Do deviants live longer? Morphology and longevity in trachyleberidid ostracodes

Lee Hsiang Liow

Abstract.—Persistent fossil taxa contravene paradigms of evolution: pervasive morphological change and taxic turnover. Comparative studies of taxic duration have often been approached from biogeographic, climatic, and ecological perspectives, with a focus on process. Here I use a morphological approach to study the pattern of longevity of a large family of marine living and fossil podocopid ostracodes, Trachyleberididae sensu lato. I test if geologically longer-lived genera are collectively morphologically more deviant from a group mean than their shorter-lived relatives by using both discrete morphological data and outline data. I discovered that long-lived genera are in general not significantly more or less morphologically deviant from the average morphology than their shorter-lived relatives. However, I found that contemporaneous subsets of long-lived trachyleberidids are often at least marginally significantly more deviant in discrete morphology than shorter-lived ones, especially in external morphology. No significant patterns of association between morphological deviation and durations in other subdivisions of the data emerged (i.e., whole data set, birth cohorts, groups of morphological characters, and outline data using both Fourier analysis and eigenshape analysis). This is in contrast to a previous finding that long-lived genera of crinoids within orders are often morphologically less deviant than their shorter-lived relatives than expected by chance.

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Introduction

The prolonged persistence of taxa in the fossil record is interesting because persistence is contrary to evolution, which implies pervasive change. The study of geologic longevity of taxa has had several guises. Longevity has been explored through the analysis of extinction probability, taxon selectivity across extinction events, extinction risk, and survivorship (Pearson 1992; Gilinsky 1994; Jablonski 1994; Jablonski and Raup 1995; McKinney 1997). Taxa with wider geographic ranges seem to have lower extinction risks, at least during ''background times'' (Jablonski 1986; Jablonski and Raup 1995), although counter-evidence also exists (Vermeij 1993). Taxa with less specialized feeding strategies also appear to have longer geologic durations, at least for Paleozoic crinoid species (Baumiller 1993). Morphological complexity has also been suggested as a correlate of longevity (Flessa et al. 1975; Anstey 1978; Ward and Signor 1983; Boyajian and Lutz 1992) although a definitive relationship between these variables is lacking. Taxa with larger body sizes, and correspond-

ingly longer generation times, turn over more slowly or are geologically more persistent than related taxa that are smaller (Van Valen 1975; Flynn et al. 1995). Some studies, however, suggest that it is not the organism that maintains the inertia of change. Instead, attributes of the environment (stability, suitability) seemingly promote their geologic longevity (Alexander 1977; Fortey 1980; Norris 1992).

In general, ecologically more specialized taxa are more prone to extinction because of smaller geographic ranges, fewer potential habitats, narrower niche breadths, and lower abundances. These generalizations have been shown for Mesozoic–Cenozoic Foraminifera genera (Banerjee and Boyajian 1996), species of carnivorous Miocene mammals (Viranta 2003), and Mississippian crinoid species (Kammer. et al. 1997, 1998). Ecological specialization was inferred from morphology in the above studies, with the implicit assumption that morphology is a proxy for ecology.

In this study, I compare ostracode genus longevities directly with their morphologies. I do this in the spirit of an empirical multivariate morphospace approach (Foote 1997; Roy

and Foote 1997 and references therein), although here, distances from a mean are utilized rather than measures of disparity. I predict that the longer the genera survive, the more morphologically average or less specialized they should be when compared with shorter-lived genera, in accordance with Simpson's (1944) ''survival of the relatively unspecialized.'' These comparisons are in the context of overall morphological variation among constituent members of a particular clade, existing or appearing during particular geologic time intervals (contemporaneous genera and birth cohorts). Morphologically average genera are potentially more general ecologically and less prone to stochastic environmental perturbations, and may have greater survivorship than morphologically deviant (= more specialized) genera. This prediction also follows from a previous finding that long-lived fossil crinoid genera throughout the Phanerozoic (either moderately or extremely long-lived) tend to be more average (less specialized, less deviant) in morphology than expected when compared with shorter-lived congeners in crinoid orders (Liow 2004). This finding contrasts with some thinking that extremely long-lived taxa or ''living fossils'' are special or exceptional (Parsons 1994; Eisner 2003).

Specifically, I examine a large family of marine podocopid ostracodes, the Trachyleberididae sensu lato, to test whether longer-lived genera are (i) morphologically average (i.e., no different collectively from shorter-lived genera); and (ii) morphologically more or less average than their shorter-lived relatives than expected. I use two independent sets of morphological data (discrete morphology and outlines) to examine the sensitivity of resulting patterns to data types. I also parse the data in several ways to validate the results on the basis of consistency and to account for some possible sampling biases. I plot various measures of morphological deviations of genera from their group mean versus their geologic durations to produce morphological deviation-duration plots.

Longer-lived taxa often appear to plot rather close to the average morphology in morphological deviation-duration plots, whereas
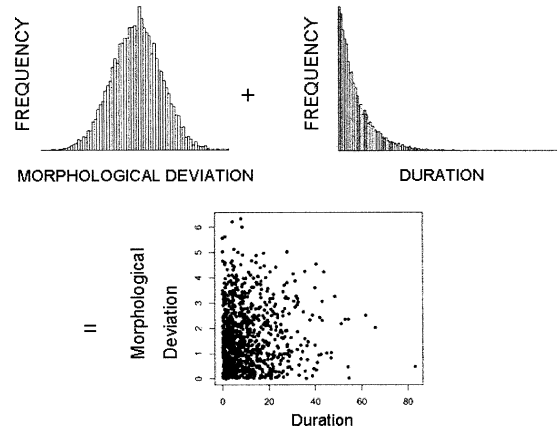

FIGURE 1. Top left, Histogram of morphological deviations drawn from a simulated normal distribution. Top right, Histogram of durations drawn from a simulated exponential distribution. Bottom, Plot of random pairing of values from top left and right, showing that the few long-lived simulated taxa are less spread out along the y-axis than shorter-lived taxa.

shorter-lived taxa span a wider range of morphologies (Liow 2004, this study). Because there are often many more shorter-lived taxa than longer-lived ones, there is a higher probability that some will have morphologies that deviate greatly from the group mean. Conversely, because there are few long-lived taxa, there is a much lower probability for any of them to be very far from the average morphology of the group (Fig. 1). The question then becomes whether they are closer or farther from the mean morphology than expected by chance alone.

In this study, I show that collective morphological deviation of long-lived trachyleberidid ostracode genera from the group mean is not significantly different from that of shorter-lived genera in most of my analyses. However, analyses of contemporaneous genera in epochs (all genera existing in a epoch, regardless of when they first or last appear) show that longer-lived taxa are sometimes collectively marginally more deviant morphologically than shorter-lived ones. This last finding, in contrast with a general pattern of nonsignificance, is discussed in light of the scale of observation as well as potential biological implications.

Data and Methods

The Organisms and the Raw Data.—Members of the Trachyleberididae sensu lato (Podocop-

ida: Cytheracea) are found in benthic sediments all over the world, from the shallowest brackish waters to the deepest oceans. It is a large family (perhaps equivalent to a higher taxonomic level in other marine invertebrates such as mollusks) that began definitively in the earliest Late Cretaceous, although trachyleberidid-like taxa have been found as early as the Jurassic (e.g., *Oligocythereis* and *Morkhovenicythereis* [see Gruendel 1975 and Lord 1979]). Members of this family are still abundant today even though many of its earlier-occurring genera are extinct. This family is heavily utilized in biostratigraphy not least because of its abundance and its frequently ornate nature, which makes taxonomic recognition less problematic than with many marine invertebrate groups or other ostracode taxa.

I constructed a relational database of species of trachyleberidid species that attempts to eliminate taxonomic synonyms. The data include the species' geographic and geologic occurrences, as well as their membership in genera. Stratigraphic ranges of genera are built from those of their component species. Using the International Stratigraphic Chart (International Commission on Stratigraphy 2004) I converted the published time of first and last appearances of species to numerical values. Durations of genera are computed as the length of absolute time between the middle of the interval in which their first species appear and the middle of the interval in which their last species disappear. The level of stratigraphic resolution for species was inevitably heterogeneous. However, instead of discarding data of a lower resolution, I included them in calculating durations for two reasons. First, because this study involves a comparison of durations, only the relative ranking of durations are really vital and a (morphologically) random distribution of species with better or poorer resolved time intervals should not bias results. Second, to discard species with less well resolved time intervals would greatly shorten known genus durations in numerous instances. Genera that are reported to occur only in one time interval are reported as having durations of zero, even though that is an impossibility. However, as before, only the approximate relative positioning of genera ac-

cording to duration is important here because binary bins of genera with long or shorter durations are used in the main analyses.

My analyses are based on 326 genera, after excluding synonyms and doubtful genera. The family was erected in 1948 (Sylvester-Bradley 1948) and many of its 300+ genera have been variously assigned to Trachyleberididae sensu stricto or one of its closely allied families (sometimes also reported as subfamilies of Trachyleberididae), e.g., Hemicytheridae, Buntoniidae, or Brachycytherinidae. Although specific assignments to family, subfamily, or tribe have fluctuated historically, general agreement on what a trachyleberidid is, sensu lato, can be assumed with relative confidence. The relationships of lower taxa in family Trachyleberididae sensu lato cannot be clearly delineated with our current knowledge, although the recognition of species within the family is not problematic by most standards.

There is no published trachyleberidid taxonomic list, although several major references, not least Hazel 1967 and van Morkhoven 1963, provided a baseline compilation of the species and genera of this family. To assess the completeness of my literature survey, I constructed sampling effort curves for species and genera. The sampling curve for genera started to flatten after about 85 days of data collection (Fig. 2). There are currently more than 4000 species in the database. Addition of species new to my database has not changed the stratigraphic ranges of genera since the time my genus-collection curve began flattening, indicating that my sampling has sufficiently traced the existing literature.

The rationale for focusing on the generic level, even though species stratigraphic range data are available for this study, is twofold. First, species stratigraphic durations are less stable than genus durations. Addition of new occurrences may often change the known geologic range of a species, unlike the case of the genus mentioned above. Second, detailed morphology is not as completely known for species such that species-level analyses will inevitably involve many more unknown character states, not to mention that the number of
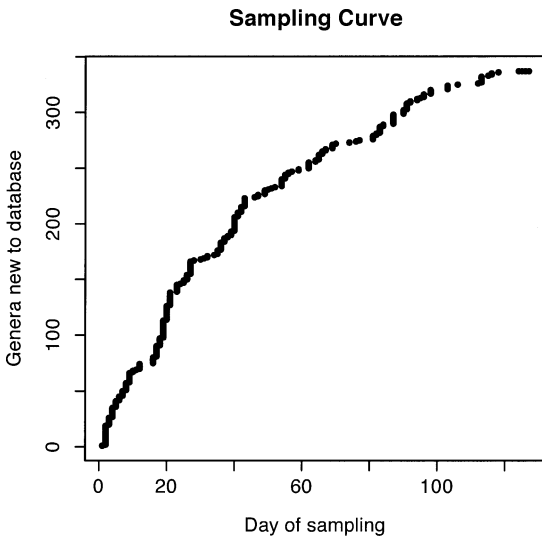
ue is simply the mean of the character states of all the genera, excluding those that were coded as ''unknown'' or ''inapplicable,'' which translates as the probability of occurrence of that character state. Similarly, for ordered multistate characters, the numerical mean of the character states is calculated. For unordered multistate characters, however, the average value is taken to be the modal state of the character and any other character state is taken as being one unit removed, regardless of the numerical coding of the character state. Lastly, for meristic characters, such as the number of denticles, natural logarithms are applied before means and distances are calculated. This transformation moderates the effects of counted characters in genera otherwise not very different from each other (e.g., denticle-poor versus denticle-rich). The different ranges of values assigned to these four character types give slightly different weights to characters of each type. However, because the ranges are not overwhelming different, and because the importance of each character and its independence from other characters is not currently known, nothing further is done to modify the degree of contribution of various characters to the overall morphospace.

As an alternative method to studying distance from a mean morphology to that described above, I also calculated principal coordinate scores (PCO) (Gower 1966). This is simply a principal components analysis (PCA) performed on the genus-to-genus morphological-distance matrix. I then calculated departures of respective PCA scores of each genus from the PCA scores averaged from all the genera included in the analysis and compared the sum of those departures with their respective genus durations.

Removal of Oversplit Taxa.—It is possible that my database contains a number of oversplit genera whose morphologies are very similar, at least on the basis of the characters used. Hence if they are not ''real'' genera, these kinds of morphologies could contribute excessively in the calculation of the family morphological mean. I removed 49 genera (see Appendix 4 online at http://dx.doi.org/10.1666/05004.s1) that are potentially oversplit and reran the analyses as above. These genera either

were first erected as subgenera or are parts of genus-complexes. The representative genera retained are the better known of the pair or group of closely related genera.

Data Treatment and Analysis: Outline Data.—I analyzed the outline coordinates in two ways in order to test the robustness of results. First, I performed PCA using the harmonics from Fourier analysis (Ferson et al. 1985). I compared the resulting PCA scores of each genus with the mean PCA scores of the family calculated from the genus PCA scores. The Fourier analysis was done using elliptical Fourier analysis (EFA) as written by Rohlf (1992). The first ten harmonics regenerated outlines precisely; thus they were used in PCA analyses and subsequent harmonics ignored. The second method used standard eigenshape analysis (MacLeod 1999), a completely different approach to studying outlines. This was chosen over the more powerful extended eigenshape analysis, which takes into account the location of homologous points around an outline. The reason is because multiple precise homologous points cannot be identified reliably on the external carapace on such a wide range of taxa. The output data are eigenshape scores, which are equivalent to PCA scores. The eigenshape scores for each genus are compared with the family mean as described earlier in this paragraph for Fourier analysis.

Defining Long-lived Genera.—There are many ways of identifying long-lived taxa in any given group (Liow 2004). Here, I define long-lived genera in three ways: (1) the most-long-lived 5% of genera, (2) the most-long-lived 10% of genera, and (3) genera having a duration greater than the midrange duration of the sample of genera included in a particular analysis. I chose to use ''long-lived'' and ''shorter-lived'' to reflect genera with long durations and those that have comparatively shorter durations, respectively, because the durations of some of the shorter-lived genera may not be ''short'' by other definitions. There are usually far fewer taxa with extended durations than those with shorter durations. Therefore, a comparison of the deviation of morphology from a group mean of long-lived versus shorter-lived taxa requires a method to deal with the huge differences in sample sizes.

TABLE 1. General duration statistics. Table listing durations (Myr) for various subsets of the data. N = no. genera; No SS = excluding single-stage genera; No Ext = excluding extant genera; −OS = minus 49 oversplit genera (Appendix 4); FA = birth cohorts with first appearances in the number (Ma) following ''FA'' till just before the value of the ''FA'' in the next column in the table; Pre Pale = genera occurring earlier than the Paleocene; Pale = genera occurring during the Paleocene; Eo = genera occurring during the Eocene; Ol = genera occurring during the Oligocene; Mi = genera occurring during the Miocene; Post Mi = genera occurring after the Miocene.

	All	No SS	No Ext	No SS No Ext		All (−OS)	No SS (−OS)	No Ext (−OS)	No SS No Ext (−OS)
N	326	271	161	136		277	225	140	117
Mean	27.4	32.6	26.1	30.9		26.6	32.7	24.9	29.8
Median	20.7	25.2	21.1	28.6		18.8	24.8	19.7	25.1
Maximum	140.5	140.5	92.8	92.8		140.5	140.5	92.8	92.8
Minimum	0.0	0.5	0.0	0.8		0.0	0.0	0.0	0.8
	FA166	FA116	FA105	FA95	FA77	FA65	FA54	FA42	FA25
N	11	14	25	35	39	33	29	14	29
Mean	46.9	42.3	54.0	43.9	36.1	42.8	29.5	24.9	17.5
Median	43.1	40.8	60.9	39.6	31.0	58.9	34.7	28.8	20.7
Maximum	140.5	122.0	101.2	92.8	77.4	63.5	53.7	41.9	25.5
Minimum	0.0	0.0	3.7	0.0	2.1	0.0	0.0	0.0	0.0
	FA15	FA5		Pre Pale	Pale	Eo	Ol	Mi	Post Mi
N	31	65		125	108	134	80	123	179
Mean	9.1	1.3		43.6	54.4	51.1	61.7	42.6	29.3
Median	8.4	0.5		39.5	59.9	51.7	62.5	37.8	16.3
Maximum	14.6	4.5		140.5	140.5	140.5	140.5	140.5	140.5
Minimum	0.0	0.0		0.0	0.0	0.0	0.0	0.0	0.0

To do this, I compared morphological deviations of rarified samples of shorter-lived trachyleberidid genera with those of long-lived ones. The number of genera picked from the shorter-lived pool depends on the number of long-lived genera identified. This rarefaction is repeated 10,000 times for each subsampled data set. On a few occasions, there are more long-lived genera by definition and when this happens, the long-lived pool is rarified instead. The proportion of times that long-lived taxa are more deviant from a mean morphology is reported as a ''p-value'' (for details see Liow 2004). A high rarefaction ''p-value'' means that long-lived taxa are significantly more deviant and a low one means that they are significantly more average when compared with shorter-lived taxa. This is a two-tailed test; hence a significant probability value will be either 0.025 (significantly less deviant) or 0.975 (significantly more deviant). Because dividing the data sets into two categories reduces statistical power, I also report probabilities and correlation values from Kendall's rank correlation by treating the data as continuous. I report uncorrected probability

values, but where significant results are found, I apply Bonferroni correction to account for the non-independence of the multiple analyses.

Results

The mean genus duration of trachyleberidids is between 26 and 33 Myr and the median between 21 and 29 Myr (Table 1) depending on whether single-stage, extant or both types of genera are excluded from the estimate. The average of species duration for trachyleberidids is about 4 Myr. The longest-lived genus is *Cythereis* (140.5 Myr) followed by *Cytheretta* (122.0 Myr) and *Pterygocythereis* (101.2 Myr) (Appendix 4). Perhaps these are ''undersplit'' or ''garbage can'' taxa, but the characters used to delineate these taxa seem to be consistent. Even if these are not ''real'' genera by some other definitions, they correspond to consistent aggregates of characters.

Morphological Deviation of Genera from Group Means (Discrete Characters).—Long-lived genera are not significantly more or less deviant from the group mean than shorter-lived genera, when compared with rarefied samples of

shorter-lived genera, using $p = 0.025$ as a cutoff in either direction. For instance, comparing all morphological characters and all genera, there are 17 long-lived genera (if long-lived is taken as the most-long-ranging 5% of all the genera). Comparing these 17 genera with 10,000 random samples of 17 shorter-lived taxa (i.e., all the other 309 genera) gives a value of 0.52 (Table 2, first row). Stated a different way, these 17 long-lived taxa are more deviant in morphology than any rarefied sample of shorter-lived taxa about 52% of the time. The same conclusion can also be drawn from Kendall's rank test, where there is no correlation between morphological deviation and duration (Table 2, $p = 0.88$). It should be noted that there are many ties in the data when subjected to Kendall's rank test, rendering inexact the p-values calculated. The statement of nonsignificant differences is true for other definitions of long-lived (the most-long-lived 5% or 10% of genera, and genera having a duration greater than the midrange duration of the group).

Next, to account for incomplete and questionable duration sampling, I eliminated genera that occur only in one stage. In doing so, the most-long-lived 5% or 10% of the taxa or those having durations greater than the midrange value, are all not more or less deviant than rarefied samples of shorter-lived taxa (Table 2). I also eliminated genera that are extant to account for one-sided range truncations. This removed taxa that have long durations and range to the Recent and possibly introduced a different bias. The relationship between morphological deviation and longevity is again nonsignificant when extant genera were removed, as when both single-staged and extant genera were removed from analysis (Table 2). Kendall's rank correlation tests also showed a nonsignificant relationship between deviation and duration for these comparisons (Table 2).

I also explored the effects of different subsets of discrete morphological characters on the analysis. Parsing the morphological characters into external, internal, muscle scars, hinge, and pores also maintained a pattern of nonsignificance with one exception. For external characters when single-stage genera were removed, the most-long-lived 5% of the genera are significantly more deviant, even after Bonferroni correction. It is possible that unknown or uncodable characters may be contributing to the general result, but a check of the proportion of uncoded characters in each subset does not show systematic bias in any direction (Table 2). Similarly, although the probability values from Kendall's ranks were less than 0.05 in few cases and one of them is significant after Bonferroni correction (muscle scars, single-stage genera removed, $p = 0.0001$), such values occur inconsistently compared with other analyses within Table 2.

I removed 49 genera (Appendix 4) that are potentially oversplit and reran the analyses as above. The pattern between morphological deviation and longevity remained mostly insignificant for various divisions and exclusions of data. The few significant and marginally significant instances are due to smaller sample sizes and a greater number of uncoded characters (Table 3) as shown by correlation tests (e.g., internal characters, single-stage genera removed, significant negative correlation between deviation and number of unknown characters, $p = 0.002$, tau $= -0.13$; other results not shown). However, an exception is one involving the external morphology of all genera and with single-stage genera removed, showing that long-lived genera may be significantly (even after Bonferroni correction in the 5% case) more deviant than shorter-lived genera. Kendall's rank test, however, shows a marginally significant positive relationship between morphological deviation and morphology, contrary to the rarefaction tests.

I checked whether removing genera with many uncoded characters changed the patterns of nonsignificance. Results are statistically nonsignificant (Table 2, last two rows).

Morphological Deviation of Genera from Group Means (Discrete Characters): Temporal Subsets.—This family is probably a monophyletic or nearly monophyletic collection of genera. However, the database is global and heterogeneous in both temporal and geographical coverage. Therefore I divided the data into temporal subsets of genera, to check whether different morphological deviation-duration patterns emerge. This is important because genera from a globally distributed data set

TABLE 2. Deviation from group mean (discrete morphology). Table showing probability values from rarefaction analysis and Kendall rank correlation tests using discrete characters to calculate morphological deviation. N = number of characters; NA = non-applicable characters; Q = characters state unknown; N-Genera: sample size; Five = proportion of times when the 5% most-long-lived genera in the group are morphologically more deviant from group mean than rarefied short-lived genera; N-Five = number of 5% most-long-lived genera; Ten = proportion of times when the 10% most-long-lived genera in the group considered are morphologically more deviant from the group mean than rarefied short-lived genera; N-Ten = number of 10% most-long-lived genera; Mid = proportion of times when those having a duration greater than that of the midrange duration of the group are morphologically more deviant from the group mean than are rarefied short-lived genera; N-Mid = number of genera that have a duration greater than that of the midrange duration of group; K's p = probability from Kendall's rank correlation test; tau = Kendall's correlation coefficient. Significant probability values are italic and those remaining significant after Bonferonni correction are underlined.

Taxa excluded	Characters	N	Mean % NA	Mean % Q	Mean % NA+Q	N-Genera	Five	N-Five	Ten	N-Ten	Mid	N-Mid	K's p	tau
None	All	87	11.58	14.85	26.43	326	0.52	17	0.37	33	0.42	25	0.88	0.00
	External	49	19.72	6.48	26.20	326	0.92	17	0.84	33	0.91	25	0.04	0.08
	Internal	38	1.03	25.75	26.78	326	0.24	17	0.56	33	0.31	25	0.14	−0.05
	Hinge	9	0.00	10.26	10.26	318	0.81	16	0.52	32	0.75	25	0.95	0.00
	Muscle scar	13	2.97	30.65	33.62	269	0.06	14	0.10	27	0.11	23	0.15	−0.06
	Pore	9	0.03	40.49	40.52	269	0.60	14	0.46	27	0.40	23	0.98	0.00
Single stage	All	87	11.46	14.70	26.16	271	0.86	14	0.33	28	0.35	25	0.57	−0.02
	External	49	19.48	6.33	25.82	271	1.00	14	0.92	28	0.90	25	0.04	0.09
	Internal	38	1.11	25.33	26.44	271	0.19	14	0.25	28	0.27	25	0.01	−0.12
	Hinge	9	0.00	10.29	10.29	261	0.21	14	0.73	27	0.72	25	0.72	−0.02
	Muscle scar	13	3.21	30.03	33.24	222	0.10	12	0.07	23	0.08	23	0.00	−0.14
	Pore	9	0.00	40.03	40.03	225	0.78	12	0.36	23	0.39	23	0.58	−0.02
Extant	All	87	11.09	18.62	29.71	161	0.30	9	0.13	17	0.51	36	0.21	−0.07
	External	49	19.15	7.04	26.19	161	0.35	9	0.30	17	0.81	36	0.63	−0.03
	Internal	38	0.69	33.57	46.32	161	0.68	9	0.52	17	0.21	36	0.49	−0.04
	Hinge	9	0.00	13.24	13.24	152	0.50	8	0.40	16	0.70	33	0.19	0.07
	Muscle scar	13	2.00	40.11	42.11	117	0.29	6	0.38	12	0.08	31	0.13	−0.09
	Pore	9	0.00	51.23	51.23	152	0.49	8	0.38	16	0.70	33	0.15	−0.09
Single stage and extant	All	87	10.85	18.86	29.70	136	0.24	7	0.23	14	0.70	35	0.50	−0.04
	External	49	18.70	7.27	25.97	136	0.30	7	0.58	14	0.92	35	0.63	0.03
	Internal	38	0.72	33.80	34.52	136	0.60	7	0.28	14	0.16	35	0.19	−0.08
	Hinge	9	0.00	13.70	13.70	129	0.31	7	0.07	13	0.68	32	0.33	0.06
	Muscle scar	13	2.11	39.83	41.94	99	0.56	5	0.79	10	0.71	30	0.99	0.00
	Pore	9	0.00	52.13	52.13	98	0.27	5	0.13	10	0.12	24	0.31	−0.07
>26 NA	All	87	—	—	17.25	219	0.92	11	0.88	22	0.82	21	0.64	0.02
>18 NA	All	87	—	—	13.04	107	0.85	6	0.81	11	0.82	12	0.47	0.05

TABLE 3. Deviation from group mean (discrete morphology) with oversplit genera removed. Table showing probability values from rarefaction analysis and Kendall's rank correlation tests with 49 oversplit genera removed (see Appendix 4 and ''Data and Methods''). Abbreviations as in Table 2.

Taxa excluded	Characters	N	N-Genera	Five	N-Five	Ten	N-Ten	Mid	N-Mid	K's p	tau
None	All	87	277	0.88	14	0.70	28	0.70	20	0.68	0.02
	External	49	277	*1.00*	14	0.95	28	*0.98*	20	*0.02*	0.10
	Internal	39	277	0.19	14	0.44	28	0.20	20	0.14	−0.06
	Hinge	9	269	0.26	14	0.17	27	0.15	20	0.34	−0.04
	Muscle scar	13	232	0.21	12	0.40	24	0.21	18	0.18	−0.06
	Pore	9	236	0.77	12	0.77	24	0.51	19	0.62	0.02
Single stage	All	87	225	0.76	12	0.57	23	0.57	20	0.48	−0.03
	External	49	225	*0.98*	12	0.97	23	0.97	20	*0.02*	0.10
	Internal	39	225	0.23	12	0.15	23	0.12	20	*0.00*	−0.15
	Hinge	9	217	0.31	11	0.17	22	0.14	20	0.36	−0.04
	Muscle scar	13	187	0.24	10	0.12	19	0.09	18	*0.00*	−0.17
	Pore	9	193	0.22	10	0.42	20	0.46	19	0.68	−0.02
Extant	All	87	140	0.39	8	0.19	15	0.47	28	0.12	−0.09
	External	49	140	0.46	8	0.36	15	0.86	28	0.55	−0.03
	Internal	39	140	0.71	8	0.13	15	*0.02*	28	0.30	−0.06
	Hinge	9	132	*0.00*	7	*0.01*	14	0.09	25	0.25	−0.07
	Muscle scar	13	140	0.58	8	0.80	15	0.63	28	0.90	−0.01
	Pore	9	105	0.22	6	0.23	11	0.27	19	0.29	−0.07
Single stage and extant	All	87	117	0.11	6	0.14	12	0.57	27	0.19	−0.08
	External	49	117	0.12	6	0.27	12	0.89	27	0.91	−0.01
	Internal	39	117	0.57	6	0.36	12	0.04	27	0.12	−0.10
	Hinge	9	112	0.97	6	0.52	12	0.71	25	0.39	−0.06
	Muscle scar	13	87	0.22	5	0.36	9	*0.01*	24	*0.01*	−0.19
	Pore	9	86	0.15	5	0.23	9	0.29	18	0.79	0.02

may not interact ecologically or phylogenetically with each other directly enough for any patterns to be discerned. Subdividing the data serves to homogenize the data so that patterns, even weak ones, may have a chance of being detected.

First, I compared the morphological deviations of long- and shorter-lived genera from their birth cohort means (a birth cohort is the subset of genera appearing within a named time interval). I divided the data into birth cohorts of 10 to 18 million years except for the Late Cretaceous and earlier (lumped as a birth cohort lasting 50 million years because the interval has only 11 genera, too few for finer subdivision). Sample sizes for each time slice are in general small and the significant values that emerge in a few instances show no consistent pattern (Table 4). Similarly, the only significant p-values for Kendall's rank test value is shown for genera first appearing at 5 Ma or later (using all and internal characters), but this may not have much weight because many of these genera will certainly continue into the future. I have included them only for completeness. On the whole, within a birth cohort,

long-lived genera are not more or less deviant from the cohort mean than their shorter-lived relatives.

A different landscape emerges when the data are divided into contemporaneous genera within a given epoch. I find that the most-long-lived 5% or 10% of genera in each epoch are more deviant from the mean of that epoch than is expected, at least marginally (Table 5) in terms of overall morphology and external morphology, although not internal morphology. The long-lived genera of each epoch do overlap (e.g., *Cythereis* is present in every single epoch analyze) but they do not belong to any one subfamily or tribe. Not all the values are significant at $p = 0.025/0.975$ or at $p = 0.0014/0.999$ after Bonferroni correction, but all except Eocene values are consistently high. However, when more genera are included in the long-lived pool (using the definition of long-lived as having a duration greater than the midrange duration value of the group), the deviations of long-lived genera from epoch means are no longer significant in numerous cases (Table 5). Kendall's rank correlation test also does not show any consistent statistical

TABLE 4. Deviation from birth cohort mean (discrete morphology). Table showing probability values from rarefaction analysis and Kendall's rank correlation tests using birth cohorts. Abbreviations as in Table 2. FA(Ma) refers to first appearance, the beginning of the interval considered. The end of one interval is the beginning of the next (= the next FA value). (R) indicates that long-lived taxa were rarified because there were more of them than short-lived ones.

FA	Characters	N	Five	N-Five	Ten	N-Ten	Mid	N-Mid	K's p	tau
166	All	11	0.91	1	*0.00*	2	*0.00*	2	0.63	−0.11
	External		0.54	1	*0.00*	2	*0.00*	2	0.45	−0.17
	Internal		0.91	1	0.38	2	0.38	2	0.19	−0.29
116	All	14	0.92	1	0.57	2	0.43	3	0.32	−0.20
	External		0.92	1	0.45	2	0.47	3	0.83	0.04
	Internal		0.92	1	0.85	2	0.86	3	0.66	0.09
105	All	25	0.43	2	0.59	3	0.10	13 (R)	0.54	0.09
	External		0.65	2	0.83	3	*0.01*	13 (R)	0.65	0.26
	Internal		0.39	2	0.24	3	0.90	13 (R)	0.08	−0.25
95	All	35	0.62	2	0.41	4	0.19	16	0.77	0.03
	External		0.49	2	0.47	4	0.98	16	0.58	0.07
	Internal		0.87	2	0.78	4	*0.00*	16	0.37	−0.11
77	All	40	0.27	3	0.42	5	*0.46*	18	0.28	−0.12
	External		0.30	3	0.43	5	*0.02*	18	0.19	−0.15
	Internal		0.51	3	0.70	5	*1.00*	18	0.65	0.05
65	All	33	0.33	2	0.41	4	0.95	23 (R)	0.40	0.10
	External		0.14	2	0.24	4	0.95	23 (R)	0.38	0.11
	Internal		0.79	2	0.91	4	0.88	23 (R)	0.66	0.05
54	All	28	0.91	2	0.97	3	*1.00*	17 (R)	0.09	0.22
	External		0.76	2	0.80	3	*0.96*	17 (R)	0.29	0.14
	Internal		0.03	2	0.11	3	0.95	17 (R)	0.17	0.18
42	All	14	0.33	1	0.41	2	0.92	9 (R)	0.77	−0.06
	External		0.21	1	*0.02*	2	0.11	9 (R)	0.18	−0.27
	Internal		0.74	2	0.91	2	*1.00*	9 (R)	0.06	0.38
25	All	29	0.04	2	*0.02*	3	*0.83*	23 (R)	0.97	0.01
	External		0.48	2	0.23	3	0.84	23 (R)	0.49	0.09
	Internal		0.04	2	0.07	3	0.91	23 (R)	0.86	0.02
15	All	31	0.63	2	0.85	4	0.54	20 (R)	0.05	−0.10
	External		0.63	2	0.09	4	0.35	20 (R)	0.58	−0.07
	Internal		0.17	2	0.40	4	0.56	20 (R)	0.86	0.02
5	All	65	0.69	4	0.62	7	*1.00*	21	0.03	0.19
	External		0.20	4	0.11	7	*0.88*	21	0.70	0.03
	Internal		0.95	4	*0.98*	7	*1.00*	21	*0.01*	0.24

TABLE 5. Deviation from time cohort mean (discrete morphology). Table showing probability values from rarefaction analysis and Kendall's rank correlation tests using contemporaneous subsets of genera. Abbreviations as Table 2.

Time	Characters	N	Five	N-Five	Ten	N-Ten	Mid	N-Mid	K's p	tau
Cretaceous	All	124	0.71	7	0.72	13	0.16	25	0.16	−0.08
	External		*0.99*	7	*0.99*	13	0.92	25	0.28	0.06
	Internal		0.33	7	0.34	13	0.39	25	0.15	−0.09
Paleocene	All	108	0.90	6	0.96	11	0.60	25	0.19	0.08
	External		*0.99*	6	*0.99*	11	0.90	25	0.04	0.13
	Internal		0.57	6	0.61	11	0.68	25	0.95	0.00
Eocene	All	134	0.88	7	0.91	14	0.43	25	0.72	0.02
	External		0.81	7	0.61	14	0.81	25	0.47	0.04
	Internal		0.46	7	0.41	14	0.68	25	0.84	0.01
Oligocene	All	79	0.73	4	0.89	8	0.62	22	0.46	0.06
	External		0.91	4	*1.00*	8	0.96	22	0.13	0.12
	Internal		0.63	4	0.26	8	0.32	22	0.46	−0.06
Miocene	All	123	0.93	7	*0.99*	13	0.82	23	0.16	0.09
	External		*0.99*	7	*1.00*	13	*0.99*	23	0.03	0.13
	Internal		0.49	7	0.55	13	0.32	23	0.49	−0.04
Post-Miocene	All	178	0.97	9	0.86	18	0.87	18	0.12	0.08
	External		*1.00*	9	*1.00*	18	*0.99*	18	*0.01*	0.13
	Internal		0.14	9	0.15	18	0.18	18	0.24	−0.06

TABLE 6. Deviation from time cohort mean (PCO of discrete morphology). Table showing probability values from rarefaction analysis and Kendall's rank correlation tests using principal coordinate scores. Abbreviations as in Table 2.

Genera	Five	N-Five	Ten	N-Ten	Mid	N-Mid	K's p	tau
All	0.61	17	0.47	33	0.37	25	0.09	0.06
All (−OS)	0.66	14	0.54	28	0.46	20	0.29	0.04
>26 Nas	0.75	11	0.81	22	0.80	21	0.30	0.04
Cretaceous	0.64	7	0.50	13	0.12	25	0.32	−0.06
Paleocene	0.65	6	0.69	11	0.23	25	0.76	0.02
Eocene	0.61	7	0.69	14	0.29	25	0.42	−0.05
Oligocene	0.27	4	0.79	8	0.38	22	0.27	0.08
Miocene	0.77	7	0.81	13	0.65	23	0.18	0.08
Post-Miocene	0.95	9	0.90	18	0.90	18	*0.00*	0.14

significance in the relationship between morphological deviation and duration.

Principal Coordinate Analysis of Discrete Morphological Data.—It may be that some character complexes, whose components are coded as separate characters, are contributing more to the overall morphological representation. To account for this possibility, I performed PCAs on the distance matrices resulting from comparing character states of genera. The first 20 components yielded between 88% and 92% of the total variance in each analysis done. The genus PCA scores of those 20 components were used in subsequent calculations of deviations of genera from a group average. Using principal coordinate scores (PCOs) to compare deviations of long- and shorter-lived genera from average scores of the entire group substantiated the previous conclusions, with one exception. Contemporaneous subsets no longer seem to have long-lived genera that are significantly more deviant from group means than shorter-lived taxa, judging from the *p*-values of the rarefaction test (Table 6). The single significant value from Kendall's rank test is for the contemporaneous group of post-Miocene genera, which includes many genera with one-sided range truncation.

Morphological Deviation of Genera from Group Means (Outline Analyses).—I performed elliptical Fourier analyses on 284 outlines representing 284 genera, creating an output of ten harmonics. These ten harmonics reproduced well the outlines of selected specimens tested. Comparing the deviation of long- and shorter-lived genera from means of the harmonics of all 284 genera, I found no significant difference between the two groups of taxa (Table 7). Principal components analysis of the ten harmonics yielded results with the first four principal components accounting for 95% of the total variation. Calculating deviation of these four principal components of long- and shorter-lived genera from means for all 284 genera yielded similar nonsignificant results (Table 7).

Using a completely different approach to comparing outlines, I found the same nonsig-

TABLE 7. Outline analyses ($n = 284$). Table showing probability values from rarefaction analysis and Kendall's rank correlation tests using outline data. 4PCS (10H) = using the first four principal components scores from the first ten harmonics; 6H = using the first ten harmonics (see text); ES = eigenshape scores; dash indicates through numbers. Other abbreviations as in Table 2.

Scores used	Five	N-Five	Ten	N-Ten	Mid	N-Mid	K's p	tau
4 PCS (10H)	0.37	15	0.37	29	0.42	25	0.40	0.03
6 H	0.37	15	0.26	29	0.39	25	0.65	0.02
ES1–10	0.92	15	0.93	29	0.92	25	0.34	0.04
ES2–9	0.79	15	0.83	29	0.79	25	0.64	0.02
ES 1	0.76	15	0.75	29	0.76	25	0.49	0.03
ES 2	0.76	15	0.94	29	0.88	25	0.96	0.00
ES 3	0.15	15	0.32	29	0.45	25	0.98	0.00
ES 4	0.56	15	0.60	29	0.85	25	0.91	0.00
ES 5	0.96	15	0.83	29	0.84	25	0.09	−0.07

nificance when comparing long and shorter-lived taxa. Standard eigenshape analysis on the 284 outlines yielded the results with the first ten eigenshape scores accounting for about 90% of the variance in outline. Combining the eigenshape scores in various ways did not change the conclusion that the outlines of longer-lived genera are no more deviant from an average outline than shorter-lived taxa, by all the definitions used (Table 7). Kendall's rank correlation tests show the same lack of significance between morphological deviation and longevity (Table 7).

It is worthwhile noting that many columns of Tables 2–7 do not correlate well for various groups of genera or character suites being tested, even though the data are more inclusive from left to right. This is because the outcomes of rarefaction analyses depend upon membership of the ''long-lived'' and ''shorter-lived'' groups. For instance, if 5% of the most long-lived genera are all quite close to the group mean, the probability value reported will be low. But moving right along the same row, the 10% most long-lived genera in the same group may now contain a genus that has very different morphology, so that the average deviation value is high and the reported probability value is greatly increased compared with the 5% case. Moving further right, the probability value may again drop because more long-lived genera (having greater than a midrange duration group) are considered such that their lower deviation values potentially swamp out the outlier first present in the 10% group. Kendall's taus (reflecting the slope of the relationship) often do not correspond in sign to rarefaction results because the relationship between morphological deviation and duration is not linear (even after ranking) and potentially quite dispersed (see Fig. 1). For example, a low rarefaction probability value signifies that a long-lived group is less deviant and we expect Kendall's test to show a negative tau, but this is not always found, regardless of whether the relationship is significant or not.

Discussion

The results presented here for trachyleberi-did ostracodes show that long-lived genera are either no different from shorter-lived genera or perhaps deviant morphologically than shorter-lived genera. This contrasts with the previous finding that genera of crinoids within a given order are morphologically less deviant than expected by chance alone (Liow 2004). One possible bias in these ostracode data is incomplete sampling, despite a thorough exploration of the literature. However, the preservation probability (per 10 Myr) is 0.28 for all trachyleberidid genera considered together, very low for genera that are still extant (0.19) and very high for genera that are extinct already (0.92) (using Foote and Raup's [1996] FreqRat). In fact, only 29 of the 326 genera are represented solely in Recent samples. This is a rather unusual situation. But it indicates that fossil trachyleberidids are very well sampled and hence the reliability of stratigraphic ranges of genera should be quite high. On the other hand, it is likely that some taxa with shorter geologic ranges may actually have their ranges slightly extended if and when members are discovered in the Recent oceans. The ''missing'' Recent genera should not systematically bias the result of this study unless they overwhelmingly lengthen durations of extinct genera, a possibility deemed unlikely because the Pliocene and Pleistocene both seem to be well sampled.

Other possible explanations for the discrepancy between the crinoid study and the current one are that (1) the patterns could be clade specific due to differences in duration distributions and biology, (2) orders (of crinoids) encompass an evolutionarily larger set of taxa than a family (Trachyleberididae) and hence produce different morphological-deviation-duration patterns, (3) the crinoid study encompassed a longer period of time (Ordovician to Eocene) than my study of ostracodes (Cretaceous to Recent), and (4) the two data sets may have different sampling artifacts.

It may be that the trachyleberidid morphological deviation-duration pattern is truly a nonexistent one, as illustrated in a theoretical null expectation (Fig. 1). This may extend to the speculation that ecological specialization is not related to geologic duration of the taxon in question. The previous statement is based upon the assumption that morphology, or at

least the chosen parts of the morphology that were coded and analyzed, is correlated with ecology such that morphological specialization equates to ecological specialization. There is, however, no empirical evidence for this relationship in ostracodes; thus this speculation is groundless for now.

Another question that arises is why the pattern of morphological deviation versus duration is different for contemporaneous subsets of genera, compared with that of either the whole data set or birth cohorts. I hypothesize that contemporaneous subsets of genera are groups that are potentially closely interacting during a particular set of global conditions. This is in contrast to all genera through the entire length of the existence of the family, because the genera at the beginning of the family's history do not directly interact with later genera. This is also in contrast to birth cohorts, which do not include all the potentially ecologically interacting genera existing during the geological interval of their origin. However, the marginally significant morphological deviation of long-lived contemporaneous genera compared with shorter-lived genera disappeared when a principal coordinates analysis was run. This is perhaps because some correlated characters that were contributing to the deviation of long-lived genera from the group mean in the distance analysis of contemporaneous genera lost some of their concerted influence on the resulting patterns from the analysis.

There are other explanations for the relationship (or the lack of one) between longevity and morphological deviation that I have not examined here. Environmental events such as climate change, sea level rise and fall may contribute to genus longevity directly or indirectly. For instance, an extinction event caused by climatic changes may directly remove certain types of morphologies to result in a new distribution of genera in morphospace. It can also remove competitors or predators from other clades that indirectly affect trachyleberidid longevity and morphospace distribution. Genera in different geographical realms could have been unevenly sampled, have experienced different regional historical events and differ in ecology. Phylogeny could also contribute to the resulting morphological deviation-duration patterns by nonrandomly contributing to certain types of morphologies or life histories or ecologies that promote taxic longevity. Lastly, interactions of external events and ecology could themselves be determinants of morphology and persistence.

Conclusions

In this study, I have used an exceptionally well sampled group of marine microfossils to test the idea of the persistence of the relatively unspecialized (Simpson 1944). Specialization is here defined as morphological deviation from a group mean. The more distant or different a genus is from a mean morphology, the more morphologically specialized it is considered to be. The closer a genus is to a mean morphology, the more morphologically average it is considered to be. Long-lived taxa were identified by using three methods: the most-long-lived 5% of the genera, the most-long-lived 10%, and taxa having durations greater than the midrange duration value of the group. Sample sizes of long-lived taxa changed according to the definition of ''long-lived'' (Liow 2004). Using rarefied sampling, I compared equivalent samples of shorter-lived and long-lived genera.

In general, long-lived trachyleberidid genera are no more or less morphologically deviant compared with shorter-lived ones. Contemporaneous subsets of genera occurring in epochs, however, ostensibly have longer-lived genera that are more deviant from the mean morphology during any one epoch. Although the results are not always statistically significant at the level of $p = 0.025/0.975$, the data do point to the possibility that longer-lived genera are more deviant from an average morphology than expected. One hypothesis, if the effect is real, is that decreased competition by specialization may aid persistence. Another possibility is that the long-lived genera in each epoch (which are not independent in successive epochs) have fewer unknown character states, so they appear more deviant. However, this cannot be the sole explanation because both when single-staged genera (= potentially less well sampled) and when genera with many unknown or inapplicable characters

were removed, long-lived genera are more deviant in their external characters and in all characters combined.

Dissecting the discrete morphological data in various other ways, including comparing birth cohorts and related groups of morphological characters separately, showed that long-lived genera are no more or less morphologically deviant than shorter-lived ones. The few exceptions to this can be attributed to low generic sample sizes and high proportions of unknown and uncodable characters. External characters may have more influence than internal ones in producing patterns of morphological deviation and longevity as shown by analyses of contemporaneous cohorts. Outline data analyzed by using two independent methods show that trachyleberidid genera that are long-lived are not more or less deviant from an average morphology than are their shorter-lived counterparts.

Specialization in discrete morphology, especially external morphology, may be positively correlated with longevity in contemporaneous subsets of trachyleberidid genera. This relationship may be true even for temporally longer contemporaneous groups of genera if discrete morphology becomes more completely known and taxonomy improved. Lateral outline data are not correlated with longevity, although they are a very important aspect of genus taxonomic identification (Bachnou et al. 2000). In this world of perpetual change, knowing why, how, and when lineages do not change for long time periods informs us in a novel way about the myriad factors contributing to radiations and turnovers.

Acknowledgments

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