

A Palaeomagnetic and Palaeobiogeographic Perspective on Latest Neoproterozoic and Early Cambrian Tectonic Events

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Abstract: During the latest Neoproterozoic to Middle Cambrian time (580-505 million years ago), the Earth underwent significant changes in palaeogeography that included rifting of a possible supercontinent and the near simultaneous formation of a second, slightly smaller supercontinent. It is against this tectonic backdrop that the Cambrian radiation occurred. While the general tectonic setting during this interval is fairly well-constrained, models of the exact palaeogeography are controversial because of the lack of reliable palaeomagnetic data from some of the continental blocks. Palaeogeographic models based on palaeomagnetic data range from: (a) a high-latitude configuration for most continents; (b) a low-latitude configuration for most continents; or (c) rapid oscillations in continental configurations triggered by inertial changes within the planet. Palaeobiogeographic data can also be used to help constrain palaeogeographic models. To this end we use vicariance patterns in olenellid trilobites to determine their compatibility with three end-member palaeogeographic models derived from palaeomagnetism for the Neoproterozoic and early Cambrian. The most congruent palaeogeographic model with respect to the palaeobiogeographic data described herein is the high-latitude configuration for most continents. Those palaeomagnetic models that predict inertial interchange true polar wander or multiple episodes of true polar wander differ significantly from the results from palaeobiogeography. The low-latitude palaeogeographic models also differ from the results from palaeobiogeography, but this may partly arise due to a lack of palaeomagnetic and palaeobiogeographic data from many parts of present day South America and Africa.

Keywords: palaeomagnetism; palaeobiogeography; trilobites; Cambrian radiation; Neoproterozoic; true polar wander.

The palaeogeography of the latest Neoproterozoic interval is the subject of considerable controversy based principally on the myriad interpretations of palaeomagnetic poles from Laurentia (Symons and Chiasson, 1991; Meert et al., 1994; Powell, 1995; Torsvik et al., 1996; Kirschvink et al., 1997; Torsvik et al., 1998; Evans, 1998; Meert, 1999; Pisarevsky et al., 2000; Meert and Van der Voo, 2001; Evans, 2003). These models can be broadly classified into three end-member reconstructions. Symons and Chiasson (1991) advocated a south polar position for Laurentia at ca.

575 Ma. Meert et al. (1994) adopted a similar position for Laurentia and placed it in a global reconstruction adjacent to the South American cratons (Fig. 1a,b). Powell (1995) also favoured a south polar position for Neoproterozoic Laurentia and placed its present-day eastern margin adjacent to Baltica and a fully assembled Gondwana (the Pannotia supercontinent). The adoption of a south polar position for Laurentia at ca. 575 Ma requires a rapid transition to lower latitudes by Middle Cambrian time (Meert et al., 1993). In contrast, Pisarevsky et al. (2000) argued for an

equatorial Laurentia in an effort to maintain a link between the Siberian craton and the arctic margin of Laurentia (Fig. 2a,b; see also Pelechaty, 1996). The third category of models attempts to harmonize both the high-latitude and low-latitude positions by proposing a series of rapid changes in palaeogeography driven by mantle mass instabilities (Kirschvink et al., 1997; Evans, 1999 and Evans, 2003). In their models, the continents rotate through as much as 90 degrees in as few as 15 million years due to multiple episodes of true polar wander (Fig. 3a,b). Each model is particularly sensitive to the palaeomagnetic data and how these are selected; therefore, a test of the models that is independent of palaeomagnetic data is highly desirable. For this reason we incorporate both palaeomagnetic and palaeobiogeographic data in our analysis.

There is a long tradition of using the analysis of palaeobiogeographic data to reconstruct the geometries of continents and their changing positions through time (e.g. Williams, 1973; Burrett and Richardson, 1980; Cocks and Fortey, 1982; Hallam, 1983; Cocks and Scotese, 1991; Fortey and Cocks, 1992; Rushton and Hughes, 1996; Lieberman and Eldredge, 1996; Lees et al., 2002). Such an approach has also been used recently in a study by Cocks and Torsvik (2002) that combined palaeobiogeographic and palaeomagnetic databases to consider Ordovician tectonics (also see McKerrow et al., 1992 and Harper et al., 1996, other studies that have combined palaeobiogeographic and palaeomagnetic datasets). Here we use palaeobiogeographic analyses of trilobites, the most diverse and abundant early Cambrian animals, in combination with palaeomagnetic data, to reconstruct

late Neoproterozoic and early Cambrian palaeogeography and consider some of the tectonic events that have been proposed for the interval.

Despite the arguments regarding the latitudinal positions of continents in Neoproterozoic times, it is universally acknowledged that there are several key tectonic events that occur during the 600-500 Ma interval. As Gondwana was assembled, the Iapetus Ocean opened (Grunow et al., 1996); the northern Iapetus Ocean between Baltica and Laurentia opened around 600 Ma (see Torsvik and Rehnström, 2002; Meert et al., 1998), and the southern Iapetus Ocean between Laurentia and several parts of present day opened around 550 Ma (Cawood et al., 2001). Rift events along the present-day western margin of Laurentia at ca. 550 Ma are poorly described, but subsidence studies suggest the development of passive margin sedimentary sequences during the latest Neoproterozoic and early Cambrian (Bond et al., 1984; Kominz, 1995). Eastern Australia was also dominated by passive margin development during the Neoproterozoic-early Cambrian interval (Preiss, 2000). Depending on the precise timing of these rifting and collisional events, a Pannotian supercontinent was either completely or nearly assembled (Powell, 1995; Dalziel, 1997; Meert and Van der Voo, 1997; Scotese et al., 1999).

In addition to the profound tectonic changes in the late Neoproterozoic and early Cambrian there are a set of profound biological changes culminating in the so called Cambrian radiation: an event that marks the proliferation of diverse representatives of most of the major animal phyla in the fossil record. Although a traditional view was that the manifestation of the Cambrian radiation

in the fossil record corresponded closely to the actual evolutionary divergence of these lineages, a growing body of evidence suggests this may not be the case. Instead, it now appears likely that the diversification of lineages comprising the Cambrian radiation faunas was underway in the Neoproterozoic, significantly before the Early Cambrian (Briggs and Fortey, 1989; Briggs et al., 1992; Conway Morris, 1993, 2000; Fortey et al., 1996, 1997; Davidson et al., 1995; Bromham et al., 1998; Xiao et al., 1998; Budd and Jensen, 2000); current debate centers on how far back these divergence events lie in the Neoproterozoic. For instance, palaeontological events have placed the divergence events in the late Vendian (e.g. Budd and Jensen, 2000; Conway Morris, 2000), somewhere before the 550-600 Ma interval (Lieberman, 2003), or back at 750 Ma (Fortey et al., 1996, 1997). Divergence estimates based on molecular clocks have placed divergence events associated with key episodes of animal evolution back to around 650 Ma (e.g. Ayala et al., 1998; Bromham et al., 1998), whereas the more distant divergence events back to 1 Ga previously proposed by molecular clock studies (e.g. Wray et al., 1996) now appear unlikely. Although there are a range of dates, these seem to straddle the breakup of Rodinia and Pannotia, suggesting that there is some correlation between the profound tectonic events of the time and the profound biological events (Fortey et al., 1996; Knoll, 1996; Dalziel, 1997). Further, the fact that many of the roots of the Cambrian divergence events extend back into the Neoproterozoic means that the patterns in early Cambrian organisms like trilobites can potentially aid in adducing

the nature and sequence of late Neoproterozoic tectonic events.

Material and Methods

Palaeomagnetic analysis

We have chosen to develop three distinct palaeogeographies based on the interpretations noted earlier in the manuscript. These palaeogeographies are based primarily on palaeomagnetic data, but geologic information (e.g. ages of rifting and collision) is used to further constrain the positioning of blocks in the absence of palaeomagnetic data. In essence, we follow the previously published reconstructions of Torsvik et al. (1996), Kirschvink et al. (1997), Pisarevsky et al. (2000), Torsvik and Rehnström (2002) and Meert and Van der Voo (2001) with slight modifications. Euler poles for each of the reconstructions are given in the appendix along with the palaeomagnetic poles used in the analysis. As with all palaeomagnetically based pre-Mesozoic reconstructions, there is additional uncertainty in determining relative palaeolongitude along with a hemispheric ambiguity (e.g. choice of polarity).

Palaeobiogeographic analysis

In order to use fossils to aid in palaeogeographic reconstructions we follow the principles described in McKerrow and Cocks (1986), Lieberman (2000), and Cocks and Torsvik (2002). Further, we use phylogenetic relationships and phylogenetic biogeographic methods to analyze the palaeobiogeographic data, following the approaches in Young (1990), Fortey and Cocks (1992),

Lieberman and Eldredge (1996), and Lieberman (1997, 2000, 2003).

More than 115 species of olenellid trilobites were considered in the biogeographic analysis. These species occur in the early Cambrian *Fallotaspis*, *Nevadella*, and *Bonnia/Olenellus* zones. Taxa evaluated occur on many of the major early Cambrian cratons including Armorica, Australia, Avalonia, Baltica, East Antarctica, eastern, southwestern, and northwestern Laurentia (with Laurentia including the Precordillera terrane), north Africa, and Siberia, and they have been subjected to phylogenetic analysis by Lieberman (1998, 1999, 2001, 2002). Eight species are from Siberia, 14 are from northern Africa-Armorica, 4 are from Avalonia, 26 are from SW Laurentia, 31 are from NW Laurentia, 26 are from eastern Laurentia, 10 are from Baltica, two are from Antarctica, and one is from Australia. (Note: some species occur in more than one region.) Taxa analyzed and their areas of occurrence are available in Lieberman (2003) or from BSL on request.

The biogeographic analysis used a modified version of Brooks Parsimony Analysis that has been described in detail by Lieberman and Eldredge (1996), and Lieberman (1997, 2000). The method converts phylogenies of organisms, in conjunction with their geographic distributions, into two separate data matrices in order to reconstruct biogeographic patterns. One, the vicariance matrix is analyzed to retrieve repeated episodes of vicariance precipitated by geological processes that isolate formerly contiguous regions. Such processes include continental rifting and sea-level fall (in the case of trilobites). The other, the geo-dispersal matrix, can be analyzed to retrieve

episodes of congruent range expansion or geo-dispersal (Lieberman and Eldredge, 1996) precipitated by geological processes that join formerly separated regions (which in trilobites include continental collision and sea-level rise). The vicariance and geo-dispersal matrices generated from this analysis are available in Lieberman (2003) or from BSL on request.

The data matrices are analyzed using the parsimony algorithm PAUP 4.08b (Swofford, 2001), with results expressed as most parsimonious vicariance and geo-dispersal trees, with each tree rooted using an outgroup; the closer two regions sit on a tree, the more recently they shared a common history. For example, a close relationship on the vicariance tree implies that regions became separated relatively recently. Similarities between the vicariance and geo-dispersal tree indicate that sea-level rise and fall had an important influence on biogeographic patterns (Lieberman and Eldredge, 1996; Lieberman, 1997, 2000). By contrast, differences between the two trees suggest that such repeating processes had less of an affect on biogeographic patterns and instead suggest tectonic processes like continental rifting or collision may have had a more fundamental effect. Parsimony based analytical methods have been frequently and successfully applied to the analysis of palaeobiogeographic patterns (e.g. Fortey and Cocks, 1992; Lieberman and Eldredge, 1996; Lieberman, 1997; Waggoner, 1999). Such methods, when implemented using PAUP 4.08b (Swofford, 2001), can also be combined with jackknife, bootstrap, and Bremer branch support analyses (Bremer, 1994) to consider the degree of support for various parts of the biogeographic tree.

Further, tree length frequency distributions (Hillis, 1991) and cladistic permutation tail probabilities (Faith, 1991; Swofford et al., 1996) also can be generated to consider how strong the biogeographic signal is in the data.

Results

Palaeobiogeographic patterns

The analysis of the two data matrices using the exhaustive search option of PAUP 4.08b (Swofford, 2001) produced one most parsimonious vicariance tree (Fig. 4) and six most parsimonious geo-dispersal trees; the strict consensus of the geo-dispersal trees is poorly resolved and therefore is not shown. Tree length frequency distributions and cladistic permutation tail probabilities each suggest strong biogeographic signal in the vicariance matrix, with values differing from random data minimally at the 0.01 and 0.001 levels respectively (Lieberman, 2003). The general lack of resolution in the consensus geo-dispersal tree indicates that there were few congruent episodes of range expansion between different regions (either due to sea-level rise or continental collision) by the trilobites considered in this analysis. Further, the lack of similarity between the vicariance and consensus geo-dispersal trees suggests tectonic events, rather than repeated episodes of sea-level rise and fall, most profoundly structured biogeographic patterns in the trilobites studied.

There are three major biogeographic groupings: Australia and East Antarctica; Baltica, eastern and northwestern Laurentia; and Siberia, north Africa/Armorica, southwestern Laurentia, and Avalonia. The various parts of the vicariance tree are well supported based on a variety of tests

conducted using PAUP with the East Antarctica/Australia grouping being the least well supported (Lieberman, 2003). This, however, is because of the relatively limited number of basal redlichiine trilobites from these regions that were sampled in this analysis. Additional analyses based on trilobites (Palmer and Rowell, 1995) and also archaeocyathans (Debrenne and Kruse, 1986) strongly reinforce the biogeographic grouping between East Antarctica and Australia. This part of eastern Gondwana is thus resolved as a distinct biogeographic region. Western Gondwana and peri-western Gondwana also group together, along with Siberia and southwestern Laurentia. Laurentia itself is a polyphyletic biogeographic region, with parts of the craton possessing trilobite faunas sharing a closer biogeographic history with Baltica, and other parts sharing a closer biogeographic history with western Gondwana, peri-western Gondwana, and Siberia.

The notion that tectonic events are driving the palaeobiogeographic patterns is consistent with the palaeomagnetic observations described earlier. Despite the lack of consensus regarding the exact palaeogeography, all of the models indicate that the opening of the Iapetus Ocean was the major tectonic event in the latest Neoproterozoic. In fact, it was the ubiquitous presence of passive margin sequences worldwide that led to Bond et al.'s (1984) suggestion that the Neoproterozoic heralded the breakup of a supercontinent. Of secondary importance was the closure of the Mawson Sea during the final stages of Gondwana assembly.

Discussion

Palaeobiogeographic patterns and timing of divergence events

The vicariance tree indicates several vicariance events in early Cambrian trilobites, and there are three major palaeobiogeographic groupings: 1) eastern Gondwana; 2) Baltica, eastern, and northwestern Laurentia; and 3) Siberia, the northern margins of western Gondwana, and southwestern Laurentia. Early vicariance events separated these three regions and their trilobites from one another either all at once or in an order that cannot be resolved. Later, vicariance separated Australian and Antarctic trilobites, Baltic, eastern, and northwestern Laurentian trilobites, and Siberian, southwestern Laurentian, Avalonian, and north African/Armorican trilobites. The vicariant biogeographic patterns are well supported by a variety of tests described above (Lieberman, 2003) and seem resilient and potentially serve as a sound template to consider the relationship between geological changes and evolution. Further, each of the regions considered have trilobites from all of the major biostratigraphic intervals in the trilobitic part of the early Cambrian (see Lieberman, 1999, 2002, 2003), suggesting that simple sampling biases related to the available strata preserved are not a likely cause of the biogeographic patterns.

The patterns of vicariance between Laurentia, Siberia, and the northern margins of western Gondwana are compatible with a distribution of trilobites across an originally unified Laurentia, Siberia, western Gondwana, and peri-western Gondwana, comprising the core elements of Pannotia. These trilobite faunas would have subsequently differentiated via vicariance as Pannotia

broke apart. The absence of resolution in the geo-dispersal tree further suggests that trilobites likely did not disperse in significant numbers between the different parts of Pannotia (especially Laurentia and western Gondwana) after they became separated. As the breakup of Pannotia is constrained to 550-600 Ma, these palaeobiogeographic patterns suggest divergence events in trilobites occurred during the Neoproterozoic, preceding the Cambrian radiation by some substantial period of time.

These results match the conclusions of Fortey et al. (1996, 1997) who argued that biogeographic patterns in trilobites indicated a Neoproterozoic origin for the group and suggested that lineages within the Trilobita were actually diverging in the Neoproterozoic. Based on the phylogenetic position of trilobites as euarthropods (e.g. Briggs et al., 1992; Wills et al., 1998) this suggests that the Cambrian radiation was well underway in the late Neoproterozoic. It also suggests that early Cambrian trilobites are a potentially useful source of information regarding latest Neoproterozoic tectonic events.

Palaeogeography

There are three end-member tectonic models discussed in this paper. Our preferred high-latitude Laurentia option (Fig. 1a,b) has palaeomagnetic support from two studies in North America (Symons and Chiasson, 1991; Meert et al., 1994) and weaker support from a study of the Sept Îles Igneous Complex (Tanczyk et al., 1987). The model does require a relatively rapid transition (minimally ~ 11 cm/yr⁻¹) from a high-latitude Laurentia at ~ 565 Ma to a more equatorial position by Middle Cambrian time (~ 508 Ma, Tapeats sandstone). If

McCausland and Hodych's (1998) documentation of a low-latitude position for the Skinner Cove volcanics of western Newfoundland is correct and if this block was attached to eastern Laurentia (the relationship of this allochthonous block to the eastern Laurentian margin is contentious) then their pole, if representative of Laurentia, requires even higher drift rates (on the order of 35-50 cm yr⁻¹). The advantage, however, of our preferred high-latitude Laurentia option at 580 Ma is that it results in a favorable geometry for the final assembly of Gondwana and the closure of the Mawson Sea between Australo-Antarctica and the bulk of Gondwana (see figure 1b compared to figure 2b).

The low-latitude Laurentia option circumvents all issues related to rapid plate motions, but it precludes a reasonable alternative explanation for the high-latitude results from the Callander and Catocin studies (Pisarevsky et al., 2000; Meert and Van der Voo, 2002). The primary argument for the low-latitude option for Laurentia was to maintain a close relationship to Siberia required by the model of Pelechaty (1996). However, recent publications by Vernikovskiy and Vernikovskaya (2001) and Khain et al. (2003) suggest that Siberia likely rifted away from the arctic margin of Laurentia starting at around 800 Ma. Unfortunately, there are no palaeomagnetic data from Siberia to unambiguously document its relationship to Laurentia and geologic comparisons are equally contentious (Meert and Torsvik, in press). Therefore, our reconstruction between Siberia and Laurentia differs slightly from that advocated by Pisarevsky et al. (2000) in that we attempt to minimize

the offset between the present-day arctic margin of Laurentia and the Siberia. In essence, we attempt to harmonize the evidence for early (ca. 800 Ma) rifting with Pelechaty's (1996) and Pisarevsky et al.'s (2000) suggestion that Siberia and Laurentia were conjoined until ~550 Ma.

A number of recent studies have important implications for the possibility of a low-latitude supercontinent at 580 Ma. Popov et al. (2002) presented results from Upper Vendian sediments from the Winter Coast of Baltic Russia. Their palaeomagnetic pole, if correct, would place Baltica at low latitudes in an inverted position (see figure 2a). Popov et al. (2002) argued that the Fen Complex pole of Meert et al. (1998) is a Permian remagnetization. However, additional palaeomagnetic data from the Lower Cambrian Dividal Group (Torsvik and Rehnström, 2002 and Rehnström and Torsvik, 2003) along with preliminary data from the 590 Ma Alnö complex of Sweden (Walderhaug et al., 2003) lend further support to the primary nature of the Fen Complex pole. We also note that our palaeobiogeographic patterns, especially the close vicariance relationship between eastern Laurentian and Baltic trilobites, seem to argue strongly against these new palaeomagnetic data which place Baltica at low latitudes while Laurentia was located at high latitudes.

There are other problematic issues related to Pisarevsky et al.'s (2000) low-latitude position of Laurentia at 580 Ma. Most evidence suggests that the opening of the Iapetus Ocean between Laurentia and the South American blocks commenced post-580 Ma (Cawood et al., 2001). Furthermore, Fitzsimons (2000) and Boger et al. (2002) suggested that final Gondwana assembly took

place around 550 Ma via the collision of Australo-Antarctica with the remainder of Gondwana. Assuming that both scenarios are correct, a rigid palaeoreconstruction would result in significant overlap between Australo-Antarctica and western Gondwana. We note, however, that by taking into account the errors in palaeomagnetic data this misfit can be alleviated. Still, such a reconstruction would require placing East Antarctica near the tip of present-day southwestern Laurentia, an alignment at odds with this and other palaeobiogeographic studies and also several palaeomagnetic analyses (e.g. Torsvik et al., 1996; Cawood et al., 2001).

Kirschvink et al. (1997) attempted to reconcile the apparent rapid drift required by the high-latitude Laurentia model shown in Figure 1 by proposing an inertial interchange true polar wander (IITPW) event during the interval from 523-508 Ma. A variation of the IITPW model was proposed by Evans (2003). The model was presented without any detailed palaeogeography, but does posit a series of Neoproterozoic-early Palaeozoic true polar wander episodes including at least one inertial interchange event. The IITPW model is somewhat more rigid than the two preceding tectonic models in that the relative palaeolongitudes shown in these figures also need to be fixed; this is unlike conventional early Palaeozoic and Precambrian palaeomagnetically based reconstructions. Assuming the Kirschvink et al. (1997) model, Figure 3a represents the configuration of the continents prior to the IITPW event. Although Kirschvink et al. (1997) claimed that this represented their 540 Ma reconstruction, in fact it was based partly on 575-565 Ma palaeomagnetic

data from Laurentia and Baltica; this explains the similarities of Figure 3 to the reconstruction in Figure 1. The main difference between Kirschvink et al.'s (1997) pre-IITPW model and the one shown in Figure 1 is that in the former Baltica is placed in the northern hemisphere (by inverting the polarity of the palaeomagnetic pole) and Siberia is also placed well away from both present-day northern Africa and the arctic margin of Laurentia. The model thus requires a wide Iapetus ocean between Laurentia and Baltica prior to the Fen complex pole at 580 Ma (Meert et al., 1998). The pre- and post-IITPW (earliest Middle Cambrian, ~510 Ma) palaeogeographies show significant differences (Figs. 3 and 5). Kirschvink et al. (1997) shows an overlap between Laurentia and Gondwana which Kirschvink et al. (1997) attributed to an incomplete dataset. The overlap, however, between the two continents is severe and would require more than 40 degrees of latitudinal displacement between western Gondwana and eastern Laurentia in order to generate an Iapetus ocean consistent with geologic data (Cawood et al., 2001). In addition, Baltica is displaced significantly from Avalonia compared to conventional views of Cambrian palaeogeography (see Cocks and Torsvik, 2002).

Our preferred palaeogeographies at 540 and 510 Ma based on palaeomagnetic data are shown in Figures 6 and 7. Figure 6 is also based on data from Torsvik and Rehnström (2001) and Cawood et al. (2001), and the Iapetus Ocean is near its maximum width while the Ægir Sea separates Baltica from Siberia. Our reconstruction at 510 Ma (Fig. 7) avoids the problems of continental overlap that Kirschvink et al. (1997) suffers from, and is in fact rather

similar to those palaeogeographies advocated by Cocks and Torsvik (2002) and Torsvik and Rehnström (2001), each of whom suggested an Iapetus Ocean of moderate width.

Relationship of palaeobiogeographic patterns to palaeogeographic and tectonic models

In several respects the recovered palaeobiogeographic patterns match results from previous studies of early Cambrian palaeobiogeography. For instance, the close palaeobiogeographic relationship between Siberia and north Africa/Armorica matches a pattern found by Lieberman (1997). In addition, the relatively close relationship between Avalonia and north Africa/Armorica was also found in studies of early Cambrian trilobites conducted by Burrett and Richardson (1980) and Fortey and Cocks (1992). Burrett and Richardson (1980), Palmer and Rowell (1995), and Debrenne and Kruse (1986) also found a close palaeobiogeographic relationship between Antarctica and Australia. Finally, Fortey and Cocks (1992) identified a close palaeobiogeographic relationship between Baltica and eastern Laurentia, a result reiterated by this analysis. The polyphyly of Laurentia in Figure 4 differs from some previous palaeobiogeographic studies (e.g. Burrett and Richardson, 1980; Fortey and Cocks, 1992; Lieberman, 1997). Part of the differences between this aspect of the results from Burrett and Richardson (1980), Lieberman (1997), and the current study may be attributable to the fact that those studies focused on a more restricted and later part of the early Cambrian. The difference between the position of Laurentia in this study and in Fortey and Cocks (1992) and again

Burrett and Richardson (1980) may be because those authors could not incorporate phylogenetic information into their palaeobiogeographic analyses. Notably, however, the polyphyly of Laurentia recovered herein agrees with some aspects of Waggoner's (1999) analysis of Vendian Ediacaran palaeobiogeography. For example, Waggoner (1999) also found that southwestern Laurentian faunas grouped with those from western Gondwana while northwestern Laurentian faunas grouped with Baltic faunas.

The biogeographic patterns resulting from analyses of the trilobites can be compared instructively to the three models of late Neoproterozoic and Early Cambrian tectonics and palaeogeography already described: for example, Kirschvink et al.'s (1997) hypothesized IITPW event. Based on their reconstructions, one might predict to find close palaeobiogeographic relationships between Baltic faunas and Siberian faunas and also potentially between Baltic faunas and Avalonian and north African/Armorican faunas. This is because all of these regions, but especially Baltica and Siberia, lie near one another both before and after Kirschvink et al.'s (1997) inferred IITPW event. None of these predicted relationships, however, was retrieved by the palaeobiogeographic analysis (Fig. 4).

Further, there are other aspects of the resulting palaeobiogeographic patterns that are counter what might be predicted if Kirschvink et al.'s (1997) version of true polar wander had occurred. This is because each of those studies predicted rapid movements of cratons and thus faunas; in accord with this one might predict palaeobiogeographic patterns among most cratons should show little or

no resolution. Instead this is manifestly not the case (see Fig. 4) as palaeobiogeographic patterns of vicariance are well resolved and also strongly supported. It is of course still conceivable that IITPW did occur, but if so it must have happened before, or after, the evolutionary and palaeobiogeographic patterns in the trilobites were produced. This minimally constricts the timing of any IITPW event and also constrains the validity of the hypothesis as a general driver and pacemaker of the Cambrian radiation (contra the arguments in Kirschvink et al., 1997), since trilobites are a key component of the Cambrian radiation fauna and appear to be unaffected, at least in a palaeobiogeographically informative manner, by such hypothesized changes. This information, in conjunction with the results from palaeomagnetism already described, casts further doubt on the validity of inferred early Cambrian or late Neoproterozoic IITPW events.

The palaeobiogeographic patterns derived from the trilobites also potentially conflict with the palaeogeographic model proposed by Pisarevsky et al. (2001) which has Laurentia in a low-latitude position (Fig. 2a,b). For example, Pisarevsky et al.'s (2001) model would predict a much closer association between Baltic faunas and faunas from Avalonia and north Africa/Armorica than the pattern actually recovered (see Fig. 4). Further, Pisarevsky et al.'s (2001) model would also predict a closer association between Siberian faunas and faunas from eastern and northwestern Laurentia, and again such a palaeobiogeographic relationship was not recovered (see Fig. 4).

Overall the results from the palaeobiogeographic analysis (Fig. 4)

accord well with our preferred palaeogeographies resulting from analysis of the palaeomagnetic data set (Figs. 1, 6, 7) such that there is a strong degree of congruence between the two data sets. For example, each analysis recognizes a close association between most of East Antarctica and Australia and these cratons likely had a common history through the Neoproterozoic and early Cambrian. Further, Baltica lies near parts of Laurentia, especially eastern Laurentia, throughout the Neoproterozoic and into the early Cambrian. The close relationship posited in the palaeobiogeographic analysis between Avalonia and north Africa/Armorica also finds support from the palaeomagnetic dataset as these regions are near one another in the late Neoproterozoic and early Cambrian. The palaeobiogeographic data also agree with aspects of the position of Siberia especially in the close palaeobiogeographic relationship between Siberia, north Africa/Armorica, and Avalonia. For this reason, we suggest that the high-latitude Laurentia model for late Neoproterozoic palaeogeography (Fig. 1) and the model for early Cambrian palaeogeography with the opening of the Iapetus Ocean between present-day eastern Laurentia and western Gondwana taking place around 540 Ma (Figs. 6 and 7) are best supported by the available palaeobiogeographic and palaeomagnetic data.

There is, however, some disagreement between the palaeobiogeographic results and the palaeomagnetic results, and this involves the grouping of southwestern Laurentian faunas with faunas from Avalonia, north Africa/Armorica, and Siberia. This is because the palaeogeographic geometry predicted by

palaeomagnetic studies should have led to a clustering of southwestern Laurentian faunas with the rest of Laurentia instead of, or more closely than, parts of western Gondwana and Siberia. The results from the palaeobiogeography and palaeoreconstructions could be compatible though if Amazonia served as a faunal link or bridge between southwestern Laurentia and other parts of western Gondwana. Unfortunately, age appropriate deposits in Amazonia are not available to test this in greater detail. Another solution that would make the one potential divergence between the palaeobiogeographic and palaeomagnetic results more compatible would be to rotate Laurentia and Baltica approximately 20 degrees counterclockwise. This, however, is currently not permissible with the available palaeomagnetic data. It is noteworthy that the palaeogeographies from both the IITPW and low-latitude Laurentia models do not provide a better fit for this aspect of our palaeobiogeographic patterns. To address the potential source of disagreement between our palaeobiogeographic and palaeomagnetic data sets, at this time we suggest the need for more extensive faunal and palaeomagnetic sampling, especially in Siberia, north Africa, Avalonia, and parts of southwestern Laurentia that have not been intensively sampled, for example, the Caborca region of Mexico.

Conclusions

Three end-member palaeogeographic models derived from palaeomagnetism are evaluated and compared with results from a phylogenetic biogeographic analysis of early Cambrian trilobites. In general, the palaeobiogeographic

patterns match palaeomagnetically derived models where Laurentia is situated at high southerly palaeolatitudes during the latest Neoproterozoic (ca. 580 Ma) and the opening of the Iapetus Ocean between present-day eastern Laurentia and western Gondwana takes place around 540 Ma. Other models, e.g. the low-latitude Laurentia and IITPW models show varying degrees of misfit with respect to patterns of trilobite vicariance. The low-latitude Laurentia and IITPW models also require some complex tectonic gyrations and the latter posits significant degrees of continental overlap. The palaeobiogeographic position of southwestern Laurentia is problematic for all the models presented here suggesting that additional palaeomagnetic and faunal sampling from this region may perhaps be worthwhile.

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Appendix: Euler Rotations for Reconstructions

Continent/Craton	Euler Latitude	Euler Longitude	Angle	Pole Used/Rotation ¹	Reference
Figure 1-580 Ma					
Laurentia	0	215	-135	<i>Callander, Catoclin-A</i>	Symons & Chiasson, 1991; Meert et al., 1994
Antarctica	27.98	98.35	+85.98	Australia	This study
Australia	46.99	115	+76.6	<i>Elatina-Yaltipena & Arumbera</i>	Sohl et al., 2000; Kirschvink, 1978
Arabian-Nubian	45.8	107.7	+108.4	Africa- Laurentia	This study
Armorica	23.6	109.2	+147.2	Africa-Laurentia	This study
Avalonia	25.3	96.7	+123.9	Africa-Laurentia	This study
Amazonia	37.3	60.5	+127.4	Africa-Laurentia	This study
Rio Plata	37.3	60.5	+127.4	Africa-Laurentia	This study
Sao Francisco	37.3	60.5	+127.4	Africa-Laurentia	This study
Congo	43.1	103	+111.3	Laurentia	This study
Kalahari	43.1	103	+111.3	Laurentia	This study
West Africa	43.1	103	+111.3	Laurentia	This study
India	63.9	162	+80.6	Africa-Laurentia	This study
Sri Lanka	70.7	224.3	+78.1	Africa-Laurentia	This study
Madagascar	48.3	93.5	+96.8	Africa-Laurentia	This study
Baltica	16.45	345	-171	<i>Fen Complex</i>	Meert et al., 1998
Siberia	43.5	323.2	+144.4	Baltica	This study
Figure 2- 580 Ma					
Laurentia	0	78	+81	<i>Average pole given in reference</i>	Pisarevsky et al., 2000
Antarctica	17.3	88.3	+78.2	Australia	This study
Australia	36.2	105	+63.2	<i>Elatina-Yaltipena & Arumbera</i>	Sohl et al., 2000; Kirschvink, 1978
Arabian-Nubian	21.1	143.9	+158.2	Africa- Laurentia	This study
Armorica	17.6	139.3	+159.4	Africa-Laurentia	This study
Avalonia	4.5	314.6	-145.1	Africa-Laurentia	This study
Amazonia	19.6	111.3	+134.8	Africa-Laurentia	This study
Rio Plata	19.6	111.3	+134.8	Africa-Laurentia	This study
Sao Francisco	19.6	111.3	+134.8	Africa-Laurentia	This study
Congo	18.7	141	+156.1	Laurentia	This study
Kalahari	18.7	141	+156.1	Laurentia	This study
West Africa	18.7	141	+156.1	Laurentia	This study
India	37.2	166.1	+161.9	Africa-Laurentia	This study
Madagascar	17.8	140.5	+142.4	Africa-Laurentia	This study
Baltica-1	14.7	0	-162.8	<i>Fen Complex pole</i>	Meert et al., 1998

Continent/Craton	Euler Latitude	Euler Longitude	Angle	Pole Used/Rotation ¹	Reference
Baltica-2	13.1	63.0	118.9	<i>White Sea Vendian</i>	Popov et al., 2002
Siberia	-4.6	246	-95.8	<i>Cisbaikalia</i> and Interpolation	Pisarevsky et al., 2000; this study
Figure 3-IITPW					
Laurentia	14.3	172	-146.5	<i>Callander Complex pole</i>	Symons and Chiasson, 1991
Baltica	47	220.9	-50.8	<i>Fen Complex pole</i>	Meert et al., 1998
Siberia	20.1	3.9	+117.3	<i>Pestrotsvet pole</i>	Kirschvink and Rozanov, 1984
Gondwana	10.2	241.1	-74.4	<i>Arumbera Sandstone-Africa</i>	Kirschvink, 1978
Avalonia	12.5	232.7	-111.5	Africa	This study fit to Africa
Armorica	6.8	240.2	-77	Africa	This study fit to Africa
Figure 5-540 Ma					
Laurentia	36.7	182.5	-148.4	Cubic spline fit	Torsvik et al., 1996
Baltica	16.6	308.5	-172.7	<i>Tornetrask Fm</i>	Torsvik & Rehnström, 2001
Gondwana	0	62.9	+72	Mean APWP	Meert, 2003
Avalonia	7.6	233.8	-109.6	Africa	This study
Armorica	3.11	62.3	+75.2	Africa	This study
Siberia	10.6	232.4	-132.2	<i>Kessyusa</i>	Pisarevsky et al., 1997
Figure 6-IITPW					
Laurentia	24.9	92.9	+96.4	<i>Tapeats sandstone</i>	Elston and Bressler, 1977
Gondwana	15	171.2	+148.5	<i>Black Mountain</i>	Ripperdan and Kirschvink, 1992
Baltica	20.1	183	+132.9	<i>Swedish Limestones</i>	Torsvik et al., 1992
Siberia	24.2	112	+156.8	<i>Moyero River</i>	Gallet and Pavlov, 1996
Avalonia	0.4	344	-125.3	Africa	This study fit to Africa
Armorica	13.7	169	+150	Africa	This study fit to Africa
Figure 7-510 Ma					
Laurentia	27.7	224	-102.2	<i>Tapeats sandstone</i>	Elston & Bressler, 1977
Gondwana	0	270	-103	Mean APWP	Meert, 2003
Baltica	16.6	321	-161.3	<i>Alum Shale-Tornetrask</i>	Torsvik & Rehnström, 2001
Siberia	0	229.6	-126.0	<i>Yunkyulyabit-Yuryakh</i>	Pisarevsky et al., 1997
Avalonia	15.2	255.5	-133.3	Africa	This study fit to Africa
Armorica	1.4	88.3	+106.6	Africa	This study fit to Africa

¹Rotations are done in the sequence indicated. For example Africa-Laurentia means that the cratons/continents were first rotated to African coordinates and then to the Laurentia reconstruction. (-) rotations are clockwise (+) rotations are anti-clockwise. If a specific pole was used for the fit, the pole is listed in italics. The age range of the poles is within error of the time frame presented in the reconstructions.

Figure Legends

Figure 1: Our preferred palaeogeography at 580 Ma assuming the high-latitude Laurentia option, which places the present-day eastern margin of Laurentia at the south pole adjacent to the Amazonian and Rio Plata cratons at 580 Ma. A) Baltica has rifted from NE-Laurentia opening the Iapetus Ocean. Siberia is positioned according to the suggestion in Hartz and Torsvik (2002). (b) Figure 1a is rotated to show the final stages of Gondwana assembly and closure of the Mawson Sea between Australo-Antarctica and the rest of Gondwana. **T** marks the approximate location of trilobite taxa used in this analysis, with several localities typically grouped together. Abbreviations are as follows: Siberia (SIB), Baltica (Bal), Avalonia (AVA), Armorica (ARM), West Africa (WAF), Sao Francisco (SAO), Rio Plata (RIO), Kalahari (KAL), Congo (CON), Antarctica (ANT), Laurentia (LAU); Arabia (Ara), India (IND), Australia (AUS), Amazonia (AMA).

Figure 2: An alternative palaeogeography at 580 Ma assuming the low-latitude Laurentia model of Pisarevsky et al. (2000). A) This reconstruction maintains the relationship of the South American cratons with eastern Laurentia and places Siberia rifted from the present-day arctic margin of Laurentia. Baltica shown in two possible orientations according to either Meert et al. (1998, shaded) or Popov et al., 2002 (unshaded) (b) Figure 2a is rotated to highlight the relationship of Australo-Antarctica to the rest of Gondwana (see also Meert and Van der Voo, 2002). **T** marks the approximate location of trilobite taxa used in this analysis, with several localities typically grouped together. Abbreviations are as follows: Siberia (SIB), Baltica (Bal), Avalonia (AVA), Armorica (ARM), West Africa (WAF), Sao Francisco (SAO), Rio Plata (RIO), Kalahari (KAL), Congo (CON), Antarctica (ANT), Laurentia (LAU); Arabia (Ara), India (IND), Australia (AUS), Amazonia (AMA).

Figure 3: (a) The pre-IITPW reconstruction at 540 Ma according to the model of Kirschvink et al. (1997). (b) Figure 3a is rotated to show the remainder of Gondwana in the pre-IITPW reconstruction. **T** marks the approximate location of trilobite taxa used in this analysis, with several localities typically grouped together. Abbreviations are as follows: Siberia (SIB), Baltica (Bal), Avalonia (AVA), Armorica (ARM), West Africa (WAF), Sao Francisco (SAO), Rio Plata (RIO), Kalahari (KAL), Congo (CON), Antarctica (ANT), Laurentia (LAU); Arabia (Ara), India (IND), Australia (AUS), Amazonia (AMA).

Figure 4: The most parsimonious vicariance tree showing palaeobiogeographic patterns in Early Cambrian olenellid trilobites. The tree shows the relative time that regions become isolated from one another due to the emergence of geographic barriers. The closer two regions sit on the tree, the more recently the geographic barriers emerged between those regions, isolating their respective trilobite faunas. The tree is rooted using an outgroup.

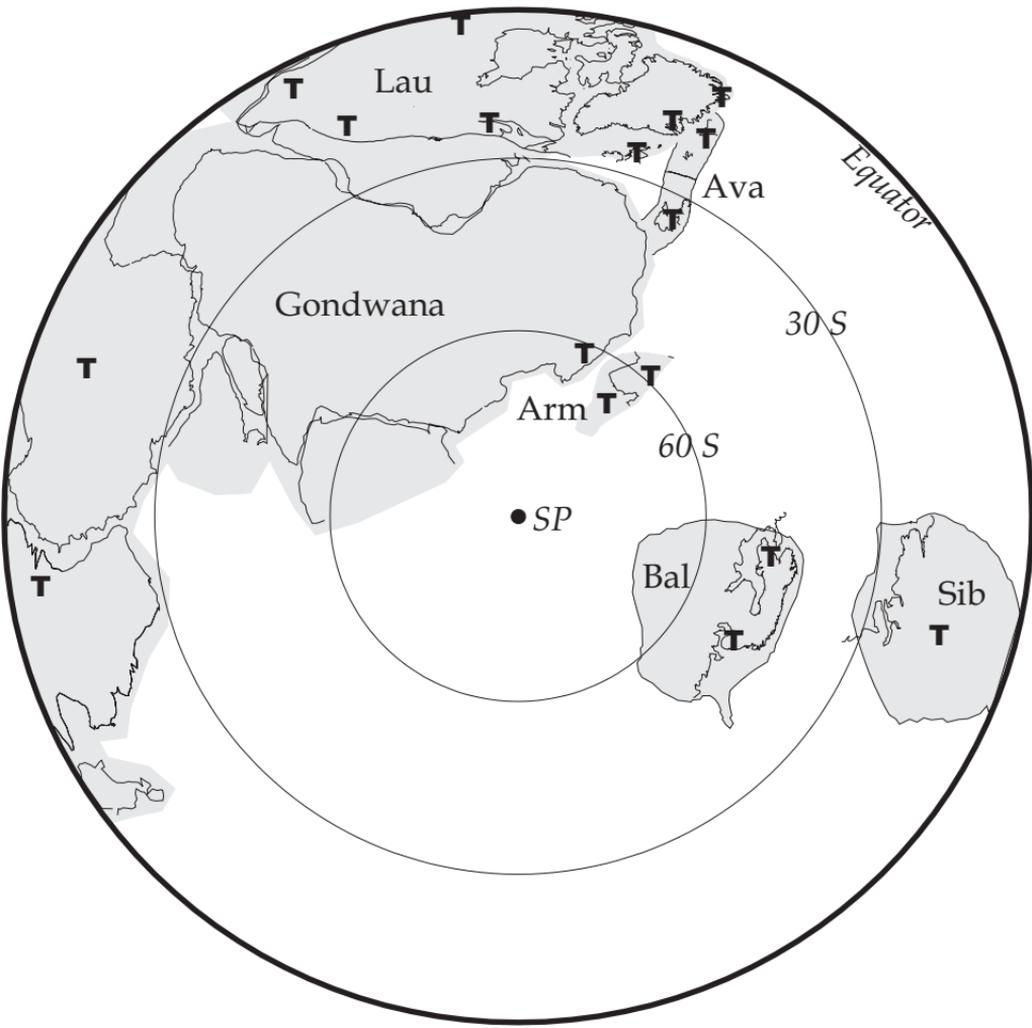
Figure 5: (a) Our preferred palaeogeographic reconstruction at 540 Ma (after Torsvik and Rehnström, 2001 and Torsvik et al., 1996) showing the opening of the Iapetus ocean

between a fully united Gondwana and Laurentia. (b) Figure 4a rotated to show the rest of Gondwana. **T** marks the approximate location of trilobite taxa used in this analysis, with several localities typically grouped together. Abbreviations are as follows: Siberia (SIB), Baltica (BAL), Avalonia (AVA), Armorica (ARM), Laurentia (LAU).

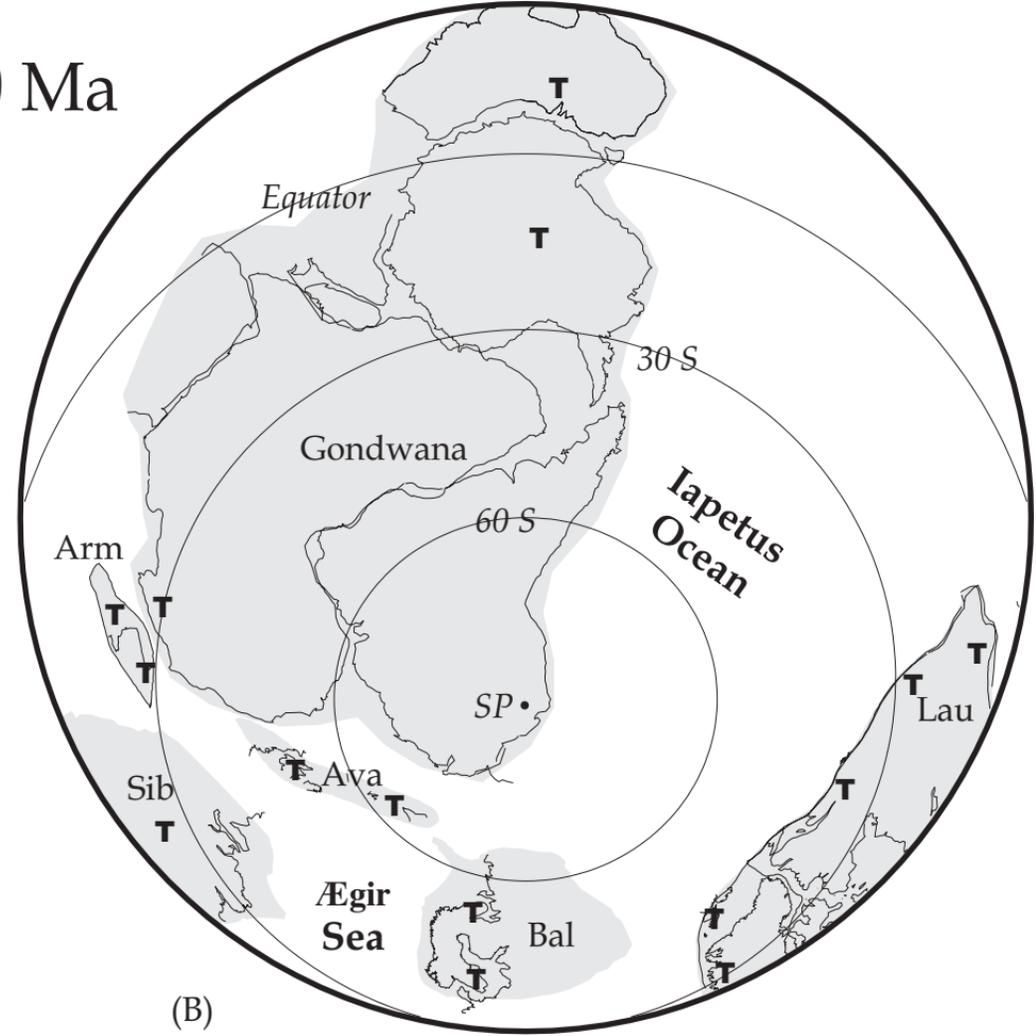
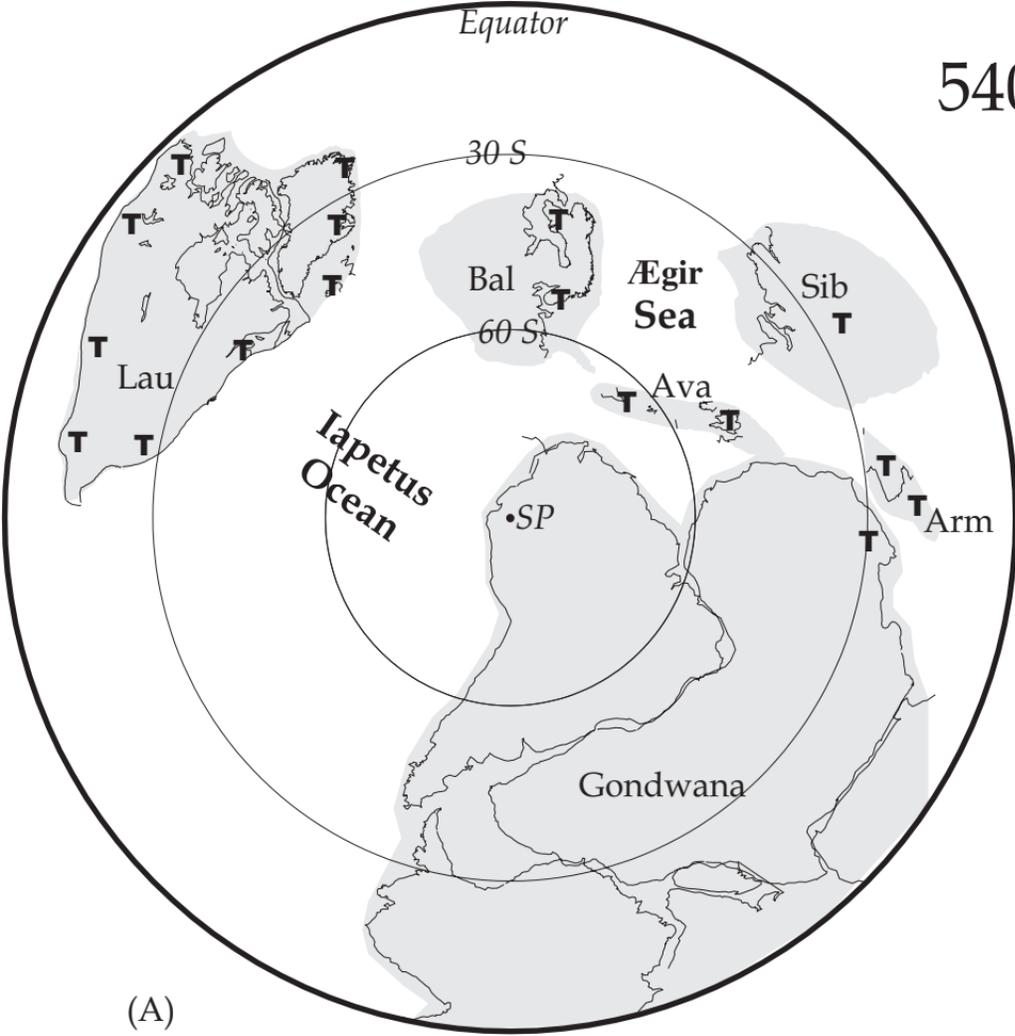
Figure 6: Post-IITPW reconstruction for 510-505 Ma based on the analysis of Kirschvink et al. (1997). **T** marks the approximate location of trilobite taxa used in this analysis, with several localities typically grouped together. Abbreviations are as follows: Siberia (SIB), Baltica (BAL), Avalonia (AVA), Armorica (ARM), Laurentia (LAU).

Figure 7: Our preferred 510 Ma reconstruction. **T** marks the approximate location of trilobite taxa used in this analysis, with several localities typically grouped together. Abbreviations are as follows: Siberia (SIB), Baltica (BAL), Avalonia (AVA), Armorica (ARM), Laurentia (LAU).

Post-IITPW (510 Ma)

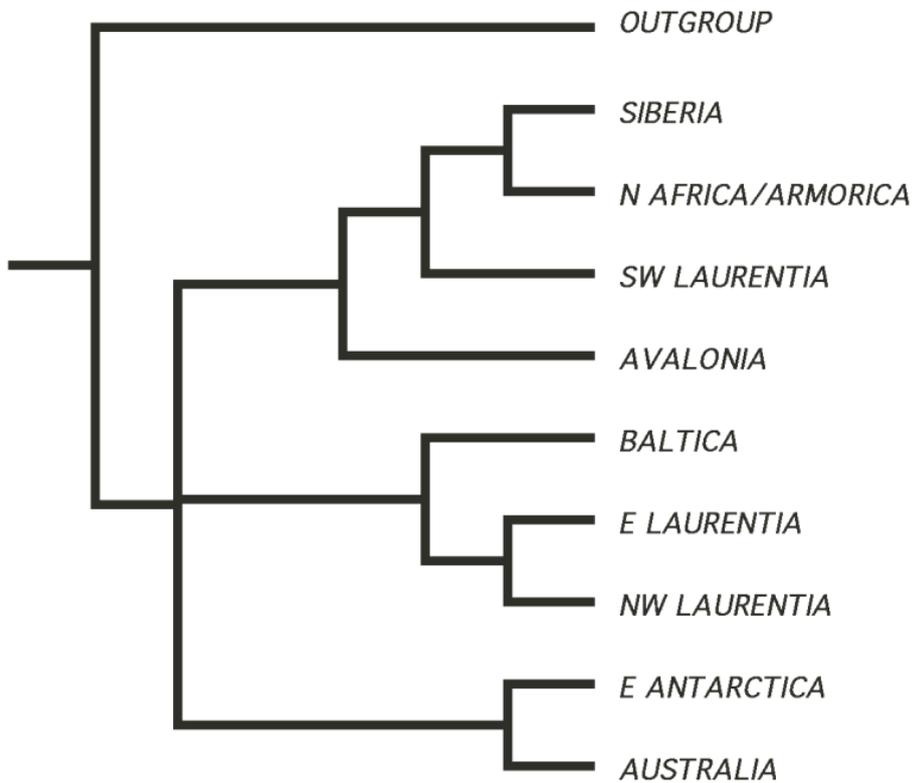


540 Ma

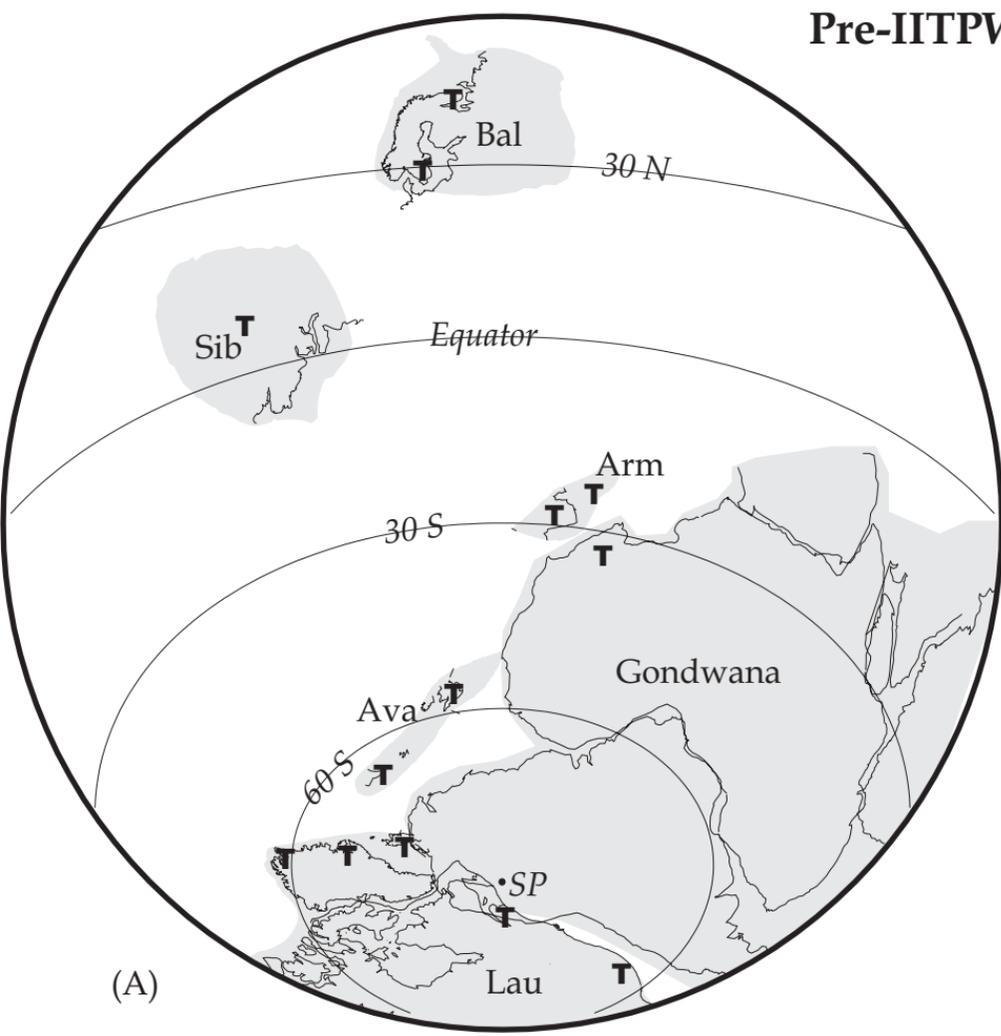


(A)

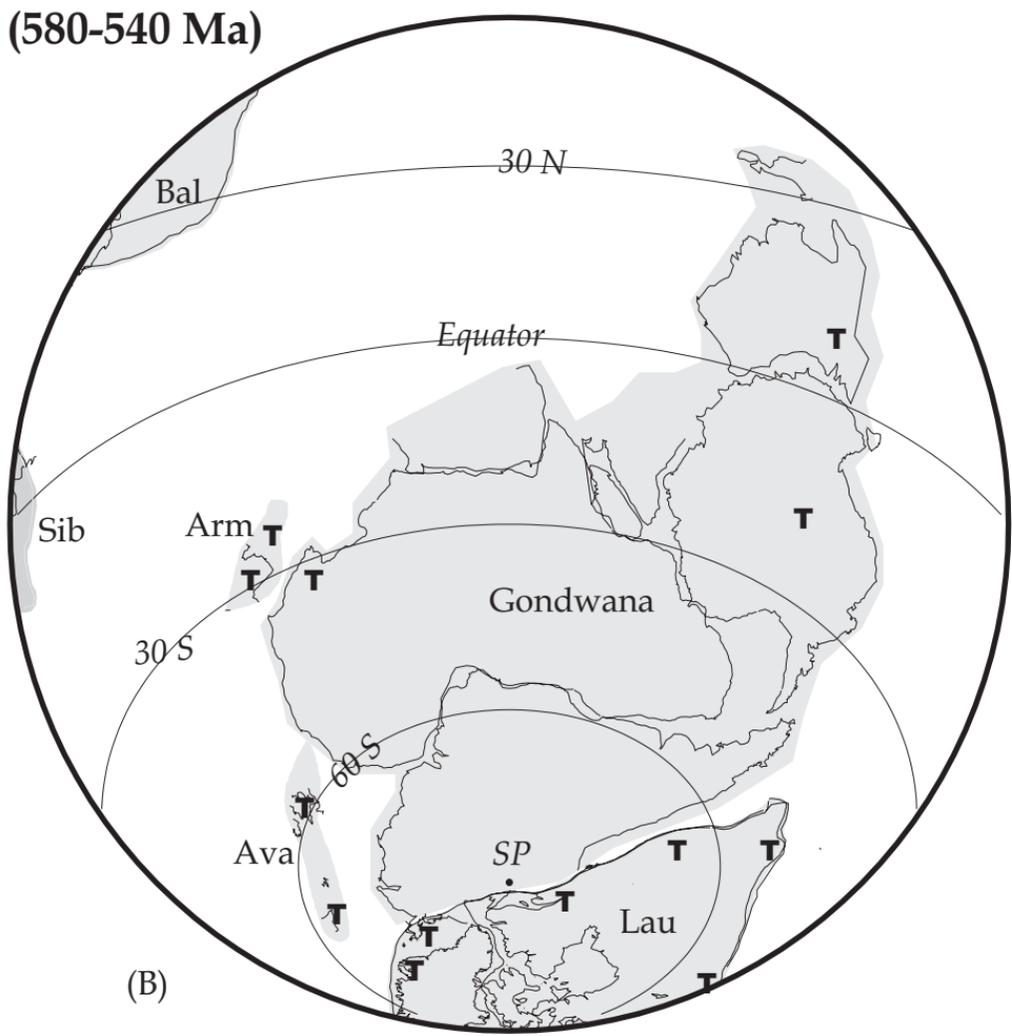
(B)



Pre-IITPW (580-540 Ma)

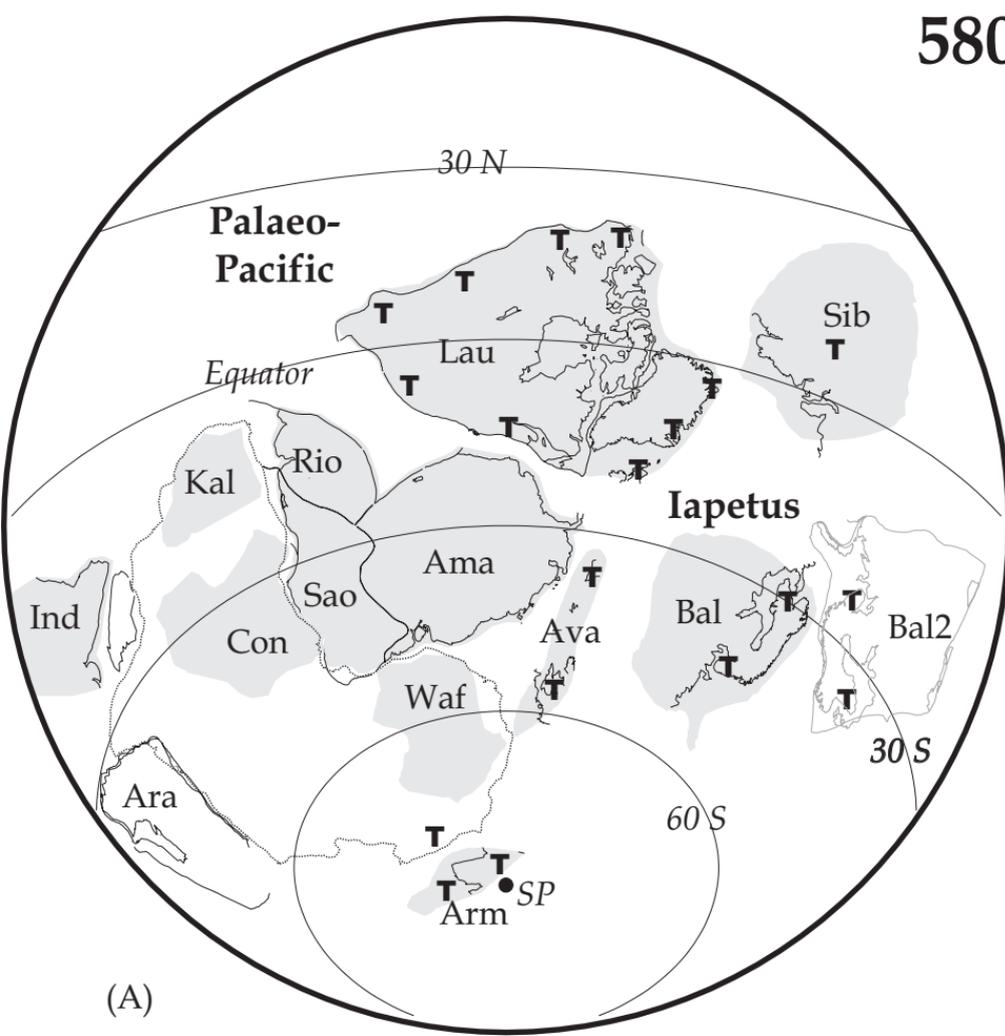


(A)

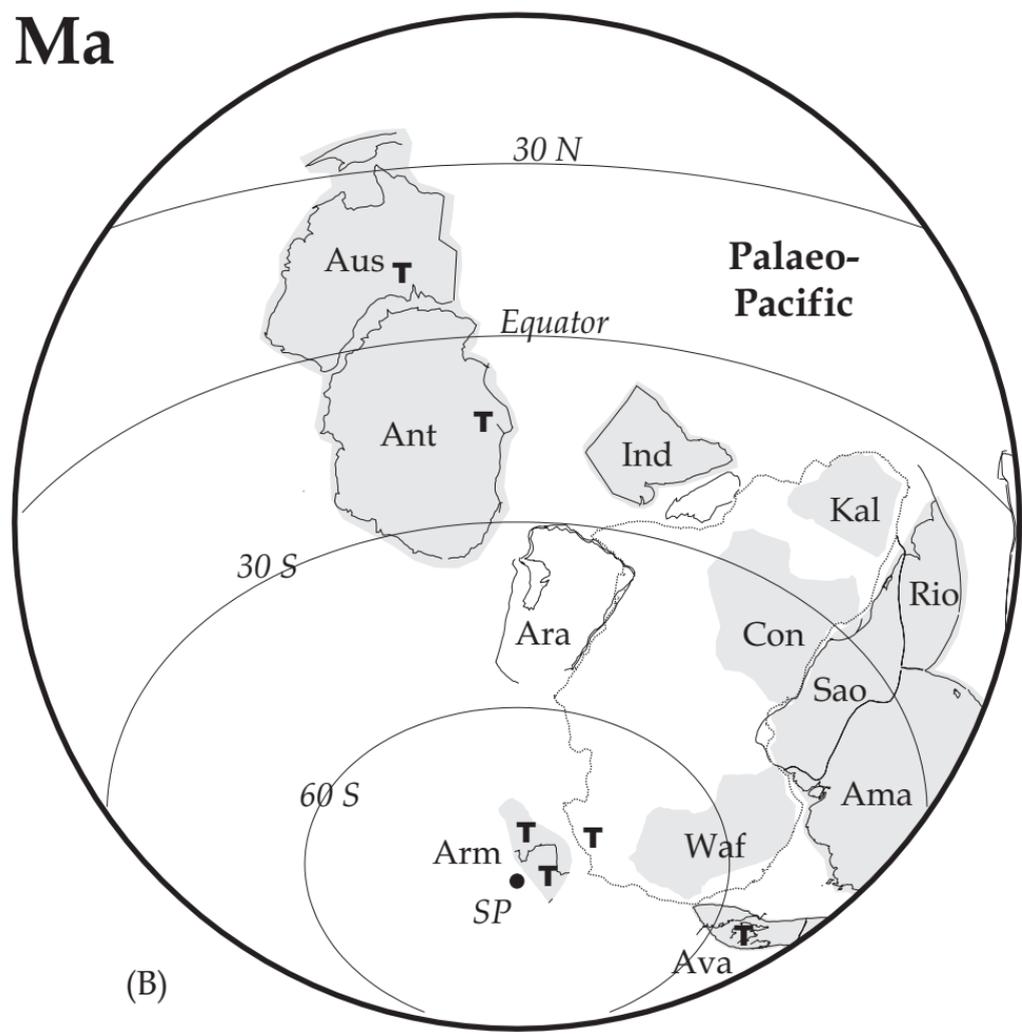


(B)

580 Ma



(A)



(B)

510 Ma

