Preservation of early and Middle Cambrian soft-bodied arthropods from the Pioche Shale, Nevada, USA

Rachel A. Moore, Bruce S. Lieberman * 

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ABSTRACT

The Early–Middle Cambrian Pioche Shale of Lincoln County, Nevada preserves a diverse array of soft-bodied ecdysozoans that are well-known from the Burgess Shale soft-bodied fauna of British Columbia, Canada. At Pioche certain genera occur both above and below the Middle Cambrian boundary, allowing a comparison of the nature of their preservation across this interval. In order to investigate the mineralization of this fauna, SEM analysis of mineral textures and element mapping of Anomalocaris, Tuzoia and Canadaspis specimens using energy dispersive X-ray spectroscopy (EDS) was undertaken. Results of these analyses show that Early Cambrian specimens are generally preserved in botryoidal hematite which is dark red in hand specimen while specimens from the Middle Cambrian are preserved as kerogenized carbon films with associated oxidized pyrite crystals and frambooids. Comparison with other Cambrian soft-bodied biotas reveals that the nature of preservation of the Middle Cambrian biota at Pioche is remarkably similar to that described for the Chengjiang soft-bodied fauna, China. There does not seem to be an adequate analogue for the Early Cambrian preservation of soft-bodied organisms at Pioche. The preservation of the fauna is discussed in relation to changing environmental conditions at the Early–Middle Cambrian boundary.

1. Introduction

The exceptional preservation and diversity of the soft-bodied animals from the Burgess Shale have made it one of the most well-known and celebrated fossil sites in the world. Since renewed interest in the Burgess Shale biota in the 1980s (Briggs et al., 1994 and references therein) a number of new, geographically widespread, Early and Middle Cambrian soft-bodied biotas have been described. These soft-bodied faunas provide important information on the timing and nature of the apparently rapid development of modern phyla, known as the ‘Cambrian explosion’ (Fortey, 2001). One of the most spectacular sites, the Early Cambrian Chengjiang biota of Yunnan, China (Hou et al., 2004), yields animals that are common to the Burgess Shale but also various unique taxa (e.g. Fuxianhuia Hou, 1987). The Pioche Shale of Nevada, USA, yields animals that are common to the Burgess Shale but also various unique taxa (e.g. Fuxianhuia Hou, 1987). The Pioche Shale of Nevada, USA, yields a less abundant soft-bodied biota than the Burgess or Chengjiang deposits, but importantly spans the Early–Middle Cambrian boundary and so has the potential to offer important insights into changes in the diversity and preservation of soft-bodied faunas at this time (Lieberman, 2003). This study contributes to our understanding of the taphonomic pathways that led to the preservation of Burgess Shale-type biotas. The mechanism by which Burgess Shale-type preservation (BST) occurs has yet to reach a consensus, however it is key to understanding the geographical distribution and temporal limitations of these soft-bodied biotas. Butterfield (1995) defined BST as carbonaceous compressions in marine shales; yet elemental mapping of Burgess Shale specimens by Orr et al. (1998) showed that aluminosilicate mineralization is also important in preserving various tissues. Both carbon films and pyrite mineralization (later altered to iron oxides) preserve Chengjiang fossils (Gabbott et al., 2004; Zhu et al., 2005), highlighting another means by which soft tissue is preserved in the Cambrian. Further study of coeval soft-bodied biotas is important to understand the taphonomic conditions that controlled preservation at these other localities.

2. Locality, age and stratigraphy

The Pioche Shale contains both Early and Middle Cambrian faunas, comprising trilobites, brachiopods, hyolithids, sponges, gastropods, eocrinoids and trace fossils. The soft-bodied bearing units of the Pioche Shale outcrop in southern Nevada in the Highland and Chief Ranges near the towns of Pioche and Caliente (Fig. 1). The Early-Middle Cambrian faunal transition occurs at the transition between the Combined Metals and Comet Shale Members (see Palmer, 1998; Sundberg and McCollum, 2000). The Lower Cambrian section contains abundant olenellid trilobites; soft-bodied animals in this part of the section occur in one or possibly more horizons that have not been well localized stratigraphically but lie within the last one-two meters of the Lower Cambrian part of the section. The Middle Cambrian part of the section contains abundant ptychopariid trilobites but no olenellids; in this part of the section soft-bodied animals occur in at least one stratigraphic horizon at each of two localities. These...
Materials and methods

The Middle Cambrian horizons have not yet been well localized stratigraphically, but each likely occurs in the lower ten to perhaps 15 m of the Middle Cambrian part of the section. The soft-bodied fauna is primarily composed of anomalocaridid carapaces, *Ottoia*, *Canadaspis* and *Perspicaris*. *Ottoia* is known only from the Early Cambrian horizons and *Canadaspis* and *Perspicaris* only occur in the Middle Cambrian horizons (Lieberman, 2003).

Detailed locality information for soft-bodied specimens are provided by Lieberman (2003).

Uncoated specimens were studied under low-vacuum conditions using a Hitachi 3500N Scanning Electron Microscope (SEM) at the Department of Earth Sciences, University of Bristol, England. Both backscatter and secondary electron images were taken. The former provide an indication of mineralogical differences and the latter provide images of surface textures. Elemental X-ray maps were obtained using an EDAX Energy Dispersive Spectrometer (EDS), using an accelerating voltage of 15 kV for all elements other than carbon, which was mapped at an accelerating voltage of 5 kV in order to minimize X-ray absorbance by surrounding material. Similar approaches have been pioneered by Orr et al. (1998) and Gabbott et al. (2004) to study soft-bodied preservation in other Cambrian fossils.

Preservation

More than 90% of the anomalocaridid material from the Pioche Shale constitutes disarticulated anterior appendages (Lieberman, 2003). The presence of disarticulated body parts indicates that most elements of the Pioche biota underwent significant decay before entering the diageneric environment. However, three possible whole-body specimens of *Anomalocaris* (KUMIP 298510, KUMIP 298511, KUMIP 293606) have been recovered from the Early Cambrian and a specimen of *Canadaspis* (KUMIP 307021) with associated appendages from the Middle Cambrian of Pioche (Lieberman, 2003), which illustrates that some carcasses entered the system at an earlier stage of decay (Briggs, 1994).

The main difference in fossils from the Early Cambrian and those from the Middle Cambrian when seen in hand specimen is the color. Specimens from the Early Cambrian are typically dark red in a pinkish-red to green matrix while those from the Middle Cambrian are dark gray with a distinct reflective film in a lighter gray matrix.

Preservation of specimens of Early Cambrian Age

Textural analysis of Early Cambrian specimens using secondary electron SEM images revealed that the habit of the fossil-preserving mineral is botryoidal (Fig. 2A and B). Along with the dark red color of the mineral in hand specimen this suggests that it is most likely to be hematite (Fe₃O₄). Element maps of *Tuzoia* and *Anomalocaris* provide further evidence for this identification because Fe is elevated in the region of the fossil (Fig. 3A and B). In *Tuzoia* elevated Fe is clearly limited to the characteristic reticulated ornament (Fig. 3A), which may have been a positive feature on the surface of the carapace in life. It is possible that the entire surface of the carapace is preserved in this way but is masked by overlying matrix in-between these ridges.

These findings agree with the XRD analysis conducted by Lieberman (2003), which showed that hematite was present in Early Cambrian specimens. Hematite is also the likely source of the red pigmentation in the shale matrix. Both the nature of shale coloration and the origin of hematite in red beds have been a source of controversy among sedimentologists (Van Houten, 1973). Red beds have traditionally been thought to indicate oxygenated depositional environments (Van Houten, 1973); however, the influence of secondary pore waters and weathering can contribute to the oxidation of iron and other minerals to generate red coloration (Küpli et al., 2000). Since many aspects of red bed formation are still poorly understood (Bensing et al., 2005) a full explanation of the method or methods by which the red shale originated at Pioche is beyond the scope of this study.

Element maps of *Anomalocaris* reveal that Al and Mg in addition to Fe are elevated in the region of the fossil (Fig. 3B). Si is not elevated in *Anomalocaris* which indicates that the Al and Mg are not in the form of silicates. Elevated Al and Mg are not evident in the specimen of *Tuzoia* (Fig. 3A).

A gray dendritic mineral occurs on the surface of fossils from the Early Cambrian and is visible in hand specimens. In secondary electron
SEM images this is seen as having a scaly habit (Fig. 2C) and element maps reveal Mn is elevated where it is present (Fig. 3A). The mineral is most likely to be pyrolusite (MnO₂). Other mapped elements (Ca, C, Na) show no elevation in this mineral or the fossil.

Pyrolusite occurs at other sites of exceptional fossil preservation, such as the Jurassic Solnhofen Lithographic Limestone (Barthel et al., 1990). This secondary mineralization is formed when Mn-rich pore waters interact with oxygenating fluids or the atmosphere (Chopard et al., 1991).

4.2. Preservation of specimens of Middle Cambrian Age

Under the secondary electron SEM beam Middle Cambrian specimens of Tuzoia and Anomalocaris show a significantly different mineralogical texture to the Early Cambrian specimens. Clay moulds, with discrete patches in which the original disseminated crystals are still present, define the fossil (Fig. 2D-G). Clusters of framboids are also present in some regions of the fossil and range from 8–10 μm in diameter (Fig. 2E and F). The framboidal habit implies the original composition was pyrite (FeS₂). Element maps confirm that Fe is abundant in the framboids and in the disseminated crystals, but EDS spot analysis on these features did not generate a sulfur peak in the resulting spectra. Element maps also failed to show an elevated signal for sulfur (Fig. 3D). The most likely explanation for this is that the original pyrite has been secondarily oxidized in a manner similar to that described by Gabbott et al. (2004) for the fossils of the Early Cambrian Chengjiang biota. Clay moulds occur over the whole surface of the fossil indicating that pyrite was originally present all over this region. The crystals that would have originally been present in the clay...
Fig. 3. Photographs and element maps of the arthropod specimens selected for study. Boxed regions in the photographs show the area of the fossil that was mapped. A: *Tuzoia nitida*, Early Cambrian Pioche Shale, Nevada (KUMIP 298507a). B: *Anomalocaris pennsylvanica*, Early Cambrian Pioche Shale, Nevada (KUMIP 298527a). C: *Tuzoia guntheri*, Middle Cambrian Pioche Shale, Nevada (KUMIP 307020b). D: *Anomalocaris cf. saron*, Middle Cambrian Pioche Shale, Nevada (KUMIP 298529a). Scale bars: photographs = 1 cm, element maps = 1 mm.
moulds were presumably lost as the rock was split or remain attached to the fossil counterpart.

The mineralization of pyrite was clearly key to the preservation of the Middle Cambrian soft-bodied biota at Pioche. The decay of soft tissues in marine environments induces the conditions that promote authigenic mineralization and therefore preservation (Briggs, 2003). However, fossil preservation relies on the rate of mineralization exceeding decay (Allison, 1988). In marine environments, such as those that prevailed at Pioche, oxygen is quickly depleted by aerobic bacterial decay of organic material thus establishing an anoxic environment (Allison, 1988). In the absence of oxygen bacteria use alternative oxidants to metabolise organic material, and in marine environments sulfate reduction dominates due to the availability of sulfur species (Allison, 1988; Grimes et al., 2001, 2002). The decaying carcasses of Canadaspis, Anomalocaris and other Pioche animals would have acted as a reducing substrate for microbial sulfate reduction, forming H2S from the seawater sulfate (Raiswell and Canfield, 1998; Gabbott et al., 2004). They would also have served as a locus for pyritization because of enhanced nucleation of pyrite on organic substrates (Grimes et al., 2001). The most likely source for the Fe required for pyrite formation is from the surrounding Fe-rich sediment, as it has been described for Chengjiang fossils by Gabbott et al. (2004). Experimental pyrite formation in plants has shown that initial pyritization can occur rapidly (within 80 days) and can produce all the mineral textures identified in fossilized plant material from the Eocene London Clay deposits, including microcrystalline euhedral forms and framboids (Butler and Rickard, 2000; Grimes et al., 2000, 2001). Framboids form when the environment is supersaturated with pyrite so that the rate of nucleation is dominant over crystal growth (Butler and Rickard, 2000).

The dissemination of available Fe to nucleation sites is an important controlling factor in the production of pyrite. Gabbott et al. (2004) suggest that the highest concentration of the constituents required for pyritization occurs where the organic material and sediment meet and frambooids appear to be more common at the sediment–fossil junction in our Middle Cambrian specimens; restriction of pyrite authigenesis to the carcass indicates that the surrounding sediment contained little or no carbon (Gabbott et al., 2004).

Element maps of a marginal spine on the Tuzoia carapace clearly show that carbon is elevated in the region of the fossil (Fig. 3C). This evidence, along with the reflective nature of the fossils in hand specimen, indicates that a carbon film is present. Carbon was not detected in the Anomalocaris appendage, which may reflect the more robust, and hence decay-resistant, nature of the Tuzoia cuticle. The carbon film in Tuzoia is present around the carapace margin and in the characteristic reticulated ornament of the carapace. The presence of organic carbon film is significant as it is a requirement of Burgess Shale-type preservation as described by Butterfield (1990, 1995, 2003).

4.2.1. Other minerals

The rare earth element (REE) phosphate mineral monazite was also found on the surface of both fossils and the surrounding shale; it occurs as crystals between 20 and 40 μm in diameter (Fig. 2H). The crystals have irregular edges and appear brighter under backscatter electron imaging due to charging related to the high atomic weight of the elements present. EDS analysis showed peaks of the rare earth elements La, Nd, Ce, Gd in addition to P. No Th peak was detected in the mineral. This agrees with an identification of low temperature, or gray, monazite, as this mineral typically has less than 1% Th (Burnett et al., 1989).

Monazite was not found in the specimens studied, although it is present in other Cambrian soft-bodied biotas including the Chengjiang (Zhu et al., 2005). This may have been due to the oxidation of pyrite in Middle Cambrian specimens which would have yielded sulfurous acid (H2SO4) (Kamei and Ohmoto, 2000), an acid that dissolves common phosphate minerals including apatite (CaPO4). Monazite, by contrast, is resistant to attack by sulfuric acid (Chang et al., 1998). Burnett et al. (1989) studied clay monazite in Belgian Cambro-Ordovician black slates and determined that similar abundances of REEs in the host rock and monazite implied a desorption of REEs from the clay and re-precipitation in the sediment during diageneis. A similar process may be responsible for the precipitation of monazite at Pioche; the irregular edges and delicate lace-like structure of the monazite crystals indicate that they are authigenic rather than detrital.

5. Conclusions

It is tempting to suggest that the differences in preservation between the Early Cambrian and Middle Cambrian soft-bodied biotas of Pioche reflect changing environmental conditions across the boundary, as Lieberman (2003) argued. However, another possible explanation is that differences in weathering account for the presence of hematite in the Early Cambrian soft-bodied fossils and its absence from Middle Cambrian soft-bodied fossils. If this is the case, and pyrite was originally present in both Early and Middle Cambrian specimens, it is still unclear what process allowed hematite to form in those from the Early Cambrian and not those in the Middle Cambrian. The extent to which weathering, and secondary re-mineralization of ions, has influenced fossil preservation is also a complicating factor in resolving the diagenesis of exceptionally preserved fossils from other localities, such as the Chengjiang.

Thus far, the preservational style of the Early Cambrian soft-bodied fossils from the Pioche seems the most distinctive. Although other Cambrian biotas show preservation of soft-bodied animals in red-orange minerals that superficially resemble those of the Pioche analysis has shown that they have different mineralogical composition (e.g., pink calcium carbonate and calcium phosphate preserves lightely sclerotized animals in the Emu Bay Shale; Briggs and Nedin, 1997; Nedin, 1997). Therefore, the preservation of the soft-bodied fauna in the Lower Cambrian part of the Pioche Shale may not have an adequate analogue, and this further highlights the great diversity of styles of soft-bodied preservation in the Cambrian. We also note that in the Lower Cambrian Latham Shale of California soft-bodied animals appear to be preserved in a grey-green shale that weathers to red (Briggs and Mount, 1982). Fossils from this locality, including Anomalocaris appendages, are most likely also preserved as kerogenized carbon films (Gaines and Droser, 2002). These fossils might usefully be targeted for future investigation of fossil mineralogy.

By contrast, the preservation of the soft-bodied fauna in the Middle Cambrian part of the Pioche Shale shows similarity to other soft-bodied faunas, in particular, the Early Cambrian Chengjiang biota. For example, both have soft tissues similarly replaced by frambooidal and disseminated oxidized pyrite, which are also less frequently preserved as carbon films (Gabbott et al., 2004; Zhu et al., 2005). This type of preservation has also been described from the Lower Cambrian Kinzers Formation of Pennsylvania, although there tissues are also replicated in aluminosilicate films (Skinner, 2005). The preservation of the Burgess Shale animals of British Columbia, Canada also bears some resemblance to the Middle Cambrian soft-bodied fauna from Pioche. This is particularly evident in the presence of carbon films. Aluminosilicate templating of more labile soft tissues and the outline of the cuticle has also been shown to be an important preservation mode in the Burgess Shale (Orr et al., 1998), but there is little evidence that this occurred in the Middle Cambrian Pioche biota. The modes of preservation observed in the Middle Cambrian of Pioche most resemble those described from the Chengjiang biota and therefore the post-burial taphonomic pathways are likely to have been similar. Therefore, the conditions that promoted the preservation of the Chengjiang biota may have a wider taphonomic significance.

Evidence for the environmental conditions that prevailed during the Early–Middle Cambrian comes from studies of key isotope species. Montañez et al. (2000) created the first high-resolution carbon isotope curve for the Cambrian and discovered a significant shift to negative δ13C values at the terminal Early Cambrian. This shift occurs just prior to the Early–Middle Cambrian boundary where a major faunal change, including a trilobite mass extinction event, has
previously been documented (Palmer, 1988). Montañez et al. (2000) interpreted the negative shift in δ^{34}C isotope values to indicate the onset of significant climatic and paleoenvironmental changes prior to the faunal turnover at the Early–Middle Cambrian boundary. The spread of anoxic bottom waters, depleted in δ^{13}C, onto shallow carbonate platforms and associated decrease in the burial rate of organic matter at the end of the Early Cambrian, due to major biomass reduction, are believed to have contributed to the negative shift in the C-isotope curve (Moitaine et al., 2000). Further evidence for the spread of anoxic waters during the Early–Middle Cambrian transition comes from independent analysis of sulfur isotopes in francolite (Hough et al., 2006). A sharp shift to high δ^{34}S values around the Early–Middle Cambrian boundary is believed to be due to increased rates of bacterial sulphate reduction leading to increased rates of pyrite burial during the spread of anoxic bottom waters over carbonate platforms (Hough et al., 2006). The development of anoxia is most likely related to a marine transgression at the end of the Early Cambrian (Montañez et al., 2000) and an episode of volcanism from the Karkarindji Large Igneous Province of northern Australia at c. 510 Ma that released vast quantities of CO2, thus triggering ocean warming during the Early Cambrian Province of northern Australia at


