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Using GIS to study palaeobiogeographic and macroevolutionary patterns in soft-bodied Cambrian arthropods

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ARTICLE INFO

Article history:

Received 15 August 2007

Received in revised form 27 March 2008

Accepted 3 April 2008

Keywords:

Cambrian

Arthropod

Soft bodied

Palaeobiogeography

Geographic Information System (GIS)

ABSTRACT

Soft-bodied Cambrian arthropods from Burgess Shale-type deposits are some of the most famous and extensively studied fossil invertebrates, but global species-level assessments of their biogeographic patterns have not previously been explored quantitatively. Here we use a newly developed occurrence database, in conjunction with Geographic Information Systems (GIS) analysis and PaleoGIS—which allows fossil locality positions to be viewed in the context of Cambrian palaeogeography—to quantitatively reconstruct geographic distribution patterns of primarily soft-bodied arthropod species. Further, we compare these patterns with those of co-occurring trilobite taxa. Soft-bodied Cambrian arthropods show both statistically larger geographic ranges and greater stratigraphic longevities than co-occurring trilobites. Many of the most widely distributed soft-bodied arthropods were likely capable of swimming, and this may in part explain their extensive distributions.

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1. Introduction

Burgess Shale-type deposits (those that preserve non-mineralized soft-parts) are known from many Lower and Middle Cambrian localities around the globe and provide a critical window on the early evolution and diversification of metazoans (Conway Morris, 1989a; Gould, 1989; Butterfield, 1995; Hagadorn, 2002). Despite intense study of the diversity, palaeoecology, and taphonomy of individual Cambrian soft-bodied biotas (e.g., Conway Morris et al., 1987; Robison, 1991; Briggs et al., 1994; Nedin, 1995; Hou and Bergström, 1997; Zhao et al., 2002; Lieberman, 2003; Hou et al., 2004; Dornbos et al., 2005; Gaines et al., 2005; Skinner, 2005; Steiner et al., 2005; Caron and Jackson, 2006; Schwimmer and Montante, 2007), little work has been done to explore and compare the global palaeobiogeographic distributions of individual species. The elucidation of such biogeographical patterns is important for our understanding of the macroevolutionary context of the Cambrian radiation (Lieberman and Meert, 2004; Meert and Lieberman, 2004; Lieberman, 2008). We use a newly constructed database of georeferenced taxon occurrence records from 51 localities, in conjunction with geographic information systems (GIS) and a reconstruction of Cambrian palaeogeography (Fig. 1), to compare distribution patterns in Early and Middle Cambrian arthropods, which are among the most diverse and abundant components of Burgess Shale-type deposits. Specifically, we compare geographic and strati-

graphic distribution patterns in species of trilobites (defined following the phylogenetic definitions of Fortey and Whittington, 1989; Edgecombe and Ramsköld, 1999) and primarily soft-bodied arthropods from Burgess Shale-type deposits to: 1) quantitatively test suggestions from the literature (Conway Morris and Robison, 1986; Conway Morris, 1989b; Lieberman, 2003) that soft-bodied arthropod species have wider geographic ranges and greater stratigraphic longevities than co-occurring trilobite species; 2) investigate whether there is an association between life habit and palaeogeographic range; and 3) examine the implied patterns of movement of arthropod species between separated palaeogeographic regions. Each of these may help to unravel macroevolutionary patterns at the beginning of the radiation of animal life.

2. Materials and methods

2.1. Database construction

A new database of arthropod species occurrence records (Table 1) from globally distributed Early and Middle Cambrian Burgess Shale-type deposits was compiled using literature sources (Table 2) and museum samples at the University of Kansas Division of Invertebrate Paleontology. Occurrence records were tabulated at the species-level because phylogenetic hypotheses supporting monophyly are lacking for most higher taxa (e.g., genera) and because it may be challenging to assign biological meaning to biogeographic patterns in higher level taxa (we did, however, evaluate the robustness of our species-level results at the genus-level for comparison; see below). Most

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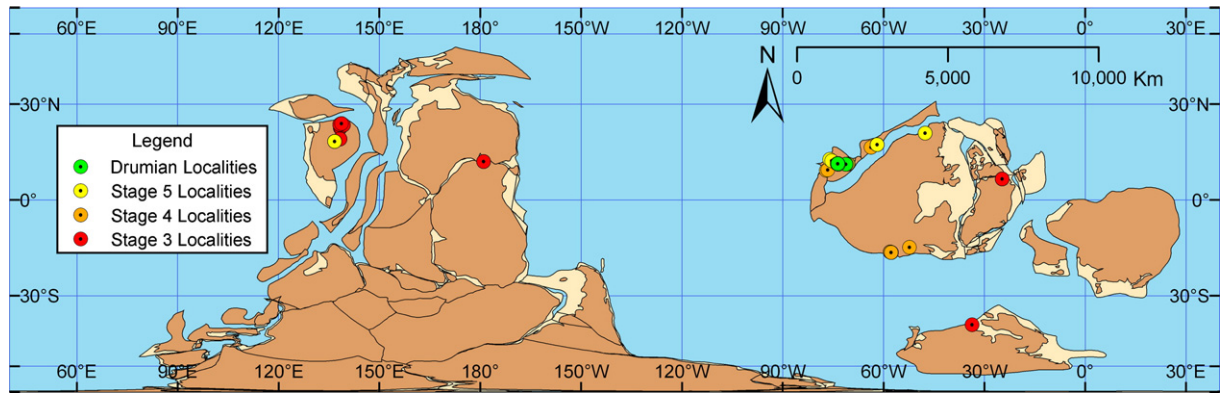


Fig. 1. Distribution of Burgess Shale-type localities and model of Cambrian palaeogeography (Ross and Scotese, 2000) utilized for this study.

occurrence records could be entered into the database without modifying their taxonomy, but some taxonomic changes were required reflecting revised taxonomic placements or identifications

(e.g., Briggs et al., 2008). Further, in some cases we chose not to follow the taxonomic placements of particular taxa where we disagreed with other authors; for example, we consider *Tuzoia getzi* and *T. nitida*

Table 1
Database of life habit, occurrence, and geographic range data for individual species. Abbreviations: A, Australia; B, benthic; BA, Baltica; C, China; EL, Eastern Laurentia; G, Greenland; N, nekitic; NB, nektobenthic; O, absent; WL, Western Laurentia; X, present

| Species | Habit | No. occurrence records | No. regions present | Regions | | | | | | Temporal stage | | | | No. temp. boundaries crossed | Geographic range | |
|--|-------|------------------------|---------------------|---------|----|---|---|---|---|----------------|---|---|---|------------------------------|------------------|---------------------------|
| | | | | WL | EL | G | C | A | B | 3 | 4 | 5 | 6 | | Distance (km) | method (km ²) |
| Non-trilobite arthropods | | | | | | | | | | | | | | | | |
| <i>Acanthomeridion serratum</i> | B | 3 | 1 | O | O | O | X | O | O | X | O | O | O | 0 | 71 | 40 |
| <i>Actaeus armatus</i> | NB | 1 | 1 | X | O | O | O | O | O | O | O | X | O | 0 | 1 | 3 |
| <i>Alalcomenaeus cambricus</i> | NB | 1 | 1 | X | O | O | O | O | O | O | O | X | O | 0 | 1 | 3 |
| <i>Amplectobelua symbrachiata</i> | N | 1 | 1 | O | O | O | X | O | O | X | O | O | O | 0 | 1 | 3 |
| <i>Amplectobelua trispinata</i> | N | 5 | 1 | O | O | O | X | O | O | X | O | O | O | 0 | 502 | 25,704 |
| <i>Anomalocaris briggsi</i> | N | 1 | 1 | O | O | O | O | X | O | X | O | O | O | 0 | 1 | 3 |
| <i>Anomalocaris canadensis</i> (& cf.) | N | 4 | 1 | X | O | O | O | O | O | O | X | X | X | 2 | 1892 | 33,481 |
| <i>Anomalocaris lineata</i> | N | 2 | 1 | O | X | O | O | O | O | O | X | O | O | 0 | 33 | 66 |
| <i>Anomalocaris pennsylvanica</i> | N | 3 | 2 | X | X | O | O | O | O | O | X | O | O | 0 | 3620 | 8505 |
| <i>Anomalocaris saron</i> (& cf.) | N | 4 | 2 | X | O | O | X | O | O | X | O | X | O | 2 | 16,352 | 935,458 |
| <i>Apioccephalus elegans</i> | ? | 1 | 1 | O | O | O | X | O | O | X | O | O | O | 0 | 1 | 3 |
| <i>Beckwithia typa</i> | B | 1 | 1 | X | O | O | O | O | O | O | O | O | X | 0 | 1 | 3 |
| <i>Branchiocaris pretiosa</i> (& ?) | NB | 4 | 1 | X | O | O | O | O | O | O | O | X | X | 1 | 1461 | 102,264 |
| <i>Branchiocaris yunnanensis</i> | NB | 5 | 1 | O | O | O | X | O | O | X | O | O | O | 0 | 126 | 3537 |
| <i>Buenaspis fortzeyi</i> | B | 1 | 1 | O | O | X | O | O | O | X | O | O | O | 0 | 1 | 3 |
| <i>Burgessia bella</i> | B | 1 | 1 | X | O | O | O | O | O | O | O | X | O | 0 | 1 | 3 |
| <i>Cambropodus gracilis</i> | B | 1 | 1 | X | O | O | O | O | O | O | O | O | X | 0 | 1 | 3 |
| <i>Canadaspis kailiensis</i> | B | 1 | 1 | O | O | O | X | O | O | O | O | X | O | 0 | 1 | 3 |
| <i>Canadaspis laevigata</i> | B | 2 | 1 | O | O | O | X | O | O | X | O | O | O | 0 | 95 | 190 |
| <i>Canadaspis ovalis</i> | B | 1 | 1 | X | O | O | O | O | O | O | O | X | O | 0 | 1 | 3 |
| <i>Canadaspis perfecta</i> (& cf.) | B | 5 | 1 | X | O | O | O | O | O | O | O | X | X | 1 | 1598 | 220,925 |
| <i>Carnarvonina venosa</i> | ? | 1 | 1 | X | O | O | O | O | O | O | O | X | O | 0 | 1 | 3 |
| <i>Cassubia infercambriensis</i> | N | 1 | 1 | O | O | O | O | O | X | X | O | O | O | 0 | 1 | 3 |
| <i>Chengjiangocaris longiformis</i> | B | 1 | 1 | O | O | O | X | O | O | X | O | O | O | 0 | 1 | 3 |
| <i>Chuanodianella? linguiformis</i> | ? | 1 | 1 | O | O | O | X | O | O | O | O | X | O | 0 | 1 | 3 |
| <i>Chuanodianella? subovata</i> | ? | 1 | 1 | O | O | O | X | O | O | O | O | X | O | 0 | 1 | 3 |
| <i>Cindarella eucalla</i> | B | 3 | 1 | O | O | O | X | O | O | X | O | O | O | 0 | 71 | 43 |
| <i>Clypepcaris pterioidea</i> | NB | 2 | 1 | O | O | O | X | O | O | X | O | O | O | 0 | 53 | 106 |
| <i>Combinivalvula chengjiangensis</i> | ? | 3 | 1 | O | O | O | X | O | O | X | O | O | O | 0 | 54 | 169 |
| <i>Comptaluta inflata</i> | NB | 1 | 1 | O | O | O | X | O | O | X | O | O | O | 0 | 1 | 3 |
| <i>Comptaluta leshanensis</i> | NB | 1 | 1 | O | O | O | X | O | O | X | O | O | O | 0 | 1 | 3 |
| <i>Cucumericrus decoratus</i> | N | 1 | 1 | O | O | O | X | O | O | X | O | O | O | 0 | 1 | 3 |
| <i>Cyathocephalus bispinosus</i> | ? | 1 | 1 | O | O | O | X | O | O | X | O | O | O | 0 | 1 | 3 |
| <i>Dianchia mirabilis</i> | ? | 1 | 1 | O | O | O | X | O | O | X | O | O | O | 0 | 1 | 3 |
| <i>Dicerocaris opisthoeces</i> | ? | 2 | 1 | X | O | O | O | O | O | O | O | O | X | 0 | 30 | 60 |
| <i>Dicranocaris guntheri</i> | NB | 7 | 1 | X | O | O | O | O | O | O | O | O | X | 0 | 11 | 18 |
| <i>Dioxycares argenta</i> | ? | 1 | 1 | X | O | O | O | O | O | O | O | X | O | 0 | 1 | 3 |
| <i>Diplopyge forcipatus</i> | ? | 1 | 1 | O | O | O | X | O | O | X | O | O | O | 0 | 1 | 3 |
| <i>Dongshanocaris foliiformis</i> | ? | 1 | 1 | O | O | O | X | O | O | X | O | O | O | 0 | 1 | 3 |
| <i>Ecnomocaris spinosa</i> | B | 2 | 1 | X | O | O | O | O | O | O | O | O | X | 0 | 30 | 60 |
| <i>Emeraldella brocki</i> | B | 1 | 1 | X | O | O | O | O | O | O | O | X | O | 0 | 1 | 3 |
| <i>Ercania minuscula</i> | B | 2 | 1 | O | O | O | X | O | O | X | O | O | O | 0 | 53 | 106 |
| <i>Forficicaris valida</i> | ? | 1 | 1 | O | O | O | X | O | O | X | O | O | O | 0 | 1 | 3 |

Table 1 (continued)

| Species | Habit | No. occurrence records | No. regions present | Regions | | | | | | Temporal stage | | | | No. temp. boundaries crossed | Geographic range | |
|---|-------|------------------------|---------------------|---------|----|---|---|---|---|----------------|---|---|---|------------------------------|----------------------|--------------------------------|
| | | | | WL | EL | G | C | A | B | 3 | 4 | 5 | 6 | | Distance method (km) | Area method (km ²) |
| Non-trilobite arthropods | | | | | | | | | | | | | | | | |
| <i>Fortiforceps foliosa</i> | NB | 2 | 1 | O | O | O | X | O | O | X | O | O | O | 0 | 53 | 106 |
| <i>Fuxianhua protensa</i> | B | 4 | 1 | O | O | O | X | O | O | X | O | O | O | 0 | 130 | 2658 |
| <i>Glossocaris oculatus</i> | ? | 1 | 1 | O | O | O | X | O | O | X | O | O | O | 0 | 1 | 3 |
| <i>Habelia optata</i> | B | 1 | 1 | X | O | O | O | O | O | O | O | X | O | 0 | 1 | 3 |
| <i>Habelia? brevicauda</i> | B | 1 | 1 | X | O | O | O | O | O | O | O | X | O | 0 | 1 | 3 |
| <i>Haikoucaris ercaiensis</i> | NB | 1 | 1 | O | O | O | X | O | O | X | O | O | O | 0 | 1 | 3 |
| <i>Helmetia expansa</i> | N | 1 | 1 | X | O | O | O | O | O | O | O | X | O | 0 | 1 | 3 |
| <i>Houghtonites gracilis</i> | ? | 1 | 1 | X | O | O | O | O | O | O | O | X | O | 0 | 1 | 3 |
| <i>Hurdia</i> sp. (Anomalocaridid Taxon) | N | 3 | 1 | X | O | O | O | O | O | O | O | X | X | 1 | 1458 | 98,133 |
| <i>Indianites? sp.</i> | ? | 1 | 1 | O | X | O | O | O | O | O | X | O | O | 0 | 1 | 3 |
| <i>Isoxys acutangulus</i> | N | 1 | 1 | X | O | O | O | O | O | O | O | X | O | 0 | 1 | 3 |
| <i>Isoxys auritus</i> | N | 6 | 1 | O | O | O | X | O | O | X | O | O | O | 0 | 125 | 8268 |
| <i>Isoxys communis</i> | N | 1 | 1 | O | O | O | O | X | O | X | O | O | O | 0 | 1 | 3 |
| <i>Isoxys curvirostratus</i> | N | 3 | 1 | O | O | O | X | O | O | X | O | O | O | 0 | 504 | 11,392 |
| <i>Isoxys longissimus</i> | N | 1 | 1 | X | O | O | O | O | O | O | O | X | O | 0 | 1 | 3 |
| <i>Isoxys paradoxus</i> | N | 4 | 1 | O | O | O | X | O | O | X | O | O | O | 0 | 513 | 15,608 |
| <i>Isoxys volucris</i> | N | 1 | 1 | O | O | X | O | O | O | X | O | O | O | 0 | 1 | 3 |
| <i>Jianfengia multisegmentalis</i> | B | 2 | 1 | O | O | O | X | O | O | X | O | O | O | 0 | 52 | 104 |
| <i>Jianshania furcatus</i> | ? | 1 | 1 | O | O | O | X | O | O | X | O | O | O | 0 | 1 | 3 |
| <i>Jiucunella paulula</i> | NB | 1 | 1 | O | O | O | X | O | O | X | O | O | O | 0 | 1 | 3 |
| <i>Kleptothule rasmussenii</i> | ? | 1 | 1 | O | O | X | O | O | O | X | O | O | O | 0 | 1 | 3 |
| <i>Kuamaia lata</i> | B | 3 | 1 | O | O | O | X | O | O | X | O | O | O | 0 | 71 | 40 |
| <i>Kuamaia muricata</i> | B | 1 | 1 | O | O | O | X | O | O | X | O | O | O | 0 | 1 | 3 |
| <i>Kunmingella douvillei</i> | NB | 6 | 1 | O | O | O | X | O | O | X | O | O | O | 0 | 147 | 9652 |
| <i>Kunmingocaris bispinosus</i> | ? | 1 | 1 | O | O | O | X | O | O | X | O | O | O | 0 | 1 | 3 |
| <i>Kunyangella cheni</i> | NB | 3 | 1 | O | O | O | X | O | O | X | O | O | O | 0 | 72 | 279 |
| <i>Laggania nathorsti</i> cf. | N | 6 | 1 | X | O | O | O | O | O | O | X | X | 1 | 1464 | 100,400 | |
| <i>Leanchoilia asiatica</i> | NB | 1 | 1 | O | O | O | X | O | O | X | O | O | O | 0 | 1 | 3 |
| <i>Leanchoilia illecebrosa</i> | NB | 6 | 1 | O | O | O | X | O | O | X | O | X | O | 2 | 633 | 19,684 |
| <i>Leanchoilia protogonia</i> | NB | 2 | 1 | X | O | O | O | O | O | O | X | X | 1 | 1462 | 2924 | |
| <i>Leanchoilia superlata</i> (& ?) | NB | 2 | 1 | X | O | O | O | O | O | O | O | X | O | 0 | 1220 | 2440 |
| <i>Leanchoilia? hanceyi</i> | NB | 2 | 1 | X | O | O | O | O | O | O | O | X | X | 1 | 287 | 574 |
| <i>Liangshanella liangshanensis</i> | NB | 1 | 1 | O | O | O | X | O | O | X | O | O | O | 0 | 1 | 3 |
| <i>Liwia</i> (& cf.) <i>plana</i> (& cf.) | B | 2 | 2 | O | O | X | O | O | X | X | O | O | O | 0 | 4937 | 9874 |
| <i>Mafangia subscalaria</i> | ? | 1 | 1 | O | O | O | X | O | O | X | O | O | O | 0 | 1 | 3 |
| <i>Mafangocaris multinodus</i> | ? | 1 | 1 | O | O | O | X | O | O | X | O | O | O | 0 | 1 | 3 |
| <i>Marrella splendens</i> | NB | 1 | 1 | X | O | O | O | O | O | O | O | X | O | 0 | 1 | 3 |
| <i>Meristosoma paradoxum</i> | B | 2 | 1 | X | O | O | O | O | O | O | O | X | O | 0 | 6 | 12 |
| <i>Misszhouia longicaudata</i> | B | 7 | 1 | O | O | O | X | O | O | X | O | O | O | 0 | 512 | 5921 |
| <i>Molaria spinifera</i> | B | 1 | 1 | X | O | O | O | O | O | O | O | X | O | 0 | 1 | 3 |
| <i>Mollisonia rara</i> | ? | 1 | 1 | X | O | O | O | O | O | O | O | X | O | 0 | 1 | 3 |
| <i>Mollisonia sinica</i> | ? | 1 | 1 | O | O | O | X | O | O | O | O | X | O | 0 | 1 | 3 |
| <i>Mollisonia symmetrica</i> | ? | 3 | 1 | X | O | O | O | O | O | O | O | X | X | 1 | 1460 | 97,171 |
| <i>Naraoia compacta</i> (& cf.) | B | 6 | 2 | X | O | O | X | O | O | O | O | X | X | 1 | 18,004 | 5,823,727 |
| <i>Naraoia halia</i> | B | 2 | 2 | X | O | O | X | O | O | X | O | X | O | 2 | 17,729 | 35,458 |
| <i>Naraoia spinifer</i> | B | 1 | 1 | X | O | O | O | O | O | O | O | X | O | 0 | 1 | 3 |
| <i>Naraoia spinosa</i> | B | 5 | 1 | O | O | O | X | O | O | X | O | O | O | 0 | 513 | 8432 |
| <i>Nettapezoura basilikos</i> | B | 1 | 1 | X | O | O | O | O | O | O | O | O | X | 0 | 1 | 3 |
| <i>Occacaris oviformis</i> | ? | 1 | 1 | O | O | O | X | O | O | X | O | O | O | 0 | 1 | 3 |
| <i>Odaraia alata</i> | N | 1 | 1 | X | O | O | O | O | O | O | O | X | O | 0 | 1 | 3 |
| <i>Odaraia? eurypetala</i> | N | 3 | 1 | O | O | O | X | O | O | X | O | O | O | 0 | 53 | 172 |
| <i>Ovalicephalus mirabilis</i> | ? | 1 | 1 | O | O | O | X | O | O | X | O | O | O | 0 | 1 | 3 |
| <i>Pahvantia hastata</i> | ? | 1 | 1 | X | O | O | O | O | O | O | O | O | X | 0 | 1 | 3 |
| <i>Parapaleomerus sinensis</i> | ? | 1 | 1 | O | O | O | X | O | O | X | O | O | O | 0 | 1 | 3 |
| <i>Parapeytoia yunnanensis</i> | N | 2 | 1 | O | O | O | X | O | O | X | O | O | O | 0 | 53 | 106 |
| <i>Paulotermis spinodorsalis</i> | B | 1 | 1 | O | O | X | O | O | O | X | O | O | O | 0 | 1 | 3 |
| <i>Pectocaris spatiosa</i> | N | 1 | 1 | O | O | O | X | O | O | X | O | O | O | 0 | 1 | 3 |
| <i>Perspiscaris</i> (& ?) <i>dilatatus</i> | NB | 5 | 1 | X | O | O | O | O | O | O | O | X | X | 1 | 1598 | 221,186 |
| <i>Perspiscaris</i> (& ?) <i>ellipsopelta</i> | NB | 2 | 1 | X | O | O | O | O | O | O | O | O | X | 0 | 7 | 14 |
| <i>Perspiscaris dictynna</i> | NB | 1 | 1 | X | O | O | O | O | O | O | O | X | O | 0 | 1 | 3 |
| <i>Perspiscaris recondita</i> | N | 1 | 1 | X | O | O | O | O | O | O | O | X | O | 0 | 1 | 3 |
| <i>Pisinnocaris subconigera</i> | ? | 1 | 1 | O | O | O | X | O | O | X | O | O | O | 0 | 1 | 3 |
| <i>Plenocaris plena</i> | NB | 1 | 1 | X | O | O | O | O | O | O | O | X | O | 0 | 1 | 3 |
| <i>Primicaris larvaformis</i> | B | 1 | 1 | O | O | O | X | O | O | X | O | O | O | 0 | 1 | 3 |
| <i>Priscansermarinus barnetti</i> | B | 1 | 1 | X | O | O | O | O | O | O | O | X | O | 0 | 1 | 3 |
| <i>Protocaris marshi</i> | ? | 1 | 1 | O | X | O | O | O | O | O | X | O | O | 0 | 1 | 3 |
| <i>Pseudoarctolepis sharpi</i> | ? | 3 | 1 | X | O | O | O | O | O | O | O | O | X | 0 | 30 | 52 |
| <i>Pseudoiulia cambriensis</i> | ? | 1 | 1 | O | O | O | X | O | O | X | O | O | O | 0 | 1 | 3 |
| <i>Pterotruncus triacanthus</i> | ? | 1 | 1 | O | O | O | X | O | O | X | O | O | O | 0 | 1 | 3 |
| <i>Pygmaclypeatus daziensis</i> | ? | 2 | 1 | O | O | O | X | O | O | X | O | O | O | 0 | 53 | 106 |
| <i>Retifacies abnormalis</i> | B | 4 | 1 | O | O | O | X | O | O | X | O | O | O | 0 | 125 | 3362 |

(continued on next page)

Table 1 (continued)

| Species | Habit | No. occurrence records | No. regions present | Regions | | | | | | Temporal stage | | | | No. temp. boundaries crossed | Geographic range | | |
|---|-------|------------------------|---------------------|---------|----|---|---|---|---|----------------|---|---|---|------------------------------|------------------|--------|-------------------------|
| | | | | WL | EL | G | C | A | B | 3 | 4 | 5 | 6 | | Distance (km) | method | Area (km ²) |
| Non-trilobite arthropods | | | | | | | | | | | | | | | | | |
| <i>Rhombicalvaria acantha</i> | ? | 1 | 1 | 0 | 0 | 0 | X | 0 | 0 | X | 0 | 0 | 0 | 0 | 0 | 1 | 3 |
| <i>Roddyia typha</i> | ? | 1 | 1 | 0 | X | 0 | 0 | 0 | 0 | 0 | X | 0 | 0 | 0 | 0 | 1 | 3 |
| <i>Sanctacaris uncata</i> | NB | 1 | 1 | X | 0 | 0 | 0 | 0 | 0 | 0 | 0 | X | 0 | 0 | 0 | 1 | 3 |
| <i>Saperion glumaceum</i> | B | 2 | 1 | 0 | 0 | 0 | X | 0 | 0 | X | 0 | 0 | 0 | 0 | 0 | 55 | 110 |
| <i>Sarotrocercus oblita</i> | N | 1 | 1 | X | 0 | 0 | 0 | 0 | 0 | 0 | 0 | X | 0 | 0 | 0 | 1 | 3 |
| <i>Serracaris lineata</i> | N | 1 | 1 | 0 | X | 0 | 0 | 0 | 0 | 0 | X | 0 | 0 | 0 | 0 | 1 | 3 |
| <i>Sidneyia inexpectans</i> | B | 1 | 1 | X | 0 | 0 | 0 | 0 | 0 | 0 | 0 | X | 0 | 0 | 0 | 1 | 3 |
| <i>Sidneyia? sinica</i> | B | 1 | 1 | 0 | 0 | 0 | X | 0 | 0 | X | 0 | 0 | 0 | 0 | 0 | 1 | 3 |
| <i>Sinoburius lunaris</i> | B | 2 | 1 | 0 | 0 | 0 | X | 0 | 0 | X | 0 | 0 | 0 | 0 | 0 | 54 | 108 |
| <i>Skania fragilis</i> | ? | 1 | 1 | X | 0 | 0 | 0 | 0 | 0 | 0 | 0 | X | 0 | 0 | 0 | 1 | 3 |
| <i>Skania sunbergi</i> | ? | 1 | 1 | 0 | 0 | 0 | X | 0 | 0 | 0 | 0 | X | 0 | 0 | 0 | 1 | 3 |
| <i>Skioldia aldna</i> | B | 2 | 1 | 0 | 0 | 0 | X | 0 | 0 | X | 0 | 0 | 0 | 0 | 0 | 480 | 960 |
| <i>Spinokunmingella typica</i> | ? | 1 | 1 | 0 | 0 | 0 | X | 0 | 0 | X | 0 | 0 | 0 | 0 | 0 | 1 | 3 |
| <i>Squamacula clypeata</i> | B | 2 | 1 | 0 | 0 | 0 | X | 0 | 0 | X | 0 | 0 | 0 | 0 | 0 | 53 | 106 |
| <i>Sunella</i> (cf.) sp. | ? | 1 | 1 | 0 | 0 | X | 0 | 0 | 0 | X | 0 | 0 | 0 | 0 | 0 | 1 | 3 |
| <i>Tanglangia caudata</i> | ? | 2 | 1 | 0 | 0 | 0 | X | 0 | 0 | X | 0 | 0 | 0 | 0 | 0 | 53 | 106 |
| <i>Tanglangia longicaudata</i> | ? | 1 | 1 | 0 | 0 | 0 | X | 0 | 0 | X | 0 | 0 | 0 | 0 | 0 | 1 | 3 |
| <i>Tegopelte gigas</i> | B | 1 | 1 | X | 0 | 0 | 0 | 0 | 0 | 0 | 0 | X | 0 | 0 | 0 | 1 | 3 |
| <i>Thelxiope palaeothallasia</i> | ? | 1 | 1 | X | 0 | 0 | 0 | 0 | 0 | 0 | 0 | X | 0 | 0 | 0 | 1 | 3 |
| <i>Tsunyiella diandongensis</i> | NB | 2 | 1 | 0 | 0 | 0 | X | 0 | 0 | X | 0 | 0 | 0 | 0 | 0 | 478 | 956 |
| <i>Tuzoia australis</i> | N | 1 | 1 | 0 | 0 | 0 | 0 | X | 0 | X | 0 | 0 | 0 | 0 | 0 | 1 | 3 |
| <i>Tuzoia bispinosa</i> | N | 1 | 1 | 0 | 0 | 0 | X | 0 | 0 | 0 | 0 | X | 0 | 0 | 0 | 1 | 3 |
| <i>Tuzoia burgessensis</i> | N | 1 | 1 | X | 0 | 0 | 0 | 0 | 0 | 0 | 0 | X | 0 | 0 | 0 | 1 | 3 |
| <i>Tuzoia canadensis</i> | N | 1 | 1 | X | 0 | 0 | 0 | 0 | 0 | 0 | 0 | X | 0 | 0 | 0 | 1 | 3 |
| <i>Tuzoia dunbari</i> (non- <i>Tuzoia</i> ; gen. ?) | ? | 1 | 1 | 0 | X | 0 | 0 | 0 | 0 | 0 | X | 0 | 0 | 0 | 0 | 1 | 3 |
| <i>Tuzoia getzi</i> | N | 1 | 1 | 0 | X | 0 | 0 | 0 | 0 | 0 | X | 0 | 0 | 0 | 0 | 1 | 3 |
| <i>Tuzoia guntheri</i> | N | 5 | 1 | X | 0 | 0 | 0 | 0 | 0 | 0 | 0 | X | X | 1 | 1 | 213 | 513 |
| <i>Tuzoia nitida</i> | N | 3 | 2 | X | X | 0 | 0 | 0 | 0 | 0 | X | X | 0 | 1 | 1 | 3691 | 56,669 |
| <i>Tuzoia polleni</i> | N | 4 | 2 | X | X | 0 | 0 | 0 | 0 | 0 | X | 0 | 0 | 0 | 0 | 3855 | 3,527,839 |
| <i>Tuzoia retifera</i> | N | 2 | 1 | X | 0 | 0 | 0 | 0 | 0 | 0 | X | 0 | 0 | 0 | 0 | 1217 | 2434 |
| <i>Tuzoia sinensis</i> | N | 1 | 1 | 0 | 0 | 0 | X | 0 | 0 | X | 0 | 0 | 0 | 0 | 0 | 1 | 3 |
| <i>Tuzoia? parva</i> | N | 1 | 1 | X | 0 | 0 | 0 | 0 | 0 | 0 | 0 | X | 0 | 0 | 0 | 1 | 3 |
| <i>Tuzoia? peterseni</i> | N | 1 | 1 | X | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | X | 0 | 0 | 1 | 3 |
| <i>Urokodia aequalis</i> | B | 3 | 1 | 0 | 0 | 0 | X | 0 | 0 | X | 0 | 0 | 0 | 0 | 0 | 71 | 37 |
| <i>Utahcaris orion</i> | NB | 2 | 1 | X | 0 | 0 | 0 | 0 | 0 | 0 | 0 | X | 0 | 0 | 0 | 5 | 10 |
| <i>Waptia fieldensis</i> (& cf.) | B | 2 | 1 | X | 0 | 0 | 0 | 0 | 0 | 0 | 0 | X | 0 | 0 | 0 | 1220 | 2440 |
| <i>Waptia ovata</i> | B | 6 | 1 | 0 | 0 | 0 | X | 0 | 0 | X | 0 | 0 | 0 | 0 | 0 | 125 | 8282 |
| <i>Wutingella binodosa</i> | NB | 1 | 1 | 0 | 0 | 0 | X | 0 | 0 | X | 0 | 0 | 0 | 0 | 0 | 1 | 3 |
| <i>Xandarella spectaculum</i> | B | 3 | 1 | 0 | 0 | 0 | X | 0 | 0 | X | 0 | 0 | 0 | 0 | 0 | 71 | 40 |
| <i>Yohoa tenuis</i> | NB | 1 | 1 | X | 0 | 0 | 0 | 0 | 0 | 0 | 0 | X | 0 | 0 | 0 | 1 | 3 |
| <i>Yunnanocaris megista</i> | ? | 1 | 1 | 0 | 0 | 0 | X | 0 | 0 | X | 0 | 0 | 0 | 0 | 0 | 1 | 3 |
| <i>Zhenghecaris shankouensis</i> | N | 1 | 1 | 0 | 0 | 0 | X | 0 | 0 | X | 0 | 0 | 0 | 0 | 0 | 1 | 3 |
| Agnostid trilobites | | | | | | | | | | | | | | | | | |
| <i>Baltagnostus centerensis</i> | N | 3 | 1 | X | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | X | 0 | 38 | 92 |
| <i>Baltagnostus eurypyx</i> | N | 2 | 1 | X | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | X | 0 | 0 | 19 | 38 |
| <i>Cotalagnostus</i> sp. | N | 1 | 1 | X | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | X | 0 | 0 | 1 | 3 |
| <i>Eoagnostus rodnyi</i> | N | 3 | 1 | 0 | X | 0 | 0 | 0 | 0 | 0 | X | 0 | 0 | 0 | 0 | 38 | 39 |
| <i>Hypagnostus parvifrons</i> | N | 2 | 1 | X | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | X | 0 | 0 | 16 | 32 |
| <i>Lejopyge lundgreni</i> | N | 1 | 1 | X | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | X | 0 | 0 | 1 | 3 |
| <i>Lejopyge rigbyi</i> | N | 1 | 1 | X | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | X | 0 | 0 | 1 | 3 |
| <i>Pagetia bootes</i> | N | 1 | 1 | X | 0 | 0 | 0 | 0 | 0 | 0 | 0 | X | 0 | 0 | 0 | 1 | 3 |
| <i>Pagetia clytia</i> | N | 1 | 1 | X | 0 | 0 | 0 | 0 | 0 | 0 | 0 | X | 0 | 0 | 0 | 1 | 3 |
| <i>Pagetia fossula</i> cf. | N | 1 | 1 | X | 0 | 0 | 0 | 0 | 0 | 0 | 0 | X | 0 | 0 | 0 | 1 | 3 |
| <i>Peronopsis bonnerensis</i> | N | 1 | 1 | X | 0 | 0 | 0 | 0 | 0 | 0 | 0 | X | 0 | 0 | 0 | 1 | 3 |
| <i>Peronopsis brighamensis</i> | N | 2 | 1 | X | 0 | 0 | 0 | 0 | 0 | 0 | 0 | X | 0 | 0 | 0 | 71 | 142 |
| <i>Peronopsis ferox</i> | N | 1 | 1 | X | 0 | 0 | 0 | 0 | 0 | 0 | 0 | X | 0 | 0 | 0 | 1 | 3 |
| <i>Peronopsis gedongensis</i> | N | 1 | 1 | 0 | 0 | 0 | X | 0 | 0 | 0 | 0 | X | 0 | 0 | 0 | 1 | 3 |
| <i>Peronopsis interstricta</i> | N | 3 | 1 | X | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | X | 0 | 0 | 38 | 152 |
| <i>Peronopsis montis</i> | N | 1 | 1 | X | 0 | 0 | 0 | 0 | 0 | 0 | 0 | X | 0 | 0 | 0 | 1 | 3 |
| <i>Peronopsis segmenta</i> | N | 1 | 1 | X | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | X | 0 | 0 | 1 | 3 |
| <i>Peronopsis taijiangensis</i> | N | 1 | 1 | 0 | 0 | 0 | X | 0 | 0 | 0 | 0 | X | 0 | 0 | 0 | 1 | 3 |
| <i>Pseudoperonopsis</i> (=Diplorrhina)? sp. | N | 1 | 1 | X | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | X | 0 | 0 | 1 | 3 |
| <i>Ptychagnostus affinis</i> | N | 1 | 1 | X | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | X | 0 | 0 | 1 | 3 |
| <i>Ptychagnostus atavus</i> | N | 3 | 1 | X | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | X | 0 | 0 | 16 | 2 |
| <i>Ptychagnostus germanus</i> | N | 2 | 1 | X | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | X | 0 | 0 | 10 | 20 |
| <i>Ptychagnostus michaeli</i> | N | 1 | 1 | X | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | X | 0 | 0 | 1 | 3 |
| <i>Ptychagnostus occultatus</i> | N | 2 | 1 | X | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | X | 0 | 0 | 10 | 20 |
| <i>Ptychagnostus praecurrens</i> | N | 1 | 1 | X | 0 | 0 | 0 | 0 | 0 | 0 | 0 | X | 0 | 0 | 0 | 1 | 3 |
| <i>Ptychagnostus punctuosus</i> | N | 1 | 1 | X | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | X | 0 | 0 | 1 | 3 |
| <i>Tsunyidiscus acilis</i> | N | 1 | 1 | 0 | 0 | 0 | X | 0 | 0 | X | 0 | 0 | 0 | 0 | 0 | 1 | 3 |
| <i>Tsunyidiscus niutitangensis</i> | N | 3 | 1 | 0 | 0 | 0 | X | 0 | 0 | X | 0 | 0 | 0 | 0 | 0 | 477 | 6997 |

Table 1 (continued)

| Species | Habit | No. occurrence records | No. regions present | Regions | | | | | | Temporal stage | | | | No. temp. boundaries crossed | Geographic range | | |
|---|-------|------------------------|---------------------|---------|----|---|---|---|---|----------------|---|---|---|------------------------------|----------------------|--------------------------------|---|
| | | | | WL | EL | G | C | A | B | 3 | 4 | 5 | 6 | | Distance method (km) | Area method (km ²) | |
| Non-agnostid trilobites | | | | | | | | | | | | | | | | | |
| <i>Achlylopsis</i> sp. | B | 1 | 1 | X | O | O | O | O | O | O | O | X | O | 0 | 1 | 3 | |
| <i>Alokistocare harrisi</i> | B | 2 | 1 | X | O | O | O | O | O | O | O | O | X | 0 | 30 | 60 | |
| <i>Alokistocare idahoense</i> | B | 1 | 1 | X | O | O | O | O | O | O | O | X | O | 0 | 1 | 3 | |
| <i>Alokistocare laticaudum</i> | B | 1 | 1 | X | O | O | O | O | O | O | O | X | O | 0 | 1 | 3 | |
| <i>Asaphiscus wheeleri</i> | B | 3 | 1 | X | O | O | O | O | O | O | O | O | X | 0 | 38 | 90 | |
| <i>Athabaskia bithus</i> | B | 1 | 1 | X | O | O | O | O | O | O | O | X | O | 0 | 1 | 3 | |
| <i>Athabaskia wasatchensis</i> | B | 1 | 1 | X | O | O | O | O | O | O | O | O | X | O | 0 | 1 | 3 |
| <i>Bathynotus</i> sp. | B | 1 | 1 | O | O | O | X | O | O | O | O | X | O | 0 | 1 | 3 | |
| <i>Bathyriscus brighamensis</i> | B | 1 | 1 | X | O | O | O | O | O | O | O | X | O | 0 | 1 | 3 | |
| <i>Bathyriscus fimbriatus</i> | B | 3 | 1 | X | O | O | O | O | O | O | O | O | X | 0 | 38 | 95 | |
| <i>Bathyriscus wasatchensis</i> | B | 2 | 1 | X | O | O | O | O | O | O | O | X | O | 0 | 5 | 10 | |
| <i>Bolaspidella contracta</i> | B | 1 | 1 | X | O | O | O | O | O | O | O | O | X | 0 | 1 | 3 | |
| <i>Bolaspidella drumensis</i> | B | 1 | 1 | X | O | O | O | O | O | O | O | O | X | 0 | 1 | 3 | |
| <i>Bolaspidella housensis</i> | B | 1 | 1 | X | O | O | O | O | O | O | O | O | X | 0 | 1 | 3 | |
| <i>Bolaspidella wellsvillensis</i> | B | 2 | 1 | X | O | O | O | O | O | O | O | O | X | 0 | 10 | 20 | |
| <i>Boniella yorkensis</i> | B | 1 | 1 | O | X | O | O | O | O | O | X | O | O | 0 | 1 | 3 | |
| <i>Bonnia sola</i> | B | 1 | 1 | O | X | O | O | O | O | O | O | X | O | 0 | 1 | 3 | |
| <i>Bonnia yorkensis</i> | B | 1 | 1 | O | X | O | O | O | O | O | X | O | O | 0 | 1 | 3 | |
| <i>Brachyaspidion microps</i> | B | 2 | 1 | X | O | O | O | O | O | O | O | O | X | 0 | 26 | 52 | |
| <i>Brachyaspidion sulcatum</i> | B | 2 | 1 | X | O | O | O | O | O | O | O | O | X | 0 | 26 | 52 | |
| <i>Buenellus higginsi</i> | B | 1 | 1 | O | O | X | O | O | O | X | O | O | O | 0 | 1 | 3 | |
| <i>Burlingia</i> sp. | B | 1 | 1 | O | O | O | X | O | O | O | O | X | O | 0 | 1 | 3 | |
| <i>Bythicheilus typicum</i> | B | 1 | 1 | X | O | O | O | O | O | O | O | X | O | 0 | 1 | 3 | |
| <i>Chancia evax</i> | B | 1 | 1 | X | O | O | O | O | O | O | O | X | O | 0 | 1 | 3 | |
| <i>Chancia palliseri</i> | B | 1 | 1 | X | O | O | O | O | O | O | O | X | O | 0 | 1 | 3 | |
| <i>Chengjiangaspis chengjiangensis</i> | B | 1 | 1 | O | O | O | X | O | O | X | O | O | O | 0 | 1 | 3 | |
| <i>Chittidilla</i> sp. | B | 1 | 1 | O | O | O | X | O | O | O | O | X | O | 0 | 1 | 3 | |
| <i>Clavaspidella anax</i> | B | 1 | 1 | X | O | O | O | O | O | O | O | O | X | O | 0 | 1 | 3 |
| <i>Danzhaiaspis</i> sp. | B | 1 | 1 | O | O | O | X | O | O | O | O | X | O | 0 | 1 | 3 | |
| <i>Dorypyge</i> sp. | B | 1 | 1 | X | O | O | O | O | O | O | O | X | O | 0 | 1 | 3 | |
| <i>Douposiella</i> sp. | B | 1 | 1 | O | O | O | X | O | O | O | O | X | O | 0 | 1 | 3 | |
| <i>Ehmaniella burgessensis</i> | B | 1 | 1 | X | O | O | O | O | O | O | O | X | O | 0 | 1 | 3 | |
| <i>Ehmaniella quadrans</i> | B | 1 | 1 | X | O | O | O | O | O | O | O | X | O | 0 | 1 | 3 | |
| <i>Ehmaniella waptaensis</i> | B | 1 | 1 | X | O | O | O | O | O | O | O | X | O | 0 | 1 | 3 | |
| <i>Elrathia</i> (cf.) <i>brevifrons</i> | B | 1 | 1 | X | O | O | O | O | O | O | O | X | O | 0 | 1 | 3 | |
| <i>Elrathia cordillerae</i> | B | 1 | 1 | X | O | O | O | O | O | O | O | X | O | 0 | 1 | 3 | |
| <i>Elrathia kingii</i> | B | 2 | 1 | X | O | O | O | O | O | O | O | O | X | 0 | 26 | 52 | |
| <i>Elrathia permulta</i> | B | 1 | 1 | X | O | O | O | O | O | O | O | X | O | 0 | 1 | 3 | |
| <i>Elrathia spencei</i> | B | 1 | 1 | X | O | O | O | O | O | O | O | X | O | 0 | 1 | 3 | |
| <i>Eoredlichia intermedia</i> | B | 5 | 1 | O | O | O | X | O | O | X | O | O | O | 0 | 130 | 2802 | |
| <i>Esmeraldina</i> (=Holmia) <i>macer</i> | B | 3 | 1 | O | X | O | O | O | O | O | X | O | O | 0 | 38 | 42 | |
| <i>Gaotaiaspis</i> sp. | B | 1 | 1 | O | O | O | X | O | O | O | O | X | O | 0 | 1 | 3 | |
| <i>Glossopleura bion</i> | B | 1 | 1 | X | O | O | O | O | O | O | O | X | O | 0 | 1 | 3 | |
| <i>Glossopleura gigantea</i> | B | 1 | 1 | X | O | O | O | O | O | O | O | X | O | 0 | 1 | 3 | |
| <i>Glossopleura utahensis</i> | B | 1 | 1 | X | O | O | O | O | O | O | O | X | O | 0 | 1 | 3 | |
| <i>Hanburia gloriosa</i> | B | 1 | 1 | X | O | O | O | O | O | O | O | X | O | 0 | 1 | 3 | |
| <i>Hemirhodon amplipyge</i> | B | 2 | 1 | X | O | O | O | O | O | O | O | O | X | 0 | 14 | 28 | |
| <i>Hsuaspis bilobata</i> | B | 1 | 1 | O | O | O | O | X | O | O | X | O | O | 0 | 1 | 3 | |
| <i>Jenkinsonia varga</i> | B | 2 | 1 | X | O | O | O | O | O | O | O | O | X | 0 | 26 | 52 | |
| <i>Jiumenia</i> sp. | B | 1 | 1 | O | O | O | X | O | O | O | O | X | O | 0 | 1 | 3 | |
| <i>Kailiella</i> sp. | B | 1 | 1 | O | O | O | X | O | O | O | O | X | O | 0 | 1 | 3 | |
| <i>Kaotaia transversa</i> | B | 1 | 1 | O | O | O | X | O | O | O | O | X | O | 0 | 1 | 3 | |
| <i>Kochina vestita</i> | B | 1 | 1 | X | O | O | O | O | O | O | O | X | O | 0 | 1 | 3 | |
| <i>Kootenia burgessensis</i> | B | 1 | 1 | X | O | O | O | O | O | O | O | X | O | 0 | 1 | 3 | |
| <i>Kootenia gracilis</i> | B | 1 | 1 | X | O | O | O | O | O | O | O | X | O | 0 | 1 | 3 | |
| <i>Kootenia mendosa</i> | B | 1 | 1 | X | O | O | O | O | O | O | O | X | O | 0 | 1 | 3 | |
| <i>Kootenia pricei</i> | B | 1 | 1 | O | X | O | O | O | O | O | X | O | O | 0 | 1 | 3 | |
| <i>Kootenia spencei</i> | B | 1 | 1 | X | O | O | O | O | O | O | O | X | O | 0 | 1 | 3 | |
| <i>Kuanyangia pustulosa</i> | B | 4 | 1 | O | O | O | X | O | O | X | O | O | O | 0 | 71 | 231 | |
| <i>Kunmingaspis</i> sp. | B | 1 | 1 | O | O | O | X | O | O | O | O | X | O | 0 | 1 | 3 | |
| <i>Kutsingocephalus</i> sp. | B | 1 | 1 | O | O | O | X | O | O | O | O | X | O | 0 | 1 | 3 | |
| <i>Lancastria rodnyi</i> | B | 2 | 1 | O | X | O | O | O | O | O | X | O | O | 0 | 5 | 10 | |
| <i>Malungia</i> (=Dolerolenus) <i>laevigata</i> | B | 1 | 1 | O | O | O | X | O | O | X | O | O | O | 0 | 1 | 3 | |
| <i>Meitania</i> sp. | B | 1 | 1 | O | O | O | X | O | O | O | O | X | O | 0 | 1 | 3 | |
| <i>Modocia brevispina</i> | B | 1 | 1 | X | O | O | O | O | O | O | O | O | X | 0 | 1 | 3 | |
| <i>Modocia laevinucha</i> | B | 2 | 1 | X | O | O | O | O | O | O | O | O | X | 0 | 13 | 26 | |
| <i>Modocia typicalis</i> | B | 1 | 1 | X | O | O | O | O | O | O | O | O | X | 0 | 1 | 3 | |
| <i>Nangaops</i> sp. | B | 1 | 1 | O | O | O | X | O | O | O | O | X | O | 0 | 1 | 3 | |
| <i>Ogygopsis typicalis</i> | B | 1 | 1 | X | O | O | O | O | O | O | O | X | O | 0 | 1 | 3 | |
| <i>Olenellus</i> (& ?) <i>crassimarginatus</i> | B | 4 | 1 | O | X | O | O | O | O | O | X | O | O | 0 | 38 | 70 | |
| <i>Olenellus getzi</i> | B | 2 | 1 | O | X | O | O | O | O | O | X | O | O | 0 | 34 | 68 | |

(continued on next page)

Table 1 (continued)

| Species | Habit | No. occurrence records | No. regions present | Regions | | | | | | Temporal stage | | | | No. temp. boundaries crossed | Geographic range | |
|--|-------|------------------------|---------------------|---------|----|---|---|---|---|----------------|---|---|---|------------------------------|------------------|--------------------------------|
| | | | | WL | EL | G | C | A | B | 3 | 4 | 5 | 6 | | Distance (km) | Area method (km ²) |
| Non-agnostid trilobites | | | | | | | | | | | | | | | | |
| <i>Olenellus rodnyi</i> | B | 4 | 1 | O | X | O | O | O | O | O | X | O | O | 0 | 38 | 70 |
| <i>Olenellus thompsoni</i> | B | 1 | 1 | O | X | O | O | O | O | O | X | O | O | 0 | 1 | 3 |
| <i>Olenoides brighamensis</i> | B | 1 | 1 | X | O | O | O | O | O | O | X | O | O | 0 | 1 | 3 |
| <i>Olenoides evansi</i> | B | 1 | 1 | X | O | O | O | O | O | O | X | O | O | 0 | 1 | 3 |
| <i>Olenoides nevadensis</i> | B | 2 | 1 | X | O | O | O | O | O | O | O | X | O | 0 | 30 | 60 |
| <i>Olenoides paraptus</i> | B | 1 | 1 | O | O | O | X | O | O | O | X | O | O | 0 | 1 | 3 |
| <i>Olenoides serratus</i> | B | 1 | 1 | X | O | O | O | O | O | O | X | O | O | 0 | 1 | 3 |
| <i>Olenoides wahsatchensis</i> | B | 1 | 1 | X | O | O | O | O | O | O | X | O | O | 0 | 1 | 3 |
| <i>Oryctocara geikei</i> | B | 2 | 1 | X | O | O | O | O | O | O | X | O | O | 0 | 71 | 142 |
| <i>Oryctocephalus burgessensis</i> | B | 1 | 1 | X | O | O | O | O | O | O | X | O | O | 0 | 1 | 3 |
| <i>Oryctocephalus matthewi</i> | B | 1 | 1 | X | O | O | O | O | O | O | X | O | O | 0 | 1 | 3 |
| <i>Oryctocephalus reynoldsi</i> | B | 1 | 1 | X | O | O | O | O | O | O | X | O | O | 0 | 1 | 3 |
| <i>Oryctocephalus walcotti</i> | B | 2 | 1 | X | O | O | O | O | O | O | X | O | O | 0 | 71 | 142 |
| <i>Parkaspis decamera</i> | B | 1 | 1 | X | O | O | O | O | O | O | X | O | O | 0 | 1 | 3 |
| <i>Probowmania</i> sp. | B | 1 | 1 | O | O | O | X | O | O | O | X | O | O | 0 | 1 | 3 |
| <i>Redlichia takoensis</i> | B | 1 | 1 | O | O | O | X | O | X | O | X | O | O | 0 | 1 | 3 |
| <i>Schmalenseeia</i> sp. | B | 1 | 1 | X | O | O | O | O | O | O | O | X | O | 0 | 1 | 3 |
| <i>Spencella</i> sp. 1 | B | 1 | 1 | X | O | O | O | O | O | O | X | O | O | 0 | 1 | 3 |
| <i>Spencella</i> sp. 2 | B | 1 | 1 | X | O | O | O | O | O | O | X | O | O | 0 | 1 | 3 |
| <i>Syspacephalus</i> (=Ptychoparella) <i>spencei</i> | B | 1 | 1 | X | O | O | O | O | O | O | X | O | O | 0 | 1 | 3 |
| <i>Thoracocare minuta</i> | B | 1 | 1 | X | O | O | O | O | O | O | X | O | O | 0 | 1 | 3 |
| <i>Trymataspis depressa</i> | B | 1 | 1 | X | O | O | O | O | O | O | O | X | O | 0 | 1 | 3 |
| <i>Wanneria walcottana</i> | B | 4 | 1 | O | X | O | O | O | O | O | X | O | O | 0 | 38 | 69 |
| <i>Wutingaspis malungensis</i> | B | 1 | 1 | O | O | O | X | O | O | X | O | O | O | 0 | 1 | 3 |
| <i>Wutingaspis tingia</i> | B | 3 | 1 | O | O | O | X | O | O | X | O | O | O | 0 | 130 | 2389 |
| <i>Xingrenaspis</i> sp. | B | 1 | 1 | O | O | O | X | O | O | O | X | O | O | 0 | 1 | 3 |
| <i>Yunnanoccephalus yunnanensis</i> | B | 4 | 1 | O | O | O | X | O | O | X | O | O | O | 0 | 71 | 238 |
| <i>Zacanthoides grabaui</i> | B | 1 | 1 | X | O | O | O | O | O | O | X | O | O | 0 | 1 | 3 |
| <i>Zacanthoides idahoensis</i> | B | 1 | 1 | X | O | O | O | O | O | O | X | O | O | 0 | 1 | 3 |

distinct taxa, whereas Vannier et al. (2007) synonymized them with *T. polleni*. Taxa identified to the genus-level but not to the species-level (e.g., “*Kunmingaspis* sp.”), were only included in the finalized database when they occurred at a single locality and in such cases were treated as separate, distinct species.

Occurrence records are from a total of 51 unique localities, six geographic regions, and 19 stratigraphic units (Tables 2 and 3; Fig. 1), ranging in age from approximately the Early Cambrian *Fallotaspis* to the Middle Cambrian *Cedaria* zones of Laurentia. Localities were defined (Table 3) as precisely as possible given the faunal reports available. We note that the number of singleton occurrences in our database (Table 1) would have increased had we been less precise in defining localities. For example, we recognize eight individual localities in the Chengjiang region of China, rather than just one. Some taxa (e.g., *Retifacies abnormalis*) in our study occur at multiple localities within the Chengjiang region, but do not occur outside of the region. Thus, had we recognized a single Chengjiang locality, *R. abnormalis* would have been assigned a single occurrence record, whereas we recognize it as occurring within four individual localities within the Chengjiang region. We expect that our approach (defining localities narrowly rather than broadly) has caused us to recognize fewer singleton taxa, but argue that our approach: 1) requires fewer arbitrary and scale-dependent boundaries to be defined; and 2) is more amenable to adding additional soft-bodied faunas to the data set as they are discovered.

The 19 stratigraphic units were each assigned to one of four temporal stage bins (Table 2) based upon a variety of lines of stratigraphic evidence, including trilobite biostratigraphy (Geyer and Shergold, 2000; Peng and Robison, 2000; Babcock et al., 2005, 2007). Two of these bins, undefined stages 3 and 4, represent the second (undefined) Cambrian series (late Early Cambrian) and two, undefined stage 5 and the Drumian Stage (formerly stage 6), represent the third Cambrian series (Middle Cambrian). Many of the trilobite species known from the Burgess Shale-type deposits considered here are also

known from other Cambrian strata that do not preserve soft-parts, but these occurrence records were not included in this study. Inclusion of these sites within our analysis of distribution patterns would effectively treat patently non-comparable localities as equivalent. By excluding occurrence records for trilobite taxa outside of Burgess Shale-type deposits we avoid artificially inflating their distribution patterns relative to soft-bodied arthropod species that would not be preserved due to taphonomic biases. This allows us to focus on what are likely to be more taphonomically equivalent patterns. While most of the non-trilobite arthropods in our database were entirely soft-bodied, a limited number had some mineralized parts (e.g., the bradoriid crustacean *Kunmingella douvillei*, which has phosphatic valves) and, like trilobites, are also known from outside Burgess Shale-type faunas.

Throughout our analyses we used a phylogenetic species concept: the same concept that most neontologists use. By necessity we assumed that the trilobite and non-trilobite species we have included in this analysis are taxonomically equivalent units of comparison. We acknowledge that if “taxonomic lumping” (i.e., an approach that recognizes considerable intraspecific morphological variability) is more prevalent in soft-bodied Cambrian arthropod species than in trilobites (which is very difficult to assess), soft-bodied taxa could potentially show artificial patterns of greater geographic ranges. In particular, there are taphonomic vagaries—including inconsistent orientation and quality of preservation—that may make many character suites difficult to interpret or compare within and among soft-bodied Cambrian arthropod taxa; these could cause several true biological species to be assigned to a single species. By contrast, trilobites tend to be character-rich and have mineralized exoskeletons, making it potentially easier to identify different species. These effects are always difficult to correct for with fossil organisms in general and long extinct Cambrian taxa in particular, but we do present genus-level analyses as a possible check on this. Resolution of the role of this potential bias will likely require comparative studies on several other

Table 2
 Summary of localities and strata (with literature sources) considered in this study, including number of individual localities (bold type), total number of species (italicized type), and number of endemic species within each spatio-temporal bin (normal type). "Stage total" gives corresponding data for all localities and regions within a single spatio-temporal bin. N.A., not applicable

| Stage | | Region | | | | | | | Stage total |
|-----------------|-------------------|---|--|--|--|--|--|----------------------|--------------------|
| | | Western Laurentia | Eastern Laurentia | Greenland | Baltica | China | Australia | | |
| Middle Cambrian | Drumian (stage 6) | Bloomington Fm., Hodges Shale Mbr. (Robison and Richards, 1981; Lieberman, 2003); Marjum Fm. (Robison and Richards, 1981; Briggs and Robison, 1984; Robison, 1984; Ubaghs and Robison, 1985; Robison, 1991; Robison and Wiley, 1995; Lieberman, 2003); Wheeler Fm. (Robison and Richards, 1981; Briggs and Robison, 1984; Robison, 1985; Conway Morris and Robison, 1986, 1988; Robison, 1991; Lieberman, 2003) 16 , 55, 44 | N.A. | N.A. | N.A. | N.A. | N.A. | N.A. | 16 , 55, 44 |
| | 5 | Mount Stephen Fm., Burgess Shale (Briggs et al., 1994; Lieberman, 2003; Vannier et al., 2007; Zhang et al., 2007; Briggs et al., 2008); Carrara Fm., Pyramid Shale Mbr. (Lieberman, 2003); Langston Fm., Spence Mbr. (Robison and Richards, 1981; Briggs and Robison, 1984; Robison, 1991; Robison and Wiley, 1995; Lieberman, 2003); Mount Cap Fm. (Butterfield and Nicholas, 1996); Pioche Fm., Comet Shale Mbr. 2 (Lieberman, 2003) 12 , 103, 89 | N.A. | N.A. | N.A. | Kaili Fm. (Huang and Yuan, 1994; Yuan and Huang, 1994; Yuan and Zhao, 1994; Zhao et al., 1994a,b; Zhang et al., 2002; Zhao et al., 2002; Hou et al., 2004; Zhu et al., 2004; Lin, 2006; Lin et al., 2006) 1 , 27, 24 | N.A. | 13 , 126, 112 | |
| Early Cambrian | 4 | Eager Fm. (Lieberman, 2003); Latham Fm. (Briggs and Mount, 1982); Pioche Fm.; Comet Shale Mbr. 1 (Lieberman, 2003) 6 , 4, 0 | Kinzers Fm. (Resser and Howell, 1938; Campbell and Kauffman, 1969; Capdevila and Conway Morris, 1999; Lieberman, 2003; Skinner, 2005); Parker Shale (Lieberman, 2003) 5 , 22, 19 | N.A. | N.A. | N.A. | N.A. | 11 , 23, 19 | |
| | 3 | N.A. | N.A. | Buen Fm. (Conway Morris et al., 1987; Budd, 1995; Williams et al., 1996; Budd, 1997; Budd and Peel, 1998; Budd, 1999a,b; Taylor, 2002) | Zawiszyn Fm. (Dzik and Lendzion, 1988) | Niutitang Fm. (Steiner et al., 2005); Yuanshan Fm. (Chen et al., 2002; Zhang et al., 2003; Hou et al., 2004; Huang et al., 2004; Steiner et al., 2005; Vannier et al., 2006, 2007; Zhang et al., 2007) | Emu Bay Shale (McHenry and Yates, 1993; Nedin, 1995, 1999; Hagadorn, 2002) | 11 , 93, 90 | |
| | | N.A. | N.A. | 1 , 7, 6 | 1 , 2, 1 | 8 , 81, 78 | 1 , 5, 5 | | |

Table 3
Georeferenced localities and supporting references. Some localities are supported by geographical information associated with particular specimens in the collections of the University of Kansas Division of Invertebrate Paleontology (KUMIP), Lawrence, Kansas

| Locality name | Lat | Long | Stratum | Stage | Zone |
|---|--------|---------|------------------------------------|-------|---|
| GL—Peary Land (Conway Morris et al., 1987) | 82.82 | -44.00 | Buen Fm. | 3 | Atdabanian–Botomian |
| AU—Kangaroo Island—Big Gully (Briggs and Nedin, 1997) | -35.57 | 137.58 | Emu Bay Shale | 3 | Botomian |
| CN—Guizhou—Zunyi (Steiner et al., 2005) | 27.70 | 106.91 | Niutitang Fm. | 3 | Atdabanian |
| CN—Yunnan—Anning (Chen et al., 2002) | 24.84 | 102.40 | Yuanshan Fm. | 3 | Atdabanian |
| CN—Yunnan—Generic Chengjiang Fauna (Hou et al., 2004) | 24.65 | 103.03 | Yuanshan Fm. | 3 | Atdabanian |
| CN—Yunnan—Haikou (Steiner et al., 2005) | 24.78 | 102.56 | Yuanshan Fm. | 3 | Atdabanian |
| CN—Yunnan—Jinning (Chen et al., 2002) | 24.71 | 102.59 | Yuanshan Fm. | 3 | Atdabanian |
| CN—Yunnan—Malong (Chen et al., 2002) | 25.42 | 103.58 | Yuanshan Fm. | 3 | Atdabanian |
| CN—Yunnan—Quijing (Steiner et al., 2005) | 25.49 | 103.79 | Yuanshan Fm. | 3 | Atdabanian |
| CN—Yunnan—Wuding (Steiner et al., 2005) | 25.56 | 102.40 | Yuanshan Fm. | 3 | Atdabanian |
| PL—Koscierzyna (Dzik and Lendzion, 1988) | 54.13 | 17.98 | Zawiszyn Fm. | 3 | Atdabanian (<i>Fallotaspis</i>) |
| CAN—BC—Cranbrook (Lieberman, 2003) | 49.56 | -115.69 | Eager Fm. | 4 | Dyeran (<i>Olenellus</i>) |
| US—PA—East Petersburg—USGS 22L (Resser and Howell, 1938) | 40.10 | -76.35 | Kinzers Fm. | 4 | Dyeran (<i>Olenellus</i>) |
| US—PA—Fruitville—USGS 12w (Resser and Howell, 1938) | 40.09 | -76.33 | Kinzers Fm. | 4 | Dyeran (<i>Olenellus</i>) |
| US—PA—Generic Kinzers Fm. (~Getz Quarry, USGS 12x) (Campbell and Kauffman, 1969) | 40.06 | -76.37 | Kinzers Fm. | 4 | Dyeran (<i>Olenellus</i>) |
| US—PA—York—USGS 8q (Resser and Howell, 1938) | 39.96 | -76.73 | Kinzers Fm. | 4 | Dyeran (<i>Olenellus</i>) |
| US—CA—Marble Mts—UCR 7602 (Briggs and Mount, 1982) | 34.54 | -115.48 | Latham Fm. | 4 | Dyeran (<i>Olenellus</i>) |
| US—CA—Providence Mts—UCR 7002 (Briggs and Mount, 1982) | 35.03 | -115.50 | Latham Fm. | 4 | Dyeran (<i>Olenellus</i>) |
| US—VT—Parker Quarry (Lieberman, 2003) | 44.74 | -73.16 | Parker Shale | 4 | Dyeran (<i>Olenellus</i>) |
| US—NV—Klondike Gap (Lieberman, 2003) | 37.76 | -114.57 | Pioche Fm., Comet Shale Mbr. 1 | 4 | Dyeran (<i>Olenellus</i>) |
| US—NV—Ruin Wash 1 (Lieberman, 2003) | 37.77 | -114.58 | Pioche Fm., Comet Shale Mbr. 1 | 4 | Dyeran (<i>Olenellus</i>) |
| US—NV—Ruin Wash 2 (Lieberman, 2003) | 37.77 | -114.57 | Pioche Fm., Comet Shale Mbr. 1 | 4 | Dyeran (<i>Olenellus</i>) |
| CAN—BC—Generic Burgess Shale (~Walcott Quarry, USNM 35k) (Briggs et al., 1994) | 51.44 | -116.48 | Burgess Shale | 5 | Marjuman (<i>Ptychagnostus praecurrens</i>) |
| US—NV—Groom Range (Lieberman, 2003) | 37.57 | -115.77 | Carrara Fm., Pyramid Shale Mbr. | 5 | <i>Eokochaspis nodosa</i> |
| CN—Guizhou—Kaili (Zhu et al., 2004) | 26.97 | 108.63 | Kaili Fm. | 5 | <i>Oryctocephalus indicus</i> |
| US—ID—Oneida Narrows (KUMIP 314280) | 42.20 | -111.79 | Langston Fm., Spence Mbr. | 5 | <i>Peronopsis bonnerensis</i> |
| US—UT—Generic Spence Mbr. (Robison, 1991) | 41.60 | -112.04 | Langston Fm., Spence Mbr. | 5 | <i>Peronopsis bonnerensis</i> |
| US—UT—Wellsville Mountains—Cataract Canyon—RAR 101 (KUMIP 314030) | 41.60 | -112.03 | Langston Fm., Spence Mbr. | 5 | <i>Peronopsis bonnerensis</i> |
| US—UT—Wellsville Mountains—Donation Canyon (Robison and Richards, 1981) | 41.61 | -112.04 | Langston Fm., Spence Mbr. | 5 | <i>Peronopsis bonnerensis</i> |
| US—UT—Wellsville Mountains—Gunther Quarry—RAR 781 (KUMIP 314263) | 41.56 | -112.01 | Langston Fm., Spence Mbr. | 5 | <i>Peronopsis bonnerensis</i> |
| US—UT—Wellsville Mountains—Hansen Canyon (Robison and Wiley, 1995) | 41.56 | -112.01 | Langston Fm., Spence Mbr. | 5 | <i>Peronopsis bonnerensis</i> |
| US—UT—Wellsville Mountains—Miners Hollow—RAR 100 (KUMIP 314040) | 41.60 | -112.04 | Langston Fm., Spence Mbr. | 5 | <i>Peronopsis bonnerensis</i> |
| CAN—NWT—Little Bear River (Butterfield and Nicholas, 1996) | 64.45 | -126.68 | Mount Cap Fm. | 5 | Delamaran (<i>Glossopleura</i>) |
| US—NV—Comet Mine (Lieberman, 2003) | 37.89 | -114.61 | Pioche Fm., Comet Shale Mbr. 2 | 5 | <i>Eokochaspis nodosa</i> |
| US—NV—One Wheel Canyon (Lieberman, 2003) | 37.92 | -114.61 | Pioche Fm., Comet Shale Mbr. 2 | 5 | <i>Eokochaspis nodosa</i> |
| US—UT—Wellsville Mountains—Baker Canyon—RAR106/10 (Robison and Richards, 1981) | 41.58 | -112.01 | Bloomington Fm., Hodges Shale Mbr. | 6 | Marjuman (<i>Ptychagnostus atavus</i>) |
| US—UT—House Range—Bird Canyon—RAR 745 (Robison and Richards, 1981) | 39.24 | -113.26 | Marjum Fm. | 6 | Marjuman (<i>Ptychagnostus punctuosus</i>) |
| US—UT—House Range—Generic Marjum Fm. (Robison, 1991) | 39.27 | -113.31 | Marjum Fm. | 6 | Marjuman (<i>Ptychagnostus punctuosus</i>) |
| US—UT—House Range—Modocia Flats—RAR 158 (Briggs et al., 2008) | 39.27 | -113.29 | Marjum Fm. | 6 | Marjuman (<i>Ptychagnostus punctuosus</i>) |
| US—UT—House Range—Red Wash—RAR 716 (Briggs et al., 2008) | 39.32 | -113.27 | Marjum Fm. | 6 | Marjuman (<i>Ptychagnostus punctuosus</i>) |
| US—UT—House Range—Sponge Gully—RAR 347 (Briggs and Robison, 1984) | 39.27 | -113.31 | Marjum Fm. | 6 | Marjuman (<i>Ptychagnostus punctuosus</i>) |
| US—UT—House Range—White Hill Quarry—RAR 811 (Ubaghs and Robison, 1985) | 39.24 | -113.33 | Marjum Fm. | 6 | Marjuman (<i>Ptychagnostus punctuosus</i>) |
| US—UT—Drum Mts. 1 (Robison and Richards, 1981) | 39.51 | -113.00 | Wheeler Fm. | 6 | Marjuman (<i>Ptychagnostus atavus</i>) |
| US—UT—Drum Mts. 2 (Robison and Richards, 1981) | 39.50 | -112.98 | Wheeler Fm. | 6 | Marjuman (<i>Ptychagnostus atavus</i>) |
| US—UT—Drum Mountains—Generic Wheeler Fm. (~RAR 712) (Conway Morris and Robison, 1986) | 39.50 | -112.99 | Wheeler Fm. | 6 | Marjuman (<i>Ptychagnostus atavus</i>) |
| US—UT—House Range—Antelope Mt. 1—RAR 116 (KUMIP 314087) | 39.29 | -113.28 | Wheeler Fm. | 6 | Marjuman (<i>Ptychagnostus atavus</i>) |
| US—UT—House Range—Antelope Mt. 2 (Briggs et al., 2008) | 39.29 | -113.28 | Wheeler Fm. | 6 | Marjuman (<i>Ptychagnostus atavus</i>) |
| US—UT—House Range—Generic Wheeler Fm. (Robison, 1991) | 39.35 | -113.28 | Wheeler Fm. | 6 | Marjuman (<i>Ptychagnostus atavus</i>) |
| US—UT—House Range—Swasey Spring—RAR 114 (Robison, 1985) | 39.40 | -113.27 | Wheeler Fm. | 6 | Marjuman (<i>Ptychagnostus atavus</i>) |
| US—UT—House Range—Wheeler Amphitheater 1—RAR 115 (Robison and Richards, 1981) | 39.35 | -113.28 | Wheeler Fm. | 6 | Marjuman (<i>Ptychagnostus atavus</i>) |
| US—UT—House Range—Wheeler Amphitheater 2 (Briggs et al., 2008) | 39.36 | -113.27 | Wheeler Fm. | 6 | Marjuman (<i>Ptychagnostus atavus</i>) |

types of organisms. We do also note that there is no reason to assume *a priori* that Cambrian animals must have had highly restricted ranges given that many marine and freshwater (e.g., Suarez-Morales et al., 2004) arthropods today have vast distributions.

In order to explore the hypothesis that life habit may have played an important role in determining the Cambrian distributions of arthropod species, we used various primary and secondary literature sources (especially Briggs and Whittington, 1985; Briggs et al., 1994;

Hou et al., 2004) to assign 240 taxa (trilobites and non-trilobites) to a particular life habit. Taxa were designated as either non-swimming (benthic) or swimming (nektobenthic and nektic) (see Briggs and Whittington, 1985); we then compared the geographic ranges of the two groups. We assumed that agnostid trilobites had nektic life habits (Robison, 1972, 1975) while all other trilobites were members of the benthos (for alternative interpretations of the life habits of agnostids, see review and literature cited by Fortey and Owens, 1999).

Information about the larval ecology of taxa would in principle be worth considering but unfortunately could not be done at this time for several reasons. First, there is little or no information regarding the larval ecology of most soft-bodied Cambrian arthropods. The situation is somewhat different for trilobites, as Chatterton and Speyer (1989) have been able to make certain inferences about trilobite larval ecology, but many of the trilobite taxa considered in our study lack the requisite information to make such inferences. For instance, olenelloid trilobites lack a calcified protaspid larval phase.

2.2. Estimation of palaeogeographic range

GIS and PaleoGIS (Ross and Scotese, 2000) were used to estimate overall palaeogeographic ranges for arthropod taxa during four temporal stages of the Early and Middle Cambrian. Because most localities lack published latitude–longitude values, coordinate data for the majority of Cambrian soft-bodied deposits were determined using literature descriptions, maps, and online geographic locator tools. The modern latitude–longitude positions of the Cambrian localities (Table 3) were then rotated onto a model of Cambrian palaeogeography using PaleoGIS (Ross and Scotese, 2000), an extension for ArcView 3.1 (ESRI Inc.), following methods described elsewhere (Rode and Lieberman, 2004; Stigall and Lieberman, 2006). All points were rotated to the target age of 511 Ma, the oldest Cambrian palaeogeographic reconstruction available in PaleoGIS that preserves all of the regions present in the data set. Other models of Cambrian palaeogeography do exist (Meert and Lieberman, 2004), but they do not differ significantly in the relative positions of Laurentia and south China, nor in the relative positions of the different parts of Laurentia, including Greenland. Since taxa from these regions form the primary components of the data set, using a different Cambrian palaeogeography is unlikely to appreciably change our results. ArcMap 9.1 (ESRI Inc.) was used to manage the biogeographic data and to calculate geographic ranges from equal area, cylindrical map projections.

In order to provide broader confidence for measures of geographic range, we calculated values in two different ways: a distance-based method and an area-based method. In the distance method, absolute minimum distances (in km) were calculated as straight lines between the furthest two points of a species' range (Fig. 2); taxa occurring at just one locality were assigned a value of 1 km. In the area method, species ranges were established by constructing polygons in ArcGIS (with occurrence points as corners), and these were then used to calculate areas in km² (Fig. 2); taxa occurring at one locality were assigned an area of 3.14 km² (equivalent to a circle with a radius of 1 km)

and taxa occurring at two localities were assigned areas of $2x \text{ km}^2$ where x equals the distance in km between the two points. The distance method provides the more conservative (i.e., minimum) assessment of geographic range, while the area method may be more biologically realistic, assuming that the presence of a taxon at separated localities requires that its constituent organisms at least occasionally traversed (e.g., by their own power or by ocean currents) the intervening space separating the localities. Although each method (and indeed any method of range reconstruction) requires some assumptions, both the distance and area methods are repeatable and involve a simple calculation; this will allow for broader comparison in future studies. In the case of taxa occupying multiple geographic regions, both measurement methods involve calculations across regions that may not have been inhabited by the taxon of interest (e.g., consider an intracratonic line or polygon connecting eastern and western Laurentia). However, these two methods were utilized because they are readily repeatable and do not require extrapolations to be made beyond the range of the available data. Calculations of geographic range for individual species sometimes included occurrence records of differing ages (i.e., fossil localities belonging to different temporal stages). In such cases we assumed that these species maintained their more ancient ranges while subsequently occupying other areas.

2.3. Assessment of spatio-temporal patterns

The resultant database and geographic range data were used to assess distribution and temporal patterns in trilobites and non-trilobite arthropod species from Cambrian soft-bodied faunas. Values of species temporal longevities may be proxies for extinction resistance (Stanley, 1979; Hansen, 1982), and we calculated these by counting the number of temporal stage boundaries crossed by a taxon. In cases where a species is absent in one temporal interval, but present in older and younger intervals, we have assumed its presence in the interval from which it is unknown. Statistics were calculated using SPSS 16.0 (SPSS Inc., 1989–2007).

3. Results

3.1. Overview of database

Our assembled database (Table 1) includes spatio-temporal occurrence data for a total of 284 species. Of these, 128 are trilobites and 156 are non-trilobite arthropods, with which we include the

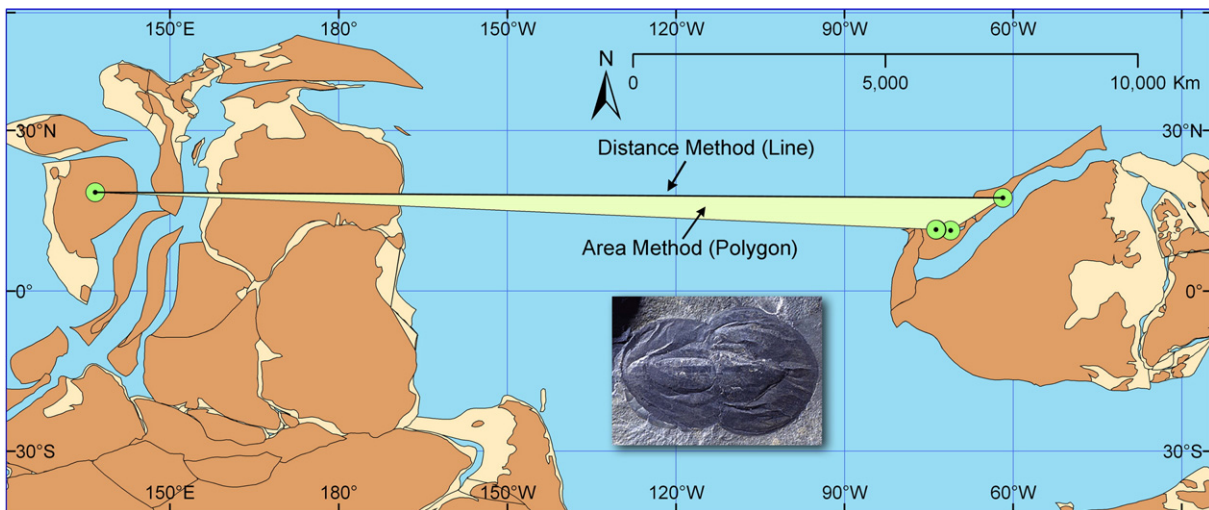


Fig. 2. Palaeobiogeographic distribution of *Naraoia compacta*, the most widely ranging Cambrian arthropod species in our analysis. Points in green are localities bearing fossils of *N. compacta*. The black line demonstrates the “distance method” of geographic range calculation and yields a value of 18,004 km; the polygon demonstrates the “area method” of geographic range calculation and yields a value of 5,823,727 km².

sclerotized appendage-bearing anomalocaridids, despite there being some question regarding their phylogenetic position relative to crown-group arthropods (Briggs and Fortey, 2005). One-hundred eighty-nine species occur at just one locality, 45 at two localities, 23 at three localities, 12 at four localities, seven at five localities, six at six localities, and two at seven localities. Only 15 species, all of which are non-trilobite arthropods, occur in more than one temporal stage interval. Further, only seven species (again, all non-trilobites) occur in more than one of the major geographic regions considered here.

3.2. Spatio-temporal patterns in trilobites versus non-trilobite arthropods

The two methods (distance- and area-based; see Methods) used to calculate the geographic ranges of individual species produced results that are correlated ($R^2=0.386$, $p<0.001$; Kendall rank correlation $\tau=0.946$, $p<0.001$). Using the distance method, we found that trilobite species ($n=128$) have an average range of 14 km ($\sigma=47$ km), while non-trilobite arthropods ($n=156$) have an average range of 584 km ($\sigma=2469$ km); these values differ significantly (Mann Whitney U -test, $p<0.01$). When the area method was used, we found that trilobite species have an average range of 115 km² ($\sigma=694$ km²) and non-trilobite arthropods have an average range of 73,138 km² ($\sigma=547,999$ km²); again, these values differ significantly (Mann Whitney U -test, $p<0.01$). The top 10% most widely ranging species are presented in Table 4, along with related regional and temporal occurrence and life habit information. The distance method identified only one trilobite species among the top 10% most widely ranging taxa and the area method identified only two, quantitatively confirming the pattern that soft-bodied arthropods tend to be much more widely ranging than trilobites.

We also found that geographic range is strongly correlated in non-trilobite arthropod species with the number of stage boundaries a species crosses when either the distance-based (Kendall rank correlation, $\tau=0.499$, $p<0.001$; Spearman rank correlation, $r_s=0.549$, $p<0.001$) or area-based ($\tau=0.489$, $p<0.001$; $r_s=0.546$, $p<0.001$) range calculation methods are used. The number of stratigraphic stage

boundaries crossed may be a proxy for extinction resistance, suggesting that there is a correlation between geographic range occupied and extinction resistance. This analysis could not be performed for trilobites because none of the trilobite species in the database occurred in more than one temporal stage.

3.3. Taxonomic robustness of results

To evaluate the robustness of our results with respect to potential taxonomic biases, we also performed similar analyses at the genus-level. Again, non-trilobite genera ($n=107$) have greater average geographic ranges (distance method average, 2592 km; area method average, 1,779,162 km²) than trilobite genera ($n=72$) (distance method average, 1436 km; area method average, 688,549 km²), although these differences are not statistically significant (Mann Whitney U -test: $p=0.690$ for distance method, $p=0.813$ for area method). A statistically significant association between extinction resistance and greater geographic range, however, exists for all of the arthropod genera in our study (distance method: $\tau=0.580$, $p<0.001$; $r_s=0.644$, $p<0.001$; area method: $\tau=0.580$, $p<0.001$; $r_s=0.647$, $p<0.001$). Nevertheless, the biological meaning of biogeographic patterns above the species-level are difficult to interpret and the Cambrian species we have included in our database were carefully vetted with respect to their taxonomic status (see Materials and methods). Further, most of these genera (trilobite and non-trilobite alike) have not been subjected to phylogenetic analyses and thus hypotheses regarding the monophyly of their component species have not been rigorously substantiated. We therefore consider the results of our species-level analyses most germane to our consideration of biogeographic patterns associated with the Cambrian radiation of arthropods.

3.4. Influence of life habit on geographic range

We found that both range calculation methods show that swimming species (nektobenthic and nektic; $n=96$) had greater

Table 4
Top 10% ($n=28$) most widely ranging species as calculated using both the distance and area methods for determining geographic range. Also provided are geographic and stratigraphic (stage) occurrence data and interpretations of life habit (italicized). Abbreviations: B, benthic; BA, Baltica; C, China; EL, eastern Laurentia; G, Greenland; N, nektic; NB, nektobenthic; S, temporal stage number; WL, western Laurentia; †Trilobite species

| Distance method | | Area method | |
|--|------------|--|--------------------------|
| Species | Range (km) | Species | Range (km ²) |
| <i>Naraoia compacta</i> (WL, C/S5, S6/B) | 18,004 | <i>Naraoia compacta</i> (WL, C/S5, S6/B) | 5,823,727 |
| <i>Naraoia halia</i> (WL, C/S3, S5/B) | 17,729 | <i>Tuzoia polleni</i> (WL, EL/S4/N) | 3,527,839 |
| <i>Anomalocaris saron</i> (WL, C/S3, S5/N) | 16,352 | <i>Anomalocaris saron</i> (WL, C/S3, S5/N) | 935,458 |
| <i>Livia plana</i> (G, BA/S3/B) | 4937 | <i>Perspicaris dilatus</i> (WL/S5, S6/NB) | 221,186 |
| <i>Tuzoia polleni</i> (WL, EL/S4/N) | 3855 | <i>Canadaspis perfecta</i> (WL/S5, S6/B) | 220,925 |
| <i>Tuzoia nitida</i> (WL, EL/S4, S5/N) | 3691 | <i>Branchiocaris pretiosa</i> (WL/S5, S6/NB) | 102,264 |
| <i>Anomalocaris pennsylvanica</i> (WL, EL/S4/N) | 3620 | <i>Laggania nathorsti</i> (WL/S5, S6/N) | 100,400 |
| <i>Anomalocaris canadensis</i> (WL/S4, S5, S6/N) | 1892 | <i>Hurdia</i> sp. (Anomalocaridid; WL/S5, S6/N) | 98,133 |
| <i>Canadaspis perfecta</i> (WL/S5, S6/B) | 1598 | <i>Mollisonia symmetrica</i> (WL/S5, S6/?) | 97,171 |
| <i>Perspicaris dilatus</i> (WL/S5, S6/NB) | 1598 | <i>Tuzoia nitida</i> (WL, EL/S4, S5/N) | 56,669 |
| <i>Laggania nathorsti</i> (WL/S5, S6/N) | 1464 | <i>Naraoia halia</i> (WL, C/S3, S5/B) | 35,458 |
| <i>Leancoilia protogonia</i> (WL/S5, S6/NB) | 1462 | <i>Anomalocaris canadensis</i> (WL/S4, S5, S6/N) | 33,481 |
| <i>Branchiocaris pretiosa</i> (WL/S5, S6/NB) | 1461 | <i>Amplectobelua trispinata</i> (C/S3/N) | 25,704 |
| <i>Mollisonia symmetrica</i> (WL/S5, S6/?) | 1460 | <i>Leancoilia illecebrosa</i> (C/S3, S5/NB) | 19,684 |
| <i>Hurdia</i> sp. (Anomalocaridid; WL/S5, S6/N) | 1458 | <i>Isoxys paradoxus</i> (C/S3/N) | 15,608 |
| <i>Leancoilia superlata</i> (WL/S5/NB) | 1220 | <i>Isoxys curvirostratus</i> (C/S3/N) | 11,392 |
| <i>Waptia fieldensis</i> (WL/S5/B) | 1220 | <i>Livia plana</i> (G, BA/S3/B) | 9874 |
| <i>Tuzoia retifera</i> (WL/S5/N) | 1217 | <i>Kunmingella douvillei</i> (C/S3/NB) | 9652 |
| <i>Leancoilia illecebrosa</i> (C/S3, S5/NB) | 633 | <i>Anomalocaris pennsylvanica</i> (WL, EL/S4/N) | 8505 |
| <i>Isoxys paradoxus</i> (C/S3/N) | 513 | <i>Naraoia spinosa</i> (C/S3/B) | 8432 |
| <i>Naraoia spinosa</i> (C/S3/B) | 513 | <i>Waptia ovata</i> (C/S3/B) | 8282 |
| <i>Misszhouia longicaudata</i> (C/S3/B) | 512 | <i>Isoxys auritus</i> (C/S3/N) | 8268 |
| <i>Isoxys curvirostratus</i> (C/S3/N) | 504 | † <i>Tsuniyidiscus niutitangensis</i> (C/S3/N) | 6997 |
| <i>Amplectobelua trispinata</i> (C/S3/N) | 502 | <i>Misszhouia longicaudata</i> (C/S3/B) | 5921 |
| <i>Skiodia alda</i> (C/S3/B) | 480 | <i>Branchiocaris yunnanensis</i> (C/S3/NB) | 3537 |
| <i>Tsuniyella diandongensis</i> (C/S3/NB) | 478 | <i>Retifacies abnormalis</i> (C/S3/B) | 3362 |
| † <i>Tsuniyidiscus niutitangensis</i> (C/S3/N) | 477 | <i>Leancoilia protogonia</i> (WL/S5, S6/NB) | 2924 |
| <i>Leancoilia hanceyi</i> (WL/S5, S6/NB) | 287 | † <i>Eoredlichia intermedia</i> (C/S3/B) | 2802 |

average geographic ranges than non-swimming species (benthic; $n=144$) (distance method, 458 versus 328 km; area method, 54,127 km² versus 42,571 km²) but Mann Whitney *U*-tests show that these differences are not significant at the 0.05 level, although are significant at the 0.07 level (distance method, $p=0.052$; area method, $p=0.066$).

4. Discussion

Our results provide strong quantitative support to earlier (Conway Morris and Robison, 1986; Conway Morris, 1989b; Lieberman, 2003) hypotheses that differences in the stratigraphic ranges of trilobites and soft-bodied arthropods correlate with differing patterns of biogeographic distribution. In fact, no trilobite species in our database existed in more than one major region; even the most widely ranging trilobite species, *Tsunyidiscus niutitangensis*, was restricted to China. While a majority of soft-bodied arthropods are also restricted to one region (96%) and one temporal interval (90%), some taxa are widely ranging geographically and/or stratigraphically, especially relative to trilobite species. We found a significant correlation between geographic range and extinction resistance among all soft-bodied arthropods in our database. This phenomenon has been demonstrated in other marine metazoan clades (e.g., Hansen, 1982; Jablonski, 1987; Jeffery and Emlet, 2003; Rode and Lieberman, 2004) and has important macroevolutionary implications (Eldredge, 1979; Vrba, 1980; Gould, 2002) for the persistence of species and clades through geological time.

Many of the most widely distributed arthropod taxa (Table 4) (with one set of exceptions discussed below) have been interpreted (Briggs et al., 1994; Hou et al., 2004) as animals that were capable of swimming (nektobenthic or nektic; Briggs and Whittington, 1985), and this may help explain their large ranges, in particular, relative to forms that were members of the benthos. For example, the flap-like abdominal limbs of the anomalocaridid genera *Anomalocaris* and *Laggania*, the bivalved crustaceans *Branchiocaris*, *Isoxys*, and *Perspicaris*, and the “great appendage” arthropod *Leancoilia* support their interpretation as members of the Cambrian nektobenthos or nekton.

The one prominent exception to this pattern involves the naraoiids. Both measurement methods used recover the trilobite-like, but soft-bodied, taxon *Naraoia compacta* as the most widely ranging species in our database (see Fig. 2); this assumes the correct identification of this species in the Kaili fauna of China (Lin et al., 2006; Zhang et al., 2007). We did not include the recent report (Schwimmer and Montante, 2007) of *N. compacta* in the Cambrian Conasauga Formation of Georgia in our analysis; doing so would have extended its range even further. The soft-parts (including limbs) of *N. compacta* are very well understood (Whittington, 1977; Briggs et al., 1994) and strongly support its interpretation as a crawling, benthic predator/scavenger (Vannier and Chen, 2002; Zhang et al., 2007). The far flung geographic distribution of *Naraoia* has been recognized elsewhere (Lin, 2006), and we found that four additional naraoiid species (*N. halia*, *N. spinosa*, *Misszhouia longicaudata*, and *Liwia plana*) are also among the most widely ranging species (Table 4). These results suggest that while the adult life habits of the taxa in our analysis may have played some role in governing their geographic ranges, other factors were likely also important. For instance, some Cambrian taxa may have had extended planktic larval stages (regardless of their adult morphologies). Unfortunately, further inquiry into this interesting area will almost certainly be limited by the fossil record itself: even if new Cambrian larval arthropods are found that occur coincidentally with the taxa analyzed here, it will be difficult (if not impossible) to link them to their adult morphologies, much less to determine their developmental modes.

Irrespective of these distinctions, our results continue to support the notion that there may be fundamental evolutionary differences between Cambrian trilobites and coeval soft-bodied arthropods. Some

of these differences may be accounted for by distinctions in adult life habit and/or larval developmental mode between different arthropod clades (e.g., most trilobite groups had benthic adults, while many—but certainly not all—soft-body arthropod taxa were nektobenthic or nektic as adults), though this needs to be examined more closely on a clade-by-clade basis; see additional discussion below. We acknowledge that greater variability in the preservation of Cambrian soft-bodied arthropods could artificially affect taxonomic identifications and this may have played some role in influencing the results of our study. Further, we cannot exclude the possibility that some of the differences between biogeographic and evolutionary patterns in trilobites and soft-bodied arthropods are attributable to this artifact. However, short of having a single worker uniformly revise (using standardized criteria for recognizing taxa irrespective of preservational type) the systematics of all species included in this study, this potential artifact is essentially impossible to quantify.

Another factor that may partly explain the biogeographic disparity between trilobites and soft-bodied arthropods is the timing of species differentiation. The initial diversification of trilobites has been related to the breakup of Pannotia between 600 and 550 Ma (Lieberman, 2002; Meert and Lieberman, 2004). Since the Eutrilobita is a derived clade of arthropods (e.g., Hendricks and Lieberman, 2007, 2008), the differentiation of the soft-bodied clades examined in this analysis is necessarily at least as old as the breakup of Pannotia. Differentiation of soft-bodied arthropods during an interval that included an intact supercontinent may have provided an opportunity for these taxa to become widespread with little subsequent speciation. Since some of the soft-bodied species analyzed herein have been shown to have much longer stratigraphic durations than co-occurring trilobites, the differences in these biogeographic scenarios for soft-bodied arthropods versus trilobites could have contributed to the disparity in biogeographic ranges observed during the Cambrian in this analysis.

Our analysis also makes it possible to examine when broadly distributed taxa developed large geographic ranges. For instance, five of the seven species that occur in more than one geographic region (Tables 1 and 4) attained a broad geographic range during the stage that included their first appearance or the subsequent stage, a pattern which may be consistent with the longer stratigraphic history hypothesis outlined above. However, the large, swimming predator *Anomalocaris saron* initially occupied a narrow range and subsequently greatly expanded its range by invading a new and distinct geographic region. *Anomalocaris saron* occurs in the Lower Cambrian Yuanshan Formation of China (Hou et al., 2004) and the Middle Cambrian Pioche Formation of Nevada (Lieberman, 2003). Assuming taxonomic equivalence of the Chinese and Laurentian forms assigned to *A. saron*, this suggests an invasion from China to western Laurentia sometime between the Early and Middle Cambrian.

We consider our data set (Table 1)—along with the results presented here—to be a baseline for future research on quantitative biogeographic patterns in Cambrian animals. Our results could be further tested by adding to or modifying our data set as additional soft-bodied arthropod faunas become better understood (e.g., those from the Early Cambrian Sinsk localities of Siberia; see Ivantsov et al., 2005; Ponomarenko, 2005) and as new faunas are discovered. In particular, we expect that the large number of singleton species occurrences in our database will be reduced as the soft-bodied Cambrian fossil record becomes better known. One area of inquiry and future research might be especially fruitful for further exploring the patterns we have documented. We have broadly compared distribution patterns in trilobite versus non-trilobite arthropods, but what patterns do individual arthropod clades show (for example at the ordinal- or family-level)? Answering this question will require new species-level phylogenetic hypotheses to be constructed for a variety of Cambrian arthropod clades. Such research also has the potential to reveal the roles of speciation and extinction in driving distribution dynamics within and between monophyletic lineages early in the

history of metazoan life. Additional future research should also focus on distributional patterns in non-arthropod, soft-bodied clades (e.g., algae, chordates, lobopods, poriferans, priapulids, and vetulicolians); are they also widespread relative to trilobites? If so, perhaps Cambrian trilobites—while having an extraordinary fossil record—are unusual in having restricted distributions relative to other taxa.

5. Conclusion

This study highlights the utility of integrating species occurrence records, reconstructions of ancient continental configurations, and GIS for analysing biogeographic patterns in extinct species, including those that lived during and shortly after the Cambrian radiation. Using a new database of arthropod occurrence records from 51 globally distributed Cambrian localities, we have provided quantitative support for the notion that soft-bodied arthropod species were more widely distributed than co-occurring trilobites. Further, we retrieved a significant correlation between geographic range and species longevity in non-trilobite species, as measured by propensity to survive across stratigraphic boundaries. Thus, our results suggest there may have been real and substantive biological differences between these types of taxa, with concomitant effects on evolutionary and biogeographic patterns. Identification of widespread species (Table 4) using the techniques outlined here opens new avenues for palaeontological investigations into the factors governing the distributions of those taxa. This is especially true when their distributions defy predictions based upon their inferred modes of life, as is the case in the benthic naraoiids. Further, our approach also provides a mechanism to identify the timing and directionality of instances of biological invasion in the fossil record (e.g., the case of *Anomalocaris saron* described above).

Acknowledgements

We thank L. Babcock for helpful discussions and N. Butterfield, E. Hermsen, R. Robison, O. E. Tetlie, and three anonymous reviewers for comments on earlier versions of this manuscript. The Yale Peabody Museum kindly allowed us to use the photograph of *Naraoia compacta* in Fig. 2. This research was supported by NSF EAR 0518976 and a Madison and Lila Self Faculty Fellowship to B.S.L.

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