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The (Paleo)Geography of Evolution: Making Sense of Changing Biology and Changing Continents

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Abstract During the voyage of the H.M.S. Beagle, Charles Darwin quickly realized that geographic isolation led to significant changes in the adaptation of local flora and fauna (Darwin 1859). Genetic isolation is one of the well-known mechanisms by which adaptation (allopatric speciation) can occur (Palumbi, *Annu Rev Ecol Syst* 25:547–72, 1994; Ricklefs, *J Avian Biol* 33:207–11, 2002; Burns et al., *Evolution* 56:1240–52, 2002; Hendry et al., *Science* 290:516–8, 2009). Evolutionary changes can also occur when landmasses converge or are “bridged.” An important and relatively recent (Pliocene Epoch) example known as the “Great American Biotic Interchange” allowed for the migration of previously isolated species into new ecological niches between North and South America (Webb 1985, *Ann Mo Bot Gard* 93:245–57, 2006; Kirby and MacFadden, *Palaeogeogr Palaeoclimatol Palaeoecol* 228:193–202, 2005). Geographic isolation (vicariance) or geographic merging (geodispersal) can occur for a variety of reasons (sea level rise, splitting of continents, mountain building). In addition, the growth of a large supercontinent (or breakup) may change the climatic zonation on the globe and form a different type of barrier for species migration. This short review paper focuses on changing paleogeography throughout the Phanerozoic and the close ties between paleogeography and the evolutionary history of life on Earth.

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Keywords

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Paleogeomagnetism and Paleogeography 36

Reconstructing past maps of the Earth requires the ability to determine both the age of the rocks and the paleoposition of the rocks at the time they formed. Modern geochronological methods such as uranium–lead (U–Pb) and argon–argon (Ar–Ar) provide precise constraints on the ages of igneous, metamorphic, and sedimentary sequences. When these geochronologic data are tied to the fossil record, it is possible to determine the rates of evolutionary change as well as pinpoint time intervals of radiation and extinction (Bowring and Erwin 1998). Advances were also made in the study of paleomagnetism that allow us to precisely determine the paleolatitude of ancient landmasses (Van der Voo 1993). The basic assumption in paleomagnetic studies is that the Earth's magnetic field behaves in a dipolar fashion when integrated over a sufficient time interval (Meert 2009). The time required for the average position of the geomagnetic field to approximate the position of the spin axis is thought to be on the order of 7,000–10,000 years. The so-called time-averaged geocentric axial dipole field (or GAD for short) allows us to use the inclination of the magnetic field to position the continents at the proper latitude. In a geocentric axial dipole field, the relationship between inclination and latitude is given by the formula:

$$\tan(\text{Inclination}) = 2 \times \tan(\text{Latitude})$$

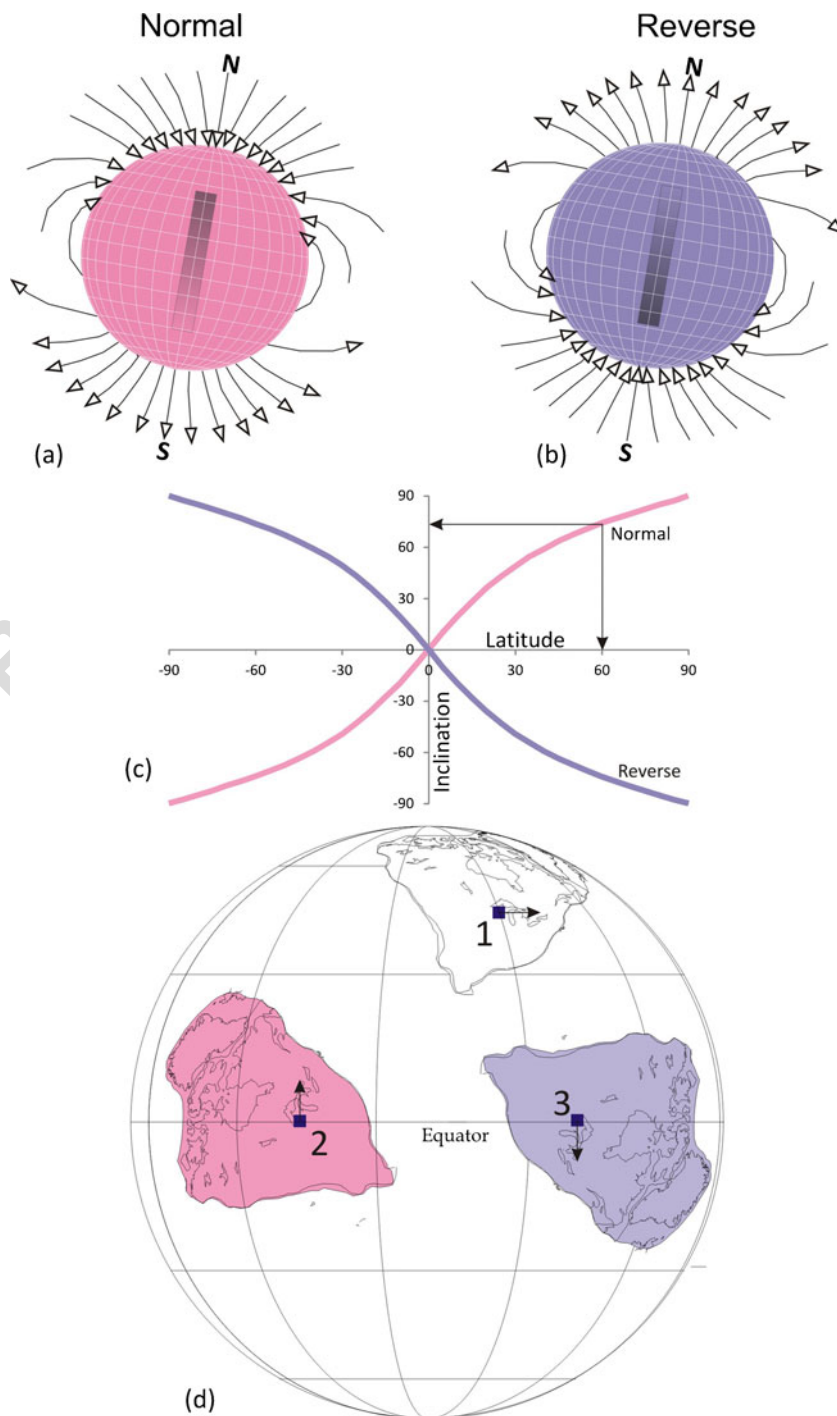
In a GAD field, the declination recorded by the rock will point either to the north geographic pole (normal field) or to the south geographic pole (reverse field). Any measured declination difference from north or south recorded by the ancient rocks thus indicates the amount of rotation the

67 continent has undergone since formation of the rock. These
 68 principles are illustrated in Fig. 1a–d. Because the geocentric
 69 axial dipolar field is symmetric, the determination of
 70 absolute paleolongitude is unconstrained in reconstructions.
 71 To help alleviate the problem of longitudinal uncertainty,
 72 paleomagnetists rely on additional data to help constrain
 73 relative paleolongitudes between the different continents.
 74 Relative paleolongitude can be constrained via ocean floor
 75 magnetic anomalies, matching geological features (such as

mountain chains) or by the distribution of certain fossils (see
 for example Cocks and Torsvik 2002). Because ocean floor
 magnetic anomalies can only be reliably traced back to
 Mesozoic time, reconstructions of Paleozoic and earlier
 continental reconstructions rely almost exclusively on faunal
 and geological comparisons (Meert and Lieberman 2004;
 Cocks and Torsvik 2002).

The mechanisms by which rocks can acquire a memory
 of an ancient magnetic field are many and varied. A

Fig. 1 **a** The structure and magnetic inclination lines for a “normal” (e.g. north seeking) geocentric axial dipole. The spin axis of the Earth is coincident with the magnetic dipole. **b** The structure and magnetic inclination lines for a “reverse” (e.g. south-seeking) geocentric axial dipole. The spin axis of the Earth is coincident with the magnetic dipole. **c** The relationship between magnetic inclination and latitude for both *Normal* (N) and *Reverse* (R) magnetic fields. As an example, the magnetic inclination at 60 degrees north in a normal field will be ~74 degrees. **d** Hypothetical sampling location on North America. The measured ancient declination in the rock is shown by the arrow and the measured ancient inclination in the rock is given as $I=0$ in this example. **2** Reconstruction of the continent assuming a normal magnetic field existed during formation of the rock. Notice how the *arrow* now points to the north and the sampling location is positioned at the equator according to the dipole formula. **3** Reconstruction of the continent assuming a reverse magnetic field existed during the formation of the rock. Notice how the declination now points due south and the sampling location is positioned at the equator according to the dipole formula



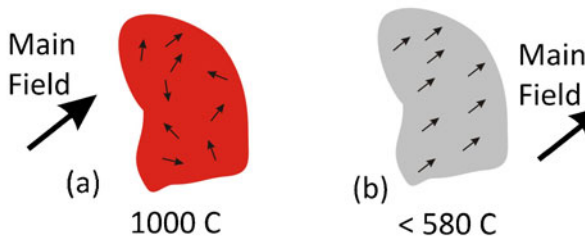
85 comprehensive discussion of remanence acquisition/de-
 86 struction/alteration in rocks is beyond the scope of this
 87 article; however, a detailed description can be found in
 88 Butler (1991). For the purposes of this paper, we review
 89 two mechanisms by which sedimentary and igneous rocks
 90 can acquire a “permanent” memory of the ancient field.
 91 Magnetic minerals in igneous rocks (in particular titanium-
 92 bearing magnetite) crystallize at elevated temperatures. As
 93 the rock cools below a certain temperature (~580 °C for pure
 94 magnetite), the magnetic spin moments in the mineral align
 95 themselves with the ambient field (in this case the ancient
 96 Earth's magnetic field). This thermoremanent magnetization
 97 (or TRM) is illustrated schematically in Fig. 2a. Once this
 98 direction is locked into the rock, it will remain locked in for
 99 extended periods of geologic time provided the rock is not
 100 subjected to significant heating or chemical changes.

101 Sedimentary rocks may acquire a memory of the ancient
 102 field in several ways. One important mechanism of remanence
 103 acquisition occurs as a grain of magnetite or hematite (rust)
 104 settles to the bottom of the ocean or lake. In the upper parts of

105 the water column, the particles are influenced by the Earth's
 106 magnetic field, but perturbations in the water column prevent
 107 alignment. As the particles reach the quieter interface between
 108 the water column and the sediments, they will align them-
 109 selves with the magnetic field and “lock-in” the direction of
 110 the field. This is the primary mode of remanence acquisition in
 111 sandstones, siltstones and clays, and is called “detrital reman-
 112 ent magnetization” and is shown in Fig. 2b. In other sedi-
 113 mentary rocks, magnetic minerals may form via chemical
 114 processes and acquire a memory of the field as they
 115 grow to a critical size. This method is called “chemical
 116 remanent magnetization”. As long as the chemical event
 117 producing the magnetization in the rocks takes place
 118 close to the time of deposition, it can be reliably used
 119 to reconstruct the continents.

120 The magnetic directions locked into the rocks can be
 121 studied by collecting oriented samples in the field and then
 122 measuring the directions recorded in those rocks back in the
 123 laboratory. In practice, paleomagnetists will sample several
 124 layers of sedimentary rock or many flows of igneous rocks
 125 to assure averaging to the GAD field.

Thermal Remanence Acquisition



Detrital Remanence Acquisition

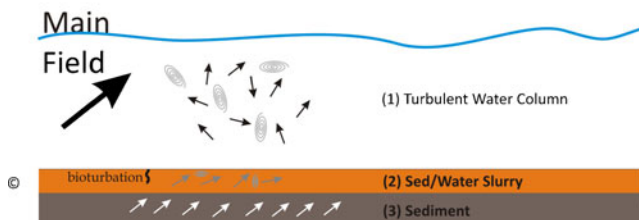


Fig. 2 a Sketch of thermal remanence acquisition in an igneous rock. Magnetite spin axes are randomly distributed in a crystallizing magma at 1,000 °C. b As the rock cools below the Curie temperature of magnetite, the spin moments align with the ambient Earth's field and become locked into the rock. c Idealized sketch of detrital remanence acquisition. As the magnetic particles fall through the water column, they show no preferential alignment due to small currents and eddies within the water column (point 1), at point (2), the particles reach the sediment water interface and begin to align with the ambient field though some minor disturbance is possible due to bioturbation or other small currents/eddies within the slurry, and at point (3) the mineral grains become permanently aligned and “locked-in” with the ambient field

Biogeography and Paleogeography: Some Examples

126 In general, reconstructions of the globe back to about 150
 127 million years can be reliably obtained by studying the pattern
 128 of ocean floor magnetic anomalies along with paleomagnetic
 129 data from the continents. Attempts to reconstruct the globe
 130 prior to 150 million years require integration of various types
 131 of data in addition to paleomagnetism in order to reliably
 132 produce paleogeographic maps. In the following sections, I
 133 show how paleogeography has influenced thinking about
 134 evolutionary changes and vice-versa for selected time slices
 135 of the Phanerozoic. The paper briefly examines the paleoge-
 136 ography/biogeography at the end of the Cretaceous Period (85
 137 million years), the end of the Paleozoic (~260 million years)
 138 and the Ediacaran–Cambrian transition (~570–530 million
 139 years) as examples of the interplays between evolutionary
 140 history and paleogeography.
 141

Late Cretaceous—85 Million Years

142 The Middle Cretaceous (from about 120–100 million years)
 143 was an interval of major changes in atmospheric chemistry,
 144 the pace of sea-floor spreading was high, the magnetic field
 145 was in a stable normal polarity “superchron” and average
 146 global temperatures were on the rise. By the late Cretaceous,
 147 the globe was ice free and a greenhouse climate resulted in
 148 elevated sea levels and further isolation of the splitting
 149 continents.
 150

151 A reconstruction of the globe at 85 million years is
 152 shown in Fig. 3. At 85 million years, the dramatic changes

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153 that occurred during the Middle Cretaceous were waning.
 154 The Earth's magnetic field which had been of a single
 155 normal polarity for the preceding 40 million years began
 156 to reverse. By 85 million years, the Atlantic Ocean between
 157 South America and Africa was open along with a wide
 158 Central Atlantic. The formation of the Atlantic and Indian
 159 Oceans separated the once landlocked Gondwana continent
 160 that consisted of India, Madagascar, Antarctica, Australia,
 161 Africa, and South America (see Fig. 4). According to
 162 many paleogeographic models, significant connections
 163 between African fauna and the other Gondwana land-
 164 masses (Fig. 3) were severely diminished due to the
 165 opening of the Southern Atlantic and Indian Oceans
 166 along with elevated sea levels (Hedges et al. 1996,
 167 2001; Gheerbrant and Rage 2006).

168 In contrast, several lines of biogeographic analysis sug-
 169 gest that there were pathways for faunal transfer between the
 170 Gondwana continents even into the Paleocene (Vences et al.
 171 2003; Sereno et al. 2004; Van Bocxlaer et al. 2006; Bossuyt
 172 et al. 2006). While isolation and rising sea levels played a
 173 large role in creating barriers to biological connections,
 174 there must have remained some pathways for significant
 175 faunal exchanges (Jacobs et al. 2011). In particular, Jacobs
 176 et al. (2011) discuss possibilities of “Noah's Ark,” “Beached
 177 Viking Funeral Ships,” and “landspans” across the Gondwana
 178 landmasses following the initial work of McKenna (1973).
 179 “Noah's Arks” are segments of continental crust that rift away
 180 from their larger landmasses and carry with them their biota.
 181 The “arks” result in initial isolation of the organisms, but they
 182 may also “dock” with a new landmass and introduce their
 183 species to a new area.

184 “Beached Viking Funeral Ships” are similar in that they
 185 are also segments of continental crust rifted from one area,

186 but these also may later collide and join new continental
 187 regions where the (extinct) biota carried on the Funeral ship
 188 are now found on a new landmass. Both “Noah's Arks,”
 189 “Docked Noah's Arks” and “Beached Viking Funeral
 190 Ships,” are expected occurrences during continental rifting
 191 and later collision (Jacobs et al. 2011).

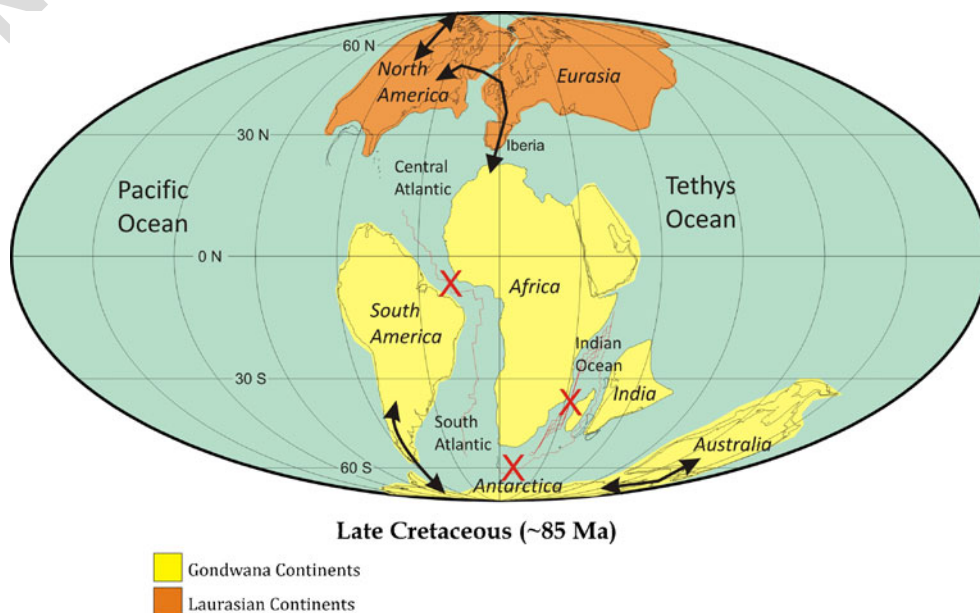
192 India and Madagascar are argued to be good examples of
 193 “Noah's Arks” formed during the rifting of Gondwana. India
 194 and Madagascar were isolated from Africa and Australo-
 195 Antarctica and ultimately from each other during the
 196 Cretaceous and Cenozoic. Jacobs et al. (2011) show that
 197 India–Madagascar shared the same “Noah's Ark” dinosaur
 198 fauna until their split in the Late Cretaceous. India was also
 199 argued to be a good example of a “beached Viking Funeral
 200 Ship” due the fact that its older vertebrate fossils now reside
 201 on the Asian continent.

202 Lastly, Jacobs et al. (2011) also propose a possible series of
 203 “landspans” between the Gondwana continents that may have
 204 allowed for transfers of biota between the various elements of
 205 land before significant separation was achieved by continuing
 206 drift; opening of the Indian, Atlantic, and Southern Oceans;
 207 and falling sea levels. Due to its long journey northward to
 208 Asia, it is possible that India interacted with island arcs or
 209 other continents before final docking resulting in a more
 210 cosmopolitan Cretaceous fauna (Chatterjee and Scotese
 211 1999; Briggs 2003; Chatterjee et al. 2009).

212 End Paleozoic/Early Mesozoic—260 Million Years

213 While the Cretaceous was a period of disaggregation of
 214 large landmasses, the end of the Paleozoic witnessed the
 215 formation of the supercontinent Pangea (Fig. 4). The bioge-
 216 ography of Pangea was influenced by geodispersal,

Fig. 3 Late Cretaceous paleogeography (~85 million years). The continents shaded in yellow outline represent the former landmasses of Gondwana and those shaded in orange represent the former landmasses of Laurasia. Laurasia + Gondwana were united in the Pangean supercontinent (see Fig. 4). The red X's denote presumed physical barriers to faunal migration across Gondwana landmasses. The arrows denote faunal pathways evident in the fossil record



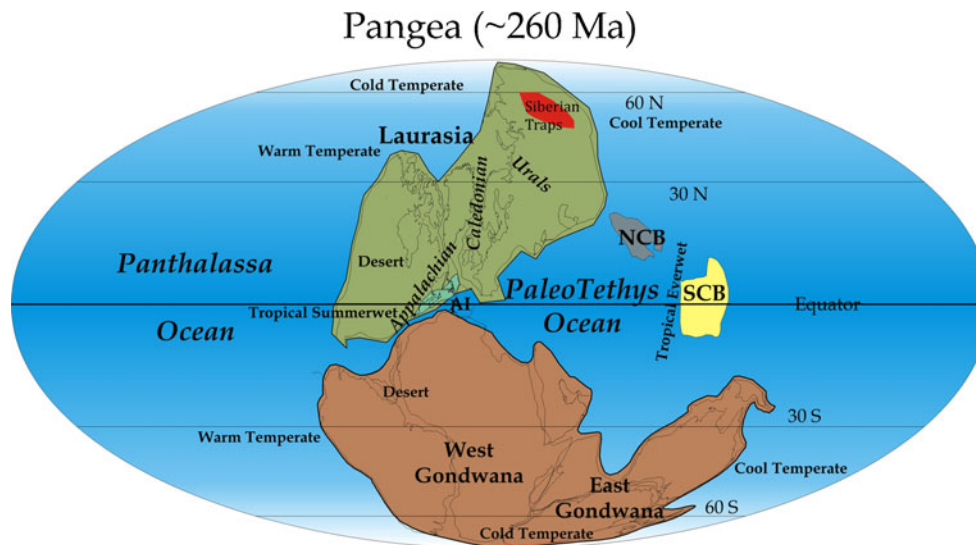


Fig. 4 The supercontinent Pangea during the Late Paleozoic (~260 million years). The supercontinent was composed of two large halves (Gondwana in the south and Laurasia in the north). The “pac-man”-shaped Paleotethyan ocean was located to the East of the supercontinent and separated from the larger Panthalassan ocean by the North China (NCB) and South China (SCB) blocks. Approximate locations of

the strong zonal climatic zones are also shown in the figure. The locations of the Appalachian, Caledonian, and Uralian Mountains are shown within Laurasia. AI = Armorica, Avalonia, and Iberia. The location of the slightly younger Siberian traps is also shown for reference

217 vicariance, and strong climatic zoning. Species were isolated
 218 ed by the uplift of major mountain chains along the suture
 219 zones of Pangea and by the lowering of sea level associated
 220 with climatic changes in the Permian, but there were also
 221 numerous opportunities for dispersal of biota across the large
 222 landmass and surrounding Panthalassic and Paleotethys
 223 Oceans (Ross and Ross 1985; Perez-Huerta 2007).

224 Pangea also extended through a wide range of climatic
 225 zones as the continental landmass stretched from pole to
 226 pole (Fig. 4). The poles were cold temperate with winter ice.
 227 Interiors of the larger continents (West Gondwana and
 228 Laurasia) were deserts and normal latitudinal zoning was
 229 present elsewhere (see Fig. 4). This strong climatic zoning
 230 may also have influenced provinciality as (for example)
 231 certain tetrapod fossils appear to be restricted to specific
 232 latitudinal zones in the absence of any physical barriers
 233 (Sidor et al. 2004; Whiteside et al. 2011).

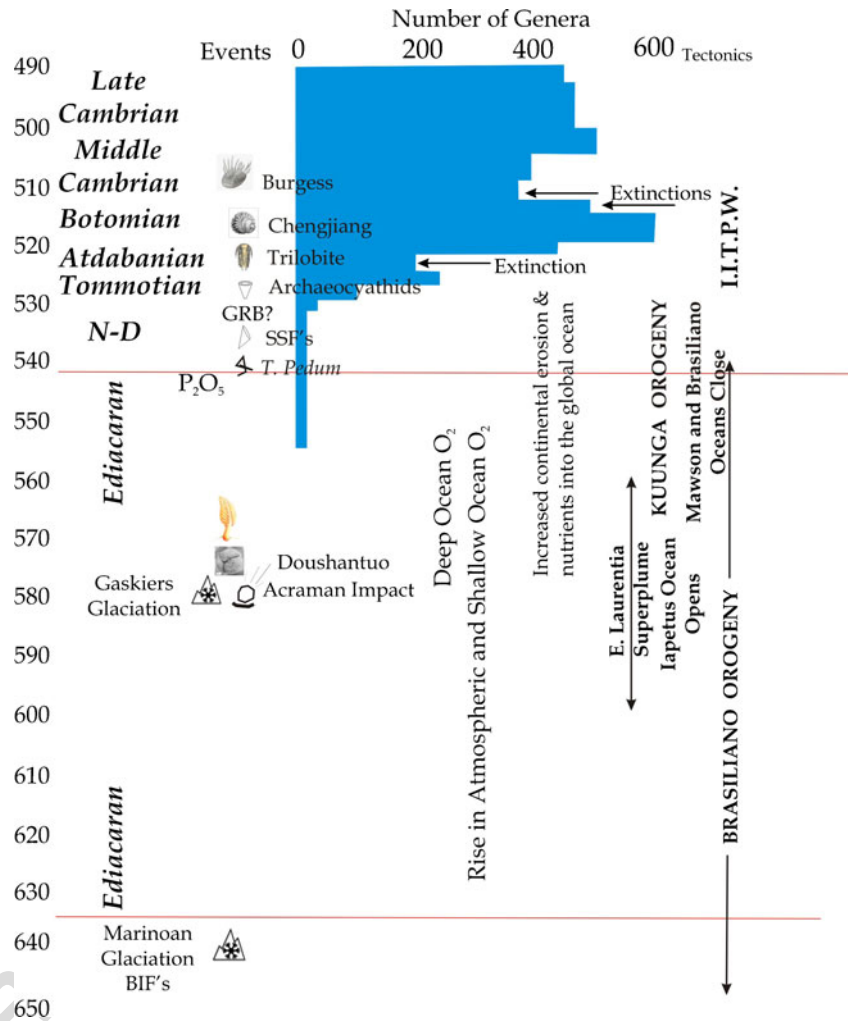
234 It is also interesting to consider the relationship between
 235 the large and connected supercontinent and the mass extinc-
 236 tion that occurred at the close of the Paleozoic (~251 million
 237 years; Benton and Twitchett 2003). Causative mechanisms
 238 for the Permian extinction are diverse and range from the
 239 effects associated with the massive volcanic outpouring of
 240 the Siberian traps, global warming, global cooling, and
 241 ocean anoxia (Benton and Twitchett 2003; Becker et al.
 242 2004). Although the exact cause of the extinction is debated,
 243 the changes in oceanic circulation brought about by the
 244 assembly of Pangea and the fact that the land surface of
 245 the Earth was mostly confined to a single hemisphere should
 246 not be underestimated.

Cambrian—542–525 Million Years 247

248 The interval from 542 to 525 million years spans the interval
 249 of the so-called “Cambrian Explosion.” In a recent article,
 250 Meert and Lieberman (2008) summarized the many “triggers”
 251 for the massive radiation of life during the Cambrian. The root
 252 cause of this expansion of the biosphere remains somewhat of
 253 a mystery though it is clear that a number of external (non-
 254 biological) and internal (biological) changes took place on the
 255 globe during this time. Figure 5 (from Meert and Lieberman
 256 2008) summarizes many of these changes.

257 The paleogeographic setting leading up to the Cambrian
 258 explosion is controversial. Well-dated paleomagnetic poles
 259 sometimes indicate vastly different (or rapidly changing)
 260 paleolatitudes for several continental blocks. In stark con-
 261 trast to modern-day rates of plate motion (approximately
 262 two to eight centimeters per year), the rate of latitudinal
 263 motion implied by some of the paleomagnetic data exceed
 264 40 centimeters per year. These rapid changes in plate con-
 265 figuration were interpreted to reflect dramatic (non-tectonic)
 266 changes in paleogeography due to true polar wander or
 267 inertial interchange true polar wander. In contrast to plate
 268 tectonic motions, true polar wander involves the motion of
 269 the entire lithosphere (+mantle) as a coherent block. True
 270 polar wander occurs due to mass imbalances within the
 271 Earth in an effort to maintain a spin axis that is coincident
 272 with the maximum inertial moment (Fig. 6). In the special
 273 case of inertial interchange true polar wander (or IITPW),
 274 the magnitude of the intermediate inertial axis exceeds the
 275 magnitude of the maximum inertial axis and causes the

Fig. 5 (After Meert and Lieberman 2008) 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 are tied to the timeline along with tectonic, climatic, catastrophic events. Abbreviations used: *GRB*, Gamma ray burst; *T. Pedum*, *Treptichnus pedum* trace fossil; *SSF's*, small shelly fossils; *BIF's*, banded iron formation; *P₂O₅*, phosphatic horizons; *IITPW*, Inertial Interchange true polar wander; *LIP*, large igneous province



276 entire lithosphere and mantle to tumble through 90 degrees
 277 in as little as 15 million years as the Earth's spin axis
 278 realigns to a stable configuration. In the most extreme, but
 279 unlikely scenario, it is argued that an IITPW event took
 280 place immediately preceding the Cambrian explosion and

served as an external trigger for the biological changes in
 Early Cambrian time (Kirschvink et al. 1997).

From the perspective of the paleomagnetist, it is difficult
 to sort out all the conflicting models using only magnetic
 data and arguments abound regarding their significance

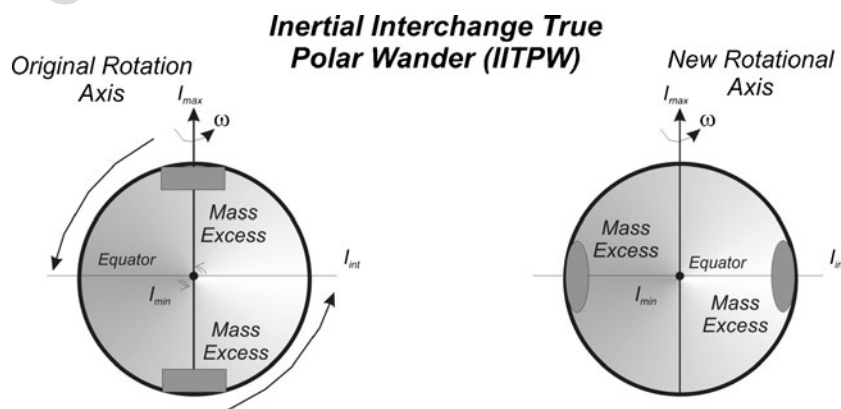
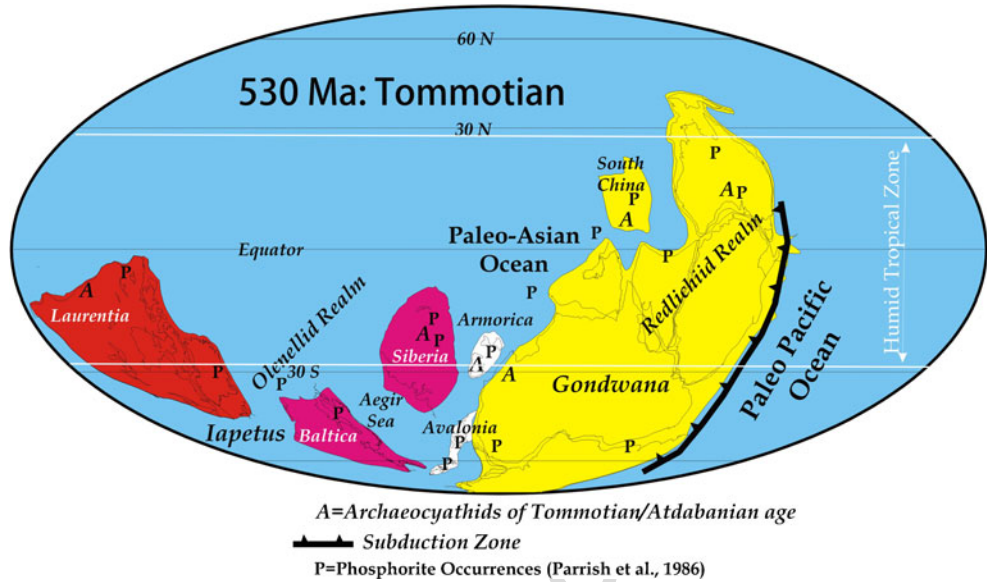


Fig. 6 Cartoon of inertial interchange true polar wander after Meert (1999). In the special case of IITPW, the maximum and intermediate axes of inertia interchange (I_{int} becomes I_{max} and vice versa). The result is that the mantle + lithosphere tumble through 90 degrees. The total

time for this reorganization can be as short as 15 million years and could result in drastic changes in paleogeography in a short period of time. (ω = rotation axis, I_{min} = minimum inertial axis, I_{int} = intermediate inertial axis, and I_{max} = maximum inertial axis)

Fig. 7 (After Meert and Lieberman 2008)
Paleogeographic reconstruction of Tommotian time. Archaeocyathin realms of Tommotian/Atdabanian time are restricted to the humid tropical zone. Locations of major phosphorite deposits are also shown in the figure



286 (Kirschvink et al. 1997; Evans 1998; Meert 1999; Meert et
 287 al. 2007). In an effort to address this conundrum, Meert and
 288 Lieberman (2004) examined the phylogeny of trilobites
 289 (with respect to paleogeography) to test the sensitivity of
 290 paleogeography to vicariance and geodispersal in early
 291 trilobite evolution. Meert and Lieberman (2004) argued
 292 that the rapid changes required by the IITPW hypothesis
 293 would not produce a robust biogeographic grouping of
 294 trilobites such as was documented by Lieberman (1997,
 295 2002). In particular, Meert and Lieberman (2004) showed that
 296 the Redlichiiina and Olenellid realms were well-established by
 297 the Early Cambrian (~530 million years) indicating that the

Eutrilobita had deeper roots into the Ediacaran period and may 298
 have originated in Siberia (Fig. 7; see also Lieberman 2002). 299
 Meert and Lieberman (2008) used one particularly conten- 300
 tious paleogeography to show that these realms were estab- 301
 lished by at least 565 million years (Fig. 8). Thus, while the 302
 physics of IITPW and TPW indicate that both are probable on 303
 Earth, the biogeographic signal of Early Cambrian trilobites 304
 argues strongly against rapid transitions in paleogeography 305
 such as those required by IITPW for the Early Cambrian (and 306
 perhaps Ediacaran). In this example, the evidence from evo- 307
 lutionary biology provides important constraints on our 308
 understanding of an otherwise contentious paleogeography. 309

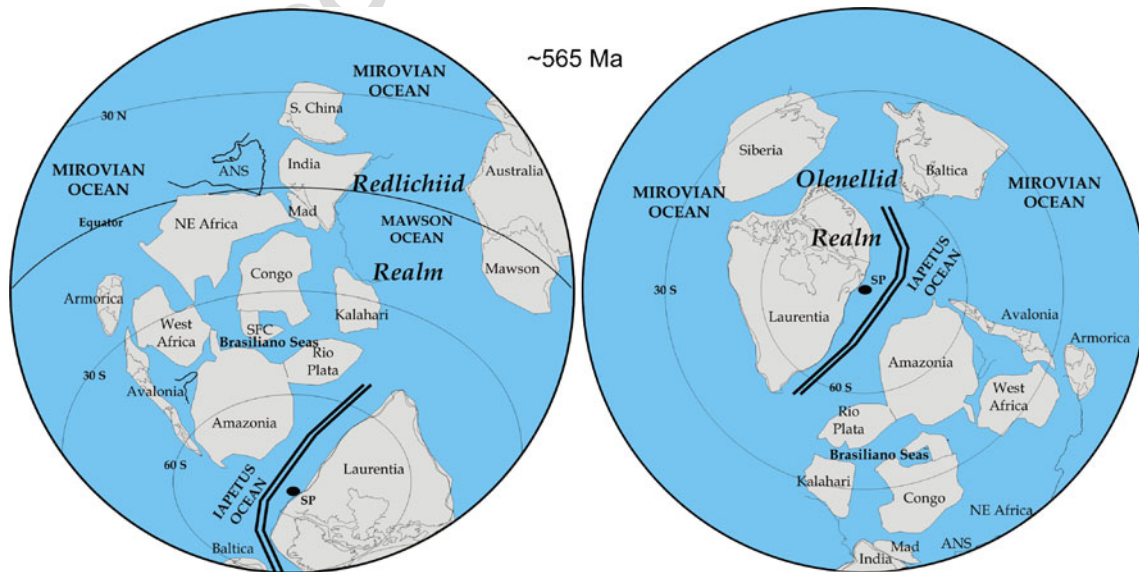


Fig. 8 Paleogeography at 565 million years after Meert and Lieberman (2004, 2008). The birthplace of the Ediacaran biota was along the borders of the Mirovian and Mawson Oceans. A close relationship between Redlichiiid fauna and the margins of the Mawson

Ocean and the Olenellid fauna with the margins of the Mirovian Ocean suggest that the eutrilobites originated and diversified prior to ~565 million years in accordance with some molecular clock studies of extant organisms

310 **Conclusions**

311 Changing paleogeography throughout Earth history played
 312 an important role in evolutionary biology. Paleogeographic
 313 changes influence evolution in myriad ways including, but
 314 not limited to, vicariance, geodispersal, and climatic zonation.
 315 Analysis of how flora and fauna are affected by
 316 changes in plate tectonic setting and concomitant changes
 317 in climate plays an important role in evaluating evolutionary
 318 change. This paper briefly reviews three intervals of time
 319 and gives examples of how biology and paleogeography are
 320 integrated into paleogeographic analyses.
 321

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