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CLIMATE-DRIVEN BODY-SIZE TRENDS IN THE OSTRACOD FAUNA OF THE DEEP INDIAN OCEAN

by GENE HUNT*, SATRIO A. WICAKSONO†‡, JULIA E. BROWN§ *and* KENNETH G. MACLEOD¶

*Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, MRC 121, P.O. Box 37012, Washington, D.C. 20013-7012, USA; e-mail hunte@si.edu
†Wesleyan University, Middletown, CT 06459, USA
‡Present address: Department of Geological Sciences, Brown University, 324 Brook Street, Box 1846, Providence, RI 02912 USA; e-mail satrio_wicaksono@brown.edu
§Department of Ecology and Evolutionary Biology, Yale University, New Haven, CT 06520-8106, USA; e-mail julia.brown@yale.edu
¶Department of Geological Sciences, University of Missouri, Columbia, MO 65211-1380, USA; e-mail MacLeodK@missouri.edu

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Abstract: Body size is a common focus of macroevolutionary, macroecological and palaeontological investigations. Here, we document body-size evolution in 19 species-level ostracod lineages from the deep Indian Ocean (Deep Sea Drilling Program Site 253) over the past 40 myr. Body-size trajectories vary across taxa and time intervals, but most lineages (16/19) show net gains in body size. Because many modern ostracod taxa are larger in colder parts of their geographical range, we compared the timing and magnitude of these size changes to established Cenozoic deep-water cooling patterns confirmed through $\delta^{18}O$ measurements of benthic foraminifera in the samples studied. These data show a significant negative correlation between size changes and temperature changes (ostracods get larger as temperatures get colder), and that systematic size increases only occur during intervals of sustained cooling. In addition, statistical support for an explicit temperature-tracking model exceeds that of purely directional evolution. We argue that this Cope's Rule pattern is driven by secular changes in the environment, rather than any universal or intrinsic advantages to larger body sizes, and we note some difficulties in the attempts to link Cope's Rule to observations made within a single generation.

Key words: body size, Cope's Rule, Bergmann's Rule, climate, Ostracoda, temperature, trends.

BODY size, probably more so than any other organismal feature, lies at the intersection of macroevolutionary and macroecological analysis. Whereas evolutionary studies track lineages and clades, macroecology focuses on the distribution of body sizes of taxa that coexist at some spatial scale. Together they offer largely complementary views of the forces shaping the body sizes of organisms and taxa. A major goal of both these approaches is to understand the factors that govern what body sizes organisms attain. These include inferring optimal sizes (Brown *et al.* 1993; Alroy 1998; Roy *et al.* 2000; Boback and Guyer 2003) and constraints on permissible sizes (Stanley 1973; Leaper *et al.* 2001), understanding the distributions of body sizes in clades or assemblages (Brown and Nicoletto 1991; Maurer *et al.* 1992; Allen and Holling 2002; Clauset and Erwin 2008), and testing the extent to which assorted biotic and abiotic factors influence organismal sizes (Lomolino 1985; Chapelle and Peck 1999; Spicer and Gaston 1999; McClain and Rex 2001; Grosholz and Ruiz 2003; Falkowski *et al.* 2005; Finkel *et al.* 2005; Finkel *et al.* 2007).

Of the various conditions that may conceivably affect body sizes, temperature has received particular attention. In many taxa, body size systematically varies with temperature, most prominently according to Bergmann's Rule, the tendency for organisms to be larger in colder parts of their geographical range (Millien *et al.* 2006). Common in mammals, Bergmann's Rule was originally explained by the heat-conserving effects of larger sizes and their resulting lower ratios of surface area relative to volume (Blackburn *et al.* 1999; Blackburn and Hawkins 2004). However, a correlation between large size and cold temperatures occurs even among some poikilothermic taxa (Strauch 1968; Partridge and Coyne 1997; Blackburn *et al.* 1999; Huey *et al.* 2000; Ashton and Feldman 2003; Blanckenhorn and Demont 2004; Olalla-Tarraga and Rodriguez 2007), and so heat conservation likely is an incomplete explanation (Blackburn *et al.* 1999). The underlying cause or causes of Bergmann's Rule in poikilotherms may lie with inter-relationships among temperature, growth rates, and mortality (Kozłowski *et al.* 2004), but until this

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question is resolved, we are in the unusual position of having good reason to believe that the pattern is adaptive (Partridge and Coyne 1997; Kingsolver and Huey 2008), but lacking a clear understanding of what, exactly, selection is acting upon. As a practical consideration, temperatures in the past can be estimated with several proxies. None of these palaeothermometers is without complication, but, when considering trends over millions of years, temperature is probably the most geologically accessible factor that is proposed to influence body size.

The spatial correlation between body size and temperature within taxa makes predictions about size evolution during intervals of net climate change. All else equal, taxa that follow Bergmann's Rule ought to get bigger when climate cools and smaller when climate warms. Moreover, these changes should manifest as phyletic change within lineages rather than sorting among lineages, and the magnitudes of change should be compatible with modern temperature–body size relationships (Hunt and Roy 2006). Several studies have demonstrated body-size patterns that are consistent with at least some of these criteria (Davis 1981; Smith *et al.* 1995; Hadly *et al.* 1998; Vrba 2005; Hunt and Roy 2006).

One commonly cited alternative for body-size trends suggests instead that there are universal selective advantages to larger body sizes, and these advantages translate over geological time into trends of increasing body size, a pattern known as Cope's Rule (Brown and Maurer 1986; Kingsolver and Pfennig 2004; Van Valkenburgh *et al.* 2004; Hone and Benton 2005; Hone *et al.* 2005). Larger organisms are said to hold many advantages over their smaller conspecifics, including more effective prey capture, better defence against predators, greater mating success and physiological benefits (Brown and Maurer 1986; Hone *et al.* 2005). Although some clade-level body-size increases are well documented (e.g. Alroy 1998; Van Valkenburgh *et al.* 2004; Hone *et al.* 2005; Novack-Gottshall and Lanier 2008), there is still debate about the frequency with which Cope's Rule holds (Jablonski 1997).

In this paper, we use the rich fossil record of deep-sea ostracods and the well-established patterns of deep-water cooling (Lear *et al.* 2000; Zachos *et al.* 2001) to test temperature as a driver of body-size evolution. Although the underlying mechanism is unclear, ostracod taxa often follow Bergmann's Rule (Hunt and Roy 2006), and previous analyses of deep-sea lineages have demonstrated size increases in selected lineages through the Cenozoic that are consistent with a climatic driver (Ayress 1994; Hunt and Roy 2006). The approach we take is a hybrid between macroevolutionary and macroecological analyses: we use lineages as evolutionary units, but do so across the entire ostracod assemblage over the past 40 million years at one site in the deep Indian Ocean (Deep Sea Drilling Program (DSDP) Site 253). Across this interval, deep waters cooled reflecting the transition from a greenhouse to an icehouse world through the Cenozoic as expressed in high latitudes where deep waters form. However, the cooling is irregular. Cooling begins at *c.* 55 Ma and continues to *c.* 30 Ma. From *c.* 30 to *c.* 14 Ma temperatures only vary over a narrow interval and then cool again from *c.* 14 Ma to the present (e.g. Lear *et al.* 2000; Zachos *et al.* 2001). During each interval of (relatively) consistent cooling, temperatures decline by *c.* 5°C. Bergmann's Rule predicts that lineages should have responded with larger body sizes during intervals of cooling but not during the interval of relative stability from *c.* 30 to *c.* 14 Ma.

In evaluating temperature as a driver of body-size changes, we compare the support for this explanation against that for alternative statistical models of a random walk and a constant directional trend towards larger bodies (Cope's Rule). We find that, although ostracod lineages have generally increased in size over time, the manner in which size changes occurred is most consistent with a model in which body sizes track changes in deep-sea temperature. These findings suggest long-term body-size trends can be driven by directional changes in environmental conditions, and therefore need not reflect universal and context-independent advantages of larger size.

MATERIALS AND METHODS

Locality and specimens

Deep Sea Drilling Program (DSDP) Site 253 is located near the southern terminus of Ninetyeast Ridge in the Indian Ocean (present position and bathymetry: 24.88°S, 87.37°E, and 1962 m). This ridge is the trace of the Indian plate over a mantle hotspot with subaerial eruptions and rapid subsidence away from the volcanic centre. Data from the more recently drilled sites from Ocean Drilling Program (ODP) 756 and 757, which bracket DSDP 253 on Ninetyeast Ridge, indicate that DSDP 253 attained near-present day lower bathyal depths sometime between 54 and 38 Ma (Peirce *et al.* 1989*a*, *b*). We sampled ostracods at 21 levels from the late Eocene to the late Pleistocene (Table 1) and placed them in time using an age-depth model constructed from published first and last occurrence datums for planktonic foraminifera and nannoplankton taxa (Text-fig. 1). Sedimentation at site 253 is generally continuous over this interval, but there is a period of lower net sediment accumulation from the early Oligocene through the mid-Miocene (Text-fig. 1).

Ostracods are abundant and usually well preserved in these samples. We traced body-size evolution in every lineage that was common enough to be subject to biometric analysis (Table 2). Ostracods, like all arthropods,

TABLE 1. List of samples studied from Deep Sea Drilling Programme (DSDP) Site 253 in the Indian Ocean.

No.	Sample	Depth in core (m)	Age (Ma)	*Cibicidoides* $\delta^{18}O$	*Oridorsalis* $\delta^{18}O$	Mg/Ca temperature
1	16/5/20–26	148.23	40.00	–	0.137 (3)	9.70
2	14/4/50–56	128.03	36.32	–	0.790 (2)	8.63
3	13/1/100–106	114.53	33.85	–	1.237 (3)	7.54
4	12/5/100–106	111.03	33.22	–	1.513 (3)	7.29
5	11/4/50–56	99.53	31.12	–	1.730 (2)	6.38
6	10/3/100–106	89.03	26.12	–	1.600 (1)	6.70
7	10/1/50–54	85.87	24.39	1.193 (3)	–	6.54
8	9/5/52–55	82.02	22.27	–	–	6.50
9	9/3/50–56	79.03	20.63	1.525 (2)	1.530 (2)	6.36
10	8/3/54–56	69.54	14.46	1.263 (3)	–	5.59
11	7/4/110–116	62.13	13.06	2.137 (3)	2.573 (3)	5.12
12	6/4/50–53	52.00	11.14	2.430 (3)	–	4.16
13	5/4/50–56	42.53	9.35	2.548 (4)	–	3.96
14	4/4/51–55	33.01	7.55	2.580 (3)	–	4.05
15	3/3/100–106	22.53	5.57	2.287 (3)	–	3.03
16	2/5/100–106	16.03	4.34	2.500 (1)	–	2.54
17	2/2/50–56	11.03	3.33	2.613 (3)	–	2.06
18	1/6/50–56	8.03	2.44	2.717 (3)	–	1.62
19	1/3/50–56	3.53	1.10	3.208 (4)	–	1.04
20	1/2/52–55	2.02	0.65	3.340 (4)	–	0.86
21	1/1/50–56	0.50	0.20	3.150 (3)	–	0.68

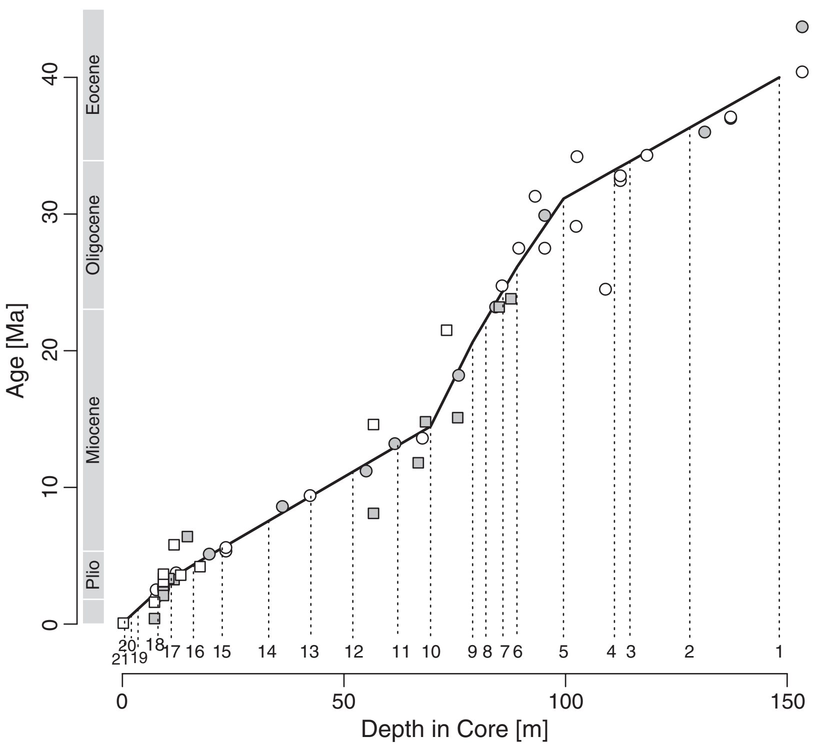
Sample names given in standard DSDP notation, as core/interval/depth in interval (in cm). Depths in core are in meters below the seafloor, and ages are estimated from the age model shown in Text-figure 1. *Oridorsalis* specimens are *O. umbonatus* and *Cibicidoides* specimens are *C. wuellerstorfi* except for sample no. 9, which are *C. perlucidus*. Means by species reported without the offset (see text), with the number of individual shells analyzed in parentheses. Mg/Ca temperatures result from linear interpolation of published curve of Lear *et al.* (2000).

moult as they grow and we analysed only individuals from the final instar (adults) in tracking body sizes. In addition to being the reproductive and therefore most biologically relevant stage, adults are a practical choice as they can be discriminated from juveniles in many taxa by their well-developed hinge teeth and inner lamellae (van Morkhoven 1962). One lineage of *Cytherella* was common through the Paleogene but was not analysed because we could not reliably distinguish juveniles from adults. In some ostracod species, males and females differ in size, and, to a lesser extent, so do left and right valves in some taxa. Sample sizes did not permit partitioning these sources of size variation in our samples. However, because the proportion of left versus right valves, and male versus female specimens should not systematically vary with either age or temperature, these heterogeneities should only add noise to the analyses.

We delimited species-level lineages by looking for morphological continuity, irrespective of body size, from sample to sample through the core. We attended to the suite of features often used to delimit ostracod species, including valve outline, characteristics of the inner lamella, and the presence, structure and position of ribs, spines and other sculptural elements of the carapace. Shape and size of the vestibule, along with valve outline and marginal pore positions, were particularly useful for recognizing species of the smooth-shelled genus *Krithe* (Coles *et al.* 1994). The taxonomy of ostracods in the deep Indian Ocean has received less attention than other regions, and although we encountered some of the same taxa as Guernet (1985), many of our species remain in open nomenclature (Text-fig. 2).

Measuring body size

We used projected valve area as a proxy for body size. Digital photographs were taken of specimens through a dissecting microscope. Using the software ImageJ (Rasband 2008), we cropped individual specimens and used thresholding to automatically detect the outline of the ostracods, which are much lighter than the black background of the micropalaeontological slides. Minor editing of the images was sometimes necessary to ensure accurate delimitation of the valves. From the thresholded image, ImageJ computed the projected area of each ostracod valve. Because the size evolution is usually best considered on a logarithmic scale (Foote 1991), we $\log_{10}$ transformed



TEXT-FIG. 1. Age model for Deep Sea Drilling Programme (DSDP) 253. Circles indicate nannofossil datums and squares are planktonic foraminifera datums. Grey-filled symbols are first appearance datums and white symbols are last appearances. The solid, black line indicates the age model. Numbers below the dotted lines correspond to sample numbers in Table 1.

all areas prior to analysis. This practice has the effect of rendering changes proportional, so that a size increase of, say, 10 per cent results in exactly the same additive increase on a log scale for both small- and large-bodied lineages. We calculated means and standard deviations for each sample, split by species, for a total of 140 sample means calculated from 672 adult individuals across 19 species-level lineages (Table 2).

TABLE 2. Taxa subjected to body-size analysis with the total number of individuals and samples included for each.

Species	No. of individuals	No. of samples
Abyssocythere sp.	34	10
Actinocythereis orientalis Guernet, 1985	22	4
Actinocythereis? sp. 4	11	5
Bradleya caeca Guernet, 1985	65	9
Cytheropteron aff. *planalatum* Guernet, 1985	49	18
Dutoitella sp. 1	83	10
Dutoitella sp. 2	23	4
Krithe sp. C	66	13
Krithe sp. D	14	3
Krithe sp. E	14	4
Krithe sp. F	21	4
Legitimocythere sp.	43	9
Marwickcythereis? aff. *reticulata* (Guernet, 1985)	95	14
Poseidonamicus anteropunctatus Whatley *et al.*, 1986	57	10
Poseidonamicus major Benson, 1972	11	4
Poseidonamicus minor Benson, 1972	20	6
Poseidonamicus nudus Benson, 1972	28	7
Poseidonamicus sp. A	8	3
Poseidonamicus sp. B	8	3

Palaeotemperature data

We used a published Mg/Ca palaeotemperature curve (Lear *et al.* 2000) to generate temperatures for samples used in analysis. Because deep waters in the oceans form in discrete areas and their temperature changes little down flow paths, deep-ocean temperatures and temperature trends are similar over wide regions. Still this curve is smoothed, low-resolution and compiled from multiple sites. Higher-resolution Mg/Ca records are available for portions of the time interval of interest (Billups and Schrag 2002, 2003), but our chronology at 253 is not resolved enough to allow for correlation to sub-million year fluctuations. The overall trajectory of the Lear *et al.* (2000) curve is similar to more recent data from ODP 747 and ODP 689, once these curves are smoothed at the same level of resolution (Billups and Schrag 2003, fig. 3). Mg/Ca palaeotemperatures at yet another site, ODP 757, differ from the others, but this curve shows strangely little variation through the Neogene and predicts unrealistically warm Pleistocene temperatures (Billups and Schrag 2003). We confirmed that trends at DSDP Site 253 follow the Lear *et al.* curve through δ^{18}O measurements on benthic foraminifera picked from the same samples from which the ostracods were analysed (Table 1).

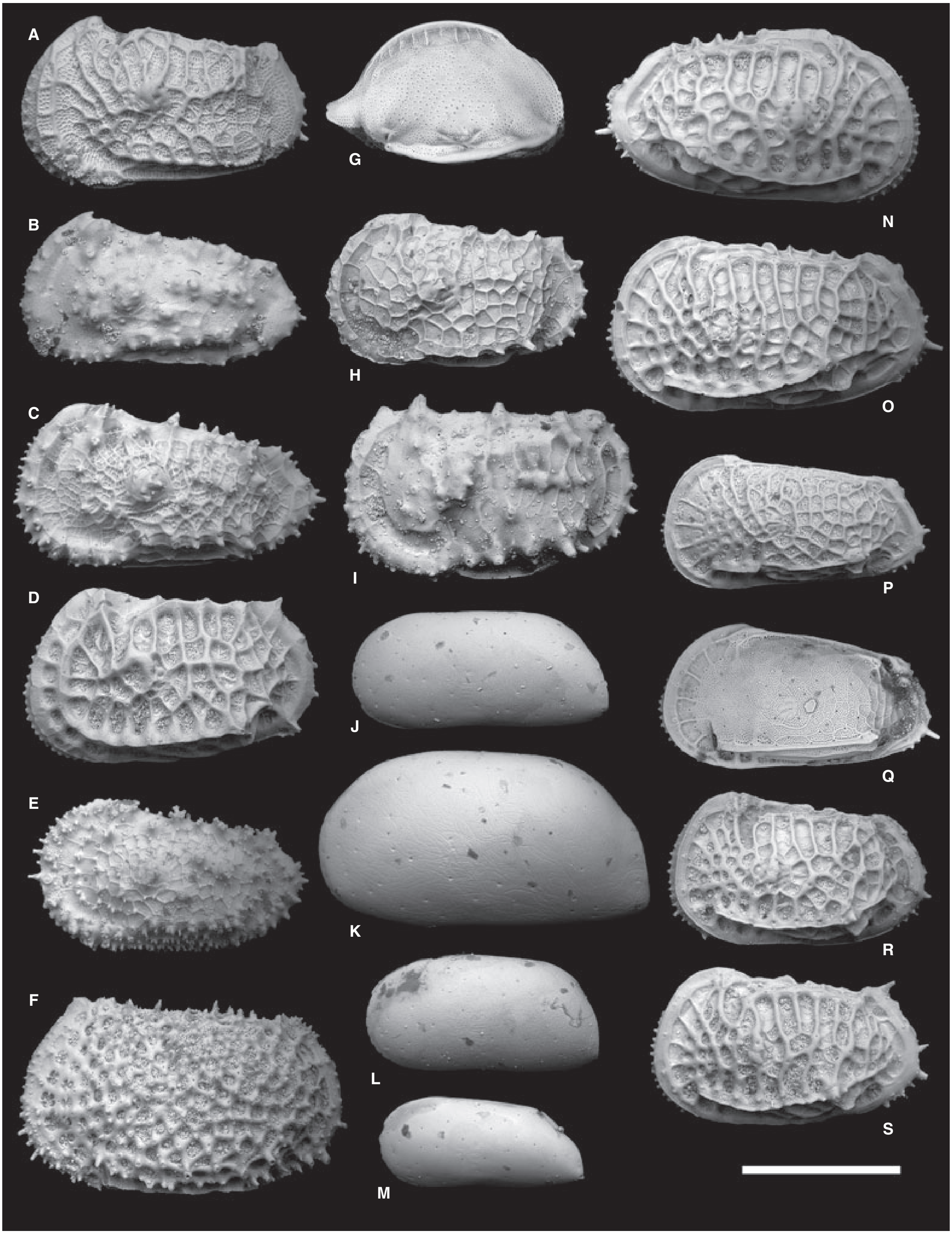
Well-preserved specimens of *Cibicidoides* and *Oridorsalis* were picked from the >125 μm size fraction and ultrasonically cleaned to remove fine adhering particles. One to four of the best-preserved individuals (*c.* 100 μg) were selected and analysed on a Kiel III carbonate device-Thermo Finnigan Delta Plus mass spectrometer in the Biogeochemistry Laboratory at University of Missouri. Results were corrected for each run based on the within-run average of multiple analyses of the NBS-19 standard. Long-term analytical precision based on uncorrected values for this standard are <0.03 and <0.06 ‰ (1 standard deviation) for carbon and oxygen measurements, respectively; for the duration of this study precision was better than the long-term average. *Cibicidoides* were available for most Neogene samples whereas *Oridorsalis* were present in most Paleogene samples (see Table 1). When integrating data from the two taxa, we used a published offset and subtracted 0.28 from *Oridorsalis* values (Katz *et al.* 2003). This offset is consistent with the two samples in which both genera were analysed (Table 1, samples 9 and 11). One sample, no. 8, did not yield usable specimens of either genus. For analytical purposes, we assigned this sample a δ^{18}O value equal to the average of its two adjacent samples. Because published deep-sea oxygen isotope curves generally show little change over this interval (Zachos, *et al.* 2001; Gupta *et al.* 2004), this procedure is not unreasonable.

As expected, both the Mg/Ca curve (Lear *et al.* 2000) and the new δ^{18}O results suggest similar temperature trends (Text-fig. 3). Because our approach to investigating the relationship between body size and temperature relies on the differences between samples rather than the overall global or regional trends, it is more relevant to compare the sample-to-sample differences in oxygen isotope values and Mg/Ca temperatures, which are moderately correlated (Spearman rank correlation $r_s = -0.49$, $p = 0.026$). Each proxy signal has strengths and weaknesses for this analysis. The oxygen isotope data were measured on foraminifera isolated from the same samples used in ostracod analyses, effectively eliminating any errors associated with correlation. However, oxygen isotopes reflect both temperature and global ice volume, and, since ice volume changed markedly over the duration of the study, the temperature change reflected by a given isotopic shift is not constant through the section. In contrast, Mg/Ca ratios are not affected by ice volume, but the measurements must be projected onto the Site 253 results and potentially important error may exist in the palaeotemperature estimates because of the uncertainty in the Cenozoic history of seawater Mg/Ca ratios (Billups and Schrag 2003; Medina-Elizalde *et al.* 2008) and variation in carbonate ion saturation (Yu and Elderfield 2008). Because it is not clear whether local oxygen isotopes or global Mg/Ca thermometry provides a more accurate estimate of the temperature history at DSDP 253, we compared ostracod size trends to both temperature proxies. Fortunately, the nontemperature components of the two records are entirely nonoverlapping, and therefore patterns shared between the curves are very likely to reflect a real temperature signal.

Data analysis

The fundamental unit in these analyses is the change in size (ΔS) from an ancestor to a descendant population in a species-level lineage. We tested the relationship between these evolutionary increments and temperature in several ways. First, we regressed each size increment against our palaeoclimate proxies, using weighted least-squares (Bowerman and O'Connell 1990) to account for differing sampling errors on each ΔS. Second, we divided the interval into three periods: an early period of cooling (40–30 Ma), a middle period of little net climate change (30–14 Ma), and a late period of cooling (14–0 Ma). The boundaries of these intervals were chosen so the generalities about temperature trends hold for both proxies (Text-fig. 3); the second boundary was set to 14 Ma so that evolutionary transitions that span the substantial cooling after sample no. 10 are allocated to the latest interval of cooling. These intervals were chosen to summarize broadly the overall trajectory of climate change and were established without reference to the body-size data. We allocated each ΔS to one of the three intervals according to the age of its descendant population and used t-tests to assess for systematic increases or decreases in body size in the three intervals.

Finally, we used a formal model-fitting approach to compare explanations of temperature tracking with that of a sustained trend (unrelated to temperature) and a random walk. The simplest of these three alternatives is a random walk, a model in which trait increases and decreases are equiprobable. This model has a single parameter, the step variance (σ^2_{step}) that determines the size of typical evolutionary steps (Hunt 2006). The trended or directional model is similar, except it has an additional parameter, the mean step (μ_{step}) that represents the bias in evolutionary change (Hunt 2006). Cope's Rule suggests that the μ_{step} for body size is usually positive, resulting in net increases over time. For temperature tracking, we consider a simple model in which the expected change in size is proportional to the change in the palaeoclimate proxy, with normally distributed variation around this expectation. We call the proportionality constant that scales temperature to size changes β, and the magnitude of variation is ε. The phenotypic response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to temperature change is geologically instantaneous according to this model, a reasonable assumption for traits that evolve rapidly in response to changes in forcing variables. More complex models can be implemented in situations in which the lag between driver and response is not negligible (Hansen 1997; Hansen *et al.*, 2008).

Each of these models – random walk, directional trend, and temperature tracking – can be fit via maximum-likelihood, and the models compared using the Akaike Information Criterion (AIC). This metric balances log-likelihood and model complexity: $\text{AIC} = -2\log L + 2K$, where $\log L$ is log-likelihood and K is the number of free model parameters. AIC scores represent the amount of information lost in approximating reality with a model, and its trade-off between goodness-of-fit and parsimony has theoretical justification (Akaike 1974; Forster and Sober 1994; Burnham and Anderson 2004). A modified version, AIC_C, performs better when sample sizes are not large. AIC_C scores for a set of models can be standardized into what are called Akaike weights, which sum to unity across candidate models. As such, they are a convenient measure of proportional support received by each model. For more in-depth treatments of model selection approaches as applied to evolutionary sequences, readers are referred to Hunt (2006, 2008*b*).

These models were fit using all the data across all lineages jointly, so we assumed that all lineages behaved similarly. Because the trajectories of most lineages are noisy and not overly long, fitting all sequences jointly allows for a more powerful test of these explanations than testing each lineage individually. Model fits were implemented using the R package paleoTS (Hunt 2008*a*), and the statistical properties of the three models are summarized in Table 3.

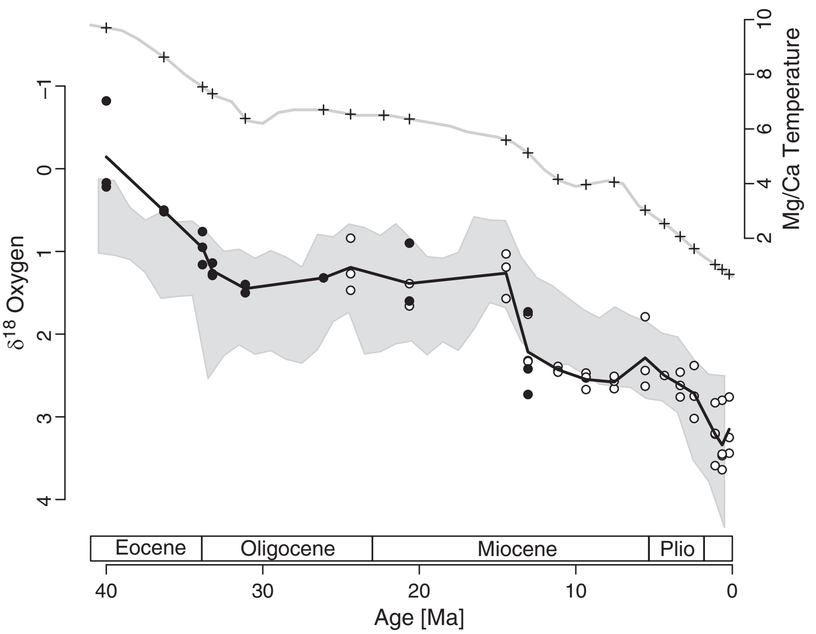
RESULTS

Trajectories of body-size evolution for all 19 lineages are shown in Text-figure 4. A variety of different patterns appear, but most lineages show net increases in body size (16/19, $p = 0.004$, binomial test). Visually, there are indications of parallel trajectories among species, for example, *Poseidonamicus anteropunctatus* and *Krithe* spF in the early to mid-Miocene, *Marwickcythereis*? aff. *reticulata* and *Poseidonamicus nudus* in the later Miocene, and *Abyssocythere* sp. and *Dutoitella* sp. 1 through much of their histories. There are also clear differences among taxa, even close relatives, including several intervals in which *Krithe* sp. C decreases in size as other *Krithe* species get larger (Text-fig. 4). Although the autecologies of deep-sea ostracods are not well known, the *Krithe* species are thought to be infaunal whereas all other taxa in this study bear the lateral ridges and flat ventral regions taken to indicate an epifaunal life habit (see Majoran and Agrenius 1995). Evolutionary trajectories reveal no obvious differences in body-size patterns according to this difference in life habit.

Despite variation among taxa, evidence for a systematic trend towards larger bodies is present only during intervals of sustained climatic cooling. With the possible exception of *Cytheropteron* aff. *planalatum*, all lineages present during the first 10 million-year interval (40–30 Ma) show significant net size increases over this time period (Text-fig. 4). When evolutionary changes are divided into three temporal windows, the mean ΔS is significantly positive during the early and late intervals, but not different from zero during the middle interval (Text-fig. 5, Table 4). The relationships between body-size changes and both temperature proxies are noisy but statistically significant (δ^{18}O: $t = 2.46$, $p = 0.0153$; Mg/Ca temperature: $t = -2.02$, $p = 0.045$; Text-fig. 6). Further, the regression slopes imply size increases of 0.017 $\log_{10}$ units (4.1 per cent) per degree of Mg/Ca cooling and 0.033 $\log_{10}$ units (7.8 per cent) per mil of δ^{18}O increase. In neither regression is the intercept significantly different from zero.

The model-fitting results are similar. The directional model receives significantly more support than the random walk model (likelihood ratio statistic = 4.87, $p = 0.027$), and the mean evolutionary step for the directional evolution model is positive, which is consistent with the increasing body sizes predicted by Cope's Rule. However,

TEXT-FIG. 2. SEM images of the species analysed in this work. All samples are from Deep Sea Drilling Programme (DSDP) 253; sample information is listed in Table 1. Scale bar in the lower right represents 500 microns. All specimens are adults, and all except for G and N are left valves. A, *Abyssocythere* sp. from sample no. 7, USNM 542222. B, *Actinocythereis orientalis* Guernet, 1985 from sample no. 1, USNM 542223. C, *Actinocythereis*? sp. 4 from sample no. 9, USNM 542224. D, *Bradleya caeca* Guernet, 1985 from sample no. 5, USNM 542225. E, *Legitimocythere* sp. from sample no. 8, USNM 542226. F, *Marwickcythereis*? aff. *reticulata* Guernet, 1985 from sample no. 7, USNM 542227. G, *Cytheropteron* aff. *planalatum* Guernet, 1985 from sample no. 18, USNM 542228. H, *Dutoitella* sp. 1 from sample no. 8, USNM 542229. I, *Dutoitella* sp. 2 from sample no. 3, USNM 542230. J, *Krithe* sp. D from sample no. 13, USNM 542231. K, *Krithe* sp. E from sample no. 15, USNM 542232. L, *Krithe* sp. F from sample no. 10, USNM 542233. M, *Krithe* sp. C from sample no. 20, USNM 542234. N, *Poseidonamicus minor* Benson, 1972 from sample no. 15, USNM 542235. O, *Poseidonamicus major* Benson, 1972 from sample no. 21, USNM 542236. P, *Poseidonamicus anteropunctatus* Whatley *et al.*, 1986 from sample no. 10, USNM 542237. Q, *Poseidonamicus nudus* Benson, 1972 from sample no. 17, USNM 542238. R, *Poseidonamicus* sp. A from sample no. 12, USNM 542239. S, *Poseidonamicus* sp. B from sample no. 12, USNM 542240.



TEXT-FIG. 3. Palaeoclimate proxies used in this study. Grey line is the smoothed Mg/Ca palaeotemperature curve from Lear *et al.* (2000); crosses indicate ages of ostracod samples. Points indicate oxygen isotope values for individual foraminifera shells (open circles = *Cibicidoides*, filled circles = *Oridorsalis*; offset applied to *Oridorsalis* points). Black line connects mean values for each sample. For comparison, the grey area shows two standard deviations on either side of interval means for the oxygen isotope compilation of deep-sea foraminiferal values (Zachos *et al.* 2008).

TABLE 3. Evolutionary models considered in this work.

Model name	Evolutionary interpretation for body-size evolution	Parameters	E(ΔS)	Var(ΔS)
Random walk	Nondirectional and unrelated to temperature	σ^2_{step}	0	$\sigma^2_{\text{step}} \cdot t$
Directional change	Unconditional trend (e.g. Cope's Rule)	μ_{step}, σ^2_{step}	$\mu_{\text{step}} \cdot t$	$\sigma^2_{\text{step}} \cdot t$
Temperature tracking	Size tracks temperature; no inherent directionality otherwise	β, ε	$\beta \cdot \Delta T$	ε

Under each model, changes in body size (ΔS) are normally distributed with means and variances that are functions of the model parameters and the duration of time (t) elapsed between ancestor and descendant populations. E(ΔS) is the expected or mean value of ΔS, Var(ΔS) is the variance of ΔS, and ΔT is the change in temperature between ancestor and descendant.

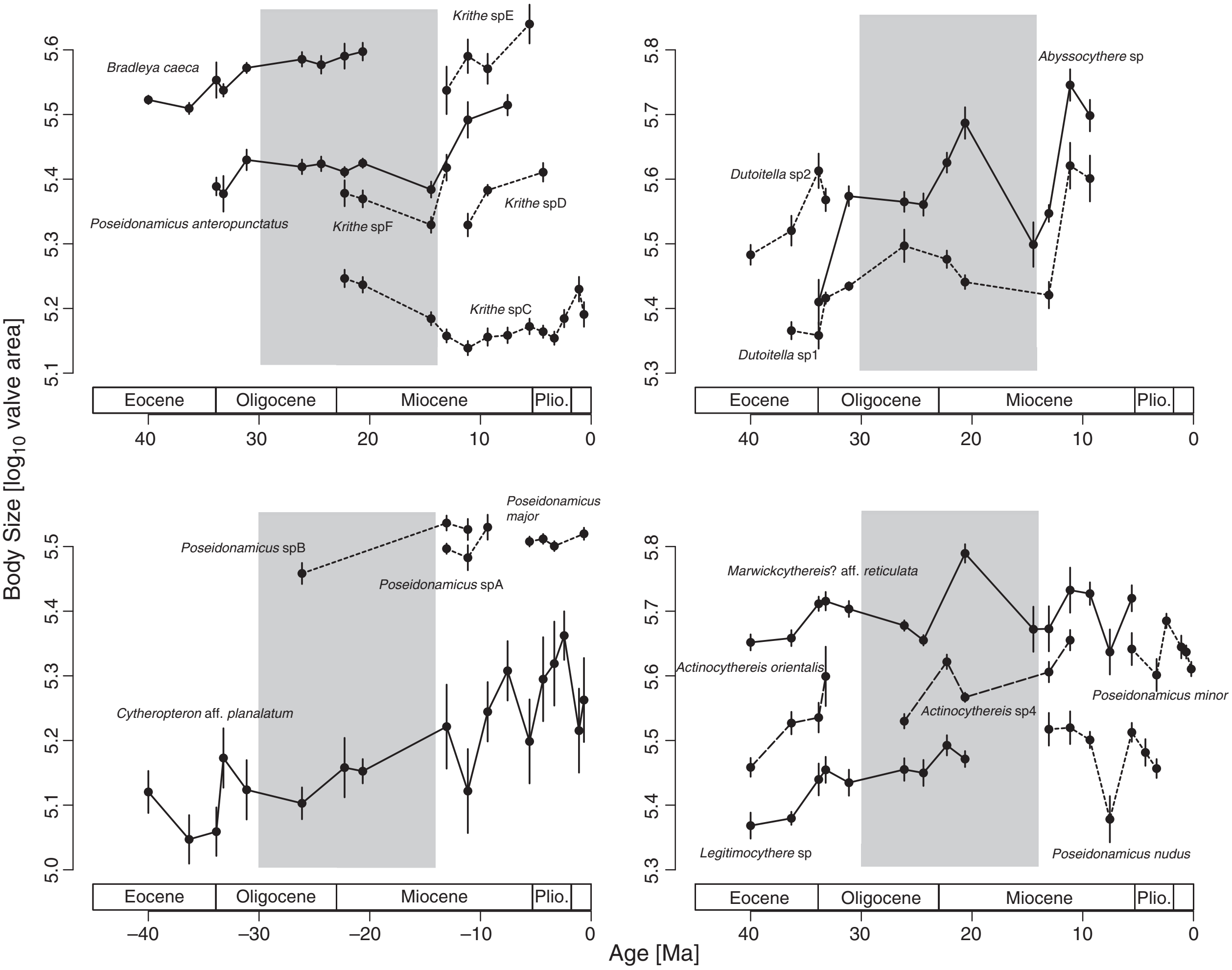
the temperature-tracking model garners greater support than a uniform increasing trend regardless of which climate proxy is used (Table 5). The coefficient β of the temperature-tracking model implies size increase of 0.024 $\log_{10}$ units (5.7 per cent) for every one degree Celsius cooling in Mg/Ca temperature and 0.046 $\log_{10}$ units (11 per cent) for every per mil of δ^{18}O increase. These parameter estimates are similar to the relationship implied by the regression of ΔS on temperature changes.

DISCUSSION

Body size and temperature at DSDP 253

The record from DSDP 253 reveals a picture over the past 40 myr in which the ostracod fauna shows a general increase in body size. This case study, like that of Sheldon (1987), documents significant and parallel trends among lineages that constitute a local fauna. The mean evolutionary step under the directional evolution model equals 0.0043, which translates to an increase of about 1 per cent per million years. This effect is moderate, but consistent at the coarsest level with Cope's Rule of increasing body sizes. Much of the literature on Cope's Rule examines patterns in genera or other higher taxa, and this study adds valuable species-level data (Alroy 1998; Hone and Benton 2005) to ongoing attempts to understand body-size evolution.

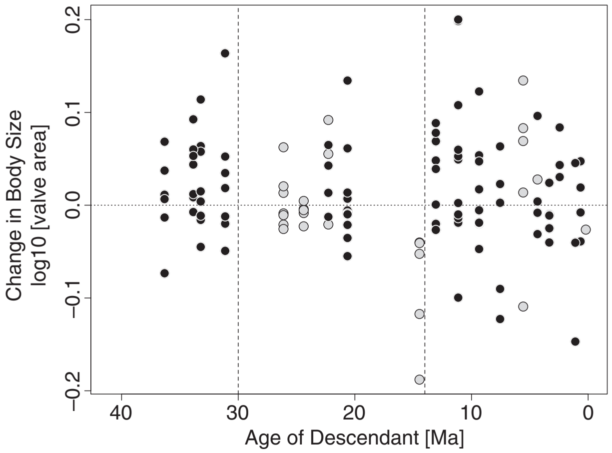
Several lines of evidence suggest that this directionality can be attributed to net directional changes in deep-water temperatures. The regression of ΔS on change in palaeotemperature proxies yields a significant slope but an intercept not significantly different from zero. If larger body sizes were favoured for reasons beyond that entailed by adaptation to temperature, such residual directionality would produce a positive intercept. Furthermore, if Cope's Rule holds regardless of environmental conditions, the strength of the increasing trend would be constant over time, and unrelated to temperature variations. Yet, changes in body size are significantly greater than zero only during the early and later



TEXT-FIG. 4. Body-size trajectories for nineteen species-level ostracod lineages at DSDP 253. Grey rectangle delimits temporal interval with little sustained cooling (30–14 Ma). Vertical axes differ across panels, but all span the same total range so size differences are comparable. Congeneric species are plotted with the same line type, and except for *Poseidonamicus*, on the same panel. Points indicate sample means, and error bars indicate standard errors.

intervals, both of which experience considerable climatic cooling. The middle interval (30–14 Ma) shows fluctuating temperatures but no net cooling and displays no significant tendency for ostracod sizes to increase. Finally, the formal model-fitting results corroborate this interpretation: a model with temperature-tracking but no Cope's Rule otherwise receives more support than a uniform trend of increasing body size, although the difference in support is not large enough to be decisive on its own. Taken together, however, these results support a view in which body sizes tend to increase when climate cools, but not otherwise.

Moreover, the magnitudes of size increase per degree cooling observed in this study are consistent with a Bergmann's rule mechanism. Our analyses indicate that, for each degree of cooling, $\log_{10}$(valve area) increases by 0.017 (according to the regression) to 0.024 (according to the temperature-tracking model). Most previous relevant work looks at linear dimensions such as valve length. On a logarithmic scale, the slopes for linear dimensions should be about half those of areas because area is proportional to length squared. Halving the above slopes results in linear increases of 2.0 per cent and 2.8 per cent per degree cooling. These estimates are consistent with size–temperature relationships in modern ostracods. For example, two species of *Echinocythereis* sampled along a depth gradient in the Gulf of Mexico (van Morkhoven 1972) show 1.6 per cent and 3.2 per cent increases in length per degree Celsius cooling, and modern populations of *Poseidonamicus major* show comparable increases of about 6 per cent (Hunt and Roy 2006). Thus, over the past 40 myr, these ostracod lineages have increased in size about as much as one would expect from temperature adaptation, given the roughly nine degrees of cooling over this interval.



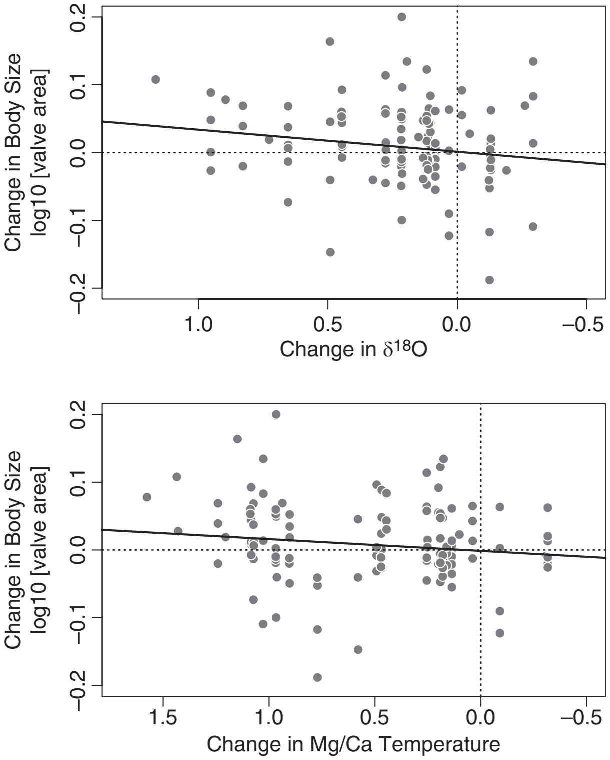
TEXT-FIG. 5. Evolutionary changes in body size plotted with respect to the age of the descendant population. Black circles indicate evolutionary increments associates with cooling and grey circles correspond to intervals of warming as indicated by oxygen isotope data. Horizontal dotted line indicates no change in size, and the vertical dashed lines delimit the three intervals discussed in the text. The earliest and latest intervals, but not the one in the middle, represent periods of sustained climatic cooling.

TABLE 4. Body size changes in three different temporal intervals.

Interval	Mean change in body size
40–30 Ma (cooling)	0.0239 (*t* = 2.48, df = 27, p = 0.019)
30–14 Ma (no net change)	−0.004 (*t* = −0.39, df = 33, p = 0.698)
14–0 Ma (cooling)	0.0176 (*t* = 2.01, df = 58, p = 0.049)

Size–temperature relationships in modern species are sometimes genetic, and sometimes ecophenotypic. Even when the latter is true, the underlying reaction norm may itself be an adaptation (Partridge and Coyne 1997; Kingsolver and Huey 2008). As usual for the fossil record, it is not possible to determine the relative contribution of each of these effects towards size changes in these ostracod lineages, although some of the size increases seem rather large to be accounted from solely by ecophenotypy (Text-fig. 4).

Other microfossil groups show body-size trajectories that also correlate with aspects of climate, but researchers have not always viewed temperature as the most likely driver. Through the Cenozoic, low-latitude assemblages of planktonic foraminifera increased in body size (Schmidt *et al.* 2004; Schmidt *et al.* 2006), while diatoms and dinoflagellate cysts assemblages became smaller-bodied (Finkel *et al.* 2005), patterns that these researchers attributed to increasing thermal stratification of the ocean. In addition, Kaiho (1998, 1999) documented body-size changes over



TEXT-FIG. 6. Plot of evolutionary size increments versus each of the climate proxies, oxygen isotope values (top panel) and Mg/Ca temperature (bottom panel). Points represent evolutionary changes from an ancestral to a descendant population across all species, each of which is associated with a change in the palaeoclimate proxies. Dotted vertical lines indicate no change in climate, dotted horizontal lines indicate no change in body size. The axis on the oxygen isotope values is reversed right to left so that decreases in temperature are towards the left in both plots. Both relationships are noisy but significant (oxygen isotopes: p = 0.015; Mg/Ca temperature: p = 0.045).

TABLE 5. Model-fitting results.

Model and climate proxy	log *L*	AIC$_C$	Akaike weight
δ^{18}O curve			
Random walk	173.93	−345.82	0.077
Directional change	176.36	−348.62	0.314
Temperature tracking	177.02	−349.95	**0.608**
Mg/Ca curve			
Random walk	173.93	−345.82	0.077
Directional change	176.36	−348.62	0.313
Temperature tracking	177.03	−349.95	**0.609**

Log-likelihoods (log*L*), small-sample Akaike Information Criterion (AIC$_C$) and Akaike weights are given. Because Akaike weights depend on the set of models compared, they need to be computed separately for the two different climate proxies. The best-supported model (in bold) is the temperature-tracking model regardless of which temperature proxy is used.

the past 120 myr in several groups of deep-sea benthic foraminifera. Similar to the ostracods at DSDP 253, benthic foraminifera generally increased in body size through the Cenozoic, and Kaiho linked this pattern to cooling temperatures and increased oxygen levels.

Untangling the ultimate drivers of these body-size patterns can be complicated because multiple factors may loosely covary with temperature trends. When several environmental factors correlate with body size, choosing among them usually relies on the strength of the background evidence for the different causal factors. For the plankton groups mentioned above, the biology of these organisms and patterns from extant assemblages support thermal stratification as a plausible driver of body-size trends. Although characteristics of surface waters may not be viable direct explanations for patterns in deep-sea benthic organisms like ostracods, Kaiho's (1998, 1999) hypothesis of oxygen-forced patterns deserves consideration. Some evidence implicates oxygen levels as a determinant of body size (Chapelle and Peck 1999; McClain and Rex 2001), but more so as a limit on maximal size for macrofauna than in determining mean size within a species (see also Spicer and Gaston 1999). Comparative data for living ostracods are limited, but the two species of *Echinocythereis* that increase in body size with depth in the Gulf of Mexico (van Morkhoven 1972) do so despite a substantial depth-related decrease in oxygen levels. At present, the available biological and palaeontological data are most consistent with temperature as the climate-related driver of the body-size trends at DSDP 253, but future work should continue to evaluate the body size–temperature link in ostracods.

Directionality, Cope's Rule and body-size trends

We emphasize that not all changes in ostracod body size during this interval are explained by temperature. Some changes are opposite in direction to that predicted by Bergmann's Rule, and these discrepancies do not arise from noise in the body-size and temperature records. For example, *Krithe* sp. C is significantly smaller in the mid-Pliocene than it is during the early Miocene, even though the Pliocene is almost certainly the colder interval (Text-fig. 3). This variability in our results is entirely expected; body size has multitudinous effects on the biology of organisms, and observed body sizes therefore should reflect compromises between many functions. Accordingly, we never expect that any single factor will completely control body sizes in natural populations.

Instead, we suggest that our results support a view in which all of the *directionality* in body-size evolution stems from trends in environmental conditions (temperature or correlated variables in this case) rather than the universal advantages of large size that are often cited as causes for Cope's Rule. The alternative, environment-independent view of Cope's Rule has found some support in a survey of selection coefficients documented by biologists working with modern, natural populations (Kingsolver and Pfennig 2004). Kingsolver and Pfennig found that traits related to body size – but not other phenotypic features – yielded selection coefficients that systematically favoured larger values. Although they considered alternative explanations, these authors viewed the disproportionately positive selection on body size as a possible proximate mechanism for Cope's Rule (Kingsolver and Pfennig 2004).

The preponderance of selection coefficients indicating selection for larger body sizes is an intriguing pattern, but one needs to be careful about relating observations occurring within a single generation to those spanning many millions of years. The fundamental difficulty is one of temporal scale and magnitude of effect, and a set of simple calculations show the disconnect between the observations of Kingsolver and Pfennig and Cope's Rule as a palaeontological phenomenon. Their median selection coefficient for body size was 0.15, and if we follow their example of typical heritability of 0.33, we expect to see a change each generation of 0.05 standard deviations (Kingsolver and Pfennig 2004, p. 1611). Consider a population of mouse-sized organisms with a mean length = 0.15 m and a standard deviation of length = 0.0075 m (this is a conservative but realistic level of variation). Under these selective conditions, this lineage will be as large as a bison (3.75 m) in 10^4 generations, and more generally, mouse-sized animals should, on average, evolve to be bison-sized in just 10 000 generations. If we assume that generations were yearly and Cope's Rule occurs over 10^7 years, we end up with a population of organisms whose mean length approaches 4 km (3750 m)! When body size is considered on a logarithmic scale, the effect is even greater, with our mice exceeding the size of celestial bodies in much fewer than a million generations. Of course, body-size increases are unlikely to persist long enough to get bison-sized mice. Nevertheless, under any set of reasonable assumptions, the problem remains that the bias towards larger sizes discovered by Kingsolver and Pfennig is far too large to produce size changes documented as Cope's Rule over 10^6–10^7 years. Conversely, if Cope's Rule were produced by a constant size advantage every generation, the magnitude of this effect would be far too small to detect in a single generation.

Kingsolver and Pfennig (2004) note that the effect of selection favouring larger sizes may be held in check by opposing selection on traits correlated with size, and they suggest that development time might be one such trait. If growth rates are equal, attaining larger body sizes requires longer periods of growth, and this extended time to develop may increase the probability of dying before reproducing. Although the available data are not extensive, there are some indications that this effect may sometimes hold (Kingsolver and Pfennig 2004; Kingsolver and Huey 2008). If general, this kind of trade-off suggests a scenario in which populations are generally close to the optimal body size they can achieve, given their available genetic variation. We might expect to see increase in body size when conditions change to shift the optimum (climate changes, the presence of new predators or prey, etc.), or when novel genetic variation allows alteration of the trade-offs between body size, time to maturity, and other linked traits.

What is the likely scope of climate-driven body-size trends? It can safely be expected to be most operative during intervals of net climatic cooling, and in taxa that often follow Bergmann's Rule. Much of the Cenozoic record of mammals fits both of these requirements, and some portion of the documented trend towards increasing size in mammals (e.g. MacFadden 1986; Alroy 1998; Van Valkenburgh *et al.* 2004) may derive from this mechanism. The keys to discriminating this from other explanations are to test correlations between size change and climate change, and then to assess whether the magnitude of size trends is consistent with a temperature driver. Size trends in deep-sea ostracods over the past 40 myr at DSDP 253 pass both tests, but the prevalence of this mechanism for other clades and environments remains largely unexplored.

CONCLUSIONS

At DSDP 253, the lineages that comprise the ostracod fauna show irregular but systematic increases in body size over the past 40 myr, a pattern that is consistent with Cope's Rule. Sizes disproportionately increase only during intervals of sustained cooling however, and multiple analyses point to an evolutionary dynamic in which all the directionality in body-size evolution is accounted for by long-term cooling trends in the deep ocean. Body-size trends can therefore arise when phenotypes track environmental or biotic changes that change directionally over time and need not reflect universal advantages of larger bodies.

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