

Clades reach highest morphological disparity early in their evolution

Martin Hughes, Sylvain Gerber, and Matthew Albion Wills¹

Department of Biology and Biochemistry, University of Bath, Bath BA2 7AY, United Kingdom

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There are few putative macroevolutionary trends or rules that withstand scrutiny. Here, we test and verify the purported tendency for animal clades to reach their maximum morphological variety relatively early in their evolutionary histories (early high disparity). We present a meta-analysis of 98 metazoan clades radiating throughout the Phanerozoic. The disparity profiles of groups through time are summarized in terms of their center of gravity (CG), with values above and below 0.50 indicating top- and bottom-heaviness, respectively. Clades that terminate at one of the “big five” mass extinction events tend to have truncated trajectories, with a significantly top-heavy CG distribution overall. The remaining 63 clades show the opposite tendency, with a significantly bottom-heavy mean CG (relatively early high disparity). Resampling tests are used to identify groups with a CG significantly above or below 0.50; clades not terminating at a mass extinction are three times more likely to be significantly bottom-heavy than top-heavy. Overall, there is no clear temporal trend in disparity profile shapes from the Cambrian to the Recent, and early high disparity is the predominant pattern throughout the Phanerozoic. Our results do not allow us to distinguish between ecological and developmental explanations for this phenomenon. To the extent that ecology has a role, however, the paucity of bottom-heavy clades radiating in the immediate wake of mass extinctions suggests that early high disparity more probably results from the evolution of key apomorphies at the base of clades rather than from physical drivers or catastrophic ecospace clearing.

macroevolution | morphological disparity | morphospace | clade shape | clade center of gravity

Evolution is usually characterized as an essentially contingent and unpredictable process (1). This makes it very difficult to identify general rules comparable to those that typify the other natural sciences. Nonetheless, the prospect of formulating and testing macroevolutionary generalities is extremely seductive, because they seem to offer fundamental insights into the manner in which evolutionary processes operate throughout Earth's history (2). Patterns of increasing diversity (measured via proxies of species richness) (3, 4) and increasing maximal organismal size within clades (Cope's rule) (5) have been perennial foci, whereas more recent attention has turned to supposed trends in increasing organismal complexity (6, 7) and the mechanisms that might generate them (8). This paper tests another putative generality, namely, the tendency for taxa to reach maximal morphological diversity (disparity) relatively early in the lifespan of their parent clade (9–17) (early high disparity).

Disparity is conceptually and empirically distinct from diversity. For example, a relatively small sample of species that differ greatly from one another morphologically (e.g., one species from each order of insects) is likely to be more disparate than a much larger sample of species that are morphologically more homogeneous (e.g., a thousand beetles). Among the first questions to be addressed using disparity indices was the perceived magnitude of the Cambrian “explosion.” From Charles Darwin (18) onward, evolutionary biologists have been perplexed by the apparently instantaneous first appearances of numerous phyla (a highly disparate sample of species) in the Cambrian fossil record (19). The

subsequent discovery of hitherto unknown fossil groups from the Cambrian Burgess Shale and similar localities added to the enigma, prompting the radical hypothesis that the disparity of metazoans peaked in the Cambrian (14, 20) and subsequent extinctions winnowed this down to much more modest levels soon thereafter. Surprisingly, a relatively small number of studies have tested this hypothesis directly in focal clades (10, 11, 21–23). These predominantly conclude that Cambrian animal groups had a disparity comparable to that of their modern counterparts (24–27). This nonetheless suggests that metazoans reached high levels of disparity relatively early in their history, the phenomenon of early high disparity. Unfortunately, such analyses are limited for two reasons. First, they discount the intervening trajectory of clade evolution. Second, the clade history is truncated both by the present and by a Precambrian fossil record that is enigmatic at best (17, 28). As a result, the focus of disparity studies has increasingly turned to clades that both originate and go extinct within the Phanerozoic (20). Once again, there is a purported tendency for clades to evolve their most disparate forms relatively early in their histories (11–14, 19, 29–31). However, the validity of this early high disparity model has never been tested systematically. If true, it represents a general macroevolutionary “rule” (19) on the broadest possible scale and is comparable to those proposed for increasing morphological complexity (6, 7) and increasing maximal organismal size within clades (2, 32).

Unfortunately, it is impossible to interpret published case studies meta-analytically for several reasons. First, the type of data used is highly variable (outlines, landmarks, and discrete characters), as is the information that these data are intended to convey (shape, form, or homologous characters of the entire organism or of particular organ systems). Second, the manner in which these data have been analyzed is equally variable, although most studies implement some form of data reduction and ordination (10, 12). Species are typically plotted within an empirical, multidimensional space defined by morphological variables (a morphospace) (33). Third, there are many possible indices of morphological disparity, and these are known to describe different aspects of morphospace occupation (34). Fourth, the manner in which trajectories of disparity through time are quantified and classified is also variable. Several of the analyses that originally spurred the debate (10, 21–23, 35) used discrete character matrices to compare anatomically very disparate forms. Many studies have recently followed similar protocols (27, 36–38), and we adopted these methods here as a unifying approach. Where discrete and continuous character data have been compared for the same sets of taxa (39), relative estimates of disparity have been similar.

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¹To whom correspondence should be addressed. E-mail: m.a.wills@bath.ac.uk.

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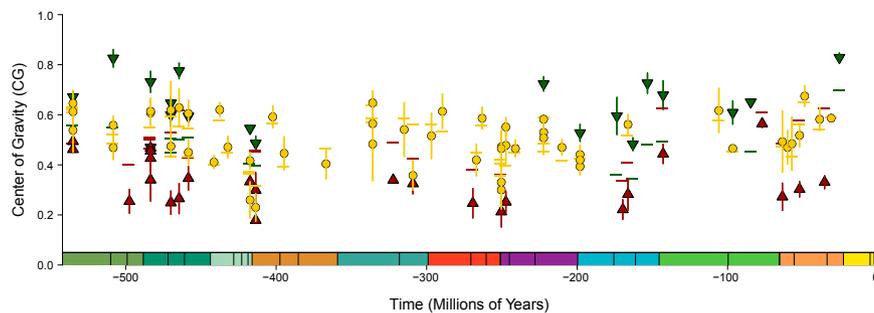


Fig. 2. Center of gravity (CG_{scaled}) values for all 98 datasets across the Phanerozoic. Case studies are sampled relatively evenly throughout this time, and there is no systemic temporal trend in disparity profile shape. Circles denote mean scaled CG (CG_{scaled}) from 1,000 bootstrap replicates of the variance-based disparity curves for each clade, plotted against the clade origination date. Vertical lines denote the SE around CG_{scaled} , derived from 1,000 bootstrap replicates. Green triangles, significantly top-heavy profiles ($CG_{scaled} > CG_i$ with $P < 0.05$); red triangles, significantly bottom-heavy profiles ($CG_{scaled} < CG_i$ with $P < 0.05$); yellow circles, profile indistinguishable from symmetrical; abscissa color scheme, International Stratigraphic Chart.

the relative frequencies of top- and bottom-heavy clades terminating at mass extinctions and at other times were different, whether including all clades ($G = 7.648$, $P = 0.006$) or only those with significant skew ($G = 13.022$, $P < 0.001$). For comparison, we also generated disparity profiles for 53 additional living clades with high diversity in the Recent (Dataset S1) (these are otherwise excluded from our sample unless stated). These extant clades (truncated by the present) had a median CG significantly greater than 0.500 ($V = 1,150$, $P < 0.001$) but indistinguishable from that for fossil clades terminating at a mass extinction ($W = 924$, $P = 0.980$).

Over half of our study clades had disparity profiles that were neither significantly top- nor bottom-heavy. However, these “symmetrical” clades may nonetheless have a variety of trajectories, with their own particular macroevolutionary implications. Most remarkable are groups [e.g., crinoids (35)] whose earliest exemplars have levels of disparity that are not significantly different from the maximum levels subsequently achieved by the clade; a simplistic null of early maximal disparity. For 29 of the 54 symmetrical groups, we were unable to reject this null. Such a pattern would be close to that often envisaged for explosive radiations (14, 49) and similar to that proposed as the trajectory for metazoans through the Phanerozoic (11). Early high patterns inevitably imply an unsampled period of cladogenesis (or the existence of ghost ranges) at the base of the clade, but this either occurs too fast for the available stratigraphic resolution or is not fossilized (11, 50). Late saturation is much less remarkable, because clades have already undergone radiation and diversification and had almost the entirety of their histories in which to colonize the extremities of their morphospaces. Although late saturation was observed in 32 symmetrical clades, 12 of these also ended at a mass extinction (and were

therefore likely to have been prematurely truncated). For this reason, we again focused on the 63 “free-evolving” clades that did not terminate at a mass extinction. Of these, the proportion (two-thirds) that were either significantly bottom-heavy or showed early saturation (two mutually compatible conceptions of early high disparity) was significantly greater than the proportion that were either significantly top-heavy or showed late saturation (late high disparity) (two-sample test for equality of proportions; $\chi^2 = 4.613$, $P = 0.016$). Therefore, clades that do not terminate at a mass extinction do indeed tend to reach their highest levels of disparity relatively early in their evolutionary histories (20). Moreover, this tendency occurs throughout the Phanerozoic.

Why Do Clades Have Early High Disparity?

What might explain the prevailing pattern of early high disparity in clade evolution (19, 51)? Both ecological and developmental explanations have been proposed, and our results remain consistent with both. The “empty ecospace” model predicts that clades will radiate and diversify more rapidly when colonizing a new environment. This colonization may occur because ecospace has been vacated by other occupants (e.g., in the wake of some other extinction, typically the result of external, physical factors) or because a hitherto inaccessible environment or other resource has been rendered viable by the acquisition of some novel, “key” adaptation (52–54) or series of characters (55) (an intrinsic, biological trigger). Morphological change under these circumstances may be rapid either because transitions are unusually large or because rates of cladogenesis are unusually high (even with “normal” step sizes at each splitting event) (29). In this context, we also note that major clades are often distinguished from their paraphyletic

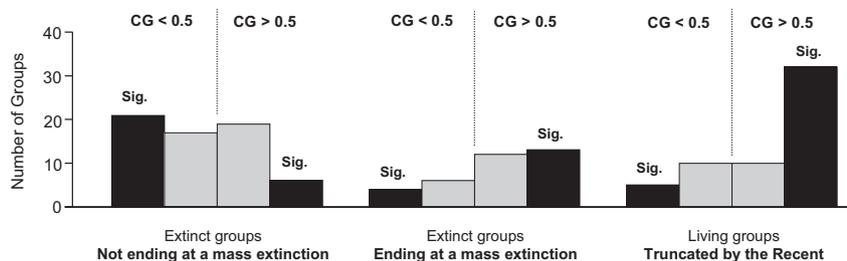


Fig. 3. Groups terminating at one of the “big five” mass extinction events (and living groups that are still diversifying) are more top-heavy than those terminating at other times. (Left) Disparity profile frequencies for extinct clades that do not terminate at a mass extinction boundary. (Center) Disparity profile frequencies for extinct clades that terminate at a mass extinction boundary. (Right) Disparity profile frequencies for living clades (truncated by the Recent). Bars to the left and right of the dotted lines indicate the frequencies of bottom-heavy ($CG < 0.5$) and top-heavy ($CG > 0.5$) clades, respectively. Black bars indicate the frequencies of significantly bottom- or top-heavy clades ($P < 0.05$), while gray bars indicate the frequencies of clades for which $P \geq 0.05$. Mass extinctions: Late Ordovician, 443.7 Ma; Late Devonian, 374.5 Ma; Late Permian, 251 Ma; Late Triassic, 199.6 Ma; and Late Cretaceous, 65.5 Ma.

progenitors because they possess distinct and defining sets of derived characters, or because an extant crown is defined relative to an extinct stem. These divisions into a clade and its residual paraphylum would otherwise often be arbitrary. For example, rather than delimiting a clade of Aves from within the paraphyletic nonavian dinosaurs, it would be possible to define a clade of Aves plus some arbitrary “depth” of theropod dinosaurs. However, birds are defined in the manner they are because they acquired a distinctive suite of apomorphies pertaining to the evolution of flight; key innovations, in this case, that also enabled them to exploit a new environment. These shifts in anatomy, physiology, behavior, and ecology may themselves explain the differential survival of crowns and stems.

More generally it is likely that global shifts in climate, sea level, and ocean chemistry [coupled with the elevated rates of extinction and turnover that these phenomena engender (56–58)] affected the availability of ecospace throughout the Phanerozoic. The only temporal pattern in disparity profile shapes detected in our data was the significant tendency toward top-heaviness in those clades terminating coincident with a mass extinction [which predominantly result from physical drivers (59)]. However, mass extinctions need not increase the subsequent availability of ecospace but may actually cause its collapse (60). The absence of any systemic trends in clade disparity patterns through time, or of any increased propensity for early high disparity in clades radiating in the immediate wake of mass extinctions (Dataset S1) suggest that if ecological mechanisms have a role, then this is more likely to be mediated via key innovations (which can evolve at any time) and the opening up of new adaptive zones rather than from ecospace clearing.

We stress that ecological and developmental explanations for early high disparity are not mutually exclusive; neither do our results allow us to distinguish between them. The hypothesis of increasing developmental constraint predicts that the increasing complexity and interdependence of ontogenetic processes with evolutionary time effectively lock down the potential for subsequent morphological innovation (14, 61–65). Such mechanisms purportedly explain why bodyplans become invariant and inflexible with time, although mechanisms by which these constraints may be lifted have been posited (66). Notable examples are the tetrapod pentadactyl limb [early tetrapods explored a range of higher digit numbers (67)], the seven cervical vertebrae of all mammals except sloths and manatees [otherwise invariant from mice to giraffes (68)] and the diagnostic head segmentation of arthropod subphyla [Cambrian genera explored numerous alternatives with relative freedom (14, 69)]. Such body patterning characters are usually controlled by *Hox* (homeobox) genes, which are also frequently exapted for other (often functionally and positionally unrelated) developmental roles (70). This increasing pleiotropy (more and more varied roles for the same regulatory genes) may account for the observed reduction of developmental lability. Testing this hypothesis would require detailed ontogenetic data far beyond the scope of this study.

The prevalence of early high disparity as the dominant pattern of clade evolution ranks alongside the well-known tendencies for increasing complexity (7, 8, 71, 72) and diversity (2, 8) underpinning putative macroevolutionary trends of the widest possible generality. Moreover, it seems to apply throughout the Phanerozoic, and not merely at times of global diversification (e.g., the early Paleozoic).

Materials and Methods

Collation of Data. We compiled published discrete morphological and stratigraphic data for 98 vertebrate and invertebrate clades radiating throughout the Phanerozoic (Dataset S2). For a subset of analyses (where expressly

stated), we also compiled morphological and stratigraphic data for an additional 53 extant clades (Dataset S2). We avoided taxonomically overlapping cases or datasets obviously derivative of others. Individual datasets were sampled at a variety of taxonomic levels, although most were familial and ordinal in their coverage. Within datasets, strict rules were applied to ensure that sampling was adequately uniform across known operational taxonomic units (OTUs) and through time, amalgamating taxa where necessary (Dataset S1).

Analyses. All analyses were conducted in R using our own scripts (Dataset S3). Empirical morphospaces were derived as multidimensional spaces in which the proximity of OTUs correlated with their morphological similarity (10, 21). Disparity was measured using the sum of variances on successive axes of the morphospace (10, 22, 73). To derive a trajectory of disparity through time, we divided the duration of the clade into time bins, defined so as to balance the competing requirements of stratigraphic resolution and sample size (73) (Fig. 1). To provide a single index of the shape of clade disparity profiles, we calculated the CG metric previously applied to paleontological diversity and disparity data (31, 40, 41). The CG in absolute time (CG_m) was given by

$$CG_m = \sum d_i t_i / \sum d_i,$$

where d_i is the disparity at the i th stratigraphic interval and t_i is the temporal midpoint in absolute time (millions of years) of the i th stratigraphic interval. We then scaled this value between the ages of the oldest (t_{oldest}) and youngest ($t_{youngest}$) representatives of the clade to yield a scaled index of observed CG (CG_{scaled}) between 0 and 1:

$$CG_{scaled} = \frac{t_{oldest} - CG_m}{t_{oldest} - t_{youngest}}.$$

If time bins were all of the same duration, then clades with uniform or symmetrical disparity profiles would have CG_{scaled} of 0.50 (midway). Clades with a relatively early disparity maximum (bottom-heavy) would have $CG_{scaled} < 0.50$, whereas those with a late disparity maximum (top-heavy) would have $CG_{scaled} > 0.50$. In practice the expected CG_{scaled} for a clade of constant disparity through time is not necessarily 0.50, but rather is determined by the durations of the time bins over which the profile was measured. This is because stratigraphic stages are of variable durations, and because taxa are not always dated to series and stages. Hence, we compared CG_{scaled} with the inherent CG_{scaled} (CG_i) for a hypothetical clade of uniform disparity spanning the same intervals. A bootstrapping test determined when this deviation was significant [clades for which >97.5% of 1,000 bootstrapped replicates lay either above or below the center of gravity inherent in the time scale (P value <0.05)] (41). Finally, we adjusted the observed scaled CG_{scaled} relative to CG_i as a zero baseline, hereafter simply CG. Clades were then partitioned into one of three categories according to CG: significantly bottom-heavy, significantly top-heavy, or indistinguishable from symmetrical. Log likelihood ratio goodness-of-fit tests (G-tests) were used to compare frequencies of different profile shapes (e.g., in different time bins).

Clades that were not significantly top- or bottom-heavy could nonetheless have a variety of profile shapes. We therefore devised an ancillary test to determine whether the taxa observed at the beginning and end of the history of each clade (those in the first and last time bins) had a disparity that could be distinguished from the maximum observed in any time bin. The disparity profile of the clade was resampled using 1,000 bootstraps of all of the OTUs in the dataset. For each replicate curve, the difference in disparity between the first (or last) intervals and the disparity maximum elsewhere in the curve was calculated, yielding a distribution. If a difference of zero was within the 95% limits of this distribution, we were unable to reject the null hypothesis of no difference between the initial disparity and the maximum achieved by the clade.

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Supporting Information

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SI Materials and Methods

Data Collation. All research articles were identified using ISI Web of Knowledge, Google Scholar, individual journal websites, and hard-copy publications. Electronic copies of data matrices were obtained from supplementary materials, standard repositories, or the original authors. Where electronic versions were unavailable, the data were transferred from .pdf to .nexus format semimanually and read into PAUP* 4.0 (1), from which a tab-delimited text file was exported.

We initially selected studies that (i) contained phylogenies derived from discrete morphological character data and (ii) contained extinct metazoan taxa. As far as possible, we selected the most inclusive and most recent studies addressing the relationships of the taxa within. We ensured that our datasets were not derivatives or subsets of one another, containing significantly overlapping sets of characters or taxa. A total of 91 publications (2–92) contained data suitable for our main disparity analysis. These either (i) comprised solely extinct taxa or (ii) could be dynamically pruned in such a way (*Taxonomic Resolution*, below) that all remaining taxa were extinct or relict and represented monophyla (Dataset S1). For two datasets we chose to use paraphyletic groups [Theropoda excluding Avialae (40), because we wished to focus on nonavian dinosaurs (93) and cladid crinoids excluding other Articulata (34)]. Data were obtained for an additional 53 living groups with disparity profiles that were truncated by the Recent (94–143). Statistics for these clades are included for comparison, but they did not contribute to the bulk of our conclusions, hence the stated sample size of 98 rather than 151.

The 91 publications in our core sample yielded data for 98 independent groups spanning the entire Phanerozoic. Four papers (20, 27, 34, 56) yielded data for more than one independent clade (Dataset S1). Of the 91 papers, just 7 had previously been used to produce empirical morphospaces, and the remaining 84 had never been used in this way. For all terminals or operational taxonomic units (OTUs) in all datasets we then determined ages of first and last fossil occurrences. Ranges were thereby coded to the stratigraphic resolution of stages, based on the 2009 International Stratigraphic Chart (144, 145). Because most of the original datasets were constructed to address phylogenetic questions, the majority required some moderation before analysis (see below).

Use of Discrete Rather Than Continuous Characters. We have used matrices of discrete characters rather than continuous ones for four reasons. First, there are many discrete matrices available in the literature, representing a largely untapped resource for meta-analysis. Second, they provide us with a sample large enough to make generalizations about disparity patterns through time. Third, they allow us to implement analyses with a unified set of methods, thereby making comparisons across a disparate sample of groups. Fourth, higher taxa tend to contain species with a wide variety of forms, such that it can become difficult to recognize all but a limited suite of homologous landmarks or code more than a degenerate set of continuous characters across all constituent species. Discrete characters offer a means by which to capture wider variations in form under these circumstances. However, we note that in other studies where disparity has been estimated using both continuous and discrete characters for the same sets of taxa, the results can be in marked agreement (146).

Taxonomic Resolution. For many datasets, it was necessary to remove outgroups. This was because cladistic matrices are often constructed by consistently sampling the ingroup, but with

piecemeal or subsequent additions of outgroup taxa. Outgroups were therefore removed for any of three reasons: (i) The outgroup OTUs did not constitute a recognized monophyletic clade with the ingroup (i.e., there were missing taxa between the ingroup and outgroup); (ii) the outgroup OTUs were sampled at a higher taxonomic level than the ingroup; or (iii) less than 50% of the outgroup OTUs were sampled, albeit at the same taxonomic level as the ingroup. In practice, outgroups were usually excluded for the second and third reasons. Retaining both classes of outgroup would have the effect of comparatively undersampling both taxonomic and morphological variation in those lineages of the total clade closest to its root. In some datasets, we also had to overcome inhomogeneity of sampling within the ingroup (e.g., some lineages were sampled at the familial level, whereas others were sampled at the ordinal level). This is problematic for variance-based indices of disparity (e.g., the sum of the variances on the axes of the ordination). Disproportionate sampling and splitting of some groups relative to others would result in a reduction of apparent variance and a shift in the centroid of the empirical morphospace toward those more intensively sampled groups. Conventional taxonomic ranks only offer a first approximation to a more even sampling strategy, but where genera are coded alongside classes (for example) it is unlikely that the sampling is unbiased with respect to either morphological or taxonomic diversity.

We first assigned OTUs to the taxonomic ranks intended by the original authors of each dataset. For example, although an author may have coded 50 named species, these may actually have been selected as exemplars of 50 genera, 50 families, or 50 taxa of some higher rank. If this was not stated explicitly in the source materials, we inferred the sampling regime with reference to the author's contemporaneous papers, or (failing this) with reference to the most congruent available taxonomic scheme. We then determined the efficiency with which this sampling scheme encoded the total number of taxa known to exist at that level. Initially we sought datasets of three types: (i) those containing all known OTUs; (ii) those not containing all OTUs but where the author gave explicit justification for their omission (e.g., uncertain assignment to the group or poor preservation); and (iii) those not adhering to a specific taxonomic scheme, but sampling OTUs with the express intention of capturing variation in morphology within the clade (93). In addition, we included datasets with less even sampling, provided we were able to amalgamate OTUs in such a way as to render them homogeneous at some higher taxonomic level. For example, if a dataset contained 20 genera, 10 of which were unique exemplars of 10 different families and 10 of which were exemplars of the same (11th) family, then we amalgamated the codes for the latter 10 genera to yield a dataset for (effectively) 11 families. Character amalgamation used modal states. Stratigraphic data were amalgamated using the oldest and youngest exemplars (total range). If our hypothetical 11 families represented all of those known within an inclusive clade (or order, in taxonomic terms), then the dataset was deemed to be effectively complete at the family level. Datasets of between 50% and 100% completeness were included provided that the coded OTUs offered reasonably even coverage of the more inclusive group. Where coverage was less than this or manifestly uneven (unless the author gave good reasons why additional OTUs were not included, for example, poor preservation or uncertain affinity to the clade in question), we amalgamated exemplars to the next highest taxonomic level. Where a dataset contained two clades, each sampled homogeneously but at two different taxonomic levels, it was split into two subclades. For example, the data set of

Carlson and Fitzgerald (27) contained two clades, one of 49 homogeneously sampled genera, the other of 20 homogeneously sampled genera. Where homogeneously sampled clades were nested within larger inhomogeneously sampled clades, OTUs were pruned from the dataset until only the homogenous clade remained. Pruning was required in 19 of our 98 datasets (Dataset S1). All preanalytical modifications to the data were implemented in Excel, and all morphological condensing was conducted in the software environment R (147) using a script written by the authors.

A potential concern was that any putative pattern of disparity profiles through time might result from the analysis of clades of markedly different taxonomic rank. For example, many metazoan phyla originate in the Cambrian and most of those that do not are without a fossil record (148). It follows that clades of higher rank and longer duration are more likely to originate in older intervals, whereas clades of genera and families (for example) can potentially originate at any time. Some of this potential bias was mitigated by the stipulation that clades must be extinct; many higher taxa not only originated in older strata but were of high diversity in the Recent, and were consequently disqualified. From our sample of 98 clades, only three spanned from the Paleozoic to the Cenozoic. Our sampling therefore preferentially selected taxa of intermediate and lower rank (orders and families). We nonetheless tested for a relationship between clade age and clade rank (Fig. S1).

Taxonomic ranks are only comparable in the very broadest terms across different metazoan groups, but we proceeded by coding subfamilies as rank one, families as rank two, superfamilies as three, up through ranks of infraorders, orders, superorders, subclasses, classes, and subphyla at rank nine. We then computed Spearman's rank correlation between taxonomic rank and the age of clade origination; this revealed a weak but significant relationship ($\rho = -0.228$, $P = 0.024$) (Fig. S1). However, when we calculated clade age as the age of its CG, the correlation between taxonomic rank and age was even weaker and no longer significant ($\rho = -0.161$, $P = 0.113$). More importantly, we tested for a relationship between taxonomic rank and CG but found no significant correlation ($\rho = -0.027$, $P = 0.791$) (Fig. S2A). We also found no difference between the median CGs for clades partitioned into familial (subfamilies, families, and superfamilies), ordinal (infraorders, orders, and superorders), and higher (subclasses, classes, subphyla, and phyla) taxonomic groups (Kruskal–Wallis test; $\chi^2 = 0.292$, $P = 0.864$). Hence, even if higher-ranking clades were preferentially sampled from older strata, this could not bias disparity profile shapes in and of itself. We also note that there was no significant correlation between clade CG and the number of OTUs as a proxy for clade size ($\rho = 0.063$, $P = 0.535$) (Fig. S2B), or between clade CG and duration of the clade ($\rho = -0.139$, $P = 0.172$) (Fig. S2C). Finally, we modeled CG as a linear function of $\ln(\text{number of OTUs}) + \ln(\text{taxonomic level of clade}) + \ln(\text{duration of clade in Myrs}) + \text{date of clade origin} + \text{taxonomic group (vertebrate or invertebrate)} + \text{demise of clade at mass extinction (yes or no)}$. The only significant variable in the full model [and the only variable retained in the minimum adequate model using the Akaike information criterion (AIC); $P < 0.001$] was the last of these: whether or not a clade went extinct coincident with a mass extinction.

Stratigraphic Resolution. After effective taxonomic ranks were ascribed to all OTUs in a matrix, stratigraphic ranges were assigned to reflect that ranking. We used the International Stratigraphic Chart 2009 (144, 145), offering a maximum resolution of 100 stages. First and last occurrences were determined at the maximum possible precision for each OTU. Taxa were assumed to persist uninterrupted between these dates. Stratigraphic range data were sourced from the Paleobiology Database (<http://paleodb.org/>), Sepkoski Online (149), *The Fossil Record 2* (150), and from other published sources (37, 57, 63, 86, 92, 151–173), including the papers containing the morphological data matrices. Ranges for higher taxa were determined by searching for those taxa directly

and by searching for all constituent taxa within them. In general, we coded the maximum duration for a given OTU. If no stratigraphic data could be found for a given OTU (and there was no evidence to suggest that it was extant) then it was noted and removed before analysis. Unranked OTUs (*incertae sedis*) were dated individually. Stratigraphic ranges for each OTU were formatted as binary matrices of absences and presences. Data taken from the Paleobiology Database and Sepkoski Online were formatted into a stratigraphic matrix using a Perl script written by Anne O'Connor, University of Bath. The script produced the binary matrix by cross-referencing the OTUs in a dataset with a reference list of taxa and dates extracted from both databases. First and last occurrences were then checked manually against other published sources. Clades were plotted according to their first occurrences.

Character Coding. Characters were coded as found in the source paper. If OTUs were to be condensed as a result of uneven sampling, character states were merged in the following way. (i) Where there was no character state conflict resulting from the condensing, no action was taken. (ii) If the character states conflicted between OTUs, we assigned the state most frequently observed within the rest of the matrix. A total of 33 studies (36 clades) contained information on the ordering of character data. For these studies the analysis was run twice to see what effect these orderings had on the disparity curves and center of gravity estimates. Fig. S3 demonstrates that these differences were undetectable; the correlation of center of gravity (CG) values (corrected for intrinsic bias) for ordered and unordered analyses across our 36 clades was extremely high (high ($\rho = 0.997$, $P < 0.001$)). Unordered data were therefore used for all further analyses, and are the basis of the results presented elsewhere. Polymorphic character codes constituted only 1.5% of all data cells. As a conservative approach, they were treated as NA before condensing taxa. Missing and/or gap state data were more prevalent. However, even at its highest concentration, it was possible to calculate pairwise distances between almost all of the taxa in all of our matrices. In cases where the condensation of taxa rendered some characters invariant, these were deleted before analysis.

Intertaxon Distance Matrices and Ordination. The above procedures resulted in one morphological character matrix and one stratigraphic presence/absence file for each of our 98 clades. All subsequent analyses were conducted within R using scripts written by S.G. and M.H. We first generated a generalized Euclidean distance matrix (174) between all pairs of OTUs. For each pair of OTUs, the difference between each comparable character state was squared, these differences summed, divided by the total number of comparable states, then square-rooted (174). A small number of morphological matrices contained one or two pairs of OTUs for which no characters were coded in common (hence it was impossible to calculate a distance between them). In these cases, the most data-deficient OTU was removed and the distances recalculated (repeated as necessary) until there were distance measures for all pairs of OTUs in the matrix. Distance matrices were ordinated using principal coordinates analysis (175) and implementing Cailleux's correction for negative and uninformative eigenvalues (176). Because scores on all coordinates were used to calculate disparity (as the sum of the univariate variances), the ordination step was primarily for visualization purposes. All distances in the ordinations (and the disparity indices inferred from them) were in precise proportion to those calculated directly from the raw character data. Nonmetric multidimensional scaling (20, 177) was not chosen because we wished to retain the metric properties of our distance matrices (178).

Quantifying Disparity. We used the sum of variance index of disparity throughout (179). This was favored because of its relative insensitivity to sample-size differences and its complete indifference

to the orientation of the coordinate axes upon which it is being calculated. The first property is useful because the number of OTUs sampled can be highly variable through time, and because larger samples will tend to have a wider distribution within their character space. Uncorrected measurements of range are sensitive to these changes in sample size, to the extent that they may largely reflect proxies of diversity. The second property is useful because although the orientation of the ordination is derived from all taxa simultaneously, taxa within a given time bin are almost invariably some subset of these. Were these subsets to have been ordinated independently, the orientation of axes would very likely have been different. Disparity was calculated for all time intervals over which each clade persisted. One thousand bootstrap replicates (180) were used at each interval to produce estimates of mean and SE. Stratigraphic resolution was to the stage, epoch, or period level depending upon the size and duration of the clade (with between 5 and 15 time intervals per clade).

Classifying Disparity Profiles. Disparity profiles were categorized according to the CG metric (181, 182). This was used to distinguish between those clades whose temporal mean disparity was located early (bottom-heavy), late (top-heavy), or in the middle of their evolutionary history (symmetrical). The center of gravity in absolute time (CG_m) was calculated as

$$CG_m = \sum d_i t_i / \sum d_i,$$

where d_i is the disparity at the i th stratigraphic interval and t_i the temporal midpoint in absolute time (millions of years) of the i th stratigraphic interval. This was then scaled between the ages of the oldest (t_{oldest}) and youngest ($t_{youngest}$) intervals to yield an index of observed CG_m (CG_{scaled}) between 0 and 1:

$$CG_{scaled} = \frac{t_{oldest} - CG_m}{t_{oldest} - t_{youngest}}.$$

The expected value of CG_{scaled} for a clade of constant disparity through time is not necessarily 0.50, but rather is determined by the durations of the time bins over which the profile was measured. This is because stratigraphic stages are not of uniform duration, nor are taxa invariably dated to series and stages. Hence, we compared the observed CG_{scaled} with the inherent CG (CG_i) for a hypothetical clade of uniform disparity spanning the same intervals. A bootstrapping test was used to determine when this deviation was significant [clades for which >97.5% of 1,000 bootstrapped replicates lay either above or below the center of gravity inherent in the timescale (P value <0.05)] (179). Finally, we adjusted the observed CG_{scaled} relative to CG_i as a baseline, hereafter referred to as simply CG.

For profiles of diversity through time, standard birth/death models of clade evolution on a regular time scale predict a mean CG of 0.5 (181, 183, 184). However, there is no analogous model for profiles of disparity through time. Many clade histories are characterized by early periods of (variously rapid) radiation and morphological diversification, but new forms must be generated by branching cladogenesis (and so clades must explore the design space progressively at some level of temporal resolution). The extinction of OTUs may also be highly selective, affecting branches in a progressive manner that reflects the structure of the tree. However, extinction can also be effectively random with respect to both the tree and the morphospace, which would tend to leave variance-based indices of disparity largely unaffected (179). We note that any model in which the random extinction of lineages is a significant factor is likely to yield top-heavy clades as a null expectation. Our use of an effective CG of 0.5 as our null is defensible in this context because we believe it to be biased against our finding more significantly bottom-heavy than top-

heavy clades (a principal conclusion of this paper). It is also defensible empirically based on our sample. The median CG of our 98 clades (corrected for intrinsic bias) was 0.501, which is indistinguishable from 0.500 ($V = 2,429$, $P = 0.992$).

Clades can only become more diverse through the progressive branching of lineages but may become less diverse because of extinctions that may be either selective (large branches) or effectively random. It is therefore noteworthy to find clades that exhibit early levels of disparity that are indistinguishable from the maximum disparity later achieved by the clade. Hence, we developed an ancillary test for those clades that were initially indistinguishable from symmetrical. The disparity profile of the clade was reconstructed using 1,000 bootstraps of all of the OTUs in the dataset. For each replicate curve, the difference in disparity between the first/second stage and the disparity maximum after the first/second stage was calculated, yielding a distribution. If a difference of zero was within the 95% limits of this distribution, we were unable to reject the null hypothesis of no difference between the initial disparity and the maximum achieved by the clade. In such cases, maximal disparity was achieved in the first stages of the clade's evolutionary history. A similar test was applied to the end of each group's history.

Finally, we implemented a test to determine whether early or late disparity was greater than the disparity we would expect for a similar number of taxa sampled from the entire history of the group (174). The null here was that taxa occupy morphospace at random with respect to our sample of empirically realized forms. This was a much more promiscuous null than we believe to be the case (again, taxa evolve through branching cladogenesis). To reject it and report early high disparity, the early colonizers of the morphospace must be significantly more disparate than the random samples (an extremely difficult test to pass). Unsurprisingly, only seven and eight datasets had early and late disparity (respectively) higher than random according to this test.

Stratigraphic Resolution Within Clades. The analysis of all 98 clades was run with temporal bins of three different sizes (stages, epochs, and periods). For each of these bin sizes, disparity profiles were categorized as described above. In a small number of cases, it became necessary to use more inclusive categories than geological periods. Specifically, the Paleozoic was partitioned into Early Paleozoic (Cambrian/Ordovician) and Late Paleozoic (Silurian–Permian) (182). Other treatments of the Paleozoic (retaining a single interval or splitting it into two bins comprising either equal numbers of epochs or with equal durations) were also implemented but made negligible difference to the overall results. The choice of stratigraphic resolution was otherwise important because not all clades had the same duration (those in our dataset had a mean duration of 15 stages or 90 million years and a SD of 12 stages or 69 million years). There was a balance between sampling at a higher temporal resolution on one hand and sampling more OTUs within each time bin on the other hand. Attempting to use too many stratigraphic subdivisions potentially results in problematic levels of noise, prohibitively large error bars, and larger numbers of intervals containing just one or no OTUs. In practice, the preferred binning regime yielded between 5 and 15 intervals. The paucity of top-heavy clades in the Cenozoic was partly a function of using entirely extinct groups. Many datasets of Cenozoic fossil taxa contained extant representatives and could not be pruned to yield an exclusively extinct subclade.

Removing the Immediate Effects of Mass Extinction. Clades terminating at mass extinction boundaries might be shaped significantly by those extinction events. Specifically, a mass extinction might truncate a clade that would otherwise have obtained a symmetrical or bottom-heavy profile of disparity through time. Such extinction-terminated clades might be expected to be flat-topped to some degree, and therefore have a potentially higher CG than

otherwise. To remove the most immediate of these effects, we reduced our sample to include only those clades not terminating at one of the big five mass extinction boundaries, namely the End Ordovician (443.7 Ma), the Late Devonian (Frasnian/Famennian boundary 374.5 Ma), the End Permian (251 Ma), the End Triassic (199.6 Ma), and the End Cretaceous (65.5 Ma). We note that broader definitions are possible for the End Ordovician and Late Devonian events, but these had no effect upon any of our statistics. A clade was deemed to terminate at a mass extinction if at least one of its constituent OTUs went extinct at the boundary but none persisted thereafter. The 35 clades terminating at a mass extinction had a mean CG significantly greater than 0.5 ($t = 3.901$, $P < 0.001$) (i.e., they were top-heavy on average). Those not terminating at a mass extinction had a mean CG significantly less than 0.5 ($t = -2.420$, $P = 0.018$), and were therefore bottom-heavy on average. Unsurprisingly, the two distributions also had significantly different medians ($t = 4.382$, $P < 0.001$).

Comparing the Distribution of Clade Disparity Profiles Within the Largest Time Bins. We first compared the frequencies of top- and bottom-heavy clade profiles in the four largest time bins (Early Paleozoic, Late Paleozoic, Mesozoic, and Cenozoic), irrespective of whether these were significant or not. A log likelihood ratio test applied to a 2×4 contingency table of all 98 clades retained the null of similar distributions within these bins ($G = 2.298$, χ^2 df = 3, $P = 0.513$). We then counted only those clades for which our bootstrapping test allowed us to reject the null hypothesis of symmetry, yielding another 2×4 contingency table, albeit with a smaller total sample size. Again, a log likelihood ratio test retained the null of similar distributions within the four time bins ($G = 3.558$, χ^2 df = 3, $P = 0.313$).

A similar suite of tests was run on only that subset of 63 clades that did not terminate at a mass extinction event. None of these revealed significant differences between Early Paleozoic, Late Paleozoic, Mesozoic, or Cenozoic time bins, irrespective of how the data were partitioned. The partition into clades with CGs above and below 0.5 ($G = 3.461$, χ^2 df = 3, $P = 0.326$) and with CGs significantly above and below 0.5 ($G = 3.943$, χ^2 df = 3, $P = 0.268$) revealed no significant differences.

Comparing the Distribution of Clade Disparity Profiles Terminating at Mass Extinctions with Those Not. Of the 35 clades that terminated at a mass extinction, 24 had a CG >0.5 . However, of the 63 clades that terminated at other times, just 25 had a CG >0.5 . A likelihood ratio test revealed that these profile frequencies were significantly different (2×2 contingency table, log likelihood test; $G = 7.519$, χ^2 df = 1, $P = 0.006$). A similar difference was observed for significantly top- and bottom-heavy clades. Thirteen from 17 significantly asymmetrical clades terminating at a mass extinction were top-heavy, whereas just 6 from 25 significantly asymmetrical clades terminating at other times were top-heavy (Fig. S4) ($G = 12.553$, χ^2 df = 1, $P < 0.001$).

Comparing the CG Distribution of Clades Radiating in the Wake of Mass Extinctions with Those Not. If early high disparity was the result of ecospace clearing in the wake of mass extinctions, then we might expect clades originating immediately after one of the big five events to have a lower median CG than those originating at other times. There were just 12 extinct clades originating in the first stage after a mass event, and 17 in the first two stages. These both showed distributions of median CG values indistinguishable from those of clades originating at other times ($W = 693$, $P = 0.970$; $W = 468$, $P = 0.608$).

Ancillary Analyses

Comparison of "Cladistic" and "Phenetic" Source Matrices. The majority of the discrete matrices analyzed in this study had been used in other contexts to infer phylogeny (hereafter "cladistic"

matrices). A small minority were not prepared with this purpose in mind (hereafter "phenetic" matrices, in the absence of a better term). Do cladists code characters differently from those researchers not intending to derive a tree? In particular, do cladists "filter" potential characters more stringently than pheneticists, applying more rigorous criteria of operational homology and thereby rejecting sources of variation that would be legitimate within analyses of morphological disparity?

All morphological data sets—whether intended for phylogenetic purposes or otherwise—necessarily sample a subset of the available universe of possible characters. Moreover, many pheneticists used concepts of homology for discrete characters that differed little from the operational definitions used by cladists (i.e., those of close compositional and relational similarity). Hence, even if rich seams of discrete phenetic data matrices were available in the literature (which, unfortunately, they are not), we believe that these would be largely similar in quality and nature to most cladistic matrices. Most pheneticists do not, for example, code states believed to be blatant analogies (wings of birds, bats, and bees) as the same state. They might, perhaps, take greater license with characters than some cladists, but this is a difference of degree rather than one of principle. By the same token, nearly all cladistic matrices contain homoplasy, and many of them retain characters that map onto globally optimal trees without supporting any nonterminal branches (i.e., they map with the maximum possible number of changes). Such characters are typically retained, even though their homology is implicitly rejected by the rest of the data.

In fact, we suspect that many cladistic matrices are more promiscuous in terms of the sampled characters than many phenetic ones. Certainly, the former are often typified by a higher ratio of characters to taxa than phenetic matrices, which is borne out in our (admittedly very modest) sample (Fig. S4). One could go a step further and include functional characters. However, such data have greater utility for investigating functional variety rather than morphological variety and disparity as usually conceived. We deliberately excluded a number of otherwise excellent datasets from our analyses for precisely this reason.

For comparison, we have analyzed the small number of discrete phenetic matrices within our sample of 98 datasets as although they were intended for phylogenetic inference, subsequently calculating the homoplasy excess ratio (HER) (185–187) for these and the other matrices in our study. The HER is relatively unbiased by dataset dimensions [unlike the ensemble consistency index (CI) and retention index (RI)]. Calculating the HER requires an estimate of the mean tree length for a large number of datasets (here 500) in which the assignment of states within characters (but across taxa) has been randomized. For this, we used a TNT (188) script implementing `xperm` followed by `xmult level 10` searches. The latter (in the absence of further `bb` searches) is very unlikely to find the full set of optimal trees but is guaranteed to find some of them (and hence the true optimal tree length, which is all that is needed within the HER calculation). The results indicate no difference in the median HER for cladistic and phenetic datasets ($W = 323$, $P = 0.917$). Hence, our cladistic matrices sample greater numbers of characters (relative to the number of taxa in the matrix) than their phenetic counterparts. However, coded cladistic and phenetic characters are indistinguishable in terms of their conflict with one another and the amounts of homoplasy that they introduce. Hence, there is no evidence (on the grounds of our admittedly modest sample) that cladists use more stringent criteria of operational homology, causing them to reject characters that others might accept.

How Closely Do Observed Intertaxon Distances Approach the Maximum Possible for a Given Dataset? Do clades reach early high disparity because they have exploited the extremes of their coded character spaces (189), or is there room for morphological expansion

throughout their histories? We addressed this simply for each of our datasets by comparing the maximum distance between taxa with the empirical distribution of all possible intertaxon distances. Where all characters are unordered, the maximum theoretical Euclidean distance between taxa was given simply by the square root of the number of characters. This was compared with the distribution of $(N^2 - N)/2$ empirically observed distances between N taxa to determine whether any observed intertaxon distances reached the theoretical maximum. We note that this contingency only implied that disparity had reached its theoretical limit where one or more observed maximum distances were between taxa

from the same time bin. Taxa might otherwise migrate through the character space, such that no individual time bin would contain taxa as distant as the theoretical maximum.

Of our 98 “extinct” and 53 “living” matrices, only 2 (18, 38) contained an empirical distance as great as the theoretical maximum. However, in neither of these cases were the maximum empirical distances observed between taxa within the same time bin. One of these had a significantly top-heavy CG, and the other was symmetrical. In these two cases, at least, character saturation (if it occurs) did not yield a low CG. We conclude that character-state saturation is not a significant problem in our analyses.

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