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(biological) changes, but radiation was enhanced and ecosystems became more complex because of the geochemical, ecological and tectonic changes occurring during Ediacaran-Cambrian periods.

March 20, 2007

Dr. M. Santosh-Editor

Dr. Santosh,

We have uploaded our contribution; "**The Neoproterozoic Assembly of Gondwana and its Relationship to the Ediacaran-Cambrian Radiation"** to the special issue of Gondwana Research per your invitation. We have also supplied the names of 5 reviewers (3 paleontologist and 2 paleomagnetists) that we feel would have useful comments on the material contained in the paper. We look forward to your comments and those of the reviewers.

Sincerely

Joseph G. Meert
Bruce S. Lieberman

The Neoproterozoic Assembly of Gondwana and its Relationship to the Ediacaran-Cambrian Radiation

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Draft

Abstract

The assembly of the Gondwana supercontinent during the waning stages of the Proterozoic provides a tectonic backdrop for the myriad biological, climatological, tectonic and geochemical changes leading up to, and including, the Cambrian radiation. A polyphase assembly of Gondwana during the East Africa, Brasiliano, Kuungan and Damaran orogenies resulted in an extensive mountain chain which delivered nutrients into a shifting oceanic realm. An analysis of key evolutionary events during this time period reveals the following (a) several fauna show well established endemism that may be rooted in a cryptic evolutionary pulse c. 580 Ma (b) the margins of the Mirovian and Mawson Oceans were the cradles for the Ediacaran fauna (c) the margins of the Iapetan and Mirovian oceans form the olenellid trilobite realm (d) the margins of the Mawson and Paleo-Asian oceans are the birthplace of the so-called Gondwana Province fauna (e) evolutionary events associated with the Cambrian radiation were likely driven by internal (biological) changes, but radiation was enhanced and ecosystems became more complex because of the geochemical, ecological and tectonic changes occurring during Ediacaran-Cambrian periods.

Key Words: Gondwana, Cambrian explosion, Ediacaran, evolution, paleogeography

Introduction

The span of geologic time that stretches from the late Neoproterozoic through the Middle Cambrian (~800-501 Ma) heralded the evolution of complex bauplans and increased bioturbation (Darwin, 1859; Walcott, 1899; Sprigg, 1947; Crimes, 1992; Signor and Lipps, 1992; Valentine, 1992; Fedonkin, 1992; McMenamin, 1998; Bowring and Erwin, 1998; Knoll, 2001; Babcock et al., 2001; Zhuralev, 2001;

Narbonne and Gehling, 2003; Narbonne, 2005; Peterson et al., 2005; Morris, 2006; Marshall, 2006; McCall, 2006; Erwin, 2006); some of the most severe glacial episodes in Earth history (Agassiz, 1842; Harland and Bidgood, 1959; Roberts, 1971, Roberts, 1976; Kirschvink, 1992; Meert and Van der Voo, 1994; Hoffman et al., 1998; Evans, 2000; Xiao, 2004; Meert, 2007); rapid changes in continental configurations (Meert et al., 1993; Kirschvink et al., 1997; Evans, 1998, Meert, 1999; Smith, 2001; Meert and Tamrat, 2003; Maloof et al., 2006); oxygenation of the atmosphere, shallow and deep oceans ; unique swings in stable isotope ratios (Garrels et al., 1973; Knoll, 1992; Canfield and Teske, 1996; Canfield and Raisewell, 1999; Berner et al., 2003; Canfield, 2005; Holland, 2006; Liang et al., 2006; Canfield et al., 2007); and a host of other enigmatic geological, geophysical and astronomical events (Williams, 1975; Williams, 1986; Walter et al., 2000; Puffer, 2002; Kirschvink and Raub, 2003; Horvath, 2003). This interval includes the Ediacaran Period (635-542 Ma), the enigmatic Nemakit-Daldynian interval (542-535 Ma) and the so-called Cambrian explosion during the Tommotian-Botomian interval (535-513 Ma). Precise causes for this unique biological period in Earth history are unknown, but speculation about the rise of animals has run the gamut from purely intrinsic biological causes (Bengston and Morris, 1992; Parker, 1998; Smith and Peterson, 2002; Peterson et al., 2005; Baker, 2006) to extrinsic triggers (Derry et al., 1994; Canfield and Teske, 1996; Hoffman et al., 1998;

Brasier and Lindsay, 2001; Kirschvink and Raub, 2003; Horvath, 2003; Squire et al., 2006) or some combination of both (Peterson et al., 2005).

Against this backdrop of climatic, evolutionary and environmental change, the southern supercontinent of Gondwana (Figure 1) was assembled (Suess, 1904-1909, Stern 1994; Meert et al., 1995; Meert and Van der Voo, 1997; Meert, 2003; Veevers, 2004; Collins and Pisarevsky, 2005; da Silva et al., 2005; Squire et al., 2006). It is of course tempting to link the biological changes that occurred at this time to the tectonic changes that resulted in the assembly of Gondwana (Brasier and Lindsay, 2001; Squires et al., 2006). The goal of this paper is to evaluate the biological, climatic and environmental changes during the interval from ~570 Ma to 500 Ma from a paleogeographic perspective.

Gondwana Assembly: The Tectonic Setting of the Cambrian Explosion

In the interval of time beginning just prior to the Ediacaran radiation and continuing on through the end of the Cambrian radiation, vestiges of the Rodinian supercontinent were assembled into the Gondwana supercontinent (Meert, 2003; Veevers, 2004; Collins and Pisarevsky, 2005). The exact timing of Gondwana assembly overlaps the period of rapid diversification of life on earth and follows the interval of global cooling and the so-called "Snowball Earth" events (Hoffman, 1998; Meert and Torsvik, 2004a). A number of models have been forwarded for Gondwana assembly. Some view the collision as a

simple unification of East Gondwana (Figure 1; India, East Antarctica, Madagascar, Australia and Sri Lanka) with West Gondwana (Figure 1; Africa and South America). These models (Yoshida, 2007; Squire et al., 2006; Yoshida, 1995) tend to oversimplify the geologic data and ignore earlier (Neoproterozoic) reconstructions that demonstrate latitudinal offsets between East Gondwana blocks (see Torsvik et al., 2001a,b; Meert, 2003; Veevers, 2004; Collins and Pisarevsky, 2005). The most extreme models hold to a Paleoproterozoic or earlier assembly of Gondwana within a long-lived supercontinent (Piper, 2007)

The foci of many recent Neoproterozoic-Cambrian paleogeographic models are regionally based. Meert (2003) for example, examines events in the eastern Gondwana, but largely ignores the events occurring simultaneously in western Gondwana (e.g. the West African, Amazonian and Rio de la Plata cratons). Tectonic reviews of Western Gondwana assembly (Alkmim et al., 2001; da Silva et al., 2005) also focus on regional events and ignore the broader tectonic framework of eastern Gondwana. The most comprehensive review of Cambrian Gondwana by Veevers (2004) suggests a series of 'counter-rotating cogs' producing orogenic pulses via oblique collisions and rotation within the mostly assembled East and West Gondwana continents.

I will briefly explain some of the most basic criticisms of the 'two-piece' or single Gondwana models (Meert, 2003; Fitzsimons, 2000; Boger and Miller, 2004; Veevers, 2004; Collins and Pisarevsky, 2005).

Assembling Gondwana: Polyphase or Simple?

There is reasonable geologic evidence for the existence of a Mesoproterozoic supercontinent (Dalziel, 1992, 1997; Meert and Torsvik, 2003; Piper, 2000; 2006). The name most commonly attached to this supercontinent is Rodinia although other names (Paleopangea) have been used (McMenamin and McMenamin, 1999; Piper, 2000). Figure 2a shows the archetypal Rodinia supercontinent (after Meert and Torsvik, 2003) and Figure 2b shows the Paleopangea configuration envisioned by Piper (2000, 2007). Several important points can be made about these supercontinental configurations. Although the positioning of individual blocks within Rodinia can be debated, the Rodinia supercontinent shows a dispersal of cratonic nuclei making up West Gondwana. East Gondwana was shown as a coherent landmass in the 'archetypal' Rodinia; however, Meert and Torsvik (2003) demonstrate that high quality paleomagnetic data from India and Australia are incompatible with a coherent East Gondwana. The Malani Igneous complex pole (India; Torsvik et al., 2001; Gregory et al., submitted) meets all 7 of Van der Voo's (1990) reliability criteria and the primary nature of its magnetization is demonstrated by a positive baked contact test. The Malani pole is supported by additional paleomagnetic and geochronologic data from the Seychelle's micrcontinent that was adjacent to India during the ~750 Ma time interval (Torsvik et al., 2001b). The Mundine dykes pole (W. Australia; Wingate et al., 2000) meets 6/7 of Van der

Voo's (1990) reliability criteria and also passes a baked contact test. Figure 3 shows the latitudinal positions of India and Australia based on the 771 ± 5 Ma Malani Igneous Province pole from India (Torsvik et al., 2001; Gregory et al, submitted) and the 755 ± 3 Ma Mundine dyke swarm (Australia). The difference between India's position in the Gondwana configuration and its position at Malani time is ~40 degrees. Even if we assume the maximum error in the paleomagnetic pole positions for Australia and India, the discrepancy in latitudinal positions is ~23 degrees (~2500 kilometers). Thus, if paleomagnetism is to make any contributions to the debate regarding the positioning of blocks within East Gondwana, these two poles form the *casus belli* for arguments against a united East Gondwana during the Neoproterozoic.

In contrast, Squire et al. (2006) defend their simplistic two plate model for Gondwana assembly on the basis of several incorrect claims regarding the polyphase model of Meert (2003) and their interpretation of detrital zircon data from eastern Gondwana. They stated that the Kuunga suture is 530-515 Ma in age whereas the paper by Meert (2003) cited an age range of 570-530 Ma for the Kuungan Orogeny. Thus, their argument that the rocks deposited on the margins of the Kuunga Orogen display detrital zircon spectra that match closely with the East African orogen and therefore negate the existence of a significant Kuunga suture is a moot point. The model of Meert (2003) would, of course, predict such a match because the Kuunga suture would have closed by 530 Ma.

Secondly, Squire et al. (2006) argue that amalgamation involved three large collisional events and the latter two collisions are too short-lived to produce such a long and tortuous mountain chain. Meert (2003) argued for two pulses related to the assembly of eastern Gondwana. The first, East African Orogeny (Stern, 1994), spanning some 130 million years and the second, Kuunga Orogeny lasted at least 40 million years (rather than the 15-30 million years cited in Squire et al., 2006). The protracted Brasiliano Orogeny (Trompette, 1997) and the closure of the Damara Belt (Gray et al., in press) are yet additional orogenic cycles related to the assembly of the Gondwana supercontinent that extend to at least the end of the Cambrian (~490 Ma; Gray et al., in press). A conservative estimate for the duration of the orogenic cycles needed to form the Gondwana supercontinent would be ~250 million years. This is comparable to the length of time needed to generate the Appalachian-Ouachita-Caledonian Orogens (Rast, 1989) that also consisted of several short to intermediate length pulses of orogenesis (Penobscottian, Taconic, Acadian, Ouachita and Alleghenian).

Lastly, Squire et al. (2006) argue that there is no arc magmatism associated with ocean closure between India and Antarctica and that the high strain zones are narrow. Both of these arguments are based on a rather limited dataset (much of East Antarctica remains hidden from our view!). Furthermore, we are looking at deeply exhumed pieces of the orogen for which significant crustal thickening has been proposed

extending some 600 km into the East Antarctic craton (see Boger and Wilson, 2005; Boger and Miller, 2004 and references therein). Since the Kuunga Orogeny also affected parts of Madagascar, Sri Lanka and western Australia, the search for arc-related rocks should not be limited to a few outcrops in Antarctica or India and as shown by Boger and Wilson (2005), the Kuunga Belt is of considerable width in some areas (see also Gray et al., in press).

A second view of the Neoproterozoic-Cambrian orogenic events within Gondwana is derived from the models of Veevers (2004) and Piper (2000, 2007). The Paleopangea configuration of Piper (2000) suggests that the Neoproterozoic to Cambrian orogenies within Gondwana are ensialic or nearly so. Piper (2000) bases his arguments on paleomagnetic data and thus, a brief discussion is necessary to explain the differences between his model and the polyphase models that are also based on paleomagnetic arguments (Meert, 2003; Collins and Pisarevsky, 2005).

Piper (2000, 2007) begins his arguments with criticisms of the Rodinia model. He lists 5 major problems with Rodinia (i) paleomagnetic test requires breakup 200 million years ahead of the geologic evidence for breakup (ii) the reconstruction separates Archean-Early Proterozoic affinities within Gondwana (iii) the stratigraphic correlations on which Rodinia was based are not consistent with the paleomagnetic data (iv) protracted breakup is inconsistent with stable isotope and passive

margin subsidence data and (v) it predicts no geodynamic mechanism for the re-organization into Gondwana.

Points (i) and (iv) are essentially the same using two different datasets. In fact, these problems are not unique to the Rodinia configuration. Meert and Torsvik (2004b) showed that the Paleopangea model also fails to account for conjugate margins to NW-Laurentia, N-Laurentia and Eastern Laurentia (Figure 2b) and the Paleopangea model also fails to explain the spike in $^{87}Sr/^{86}Sr$ ratios in the Cambrian (Figure 4) or the relatively low $^{87}Sr/^{86}Sr$ ratios in the 800-700 Ma interval (Meert and Torsvik, 2004b).

Point (ii) raised by Piper is an interesting one. Piper relies on the model of Rogers (1996) for the existence of united Archean and Paleoproterozoic crustal segments within Gondwana (Ur and Atlantica). The crustal continuity of these segments is based on the similarity of their cratonization ages. Rogers (1996) argues, for example in the case of Ur that the probability of all the crust stabilized by 3.0 Ga is unlikely to have assembled into one area of Pangea. Thus, the contention is that the Kaapvaal (S. Africa), Pilbara (Australia), W. Dharwar and Singhbhum (India) were in close proximity by the end of the Archean. However, Rogers (1996) notes that tests of this hypothesis are very difficult and it requires many orogenic belts between the cratons to be intracratonic. Furthermore, why is it that the Mesozoic rifting of Pangea was able to

separate Archean nuclei whereas the previous 2750 million years of drift were unable to accomplish this feat?

Point (iii) argues that stratigraphic correlations used to justify Rodinia are not consistent with the paleomagnetic data. This problem holds for the Paleopangea model as well. As noted by Meert and Torsvik (2004b), the Paleopangea model depends more on paleomagnetic noise than signal. In lumping good, bad and ugly paleomagnetic results into a contouring program, one is liable to come out with clusters of data (Piper 2007), but what conclusions can be made using such a method? Piper (2007) argues that the clusters signify cratonic coherence for incredibly long periods time (nearly 2100 Ma of time)! Meert and Torsvik (2004b) and Van der Voo and Meert (1991) showed clearly that a careful examination of the paleomagnetic data used by Piper is wholly inconsistent with a single-plate model for Paleopangea.

Point (v) makes the assertion that the Paleopangean configuration is similar in shape to the Neozoic Pangea and therefore reflects some underlying stable mantle configuration that is similar to the present-day geoid. While such a configuration may be stable for a short time interval, Proterozoic paleomagnetic data are indicating that (a) continents moved relative to the mantle during the 1300-500 Ma time frame and (b) continents moved relative to one another during this interval (Meert and Torsvik, 2004b). Thus, an argument favoring cycling of continents around the globe due to geoid forces may be valid, but the argument that

there is only one stable configuration of that geoid has yet to be demonstrated. It is likely that plate motion (especially subduction) plays a major role in creating a dynamic feedback loop with the mantle, and hence affects the shape of the non-hydrostatic geoid (Gurnis and Torsvik, 1994; Evans, 1998; Meert and Tamrat, 2004).

Environmental, Climatic and Biologic Links to Gondwana Assembly and Opening of the Iapetan Ocean

The breakup of a pre-existing supercontinent followed by the formation of the Gondwana formed the tectonic backdrop for the myriad environmental, climatic and biologic changes that occurred during the Neoproterozoic-Cambrian interval (Figure 4). It is a useful exercise to examine how the plate re-organization may have influenced climate and the ecology of the Ediacaran-Cambrian biologic revolution. The exact role played by tectonic reorganization in the events of the Neoproterozoic is only beginning to be recognized. The late Neoproterozoic glaciations are thought to have generated a series of 'bottleneck and flush' episodes of evolution (Hoffman et al, 1998). If these glaciations are themselves the result of the enhancement of physical and chemical weathering following supercontinental breakup, then a link between tectonic changes and evolutionary changes can be made (Hoffman et al., 1998; Donnadiue et al., 2004).

Numerous authors suggest that geochemical changes in the oceanic and atmospheric reservoirs were the direct result of changing

plate motions (Dalziel, 1997; Brasier and Linsday, 2001; Kirschvink and Raub, 2003,). The boldest of these proposals suggests that the mountainous regions of the assembled Gondwana supercontinent (Figure 1) supplied the nutrients necessary for the biologic revolution (Brasier and Lindsay, 2001; Squire et al., 2006).

The rise of oxygen levels in the Neoproterozoic is also considered as a possible 'trigger' for the Cambrian radiation (Acquisti et al., 2007; Canfield and Teske, 1996; Canfield et al., 2007; Holland, 2006; Liang et al., 2006). The association between tectonics and oxygenation of the atmosphere and oceans may be less obvious. Canfield et al. (2007) argue that the deep oceanic realm was anoxic and iron-rich prior to the Gaskiers glaciation (~580 Ma). Canfield et al. (2007) suggest that following the Gaskiers glaciation a feedback mechanism developed that resulted in an increase in oxygen in both the atmosphere and the deep ocean. According to their model, glacial melting results in an increase of nutrient supply to the ocean. The increase in nutrients results in a concomitant rise in primary productivity which, in turn, causes a rise in atmospheric and deep oceanic oxygen levels.

It should be noted that the system proposed by Canfield et al. (2007) might not have been caused solely by glacial melting. It appears that the Gaskiers glaciations were not as extensive as their Neoproterozoic counterparts (Figure 5) and therefore, the addition of nutrients to the ocean via glacial runoff might be of little importance in

comparison to the volume of nutrients delivered via fluvial systems draining the high elevations of the East African, Brasiliano and Kuungan orogens (Figure 1) that formed during the assembly of Gondwana (Brasier and Lindsay, 2001; Meert, 2003; Squires et al., 2006). Circulation in the deep oceans may also have been enhanced by the redistribution of landmasses and the resultant changes in oceanic currents. For example, the models for Gondwana assembly given above posit the closure of the Brasiliano, Mozambique and Mawson oceans during 650-530 Ma interval along with the opening of the Iapetan Ocean at around 580 Ma. These plate tectonic movements resulted in a continental exodus from the south polar regions (Figure 5). The resulting reconfiguration of the plates likely changed the oceanic circulation patterns and established the delivery system of dense-oxygenated and nutrient rich circumpolar waters (derived from the tropics) to the deeper oceanic realms.

Cradles of Life: Clues from Biogeography

The polyphase models of Gondwana assembly (Meert, 2003; Boger et al., 2004; Collins and Pisarevsky, 2005) disagree slightly regarding the geographic outlines of the various pieces that amalgamated into the Gondwana continent, but the overall timing of that assembly is generally considered to overlap with the Ediacaran-Cambrian boundary and the Cambrian explosion. We present a series of paleogeographic maps for the Ediacaran-Cambrian and explore possible interplays between the

biologic events in the Cambrian and review potential external triggers for those biological events. We note at the outset of the discussion that the model presented below is one of myriad plate models proposed for the Ediacaran-Early Cambrian interval; however, based upon the aforementioned paleomagnetic data from India-Australia we reject, *a priori*, scenarios that involve a fully formed Neoproterozoic East Gondwana.

565 Ma

The paleogeography of the 600-510 Ma time interval is only poorly constrained (Meert and Powell, 2001). Kirschvink et al. (1997) proposed an episode of inertial interchange true polar wander during the period of time corresponding to the Cambrian explosion (~523-508 Ma). Evans (1998) expanded on this idea and has proposed a series of inertial interchange events during the 600-510 Ma interval. Both of these analyses suffer from the same poorly constrained database as the more conventional plate models (Meert, 1999; Meert and Lieberman, 2004). Thus, it can be instructive to use biogeographic information as an adjunct to the more quantitative paleomagnetic methods. The following analysis assumes the 'high-latitude' model for Laurentia. Other models such as a low-latitude Laurentia were discussed elsewhere (Pisarevsky et al., 2000; Meert and Lieberman, 2004). The reconstruction follows that of Meert and Lieberman (2004) with two changes. First, we interpolate the position of Baltica based on a position between the recently

published 610 Ma Egersund dykes (Walderhaug et al., 2007) and the Winter Coast and related 555 Ma poles (Popov et al., 2002,2005; Iglesia-Llanos et al., 2005; Nawrocki et al, 2004). Secondly, we position Siberia off the Arctic margin of Laurentia (Pisarevsky et al., 2000).

Meert and Lieberman (2004) used a phylogenetic biogeographic analysis of trilobites to reconstruct the history of vicariance and geodispersal in early trilobite evolution. They noted that the vicariance patterns of olenellid trilobites were consistent with two models of plate configurations for the Ediacaran-Cambrian interval, but not so for the inertial interchange model of Kirschvink et al. (1997). That conclusion is based on the recognition that rapid changes in plate configuration would not favor a robust paleogeographic grouping of trilobites such as observed in the analysis conducted by Lieberman (1997, 2002). The biogeographic analyses of Lieberman (2002) Meert and Lieberman (2004) also concluded that the bilaterian ancestor of the olenellid trilobites likely arose in the area of Siberia ~580 Ma and therefore trilobites had a cryptic evolutionary history prior to their appearance in the fossil record.

In this analysis, we look at both paleogeography and biogeography of the Ediacaran fauna (Waggoner, 1999) and trilobites (Meert and Lieberman, 2004) to see if there is a paleogeographic solution that is parsimonious based on two independently analyzed datasets.

Waggoner (1999, 2003) conducted a parsimony analysis of endemism (PAE) and phenetic clustering of Ediacaran biota. These

methods do not utilize detailed information about evolutionary relationships, contra the methods used by Meert and Lieberman (2004), but in this particular case, because the evolutionary relationships of the Ediacara are so poorly constrained this was necessary. Although Grazhdankin (2003) recently has challenged aspects of the analysis of Waggoner (1999), Waggoner's (1999) results are still worth considering. Those analyses revealed a tripartite grouping of the Ediacara that Waggoner (2003) referred to as the Avalon, Nama and White Sea Assemblages. Figure 6a shows the results of the analysis by Waggoner (2003) and Figure 6b shows the locations of major Ediacaran finds according to Marshall (2006). Group 1 (E1 in Figure 5) are known from NW-Laurentia, Siberia, Baltica and Australia. Group 2 (E2 in Figure 5) biota indicates a clustering of Namibian, South China, SW-Laurentian and South American fauna. The third grouping (E3 in fig 5) of Ediacaran fauna are found in the Charnwood Forest (UK), Newfoundland and the Carolina Slate Belt of North Carolina. Although these areas are now widely dispersed, they all likely originated near the margins of Gondwana (Avalonia or Armorica). Additional Ediacaran finds that were not used in Waggoner's (1999) analysis are indicated by ★ on Figure 5.

Our paleogeography provides a good fit for the E2 grouping in SW-Laurentia, Namibia and South America, but South China falls well away from the E2 grouping. De (2006) reported finding E2-type Ediacaran fauna in the Vindhyanchal basin of India which would create a more

favorable N-S trending E2 coastline, but the fossils in India remain contentious due to the fact that paleomagnetic and geochronologic data favor a much greater age (~1000 Ma) for the Upper Vindhyan sediments (Malone et al., submitted; Gregory et al., 2006; Deb et al., 2007). In order to square patterns of the biogeography of the Ediacara biota it is paleomagnetically possible to place South China closer to the Kalahari craton; this, however, makes little sense in terms of the more robust paleogeography of the Cambrian that we discuss more fully below and would require rapid and complex motion to arrive at the ~530 Ma paleogeographic setting.

The E1 grouping of Ediacaran fauna is also nicely constrained in our reconstruction, particularly between Siberia, Baltica and NW-Laurentia (White Sea Assemblage). Australia and northern India also fall into the E1 grouping though they are more distant to the White Sea connection. We place the E1 fauna within the larger Mirovian Ocean. The continental margins along the Mirovian Ocean were proposed as the birthplace of the early metazoans (McMenamin and McMenamin, 1990) and this conclusion accords with the paleogeography shown in Figure 5.

The E3 fauna are restricted to the peri-Gondwana region near Avalonia and Armorica (Figure 5).

We also note here that analyses of the distribution of Lower Cambrian archaeocyathids, small shelly fossils (SSF's) and the redlichiid trilobites form the so-called Gondwanan Province (Palmer and Rowell,

1995; Debrenne and Cruse, 1989; Joshi et al., 1989; Brock and Cooper, 1993). This grouping is also well constrained in our reconstruction of the regions bordering the Mawson Ocean (Figure 5). Fortey et al. (1996) noted that the biogeographic separation of the redlichiid and olenellid realms were already apparent in the Early Cambrian as did Meert and Lieberman (2004) and Lieberman (2002). Since the trilobites are a monophyletic clade, the biogeographic separation observed in the Cambrian is also suggestive of the fact that the trilobites had evolutionary roots established prior to their appearance in the fossil record. In addition to the evidence described above that the trilobites had established evolutionary roots prior to their appearance in the fossil record, the paleogeography shown here further suggests that the trilobites colonized Gondwana from Siberia.

Waggoner (1999) suggested that the Ediacara fauna may have evolved and diverged along the margins of a once united eastern Gondwana adjacent to western North America in a so called Rodinia configuration that straddled the equator. One potential issue with this reconstruction is that these regions had rifted apart from one another literally hundreds of millions of years earlier. This disparity may be caused by the fact that Waggoner (1999) lacked phylogenies for the Ediacara biota and thus could not determine whether the biogeographic patterns he recovered were produced by vicariance, and thus were coincident with the much earlier fragmentation of Rodinia, or were

caused by geodispersal that occurred some indeterminate period after the parts of Rodinia had fragmented. Waggoner (1999) noted other possible explanations for the disparity between the reconstruction of the type shown in Figure 2a and Figure 6 Among them is the notion that the vicariant pattern evidenced in his analysis is simply due to the poorly resolved phylogenies of the Ediacaran fauna. It may also arise from different environments of deposition. For example, Crimes (2001) argued that the Ediacara fauna found in Australia (E1), Namibia (E2), Siberia (E1) and Baltica (E1) were shallow-water communities whereas those of Avalonia (E3 including Charnwood, Newfoundland, and the Carolina Slate Belt) and NW Canada (E1) are deep-water organisms. Clearly more work is needed to understand the exact environment and nature of the Ediacara fauna, but the resolved biogeographic pattern described here might also reveal a deeper root and older origin for the Ediacarans.

Cambrian Reconstructions: Cambrian Explosion

By the earliest Cambrian (~540-530 Ma), Gondwana assembly was largely complete with the exception of small oceanic basins in the region of the Kalahari craton (Figure 7; Meert and Lieberman, Gray et al., in press). Gondwana stretched from the South pole (South America) to the lower latitudes of the northern hemisphere (Australia). Global sea level changes during the Cambrian resulted in the inundation of the margins of most continental blocks although Gondwana remained largely emergent during the Cambrian following its assembly (Veevers, 2004).

The locus of subduction that closed up the Mawson Ocean jumped to the Paleo-Pacific margin of Gondwana. The Ediacaran-Cambrian boundary is marked by the appearance of *Treptichnus pedum* (Droser and King, 2001; Valentine, 2002).

The Tommotian brought with it the first of the archaeocyathid reefs. These reefs appear to have originated in Siberia within the humid tropical zone (see also Debrenne, 1992; Cocks and Torsvik, 2007). The archaeocyathids of the Tommotian-Atdabanian interval are designated by "A" in Figure 7. Additional Tommotian-Atdabanian archaeocyathid fossils are found in regions bordering Paleo-Asian ocean margins (e.g. present-day North Africa, Arabia and northern India (Debrenne, 1992). All are located to within ± 30 degrees of the equator in the reconstruction and this is consistent with previous conclusions regarding their tropical endemism (Debrenne, 1992; Cocks and Torsvik, 2007).

The Tommotian interval also marks the beginnings of the so-called Cambrian explosion. The diversity at the genus level (Figure 4) increased markedly during the Tommotian and reaches an early zenith during the Botomian. Thus, in the absence of any additional evidence, it is tempting to look for possible 'triggers' to this evolutionary pulse in the interval immediately preceding the Tommotian interval although some schools of thought posit that the sudden appearance of phyla was the inevitable consequence of a planet undergoing cumulative and irreversible change (Butterfield et al., 2003; Conway-Morris, 2006).

Certainly there is no shortage of hypothesized 'triggers' for the radiation observed in the fossil record.

Accepting for the moment that either a single event or multiple overlapping events resulted in conditions that favored a large radiation, we can look at the available datasets to examine the timing of each of the potential triggers. The discussion that follows is not meant to be exhaustive (in part because such a review would be exhausting!). Triggering mechanisms range from the simple and 'internal', for example Conway-Morris' (2006) inevitable consequence model or the development of HOX genes (Peterson et al., 2005) to complex models involving 'external' triggers such as inertial interchange true polar wander events, orogenesis and gamma-ray bursts (Kirschvink et al., 1997; Squire et al., 2006; Horvath, 2003).

In terms of 'external' triggers, both oxygenation of the deep oceans following the Gaskiers glaciation and the supply of nutrients from the rising "Trans-Gondwanan" (TG) mountains deserve some attention in this paper. Figure 4 shows the rise in $^{87}Sr/^{86}Sr$ levels in seawater following the Gaskiers glaciation presumably related to the influx of radiogenic strontium into the oceans from the TG mountains (see also Squire et al., 2006). Canfield et al. (2007) also note that this same interval of time shows evidence for a rise in oxygen levels in the deep oceans and atmospheres. Both of these 'external' triggers were argued to be important events in the rise of the metazoans. However, if the real

increase in biodiversity occurred significantly before the Tommotian interval as suggested by biogeographic and molecular clock analyses, then the oxygenation and increased nutrient flux delivered by the TG mountains become less important as drivers for the biological radiation.

We might then look at events at ~580 Ma for their potential influence on the evolution of metazoans. In particular, two events take place at this time that are worthy of consideration. The first is the Acraman impact (Figure 5). Impactogens in the geologic record are associated with extinction/radiation events with the most notable at the Cretaceous-Tertiary boundary (K-T, Alvarez et al., 1980; Rampino and Strothers, 1984). In addition to impactogens, the eruptions of large volumes of basaltic magmatism and the formation of Large Igneous Provinces have also been linked to extinction/radiation events in the fossil record (Renne and Basu, 1991; Glass and Phillips, 2006). The magmatic activity of the Laurentian superplume corresponds closely in time to the Acraman impact and invites comparisons to events at the Cretaceous-Tertiary boundary (K-T boundary; e.g. Deccan Traps and Chixulub crater). Thus, it is possible that the zenith of the Ediacara fauna followed an extinction event brought on by climatological/geochemical events during/following the impact at Acraman and the outpouring of lava via the Laurentian superplume. The situation would be somewhat analogous to the Cenozoic rise of mammals

that was facilitated by the clearing of the dominant reptilian ecological niche at the K-T boundary.

Internal, or biological triggers, are also popular for explaining the rise of the metazoans. The 'arms-race' model (Stanley, 1973; Babcock, 2003; Zhu et al., 2004) calls on the development of predatory behavior in the earliest Cambrian organisms driving a rapid push for defensive and offensive weapons in order to survive. In this scenario, the principal defense is the evolutionary development of hard shells which also happen to be more easily preserved in the fossil record (Peterson et al., 2005; Fedonkin, 2003). The arms race may also have resulted in an increase in body size of the organisms (as both a defensive and offensive measure) that would also provide for easier detection within the fossil record (Peterson et al., 2005).

HOX genes are the so-called 'biological architects' because of their function in the triggering of genetic development of body parts. The development of HOX genes prior to the Cambrian radiation, perhaps driving the arms race is another 'internal trigger' proposed for the Cambrian radiation (Peterson et al., 2005).

Taking a larger view of the Cambrian radiation and acknowledging our acceptance of a somewhat deeply rooted origin of metazoans and bilaterians (Figure 8; 600-580 Ma), we propose the following potential scenario for the Cambrian explosion of animal life that combines the aforementioned external and internal triggers into an explanation for the

observations in the fossil record. The 565 Ma paleogeography suggests that significant endemism had developed in the Ediacara fauna. Following the analysis of Waggoner (1999, 2003), three distinct biogeographic groupings of the Ediacara fauna are potentially recognized (see Figure 5). Furthermore, the endemism shown by redlichiid and olenellid trilobites is also suggestive of an earlier, albeit cryptic presence in the fossil record (Meert and Lieberman, 2004; Lieberman, 1997, 2002). The so-called Gondwana Province of redlichiids, archaeocyathids and small-shelly fauna colonized the tropical waters of the Mawson ocean whereas the olenellids colonized mid-high latitudes in Siberia, Baltica and Laurentia. By Tommotian time, the Mawson Ocean had closed and Archaeocyathid reefs were present in the Humid tropical zone. Veevers (2004) indicates that although this is a time of global sea-level rise, much of the interior of Gondwana remained emergent. In a united Gondwana scenario, these interior elevations would have provided an effective barrier thus preventing establishment of the strong provinciality in the Gondwana Province fauna (Figures 1 and 5). This may provide further evidence that these faunas had their roots extending back to the time when the Mawson Ocean was still open in the tropics.

As noted by Brasier and Lindsay (2001) and again later by Squire et al. (2006), the formation of a series of trans-Gondwanan mountains would have provided an effective source of rich nutrients to the equatorial waters. In addition, the closure of the Mawson Ocean coupled

with the opening of the Iapetan Ocean would result in opening of a south polar ocean setting up a source and sink for oxygen-rich waters. This deep-water oxygenation event coupled to the erosion of rising mountain chains (Canfield et al., 2007; Squire et al., 2006; Brasier and Lindsay, 2001) accomplished two things. The upwelling of P_2O_5 and Fe-rich waters caused by increased equator-pole circulation provided essential nutrients to the hospitable zones of the ocean (Brasier, 1992). Phosphate deposition during the Doushantuo (~570 Ma) aided in fossil preservation. The pulse of phosphate deposition during the Nemakit-Daldynian interval reflects increased biological productivity of organisms now able to secrete hard parts that also aided in preservation of the organisms. Thus, the cryptic evolutionary record suggested by molecular clocks (Figure 8), phylogenetic analyses and biogeography is real. Delivery of essential nutrients during the Nemakit- Daldynian and early Cambrian time may have helped accelerate the 'arms race' and also led to a rapidly increasing biodiversity, but significant diversity existed prior to the Cambrian explosion.

Conclusions

The formation of the Gondwana supercontinent in the Cambrian followed the last of the severe glaciations in the Neoproterozoic and overlaps with the radiation of the Ediacara and the so-called "Cambrian Explosion". The 'explosiveness' of the radiation in the fossil record has been questioned by studies of molecular clocks, phylogenetic analyses of

trilobites and biogeography (Peterson et al., 2004, 2005; Meert and Lieberman, 2004; Lieberman, 2002; Lieberman, 1997). In spite of the problems with molecular clock analyses (Benton and Ayala, 2003; Peterson et al., 2005), the temporal sequence of evolutionary events recorded in more recent analyses of molecular clocks is on the whole consistent with the fossil record and also the inferences made in this paper regarding the paleobiogeography of the Ediacaran-Cambrian interval. Specifically, molecular clocks indicate that the Metazoans are rooted to near the last of the severe glacial epochs of the Neoproterozoic (the Marinoan at ~635 Ma). The bilaterians emerged according to molecular clock analyses prior to the Gaskiers glaciation (~600 Ma). The trilobite stem groups originated sometime between 600-550 Ma. This timing is consistent with the conclusions reported in this paper. Our reconstruction at 565 Ma shows that the Ediacara fauna had a well established provinciality suggesting that they may have originated shortly after the impact event at Acraman and during the outpouring of lavas from the Laurentian superplume. Even more striking is the biogeographic split between the redlichiid and olenellid trilobites already present with their first appearance in the fossil record. A related conclusion is that the trilobites originated in Siberia (~580 Ma) and that the ancestors to the redlichiids had established the Mawson Ocean margins as their home and the olenellids developed along the Iapetan and Mirovian ocean margins (see also Meert and Lieberman, 2004). Both

of these observations are consistent with the view that the roots of the Cambrian explosion extend some 50-70 million years before its expression in the fossil record.

Given that the Cambrian explosion was somewhat more of a slow burn than a true explosion, the notion of some external or internal triggering mechanism should explore events occurring over a wider expanse of time. Based on the biogeographic distribution of trilobites, any triggering mechanisms that focus on tectonic events immediately preceding their appearance in the fossil record should be ruled out as a direct cause. If the analysis here is correct, then the inertial interchange true polar wander (IITPW) hypothesis for the Cambrian radiation can be ruled out. As noted by Meert and Lieberman (2004), it seems highly unlikely that such endemism could arise in the rapidly changing geography required by the IITPW hypothesis.

On the other hand, the myriad environmental factors including increased oxygenation of the atmosphere, increased oxygenation of the deep oceans, increased delivery of nutrient rich water to the tropics, and changes in seawater chemistry all may have led to increasing organism body size and greater availability of the materials necessary to allow secretion of hard parts that ultimately favor fossil preservation. Thus, these should not be viewed strictly as external driving forces for the radiation and the biological/behavioral causes (Hox genes, arms-race) should be considered in conjunction with the various other

environmental causes of the evolutionary changes leading up to and including the Cambrian explosion.

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Figure Legends

Figure 1: The Gondwana supercontinent. West Gondwana is shaded in light blue and East Gondwana is shaded yellow. Neoproterozoic orogenic belts criss-cross the supercontinent. Those associated with the final amalgamation of the supercontinent are the East African orogen (red), the Brasiliano-Damara orogen (blue) and the Kuungan orogen (green).

Figure 2: (a) The archetypal Rodinia supercontinent with East Gondwana juxtaposed against the present-day western margin of Laurentia and the elements of West Gondwana along the present-day eastern and southern margins of Laurentia. (b) The Paleopangea configuration of Piper (2006). CRM=Cambrian rifted margins; dashed lines are Neoproterozoic collisional belts within Gondwana (both after Meert and Torsvik, 2004b)

Figure 3: Paleomagnetically-based reconstruction of Australia, Antarctica and India. India is placed according to paleomagnetic data from the Malani igneous province (Torsvik et al., 2001; Gregory et al., submitted) and Australia is placed according to the Mundine dyke swarm (Wingate et al., 2000). There is a latitudinal offset of ~41° from India's presumed East Gondwana position (see also Figure 1).

Figure 4: Timeline of Gondwana assembly and major 'events' in earth history during the Ediacaran-Cambrian interval. Blue shading shows the approximate number of genera present during the late Ediacaran through Late Cambrian. Major faunal developments discussed in this paper are tied to the timeline along with tectonic, climatic, catastrophic events and idealized Cambrian $\delta^{13}C$ and Ediacaran-Cambrian $^{87}Sr/^{86}Sr$ curves. Abbreviations used: GRB=Gamma ray burst, *T. Pedum= Treptichnus pedum* trace fossil, SSF's=small shelly fossils, BIF's=Banded Iron Formation, P_2O_5=phosphatic horizons, IITPW=Intertial Interchange true polar wander; LIP=Large Igneous Province.

Figure 5: Paleogeography at 565 Ma. The birthplace of the Ediacaran biota was along the borders of the Mirovian and Mawson Oceans. A close relationship between Gondwana Province fauna and the margins of the Mawson Ocean and Olenellid fauna with the margins of the Mirovian Ocean suggest that the eutrilobites originated and diversified prior to ~ 565 Ma in accordance with some molecular clock studies of extant organisms. Gaskiers glacial deposits are limited to latitudes above ~40 S suggesting that

they are more in line with Phanerozoic type glaciations. The Acraman impact site is located in south-central Australia.

Figure 6: (a) Cladistic parsimony analysis of endemicity of Ediacaran fauna showing the single shortest tree according to Waggoner (2003). (b) Distribution of major Ediacaran fossil locations after McCall (2006).

Figure 7: Paleogeographic reconstruction of Tommotian time. Archaeocyathin realms of Tommotian/Atdabanian time are restricted to the humid tropical zone. Locations of major phosphorite deposits according to Parrish et al. (1986) are also shown in the Figure.

Figure 8: Molecular clock analysis according to Peterson et al. (2004). According to this analysis the last common ancestor of bilaterians diverged sometime between 573-653 Ma with the total group bilateria divergence at 615 Ma. According to the biogeographic analysis in this paper, we would place the ancestors of eutrilobites around 573 Ma shortly after the Acraman impact and Laurentian superplume events. The Kalkirindji LIP took place at about the same time as Middle Cambrian extinction (see Figure 4).

Figure

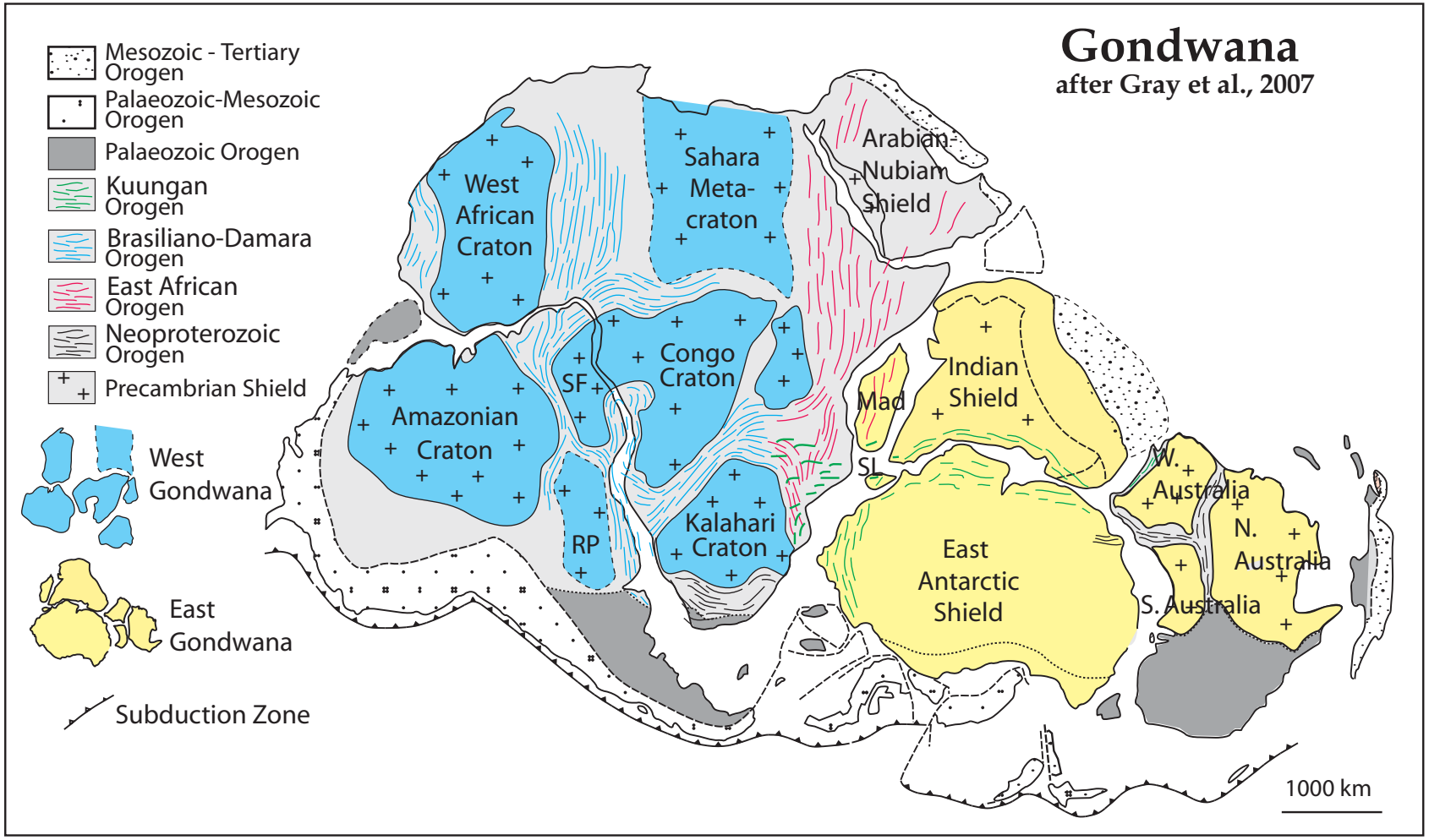
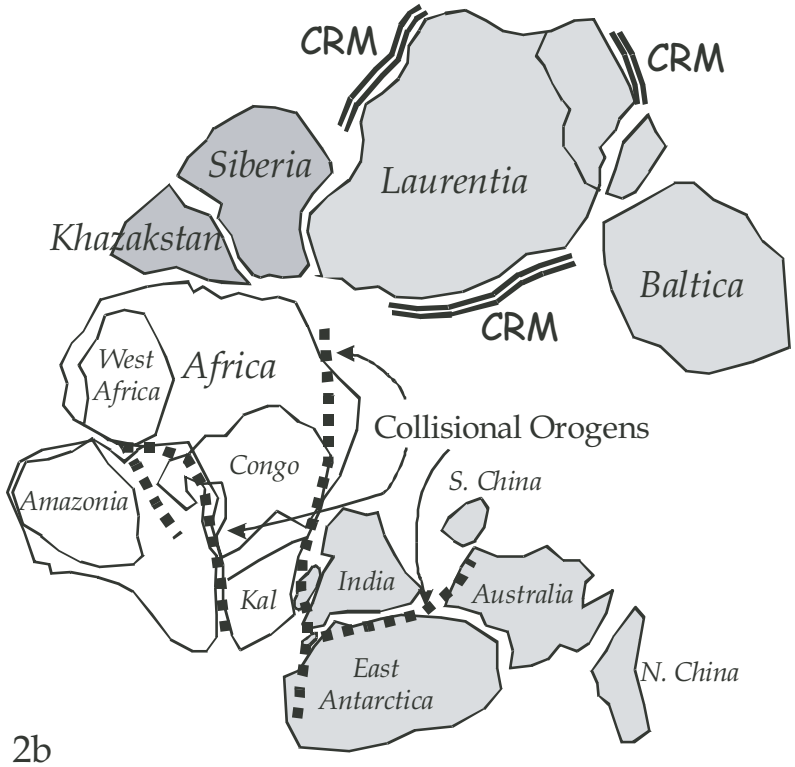

Gondwana
after Gray et al., 2007
Mesozoic - Tertiary Orogen
Palaeozoic-Mesozoic Orogen
Palaeozoic Orogen
Kuungan Orogen
Brasiliano-Damara Orogen
East African Orogen
Neoproterozoic Orogen
Precambrian Shield
West Gondwana
East Gondwana
Subduction Zone
West African Craton
Sahara Meta-craton
Arabian-Nubian Shield
Amazonian Craton
SF
Congo Craton
Mad
Indian Shield
SL
RP
Kalahari Craton
East Antarctic Shield
W. Australia
N. Australia
S. Australia
1000 km

Figure2

2a

"Paleopangea"



2b

Figure3

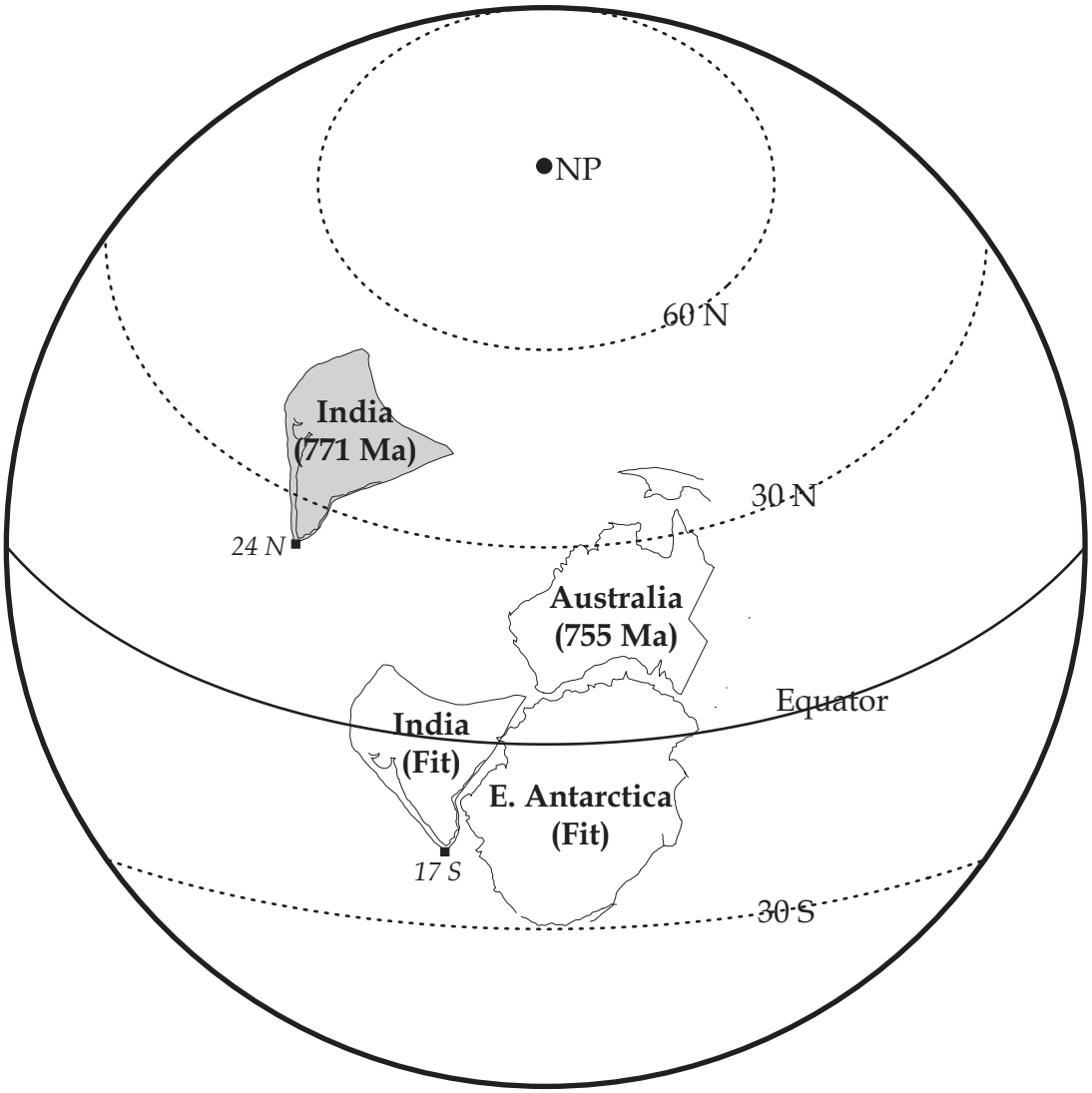

NP
60 N
India
(771 Ma)
30 N
24 N
Australia
(755 Ma)
Equator
India
(Fit)
E. Antarctica
(Fit)
17 S
30 S

Figure4

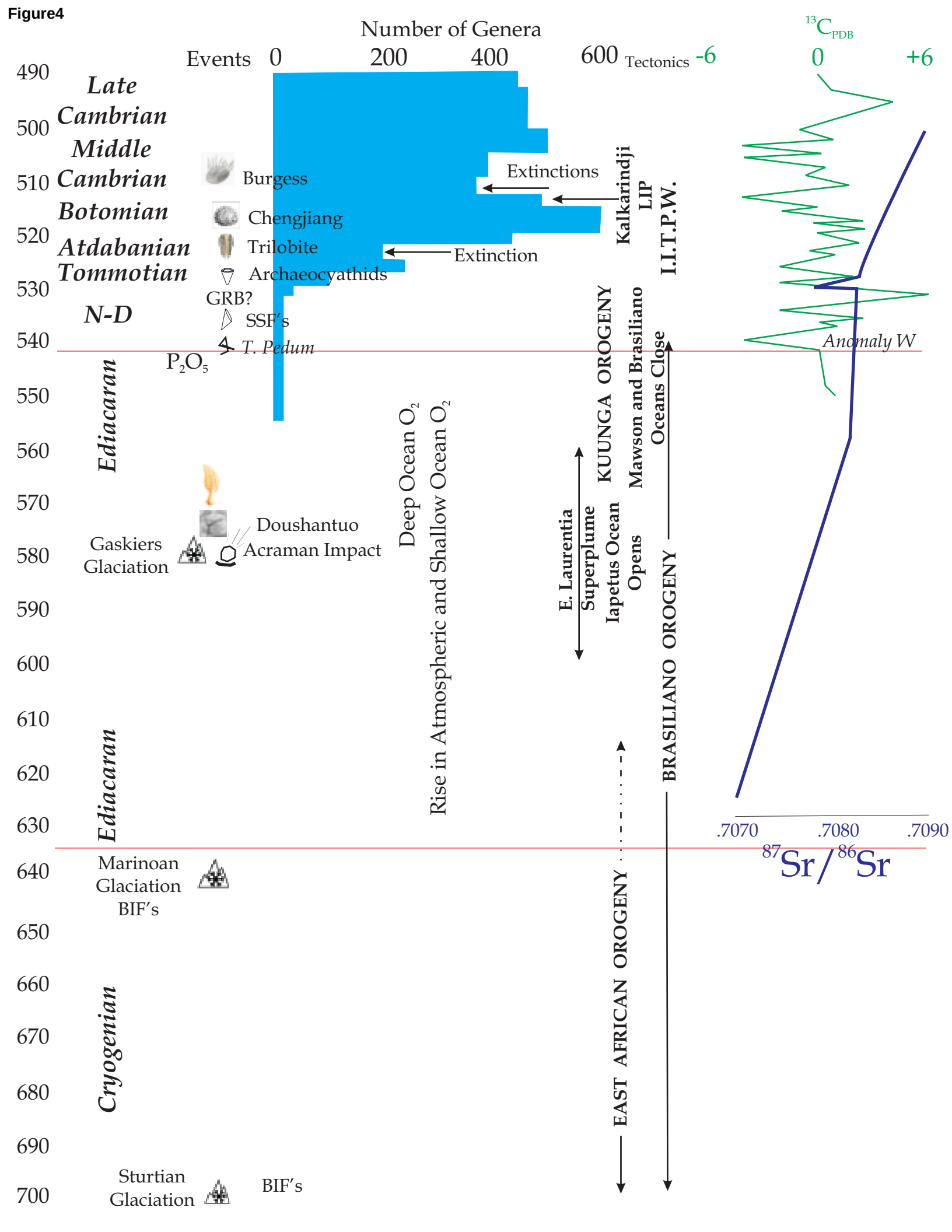

Number of Genera
Events
0
200
400
600
Tectonics
-6
0
+6
$^{13}C_{PDB}$
490
500
510
520
530
540
550
560
570
580
590
600
610
620
630
640
650
660
670
680
690
700
Late Cambrian
Middle Cambrian
Botomian
Atdabanian
Tommotian
N-D
Ediacaran
Ediacaran
Cryogenian
Burgess
Chengjiang
Trilobite
Archaeocyathids
GRB?
SSF's
T. Pedum
P_2O_5
Extinctions
Extinction
Kalkarindji LIP
I.I.T.P.W.
Anomaly W
Deep Ocean O_2
Rise in Atmospheric and Shallow Ocean O_2
KUUNGA OROGENY
Mawson and Brasiliano Oceans Close
E. Laurentia Superplume
Iapetus Ocean Opens
BRASILIANO OROGENY
EAST AFRICAN OROGENY
Doushantuo
Acraman Impact
Gaskiers Glaciation
Marinoan Glaciation
BIF's
Sturtian Glaciation
BIF's
.7070
.7080
.7090
$^{87}Sr/^{86}Sr$

Figure5

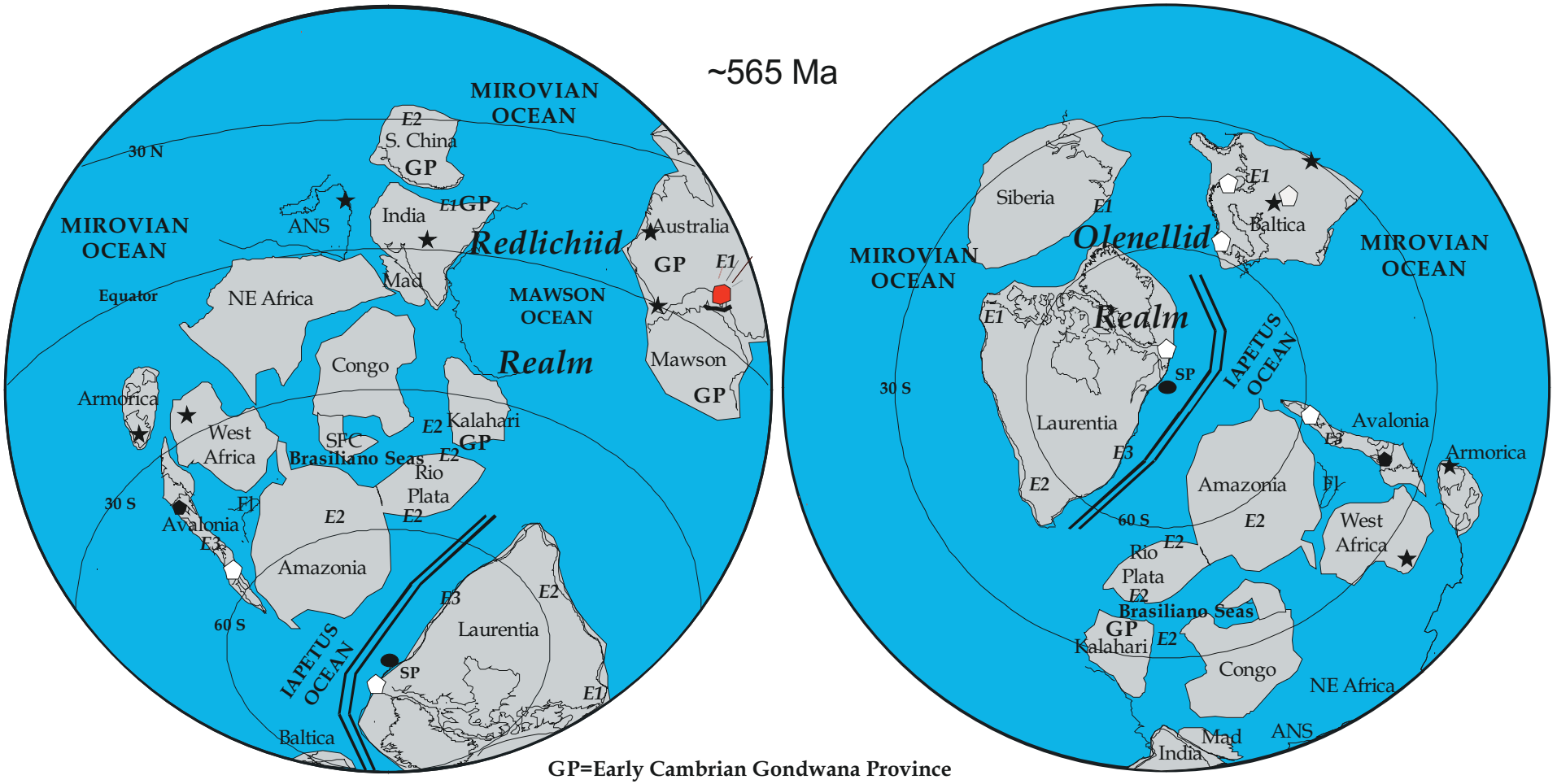
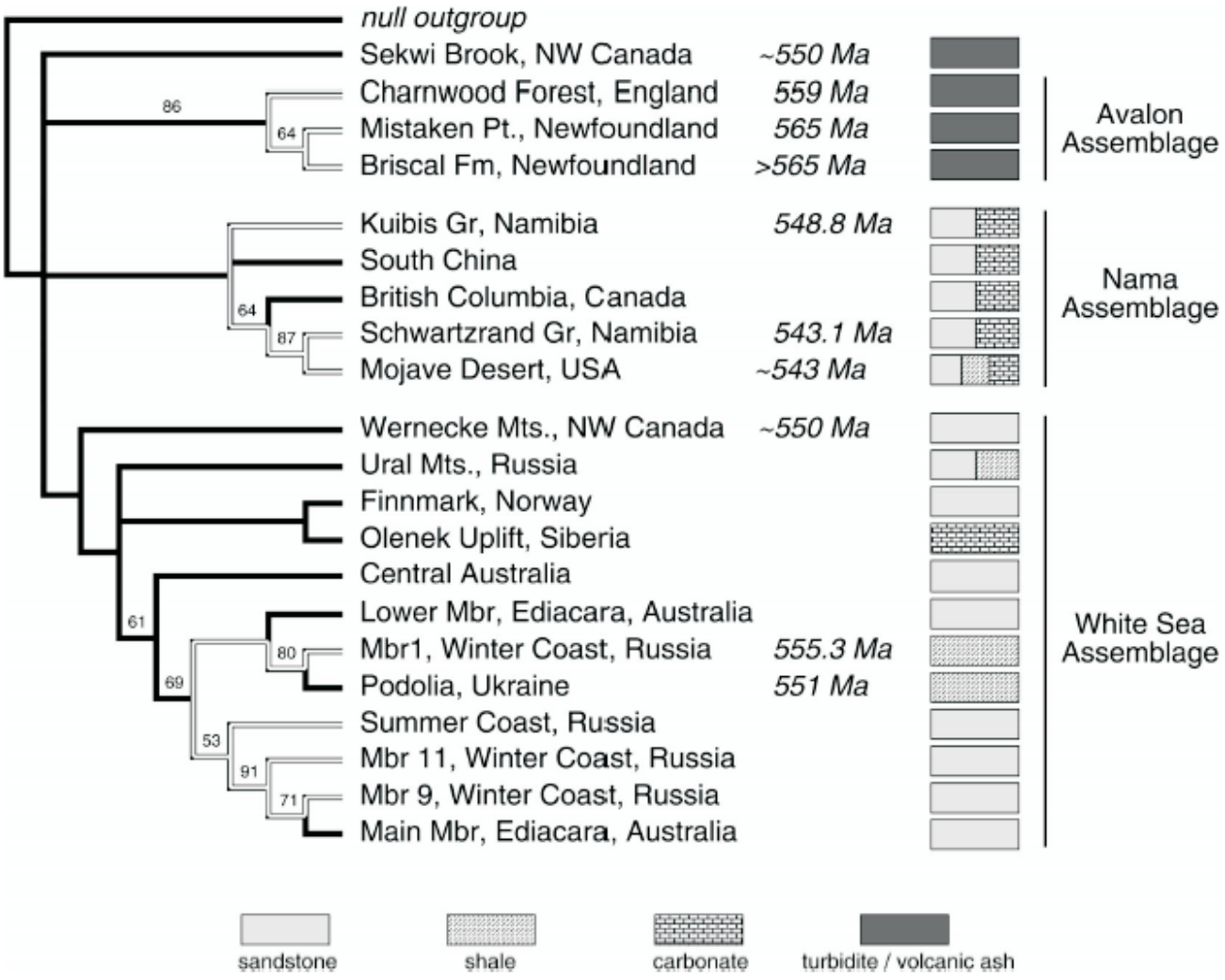
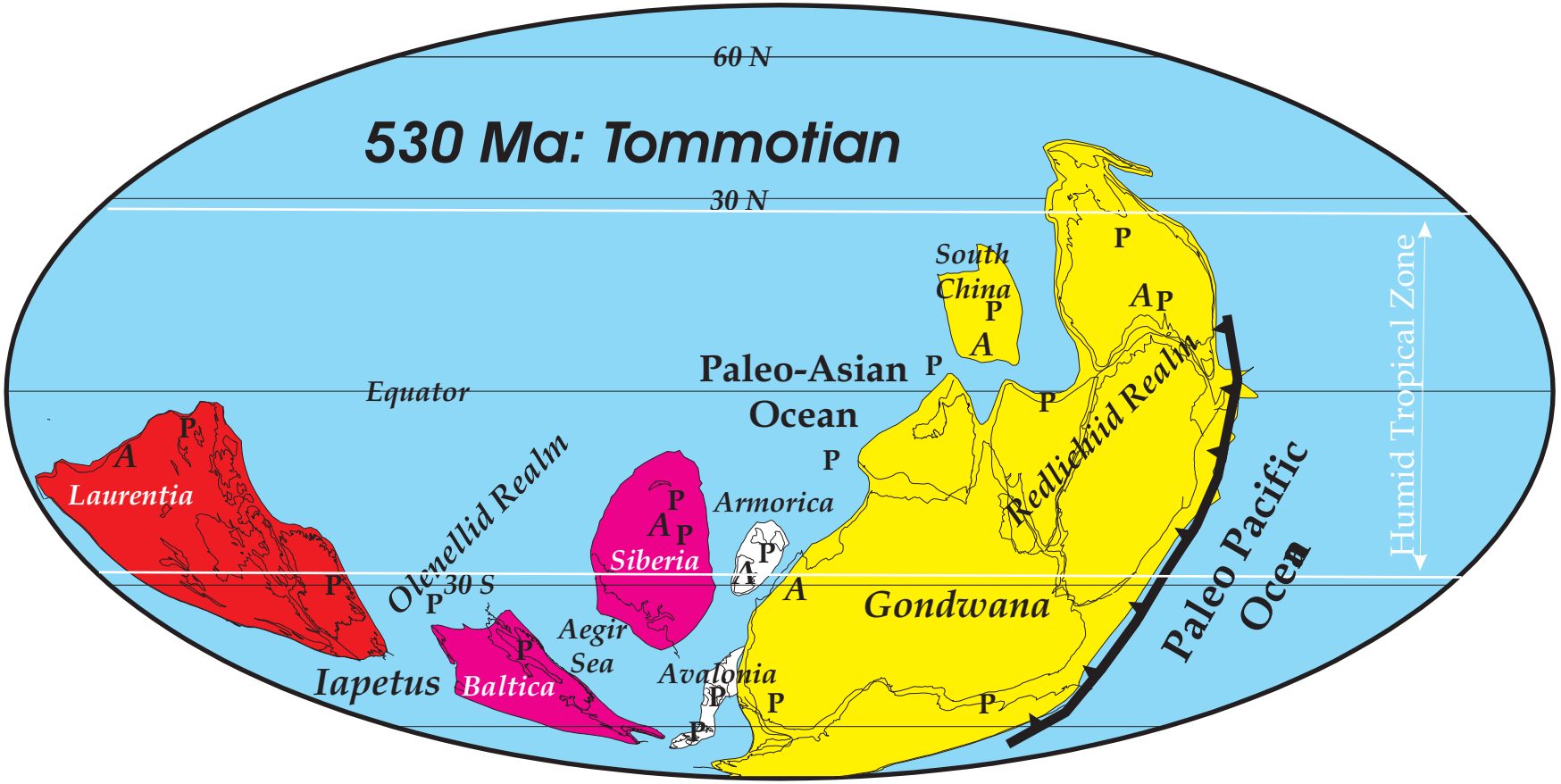

~565 Ma
MIROVIAN OCEAN
30 N
Equator
30 S
60 S
E2
S. China
GP
India
E1GP
ANS
Redlichiid
Australia
GP
E1
Mad
NE Africa
MAWSON OCEAN
Realm
Congo
Mawson
GP
Armorica
West Africa
SFC
Brasiliano Seas
E2
Kalahari
GP
E2
Rio Plata
E2
E1
Avalonia
E3
E2
Amazonia
E3
E2
Laurentia
SP
E1
IAPETUS OCEAN
Baltica
Siberia
E1
Olenellid
E1
Baltica
MIROVIAN OCEAN
MIROVIAN OCEAN
E1
Realm
SP
IAPETUS OCEAN
30 S
Laurentia
E3
E2
Avalonia
E3
Armorica
Amazonia
E1
60 S
E2
West Africa
Rio Plata
E2
E2
Brasiliano Seas
GP
Kalahari
E2
Congo
NE Africa
India
Mad
ANS
GP=Early Cambrian Gondwana Province
Gaskiers Glacial deposits
Ediacaran fossil locations not used by Waggoner (1999)
E1=Ediacaran province 1, E2=province 2, E3=province 3
Acraman Impact Site (580 Ma)

Figure6


null outgroup
Sekwi Brook, NW Canada ~550 Ma
Charnwood Forest, England 559 Ma
Mistaken Pt., Newfoundland 565 Ma
Briscal Fm, Newfoundland >565 Ma
Avalon Assemblage
Kuibis Gr, Namibia 548.8 Ma
South China
British Columbia, Canada
Schwartzrand Gr, Namibia 543.1 Ma
Mojave Desert, USA ~543 Ma
Nama Assemblage
Wernecke Mts., NW Canada ~550 Ma
Ural Mts., Russia
Finnmark, Norway
Olenek Uplift, Siberia
Central Australia
Lower Mbr, Ediacara, Australia
Mbr1, Winter Coast, Russia 555.3 Ma
Podolia, Ukraine 551 Ma
Summer Coast, Russia
Mbr 11, Winter Coast, Russia
Mbr 9, Winter Coast, Russia
Main Mbr, Ediacara, Australia
White Sea Assemblage
86
64
64
87
61
80
69
53
91
71
sandstone
shale
carbonate
turbidite / volcanic ash

Sites of Ediacara-type terminal Proterozoic faunas

Figure7

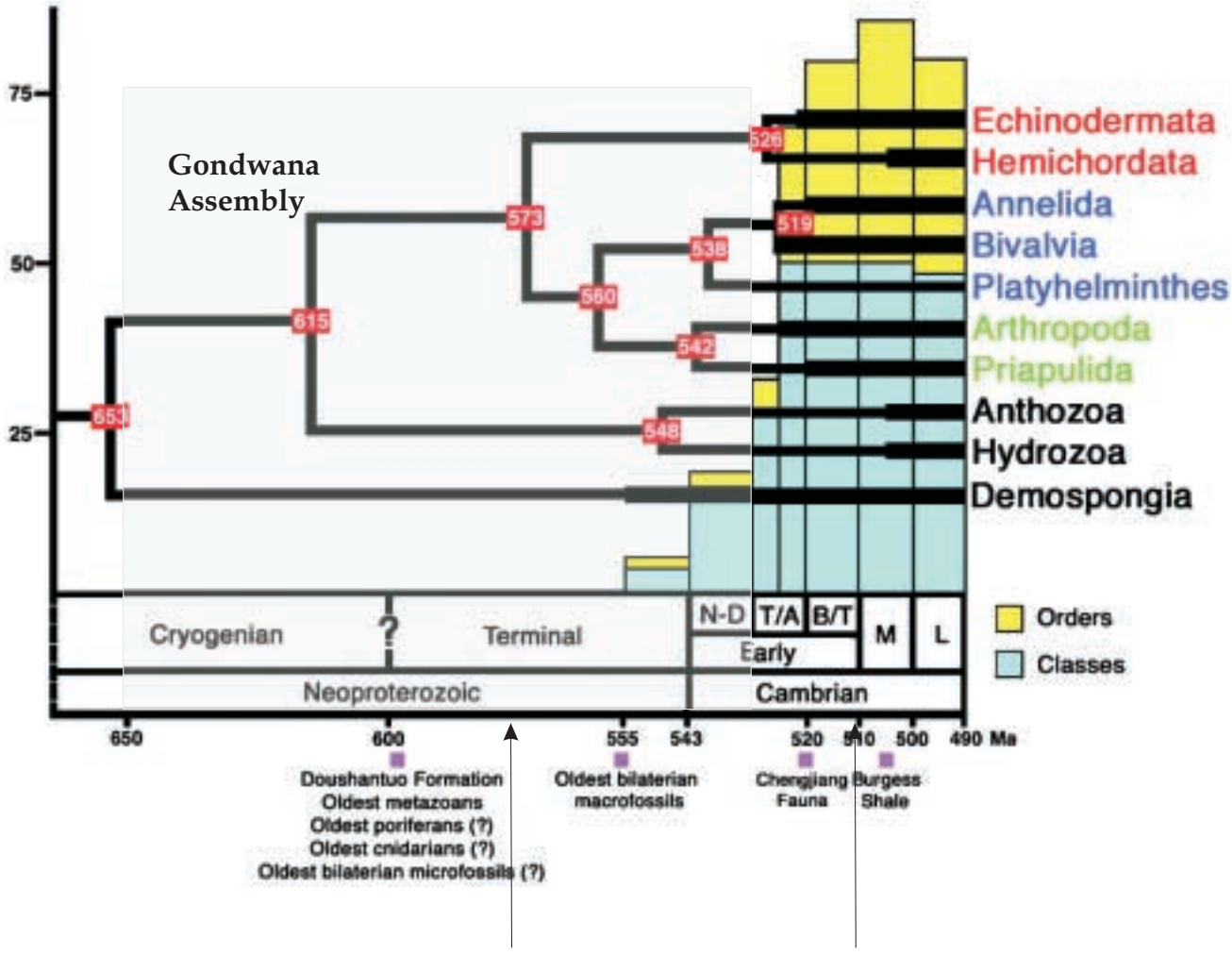


A=Archaeocyathids of Tommotian/Atdabanian age

Subduction Zone

P=Phosphorite Occurrences (Parrish et al., 1986)

Figure8


75
50
25
Gondwana
Assembly
653
615
573
560
548
538
542
526
519
Echinodermata
Hemichordata
Annelida
Bivalvia
Platyhelminthes
Arthropoda
Priapulida
Anthozoa
Hydrozoa
Demospongia
Cryogenian
?
Terminal
N-D
T/A
B/T
M
L
Early
Neoproterozoic
Cambrian
Orders
Classes
650
600
555
543
520
500
490 Ma
Doushantuo Formation
Oldest metazoans
Oldest poriferans (?)
Oldest cnidarians (?)
Oldest bilaterian microfossils (?)
Oldest bilaterian
macrofossils
Chengjiang
Fauna
Burgess
Shale
Acraman Impact
Laurentian Superplume
Kalkirindji LIP