

Direct evidence for predation on trilobites in the Cambrian

M.-Y. Zhu^{1*}, J. Vannier², H. Van Iten³ and Y.-L. Zhao⁴

¹State Key Laboratory of Palaeobiology and Stratigraphy (LPS), Nanjing Institute of Geology and Palaeontology, Chinese Academy of Science, Nanjing 210008, China

²Université Claude Bernard Lyon 1, Bâtiment GEODE-2, rue Raphaël Dubois, 69622 Villeurbanne cedex, France

³Department of Geology, Hanover College, Hanover, IN 47243, USA

⁴Department of Resource Engineering, Guizhou University of Technology, Guiyang 550003, China

* Author for correspondence (myzhu@nigpas.ac.cn).

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A fossil arthropod similar to *Fuxianhuia* and displaying an exceptionally well-preserved alimentary canal with *in situ* gut contents is reported from the lower Middle Cambrian (ca. 510 Myr ago) of South China. Three-dimensionally preserved, paired phosphatic nodules, arranged in series along both sides of the gut and containing spherical bacteria, probably represent serial digestive glands. The gut is filled with fragments of the eodiscoid trilobite, *Pagetia*. The well-developed digestive glands and the fragmentary trilobite remains suggest (i) that the arthropod was a durophagous, possibly selective predator, and (ii) that small trilobites such as eodiscoids were a major food source in Cambrian marine ecosystems. This fossil association augments the small number of previously described associations providing more or less direct evidence of predator-prey relationships in Cambrian epibenthic communities.

Keywords: predation; trilobites; Arthropoda; Cambrian; South China

1. INTRODUCTION

Predator-prey systems play a central role in animal evolution. However, the nature of such systems in marine environments of the Cambrian world and the role of predation in the explosive radiation of metazoans during the Early Cambrian remain controversial. It has long been assumed that predation was a major selective force in the origin of mineralized exoskeletons (Vermeij 1990), and that it was one of the causes of the Cambrian explosion (Stanley 1973). Unfortunately, evidence of predation in the Cambrian is largely circumstantial, consisting in part of the following: (i) skeletal structures that may have served a defensive function in numerous groups such as halkieriids, *Wiwaxia* and lobopodians; (ii) probable drill holes in mineralized skeletons (Conway Morris & Bengtson 1994); (iii) probable bite marks and healed injuries in the exoskeletons of trilobites and trilobite-like animals (see Babcock (2003) for a review); and (iv) possible foraging or hunting traces left by trilobites or other arthropods that may have preyed on infaunal worms

(Jensen 1990). Analyses of the functional morphology of Cambrian arthropods provide additional indirect evidence that certain trilobites (Fortey & Owens 1999), anomalocarids (Chen *et al.* 1994) and *Naraoia* (Vannier & Chen 2002) were predators. Other non-arthropod predators included infaunal worms (Conway Morris 1977), mid-water animals such as eldoniids (Zhu *et al.* 2002) and chaetognaths (Chen & Huang 2002).

The only previously documented, direct evidence of predator-prey relationships in Cambrian ecosystems consists of skeletal remains preserved in the alimentary canal of *Ottoia* (a 'worm') and *Sidneyia* (an arthropod) from the Middle Cambrian Burgess Shale (Conway Morris 1977; Bruton 1981). In this paper we report on a possible new arthropod with well-preserved gut contents from the Middle Cambrian of South China. We argue that the arthropod preyed on live trilobites and that it provides additional direct evidence of predator-prey relationships in the Cambrian.

2. FOSSIL MATERIAL: THE KAILI LAGERSTÄTTE

The fossil arthropod described here was collected from the middle member of the lower Middle Cambrian Kaili Formation (Taijiang County, Guizhou Province), a transgressive-regressive siliciclastic sequence originally deposited below the fair-weather wave base near the distal margin of the Yangtze Platform (South China). The middle member contains the Kaili Lagerstätte, a major Burgess Shale-type fauna (Zhao *et al.* 2002). The Kaili fauna contains typical components of both the Early Cambrian Chengjiang (e.g. *Microdictyon*, *Naraoia*, *Anomalocaris*) and the Middle Cambrian Burgess Shale (e.g. *Wiwaxia*, *Marella*, *Canadaspis*) faunas, and thus provides a unique window on the Early-Middle Cambrian transition interval in the history of life.

3. THE ARTHROPOD PREDATOR

(a) Morphology

The Kaili arthropod specimen (figure 1; also see electronic Appendix A, figure 3) measures ca. 8 cm long by 5 cm wide. Part of the head section and the posterior portion of the body are missing (figure 1*a,b*). The original carapace was weakly mineralized and flattened dorso-ventrally, a condition that has been accentuated by post-mortem compaction. The trunk tapers gradually posteriorly and is composed of at least 18 articulated segments showing lateral pleurae and a central axis. The non-segmented head shield is short and hemispherical (figure 1*a*). Straddling the sagittal axis of the head shield is a poorly defined rounded feature that may be a hypostome. The right side of the specimen lies obliquely to bedding and exposes several large, flat appendages resembling exopod flaps. The appendages reach the outer margin of the pleurae and exhibit oblique fine wrinkles that may represent gill-like features. No evidence of a former endopodite is discernible.

The axial part of the trunk has been broken to reveal the alimentary canal, which contains numerous shell fragments distributed along its entire length (figure 1*a,b*). The alimentary canal is flanked by two types of paired features: brown-coloured imprints having a subrectangular or lobate outline (figure 1*a-c*); and three-dimensionally preserved, dark-coloured nodules that contact the margins of the gut (figure 1*a-c*). The brownish imprints can be

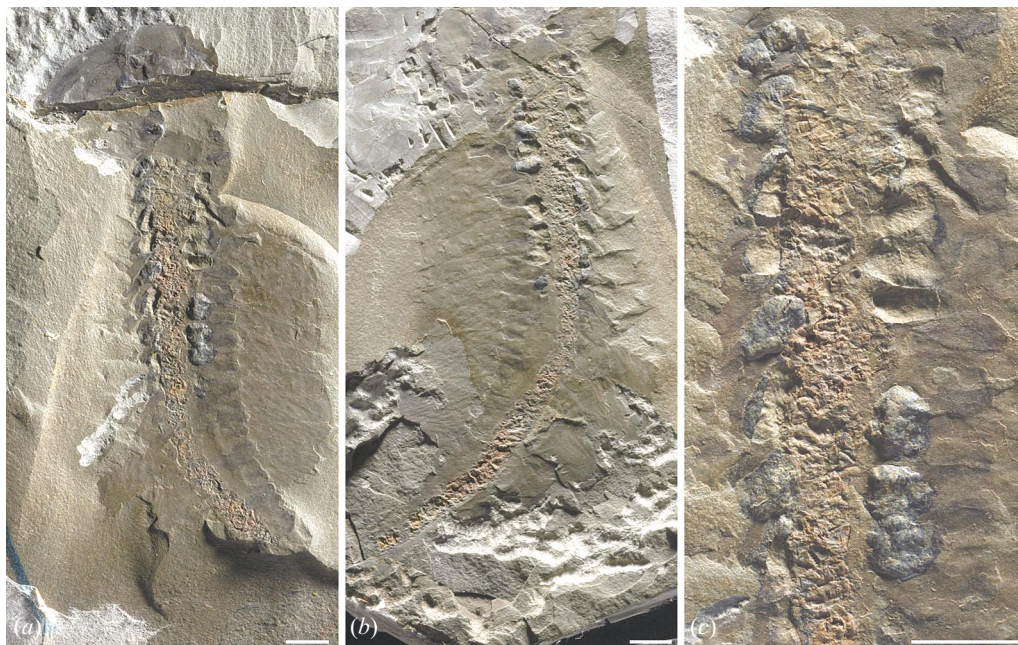


Figure 1. An unnamed arthropod with gut contents from the Middle Cambrian Kaili Formation, Taijiang County, Guizhou Province, South China. The specimen is housed in the collections of the Palaeontological Institute of the Guizhou University of Technology. (a) View of the entire specimen showing the (partial) cephalic shield and the alimentary canal with preserved gut contents, GM-9-1-510a. (b) Counterpart of the specimen showing the posterior part of the body, GM-9-1-305b. (c) Details of the gut contents, digestive glands, and traces of possible limb musculature and basal parts (brownish imprints) along both sides of the gut. Scale bars, 5 mm.

interpreted as traces of muscle bundles that connected the appendages to the axis. Similar features, likewise interpreted as muscles, occur in other Cambrian arthropods including *Kerygmachela* (Budd 1998). The relatively large size of the imprints in the Kaili arthropod may indicate that the appendages were provided with powerful gnathobases.

The dark-coloured nodules are apatitic (as indicated by X-ray analysis), and the boundary between them and the surrounding mudstone matrix is sharp. Some nodules exhibit a surficial network of fine radiating lines that form bunch-like structures (figure 1c). At least in the anterior part of the trunk, each segment appears to bear a single pair of nodules.

We interpret the nodules as serially repeated digestive glands. This hypothesis is supported by comparisons with extant arthropods (Vannier & Chen 2002) and by the presence of similar paired features in other fossil arthropods (Butterfield 2002; Vannier & Chen 2002).

Together with the three-dimensional preservation of the dark-coloured nodules, the presence in these structures of numerous spherical bacteria (figure 2a–d) suggests that the nodules underwent very early, bacterially mediated phosphatization that prevented them from becoming compacted. Similar phosphatic preservation of non-mineralized structures has been reported in numerous fossil groups throughout the stratigraphical record (Briggs *et al.* 1993). The phosphatized bacteria in the Kaili arthropod have an average diameter of 1 μm (figure 2a–d) and probably represent autolithified bacteria (e.g. Hirschler *et al.* 1990). Similar microspherules found in homologous structures ('midgut glands') in the Cambrian arthropod *Leanchoilia* may also be autolithified bacteria, rather than

cellular features or metabolic by-products (Butterfield 2002).

(b) *Affinities*

The Kaili specimen differs clearly from previously described Kaili arthropods. It is most similar to Early Cambrian *Fuxianhuia* (Chen *et al.* 1995), with which it shares a segmented trunk that tapers posteriorly, a small hemispherical head shield and large flat exopod flaps. Whether the new arthropod possessed additional features of *Fuxianhuia*, for example a frontal eye-bearing sclerite, sub-chelate head appendages, long-segmented endopods and a narrow abdomen, is uncertain. Also, the exoskeleton of *Fuxianhuia* is substantially thicker and has a more clearly defined central axis than that of the new arthropod. At this point, then, the affinities of the new Kaili arthropod are uncertain, and we cannot name it.

4. GUT CONTENTS

The alimentary canal of the Kaili arthropod is occupied by a nearly uniform aggregation of millimetre-sized, broken skeletal elements (figure 1). Most of the elements are stacked on top of each other and are difficult to identify under reflected light. Scanning electron microscopy (SEM) revealed the presence of cephalic, pygidial and pleural fragments of eodiscoid trilobites (figure 2e,f). Several fragments of the periglabella field exhibit scrobicules, a typical feature of many eodiscoids including *Pagetia*, the only eodiscoid genus present in the Kaili fauna (Yuan *et al.* 2002; five species represented). The fragmentary eodiscoid elements present in the arthropod gut cannot be identified at the species level. The remaining and dominant fraction of the gut contents consists of spiny, flat,

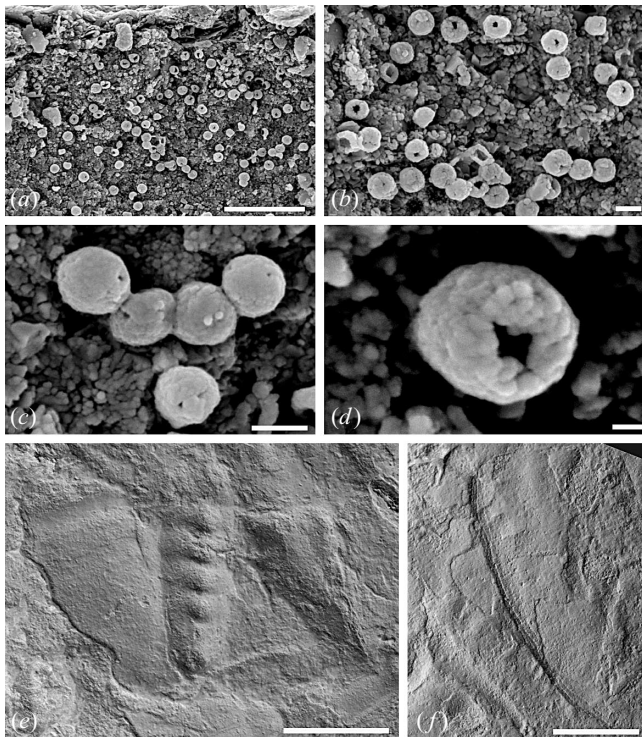


Figure 2. (a–d) SEM images of phosphatized digestive glands with spherical bacteria. (a) General view of a transverse section. (b,c) Clusters of bacteria. (d) Detail of bacteria. (e,f) SEM images of eodiscoid trilobite fragments in the gut of the Kaili arthropod. (e) Pygidium of *Pagetia*. (f) Nearly complete eodiscoid librigena. Scale bars: (a) 10 µm; (b,c) 1 µm; (d) 200 µm; and (e,f) 500 µm.

slightly convex and lobate exoskeletal elements that may also belong to eodiscoids.

We believe that this well-delimited aggregation of skeletal elements represents the remains of ingested live prey. Our interpretation is based on a combination of six independent lines of evidence: (i) the skeletal elements are fragmentary (broken); (ii) the elements are restricted to the alimentary canal (they are absent from the exposed rock matrix surrounding the arthropod); (iii) the elements are distributed uniformly, from the oral to the anal ends of the gut, and fill almost the entire gut lumen; (iv) the size of the elements is relatively uniform (from 2.5 mm to 6 mm long) and is less than or equal to the gut diameter (ca. 6 mm maximum); (v) all of the identifiable elements belong to eodiscoid trilobites; and (vi) the arthropod was buried rapidly in an event deposit. Taken together, these six lines of evidence tend to rule out alternative hypotheses such as (i) coincidental association of the arthropod and the trilobite fragments, (ii) introduction of the trilobite fragments into the gut of the dead arthropod by water currents, and (iii) scavenging on dead trilobites. Scavenging of dead animals is unlikely because the vast majority of present-day scavengers (e.g. crustaceans) are non-selective feeders (Vannier *et al.* 1998), and the gut contents of the Kaili arthropod appear to belong to the same genus.

5. DISCUSSION

A carnivorous habit for the Kaili arthropod is suggested by the taxonomically uniform composition of its gut contents (eodiscoid trilobites) and by the presence of well-

developed digestive glands arrayed along the gut. Such glands are present in numerous additional Cambrian arthropods with probable predatory habits such as *Naraoia* and *Leanchoilia* (Butterfield 2002; Vannier & Chen 2002). The lack of detailed information on the anatomy of the head and trunk appendages precludes the precise reconstruction of the feeding techniques of the Kaili arthropod. If it was durophagous, then future discoveries of specimens possessing well-preserved, better exposed appendages may reveal the presence of gnathobases, which if present would have aided in seizing, macerating and directing eodiscoid fragments to the animal's mouth. The apparently uniform composition of the gut contents suggests that the arthropod was a selective feeder, preying upon the most abundant skeletonized epibenthic organism present in the Kaili biota.

The present study suggests that eodiscoid trilobites (electronic Appendix A, figure 3e), which flourished during Early Cambrian times, were a major food source for larger animals. The hypothesis that eodiscoids were prey animals is also supported by the presence of minute predation scars on the margins of small pygidia (Babcock 2003). Small epibenthic animals such as eodiscoid trilobites, hyoliths and bradoriids, which lived close to the water–sediment interface, probably were subjected to high, multidirectional predation pressure from a variety of epibenthic, endobenthic and nektonic animals (Babcock 2003). Together with evidence previously described, the new evidence here documented indicates that diverse and complex predator–prey relationships were firmly established in the Middle Cambrian marine ecosystem.

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