Exceptional Fossil Preservation and the Cambrian Explosion[1]

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SYNOPSIS. Exceptionally preserved, non-biomineralizing fossils contribute importantly to resolving details of the Cambrian explosion, but little to its overall patterns. Six distinct "types" of exceptional preservation are identified for the terminal Proterozoic-Cambrian interval, each of which is dependent on particular taphonomic circumstances, typically restricted both in space and time. Taphonomic pathways yielding exceptional preservation were particularly variable through the Proterozoic-Cambrian transition, at least in part a consequence of contemporaneous evolutionary innovations. Combined with the reasonably continuous record of "Doushantuo-type preservation," and the fundamentally more robust records of shelly fossils, phytoplankton cysts and trace fossils, these taphonomic perturbations contribute to the documentation of major evolutionary and biogeochemical shifts through the terminal Proterozoic and early Cambrian.

Appreciation of the relationship between taphonomic pathway and fossil expression serves as a useful tool for interpreting exceptionally preserved, often problematic, early Cambrian fossils. In shale facies, for example, flattened non-biomineralizing structures typically represent the remains of degradation-resistant acellular and extracellular "tissues" such as chaetae and cuticles, whereas three-dimensional preservation represents labile cellular tissues with a propensity for attracting and precipitating early diagenetic minerals. Such distinction helps to identify the acuticular integument of hyolithids, the chaetae-like nature of *Wiwaxia* sclerites, the chaetognath-like integument of *Amiskwia*, the midgut glands of various Burgess Shale arthropods, and the misidentification of deposit-feeding arthropods in the Chengjiang biota. By the same reasoning, putative lobopods in the Sirius Passet biota and putative deuterostomes in the Chengiang biota are better interpreted as arthropods.

INTRODUCTION

The Cambrian explosion is a phenomenon recognised solely from the fossil record, so it is imperative that the processes responsible for fossilisation be well understood. Insofar as the majority of fossils are biomineralized skeletons, it is worth asking whether the sudden increase of fossil diversity and abundance in the early Cambrian represents not so much an "explosion" of animal diversity as the rapid expansion of biomineralization (Runnegar, 1982). Certainly the Cambrian record is deeply biased in favour of shelly fossils, as revealed by the exceptionally preserved Burgess Shale and Chengjiang biotas, where the vast majority of taxa and individuals were non-biomineralizing (Conway Morris, 1986; Chen and Zhou, 1997). By the same token, however, the existence of Burgess Shale-type biotas suggests that the Cambrian explosion could have proceeded quite independently of widespread biomineralization. If so, then one way of avoiding the bias of the shelly fossil record might be simply to ignore it. Here I will consider taphonomic issues relating to non-biomineralizing components of Proterozoic-Cambrian transition with an eye both to testing the Cambrian explosion hypothesis, and as a tool to be used in the interpretation of problematic fossils.

THE PROTEROZOIC-CAMBRIAN RECORD OF NON-BIOMINERALIZING ORGANISMS

There is a rich record of non-biomineralizing fossils through Proterozoic-Cambrian transition. It is expressed in a variety of taphonomic modes, ranging from silica permineralization in peritidal carbonates ("Bitter Springs-type preservation") to carbonaceous compressions in shales ("Burgess Shale-type preservation"), phosphate mineralization in shallow marine phosphorite/carbonates ("Doushantuo-type preservation"), casts and moulds on and within sandstones ("Ediacaran-type preservation"), phosphate mineralization within carbonate concretions ("Orsten-type preservation") and pyritization in shales ("Beecher's Trilobite-type preservation"). In addition to these "exceptionally" preserved body fossils, there is of course valuable information to be recovered from the more conventional records of shelly fossils, organic-walled microfossils (*e.g.,* acritarchs) and biologically induced sedimentary structures (*e.g.,* microbialites and trace fossils). Each of these is capable of capturing some, but never all, contemporaneous diversity, simply because each is limited to particular sedimentary facies and requires more or less specific pre- and post-depositional circumstances for fossilisation (Allison, 1988). Less immediately obvious is the fact that these conducive facies and circumstances are not evenly, or even randomly distributed through time (Allison and Briggs, 1993; Butterfield, 1995; Kowalewski and Flessa, 1996), and that the pathways leading to the preservation of some kinds of tissue preclude the preservation of others. In other words, the fossil record can

never be read literally, and any meaningful assessment must be prefaced by a thorough understanding of the environmental, diagenetic and temporal controls on particular taphonomic pathways.

Bitter Springs-type preservation

Microbial mat biotas dominated by cyanobacteria, are commonly preserved in Meso- and Neoproterozoic carbonate facies, the first well-documented case being the Bitter Springs biota of central Australia (Schopf, 1968). Such microfossils are preserved in three dimensions due to the very early (*i.e.,* prior to degradational collapse) diagenetic emplacement of silica, from which point they become more or less impervious to subsequent diagenetic, and even low grade metamorphic alteration (Knoll, 1992). The quality of preservation can be spectacular but, unfortunately, the view is profoundly biased. The Bitter Springs-type "taphonomic window" is limited to conspicuously shallow-water/supratidal carbonate environments and is conspicuously absent in the Phanerozoic. The reason lies in the disjunct history of silica biogeochemistry. Prior to the appearance of silica biomineralizers in the terminal Proterozoic, surface waters of the oceans would have been saturated with respect to silica, and supersaturated in restricted peritidal settings (Maliva *et al.*, 1989). These restricted environments would also have been dominated by prolific microbial mats which, as they decayed, served as foci for the nucleation and precipitation of silica (Knoll, 1985). Such paleoenvironments were far from equable and, with a few notable exceptions (*e.g.,* Zhang *et al.*, 1998; Butterfield, 2000), tended to exclude eukaryotic organisms. So despite its exceptional preservation, this taphonomic mode fails to offer even a broad approximation of paleodiversity. Moreover, the disappearance of Bitter Springs type biotas at the end of the Proterozoic in no way reflects biological extinction; rather, it is a taphonomic signal induced by the evolution of silica-biomineralizing sponges and consequent draw-down of marine silica concentrations.

Burgess Shale-type preservation

The bias of Bitter Springs-type taphonomy is starkly exposed by comparison with coeval fossil assemblages preserved in fine-grained siliciclastic sediments. These shales and siltstones typically represent less restricted paleoenvironments and, not surprisingly, yield a fundamentally greater diversity of early eukaryotic organisms (*e.g.,* Butterfield *et al.*, 1994; Butterfield and Rainbird, 1998). Moreover, there is at least a broad degree of continuity through the Proterozoic-Cambrian transition with the relatively widespread occurrence of carbonaceous compression fossils in both the (pre-glacial) Neoproterozoic and early-middle Cambrian (Butterfield, 1995). Even so, major biases remain. Of these, the most obvious is the disappearance of such "Burgess Shale-type" preservation at the end of the middle Cambrian. The loss of this taphonomic pathway has yet to be convincingly explained, but it does raise the issue of how to interpret the similar dearth of Burgess Shale-type fossils through the last 150 million years of the Neoproterozoic. Is this a real evolutionary signal, or merely the opening and closing of a taphonomic window?

Burgess Shale-type preservation is defined as the "exceptional" preservation of non-mineralizing organisms as carbonaceous compressions in marine shales (Butterfield, 1995). Recognition and analysis of this taphonomic mode in the Burgess Shale and comparable biotas has contributed importantly to their interpretation at various levels (Butterfield, 1990a, b, 2002). Burgess Shale-type fossils notably retain the outline of their three-dimensional precursors through the process of flattening, a consequence of the rapid degradation and collapse of supporting cellular tissues (Briggs and Williams, 1981). What remains is a residue of recalcitrant *extracellular* structures such as cuticle, chaetae and jaws (Briggs and Kear, 1993)—handily for paleontologists, it is these same structures that tend to define the external morphology of many non-biomineralizing invertebrates. Even so, there is large diversity of forms that lack such recalcitrant tissues and are simply not preservable under Burgess Shale-type conditions. Thus the predominance in Burgess Shale-type biotas of cuticularized arthropods, priapulids and polychaetes, and the *absence* of acuticular flatworms, mesozoans, nemerteans, unshelled molluscs, etc. cannot alone be taken as of particular evolutionary or ecological significance. In this light, one possible explanation for the early Cambrian appearance of Burgess Shale-type fossils is simply the widespread evolution of metazoan cuticles, chaetae, etc., at more or less the same time as the expansion of biomineralization. On the basis of Burgess Shale-type fossil record alone, there is no reason to rule out a diversity of true soft-bodied metazoans in the terminal Proterozoic.

The taphonomic processes responsible for Burgess Shale fossils have been debated at length with explanations ranging from simple absence of bioturbation (Allison and Briggs, 1993), to the mechanical properties of embedding clays (Wollanke and Zimmerle, 1990), early aluminosilicate diagenesis (Orr *et al.*, 1998), inhibition of degradation due to enzyme adsorption on and within clay minerals (Butterfield, 1990a, 1995), and inhibition of degradation due to Fe^{2+} adsorption on structural biopolymers (Petrovich, 2001). Whatever the particular combination of circumstances, it is clear that the resulting fossils represent structures at the recalcitrant end of a "chemical reactivity spectrum," and that their fossilization results from further reduction and indeed termination of degradative chemistry. Given the powerful inhibitory and/or catalytic effects of certain mineral- and clay-organic systems (Butterfield, 1995; Ransom *et al.*, 1998; Lewan, 1998; Kennedy *et al.*, 2002) and the specific range of lithologies and TOC values in which Burgess Shale-type preservation is expressed, there is little doubt that interactions between carcasses and enclos-

ing sediments play a key role in terminating degra-dation. Insofar as such interactions are likely to have changed through time (*e.g.,* secular changes in average clay mineralogy, marine chemistry, exchange cations, etc.), these may also account for secular changes in the expression of Burgess Shale-type preservation, not least its common occurrence in the early and middle Neoproterozoic, marked decline in the terminal Pro-terozoic (see Xiao *et al.* [2002] for a possible excep-tion), and brief but spectacular return in the early and middle Cambrian (Butterfield, 1995). The terminal Proterozoic interruption in this taphonomic pathway is unfortunate in that it is precisely this *ca.* 150 million year interval where the key transitions to Phanerozoic biology are likely to be found. All that can be directly concluded on the basis of Burgess Shale-type preser-vation is that metazoans with substantial cuticles ap-peared sometime during the terminal Proterozoic and/ or earliest Cambrian—there is no evidence of such forms in the early-middle Neoproterozoic, despite the conspicuous occurrence of Burgess Shale-type pres-ervation (*e.g.,* Butterfield *et al.*, 1994; Butterfield, 1995; Butterfield and Rainbird, 1998).

Doushantuo-type preservation

It is, however, possible to capture cells and genuine soft-tissues in the fossil record. Not as organic-walled residua, but through a process of early diagenetic min-eralization. Phosphate mineralization offers a particu-larly important view of the Cambrian explosion, partly because of its potential to see beyond cuticles and cell walls, but also because it appears to document "nor-mal" marine environments more or less continuously through the Proterozoic-Cambrian transition. Early diagenetic phosphatization (*i.e.,* phosphate perminer-alization prior to the degradational collapse of cells and cellular tissues) is spectacularly displayed in shal-low-water, relatively high energy, carbonate facies of the terminal Proterozoic Doushantuo Formation of southern China. In addition to a high diversity of ac-ritarchs (unicellular protists of unknown affinity) (Zhang *et al.*, 1998), the Doushantuo phosphorites have yielded evidence of both embryonic and adult metazoans (Xiao *et al.*, 1998, 2001). The occurrence of similar acritarchs as two-dimensional compression fossils in age-equivalent shales (*e.g.,* Zang and Walter, 1992) indicates that some Doushantou fossils had deg-radation-resistant walls, but this was certainly not nec-essarily or universally the case. Indeed, the best ex-planation for early emplacement of the permineralizing phosphate is its attraction to labile, chemically reactive substrates such as degrading cell cytoplasm (Xiao and Knoll, 1999; Sagemann *et al.*, 1999). Metazoan cells, including those of embryos, notably lack cell walls or comparable structures (see Xiao, 2002). In other words, Doushantuo-type preservation potentially pro-vides a record of true soft-bodied (acuticular) organ-isms that are not preservable under Burgess Shale-type conditions.

Although chemically reactive substrates provide a

focus for permineralization, the primary cause of Doushantuo-type preservation is the elevated avail-ability of phosphate. Thus, the abundance of major phosphorite deposition in the terminal Proterozoic through to the middle Cambrian is a key component of the Doushantuo-type taphonomic window (Brasier, 1990; Cook, 1992; Porter, 2002). Despite marked geo-chemical differences between the Proterozoic and Cambrian phosphorites (Shen *et al.*, 2000), there does appear to be broad similarity in depositional environ-ments (typically shallow-shelf carbonate facies) and the "kind" of fossils represented (*e.g.,* metazoan em-bryos; Xiao *et al.*, 1998; Bengtson and Zhao, 1997; Kouchinsky *et al.*, 1999) throughout this extended in-terval of phosphogenesis. If so, then the absence of phosphatic shells and secondarily phosphatized shells from Doushantuo-age phosphorites would appear to be a real evolutionary signal. Moreover, the Terminal Pro-terozoic absence of phosphatic steinkerns (internal moulds) points to a genuine absence of even non-min-eralizing equivalents of Cambrian shelly fossils.

Doushantuo-type preservation may offer a more continuous record through terminal Proterozoic-Cam-brian transition than Burgess Shale-type fossils, but it is far from complete. Most Doushantuo-type fossils, for example, tend to be microscopic, and do not at all reflect the diversity recorded in coeval Burgess Shale-type assemblages: Cambrian taxa recognised in both taphonomic modes are limited to occasional worm fragments (*e.g.,* Mueller and Hinz-Schallreuter, 1993), a few shelly forms (*e.g.,* chancelloriids and hyoliths; Butterfield and Nicholas, 1996) and some *Wiwaxia*-like sclerites (Porter, 2000). Of somewhat greater con-cern is the temporal distribution of Doushantuo-type phosphorites. In the absence of comparable deposits before Doushantuo-time, it is difficult to assess the ear-lier history of organisms lacking recalcitrant cell walls or cuticles. By the same token, the *disappearance* of Doushantuo-type phosphorites at the end of the middle Cambrian, curiously coincident with the demise of Burgess Shale-type preservation, precludes any defin-itive statement regarding the fate of those taxa limited to this taphonomic mode.

Örsten-type preservation

Exceptional preservation through phosphatization occurs in an alternative mode, in deeper water settings not associated with major phosphogenesis, and pur-portedly mineralizing just the outer surfaces of small cuticular organisms, primarily arthropods. The classic locality for this taphonomic mode is in the Late Cam-brian örsten of southern Sweden (Mass and Waloszek, 2001), and it remains to be seen whether direct com-parisons have been encountered elsewhere. Despite the spectacular anatomical resolution provided by these fossils, the taphonomic processes have yet to be seri-ously investigated—what, for example, is the attrac-tion of phosphate to relatively inert cuticle? If örsten-type preservation is indeed limited to external cuticular structures, its preservational biases are comparable to

those in the Burgess Shale, though with the added advantage of three-dimensionality. Örsten-type fossils are also notably limited to conspicuously small organisms (<2 mm), possibly a reflection of original community structure, but more likely an artifact of taphonomy.

Ediacara-type preservation

Complex macrofossils make their first appearance in the fossil record as casts and moulds on and within terminal Proterozoic sandstones and siltstones, from strand-plain through to relatively deep-water facies. These so-called Ediacaran fossils stand as a fascinating and largely problematic prelude to the Cambrian explosion, first appearing at *ca.* 570 Ma and continuing up to the base of the Cambrian, at which point they and their preservational mode effectively, if not entirely (*e.g.,* Jensen *et al.*, 1999), disappear. Gehling (1999) has argued that the preservation of at least some of these soft-bodied organisms was a consequence of overgrowing microbial mats and their induction of early diagenetic cements, a phenomenon lost with the appearance of mat-disturbing metazoans. Although this "death mask" hypothesis does not explain the preservation of three-dimensional Ediacarans that occur *within* beds (*e.g., Pteridinium* and *Ernietta*), it is likely that the early Cambrian increase in depth and intensity of bioturbation (Jensen, this volume) does account for the general disappearance of Ediacaran-type fossils, a taphonomic explanation that obviates the tendency to invoke coincident mass extinction. More interesting, perhaps, is consideration of what the *first* appearance of Ediacaran-type fossils signifies. If preservation was a function of sediment stability and undisturbed microbial mats—pervasive throughout the Archean and Proterozoic—then the first stratigraphic appearance of Ediacaran-type fossils at around 570 Ma may well be reflecting the first appearance of large benthic organisms.

Beecher's Trilobite-type preservation

Non-biomineralizing tissues can also be preserved through pyritization, the classic example being trilobite appendages in black shales of the Upper Ordovician Beecher's Trilobite Bed, New York (Briggs *et al.*, 1991). Like most other types of mineralization, this pyrite emplacement appears to be associated with relatively labile cellular tissues, hence its typically three-dimensional expression. Unlike Doushantuo-type preservation, however, there is no evidence of any remaining cellular structure, and the pyrite is probably better interpreted as mouldic, forming within cavities defined by recalcitrant cuticle (see Otto, 2000). Such a habit is nicely illustrated in arthropod appendages from the Lower Cambrian Mount Cap Formation (Butterfield, 1994) where the presence of three-dimensional pyrite euhedra within the otherwise flattened organic-walled cuticles (representing Burgess Shale-type preservation) confirms the pre-collapse emplacement of the pyrite, but with no real reflection of the original tissues
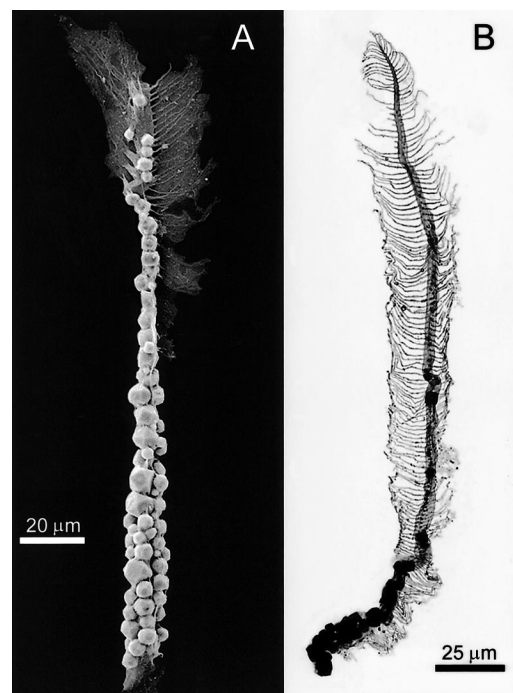

FIG. 1. Acid-isolated arthropod setae from the Lower Cambrian Mount Cap Formation (Butterfield, 1994) showing both Burgess Shale-type (*i.e.,* organic-carbon compressions) and Beecher's Trilobite-type (*i.e.,* mouldic pyrite) preservation. Although the cuticular organic-carbon films preserve most of the fine detail, it is the early diagenetic pyrite that captures the original three-dimensionality. A is an SEM micrograph of a specimen with most of the setal shaft packed with pyrite euhedra. B is a transmitted light micrograph of a specimen with pyrite formed only at the base.

or cells (Fig. 1). Mouldic pyrite also occurs within the carbonaceous sheaths of coiled filamentous microbes from the terminal Proterozoic of Ukraine (Burzin, 1995) and a middle Cambrian hemichordate from Siberia (Durman and Sennikov, 1993). The mouldic nature of internal pyrite is unambiguous in the case of three-dimensionally preserved chuariids from the terminal Proterozoic of China (Yuan *et al.*, 2001), where the presence of prominent medial splits clearly documents the prior release of cell contents. If this mode of emplacement is generally the case, then it would appear that Beecher's Trilobite-type preservation is incapable of capturing forms without a cuticle or comparably recalcitrant structure that would serve to support and define a mould. In other words, it has the same limitations inherent to Burgess Shale-type and örsten-type preservation. The exception to this rule are putative pyritized ophiuroid tube-feet (which lack a recalcitrant cuticle) from upper Ordovician and Devonian black shales (Glass and Blake, 2002); if true, the mechanism by which this occurred remains to be explained.

EXCEPTIONAL PRESERVATION AND THE CAMBRIAN EXPLOSION

Exceptionally preserved fossils, more or less by definition, provide an unreliable measure for assessing

evolutionary timing or trends. Most of the above "types" of preservation are sufficiently rare and restricted in time to frustrate statistical analysis, and all are limited to particular, probably untypical, paleoenvironments. Certainly the records of örsten-type and Beecher's Trilobite-type preservation are too sparse to provide anything other than a glimpse of otherwise invisible paleodiversity, and Bitter Springs-type preservation merely documents the deep evolutionary conservatism of intertidal/supratidal microbial mats—interesting to be sure, but of limited importance to understanding the rise and radiation of metazoans. Burgess Shale-type, Doushantuo-type and Ediacara-type preservation have greater potential for resolving evolutionary patterns (Conway Morris, 1989; Cook, 1992; Jenkins, 1992; Butterfield, 1995), but even these are constrained by larger-scale controls on taphonomic pathways: both the early Cambrian reappearance and the Upper Cambrian disappearance of Burgess Shale-type fossils result from a shifting potential in the preservation of organic-walled fossils (Butterfield, 1995); the terminal Proterozoic to middle Cambrian occurrence of Doushantuo-type preservation is a consequence of contemporaneous phosphogenesis; and the disappearance of Ediacaran-type fossils coincides conspicuously with the onset of significant bioturbation.

All is not lost, however. Doushantuo-type preservation offers an important and relatively continuous view, at least of a particular facies, through the Proterozoic-Cambrian transition. And there is a reasonable argument, stemming from the conservatism of microbial mats and their probable role in preserving at least some Ediacaran fossils (Gehling, 1999), for a more or less literal interpretation of the first appearance of diverse Ediacaran biotas. More important, however, are broad-scale patterns and trends drawn from the more conventional fossil record. Mineralized skeletons, for example, are fundamentally more likely to enter the fossil record than non-mineralized tissues, and their rapid expansion in the early Cambrian is a straightforward record of major radiation. Whether or not it is possible to imagine an non-mineralizing archaeocyath or brachiopod or echinoderm, this new-found capacity for biomineralization, in the form of rigid skeletons, bioclasts and reefs, contributed fundamentally to the ecological/evolutionary feedback that fuelled, and indeed defined, the Cambrian explosion.

Organic-walled microfossils, particularly those representing phytoplankton cysts, undergo a major radiation coincident with the Cambrian "explosion" of large animals and biomineralization (Butterfield, 1997). As with all fossils, these unicellular cysts passed through a variety of taphonomic filters; however, there is good reason to believe that they were largely indifferent to the delicate taphonomic balances controlling "exceptional" preservation. Not only is there a relatively continuous record of phytoplankton cysts from the beginning of the Proterozoic (Butterfield, 1997, 2001), but the walls of such cysts are known to be composed of highly recalcitrant aliphatic

compounds (e.g., "sporopollenin," "algaenan," etc.; Tegelaar et al., 1989) which under most conditions are at least as robust as mineralized hard parts. The sudden introduction of diverse acanthomorphic phytoplankton in the early Cambrian, following some two billion years of successful but merely sphaeromorphic membership, points unambiguously to a fundamental shift in pelagic ecology, including the primary productivity responsible for the vast majority of marine metabolism. The connection between the evolutionary radiation of phytoplankton on the one hand, and large animals on the other is best explained by the evolution of small, pelagic metazoans—zooplankton—the evolution of which carried profound ecological, evolutionary and biogeochemical implications (Butterfield, 1997, 2001). So, although the first fossil occurrence of filter-feeding zooplankton in the late Early Cambrian (Fig. 1; Butterfield, 1994) only tenuously constrains the true first appearance of this habit, the "explosive" radiation of ornamented phytoplankton cysts in the middle early Cambrian (i.e., Tommotian; Zhuravlev, 2001) documents precisely the timing of metazoan expansion into the plankton.

Like phytoplankton cysts, sedimentary trace fossils do not require exceptional circumstances for their preservation. The fundamental increase in diversity and intensity of infaunal activity in the early Cambrian (Jensen, 2003) documents the arrival of Phanerozoic-style ecosystems quite independently of any body fossils. By the same token, the marked decline in the abundance and diversity of sedimentary microbialites across the Proterozoic-Cambrian boundary most likely reflects the activities of newly introduced grazers and burrowers—and leading, inadvertently, to the demise of Ediacaran-type preservation.

In summary, the fact of the Cambrian explosion is most clearly and consistently recorded in the conventional fossil record, simply because it is unexceptional. Exceptionally preserved biotas add fascinating detail but, on their own, are not able to define large-scale patterns. Even so, the marked shifts in taphonomic pathways through the Proterozoic-Cambrian interval can be tied to major biological/biogeochemical innovations of that time, most obviously so in the case of disappearing Bitter Springs-type and Ediacaran-type preservation, but also, it seems, for the early Cambrian reintroduction of Burgess Shale-type preservation (Butterfield, 1995): Insofar as Burgess Shale-type preservation is related to early diagenesis, including clay mineralogy, exchange cations, pH, Eh, and etc., I suggest that the reopening of this taphonomic window was causally correlated with the introduction of widespread biomineralization, bioturbation and/or zooplankton, all of which would have induced substantial shifts in contemporaneous marine chemistry.

Doushantuo-type preservation traverses the Terminal Proterozoic-Cambrian boundary and the absence of phosphatic steinkerns in the Terminal Proterozoic reliably documents the absence of even non-mineralized Cambrian-style sclerites at that time. To a degree,

it also records the terminal Proterozoic absence of diverse, acuticular metazoans that would have remained invisible under Burgess Shale-type preservation. This insight, however, is limited by long term fluctuations in phosphogenesis, which are conventionally interpreted as resulting from tectonically induced shifts in marine circulation. According to Brasier (1992), the increase in sedimentary phosphates in the terminal Proterozoic was a bottom-up *cause* of the Cambrian explosion. There is, however, no indication that the Proterozoic was in any way starved of primary production, and it may be that the various biogeochemical perturbations of the Proterozoic-Cambrian interval were in fact a top-down *consequence* of contemporaneous biological innovations (Butterfield, 1997, 2001). If this was the case, then the taphonomic window offered by Doushantuo-type preservation is itself a record of fundamental changes in an evolving biosphere, just as in the case of Bitter Springs-type, Ediacaran-type and Burgess Shale-type preservation.

EXCEPTIONAL PRESERVATION AND THE INTERPRETATION OF PROBLEMATIC FOSSILS

During the fossilization process some components of a once living organism are inevitably lost while others are preserved, a function determined by original tissue histology and early diagenesis. In the conventional fossil record, for example, it is largely the decay-resistance of mineralized hard parts that accounts for their preferential preservation. Likewise, the relative recalcitrance of various non-mineralizing tissues such as algal cyst walls, graptolite periderm, polychaete chaetae and arthropod cuticles contributes to their enhanced preservation potential. But there is more to exceptional preservation than resistance to biodegradation. When it comes to the early diagenetic mineralization of non-mineralizing tissues, for example, it is the more labile structures that tend to be preserved, a consequence of their exaggerated chemical reactivity and consequent attraction of precipitating mineral ions. In other words, there are two broad modes of exceptional preservation which represent essentially opposite ends of a "chemical reactivity spectrum:" on the one hand relatively decay-resistant acellular and extracellular structures such as chaetae and cuticles, and on the other highly labile, degradation-prone, cellular ones such as internal tissues and organs. Recognition of these two discrete modes gives rise to a simple deductive rule, at least for shale-hosted fossils: structures preserved as two-dimensional carbonaceous compressions represent resistant acellular and extracellular histologies, whereas those preserved three-dimensionally, due to early diagenetic mineralization, are likely to represent chemically labile cellular histologies. Such resolution can provide key evidence for the interpretation of problematic fossils.

The relationship between differential preservation and original histology is nicely illustrated by the hyolithids, a group of common but problematic early Paleozoic fossils with a four-part calcareous skeleton (Fig. 2B). Despite the common occurrence of articulated hylothids in Burgess Shale-type assemblages (Yochelson, 1961; Butterfield and Nicholas, 1996), there are no recorded examples of the body-wall itself. Given the abundance of associated carbonaceous compressions, this absence is convincing evidence for hyolithids having had an acuticular, cellular integument. This in turn stands as circumstantial evidence for interpreting them as more closely related to molluscs than, say, sipunculids (*cf.*, Runnegar *et al.*, 1975; Runnegar, 1980): unlike sipunculids, molluscs lack a robust body-wall cuticle.

Hyolithids are also known from secondarily phosphatized and pyritized shells and steinkerns (Bengtson *et al.*, 1990; Butterfield, 1996), but again there is no evidence of a preserved body-wall. Insofar as Beecher's Trilobite-type preservation requires a cuticular envelope, the lack of pyritized hyolithid soft parts is not surprising. The absence of phosphatized hyolithids is more problematic however, especially given the Doushantuo-type preservation of various embryos (Xiao *et al.*, 1998; Bengtson and Zhao, 1997; Kouchinsky *et al.*, 1999), and at least the potential for extensive Santana-type phosphatization of muscle (Martill, 1990). Even so, a hyolithid from the middle Cambrian Mount Cap Formation does show preferential phosphatization of a simple loop-shaped gut (Fig. 2A), a clear reflection of histological selectivity, presumably because the gut offered a fundamentally more reactive substrate for early mineralization than adjacent tissues and organs.

As discussed above, Burgess Shale-type preservation is expressed as flattened carbonaceous films representing the relatively recalcitrant acellular remains of metazoans (plus the cell walls of plant protists). This alone provides useful histological resolution, but there is also potential for recognizing a preservational/histological gradient within these potentially preservable structures. In the case of the Burgess Shale polychaetes, for example, both the body-wall cuticle and chaetae may be preserved (Conway Morris, 1979), but the fossil chaetae are conspicuously more coherent and robust, to the extent that they can be readily isolated from the rock matrix with HF acid (Butterfield, 1990*a*, *b*). Such differential preservation accords with the relative histologies of the two structures, polychaete chaetae being inherently tougher and more recalcitrant than the body-wall cuticle (Briggs and Kear, 1993).

A similar argument can be applied to the interpretation of *Wiwaxia*, a problematic "worm" from the Burgess Shale that Walcott (1911) compared to modern polychaetous scale-worms. Conway Morris (1985) correctly noted major anatomical differences between *Wiwaxia* sclerites and the scales/elytra of scale-worms, not least that *Wiwaxia* sclerites have a basal stalk that insert into follicles of the body-wall, whereas elytra are little more than outgrowths of the body-wall. In this respect, as indeed in their microstructure, the sclerites of *Wiwaxia* are fundamentally more compa-
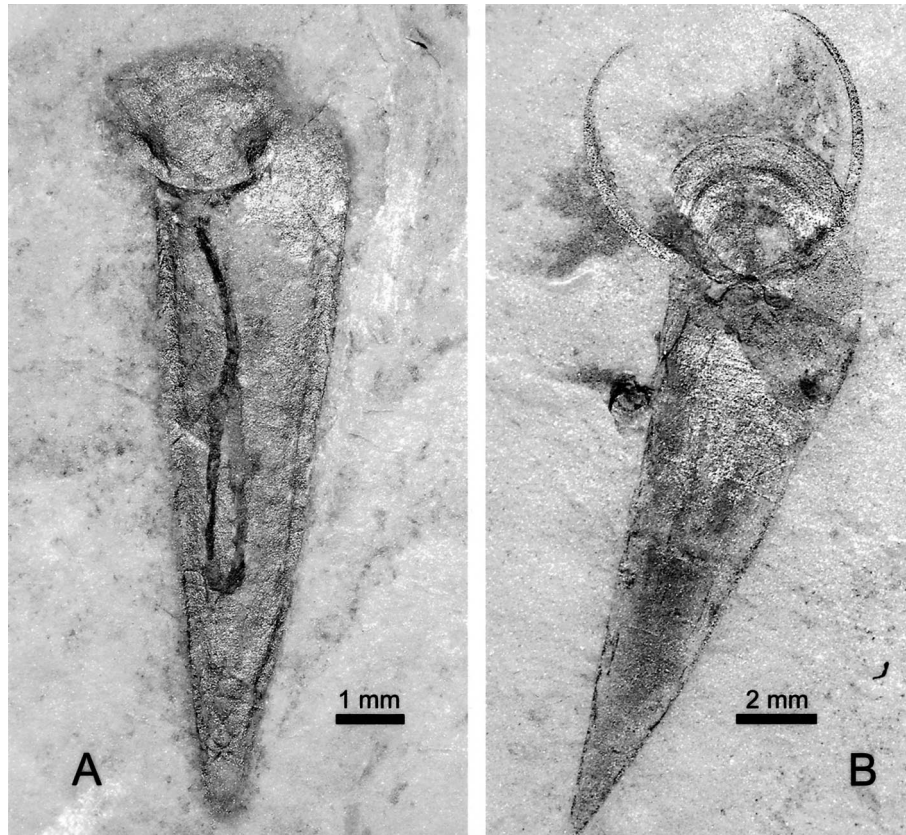
FIG. 2.   Bedding-plane hyolithids from the middle Cambrian Mount Cap Formation (Butterfield and Nicholas, 1996) showing the articulated four-part skeleton (B) and simple, loop-shaped phosphatized gut (A). In both cases the fossils occur as more or less two dimensional compression fossils, defined by the preservation of a relatively recalcitrant organic-carbon periostracum; the original skeletal carbonate appears to have been lost during early diagenesis, hence the flattening. Despite the obvious presence of an intact carcass in A, the body wall has not been preserved—compelling evidence for an acuticular integument. The phosphatic gut of A is three dimensionally preserved, as are the moulds of hexact sponge spicules superimposed on the conch.

rable to polychaete chaetae (Butterfield, 1990*b*). A chaeta-like interpretation is also supported by taphonomic/histologic evidence: like polychaete chaetae, organic-walled *Wiwaxia* sclerites are conspicuously more robust than the associated body wall cuticle (Conway Morris, 1985), and are similarly extractable from the rock matrix (Butterfield, 1990*b*). This taphonomic recalcitrance is at least partially responsible for the remarkably widespread occurrence of *Wiwaxia* sclerites which are now known from five localities in western Laurentia (Walcott, 1911; Conway Morris and Robison, 1988; Butterfield, 1994, 2000), as well as the Kali biota of southern China (Zhao *et al.*, 1994). The presence of microscopic but nevertheless three-dimensional pyrite euhedra at the base some *Wiwaxia* sclerites suggests the presence of a more degradation-prone medullary zone (Fig. 3A), a habit entirely in keeping with the structure of certain modern polychaete chaetae (*e.g.,* Gustus and Cloney, 1973), and in no way comparable to the much larger internal spaces characteristic of, for example, halkieriid sclerites. Despite its chaeta-like sclerites, *Wiwaxia* is not directly comparable to any modern polychaete, lacking, for example, both ventral neurochaetae and internal acicula,

both of which would be expected to preserve under Burgess Shale-type conditions. It is probably best interpreted as a stem-group annelid.

Intermediate between the discrete preservation of cuticular structures of most Burgess Shale-type fossils and the non-preservation (or amorphous preservation in the form of an ''organic stain''; see Whittington, 1971; Butterfield, 1990*a*) of cellular tissues, is that expressed in the problematic Burgess Shale fossil *Amiskwia*. Although its overall form is that of a chaetognath, Conway Morris (1977) has argued against such assignment because of the absence of expected chaetognath-like grasping spines and a ''gelatinous'' constitution, as suggested by its unusually non-reflective preservation and the clarity of its ''internal organs.'' Interestingly, extant chaetognaths do not have a cuticle, but their unique integument includes an unusually tough acellular basement membrane (Ahnelt, 1984; Shinn, 1997) that might well be considered of a taphonomically intermediate grade—less robustly preservable than true cuticle (under Burgess Shale-type conditions), but much more so than simple cellular tissue. This offers a ready explanation for the ''gelatinous'' habit of the *Amiskwia* body wall, whereas the
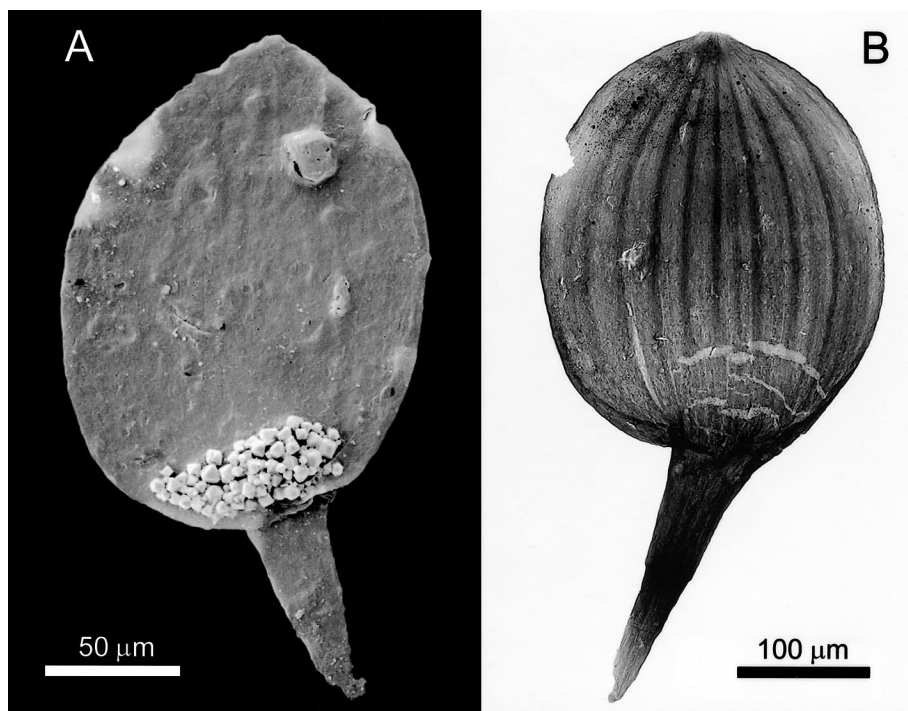
FIG. 3. Acid-isolated carbonaceous *Wiwaxia* sclerites from the Lower Cambrian Mount Cap Formation (Butterfield, 1994); such preservation is evidence of an originally robust acellular "histology." The pyrite euhedra at the base of the blade in A (SEM), as well as the similarly positioned cracks in the specimen in B (light micrograph), indicate the presence of a slight medullary lumen, not unlike that seen in the compound chaetae of the modern polychaete *Neriesis* (*cf.*, Gustus and Cloney, 1973).

prominent reflective area on its head (Conway Morris, 1977) accords taphonomically with the "mask" of robust cuticular structures that reinforces the head and grasping apparatus of extant chaetognaths (*cf.*, Ahnelt, 1984; Shinn, 1997). Other features of *Amiskwia* remain to be resolved (*e.g.,* the anterior, bi-lobed structures preserved in three-dimensions—presumably permineralized cellular organs), but the combination of chaetognath-like form and body-wall histology argues compelling case for a close phylogenetic relationship.

The overwhelming majority of non-mineralizing organisms preserved in the Burgess Shale are preserved as two-dimensional compression fossils representing external cuticular structures. A number of arthropods, however, also feature conspicuously three-dimensional phosphatized gut structures, most notably *Leanchoilia* (Fig. 4), *Odaraia*, *Canadaspis*, *Perspicaris*, *Sydneyia*, *Anomalocaris* and *Opabinia*. Analysis of the *Leanchoilia* gut, including thin-section examination of exceptionally preserved sub-cellular anatomy, has identified the mineralized tissue as serially repeated midgut glands, the details of which contribute important paleoecolgical and phylogenetic resolution (Butterfield, 2002). The deeper significance, however, lies in appreciation of the differential taphonomy. All of these Burgess arthropods are represented by two distinct taphonomic modes: on the one hand relatively recalcitrant cuticles that have survived degradational collapse and sedimentary compaction despite the loss of their third dimension, and on the other highly labile

midgut glands which have retained their three-dimensional form through early diagenetic mineralization. Once again, these disparate preservational modes reflect fundamental histological differences, and go some way to explaining their juxtapostion in a single fossil. It is at the histological extremes where the taphonomic balance is most easily tipped towards fossilization, with recalcitrant cuticle inherently prone to organic preservation, and labile midgut glands to early mineralization (particularly as arthropod midgut glands tend to contain an abundance of unordered calcium phosphate [Butterfield, 2002]). By contrast, more "intermediate" tissue types, such as muscle, have no inherent propensity for either organic preservation or mineralization, hence its absence in the Burgess Shale.

The combination of flattened cuticular structures and three-dimensional gut structures is encountered in other Burgess Shale-type occurrences, most notably the Lower Cambrian Sirius Passet biota of north Greenland and the Chengjiang biota of China. Despite the later-stage taphonomic alteration experienced by these two biotas—respectively, high temperature metamorphism and intense weathering—the simple relationship of histology and preservational style can still be applied. Thus the three-dimensional axial trace and related structures of the Sirius Passet fossils *Kerygmachela* and *Pambdelurion* are better interpreted as expressions of internal, permineralization-prone midgut glands than external lobopod-type body walls and legs (Butterfield, 2002). In the Chengjiang biota, most
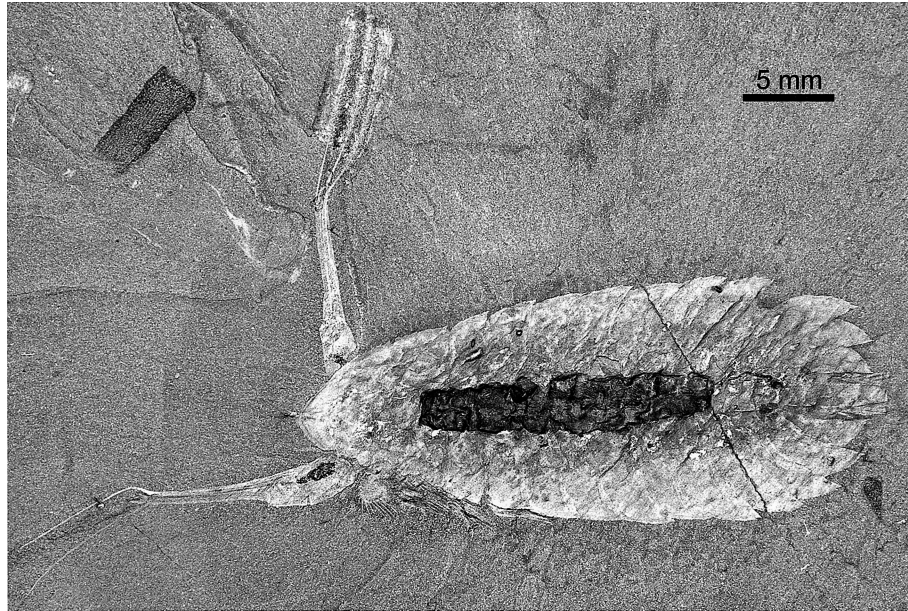
FIG. 4.   Bedding plane specimen of *Leanchoilia superlata* from the middle Cambrian Burgess Shale (Butterfield, 2002) showing characteristic flattening of degradation-resistant cuticle (original organic-carbon preservation) and three dimensional preservation of labile mid-gut glands (early diagenetic phosphatization). The juxtaposton of these two distinct taphonomic modes relates directly to their original histology, representing opposite ends of the histological/taphonomic spectrum.

of the three-dimensional structures have been correctly identified as gut traces (*e.g.,* in *Naraoia*, *Leanchoilia*, *Fuxianhuia*, *Clypecaris*, etc.) but, because they are now defined by clay minerals, have been mistakenly interpreted as evidence of a deposit-feeding habit, this despite the fact that such guts are functionally incompatible with a mud diet, and are accompanied by feeding apparatus clearly unrelated to such a mode of life (Butterfield, 2002). Such taphonomic/histologic resolution has obvious autecological, but also larger-scale evolutionary implications: by eliminating the only direct evidence of deposit feeding in the Cambrian, it is worth considering whether deposit feeding represents a relatively derived habit, perhaps not generally exploited until after the Cambrian (Butterfield and Jensen, 2001).

Taphonomic analysis may also contribute to the resolution of *Vetulicola*, a problematic Chengiang fossil that has recently been interpreted as a primitive deuterostome (Shu *et al.*, 2001). In overall form *Vetulicola* looks like an arthropod with an anterior, more or less bi-valved carapace, and a posterior segmented tail. Shu *et al.* (2001), however, consider these to be merely convergent with arthropods and focus instead on the five prominent paired structures borne by the anterior region, which they interpret as gills. Whether even a permissive character analysis (*cf.*, Peterson, 1995) supports a deuterostome affiliation remains to be seen, but it is useful to consider the taphonomy/histology of the various components of *Vetulicola*. For example, both the "bivalved" anterior carapace and segmented tail are preserved as flattened films and were clearly derived from recalcitrant non-mineralizing precursors; combined with their inter-segmental arthrodial membranes, they are indistinguishable from typical arthropod cuticle preserved in the Chengjiang. In conspicuous contrast, the five paired anterior structures are prominently preserved in three dimensions, which Shu *et al.* (2001, p. 421) interpret as essentially hollow structures variably filled with fine-grained "sediment." Such an interpretation, however, fails to account for their three-dimensional expression—any such infillings would have experienced the same *ca.* 10:1 compaction of the surrounding sediment, resulting in no substantial relief (Butterfield, 2002). The better explanation, as for the three-dimensionally preserved midgut glands, is that they represent early, pre-collapse, permineralizations (probably phosphatic) that were subsequently altered to clay minerals by intense weathering. This does not rule out the possibility that the anterior paired structures of *Vetulicola* might be gills—like midgut glands, they too might have been histologically prone to the attraction and precipitation of mineral ions. It does, however, suggest an alternative, more parsimonious interpretation, *i.e.,* that *Vetulicola* was an arthropod characterised not only by an arthropod-like cuticle and carapace, but also five serially repeated pairs of arthropod-like midgut glands.

CONCLUSION

Fossils provide the only direct record of ancient life, but there is limited value in treating all occurrences as comparable. Particularly in the case of exceptional preservation, fossilization is intimately related to original histology, ecology, depositional environment, and early diagenesis, all of which are known to have changed through time, and conspicuously so through the Proterozoic-Cambrian transition. Meaningful inter-

pretation of the fossil record thus requires the identification of contributing taphonomic pathways and their differential distribution in both time and space. By understanding the local controls on particular taphonomic pathways, it should be possible to assess the broader-scale significance of fossil data.

At one level, the topics of "exceptional preservation" and the "Cambrian explosion" are incompatible simply because they represent phenomena recorded at entirely different scales. By its very nature, exceptional preservation provides high resolved, but inevitably localised snapshots of standing diversity, whereas documentation of major evolutionary events requires abundant, widespread, statistically robust data. Even so, there is a marked correlation between the Cambrian explosion, as recorded by the robust data of shells, phytoplankton cysts and trace fossils, and exceptionally preserved biotas containing unambiguous, Phanerozoic-style metazoans. Taphonomic pathways yielding exceptional preservation are also encountered in the terminal Proterozoic, but here the identifiable metazoans appear to be of a fundamentally more primitive aspect, even when viewed through the same taphonomic window (*e.g.,* Doushantuo-type preservation). Insofar as the marked perturbations in taphonomic pathways associated with this Proterozoic-Cambrian transition were self-induced—a *consequence* of the biological innovations that define the Cambrian explosion—there is good reason to consider the abundance of metazoan diversity documented in Burgess Shale-type biotas as bona fide additions to marine ecosystems, and by extension, as early stem-group representatives of Phanerozoic clades (*cf.*, Budd and Jensen, 2000).

The real contribution of exceptional preservation, however, is the detail it provides at the much smaller, snapshot, scale, not so much defining the Cambrian explosion as filling in gaps left by the shelly and trace fossil records. Although never providing a complete view of local diversity, some exceptionally preserved biotas may offer a reasonable estimate, particularly given the regular recurrence of certain taxa in certain facies, such as occurs in Ediacara-type and Burgess Shale-type fossil assemblages. Differences within these facies-specific, taphonomically equivalent assemblages are potentially significant, though the underlying causes will require independent assessment. The absence of polychaetes or *Wiwaxia* in the Lower Cambrian Chengjiang biota, for example, may well be "real," but is this a function of evolution, biogeography, or merely local ecology? The answer lies in broader sampling, the perennial Achilles heel of exceptional preservation.

Recognition that different "tissue" types will follow distinct taphonomic pathways provides an important tool for interpreting problematic exceptionally preserved fossils, and a welcome corrective for what has become a litany of misinterpretation. In other words, any interpretation of a fossil structure must be taphonomically accountable—it must make taphonomic sense in the context of its original histology, depositional environment and geological history. For those who would recognise fossilized muscles or nerves, or gills or embryos, it is no longer sufficient to make claims from simple geometrical comparison. Exceptionally preserved fossils are more than just shapes in rocks and, when appreciated taphonomically, can yield exceptionally fine paleobiological resolution.

ACKNOWLEDGMENTS

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