

## A palaeomagnetic and palaeobiogeographical perspective on latest Neoproterozoic and early Cambrian tectonic events

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**Abstract:** During the latest Neoproterozoic to Mid-Cambrian time (580–505 Ma 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. Although 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. Palaeogeographical models based on palaeomagnetic data range from a high-latitude configuration for most continents, to a low-latitude configuration for most continents, or to rapid oscillations in continental configurations triggered by inertial changes within the planet. Palaeobiogeographical data can also be used to help constrain palaeogeographical models. To this end we use vicariance patterns in olenellid trilobites to determine their compatibility with three end-member palaeogeographical models derived from palaeomagnetic data for the Neoproterozoic and early Cambrian. The most congruent palaeogeographical model with respect to the palaeobiogeographical 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 palaeogeographical models also differ from the results from palaeobiogeography, but this may partly arise because of a lack of palaeomagnetic and palaeobiogeographical data from many parts of present-day South America and Africa.

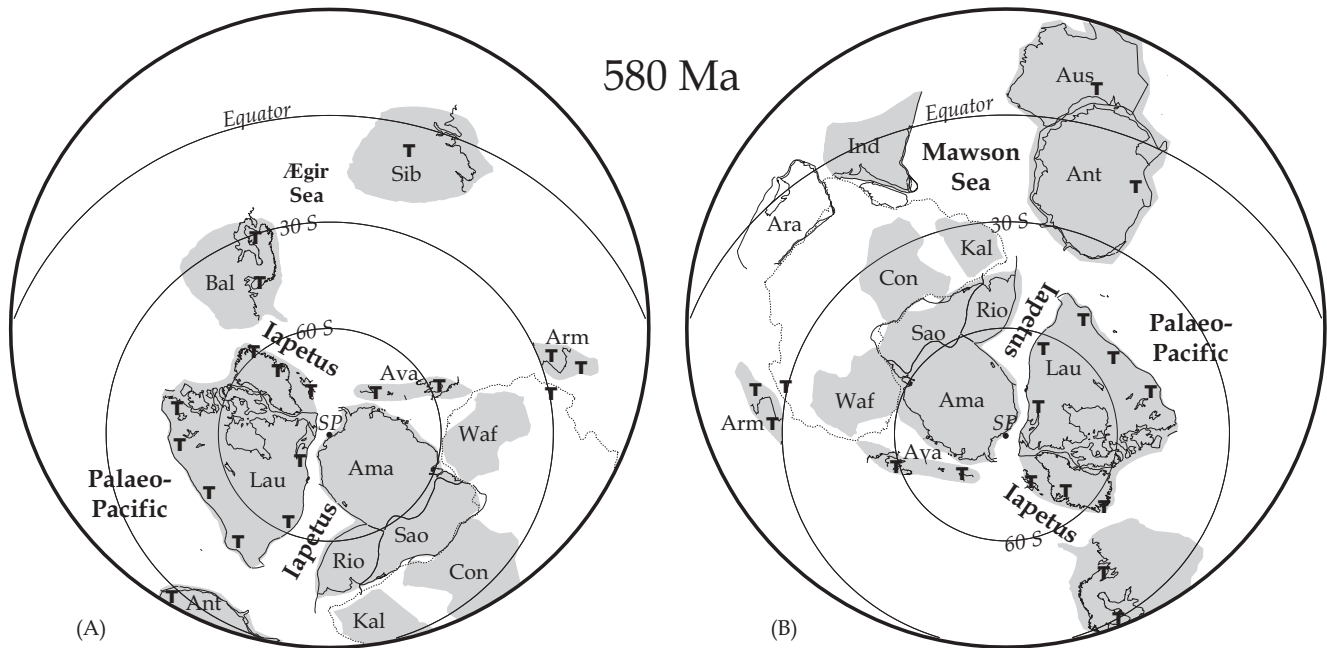
**Keywords:** Cambrian, Neoproterozoic, polar wandering, biogeography, trilobites.

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 & Chiasson 1991; Meert *et al.* 1994; Powell 1995; Torsvik *et al.* 1996, 1998; Kirschvink *et al.* 1997; Evans 1998, 2003; Meert 1999; Pisarevsky *et al.* 2000; Meert & Van der Voo 2001). These models can be broadly classified into three end-member reconstructions. Symons & Chiasson (1991) advocated a south polar position for Laurentia at *c.* 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 and 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 *c.* 575 Ma requires a rapid transition to lower latitudes by Mid-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 and 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 1998, 2003). In this group of models, the continents rotate through as much as 90° in as few as 15 Ma as a result of multiple episodes of true polar wander (Fig. 3a and b). Each model is particularly sensitive to the palaeomagnetic data and

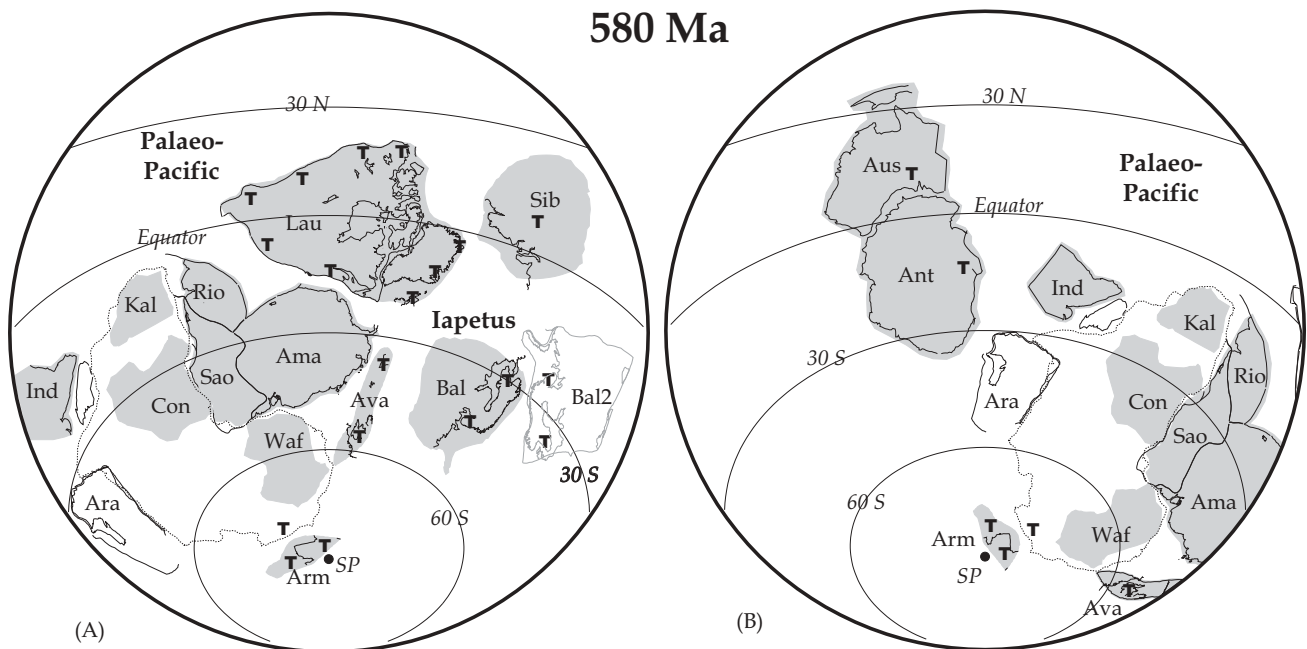
how these are selected; therefore, a test of the models that is independent of palaeomagnetic data is highly desirable. For this reason we incorporate both palaeomagnetic and palaeobiogeographical data in our analysis.

There is a long tradition of using the analysis of palaeobiogeographical data to reconstruct the geometries of continents and their changing positions through time (e.g. Williams 1973; Burrett & Richardson 1980; Cocks & Fortey 1982; Hallam 1983; Cocks & Scotese 1991; Fortey & Cocks 1992; Lieberman & Eldredge 1996; Rushton & Hughes 1996; Lees *et al.* 2002). Such an approach has also been used recently in a study by Cocks & Torsvik (2002) that combined palaeobiogeographical and palaeomagnetic databases to consider Ordovician tectonics (also see McKerrow *et al.* (1992) and Harper *et al.* (1996), other studies that have combined palaeobiogeographical and palaeomagnetic datasets). Here we use palaeobiogeographical 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 occurred 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 Meert *et al.* 1998; Torsvik & Rehnström 2001), and



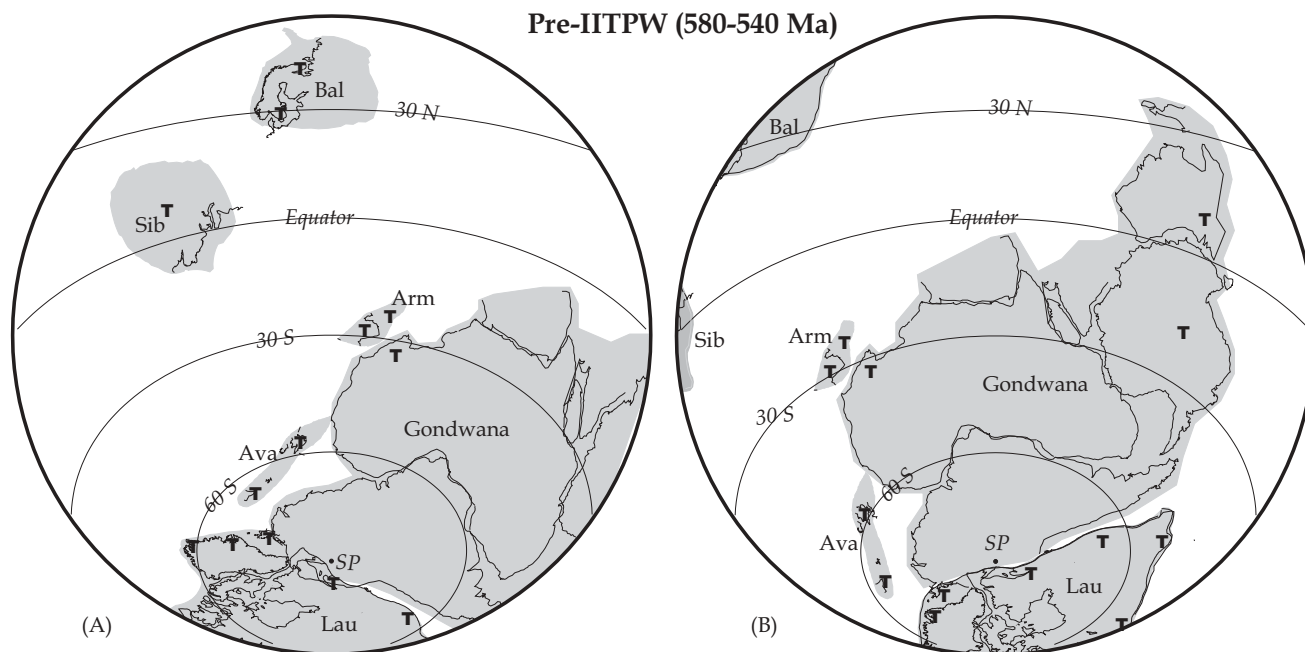
**Fig. 1.** Our preferred palaeogeography at 580 Ma assuming the high-latitude Laurentia option, which places the present-day eastern margin of Laurentia at the south pole adjacent to the Amazonian and Rio Plata cratons at 580 Ma. (a) Baltica has rifted from NE Laurentia, opening the Iapetus Ocean. Siberia is positioned according to the suggestion by Hartz & Torsvik (2002). (b) rotation of (a) to show the final stages of Gondwana assembly and closure of the Mawson Sea between Australo-Antarctica and the rest of Gondwana. T, approximate location of trilobite taxa used in this analysis, with several localities typically grouped together. Sib, Siberia; Bal, Baltica; Ava, Avalonia; Arm, Armorica; Waf, West Africa; Sao, São Francisco; Rio, Rio Plata; Kal, Kalahari; Con, Congo; Ant, Antarctica; Lau, Laurentia; Ara, Arabia; Ind, India; Aus, Australia; Ama, Amazonia.



**Fig. 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 is shown in two possible orientations according to either Meert *et al.* (1998, shaded) or Popov *et al.* (2002, unshaded). (b) rotation of (a) to highlight the relationship of Australo-Antarctica to the rest of Gondwana (see also Meert & Van der Voo 2001). Abbreviations as in Figure 1.

the southern Iapetus Ocean between Laurentia and several parts of present-day South America opened around 550 Ma (Cawood *et al.* 2001). Rift events along the present-day western margin of Laurentia at *c.* 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 Neoproter-



**Fig. 3.** (a) The pre-IITPW reconstruction at 540 Ma according to the model of Kirschvink *et al.* (1997). (b) rotation of (a) to show the remainder of Gondwana in the pre-IITPW reconstruction. Abbreviations as in Figure 1.

ozoic–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 & Van der Voo 1997; Meert *et al.* 1998; 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 under way in the Neoproterozoic, significantly before the Early Cambrian (Briggs & Fortey 1989; Briggs *et al.* 1992; Conway Morris 1993, 2000; Davidson *et al.* 1995; Fortey *et al.* 1996, 1997; Bromham *et al.* 1998; Xiao *et al.* 1998; Budd & Jensen 2000); current debate centres 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 & 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 such as 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 above. These palaeogeographies are based primarily on palaeomagnetic data, but geological 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), Meert & Van der Voo (2001) and Torsvik & Rehnström (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).

### *Palaeobiogeographical analysis*

To use fossils to aid in palaeogeographical reconstructions we follow the principles described by McKerrow & Cocks (1986), Lieberman (2000) and Cocks & Torsvik (2002). Further, we use phylogenetic relationships and phylogenetic biogeographical methods to analyse the palaeobiogeographical data, following the approaches of Young (1990), Fortey & Cocks (1992), Lieberman & Eldredge (1996) and Lieberman (1997, 2000, 2003).

More than 115 species of olenellid trilobites were considered in the biogeographical 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 Armórica,

Australia, Avalonia, Baltica, East Antarctica, eastern, SW and NW 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, four 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. (Some species occur in more than one region.) Taxa analysed and their areas of occurrence have been described by Lieberman (2003) or are available from B.S.L. on request.

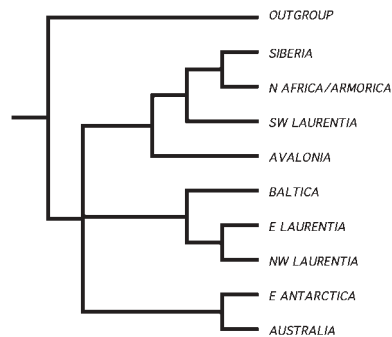
The biogeographical analysis used a modified version of Brooks Parsimony Analysis that has been described in detail by Lieberman & Eldredge (1996) and Lieberman (1997, 2000). The method converts phylogenies of organisms, in conjunction with their geographical distributions, into two separate data matrices to reconstruct biogeographical patterns. One, the vicariance matrix, is analysed 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 analysed to retrieve episodes of congruent range expansion or geo-dispersal (Lieberman & 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 have been described by Lieberman (2003) or are available from B.S.L. on request.

The data matrices are analysed 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 biogeographical patterns (Lieberman & Eldredge 1996; Lieberman 1997, 2000). By contrast, differences between the two trees suggest that such repeating processes had less of an effect on biogeographical patterns and instead suggest that tectonic processes such as 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 palaeobiogeographical patterns (e.g. Fortey & Cocks 1992; Lieberman & 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 biogeographical 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 biogeographical signal is in the data.

## Results

### *Palaeobiogeographical 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 a strong biogeographical 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 (as a result of either 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 that tectonic events, rather than repeated episodes of sea-level rise and fall,



**Fig. 4.** The most parsimonious vicariance tree showing palaeobiogeographical patterns in early Cambrian olenellid trilobites. The tree shows the relative time at which regions become isolated from one another as a result of the emergence of geographical barriers. The closer two regions sit on the tree, the more recently the geographical barriers emerged between those regions, isolating their respective trilobite faunas. The tree is rooted using an outgroup.

most profoundly structured the biogeographical patterns in the trilobites studied.

There are three major biogeographical groupings: Australia and East Antarctica; Baltica, eastern and NW Laurentia; and Siberia, north Africa–Armorica, SW 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 & Rowell 1995) and also archaeocyathans (Debrenne & Kruse 1986) strongly reinforce the biogeographical grouping between East Antarctica and Australia. This part of eastern Gondwana is thus resolved as a distinct biogeographical region. Western Gondwana and peri-western Gondwana also group together, along with Siberia and SW Laurentia. Laurentia itself is a polyphyletic biogeographical region, with parts of the craton possessing trilobite faunas sharing a closer biogeographical history with Baltica, and other parts sharing a closer biogeographical history with western Gondwana, peri-western Gondwana and Siberia.

The notion that tectonic events are driving the palaeobiogeographical patterns is consistent with the palaeomagnetic observations described above. 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 the suggestion by Bond *et al.* (1984) 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

### *Palaeobiogeographical patterns and timing of divergence events*

The vicariance tree indicates several vicariance events in early Cambrian trilobites, and there are three major palaeobiogeographical groupings: (1) eastern Gondwana; (2) Baltica, and eastern

and NW Laurentia; (3) Siberia, the northern margins of western Gondwana and SW 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, and eastern and NW Laurentian trilobites, and Siberian, SW Laurentian, Avalonian and north African–Armorican trilobites. The vicariant biogeographical 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 has trilobites from all of the major biostratigraphical 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 biogeographical 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, forming 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 probably 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 palaeobiogeographical patterns suggest that 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 biogeographical patterns in trilobites indicated a Neoproterozoic origin for the group and suggested that lineages within the Trilobita were actually diverging in the Neoproterozoic. On the basis of 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 under way 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 and b) has palaeomagnetic support from two studies in North America (Symons & 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  $c. 11 \text{ cm a}^{-1}$ ) from a high-latitude Laurentia at  $c. 565 \text{ Ma}$  to a more equatorial position by Mid-Cambrian time ( $c. 508 \text{ Ma}$ , Tapeats sandstone). If the documentation by McCausland & Hodych (1998) of a low-latitude position for the Skinner Cove volcanic rocks 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 (of the order of  $35\text{--}50 \text{ cm a}^{-1}$ ). The advantage, however, of our preferred high-latitude Laurentia option at 580 Ma is that it results in a favourable geometry for the final assembly of Gondwana and the closure of the Mawson Sea between Australo-Antarctica and the bulk of Gondwana (see Fig. 1b compared with Fig. 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 Catoctin studies (Pisarevsky *et al.* 2000; Meert & Van der Voo 2001). 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 & Vernikovskaya (2001) and Khain *et al.* (2003) suggest that Siberia probably 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 geological comparisons are equally contentious (Meert & Torsvik 2004). 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 ( $c. 800 \text{ Ma}$ ) rifting with the suggestion by Pelechaty (1996) and Pisarevsky *et al.* (2000) that Siberia and Laurentia were conjoined until  $c. 550 \text{ Ma}$ .

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 Fig. 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 & Rehnström 2002; Rehnström & Torsvik 2004) 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 palaeobiogeographical 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.

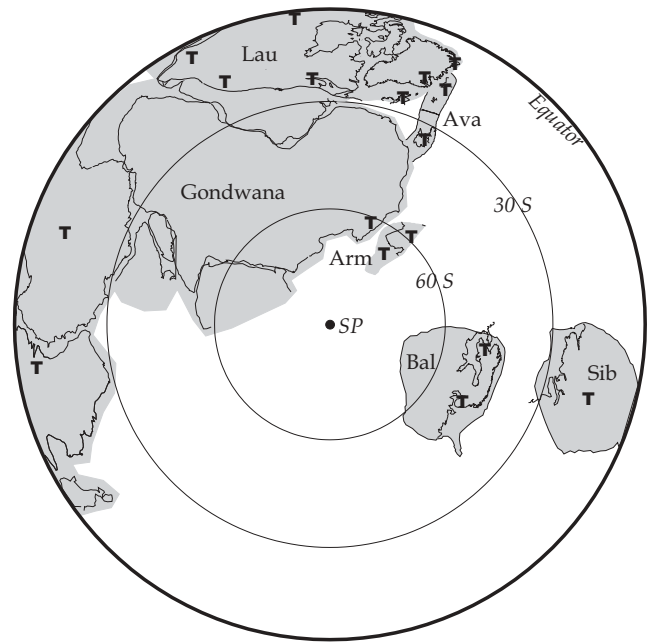
There are other problematic issues related to the Pisarevsky *et al.* (2000) low-latitude position of Laurentia at 580 Ma. Most evidence suggests that the opening of the Iapetus Ocean between Laurentia and the South American blocks commenced post-580 Ma (Cawood *et al.* 2001). Furthermore, Fitzsimons (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 SW Laurentia, an alignment at odds with this and other palaeobiogeographical 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 to 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 the pre-IITPW model of Kirschvink *et al.* (1997) 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 Mid-Cambrian, *c.* 510 Ma) palaeogeographies show significant differences (Figs 3 and 6). Kirschvink *et al.* (1997) showed an overlap between Laurentia and Gondwana, which they attributed to an incomplete dataset. The overlap, however, between the two continents is severe and would require more than 40° of latitudinal displacement between western Gondwana and eastern Laurentia to generate a Iapetus ocean consistent with geological data (Cawood *et al.* 2001). In addition, Baltica is displaced significantly from Avalonia compared with conventional views of Cambrian palaeogeography (see Cocks & Torsvik 2002).

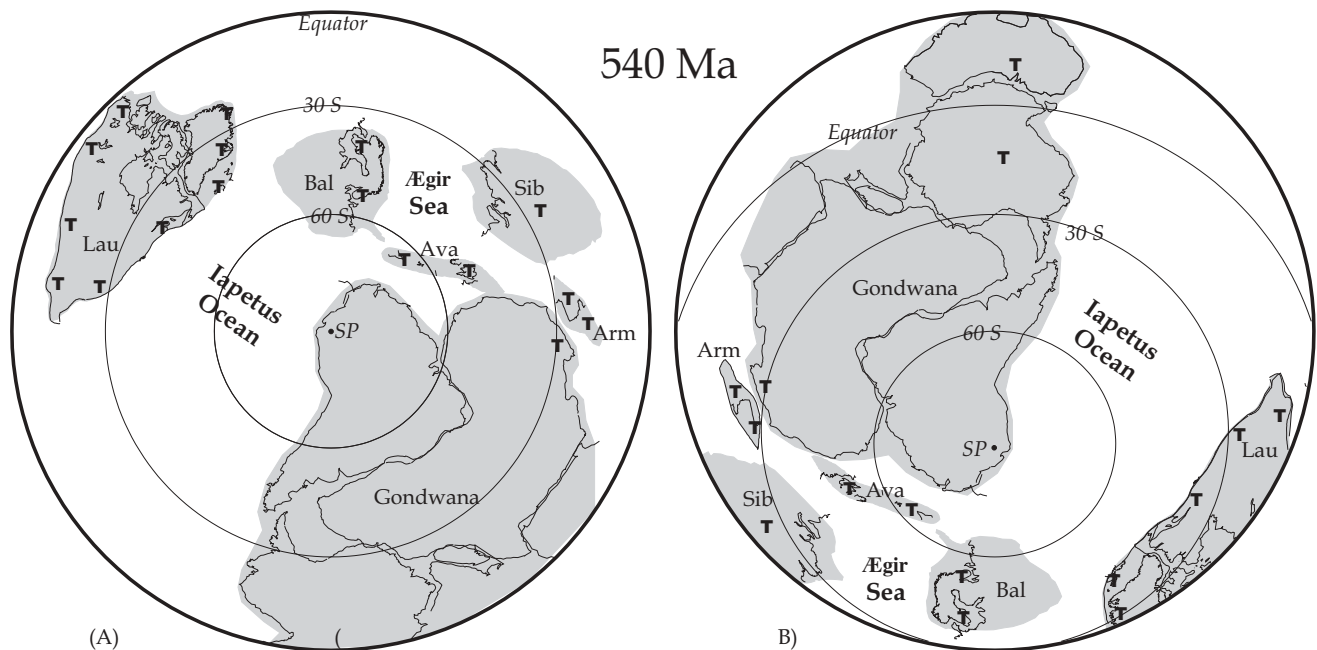
Our preferred palaeogeographies at 540 and 510 Ma based on palaeomagnetic data are shown in Figures 5 & 7. Figure 5 is also based on data from Torsvik & Rehnström (2001) and Cawood *et al.* (2001); the Iapetus Ocean is near its maximum width and the Ægir Sea separates Baltica from Siberia. Our reconstruction at 510 Ma (Fig. 7) avoids the problems of continental overlap that the model of Kirschvink *et al.* (1997)

### Post-IITPW (510 Ma)



**Fig. 6.** Post-IITPW reconstruction for 510–505 Ma based on the analysis of Kirschvink *et al.* (1997). Abbreviations as in Figure 1.

suffers from, and is in fact rather similar to those palaeogeographies advocated by Torsvik & Rehnström (2001) and Cocks & Torsvik (2002), each of whom suggested a Iapetus Ocean of moderate width.



**Fig. 5.** (a) Our preferred palaeogeographical reconstruction at 540 Ma (after Torsvik *et al.* 1996; Torsvik & Rehnström 2001) showing the opening of the Iapetus ocean between a fully united Gondwana and Laurentia. (b) rotation of (a) to show the rest of Gondwana. Abbreviations as in Figure 1.

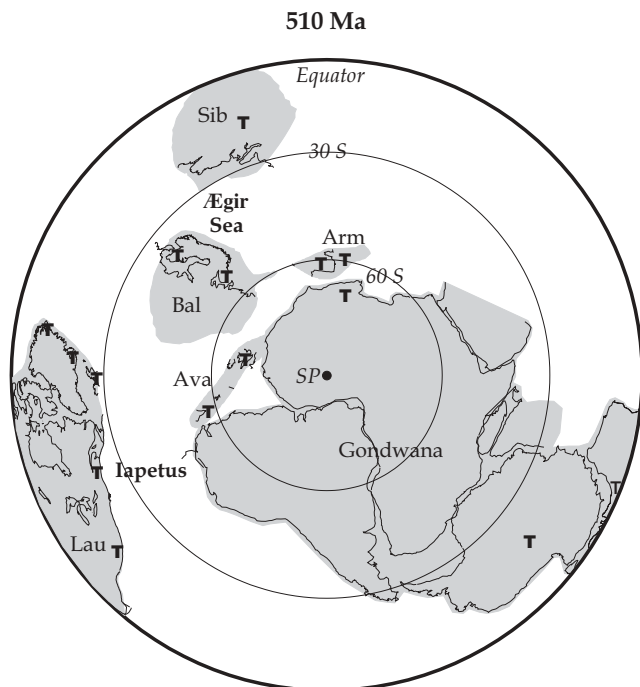


Fig. 7. Our preferred 510 Ma reconstruction. Abbreviations as in Figure 1.

#### *Relationship of palaeobiogeographical patterns to palaeogeographical and tectonic models*

In several respects the recovered palaeobiogeographical patterns match results from previous studies of early Cambrian palaeobiogeography. For instance, the close palaeobiogeographical 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 & Richardson (1980) and Fortey & Cocks (1992). Burrett & Richardson (1980), Debrenne & Kruse (1986) and Palmer & Rowell (1995) also found a close palaeobiogeographical relationship between Antarctica and Australia. Finally, Fortey & Cocks (1992) identified a close palaeobiogeographical relationship between Baltica and eastern Laurentia, a result reiterated by this analysis. The polyphyly of Laurentia in Figure 4 differs from some previous palaeobiogeographical studies (e.g. Burrett & Richardson 1980; Fortey & Cocks 1992; Lieberman 1997). Part of the differences between this aspect of the results from Burrett & 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 those by Burrett & Richardson (1980) and Fortey & Cocks (1992) may be because those workers could not incorporate phylogenetic information into their palaeobiogeographical analyses. Notably, however, the polyphyly of Laurentia recovered herein agrees with some aspects of the analysis by Waggoner (1999) of Vendian Ediacaran palaeobiogeography. For example, Waggoner (1999) also found that SW Laurentian faunas grouped with those from western Gondwana whereas NW Laurentian faunas grouped with Baltic faunas.

The biogeographical patterns resulting from analyses of the trilobites can be compared instructively with the three models of

late Neoproterozoic and early Cambrian tectonics and palaeogeography described above: for example, the IITPW event hypothesized by Kirschvink *et al.* (1997). On the basis of their reconstructions, one might predict to find close palaeobiogeographical 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 the inferred IITPW event of Kirschvink *et al.* (1997). None of these predicted relationships, however, was retrieved by the palaeobiogeographical analysis (Fig. 4).

Further, there are other aspects of the resulting palaeobiogeographical patterns that are counter what might be predicted if the Kirschvink *et al.* (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 that palaeobiogeographical patterns among most cratons should show little or no resolution. Instead this is manifestly not the case (see Fig. 4), as palaeobiogeographical 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 palaeobiogeographical 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 of Kirschvink *et al.* 1997), as 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 described above, casts further doubt on the validity of inferred early Cambrian or late Neoproterozoic IITPW events.

The palaeobiogeographical patterns derived from the trilobites also potentially conflict with the palaeogeographical model proposed by Pisarevsky *et al.* (2000), which has Laurentia in a low-latitude position (Fig. 2a and b). For example, their 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, the model of Pisarevsky *et al.* (2000) would also predict a closer association between Siberian faunas and faunas from eastern and NW Laurentia, and again such a palaeobiogeographical relationship was not recovered (see Fig. 4).

Overall the results from the palaeobiogeographical analysis (Fig. 4) accord well with our preferred palaeogeographies resulting from analysis of the palaeomagnetic dataset (Figs 1, 5 and 7) such that there is a strong degree of congruence between the two datasets. For example, each analysis recognizes a close association between most of East Antarctica and Australia, and these cratons probably 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 palaeobiogeographical 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 palaeobiogeographical data also agree with aspects of the position of Siberia especially in the close palaeobiogeographical 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 5 and 7) are best supported by the available palaeobiogeographical and palaeomagnetic data.

There is, however, some disagreement between the palaeobiogeographical results and the palaeomagnetic results, and this involves the grouping of SW Laurentian faunas with faunas from Avalonia, north Africa–Armorica and Siberia. This is because the palaeogeographical geometry predicted by palaeomagnetic studies should have led to a clustering of SW 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, however, if Amazonia served as a faunal link or bridge between SW 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 palaeobiogeographical and palaeomagnetic results more compatible would be to rotate Laurentia and Baltica approximately 20° 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 palaeobiogeographical patterns. To address the potential source of disagreement between our palaeobiogeographical and palaeomagnetic datasets, at this time we suggest the need for more extensive faunal and palaeomagnetic sampling, especially in Siberia, north Africa, Avalonia and

parts of SW Laurentia that have not been intensively sampled, for example, the Caborca region of Mexico.

## Conclusions

Three end-member palaeogeographical models derived from palaeomagnetism are evaluated and compared with results from a phylogenetic biogeographical analysis of early Cambrian trilobites. In general, the palaeobiogeographical patterns match palaeomagnetically derived models where Laurentia is situated at high southerly palaeolatitudes during the latest Neoproterozoic (*c.* 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 palaeobiogeographical position of SW Laurentia is problematic for all the models presented here, suggesting that additional palaeomagnetic and faunal sampling from this region may perhaps be worth while.

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## Appendix: Euler rotations for reconstructions

Continent/craton	Euler latitude	Euler longitude	Angle	Pole used/Rotation*	Reference
<i>Figure 1; 580 Ma</i>					
Laurentia	0	215	−135	<i>Callander, Catocotin-A</i>	Symons & Chiasson 1991; Meert <i>et al.</i> 1994
Antarctica	27.98	98.35	+85.98	Australia	This study
Australia	46.99	115	+76.6	<i>Elatina–Yaltipena &amp; Arumbera</i>	Kirschvink 1978; Sohl <i>et al.</i> 1999
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
Río Plata	37.3	60.5	+127.4	Africa–Laurentia	This study
São 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 <i>et al.</i> 1998
Siberia	43.5	323.2	+144.4	Baltica	This study
<i>Figure 2; 580 Ma</i>					
Laurentia	0	78	+81	<i>Average pole given in reference</i>	Pisarevsky <i>et al.</i> 2000
Antarctica	17.3	88.3	+78.2	Australia	This study
Australia	36.2	105	+63.2	<i>Elatina–Yaltipena &amp; Arumbera</i>	Kirschvink 1978; Sohl <i>et al.</i> 1999
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
Río Plata	19.6	111.3	+134.8	Africa–Laurentia	This study
São 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

(Continued)



## Appendix. Continued

Continent/craton	Euler latitude	Euler longitude	Angle	Pole used/Rotation*	Reference
Madagascar	17.8	140.5	+142.4	Africa–Laurentia	This study
Baltica-1	14.7	0	–162.8	<i>Fen Complex pole</i>	Meert <i>et al.</i> 1998
Baltica-2	13.1	63.0	118.9	<i>Vendian</i>	Popov <i>et al.</i> 2002
Siberia	–4.6	246	–95.8	<i>Cisbaikalia</i> and interpolation	Pisarevsky <i>et al.</i> 2000; this study
<i>Figure 3; IITPW</i>					
Laurentia	14.3	172	–146.5	<i>Callander Complex pole</i>	Symons & Chiasson 1991
Baltica	47	220.9	–50.8	<i>Fen Complex pole</i>	Meert <i>et al.</i> 1998
Siberia	20.1	3.9	+117.3	<i>Pestrotsvet pole</i>	Kirschvink & Rozanov 1984
Gondwana	10.2	241.1	–74.4	<i>Arumbera Sandstone</i> –Africa	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
<i>Figure 5; 540 Ma</i>					
Laurentia	36.7	182.5	–148.4	Cubic spline fit	Torsvik <i>et al.</i> 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 <i>et al.</i> 1997
<i>Figure 6; IITPW</i>					
Laurentia	24.9	92.9	+96.4	<i>Tapeats sandstone</i>	Elston & Bressler 1977
Gondwana	15	171.2	+148.5	<i>Black Mountain</i>	Ripperdan & Kirschvink 1992
Baltica	20.1	183	+132.9	<i>Swedish Limestones</i>	Torsvik & Trench 1991
Siberia	24.2	112	+156.8	<i>Moyero River</i>	Gallet & 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
<i>Figure 7; 510 Ma</i>					
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>Yunkulyabit–Yuryakh</i>	Pisarevsky <i>et al.</i> 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

\*Rotations are performed 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 anticlockwise. If a specific pole was used for the fit, the pole is listed in italics. The age range of the poles is within the error of the time frame presented in the reconstructions.

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