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Reconstructing the diet of a 505-million-year-old arthropod: *Sidneyia inexpectans* from the Burgess Shale fauna

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The feeding ecology of the 505-million-year-old arthropod *Sidneyia inexpectans* from the middle Cambrian (Series 3, Stage 5) Burgess Shale fauna (British Columbia, Canada) is revealed by three lines of evidence: the structure of its digestive system, the fossilized contents of its gut and the functional anatomy of its appendages. The digestive tract of *Sidneyia* is straight, tubular and relatively narrow in the trunk region. It is enlarged into a pear-shaped area in the cephalic region and stretches notably to form a large pocket in the abdomen. The mouth is ventral, posteriorly directed and leads to the midgut via a short tubular structure interpreted as the oesophagus. Anteriorly, three pairs of glands with internal, branching tubular structures open into the digestive tract. These glands have equivalents in various Cambrian arthropod taxa (e.g. naraoiids) and modern arthropods. Their primary function was most likely to digest and assimilate food. The abdominal pocket of *Sidneyia* concentrates undigested skeletal elements and various residues. It is interpreted here as the functional analogue of the stercoral pocket of some extant terrestrial arachnids (e.g. Araneae, Solifugae), whose primary function is to store food residuals and excretory material until defecation. Analysis of the gut contents indicates that *Sidneyia* fed largely on small ptychopariid trilobites, brachiopods, possibly agnostids, worms and other undetermined animals. *Sidneyia* was primarily a durophagous carnivore with predatory and/or scavenging habits, feeding on small invertebrates that lived at the water-sediment interface. There is no evidence for selective feeding. Its food items (e.g. living prey or dead material) were grasped and manipulated ventrally by its anterior appendages, then macerated into ingestible fragments and conveyed to the mouth via the converging action of strong molar-like gnathobases. Digestion probably took place within the anterior midgut via enzymes secreted in the glands. Residues were transported through the digestive tract into the abdominal pocket. The storage of faeces suggests infrequent feeding. The early diagenetic three-dimensional preservation of the digestive glands and abdominal pocket may be due to the capacity of *Sidneyia* to store Phosphorus and Calcium (e.g. spherites) in its digestive tissues during life as do, for example, modern horseshoe crabs.

1. Introduction

Reconstructing the diet of ca 500-million-year-old animals presents a scientific challenge with important implications regarding the level of interactivity within early marine

communities and the construction of the very first modern-style trophic webs. The exceptional preservation of fossils from several Cambrian Lagerstätten has allowed scientists to reconstruct the feeding ecologies of early animals with astonishing accuracy, as exemplified by recent studies on carnivorous worms (Vannier, 2012), anomalocaridids (Vinther et al., 2014), trilobites (Lerosey-Aubril et al., 2012) and other arthropods (Zhu et al., 2004; Haug et al., 2012b). Here we focus on *Sidneyia inexpectans* (Walcott, 1911; Bruton, 1981), an iconic arthropod of the middle Cambrian (Series 3, Stage 5; ca 505 Ma) Burgess Shale biota from British Columbia, Canada. Its feeding ecology is inferred using three lines

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of evidence: the structure of its digestive system, the fossilized contents of its gut, and the functional morphology of its appendages. Comparisons with modern chelicerates (e.g. spiders, horseshoe crabs) are made to reconstruct key-aspects of its biomechanics of feeding and to elucidate the phosphatic preservation of its digestive structures.

2. Material and methods

2.1. Fossil material

Most of the fossil material studied here (Table Sup. 1,2) comes from: 1) the Walcott Quarry Shale Member, characterized by fossiliferous, finely laminated, calcareous siltstones and silty graphitic mudstones; and 2) the slightly younger Raymond Quarry Shale Member, characterized by grey, greenish and brown layered blocky-slaty mudstones (see Briggs et al., 1994; Fletcher and Collins, 1998, 2003, 2009; Caron and Jackson, 2008; Collins, 2009). The *Sidneyia inexpectans* specimens deposited in the collections of the National Museum of Natural History, Smithsonian Institution, Washington D.C. (USNM) were mainly collected from the Phyllopod Bed within the Walcott Quarry Shale Member. The great majority of those housed at the Royal Ontario Museum (ROM) were collected from both the Raymond Quarry Shale Member and Walcott Quarry Shale Member (RQ, RT and WQ, WT numbers, respectively) in successive seasons of excavations and talus picking (RT, WT) between 1975 and 2000, by ROM parties led by D. Collins. A few specimens come from the Emerald Lake Oncolite Member, about 30 m above the floor of Raymond's Quarry (Fletcher and Collins, 1998). Additional material comes from localities that were more recently exploited by the ROM (field campaigns led by J.-B. Caron) ca 40 km southeast of the type area (Raymond and Walcott's Quarries, near Field) in the northern part of the Kootenay National Park, British Columbia: ten specimens from the Stanley Glacier area (STAN in Table Sup. 2; Caron et al., 2010) and two specimens from Marble Canyon (MCC in Table Sup. 2; Caron et al., 2014) in the uppermost part of the Stephen Shale ('thin' Stephen) and Burgess Shale Formations ('thick' Stephen) respectively.

A total of 136 specimens was selected for detailed observations and analyses under a stereomicroscope (see list in Table Sup. 1,2).

2.2. Recent material

Six specimens of the horseshoe crab *Limulus polyphemus* were purchased from the Woods Hole Oceanographic Institution (Massachusetts, United States) for anatomical comparisons (digestive system, appendages) with *S. inexpectans*. Horseshoe crabs were collected near the marine station, kept in the laboratory for a few days, fed with mashed *Mytilus edulis* and *Crepidula fornicata* before being euthanized with clove oil, put in 70% ethanol and shipped to Lyon. One specimen was deep-frozen in diluted ethanol (ca -57 °C) and cut across its sagittal plane with a wire saw before being photographed. Other specimens were dissected in 70% ethanol in order to observe details of their internal anatomy (e.g. hepatopancreas) and to sample gut contents for microscopic observations and analyses. A specimen of the spider *Leucorchestris* sp. (Araneae, Sparassidae) from Namibia was dissected in 70% ethanol for observations of its stercoral pocket.

2.3. Methods, techniques and terminology

Microscopic observations (Leica MZ125 stereomicroscope equipped with Plan 1.0× and Planapo 1.6× lenses, digital camera and Leica LAS 3.7.0 imaging system with multifocus option) and digital light photography (D3X-Nikon camera with Nikon Micro-

Nikkor 60 mm lens) with cross-polarized light techniques to increase contrast of anatomical features were used routinely. Scanning electron microscopy (FEI Quanta FEG 250) and Energy dispersive X-ray spectroscopy (EDX) analysis were used to study the detailed morphology and chemical composition of the fossil and Recent materials. Images were acquired with Secondary Electron (SE) and Back-Scattered (BSE) Electron detectors at 15 KV and under high vacuum, with no sputter coating. Some low-relief specimens were coated with ammonium chloride (NH₄Cl) sublimate or immersed in water before being observed under the stereomicroscope and photographed.

Head, thorax, abdomen and their adjectives are used here as descriptive terms and do not imply homologies with their equivalents in extant arthropods. The head of *S. inexpectans* corresponds to the shield-bearing anterior tagma (cephalon), the thorax to the limb-bearing trunk region and the abdomen to the limbless trunk region.

3. External morphology and affinities of *Sidneyia inexpectans*

The most accurate description of *S. inexpectans* Walcott, 1911 remains that of Bruton (1981) who reconstructed the overall external anatomy of this iconic arthropod of the Burgess Shale and discussed its possible lifestyle. Only Stein (2013) challenged some aspects of Bruton's interpretation, especially the head and appendage structure.

Sidneyia is a low-vaulted, oval-shaped arthropod with its dorsal exoskeleton clearly divided into three regions: a cephalon, a thorax and an abdomen (Fig. 1). The anteriormost exoskeletal element forms a short hemielliptical cephalic shield (CS) that bears lateral notches from which multi-annulated antennulae and small stalked eyes protrude. It is followed by nine imbricated dome-shaped thoracic tergites each composed of a broad medial area and pointed pleurae directed posteriorly. The body of *Sidneyia* terminates with two cylindrical abdominal sclerites and a tail fan. The latter consists of a central, triangular, moderately swollen telson flanked with paired (possibly two-folded) thin flap-like structures arising from the rear margin of the second abdominal somite (Fig. 1C and D). Rare specimens preserved in lateral view (Fig. 2) confirm that CS has a rounded frontal margin and extends ventrally but do not confirm the presence of a ventral cephalic doublure *sensu* Bruton (1981). We agree with Stein (2013) that *Sidneyia* had most probably a hypostome attached to its CS via a hypostomal suture that probably functioned during molting as in modern horseshoe crabs.

Sidneyia has nine pairs of post-antennal appendages (Fig. 1E,F) that are characterized by particularly large basipods and robust attachments to the body (Fig. 3). The basipods exhibit large gnathobases directed towards the animal's midline in natural position (Fig. 3E). These gnathobases are made of strongly sclerotized elements which are teeth-like in the anterior appendages and seem to be more spine-like in the posterior ones. The endopod has seven podomeres, the four proximal ones bearing a bunch of thin spines, the 3 distal ones being armed with stout claw-like elements (Fig. 3H). The endopods of at least the 3 anteriormost post-antennal appendages seem to end up as a three-folded pincer-like structure suggesting a possible prehensile function (Fig. 3J-L). Post-antennal appendages 4-9 are characterized by well-developed exopods fringed with numerous blade-like lamellae interpreted as gills (Fig. 3I; see Bruton, 1981 and Stein, 2013 for more details). The presence of such gills in appendages 1-3 (Stein, 2013) is not confirmed here. Juveniles have an overall external morphology comparable to that of adults (Fig. 1F,G).

Although the phylogenetic position of *S. inexpectans* within the Arthropoda has been debated for more than a century (see Stein,

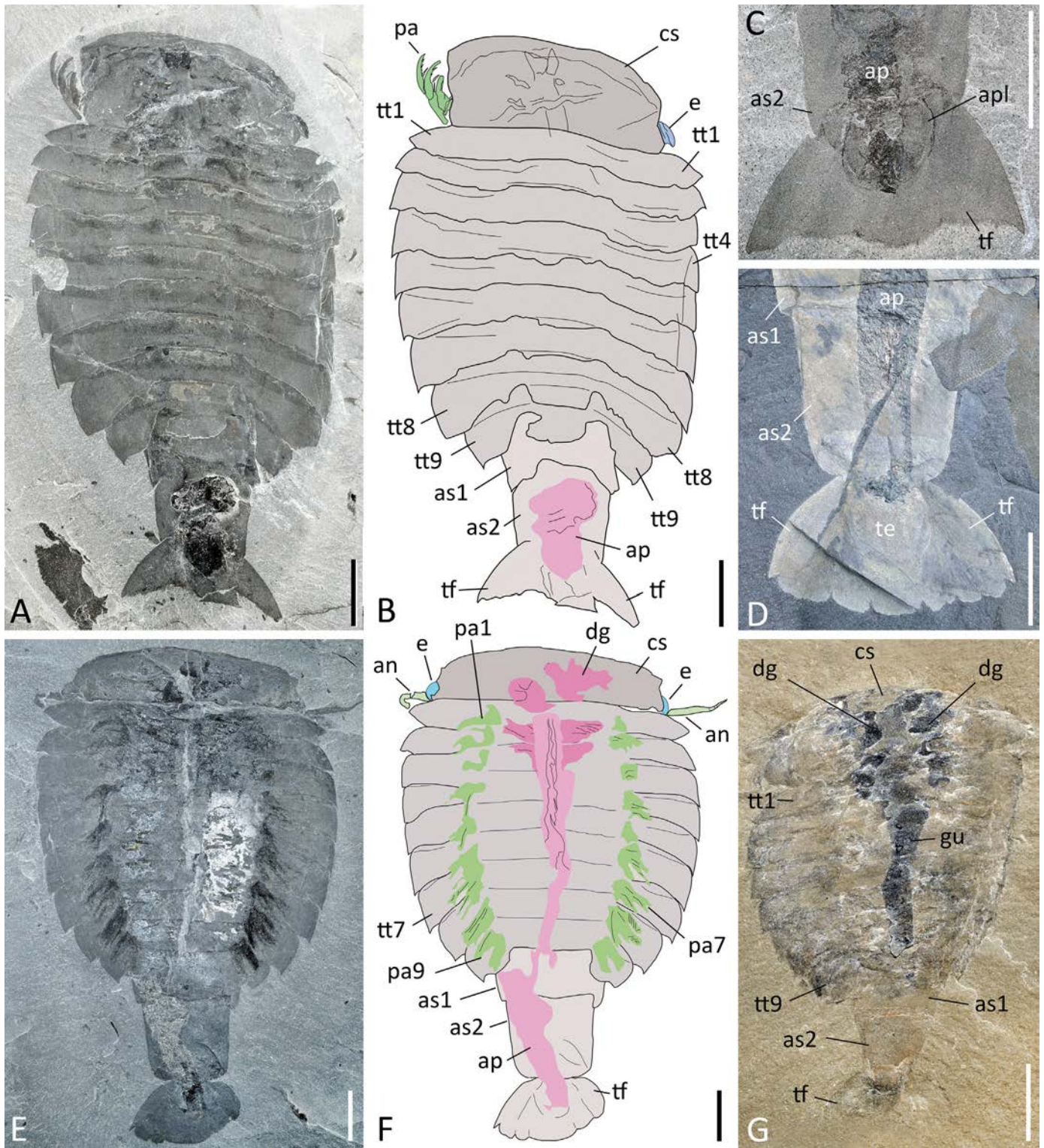


Fig. 1. General morphology of *Sidneyia inexpectans* Walcott, 1911 from the middle Cambrian (Series 3, Stage 5) Cambrian Burgess Shale, British Columbia, Canada. (A–B) USNM 269165, complete specimen in dorsal view. (C) ROM 61118.1, abdominal termination in ventral view showing possible elliptical anal plate. (D) ROM 63375, abdominal termination in dorsal view showing tail fan. (E–F) ROM 63377, complete specimen in ventral view showing distal part of post-antennal appendages. (G) ROM 63361, juvenile. Scale bars: 1 cm in A–F; 5 mm in G. Abbreviations: an, antenna; ap, abdominal pocket; apl, anal plate; as1–as2, 1st–2nd abdominal segment; cs, cephalic shield; dg, digestive gland; e, eye; gu, gut; pa1–pa9, 1st–9th pair of post-antennal appendages; te, telson; tf, tail fan; tt1–tt9, 1st–9th trunk tergite.

2013 for a recent review), no real consensus has emerged. This taxon has often been associated with *Emeraldella* to form the Xenopoda (sometimes with a third arthropod from the Burgess Shale, *Molaria*), but most phylogenetic analyses have failed to

resolve this group as monophyletic (e.g. Wills et al., 1995; Cotton and Braddy, 2004; Ortega-Hernández et al., 2013; Legg et al., 2013). More recently, Ortega-Hernández et al. (2013) have formally characterized the clade Vicissicaudata, which regroups

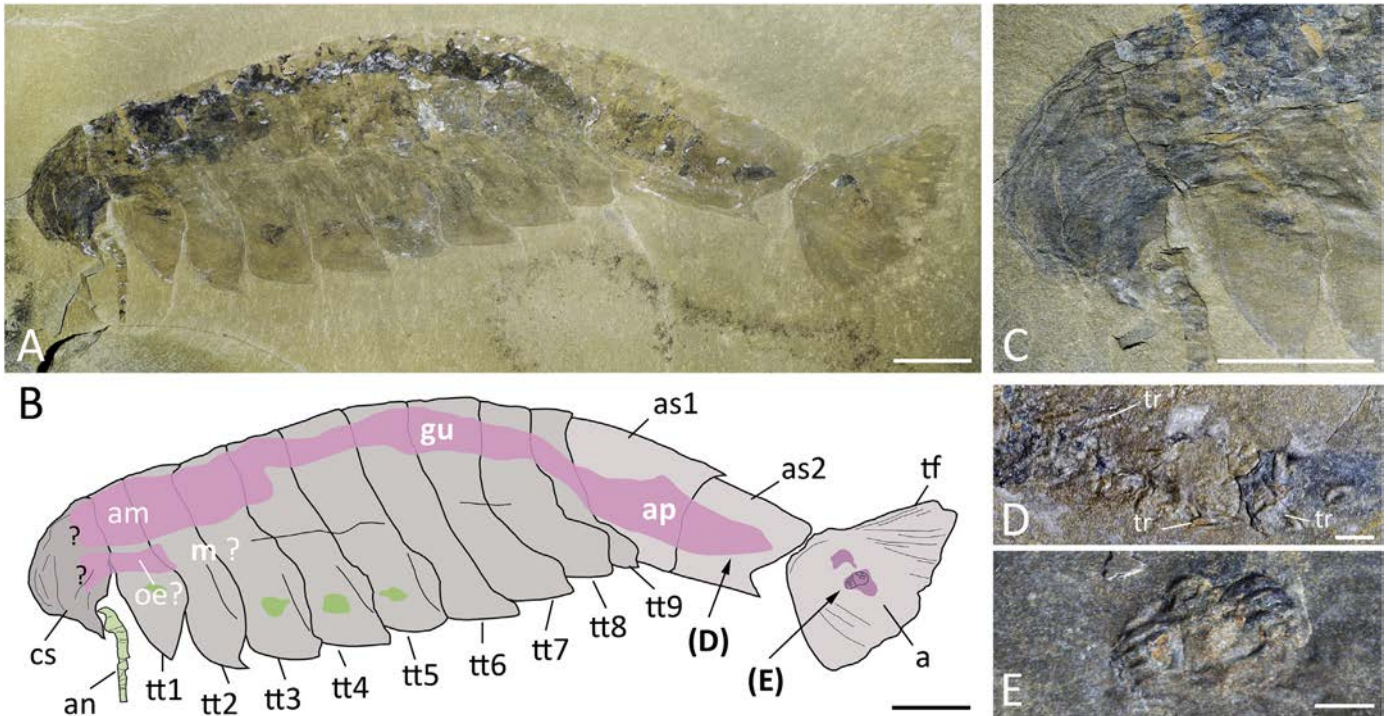


Fig. 2. General morphology of *Sidneyia inexpectans* Walcott, 1911 from the middle Cambrian (Series 3, Stage 5) Burgess Shale, British Columbia, Canada; ROM 63380, complete specimen in lateral view. (A–B) General view. (C) Details of head shield. (D) Exoskeletal fragments in AP (for location see B). (E) Trilobite fragment in posterior part of AP (for location see B). Scale bars: 1 cm in A–C; 1 mm in D and E. Abbreviations: a, anus; am, anterior midgut; an, antenna; ap, abdominal pocket; as1–as2, 1st–2nd abdominal sclerite; cs, cephalic shield; gu, gut; m?, possible mouth opening; oe?, possible oesophagus; tf, tail fan; tr, trilobite fragments; tt1–tt9, 1st–9th trunk tergite; ?, outline of anteriormost gut uncertain.

Sidneyia and the other ‘xenopods’, and two well-supported groups of Palaeozoic arthropods, the Aglaspidida and the Cheloniellida. However, this new clade only relies on a single shared character and none of the phylogenetic analyses that have identified it agreed on the relationships between its different components. Moreover, while the vicissicaudates were resolved as the sister taxon of a clade regrouping crustaceans and marrellomorphs by Ortega-Hernández et al. (2013), other studies have resolved them as the sister taxon of chelicerates (e.g. Legg et al., 2013) or of a clade regrouping chelicerates and megacheira (Edgecombe et al., 2011). Finally, recent studies suggest that *Sidneyia* might in fact be a stem-chelicerate rather than a vicissicaudate (Legg, 2014a, b).

4. Morphology of the digestive system of *Sidneyia inexpectans*

4.1. General features

The gut tract of *S. inexpectans* is straight, tubular and relatively narrow through the thoracic region, but stretches both anteriorly and notably posteriorly to form a large elliptical pocket. Rare specimens preserved in lateral compression show that the digestive tract runs parallel and close to the axial roof of the exoskeleton and slopes down in the abdominal region (Fig. 2A,B). The anus opens ventrally at the telson level and seems to be covered by a circular anal plate attached along the posterior margin of the second abdominal sclerite (Fig. 1C). The digestive glands and the abdominal pocket are by far the best preserved features of the digestive system of *Sidneyia* due to the early diagenetic mineralisation of their soft tissues and lumina in phosphate.

4.2. Digestive glands and anterior gut

Three pairs of conspicuous features often occur in the cephalic region and the anterior thorax up to the third segment. They are preserved in three dimensions in contrast to most anatomical and exoskeletal features that are strongly compressed. They are mineralised in calcium phosphate with frequent cauliflower-like microcrystals of ca 0.5 μm in diameter (see Fig. 4G and Energy Dispersive X-ray Spectroscopy (EDX) analysis in Fig. 4H–J). The features are interpreted as paired digestive glands owing to their symmetrical arrangement on both sides of the sagittal plane of the animal (Fig. 4A–F). They seem to attach along the wall of the anterior part of the gut although the exact outlines of this wall are not clearly defined. These assumed digestive glands have morphofunctional equivalents in various Cambrian arthropods such as *Squamacula* (Paterson et al., 2012) and naraoiids (Vannier and Chen, 2002; Zhang et al., 2007). Their relatively irregular outline suggests that they were soft organs possibly resembling the digestive glands of extant crustaceans (e.g. Icelly and Nott, 1992; Felgenhauer, 1992) and chelicerates (Fage, 1949; Fahrenbach, 1999; Botton and Shuster, 2003). The anteriormost pair has the largest size, the broadest base, and forms wing-shaped pointed extensions into the head region. The second pair is shorter and splits into two lobes distally and the third one has a more elongated spindle-shape. They are located between the cephalic shield and the third trunk segment. Each gland is made up of closely packed, curved and relatively long tubules of ca 150–300 μm in diameter. The tubules ramify distally and end up blindly along the margin of the gland (Fig. 5 and Fig. Sup. 1). They appear to be radiating from the attachment area of the gland although the way they open into the anterior gut lumen (via a single primary duct or several?) is unclear. An intersegmental

disposition of these glands is suggested by their insertion sites on the gut at the boundaries between cephalon/tergite 1, tergite 1/tergite 2, and tergite 2/tergite 3 (Fig. 4A–H). A similar distribution pattern of digestive glands has been described in various Cambrian arthropods (Lerosey-Aubril et al., 2012; Ortega-Hernández and Brena, 2012; Vannier et al., 2014; Lerosey-Aubril, 2015). By their lobate shape, tubular network and tubule average diameter, the digestive glands of *S. inexpectans* recall the hepatopancreatic tissue of modern crustaceans (Fig. Sup. 1G,H) that secretes digestive enzymes and assimilates food. The anterior part of the gut between the glands, although poorly delimited, is pear-shaped (Fig. 4C,F) and is interpreted as the anteriormost region of the midgut. Its swollen shape suggests a possible function in food storage and processing.

4.3. Oesophagus and mouth

Two specimens of *Sidneyia* show a short cylindrical feature within the sagittal plane of their body that runs across the boundary between the cephalic shield (CS) and at least the first trunk tergite (Fig. Sup. 2). This tube-like feature is less than 10 mm long and is lined with a ca 1 mm thick wall rich in carbon (EDX analysis and SEM backscattered images; Fig. Sup. 2B,C) and slightly expands posteriorly in a funnel-like manner. This feature is interpreted as the possible oesophagus of *Sidneyia*. In most modern arthropods, the oesophagus is lined with cuticle and is associated with ring muscles whose peristaltic contractions convey food into the gut (Fig. Sup. 2F,G). The thick wall of the possible oesophagus of *Sidneyia* may represent the remains of a comparable musculature. In the laterally compressed specimen (Fig. 2), the assumed oesophagus lies ventral to the anterior part of the gut but how it connects to it remains unclear, probably because of the overlap of various anatomical features present in the head region. However, the oesophagus seems to loop upwards to join the midgut. The flared end of the assumed oesophagus (Fig. Sup. 2B) is likely to represent the mouth of *Sidneyia* that clearly opened ventrally and posteriorly in a sagittal position, and probably close to the posterior margin of the first trunk segment. The anterior part of the digestive system of trilobites displayed a similar loop and posteriorly oriented mouth opening (Chatterton et al., 1994; Lerosey-Aubril et al., 2011).

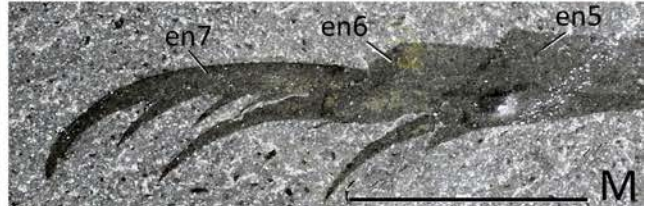
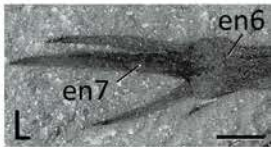
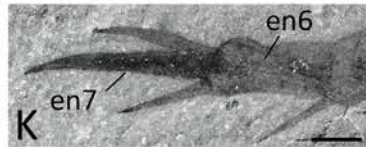
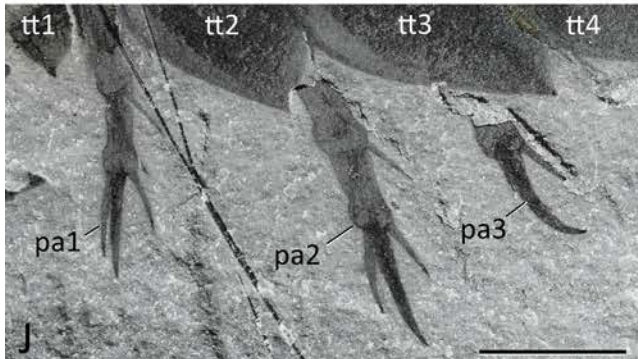
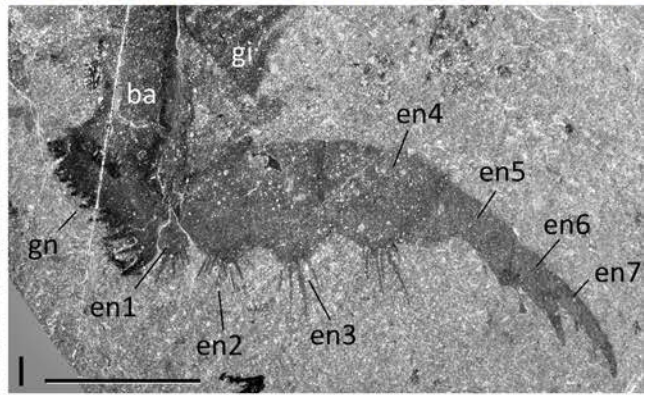
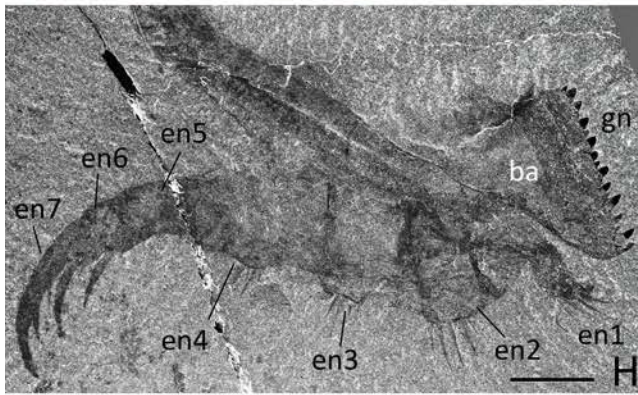
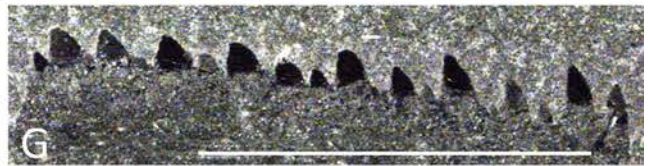
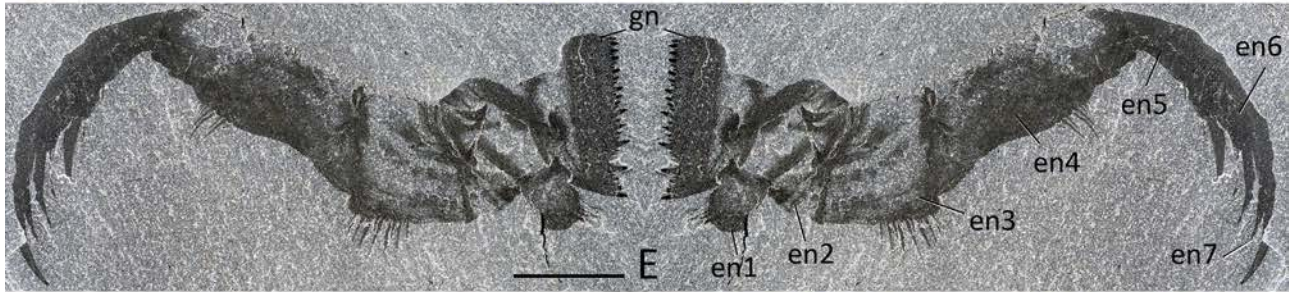
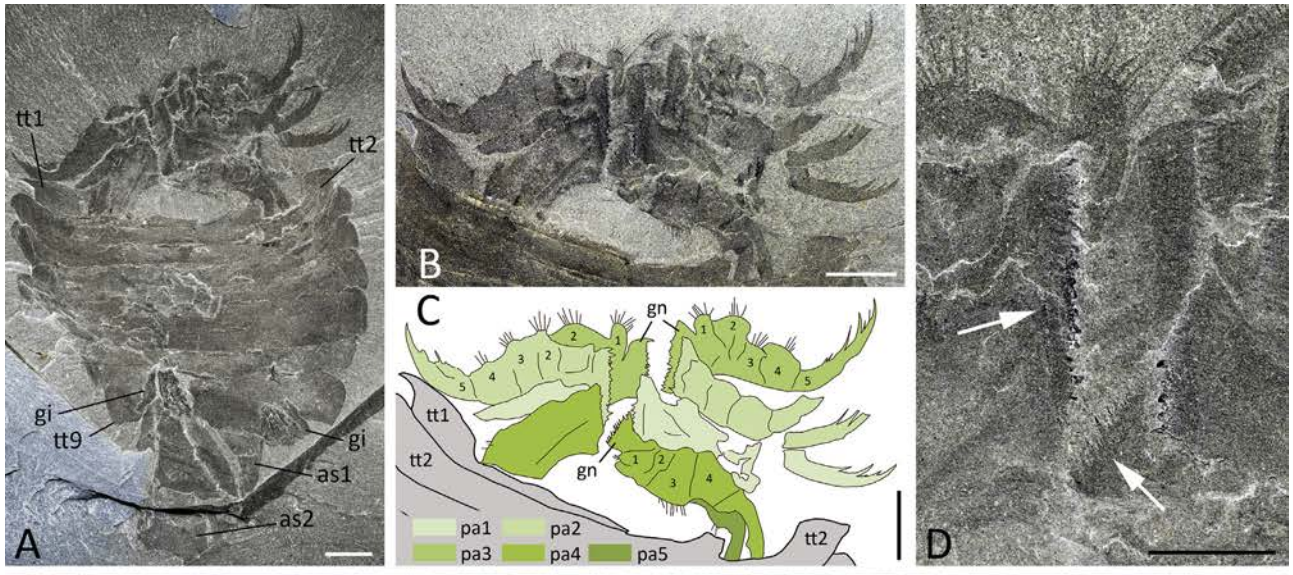
4.4. Abdominal pocket

The gut of *Sidneyia* stretches markedly and relatively abruptly at the level of the posterior margin of the last trunk tergite to form a spacious, elongated abdominal pocket (AP) that fills a large portion of the abdomen being encased by the two cylindrical abdominal sclerites (Figs. 4A and 6; Fig. Sup. 3). The AP tapers gently at the telson level down to the anus opening. In dorsal view, the AP has a consistent elliptical or inverted pear-shaped outline. In numerous specimens, the AP is the only part of the digestive system to be preserved. By contrast with the digestive glands and the middle part of the gut, the AP has sharp, well-defined boundaries (Fig. 6A–C). The AP is typically filled with three-dimensionally preserved material (called gut contents here) that consists of more or less abundant exoskeletal elements of invertebrates (e.g. trilobite trunk tergites, cephalia and pygidia) embedded in a mineralized matrix. No other region of the gut concentrates undigested elements in such a way, indicating that the AP had the probable function of storing food residuals. Moreover, very few specimens of *Sidneyia* have an empty AP. These two characteristics suggest that food did not run through the gut in a continuous flow and that the undigested fraction accumulated in the AP for some time before defecation. This feature is unique among Cambrian

arthropods described so far and no exact equivalent of the AP of *Sidneyia* occurs in extant arthropods. However, interesting comparisons can be made with modern Arachnida such as the Amblypygi (Weygoldt, 2000), Anactinotrichida (Coons and Alberti, 1999), Araneae (Felgenhauer, 1999; Foelix, 2010), Pseudoscorpiones (Vachon, 1968), Ricinulei (Talarico et al., 2011) and Solifugae (Klann and Alberti, 2010). In these groups, the posterior portion of the midgut or the hindgut (in the Solifugae only) forms a pouch, the so-called stercoral pocket, that serves as a reservoir for fecal material (Fig. Sup. 4). In the Araneae and Solifugae (at least), this pocket is surrounded by variously orientated muscle fibres. The stercoral pocket is assumed to perform various functions such as the storage of digested food and excretory material or even the reabsorption of water (Ueda, 1974; Butt and Taylor, 1986; Tillinghast, 1986; Coons and Alberti, 1999; Felgenhauer, 1999; Farley, 1999; Foelix, 2010; Klann and Alberti, 2010; Talarico et al., 2011). When empty, the AP of *Sidneyia* shows lineated transverse or criss-crossed structures (Fig. 6D–I) that clearly belong to the wall of the AP and cannot be mistaken for gut contents. These structures represent either transverse folds in the wall of the AP and/or muscle fibres. One *Sidneyia* specimen displays a particularly well-preserved criss-crossed network of fibre-like structures (Fig. 6D–I) that seems to be lining the wall of the AP. They are comparable in size and overall arrangement to the muscle fibres that surround the stercoral pocket of modern chelicerates (Fig. Sup. 4F,I). The AP was probably flexible, being able to stretch in order to accommodate the successive input of food residuals, as indicated by its more or less inflated shape (Fig. 6; Figs. Sup. 3,4). In rare specimens (see also Caron et al., 2014), the AP appears to have been extruded from the abdomen (Fig. Sup. 5) as the possible result of a stress that may have preceded the animal's death. In conclusion, the AP is interpreted here as a possible functional analogue of the stercoral pocket of some modern chelicerates, the role of its assumed musculature being to expel food residuals and excretory material outside.

5. Gut contents of *Sidneyia inexpectans*

Recognisable, whole or fragmented exoskeletal elements (e.g. trilobite sclerites) and undetermined debris of most probably biological origin (e.g. black patches suggesting organic-rich material) were observed in the gut of 94 specimens of *Sidneyia* (Table 1). The vast majority of these elements are concentrated in the AP but some of them occasionally occur in the anterior and middle parts of the gut. SEM observations and EDX analysis of gut contents indicate that the material contained in the AP is particularly rich in Calcium and Phosphorus and therefore likely represents calcium phosphate (Fig. Sup. 6). Natural sections through this material show that it is often capped with a thin layer of phyllosilicates that are similar (elemental composition, texture) to those of the host rock (Fig. Sup. 6A,B). Elemental mapping of the exposed surface of gut contents confirms that calcium phosphate does not occur outside the boundary of the AP (Fig. 7, Fig. Sup. 6G). It is likely to have precipitated during early diagenesis within the AP and before the post-mortem collapse of the gut structures. Carbon is scattered all over the AP with patches of carbon films in places. Some exoskeletal elements have a phosphatic composition perhaps inherited from their original chemistry (Fig. Sup. 6E,F), typically the phosphatic shell of inarticulated brachiopods. Even in those cases, however, it cannot be entirely ruled out that diagenetic phosphatisation occurred, considering that they are embedded within a matrix of calcium phosphate. More surprisingly, EDX analyses of trilobite sclerites show no clear Phosphorus or Calcium signals (Fig. 7A,C,D) suggesting that their 3D-preservation may be due to aluminosilicate coatings or replacement (see Butterfield et al., 2007). Pyrite, identified by the co-occurrence of Sulphur and Iron (Fig. 7G,I), is



present in isolated spots and rarely prevalent. The origin of calcium phosphate in the gut contents and digestive glands of *Sidneyia* is discussed later in this paper (see section 6.4).

5.1. Food remains within the anterior gut

Remains of brachiopod shells concentrated between the first digestive glands were found in one specimen of *Sidneyia* (Fig. 8E–J). They consist of broken elements and an almost complete valve (length and width approx. 2.5 and 1.5 mm) bearing symmetrical radiating ribs. These brachiopod elements may belong to *Nisusia burgessensis* Walcott, 1924 (see Briggs et al., 1994, p. 109). Their occurrence suggests that the enlarged interspace between the digestive glands received freshly ingested food. More questionable is the presence in one specimen of *Sidneyia* of a cluster of 5 agnostids (*Ptychagnostus praecurrens* Westergaard, 1936) in the central part of the cephalic shield (Fig. 8A–D; see also Bruton, 1981, Fig. 99). These agnostids have a small size (cephalon width less than 3.5 mm) and are neither disarticulated nor broken apart, except for one specimen. This rounded cluster is located under the central part of the cephalic shield (Fig. 8B), thus matching the assumed position of the anteriormost part of the midgut housing freshly ingested food. However, the lack of visible landmarks such as the remains of digestive glands or gut boundaries makes it difficult to ascertain whether these agnostids are effectively ingested items preserved within the anterior midgut or result from chance superposition with *Sidneyia*. Agnostids such as *Ptychagnostus* are extremely abundant in the Burgess Shale (Caron and Jackson, 2008) and are often superimposed on the external surface of larger animals or within cavities (Chatterton et al., 2003). Based on other Cambrian occurrences, Fatka et al. (2009) and Fatka and Szabad (2011) also suggested that agnostids, because of their small size, could move into the cavities of carcasses for sheltering or scavenging. A group of agnostids may have effectively penetrated into the decaying carcass of *Sidneyia*, its cephalic shield offering a potential shelter and source of food. These two hypotheses (ingestion versus sheltering/scavenging behaviour) need to be tested by additional fossil evidence.

5.2. Food remains within the middle part of the gut

The middle part of the gut is relatively narrow and cylindrical (Fig. 2). Unlike the AP and the digestive glands, its external boundaries are usually poorly defined, discontinuous, if not absent. However, one specimen shows closely packed clusters of disarticulated sclerites of ptychopariid trilobites, possibly *Ehmaniella burgessensis* Rasetti, 1951, distributed along the midline of the body between the 5th and 8th trunk tergites (Fig. 9A,C). Their location, their disarticulated and/or fragmentary state, and the fact that they form clusters strongly suggest that they represent ingested elements that were transiting through the midgut and do not result from chance superposition. Similarly, an agnostid cephalon (presumably belonging to *Ptychagnostus praecurrens*) and a cluster of trilobite elements were found in the middle part of the gut of two other specimens (Fig. Sup. 7D–G). Some doubts remain however when elements overreach the assumed outer boundaries of the gut.

This is typically the case of some elongated, curved, exoskeletal elements (e.g. Fig. Sup. 7A–C). Rather than storing food, the main function of this part of the digestive tract was most probably to ensure the transit of undigested residuals towards the AP, which would explain that gut contents rarely occur there. Insufficient concentration of Phosphorus and Calcium in the middle part of the gut due to its transit function may explain its poor preservation compared with that of the digestive glands and the AP.

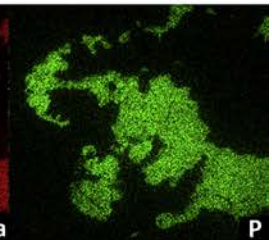
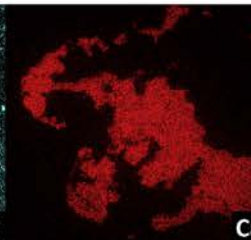
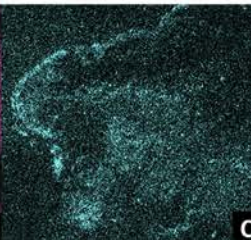
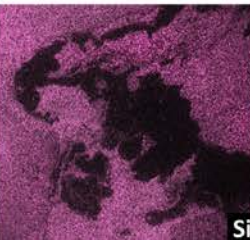
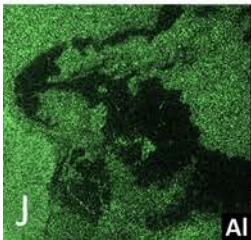
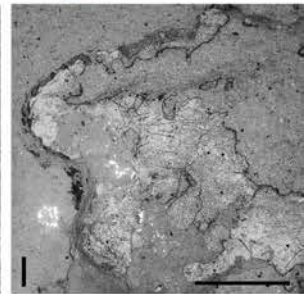
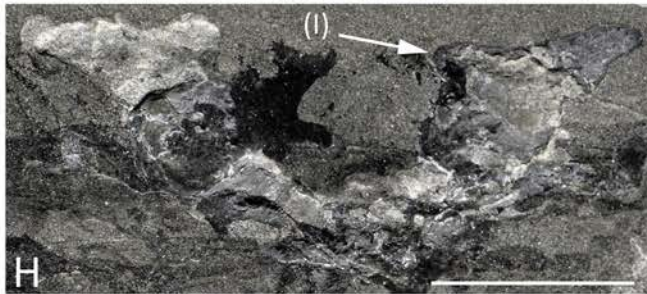
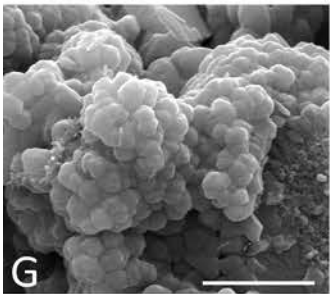
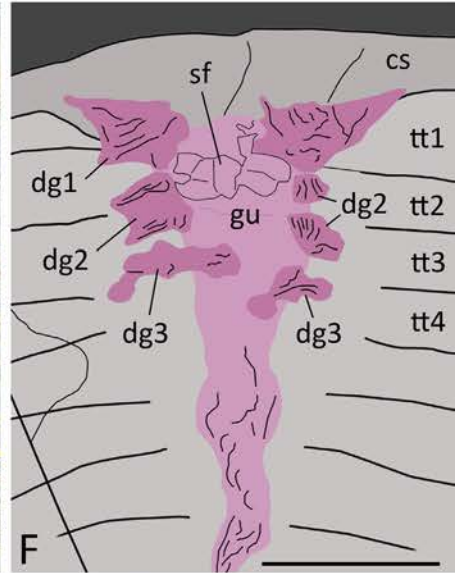
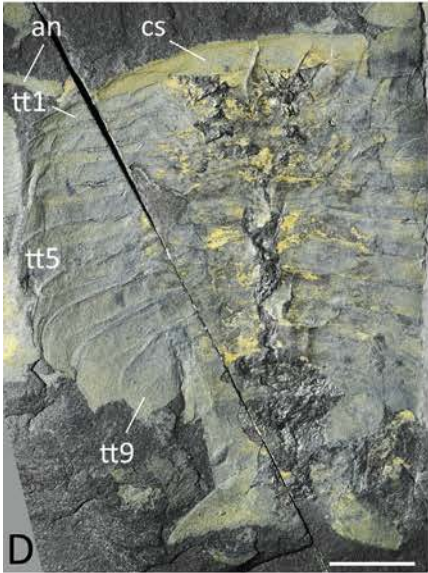
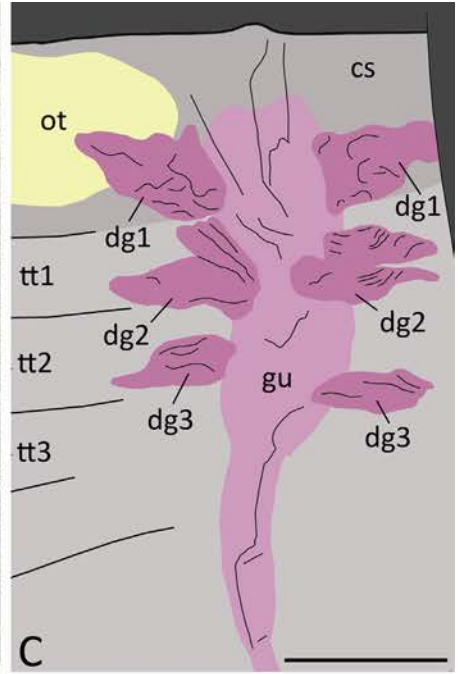
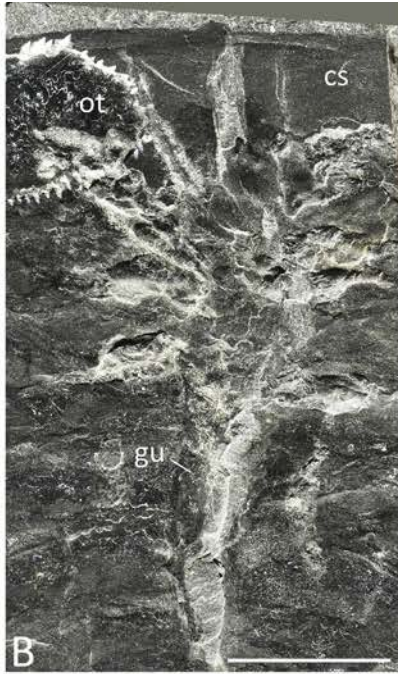
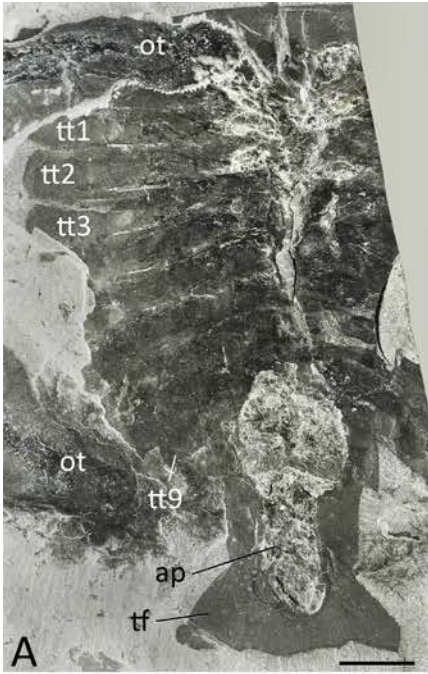
5.3. Food remains within the abdominal pocket

5.3.1. Trilobites

Trilobite elements are by far the most frequent exoskeletal remains within the AP of *S. inexpectans*. They were found in at least 13% of the *Sidneyia* specimens where gut contents are present in the AP (Table 1). The trilobite elements are typically whole or broken cephalons and pygidia, and more or less disarticulated thoracic tergites. Their overall morphology (e.g. cephalon) and ornament (e.g. pustules) best compare to *Ehmaniella burgessensis*, suggesting that it was the most frequent trilobite ingested by *Sidneyia*. *E. burgessensis* is common in the Burgess Shale biota and is very often associated with *Sidneyia* on numerous rock slabs. The majority of ingested trilobites belong to juvenile stages (probably meraspis).

The size of exoskeletal elements found in the AP is a good indicator of the size range of trilobites that *Sidneyia* had the ability to ingest. One complete subadult specimen of *Sidneyia* (ca 90 mm long) displays a cephalon in its AP that corresponds to a juvenile stage of *E. burgessensis* of approximately 5.5 mm long and 3.5 mm wide (Fig. 9A–E). Similarly, an almost complete undetermined juvenile trilobite (not *Ehmaniella*; possibly a corynexochid such as *Olenoides* or *Kootenia*, based on its long pleural spines) of about 3 mm long and 2.3 mm wide occurs within the AP of another specimen of *Sidneyia* (Fig. Sup. 7L,M). The assumed oesophagus of *Sidneyia* had a diameter of about 1 mm with a possible funnel-shaped mouth opening reaching about 2.5 mm wide or more (Fig. Sup. 2B). This size range is consistent with the ingestion of such small trilobites provided that the oesophagus could slightly stretch open to allow food to pass into the anterior midgut. It is the case in the majority of modern crustaceans in which the oesophagus is a tube equipped with ring muscles that can expand and contract (e.g. in myodocope ostracods; Fig. Sup. 2F,G). The trilobite elements often show obvious signs of disarticulation and breakage (Fig. 9E–G) that probably resulted from the grinding action of gnathobases (Fig. 3) prior to ingestion. No appendages of trilobites were found in the AP of *S. inexpectans*. Their non-biomineralized cuticle and internal soft tissues (e.g. muscles) were probably resorbed through enzymatic digestion in the anterior part of the gut. The absence of large exoskeletal fragments in the AP indicates that *Sidneyia* neither preyed upon nor scavenged on adult or subadult trilobites. This selectivity towards feeding on immature individuals might have been related to the fact that the appendages of *Sidneyia*, especially their gnathobases, were not powerful and/or resistant enough to break the heavily mineralized cuticle of adult trilobites. We must also consider that adult trilobites could probably escape more easily and were possibly less abundant than juveniles.

Fig. 3. Post-antennal appendages of *Sidneyia inexpectans* Walcott, 1911 from the middle Cambrian (Series 3, Stage 5) Burgess Shale, British Columbia, Canada. (A–D) ROM 63123, disarticulated specimen with cephalic shield removed showing the four anteriormost postantennal appendages, general view, appendages and details of gnathobases. (E, F) ROM 63376, appendage with its mirror image to emphasize the assumed grinding function of the opposing gnathobases, general view and details of gnathobase spiny features. (G, H) ROM 63370, appendage, details of gnathobase and general view. (I) ROM 63382.1, appendage showing remains of possible exopodial gills. (J–L) ROM 63362, tip of the three anteriormost postantennal appendages, general view and details of second and first appendage, respectively (note their pincer-like aspect in dorsal view). (M) ROM 63388.1, tip of postantennal appendage showing secondary spines on the last podomere. Scale bars: 1 cm in A–D; 5 mm in E–K, N; 1 mm in L, M. Abbreviations: as1–as2, 1st–2nd abdominal segment; ba, basipod; en1–en7, 1st–7th endopod podomere; gi, gill (on exopod); gn, gnathobase; pa1–pa9, 1st–9th pair of post-antennal appendages; tt1–tt9, 1st–9th trunk tergite.



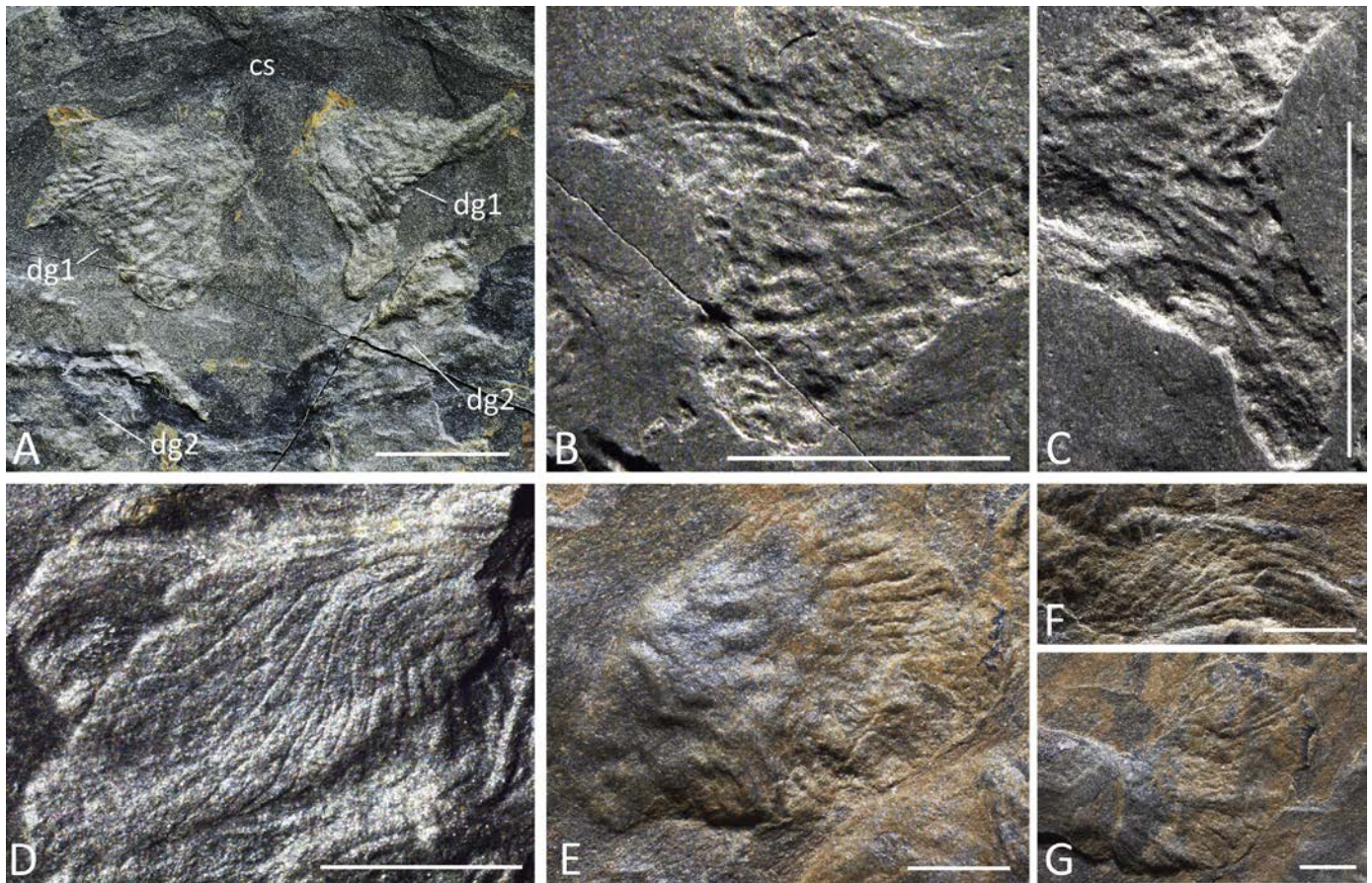


Fig. 5. Internal features of the digestive glands of *Sidneyia inexpectans* Walcott, 1911 from the middle Cambrian (Series 3, Stage 5) Burgess Shale, British Columbia, Canada. (A–C) ROM 63384, general view and details of the first pair of digestive glands. (D) ROM 63365, left gland, first pair, showing ramified closely packed tubules. (E–G) ROM 63369, left gland of the second pair, right gland of the second pair and right gland of the third pair, details of ramified and radiating network. Scales bars: 5 mm in A–C, 2 mm in D; 1 mm in E–G. Abbreviations: cs, cephalic shield; dg1–dg3, 1st–3rd pair of digestive glands.

5.3.2. Brachiopods

Brachiopods are less frequent (ca 6%; Table 1) than trilobites in the AP of *Sidneyia* and are represented by various species, none of them being dominant. Shell fragments of *Micromitra burgessensis* (Resser, 1938), with their readily recognizable reticulated ornament are present in one specimen (Fig. 10A–C). Costellate, articulate brachiopods also occur in a few specimens and most probably belong to *Diraphora bellicostata*, Walcott, 1924 or *Nisusia burgessensis* (Walcott, 1889) (Fig. 10F–H). Another form represented by three valves bearing fine concentric growth lines was found in the AP of one specimen of *Sidneyia* (Figs. 6B and 10D,E) and might belong to *Lingulella waptaensis* Walcott, 1924.

5.3.3. Bradoriid arthropods?

More enigmatic are tiny skeletal elements of less than a millimetre length that occur in at least two specimens of *Sidneyia* (Fig. 10M, Fig. Sup. 8). Although partly covered by sediment, their outline seems to be circular with no dividing line possibly representing a hinge of a dorsal fold such as in the shell/carapace of

typical ‘bivalved’ invertebrates (e.g. brachiopods, arthropods). They are preserved in calcium phosphate and are characterized by a very fine, concentrically arranged reticulated ornament and a ridge running parallel to the margin. Their overall morphology, ornamented pattern and chemical composition recall those of bradoriid arthropods, especially *Flumenoglacies michaeli* Andersson, 2014 from the middle Cambrian Stephen Formation of British Columbia, Canada (Andersson, 2014). However, this bradoriid species has not been reported so far in the Burgess Shale Formation. Resemblances with the ornament of *Zepaera* sp. (Wrona, 2009) and *Kunmingella* sp. (Zhang, 2007) are also worth being noted. Perhaps these enigmatic tiny remains belong to a new bradoriid species (J.-B. Caron personal communication). The lack of dorsal split (e.g. fold) and antero–posterior polarity that normally characterize the carapace of subadult bradoriids might indicate that these tiny shells are juvenile stages. Univalved, subcircular carapaces with an almost circular outline have been reported in the juvenile stages of bradoriids such as *Kunmingella douvillei* (Mansuy, 1912) from the early Cambrian of China (Zhang, 2007; pl. 1). The AP

Fig. 4. General morphology and chemical composition of the digestive glands of *Sidneyia inexpectans* Walcott, 1911 from the middle Cambrian (Series 3, Stage 5) Burgess Shale, British Columbia, Canada. (A–C) USNM 250218, almost complete specimen showing three pairs of digestive glands, gut and stercoral pocket, general view and details of glands. (D–F) ROM 56945 with almost complete digestive system, general view and details of digestive glands. (G) ROM 63389,1, apatite microcrystals within a three-dimensionally preserved digestive gland. (H–J) USNM 268575, first pair of digestive glands showing bilateral symmetry, general view, detail and EDX elemental mapping of the area re-presented in I. Scale bars: 1 cm in A–F; 5 mm in H; 1 mm in I; 2 μ m in G. G–I are SEM images (I is a backscattered image). Abbreviations: an, antenna; ap, abdominal pocket; cs, cephalic shield; dg1–dg3, 1st–3rd pair of digestive glands; gu, gut; ot, *Ottoia prolifica* (priapulid worm) associated with *Sidneyia*; sf, shell fragments (brachiopods); tf, tail fan; tt1–tt9, 1st–9th trunk tergite.

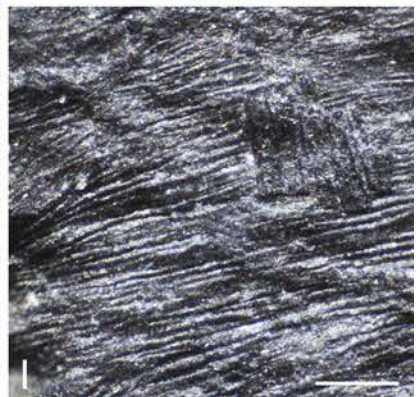
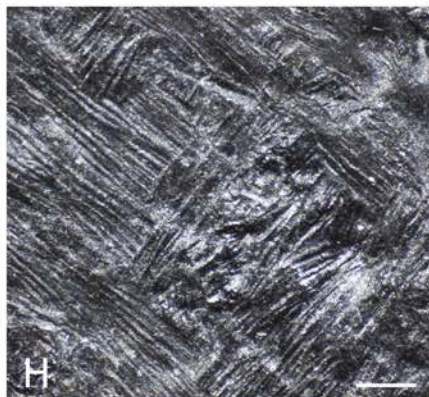
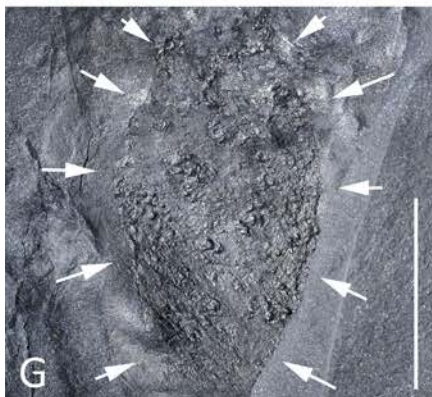
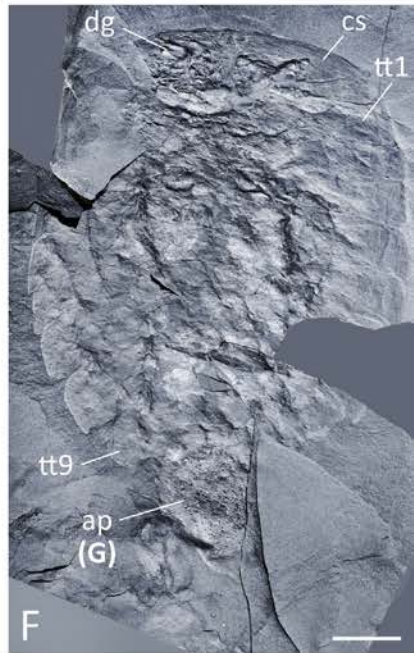
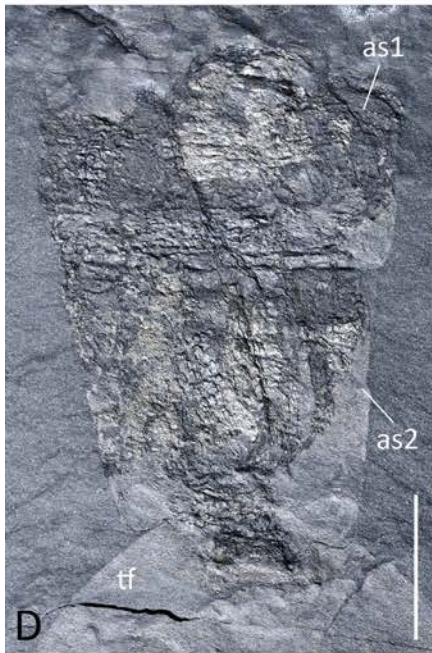
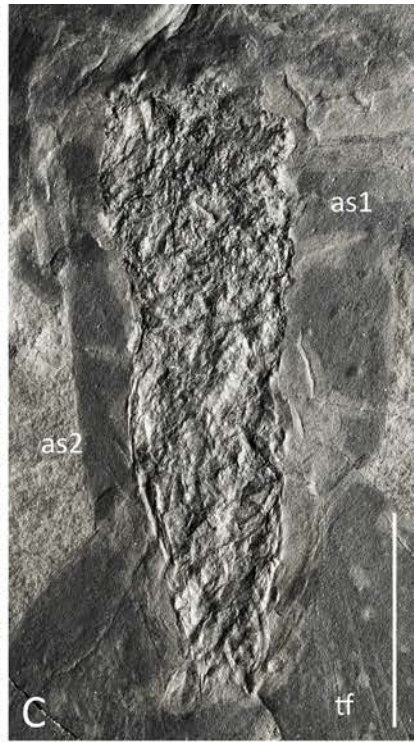
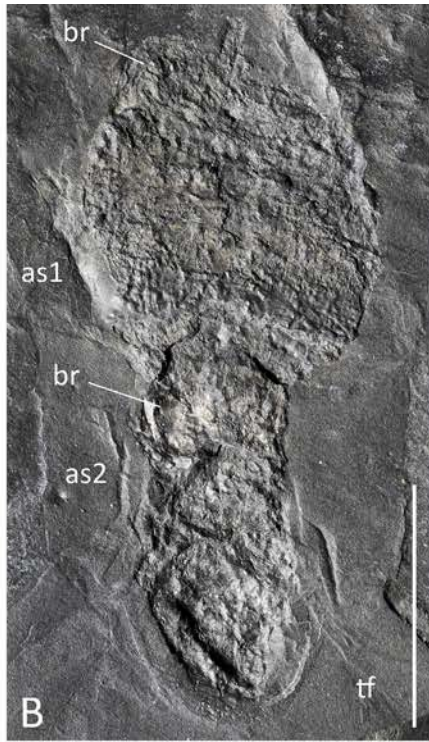
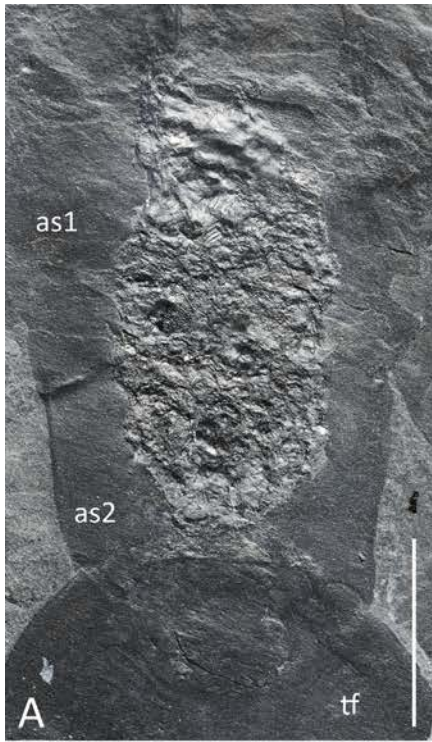


Table 1

Count data of the gut contents of *Sidneyia inexpectans* Walcott, 1911 from the middle Cambrian (Series 3, Stage 5) Burgess Shale, British Columbia, Canada. The three columns correspond to the number of *Sidneyia* specimens with specific gut contents (e.g. trilobite elements) in the anterior part (between the digestive glands), the middle part of the gut and the abdominal pocket. The total number of *Sidneyia* specimens with gut contents is 94. USNM, collections of the National Museum of Natural History, Smithsonian Institution, Washington D.C.; ROM, collections of the Royal Ontario Museum, Toronto, Canada. RQ/RT, Raymond Quarry/Talus; WQ/WT, Walcott Quarry/Talus; others, specimens from other localities (see Table Sup. 2).

| | Anterior part | Middle part | Abdominal pocket |
|--|---------------|-------------|------------------|
| Trilobites | 0 | 3 | 12 |
| Possible trilobites | 0 | 0 | 6 |
| Agnostids | 1 | 1 | 0 |
| Possible agnostids | 0 | 0 | 0 |
| Brachiopods | 1 | 0 | 5 |
| Possible brachiopods | 0 | 0 | 1 |
| Other skeletal/cuticular/granular elements | | | |
| Possible worms | 0 | 0 | 2 |
| Possible bradoriids | 0 | 0 | 3 |
| Elongated curved elements | 0 | 0 | 6 |
| Undetermined fragments/elements | 0 | 0 | 73 |
| Number of <i>Sidneyia</i> specimens with gut contents | | | |
| USNM | 1 | 2 | 29 |
| ROM (RQ/RT) | 0 | 1 | 24 |
| ROM (WQ/WT) | 1 | 6 | 35 |
| ROM (others) | 0 | 0 | 6 |
| Total | 2 | 9 | 94 |

of one specimen of *Sidneyia* contains a pustulated shelly fragment also of possible bradoriid origin (Fig. 10I–L). Finally, it is important to note that the bradoriid *Liangshanella burgessensis* Siveter and Williams, 1997 which is by far the most abundant animal in the Greater Phyllopod Bed of the Walcott Quarry Shale Member (Caron and Jackson, 2008) does not occur in the AP of *Sidneyia*.

5.3.4. Other animal groups

Approximately five-to-eight millimetre long, slender, slightly curved elements occur in the AP of a few specimens of *S. inexpectans* or are adjacent to it (Fig. Sup. 9). They are preserved in aluminosilicates, iron oxides, calcium phosphate (Fig. Sup. 9C,D) or partly as carbon films (Fig. Sup. 9F,H). Whether some of these elongated elements belong to gut contents or are superimposed to them by chance is uneasy to determine (e.g. Fig. Sup. 9B,C). Their shape recalls that of various sclerites of Burgess Shale animals such as the helens of hyolithids (e.g. *Haplophrentis carinatus* (Matthew, 1899) or the long spiny sclerites of the halwaxiid *Orthrozanclus reburrus* (see Conway Morris and Caron, 2007)). However, considering the lack of conical hyolithid shells within the AP (see Vannier, 2012) and the fact that the curved elements are never numerous, it seems unlikely that *Sidneyia* actually fed on either of these two animals. Some of the slightly curved elements superficially resemble the tubes of *Tubulella flagellum* Matthew, 1899 (see Van Iten et al., 2012), a possible sessile but poorly documented cnidarian from the Burgess Shale (Fig. Sup. 9F–H). The arthropod *Marrella splendens* Walcott, 1912 (Garcia-Bellido and Collins, 2006) would appear as an interesting alternative if we consider that the curved elements found in the AP of *Sidneyia* might be the undigested head spines of this extremely abundant arthropod of the Burgess Shale. However, the presumed high mobility of *Marrella* on and above the seafloor probably strongly reduced its chances to be captured alive by epibenthic consumers such as *Sidneyia*. Regardless of their origin, the curved elements are relatively rare and

simply may have been ingested by chance along with consumable food. Rare annulated fragments were also found within the AP of two specimens of *Sidneyia* (Fig. Sup. 9I–K). Based on their tubular shape and wrinkled appearance, they are tentatively interpreted as cuticular remains of worms, possibly of juvenile stages of *Ottoia prolifica*, a common priapulid worm of the Burgess Shale fauna (Conway Morris, 1977; Vannier, 2012).

6. Discussion

6.1. The feeding mode of *Sidneyia inexpectans*

Numerous Cambrian arthropods with assumed predatorial habits (e.g. anomalocaridids, *Isoxys*, *Kodymirus*, *Yohioia*; Vannier et al., 2009, 2014; Haug et al., 2012a,b; Daley et al., 2013; Lamsdell et al., 2013; Legg and Vannier, 2013; Daley and Edgecombe, 2014; Cong et al., 2014) had well-developed grasping frontal appendages. *S. inexpectans* lacked such prehensile appendages pointing forwards. Its flexible, flagelliform antennae (Fig. 8A,B) had an obvious sensory function and were not involved in manipulating food. Moving food to the ventral gnathobases (Fig. 3E) seems to have been the initial step of the feeding process. Although the primary function of ventral endopods was locomotion, we assume that the most anterior ones played an important role in manipulating food and moving it to the gnathobases. Their claw-like termination, articulated design and possible pincer-like structure (Fig. 3) strongly suggest capacities for pushing, seizing and directing small prey or food particles to the mouth area. One specimen of *Sidneyia* preserved in ventral view clearly shows that the basal parts of the four anteriormost appendages converged towards the sagittal axis of the animal where the posteriorly directed mouth was supposed to open (Fig. 11A,B). The converging motion of the gnathobases had the effect of disarticulating and crushing food such as the exoskeleton of small trilobites and the

Fig. 6. Abdominal pocket of *Sidneyia inexpectans* Walcott, 1911 from the middle Cambrian (Series 3, Stage 5) Burgess Shale, British Columbia, Canada. (A) ROM 63385.1, with elliptical shape. (B) USNM 250218, with inverted bottle shape. (C) USNM 57489, with elliptical elongate shape. (D) ROM 63194, AP with striated wall. (E–I) ROM 63373, elliptical pocket with crisscrossed fibre-like structures; simplified line drawing, general view of specimen, general view of AP (white arrows indicate outline), details of fibre-like networks. Scale bars: 1 cm in A–G; 200 µm in H and I. Abbreviations: ap, abdominal pocket; as1–as2, 1st and 2nd abdominal sclerites; br, brachiopod shell fragments; cs, cephalic shield; tf, tail fan; tt1–tt9, 1st to 9th trunk tergite.

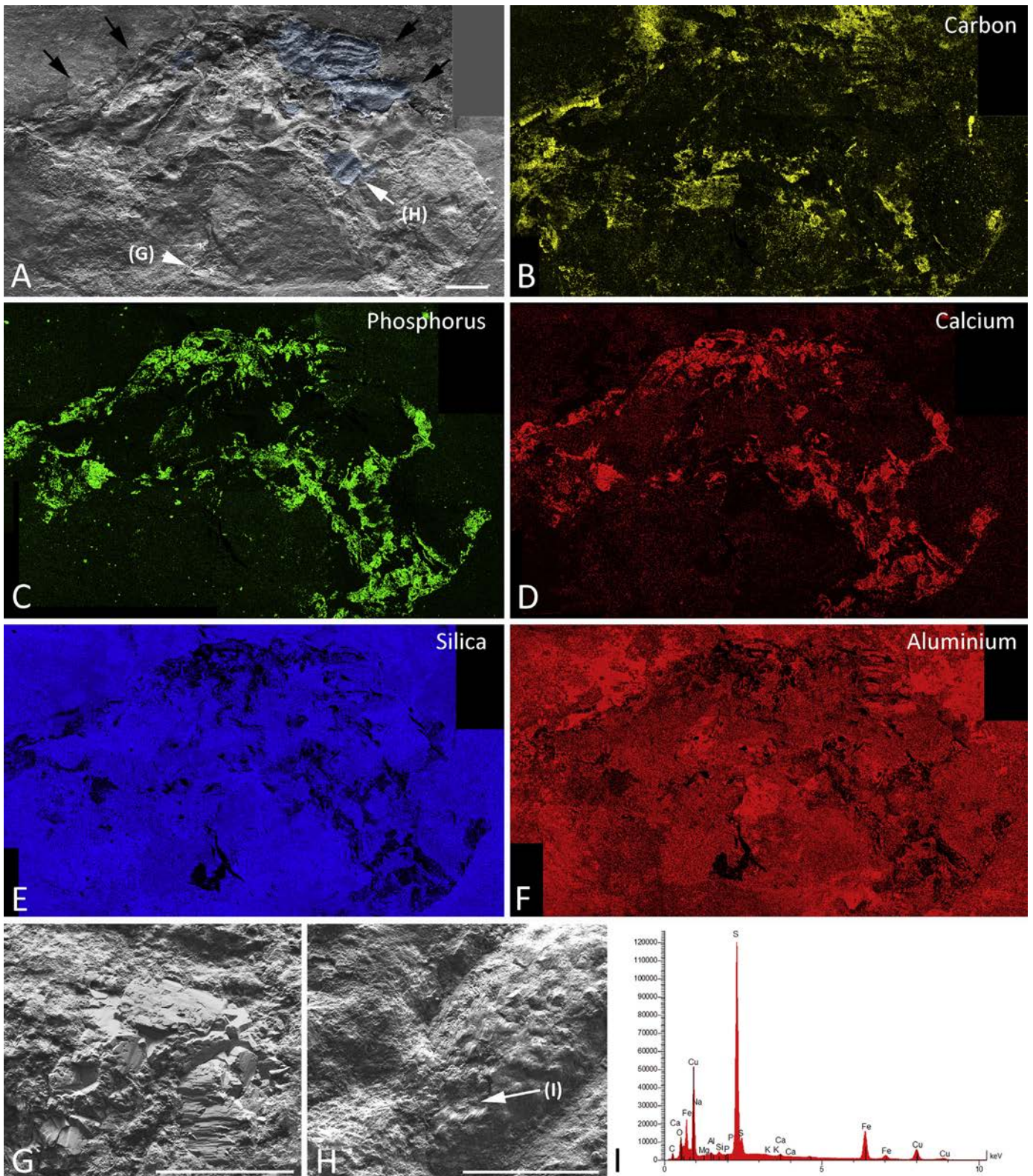


Fig. 7. EDX analyses and elemental mapping of the gut contents of *Sidneyia inexpectans* Walcott, 1911 from the middle Cambrian (Series 3, Stage 5) Burgess Shale, British Columbia, Canada; ROM 60744.1. (A) General view with exoskeletal elements highlighted in blue (location in Fig. 9C; boundaries of abdominal pocket indicated by black arrows). (B–F) Carbon, Phosphorus, Calcium, Silica and Aluminium maps, respectively. (G–I) Pyrite spots (location indicated in A) and EDX analysis showing Sulphur and Iron occurrences. A, G, H are SEM images. Scale bars: 1 mm in A,–F; 500 μ m in G; 300 μ m in H.

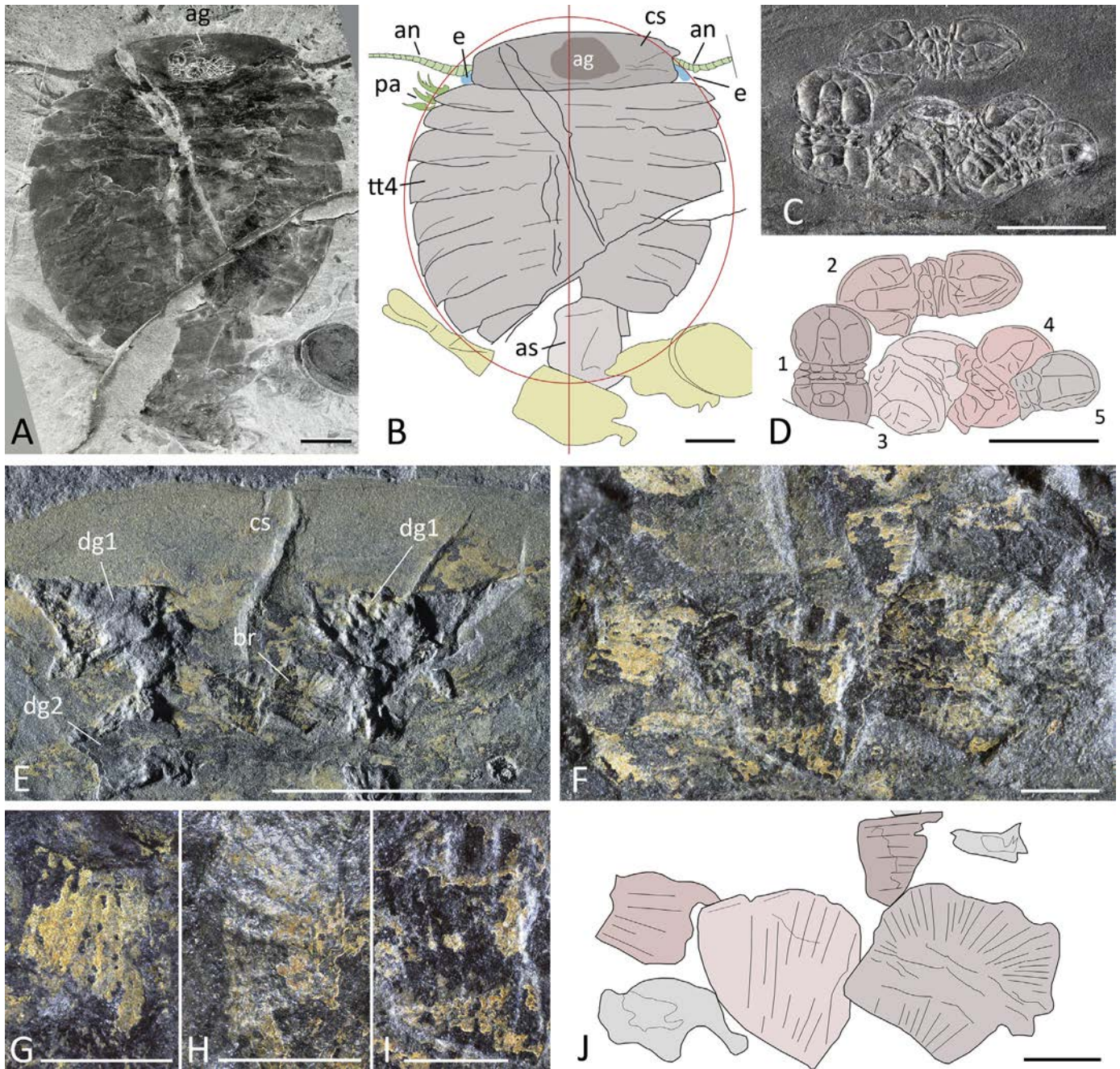
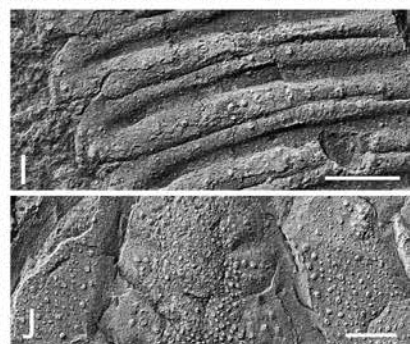
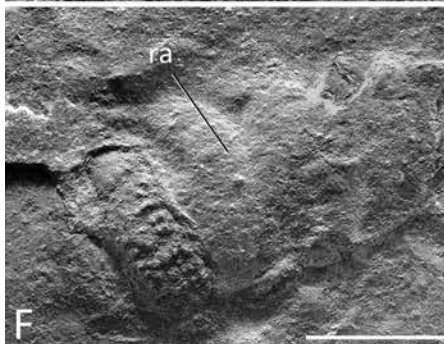
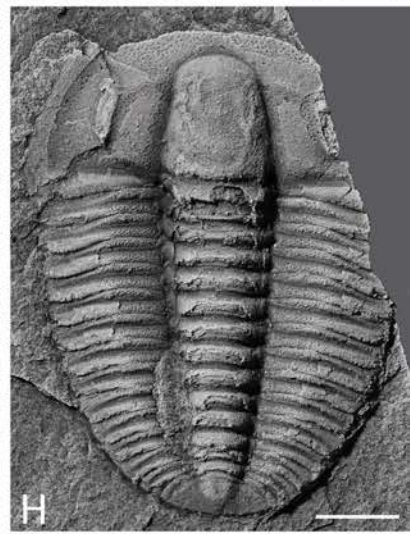
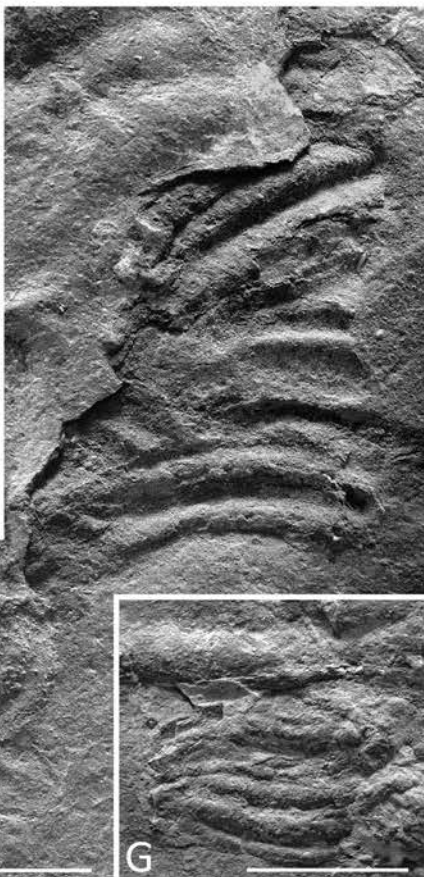
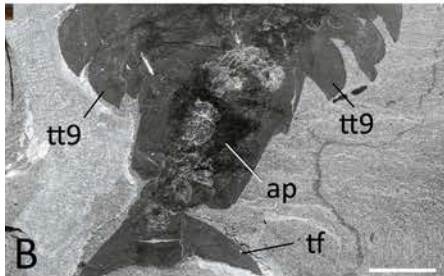
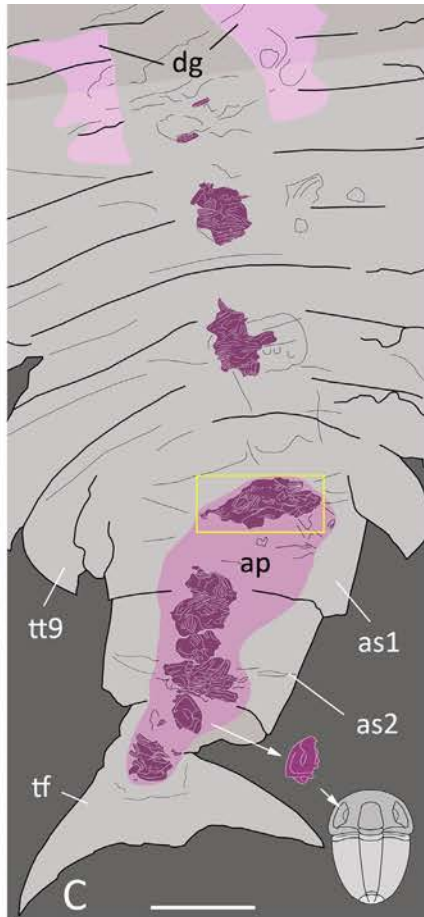
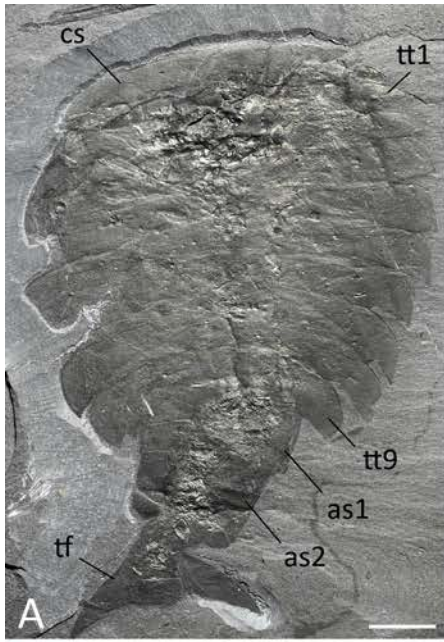


Fig. 8. Exoskeletal elements in the anterior part of the gut of *Sidneyia inexpectans* Walcott, 1911 from the middle Cambrian (Series 3, Stage 5) Burgess Shale, British Columbia, Canada. (A–D) USNM 269164, general view and details of agnostid specimens clustered in the central part of the cephalic shield where the anterior gut occurs (gut structures not preserved). (E–J) ROM 56945.1, brachiopod fragments between the first pair of digestive glands, interpreted as being located within the anterior part of the gut; general view, details of the whole cluster and of individual fragments. Scale bars: 1 cm in A, B and E; 5 mm in C and D; 1 mm in F–J. Abbreviations: ag, agnostid cluster; an, antenna; as, abdominal sclerite; br, brachiopod fragments; cs, cephalic shield; dg1–dg2, 1st and 2nd pair of digestive glands; e, eye; pa, postantennal appendage; tt4, 4th trunk tergite.

shells of brachiopods prior to its ingestion through the oesophagus. The physical breakdown of food exerted by the gnathobases was sufficient for millimetre-sized items to be sucked into the gut via the assumed peristaltic contractions of the oesophagus (Fig. Sup. 2). The grinding power of gnathobases was however limited since no thick sclerotized or mineralised fragments are found within the gut contents of *Sidneyia*. A comparable mechanism, involving opposing and converging pairs of gnathobases, has been observed in modern horseshoe crabs (Fig. 11C,E), that easily crush the shells of small bivalves and soft-bodied animals (Botton and Shuster, 2003). In *L.*

polyphemus, food is pushed into the funnel-like mouth opening by the spiny tips of gnathobases and pumped into the oesophagus (Fig. 12). In *Sidneyia*, ingested food passed from the oesophagus into the pear-shaped anterior part of the midgut that probably functioned as a temporary storage pocket. The enzymatic chemical breakdown of food most probably took place within this structure, enzymes being secreted within the tubules of the digestive glands attached to it and drained into the anterior midgut through ducts. The digestive glands of *Sidneyia* performed the same function as the hepatopancreas of modern horseshoe crabs and crustaceans



(Fig. Sup. 1G,H). The relatively small diameter of their tubules (less than 200 μm) was not consistent with food particles entering the ramified network of the glands. Where assimilation took place is less clear. In modern horseshoe crabs, lipids, glycogen and proteins resulting from digestion are stored in connective tissues surrounding the tubules of the hepatopancreas (Fahrenbach, 1999). Similarly, the digestive glands of *Sidneyia* formed relatively large organs that most probably housed tubules and storage tissues with various cellular types for both digestion and assimilation. After a short transit through the middle part of the gut, digested food residuals (mainly shell fragments and sclerotized exoskeletal elements) and excretory material accumulated within the abdominal pocket. Although this pocket may be seen as a functional equivalent to the stercoral pocket of modern arachnids, important differences should be noted. In some arachnids (Araneae, Ricinulei), the pocket is a diverticle of the gut (extensible blind sack; Fig. Sup. 4; Ludwig et al., 1994; Foelix, 2010; Talarico et al., 2011), whereas it runs in straight continuity with the digestive tract in *Sidneyia*. The abdominal pocket of *Sidneyia* was probably lined by muscle fibres (Fig. 6) arranged in different directions allowing residues to be excreted through circular and/or longitudinal muscular contractions. Although morphofunctional comparisons with horseshoe crabs are valuable (Figs. 11 and 12), the digestive system of *Sidneyia* seems to differ markedly from that of *L. polyphemus* (Fig. 12A; Fahrenbach, 1999). *Sidneyia* displays a swelling in its anterior midgut but does not seem to have possessed a gizzard for mashing food material as in modern horseshoe crabs (Fig. 12A). The hepatopancreas, which occupies much of the prosoma in *Limulus* (Packard, 1880; Fahrenbach, 1999; Shuster and Sekiguchi, 2003), is represented in *Sidneyia* by much smaller glands in proportion to the body size of the animal (Fig. 4). The storage of faeces within the abdominal pocket suggests infrequent feeding.

6.2. The diet of *Sidneyia inexpectans*

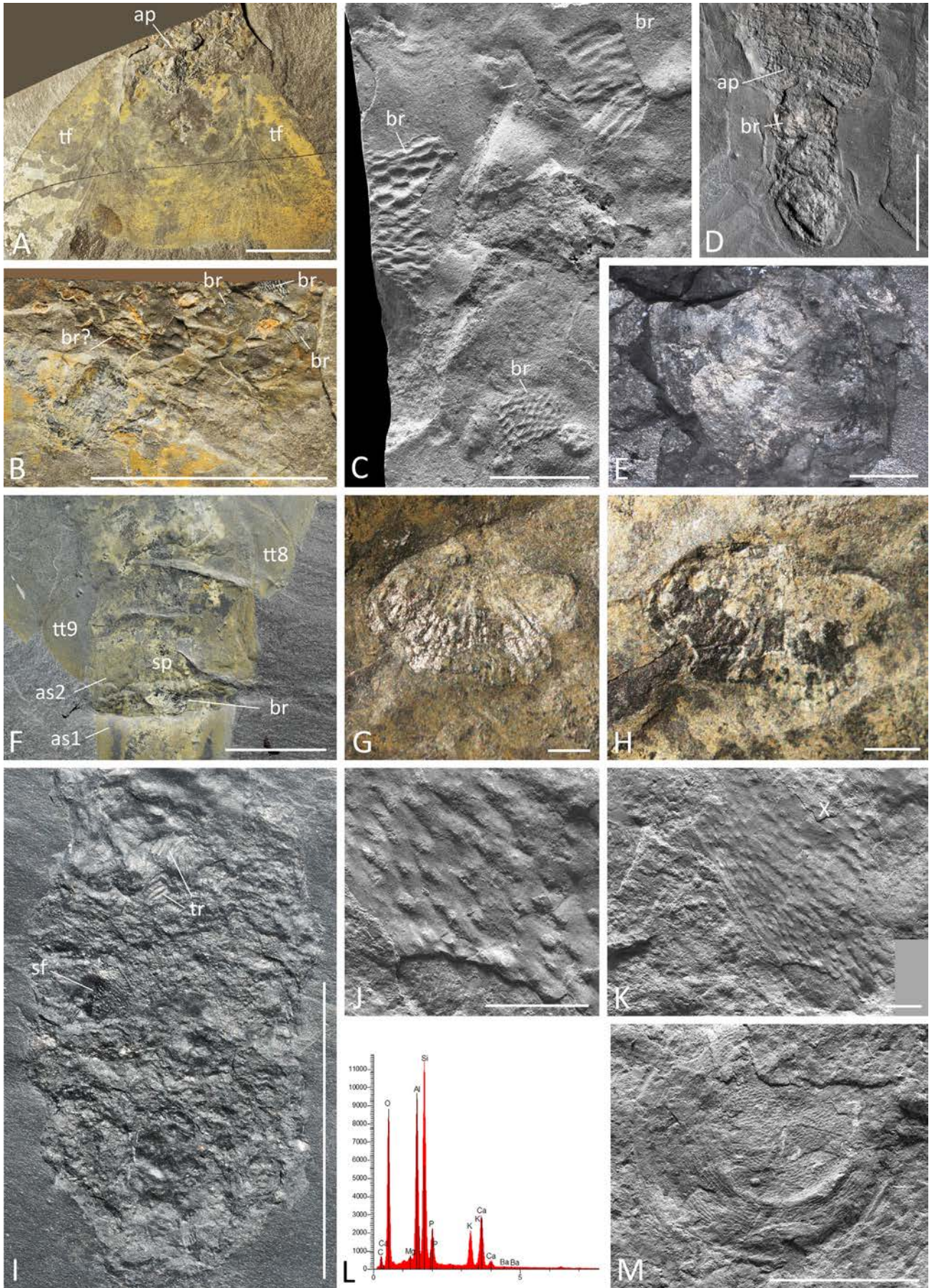
Sidneyia fed upon a variety of organisms such as trilobites, brachiopods, possibly agnostids and priapulid worms and various undetermined invertebrates represented by their exoskeletal elements (e.g. possible bradoriids, *Marrella*). Juvenile stages of trilobites seem to have been the most frequent prey of *Sidneyia* as indicated by the relatively large number of their exoskeletal fragments stored in the AP. Some elements might have been ingested incidentally (e.g. some elongated/curved elements; see section 5.3.4). *Sidneyia* was not a sediment eater, no significant proportion of sediment being ever found in its gut. The overall shape and appendage design of *Sidneyia* is typical of an epibenthic crawler that fed on small sessile or relatively slow moving animals living at the water-sediment interface. Bradoriids overwhelmingly represented by *Liangshanella*, agnostids and small trilobites such as *Ehmaniella* were among the most abundant arthropods of the Burgess Shale biota (e.g. Caron and Jackson, 2008 and J.-B. Caron, personal communication) as indicated by their numerical abundance on rock slabs. Whereas *Sidneyia* did feed on small trilobites and possibly agnostids, *Liangshanella* was absent from its diet. This might stem from the possibility that *Liangshanella* was a vagile, swimming arthropod that *Sidneyia* could not capture.

Hyaloliths that were a major food source for the carnivorous worm *Ottoia prolifica* (Vannier, 2012) are absent from the gut contents of *Sidneyia*. Whether hyaloliths were avoided by *Sidneyia* relative to other food items is impossible to ascertain. Contrasting with *Sidneyia*, the feeding mechanism of *Ottoia* involved no appendages and was based on the pharyngeal eversion/inversion that drew prey into the gut, a mechanism that may have favoured the ingestion of slender, conical organisms such as hyaloliths. Perhaps, the functional morphology of the mouth and oesophagus of *Sidneyia* did not permit such food items to be ingested easily. Although the ventral appendages of *Sidneyia* were obviously able to manipulate a wide range of live and dead food items (e.g. via their gnathobases), only a small proportion of them could probably find its way to the mouth to be eventually ingested via the oesophagus. *Sidneyia* was possibly a predator but may have had scavenging habits as well. We see no biomechanical constraints that would have prevented this arthropod from processing carcasses and extracting food from them through the tearing and grinding action of its gnathobases. The food items that could be identified with certainty in the gut contents of *Sidneyia* may account for a small fraction of the actual diet of *Sidneyia*, which possibly fed upon a much more diverse food source including a great variety of soft-bodied animals and larval stages. We must keep in mind that soft tissues (e.g. plucked from carcasses) and thin cuticular elements may have been completely resorbed through digestion, leaving no identifiable traces in gut contents. No fossil evidence suggests that *Sidneyia* was a selective feeder. Its indiscriminate feeding mode, however, must have been strongly constrained by biomechanical factors, such as the diameter of the oesophagus and the grinding power of ventral appendages.

Sidneyia provides by far the most detailed and valuable source of information concerning the diet and the feeding mode of a Cambrian arthropod. Indeed, if we except the pioneer descriptions of *Sidneyia* by Bruton (1981), ingested food items have been described in three Cambrian arthropods only (one specimen in each case). Eodiscoid sclerites (*Pagetia*; Zhu et al., 2004) were recognized in the gut a “*Fuxianhuia*-like” arthropod from the middle Cambrian Kaili biota (ca 508 Ma, China; Zhao, 2011). This specimen has a series of well-developed paired digestive glands preserved in phosphate. But unlike *Sidneyia*, they are uniformly distributed along the major part of its gut and the gut tract is filled with trilobite sclerites throughout its length. The holotype of the arthropod *Utahcaris* from the middle Cambrian Spence Shale of Utah preserves a cluster of fragmented sclerites of trilobites under its cephalon, which was interpreted as stomach contents by Conway Morris and Robison (1988). Information concerning the diet of early Cambrian arthropods is extremely fragmentary. However, a new arthropod from the Emu Bay Shale Lagerstätte (Cambrian Series 2, Stage 4), probably allied to *Sanctacaris* and *Utahcaris* (Jago et al., 2014), has identifiable fragments of the trilobite *Estaingia bilobata* (Pocock, 1964) in its gut. Whether this arthropod was a predator or a scavenger could not be determined.

These arthropods from Kaili, the Spence Shale and the Emu Bay Shale, and *S. inexpectans* all indicate that small epibenthic arthropods such as the juvenile stages of trilobites and agnostids

Fig. 9. Trilobite elements in the digestive tract of *Sidneyia inexpectans* Walcott, 1911 from the middle Cambrian (Series 3, Stage 5) Burgess Shale, British Columbia, Canada. (A–G) ROM 60744.1. (A, B) General view in normal and polarized light. (C) Distribution of exoskeletal elements (in purple) within AP and within the central part of the gut; yellow frame indicates analysed (elemental mapping) area in Fig. 7; small trilobite represented at the same scale as *Sidneyia* to show the approximate size of ingested prey. (D) Concentration of various trilobite elements in the abdominal pocket. (E–G) Details of trilobite elements (*Ehmaniella burgessensis*); right half of cephalon, pustulose rachis of posterior trunk and disarticulated tergites, and tergite tips, respectively. (H–J) *Ehmaniella burgessensis* from the Burgess Shale (not in gut contents). (H) ROM 60759, juvenile of about the same size as that in (C). (I, J) ROM 60670, details of trunk tergites and pustulose glabella. E–G are SEM images. Scale bars: 1 cm in A, B; 5 mm in C; 1 mm in D–J. Abbreviations: ap, abdominal pocket; as1–as2, 1st and 2nd abdominal sclerites; ce, cephalon; cs, cephalic shield; dg, digestive gland; gl, glabella; ra, rachis; te, thoracic elements; tf, tail fan; tt1–tt9, 1st to 9th trunk tergite.



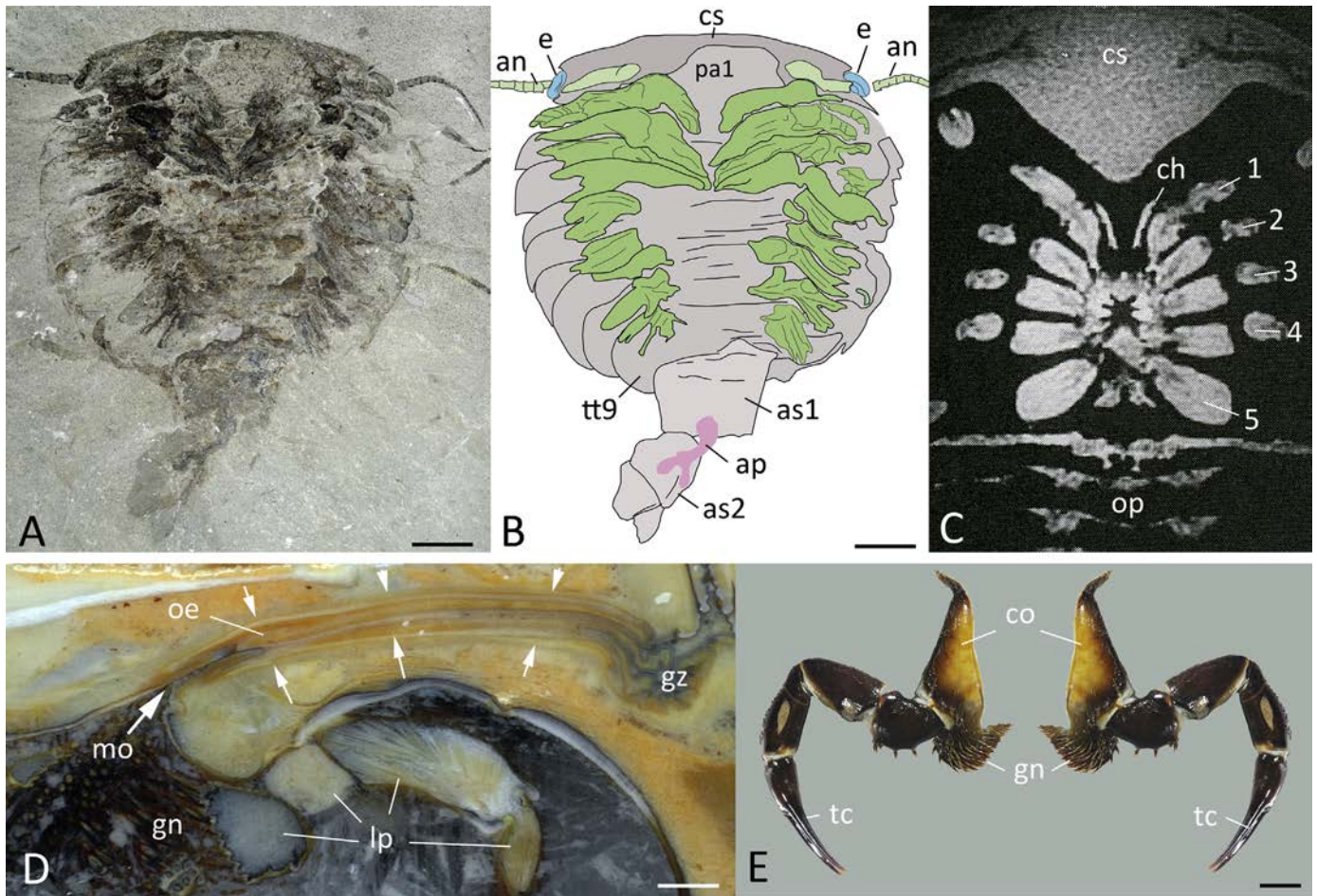


Fig. 11. Role of gnathobases in food processing: comparisons between *Sidneyia inexpectans* from the middle Cambrian (Series 3, Stage 5) Burgess Shale (British Columbia, Canada) and modern horseshoe crabs. (A, B) ROM 59945, ventral view showing the outlines of post-antennal appendages; the gnathobases of the four anteriormost appendages converge towards the mouth. (C) Magnetic Resonance Image (MRI) through a live female horseshoe crab (*Limulus polyphemus*) showing the “teeth-like” radiating orientation of gnathobases around the mouth (courtesy Mark. L. Botton). (D) Sagittal section through a deep-frozen specimen of *L. polyphemus* showing gnathobases in contact with mouth opening (white arrows indicate oesophagus). (E) Leg of *L. polyphemus* and its mirror image to show gnathobases on both sides of the mouth (not shown); compare with Fig. 3F. Scale bars: 1 cm. Abbreviations: an, antenna; ap, abdominal pocket; as1–as2, 1st and 2nd abdominal sclerite; ch, chelicera; cs, cephalic shield; e, eye; gn, gnathobasis; gz, gizzard; lp, leg podomeres in section; mo, mouth opening; oe, oesophagus; op, opisthosoma; pa1, 1st pair of postantennal appendages; tc, terminal claw; tt9, 9th trunk tergite; 1–5, 1st–5th pair of leg.

were an important source of food for much larger arthropods in Cambrian ecosystems.

6.3. Ecological impact of *Sidneyia inexpectans*

Sidneyia was a relatively large (maximum length ca 160 mm) epibenthic arthropod with predatory and possibly scavenging habits. Although it is difficult to have a precise idea of its population density, *Sidneyia* is a frequent arthropod throughout the Greater Phyllopod Bed (Walcott Quarry) of the Burgess Shale (Caron and Jackson, 2008) and is very common in the Raymond Quarry (J.-B. Caron, personal communication). The impact of *Sidneyia* predation on the populations of small epibenthic arthropods, such as trilobites (e.g. *Ehmaniella*), should be

considered, because it especially affected juveniles. Although it is impossible to make a quantitative assessment of predation pressure in the Burgess Shale biota, recent models support this hypothesis. Thin-shelled bivalves (e.g. *Mytilus*, *Mya* and *Spisula*) are one of the major sources of food for modern horseshoe crabs, such as *L. polyphemus* (Botton, 1984; Botton and Shuster, 2003). Quantitative studies demonstrate the predation impact of horseshoe crabs on these bivalve populations (Botton and Shuster, 2003). The fact that they preferentially feed on individuals within a specific size range seems to have an important effect on the composition, growth and survival of these populations. That *Sidneyia* may have exerted a comparable pressure on certain trilobite populations should not be excluded. *Sidneyia* may have been an occasional scavenger on various carcasses of

Fig. 10. Brachiopod and other “shelly” elements in the abdominal pocket of *Sidneyia inexpectans* Walcott, 1911 from the middle Cambrian (Series 3, Stage 5) Burgess Shale, British Columbia, Canada. (A–C) USNM 269163, abdominal end with incomplete AP, general view and details showing fragments of the brachiopod *Mitromitra burgessensis*. (D,E) USNM 250218, detail of AP with an undet. brachiopod (possibly *Lingulella waptaensis*) in it; one more fragment of presumably the same form occur in AP (see location in Fig. 6B). (F–H) ROM 63387.1, brachiopod bearing radiating ribs, possibly within AP. (I–L) ROM 63385.1, abdominal pocket with trilobite and shelly fragments, details and chemical composition (apatite; EDX) of the shelly fragment. (M) USNM 269124, undet. reticulated shell element, general view (see also Fig. Sup. 8). B, J, K, M are SEM images. Scale bars: 1 cm in A, B, D–F and I; 1 mm in C, E, G, H; 500 μm in M; 300 μm in J and K. Abbreviations: ap, abdominal pocket; as1–as2, 1st and 2nd abdominal sclerite; br, brachiopod; sf, shell fragments; tf, tail fan; tt8–tt9, 8th and 9th tergite; x, location of EDX analysis in L.

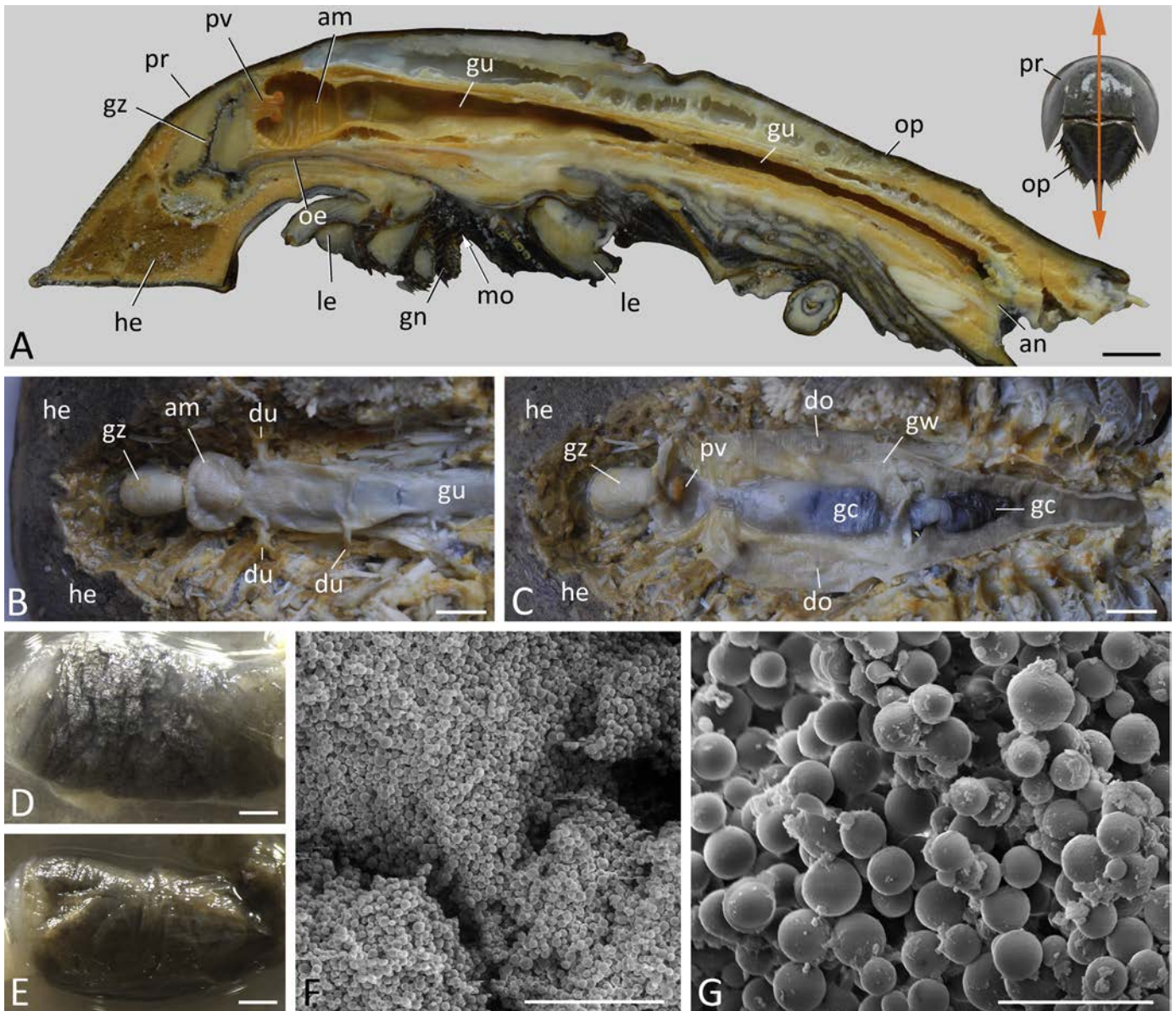


Fig. 12. Digestive system of *Limulus polyphemus*. (A) Sagittal section through a deep-frozen specimen. (B, C) Dissected specimen showing external and internal features of gut. (D, E) Gut contents wrapped in a thin membrane in the anterior and posterior part of the gut, respectively. (F, G) High concentration of phosphatic (EDX analysis) spherites in gut contents from the posterior part of the gut, general view and details. F, G are SEM images. Scale bars: 2 cm in A; 1 cm in B, C; 2 mm in D, E; 100 μ m in F; 20 μ m in G. Abbreviations: am, anterior midgut; an, anus; do, opening of hepatopancreatic duct; du, hepatopancreatic duct opening into the gut lumen; gc, gut content; gn, gnathobasis; gu, gut; gw, gut wall; gz, gizzard; he, hepatopancreas; le, leg; mo, mouth opening; oe, oesophagus; op, opisthosoma; pr, prosoma; pv, pyloric valve.

small or larger invertebrates. Its role as a possible epibenthic recycler should be considered.

6.4. Phosphatic preservation of the digestive system of *Sidneyia inexpectans*

Phosphatic mineralisation is responsible for the three-dimensional preservation of the major part of the digestive system of *Sidneyia*, especially its digestive glands and AP (Figs. 4 and 7, respectively). This questions the origin of phosphorus and calcium that led to the mineralisation and preservation of the digestive soft tissues. In numerous extant arthropods, the epithelial cells of the midgut or the midgut glands contain calcium phosphate mineral concretions (spherites). These spherites play an important role in the storage of P and Ca and are usually released

into the gut lumen to be eventually recycled in vital processes such as moulting (hardening of the new cuticle). This is clearly exemplified by horseshoe crabs in which the absorptive cells of the hepatopancreas release important quantities of calcium phosphate spherites into the lumen of tubules (Fahrenbach, 1999; Botton and Shuster, 2003) that pass into the alimentary canal and add to faeces (Lockhead, 1950). An adult specimen of *L. polyphemus* was dissected in order to analyse its gut contents (Fig. 12). They appeared in the form of a shapeless mass of undigested residues wrapped within a thin translucent membrane (Fig. 12D,E), the posteriormost part being filled with spherites (Fig. 12F,G). These spherites of about 5–10 μ m in diameter have a phosphatic composition (EDX analysis). If we assume that *Sidneyia* had comparable physiological capacities to produce, store and recycle phosphate, then the 3D-preservation of its digestive

glands could be easily explained by early mineralisation processes driven from an internal *in situ* source of P and Ca, possibly in the form of spherites. However, the clustered apatite microcrystals (<0.5 µm; Fig. 4G) found in the digestive glands of *Sidneyia* are much smaller than the phosphatic spherites of *Limulus*. They might represent a recrystallized form of original spherites that were resorbed immediately after death. The concentration of spherites in the posterior gut of *Limulus* (Fig. 12) also offers a convincing explanation for the presence of phosphate in the abdominal pocket of *Sidneyia*. Again, the presence of P and Ca *in situ* among undigested residues might explain the post-mortem mineralization of both the surrounding muscles of the AP and the gut contents themselves. A comparable process has been proposed to explain the 3D-preservation of the digestive structures of *Leaenchoilia* from the Burgess Shale (Butterfield, 2002) and trilobites from the Weeks Formation (Lerosey-Aubril et al., 2012). The midgut glands of *Leaenchoilia* contain numerous microspheres (diameter 2–3 µm) that may correspond to the intracellular spherites found in the midgut glands of modern arthropods (Butterfield, 2002). The replacement of soft tissues with calcium phosphate, whatever its origin, requires special physicochemical conditions. Decay experiments with shrimps show that the mineralisation of soft tissues in phosphate starts within two weeks after death and requires an elevated concentration of phosphate in sediment pore waters and a drop in pH, and is favoured by a system closed to diffusion (Briggs and Kear, 1993, 1994; Hof and Briggs, 1997). The abdominal pocket and the blind tubular network of the digestive glands of *Sidneyia* both show all the characteristics of relatively closed systems in which phosphatic precipitation may have been optimal.

7. Conclusion

Our study reveals major functional aspects of the digestive system of a Cambrian arthropod with unprecedented accuracy allowing precise comparisons with extant arthropods. *S. inexpectans* displays a remarkable set of digestive glands and a spacious abdominal pocket for storing undigested elements. This pocket has no functional equivalent in extant arthropods except some arachnids. The analysis of its gut contents tells us about the diet of *Sidneyia* that included juveniles of trilobites, brachiopods and other epibenthic invertebrates.

Taking *Sidneyia* as an example, we show that significant information on the feeding ecology and digestive systems of early arthropods can be obtained through the detailed observation of fossils from Konservat-Lagerstätten, which invites further research on the Cambrian and Ordovician Burgess Shale-type exceptional biotas. Our approach, which considers fossils more as living entities than as dead organisms preserved in rocks, has great potential to unveil many aspects of the early organization and functioning of animal life that are still unknown or have to be exploited. This type of approach has been used recently to characterize key-anatomical features of early animals, such as the nervous, sensory and digestive systems of arthropods (e.g. Ma et al., 2012; Strausfeld et al., in this issue; Lerosey-Aubril et al., 2012; Vannier et al., 2014), to analyse their gut contents (e.g. worms; Vannier, 2012), and to reconstruct their functional morphology via computer modelling (e.g. Haug et al., 2012b). Recent studies have attempted to reconstruct Cambrian food webs via the computerized analyses of data obtained from the Chengjiang and Burgess Shale biotas (Dunne et al., 2008). They provide the opportunity to compare the trophic complexity at different stages in the evolution of life on Earth. However, the validity of these computerized models is dependent on the quality of data obtained from the literature and often suffers from erroneous or incomplete assumptions and crude

extrapolations based on recent biological models. Future palaeoecological models need to be directed by new and more reliable information sources such as those presented here.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.asd.2015.09.003>.

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