

Fossilised guts in trilobites from the Upper Ordovician Letná Formation (Prague Basin, Czech Republic)

OLDŘICH FATKA, RUDY LEROSEY-AUBRIL, PETR BUDIL & ŠTĚPÁN RAK



The preservation of digestive structures of trilobites is extremely rare. Here we describe two new examples of trilobites from the Upper Ordovician Letná Formation (Prague Basin, Czech Republic), which display remains of the digestive system. The first specimen, assigned to *Selenopeltis buchi* (Barrande, 1846), exhibits cavities under the posterior part of the glabella and the axis of most thoracic segments. These cavities are interpreted as remains of metamerically paired digestive caeca and constitute the first example of preserved digestive structures in the order Odontopleurida. The second specimen belongs to *Birmanites ingens* (Barrande, 1852) and displays a tube-like structure, filled with a finely-grained material, that runs under the axial lobe of the entire trunk. We interpret this structure as a gut infilling similar to that repeatedly observed in the Moroccan *Basilicus calzadai*. These specimens confirm that the depositional environment of the Letná Formation was locally favourable to soft-tissue preservation. They also further document the presence of two different types of digestive systems in trilobites. The possibility that different processes might have been involved in the preservation of different parts of the trilobite gut is discussed, and several criteria to differentiate genuine gut remains from scavenger burrows are proposed. • Key words: trilobites, digestive system, soft-tissue preservation, Letná Formation, Upper Ordovician, Czech Republic.

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With almost 4,000 genera (Jell & Adrain 2003) and more than 20,500 species (Adrain 2008) described, trilobites represent one of the best documented fossil groups of the Palaeozoic Era. Despite this impressive record, clearly suggesting that trilobites were one of the most important components of marine invertebrate communities of that time, our knowledge of their internal anatomy is surprisingly limited. Recently, Lerosey-Aubril *et al.* (2011) reported that remains of the digestive system of trilobites had been described in less than 25 species and in most cases, from a single specimen only. If the few examples omitted in this work (Kordule 2006, Alberti 2009) or reported/illustrated since its publication (Corbacho 2011, Eriksson & Terfelt 2012, Lerosey-Aubril *et al.* 2012, Zhu *et al.* submitted) are considered, it appears that the morphology of the digestive system of trilobites is partially known in some 0.7% of the genera and 0.15% of the species. There is not

a single report for four of its ten orders (*i.e.* Harpetida, Odontopleurida, Proetida, and Agnostida, assuming that these latter are trilobites). However, understanding the anatomy of trilobite digestive system and its evolution through time could permit a better assessment of the diversity of their feeding habits and of their position(s) within marine food webs in the Palaeozoic.

The Lower Palaeozoic of the Barrandian area (Czech Republic) has significantly contributed to the documentation of the morphology of trilobite digestive systems. Indeed, putative remains of digestive structures have been described or illustrated in four trilobite genera from this area in the past: *Conocoryphe* (Cambrian, 2 specimens; Budil & Fatka 2008; Fatka *et al.* 2008), *Dalmanitina* (Ordovician, 1 specimen; Šnajdr 1991), *Deanaspis* (Ordovician, 22 specimens; Barrande 1852; Beyrich 1846; Přibyl & Vaněk 1969; Šnajdr 1990, 1991), and *Ptychoparia*

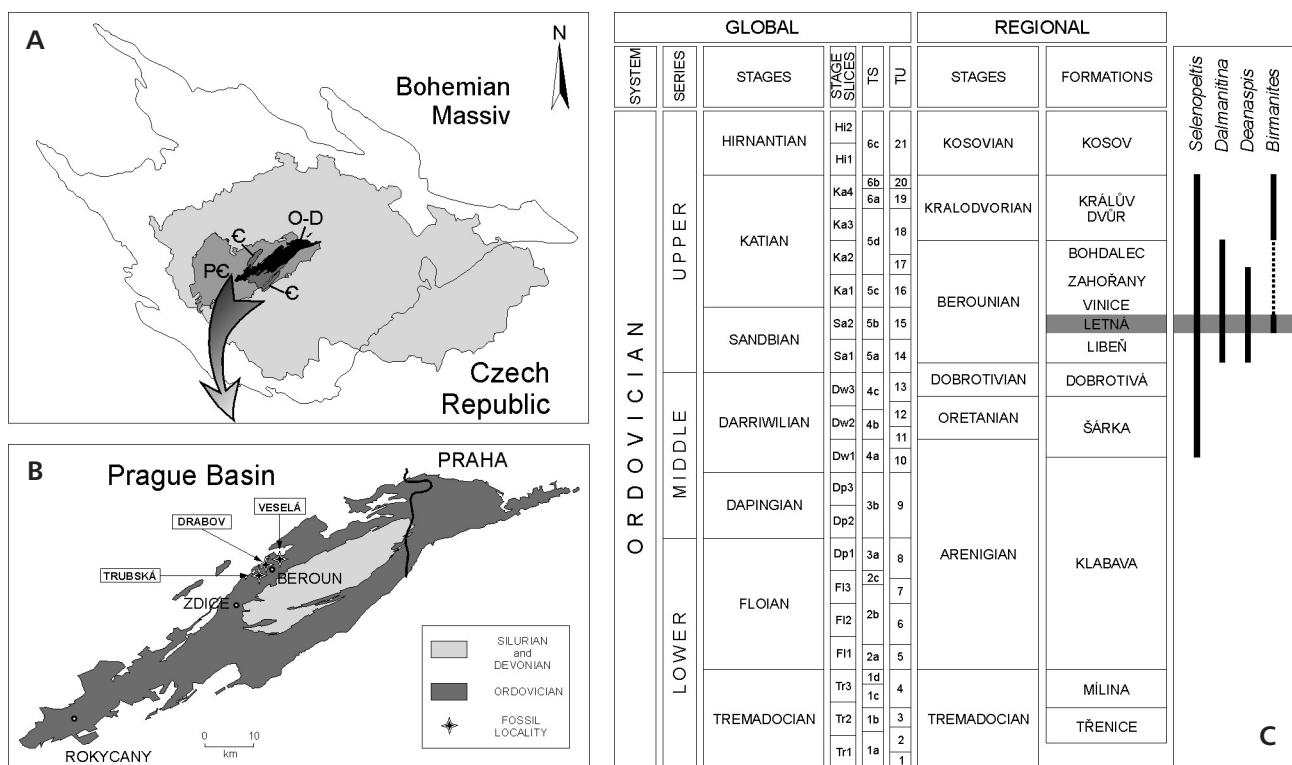


Figure 1. A – map of the Czech Republic and the Barrandian area. • B – sketch map of the Prague Basin showing location of the Drabov, Veselá and Trubská outcrops at which the exceptionally preserved trilobites with soft parts have been found. • C – stratigraphy of the Ordovician of the Prague Basin with marked level at which the trilobite specimens were collected (stratigraphy modified from Budil *et al.* 2011).

(Cambrian, 3 specimens; Jaekel 1901, Šnajdr 1958, Kordule 2006). In this contribution, we described two additional examples of fossilized digestive structures in Ordovician trilobites from the Czech Republic. This includes the first report of the preservation of such structures in the order Odontopleurida.

Material and methods

The first specimen (NML 15662) described herein belongs to the original collection of Barrande deposited at the National Museum (Prague University). It has been collected in the Upper Ordovician Letná Formation at the locality of Veselá, near the city of Beroun (Fig. 1), and is assigned to *Selenopeltis buchi* (Barrande, 1846) (for a recent revision of the genus *Selenopeltis*, see Bruton 2008). In Barrande's monograph (1852, pl. 37, fig. 25), an idealised reconstruction of this specimen was illustrated, which omitted the presence of the putative remains of digestive structures described herein.

The second specimen investigated (NML 38812) is a large asaphid that we attribute to *Birmanites ingens* (Barrande, 1846). It has also been collected in the Letná Formation, but at the locality of Trubská (Fig. 1), by Mr. Bartoníček who kindly donated it to the National Museum,

Prague. *Asaphus ingens* Barrande, 1846 has been considered the type species of a new genus, *Megasaphus*, by Kácha & Petr (1996), but as correctly pointed out by Vaněk (1997), the diagnostic characters of this new taxon were in fact typical of the genus *Birmanites* Sheng, 1934. *Megasaphus* was therefore logically considered a subjective junior synonym of *Birmanites* by Vaněk, a view later followed by Shaw (2000) and Vaněk & Valíček (2001) and accepted herein.

For comparative purposes, a specimen of *Basiliscus calzadai* Corbacho, 2011 from the Izegguirene Formation (Upper Ordovician) in Jbel Tijarfaouine (Morocco), initially illustrated in Van Roy (2006, fig. 1.14b), is refigured herein. It exhibits remains of the digestive tract, the morphology and preservation of which are strikingly similar to that encountered in the specimen of *Birmanites ingens*. This specimen (SMF 96342) from Morocco has been generously donated by P. Van Roy to the Senckenberg Research Institute of Frankfurt am Main, Germany.

All the specimens considered herein have been studied using optical microscopes (Microscope NIKON SMZ 1500, Leica S8APO). Photographs of specimens NML 38812, NML 15662, and MCZ 184156 were taken using a digital camera Camera NIKON D 300 after being coated with ammonium chloride. Specimen SMF 96342 was left uncoated and photographed using a digital camera

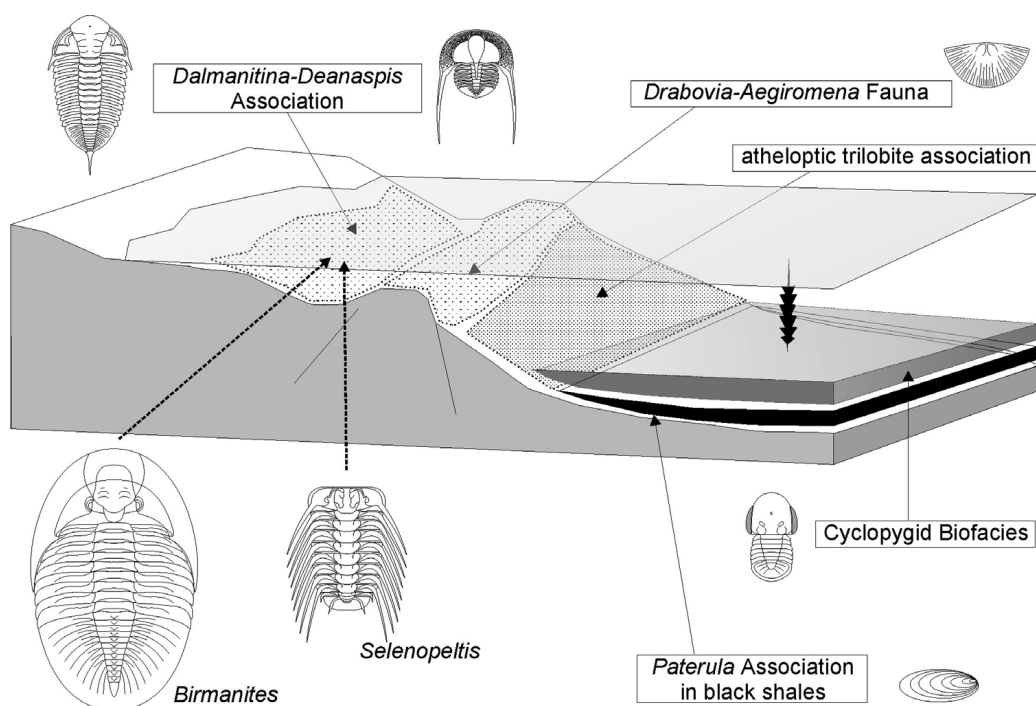


Figure 2. Sketch representing the distribution of the different biofacies associated with the late Sandbian Letná Formation. Shallowing of the basin with quartzitic sands and greywackes inshore, siltstones and black shales offshore. *Drabovia-Aegiromena* Fauna with rich brachiopod associations (*Drabovia* Community, *Bicuspina* Community), non-trilobite arthropods and the trilobite *Dalmanitina-Deanaspis* Association are characteristic for the inshore quartzose sandstones, while a poor atheloptic trilobite association is typical for the offshore slope settings. Rare graptolites, Cyclopygid Biofacies and the *Paterula* Association dominate in poorly oxygenated black shales in central parts of the basin. Modified after Fatka & Mergl (2009, fig. 11g).

Panasonic DMC-TZ18 (macro mode) to permit colour differences between the putative digestive tract and the exoskeleton to be visible. The drawings of the specimens were made from these photographs using Corel Draw X3 and Photoshop CS5. Lastly, the terminology used below follows that proposed by Whittington *et al.* (1997), including the following abbreviations: exs. – exsagittal, sag. – sagittal, tr. – transverse.

The Letná Formation and its faunal assemblages

The concept of the Letná Formation has been initially proposed by Kettner & Prantl (1948) for a thick complex of quartzose sandstone, greywacke, siltstone and pelites rapidly alternating vertically. This concept was later formalized and detailed by Havlíček & Vaněk (1966) and Havlíček (1992, 1998). The Letná Formation is the thickest lithostratigraphic unit of the Ordovician of the Prague Basin, exceeding locally 600 m in thickness between Prague and Beroun. Its lower boundary corresponds to the onset of a thick, rhythmically bedded quartzose sandstones, bioturbated quartzose sandstones, siltstones and greywackes (Kukal 1958, 1998). It outcrops in many localities, but only some of them have yielded fossils. Chlupáč (1965) recog-

nized three main fossiliferous levels within the Letná Formation from the study of various outcrops in the Děd Hill (“Drabow”, now Drabov; Fig. 1B), but at present it is still not clear whether these levels could all be identified elsewhere in the Prague Basin.

A rather diverse fauna composed of brachiopods, trilobites, echinoderms, conularids, and non-trilobite arthropods (Havlíček & Vaněk 1966, Havlíček 1998) has been found in outcrops located between Zdice and Chrastenice. This area probably represented a rather shallow environment in the north-western part of the basin (Šnajdr 1956, Havlíček 1992). The fossils are usually fragmentary and preserved as internal or external moulds associated with angular claystone fragments within quartzose sandstones to siltstones. Accumulations of these fossil remains are commonly found in thick-bedded quartzose sandstones of light-grey and yellow or grey-brown colour (see Šnajdr 1990), which might have been deposited in areas sheltered from wave activity by sand bars (Chlupáč 1965).

Fossil associations of the Letná Formation have been intensively studied by Havlíček (1982), Havlíček & Vaněk (1966, 1990), Havlíček & Fatka (1992), more recently the earlier data were summarized and discussed by Servais *et al.* (2008) and Fatka & Mergl (2009). Locally common ichnofossils were studied by Mikuláš (1998a). Five major fossil associations are usually distinguished in

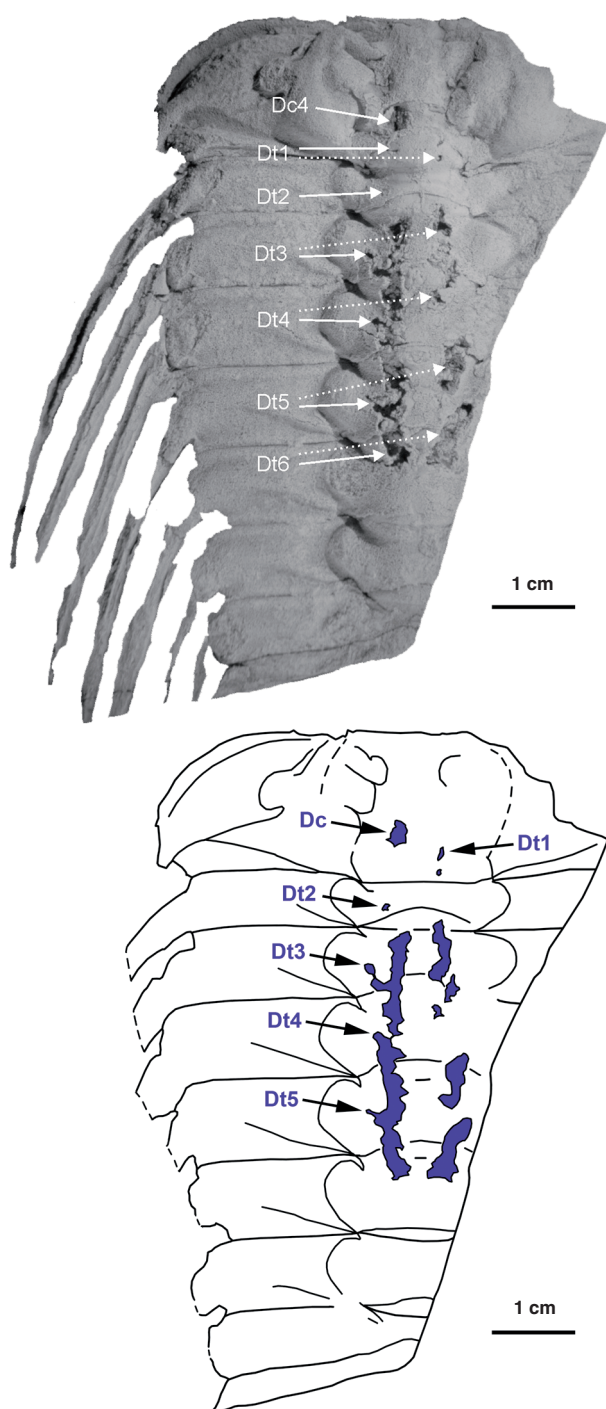


Figure 3. *Selenopeltis buchi* (Barrande, 1846), National Museum in Prague, NML 15662, Upper Ordovician Sandbian (= Berounian Regional Stage), Letná Formation, the locality Veselá near Beroun. • A – a photograph of the internal mould. • B – interpretative sketch. Dc – pairs of cephalic gut diverticulae, Dt – pairs of thoracic gut diverticulae.

this formation (Fatka & Mergl 2009, Havlíček 1998; Fig. 2). The rich brachiopod dominated *Drabovia* Community is associated with shallow water, well-sorted quartzose sandstones. The *Bicuspina* Community, which

probably represents a slightly deeper environment, is typically found in the poorly sorted greywackes of the higher horizons of the Letná Formation (e.g., Havlíček 1982). These two communities constitute the *Drabovia-Aegiro-mena* Fauna. In more proximal environments, this fauna is replaced by the trilobite dominated *Dalmanitina-Deanaspis* Association, which contains *Birmanites ingens* and *Selenopeltis buchi*. The more distal, probably deeper parts of the basin are characterized by a poorly diversified atheloptic assemblage of trilobites associated with rare graptolites. Lastly, trilobites of the so-called Cyclopygid Biofacies (Fatka & Mergl 2009, fig. 11g) and brachiopods of the *Paterula* Association are typical for the deepest portions of the Prague Basin (Fig. 2). Interdital (*Skolithos* ichnofacies) and near shore (*Cruziana* ichnofacies) environments are also evidenced by ichnofossils (Chlupáč & Kukal 1988; Mikuláš 1998a, b, 1999).

Fossilised gut remains have been observed in only four of the twenty or so trilobite species (Havlíček & Vaněk 1966, Šnajdr 1956, Vaněk & Valíček 2001) present in the Letná Formation: *Birmanites ingens* (herein), *Dalmanitina socialis* (see Šnajdr 1991), *Deanaspis goldfussi* (e.g. Šnajdr 1991), and *Selenopeltis buchi* (herein). These four trilobites belong to the *Dalmanitina-Deanaspis* Association, characterizing rather proximal and shallow environments of the Letná Formation. Interestingly, most of the non-trilobite arthropods discovered in this formation, including forms with non-mineralized exoskeleton, are also found associated with *D. goldfussi* and/or *D. socialis* (e.g. Chlupáč 1965, Rak *et al.* 2009, Ortega-Hernández *et al.* 2010). This suggests that the development of conditions conducive to soft-tissue fossilization was not uncommon in the environment represented by the *Dalmanitina-Deanaspis* Association.

Results

Specimen NML 15662 (Fig. 3). – This specimen of *Selenopeltis buchi* (Barrande, 1846) is the internal mould of an originally entire, articulated individual. However, the posterior part of the trunk (*i.e.* posterior to the eighth thoracic segment) is missing as well as most of the right part of the dorsal exoskeleton. The portion preserved is 76 mm long (sag.), which suggests it belongs to a holaspide stage. The fact that the left librigena is still connected to the cranidium indicates that the specimen is not an exuvia.

The axial lobe displays slightly abaxially located cavities under the posterior half of the glabella and the anterior portion of the thoracic axis (up to the fifth segment). Under some thoracic axial rings, these cavities are observed on both sides of the sagittal axis, suggesting that they were initially paired structures. On the left side of the axis, where the cavities are more developed, they seem to be part of a single,

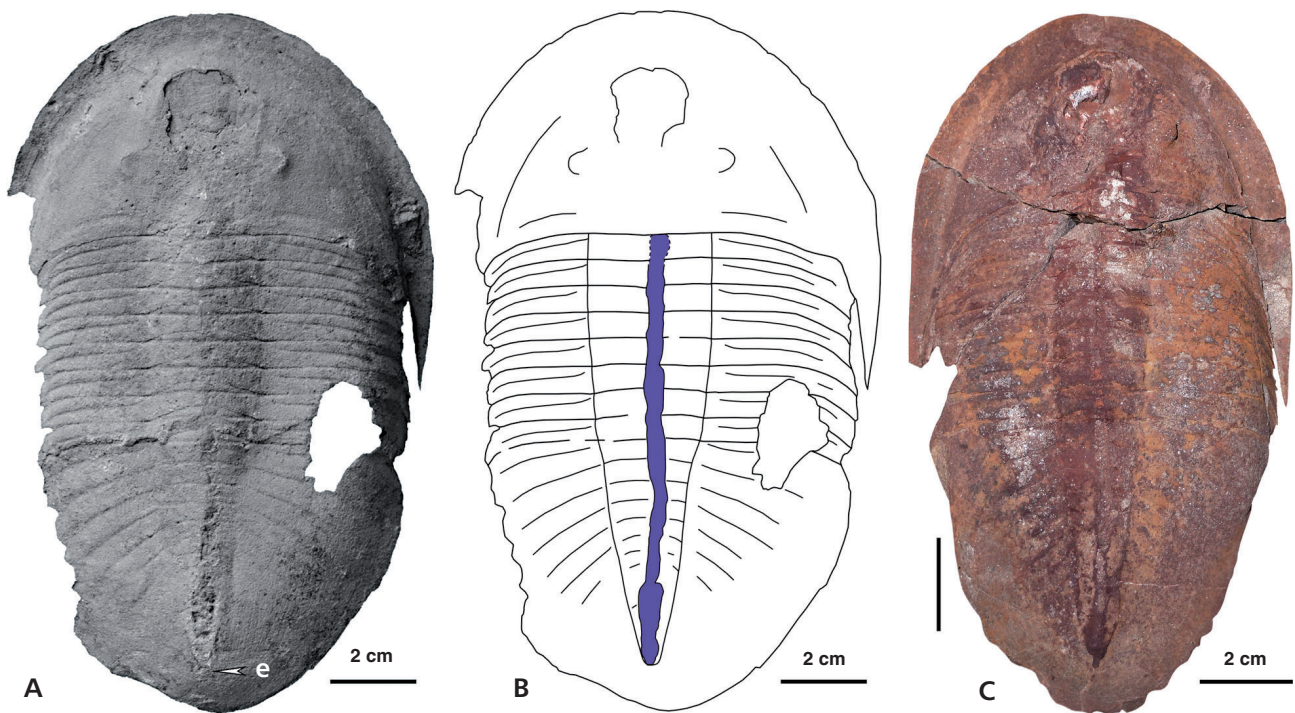


Figure 4. Internal mould of *Birmanites ingens* (Barrande, 1852), National Museum in Prague, NML 38812; Upper Ordovician Sandbian (= Berounian Regional Stage), Letná Formation, Beroun locality. • A – a photograph of the internal mould. • B – interpretative sketch. *Basilicus calzadai* Corbacho, 2011, Senckenberg Research Institute Frankfurt am Main, SMF 96342; Upper Ordovician, Izegguirene Formation, Jbel Tijarfaouine, Morocco, initially illustrated in Van Roy (2006, fig. 1.14b). • C – a photograph of the internal mould. e – termination of the intestine.

elongate structure. A careful examination, however, shows that the cavities are shallower at the junctions of axial rings. Here, they probably represent bridges that appeared later during diagenesis between the deeper cavities located under the axial rings. We interpret these deeper cavities as the remains of metamERICALLY paired, digestive caeca. Although not visible on both sides under all the segments concerned, we hypothesize that *S. buchi* possessed at least six pairs of such structures associated with the posteriormost cephalic segment and the five anteriormost thoracic segments. The absence of cavities under the axial rings of thoracic segments 6 to 8 might be due to the absence of digestive caeca associated with these segments or the fact that the above lying material has not collapsed, as in the case of the right sides of several, more anteriorly located axial rings.

Specimen NML 38812 (Fig. 4A, B). – This specimen of *Birmanites ingens* (Barrande, 1852) is also the internal mould of an entire, articulated individual. It measures 154 mm in length (sag.) and 85 mm (tr.) in width and exhibits eight thoracic segments, suggesting it corresponds to a late holaspide growth stage. Both the librigenae and the hypostome are still in the *in situ* positions, which demonstrate that the specimen represents a carcass.

The remains of a simple digestive tract are visible under the axis from the second (possibly the first) thoracic segment to the tip of the pygidial axis in the form of an infilling

(Fig. 4B). The nature of this infilling is unknown, but it is more finely grained than the matrix surrounding the specimen. The alimentary canal is straight, running sagittally up to the fourth pygidial axial rings, where it slightly bent to the left. Faintly expressed under the few anteriormost thoracic segments, it becomes more apparent from the 4th thoracic segment rearwards, due to abrasion of the medial part of the axis. In the posterior portion of the pygidial axis, the material filling the gut itself seems to have suffered from weathering. In the cephalic region, the anterior portion of the glabella has collapsed, allowing the hypostome, still in *in situ* position, to be observed. The cavity hence formed clearly represents the space enclosed by the hypostome rather than remains of crop. This is confirmed by the absence of connection between this cavity and remain of the digestive tract visible under the trunk axis.

Discussions

Morphology of trilobite guts

It has been hypothesized that at least two different types of digestive systems were present in trilobites (Chatterton *et al.* 1994, Leroosey-Aubril *et al.* 2011). The two specimens described herein exemplify these two morphologies of the trilobite gut.

In *Birmanites*, only a simple, rather large digestive tract is visible under the trunk axis. Recently illustrated specimens of *Basilicus calzadai* Corbacho, 2011 (Van Roy 2006, fig. 1.14b and Fig. 4C herein; Corbacho 2011, pl. I, figs 1–3) from the Ordovician of Morocco, confirm that this gut morphology was common in large Ordovician asaphids. A simple alimentary canal devoid of digestive caeca has also been reported/illustrated in *Deanaspis goldfussi* (see Šnajdr 1991) and *Isotelus maximus* (see English & Babcock 2007), as well as in various non-asaphid trilobites (Lerosey-Aubril *et al.* 2011, table 1). Interestingly, all these examples but one concern post-Cambrian taxa, which suggests that a simple gut devoid of digestive caeca might be a derived character for trilobites. Lerosey-Aubril *et al.* (2011) made the assumption that a simple intestine under the trunk axis might have been associated with the differentiation of the foregut into a crop anteriorly (*i.e.* a pouch-like structure under the glabella). The presence of a crop in trilobites have been repeatedly reported, but as recently argued by Lerosey-Aubril *et al.* (2011), it has been convincingly illustrated in *Deanaspis goldfussi* (see Šnajdr 1991) and *Triarthrus eatoni* (see Cisne 1981) only. As discussed above, the anterior portion of the gut is not preserved in the specimen of *B. ingens* studied herein, the large cavity present in the anterior portion of the cephalic axis more likely representing the space enclosed within the hypostome rather than a crop. However, it has been suggested that the presence of a crop was associated with the development of a rather large frontal glabellar lobe (Lerosey-Aubril *et al.* 2011) and indeed, this region of the axis is well-developed in *D. goldfussi* and *T. eatoni*. In *Nobiliasaphus nobilis*, another Ordovician asaphid, muscle scars in this part of the glabella have been interpreted as indicative of the presence of an extrinsic musculature associated with a small crop (Lerosey-Aubril *et al.* 2011). Considering that *Basilicus*, *Birmanites*, and *Nobiliasaphus* exhibit rather similar glabellar morphologies, it seems reasonable to assume that representatives of the former two genera might have also possessed a modest crop, in addition to the simple digestive tract repeatedly observed under their trunk axis.

The specimen of *S. buchi* studied herein suggests that the digestive system in this taxon probably comprised several pairs of digestive caeca. Digestive caeca have been described (or at least illustrated) in a great variety of trilobites (Lerosey-Aubril *et al.* 2011, table 1), but this is the first report of the presence of such structures 1) in a post-Cambrian trilobite and 2) within the order Odontopleurida. Simple outpocketings of the digestive tract are also known in various Cambrian arthropods (*e.g.* *Cindarella* – Ramsköld *et al.* 1997; *Misszhouia* – Vannier & Chen 2002), which gives further credence for their presence being a plesiomorphic character for trilobites. Unlike naraoids, however, no digestive caeca seemed to have occurred un-

der the posterior portion of the trunk in trilobites (Lerosey-Aubril *et al.* 2012), which could explain why no cavities are observed associated with the 6th–8th thoracic segments on our specimen. Alternatives could be that the last three pairs of thoracic digestive caeca have simply not been preserved or that they are still hidden by the dorsal exoskeleton. The outlines of the cavities are poorly defined but interestingly, it seems they were associated with structures that projected toward the lobe-like abaxial extensions of the axial rings. Considering the relative sizes of digestive caeca and axial rings in other trilobites (*e.g.* Lerosey-Aubril *et al.* 2012), it seems unlikely that the digestive caeca fully occupied these lateral extensions of the axial rings in *S. buchi* or only if they were able to dramatically dilate when filled with food. It remains that the rather unusual morphology of the trunk axis in *Selenopeltis* might have well been related to the presence of digestive caeca, which would suggest that paired digestive caeca also occurred under the posteriormost thoracic axial rings, since they do not differ in shape compared to more anterior ones. If confirmed by further findings, this would constitute a rare case of a direct correspondence between the morphologies of the gut and the dorsal exoskeleton.

The recent discovery of a juvenile hypostome associated with fossilized soft-tissues (including digestive structures) in the Cambrian Orsten Lagerstätte somewhat challenges the view of mutually exclusive occurrences of a crop and digestive caeca in trilobites (Eriksson & Terfelt 2012). Indeed, this specimen, tentatively assigned to an olenid, exhibits a well-developed crop followed by a narrower alimentary canal, which was said to be associated with two pairs of digestive caeca. However, unlike the oesophagus, the crop, and the anterior portion of the intestine, these putative digestive caeca are not really obvious on the synchrotron 3D-tomographic reconstructions provided by Eriksson & Terfelt (2012). In addition, they are described as arising from the lower (*i.e.* ventral) side of the intestine, while they are known to insert latero-dorsally on the digestive tract in other trilobites (*e.g.* Lerosey-Aubril *et al.* 2012). Anyway, the description of this specimen remains interesting, but it should be kept in mind that it represents a very early growth stage, while the “two types” model for the trilobite gut emerged from the study of adult (holaspid) forms. It is most likely that the digestive system of trilobites, like that of most modern arthropods, underwent significant changes during ontogeny, especially in taxa having different feeding habits during their life cycle. Eriksson & Terfelt (2012) hypothesized that the hypostome they described likely under-covered a larger part of the body than the glabellar area. A large, protective hypostome/labrum is known in larval/juvenile stages of trilobites (*e.g.* Lerosey-Aubril & Feist 2005, fig. 3.14) and modern crustaceans (*e.g.* Olesen 2005), which are thought/known to be pelagic forms and

mostly filter-feeders. This feeding strategy could explain the presence of a large crop in this early juvenile specimen. Thus, it cannot be excluded that the co-occurrence of a crop and digestive caeca in this individual might have been transitory, evidencing the passage from a filter-feeding habit in planktonic larvae to another feeding strategy in benthic adults, which did not necessarily involve the presence of well-developed crop.

Gut preservation in trilobites

Three different types of remains of digestive structures have been described in trilobites: infillings, cavities, and dark markings on an exoskeleton/internal mould. In cases of infillings, various materials have been shown to replace the gut lumen, such as calcium carbonate (English & Babcock 2007), calcium phosphate (Chatterton *et al.* 1994, Leroosey-Aubril *et al.* 2012, Eriksson & Terfelt 2012), quartz (Babcock & Peel 2007), or pyrite (Stürmer & Bergström 1973; Bruton & Haas 1999; Cisne 1975, 1981). Interestingly, a sediment filling of the gut has rarely been demonstrated in trilobites (Zhu *et al.* submitted), while it has been supposedly observed in many Cambrian arthropods and interpreted as indicative of them being deposit-feeders (*e.g.* Hou *et al.* 2004, Bergström *et al.* 2007 and references therein). Anyway, this diversity of remains suggests that various processes have likely been involved in the preservation of trilobite guts.

The two trilobites described herein exhibit different types of remains of the digestive system, an infilling in *B. ingens* and cavities in *S. buchi*. The size of the rock sample bearing the specimen of *B. ingens* prevented compositional analyses (*e.g.* EDX) of its gut infilling and its matrix to be performed, but these two materials clearly have different aspects, with the material filling the gut being much finely-grained compared to the matrix. A similar difference in aspects has been reported by Šnajdr (1991) in *Deanaspis goldfussi* (also from the Letná Formation; see his pl. 3, fig. 13, pl. 4, fig. 15) and it can also be observed in the specimen of *Basilicus calzadai* from the Upper Ordovician of Morocco available to us. This suggests that if these gut infillings represent sediments, the larger grains have been sorted out before ingestion, possibly through the action of appendage gnathobases.

The fact that the two specimens described herein illustrate two modes of preservation of digestive structures (infilling vs. cavities) might seem surprising, considering that both are associated with similar lithologies (*i.e.* quartzose sandstones) and were collected from the same lithostratigraphical unit (*i.e.* the Letná Formation). One could argue that they actually document a similar preservation mode at different diagenetic stages. Indeed, these two types of remains can sometimes co-occur in a single specimen or in

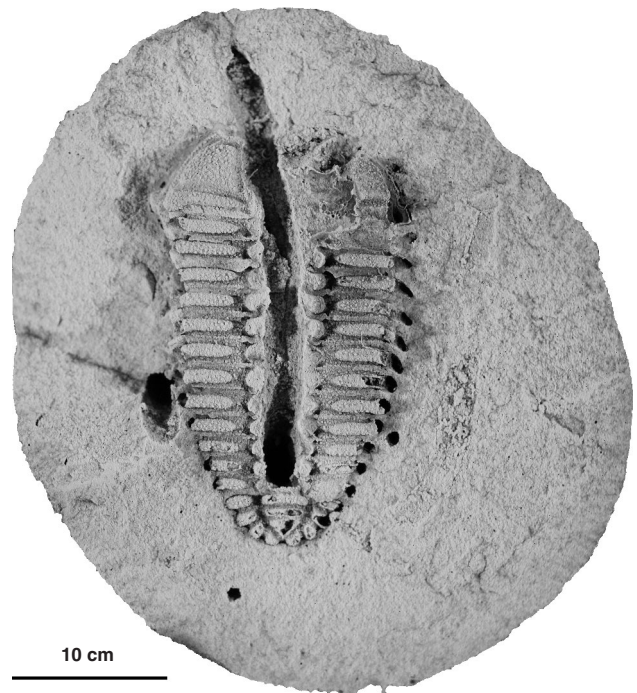


Figure 5. Internal mould of *Placoparia cambriensis*, with “worm” burrow in axial part, Museum of Comparative Zoology at Harvard University, MCZ 193179, Middle Ordovician Darriwilian (= Oretanian Regional Stage), Šárka Formation, locality ?Osek near Rokycany.

different specimens of the same species, as observed in *Buenellus higginsi* (see Babcock & Peel 2007, compare their figs 2A and 3A) or *Deanaspis goldfussi* (see Šnajdr 1990, p. 67). Consequently, it could be hypothesized that in all these cases, the digestive system was filled by the same material in all specimens, but dissolved in some of them only (Babcock & Peel 2007). However, this scenario is hardly applicable to *S. buchi*. Indeed, the odontopleurid specimen is the only one from the Letná Formation to exhibit remains of digestive caeca and no evidence of preserved intestine. Interestingly, infillings of digestive caeca have as-yet only been observed in cases of phosphatisation (Chatterton *et al.* 1994, Eriksson & Terfelt 2012, Leroosey-Aubril *et al.* 2012). A possible exception to this might be the specimen of *Ptychoparia dubinka* Kordule, 2006 figured by Jaekel (1901, pls 4, 5), for which nothing is known about the nature of the gut infilling. Considering that the infillings of the tract do not present the characteristic aspect of phosphatic materials in the trilobites from the Letná Formation, the question of whether different processes might have been involved in the fossilization of the digestive caeca and the alimentary canal can be raised. It has been shown that different types of preservation for these two structures can occur in a single specimen in trilobites or non-trilobite arthropods (Zhu *et al.* submitted for references). Moreover, Babcock & Peel (2007; see also Blaker & Peel 1997) illustrated many specimens of

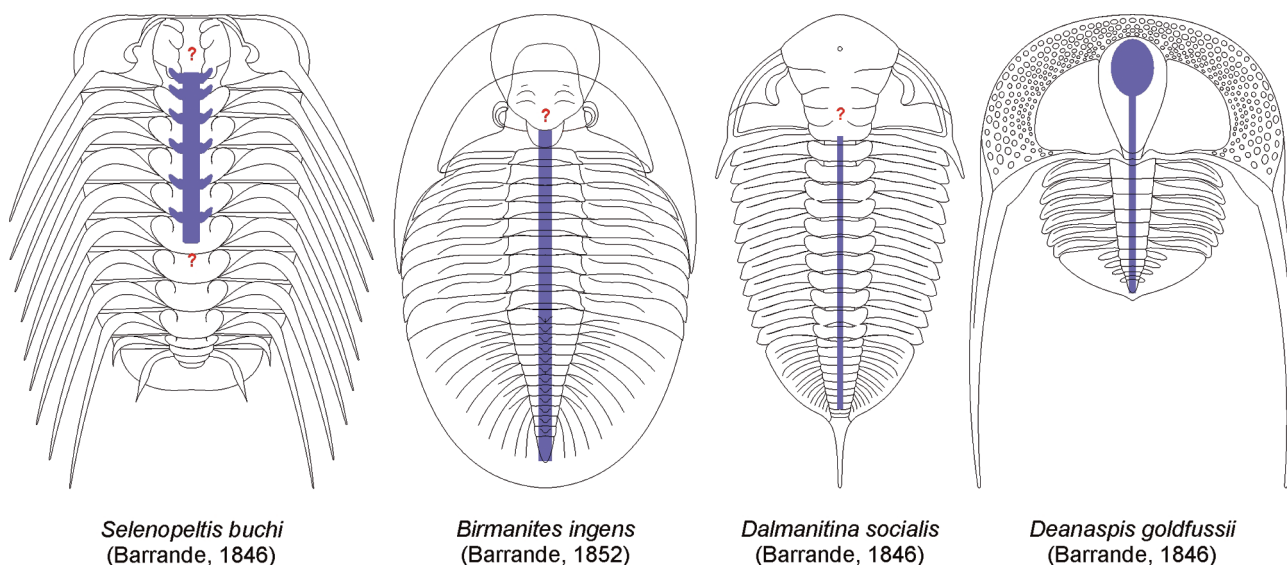


Figure 6. Morphology of the preserved parts of the digestive system in the cephalic, thoracic and pygidial regions of trilobites in the Letná Formation. All specimens in dorsal view.

B. higginsii with remains of the digestive system. However, if both the digestive tract and the digestive caeca can be represented by cavities on these specimens, an infilling-type of preservation was only illustrated for the tract, again suggesting that these different parts of the digestive system might have been filled by different materials at death or soon after. It could not be excluded, that all ingested food was immediately transported into and digested inside of the digestive caeca (= diverticulae), while the gut alone stays empty. These observations emphasize the need for thorough investigations on the modes of preservation of trilobite digestive structures to properly address the questions of their morphology, their variability, and their evolution through time. However, as far as the trilobites from the Letná Formation are concerned, the absence of digestive caeca in some species likely indicates anatomical differences, since if their preservation was possible in *S. buchi*, there is no reason to believe it was different for the other taxa occurring in the same beds.

It may be appropriate to make a final remark about the risk of misinterpreting *Planolites*- or *Skolithos*-like ichnofossils as gut remains of trilobites. Indeed, as pointed out by Shaw (1995), the association of these trace fossils and trilobites is common in Ordovician trinucleids from Bohemia, as well as in the supposedly semi-infaunal *Placoparia* (Fig. 5). This kind of ichnofossils may mimic the remains of a digestive tract left empty after dissolution of the material initially filling it. However, a careful examination will reveal that in most cases they differ from gut infillings by one of the following criteria: 1) they usually have a larger diameter relative to the width of the axis, 2) their margins are often not sharp but partially dissolved, 3) they commonly extend outside the axial lobe, if not the body of the trilobite (Fig. 5),

and 4) they frequently display a more tortuous route (the digestive tract of trilobites is essentially straight). However, as noticed by Babcock & Peel (2007) and confirmed by our own observations on various Ordovician trinucleoids, the vermiform scavengers supposedly at the origin of these burrows might have targetted preferentially the gut tract of the decaying trilobite. Therefore, it is particularly important to remain careful when interpreting semi-tubular cavities under the axial region of a trilobite, especially when they extend under a short portion of the axial lobe only and they are not associated with remains of digestive caeca.

Summary

The two new trilobites with remains of digestive structures described herein confirmed that the depositional environment of the Letná Formation was favourable for soft-tissue preservation. They also confirm that at least two types of digestive system were present in trilobites (Chatterton *et al.* 1994, Lerosey-Aubril *et al.* 2011). In the Letná Formation, a simple digestive tract, possibly associated with a crop under the glabella, was present in the dalmanitid *Dalmanitina socialis* and the asaphid *Birmanites ingens* and the trinucleid *Deanaspis goldfussi* (Fig. 6). In contrast, the specimen of *Selenopeltis buchi* constitutes the first example of a trilobite gut with digestive caeca in this Ordovician Lagerstätte. It also represents the only post-Cambrian occurrence of this type of gut known to date and the first example of gut preservation in the Odontopleurida. If the presence of two types of digestive systems in the trilobites from the Letná Formation is rather well-established, we raise the question of the possible involvement of different

processes in the preservation of the digestive tract of trilobites on the one hand, and their digestive caeca on the other. This scenario would explain the absence of digestive caeca in some previously described examples of simple digestive systems in this group. In conclusion, it seems to us that a confident description of the diversity of digestive systems in these extinct arthropods will not be possible until the processes involved in its various modes of preservation are more thoroughly investigated (e.g. Lerosee-Aubril et al. 2012).

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