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Palaeogeography, Palaeoclimatology, Palaeoecology 258 (2008) 222–256

PALAEO

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Paleoecology of the Greater Phyllopod Bed community, Burgess Shale

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Accepted 3 May 2007

Abstract

To better understand temporal variations in species diversity and composition, ecological attributes, and environmental influences for the Middle Cambrian Burgess Shale community, we studied 50,900 fossil specimens belonging to 158 genera (mostly monospecific and non-biomineralized) representing 17 major taxonomic groups and 17 ecological categories. Fossils were collected *in situ* from within 26 massive siliciclastic mudstone beds of the Greater Phyllopod Bed (Walcott Quarry — Fossil Ridge). Previous taphonomic studies have demonstrated that each bed represents a single obrution event capturing a predominantly benthic community represented by census- and time-averaged assemblages, preserved within habitat. The Greater Phyllopod Bed (GPB) corresponds to an estimated depositional interval of 10 to 100 KA and thus potentially preserves community patterns in ecological and short-term evolutionary time.

The community is dominated by epibenthic vagile deposit feeders and sessile suspension feeders, represented primarily by arthropods and sponges. Most species are characterized by low abundance and short stratigraphic range and usually do not recur through the section. It is likely that these are stenotopic forms (i.e., tolerant of a narrow range of habitats, or having a narrow geographical distribution). The few recurrent species tend to be numerically abundant and may represent eurytopic organisms (i.e., tolerant of a wide range of habitats, or having a wide geographical distribution). Rarefaction curves demonstrate variation in species richness through the GPB and suggest that more stenotopic species could still be discovered with additional sampling. Comparisons between richness and evenness trends suggest that the community is relatively stable overall, despite gradual species turnover through time, especially in assemblages from younger beds. Less diverse assemblages with low species evenness possibly represent the onset of less favourable environmental conditions.

Fossil occurrences in individual beds were analysed using a range of statistical techniques (Correspondence Analysis, Canonical Correspondence Analysis, Minimum Spanning Tree, Indicator Species Analysis, Mantel Test) to extract community patterns. Results suggest the presence of four fossil assemblages based on distinct species associations. The different assemblages presumably reflect variations in environmental and ecological conditions, some acting through time, leading to species turnover. "Disturbances" (e.g., changes in paleo-redox conditions), differences in substrate firmness, and limited taphonomic biases are probably the main factors contributing to community structure. The influence of ecological factors, however, is also predicted from non-random patterns of species recurrences in successive events. Preliminary comparisons with Lower Cambrian Chengjiang-type assemblages of southern China suggest that the overall structure and ecology of Cambrian communities remained relatively stable until at least the Middle Cambrian in subtidal siliciclastic soft substrate environments.

Comparisons with modern marine benthic ecosystems further suggest the Burgess Shale community was probably highly dependent on immigration from a regional pool of species after each burial event. This could support the view that species

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doi:10.1016/j.palaeo.2007.05.023

availability, habitat characteristics, and recolonisation processes were more important in structuring the community in the long-term than species interactions or environmental variations at a local scale.

Keywords: Middle Cambrian; Paleoecology; Community structure; Temporal patterns; Multivariate methods

1. Introduction

Konservat Lagerstätten of Cambrian age (e.g., Burgess Shale and Chengjiang), characterized by the exceptional preservation of large numbers of non-biomineralizing organisms, demonstrate that complex marine benthic and pelagic communities flourished soon after the Precambrian-Cambrian transition (Whittington, 1985; Chen and Zhou, 1997; Hou et al., 2004). These sites are rich sources of biological and ecological information not available from most conventional Cambrian fossil deposits (Conway Morris, 1986). A high degree of stratigraphic continuity, an abundance and diversity of preserved soft-bodied animals, limited taxonomic control on post-burial decay and transport (Caron and Jackson, 2006), and a crucial position in the fossil record, make the Burgess Shale an ideal terrain for investigating long-term temporal dynamics of populations and patterns of species assembly. The main goal of this study is to analyse historical community patterns based on abundance data collected from discrete fossiliferous beds in the Burgess Shale Walcott Quarry. Analyses of patterns of species assembly, diversity, and abundance are crucial to our understanding of the structure of the earliest complex animal communities and the way in which they functioned following the "Cambrian explosion."

2. Burgess Shale biota

2.1. Previous quantitative studies

The most systematic paleoecological analysis of the Burgess Shale to date was based on an estimated 73,300 specimens from a two-metre thick section called the "Phyllopod Bed" (PB) (Conway Morris, 1986). The PB represents an informal rock unit in the Walcott Quarry (see Whittington, 1971). As emphasized elsewhere in greater detail (Caron, 2005), previous collections of Burgess Shale fossils from the PB lack information regarding the exact temporal ordering of the fossils. For example, Walcott's collection was assembled by extracting large blocks of shale using explosives and the blocks were transported to his camp to be split for fossils (Whittington, 1971). Unfortunately, this sampling procedure erased valuable information on the detailed stratigraphical origin of the fossils (at the level of individual beds). Subsequent expeditions by the Geological Survey of Canada (GSC) sampled sections of the PB based on rock thickness, in feet (Whittington, 1971). However, a one-foot thick interval of rock usually encompasses many different fossiliferous beds. Conway Morris estimated there were about 50 of these beds in the PB (Conway Morris, 1986), but unfortunately the fossil content of the individual levels was unknown. Therefore, Conway Morris had no other recourse than to study the PB community as an induced time-averaged assemblage of unknown duration (Conway Morris, 1986), thus removing the potential temporal record of variations in taphonomic and biologic processes. Problems related to sampling techniques probably contributed to additional biases when analyzing Burgess Shale collections (Conway Morris, 1986). For example, it is worth noting that most specimens from the Walcott collection have been separated from their associated biota. Slabs were trimmed closely around the specimens, and stored by taxonomic groups in keeping with museum collection management practices of the time. This process almost certainly removed additional associated taxa that were not specifically targeted for collection in the field. Moreover, the parts and counterparts of nearly 95% of specimens in the Walcott collection have been separated; this in turn may have greatly inflated the number of individual specimens counted and studied despite attempts to correct this bias (Conway Morris, 1986). Conway Morris' study gives, at best, a temporally condensed view of the community composition of the PB, which might be of advantage in eliminating short-term stochastic noise. It is likely, however, that sampling problems supersede short-term variability. Therefore, a re-evaluation of the PB community based on appropriate samples of individual fossiliferous beds using consistent collecting methods has been long overdue.

2.2. Locality, geological setting and sedimentology

Fossils with and without non-biomineralized preservation (NBP) used in this study were collected *in situ* by Royal Ontario Museum teams from discrete individual mudstone beds within the “Greater Phyllopod Bed” (GPB) on Fossil Ridge, north of the town of Field, British Columbia (see locality map in Caron and Jackson, 2006). The GPB is an informal seven-metre thick rock unit within the Walcott Quarry Member of the Burgess Shale Formation (Fletcher and Collins, 1998; Caron and Jackson, 2006). The Burgess Shale Formation corresponds to a relatively deep-water depositional setting, below storm wave base, situated at the basinward edge of a regional carbonate bank limited by the Cathedral Escarpment (Aitken and McIlreath, 1984).

Recent sedimentological investigations (Gostlin, 2006) have shown that the GPB is composed predominantly of centimetre-scale interbedded siliceous mudstones and calcisiltites. The vast majority of fine-grained siliciclastic beds are massive, have sharp bases, are not graded or coupled, and are not related to the calcisiltites as previously described (Piper, 1972). Most of the siliciclastic beds contain fossils with NBP and can be interpreted as obrution deposits (Caron and Jackson, 2006). Detailed sedimentological analyses of typical fine-grained siliciclastic horizons with NBP have failed to show any significant differences between beds (Gostlin, 2006).

2.3. Taphonomy

Recent biostratinomic studies based on qualitative and quantitative data (Caron, 2005; Caron and Jackson, 2006), suggested that transport of the biota in the GPB was minimal and that each obrution event is composed of census- and time-averaged assemblages. Most organisms lived, died and were preserved within their original habitat (assuming that they were transported at all) and were buried catastrophically during obrution events. Live and dead organisms were probably engulfed in high-density fluidized mud-flows in the nepheloid layer, generated within the basin, directly at the bottom of the Cathedral Escarpment (Allison and Brett, 1995), rather than in distal turbidites or storm deposits (Piper, 1972).

Gostlin (2006) suggested that the general conditions inhibiting decay and enhancing stabilization and preservation of soft tissues were constant across the GPB and not dependent on a particular redox condition or carbonate/aluminosilicate ratio; instead these conditions were probably influenced more by the grain size of the host sediment (see also Orr et al., 2003). Therefore, similar preservation is expected within the same lithofacies, and in particular within siliciclastic mudstone layers with NBP. This agrees with quantitative patterns of preservation across the GPB. Rarefaction curves suggest that preburial decay had no effect on species richness (Caron, 2005; Caron and Jackson, 2006). Therefore the effect of time-averaging through preburial decay is not an important controlling factor in the community. Early stabilization and/or early mineralisation of soft tissues must have occurred soon after burial across a wide range of taxa with NBP to explain the preservation of many body plans in the same bed. Overall, taphonomic biases appear to have had only limited effects on the original community structure (Caron and Jackson, 2006).

3. Material and methods

3.1. Terminologies

A bed assemblage (BA) represents the sum of all fossils (i.e., soft-bodied and shelly organisms) counted from within the thickness of massive fine-grained siliciclastic beds with NBP (see details in Caron, 2005; Caron and Jackson, 2006). [Note the use of “BA” in this study is not to be confused with “benthic assemblage” *sensu* Boucot, 1975, which refers to depth-zoned groups of communities]. Census counts of all macrofossils (i.e., specimens with one dimension >0.5 mm) were made on all slabs collected from the GPB (see Caron, 2005). BAs were not distributed evenly through the GPB, and vary in thickness from 2 to 170 mm (mean 30 mm) (Fig. 1). Following Rosenzweig (1995), we tested the amount of sampling bias using Fisher's α diversity index. Fisher's α does not depend on sample size and is based on the assumption that species abundances follow a log-series distribution (Fisher et al., 1943). However, even if the distribution of the population under study is different from a log-series distribution, it is not usually a problem (Rosenzweig, 1995). Fisher's α curves were obtained using the EstimateS© package (Colwell and Coddington, 1994). Fisher's α rises with an increasing number of species ($r=0.70$ $p<0.001$), demonstrating that overall the increase in number of species is not due to sampling biases (Fisher's α is not affected by variation in number of individuals), but due to historical factors (see also Caron, 2005).

The base of the PB was used as the main datum for measuring (in centimetres) the position of the strata above (+) and below (−) (Fig. 1). For example, BA-400 is roughly 400 cm below the base of the PB. Two BAs come from the PB itself: the Great *Eldonia* layer (BA + 120) and the Great *Marrella* layer (BA 0) of Walcott (1912).

3.2. Taxonomic and ecological groups

Identification was made to species level wherever possible (Table 1). In the rare instances where species identity was uncertain (most taxa are monospecific), determination was made to the genus level. New and undescribed species ($N=67$) were also included. Species were first grouped in higher taxonomic subdivisions, at the phylum level if possible, to give a general summary of composition (Fig. 2). The traditional definition of a "phylum" is expanded here to include a number of problematic taxa possibly representing stem-group members. Life and trophic groups of all species were divided into broad categories (Fig. 3) similar to the ones used in Conway Morris (1986). Four main categories of life habits were recognized: infaunal (I) and epifaunal (E) (sessile [S] or vagile [V]), nektobenthic (NK), and pelagic (P). Four trophic categories were also employed: suspension (SU), deposit (DE), hunter and/or scavenger (HS), and grazer (GR). Epibenthic primary producers (EPP) and species with unknown life habit and/or feeding type were also included (UN, Table 1). Contrary to Conway Morris (1986), we did not attempt to differentiate between high- and low-level suspension feeders and between deposit collectors and swallowers. Each species is assigned to a single life and trophic group, in agreement with published references (see Conway Morris, 1986; Briggs et al., 1994). Hypotheses of mode of life for new species are based on relative abundance, species associations, and comparisons with the functional morphology of fossil or extant species.

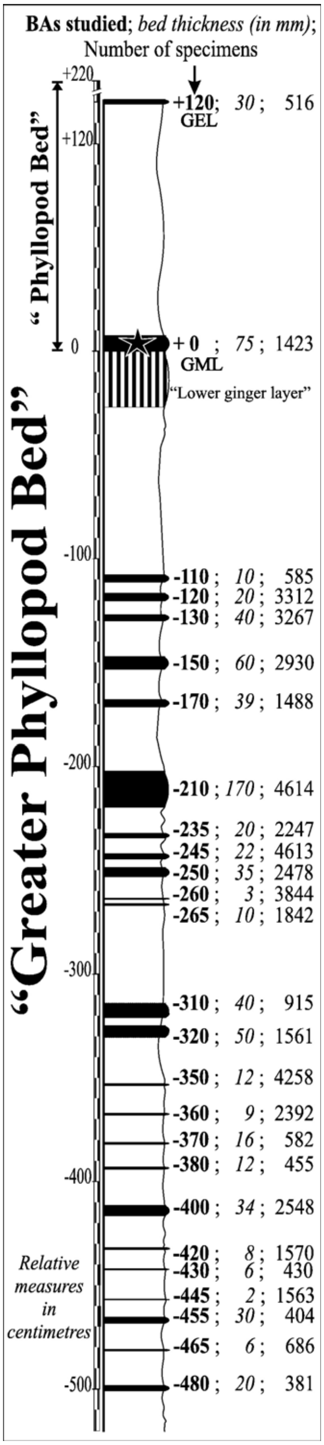


Fig. 1. Simplified stratigraphic section of the GPB. Only the 26 bedding assemblage (BA) with more than 300 specimens studied herein are represented (see text for details). The stratigraphic reference datum ("0" level) was fixed at the top of the "lower ginger layer", representing the base of the "Phyllopod Bed". Fossiliferous beds were ordered by approximate vertical distance from the stratigraphic reference datum to the top of the individual beds (see Caron and Jackson, 2006 for more details). GML = Great *Marrella* Layer, GEL = Great *Eldonia* Layer (Walcott, 1912).

3.3. Counts of specimens

A specimen is usually complete and articulated, but it can also be disarticulated with parts in close anatomical proximity. In rare cases, the number of specimens was estimated from individual elements (e.g., *Laggania*), and conservative estimates were provided for some other taxa (e.g., bradoriids, see Caron and Jackson, 2006). The specimens from all collected slabs were pooled per BA because numbers of individuals and species on slab surfaces were too small to be analyzed separately in a meaningful way. A total of 15,875 slabs were studied, 81% of which constituted both part and counterpart. To reduce sampling artefacts and to allow sufficient confidence for comparative

Table 1
Taxonomic composition of the Greater Phyllopod Bed per main taxonomic and ecological groupings (abbreviated names of taxa in brackets). See also Figs. 2 and 3

Algae+ Cyanobacteria	EPP	Algae A to G (Alga A to G), *Bosworthia* spp. (Bosw), *Dalyia* spp. (Daly), *Dictyophycus gracilis* (Dict), *Marpolia spissa* (Marp), *Morania* spp. (Mora), *Wahpia* spp. (Wahp), *Waputikia ramosa* (Wapu), *Yuknessia simplex* (Yukn)
Annelida	EVDE	*Stephenoscolex argutus* (Step)
	EVGR	*Wiwaxia corrugata* (Wiwa) [this species is now attributed to the Mollusca, see Caron et al., 2006]
	IVDE	*Burgessochaeta setigera* (Bur se.), Polychaeta B to D (Poly B to D)
	IVHS	*Peronochaeta dubia* (Pero)
	NKHS	*Canadia spinosa* (Can s.)
	PESU	*Insolicorypha psygma* (Insol)
Arthropoda	ESSU	*Priscansermarinus barnetti* (Pris)
	EVDE	Arthropoda C (Arthr C), *Burgessia bella* (Burg b.), *Canadaspis perfecta* (Can p.), *Chancia palliseri* (Chan p.), *Ehmaniella burgessensis* (Ehm b.), *Ehmaniella waptaensis* (Ehm w.), *Elrathia permulta* (Elra p.), *Elrathina cordillerae* (Elr c.), *Hanburia gloriosa* (Han g.), *Marrella splendens* (Marr), *Mollisonia* spp. (Molli), *Waptia fieldensis* (Wapt)
	EVHS	Arthropoda A, F (Arthr A, F), *Emeraldella brocki* (Emer), *Habelia brevicauda* (Hab b.), *Habelia optata* (Hab o.), *Kootenia burgessensis* (Koot), *Molaria spinifera* (Mola), *Naraoia compacta* (Nara c.), *Naraoia spinifer* (Nara s.), *Olenoides serratus* (Olen), *Oryctocephalus burgessensis* (Oryc b.), *Oryctocephalus matthewi* (Oryc m.), *Sidneyia inexpectans* (Sidn)
	NKDE	Arthropoda E (Arthr E), *Pagetia bootes* (Page), *Perspicaris dictynna* (Per d.), *Plenocaris plena* (Plen), *Ptychagnostus praecurrens* (Ptyc)
	NKHS	*Alalcomenaeus cambricus* (Alal), *Alalcomenaeus cambricus* putative juveniles (Alal (Juv.)), *Branchiocaris pretiosa* (Bran p.), *Leanchoilia persephone* (Lean p.), *Leanchoilia superlata* (Lean s.), *Yohoia tenuis* (Yoho)
	NKSU	*Helmetia expansa* (Helm e.), *Liangshanella burgessensis* (Lian), *Liangshanella* sp. A (Lian A), Trilobita Larvae (Tril (L))
	PEHS	Dinocarida A, B, (Dino A, B), *Hurdia* sp. (Hur sp.), *Isoxys acutangulus* (Isox a.), *Isoxys longissimus* (Isox l.), *Laggania cambrica* (Lagg), *Opabinia regalis* (Opab)
	PESU	*Odaraia alata* (Odar), *Perspicaris recondita* (Per r.), *Sarotrocercus oblita* (Saro), *Tuzoia* sp. A, *Tuzoia* sp. B (Tuz A, B) [Morph A is probably *T. retifera* and Morph B=*T. canadensis* see Vannier et al, 2007]
	UNUN	Arthropoda B, G, H, I, J, K, (Arthr B, G, H, I, J, K), *Skania fragilis* (Skan)
Brachiopoda	ISSU	*Acrothyra gregaria* (Acro), *Lingulella* sp. A (Ling A) [now described as *Acanthotretella spinosa* in Holmer and Caron, 2006], *Lingulella waptaensis* (Ling w.), *Paterina zenobia* (Pate)
	ESSU	Brachiopoda A (Brach A), *Diraphora bellicostata* (Dira), *Micromitra burgessensis* (Micr), *Nisusia burgessensis* (Nisu)
Chaetognatha	NKHS	Chaetognatha (Chae)
Chancellorid	ESSU	*Chancelloria eros* (Chan e.)
Chordata	PESU	*Pikaia gracilens* (Pika)
Cnidaria	ESSU	*Cambrorhytium fragilis* (Cam f.), *Cambrorhytium major* (Camb m.), *Tubullela* sp. (Tubu)
	ESHS	*Mackenzia costalis* (Mack)
Ctenophora	PEHS	*Ctenorhabdotus* sp. (Cteno)
Echinodermata	ESSU	Echinodermata A (Echin A), *Echmatocrinus brachiatus* (Echm b.), *Gogia* sp. (Gog), *Walcottidiscus* spp. (Walc)
	EVDE	Holothuroidea A (Holo A)
	NKHS	*Eldonia ludwigi* (Eldo)
Hemichordata	ESSU	*Chaunograptus scandens* (Chaun)
	ISSU	Hemichordata A (Hemi A)
	IVDE	*Oesia disjuncta* (=*Ottoia tenuis*, Oesi)
Hyolitha	ESDE	*Haplophrentis carinatus* (Hapl)
Mollusca	EVGR	*Odontogriphus omalus* (Odon) [see Caron et al., 2006], *Scenella amii* (Scen)
Onychophora	EVHS	*Aysheaia pedunculata* (Aysh), *Hallucigenia* sp. A (Hal A), *Hallucigenia sparsa* (Hal s.), Onychophora A (Ony A)
Plathyhelminthes?	PEHS	Plathyhelmintha? A (Plath A)
Porifera	ESSU	*Capsospongia undulata* (Caps), *Choia* spp. (Choi), *Crumillospongia* spp. (Crum), *Diagoniella hindei* (Diag), *Eiffelia globosa* (Eiff), *Falospongia falata* (Falos), *Fieldospongia bellilineata* (Field b.), *Halicondrites elissa* (Hali e), *Hamptonia bowerbanki* (Hamp), *Hazelia* spp. (Haz sp.), *Leptomitus lineatus* (Lept), *Petaloptyon danei* (Petal), *Pirania muricata* (Pira), Porifera A to D (Por A to D) [porifera B is described as *Hazelia lobata* and porifera D to *Leptomitus undulates in* Rigby and Collins 2004], *Protospongia hicksi* (Prot), *Takakkawia lineata* (Taka), *Vauxia* spp. *(Vaux)*, *Wapkia* sp. (Wapk)
Priapulida	IVDE	*Fieldia lanceolata* (Field 1.)
	IVHS	*Ancalagon minor* (Anc), *Louisella pedunculata* (Loui p.), *Ottoia prolifica* (Otto), Priapulida A and B (*Priap A and B*), *Selkirkia columbia* (Selk), *Selkirkia* sp. A (Selk A)

Table 1 (*continued*)

Unknown	ESSU	*Dinomischus sagittiformis* (Dino s.), *Petaloptyon* sp. (Petal sp.)
	EVDE	“Creeposaurus” (Creep), *Portalia mira* (Port), *Scleritomorph A and C* (Scl A and C)
	EVGR	Scleritomorph B (Scl B)
	EVSU	Indet C (Ind C)
	EVUN	Worm-like A, B, D, E (Worm A, B, D, E)
	NKSU	“Woolly bear” (Wool)
	PESU	“Siamese-lantern-like” (Siam), *Amiskwia sagittiformis* (Amis)
	UNUN	Indet A, B, D to L (Ind A, B, D, L), *Pollingeria grandis* (Poll)

studies, only those 26 BAs with more than 300 specimens present were selected for this study. The final data matrix contains 50,900 specimens, assigned to 172 taxa within 26 BAs and represents the original source of data for this study (see the full data matrix in Caron and Jackson, 2006).

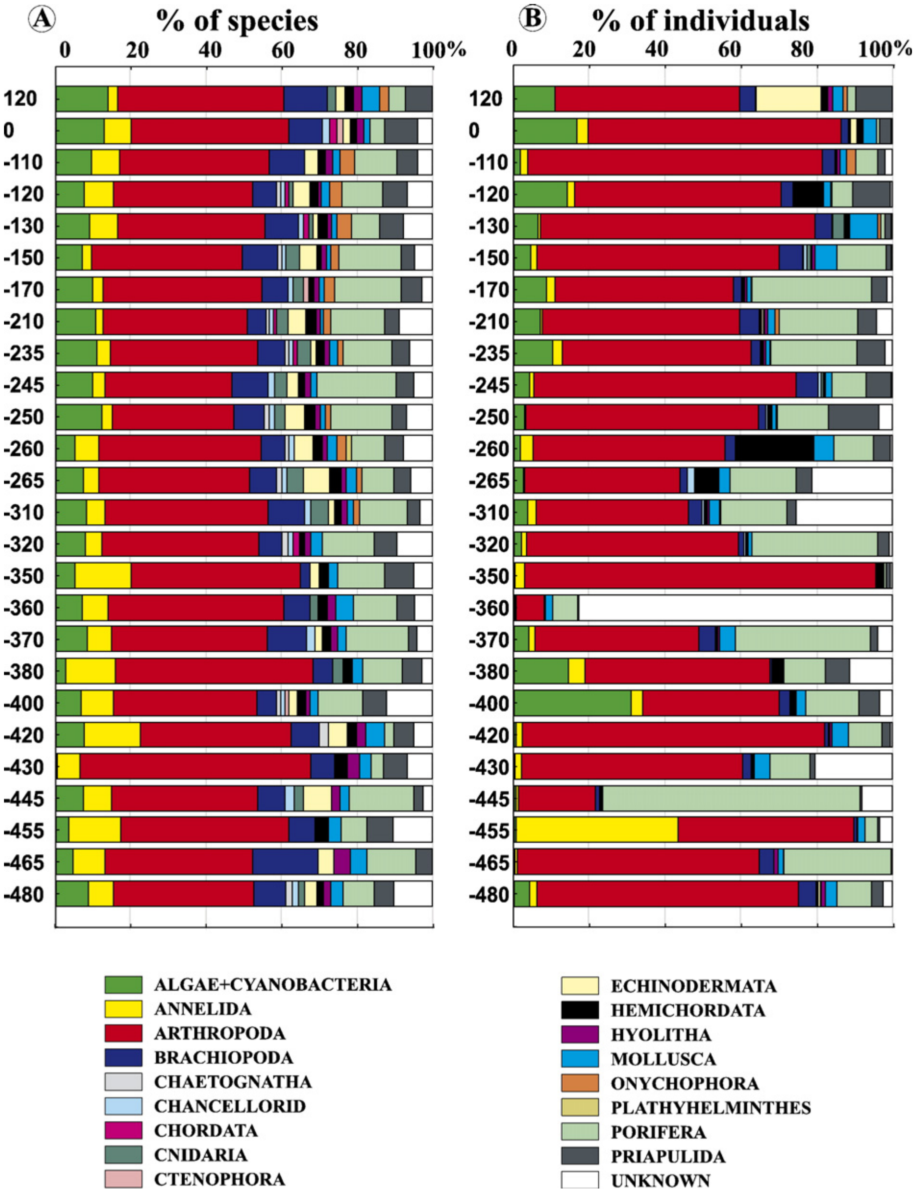


Fig. 2. Relative abundance within larger taxonomic groupings of: A) species; and B) individuals. See Table 1.

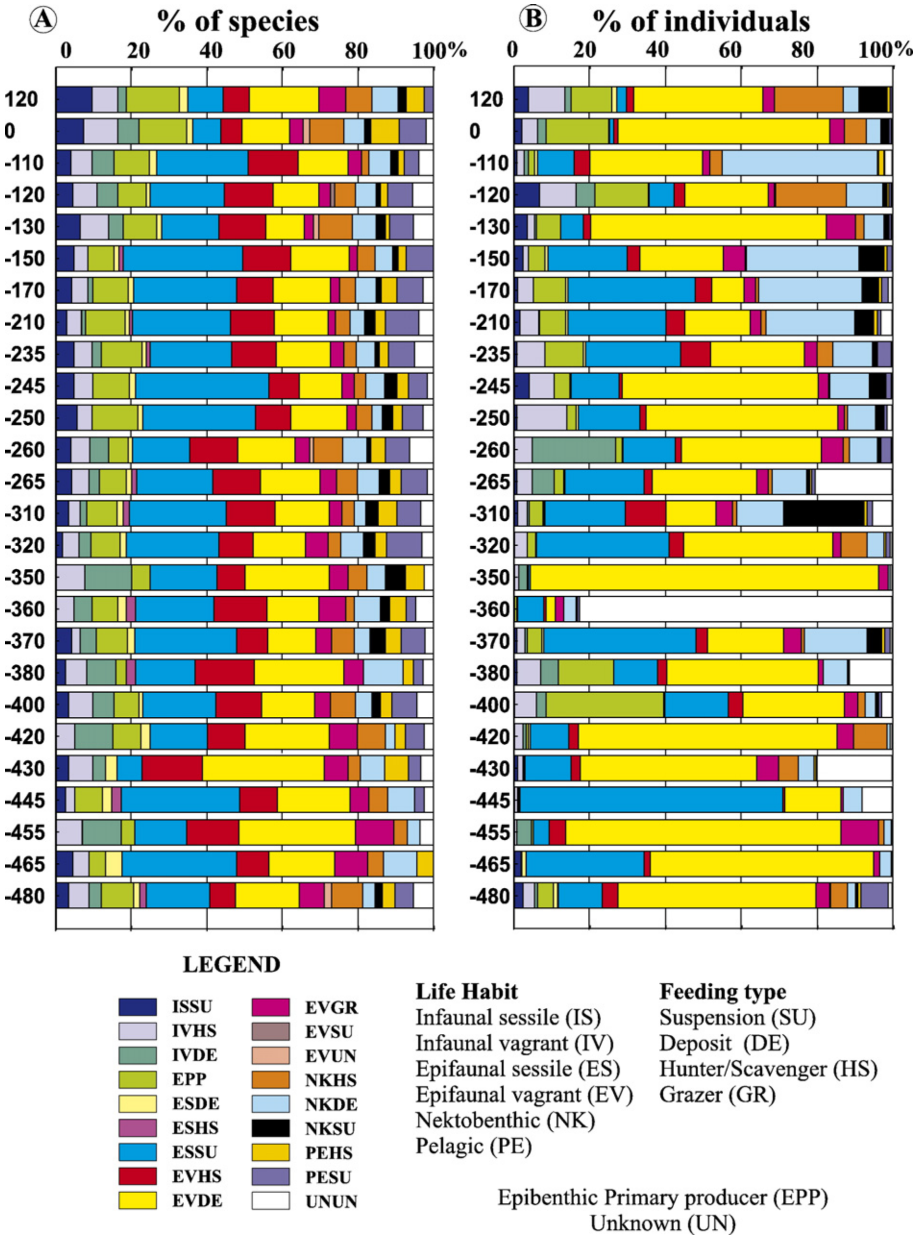


Fig. 3. Relative abundance within ecological groupings of: A) species; and B) individuals. See Table 1.

3.4. Multivariate methods

In order to summarize community patterns and to discover potential environmental and, or, ecological gradients we applied Correspondence Analysis (CA) (Gauch, 1982; Jackson, 1997), and Canonical Correspondence Analysis (CCA) (ter Braak, 1986), which both take into account species identity and abundance. CA is an indirect gradient analysis designed to summarize patterns in species composition without assuming whether this composition reflects biotic or abiotic influences, whereas CCA is a direct gradient analysis in which the species matrix is compared to a second independent data matrix and tested for relationship. CCA has an implicit assumption that the pattern in community composition is due to the factors in the second matrix, typically environmental variables. Single linkage cluster analysis was used in association with the CA in order to verify whether the CA plots provided a good multivariate summary (Legendre and Legendre, 1998). A Minimum Spanning Tree (MST) was superimposed on the ordination diagram and reflects changes in the composition of main clusters (Legendre and Legendre, 1998). Shorter branches in the MST indicate species showing similar association (i.e., occurring together in BAs across the GPB).

For all multivariate analyses, rare species were eliminated before computation, given that these species tend to be at the extreme ends of ordination scores (which are often compressed by CA) and provide little information regarding community patterns. Rare species were defined as those which occur in only one BA or have a cumulative relative abundance across all 26 BAs of less than 0.5%. Because the range of abundance varied considerably among species, the final data table was log transformed ($\mathrm{Log}_{10}\,(X+1)$) to give more equal weighting (Gauch, 1982; Legendre and Legendre, 1998). NTSYS© version 2.02 for PC (Rohlf, 2002) was used for both the CA ordination and classification methods. For CCA we tested the null hypothesis that there is no relationship between the temporal order of BAs and the pattern of species composition in the "species" matrix (along the first axis) using the CANOCO software (ter Braak and Smilauer, 1998).

We used Indicator Species Analysis (IndVal) (Dufrêne and Legendre, 1997) to determine whether some species are characteristic of particular groups of BAs defined from CA diagrams generated by PC-ORD (McCune and Mefford, 1999; McCune and Grace, 2002). The indicator value is maximum (100%) when all the individuals of a given species are present in all BAs of a given group (i.e., absent in any BAs from all the other groups).

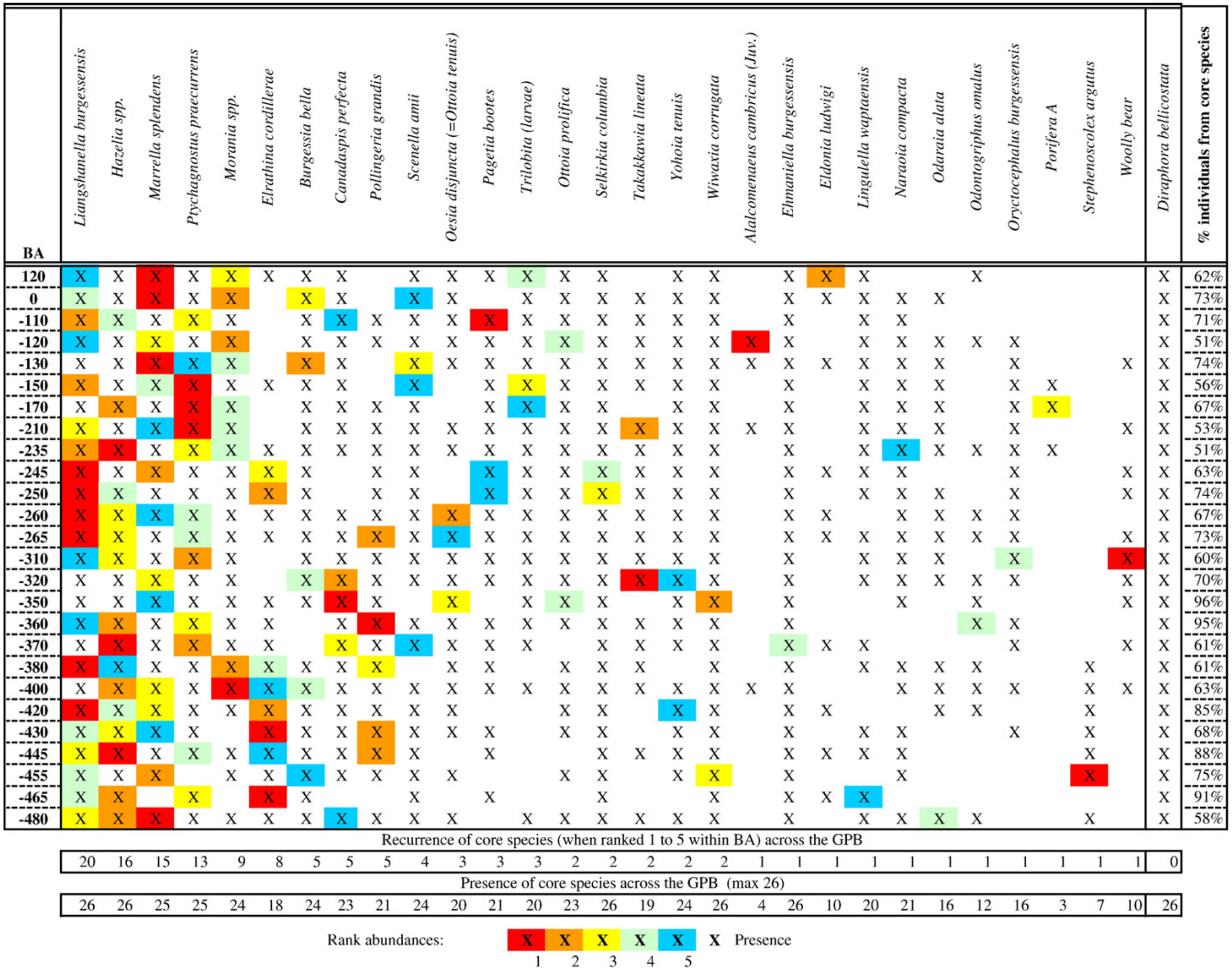
4. The GPB community

4.1. Concepts of "community" and temporal scale

Following Fauth et al. (1996) we use the term "community" to mean associations of organisms occurring at a specified place and time. In this study the GPB community comes from a seven metre-thick stratigraphic unit with a clear lower boundary (i.e., top of Wash Limestone Member), and upper boundary (i.e., top of the Upper Ginger layer; see Fletcher and Collins, 1998). The GPB does not contain any internal unconformities (e.g., erosional or non-depositional) or major faults and represents only a very small portion of the *Bathyuriscus–Elrathina* trilobite biozone (Fletcher and Collins, 1998). Depending on the estimate of the duration of this trilobite biozone itself, and taking into account its entire thickness (which represents about 20% of the Cambrian strata in the region, Aitken, 1997), the duration of the GPB was estimated to be between 10 ka and 100 ka, based on a constant sedimentation rate (K.E. Gostlin, pers. comm., 2004). According to Gostlin (2006), the calcisiltite beds between obrution beds represent gradual background accumulation of sediments (presumably over many years). If the duration of the GPB is estimated from comparisons with observed sedimentation rates in modern settings (about 0.1 m/1000 years — K.E. Gostlin, pers. comm., 2004; Stow, 1994), a fairly similar value was obtained. The lack of internal hiatuses in the GPB suggests that there were no major long-term environmental shifts in the area of deposition (Gostlin, 2006). This is supported by the fact that about 75% of species are present in both the oldest and the youngest BAs of the GPB. In other words, an estimated duration of 10 to 100 KA is probably realistic, placing the GPB community patterns in the context of ecological and short-term evolutionary time frames.

4.2. General abundance patterns

A constant relative proportion of species per phylum indicates the stability of ecologic structure throughout the studied interval. Percentage composition of individuals highlights the taxonomic dominance in the community. For example, arthropods represent the dominant taxonomic group in all BAs in both species and individual richness (Fig. 2A and B). Sponges rank second in dominance in most BAs (Fig. 2A and B). Taxonomic groups represented by one or a few species have in generally fewer individuals in most BAs, but there are exceptions (e.g., 40% of individuals in BA −455 are annelids). The community is dominated by epifaunal organisms (Fig. 3; ESDE, ESHS, ESSU, EVHS, EVDE, EVGR, EVSU, EVUN) comprising, on average, 63.9% of the species (from 45.5% in BA 0 to 78.0% in BA −445) and 69.2% of the individuals (from 12.8% in BA −360 to 95.4% in BA −350). Epibenthic, vagile deposit feeders (EVDE) are the dominant group in this category, representing, on average, 38.2% of the individuals and 16.8% of the species, followed by the epibenthic sessile suspension feeders (ESSU) and the epibenthic vagile hunters or scavengers (EVHS). Infaunal organisms represent 12.7% of the species and 7.4% of the individuals across BAs (Fig. 3; ISSU, IVHS, IVDE). Among those, vagile hunters or scavengers (IVHS) represent the largest group (species: 3.9%; individuals: 5.2%). The nektobenthos (Fig. 3; NKHS, NKDE, NKSU) averaged 12.1% of the species (from 6.9% in BA −455 to 16.3% in BA +120), and 15.7% of the specimens (from 0.7% in BA −350 to 44.8% in BA −110). Putative pelagic animals (Fig. 3; PEHS, PESU) represent a small fraction of both the total number of species (8.3% in average, from 0% in BA −455 to 12.3% in BA −320) and the total number of specimens (1.5% in average, from 0% in BA −455 to an exceptional 7.9% in BA −480).



BA	*Liangshanella burgessensis*	*Hazelia spp.*	*Marrella splendens*	*Ptychagnostus praecurrens*	*Morania spp.*	*Elrathina cordillerae*	*Burgessia bella*	*Canadaspis perfecta*	*Pollingeria grandis*	*Scenella amii*	*Oesia disjuncta (=Ottoia tenuis)*	*Pagetia bootes*	*Trilobita (larvae)*	*Ottoia prolifica*	*Selkirkia columbia*	*Takakkawia lineata*	*Yohoia tenuis*	*Wiwaxia corrugata*	*Alalcomenaeus cambricus (Juv.)*	*Ehmaniella burgessensis*	*Eldonia ludwigi*	*Lingulella waptaensis*	*Naraoia compacta*	*Odaraia alata*	*Odontogriphus omalus*	*Oryctocephalus burgessensis*	*Porifera A*	*Stephenoscolex argutus*	*Woolly bear*	*Diraphora bellicostata*	**% individuals from core species**
120	🟦X	X	🟥X	X	🟨X	X	X	X		X	X	X	🟩X	X	X		X	X		X	🟧X	X			X					X	62%
0	🟩X	X	🟥X	X	🟧X		🟨X	X		🟦X	X		X	X	X	X	X	X		X	X	X	X	X						X	73%
-110	🟧X	🟩X	X	🟨X	X		X	🟦X	X	X	X	🟥X	X	X	X	X	X	X		X		X	X							X	71%
-120	🟦X	X	🟨X	X	🟧X		X	X	X	X	X	X	X	🟩X	X	X	X	X	🟥X	X		X	X	X	X	X				X	51%
-130	X	X	🟥X	🟦X	🟩X		🟧X	X		🟨X	X	X	X	X	X	X	X	X	X	X	X	X	X	X		X			X	X	74%
-150	🟧X	X	🟩X	🟥X	X	X	X	X		🟦X		X	🟨X	X	X	X	X	X		X		X	X	X		X	X			X	56%
-170	X	🟧X	X	🟥X	🟩X		X	X	X	X		X	🟦X	X	X		X	X		X		X	X	X		X	🟨X			X	67%
-210	🟨X	X	🟦X	🟥X	🟩X		X	X	X	X	X	X	X	X	X	🟧X	X	X	X	X		X	X	X		X			X	X	53%
-235	🟧X	🟥X	X	🟨X	🟩X	X	X	X	X	X	X	X	X	X	X	X	X	X		X		X	🟦X	X	X	X	X			X	51%
-245	🟥X	X	🟧X	X	X	🟨X	X		X	X		🟦X	X	X	🟩X	X	X	X		X	X	X	X			X			X	X	63%
-250	🟥X	🟩X	X	X	X	🟧X	X		X	X		🟦X	X	X	🟨X	X	X	X		X		X	X	X		X			X	X	74%
-260	🟥X	🟨X	🟦X	🟩X	X	X	X	X	X	X	🟧X	X	X	X	X	X	X	X		X	X		X	X	X	X				X	67%
-265	🟥X	🟨X	X	🟩X	X	X	X	X	🟧X	X	🟦X	X	X	X	X	X	X	X		X	X	X	X	X	X	X			X	X	73%
-310	🟦X	🟨X	X	🟧X	X		X	X	X	X	X	X	X	X	X	X	X	X		X		X	X	X		🟩X			🟥X	X	60%
-320	X	X	🟨X	X	X		🟩X	🟧X	X	X	X	X	X	X	X	🟥X	🟦X	X		X		X	X	X	X	X			X	X	70%
-350	X	X	🟦X	X	X	X	X	🟥X	X		🟨X		X	🟩X	X		X	🟧X		X			X		X				X	X	96%
-360	🟦X	🟧X	X	🟨X	X	X		X	🟥X	X	X	X	X	X	X	X	X	X		X					🟩X	X				X	95%
-370	X	🟥X	X	🟧X	X	X		🟨X	X	🟦X	X	X	X		X	X	X	X		🟩X	X	X				X			X	X	61%
-380	🟥X	🟦X	X	X	🟧X	🟩X	X	X	🟨X		X	X		X	X	X		X		X		X	X	X	X			X		X	61%
-400	X	🟧X	🟨X	X	🟥X	🟦X	🟩X	X	X	X	X	X	X	X	X	X	X	X	X	X			X	X	X	X		X	X	X	63%
-420	🟥X	🟩X	🟨X	X	X	🟧X	X	X	X	X	X			X	X		🟦X	X		X	X			X	X			X		X	85%
-430	🟩X	🟨X	🟦X	X		🟥X	X	X	🟧X	X	X	X		X	X		X	X		X		X	X			X		X		X	68%
-445	🟨X	🟥X	X	🟩X	X	🟦X	X	X	🟧X	X		X			X	X	X	X		X	X	X	X					X		X	88%
-455	🟩X	X	🟧X		X	X	🟦X	X	X	X	X			X	X		X	🟨X		X			X					🟥X		X	75%
-465	🟩X	🟧X		🟨X		🟥X	X			X		X			X			X		X	X	🟦X								X	91%
-480	🟨X	🟧X	🟥X	X	X	X	X	🟦X	X	X	X		X	X	X	X	X	X		X		X	X	🟩X	X			X		X	58%
Recurrence of core species (when ranked 1 to 5 within BA) across the GPB	20	16	15	13	9	8	5	5	5	4	3	3	3	2	2	2	2	2	1	1	1	1	1	1	1	1	1	1	1	0	
Presence of core species across the GPB (max 26)	26	26	25	25	24	18	24	23	21	24	20	21	20	23	26	19	24	26	4	26	10	20	21	16	12	16	3	7	10	26	

Rank abundances:	🟥X	🟧X	🟨X	🟩X	🟦X	**X** Presence
	1	2	3	4	5	

Fig. 4. Core species in the GPB, ordered from most recurrent (left) to least recurrent (right). The different rank abundances within the core species are differentiated. When a core species is simply present (i.e., not necessarily ranking within the 5 most abundant species) a cross was added, so that rank abundances and recurrence patterns can be visually compared. *Diraphora bellicostata* on the right of the table represents the only species co-occurring in all 26BAs but which does not belong to the core species in at least one BA. The cumulative percentage of individuals represented by the core species is also tabulated on the rightmost column.

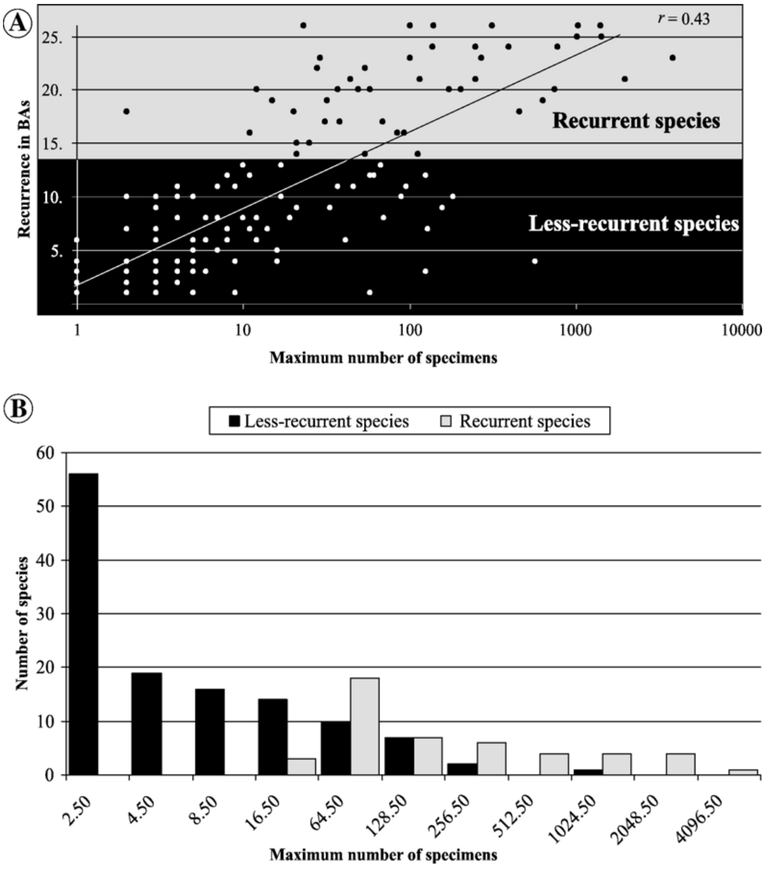


Fig. 5. Comparisons of the distributions of recurrent and less-recurrent species in the GPB. Recurrent species are defined as species present in 14 to 26 BAs. Less-recurrent species are defined as species present in 1 to 13 BAs (i.e., 50% of the BAs). A) Comparisons between recurrence of species and the maximum number of individuals present at any given BA through the GPB. B) Abundance distribution of recurrent and less-recurrent species. Abundance classes are octave (log2 classes). 0.5 was added to the upper boundary to each abundance class to assign species abundance unambiguously. Recurrence and abundance patterns were studied following Magurran and Henderson (2003). Less-recurrent species seem to follow a log-series distribution, whereas recurrent species tend to follow a log-normal distribution. However, observed frequency distributions for both groups of species were significantly different from those expected from the log-series distribution (Kolmogorov−Smirnov tests $p<0.01$). On the other hand, both distributions are consistent with expected truncated log-normal distributions (Kolmogorov−Smirnov tests $p>0.05$).

4.3. Core species

Core species are defined herein as the five species with the highest raw abundance (number of individuals per BA). Overall, these five are relatively stable in their abundance ranking across the BAs in the GPB (Fig. 4). *Liangshanella* sp. is the most abundant species with 20 occurrences across the GPB (the number of BAs in which the species represented one of the top-five ranked taxa in abundance out of a maximum of 26 BAs considered), followed by *Hazelia* spp. (16), *Marrella splendens* (15), *Ptychagnostus praecurrens* (13) and *Morania* spp. (9). In a previous study of the PB, Conway Morris (1986) considered that *M. splendens* was the most abundant species, followed by "*Ottoia*" *tenuis*, *Canadaspis perfecta*, *Burgessia bella* and *Ottoia prolifica*. However, with the exception of *M. splendens* (particularly in the GML but also in the GEL, the two layers from the PB sampled by the Royal Ontario Museum, Fig. 1), the other species are not particularly abundant in the GPB. It is striking that the small bradoriid *Liangshanella* sp. only ranks 11th with a mere 0.5% of number of individuals in the PB (Conway Morris, 1986) whereas this species is by far the most abundant in the GPB (around 12% of all individuals collected). *Liangshanella* sp. is a core species in both the GML and GEL, so it seems likely that small and common shelly fossils like *Liangshanella* sp. were under-sampled by Walcott and/or selectively counted by Conway Morris. In the GPB the most abundant species are usually represented by several times as many individuals as the next in rank (Appendix A). For example, in BA −350, the arthropod *Canadaspis* comprises almost 90% of all individuals. In this BA, the five most abundant species represent about 96% of all individuals (Fig. 4).

Overall, it is difficult to detect any major shifts in species identity within the core species across the GPB based on Fig. 4 alone. Conway Morris (1986) speculated that it might be possible to detect potential negative associations due to competition for similar resource between species from the same ecological groups. In order for competition to be important in determining composition, one or more resources must be limited in supply. Unfortunately, there are no means to assess such limitations from the fossil record.

4.4. Relationship between recurrence and abundance patterns

Fig. 4 shows that when a species is abundant in one BA (a core species) then this species tends to recur in many other BAs. Relationships between recurrence and abundance patterns were studied using all (including core) species following the methodology outlined by Magurran and Henderson (2003) (Fig. 5). Recurrent (or common) species were defined as those present in 14 to 26 BAs; less recurrent (or rare) species were defined as those present in fewer than 13 BAs. Comparisons between recurrence and the maximum number of individuals in any given BA per species show that numerically abundant species are usually recurrent ($r = 0.43$, $p < 0.0001$, Fig. 5 A). However, recurrent species are not dominant in number of species (Fig. 6); recurrent species represent 88% of the total number of individuals, despite representing only 27% of the total number of species ($n = 47$, Fig. 6). Only six species are present in all 26 BAs (Fig. 4; with the exception of *Diraphora bellicostata*, all six species appear at least once in the core species). These patterns demonstrate that most species lack temporal persistence or are rare enough to have been missed in some BAs. Interestingly, Fig. 6 fails to show the bimodal distribution typically found in modern ecological communities (Hanski, 1982) indicating that there are fewer species that are very common in their occurrence in the GBP.

4.5. Eurytopic vs. stenotopic species

The range chart of occurrences in the GPB (Appendix B), combined with recurrence patterns, provide a potential means to identify eurytopic and stenotopic species. Recurrent species with a longer stratigraphical range could possibly represent more generalist (or eurytopic) forms capable of surviving under a greater range of environmental conditions, or they could also represent species with wider geographical distribution. Species recurrent within a short stratigraphical range could be interpreted as tolerant of a narrower range of environmental conditions (stenotopic species). The 6 species present in all BAs (Fig. 4), and most core species can confidently be interpreted as generalists.

4.6. Species richness and evenness

4.6.1. Rarefaction

In our study we used the rarefaction method developed by Sanders (1968) to estimate the number of species expected from smaller size samples with fewer individuals (Caron, 2005; Caron and Jackson, 2006). Rarefaction curves differ in length along the horizontal axis, shape, and

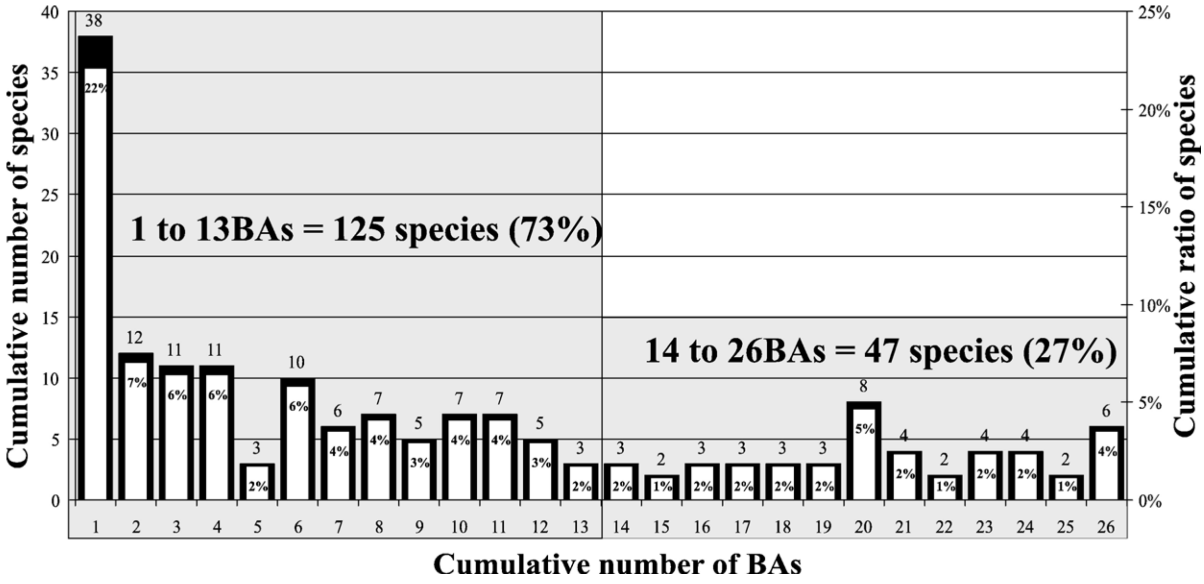


Fig. 6. Variations in number and ratio of species with cumulative number of BAs.

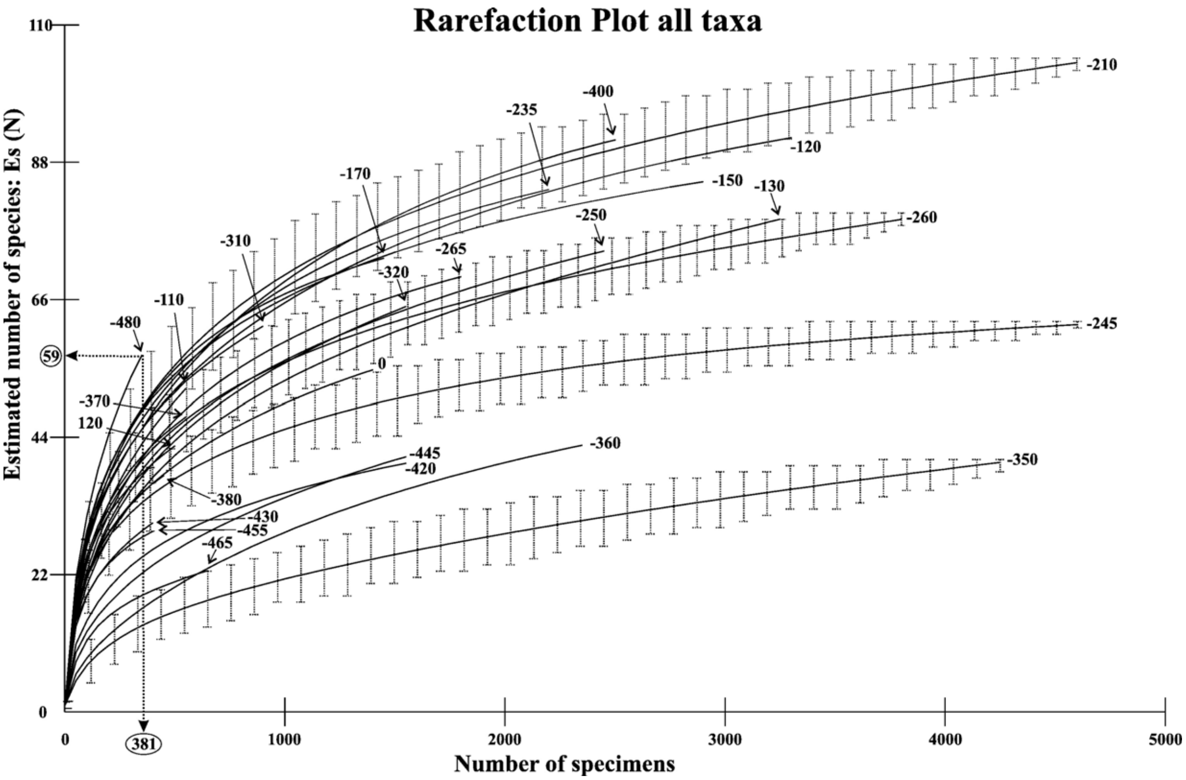


Fig. 7. Species richness estimates in the GPB at varying number of specimens using rarefaction curves based on all taxa. Confidence intervals (at 95%) are presented for only a few BAs (−210, −245, −260 and −350) for clarity. Rarefaction curves were calculated using ECOSIM© (Gotelli and Entsminger, 2001), and BioDiversity Pro© (McAleece, 1999). In both rarefaction programs, the expected numbers of species richness are derived from a modified version of Sanders' (1968) original algorithm (Hurlbert, 1971; Heck et al., 1975; Gotelli and Entsminger, 2001). In ECOSIM, calculations are 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. Expected numbers of species with their confidence intervals (fixed at 95%) were rarefied to the lowest number of specimens among the 26 BAs studied (381 specimens from BA −480, representing 59 estimated species).

in relative position to each other (Fig. 7). Length along the horizontal axis is determined by the number of specimens collected in the field. Most rarefaction curves (Fig. 7) have not yet reached an asymptote, supporting the idea that with additional sampling more species (probably stenotopic ones) could still be found in most BAs. This trend is also

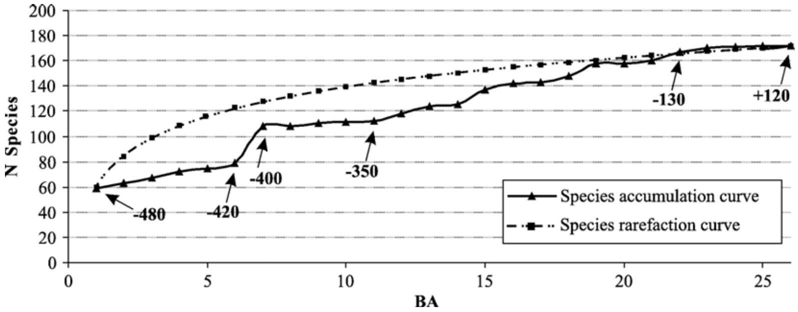


Fig. 8. Species-accumulation and rarefaction curves of the GPB (These curves were obtained by adding species from the oldest BA, −480, to the youngest BA, +120. The addition of some species-rich BAs, e.g., −400, greatly influences the shape of the species-accumulation curve). Species-accumulation curve represent the rate of accumulation of new species over the duration of the GPB and was computed with the total number of individuals of each species present in each BA, using the statistical package EstimateS© (Version 6.0b1) (Colwell and Coddington 1994). To detect whether "time" (order of BAs) is an important unidirectional factor in determining the shape of the accumulation curve, or whether time represents a mere fluctuation without particular direction to the number of species randomized curves (500 times) were computed to remove the effect of sample order producing smooth sample accumulation curves equivalent to sample-based rarefaction curves (Gotelli and Colwell, 2001).

revealed when species-accumulation curves are computed with the total number of individuals of each species present in each BA across the GPB, and even when these curves are randomized (Species rarefaction curve) to remove the effect of sample order (Fig. 8).

When estimates for species richness are compared for the same number of specimens and when the confidence limits for these curves are taken into account, it is possible to determine distinct variations among BAs (Fig. 7). For example, BA −210 does not lie within the confidence interval of BA −350 (except at very low number of specimens) and therefore has a different diversity level. However, BA −130 always lies within confidence levels of BA −260 and their diversity levels thus do not differ. Overall, BAs with large numbers of specimens are not particularly species rich; in fact, BA −350 is one of the least diverse fossil assemblages (even when confidence intervals are taken into account), despite containing more than 4000 specimens. In this BA, most specimens belong to a single arthropod species, *Canadaspis* (see pie plots, Appendix A). With some exceptions (BAs −370 to −400 and −480), older BAs (from BA −350 down) tend to have lower diversity levels than younger BAs (Fig. 7).

4.6.2. Species diversity trends

The shape of the rarefaction curves is determined by the type of abundance distribution of the species. In order to track changes in evenness, we compared the slopes of linear regression lines from Whittaker plots (Whittaker, 1965) also known as rank-abundance plots or dominance/diversity curves (Appendix A). Species evenness is here defined as the variability in species abundance (Magurran, 2004). When evenness and richness trends are compared (Fig. 9), it is clear that differences in species evenness are paralleled by similar trends in species richness. In particular, the number of specimens per species is more equal in BAs with more species. To help interpret the results, we used the following scheme: if both the estimated number of species and evenness levels are greater than their respective average across the GPB, then these BAs are referred to as type "A." Type "B" is the reverse and represents BAs with less species and lower evenness levels compared to average. Based on this classification, the GPB can roughly be divided into five main intervals from the oldest to the youngest assemblage. Starting from BA −480 (representing the BA with the highest richness and evenness levels found in the GPB), the community suddenly shifts to five impoverished assemblages (type B: BAs −465 to −420) which are typically characterized by having one or a few very abundant species (e.g., *Elrathina cordillerae* in BA −465; *Hazelia* spp. in BA −445). From BA −400 to BA −370 the community returns to more diverse and even assemblages (with the exception of BA −380) before declining again to BAs of type B with BA −350 and BA −360. However from BA −320 onward all the youngest BAs are of type A (BA −245 is the only possible exception). These patterns support the view of a major ecological and, or, environmental change after BA −480 and in particular between BA −465 and −420.

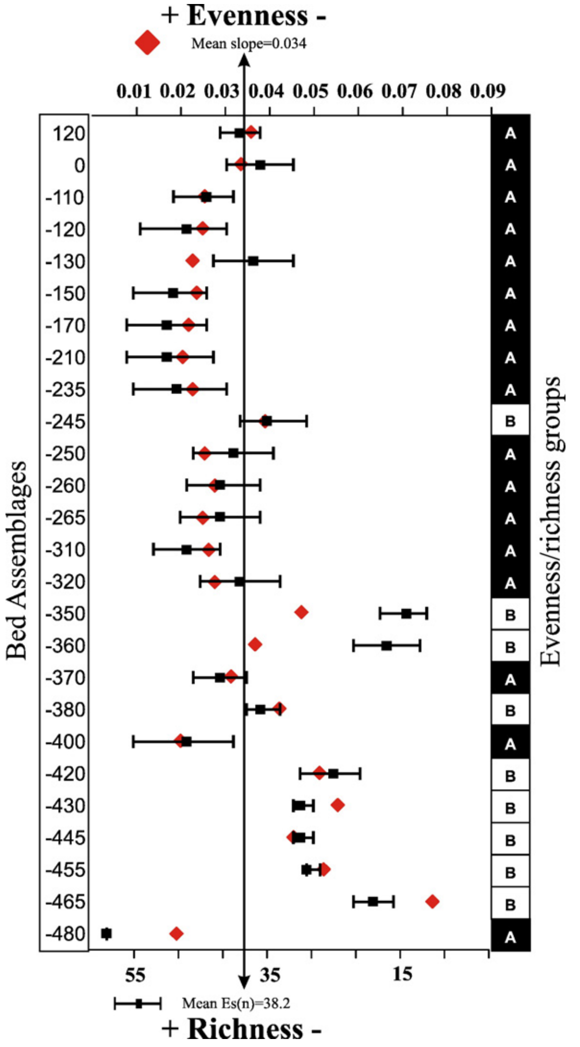


Fig. 9. Comparison between temporal patterns of species evenness and richness in the GPB. The slope of the regression lines and the number of estimated species (Es (*n*), with 381 specimens) are displayed sequentially per BA with the youngest BA on top. To facilitate interpretation, the mean of the slope of the linear regression lines across BAs and the mean of estimated species are also displayed. Species richness and evenness increase towards the left side of the diagram, and decrease towards the right side. Evenness/richness groups are displayed on the right side of the figure. Group "A" represents BAs with high species evenness and richness and group "B" represents BAs with relatively lower species evenness and richness. Distinction between groups "A" or "B" is based on the position of the slope of the linear regression line in relation to the mean of the slope of the linear regression lines across BAs and the mean of estimated species.

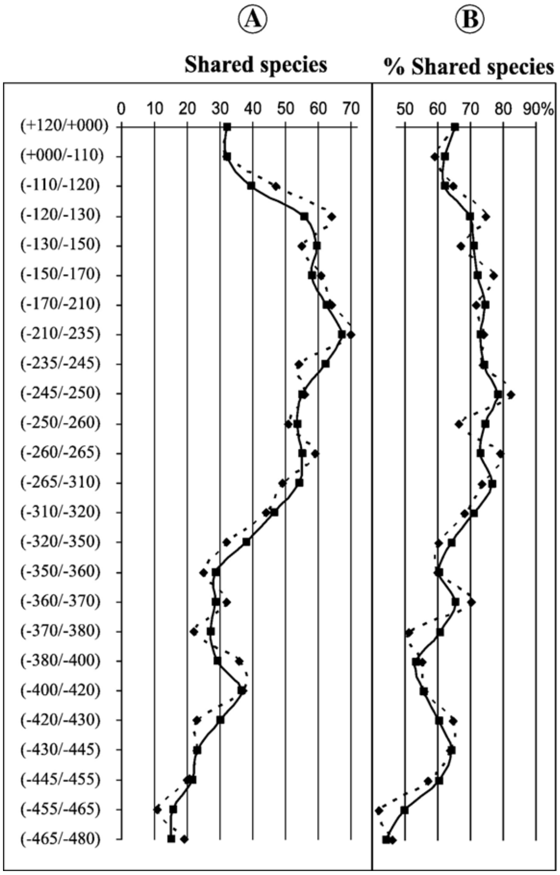


Fig. 10. Pairwise comparisons of successive BAs, using raw indices and moving averages: A) Shared species; B) ratio of shared species. Dashed lines represent raw indexes and plain lines represent moving averages.

4.7. Turnover patterns

We used a Mantel test (Mantel, 1967; Jackson and Somers, 1989) to assess whether or not species composition changed through time, or whether species composition was random. Results show that a positive relationship ($r = 0.48$) exists between the species and time matrices [Time was ranked from 1 to 26, with 26 representing the oldest BA (i.e., BA −480). The distance matrix between different BAs was based on the presence-absence matrix of species using the Jaccard coefficient. The "time" similarity matrix was calculated using the Euclidean distance]. This relationship is statistically significant ($p < 0.0001$) based on a randomization test. Thus, we can conclude that BAs that differ more in their sequence also show greater differences in their species composition. Turnover patterns were measured using different presence-absence (% shared species, and Jaccard) and quantitative (modified Morisita–Horn) coefficients (see Magurran, 2004). All calculations were based on pairwise comparisons of successive BAs, which is the standard procedure in most beta-diversity studies (Koleff et al., 2003). We obtained similar trends when all indices were rescaled (0 to 100) showing that, overall, the inclusion of abundance data does not change patterns observed from presence-absence data. For simplicity only the ratio of shared species is discussed here (Fig. 10). This ratio is relatively stable and varies from 50% to about 80%. Relatively high percentages of shared species occur in many successive BAs. If a threshold is set arbitrarily at 60% (i.e., six out of 10 species are common to two successive BAs), then most pairs of BAs are well above this threshold. This in turn indicates that many species are recurrent through the GPB within short-term intervals (successive BAs).

Patterns of species turnover can be visually estimated using the range chart of species occurrences in the GPB sorted by first and last appearance (Appendix B). In this graphic, it seems that species with shorter temporal range (to the right of the diagram) are located in younger BAs thus suggesting that species turnover might also happen through longer term intervals.

5. Community patterns

5.1. Results

The first and the second CA axes (Fig. 11) account for more than 30% of the variation (15.6% and 15% respectively). Ranks of taxa or BAs along the first axis showed that taxa with similar relative abundance or which occur in the same BAs tend to be grouped together (Appendix C). The MST of species (Appendix D) shows that taxa that are near the base of the cluster (i.e., connected by thicker lines) and close to the centre of the ordination diagram tend to be associated with many other taxa, and are usually relatively abundant in most BAs (Appendix C). Conversely, taxa at the end of the thin dashed lines tend to be relatively isolated, have restricted associations, and occur in few BAs (e.g., *Pikaia*, Fig. 11, see also Appendix C). Species close together (in terms of their minimum-length of connectors from the MST) tend to systematically co-occur in most BAs. Groups of species are more difficult to extract than groups of BAs, due to the large number of species included in this analysis. The MST of BAs shows the presence of four main groups (Fig. 12) based on the ordination result.

With the exception of BAs +120 and −110 which are more centrally located in the ordination plot, Group 1 is composed of BAs and species present mostly on the extreme left side (BAs: −150, 170, −210, −245, −250, −310, and −370). Common taxa in these BAs include almost all sponges known from the GPB. Species of *Leptomitus, Choia, Wapkia,* and *Protospongia* are all indicators of Group 1 (Fig. 12, see also Appendix E). Other species in

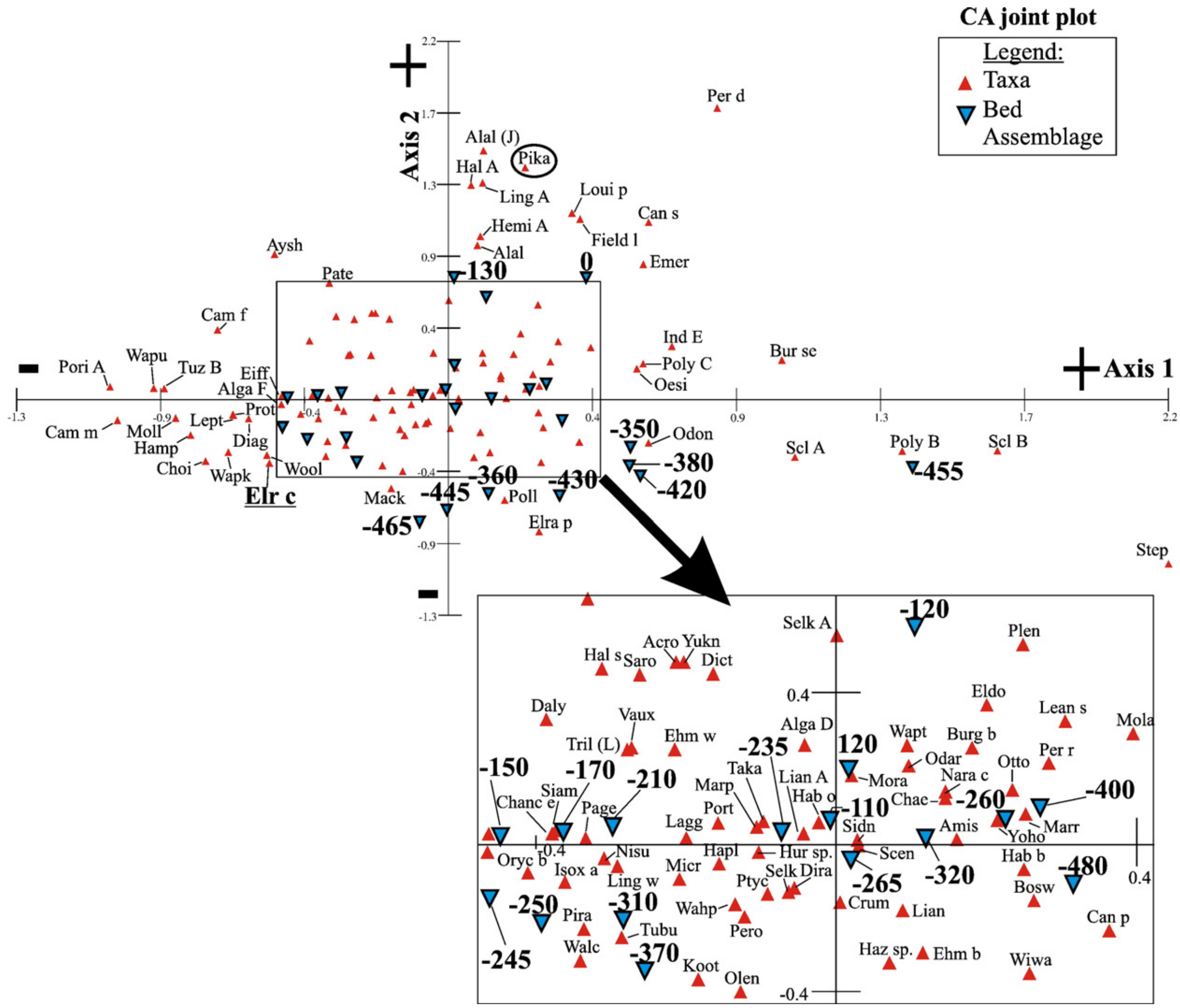


Fig. 11. CA ordination diagram of the species and BAs from the Greater Phyllopod Bed. The middle part of the ordination diagram was enlarged for clarity. See Table 1 for complete names of taxa. The first axis may represent a gradient of benthic oxygen level from low to high starting from the left of the diagram. Note the position of the trilobite species *Elrathina cordillerae* (Elr c in bold and underlined) on the left side of the diagram along the first axis. The second axis may represent a turnover gradient. *Pikaia gracilens* (Pika), emphasized by a circle along the second axis tends to be restricted to a few BAs.

Group 1 include brachiopods (e.g., *Micromitra burgessensis*), trilobites (e.g., *Elrathina cordillerae*), and putative tubiculous cnidarians (e.g., *Cambrorhytium* spp.). Overall, most BAs from Group 1 are characterized by having a greater number of suspension filter feeding organisms.

BAs from Group 2 (BAs: −235, −260, −265, −320 and −480) are at the centre of the ordination diagram, which indicates that they contain a set of species typically common in most other BAs from the other three groups. BA −360 is more isolated. Because species present in Group 2 are common to most BAs, they probably represent eurytopic species with a broader ability to adapt to variations of the environment. Significant indicator species (*IVs*) from Group 2 are represented by only three taxa: *Odontogriphus omalus, Amiskwia sagittiformis,* and *Habelia brevicauda* (Fig. 12). A low number of indicator species is expected because species at the centre of the ordination diagram are common to most BAs and are not particularly indicative of any one group.

Group 3 is relatively distinct in the ordination diagram along the 2nd axis; it is composed of three BAs (0, −120, and −130) and differs in terms of species composition and has more indicator species than all other groups of BAs (Fig. 12). Most taxa typical of Group 3 are farther away from the centre of the ordination diagram, and are often rare in most BAs outside those of Group 3 (e.g., *Peronochaeta dubia* has the highest *IV* (97.7%) of all species studied see Appendix E). Interestingly BAs from Group 3 are among

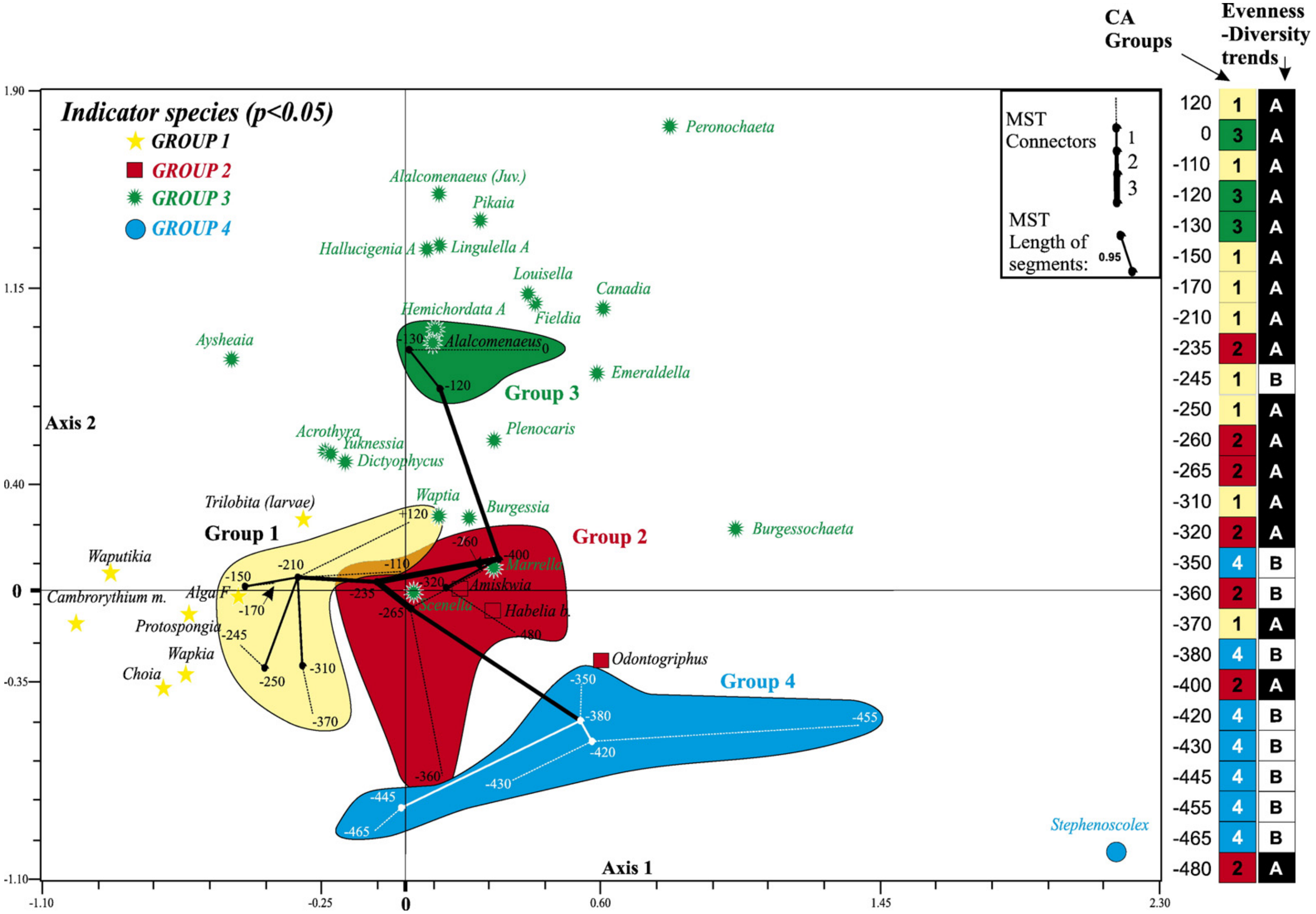


Fig. 12. Minimum Spanning Tree (MST) of the BAs from the Greater Phyllopod Bed superposed on the CA diagram. Connectors (lines of the MST connecting two entities) were represented with different thicknesses according to their clustering position. The thinnest lines connect "the tip of the branches" of the clusters, whereas the thicker lines represent increasingly larger clusters towards the base of the clustering diagram. The MST tree of the BAs suggests the existence of four main groups. Position of indicator species in the CA ordination diagram with $p < 0.05$ and for each of the four groups of BAs are also identified. See also Appendix E, for indicator value (IVs) scores. The CA groups are compared with evenness/diversity trends from Fig. 9.

the youngest in the GPB and the high proportion of indicator species in these BAs probably relates to the empirical pattern of species turnover already observed in younger BAs (Appendix B). Thus it is likely that the second axis of the CA diagram corresponds to a gradient of species turnover. Between group differences along this second axis probably represent long-term turnover trends whereas short-term trends would be represented by minor differences of position of each BA among each group.

Group 4 mostly occupies the lower right hand side of the ordination diagram (BAs −350, −380, −420, −430, −445, −455 and −465). The isolation of BA −455 is due to the high abundance of the rare worm *Stephenoscolex argutus* which is the only species having a statistically significant *IV* in this group (Appendix E). The positions of BAs −350 and −380 are, to a lesser extent, probably influenced by the dominance of *Canadaspis* (Appendices A, B and C). Similarly, *Pollingeria grandis* is abundant in BAs −380 and −430, and the position of this species is somewhat intermediate between the previous BAs, and a BA from Group 2, where it also has a very high ratio of occurrence (BA −360). BAs −445 and −465 have high ratios of sponges which explains their position to the left of the ordination diagram closer to Group 1. Group 4 differs from most other groups in that it contains only BAs with low species richness and evenness (Type B, Fig. 9). The extreme right hand of the ordination diagram is dominated by polychaete worms (Fig. 11), suggesting that such species could be more stenotopic and confirming that the first axis of the ordination diagram is influenced by environmental and/or ecological gradient(s). Patterns of BAs from Group 4 support the view that the second axis represents a gradient of species turnover. This is based on their positions (opposite to Group 3) along the second axis and on the fact that these are among the oldest BAs in the GPB.

5.2. Relationship between CA-CCA

The hypothesis that the second CA axis represents a gradient of species turnover over time was tested using CCA. The species-time correlation on the first axis of the CCA is very high ($r=0.917$, F-ratio$=3.26$, $p=0.001$), demonstrating species pattern along the first axis is strongly correlated with environmental and/or ecological factors acting through time (Appendix F). In other words, the position of the species along the first axis of the CCA diagram represents a summary of turnover patterns in the GPB. Interestingly, the pattern of BAs along the first axis of the CCA ordination diagram is similar to the pattern of BAs along the second axis of the CA ordination diagram (Fig. 12). Groups of BAs (1 to 4) characterized in the CA ordination diagram with MST, can also be recognized in the CCA diagram, albeit with some minor variations. When the temporal succession is compared against the BA scores along both CA axes, the first axis is more weakly correlated ($r=0.43$, $p=0.025$) than the second axis ($r=-0.78$, $p<0.0001$).

6. Discussion and conclusions

Deciphering the different processes behind community patterns is a complex matter because of a multitude of biotic and abiotic factors acting on multiple temporal and spatial scales (Ricklefs and Schluter, 1993). The study of any fossil community is further complicated by various degrees of taphonomic biases and by the possibility that patterns extend in evolutionary time. The data presented in this study, however, provide some insights on a number of environmental and ecological factors which might have been important in controlling patterns observed.

6.1. Environmental factors

As in other obrution deposits with NBP (Brett and Seilacher, 1991), it is likely that many organisms were killed or affected by environmental changes (considered herein as disturbances) just prior to and/or during the burial event. These could include variations in paleo-redox conditions (discussed below), substrate consistency, increased salinity, or possibly even H_2S or CH_4 poisoning. For example, if the pelagic mode of life of the animal *Eldonia ludwigi* is interpreted correctly, the large numbers of specimens found together supports the view that entire populations were poisoned in the water column and rapidly sank to the sea bed sea just prior to being interred. It is possible that many poisoning events might have occurred between two successive mud-flows but only the one immediately preceding burial could eventually be detected from the fossil assemblages (a “death” assemblage — see Caron and Jackson, 2006). Here we use the term disturbance (*sensu* Sousa, 2000) to describe the death of a number of resident individuals, or the removal of some species in sufficient quantity to affect the abundance of others.

6.1.1. Paleo-redox conditions

A number of studies (Allison and Brett, 1995; Powell et al., 2003) have suggested that the Burgess Shale community was deposited under an oscillating oxycline which was thought to have had a crucial role in regulating the community. Paleo-redox conditions have been estimated in various ways for the Burgess Shale and the merits and validity of each of these methods have been questioned (i.e., ichnofossils, pyrite content and trace metals; for a review and critique, see Powell et al., 2003). Detailed microstratigraphic studies and estimation of paleo-redox conditions using ichnological criteria in the Wheeler Formation led Gaines and Droser (2003) to speculate that the “ptychopariid” trilobite *Elrathia kingii* was probably living in an exaerobic environment. In the Burgess Shale, *Elrathina cordillerae* is the most abundant “ptychopariid” and one of the five most abundant species in 8 out of 26 BAs in this study (Fig. 4). This species is located on the left side of the first axis of our CA ordination diagram (see Fig. 12), suggesting it may have inhabited a more specific environment (=stenotopic species) than more commonly encountered taxa. *Elrathina cordillerae* is often present in assemblages dominated by sponges (in Group 1 in particular). If *Elrathina cordillerae* represents a valid indicator for low benthic oxygen levels (possibly including sponges), then the first axis of the CA diagram could potentially represent a paleo-redox gradient with the oxygen level increasing towards the right side of the diagram. Interestingly, all putative shallow infaunal organisms, such as *Ottoia prolifica* are positioned at the right side of the ordination diagram, in a presumably more oxygenated benthic environment. The rarity of these species in BAs to the left side of the diagram is consistent with what we would expect if the critical anoxic boundary were at the sediment-water interface and the mud were anoxic in these BAs. It is worth noting that BAs on the left side of the diagram in which *Elrathina cordillerae* is dominant (e.g., −465, −250), belong to different groupings, demonstrating that if variations in oxygen levels occurred, they do not seem to have affected groupings of BAs themselves. In other words, paleo-redox conditions might represent a relatively important factor controlling the community structure within a short-term interval, but repeated short-term paleo-redox variations may not have had a profound impact on long-term community changes through the GPB. Additional data on paleo-redox conditions, based on more extensive and detailed geochemical and microstratigraphic studies, would be needed to validate this hypothesis.

6.1.2. Substrate type and ecological consequences

Dornbos et al. (2005) recognised different types of benthic suspension feeding animals in the Burgess Shale, based on morphological adaptations to substrate firmness; some were better suited to firm, Proterozoic-type substrates and others to soupier, bioturbated Phanerozoic-type substrates. They further suggested that animals adapted to Proterozoic-style substrates were predominant in relative numbers of species due to the presence of seafloor microbial mats. The rarity of infaunal traces in the Burgess Shale, and patterns of species association, provide additional arguments for the model presented by Dornbos et al. (2005). Grazing is a more common form of feeding in the Burgess Shale than previously recognized. For example, *Odontogriphus* and *Wiwaxia* were recently redescribed as grazing radula-bearing molluscs, with the suggestion that the co-occurring macrobenthic cyanobacterium *Morania confluens* could have represented an important food source for these animals (Caron et al., 2006). Detecting any particular trends in substrate texture based on the species categories defined by Dornbos et al. (2004) as proxies for substrate type is not, however, straightforward (see Fig. 10). The position of these species in the CA ordination diagram does not seem to be related to particular groups of species and BAs. This in turn suggests that each BA records the presence of animals living on both substrate types. Animals adapted to less stable substrates probably cohabited with others living on localized patches of microbially stabilized seafloor. Interestingly, *M. confluens* occupies a central position in our CA ordination diagram, suggesting that this taxon is widespread and abundant across the GPB and had a profound impact on the texture of the substrate. As previously discussed (see also Caron, 2005; Caron and Jackson, 2006), the presence of the sheet-like *Morania* in most BAs may have another important ecological implication. The association of numerous juveniles of many arthropods, in particular *Alalcomenaeus cambricus* and trilobite larvae, suggests that this blue-green “alga” provided a potential food supply, as well as shelter from predators, during development and growth (Caron, 2002). The role of cyanobacteria and algae in the recruitment of larvae and juveniles of marine invertebrates is recognised as an important structuring factor of modern benthic communities (Morse, 1992).

6.1.3. Ecological effects of environmental disturbances

Disturbances are thought to initiate temporal and spatial heterogeneity in the structure and dynamics of natural communities (Sousa, 1984), and have often been associated with the processes of succession (i.e., changes in a particular order of the species composition after disturbances; see review in Platt and Connell, 2003 and below). In modern marine environments, large-scale physical disturbances such as deep sea currents, or storm-generated currents in shallower waters, are not favourable for the development of species-rich communities (Grassle and Maciolek, 1992). In the GPB, a single species is very abundant in a few BAs (e.g., *Canadaspis* in BA −350 represents 90% of all individuals, Appendix A). However, with the exception of these particular BAs in which major physical disturbances could explain patterns of species abundance, the most abundant species in most BAs comprise 15 to 30% of the total number of individuals. This range is closer to typical deep sea communities, in which a few dominant species account for fewer than 10% of individuals, in the absence of large-scale disturbance events (Grassle and Maciolek, 1992). This may support the view that only a small area of the seabed was affected by the burial events and that the community quickly recovered with recruitment from adjacent patches of species. Quick recovery is evidenced by the nearly identical species composition of successive pairs of BAs. In the longer-term, "turnover" of rare species and recurrence of abundant species may be controlled in part by the ability of individuals to disperse and recolonise after each burial event. High frequency burial events would have limited the settlement of more specialized species. Species with widespread geographical ranges, e.g., *Ptychagnostus praeccurrens* are more likely to have a greater ability to recolonise at a local scale than more spatially and temporally restricted species, as noted by Hanski (1982). As mentioned above, it is possible that recurrent species represent more opportunistic organisms, capable of quickly recolonising the environment after each disturbance event. These disturbance-adapted species may have short-lived populations but enhanced species longevity (Sheldon, 1993).

6.2. Ecological factors

Many authors have argued that predation has played a crucial role in structuring communities, especially during the Cambrian explosion (Conway Morris, 1986; Bengtson, 2002; Babcock, 2003). In the Burgess Shale and other Cambrian Lagerstätten, predator-prey relationships have been identified from direct evidence such as shelly remains in gut contents (Conway Morris, 1977; Bruton, 1981; Zhu et al., 2004) and in coprolitic aggregates (Vannier and Chen, 2005), as well as from indirect evidence including presumed adaptations for predation (e.g., *Anomalocaris*; Whittington and Briggs, 1985), putative antipredator morphologies (e.g., rows of spines on *Hallucigenia*), and healed injuries potentially representing bite marks on trilobites by large predators (Rudkin, 1979; Conway Morris and Jenkins, 1985; Pratt, 1998; Nedin, 1999). In most modern environments, predators regulate prey populations and potentially alter the species composition of communities (Jackson et al., 2001). Predation is also believed to have a major impact on competitive interactions (see review in Chase et al., 2002). For example, some predators feed exclusively on a single prey organism, which leads to reduced interspecific competition among remaining species. In modern settings, experimental studies could determine whether a given predator influences community patterns, but even so, predation may not be the only reason for the demise of a given prey species (which might simply be a weak competitor for resources). In light of these challenges in interpreting the modern environment, it is not obvious that predators had a major impact in regulating Cambrian communities, where even direct fossil evidence of predation does not preclude the operation of other biological processes. Competition, as noted above for instance, has long been recognized as an important agent of natural selection (Cody and Diamond, 1975), but it is difficult to formally quantify even in neontological settings. Whether competition was a significant factor during Middle Cambrian times is impossible to determine unambiguously, because competitive relationships do not leave tangible evidence and can only be inferred. The impact of commensalism and other inter-species interactions on structuring the community is also very difficult to evaluate. Only circumstantial evidence of such interactions is preserved. For example, specimens of the small brachiopod *Micromitra burgessensis* with setae protruding around the shell margins, are often found attached to spicules of the sponge *Pirania muricata* (Whittington, 1985). In this kind of interaction, the "guest" species would be raised above the soft muddy bottom, avoiding fouling and increasing filtering efficiency. *M. burgessensis* and *P. muricata* are close together in our CA ordination diagram (Fig. 11). Such an association supports the view that the observed patterns can yield ecologically meaningful interpretations. Our quantitative results also demonstrate that interactions between these two species were recurrent through time across the GPB.

6.3. Comparisons with coeval deposits

Fossils with NBP are also found in Early and Middle Cambrian strata of south-west China in shallow to deeper environments (Chen et al., 1997; Luo et al., 1999; Hou et al., 2004; Steiner et al., 2005). Most of these localities are referred to as Chengjiang-type deposits from the name of the first outcrop investigated in Yunnan, which has yielded soft-bodied animals (Zhang and Hou, 1985). Despite the discovery of abundant and diverse organisms from numerous Chengjiang-type deposits, very little is known about the community structure and functioning of these biotas (Steiner et al., 2005). This is due to a lack of detailed faunal inventories and fine-scale sedimentological and geochemical investigations, particularly at the key Chengjiang localities. Traditionally, individual studies of the Chengjiang biota have focused on a small number of fossil specimens, with little attention given to their exact stratigraphic origin and paleoenvironmental setting. Unfortunately, this approach has led to the loss of crucial information concerning variations in depositional environments and associated biotas. The lack of controlled sampling from individual depositional events, the mixing of specimens from different localities, and the dispersal of specimens in different collections are additional obstacles for carrying out comprehensive quantitative ecological studies of the Chengjiang biota (Zhu et al., 2005).

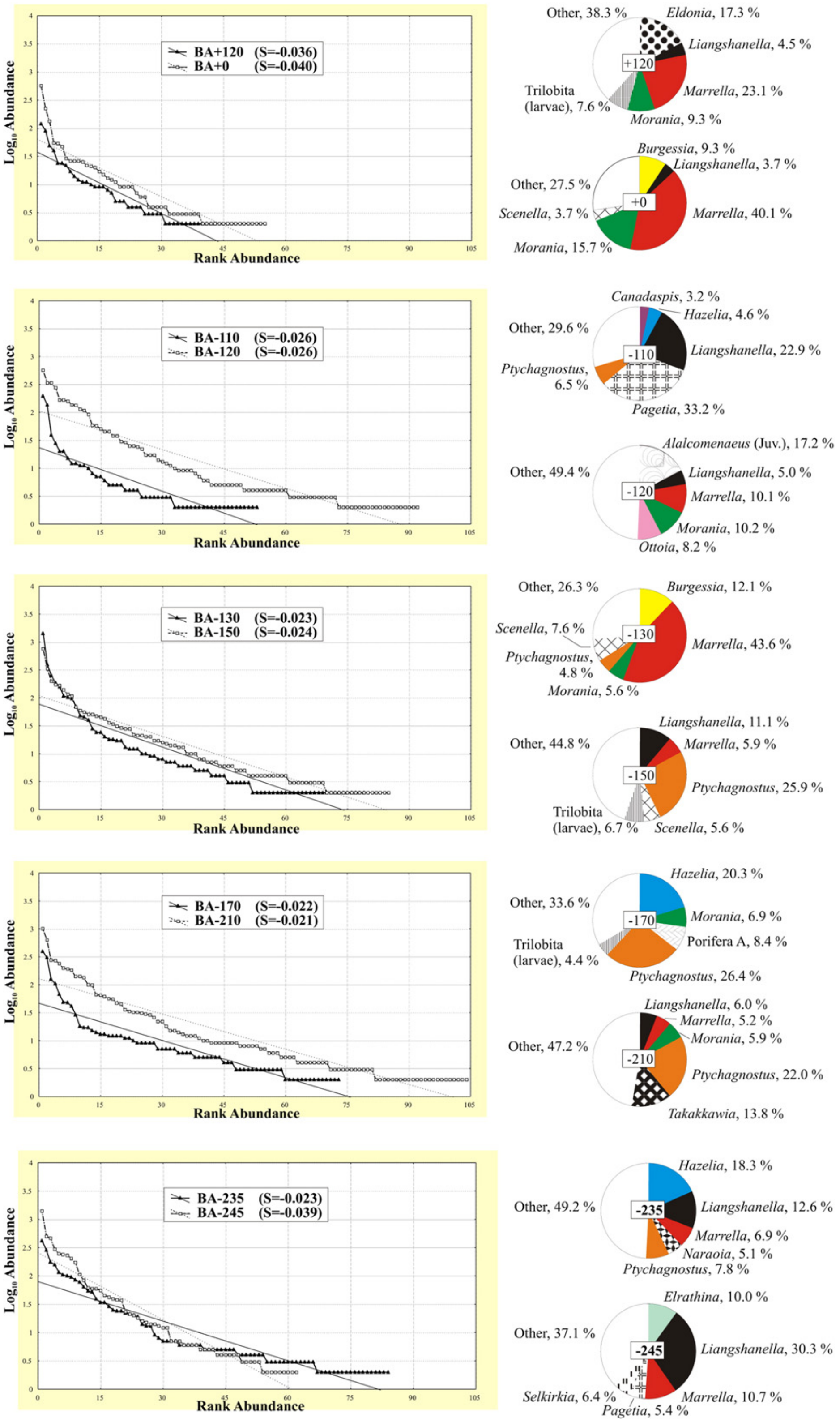
Despite these problems, preliminary estimates based on published reports representing a mix of different assemblages from different localities support the view that arthropods were dominant in Chengjiang-type deposits in terms of both relative abundance (60%), and number of genera, followed by the "algae and bacteria" (30%), with most other species representing 3% or less of individuals (see Fig. 2.2.7.1 Hou et al., 2004). Subjective estimates of abundance from existing collections suggest that different localities have slightly different assemblages in terms of composition and abundance levels. For example, Chengjiang and Haikou are both dominated by arthropods but Haikou has more priapulids and fewer sponges than Chengjiang. In both sites, some beds (or accumulation layers) are dominated by one or a few species — *Cricocosmia jinningensis* was estimated to reach densities of up to 4000 individuals per square meter in Haikou (Steiner et al., 2005). Differences in species composition between Chengjiang-type localities are thought to reveal genuine ecological (habitat) differences in community composition (Steiner et al., 2005). Variations are unlikely to be due to differences in preservational modes or sedimentology because fossils are preserved in the same way in all the massive mudstone layers, and are interpreted to be parautochthonous (Steiner et al., 2005). Since the degree of preservation in both Burgess Shale and Chengjiang-type localities is very similar, some shared community attributes, such as the predominance of arthropods and sponges, could represent ecologically meaningful signals. Thus, it is possible that the structure and functioning of the Cambrian soft-bottom community in shallow to deeper environments remained stable until the Middle Cambrian (in terms of overall taxonomic composition and ecological categories). The Burgess Shale and Chengjiang biotas were located on different tectonic plates (Laurentia and Gondwana respectively) during the Lower to Middle Cambrian (McKerrow et al., 1992, see also Meert and Lieberman, 2004), suggesting that time, and mechanisms of origin and dispersion are likely to be important factors controlling community patterns at both sites. Field projects are now underway to systematically collect data from Chengjiang-type localities, bed by bed, within single sections (Zhao et al., 2006). This methodology yields optimal results for quantitative comparative studies (particularly of temporal patterns within and between communities) with the GPB. Such comparative approaches to the analysis of the structure and functioning of different Cambrian communities should provide insight into the variability of ecological patterns at different temporal and spatial scales, and greatly expand our knowledge of the ecology of Cambrian communities.

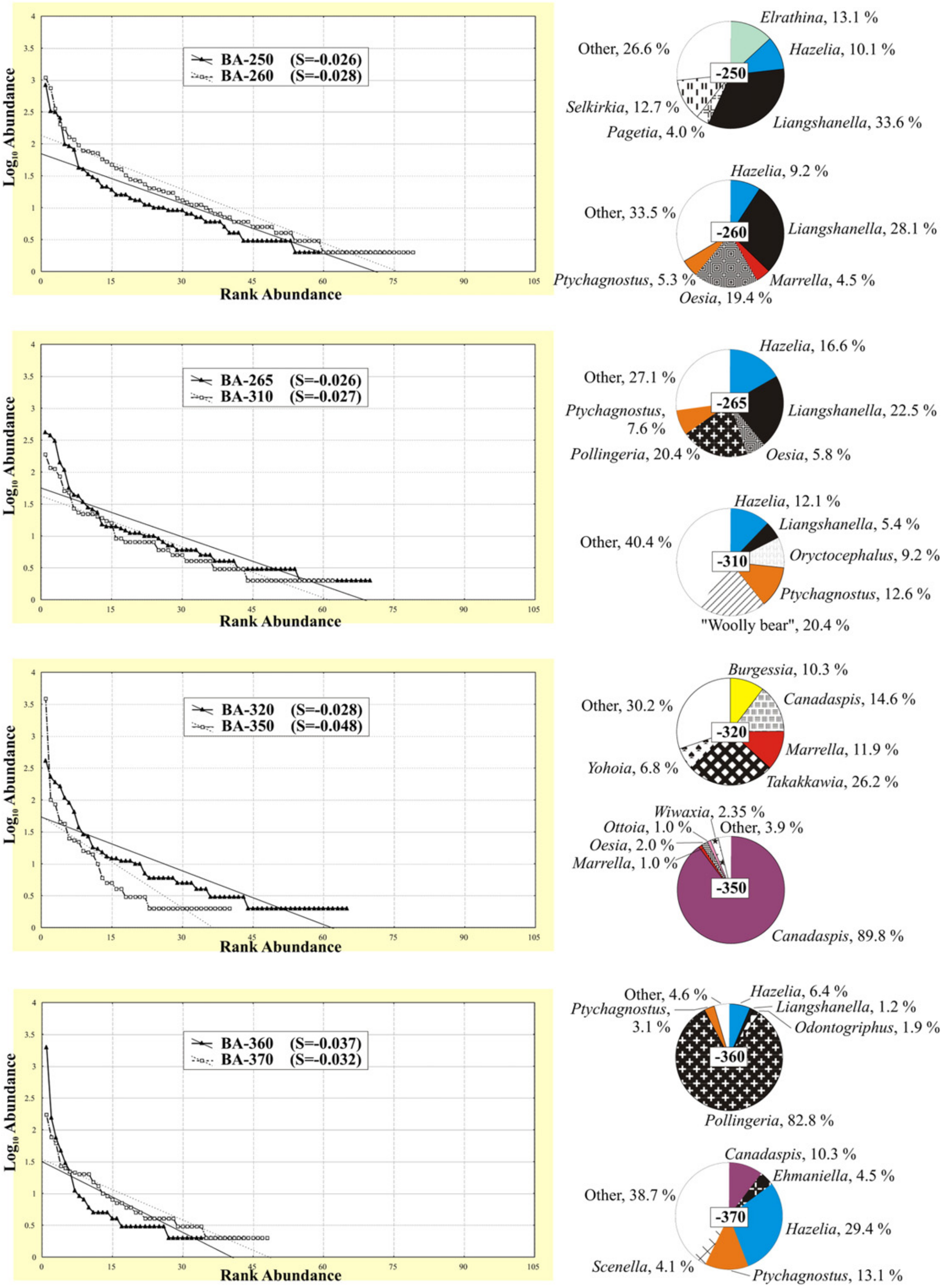
6.4. Comparisons with modern analogues

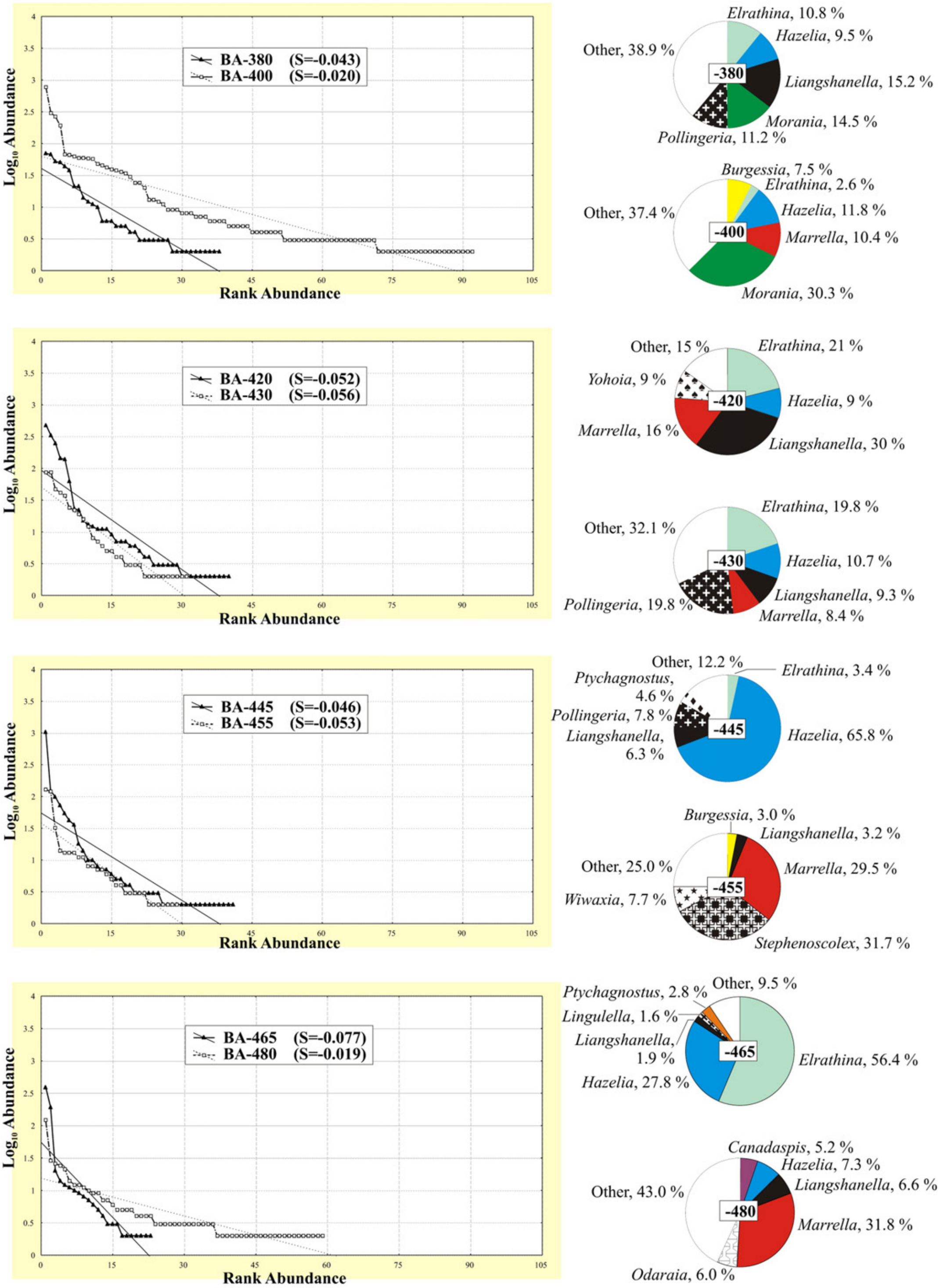
Interestingly, community trends from the GPB are similar in many respects to those of modern marine benthic communities. In particular, most species in modern benthic faunas have small spatial ranges (Ellingsen and Gray, 2002), which could be comparable to small temporal ranges of species in the GPB (for discussion see McKinney and Frederick, 1999). Moreover, the fact that the species-accumulation curve of the GPB (Fig. 8) does not approach an asymptote demonstrates that the count of species in the GPB is not exhaustive. This is also typical of modern benthic communities in which all species are rarely recovered in a series of samples obtained with grabs or corers (Gray, 2002). In modern marine benthic faunas, local species richness is thought to be controlled primarily by regional richness, which may explain why more species, especially rare ones, are still added with more surface area sampled. For Gray (2002) and others (e.g., Grassle and Maciolek, 1992), these faunas are probably "unsaturated" in the sense that species interactions do not constrain local richness. Moreover, Gray (2002) suggested that this unsaturated model from marine benthic communities could have an interesting parallel with Hubbell's neutral theory (Hubbell, 2001), and, in particular, with the example of an unsaturated forest in which the population dynamics of each species is independent of one another. Because most marine benthic communities do not have barriers to dispersal, and competition among species is weak, the neutral theory may have a particularly sound application in marine communities and in the GPB community. In this context as well, the role of predation in structuring the Burgess Shale community and other Cambrian communities may not have been as important as many authors have suggested (e.g., Conway Morris, 1986).

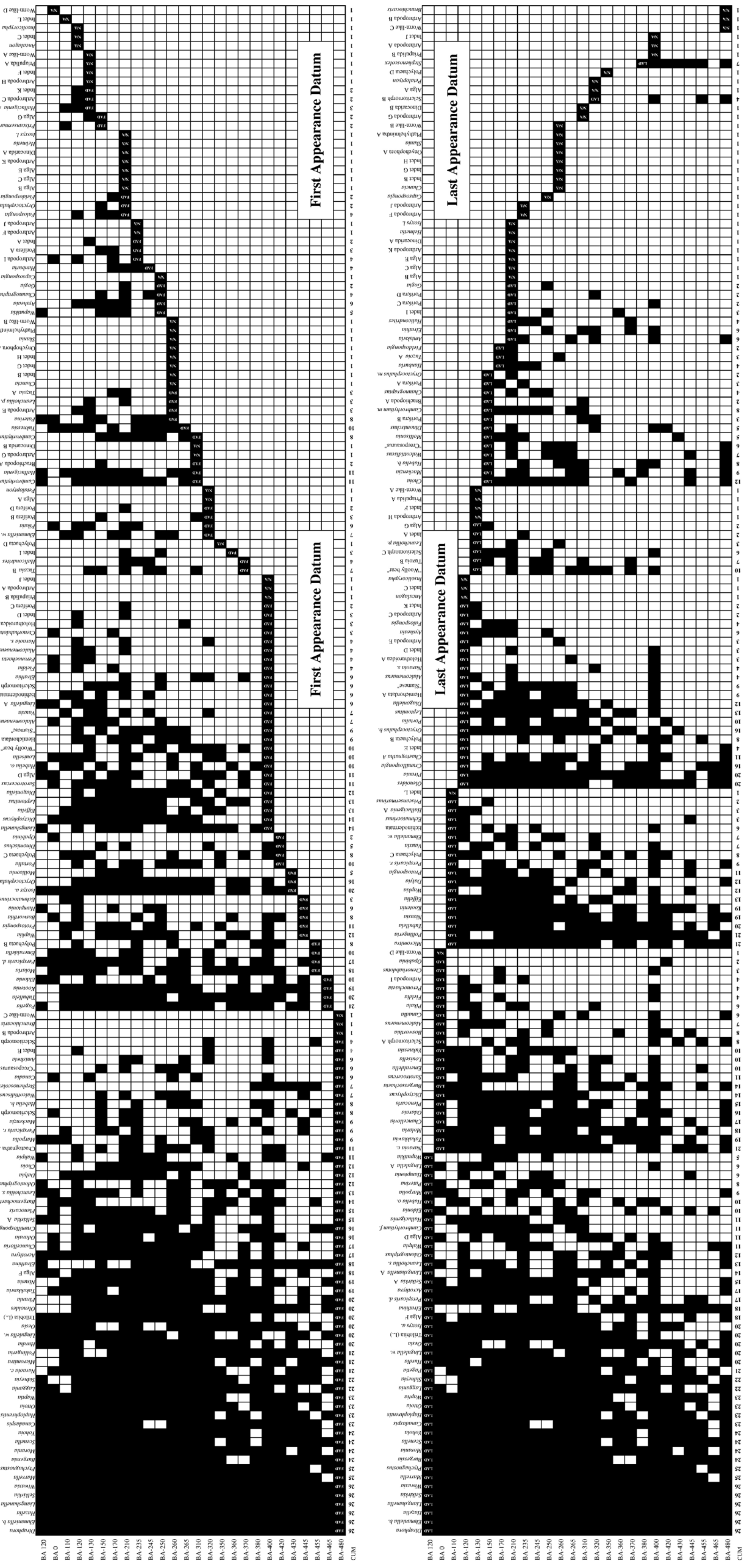
7. Summary

One hundred and seventy-two species from 17 major taxonomic groups and ecological categories


Log10 Abundance
Rank Abundance
0
15
30
45
60
75
90
105
0
0.5
1
1.5
2
2.5
3
3.5
4
BA+120 (S=-0.036)
BA+0 (S=-0.040)
Other, 38.3 %
Eldonia, 17.3 %
Liangshanella, 4.5 %
+120
Trilobita (larvae), 7.6 %
Marrella, 23.1 %
Morania, 9.3 %
Burgessia, 9.3 %
Liangshanella, 3.7 %
Other, 27.5 %
+0
Scenella, 3.7 %
Marrella, 40.1 %
Morania, 15.7 %
BA-110 (S=-0.026)
BA-120 (S=-0.026)
Canadaspis, 3.2 %
Hazelia, 4.6 %
Other, 29.6 %
Liangshanella, 22.9 %
-110
Ptychagnostus, 6.5 %
Pagetia, 33.2 %
Alalcomenaeus (Juv.), 17.2 %
Other, 49.4 %
Liangshanella, 5.0 %
-120
Marrella, 10.1 %
Morania, 10.2 %
Ottoia, 8.2 %
BA-130 (S=-0.023)
BA-150 (S=-0.024)
Other, 26.3 %
Burgessia, 12.1 %
Scenella, 7.6 %
-130
Marrella, 43.6 %
Ptychagnostus, 4.8 %
Morania, 5.6 %
Liangshanella, 11.1 %
Other, 44.8 %
Marrella, 5.9 %
-150
Ptychagnostus, 25.9 %
Trilobita (larvae), 6.7 %
Scenella, 5.6 %
BA-170 (S=-0.022)
BA-210 (S=-0.021)
Hazelia, 20.3 %
Other, 33.6 %
-170
Morania, 6.9 %
Porifera A, 8.4 %
Trilobita (larvae), 4.4 %
Ptychagnostus, 26.4 %
Liangshanella, 6.0 %
Marrella, 5.2 %
Morania, 5.9 %
Other, 47.2 %
-210
Ptychagnostus, 22.0 %
Takakkawia, 13.8 %
BA-235 (S=-0.023)
BA-245 (S=-0.039)
Hazelia, 18.3 %
Other, 49.2 %
-235
Liangshanella, 12.6 %
Marrella, 6.9 %
Naraoia, 5.1 %
Ptychagnostus, 7.8 %
Elrathina, 10.0 %
Other, 37.1 %
-245
Liangshanella, 30.3 %
Selkirkia, 6.4 %
Marrella, 10.7 %
Pagetia, 5.4 %


BA-250 (S=-0.026)
BA-260 (S=-0.028)
Log10 Abundance
Rank Abundance
0
0.5
1
1.5
2
2.5
3
3.5
4
0
15
30
45
60
75
90
105
Elrathina, 13.1 %
Other, 26.6 %
Hazelia, 10.1 %
-250
Selkirkia, 12.7 %
Pagetia, 4.0 %
Liangshanella, 33.6 %
Hazelia, 9.2 %
Other, 33.5 %
-260
Liangshanella, 28.1 %
Ptychagnostus, 5.3 %
Marrella, 4.5 %
Oesia, 19.4 %
BA-265 (S=-0.026)
BA-310 (S=-0.027)
Hazelia, 16.6 %
Other, 27.1 %
-265
Liangshanella, 22.5 %
Ptychagnostus, 7.6 %
Pollingeria, 20.4 %
Oesia, 5.8 %
Hazelia, 12.1 %
Liangshanella, 5.4 %
Other, 40.4 %
Oryctocephalus, 9.2 %
-310
Ptychagnostus, 12.6 %
"Woolly bear", 20.4 %
BA-320 (S=-0.028)
BA-350 (S=-0.048)
Burgessia, 10.3 %
Other, 30.2 %
Canadaspis, 14.6 %
-320
Marrella, 11.9 %
Yohoia, 6.8 %
Takakkawia, 26.2 %
Wiwaxia, 2.35 %
Ottoia, 1.0 %
Other, 3.9 %
Oesia, 2.0 %
Marrella, 1.0 %
-350
Canadaspis, 89.8 %
BA-360 (S=-0.037)
BA-370 (S=-0.032)
Other, 4.6 %
Hazelia, 6.4 %
Ptychagnostus, 3.1 %
Liangshanella, 1.2 %
Odontogriphus, 1.9 %
-360
Pollingeria, 82.8 %
Canadaspis, 10.3 %
Ehmaniella, 4.5 %
Other, 38.7 %
-370
Hazelia, 29.4 %
Scenella, 4.1 %
Ptychagnostus, 13.1 %


BA-380 (S=-0.043)
BA-400 (S=-0.020)
Log10 Abundance
Rank Abundance
0
0.5
1
1.5
2
2.5
3
3.5
4
0
15
30
45
60
75
90
105
-380
Elrathina, 10.8 %
Hazelia, 9.5 %
Liangshanella, 15.2 %
Morania, 14.5 %
Pollingeria, 11.2 %
Other, 38.9 %
-400
Burgessia, 7.5 %
Elrathina, 2.6 %
Hazelia, 11.8 %
Marrella, 10.4 %
Morania, 30.3 %
Other, 37.4 %
BA-420 (S=-0.052)
BA-430 (S=-0.056)
-420
Other, 15 %
Elrathina, 21 %
Yohoia, 9 %
Hazelia, 9 %
Marrella, 16 %
Liangshanella, 30 %
-430
Elrathina, 19.8 %
Other, 32.1 %
Hazelia, 10.7 %
Liangshanella, 9.3 %
Pollingeria, 19.8 %
Marrella, 8.4 %
BA-445 (S=-0.046)
BA-455 (S=-0.053)
-445
Other, 12.2 %
Elrathina, 3.4 %
Ptychagnostus, 4.6 %
Pollingeria, 7.8 %
Liangshanella, 6.3 %
Hazelia, 65.8 %
-455
Burgessia, 3.0 %
Liangshanella, 3.2 %
Other, 25.0 %
Marrella, 29.5 %
Wiwaxia, 7.7 %
Stephenoscolex, 31.7 %
BA-465 (S=-0.077)
BA-480 (S=-0.019)
-465
Ptychagnostus, 2.8 %
Other, 9.5 %
Lingulella, 1.6 %
Liangshanella, 1.9 %
Elrathina, 56.4 %
Hazelia, 27.8 %
-480
Canadaspis, 5.2 %
Hazelia, 7.3 %
Other, 43.0 %
Liangshanella, 6.6 %
Marrella, 31.8 %
Odaraia, 6.0 %


First Appearance Datum
First Appearance Datum
Last Appearance Datum
Last Appearance Datum
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BA 0
BA 110
BA 120
BA 130
BA 150
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BA 245
BA 250
BA 260
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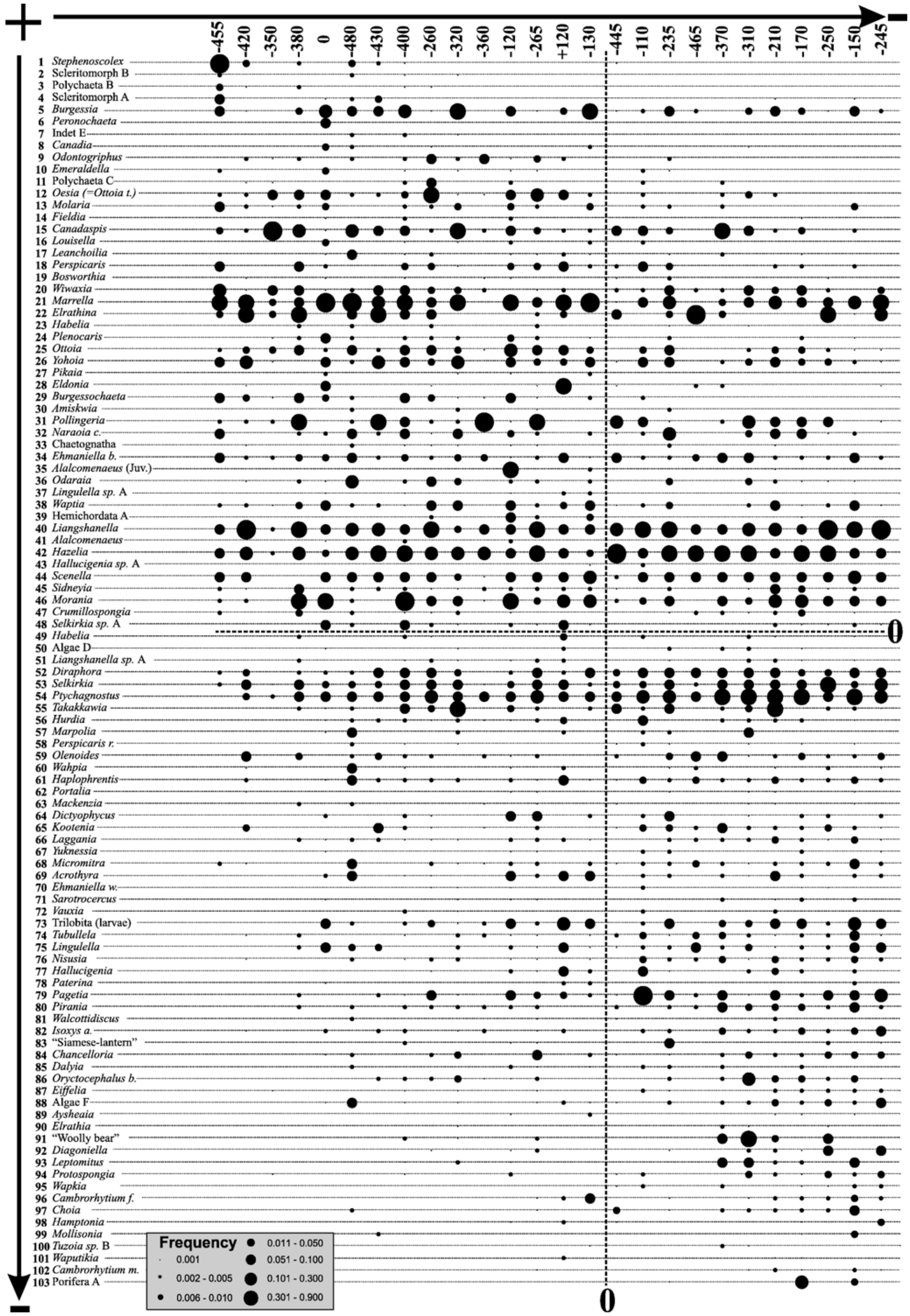
BA 455
BA 465
BA 480
CUM



(based on life and feeding habits) are recognised from more than 50,000 specimens in 26 BAs sampled through the Greater Phyllopod Bed (GPB) community. Variations in relative species composition of each group are relatively moderate compared to variations in percentage composition of individuals. Arthropods, followed by sponges, dominate in numbers of individuals and taxa. On average, epibenthic organisms (mostly vagile deposit feeders and sessile suspension feeders) comprise almost two-thirds of the total number of species and individuals. The pelagic component has fewer species (8.3%) and represents a trivial proportion of individuals (1.5%). In all BAs a few species dominate in their relative abundance. The five most abundant species typically represent one-half to more than three-quarters of specimens present in most BAs. The most abundant species is usually represented by many more individuals than the next in rank. Species that are abundant in any given BA are usually recurrent.

Species richness estimates derived from rarefaction curves demonstrate that the number of species between BAs varies significantly. Most rarefaction curves have not yet reached an asymptote, which suggests that more species (especially rare ones) may still be found in most BAs with additional sampling. Comparisons between abundance and species richness show that there is a positive correlation between evenness and richness, such that BAs with relatively high species evenness also have more species. In general, younger BAs have higher species evenness and richness than older BAs, revealing variations in diversity trends across the GPB. Relatively high percentages of shared species occur in many successive pairs of BAs, but a minority of species (25%), co-occur in a little more than half the number of assemblages, demonstrating that most species lack temporal persistence. The presence of similar BAs (in terms of species diversity) at the far temporal extremes of the GPB, however, implies that the community was able to recover similar species assemblages, composed mostly of persistent forms, and return to a state closely approximating equilibrium. Results from Mantel tests support the view that the community is influenced by long-term and non-random biotic factors.

Correspondence Analysis and Minimum Spanning Tree results suggest the existence of four structural groups composed of distinct fossil assemblages. Taxa co-occurring in different BAs tend to be grouped together in the ordination diagram, which provides, in conjunction with the Minimum Spanning Tree, a potential ecological “road-map” of species relationships. Indicator Species Analysis supports the presence of certain species that show a strong fidelity to particular groups but are seldom found in other groups.

These results summarize patterns of variation in the composition and structure of the GPB community and provide evidence for recurrence of groups within BAs and changes in community composition between groups and BAs. These patterns might be controlled by different environmental (e.g., paleo-redox conditions, substrate type) and ecological factors acting at different temporal scales. Based on comparisons with modern open marine communities, the ability of individuals to recolonise after each burial event and substrate availability were probably more important in controlling the structure of the GPB community than were species interactions.

Acknowledgements

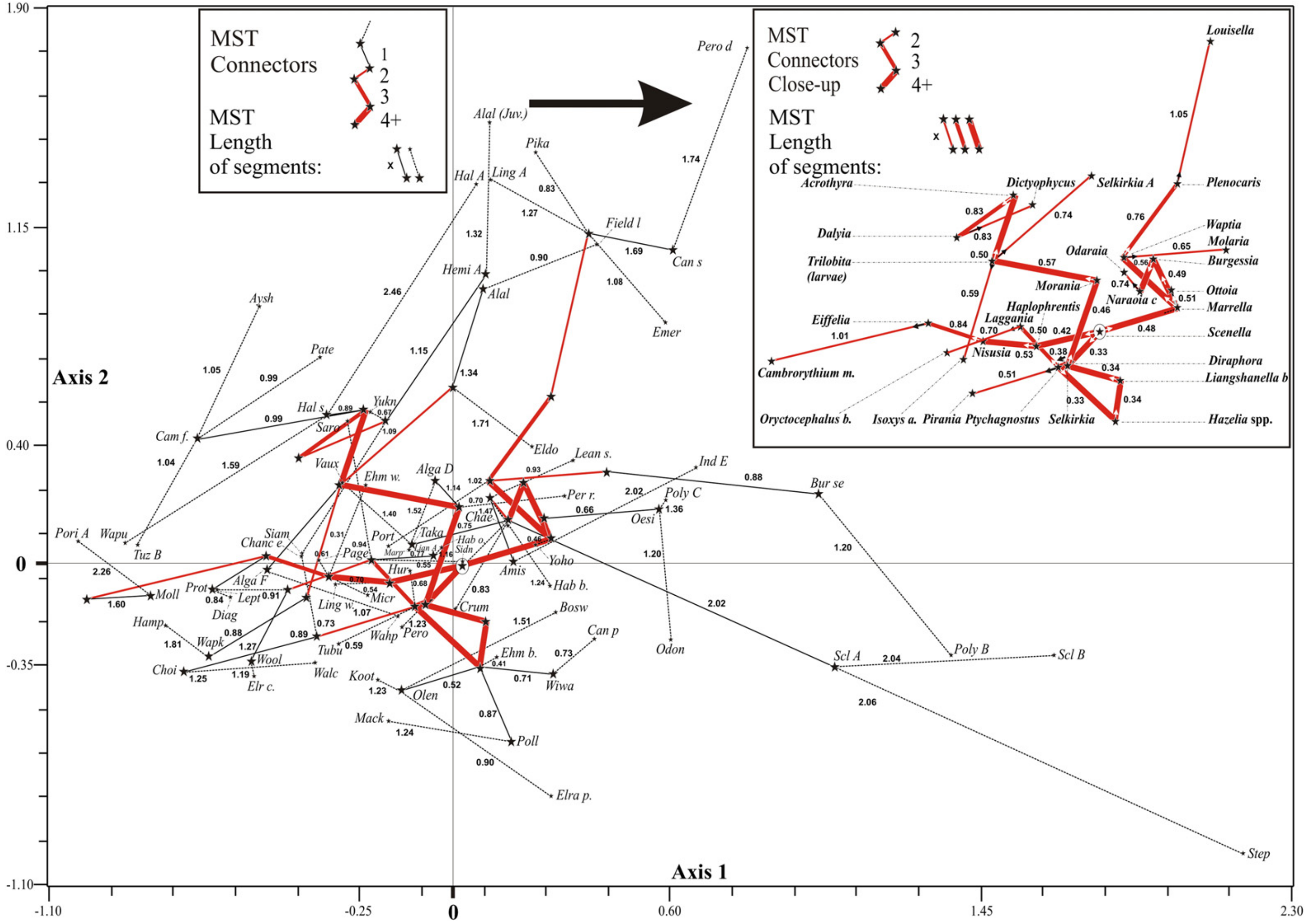
This research was undertaken as part of a PhD thesis (J.B. Caron) supported by doctoral fellowships from the University of Toronto (Department of Zoology) and a Natural Sciences and Engineering Research Council of Canada Discovery Grant to D.A Jackson. We are grateful for feedback from Derek Briggs, Dale Calder, Des Collins and Dave Rudkin. The present manuscript benefited from the constructive comments of Alex Lin and an anonymous referee; Carl Brett, Nick Butterfield, Steve Dornbos, Mark Patzkowsky and Jean Vannier critically reviewed earlier versions. Dave Rudkin and Sarah Scharf provided a careful editing of various portions of this manuscript. We thank the staff of the Paleobiology section (Department of Natural History) of the Royal Ontario Museum and, in particular, Des Collins for access to the material, and Janet Waddington, Brian Iwama and Peter Fenton for assistance in the collections. Permission to collect Burgess Shale fossils was given to Des Collins by Parks Canada.

Appendix A

Species abundance patterns in the GPB using Whittaker plots (Whittaker, 1965) and pie chart diagrams. Whittaker plots, also known as rank-abundance plots or dominance/diversity curves, are especially designed to compare patterns of species evenness (or variability in species abundance, see Magurran, 2004). Whittaker plots were drawn with the rank order of abundance of each species on the *X* axis (from most to least abundant), and the log10 transformed abundance value for each species on the *Y* axis. The slope of linear regression lines from the Whittaker plots is used as a descriptive statistical measure to track changes in community structure without implicitly testing a scenario of niche apportionment (Tokeshi, 1993)(see Fig. 9). Pie chart diagrams were drawn in order to display the identity and variation in relative abundance of the five most abundant species compared to all the other species present per BAs.

Appendix D

MST of 103 species from the Greater Phyllopod Bed. Taxa that are near the base of the cluster (i.e., connected by thicker lines) tend to be associated with many other taxa, and are usually relatively abundant in most BAs (See species within the enlarged frame and Appendix C). Species close together (in terms of their minimum-length of connectors from the MST) tend to systematically co-occur in most BAs. Taxa at the end of lines tend to be rare.



Appendix B

Presence-absence and First Appearance Datums (FADs) and Last Appearance Datums (LADs) of all taxa across 26 bedding assemblages (BAs) with more than 300 specimens from the GPB. N/A represents species present in a single BA (=unique). CUM represents the cumulative presence of each taxa per BA across the 26 BAs.

Appendix C

Ranked scores of the species and BAs in relation to their position along the CA first axis from the GPB (see Fig. 11). Relative abundance of each species in each BA is represented by plain circles of variable diameter within one of seven classes of abundance. The relative position of the ordination origin along the first axis is emphasized for both the species and the BAs ("0" and cross lines). Species with similar abundances tend to be grouped together.

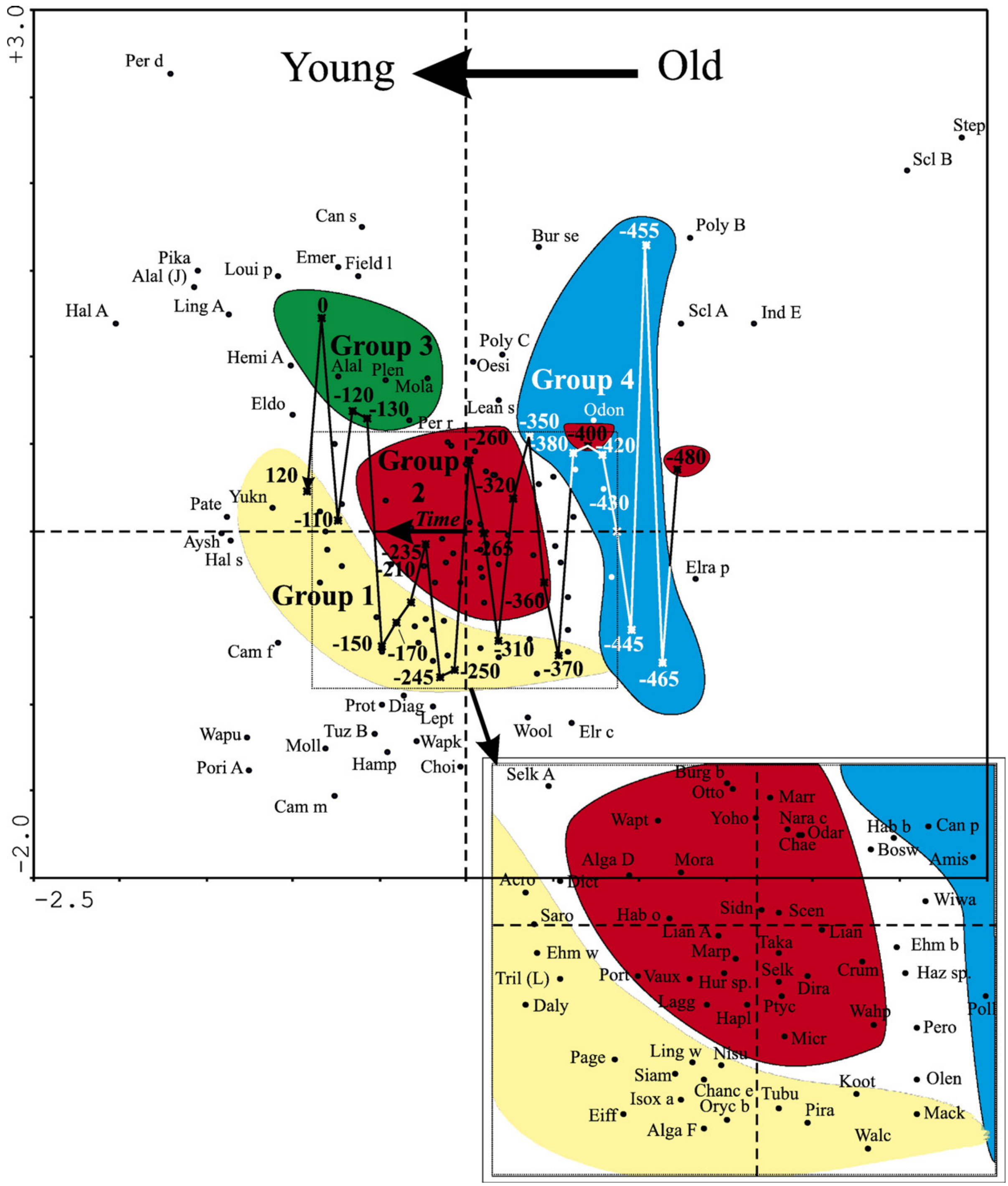
Appendix E

Results indicator Species Analysis. Results are presented per groups and are ranked according to the observed indicator value *IV* (in %). Means and standard deviations are from the observed randomized indicator groups. Only species with $p < 0.05$ are presented. (See also Fig. 12).

Appendix F

CCA ordination diagram with the species matrix compared to the temporal order of BAs. The middle part of the ordination diagram is enlarged. The BAs are ranked from right to left along the first axis and according to their stratigraphic order in the GPB. BAs

Species	Group	Observed *IV*	Mean *IV*	Sdev. *IV*	*p*-value
Algae F	1	68.2	41.6	13.12	*0.047*
Isoxys acutangulus	1	66.4	41.5	11.68	*0.041*
Leptomitus lineatus	1	65.8	36.2	13.64	*0.036*
Choia sp.	1	64.2	35.2	13.95	*0.039*
Trilobita (larvae)	1	62.9	40	11	*0.039*
Wapkia grandis	1	61.3	30.5	11.78	*0.028*
Cambrorhytium major	1	61.2	26.1	12	*0.021*
Protospongia hicksi	1	58	29.2	11.79	*0.03*
Waputikia ramosa	1	55.6	21.2	11.15	*0.016*
Odontogriphus omalus	2	90.1	36.6	13.92	*0.002*
Amiskwia sagittiformis	2	67.1	22	11.44	*0.008*
Habelia brevicauda	2	65.6	28.4	13.28	*0.01*
Peronochaeta dubia	3	97.7	29.4	12.35	*0.002*
Pikaia gracilens	3	91.6	43.6	8.83	*0.001*
Louisella pedunculata	3	90.5	22.9	11.2	*0.001*
Lingulella sp. A	3	89.6	27.9	11.43	*0.004*
Alalcomenaeus cambricus	3	78.4	23.2	12.37	*0.006*
Emeraldella brocki	3	76.6	24.3	12.92	*0.002*
Acrothyra gregaria	3	73.3	32.5	10.44	*0.01*
Plenocaris plena	3	72.6	33.9	9.62	*0.004*
Burgessia bella	3	71	25.8	12.35	*0.014*
Marrella splendens	3	70.1	25.4	12.62	*0.001*
Alalcomenaeus cambricus (Juv.)	3	66.5	37.8	12.01	*0.006*
Dictyophycus gracilis	3	64.5	44.7	10.39	*0.041*
Hemichordata A	3	64	18.2	10.43	*0.036*
Molaria spinifera	3	63.7	25.5	9.88	*0.005*
Burgessochaeta setigera	3	63.6	20.4	10.68	*0.021*
Waptia fieldensis	3	63.6	33	11.68	*0.035*
Canadia spinosa	3	57.2	22.9	12.24	*0.023*
Hallucigenia sp. A	3	55.6	24.6	13.03	*0.015*
Scenella amii	3	54.9	41.9	10.02	*0.036*
Aysheaia pedunculata	3	54.1	35.9	15.2	*0.022*
Yuknessia simplex	3	53.8	38.7	7.98	*0.017*
Fieldia lanceolata	3	53.4	35.5	13.2	*0.02*
Stephenoscolex argutus	4	69	32.2	14.09	*0.01*



are connected by lines for clarity. Areas with different shadings of gray or colors are based on the groups from the CA ordination diagram (Fig. 12). The first axis of the CCA ordination diagram accounts for 12% of the variance of the data, whereas the second axis represents 15.4% of the variance. Both matrices (species and time) are correlated confirming that turnover did occur. (See Table 1 for complete names of taxa).

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