The oldest known digestive system consisting of both paired digestive glands and a crop from exceptionally preserved trilobites of the Guanshan Biota (Early Cambrian, China)

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Abstract

The early Cambrian Guanshan biota of eastern Yunnan, China, contains exceptionally preserved animals and algae. Most diverse and abundant are the arthropods, of which there are at least 11 species of trilobites represented by numerous specimens. Many trilobite specimens show soft-body preservation via iron oxide pseudomorphs of pyrite replacement. Here we describe digestive structures from two species of trilobite, *Palaeolenus lantenoisi* and *Redlichia mansuyi*. Multiple specimens of both species contain the preserved remains of an expanded stomach region (a "crop") under the glabella, a structure which has not been observed in trilobites this old, despite numerous examples of trilobite gut traces from other Cambrian Lagerstätten. In addition, at least one specimen of *Palaeolenus lantenoisi* shows the preservation of an unusual combination of digestive structures: a crop and paired digestive glands along the alimentary tract. This combination of digestive structures has also never been observed in trilobites this old, and is rare in general, with prior evidence of it from one juvenile trilobite specimen from the late Cambrian Orsten fauna of Sweden and possibly one adult trilobite specimen from the Early Ordovician Fezouata Lagerstätte. The variation in the fidelity of preservation of digestive structures within and across different Lagerstätten may be due to variation in the type, quality, and point of digestion of food among specimens in addition to differences in mode of preservation. The presence and combination of these digestive features in the Guanshan trilobites contradicts current models of how the trilobite digestive system was structured and evolved over time. Most notably, the crop is not a derived structure as previously proposed, although it is possible that the relative size of the crop increased over the evolutionary history of the clade.

Introduction

Although the trilobite fossil record is rich in terms of diversity and abundance, most species are known only from certain heavily mineralized exoskeletal sclerites. Non-mineralized parts,

including appendages and organ systems, are preserved only under exceptional conditions, and
thus are known for only a very small fraction of species. For example, traces of the digestive system are known for no more than 42 species (Table 1) of the almost 20,000 species known to
date [1]. For most of these species, reconstruction of the digestive system is based only on one
specimen (Table 1). The most commonly preserved structure is the alimentary canal which
runs the length of the thorax along the axis. In several of these species, the alimentary canal has
lobe-like features that do not extend to the genal regions of the trilobite. These have been interpreted as digestive glands, or paired metameric lateral expansions of the digestive tract (also
called digestive caeca, midgut glands, or gut diverticula, but see [2] for a distinction between
glands and diverticula in Cambrian lobopodians). More rarely there is evidence of an expanded
region of the canal under the glabella; this has been interpreted as a stomach, or crop.

The taxa with the most compelling evidence for a crop, such as *Deanaspis goldfussi* and
Wenndorfia mutabilis, do not appear to have digestive glands (Table 1). As a result, it has been
hypothesized that there are two main digestive systems in trilobites: one with a crop and simple
alimentary canal, and one with a canal characterized by digestive glands under the cranidium (the
medial sclerite of the head shield), and along at least some of the thoracic segments [29, fig 6; see
also 13, 18, 23]. Thus far, there have been two possible exceptions to this pattern. The first is the
remains of the digestive system attached to a juvenile hypostome (a sclerite on the ventral side of
the trilobite below the cranidium) tentatively assigned to the genus *Sphaerophthalmus* [20, fig 1].
The specimen was imaged using synchrotron-radiation X-ray tomography, and as a result, the
authors were able to discern delicate features, such as a J-shaped esophagus indicating that the
mouth was ventrally and posteriorly directed. They also located a relatively large expanded region
which they interpreted as the crop, and several pairs of lobe-like extensions on the alimentary
canal which they interpreted as digestive glands. Some doubt has been raised over the latter interpretation, primarily because the lobes project ventrally rather than latero-dorsally, as in adult trilobites [23]. Even if they are digestive glands, the fact that the specimen represents a very early
growth stage (early meraspid) has kept open the possibility that the crop decreased in relative size
over ontogeny, in which case the two-type model based on adult morphologies would still be valid
[7, 20, 23]. The second is the remains of the digestive system in an adult specimen of the trilobite
Megistaspis (Ekeraspis) hammondi from the early Ordovician Fezouata Lagerstätte [27, fig 1b-d].
In this specimen, the putative crop is narrow, taking up only one-quarter of the width of the glabella, similar in width to the alimentary tract spanned by the gut diverticula.

The adult specimens with the most compelling evidence for a crop (Table 1), or with
enlarged glabellas and muscle scars that may have supported a crop [29], are from geologically
younger species (post-Cambrian). Because of this, it has been suggested that the digestive system characterized by a crop and simple alimentary canal may be more derived evolutionarily
than the digestive system characterized by digestive glands [29].

Here we report on multiple specimens of two trilobite species from the Guanshan Biota
(Cambrian Series 2, early stage 4) that show compelling evidence for a crop. In one species,
Redlichia mansuyi Resser et Endo, 1937, the crop is located under the anterior region of a glabella, even though it narrows anteriorly. The other species, *Palaeolenus lantenoisi* Mansuyi,
1912, also has digestive glands. Both the presence of the crop in early trilobites and the association of the crop with a narrow glabella and digestive glands contradict previous conclusions
drawn about the structure of the trilobite digestive system and its evolution.

The Guanshan biota

The Guanshan biota is a Burgess Shale-type fossil biota [38]. Soft-bodied fossils range from the
Palaeolenus biozone to the *Megapalaeolenus* biozone of the regional Canglangpuan Stage of

Table 1. Trilobite taxa for which part of the digestive system has been described.

Family	Taxon	Age	Cr	Dg	Ac	No	Ref	Figure
Ellipsocephalidae	*Bergeroniaspis lenaica*	E Camb		X	X	1	[3]	Fig 10, Plate 25, fig 1a
Nevadiidae	*Buenellus higginsi*	E Camb		X	X	Mul	[4]	Figs 2–3
Redlichiidae	*Eoredlichia intermedia*	E Camb	?	X	X	Mul	[5]	Figs 14–15
							[6]	Figs 4E, 7A, 7E
							[7]	Fig 5
Redlichiidae	*Kuanyangia bella*	E Camb	?	X	X	1	[8]	Fig 65
Oryctocephalidae	*Metabalangia yupingensis*	E Camb	X?			1	[9]	Plate 3, fig 6
Corynexochidae	*Olenoides paraptus*	E Camb	?	X	X	2	[10]	Plate 13, fig 3
							[11]	Fig 1A
Oryctocephalidae	*Oryctocephalus indicus*	E Camb			X	1	[9]	Plate 3, fig 4
Yunnanocephalidae	*Yunnanocephalus? Sp.*	E Camb		X		1	[12]	Fig 7D
Crepicephalidae	*Coosella kieri*	M Camb		X	?	1	[13]	Figs 1F, 3H
Alokisotcaridae	*Elrathia kingii*	M Camb	X		?	2	[14]	Figs 2–3
Llanoaspididae	*Genevievella granulatus*	M Camb		X	X	1	[13]	Figs 1G, 3I-M, 3O
Ptychopariidae	*Jiumenia anhuiensis?*	M Camb			X	1	[7]	Fig 2
Undetermined	*Meniscopsia beebei*	M Camb		X	X	Mul	[13]	Figs 1A-E, 3A-G, 3N
Corynexochidae	*Olenoides serratus*	M Camb		?	X	1	[15]	text-fig 4, Plate 19
Ptychopariidae	*Ptychoparia striata*	M Camb		X	X?	2	[16]	Fig 1M
							[17]	Plate 4–5
Parabolinoididae	*Orygmaspis contracta*	L Camb		X	X	1	[18]	Fig 5
Ptercephaliidae	*Pterocephalia norfordii*	L Camb	?	X	X	Mul	[19]	Figs 1–5
Olenidae	*Sphaerophthalmus?*	L Camb	X	X	X	1	[20]	Figs 1–2
Calymenidae	*Conocoryphe sp.*	Camb		X		1	[21]	Figs 1.2, 1.3
Asaphidae	*Basilicus calzadai*	L Ord	?	?	X	3	[22]	Fig 1.2, 1.3
							[23]	Fig 4C
Asaphidae	*Birmanites ingens*	L Ord	?		X	1	[23]	Fig 4C
Dalmanitidae	*Dalmanitina socialis*	L Ord			X	1	[24]	Plate III, fig 14
Trinucleidae	*Deanaspis goldfussi*	L Ord	X		X	Mul	[24]	Plate I-IV
Calymenidae	*Flexicalymene pragensis*	L Ord			?	1	[25]	Fig 5
Asaphidae	*Isotelus maximus*	L Ord			X	1	[26]	Fig 1B, 1A?
Odontopleuridae	*Selenopeltis buchi*	L Ord		X		1	[23]	Fig 3
Asaphidae	*Megistaspis (Ekeraspis) hammondi*	L Ord	X?	X	X	1	[27]	Fig 1b-d
Olenidae	*Triarthrus eatoni*	L Ord	?		X	?	[28, 29]	
Cheiruridae	*Ceraurus pleurexanthemus*	M Ord			X	1	[30]	Plate 78
Calymenidae	*Colpocoryphe bohemica*	M Ord			X	1	[25]	Fig 4
Calymenidae	*Colpocoryphe cf. bohemica*	M Ord		X	X	1	[25]	Fig 3
Calymenidae	*Flexicalymene senaria*	M Ord			?	1*	[31]	p. 80
Calymenidae	*Flexicalymene senaria*	M Ord			?	Dr*	[32]	Plate 4, fig 6; Plate 6, fig 2
Illaenidae	*Illaenus crassicauda*	M Ord			X	Dr	[33]	Plate 1, fig 12
Pliomeridae	*Placoparia cambriensis*	M Ord			X	1	[34]	Fig 1–4, 6
Tropidocoryphidae	*Cornuproetus cornutus*	M Dev	?			1	[14]	Fig 5A
Homalonotidae	*Wenndorfia mutabilis*	U Dev	X		X	1	[35]	Fig 1
Acastidae	*Asteropyge sp.*	Dev			X	?	[29, 36]	Plates 22–23
Phacopidae	*Phacops sp.*	Dev			X	?	[29, 36]	Plates 16–21
Redlichiidae	*Redlichia mai*	E Camb			X	2	[37]	Plates 113–114
Redlichiidae	*Redlichia noetligi*	E Camb	?			1	[37]	Plate 108
Palaeolenidae	*Palaeolenus lantenoisi*	E Camb	X	X	X	Mul	[37]	Plate 1, 123

(*Continued*)

Table 1. (*Continued*)

Family	Taxon	Age	Cr	Dg	Ac	No	Ref	Figure
							This study	Figs 1–3
Redlichiidae	*Redlichia mansuyi*	E Camb	X			Mul	[37]	Plate 44, 45, 112
							This study	Fig 1, 3, 4

Cr = crop; Dg = digestive glands; Ac = alimentary canal; No = number of specimens. E = Early; M = Middle; L = Late; Camb = Cambrian; Ord = Ordovician; Dev = Devonian.

* = specimen is a thin section through fossil; Mul = multiple specimens; Dr = Drawing only.

South China. The Guanshan biota is thus slightly younger that the celebrated Chengjiang biota, older than the Kaili fauna (Guizhou), and temporally equivalent to the Balang fauna (Guizhou), Shipai fauna (Hubei), Sinsk biota (Siberia), and Emu Bay Shale biota (south Australia) [39]. It may also be temporally equivalent to the Sirius Passet biota, but is more likely younger [4]. The biota is preserved within the Wulongqing Formation and is widely exposed in the Kunming-Wuding and Malong-Yiliang areas in eastern Yunnan, China [39]. At least 60 taxa belonging to 10 metazoan groups and algae have been identified, including 11 trilobite species [37, 39, 40]. Previous descriptions of the biota have noted the preservation of non-mineralized ("soft-body") anatomical features of the trilobites, including gut traces, antennae, and other appendages [37, 39], but have not described them in detail. It appears that appendages and antennae are rare, especially compared to gut traces.

Burgess Shale-type exceptional preservation has been the focus of considerable research, particularly the eponymous site in southwestern Canada and the Chengjiang biota of south China [38, 41–45]. The taphonomy of the Guanshan biota is most similar to that of the Chengjiang biota [46, 47]. Both the Chengjiang and Guanshan biotas are unusual among Burgess-Shale type fossils for having limited pyritization of non-mineralized features [38], although pyrite framboidal crystals and spherical aggregates have typically been replaced with iron oxide pseudomorphs, especially in weathered specimens [46]. Pyrite precipitation usually occurs in anoxic conditions where there is a release of sulfides from decaying organic tissues [41]. However, the formation of large euhedral crystals requires some resupply of constituents, and therefore, some diffusion in and out of the system. In addition, the formation of framboids requires nucleation and is favored under more oxidizing conditions [7]. Geochemical data from the Guanshan indicates an absence of oxygen-depleted conditions during deposition, suggesting that iron enrichment occurred during late diagenesis and subsequent alteration during weathering of exposed rocks [46]. Based on this, Forchielli et al. [46] proposed that pyrite formation occurred during late diagenesis via sulfate-reducing bacterial activity. Vannier et al. [2] drew similar conclusions from study of gut traces in lobopodians of the Chengjiang biota. Dissolution of the dorsal exoskeleton may have resulted from release of sulfuric acid during oxidation of pyrite [48].

Materials and methods

Specimens were collected from the lower Cambrian Wulongqing Formation in the Gaoloufang section near Guangwei Village in southern Kunming, the capital city of Yunnan Province of China, during a collecting campaign of 10 local people, organized by Z. Zhang during the spring of 2014 to the autumn of 2015. The fossils were recovered from a 40–50 m thick, fine-grained laminated mudstone, occasionally intercalated with thin layers of siltstone or sandstone. Abundant silt-mud couplets with normal grading are commonly observed within the

mudstone layers containing the trilobite fossils. The Wulongqing Formation contains two tri-
lobite zones: the upper part of *Palaeolenus* Zone and the lower *Megapalaeolenus* Zone. The
stratigraphic level of the specimens presented here unquestionably belong to the *Palaeolenus*
Zone, generally thought to correlate with the upper Botomian Stage of the early Cambrian in
Siberia [49]. Details of the stratigraphy and fossil localities were provided in Hu et al.[37, 39,
50]. A total of 270 specimens of *Palaeolenus spp.* and *Redlichia spp.* were collected, mostly by
cracking out manually, and then transported by truck to the Early Life Institute (ELI) in the
Department of Geology, Northwest University, Xi'an. No permits were required for the
described study, which complied with all relevant regulations.

The specimens are deposited in the ELI and the Department of Geology of Northwest Uni-
versity, Xi'an, China. They were examined and observed under an Olympus Zoom Stereo
Microscope, and photographed with the photomicrographic system of the Zeiss Smart Zoom
5, with different angles of illumination for particular views when high contrast images were
required. Backscatter scanning electron microscopy (BSEM) and energy dispersive X-ray spec-
trometry (EDS) of uncoated fossils was performed using a Quanta 450 FEG at 20.0 kV, 60 Pa
and WD of 11.4 mm at the State Key Laboratory of Continental Dynamics, Northwest Univer-
sity, Xi'an.

Results

Most trilobite specimens from the Wulongqing Formation are complete or partially articulated
(Figure A in S1 File). In particular, specimens have articulated librigena and sometimes the
hypostome is evident. Both of these features indicate that such specimens are body fossils
rather than exuvia (molted exoskeletons). The mineralized exoskeleton is preserved with some
relief, but is largely compressed with minor fracturing and occasional lateral distortion. Some-
times this fracturing is concentrated along suture lines, but such "gape sutures" can occur on
carcasses that were exposed to physical disturbance such as the compaction seen here [51].
The original calcareous cuticle appears to have been lost during diagenesis, but surface orna-
mentation was retained in impressions.

The anterior part of the glabella in several of the trilobite specimens is enlarged and charac-
terized by dark brown or red staining (Fig 1 and Fig A in S1 File), which we interpret to be the
remains of an expanded stomach, or crop. In some cases, secondary loss during weathering
has occurred, leaving a cavity lined with iron-oxide spherical aggregates or framboids where
the crop was (Fig 1C, 1F and 1H, Fig A in S1 File; see also Figs 3 and 4). In other cases, material
that occupied what is now a cavity on the part is preserved on the counterpart. Such cavities
are distinct from the crushed glabellas seen in some complete exuvia [51, 52]. In both *Palaeole-
nus lantenoisi* and *Redlichia mansuyi*, the crop is located at the anteriormost part of the glabella
but may extend as far back as S1 (Fig 1F and 1H). Because the crop is contained within the gla-
bella, it is relatively less wide compared to the width of the cephalon in *Redlichia spp.*, than in
Palaeolenus lantenoisi, because of the anterior narrowing of the glabella in the former. In gen-
eral, the crop is elliptical in shape but not always symmetrically preserved. The crop is the
most frequently preserved part of the digestive system. Red staining along the axis is less fre-
quent and usually more diffuse (Fig 1A and 1D). Occasionally the red staining along the axis
extends past the posterior margin of the pygidium, possibly representing extruded gut contents
forced out by depositional compaction (e.g., Fig 1A).

In one specimen of *Palaeolenus lantenoisi*, there is evidence of digestive glands just poste-
rior to the enlarged area (Figs 1A and 2). The putative digestive glands are preserved as weath-
ered areas with red staining, and their shape is consistent with other descriptions of digestive
glands in trilobites [13, 19]: they are lobate in form, constrained within the axis, narrower than
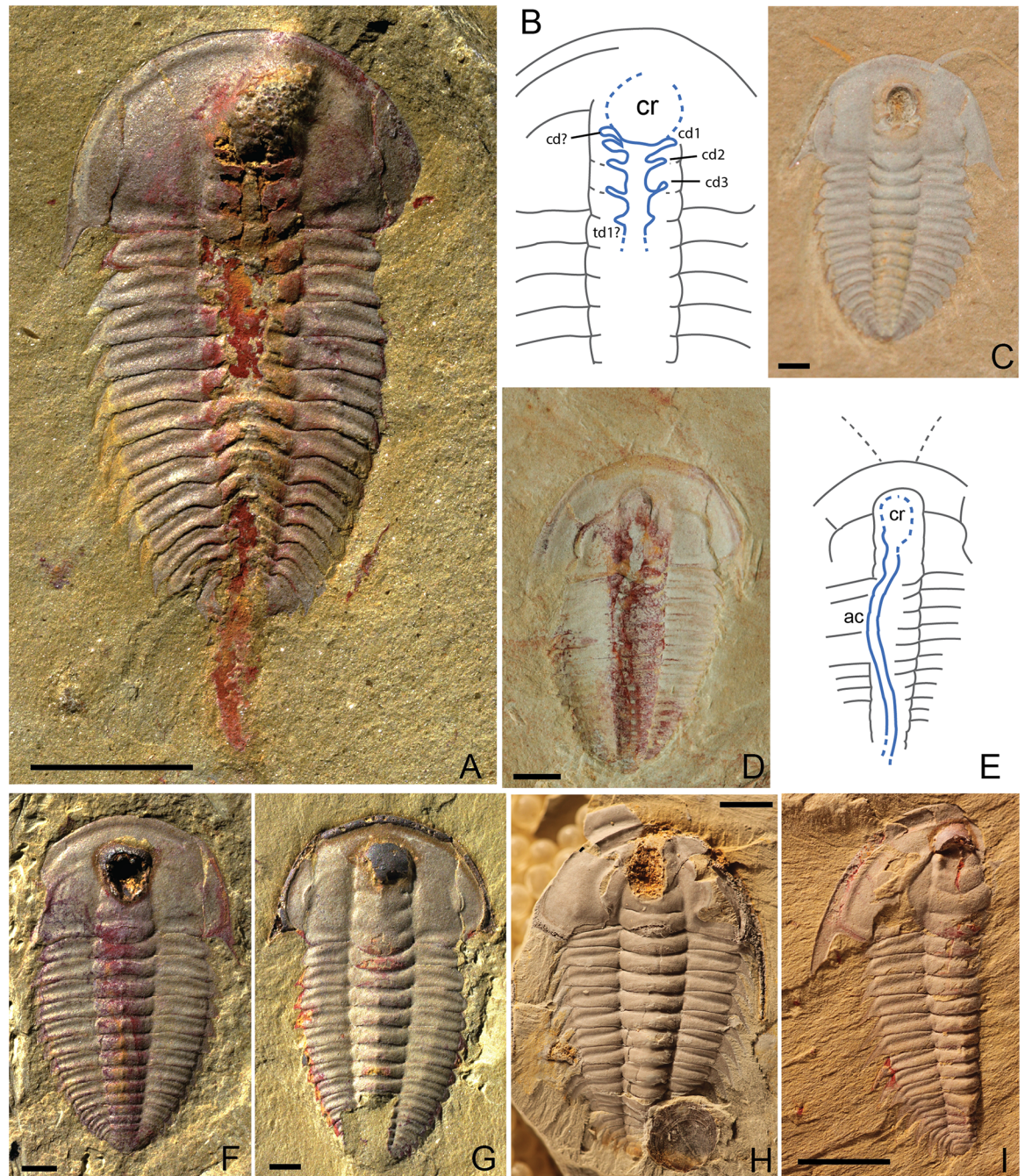
Fig 1. Evidence for crop and digestive glands in Guanshan trilobites. (A) *Palaeolenus lantenoisi* showing evidence of crop, digestive glands, alimentary canal along thorax, and excreted waste posterior to pygidium, GLF WLQ 228A. (B) Line drawing of (A). Cr = crop; cd = cephalic digestive glands; td = thoracic digestive glands. (C) *Palaeolenus lantenoisi*, showing crop cavity and antennae but no alimentary canal. (D) *Palaeolenus lantenoisi*, showing antennae, crop and alimentary canal but not preserving obvious digestive glands. (E) Line drawing of (D). Cr = crop; ac = alimentary canal. (F) *Palaeolenus lantenoisi*, showing crop cavity and only diffuse iron staining on thorax, GLF WLQ 174. (G) *Palaeolenus lantenoisi*, showing crop and no additional iron staining, GLF WLQ 214A. (H) *Redlichia mansuyi* showing cavity where crop would be located, GLF WLQ 216A. (I) *Redlichia mansuyi* showing crop and some additional iron staining, GLF WLQ 245A. Scale bar for (A), (H-I) = 5 mm; scale bar for all other = 1 mm.
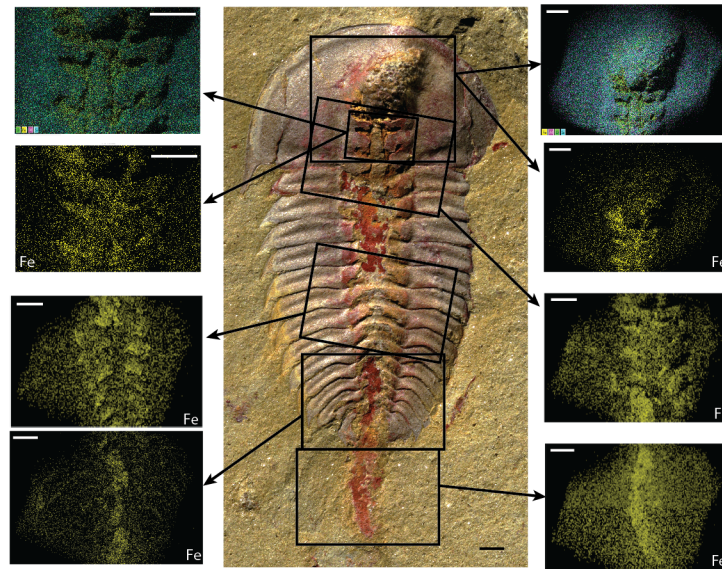
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Fig 2. Iron concentrations in digestive tract of *Palaeolenus lantenoisi*, GLF WLQ 228A. Scale bars = 1 mm. Top right and left panels show elemental maps of Fe (yellow), Si (pink), O (green), and Al (cyan) concentrations in the areas indicated by black rectangles in the central photography. All other panels show elemental maps of just Fe concentrations (yellow) in the indicated areas. Note that here and in elemental maps in other figures, some areas where iron concentrations are expected but not evident are in 'shadow' due to the orientation of the specimen or because that part of the specimen is outside of the width of detection, so no elemental composition is available (compare the top two panels showing Fe, Si, O, and Al with those just below showing only Fe). See Figs B-G in S1 File for additional elemental maps of different parts of this specimen.

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the sagittal alimentary tube, and branch dorso-laterally. They are also distributed one pair per segment; this is evident by the positioning of each pair along a glabellar furrow (cd1-3) or where the posterior margin of the occipital ring articulates with the anteriormost thoracic segment (td1). Thus they are associated with the tergite-tergite junction described by Lerosey-Aubril et al. [13] and supported by gene expression patterns in Panarthropoda [53]. We have not discovered any *Redlichia* specimens with obvious impressions of gut diverticula.

Elemental mapping of specimens of both *Palaeolenus lantenoisi* and *Redlichia* spp. shows that the areas with brown and red staining have high concentrations of iron (Figs 2–4). Oxygen is in high abundance and evenly distributed across the specimen and the matrix, including areas where Fe is concentrated (Figs B-P in S1 File). This indicates that the red staining is composed of iron oxides. Si, Al, and K are usually in high abundance and evenly distributed across the matrix and the impression of the exoskeleton, but frequently absent where Fe is concentrated (e.g., Fig 2, Figs L, N, and P in S1 File). Mg, Ti, C, and Ca are less abundant but generally evenly distributed (e.g., Figs B, I, and M in S1 File). S, Na, and P are only sometimes abundant in high enough quantities to be detected (e.g., Figs C, D, E, G, J and M in S1 File); W (e.g., Fig H in S1 File), Cu (e.g., Figs J and M in S1 File), and N (Fig O in S1 File) are rare.

Iron oxide concentrations are usually highest in the anterior part of the glabella, where the crop would have been (Fig 3B–3E, 3G and 3K). Iron oxide is also frequently concentrated along the cephalic margin (Fig 3E), the thoracic and pygidial pleural spines (Fig 3H), and at the articulating half-rings of the thorax (Fig 3E and 3H). These three areas of the exoskeleton were characterized by a tight fold called the doublure; organic material may have been more protected against decay in these areas.
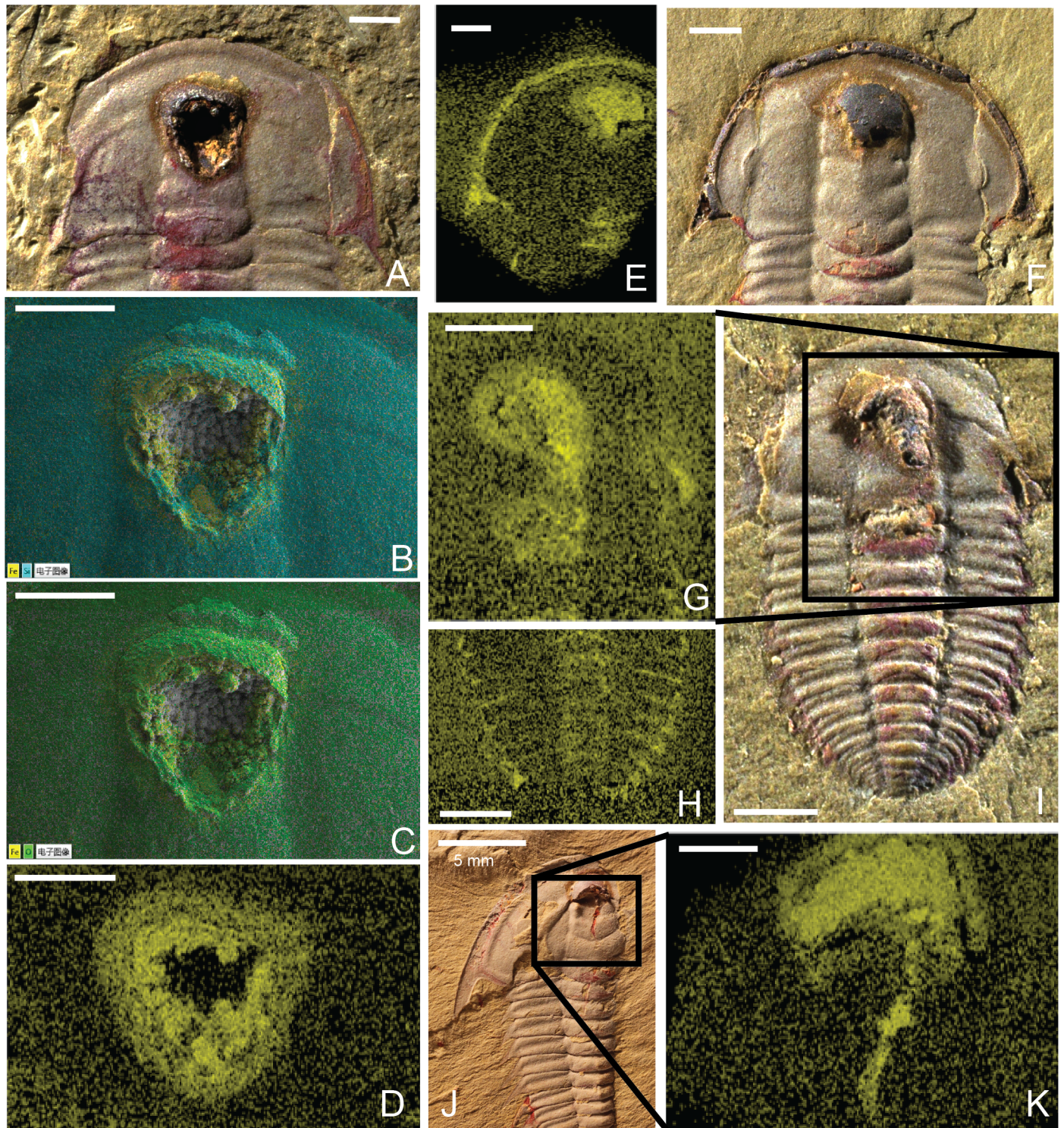
Fig 3. Overview of soft-body preservation. (A) *Palaeolenus lantenoisi*, GLF WLQ 174. (B) Elemental maps of Si (cyan) and Fe (yellow) overlain on SEM image of iron oxide framboids in crop of specimen shown in 3A. (C) Elemental maps of O (green) and Fe (yellow) overlain on SEM image of iron oxide framboids in crop of specimen shown in 3A. (D) Elemental map showing Fe concentration (yellow) at crop of specimen shown in 3A. There is no indication of iron in the center of the image because the framboids at the back of the cavity are outside the width of the detection field (see also 3B, 3C). (E) Elemental map showing Fe concentration (yellow) under left-hand side of doublure of cephalon, articulating half-rings on thoracic segments, and at crop for specimen shown in 3F. (F) *Palaeolenus lantenoisi*, GLF WLQ 214A. (G) Elemental map showing Fe concentration (yellow) at crop, posterior part of glabella, and palpebral lobe of specimen shown in 3I. (H) Elemental map showing Fe concentration (yellow) at thoracic and pygidial pleural spines

of specimen shown in 3I. (I) *Palaeolenus latenoisi*, GLF WLQ 212A. (J) *Redlichia mansuyi*, GLF WLQ 245A. (K) Elemental map showing Fe concentration (yellow) at crop of specimen shown in 3J. Scale bar = 1 mm except where indicated. See Figs H-L in S1 File for additional elemental maps for these specimens. See Figs M-N in S1 File for additional elemental maps of pleural areas in *Redlichia spp.*

Spherical aggregates of iron oxides are most frequently preserved in the crop cavities (Fig 4); these aggregates are in the same size range as those reported from other Guanshan fossils [46]. Occasionally iron oxide framboids are present (Fig 3B and 3C). The spherical aggregates are comprised of O (43.9%) Fe (29.0%), Si (11.9%), Al (6.1%) (Fig 4 and Fig Q in S1 File).

Of the 270 specimens examined, 118 belong to *Palaeolenus*, and 152 belong to *Redlichia*. 21 of the *Palaeolenus* specimens contained some evidence of soft-body preservation, and 19 of these contained evidence of gut traces specifically. 24 of the *Redlichia* specimens contained some evidence of soft-body preservation, but only 8 of these contained evidence of gut traces specifically.

Discussion

The specimens examined herein have all been weathered (compare Figs 1–4 with Forchielli et al. [46], fig 2). The matrix and exoskeletal molds show high concentrations of Si, K, and Al. In contrast, Fe is sparce in the matrix and molds, but is the primary component of the gut
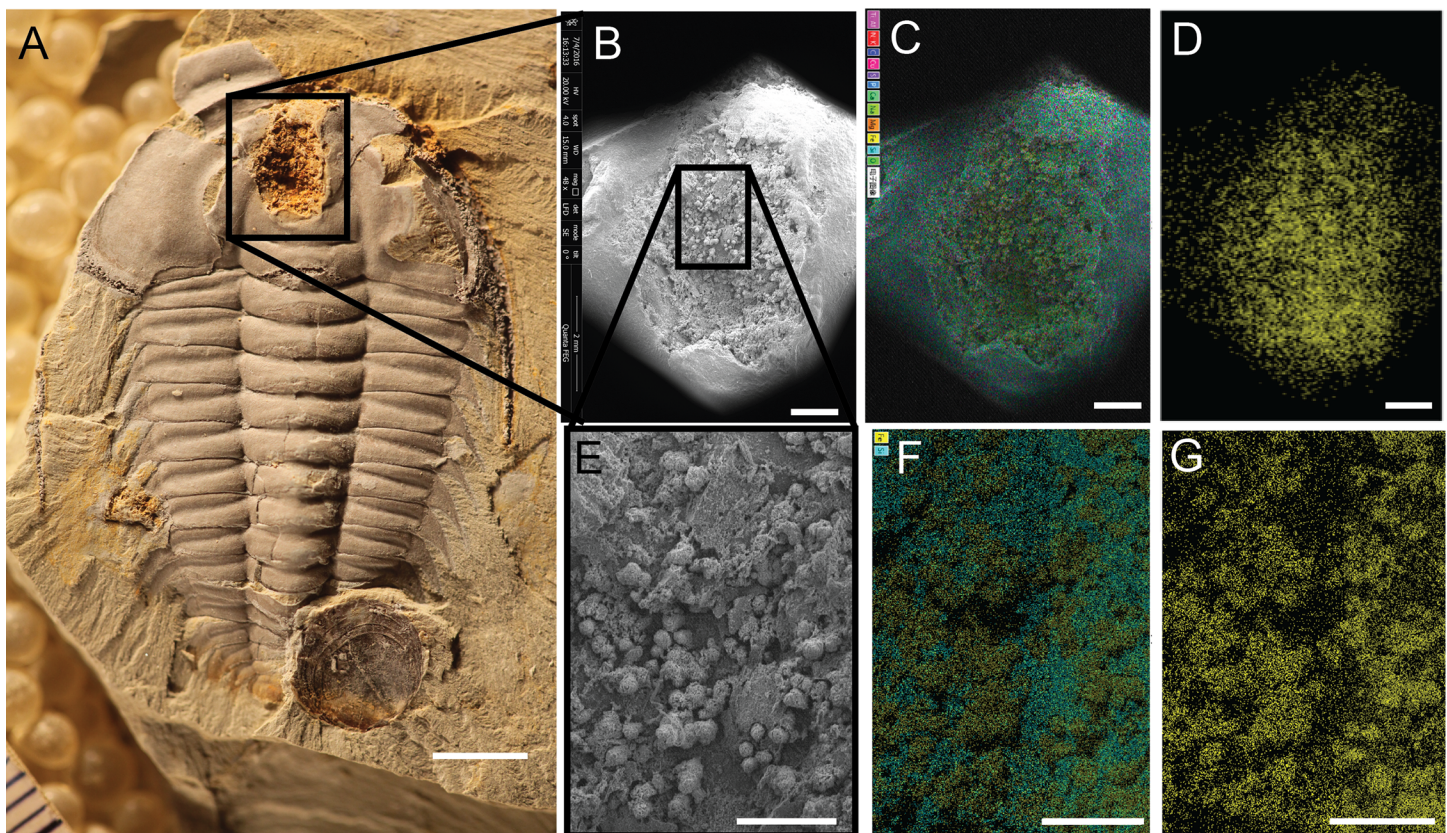

Fig 4. Spherical aggregates of iron oxide in crop of *Redlichia mansuyi*, GLF WLQ 216A. (A) Photograph of entire specimen. (B) SEM image of crop outlined in (A). (C) SEM image overlain by elemental mapping: Ti, Al (fuchsia); N, K (red); C (dark blue); Cu (pink); S (violet); P (light blue); Ca (blue-green); Na (yellow-green); Mg (orange); Fe (yellow); Si (cyan); O (green). (D) Elemental map of just iron in area shown in B and C. (E) SEM image of area outlined in (B). (F) SEM image overlain by elemental mapping: Fe (yellow); Si (cyan). (G) Elemental map of iron in area shown in E and F. Scale bar for (A) = 5 mm; scale bar for (B-D) = 1 mm; scale bar for (E-G) = 500 microns. See Figs O-P in S1 File for additional elemental maps for this specimen.

traces, along with O. This distribution of elements has been seen in other trilobite specimens preserving gut traces. For example, the molds of trilobite specimens from the Kaili biota are composed of clay minerals with iron oxides [11], and pyrite formation and iron oxides are associated with preservation of the stomach in *Elrathia* [14]. Trilobites of the Chengjiang biota show both iron staining at digestive glands as well as the cephalic margin and pleural spines [e.g., ref 12, fig 7D], but pyrite habit in the Chengjiang biota varies in association with variation in the decay susceptibility of the soft tissues [48]. Even though the presence of iron is more diffuse in Guanshan fossils than in Chengjiang fossils [46], iron concentrations in trilobites of the Guanshan biota appear to be similar in distribution and habit.

In the Guanshan trilobites, most of the topographical resistance to compaction occurred where there was soft-body preservation. Most notably, the crop retains dimensionality, even though the exoskeleton surrounding it was flattened. This characteristic is consistent with specimens from the Burgess Shale, even though the type of mineral replacement was different [42]. Given current understanding of pyrite formation in the Guanshan and Chengjiang deposits [46], however, the three-dimensional preservation of some parts of the gut is more likely due to selective syndiagenetic anaerobic microbial decay of the internal issues or organs [54] than to early pre-compaction mineralization [42, 43]. In the former scenario, gaseous accumulations from decay could have helped to prevent compaction of the gut tissues.

Mineral infilling of some trilobite gut traces has led authors to suggest that the gut was fluid-filled [4, 54], and even that trilobites might have liquefied the prey as some arachnids do [4]. Although the latter remains speculative, there does seem to be a lack of convincing evidence that trilobites consumed large quantities of sediment as deposit feeders. For example, Al, Si, and Mg concentrations that have been reported from trilobite gut traces, and would be indicative of internal sediment processing, may actually reflect the matrix composition below the gut trace [11]. Although it is likely that trilobites were at least somewhat selective in what they consumed, interpretations of feeding behavior and trophic level based on the morphology and elemental composition of preserved gut traces remain controversial.

The Guanshan material is the first convincing evidence for a crop in early Cambrian trilobites. The frequency with which the crop is represented by an iron-oxide lined cavity provides a new search image for this part of the digestive system in fossil specimens. Only once before has a cavity been interpreted as a crop [*Deanaspis goldfussi*, 24]. Fatka et al. [23] note a similar depression in the anterior part of the glabella of *Birmanites ingens*, but conclude that while this cavity represents space enclosed by the hypostome, it cannot represent a crop because there is no obvious preservation of the digestive tract between this space and where it is visible in the thorax. However, differential preservation of the gut trace within individual specimens is not uncommon (see below). Furthermore, it is certain that the digestive system did continue under the cranidium to the mouth, even if it is not preserved. Thus, whether *Birmanites ingens* had a crop or not remains an open question.

Similarly, it is also possible that the cavities in the anterior part of the glabella in three specimens of *Basilicus calzadai* from the Izeguirene Formation of Morocco represent the remains of the crop in this species [22, 23]. In addition one specimen of *Basilicus calzadai* shows a pair of small circular cavities on either side of the alimentary canal at the anteriormost axial segment, and another fainter pair within the glabella [22, fig 1.2]. Although preservation is not good enough to be conclusive, *Basilicus calzadai* may be another example of a trilobite with both crop and digestive glands. As such, there is now evidence for this digestive system in at least four species spanning the Cambrian (*Palaeolenus lantenoisi* and *Sphaeropthalmus*? *sp.*) and Ordovician (*Basilicus calzadai* and *Megistaspis (Ekeraspis) hammondi*).

Gutiérrez-Marco and colleagues [27] interpreted the combination of a crop and digestive glands in *Megistaspis (Ekeraspis) hammondi* to be a new "type 3" trilobite digestive system.

However, we suspect that at least some previous classifications may have been misled by taphonomic variabililty. In addition to the relatively small number of specimens (16% of *Palaeolenus* specimens and 5% of *Redlichia* specimens) that show gut trace preservation in the Guanshan material, there is considerable variation in the fidelity of gut trace preservation among specimens, despite having been collected from the same outcrop (Figs 1–4, Fig A in S1 File). Inconsistent preservation was also observed among specimens of *Buenellus ingens* from Sirius Passet [4]. Lin [11] went so far as to suggest that when the alimentary canal was preserved in *Olenoides paraptus*, paired axial markings were not visible, and vice versa; in other words, one feature was always preserved at the exclusion of the other. In individual specimens, it is possible that different concentrations of sediment and organic material along the digestive tract could result in differential preservation of different regions [6, 7, 23]. Thus even under the same taphonomic conditions, differential preservation would be a natural consequence of individual variation in the type and quantity of food, as well as the point in digestion of that food at death and burial. This emphasizes the importance of multiple specimens for describing the digestive system of a species [13].

The preservation of a crop in two early Cambrian Stage 4 trilobites (of different taxonomic orders) indicates that the presence of the crop is not only a feature of geologically younger trilobites, as previously suggested [29]. However, the crops in *Palaeolenus lantenoisi* and *Redlichia* are no larger than the anterior part of the glabella, which is relatively narrow in both species, and even narrows anteriorly in *Redlichia*. Taxa with expanded glabella could have accommodated a much larger crop (e.g., *Phacops*), in which case there may still be evolutionary trends toward relatively larger crops over time [29].

Supporting information

S1 File. Supporting figures A-Q.
(PDF)

Acknowledgments

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