New Information about the Internal Anatomy and Taphonomic History of Trilobites Revealed through CT Scanning

Senior Thesis

Submitted in partial fulfillment of the requirements for the

Bachelor of Science Degree

at The Ohio State University

By

Michael A. Rutana
The Ohio State University
2015

Approved by

Loren E. Babcock, Advisor

School of Earth Sciences

TABLE OF CONTENTS

Abstract	iv
Acknowledgments	V
Table of Figures	V1
Introduction	1
Methods	3
Materials	3
Computed Tomography	3
Results	4
Elrathia kingii Scans	4
Modocia laevinucha Scans	4
Hemirhodon amplipyge Scans	5
Alokistokare idahoensis Scans	5
Olenoides nevadensis Scans	5
Labiostria westropi Scans	6
Isoteloides flexus Scans	6
Flexicalymene retrorsa Scans	6
Discussion	7
Trilobite Diet	7
Digestive System Models	8
Conclusions	9
Future Work	10
References	11
Figures	13

Abstract

X-ray computed tomography (CT or XCT) scans were made of eight trilobite species hypothesized to have internal remains preserved through early diagenetic processes. Specimens range in age from Cambrian Epoch 3 to Late Ordovician. XCT scans reveal early mineralization lining the digestive systems. Studied forms show either a non-bifurcate digestive system architecture (interpreted as primitive) or a bifurcate architecture (interpreted as derived). Taxa showing a non-bifurcate architecture are Elrathia kingii, Modocia laevinucha, Labiostria westropi, Alokistocare idahoensis, Olenoides nevadensis, Hemirhodon amplipyge, (all Cambrian), and Flexicalymene retrorsa (Ordovician). Isoteloides flexus (Ordovician) shows a bifurcate digestive system architecture. Fossilization of the digestive tract resulted from early mineralization around decaying soft parts. Early diagenetic mineralization must have occurred quickly after death of the animal, possibly beginning within days to a few weeks. It must have begun before significant decay of the animal had occurred. The mineralization that occurred around the digestive tract contrasted with the taphonomic processes that affected the calcite-reinforced exoskeleton and the appendages. In all of the studied examples, the appendages have been lost. CT imaging also reveals that preserved guts can be used as geopetal indicators. Unfilled or later-stage mineralization within fluid-filled internal cavities, recognizable in scans, indicates stratigraphic-top direction.

Acknowledgments

I would like to thank my advisor, Dr. Loren E. Babcock, for providing me with the opportunity to work with him as well as providing guidance, support, and advice while I was working on this project. Dr. Richard A. Robison donated a large number of trilobite fossils to work on; these samples were invaluable and made up a bulk of the samples analyzed. Dr. Ann Cook graciously provided use of a Neurologica CereTom CT Scanner. Without this equipment, this research would have been impossible. I would also like to thank Jessica Kastigar for her time, advice, and assistance in the lab. A big thank you to all the friends that I made in the department for their company, support, and making my time here a great experience. Additional thanks go to the Shell Exploration and Production Company for providing funding through the Shell Undergraduate Research Experience, which gave me the opportunity to perform this research. Lastly, I would like to thank my family for their unconditional love and support throughout my time at Ohio State.

Table of Figures

Figure 1. Elrathia kingii	13
Figure 2. Modocia laevinucha.	
Figure 3. Hemirhodon amplipyge	
Figure 4. Alokistocare idahoensis.	
Figure 5. Olenoides nevadensis.	
Figure 6. Labiostria westropi	
Figure 7. Isoteloides flexus	
Figure 8. Flexicalymene retrorsa	

Introduction

The trilobite is one of the most familiar fossil organisms, and one of the most commonly preserved in Paleozoic rocks. However, aside from a relatively few exceptionally preserved specimens little is known of their internal and nonbiomineralized anatomy. Approximately 50 species of trilobites are now known to have preserved internal soft parts (e.g., Whittington, 1997; Robison and Babcock, 2011; Lerosey-Aubril et al., 2012; Robison et al., 2015). Some of the better known, recently described examples of Cambrian taxa with nonbiomineralized remains are *Coosella kieri* (Robison and Babcock 2011) and *Meniscopsia beebei* (Robison and Babcock, 2011; Lerosey-Aubril et. al, 2012; Robison et al., 2015); some recently described Ordovician taxa are *Isotelus maximus* (Babcock, 2003; English and Babcock, 2007). All of these instances of nonbiomineralized remains come from Konservat-Lagerstätten, or deposits of exceptional preservation.

The animal body-fossil record is dominated by remains of hard parts, and nonbiomineralized anatomy, including appendages and internal organs, generally have a low preservation potential. One of the major taphonomic filters affecting the preservation of nonbiomineralized trilobite anatomy is that chitinous appendages and nutrient-rich internal organs are a major source of food for predators and scavengers, as well as microbial decomposers (Babcock, 2003). Preservation of nonbiomineralized trilobite anatomy varies, as some specimens have both appendages and internal soft-parts preserved (e.g., Whittington, 1997; Babcock, 2003; English and Babcock, 2007; Robison et al., 2015), and others have appendages but no apparent internal anatomy preserved (e.g., Whittington, 1997) or they have internal anatomy but no appendages preserved (e.g., Robison and Babcock, 2011; Lerosey-Aubril et. al, 2012; Robison et al., 2015). This exceptional preservation of trilobites is interpreted as having occurred quickly after death (Robison and Babcock, 2011). Within

the Wheeler and Marjum formations of Utah, nonbiomineralized remains have been preserved through mineral replication by means of microbial biofilms (English and Babcock, 2007; Robison and Babcock, 2011; Robison et al., 2015).

The nonbiomineralized anatomy of trilobites can be studied using invasive or destructive preparation techniques or through non-invasive imaging. In some examples, internal nonbiomineralized anatomy is apparent through surface examination (e.g., Babcock, 2003; Robison and Babcock, 2011). Other more invasive techniques can reveal nonbiomineralized anatomy, but they risk destroying the specimen. Recently, non-invasive techniques, including computed tomography (CT) and microtomography (micro-CT), have provided considerable insight into the anatomy of trilobites without risk of destroying specimens (Eriksson and Terfelt, 2012). Robison and Babcock (2011) provided criteria for predicting the presence of fossilized remains of the digestive tract in specimens in which there is little outward evidence of their presence below the dorsal exoskeleton.

The purpose of this paper is to describe and interpret the nonbiomineralized remains in representatives of eight trilobite species from high-resolution CT imagery. Each of the studied specimens was identified as likely having preserved guts using the criteria of crushed glabellas described by Robison and Babcock (2011). Cambrian taxa imaged were *Elrathia kingii* (Meek, 1870), *Modocia laevinucha* Robison, 1964, *Hemirhodon amplipyge* Robison, 1964, *Alokistokare idahoensis* (Resser, 1938), *Olenoides nevadensis* (Meek, 1877), and *Labiostria westropi* Chatterton and Ludvigsen, 1998.

Ordovician taxa imaged were *Isoteloides flexus* (Hintze, 1952) and *Flexicalymene retrosa* (Foerste, 1910).

Methods

Materials

Several hundred trilobite specimens from various localites, mostly Utah, Ohio, and British Columbia, were examined for evidence of preserved nonbiomineralized anatomy. From this collection, approximately forty trilobites from thirteen genera were selected for detailed studies using CT scanning techniques. Trilobites were selected to be scanned based on whether or not the glabella was compacted. Specimens having both compacted and uncompacted glabellas were scanned. Robison & Babcock (2011) hypothesized that compacted glabellas in articulated specimens resulted from collapse of stomach chambers that were fluid-filled, rather than sediment filled, at the time of burial. This hypothesis is a corollary to the interpretation that most trilobites were non-durophagous predators (Babcock, 2003). Trilobites that show preserved stomach cavities also often show fossilized remains of the midgut region including digestive glands. Trilobite sizes ranged from 1.8 cm to 10.1 cm.

Computed Tomography

A portable Neurologica CereTom CT scanner, housed at The Ohio State University's School of Earth Sciences, was used to create CT images of the selected specimens. The CereTom portable CT scanner has eight x-ray detectors that rotate around a sample opposite an x-ray generator, which generates hundreds of images that can be compiled into two-dimensional and three-dimensional models using the machine's in-house software. Trilobites were scanned using an axial protocol of 0.625 x 0.625 millimeters, which is the highest resolution the scanner can produce. DIACOM images were transferred from the CT scanner to a personal computer and reanalyzed in ImageJ (National Institutes of Health, 2011) for conversion from DIACOM files to jpeg files that are readable by a computer.

Results

Elrathia kingii Scans

A single dorsal exoskeleton of *Elrathia kingii* (Fig. 1) collected from the Wheeler Formation (Cambrian: Drumian Stage) of Millard County, Utah, was scanned for evidence of preserved nonbiomineralized internal anatomy. CT images of the 2.7 cm trilobite reveal a high-density balloon-shaped mass directly beneath the glabella. This is interpreted as the stomach (foregut) of the trilobite. Another high-density structure which extends from the posterior glabella down the axial lobe and gradually tapers in width to the tip of the pygidium, can also be seen in the CT images. This style of post-cephalic digestive tract is interpreted to be primitive based on criteria published by Lerosy-Aubril et al. (2012).

Modocia laevinucha Scans

Two exoskeletons of *Modocia laevinucha* (Robison 1964) collected from the Marjum Formation (Cambrian: Drumian Stage) of the House Range of Millard County, Utah, were scanned for evidence of preserved nonbiomineralized internal anatomy. Imagery captured from the Neurologica CereTom portable CT scanner showed an excellent view of the balloon-shaped foregut and primitive post-cephalic digestive system. One specimen (Fig. 2) displayed a high-density artifact separate from the trilobite, which appears to be a mass of pyrite. The same specimen also displayed a high-density artifact surrounding the trilobite. It is possible that this is a preserved and pyritized biofilm that surrounded the specimen shortly after the death of the organism (compare English and Babcock, 2007).

Hemirhodon amplipyge Scans

A single exoskeleton of *Hemirhodon amplipyge* (Fig. 3) collected from the Marjum Formation (Cambrian: Drumian Stage) of the House Range of Millard County, Utah, was scanned for evidence of preserved nonbiomineralized internal anatomy. This trilobite was the largest scanned, 10.1 cm. A double-lobed, possibly bifurcate (Lerosey-Aubril et al., 2012) stomach is preserved in the specimen, but there is no evidence of a post-cephalic digestive tract. A bean-shaped structure along the midgut region of the trilobite appears to have a higher density than the surrounding exoskeleton, but its origin is unknown. Several other anomalous high-density locations within the trilobite were detected, and these appeared to be masses of pyrite within the specimen.

Alokistokare idahoensis Scans

One exoskeleton of *Alokistokare idahoensis* (Fig. 4) collected from the Spence Shale (Cambrian: Stage 5) of Box Elder County, Utah, was scanned for evidence of preserved nonbiomineralized internal anatomy. This trilobite was the smallest one scanned, 1.8 cm. Trilobites smaller than this would require higher resolution scans from a Micro-CT scanner to produce accurate imagery. A small primitive balloon-shaped foregut and tapering post-cephalic digestive system can be seen in the CT imagery.

Olenoides nevadensis Scans

A single exoskeleton of *Olenoides nevadensis* (Fig. 5) collected from the Wheeler Formation (Cambrian: Drumian Stage) of Millard County, Utah, was scanned for evidence of preserved nonbiomineralized internal anatomy. This specimen is preserved in a small concretion formed by cone-in-calcite that attached to the ventral surface of the exoskeleton (see Bright, 1959; Robison and Babcock, 2011). When scanned, the trilobite exhibited a digestive tract preserved at an angle. This indicates a possible post-mortem shift of the digestive tract. The stomach of the organism is well

preserved; it has an ovoid appearance, which contrasts with the balloon-shaped foreguts of *Elrathia*, *Modocia*, and *Alokistokare*.

Labiostria westropi Scans

One exoskeleton of *Labiostria westropi* (Fig. 6) collected from the McKay Group (Cambrian: Furongian Epoch) in British Columbia was scanned for evidence of preserved nonbiomineralized internal anatomy. A primitive balloon-shaped foregut and tapering post-cephalic digestive system can be seen in the CT scan. A small hole in the glabella appeared as a low-density region in the CT scan. In this low-density region, the preserved foregut is replaced by infill. The high-density artifact to the right of the trilobite is a pyrite mass.

Isoteloides flexus Scans

One exoskeleton of *Isoteloides flexus* (Fig. 7) collected from the Fillmore Formation (Lower Ordovician) in the Confusion Range of Utah was scanned for evidence of preserved nonbiomineralized internal anatomy. A double-lobed, or bifurcate, foregut is preserved in the specimen. The post-cephalic part of the digestive tract, which extends through the axis, appears to show elongate, paired enlargements. Two symmetrical high-density regions flanking the axial lobe within the midgut region are interpreted to be midgut glands. This style of post-cephalic digestive system is interpreted to be bifurcate and derived based on the criteria published by Lerosey-Aubril et al. (2012).

Flexicalymene retrorsa Scans

A single exoskeleton of *Flexicalymene retrorsa* (Fig. 8), collected from the Richmond Group (Upper Ordovician) of southwestern Ohio, was scanned for evidence of preserved nonbiomineralized internal anatomy. There is no evidence of a preserved foregut or a complete

digestive tract within this enrolled trilobite, but there is a high-density mass in the midgut region.

This is interpreted to be a remnant of the digestive tract. This digestive tract remnant can be used as a geopetal indicator to determine stratigraphic-top direction.

Discussion

Trilobite Diet

Several possible feeding methods of trilobites were reviewed by Fortey and Owens (1999). These include predation, both as an active carnivore and as a scavenger, parasitism, particle feeding, and filter feeding. Non-durophagous predation is inferred to be the primitive feeding method of trilobites (Fortey and Owens, 1999; Babcock, 2003). An active carnivorous lifestyle is suggested by specimens of the trace fossil *Rusophycus*, a trilobite trace fossil, intersecting *Planolites* and other similar "worm" traces (e.g., Babcock, 2003; English and Babcock, 2007). Mineral-filled gut tracts suggest that a number of trilobites had fluid-filled, rather than sediment-filled or skeleton-filled guts, at the time of death and burial. Fluid filling of the gut suggests a predaceous life habit similar to that of extant spiders and scorpions (Babcock, 2003).

Based on nonbiomineralized anatomical evidence shown in CT scans, every trilobite species scanned in this study, with the exception of *Flexicalymene retrorsa*, can be inferred to have been a non-sclerite-ingesting predator. In each of the fossils scanned, the presence of a crushed glabella directly correlated with the preservation of some nonbiomineralized internal anatomy along the digestive tract. In contrast, all scans made of specimens having uncrushed glabellas failed to evidence of preserved nonbiomineralized internal anatomy. A crushed glabella suggests that the gut was fluid-filled rather than sediment-filled at the time of death (Babcock, 2003; Robison and Babcock, 2011).

Digestive System Models

Two models for the polymerid trilobite digestive system were discussed by Lerosey-Aubril et al. (2012). One form is simple, consisting of a round, balloon-shaped stomach ventral to the anterior glabella that is connected to a backward-tapering, post-cephalic digestive tract extending to the pygidial axis with no evidence of midgut glands. The other form is more complex, consisting of a long, backward-tapering, post-cephalic digestive tract with paired foregut and midgut glands (Robison and Babcock, 2011; Lerosey-Aubril et al., 2012). All trilobites scanned, with the exception of *Hemirhodon amplipyge* (Fig. 3) and *Isoteloides flexus* (Fig. 7), were observed to possess simple, or primitive, digestive architecture. Both *H. amplipyge* and *I. flexus* were observed to possess a more complex, or bifurcate, digestive architecture. Scans of *H. amplipyge* did not provide evidence of paired midgut glands or a post-cephalic digestive tract, although the paired, or dual-lobed, foregut was still present.

Conclusions

X-ray computed tomography has provided insight into the anatomy of the digestive systems of eight trilobite species. Preservation of the digestive tract in these forms suggests that a large percentage of trilobites were predators that liquefied prey prior to ingestion (Fortey and Owens, 1999). Early diagenetic mineralization of the digestive tract and other nonbiomineralized anatomy must have occurred quickly after animal death, before the animals had decayed significantly. This mineralization contrasted with the taphonomic processes that affected the calcite exoskeleton and appendages. In all specimens the appendages have been lost, which indicates that dagenesis of the digestive tract occurred prior to appendage disarticulation. This constrains the timing of early diagenesis of the internal anatomy to a few days or weeks following death (Babcock et al., 2000). Preserved digestive tracts can also be used as geopetal indicators.

Two forms of digestive system architecture, as modeled by Lerosey-Aubril et al. (2012), were identified in the studied taxa. Cambrian species showing simple, or primitive, digestive tract architecture are *Elrathia kingii*, *Modocia laevinucha*, *Labiostria westropi*, *Alokistokare idahoensis*, and *Olenoides nevadensis*; the Ordovician *Flexicalymene retrorsa* also shows primitive architecture. Taxa showing complex, or bifurcate, digestive tract architecture are *Hemirhodon amplipyge* (Cambrian) and *Isoteloides flexus* (Ordovician).

Future Work

The fossils illustrated here provide further information about the internal soft parts of trilobites. Patterns of digestive systems appear to follow the model of Lerosey-Aubril et al. (2012). Future work could be aimed at establishing whether digestive systems or other nonbiomineralized anatomy can be imaged in other non-trilobite arthropod fossils. The results may be helpful in elucidating the phylogenetic relationships of trilobites to other groups, including groups such as the agnostoids, whose affinities are currently unresolved.

References

- BABCOCK, L. E. 2003. Trilobites in Paleozoic predator-prey systems, and their role in reorganization of early Paleozoic ecosystems, p. 55-92. *In* P. H. Kelley, M. Kowalewski, and T. A. Hansen (eds.), Predator-prey Interactions in the Fossil Record. Kluwer Academic/Plenum Publishers. New York.
- BABCOCK, L. E., D. F. MERRIAM, and R. R. WEST. 2000. *Paleolimulus*, an early limuline (Xiphosurida), from Pennsylvanian-Permian Lagerstätten of Kansas, and taphonomic comparison with modern *Limulus*. Lethaia, 33:129-141.
- BRIGHT, R. C. 1959. A paleoecologic and biometric study of the Middle Cambrian trilobite *Elrathia kingii* (Meek). Journal of Paleontology, 33:83–98.
- CHATTERTON, B. D. E. & R. LUDVIGSEN, 1998. Upper Steptoean (Upper Cambrian) trilobites from the McKay group of southeastern British Columbia, Canada. Memoir (The Paleontological Society), 49, Supplement J. Paleont. 72 (2): pp. 1-43.
- ENGLISH, A. M. & L. E. BABCOCK. 2007. Feeding behaviour of two Ordovician trilobites inferred from trace fossils and non-biomineralized anatomy, Ohio and Kentucky, USA. Association of Australasian Palaeontologists Memoir, 34:537-544.
- ERIKSSON, M. E. & F. TERFELT. 2012. Exceptionally Preserved Cambrian Trilobite Digestive System Revealed in 3D by Synchrotron-Radiation X-Ray Tomographic Microscopy. PLOS One, DOI: 10.1371/journal.pone.0035625.
- FOERSTE, A.F. 1910. Bulletins of the Scientific Laboratories of Dennison University 1910 (16):84
- FORTEY, R. A. & A. W. OWENS. 1999. Feeding habits in trilobites. Palaeontology, 42:429-465.
- HINTZE, L.F. 1952. Lower Ordovician trilobites from western Utah and eastern Nevada. Utah Geological and Mineralogical Survey Bulletin 48:249 p.
- LEROSEY-AUBRIL, R., T. A. HEGNA, C. KIER, E. BONINO, J. HABERSETZER, and M. CARRÉ. 2012. Controls on gut phosphatisation: the trilobites from the Weeks Formation Lagerstätte (Cambrian; Utah). PLoS ONE, 7:1-9.
- MEEK, F. B. 1870. Descriptions of fossils collected by the U.S. Geological Survey under the charge of Clarence King, esq. Academy of Natural Sciences of Philadelphia Proceedings, 14:54-64.
- MEEK, F. B. 1877. Paleontology. United States Geological Exploration of the Fortieth Parallel 4(1):1–197.
- NATIONAL INSTITUTE OF HEALTH. 2011. ImageJ (Version 1.48s) [Computer Program]. Available at http://rsbweb.nih.gov/ij/download.html.

- RESSER, C.E. 1938. Middle Cambrian fossils from Pend Oreille Lake, Idaho. Smithsonian Miscellaneous Collections 97(3):1-12
- ROBISON, R.A. 1964. Late Middle Cambrian faunas from western Utah. Journal of Paleontology 38:510–566.
- ROBISON, R.A. & L.E. BABCOCK, 2011. Paleoecology and taphonomy of some new trilobites from Cambrian (Series 3) Lagerstätten of Utah, USA. Museum of Northern Arizona Bulletin, 67:275-276.
- ROBISON, R.A., L.E. BABCOCK, V.G. GUNTHER. 2015. Exceptional Cambrian Fossils from Utah: A Window into the Age of Trilobites. Utah Geological Survey Miscellaneous Publications 15-1.
- WHITTINGTON H.B., 1997. The trilobite body, p. O87-O135. In Kaesler, R.L. (editor), Treatise on Invertebrate Paleontology, Part O, Revised, Trilobita. Introduction, Order Agnostina, Order Redlichiida. Geological Society of America & University of Kansas; Boulder, Colorado, Lawrence.

Figures



Figure 1. *Elrathia kingii* (Meeks, 1870) from the Wheeler Formation (Cambrian: Drumian Stage), Millard County, Utah. Left, dorsal surface of exoskeleton; arrows point to glabella and axial lobe. Right, CT scan showing high-density regions interpreted as the stomach and post-cephalic digestive system.

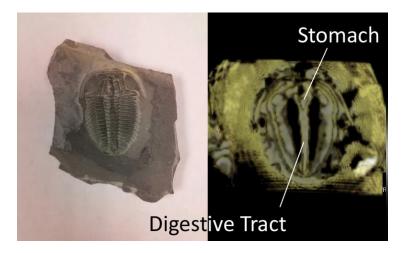


Figure 2. *Modocia laevinucha* Robison, 1964 from the Marjum Formation (Cambrian: Drumian Stage), Millard County, Utah. Left, dorsal surface of exoskeleton. Right, CT scan showing a well-preserved primitive stomach and digestive tract (compare Lerosey-Aubril et al., 2012). A possible pyritized biofilm surrounds the trilobite. The high-density region to the right of the trilobite is a pyrite mass.

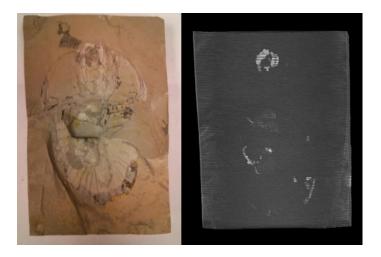


Figure 3. Hemirhodon amplipyge Robison, 1964 from the Marjum Formation (Cambrian: Drumian Stage) Millard County, Utah. Left, dorsal surface of exoskeleton. Right, CT scan showing a double-lobed, possibly bifurcate foregut (compare Lerosey-Aubril et al., 2012). Several small high density areas throughout thorax and pygidium are pyrite masses.



Figure 4. *Alokistocare idahoensis* (Resser, 1938) from the Spence Shale (Cambrian Stage 5), Box Elder County, Utah. Left, dorsal surface of exoskeleton. Right, CT scan showing a well-preserved, primitive stomach and digestive tract.



Figure 5. Olenoides nevadensis (Meek, 1877) from the Wheeler Formation (Cambrian: Drumian Stage), Millard County, Utah. Left, dorsal surface of exoskeleton. Right, CT scan showing a primitive ovoid foregut and angled digestive tract.



Figure 6. Labiostria westropi Chatterton and Ludvigsen, 1998 from the McKay Group (Cambrian: Furongian Series), near Cranbrook, British Columbia). Left, dorsal surface of exoskeleton. Right, CT scan showing a well-preserved, primitive stomach and digestive tract. The high-density region to the right of the trilobite is a pyrite mass.

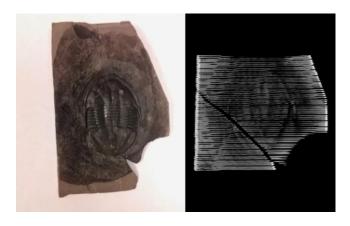


Figure 7. *Isoteloides flexus* (Hintze, 1952) from the Fillmore Formation (Lower Ordovician) Confusion Range, Utah. Left, dorsal surface of exoskeleton. Right, CT scan showing a well-preserved, bifurcate stomach and digestive tracts (compare Lerosey-Aubril et al., 2012). Two outer high-density regions within the midgut are interpreted as midgut glands.



Figure 8. Flexicalymene retrorsa (Foerste, 1910) from the Richmond Group (Upper Ordovician), southwestern Ohio. Left, surface of exoskeleton. Right, CT scan showing a possible digestive tract remnant within the thorax.