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Testing the Order of the Fossil Record: Preliminary Observations on Stratigraphic-clade Congruence and Its Implications for Models of Evolution and Creation

Kathryn McGuire

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TESTING THE ORDER OF THE FOSSIL RECORD: PRELIMINARY OBSERVATIONS ON STRATIGRAPHIC-CLADE CONGRUENCE AND ITS IMPLICATIONS FOR MODELS OF EVOLUTION AND CREATION

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ABSTRACT

One important category of fossil evidence for evolution is the congruence between the order in which groups appear in the fossil record and the order predicted from evolutionary phylogenies based on morphology. However, creationists have only rarely scrutinized the order of the fossil record. We therefore compiled a dataset of 2,721 published phylogenies and assembled first appearance data for all the taxa in the phylogenies. After assigning clade and age ranks we used Spearman's Rank Correlation to measure the fit between the clade and age ranks. Almost three-quarters of our phylogenies (1,989 or 73.1%) showed statistically significant correlation (p < 0.05). However, only 684 (25.1%) showed high correlation (p < 0.05 and Spearman rho > 0.75). Stratigraphically, correlations seem to be higher in the Mesozoic (37.8% high correlation) than in either the Paleozoic (25.1% high correlation) or Cenozoic (12.3% high correlation). More specific comparisons are difficult because the t-statistic from which the significance of the Spearman rho is calculated is correlated with the number of taxa, leading to potentially spurious significance for phylogenies with large taxon samples. In addition, our dataset suffers from considerable redundancy (for example, each dinosaur species is represented on average at least 20.4 times). Here, we devise a simulation-based method to overcome the taxon sample size problem, but dealing with redundancy will require additional manual curation. Still, the dataset we have compiled is the largest set of phylogenies ever evaluated for stratigraphic congruence and will provide an excellent basis for future research.

KEYWORDS

stratigraphy, phylogenetic trees, ecological zonation, paleontology, cladistics, congruence, fossil record

I. INTRODUCTION

The fossil record is widely regarded as primary evidence for macroevolutionary theory (e.g. Cuffey 1984; Prothero 2007; Coyne 2009). One important category of fossil evidence for evolution is the congruence between the order in which groups appear in the fossil record and the order predicted from evolutionary phylogenies based on morphology (e.g. Ridley 2004, pp.65-66). Over the past few decades, paleontologists have increasingly studied the stratigraphic congruence of phylogenetic hypotheses (e.g. Benton and Storrs 1994; Benton and Hitchin 1997; Wagner 1998; O'Connor et al. 2011; O'Connor and Wills 2016), but only rarely have creationists carefully scrutinized the order of the fossil record. We therefore set out to conduct a large-sample study of congruence between first fossil appearances and the order of branching in evolutionary phylogenies. About thirty years ago, some preliminary work in this area was carried out by Wise (n.d.a.), who constructed cladograms for 7 kingdoms, 101 phyla, and 266 classes using a taxonomic scheme modified from Margulis and Schwartz (1988). From the cladograms, 144 predicted evolutionary series were derived: 3 series of kingdoms, 1 series of divisions, 62 series of phyla, 6 series of subphyla, and 72 series of classes. Spearman's Rank Correlation (SRC) was used to compare the order of first appearances in the fossil record with the order of first appearances in the cladograms for all 144 series. Only 5 out of the 144 series showed a significant correlation at the 95% confidence level between the predicted and observed order of first appearances. The remainder were basically random with respect to the predicted evolutionary order. The 5 series that showed significant correlation were 4 series of plant phyla and 1 series of arthropod classes. In all 5 cases, the order of appearance in the fossil record correlates with an

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increase in terrestriality and independence of standing water. Wise (n.d.b.) suggested this may represent an ecological, rather than an evolutionary, gradient, and that the advance of the Flood waters from sea to land may be all that is needed to explain the small handful of examples where the stratigraphic order agrees with evolutionary phylogeny. The strong stratigraphic-clade congruence for vascular plant divisions and classes (SRC=0.994, p << 0.001) was one of the factors that led Wise (2003) to develop the floating forest model, in which he reconstructed the plants of the Paleozoic as a supercontinent-sized pre-Flood biome growing over the deep ocean and broken apart and buried from the outside in during the Flood.

The importance of stratigraphic congruence is not merely as a test for evolutionary claims. While the first order interpretation is the correspondence between cladistic order and stratigraphic order, many higher order questions can also be explored. For example, as seen in Wise's (n.d.b.) work, stratigraphic congruence can suggest alternative interpretations of the trends in the fossil record. Wise's work suggests that there might be a difference between ecologies, possibly between marine and terrestrial vertebrates. Additionally, we might expect to see a difference between stratigraphic congruence for fossils preserved in the Flood vs. those from before or after the Flood.

Questions around stratigraphic-clade congruence have also been explored in the conventional literature. The reported results have been mixed. For example: Norell and Novacek (1992a, b) examined 38 vertebrate groups and concluded that in most cases there was a general correspondence between superpositional order and the sequence of branching in the cladograms. However, the degree of fit varied widely. Benton and Hitchin (1997) examined 384 cladograms of echinoderms, fishes, and tetrapods with fewer than 40% showing statistically significant congruence between cladistic and stratigraphic data. They reported that this result contradicted findings on smaller samples of cladograms. Wills (2001) examined 179 cladograms of arthropods, along with 510 tetrapod and 157 fish cladograms for comparison. He found that arthropod cladograms showed significantly worse congruence than tetrapods. O'Connor and Wills (2016) analyzed 647 animal and plant cladograms and found significant variations in the degree of congruence across the Phanerozoic, with parts of the fossil record with a higher proportion of arthropods showing poorer overall congruence and parts of the record with a higher proportion of tetrapods showing higher overall congruence. Benton (2001) assessed 1,000 published phylogenies and found that there was little change in congruence throughout the twentieth century despite revolutionary change in methods and data sources.

Here, we present a new database of 2,721 published phylogenies, all of which have been evaluated for their stratigraphic correlations based on first appearance dates recorded in the Paleobiology Database (PBDB; https://paleobiodb.org). Our taxon sample is heavily biased towards vertebrates, and among the vertebrates towards dinosaurs, but the database and our procedure provide the means for new creationist evaluations of the fossil record, by analysis of our current data and by application of our ongoing methodological work to nonvertebrate groups. Here we show the utility of this dataset by examining two important questions: 1) Is there an evolutionary order to the fossil record? 2) Are there differences between post-Flood and Flood strata?

II. MATERIALS AND METHODS

We assembled a dataset of 2,721 phylogenies, including most phylogenies compiled from published papers on Graeme T. Lloyd's website (http://www.graemetlloyd.com/matr.html) as of June 2022. We chose to use these phylogenies for several reasons: (1) Lloyd is a well-known expert on this subject, (2) we needed phylogenies mostly based on fossil taxa, not extant species, and (3) the collection includes many phylogenies in digital formats, enabling us to process more trees. We also selected some additional published phylogenies reflecting the interests of our co-authors. We then assembled first appearance data for all the taxa in our phylogenies from the PBDB. In order to ensure reliable statistics, any phylogenies with fewer than 10 taxa were excluded from our dataset, as well as any taxa in the remaining phylogenies for which first appearance data were not available in the PBDB. This resulted in the exclusion of all phylogenies for plants and unicellular organisms. For phylogenies with exactly the same taxon sample, we calculated clade and stratigraphic rank correlation first, then selected the phylogeny with the best correlation. As a result, there should be no trees in our dataset that sample exactly the same set of taxa, but the overlap in taxic coverage could be considerable.

A. Assigning Ranks

To rank the phylogenies, we followed this procedure: Firstly, the root was identified and followed to the subsequent taxa(on) or node(s). Both the node(s) and/or taxa(on) were given the rank of 1 (see Fig. 1). When the node leads to a taxon, the taxon was assigned a fixed



Figure 1. A sample tree illustrating the clade ranking strategy. Modified from Gahn and Kammer (2002, Fig. 2(1)).

"relative rank" the same as its "parent" node. However, if the node led to another node, the "child" node was given a rank one integer higher than the "parent" node. This procedure was applied to all subsequent nodes and taxa until every taxon in the tree had been assigned a relative rank. To assign a "final rank" to each taxon, they were entered into a spreadsheet and sorted by their relative ranks from lowest to highest. They were then assigned an ordered number from 1 to n. If only one taxon was associated with a given relative rank, the ordered number of that taxon became its final rank. If there were three or fewer taxa associated with the same relative rank, the lowest of their ordered numbers became their final rank. If there were four or more taxa associated with the same relative rank, the average of their ordered numbers was calculated and became their final rank.

To assign age ranks, we obtained first appearance dates from the PBDB, ordered them, and assigned ranks beginning with the oldest. Taxa with no date listed in the PBDB were eliminated from the calculations. In this way, the lowest ranks correspond to the basalmost branches of the tree and the earliest appearance in the fossil record.

B. Correlating the Ranks

We used Spearman's Rank Correlation (SRC) to measure the fit between the clade ranks and the age ranks. SRC is monotonic, which means that it measures order as opposed to linearity. In macroevolutionary theory, we would expect taxa to make their first fossil appearances in the same order that those taxa evolved, all other things being equal. If clade ranks and age ranks are completely congruent, a straight line with a slope of 1 is expected, regardless of whether the relationship is strictly linear. This would mean that taxa that are believed to have evolved first always appear earlier in the fossil record than taxa that are believed to have evolved later. Negative SRC values are also possible, demonstrating the opposite trend. We calculated the SRC coefficient (rho) for each tree based on our age and clade ranks using Python. All additional analyses were conducted in R.

C. Simulations

To simulate the correlation of large sets of points, we began with the empirical distribution of taxon sample sizes from our database of phylogenies. For each real phylogeny, we created a set of points consisting of exact rank matches, e.g. (1,1), (2,2), (3,3)...(n,n), where n = the number of taxa in that phylogeny. We then scrambled a set

percentage of those points, so that only the remaining unscrambled points were perfectly correlated. We repeated this procedure for every phylogeny in our database. We then calculated Spearman's rho and *p*-values for each of these sets of points. In this way, we could simulate correlations with the precise taxon sample sizes of our real phylogenies while evaluating different fractions of perfectly correlated points. Following this procedure, we produced four separate sets of simulated correlations, one each for 60%, 50%, 40%, and 30% randomized points, thus giving an expected correlation of approximately 0.4, 0.5, 0.6, and 0.7. These fractions of randomized points were chosen specifically to match the spread of correlations among our real phylogenies.

III. RESULTS

Our full dataset consists of 2,721 phylogenies that were ranked by clade and age. The phylogenies are almost entirely Phanerozoic. Only three phylogenies included Proterozoic taxa; all three were Porifera phylogenies that spanned the Precambrian to the Cenozoic. Slightly more than half of the phylogenies had their first appearance in the Mesozoic (1401, 51%). Only 132 phylogenies (4.9%) span the entire Phanerozoic, from the Paleozoic to Cenozoic (Table 1).

For convenience in future studies, we assigned one of 38 higher-order taxonomic "groups" to every phylogeny, based on classifications from Graeme Lloyd's website. The traditional Linnean-type rank of these groups varied from mammal orders to entire phyla (e.g. echinoderms or hemichordates). The five largest groups were the dinosaurs (655 phylogenies, 24.0%), the non-dinosaurian archosauromorphs (351, 12.9%), non-mammalian synapsids (164, 6.0%), Mesozoic mammals (158, 5.8%), and cetaceans (148, 5.4%). Collectively, these five groups account for 1,476 phylogenies (54.2%). The mean number of phylogenies for a group is 71.6, while the median is 30.5. The number of phylogenies for each group is shown in Fig. 2 and listed in Table 2.

We selected phylogenies for our study based on completely unique taxon samples. For papers where multiple tree topologies were published for a single set of taxa, we calculated clade ranks and correlations for all trees, then chose the tree with the best correlation for our dataset. Although this strategy reduced "absolute" redundancy of phylogenies using the exact same taxon sample, our dataset nevertheless contains a great deal of "relative" redundancy. For example,

Table 1. Breakdown of Phanerozoic phylogenies by stratigraphic coverage.		Stratigraphically Highest Taxon		
		Cenozoic	Mesozoic	Paleozoic
Stratigraphically Lowest Taxon	Cenozoic	543 (20.0%)		
	Mesozoic	710 (26.1%)	691 (25.4%)	
	Paleozoic	132 (4.9%)	435 (16.0%)	207 (7.6%)



Figure 2. Number of phylogenies by each taxonomic group.

two phylogenies that matched 95% of their taxa would not be considered redundant by our measure, since they do not have exactly the same taxon sample. This is likely to skew our results in unpredictable ways, depending on which taxa occur more frequently in the "group" under consideration. For instance, our sample of 655 dinosaur phylogenies has a total of 22,974 taxa (mean 35.1), but a recent evaluation of the PBDB revealed only 1,124 currently named dinosaur species (Starrfelt and Liow 2016). Consequently, each species is represented on average at least 20.4 times. Thus, additional work will be needed to better evaluate the question of redundancy and how best to deal with it.

A. Correlations

Overall, 1,989 of our 2,721 phylogenies exhibited statistically significant correlation (p < 0.05). That is well over a majority of the phylogenies (73.1%), but when we simultaneously consider the actual correlation coefficient (Spearman rho), the numbers change dramatically. We defined "high correlation" phylogenies as those with statistically significant correlations (p < 0.05) and a Spearman rho > 0.75. For the entire set of phylogenies, there are only 684 (25.1%) that are classified as high correlation.

Considered stratigraphically, phylogenies that contain only Paleozoic taxa also have 25.1% that are highly correlated, but phylogenies that include Cenozoic taxa appear to have less frequent high correlations. In particular, only 12.3% of phylogenies that include only Cenozoic taxa are highly correlated. In contrast, phylogenies with only Mesozoic taxa have substantially more that are highly correlated (37.8%). Considered taxonomically, a surprisingly high fraction of high correlation phylogenies occurs among the sarcopterygians and "early" tetrapods (54.3% high correlation), non-mammalian synapsids (45.1% high correlation), and dinosaurs (31.1% high correlation).

Should these correlations be considered paleontologically significant? While we could easily run a statistical test to determine if one set of correlations is significantly higher or lower than another set, several factors urge caution in interpreting these results. First, as we have mentioned, our dataset suffers from considerable redundancy, which must be addressed manually. Beyond that, though, we also see a significant correlation between the taxon sample size and the t-statistic by which the statistical significance of the Spearman rho is calculated (Fig. 3). For example, we observed that 37.8% of phylogenies that contained only Mesozoic taxa were high correlation, and those high correlation phylogenies had an average of 33.7 taxa. In contrast, the 12.3% of Cenozoic-only high correlation phylogenies had an average of only 27.6 taxa. If we are to compare different sets of phylogenies, we would either have to utilize samples with the same taxon sample sizes (unlikely) or in some manner adjust for differences in taxon sample size.

B. Simulations

We simulated rank correlations by randomly selecting data points from a distribution of points of specified correlation (Fig. 4). By using the same taxon sample sizes as in our set of phylogenies, any set of empirical correlations can be directly compared to a simulation. For all 2,721 phylogenies, the simulations only poorly match the empirical distribution of correlations. Above the median correlation, the empirical distribution of correlations fall between points drawn randomly from a population with a true correlation between 0.6 and 0.7. Below the median correlation, no single simulation best matches the empirical distribution of correlation coefficients. These results suggest that, at best, our set of 2,721 phylogenies represents a random sample from an approximately 65% correlation between the order of

Table 2. Breakdown of phylogenies by group	. Group labels are largely taken from	Graeme T. Lloyd.
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GROUP	NUMBER OF PHYLOGENIES	% OF TOTAL PHYLOGENIES	MEAN NUMBER OF TAXA PER PHYLOGENY
Actinopterygians	27	0.99	20.7
Afroinsectiphilians	10	0.37	24.3
Brachiopods	7	0.26	16.4
Carnivores	40	1.47	18.2
Cenozoic birds	86	3.16	25.7
Cetaceans	148	5.44	40.7
Chiropterans	3	0.11	19.7
Echinoderms	16	0.59	24.4
Gastropods	1	0.04	15
Hemichordates	1	0.04	17
Hyracoideans	2	0.07	33.8
Ichthyopterygians	60	2.21	30.8
Lagomorphs	2	0.07	63
Lipotyphlans	3	0.11	13
Marsupials	68	2.5	20.5
Mesozoic dinosaurs	655	24.07	35.1
Mesozoic mammals	158	5.81	46.4
Monotremes	1	0.04	90
Non-amniote tetrapods	130	4.78	25.3
Non-bilaterian metazoans	4	0.15	65.5
Non-cetacean artiodactyls	7	0.26	22.4
Non-diapsid reptiles	53	1.95	20.8
Non-dinosaurian archosauromorphs	351	12.9	44.8
Non-mammalian synapsids	164	6.03	32.2
Non-osteichthyan vertebrates	23	0.85	26.4
Non-saurian diapsids	34	1.25	31.6
Non-squamate lepidosauromorphs	34	1.25	24.6
Perissodactyls	50	1.84	20.2
Piscine sarcopterygians and "early" tetrapods	138	5.07	28.5
Primates	111	4.08	34.6
Proboscideans	9	0.33	18.7
Pterosaurs	17	0.62	32
Rodents	16	0.59	24.2
Sauropterygians	89	3.27	34.1
Sirenians	3	0.11	30.7
Squamates	71	2.61	32.4
Turtles	103	3.79	35.1
Xenarthrans	26	0.96	23.4





log(Number of Taxa)

Figure 3. t-statistics calculated from Spearman rho values are correlated with the number of points in the correlation (i.e. the number of taxa in the phylogeny).



Figure 4. Distribution of Spearman rho correlations for all 2,721 phylogenies (black). Shown in color are models controlled for taxon sample size. Purple: 60% randomized, blue: 50% randomized, green: 40% randomized, red: 30% randomized.

the fossil record and the putative phylogenetic order.

We repeated separate simulations for each set of stratigraphic categories indicated above (Fig. 5). In this case, the empirical distributions of correlations cannot be compared directly because the taxon sample sizes differ, but each empirical distribution can be compared to corresponding simulations. Since the simulations come from the same underlying model of correlated points, this gives us a means to say something about the differences between the stratigraphic categories.

Our simulations do indicate that the phylogenies with only Mesozoic taxa appear to be notably more correlated than phylogenies with only Cenozoic taxa. Above the median, the Mesozoic-only phylogenies closely match the simulations from a 70% correlated set of points. This is also true for phylogenies involving both Paleozoic and Mesozoic taxa. For phylogenies with just Cenozoic taxa, the empirical distribution of correlations closely matches the simulations from a 60% correlated set of points. Phylogenies involving only Paleozoic or the entire Phanerozoic taxa also seem closely aligned to the 60% correlated set of simulations. Thus the apparent reduction in high correlation phylogenies in Cenozoic-only phylogenies may be an artifact, while the increase in high correlation phylogenies in the Mesozoic-only phylogenies appears to reflect a real difference.

III. DISCUSSION

CZ only

Although the results reported by Wise (n.d.a.) are of potentially great significance to the creation model, there are several limitations to his study, namely: (1) it was never published in a peer-reviewed journal, (2) it focused only on higher taxonomic categories (kingdoms, phyla, classes), and (3) it focused narrowly on the question of whether

evolutionary phylogeny matched stratigraphy. The dataset we have assembled will allow a broader study (1) encompassing more taxonomic levels, and (2) making comparisons between supra- and intra-baraminic groups and (3) between different parts of the stratigraphic record (Palaeozoic vs. Mesozoic vs. Cenozoic). These new data will be valuable in addressing many outstanding questions within creationism, potentially including questions about Flood boundaries, holobaramin identification, the nature of the pre-Flood world, and why people believe that the fossil record so strongly supports an evolutionary interpretation.

For example, with regard to the last question of why people believe the fossil record reveals the evolution of life, we note that our results indicate that the fossil record is only 70% correlated with the morphology of the creatures it contains. The correlation appears to go up in the Mesozoic. Given that our simulations still do not closely match the distribution of empirical correlations, this conclusion is likely to change with further refinements to our dataset and to our simulations. Still, one can more easily understand why a paleontologist might claim that the fossil record is the best evidence for evolution. On the other hand, those who claim that the fossil record is a "precise" or "exact" match to what we would expect if evolution were true are not likely to be correct.

These conclusions must be tempered by a number of technical considerations. First, our conclusions rest on the idea that reconstructed phylogenies somehow reflect "true" evolutionary relationships. Since there are numerous reasons to question the validity of particular phylogenies (taxon sample bias, character sample bias, biases from phylogenetic reconstruction methodology) and the entire phylogenetic enterprise (evolution may be more reticulate), observing



Figure 5. Distribution of Spearman rho correlations for phylogenies according to stratigraphic coverage. For key to models, see Figure 4.

a correlation between phylogenies and the fossil record may only be telling us about the ordering of fossils rather than anything evolutionary. Second, the clade ranking process is itself artificial, since the point at which two taxa share a common ancestor may not be the point at which those taxa began to exist as recognizably distinct species. Third, except for species with an abundant fossil record, the first appearance date on which these ranks are based can only be coarsely related to the actual first appearances of those species, especially for species known from only one occurrence. This is even more important if the fossil record represents hundreds of millions of years and only very sparsely samples the species alive during that interval. Still, the high level of correlation seen here is quite impressive, perhaps even too impressive. Future work should focus on the effects of stochastically sampling a very sparse fossil record and alternative methods of evaluating morphological similarity.

We also document here a notable difference in correlations based on the stratigraphic range of the taxa involved, that may shed light on the nature of the Flood, the pre-Flood world, and post-Flood recovery. We noted that correlations in the Mesozoic were greater than correlations in the Cenozoic and the Paleozoic. With our simulations that control for taxon sample size, we see that this difference is not merely a difference of taxon sampling. It could be a difference in redundancy, if, as we noted above, the sampling of dinosaur phylogenies in particular indicates a highly redundant dataset. Interestingly, both Wills (2007) and O'Connor et al. (2011) made similar observations. Although they used different methods and datasets for calculating congruence, both found a convex pattern in their results, with congruence peaking in the Mesozoic and deteriorating to the present. Both attribute this pattern, at least in part, to the changes in proportions of higher taxa through time.

If these differences do reflect real differences in correlation between taxon and stratigraphic order, then Flood models ought to grapple with these differences. For example, any Flood model that does not include the Paleozoic or even part of the Paleozoic in the Flood sediments must account for the ordering of fossils in the Paleozoic. Alternatively, Flood models that recognize most of the Phanerozoic as Flood deposits should account for the change in correlation seen as Flood deposition moves from Paleozoic to Mesozoic to Cenozoic. In particular, what could cause a sharp spike in correlation at the mid-Flood (Mesozoic)? Finally, Flood models that place the Flood/ post-Flood boundary at the base of the Cenozoic ought to address the increasing correlation seen from Paleozoic to Mesozoic (early to late Flood) and why the post-Flood (Cenozoic) is roughly as correlated as the earliest Flood sediments (Paleozoic).

Regardless of the Flood model, answering any of these questions must engage at least two different issues: the nature of the pre-Flood world and the mechanism of the Flood. Since patterns in the Flood record are not evolutionary, they arise instead from the geography of the world at the start of the Flood and the way the creatures were deposited in sediments during the Flood. At its most general, the issue of geography addresses where creatures lived, and in our modern world, we see that this question relates to both continental/regional differences as well as elevational differences. More specifically, Flood deposition might have been influenced by factors such as how far inland species lived, which coast the coastal species lived on, or mountainous barriers to the Flood waters that would either be eroded in the Flood or serve as accumulation points.

Historically, perceptions of the mechanism of the Flood have varied widely. Early modern scholars imagined a very simple Flood in which heavy rain inundated the entire land (e.g. Burnet 1684; Woodward 1695), while more recent models have invoked more advanced ideas such as a vapor canopy (Dillow 1981) or catastrophic plate tectonics (Austin et al. 1994). Each of these models would deposit corpses in different ways, involving many complex factors such as the energy levels of the Flood waters, how the Flood waters interacted with the geography of the pre-Flood world, and whether the Flood began in the oceans or on the land.

Our work here represents just the beginning of what we hope will become a new era of examining in much greater detail the order of the fossil record. Our future work will examine our dataset in more detail to alleviate redundancy, seek and assess alternative metrics for ranking taxa and assessing agreement with the fossil record, and develop more sophisticated models of evolution and the Flood to help us understand the patterns we actually observe. We also want to extend the dataset to include more invertebrates and even microfossils, such as diatoms or foraminifera. We look forward to exciting new discoveries as we continue to work with these data.

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