BURGESS SHALE-TYPE PRESERVATION AND ITS DISTRIBUTION IN SPACE AND TIME

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ABSTRACT.—Burgess Shale-type fossil assemblages provide a unique record of animal life in the immediate aftermath of the so-called "Cambrian explosion." While most soft-bodied faunas in the rock record were conserved by mineral replication of soft tissues, Burgess Shale-type preservation involved the conservation of whole assemblages of soft-bodied animals as primary carbonaceous remains, often preserved in extraordinary anatomical detail. Burgess Shale-type preservation resulted from a combination of influences operating at both local and global scales that acted to drastically slow microbial degradation in the early burial environment, resulting in incomplete decomposition and the conservation of soft-bodied animals, many of which are otherwise unknown from the fossil record. While Burgess Shale-type fossil assemblages are primarily restricted to early and middle Cambrian strata (Series 2–3), their anomalous preservation is a pervasive phenomenon that occurs widely in mudstone successions deposited on multiple paleocontinents. Herein, circumstances that led to the preservation of Burgess Shale-type fossils in Cambrian strata worldwide are reviewed. A three-tiered rank classification of the more than 50 Burgess Shale-type deposits now known is proposed and is used to consider the hierarchy of controls that regulated the operation of Burgess Shale-type preservation in space and time, ultimately determining the total number of preserved taxa and the fidelity of preservation in each deposit. While Burgess Shale-type preservation is a unique taphonomic mode that ultimately was regulated by the influence of global seawater chemistry upon the early diagenetic environment, physical depositional (biostratinomic) controls are shown to have been critical in determining the total number of taxa preserved in fossil assemblages, and hence, in regulating many of the important differences among Burgess Shale-type deposits.

INTRODUCTION

Burgess Shale-type fossil assemblages provide, by far, the best records of the development of complex life on Earth following the "Cambrian explosion." Fossils from these deposits are the primary basis for understanding phylogenetic patterns of the Cambrian explosion, as well as patterns of morphological diversity and disparity of the Cambrian fauna (Conway Morris, 1989a; Wills et al., 1994; Budd and Jensen, 2000; Briggs and Fortey, 2005; Marshall, 2006; Erwin et al., 2011). Exceptionally preserved assemblages occur abundantly in early and middle Cambrian strata found worldwide (Conway Morris, 1989b; Allison and Briggs, 1993) and the Burgess Shale-type taphonomic pathway for the conservation of nearly complete soft-bodied fossil assemblages may have persisted into the early Ordovician (Van Roy et al., 2010). Burgess Shale-type preservation represents a unique and non-analogous taphonomic phenomenon that was widespread in Cambrian marine environments and largely disappeared from the marine rock record thereafter (Allison and Briggs, 1993; Butterfield, 1995).

BURGESS SHALE-TYPE PRESERVATION AS A TAPHONOMIC MODE

Preservation of soft-bodied fossils as carbonaceous remains

Most instances of soft-tissue preservation in the fossil record involve the replication of soft-tissues by minerals precipitated in the early burial environment (Briggs, 2003), by means of reactions under microbial control. Conversely, Burgess Shale-type preservation (Butterfield, 2003) represents the conservation of primary organic tissues as thin (<1 μm) carbonaceous films (Fig. 1), a pathway that requires suppression of the processes that typically lead to the
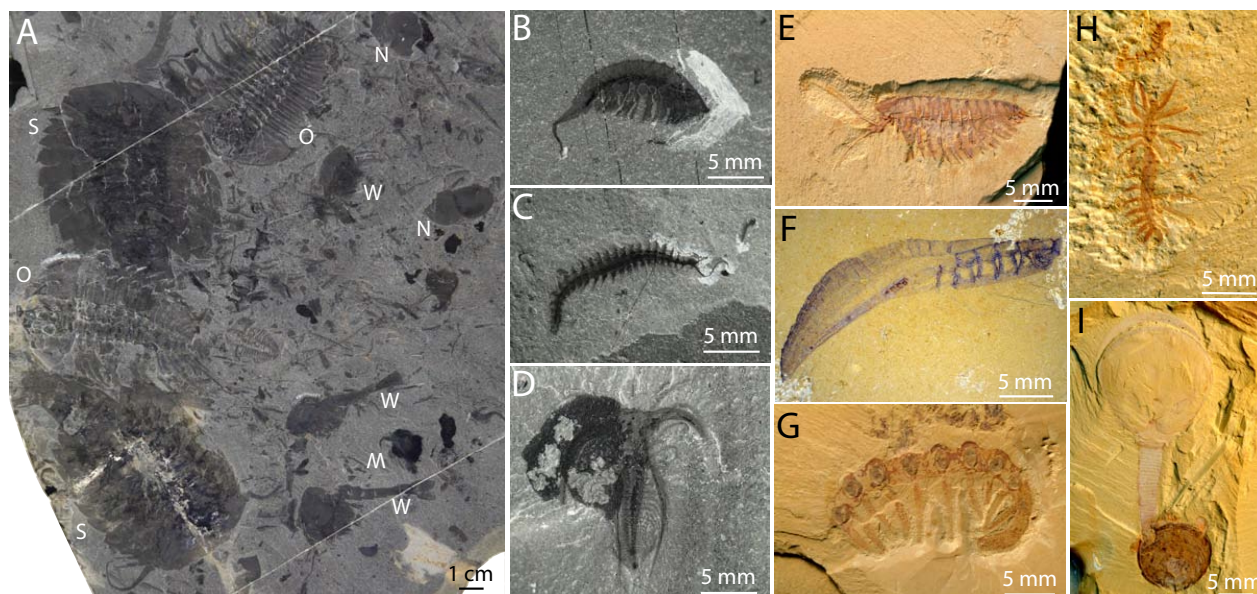
FIGURE *1*.—Examples of Burgess Shale-type fossils from the middle Cambrian (Series 3) Burgess Shale (A–D) and early Cambrian (Series 2) Chengjiang (E–I) biotas. A) Bedding-plane assemblage from the Walcott Quarry, Royal Ontario Museum, including the soft-bodied arthropods *Sydneyia inexpectans* (S), *Naroia compacta* (N), *Waptia fieldensis* (W), and *Marrella splendens* (M), and trilobite *Olenoides serratus* (O) with soft parts preserved in addition to mineralized carapace; ROM 57772. B, C) Soft-bodied fossils of the Marble Canyon assemblage (from Caron et al., 2014): B) *Molaria spinifera* (Arthropoda), ROM 62973; C) *Burgessochaeta* cf. *setigera* (*Polychaeta*), ROM 62972. D) *Marrella splendens* (Arthropoda), ROM 62969. E) *Leanchoilia illecebrosa* (Arthropoda). F) *Yunnanozoon lividum* (Chordata?). (G) *Microdictyon* (Lobopodia). H) *Luolishania longicruris* (Lobopodia). I) *Longtancunella chengjiangensis* (Brachiopoda). Images A–D courtesy of Jean-Bernard Caron, Royal Ontario Museum, E–I courtesy of Hou Xianguang, Yunnan University.

degradation of soft tissues. This means of preservation was first conclusively identified by Butterfield (1990, 1995), who isolated organic elements of Burgess Shale fossils by maceration in HF. Contradictory findings were soon reported by Orr et al. (1998), who used in-situ analysis by electron microprobe to determine the elemental composition of two Burgess Shale arthropods. Elemental maps revealed that the fossils are comprised of templates of aluminosilicate minerals that, importantly, vary in composition among discrete anatomical aspects of fossils, with carbonaceous remains also present. On this basis, Orr et al. (1998) interpreted that the primary means of fossil preservation in the Burgess Shale was replacement of soft tissues by clay minerals shortly after burial. However, evidence for a late metamorphic origin of aluminosilicate coatings associated with Burgess Shale fossils was provided by Butterfield et al. (2007). Elemental mapping was used in combination with petrographic and textural (e.g. cross-cutting relationships) observations to demonstrate that replacement of Burgess Shale fossils by aluminosilicates occurred during greenschist facies metamorphism of the Burgess Shale (Powell, 2003), and not during early diagenesis; thus, aluminosilicification was not involved in the original preservation of the biota (Butterfield et al., 2007). This case was supported by observations of late-stage aluminosilicification of trilobite carapaces and of calcitic veins that crosscut the samples, as well as by the presence of metamorphically derived aluminosilicates as coatings on Carboniferous ferns (Butterfield et al., 2007) and Ordovician–Silurian graptolites (Page et al., 2008) that also were originally preserved as carbonaceous compressions. Tissue-specific variation in the elemental composition of aluminosilicate templates was verified as resulting from metamorphic, rather than early diagenetic processes (Page et al., 2008). These investigations revealed that aluminosilicification of carbonaceous fossil remains is an expected product of metamorphism of mudstones. More importantly, they demonstrated that the original pathway of extraordinary preservation in the Burgess Shale was the conservation of carbonaceous organic remains.

Burgess Shale-type preservation, originally

defined by Butterfield (1995, p. 1) as the preservation of "carbonaceous compressions in fully marine sediments," is now understood to be the primary mode of preservation in the great majority of Cambrian Lagerstätten found worldwide (Gabbott et al., 2004; Hu, 2005; Gaines et al., 2008; Forchielli et al., 2014). Although carbonaceous preservation occurs throughout the fossil record, later Phanerozoic marine examples typically include only selected refractory tissues (although see Liu et al., 2006; von Bitter et al., 2007) such as those of algae, plants, and graptolite or eurypterid cuticle (Butterfield, 1995), and do not compare to Burgess Shale-type preservation in either anatomical detail or in faunal diversity that is captured in carbonaceous remains. The prevalence of this taphonomic pathway in Cambrian strata (Allison and Briggs, 1993) requires widespread, similar, favorable chemical conditions and physical depositional environments in early Phanerozoic continental seaways (see below).

Auxiliary mineralization of selected soft tissues

Mineralization of selected tissues may occur in association with carbonaceous remains of Burgess Shale-type fossils. While mineral replacement of soft tissues sometimes preserves anatomical detail that would otherwise be lost, mineralization is auxiliary to the primary carbonaceous taphonomic mode at the scale of individual fossils. The most important pathways of selective soft tissue mineralization in Burgess Shale-type fossils are replacement by calcium phosphate (see Schiffbauer et al., 2014**)** and by pyrite **(**see Farrell, 2014).

Phosphatization is primarily restricted to guts, in particular those of arthropods, in which digestive glands are sometimes preserved (Butterfield, 2002). Precipitation of phosphate minerals in these fossils is problematic. While the gut tracts of particular animals provided chemical microenvironments that favored the precipitation of phosphate (e.g., Butterfield, 2002; Lerosey-Aubril et al., 2012), mass-balance considerations imply the necessity of an additional source of P from outside the gut. This source is difficult to account for in the typically organic-poor sediments in which Burgess Shale-type preservation occurs (Gaines et al., 2012c). This auxiliary pathway, however, exhibits a strong taxonomic selectivity and occurs overall in relatively few genera, suggesting that originally high concentrations of phosphate in the gut glands or in the diet of these taxa may have been important to phosphate mineralization (Butterfield, 2002; Lerosey-Aubril et al., 2012). Phosphatization of gut anatomy is common within some taxa, e.g., *Leanchoilia* (Butterfield, 2002), but it is not ubiquitous in any taxon.

Limited pyritization of aspects of soft-bodied fossils is most common in the Chengjiang deposit (Gabbott et al., 2004), but has been reported in rare examples from the Burgess Shale and elsewhere (e.g., García-Bellido and Collins, 2006). Precipitation of sedimentary pyrite during early diagenesis occurs in anaerobic sediments as a byproduct of microbial reduction of iron and sulfate during organic decomposition (Berner, 1984; Raiswell and Berner, 1986). During iron reduction, Fe(III), derived largely from Fe-oxides and oxyhydroxides, is used as a terminal electron acceptor and is reduced to Fe(II), which is liberated to solution where it may react with sulfide compounds generated by microbial sulfate reduction to form Fe-sulfides (e.g., Canfield et al., 1992). Pyritization of soft tissues (see Farrell, 2014) is favored by low organic carbon content of sediments, which serves to localize microbial reactions around fossil carcasses (Briggs et al., 1991, 1996; Raiswell et al., 2008; Farrell et al., 2013). While this is consistent with the sediments of Burgess Shale-type deposits, pyritization in these deposits was limited in its extent due to strongly reduced availability of SO_4^{2-} in the early burial environment, as indicated by $\delta^{34}S$ of sedimentary pyrite (Gaines et al., 2012c), described below. As a result, when pyrite is present in Burgess Shale-type fossils, it is frequently concentrated around soft tissues that are especially labile (Gabbott et al., 2004) and served as nuclei for early microbial activity.

Pyritization of aspects of soft-bodied fossils is most common in the Chengjiang deposit (Gabbott et al., 2004). However, the extent of early pyritization in Chengjiang fossils has proven difficult to assess due to extensive weathering under a humid, monsoonal climate, which has substantially altered the primary composition of the host rocks and the Chengjiang fossils to a depth of ~20 m (Gaines et al., 2012c; Ma et al., 2012; Forchielli et al., 2014). A comprehensive analysis of the effects of weathering on the Chengjiang fossils was undertaken by Forchielli et al. (2014), who characterized the elemental composition of fossils and the mineralogic and chemical composition of the host mudstones across a weathering gradient. The results of this

study confirmed earlier suggestions (Hu, 2005; Forchielli et al., 2012) that pyritization in Chengjiang fossils was limited to discrete anatomical aspects, and verified the dominance of carbonaceous preservation in unweathered specimens. With weathering, Chengjiang fossils were shown to progressively lose carbon and to acquire coatings of Fe-oxides derived from the oxidation of pyrite in the enclosing mudstones (as evidenced by the loss of S) and resulting from the redistribution of Fe along voids and cracks, including those associated with Burgess Shale-type fossils (Forchielli et al., 2014). Thus, the characteristic reddish aspect of Chengjiang fossils (Fig. 1E–I) resulted from alteration accompanying weathering rather than from a different taphonomic pathway, such as the growth of thin pyrite envelopes around carcasses. In the unweathered condition, Chengjiang fossils closely resemble the appearance of those from the Burgess Shale and elsewhere (Forchielli et al., 2014). These findings underscore the importance of fresh, unaltered fossil material for the accurate assessment of taphonomic mode in exceptionally preserved fossils.

Burgess Shale-type preservation: definition

Although other auxiliary modes of preservation may occur in association within fossils primarily preserved via Burgess Shale-type preservation, these modes occur rarely, and predominantly in specific anatomical attributes of a minority of taxa (Butterfield, 2002; Gabbott et al., 2004; García-Bellido and Collins, 2006; Lerosey-Aubril et al., 2012). A small number of deposits dominated by Burgess Shale-type preservation also contain examples of soft-bodied preservation within concretions (Schwimmer and Montante, 2007; Van Roy and Briggs, 2011; Gaines et al., 2012a), a wholly different means of preservation (see McCoy, 2014). However, concretions and other modes of exceptional preservation do not occur in the same beds in which Burgess Shale-type preservation occurs. Here, the term "Burgess Shale-type preservation" is used to define occurrences of exceptional preservation of soft-bodied fossils as primary carbonaceous remains as originally defined by Butterfield (1995, 2003). This mode of preservation was widespread in early and middle Cambrian epicratonic seaways, and often occurs pervasively across large stratigraphic intervals (10s of meters) in many of the deposits in which it occurs. The term "Burgess Shale-type fauna" has generally been used in the literature to refer to the global soft-bodied fauna of the Cambrian, including members of which that are represented in younger Lagerstätten (e.g., Conway Morris, 1989b). While Burgess Shale-type faunas are overwhelmingly represented by Burgess Shale-type preservation, a specific mode of preservation is not implied by this term, which is herein avoided for clarity.

BURGESS SHALE-TYPE DEPOSITS: A GLOBAL EARLY PHANEROZOIC PHENOMENON

Burgess Shale-type deposits: definition

In this paper, the term 'Burgess Shale-type deposit' is used to refer to bodies of sedimentary rock that contain exceptional biotas preserved via Burgess Shale-type preservation as defined above. While the Burgess Shale biota occurs globally (Conway Morris, 1989b), the original taphonomic mode of exceptional biotas at a few localities is presently uncertain due to extensive metamorphism and/or weathering, which has substantially altered the primary composition of soft-bodied fossils. These include most prominently the early Cambrian Emu Bay Shale (Briggs and Nedin, 1997; Lee et al., 2011) and Sirius Passet (Budd, 2011) deposits. While the overall mode of preservation as two-dimensional compression fossils is superficially similar, early and/or late diagenetic mineralization is also particularly prominent in these two deposits (Briggs and Nedin, 1997; Budd, 2011; Paterson et al., 2011), and the degree to which Burgess Shale-type preservation was involved in fossilization, if at all, is unclear. Therefore, the Emu Bay and Sirius Passet deposits are explicitly excluded from considerations of the circumstances of Burgess Shale-type preservation that follow here, as are all other deposits for which the mode of original preservation remains ambiguous, such as the late Cambrian Weeks Formation (Lerosey-Aubril et al., 2013).

A few prominent deposits of Ediacaran age also contain algal and problematic fossils preserved in whole (Zhu et al., 2008; Xiao et al., 2013; Wang et al., 2014) or in part (Cai et al., 2012) as carbonaceous compressions, and older Proterozoic examples also occur (Butterfield, 1995; Gaines et al., 2008). At present, the depositional and early diagenetic settings of these deposits have not yet been comprehensively investigated, and therefore, these Precambrian

examples of carbonaceous preservation are also excluded from discussion herein. It should be noted, however, that investigation of these deposits represents a promising avenue for further research.

Distribution of Burgess Shale-type deposits in the Early Phanerozoic

It has long been recognized that Cambrian strata are unusually enriched in soft-bodied biotas, even when rock volume is taken into account (Allison and Briggs, 1993). This apparent "taphonomic window" has been the subject of much interest over the last two decades (Aronson, 1993; Allison and Briggs, 1993, 1994; Butterfield, 1995, 2003; Brasier and Lindsay, 2001; Orr et al., 2003; Gaines et al., 2005, 2012b,c). Although several modes of exceptional preservation occur in early Phanerozoic strata, including most prominently Orsten-type preservation (Walossek and Müller, 1998; Zhang et al., 2007b) as well as Ediacaran-like preservation (Hagadorn et al., 2002; Alessandrello and Bracchi, 2003), the signal of the taphonomic window is, by far, dominated by Burgess Shale-type deposits (Conway Morris, 1989b; Allison and Briggs, 1993). The underlying causes of this greatly enhanced Cambrian fossil record and its limitation in time and space may be determined only through a process-based understanding of Burgess Shale-type preservation.

The number of Burgess Shale-type deposits presently known from Cambrian strata is difficult to estimate, but certainly exceeds 50 deposits, primarily of early and middle Cambrian (Series 2–3) age. Conway Morris (1989b) provided a compilation of Burgess Shale-type deposits, but intensive research in recent decades has resulted in the discovery of dozens of new localities (Lieberman, 2003; Steiner et al., 2005; Caron et al., 2010, 2014; Kimmig and Pratt, 2013), and a more recent compilation has not yet been provided. In such a future compilation, it would be useful to distinguish Burgess Shale-type preservation from other modes of preservation using data on taphonomic mode now available for many of the deposits. It would also be useful to tabulate by formation as well as by individual locality within each formation (Conway Morris, 1989b), owing to geographically widespread exceptional preservation that occurs at many sampled localities within many of the individual formations (e.g., Fletcher and Collins, 1998, 2003; Hu, 2005; Gaines and Droser, 2010; Caron et al., 2010, 2014).

The most prominent feature of the Allison and Briggs (1993) compilation was the sharp decline in exceptional preservation following the middle Cambrian, inferred to signify the closure of the early Phanerozoic taphonomic window. However, the discovery of Burgess Shale-type fossils within a small number deposits of late Cambrian (Series 4) age (Vaccari et al., 2004; García-Bellido and Aceñolaza, 2011) suggests that the Burgess Shale-type window remained open while facies favorable to preservation exhibit a sharp decline in the sedimentary records of most paleocontinents (Gaines et al., 2013).

The early Ordovician Fezouata biota of Morocco (Van Roy et al., 2010) is perhaps the most important new soft-bodied assemblage to be reported from early Phanerozoic strata in recent decades. Both Burgess Shale taxa and those typical of the later Ordovician are represented in its abundant and diverse faunas. Fezouata soft-bodied fossils are characteristically strongly weathered (Van Roy et al., 2010), and although the primary taphonomic pathway remains unclear, the mode of preservation of Fezouata fossils superficially appears to be consistent with Burgess Shale-type preservation. If the Fezouata deposit indeed is a Burgess Shale-type deposit, then this pathway must have persisted across the Cambrian and into the early Ordovician. This possibility is taken into account in the discussion that follows.

Were Burgess Shale-type biotas 'burrowed away?'

In their 1993 analysis of trends in exceptional preservation across the Phanerozoic, Allison and Briggs advanced the hypothesis that exceptionally preserved biotas were 'burrowed away' from the post-Cambrian sedimentary record (Allison and Briggs, 1993; Orr et al., 2003) as a result of increasing sediment mixing by infaunal organisms (Droser and Bottjer, 1988, 1989). Aronson (1993) modeled the increases in depth and extent of bioturbation that would be required to account for the decline in exceptional preservation, and considered such increases to be far larger than those observed across the early Paleozoic. This finding is in agreement with detailed ichnologic observations from Cambrian strata (Tarhan and Droser, 2014).

Other work has suggested that the settings of Burgess Shale-type deposits likely rendered large portions of the deposits invulnerable to

TABLE *1*.—A proposed rank classification of Burgess Shale-type deposits.

	Total Number of Soft-Bodied taxa	Fidelity of Soft-Bodied Preservation	Abundance of Soft-Bodied Fossils	Examples
Tier 1	> 100 taxa Large % Endemic	High: eyes, guts, limbs, etc. common	High	Burgess, Chengjiang
Tier 2	< 100 taxa Small % Endemic	Intermediate: carapace and algal/bacterial fossils dominant	Intermediate: (Range: Low–High)	Guanshan, Kaili, Marjum, Spence
Tier 3	< 10 taxa	Low: carapace, cuticle, algal/bacterial fossils only	Low	Latham, Indian Springs, Zawiszyn

bioturbation. Paleoenvironmental data from Burgess Shale-type deposits has confirmed that Burgess Shale-type preservation is strongly favored under anoxic benthic conditions, which exclude the possibility of bioturbation (Gaines and Droser, 2010). While bioturbation clearly limited the extent of Burgess Shale-type preservation in Cambrian strata (Allison and Brett, 1995), a post-Cambrian increase in bioturbation would not have affected preservation potential in the two most important deposits. Because the fossil-bearing intervals of the Chengjiang and the Walcott Quarry member of the Burgess Shale were deposited in whole or in large part under sustained anoxic conditions, which are not susceptible to sediment mixing by bioturbation, preservation potential in comparable settings later in the Phanerozoic would not have been affected (Gaines et al., 2012b, references therein). These results imply that other controls were responsible for limiting Burgess Shale-type preservation and its distribution in time.

A proposed rank classification of Burgess Shale-type deposits

Burgess Shale-type deposits share a common mode of preservation, yet they are not equally informative. As has been long recognized (Conway Morris 1989a, b; Hagadorn, 2002), the deposits encompass a broad spectrum of abundance, number of preserved taxa, and quality of soft-bodied preservation, yet there has been no formal attempt to rank or classify the deposits. For the purposes of this contribution, I propose a three-tier classification scheme to group Burgess Shale-type deposits according to their overall paleontological importance (Table 1).

Because the total number of known soft-bodied taxa, or taxonomic richness, is the critical feature that determines each deposit's contribution to understanding phylogenetic patterns and morphological disparity of the Cambrian biota (Conway Morris, 1989a; Briggs et al., 1992; Budd and Jensen, 2000; Marshall, 2006; Erwin et al., 2011), total number of soft-bodied taxa is the most important criterion for classifying the deposits. Because the total number of taxa preserved in Burgess Shale-type fossil assemblages is often correlated with the fidelity of preservation, especially of labile (non-cuticle) tissues, classification of the deposits into three tiers is straightforward, and provides useful insight into important differences among the deposits, as discussed below. It must be emphasized, however, that this classification is based on total sum of soft-bodied taxa presently known from each of the deposits and does not attempt to account for rock volume, sampling intensity, or collection bias. Especially given that collection efforts have varied widely among the deposits, any deposit has the potential to rise from one tier to the next with increased collection or the discovery of new localities. It is also important to note that within individual deposits, fossil density and fidelity of preservation vary widely by stratigraphic horizon as well as by locality, for reasons considered below. This simplistic classification scheme is therefore intended only to provide a framework for considering the prominent first-order differences among the deposits.

Tier 1 deposits.—These include only the Burgess Shale and Chengjiang, which are distinguished by an exceptionally high taxonomic richness (>100 taxa) of soft-bodied fossils that clearly separates them from other Burgess Shale-

type deposits (Briggs et al., 1994; Hou et al., 2008). The high taxonomic richness captured in these two deposits is presumably due in part to the consistently high fidelity of preservation, found in many intervals, of labile anatomical features (e.g., eyes, gills, neural tissue), which are comprised of the tissues most readily lost to decomposition in the early burial environment (Fig. 1; Briggs et al., 1994; Hou et al., 2008; Sansom et al., 2010; Caron et al., 2014; Ma et al., 2012, 2014). Therefore, the preservation potential for organisms lacking robust organic cuticle was optimized in these two deposits, and the potential for preservation bias among taxa was minimized. Preservation of soft-tissue in taxa that possessed mineralized skeletons, most prominently trilobites and brachiopods, is common in the Tier 1 assemblages, but occurs only rarely in subordinate deposits.

Richness of the assemblages is also related to the density of fossils in each deposit. Absolute abundance of soft-bodied fossils per unit volume of rock is far greater in the Walcott Quarry and Marble Canyon assemblages of the Burgess Shale than at any Chengjiang locality (Caron and Jackson, 2006, 2008; Zhao et al., 2009; Caron et al., 2014). However, Burgess Shale fossil assemblages occur most prominently in concentrations that are localized at the front of the Cathedral escarpment (see below; Aitken, 1971, 1997; Collins et al., 1983; Fletcher and Collins, 1998, 2003; Caron et al., 2014). By comparison, fossil assemblages at Chengjiang are considerably less abundant, with the exception of 'cluster' assemblages dominated by single taxa (Hu, 2005; Zhao et al., 2009). Furthermore, Chengjiang fossils are found across a much larger geographic area in relatively continuous outcrop (Hu, 2005). Fossils occur in soft, weathered rock that is easily worked by hand tools, and has been intensively collected by a number of research groups since its discovery in 1984 (Hou et al., 2008), resulting in an exceptionally high number of soft-bodied taxa, although sampling biases are prominent (Zhao et al., 2012).

Tier 2 deposits.—These deposits, characterized by an intermediate richness of soft-bodied taxa (10–100 taxa), include the great majority of reported Burgess Shale-type deposits, most prominently including the Kaili (Series 2–3), Guanshan (Series 2), Nuititang (Series 1–2), Balang (Series 2), and Tsinghsutung (Series 2) deposits of South China (Peng et al., 2005; Steiner et al., 2005; Zhao et al., 2005; Hu et al.,

2010; Sun et al., 2013), and the Mount Cap (Series 2), Pioche (Series 2–3), Spence (Series 3), Wheeler (Series 3), and Marjum (Series 3) deposits of Laurentia (Robison, 1991; Butterfield, 1994; Lieberman, 2003; Briggs et al., 2008). Preservation of anatomical detail in macrofossils is typically subsidiary to that found in Tier 1 deposits, and preservation is most often restricted to relatively robust anatomical tissues such as arthropod and worm cuticle, and algae, although important exceptions to this generalization do occur in Tier 2 deposits (Zhao et al., 2005; Briggs et al., 2008). Maximum taxonomic richness of individual beds is low compared to the richest beds of the Tier 1 deposits (Caron and Jackson, 2006, 2007; Zhao et al., 2009), and abundance of soft-bodied fossils in individual beds ranges from low to high; possible influences on this pattern are considered below.

Tier 3 deposits—Tier 3 deposits are distinguished by low richness (<10 taxa) of soft-bodied faunas, which characteristically are known only from isolated occurrences of individual soft-bodied fossils, typically represented by arthropod and worm cuticle or algae. Examples of Tier 3 deposits include the Kinzers, Parker, Latham, and Indian Springs deposits of Laurentia (Series 2; Conway Morris, 1989b; Gaines and Droser, 2002; Skinner, 2005; English and Babcock, 2010) and the Zawiszyn deposit of Baltica (Series 2; Conway Morris, 1989b). Burgess Shale-type preservation is quite rare in most Tier 3 deposits, suggesting that conditions favorable to fossilization were present only infrequently during their accumulation, and that the number of soft-bodied taxa is unlikely to rise substantially with future collection (e.g., Latham, Indian Springs). In other deposits, however, the total number of soft-bodied taxa appears to be limited by exposure (e.g., Kinzers, Zawiszyn), and could rise with future exploration.

THE TAPHONOMIC PATHWAY FOR BURGESS SHALE-TYPE PRESERVATION

History of research

Rapid burial and anoxia.—It has long been recognized that rapid burial is an important limiting requirement for exceptional preservation in Burgess Shale-type deposits and elsewhere (e.g., Whittington, 1971; Piper, 1972; Conway Morris, 1986), and event-driven sedimentation of fossil-bearing horizons has been confirmed for all deposits that have been investigated to date (Zhu

et al., 2001; Caron and Jackson, 2006; Gabbott et al., 2008; Zhao et al., 2009; Gaines et al., 2011, 2012c; Caron et al., 2014). Because most Burgess Shale-type deposits are characterized by exclusively fine-grained sediments, event-driven deposition must be established using sediment microfabric and lateral facies associations (Gaines et al., 2011, 2012c). Prominent grading in beds bearing Burgess Shale-type fossils occurs consistently at Chengjiang, where partial turbidite sequences are recognized (Zhu et al., 2001; Hu, 2005), as well as in other subordinate deposits (e.g., Gaines and Droser, 2002). Exceptionally preserved fossils typically occur within discrete event beds, rather than at bed junctions, as would be expected if smothered in situ on the seafloor (Gaines and Droser, 2010; Gaines et al., 2012c). Although examples of in-situ burial at bed junctions are present in some deposits (e.g., Gaines and Droser, 2005), such cases appear to be rare.

Early research on the preservation of the Burgess Shale biota emphasized the role of benthic anoxia in slowing the decomposition of fossils in the early burial environment (e.g., Conway Morris, 1986). This conclusion requires that fossil assemblages were in large part transported across a chemocline that separated habitable benthic environments from adjacent anoxic environments, characterized by Conway Morris as the 'pre-slide' and 'post-slide' environments (Conway Morris, 1986). This interpretation is supported by the orientations of fossils relative to bedding within event-deposited beds (Whittington 1971; Zhang et al., 2006; Zhang and Hou, 2007; Caron et al., 2014). Experimental work has confirmed that freshly killed soft-bodied arthropods can withstand such transport without fragmentation (Allison, 1986), which is in line with taphonomic evidence (Caron and Jackson, 2006; Zhang et al., 2006; Zhang and Hou, 2007).

While rapid burial in close proximity to a sharp chemocline has been demonstrated for Tier 1 deposits and many of the Tier 2 deposits (Allison and Brett, 1995; Gaines and Droser, 2003, 2005, 2010; Gostlin, 2006; Gabbott et al., 2008; Gaines et al., 2012b), experimental data and observations from modern settings indicate that anoxia alone is insufficient to cause Burgess Shale-type preservation (Henrichs and Reeburgh, 1987; Allison, 1988; Butterfield, 1990, 1995; Lee, 1992). Therefore, anoxia in the early benthic environment is considered a necessary but insufficient prerequisite for Burgess Shale-type preservation (Allison, 1988; Butterfield, 1990; Gaines and Droser, 2010), as is rapid burial. The preservation of Burgess Shale-type assemblages worldwide was facilitated in part by widespread anaerobic conditions in Cambrian epicontinental seas (e.g., Gill et al., 2011), but this condition is not unique to the early Paleozoic rock record, and therefore it cannot account for the taphonomic window.

Preservation of Burgess Shale-type fossils as carbonaceous remains necessitates either the special protection of organic material from the normal processes of microbial decomposition or the large-scale suppression of those processes within sediments of the early burial environment (Gaines et al., 2008).

The clay mineral hypothesis.—The first hypothesis to account for Burgess Shale-type preservation was offered by Butterfield (1995), who proposed that preservation occurred via clay mineral-organic interactions. Recognizing that some highly reactive clay mineral species have the capacity to limit microbial activity by direct adsorption of enzymes involved in organic decomposition, Butterfield proposed that unusually reactive clay minerals, such as Fe or Mg-rich smectites, were common in Cambrian sedimentary environments. This possibility was discounted by Powell (2003), who used whole-rock geochemistry to determine that the primary clay mineral assemblage present in the Burgess Shale was not unusual, as has also been confirmed for the Chengjiang (Forchielli et al., 2014) and several Tier 2 deposits (Curtin and Gaines, 2011). Experimental work (Wilson, 2006) has suggested a possible role for the clay mineral kaolinite in polymerization of some organic tissues, increasing their resistance to decay. However, geochemical studies of Burgess Shale-type sediments show that kaolinite comprised only a small fraction of the primary clay mineral assemblage, if kaolinite was present at all (Powell, 2003; Curtin and Gaines, 2011, Forchielli et al., 2014).

The Fe-adsorption hypothesis.—Another hypothesis for protection of organic fossils from the normal processes of microbial decay was suggested by Petrovich (2001), who proposed that adsorption of Fe(II) onto chitin and other biopolymers led to degradation resistance. In this view, fossils were physically armored against the action of microbial enzymes by coatings of Fe(II), suggested to have adsorbed selectively onto fossil

tissues from solution in the anoxic early burial environment. Subsequent elemental mapping of fossils from a number of deposits, however, has excluded a systematic association of Fe with organic remains in unweathered fossil material (Hu, 2005; Gaines et al., 2008; Forchielli et al., 2014). While secondary Fe-oxide coatings resulting from oxidative weathering of sedimentary pyrite are commonly associated with weathered specimens from a majority of the deposits, it has been demonstrated that Fe was not involved in Burgess Shale-type preservation except through limited pyritization of discrete anatomical aspects of some specimens (Butterfield, 2009; Forchielli et al., 2014).

Inhibition of decay by early sealing of the burial environment.—Preservation by early suppression of microbial activity in the sediments was hypothesized by Gaines et al. (2005), and subsequently supported by geochemical and petrographic data from a broad survey of Burgess Shale-type deposits, including both Tier 1 deposits and six of the most important Tier 2 deposits (Gaines et al., 2012c). Preservation as carbonaceous remains was determined to have resulted from a three-step process that involved: 1) limited transportation of fossils and rapid burial in exclusively fine-grained, clay-rich sediments; 2) low concentrations of sulfate in the global ocean and low concentrations of oxygen at the sites of burial, which limited the pace of microbial degradation; and 3) early sealing of the burial environment by pervasive carbonate cements at bed tops, which further restricted the diffusion of oxidants required to sustain organic decomposition and ultimately resulted in the conservation of fossils as primary organic remains (Gaines et al., 2012c). These steps are described in detail below. Important differences in taxonomic richness and in the fidelity of preservation among the Burgess Shale-type biotas found globally are shown to result primarily from variations in the conditions surrounding steps 1 and 2.

Physical depositional settings of Burgess Shale-type deposits

Burgess Shale-type deposits occur with greatest frequency in outer-shelf environments that lay near the seaward margins of expansive carbonate platforms, including the "outer detrital belt" of Laurentia (Robison, 1960), and comparable settings of other paleocontinents. These deposits represent mixed siliciclastic-carbonate ramp settings that accumulated on low-angle slopes (Rees, 1986; Liddell et al., 1997; Elrick and Snider, 2002; Brett et al., 2009; Halgedahl et al., 2009; Gaines et al., 2011). Notably, both the Walcott Quarry and Marble Canyon localities of the Burgess Shale and the multiple localities of the Chengjiang deposit represent exceptions to this pattern. The Burgess Shale was deposited at the edge of a carbonate platform; however, it occurs in direct association with the Cathedral Escarpment, a prominent break in submarine topography that provided a steep local slope (Aitken, 1971, 1997; Fletcher and Collins, 1998, 2003; Caron et al., 2014). A minority of Burgess Shale-type deposits, including the Chengjiang, are not associated with a carbonate platform, but instead lie offshore of broad clastic shelves (Zhu et al., 2001; Gaines and Droser, 2002).

Most Burgess Shale-type deposits occur >100 km from the paleo-margin of continental crust, and the inland nature of the connection between these environments and the global ocean is unclear. Many prominent deposits, such as the Chengjiang (Zhu et al., 2001; Hu, 2005) and the Wheeler and Marjum deposits (Rees, 1986), are interpreted to have accumulated in actively subsiding local basins with complex regional submarine topography. In these settings, as well as those of epicratonic seas more broadly, restricted circulation with the open ocean may have been an important factor in promoting and sustaining anoxia in deeper water masses (e.g., Peters, 2009). Early Paleozoic epicratonic seas may have been further vulnerable to restricted circulation by means of thermal stratification due to the low latitude configuration of landmasses (Brasier and Lindsay, 2001) and the Phanerozoic maximum in pCO$_2$ that spans this interval (Berner, 2006).

The frequency and stratigraphic extent of Burgess Shale-type preservation varies widely among the deposits and among localities within them. In some cases, Burgess Shale-type preservation occurs consistently across meters of continuous section, while in others, preservation is confined to narrow (mm-scale) stratigraphic intervals (Gaines and Droser, 2010). The specific stratigraphic intervals that contain Burgess Shale-type preservation worldwide share two fundamental aspects of the physical depositional environment: 1) accumulation below (or near) maximum Storm Wave Base (SWB); and 2) rapid, event-driven deposition of a clay-dominated size

fraction from bottom-flowing density currents (Zhu et al., 2001; Gabbott et al., 2008; Gaines and Droser, 2010; Gaines et al., 2012c). Depositional regimes that prevailed at each setting during deposition of Burgess Shale-type intervals permitted nearly 100% accumulation in the near (Chengjiang) or complete absence (most others) of scour or reworking (Zhu et al., 2001, Hu, 2005; Gaines and Droser, 2005, 2010; Zhao et al., 2009; Gaines et al., 2012c). Within this broadly similar depositional context, significant variation in the physical magnitude of individual depositional events is prominent in the Burgess Shale and in the Chengjiang. Tier 2 and 3 Burgess Shale-type deposits are comprised of event-deposited claystone laminae that are millimeters in thickness (Gaines and Droser, 2002, 2010; Gaines et al., 2011, 2012c). By comparison, the thickness of individual event-deposited claystone beds ranges up to 8 cm in thickness in the Burgess Shale (Gabbott et al., 2008; Caron et al., 2014), and may exceed 10 cm at Chengjiang, where in a minority of cases, the D–E portion of the turbidite succession is present (Zhu et al., 2001; Zhao et al., 2009). As all evidence suggests, if physical depositional energy may be reliably assumed to correspond to bed thickness, then the Tier 1 deposits may be clearly distinguished from all subordinate deposits by the presence of elevated depositional energy. Thus, the efficiency of transportation of fossil assemblages appears to have been the critical factor that set Tier 1 Burgess Shale-type assemblages apart from the other deposits. Similar evidence for enhanced physical energy is also present in the early Ordovician Fezouata deposit, although its status as a Burgess Shale-type deposit is unclear.

It must also be noted that the physical depositional conditions shared among Burgess Shale-type intervals of the deposits are widespread in the Phanerozoic rock record. Although Burgess Shale-type preservation is restricted to specific depositional settings that promoted limited transport and rapid burial of soft-bodied fossils in claystone sediments, other factors were ultimately responsible for exceptional preservation.

Paleo-redox settings of Burgess Shale-type deposits

The benthic settings represented in Burgess Shale-type deposits are characterized by oxygen deficiency, and range from sustained anoxia to deposition near a fluctuating oxycline with high-frequency oscillation between anoxic and dysoxic conditions (Gaines and Droser, 2010, Gaines et al., 2012b). The use of geochemical proxies to delineate benthic redox conditions in Burgess Shale-type deposits is complicated by several factors. Because most geochemical redox proxies are based upon the concentrations of redox-sensitive elements delivered from an anoxic water column to the sediments (e.g., Poulton and Canfield, 2005; Tribovillard et al., 2006), these proxies are most effective when sedimentation is slow and relatively continuous, and sediments are overlain by a thick anoxic water mass. Neither is the case for Burgess Shale-type deposits. Event-driven sedimentation, which characterizes all Burgess Shale-type deposits (see above), acted to dilute any signal of Fe or trace-element enrichment (Hammarlund, 2007), as also observed in other settings (e.g., Farrell et al., 2013). Furthermore, the prevalence of near-bottom anoxia in Burgess Shale-type deposits, as interpreted from paleontological, ichnologic, and taphonomic evidence (Gaines and Droser, 2005, 2010; Garson et al., 2012), indicates that the sites of deposition were not overlain by thick anoxic water masses. This interpretation suggests that Fe and trace-element enrichments should not be expected (Gaines and Droser, 2010).

Despite the lack of a clear geochemical proxy for reconstructing paleoredox environments of Burgess Shale-type deposits, the presence, depth and intensity of bioturbation can provide a useful means of assessing relative oxygen concentrations within the deposits (Gaines and Droser, 2005, 2010; Gaines et al., 2012b). Burgess Shale-type deposits all contain intervals that are not bioturbated as well as those in which shallow (<10 mm), low-intensity bioturbation is prevalent (Allison and Brett, 1995; Gaines and Droser, 2003, 2005, 2010; Dornbos et al., 2005; Gostlin, 2006; Gabbott et al., 2008; Gaines et al., 2011, 2012b, Mángano, 2011; Garson et al., 2012; Minter et al., 2012). These two types of settings occur in greatly different proportions among and within Burgess Shale-type deposits, and frequently occur interbedded in repeated, close (mm-scale) association.

While the co-occurrence of bioturbation and Burgess Shale-type preservation in individual beds is known from numerous examples (Wang et al., 2004; Zhang et al., 2007a; Gaines and Droser, 2010; Lin et al., 2010; Gaines, 2011; Mángano, 2011; Gaines et al., 2012b, Garson et al., 2012), it is clear that Burgess Shale-type preservation is

strongly favored in the absence of bioturbation, and that the quality of Burgess Shale-type preservation is often diminished in the presence of bioturbation (e.g., Lin et al., 2010). Because trace fossils are well preserved in sedimentary facies that are otherwise identical to those that lack bioturbation, the absence of bioturbation from critical intervals of Burgess Shale-type deposits cannot be ascribed to preservational bias. Instead, this pattern reflects the general exclusion of benthic fauna from the intervals of each deposit that lack bioturbation entirely. By analog with the modern (e.g., Savrda et al., 1984; Savrda and Bottjer, 1986), these intervals, which include the critical fossil-bearing portions of the Walcott Quarry Member of the Burgess Shale (Gostlin, 2006; Gabbott et al., 2008) and the Chengjiang (Dornbos et al., 2005; Hu, 2005; Gaines et al., 2012b), are interpreted to have accumulated under anoxic benthic conditions (but see Powell et al., 2003; Caron and Jackson, 2006).

Thus, it is clear that Burgess Shale-type preservation is most strongly favored under anoxic bottom waters, but may occur in close association with weakly oxygenated benthic environments. These findings have validated earlier models of transportation of Burgess Shale-type fossil assemblages across the chemocline and burial under anoxic conditions (e.g., Conway Morris 1986), as also supported by the orientations of individual fossils within event-deposited mudstone beds (Gostlin, 2006; Zhang et al., 2006, 2007a; Gabbott et al., 2008; Zhao et al., 2009; Caron et al., 2014). However, they also reveal additional subtleties, including the possibility in rare cases of in-situ preservation of fossil assemblages lying close to the chemocline (Gaines and Droser, 2010; Garson et al., 2012).

All Burgess Shale-type deposits examined to date have been associated with the close juxtaposition of anoxic and oxygenated water masses. Transportation of fossil assemblages from the living environment to an anoxic preservational trap was most strongly favored by elevated physical energy of depositional events, as described above.

Again, this depositional setting is not unlike those found in the modern ocean and throughout the Phanerozoic rock record. While this particular setting was certainly important in promoting preservation, other factors operating in the early burial environment ultimately controlled Burgess Shale-type preservation.

Preservation of organic fossils by sealing of the early burial environment

Fossil-bearing mudstones of Burgess Shale-type deposits worldwide are characterized by prominent early diagenetic carbonate cements that are concentrated at bed tops and penetrate downwards (Fig. 2; Gaines et al., 2005, 2012c, d). Although bed-capping cements are rapidly lost to weathering, analysis of fresh, unaltered material has revealed that these features are pervasive in each of the deposits studied to date (Gaines et al., 2012c). Textural data show that carbonate growth was early, and resulted in displacement of clay particles prior to compaction or significant overpressure. The presence of bed-capping cements in synsedimentary soft-sediment deformation features (seafloor slumping) indicates that cements were emplaced at or near the sediment-water interface (Gaines et al., 2012c). Carbon isotope values of the cements lie within the range of seawater values, indicating that cements precipitated directly from seawater (Gaines et al., 2012c).

The precipitation of seafloor cements following burial had a profound influence on the processes of microbial decomposition in the sediments. Sulfur isotope data from sedimentary pyrite reveal that sulfate reduction, the primary pathway for the degradation of organic matter in marine sediments in the absence of O_2 (Jørgensen, 1982), was severely inhibited by early sealing of the burial environment (Gaines et al., 2012c). Tissue loss occurred via limited sulfate reduction, as well as by the far less efficient pathways of methanogenesis and fermentation. Although Burgess Shale-type fossils have lost >99% of their volume to decay (Gaines et al., 2012d), decay was sufficiently restricted that it did not reach completion, and macrofossils were conserved as organic films. The remarkable anatomical detail captured in Burgess Shale-type fossils resulted from the firm and fine-grained nature of sediments, which aided in the retention of fine anatomical features—including those of labile tissues (Gaines et al., 2012c)—after organic tissues lost structural integrity and collapsed into two dimensions as they underwent degradation (Briggs and Kear, 1994).
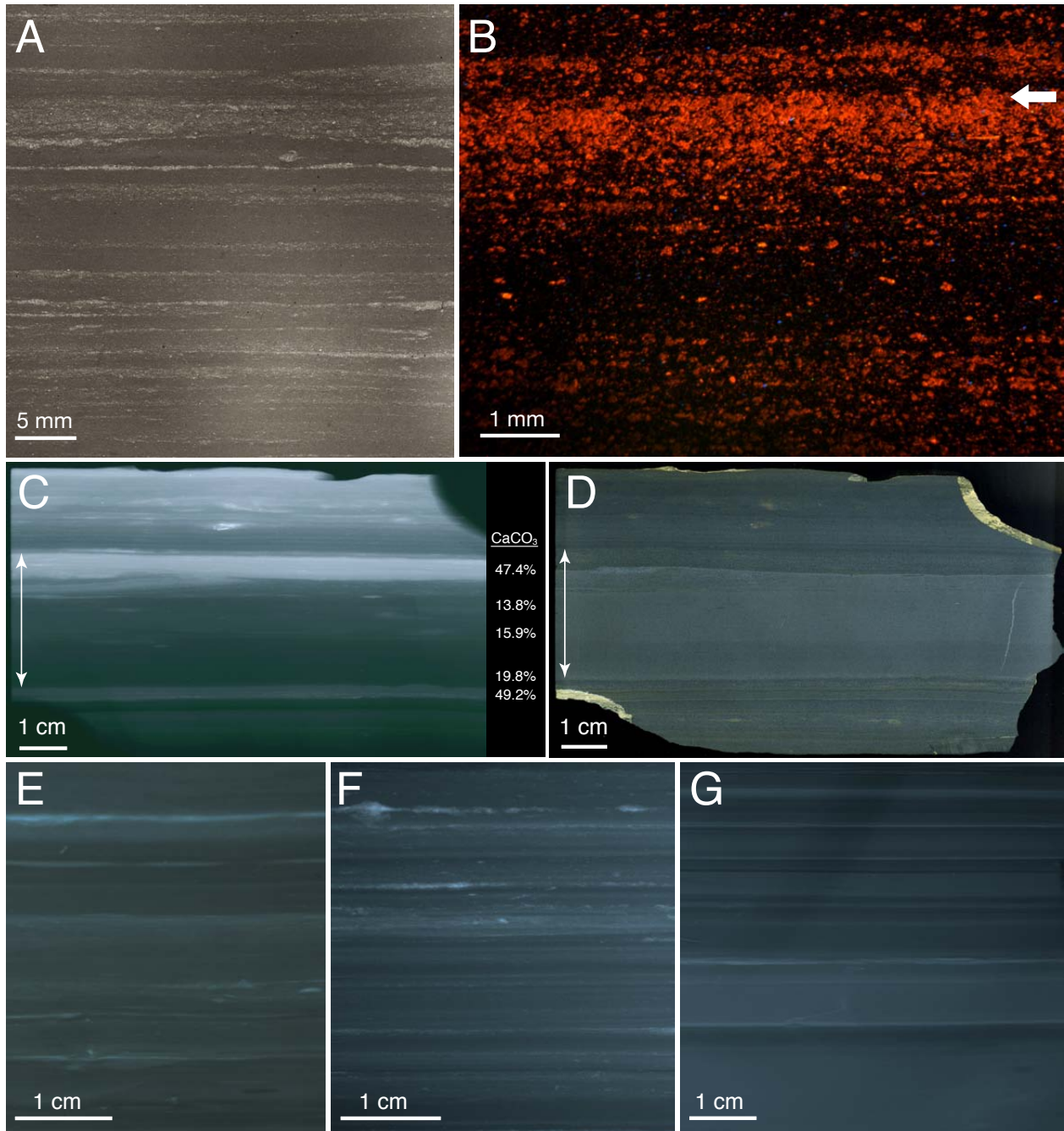
FIGURE *2.*—Carbonate cements in claystones bearing Burgess Shale-type preservation. Thin section micrographs (A, B), polished slab (D) and X-radiograph (C–E). A) Thin section of Marjum Formation shown in transmitted light. Carbonate cements at bed tops appear bright, clay-rich bed bases appear gray. B) Cathodoluminescence micrograph of thin section of fossil-bearing interval of Kaili Formation, arrow marks top (upper) of a typical claystone lamina, 3 mm in thickness. Carbonates, which exhibit bright orange luminesce, are concentrated at bed tops and become less abundant down bed. The dark, non-luminescent portions of the image are clay-rich with subsidiary carbonate dispersed throughout the claystone fabric. X-radiograph (C) and polished slab (D) of Burgess Shale containing Walcott's Great *Eldonia* Layer (GEL) (arrow), ROM #63065. The distribution of bed-capping authigenic carbonate cements is clearly seen in X-radiograph, where bright areas correspond to high wt.% $CaCO_3$ (data derived from spot-drilled samples). Extensive bed-capping cement is present at the top of the GEL as well as at the tops of the thin, millimeter-scale beds that overlie it. (E–G) X-radiographs of slab samples of claystones bearing Burgess Shale-type preservation. Carbonate-rich portions of event-deposited laminae are less easily penetrated by X-rays and appear bright in X-radiograph, whereas clay-rich portions appear dark in color, revealing concentration of carbonate cements at the tops of individual mm-scale laminae. E) "thin" Stephen Formation, Stanley Glacier locality ROM #59951. F) Wheeler Formation, Drum Mountains locality. G) Marjum Formation, Marjum Pass Locality.

BURGESS SHALE-TYPE PRESERVATION
IN TIME AND SPACE

Controls on the temporal distribution of Burgess Shale-type preservation

Widespread Burgess Shale-type preservation in the early and middle Cambrian was promoted by: 1) transportation of fossil assemblages across the chemocline, 2) rapid burial under predominantly anoxic benthic conditions, and 3) severe inhibition of microbial degradation of soft tissues by early cementation and sealing of the burial environment. While conditions 1 and 2 are common throughout the Phanerozoic marine rock record, condition 3 is restricted to early Phanerozoic strata. The distribution of Burgess Shale-type deposits in time appears to have resulted from the chemical conditions that prevailed in epicratonic seaways during the rise of animal life and its subsequent establishment in shallow-marine environments globally.

The role of ocean chemistry.—The final and critical step in Burgess Shale-type preservation was the emplacement of pervasive bed-capping cements at the seafloor (Fig. 2). Early marine carbonate cements in Burgess Shale-type deposits and in a range of other marine environments have been taken as evidence of alkaline conditions in the Cambrian oceans. These conditions resulted from a greatly enhanced flux of continental weathering products to the oceans due to exposure of reactive basement rocks to atmospheric chemical weathering over an area that is unprecedented in the rock record, and included the interiors of most continental cratons (Peters and Gaines, 2012). A whole-rock chemical database of Cambrian shales, including Burgess Shale-type deposits, demonstrated that Cambrian shales are significantly enriched in Ca and depleted in Si relative to composite shale standards (Peters and Gaines, 2012), revealing strongly elevated carbonate content as compared to average shale. This evidence, as well as that of anomalous carbonate cementation in other depositional facies (Peters and Gaines, 2012), indicates that early carbonate cements precipitated broadly in Cambrian epicontinental seas. Under these favorable conditions, Burgess Shale-type preservation was promoted wherever fine-grained clastic depositional environments with event-dominated sedimentation intersected the chemocline.

In addition to high alkalinity, Burgess Shale-type preservation was also favored by low concentrations of oxygen and sulfate in the Cambrian oceans. Although anoxic and low-sulfate conditions were widespread in Cambrian marine environments (Brennan et al., 2004; Dahl et al., 2010; Gill et al., 2011; Gaines et al., 2012c), these conditions developed repeatedly in marine environments of epicratonic seas throughout the Phanerozoic rock record. Therefore, the chemical conditions that favored the development of carbonate cements are of primary importance in understanding the temporal distribution of Burgess Shale-type preservation. Data from multiple sedimentary environments indicates that conditions favorable to early cementation were maintained across the early Cambrian–early Ordovician as reactive basement rocks of the continental interiors were progressively reburied underneath sedimentary rocks of the Sauk Sequence, and protected from atmospheric weathering (Peters and Gaines, 2012). Thus, chemical conditions favoring Burgess Shale-type preservation are predicted to have persisted through the early Ordovician despite the apparent decline of this taphonomic pathway after the middle Cambrian (Allison and Briggs, 1993).

Recently discovered late Cambrian (e.g., Vaccari et al., 2004; García-Bellido and Aceñolaza, 2011) and early Ordovician (Van Roy et al., 2010) examples of Burgess Shale-like assemblages suggest that the taphonomic window for Burgess Shale-type preservation did remain open during this time. The post-middle Cambrian decline of Burgess Shale-type preservation may be correlated to a decline in the area of favorable outer detrital belt environments, which became displaced from continental seaways due to the expansion of carbonate platforms during the late Cambrian and early Ordovician (Gaines et al., 2013). These findings also suggest that additional Burgess Shale-type assemblages should be present in late Cambrian and early Ordovician strata wherever favorable depositional environments as described above developed.

Burgess Shale-type preservation in space: what factors controlled the differences among Burgess Shale-type deposits?

While early carbonate cementation was pervasive in Cambrian marine environments, Burgess Shale-type preservation was restricted to environments that promoted transportation of fossil assemblages across the chemocline and rapid burial in fine-grained sediments. The differences in the number of soft-bodied taxa
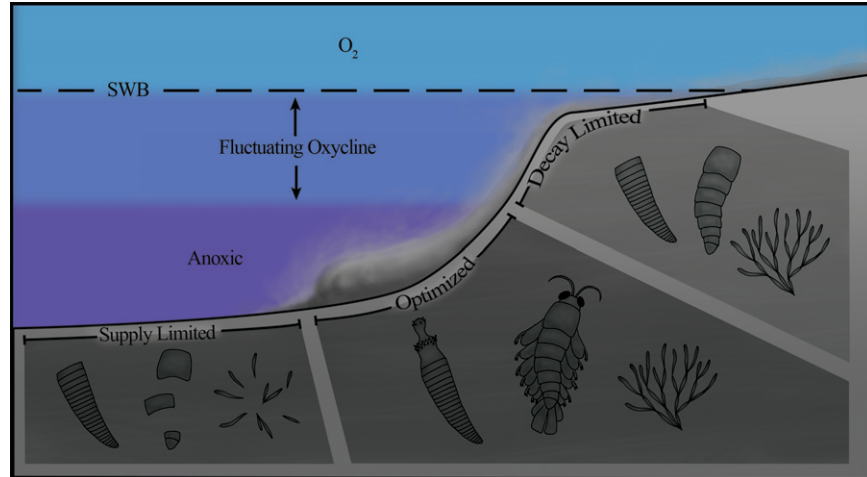
FIGURE *3*.—Depositional and taphonomic setting of the Burgess Shale at the front of the Cathedral Escarpment, with anoxic and oxygenated water masses separated by a fluctuating oxycline. SWB indicates maximum storm wave base. Physical depositional energy was maximized by the steep slope at the front of the escarpment, which greatly enhanced the potential for transport of fossil assemblages across the oxycline. Potential for preservation of taxonomically diverse and abundant fossil assemblages was maximized in settings lying immediately below the oxycline, where required transport distance was minimized. Preservation potential in the early burial environments of areas of the seafloor lying downslope from this zone was high, however, number of preserved taxa and fossil density were limited by the greater distance of transportation required for fossil benthos to reach these more distal environments ("Supply Limited"). Preservation potential in regions of the seafloor lying upslope from this zone was limited by the prevalence of oxic conditions in the benthic environment, which, when present, resulted in complete decomposition of soft tissues ("Decay Limited"). In these more proximal settings, soft-bodied preservation was favored in intervals in which anoxic conditions developed.
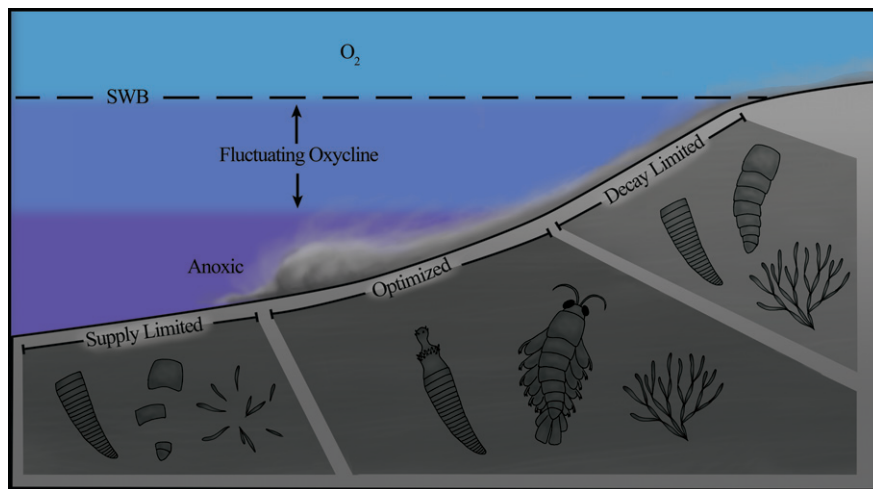

FIGURE *4*.—Depositional and taphonomic setting of the Chengjiang, showing location of the chemocline with respect to the loci of preservation and to maximum storm wave base (SWB). High physical depositional energy facilitated transport of fossil assemblages across the oxycline, in many cases over greater distances than in the Burgess Shale (Figure 3). Preservation of taxonomically diverse and abundant fossil assemblages was maximized in settings lying near the oxycline where required transport distance was minimized. Preservation potential in environments of the seafloor lying downslope from this zone was high, but limited by energy required to transport organisms to more distal environments ("Supply Limited"). Preservation potential in environments lying upslope was limited by frequent oxic conditions in the benthic environment ("Decay Limited"). Soft-bodied preservation was favored in intervals in which anoxic conditions developed.

preserved, fossil density, and fidelity of preservation that exist among Burgess Shale-type deposits may be shown to have resulted from subtle but important differences in physical depositional setting and proximity of the chemocline. Preservation potential was optimized under sustained anoxic conditions in the benthic environment (Gaines and Droser, 2010), a condition that requires transportation of fossil assemblages from the living environments to a downslope preservational trap. The preservation of Burgess Shale-type assemblages also required rapid burial in claystone sediments, which, in most cases, occurred under relatively low depositional energy.

The Burgess Shale and Chengjiang.—Both of the Tier 1 deposits represent special cases in which the physical depositional energy was enhanced relative to the other deposits, promoting periodic entrainment of whole assemblages, transportation across a well-developed chemocline, and rapid burial in often thick (up to 10 cm) claystone beds (see above). In the Chengjiang, and in the Walcott Quarry and Marble Canyon assemblages of the Burgess Shale, evidence of transportation in turbid flows followed by rapid deposition is conspicuous in the orientations of individual fossils (Whittington, 1971; Gostlin, 2006; Zhang et al., 2006; Zhang and Hou, 2007; Gabbott et al., 2008; Caron et al., 2014).

In the Burgess Shale (Fig. 3), physical energy of transportation and deposition was enhanced by the steep slope at the front of the Cathedral Escarpment that lay near the angle of repose (Conway Morris, 1986; Fletcher and Collins, 1998, 2003; Caron et al., 2014). Periodic failure of this slope, presumably under the influence of storm wave disturbance, is interpreted to have led to the development of dense, mud-rich slurries that promoted greater transport efficiency (Gabbott et al., 2008). The steep nature of the slope also greatly reduced the minimum transport distance required to move organisms across the chemocline.

At Chengjiang (Fig. 4), depositional energy was enhanced by the descent of storm-generated turbidity currents from the shelf into a fault-bounded basin (Zhu et al., 2001; Hu, 2005), resulting in the deposition of thick distal turbidite claystone beds that bear Burgess Shale-type fossils (Zhu et al., 2001; Zhao et al., 2009). Depositional energy was elevated relative to that of most other Burgess Shale-type deposits due to

proximity of the basin to a storm-influenced clastic shelf: in most other cases, the depositional basins of Burgess Shale-type deposits were separated from clastic shelfal environments by broad carbonate platforms that reached up to hundreds of kilometers in width, and served to sequester a large fraction of clastic sediments in nearshore environments of the inner detrital belt. The direct proximity of the Chengjiang basin, which lay below storm wave base, to the storm-influenced shelf (Zhu et al., 2001; Hu, 2005) provided a depositional regime dominated by larger magnitude sediment-gravity flows than are observed in other Burgess Shale-type deposits, even those that occur within the inner detrital belt (see below). This setting facilitated the transportation of soft-bodied fossil assemblages across greater distances than in the Burgess Shale or in Tier 2 and 3 deposits, as evidenced by patterns of fossil orientation indicative of gravitational settling of fossils during burial (Zhang and Hou, 2007).

In both the Burgess Shale and Chengjiang (Figs. 3, 4), the preservation of abundant and diverse assemblages was optimized in a zone that lay immediately below the chemocline, where potential for delivery to the anoxic environment was greatest, and was accompanied by rapid burial. Preservation potential of fossils in environments lying downslope from this zone was limited by the capacity of bottom-flowing currents to transport fossils from habitable benthic environments farther upslope, and are herein termed "supply limited" environments. The preservation potential in environments upslope from the optimized zone was limited by the presence of oxygen, which promoted more rapid decay in the days to weeks following burial. Thus, the potential for Burgess Shale-type preservation may be considered to have been decay-limited in these environments.

In the Chengjiang, the optimized zone for Burgess Shale-type preservation and the "decay-limited" zones tend to occur in >10m thick stratigraphic intervals and are not closely interbedded (Dornbos et al., 2005; Gaines et al., 2012b). In the Burgess Shale (Raymond Quarry, Marble Canyon, and Stanley Glacier assemblages), however, these zones may be interbedded at the cm- to mm-scale (Allison and Brett, 1995, Caron et al., 2010, 2014), reflecting migration of chemical environments under a fluctuating oxycline (Gaines and Droser, 2010). The development of decay-limited conditions
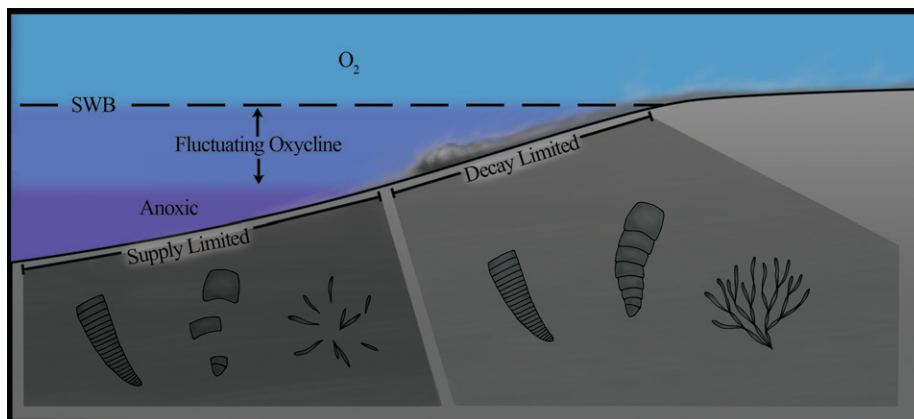
FIGURE *5.*—Depositional and taphonomic setting of Burgess Shale-type deposits in Outer Detrital Belt environments, showing location of the chemocline with respect to the loci of preservation and to maximum storm wave base (SWB). These environments were characterized by low angle slopes, with reduced physical depositional energy that limited the ability of bottom-flowing currents to transport soft-bodied fossils across chemoclines ("Supply Limited"). As a result, preservation of molts, dead organisms, and hydrodynamically-light (i.e., algal/bacterial) forms is dominant in the record of soft-bodied fossils. Preservation of labile tissues is infrequent in outer detrital belt environments, but was favored in environments lying near the chemocline, or by the delivery of pelagic organisms to more distal environments followed by rapid burial. Preservation potential in regions of the seafloor lying upslope from this zone was limited by the prevalence of oxic conditions in the benthic environment, which, when present, resulted in complete decomposition of soft tissues ("Decay Limited"). Soft-bodied preservation was favored in intervals in which anoxic conditions developed.

over fossil assemblages originally buried under optimized conditions may have had consequences for the fidelity of preservation in these instances. However, processes important to the conservation of organic remains of Burgess Shale-type fossils are interpreted to have been operative in the first few weeks following burial (Briggs and Kear, 1994; Gaines et al., 2012c); thus, the longer-term migration of chemical environments is not expected to have influenced the preservation of fossils buried immediately below the sediment-water interface.

Outer detrital belt settings.—The majority of Burgess Shale-type deposits, including most of the Tier 2 and Tier 3 deposits, occur in outer detrital belt environments (Fig. 5; Robison, 1960), characterized by relatively low-angle, mixed siliciclastic-carbonate slopes that descended from carbonate platforms towards the seaward margins of the continental crust (Rees, 1986; Liddell et al., 1997; Elrick and Snider 2002; Brett et al., 2009; Halgedahl et al., 2009; Gaines et al., 2011). The Burgess Shale-type fossil-bearing intervals of these deposits are comprised of amalgamated mm-scale claystone beds. These beds were deposited from bottom-flowing currents that are interpreted to have typically lacked the transport energy required to move fossil assemblages *en masse*. Most commonly, exceptional fossils found

in these deposits represent molts and/or dead and partially decomposed specimens, in addition to a hydrodynamically light fraction dominated by algal fragments (Gaines and Droser, 2005, 2010; Gaines et al., 2012b; Garson et al., 2012). In the distal portion of these settings, fossils may occur in great density, but exhibit very low overall taxonomic richness, and fossils of animals are rare (Gaines and Droser, 2010). These include the Kaili (Series 2–3), Balang (Series 2), and Tsinghsutung (Series 2) deposits of South China (Peng et al., 2005; Steiner et al., 2005; Zhao et al., 2005; Sun et al., 2013), and Pioche (Series 2–3), Spence (Series 3), Wheeler (Series 3), and Marjum (Series 3) deposits of Laurentia (Robison, 1991; Lieberman, 2003; Briggs et al., 2008; Webster et al., 2008). In many cases, beds deposited under supply-limited conditions are closely (mm-scale) interbedded with those deposited under decay-limited conditions (Gaines and Droser, 2003, 2005, 2010; Wang et al., 2004; Webster et al., 2008; Caron et al., 2010; Lin et al., 2010; Gaines, 2011; Gaines et al., 2012b; Garson et al., 2012) although this is not expected to have affected preservation potential of fossils in the shallow burial environment, as discussed above.

Examples of soft-bodied fossils bearing limbs, organs, and other labile tissues are well known from these deposits, although they are
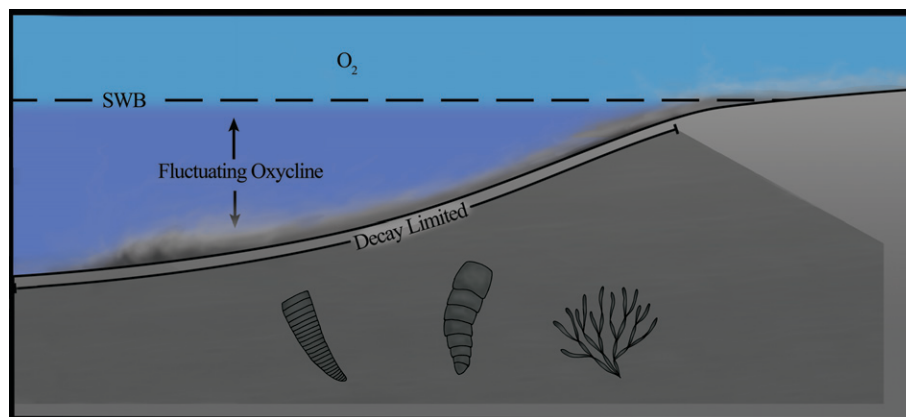
FIGURE *6.*—Depositional and taphonomic setting of Burgess Shale-type deposits in Inner Detrital Belt environments, showing location of the chemocline with respect to the loci of preservation and to maximum storm wave base (SWB). Elevated physical depositional energy favored transportation and rapid burial of fossil assemblages, but preservation was limited by the prevalence of oxic conditions in the benthic environment, which resulted in complete decomposition of soft tissues ("Decay Limited"). Frequent scour and reworking associated with deposition of a silt or fine-sand fraction also acted to limit preservation potential. Burgess Shale-type preservation in these settings occurred very rarely when anoxic benthic conditions developed and when physical depositional energy was also reduced.

much more rare than fossil cuticle (typically of arthropods and worms) and algal/bacterial forms (e.g., Handle and Powell, 2012). The examples of high-fidelity preservation in these deposits suggest that the potential for high-fidelity preservation was present in large portions of them, but that preservation was limited by the delivery of live or freshly killed organisms (supply limited). Rarely, high-fidelity preservation occurred in settings near the chemocline or via the delivery of freshly killed pelagic organisms to more distal settings, followed by rapid burial. The total number of taxa preserved in the great majority of Burgess Shale-type deposits appears to have been supply limited, with overall number of taxa and fidelity of preservation constrained primarily by biostratinomic rather than diagenetic factors.

Inner detrital belt settings.—A minority of Tier 2 and Tier 3 deposits occur in mudstone-dominated inner detrital belt settings (Fig. 6) where conditions promoting decay were more limiting to preservation than transport energy. Important among these conditions were greater availability of oxygen during deposition, and sediment reworking resulting from elevated physical energy, both of which are features of shallower water depth and more proximal depositional environment than that of typical Burgess Shale-type settings. These distal shelf deposits include the Latham (Gaines and Droser, 2002) and Indian Springs (English and Babcock,

2010) deposits, belonging to Series 2 of Laurentia. In each, exceptional preservation of macrofossils is rare, and occurs in infrequent intervals that accumulated below the chemocline (Gaines and Droser, 2002). Throughout the majority of each of these deposits, the probability of Burgess Shale-type preservation was precluded by oxygen concentrations that accelerated decay and promoted colonization by an infauna and the irrigation of sediment pore-waters, despite the development of carbonate cements at bed tops. Individual depositional beds rarely exceed 10 mm in thickness, but each typically contains a silt or fine sand fraction at the bed base that contributed to frequent scour and reworking of underlying beds (e.g., Gaines and Droser, 2002), which is not observed in most other Burgess Shale-type settings. Prevalence of oxic conditions during the accumulation of these deposits and disturbance of the early burial environment by bioturbation, scour, and reworking served to limit the number of taxa preserved and the fidelity of exceptional preservation in these decay-limited settings, from which only rare examples of Burgess Shale-type preservation are known. Rarely, Burgess Shale-type fossils were conserved when infrequent anoxic conditions developed, and when reworking and bioturbation were minimized.

CONCLUSIONS

1) Burgess Shale-type preservation is a

unique taphonomic pathway that is defined by the conservation of whole assemblages of soft-bodied fossils as primary carbonaceous remains (Butterfield 1995, 2003; Butterfield et al., 2007; Gaines et al., 2008)—a pathway that does not occur in modern marine environments or in the great majority of the Phanerozoic rock record.

2) The Burgess Shale-type taphonomic pathway was widespread in early and middle Cambrian settings, and was permitted wherever fine-grained clastic depositional environments characterized by event-based deposition intersected the redox boundary at the seafloor.

3) Burgess Shale-type preservation declines sharply after the middle Cambrian (Allison and Briggs, 1993), but this pathway may have persisted into the late Cambrian (Vaccari et al., 2004; García-Bellido and Aceñolaza, 2011) and the early Ordovician (Van Roy et al., 2010). The signal of the early Phanerozoic taphonomic window (Allison and Briggs, 1993; Orr et al., 2003) for exceptional preservation is statistically dominated by Burgess Shale-type fossil assemblages.

4) Burgess Shale-type preservation ultimately resulted from early sealing of the burial environment by carbonate cements emplaced at the seafloor shortly after deposition. These cements acted to restrict the diffusion of oxidants into the sediments, thereby retarding the processes of microbial decomposition in the sediments at large, resulting in incomplete decay of organic remains and the conservation of morphology in carbonaceous films (Gaines et al., 2005, 2012c). Low concentrations of oxygen and sulfate in the Cambrian oceans also contributed to the slowing of decomposition, but these conditions are not unique to the early Phanerozoic, and therefore cannot account for Burgess Shale-type preservation. The non-analogue condition that was responsible for Burgess Shale-type preservation was the high alkalinity of the Cambrian oceans, which promoted early carbonate cementation at the seafloor in Burgess Shale-type deposits and across multiple marine depositional environments during the Cambrian (Peters and Gaines, 2012). While this control over Burgess Shale-type preservation was global in extent, local physical depositional and chemical conditions, specifically proximity to the oxycline, determined where Burgess Shale-type preservation occurred.

5) Prominent differences in total number of preserved taxa and in fidelity of preservation among Burgess Shale-type deposits resulted from biostratinomic factors that controlled the potential for transportation of soft-bodied fossils across chemical gradients and their rapid burial in fine-grained sediments. The Chengjiang and Burgess Shale contain the greatest number of soft-bodied forms because of enhanced transport energy, and, in the Burgess Shale, reduced minimum transport distance required to move organisms across the chemocline.

6) Although distal muddy environments favorable to preservation appear to decline across the late Cambrian and early Ordovician, additional Burgess Shale-type assemblages should be present in strata of these ages wherever favorable physical depositional and local chemical conditions developed.

ACKNOWLEDGMENTS

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