



Comparisons between Cambrian Lagerstätten assemblages using multivariate, parsimony and Bayesian methods



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ABSTRACT

Exceptional fossil deposits exhibiting soft-part preservation, or *Konservat-Lagerstätten*, are prevalent in Cambrian rocks and provide detailed information on fossil assemblages not available from conventional deposits. It has long been recognised that many of these assemblages exhibit certain taxonomic similarities, with many elements seemingly having cosmopolitan distributions. These types of assemblages, particularly those of Cambrian age, have become known as Burgess Shale-type (BST) biotas, named for the famous deposit in the Canadian Rocky Mountains where fossils preserved in this way were first discovered. This study provides the first broad-scale analysis of the assemblage relationships between all major BST biotas. We compiled a database of the presences and absences of over 600 genera within 12 Lagerstätten from Laurentia, Siberia, South China and East Gondwana, ranging in age from Cambrian Series 2 through Series 3 (late-early to middle Cambrian; c. 518–502 Ma), and analysed this using a variety of quantitative methods in order to investigate the relationships between these sites. Non-metric multidimensional scaling (NMDS) ordination, cluster analysis and Parsimony Analysis of Endemism (PAE) were used to group localities and examine relationships. We also used Bayesian inference and illustrate the benefits of this approach to biogeographic studies. Results suggest that both space and time have important effects on the taxonomic constitution of BST biotas, and that the similarity of these assemblages appears to increase from Series 2 through Series 3, largely driven by increases in cosmopolitanism of biomineralised taxa such as trilobites and brachiopods. There is also evidence of higher-level taxonomic turnover across this period. Endemic taxa help amplify these patterns, despite their frequent exclusion from biogeographic analyses.

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1. Introduction

1.1. Background

Cambrian *Konservat-Lagerstätten* – fossil deposits exhibiting exceptional preservation of soft parts – offer great insight into the diversity and ecology of early communities following the ‘Cambrian explosion’ (Conway Morris, 1985). As well as providing enhanced biological information about individual organisms, they also provide a more faithful representation of the full diversity and relative abundances of taxa present within these communities. This information should allow us to undertake not only more informative and unbiased ecological analysis of these early communities, but also to examine their biogeographic relationships based on shared taxa. The former has been undertaken for

several Cambrian Lagerstätten (e.g. Conway Morris, 1986; Ivantsov et al., 2005; Caron and Jackson, 2008; Dornbos and Chen, 2008; Zhao et al., 2010, 2014); the latter has also been pursued (e.g. Hendricks and Lieberman, 2007; Hendricks et al., 2008; Hendricks, 2013) and is the focus of the present contribution.

It is well known that many Cambrian Lagerstätten share common faunal elements. A substantial number of genera found within these assemblages exhibit largely cosmopolitan distributions, e.g. the sponges *Choia*, *Hazelia*, *Leptomitus* and *Protospongia*, sponge-like *Chancelloria*, cnidarian *Byronia*, brachiopods *Lingulella* and *Nisusia*, anomalocaridid *Anomalocaris*, lobopodian *Hallucigenia*, the euarthropods *Canadaspis*, *Isoxys*, *Leancoilia*, *Liangshanella*, *Naraoia* and *Tuzoia*, priapulid *Selkirkia*, and the enigmatic taxa *Haplophrentis*, *Wiwaxia*, *Eldonia* and *Dinomischus*. It is likely that at least some of these had larval stages capable of long distance dispersal via ocean currents (García-Bellido et al., 2007; Han et al., 2008; Zhao et al., 2011). These taxa are not particularly informative in a biogeographic sense, as their broad distributions provide little evidence when attempting to draw conclusions about relationships between localities; however, their shared presences suggest that we are looking at similar types of communities. These have

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been termed Burgess Shale-type (BST) biotas, named for the famous Cambrian Series 3 deposit in the Canadian Rocky Mountains.

1.2. Previous work

Comparisons between BST biotas have been made by many authors; however, these have not always employed quantitative analysis. One exception is the work of Hendricks et al. (2008), who used species occurrence data and continental reconstructions to examine the geographic and temporal distribution of Cambrian arthropods, and showed that soft-bodied species had wider geographic and stratigraphic ranges than contemporaneous trilobites. Hendricks (2013) conducted a similar analysis of a wider range of Cambrian metazoan phyla, as well as algae and cyanobacteria, and showed that patterns varied across different clades, and that geographic range of species (and genera) was positively correlated with temporal persistence. However, these studies focused on distributions of individual taxa rather than on assemblage similarity as a whole. One of the few dedicated studies to focus on broad-scale assemblage similarity between Cambrian Lagerstätten was that undertaken by Han et al. (2008), who listed shared genera for a number of site comparisons as part of their analysis, in particular focusing on associations between sites in Laurentia and South China. They suggested that the Chengjiang (Series 2) and Burgess Shale (Series 3) assemblages were closely related based on qualitative analysis of shared genera, and that the development of pelagic larvae may have resulted in the worldwide distribution of BST biotas. Similarities between the Chengjiang and Burgess Shale assemblages have also been mentioned by other authors (e.g. Conway Morris, 1989, 1998; Babcock et al., 2001). Common generic occurrences between the Kaili Biota (Series 3), and the Burgess Shale and Chengjiang Lagerstätten were discussed by Zhao et al. (2005), who presented figures of 38 and 30 shared genera respectively, and suggested that the greater similarity with the Laurentian site was possibly due to elements of middle-to-outer shelf faunas becoming more stable and widespread by this time. It was suggested by Zhao et al. (2011) that the similarity in age (as well as environment) between Kaili and the Laurentian Burgess Shale and Spence Shale (Utah, USA), may partially account for the similarity seen between these assemblages, and that perhaps age was a greater determinant of assemblage than geography during the late-early to middle Cambrian. Similar features between the Sinsk Biota of Siberia and the Burgess Shale assemblage (the Phyllopod Bed in particular) were noted by Ivantsov et al. (2005), including co-occurrence of a small number of genera. Numerous studies have acknowledged the existence of shared taxa (mostly at genus level) between the Emu Bay Shale (EBS) from South Australia, and other Cambrian Series 2 Lagerstätten in South China; this association has been strengthened in recent years with the discovery of new taxa from the EBS with Chinese representatives (Paterson and Jago, 2006; Paterson et al., 2010, 2012, 2015, 2016). Similarities between Laurentian Series 3 Lagerstätten, such as between those in Utah and the Burgess Shale, are well known (e.g. Hagadorn, 2002; Briggs et al., 2008).

Previous palaeoecological analyses have compared the ecological attributes of BST biotas, e.g. patterns in species abundances, species diversity and phylum-level abundance. (e.g. Ivantsov et al., 2005; Caron and Jackson, 2008; Dornbos and Chen, 2008; Zhao et al., 2014). Ecological comparison of different assemblages has also been undertaken between subsets of individual Lagerstätten, both temporally (e.g. the 'bedding assemblages' from the Burgess Shale's Phyllopod Bed: Caron and Jackson, 2008), or spatially (e.g. the comparison of individual localities of the Chengjiang Biota: Zhao et al., 2012).

The majority of comments relating to taxonomic and biogeographic similarity between BST biotas have been made within studies mostly dedicated to other fields, e.g. palaeobiology and palaeoecology. The literature on the biogeography of these deposits is sparse, simply due to the fact that the spread of sites through space and time might make them seem poor candidates for biogeographic study – at least when

considered in isolation. It is important to note that within the biotas there are many different groups that may show completely different biogeographic patterns due to factors such as the history of individual lineages and their dispersal abilities. It has been shown, for example, that early Cambrian trilobite distributions are possibly a vicariant result of the breakup of the short-lived supercontinent Pannotia during the late Neoproterozoic (Lieberman, 2003; Meert and Lieberman, 2004), whereas the distribution of non-trilobite arachnomorph arthropods is more likely a result of other factors such as dispersal ability and sea level change (Hendricks and Lieberman, 2007). For traditional biogeographic purposes it is more sensible to focus on mineralised groups that have wide collective distributions across space and time, such as trilobites (Álvarez et al., 2013; Hally and Paterson, 2014) and/or on clades with robust phylogenetic hypotheses (Lieberman, 2003; Hendricks and Lieberman, 2007). Unfortunately, many groups present within BST biotas do not display these characteristics. Despite this, Cambrian Lagerstätten still contain important biogeographic information that should be considered. The resolution with which we can view these exceptionally preserved assemblages, i.e. the fact that they provide a more faithful representation of taxa present than conventional fossil deposits, means that we can analyse taxonomic associations in greater detail, and then suggest what factors may be responsible for the relationships we see based on the characteristics of the sites in question.

Here we undertake the first quantitative analysis of the taxonomic relationships between all major BST biotas. The importance of these deposits to our understanding of early animal life and evolution has resulted in considerable scholarly attention, and the resulting literature has allowed for the compilation of a substantial database of generic occurrence to be constructed. We analyse this database using a variety of statistical methods to provide insights into how and why BST biotas are related. Our analyses are based on a 'whole of assemblage' perspective (i.e. all genera present at a site were considered, regardless of their biomineralisation), which provides the most informed comparison of biotas and thus a more complete view of the overall diversity of Lagerstätten assemblages compared to conventional deposits.

1.3. Locations and relative ages

In this study we consider 12 BST biotas from East Gondwana (Emu Bay Shale), South China (Chengjiang, Kaili, Guanshan, Balang), Laurentia (Burgess, Wheeler, Spence and Kinzers Shales, the Marjum Formation, and Sirius Passet) and Siberia (Sinsk) (Fig. 1), and ranging in age from Series 2 through Series 3 (formerly late-early through middle Cambrian; Table 1). Absolute ages are estimated below and are based on correlation with the Cambrian timescale presented in Peng et al. (2012, Fig. 19.3), unless otherwise stated.

The Chengjiang Biota occurs within the Maotianshan Shale – the middle member of the Yu'an-shan Formation based on the organisation of MacKenzie et al. (2015; as per Hu, 2005; Zhao et al., 2012), overlying the 'Black Shale' and underlying the 'Upper Siltstone' members. Fossils of the Chengjiang Biota occur primarily in the middle-to-upper part of the Maotianshan Shale member, essentially in the middle of the Yu'an-shan Formation (MacKenzie et al., 2015). This is consistent with a mid-late Atdabanian age (e.g. Steiner et al., 2007), or c. 518 Ma based on correlation with Fig. 19.11 of Peng et al. (2012). The Sirius Passet Lagerstätte (lower Buen Formation) is stratigraphically poorly constrained and its position based mainly on the nevadiid affinities of the trilobite *Buenellus* and subsequent correlation with the *Nevadella* trilobite zone of Laurentia (Babcock and Peel, 2007), the middle of which is dated to around 517 Ma. Incidentally, this is the same age tentatively assigned to Sirius Passet by Budd (2011). Based on the presence of the Sinsk Biota within the *Bergeroniellus gurarii* zone (Astashkin et al., 1990) we estimate an age of 515 Ma. The age of the Balang Formation is approximately 514 Ma based on placement within the *Arthrocephalus chavezui* zone (Yan et al., 2014). The Guanshan Biota

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