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TAPHONOMY OF THE GREATER PHYLLOPOD BED COMMUNITY, BURGESS SHALE

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ABSTRACT

The degree to which the original community composition of the Middle Cambrian Burgess Shale was altered through transport and decay and how taphonomic conditions varied through time and across taxa is poorly understood. To address these issues, variation in fossil preservation was analyzed through a vertical succession of 26 bed assemblages, each representing a single obrution event, within the 7-m-thick Greater Phyllopod Bed of the Walcott Quarry. More than 50,000 specimens belonging to 158 genera—mostly benthic, monospecific and nonbiomineralized—were included in this analysis. The decay gradient of the polychaete *Burgessochaeta setigera* was used as a taphonomic threshold to estimate how far decay had proceeded in each bed assemblage.

Qualitative comparisons of the degree of preservation of 15 species, representing an array of different body plans, demonstrate that all bed assemblages contain a mix of articulated and *in situ* dissociated or completely dissociated organisms interpreted respectively as census- and time-averaged assemblages. Furthermore: (1) most organisms studied were preserved within their habitat and only slightly disturbed during burial; (2) most decay processes took place prior to burial and resulted in disarticulation of organisms at the time of burial; (3) the degree of disarticulation was variable within individuals of the same population and between populations; and (4) early mineralization of tissues across all body plans occurred soon after burial.

Canonical correspondence analysis summarizes the apparent variations in the amount of preburial decay, or time averaging, across species, individuals, and bed assemblages. The effect of time averaging, however, must have been limited because rarefaction curves reveal no link between decay and species richness. This suggests that decay is not an important community controlling factor. Overall, our data suggest that transport was trivial and the traditional distinction between a pre- and postslide environment is unnecessary. It is likely that all specimens present at the time of burial would have been preserved independent of their original tissue composition and degree of preburial decay.

The presence of extensive sheets of *Morania confluens*, a putative benthic cyanobacterium, in most bed assemblages suggests that it: (1) provided a stable substrate and food source for a number of benthic metazoans, and (2) played a possible role in the preservation of nonbiomineralized animals, acting as a barrier in maintaining local anoxic pore-water conditions.

INTRODUCTION

Following the discovery of the main site in 1909 by Charles Walcott of the Smithsonian Institution (Walcott, 1911), the Middle Cambrian Burgess Shale has become the best known *Konservat Lagerstätte* in the fossil record (Seilacher, 1990; Briggs et al., 1994; Briggs, 2001). Thanks in particular to the preservation of nonbiomineralized organisms, the Burgess Shale provides important paleoecological insights into a Middle Cambrian community which otherwise would not be available from the study of the biomineralized component alone (Conway Morris, 1986). This site also represents a crucial benchmark for studying body plans and the evolution of early animals in the interval immediately after the most important metazoan radiation of the Phanerozoic, the famous Cambrian explosion (Gould, 1989; Conway Morris, 1998).

Meaningful evaluation of the evolutionary and ecological significance of the Burgess Shale biota relies on understanding better the taphonomic factors responsible for preservation of nonbiomineralized organisms. These factors include preburial (biostratinomy) and postburial (diagenesis) processes. However, the degree to which the original community composition of the Middle Cambrian Burgess Shale was altered through transport and decay and how taphonomic conditions varied through time and across taxa is still poorly understood. In this study qualitative and quantitative data were used at the scale of entire fossil assemblages and from a series of individual bed assemblages with preservation of nonbiomineralized organisms to test whether or not: (1) the Burgess Shale biota was subject to significant transport prior to burial; and (2) decay was a significant factor in altering the structure and species-level diversity of fossil assemblages. Transport and decay biases were estimated on the basis of: (1) semiquantitative comparisons between the degree of preservation of the polychaete worm *Burgessochaeta setigera* across bed assemblages and 14 other taxa representing a wide range of taxa and body plans; (2) quantitative analyses of how well community structure (abundance and species composition) from entire bed assemblages are related to the degree of preservation of *Burgessochaeta*, and how these patterns changed through time; and (3) quantitative analyses that test whether diversity levels across bed assemblages are related to variation in the degree of preservation of *Burgessochaeta*.

PREVIOUS QUANTITATIVE TAPHONOMIC STUDIES

Earlier taphonomic studies of the Burgess Shale utilized only a few selected taxa and specimens, often those numerically dominant in museum collections, as well as limited sedimentological and geochemical data to formulate general hypotheses concerning the biostratinomic and diagenetic factors responsible for nonbiomineralized preservation. Specimens and samples employed in these studies (e.g., Whittington, 1971a, 1971b) typically had been collected with little information concerning their exact origin in a stratigraphic context. The only attempt at a quantitative assessment of the Burgess Shale (Conway Morris, 1986) was based on material collected from the Phyllopod Bed by Walcott and later by the Geological Survey of Canada. The Phyllopod Bed represents a 2-m-thick stratigraphic section which was at that time (Piper, 1972) interpreted as a sequence of distal turbidites deposited from a series of individual slumps, each of which incorporated a snapshot of the biota inhabiting the local seafloor. Such successive temporal sampling was considered to be analogous to the sampling of a modern benthic community by a series of sediment grabs or a towed sledge (Conway Morris, 1986, p. 433). The analysis of the fossil content at the level of each depositional

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event (slump) in the Phyllopod Bed would have been ideal (Conway Morris, 1986), but unfortunately, with few exceptions (Walcott, 1912), Walcott did not record the stratigraphic levels at which he found specimens in his original excavations. Thus, the Phyllopod Bed could be studied only as an induced time-averaged assemblage of unknown duration, possibly representing up to 50 separate depositional events (Conway Morris, 1986). Problems related to sampling techniques (e.g., separation of most parts and counterparts of specimens) further reduced the reliability of ecological signals inferred from subsequent analyses based on the Walcott collection (see Conway Morris, 1986).

EVALUATION OF PRESERVATION BIASES USING MODERN AND FOSSIL DATA

Decay experiments on modern marine invertebrate taxa have proved to be a particularly promising and useful baseline for evaluating decay-induced morphological change, decay rate, and preservation biases (Allison, 1986, 1990; Plotnick and Thomas, 1986; Allison and Briggs, 1991a, 1991b; Briggs and Kear, 1993, 1994a, 1994b; Babcock and Chang, 1997; Sagemann et al., 1999; Babcock et al., 2000). In one seminal paper, Briggs and Kear (1993) conducted a series of decay experiments on the modern marine polychaete *Nereis virens*. Decay was studied in terms of morphological change, weight loss, and change in chemical composition. Specimens were killed and transferred to separate experimental vessels containing artificial sea water, and subjected to a range of conditions to study variations in decay in response to differences in oxygen level, agitation, sediment, and degrading agents. Briggs and Kear (1993) described five stages in the decay of polychaete carcasses based on discrete morphological changes: (1) whole or shrivelled; (2) flaccid; (3) with unsupported gut; (4) preserved as a cuticle sac (gut fully decayed); and (5) with jaws and setae preserved only. Only the sclerotized tissues (jaws) survived more than 30 days in all experiments. They concluded that if a given fossil assemblage contains very well-preserved polychaetes then the recorded diversity should be higher than that within an assemblage containing poorly preserved polychaetes. Their hypothesis (Briggs and Kear, 1993) was intuitively based on the fact that polychaetes decay more quickly than many other nonbiomineralized taxa, including arthropods (Allison, 1986), and that these five stages could therefore be used to measure generally how far decay had proceeded before it was halted (see taphonomic threshold in Briggs and Kear, 1993). In identifying the Burgess Shale as a prime example of where this might be applied, Briggs and Kear (1993) cited the exquisite preservation of various polychaetes in the biota as an indication that decay was quickly halted, presumably across multiple animal body plans, thereby enhancing species-level diversity. This assumption, however, has never been evaluated at the scale of multispecies assemblages and from individual bed assemblages.

LOCALITY AND STRATIGRAPHY

Material used for this study came from the Walcott Quarry Member (Fig. 1A) of the Burgess Shale Formation (see Fletcher and Collins, 1998). This formation, formerly known as the thick Stephen formation, corresponds to a relatively deep-basinal depositional setting situated at the basinward edge of a regional carbonate bank limited by the Cathedral Escarpment (Aitken and McIlreath, 1984). Fossils were collected on Fossil Ridge, north of the town of Field, British Columbia (Fig. 1A) by Royal Ontario Museum field crews between 1993 and 2000. All material used in this study comes from the Greater Phyllopod Bed (GPB, Figs. 1B–1D). The GPB succession is about 7 m thick and corresponds to the stratigraphic interval extending down from the top of the Phyllopod Bed in the historical Walcott Quarry to the top of the Wash Limestone Member about 5 meters below the original Walcott Quarry floor (Figs. 1B–1D).

The GPB is composed of centimeter-scale interbedded fine-grained siliceous mudstones and calcisiltites (Fig. 2; Gostlin, 2006). The two lithologies often separate along bedding planes. The fine-grained siliciclastic beds are massive, have sharp bases, and are not graded or coupled as previously described by Piper (1972). They often contain fossils showing preservation of nonbiomineralized parts (referred herein as beds with nonbiomineralized preservation or NBP). Coupled beds have been reported in other Cambrian *Lagerstätten* in mudstone layers with NBP but are associated with different depositional environments (e.g., Gaines et al., 2005). The layers between the mudstone beds with NBP are composed of coarser-grained calcisiltite sediments with shelly (e.g., *Scenella*, hyoliths, trilobites) or more rarely nonbiomineralized (e.g., *Selkirkia* tubes) organisms. The putative monoplacophoran *Scenella* often occurs in large concentrations, with shells oriented convex up and presumably in life position, in calcisiltite beds (see also Babcock and Robison, 1988). Allison and Brett (1995) proposed that organisms preserved in the Phyllopod Bed were engulfed in high-density fluidized mudflows, instead of distal turbidites or storm deposits. Gostlin (2006) interprets the mudstone beds with NBP as the result of storm-generated back currents transporting sediment from the platform in a manner consistent with the depositional model of Aitken and McIlreath (1990). All previous studies agree that the nonbiomineralized organisms were buried very quickly, and in this context each depositional event with NBP can be regarded as an obrution deposit (see also Seilacher, 1990).

Individual mudstone beds with NBP studied here vary in thickness from 2 mm to more than 100 mm (Fig. 1D). Fossiliferous beds were ordered by approximate vertical distance from the stratigraphic reference datum—0 level, the original floor of the Walcott Quarry (Fig. 1)—to the top of the bed in question (e.g., bed assemblage -210 is about -210 cm below the reference datum; Fig. 1). The distance between the datum and the top of the bed may vary along the quarry due to lateral variation in thickness of the siliciclastic and calcisiltite beds, and is therefore a relative measure (Fig. 1D). In this study, a bed assemblage (BA) represents all fossils collected in a single fine-grained siliciclastic mudstone bed with NBP (Nota: a BA in this study is different from a benthic assemblage *sensu* Boucot, 1975, which refers to depth zoned groups of communities). These beds were sampled sequentially and independently (Fig. 1D) within defined sample areas (Fig. 1E; Caron, 2005b). In some instances the tops and bottoms of slabs and orientations of individual fossils were recorded in the field, but these parameters were not noted systematically for every slab.

MATERIAL

In this study 15,875 slabs containing 68,850 fossils from 36 bed units with NBP through the GPB were systematically surveyed and censused (Fig. 1D, Supplementary Material 1^2) in order to reconstruct the overall taphonomic history (Caron, 2005b). In conducting the census, taxa were identified to species level where possible, the number of individuals for each taxon was computed per BA, and direct fossil associations and the degree of preservation of specimens (e.g., disarticulation) were assessed qualitatively. Most specimens (81%) are preserved with both parts and counterparts and have been counted only once. Most counterparts of the remaining specimens (19%) were discarded in the field because they were too damaged to be collected. In a few cases, parts and counterparts were accidentally separated and inventoried under different field numbers. When identified, such mistakes were corrected, but it is still possible that a very small minority of specimens were counted twice. To avoid integrating fossils from potentially nonisochronous beds and because of intense weathering between beds, only specimens within the thickness of fine-grained siliciclastic individual mudstone beds with NBP were counted. Specimens present within calcisiltite beds or on bedding surfaces in contact with calcisiltite beds were observed but not counted. Slabs were examined under a binocular microscope, and all specimens >0.5 mm in minimum dimension were censused. Where fossils occurred in overlapping clusters, only the specimens that appeared on the surface were identified and counted. Disarticulated or dissociated specimens with parts usually in close anatomical proximity were counted as one individual.

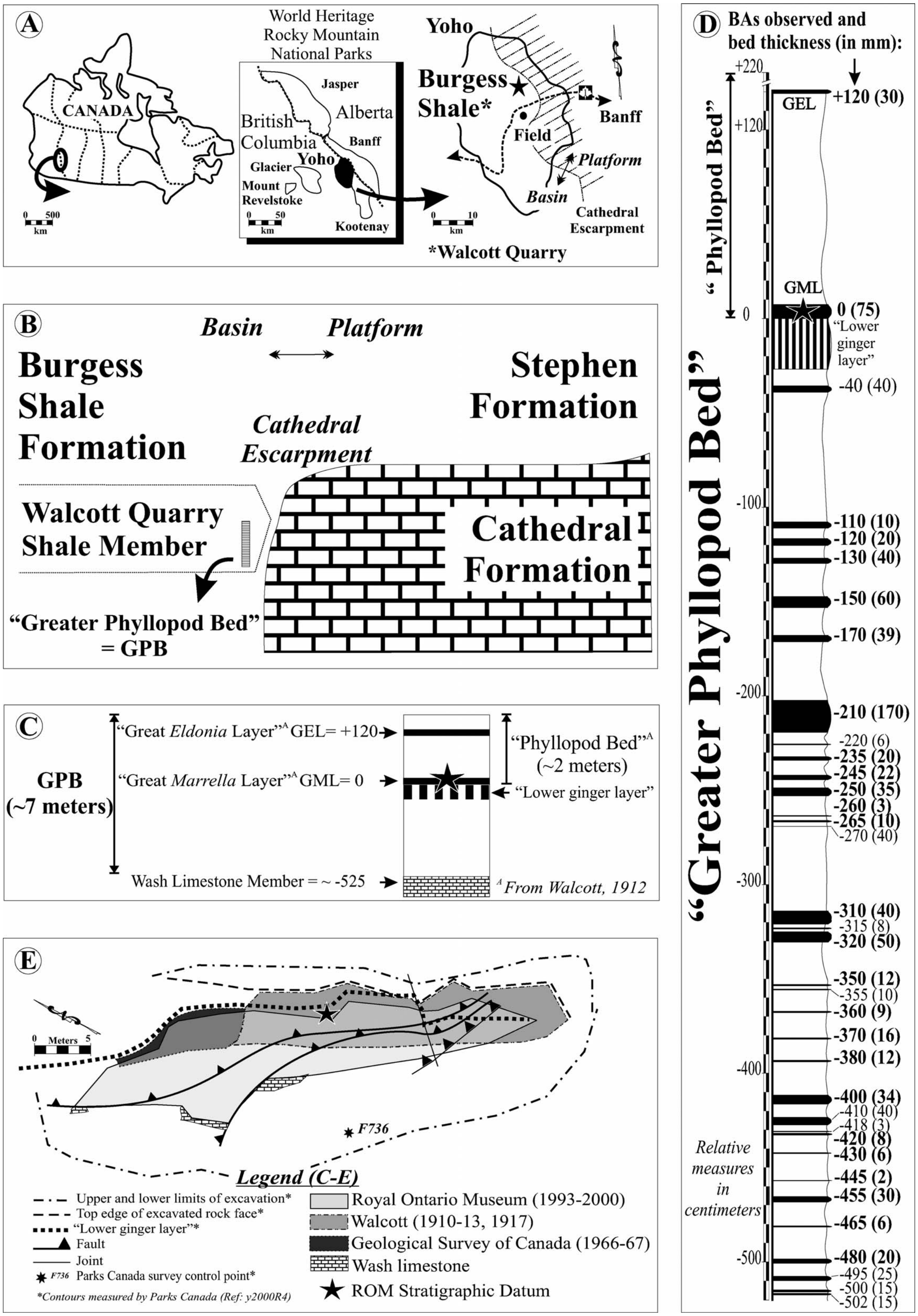

FIGURE 1—Location and stratigraphic origin of fossil material collected by the Royal Ontario Museum from the Burgess Shale. (A) Location of the Walcott Quarry, and relative position of the Cathedral Escarpment. (B–C) Schematic cross views of the Greater Phyllopod Bed (GBP) (B) in relation to the Cathedral Escarpment (modified from Fletcher and Collins, 1998); (C) in relation to the Phyllopod Bed. (D) Simplified stratigraphic section of the Greater Phyllopod Bed. Numbers on the right represent the names and respective thicknesses of BAs from fine-grained siliciclastic mudstone beds with nonbiomineralized preservation. 26 BAs with at least 300 specimens were analyzed in this study (represented in bold and in larger font). (E) Approximate areas of successive historical excavations in the Walcott Quarry.

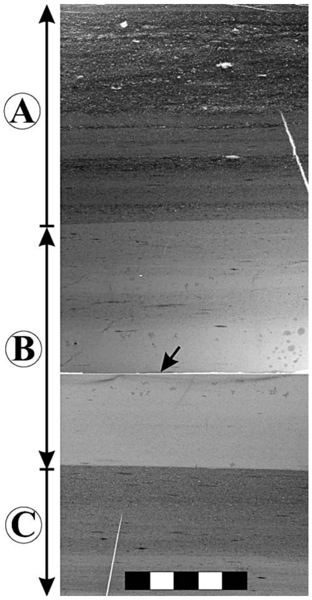

FIGURE 2—Typical thin section from the GPB (+60 level, courtesy Kevin Gostlin). Scale bar: = 10 mm. The uppermost layer (A) is a calcisiltite. The light grey layer (B) in the center corresponds to a continuous and massive fine-grained siliciclastic bed with high quality nonbiomineralized preservation (BA +60). This layer has split along fossils of *Marrella* (black arrow). The siliciclastic layer at the base (C) is slightly more coarse grained. The 3 layers present on this thin section are not genetically related and represent different depositional events.

The dataset used in this study was reduced to 50,900 specimens, assigned to 170 species (158 genera) in 26 BAs. Isolated or broken parts of unidentified taxa, and isolated sclerites of *Wiwaxia* or *Chancelloria*, were excluded. In rare cases the number of specimens was estimated from individual elements (for example, see *Laggania* in Supplementary Material 1[2]). Conservative estimates of the numbers of specimens are provided for some other taxa, either because the shape of an entire specimen was poorly known or because taxa occurred in clusters and different individuals were not easily distinguishable (e.g., the valves of bradoriids; see Supplementary Material 1[2]). The numbers of trilobite larvae and presumed juveniles of *Alalcomenaeus* sp. (Caron, 2002) were coded in separate categories as species to acknowledge that age difference may be an important factor in the structure of the BAs. New and undescribed organisms (N = 61) were also included, and often represent distinct species of unknown higher taxonomic groups (e.g., Arthropoda A, Indet. A, Woolly Bear). To allow significant confidence for comparative studies, the following BAs with less than 300 specimens were excluded from the analyses: -040, -220, -270, -315, -355, -410, -418, -495, -500, and -502.

QUANTITATIVE METHODS

In order to assess whether the nature of the organism was an important factor controlling the structure and diversity of the GPB community, a dataset (N = 50,900) was analysed using different quantitative approaches. First, the degree of preservation of 14 species + *Burgessochaeta* was compared (Supplementary Material 2[2]). These species were chosen for three main reasons: (1) they belong to different groups of organisms with a wide range of body plans; (2) they are composed of many parts, and all or individual portions of their external anatomy can be easily identified; and (3) they display a range of preservation easily separated across BAs into two broad categories (Supplementary Material 2[2]). Category 1 represents individuals that are complete, often with preservation of nonbiomineralized parts, and hence do not show evidence of physical damage or dissociation. By contrast, Category 2 represents usually disarticulated or dissociated individuals, often with parts in close anatomical proximity. Category 2 also includes empty tubes of the priapulid worm *Selkirkia* (see Supplementary Material 2[2]). The two preservational categories for the polychaetes *Burgessochaeta* and *Canadia* were obtained by comparison with stages of morphological change observed during the experimental decay of the modern polychaete *Nereis* (Briggs and Kear, 1993), under the assumptions that decay processes and the sequence of morphological stages are broadly similar in both Cambrian and Recent polychaetes.

Given that not all different stages of decay are easily recognizable in *Burgessochaeta* and *Canadia*, those defined as 1 to 5 by Briggs and Kear (1993) were pooled into two main categories: (1) representing whole, shrivelled, or flaccid animals (Figs. 3A and 3G); and (2) animals with unsupported gut and dissociated setae (Figs. 3B–3F, 3H). Specimens in Category 1 are typically complete with all setae and parapodia (Fig. 3A). Often, the gut is also present (85% of specimens) and is preserved in three dimensions, possibly filled with sediment (47% of specimens). The gut is straight and does not show any sign of rupture. By contrast, in specimens in Category 2, decay has altered the body wall, and parapodia are detached (Fig. 3B) or missing in some specimens (Fig. 3E). The gut tends to vary in diameter and is sometimes ruptured (Fig. 3C, D). Remains of the body wall are still visible in the most severely affected specimens (Fig. 3F). *Burgessochaeta* and *Canadia* do not have sclerotized pharyngeal teeth (jaws), and individual isolated setae were not recognized; therefore, stage 5 of Briggs and Kear (1993) is not relevant to this study.

For each BA and for the 15 species, three different parameters were observed: (1) number of species represented by specimens in Category 1; (2) number of species represented by specimens in Category 2; and (3) number of species that had specimens in both Categories 1 and 2. For convenience, the terms articulated and disarticulated are used to refer to preservational Categories 1 and 2, respectively. Each of these parameters was divided by the total number of species present per BA (maximum 15), and three different ratios were obtained (Fig. 4): species represented by articulated specimens (% Art), species represented by disarticulated specimens (% Dis), and species with both articulated and disarticulated specimens (% Art-Dis).

In the second part of this study, canonical correspondence analysis (CCA) (ter Braak, 1986; Borcard et al., 1992; Palmer, 1993; ter Braak and Verdonschot, 1995) was used to explore how patterns of preservation vary across species and BAs. For CCA, the stages of decay of *Burgessochaeta* were coded as either 1 (representing preservational Category 1) or 2 (representing preservational Category 2). Often, *Burgessochaeta* displays a range of preservation within the same BA. In such cases, the assigned category is based on specimens with the best preservation (i.e., representing the least amount of decay). *Burgessochaeta* is absent in 12 BAs, and to test whether or not its absence is due to decay a third category was used, representing a presumably higher level of degradation resulting in total removal. Thus, the three categories represent a gradient of decay from 1 (least) to 3 (high enough to eliminate *Burgessochaeta*).

Results were compared with CCAs treating only those BAs containing polychaetes in Categories 1 and 2 (N = 14). To evaluate whether certain categories were more common in some BAs than others, the BA-Species table included the number of specimens of species coded in Categories 1 and 2 (Supplementary Material 2[2]). The abundance of *Burgessochaeta* was excluded from the species table to avoid redundancy in the analysis, because it had already been used as a proxy for the inferred decay gradient. Rare species were eliminated, in particular where species occurred in fewer than two BAs and where the cumulative relative abundance of species across all BAs was less than 0.5%. Deletion of rare species did not affect important patterns in the data and is a recommended practice, given that rare species tend to be at the extreme ends of ordination scores (Legendre and Legendre, 1998). The final matrix contained 26 BAs and 116 species (Supplementary Material 3[2]). Because the range of abundance varied considerably among species, the final data table was further

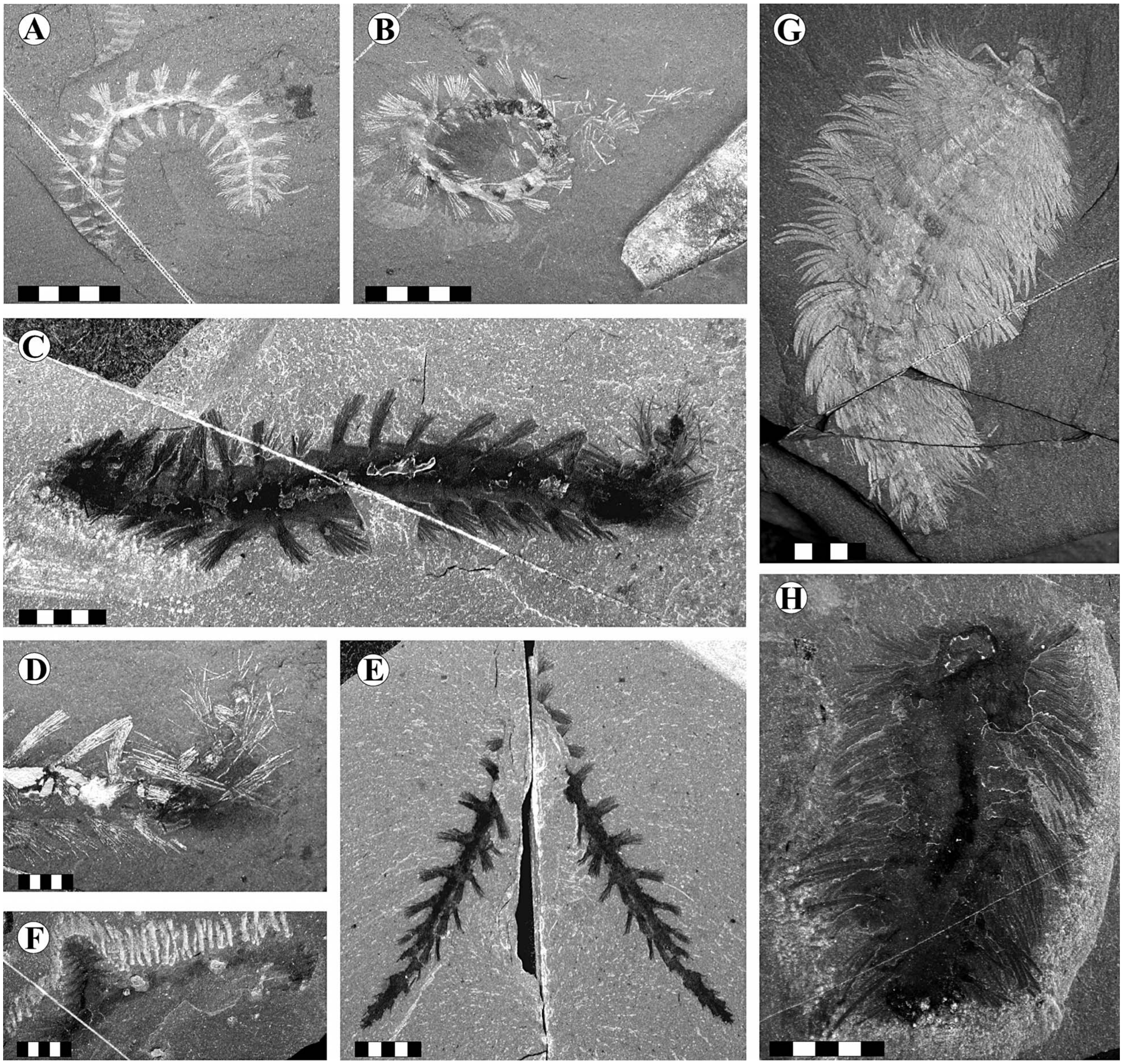

FIGURE 3—Morphological categories of decay of *Burgessochaeta setigera* (A–F) and *Canadia spinosa* (G–H). Scale bars: A = 10 mm; B, C, E, G, H = 5 mm; D, F = 2.5 mm. (A) Specimen with complete gut and gut content (Category 1) (ROM 56967, BA-120). (B–F) Specimens in Category 2 of preservation. (B) Dissociated setae (ROM 56968, BA-120). (C–D) Preferential dissociation of setae at the posterior part of the body, and unsupported gut (ROM 56969, BA-120); (C) Overall view; (D) Close-up. (E) Part and counterpart of the same specimen, with setae missing at the posterior part of the body and partially decayed gut (ROM 56970, BA-400). (F) Specimen with traces of gut and setae, preserved as a cuticle bag (specimen # 15, ROM 56971, BA-455). (G) Complete specimen (Category 1) (ROM 56972, BA 0). (H) Specimen with partially decayed gut (Category 2) (ROM 56973, BA-480).

log transformed to provide more equal weights to all species (Gauch, 1982; Legendre and Legendre, 1998).

The CANOCO program (ter Braak and Smilauer, 1998) was used for all CCAs. Analyses were performed with axes scaled using symmetric and biplot scaling. The significance of the decay variable was established by determining the importance of the first canonical axis using Monte Carlo testing. Monte Carlo tests were performed using random seeds, and with the maximal number of runs allowed by CANOCO (9998 runs), with randomized data and unrestricted permutations (full model option in CANOCO). The null hypothesis tested was a random relationship between the species data and the decay gradient data (ter Braak and Smilauer, 1998).

In the last part of this study the rarefaction method (Sanders, 1968) was used to estimate the number of species expected in each BA (see further discussions in Caron, 2005b). For the purposes of this study two individual-based rarefaction curves were computed, and species richness in both analyses was compared to the preservation of *Burgessochaeta*. The rarefaction analyses were based on (1) all arthropods and (2) all taxa. Expected numbers of species with their 95% confidence intervals were rarefied to the lowest number of specimens among the 26 BAs studied (381 specimens from BA-480). Rarefaction curves were calculated using ECOSIM© (Gotelli and Entsminger, 2001), and BioDiversity Pro© (McAleece, 1999). In both rarefaction programs, the expected species richness was derived from a modified version of Sanders' (1968) original algorithm (Hurlbert, 1971; Heck et al., 1975; Gotelli and Entsminger, 2001). In ECOSIM, calculations were repeated by 1000 random iterations to generate mean, variance, and confidence intervals of species diversity (Gotelli and Entsminger, 2001). Individual curves, and individual analyses at specific numbers of individuals (knots), were computed using ECOSIM with species richness as the default species diversity index. The

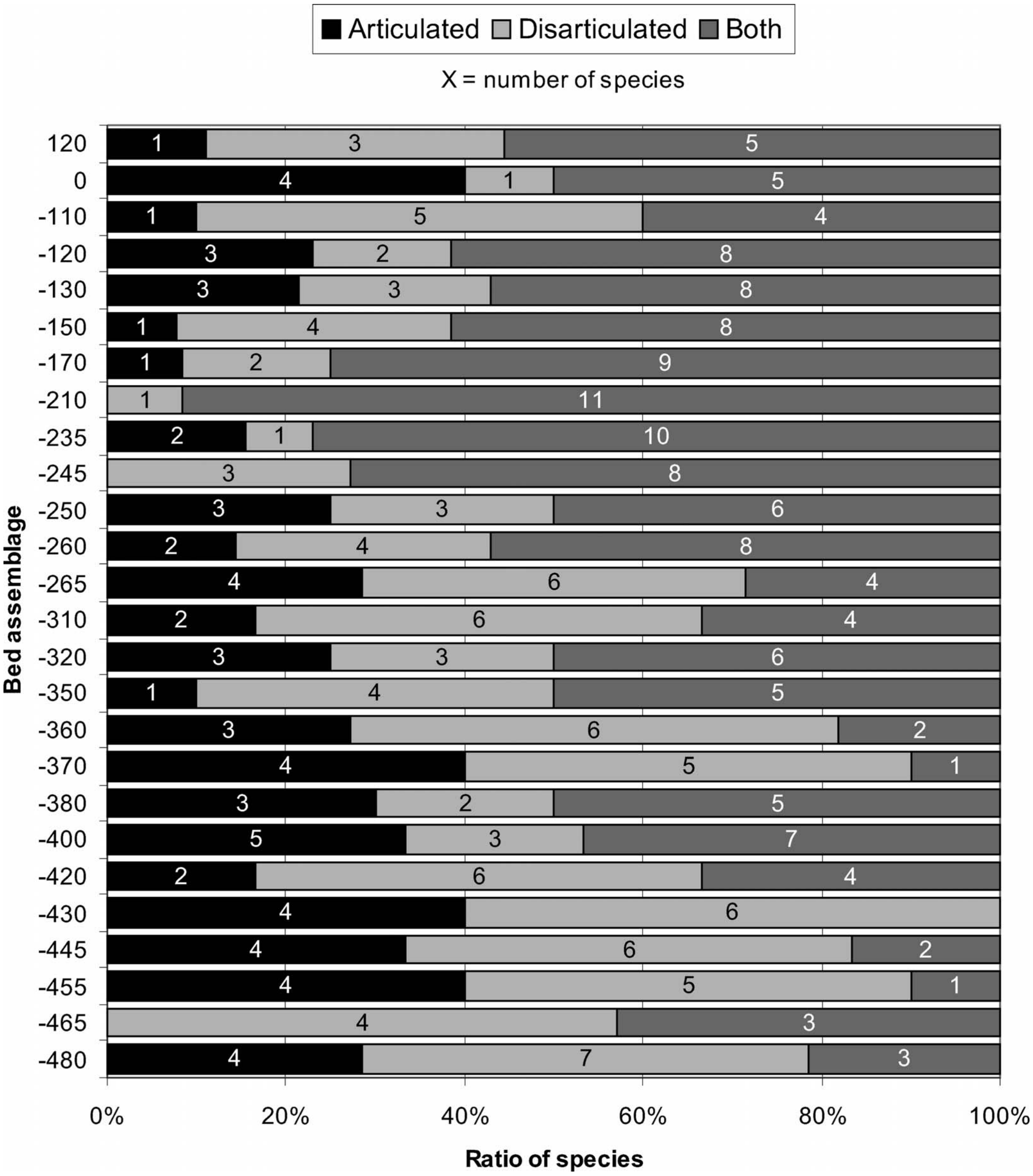

FIGURE 4—Ratios of species representing articulated specimens (% Art), disarticulated specimens (% Dis), and both articulated and disarticulated specimens (% Art-Dis) per BA. The terms articulated and disarticulated encompass the Categories 1 and 2 of preservation respectively, and were calculated based on the 15 species present in Supplementary Material 2[2]; see text for details.

results of the two analyses were very similar, and only the rarefaction curved based on all taxa is presented in this paper (Caron, 2005b).

RESULTS

General Preservation Patterns

Specimens of many taxa show slight disarticulation of parts that remain in close anatomical proximity (Supplementary Materials 4–5[2]: *Olenoides*, *Canadaspis*, *Elrathina*, *Marrella*, *Waptia*, *Micromitra*, *Wiwaxia*) and are preserved in the same BAs with articulated remains of the same species (see also Caron, 2005b). This general trend is summarized in Figure 4 based on 15 species (Supplementary Material 2[2]). Articulated specimens occur in all BAs, often in association with disarticulated remains of the same species. The ratio of species known from both articulated and disarticulated specimens decreases in older BAs. Overall, there are fewer species with articulated specimens than species with disarticulated specimens (means across BAs: 65% and 78%, respectively).

Quantitative Comparisons

Ordination Diagram.—With just one environmental variable used in the analysis—the inferred decay gradient—only the first axis of the ordination diagram can be interpreted in relation to decay (Fig. 5). The Monte Carlo test strongly rejected ($p = 0.0002$) the null hypothesis that the relationship between the species and decay gradient matrix is random. Therefore, the species structure appears to be related to the pattern of decay in *Burgessochaeta* (Fig. 5; the first axis of CCA explained 10.6% of the variation). In other words, the relative positions of the species in the CCA along the first axis provide an indication of the extent to which different taxa were affected by decay. Variation on the second axis could be interpreted as a standard correspondence analysis axis of the residual information. On this second axis, species and BAs are ordered according to their relationships in relation to environmental and/or ecological variations to each other but not to decay. The direction of the arrows of the pseudospecies is identical in most taxa and follows the direction of the decay gradient of *Burgessochaeta* (Figs. 5A–5B). The ordination diagram

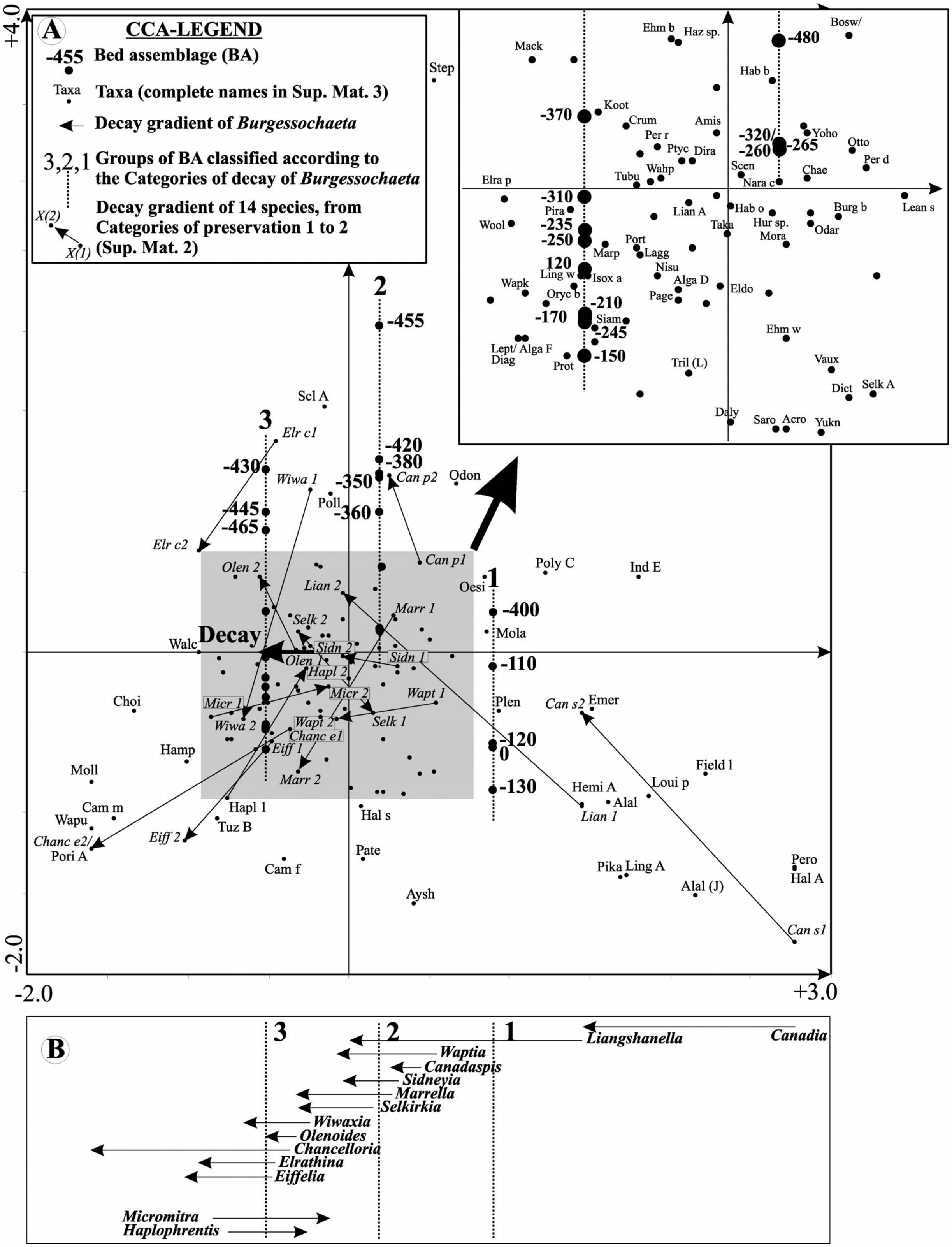

FIGURE 5—Results of CCA analysis. (A) CCA diagram. (B) Summary diagram of the projected scores of individual species along the first axis of the CCA diagram in relation to the decay gradient in *Burgessochaeta*. More specimens of many species are found in their disarticulated states in BAs on the left side of the ordination diagram than in BAs on the right side. (See Supplementary Material 3^2 for complete names)

(Fig. 5A) can be divided further into three different sections in relation to the putative decay gradient defined by *Burgessochaeta*.

1. Those species present on the right side of the ordination diagram tend to be clearly associated with *Burgessochaeta* in Category 1 in similar BAs (right vertical dashed line in Fig. 5). These belong to a wide range of nonbiomineralized taxa including: most polychaetes (*Canadia*, *Peronochaeta*, Polychaetes B and C); one onychophoran (*Hallucigenia* A); priapulids (*Fieldia*, *Louisella*); chordates and hemichordates (*Pikaia*, hemichordata A, *Oesia*); many nonbiomineralized arthropods (*Alalcomenaeus*, *Liangshanella*, *Emeraldella*, *Plenocaris*, *Molaria*); and a variety of other organisms including an indeterminate soft-shell lingulid with pedicle (*Lingulella* A). Interestingly, presumed juvenile molts of the arthropod *Alalcomenaeus* (Caron, 2002) are abundant in some of these BAs and particularly in -120 (Alal (J) in Fig. 5A).
2. Species close to the center of the ordination (middle vertical dashed line in Fig. 5) tend to be abundant and widely distributed across BAs. The dashed line 2 is very close to the center of the ordination diagram, given that *Burgessochaeta* in Category 2 is relatively common in most BAs. By extension, the presence of *Liangshanella*, *Waptia*, *Canadaspis*, *Sidneyia*, *Selkirkia*, *Micromitra*, and *Haplophrenti*s close to the center of the ordination diagram indicates that many specimens of these species are common to most BAs at an advanced stage of decay (Category 2, Supplementary Material 2[2]). Some species seem to be common to many BAs in a pristine stage of preservation (Category 1) as well (e.g., *Waptia*, *Marrella*, *Canadaspis*, and *Sidneyia*). Preservation of the nonbiomineralized anatomy of some species, however, is often restricted to just a few BAs (e.g., *Micromitra* with setae, Category 1; BA-150, BA-210). Complete and dissociated specimens of *Canadaspis* seem to be particularly abundant in BA-350. Numerous slabs from this BA have been collected with hundreds of specimens literally covering the entire rock surface (Supplementary Material 5A[2]). Roughly one third of these specimens appear to be articulated. This suggests that BA-350 may represent a mass mortality or molting event.
3. Species on the left side of the ordination (left vertical dashed line in Fig. 5, i.e., present without specimens of *Burgessochaeta*, which have presumably decayed completely) tend to have more disarticulated or dissociated specimens or are lacking in nonbiomineralized parts. Mineralized taxa are also abundant in most of these BAs, especially trilobites and brachiopods. The presumption that the absence of *Burgessochaeta* in these BAs is related to an increase in decay may be validated by the fact that numerous dissociated or disarticulated specimens of *Olenoides* (Supplementary Material 4[2]), and *Marrella*, *Sidneyia*, *Waptia*, *Eiffelia*, and *Wiwaxia* are present (Supplementary Material 5[2]). Greater abundance of disarticulated or dissociated specimens, however, seems to occur in only a limited number of BAs (particularly -150, -170, -210, -245). Many species preserving nonbiomineralized anatomy are also present in BAs without *Burgessochaeta*, including, for example, the putative cnidarian *Mackenzia* in BA-150 and BA-210. Various species of polychaetes are also present in BAs -150, -170, and -210 (Supplementary Material 1[2]).

Rarefaction Curves.—When the overall shapes and relative positions of the rarefaction curves are compared, BAs with *Burgessochaeta* showing Category 1 preservation occupy an intermediate to upper range of expected richness across all taxa (Figs. 6A–6B). Moreover, the relative species rank order for each BA is similar: BA-400 consistently has more species than BAs -120, -110, -130, and 0 (in descending number of species). When the curves are rarefied to 381 specimens, the confidence intervals of most BAs fit within the limits of BAs with *Burgessochaeta* in Category 1 (Fig. 6B). Some BAs, however, are distinctly less diverse and do not contain *Burgessochaeta* in Category 1 (-350, -360, -420, -430, -445, -455, and -465). These patterns are clearly seen on the rarefaction curves themselves and seem to be consistent with an increasing number of specimens. The BAs with *Burgessochaeta* in only Category 2 occur at variable species richness levels in both data sets: from very low (-350, -360, -420, -455), to moderate (-380, -260, -265, -320), to very high (-480). When BAs with *Burgessochaeta* in Categories 1 and 2 are compared, it seems that most BAs with better preserved polychaetes do not have significantly more species than BAs with less well preserved specimens (e.g., compare BA-480 with BA 0). Various species of polychaetes are present in five of the 26 BAs in which *Burgessochaeta* is absent: *Canadia* (-310), Type B polychaete (-235), Type C polychaete (-370), and *Stephenoscolex argutus* (-430, -445). There is no particular trend associated with these BAs, however, in terms of total number of species preserved (Fig. 6). More importantly, such BAs as -210 or -150 without any polychaetes, and with a large number of specimens, have more species than most BAs containing polychaetes with comparable numbers of specimens collected (Fig. 6: e.g., BA-130 or BA-260).

INTERPRETATIONS

A BA is typically composed of a mixture of articulated, *in situ* dissociated (i.e., parts dissociated but remaining in close anatomical proximity) and disarticulated organisms preserved together. Articulated specimens are interpreted as representing animals buried alive whereas dissociated animals probably died shortly before burial. Such an association of specimens within the same bed assemblage resembles, though does not equal, death and life assemblages found in the same local environment in modern settings (Staff et al., 1986). In the following part of this discussion, the term census assemblage (vs. Kidwell and Flessa, 1995) refers to specimens buried alive, whereas the term time-averaged assemblage refers to specimens buried shortly after death.

The relative ratio of species in different states of preservation varies through time, and in some instances the proportion of the time-averaged assemblage is much higher than the proportion of the census assemblage. This demonstrates that the event of burial is not always the main cause of death for many organisms. The finding of fossil census and time-averaged assemblages suggest that most organisms from the GPB community, in particular those living in or on the benthos, are probably preserved within habitat. This conclusion is in agreement with published paleontological evidence as well as studies of modern marine environments, which indicate that skeletal concentrations are not distributed randomly (Kidwell et al., 1986). Dissociated or disarticulated organisms which are found together with more complete specimens (life assemblage) are rarely transported out of the original community habitat and are often preserved *in situ* or near *in situ* (Kidwell and Flessa, 1995). This last conclusion was derived from studies of communities based on animals with shelly parts, but there are no reasons why such a conclusion could not be applicable to benthic nonbiomineralized organisms.

It has been shown from modern taphonomic experiments that disarticulation and fragmentation of nonbiomineralized carcasses is not related to the nature and distance of transport but rather to the amount of decay before burial: decay-induced disarticulation may occur even with minimal transport at the sediment-water interface if decay processes had already commenced (Allison, 1986). If some organisms were already dead and had already decayed in the preslide environment (*sensu* Conway Morris, 1986), then it is likely that any significant transport of the biota within a turbulent cloud of sediment would have completely disarticulated these carcasses, and only bits and pieces would have been found in the postslide environment. If the community had been killed en masse by the event of burial and transported rapidly away from the living habitat, then only perfectly articulated organisms would be expected to be found and possibly a few disarticulated parts of some shelly organisms. The finding of disarticulated specimens only might be interpreted in the same way. Specimens could have been transported en masse away from the living habitat but could have been deposited relatively slowly allowing decay and disarticulation at the site of deposition prior to burial. Neither of these scenarios is supported by the fossil evidence.

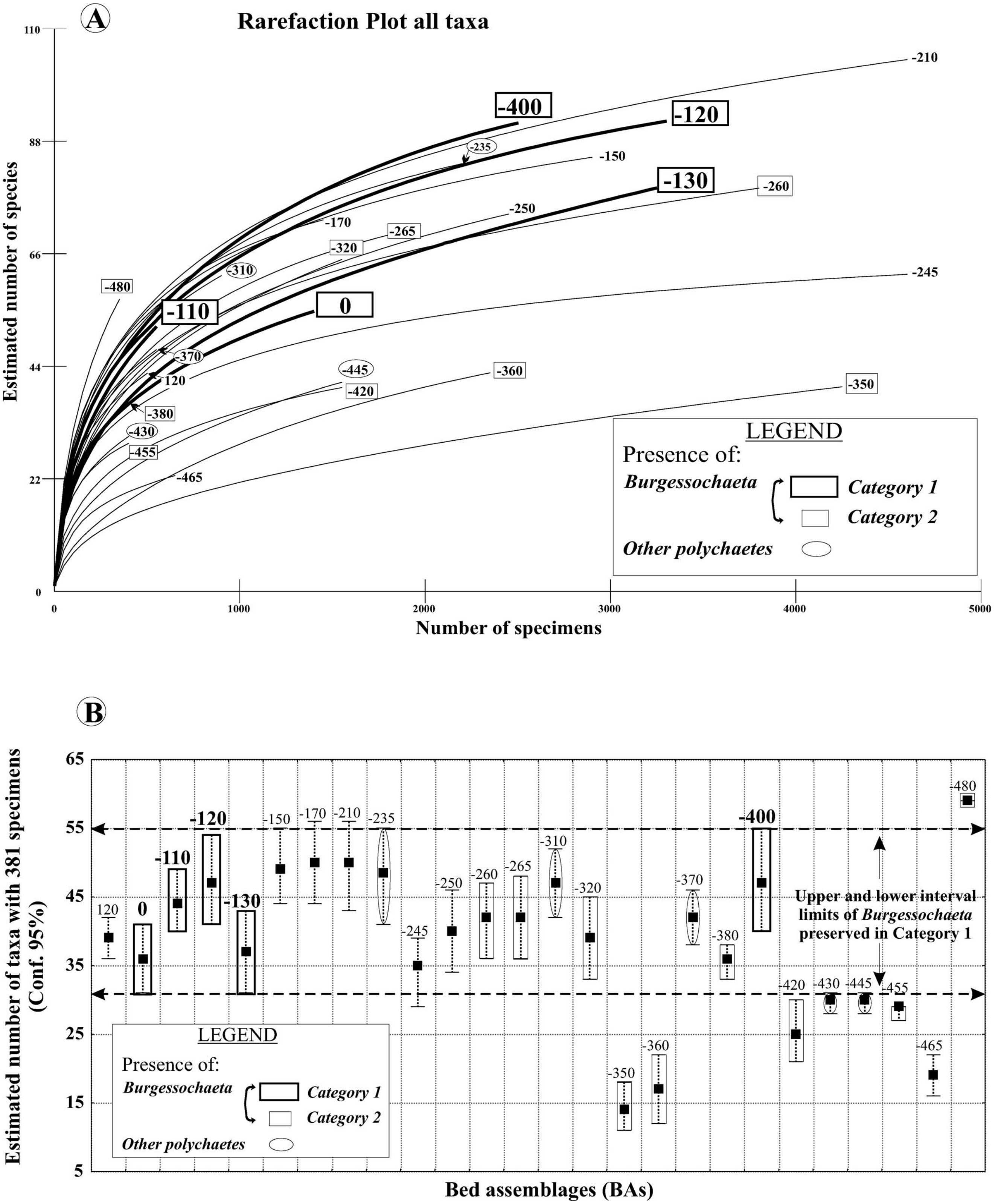

FIGURE 6—Rarefaction curves of 26 BAs from the GPB based on all taxa in relation to the preservation of *Burgessochaeta* and the presence of other polychaetes. (A) Expected number of species with a decreasing number of specimens. (B) Expected number of species with their confidence intervals (95%) rarefied to 381 specimens. (See text for details).

The apparent increase of dissociated carcasses toward the left of the ordination diagram (shown by the decay gradient of 12 species; Fig. 5) and the positive relationship between the overall species structure and the pattern of decay of *Burgessochaeta* may be exaggerated if the lack of *Burgessochaeta* in some BAs is not due to decay, as assumed. The absence of *Burgessochaeta* in some BAs is probably not related to an increase of decay during and after burial, because BAs without *Burgessochaeta* include a number of well preserved and articulated nonbiomineralized species. This absence most likely results from decay prior to burial and possibly from fluctuations in original abundance, reflecting turnover of populations. Similar patterns were obtained when the BAs lacking *Burgessochaeta* were removed (Caron 2005b, unpublished results). Therefore, BAs to the left of the ordination diagram could represent environments in which the residence time of carcasses at the surface of the sediment prior to burial was longer than in BAs at the right of the ordination diagram. This would explain the apparent increase in dissociated carcasses toward the left of the CCA diagram. Rarefaction curves, however, demonstrate that the number of species is not significantly different in BAs with or without *Burgessochaeta*. This result is related to the fact that most taxa are normally represented by individuals that have been buried alive, even if others have decayed prior to burial.

DISCUSSION

Depositional Environment

In the taphonomic model of Conway Morris (1979), mudflows carried live and dead organisms from a preslide to a postslide environment with an estimated lateral travel distance of 2 km and a vertical displacement of around 70 m. In this model, the postslide environment was thought to lie in a relatively deep-water setting, along a steep carbonate platform (Cathedral Escarpment) below the photic zone, and would have been inimical to life, including for scavengers and other metazoan grazers or heterotrophic bacteria (Conway Morris, 1986).

In past studies, the apparent absence of infaunal burrowers was taken as the main evidence that the biota was not living where it was buried (Piper, 1972; Conway Morris, 1986). Ichnofossils are rare but not absent in the Greater Phyllopod bed. A few samples of macroscopic burrows in mudstone beds with nonbiomineralized preservation have been collected in the GPB (Fig. 7A). The presence of rare traces (Fig. 7B) provides evidence that some animals were alive in the sediment soon after burial. The lower frequency of occurrence of larger burrows in the GPB compared to beds higher in the section (e.g., Raymond Quarry: see Allison and Brett, 1995) could have been controlled by fluctuations in oxygen levels at the sediment-water interface. Powell et al. (2003) suggested that the Burgess Shale community was preserved within an exaerobic zone, in which pore water in the mud was anoxic but overlying seawater was oxygenated and favorable to life. Such a model provides a simple explanation for the absence of deep vertical burrowing in these sediments (see also discussions in Orr et al., 2003). Another explanation is that most burrows in the GBP were shallow and present only in the uppermost water-saturated layer of sediment.

One of the rare infaunal animals that could have produced large burrows in the GPB is the priapulid worm *Ottoia* (Conway Morris, 1977). In beds of the Raymond Quarry, *Ottoia* is sometimes associated with a putative organic-walled tube or feeding burrow (Devereux, 2001). These burrows were thought to be shallow and parallel to the sediment surface (Devereux, 2001), and not U-shaped, contrary to previous interpretations (Conway Morris and Whittington, 1979). The rarity of these burrows in the Raymond Quarry was, in part, interpreted to be the consequence of the obrution event itself remobilizing the topmost water-saturated layer of sediment. Devereux (2001) also suggested that the rarity of feeding burrows of *Ottoia* in the Raymond Quarry could be the result of sudden changes in oxygenation. The sediment interface was certainly not firm in the GPB, as evidenced by the occurrence of numerous organisms attached to shelly remains which presumably served as anchors (Caron, 2005b; see also Dornbos et al., 2005).

Conway Morris (1986) suggested that the presence of numerous individuals preserved at various angles to the bedding planes, the presence of sediment between appendages of arthropods, and preferential orientations of vacant tubes of the priapulid worm *Selkirkia* all provided evidence for transportation to the site of burial. The variable orientation of many arthropods with respect to bedding planes and the presence of sediment between appendages does not necessarily require *large-scale* transport. Based on a study of *Marrella*, Whittington originally envisaged only moderate or no transport of the biota (Whittington, 1971a, 1971b, but see 1980). Most specimens of *Marrella* in the GPB are preserved parallel to bedding (Caron, unpublished data), suggesting little or no transport. Preferential orientation of empty *Selkirkia* tubes (Conway Morris, 1986) has been interpreted as a consequence of minor currents at the time of burial. There is no evidence of preferential orientation of empty *Selkirkia* tubes in the BAs analyzed in this study, however (Supplementary Material 5N[2]). It is possible that many of the *Selkirkia* tubes studied by Conway Morris came from calcisiltite beds, owing to sampling artefact, and thus represent fossils accumulated under different depositional conditions.

Decay processes and the degree of disarticulation for various species in the Phyllopod Bed (*Ottoia prolifica*: Conway Morris, 1977, p. 30; polychaetes: Conway Morris, 1979, p. 266; *Sidneyia*: Bruton, 1981, p. 624; and *Wiwaxia*: Conway Morris, 1985, p. 521) have been related to varying amounts of preburial transportation. The timing of death, burial, and decay of many organisms, however, remained largely inferential in most cases (Whittington, 1985, p. 129). For example, decay of *Wiwaxia* may have proceeded before or during its deposition (Conway Morris, 1985, p. 521). As explained here, the recovery of fossil census and time-averaged components together is the best criterion on which to argue that most benthic organisms in the GPB were only slightly disturbed by the event of burial itself and were preserved within habitat.

This last conclusion, however, should be flexible and may depend on the particular position of each organism at the time of burial. For example, the rarity of specimens of *Tuzoia* preserved with eyes is interpreted to be due to a free-swimming life style (Vannier et al., in press) rather than to a unique chemical composition of the nonbiomineralized parts. Empty carapaces of *Tuzoia*, presumably representing molts or carcasses, may have been transported by currents prior to burial. Transport of remains of other inferred pelagic or nekto-benthic organisms with shelly or heavily sclerotized components (e.g., see Table 1 in Conway Morris, 1986) is very likely. Some of these species (i.e., bradoriids, and *Isoxys*) have now been found with parts of their nonbiomineralized tissues, but such occurrences remain very rare (Caron, 2005b). If the presence of dissociated and oriented sclerites of the putative polychaete *Wiwaxia* (Supplementary Material 5M[2]) provides an average benchmark of transport among mobile epifaunal species, then it becomes clear that transport must have been very limited. Transported elements of pelagic organisms would most likely have been carried short distances within the basin or derived from the platform.

Because the GPB community is composed mostly of organisms living on or in the benthos, representing about 75% of all species and individuals on average (Caron, 2005b), the potential mix of some transported elements probably did not significantly affect the overall bed assemblages. Although some range in degree of disturbance cannot be denied, the data presented herein support the conclusion that transport was trivial and the distinction between a preslide and postslide environment is unnecessary.

Most organisms from the Greater Phyllopod Bed probably lived, died, decayed, and were buried in the same local environment (Fig. 8). There are numerous fossil occurrences through the GPB that corroborate this interpretation. It is impossible here to provide a detailed and exhaustive list for each BA, and only a few examples are provided as follows (see also Caron, 2005b). Articulated molts of trilobites and other arthropods are interpreted as evidence of near *in situ* burial (Fortey, 1975) and rapid

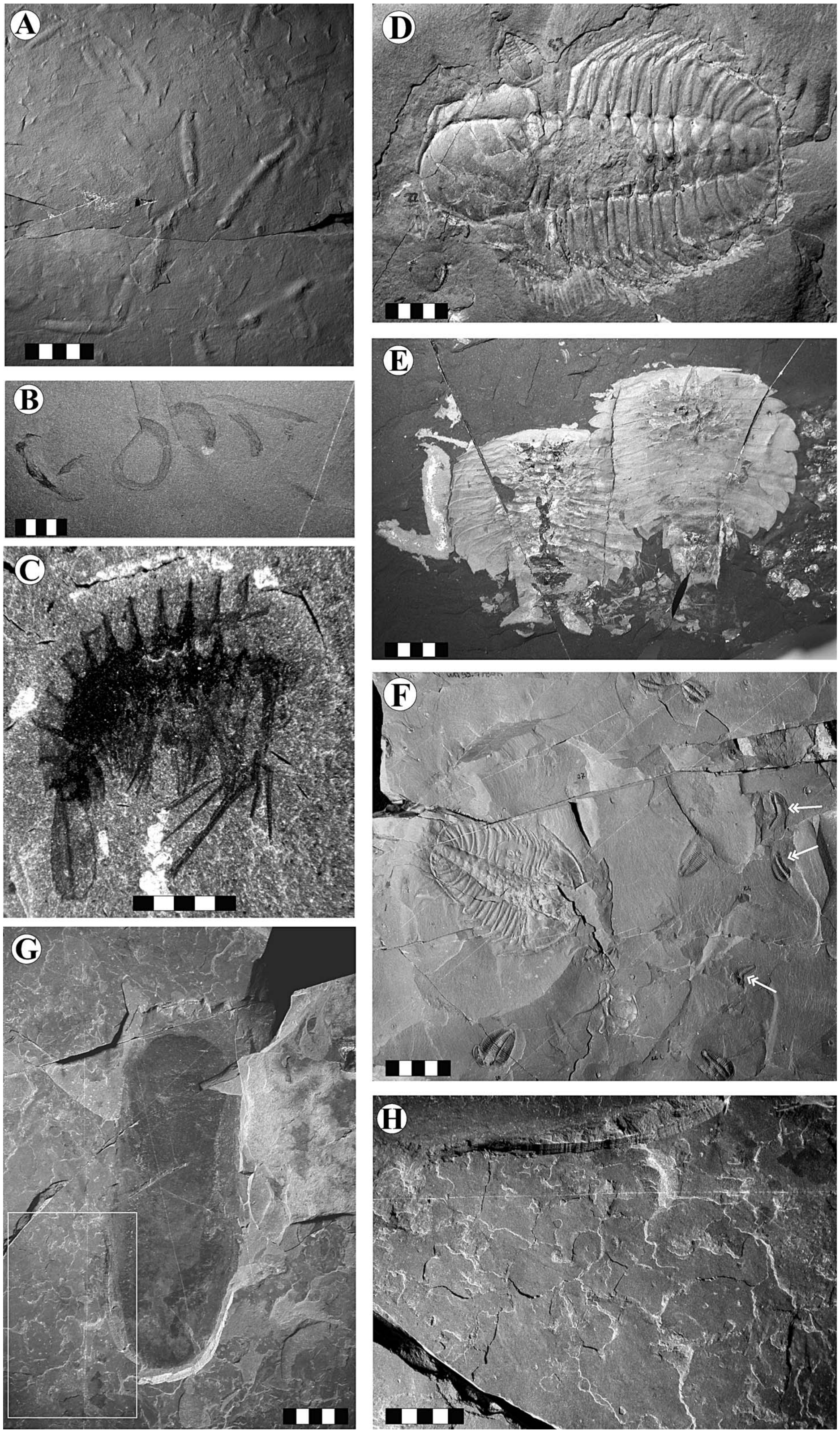

FIGURE 7—Within habitat assemblages inferred from qualitative fossil evidence in the GPB (See also Supplementary Material 6[2]). Scale bars: A = 40 mm; F = 30 mm; E, G = 20 mm; D, H = 10 mm; B = 5 mm; C = 2 mm. (A) Macroburrows (ROM 57710, BA-50). (B) Microburrow of an indeterminate organism (ROM 56978, BA-370). Putative molts (C–E); (C) Juvenile of *Alalcomenaeus* (ROM 57711, BA-120); (D) *Olenoides* (ROM 56631, BA-465); (E) *Sidneyia* freshly molted (left) with its putative exuviae (right) (ROM 56945, BA-210): (F) Outstretched and articulated *Olenoides* with nonbiomineralized preservation (center left), and numerous specimens of the trilobite *Elrathina cordillerae* in enrolled positions (double white arrows) (ROM 56632; BA-420). (G–H) Large specimen of *Odontogriphus* directly superposed on a layer of the putative cyanobacterium *Morania* covering the entire surface of the slab (ROM 57712; BA-400). *Morania* is at the base of the mudstone bed. (G) Overall view; (H) Detail of *Morania* from G, showing cohesive behavior and wavy-crinkly character of laminae.

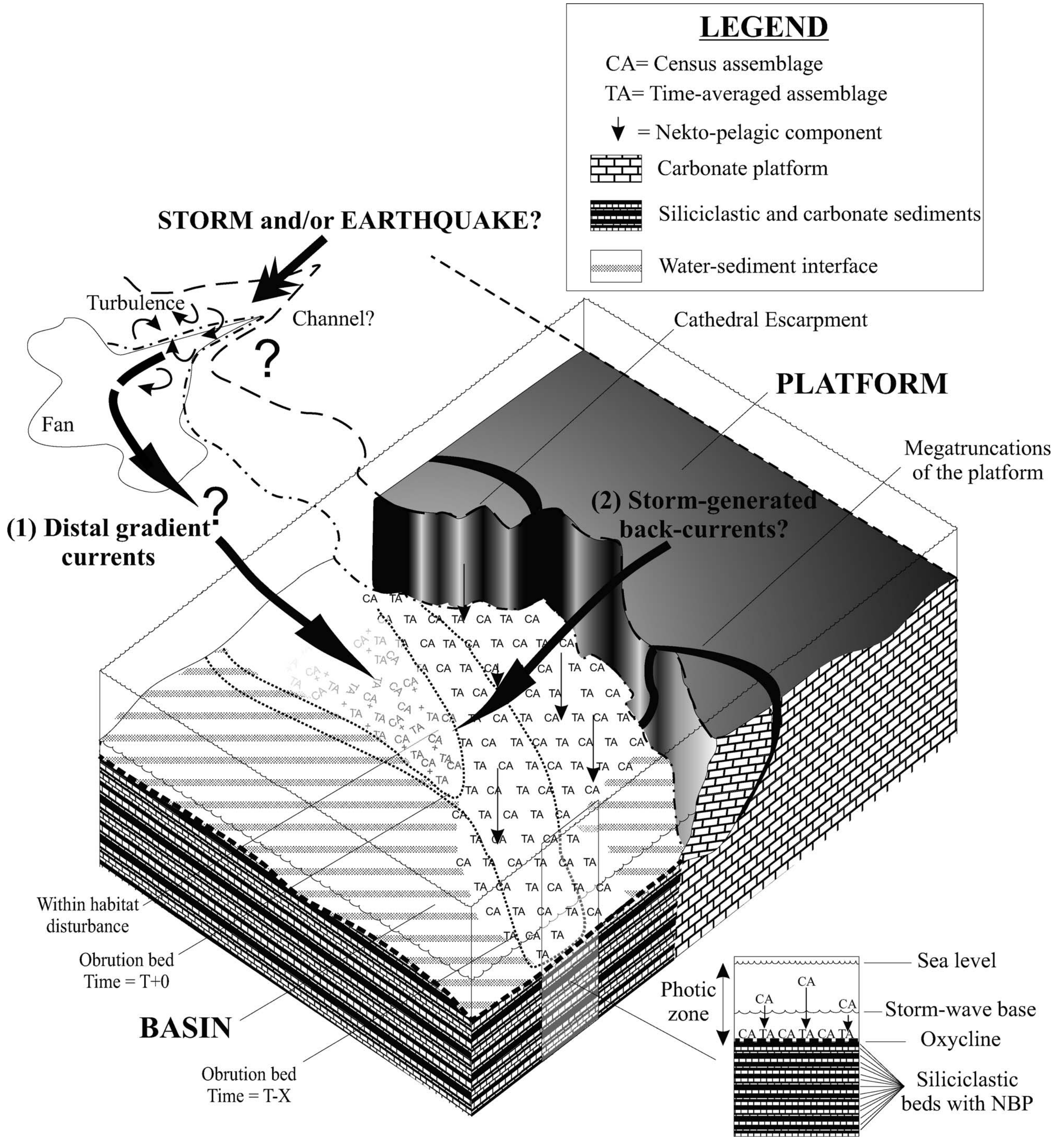

FIGURE 8—Paleoenvironmental synthesis. Sedimentological and biostratinomic evidence show that the biota was buried rapidly, either by high-density fluidized mudflows traveling parallel to the Cathedral Escarpment (1, see Allison and Brett, 1995), or by storm-generated back currents directly from the platform (2, see Aitken and McIlreath, 1990; Gostlin, 2006). In the first hypothesis, gravity mudslides may have originated along the outer carbonate platform margin, possibly within the fan of a hypothetical channel (T.P. Fletcher, personal communication, 1999). These mudslides probably originated during periods of increased turbulence (e.g., storms or earthquakes). The presence of megatruncations along the platform provides evidence of seismic activity and large-scale slumps (Stewart et al., 1993). Based on this study, most of the biota is thought to have been living at the base of the Cathedral Escarpment at the time of burial; see text for details.

entombment in obrution *Lagerstätten* deposits (Speyer, 1987; Whittington, 1990; Karim and Westrop, 2002). In the GPB, molts of *Olenoides* (in BAs -150, -170, -210, -245, -420, and -465; Fig. 7D), *Sidneyia* (BA -210; Fig. 7E), and juveniles of *Alalcomenaeus* (Caron, 2002; BAs -120 and -130; Fig. 7C) have been observed. Direct species associations and clusters provide additional arguments that many specimens were stunned and died close to where they lived. A selection of examples includes: the association of enrolled specimens of the trilobite *Elrathina cordillerae* with preserved soft parts together with molts and pristine specimens of *Olenoides* (e.g., BA-420, Fig. 7F); the presence of numerous ptychagnostids and *Pagetia* in vacant tubes of the priapulid worm *Selkirkia* (see Chatterton et al., 2003); and clusters of the large arthropod *Canadaspis perfecta* reaching hundreds of specimens per meter square, with no sediment between overlapping specimens (BA-350, Supplementary Material 5A[2]; see also clusters of bradorids and *Selkirkia*, Supplementary Material 5G[2] and 5N[2], respectively).

Some previous studies have suggested *in situ* burial of parts or all of the Burgess Shale community (Allison and Brett, 1995; Powell et al., 2003). Based on a study of samples and field observations from the Raymond Quarry, Allison and Brett (1995) concluded that the Burgess Shale was deposited under fluctuating benthic redox conditions. They (Allison and Brett, 1995) suggested that nonbiomineralized fossils would have been preserved exclusively during times of benthic anoxia, and that *in situ,* low-diversity assemblages of *r*-selected organisms would have colonized the seafloor during times of available benthic oxygen, forming shelly accumulations. Evidence for *in situ* burial included the presence of articulated molts of trilobites and burrows. This model of preservation, however, is challenged by detailed studies of the Raymond Quarry community (Devereux, 2001). Devereux (2001) has shown that *in situ* burial can be inferred in layers associated with nonbiomineralized organisms, including the priapulid *Ottoia* preserved in its putative feeding burrow, molts of *Sidneyia*, and numerous sessile organisms with holdfasts attached to shelly substrates. The occurrence of large numbers of the nonbiomineralized animal *Banffia constricta* in beds from the Emerald Lake Oncolite Member, located above the Raymond Quarry, with ichnofossils on the same surface, provides additional evidence for *in situ* burial in the presence of some local oxygen (Caron, 2005a).

A cluster of *Ottoia* specimens around a freshly molted instar of the arthropod *Sidneyia* from the Raymond Quarry was interpreted as an *in situ* assemblage and evidence of scavenging (Bruton, 2001). Such associations have also been noticed in the GPB (Caron, 2005b). In the study by Powell et al. (2003), *in situ* burial in the Walcott Quarry was inferred from the presence of surficial traces. They also concluded, on the basis of geochemical evidence, that the bottom waters must have been oxygenated at the time of burial. The previous study relied on hand samples collected from different stratigraphic horizons with and without NBP. Paleo-redox conditions were estimated from the study of trace metals, and it was shown that the pattern of redox-sensitive elements was not different between beds with NBP and those without (Powell et al., 2003). Unfortunately, without a detailed analysis of samples from fossil-bearing beds at the level of individual BAs (i.e., as defined in this study) it is possible that some of these samples may have recorded both anoxic and oxic benthic conditions, resulting in an averaged exaerobic result (Gaines, R.R., personal communication, 2005). Detailed geochemical analyses in the GPB (at the level of individual BAs) are necessary to determine whether or not nonbiomineralized organisms were preserved exclusively during times of benthic anoxia.

Decay Biases

Most taphonomic research on the Burgess Shale has concentrated on diagenetic mechanisms leading to NBP (Butterfield, 1990, 1995, 1996, 2002, 2003; Towe, 1996; Orr et al., 1998; Petrovich, 2001), and these studies have certainly brought about a better understanding of fossilization processes for individual taxa. Butterfield (1990, 1995, 1996, 2003) suggested that the community composition of the Burgess Shale is strongly biased toward the preservation of organisms with recalcitrant tissues (e.g., cuticles, chaetae), thereby eliminating organisms with low preservation potential such as those without a cuticle (e.g., flatworms). The discovery of three-dimensional phosphatized midgut glands (Butterfield, 2002, 2003), however, supports the view that at least in some cases, some of the most labile tissues have a very high preservation potential, in particular when the gut content promotes authigenic mineralization. The fact that organic carbon is documented in a number of taxa demonstrates that the preservation of nonbiomineralized tissues is governed by a variety of taphonomic pathways (see also Petrovich, 2001; Briggs, 2003), which could have operated simultaneously even within the same organism soon after burial. These pathways could be related to different susceptibilities of nonbiomineralized tissues to decay, the more recalcitrant parts being preserved as organic compressions and the more labile parts (e.g., gut diverticulae) becoming phosphatized (Butterfield, 2002, 2003) or preserved as clay minerals (Orr et al., 1998; Orr et al., 2003; Gabbott et al., 2004; Zhu et al., 2005). Experimental taphonomic studies have shown that authigenic mineralization appears to be controlled by microbial activity and therefore a minimum amount of decay is necessary for preservation of nonbiomineralized parts (Sagemann et al., 1999).

In the GPB, many species from body plans with very low preservational potential are present in most BAs (Supplementary Material 6[2]) including cnidarians (*Mackenzia*), ctenophores (*Ctenorhabdotus*), chaetognaths, hemichordates (*Ottoia tenuis* + Hemichordata A), putative holothurians (Holothuroidea A, *Portalia mira*, *Eldonia*), and chordates (e.g., *Pikaia*). *Odontogriphus*, regarded originally as a lophophorate (Conway Morris, 1976), is a nonshelled mollusc and most likely lacked a resilient cuticle (Caron et al., 2006). Because most previous authors agree that stabilization and early mineralization occurred soon after burial, which is evidenced by the occurrence of complete and dissociated nonbiomineralized organisms of various species in each BA, it is possible that all specimens present at the time of burial were likely preserved independent of their original tissue composition and state of decay.

Ecological Importance of Bacterial Mats

Powel et al. (2003) speculated that the finding in the Walcott Quarry of the calcareous bacterium *Girvanella* (probably *Obruchevella;* see Mankiewicz, 1992) intertwined with less common filaments composed of pyritic spheres (5–10 μm) might represent a mixed cyanobacterial–chemosynthetic consortium probably living at the limit of the photic zone. This idea was reinforced by the finding of surficial traces on one calsisiltite slab, possibly produced by the putative monoplacophoran mollusc *Scenella* (Powell et al., 2003). The evidence of grazing traces is problematic; inasmuch as the only reported link between the traces and *Scenella* was a similar width (see Fig. 6 in Powell et al., 2003), and the authors did not provide any evidence of preservation of mats *per se* (Schieber, 1999). Bacterial filaments were seen only in petrographic thin sections from calcareous beds, but, surprisingly, a thin section of the slab with putative traces was not provided. Despite these problems, Powell et al. (2003) speculated that the Burgess Shale substrate may have maintained a mat-based ecology typical of Precambrian communities. Large and discrete megascopic sheets of the putative benthic cyanobacterium *Morania* (Satterthwait, 1976) are present in many BAs in dense aggregates often covering entire slab surfaces (especially in BAs -380, -400; Figs. 7G–7H). *Morania* is preserved as microscopic pyritized filaments (figs. 3–4, pl. 1 in Satterthwait, 1976) and appear similar to the filaments described from calcareous beds by Powell et al. (2003, fig. 5B). Based on the criteria of Schieber (1999), the matlike aspect of *Morania* includes cohesive behavior, wavy-crinkly character of laminae, and irregular wrinkled bed surfaces (see Fig. 7H). Due to its abundance (present on about a third of all slabs studied in the GPB) it is possible that *Morania* played a role in the preservation of nonbiomineralized animals. *Morania* would have acted as a barrier in controlling exchange between pore waters and bottom waters (see also Wilby et al., 1996), presumably creating patches of anoxic mud at a local level directly under colonies. *Morania* may also have served an important ecological function in the community as a food source for grazers (Caron et al., 2006) and as a substrate for a number of mobile and sessile benthic metazoans adapted to typical Proterozoic-style soft substrates (Dornbos et al., 2005). The idea that the Burgess Shale substrate may have maintained a level of mat-based ecology more typical of Proterozoic environments is partially validated by this study, despite the fact that *Morania* does not grow as a continuous mat covering (see also Seilacher and Pflüger, 1994; Bottjer et al., 2000; Dornbos et al., 2004; Dornbos et al., 2005). A detailed study of *Morania* and its relationship with the biota and the depositional environment, however, is beyond the scope of this paper.

CONCLUSIONS

Variation in quality of preservation across taxonomic groups, populations, and individuals in single BAs is attributable to decay processes prior to burial combined with limited disturbance during burial. Most organisms are preserved within habitat, judging principally by the presence of fossil census and time-averaged assemblages. The relative position of the species in the CCA ordination diagram indicates the extent to which different taxa are affected by preburial decay. As predicted by experimental studies, polychaetes decay more rapidly than arthropods, and seem to be absent in some time-averaged assemblages. The number of species is not greater in BAs with well-preserved specimens of *Burgessochaeta*, however, and this strongly suggests that preservation biases have not affected the overall diversity of the Burgess Shale.

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