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WAS THE CAMBRIAN EXPLOSION BOTH AN EFFECT AND AN ARTIFACT OF TRUE POLAR WANDER?

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ABSTRACT. Charles Darwin suspected that the Cambrian "explosion" might be an artifact of fossil preservation. A more recent, initially controversial hypothesis that repeated true polar wander (TPW) triggered the Ediacaran-Cambrian explosion of animal life has been supported by numerous paleomagnetic and geochronologic refinements. These data imply ~75° of TPW between 535 and 515 million years ago, coinciding with the paleontologically observed rise in metazoan diversity and disparity. We show here that this evolutionary trend is explained simply by the well known ecology-driven increase of diversity in low latitudes, coupled by other ecological effects as well as the enhanced deposition of sedimentary rocks during TPW-driven sea-level transgressions. During the Cambrian TPW event, Laurentia and parts of Gondwanaland moved into the equatorial zone while experiencing local TPW-induced transgressions; these areas dominate the paleontological record of the time. Although diversity might thus be considered partly artifactual, TPW acted on Cambrian biogeography to increase net diversity; and enhanced rates of origination and extinction also could increase disparity, especially if Early Cambrian TPW occurred at a time when genetic regulatory networks were critically poised for expansion and exaptation.

Keywords: Cambrian explosion, True Polar Wander, plate tectonics, diversity, paleogeography

INTRODUCTION

TPW, the inertially-conserved migration of a planet's entire solid body relative to its spin axis, that is, net slip on the core-mantle boundary, can occur at rates commensurate with or notably faster than normal plate tectonic motions (Tsai and Stevenson, 2007). TPW is expected of any quasi-rigid, self-gravitating planet or moon with active geodynamics. On Earth, the implications of TPW for surface proxy records of isotopic (Maloof and others, 2006) and relative sea-level (Mound and Mitrovica, 1998; Mound and others, 1999) changes have been explored, whereas the possible ecological effects on biota due to rapid TPW-related paleogeographic change so far have received only broad, speculative treatment (Kirschvink and Raub, 2003; Raub and others, 2007). This paper uses recently established temporal synchrony of the rapid Early Cambrian rotation of Gondwanaland via TPW (Kirschvink, 1992; Kirschvink and others, 1997; Mitchell and others, 2010) and the updated paleontological diversity database-definition of the Cambrian explosion (Maloof and others, 2010a) (fig. 1) to construct a specific paleogeographic test of the proposed causation.

Unlike younger, smaller TPW events in Phanerozoic time that are documented for most, if not all, major continents (van der Voo, 1994; Steinberger and Torsvik, 2008; Doubrovine and others, 2012; Torsvik and others, 2014), strong paleomagnetic support for Early Cambrian TPW is largely based on the well-sampled Gondwanaland

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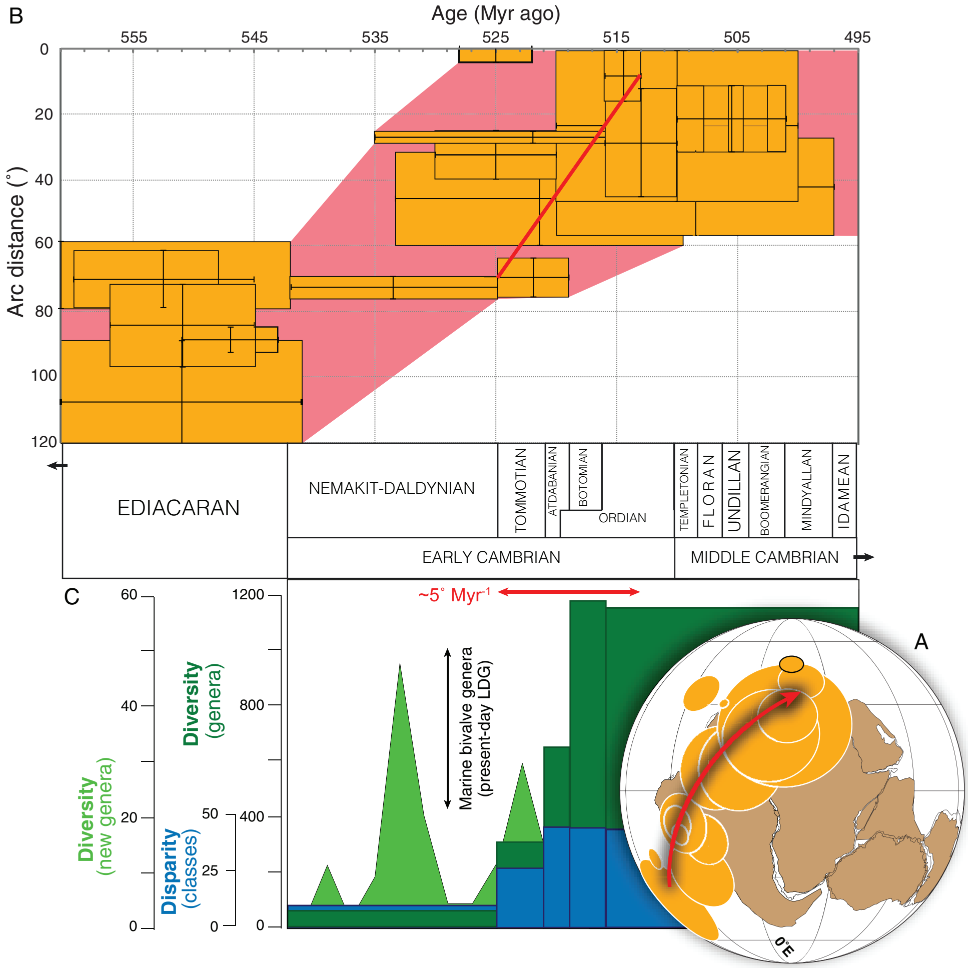

Fig. 1. Correlation between TPW and the Cambrian explosion. (A) End Ediacaran and Early and Middle Cambrian paleomagnetic poles for Gondwanaland [see Mitchell and others (2010) for Gondwanaland paleopole information, which is updated from Meert (2003)]. Red arrow is an apparent polar wander path. (B) Paleomagnetic poles in panel A plotted according to arc distance from the black outlined pole (Wyatt Formation from East Antarctica). The red line honors all individual paleopole uncertainties during the interval of fastest TPW and the red envelope represents the collective uncertainty. (C) Diversity (Foote, 2003) and disparity (Bowring and others, 1993) curves for Early and Middle Cambrian time as boxed histogram series. Diversity specific to new genera also figured as light green "spikes" in Early Cambrian time (Maloof and others, 2010a). The presence of huge new genera origination anomalies despite overall flat cumulative diversity underscores the simultaneous increase in extinction rate. The Early Cambrian time scale has been recently refined (Maloof and others, 2005; Maloof and others, 2010a; Maloof and others, 2010b). For comparison, an average diversity range is presented for the present-day LDG of marine bivalve genera along meridional transects of the East Atlantic and West Pacific (Roy and others, 1998).

paleomagnetic database (Mitchell and others, 2010). In particular, evidence for TPW from Laurentia is lacking at present with the exception of unpublished data presented in abstract only (Barr and Kirschvink, 1983; Kirschvink and others, 1997). While ongoing paleomagnetic investigations focus on Laurentia, Siberia, and other under-constrained continents, confirmation or rejection of the Cambrian TPW hypothesis will depend on building substantive datasets from multiple paleoplates. A single continent appearing to be in “standstill,” for example, could still be compatible with a global TPW scenario if that particular plate’s tectonic velocity were equal and opposite manner to the sense of global TPW rotation (Evans, 2003). The global paleomagnetic database begins to reach sufficiency to test a multiple-event TPW hypothesis when expanded across both Ediacaran and Cambrian time. Such a test fails to reject multiple episodes of significant TPW; moreover, by assuming paleomagnetic dispersion among the continental nuclei does in fact reflect repeated TPW, it is possible to reconstruct the essential architecture of Gondwanaland from subsequently dispersed continental nuclei, *independent* of the conventional Gondwanaland restoration mechanism closing ocean basins across marine magnetic anomalies and using tectonic piercing points (Raub and others, 2007). In sum, evidence for Early Cambrian TPW, although not unanimous, is compelling.

The latitudinal diversity gradient (LDG) is one of the largest-scale observable patterns common to marine and terrestrial ecosystems (Pianka, 1966; Roy and others, 1998). The origin of the LDG likely takes root in basic biophysical principles including mass and energy balance, metabolic scaling, generation times, productivity and nutrient availability, and ecospace, among other feasible, interrelated explanations (Brown, 2014). Because the LDG is established in the solar reference frame, TPW rotates all continents simultaneously relative to the LDG, except those areas very close to the TPW rotation axis on the equator. As a result, most ecosystems would expand, diminish, or migrate in response. As with relative sea-level changes (Mound and Mitrovica, 1998), TPW would cause diversity increases and decreases in a global quadrential pattern (fig. 2). Equatorward shifting margins would experience diversity increase and enhanced origination rates relative to extinction rates. Poleward-shifting continental margins would experience diversity reduction and be prone to relatively higher extinction rates compared to origination rates. Quadrants of elevated extinction as well as origination would be predicted by the TPW event, although quadrants in the elevated zones also experience sea-level transgressions that produce other ecological effects and also enhance fossil preservation (see below).

In fact, elevated rates of both origination and extinction characterize the Cambrian explosion, with origination only relatively higher than extinction overall and thus netting a diversity increase (Bowring and others, 1993; Foote, 2003; Bambach and others, 2004). Diversity changes by quadrential TPW offers a unifying explanation for why rates of Early Cambrian origination and extinction simultaneously increased and why origination prevailed.

ENVIRONMENTAL EFFECTS AND PRESERVATIONAL ARTIFACTS

TPW dynamics make predictions for LDG and sea-level change for a prescribed paleogeography, which can be tested against the rock record. For relatively quick TPW events, the viscous relaxation of Earth’s spin bulge is much slower than the fluid response of the equipotential ocean surface; this yields a quadrential response of relative sea level change (Mound and others, 1999), where Earth’s hydrostatic bulge has a ~10 km radius effect. These itinerant but dramatic sea level changes ultimately will be compensated by a relaxation (transgression or regression) back toward the antecedent state. The TPW-LDG model, additionally taking into account the relative tectonic drift of continents over long time scales, may be of great importance for understanding the correlates and causes of the LDG, both at present and in the past (Allison and Briggs, 1993). During TPW, this association of LDG biodiversification with transgression, and the corresponding diminished biodiversity associated with regression, will yield a net fossil record of diversification both for ecological (LDG and transgression ecological) and preservational [stratigraphic, geographic (Peters and Gaines, 2012)] reasons.

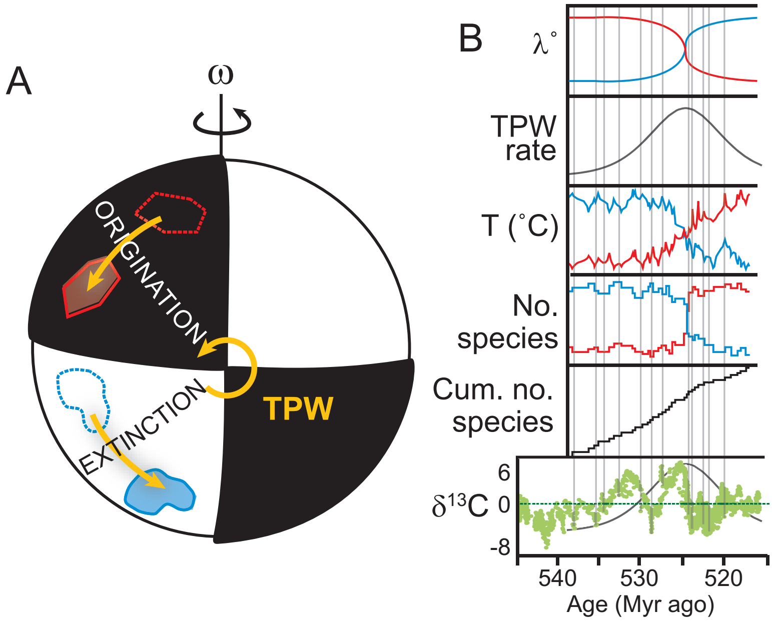

Fig. 2. TPW-LDG model. (A) Schematic illustration of the approximate spatial geometry of diversity changes induced by TPW for two continents in different original positions (red and blue). Black quadrants represent areas of dominant origination rate anomaly, and white quadrants represent areas of dominant extinction rate anomaly. (B) Schematic correlations of paleolatitude (λ°), TPW rate, sea-surface temperature (T°C), number of species, and cumulative number of species for two different continents (red and blue from fig. 2A) with the actual inorganic carbon isotope curve for Early Cambrian time (Maloof and others, 2005; Maloof and others, 2010a; Maloof and others, 2010b). Paleolatitude and TPW rate (from fig. 1) and the carbon isotope curve are all calibrated in time. Vertical lines indicate peaks in the carbon isotope record, interpreted here as (for example) methane clathrates being destabilized by combined sea level, temperature, and sediment advection effects during TPW (Kirschvink and Raub, 2003). Species diversity response is schematized (compare fig. 1C).

Oceanographic effects of TPW are thought to enhance the accrual of genetic mutations by intermittently warming the planet via greenhouse-gas "pulses" and diminishing average generation time (Kirschvink and Raub, 2003) via energy-equivalence relations (Allen and others, 2002). Accrued mutations promote higher diversity for a given disparity provided that genetic mutations are the limiting factor on diversification. It is crucial to note that a single, multimillion-year long TPW event could foster dozens of hyperthermal events because of a prolonged legacy of eddy instability in the oceans (Kirschvink and Raub, 2003). Coastline boundaries, topographic features, and winds, all of which will change during a TPW episode, largely influence current patterns. Winds are dominated by equator to pole heat transport and the Coriolis effect and remain somewhat stable with respect to the spin axis, but their orientation with respect to coastlines and mountain belts will change during the TPW event, thereby periodically forcing ocean circulation patterns to reorganize (Raub and othes, 2007). Biogeographic effects of TPW were hypothesized to enhance allopatric fixation of novel mutations (Kirschvink and Raub, 2003)—again by reorganizing ocean currents, zones of upwelling, loci and seasonality of high primary productivity (Raub and others, 2007) and by flooding low-relief continental margins to create new, expansive littoral and inner neritic zones in Earth's quadrants that shift equatorward. Our theory combines the effects of rapid TPW on regional sea-level (Mound and Mitrovica, 1998; Mound and others, 1999), and consequently on the remineralization of organic matter and the destabilization of methane hydrate (Kirschvink and others, 1997), in addition to diversity changes brought about as environments migrated relative to the paleoequator (the LDG).

Nearly 20 large fluctuations in $\delta^{13}C_{carb}$ have been documented during Early Cambrian time and form the basis of global chronostratigraphic correlations (Maloof and others, 2005; Maloof and others, 2010a; Maloof and others, 2010b). Seafloor methane clathrates could become destabilized in areas experiencing TPW-induced sea-level fall, while new clathrate reservoirs could form in TPW transgressed continental shelves (Kirschvink and Raub, 2003). Global clathrate reservoirs should be rejuvenated during TPW reorientation, as long time scale ($>$1 Myr) $\delta^{13}C$ excursions could be sustained by prolonged release of clathrate. The global pattern, however, would not necessarily be simple to model because methane hydrate is rarely stable, for example at shelf depths ($<$300 m) in extrapolar regions because bottom waters are too warm. Atmospheric residence time of methane scales roughly quadratically with concentration (Bjerrum and Canfield, 2011). Lateral sediment advection would be a spatially and temporally heterogeneous destabilizing mechanism, releasing a particular greenhouse gas reservoir at a certain time, and another elsewhere, later on, driven by aforementioned episodic circulation changes. In addition, respiration of remineralized organic carbon weathered from TPW-exposed shelves could further liberate significant greenhouse gas from regional-scale sources at million-year time scales (Kirschvink and Raub, 2003). Evocatively, Earth during TPW might have been comprised of multiple warming-cooling cycles ramping up diversity, and then fixing it, then ramping it up again, producing the evolutionary acceleration known as the Cambrian explosion (fig. 2). At the end of Cambrian TPW, net greater continental margin area—independent of sea level—had moved into low latitudes, and the LDG superimposed on this change also accounts for the directionality of Cambrian diversity growth.

The age of peak TPW rate at *ca.* 525 Ma is coincident, possibly causally, with the aragonite-to-calcite transition in seawater chemistry and early carbonate biomineralization (Porter, 2007). At elevated temperatures, seawater with lower Mg/Ca ratios precipitates low-Mg calcite inorganically (Morse and others, 1997), whereas at ever higher Mg/Ca ratios, high-Mg calcite and aragonite are the favored inorganic precipitates (Lowenstein and others, 2001), although ambient temperature does have an effect, particularly tending to dissolve aragonite. Even though most animals grow skeletons independent of ambient ocean conditions (Weiner and Dove, 2003), seawater chemistry nevertheless influences skeletal mineralogy indirectly through physiological effects (Knoll, 2003). TPW ought to affect global seawater Mg/Ca in several ways.

Most fundamentally, seawater Mg/Ca is buffered by hydrothermal exchange with ocean crust, mostly near the mid-ocean ridge system. It is not easy to reconstruct the topology of Cambrian ocean ridges, but it is easy to expect the quadrential sea level anomalies associated with TPW to enhance hydrothermal exchange in the polar regions by elevating ridges relative to mean sea level, leading to decompression melting and spreading rate increase. Because post-TPW continents were preferentially migrated toward the equator, there would have been net decrease in available area for equatorial ridges, so it is at least possible that TPW was accompanied by net increase in ridge-proximal hydrothermal burial of Mg.

We suspect that at least as importantly, wherever the location of Cambrian subduction zones, forebulges would have been mostly subject to significant change in hydrostatic bending stress during significant polar wander (with some azimuthal dependence). Whereas hydrothermal exchange near the mid-ocean ridge is limited to the top several km of crust, limited by high-temperature dissolution of sulphate minerals and limited surficial exposure of ultramafic rocks, fluid exchange associated with bending-related cracks at a subducting forebulge can penetrate the entire crust and serpentinize the mantle lithosphere. Whether deep forebulge cracks were closing while shallow forebulge cracks were opening (equatorward TPW subduction zones), or whether the bottoms of forebulge plates were more prone to tension than at shallower levels (poleward TPW subduction zones), new space for Mg mineral precipitation would have been created, resulting in fast, marked decrease in bulk ocean Mg/Ca.

Finally, respecting the specific arrangement of Cambrian continents, the increasingly shallow-water, and warmer environments on flooded Laurentian epicontinental seas during the apex of the TPW motion could also have favored a transition to calcitic taxa. In concert, these three phenomena caused by TPW may have directly influenced the remarkably abrupt and severe shift from aragonite to calcite seas *ca.* 525 to 515 Ma (Zhuravlev and Wood, 2008).

DYNAMIC EARLY CAMBRIAN BIOGEOGRAPHY

During rapid TPW events, paleomagnetic data can provide “absolute” paleogeographic reconstructions, constraining both the paleolatitude and paleolongitude of biogeographic provinces (Kirschvink and others, 1997; Mitchell and others, 2012). Biogeography during Early Cambrian TPW just happens to be such that most continents either remain in the low-latitude LDG peak, or else experience origination rather than extinction anomalies (fig. 3). In pre-TPW Early Cambrian time, there were at least six distinct biogeographic provinces: **East Gondwanaland** (Australian Centralian superbasin including Georgina and Adelaide sub-basins + East Antarctica ± South China), **West Gondwanaland** (Indian Salt Ranges + Arabia/Nubia + southern Africa ± South China), **polar Iapetus** (northeast Amazonia + eastern Laurentia + East Avalon ± West Avalon), **tropical Iapetus** (southwest Amazonia + Rio de la Plata + western Baltica ± West Avalon), **Panthalassa** (eastern Baltica + western Laurentia), and **Siberia**. Here we consider LDG-based origination/extinction predictions for each of these biogeographic provinces according to paleogeographic reconstructions over 60° of the ~75° of the TPW arc, in 20° increments, spanning the time interval from 545 to 510 Ma (fig. 3).

East Gondwanaland, rotating near the equatorial TPW axis, should show little LDG effect but retain relatively high diversity because of its low-latitude position (Kirschvink and Raub, 2003). In **West Gondwanaland**, the LDG should promote an origination anomaly >525 Ma and an extinction anomaly <525 Ma; but proximity to the TPW axis may yield varied responses based on location within the province. For **polar Iapetus**, the LDG will promote an origination anomaly throughout the TPW interval. **Tropical Iapetus** will similarly experience a prolonged LDG-promoted origination anomaly. **Panthalassa** also will experience a persistent LDG-origination anomaly, particularly for Baltica, although its reconstruction is paleomagnetically relatively uncertain (Llanos and others, 2005; Meert, 2013). Finally, the **Siberian** province, also of relatively uncertain paleogeographic reconstruction, should experience a minor LDG effect as it rotates proximal to the TPW axis in low to middle latitudes throughout Cambrian time (Kirschvink and others, 1997). As with **East Gondwanaland**, **Siberian** TPW-affected diversity should be dominated by energy-equivalence and allopatry (Kirschvink and Raub, 2003).

TPW-driven sea-level change was the first hypothesis to explain the presence of the Sauk transgression in North America during the TPW event, and its complete absence on the Baltic Platform (Mound and others, 1999). The Middle Cambrian diversity spike in Laurentia associated with Sauk transgressions (Peters, 2006)—and possibly even the environmental conditions amenable to large-scale shelf instability and exceptional preservation of the Burgess Shale fauna (Butterfield, 1990)—may be attributed to translation of that continent via TPW from high southern latitudes to a position straddling the equator (Kirschvink and others, 1997). This shift to low latitudes would trigger elevated levels of origination. It would also increase rates of

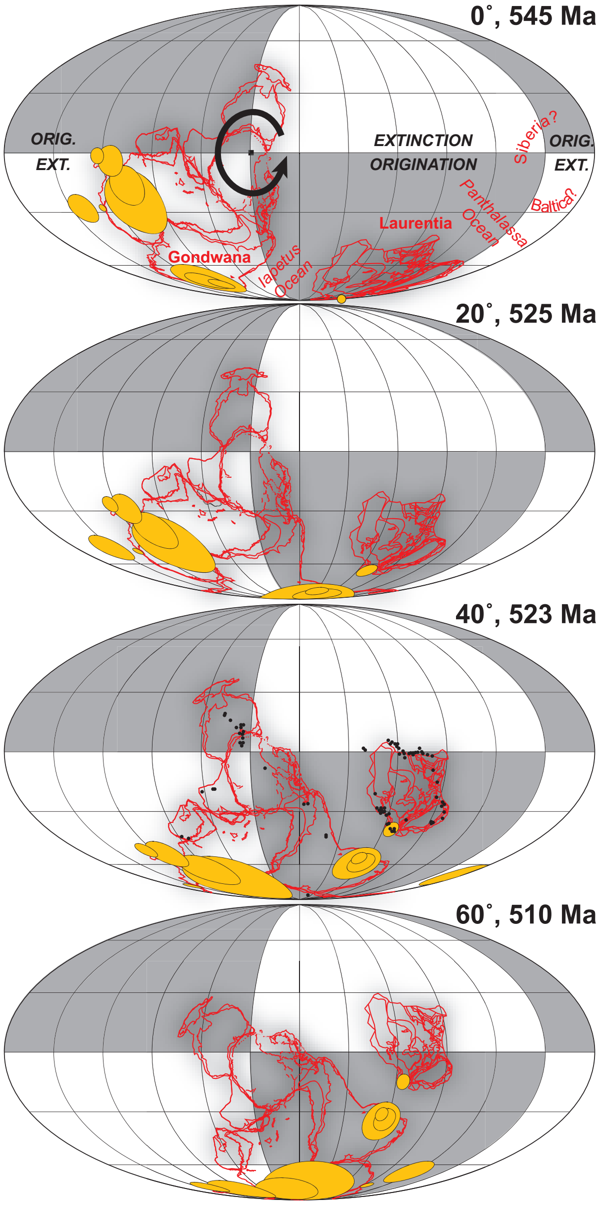

Fig. 3. Paleogeography throughout the Early Cambrian TPW event. Reconstructions of well-constrained continents Gondwanaland and Laurentia during Early Cambrian TPW. Continents with uncertain reconstructions are excluded but discussed in text. Maps are in 20° increments, with time of the 60 to 75° event scaled according to figure 1B. Yellow ellipses are a selection of paleomagnetic poles from figure 1A; not all are shown in order to keep continent outlines (red) visible [see Kirschvink and others (1997) and Barr and Kirschvink (1983) for Laurentia paleopole information]. Quadrant shading follows zones of origination and extinction during TPW event. The Iapetus paleoocean is labeled between West Gondwanaland and Laurentia. Black dots depict Early Cambrian fossil collections from the Paleobiology Database (only fossils from reconstructed continents are shown; see figure 4 for complete collection and figure 5 for a comparison between origination and extinction quadrants). See text for discussion of environmental effects and preservational artifacts for each biographic province.

continental weathering that drive organic carbon burial in tropical river deltas such as the modern Amazon (Berner, 1982). Enhanced primary productivity and nutrient replete conditions promote ecological tiering, behavioral specialization, and predator-prey escalation. Anomalously strong Cambrian continental weathering has previously been invoked (Peters and Gaines, 2012) to increase seawater alkalinity, promoting widespread exaptation of biomineralization (Kirschvink and Hagadorn, 2000). The novelty of Cambrian TPW-induced transgression onto low-freeboard continental interiors would have opened niches for these tiered, specialized communities of "hopeful monsters" to occupy. Each of these consequences has been identified separately as a characteristic of the Cambrian Explosion; our hypothesis herein sets a common context and specific environmental reason for their coincidence *ca.* 535 to 515 Ma.

TPW-transgressed interior seaways would be subject to micro-environmental pressures to which open margins are not prone. Continental tectonic influence on regional climate, nutrient availability, and sedimentation rate, and tectonic events that might fragment or isolate ecospace all would tend to promote allopatric speciation and provincialism. Simultaneously, shallow seaways linking disparate provinces would promote migration. The rich Cambrian fossil records of Baltica and East Avalon are marked paradoxically by increased cosmopolitan as well as increased provincial fauna. This duality is a predicted consequence of our TPW-LDG hypothesis. Diversity, once fixed during transgression, may migrate out and increase competitive selection pressures during post-TPW sea level relaxation. This irreversibility of diversification also is an attractive predisposition of TPW-transgression coinciding with the global LDG peak.

We would expect a noticeable drop in originations for West Gondwanaland (Salt Ranges, Arabia, Africa, and possibly South China); it is unclear whether any effect would be noticeable for East Gondwanaland, which remains continually near the equator. Although its position is more indeterminate, two independent paleomagnetic studies suggest Siberia rotated significantly and translated slightly from low to mid latitudes in Early Cambrian time, possibly indicating elevated extinction (Kirschvink and Rozanov, 1984; Gallet and others, 2003). These diversity predictions for each biogeographic realm are broadly supported by Early and Middle Cambrian fossil collections compiled in the Paleobiology database (www.fossilworks.org): almost all collections derive from origination-quadrant continents and few come from extinction-quadrant continents (figs. 3 and 4). Fossil collections are admittedly biased by preservation, exposure of the rock record, and intensity of systematic study. Numerous stratigraphic sequences occur in West Gondwanaland, however, none are very fossiliferous, most are quartz-rich units that are thought to be part of the larger Gondwanaland "super-fan system" (Squire and others, 2006).

Considering the overall pattern, it is noteworthy that the earliest Cambrian global biography was dominated by continental shelves moving toward the equator, thereby biasing the paleontological database with sediments from geographic areas that experienced TPW-induced origination-quadrant anomalies instead of extinction anomalies. Genera data from modern marine bivalves, comparable to those in Cambrian oceans, show a doubling of diversity from pole to equator (Roy and others, 1998)—an effect the magnitude of which approximates most of the observed Cambrian explosion (fig. 1C).

As absolute levels of diversity in the LDG are low near the poles and high near the equator, relative origination or extinction anomalies should always be most influential on global diversity for continents moving into or out of the tropics. As a result of these broad provincial patterns, the global biodiversity signal *ca.* 525 Ma should have been dominated by TPW-induced origination anomalies focused on northeast Amazonia, eastern Laurentia, East Avalon, eastern Baltica, and to a lesser extent western Lauren-

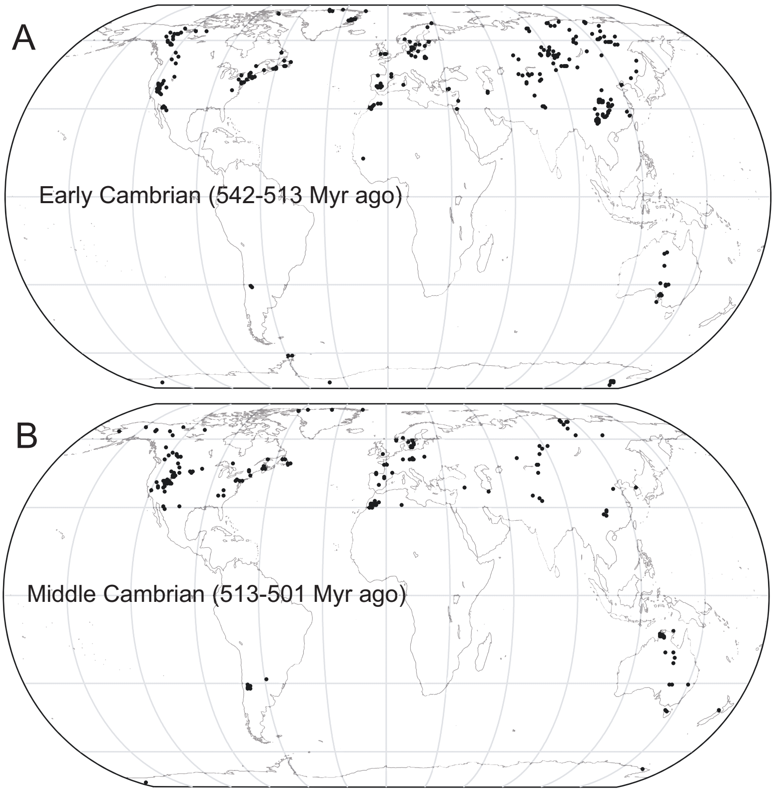

Fig. 4. Fossil collections from the Paleobiology Database. (A) Early Cambrian collections. (B) Middle Cambrian collections. See text for discussion.

tia and West Avalon. The fossil record broadly accords with this prediction (figs. 3, 4 and 5), although caution is warranted because the regions inferred to have rotated poleward naturally experienced sea-level regressions, which are not as good at preserving fossil-rich sediments.

At a global scale, biogeography displays an overwhelming dominance of Cambrian explosion fossil localities in sea level transgression and origination quadrants. Note that most Early Cambrian fossils reconstruct in origination zones (figs. 3 and 5). Strictly speaking, fossil collections are not the same as fossil diversity. Nonetheless, the dominance of fossils collected from origination quadrants supports the TPW-LDG model for Early Cambrian time (fig. 5). Continents in extinction quadrants, by comparison, yield 10 to 50 percent less fossil collections than those in origination quadrants. The uptick in fossil occurrences in extinction quadrants by 510 Ma may herald the cessation of the explosive diversification promoted by TPW. Further investigation of well-sampled provinces may further suggest more diversity per collection, in addition to more fossil abundance, in origination quadrants. Alternatively, the TPW-LDG model could be tested by definitively reconstructing Siberia and Baltica, which are well studied paleontologically.

IMPLICATIONS

It has recently been recognized that Metazoa have a deep, cryptic ancestry extending back through Ediacaran time. Molecular clocks (Erwin and others, 2011), biomarkers

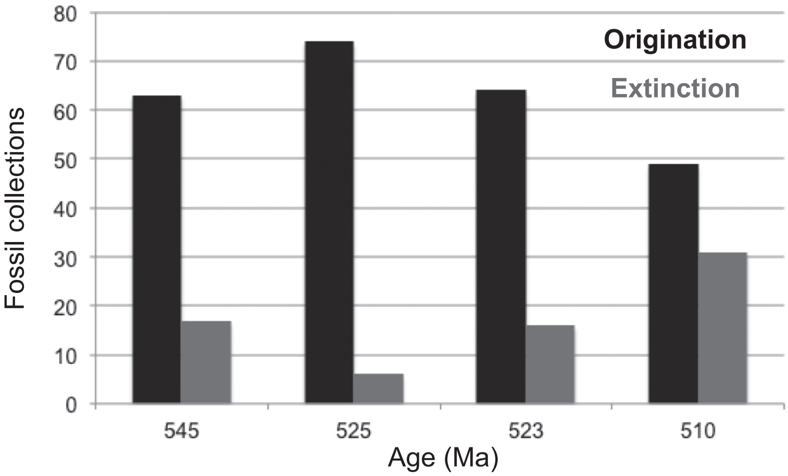

Fig. 5. Number of fossil collections in origination and extinction quadrants through time. Calculated for fossil collections in each quadrant for each time slice throughout the TPW rotation depicted in figure 3.

(Love and others, 2009), Ediacara faunal animal ancestors (Narbonne, 2005), terminal Ediacaran biomineralization (Wood and others, 2002), and Ediacaran-Cambrian secular diversification of ichnofauna (Seilacher and others, 2005) all predate the iconic Cambrian explosion. These early innovations, while environmentally revolutionary in their own ways (Sperling and others, 2013), failed to spawn an "explosion" of lineage diversity or morphological disparity until Cambrian time. We suggest that the timing and magnitude of this "explosion" reflects the coincidence of genomic sophistication with special, quadrential biogeography and low freeboard suitable for continental flooding by TPW-driven transgression. By this we maintain that a certain amount of time followed, for example, stem group triploblastic origination before genetic regulatory mechanisms and other elements of genomic architecture (Erwin and others, 2011) were sufficiently organized, duplicated, and transposed to be poised for repeated, independent innovations of wholesale body plan (Davidson and others, 1995).

Recognition of the stochastic aspect of body plan innovation is important for any understanding of the Cambrian explosion (Marshall, 2006). While diversity probably increments in proportion to increase of genetic mutations modulated by allopatric environmental effects, disparity (the evolutionary count of different body plans) should depend mostly on wholesale re-organization of genetic cassettes by exaptation of biochemical pathways and genetic regulatory mechanisms (Davidson and others, 1995). In principle, early Paleozoic TPW can provide a causal explanation for both diversity and disparity increases by increasing diversity at a time when genetic patterns were being generated (Kirschvink and others, 1997; Kirschvink and Raub, 2003). Phylogenetic and physiological innovation among Metazoa has become widely recognized as much as 100 Myr prior to the Cambrian explosion (Erwin and others, 2011). We suggest that the iconic early Cambrian phylum-level diversification strongly reflects the chance coincidences of TPW acting upon the paleogeography of that age.

The TPW-LDG hypothesis is more specifically testable than previous Cambrian Explosion hypotheses which neglect paleogeography altogether, or assume static continental drift. When simple TPW-associated allopatric speciation effects are considered for the contingent biogeography of Early Cambrian time, enhanced evolutionary rates are expected as an effect of varying one boundary condition—paleogeography—alone (figs. 3 and 5). That TPW-driven sea level anomalies also should promote ecological tiering, specialization, and allopatry while increasing gross ecospace further underscores the unifying potential of our hypothesis. We acknowledge that other processes exist which are important to the functioning of an ecosystem, and which surely affect species diversity. There may have been previous TPW episodes in Ediacaran time (Raub and others, 2007; Mitchell and others, 2011) during the cryptic metazoan ancestry, however global paleogeography was not yet suited to exploit the consequences for the LDG of those specific TPW rotations. Atmospheric oxygenation proceeded apace through the Ediacaran Period expanding available niches and hosting ever more sophisticated ecological tiering, but until genetic regulatory mechanisms passed census, connectivity, and redundancy thresholds in Cambrian time, wholesale innovations to disparity limited the biosphere's capacity for sympatry and allopatry to boost diversity. We maintain that the TPW-LDG hypothesis developed herein is both more specifically testable and more likely to dominate the response of diversity dynamics to physical paleogeographic changes.

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