Biogeographic and Biological Comparisons Between the Emu Bay Shale (Kangaroo Island, South Australia) and Other Cambrian Burgess Shale-Type Biotas

James Dougal Holmes
B.Sc B.Ec

Thesis submitted for the degree of

Master of Philosophy

School of Biological Sciences
Faculty of Sciences
University of Adelaide
October 2016
Contents

Figures and Tables........................................................................................................vi
Abstract............................................................................................................................vii
Declaration.........................................................................................................................ix
Acknowledgements..........................................................................................................x

Chapter 1 – Introduction....................................................................................................1
   1.1 Contextual statement.................................................................................................2

Chapter 2 – Background....................................................................................................3
   2.1 Konservat-Lagerstätten and Burgess Shale-type (BST) biotas.................................4
   2.2 History of the Emu Bay Shale...................................................................................6
   2.3 Geology and environment.........................................................................................9
   2.4 Preservation..............................................................................................................11
   2.5 Biota.........................................................................................................................11
   2.6 Palaeogeography.......................................................................................................14
   2.7 Biogeographic associations.......................................................................................16
   2.8 Moulting in Emu Bay Shale trilobites.......................................................................17
   2.9 References...............................................................................................................19

Chapter 3 – Quantitative comparison of Cambrian Lagerstätten assemblages in space and time ..............................................................28
   3.1 Abstract...................................................................................................................29
   3.2 Introduction..............................................................................................................31
<table>
<thead>
<tr>
<th>Section</th>
<th>Title</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>3.2.1</td>
<td>Background</td>
<td>31</td>
</tr>
<tr>
<td>3.2.2</td>
<td>Previous work</td>
<td>32</td>
</tr>
<tr>
<td>3.2.3</td>
<td>Locations and relative ages</td>
<td>35</td>
</tr>
<tr>
<td>3.2.4</td>
<td>Considerations in comparing assemblages</td>
<td>40</td>
</tr>
<tr>
<td>3.3</td>
<td>Data and methodology</td>
<td>44</td>
</tr>
<tr>
<td>3.3.1</td>
<td>General considerations</td>
<td>44</td>
</tr>
<tr>
<td>3.3.2</td>
<td>Statistical modelling</td>
<td>45</td>
</tr>
<tr>
<td>3.3.3</td>
<td>Ordinations and cluster analysis</td>
<td>47</td>
</tr>
<tr>
<td>3.3.4</td>
<td>Parsimony and Bayesian analysis</td>
<td>48</td>
</tr>
<tr>
<td>3.3.5</td>
<td>Phyla diversity</td>
<td>50</td>
</tr>
<tr>
<td>3.4</td>
<td>Results</td>
<td>50</td>
</tr>
<tr>
<td>3.4.1</td>
<td>Statistical modelling</td>
<td>50</td>
</tr>
<tr>
<td>3.4.2</td>
<td>Ordinations and cluster analysis</td>
<td>51</td>
</tr>
<tr>
<td>3.4.3</td>
<td>PAE and Bayesian analysis</td>
<td>55</td>
</tr>
<tr>
<td>3.4.4</td>
<td>Phyla diversity</td>
<td>57</td>
</tr>
<tr>
<td>3.5</td>
<td>Discussion</td>
<td>58</td>
</tr>
<tr>
<td>3.5.1</td>
<td>General palaeobiogeographic patterns</td>
<td>58</td>
</tr>
<tr>
<td>3.5.2</td>
<td>Individual comparisons</td>
<td>61</td>
</tr>
<tr>
<td>3.5.3</td>
<td>Phyla diversity</td>
<td>68</td>
</tr>
<tr>
<td>3.6</td>
<td>Conclusions</td>
<td>71</td>
</tr>
<tr>
<td>3.7</td>
<td>Acknowledgements</td>
<td>72</td>
</tr>
<tr>
<td>3.8</td>
<td>References</td>
<td>73</td>
</tr>
</tbody>
</table>
Chapter 4 – Variable trilobite moulting behaviour preserved in the Emu Bay Shale, South Australia .................................................................85

4.1 Abstract .........................................................................................86
4.2 Introduction ....................................................................................88
4.3 Location, geological setting and age .............................................89
4.4 Material and methods .................................................................92
4.5 Results ..........................................................................................93
  4.5.1 Descriptions of recognised moult configurations ....................93
  4.5.2 Description of moulting in *Estaingia bilobata* Pocock, 1964 .....97
  4.5.3 Description of moulting in *Redlichia takooensis* Lu, 1950 .......101
4.6 Discussion ......................................................................................105
  4.6.1 Inferred moulting behaviour of *Estaingia bilobata* .................105
  4.6.2 Inferred moulting behaviour of *Redlichia takooensis* ............108
  4.6.3 Comparisons with other Cambrian trilobites and localities .....111
  4.6.4 Recognising moult configurations ........................................113
4.7 Conclusions ..................................................................................117
4.8 Acknowledgements .......................................................................118
4.9 References .....................................................................................119

Chapter 5 – Conclusions ....................................................................124

5.1 Summary ......................................................................................125
5.2 Future directions ..........................................................................127
Chapter 6 – Appendices ..................................................................................129

6.1 Electronic Supplementary Material ................................................................130

6.2 Supplementary Material for Chapter 3 ..........................................................131

6.3 References .................................................................................................147
Figures and Tables

Chapter 2

Figure 2.1: Map showing localities of the Emu Bay Shale ........................................... 5
Figure 2.2: Big Gully with Buck Quarry (bottom right) and Daily Quarry (centre) ...... 7
Figure 2.3: Generalised costal section of the Cambrian succession near Big Gully.. 8
Figure 2.4: Faunal slab from the EBS Lagerstätte (Buck Quarry)............................... 12
Figure 2.5: Cambrian continental reconstruction as at 510 Ma................................. 15
Figure 2.6: Simplified biomineralised anatomy of the trilobite Estaingia bilobata .... 18

Chapter 3

Figure 3.1: Cambrian continental reconstruction showing hypothesised locations of Cambrian Lagerstätten (as at 510 Ma). ................................................................. 36
Table 3.1: Estimated age, location, number of genera, and number of shared/endemic genera for each of the 12 Cambrian Lagerstätten................................. 38
Figure 3.2: Non-metric multidimensional scaling (NMDS) ordination plots of major BST biotas based on presence/absence of genera ................................................. 52
Figure 3.3: UPGMA cluster analysis dendrograms depicting assemblage distance between major BST biotas based on presence/absence of genera ................................ 54
Figure 3.4: A. PAE phylogram (single shortest tree of 752 steps). B. Bayesian majority-rule consensus tree......................................................................................... 56
Figure 3.5: Composition of the 12 Cambrian Lagerstätten assemblages considered in this study in order of age, based on number of genera per phylum .............. 57
Figure 3.6: Biplot and linear regression of age difference vs shared genera between Laurentian Lagerstätten....................................................................................... 65
Figure 3.7: Relative proportions and linear regression trendlines for trilobites, non-trilobite arthropods, and total arthropods through time ........................................... 70

Chapter 4

Figure 4.1: Moult configurations discussed in the text (based on Estaingia bilobata Pocock, 1964) ........................................................................................................ 96
Figure 4.2: Example moult configurations of Estaingia bilobata Pocock, 1964........ 98
Figure 4.3: Example moult configurations of Estaingia bilobata Pocock, 1964........ 100
Figure 4.4: Example moult configurations of Redlichia takooensis Lu, 1950 ......... 103

Chapter 6

Supplementary Table 6.1: Presence/absence matrix of genera at 12 Cambrian Lagerstätten analysed in Chapter 3................................................................. 131
Supplementary Table 6.2: Mantel test results ...................................... Error! Bookmark not defined.
Supplementary Table 6.3: MRM results ................................................ 144
Supplementary Table 6.4: Table of references used in construction of the presence/absence matrix analysed in Chapter 3........................ 146
Abstract

*Konservat-Lagerstätten*, or fossil deposits exhibiting exceptional preservation of non-biomineralised material, are particularly prevalent in the Cambrian, and offer us great insight into the evolution and ecology of early animals and communities. The Emu Bay Shale (EBS) from the north coast of Kangaroo Island, South Australia, houses an early Cambrian (Series 3 – c. 514 Ma) Lagerstätte that contains over 50 species, including sponges, brachiopods, molluscs, annelids, priapulids, lobopodians, arthropods, vetulicolians, and several problematic taxa, making it the most diverse Burgess Shale-type (BST) biota in the southern hemisphere. While considerable work in describing taxa from the EBS Lagerstätte has been completed, less has been undertaken that focuses on the relationships between this and other Cambrian BST biotas. This project aims to examine some of the links between the EBS Lagerstätte and similar deposits from around the world, including the Burgess Shale (Canada), Chengjiang (China) and Sirius Passet (Greenland) biotas, amongst others. To this end, the project has two major parts.

The first section aims to examine the biogeographic relationships between major Cambrian BST biotas from a global perspective. A substantial database of generic occurrence was constructed from the published literature, and analysed using various multivariate techniques in order to examine the relationships between these exceptionally preserved assemblages. Results suggest that both geographic distance and differences in age have an effect on the composition of BST biotas, and that assemblage similarity appears to increase through the Cambrian. The EBS
biota is most closely related to other Gondwanan sites in South China, most likely reflecting a regional relationship.

The second section involves a more focused description and interpretation of a single element of the EBS biota, namely an examination of the moulting habits of two common trilobite species from the Emu Bay Shale, *Estaingia bilobata* Pocock, 1964 and *Redlichia takooensis* Lu, 1950, and how this compares with other BST assemblages. Specimens from the EBS were examined and arrangements of exoskeletal elements likely representing moult ensembles identified, from which moulting behaviour was then inferred and compared. Analysis reveals that the EBS preserves a record of trilobite moulting unparalleled within other exceptionally preserved assemblages, representing a range of trilobite moulting behaviours, likely due to minimal water movement and relatively rapid burial within the biota’s unique inshore depositional setting.

The unusual depositional setting of the EBS Lagerstätte seems to have had a minimal effect on the types of organisms present with the assemblage compared to other BST biotas. In contrast, this setting seems to have facilitated the preservation of an exceptional moulting record not found at other sites, including BST deposits. This, coupled with the unique preservation of certain structures such as eyes, confirms that the EBS is of great importance in elucidating the evolution of early animals and communities.
Declaration

I, James Dougal Holmes, certify that this work contains no material which has been accepted for the award of any other degree or diploma in my name in any university or other tertiary institution and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text. In addition, I certify that no part of this work will, in the future, be used in a submission in my name for any other degree or diploma in any university or other tertiary institution without the prior approval of the University of Adelaide and where applicable, any partner institution responsible for the joint award of this degree.

I give consent to this copy of my thesis when deposited in the University Library, being made available for loan and photocopying, subject to the provisions of the Copyright Act 1968. The author acknowledges that copyright of published works contained within this thesis resides with the copyright holder(s) of those works. I also give permission for the digital version of my thesis to be made available on the web, via the University's digital research repository, the Library Search and also through web search engines, unless permission has been granted by the University to restrict access for a period of time.

James Dougal Holmes

1st December 2016
Acknowledgements

I would like to thank my supervisors, Dr Diego García-Bellido, Prof Mike Lee and Prof Corey Bradshaw, for the time and effort they have invested in supporting me through my candidature.

Thanks to my collaborators Allison Daley and in particular Harriet Drage, for their efforts and patience in working with me on the Emu Bay Shale trilobites.

I would like to thank staff, students, volunteers and associates of the South Australian Museum, as well as the University of Adelaide, the University of South Australia, and the University of New England, for their invaluable assistance, collection of material, and for giving up their time to help me, in particular Ronda Atkinson, Mary-Anne Binnie, Felicity Coutts, Jim Gehling, Jim Jago, Katrina Kenny, Justin Payne, John Paterson and Natalie Schroeder.

I would like to thank Paul and Carmen Buck for generously allowing access to the Emu Bay Shale field site on their property.

Finally, thanks to my family - to my parents for always encouraging me, and in particular to my fiancé Lily Reid for her help, patience and unwavering support of me in everything I do.