Early Bursts of Disparity and the Reorganization of Character Integration

Peter J. Wagner

Dept. of Earth & Atmospheric Sciences, and School of Biological Sciences

University of Nebraska

Lincoln, NE 20560

pjwagner3@gmail.com

Abstract

Evolutionary biologists commonly explain “early bursts” of morphological disparity (i.e., diversity of anatomical types) in terms of subsequent integration among characters reducing probabilities of characters change. However, modules of linked characters themselves evolve, changing which characters are linked to one another and potentially allowing for rapid increases in disparity. Early bursts fit the expectations of integration/modularity reorganization in two ways: early disparity exceeds the expectations of simple independent change models, and early bursts correlate with stratigraphic incompatibility suggesting that multicharacter changes are followed by independent changes. This suggests that integrated changes sustained by the beneficial effects of some characters lead to selection for reduced integration among those characters, allowing both for reversals to primitive states for some characters and still different novel states for others. Subsequent reorganization of integration and modularity later constrains disparity. Thus, although modularity and integration might limit disparity most of the time, they periodically elevate disparity greatly.

Introduction

A common pattern in the fossil record is for the range of distinct anatomical forms (i.e., morphological disparity) to be high early in clade histories (Erwin 2007, Hughes et al. 2013). Explanations for such “early bursts” of disparity invoke theory from both ecology and evolutionary-developmental biology (Foote 1994, Wagner 1995b, Foote 1996a, Ciampaglio 2002, Gerber 2013): the former posits reduced opportunities for novel anatomies to succeed and the latter posits reduced opportunities for novel anatomies to arise. The predictions stemming from those models typically are framed in the context of systematic theory. This views characters (i.e., specific anatomical structures) as homologies and the units of morphological evolution (Patterson 1982). Combining these theories provides two explanations for early bursts of disparity. The first is that ecology and development limit plausible novel states, resulting in clades that rapidly exhaust the possible states to add little disparity even if rates of character change remain constant (Foote 1994, Wagner 2000b). The second is that frequencies of character change decrease, resulting in fewer opportunities for novel states to arise and/or flourish (Foote 1996a) and thus reduced increase of disparity.

Evolutionary-developmental theory also offers a model of homology and units of morphologic evolution that differs from that of systematic theory, and that provides an explanation for why evolvability should sometimes increase then decrease and thus create bursts of disparity (Wagner and Altenberg 1996). This theory treats character complexes (modules) as the unit of change, with distinct character states often appearing through interactions with other characters in the same complex rather than through independent processes (Wagner 1989). Although tighter integration among characters within a module should limit evolvability and disparity (Goswami and Polly 2010), modules themselves evolve by breaking up and reforming anew (Wagner 1996), resulting in different integration patterns among characters (Eble 2004, Goswami 2006). Intervals of integration/modularity reorganization among characters should elevate both rates of character change and thus encourage the evolution of novelties that greatly increases disparity (Davidson and Erwin 2006, Wagner 2007). If integration/modularity reorganization commonly delimits what paleontologists recognize as higher taxa, then this provides a third explanation for early bursts of disparity.

The three models for generating early bursts of disparity (exhaustion, elevated early rates of change and integration/modularity reorganization) all make unique predictions about the relationship between early disparity and both character compatibility and stratigraphic compatibility (Table 1). Character compatibility (Le

Quesne 1969) measures whether pairs of characters necessarily require parallelisms or reversals. As frequencies of change among character states increase, reversals and parallelisms also increase and levels of compatibility decrease (O'Keefe and Wagner 2001). Simple inverse modeling can determine a (uniform) rate of independent character changes that maximizes the probability of observed compatibility within clade (Wagner and Estabrook 2015). If early disparity exceeds the expected disparity given this best uniform rate model, then we can reject exhaustion as the primary culprit of an early burst. The same approach applied only to the earliest taxa can establish the 2-rate (early vs. late) models of independent change maximizing the probability of compatibility among those early taxa (see Materials and Methods). If early disparity exceeds that expected from the 2-rate model of independent change, then we can reject elevated early rates of independent change as the sole cause of an early burst.

In addition to predicting that early disparity will exceed expectations given any independent change model (**Table 1**), the integration/modularity reorganization model predicts that stratigraphic compatibility also should be low. This premise is supported both by simulations and by unusually high stratigraphic compatibility in Cambrian trilobites (Wagner and Estabrook 2015), which show low phylogenetic conservation of integration patterns relative to later trilobites (Webster 2007, Webster and Zelditch 2011). Thus, integration/modularity reorganization predicts that early disparity exceeding the expectations of 2-rate models of independent change will correspond to overly low stratigraphic incompatibility given the same 2-rates models.

Table 1.

Alternative models for early bursts of disparity (D), expected early disparity ($E[\text{early } D]$) and their expected associations. “Model” refers to the pattern underlying an early burst of disparity. “Expectations” reflect both first principles and also outcomes of Monte Carlo analyses (see Methods).

Model	Expectations
Exhaustion/Saturation	Early $D \leq E[\text{early } D]$ given uniform rate of independent character change maximizing the probability of character compatibility among all taxa (= 1-rate model).
Elevated Early Rates of Change	Early $D > E[\text{early } D]$ given best 1-rate model of independent change; Early $D \leq E[\text{early } D]$ given independent change maximizing the probability of compatibility among the early and late taxa separately (= 2-rate model).
Integration/Modularity Reorganization	Early $D > E[\text{early } D]$ given best 1-rate model; Early $D > E[\text{early } D]$ given best 2-rate model; (Early $D - E[\text{early } D]$) correlates with stratigraphic incompatibility.

Materials and Methods

Data assembly

The analyses cover 257 published character matrices of 13+ ingroup taxa that were originally assembled for phylogenetic analyses (Appendix S1; <http://datadryad.org/resource/doi:10.5061/dryad.h5971>). Only data sets with 13+ ingroup taxa were used in order to have a sample of at least 4 species when looking at disparity and rates in the earliest third of clade evolution. Because the tested hypotheses concern shifts at low taxonomic levels, only analyses of species or genera are used. This also avoids the heterogeneity in phylogenetic branch durations expected when analyzed taxa of variable ranks and taxonomic richness are analyzed. The one exception made for this rule is studies focusing on early members of clades that included token representation of later members. If the representatives were the oldest members of the derived taxon, then that stem-member was included. Otherwise, the taxon was excluded and only the older taxa were examined. Extant taxa are included only if they have fossil representatives. I exclude any characters not coded for extinct taxa these probably are non-fossilizable. I also exclude characters that are invariant within the ingroup. Polymorphic characters (i.e., those in which 2+ conditions are observed in the same taxon) are set to states that maximized their stratigraphic compatibility. First and last appearance data come from several sources, with the original publications and the Paleobiology Database (<http://www.paleobiodb.org/>) being the two primary sources. Stratigraphic ranges for extant taxa reflect the first and last fossil occurrences of those taxa.

Disparity calculations

Disparity is measured here as the average pairwise dissimilarity among characters (Foote 1992, 1994, 1996b). Multistate characters are unordered, which means that any taxa are considered either different or the same for any character. This makes disparity:

$$\frac{\sum_{s_A=1}^{S-1} \sum_{s_B=s_A+1}^S \frac{\sum_{n=1}^N \text{differing states}}{\text{comparable characters}}}{S}$$

where S is the number of taxa, N is the number of characters, and “comparable characters” are all characters for which two contrasted taxa have an observed state rather than an unknown condition. The biggest factor increasing average pairwise dissimilarity is the addition of novel character states: with complete exhaustion of available character states, we expect disparity to peak at $v/(v+1)$, where v is the

Fig. 1. Cumulative vs. standing disparity and richness for *Floweria* species. (A) 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 a 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 $S=1$.

average number of novel (derived) states per character (Lupia 1999). This also means that simply adding new combinations and “filling” morphospace can decrease disparity. Analyses calculate disparity among all S taxa and for the earliest $S/2$ taxa (Wagner and Estabrook 2014) see (Table 2 and Fig. 1). Analyses using the earliest $S/3$ taxa are presented in the supplementary material. Using all taxa rather than standing diversity removes the effects of differential extinction or active trends on disparity patterns. When there are an odd number of taxa, I round up (e.g., the first seven taxa given either 13 or 14 total taxa). In cases where stratigraphic binning creates “ties” for taxon $S/2$, the taxa creating the least disparity among the first $S/2$ are chosen. So, if there are 21 taxa, and species 9, 10, 11 and 12 all appear in the same interval, whichever three of those species add least to total disparity are used along with taxa 1-8.

Early bursts are measured as the how many times greater (or less) observed disparity is among the first $S/2$ taxa and expected disparity among those taxa given the Monte Carlo tests described below. Note that this is atypical of paleontological studies: usually disparity is measured solely given contemporaneous (or roughly contemporaneous) taxa (Foote 1991, 1992, 1993a, Hughes et al. 2013). Instead, it is closer to studies contrasting relative diversity among whole subclades (Foote 1993b, Wagner 1997). It also is akin to studies looking at the disparity

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	•

Table 2. Pairwise dissimilarities among Devonian *Floweria* species. *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. magnacitrix*; *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. See Fig. 1.

encompassed by whole clades within phylogenies of extant taxa (Harmon et al. 2010, Rabosky et al. 2013).

Measuring compatibility and stratigraphic compatibility

Compatible characters have 3 of 4 possible combinations if the characters are binary (e.g., **00**, **10** and **01**) (Le Quesne 1969, Estabrook et al. 1975). Multistate characters are considered unordered; compatibility reflects whether all binary breakdowns have three or fewer combinations as well as whether the collection of state-pairs demands parallelism or reversal (Estabrook et al. 1975, Wagner and Estabrook 2014). Note that treating multistate characters as unordered maximizes their compatibility as combinations that are considered compatible given unordered change are considered incompatible given ordered change because some parallel “decrease” or “increase” is invoked even if the final combination of character states is unique (Meacham 1984, Salisbury 1999, Hoyal Cuthill 2015). As

frequencies of homoplasy (i.e., reversals or parallelisms) increase, compatibility decreases.

Stratigraphic compatibility represents compatible character pairs in which each combination of characters appears in the fossil record in an order consistent with a simple character state tree (Estabrook and McMorris 2006). For the set **00**, **10** and **01**, this requires that oldest species bearing **00** occurs in older strata than the oldest species bearing **10** and/or **01**. If the oldest species with the intermediate character pair is older than (or as old as) either of those other two species, then the fossil record is consistent with simple trees positing no homoplasy and no basic gaps in the fossil record. Because stratigraphic compatibility utilizes only compatible characters, it is uncorrelated with frequencies of homoplasy. Because compatible characters are based on rates of change relative to rates of taxon sampling, stratigraphic compatibility also is uncorrelated with per-lineage sampling intensity (Wagner and Estabrook 2015). Instead, the two primary models decreasing stratigraphic compatibility are elevated rates of early change and correlated change followed by independent change (Wagner and Estabrook 2015).

Monte Carlo tests estimating independent change rates using character compatibility

For S taxa with N characters, there will be some range of changes (“steps”) that maximize the probability of observed compatibility and the observed number of novel states assuming independent change (O’Keefe and Wagner 2001, Wagner 2012, Wagner and Estabrook 2015). This is assessed using Monte Carlo analyses that simulate phylogenies of S taxa (= number of sampled ingroup taxa) using rates of cladogenesis, extinction and sampling appropriate to each analyzed clade (Wagner and Estabrook 2014, 2015). The analyses evolve one step at a time over N characters (= variable fossilizable characters in the original dataset) and track the average compatibility at X steps in order to estimate the likelihood of X steps given observed compatibility. The probability of any individual character changing is uniform, as this adds a conservative bias to the analyses by making it easier to derive each state with the minimum steps necessary (Wagner et al. 2006) and thus maximizes the likely compatibility associated with N novel states. Character state evolution also is unordered, as this minimizes the expected number of changes needed to evolve all N states in an N -state character (Foote 1994, Wagner 2000b), and thus maximizes the likely compatibility associated with the whole character space. These analyses are repeated 1000 times to find the X maximizing the probability of observed compatibility is used for the uniform (1-rate) model of change. This is repeated using the earliest $S/2$ (or $S/3$) taxa, where the “first” $S/2$ (or $S/3$) taxa always are the same as for the disparity analyses. Now X is found that

simultaneously maximizes the probability of the observed compatibility given only the earliest taxa and the probability of having as many derived character states as actually observed among the earliest taxa.

Although it is possible to model modules of integrated characters, even simple models involve many more than two varying parameters (Gerber et al. 2011). Moreover, because the number of characters per module and the number of modules with a collection of characters all can vary, this rapidly becomes unfeasible when evaluating large numbers of datasets. Because we expect stratigraphic compatibility to drop precipitously in the presence of integration/modularity reorganization, correlations between stratigraphic compatibility and disparity are used instead of inverse modeling of integration/modularity reorganization.

Monte Carlo analyses for expected early disparity and stratigraphic compatibility

The most likely whole-clade (1-rate) and early vs. late (2-rate) models of independent change from the first set of Monte Carlo analyses then are used in a second set of Monte Carlo analyses that tally disparity among the first $S/2$ (or $S/3$) as a proportion of disparity among all S taxa given either the 1-rate or 2-rate models of independent change. These same analyses also are used to estimate expected stratigraphic compatibility. The simulations assume budding cladogenesis, in which ancestral morphospecies persist after speciation and can give rise to any number of descendants (Raup and Gould 1974), rather than bifurcating cladogenesis, in which ancestors become pseudo-extinct upon branching and thus give rise to only 2 descendants (Slowinski and Guyer 1989). The simulations also assume exponential growth. Neither has any effect on disparity as calculated here, but budding and exponential models both generate lower stratigraphic compatibility than do bifurcating and richness-dependent diversification models such as logistic (Sepkoski 1979) or hierarchical (Brayard et al. 2009) models (Wagner and Estabrook 2015). The simulations again assume unordered character state change for multistate characters, which again maximizes both expected disparity and expected compatibility at X steps. As before, evolutionary and sampling parameters appropriate to each clade are used (Wagner and Estabrook 2014, 2015).

Fig. 2. Deviations from expected disparity (D) among the first $S/2$ of S taxa given the uniform rates of independent change that maximize the probability of observed compatibility. Deviations are on a log-scale so that one-half and twice of expected D represent the same absolute deviation. (A) Deviations over time. $\tau = -0.039$, $p = 0.379$. (B) Deviations against the ratio between early and late rates maximizing the probability of compatibility among the first $S/2$ taxa. Molluscs+Brachiopods (purple shells): $\tau = 0.383$, $p = 1.0 \times 10^{-4}$; Arthropods (orange trilobites): $\tau = 0.443$, $p = 4.6 \times 10^{-6}$; Echinoderms (blue stars): $\tau = 0.411$, $p = 2.0 \times 10^{-4}$; Chordates (green fishes): $\tau = 0.488$, $p = 3.6 \times 10^{-15}$.

The analyses use 1000 simulations for both rate models. Each run calculates disparity at $S/2$ (or $S/3$) using the same criteria as used for the original data. The median disparity at $S/2$ (or $S/3$) taxa from those 1000 replicates is used for the expected early disparity given the 1-rate or 2-rate model. The median stratigraphic compatibility at $S/2$ (or $S/3$) from the analyses using the 2-rate model is used for the expected stratigraphic compatibility. Analyses were conducted using programs written in C that are available at <http://dx.doi.org/10.5061/dryad.h5971>.

Wilcoxon signed rank tests, a nonparametric analog of the t-test, assess whether deviations from expected early disparity are biased in favor of more and/or larger early bursts (excess positive ranks) or delayed bursts (excess negative ranks). Because the tests use ratios of observed to expected, the ratios are log-transformed so that early disparity 1.5 times expected has the same absolute rank as early disparity 0.67 times expected. Thus, any positive deviation can have an identically ranked negative deviation. Kendall's rank correlation tests are used to assess correlations between the ratios of observed and expected early disparity with time, early rates and stratigraphic compatibility.

Results

Early bursts of disparity exceeding expectations given character compatibility and uniform frequencies of change (i.e., the exhaustion model) occur in 203 of the 257

clades examined (**Fig. 2A**). Many of the deviations are quite large: in 91 cases, the deviations are significant at $p \leq 0.05$ (**Fig. 3**). Within each of brachiopods+molluscs, arthropods, echinoderms and chordates, significantly more than half of studies show excess early disparity (**Table 3**). The summed ranks of absolute deviations (log-transformed so that one half and twice expected disparity have the same absolute rank) is significantly biased towards excess early disparity. The pattern also is common throughout the Phanerozoic: significantly more clades than half of studies show excess early disparity in 8 of 11 periods, and the summed ranks are biased significantly in favor of excess early disparity in 9 of 11 periods (**Table 4**). Differences between observed and expected disparity given the exhaustion model correlate with the relative difference between early rates and late rates from 2-rate

Table 3. Deviations from expected early disparity within major taxonomic groups. “Studies” refers to the number of published matrices represent clades used. “Excess” gives the number of studies with excess disparity in the first half of clade evolution given a single rate (“1-Rate”) and given separate early and late rates (“2-Rates”), with the early rate maximizing the probability of character compatibility given the earliest $S/2$ of S total taxa. The significance is the binomial probability of that many excess cases given the total studies and an expectation of 50%. “ ΣR ” gives the signed rank statistic, which ranks deviations by absolute values but then gives each rank a +/- based on the original statistic. Deviations are ranked after log-transformation, so half the expected disparity has the same rank as twice the expected disparity. Significance is assessed on the expectation that $\Sigma R=0$.

Taxa	Studies	1-Rate		1-Rate		2-Rates		2-Rates	
		Excess	p	ΣR	p	Excess	p	ΣR	p
Brachiopods									
+Molluscs	49	43	7.6×10^{-9}	989	4.4×10^{-7}	35	1.4×10^{-3}	749	9.8×10^{-5}
Arthropods	51	40	1.5×10^{-5}	872	2.2×10^{-5}	33	0.024	570	3.8×10^{-3}
Echinoderms	38	35	5.4×10^{-9}	653	1.1×10^{-6}	28	1.7×10^{-3}	525	7.0×10^{-5}
Chordates	119	85	1.3×10^{-6}	3441	1.9×10^{-6}	78	2.9×10^{-4}	2222	1.6×10^{-3}

models for each clade (**Fig. 2B**; $\tau=0.470$; $p<10^{-20}$). This association is significant within all four general taxonomic partitions. The associations between early bursts and best-fit early rates are positive in all 11 periods, and significant at $p \leq 0.06$ in 9 of 11 periods. Thus, both disparity and compatibility patterns deviate from the expectations of the exhaustion model.

Fig. 4. Deviations from expected disparity (D) among the first $S/2$ of S taxa given the early rates of independent change that maximize the probability of observed compatibility among the first $S/2$ taxa. See Fig. 1 for further details. (A) Deviations over time. $\tau = -0.035$, $p = 0.421$. (B) Disparity deviations against deviations from expected stratigraphic compatibility given the same 2-rate model. Molluscs+Brachiopods (purple shells): $\tau = -0.191$, $p = 0.053$; Arthropods (orange trilobites): $\tau = -0.343$, $p = 3.9 \times 10^{-4}$; Echinoderms (blue stars): $\tau = -0.165$, $p = 0.145$; Chordates (green fishes): $\tau = 0.301$, $p = 1.3 \times 10^{-6}$.

Table 4. Deviations from expected early disparity over time. “Periods” give geochronological periods of the plurality of taxa within any one clade. See Table 3 for further details.

Period	Studies	1-Rate		1-Rate		2-Rates		2-Rates	
		Excess	<i>p</i>	ΣR	<i>p</i>	Excess	<i>p</i>	ΣR	<i>p</i>
Cambrian	21	17	3.6×10^{-3}	131	0.011	14	0.095	95	0.049
Ordovician	42	36	1.4×10^{-6}	731	2.4×10^{-6}	31	1.4×10^{-3}	533	4.3×10^{-4}
Silurian	14	11	0.029	67	0.018	11	0.029	51	0.055
Devonian	29	26	7.6×10^{-6}	395	9.7×10^{-6}	22	4.1×10^{-3}	313	3.6×10^{-4}
Carboniferous	12	9	0.073	32	0.105	8	0.194	18	0.240
Permian	11	10	5.9×10^{-3}	62	2.9×10^{-3}	10	5.9×10^{-3}	54	8.2×10^{-3}
Triassic	16	13	0.011	70	0.035	12	0.038	60	0.060
Jurassic	21	14	0.095	85	0.070	10	0.500	25	0.332
Cretaceous	38	30	2.4×10^{-4}	509	6.2×10^{-5}	22	0.209	229	0.048
Paleogene	41	28	0.014	427	2.8×10^{-3}	25	0.106	267	0.042
Neogene	12	9	0.073	30	0.136	9	0.073	28	0.120

Early bursts of disparity exceed expectations given separate early/late frequencies of change in 174 of 257 clades (**Fig. 4A**). In 40 cases, the deviations are significant at $p \leq 0.05$ (**Fig. 5**). Excess early disparity deviates significantly from the expectations of best-fit single-rate models within the basic taxonomic partitions (**Table 3**). In every period but the Jurassic, over half of the clades show greater disparity than predicted by elevated early rates, with five periods showing deviations significant at $p \leq 0.05$ (**Table 4**). All 11 periods have ranked absolute deviations favoring positive (excess) disparity, with 8 of 11 periods deviating from a symmetrical distribution around zero at $p \leq 0.06$. Thus, early bursts of disparity typically exceed the expectations of plausible elevated early rates of independent change (Table 1).

Disparity exceeding 2-rate independent change models correlates negatively with stratigraphic compatibility within clades (Fig. 2B; $\tau = -0.277$; $p = 1.7 \times 10^{-10}$). This association exists in all 11 periods, although it is rarely significant (**Table 4**). The associations also are negative in all four higher taxonomic partitions (Table 2) and significant at $p \leq 0.05$ for all groups save echinoderms. Thus, as predicted by the integration/modularity reorganization models, early bursts of disparity deviating further from the expectations of independent character change correspond to a greater tendency for compatible sets of character pairs to appear out of order in the fossil record.

Discussion

There are many reasons to think that these results are conservative. One, Monte Carlo tests looking at disparity and rate shifts among the earliest *S*/3 taxa generate

nearly identical results (**Table S1-2, Figs. S1-S4**). This indicates that the early bursts are concentrated even earlier in clade histories than simply anytime in the first half. Two, the evolutionary models used by the Monte Carlo tests (see Methods) were chosen to minimize expected stratigraphic compatibility (Wagner and Estabrook 2015), and thus minimize any association between excess stratigraphic incompatibility and excess disparity. Three, although there is copious evidence for rate heterogeneity among characters (Wagner 2012; Harrison and Larsson 2015), these tests assume homogeneous rates among characters. Homogeneous rates minimize the expected number of changes (and thus maximize the possible compatibility) necessary to evolve numerous derived states. This exaggerates how easily both high disparity and high compatibility are evolved simultaneously. Four, the analyses attribute as much disparity as possible to 2-rate

independent change models before considering the predictions of the integration/modularity reorganization model. Thus, much of the change that the integration/modularity reorganization model would generate is attributed to elevated independent change. Five, systematists are counseled to exclude characters that might be correlated with other characters (Patterson 1982). The low levels of stratigraphic incompatibility argue that systematists are not completely successful at doing this, but the practice still biases these data against corroborating hypotheses invoking correlated change.

Other explanations also fail to account for the results. For example, low sampling of early taxa might elevate early disparity (Foote 1996a). However, there is no reason to think that per-taxon sampling typically is low early in clade histories. Moreover, paleontologists often target early members of clades for phylogenetic studies out of concern that parallelisms and reversals among later taxa will distort basic relationships (Smith 2001). Regardless, the 2-rate models double as low early sampling models (Wagner and Estabrook 2015): one way to get separate early per-branch rates of change is to have different early sampling rates that mean fewer (or more) unsampled ancestors exist along each branch (Foote et al. 1999; Wagner 2000a). Thus, disparity exceeding the 2-rate models and the correlation of this excess disparity with stratigraphic compatibility demand explanations other than sampling.

These results corroborate other meta-analyses showing that early bursts are common in paleontological data (Hughes et al. 2013). However, because this study uses cumulative disparity rather than contemporaneous disparity, these results cannot be attributed to high early taxonomic richness (see Foote 1996a). By establishing expected disparity through character compatibility, these results also show that early bursts are not driven by exhaustion of character states. Finally, the results indicate early bursts often are more than just elevated rates of independent character change: too often, the numbers of independent changes needed to generate the early disparity should also precipitate many more reversals and parallelisms than the observed character compatibility among early taxa allows. Correlated change associated with integration circumvents this by concentrating N changes in N characters, which maximizes disparity while retaining high character compatibility among characters within the altered suite (O'Keefe and Wagner 2001). Thus, correlated change within integrated modules allows both high disparity and high compatibility when independent change will not.

The integration/modularity reorganization model and the early bursts it induces is consistent the expected effects of Gene Regulatory Networks (Davidson and Erwin

2006) and Character Identity Networks (Wagner 2007). The impetus would be the rare circumstance in which one or more novelties generated by change to a character complex is an innovation (Erwin 2012) that outweighs any maladaptive effects of changing other characters in the same complex (Davidson and Erwin 2010). In principle, this would introduce strong selection for reducing integration or other linkages among characters, i.e., parcellation (Wagner 1996), in the same module as the innovation(s) (Polly 1998), which in turn would allow other characters to either return to functionally superior primitive conditions (creating stratigraphic incompatibility) or develop still different states (creating further disparity). If the innovation(s) opens up new ecologic opportunities and/or alters functional interactions with characters in other modules, then the stage is set for selection favoring reorganization of integration among other character modules (Davidson and Erwin 2006, Goswami 2006, Davidson and Erwin 2010, Erwin 2012). This might also provide a link between elevated origination and elevated disparity/evolvability if the innovation(s) in question affect origination/extinction probabilities (Erwin 2012, Rabosky et al. 2013). Subsequent evolution of integration networks within the new modules would later diminish evolvability and discourage additional disparity.

An integration/modularity reorganization model further erodes the false dichotomy between “developmental constraints” and “ecological restrictions” (Erwin 2007). If unusual ecological opportunities help create circumstances where the benefits of one novelty or a few novelties outweigh the drawbacks of associated changes (Polly 1998), then parcellation of modules due ecological pressures and any variation in developmental parameters should alter the ease in which taxa can achieve different combinations of character states and different adaptive peaks (Marshall 2014). If so, then examination of individual clades might suggest ecological “cues” associated with increases in disparity and low stratigraphic compatibility (see Gerber 2013).

A question that might arise is: given that all early bursts are actually “delayed bursts” within a larger clade (Hopkins and Smith 2015), why does elevated disparity always occur early in our prior definitions of taxa? A simple explanation is that: 1) systematists choose groups of species for phylogenetic (or disparity) analyses based on prior higher taxonomic definitions; and, 2) prior higher taxonomic definitions are based on amounts of difference and apparent “gaps” in character space separating that cluster of species from other clusters of species. Gaps in character space subsequently recognized by taxonomists as distinguishing higher taxa would be side effect of correlated changes followed by reorganization of sets of integrated or otherwise linked characters. In other words, the evolvability

and disparity accompanying integration/modularity reorganization produce the anatomical differences that systematists use to decide which taxa to include in phylogenetic analyses, and thus establishes the “early” portions of higher taxon histories (Davidson and Erwin 2006,2010).

Conclusion

We have long modeled early bursts using models assuming that individual characters had unusually high rates of evolution. Models concerning shifts intrinsic constraints and/or ecological limits simply assumed that these shifts depressed frequencies of independent change. However, these models are inadequate to explain the bursts of disparity and observed compatibility that we do see. Instead, the observed patterns are consistent with correlated change among suites of characters rapidly elevating disparity, with subsequent changes including not simply novel character states that further add to disparity, but uncoupling of existing linkages that allow for reversals to prior conditions. Thus, modeling expected morphological change early in the evolution of major groups should explicitly allow for not just elevated rates, but also correlated change followed by independent change in some suites of characters.

References

- Abdala, F. 2007. Redescription of *Platycraniellus elegans* (Therapsida, Cynodontia) from the Lower Triassic of South Africa, and the cladistic relationships of eutheriodonts. *Palaeontology* 50:591 - 618.
- Abdala, F., and A. M. Ribeiro. 2003. A new traversodontid cynodont from the Santa Maria Formation (Ladinian-Carnian) of southern Brazil, with a phylogenetic analysis of Gondwanan traversodontids. *Zoological Journal of the Linnean Society* 139:529 - 545.
- Adrain, J. M. 1998. Systematics of the Acanthoparyphinae (Trilobita), with species from the Silurian of Arctic Canada. *Journal of Paleontology* 72:698 - 718.
- Adrain, J. M., B. D. E. Chatterton, and G. J. Kloc. 2008. Systematics of the Koneprusiine trilobites, with new taxa from the Silurian and Devonian of Laurentia. *Journal of Paleontology* 82:657-675.
- Adrain, J. M., and G. D. Edgecombe. 1997. Silurian (Wenlock) calymenid trilobites from the Cape Phillips Formation, Central Canadian Arctic. *Journal of Paleontology* 71:657 - 682.
- Adrain, J. M., S. R. Westrop, E. Landing, and R. A. Fortey. 2001. Systematics of the Ordovician trilobites *Ischyrotoma* and *Dimeropygiella*, with species from the type Ibexian area, western U.S.A. *Journal of Paleontology* 75:947 – 971.

- Ahlberg, P. E., J. A. Clack, E. Luksevics, H. Blom, and I. Zupins. 2008. *Ventastega curonica* and the origin of tetrapod morphology. *Nature* 453:1199-1204.
- Alroy, J. 1995. Continuous track analysis: a new phylogenetic and biogeographic method. *Systematic Biology* 44:152 - 178.
- Amati, L., R. M. Feldmann, and J.-P. Zonneveld. 2004. A new family of Triassic lobsters (Decapoda: Astacidea) from British Columbia and its phylogenetic context. *Journal of Paleontology* 78:150-168.
- Amati, L., and S. R. Westrop. 2004. A systematic revision of *Thaleops* (Trilobita: Illaenidae) with new species from the Middle and Late Ordovician of Oklahoma and New York. *Journal of Systematic Palaeontology* 2:207-256.
- Andres, B., J. M. Clark, and X. Xing. 2010. A new rhamphorhynchid pterosaur from the Upper Jurassic of Xinjiang, China, and the phylogenetic relationships of basal pterosaurs. *Journal of Vertebrate Paleontology* 30:163 - 187.
- Angielczyk, K. D. 2002. Redescription, phylogenetic position, and stratigraphic significance of the dicynodont genus *Odontocyclops* (Synapsida: Anomodontia). *Journal of Paleontology* 76:1047 - 1059.
- . 2007. New specimens of the Tanzanian dicynodont “*Cryptocynodon parringtoni*” von Huene, 1942 (Therapsida, Anomodontia), with an expanded analysis of Permian dicynodont phylogeny. *Journal of Vertebrate Paleontology* 27:116 - 131.
- Archibald, J. D., A. O. Averianov, and E. G. Ekdale. 2001. Late Cretaceous relatives of rabbits, rodents, and other extant eutherian mammals. *Nature* 414:62-65.
- Arratia, G. 1996. Reassessment of the phylogenetic relationships of certain Jurassic teleosts and their implications on teleostean phylogeny. Pp. 219 - 242 in G. Arratia and G. Viohl, eds. *Mesozoic Fishes – Systematics and Paleoecology*. Verlag, München.
- Arratia, G., and H. Tischlinger. 2010. The first record of Late Jurassic crossognathiform fishes from Europe and their phylogenetic importance for teleostean phylogeny. *Fossil Record* 13:317-341.
- Ausich, W. I. 1998a. Early phylogeny and subclass division of the Crinoidea (Phylum Echinodermata). *Journal of Paleontology* 72:499 - 510.
- . 1998b. Phylogeny of Arenig to Caradoc crinoids (Phylum Echinodermata) and suprageneric classification of the Crinoidea. *The University of Kansas Paleontological Contributions* 9:1 - 36.
- Ausich, W. I., and T. W. Kammer. 2008. Evolution and extinction of a Paleozoic crinoid clade: phylogenetics, paleogeography, and environmental distribution of the periechocrinids. Pp. 145 - 171 in W. I. Ausich and G. D. Webster, eds. *Echinoderm paleobiology*. Indiana University Press, Bloomington.

- Babcock, L. E. 1994. Systematics and phylogenetics of polymeroid trilobites from the Henson Gletscher and Kap Stanton Formations (Middle Cambrian), North Greenland. *Grønlands Geologiske Undersøgelse Bulletin* 169:79 - 127.
- Barras, C. G. 2007. Phylogeny of the Jurassic to Early Cretaceous ‘disasteroid’ echinoids (Echinoidea; Echinodermata) and the origins of spatangoids and holasteroids. *Journal of Systematic Palaeontology* 5:133 - 161.
- Bell, G. L., Jr. 1997. A phylogenetic revision of North American and Adriatic Mosasauroidea. Pp. 293 - 332 in J. M. Callaway and E. L. Nicholls, eds. *Ancient marine reptiles*. Academic Press, San Diego.
- Benedetto, J. 2009. *Chaniella* a new lower Tremadocian (Ordovician) brachiopod from northwestern Argentina and its phylogenetic relationships within basal rhynchonelliforms. *Paläontologische Zeitschrift* 83:393-405.
- Benson, R., M. Carrano, and S. Brusatte. 2010. A new clade of archaic large-bodied predatory dinosaurs (Theropoda: Allosauroidea) that survived to the latest Mesozoic. *Naturwissenschaften* 97:71-78.
- Benson, R. B. J. 2012. Interrelationships of basal synapsids: cranial and postcranial morphological partitions suggest different topologies. *Journal of Systematic Palaeontology* 10:601-624.
- Bentley, C. J., and J. B. Jago. 2004. Wuaniid trilobites of Australia. *Memoirs of the Association of Australasian Palaeontologists* 30:179 - 191.
- Bisconti, M. 2007. A new basal balaenopterid whale from the Pliocene of northern Italy. *Palaeontology* 50:1103 - 1122.
- Blake, D. B. 2010. *Comptoniaster adamsi* nov. sp. (Echinodermata, Asteroidea) from the middle Cretaceous of Texas and its phylogenetic position. *Geobios* 43:179-190.
- Bloch, J. I., D. C. Fisher, K. D. Rose, and P. D. Gingerich. 2001. Stratocladistic analysis of Paleocene Carpolestidae (Mammalia, Plesiadapiformes) with description of a new late Tiffanian genus. *Journal of Vertebrate Paleontology* 21:119–131.
- Bodenbender, B. E. 1995. Morphological, crystallographic, and stratigraphic data in cladistic analyses of blastoid phylogeny. *Contributions from the Museum of Paleontology, the University of Michigan* 29:201 - 257.
- Boisserie, J.-R. 2005. The phylogeny and taxonomy of Hippopotamidae (Mammalia: Artiodactyla): a review based on morphology and cladistic analysis. *Zoological Journal of the Linnean Society* 143:1 - 26.
- Botha, J., F. Abdala, and R. Smith. 2007. The oldest cynodont: new clues on the origin and early diversification of the Cynodontia. *Zoological Journal of the Linnean Society* 149:477-492.

- Brayard, A., G. Escarguel, H. Bucher, C. Monnet, T. Bruhwiler, N. Goudemand, T. Galfetti, and J. Guex. 2009. Good genes and good luck: ammonoid diversity and the End-Permian Mass Extinction. *Science* 325:1118 - 1121.
- Brezinski, D. K. 2003. Evolutionary and biogeographical implications of phylogenetic analysis of the Late Palaeozoic trilobite *Paladin*. *Special Papers in Palaeontology* 70:363 - 375.
- . 2005. Paleobiogeographic patterns in Late Mississippian trilobites of the United States with new species from Montana. *Annals of the Carnegie Museum* 74:77 - 89.
- Brochu, C. A. 1997. Morphology, fossils, divergence timing, and the phylogenetic relationships of *Gavialis*. *Systematic Biology* 46:479 - 522.
- Brower, J. C. 2001. Flexible crinoids from the Upper Ordovician Maquoketa formation of the northern midcontinent and the evolution of early flexible crinoids. *Journal of Paleontology* 75:370 - 382.
- Brusatte, S. L., M. J. Benton, J. B. Desojo, and M. C. Langer. 2010a. The higher-level phylogeny of Archosauria (Tetrapoda: Diapsida). *Journal of Systematic Palaeontology* 8:3 - 47.
- Brusatte, S. L., M. A. Norell, T. D. Carr, G. M. Erickson, J. R. Hutchinson, A. M. Balanoff, G. S. Bever, J. N. Choiniere, P. J. Makovicky, and X. Xu. 2010b. Tyrannosaur paleobiology: new research on ancient exemplar organisms. *Science* 329:1481-1485.
- Campbell, M. J., and B. D. E. Chatterton. 2007. Late Ordovician and Silurian lichid trilobites from Northwestern Canada: *Hemiarges*, *Borealarges*, and *Richterarges*. *Journal of Paleontology* 81:1348 - 1364.
- Candela, Y. 2010. Phylogenetic relationships of leptellinid brachiopods. *Alcheringa* 35:413-426.
- Carlini, A. A., M. R. Ciancio, J. J. Flynn, G. J. Scillato-Yané, and A. R. Wyss. 2009. The phylogenetic and biostratigraphic significance of new armadillos (Mammalia, Xenarthra, Dasypodidae, Euphractinae) from the Tinguirirican (Early Oligocene) of Chile. *Journal of Systematic Palaeontology* 7:489-503.
- Carlson, S. J., and P. C. Fitzgerald. 2007. Sampling taxa, estimating phylogeny and inferring macroevolution: an example from Devonian terebratulide brachiopods. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* 98:311-325.
- Carr, R. K., and W. J. Hlavin. 2010. Two new species of *Dunkleosteus* Lehman, 1956, from the Ohio Shale Formation (USA, Famennian) and the Kettle Point Formation (Canada, Upper Devonian), and a cladistic analysis of the Eubrachythoraci (Placodermi, Arthrodira). *Zoological Journal of the Linnean Society* 159:195 - 222.

- Carrano, M. T., and S. D. Sampson. 2008. The phylogeny of Ceratosauria (Dinosauria). *Journal of Systematic Palaeontology* 6:183-236.
- Cavin, L., V. Suteethorn, E. Buffetaut, and H. Tong. 2007. A new Thai Mesozoic lungfish (Sarcopterygii, Dipnoi) with an insight into post-Palaeozoic dipnoan evolution. *Zoological Journal of the Linnean Society* 149:141-177.
- Chatterton, B. D. E., G. D. Edgecombe, B. G. Waisfeld, and N. E. Vaccari. 1998. Ontogeny and systematics of Toernquistiidae (Trilobita, Proetida) from the Ordovician of the Argentine Precordillera. *Journal of Paleontology* 72:273 - 303.
- Christiansen, P., and N. Bonde. 2002. A new species of gigantic mosasaur from the Late Cretaceous of Israel. *Journal of Vertebrate Paleontology* 22:629 - 644.
- Ciampaglio, C. N. 2002. Determining the role that ecological and developmental constraints play in controlling disparity: examples from the crinoid and blastozoan fossil record. *Evolution and Development* 4:170 - 188.
- Cisneros, J. C. 2008. Phylogenetic relationships of procolophonid parareptiles with remarks on their geological record. *Journal of Systematic Palaeontology* 6:345-366
- Clement, G. 2005. A new coelacanth (Actinistia, Sarcopterygii) from the Jurassic of France, and the question of the closest fossil relative to Latimeria. *Journal of Vertebrate Paleontology* 25:481 - 491.
- Cloutier, R. 1991. Patterns, trends and rates of evolution within the Actinistia. *Environmental Biology of Fishes* 32:23 - 58.
- Cloutier, R., and P. E. Ahlberg. 1995. Morphology, characters, and the interrelationships of basal sarcopterygians. Pp. 445 - 479 in M. L. J. Stiassny and L. Parenti, eds. *Interrelationships of fishes, II*. Academic Press, London.
- Congreve, C. R., and B. S. Lieberman. 2010. Phylogenetic and biogeographic analysis of deiphonine trilobites. *Journal of Paleontology* 84:128 – 136.
- . 2011. Phylogenetic and biogeographic analysis of sphaerexochine trilobites. *PLoS ONE* 6:e21304.
- Cotton, T. J. 2001. The phylogeny and systematics of blind Cambrian ptychoparioid trilobites. *Palaeontology* 44:167 - 207.
- Cotton, T. J., and S. J. Braddy. 2003. The phylogeny of arachnomorph arthropods and the origin of the Chelicerata. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* 94:169-193.
- Cotton, T. J., and R. A. Fortey. 2005. Comparative morphology and relationships of the Agnostida. Pp. 95-136 in S. Koenemann and R. A. Jenner, eds. *Crustacea and arthropod relationships*. Taylor & Francis, Boca Raton.
- Cripps, A. P. 1991. A cladistic analysis of the cornutes (stem chordates). *Zoological Journal of the Linnean Society* 102:333 - 366.

- Crônier, C. 2003. Systematic relationships of the blind phacopine trilobite *Trimerocephalus*, with a new species from Causses-et-Veyran, Montagne Noire. *Acta Palaeontologica Polonica* 48:55 - 70.
- Cusack, M., A. Williams, and J. O. Buckman. 1999. Chemico-structural evolution of linguloid brachiopod shells. *Palaeontology* 42:799 - 840.
- D'Emic, M. D. 2012. The early evolution of titanosauriform sauropod dinosaurs. *Zoological Journal of the Linnean Society* 166:624-671.
- Daley, P. E. J. 1992. The anatomy of the solute *Girvanicystis batheri* (?Chordata) from the Upper Ordovician of Scotland and a new species of *Girvanicystis* from the Upper Ordovician of South Wales. *Zoological Journal of the Linnean Society* 105:353 - 375.
- Damiani, R. J. 2001. A systematic revision and phylogenetic analysis of Triassic mastodonsauroids (Temnospondyli: Stereospondyli). *Zoological Journal of the Linnean Society* 133:379 – 482.
- Damiani, R. J., C. Vasconcelos, A. Renaut, J. Hancox, and A. Yates. 2007. *Dolichuranus primaevus* (Therapsida: Anomodontia) from the Middle Triassic of Namibia and its phylogenetic relationships. *Palaeontology* 50:1531 - 1546.
- Dashzeveg, D., and J. Meng. 1998. New Eocene ctenodactyloid rodents from the Eastern Gobi Desert of Mongolia and a phylogenetic analysis of ctenodactyloids based on dental features. *American Museum Novitates* 3246:1 - 20.
- Davidson, E. H., and D. H. Erwin. 2006. Gene Regulatory Networks and the evolution of animal body plans. *Science* 311:796-800.
- Davidson, E. H., and D. H. Erwin. 2010. Evolutionary innovation and stability in animal gene networks. *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution* 314B:182-186.
- de Maintenon, M. J. 2005. Phylogenetic relationships of the tropical American columbellid taxa *Conella*, *Eurypyrene*, and *Parametaria* (Gastropoda: Neogastropoda). *Journal of Paleontology* 79:497 - 508.
- Dean Shackleton, J. 2005. Skeletal homologies, phylogeny and classification of the earliest asterozoan echinoderms. *Journal of Systematic Palaeontology* 3:29-114.
- Dewing, K. 2004. Shell structure and its bearing on the phylogeny of Late Ordovician-Early Silurian strophomenoid brachiopods from Anticosti Island, Quebec. *Journal of Paleontology* 78:275 - 286.
- Dietze, K. 2000. A revision of paramblypterid and amblypterid actinopterygians from Upper Carboniferous - Lower Permian lacustrine deposits of Central Europe. *Palaeontology* 43:927 - 966.
- Dilkes, D. W. 1998. The early Triassic rhynchosaur *Mesosuchus browni* and the interrelationships of basal archosauromorph reptiles. *Philosophical*

- Transactions of the Royal Society of London Series B: Biological Sciences 353:501 - 541.
- Donoghue, P. C. J. 2001. Conodonts meet cladistics: recovering relationships and assessing the completeness of the fossil record. *Palaeontology* 44:65 - 93.
- Dortangs, R. W., A. S. Schulp, E. W. A. Mulder, J. W. M. Jagt, H. H. G. Peeters, and D. T. d. Graaf. 2002. A large new mosasaur from the Upper Cretaceous of the Netherlands. *Netherlands Journal of Geosciences* 81:1 - 8.
- Dupret, V. 2004. The phylogenetic relationships between actinolepids (Placodermi: Arthrodira) and other arthrodire (phlyctaeniids and brachythoracids). *Fossils and Strata* 50:44 - 55.
- Dupret, V., and M. Zhu. 2007. The earliest phyllolepid (Placodermi, Arthrodira) from the Late Lochkovian (Early Devonian) of Yunnan (South China). *Geological Magazine* 145:257 - 278.
- Ebach, M. C. 2002. Lower Devonian trilobites from Cobar, New South Wales. *Records of the Western Australian Museum* 20:353 - 378.
- Ebach, M. C., and S. T. Ah Yong. 2001. Phylogeny of the trilobite subgenus *Acanthopyge* (*Lobopyge*). *Cladistics* 17:1 - 10.
- Ebbestad, J. O. R., and G. E. Budd. 2002. Burlingiid trilobites from Norway, with a discussion of their affinities and relationships. *Palaeontology* 45:1171 - 1195.
- Eble, G. J. 2004. The macroevolution of phenotypic integration. Pp. 253 - 273 in M. Pigliucci and K. Preston, eds. *Phenotypic integration: studying the ecology and evolution of complex phenotypes*. Oxford University Press, Oxford.
- Edgecombe, G., and L. Ramsköld. 1994. Earliest Devonian phacopide trilobites from central Bolivia. *Paläontologische Zeitschrift* 68:397-410.
- Erwin, D. H. 2007. Disparity: morphological pattern and developmental context. *Palaeontology* 50:57-73.
- . 2012. Novelties that change carrying capacity. *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution* 318:460 - 465.
- Estabrook, G. F., C. S. Johnson, Jr., and F. R. McMorris. 1975. An idealized concept of the true cladistic character. *Mathematical Biosciences* 23:263 - 272.
- Estabrook, G. F., and F. R. McMorris. 2006. The compatibility of stratigraphic and comparative constraints on estimates of ancestor–descendant relations. *Systematics and Biodiversity* 4:9 - 17.
- Finarelli, J. A., and W. C. Clyde. 2004. Reassessing hominoid phylogeny: evaluating congruence in the morphological and temporal data. *Paleobiology* 30:614 - 651.
- Foote, M. 1991. Morphological and taxonomic diversity in a clade's history: the blastoid record and stochastic simulations. *Contributions from the Museum of Paleontology, the University of Michigan* 28:101 - 140.

-
- _____. 1992. Paleozoic record of morphological diversity in blastozoan echinoderms. *Proceedings of the National Academy of Sciences, USA* 89:7325 - 7329.
- _____. 1993a. Discordance and concordance between morphological and taxonomic diversity. *Paleobiology* 19:185 - 204.
- _____. 1993b. Contributions of individual taxa to overall morphological disparity. *Paleobiology* 19:403 - 419.
- _____. 1994. Morphological disparity in Ordovician - Devonian crinoids and the early saturation of morphological space. *Paleobiology* 20:320 - 344.
- _____. 1996a. Models of morphologic diversification. Pp. 62 - 86 in D. Jablonski, D. H. Erwin and J. H. Lipps, eds. *Evolutionary paleobiology: essays in honor of James W. Valentine*. University of Chicago Press, Chicago.
- _____. 1996b. Ecological controls on the evolutionary recovery of Post-Paleozoic crinoids. *Science* 274:1492 - 1495.
- Foot, M., J. P. Hunter, C. M. Janis, and J. J. Sepkoski, Jr. 1999. Evolutionary and preservational constraints on origins of biologic groups: divergence times of eutherian mammals. *Science* 283:1310 - 1314.
- Forey, P. L. 1991. *Latimeria chalumnae* and its pedigree. *Environmental Biology of Fishes* 32:75 - 97.
- Friedman, M. 2007. The interrelationships of Devonian lungfishes (Sarcopterygii: Dipnoi) as inferred from neurocranial evidence and new data from the genus *Soederberghia* Lehman, 1959. *Zoological Journal of the Linnean Society* 151:115-171.
- Fröbisch, J. 2007. The cranial anatomy of *Kombuisia frerensis* Hotton (Synapsida, Dicynodontia) and a new phylogeny of anomodont therapsids. *Zoological Journal of the Linnean Society* 150:117-144.
- Froehlich, D. J. 2002. Quo vadis *Eohippus*? The systematics and taxonomy of the early Eocene equids (Perissodactyla). *Zoological Journal of the Linnean Society* 134:141 - 256.
- Gahn, F. J., and T. W. Kammer. 2002. The cladid crinoid *Barycrinus* from the Burlington Limestone (Early Osagean) and the phylogenetics of Mississippian botryocrinids. *Journal of Paleontology* 76:123 - 133.
- Gasparini, Z., D. Pol, and L. A. Spalletti. 2006. An unusual marine crocodyliform from the Jurassic-Cretaceous boundary of Patagonia. *Science* 311:70-73.
- Gelfo, J. N., G. M. Lopez, and M. Bond. 2008. A new Xenungulata (Mammalia) from the Paleocene of Patagonia, Argentina. *Journal of Paleontology* 82:329 - 335.
-

- Geraads, D., C. Blondel, A. Likius, H. T. Mackaye, P. Vignaud, and M. Brunet. 2008. New Hippotragini (Bovidae, Mammalia) from the Late Miocene of Toros-Menalla (Chad). *Journal of Vertebrate Paleontology* 28:231-242.
- Gerber, S. 2013. On the relationship between the macroevolutionary trajectories of morphological integration and morphological disparity. *PLoS One* 8:e63913.
- Gerber, S., G. J. Eble, and P. Neige. 2011. Developmental aspects of morphological disparity dynamics: a simple analytical exploration. *Paleobiology* 37:237-251.
- Goin, F. J., A. M. Candela, M. A. Abello, and E. V. Oliveira. 2009. Earliest South American paucituberculatans and their significance in the understanding of 'pseudodiprotodont' marsupial radiations. *Zoological Journal of the Linnean Society* 155:867-884.
- Goswami, A. 2006. Cranial modularity shifts during mammalian evolution. *The American Naturalist* 168:270-280.
- Goswami, A., and P. D. Polly. 2010. The influence of modularity on cranial morphological disparity in Carnivora and Primates (Mammalia). *PLoS One* 5:e9517.
- Grande, L., and W. E. Bemis. 1998. A comprehensive phylogenetic study of Amiid fishes (Amiidae) based on comparative skeletal anatomy. An empirical search for interconnected patterns of natural history. *Memoirs of the Society of Vertebrate Paleontology* 4:1 - 690.
- Grégoire, M., J. Guo, and K. C. Beard. 2004. A new small dichobunid artiodactyl from Shanghuang (Middle Eocene, eastern China): implications for the early evolution of proto-selenodonts in Asia. *Bulletin of Carnegie Museum of Natural History* 36:177-197.
- Haasl, D. M. 2000. Phylogenetic relationships among nassariid gastropods. *Journal of Paleontology* 74:839 - 852.
- Hanger, R. A., and E. E. Strong. 2000. Phylogeny of the Anopliidae (Brachiopoda: Chonetidina). *Historical Biology* 14:285 - 298.
- Harmon, L. J., J. B. Losos, T. Jonathan Davies, R. G. Gillespie, J. L. Gittleman, W. Bryan Jennings, K. H. Kozak, M. A. McPeck, F. Moreno-Roark, T. J. Near, A. Purvis, R. E. Ricklefs, D. Schluter, J. A. Schulte II, O. Seehausen, B. L. Sidlauskas, O. Torres-Carvajal, J. T. Weir, and A. Ø. Mooers. 2010. Early bursts of body size and shape evolution are rare in comparative data. *Evolution* 64:2385-2396.
- Harris, J. D. 2006. The significance of *Suuwassea emilieae* (Dinosauria: Sauropoda) for flagellicaudatan intrarelationships and evolution. *Journal of Systematic Palaeontology* 4:185 - 198.

- Harrison, L., and H. C. E. Larsson. 2015. Among-character rate variation distributions in phylogenetic analysis of discrete morphological characters. *Systematic Biology* 64:307 - 324.
- Harvey, E. W., and W. I. Ausich. 1997. Phylogeny of calceocrinid crinoids (Paleozoic: Echinodermata): biogeography and mosaic evolution. *Journal of Paleontology* 71:299 - 305.
- Holbrook, L. T. 2001. Comparative osteology of early Tertiary tapiromorphs (Mammalia, Perissodactyla). *Zoological Journal of the Linnean Society* 132:1 - 54.
- Hooker, J. J., and D. Dashzeveg. 2004. The origin of chalicotheres (Perissodactyla, Mammalia). *Palaeontology* 47:1363 – 1386.
- Hooker, J. J., and D. E. Russell. 2012. Early Palaeogene Louisinidae (Macroscelidea, Mammalia), their relationships and north European diversity. *Zoological Journal of the Linnean Society* 164:856-936.
- Hopkins, M. J. 2011. Species-level phylogenetic analysis of pterocephaliids (Trilobita, Cambrian) from the Great Basin, Western USA. *Journal of Paleontology* 85:1128-1153.
- Hopkins, M. J., and A. B. Smith. 2015. Dynamic evolutionary change in post-Paleozoic echinoids and the importance of scale when interpreting changes in rates of evolution. *Proceedings of the National Academy of Sciences* 112:3758–3763.
- Hopkins, S. S. B. 2008. Phylogeny and evolutionary history of the Aplodontoidea (Mammalia: Rodentia). *Zoological Journal of the Linnean Society* 153:769-838.
- Hoyal Cuthill, J. 2015. The size of the character state space affects the occurrence and detection of homoplasy: Modelling the probability of incompatibility for unordered phylogenetic characters. *Journal of Theoretical Biology* 366:24-32.
- Huelsenbeck, J. P. 1994. Comparing the stratigraphic record to estimates of phylogeny. *Paleobiology* 20:470 - 483.
- Hughes, M., S. Gerber, and M. A. Wills. 2013. Clades reach highest morphological disparity early in their evolution. *Proceedings of the National Academy of Sciences* 110:13875-13879.
- Hughes, N. C., and A. W. A. Rushton. 1990. Computer-aided restoration of a Late Cambrian ceratopygid trilobite from Wales, and its phylogenetic implications. *Palaeontology* 33:429-445.
- Huttenlocker, A. 2009. An investigation into the cladistic relationships and monophyly of therocephalian therapsids (Amniota: Synapsida). *Zoological Journal of the Linnean Society* 157:865-891.
- Huttenlocker, A. K., C. A. Sidor, and R. M. H. Smith. 2011. A new specimen of *Promoschorhynchus* (Therapsida: Therocephalia: Akidnognathidae) from the

- Lower Triassic of South Africa and its implications for theriodont survivorship across the Permo-Triassic boundary. *Journal of Vertebrate Paleontology* 31:405-421.
- Hwang, S. H., M. A. Norell, J. I. Qiang, and G. A. O. Keqin. 2002. New specimens of *Microraptor zhaoianus* (Theropoda: Dromaeosauridae) from northeastern China. *American Museum Novitates* 381:1 - 44.
- Jeffery, C. H. 1999. A reappraisal of the phylogenetic relationships of somaliasterid echinoids. *Palaeontology* 42:1027 - 1042.
- Jeffery, C. H., and R. B. Emlet. 2003. Macroevolutionary consequences of developmental mode in temnopleurid echinoids from the Tertiary of Southern Australia. *Evolution* 57:1031-1048.
- Jiang, H., R. J. Aldridge, X. Lai, C. Yan, and Y. Sun. 2011. Phylogeny of the conodont genera *Hindeodus* and *Isarcicella* across the Permian–Triassic boundary. *Lethaia* 44:374 - 382.
- Jin, J., and L. E. Popov. 2008. A new genus of Late Ordovician-Early Silurian pentameride brachiopods and its phylogenetic relationships. *Acta Palaeontologica Polonica* 53:221-236.
- Johanson, Z., J. A. Long, J. A. Talent, P. Janvier, and J. W. Warren. 2006. Oldest coelacanth, from the Early Devonian of Australia. *Biology Letters* 2:443-446.
- Johnson, H. G., D. K. Elliott, and J. H. Wittke. 2000. A new actinolepid arthrodire (Class Placodermi) from the Lower Devonian Sevy Dolomite, east-central Nevada. *Zoological Journal of the Linnean Society* 129:241 – 266.
- Joyce, W. G. 2007. Phylogenetic relationships of Mesozoic turtles. *Bulletin of the Peabody Museum of Natural History* 48:3-102.
- Kammer, T. W., and F. J. Gahn. 2003. Primitive cladid crinoids from the early Osagean Burlington Limestone and the phylogenetics of Mississippian species of *Cyathocrinites*. *Journal of Paleontology* 77:121 - 138.
- Kammerer, C. F., J. J. Flynn, L. Ranivoharimanana, and R. R. Wyss. 2008. New material of *Menadon besairiei* (Cynodontia: Traversodontidae) from the Triassic of Madagascar. *Journal of Vertebrate Paleontology* 28:445-462.
- Karasawa, H., and C. E. Schweitzer. 2006. A new classification of the Xanthoidea sensu lato (Crustacea: Decapoda: Brachyura) based on phylogenetic analysis and traditional systematics and evaluation of all fossil Xanthoidea sensu lato. *Contributions to Zoology* 75:23 - 73.
- Kellner, A. W. A., A. E. P. Pinheiro, and D. A. Campos. 2014. A new sebecid from the Paleogene of Brazil and the crocodyliform radiation after the K–Pg Boundary. *PLoS ONE* 9:e81386.
- Kielan-Jaworowska, Z., and J. H. Hurum. 2001. Phylogeny and systematics of multituberculate mammals. *Palaeontology* 44:389-429.

- Kohno, N. 2006. A new Miocene odobenid (Mammalia: Carnivora) from Hokkaido, Japan, and its implications for odobenid phylogeny. *Journal of Vertebrate Paleontology* 26:411-421.
- Korn, D. 1997. Evolution of the Goniatitaceae and Viséan-Namurian biogeography. *Acta Palaeontologica Polonica* 42:177 - 199.
- Kroh, A. 2007. *Hemipatagus*, a misinterpreted lovenioid (Echinodermata: Echinoidea). *Journal of Systematic Palaeontology* 5:163 - 192.
- Lamsdell, J. C., S. J. Braddy, and O. E. Tetlie. 2010. The systematics and phylogeny of the Stylonurina (Arthropoda: Chelicerata: Eurypterida). *Journal of Systematic Palaeontology* 8:49 - 61.
- Laurin, M., and R. Soler-Gijón. 2006. The oldest known stegocephalian (Sarcopterygii: Temnospondyli) from Spain. *Journal of Vertebrate Paleontology* 26:284 - 299.
- Le Quesne, W. J. 1969. A method of selection of characters in numerical taxonomy. *Systematic Zoology* 18:201 - 205.
- Lee, S.-b., D.-C. Lee, and D. K. Choi. 2008. Cambrian-Ordovician trilobite family Missisquoiidae Hupè, 1955: systematic revision and palaeogeographical considerations based on cladistic analysis. *Palaeogeography, Palaeoclimatology, Palaeoecology* 260:315-341.
- Lefebvre, B. 2001. A critical comment on ‘ankyroids’ (Echinodermata, Stylophora). *Geobios* 34:597 - 627.
- Leighton, L. R., and C. G. Maples. 2002. Evaluating internal versus external characters: phylogenetic analyses of the Echinoconchidae, Buxtoniinae, and Juresaniinae (Phylum: Brachiopoda). *Journal of Paleontology* 76:659 - 671.
- Lieberman, B. S. 1993. Systematics and biogeography of the “*Metacryphaeus* group” Calmoniidae (Trilobita, Devonian), with comments on adaptive radiations and the geological history of the Malvinokaffric Realm. *Journal of Paleontology* 67:549 - 570.
- . 1994. Evolution of the trilobite subfamily Proetinae Salter, 1864, and the origin, diversification, evolutionary affinity, and extinction of the Middle Devonian proetid fauna of eastern North America. *Bulletin of the American Museum of Natural History* 223:1 - 176.
- . 1999. Testing the Darwinian legacy of the Cambrian radiation using trilobite phylogeny and biogeography. *Journal of Paleontology* 73:176 - 181.
- . 2001. Phylogenetic analysis of the Olenellina Walcott, 1890 (Trilobita, Cambrian). *Journal of Paleontology* 75:96 - 115.
- . 2002. Phylogenetic analysis of some basal Early Cambrian trilobites, the biogeographic origins of the Eutrilobita, and the timing of the Cambrian radiation. *Journal of Paleontology* 76:692-708.

- Lieberman, B. S., G. D. Edgecombe, and N. Eldredge. 1991. Systematics and biogeography of the “*Malvinella* group,” Calmoniidae (Trilobita, Devonian). *Journal of Paleontology* 65:824 - 843.
- Lieberman, B. S., and G. J. Kloc. 1997. Evolutionary and biogeographic patterns in the Asteropyginae (Trilobita, Devonian) Delo, 1935. *Bulletin of the American Museum of Natural History* 232:1 - 127.
- López-Antoñanzas, R., and S. Sen. 2006. New Saudi Arabian Miocene jumping mouse (Zapodidae): systematics and phylogeny. *Journal of Vertebrate Paleontology* 26:170-181.
- López-Arbarello, A. 2012. Phylogenetic interrelationships of ginglymodian fishes (Actinopterygii: Neopterygii). *PLoS ONE* 7:e39370.
- López-Arbarello, A., and A. M. Zavattieri. 2008. Systematic revision of *Pseudobeaconia* Bordas, 1944, and *Mendocinichthys* Whitley, 1953 (Actinopterygii: 'Perleidiformes') from the Triassic of Argentina. *Palaeontology* 51:1025 - 1052.
- Lü, J., D. M. Unwin, X. Jin, Y. Liu, and Q. Ji. 2010. Evidence for modular evolution in a long-tailed pterosaur with a pterodactyloid skull. *Proceedings of the Royal Society B: Biological Sciences* 277:383 - 389.
- Lupia, R. 1999. Discordant morphological disparity and taxonomic diversity during the Cretaceous angiosperm radiation: North American pollen record. *Paleobiology* 25:1 - 28.
- Lyson, T. R., and W. G. Joyce. 2009. A new species of *Palatobaena* (Testudines: Baenidae) and a Maximum Parsimony and Bayesian phylogenetic analysis of Baenidae. *Journal of Paleontology* 83:457 - 470.
- Makovicky, P. J., and M. A. Norell. 2006. *Yamaceratops dorn gobiensis*, a new primitive ceratopsian (Dinosauria: Ornithischia) from the Cretaceous of Mongolia. *American Museum Novitates* 3530:1 - 42.
- Makovicky, P. J., and H.-D. Sues. 1998. Anatomy and phylogenetic relationships of the theropod dinosaur *Microvenator celer* from the Lower Cretaceous of Montana. *American Museum Novitates* 3240:1 - 27.
- Marivaux, L., M. Adaci, M. Bensalah, H. G. Rodrigues, L. Hautier, M. h. Mahboubi, F. Mebrouk, R. Tabuce, and M. Vianey-Liaud. 2011. Zegdoumyidae (Rodentia, Mammalia), stem anomaluroid rodents from the Early to Middle Eocene of Algeria (Gour Lazib, Western Sahara): new dental evidence. *Journal of Systematic Palaeontology* 9:563-588.
- Marshall, C. R. 2014. The evolution of morphogenetic fitness landscapes: conceptualising the interplay between the developmental and ecological drivers of morphological innovation. *Australian Journal of Zoology* 62:3-17.
- McDonald, A. T. 2012. Phylogeny of basal iguanodonts (Dinosauria: Ornithischia): an update. *PLoS ONE* 7:e36745.

- McGowan, A. J., and A. B. Smith. 2007. Ammonoids across the Permian/Triassic boundary: a cladistic perspective. *Palaeontology* 50:573-590.
- Meacham, C. A. 1984. The role of hypothesized direction of characters in the estimation of evolutionary history. *Taxon* 33:26-38.
- Merle, D., and J.-M. Pacaud. 2003. New species of *Eocithara* Fischer, 1883 (Mollusca, Gastropoda, Harpidae) from the Early Paleogene with phylogenetic analysis of the Harpidae. *Geodiversitas* 26:61 - 87.
- Métais, G. 2006. New basal selenodont artiodactyls from the Pondaung Formation (Late Middle Eocene, Myanmar and the phylogenetic relationships of early ruminants. *Annals of Carnegie Museum* 75:51 - 67.
- Métais, G., J. Guo, and K. C. Beard. 2004. A new small dichobunid artiodactyl from Shanghuang (Middle Eocene, Eastern China): Implications for the early evolution of proto-selenodonts in Asia. *Bulletin of Carnegie Museum of Natural History* 36:177-197.
- Michaux, B. 1989. Cladograms can reconstruct phylogenies: an example from the fossil record. *Alcheringa* 13:21 - 36.
- Mihlbachler, M. C. 2008. Species taxonomy, phylogeny, and biogeography of the Brontotheriidae (Mammalia: Perissodactyla). *Bulletin of the American Museum of Natural History* 311:1 - 475.
- Mitchell, S. F. 2013. Revision of the Antillocaprinidae Mac Gillavry (Hippuritida, Bivalvia) and their position within the Caprinoidea d'Orbigny. *Geobios* 46:423-446.
- Monari, S. 2009. Phylogeny and biogeography of pholadid Bivalve *Barnea* (*Anchomasa*) with considerations on the phylogeny of Pholadoidea. *Acta Palaeontologica Polonica* 54:315-335.
- Monks, N. 1999. Cladistic analysis of Albian heteromorph ammonites. *Palaeontology* 42:907 - 925.
- . 2000. Functional morphology, ecology, and evolution of the Scaphitaceae Gill, 1871 (Cephalopoda). *Journal of Molluscan Studies* 66:205-216.
- . 2002. Cladistic analysis of a problematic ammonite group: the Hamitidae (Cretaceous, Albian-Turonian) and proposals for new cladistic terms. *Palaeontology* 45:689 - 707.
- Motani, R. 1999. Phylogeny of the Ichthyopterygia. *Journal of Vertebrate Paleontology* 19:473 - 496.
- Nardin, E., and J. Bohatý. 2013. A new pleurocystitid blastozoan from the Middle Devonian of the Eifel (Germany) and its phylogenetic importance. *Acta Palaeontologica Polonica* 58:533-544.

- Nasif, N. L., S. Musalem, and E. Cerdeño. 2000. A new toxodont from the Late Miocene of Catamarca, Argentina, and a phylogenetic analysis of the Toxodontidae. *Journal of Vertebrate Paleontology* 20:591-600.
- Ni, X., J. Meng, K. C. Beard, D. L. Gebo, Y. Wang, and C. Li. 2010. A new tarkadectine primate from the Eocene of Inner Mongolia, China: phylogenetic and biogeographic implications. *Proceedings of the Royal Society B: Biological Sciences* 277:247-256.
- Nützel, A., D. H. Erwin, and R. H. Mapes. 2000. Identity and phylogeny of the Late Paleozoic Subulitoidea (Gastropoda). *Journal of Paleontology* 74:575 - 598.
- O'Keefe, F. R. 2001. A cladistic analysis and taxonomic revision of the Plesiosauria (Reptilia: Sauropterygia). *Acta Zoologica Fennica* 213:1 - 63.
- O'Keefe, F. R., and P. J. Wagner. 2001. Inferring and testing hypotheses of correlated character evolution by using character compatibility. *Systematic Biology* 50:657 - 675.
- Ösi, A. 2005. *Hungarosaurus tormai*, a new ankylosaur (Dinosauria) from the Upper Cretaceous of Hungary. *Journal of Vertebrate Paleontology* 25:370-383.
- Parsley, R. L. 1997. The echinoderm classes Stylophora and Homoiostelea: non Calcichordata. Pp. 225 - 248 in J. A. Waters and C. G. Maples, eds. *Geobiology of echinoderms*. The Paleontological Society, Knoxville.
- Parsley, R. L., and C. D. Sumrall. 2007. New recumbent echinoderm genera from the Bois d'Arc Formation: Lower Devonian (Lochkovian) of Coal County, Oklahoma. *Journal of Paleontology* 81:1486–1493.
- Paterson, J. R., and G. D. Edgecombe. 2006. The Early Cambrian trilobite family Emuellidae Pocock, 1970: systematic position and revision of Australian species. *Journal of Paleontology* 80:496-513.
- Patterson, C. 1982. Morphological characters and homology. Pp. 21 - 74 in K. A. Joysey and A. E. Friday, eds. *Problems of phylogenetic reconstruction*. Academic Press, London.
- Pernègre, V. N., and D. K. Elliott. 2008. Phylogeny of the Pteraspidoformes (Heterostraci), Silurian–Devonian jawless vertebrates. *Zoologica Scripta* 37:391-403.
- Piras, P., and A. D. Buscalioni. 2006. *Diplocynodon muelleri* comb. nov., an Oligocene diplocynodontine alligatoroid from Catalonia (Ebro Basin, Lleida Province, Spain). *Journal of Vertebrate Paleontology* 26:608-620.
- Pol, D., J. M. Leardi, A. Lecuona, and M. Krause. 2012. Postcranial anatomy of *Sebecus icaeorhinus* (Crocodyliformes, Sebecidae) from the Eocene of Patagonia. *Journal of Vertebrate Paleontology* 32:328-354.
- Pollitt, J. R., R. A. Fortey, and M. A. Wills. 2005. Systematics of the trilobite families Lichidae Hawle & Corda, 1847 and Lichakephalidae Tripp, 1957: the

- application of Bayesian inference to morphological data. *Journal of Systematic Palaeontology* 3:225 - 241.
- Polly, P. D. 1996. The skeleton of *Gazinocyon vulpeculus* gen. et. comb nov. and the cladistic relationships of Hyaenodontidae (Eutheria, Mammalia). *Journal of Vertebrate Paleontology* 16:303 - 319.
- Polly, P. D. 1998. Variability, selection, and constraints: development and evolution in viverravid (Carnivora, Mammalia) molar morphology. *Paleobiology* 24:409 - 429.
- Popov, L. E., I. F. Nikitin, and E. V. Sokiran. 1999. The earliest atrypides and athyridides (Brachiopoda) from the Ordovician of Kazakhstan. *Palaeontology* 42:625-661.
- Popov, L. E., O. Vinn, and O. I. Nikitina. 2001. Brachiopods of the redefined family Tritoechiidae from the Ordovician of Kazakhstan and South Urals. *Geobios* 34:131-155.
- Prado, J. L., and M. T. Alberdi. 1996. A cladistic analysis of the horses of the tribe Equini. *Palaeontology* 39:663 - 680.
- Prieto-Márquez, A. 2010. Global phylogeny of Hadrosauridae (Dinosauria: Ornithopoda) using parsimony and Bayesian methods. *Zoological Journal of the Linnean Society* 159:435-502.
- Pujos, F., G. De Iuliis, C. Argot, and L. Werdelin. 2007. A peculiar climbing Megalonychidae from the Pleistocene of Peru and its implication for sloth history. *Zoological Journal of the Linnean Society* 149:179-235.
- Rabosky, D. L., F. Santini, J. Eastman, S. A. Smith, B. Sidlauskas, J. Chang, and M. E. Alfaro. 2013. Rates of speciation and morphological evolution are correlated across the largest vertebrate radiation. *Nature Communications* 4:nc2958.
- Ramsköld, L., and B. D. E. Chatterton. 1991. Revision and subdivision of the polyphyletic '*Leonaspis*' (Trilobita). *Transactions of the Royal Society of Edinburgh: Earth Sciences* 82:333 - 371.
- Ramsköld, L., and L. Werdelin. 1991. The phylogeny and evolution of some phacopid trilobites. *Cladistics* 7:29 - 74.
- Raup, D. M., and S. J. Gould. 1974. Stochastic simulation and evolution of morphology - towards a nomothetic paleontology. *Systematic Zoology* 23:305 - 322.
- Reynoso, V.-H. 1996. A Middle Jurassic *Sphenodon*-like sphenodontian (Diapsida: Lepidosauria) from Huizachal Canyon, Tamaulipas, Mexico. *Journal of Vertebrate Paleontology* 16:210-221.
- Rode, A. L. 2004. Phylogenetic revision of *Leptodesma* (*Leiopteria*) (Devonian: Bivalvia). *Postilla* 229:1 - 26.

- Rode, A. L., and L. E. Babcock. 2003. Phylogeny of fossil and extant freshwater crayfish and some closely related nephropid lobsters. *Journal of Crustacean Biology* 23:418 – 435.
- Rode, A. L., and B. S. Lieberman. 2002. Phylogenetic and biogeographic analysis of Devonian phyllocarid crustaceans. *Journal of Paleontology* 76:271 - 286.
- Roopnarine, P. D. 2001. A history of diversification, extinction, and invasion in tropical America as derived from species-level phylogenies of chionine genera (Family Veneridae). *Journal of Paleontology* 75:644 - 657.
- Rougier, G. W., S. Isaji, and M. Manabe. 2007. An Early Cretaceous mammal from the Kuwajima Formation (Tetori Group), Japan, and a reassessment of triconodont phylogeny. *Annals of the Carnegie Museum* 76:73-115.
- Rougier, G. W., M. J. Novacek, M. C. McKenna, and J. R. Wible. 2001. Gobiconodonts from the Early Cretaceous of Oshih (Ashile), Mongolia. *American Museum Novitates* 3348:1-30.
- Rulleau, L., M. Bécaud, and P. Neige. 2003. Ammonites generally classified in the Bouleiceratinae sub-family (Hildoceratidae, Toarcian): phylogenetic, biogeographic and systematic perspective. *Geobios* 36:317 - 348.
- Ruta, M. 1997. A new mitrate from the Lower Ordovician of Southern France. *Palaeontology* 40:363 - 383.
- . 1999. A cladistic analysis of the anomalocystitid mitrates. *Zoological Journal of the Linnean Society* 127:345 – 421.
- Ruta, M., and J. N. Theron. 1997. Two Devonian mitrates from South Africa. *Palaeontology* 40:201 - 243.
- Salisbury, B. A. 1999. Strongest evidence in compatibility: clique and tree evaluation using apparent phylogenetic signal. *Taxon* 48:755-766.
- Salisbury, S. W., R. E. Molnar, E. Frey, and P. M. Willis. 2006. The origin of modern crocodyliforms: new evidence from the Cretaceous of Australia. *Proceedings of the Royal Society B: Biological Sciences* 273:2439 – 2448.
- Sampson, S. D., M. A. Loewen, A. A. Farke, E. M. Roberts, C. A. Forster, J. A. Smith, and A. L. Titus. 2010. New horned dinosaurs from Utah provide evidence for intracontinental dinosaur endemism. *PLoS Biol* 5:1 - 12.
- Sansom, R. S. 2008. The origin and early evolution of the Osteostraci (Vertebrata): a phylogeny for the Thyestiida. *Journal of Systematic Palaeontology* 6:317 - 332.
- Santini, F., and J. C. Tyler. 2003. A phylogeny of the families of fossil and extant tetraodontiform fishes (Acanthomorpha, Tetraodontiformes), Upper Cretaceous to Recent. *Zoological Journal of the Linnean Society* 139:565 - 617.

- Saucède, T., R. Mooi, and B. David. 2007. Phylogeny and origin of Jurassic irregular echinoids (Echinodermata: Echinoidea). *Geological Magazine* 144:333 - 359.
- Saucède, T., and D. Neraudeau. 2006. An 'Elvis' echinoid, *Nucleopygus (Jolyclypus) jolyi*, from the Cenomanian of France: phylogenetic analysis, sexual dimorphism and neotype designation. *Cretaceous Research* 27:542-554.
- Schneider, J. A. 1998a. Phylogeny of stem-group eucardiids (Bivalvia: Cardiidae) and the significance of the transitional fossil *Perucardia*. *Malacologia* 40:37 - 62.
- . 1998b. Phylogeny of the Cardiidae (Bivalvia): phylogenetic relationship and morphologic evolution within the subfamilies Clinocardiinae, Lymnocardiinae, Fraginae and Tridacninae. *Malacologia* 40:321 - 373.
- Schoch, R. R. 2008a. A new stereospondyl from the German Middle Triassic, and the origin of the Metoposauridae. *Zoological Journal of the Linnean Society* 152:79-113.
- . 2008b. The Capitosauria (Amphibia): characters, phylogeny, and stratigraphy. *Palaeodiversity* 1:189–226.
- Schoch, R. R., and A. R. Milner. 2008. The intrarelationships and evolutionary history of the temnospondyl family Branchiosauridae. *Journal of Systematic Palaeontology* 6:409 - 431.
- Schram, F. R., C. H. J. Hof, and F. A. Steeman. 1999. Thylacocephala (Arthropoda: Crustacea?) from the Cretaceous of Lebanon and implications for Thylacocephalan systematics. *Palaeontology* 52:769 - 797.
- Sepkoski, J. J., Jr. 1979. A kinetic model of Phanerozoic taxonomic diversity. II. Early Phanerozoic families and multiple equilibria. *Paleobiology* 5:222 - 251.
- Shockey, B. J. 1997. Two new notoungulates (Family Notohippidae) from the Salla Beds of Bolivia (Deseadan: late Oligocene): systematics and functional morphology. *Journal of Vertebrate Paleontology* 17:584-599.
- Shoshani, J., R. C. Walter, M. Abraha, S. Berhe, P. Tassy, W. J. Sanders, G. H. Marchant, Y. Libsekal, T. Ghirmai, and D. Zinner. 2006. A proboscidean from the Late Oligocene of Eritrea, a "missing link" between early Elephantiformes and Elephantimorpha, and biogeographic implications. *Proceedings of the National Academy of Sciences* 103:17296 - 17301.
- Sidor, C. A., F. R. O'Keefe, R. Damiani, J. S. Steyer, R. M. H. Smith, H. C. E. Larsson, P. C. Sereno, O. Ide, and A. Maga. 2005. Permian tetrapods from the Sahara show climate-controlled endemism in Pangaea. *Nature* 434:886-889.
- Simões, M. G., A. C. Marques, L. H. Cruz de Mello, and L. E. Anelli. 1997. Phylogenetic analysis of the genera of the extinct family Megadesmidae (Bivalvia, Anomalodesmata), with remarks on its paleoecology and taxonomy. *Journal of Comparative Biology* 2:75 - 90.

- Skelton, P. W., and A. B. Smith. 2000. A preliminary phylogeny for rudist bivalves: sifting clades from grades. Pp. 97 - 127 in E. M. Harper, J. D. Taylor and J. A. Crame, eds. The evolutionary biology of the Bivalvia. Special Publication of the Geological Society, London, Geological Society, London.
- Slowinski, J. B., and C. Guyer. 1989. Testing null models in questions of evolutionary success. *Systematic Zoology* 38:189 - 191.
- Smith, A. B. 1994. Triassic echinoids from Peru. *Palaeontographica Abteilung A* 233:177 - 202.
- . 2001. Probing the cassiduloid origins of clypeasteroid echinoids using stratigraphically restricted parsimony analysis. *Paleobiology* 27:392 - 404.
- . 2004. Phylogeny and systematics of holasteroid echinoids and their migration into the Deep-sea. *Palaeontology* 47:123-150.
- . 2007. Intrinsic versus extrinsic biases in the fossil record: contrasting the fossil record of echinoids in the Triassic and early Jurassic using sampling data, phylogenetic analysis, and molecular clocks. *Paleobiology* 33:310-323.
- Smith, A. B., and C. W. Wright. 1993. British Cretaceous echinoids. Part 3, Stirodonta 2 (Hemicidaroida, Arbacioida and Phymosomatoida, Part 1). *Monograph of the Palaeontological Society* 147:199 - 267.
- Smith, A. B., and S. Zamora. 2009. Rooting phylogenies of problematic fossil taxa; a case study using cinctans (stem-group echinoderms). *Palaeontology* 52:803-821.
- Solé, F. 2013. New proviverrine genus from the Early Eocene of Europe and the first phylogeny of Late Palaeocene–Middle Eocene hyaenodontidans (Mammalia). *Journal of Systematic Palaeontology* 11:375 - 398.
- Steyer, J. S., R. Damiani, C. A. Sidor, F. R. O'Keefe, H. C. E. Larsson, A. Maga, and O. Ide. 2006. The vertebrate fauna of the Upper Permian of Niger. IV. *Nigerpeton ricqlesi* (Temnospondyli: Cochleosauridae), and the edopoid colonization of Gondwana. *Journal of Vertebrate Paleontology* 26:18-28.
- Stigall Rode, A. L. 2005. Systematic revision of the Middle and Late Devonian brachiopods *Schizophoria* (*Schizophoria*) and '*Schuchertella*' from North America. *Journal of Systematic Palaeontology* 3:133 - 167.
- Stocker, M. R. 2010. A new taxon of phytosaur (Archosauria: Pseudosuchia) from the Late Triassic (Norian) Sonsela Member (Chinle Formation) in Arizona, and a critical reevaluation of *Leptosuchus* Case, 1922. *Palaeontology* 53:997-1022.
- . 2012. A new phytosaur (Archosauriformes, Phytosauria) from the Lot's Wife beds (Sonsela Member) within the Chinle Formation

- (Upper Triassic) of Petrified Forest National Park, Arizona. *Journal of Vertebrate Paleontology* 32:573-586.
- Stockley, B., A. B. Smith, T. Littlewood, H. A. Lessios, and J. A. Mackenzie-Dodds. 2005. Phylogenetic relationships of spatangoid sea urchins (Echinoidea): taxon sampling density and congruence between morphological and molecular estimates. *Zoologica Scripta* 34:447-468.
- Strait, D. S., and F. E. Grine. 2004. Inferring hominoid and early hominid phylogeny using craniodental characters: the role of fossil taxa. *Journal of Human Evolution* 47:399-452.
- Sues, H.-D., and A. Averianov. 2009. A new basal hadrosauroid dinosaur from the Late Cretaceous of Uzbekistan and the early radiation of duck-billed dinosaurs. *Proceedings of the Royal Society B: Biological Sciences* 276:2549-2555.
- Sumrall, C. D., and F. J. Gahn. 2006. Morphological and systematic reinterpretation of two enigmatic edrioasteroids (Echinodermata) from Canada. *Canadian Journal of Earth Sciences* 43:497 - 507.
- Sumrall, C. D., and J. Sprinkle. 1995. Plating and pectinirhombs of the Ordovician rhombiferan *Plethoschisma*. *Journal of Paleontology* 69:772 - 779.
- Sumrall, C. D., and S. Zamora. 2011. Ordovician edrioasteroids from Morocco: faunal exchanges across the Rheic Ocean. *Journal of Systematic Palaeontology* 9:425-454.
- Sundberg, F. A. 1999. Redescription of *Alokistocare subcoronatum* (Hall and Whitfield, 1877), the type species of *Alokistocare*, and the status of Alokistocaridae Resser, 1939b (Ptychopariidae: Trilobita, Middle Cambrian. *Journal of Paleontology* 73:1126 - 1143.
- . 2004. Cladistic analysis of Early-Middle Cambrian kochaspid trilobites (Ptychopariida). *Journal of Paleontology* 78:920 - 940.
- Sundberg, F. A. 2006. Taxonomic assignment of the Cambrian trilobite *Tonkinella* Mansuy, 1916 (Corynexochida), with a new species from California. *Memoirs of the Association of Australasian Palaeontologists* 32:59 - 74.
- Sundberg, F. A., and L. B. McCollum. 1997. Oryctocephalids (Corynexochida: Trilobita) of the Lower-Middle Cambrian boundary interval from California and Nevada. *Journal of Paleontology* 77:1065 - 1090.
- Suter, S. J. 1994. Cladistic analysis of cassiduloid echinoids: trying to see the phylogeny for the trees. *Biological Journal of the Linnean Society* 53:31 - 72.
- Swartz, B. A. 2009. Devonian actinopterygian phylogeny and evolution based on a redescription of *Stegotrachelus finlayi*. *Zoological Journal of the Linnean Society* 156:750-784.

- Tetlie, O. E. 2006. Two new Silurian species of *Eurypterus* (Chelicerata: Eurypterida) from Norway and Canada and the phylogeny of the genus. *Journal of Systematic Palaeontology* 4:397 - 412.
- Tetlie, O. E., and M. B. Cuggy. 2007. Phylogeny of the basal swimming eurypterids (Chelicerata; Eurypterida; Eurypterina). *Journal of Systematic Palaeontology* 5:345-356.
- Thompson, R. S., J. C. Parish, S. C. R. Maidment, and P. M. Barrett. 2012. Phylogeny of the ankylosaurian dinosaurs (Ornithischia: Thyreophora). *Journal of Systematic Palaeontology* 10:301-312.
- Thorne, P. M., M. Ruta, and M. J. Benton. 2011. Resetting the evolution of marine reptiles at the Triassic-Jurassic boundary. *Proceedings of the National Academy of Sciences* 108:8339-8344.
- Tinn, O., and T. Meidla. 2004. Phylogenetic relationships of Early–Middle Ordovician ostracods of Baltoscandia. *Palaeontology* 47:199 - 221.
- Tsuji, L. A., J. Müller, and R. R. Reisz. 2010. *Microleter mckinzieorum* gen. et sp. nov. from the Lower Permian of Oklahoma: the basalmost parareptile from Laurasia. *Journal of Systematic Palaeontology* 8:245-255.
- Turvey, S. T. 2002. Phylogeny of the Reedocalymeninae (Trilobita): implications for Early Ordovician biogeography of Gondwana. Pp. 53 - 68 in J. A. Crame and A. W. Owen, eds. *Palaeobiogeography and biodiversity change: the Ordovician and Mesozoic-Cenozoic radiations*. Geological Society of London, Special Publications, London.
- Uhen, M. D., and P. D. Gingerich. 2001. New genus of dorudontine archaeocete (Cetacea) from the middle-to-late Eocene of South Carolina. *Marine Mammal Science* 17:1-34.
- Vermeij, G. J., and S. J. Carlson. 2000. The muricid gastropod subfamily Rapaninae: phylogeny and ecological history. *Paleobiology* 26:19 - 46.
- Villier, L., D. Blake, J. Jagt, and M. Kutscher. 2004. A preliminary phylogeny of the Pterasteridae (Echinodermata, Asteroidea) and the first fossil record: Late Cretaceous of Germany and Belgium. *Paläontologische Zeitschrift* 78:281-299.
- Wagner, G. P. 1989. The origin of morphological characters and the biological basis of homology. *Evolution* 43:1157 - 1171.
- . 1996. Homologues, natural kinds and the evolution of modularity. *American Zoologist* 36:36-43.
- . 2007. The developmental genetics of homology. *Nature Reviews Genetics* 8:473-479.
- Wagner, G. P., and L. Altenberg. 1996. Complex adaptations and the evolution of evolvability. *Evolution* 50:967 - 976.
- Wagner, P. J. 1995a. Stratigraphic tests of cladistic hypotheses. *Paleobiology* 21:153 - 178.

-
- _____. 1995b. Testing evolutionary constraint hypotheses with early Paleozoic gastropods. *Paleobiology* 21:248 - 272.
- _____. 1997. Patterns of morphologic diversification among the Rostroconchia. *Paleobiology* 23:115 - 150.
- _____. 1999a. The utility of fossil data in phylogenetic analyses: a likelihood example using Ordovician-Silurian species of the Lophospiridae (Gastropoda: Murchisoniina). *American Malacological Bulletin* 15:1 - 31.
- _____. 1999b. Phylogenetic relationships of the earliest anisostrophically coiled gastropods. *Smithsonian Contributions to Paleobiology* 88:1 - 132.
- _____. 2000a. The quality of the fossil record and the accuracy of phylogenetic inferences about sampling and diversity. *Systematic Biology* 49:65 - 86.
- _____. 2000b. Exhaustion of cladistic character states among fossil taxa. *Evolution* 54:365 - 386.
- _____. 2001. Gastropod phylogenetics: progress, problems and implications. *Journal of Paleontology* 75:1128 - 1140.
- _____. 2012. Modelling rate distributions using character compatibility: implications for morphological evolution among fossil invertebrates. *Biology Letters* 8:143 - 146.
- Wagner, P. J., and G. F. Estabrook. 2014. Trait-based diversification shifts reflect differential extinction among fossil taxa. *Proceedings of the National Academy of Sciences* 111:16419-16424.
- _____. 2015. The implications of stratigraphic compatibility for character integration among fossil taxa. *Systematic Biology* 64:838 - 852.
- Wagner, P. J., M. Ruta, and M. I. Coates. 2006. Evolutionary patterns in early tetrapods. II. Differing constraints on available character space among clades. *Proceedings of the Royal Society of London, Series B. Biological Sciences* 273:2113 - 2118.
- Waisfeld, B. G., N. E. Vaccari, B. D. E. Chatterton, and G. D. Edgecombe. 2001. Systematics of Shumardiidae (Trilobita), with new species from the Ordovician of Argentina. *Journal of Paleontology* 75:827 - 859.
- Wang, X., M. C. McKenna, and D. Dashzeveg. 2005. *Amphicticeps* and *Amphicynodon* (Arctoidea, Carnivora) from Hsanda Gol Formation, Central Mongolia and phylogeny of basal arctoids with comments on zoogeography. *American Museum Novitates* 3483:1 - 57.
- Wang, X., R. H. Tedford, and B. E. Taylor. 1999. Phylogenetic systematics of the Borophaginae (Carnivora: Canidae). *Bulletin of the American Museum of Natural History* 243:1-392.
-

- Warren, A., and C. Marsicano. 2000. A phylogeny of the Brachyopoidea (Temnospondyli, Stereospondyli). *Journal of Vertebrate Paleontology* 20:462-483.
- Webster, M. 2007. A Cambrian peak in morphological variation within trilobite species. *Science* 317:499-502.
- Webster, M., and M. L. Zelditch. 2011. Evolutionary lability of integration in Cambrian ptychoparioid trilobites. *Evolutionary Biology* 38:144-162.
- Weishampel, D. B., C.-M. Jianu, Z. Csiki, and D. B. Norman. 2003. Osteology and phylogeny of *Zalmoxes* (n.g), an unusual euornithopod dinosaur from the latest Cretaceous of Romania. *Journal of Systematic Palaeontology* 1:65 - 123.
- Wenwei, Y., R. A. Fortey, and S. T. Turvey. 2006. Ontogeny and relationships of the trilobite *Pseudopetigurus* Prantl and Přibyl. *Palaeontology* 49:537 - 546.
- Werdelin, L., and N. Solounias. 1991. The Hyaenidae: taxonomic systematics and evolution. *Fossils and Strata* 30:1 - 104.
- Wesley-Hunt, G. D., and J. J. Flynn. 2005. Phylogeny of the Carnivora: basal relationships among the carnivoramorphans, and assessment of the position of “Miacoidea” relative to crown-clade Carnivora. *Journal of Systematic Palaeontology* 3:1 - 28.
- Westrop, S. R., R. Ludvigsen, and C. H. Kindle. 1996. Marjuman (Cambrian) agnostoid trilobites of the Cow Head Group, western Newfoundland. *Journal of Paleontology* 70:804 - 829.
- Whitlock, J. A. 2011. A phylogenetic analysis of Diplodocoidea (Saurischia: Sauropoda). *Zoological Journal of the Linnean Society* 161:872-915.
- Wickström, L. M., and P. C. J. Donoghue. 2005. Cladograms, phylogenies and the veracity of the conodont fossil record. *Special Papers in Palaeontology* 73:185 - 218.
- Wilkinson, L. E., M. T. Young, and M. J. Benton. 2008. A new metriorhynchid crocodile (Mesoeucrocodylia: Thalattosuchia) from the Kimmeridgian (Upper Jurassic) of Wiltshire, UK. *Palaeontology* 51:1307-1333.
- Williamson, T. E., and T. D. Carr. 2007. *Bomburia* and *Ellipsodon* (Mammalia: Mioclaenidae) from the Early Paleocene of New Mexico. *Journal of Paleontology* 81:966-985.
- Wilson, M. V. H., and A. M. Murray. 2008. Osteoglossomorpha: phylogeny, biogeography, and fossil record and the significance of key African and Chinese fossil taxa. Geological Society, London, Special Publications 295:185-219.
- Wu, X.-c., D. B. Brinkman, D. A. Eberth, and D. R. Braman. 2007. A new ceratopsid dinosaur (Ornithischia) from the uppermost Horseshoe Canyon Formation (upper Maastrichtian), Alberta, Canada. *Canadian Journal of Earth Sciences* 44:1243-1265.

- Xu, G.-H., and K.-Q. Gao. 2011. A new scanilepiform from the Lower Triassic of northern Gansu Province, China, and phylogenetic relationships of non-teleostean Actinopterygii. *Zoological Journal of the Linnean Society* 161:595-612.
- Xu, X., Y.-N. Cheng, X.-L. Wang, and C.-H. Chang. 2002a. An unusual oviraptorosaurian dinosaur from China. *Nature* 419:291 - 293.
- Xu, X., M. A. Norell, X.-l. Wang, P. J. Makovicky, and X.-c. Wu. 2002b. A basal troodontid from the Early Cretaceous of China. *Nature* 415:780-784.
- Yacobucci, M. M. 1999. Plasticity of developmental timing as the underlying cause of high speciation rates in ammonoids. An example from the Cenomanian Western Interior Seaway of North America. Pp. 59 - 77 in F. Olóriz and F. J. Rodriguez-Tovar, eds. *Advancing research on living and fossil cephalopods*. Kluwer Academic / Plenum, New York.
- Yates, A. M. 2003. A new species of the primitive dinosaur *Thecodontosaurus* (Saurischia: Sauropodomorpha) and its implications for the systematics of early dinosaurs. *Journal of Systematic Palaeontology* 1:1-42.
- Young, M. T., and M. B. De Andrade. 2009. What is *Geosaurus*? Redescription of *Geosaurus giganteus* (Thalattosuchia: Metriorhynchidae) from the Upper Jurassic of Bayern, Germany. *Zoological Journal of the Linnean Society* 157:551-585.
- Zaher, H., D. Pol, A. B. Carvalho, C. Riccomini, D. Campos, and W. Nava. 2006. Redescription of the cranial morphology of *Mariliasuchus amarali*, and its phylogenetic affinities (Crocodyliformes, Notosuchia). *American Museum Novitates* 3512:1 - 40.
- Zhao, X., Z. Cheng, X. Xu, and P. J. Makovicky. 2006. A new ceratopsian from the Upper Jurassic Houcheng Formation of Hebei, China. *Acta Geologica Sinica* 80:467 - 473.
- Zheng, X., X. Xu, H. You, Q. Zhao, and Z. Dong. 2010. A short-armed dromaeosaurid from the Jehol Group of China with implications for early dromaeosaurid evolution. *Proceedings of the Royal Society B: Biological Sciences* 277:211-217.
- Zhu, M., X. Yu, and P. E. Ahlberg. 2001. A primitive sarcopterygian fish with an eyestalk. *Nature* 410:81 - 84.

ACKNOWLEDGEMENTS

For comments and discussion, I thank D. H. Erwin & S. K. Lyons. This is Paleobiology Database Publication XXX.

Supplementary Materials:

Supplementary Figures & Tables repeating analyses looking at disparity at $S/3$.

Figures S1-S2

Tables S1-S4

Appendix S1. Full results for 257 clades.

Fig. S1. Deviations from expected disparity (D) among the first $S/3$ of S taxa given the expectations of uniform rates of independent change. Deviations are on a log-scale so that half of expected D is the same distance from 1.0 as twice expected D . For each clade, the uniform rate model maximizes the probability of observed character compatibility. **(A)** Deviations over time. $\tau = -0.037$, $p = 0.403$. **(B)** Molluscs+Brachiopods (purple shells): $\tau = 0.493$, $p = 6.0 \times 10^{-7}$; Arthropods (orange trilobites): $\tau = 0.391$, $p = 5.0 \times 10^{-5}$; Echinoderms (blue stars): $\tau = 0.516$, $p = 1.8 \times 10^{-6}$; Chordates (green fishes): $\tau = 0.414$, $p = 2.5 \times 10^{-11}$.

Fig. S2. Probabilities of observed disparity (D) accumulated during the first half of clade evolution ($S/3$) given the best-fit uniform rate of independent change for all S taxa in each clade. Significance based on 1000 Monte Carlo replications. Best-fit uniform rates maximize the probability of observed character compatibility for all S taxa. Dashed lines show the expected number of studies at each p -value.

Fig. S3. Deviations from expected disparity (D) among the first $S/3$ of S taxa given the expectations of separate early and late rates of independent change. Deviations are on a log-scale so that half of expected D is the same distance from 1.0 as twice expected D . For each clade, the uniform rate model maximizes the probability of observed character compatibility among the first $S/3$ taxa. (A) Deviations over time. $\tau=-0.034$, $p=0.429$. (B) Deviations vs deviations from expected stratigraphic compatibility. Molluscs+Brachiopods (purple shells): $\tau=-0.227$, $p=0.021$; Arthropods (orange trilobites): $\tau=-0.309$, $p=1.3 \times 10^{-3}$; Echinoderms (blue stars): $\tau=-0.138$, $p=0.223$; Chordates (green fishes): $\tau=0.315$, $p=3.7 \times 10^{-7}$.

Table S1. Deviations from expected disparity at $S/3$ taxa within major taxonomic groups. “Studies” refers to the number of published matrices represent clades used. “Excess” gives the number of studies with excess disparity in the first half of clade evolution given a single rate (“1-Rate”) and given separate early and late rates (“2-Rates”), with the early rate maximizing the probability of character compatibility given the earliest $S/3$ of S total taxa. The significance is the binomial probability of that many excess cases given the total studies and an expectation of 50%. “ $\sum R$ ” gives the signed rank statistic, which ranks deviations by absolute values but then gives each rank a +/- based on the original statistic. Deviations are ranked after log-transformation, so half the expected disparity has the same rank as twice the expected disparity. Significance is assessed on the expectation that $\sum R=0$.

Taxa	Studies	1-Rate		1-Rate		2-Rates		2-Rates	
		Excess	p	$\sum R$	p	Excess	p	$\sum R$	p
Brachiopods									
+Molluscs	49	42	5.7×10^{-8}	979	5.6×10^{-7}	38	3.9×10^{-5}	817	1.3×10^{-4}
Arthropods	51	40	1.5×10^{-5}	868	2.4×10^{-5}	33	0.024	578	0.015
Echinoderms	38	35	5.4×10^{-9}	651	1.2×10^{-6}	29	2.4×10^{-4}	555	2.4×10^{-5}
Chordates	119	85	1.3×10^{-6}	3510	1.6×10^{-6}	75	3.2×10^{-3}	2432	6.4×10^{-3}

Table S2. Deviations from expected disparity at $S/3$ over time. “Periods” give geochronological periods of the plurality of taxa within any one clade. “Studies” refers to the number of published matrices represent clades used. “Excess” gives the number of studies with excess disparity in the first half of clade evolution given a single rate (“1-Rate”) and given separate early and late rates (“2-Rates”), with the early rate maximizing the probability of character compatibility given the earliest $S/3$ of S total taxa. The significance is the binomial probability of that many excess cases given the total studies and an expectation of 50%. “ ΣR ” gives the signed rank statistic, which ranks deviations by absolute values but then gives each rank a +/- based on the original statistic. Deviations are ranked after log-transformation, so half the expected disparity has the same rank as twice the expected disparity. Significance is assessed on the expectation that $\Sigma R=0$.

Period	Studies	1-Rate		1-Rate		2-Rates		2-Rates	
		Excess	p	ΣR	p	Excess	p	ΣR	p
Cambrian	21	17	3.6×10^{-3}	135	9.5×10^{-3}	14	0.095	87	0.065
Ordovician	42	36	1.4×10^{-6}	727	2.7×10^{-6}	31	1.4×10^{-3}	573	1.7×10^{-4}
Silurian	14	11	0.029	67	0.018	11	0.029	47	0.070
Devonian	29	26	7.6×10^{-6}	389	1.3×10^{-5}	24	2.7×10^{-4}	337	1.3×10^{-4}
Carboniferous	12	9	0.073	32	0.105	7	0.387	30	0.120
Permian	11	10	5.9×10^{-3}	62	2.9×10^{-3}	9	0.033	56	6.4×10^{-3}
Triassic	16	13	0.011	70	0.035	12	0.038	72	0.031
Jurassic	21	14	0.095	87	0.065	12	0.332	45	0.217
Cretaceous	38	29	8.3×10^{-4}	525	7.0×10^{-5}	21	0.314	295	0.016
Paleogene	41	28	0.014	425	2.9×10^{-3}	25	0.106	265	0.043
Neogene	12	9	0.073	28	0.136	9	0.073	26	0.154

Appendix S1. Data sets, disparity and expectations from Monte Carlo tests.

Taxon	Study	Period	S	Ch	N	$D_{S/2}$	1-Rate			E. Rate			2-Rate			$\Delta[SC]$	Source(s)
							$E[D_{S/2}]$	p		L. Rate	$E[D_{S/2}]$	p		$E[D_{S/2}]$	p		
Brachiopoda	Anopliidae	S	28	31	42	0.962	0.891	0.102		2.340	0.933	0.321		0.933	0.321	0.099	Hanger and Strong 2000
Brachiopoda	Atrypidae	O	25	27	73	0.993	0.863	0.019		4.222	0.930	0.208		0.930	0.208	0.026	Popov et al. 1999
Brachiopoda	Billingsellida	Cm	20	24	40	0.867	0.852	0.423		1.781	0.891	0.591		0.891	0.591	-0.008	Benedetto 2009
Brachiopoda	Echinoconchidae	D	14	24	29	0.887	0.846	0.355		1.909	0.890	0.505		0.890	0.505	0.024	Leighton and Maples 2002
Brachiopoda	Floweria	D	14	28	34	1.073	0.864	0.011		1.450	0.899	0.022		0.899	0.022	-0.121	Stigall Rode 2005
Brachiopoda	Leptenellidae	O	23	20	35	0.965	0.863	0.077		2.560	0.929	0.324		0.929	0.324	0.113	Candela 2010
Brachiopoda	Linguloidea	Cm	23	45	77	0.949	0.830	0.042		1.857	0.889	0.197		0.889	0.197	0.005	Cusack et al. 1999
Brachiopoda	Orbirhynchia	K	16	22	32	0.825	0.824	0.496		1.818	0.885	0.691		0.885	0.691	-0.020	Monks 2000
Brachiopoda	Parastrophinidae	O	26	34	71	1.051	0.852	0.002		4.679	0.902	0.035		0.902	0.035	0.000	Jin and Popov 2008
Brachiopoda	Schizophoria	D	22	36	42	1.000	0.876	0.017		1.782	0.918	0.104		0.918	0.104	0.021	Stigall Rode 2005
Brachiopoda	Strophomenoidea	O	14	13	22	1.054	0.902	0.040		1.714	0.939	0.086		0.939	0.086	-0.145	Dewing 2004
Brachiopoda	Terebratuloidea	D	78	42	71	0.955	0.850	0.010		2.200	0.881	0.082		0.881	0.082	0.024	Carlson and Fitzgerald 2007
Brachiopoda	Tritoechiidae	O	13	24	45	0.830	0.872	0.665		0.953	0.877	0.682		0.877	0.682	-0.055	Popov et al. 2001
Rostroconchia	Conocardioidea	D	43	53	87	0.861	0.827	0.291		1.859	0.864	0.520		0.864	0.520	-0.028	Wagner 1997
Rostroconchia	Eopteriidae	O	20	44	61	0.943	0.840	0.125		1.109	0.845	0.136		0.845	0.136	0.011	Wagner 1997
Rostroconchia	Pseudobigaleaidea	S	24	62	101	0.881	0.822	0.199		1.671	0.874	0.456		0.874	0.456	-0.028	Wagner 1997
Rostroconchia	Ribeiriidae	O	27	34	68	0.985	0.854	0.018		2.306	0.906	0.145		0.906	0.145	0.005	Wagner 1997
Rostroconchia	Technophoridae	O	14	40	61	1.021	0.828	0.021		1.333	0.856	0.042		0.856	0.042	-0.013	Wagner 1997
Bivalvia	Caprinoidea	K	23	23	29	0.617	0.785	0.923		1.000	0.804	0.938		0.804	0.938	0.000	Mitchell 2013
Bivalvia	Cardiidae	Pg	33	24	42	0.981	0.811	0.014		2.000	0.864	0.071		0.864	0.071	-0.014	Schneider 1998b
Bivalvia	Chione	Pg	19	22	30	1.188	0.851	0.000		3.412	0.937	0.005		0.937	0.005	-0.090	Roopnarine 2001
Bivalvia	Chionopsis	Pg	19	23	35	1.153	0.838	0.000		3.353	0.925	0.017		0.925	0.017	-0.140	Roopnarine 2001
Bivalvia	Eucardiidae	K	20	16	36	0.909	0.871	0.341		1.870	0.918	0.545		0.918	0.545	-0.054	Schneider 1998a
Bivalvia	Hippuritoidea	K	36	32	36	0.821	0.774	0.318		1.241	0.801	0.410		0.801	0.410	0.000	Skelton and Smith 2000
Bivalvia	Leptodesma	D	22	27	31	0.899	0.858	0.286		1.289	0.882	0.401		0.882	0.401	0.025	Rode 2004
Bivalvia	Megadesmidae	P	15	21	27	0.972	0.791	0.056		1.611	0.861	0.168		0.861	0.168	0.018	Simões et al. 1997
Bivalvia	Ostreaoidea	K	34	30	37	0.821	0.777	0.295		1.783	0.836	0.564		0.836	0.564	0.006	Huelsenbeck 1994
Bivalvia	Pholadidae	K	25	23	26	1.057	0.810	0.010		4.333	0.880	0.096		0.880	0.096	-0.079	Monari 2009
Cephalopoda	Acanthoceratidae	K	20	32	103	1.029	0.907	0.002		1.484	0.935	0.027		0.935	0.027	0.045	Yacobucci 1999
Cephalopoda	Ceratitida	P	32	55	77	0.896	0.829	0.125		1.778	0.877	0.387		0.877	0.387	0.022	McGowan and Smith 2007

Taxon	Study	Period	<i>S</i>	Ch	N	$D_{S/2}$	1-Rate			E. Rate			2-Rate			$\Delta[\text{SC}]$	Source(s)
							$E[D_{S/2}]$	p		L. Rate	$E[D_{S/2}]$	p					
Cephalopoda	Goniatioidea	C	13	24	24	0.654	0.746	0.727		0.875	0.761	0.749				0.049	Korn 1997
Cephalopoda	Hamitidae	K	27	30	43	0.691	0.771	0.757		1.500	0.818	0.885				0.013	Monks 2002
Cephalopoda	Hildoceratidae	J	17	19	27	0.828	0.874	0.713		0.872	0.874	0.713				-0.022	Rulleau et al. 2003
Cephalopoda	Scaphitacoidea	K	13	18	23	0.869	0.755	0.232		1.818	0.878	0.520				0.053	Monks 2000
Cephalopoda	Turrilitoidea	K	26	26	29	0.929	0.768	0.065		1.882	0.835	0.240				0.041	Monks 1999
Tergomya	Cyrtelloidea	O	21	41	68	1.081	0.818	0.001		3.600	0.882	0.024				-0.034	Wagner 2001
Gastropoda	Ancillinae	Pg	30	36	36	0.974	0.771	0.008		2.038	0.833	0.061				-0.027	Michaux 1989
Gastropoda	Bucaniidae	J	40	46	88	0.967	0.839	0.025		2.015	0.870	0.073				-0.019	Wagner 2001
Gastropoda	Columbellidae	Ng	24	30	43	0.946	0.840	0.101		1.452	0.863	0.148				0.041	de Maintenon 2005
Gastropoda	Eotomarioidea	O	40	69	137	0.904	0.815	0.062		1.812	0.854	0.227				-0.044	Wagner 1999b
Gastropoda	Harpidae	Pg	18	28	43	0.836	0.789	0.325		2.150	0.844	0.527				-0.091	Merle and Pacaud 2003
Gastropoda	Hormotomidae	O	34	67	122	0.950	0.809	0.019		1.805	0.851	0.094				-0.006	Wagner 1999b
Gastropoda	Macluritidae	O	18	50	84	0.939	0.846	0.114		1.538	0.875	0.215				-0.014	Wagner 1999b
Gastropoda	Nassariidae	Pg	26	25	36	0.959	0.837	0.046		1.697	0.875	0.150				-0.042	Haas 2000
Gastropoda	Rapaninae	Pg	27	32	44	0.992	0.854	0.014		7.000	0.946	0.304				0.058	Vermeij and Carlson 2000
Gastropoda	Sinuitidae	O	16	31	47	0.773	0.831	0.703		1.000	0.831	0.703				-0.010	Wagner 2001
Gastropoda	Subulitoidea	C	27	17	28	0.950	0.850	0.098		1.214	0.866	0.142				0.014	Nützel et al. 2000
Gastropoda	Trochonematoidea	O	55	43	64	0.927	0.827	0.039		1.184	0.842	0.070				0.001	Wagner 1995a; 1999a
Gastropoda	Tropidodiscidae	O	22	33	57	1.019	0.826	0.012		2.182	0.866	0.053				-0.025	Wagner 2001
Trilobita	Agnostoidea	Cm	82	80	113	0.980	0.822	0.003		1.650	0.838	0.005				0.006	Cotton and Fortey 2005
Trilobita	Agnostoidea	Cm	43	28	43	0.986	0.844	0.008		2.200	0.877	0.046				-0.003	Westrop et al. 1996
Trilobita	Alokistocaridae	Cm	19	50	101	1.020	0.893	0.017		2.139	0.936	0.117				-0.040	Sundberg 1999
Trilobita	Basal Trilobita	Cm	16	29	40	0.927	0.851	0.184		0.514	0.802	0.095				0.007	Lieberman 2002
Trilobita	Burlingiidae	Cm	16	18	18	0.658	0.877	0.984		0.600	0.832	0.944				0.008	Ebbestad and Budd 2002
Trilobita	Emuellidae	Cm	15	34	37	0.674	0.825	0.899		0.818	0.825	0.899				0.037	Paterson and Edgecombe 2006
Trilobita	Iwayaspidinae	Cm	14	23	30	0.920	0.881	0.331		2.455	0.933	0.551				0.054	Hughes and Rushton 1990
Trilobita	Kochaspidae	Cm	66	70	149	0.960	0.857	0.007		2.255	0.919	0.160				0.010	Sundberg 2004
Trilobita	Missisquoiidae	Cm	22	40	58	0.880	0.888	0.555		1.083	0.900	0.632				-0.040	Lee et al. 2008
Trilobita	Nevadoidea	Cm	22	57	80	0.981	0.888	0.077		0.852	0.883	0.072				0.017	Lieberman 2001
Trilobita	Olenelloidea	Cm	26	79	136	0.982	0.898	0.020		1.212	0.917	0.058				-0.007	Lieberman 1999
Trilobita	Oryctocephalidae	Cm	22	36	76	1.043	0.878	0.002		2.604	0.909	0.031				-0.066	Sundberg and McCollum 1997

Taxon	Study	Period	<i>S</i>	Ch	N	<i>D_{S/2}</i>	1-Rate		<u>E. Rate</u>	2-Rate		$\Delta[SC]$	Source(s)
							<i>E[D_{S/2}]</i>	<i>p</i>	L. Rate	<i>E[D_{S/2}]</i>	<i>p</i>		
Trilobita	Oryctocephalinae	Cm	24	20	42	1.056	0.864	0.003	2.063	0.923	0.027	-0.022	Sundberg 2006
Trilobita	Polymeroidea	Cm	19	26	41	0.719	0.789	0.728	1.296	0.830	0.850	0.024	Babcock 1994
Trilobita	Pterocephaliidae	Cm	36	45	71	0.861	0.825	0.289	1.731	0.861	0.506	-0.001	Hopkins 2011
Trilobita	Ptychoparioidea	Cm	48	72	113	0.912	0.813	0.066	2.256	0.849	0.194	-0.003	Cotton 2001
Trilobita	Wuaniidae	Cm	37	14	25	0.931	0.878	0.187	1.146	0.895	0.245	0.000	Bentley and Jago 2004
Trilobita	Acanthoparyphinae	O	24	39	50	0.692	0.792	0.881	1.333	0.827	0.944	-0.020	Adrain 1998
Trilobita	Deiphoninae	O	21	27	29	0.787	0.866	0.824	0.920	0.875	0.849	-0.083	Congreve and Lieberman 2010
Trilobita	Dimeropygidae	O	18	25	35	0.836	0.807	0.370	5.778	0.944	0.773	0.057	Adrain et al. 2001
Trilobita	Illaenidae	O	28	20	40	1.053	0.847	0.003	3.421	0.892	0.030	-0.134	Amati et al. 2004
Trilobita	Pseudopetigurus	O	17	25	40	0.911	0.873	0.330	1.225	0.888	0.395	-0.137	Wenwei et al. 2006
Trilobita	Reedocalymeninae	O	32	25	33	0.831	0.840	0.546	0.882	0.831	0.499	-0.037	Turvey 2002
Trilobita	Shumardiidae	O	33	52	99	0.867	0.862	0.453	1.197	0.884	0.634	0.039	Waisfeld et al. 2001
Trilobita	Sphaerexochinae	O	31	39	46	0.902	0.856	0.234	2.133	0.913	0.564	0.012	Congreve and Lieberman 2011
Trilobita	Toernquistiidae	O	38	55	85	0.851	0.842	0.438	1.216	0.864	0.610	-0.004	Chatterton et al. 1998
Trilobita	Acanthopgye	S	25	15	23	0.954	0.893	0.203	1.815	0.921	0.321	-0.059	Ebach and Ah Yong 2001
Trilobita	Encrinurinae	S	32	40	56	0.997	0.798	0.002	3.069	0.899	0.125	-0.057	Adrain and Edgecombe 1997
Trilobita	Odontopleuridae	S	62	35	57	0.954	0.828	0.009	1.190	0.841	0.018	-0.106	Ramsköld and Chatterton 1991
Trilobita	Phacopidae	S	50	32	86	0.826	0.865	0.748	2.000	0.888	0.849	0.008	Ramsköld and Werdelin 1991; Edgecombe and Ramsköld 1994; Ebach 2002
Trilobita	Trochurinae	S	19	21	37	0.815	0.861	0.710	1.175	0.887	0.825	0.045	Campbell and Chatterton 2007
Trilobita	Asteropyginae	D	38	66	104	0.988	0.860	0.006	2.490	0.899	0.085	0.008	Lieberman and Kloc 1997
Trilobita	Basidechenella	D	16	25	32	1.144	0.815	0.000	2.182	0.887	0.009	-0.171	Lieberman 1994
Trilobita	Dechenella	D	17	47	68	1.043	0.881	0.010	1.917	0.926	0.063	-0.066	Lieberman et al. 1991
Trilobita	Koneprusiinae	D	39	23	32	0.921	0.836	0.110	1.226	0.855	0.160	-0.055	Lieberman 1993
Trilobita	Malvinella	D	14	51	61	0.993	0.880	0.085	1.388	0.906	0.146	0.021	Lieberman 1994
Trilobita	Metacryphaeus	D	17	38	48	0.937	0.832	0.128	1.489	0.855	0.220	0.052	Adrain et al. 2008
Trilobita	Proetidae	D	21	52	58	0.866	0.825	0.303	1.145	0.844	0.389	0.015	Lieberman 1994
Trilobita	Trimeroccephalus	D	14	23	33	1.347	0.781	0.000	5.714	0.924	0.013	-0.035	Crônier 2003
Trilobita	Phillipsidae	C	28	30	38	0.980	0.890	0.034	0.717	0.866	0.019	-0.083	Brezinski 2003; 2005
Trilobita	Lichoidea	O	36	48	89	0.995	0.854	0.006	2.025	0.902	0.065	-0.009	Pollitt et al. 2005

Taxon	Study	Period	<i>S</i>	Ch	N	$D_{S/2}$	1-Rate			E. Rate			2-Rate			$\Delta[SC]$	Source(s)
							$E[D_{S/2}]$	p		L. Rate	$E[D_{S/2}]$	p					
Chelicerata	Early Arachnomorpha	Cm	24	38	51	0.879	0.789	0.172		1.417	0.817	0.270				-0.024	Cotton and Braddy 2003
Chelicerata	Eurypetridae	S	23	33	63	0.947	0.851	0.125		1.067	0.864	0.154				-0.022	Tetlie and Cuggy 2007
Chelicerata	Eurypetrus	S	13	20	27	1.021	0.832	0.117		1.500	0.891	0.208				-0.188	Tetlie 2006
Chelicerata	Stylonurina	S	23	45	45	0.887	0.759	0.127		1.222	0.795	0.191				0.019	Lamsdell et al. 2010
Crustacea	Astacidae	J	17	28	45	0.841	0.879	0.675		1.091	0.893	0.740				0.023	Rode and Babcock 2003
Crustacea	Astacoidea	J	23	21	39	0.831	0.816	0.450		1.194	0.849	0.574				0.001	Amati and Westrop 2004
Crustacea	Beyrichiocopa	O	34	39	48	0.902	0.770	0.069		1.412	0.802	0.131				-0.008	Tinn and Meidla 2004
Crustacea	Phyllocarida	D	41	54	83	0.872	0.813	0.158		1.938	0.880	0.547				-0.051	Rode and Lieberman 2002
Crustacea	Thylacocephala	D	18	15	36	0.802	0.876	0.816		1.083	0.886	0.853				0.034	Schram et al. 1999
Crustacea	Xanthoidea	Pg	21	62	64	1.075	0.780	0.000		6.353	0.908	0.123				-0.028	Karasawa and Schweitzer 2006
Cincta	Cincta	Cm	21	56	79	0.875	0.792	0.146		1.262	0.830	0.274				-0.012	Smith and Zamora 2009
Stylophora	Anomalocystitidae	O	20	97	97	0.993	0.829	0.004		1.935	0.894	0.093				0.005	Ruta 1999
Stylophora	Cornuta	O	32	72	78	0.941	0.786	0.010		1.770	0.849	0.130				-0.065	Cripps 1991
Stylophora	Cornuta	O	22	34	34	0.968	0.763	0.028		1.727	0.835	0.119				-0.026	Daley 1992
Stylophora	Cornuta	O	28	18	36	0.876	0.831	0.276		2.000	0.895	0.594				-0.080	Lefebvre 2001
Stylophora	Dendrocystitidae	O	15	16	25	0.915	0.853	0.259		0.778	0.848	0.259				-0.041	Parsley 1997; Parsley and Sumrall 2007
Stylophora	Mitrata	O	13	38	44	0.841	0.769	0.291		5.556	0.878	0.567				-0.085	Ruta and Theron 1997
Stylophora	Mitrata	O	17	76	134	0.927	0.820	0.085		2.388	0.907	0.409				0.008	Ruta 1997
Stylophora	Stylophora	O	42	42	91	0.889	0.818	0.139		1.300	0.833	0.195				0.019	Parsley 1997
Edrioasteroidea	Edrioasteroidea	O	15	24	27	0.640	0.788	0.846		1.150	0.806	0.872				0.077	Sumrall and Gahn 2006
Edrioasteroidea	Isorophida	O	13	23	24	1.194	0.789	0.001		5.833	0.913	0.050				-0.071	Sumrall and Zamora 2011
Asterozoa	Asterozoa	O	36	142	156	1.017	0.767	0.000		2.151	0.810	0.009				-0.016	Dean Shackleton 2005
Asterozoa	Goniasteridae	J	21	68	71	0.851	0.832	0.417		1.182	0.864	0.573				0.034	Blake 2010
Blastozoa	Blastoidea	D	68	93	153	0.910	0.806	0.029		2.100	0.856	0.193				0.024	Bodenbender 1995
Blastozoa	Pleurocystitidae	D	13	21	24	1.180	0.784	0.002		5.333	0.899	0.056				-0.087	Sumrall and Sprinkle 1995; Parsley and Sumrall 2007; Nardin and Bohatý 2013
Crinoidea	Basal Crinoidea	O	33	25	69	1.013	0.889	0.008		2.472	0.939	0.097				-0.037	Ausich 1998a
Crinoidea	Botryocrinidae	C	13	14	21	0.838	0.824	0.460		1.571	0.895	0.653				-0.016	Gahn and Kammer 2002
Crinoidea	Calceocrinidae	S	22	17	32	1.027	0.878	0.012		1.100	0.892	0.031				0.072	Harvey and Ausich 1997
Crinoidea	Camerata	O	28	27	72	1.028	0.885	0.003		1.845	0.926	0.035				-0.017	Ausich 1998b

Taxon	Study	Period	<i>S</i>	Ch	N	$D_{S/2}$	1-Rate			E. Rate			2-Rate			$\Delta[SC]$ Source(s)
							$E[D_{S/2}]$	p		L. Rate	$E[D_{S/2}]$	p				
Crinoidea	Cladida	O	27	21	46	1.060	0.827	0.002		2.200	0.893	0.034				-0.007 Ausich 1998b
Crinoidea	Cupulocrinidae	O	13	19	34	1.002	0.815	0.048		4.300	0.934	0.337				-0.090 Brower 2001
Crinoidea	Cyathocrinites	C	14	14	17	0.787	0.810	0.578		0.941	0.802	0.553				-0.022 Kammer and Gahn 2003
Crinoidea	Disparida	O	45	31	77	0.965	0.844	0.021		1.678	0.885	0.097				0.011 Ausich 1998b
Crinoidea	Pereichocrinidae	D	20	32	42	1.035	0.880	0.011		3.097	0.950	0.147				0.088 Ausich and Kammer 2008
Echinoidea	Arbacoidea	K	21	40	48	0.706	0.763	0.723		1.375	0.814	0.843				-0.022 Smith and Wright 1993
Echinoidea	Arbacoidea	Tr	25	26	41	1.052	0.854	0.004		1.938	0.878	0.015				-0.153 Smith 1994
Echinoidea	Cassiduloidea	K	69	38	57	0.808	0.796	0.417		1.745	0.824	0.575				-0.008 Suter 1994
Echinoidea	Cassiduloidea	K	49	31	47	0.947	0.799	0.017		2.533	0.852	0.107				-0.087 Saucède and Neraudeau 2006
Echinoidea	Clypeasteroidea	K	43	42	61	0.976	0.786	0.002		4.400	0.875	0.149				-0.006 Smith 2001
Echinoidea	Disasteroidea	K	26	19	28	0.941	0.817	0.093		1.320	0.840	0.138				0.033 Barras 2007
Echinoidea	Holasteroidea	K	43	34	51	0.816	0.798	0.396		1.216	0.819	0.518				-0.023 Smith 2004
Echinoidea	Irregularia	J	27	37	50	0.968	0.819	0.020		2.026	0.887	0.154				-0.091 Saucède et al. 2007
Echinoidea	Loveniidae	Pg	14	38	61	1.003	0.914	0.093		1.385	0.940	0.178				-0.047 Kroh 2007
Echinoidea	Mesozoic Echinoidea	Tr	46	54	77	0.806	0.783	0.355		1.583	0.817	0.560				0.000 Smith 2007
Echinoidea	Somaliasteridae	K	19	24	31	1.031	0.806	0.007		1.360	0.848	0.047				-0.071 Jeffery 1999
Echinoidea	Spatangoidea	Pg	50	68	104	0.892	0.787	0.049		1.859	0.839	0.248				0.022 Stockley et al. 2005
Echinoidea	Temnopleuridae	Pg	16	36	47	1.074	0.835	0.004		1.889	0.867	0.021				-0.038 Jeffery and Emlet 2003
Echinoidea	Toxasteridae	J	35	35	62	0.963	0.829	0.014		1.377	0.849	0.033				-0.039 Villier et al. 2004
Conodonta	Hindeodus-Isarcicella	P	21	20	20	0.763	0.793	0.604		1.529	0.851	0.765				0.036 Jiang et al. 2011
Conodonta	Kockelella	S	17	36	36	0.580	0.824	0.972		0.702	0.814	0.970				0.040 Wickström and Donoghue 2005
Conodonta	Palmatolepis	D	15	25	26	0.755	0.742	0.469		1.846	0.868	0.743				-0.002 Donoghue 2001
Cephalaspida	Thyestiidae	S	18	31	40	0.920	0.895	0.361		1.031	0.908	0.422				-0.039 Sansom 2008
Placoderma	Pteraspidoformes	D	26	59	98	1.002	0.859	0.011		1.804	0.885	0.025				-0.082 Pernègre and Elliott 2008
Placoderma	Actinolepidae	S	18	37	37	0.878	0.812	0.254		1.139	0.827	0.328				0.038 Johnson et al. 2000
Placoderma	Arthrodira	D	31	54	56	0.814	0.824	0.538		0.656	0.802	0.446				-0.012 Dupret 2004
Placoderma	Eubrachythoraci	D	19	48	61	0.963	0.885	0.198		0.737	0.880	0.173				0.021 Carr and Hlavin 2010
Placoderma	Phyllolepidae	D	38	63	64	0.755	0.806	0.756		0.504	0.773	0.581				-0.042 Dupret and Zhu 2007
Actinopterygia	Amblypteridae	C	50	57	90	0.903	0.841	0.105		1.748	0.885	0.384				0.017 Dietze 2000
Actinopterygia	Amiidae	Pg	21	45	48	1.019	0.735	0.013		4.636	0.873	0.201				-0.054 Grande and Bemis 1998

Taxon	Study	Period	S	Ch	N	$D_{S/2}$	1-Rate $E[D_{S/2}]$	p	E. Rate L. Rate	2-Rate $E[D_{S/2}]$	p	$\Delta[SC]$ Source(s)
Actinopterygia	Basal Teleostei	J	26	126	160	0.903	0.784	0.071	1.523	0.807	0.133	0.011 Arratia 1996; Arratia and Tischlinger 2010
Actinopterygia	Palaeonisciformes	D	15	44	53	0.903	0.798	0.143	0.882	0.811	0.170	-0.037 Swartz 2009
Actinopterygia	Ginglymodi	Pg	27	70	88	0.746	0.819	0.818	0.950	0.825	0.845	0.012 López-Arbarello and Zavattieri 2008; López-Arbarello 2012
Actinopterygia	Osteoglossomorphes	Tr	18	65	88	0.851	0.839	0.446	0.817	0.824	0.372	-0.010 Wilson and Murray 2008
Actinopterygia	Perleidiformes	Tr	14	27	32	0.966	0.827	0.068	1.300	0.861	0.141	-0.066 López-Arbarello and Zavattieri 2008
Actinopterygia	Scanalepiformes	D	13	50	57	0.826	0.809	0.429	1.531	0.865	0.635	0.072 Xu and Gao 2011
Actinopterygia	Tetradontiformes	D	36	58	88	1.080	0.818	0.000	14.167	0.882	0.015	0.030 Santini and Tyler 2003
Sarcopterygia	Basal Sarcopterygia	C	32	140	158	0.973	0.782	0.008	2.553	0.842	0.090	-0.013 Cloutier and Ahlberg 1995
Sarcopterygia	Basal Sarcopterygia	C	25	147	167	0.946	0.789	0.019	1.542	0.839	0.082	-0.057 Zhu et al. 2001
Sarcopterygia	Coelocanthiformes	C	30	72	94	0.872	0.855	0.394	1.280	0.866	0.466	0.002 Cloutier 1991
Sarcopterygia	Coelocanthiformes	Tr	24	101	106	0.742	0.813	0.769	1.114	0.824	0.809	0.029 Forey 1991; Clement 2005
Sarcopterygia	Devonian Dipnoi	D	26	59	61	0.942	0.804	0.049	1.267	0.820	0.079	-0.123 Friedman 2007
Sarcopterygia	Mesozoic Dipnoi	D	16	14	22	1.110	0.840	0.006	2.000	0.879	0.026	-0.029 Cavin et al. 2007
Sarcopterygia	Rhipidistia	Pg	30	99	112	1.125	0.782	0.000	4.390	0.905	0.022	-0.040 Johanson et al. 2006
Tetrapoda	Early Tetrapoda	C	21	109	136	0.715	0.823	0.889	0.955	0.831	0.897	-0.003 Ahlberg et al. 2008
Temnospondyla	Brachyopoidea	P	21	45	54	1.023	0.808	0.006	1.744	0.873	0.061	-0.027 Warren and Marsicano 2000; Damiani et al. 2007
Temnospondyla	Branchiosauridae	P	19	40	47	1.053	0.782	0.004	2.958	0.893	0.084	-0.108 Schoch and Milner 2008
Temnospondyla	Capitosauria	Tr	22	42	49	0.879	0.808	0.199	0.619	0.766	0.117	-0.023 Schoch 2008b
Temnospondyla	Edopoidea	C	15	42	51	0.932	0.906	0.366	0.644	0.898	0.307	-0.102 Sidor et al. 2005; Steyer et al. 2006
Temnospondyla	Mastodonsauroidea	P	21	38	41	0.972	0.844	0.058	1.408	0.873	0.116	-0.099 Damiani 2001
Temnospondyla	Stegocephalia	C	16	59	67	0.945	0.881	0.206	0.937	0.881	0.206	0.028 Laurin and Soler-Gijón 2006
Temnospondyla	Stereospondylia	P	15	83	89	0.899	0.825	0.194	1.062	0.849	0.275	-0.026 Schoch 2008a
Synapsida	Basal Synapsida	P	17	46	56	1.100	0.829	0.002	1.667	0.890	0.018	-0.171 Benson 2012
Therapsida	Anomodontia	P	30	69	99	0.999	0.828	0.002	2.313	0.904	0.101	-0.044 Angielczyk 2002; Fröbisch 2007
Therapsida	Cynodontia	P	16	56	73	0.856	0.834	0.405	1.070	0.840	0.444	-0.044 Botha et al. 2007
Therapsida	Dicynodontia	Tr	29	60	89	0.970	0.834	0.024	1.551	0.860	0.069	-0.020 Angielczyk 2007
Therapsida	Eutheriodontia	Tr	23	79	113	0.676	0.828	0.974	1.235	0.861	0.992	0.000 Abdala 2007

Taxon	Study	Period	S	Ch	N	$D_{S/2}$	1-Rate		<u>E. Rate</u>	2-Rate		$\Delta[SC]$	Source(s)
							$E[D_{S/2}]$	p	L. Rate	$E[D_{S/2}]$	p		
Therapsida	Eutherocephalia	Tr	21	70	82	0.886	0.805	0.133	1.444	0.861	0.371	-0.033	Huttenlocker 2009; Huttenlocker et al. 2011
Therapsida	Traversodontidae	Tr	16	39	47	0.893	0.844	0.306	1.326	0.861	0.376	0.001	Abdala and Ribeiro 2003; Kammerer et al. 2008
Mammalia	Amphilestidae	K	20	56	71	0.921	0.786	0.091	2.054	0.834	0.209	-0.056	Rougier et al. 2007
Mammalia	Anomaluroidea	Pg	14	100	149	1.116	0.836	0.000	2.119	0.897	0.017	-0.084	Marivaux et al. 2011
Mammalia	Arctoidea	Pg	20	32	44	0.741	0.826	0.822	0.898	0.819	0.795	0.002	Wang et al. 2005
Mammalia	Basal Aplodontoidea	Pg	61	194	253	0.767	0.831	0.877	0.725	0.819	0.821	0.033	Hopkins 2008
Mammalia	Basal Cetacea	Pg	17	38	63	0.855	0.841	0.439	1.561	0.867	0.547	-0.017	Uhen and Gingerich 2001
Mammalia	Basal Ctenodactyloidea	Pg	14	21	29	0.783	0.843	0.687	0.719	0.826	0.620	0.050	Dashzeveg and Meng 1998
Mammalia	Borophaginae	Pg	66	76	119	0.683	0.777	0.931	1.107	0.781	0.941	0.007	Wang et al. 1999
Mammalia	Brontotheriidae	Pg	47	73	112	0.890	0.797	0.096	1.545	0.830	0.202	0.012	Mihlbachler 2008
Mammalia	Carnivoramorpha	Pg	24	78	110	0.817	0.825	0.546	1.362	0.852	0.677	0.016	Wesley-Hunt and Flynn 2005
Mammalia	Carpolestidae	Pg	13	25	42	0.763	0.827	0.690	0.900	0.840	0.717	-0.008	Bloch et al. 2001
Mammalia	Ceratomorpha	Pg	22	24	31	0.582	0.786	0.942	0.645	0.724	0.867	-0.044	Holbrook 2001
Mammalia	Chalicotheriidae	Pg	17	39	62	0.883	0.865	0.399	0.327	0.800	0.194	0.055	Hooker and Dashzeveg 2004
Mammalia	Cretaceous Eutheria	K	23	69	111	0.927	0.844	0.125	1.459	0.873	0.267	-0.005	Archibald et al. 2001
Mammalia	Dichobunidae	Pg	23	26	36	0.764	0.852	0.846	0.857	0.852	0.846	-0.015	Métais et al. 2004
Mammalia	Elephantiformes	Ng	31	54	67	0.975	0.791	0.011	2.189	0.862	0.110	-0.020	Shoshani et al. 2006
Mammalia	Eocene Equidae	Pg	18	58	68	0.633	0.796	0.931	0.940	0.796	0.931	0.014	Froehlich 2002
Mammalia	Eotheria	J	21	55	70	0.961	0.797	0.036	2.595	0.879	0.227	0.008	Rougier et al. 2001
Mammalia	Equidae	Pg	17	52	82	0.838	0.852	0.560	1.758	0.891	0.717	0.024	Alroy 1995
Mammalia	Equinae	Ng	19	32	55	0.946	0.848	0.098	2.514	0.943	0.479	-0.035	Prado and Alberdi 1996
Mammalia	Hippopotamidae	Pg	16	31	39	0.888	0.828	0.277	1.517	0.860	0.408	-0.043	Boisserie 2005
Mammalia	Hippotragini	Ng	15	22	27	1.005	0.772	0.046	2.077	0.867	0.181	-0.106	Geraads et al. 2008
Mammalia	Hominidae	Ng	14	87	146	0.872	0.863	0.463	0.520	0.807	0.264	-0.024	Strait and Grine 2004
Mammalia	Hominoidea	Ng	14	125	149	0.647	0.881	0.989	0.289	0.813	0.910	-0.036	Finarelli and Clyde 2004
Mammalia	Hyaenidae	Ng	18	19	26	1.017	0.872	0.295	1.125	0.893	0.397	-0.242	Werdelin and Solounias 1991
Mammalia	Hyaenodontida	Pg	34	59	75	0.876	0.813	0.178	1.716	0.857	0.391	0.021	Polly 1996; Solé 2013
Mammalia	Louisinidae	Pg	22	66	128	1.007	0.853	0.014	1.358	0.868	0.030	-0.019	Hooker and Russell 2012
Mammalia	Megalochinidae	Ng	14	41	65	0.986	0.877	0.086	1.917	0.915	0.210	-0.004	Pujos et al. 2007

Taxon	Study	Period	S	Ch	N	$D_{S/2}$	1-Rate			E. Rate			2-Rate			$\Delta[\text{SC}]$ Source(s)
							$E[D_{S/2}]$	p		L. Rate	$E[D_{S/2}]$	p				
Mammalia	Megalonychidae	Ng	14	17	27	0.781	0.864	0.816		0.722	0.839	0.722				-0.005 Carlini et al. 2009
Mammalia	Mioclaenidae	Pg	31	50	73	0.873	0.836	0.297		0.881	0.836	0.297				-0.034 Williamson and Carr 2007
Mammalia	Multituberculata	K	32	60	91	0.840	0.845	0.528		1.682	0.869	0.639				0.087 Kielan-Jaworowska and Hurum 2001
Mammalia	Mysticetiidae	Ng	32	149	222	1.036	0.812	0.000		2.129	0.852	0.014				-0.088 Bisconti 2007
Mammalia	Notoungulata	Pg	17	28	32	0.846	0.763	0.266		3.200	0.839	0.482				0.028 Shockey 1997
Mammalia	Odobenidae	Ng	14	42	64	0.594	0.811	0.963		0.357	0.720	0.764				0.033 Kohno 2006
Mammalia	Omomyidae	Pg	29	279	391	0.851	0.806	0.227		1.874	0.878	0.643				0.022 Ni et al. 2010
Mammalia	Paucituberculata	Pg	21	42	62	0.775	0.840	0.807		0.905	0.840	0.807				-0.017 Goin et al. 2009
Mammalia	Protoselendonta	Pg	23	26	36	0.764	0.845	0.862		0.860	0.845	0.862				-0.015 Grégoire et al. 2004
Mammalia	Selenodonta	Pg	22	57	76	1.020	0.906	0.024		1.774	0.934	0.078				0.071 Métais 2006
Mammalia	Toxodontidae	Ng	20	56	79	1.027	0.867	0.012		0.893	0.864	0.007				0.021 Nasif et al. 2000
Mammalia	Xenungulata	Pg	22	20	49	0.976	0.881	0.067		2.029	0.916	0.190				-0.037 Gelfo et al. 2008
Mammalia	Zapodidae	Pg	25	28	36	0.867	0.833	0.322		1.022	0.837	0.343				-0.018 López-Antoñanzas and Sen 2006
Anapsida	Ankyramorpha	P	19	86	100	1.063	0.824	0.001		2.083	0.898	0.029				-0.035 Tsuji et al. 2010
Anapsida	Baenidae	K	14	51	57	0.971	0.832	0.099		0.932	0.832	0.099				0.031 Lyson and Joyce 2009
Anapsida	Basal Testudinata	J	33	90	102	0.993	0.775	0.012		1.661	0.802	0.043				0.017 Joyce 2007
Anapsida	Procolophonoidea	Tr	21	37	52	0.731	0.806	0.798		1.227	0.839	0.876				0.022 Cisneros 2008
Ichthyosauria	Ichthyosauria	J	31	93	120	0.871	0.798	0.164		2.028	0.878	0.527				-0.017 Motani 1999; Thorne et al. 2011
Sauropterygia	Mosasauroidea	K	33	89	108	0.926	0.827	0.058		1.160	0.844	0.090				-0.045 Bell 1997; Christiansen and Bonde 2002; Dortangs et al. 2002
Sauropterygia	Plesiosauroidea	J	32	132	165	0.784	0.845	0.817		0.959	0.845	0.817				0.003 O'Keefe 2001
Sauropterygia	Sphenodontia	Tr	22	47	63	1.011	0.880	0.020		1.577	0.909	0.075				-0.020 Reynoso 1996
Archosauria	Archosauromorpha	Tr	20	130	153	0.887	0.837	0.255		1.471	0.859	0.356				0.053 Dilkes 1998
Archosauria	Basal Crocodyliformes	K	33	128	159	0.967	0.810	0.008		2.063	0.869	0.117				-0.066 Salisbury et al. 2006
Archosauria	Basal Crurotarsia	Tr	20	125	136	0.931	0.858	0.170		0.761	0.842	0.110				-0.032 Brusatte et al. 2010a
Archosauria	Crocodylia	K	48	138	172	0.938	0.822	0.029		1.272	0.832	0.049				-0.033 Brochu 1997; Zaher et al. 2006
Archosauria	Diplocynodontinae	Pg	35	114	136	1.070	0.797	0.000		2.554	0.890	0.023				-0.061 Piras and Buscalioni 2006
Archosauria	Metriorhynchidae	J	34	63	89	0.876	0.772	0.130		1.451	0.804	0.221				0.016 Young and De Andrade 2009
Archosauria	Metriorhynchinae	J	18	42	67	0.612	0.797	0.958		0.610	0.777	0.913				0.062 Wilkinson et al. 2008
Archosauria	Phytosauridae	Tr	18	29	36	0.922	0.871	0.296		0.508	0.844	0.235				-0.089 Stocker 2010; Stocker 2012

Taxon	Study	Period	S	Ch	N	$D_{S/2}$	1-Rate		E. Rate		2-Rate		$\Delta[SC]$	Source(s)
							$E[D_{S/2}]$	p	L. Rate	$E[D_{S/2}]$	p			
Archosauria	Protosuchidae	J	14	134	147	0.876	0.823	0.287	0.993	0.823	0.287	0.008	Gasparini et al. 2006	
Archosauria	Sebecosuchia	Pg	16	29	36	1.045	0.786	0.042	1.136	0.802	0.050	-0.054	Pol et al. 2012; Kellner et al. 2014	
Archosauria	Basal Pterosauria	J	18	71	82	0.916	0.797	0.111	2.585	0.877	0.376	0.013	Andres et al. 2010	
Archosauria	Pterosauria	J	56	117	160	0.877	0.802	0.114	1.789	0.835	0.255	-0.030	Lü et al. 2010	
Archosauria	Ankylosauria	K	45	140	149	0.869	0.886	0.629	1.485	0.901	0.727	0.010	Thompson et al. 2012	
Archosauria	Ankylosauroidea	K	16	54	65	0.933	0.918	0.422	1.009	0.926	0.461	0.051	Ösi 2005	
Archosauria	Basal Iguanodontia	J	21	31	38	0.856	0.848	0.470	1.515	0.900	0.668	0.045	McDonald 2012	
Archosauria	Ceratopsidae	K	13	17	22	0.816	0.767	0.352	2.750	0.911	0.666	-0.014	Wu et al. 2007	
Archosauria	Ceratosauria	K	18	27	28	0.928	0.803	0.215	4.875	0.957	0.567	0.001	Carrano and Sampson 2008	
Archosauria	Chasmosaurinae	K	18	61	75	0.844	0.844	0.501	1.123	0.851	0.534	0.020	Sampson et al. 2010	
Archosauria	Deinonychosauria	K	17	75	83	1.038	0.812	0.010	1.926	0.856	0.049	0.053	Makovicky and Sues 1998; Xu et al. 2002a; Hwang et al. 2002	
Archosauria	Diplodocoidea	J	20	106	107	0.723	0.798	0.759	1.133	0.810	0.796	0.035	Whitlock 2011	
Archosauria	Dromaeosauridae	K	17	108	115	1.167	0.832	0.003	3.476	0.899	0.022	-0.055	Zheng et al. 2010	
Archosauria	Hadrosauroidea	K	29	126	143	0.929	0.774	0.011	2.145	0.856	0.195	-0.063	Sues and Averianov 2009	
Archosauria	Megalosauroidea	J	15	34	37	0.545	0.762	0.953	0.629	0.729	0.921	-0.021	Benson et al. 2010	
Archosauria	Neoceratopsia	K	18	110	131	0.806	0.815	0.537	0.795	0.799	0.476	-0.008	Makovicky and Norell 2006; Zhao et al. 2006	
Archosauria	Ornithopoda	K	14	72	75	0.874	0.845	0.375	1.169	0.860	0.437	-0.140	Weishampel et al. 2003	
Archosauria	Oviraptorosauria	K	13	39	42	1.236	0.825	0.003	10.800	0.931	0.047	-0.114	Xu et al. 2002b; Xu et al. 2002a	
Archosauria	Prosauropoda	Tr	15	110	110	1.018	0.845	0.035	1.211	0.870	0.061	0.039	Yates 2003	
Archosauria	Saurolophidae	K	28	210	295	0.969	0.813	0.011	1.361	0.849	0.029	-0.046	Prieto-Márquez 2010	
Archosauria	Sauropoda	J	28	270	340	0.847	0.858	0.595	1.142	0.875	0.683	0.033	Harris 2006	
Archosauria	Titanosauriformes	K	21	64	67	0.786	0.779	0.478	1.333	0.818	0.602	-0.041	D'Emic 2012	
Archosauria	Tyransauroidae	K	19	284	324	0.658	0.759	0.879	1.631	0.817	0.953	0.014	Brusatte et al. 2010b	

“Period” gives the geochronological period from which most taxa in an analysis are known: Cm=Cambrian; O=Ordovician; S=Silurian; D=Devonian; C=Carboniferous; P=Permian; Tr=Triassic; J=Jurassic; K=Cretaceous; Pg=Paleogene; Ng=Neogene. “S” = Number of taxa. “Ch”= Number of characters. “N” = Number of novel states (= Number of characters if all characters are binary). $D_{S/2}$ = Disparity as average pairwise dissimilarity between taxa among the first half of all S taxa. This is a proportion of

the disparity among all S taxa; note that disparity can decrease (yielding $D_{S/2} > 1$) when the latter half of diversification largely fills in existing morphospace. $E[D_{S/2}]$ gives the expected disparity among the first $S/2$ taxa given either a uniform rate (1-rate) of independent change or a separate early and late rate (2-Rate) of change given 1000 Monte Carlo simulations, where the rates maximize the probability of the observed compatibility among either all S taxa (1-Rate) or the earliest $S/2$ taxa (2-rate). $P[D_{S/2}]$ gives the proportion of Monte Carlo runs generating $D_{S/2}$ equaling or surpassing the observed. $\frac{\text{Early Rate}}{\text{Late Rate}}$ gives the proportional difference between the early and late rates. $\Delta[\text{SC}]$ gives the difference between observed and expected stratigraphic compatibility based on the same Monte Carlo analyses assuming the 2-rate model of independent change.