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# Trait-based diversification shifts reflect differential extinction among fossil taxa

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Evolution provides many cases of apparent shifts in diversification associated with particular anatomical traits. Three general models connect these patterns to anatomical evolution: (i) elevated net extinction of taxa bearing particular traits, (ii) elevated net speciation of taxa bearing particular traits, and (iii) elevated evolvability expanding the range of anatomies available to some species. Trait-based diversification shifts predict elevated hierarchical stratigraphic compatibility (i.e., primitive→derived→highly derived sequences) among pairs of anatomical characters. The three specific models further predict (i) early loss of diversity for taxa retaining primitive conditions (elevated net extinction), (ii) increased diversification among later members of a clade (elevated net speciation), and (iii) increased disparity among later members in a clade (elevated evolvability). Analyses of 319 anatomical and stratigraphic datasets for fossil species and genera show that hierarchical stratigraphic compatibility exceeds the expectations of trait-independent diversification in the vast majority of cases, which was expected if trait-dependent diversification shifts are common. Excess hierarchical stratigraphic compatibility correlates with early loss of diversity for groups retaining primitive conditions rather than delayed bursts of diversity or disparity across entire clades. Cambrian clades (predominantly trilobites) alone fit null expectations well. However, it is not clear whether evolution was unusual among Cambrian taxa or only early trilobites. At least among post-Cambrian taxa, these results implicate models, such as competition and extinction selectivity/resistance, as major drivers of trait-based diversification shifts at the species and genus levels while contradicting the predictions of elevated net speciation and elevated evolvability models.

trait-based diversification | extinction | evolvability | speciation | Cambrian

A basic question in evolution is whether shifts in taxonomic and/or morphologic diversification are tied to particular anatomical traits. The fossil record includes many examples of taxa possessing one set of traits losing diversity over time, whereas other taxa with different sets of traits gain diversity (1–4). Similarly, phylogenies of extant taxa often suggest that speciose subclades possessing derived traits were once much less diverse than the remainder of the clade diagnosed by primitive traits (5–7). In a different vein, morphospace studies often indicate that particular subclades diversify in regions of morphospace seemingly off limits to the remainder of the clade (8–10). Three models of trait-based diversification shifts explain these patterns. Model 1 (elevated net extinction) posits elevated extinction rates and/or decreased origination rates among taxa with primitive traits (11, 12). Model 2 (elevated net speciation) posits elevated speciation rates and/or decreased extinction rates among some taxa with derived traits (11, 13, 14). Model 3 (elevated evolvability) posits that some characters vary only among some derived taxa and not among the remainder of the clade (3, 15). These models are not mutually exclusive: elevated evolvability might elevate net speciation (models 2 and 3) (16), or elevated speciation in one part of a clade might induce elevated extinction in another part of a clade (models 1 and 2) (17). However, we do not know whether any of these three models predominates or even whether trait-based diversification shifts are the norm at low taxonomic (e.g., species and genus) levels.

## Model Predictions

We can test whether traits correlate with diversification shifts on phylogenies of extant taxa (13, 14). However, accurately estimating extinction rates and recognizing lost diversity given only extant taxa are notoriously difficult (18, 19), both of which bias such tests against supporting the elevated net extinction model (20). Modifying these tests to include taxa sampled in different time intervals rather than from just the present should improve extinction rate estimates (21). Even then, error in phylogenetic reconstructions for fossil taxa is biased toward elevating early diversification rates (22). Such error biases inferred trees against supporting differential net cladogenesis and possibly, against elevated evolvability.

Trait-based diversification and trait-independent diversification make different predictions about the fossil record without reference to specific phylogenies (9, 10, 23–25). Stratigraphic patterns among compatible character pairs are one example. Character pairs are compatible if there are phylogenies that do not require parallelism or convergence for either character (26, 27). If both characters have two states, then at most, only three of four possible combinations evolve. Such pairs are stratigraphically compatible (28) if they fit one of two patterns. Suppose that we label the character states on the oldest-known species 0. Hierarchical stratigraphic compatibility (HSC) is species with 00 occurring in the oldest strata, species with 10 appearing in younger strata, and species with 11 appearing in still younger strata. HSC is consistent with a 00→10→11 sequence of evolution. Divergent stratigraphic compatibility (DSC) is species with 00 occurring in the oldest strata,

## Significance

Shifts in biological diversity often are associated with particular anatomical traits. Anatomical data from over 300 clades of brachiopods, molluscs, arthropods, echinoderms, and chordates show that trait-based diversification shifts are common at even fairly low (genus and species) taxonomic levels. Cambrian taxa present the lone major exception. Among post-Cambrian taxa, diversification shifts correlate strongly with elevated net extinction of primitive taxa rather than elevated net speciation of derived taxa or increased morphological disparity among derived taxa. This finding emphasizes the importance of extinction in shaping morphological and phylogenetic diversity among closely related species and genera as well as suggests another way in which Cambrian evolution was unique.

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Data deposition: The datasets used in this paper have been deposited in The Paleobiology Database, [www.paleobiodb.org/cgi-bin/bridge.pl?a=nexusFileSearch](http://www.paleobiodb.org/cgi-bin/bridge.pl?a=nexusFileSearch) (reference no. 53093).

See Commentary on page 16240.

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with some species bearing **10** and different species bearing **01** appearing in younger strata. DSC is consistent with a **10** ← **00** → **01** sequence of evolution.

Compatible characters should represent slowly evolving characters (26, 27). Simulations confirm this expectation (29) (*SI Appendix, Fig. S4*). If characters change infrequently, then there usually will be several species bearing **00** (hereafter, a paraclade) (30) contemporaneous with the first species bearing **10** (31). Under trait-independent diversification, that paraclade should generate more total descendants than the sole-derived species (30) and thus, generate more opportunities for a **00**→**01** transition (DSC) than for a **10**→**11** transition (HSC). Simulations show that, given trait-independent diversification and no addition to character space, fewer than 40% of stratigraphically compatible pairs should be HSC (*SI Appendix, Fig. S5*). These expectations hold over a wide range of per-taxon sampling rates and evolutionary models (*SI Appendix, Fig. S5*) (note that the same simulations show that we should sample state pairs in correct order for 95% of compatible character pairs).

Increasing net extinction rates within paraclades retaining **00** pairs (model 1) reduces the chance of a **00**→**01** transition (and DSC) by reducing the expected descendants from paraclade members. Similarly, increasing net speciation rates for species with **10** (model 2) elevates the probability of a **10**→**11** transition (and HSC) by elevating the expected descendants of the species with **10**. Finally, increasing the number of evolvable characters for the subclade diagnosed by **10** (model 3) introduces a suite of characters for which **10**→**11** (and HSC) is the only probable transition. Thus, all three models elevate expected HSC.

Models 1–3 make unique predictions about correlations between HSC and different paleontological patterns. Elevated net extinction and elevated net speciation (models 1 and 2) make distinct predictions about stratigraphic distributions of species within paraclades and whole clades, respectively. Elevated net extinction (model 1) predicts that the pooled stratigraphic distributions of species retaining primitive conditions should have lower centers of gravity than other models predict (32, 33). Elevated net speciation (model 2) predicts that the pooled stratigraphic distributions for the clade should have a higher center of gravity than other models predict.

Elevated evolvability (model 3) makes unique predictions regarding morphological diversity (disparity) relative to models 1 and 2. If fewer characters can change among early species than some derived species, then the disparity among all  $S/2$  early species will be lower than expected given the total character space and likely rates of change (34, 35). These predictions apply to cumulative disparity (i.e., disparity among all  $S/2$  species) rather than standing disparity (i.e., species extant halfway through a clade's history), because extinction often greatly affects standing disparity (36) (*Materials and Methods* and *SI Appendix, Fig. S5*).

We apply stratigraphic compatibility, center of gravity, and cumulative disparity analyses to 319 published character matrices of fossil species and genera to ask three questions. (i) Are patterns consistent with trait-based diversification shifts truly common among fossil taxa at low taxonomic levels? (ii) Do these patterns vary among taxonomic groups and/or over time? (iii) Is there any general association with the expectations of elevated net extinction, elevated net speciation, or elevated evolvability?

## Results

**Excess HSC.** HSC exceeds expectations of trait-independent diversification in the vast majority of the clades (Fig. 1, Table 1, and *SI Appendix, Table S3*, results under alternative models). Only arthropods fail to have significantly more than 50% of clades with excess HSC. Major deviations are particularly common: 37–53% of clades show excess HSC deviations that 25% or fewer clades should show; 12–29% of clades show deviations that only 5% or fewer clades should show (Table 1 and *SI Appendix, Fig. S7*).

Temporally, only Cambrian clades fit null expectations (Fig. 2); excess HSC is common thereafter, with only the Carboniferous failing to show excess HSC in significantly more than 50%

of clades at  $P \leq 0.05$ . Pairwise contrasts in excess HSC between periods (*SI Appendix, Table S4*) show the Cambrian to be significantly different from all periods save the Carboniferous; however, only one of the remaining 45 contrasts (Ordovician vs. Paleogene) is significant at  $P \leq 0.05$ .

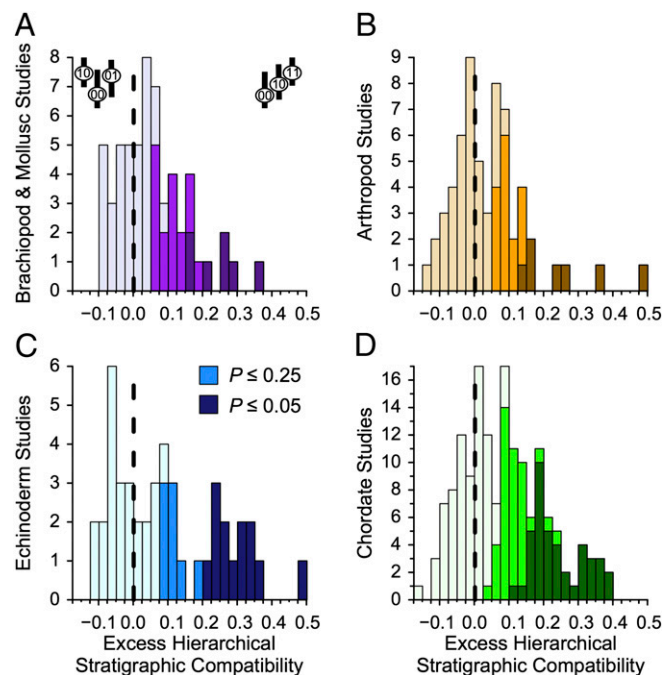
## Associations Between Excess HSC and Other Evolutionary Patterns.

Clades with excess HSC typically have lower centers of gravity for paraclades retaining **00** pairs than expected given trait-independent diversification and origination, extinction, sampling, and character change parameters appropriate to each clade (*Materials and Methods*). This association (Fig. 3A) is highly significant for all clades (Kendall's  $\tau = -0.329$ ,  $P = 1.7 \times 10^{-18}$ ) and among brachiopod and mollusc, arthropod, echinoderm, and chordate clades separately (Table 2). The associations also are significant for Ordovician-Permian and Meso-Cenozoic clades but not Cambrian clades (Table 2). Excess HSC is also associated with whole clades having lower than expected centers of gravity. This association is much weaker than the HSC–paraclade association, and it is significant only among chordate and Meso-Cenozoic clades (Table 2). Finally, no significant associations exist between excess HSC and deviations from expected cumulative disparity (Table 2).

## Discussion

Our results strongly corroborate elevated net extinction (model 1), strongly contradict elevated net speciation (model 2), and are unresponsive of elevated evolvability (model 3). Before discussing the implications of these models in additional detail, we will first consider whether very different models might explain our results.

**Alternative Explanations for Excess HSC.** We should sample 95% of state pairs for compatible characters in correct order, regardless



**Fig. 1.** Deviations between observed and expected HSC for fossil (A) brachiopods and molluscs; (B) arthropods; (C) echinoderms; and (D) chordates. Positive numbers mean that **00**→**10**→**11** (upper right cartoon in A) sequences exceed Monte Carlo-generated expectations assuming continuous trait-independent diversification with empirically estimated origination, extinction, and sampling rates and simulated character evolution matching observed compatibility for each dataset. Negative numbers mean that **10**←**00**→**01** sequences (upper left cartoon in A) exceed those same expectations. Shades correspond to the significance of the deviations.

**Table 1. Cases of excess HSC at Monte Carlo significances of  $P \leq 0.05$ ,  $P \leq 0.25$ , and  $P < 0.50$  assuming trait-independent diversification**

Group	<i>N</i>	$P$ (HSC) $\leq 0.05$	$P$ (HSC) $\leq 0.25$	$P$ (HSC) $< 0.50$
Brachiopods and molluscs	57	7 ( $7.2 \times 10^{-3}$ )	23 ( $3.5 \times 10^{-3}$ )	39 ( $1.6 \times 10^{-3}$ )
Arthropods	60	7 ( $9.8 \times 10^{-3}$ )	22 ( $4.3 \times 10^{-4}$ )	35 (0.078)
Echinoderms	45	13 ( $2.3 \times 10^{-8}$ )	21 ( $4.6 \times 10^{-4}$ )	29 (0.018)
Chordates	157	41 ( $1.4 \times 10^{-18}$ )	83 ( $7.7 \times 10^{-14}$ )	117 ( $3.0 \times 10^{-10}$ )

Cases from each major group showing different levels of significance for excess HSC (measured as the proportion of Monte Carlo runs with equal or greater HSC). All cases with  $P \leq 0.05$  are also counted as  $P \leq 0.25$  and  $P < 0.50$ . Numbers in parentheses give binomial probabilities of these outcomes given expectations of 5%, 25%, and 50% of datasets. Fig. 1 describes the test.

of average per-taxon sampling rates (*SI Appendix, Fig. S5*). However, if species with derived states have vastly higher sampling rates than species with primitive states, then we could sample more state pairs out of order. We consider this an unlikely explanation for two reasons. First, such changes in preservation potential should be as apt to convert HSC to DSC as DSC to HSC. Second, it is an improbable explanation on first principles: traits, such as basic skeletal mineralogy or environmental preference, that greatly alter preservation potential rarely vary among closely related species and genera (37, 38). Instead, the vast majority of character states are variations on features with very similar preservation potentials (e.g., shapes on some region of bone or calcitic shell).

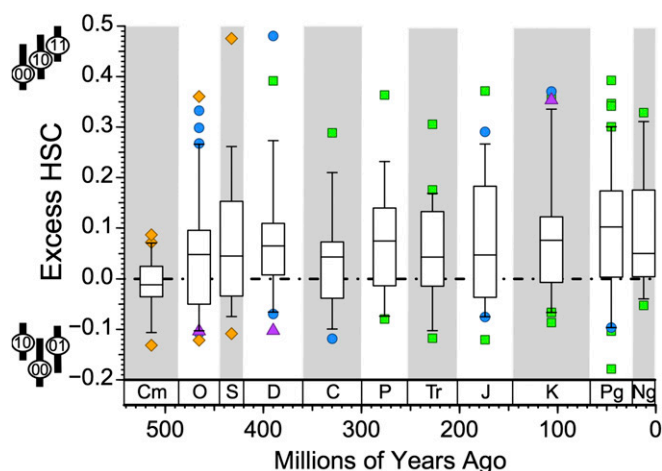
Our Monte Carlo tests use diversification models that maximize expected HSC. However, pervasive anagenesis is a very different model that also will generate copious HSC. If all species in a given dataset are morphospecies from a single anagenetically evolving lineage, then only HSC can be common: a **00**→**10** transition eliminates the sole (morpho-) species bearing **00**. A **00**→**01** transition requires that the lineage first revert back to **00**. Anagenesis also predicts that HSC is anagenetic: species with **00** do not occur in younger strata than the first species with **10**. Anagenetic HSC is much more frequent than predicted by trait-independent diversification (*SI Appendix, Fig. S8A*). However, very few datasets analyzed here are good candidates for being anagenetic lineages. Most datasets include numerous clearly contemporaneous species,

and reconstructed phylogenies typically imply numerous subclades within each clade. Notably, trait-independent diversification under bifurcation models that mix anagenesis and cladogenesis predicts less HSC than it does under budding models with only cladogenesis (*SI Appendix, Fig. S5*). Our Monte Carlo tests assume the budding model. As such, assuming no anagenesis makes our results conservative (*SI Appendix, Fig. S9 and Table S3*).

An evolutionary explanation for reduced durations of paraclades relative to expected paraclade durations is that turnover rates decrease over time within clades. If this happens within individual clades that we analyze, then early paraclades should have shorter durations than expected given our null model. This pattern is well-documented for the Phanerozoic as a whole (39). However, stage-to-stage variation in turnover is considerable for both metazoans (39) and larger taxonomic groups (e.g., gastropods or mammals) (40–42), which means that turnover actually varies considerably over the timespans covered by the datasets that we analyze. Moreover, individual clades often have early origination rates that are much higher than extinction rates (3, 41–44), which elevates DSC rather than HSC (*SI Appendix, Fig. S5D*).

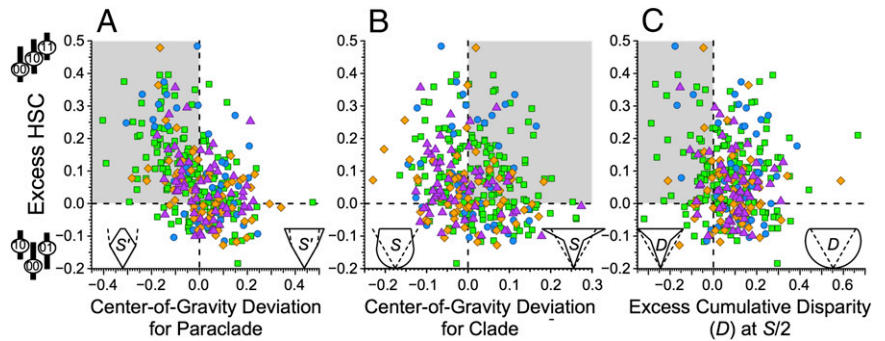
Paleontologists choose species and genera for phylogenetic analyses to address particular issues, which might, in turn, bias our results. For example, workers compile many phylogenetic datasets to examine biogeographic patterns (45–47). However, biogeographic differentiation should encourage the subclade divergence and thus, should generate more DSC than null models. Other phylogenetic datasets deliberately target the oldest members of clades to unravel subclade relationships because of a concern that homoplasy among late-appearing members of subclades will confound relationships among those subclades (48–50). Deliberately targeting early members of subclades should elevate DSC. Finally, high diversification rates early in clade history also would elevate DSC (see above).

Many of the clades that we analyze actually are paraclades within larger clades. Paraclades do not affect the implications of our results. Suppose that Eocene species show high HSC and correspondingly low centers of gravity among paraclades with primitive states. The implied relationship between primitive states and elevated net extinction in the Eocene follows if the clade went extinct at the end of the Eocene or if the clade includes unanalyzed Oligocene species. Alternatively, a group might be paraphyletic relative to a contemporaneous taxon that is so different that workers have not analyzed them together. Again, subsequent evolution has no bearing on the history of character states within the paraphyletic group; moreover, if the daughter taxon is that different from its ancestors, then there probably are few character states that can be coded easily in both groups to reveal DSC. Finally, our finding that paraclades with primitive states have unusually low centers of gravity is not an artifact of parafyly. We report the difference between expected metrics given trait-independent diversification and observed metrics; regardless of whether expected centers of gravity for paraclades are low or high (33), we find that the observed centers of gravity are too low.



**Fig. 2.** Deviations between observed and expected HSC over time given budding cladogenesis. Colors denote higher taxonomic group like in Fig. 1. Binomial probabilities of deviations from an expectation of 50% excess HSC are Cambrian (Cm):  $P = 0.584$  (11 of 22); Ordovician (O):  $P = 0.049$  (32 of 53); Silurian (S):  $P = 0.025$  (12 of 17); Devonian (D):  $P = 9.6 \times 10^{-5}$  (25 of 31); Carboniferous (C):  $P = 0.072$  (11 of 17); Permian (P):  $P = 0.018$  (11 of 15); Triassic (Tr):  $P = 5.3 \times 10^{-3}$  (17 of 23); Jurassic (J):  $P = 0.026$  (18 of 27); Cretaceous (K):  $P = 1.1 \times 10^{-4}$  (36 of 48); Paleogene (Pg):  $P = 2.9 \times 10^{-5}$  (39 of 51); and Neogene (Ng):  $P = 2.9 \times 10^{-5}$  (12 of 15).

**Fig. 3.** Associations between excess HSC and other paleontological patterns. Colors and shapes are the same as in Figs. 1 and 2. All points plot the differences between observation and expectation given continuous trait-independent diversification and no change of character space. Cartoons on the x axis idealize those deviations from the null model, with dashed lines giving expectations and solid lines giving possible patterns (*D*, cumulative disparity; *S*, richness). Gray boxes reflect predicted associations with HSC given (A) elevated net extinction, (B) elevated net speciation, and (C) elevated evolvability. (A) Observed minus expected centers of gravity for paraclades retaining 00 combinations (where 0 denotes the oldest appearing state). (B) Observed minus expected centers of gravity for whole clades. (C) Excess cumulative disparity among the first *S*/2 taxa in a clade of *S* taxa. Additional information is in Figs. 1 and 2.



**General Models of Elevated Net Extinction.** We conclude that elevated net extinction of paraclades retaining primitive conditions (model 1) drives most trait-based diversification shifts at low taxonomic levels. Paleontologists have proposed several explanations for elevated net extinction, including competition (43, 51, 52) and biased survivorship over extinction pulses (53). Competition models, such as coupled logistic diversification, are particularly appealing, because they offer mechanisms for actively eliminating paraclades while not necessarily greatly increasing the overall diversity of a clade (1, 43, 52). Competition also predicts the elevated anagenetic HSC discussed above by linking elevated net extinction to the appearance of derived species (*SI Appendix, Fig. S12*). Competition with members of other clades could have the same effect (with or without logistic diversification) if it induces new states through mechanisms, such as character displacement (54), in some lineages while elevating net extinction in paraclades. Under either case, elevated net extinction might reflect decreased origination rates rather than increased extinction rates among lineages within paraclades (32).

Extinction resistance/selectivity favoring some derived taxa (24, 53) is another plausible model. Although few of the datasets examined here span mass extinctions, many of them span extinction pulses (55). Like competition models, extinction resistance for a derived subclade predicts lower centers of gravity for many paraclades than expected without selective extinction pulses. However, extinction resistance/selectivity does not predict unusually high anagenetic HSC: The mechanism for paraclade extinction does not coincide with the appearance of derived traits. Moreover, we have empirical examples of extinction resistance associated with primitive traits (23, 56) as well as many cases in which there is no obvious selectivity at all (57). These considerations make extinction resistance/selectivity a less reliable and less powerful explanation; however, we cannot discount it entirely.

**On the Viability of the Elevated Evolvability and Elevated Net Cladogenesis Models.** Our results do not support the idea that elevated evolvability (model 3) drives trait-based diversification shifts. The vast majority of clades showing excess HSC shows more disparity among early species than expected rather than less disparity. High early disparity corroborates the idea that clades rapidly exhaust available character states (34, 58). It also raises the possibility that evolvability is greatest early in clade history (25). If so, then pooling datasets to examine (say) the Carnivora as a whole might reveal associations between elevated evolvability and the founding of major clades that do not exist with the families and subfamilies examined here (16, 59).

Our results flatly contradict the idea that elevated net speciation (model 2) drives trait-based diversification shifts. The associations between clade centers of gravity and HSC actually are opposite of the model's predictions. A corollary prediction (i.e., that major taxonomic groups with many examples of excess HSC should show rising net origination rates over time) is also incorrect. Most Cenozoic mammal clades show excess HSC (*SI Appendix, Fig. S11B*) without any trend in net origination rates (42). Even more damning, most Silurian-Carboniferous trilobite clades show excess HSC (*SI Appendix, Fig. S11A*) while showing decreasing net origination rates (40). Thus, our results are another caution that the common inference of elevated net speciation from phylogenies of extant taxa is an artifact of those trees being unable to support elevated net extinction models (18–21, 60).

**Why Is the Cambrian Different?** Cambrian clades alone show neither pervasive excess HSC nor a correlation between excess HSC and low centers of gravity for paraclades. This evidence of (relatively) high divergence might reflect the radiation of clades into new ecospace, allowing for unusually high numbers of subclades to diversify (61, 62), which in turn, might generate enough DSC to cancel out excess HSC within subclades. However, major radiations in the Ordovician, Triassic, and Paleogene contradict this

**Table 2. Associations between excess HSC and other paleontological patterns**

Group	Paraclade CG		Clade CG		CD at <i>S</i> /2	
	$\tau$	<i>P</i>	$\tau$	<i>P</i>	$\tau$	<i>P</i>
Brachiopods and molluscs	-0.234	0.010	-0.135	0.139	-0.068	0.453
Arthropods	-0.307	$5.2 \times 10^{-4}$	-0.077	0.386	-0.047	0.592
Echinoderms	-0.274	$8.0 \times 10^{-3}$	-0.151	0.145	-0.028	0.784
Chordates	-0.367	$8.7 \times 10^{-12}$	-0.161	$2.8 \times 10^{-3}$	-0.048	0.373
Cambrian	-0.074	0.631	-0.017	0.910	0.052	0.735
Paleozoic	-0.236	$6.2 \times 10^{-5}$	-0.064	0.277	-0.025	0.666
Meso-Cenozoic	-0.398	$4.6 \times 10^{-14}$	-0.175	$9.3 \times 10^{-4}$	-0.058	0.269

Associations between excess HSC and deviations from expected paraclade and clade centers of gravity (CGs) and cumulative disparity (CD) halfway through clade history (*S*/2) broken down by taxonomic group and time.  $\tau$  gives Kendall's rank correlation statistic.

idea by generating frequent excess HSC (Fig. 2), despite having many plausible examples of clades radiating into “vacated” ecospace.

Nearly all Cambrian datasets represent trilobites. Thus, the Cambrian pattern might corroborate the biomere model (56), which posits that trilobites retaining primitive states selectively survived extinction pulses in the Cambrian. Such extinction would offset background loss of taxa retaining primitive states (63). Notably, post-Cambrian trilobites (and particularly, Silurian-Carboniferous trilobites) show HSC patterns comparable with other metazoans (*SI Appendix, Fig. S10 and Table S4*). Moreover, arthropods show a significant association between excess HSC and overly low paraclade centers of gravity, although 50 of 60 clades are trilobites (Table 2). Assessing whether this reflects something different about Cambrian trilobites or the Cambrian as a whole requires data from Cambrian molluscs, echinoderms, etc. Nevertheless, it does suggest yet another way in which Cambrian evolution was unique.

## Conclusions

After the Cambrian, HSC among closely related species and genera greatly exceeds the expectations of trait-independent diversification. Our finding indicates that trait-based diversification shifts are common at low taxonomic levels. The pattern corresponds with paraphyletic groups retaining primitive conditions losing diversity faster than predicted by trait-independent diversification. Thus, elevated net extinction seems to be the primary driver of trait-based diversity shifts. Our results strongly contradict the idea that elevated net speciation within derived subclades is common, although elevated net speciation is a conclusion of many studies using phylogenies of extant species. Increased evolvability among anatomical characters also does not explain diversification shifts, although elevated evolvability might be important for the founding of the analyzed taxa. Future work should focus on assessing why we do not see clear signs of trait-based diversification shifts among Cambrian taxa and means of recognizing elevated net extinction among taxa lacking fossil records.

## Materials and Methods

**Datasets.** We analyze 319 published character matrices, all of which were assembled for phylogenetic analyses (*SI Appendix, Tables S5 and S6*). We focus on species- and genus-level datasets, because (i) we are interested in whether patterns associated with trait-based diversification shifts occur at low taxonomic levels, (ii) species- and genus-level analyses minimize the potential for uneven species richness among taxa hiding evidence of divergence, and (iii) using species and genera instead of (say) families minimizes cases where characters used to diagnose a taxon are absent in the oldest known members of that taxon. We made exceptions for studies focusing on early members of clades that include token members of groups that diversify after the study interval of the dataset (e.g., late Eocene representatives of subfamilies that diversify in the Oligocene are included in an analysis of Eocene species). We also exclude outgroup taxa, because outgroups usually represent a small fraction of the richness in a related clade. The vast majority of our datasets lacks any extant species or genera; however, any extant taxa in a dataset are included only if they have fossil representatives.

We set polymorphic characters to states that maximized their stratigraphic compatibility. In studies including extant species, we exclude any characters not coded for extinct taxa on the assumption that they are not fossilizable characters. We also exclude characters that are invariant within the ingroup.

We derive first and last appearance data from several sources, with the original publications and the Paleobiology Database ([paleobiodb.org](http://paleobiodb.org)) being the two biggest sources. Stratigraphic ranges for extant taxa reflect the first and last fossil occurrences rather than assuming that those taxa survive to the present.

**Metrics.** Our analyses measure compatibility, stratigraphic compatibility, center of gravity, and morphological disparity. Compatible characters have three of four possible combinations if the characters are binary (26, 27); if one or both characters have three or more states, then we first assess whether the pair is compatible (*SI Appendix, Fig. S1*), and then, we tally all binary breakdowns of the two characters with three of four possible pairs (*SI Appendix, Figs. S2 and S3*) (note that inapplicable and unknown conditions always are excluded from combinations). Our approach therefore treats all multistate characters as unordered, which maximizes their compatibility (27)

and standardizes the inconsistent use of ordered characters among workers. We tally stratigraphic compatibility as all compatible pairs with three of four states in which species with the intermediate pair (e.g., 00 given 00, 10, and 01) do not appear last in the fossil record (28). (Note that 0 represents the first appearing state, regardless of whether those states were coded 0 in the real data.) We tally hierarchical and DSC as described in the text; in cases where species with 00 and 10 first appear in the oldest strata before species with 11, it is not clear which state for the first character appears first, and the data are consistent with both HSC and DSC. We tally such cases as one-half HSC and one-half DSC. We then use the proportion of stratigraphically compatible pairs that are HSC for comparison with Monte Carlo expectations (see below).

We calculate center of gravity following several prior studies (32, 33) using the stratigraphic ranges of the taxa in the dataset. We did this first for the entire clade (total clade center of gravity). For the average paraclade center of gravity within each clade, we took every HSC pair and then measured the center of gravity for the assemblage of taxa retaining the 00 condition (with 0 representing the oldest appearing states, regardless of the actual number used in the dataset). We then estimated the average center of gravity of those paraclades. (If a character pair is one-half HSC because of two states appearing in the oldest strata, then the pair is given half-weight; see above.) This average was then rescaled to the total clade center of gravity for comparisons with Monte Carlo expectations (see below).

We measure morphological disparity as the average pairwise dissimilarity among species [i.e., the differing characters between two taxa/characters coded for both taxa (64)]. We use cumulative disparity rather than standing disparity (i.e., the average pairwise dissimilarity among all  $S$  taxa in a dataset and the average pairwise dissimilarity among the oldest  $S/2$  taxa in that dataset). In cases where clades passed  $S/2$  taxa partway through a stratigraphic interval, we estimate the disparity at  $S/2$  assuming a log-linear relationship between disparity and richness (35). Suppose that a dataset with 29 species has 10 species through time 3 and 20 species through time 4 and that the average pairwise dissimilarity among the first 10 species is 0.4, whereas the average pairwise dissimilarity among the first 20 species is 0.5. Species 15 represents the halfway point. The cumulative disparity among the first 15 species is  $0.4 + (\ln[15] - \ln[10]) \times 0.5 - 0.4 / (\ln[20] - \ln[10]) = 0.453$  (*SI Appendix, Fig. S6*). We rescale ( $\mu$  pairwise dissimilarity among  $S/2$ ) /  $\mu$  pairwise dissimilarity among  $S$  for comparison with Monte Carlo expectations (see below).

**Monte Carlo Analyses.** We use Monte Carlo analyses to estimate expected HSC, centers of gravity, and cumulative disparities. Unlike bootstrapping or permutation tests in similar analyses (25), Monte Carlo tests assume that some phylogeny underlies character and stratigraphic distributions. For each clade of  $S$  taxa, 1,001 phylogenies are simulated using origination and extinction rates estimated from the stratigraphic ranges of the original data until  $S$  taxa are sampled given sampling rates estimated from the same stratigraphic data. Usually, origination, extinction, and sampling are empirically estimated based on the proportions of taxa known from one, two, three, etc. intervals (65). For datasets with taxa limited to one or two intervals, we used a preliminary set of simulations to find rates maximizing the probability of observing  $S$  taxa over  $X$  intervals, with  $X$  being the number of intervals in the dataset. Origination and extinction rates are constant, which matches the null hypothesis. Also, continuous exponential diversification generates more HSC than alternative models, such as logistic diversification (*SI Appendix, Fig. S5D*). We simulated phylogenies under both budding cladogenesis (where species can have descendants as long as they persist) and bifurcating cladogenesis (where morphospecies disappear anagenetically on giving rise to two descendants) but present only the budding results, because budding promotes more HSC (and thus, more conservative results) than bifurcation by allowing single species to have three or more descendants instead of only two descendants (*SI Appendix, Fig. S5*). We simulate morphological evolution among the same numbers of characters and states as the original dataset. Change ceases when compatibility among simulated characters matches that of the original dataset (66) and thus, at a likely overall amount (*SI Appendix, Fig. S4*).

The Monte Carlo tests generate:

- i) expected HSC given continuous, trait-independent diversification over phylogeny generated under plausible rates of origination, extinction, sampling, and change;
- ii) expected paraclade and clade center of gravity given continuous, trait-independent diversification over phylogeny under plausible rates of origination, extinction, sampling, and change; and
- iii) expected cumulative disparity at  $S/2$  over phylogeny given plausible and consistent rates of change in a single character space.

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## Supporting Information

### SI Methods

**Compatibility for Unordered Multistate Characters.** Compatibility is easy to calculate for binary characters: any pair with 3 or fewer combinations (state-pairs) fits any number of trees with only one derivation per state (Fig. S1A). However, once a 4<sup>th</sup> combination appears, then there must have been a parallelism or reversal in one or both characters (1, 2). It is slightly more difficult to calculate compatibility if one character has 3+ states. The characters clearly are incompatible if every possible combination is present. However, incompatibility is possible with fewer than the maximum number of state-pairs. Here, we calculate multistate character compatibility by breaking down the characters into all possible binary comparisons. There are two criteria for compatibility: 1) all of the binary comparisons must have fewer than 4 combinations; 2) at least one state-pair must not be the intermediate pair in any of those comparisons.

Consider two 3-state characters with the following state-pairs. Italics denote the state-pair that is intermediate between the other two. For all comparisons, there are fewer than four state-

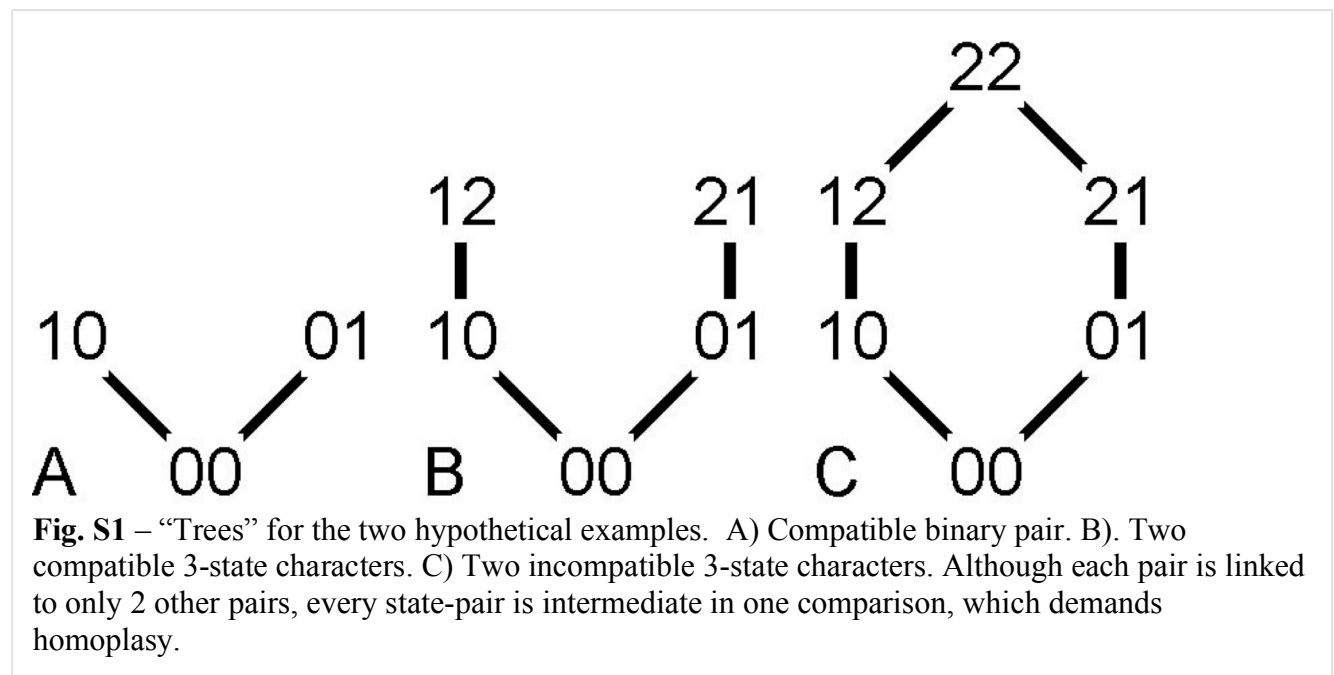
Data	Binary Breakdowns								
<b>00</b>	<i>00</i>	<b>00</b>		<b>00</b>					
<b>01</b>	<b>10</b>		<b>01</b>	<i>01</i>	<b>01</b>				
<b>10</b>	<b>01</b>	<i>10</i>				<b>10</b>	<b>10</b>		
<b>12</b>		<b>12</b>	<b>12</b>				<b>12</b>	<b>12</b>	
<b>21</b>				<b>21</b>	<b>21</b>	<b>21</b>		<b>21</b>	

pairs. Moreover, two of those state-pairs (**12** & **21**) are not the intermediate state-pair in any of its combinations. We can create a character state tree that does not demand homoplasy (Fig. S1B), meaning that the characters are compatible.



Now, consider a similar pair of characters that have one extra state-pair, 22. Again, italicized pairs are the “intermediate” state-pair in each comparison. In all cases, there are fewer than four state-pairs. However, every state-pair now is intermediate in one breakdown. This means that we cannot draw a tree with open branches; instead, there must be a parallelism or reversal somewhere and the characters are incompatible (Fig. S1C).

Data		Binary Breakdowns							
00	<i>00</i>	00	00	00	00				
01	10		01	<i>01</i>		01			
10	<i>01</i>	<i>10</i>					10	10	
12		12	12					<i>12</i>	12
21				21		<i>21</i>	21		<i>21</i>
22					22	<i>22</i>		<i>22</i>	<i>22</i>



Finally, when dealing with more than 3 states per character, the same routine must be broken down to ensure that there are no “closed circuits” among any state trio (e.g., Fig. S1C).

### Stratigraphic Compatibility for Unordered Multistate Characters.

We examine stratigraphic compatibility for all binary breakdowns with three combinations. For a binary + 3-

state character, we can have

two comparisons. This can

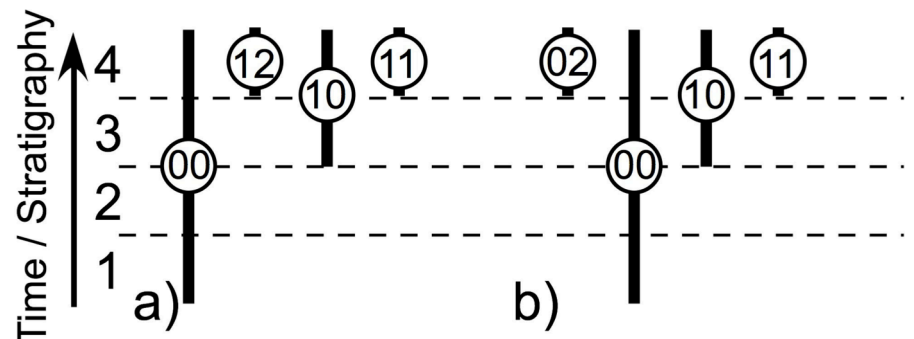
generate two hierarchical

(HSC) pairs (Fig. S2A) if a

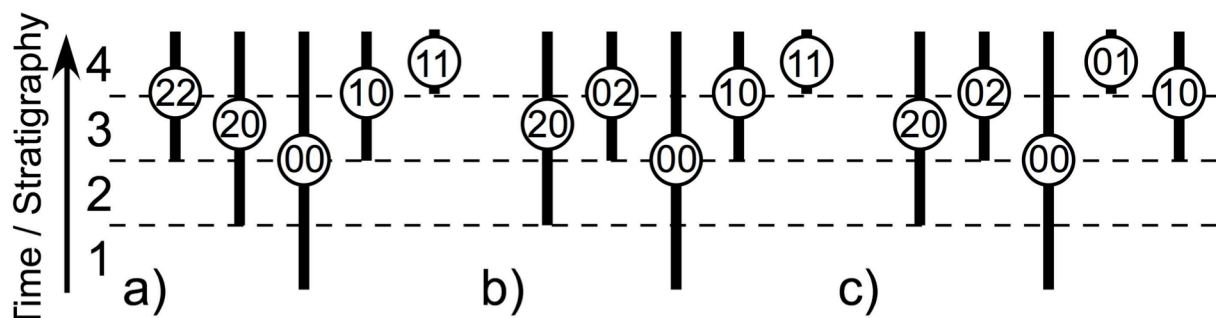
derived pair (e.g., 10) is

intermediate on two

sequences. Alternatively,



**Fig. S2** – A 2-state and 3-state character pair. A. Two case of hierarchical stratigraphic compatibility (HSC;  $00 \rightarrow 10 \rightarrow 11$  and  $00 \rightarrow 10 \rightarrow 12$ ). B. One case of HSC ( $00 \rightarrow 10 \rightarrow 11$ ) and one case of divergent stratigraphic compatibility (DSC;  $00 \rightarrow 10 \rightarrow 02$ ).



**Fig. S3** – Two 3-state character pair. A. Two case of HSC ( $00 \rightarrow 10 \rightarrow 11$  and  $00 \rightarrow 20 \rightarrow 22$ ). B. One case of HSC ( $00 \rightarrow 10 \rightarrow 11$ ) and two cases of DSC ( $00 \rightarrow 10 \rightarrow 02$  and  $00 \rightarrow 20 \rightarrow 02$ ). C. Four cases of DSC ( $00 \rightarrow 10 \rightarrow 01$ ,  $00 \rightarrow 20 \rightarrow 01$ ,  $00 \rightarrow 10 \rightarrow 02$  and  $00 \rightarrow 20 \rightarrow 02$ ).

this can generate one HSC and one divergent (DSC) pair if the oldest combination (**00**) is

intermediate on one sequence but not on the other (Fig. S2B). If both characters have 3-states,

then we can see two HSC cases (Fig. S3A). However, we can see up to four DSC cases if we get

all four possible binary breakdowns with the oldest combination intermediate each time (Fig.

S3C). Note also that this example is compatible if we assume unordered character state

evolution.

**On the Relationship between Compatibility and Homoplasy.** The first principles deduction

that numbers of compatible

character-pairs should decrease as

amounts of homoplasy increase is

easy to verify through simulations

(4-6). We repeat these here (Fig.

S4), in simulations using 32 taxa

with 100 binary characters (and

thus 100 derived states). As the

number of changes per derived

state increases (i.e., as the number

of homoplasies increases),

compatibility for the whole matrix

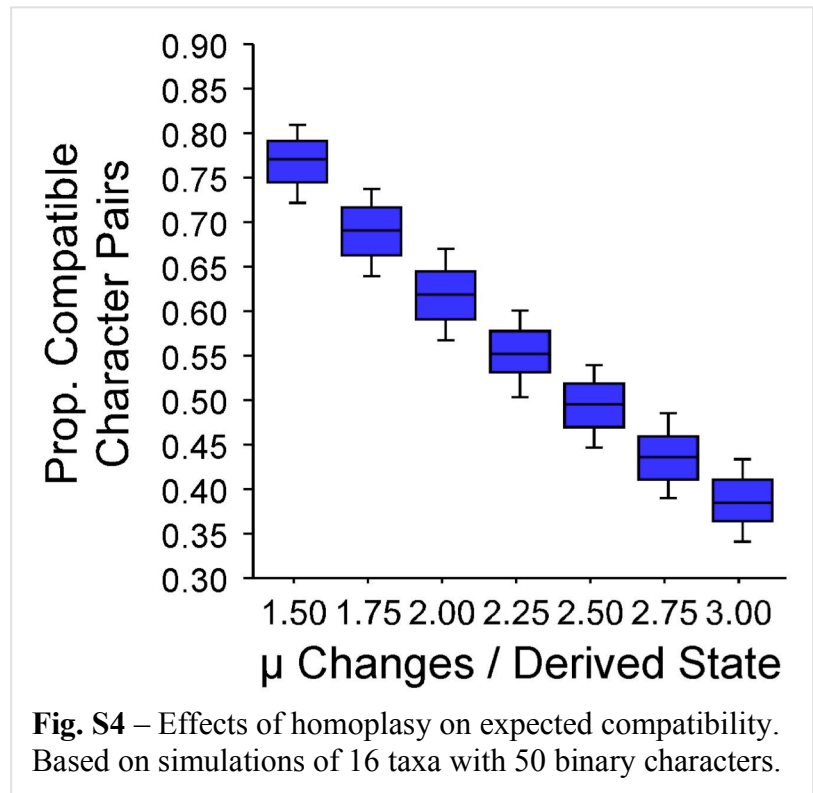
decreases. This illustrates that simulations can generate a probabilistic distribution of expected

compatibility given  $X$  changes among  $Y$  characters with  $Z$  derived states. For our purposes,

when simulations of  $S$  taxa with  $Y$  characters and  $Z$  derived states matches compatibility

observed in a real dataset of  $S$  taxa with  $Y$  characters and  $Z$  derived states, then the simulation

has used a plausible number of total changes.



**The Effects of Different Sampling and Evolutionary Parameters on Expected Hierarchical**

**Stratigraphic Compatibility.** We simulate the evolution of 32 taxa with 100 binary characters

to explore the effects of a variety of sampling and evolutionary parameters on the expectations of

both general stratigraphic compatibility (GSC) and hierarchical stratigraphic compatibility (HSC;

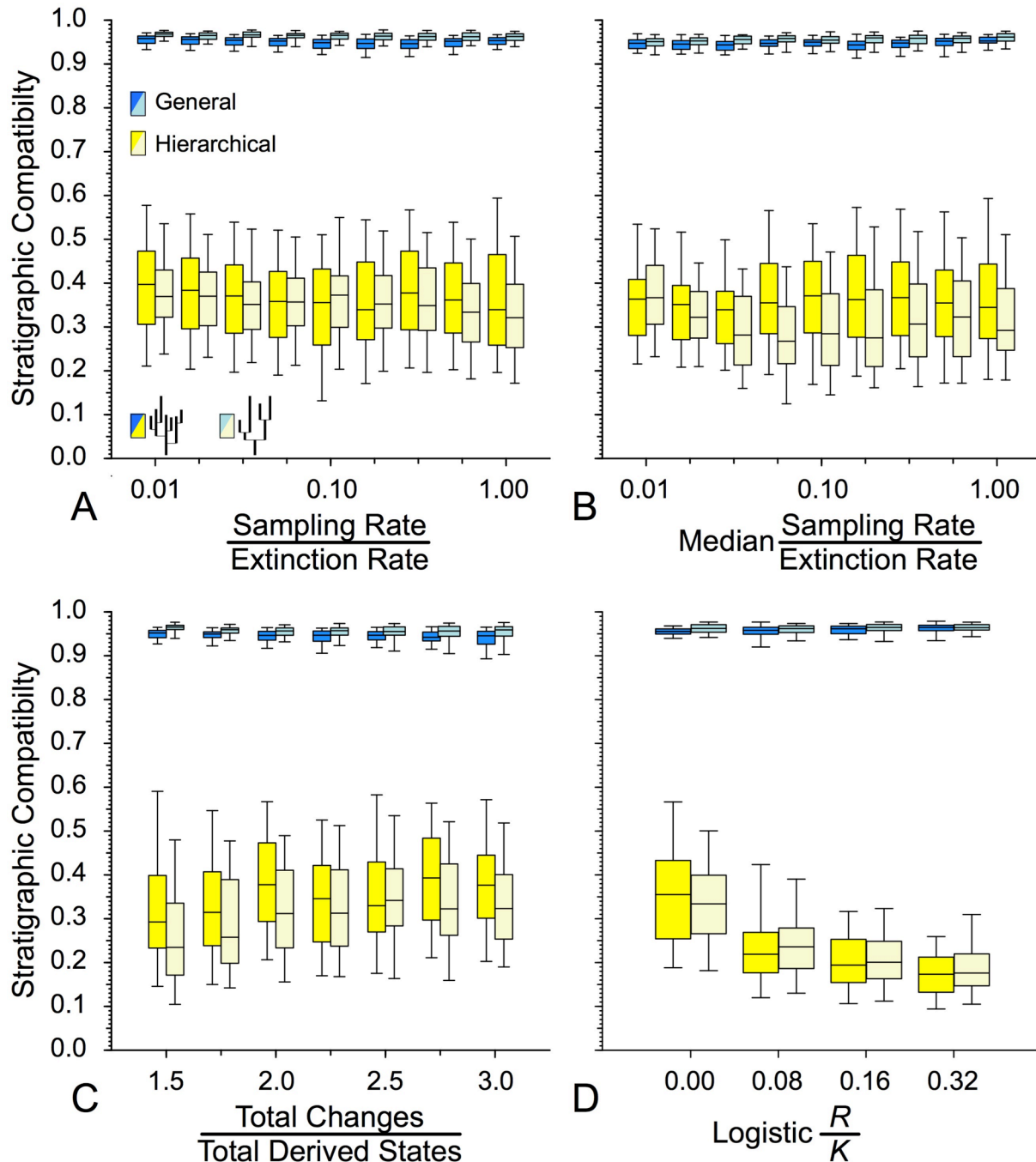
see main text). The varying parameters include: 1) basic speciation/cladogenetic model; 2) typical sampling intensity; 3) temporal variation in sampling intensity; 4) frequencies of homoplasy; and, 5) continuous exponential versus logistic diversification over different logistic parameters. We assess the effects of speciation models by using both budding and bifurcating cladogenesis. The budding model is used in many Monte Carlo analyses conducted by paleobiologists (7-11) and it is the expectation of speciation models such as punctuated equilibrium (12). For the genus-level, budding is an expectation among polytypic genera even if speciation is anagenetic: even if one species anagenetically evolves so much that later (morpho)species are placed in another genus, other species from the “ancestral” genus will persist. The bifurcating model is frequently assumed in neontological analyses (e.g., 14). If rates of anagenesis match those of cladogenesis, then bifurcating patterns will be common. Models such as vicariance also predict bifurcating patterns (15). The primary difference is that ancestral species persist after speciation in the budding model and thus a single species can have any number of descendants, whereas ancestral species become anagenetically extinct (“pseudoextinct”; 16) at cladogenesis and give rise to two descendants in the bifurcating model. Pseudo-extinction raises expected stratigraphic compatibility slightly by making it impossible for ancestors to first appear in younger strata than their descendants (Fig. 3A-D). However, budding generally raises expected HSC by making it easier for a single species to have multiple descendants without shifts in speciation rates (Fig. 3A-D).

We address two effects of sampling intensity: that of relatively good/poor sampling, and that of variation in sampling over time. This is critical because different higher taxonomic groups have different general sampling rates: e.g., molluscs typically show higher preservation rates than do fishes (17). We examine expectations given the same general rate of character change

per sampled taxon (here, 1.5 changes per character state) and assuming exponential diversification with both budding and bifurcating models. The cladogenesis rates are  $1.1\times$  extinction rates. We give the sampling rates relative to extinction rates; when these are equal, then we expect to sample a species of median duration once; at 0.01 we expect to sample 1% of taxa with median durations. We expect GSC in 90-95% of compatible character pairs over all ranges of sampling (Fig. S5A); as noted above, we expect slightly higher GSC given bifurcating cladogenesis than given budding cladogenesis. Expectations for HSC also show little trend, with an expectation of approximately 40% over all sampling rates, with slightly higher expectations with budding cladogenesis rather than bifurcating cladogenesis.

In addition to varying among taxa, sampling intensity also can vary fairly substantially over time within higher taxonomic groups (e.g., 18, 19). This *decreases* rather than increases the expected stratigraphic gaps implied by phylogenies (20) and thus might affect stratigraphic compatibility. Therefore, we repeat the simulations with lognormal variation in the sampling rates. We scale the variation so that every standard deviation doubles the rate; thus, 15.8% of “stages” have more than twice the median sampling rate and 15.8% have less than one half the median sampling rate; 2.2% have more than four times the median sampling rate, and 2.2% have less than one quarter the median sampling rate, etc. This has little effect on the expected GSC (Fig S3B). Variable sampling decreases expected HSC among stratigraphically compatible pairs, albeit only very slightly. This suggests that our overall results are slightly conservative.

To assess the effect of homoplasy, we repeat the simulations over a wide range of rates of character-change. Sampling rates here is  $0.31\times$  extinction rates and diversification is exponential. We again use both budding and bifurcating cladogenetic models. As frequencies of homoplasy increase, expected GSC drops slightly whereas the expected HSC increases slightly



**Fig. S5** – Simulated expectations for general (GSC) and hierarchical (HSC) stratigraphic compatibility using 32 taxa and 100 binary characters. Dark shades give expectations from budding cladogenesis and pale shades give expectations from bifurcating cladogenesis. (A) Sampling intensity relative to extinction intensity. (B) Sampling intensity varying over time. (C) Effects of homoplasy. (D) Effects of logistic diversification.  $R$  is the intrinsic rate of diversification. Equilibrium richness  $K=\infty$  at  $R/K = 0$ , making diversification exponential;  $K=25$  in all other cases. Diversification is exponential in (A), (B) and (C). Characters average 1.5 changes per derived state in (A), (B) and (D); Sampling intensity is uniform and  $0.31 \times$  the extinction rate in (C) and (D).

(Fig. S5C). Again, expected GSC is slightly higher given bifurcation and expected HSC is slightly higher given budding.

Numerous paleontological studies (21-24) and some molecular studies (25) suggest that diversification is not exponential, but instead decreases as standing richness increases. We use logistic diversification (e.g., 26) to assess the possible effects of decreasing net origination over time. Under this model,

$$\Delta S = RS\left(1 - \frac{S}{K}\right)$$

where  $S$  is the standing richness,  $\Delta S$  is the change in richness,  $R$  is an intrinsic rate of increase, and  $K$  is the equilibrium richness (27). We assume constant extinction rates ( $\mu$ ), which means that cladogenesis rate  $\lambda$  shifts so that:

$$\lambda = \mu + \ln(S + \Delta S) - \ln(S) \text{ (see 28).}$$

Thus, as  $R$  increases relative to  $K$ , the difference between  $\mu$  and initial  $\lambda$  increases and the time required to reach  $K$  decreases. (Thus, exponential diversification is essentially a special case of logistic diversification in which  $K=\infty$  and thus  $R/K$  is essentially 0). We expect slightly more GSC given logistic diversification than we do given exponential diversification; we also expect markedly less HSC given logistic diversification than we do given exponential diversification ( $R/K = 0$ ; Fig. S5D). Within different logistic systems, expectations for both GSC and HSC become more pronounced as  $R$  (and thus early cladogenesis rates) increases relative to  $K$ . Both patterns simply reflect speciation rates being highest among taxa that have had the fewest chances to accumulate derivations. Thus, **00** taxa frequently have (over their history) higher speciation rates than **01** taxa, which in turn elevates expected divergent stratigraphic compatibility for the same reasons that elevated net speciation would elevate expected HSC. More complex richness-dependent diversification models such as hierarchical diversification

(e.g., 29) typically predict more rapid early rises in diversity than do logistic models do. Thus, the differences between exponential and richness-dependent models should become more pronounced as the intrinsic rate of diversification increases relative to maximum richness.

**Estimating Cumulative Disparity for the First Half of Clade Evolution.** Disparity studies typically examine relative amounts of disparity (however measured) in different time units or different clades. However, the relevant hypotheses here make explicit predictions about the cumulative character space (= morphospace) occupied by a clade; that is, the size of the character

**Table S1. Estimating Cumulative Disparity at  $S/2$  among Devonian *Floweria* species (3).**

Taxon	<i>F. be.</i>	<i>F. de.</i>	<i>F. pa.</i>	<i>F. pe.</i>	<i>F. an.</i>	<i>F. ar.</i>	<i>F. co.</i>	<i>F. cr.</i>	<i>F. li.</i>	<i>F. ch.</i>	<i>F. io.</i>	<i>F. ma.</i>	<i>F. pr.</i>	<i>F. tr.</i>
<i>F. be.</i>	•	0.520	0.643	0.536	0.536	0.464	0.375	0.375	0.583	0.464	0.444	0.583	0.500	0.542
<i>F. de.</i>	0.520	•	0.720	0.720	0.240	0.640	0.208	0.500	0.208	0.400	0.417	0.667	0.400	0.500
<i>F. pa.</i>	0.643	0.720	•	0.179	0.571	0.321	0.750	0.625	0.708	0.464	0.556	0.333	0.607	0.458
<i>F. pe.</i>	0.536	0.720	0.179	•	0.536	0.393	0.708	0.667	0.667	0.429	0.556	0.375	0.643	0.500
<i>F. an.</i>	0.536	0.240	0.571	0.536	•	0.643	0.292	0.542	0.250	0.321	0.296	0.625	0.321	0.542
<i>F. ar.</i>	0.464	0.640	0.321	0.393	0.643	•	0.667	0.500	0.792	0.429	0.667	0.333	0.679	0.458
<i>F. co.</i>	0.375	0.208	0.750	0.708	0.292	0.667	•	0.333	0.208	0.458	0.208	0.708	0.208	0.500
<i>F. cr.</i>	0.375	0.500	0.625	0.667	0.542	0.500	0.333	•	0.458	0.458	0.375	0.625	0.458	0.583
<i>F. li.</i>	0.583	0.208	0.708	0.667	0.250	0.792	0.208	0.458	•	0.417	0.333	0.708	0.333	0.542
<i>F. ch.</i>	0.464	0.400	0.464	0.429	0.321	0.429	0.458	0.458	0.417	•	0.481	0.375	0.571	0.458
<i>F. io.</i>	0.444	0.417	0.556	0.556	0.296	0.667	0.208	0.375	0.333	0.481	•	0.667	0.074	0.458
<i>F. ma.</i>	0.583	0.667	0.333	0.375	0.625	0.333	0.708	0.625	0.708	0.375	0.667	•	0.667	0.208
<i>F. pr.</i>	0.500	0.400	0.607	0.643	0.321	0.679	0.208	0.458	0.333	0.571	0.074	0.667	•	0.458
<i>F. tr.</i>	0.542	0.500	0.458	0.500	0.542	0.458	0.500	0.583	0.542	0.458	0.458	0.208	0.458	•

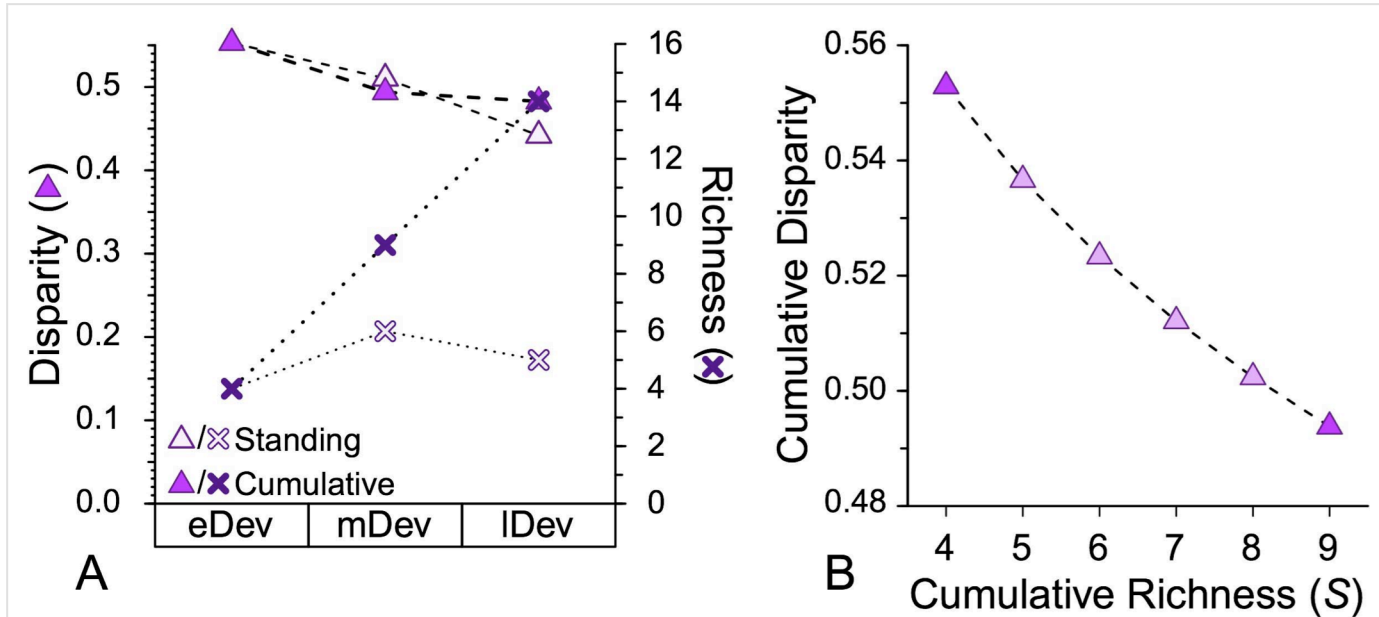
*F. be.*=*Floweria becraftensis*; *F. de.*=*F. deformis*; *F. pa.*=*F. pandora*; *F. pe.*=*F. perversa*; *F. an.*=*F. anomala*; *F. ar.*=*F. arctostriata*; *F. co.*=*F. cornucopia*; *F. cr.*=*F. crassa*; *F. li.*=*F. lirella*; *F. ch.*=*F. chemungensis*; *F. io.*=*F. iowensis*; *F. ma.*=*F. magnacatrix*; *F. pr.*=*F. prava*; *F. tr.*=*F. transversalis*. Numbers give pairwise dissimilarity between species, i.e. the number differing characters divided by the number of characters for which both species are coded. This is done after polymorphic characters are fixed to the state maximizing stratigraphic compatibility. Cumulative disparity is estimated from the average pairwise dissimilarity among: 1) *F. becraftensis* – *F. perversa* (the four early Devonian species); 2) *F. becraftensis* – *F. lirella* (the nine early-middle Devonian species); and, 3) *F. becraftensis* – *F. transversalis* (the 14 total species). Note that *F. perversa* survives into the Middle Devonian. The final number gives the cumulative disparity for all 14 species. The disparity for the first 7.5 species (i.e., the first half of *Floweria* evolution) is interpolated from the first and second numbers assuming a linear change in disparity with a logarithmic change in richness (13; Fig. S6).



space occupied by all  $S$  species in a clade. Elevated evolvability predicts that available character space is greater at the end of clade evolution than it was at the onset, whereas the null hypothesis predicts that there are no major additions to character space. If elevated evolvability is correct, then the cumulative disparity among early members of the clade (say, the first  $S/2$  species) should be less than expected if the entire character space is available to all species and that rates of change are reasonably consistent through time. The null hypothesis (no major addition of characters to any derived taxa) predicts that cumulative disparity at  $S/2$  is simply a product of the size of total character space and the average overall rate of change (13).

We present an empirical example of how we estimate cumulative disparity at  $S/2$  using 14 Devonian brachiopod species from the genus *Floweria* (3). Table S1 gives the average pairwise dissimilarity between each species, which is a common metric of disparity (e.g., 30). We separate these species into three general stratigraphic units: Early Devonian (*F. becraftensis* – *F. perversa*), Middle Devonian (*F. anomala* – *F. lirella*) and Late Devonian (*F. chemungensis* – *F. transversalis*). The key difference between our approach and typical approaches is that we estimate disparity not among just Middle Devonian or Late Devonian species, but among all species sampled in through the Middle Devonian or Late Devonian; thus, cumulative disparity for the first 9 species (i.e., through the middle Devonian) is the average of the pairwise dissimilarities among the first 9 species in Table S1, and the cumulative disparity for the entire clade is the average of all disparities in Table S1 (Fig. S6A).

As often is the case, the stratigraphic divisions do not neatly partition the 14 species into a first and second half; moreover, the true midpoint for 14 species is at 7.5 species because clades start with one species, not zero. Therefore, we interpolate cumulative disparity at  $S/2$  assuming a log-linear relationship between richness and disparity (13, 31). For example, the average



**Fig. S6** – Cumulative vs. standing disparity and richness for *Floweria* species (A) and interpolated cumulative disparity halfway through clade evolution (B). Cumulative richness and disparity sum all species sampled through the Middle or Late Devonian, whereas standing richness and disparity reflect only species present at those times. (B) Interpolates the shift in disparity from the Early Devonian (i.e., the first 4 species) and the Middle Devonian (i.e., the first 9 species). The pale triangles give the estimated cumulative disparity assuming an linear increase change in disparity with an exponential change in richness. Finally, note that the actual midpoint here (and in all clades with even numbers of species) used is at  $S=7.5$ , as clade evolution starts at  $S=1$ .

pairwise dissimilarity among the first 4 species is 0.553 whereas the average pairwise

dissimilarity is 0.494 among the first 9 species. Therefore, the slope is:  $\frac{0.553-0.494}{\ln(9)-\ln(4)}=-0.073$ , and

the interpolated disparity among the first 5 species is  $0.553-0.073 \times (\ln[5]-\ln[4])=0.537$  (Fig.

S6B). Isolated experiments show that we obtain nearly identical values if we randomly order the

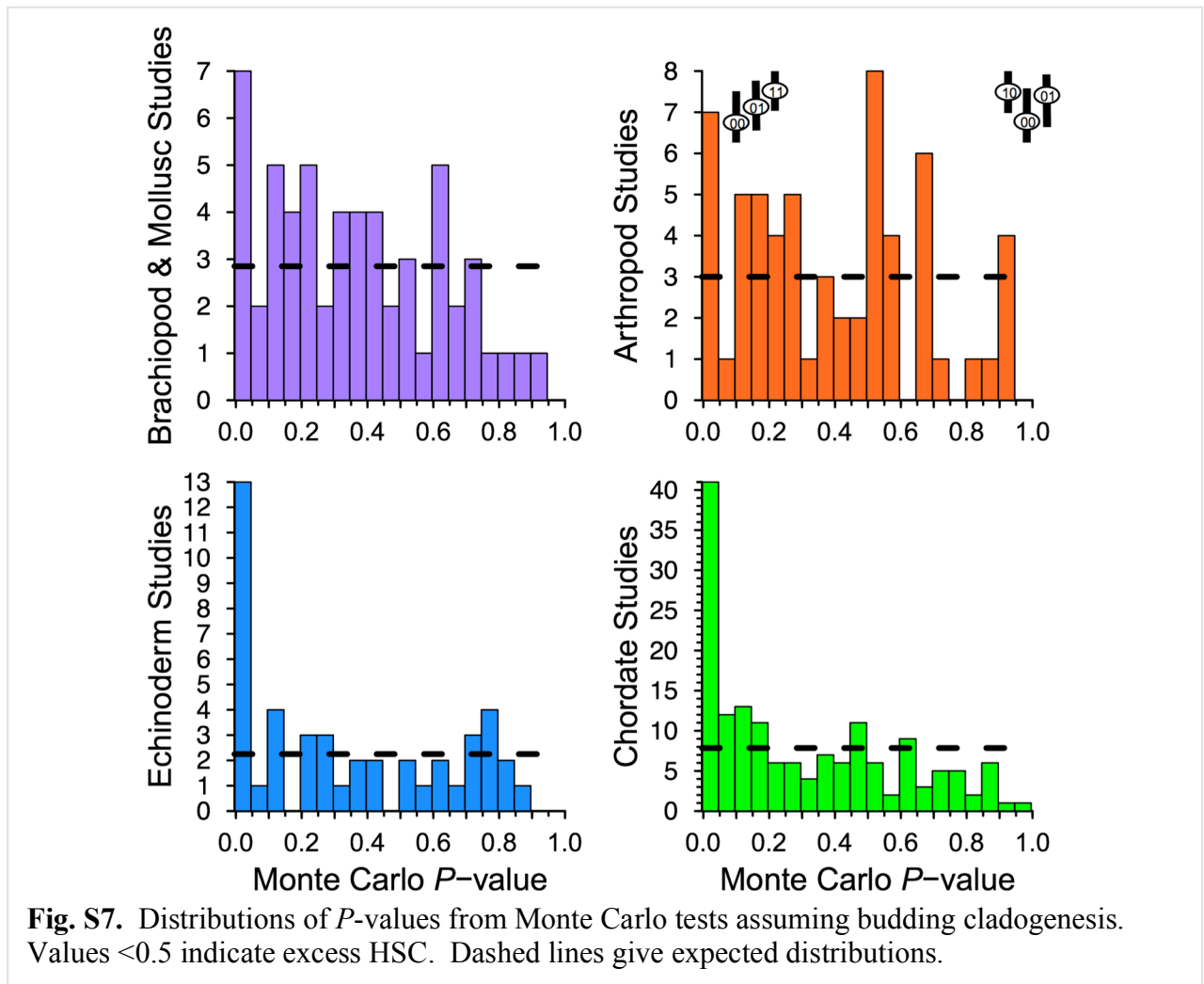
5 Middle Devonian species repeatedly and take average cumulative disparities; as this is

computationally more time consuming, we used interpolation instead.

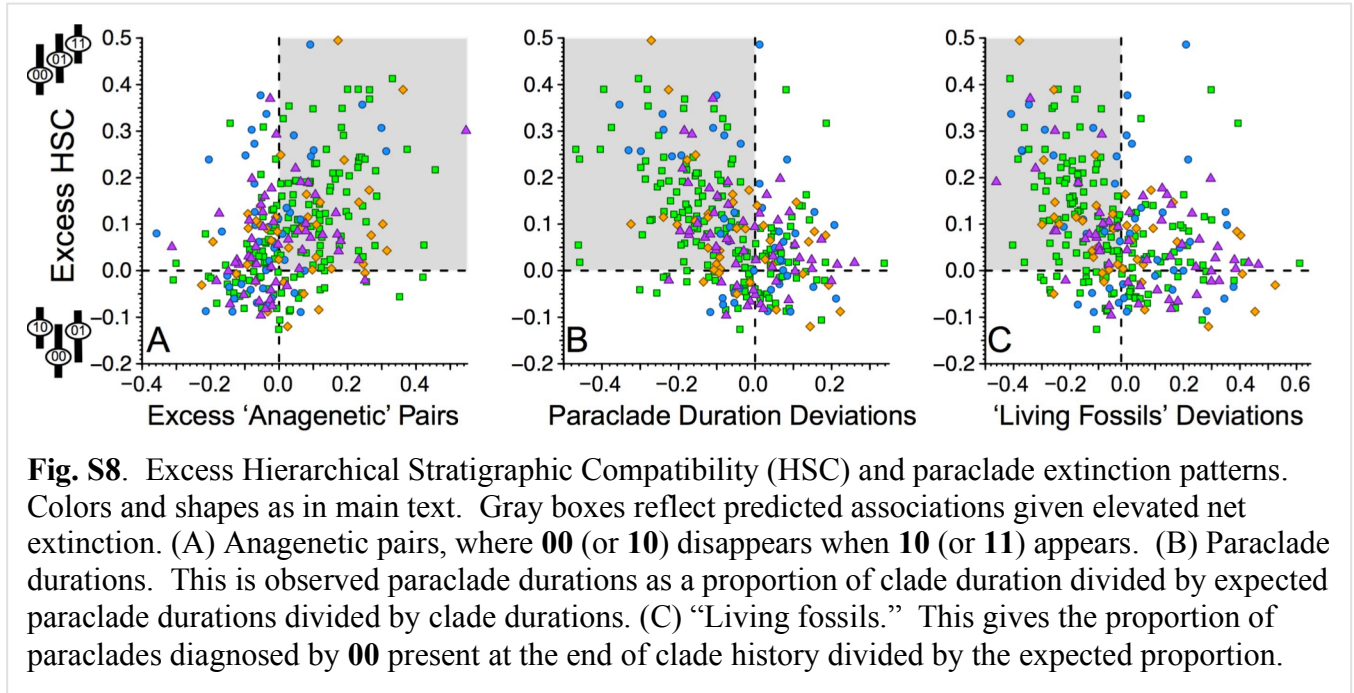
Finally, note that disparity actually decreases in this group, which is not uncommon (see Table S7). This simply reflects the rapid exhaustion of character space, which is common among fossil taxa (32), resulting in later evolution generating new combinations of existing character states and filling in character space, which in turn reduces disparity.

## SI Results

**Additional Summaries of Results Presented in Main Text.** The  $P$ -values from multiple independent tests should follow a uniform distribution. Table 1 in the main text shows this is not the case. A histogram of the  $P$ -values further emphasizes this (Fig. S7).



**Additional Correlations between Paraclade Durations and HSC.** Excess HSC shows a strong correlation with paraclade center-of-gravity (CG) that is lower than expected given trait-independent diversification. Additional correlations exist showing that paraclades retaining primitive state-pairs go extinct earlier than expected given null models of diversification.



**Fig. S8.** Excess Hierarchical Stratigraphic Compatibility (HSC) and paraclade extinction patterns. Colors and shapes as in main text. Gray boxes reflect predicted associations given elevated net extinction. (A) Anagenetic pairs, where **00** (or **10**) disappears when **10** (or **11**) appears. (B) Paraclade durations. This is observed paraclade durations as a proportion of clade duration divided by expected paraclade durations divided by clade durations. (C) “Living fossils.” This gives the proportion of paraclades diagnosed by **00** present at the end of clade history divided by the expected proportion.

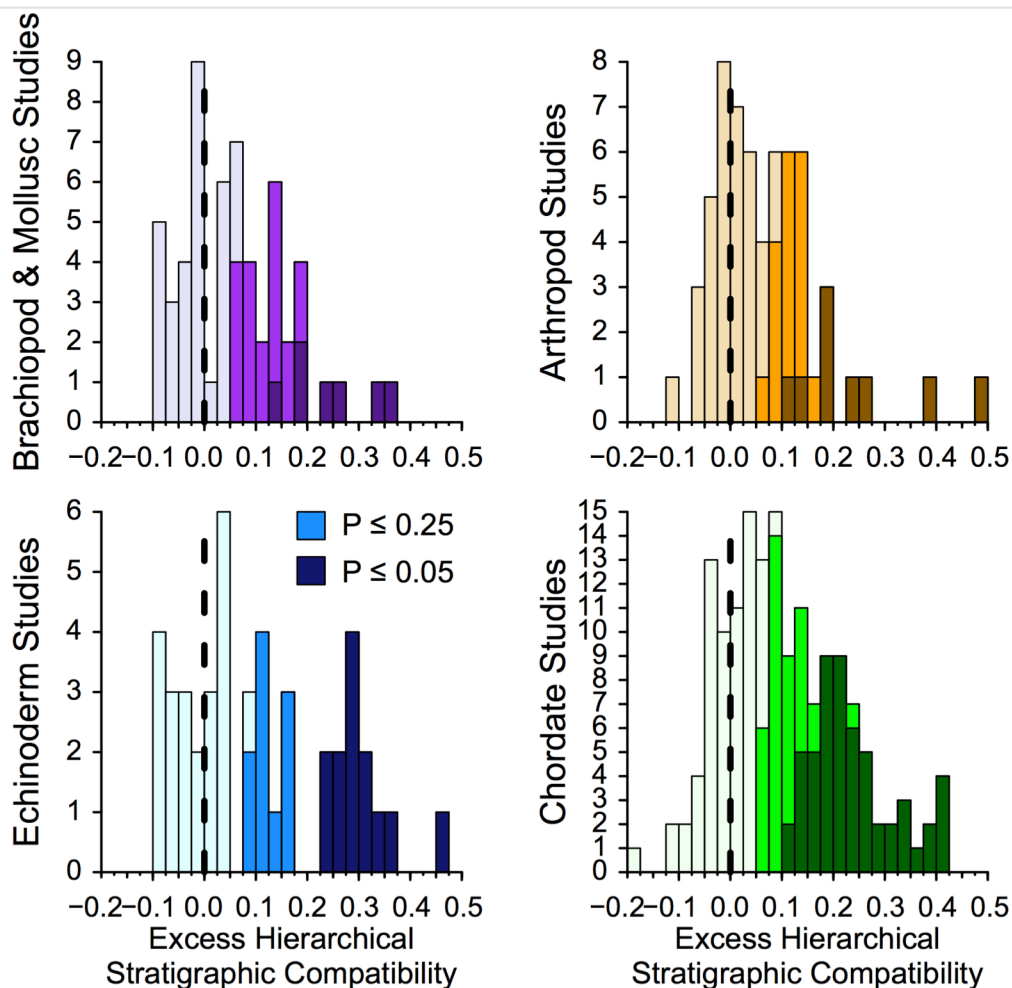
“Anagenetic” HSC pairs are those where the last taxa scored **00** occur in the same or prior interval as the first taxa scored **10**. (We allow for **00**-taxa and **10**-taxa to occur in the same intervals because we use broad intervals such as stages in which both anagenetic ancestor and descendant are present.) “Anagenetic” patterns tend to increase as HSC increases (Kendall’s  $\tau=0.248$ ,  $P=4.2\times 10^{-11}$ ; Fig. S8A). We measure paraclade duration as the proportion of a clade’s history that a paraclade retaining any **00** state-pair persists. Paraclade durations decrease as HSC increases (Kendall’s  $\tau=-0.298$ ,  $P=2.2\times 10^{-15}$ ; Fig. S8B). The frequency of “living fossils” (paraclades bearing **00** state-pairs extant late in clade history) is important for neontological studies. “Living fossil” paraclades decrease as HSC increases (Kendall’s  $\tau=-0.247$ ,  $P=4.8\times 10^{-11}$ ; Fig. S8C).

**Results given Bifurcating Cladogenesis.** Tests assuming bifurcating cladogenesis provide slightly more emphatic support for our conclusions (Table S3; Fig. S9). Thus, our conclusions do not depend on a particular model of speciation/cladogenesis prevailing.

**Table S3. Cases of excess Hierarchical Stratigraphic Compatibility (HSC) at Monte Carlo significance of  $P \leq 0.05$ ,  $\leq 0.25$  and  $< 0.50$  assuming Bifurcating Cladogenesis.**

Group	N	$P[\text{HSC}] \leq 0.05$	$P[\text{HSC}] \leq 0.25$	$P[\text{HSC}] < 0.50$
Brachiopods + Molluscs	57	7 ( $7.2 \times 10^{-3}$ )	26 ( $2.1 \times 10^{-4}$ )	36 (0.017)
Arthropods	60	9 ( $7.4 \times 10^{-4}$ )	25 ( $1.5 \times 10^{-3}$ )	43 ( $2.0 \times 10^{-4}$ )
Echinoderms	45	13 ( $2.3 \times 10^{-8}$ )	23 ( $4.4 \times 10^{-5}$ )	33 ( $4.1 \times 10^{-4}$ )
Chordates	153	54 ( $3.2 \times 10^{-31}$ )	88 ( $7.7 \times 10^{-20}$ )	121 ( $2.9 \times 10^{-14}$ )

Numbers of clades from each major group showing different levels of significance for excess HSC. Numbers in parentheses give binomial probabilities of these outcomes given an expectation of uniform distributions of binomial  $P$  values.



**Fig. S9.** Deviations from expectations given bifurcating cladogenesis. Observed hierarchical stratigraphic compatibility deviates even further from expectations than under the budding model. Shading denotes general significance of deviations.

**Table S4. Period-by-Period contrasts of HSC Deviations assuming Budding Cladogenesis.**

Period	Cm	O	S	D	C	P	Tr	J	K	Pg	Ng
Cambrian	•	0.042	0.040	$8 \times 10^{-4}$	0.169	0.015	0.018	0.026	$5 \times 10^{-4}$	$5 \times 10^{-4}$	$4 \times 10^{-3}$
Ordovician	<b>0.794</b>	•	0.485	0.230	0.737	0.355	0.591	0.396	0.090	0.048	0.206
Silurian	<b>0.837</b>	0.975	•	0.974	0.540	0.955	0.547	0.772	0.935	0.887	0.766
Devonian	<b>0.689</b>	0.943	1.000	•	0.281	0.944	0.681	0.876	0.964	0.491	0.761
Carboniferous	0.891	1.017	1.073	1.065	•	0.273	0.662	0.360	0.156	0.128	0.234
Permian	<b>0.816</b>	0.968	1.008	0.996	0.898	•	0.665	1.000	0.771	0.646	0.694
Triassic	<b>0.796</b>	0.977	1.071	1.028	0.950	1.061	•	0.627	0.589	0.321	0.411
Jurassic	<b>0.801</b>	0.960	1.031	1.015	0.898	1.005	0.962	•	0.639	0.636	0.604
Cretaceous	<b>0.645</b>	0.907	0.997	0.996	0.830	0.960	0.947	0.959	•	0.674	0.828
Paleogene	<b>0.644</b>	<b>0.890</b>	0.982	0.942	0.821	0.943	0.905	0.962	0.975	•	0.982
Neogene	<b>0.778</b>	0.952	0.970	0.987	0.888	0.960	0.939	0.963	0.991	1.000	•

Lower left gives summed ranks for the older interval divided by the expected summed ranks given the null hypothesis. Numbers less than one indicate that deviations for the older period are lower than expected given the null hypothesis. Bold values indicate “significant” differences. Upper right gives the probability of the distributions of ranked HSC deviations given the same null hypothesis as assessed by a Mann-Whitney test.

**Period-by-Period Contrasts.** The Cambrian is unique for not deviating strongly from the expectations of trait-independent diversification. Mann-Whitney tests (Table S4) show that the Cambrian deviations are significantly lower than those for all intervals other than the Cambrian. Among the remaining 45 contrasts, only Ordovician and Paleogene datasets differ significantly in excess HSC. This is well within the expectations of Type I error.

**Cambrian vs. Post-Cambrian Arthropods.** The Cambrian vs. Post-Cambrian pattern in HSC almost entirely reflects Cambrian trilobites. This distinction is very strong within arthropods alone (Fig. S10; Table S5. Cambrian arthropods fit the null expectations very well. In contrast,

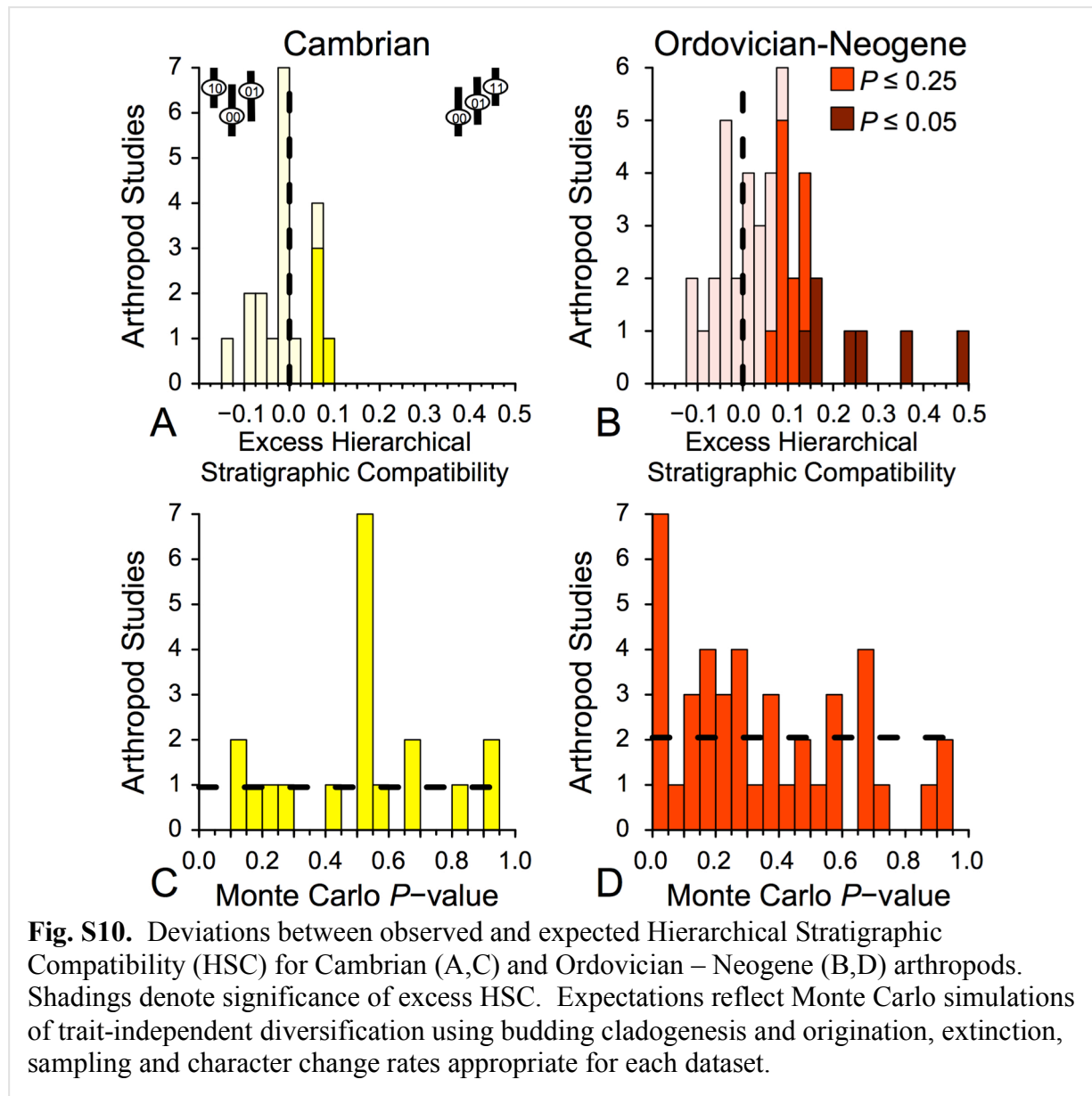
**Table S5. Numbers of cases of excess Hierarchical Stratigraphic Compatibility (HSC) at Monte Carlo significance of  $P \leq 0.05$ ,  $\leq 0.25$  and  $< 0.50$  for Arthropods only.**

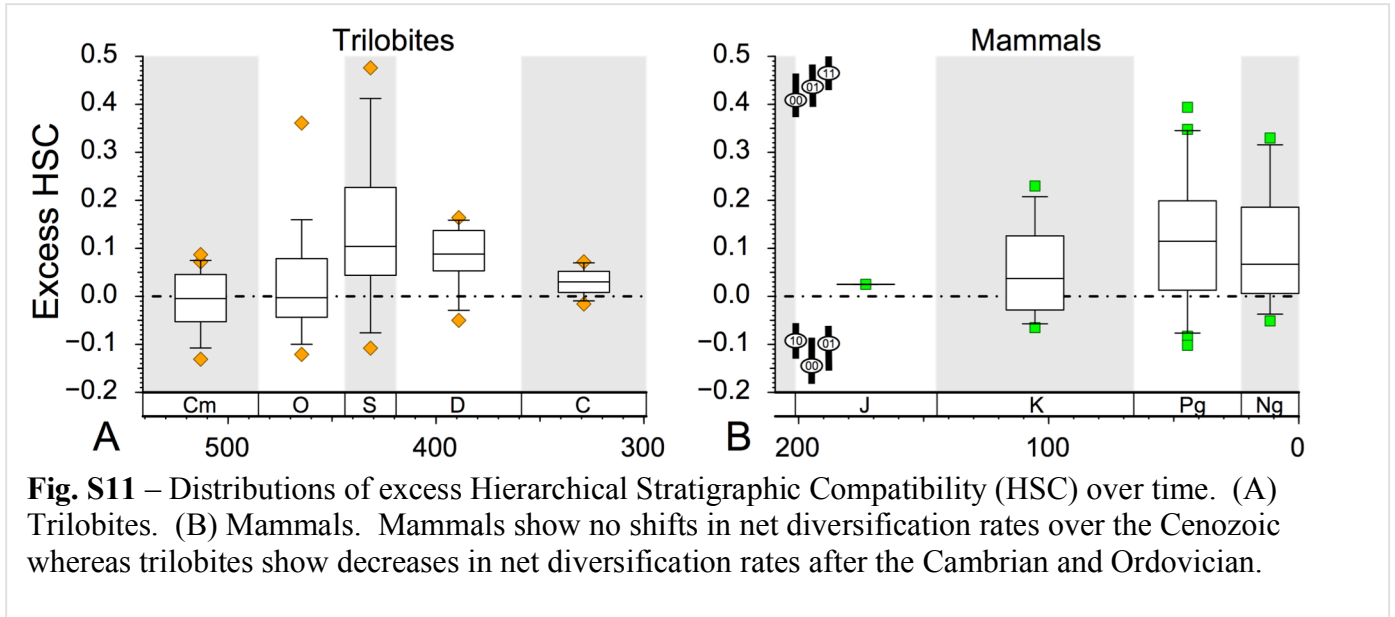
Group	N	$P[\text{HSC}] \leq 0.05$	$P[\text{HSC}] \leq 0.25$	$P[\text{HSC}] < 0.50$
Cambrian	19	0 (0.377)	4 (0.465)	6 (0.916)
Post-Cambrian				
All Arthropods	41	7 ( $8.5 \times 10^{-4}$ )	18 ( $2.4 \times 10^{-3}$ )	29 ( $2.2 \times 10^{-3}$ )
Trilobites Only	31	6 ( $7.1 \times 10^{-4}$ )	13 (0.012)	21 (0.015)

Numbers of clades from each major group showing different levels of significance for excess HSC. Numbers in parentheses give binomial probabilities of these outcomes given an expectation of uniform distributions of binomial  $P$  values.

Ordovician – Neogene arthropods deviate from null expectations as strongly as do echinoderms or vertebrates.

The bulk (30 of 40) of the post-Cambrian studies also represent trilobites. Thus, this pattern largely reflects Cambrian vs. Post-Cambrian trilobites (see also Fig. S11A below). Note, however, that Ordovician trilobites fail to show strong excess HSC patterns, too (Fig. S11A).





### Patterns of Hierarchical Stratigraphic Compatibility against General Patterns of

**Diversification.** Elevated net speciation posits that subclades within a larger clade sometimes produce daughter lineages at a higher rate than the rest of the clade. If elevated net speciation is a primary driver of HSC, then we do not expect to see excess HSC when net speciation rates are stable or decreasing. We illustrate two examples showing that excess HSC often is unassociated with increased diversification rates. Mammals (Fig. S11B) show considerable excess HSC throughout their history. However, net speciation rates do not show increase over that time (23). Trilobites commonly show excess HSC after the Ordovician (Fig. S11A). However, not only do net speciation rates not increase, they instead decrease (33). Conversely, HSC patterns among trilobites do not deviate from the expectations of trait-independent change when their net speciation rates are highest in the Cambrian.

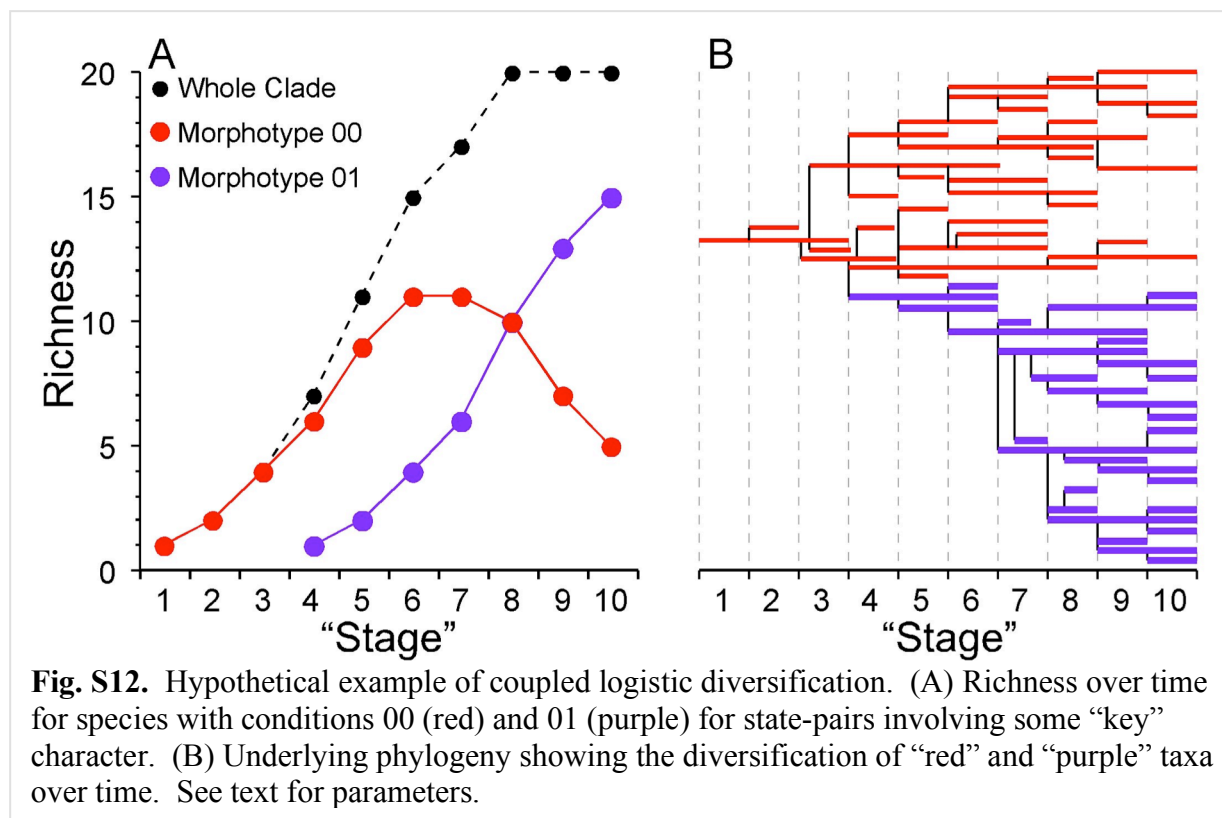
### SI Discussion

**A Hypothetical Example of Coupled Logistic Diversification.** Sepkoski (27) proposed a fairly simple equation for diversification patterns of two “competing” groups:



$$\Delta S_i = R_i S_i \left(1 - \frac{S_i + c_{ij} S_j}{K}\right)$$

where  $S$  is the richness of the group,  $R$  is the “intrinsic” net diversification,  $K$  is the equilibrium richness,  $c_{ij}$  is the effect of Group  $j$  on Group  $i$ , and  $\Delta S_i$  is the expected change in richness over time for group  $i$  or  $j$ . Here we illustrate a simple hypothetical example, generated with  $R_1=R_2=1.5$ , and  $K_1=K_2=20$  (Fig. S12A). Instead of two competing clades, Group 1 represents a paraclade of taxa diagnosed by primitive condition **00** whereas Group 2 represents a derived subclade of taxa diagnosed by a derived condition **01** (Fig. S12B). Declining origination rates rather than increasing extinction rates drive the decline of the paraclade here. Moreover, net diversification rates for the *entire* clade also do not change: the decline in origination rates for the paraclade is offset by elevated rates in the subclade. The negative net diversification of a paraphyletic portion of the clade also would encourage “anagenetic” HSC by increasing the chances of the last “red” lineages bearing some **00** conditions disappears shortly after some



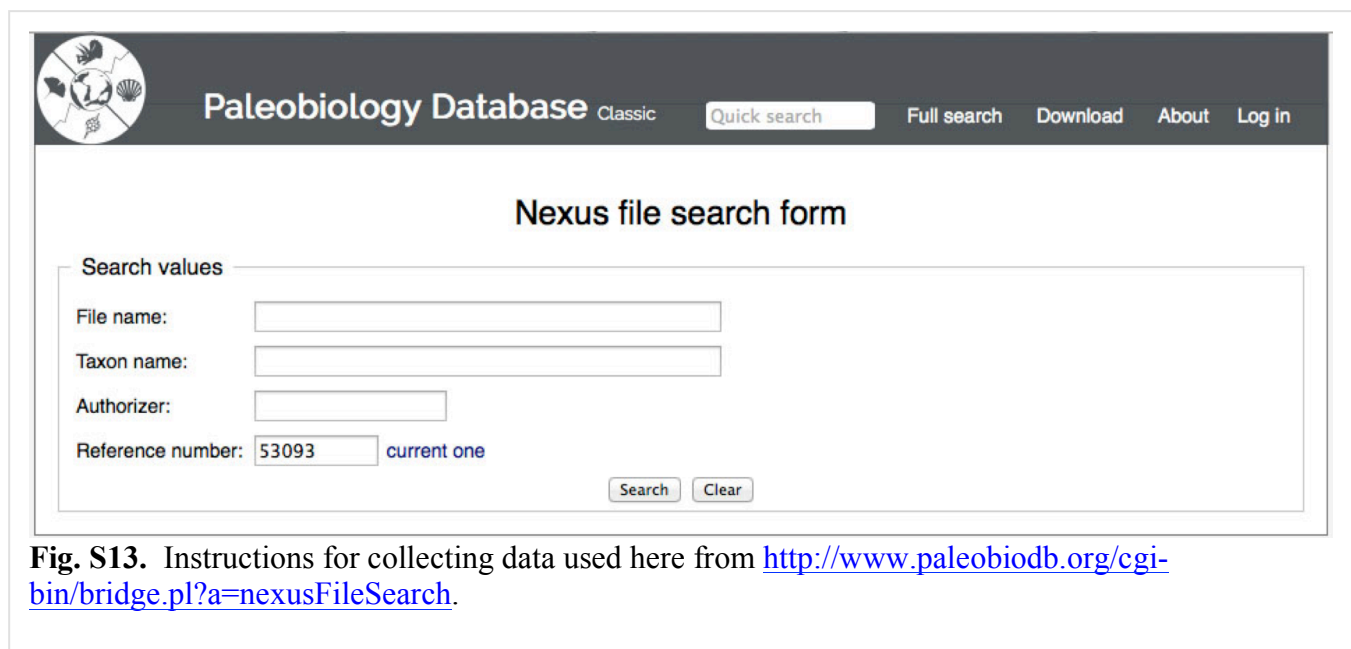
“purple” lineage bearing a new **01** condition evolves.

Finally, note that phylogenetic pattern in Fig. S12B would create the illusion of elevated net speciation if we analyzed only the taxa from the final “stage.” This reflects two things. One, because the five “living fossil” lineages from the **00** paraclade provide no evidence of greater past diversity, they will actively mislead estimates of net diversification at the base of the tree. This leads to the second problem. The boost in net diversification among the “purple” lineages now appears to be a shift in rates. However, 1) diversification rates actually are *lower* than the net diversification rates at the base of the tree, and 2) the only “new” parameters introduced are those reflecting the advantage of the purple lineages over the red lineages.

## SI Data

**Accessing NEXUS files.** The character matrices used in this study can be accessed at:

<http://www.paleobiodb.org/cgi-bin/bridge.pl?a=nexusFileSearch>. Enter “53093” under the reference number to return the relevant files (Fig. S13).



The image shows a screenshot of the Paleobiology Database website's Nexus file search form. The page header includes the Paleobiology Database logo, the text "Paleobiology Database Classic", and navigation links for "Quick search", "Full search", "Download", "About", and "Log in". The main content area is titled "Nexus file search form" and contains a "Search values" section with four input fields: "File name:", "Taxon name:", "Authorizer:", and "Reference number:". The "Reference number" field contains the value "53093" and a link labeled "current one". Below the input fields are "Search" and "Clear" buttons.

**Fig. S13.** Instructions for collecting data used here from <http://www.paleobiodb.org/cgi-bin/bridge.pl?a=nexusFileSearch>.

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**Table S5. Observed vs. Expected Hierarchical Stratigraphic Compatibility (HSC)**

Higher Taxon	Analyzed Taxon	Per.	OTU	SCP	Obs. HSC	E[HSC Bud]	<i>P</i>	E[HSC Bif]	<i>P</i>	Ref.
Brachiopod	Anopliidae	3	28	160	0.406	0.458	0.689	0.462	0.719	1
Brachiopod	Atrypidae	2	25	438	0.502	0.429	0.215	0.424	0.167	2
Brachiopod	Billingsellida	1	20	214	0.474	0.435	0.344	0.434	0.334	3
Brachiopod	Echinoconchidae	4	14	174	0.534	0.494	0.387	0.496	0.381	4
Brachiopod	<i>Floweria</i>	4	14	180	0.433	0.532	0.906	0.511	0.858	5
Brachiopod	<i>Kutchithyris</i>	8	12	180	0.547	0.472	0.248	0.472	0.242	6
Brachiopod	Leptenellidae	2	23	103	0.345	0.429	0.756	0.441	0.828	7
Brachiopod	Leptestiidae	2	10	193	0.661	0.502	0.046	0.513	0.040	8
Brachiopod	Linguloidea	1	23	866	0.383	0.407	0.604	0.413	0.629	9
Brachiopod	<i>Orbirhynchia</i>	9	16	162	0.809	0.514	0.009	0.461	0.004	10
Brachiopod	Parastrophinidae	2	26	518	0.486	0.418	0.234	0.420	0.234	11
Brachiopod	<i>Plaesiomys</i>	2	10	50	0.780	0.527	0.049	0.542	0.043	12
Brachiopod	<i>Schizophoria</i>	4	22	214	0.584	0.486	0.176	0.453	0.085	5
Brachiopod	Strophomenoidea	2	14	33	0.409	0.500	0.725	0.500	0.758	13
Brachiopod	Terebratuloidea	4	78	309	0.388	0.352	0.376	0.339	0.317	14
Brachiopod	Tritoechiidae	2	13	394	0.426	0.526	0.858	0.498	0.821	15
Brachiopod	Virgianidae	2	12	449	0.392	0.476	0.822	0.477	0.854	16
Rostroconch	Conocardioidea	4	43	962	0.448	0.347	0.134	0.346	0.122	17
Rostroconch	Eopteriidae	2	20	699	0.522	0.438	0.155	0.430	0.113	17
Rostroconch	Pseudobigaleaidae	3	24	1731	0.506	0.458	0.292	0.401	0.093	17
Rostroconch	Ribeiriidae	2	27	615	0.498	0.431	0.230	0.425	0.183	17
Rostroconch	Technophoridae	2	14	869	0.498	0.449	0.318	0.451	0.287	17
Bivalve	Caprinoidea	9	23	311	0.706	0.349	0.004	0.343	0.006	18
Bivalve	Cardiidae	10	33	356	0.367	0.336	0.410	0.383	0.563	19
Bivalve	<i>Chione</i>	10	19	112	0.567	0.440	0.130	0.437	0.135	20
Bivalve	<i>Chionopsis</i>	10	19	164	0.427	0.420	0.468	0.430	0.521	20
Bivalve	Corbulidae	9	12	2828	0.476	0.491	0.599	0.489	0.580	21
Bivalve	Eucardiidae	9	20	156	0.715	0.441	0.026	0.461	0.021	22
Bivalve	Hippuritoidea	9	36	427	0.489	0.280	0.045	0.305	0.039	23

“Per..” gives Period of peak richness (1=Cambrian, 2=Ordovician, 3=Silurian, 4=Devonian, 5=Carboniferous, 6=Permian, 7=Triassic, 8=Jurassic, 9=Cretaceous, 10=Paleogene, 11=Neogene). OTU=number of taxa examined. SCP = Stratigraphically Compatible Pairs. E[HSC] gives expected HSC under given either budding (Bud) or Bifurcating (Bif) cladogenesis.

Higher Taxon	Analyzed Taxon	Per.	OTU	SCP	Obs.	HSC	E[HSC Bud]	<i>P</i>	E[HSC Bif]	<i>P</i>	Ref.
Bivalve	<i>Leptodesma</i>	4	22	128	0.492	0.500	0.518	0.437	0.255	24	
Bivalve	Megadesmidae	6	15	213	0.498	0.478	0.445	0.414	0.220	25	
Bivalve	Ostreaoidea	9	34	439	0.295	0.304	0.536	0.316	0.590	26	
Bivalve	Pholadidae	9	25	197	0.492	0.385	0.177	0.325	0.083	27	
Cephalopod	Acanthoceratidae	9	20	562	0.482	0.468	0.447	0.486	0.517	28	
Cephalopod	Ceratitida	6	32	891	0.299	0.365	0.746	0.383	0.854	29	
Cephalopod	Goniatitoidea	5	13	244	0.545	0.381	0.157	0.369	0.096	30	
Cephalopod	Hamitidae	9	27	651	0.326	0.320	0.484	0.335	0.538	31	
Cephalopod	Hammatoceratinae	8	11	60	0.467	0.524	0.652	0.517	0.653	32	
Cephalopod	Hildoceratidae	8	17	85	0.535	0.476	0.306	0.475	0.310	33	
Cephalopod	Scaphitacoidea	9	13	189	0.563	0.397	0.146	0.392	0.108	10	
Cephalopod	<i>Semiformiceras</i>	8	11	110	0.532	0.566	0.628	0.535	0.523	34	
Cephalopod	Turrilitoidea	9	26	316	0.503	0.320	0.078	0.322	0.076	35	
Tergomyan	Cyrtonelloidea	2	21	920	0.486	0.426	0.226	0.411	0.175	36	
Gastropod	Ancillinae	10	30	376	0.418	0.334	0.267	0.337	0.235	37	
Gastropod	Bucaniidae	8	40	1034	0.346	0.376	0.631	0.366	0.580	36	
Gastropod	Columbellidae	11	24	304	0.474	0.454	0.427	0.452	0.402	38	
Gastropod	Eotomarioidea	2	40	2363	0.372	0.346	0.384	0.343	0.350	39	
Gastropod	Harpidae	10	18	357	0.520	0.402	0.135	0.394	0.120	40	
Gastropod	Hormotomidae	2	34	2778	0.308	0.355	0.713	0.355	0.746	39	
Gastropod	Macluritidae	2	18	1434	0.611	0.436	0.021	0.431	0.010	39	
Gastropod	Muricidae	10	18	566	0.549	0.399	0.097	0.404	0.078	41	
Gastropod	Nassariidae	10	26	185	0.443	0.406	0.385	0.401	0.336	42	
Gastropod	Rapaninae	10	27	206	0.379	0.411	0.630	0.428	0.692	43	
Gastropod	Sinuitidae	2	16	465	0.492	0.437	0.319	0.437	0.272	36	
Gastropod	Subulitoidea	5	27	132	0.386	0.413	0.613	0.413	0.626	44	
Gastropod	Trochonematoidea	2	55	469	0.319	0.332	0.548	0.326	0.521	45, 46	
Gastropod	Tropidodiscidae	2	22	596	0.537	0.413	0.116	0.405	0.078	36	
Trilobite	Agnostoidea	1	82	1786	0.351	0.284	0.232	0.272	0.158	47	
Trilobite	Agnostoidea	1	43	231	0.348	0.377	0.592	0.372	0.597	48	
Trilobite	Alokistocaridae	1	19	1160	0.459	0.468	0.537	0.469	0.570	49	
Trilobite	Basal Trilobita	1	17	241	0.647	0.557	0.125	0.531	0.073	50	
Trilobite	Burlingiidae	1	16	71	0.570	0.500	0.285	0.479	0.229	51	



Higher Taxon	Analyzed Taxon	Per.	OTU	SCP	Obs.	HSC	E[HSC Bud]	<i>P</i>	E[HSC Bif]	<i>P</i>	Ref.
Trilobite	Emuellidae	1	15	348	0.330	0.458	0.911	0.446	0.923	52	
Trilobite	Euptychaspidinae	1	12	273	0.443	0.455	0.536	0.440	0.492	53	
Trilobite	Iwayaspidinae	1	14	137	0.423	0.478	0.696	0.481	0.721	54	
Trilobite	Kochaspidae	1	66	1344	0.385	0.447	0.810	0.380	0.463	55	
Trilobite	Missisquoiidae	1	22	331	0.418	0.516	0.919	0.484	0.842	56	
Trilobite	Nevadoidea	1	22	686	0.493	0.495	0.511	0.488	0.467	57	
Trilobite	Olenelloidea	1	26	921	0.584	0.509	0.145	0.480	0.050	58	
Trilobite	Oryctocephalidae	1	22	493	0.526	0.458	0.191	0.451	0.151	59	
Trilobite	Oryctocephalinae	1	24	189	0.497	0.503	0.518	0.464	0.341	60	
Trilobite	Polymeroidea	1	19	438	0.372	0.373	0.504	0.383	0.556	61	
Trilobite	Pterocephaliidae	1	36	625	0.397	0.381	0.434	0.387	0.461	62	
Trilobite	Ptychoparioidea	1	48	2144	0.397	0.399	0.512	0.358	0.323	63	
Trilobite	Wuaniidae	1	37	13	0.385	0.467	0.658	0.400	0.529	64	
Trilobite	Acanthoparyphinae	2	24	644	0.469	0.474	0.510	0.400	0.274	65	
Trilobite	<i>Ceratocara</i>	2	10	141	0.564	0.590	0.594	0.565	0.507	66	
Trilobite	Deiphoninae	2	21	115	0.443	0.489	0.663	0.460	0.575	67	
Trilobite	Dimeropygidae	2	18	306	0.497	0.517	0.556	0.457	0.358	68	
Trilobite	Illaeidae	2	28	214	0.418	0.417	0.493	0.409	0.458	69	
Trilobite	<i>Ovalocephalus</i>	2	10	215	0.853	0.489	0.001	0.456	0.001	70	
Trilobite	<i>Pseudopetigurus</i>	2	17	210	0.581	0.486	0.162	0.456	0.085	71	
Trilobite	<i>Pseudosphaerexochus</i>	2	10	216	0.412	0.486	0.730	0.450	0.635	72	
Trilobite	Reedocalymeninae	2	32	146	0.479	0.400	0.255	0.403	0.256	73	
Trilobite	Shumardiidae	2	33	584	0.423	0.506	0.910	0.463	0.756	74	
Trilobite	Sphaerexochinae	2	31	402	0.552	0.474	0.212	0.402	0.068	75	
Trilobite	<i>Stenoblepharum</i>	2	10	169	0.521	0.479	0.357	0.474	0.336	76	
Trilobite	Tetralichinae	2	11	104	0.644	0.542	0.179	0.520	0.137	77	
Trilobite	Toernquistiidae	2	38	756	0.319	0.437	0.909	0.386	0.757	78	
Trilobite	<i>Acanthopgye</i>	3	25	40	0.725	0.469	0.050	0.475	0.033	79	
Trilobite	<i>Edgecombeaspis</i>	3	9	88	0.966	0.487	<0.001	0.468	<0.001	80	
Trilobite	Encrinurinae	3	32	596	0.345	0.450	0.864	0.370	0.605	81	
Trilobite	Odontopleuridae	3	62	357	0.457	0.398	0.283	0.313	0.075	82	
Trilobite	Phacopidae	3	50	311	0.441	0.401	0.325	0.385	0.265	83-85	
Trilobite	Trochurinae	3	19	163	0.650	0.491	0.047	0.458	0.022	86	

Higher Taxon	Analyzed Taxon	Per.	OTU	SCP	Obs.	HSC	E[HSC Bud]	<i>P</i>	E[HSC Bif]	<i>P</i>	Ref.
Trilobite	<i>Asteropyginae</i>	4	38	855	0.367	0.414	0.669	0.411	0.689	87	
Trilobite	<i>Basidechenella</i>	4	16	186	0.581	0.496	0.195	0.454	0.078	88	
Trilobite	<i>Dechenella</i>	4	17	598	0.607	0.472	0.049	0.470	0.039	88	
Trilobite	<i>Koneprusiinae</i>	4	39	116	0.647	0.500	0.084	0.455	0.046	89	
Trilobite	<i>Malvinella</i>	4	14	817	0.537	0.520	0.413	0.520	0.424	90	
Trilobite	<i>Metacryphaeus</i>	4	17	525	0.635	0.468	0.030	0.448	0.018	91	
Trilobite	Proetidae	4	21	696	0.514	0.422	0.171	0.419	0.155	88	
Trilobite	<i>Trimerocephalus</i>	4	14	294	0.558	0.488	0.295	0.409	0.085	92	
Trilobite	<i>Kaskia</i>	5	19	146	0.449	0.462	0.548	0.451	0.507	93	
Trilobite	Phillipsidae	5	21	108	0.532	0.457	0.287	0.460	0.273	94, 95	
Trilobite	Lichoidea	2	36	804	0.521	0.413	0.118	0.412	0.090	96	
Chelicerate	Adelophthalmoidea	3	12	155	0.629	0.496	0.121	0.465	0.067	97	
Chelicerate	Cambrian Arachnomorpha	1	24	742	0.357	0.384	0.593	0.379	0.604	98	
Chelicerate	Eurypetriidae	3	23	660	0.472	0.449	0.393	0.455	0.405	99	
Chelicerate	<i>Eurypterus</i>	3	13	144	0.562	0.513	0.369	0.474	0.259	100	
Chelicerate	Stylonurina	3	23	631	0.368	0.408	0.660	0.397	0.617	101	
Crustacean	Astacidae	8	17	253	0.731	0.498	0.005	0.472	<0.001	102	
Crustacean	Astacidae	8	23	375	0.488	0.357	0.134	0.380	0.155	103	
Crustacean	Beyrichiocopa	2	34	464	0.417	0.339	0.201	0.333	0.174	104	
Crustacean	Phyllocarida	4	41	1288	0.503	0.431	0.236	0.359	0.052	105	
Crustacean	Thylacocephala	4	18	125	0.548	0.538	0.474	0.505	0.317	106	
Crustacean	Xanthoidea	10	21	1255	0.399	0.450	0.697	0.373	0.386	107	
Stylophoran	Anomalocystitidae	2	20	2267	0.374	0.478	0.892	0.439	0.807	108	
Stylophoran	Chauvelicystinae	2	12	73	0.637	0.553	0.244	0.515	0.168	109	
Stylophoran	Cincta	1	21	1702	0.427	0.459	0.622	0.396	0.364	110	
Stylophoran	Cornuta	2	32	1662	0.364	0.415	0.707	0.353	0.443	111	
Stylophoran	Cornuta	2	22	383	0.520	0.424	0.227	0.363	0.073	112	
Stylophoran	Cornuta	2	28	226	0.416	0.433	0.555	0.377	0.343	113	
Stylophoran	Dendrocystitidae	2	15	107	0.561	0.492	0.285	0.446	0.148	114, 115	
Stylophoran	Mitrata	2	13	577	0.791	0.455	0.005	0.420	<0.001	116	
Stylophoran	Mitrata	2	17	4167	0.433	0.486	0.728	0.435	0.508	117	
Stylophoran	Stylophora	2	42	1966	0.446	0.337	0.107	0.318	0.069	114	
Edrioasteroid	Agelacrinitinae	4	10	30	1.000	0.516	0.004	0.526	0.005	118	

Higher Taxon	Analyzed Taxon	Per.	OTU	SCP	Obs.	HSC	E[HSC Bud]	<i>P</i>	E[HSC Bif]	<i>P</i>	Ref.
Edrioasteroid	Edrioasteroidea	2	15	192	0.776	0.474	0.021	0.476	0.022	119	
Edrioasteroid	Isorophida	2	11	42	0.631	0.454	0.099	0.459	0.071	120	
Asterozoan	Asterozoa	2	36	7260	0.350	0.350	0.508	0.321	0.365	121	
Asterozoan	Goniasteridae	8	21	1151	0.424	0.496	0.795	0.450	0.638	122	
Blastozoan	Blastoidea	4	68	2863	0.390	0.341	0.272	0.340	0.254	123	
Blastozoan	Glyptocystitidae	3	11	109	0.766	0.518	0.008	0.497	0.003	124	
Blastozoan	Pleurocystitidae	2	12	147	0.782	0.524	0.033	0.507	0.033	125	
Crinoid	Basal Crinoidea	2	33	143	0.409	0.437	0.603	0.441	0.634	126	
Crinoid	Botryocrinidae	5	13	88	0.369	0.450	0.759	0.456	0.798	127	
Crinoid	Calceocrinidae	3	22	99	0.692	0.454	0.045	0.455	0.025	128	
Crinoid	Camerata	2	28	439	0.432	0.414	0.420	0.421	0.453	129	
Crinoid	Cladida	2	27	308	0.305	0.372	0.764	0.391	0.850	129	
Crinoid	Cupulocrinidae	2	13	237	0.741	0.527	0.024	0.461	0.001	130	
Crinoid	<i>Cyathocrinites</i>	5	14	74	0.399	0.514	0.846	0.459	0.708	131	
Crinoid	Disparida	2	45	648	0.299	0.349	0.720	0.355	0.770	129	
Crinoid	<i>Mespilocrinus</i>	5	10	40	0.562	0.508	0.363	0.449	0.234	132	
Crinoid	Pereichocrinidae	4	20	258	0.391	0.457	0.788	0.473	0.851	133	
Echinoid	Arbacoidea	9	21	749	0.730	0.395	0.011	0.410	0.005	134	
Echinoid	Arbacoidea	7	25	224	0.538	0.410	0.109	0.384	0.063	135	
Echinoid	Cassiduloidea	9	69	620	0.318	0.281	0.362	0.274	0.309	136	
Echinoid	Cassiduloidea	9	49	382	0.651	0.277	0.001	0.309	<0.001	137	
Echinoid	Clypeasteroidea	9	43	695	0.355	0.298	0.304	0.319	0.346	138	
Echinoid	Disasteroidea	9	26	189	0.696	0.391	0.007	0.411	0.016	139	
Echinoid	Holasteroidea	9	43	478	0.341	0.319	0.430	0.338	0.489	140	
Echinoid	Hypsaleriinae	9	10	44	0.568	0.489	0.297	0.471	0.259	134	
Echinoid	Irregularia	8	27	401	0.613	0.376	0.011	0.386	0.013	141	
Echinoid	Loveniidae	10	14	626	0.450	0.484	0.654	0.485	0.696	142	
Echinoid	Mesozoic Echinoidea	7	46	1471	0.444	0.323	0.107	0.331	0.081	143	
Echinoid	Ordovician Echinoidea	2	11	206	0.745	0.474	0.015	0.467	0.003	144	
Echinoid	Somaliasteridae	9	19	190	0.479	0.386	0.232	0.394	0.244	145	
Echinoid	Spatangoidea	10	50	1910	0.410	0.287	0.116	0.319	0.126	146	
Echinoid	Spatangoidea	9	37	635	0.350	0.361	0.544	0.373	0.601	147	
Echinoid	Temnopleuridae	10	16	400	0.360	0.453	0.819	0.441	0.844	148	

Higher Taxon	Analyzed Taxon	Per.	OTU	SCP	Obs.	HSC	E[HSC Bud]	<i>P</i>	E[HSC Bif]	<i>P</i>	Ref.
Echinoid	Toxasteridae	8	35	474	0.661	0.367	0.003	0.340	0.001	149	
Conodont	<i>Hindeodus–Isarcicella</i>	6	21	113	0.465	0.389	0.275	0.402	0.307	150	
Conodont	<i>Kockelella</i>	3	17	311	0.595	0.453	0.070	0.446	0.035	151	
Conodont	<i>Palmatolepis</i>	4	15	233	0.442	0.424	0.467	0.383	0.308	152	
Cephalaspid	Thyestiidae	3	18	274	0.478	0.508	0.628	0.513	0.639	153	
Pteraspid	Pteraspidiformes	4	26	902	0.639	0.447	0.005	0.443	0.004	154	
Placoderm	Actinolepidae	3	18	446	0.410	0.443	0.617	0.407	0.486	155	
Placoderm	Arthrodira	4	31	731	0.486	0.428	0.304	0.429	0.268	156	
Placoderm	Bothriolepidae	4	12	100	0.650	0.403	0.109	0.413	0.107	157	
Placoderm	Eubrachythoraci	4	19	799	0.557	0.494	0.194	0.485	0.161	158	
Placoderm	Phyllolepidae	4	38	940	0.457	0.385	0.235	0.380	0.197	159	
Placoderm	Selenosteidae	4	10	62	0.476	0.509	0.613	0.491	0.564	160	
Chondrichthian	Basal Chondrichthyes	5	10	74	0.493	0.489	0.491	0.489	0.489	161	
Actinopterygian	Amblypteridae	5	50	771	0.694	0.402	<0.001	0.340	<0.001	162	
Actinopterygian	Amiidae	10	21	771	0.350	0.372	0.560	0.313	0.341	163	
Actinopterygian	Basal Teleostei	8	26	7451	0.557	0.381	0.025	0.358	0.015	164, 165	
Actinopterygian	Devonian Palaeonisciformes	4	15	821	0.523	0.521	0.492	0.453	0.207	166	
Actinopterygian	Ginglymodi	10	27	1869	0.428	0.412	0.439	0.398	0.389	167, 168	
Actinopterygian	Osteoglossomorphes	7	18	1392	0.449	0.466	0.608	0.473	0.639	169	
Actinopterygian	Perleidiformes	7	14	240	0.433	0.498	0.756	0.463	0.633	167	
Actinopterygian	Scanalepiformes	4	13	1014	0.470	0.473	0.507	0.430	0.353	170	
Actinopterygian	Tetradontiformes	4	36	1688	0.547	0.440	0.122	0.384	0.025	171	
Sarcopterygian	Basal Sarcopterygia	5	32	6829	0.443	0.385	0.285	0.392	0.281	172	
Sarcopterygian	Basal Sarcopterygia	5	25	6580	0.472	0.408	0.240	0.413	0.243	173	
Sarcopterygian	Coelocanthiformes	5	30	1535	0.533	0.457	0.193	0.416	0.074	174	
Sarcopterygian	Coelocanthiformes	7	24	3201	0.739	0.430	<0.001	0.433	<0.001	175, 176	
Sarcopterygian	Devonian Dipnoi	4	26	1164	0.573	0.419	0.065	0.413	0.040	177	
Sarcopterygian	Mesozoic Dipnoi	4	16	100	0.890	0.495	<0.001	0.468	<0.001	178	
Sarcopterygian	Rhipidistia	10	30	3196	0.603	0.401	0.014	0.401	0.010	179	
Tetrapod	Early Tetrapoda	5	21	4646	0.714	0.504	0.001	0.457	<0.001	180	
Temnospondyl	Basal Temnospondyli	5	10	1047	0.455	0.531	0.780	0.476	0.589	181	
Temnospondyl	Brachyopoidea	6	21	634	0.421	0.465	0.720	0.431	0.555	182, 183	
Temnospondyl	Branchiosauridae	6	19	484	0.606	0.419	0.044	0.415	0.025	184	

Higher Taxon	Analyzed Taxon	Per.	OTU	SCP	Obs.	HSC	E[HSC Bud]	<i>P</i>	E[HSC Bif]	<i>P</i>	Ref.
Temnospondyl	Capitosauria	7	22	648	0.596		0.449	0.077	0.384	0.010	185
Temnospondyl	Capitosauridae	6	11	333	0.683		0.524	0.029	0.517	0.015	186
Temnospondyl	Dvinosauridae	5	10	858	0.528		0.518	0.446	0.512	0.409	187
Temnospondyl	Edopoidea	5	15	304	0.704		0.535	0.016	0.519	0.006	188, 189
Temnospondyl	Mastodonsauroida	6	21	292	0.560		0.471	0.214	0.464	0.186	190
Temnospondyl	Rhytidosteoidea	6	11	52	0.740		0.530	0.068	0.445	0.022	191
Temnospondyl	Stegocephalia	5	16	818	0.416		0.501	0.909	0.480	0.851	192
Temnospondyl	Stereospondylia	6	15	1965	0.544		0.464	0.196	0.464	0.179	193
Synapsid	Basal Synapsida	6	17	619	0.448		0.524	0.827	0.481	0.668	194
Synapsid	Varanopidae	7	10	50	0.660		0.576	0.263	0.556	0.207	195
Synapsid	Anomodontia	6	30	2241	0.422		0.449	0.619	0.386	0.324	196, 197
Synapsid	Cynodontia	6	16	1155	0.494		0.458	0.351	0.435	0.252	198
Synapsid	Dicynodontia	7	29	1620	0.458		0.411	0.300	0.403	0.240	199
Synapsid	Eutheriodontia	7	23	2648	0.621		0.464	0.025	0.410	0.004	200
Synapsid	Eutherocephalia	7	21	1629	0.378		0.475	0.863	0.426	0.709	201; 202
Synapsid	Traversodontidae	7	16	511	0.634		0.455	0.023	0.455	0.024	203, 204
Synapsid	Amphilestidae	9	20	1381	0.339		0.402	0.760	0.397	0.761	205
Synapsid	Anomaluroidea	10	14	4889	0.610		0.503	0.112	0.462	0.026	206
Synapsid	Anthracotheriidae	10	9	95	0.421		0.464	0.601	0.454	0.588	207
Synapsid	Arctoidea	10	20	375	0.327		0.427	0.876	0.422	0.895	208
Synapsid	Basal Aplodontioidea	10	61	11758	0.507		0.394	0.040	0.378	0.020	209
Synapsid	Basal Cetacea	10	17	714	0.676		0.459	0.010	0.463	0.008	210
Synapsid	Basal Ctenodactyloidea	10	14	185	0.535		0.467	0.283	0.458	0.216	211
Synapsid	Basal Ruminantia	10	10	292	0.522		0.489	0.367	0.487	0.362	212
Synapsid	Borhyaenoidea	10	10	493	0.792		0.447	0.008	0.450	0.010	213
Synapsid	Borophaginae	10	66	3528	0.431		0.285	0.037	0.279	0.029	214
Synapsid	Brontotheriidae	10	47	3113	0.658		0.354	<0.001	0.343	<0.001	215
Synapsid	Carnivoramorpha	10	24	2210	0.542		0.412	0.086	0.416	0.060	216
Synapsid	Carpolestidae	10	13	392	0.801		0.451	0.001	0.453	0.003	217
Synapsid	Ceratomorpha	10	22	273	0.438		0.429	0.481	0.430	0.480	218
Synapsid	Chalicotheriidae	10	17	814	0.452		0.471	0.603	0.476	0.623	219
Synapsid	<i>Cormohipparion</i>	11	12	1356	0.749		0.519	0.008	0.480	0.001	220
Synapsid	Cretaceous Eutheria	9	23	2170	0.551		0.455	0.120	0.452	0.112	221

Higher Taxon	Analyzed Taxon	Per.	OTU	SCP	Obs.	HSC	E[HSC Bud]	<i>P</i>	E[HSC Bif]	<i>P</i>	Ref.
Synapsid	Dichobunidae	10	23	186	0.672	0.473	0.018	0.433	0.009	222	
Synapsid	Didolodontidae	10	13	74	0.541	0.464	0.325	0.402	0.175	223	
Synapsid	Elephantiformes	11	31	1101	0.658	0.347	0.002	0.360	0.001	224	
Synapsid	Eocene Equidae	10	18	1325	0.830	0.434	<0.001	0.420	<0.001	225	
Synapsid	Eotheria	8	21	1341	0.433	0.408	0.423	0.413	0.396	226	
Synapsid	Equidae	10	17	1151	0.712	0.479	0.002	0.442	<0.001	227	
Synapsid	Equinae	11	19	506	0.539	0.492	0.303	0.457	0.176	228	
Synapsid	Hathliacynidae	10	10	658	0.742	0.486	0.003	0.496	0.004	229	
Synapsid	Hippopotamidae	10	16	366	0.548	0.444	0.160	0.442	0.136	230	
Synapsid	Hippotragini	11	15	181	0.395	0.421	0.579	0.420	0.589	231	
Synapsid	Hominidae	11	14	4309	0.581	0.526	0.197	0.499	0.070	232	
Synapsid	Hominoidea	11	14	4783	0.722	0.526	<0.001	0.515	<0.001	233	
Synapsid	Hyaenidae	11	18	77	0.494	0.452	0.375	0.446	0.354	234	
Synapsid	Hyaenodontida	10	34	983	0.551	0.373	0.018	0.366	0.011	235, 236	
Synapsid	Hypsodontidae	10	11	239	0.435	0.502	0.751	0.467	0.640	237	
Synapsid	Louisinidae	10	22	2712	0.560	0.452	0.083	0.445	0.047	238	
Synapsid	Machairodontinae	11	12	399	0.695	0.526	0.021	0.489	0.009	239	
Synapsid	Megalochinidae	11	14	770	0.569	0.482	0.144	0.484	0.130	240	
Synapsid	Megalonychidae	11	14	106	0.524	0.523	0.499	0.491	0.381	241	
Synapsid	Mioclaenidae	10	31	831	0.412	0.399	0.450	0.391	0.411	242	
Synapsid	Multituberculata	9	32	1424	0.702	0.470	<0.001	0.466	<0.001	243	
Synapsid	Mustellidae	11	9	743	0.518	0.528	0.540	0.496	0.378	244	
Synapsid	Mysticetiidae	11	32	9722	0.498	0.390	0.117	0.388	0.086	245	
Synapsid	Nimravinae	10	11	428	0.463	0.494	0.612	0.498	0.644	246	
Synapsid	Notohippidae	10	17	309	0.579	0.380	0.082	0.359	0.045	247	
Synapsid	Odobenidae	11	15	1157	0.777	0.445	0.003	0.445	0.001	248	
Synapsid	Omomyidae	10	29	35489	0.356	0.437	0.851	0.390	0.673	249	
Synapsid	Paucituberculata	10	21	713	0.616	0.525	0.157	0.475	0.045	250	
Synapsid	Perissodactyla	10	10	467	0.498	0.487	0.442	0.487	0.452	237	
Synapsid	Protoselendonta	10	23	186	0.672	0.480	0.040	0.437	0.008	251	
Synapsid	Selenodonta	10	22	1107	0.696	0.472	<0.001	0.469	<0.001	252	
Synapsid	Splacotheriidae	9	11	132	0.564	0.579	0.541	0.549	0.446	253	
Synapsid	Taeniodonta	10	10	723	0.632	0.509	0.059	0.503	0.055	254	

Higher Taxon	Analyzed Taxon	Per.	OTU	SCP	Obs.	HSC	E[HSC Bud]	<i>P</i>	E[HSC Bif]	<i>P</i>	Ref.
Synapsid	Toxodontidae	11	20	1275	0.421		0.470	0.729	0.467	0.737	255
Synapsid	Xenungulata	10	22	128	0.582		0.454	0.107	0.449	0.088	256
Synapsid	Zapodidae	10	25	223	0.619		0.442	0.039	0.423	0.024	257
Anapsid	Ankyramorpha	6	19	2329	0.565		0.487	0.164	0.442	0.053	258
Anapsid	Baenidae	9	14	802	0.587		0.491	0.152	0.491	0.107	259
Anapsid	Basal Testudinata	8	33	3076	0.755		0.380	<0.001	0.349	<0.001	260
Anapsid	Leptopleuroninae	7	10	455	0.542		0.499	0.357	0.491	0.289	261
Anapsid	Millerettidae	6	10	422	0.698		0.564	0.081	0.547	0.032	262
Anapsid	Nanhsiungchelyidae	9	10	154	0.484		0.542	0.652	0.469	0.459	263
Anapsid	Procolophonoidea	7	21	865	0.636		0.502	0.057	0.454	0.010	264
Ichthyosaur	Ichthyosauria	8	31	3904	0.676		0.425	0.001	0.411	<0.001	265, 266
Sauropterygian	Mosasauridae	9	33	2183	0.484		0.452	0.322	0.398	0.099	267-269
Sauropterygian	Cryptocleidoidea	9	11	1174	0.445		0.508	0.729	0.503	0.744	270
Sauropterygian	<i>Nothosaurus</i>	7	11	138	0.656		0.515	0.101	0.487	0.056	271
Sauropterygian	Placodontia	7	10	1436	0.537		0.511	0.363	0.509	0.338	272
Sauropterygian	Plesiosauridae	8	11	300	0.360		0.477	0.863	0.481	0.876	273
Sauropterygian	Plesiosauroidea	8	32	5881	0.527		0.436	0.108	0.428	0.097	274
Sauropterygian	Polycotylidae	9	10	433	0.582		0.501	0.244	0.515	0.260	275
Sauropterygian	Sphenodontia	7	22	771	0.506		0.501	0.482	0.478	0.319	276
Archosaur	Archosauromorpha	7	20	6293	0.442		0.437	0.478	0.425	0.432	277
Archosaur	Basal Crocodylia	7	11	95	0.363		0.477	0.805	0.481	0.849	278
Archosaur	Basal Crocodyliformes	9	33	5966	0.437		0.434	0.487	0.370	0.214	279
Archosaur	Basal Crurotarsia	7	20	4607	0.417		0.501	0.893	0.464	0.772	280
Archosaur	Chroniosuchia	6	12	121	0.876		0.509	0.008	0.489	0.008	281
Archosaur	Crocodylia	9	48	6662	0.500		0.388	0.080	0.358	0.048	282, 283
Archosaur	Diplocynodontinae	10	35	4718	0.563		0.421	0.088	0.362	0.008	284
Archosaur	Dyrosauridae	9	10	153	0.529		0.524	0.491	0.500	0.370	285
Archosaur	Metriorhynchidae	8	34	2335	0.407		0.379	0.391	0.368	0.322	286
Archosaur	Metriorhynchinae	8	18	1138	0.454		0.430	0.417	0.415	0.324	287
Archosaur	Phytosauridae	7	10	1045	0.688		0.532	0.029	0.497	0.010	288
Archosaur	Phytosauroidea	7	18	240	0.558		0.512	0.297	0.433	0.023	289, 290
Archosaur	Protosuchidae	8	14	5979	0.472		0.526	0.730	0.489	0.579	291
Archosaur	Sebecosuchia	10	16	295	0.235		0.419	0.981	0.399	0.978	292, 293

Higher Taxon	Analyzed Taxon	Per.	OTU	SCP	Obs.	HSC	E[HSC Bud]	<i>P</i>	E[HSC Bif]	<i>P</i>	Ref.
Archosaur	Thalattosauriformes	7	12	87	0.454	0.528	0.778	0.496	0.691	294	
Archosaur	Basal Pterosauria	8	18	1878	0.660	0.480	0.026	0.429	0.004	295	
Archosaur	Pterosauria	8	56	6076	0.449	0.342	0.109	0.337	0.095	296	
Archosaur	Allosauroidae	8	12	367	0.733	0.527	0.010	0.511	0.004	297	
Archosaur	Ankylosauria	9	45	3872	0.544	0.462	0.111	0.459	0.088	298	
Archosaur	Ankylosauroidae	9	16	741	0.549	0.513	0.245	0.520	0.279	299	
Archosaur	Basal Iguanodontia	8	21	272	0.759	0.532	0.008	0.504	0.001	300	
Archosaur	Carcharodontosauria	9	14	384	0.613	0.487	0.147	0.479	0.118	301	
Archosaur	Ceratopsidae	9	13	109	0.569	0.575	0.514	0.487	0.273	302	
Archosaur	Ceratosauria	9	18	1441	0.644	0.520	0.187	0.488	0.053	303	
Archosaur	Chasmosaurinae	9	18	1491	0.547	0.451	0.168	0.443	0.100	304	
Archosaur	Deinonychosauria	9	17	1391	0.471	0.499	0.625	0.489	0.586	305-307	
Archosaur	Diplodocoidea	8	20	3632	0.421	0.433	0.548	0.432	0.535	308	
Archosaur	Dromaeosauridae	9	17	2385	0.401	0.455	0.745	0.453	0.760	309	
Archosaur	Euornithopoda	8	10	121	0.488	0.529	0.698	0.526	0.692	310	
Archosaur	Hadrosaurinae	9	10	2031	0.482	0.492	0.530	0.493	0.541	311	
Archosaur	Hadrosauroidae	9	29	5866	0.769	0.456	0.001	0.369	<0.001	312	
Archosaur	Megalosauroidae	8	19	2757	0.474	0.521	0.677	0.480	0.531	301	
Archosaur	Neoceratopsia	9	18	4413	0.537	0.446	0.201	0.456	0.175	313, 314	
Archosaur	Ornithopoda	9	14	1203	0.379	0.462	0.859	0.469	0.904	315	
Archosaur	Oviraptorosauria	9	13	249	0.512	0.470	0.356	0.467	0.340	306, 316	
Archosaur	Prosauropoda	7	15	2786	0.549	0.452	0.176	0.456	0.168	317	
Archosaur	Saurolophidae	9	28	18063	0.472	0.468	0.482	0.411	0.183	318	
Archosaur	Sauropoda	8	28	28844	0.471	0.467	0.483	0.425	0.276	319	
Archosaur	Titanosauriformes	9	21	1258	0.579	0.458	0.124	0.445	0.101	320	
Archosaur	Tyransauroidae	9	19	25404	0.858	0.499	<0.001	0.443	<0.001	321	



**Table S6. Differences between Observations and Expectations for Parameters Hypothesized to Elevate Hierarchical Stratigraphic Compatibility.**

Analyzed Taxon	Cum. Disp. $\frac{S}{2}$		Clade CG		Paracl. CG		Pair Anag.		Paracl. Dur.		"Living Fossils"	
	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.
Anopliidae	0.962	0.890	0.436	0.444	0.677	0.619	0.069	0.134	0.696	0.672	0.554	0.315
Atrypidae	0.993	0.854	0.437	0.447	0.324	0.292	0.223	0.351	0.318	0.275	0.160	0.129
Billingsellida	0.867	0.847	0.368	0.452	0.406	0.496	0.190	0.247	0.446	0.508	0.338	0.237
Echinoconchidae	0.887	0.858	0.394	0.461	0.590	0.605	0.320	0.220	0.695	0.652	0.375	0.291
<i>Floweria</i>	1.051	0.872	0.476	0.444	0.653	0.645	0.269	0.324	0.732	0.701	0.611	0.431
<i>Kutchithyris</i>	0.927	0.861	0.409	0.456	0.415	0.563	0.289	0.310	0.461	0.595	0.198	0.296
Leptenellidae	0.965	0.875	0.529	0.439	0.557	0.496	0.106	0.173	0.540	0.521	0.300	0.261
Leptestiidae	0.885	0.903	0.375	0.472	0.477	0.436	0.486	0.492	0.531	0.421	0.447	0.172
Linguloidea	0.949	0.832	0.552	0.435	0.538	0.471	0.216	0.225	0.524	0.495	0.177	0.246
Orbirhynchia	0.825	0.818	0.511	0.442	0.451	0.502	0.853	0.317	0.355	0.532	0.040	0.286
Parastrophinidae	1.051	0.846	0.534	0.474	0.395	0.388	0.124	0.265	0.361	0.384	0.117	0.167
<i>Plaesiomys</i>	1.023	0.929	0.469	0.464	0.999	0.786	<0.001	0.125	0.994	0.888	0.974	0.423
<i>Schizophoria</i>	1.000	0.867	0.460	0.442	0.772	0.696	0.052	0.146	0.826	0.756	0.591	0.443
Strophomenoidea	1.054	0.913	0.396	0.459	0.505	0.503	0.074	0.214	0.556	0.521	0.556	0.235
Terebratuloidea	0.955	0.829	0.435	0.432	0.695	0.513	0.056	0.083	0.699	0.560	0.533	0.239
Tritoechiidae	0.830	0.855	0.643	0.465	0.352	0.370	0.385	0.514	0.350	0.354	0.162	0.145
Virgianidae	0.974	0.859	0.554	0.458	0.443	0.389	0.205	0.445	0.442	0.373	0.286	0.164
Conocardioidea	0.861	0.812	0.488	0.459	0.437	0.510	0.191	0.148	0.425	0.527	0.263	0.238
Eopteriidae	0.943	0.842	0.576	0.478	0.475	0.551	0.304	0.293	0.445	0.529	0.137	0.219
Pseudobigaleidae	0.881	0.818	0.427	0.439	0.445	0.461	0.513	0.355	0.429	0.469	0.283	0.240
Ribeiriidae	0.985	0.853	0.545	0.451	0.329	0.427	0.316	0.251	0.321	0.446	0.202	0.212
Technophoridae	1.021	0.818	0.536	0.466	0.410	0.475	0.258	0.414	0.430	0.453	0.197	0.195
Caprinoidea	0.617	0.771	0.347	0.462	0.428	0.530	0.178	0.282	0.526	0.558	0.069	0.250
Cardiidae	0.981	0.825	0.352	0.426	0.579	0.447	0.008	0.161	0.623	0.466	0.623	0.215
<i>Chione</i>	1.188	0.866	0.373	0.440	0.559	0.603	0.051	0.153	0.628	0.662	0.628	0.324

“Disp.  $\frac{S}{2}$ ” = cumulative clade disparity after half of taxa have evolved. “Clade CG” gives center of gravity for the whole clade.

“Paracl. CG” gives the CG for paraclades diagnosed with states **00** from HSC pairs. “Pair Anag.” Gives state-pairs in which the older state-pair disappears at the same time the derived pair appears from HSC pairs. “Paracl.” Duration gives duration of paraclades diagnosed by **00** from HSC character-pairs. Duration is as a proportion of the entire clade. “Living fossils” gives the proportion of paraclades diagnosed by **00** that are still extant at the end of a study.

Analyzed Taxon	Cum. Disp. $\frac{S}{2}$		Clade CG		Paracl. CG		Pair Anag.		Paracl. Dur.		"Living Fossils"	
	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.
<i>Chionopsis</i>	1.153	0.842	0.407	0.439	0.764	0.539	0.007	0.195	0.870	0.572	0.840	0.293
Corbulidae	0.896	0.867	0.344	0.451	0.547	0.434	0.179	0.419	0.588	0.434	0.587	0.196
Eucardiidae	0.909	0.879	0.406	0.448	0.237	0.364	0.204	0.317	0.248	0.368	0.162	0.160
Hippuritoidea	0.821	0.780	0.350	0.417	0.497	0.674	0.117	0.104	0.614	0.761	0.249	0.392
<i>Leptodesma</i>	0.899	0.857	0.712	0.439	0.803	0.705	0.044	0.165	1.000	0.776	1.000	0.500
Megadesmidae	0.972	0.802	0.384	0.444	0.607	0.568	<0.001	0.338	0.707	0.603	0.707	0.337
Ostreaoidea	0.821	0.779	0.434	0.417	0.792	0.605	0.077	0.134	0.758	0.661	0.711	0.350
Pholadidae	1.057	0.775	0.388	0.461	0.651	0.606	<0.001	0.219	0.726	0.645	0.656	0.274
Acanthoceratidae	1.029	0.907	0.394	0.435	0.239	0.252	0.147	0.362	0.259	0.228	0.222	0.109
Ceratitida	0.896	0.835	0.392	0.420	0.671	0.587	0.060	0.122	0.743	0.627	0.574	0.321
Goniatitoidea	0.654	0.761	0.410	0.450	0.671	0.666	0.274	0.287	0.787	0.729	0.075	0.336
Hamitidae	0.691	0.769	0.353	0.439	0.461	0.493	0.123	0.256	0.521	0.509	0.286	0.261
Hammatoceratinae	0.992	0.910	0.335	0.451	0.660	0.633	0.036	0.200	0.729	0.688	0.714	0.333
Hildoceratidae	0.828	0.887	0.497	0.451	0.492	0.577	0.275	0.160	0.532	0.613	0.286	0.300
Scaphitacoidea	0.869	0.786	0.376	0.455	0.417	0.547	0.228	0.333	0.525	0.578	0.525	0.270
<i>Semiformiceras</i>	0.791	0.865	0.532	0.452	0.254	0.398	0.726	0.522	0.214	0.393	0.023	0.167
Turrilitoidea	0.929	0.771	0.342	0.441	0.698	0.641	0.047	0.179	0.833	0.699	0.805	0.355
Cyrtonelloidea	1.081	0.819	0.397	0.471	0.397	0.461	0.406	0.386	0.356	0.415	0.197	0.186
Ancillinae	0.974	0.790	0.450	0.425	0.885	0.743	0.038	0.081	0.893	0.856	0.599	0.443
Bucaniidae	0.967	0.824	0.571	0.462	0.403	0.425	0.164	0.223	0.401	0.435	0.290	0.189
Columbellidae	0.946	0.841	0.384	0.466	0.693	0.512	0.458	0.277	0.742	0.528	0.740	0.217
Eotomarioidea	0.904	0.812	0.373	0.444	0.490	0.414	0.064	0.200	0.518	0.429	0.454	0.201
Harpidae	0.836	0.800	0.424	0.465	0.507	0.444	0.247	0.387	0.600	0.433	0.318	0.188
Hormotomidae	0.950	0.809	0.455	0.442	0.450	0.445	0.186	0.214	0.460	0.468	0.376	0.227
Macluritidae	0.939	0.837	0.462	0.460	0.358	0.460	0.310	0.301	0.356	0.467	0.165	0.219
Muricidae	0.749	0.820	0.350	0.439	0.445	0.530	0.129	0.236	0.519	0.562	0.458	0.287
Nassariidae	0.959	0.835	0.319	0.446	0.482	0.579	0.186	0.160	0.551	0.611	0.418	0.292
Rapaninae	0.992	0.868	0.336	0.430	0.740	0.624	<0.001	0.110	0.780	0.681	0.780	0.324
Sinuitidae	0.773	0.839	0.472	0.464	0.675	0.477	0.287	0.353	0.736	0.485	0.606	0.219
Subulitoidea	0.950	0.843	0.387	0.449	0.725	0.547	0.034	0.272	0.753	0.489	0.706	0.245
Trochonematoidea	0.927	0.804	0.357	0.458	0.743	0.536	0.109	0.070	0.782	0.588	0.782	0.240
Tropidodiscidae	1.019	0.821	0.391	0.469	0.342	0.422	0.440	0.347	0.369	0.409	0.179	0.180

Analyzed Taxon	Cum. Disp. $\frac{S}{2}$		Clade CG		Paracl. CG		Pair Anag.		Paracl. Dur.		"Living Fossils"	
	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.
Agnostoidea	0.980	0.771	0.661	0.478	0.688	0.551	0.034	0.067	0.667	0.625	0.606	0.227
Agnostoidea	0.986	0.831	0.426	0.460	0.567	0.516	0.102	0.104	0.563	0.551	0.373	0.232
Alokistocaridae	1.020	0.886	0.467	0.464	0.363	0.386	0.365	0.382	0.368	0.372	0.205	0.164
Basal Trilobita	0.894	0.868	0.402	0.446	0.796	0.565	0.293	0.376	0.797	0.598	0.741	0.325
Burlingiidae	0.658	0.868	0.436	0.442	0.515	0.735	0.389	0.227	0.564	0.797	0.029	0.412
Emuellidae	0.674	0.832	0.541	0.471	0.733	0.634	0.122	0.289	0.751	0.671	0.338	0.286
Euptychaspidinae	0.976	0.803	0.478	0.473	0.828	0.487	0.283	0.503	0.757	0.477	0.329	0.188
Iwayaspidinae	0.920	0.887	0.356	0.453	0.805	0.616	0.017	0.226	0.879	0.656	0.879	0.327
Kochaspidae	0.960	0.826	0.563	0.447	0.449	0.412	0.240	0.261	0.429	0.390	0.291	0.184
Missisquoiidae	0.880	0.896	0.462	0.437	0.647	0.579	0.262	0.252	0.632	0.570	0.304	0.302
Nevadoidea	0.981	0.887	0.642	0.487	0.615	0.548	0.211	0.282	0.577	0.558	0.332	0.225
Olenelloidea	0.982	0.893	0.404	0.436	0.514	0.505	0.206	0.212	0.550	0.520	0.251	0.276
Oryctocephalidae	1.043	0.863	0.506	0.482	0.225	0.370	0.287	0.365	0.240	0.350	0.079	0.146
Oryctocephalinae	1.056	0.843	0.420	0.441	0.413	0.398	0.356	0.398	0.428	0.403	0.357	0.207
Polymeroidea	0.719	0.793	0.458	0.439	0.766	0.472	0.112	0.286	0.840	0.479	0.814	0.245
Pterocephaliidae	0.861	0.825	0.435	0.435	0.599	0.518	0.113	0.132	0.604	0.554	0.560	0.259
Ptychoparioidea	0.912	0.785	0.417	0.466	0.534	0.467	0.299	0.247	0.621	0.475	0.545	0.189
Wuaniidae	0.931	0.879	0.392	0.441	0.490	0.495	<0.001	0.062	0.600	0.533	0.333	0.250
Acanthoparyphinae	0.692	0.781	0.515	0.438	0.448	0.572	0.330	0.241	0.496	0.596	0.255	0.309
<i>Ceratocara</i>	1.022	0.879	0.333	0.449	0.785	0.694	0.230	0.371	0.884	0.753	0.837	0.394
Deiphoninae	0.787	0.874	0.518	0.438	0.687	0.710	0.230	0.160	0.747	0.790	0.208	0.436
Dimeropygidae	0.836	0.797	0.583	0.448	0.478	0.500	0.592	0.364	0.451	0.517	0.191	0.235
Illaenidae	1.053	0.835	0.505	0.461	0.443	0.370	0.131	0.292	0.465	0.361	0.315	0.154
<i>Ovalocephalus</i>	0.950	0.788	0.442	0.443	0.257	0.429	0.857	0.545	0.251	0.432	<0.001	0.197
<i>Pseudopetigurus</i>	0.911	0.862	0.579	0.471	0.377	0.468	0.242	0.374	0.375	0.465	0.150	0.202
<i>Pseudosphaerexochus</i>	0.948	0.785	0.442	0.450	0.685	0.680	0.362	0.382	0.790	0.747	0.692	0.412
Reedocalymeninae	0.831	0.837	0.418	0.442	0.635	0.597	0.125	0.086	0.663	0.671	0.557	0.320
Shumardiidae	0.867	0.858	0.511	0.442	0.535	0.457	0.432	0.326	0.499	0.432	0.302	0.228
Sphaerexochinae	0.902	0.836	0.516	0.441	0.359	0.641	0.457	0.178	0.350	0.640	0.081	0.270
<i>Stenoblepharum</i>	0.936	0.843	0.449	0.469	0.381	0.489	0.386	0.456	0.454	0.485	0.234	0.206
Tetralichinae	0.878	0.852	0.500	0.448	0.540	0.575	0.470	0.491	0.496	0.598	0.164	0.308
Toernquistiidae	0.851	0.820	0.461	0.439	0.686	0.532	0.166	0.147	0.692	0.558	0.547	0.270

Analyzed Taxon	Cum. Disp. $\frac{S}{2}$		Clade CG		Paracl. CG		Pair Anag.		Paracl. Dur.		"Living Fossils"	
	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.
<i>Acanthopgye</i>	0.954	0.891	0.315	0.468	0.395	0.536	0.172	0.229	0.433	0.522	0.222	0.217
<i>Edgecombeaspis</i>	0.748	0.793	0.491	0.472	0.384	0.548	0.635	0.532	0.378	0.553	<0.001	0.213
Encrinurinae	0.997	0.783	0.381	0.438	0.713	0.515	0.196	0.240	0.776	0.545	0.738	0.263
Odontopleuridae	0.954	0.808	0.479	0.435	0.606	0.490	0.143	0.179	0.562	0.513	0.269	0.241
Phacopidae	0.826	0.854	0.544	0.467	0.271	0.303	0.520	0.251	0.236	0.288	0.064	0.123
Trochurinae	0.815	0.858	0.462	0.443	0.430	0.457	0.373	0.302	0.428	0.470	0.286	0.266
Asteropyginae	0.988	0.855	0.422	0.455	0.588	0.549	0.107	0.128	0.614	0.588	0.448	0.260
<i>Basidechenella</i>	1.144	0.802	0.550	0.448	0.515	0.613	0.338	0.386	0.585	0.599	0.279	0.303
Calmoniidae	0.993	0.878	0.397	0.463	0.570	0.586	0.343	0.330	0.598	0.608	0.276	0.246
Calmoniidae	0.937	0.832	0.278	0.480	0.554	0.575	0.489	0.297	0.665	0.582	0.519	0.237
<i>Dechenella</i>	1.043	0.871	0.325	0.466	0.524	0.530	0.149	0.291	0.622	0.540	0.275	0.243
Koneprusiinae	0.921	0.833	0.409	0.435	0.701	0.570	0.513	0.288	0.676	0.567	0.460	0.278
Proetidae	0.866	0.843	0.432	0.441	0.752	0.711	0.037	0.130	0.833	0.769	0.559	0.394
<i>Trimerocephalus</i>	1.347	0.759	0.324	0.444	0.420	0.488	0.416	0.525	0.472	0.503	0.310	0.238
<i>Kaskia</i>	0.877	0.878	0.459	0.463	0.792	0.655	0.252	0.144	0.686	0.710	0.492	0.322
Phillipsidae	1.036	0.853	0.561	0.457	0.647	0.645	0.170	0.097	0.566	0.715	0.200	0.303
Lichoidea	0.995	0.856	0.480	0.428	0.293	0.508	0.236	0.197	0.281	0.489	0.057	0.231
Adelophthalmoidea	0.816	0.785	0.534	0.470	0.540	0.612	0.626	0.583	0.554	0.523	0.032	0.177
Cambrian Arachnomorpha	0.879	0.785	0.433	0.461	0.513	0.502	0.121	0.336	0.603	0.500	0.448	0.215
Eurypetriidae	0.947	0.842	0.456	0.478	0.466	0.371	0.368	0.481	0.443	0.337	0.251	0.132
<i>Eurypterus</i>	1.021	0.808	0.420	0.463	0.607	0.392	0.438	0.707	0.588	0.366	0.324	0.079
Stylonurina	0.887	0.782	0.622	0.451	0.659	0.664	0.167	0.312	0.613	0.665	0.344	0.289
Astacidae	0.841	0.883	0.457	0.461	0.394	0.489	0.473	0.325	0.372	0.503	0.034	0.233
Astacidae	0.831	0.839	0.350	0.435	0.305	0.432	0.093	0.263	0.339	0.435	0.241	0.217
Beyrichiocopa	0.902	0.769	0.319	0.441	0.780	0.597	0.164	0.225	0.806	0.603	0.782	0.275
Phyllocarida	0.872	0.787	0.207	0.438	0.654	0.484	0.489	0.236	0.688	0.497	0.655	0.246
Thylacocephala	0.802	0.881	0.528	0.442	0.225	0.328	0.693	0.463	0.231	0.325	0.155	0.177
Xanthoidea	1.075	0.762	0.338	0.441	0.906	0.687	<0.001	0.249	0.967	0.758	0.967	0.411
Anomalocystitidae	0.993	0.826	0.444	0.441	0.617	0.724	0.229	0.184	0.709	0.803	0.387	0.449
Chauvelicystinae	1.151	0.858	0.429	0.452	0.571	0.463	0.274	0.466	0.576	0.483	0.205	0.242
Cincta	0.883	0.772	0.405	0.443	0.425	0.488	0.242	0.382	0.467	0.508	0.232	0.248
Cornuta	0.941	0.766	0.549	0.439	0.732	0.644	0.143	0.206	0.694	0.711	0.357	0.366

Analyzed Taxon	Cum. Disp. $\frac{S}{2}$		Clade CG		Paracl. CG		Pair Anag.		Paracl. Dur.		"Living Fossils"	
	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.
Cornuta	0.968	0.763	0.474	0.444	0.650	0.698	0.207	0.230	0.704	0.767	0.467	0.412
Cornuta	0.876	0.818	0.587	0.440	0.469	0.375	0.144	0.323	0.484	0.378	0.320	0.200
Dendrocystitidae	0.915	0.864	0.424	0.443	0.385	0.490	0.350	0.371	0.437	0.510	0.154	0.275
Mitrata	0.841	0.742	0.457	0.469	0.296	0.535	0.624	0.459	0.290	0.544	0.005	0.212
Mitrata	0.927	0.800	0.583	0.435	0.395	0.413	0.434	0.410	0.380	0.404	0.113	0.206
Stylophora	0.889	0.784	0.590	0.479	0.261	0.318	0.305	0.317	0.213	0.304	0.053	0.127
Agelacrinitinae	0.727	0.904	0.394	0.458	0.547	0.556	0.383	0.357	0.628	0.556	0.567	0.250
Edrioasteroidea	0.640	0.808	0.477	0.483	0.573	0.578	0.233	0.349	0.632	0.576	0.374	0.191
Isorophida	1.197	0.812	0.540	0.465	0.874	0.666	0.170	0.333	0.800	0.683	0.429	0.289
Asterozoa	1.017	0.751	0.494	0.462	0.751	0.607	0.136	0.232	0.785	0.631	0.577	0.264
Goniasteridae	0.851	0.831	0.490	0.443	0.693	0.661	0.189	0.272	0.696	0.729	0.403	0.391
Blastoidea	0.910	0.798	0.482	0.428	0.572	0.518	0.125	0.174	0.492	0.531	0.300	0.241
Glyptocystitidae	0.875	0.852	0.483	0.443	0.309	0.615	0.500	0.429	0.317	0.622	0.025	0.346
Pleurocystitidae	1.055	0.835	0.491	0.468	0.418	0.612	0.585	0.370	0.406	0.598	0.049	0.212
Basal Crinoidea	1.013	0.892	0.425	0.433	0.387	0.312	0.111	0.282	0.392	0.308	0.184	0.143
Botryocrinidae	0.838	0.849	0.514	0.450	0.497	0.524	0.215	0.328	0.499	0.530	0.188	0.245
Calceocrinidae	1.027	0.882	0.597	0.432	0.310	0.442	0.069	0.234	0.298	0.458	0.048	0.222
Camerata	1.028	0.876	0.302	0.429	0.396	0.357	0.231	0.285	0.449	0.360	0.338	0.181
Cladida	1.060	0.826	0.326	0.426	0.558	0.375	0.080	0.278	0.603	0.372	0.581	0.184
Cupulocrinidae	1.002	0.804	0.411	0.446	0.440	0.402	0.318	0.575	0.524	0.409	0.458	0.205
<i>Cyathocrinites</i>	0.787	0.818	0.548	0.439	0.714	0.610	0.136	0.378	0.727	0.657	0.727	0.393
Disparida	0.965	0.849	0.420	0.428	0.406	0.358	0.081	0.217	0.436	0.367	0.410	0.179
Mespilocrinus	0.959	0.781	0.452	0.444	0.745	0.582	0.122	0.514	0.761	0.616	0.364	0.286
Pereichocrinidae	1.035	0.877	0.503	0.439	0.633	0.635	0.129	0.205	0.616	0.662	0.425	0.321
Arbacoidea	0.706	0.799	0.553	0.441	0.466	0.602	0.056	0.160	0.465	0.658	0.033	0.289
Arbacoidea	1.052	0.838	0.398	0.483	0.548	0.454	0.203	0.272	0.579	0.464	0.381	0.180
Cassiduloidea	0.808	0.780	0.416	0.437	0.561	0.478	0.055	0.099	0.624	0.525	0.539	0.233
Cassiduloidea	0.947	0.818	0.376	0.404	0.410	0.558	0.008	0.090	0.529	0.610	0.444	0.315
Clypeasteroidea	0.976	0.810	0.386	0.411	0.651	0.559	0.006	0.099	0.728	0.625	0.676	0.322
Disasteroidea	0.941	0.824	0.518	0.428	0.374	0.546	0.049	0.182	0.347	0.556	0.085	0.267
Holasteroidea	0.816	0.801	0.410	0.419	0.621	0.536	0.040	0.104	0.665	0.591	0.432	0.296
Hypsaleriniinae	0.680	0.827	0.417	0.462	0.797	0.592	0.280	0.409	0.919	0.623	0.792	0.313

Analyzed Taxon	Cum. Disp. $\frac{S}{2}$		Clade CG		Paracl. CG		Pair Anag.		Paracl. Dur.		"Living Fossils"	
	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.
Irregularia	0.968	0.835	0.385	0.424	0.421	0.608	0.189	0.132	0.478	0.664	0.438	0.333
Loveniidae	1.003	0.913	0.458	0.446	0.666	0.511	0.060	0.292	0.706	0.520	0.702	0.234
Mesozoic Echinoidea	0.806	0.776	0.279	0.424	0.486	0.532	0.172	0.183	0.552	0.566	0.505	0.281
Ordovician Echinoidea	1.097	0.845	0.536	0.478	0.657	0.508	0.340	0.509	0.577	0.483	0.361	0.182
Somaliasteridae	1.031	0.818	0.402	0.441	0.633	0.602	0.088	0.185	0.642	0.653	0.242	0.329
Spatangoidea	0.892	0.813	0.283	0.398	0.649	0.541	0.002	0.107	0.766	0.595	0.764	0.309
Spatangoidea	0.964	0.831	0.304	0.415	0.504	0.513	0.162	0.121	0.590	0.559	0.583	0.287
Temnopleuridae	1.074	0.833	0.568	0.471	0.806	0.564	0.057	0.263	0.760	0.586	0.417	0.257
Toxasteridae	0.963	0.812	0.345	0.468	0.346	0.441	0.431	0.177	0.397	0.454	0.193	0.202
<i>Hindeodus–Isarcicella</i>	0.763	0.820	0.490	0.439	0.799	0.741	0.124	0.117	0.950	0.870	0.583	0.423
<i>Kockelella</i>	0.580	0.841	0.416	0.483	0.755	0.678	0.327	0.355	0.713	0.662	0.514	0.258
<i>Palmatolepis</i>	0.755	0.750	0.388	0.443	0.714	0.658	0.248	0.339	0.768	0.709	0.175	0.365
Thyestiidae	0.919	0.891	0.661	0.462	0.703	0.584	0.073	0.314	0.640	0.586	0.192	0.242
Pteraspidiformes	1.002	0.842	0.507	0.468	0.483	0.466	0.248	0.230	0.492	0.477	0.216	0.202
Actinolepidae	0.878	0.788	0.461	0.462	0.629	0.687	0.235	0.270	0.683	0.708	0.134	0.315
Arthrodira	0.825	0.807	0.598	0.462	0.607	0.641	0.259	0.195	0.602	0.667	0.319	0.276
Bothriolepidae	0.435	0.721	0.534	0.494	0.288	0.529	0.623	0.506	0.313	0.526	0.015	0.107
Eubrachythoraci	0.963	0.861	0.361	0.481	0.622	0.527	0.403	0.394	0.671	0.521	0.265	0.201
Phyllolepidae	0.755	0.794	0.585	0.460	0.640	0.686	0.167	0.176	0.667	0.719	0.361	0.297
Selenosteidae	0.659	0.787	0.489	0.452	0.714	0.726	0.729	0.510	0.552	0.705	0.250	0.345
Basal Chondrichthyes	0.994	0.833	0.410	0.500	0.955	0.482	0.082	0.474	1.000	0.479	1.000	0.147
Amblypteridae	0.903	0.819	0.593	0.439	0.359	0.522	0.298	0.115	0.305	0.543	0.096	0.285
Amiidae	1.019	0.725	0.535	0.458	0.712	0.611	0.342	0.326	0.691	0.624	0.532	0.276
Basal Teleostei	0.903	0.778	0.472	0.478	0.414	0.525	0.297	0.286	0.405	0.551	0.181	0.227
Devonian Palaeonisciformes	0.903	0.784	0.456	0.446	0.585	0.570	0.420	0.497	0.647	0.591	0.390	0.278
Ginglymodi	0.746	0.810	0.396	0.469	0.620	0.555	0.429	0.249	0.652	0.583	0.544	0.246
Osteoglossomorphes	0.848	0.838	0.483	0.451	0.609	0.539	0.251	0.396	0.635	0.500	0.494	0.214
Perleidiformes	0.966	0.842	0.454	0.445	0.663	0.628	0.200	0.341	0.704	0.663	0.444	0.363
Scanalepiformes	0.826	0.806	0.614	0.448	0.670	0.595	0.545	0.474	0.612	0.599	0.334	0.262
Tetradontiformes	1.080	0.781	0.528	0.440	0.328	0.482	0.530	0.358	0.339	0.471	0.124	0.205
Basal Sarcopterygia	0.973	0.770	0.548	0.448	0.703	0.611	0.122	0.289	0.676	0.608	0.380	0.256
Basal Sarcopterygia	0.946	0.783	0.402	0.451	0.663	0.690	0.184	0.281	0.677	0.631	0.448	0.294

Analyzed Taxon	Cum. Disp. $\frac{S}{2}$		Clade CG		Paracl. CG		Pair Anag.		Paracl. Dur.		"Living Fossils"	
	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.
Coelocanthiformes	0.872	0.834	0.620	0.435	0.335	0.594	0.383	0.298	0.309	0.585	0.110	0.279
Coelocanthiformes	0.742	0.805	0.570	0.468	0.371	0.613	0.395	0.290	0.365	0.653	0.031	0.261
Devonian Dipnoi	0.945	0.809	0.425	0.457	0.738	0.614	0.293	0.329	0.817	0.604	0.569	0.248
Mesozoic Dipnoi	1.110	0.837	0.540	0.479	0.275	0.441	0.697	0.531	0.205	0.390	0.080	0.140
Rhipidistia	1.125	0.774	0.463	0.453	0.529	0.592	0.184	0.307	0.577	0.599	0.193	0.252
Early Tetrapoda	0.714	0.819	0.591	0.433	0.286	0.535	0.609	0.397	0.297	0.569	0.069	0.262
Basal Temnospondyli	1.073	0.804	0.525	0.446	0.607	0.555	0.368	0.524	0.647	0.604	0.294	0.292
Brachyopoidea	1.023	0.785	0.700	0.439	0.613	0.618	0.214	0.384	0.588	0.598	0.321	0.299
Branchiosauridae	1.053	0.817	0.477	0.462	0.416	0.604	0.322	0.219	0.445	0.656	0.252	0.287
Capitosauria	0.879	0.779	0.518	0.442	0.564	0.628	0.187	0.254	0.584	0.670	0.168	0.348
Capitosauridae	1.111	0.897	0.430	0.455	0.569	0.619	0.607	0.355	0.566	0.660	0.243	0.346
Dvinosauridae	0.850	0.888	0.514	0.492	0.588	0.600	0.451	0.394	0.554	0.612	0.222	0.237
Edopoidea	0.932	0.916	0.516	0.461	0.570	0.617	0.364	0.264	0.563	0.657	0.150	0.302
Mastodonsauroidea	0.972	0.845	0.513	0.458	0.675	0.683	0.150	0.120	0.669	0.761	0.480	0.322
Rhytidosteoidea	1.434	0.767	0.456	0.446	0.645	0.629	0.506	0.545	0.628	0.676	0.192	0.310
Stegocephalia	0.945	0.877	0.436	0.472	0.625	0.668	0.269	0.271	0.667	0.669	0.379	0.304
Stereospondylia	0.899	0.822	0.380	0.450	0.693	0.657	0.189	0.276	0.751	0.721	0.688	0.334
Basal Synapsida	1.100	0.803	0.397	0.443	0.582	0.546	0.318	0.448	0.619	0.567	0.300	0.261
Varanopidae	1.182	0.831	0.350	0.454	0.682	0.619	0.515	0.445	0.775	0.658	0.515	0.333
Anomodontia	0.999	0.811	0.508	0.440	0.412	0.514	0.334	0.317	0.421	0.519	0.196	0.239
Cynodontia	0.856	0.827	0.382	0.479	0.540	0.518	0.518	0.371	0.584	0.527	0.335	0.210
Dicynodontia	0.970	0.820	0.472	0.466	0.606	0.504	0.147	0.313	0.591	0.479	0.232	0.203
Eutheriodontia	0.676	0.816	0.481	0.437	0.364	0.542	0.466	0.286	0.367	0.557	0.159	0.295
Eutherocephalia	0.886	0.806	0.585	0.439	0.748	0.600	0.165	0.282	0.765	0.652	0.378	0.335
Traversodontidae	0.893	0.842	0.535	0.469	0.420	0.598	0.383	0.318	0.429	0.601	0.067	0.252
Amphilestidae	0.921	0.790	0.606	0.463	0.589	0.524	0.261	0.350	0.571	0.537	0.086	0.235
Anomaluroidea	1.116	0.823	0.543	0.447	0.303	0.488	0.506	0.422	0.322	0.496	0.098	0.240
Anthracotheriidae	1.098	0.797	0.516	0.462	0.854	0.624	0.237	0.435	0.956	0.652	0.824	0.254
Arctoidea	0.741	0.829	0.559	0.449	0.770	0.555	0.216	0.250	0.716	0.569	0.321	0.279
Basal Aplodontoidea	0.767	0.795	0.345	0.459	0.693	0.575	0.109	0.196	0.741	0.594	0.601	0.235
Basal Cetacea	0.855	0.823	0.459	0.483	0.240	0.430	0.703	0.536	0.217	0.360	0.056	0.134
Basal Ctenodactyloidea	0.783	0.857	0.506	0.471	0.657	0.533	0.444	0.365	0.683	0.522	0.385	0.224

Analyzed Taxon	Cum. Disp. $\frac{S}{2}$		Clade CG		Paracl. CG		Pair Anag.		Paracl. Dur.		"Living Fossils"	
	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.
Basal Ruminantia	1.002	0.864	0.544	0.469	0.606	0.545	0.261	0.407	0.676	0.551	0.323	0.240
Borhyaenoidea	0.837	0.760	0.527	0.466	0.332	0.477	0.486	0.567	0.299	0.469	0.039	0.157
Borophaginae	0.683	0.771	0.497	0.439	0.421	0.479	0.158	0.154	0.397	0.514	0.137	0.234
Brontotheriidae	0.890	0.783	0.453	0.457	0.454	0.486	0.135	0.233	0.468	0.483	0.151	0.207
Carnivoromorpha	0.817	0.833	0.410	0.440	0.478	0.560	0.162	0.231	0.507	0.578	0.335	0.277
Carpolestidae	0.763	0.800	0.536	0.471	0.336	0.355	0.595	0.608	0.299	0.319	0.102	0.111
Ceratomorpha	0.582	0.810	0.577	0.436	0.684	0.584	0.126	0.266	0.817	0.573	0.804	0.280
Chalicotheriidae	0.883	0.863	0.611	0.462	0.667	0.494	0.099	0.377	0.652	0.482	0.177	0.209
Cormohipparion	1.084	0.839	0.367	0.438	0.161	0.308	0.836	0.620	0.150	0.291	0.042	0.124
Cretaceous Eutheria	0.927	0.844	0.424	0.469	0.509	0.464	0.296	0.379	0.469	0.454	0.271	0.191
Dichobunidae	0.764	0.828	0.388	0.437	0.405	0.569	0.448	0.279	0.442	0.581	0.168	0.296
Didolodontidae	0.850	0.776	0.643	0.441	0.411	0.634	0.325	0.375	0.392	0.706	<0.001	0.378
Elephantiformes	0.975	0.799	0.328	0.422	0.718	0.604	0.040	0.244	0.827	0.600	0.772	0.291
Eocene Equidae	0.633	0.797	0.438	0.466	0.456	0.586	0.536	0.273	0.416	0.633	0.034	0.278
Eotheria	0.961	0.813	0.483	0.444	0.568	0.562	0.223	0.279	0.554	0.598	0.262	0.292
Equidae	0.838	0.829	0.494	0.464	0.299	0.468	0.545	0.375	0.298	0.469	0.082	0.208
Equinae	0.946	0.849	0.548	0.446	0.339	0.473	0.486	0.329	0.312	0.495	0.085	0.279
Hathliacynidae	1.072	0.826	0.357	0.462	0.204	0.609	0.482	0.440	0.250	0.621	0.090	0.280
Hippopotamidae	0.888	0.834	0.481	0.456	0.335	0.602	0.349	0.302	0.381	0.588	0.112	0.271
Hippotragini	1.005	0.778	0.452	0.448	0.580	0.537	0.224	0.402	0.630	0.570	0.385	0.268
Hominidae	0.872	0.872	0.397	0.440	0.390	0.522	0.500	0.581	0.322	0.448	0.108	0.220
Hominoidea	0.647	0.857	0.520	0.480	0.487	0.461	0.537	0.592	0.494	0.469	0.026	0.168
Hyaenidae	0.917	0.868	0.431	0.440	0.511	0.647	0.118	0.194	0.548	0.679	0.208	0.340
Hyaenodontida	0.876	0.814	0.487	0.440	0.529	0.668	0.139	0.120	0.489	0.675	0.202	0.330
Hypsodontidae	0.684	0.806	0.525	0.450	0.571	0.490	0.550	0.515	0.587	0.506	0.304	0.239
Louisinidae	1.007	0.843	0.566	0.482	0.368	0.366	0.451	0.426	0.346	0.350	0.223	0.139
Machairodontinae	1.059	0.843	0.425	0.444	0.386	0.502	0.461	0.467	0.419	0.529	0.191	0.269
Megalochinidae	0.986	0.876	0.299	0.464	0.514	0.487	0.301	0.412	0.579	0.463	0.500	0.202
Megalonychidae	0.781	0.883	0.467	0.443	0.636	0.509	0.252	0.341	0.629	0.534	0.549	0.308
Mioclaenidae	0.873	0.822	0.587	0.451	0.670	0.540	0.083	0.164	0.679	0.571	0.513	0.261
Multituberculata	0.840	0.844	0.405	0.461	0.359	0.547	0.498	0.344	0.281	0.496	0.138	0.218
Mustellidae	0.641	0.775	0.551	0.454	0.669	0.646	0.501	0.631	0.680	0.618	0.294	0.272



Analyzed Taxon	Cum. Disp. $\frac{S}{2}$		Clade CG		Paracl. CG		Pair Anag.		Paracl. Dur.		"Living Fossils"	
	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.
Mysticetiidae	1.036	0.801	0.488	0.464	0.724	0.487	0.254	0.275	0.695	0.494	0.602	0.209
Nimravinae	1.073	0.833	0.451	0.465	0.631	0.490	0.222	0.626	0.639	0.379	0.511	0.134
Notohippidae	0.846	0.777	0.353	0.481	0.470	0.539	0.510	0.396	0.501	0.515	0.092	0.193
Odobenidae	0.607	0.823	0.448	0.467	0.308	0.411	0.567	0.493	0.314	0.404	0.018	0.155
Omomyidae	0.851	0.785	0.595	0.440	0.571	0.530	0.119	0.326	0.621	0.551	0.369	0.307
Paucituberculata	0.775	0.818	0.422	0.441	0.464	0.496	0.607	0.362	0.458	0.510	0.197	0.254
Perissodactyla	0.789	0.868	0.401	0.458	0.456	0.466	0.347	0.457	0.487	0.460	0.370	0.212
Protoselendonta	0.764	0.819	0.396	0.440	0.448	0.551	0.448	0.309	0.450	0.564	0.168	0.293
Selenodonta	1.020	0.892	0.561	0.458	0.457	0.580	0.316	0.298	0.444	0.548	0.119	0.235
Splacotheriidae	0.880	0.817	0.555	0.445	0.604	0.706	0.862	0.452	0.500	0.710	0.070	0.333
Taeniodonta	0.986	0.865	0.519	0.475	0.319	0.410	0.673	0.621	0.218	0.359	0.055	0.128
Toxodontidae	1.027	0.861	0.490	0.454	0.643	0.553	0.198	0.331	0.591	0.521	0.324	0.222
Xenungulata	0.976	0.875	0.392	0.460	0.470	0.315	0.248	0.332	0.451	0.294	0.295	0.134
Zapodidae	0.867	0.822	0.455	0.468	0.611	0.568	0.167	0.225	0.596	0.610	0.231	0.250
Ankyramorpha	1.063	0.798	0.530	0.441	0.592	0.653	0.358	0.351	0.563	0.645	0.259	0.332
Baenidae	0.971	0.816	0.532	0.481	0.433	0.565	0.442	0.499	0.407	0.536	0.121	0.200
Basal Testudinata	0.993	0.780	0.428	0.469	0.198	0.513	0.489	0.370	0.237	0.515	0.084	0.194
Leptopleuroninae	0.982	0.825	0.486	0.479	0.310	0.571	0.829	0.505	0.274	0.574	0.005	0.213
Millerettidae	0.959	0.881	0.353	0.460	0.658	0.552	0.675	0.501	0.737	0.561	0.152	0.235
Nanhsiungchelyidae	0.922	0.784	0.444	0.446	0.546	0.587	0.466	0.648	0.577	0.577	0.300	0.224
Procolophonoidea	0.737	0.786	0.585	0.446	0.431	0.565	0.583	0.499	0.351	0.505	0.054	0.220
Cryptocleidoidea	0.801	0.836	0.479	0.472	0.324	0.442	0.536	0.626	0.306	0.431	0.078	0.138
Ichthyosauria	0.871	0.802	0.602	0.455	0.218	0.496	0.621	0.331	0.188	0.524	0.026	0.215
Mosasauridae	0.926	0.801	0.377	0.430	0.579	0.637	0.303	0.252	0.637	0.651	0.545	0.350
Nothosaurus	1.131	0.820	0.423	0.447	0.533	0.573	0.403	0.433	0.551	0.602	0.349	0.310
Placodontia	0.870	0.901	0.525	0.467	0.635	0.553	0.303	0.508	0.595	0.538	0.173	0.218
Plesiosauridae	0.756	0.799	0.521	0.490	0.699	0.562	0.370	0.453	0.693	0.588	0.296	0.202
Plesiosauroidea	0.785	0.816	0.546	0.465	0.599	0.563	0.262	0.284	0.565	0.570	0.288	0.231
Polycotylidae	0.719	0.780	0.442	0.474	0.517	0.558	0.334	0.631	0.549	0.507	0.381	0.183
Sphenodontia	1.011	0.848	0.542	0.448	0.537	0.571	0.442	0.394	0.457	0.527	0.206	0.225
Archosauromorpha	0.887	0.810	0.597	0.485	0.641	0.567	0.347	0.338	0.493	0.561	0.210	0.219
Basal Crocodylia	0.983	0.874	0.528	0.466	0.742	0.565	0.370	0.468	0.883	0.590	0.667	0.233

Analyzed Taxon	Cum. Disp. $\frac{S}{2}$		Clade CG		Paracl. CG		Pair Anag.		Paracl. Dur.		"Living Fossils"	
	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.
Basal Crocodyliformes	0.967	0.784	0.380	0.446	0.593	0.556	0.241	0.318	0.585	0.569	0.276	0.248
Basal Crurotarsia	0.931	0.824	0.567	0.442	0.635	0.661	0.359	0.434	0.690	0.621	0.467	0.273
Chroniosuchia	0.548	0.815	0.483	0.482	0.553	0.513	0.535	0.397	0.745	0.524	0.677	0.162
Crocodylia	0.938	0.782	0.345	0.480	0.531	0.579	0.352	0.274	0.588	0.543	0.342	0.210
Diplocynodontinae	1.070	0.773	0.512	0.425	0.375	0.598	0.388	0.295	0.381	0.588	0.093	0.263
Dyrosauridae	1.024	0.843	0.700	0.447	0.286	0.579	0.358	0.430	0.207	0.621	<0.001	0.306
Metriorhynchidae	0.876	0.774	0.527	0.464	0.568	0.419	0.322	0.404	0.509	0.404	0.220	0.165
Metriorhynchinae	0.612	0.806	0.650	0.480	0.436	0.375	0.557	0.531	0.431	0.335	0.187	0.123
Phytosauridae	0.766	0.824	0.417	0.450	0.382	0.510	0.741	0.556	0.401	0.536	0.109	0.278
Phytosauroida	0.922	0.838	0.386	0.388	0.725	0.662	0.729	0.453	0.864	0.746	0.854	0.602
Protosuchidae	0.876	0.806	0.452	0.447	0.480	0.567	0.620	0.525	0.580	0.584	0.453	0.256
Sebecosuchia	1.045	0.749	0.444	0.472	0.662	0.503	0.402	0.544	0.590	0.452	0.380	0.162
Thalattosauriformes	0.903	0.851	0.563	0.444	0.616	0.663	0.791	0.451	0.679	0.667	0.441	0.371
Basal Pterosauria	0.916	0.793	0.473	0.450	0.390	0.564	0.466	0.423	0.447	0.585	0.173	0.262
Pterosauria	0.877	0.793	0.458	0.452	0.404	0.539	0.177	0.199	0.411	0.559	0.127	0.227
Allosauroida	0.949	0.896	0.333	0.447	0.397	0.656	0.842	0.432	0.535	0.669	0.236	0.292
Ankylosauria	0.869	0.838	0.416	0.474	0.709	0.663	0.209	0.306	0.750	0.620	0.538	0.245
Ankylosauroida	0.933	0.915	0.411	0.465	0.637	0.629	0.381	0.394	0.649	0.586	0.399	0.259
Basal Iguanodontia	0.856	0.837	0.400	0.446	0.458	0.520	0.653	0.556	0.488	0.523	0.138	0.218
Carcharodontosauria	1.052	0.797	0.612	0.474	0.430	0.591	0.540	0.657	0.414	0.440	0.114	0.140
Ceratopsidae	0.816	0.779	0.402	0.449	0.548	0.489	0.411	0.595	0.567	0.506	0.500	0.222
Ceratosauria	1.061	0.815	0.365	0.439	0.251	0.641	0.762	0.677	0.324	0.495	0.196	0.146
Chasmosaurinae	0.844	0.831	0.484	0.462	0.546	0.564	0.393	0.353	0.528	0.571	0.070	0.238
Deinonychosauria	1.038	0.796	0.494	0.461	0.595	0.528	0.443	0.614	0.650	0.450	0.159	0.156
Diplodocoidea	0.723	0.802	0.620	0.457	0.507	0.656	0.112	0.426	0.449	0.583	0.081	0.213
Dromaeosauridae	1.167	0.811	0.368	0.461	0.574	0.618	0.368	0.519	0.607	0.512	0.330	0.188
Euornithopoda	1.166	0.888	0.552	0.486	0.461	0.637	0.585	0.582	0.399	0.565	0.082	0.212
Hadrosaurinae	0.847	0.821	0.500	0.472	0.770	0.529	0.311	0.507	0.795	0.538	0.638	0.204
Hadrosauroida	0.929	0.738	0.334	0.440	0.433	0.593	0.309	0.313	0.545	0.621	0.356	0.284
Megalosauroida	0.549	0.869	0.699	0.438	0.692	0.549	0.478	0.579	0.577	0.534	0.143	0.190
Neoceratopsia	0.806	0.809	0.401	0.467	0.480	0.560	0.464	0.456	0.457	0.503	0.211	0.200
Ornithopoda	0.874	0.838	0.471	0.460	0.752	0.692	0.201	0.298	0.719	0.686	0.353	0.302

Analyzed Taxon	Cum. Disp. $\frac{S}{2}$		Clade CG		Paracl. CG		Pair Anag.		Paracl. Dur.		"Living Fossils"	
	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.
Oviraptorosauria	1.236	0.795	0.382	0.466	0.632	0.556	0.563	0.595	0.669	0.477	0.343	0.152
Prosauropoda	1.018	0.821	0.563	0.462	0.526	0.665	0.250	0.396	0.549	0.620	0.332	0.256
Saurolophidae	0.969	0.781	0.433	0.443	0.710	0.547	0.279	0.373	0.635	0.515	0.436	0.241
Titanosauriformes	0.786	0.816	0.518	0.452	0.558	0.578	0.361	0.408	0.530	0.616	0.086	0.259
Sauropoda	0.846	0.817	0.500	0.442	0.583	0.608	0.352	0.396	0.449	0.541	0.130	0.228
Tyranosauroida	0.658	0.736	0.357	0.440	0.439	0.584	0.706	0.459	0.409	0.579	0.103	0.255

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