

HOW SPECIES LONGEVITY, INTRASPECIFIC MORPHOLOGICAL VARIATION, AND GEOGRAPHIC RANGE SIZE ARE RELATED: A COMPARISON USING LATE CAMBRIAN TRILOBITES

Melanie J. Hopkins^{1,2,3}

¹Department of the Geophysical Sciences, University of Chicago, 5734 S. Ellis Ave, Chicago IL 60637

²E-mail: mhopkins@fieldmuseum.org

Received January 31, 2011

Accepted May 26, 2011

Data Archived: Dryad doi:10.5061/dryad.rm73j

Phenotypic variation is fundamental to evolutionary change. Variation not only evinces the connectivity of populations but it is also associated with the adaptability and evolvability of taxa. Despite the potential importance of morphological variation in structuring evolutionary patterns, little is known about how relative differences in intraspecific morphological variation and its geographic structure are linked to differences in species longevity. This study offers a novel combination of analyses that reveal the quantitative relationships among intraspecific variation, geographic range size and duration in the fossil record using late Cambrian trilobites. Results show that geographic range size and duration are positively correlated. Surprisingly, longer lived species tend to have less intraspecific variation. Phylogenetic effects were also explored and found not to determine the association between these variables. However, the distribution of geographic range sizes shows strong phylogenetic signal. In light of previous work, one possible explanation for these results is that species with shorter durations have comparatively higher rates of morphological evolution, reflected in higher phenotypic variation overall.

KEY WORDS: Duration, evolutionary rates, morphological evolution, paleobiology, phylogenetic signal.

Since Darwin, biologists have recognized that evolutionary change requires the presence of variation. Phenotypic variation, in particular, is the raw material for natural selection (Van Valen 1974; West-Eberhard 2005), and considerable research is focused on the determinants of and constraints on the generation of phenotypic variation (Carroll et al. 2005; Hallgrímsson and Hall 2005; Gilbert and Epel 2009), the role of phenotypic variation and its geographic structure in maintaining reproductive isolation between species (Coyne and Orr 2004) and driving speciation (Endler

1977; West-Eberhard 2003), and the degree to which there is a correspondence between morphological variation within populations and morphological divergence between populations or species (e.g., Merila and Bjorklund 1999; Badyaev and Foresman 2000; Badyaev and Hill 2000; Merila and Bjorklund 2004; Marroig and Cheverud 2005; Renaud et al. 2006; Hunt 2007a).

Both within- and between-population variation might influence longevity and extinction. Models indicate that both genetic variability and plasticity promote persistence or adaptability of a population in the face of cyclical, directional, or otherwise predictable environmental change (Lande and Shannon 1996; Reed et al. 2010). In addition, morphological variation and niche

³Current address: Department of Geology, Field Museum of Natural History, 1400 S. Lake Shore Dr., Chicago, IL 60605.

breadth are associated in some taxa (e.g., Van Valen 1965; Findley and Black 1983; Galeotti and Rubolini 2004; Bolnick et al. 2007), and there is evidence that niche breadth promotes species longevity (Kammer et al. 1997, 1998). Thus, a species with relatively high morphological variation may tolerate a range of environmental conditions that is more extensive than a morphologically invariant species, improving its likelihood of surviving environmental perturbations, and thereby its persistence.

Morphological variation may also increase as species encounter new environments or are subject to environmental change. For example, within-population morphological variation has been shown to increase under adverse conditions within a variety of organisms (e.g., Hoffmann and Parsons 1997, and references therein). This could be due to an increase in the generation of new variation or due to an increase in developmental instability resulting in the expression of previously accumulated but developmentally suppressed variation (Badyaev et al. 2005, and references therein). Thus, at an ecological scale, low intrapopulation variation could be the result of stress resistance. Stress resistance might promote species stability by making species less susceptible to environmental perturbations as well as decreasing the variation available to natural selection. In such situations, stress resistance results confers longevity despite reducing morphological variation.

Similarly, stabilizing selection is produced by both abiotic (e.g., the external environment) and biotic (e.g., competition) factors that mediate stasis by eliminating extreme morphologies that are less fit. In this situation, taxa with lower variation may be longer lived because stabilizing selection is ultimately conferring evolutionary stability. In contrast, when morphological variation facilitates population-level response to changes in local selection pressures, morphologically variable species may be more likely to experience divergence between populations, ultimately increasing rates of morphological evolution.

Despite the potential importance of morphological variation in structuring evolutionary patterns, little is known about how different patterns of intraspecific variation across species are related empirically to differences in species longevity, in part because previous paleontological work has largely focused on extinction at higher taxonomic levels. I investigate these possibilities here by analyzing the association between intraspecific morphological variation and species duration in pterocephaliid trilobite species from the Steptoean (Furongian, Cambrian). Because previous work has shown a strong association between geographic range size and duration (e.g., Buzas and Culver 1984; Jablonski and Roy 2003; Liow 2007; Powell 2007; Foote et al. 2008), and because the geographic structure of populations is fundamental in creating, structuring, and maintaining morphological variation (e.g., Avise 2000; Grosberg and Cunningham 2001; DeWitt and Scheiner 2004; Russell and Bauer 2005; Hopkins and Thurman

2010), I also examine the association between these variables and geographic range size. To quantify these variables, I employed geometric morphometrics, paleoreconstruction of occurrence localities, and quantitative biostratigraphic methods based in graphic correlation. Because each species within this clade shared some evolutionary history with all of the other species, variables may covary simply because of a shared phylogenetic history. To test this possibility for these variables, phylogenetic signal in each variable was assessed using a recent phylogenetic analysis of several pterocephaliid genera (Hopkins 2011). By focusing on the fossil record, this study is able to provide a novel example of how expectations regarding the influence of variation on evolutionary divergence and rates of evolution at ecological scales, where species longevity is not observable, may be extrapolated and studied at macroevolutionary scales.

Materials

The Trilobita are an entirely extinct class of arthropods. However, because their exoskeletons were highly impregnated with calcite, they had a high preservation potential among marine invertebrates. In fact, late Cambrian trilobites of North America have arguably one of the best-known fossil records of any fossil group at any time (Adrain and Westrop 2001) and are the earliest morphologically complex macroscopic animals to be preserved in high abundance. In the Cambrian, assemblages from most depositional environments on the continental shelf are dominated by trilobite sclerites and the geographic and stratigraphic distributions of trilobite species have historically received considerable study because they are the primary biostratigraphic indicators of the Cambrian.

The 38 trilobite species used in this analysis belong to either the family Pterocephaliidae Kobayashi, 1935, or the family Aphelepididae Palmer, 1960 (sensu Jell and Adrain 2003). Both families comprise species that occur across the United States but because the stratigraphic interval in which they occur (the Steptoean Stage [Furongian, Cambrian]) is more complete and the fossil material is generally better preserved or more accessible at Great Basin localities, this study focuses on species that occur at least in part in the Great Basin. All species are restricted to the Steptoean Stage, which began around 499 million year ago (Mya) and lasted about four million years (Peng and Babcock 2008). The Steptoean Stage is coincident with an interval of time previously described as the “Pterocephaliid biore” (Ludvigsen and Westrop 1985), coined by Palmer (1965a) to describe one of several sequential intervals of trilobite diversification and extinction. Although the extent to which higher taxonomic trilobite clades were truly restricted to the stage in which they dominate is debated (Hughes 2001), genera chosen for this study were both prevalent during but restricted to the Steptoean stage.

Variation was estimated using geometric morphometrics methods (Bookstein 1991; Zelditch et al. 2004). To reduce conflation of variation within fossil species with the definition of the species itself, the species used in this study were defined under one taxonomic rubric, summarized in Palmer (1960, 1962, 1965b). Because the systematic work undertaken by Palmer was done, at least in part, in the service of biostratigraphy (i.e., with the goal of dividing the geologic record into intervals defined by the appearance of new taxa), it is conceivable that Palmer's concept of a species was governed to some extent by its longevity. Thus the variation that was tolerated as intraspecific variation from a narrow stratigraphic range may have been considered diagnostic if witnessed over a longer range (N. Hughes, pers. comm.). However, variation was estimated only from species where their designation withstood reexamination of old and new material with no consideration to the stratigraphic or geographic extent over which samples were taken. Herein, a species is defined as the smallest aggregation of comparable individuals diagnosable by a unique combination of characters. Characters may include both discrete and continuous characters and are taken from all available sclerites. For the clades analyzed here, discrete pygidial (tail shield) characters and ornamentation are the most useful for delimiting cogenics (Hopkins 2011). For a detailed application of this species concept to Cambrian trilobites, see also Hopkins and Webster (2009) and Webster (2009).

Specimens were obtained from field collections and from collections made by A.R. Palmer and held at the U.S. Geological Survey and the Institute for Cambrian Studies, University of Chicago (Table S1). Because most of the trilobite fossil record during the Steptoean is comprised of assemblages of disarticulated sclerites, variation was estimated from the cranidium, or the medial sclerite of the head shield. The cranidium was chosen because it shows more morphological complexity than other sclerites and comprises ecologically relevant features such as the eyes. Although there is some overlap in the morphological characters used to discriminate species and those captured by the landmark data (see Methods below), specimens were assigned to species prior to collection of landmark data. Thus the set of characters used to identify specimens and the set of characters used to estimate variation are not coincident. In fact, if one were to use only the landmark data, it would be very difficult to discriminate species of this clade as species overlap considerably in morphospace (data not shown).

Some systematic uncertainty remains for two of the included species: *Aphelaspis haguei* (Hall and Whitfield, 1877) and *A. subditus* Palmer 1962. These two species are difficult to distinguish from one another and *A. subditus* may actually be a junior synonym of *A. haguei* (Hopkins 2011). These two species are so similar in geographic range size, stratigraphic duration, and morphology, however, that synonymizing these species and esti-

imating each variable from the pooled sample did not change the results.

DATASETS

Because of the differences in data availability across the variables considered, a total of three datasets were used for study. The first consists of estimates of duration and geographic range size for most pterocephaliids and aphelaspids that occur, at least partially, in the Great Basin (Table 1); this dataset is referred to as the "All" dataset hereafter (38 species). The second is a subset of these taxa that were included in a phylogenetic analysis of several genera belonging to the Pterocephaliidae or Aphelaspidae (Hopkins 2011). This dataset is referred to as the "Phylo" dataset in the results and excludes species of *Litocephalus* and *Eugoncare* as well as *Aphelaspis brachyphasis* and *A. buttsi* (30 species). The third is a subset of these taxa for which variation data were also available; this dataset is referred to as the "Var" dataset (17 species, Table 3).

Methods

ESTIMATING GEOGRAPHIC RANGE SIZE

Continent-wide species occurrences for the focal species of this study (Table 1) were compiled from the literature (Tables S2 and S3), from field work, or estimated using Google Earth.

Geographic range size was estimated in two ways. First, because trilobites inhabited continental shelf environments, their geographic range may be represented by a distance along the coastline. Because the Cambrian coastline of Laurentia (the paleo-North American continent) is known only at a very coarse resolution, the coastal distance was estimated using the Great Circle distance between the two most geographically separated occurrences, tabulated using the `earth.dist` function from the "fossil" package written for the R statistical programming language (R Development Core Team 2005; Vavrek 2007). Species that have been found only at one location were assigned an arbitrarily low value of 10 km for the maximum Great Circle distance. There was no need to transform geographic coordinates to paleo-coordinates before calculating Great Circle distances because paleoreconstruction of the overall position of Laurentia treats the continent as a rigid unit, ignoring potential contributions from local tectonic deformation (such as the extension of the Great Basin or shortening from the Laramide and Sevier orogenies). Thus estimates of Great Circle distances between localities would not be altered by transformation to paleocoordinates (D. Rowley, pers. comm.).

Paleo-coordinates were used instead to estimate the latitudinal extent over which each species occurred. The mean pole position was determined from five paleopoles estimated from rock units of the late Cambrian (summarized in McCausland et al. 2007) and then used to rotate the modern latitudes to paleolatitudes for each locality. Because of the paucity of paleopoles, the coarse correlation of the rock units, and the uncertainty in

Table 1. Estimated species geographic range sizes. Relative maximum Great Circle distance and relative latitudinal extent calculated by dividing each by the total range possible (bottom of table) during the part of the Steptoean when the species occurred, listed under "Biozone occur."

Species	Family	Biozone occur.	# loc.	Max. GC dist. (km)	Rel. max. GC dist.	Lat. extent	Rel. lat. extent	Rel. Abund.
<i>Aphelaspis brachyphasis</i> Palmer 1962	Aphelaspidae	Aph	3	537.60	0.11	1.9	0.04	C
<i>Aphelaspis buttsi</i> (Kobayashi, 1936)	Aphelaspidae	Aph	4	2848.13	0.57	25.5	0.59	R
<i>Aphelaspis haguei</i> (Hall and Whitfield, 1877)	Aphelaspidae	Aph	12	4275.20	0.86	29.0	0.68	MC
<i>Aphelaspis longispina</i> Palmer, 1965a	Aphelaspidae	Aph	1	10.00	0.002	0.01	0.0002	R
<i>Aphelaspis subditus</i> Palmer, 1962	Aphelaspidae	Aph	11	3761.29	0.75	7.7	0.18	C
<i>Cernuolimbis depressus</i> Palmer, 1960	Pteroccephaliidae	Du	5	2785.73	0.87	4.0	0.65	R
<i>Cernuolimbis granulatus</i> Palmer, 1965a	Pteroccephaliidae	Du	9	522.98	0.16	3.2	0.52	MC
<i>Cernuolimbis taevifrons</i> Palmer, 1965a	Pteroccephaliidae	Pre	3	474.37	0.15	1.2	0.19	MR
<i>Cernuolimbis orygnatos</i> Palmer, 1960	Pteroccephaliidae	Du	4	2785.73	0.87	3.5	0.56	MR
<i>Cernuolimbis semigranulosus</i> Palmer, 1960	Pteroccephaliidae	Du	2	334.02	0.10	0.5	0.08	MR
<i>Dicanthopyge convergens</i> Palmer, 1965a	Aphelaspidae	Dic	11	428.84	0.13	2.2	0.35	MR
<i>Dicanthopyge quadrata</i> Palmer, 1965a	Aphelaspidae	Dic	15	462.38	0.14	2.4	0.39	MR
<i>Dicanthopyge reductus</i> Palmer, 1965a	Aphelaspidae	Dic	3	125.23	0.04	1.1	0.18	MR
<i>Eugonocare (Olenaspella) regularis</i> (Palmer, 1962)	Aphelaspidae	Aph-Pre	11	4098.99	0.82	13.5	0.31	MC
<i>Eugonocare (Olenaspella) separata</i> (Palmer, 1962)	Aphelaspidae	Aph	6	4367.57	0.87	27.7	0.65	MC
<i>Housia ovata</i> Palmer, 1960	Pteroccephaliidae	Elv	11	2382.97	0.49	21.3	0.50	C
<i>Litocephalus bilobus</i> (Hall and Whitfield, 1877)	Aphelaspidae	Du	2	2713.47	0.85	3.2	0.52	C
<i>Litocephalus expansa</i> (Palmer, 1960)	Aphelaspidae	Du	4	328.70	0.10	0.5	0.08	R
<i>Litocephalus granulomarginatus</i> Palmer, 1960	Aphelaspidae	Du	2	125.03	0.04	0.4	0.06	R
<i>Litocephalus verruculapeza</i> Palmer, 1960	Aphelaspidae	Du	2	109.74	0.03	0.8	0.13	R
<i>Parahousia constricta</i> Palmer, 1960	Pteroccephaliidae	Elv	6	2190.89	0.45	19.7	0.46	MR
<i>Parahousia subequalis</i> Palmer, 1965a	Pteroccephaliidae	Elv	2	68.28	0.01	0.5	0.01	MR
<i>Prehousia alata</i> Palmer, 1960	Pteroccephaliidae	Pre	10	418.32	0.13	2.0	0.32	C
<i>Prehousia diverta</i> Palmer, 1965a	Pteroccephaliidae	Du	11	442.59	0.14	2.8	0.45	MR
<i>Prehousia impolita</i> Palmer, 1965a	Pteroccephaliidae	Pre	5	409.57	0.13	1.4	0.22	MR
<i>Prehousia indenta</i> Palmer, 1965a	Pteroccephaliidae	Pre	10	537.90	0.17	3.0	0.48	C
<i>Prehousia prima</i> Palmer, 1965a	Pteroccephaliidae	Pre	4	241.27	0.08	1.3	0.21	C
"Prehousia" semicircularis (Palmer, 1960)	Pteroccephaliidae	Du	1	10.00	0.003	0.01	0.0016	R
<i>Pteroccephalia concava</i> Palmer, 1954	Pteroccephaliidae	Du	7	482.69	0.15	1.6	0.26	MC
<i>Pteroccephalia elongata</i> Palmer, 1960	Pteroccephaliidae	Du	2	109.74	0.03	0.8	0.13	MR
<i>Pteroccephalia sanctisabae</i> Roemer, 1849	Pteroccephaliidae	Elv	20	2894.91	0.59	20.5	0.48	MC
<i>Sigmocheilus flabellifer</i> (Hall and Whitfield, 1877)	Pteroccephaliidae	Du-Elv	10	409.62	0.08	2.0	0.05	MC
<i>Sigmocheilus grata</i> (Resser, 1942)	Pteroccephaliidae	Du	5	417.00	0.13	0.8	0.13	MC
<i>Sigmocheilus notha</i> (Resser, 1942)	Pteroccephaliidae	Du	10	482.08	0.15	2.6	0.42	C
<i>Sigmocheilus pogonipensis</i> (Resser, 1942)	Pteroccephaliidae	Du-Elv	6	361.23	0.07	1.0	0.02	MR
<i>Strigambitus bilobus</i> Palmer, 1965a	Pteroccephaliidae	Du	3	307.67	0.10	0.6	0.10	MR
<i>Strigambitus transversus</i> Palmer, 1965a	Pteroccephaliidae	Du	8	435.37	0.14	2.0	0.32	MC
<i>Strigambitus utahensis</i> (Resser, 1942)	Pteroccephaliidae	Du	9	522.98	0.16	3.2	0.52	MR
Total range possible-Aphelaspis			64	4998.40		42.9		
Total range possible-Dican.-Dunder.			43	3193.20		6.2		
Total range possible-Elvinia			70	4913.16		42.9		

loc. = number of known occurrences in North America. Aph = *Aphelaspis*; Dic = *Dicanthopyge*; Du = *Dunderbergia*; Pre = *Prehousia*; Elv = *Elvinia*. Rel. Abund. = Palmer (1965b) qualitative appraisal of relative abundance of species within faunal assemblages in which they are found. R = rare; MR = moderately rare; MC = moderately common; C = common.

Table 2. Duration estimates. Values in parenthesis are 95% confidence intervals based on compilation of equally good solutions to the correlation problem. See text for details.

Species	Duration (m)
<i>Aphelaspis brachyphasis</i>	11.62 (6.47–14.69)
<i>Aphelaspis buttsi</i>	14.89 (6.39–34.43)
<i>Aphelaspis haguei</i>	18.98 (13.89–24.65)
<i>Aphelaspis longispina</i>	1.71 (0.00–11.30)
<i>Aphelaspis subditus</i>	13.43 (16.83–17.98)
<i>Cernuolimbus depressus</i>	100.48 (88.70–111.75)
<i>Cernuolimbus granulosus</i>	12.23 (5.00–21.29)
<i>Cernuolimbus laevifrons</i>	10.49 (0.00–21.29)
<i>Cernuolimbus orygmatus</i>	89.27 (61.21–107.33)
<i>Cernuolimbus semigranulosus</i>	48.67 (2.30–146.15)
<i>Dicanthopyge convergens</i>	12.80 (10.79–18.18)
<i>Dicanthopyge quadrata</i>	16.97 (13.16–22.80)
<i>Dicanthopyge reductus</i>	7.72 (0.00–13.79)
<i>Eugonocare regularis</i>	53.37 (47.13–59.16)
<i>Eugonocare separata</i>	13.58 (11.50–16.60)
<i>Housia ovata</i>	53.61 (49.21–58.30)
<i>Litocephalus bilobus</i>	93.07 (79.26–102.06)
<i>Litocephalus expansa</i>	14.24 (8.26–20.16)
<i>Litocephalus granulosus</i>	0.46 (0.00–7.05)
<i>Litocephalus verruculapeza</i>	14.35 (7.94–19.88)
<i>Parahousia constricta</i>	25.94 (16.35–34.35)
<i>Parahousia subequalis</i>	11.37 (7.30–16.73)
<i>Prehousia alata</i>	52.74 (45.56–57.38)
<i>Prehousia diverta</i>	34.21 (23.87–39.49)
<i>Prehousia impolita</i>	0.22 (0.00–1.48)
<i>Prehousia indenta</i>	2.03 (0.95–4.19)
<i>Prehousia prima</i>	29.68 (19.27–42.89)
<i>“Prehousia” semicircularis</i>	50.03 (0.78–132.08)
<i>Pterocephalia concava</i>	14.71 (7.04–23.64)
<i>Pterocephalia elongata</i>	14.95 (7.94–21.37)
<i>Pterocephalia sanctisabae</i>	62.08 (59.98–66.81)
<i>Sigmocheilus flabellifer</i>	37.40 (25.36–48.12)
<i>Sigmocheilus grata</i>	11.70 (5.71–24.31)
<i>Sigmocheilus notha</i>	9.85 (5.82–17.65)
<i>Sigmocheilus pogonipensis</i>	24.63 (21.19–30.06)
<i>Strigambitus bilobus</i>	9.31 (0.00–23.15)
<i>Strigambitus transversus</i>	10.79 (2.52–21.68)
<i>Strigambitus utahensis</i>	5.22 (0.00–16.31)

estimation of paleopoles from Paleozoic rock units in general, the mean pole position was also calculated from subsets of the paleopoles (Table S4). Although the correspondence becomes worse as the number of paleopoles decreases, the mean pole position remains fairly stable across subsets, with the result that the paleolatitudinal estimates are all highly correlated among the sets of paleopoles ($R = 0.992$ – 0.999 , $df = 96$, $P < 0.0001$).

The paleo-latitudinal range of each species was estimated based on these approximations. Species known from only one

locality were assigned an arbitrarily low paleo-latitudinal range of 0.01 degree. The paleo-latitudinal ranges of each species were also highly correlated across each set of paleopoles ($R = 0.993$ – 0.999 , $df = 39$, $P < 0.0001$). For the remainder of this study, only the results for the largest dataset (five paleopoles) are reported and are hereafter referred to as the latitudinal extent of each species.

A Laurentian-wide marine regression (Sauk II–Sauk III) occurred during the Steptoean (e.g., Saltzman et al. 2004). As a result, many localities across the continent are missing strata or preserve unfossiliferous strata from the interval between the *Aphelaspis* and *Elvinia* biozones (Fig. 1). It is conceivable that, during this regression, there was less shelf space for species to occupy and thus a smaller “maximum” geographic range size that could be obtained. To make geographic range sizes comparable across different biozones, the extent of continental shelf available during the *Aphelaspis* biozone, middle Steptoean (*Dicanthopyge* to *Dunderbergia* biozones) and *Elvinia* biozone was estimated from outcrop data (Fig. 2A–C). The geographic range estimated for each species was then standardized by the shelf size for the interval in which they occurred by dividing the observed range by the maximum size possible for the interval. Because this transformation ignores known biofacies and water depth associations that also might restrict geographic ranges (e.g., some Canadian occurrences during the middle Steptoean are considered to be offshore deposits [Pratt 1992]), both the original and the relative range estimates are presented (Table 1).

The transformation had little effect on the distribution of the maximum Great Circle distances (Spearman’s $\rho = 0.96$, $P < 0.001$) but did appear to make the range size estimates for latitudinal extent more comparable. For example, during the Cambrian, the Laurentian continent was rotated about 90 degrees clockwise relative to its current position and sat on the equator (Miall and Blakey 2008). Outcrop localities in the interior of the continent (e.g., Texas, Tennessee) available in the *Aphelaspis* and *Elvinia* biozones but not during the regression (Fig. 2A–C) were thus at higher latitudes relative to Great Basin occurrences (Table S3–S4). As a result, all species with a latitudinal extent greater than 6.2 degrees occurred either in the *Aphelaspis* or *Elvinia* biozones (Table 1), when continental shelf at higher latitudes was available for habitation. Some species occurring during these time intervals were still restricted to small latitudinal ranges, however (e.g., *A. subditus*, *Aphelaspis longispina*, and *Parahousia subequalis*, Table 1).

ESTIMATING SPECIES DURATION

Neither regional geologic stages nor biozones resolve time finely enough to document relative species durations during the Steptoean (Fig. 1). To construct a higher resolution timescale, relative durations were estimated using a composite section of

Table 3. Estimates of intraspecific variation. “Raw” variation is estimated from the sample before standardizing for allometry. “Size-stand.” variation is estimated from the sample after standardizing for allometry. Values in parenthesis show 95% confidence intervals around estimate based on bootstrapping. See text for details.

Species	Loc.	Coll.	N	“Raw” variation ($\times 10^3$)	Size-stand. Variation ($\times 10^3$)
<i>Aphelaspis haguei</i>	4	7	40	2.19 (1.65–2.64)	1.75 (1.38–2.05)
<i>Aphelaspis longispina</i>	1	2	26	2.67 (1.98–3.02)	2.17 (1.60–2.51)
<i>Aphelaspis subditus</i>	7	11	64	2.46 (2.12–2.72)	2.18 (1.84–2.43)
<i>Cernuolimbus granulatus</i>	4	6	23	2.55 (1.80–3.08)	2.33 (1.59–2.90)
<i>Dicanthopyge convergens</i>	5	5	10	3.69 (2.43–4.11)	2.82 (1.67–3.22)
<i>Dicanthopyge quadrata</i>	5	8	52	2.58 (2.19–2.92)	2.11 (1.71–2.39)
<i>Prehousia alata</i>	6	9	24	2.23 (1.74–2.55)	1.73 (1.29–2.03)
<i>Prehousia diverta</i>	5	8	19	2.72 (2.07–3.07)	2.07 (1.47–2.35)
<i>Prehousia impolita</i>	3	5	17	2.06 (1.45–2.44)	1.71 (1.14–2.00)
<i>Prehousia indenta</i>	7	11	47	2.30 (1.90–2.64)	2.15 (1.73–2.45)
<i>Prehousia prima</i>	3	5	23	2.30 (1.69–2.80)	2.23 (1.68–2.66)
<i>Pterocephalia concava</i>	4	7	12	6.16 (3.39–8.07)	2.11 (1.36–2.49)
<i>Sigmocheilus flabellifer</i>	5	9	24	2.09 (1.60–2.38)	1.79 (1.38–2.07)
<i>Sigmocheilus notha</i>	4	9	32	4.86 (3.80–5.55)	2.58 (1.96–3.02)
<i>Sigmocheilus pogonipensis</i>	4	7	41	2.37 (1.92–2.66)	2.16 (1.66–2.52)
<i>Strigambitus bilobus</i>	3	4	19	3.83 (2.81–4.56)	2.67 (1.93–3.08)
<i>Strigambitus utahensis</i>	4	4	26	1.99 (1.46–2.34)	1.67 (1.15–1.97)
<i>A. haguei</i> + <i>A. subditus</i>	9	14	104	2.54 (2.26–2.77)	2.20 (1.94–2.41)
Orientation Error	NA	NA	20	0.13 (0.10–0.17)	NA
Digitization error	NA	NA	20	0.04 (0.03–0.05)	NA

“Loc.” = number of localities sampled. “Coll.” = number of collections sampled. “N” = total sample size across all collections.

continent-wide (Laurentian) occurrences of Steptoean taxa produced using constrained optimization software (CONOP, Sadler 2003). In CONOP, composite sections are built by finding the optimal sequence of events. When the order of events preserved locally contradicts the order of events preserved somewhere else, range extensions are applied to shared taxa until the order is consistent across all sections under consideration. The optimal solution is the one that requires the lowest summed range extensions for all taxa across all sections.

All published stratigraphic sections that included at least part of the Steptoean Stage of Laurentia contributed to the composite section (i.e., were included in the CONOP analysis). In addition, stratigraphic sections immediately overlying and underlying the Stage were included to eliminate edge effects from artificial truncation of taxon ranges. To increase the independency between the construction of the time scale and the duration estimates, construction of composite section excluded the focal species but incorporated carbon isotope data as well as taxon ranges (Fig. 1). Following this, the first appearances (FAs) and last appearances (LAs) of the focal taxa were located within the optimal solution and the relative placement of all events was scaled by stratigraphic thickness using a scaling option that best approximates actual time, particularly over intervals where rapid origination or extinction took place (Sadler 2003). Relative durations were then

estimated by finding the thickness between the composite FA and LA for each focal species. The total thickness of the Steptoean Stage in the scaled composite section is about 200 m, close to the average local thickness (Palmer 1965b; Hintze and Palmer 1976; Hopkins 2010).

Analogous to phylogenetic analysis, there may be many “best” solutions in which any given event can occupy a range of relative positions (the “best-fit interval,” Sadler and Cooper 2003; Cody et al. 2008). The ramification of this for biostratigraphic purposes is a reduction in resolving power as some runs of events must collapse into clusters (Sadler 2004). However, this situation was capitalized on here by using a compilation of equally good solutions to determine the reliability of each duration estimate. To assess the stability of duration estimates, 10 composite sections with equally low penalties were compiled, and then 10 sets of estimates compiled from each solution, for a total of 100 duration estimates based on 10 composite sections. The distribution of estimates was then used to calculate 95% confidence intervals for the estimated duration of each focal taxon. Because of their extremely large confidence intervals, “*Prehousia*” *semicircularis* and *Cernuolimbus semigranulosus* were excluded from the analyses (Table 2).

More extensive discussion of all steps outlined in this section may be found in Hopkins (2010).

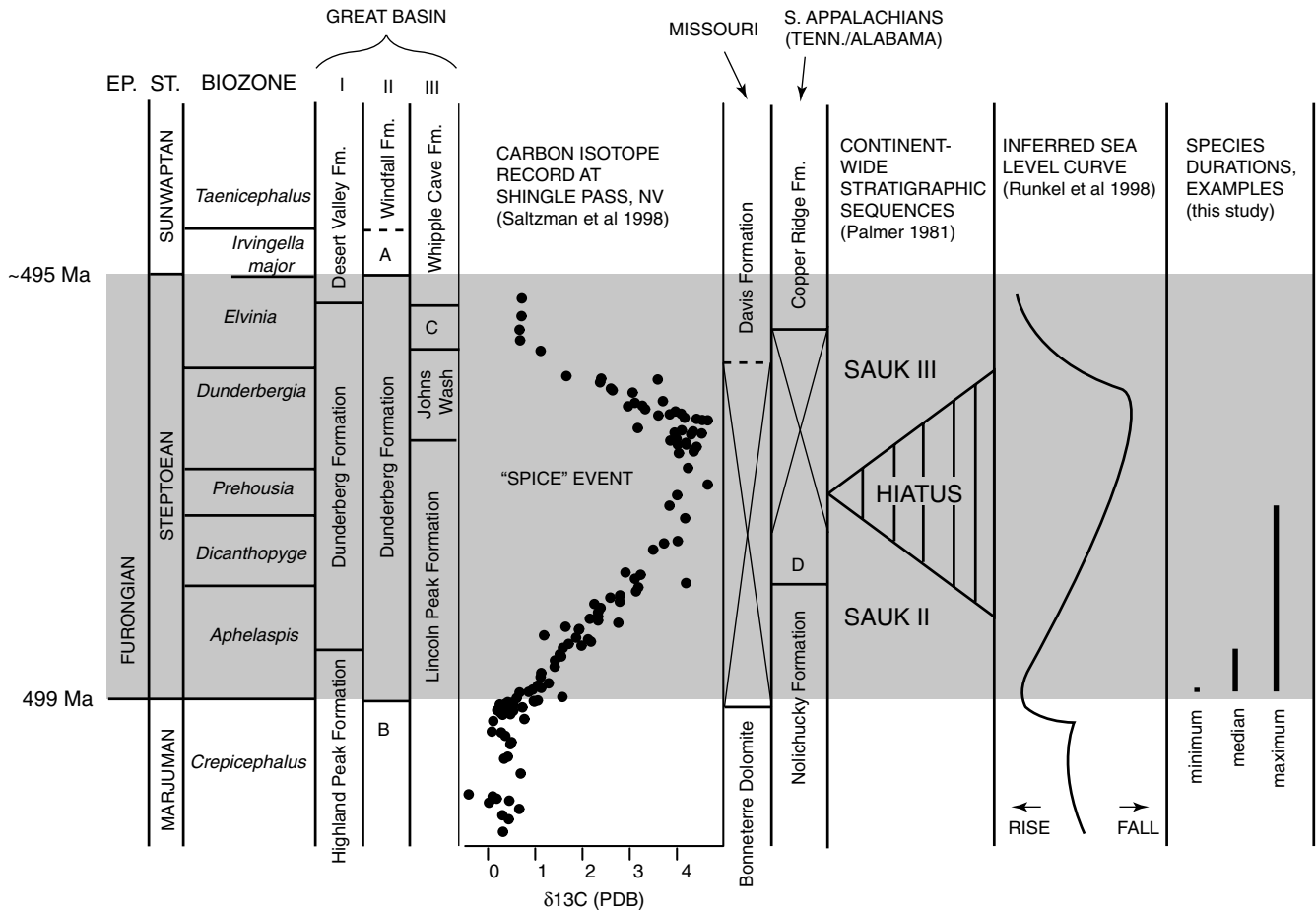


Figure 1. Stratigraphic column showing local geologic formations, biozones, and major features of the Steptoean Stage (shaded area) of North America. Note that the geologic record continues throughout sections in the Great Basin whereas there is a gap in the rock record ("X" symbol) at mid- and eastern-continent outcrop localities, such as Missouri or Tennessee. The hiatus in the rock record at the latter localities is the result of a continent-wide sea-level drop, ultimately precluding deposition of sediments in these areas. Coincident with sea-level fall during this interval is a positive carbon isotope excursion (the "SPICE" interval). Locality symbols: I = Pahrnatag Range, Nevada; II = Cherry Creek and Duck Creek Ranges, Nevada; III = Snake Range and Shingle Pass, Nevada. Additional lithologic units: A = Barton Canyon Limestone; B = Hamburg Limestone/Raiff Formation; C = Corset Spring Shale; D = Maynardville Limestone. EP = Epoch; ST = North American Stage. Example of species durations aligned for comparative purposes and does not indicate relative stratigraphic position of shortest-lived and longest-lived species in section.

ESTIMATING MORPHOLOGICAL VARIATION

Silicified specimens were removed from the limestone bed by dissolution of the carbonate matrix in dilute acetic acid. The specimens were then picked from the remaining insoluble residue and blackened with India ink. Limestone specimens were prepared from crack-out using a micro-scribe. All specimens were whitened with ammonium chloride prior to photography. Cranidia were oriented for photography in dorsal view such that the palpebral lobes were horizontal, following Shaw (1957).

Landmark coordinates were obtained from the photographs using ImageJ 1.36b (Rasband 2006). A total of 15 landmarks were chosen that summarize the overall shape of the cranidium (Fig. 3). All paired landmarks were averaged across the sagittal axis because the right and left sides cannot be regarded as independent (Zelditch et al. 2004; Zelditch 2005), reducing the total number of landmarks used to 10. Some researchers prefer to base the consensus shape on a joint Procrustes fit of all the landmark configurations and their mirror images because this method can handle asymmetry in the landmarks on the sagittal axis and provides a more compact description of the variation by reducing the dimensionality (Klingenberg et al. 2002). This method is more readily applied when the entire configuration of landmarks is measurable for all specimens; in contrast, averaging across the sagittal axis prior to applying Procrustes superimposition allowed me to include specimens where only one paired landmark could be digitized. Fortunately, the difference between these two methods is small as long as the cranidia are nearly symmetric

tal axis because the right and left sides cannot be regarded as independent (Zelditch et al. 2004; Zelditch 2005), reducing the total number of landmarks used to 10. Some researchers prefer to base the consensus shape on a joint Procrustes fit of all the landmark configurations and their mirror images because this method can handle asymmetry in the landmarks on the sagittal axis and provides a more compact description of the variation by reducing the dimensionality (Klingenberg et al. 2002). This method is more readily applied when the entire configuration of landmarks is measurable for all specimens; in contrast, averaging across the sagittal axis prior to applying Procrustes superimposition allowed me to include specimens where only one paired landmark could be digitized. Fortunately, the difference between these two methods is small as long as the cranidia are nearly symmetric

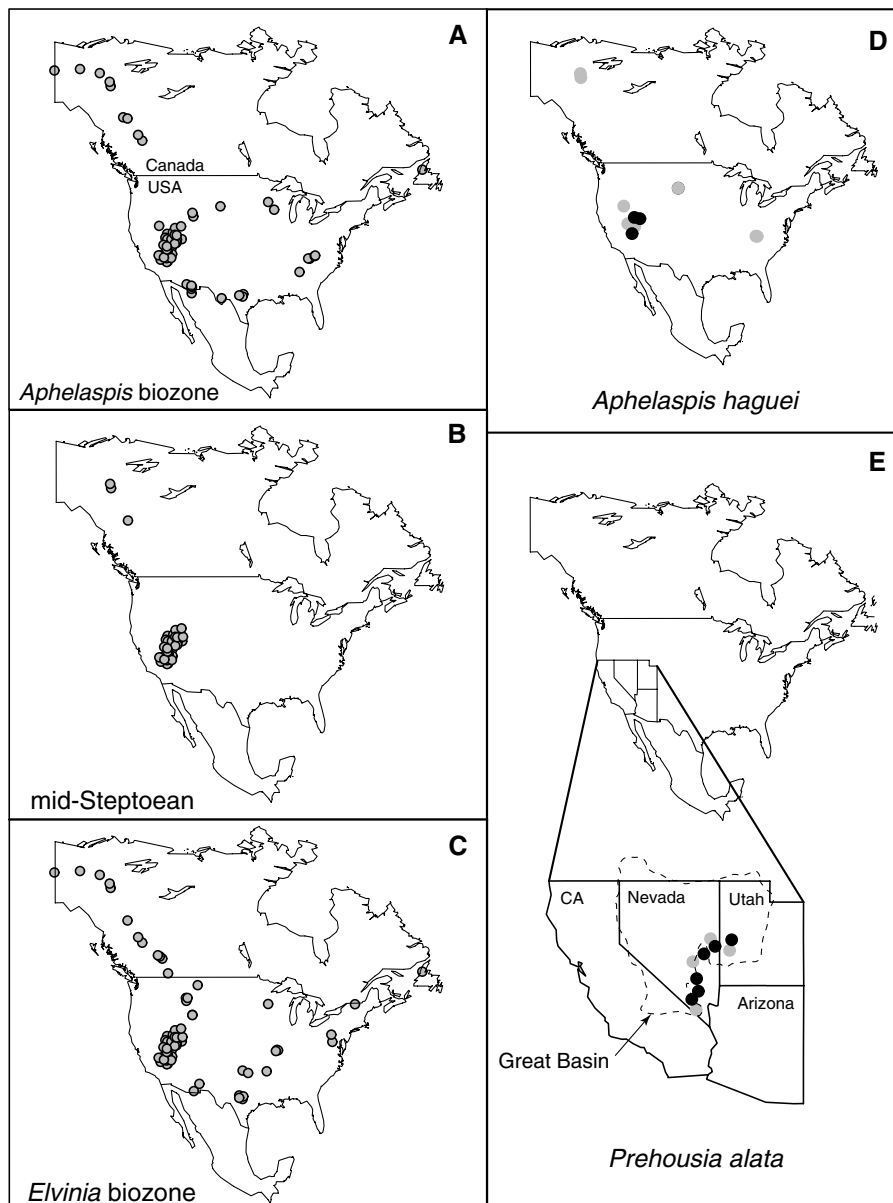


Figure 2. Outcrop localities in North America during the *Aphelaspis* biozone (A), the middle Steptoean (B), and the *Elvinia* biozone (C) and known occurrences for representative taxa sampled for variation estimates (D, E). For (D) and (E), black dots show sampled localities, gray dots show additional occurrences. Dashed line shows perimeter of Great Basin region of the western United States. See Tables S2 and S3 for detailed locality information, including geographic coordinates, and species occurrences and Figure S1 for additional species maps.

(C. Klingenberg, pers. comm.), which is the case for all species examined here.

All statistical analyses were performed using partial and uniform warp scores, which are derived from thin-plate spline decomposition of the landmark coordinates (Rohlf 1990; Bookstein 1991; Zelditch et al. 2004). The degree of variation in each sample and across species was estimated by finding the sum of the variances of the partial warps, which is equivalent to the mean squared Procrustes distances to the sample mean (*MD* of Zelditch et al. 2004, after Foote, 1993). Confidence intervals

were calculated by resampling with replacement (1600 bootstraps, Table 3).

Samples of silicified specimens tend to capture smaller specimens while only larger usable specimens were obtained from limestone samples due to limits in preparation precision. Thus collections often, but not always, include specimens of the mean size of the species. While all specimens used in the study are believed to be holaspids (specimens that have reached the terminal state of maturity based on the cessation of new thoracic segment release), these specimens vary in size both within and across species

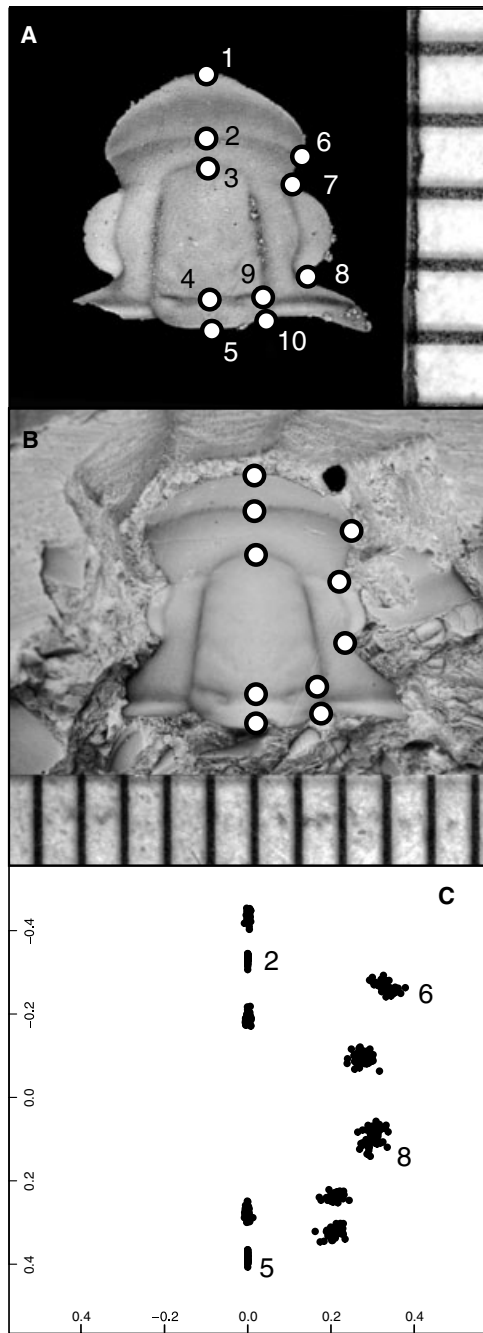


Figure 3. Landmarks chosen for morphometric analysis. Photographs showing chosen landmarks for crania on a silicified specimen of *Sigmocheilus notha* (A) and specimen of *Prehousia indenta* in limestone (B). Scale bar in millimeters. See supporting information for description of landmarks. (C) Superimposed landmark configurations for *Prehousia indenta* ($N = 47$). Superimposition method shown is sliding baseline registration, appropriate for visual assessment of landmark variation in bilaterally symmetric organisms. This aligns all landmark configurations to two axial landmarks (here, 2 and 5), allowing variation only along the sagittal axis for these two landmarks (Webster et al., 2001; Kim et al., 2002). Statistical analyses were performed using partial Procrustes coordinates (see text).

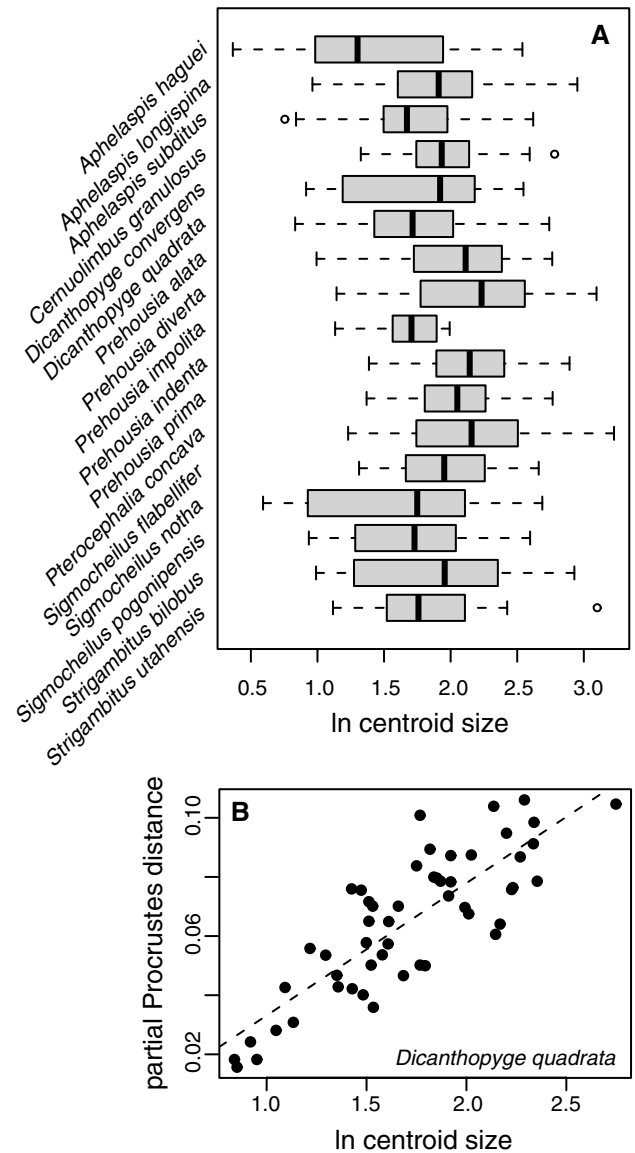


Figure 4. Size distributions for all species and example of shape change during development. (A) Box plots of \ln centroid size distributions for each species for which variation estimates could be obtained. A \ln centroid size of 2.4 is equivalent to approximately 1 cm in cranium length. Open circles indicate statistical outliers. (B) Allometric growth in *Dicanthopyge quadrata*. Shape difference is measured as the partial Procrustes distance between the shape of each specimen and the mean shape of the smallest three specimens. The dashed line is a linear regression line.

(Fig. 4). Allometric growth can inflate estimates of variation for samples of specimens with larger size ranges. The presence of allometry was assessed separately for each species by comparing the natural log of centroid size (\ln centroid size) to the partial Procrustes distance (the distance between two landmark configurations when both are centered, scaled to unit centroid size, and rotated to minimize the sum of squared distances between their corresponding landmarks) of each specimen from the mean of

the smallest three specimens (Zelditch et al. 2004; Webster 2007; Tomašových et al. 2008; Hopkins and Webster 2009; Hopkins and Thurman 2010). All species exhibit some allometric growth (see Fig. 4 for an example) but comparison of the partial warp and uniform warp scores against \ln centroid size indicated that shape changes linearly with size for all species (data not shown). Because allometric shape change is linear in a log-transformed space, each specimen could be size-standardized based on the ontogenetic trajectory of its species. First, multiple regression of the partial and uniform warps against \ln centroid size was used to predict the shape of an individual at the mean size for each species. The variation in the sample not due to allometry was preserved in the residuals from the regression (Zelditch et al. 2004; Webber and Hunda 2007; Hopkins and Webster 2009; Kim et al. 2009; Hopkins and Thurman 2010). Using this method to account for allometry assumes that the allometric trajectories estimated from different collections belonging to the same species are the same, that is, that different populations are growing in the same way. The ubiquitous presence of geographic variation across species (Ridley 1996, p. 426) warns that this might not always be the case. However, for all species in this study where collection-level sample sizes were sufficient to test for this possibility, allometric trajectories were not significantly different despite size range differences among some samples (Table S5). In addition, size-standardization in species showing allometric growth necessarily decreased the overall variation in each sample but the difference is usually minor compared to the amount of variation that remains (Table 3).

Apparent morphological variation is also inflated through measurement error by the operator. Orientation error was assessed by remounting and rephotographing one randomly selected specimen 20 times (PalataPR51.01 [*Prehousia alata* from the Pahrana-gat Range, Nevada]). Digitization error was assessed by obtaining landmarks coordinates from one randomly selected photograph 20 times. Because the magnitude of the variation introduced by inconsistent orientation or digitization is at least an order of magnitude smaller than the intraspecific variation assessed in any species, measurement error was deemed negligible (Table 3).

Morphometric analyses were performed using the Integrated Morphometrics Package (IMP) (Sheets 2003b).

TESTING FOR PHYLOGENETIC SIGNAL IN TRAIT DISTRIBUTION

Phylogenetic signal in the distribution of geographic range size, duration, and amount of variation was investigated by applying Pagel's λ measure of phylogenetic correlation (Pagel 1999; Freckleton et al. 2002) to a phylogeny of Great Basin pteroccephaliids (Hopkins, 2011). A λ value of 0 indicates that the trait distribution is independent of phylogeny and a λ value of 1 indicates that traits are evolving according to Brownian motion along

the given phylogeny; thus the maximum likelihood value of λ indicates the effect strength of phylogeny on the distribution of the trait data (Freckleton et al. 2002; Freckleton 2009). These values can be tested to see if traits exhibit significant phylogenetic dependence by comparing the log likelihood of the maximum likelihood value of λ to the log likelihood of the data at an alternative value of λ . This diagnostic shows low Type I error rates, even at small sample sizes ($N < 20$, Freckleton et al. 2002).

For comparison, Blomberg's K metric was also calculated and the associated permutation tests were performed (Blomberg et al. 2003). λ was calculated using the `fitContinuous` function in the "GEIGER" package in R; sampling error for duration and variation was included using the `meserr` argument (Harmon et al. 2008). K was calculated using the "Picante" package in R (Kembel et al. 2010).

In the absence of measures such as absolute age dates or molecular data, many studies assume equal branch lengths (e.g., see summary of studies in Blomberg et al. 2003). Although absolute dates are not known for the occurrences of the species in this study, relative stratigraphic position can be inferred from the composite sections used to estimate species duration (above, see also Hopkins [2010]) and used to scale branch lengths (Fig. 5). Net sedimentation rate determines the relationship between stratigraphic position and time; at any given locality, the less variable the rate is, the more stratigraphy is proportional to time. Here, variation in sedimentation rates within and across sections is mediated by both the process of correlation as well as the specific scaling option chosen (see above). Branches that are not constrained by FAs were conservatively assumed to represent geologically instantaneous branching and were assigned an arbitrarily low value of 0.01. Although λ is sensitive to very small and zero branch lengths (Ruta et al. 2006; Brusatte et al. 2008), setting higher minimum branch lengths for the trees did not change the results. Hopkins (2011) analyzed four character matrices each treating continuous characters in different ways: using finite mixture coding (Strait et al. 1996; Sheets 2003a) to code continuous characters, and using gap-weighting (Thiele 1993) to code continuous characters, or excluding continuous characters altogether all produced different consensus trees, whereas treating continuous characters "as such" (Goloboff et al. 2006) produced the same most parsimonious tree as gap-weighting after pruning. In this study, scaling was applied to the three different phylogenetic hypotheses and the results of these tests were compared to the same trees scaled to equal branch lengths (all = 1).

In addition to the phylogenetic signal diagnostics, phylogenetic generalized least squares (PGLS) was applied to the dataset to assess the dependence of evolutionary history on the apparent relationships between variables (Martins and Hansen 1997; Pagel 1997; Cunningham et al. 1998; Garland and Ives 2000; Rohlf 2001; Garland et al. 2005; Paradis 2006; Rohlf 2006). PGLS was

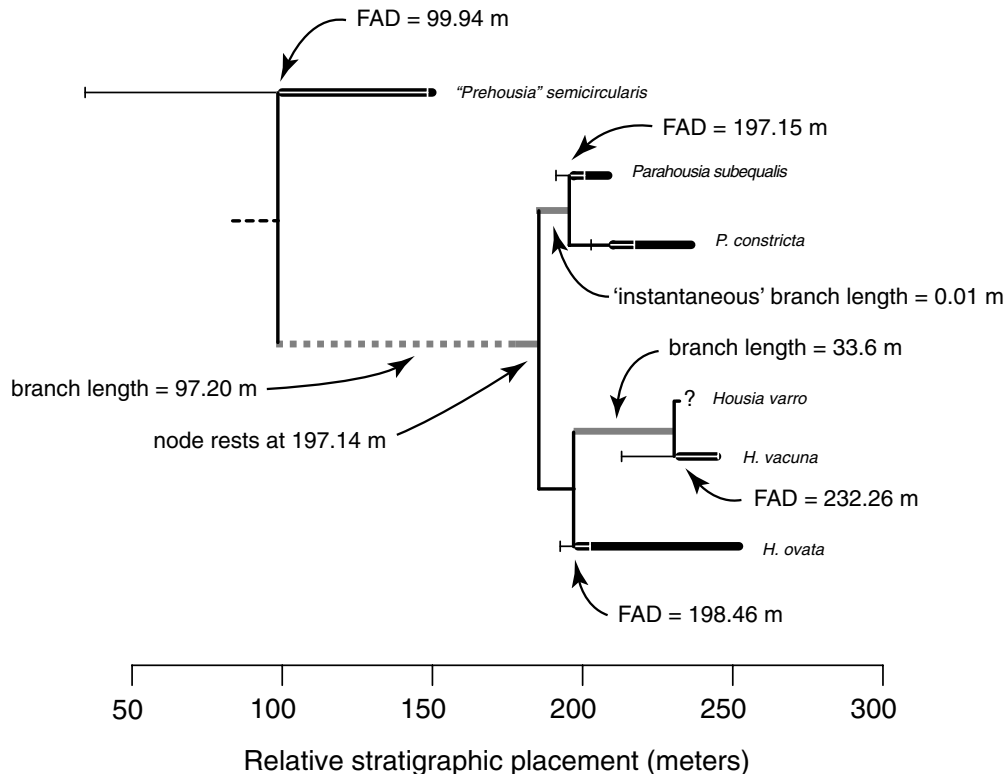


Figure 5. Portion of one phylogenetic hypothesis showing how branches are assigned lengths based on the relative placement of first appearances of the tree tips (FADs). Thick black bars show the stratigraphic range for each species; gray bars show branches being estimated from FADs. Error bars show the confidence intervals around the first appearances of each taxon. "?" = FA unknown for taxon; branches that are not pinned by first appearances are conservatively assumed to represent a geologically instantaneous amount of time and assigned an arbitrarily low value of 0.01 m.

performed using COMPARE 4.6 (Martins 2004) with the best-fit value of α selected through maximum likelihood. Consensus trees were resolved arbitrarily by setting internal branch lengths to zero (Purvis and Garland 1993). Analyses were run with branch lengths scaled to both relative stratigraphic position and with equal branch lengths.

SAMPLING BIAS AND MISSING DATA

Variance metrics are relatively insensitive to sample size and give a better indication of the relative dissimilarity between forms than other variation metrics, such as range (Foote 1992; Wills 2001). However, variation estimates may be influenced by an increase in the number of localities sampled, particularly for species that show geographic variation. Because it was not feasible to sample all known occurrences of these species (Fig. 2D, E, and Fig. S1), variation estimates were compared to the number of specimens, number of collections, number of localities, and the percent of the geographic range represented in the sample, none of which appear to be systematically biasing the variation estimates (Fig. S2).

In addition, rarefaction curves were produced by subsampling size-standardized landmark configurations by number of

localities (1000 iterations). Rarefaction routines were written in R, using functions from the "shapes" package (Dryden 2009). For each iteration, a specified number of localities were randomly selected and all specimens available from those localities were used to estimate variation in the landmark configurations. Small total sample size prohibited subsampling by both number of specimens and localities. Thus, because of variation in sample size among localities, subsampling by locality produced different sized subsets of landmark configurations for the same number of localities. When subsampling by localities, the estimated variation initially increases with more localities but stabilizes when three or more localities are sampled (Fig. S3). All species included in the analysis were sampled from at least three localities with the exception of *A. longispina*, known to occur only in the Duck Creek Range of Nevada (Table 3, Fig. S1). Subsampling by number of specimens was also performed, but, following the suggestion of one reviewer, results were disregarded in favor of bootstrapped confidence intervals that more reliably indicate degrees of uncertainty at smaller sample sizes.

In addition to unsampled specimens, unsampled species may also bias the results if the distribution of the missing taxa is not completely random (Nakagawa and Freckleton 2008;

Table 4A. Correlations between duration and geographic range size. Statistically significant values are in bold.

Dataset	N	Variable	Duration (m)	
			R	Spearman's ρ
All	36	Max. GC dist (km)	0.49**	0.43**
		Rel. max GC dist	0.64***	0.46**
		Lat. extent	0.16	0.50**
		Rel. lat. extent	0.42**	0.36*
Phylo	28	Max. GC dist (km)	0.52**	0.39*
		Rel. max GC dist	0.65***	0.39*
		Lat. extent	0.27	0.48**
		Rel. lat. extent	0.42*	0.31
Var	17	Max. GC dist (km)	−0.02	−0.06
		Rel. max GC dist	−0.02	−0.06
		Lat. extent	0.02	0.04
		Rel. lat. extent	−0.08	−0.07

* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.

Freckleton 2009). In this study, missing data are likely to be biased by one of two things. First, geographic range size and duration estimates were estimated for species that occur in the Great Basin but not for cogenics that occur only in other parts of Laurentia, thus not all taxa included in the phylogenetic analysis were sampled. As a result, if there is a relationship between phylogenetic affinity and biogeography, then some parts of the tree will be more pruned than other parts of the tree. However, inspection of the relative placement of taxa within genera across the different phylogenetic analyses (Hopkins, 2011) suggests that for geographic range size and duration, this is not the case. In contrast, some parts of the tree are pruned more severely than others when only species with variation data are left.

Second, missing data might also be biased by abundance, such that data on rare species are more likely to be missing than for common species (Kunin and Gaston 1997; Nakagawa and Freckleton 2008). In particular, rare species are less likely to occur in large enough samples to be available for variation estimates. The latter situation is surely true for this study, but I can think of no a priori reason for a systematic difference in the *amount* of variation expressed by a species by virtue of its being rare rather than common.

Results

BIVARIATE COMPARISONS

Bivariate comparisons support a positive association between geographic range size and species duration, regardless of the geographic range size or duration metric used (Table 4A, 4B, and Fig. 6 [only “All” dataset shown]). This is consistent with previous analyses showing a positive relationship between geographic

Table 4B. Correlations between variation, geographic range size, and duration.

Dataset	N	Variable	Variation	
			R	Spearman's ρ
Var	17	Max. GC dist (km)	−0.21	−0.18
		Rel. max GC dist	−0.21	−0.16
		Lat. extent	−0.29	−0.20
		Rel. lat. extent	−0.14	−0.23
		Duration (meters)	−0.27	−0.18

range size and duration in many clades (e.g., Buzas and Culver 1984; Jablonski and Roy 2003; Liow 2007; Powell 2007; Foote et al. 2008), at least during background extinction intervals. However, the spread of data resembles what has been referred to in the macroecology literature (e.g., Blackburn and Gaston 1998) as “polygon-shaped” (or “triangle-shaped”) associations, with data-points falling within some areas of bivariate plots but not in others (this sort of relationship is not uncommon in macroecological studies but analytical methods for such associations remain limited [Blackburn and Gaston 1998; Gotelli 2001; Gaston 2003]). As a result, Steptoean trilobite species with large geographic range sizes do not necessarily live a relatively long time; rather, there is a lack of long-lived species with narrow geographic ranges.

The three taxa with latitudinal extents around 5 degrees and durations of over 80 m (Fig. 6C) occurred in the middle of the Steptoean stage when the total continental shelf available for habitation was reduced relative to earlier and later in time. These taxa thus occupied a relatively high proportion of the area available, and standardizing for this shifts their position to the right (Fig. 6D).

There is a gap in the distribution of durations for species with wide relative geographic ranges, both relative maximum Great Circle distance and relative latitudinal extent (Fig. 6B,D). For both measures of geographic range size, however, both short-lived and long-lived widespread groups of taxa contain species from each subfamily or family and most genera (Tables 1 and 2). Both contain stratigraphically older and younger species, both contain species that range across the width of the shelf (Pratt 1992), and both contain common and rare species (Palmer 1965b); other ecological data that may be relevant (such as larval type) is not currently known for these taxa. The apparent bimodal distribution of stratigraphic durations in wide-ranging taxa may be real, but no explanation for this distribution is evident from the available data. The geographically restricted taxa also occupy a triangle-shaped space in the plot but there is no linear or rank-order correlation between the variables (Fig. 6E).

The data indicate a weak negative association between morphological variation and geographic range size but the data are

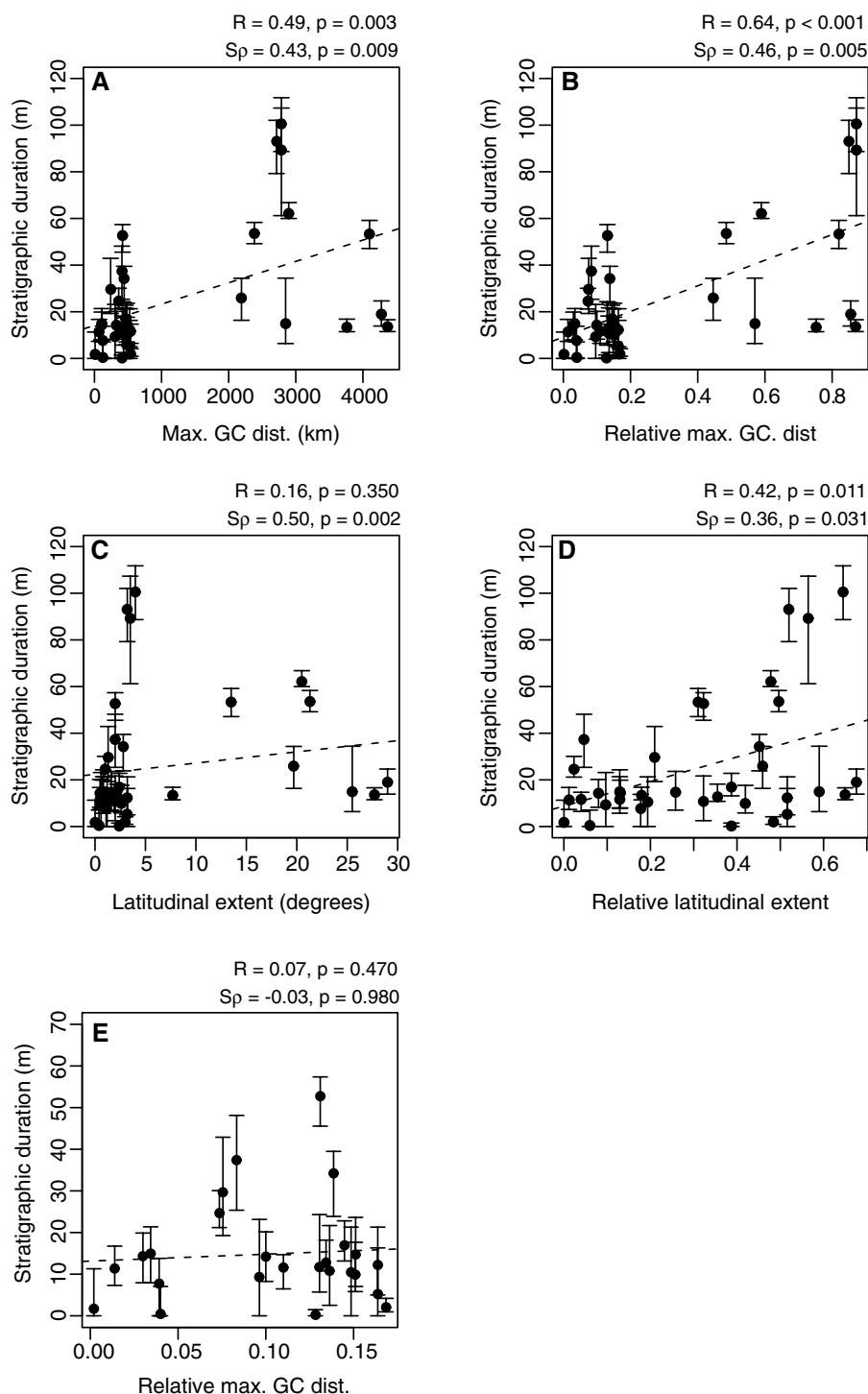


Figure 6. Bivariate plots showing the relationship between stratigraphic duration and geographic range size for the “All” dataset ($N = 36$). Error bars on duration estimates based on compiled equally good composite sections. R = Pearson product-moment correlation coefficient; S_p = Spearman rank-order correlation coefficient. Data distribution and statistics are similar for the “Phylo” dataset ($N = 28$). (A–D) All taxa. (E) Relative maximum Great Circle distance versus stratigraphic duration for geographically restricted taxa (relative maximum Great Circle distance < 0.2). This plot is a larger view of the lower left-hand corner of 7B but regression line and statistics are based on just this subset of data.

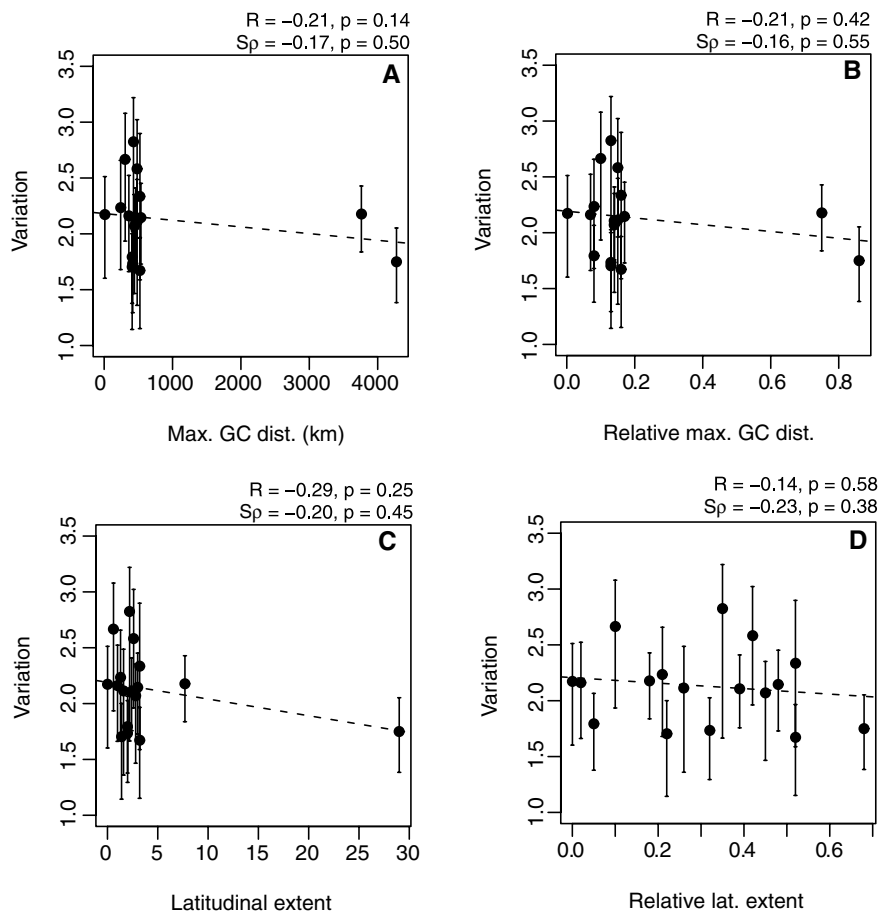


Figure 7. Bivariate plots showing the relationship between size-standardized variation and geographic range size. Error bars on variation estimates based on resampling by bootstrapping (see text). R = Pearson product moment correlation coefficient; S_p = Spearman rank-order correlation coefficient.

scattered across the plot (Fig. 7) leaving little support for an association between these variables. Considering the ubiquity of geographic variation across species, the absence of a positive relationship between these two variables may be surprising. Nonetheless, the same result has been found in other organisms (extant fiddler crabs, Hopkins and Thurman 2010).

The data also indicate a weak negative association between morphological variation and duration (Fig. 8), but in contrast to the comparison of variation and geographic range size, the data occupy only one part of the graph, again indicating a “triangular” relationship between these two variables rather than a linear association. If any argument can be made that there is an association between these two variables, it appears that species with less variation in cranial shape do not necessarily live a relatively long time; rather, there is a lack of long-lived species with high levels of variation within this clade.

The data distribution and correlation statistics between geographic range size and duration are similar for the “Phylo” dataset ($N = 28$, Table 4A), but the relationship between geographic range size and duration is not captured in the “Var” dataset ($N = 17$),

because widely distributed and long-lived taxa are not among the subset (Table 4B). Although geographic range size is not explicitly being held constant here, the effect of geographic range size on duration in this dataset is essentially negligible and partial correlation coefficients reflect this (they are consistent). Small sample size precludes application of other analytical tools, such as path analysis (Shipley 2000), to investigate the simultaneous interaction of these three variables.

PHYLOGENETIC SIGNAL

Duration estimates show maximum likelihood values of $\lambda = 0$ across all datasets, indicating no phylogenetic signal in the distribution of duration estimates (Table 5, see also Table S6 for full results). These results did not depend on the inclusion of estimation error in their estimation. Surprisingly, variation also shows no phylogenetic signal across all phylogenetic hypotheses. In this case, however, the incorporation of estimation error in the calculation of λ was important: if not included, λ values for variation are as high as 0.82 (and significantly different from 0) when branches were scaled to stratigraphic thickness.

Table 5. Range of λ values for each variable across all three phylogenetic hypotheses and the “Phylo” and “Var” datasets. λ values significantly different from 0 are bolded. N = number of species in analyzed datasets.

Variable	Branch lengths scaled to relative stratigraphic placement (meters)	Equal branch lengths (all = 1)	N
Max. GC dist (km)	0.75–0.97***	0.50–1.00***	28,17
Rel. max GC dist	0.97–1.00***	0.85–1.00***	28,17
Lat. extent	0.96–1.00***	0.93–1.00***	28,17
Rel. lat. extent	0.91–0.95***	0.00–0.88*	28,17
Duration (meters)	0.00	0.00	28,17
Variation	0.00	0.00	17

* < 0.05, ** < 0.01, *** < 0.001.

λ values for geographic range size consistently show a high degree of phylogenetic dependence across all topologies, datasets, and scaling methods. In many cases, particularly for maximum Great Circle distance, λ is equal to or not significantly different from 1, indicating that geographic range size covaries as would be predicted from a Brownian model of evolution.

Blomberg’s K values for geographic range size are also considerably and consistently higher than K values for variation and duration (Table S7). In addition, K values for geographic range size are also often over 1, indicating that the distribution of geographic range sizes are typically more similar than expected. However, permutation tests resulted in low but rarely significant P -values (Table S7), perhaps due to a lack of power at these sample sizes. Overall, these results suggest that geographic range size is much more strongly correlated with phylogeny in these taxa than either variation or duration.

Phylogenetic generalized least squares methods (PGLS) assume that the traits under study are linearly associated with one another. There appears to be some capacity for accounting for nonlinear relationships (although “line-based”, such as curvilinear) but the ability of this method to deal with various kinds of nonlinearity—particularly “polygonal-shaped” associations—has not been treated in detail and may actually be misleading in regards to the biological inferences being made (Quader et al. 2004). Regardless, results from PGLS of the trilobite species of this study were consistent with those produced from conventional bivariate analyses (Table S8). At least one other study looking at similarly associated ecological variables with low-to-moderate phylogenetic signal has also found that results from phylogenetic comparative methods were consistent with results from conventional bivariate statistics (Diniz-Filho and Torres 2002).

Thus, based on both the lack of phylogenetic signal in some variables and the results of the PGLS, there is no indication that phylogenetic history is conflating or obscuring the relationships

between geographic range size, variation, and duration in this clade.

Discussion

The results presented above suggest that at least in this clade, short-ranging taxa may exhibit a range of variation in cranial shape and may be either geographically restricted or widespread, whereas long-ranging species tend to be widespread and/or have less variation. This pattern of association between variables is not simply a result of shared evolutionary history.

Geographic range size does show considerable dependence on phylogeny in this clade of trilobites, and, in fact, is correlated with phylogeny in many, if not all, clades where it has been investigated (Jablonski 1987; Freckleton et al. 2002; Hunt et al. 2005; Jablonski and Hunt 2006; Waldron 2007; Mouillot and Gaston 2009, this study), as may be range limits as well (at least for genera, Roy et al. 2009b). Mouillot and Gaston (2009) found that geographic range size heritability was enhanced for closely related species whose ranges overlap, most likely because these species share common environmental conditions and presumably share other ecological characteristics that affect geographic range size. This may explain the strong phylogenetic signal in this study relative to other studies because all of these species occurred, at least in part, in the Great Basin region.

Widespread species may have a tendency to live longer because they are less susceptible to local extinction. Geographic range might also be correlated with duration because of covarying factors, such as dispersal ability, climate or environmental tolerance or breadth, and absolute population size (e.g., Hansen 1980; Stanley 1986; Kammer et al. 1997; Liow 2007; Powell 2007). Alternatively, long-lived species might have achieved a wide geographic range because they lived long enough to establish populations further from their site of origin (Foote et al. 2008).

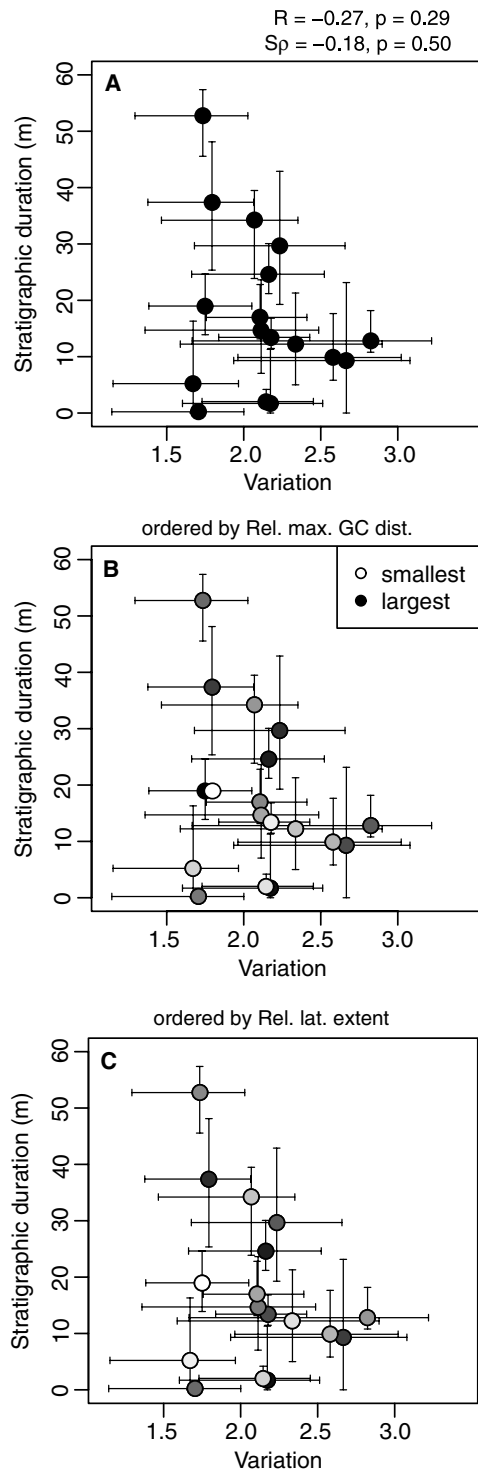


Figure 8. Bivariate plots showing the relationship between size-standardized variation and stratigraphic duration (A) and coded to show rank order of geographic range sizes (B, C). Error bars on variation estimates based on resampling by bootstrapping (see text). Error bars on duration estimates based on compiled equally good composite sections. R = Pearson product moment correlation coefficient; S_p = Spearman rank-order correlation coefficient. (B) Coded by relative maximum Great Circle distance. (C) Coded by relative latitudinal extent; legend in (B) also applies to (C).

Local abundance, geographic range size, and extinction risk covary in many groups (Gaston and Blackburn 2000; Gaston 2003; but see Kiessling and Aberhan 2007). Although relative abundance data have not been compiled for Steptoean trilobite collections, Palmer (1965b) made a subjective appraisal of relative abundance of Great Basin species in the faunal assemblages in which he found them (Table 1). By coding his categories (rare = 1, moderately rare = 2, moderately common = 3, and common = 4), I was able to make a preliminary comparison of local abundance and geographic range size. Abundance is significantly positively correlated with all geographic range size metrics except relative latitudinal extent (Spearman's $\rho = 0.38$ – 0.49 , $P = 0.018$ – 0.002). Further investigation of the importance of abundance in the evolution of this clade is beyond the scope of this dataset. However, where it has been assessed in marine invertebrates, abundance appears to have only an indirect effect on extinction risk through its association with geographic range size (Harnik 2011).

Statistically, it is possible for one trait showing phylogenetic signal (geographic range size) to be correlated with a trait lacking phylogenetic signal (duration) because these variables are not linearly related. The lack of phylogenetic signal in duration in this clade of trilobites appears to contradict other studies documenting extinction selectivity across many fossil and extant groups (e.g., McKinney 1997; Purvis 2008; Janevski and Baumiller 2009; Roy et al. 2009a; Green et al. 2011). In contrast to this work, however, this study is limited to a clade of closely related species that shared numerous ecological and life-history strategies with overlapping geographic ranges. Even if extinction is random at this scale, extinction selection could still be operating on characters that are shared by the group, effectively acting at higher taxonomic levels inclusive of the group. The frequency with which duration shows different degrees of phylogenetic signal at different taxonomic levels would be straightforward to test but would require species-level phylogenies with sufficient taxonomic breadth and corresponding species duration estimates.

Similarly, the pattern of association between variation and duration appears to contradict a previous study that found morphological variability to promote longevity in ostracods (Liow 2007). Although Liow found that species or genera with highly variable subspecies or species (as reported from taxonomic descriptions) were among the longest lived, she did not investigate whether those variable subspecies or species were themselves long-lived. Genera with morphologically variable species may tend to accumulate more species over time, ultimately promoting genus longevity, even if many of the morphologically variable species themselves are not long-lived.

Crucial to the interpretation of these results is the recognition that within-species variation as measured herein is the amount of morphospace occupied by a species across time and space, that is, across all sampled populations. For example, among sister species

of bivalves within which only one survived the Plio-Pleistocene extinction interval, survivors typically expressed more morphological variation than victims (Kolbe et al. 2011). However, both the sign and magnitude of the difference in variation between survivors and victims depended on whether the variation under consideration was the average population-level variation or the variation pooled across populations. The apparent role of variation in driving evolutionary rates or persistence may often depend on the focal level (population vs. species), particularly as some mechanisms by which variation influences extinction involve one source but not the other.

Thus, although both stress resistance and stabilizing selection influence population-level variation (see Introduction), these factors may affect species-level variation in a number of ways or not at all. In particular, the adequacy of stabilizing selection as a mechanism for long-term stasis requires that selective optima be preserved over a narrow range across traits and over significant amounts of time (Hansen and Houle 2004; Futuyma 2010). Possible mechanisms for providing a stable optimum across environments or as environmental parameters are changing include niche tracking (Eldredge 1999; Gould 2002), differential degrees of plasticity across characters (Wake et al. 1983), averaging across semi-independent populations that track environmental changes separately (Stanley and Yang 1987; Lieberman and Dudgeon 1996), and variation in selection strength across the geographic range of a taxon (Holt and Gaines 1992; Holt 1996). As a general pattern, these mechanisms assume that stabilizing selection is common and strong, which may not be the case (Kingsolver et al. 2001; Hansen and Houle 2004; but see Walsh and Blows 2009). Finally, models that purport to demonstrate that stabilizing selection is a sufficient driver to explain stasis at higher taxonomic levels (e.g., Estes and Arnold 2007) have not been applied to networks of populations. In fact, the entire spatio-temporal history of a species may reveal less morphological change overall than what is documented in local subsets of a species lineage (Eldredge et al. 2005).

Instead, the pattern documented in this clade of trilobites may be indicating a relationship between rates of morphological evolution and geographic variation. For example, fiddler crab species with more carapace variation show more geographic structure of variation—in other words, species with higher morphological variation are characterized by more population-level difference in morphology, not higher population-level variation (Hopkins and Thurman 2010). Similarly, observed variance increases linearly, if slowly, as populations are increasingly time-averaged (Hunt 2004), at least in the frequent situation where within-lineage change is best described as an unbiased random walk (Hunt 2007b). Thus, greater variation within some trilobite species in this clade could simply reflect more distinct geographic or temporal structure of that variation. For example, the placement and

orientation of the eyes relative to the rest of the cranium has already been shown to vary with water depth in some trilobites (Webber and Hunda 2007; Hopkins and Webster 2008) and the mean number of pygidial axial rings varies in time in others (Cisne et al. 1980; Sheldon 1987). Divergence between populations may occur because of adaptation to local selection pressures or because populations are able to respond plastically to different environmental cues in either a spatial or temporal context, or both. In either case, divergence can precede reproductive isolation, even as it contributes to isolation and speciation through the origination of developmental differences among populations (West-Eberhard 2003).

One optimistic view proposes that speciation provides enough permanence of morphological changes to be registered in the fossil record, and perhaps that we can expect evolutionary changes in the fossil record to be associated with speciation (Futuyma 1987). At the very least, morphological characters that are expressed consistently in time and space (i.e., with enough “permanence”) can be used to identify discrete biological units (i.e., fossil species), whereas variation in other morphological characters pooled across time and space give an indication of the morphological breadth that each species explored. Nonetheless, spatial or temporal divergence of most populations may frequently be too short-lived to be captured in the fossil record due to interbreeding with nondivergent populations (Futuyma 2010). Because of this, lineages with high rates of morphological evolution may typically appear in the fossil record as relatively short-lived but more variable taxa.

ACKNOWLEDGMENTS

I thank M. Webster, S. Westrop, D. Jablonski, M. Foote, M. LaBarbara, S. Lidgard, and A.R. (Pete) Palmer for invaluable guidance and support of this project at many stages. I also thank D. Rowley for his help with paleo-latitude reconstructions and P. Sadler for guidance in using CONOP. I am indebted to K. McKinney at the U.S. Geological Survey in Denver for his help in sorting material and arranging loans. I am also indebted to G. Dechman and C. Stevenson for all of their help and support in the field. Thanks to J. Spicer, C. Hopkins, D. Hopkins, T. Mason, and M. Webster for field assistance, to A. Sprunger of the Desert National Wildlife Refuge for providing collecting permits and facilitating field work in the Desert Range, and to M. Webster for access to the Institute for Cambrian Studies library and specimen collection. G. Hunt, N. Hughes, and the associate editor, C. Klingenberg, provided exceptionally helpful and thoughtful reviews. Field and laboratory work were supported by funding from the Paleontological Society (Gould Grant-in-Aid), the Society for Sedimentary Research, the Institute for Cambrian Studies, the American Museum of Natural History (Theodore Roosevelt Memorial Fund), the Geological Society of America, and the Department of the Geophysical Sciences, University of Chicago (Gurley Fund).

LITERATURE CITED

Adrain, J. M., and S. R. Westrop. 2001. Stratigraphy, phylogeny, and species sampling in time and space. Pp. 291–322 in J. M. Adrain,

- G. D. Edgecombe and B. S. Lieberman, eds. Fossils, phylogeny, and form. Kluwer Academic/Plenum Publishers, New York.
- Avise, J. C. 2000. *Phylogeography: the history and formation of species*. Harvard Univ. Press, Cambridge, MA.
- Badyaev, A. V., and K. R. Foresman. 2000. Extreme environmental change and evolution: stress-induced morphological variation is strongly concordant with patterns of evolutionary divergence in shrew mandibles. *Proc. R. Soc. Lond. B* 267:371–377.
- Badyaev, A. V., and G. E. Hill. 2000. The evolution of sexual dimorphism in the house finch. I. Population divergence in morphological covariance structure. *Evolution* 54:1784–1794.
- Badyaev, A. V., K. R. Foresman, and R. L. Young. 2005. Evolution of morphological integration: developmental accommodation of stress-induced variation. *Am. Nat.* 166:382–395.
- Blackburn, T. M., and K. J. Gaston. 1998. Some methodological issues in macroecology. *Am. Nat.* 151:68–83.
- Blomberg, S. P., R. Garland, Jr., and A. R. Ives. 2003. Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution* 57:717–745.
- Bolnick, D. I., R. Svanback, M. S. Araujo, and L. Persson. 2007. Comparative support for the niche variation hypothesis that more generalized populations also are more heterogeneous. *Proc. Natl. Acad. Sci. USA* 104:10075–10079.
- Bookstein, F. L. 1991. *Morphometric tools for landmark data: geometry and biology*. Cambridge Univ. Press, Cambridge, MA.
- Brusatte, S. L., M. J. Benton, M. Ruta, and G. T. Lloyd. 2008. Superiority, competition, and opportunism in the evolutionary radiation of dinosaurs. *Science* 321:1485–1488.
- Buzas, S. J., and S. J. Culver. 1984. Species duration and evolution: benthic foraminifera on the Atlantic continental margin of North America. *Science* 225:829–830.
- Carroll, S. B., J. K. Grenier, and S. D. Weatherbee. 2005. *From DNA to diversity: molecular genetics and the evolution of animal design*. 2nd ed. Blackwell Publishing, Malden, MA.
- Cisne, J. L., G. O. Chandlee, B. D. Rabe, and J. A. Cohen. 1980. Geographic variation and episodic evolution in an Ordovician trilobite. *Science* 209:925–927.
- Cody, R. D., R. H. Levy, D. M. Harwood, and P. M. Sadler. 2008. Thinking outside the zone: high-resolution quantitative diatom biochronology for the Antarctic Neogene. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 260:92–121.
- Coyne, J. A., and H. A. Orr. 2004. *Speciation*. Sinauer, Sunderland, MA.
- Cunningham, C. W., K. E. Omland, and T. H. Oakley. 1998. Reconstructing ancestral character states: a critical reappraisal. *Trends Ecol. Evol.* 13:361–366.
- DeWitt, T. G., and S. M. Scheiner. 2004. *Phenotypic plasticity: functional and conceptual approaches*. Oxford Univ. Press, Oxford.
- Diniz-Filho, J. A. F., and N. M. Torres. 2002. Phylogenetic comparative methods and the geographic range size-body size relationship in new world terrestrial Carnivora. *Evol. Ecol.* 16:351–367.
- Dryden, I. 2009. shapes: statistical shape analysis. Available at: <http://cran.r-project.org/web/packages/shapes/index.html>.
- Eldredge, N. 1999. *The pattern of evolution*. W.H. Freeman, New York.
- Eldredge, N., J. N. Thompson, P. M. Brakefield, S. Gavrilets, D. Jablonski, J. B. C. Jackson, R. E. Lenski, B. S. Lieberman, M. A. McPeck, and W. Miller, III. 2005. The dynamics of evolutionary stasis. Pp. 133–145 in E. S. Vrba and N. Eldredge, eds. *Macroevolution: diversity, disparity, contingency*. *Paleobiology* 31(Suppl.).
- Endler, J. A. 1977. *Geographic variation, speciation, and clines*. Princeton Univ. Press, Princeton, NJ.
- Estes, E., and S. J. Arnold. 2007. Resolving the paradox of stasis: models with stabilizing selection explain evolutionary divergence on all timescales. *Am. Nat.* 169:227–244.
- Findley, J. S., and H. Black. 1983. Morphological and dietary structuring of a Zambian insectivorous bat community. *Ecology* 64:625–630.
- Foote, M. 1992. Rarefaction analysis of morphological and taxonomic diversity. *Paleobiology* 18:1–16.
- . 1993. Contributions of individual taxa to overall morphological disparity. *Paleobiology* 19:403–419.
- Foote, M., J. S. Crampton, A. G. Beu, and B. N. Cooper. 2008. On the bidirectional relationship between geographic range and taxonomic duration. *Paleobiology* 34:421–433.
- Freckleton, R. P. 2009. The seven deadly sins of comparative analysis. *J. Evol. Biol.* 22:1367–1375.
- Freckleton, R. P., P. H. Harvey, and M. Pagel. 2002. Phylogenetic analysis and comparative data: a test and review of evidence. *Am. Nat.* 160:712–726.
- Futuyma, D. J. 1987. On the role of species in anagenesis. *Am. Nat.* 130:465–473.
- . 2010. Evolutionary constraint and ecological consequences. *Evolution* 64:1865–1884.
- Galeotti, P., and D. Rubolini. 2004. The niche variation hypothesis and the evolution of colour polymorphism in birds: a comparative study of owls, nightjars, and raptors. *Biol. J. Linn. Soc.* 82:237–248.
- Garland, R., Jr., and A. R. Ives. 2000. Using the past to predict the present: confidence intervals for regression equations in phylogenetic comparative methods. *Am. Nat.* 155:346–364.
- Garland, R., Jr., A. F. Bennett, and E. L. Rezende. 2005. Phylogenetic approaches in comparative physiology. *J. Exp. Biol.* 208:3015–3035.
- Gaston, K. J. 2003. *The structure and dynamics of geographic ranges*. Oxford Univ. Press, Oxford.
- Gaston, K. J., and T. M. Blackburn. 2000. *Pattern and process in macroecology*. Blackwell Science, Oxford.
- Gilbert, S. F., and D. Epel. 2009. *Ecological developmental biology: integrating epigenetics, medicine, and evolution*. Sinauer Associates Inc., Sunderland, MA.
- Goloboff, P. A., C. I. Mattoni, and A. S. Quinteros. 2006. Continuous characters analyzed as such. *Cladistics* 22:589–601.
- Gotelli, N. J. 2001. Research frontiers in null model analysis. *Glob. Ecol. Biogeogr.* 10:337–343.
- Gould, S. J. 2002. *The structure of evolutionary theory*. Belknap Press, Harvard Univ. Press, Cambridge, MA.
- Green, W. A., G. Hunt, S. L. Wing, and W. A. DiMichele. 2011. Does extinction wield an axe or pruning shears? How interactions between phylogeny and ecology affect patterns of extinction. *Paleobiology* 37:72–91.
- Grosberg, R. K., and C. W. Cunningham. 2001. Genetic structure in the sea: from populations to communities. Pp. 61–84 in M. D. Bertness, S. D. Gaines and M. E. Hay, eds. *Marine community ecology*. Sinauer Associates, Inc., Sunderland, MA.
- Hall, J., and R. P. Whitfield. 1877. *Paleontology: fossils of the Potsdam Group*. U.S. Geological Exploration 40th Parallel 4:199–231.
- Hallgrímsson, B., and B. K. Hall. 2005. *Variation: a central concept in biology*. Elsevier Academic Press, New York.
- Hansen, T. A. 1980. Influence of larval dispersal and geographic distribution on species longevity in neogastropods. *Paleobiology* 6:193–207.
- Hansen, T. F., and D. Houle. 2004. Evolvability, stabilizing selection, and the problem of stasis. Pp. 130–150 in M. Pigliucci and K. Preston, eds. *Phenotypic integration: studying the ecology and evolution of complex phenotypes*. Oxford Univ. Press, Oxford.
- Harmon, L. J., J. Weir, C. Brock, R. Glor, and W. Challenger. 2008. GEIGER: investigating evolutionary diversification. *Bioinformatics* 24:129–131.

- Harnik, P. G. 2011. Direct and indirect effects of biological factors on extinction risk in fossil bivalves. *Proceedings of the National Academy of Sciences USA*. *In press*.
- Hintze, L. F., and A. R. Palmer. 1976. Upper Cambrian orr formation: its subdivisions and correlatives in western Utah. *U.S. Geol. Surv. Prof. Pap.* 1405-G, 1–25.
- Hoffmann, A. A., and P. A. Parsons. 1997. *Extreme environmental change and evolution*. Cambridge Univ. Press, Cambridge.
- Holt, R. D. 1996. Demographic constraints in evolution: toward unifying the evolutionary theories of senescence and niche conservatism. *Evol. Ecol.* 10:1–11.
- Holt, R. D., and M. S. Gaines. 1992. Analysis of adaptation in heterogeneous landscapes: implications for the evolution of fundamental niches. *Evol. Ecol.* 6:433–447.
- Hopkins, M. J. 2010. Intraspecific variation, its geographic structure, and the relationship between variation and duration, with examples from Cambrian trilobites and Recent fiddler crabs. Unpublished Ph.D. dissertation, University of Chicago, Chicago.
- . 2011. Species-level phylogenetic analysis of some pteropodliids (Trilobita) from the Great Basin, western USA. *J. Paleontol.* 85. *In press*.
- Hopkins, M. J., and M. Webster. 2008. Morphological and ontogenetic change in the “Early” Cambrian trilobite *Zacanthopsis* during an interval of environmental change. Pp. 185–187 in I. Rabano, R. Gozolo and D. C. Garcia-Bellido, eds. *Advances in trilobite research*. Instituto Geologico y Minero de Espana, Cuadernos del Museo Geominero 9, Madrid.
- . 2009. Ontogeny and geographic variation of a new species of the corynexochine trilobite *Zacanthopsis* (Dyeran, Cambrian). *J. Paleontol.* 83:524–547.
- Hopkins, M. J., and C. L. Thurman. 2010. The geographic structure of morphological variation in eight species of fiddler crabs (Ocypodidae: genus *Uca*) from the eastern United States and Mexico. *Biol. J. Linn. Soc.* 100:248–270.
- Hughes, N. C. 2001. Ecologic evolution of Cambrian trilobites. Pp. 370–403 in A. Y. Zhuravlev and R. Riding, eds. *The ecology of the Cambrian radiation*. Columbia Univ. Press, New York.
- Hunt, G. 2004. Phenotypic variation in fossil species: modeling the consequences of time-averaging. *Paleobiology* 30:426–443.
- . 2007a. Evolutionary divergence in directions of high phenotypic variance in the ostracode genus *Poseidonamicus*. *Evolution* 61:1560–1576.
- . 2007b. The relative importance of directional change, random walks, and stasis in the evolution of fossil lineages. *Proc. Natl. Acad. Sci. USA* 104:18404–18408.
- Hunt, G., K. Roy, and D. Jablonski. 2005. Species-level heritability reaffirmed: a comment on “On the heritability of geographic range sizes”. *Am. Nat.* 166:129–135.
- Jablonski, D. 1987. Heritability at the species level: analysis of geographic ranges of Cretaceous mollusks. *Science* 238:360–363.
- Jablonski, D., and K. Roy. 2003. Geographical range and speciation in fossil and living molluscs. *Proc. R. Soc. Lond. B* 270:401–406.
- Jablonski, D., and G. Hunt. 2006. Larval ecology, geographic range, and species survivorship in Cretaceous mollusks: organismic versus species-level explanations. *Am. Nat.* 168:556–564.
- Janevski, G. A., and T. K. Baumiller. 2009. Evidence for extinction selectivity throughout the marine invertebrate fossil record. *Paleobiology* 35:553–564.
- Jell, P. A., and J. M. Adrain. 2003. Available generic names for trilobites. *Mem. Queensl. Mus.* 48:331–553.
- Kammer, T. W., T. K. Baumiller, and W. I. Ausich. 1997. Species longevity as a function of niche breadth: evidence from fossil crinoids. *Geology* 25:219–222.
- . 1998. Evolutionary significance of differential species longevity in Osagean-Meramecian (Mississippian) crinoid clades. *Paleobiology* 24:155–176.
- Kembel, S. W., P. D. Cowan, M. R. Helmus, W. K. Cornwell, H. Morlon, D. D. Ackerly, S. P. Blomberg, and C. O. Webb. 2010. Picante: R tools for integrating phylogenies and ecology. *Bioinformatics* 26:1463–1464.
- Kiessling, W., and M. Aberhan. 2007. Geographical distribution and extinction risk: lessons from Triassic-Jurassic marine benthic organisms. *J. Biogeogr.* 34:1473–1489.
- Kim, K., H. D. Sheets, R. A. Haney, and C. E. Mitchell. 2002. Morphometric analysis of ontogeny and allometry of the Middle Ordovician trilobite *Triarthrus becki*. *Paleobiology* 28:364–377.
- Kim, K., H. D. Sheets, and C. E. Mitchell. 2009. Geographic and stratigraphic change in the morphology of *Triarthrus beckii* (Green) (Trilobita): a test of the *Plus ça change* model of evolution. *Lethaia* 42:108–125.
- Kingsolver, J. G., H. E. Hoekstra, J. M. Hoekstra, D. Berrigan, S. N. Vignieri, C. E. Hill, A. Hoang, P. Gibert, and P. Beerli. 2001. The strength of phenotypic selection in natural populations. *Am. Nat.* 157:245–261.
- Klingenberg, C. P., M. Barluenga, and A. Meyer. 2002. Shape analysis of symmetric structures: quantifying variation among individuals and asymmetry. *Evolution* 56:1909–1920.
- Kobayashi, T. 1935. The Cambro-Ordovician formations and faunas of South Chosen. *Paleontology*. Part 3: Cambrian faunas of South Chosen with a special study on the Cambrian trilobite genera and families. *J. Faculty Sci.* 4:49–344.
- Kolbe, S. E., R. Lockwood, and G. Hunt. 2011. Does morphological variation buffer against extinction? A test using veneroid bivalves from the Pliocene-Pleistocene of Florida. *Paleobiology* 37:355–368.
- Kunin, W. E., and K. J. Gaston. 1997. *The biology of rarity: causes and consequences of rare-common differences*. Chapman and Hall, New York.
- Lande, R., and S. Shannon. 1996. The role of genetic variation in adaptation and population persistence in a changing environment. *Evolution* 50:434–437.
- Lieberman, B. S., and S. Dudgeon. 1996. An evaluation of stabilizing selection as a mechanism for stasis. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 127:229–238.
- Liow, L. H. 2007. Does versatility as measured by geographic range, bathymetric range and morphological variability contribute to taxon longevity? *Glob. Ecol. Biogeogr.* 116:117–128.
- Ludvigsen, R., and S. R. Westrop. 1985. Three new Upper Cambrian stages for North America. *Geology* 13:139–143.
- Marroig, G., and J. M. Cheverud. 2005. Size as a line of least evolutionary resistance: diet and adaptive morphological radiation in New World monkeys. *Evolution* 59:1128–1142.
- Martins, E. P. 2004. COMPARE 4.6b: Computer programs for the statistical analysis of comparative data. Available at <http://compare.bio.indiana.edu>.
- Martins, E. P., and T. F. Hansen. 1997. Phylogenies and the comparative method: a general approach to incorporating phylogenetic information into the analysis of interspecific data. *Am. Nat.* 149:646–667.
- McCausland, P. J. A., R. Van der Voo, and C. M. Hall. 2007. Circum-Iapetus paleogeography of the Precambrian-Cambrian transition with a new paleomagnetic constraint from Laurentia. *Precambrian Res.* 156:125–152.
- McKinney, M. L. 1997. Extinction vulnerability and selectivity: combining ecological and paleontological views. *Annu. Rev. Ecol. Evol. Syst.* 28:495–516.

- Merila, J., and M. Bjorklund. 1999. Population divergence and morphometric integration in the greenfinch (*Carduelis chloris*)—evolution against the trajectory of least resistance? *J. Evol. Biol.* 12:103–112.
- Merila, J., and M. Bjorklund. 2004. Phenotypic integration as a constraint and adaptation. Pp. 107–129 in M. Pigliucci and K. Preston, eds. *Phenotypic integration: studying the ecology and evolution of complex phenotypes*. Oxford Univ. Press, Oxford.
- Miall, A. D., and R. C. Blakey. 2008. The Phanerozoic tectonic and sedimentary evolution of North America. Pp. 1–29 in A. D. Miall, ed. *Sedimentary basins of the United States and Canada*. Elsevier, Amsterdam.
- Mouillot, D., and K. J. Gaston. 2009. Spatial overlap enhances geographic range size conservatism. *Ecography* 32:671–675.
- Nakagawa, S., and R. P. Freckleton. 2008. Missing inaction: the dangers of ignoring missing data. *Trends Ecol. Evol.* 23:592–596.
- Pagel, M. 1997. Inferring evolutionary processes from phylogenies. *Zool. Scr.* 26:331–348.
- . 1999. Inferring the historical patterns of biological evolution. *Nature* 401:877–884.
- Palmer, A. R. 1960. Trilobites of the Upper Cambrian Dunderberg Shale, Eureka District, Nevada. U.S. Geol. Surv. Prof. Pap. 334-C:53–109.
- . 1962. *Glyptagnostus* and associated trilobites in the United States. U.S. Geol. Surv. Prof. Pap. 374-F, 1–49.
- . 1965a. Biome: a new kind of biostratigraphic unit. *J. Paleontol.* 39:149–153.
- . 1965b. Trilobites of the Late Cambrian Pteropcephaliid biome in the Great Basin, United States. U.S. Geol. Surv. Prof. Pap. 493, 1–105.
- Palmer, A. R. 1981. Subdivision of the Sauk sequence. Pp. 160–162 in M. E. Taylor, ed. *Short papers for the Second International Symposium on the Cambrian System*. U.S. Geological Survey Open-File Report 81-743.
- Paradis, E. 2006. Analysis of phylogenetics and evolution with R. Springer, New York.
- Peng, S., and L. E. Babcock. 2008. Cambrian period. Pp. 37–46 in J. G. Ogg, G. Ogg and F. M. Gradstein, eds. *The Concise Geologic time scale*. Cambridge Univ. Press, Cambridge.
- Powell, M. G. 2007. Geographic range and genus longevity of late Paleozoic brachiopods. *Paleobiology* 33:530–546.
- Pratt, B. R. 1992. Trilobites of the Marjuman and Steptoean stages (Upper Cambrian), Rabbitkettle Formation, southern Mackenzie Mountains, northwest Canada. *Paleontographica Canadiana* No. 9.
- Purvis, A. 2008. Phylogenetic approaches to the study of extinction. *Annu. Rev. Ecol. Evol. Syst.* 39:301–319.
- Purvis, A., and R. Garland, Jr. 1993. Polytomies in comparative analyses of continuous characters. *Syst. Biol.* 42:569–575.
- Quader, S., K. Isvaran, R. E. Hale, B. G. Miner, and N. E. Seavy. 2004. Nonlinear relationships and phylogenetically independent contrasts. *J. Evol. Biol.* 17:709–715.
- R. Development Core Team. 2005. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rasband, W. S. 2006. ImageJ 1.36b. Available at: <http://rsb.info.nih.gov/ij/>.
- Reed, T. E., R. S. Waples, D. E. Schindler, J. J. Hard, and M. T. Kinnison. 2010. Phenotypic plasticity and population viability: the importance of environmental predicatability. *Proc. R. Soc. Lond. B* 277:3391–3400.
- Renaud, S., J.-C. Auffray, and J. Michaux. 2006. Conserved phenotypic variation patterns: evolution along lines of least resistance, and departure due to selection in fossil rodents. *Evolution* 60:1701–1717.
- Ridley, M. 1996. *Evolution*. 2nd ed. Blackwell Scientific, Cambridge, MA.
- Rohlf, F. J. 1990. Rotational fit (Procrustes) methods. Pp. 227–236 in F. J. Rohlf and F. L. Bookstein, eds. *Proceedings of the Michigan Morphometrics Workshop*. Univ. of Michigan Museum of Zoology Special Publication.
- . 2001. Comparative methods for the analysis of continuous variables: geometric interpretations. *Evolution* 55:2143–2160.
- . 2006. A comment on phylogenetic correction. *Evolution* 60:1509–1515.
- Roy, K., G. Hunt, and D. Jablonski. 2009a. Phylogenetic conservatism of extinctions in marine bivalves. *Science* 325:733–737.
- Roy, K., G. Hunt, D. Jablonski, A. Z. Krug, and J. W. Valentine. 2009b. A macroevolutionary perspective on species range limits. *Proc. R. Soc. Lond. B* 276:1485–1493.
- Runkel, A. C., J. F. Miller, R. M. McKay, A. R. Palmer, and J. F. Taylor. 2007. High-resolution sequence stratigraphy of lower Paleozoic sheet sandstones in central North America: The role of special conditions of cratonic interiors in development of stratal architecture. *Geol. Soc. Am. Bull.* 119:860–881.
- Russell, A. P., and A. M. Bauer. 2005. Variation in structure and its relationship to function: correlation, explanation, and extrapolation. Pp. 399–434 in B. Hallgrímsson and B. K. Hall, eds. *Variation: a central concept in biology*. Elsevier Academic Press, New York.
- Ruta, M., P. J. Wagner, and M. I. Coates. 2006. Evolutionary patterns in early tetrapods. I. Rapid initial diversification followed by decrease in rates of character change. *Proc. R. Soc. Lond. B* 273:2107–2111.
- Sadler, P. M. 2004. Quantitative biostratigraphy—achieving finer resolution in global correlation. *Annu. Rev. Earth Pl. Sci.* 32:187–213.
- Sadler, P. M., W. G. Kemple, and M. A. Kooser. 2003. Contents of the compact disc: CONOP9 programs for solving the stratigraphic correlation and seriation problems as constrained optimization. Pp. 461–465 in P. J. Harries, ed. *Approaches in high-resolution stratigraphic paleontology*, Kluwer Academic Publishers, Netherlands.
- Sadler, P. M., and R. A. Cooper. 2003. Best-fit intervals and consensus sequences. Pp. 49–94 in P. J. Harries, ed. *Approaches in high-resolution stratigraphic paleontology*. Kluwer Academic Publishers, Netherlands.
- Saltzman, M. R., B. Runnegar, and K. C. Lohmann. 1998. Carbon isotope stratigraphy of Upper Cambrian (Steptoean Stage) sequences of the eastern Great Basin: record of a global oceanographic event. *Geol. Soc. Am. Bull.* 110:285–297.
- Saltzman, M. R., C. A. Cowen, A. C. Runkel, B. Runnegar, M. C. Stewart, and A. R. Palmer. 2004. The Late Cambrian SPICE ($\delta^{13}\text{C}$) event and the Sauk II-Sauk III regression: new evidence from Laurentian basins in Utah, Iowa, and Newfoundland. *J. Sediment. Res.* 74:366–377.
- Shaw, A. B. 1957. Quantitative trilobite studies II. Measurement of the dorsal shell of non-agnostidean trilobites. *J. Paleontol.* 31:193–207.
- Sheets, H. D. 2003a. FMCBox. Available at <http://www3.canisius.edu/sheets/morphosoft.html>.
- . 2003b. Integrated morphometrics package. Available at <http://www3.canisius.edu/sheets/morphosoft.html>.
- Sheldon, P. R. 1987. Parallel gradualistic evolution of Ordovician trilobites. *Nature* 330:561–563.
- Shipley, B. 2000. *Cause and correlation in biology: a user's guide to path analysis, structural equations and causal inference*. Cambridge Univ. Press, Cambridge.
- Stanley, S. M. 1986. Population size, extinction, and speciation: the fission effect in Neogene Bivalvia. *Paleobiology* 12:89–110.
- Stanley, S. M., and X. Yang. 1987. Approximate evolutionary stasis for bivalve morphology over millions of years: a multivariate, multilineage study. *Paleobiology* 13:113–139.
- Strait, D. S., M. A. Moniz, and P. T. Strait. 1996. Finite mixture coding: a new approach to coding continuous characters. *Syst. Biol.* 45:67–78.
- Thiele, K. 1993. The holy grail of the perfect character: the cladistic treatment of morphometric data. *Cladistics* 9:275–304.
- Tomašových, A., S. J. Carlson, and M. LaBarbara. 2008. Ontogenetic niche shift in the brachiopod *Terebratalia transversa*: relationship between the

- loss of rotation ability and allometric growth. *Palaeontology* 51:1471–1496.
- Van Valen, L. 1965. Morphological variation and width of ecological niche. *Am. Nat.* 159:377–390.
- . 1974. The statistics of variation. *Evol. Theory*:433–443.
- Vavrek, M. 2007. Fossil: palaeoecological and palaeogeographical analysis tools. Available at <http://cran.r-project.org/web/packages/fossil/index.html>.
- Wake, D. B., G. Roth, and M. H. Wake. 1983. On the problem of stasis in organismal evolution. *J. Theor. Biol.* 101:211–224.
- Waldron, A. 2007. Null models of geographic range size evolution reaffirm its heritability. *Am. Nat.* 170:221–231.
- Walsh, B., and M. W. Blows. 2009. Abundant genetic variation + strong selection = multivariate genetic constraints: a geometric view of adaptation. *Annu. Rev. Ecol. Evol. Syst.* 40:41–59.
- Webber, A. J., and B. R. Hunda. 2007. Quantitatively comparing morphological trends to environment in the fossil record (Cincinnatian Series, Upper Ordovician). *Evolution* 61:1455–1465.
- Webster, M. 2007. Ontogeny and evolution of the Early Cambrian trilobite genus *Nephrolenellus* (Olenelloidea). *J. Paleontol.* 81:1168–1193.
- . 2009. Systematic revision of the Cambrian trilobite *Bathynotus* Hall, 1860, with documentation of new occurrences in western Laurentia and implications for intercontinental biostratigraphic correlation. *Memoirs of the Association of Australasian Palaeontologists* 37:369–407.
- Webster, M., H. D. Sheets, and N. C. Hughes. 2001. Allometric patterning in trilobite ontogeny: testing for heterochrony in *Nephrolenellus*. Pp. 105–144 in M. L. Zelditch, ed. *Beyond heterochrony: the evolution of development*. Wiley-Liss, Inc., New York.
- West-Eberhard, M. J. 2003. *Developmental plasticity and evolution*. Oxford Univ. Press, Oxford.
- . 2005. Developmental plasticity and the origin of species differences. *Proc. Natl. Acad. Sci. USA* 102:6543–6549.
- Wills, M. A. 2001. Morphological disparity: a primer. Pp. 55–145 in J. M. Adrain, G. D. Edgecombe and B. S. Lieberman, eds. *Fossils, phylogeny, and form: an analytical approach*. Kluwer Academic/Plenum Publishers, New York.
- Zelditch, M. L. 2005. Developmental regulation of variation. Pp. 249–276 in B. Hallgrímsson and B. K. Hall, eds. *Variation: a central concept in biology*. Elsevier Academic Press, New York.
- Zelditch, M. L., D. L. Swiderski, H. D. Sheets, and W. L. Fink. 2004. *Geometric morphometrics for biologists*. Elsevier Academic Press, New York.

Associate Editor: C. Klingenberg

Supporting Information

The following supporting information is available for this article:

Figure S1. Maps showing the known occurrences for taxa sampled for variation estimates but not shown in Figure 4.

Figure S2. Plots showing size-standardized variation against potential sampling biases.

Figure S3. Rarefaction plots.

Table S1. Collections that yielded specimens for variation estimates.

Table S2. Locality, formation, and reference information for all Steptoean outcrops in North America.

Table S3. Species occurrences and geographic coordinates.

Table S4. Paleolatitudinal estimates and statistics for each mean pole position estimate.

Table S5. Results from test for statistical significance between allometric trajectories estimated from different collections belonging to the same species.

Table S6. Results from the λ test for phylogenetic signal.

Table S7. Blomberg's K metric for phylogenetic signal.

Table S8. Results from phylogenetic least squares analysis.

Supporting Information may be found in the online version of this article.

Please note: Wiley-Blackwell is not responsible for the content or functionality of any supporting information supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.