

angle equals  $5.8^\circ$ . Two permutation-type tests evaluated these figures by generating a large number of random permutations for both the trend and plunge angles and calculating the average difference in trend and plunge angles for each permutation. 10,000 permutations of the trend angles yielded no case with an average difference of less than  $12.1^\circ$ . 10,000 permutations of the plunge angles provided only six cases with an average difference of less than  $5.8^\circ$ . Trend and plunge data also indicate a non-random distribution.

Analysis of MOR 963 followed the same procedures, except that egg tops were used rather than bottoms. The simulation study used a  $D_{\min} = 5.3$  cm, a 7-sided polygon with an area of  $0.1 \text{ m}^2$ , and yielded  $P = 0.342$ , neither supporting nor contradicting a paired-egg hypothesis. The top-down preparation of MOR 963 did not permit accurate measurement of egg trends and plunges, nor use of the two permutation-type tests. Egg spacing, trend and plunge data are available from D.J.V.

Received 23 July; accepted 11 November 1996.

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**Acknowledgements:** We thank the Museum of the Rockies, Montana State University, the Old Trail Museum, M. Lange and the rest of the MOR's 1994 Field School participants, P. Leiggi, Y. Katsura, T. Weaver, C. Trueman, the families of V. and L. Carrol, E. Bray, R. Jackson, K. Carpenter, K. Alf, G. Erickson and G. Dyke; we thank P. Currie, K. Padian, R. Rogers and H. Temrin for critically reading early drafts of the manuscript. B. Selyem (MOR) provided egg photos.

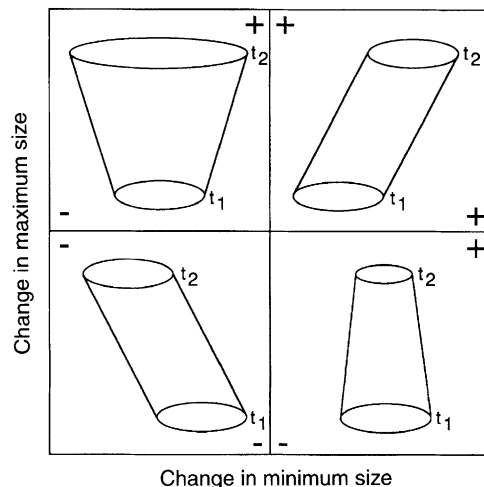
Correspondence and requests for materials should be addressed to D.J.V. (e-mail: otmdjv@3rivers.net).

## Body-size evolution in Cretaceous molluscs and the status of Cope's rule

David Jablonski

Department of Geophysical Sciences, University of Chicago,  
5734 South Ellis Avenue, Chicago, Illinois 60637, USA

Cope's rule, the tendency for lineages to evolve to larger body size, is widely seen as a pervasive evolutionary pattern<sup>1–4</sup>. However, only a few studies<sup>5–8</sup> have gone beyond enumerating isolated examples to assess its overall frequency relative to body-size decrease or stasis. Thus, although size is clearly an important parameter for microevolution and ecology<sup>9–14</sup>, including conservation biology<sup>10</sup>, its impact on large-scale patterns remains poorly

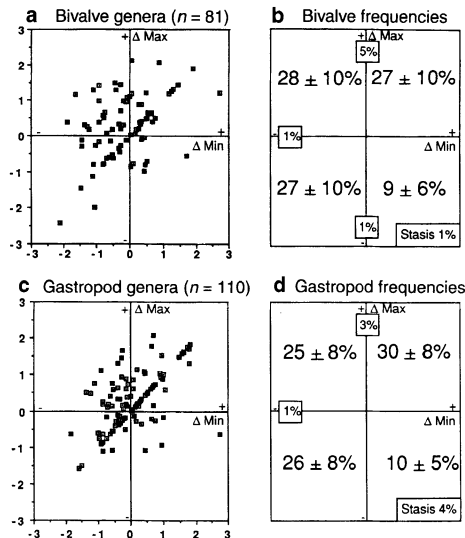


**Figure 1** A graphical approach to the analysis of evolutionary changes in body size, with each quadrant representing a different temporal pattern, as shown schematically. ( $t_1$  = time 1;  $t_2$  = a subsequent time 2.) The vertical axis is the change in the upper bound of the size distribution of the species in a lineage, and the horizontal axis is the change in the lower bound of the size distribution. Each clade can thus be plotted as a point determined by the behaviour of its upper and lower size bounds (in this study, the maximum recorded size of the largest and smallest species, respectively). The top-right quadrant represents Cope's rule, the bottom-left quadrant a directional evolutionary size decrease, the top-left an increase in the range of body sizes or 'increase in variance', and the bottom-right a decrease in size range.

understood. The prevalence of Cope's rule is even more uncertain, as some reported cases of evolutionary size increase may actually represent an expansion of a clade's size range (a pattern generally termed an 'increase in variance', although not necessarily in the formal statistical sense) rather than a phyletic, directional trend<sup>15–18</sup>. I have performed a comprehensive census of body-size changes in a large fauna of Cretaceous bivalve and gastropod genera. A directional net increase in body size (including the loss of small-sized species and thus representing Cope's rule in the strict sense) is no more frequent than an increase in size range among species or a net evolutionary size decrease. Thus the undisputed ecological importance of body size does not translate into a preferred macroevolutionary pattern.

The Late Cretaceous (Late Santonian–Maastrichtian) deposits of the Gulf and Atlantic Coastal Plain of North America contain a rich and well-preserved marine molluscan fauna<sup>19</sup>. This period of 16 Myr, which can be divided into increments of 2 Myr, contains 191 bivalve and gastropod lineages that are generally afforded genus or subgenus rank<sup>20</sup>. (The genus is a standard level of analysis for body-size trends, as discussions of Cope's rule have almost always involved claims about large-scale patterns<sup>8,16,21</sup>; genera and subgenera are here treated equivalently as operational units because the distinction between the two ranks is often arbitrary.) Several apparently paraphyletic taxa were amalgamated for this analysis, but most of the genera and subgenera originated before the study interval, thereby reducing the number of potential paraphyly-derived artefacts.

The data consist of adult sizes for each genus at the beginning and the end of the study interval, as determined by the geometric mean of height and length<sup>22</sup> of the largest known specimen of each constituent species. Sizes were obtained for all described species and a number of undescribed ones (total  $n = 1,086$ ), but the rudist bivalves were excluded as they were considered too rare and fragmentary in this region for meaningful measurement. Maximum sizes were used to exclude immature specimens (most of these species exhibit indeterminate growth<sup>23</sup>), but results are not qualitatively different when median sizes are taken for groups of probably

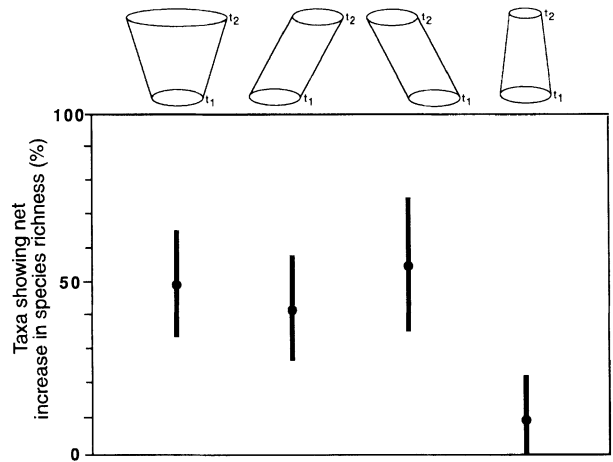


**Figure 2** Evolutionary patterns of size change in genera and subgenera of Late Cretaceous bivalves (a, b) and gastropods (c, d) over 16 Myr. Sizes were log<sub>2</sub>-transformed, so that, for example, an increase of unit 1 represents a doubling, and a corresponding decrease a halving, of body size; 95% confidence limits on frequencies calculated following ref. 27, ΔMax = change in upper bound of adult sizes; ΔMin = change in lower bound of adult sizes.

adults in the 50 best-sampled genera. Because shapes are relatively constant within genera, and because many causal explanations involve volume-correlated parameters (such as gonad output, physiological inertia, size refuges from predation), more elaborate measures such as the first principal component of a multivariate morphometric analysis were not used. Analysis at this taxonomic level may lose details of individual species transitions (but see below for data on phyletic trends), but it allows the partitioning of large-scale trends according to net directional or diffusional dynamics in a large number of discrete phylogenetic units.

The evolution of body size can be analysed using the scheme shown in Fig. 1, with each taxon plotted as a point determined by the change in both extremes of its size range, as defined by the largest and smallest species. Taking this approach, the bivalve and gastropod genera show similar patterns of body-size evolution, with statistically equivalent frequencies of net directional size increase (27–30%), net size decrease (26–27%), and increased variance (25–28%) (Fig. 2). The paucity of taxa exhibiting either a decrease in variance or stasis conforms to the expectation if body sizes commonly evolve within genera as a diffusion process. Only 3–5% of the taxa exhibit stasis at the lower bound while expanding towards greater sizes; this suggests that few of these molluscs are near a clade-specific or general size limit, which can impose apparent directionality on diffusive or passive trends<sup>15,18</sup>. (By tallying taxa according to the loss or accretion of species at their lower as well as upper size bounds, these analyses essentially correspond to McShea's<sup>18</sup> 'test based on the behavior of the minimum' for distinguishing passive from active, or directional, trends.)

The alignment of taxa on the diagonal in the upper right and lower left quadrants is in a sense an artefact of the analytical technique. Those points represent lineages that were monospecific in both their first and last time increment; the lone species is by default both smallest and largest in its time interval, so that any net size increase or decrease inevitably plots as a symmetrical change with respect to both minimum and maximum size. This subset of the data, which provides one estimate of the relative frequencies of phyletic size change, also shows no significant tendency towards Cope's rule (16 ± 8% of all bivalve genera show this phyletic size increase, 14 ± 8% show size decrease; 18 ± 7% of all gastropod genera show phyletic size increase, 15 ± 7% show size decrease).



**Figure 3** Percentage of taxa exhibiting a net increase in species richness. The increased-variance category is not significantly dominated by taxa showing a net increase in species numbers, relative to taxa showing directional size trends (*G*-tests on raw data, with Williams' correction). This suggests that the increased-variance pattern is not simply an artefact of sampling more species late in the study interval. The decreased-variance pattern is significantly concentrated in clades with declining species richness, as expected if body sizes evolve as a random walk. Taxa constrained by monospecific start and finish are omitted, as are those in which the upper and/or lower bound is static; 95% confidence limits on frequencies calculated following ref. 27.

If taxa that fall on the diagonal are omitted, then the 'increased variance' quadrant is most heavily occupied (39% and 40% of the remaining genera of bivalves ( $n = 57$ ) and gastropods ( $n = 70$ ), respectively), and the quadrants presenting Cope's rule and net size decrease still have equal frequencies (17–18% and 18–20%, respectively). As before, an evolutionary decrease in variance is less common, although no longer significantly so (11–16%), and stasis is seen least of all. Again, this is the pattern expected for a large population of clades branching stochastically to larger and smaller sizes. The slightly greater proportion of points in the upper half of Fig. 2a ( $60 \pm 10\%$ ) and Fig. 2c ( $58 \pm 9\%$ ) derives from the rarity of 'decreased variance' clades relative to those that increase their size range or show size trends upwards or downwards, rather than from any overall tendency towards Cope's rule.

These results are unlikely to be artefacts of taxonomic practice or the geographic limits of the study. Incorporation of extraprovincial species, or correction of any remaining paraphyletic taxa by merging them into monophyletic units, would be as likely to create an increase or decrease in size range as to generate a directional pattern. A pattern typical of Cope's rule, for example, would be produced only by the addition of a smaller species at the start of a formerly increased-variance clade, or by the addition of a larger species at the end of a formerly decreased-variance clade. Conversely, Cope's rule would be converted to decreased variance by the addition of a larger species at the start of the study interval, or to increased variance by the addition of a smaller species at the end of the study interval.

The youngest time increment, the *Haustator bilira* biostratigraphic zone, has more localities than the oldest time increment, and this difference might artificially increase size ranges within a genus through time. However, when the three oldest time increments of the study interval are pooled to raise the number of localities to about 150, as in the youngest time increment, the resulting changes in frequency are statistically negligible—frequencies in the upper right quadrant (i.e. Cope's rule), for example, are  $32 \pm 10\%$  and  $30 \pm 8\%$ , for bivalves and gastropods respectively—suggesting that sampling does not create the overall pattern. Indeed, by summing the evolutionary spread of body sizes in the initial intervals, this procedure must artificially reduce the number of taxa

falling into the increased-variance quadrant. Further, the proportion of clades exhibiting a net increase in species richness is no higher for the increased-variance group than for the directional-change groups (Fig. 3), so the observed patterns are again unlikely to be sampling artefacts. By indicating that patterns are not driven by changes in sample size, these tests suggest that the observed expansions or contractions in size range represent true changes in variance.

The analyses presented here do not support Cope's rule as an evolutionary generalization, and provide the most extensive empirical evidence yet for the 'increased variance' pattern as an equally important pathway in body-size evolution. The selective forces often held to drive Cope's rule (for example, advantages of large size in defence, mating success, predatory ability, and resistance to environmental extremes<sup>1-4,21,26</sup>) generally imply the evolutionary loss of small-bodied forms. However, the fossil record shows that increases in the maximum body size within clades do not require such mechanisms, but can simply represent one limb of an expanding size range, and that directional decreases in sizes are no less frequent than directional increases. This apparently random evolution of body size in Cretaceous molluscs need not imply the absence of driving mechanisms, but could result from the interaction of many factors which have effects so context specific and scale dependent that unitary patterns fail to emerge<sup>18</sup>. Large size is not universally advantageous, and multiple pressures operate on body size and taxon-specific correlates that range from age at first reproduction to allometric morphologies<sup>13,16</sup>. Thus lineages collectively fail to follow a single, predictable size trajectory as their species diffuse or shift through size changes. Extinction probability also need not be strongly related to size<sup>24,25</sup>. Despite its importance in microevolution and ecology<sup>9-14</sup>, size plays a surprisingly weak or unpredictable role at larger scales, reinforcing the view that macroevolutionary patterns need not be simple extensions of those seen at the level of individual organisms over microevolutionary time. □

Received 13 May; accepted 23 October 1996.

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**Acknowledgements:** I thank S. Calzada, R. J. Cleavelly, A. V. Dhondt, D. L. Dockery, C. Heinberg, C. C. Johnson, E. G. Kauffman, G. R. Kennedy, M. Machalski, N. J. Morris, L. R. Saul, N. F. Sohl and G. L. Wingard for access to collections and unpublished information; J. Walsh for assistance with data entry; and W. D. Allmon, M. J. Benton, D. H. Erwin, M. Foote, S. J. Gould, S. M. Kidwell, B. A. Maurer, F. K. McKinney, A. I. Miller, P. Pearson, K. Roy, S. M. Stanley, P. J. Wagner and P. D. Ward for comments. This work was supported by the US National Science Foundation.

Correspondence and requests for materials should be addressed to the author (e-mail: djablons@midway.uchicago.edu).

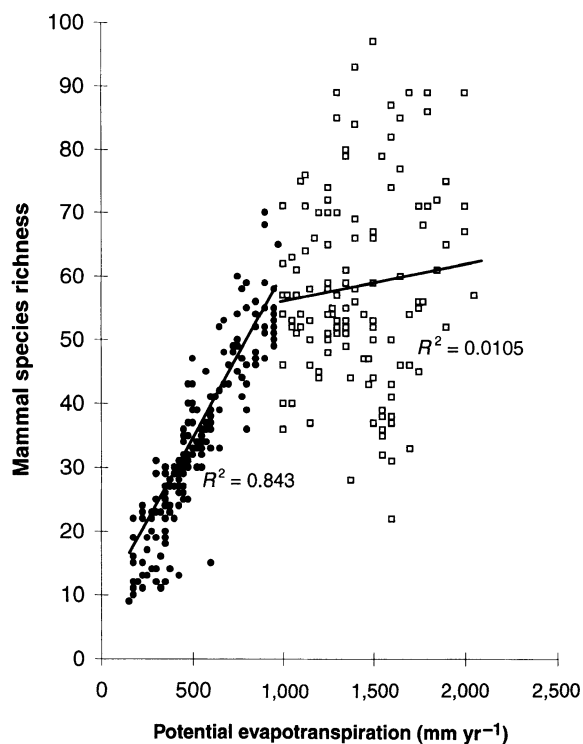
# Habitat heterogeneity as a determinant of mammal species richness in high-energy regions

Jeremy T. Kerr & Laurence Packer

Department of Biology, York University, 4700 Keele Street, North York, Ontario M3J 1P3, Canada

A fundamental problem in ecological research is to explain large-scale gradients in species richness<sup>1,2</sup>. Although many causative agents for this phenomenon have been suggested, the species richness-energy hypothesis has received the strongest empirical support<sup>3-6</sup>: this hypothesis states that higher energy availability provides a broader resource base, permitting more species to coexist. Here we show that the species richness-energy hypothesis applies to North American mammals only over a limited geographical area in which climatic energy levels are low (Alaska and most of Canada), rather than on a continental scale as had previously been accepted<sup>6</sup>. In relatively high-energy regions of North America, corresponding to most of the continental United States and southern Canada, we find that mammal species richness is best predicted by topographic heterogeneity and local variation in energy availability. Our results contradict previous studies of large-scale richness patterns that dismissed the importance of habitat heterogeneity<sup>2,7-9</sup>, and have implications for climate change research.

Climatic factors, environmental stability, land area, habitat heterogeneity, historical influences (such as Pleistocene glaciations) and energy availability are the factors most often discussed as determinants of regional variability in species richness<sup>8-13</sup>. Energy



**Figure 1** The relationship between PET and mammal species richness in North America. In areas where PET < 1,000 mm yr<sup>-1</sup>, PET explains 84% of the variance in mammal richness ( $F = 1.096, P \ll 0.0001$ ). South of this zone, however, PET is unrelated to mammal richness ( $F = 1.35, P = 0.248$ ).