Resolving Details of the Nonbiomineralized Anatomy of Trilobites Using Computed Tomographic Imaging Techniques

Thesis

Presented in Partial Fulfillment of the Requirements for the Master of Science in the Graduate School of The Ohio State University

By

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2013

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Abstract

Remains of two trilobite species, *Elrathia kingii* from the Wheeler Formation (Cambrian Series 3), Utah, and *Cornuproetus cornutus* from the Hamar Laghdad Formation (Middle Devonian), Alnif, Morocco, were studied using computed tomographic (CT) and microtomographic (micro-CT) imaging techniques for evidence of nonbiomineralized alimentary structures. Specimens of *E. kingii* showing simple digestive tracts are complete dorsal exoskeletons preserved with cone-in-cone concretions on the ventral side. Inferred stomach and intestinal structures are preserved in framboidal pyrite, likely resulting from replication by a microbial biofilm. *C. cornutus* is preserved in nonconcretionary limestone with calcite spar lining the stomach ventral to the glabella. Neither species shows sediment or macerated sclerites of any kind in the gut, which tends to rule out the possibilities that they were sediment deposit-feeders or sclerite-ingesting durophagous carnivores. Instead, the presence of early diagenetic minerals in the guts of *E. kingii* and *C. cornutus* favors an interpretation of a carnivorous feeding strategy involving separation of skeletal parts of prey prior to ingestion.
Dedication

This manuscript is dedicated to my parents for encouraging me to go into the field of paleontology and to Lee Gray for inspiring me to continue.
Acknowledgments

I would like to thank Loren E. Babcock for providing most of the specimens used in this study and providing guidance in the completion of the work. Daniel F. Merriam (Kansas Geological Survey) provided specimens of *Ditomopyge decurtata* for study, but which are not reported on here. I would also like to thank William Ausich and Matthew Saltzman for their helpful advice through the completion of my studies and Stig Bergström for his contribution to my thesis defense. Soo-Yeun Ahn from The University of Akron supplied environmental scanning electron microscope images. Garrett Noble and Kyle Bodnyk from The Ohio State University’s School of Biomedical Engineering provided help and advice with the microtomography scans. Richard Hart provided access to the microtomography facility in The Ohio State University’s School of Biomedical Engineering and Ann Cook provided access to the computed tomography scanner in The Ohio State University’s School of Earth Sciences. Funding for the project was provided by Loren Babcock and the Friends of Orton Hall Fund of The Ohio State University.
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Chapter 1: Introduction

Much of the information about the nonbiomineralized anatomy of trilobites comes from exceptionally preserved specimens representing a relatively small number of taxa. Nonbiomineralized remains have been described from approximately 40 species, which represents approximately 0.04% of the described species. Some of the more exquisite examples of nonbiomineralized preservation are documented from specimens of *Phacops* sp. (Stürmer and Bergström, 1973), *Olenoides serratus* (Whittington, 1975, 1980), *Triarthrus eatoni* (Cisne, 1981), *Agnostus pisiformis* (Müller and Walossek, 1987), *Pterocephalia* sp. (Chatterton et al., 1994), *Buenellus higginisi* (Babcock and Peel, 2007), *Isotelus maximus* (Babcock, 2003; English and Babcock, 2007), *Coosella kieri* (Robison and Babcock, 2011), *Meniscopsia beebei* (Robison and Babcock, 2011; Lerosey-Aubril et al. 2012), *Sphaerophthalmus*? (Eriksson and Terfelt, 2012), *Selenopeltis buchi*, and *Biramites ingens* (Fatka et al., 2013) from Konservat-lagerstätten (deposits of exceptional preservation) in North America, Europe, and Asia. Preservation of nonbiomineralized anatomy of trilobites varies. In some material, appendages are present and internal structures are not. In others, internal structures are present and appendages are not, or both appendages and internal structures are preserved. Trace fossils in sediment have been used to supplement information on the ventral anatomy of trilobites (Jensen, 1990;
Brandt et al., 1995; Babcock, 2003; English and Babcock, 2007), but the information provided by trace fossils is limited to details of external anatomy.

Exceptional preservation of trilobites and other marine organisms is inferred to have occurred quickly after death (Briggs et al., 1994; Babcock and Chang, 1997; Babcock et al., 2001; Butterfield, 2002; Zhu et al., 2005; Ciampaglio et al., 2006; Robison and Babcock, 2011). Mineral replication of nonbiomineralized tissues was likely mediated by microbial biofilms in most examples (see Borkow and Babcock, 2003; Maas et al., 2006; English and Babcock, 2007; Lerosey-Aubril et al., 2010, 2012; Babcock and Robison, 2011). Mineral replication or fill of various types has been described (e.g., Stürmer and Bergström, 1973; Whittington, 1980; Cisne, 1981; Müller and Walossek, 1987; Orr et al., 1998; Babcock, 2003; Zhu et al., 2005; English and Babcock, 2007; Robison and Babcock, 2011). Among the preservational agents of nonbiomineralized anatomy of trilobites are calcium phosphate (Chatterton et al., 1994; Robison and Babcock, 2011; Lerosey-Aubril et al., 2010, 2012; Eriksson and Terfelt, 2012), calcium carbonate (Chatterton et al., 1994; English and Babcock, 2007), iron sulfide (Stürmer and Bergström, 1973; Cisne, 1982), aluminosilicates (Whittington, 1980), and silica (Babcock and Peel, 2007).

Nonbiomineralized trilobite anatomy can be studied either through surface examination of fortuitously broken or well-prepared specimens, or through non-invasive imaging techniques. In comparatively rare examples, alimentary structures, limbs, or other nonbiomineralized structures are evident in trilobites with surface examination (see for example Chatterton et al., 1994; Babcock, 2003; Babcock and Peel, 2007; Robison...
and Babcock, 2011; Fatka et al., 2013). Serial grinding and serial sectioning can reveal nonbiomineralized anatomy (Walcott, 1881), but this leads to destruction of specimens (Sutton et al., 2001). Non-invasive techniques (see for review Sutton, 2008), such as X-ray imaging technology, have long been known to be effective for discerning nonbiomineralized structures in unprepared and unexposed specimens (Stürmer and Bergström, 1973; Cisne, 1981).

In recent years, standard x-ray imaging has been surpassed in utility by other non-invasive techniques, including computed tomography (CT), microtomography (micro-CT), and synchrotron radiation imaging. Such techniques make it possible to gain more insight into the anatomy of various arthropods without destroying the specimens. Computer-based imaging has revealed, for example, insect and arachnid inclusions in opaque amber (Dierick et al., 2007; Penney et al., 2007; Soriano et al., 2010), external anatomy of arthropods preserved in siderite (Garwood et al., 2009; Garwood and Sutton, 2010), and internal anatomy of the meraspid stage of a trilobite (Eriksson and Terfelt, 2012).

The purpose of this paper is to describe and interpret internal structures in two species of Paleozoic trilobites from high-resolution CT images. Three specimens are interpreted to have three-dimensionally preserved digestive structures. These are compared to previous anatomical and ecological models, and the new information helps to further constrain feeding strategies of the studied trilobite taxa.
Materials – Several hundred Paleozoic trilobite specimens from various localities were examined for evidence of possible nonbiomineralized anatomy and, from among them, nine were selected for detailed study using CT scanning techniques. Selections were made partly based on specimen size, as the samples were restricted by the 60 mm diameter of the specimen chamber inside the micro-CT scanner. Small, complete, inferred corpses were selected for micro-CT preview scans to determine if they could be penetrated by an x-ray source and if a discernible image could be produced. Full micro-CT and CT scans were conducted on the specimens that fulfilled these criteria.

Seven *Elrathia kingii* (Meek, 1870) from the Wheeler Formation (Cambrian Series 3), House Range, Utah, USA, and one *Cornuproetus cornutus* (Goldfuss, 1843) from the Hamar Laghdad Formation (Middle Devonian) near Alnif, Morocco, were scanned for evidence of nonbiomineralized anatomy. Five *E. kingii* specimens were later rejected for further study due to lack of evidence of internal structures.

Repositories. – Illustrated specimens are deposited in the Paleontological Research Institution, Ithaca, New York (PRI), USA.
Methods – Techniques used for study of trilobite specimens were microtomography (micro-CT), computed tomography (CT), and environmental scanning electron microscopy with energy-dispersive x-ray (ESEM/EDX).

Microtomography

Microtomography was conducted using a Skyscan 1172 high resolution micro-CT scanner at The Ohio State University’s Department of Biomedical Engineering. The micro-CT scanner produced hundreds of 0.8 to 27 μm resolution images at different angles for each sample. Specimens were placed on a metal disk that rotated to expose all parts of the specimen to a single X-ray source. Elrathia kingii specimens were wedged between two pieces of styrofoam inside a plastic tube to reduce the effects of vibrations of the machine on image quality (Figure 1). Quick scans were generated to see if a discernible image could be produced from the specimen and if the specimen contained internal fluctuations in density that could indicate the presence of

![Micro-CT scanner](image)

Figure 1. Micro-CT scanner. A, Skyscan 1172 micro-CT scanner with a trilobite specimen in the sample chamber. B. Close-up of the sample chamber.
internal structures. Full scans were completed on trilobites that met these criteria using an aluminum-copper filter to increase resolution. Some specimens contained too much high density material in the matrix, resulting in black images in which structures of the trilobite could not be differentiated from the matrix. Due to lack of visibility, these specimens were rejected for further study.

The following settings were used to create micro-CT images for the three trilobite specimens used in this study. Exposure time for PRI 0000A was 260 ms, and source current was 141 μA; exposure time for PRI 0000B was 180 ms; PRI 0000C was scanned using a 180 ms exposure time. The source current for PRI 0000B and PRI 0000C was 100 μA. All three specimens were scanned using a frame averaging of 6 and an image pixel size of 27.20 μm. More than one-thousand TIF files were generated for each specimen.

Raw images from the micro-CT scanner were uploaded to NRecon (Bruker MicroCT, 2012) to be sectioned for later three-dimensional imaging. Transverse slices of each raw image were generated at intervals of 27 μm, using a ring artifact reduction of 20 and a beam-hardening correction of 20% to decrease the effects of artifacts created by the scanner. Images generated by NRecon were uploaded to CTvox (Bruker MicroCT, 2012) to create three-dimensional computer reconstructions of each specimen that could be rotated, sectioned at any angle, and enhanced.

Computed Tomography

A portable Neurologica CereTom CT scanner was used at The Ohio State University School of Earth Sciences to create CT images of the specimens for
comparison with micro-CT images. The CereTom scanner has eight x-ray detectors that rotate around a sample opposite an x-ray tube, generating hundreds of images that can be compiled into interactive two-dimensional and three-dimensional models using the machine’s software. Trilobites were scanned using an axial protocol at a resolution of 0.625 x 0.625 millimeters, which is the highest possible resolution generated by the scanner. DIACOM images were captured directly from the CT scanner software and uploaded to ImageJ (National Institutes of Health, 2011) for conversion from the DIACOM files to jpeg files that are readable by a computer.

Scanning Electron Microscopy

A Quanta 200 Environmental Scanning Electron Microscope (ESEM) was used by Soo-Yeun Ahn to study surface-exposed features of Elrathia kingii specimens, including PRI 0000A and PRI 0000D, at The University of Akron’s Geology Department. Whole specimens were initially scanned for evidence of bacterial preservation. PRI 0000D, was cut between the thorax and cephalon for further imaging and EDX (chemical) analysis. PRI 0000A was left uncut. No tomographic analyses were conducted on PRI 0000D.
Chapter 3: Scans of *Elrathia kingii*

Two outstretched, complete dorsal exoskeletons of *Elrathia kingii* (Figure 2, 3) were scanned for evidence of nonbiomineralized internal anatomy. These specimens were previously discussed in an abstract by Babcock and Robison (2011) before CT scans were obtained. The specimens, similar to many trilobites from the Wheeler and Marjum formations of Utah, are compressed and preserved with white calcite cone-in-cone structures on the undersides (see Bright, 1959; Robison, 1964, 1971; Hintze and Robison, 1987; Seilacher, 2001; Gaines and Droser, 2003; Robison and Babcock, 2011). These cone-in-cone structures, which are geopetal indicators preserved on the stratigraphic downward sides of polymerid trilobites and agnostoids (Bright, 1959; Robison, 1964; Gaines and Droser, 2003, 2005; Brett et al., 2009; Robison and Babcock, 2011), are interpreted as a form of concretionary calcite (Babcock and Robison, 2011; Robison and Babcock, 2011). The glabella of PRI 0000A (Figure 2A) is crushed, presumably due to the weight of overlying sediment on a gut that was not reinforced by sediment fill shortly after the trilobite died (Robison and Babcock, 2011). Scouring on the exoskeleton of PRI 0000B suggests that the specimen was prepared prior to study and much of the anterior glabella was removed, exposing a 2 mm long area with pyrite and limonite (Figure 3A).
When imaged using ESEM, PRI 0000A has a few pyrite framboids that may have been associated with bacterial preservation of soft tissues (Figure 4A). Another E. kingii specimen from the Wheeler Formation, PRI 0000D (Figure 4B), has many pyrite framboids replicating inferred soft tissues in the axial lobe between the exoskeleton and the ventral cone-in-cone calcification (Figure 4C, D). Framboidal pyrite is interpreted as having a microbial origin, and it is likely that pyrite lining cracks in the glabella of PRI 0000A and the pyrite mass in the glabella of PRI 0000B resulted from the early diagenesis of a microbial biofilm (see Borkow and Babcock, 2003; Babcock et al., 2005; English and Babcock, 2007). Much of the pyrite has been replaced by iron oxide (limonite).

CT and micro-CT images have revealed internal structures in both Elrathia kingii specimens (Figure 2B-G, 3B-D). Bright, high density masses occur in the glabellas of both PRI 0000A and PRI 0000B, which correspond to the pyrite visible on the surface (Figures 2A-D, F, G, 3A-D). In PRI 0000B, the center of the glabellar mass is ventrally convex. The convex area increases in width toward the center and tapers slightly posteriorly, although not to a point. Two thin lateral structures occur on both sides of the central mass and also gradually decrease in width toward the posterior (Figure 3C). Another high density structure extends from the posterior glabella through the axial lobe and gradually tapers in width to the tip of the axis of the pygidium of PRI 0000A (Figures 2F, G).

Pyritized material in the glabella of PRI 0000A and PRI 0000B is inferred to be the result of early diagenetic mineralization of a biofilm-coated hypostome and presumed
stomach material. In PRI 0000A, pyrite is thickest in the cracks of the glabella (Figure 2B, D), suggesting that pyritization occurred shortly after the glabella and underlying stomach were crushed by the weight of overlying sediment. Pyritization evidently continued after this time, perhaps stimulated in part by fluid from the stomach that seeped into the cracks. The pyritized mass in the anterior glabella of PRI 0000B includes the hypostome in its original position. The mass is convex in the center on the ventral side (Figures 3C, D). The thin, lateral, high density structures on either side of the convex mass are not similar in size and appear to be connected to it anteriorly and ventrally rather than projecting laterally from a single point, as would be expected if they were foregut glands (see for example Babcock and Peel, 2007; Robison and Babcock, 2011; Lerosey-Aubril et al., 2012; Fatka et al., 2013). It is possible that these structures are a pyritized biofilm covering the hypostome.

The thoracic and pygidial axis of PRI 0000A is lined with pyrite, which appears to connect to the pyrite in the glabella (Figures 3F, G), suggesting that both the intestine and parts of the stomach are preserved in this specimen. Neither the stomach material preserved in PRI 0000B (Figure 3E, F) nor the digestive tract preserved in PRI 0000A (Figure 2H) contain sediment or evidence of skeletal material. There is also no evidence of midgut glands and it is probable that the stomach, when inflated, was large and sac-like (compare Harrington, 1959; Stürmer and Bergström, 1973; Cisne, 1981; Lerosey-Aubril et al., 2010; Robison and Babcock, 2011; Lerosey-Aubril et al., 2012).

Preservation of nonbiomineralized tissues in trilobites seems to follow two endmember modes: 1, replication of external body parts such as appendages (as
expressed, for example in Orsten-type deposits; Müller and Walossek, 1987; Waloszek, 2003; Dong et al., 2005; Eriksson and Terfelt, 2012, and the Burgess Shale; Whittington, 1975, 1980; Briggs et al., 1994); and 2, mineral infilling of digestive structures (as expressed, for example, in the Sirius Passet Lagerstätte; Babcock and Peel, 2007, and the Utah Lagerstätten; Robison and Babcock, 2011; Lerosey-Aubril et al., 2012). Some occurrences of nonbiomineralized preservation in trilobites include a combination of the two endmember modes (e.g., Stürmer and Bergström, 1973; Cisne, 1981; Babcock, 2003; Babcock and Peel, 2007). The preservation of internal structures in specimens of *E. kingii* described here follows the pattern of mineral infilling of digestive structures without preservation of appendages or other external nonbiomineralized anatomy.
Figure 2. Digestive structures in *Elrathia kingii*, PRI 0000A. A, Dorsal view of the specimen. B, micro-CT dorsal view. C, CT dorsal view. White areas in the trilobite axis and around the periphery are an artifact reflecting the topography of the dorsal exoskeleton and do not represent digestive structures. D. Slice across the center of the glabella. Dorsal toward top. E. Slice across thoracic segment 2. Dorsal toward top. F, Micro-CT MIP image. The calcite of the exoskeleton and ventral cone-in-cone structure have been made transparent, making high density internal structures visible. G, Sagittal slice through the axial lobe of the specimen. Dorsal toward the left and anterior toward the top. Brightness of the anterior and posterior ends may be an artifact of the micro-CT scanner. H, Interpretive drawing of internal structures in PRI 0000A based on CT and micro-CT images. Hypostomal and stomach material is dark gray and intestinal material is light gray. Abbreviations: h, structure ventral to the glabella interpreted as a biofilm-coated hypostome and possible stomach material; i, elongate structure ventral to the axis interpreted as the intestine. Scale bars: 5 mm.
Figure 3
Figure 3. Digestive structures in *Elrathia kingii*, PRI 0000B. A, Dorsal view of the specimen. B, Micro-CT dorsal view. C, Transverse slice across the anterior glabella. Dorsal toward the top. D, Sagittal slice through the cephalon. Dorsal toward the top and anterior toward the left. E, Interpretive drawing of the dorsal side of the cephalon with the glabella outlined in a dotted line and internal structures illustrated in their positions beneath the glabella. The hypostome is interpreted to be ventral to the stomach beneath the anterior glabella. F, Interpretive drawing of the specimen. The hypostome, inferred to have been biofilm-coated at the time of early diagenesis, and stomach are shown in gray. Abbreviation: s, stomach. Scale bars: 5 mm.
Figure 4. ESEM images made from specimens of *Elrathia kingii*, PRI 0000A and PRI 0000D. A, Surface of the thorax of PRI 0000A. B-D, *Elrathia kingii*, PRI 0000D, B, PRI 0000D before the specimen was cut for ESEM analysis. C, Axial lobe of thoracic segment 1 showing the exoskeleton (ex), frambooidal pyrite in the gut (gt), and the top of the cone-in-cone structure (cc) on the ventral side of the trilobite D. Scale bars: A, 200 μm. B, 5 mm. C, 100 μm. D, 20 μm.
Chapter 4: Scans of *Cornuproetus cornutus*

A specimen of *Cornuproetus cornutus* (PRI 0000C; Figure 5A) is preserved complete and partially enrolled in non-concretionary, medium gray limestone. The glabella is inflated and the posterior 6 mm is lined with white calcite spar that extends 1 mm into the occipital ring, which may have resulted from early crystallization of a fluid-filled stomach (Figures 5A, B).

The stomach is visible on external examination, but is not expressed in CT and micro-CT images (Figure 5 C-H), apparently because of minor density differences between the calcite spar and limestone matrix. It appears to be the only preserved internal structure in the *C. cornutus* specimen. There is a smaller high density mass visible in both the CT and micro-CT images approximately 1.1 mm below the external surface of the glabella (Figures 5D-I). However, the small mass cannot be positively linked to an internal structure of the trilobite due to the presence of eight similar high density masses that occur throughout the limestone matrix (Figures 5J, K). Additional masses inside the matrix are also expressed as thin lines of pyrite visible on the surface (Figures 5L, M). They appear to be pyritized burrows excavated shortly after final burial of the trilobite.
Figure 5. Internal structures in *Cornuproetus cornutus*. A, anterior dorsal view of *Cornuproetus cornutus*, PRI 0000C. B, detail of calcite spar lining the stomach wall. C, micro-CT anterior dorsal view of specimen. White material in the genal spines is likely due to artifact from the micro-CT scanner. D-H, tomographic images of bright high density mass ventral to the glabella. D, E, CT (D) and micro-CT (E) sagittal section, anterior left. F, G, CT (F) and micro-CT (G) with dorsal 1.5 mm of the glabella removed. Yellow material in F represents the topography of the specimen. H, transverse section through center of glabella. Dorsal toward top. I, drawing illustrating size difference between the calcite spar visible on the specimen (dark gray), interpreted as the stomach, and the high density mass viewed in CT and micro-CT scans (light gray). J, K, CT scans showing positions of trace fossils. Arrow points to high density mass in the glabella. Insets show the position of specimen. L, M, posterior view of specimen (L) and corresponding micro-CT image (M). Arrows indicate pyritized a trace fossil visible on the surface of PRI 0000C and in the micro-CT scan. Scale bars: 10 mm.
Chapter 5: Discussion

Trilobite Feeding Strategies

Possible feeding strategies of trilobites were reviewed by Fortey and Owens (1999). They include predation, both active carnivory and scavenging, parasitism, particle feeding, and filter feeding. Non-durophagous predation is considered the primitive feeding mode of trilobites (Fortey and Owens, 1999; Babcock, 2003). Active carnivory is suggested by specimens of the trace fossil Rusophycus, which is typically inferred to have been constructed by trilobites, shown to be intersecting Planolites-type traces, interpreted to have been constructed by “worms” (Jensen, 1990; Brandt et al., 1995; Babcock, 2003, 2009; English and Babcock, 2007), spinose limb morphology that may have aided in the grasping of prey (Stürmer and Bergström, 1973; Whittington, 1975, 1980; Hughes, 2001; Babcock, 2003), and the presence of a diagenetically mineralized gut or crushed glabella (Robison and Babcock, 2011). Rigid hypostomal attachment and a forked posterior margin of the hypostome (Fortey and Owens, 1999; Babcock, 2003) have also been attributed to a carnivorous habit, although longer forked morphologies (e.g., Hypodicranotus striatulus) may have been too cumbersome to have been used for the manipulation of prey (Hegna, 2009). Pre-liquifying of prey before ingestion has been inferred for trilobites with diagenetically mineralized digestive tracts, such as Buenellus
*higginsi* (Babcock and Peel, 2007). Due to their small size and possibly well-developed digestive glands, agnostoids have been suggested to have had a parasitic feeding mode like that of extant parasitic copepods (Bergström, 1973), however there is no confirmed evidence of parasitism in any agnostoid (Fortey and Owen, 1999), and a parasitic mode of feeding has not been inferred for polymerid trilobites. A particle feeding strategy would be suggested by the presence of sediment in the alimentary canal similar to that in the related nektaspid arachnomorph, *Naraoia spinosa* (Babcock and Chang, 1997; Vannier and Chen, 2002; Bergström et al., 2007), but such a feature has not been confirmed in a trilobite (confer Chatterton et al., 1994, who illustrated trilobites with mineral-filled alimentary tracts), although it has not been ruled out for *Deanaspis goldfussi* (Barrande, 1852). Having a hypostome that is not strengthened by attachment to the cephalic doublure might also imply a particle-feeding strategy. Natant hypostomes usually have a box-like or smooth posterior edge, rather than developing a forked margin, which Fortey and Owens (1999) attributed to a particle-feeding strategy. Trilobites, such as harpiids and trinucleiid, which have a large, convex cephalon that may have aided in the circulation of currents around the trilobite are inferred to have been filter feeders (Fortey and Owen, 1999).

Based on nonbiomineralized anatomical evidence (namely gut tracts preserved through early diagenetic mineralization), *Elrathia kingii* and *Cornuproetus cornutus* are here considered to have been non-sclerite-ingesting predators. *E. kingii* was previously interpreted as a particle-feeder because of its natant, box-like hypostome (Fortey and Owens, 1999; Gaines and Droser, 2003). However, many articulated specimens with
attached librigenae, including PRI 0000A, have crushed glabellas. A crushed glabella suggests that the gut was fluid-filled rather than sediment-filled at the time of death (Robison and Babcock, 2011). The lack of mud infill indicates that mud did not enter the gut tract after death (see Butterfield, 2002) nor was it ingested during life (Babcock, 2003; Babcock and Peel, 2007).

It has been speculated that mineralization of the alimentary tract of trilobites and the *Leanchoilia* (Butterfield, 2002; Babcock et al., 2012) has been associated with a fluid-filled gut, possibly resulting from a predatory habit similar to that of some modern chelicerate arthropods, in which prey is liquefied and then consumed (Babcock, 2003; Babcock and Peel, 2007). Alternatively, these ancient arthropods may have separated sclerite pieces from digestible food before swallowing it (Robison and Babcock, 2011). Alimentary structures in PRI 0000A and PRI 0000B are mineralized. Likewise, the stomach of *C. cornutus* is lined with calcite spar rather than sediment, indicating this trilobite was not a sediment-deposit feeder. Neither external examinations nor internal scans of any of the trilobite taxa studied have revealed the presence of sclerites in digestive structures, which is consistent with an interpretation of a prey-liquifying, carnivorous feeding habit (Babcock, 2003; Babcock and Peel, 2007).

**Models for the Trilobite Digestive System**

Two models for the polymerid trilobite digestive system were discussed by Lerosey-Aubril et al. (2012). One form is complex, consisting of a long, posteriorly tapering alimentary canal with paired foregut and midgut glands (see for example
Chatterton et al., 1994; Babcock and Peel, 2007; Robison and Babcock, 2011; Lerosey-Aubril et al., 2012; Fatka et al., 2013). The other form is simple, with a round, sac-like stomach ventral to the anterior glabella that is connected to a thin, posteriorly tapering intestine that extends to the pygidial axis with no evidence of midgut glands (see for example Stürmer and Bergström, 1973; Cisne, 1981, Fatka et al., 2013). A large stomach is visible in the anterior glabella of PRI 0000B, and the ruptured(?) stomach of PRI 0000A was probably large and sac-like prior to compression. Micro-CT scans of PRI 0000A also have a posteriorly tapering intestine down the axis of the trilobite. *Elrathia kingii* had a simple gut (Figure 6), making it the second Cambrian trilobite reported with this presumably derived morphology (see Fatka et al., 2013).

The morphology in *Cornuproetus cornutus* is difficult to diagnose due to the lack of preserved soft-parts in the thoracic axial lobe of PRI 0000C. However, the stomach appears to be large compared to the overall size of the glabella, and there does not appear to be evidence of foregut glands.

Eriksson and Terfelt (2012) illustrated a larval trilobite from the Cambrian of Sweden that had a gut seemingly constricted lengthwise at the center. Robison and Babcock (2011) and Lerosey-Aubril et al. (2012) also illustrated a trilobite from the Cambrian of Utah (*Coosella kieri*) that has such a longitudinally constricted gut tract. Specimens of *E. kingii* illustrated here do not have any obvious central constriction, and the illustrated specimen of *C. cornutus* does not provide enough information to determine whether it had a central constriction in the anterior part of the digestive system.
Figure 6. Reconstruction of the morphology of the *Elrathia kingii* alimentary canal, including the stomach in the anterior glabella and intestine, in dorsal view.
References


