

Paleozoic geomagnetism shapes vertebrate evolution

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Background. Despite a fifty-year failure of paleontologists to find a viable connection between geomagnetic polarity reversals and evolutionary patterns, recent databases show that the early appearance, radiation, and diversification of Paleozoic vertebrates tends to occur during periods having frequent collapses of the Earth's geomagnetic field. The transition time during the collapse of the Earth's protective magnetic shield can last thousands of years, and the effects on biota are unknown. Solar and cosmic radiation, volcanism, weather alteration, low-frequency electromagnetic fields, depletion of ozone, and the stripping of atmospheric oxygen have been proposed as possible causes, but previous studies have found no effects.

Methods. Using published databases, we compiled a spreadsheet that shows the first appearance of 1809 age-dated genera with each genus assigned to one of 28 taxonomic groups. From Gradstein's Geologic Time Scale 2012, we delineated 17 Paleozoic zones with either high or low levels of polarity reversals.

Results. From our compilation, we counted 508 Paleozoic vertebrates that first appeared within 20 million-years of the origin of their clade or natural group. These genera represent the initial radiation and diversification of individual Paleozoic vertebrate clades. After compensating for sample-size and external geologic biases, the resulting Pearson's coefficient between these genera and polarity zones equals 0.781. Using 11 commonly accepted clades and assuming a natural competition existed between them, we counted each genus from a clade's inception until it was bypassed by a subsequent clade. Here, Pearson's equals 0.901 with a p-value of <0.000001 . In a blindfold study, we separated the Paleozoic into a dozen equally-sized temporal bins, then 13 bins, up to 31 bins. The mean Pearson coefficient for these bins is 0.810. After calculating coefficients for four distinct taxonomies, two paleomagnetic systems, three systematics for age-dating within geologic stages, and seven independent spreadsheets, the results suggest a strong relationship exists between Paleozoic vertebrates and polarity reversals.

In addition, the earliest species of the major divisions of Paleozoic vertebrates (jawless fish, armored fish, jawed fish, cartilage fish, fish with bones, lobe-finned fish, tetrapods, amphibians, reptiles, and synapsids) first appeared in zones with relatively high levels of polarity reversals.

Discussion. The question: is this apparent connection between geomagnetism and the evolution of Paleozoic vertebrate due to environmental or biologic factors. If biologic, why are vertebrates the only biota effected? And after an indeterminate period of time, how do vertebrate families become immune to the ongoing effects of polarity reversals?

Introduction

Geomagnetic polarity reversals have occurred randomly throughout the Phanerozoic at a rate of two or three times per million years. The transition between the collapse of the Earth's protective magnetic shield and its subsequent regeneration can last thousands of years, and no one knows what the effects on biota during this interim have been in the past or might be in the future. Numerous researchers have searched for answers, both pro and con (Glassmeier, 2010). Uffen first raised the possibility that polarity reversals could increase extinction rates due to harmful solar and cosmic radiation (Uffen, 1963). Others soon pointed out the Earth's atmosphere is our primary shield despite a potential loss of ozone (Crutzen, 1975). Secular variations of a weakening geomagnetic field intensity show enhanced cosmic-ray production of ^{10}Be and ^{36}Cl in the stratosphere (McHargue, 2000). Reinforcing this view, age-dated Greenland ice cores show increasing concentrations of ^{10}Be during polarity excursions (Raisbeck, 2006). Despite active DNA repair mechanisms, all life forms are susceptible to high levels of UV exposure (Glassmeier, 2010). Volcanism (Courtilow, 2007), weather alteration (Harrison, 1974), low-frequency electromagnetic fields (Liboff, 2013), depletion of ozone (Huang, 2017), and the stripping of atmospheric oxygen (Wei, 2014) have been proposed as possible culprits, but Glassmeier and Vogt in their review of *Magnetic Polarity Transitions and Biospheric effects* listed numerous causations but found no evidence of effects (Glassmeier, 2010). Pechersky's study found minimal correlation between biozones and geomagnetic polarity (Pechersky, 2012). And analysis of Sepkoski's 2002 marine fossil compendium shows virtually no alignment of biota and polarity reversals—with one exception, family-level Paleozoic vertebrates.

The Paleozoic is the only geologic era of the Phanerozoic with two polarity superchrons (the Kiaman and Moyero) plus six polarity chrons lasting more than 6 myr. The question: can these polarity chrons be correlated with Paleozoic vertebrates using current taxonomic compilations.

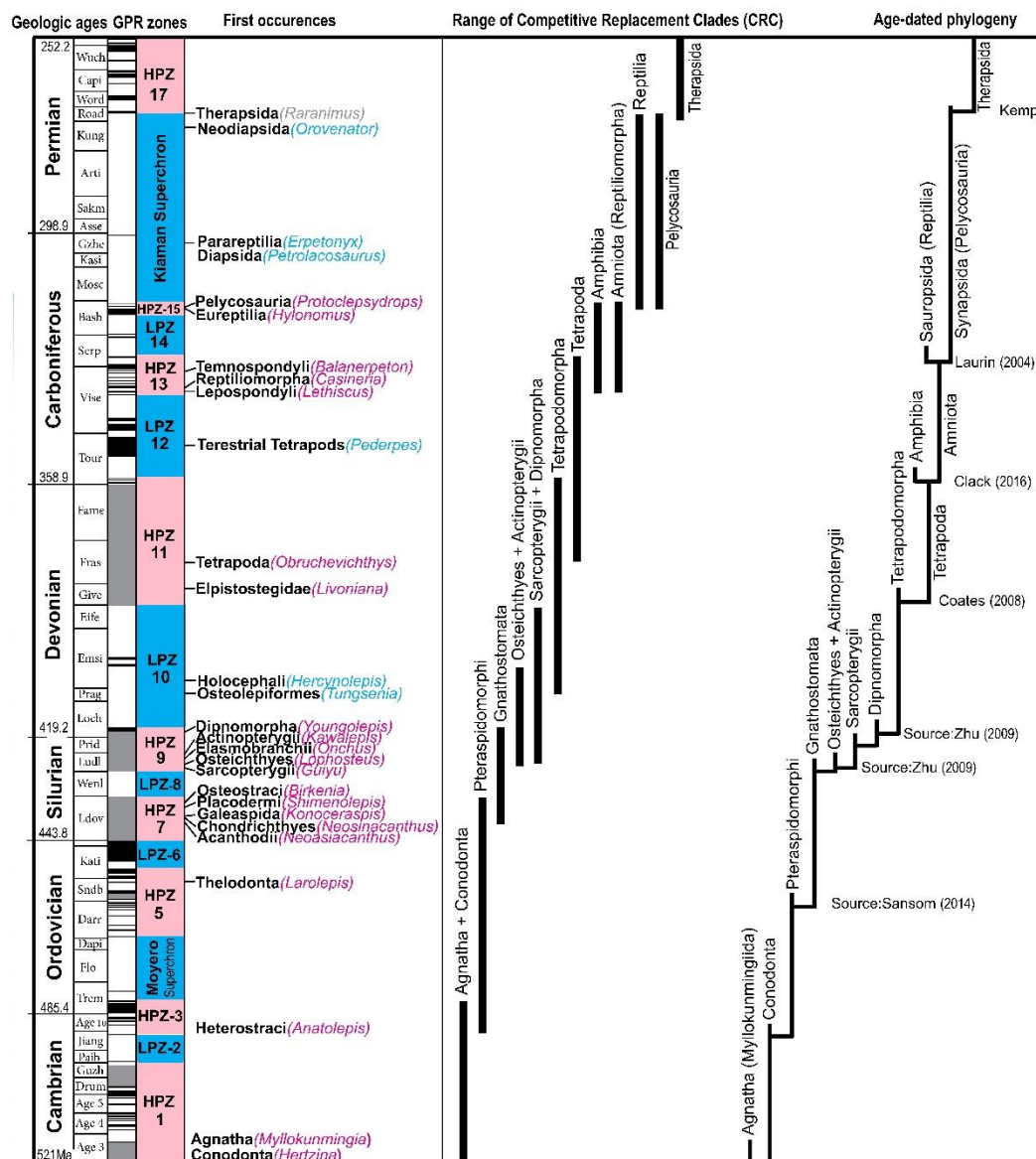
Methods

The Paleobiology database (paleodb.org) is an ideal source to build a compilation of genus-level Paleozoic vertebrates, but it is not yet fully complete. Therefore, we added Benton's list of terrestrial vertebrates from the supplemental in *The first half of tetrapod evolution* (Benton, 2013), plus data from Zhao and Zhu's *Siluro-Devonian vertebrate biostratigraphy and biogeography of China* (Zhao, 2009), and Sepkoski's 2002 marine compendium. From these sources, we compiled a spreadsheet that lists the first appearance (FAD) of 1809 genera that are dated by geologic stage as specified by The Geologic Time Scale 2012 (Gradstein, 2012). In addition, each genus was assigned to one of 28 taxonomic groups as defined by Paleobiology or by Benton in the appendix of his book, *Vertebrate Palaeontology* (Benton, 2013). Fossilworks (fossilworks.org) clarified taxon classification when necessary.

We dated 303 individual Paleozoic geomagnetic polarity reversals taken from Gradstein, 2012, Ogg, 2016, Hansma, 2015, Lanci, 2013, Hounslow, 2016, and Opdyke, 2009. From their data, we delineated nine Paleozoic zones with high levels of polarity reversals (HPZ) lasting 130.4 million years (myr), and eight low-level polarity zones (LPZ) lasted 138.4 myr. See Figure 1. Each of the 1809 genera was assigned to a specific polarity zone (see supplemental, Data S1).

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Figure 1 Polarity Reversals and Distribution of Paleozoic vertebrates.



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Columns (1) and (2): geologic periods and stages age-dated from Gradstein 2012. Column (3): geomagnetic polarity reversals from multiple sources (black is normal polarity; white is reversed; gray represents multiple reversals). Column (4): high (red) and low polarity (blue) zones. Column (5): FAD of originating genus of 28 clades. Column (6): Ranges of competitive replacement clades (CRC) from their origination until bypassed by a succeeding clade. Column (7): Possible age-dated phylogeny of Paleozoic vertebrates, with sources.

An insignificant 52.9% (958/1809) of the compiled genera originated in high polarity zones. Neither marine fauna at 51.0% (577/1131), nor post-Devonian tetrapods at 56.2%, (678/381) showed significant improvement. Nonetheless, the first appearance of every major divisions of Paleozoic vertebrates (agnathans, conodonts, pteraspidomorphs, gnathostomes, osteichthyans, actinopterygians, sarcopterygians, tetrapods, amphibians, reptiles, and synapsids) occurred in high-polarity zones. Twenty-three of Benton's 28 class-level natural groups and monophyletic clades of vertebrates (82.1%) first appeared in high polarity zones (see Table 1).

We used multiple sources to define the originating species and its FAD of 28 monophyletic and polyphyletic clades (Table 1). The post-origin time of an individual genus is the time in millions of years (myr) after the FAD of the clade's originating genus. We counted all genera with a post-origin time of less than 5 myr, then calculated the percentages of genera originating in high polarity zones compared to the total genera. Likewise, we found the percentages of high-polarity genera with a post-origin time of zero to 10 myr, then 0-15 myr, stepwise up to 50 million years. Figure 2a shows the percentages for the intervals, 0-5 myr through 0-50 myr. Note the percentage falloff after 20 myr.

Now, the question becomes more specific: does the early radiation and diversification of a clade or natural group correlate with polarity reversals?

Results

From our final compilation of 1809 genera, we counted 508 Paleozoic vertebrates (abbreviated 20G) with a post-origin time of less than 20 million-years. These 20G genera represent the initial radiation and diversification of individual Paleozoic vertebrate clades. 74% of the 508 20G genera are found in high-polarity zones.

Extrinsic biases such as outcrop area and accessibility are known to affect the distribution of fossils (Peters, 2001). Sample-size is a potential problem (for example, we have only five actinopterygians compared to over 200 therapsids). To partially nullify these biases, we simply divided the 20G genera by the total genera within each polarity zone (see Tables 2 and 3), then correlated those percentages to the rate of polarity reversals per million years for each of our 8 high and 7 low polarity zones. The resulting Pearson's correlation coefficient equals 0.674 with a p-value of .00303. After correcting for the Cambrian problem (see calculations section), Pearson's equals 0.781 with a p-value of .0003.

The 20G vertebrates represent the original diversification and radiation of vertebrate clades. They are defined as all genera found within a twenty-million period after the FAD of the originating fossil of each clade, but new discoveries can alter those dates, and the twenty-million-year cutoff, although statistically significant, is obviously arbitrary. Nor will Benton's—or anyone's—choice of clades be universally accepted. In reality, reclassification of a single genus might disrupt the 20G statistical results.

A more reliable and simplified system is to replace the 28 clades with only 11 commonly-accepted major groups, and assume a natural competition exists between them. The Early Cambrian 'agnathans' (including conodonts) are counted as positive until the first appearance of

the pteraspidomorphs with their protective scales and armor; the jawless fish until the gnathostomes; the jawed fish until the osteichthyans; the bony fish until the sarcopterygians; the lobe-finned fish until the tetrapodomorphs; the tetrapodomorphs until the Upper Devonian tetrapods; the early tetrapods until the amphibians; the temnospondyls and lepospondyls until the amniotes; the reptiles and pelycosaurs until the therapsids. We counted each genus from a clade's inception until it was bypassed by a subsequent clade. 538 Paleozoic genera were assigned as positive to these competitive replacement clades (CRC). 397 of the CRC genera (73.8%) are found in high-polarity zones. Pearson's correlation equals 0.691 with a p-value of .00215. After correcting for the Cambrian problem (see calculations section), Pearson's equals 0.901 with a p-value of <0.000001.

Choosing the boundary of a paleomagnetic zones is somewhat arbitrary, and so in a blindfold study, we separated the Paleozoic into a dozen equally-sized temporal bins (<12 bins are statistically insignificant). For each bin, we counted the CRC genera, total genera, and number of polarity reversals, then we compared the polarity reversals to the CRC genera divided by the total genera within each bin. Pearson's correlation equals 0.846. We also separated the Paleozoic into 13 bins (Pearson's $\rho=0.865$), then 14 bins (Pearson's $\rho=0.864$), and up to 30 equally-sized bins. For 15 bins, $r=0.831$; 16 bins, $r=0.839$; 17 bins, $r=0.847$; 18 bins, $r=0.847$; 19 bins, $r=0.834$; 20 bins, $r=0.785$; 21 bins, $r=0.792$; 22 bins, $r=0.784$; 23 bins, $r=0.731$; 24 bins, $r=0.786$; 25 bins, $r=0.813$; 26 bins, $r=0.791$; 27 bins, $r=0.83$; 28 bins, $r=0.818$; 29 bins, $r=0.738$; 30 bins, $r=0.741$. For CRC genera, the mean Pearson's correlation coefficient for these 19 bins is 0.810. For 20G genera, the mean Pearson's correlation is 0.602. No corrections were made for the Cambrian genera when calculating bins.

It is apparent that Paleozoic vertebrates originated and radiated in alignment with polarity reversals. Each of the 10 major divisions of Paleozoic vertebrates first appear in a high-polarity zone. Table 4 shows correlation coefficients and p-values for four taxonomies (Paleobiology's, Benton's classification, a final composite system, and the competitive replacement clades); two paleomagnetic references (Gradstein, 2012, et al. and Ogg, 2016); occurrences vs. total genera; basal, median, and proportional dating of geologic stages; 20G and CDC genera with seven independent spreadsheets (see the Detailed Methodology section for a description of the seven spreadsheets). After correcting for the Cambrian problem, the CRC genera have an average p-value of <0.001 (highly significant); half of the 20G systems are <0.001 (highly significant) and the other half, <0.05 (significant). These results, shown in Table 4, strongly suggest a relationship exists between Paleozoic vertebrates and geomagnetic polarity reversals.

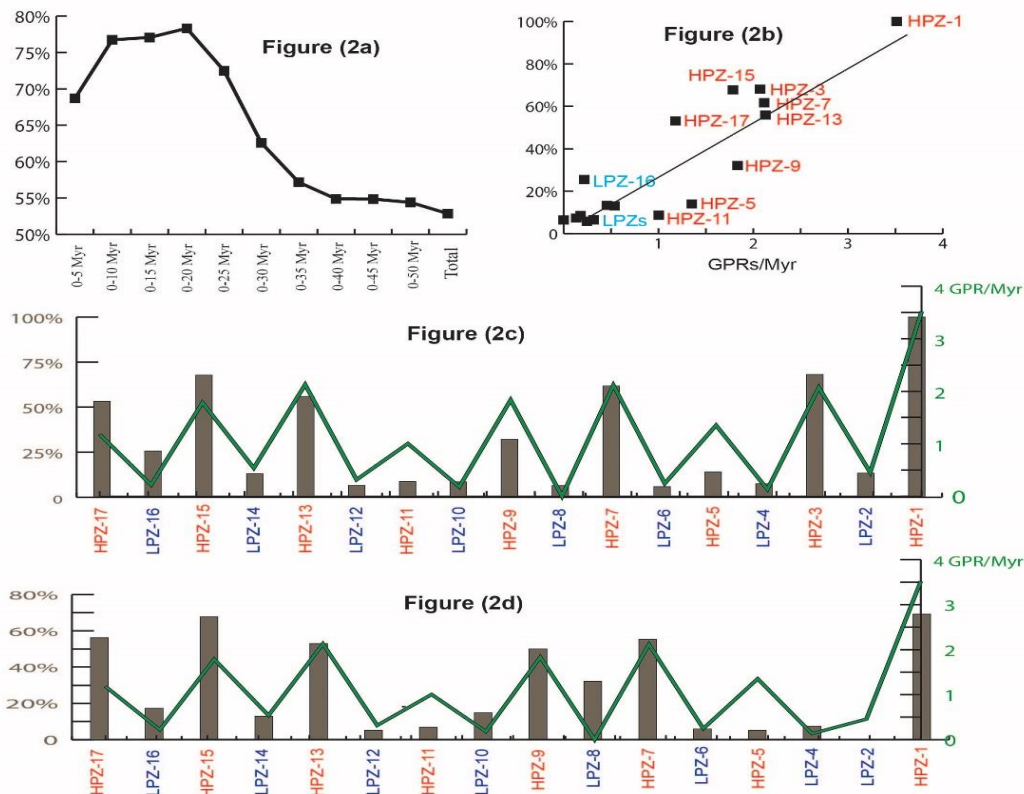
165 **Table 1 | FAD of earliest known species of Paleozoic clades** (reds are high-polarity zones).

Major Clades	Genus	Geologic stage	Range	Median	Zone	Source
Synapsida (Pelycosauria)	Protoclepsyrops	Westphalian A	318.6-317.8	318.2	HPZ-15	Paleobiology
Reptilia (Eureptilia)	Hylozoum	Westphalian A	318.6-317.8	318.2	HPZ-15	Paleobiology
Amniota (Reptiliomorpha)	Casineria	Asbian	336.5-332	334.2	HPZ-13	Paleobiology; See Note 1
Amphibia (Lepospondyli)	Lethiscus	Early Asbian	336.5-334.2	335.4	HPZ-13	See Note 1
Tetrapoda	Obruchevichthys	Frasnian	382.7-372.2	377.4	HPZ-11	Paleobiology
Osteichthyes	Lophosteus	Late Gorstian	426.5-425.6	426	HPZ-9	Sepkoski
Sarcopterygii	Guigu	Gorstian	427.4-425.6	426.5	HPZ-9	Zhoa & Zhu
Gnathostomata (Placodermi)	Shimenolepis	Middle Telychian	436.8-435.1	436	HPZ-7	Zhoa & Zhu
Pteraspidomorphi	Anatolepis	Sunwaptan, Mid	490.8-488.5	489.6	HPZ-3	Smith (2007); see Note 4
Agnatha	Myllokunmingia	Aldabanian	521-516.1	518.6	HPZ-1	Paleobiology
Benton's Clades						
Lepidosauromorpha	Lacertulus	Early Wuchiapingian	259.8-257	258.4	HPZ-17	Paleobiology
Archosauromorpha	Eorasaurus	Capitanian	265.1-254.2	259.7	HPZ-17	Paleobiology
Neodiapsida	Orovenator	Kungurian	279.3-272.3	272.3	LPZ-16	Paleobiology
Parareptilia	Erpetonyx	Gzhelian	303.7-298.9	301.3	LPZ-16	Paleobiology
Diapsida	Petrolacosaurus	Missourian	306-303.7	304.8	LPZ-16	Paleobiology
Batrachomorpha (Temnospondyli)	Balanerpeton	Early Brigantian	332-331.4	331.7	HPZ-13	Paleobiology w/Stratcomments
Tetrapodomorpha	Tungsenia	Late Pragian	409.2-407.6	408.4	LPZ-10	Lu (2012); see Note 2
Chondrichthyes (Subterbranchialia)	Petalodus	Famennian	372.2-358.9	365.5	HPZ-11	Zhoa & Zhu
Chondrichthyes (Holocephali)	Hercynolepis	Early Emsian	407.6-400.4	404	LPZ-10	Zhoa & Zhu
Dipnomorpha	Youngolepis	Early Lochkovian	419.2-416.4	417.8	HPZ-9	Zhoa & Zhu
Actinopterygii	Kawalepis	Late Ludfordian	424.3-423	423.6	HPZ-9	Zhoa & Zhu
Actinopteri	Ligulalepis	Late Ludfordian	424.3-423	423.6	HPZ-9	Zhoa & Zhu
Chondrichthyes (Elasmobranchii)	Onchus	Ludfordian	425.6-423	424.3	HPZ-9	Paleobiology
Osteostraci	Birkenia	Late Llandovery	438.6-430.4	434.5	HPZ-7	Paleobiology w/Stratcomments
Chondrichthyes	Neosinacanthus	Early Telychian	438.5-436.8	437.6	HPZ-7	Zhu (1998); see Note 3
Acanthodii	Neosinacanthus	Early Telychian	438.5-436.8	437.6	HPZ-7	Zhu (1998); see Note 3
Galeaspidia	Konoceraspis	Early Telychian	438.5-436.8	437.6	HPZ-7	Zhoa & Zhu
Chordata (Conodonts)	Hertzina	Nemakit-Daldynian	530.7-525.3	528	HPZ-1	Paleobiology
Additional Clades						
Synapsida (Therapsida)	Raranimus	Mid-late Roadian	271.7-268.8	269.95	LPZ-16	see note 5
Carboniferous Tetrapoda	Pederpes	Ivorian	351.3-346.7	349	LPZ-12	Paleobiology
Elpistostegidae	Livoniana	Late Givetian	384.37-382.7	383.535	HPZ-11	Paleobiology
Thelodontia	Larolepis	Franklinian	460.9-449.5	455.2	HPZ-5	Paleobiology

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167 Note 1: *Casineria* (Cheese Bay Shrimp Bed) and *Lethiscus* (Wardie Shales) were discovered in the *Perotrilites*
168 *tessellatus*/*Schulzospira campyloptera* microspore zone (Late Holkerian to Early Asbian). *Casineria* is listed as
169 Asbian. Wardie Shales were deposited slightly before the Cheese Bay Shrimp, thus *Lethiscus* is Early Asbian
170 (Van Tuinen, 2004; Paton, 1999). Note 2: *Tungsenia* is the earliest known tetrapodomorph (Lu, 2012). Note 3:
171 *Neosinacanthus* is an acanthodian, based on the number of ridges on the fin spines (Zhu, 1998). Note 4: *Anatolepis*
172 is a pteraspidomorph. Note 5: *Raranimus* replaces *Tetraceratops* as the earliest therapsid. It is improbable that
173 *Raranimus*, is Early Roadian (Kemp 2006; Liu 2009). Li equates *Raranimus* to Zone II in Russia which is likely
174 Middle Roadian (Liu, 2001,2009).

175 **Figure 2**



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177 **Figure 2a** shows percentages of Paleozoic vertebrate genera discovered in high-polarity zones relative to
 178 the total genera from 0-5, 0-10 myr, to 0-50 myr. Note the falloff after 20 myr. ‘Total’ is the percentage
 179 for all 1809 genera.

180 **Figure 2b** is a scatter plot of polarity zones comparing the reversals per myr to the CRC genera divided
 181 by the total genera within each zone. The CRC (competitive replacement clades) are active clades early in
 182 their diversification until bypassed by a more-successful clade. Reds are high-polarity zones; blues are
 183 low-polarity zones.

184 **Figure 2c** is the bar graph of the CRC genera (the zigzag lines are polarity reversals per myr). HPZ-1 has
 185 a percentage of 100% which may be too high, but it is balanced by HPZ-11 where the number of marine
 186 tetrapods is low compared to the large numbers of Devonian fish.

187 **Figure 2d** is the bar graph for 20G genera. The earliest genera of a clade represents the initial radiation of
 188 that clade. The 20G genera are all genera with a post-origin time of less than 20 myr following the
 189 original FAD of the earliest species of that clade. For example: *Guiyu*, the originating sarcopterygian, was
 190 discovered in the Gorstian Stage of the Upper Silurian which is dated at 427.4 to 425.6 Ma (median age is
 191 426.50 Ma). *Porolepis* is date at 404.03 Ma. Therefore, *Porolepis* has a post-origin time of 22.47 myr,
 192 median age. Note that HPZ-3 is void of all species and was eliminated (see Calculations Section).

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Discussion

Although the statistical evidence connects the fossil record of Paleozoic vertebrates to polarity reversals, it does not determine if the causation is extrinsic (geologic) or intrinsic (biologic). Nor does it answer a larger question: Do polarity reversals directly affect vertebrate evolution due to increasing mutation rates?

Fossilization is dependent on positive environmental conditions such as rapid burial or anoxia. Poor environmental conditions can cause gaps in the fossil record. Romer's Gap (LPZ-12) of the Early Carboniferous is now thought to be a sampling artifact (Anderson, 2015; Clack, 2016), but other gaps exist. The Middle Carboniferous Namurian Stage (LPZ-14) has been called a gap in the tetrapod record (Clack, 2012). Olsen's gap runs between the last occurrence of pelycosaurs in North America until the earliest appearance of therapsids in the uppermost Kiaman superchron (LPZ-16). The Moyero Superchron (LPZ-4), shows active diversification of conodonts but limited signs of agnathan vertebrates. The Cambrian Paibian/Jiangshanian (LPZ-2) gap has only two originating conodonts, while the Upper Ordovician LPZ-6 is void of any vertebrates other than conodonts. That these gaps correlate with low-polarity zones implies the causation is environmental, not biologic.

The first appearance of a genus is not the origin of the species, and ghost lineages can be extensive. Age-dated phylogenies, dependent on molecular or morphological variation, attempt to date the origin, but phylogenetic analysis is often impaired by a lack of articulated fossils—and parsimony is never a grantor of accuracy. Worse, results are prone to differing opinions or new discoveries. The amniote/amphibian divergence is now placed in the earliest Carboniferous (HPZ-11)(Clack, 2016). *If* this phylogeny is confirmed, and *if* Zhu's minimal phylogenetic dates for the osteichthyans, actinopterygians, sarcopterygians, dipnomorphs, and tetrapodomorphs are upheld (Zhu, 2009), and *if* the earliest pteraspidomorph is dated no more than a million years prior to the single scale of *Anatolepis* that was discovered in the Middle Sunwaptan (multiple scales were found in the Upper Sunwaptan)(Smith, 2007), and *if* limb-bearing tetrapods originated in the Late Devonian (Coates, 2008), and assuming the Polish tetrapod trackways are actually fish nests or feeding traces (Lucas, 2015), and *if* Laurin's estimated synapsid/sauropsids node is correct (Laurin, 2004) and *if* the true identity of the poorly preserved and fragmented early Kazanian Russian fossils are not therapsids (Kemp, 2006), then it's *not impossible* that every major clade of Paleozoic vertebrates originated in a high-polarity zone, and *if so*, the causation for the connection between polarity reversals and vertebrates would be biologic, not environmental.

Volcanic activity, weather alteration, and the depletion of ozone have been linked to geomagnetic polarity reversals. But if these external causations are the connection between Paleozoic vertebrate evolution and geomagnetism, then why are only vertebrates affected? Why not invertebrates? And after an indeterminant period of time (we used 20 myr), how do vertebrate families become immune to the ongoing effects of polarity reversals? Are DNA repair mechanisms involved?

In reality, any usage of taxonomic group might be considered faulty. Evolution is a continuum with natural groups and clades merely artificial tools useful for clarification. Nonetheless, the continuum of evolution does not keep mutation rates from increasing periodically, nor does it keep the pace of evolution from accelerating during geomagnetic polarity collapses.

Detailed Methodology

Generating the seven Paleozoic compilations

Originally, we compiled a list of over 2000 Paleozoic vertebrate genera taken from multiple sources, but this early compilation lacked repeatability. Therefore, we limited our sources to the Paleobiology Database (Feb 9, 2017, upgraded Sept 17, 2017), Sepkoski's 2002 marine compilation, Benton's 2013 compilation in *The first half of tetrapod evolution*, plus Zhao and Zhu's 2010 *Siluro-Devonian vertebrate biostratigraphy and biogeography of China*. A single source would be ideal, but the Paleobiology Database lacks many marine and terrestrial vertebrates, and their Phylum/Class/Order/Family taxonomy is often inadequate. We used Gradstein 2012 to date the geologic stages, and Paleobiology's "stratcomments" column for precise dating. Any genus, imprecisely dated at >20 myr, was removed. Fossilworks was referenced when necessary, but any genus not listed by the four main sources was ignored for statistical analysis. Duplicate genera often occurred with our four sources. If so, Sepkoski had low priority. Otherwise, we chose the earliest, most precise date.

For our first four spreadsheets, the clades and natural groups were defined by the four original compilations. For variation, we switched to Benton's classification of vertebrate classes from the appendix of his book, *Vertebrate Palaeontology*. For our final composite compilation, we reinstalled the Thelodonts and Osteostraci, and separated the four Elpistostegidae genera from the "tetrapodomorphs". The tetrapods were divided into Upper Devonian marine genera and Carboniferous tetrapods. We combined Lepidosauromorpha and Archosauromorpha within Neodiapsida, and switched *Tetraceratops* and *Dimacrodon* from therapsids to pelycosaurs.

But any complete, balanced, accurate, and impartial Paleozoic compilation from whatever source, should reach equivalent conclusions.

Generating Geomagnetic Polarity Zones

Gradstein and Ogg 2012, with updated data from Hansma¹⁸, Lanci¹⁹, Hounslow²⁰, Ogg 2016¹⁷ and Opdyke²¹, was used to individually date 303 Paleozoic geomagnetic polarity reversals and to define 9 high-level and 8 low-level polarity zones. Post-Cambrian, 193 polarity reversals occurred in 233.4 million years (0.827 polarity reversals per million years). This 0.827 value was used as a guide to delineate polarity zones. We extended the high-polarity zones by .2 myr after the uppermost polarity reversal in a zone (excluding the Silurian). The high-polarity zones equal 130.4 myr; the low-polarity zones equal 138.4 myr. See a list of individual polarity reversals below.

Lanci's used zircons in his 2013 report on the *Upper Permian magnetic stratigraphy of the lower Beaufort Group in the Karoo Basin of South Africa* to accurately date the base of the Illawara polarity zone (top of the Kiaman superchron) at ~270 mya. He correlates his N3 polarity chron with the Wordian normal, which would place the Eodicynodon AZ into the middle or late Capitanian. It seems more likely, the N3 is an outlier of the Upper Permian Illawarra superchron and should be placed in the Roadian. This has minor effect on our statistics, but potentially could help explain the explosive origin of the therapsids (Kemp, 2005, 2006, 2012) and their possible connection to polarity reversals.

Polarity reversals of post-Jurassic profiles taken from seafloor studies are highly reliable, but Paleozoic geomagnetism needs multiple sites from around the world, and future studies could alter these 17 polarity zones.

Statistical analysis

The basal age or median age of a geologic stage can be used to date fossils, but geologic stages are often split by polarity zones. For example, the Lochkovian, lasting from 419.2 to 410.8 Ma, is split by the contact of HPZ-9 and LPZ-10 at 416.5 Ma. Only 32% of the Lochkovian is in a high-polarity zone, but when the basal date is used for calculations, 100% of the 41 Lochkovian genera fall into HPZ-9 (zero percent when the median age is used). To solve this problem, we proportionally divided the Lochkovian, and put 28 genera in LPZ-10 and 13 genera in HPZ-9. This way, when only two genera are in a geologic stage or sub-stage, one is placed at the upper two thirds; the other, at the lower third. Proportionality is our preferred dating systematic.

The Cambrian presents a unique problem. There are 13 genera in the Early Cambrian HPZ-1, followed by 2 genera in LPZ-2, and 32 in the Late Cambrian HPZ-3 (See Table 2). This distribution is positive to our hypothesis, but when we divide the two 20G genera by the total of two genera in LPZ-2, the results equal 100%. To compensate, we add the 13 genera from HPZ-1 to the two genera from LPZ-2 and use 15 as the total genera in LPZ-2, lowering the percentage from 100% to a more reasonable 12.5%. Likewise, for HPZ-3, the 32 genera are divided by the total of 47 (13+2+32=47). For 20G genera, the conodonts in HPZ-3 extend past their 20 million-year cutoff leaving a void, and to compensate, we delete HPZ-3 (see Table B and Figure 2d).

A potential problem to this hypothesis: if the FAD of every originating genus first appeared at the base of a high-polarity zone that lasted exactly 20 million-years, then 100% of the 20G genera would be found in high-polarity zones. In reality, the total possible years for our 28 clades is 560 myr with 283.92 myr in high-polarity zones (50.7%).

To calculate equal-sized polarity bins, the post-Terreneuvian Paleozoic lasted for 268.8 myr (521 to 252.2 myr). Therefore, for 20 bins, each bin equals 13.44 myr. Excel automatically counts the total number of genera, the total number of 20G or CRC genera, and the number of polarity reversals for any number of bins, 12 to 31. No corrections for the Cambrian genera are made when calculating bins.

Table 2 | Geomagnetic polarity zones and Total Distribution of Paleozoic Vertebrates.

Tables 2 and 3 are combined to calculate coefficients with results in Table 4.

Polarity Zones		Duration		Reversals		Total Distribution			Occurrences	
Zone (a)	Geologic stages (b)	Ma (c)	Myr (d)	GPRs	perMyr	Proportion	Basal	Mid(i)	Basal	Mid(k)
HPZ-17	Late Permian	270-252.2	17.8	21	1.18	415	395	411	1464	1534
LPZ-16	Kiaman Superchron	316-270	46	10	0.22	403	415	403	2162	2118
HPZ-15	Westphalian A & B	318.8-316	2.8	5	1.79	31	24	32	133	106
LPZ-14	Late Serpukhovian-Early Bashkirian	328.1-318.8	9.3	5	0.54	46	58	48	237	266
HPZ-13	Late Viséan	337.5-328.1	9.4	20	2.13	35	37	33	89	81
LPZ-12	Romer's Gap	356.5-337.5	19	6	0.32	76	57	80	321	691
HPZ-11	Late Devonian	388.4-356.5	31.9	32	1.00	219	237	214	4784	4429
LPZ-10	Middle Devonian	416.5-388.4	28.1	5	0.18	222	193	239	2380	3788
HPZ-9	Late Silurian-Early Lochkovian	427.4-416.5	10.9	20	1.83	106	138	92	3393	1958
LPZ-8	Wenlock Stage	433.4-427.4	6	0	0.00	31	31	31	2894	2889
HPZ-7	Early Silurian	443.8-433.4	10.4	22	2.12	47	48	48	1166	1174
LPZ-6	Katian	452-443.8	8.2	2	0.24	17	14	15	528	877
HPZ-5	Middle Ordovician	466.8-452	14.8	20	1.35	57	52	57	1304	1070
LPZ-4	Moyero Superchron	482-466.8	15.2	2	0.13	54	47	67	707	1031
HPZ-3	Age 10, Late Cambrian	490.2-482	8.2	17	2.07	32	46	21	561	98
LPZ-2	Early Furongian	496.8-490.2	6.6	3	0.45	2	1	2	68	77
HPZ-1	Early Cambrian	521-496.8	24.2	85	3.51	13	15	13	85	85

Table 2 shows the 17 high (red) and low polarity zones (blue), their range (Ma), duration (myr), number of polarity reversals, reversals per million years, and distribution of total genera in each polarity zone using the median age, basal age, and proportional age of geologic stages used in this compilation. The distribution of genera is generated from our seven Excel spreadsheets can be found in the supplemental, Data S1. Occurrences are taken from the count of total Paleozoic genera in the Paleobiology database.

323 **Table 3 | Distribution of Paleozoic vertebrate genera from individual spreadsheets.**

Polarity zones (a)	20G genera (initial radiation)								CRC genera (competitive replacement)										
	Proportional dating of geologic stages																	Mid	Base
	GPRs from Gradstein, et al.							Ogg (2016)	GPRs from Gradstein, et al.										
	Paleobiology.org (b)	plus Sepkoski's compilation	plus Benton's compilation	plus Zhao & Zhu (e)	Corrected dating (f)	Benton's classification	Final Taxonomy (h)	Final Taxonomy (i)	Final Taxonomy (j)	Paleobiology.org (k)	plus Sepkoski's compilation	plus Benton's compilation	plus Zhao & Zhu (n)	Corrected dating (o)	Benton's classification	Final Taxonomy (q)	Final Taxonomy (r)	Final Taxonomy (s)	
HPZ-17	135	235	235	234	234	233	233	221	207	124	126	219	221	220	221	220	219	214	
LPZ-16	63	72	72	71	71	70	70	80	116	95	94	102	100	104	104	103	104	109	
HPZ-15	12	20	20	21	21	21	21	24	22	12	12	20	20	21	21	21	22	13	
LPZ-14	2	6	6	6	6	6	6	5	5	2	2	6	6	6	6	6	5	12	
HPZ-13	7	11	11	13	13	18	18	17	18	13	13	17	17	19	19	19	18	20	
LPZ-12	1	2	2	0	1	4	4	5	6	2	2	6	6	4	5	5	6	5	
HPZ-11	7	14	14	14	12	15	15	15	19	7	7	13	14	14	20	19	19	20	
LPZ-10	26	32	28	27	33	33	33	35	20	8	10	11	20	20	20	19	23	19	
HPZ-9	21	39	52	53	53	53	53	51	33	12	24	24	33	34	34	34	30	34	
LPZ-8	6	9	11	10	10	10	10	10	2	0	0	0	2	2	2	2	2	2	
HPZ-7	6	6	27	27	22	26	26	26	29	8	8	8	29	29	29	29	29	29	
LPZ-6	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	0	0	
HPZ-5	3	3	3	3	1	3	3	2	5	7	9	9	9	8	8	8	9	9	
LPZ-4	3	4	4	4	4	4	4	5	7	3	4	4	4	4	4	4	15	4	
HPZ-3	0	0	0	1	1	1	1	1	32	27	28	28	28	32	32	32	21	31	
LPZ-2	0	0	0	0	0	0	0	0	2	2	2	2	2	2	2	2	2	1	
HPZ-1	9	9	9	9	9	9	9	13	13	13	13	13	13	13	13	13	13	15	

324

325

326 Table 3 shows the distribution of individual 20G and CRC genera placed in 17 polarity zones using

327 proportional, median, and basal dates. Geomagnetic polarity reversal (GPRs) determine the boundaries of

328 polarity zones. Polarity reversals from Gradstein (2012) with updates from Hansma, Lanci, Hounslow,

329 Ogg 2016 and Opdyke are detailed, but Ogg (2016) is easier to compile. The distribution of genera is

330 taken from our seven spreadsheets found in the supplemental, Data S1. The first spreadsheet is

331 Paleobiology only; the 2nd adds Sepkoski; the 3rd adds Benton's terrestrial vertebrates; the 4th adds data

332 from China; the 5th uses Stratcomments from Paleobiology; the 6th uses Benton's phylogeny; the 7th is a

333 compilation. The yellow rows of the Cambrian zones negatively disrupt the statistical results. For

334 example, the two genera in LPZ-2 when divided by the total distribution from LPZ-2 in Table 2 equals

335 100%.

Table 4 Pearson's coefficient calculations and p-values taken from data in Table 1 and Table 2 (The red results, due to the Cambrian statistical anomaly are relatively poor; Dark greens are highly significant).

Phylogenetic systems	Geomagnetic polarity	Dating systems	Spreadsheets	Pearson (uncorrected)	p-value (uncorrected)	Corrected Pearson's	Corrected p-values	Corrections
20G genera	Gradstein's GPRs	Proportional dating	Paleobiologyg.org	0.6387	0.005779	0.7361	0.001149	HPZ-3 is deleted
			plus Sepkoski's compilation	0.5993	0.011003	0.7014	0.002464	
			plus Benton's compilation	0.5535	0.021177	0.6563	0.005759	
			plus Zhao & Zhu	0.6266	0.007107	0.7414	0.001011	
			Corrected dating	0.66	0.004094	0.7618	0.000605	
			Benton's classification	0.6445	0.005224	0.742	0.000999	
			Final taxonomy	0.6736	0.003033	0.7812	0.000352	
CRC genera	Ogg (2016)		Final taxonomy	0.7225	0.00105	0.7057	0.0016	Cambrian percentages are corrected
	Gradstein's GPRs		Final taxonomy	0.5236	0.031	0.764	0.000357	
			Paleobiologyg.org	0.5628	0.01866	0.8236	0.000048	
			plus Sepkoski's compilation	0.5824	0.014163	0.8483	0.000017	
			plus Benton's compilation	0.6025	0.010482	0.8218	0.000052	
			plus Zhao & Zhu	0.6836	0.00248	0.8988	0.0000009	
			Corrected dating	0.6884	0.002246	0.8978	0.000001	
			Benton's classification	0.6903	0.002162	0.901	0.0000008	
			Final taxonomy	0.6905	0.00215	0.9014	0.0000008	
	Mid	Final taxonomy	0.6798	0.002682	0.8873	0.000002		
Base	Final taxonomy	0.6673	0.003363	0.8907	0.000002			
Occurrences	Final taxonomy, Mid		0.6547	0.004344	No corrections			
Occurrences	Final taxonomy, Base		0.6391	0.005747				

Coefficient results are calculated using Tables 2 and 3. Table 2 lists the number of **GPRs** in a polarity zone (column 2e), the **Duration Myr** (column 2d), and the **Total distribution** of all genera, using **Proportional dating** (column 2g), **Mid-point** (2i), and **Basal** dating (2h) of geologic stages. Correlation coefficients are calculated by comparing **Reversals per Myr** (Table 2f) to **20G genera** (Table 3, columns b to h) or **CRC genera** (Table 3, columns k to q) divided by the **Total Distribution** (Table 2, columns g to i) within **Polarity Zones** (Table 2, columns a and b). **Occurrences** are calculated using columns 2j and 2k. The **Corrected dating** spreadsheet of 1809 genera was an improvement by using the "Stratcomments" column in paleobiology.org.

349 **Individual Paleozoic polarity reversals** (reds are high polarity zones; blues are low polarity
350 zones).

351 HPZ-17 (Guadalupian to Lopingian, Upper Permian): 252.46⁴, 252.83⁴, 253.0⁴, 253.36⁴, 253.72⁴,
352 254.11⁴, 254.35⁴, 255.21⁴, 257.20⁴, 257.98⁴, 258.18⁴, 258.82⁴, 259.7⁴, 264.10⁴, 264.42⁴, 264.86⁴,
353 266.07⁴, 266.63³, 267.63³, 268.69³, 270.0³.

354 LPZ-16 (Kiaman Superchron, Upper Carboniferous to Lower Permian): 286.3, 297.3, 299.1,
355 299.3, 300.4, 300.8, 304.4, 308.7, 310.7, 311.75.

356 HPZ-15 (Upper Bashkirian): 316.2⁵, 317.0, 318.6⁴, 318.7⁴, 318.8⁴.

357 LPZ-14 (Upper Serpukhovian to Lower Bashkirian): 319.45, 322.7, 324.3, 326.92⁴, 327.43⁴.

358 HPZ-13 (Middle Viséan to Lower Serpukhovian, Carboniferous): 328.3, 328.65, 330.6, 331.3,
359 331.8, 331.9, 332.2, 332.3, 333.2, 333.35, 334.05, 334.25, 334.75, 334.9, 335.2, 335.7, 336.6,
360 336.8, 337.3, 337.5.

361 LPZ-12 (Romer's Gap, Early Tournaisian to Middle Viséan, Carboniferous): 343.0, 343.7,
362 344.3, 346.0, 347.45, 352.35.

363 HPZ-11 (Givetian to Famennian, Upper Devonian, plus Early Tournaisian): 356.7, 356.85,
364 357.6, 357.75, 358.4, 358.75, 360¹, 363.6¹, 364.7¹, 365.2¹, 367.7¹, 370.4¹, 371.5¹, 372.8¹, 373.3¹,
365 373.8¹, 375¹, 376.1¹, 377.3¹, 378.3¹, 378.65¹, 378.9¹, 379.3¹, 380.3¹, 381.6, 382.5², 383.1²,
366 384.3², 386.4², 387.1², 387.7².

367 LPZ-10 (Middle Lochkovian to Eifelian, Lower Devonian): 393.3, 400.24, 400.76, 401.6²,
368 402.5².

369 HPZ-9 (Ludlow to Pridoli Stages, Upper Silurian; Lower Lochkovian): 416.7, 418.2, 418.9, 419,
370 419.4, 419.9, 420.4, 420.9, 421.4, 421.9, 422.4, 422.9, 423.4, 423.9, 424.4, 424.9, 425.4, 425.9,
371 426.4, 426.9, 427.4.

372 HPZ-8 (Wenlock Stage, Middle Silurian): None.

373 HPZ-7 (Llandovery, Lower Silurian): 433.5, 433.8, 434.3, 434.8, 435.3, 435.8, 436.3, 436.8,
374 437.3, 437.8, 438.3, 438.8, 439.3, 439.8, 440.3, 440.8, 441.3, 441.8, 442.3, 442.8, 443.3, 443.8.

375 LPZ-6 (Middle Katian to Hirnantian, Ordovician): 448.9, 450.7.

376 HPZ-5 (Darriwilian to Lower Katian): 452.2, 452.34, 453, 453.6, 454.0⁴, 454.73⁴, 457.26⁴,
377 457.7⁴, 458.26⁴, 459.19⁴, 459.68⁴, 461.21⁴, 461.73⁴, 462.11⁴, 462.32⁴, 462.76⁴, 463.56⁴, 464.6⁴,
378 466.0⁴, 466.8⁴.

379 LPZ-4 (Moyero Superchron, Upper Tremadocian to Lower Darriwilian): 479.95, 480.1.

380 HPZ-3 (Cambrian Age 10 to Lower Tremadocian): 482.2, 482.7, 482.9, 484.35, 484.6, 484.8,
381 485.3, 485.9, 486.75, 486.95, 487.1, 487.2, 487.3, 487.8, 488.1⁴, 490.05⁴, 490.2⁴.

382 LPZ-2 (Paibian to Upper Jiangshanian): 492⁴, 492.2⁴, 495⁴.

383 HPZ-1 (Lower Cambrian): 497⁴, 497.4, 497.55, 497.7, 497.85, 498.0, 498.1, 498.2, 498.3,
384 498.75, 498.95, 499.0, 499.15, 499.45, 499.6, 499.68, 499.75, 499.83, 499.9, 500.65, 500.75,
385 500.8, 501.1, 501.25, 501.45, 501.55, 501.65, 501.75, 501.8, 502.1, 502.2, 502.35, 502.8, 503.13,
386 503.6, 503.75, 504.1, 504.75, 505.3, 505.55, 506.7, 507.2, 508.9, 509.2, 509.52, 509.7, 510.17,
387 510.32, 510.6, 510.8, 511.72, 511.95, 512.05, 512.25, 512.4, 512.9, 513.4, 513.9, 514.4, 514.9,
388 515.4, 515.9, 516.18, 516.35, 517, 517.5, 517.6, 517.75, 517.85, 518.25, 518.35, 518.6, 518.64,

389 518.7, 518.85, 519.25, 519.25, 519.4, 519.55. 519.7, 520.2, 520.35, 520.6, 520.75, 520.85,
390 520.95.

391

392 Superscripts: 1 is for Ogg (2016); 2 is for Hansma (2015); 3 is for Lanci (2013); 4 is for
393 Hounslow (2016); 5 is for Opdyke (2014). Polarity reversals without superscripts are from
394 Gradstein (2012).

395

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