

Graptoloid diversity and disparity became decoupled during the Ordovician mass extinction

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The morphological study of extinct taxa allows for analysis of a diverse set of macroevolutionary hypotheses, including testing for change in the magnitude of morphological divergence, extinction selectivity on form, and the ecological context of radiations. Late Ordovician graptoloids experienced a phylogenetic bottleneck at the Hirnantian mass extinction (~445 Ma), when a major clade of graptoloids was driven to extinction while another clade simultaneously radiated. In this study, we developed a dataset of 49 ecologically relevant characters for 183 species with which we tested two main hypotheses: (i) could the biased survival of one graptoloid clade over another have resulted from morphological selectivity alone and (ii) are the temporal patterns of morphological disparity and innovation during the recovery consistent with an interpretation as an adaptive radiation resulting from ecological release? We find that a general model of morphological selectivity has a low probability of producing the observed pattern of taxonomic selectivity. Contrary to predictions from theory on adaptive radiations and ecological speciation, changes in disparity and species richness are uncoupled. We also find that the early recovery is unexpectedly characterized by relatively low morphological disparity and innovation, despite also being an interval of elevated speciation. Because it is necessary to invoke factors other than ecology to explain the graptoloid recovery, more complex models may be needed to explain recovery dynamics after mass extinctions.

graptolites | macroevolution | selection | diversification | nonadaptive radiation

Mass extinction events are defined by their effect on taxonomic diversity, but they also have profound impacts on the biotic diversity of morphology and ecology (1–3). Quantitative assessments of morphological diversity, i.e., disparity, can shed light on the selectivity of extinction and add to our understanding of the ecological context of recovery patterns after extinction events (4, 5).

In this paper, we quantify the morphological dynamics of the Graptoloidea during the end-Ordovician mass extinction, which began ~445 million years ago. This event is composed of two separate extinction episodes during the Hirnantian Stage (6) and is commonly referred to as the Hirnantian mass extinction (HME). These episodes of increased extinction rate are associated with the initiation and termination of a global cooling period in the first half of the Hirnantian, during which sea-surface temperatures dropped ~5 °C (7, 8).

Graptoloids are an extinct clade of colonial zooplankton (Hemichordata) noted for their well-sampled fossil record and high rate of species turnover (9–11). Previous work on the effect of the HME on the Graptoloidea has revealed a tumultuous and complex pattern. The graptoloids experienced some of the highest extinction intensities among marine invertebrates during the HME (12), and the surviving taxa were a limited sample of pre-HME lineages. Before the mass extinction event, graptoloid lineages can be divided into two monophyletic clades that diverged more than 20 million years before the HME: the Neograptina and the Diplograptina (13, 14). Although the Diplograptina were much more species-rich and morphologically disparate before the

HME (Fig. 1), they were driven to extinction during the Hirnantian glaciation (7, 15). In contrast, the Neograptina simultaneously speciated rapidly after the first extinction episode of the HME (15).

The changes in morphological diversity during this interval have not been studied quantitatively. Previous work suggests that only a single morphotype survived the HME (16, 17) and that the number of morphotypes recovered in the Silurian. Mitchell (18) demonstrated that the Silurian Neograptina evolved a number of morphologies that converged upon pre-Hirnantian diplograptine forms. Overall, this work suggests that the Hirnantian diversification of the Neograptina was an adaptive radiation sparked by the removal of their diplograptine competitors (7), in agreement with a common interpretation that, during recovery intervals, diversification is driven by ecological opportunity available after a mass extinction removes competitors (19–22). Morphological data provide a means by which to further test this hypothesis.

The protracted nature of the HME and the well-sampled fossil record of the graptoloids allows for a high-resolution examination of processes throughout the mass extinction event. Our study covers ~9 million years, divided into 10 biostratigraphic zones (*SI Text*). In many studies of morphological disparity, 9 million years would be resolved to one or two temporal bins. The relatively high temporal resolution afforded by the graptolite record provides a unique opportunity to examine macroevolutionary change at the scale of species durations and therefore to potentially recover much more detailed insights into the processes of recovery from mass extinction than would otherwise be possible.

In this paper, we analyze the patterns and processes of disparity change in Late Ordovician and Early Silurian Graptoloidea by using a multivariate dataset of 49 morphological characters for 183 species (*Dataset 1*). We use our data to analyze the support for two main hypotheses. First, we use resampling simulations to test whether morphological selectivity alone can explain the preferential survival of the Neograptina during the two extinction episodes of the HME. Chen et al. (7) established that the survival and proliferation of the Neograptina during the Hirnantian cannot be explained by stochastic non-selective processes, but it is unclear whether this pattern results from selection for the relatively simple morphology of Late

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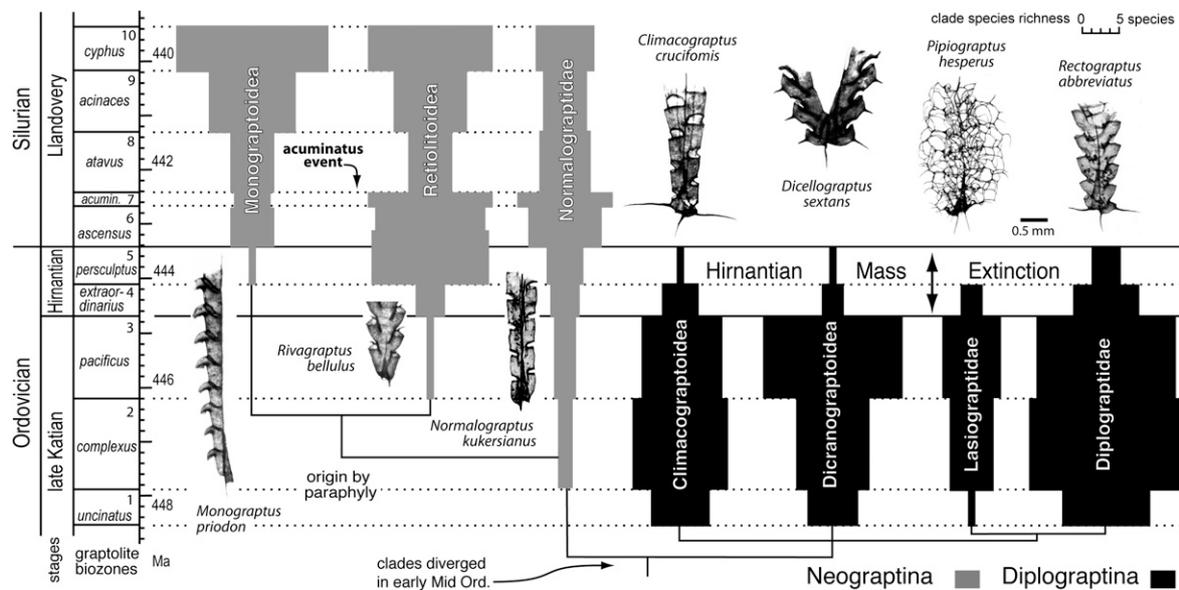


Fig. 1. Spindle diagrams and phylogenetic relationships of groups examined in this analysis, plotted through the ten graptolite biostratigraphic zones the comprise the study interval. Width of spindles corresponds to species richness per interval (scale bar at top right). Colonies of typical members of each group illustrate some of the morphologic diversity of colony forms (imaged in transmitted infrared illumination; see scale bar). Phylogenetic relationships are taken from previous cladistic analyses (13, 40). Absolute time scale for the zones is taken from Sadler et al. (39). Note that the lack of neograptine species in the *uncinatus* Zone reflects the rarity of normalograptid taxa in that interval rather than a poorly sampled record (45).

Ordovician neograptines or unobserved variation in another set of traits, such as physiological tolerances (23).

Second, we evaluate whether the graptoloid recovery is consistent with the postulated model of diversification mediated by ecology. Under a model of adaptive radiation where ecological opportunity promotes diversification, morphological and taxonomic diversity should correlate from interval to interval as new species fill the available ecospace. If the graptoloid recovery was primarily driven by ecological opportunity, there should be a close relationship between species richness and morphological disparity as the neograptines diversify. Theory on adaptive radiations also predicts that morphological variation should accumulate early in the radiation of the neograptines and the rate should subsequently slow down (24, 25). Thus, any evidence of a shift in the rate of morphological change should be in the Early Hirnantian when the neograptines first begin to diversify (Fig. 1). To evaluate changes in the rate of morphological evolution during our study interval, we developed measures of the morphological difference between new species and their potential ancestors in the previous time interval (*Materials and Methods*). We refer to this basic quantity as innovation and used several different measures as proxies for the magnitude of morphological divergence in a given time interval. As an alternative to the ecological model, trait evolution might be constrained by intrinsic factors such as canalized developmental processes, and thus rate of trait change may show no change during the recovery despite the increased rates of speciation (19). A third possibility is that morphological innovation may increase late in the recovery, implying a different scenario than either of these hypotheses.*

Results

Morphological Selectivity of Extinction Patterns. Both of the extinction episodes during the HME displayed patterns that suggest a preferential survival of the Neograptina over the Diplograptina. Their differential response to these extinction events and the bias

in speciation rates during the Hirnantian are the factors that resulted in the subsequent phylogenetic bottleneck of the Graptoloidea. We used repeated sampling simulations to test whether selection for neograptine-like characteristics is the only causal factor necessary to explain the Neograptina survival patterns. These simulations included selective survival of neograptine-like morphology and preserved the same extinction intensity as the two extinction episodes (*Materials and Methods*). If morphological selectivity is a sufficient explanation, these simulations of the extinction episodes should often produce computer-generated survivor faunas with a proportion of neograptines like that observed in the fossil record.

Our resampling analyses for both extinction episodes found that, under a scenario of direct selection for neograptine morphology, there was a small but tangible probability of producing the observed neograptine survivorship patterns (for the Katian–Hirnantian extinction, $P < 0.09$; for the Hirnantian–Llandovery extinction, $P < 0.06$; each with 10,000 simulations). Typical thresholds for statistical acceptance ($\alpha = 0.05$) would cause us to marginally accept the hypothesis that the observed survivorship patterns could have been produced by morphological selectivity, except that these calculated probabilities consider the events as occurring independently. We may be more interested in the capability of morphological selectivity to explain high neograptine survival at both of the extinction episodes, rather than considering each episode separately. The joint probability for the observed survivorship patterns at both extinction episodes under a model of morphological selectivity is very low ($P < 0.006$). These results indicate that the survival of the Neograptina during the HME probably did not occur as a sole result of a selective advantage afforded by their colony morphology.

The improbability of morphological selection for neograptine-like forms is partly attributable to morphological convergence. Pre-HME neograptines and some diplograptine lineages were strongly convergent, particularly in late growth stages (13, 26). In our analysis, this convergence places many diplograptine species close to the Neograptina centroid, and thus the survival of these taxa is nearly as likely as the survival of the neograptines themselves.

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Comparison of Species Richness and Morphological Disparity. If patterns of taxonomic diversity represent the contraction and expansion of taxa in ecospace, then changes in species richness should track changes in the relative disparity of morphology. This effect should be particularly evident during the Hirnantian, if ecological opportunity was a driving factor of the rapid diversification of the Neograptina. Species richness and morphological disparity, measured as mean pair-wise distance (*Materials and Methods*), do share a superficially similar pattern over our entire study interval (Fig. 2). Both richness and disparity decrease prominently after the first extinction episode of the HME. However, the drop in disparity lags behind the decline in species richness, and disparity falls farther than species richness compared with their respective preceding maxima before the HME. Disparity also increases more steadily and gradually than species richness after the first extinction episode of the HME. Richness drops again during a minor extinction event at the end of the *acuminatus* Zone (AZE) (27). Surprisingly, this extinction event also marks an increase in morphological disparity, although this shift is not statistically significant (Fig. 2). Thus, patterns of morphological disparity and species richness are somewhat discordant in the interval from the start of the Hirnantian until several million years into the recovery.

Statistical analysis of the data supports the lack of a correlation between these two diversity metrics during the recovery. As our focus is testing the role of ecological opportunity during the recovery, we considered only the time intervals after the first extinction episode of the HME when the Neograptina diversification begins. Taking first differences for richness and disparity to remove the correlations induced by their general trends, we find no significant relationship by using either the absolute differences (Pearson's product moment correlation test; $P = 0.41$) or the ranked differences (Spearman's rank correlation test; $P = 0.34$). Under the ecological diversification hypothesis, it is possible that species richness might instead lag behind disparity if there was an "early burst" of rapid morphological evolution (25), which can be tested by lagging the time series in either direction so that changes in one metric are associated with changes in the other metric in the previous or next interval. However, such lagging also does not produce any significant correlations (all P values >0.3). Our inability to find strong correlations may result in part from the small number of intervals analyzed. Stronger evidence for the decoupling between the processes that create disparity and richness come from our measurements of morphological innovation.

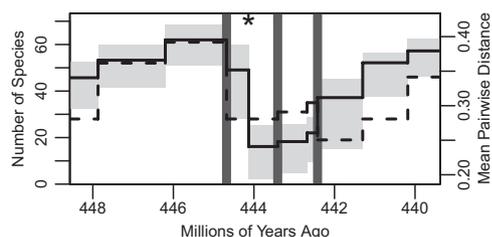


Fig. 2. Species richness and morphological disparity in graptolite zones. The dashed line is the total species richness in that zone, and the thick black line is the morphological disparity, measured as the mean pair-wise distance between taxa. The light gray boxes are 95% quantiles of mean pair-wise distance based on 1,000 bootstraps. Asterisks represent significant shifts in disparity, based on resampling tests with 1,000 bootstraps ($P < 0.05$, Bonferroni-corrected) (46). The dark gray vertical lines represent the following extinction events: the first Hirnantian extinction pulse at the onset of glaciation, the second Hirnantian extinction pulse as the glacial interval ended, and the extinction event at the end of the AZE in the Early Silurian.

Drop in Morphological Innovation During the HME. By all three estimates of morphological innovation, the magnitude of morphological change was relatively high during the late Katian but decreased sharply at the onset of the HME (Fig. 3). Although dynamics in the early Silurian are somewhat uncertain, all three metrics indicate a decrease in the morphological innovation of new species during the HME. Innovation did not return to pre-HME levels until at least 1 or 2 million years later. In addition, changes in morphological innovation and morphological diversity appear to be correlated, although this is not a necessary expectation based on first principles.

Given these results, we also examined mean nearest-neighbor distance (NND) for each zone, a measure of the relative clustering of taxa in morphospace (28). If rates of morphological evolution did drop during the HME, then lower NND and thus higher clustering would be expected during the Hirnantian. We found NND to be very similar to the pattern shown for disparity in Fig. 2, with a decrease in the Hirnantian and an increase after the AZE (Fig. S1). This finding implies that the drop in morphological diversity in the Hirnantian was the result of increased morphological clustering of both new species and survivors.

Altogether, the available evidence suggests that the Neograptina diversification during the HME exhibited less morphological divergence than characterized pre-HME graptoloids, based on the low observed innovation relative to the ancestral stock. The magnitude of morphological innovation did not initially increase above "background" pre-HME levels, contrary to the expectations of the ecological diversification hypothesis. Instead, mean innovation actually decreased in response to the mass extinction and remained at low levels for millions of years, despite the Hirnantian being an interval of increased speciation rates for the Neograptina (7). This decrease produced a large number of species that were much more clustered in morphospace than in pre-HME faunas.

The AZE apparently had the effect of thinning out the occupation of the morphospace by decreasing species richness and morphospace clustering without reducing the span of species

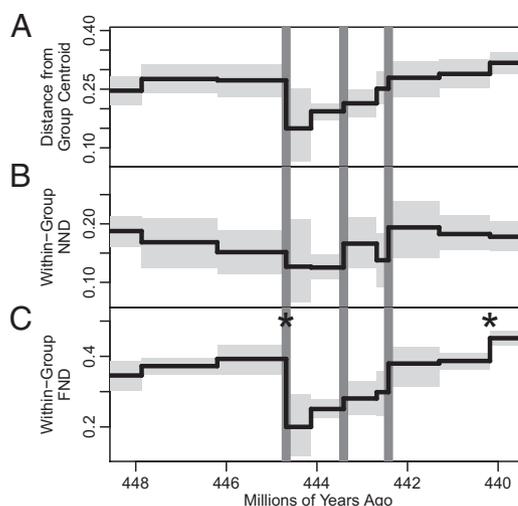


Fig. 3. Morphological innovation of new species over time. Three different metrics for mean morphological innovation of new species are plotted for each time interval. (A) The distance of a new species from the centroid of its taxonomic group in the prior zone, in principle coordinates. (B) The distance between a new species and its nearest neighbor within the same group and in the prior zone. (C) The distance between a new species and its farthest neighbor within the same group and in the prior zone. The light gray boxes represent 95% quantiles, asterisks represent significant differences between zones, and dark gray bars represent extinction events as described in the legend for Fig. 2.

across the morphospace. Although this minor extinction event clearly had an effect on the pattern of disparity and clustering, the event did not have a statistically significant effect on morphological innovation (Fig. 3). In the intervals after the AZE, species richness, disparity, and innovation all increased. These trends match our theoretical expectations for an adaptive radiation driven by ecological opportunity, yet this condition did not develop until several million years after the neograptines began to rapidly diversify.

Measurements of NND depend on sampling size. If intervals of lower diversity also were poorly sampled, estimated NNDs would be inflated even if NND changed very little across intervals (29). We find the opposite trend, with mean NND and the NND-based innovation metric decreasing with species richness. Therefore, the expected bias attributable to variable species richness only reinforces our conclusion that, although the Neograptina radiated in the early Hirnantian, new species were less morphologically divergent, and all taxa present were more clustered in morphospace.

Our analyses of innovation and disparity were for all graptoloid species included in our dataset. We did not analyze the innovation metrics of the Neograptina alone. Thus, it is possible that the decrease in the Hirnantian may reflect a low level of morphological innovation for Ordovician neograptines in general, which would agree with previous assessments of the clade as morphologically conservative (7). However, the small number of neograptine taxa known before the HME makes it difficult to quantitatively assess their characteristic level of morphological divergence.

Discussion

Extinction Selectivity During the Hirnantian. We found that simulations of selective survival for species with neograptine-like morphology during the HME rarely produced the patterns of neograptine survival observed at both extinction episodes. Thus, we were able to test and reject a standing hypothesis that selectivity for general colony form in the Hirnantian is the principal cause for the survival of the Neograptina over the Diplograptina (7, 16). Although these tests do not reject the possibility that selective extinction may have favored specific morphological characters found among the Neograptina, it is not clear that any of the uniquely neograptine traits could be the basis for their unlikely survival. The more likely alternative is that the survival of the Neograptina was the result of selection for nonmorphological traits, such as larger biogeographic ranges or clade-specific physiological preferences for environmental conditions prevalent during the Hirnantian (7, 23, 30).

Models of Morphological Diversification. Before this study, diversification after the first extinction episode of the HME appeared to be consistent with a simple model of ecological opportunity. However, the results of our quantitative morphological analysis are difficult to reconcile with such an interpretation. If the species richness of graptoloids only depended on the amount of ecospace that could be occupied, we would have expected a stronger relationship between species richness and morphological disparity during the neograptine radiation. The high degree of morphospace clustering and low disparity and innovation after the first extinction episode of the HME implies that the initial speciation of the Neograptina had essentially the opposite character of that expected from ecological diversification. Furthermore, the initial decrease and subsequent lag in morphological innovation for at least 2 million years after the start of the Hirnantian is also difficult to reconcile with the ecological opportunity model. Instead, the observed pattern of morphological evolution appears to have been a function of factors beyond the loss of diplograptine competitors. This pattern is also not compatible with a model of morphological evolution controlled by intrinsic constraints, where aspects of

evolutionary history and entrenched colony architecture permanently dampened the ability of the Neograptina to diverge morphologically. If this model were true, no shift to pre-HME levels of morphological innovation would be observed, yet there is a shift to an adaptive radiation-like pattern of morphological diversification after the AZE.

It is possible that this mismatch results from a failure of our assumption that the morphology of graptoloid colonies is a good predictor of their functional ecology and, thus, that morphological diversity can be used as a proxy for ecological diversity. Previous work has demonstrated links between graptoloid form, hydrodynamics, and overall ecology (31–33), supporting our claim that variation in graptoloid morphology reflects real ecological differences. However, some recent work has shown that functional diversity and morphological diversity can be discordant (34, 35). Additional experimental work is needed in graptoloids to allow the direct estimation of functionally relevant traits from fossil morphology. The functional diversity of graptoloids can be estimated with such measurements and compared with morphological diversity to understand the strength of the form–function relationship.

If our analysis is capturing ecologically meaningful aspects of graptoloid morphology, some explanation other than ecologic competition is necessary to explain the delayed morphological recovery among the Neograptina. Any such explanation must account for both the observed increase in speciation rate and the depressed level of morphological innovation during the Hirnantian. For example, morphological diversification may have been depressed during the early recovery by a degraded physical environment (7, 27), a lack of complex ecological interactions (36), or restrictive developmental constraints (26). The pattern of graptoloid species richness increasing with little morphological diversification is similar to the nonadaptive radiations described in some extant groups (37, 38), where lineages diverge in traits unrelated to morphology, such as life history or reproduction. There is no theoretical explanation for why a nonadaptive radiation would later shift to high levels of morphological differentiation, however, as occurs in the early Silurian. In *SI Text*, we further explore these explanations for the decreased morphological innovation during the recovery and suggest the evidence necessary to test them.

Conclusions

Our testing of morphological selectivity and ecological diversification in the Paleozoic graptoloids has rejected two hypotheses suggested by prior work. Our quantitative assessment of morphology gave us an additional dimension to test and reject inferences based on studies of taxonomic diversity and phylogenetic relationships. This study also demonstrated the presence of a varied and very fine-grained pattern of macroevolutionary lags between species richness and morphological disparity—temporal offsets of nearly the same length as the species durations themselves and that, consequently, would have been entirely invisible at the temporal scale used in many studies of morphological disparity in the fossil record (bins on the order of 5 million years or more). This fact expresses the need for high-resolution studies in macroevolution, which in turn depend on high-resolution geochronologies and all of the work that they entail (39). Continued study of taxonomic, morphological, and phylogenetic patterns of evolution in highly resolved fossil records has the potential to add greatly to our knowledge of evolutionary dynamics.

Materials and Methods

For the purposes of this study, we created a dataset of 45 discrete traits and 4 continuous traits, coded for 183 graptoloid species ([Dataset S1](#)). Our choice of morphological characters focused on features of the individual zooid tubes as well as those of the overall colonial edifice, particularly those traits that have been discussed as being functionally important. Data for species came

from previously published systematic descriptions and figures, with a small portion coming from new observations (see [Dataset S1](#) for complete details). We included all graptoloid species from our chosen time interval that are sufficiently well known to be adequately coded for this analysis. The resulting data matrix was only missing data for 3% of all possible species/trait entries. Species were assigned to graptolite biostratigraphic zones (Fig. 1) and phylogenetically defined groups by using the most recent systematic literature (13, 39, 40) (also see [SI Text](#) and [Dataset S1](#) for additional details on these assignments).

For many of the calculations in this work, we used pair-wise distances between taxa, calculated based on the number of character states that differed among each pair of taxa. Our continuous characters are coded as ranges, following standard reporting in graptoloid systematics. Two taxa are considered to differ in a continuous character if their ranges did not overlap. We chose mean pair-wise distance as our measure of morphological disparity, which is notably robust to changes in number of species sampled (41) and thus well-suited for this study given the large changes in observed species richness.

Some of our analyses required the calculation of an average form for all taxa or a particular selection of taxa. We did this by applying a principal coordinate analysis (PCO) to the pair-wise distance matrix, using functions from the R library *ape* (42) with a Lingoes correction (43). This ordination method builds a multidimensional morphospace within which group centroids can be calculated and taken as representative of the “average” morphology for a group. Centroids were calculated for all principal coordinate axes with positive eigenvectors and the Euclidean distance used as the distance between centroids. The sum of the first four relative corrected eigenvalues is less than 0.1, indicating that much of the variance in our data is not represented along the first four axes of the PCO ordination. Although this finding precludes a simple discussion or illustration of the morphospace, this spreading of variance across a wide number of PCO axes implies that graptoloid evolution in our study interval was highly mosaic, with few well-developed character complexes.

We used resampling simulations to test whether extinction selectivity during the HME depended on morphological features. Testing proceeded in two steps. First, we began with a relatively simple analytical framework that only tested whether the observed bias of taxonomic survival across graptoloid clades could be produced via random extinction. In this basic analysis, we resampled the species present before each extinction episode to create simulated sets of survivors. These species were always sampled with uniform probability. The number of survivors sampled was constrained to be the same as observed in the fossil record. Because we wished to test whether the pattern of neograptine survival could be produced with no preferential bias in extinction, we measured the proportion of simulated sets with at least as many range-through neograptine survivors as in the observed data. Over thousands of simulations, the proportion of runs that match or exceed the number of range-through neograptine survivors should be equal to the probability of observing such high neograptine survival under a model of extinction random with respect to clade membership. We applied this analysis separately to the two extinction episodes of the HME by sampling from the species present in the *pacificus* and *persculptus* zones and comparing the simulated survivors to the number of range-through neograptine species observed in the subsequent biozones. The resampling analyses for these two individual extinction episodes were separate and independent simulations. Our simulations of random extinction rarely produced as many neograptine survivors as in the observed data ($P < 0.02$ for both episodes, with 10,000 simulations each). The joint probability of both extinction episodes having such large numbers of neograptine survivors is even lower ($P < 10^{-3}$). These results strongly reject random extinction as a likely cause of neograptine survivorship during the HME, in agreement with the analyses by Chen et al. (7), who focused on the record of these events in the Yangtze Platform succession.

Secondly, the test for taxonomic selectivity described above was extended to include morphological selectivity by varying the species-specific probabilities of survival. All other aspects of the resampling procedure were retained, such as the species lists and the survivorship pattern criteria. The probability of a particular species being sampled for survival was calculated as a function of the multidimensional distance of that species from the centroid of neograptine species in the interval before the extinction episode. This calculation assumes a model of linear selection for species with more neograptine-like colony forms. These probabilities were measured as the similarity of individual species to the neograptine centroid along the PCO axes (see above), such that species closest to neograptine forms had the highest relative values. These similarities were then transformed to sum to unity.

Typically, the tempo of trait evolution is estimated as rates of change on a phylogeny (25, 44), but a majority of the taxa in this study cannot be placed on present phylogenetic hypotheses. Instead, we developed three related metrics to estimate the degree of morphological divergence exhibited by new species, which we call morphological innovation, calculated as the morphological distance between a new taxon and its assumed ancestors in the previous time interval. Innovation estimates are analogous but not equivalent to an estimate of the rate of trait evolution because innovation is measured relative to new species and not units of time. The first innovation metric is the distance of a new species from the centroid of its taxonomic group in the previous zone, measured as the Euclidean distance along the PCO axes. The second metric, a modification of NNDs mentioned above, measures the pair-wise dissimilarity between a new species and the single species in the previous zone that is most similar and in the same group. The third metric is similar to the second but instead computes the distance between a new species and the most dissimilar same-group species in the previous zone.

These individual measures of innovation cannot be considered precise estimates of the degree of trait change, but together they effectively bracket the expected range of possibilities. The first metric provides an estimate of how innovative an average new species might be, whereas the latter two metrics estimate the minimum and maximum amounts of morphological divergence per new species, assuming that the species in the previous zone represent an accurate estimate of the ancestral stock. Given that ancestors are more likely to be close in morphospace to their descendants than not, the NND-based metric may be the more accurate estimate of morphological divergence.

These metrics were calculated for newly appearing species in every graptolite zone, based on a comparison with the potential ancestors in the previous zone. For the first monograptoid species in the *persculptus* Zone and the first retiolitid species in the *pacificus* Zone, the ancestral stock for the three innovation metrics was defined as being among the normalograptids of the previous interval. The measurements for each new species were combined into zonal sets to calculate both mean innovation and 95% quantiles for each time interval.

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