Climate change, body size evolution, and Cope's Rule in deep-sea ostracodes

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Causes of macroevolutionary trends in body size, such as Cope's Rule, the tendency of body size to increase over time, remain poorly understood. We used size measurements from Cenozoic populations of the ostracode genus *Poseidonamicus*, in conjunction with phylogeny and paleotemperature estimates, to show that climatic cooling leads to significant increases in body size, both overall and within individual lineages. The magnitude of size increase due to Cenozoic cooling is consistent with temperature–size relationships in geographically separated modern populations (Bergmann's Rule). Thus population-level phenotypic evolution in response to climate change can be an important determinant of macroevolutionary trends in body size.

Bergmann's Rule | Ostracoda | temperature

Body size has long been considered one of the most important traits of an organism, because it influences nearly every aspect of the biology of the organism (1, 2). Despite its obvious biological importance, the processes that determine patterns of body size evolution, such as the tendency of size to increase over geological time [commonly known as Cope's Rule (3–5)], remain poorly understood. Existing explanations of Cope's Rule range from a general fitness advantage of large body size (4, 6, 7) to an increase in body size variance in a clade as it diversifies from a small ancestor (8, 9), but most of these models ignore the environmental context within which size evolution takes place. This is surprising, given that in many living species, size often varies predictably with environmental conditions (10), and it has been shown that body size can change in response to climatic change (11, 12). Thus it seems likely that changes in the physical environment should exert a strong influence on the nature and directionality of body size evolution.

Of the environmental factors known to influence body size, temperature is one of the strongest and most pervasive. Bergmann's Rule, an inverse correlation between body size and temperature within a species' range, is well documented in many endothermic and ectothermic animals (10, 13, 14). Over longer time periods, body sizes have been shown to change predictably in response to climatic fluctuations (11, 12, 15, 16). Such correlations between body size and temperature have led to the suggestion that Cope's Rule may simply be an evolutionary manifestation of Bergmann's Rule; species and lineages that conform to Bergmann's Rule should evolve toward larger sizes during episodes of climatic cooling. Even though this hypothesis was first proposed over a half-century ago (17, 18) and has been restated several times since (19–21), it has never been tested empirically.

Here we evaluate this Cope–Bergmann hypothesis using the fossil record of body size evolution in the deep-sea ostracode genus *Poseidonamicus*. Ostracodes are small bivalved crustaceans that form an important component of the marine biota and are abundantly preserved in fossil deposits. Body size in living podocopid ostracodes such as *Poseidonamicus* commonly varies with temperature as predicted by Bergmann's Rule, with larger body sizes associated with colder temperatures (see *Supporting Text*, Table 3, and Figs. 4–6, which are published as supporting

information on the PNAS web site). This temperature dependence, when combined with the rich fossil record of *Poseidonamicus*, provides a unique opportunity to test the hypothesized connection between body size evolution and global climate change.

We use a combined data set of body sizes, phylogenetic relationships, and paleotemperatures to test three specific predictions of the hypothesis that body size increases in these ostracodes are primarily a response to climatic cooling: (*i*) temporal changes in body size and temperature should be tightly and negatively correlated; (*ii*) increased body sizes should be attributable to evolutionary changes within lineages, rather than sorting among lineages; and (*iii*) the slope of the temperature–size relationship over evolutionary time should be consistent with the same relationship in geographically separated modern populations.

Results and Discussion

Body size in *Poseidonamicus* has increased greatly over the past 40 million years, consistent with the expectations of Cope's Rule (Fig. 1). This trend is evident both in raw data (Fig. 1*A*) and when populations are binned into million-year intervals (Fig. 1*C*). The oldest population in the analysis is also the smallest, with a mean length of <550 μm. Modern populations are nearly 50% larger, averaging >800 μm in length. Most of this increase is concentrated in the first and last 10 million years of this interval, with 20 million years of relatively stable body size in between. The temporal trend in body size mirrors the trajectory of bottom-water temperature, which cooled most rapidly in the first and last 10 million years of this interval (Fig. 1*C*). This qualitative match is confirmed by two statistical analyses: regression of the binned body size data (Fig. 1*C*) on bottom-water temperature yields a highly significant negative relationship (Table 1), as does the same regression using population means (Table 1). Thus, the first prediction is well supported: as bottom-water temperatures cooled, body size in these ostracodes increased.

In agreement with the second prediction of the Cope–Bergmann hypothesis, an inverse correlation between temperature and body size is evident within individual species of *Poseidonamicus*; populations from colder intervals tend to be larger than closely related populations from warmer intervals (Fig. 1*B*). Linear regressions find significant negative relationships between body size and temperature within most species of *Poseidonamicus* (Fig. 2 and Table 2; see also ref. 22). The species that deviate from this pattern (*Poseidonamicus miocenicus* and *Poseidonamicus riograndensis*) occur mostly within very narrow temperature ranges, offering little power to detect body size–temperature relationships. In keeping with the second prediction, the temporal trend in body size reflects evolution occurring

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Fig. 1. Body size evolution in the genus *Poseidonamicus*. (*A*) Population-level body size patterns, shown for individual specimens (small orange circles) and population means (larger open squares). (*B*) Populations shown connected according to their phylogenetic relationships. Populations from four species indicated by colored circles: *Poseidonamicus rudis* (red), *Poseidonamicus dinglei* (green), *P. major* (blue), and *P. pintoi* (orange); all other species are shown in gray. (*C*) Mean body size within million-year temporal bins (dotted lines; numbers indicate how many populations were included in each bin), plotted with a bottom-water temperature curve inferred from Mg/Ca paleothermometry (light-blue solid line).

Fig. 2. Slope of the body size–paleotemperature relationship within nine species of *Poseidonamicus*. Most species show a significantly negative slope between body size and temperature, indicating a tendency for body size to increase in response to climatic cooling (horizontal lines show 95% confidence interval on the slope estimate; vertical dotted line indicates a slope of zero). Also shown is the body size–temperature slope among modern populations of *P. major* (gray line, open circle; see also Fig. 4). The last row shows the summary estimate of within-species slope according to a metaanalysis (filled square, with a line indicating the 95% confidence interval).

within species: as climate cooled over the Cenozoic, multiple lineages within *Poseidonamicus* responded in parallel by getting larger.

The final and most stringent prediction of the hypothesis that Bergmann's and Cope's Rules are related phenomena is that the

slope of the temperature–body size relationship over time should be quantitatively similar to the same relationship among geographically separated modern populations. Among species of *Poseidonamicus* with a negative relationship between body size and paleotemperature during the Cenozoic, slopes range from −15 to −90 μm/°C, with a metaanalysis summary over all species of −28.7 μm/°C (Table 2, Fig. 2). In other words, for every degree Celsius of climatic cooling, *Poseidonamicus* species increased in length by an average of ≈29 μm. The temperature–body size slope among geographically separated modern populations of *Poseidonamicus major* (the only extant species of *Poseidonamicus* with sufficient available data) is not significantly different from this summary slope estimate (Fig. 2; see also Fig. 4). Very similar body size–temperature slopes also occur among bathymetrically separated modern populations of two species of the related genus *Echinocythereis* (Fig. 5).

Thus, for *Poseidonamicus*, climate is clearly a major determinant of body size evolution: body size increases significantly over time in concert with cooling; this size increase occurs through parallel evolutionary responses within multiple lineages; and finally, the magnitude of size increase is commensurate with the amount of change expected, given the extent of Cenozoic cooling and the slope of the temperature–size relationship among modern ostracode populations.

As with any paleontological pattern, it is necessary to consider the effects of potential biases due to imperfect preservation and incomplete sampling. Overall preservation in the samples used here is quite good, and the measured specimens were always found with much smaller and much larger microfossils, making it very unlikely that body size estimates were biased by dissolution or other preservational effects. In addition, the temperature–body size correlation in *Poseidonamicus* cannot be explained by the changing distribution of sample depths over the study interval. Consistent with Bergmann's Rule, individuals from deeper sites (and hence colder waters) tend to be larger than those from shallower sites (Fig. 3). However, body size

Table 1. Body size and paleotemperature relationships in *Poseidonamicus*

Model	Data	Analysis	Regression coefficients
$L \sim T$	Mean valve length in 1 million-year bins	Ordinary least squares	$b_T = -12.29$**
$L \sim T$	Mean valve length in 1 million-year bins	Generalized least squares, accounting for temporal autocorrelation	$b_T = -13.68$*
$L \sim T$	Mean valve length in 106 populations	GEE accounting for phylogeny	$b_T = -14.81$***
$L \sim T + D$	Mean valve length in 106 populations	GEE accounting for phylogeny	$b_T = -12.64$***
			$b_D = 23.42$***

Body size was measured as valve length (*L*) in micrometers; paleotemperature (*T*) in °C was derived from a published Mg/Ca curve, and (*D*) is sample bathymetric depth in kilometers below the sea surface. Estimated regression coefficients for temperature (b_T) and depth (b_D) are given in the last column. ***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$.

trajectories for samples in the shallow (<1,800 m) and intermediate (1,800–3,000 m) depth categories show body size trajectories very similar to each other (Fig. 3), consistent with a common response to climate change. Furthermore, multiple regression results show that depth influences body size in the predicted direction (deeper populations, living in colder waters, tend to be larger-bodied), but the effects of paleotemperature remain significant. This pattern holds across the genus as a whole (Table 1) and within the two species (*P. major* and *Poseidonamicus pintoi*) with sufficient spatiotemporal coverage to be analyzed separately (Table 2). Thus, although body size generally increases with depth, paleotemperature has a strong and independent effect on body size evolution, even after accounting for the bathymetric distribution of samples.

The negative relationship between paleotemperature and body size within individual species of *Poseidonamicus* indicates that the Cenozoic size increase is largely a result of within-lineage phenotypic evolution. Other proposed mechanisms for Cope's Rule are not strongly supported by our data. Although it is possible that origination and/or extinction rates are related to body size, size-selective turnover is unlikely to have had a strong effect because *Poseidonamicus* species have very long durations and correspondingly slow turnover rates (23). In fact, substantial size differences are observed even between intervals separated by almost no species turnover, such as the late Pliocene and the

Recent. In addition, the model of Cope's Rule as passive diffusion from an ancestor located near a lower limit of permissible body sizes (8, 24) can also be rejected in this case, because it is inconsistent with widespread body size increases within lineages and with the pattern of increasing minimum size during intervals of cooling (Fig. 1). Furthermore, because many related ostracode taxa are smaller-bodied than the smallest specimens in the present study, it is unlikely that *Poseidonamicus* is anywhere near a lower structural limit for ostracode body size.

As in any phenotypic study of fossils, we cannot determine what proportion of the observed size trend has a genetic versus ecophenotypic basis, although there are grounds to suspect that both mechanisms are involved. It is common for ectotherms to exhibit reaction norms in which individuals grow larger at colder temperatures (10, 25, 26), and a few studies indicate this may hold for ostracodes (27, 28). However, laboratory-rearing experiments have shown that many temperature-based body size clines have a genetic basis (25, 29–31). The two possibilities are not as distinct as would first appear, because even thermally plastic body size changes are generally thought to be adaptive (25, 29). Despite the agreement that natural selection shapes both plastic and genetic relationships between body size and temperature, it has proven surprisingly difficult to establish why larger body size should be favored in colder environments. The original explanation for Bergmann's Rule in mammals (larger bodies conserve more heat because of lower surface area-to-volume ratios) does not apply to ectotherms (10). A number of

Table 2. Regression of body size (*L*) on paleotemperature (*T*) within individual species of *Poseidonamicus*

Species	Model	Coefficients	R^2
		Regression results	
P. rudis	$L \sim T$	$b_T = -16.5$*	0.78
P. dinglei	$L \sim T$	$b_T = -32.5$*	0.60
P. riograndensis	$L \sim T$	$b_T = 4.2$	0.09
P. pintoi	$L \sim T$	$b_T = -89.0$***	0.77
	$L \sim T + D$	$b_T = -62.2$***, $b_D = 24.0$*	0.86
Poseidonamicus species 3	$L \sim T$	$b_T = -41.7$***	0.87
Poseidonamicus species 4	$L \sim T$	$b_T = -53.4$**	0.81
P. miocenicus	$L \sim T$	$b_T = 3.3$	0.01
P. minor	$L \sim T$	$b_T = -15.3$	0.10
P. major	$L \sim T$	$b_T = -27.2$**	0.50
	$L \sim T + D$	$b_T = -24.8$**, $b_D = 17.1$	0.59
Summary estimate	$L \sim T$	$b_T = -28.7$***	

Only species with six or more sampled populations were analyzed. For the two species with adequate data, *P. pintoi* and *P. major,* we fit an additional model which included sample depth (*D,* in kilometers) along with paleotemperature. The last row gives the metaanalysis summary estimate of the within-species slope of valve length on paleotemperature across all species. R^2, coefficient of determination; otherwise, conventions as for Table 1.
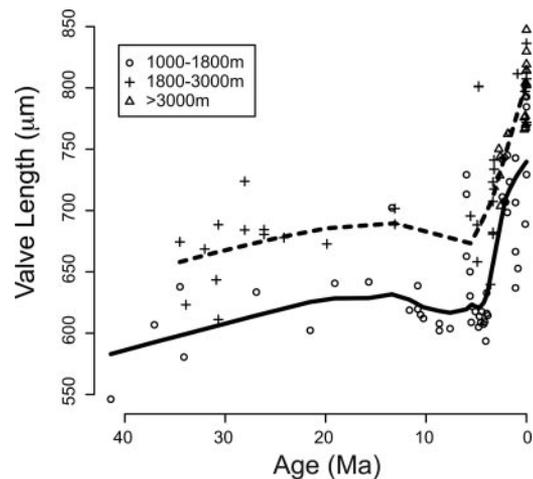
Fig. 3. Body size in *Poseidonamicus*, with populations divided into bathymetric categories. Lines indicate lowess smoothing function for the shallowest localities (1,000–1,800 m, solid line) and localities from intermediate depths (1,800–3,000 m, dotted line). The deepest depth bin (>3,000 m) includes only samples <3 million years old; its lowess function is quite similar to the intermediate depth group and is not shown for clarity.

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alternate mechanisms have been proposed involving temperature-related variation in seasonality, growth constraints, oxygen requirement, and nutritional stress, among others (10, 32, 33), but all suffer from a lack of generality or empirical support. Some recent work suggests that resolving this puzzle will involve understanding the interactions among metabolic rates, mortality schedules, and temperature in the context of life history evolution (25, 34), although definitive answers are still elusive (32).

Clearly, temperature is not the only factor likely to influence body size evolution. Other factors, such as changes in primary production associated with climate change, could also play a role, because food availability for deep-sea benthic animals such as *Poseidonamicus* is related to surface ocean productivity that is exported to the sea floor. Our data do not permit direct tests of whether changes in primary production influence body size evolution. However, we do note that high-latitude sites, which in the modern ocean have relatively high annual productivity, do not yield anomalously large *Poseidonamicus* specimens, and there is no overall correlation between absolute latitude and body size ($r = -0.04$, $n = 106$, $P = 0.71$). This suggests that the effect of productivity changes on body size evolution of these ostracodes is likely to be small compared with temperature effects.

Various aspects of species ecology and life history must also be important evolutionary determinants of body size. However, these influences need not produce inherently directional temporal change, at least on macroevolutionary timescales. If the temperature dependence of body size is an important contributor to Cope's Rule in general, we would predict that for taxa whose modern representatives follow Bergmann's Rule, net increases in body size should be especially common during intervals of climatic cooling. This prediction is consistent with the canonical example of Cope's Rule in mammals (5), where many living species show Bergmann's Rule (14, 35) and the evolutionary increase in body size coincided with dramatic Cenozoic climatic cooling. In contrast, the well documented absence of Cope's Rule in late Cretaceous mollusks (36) occurred during a period of essentially warm and stable climates. Further studies that track body size through both cooling and warming intervals while incorporating temperature–size relationships in related modern populations should help to delimit the frequency with which temperature change drives body size evolution.

Specific mechanisms aside, the results presented here provide strong support for the hypothesis that Bergmann's and Cope's Rules can be related phenomena, both involving temperature-related changes in body size. This finding is consistent with the idea that the macroevolutionary pattern of Cope's Rule can result from microevolutionary processes occurring within populations (6, 37). More importantly, our results also show that this connection between micro- and macroevolution can be mediated by prevailing climate. Evolution towards large body size in *Poseidonamicus* is not a constant tendency but rather is pronounced only during intervals of climatic cooling. Such environmental mediation of body size evolution may also explain why, despite the putative selective advantage of large body size, taxa do not increase in size universally or indefinitely (38).

Existing models of body size evolution have largely ignored the role of the external environment. Yet there is emerging evidence that changes in the physical environment can have a major influence on patterns of body size evolution (11, 15, 39). This suggests that our understanding of the dynamics of body size evolution will be incomplete without mechanistic insight as to how temperature and other abiotic factors modulate body size. These processes, although poorly understood at present (26, 29, 32, 40), are likely to be important determinants of body size evolution in the distant past, as well as biotic responses to future global climate change.

Materials and Methods

Study Samples and Body Size Data. We measured body size as valve length in 1,353 individuals from 106 populations representing 19 deep-sea species of *Poseidonamicus*. Samples used in this study derive primarily from cores from the Deep Sea Drilling Project (DSDP), supplemented with some dredge samples. These samples range from the Eocene to the Recent, recording >40 million years of body size evolution. Sample ages were estimated by using revised age models based on biostratigraphic events, mostly from the Initial Reports of the DSDP, updated to recent syntheses of Cenozoic chronology (41, 42). These age models are available upon request from the authors. Specimens from the same dredge or core sample (or in some cases, from multiple closely spaced core samples) were aggregated into populations for analysis. Mean body sizes, paleotemperatures, and ages for all analyzed populations are listed in Table 4, which is published as supporting information on the PNAS web site.

Anterior–posterior length was measured from digital scanning electron microscopic images of individual *Poseidonamicus* valves using the software TPSDIG (43). Only individuals from the last juvenile instar were included in the analysis. Growth in podocopid ostracode species is determinate, with a fixed number of molt stages, usually nine (44). In *Poseidonamicus*, instars can be readily identified on the basis of size clusters (45) and instar-specific morphological characters (46). We analyzed the last juvenile rather than adult instar, because the former were generally more abundant than the latter, which allowed for the inclusion of more populations, and more measurable individuals per population. In addition, sexual dimorphism in the adult carapace requires that males and females be analyzed separately, further lowering sample sizes. The carapace length of the last juvenile instar is highly correlated with that of the adults ($r = 0.99$ for populations with at least five individuals in each instar, $n = 51$), and therefore valve length in the last juvenile instar is an excellent proxy for adult body size. Left and right valves of this instar do not differ in length and were pooled within samples.

All analyses were performed by using population means (rather than individual specimens) as the unit of analysis so that samples with many individuals would not disproportionately influence the results. We did not omit samples with few individuals, because differences among populations were large relative to variation within populations (within-population coefficients of variation averaged ≈3.0). Consequently, even imprecisely estimated population means could inform between-species differences. Sensitivity analyses show that our results do not differ qualitatively if we omit populations represented by fewer than five individuals. In addition, log-transforming body size does not have any substantial effect on the results presented.

Temperature Data. We traced temperature change over the past 40 million years using the curve published by Lear *et al.* (47) on the basis of Mg/Ca thermometry from multiple deep-sea sites. Magnesium–calcium temperature curves have been found to correlate with the more established oxygen isotope curves (47–49), but unlike oxygen isotope values, they are unaffected by changes in global ice volume and are therefore easier to relate directly to temperature. We digitized figure 1*C* of Lear *et al.* (47) with the software WINDIG (50) and used linear interpolation to estimate paleotemperature for sample ages between digitized points of this curve. This temperature curve is a long-term smoothed record suited for reconstructing the broad features of a ≈12°C cooling over the Cenozoic. Although there are interesting changes in climate that occur at higher frequencies than can be resolved with this record, the scope and resolution of the Lear *et al.* (47) curve match that of the fossil record of body size evolution in *Poseidonamicus*. Note that Mg/Ca values reflect the temperature of the high-latitude source waters for deep-water

masses rather than the temperature at the site of deposition (51). Because deep-water circulation patterns propagate these water masses through the world ocean, deep-sea temperature signals are largely global rather than local in nature. Although there is general decrease in temperature with increasing depth, we account for this analytically by including sample bathymetry in our statistical models (see below).

Time-Series Analysis. To more formally characterize overall body size trends in *Poseidonamicus*, we divided the timescale into 1 million-year bins and calculated the mean valve length for all populations within each bin. Twenty-two of the 42 million-year bins were represented by at least one population, spanning interval midpoints of 41.5–0.5 millions of years before the present. For each of these occupied bins, deep-sea temperature was estimated by linear interpolation of the Mg/Ca curve. This resulted in two time series, one for body size and one for temperature, each with the same temporal spacing. We used linear regression to test for significant association between the two time series. To account for dependence due to temporal autocorrelation, we modeled the regression residuals as an autoregressive (AR) process, selecting the best-fitting model by the Akaike Information Criterion. This best AR model was used to estimate the dependence among observations, and this dependence was accounted for by using generalized least squares (see ref. 52).

Body Size–Temperature Relationship Among Populations. We evaluated the relationship between body size and temperature among all deep-sea *Poseidonamicus* populations using standard comparative methods to account for phylogenetic dependence. We fit two regression models: body size as a linear function of temperature and body size as a function of both temperature and sample depth. Generalized estimating equations (GEE) were used to accommodate phylogenetic dependence among samples (53).

The phylogenetic hypothesis that forms the basis for these comparative analyses is based on Hunt's (46) study of the genus *Poseidonamicus*. This study defined a set of morphological characters describing variation in valve shape and structure, presence/absence and location of sensory pore canals, and reticulum structure. Standard phylogenetic methods were used to infer relationships among populations, which were not lumped into species *a priori*. Rather, species-level taxonomy was overlain onto the phylogenetic relationships among populations. In applying the results of this phylogenetic study to the present analysis, two issues needed to be addressed. First, uncertainty in phylogenetic relationships had to be resolved. Second, sample ages had to be translated into estimated branch lengths on the phylogeny.

There were three sources of phylogenetic uncertainty. First, some of the populations in the present analysis (especially those with few specimens) were not included in the previous phylogenetic analysis (46). The phylogenetic position of these omitted populations were set by adding each to the least-inclusive clade to which it could be unambiguously assigned based on the coded characters. The second source of phylogenetic uncertainty stems from the fact that some populations were lumped to create terminal taxa in the phylogenetic analysis. Such composite terminal taxa in the phylogenetic study were replaced by an unresolved polytomy of their constituent populations. The third and final source of phylogenetic ambiguity was the presence of multiple equally parsimonious trees (46). Because GEE approaches require a fully bifurcating tree, it was necessary to resolve all polytomies stemming from these three sources of ambiguity. To do so, we relied on stratigraphic information: all polytomies were resolved into pectinate clades with taxa in stratigraphic order from old (at the base) to young (at the tips). This approach follows a long tradition in paleontology of using

the age of taxa to inform phylogeny and is similar in spirit to strato-cladistic (54) and strato-likelihood (55) methods. Our protocol actually makes rather limited use of stratigraphy, because age information is never used to overturn character evidence; only those relationships not resolved by character data are informed by stratigraphic ordering.

We calculated phylogenetic branch lengths using the stratigraphic ages of the terminal taxa. Each internal node in the tree was assigned the age of the oldest terminal taxon it includes. These estimates have somewhat different properties than those calculated from molecular divergences but are appropriate for phylogenies with extinct taxa for which molecular estimates of branch lengths are unobtainable. Allowing a node to be the age of its oldest terminal taxon yields some branch lengths of zero length, which are not permitted when using GEEs. We resolved this problem by extending zero-length branches by an arbitrary fixed length of 0.1 million years; results are essentially unchanged if the extension is much smaller (0.01 million years) or much greater (10 million years).

As in any large phylogenetic analysis, there are surely uncertainties and inaccuracies in the final hypothesis of relationships. However, it is important to note that the inferred phylogenetic relationships have only the limited role of modeling the dependence among populations in this analysis. Because the major features of this phylogeny are well supported by character data (46), the inferred dependence among populations is not likely to be very sensitive to the exact topology used. In fact, resolving phylogenetic uncertainty arbitrarily (rather than on the basis of stratigraphic order) yielded results very similar to those presented, as did nonphylogenetic versions of the analyses reported here.

In addition to examining trends across the clade as a whole, we also analyzed the temperature–body size relationship within the nine *Poseidonamicus* species represented by at least six populations in this study. We used linear regression to estimate the within-species slope of body size as a function of temperature; a random effects metaanalysis provided a summary slope estimated across all nine species (56). For the two best-represented species (*P. pintoi* and *P. major*), we also performed a multiple regression of body size on paleotemperature and bathymetric depth.

Sample Depths over Time. Within this dataset, sampling with respect to water depth is not even over time; most of the very deep samples studied are quite young (<3 million years old). Because temperature decreases with depth, this sampling pattern could potentially influence observed trends in body size. We used two independent approaches to test this possibility. First, we divided populations into bathymetric categories at natural breaks in the distribution of sample depths at 1,800 and 3,000 m and used a lowess smoothing function (57) to highlight body size trends separately within these depth categories over time (there are no depth trends over time within these bathymetric categories). Second, we statistically accounted for the effects of sample depth using a multiple regression model in which body size is predicted jointly by Mg/Ca paleotemperature and sample depth (as described in *Body Size–Temperature Relationship Among Populations*). In this model, we used modern bathymetry to estimate locality depths at the time of sediment deposition. For nearly all sites, geophysical and faunal data indicate little change in bathymetry from the time of deposition to the present day. For the handful of sites that have subsided detectably since the sampled strata were deposited, the magnitude of bathymetric change is modest enough (a few hundred meters or less) to constitute only a minor source of error.

All analyses were performed by using the statistical programming environment R (58). The GEE comparative analysis used the ANALYSES OF PHYLOGENETICS AND EVOLUTION package available for R (53).

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