

ACTIVE TRENDS, PASSIVE TRENDS, COPE'S RULE AND TEMPORAL SCALING: NEW CATEGORIZATION OF CLADOGENETIC CHANGES IN BODY SIZE

JERZY TRAMMER^a and ANDRZEJ KAIM^{b*}

^a*Instytut Geologii Podstawowej, Uniwersytet Warszawski, ul. Żwirki i Wigury 93, PL-02-089 Warszawa, Poland and* ^b*Instytut Paleobiologii, Polska Akademia Nauk, ul. Twarda 51/55, PL-00-818 Warszawa, Poland*

Regimes of cladogenetic change in body size recognized in the fossil record are related to the time scales over which they are observed. A new categorization of regimes of cladogenetic size change is proposed: this scheme includes seventeen types. In a random distribution, the pure, single-cause regimes are rare (0.01 probability of appearance) while mixed regimes, resulting from the simultaneous operation of two or more causes are frequent (0.115 probability of appearance). Some regimes seem to be nonrandomly distributed.

Keywords: Body size; Evolutionary size change; Cope's Rule; Evolutionary trends

This paper is dedicated to the founding fathers of paleobiology

INTRODUCTION

According to Jablonski (1996, 1997), there are four types, or regimes, of cladogenetic change in body size: an active, directional trend towards larger body sizes, or Cope's Rule in the strict sense; an active trend towards smaller sizes, or the opposite of Cope's Rule in the strict sense; a passive trend called "increase in variance" which involves an increase in the range of body sizes; and finally a "decrease in variance" trend that, theoretically, may or may not be driven, or active, as a product of selection against extremes (Gould 1988). We recognize a fifth type in addition to those of Jablonski (1996, 1997), that of no change, or stasis. These patterns are easily recognized by exploring the behavior of maximum and minimum body size in an evolving clade (Figure 1). There are also body size

* Corresponding author: e-mail: kaim@twarda.pan.pl.

trends where it is difficult to determine, without further tests (McShea 1994), whether they represent Cope's Rule in the strict sense or an increase in variance (Figure 1).

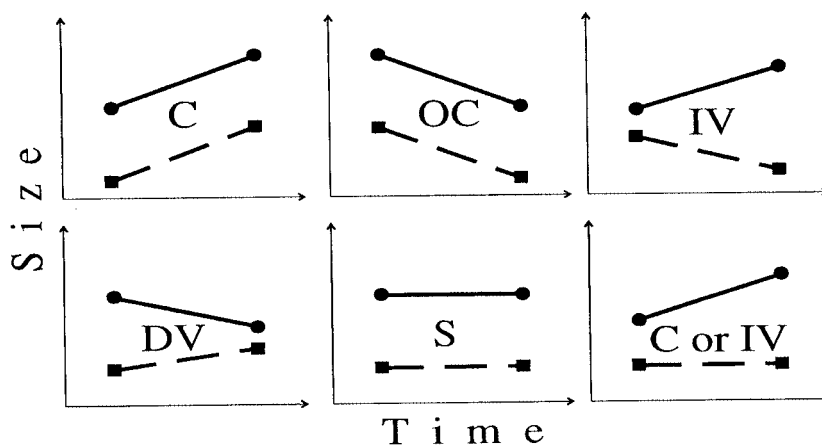


FIGURE 1 Regimes of cladogenetic change in body size characterized by the changes in the maximum (solid line) and minimum (dashed line) sizes of species in the evolving clade. Modified after Jablonski (1996, 1997) and McShea (1994). **C** Cope's Rule in the strict sense, **OC** opposite of Cope's Rule in the strict sense, **IV** increase in variance, **DV** decrease in variance, **C or IV** Cope's Rule or increase in variance, **S** no change or stasis

The aim of the present contribution is to show that the type, or regime, of body size change one recognizes depends largely on the length of the time interval examined. In a sense, this problem is a variant of the question of time averaging discussed by Gingerich (1983), who showed that rates of evolution are inversely proportional to the length of the time interval over which they are calculated.

Consider the well-known evolutionary trends among Neogene planktonic foraminiferans, set up by Gould (1988; see also Norris 1991; Arnold et al. 1995) as a typical example of the pattern of body size change that involves a passive increase in variance (Figure 2). If this data set is analyzed as a whole, over its entire 36 million year interval, considering only its end points, there is an increase in variance, as the maximum size increased and the smallest size decreased (compare with Figure 1). But, when the data set is divided into shorter, three million year intervals and each interval is considered separately, the long-term trend is seen to consist of a mixture of passive and active regimes of body size change (Figure 2).

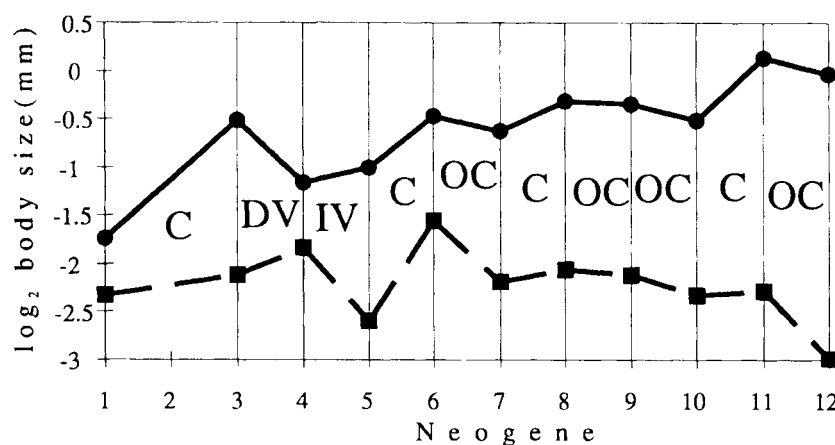


FIGURE 2 Evolution of size change in Neogene planktonic foraminifera. The long-term passive increase in variance of cladogenetic body size is shown to be the net outcome of a variety of active and passive regimes of change, when the data are analyzed over three-million-year intervals. Modified after Gould (1988, his Figure 5). For annotations referring to regimes of change in body size, see Figure 1

There were four periods with changes conforming to Cope's Rule in the strict sense. Together they comprised 45% of the duration of the trend. The other active pattern of change, opposing Cope's Rule, also occurred four times. This pattern extended over 36% of the time. Passive increase in variance appeared only once, as did the regime of decreasing variance. These two intervals spanned 19% of the duration of the trend. Paradoxically, the trend selected as a typical example of evolutionary change in body size brought about by a passive increase in variance is revealed to consist of active trends, with alternating directions of change, though 81% of its duration.

The ecological literature is full of examples of body size increases, decreases and reversals (e.g. Lister 1989; Petren and Case 1997) that lasted only a few thousands of years. In spite of these observations, paleontologists working in "deep time" (Gould 1987) have repeatedly been inclined to believe that long-term evolutionary tendencies have resulted from the same dominating factors, operating throughout their histories. In fact, these long-term trends may have been scale-related, representing a mixture of effects that were products of various secondary regimes of change (compare Hennigsmoen 1964; Stanley 1979; Hoffman 1989; McShea 1994; Jablonsky 1997).

NEW CATEGORIZATION OF CLADOGENETIC CHANGES IN BODY SIZE

Theoretical Analysis


















As shown above, Jablonski's (1996, 1997) scheme with its four types of change (Figure 1) is a very useful analytical tool. It is too general, however, to model and define all the basic situations that are involved in cladogenetic body size change. We therefore propose a more complete categorization of size changes. Our scheme includes seventeen types of change. For example, in place of the regime Jablonski called "Cope's Rule in the strict sense" we recognize three regimes: pure Cope's Rule, Cope's Rule with increasing variance, and Cope's Rule with decreasing variance. Following Gould (1988) and Jablonski (1997) we use the term "increase in variance" not necessarily in a formal statistical sense. Definitions of all our individual regimes are given in Table I and their names are shown in Table II. Examples of possible mechanisms by which each pattern might arise (albeit not all those that are theoretically conceivable) are presented in Table III.

TABLE I Definitions of proposed regimes of cladogenetic change in body size. Solid lines show changes in the maximum size of taxa in the evolving clade; dashed lines show changes in the minimum size. The slopes of these lines characterize the rate of change in maximum body size within the clade (r_{max}) and the rate of change in minimum body size (r_{min}). Letter notations used to refer to the regimes are defined in Table II

	maximum increasing $ r_{max} < r_{min} $	maximum increasing $ r_{max} > r_{min} $	maximum increasing $ r_{max} = r_{min} $	maximum constant	maximum decreasing $ r_{max} = r_{min} $	maximum decreasing $ r_{max} > r_{min} $	maximum decreasing $ r_{max} < r_{min} $
minimum increasing	C ₃	C ₂	C ₁	C/DV	DV ₁	DV ₂	DV ₃
minimum constant		C/IV		S		OC/DV	
minimum decreasing	IV ₃	IV ₂	IV ₁	OC/IV	OC ₁	OC ₂	OC ₃

We have also located our regimes on Jablonski's (1996, 1997) square, where each mode of cladogenetic change in body size may be plotted (Figure 3). Eight regimes occupy triangles within the square, eight lie on lines and one regime

TABLE II Names and letter notations of the proposed regimes of cladogenetic change in body size. Solid lines show changes in maximum size and dashed lines show changes in minimum size, within the clade, as in Table I

Letter notation	Name of regime
 C ₁	pure Cope's rule
 C ₂	Cope's rule with increase in variance
 C ₃	Cope's rule with decrease in variance
 OC ₁	pure opposite Cope's rule
 OC ₂	opposite Cope's rule with decrease in variance
 OC ₃	opposite Cope's rule with increase in variance
 IV ₁	pure (symmetrical) increase in variance
 IV ₂	increase in variance with increasing mean
 IV ₃	increase in variance with decreasing mean
 DV ₁	pure (symmetrical) decrease in variance
 DV ₂	decrease in variance with decreasing mean
 DV ₃	decrease in variance with increasing mean
 C/IV	transitional regime between increase in variance and Cope's rule
 C/DV	transitional regime between Cope's rule and decrease in variance
 OC/DV	transitional regime between decrease in variance and opposite Cope's rule
 OC/IV	transitional regime between opposite Cope's rule and increase in variance
 S	stasis

(stasis) occupies a single point at the centre. These regimes thus consist of mathematical sets that are not equally numerous. Stasis is represented by a set with only one element. Those regimes that are located on lines include more elements (possible patterns of size change). Finally, the regimes that occupy triangles embrace the most possibilities of change.

TABLE III Potential evolutionary mechanisms able to produce the regimes of cladogenetic change in body size. The direction of the trend in the mean for each regime is shown in the last column. "Diffusion" here means cladogenetic diffusion in the sense of McKinney (1990) and McShea (1994). For letter annotations referring to the regimes, consult Table II

MECHANISM		TYPE OF REGIME		Direction of trend in the mean
1. PURE				
Directional force	up	C_1		up
	down	OC_1		down
Diffusion		IV_1		no trend
Selection against extremes		DV_1		no trend
2. MIXED				
Resulting from directional force (up) and diffusion	force stronger than diffusion	C_2		up
	diffusion stronger than force	IV_2		up
Resulting from directional force (down) and diffusion	force stronger than diffusion	OC_3		down
	diffusion stronger than force	IV_3		down
Resulting from directional force (up) and selection against extremes	force stronger than selection	C_3		up
	selection stronger than force	DV_3		up
Resulting from directional force (down) and selection against extremes	force stronger than selection	OC_2		down
	selection stronger than force	DV_2		down
3. WITH BOUNDS				
Diffusion with lower bound or directional force (up) with lower bound		C/IV		up
Diffusion with upper bound or directional force (down) with upper bound		OC/IV		down
Directional force (down) with lower bound or selection against extremes with lower bound		OC/DV		down
Directional force (up) with upper bound or selection against extremes with upper bound		C/DV		up
4. NO FORCE OR TWO BOUNDS				
No force or two (lower and upper) bounds		S		no trend

In general, the number of elements included in an individual regime is proportional to the area occupied by that regime within Jablonski's square. Each of the eight triangles occupies 12.5% of the area of the square. Lines have no area;

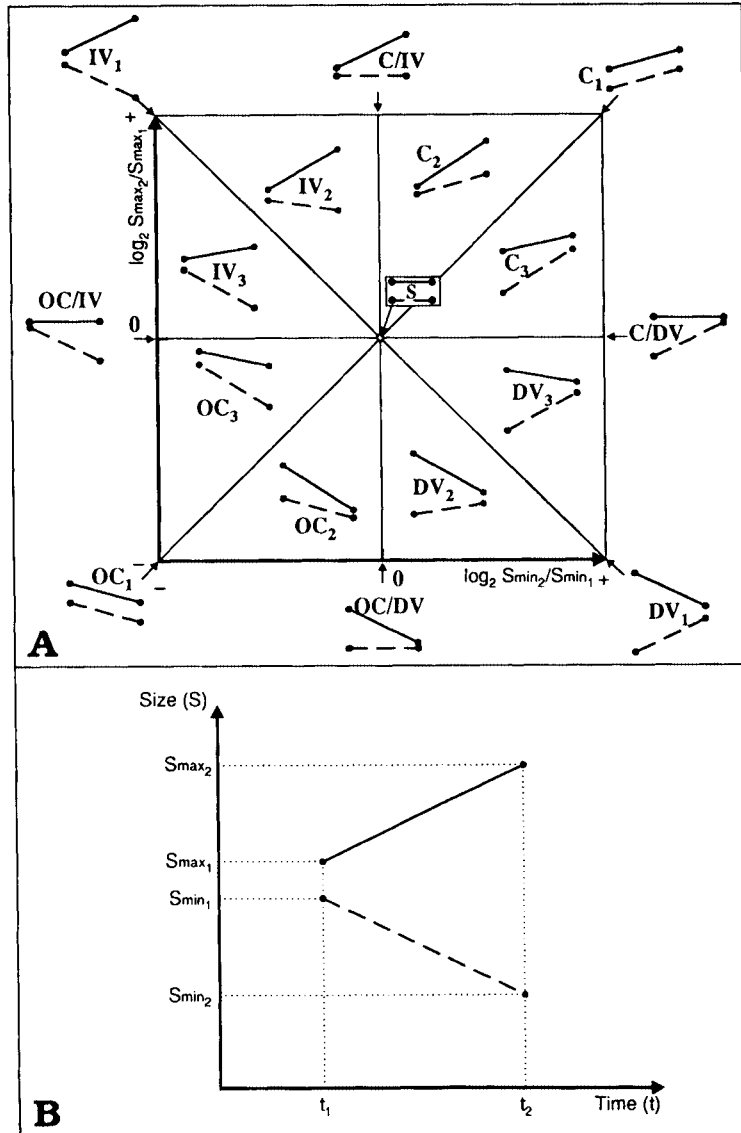


FIGURE 3 A. Distribution of the proposed regimes of cladogenetic change in body size within Jablonski's (1996, 1997) square. Given a random distribution, the frequency of occurrence of each regime should be proportional to the area it occupies within the square. B. Coordinates used to plot points on the square. S_{max1} maximum body size in a given clade at time t_1 ; S_{max2} maximum body size in a given clade at time t_2 ; S_{min1} minimum body size in a given clade at time t_1 ; S_{min2} minimum body size in a given clade at time t_2 . For annotations referring to regimes of change in body size, see Table II

operationally we treat them as very elongated rectangles, each representing 1% of the square. The choice of 1% is arbitrary but pragmatic: it includes cases that would not normally be statistically differentiable from those lying on the line. The transformation of lines into rectangles reduces the areas of the triangles. Thus we have eight triangles, each constituting 11.5% of the area of the square, and eight rectangles, each representing 1% of its surface. As the number of elements (possibilities of size change) in each regime is proportional to the area occupied in the diagram, we have eight regimes that each include 11.5% of the possibilities of change and eight others that each include 1% of the possibilities. If causes (forces, constraints, diffusion, etc.) operate at random, generating patterns of evolutionary size change, the probability of occurrence of the 11.5% regimes should be 0.115 and that of the 1% regimes should amount to 0.01 (Table IV).

TABLE IV Probabilities of occurrence of regimes of change in body size, assuming forces and/or constraints that produce them operate at random. A detailed explanation of the rationale for this model is provided in the text

<i>Types of regime</i>	<i>Probability</i>
$C_3, C_2, IV_2, IV_3, OC_3, OC_2, DV_2, DV_3$	0.115
$C_1, IV/C, IV_1, IV/OC, OC_1, OC/DV, DV_1, C/DV$	0.01
S	close upon 0

This theoretical analysis leads to interesting conclusions. The “linear” ($p = 0.01$) regimes (Figure 3) are “pure” in the sense that they result from the action of one main cause (directional force, diffusion, etc.), generating patterns such as pure Cope's Rule and pure (symmetrical) increase in variance (see Tables II and III). On the other hand, the “triangular” ($p = 0.115$) regimes (Figure 3) are “mixed” regimes. They result from two causes acting together (directional force plus diffusion, for example), yielding patterns such as Cope's Rule with increasing variance, or increasing variance with increasing mean size (see Tables II and III). This analysis implies that, if patterns of evolutionary size change are randomly distributed, every “pure” regime should be rare in nature (0.01 probability of occurrence), while “mixed” regimes should be relatively common (each with 0.115 probability of occurrence). Finally, stasis (operationally defined as no change in size within the range of measurement errors) should be extremely rare, with a probability of occurrence near zero.

Empirical Investigations

We undertook an empirical study to elucidate two problems. First, we wished to determine the actual frequencies of the regimes in nature, to determine whether or not they are randomly distributed. Secondly, we wanted to determine whether or not the frequency distributions of the regimes differ from one another on various time scales. In other words, are some regimes preferred on certain time scales, or not?

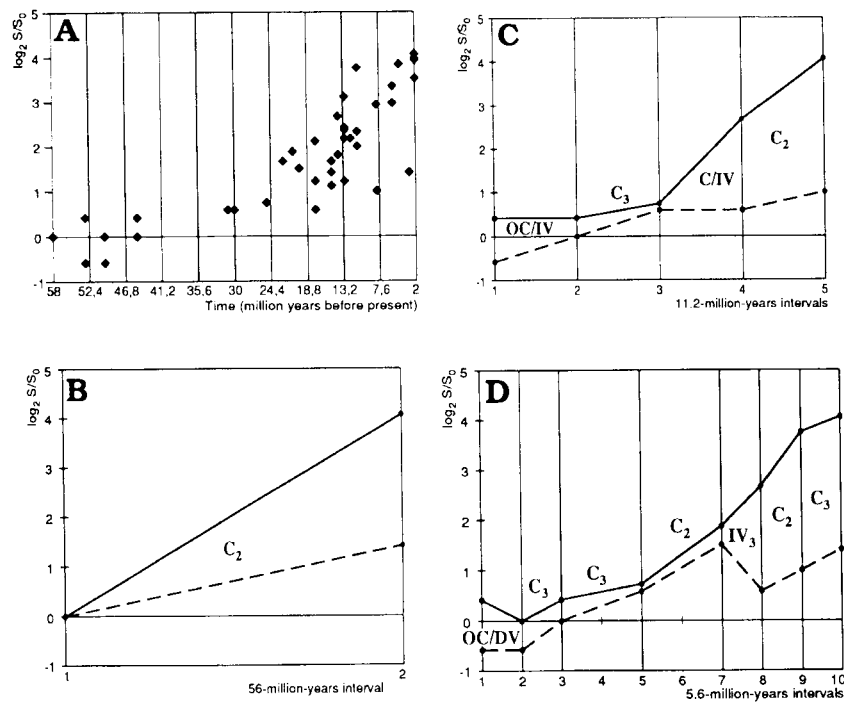


FIGURE 4 Regimes of cladogenetic change in body size observed in the equid clade at various time scales. A. Sizes at first appearance of equid species (from MacFadden 1986) plotted against geologic time. B. The long-term regime of size change for the whole 56 million year interval. C. Shorter-term regimes of change for five 11.2-million-year intervals. D. The shortest-term regimes recognized here, comprising ten 5.6 million year intervals. S_0 size (body mass) of the earliest species in the clade. S size (body-mass) of all other species in the clade. For annotations referring to regimes of change in body size, see Table II

We gathered our data in the following way, exemplified here by an analysis of the 56 million year span of body size evolution in horses (Figure 4). We plotted (in this case after MacFadden 1986) the sizes at first appearance of species that comprise the clade against the geologic time scale (Figure 4a). The sizes of species in all the groups we studied were measured as body mass or the cube of body length. Then, we determined the regime of long-term size change, taking only

body sizes at the beginning and at the end of the clade's history into consideration (Figure 4b and Table V). Next, we examined the data set in relation to five shorter intervals, each in this case 11.2 million years long, and diagnosed the regime of change in body size separately for each interval (Figure 4c and Table V). Finally, we further divided the data set into ten 5.6-million year intervals, here called the shortest-term intervals, and determined the regimes of change in body size at this temporal scale (Figure 4d and Table V).

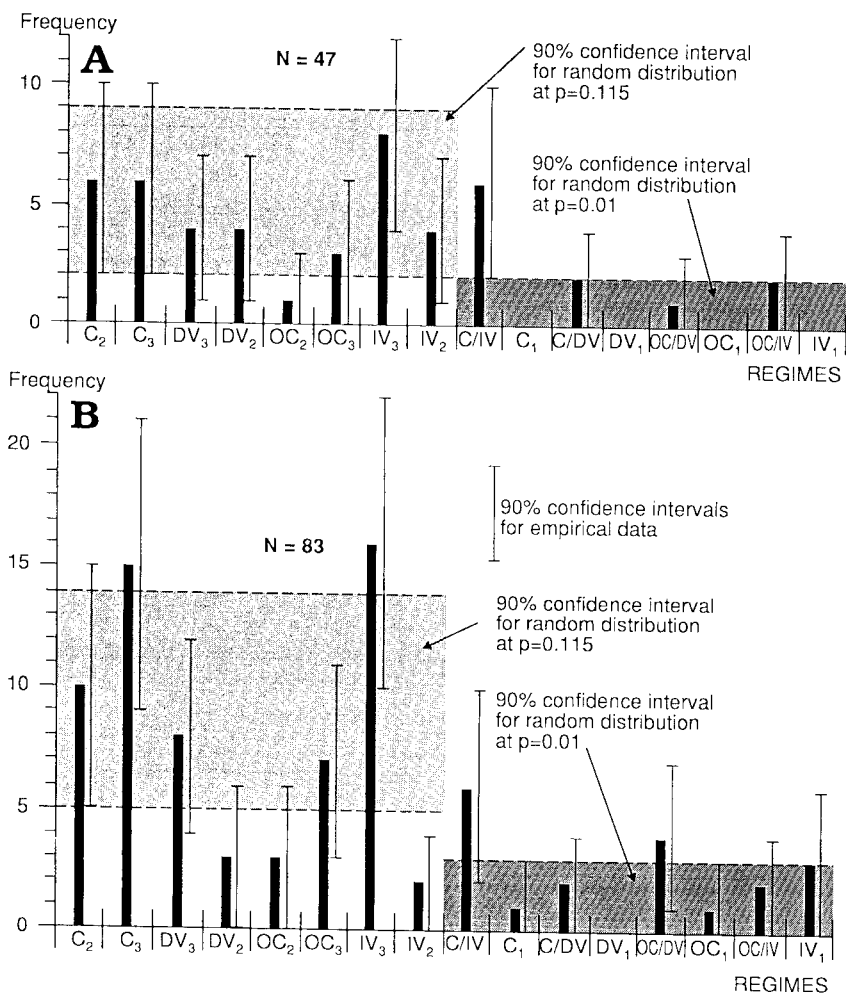


FIGURE 5 Frequency distributions of regimes of cladogenetic change in body size observed on different time scales in eight groups of organisms (see Table V). A. Frequencies of shorter-term regimes. B. Frequencies of shortest-term regimes. C_3 , DV_2 , OC_2 , IV_3 , IV_2 , C/IV , and OC/DV regimes seem to be non randomly distributed. For annotations referring to regimes of change in body size, see Table II

TABLE V Patterns of cladogenetic change in body size exhibited on different time scales in the evolution of eight groups of organisms. For the mode of analysis, see Figure 4. For letter annotations referring to the regimes, consult Table II. Sources of data are listed in the last column

Systematic group	Type of long-term regime	Duration of long-term regime (My)	Types of shorter-term regimes of that long-term regime is composed (in order of appearance)	Types of shortest-term regimes of that long-term regime is composed (in order of appearance)	Source of data
Pelycosaurs	IV ₂	23	IV ₃ , C ₃ , OC/IV, IV ₃ 4,6-million-years-intervals	OC ₃ , OC ₃ , C ₂ , IV ₃ , OC/IV, IV ₃ , C ₃ 2,3-million-years-intervals	McKinney 1990
Equids	C ₂	56	OC/IV, C ₃ , C/IV, C ₂ 11,2-million-years-intervals	OC/DV, C ₃ , C ₃ , C ₂ , IV ₃ , C ₂ , C ₃ 5,6-million-years-intervals	MacFadden 1986
Hesperocyonines	C ₂	19,5	C ₂ , DV ₂ , C ₃ 4,9-million-years-intervals	IV ₁ , C ₃ , C ₂ , DV ₂ , C ₃ 2,45-million-years-intervals	Wang 1994
Cetaceans	IV ₂	55	C/DV, IV ₃ , C/IV, IV ₂ 11-million-years-intervals	C ₁ OC/IV, C/IV, IV ₃ , C ₂ , DV ₃ , IV ₃ 5,5-million-years-intervals	McKinney 1990
Proboscideans	IV/C	35	C ₂ , C/IV, C/IV, IV ₂ , 5-million-years-intervals	C ₂ , C/IV, DV ₃ , C/IV, IV ₃ , C ₃ , IV ₃ , C ₃ , IV ₃ , C ₃ OC ₃ 1,25-million-years-intervals	McKinney 1990
Cretaceous planktonic foraminiferans	IV/C	61,5	C/IV, C/DV, IV ₃ , DV ₃ , C/IV, IV ₃ , DV ₂ , IV ₂ 5,6-million-years-intervals	C/IV, C ₂ , C/DV, DV ₃ , IV ₃ , IV ₃ , DV ₃ , OC ₃ , C/IV, OC/DV, IV ₃ , DV ₂ , IV ₂ , DV ₃ 2,8-million-years-intervals	Gould 1988
Paleogene planktonic foraminiferans	C ₃	29,5	C ₃ , DV ₃ , OC ₃ , DV ₂ , IV ₂ C ₃ , OC ₂ , C ₂ , DV ₃ , OC ₃ 2,7-million-years-intervals,	C ₃ , C ₂ , OC ₂ , C ₃ , OC ₂ , IV ₂ , C ₃ , OC ₃ , DV ₃ , IV ₃ , C ₃ , IV ₁ , OC ₂ , IV ₃ , C ₂ DV ₃ , C ₂ , OC ₁ , IV ₃ 1,35-million-years-intervals	Gould 1988
Neogene planktonic foraminiferans	IV ₃	35	C ₂ , DV ₂ , IV ₃ , C ₃ , IV ₃ , C ₂ , OC/DV, DV ₃ , IV ₃ , OC ₃ 3-million-years-intervals	C ₂ , DV ₂ , IV ₃ , C ₃ , IV ₃ , C/DV, OC ₃ , C/IV, OC/DV, OC/DV, C ₃ , IV ₃ , DV ₃ , IV ₁ , OC ₃ 1,5-million-years-intervals	Gould 1988
			Σ=47	Σ=83	

We applied this procedure to the evolutionary histories of change in body size in eight groups of organisms, obtaining 47 records of shorter-term regimes of change and 83 records of the shortest-term regimes of change. Full details of these data sets and their sources are given in Table V. The data set for the shortest intervals is not twice as large as that for the next longer intervals because the observations were occasionally not distributed closely enough to occur in every shortest-term interval.

Summarizing these results, we plotted two frequency distributions: one for the shorter-term regimes (Figure 5a) and the other for the shortest-term regimes (Figure 5b). We have also shown two 90% confidence intervals for random distributions of frequencies on each plot: one for the 0.115 probability regimes and one for the 0.01 probability regimes.

CONCLUSIONS

The results of our analysis, displayed in Figure 5, suggest the following conclusions:

1. Almost all the theoretically imaginable regimes, with the exception of stasis and a symmetrical decrease in variance, were observed in our empirical data set. Consequently, they are shown to exist in nature.
2. The prediction that in a random distribution there should be two groups of regimes with different frequencies, rare 0.01 probability regimes and much more common 0.115 probability regimes, is supported by our data. Strictly speaking, it cannot be rejected (Figure 5).
3. The frequency distributions of regimes at shorter and longer time scales do not differ fundamentally (compare Figure 5a with Figure 5b). More types of regimes are represented in the shortest-term data set but this is not surprising, as this constitutes a larger sample.
4. Some regimes are most probably not distributed at random. The C_3 , IV_3 , C/IV and OC/DV regimes seem to occur too frequently, while DV_2 , OC_2 and IV_2 regimes occur too rarely to be random (see especially Figure 5b). The high frequencies of C/IV and OC/DV regimes, both of which involve the influence of a lower bound (see Table III), suggests that lower bounds are frequent constraints on size in nature.
5. What kinds of evolutionary trends are more frequent, active, directional trends or diffusive, passive ones? This issue has been discussed by Gould (1988) and Jablonski (1996, 1997), among others. Our results provide the following answer: mixed trends, both active and passive, are most common.

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