Biogeography and the Cambrian radiation of arachnomorph arthropods

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Biogeographic patterns in primarily Cambrian arachnomorph taxa are investigated using a recently constructed phylogenetic hypothesis in order to explore the biogeographic context of the Cambrian radiation. A modified version of Brooks Parsimony Analysis is employed to elucidate patterns of vicariance and geodispersal in taxa from six regions (Laurentia, Baltica, Siberia, Australia, Africa and China). Well resolved vicariance and geodispersal trees are very similar and reconstruct Laurentia and China as sister areas. This close area relationship between Laurentia and China provides extensive evidence for congruent vicariance and range expansion in Cambrian arachnomorphs, while data from trilobites do not show this pattern. Our results imply that cyclic events (such as sea-level change), in conjunction with dispersal ability, may have been more important than tectonic events in generating the biogeographic patterns we observed in Cambrian arachnomorphs. Further, the greater degree of dispersal in various non-trilobite arachnomorph lineages relative to trilobites is correlated with greater extinction resistance across the early-Middle Cambrian boundary.

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ONE of John Shergold's abiding research interests, and an area in which he made fundamental contributions to the fields of palaeontology and geology, was the study of Cambrian arthropods in general, and trilobites in particular (e.g., Shergold 1977, 1988, 1991; Shergold *et al*. 1990; Shergold & Laurie 1997). Here we focus on what Cambrian arthropods, including trilobites, can tell us about the nature of evolutionary and biogeographic patterns, and their relationship to geological changes, during a key episode in the history of life, the Cambrian radiation. The first appearance of animal life in Cambrian strata has stimulated the curiosity of naturalists ever since Buckland (1836). A growing body of evidence, from studies of molecular sequence evolution to trilobite biogeography, supports the hypothesis that bilaterian lineages originated and began to diverge at the end of the Neoproterozoic, perhaps a few tens of millions of years before their first appearance in the fossil record (e.g., Meert & Lieberman 2004; Peterson *et al*. 2004).

Much recent attention has focused on the roles that extrinsic environmental or geological factors may have played in the Cambrian radiation (Hoffman 1991; Knoll 1996; Dalziel 1997; Lieberman 1997; Veevers *et al*. 1997; Hoffman *et al*. 1998). The late Neoproterozoic to early Cambrian was a period of substantial tectonic activity and Meert & Lieberman (2004; also see references therein) provided a recent review of these events, which are briefly recounted here. The supercontinent Rodinia broke apart ca. 750 Ma, with major rifting occurring between western Laurentia and Gondwana (Australia, East Antarctica and South China). Around 600 Ma, the ephemeral supercontinent Pannotia formed. Pannotia rifted apart during the subsequent 50 million years (550-600 Ma), resulting in four distinct land masses by the beginning of the Cambrian: Laurentia; Baltica (Scandinavia and eastern Europe); Siberia; and Gondwana (including South America, Africa, Antarctica, Australia, India, North and South China, Avalonia, and western and central Europe).

Of interest here are the roles that tectonic factors may have played in the early evolution and radiation of arachnomorph arthropods, which
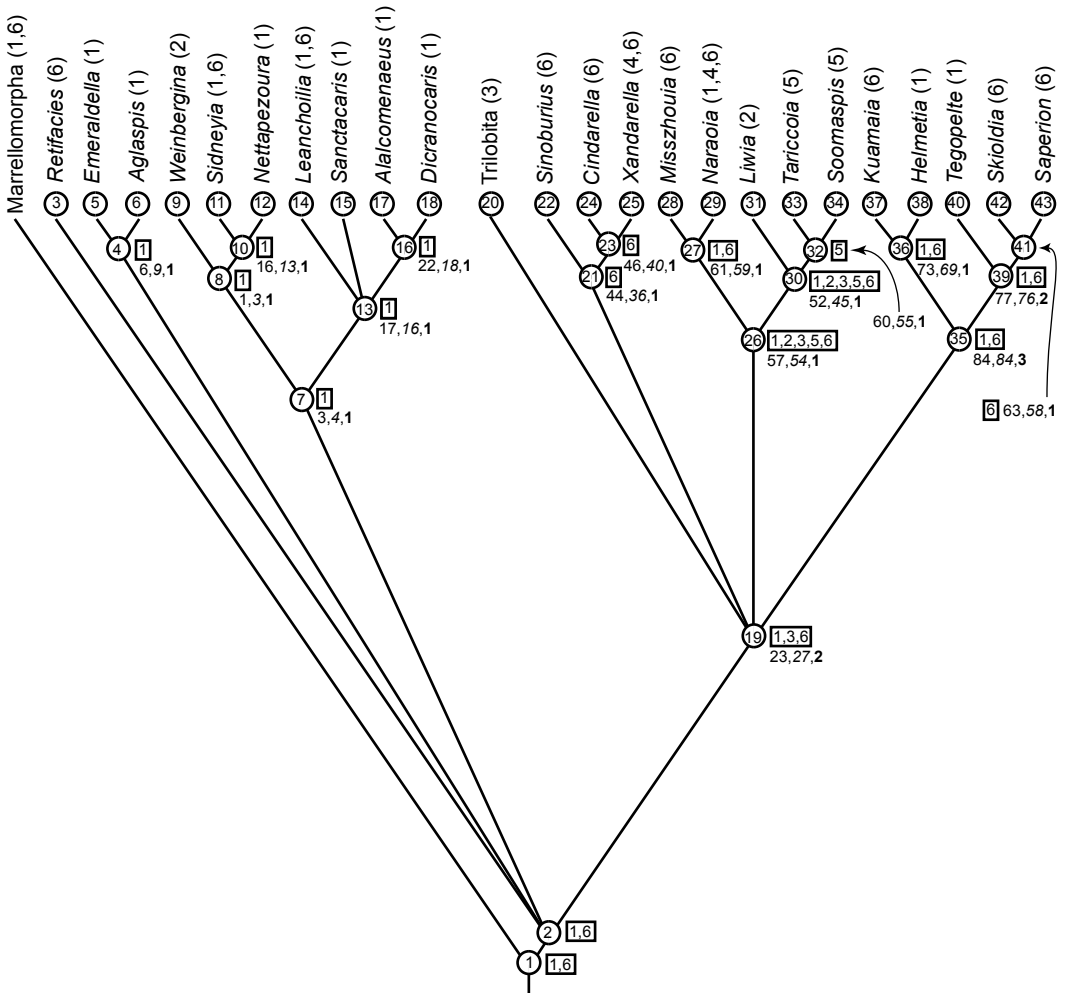
Fig. 1. Combined phylogenetic hypothesis (Hendricks & Lieberman in press) of arachnomorph relationships (strict consensus of 12 most parsimonious trees, each of 78 steps and with CI = 0.62 and RI = 0.75; the consensus has 82 steps) and area cladogram resulting from substituting biogeographic character states for taxon names and mapping biogeographic characters to ancestral nodes. Numbers adjacent to taxon names refer to geographic occurrence records (also see Table 1): 1) Laurentia; 2) Baltica; 3) Siberia; 4) Australia; 5) Africa; and 6) China. Geographic data for "Marrellomorpha" are derived from *Marrella* and geographic data for *Weinbergina* are derived from *Eolimulus* and *Paleomerus* (see text for details); further, "Trilobita" represents a sister-group relationship found for *Eoredlichia* and *Olenoides* by Hendricks & Lieberman (in press). Numbers in boxes are biogeographic regions reconstructed at ancestral nodes using Fitch (1971) optimisation as described by Lieberman (2000). Numbers in circles refer to nodes or terminals developed into biogeographical characters shown in Tables 2 and 3. Numbers in boxes are support values [normal type, bootstrap support (Felsenstein 1985); italicised type, jackknife support (Farris *et al.* 1996); bold type, Bremer support (Bremer 1988, 1994)] calculated for the phylogenetic hypothesis of Hendricks & Lieberman (in press, fig. 3).

include trilobites, chelicerates and many poorly scleritised, enigmatic arthropods only known from Burgess Shale-type deposits. Our study considers over 20 relevant, early Palaeozoic arachnomorph taxa. It was not possible, however, to consider every taxon that has been treated as an arachnomorph (or close relative) in our study. For example, we did not explore the phylogenetic position of the pycnogonids relative to Cambrian arachnomorphs and crown-group chelicerates. Biogeographic patterns in these other taxa are outside the scope of this paper, and the interested reader is referred to discussions on the phylogenetic status of the arachnomorphs by Wills *et al.* (1998), Edgecombe & Ramsköld (1999), Budd (2002), Cotton & Braddy (2004), Scholtz & Edgecombe (2006) and Hendricks & Lieberman (in press), and references therein.

It has been previously demonstrated (Lieberman 2003a, b; Lieberman & Meert 2004; Meert & Lieberman 2004) that vicariant biogeographic patterns (those involving the fragmentation of geographic areas, with subsequent lineage diversification and range contraction) in early Cambrian trilobites are congruent with the 600-550 Ma breakup of Pannotia. Further, analyses of patterns of geodispersal (those involving the joining of geographic areas, with subsequent range expansion) in early Cambrian trilobites show little evidence for significant amounts of congruent dispersal or range expansion between tectonic regions (Lieberman 2003a; Lieberman & Meert 2004; Meert & Lieberman 2004). Indeed, many early Cambrian trilobites are highly endemic. For example, among more than 100 species of early Cambrian olenelline trilobites, all were confined to a single craton and only one species occurred in more than one tectonic basin (Lieberman 1997, 1999, 2001, 2003c). On the face of it, however, this pattern of endemicity is not present in many of the Cambrian Burgess Shale-type arthropod taxa, including many non-trilobite arachnomorphs; for instance, some of these taxa are known to occur in multiple tectonic basins (Lieberman 2003c). Here we use new analyses to study biogeographic patterns of vicariance and geodispersal in primarily Cambrian arachnomorphs in order to better understand the biogeographic context of the Cambrian radiation and to consider how these patterns compare to those that have been previously observed in trilobite taxa.

METHODS AND MATERIALS

A variety of methods have been developed to explore phylogenetic biogeographic patterns (e.g., Ebach & Edgecombe 2001). Our study utilised a modified version of Brooks Parsimony Analysis (BPA) to consider biogeographic patterns in Cambrian arachnomorphs; this method was chosen because it allows examination of both patterns of vicariance and patterns of geodispersal. The modified BPA methodology used here has been described in detail previously (Lieberman & Eldredge 1996; Lieberman 1997, 2000). The method relies on first constructing an area cladogram by replacing the terminal taxa from a phylogenetic hypothesis with the geographic regions occupied by those taxa. Geographic occurrences are then reconstructed at the nodes of the cladogram using Fitch (1971) optimisation (see Lieberman, 2000, p. 121-123), a parsimony algorithm. Once constructed, information from the area cladogram is used to explore how the geographic distributions of taxa changed during cladogenesis by creating two data matrices: one designed to retrieve congruent episodes of vicariance; the other designed to retrieve congruent episodes of geodispersal. Each data matrix is then individually analysed using a parsimony algorithm. The results are expressed as a most parsimonious tree (or consensus tree) depicting, respectively, the best supported congruent patterns of vicariance and the best supported congruent patterns of geodispersal in the data. A recently constructed phylogenetic hypothesis for mostly Cambrian, Palaeozoic arachnomorph taxa (Hendricks & Lieberman in press) forms the basis of this study. Our phylogenetic hypothesis (see Fig. 1) was built by modification of, and addition to, a character matrix previously published by Edgecombe & Ramsköld (1999) and included a total of 26 terminal taxa. The topology shown (Fig. 1) is the strict consensus (with all unsupported nodes collapsed) of 12 most parsimonious trees, each of 78 steps.

Some changes were made to the phylogenetic hypothesis of Hendricks & Lieberman (in press) for the purposes of the present study. In particular, because the goal of the present study was to deduce patterns of biogeography in Cambrian arachnomorphs (see Table 1), two of the Devonian-aged terminal taxa were replaced on the tree by Cambrian taxa considered to be either nearly equivalent or closely related. These two changes included: 1) replacing the composite outgroup terminal "Marrellomorpha", which comprises both the Cambrian taxon *Marrella* and the Devonian taxon *Mimetaster*, with just *Marrella*; and 2) substituting either *Eolimulus* or *Paleomerus*, both Cambrian taxa, for the Devonian chelicerate *Weinbergina*. We acknowledge that because information about the appendages of *Eolimulus* and *Paleomerus* are lacking, their phylogenetic positions cannot be confidently established. For the purposes of the present study, however, we assume that one (or both) may be on the xiphosuran stem lineage and are thus appropriate placeholders for *Weinbergina*, especially because all three taxa share a similar palaeogeographic provenance (Baltica). Additionally, the trilobite genera *Eoredlichia* and *Olenoides*, found to be sister taxa in the earlier analysis, were fused into a single terminal labeled here simply as "Trilobita" (as shown in Fig. 1). With the exceptions of the Ordovician taxa *Tariccoia* and *Soomaspis*, these changes resulted in all terminal taxa being Cambrian in age.

Global geographic occurrence data for all taxa considered in this study were collected from a comprehensive review of the relevant literature, especially the work of Raasch (1939), Bergström (1968), Dzik & Lendzion (1988), Hammann *et*

Taxon	Laurentia (1)	Baltica (2)	Siberia (3)	Australia (4)	Africa (5)	China (6)
Aglaspis Hall, 1862	Raasch 1939					
Alalcomenaeus Simonetta, 1970	Robison 1991; Briggs et al. 1994					
Cindarella Chen, Ramsköld, Edgecombe & Zhou in Chen *et al.*, 1996						Hou *et al.* 2004
Dicranocaris Briggs *et al.*, in press	Briggs *et al.* in press					
Emeraldella Walcott, 1912	Robison 1991; Briggs et al. 1994					
Eolimulus Bergström, 1968 (Placeholder for *Weinbergina*)		Bergström 1968				
Helmetia Walcott, 1918	Briggs *et al.* 1994					
Kuamaia Hou, 1987						Hou *et al.* 2004
Leanchoilia Walcott, 1912	Robison 1991; Briggs et al. 1994					Zhao *et al.* 2002; Hou *et al.* 2004
Liwia Dzik & Lendzion, 1988		Dzik & Lendzion 1988				
Marrella Walcott, 1912 (Placeholder for Marrellomorpha)	Briggs *et al.* 1994					*Zhao et al.* 2002
Misszhouia Chen *et al.*, 1997						Hou *et al.* 2004; Steiner *et al.* 2005
Naraoia Walcott, 1912	Robison 1991; Briggs *et al.* 1994; Zhang *et al.* 2007			Nedin 1999		Hou *et al.* 2004; Steiner *et al.* 2005; Lin 2006; Zhang *et al.* 2007
Nettapezoura Briggs *et al.*, in press	Briggs *et al.* in press					
Paleomerus Størmer, 1956 (Placeholder for *Weinbergina*)		Tetlie & Moore 2004				
Retifacies Hou *et al.*, 1989						Hou *et al.* 2004
Sanctacaris Briggs & Collins, 1988	Briggs *et al.* 1994					
Saperion Hou *et al.*, 1991						Hou *et al.* 2004
Sidneyia Walcott, 1911	Briggs *et al.* 1994					Hou *et al.* 2004
Sinoburius Hou *et al.*, 1991						Hou *et al.* 2004
Skioldia Hou & Bergström, 1997						Hou *et al.* 2004; Steiner *et al.* 2005
Soomaspis Fortey & Theron, 1994					Fortey & Theron 1994	
Tariccoia Hammann *et al.*, 1990					Hammann *et al.* 1990	
Tegopelte Simonetta & Delle Cave, 1975	Briggs *et al.* 1994					
Trilobita (Placeholder for *Eoredlichia* and *Olenoides*)			Lieberman 2002			
Xandarella Hou *et al.*, 1991				Hagadorn 2002		Hou *et al.* 2004

Table 1. Regional biogeographic occurrence data (presence indicated by reference) for the arachnomorph taxa considered in this study. Presence in a region is indicated by a recent reference.

al. (1990), Robison (1991), Briggs *et al.* (1994), Fortey & Theron (1994), Nedin (1999), Hagadorn (2002), Zhao *et al.* (2002), Hou *et al.* (2004), Tetlie & Moore (2004), Steiner *et al.* (2005), Lin (2006), Zhang *et al.* (2007) and Briggs *et al.* (in press). We grouped these occurrence records into six major tectonic provinces or areas of endemism: 1) Laurentia (including taxa from present day British Columbia, Greenland, Pennsylvania, Utah and Wisconsin); 2) Baltica (Poland and Sweden); 3) Siberia; 4) Australia (in this case the lower Cambrian deposits from Kangaroo Island); 5) Africa (in this case South Africa and Sardinia, which sat close to the margins of the African craton; Meert & Lieberman 2004); and 6) China (in this case Yunnan and Guizhou provinces).

These occurrence data are summarised in Table 1. The assignment of the biogeographic state of the Trilobita to Siberia is based upon the phylogenetic biogeographic analysis of Lieberman (2002), which reconstructed Siberia as the region where eutrilobites originated. Additionally, a hypothetical, ancestral outgroup region (0) was created to provide polarity for the biogeographic character data in the six ingroup regions; see further details below.

Some geographical assignments of taxa remain controversial. Relevant examples include the occurrence records for *Alalcomenaeus*, *Sidneyia* and *Naraoia*. It has been suggested (e.g., Briggs & Collins 1999) that a small number of Chengjiang specimens referred to *Leanchoilia*

	1	2	3	4	5	6	7	8	9	1 0	1 1	1 2	1 3	1 4	1 5	1 6	1 7	1 8	1 9	2 0	2 1	2 2	2 3	2 4	2 5	2 6	2 7	2 8	2 9	3 0	3 1	3 2	3 3	3 4	3 5	3 6	3 7	3 8	3 9	4 0	4 1	4 2	4 3
Ancestor (0)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Laurentia (1)	1	1	1	2	1	1	2	1	0	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	1	2	1	1	1	1	1	0	0	2	1	1	2	1	2	1	0	0
Baltica (2)	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	2	1	0	0	0	0	0	0	0	0	0	0	0	0
Siberia (3)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	1	0	0	0	0	1	1	0	0	1	1	1	0	0	1	0	0	0	0	0	0	0	0
Australia (4)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Africa (5)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	1	2	1	1	0	0	0	0	0	0	0	0	0	0
China (6)	1	1	2	1	0	0	1	0	0	0	1	0	0	1	0	0	0	0	1	1	2	1	1	1	1	1	2	2	1	1	1	1	0	0	2	1	2	1	1	1	2	1	1

Table 2. Matrix of biogeographical characters and character states used in the analysis of vicariance. State 0 signifies the primitive condition (absent) and states 1 and 2 signify the derived conditions (present). All characters treated as ordered (additive). Characters 5, 6, 8-10, 12, 13, 15-18, 22-24, 33, 34, 42 and 43 are uninformative and were deactivated prior to cladistic analysis.

may be *Alalcomenaeus*, though this assignment has not yet been conclusively determined and several recent publications do not recognise this taxon as occurring in China (Hou *et al*. 2004; Steiner *et al*. 2005). Therefore, we do not treat *Alalcomenaeus* as occurring in China in this study. *Sidneyia*—first described from the Burgess Shale of Laurentia by Walcott (1911) as *S. inexpectans*—has been reported (Zhang *et al*. 2002) to occur in the Chengjiang as *S. sinica*, though Briggs *et al*. (in press) challenge this generic assignment. Nevertheless, Briggs *et al*. (in press) argue that *S. sinica* is similar to *Sidneyia inexpectans* in many respects and was likely closely related. Hence, we have chosen to include an occurrence record for *Sidneyia* in China. Recently, Lin *et al*. (2006) and Zhang *et al*. (2007) challenged Nedin's (1999) identification of *Naraoia* in the Emu Bay Shale, claiming instead that Nedin's material may represent *Primicaris* or *Skania*. Nedin's (1999, fig. 2a) figured specimen is somewhat poorly preserved and in general form could be compatible with an interpretation either as *Naraoia*, *Primicaris* or *Skania*. Specimens of *Naraoia* tend to be larger than specimens of *Primicaris* and *Skania* (see sizes for these taxa presented by Zhang *et al*. 2003; Lin *et al*. 2006), however, and the size of Nedin's (1999, fig. 2a) figured specimen (ca. 12 mm) from the Emu Bay Shale is within the range of *Naraoia*, but appears to be too large for the other two taxa. Thus, until decisive Emu Bay Shale specimens present themselves to the contrary, we follow Nedin's (1999) identification of his material from the Emu Bay Shale, South Australia.

We acknowledge the possibility that potential biases may have led to some true taxon occurrence records going unrecognised due to either their missing fossil record (not being fossilised due to taphonomic biases) or their lack of collection to date. This is a challenging problem without a simple solution: how should one weigh negative occurrence evidence? We argue that the distributional patterns considered here could be easily tested, further evaluated and modified, if need be, as new fossil discoveries are made.

We replaced the terminal taxon names on our phylogenetic hypothesis (Hendricks & Lieberman in press) with their associated geographic occurrence data (tectonic provinces 1-6); see Figure 1. Next, unordered Fitch optimisation (Fitch 1971) was used to optimise the geographic states on the tree topology, as described by Lieberman (2000, p. 121-123). This resulted in an area cladogram (see Fig. 1) that could be used to construct a vicariance matrix and a geodispersal matrix, which are respectively designed to discover congruent historical episodes of vicariance and range expansion (Lieberman 2003a). These matrices were constructed and coded from the area cladogram (Fig. 1) following the methodology described by Lieberman (2000, p. 144-150). All characters were treated as ordered (=additive), with a vicariant transition between a region denoted by a transition from state '1' to state '2' in the vicariance matrix; similarly, a transition involving range expansion would be denoted by a transition from state '1' to state '2' in the geodispersal matrix. The vicariance matrix is shown in Table 2 and the geodispersal matrix is shown in Table 3. In both cases, all biogeographic characters for the hypothetical ancestral outgroup region (0) were coded as absent in order to provide polarity to the characters in the ingroup regions. These matrices were used to reconstruct the best supported vicariance and geodispersal topologies using the parsimony criterion, which may be interpreted as follows: on a vicariance tree (or a consensus of multiple trees), the closer two regions sit on the tree, the more recently they were separated (Lieberman 2003a); the closer two regions sit on the geodispersal tree, the more recently they were joined (Lieberman 2003a). Significant amounts of similarity between the two trees may suggest that the same environmental processes responsible for vicariance were also responsible for geodispersal (e.g., cyclic processes such as sea-level change). By contrast,

	1	2	3	4	5	6	7	8	9	1 0	1 1	1 2	1 3	1 4	1 5	1 6	1 7	1 8	1 9	2 0	2 1	2 2	2 3	2 4	2 5	2 6	2 7	2 8	2 9	3 0	3 1	3 2	3 3	3 4	3 5	3 6	3 7	3 8	3 9	4 0	4 1	4 2	4 3
Ancestor (0)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Laurentia (1)	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	1	1	0	1	1	0	0	0	0	1	1	0	1	1	1	0	0	0	
Baltica (2)	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	
Siberia (3)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	
Australia (4)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Africa (5)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1	0	1	1	1	0	0	0	0	0	0	0	0	0		
China (6)	1	1	1	0	0	0	0	0	0	0	2	0	0	2	0	0	0	0	1	0	1	1	1	1	1	1	1	1	1	1	0	0	0	0	1	1	1	0	1	0	1	1	1

Table 3. Matrix of biogeographical characters and character states used in the analysis of geodispersal. State 0 signifies the primitive condition (absent) and states 1 and 2 signify the derived conditions (present). All characters treated as ordered (additive). Characters 3-8, 10, 12, 13, 15-18, 20-24, 28, 31-34, 37, 38 and 40-43 are uninformative and were deactivated prior to cladistic analysis.

significant differences between the two trees may suggest that tectonic events, a single profound episode of sea-level rise (or fall), or chance dispersal events may have played more important roles in influencing the observed biogeographic patterns in a given group (Lieberman 2003a); see Lieberman & Eldredge (1996) and Lieberman (1997, 2000) for additional discussion.

The vicariance and geodispersal matrices were managed using WinClada (Nixon 1999-2002) and heuristic parsimony analyses were independently carried out on each matrix using NONA 2.0 (Goloboff 1999). Prior to each parsimony analysis, all uninformative characters were selected and deactivated using WinClada. The matrices were then submitted to NONA for analysis. The tree-bisection reconnection (TBR) algorithm of Swofford & Olsen (1990) was used in NONA to search for most parsimonious tree (MPT) topologies. Each analysis involved 2,500 replications (during each replication, 15 trees were stored in memory for branch-swapping) and space was held in memory to store up to 10,000 trees. After this search, the shortest MPT's were swapped to completion and only unique trees were saved. The command line for this search sequence in NONA is "h10000; h/15; mult*2500; max*; unique; sv* filename.tre sv/;". Ensemble consistency index (CI; Kluge & Farris 1969) and retention index (RI; Farris 1989) values were then computed using NONA's "fit;" command. Saved trees were imported into WinClada for study and nodes lacking character support were collapsed. Additionally, bootstrap (Felsenstein 1985) and jackknife support (Farris *et al*. 1996) values were calculated for each matrix using NONA (executed through WinClada).

RESULTS
The parsimony analysis of the vicariance matrix resulted in the discovery of a single most parsimonious tree of length 41 steps (CI = 0.95; RI = 0.93), which is shown in Figure 2A. The

tree is well resolved. Note, however, that no characters support separation of Africa from Baltica, resulting in a collapsed node; thus, it is not clear whether Baltica is positioned basal to Africa, or vice-versa.

The analysis of the geodispersal matrix resulted in the discovery of a single most parsimonious tree of length 24 steps (CI = 0.87, RI = 0.82), which is shown in Figure 2B. This well resolved tree features two major groupings: 1) a monophyletic area composed of Siberia, Laurentia and China; and 2) a sister-area relationship for Baltica and Africa. These two groupings in turn have a sister-group relationship, with Australia positioned (relatively) one node down the tree.

The vicariance (Fig. 2A) and geodispersal (Fig. 2B) trees are very similar in appearance. Both show a derived sister-area relationship between Laurentia and China and show Siberia one node "down the tree" from this grouping. Further, both show a basal position for Australia. As described above, and shown in Figure 2A-B, the vicariance and geodispersal trees differ only in their relative placements of Baltica and Africa.

DISCUSSION AND CONCLUSIONS
The results from the analysis of phylogenetic biogeographic patterns in predominantly Cambrian arachnomorphs are rather different from the results that have been observed previously in Cambrian trilobites (Lieberman 2002, 2003a). In particular, the most parsimonious patterns of geodispersal are well resolved for the arachnomorphs (Fig. 2B), whereas the patterns from the trilobites showed relatively little resolution. This suggests that the arachnomorphs experienced significantly more congruent episodes of range expansion during the Cambrian than trilobites did. Another fundamental difference between the biogeographic patterns in arachnomorphs and trilobites involves the association between the faunas of Laurentia and China. These regions are sister areas in both the arachnomorph vicariance and geodispersal
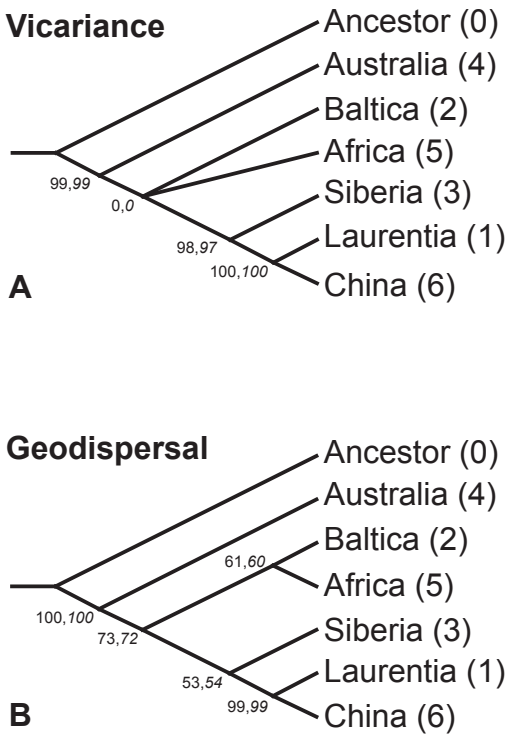
Vicariance

A

Geodispersal

B

Fig. 2. Single most parsimonious area cladograms resulting from modified Brooks Parsimony Analyses of the vicariance (2A; see Table 2) and geodispersal (2B; see Table 3) matrices. Values at nodes are bootstrap (normal type) and jackknife (italicised type) support values. The vicariance tree (2A) is 41 steps in length (CI = 0.95; RI = 0.93); one node is collapsed due to lack of character support. The geodispersal tree is 24 steps in length (CI = 0.87, RI = 0.82) and is completely resolved.

trees (Fig. 2A-B); by contrast, the trilobite faunas of Laurentia and China do not have a close area relationship. Our recovered pattern is part of a more general pattern that other authors have recognised. For instance, of the 112 early Cambrian trilobite taxa from the western Gondwanan margin considered in the study by Álvaro *et al*. (2003, fig. 5), only one genus (*Serrodiscus*) is found in both Laurentia and China. Similarly, of 94 Middle Cambrian trilobite genera (also from western Gondwana), Álvaro *et al*. (2003, fig. 6) reported only eight (*Centropleura*, *Diplagnostus*, *Doryagnostus*, *Hypagnostus*, *Lejopyge*, *Oidalagnostus*, *Peratagnostus* and *Ptychagnostus*) common to Laurentia and China. [Of these nine Cambrian trilobite genera, only *Centropleura* belongs to the polymeroid trilobite clade; the other eight taxa are 'miomeroids'. The latter likely had a pelagic lifestyle and consequently were more widely distributed than polymeroids (Laurie 1988; Shergold *et al*. 1990;

Shergold & Laurie 1997)]. By contrast, the Cambrian Burgess Shale-type faunas of Laurentia and China share many elements in common, including arachnomorphs.

Still, on tectonic grounds, it is somewhat unexpected to find such a close area relationship between Laurentia and China (Fig. 2A): these two regions were last in tectonic contact about 750 Ma (see Meert & Lieberman 2004, but also see Veevers *et al*. 1997 for an alternative breakup time). The close association between Laurentia and China in our area cladograms may be partly related to the fact that the most diverse and well known Cambrian arthropod faunas occur in Laurentia (for example, the Middle Cambrian Burgess Shale biota [e.g., Briggs *et al*. 1994] and biotas of similar age from Utah [e.g., Robison 1991; Briggs *et al*. in press]) and China (for example the Chengjiang biota [e.g., Hou *et al*. 2004]). It has been shown previously that low diversity faunas can sometimes map "down the tree" in phylogenetic biogeographic analyses, causing high diversity faunas to potentially group together (Fortey & Cocks 1992). We acknowledge this potential bias. However, it is worth noting that the close area relationship we recovered here between Laurentia and China does seem to reflect a truly different pattern from the one uncovered in the trilobites. In particular, while the non-trilobite faunas of Laurentia and China share many elements in common (e.g., see discussion above), the trilobites that co-occur in the early Cambrian Chengjiang biota and other early Cambrian or Middle Cambrian Burgess Shale-type faunas in Laurentia share very few elements in common. Further, many non-trilobite arthropod genera (for instance, the arachnomorphs *Leanchoilia* and *Naraoia*, as well as *Anomalocaris*, *Branchiocaris*, *Canadaspis*, *Isoxys*, *Marrella*, *Tuzoia* and *Waptia*) are widely distributed, and occur in both Laurentia and China. This too, as mentioned above, is very different from the trilobites, which tend to be much more narrowly distributed, except in the case of the agnostoids (Shergold & Laurie 1997). We are not alone in recognising a biotic association between Laurentia and China near the beginning of the Phanerozoic: Waggoner (1999) recovered a biogeographic association between some Ediacaran taxa from southwestern Laurentia and south China, although our data are based on different methods, and other aspects of our results are very different.

When dispersal is minimal or absent, the timing of tectonic events—for example, the age when two regions that are now separated were last joined and homogeneous—can potentially be used to constrain the age of origination of monophyletic groups. For example, studies of
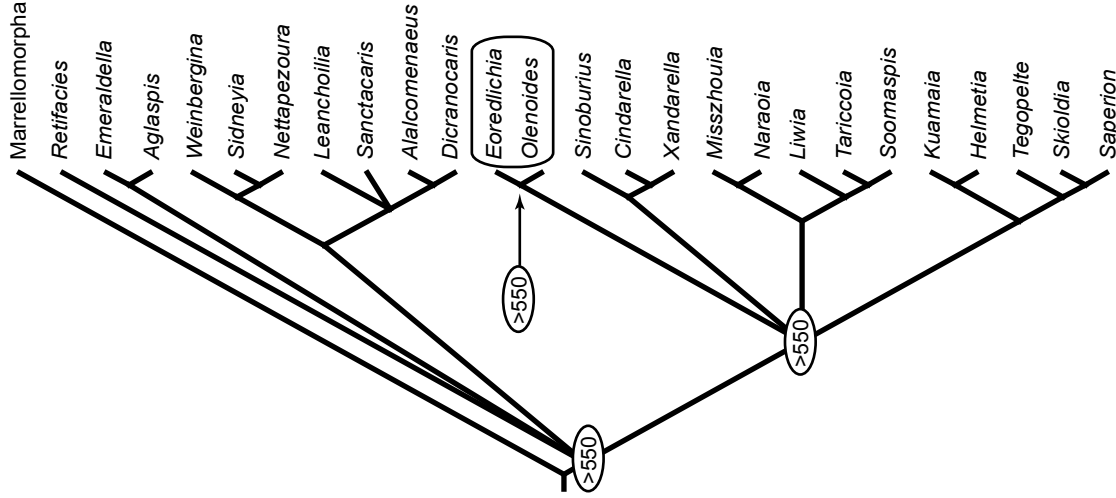
otherwise, in trilobite lineages. By contrast, the congruent patterns of vicariance and geodispersal observed here in arachnomorphs (particularly between Laurentia and China) mean that the tectonic vicariance between these regions does not equate to the last time of contact between their respective faunas. This is because dispersing lineages could recolonise regions after they were no longer in contact geologically. Still, the fact that biogeographic patterns indicate that trilobites likely originated somewhere in the interval of 600-550 Ma (Lieberman 2003a; Lieberman & Meert 2004) can be used as a phylogenetic constraint on the origination time of a whole host of arachnomorph lineages. In particular, these lineages—including the true chelicerates—must have minimally also commenced diverging by 600-550 Ma (Fig. 3).

The failure of Australia to biogeographically group with China also differs from the inferred sequence of late Neoproterozoic and early Cambrian tectonic events (Lieberman & Meert 2004; Meert & Lieberman 2004). This, and the fact that there are very strong similarities between our vicariance and geodispersal trees (Fig. 2A-B), may suggest that in the case of these arachnomorphs, tectonics was not the primary factor that governed diversification. Instead, the processes producing the pattern in the vicariance tree may have been those driving the patterns in the geodispersal tree (Lieberman 2000) and likely included cyclic processes including repeated episodes of sea-level rise and fall.

The palaeobiogeographic patterns described herein also have the potential to inform our understanding of macroevolutionary processes operating during (and immediately prior to) the Cambrian radiation. This is because Cambrian trilobites and many non-trilobite arthropods show not only differing biogeographical patterns, but also different patterns of extinction across the early-Middle Cambrian boundary, as has been noted previously (Conway Morris & Robison 1986; Conway Morris 1989; Lieberman 2003c). These two aspects may be related. Highly endemic early Cambrian trilobites show significant taxonomic turnover at the early-Middle Cambrian boundary (Palmer 1998; Lieberman 2003c), while many other non-trilobite taxa cross this boundary unscathed. This extinction resistance is in fact reflected in the faunal similarities between the early Cambrian Chengjiang fauna of China and other Cambrian faunas in Laurentia, including the Middle Cambrian Burgess Shale fauna of British Columbia and the Middle Cambrian Pioche Shale of Nevada (e.g., Lieberman 2003c). The topic of the causal link between broad geographic range and extinction resistance has been frequently

Fig. 3. Strict consensus of the 12 most parsimonious trees found in the analysis of Hendricks & Lieberman (in press) with minimum of origination (in millions of years ago) mapped at some nodes. Biogeographic data suggest that trilobites (represented here by *Eoredlichia* and *Olenoides*) originated by 550-600 Ma. The derived position of the trilobites in this tree implies that many other arachnomorph taxa must also have originated by no later than 550 Ma.

trilobite palaeobiogeography were used to make inferences about the timing of the Cambrian radiation (e.g., Lieberman 2003b; Meert & Lieberman 2004). This was possible because not only did the vicariance patterns in trilobites match the pattern predicted for the 600-550 Ma breakup of Pannotia, but also there was very limited evidence for any kind of dispersal, congruent or

supported (Eldredge 1979; Stanley 1979; Vrba 1980; Hansen 1982; Gould 2002) and we hypothesise that such an association may have been important for the early evolution and persistence of many metazoan taxa. In particular, the relatively endemic nature of certain early Cambrian trilobites, especially the olenellines, would have made them more susceptible to extinction, whereas by contrast, more broadly distributed Cambrian non-trilobite arthropod taxa would have been naturally extinction resistant. This, however, remains to be studied in greater detail.

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