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Power formula for Cope's rule

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ABSTRACT

Relative maximum body size (the ratio of maximum body size to the size of first species) in a radiating clade is a power function of diversity, so that relative maximum size increases approximatively with the square root of diversity. Thus, relative maximum body size increases at a decreasing rate with diversity. This relates to the whole spectrum of organisms of different complexity and ecology, from foraminiferans to vertebrates.

Keywords: allometry, body size, Cope's rule, evolutionary size change.

INTRODUCTION

The aim of this study was to analyse quantitatively Cope's rule, which is understood here only to be an increase in maximum body size during the evolutionary radiation of a clade. The mechanism behind Cope's rule is not at issue here.

The position of such a neutral approach is thus outside the current discussion on Cope's rule. Regardless of whether Cope's rule represents active directional trends towards larger sizes (Maurer *et al.*, 1992; Maurer, 1998; Alroy, 1998), passive diffusions (Stanley, 1973; Gould, 1988, 1997; Jablonski, 1997) or both (Trammer and Kaim, 1999), maximum size generally increased during radiations (McKinney, 1990; McShea, 1994; Trammer and Kaim, 1997).

METHODS

I examined the relationship between the rate of increase of clade diversity, or the number of species, and the rate of increase of its maximum size. The diversity and size data used were from such various fossil groups as planktonic foraminiferans, through rhynchonellid brachiopods and ammonites to pelycosaurs and Cenozoic mammals (Table 1). To make the comparison of the fossils of such different sizes possible, I denote the earliest known and contemporaneous values of maximum body length and diversity for a given goup as S_0 and N_0, respectively, and I present all the younger values of maximum size (S) and diversity (N) as ratios of S and S_0 (S/S_0) and N and N_0 (N/N_0). These ratios may be termed 'relative maximum size' (= S/S_0) and 'relative diversity' (= N/N_0).

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Table 1. Raw data used in the regression analysis

Group	Age (MY BP)	Diversity (N)	Relative diversity (N/N_0)	Maximum size (S)	Relative size (S/S_0)	Source of data
				Test diameter (mm)		
Cretaceous	118	2 (= N_0)	1	0.225 (= S_0)	1	Norris (1991)
foraminifera	108	15	7.5	0.69	3.07	
	94	23	11.5	0.80	3.55	
	88	38	19	0.88	3.90	
	80	50	25	0.90	4	
Paleogene	64	6 (= N_0)	1	0.24 (= S_0)	1	Norris (1991)
foraminifera	57	22	3.67	0.72	3	
	43	45	7.5	1.09	4.54	
	38	39	6.5	1.04	4.33	
Neogene	32	25 (= N_0)	1	0.34 (= S_0)	1	Norris (1991)
foraminifera	20	59	2.36	0.71	2.09	
	12	64	2.56	0.89	2.62	
	3	68	2.72	1.05	3.09	
				Shell length (mm)		
Rhynchonellida	480–450	70 (= N_0)	1	26 (= S_0)	1	Stanley (1973)
	440–410	85	1.21	52	2	
	410–363	101	1.44	74	2.85	
				Shell diameter (cm)		
Ammonites	210–206	30 (= N_0)	1	20 (= S_0)	1	Stanley (1973)
	206–202	42	1.4	26	1.3	
	173–166	84	2.8	44	2.2	
	160–155	160	5.3	62	3.1	
				$(Body\ weight)^{1/3}$ (kg)		
Pelycosaurs	291	2 (= N_0)	1	2.46 (= S_0)	1	McKinney (1990)
	288	4	2	4.48	1.82	
	277	13	6.5	4.93	2	
	272	16	8	6.69	2.72	
				Molar length (mm)		
Rodents	55–40	47 (= N_0)	1	6.5 (= S_0)	1	Stanley (1973)
	25–5	58	1.23	9.5	1.46	
	5–1.7	85	1.81	14	2.15	
				Lower tooth length (mm)		
Hesperocyoninaes	38	1 (= N_0)	1	4.5 (= S_0)	1	Wang (1994)
	34	3	3	7.2	1.6	
	29	7	7	14	3.11	
				$(Body\ mass)^{1/3}$ (kg)		
All Cenozoic	65	6 (= N_0)	1	1.54 (= S_0)	1	Alroy (1998)
mammals	64	33	5.5	4.78	3.1	
	60	55	9.16	6.45	4.18	
	55	74	12.3	8.14	5.28	
	45	53	8.8	12.56	8.15	
	35	67	11.16	17.53	11.14	

Note: The underlined data were excluded from the regression. N_0 = the earliest known diversity for a given group, S_0 = the earliest known maximum size (body length) for a given group.

From the published literature, I found 36 such pairs of relative diversity and relative size values (Table 1), but only 34 were used in the regression analysis because the remaining pair was rejected as exceptional (see 'Results'). To estimate the parameters of the relationship between relative size and relative diversity, I used linear regression with transformation of the data to their logarithmic equivalents and re-transformation back to anti-logarithms (Fig. 1).

The data used (Table 1) are not of equal quality. Data for foraminiferans, pelycosaurs, hesperocyoninaes and mammals (26 pairs in total) represent instants in time, but the data for the remaining groups – rhynchonellids, ammonites and rodents (10 pairs) – represent intervals of time. For each systematic group, the intervals are usually of similar length, but a few are not. This may induce errors, which, if present, with others will represent residual errors.

RESULTS

Using regression analysis, I obtained a power formula that shows that relative maximum body size increases with relative diversity:

$$S/S_0 = 1.23(N/N_0)^{0.488} \quad (1)$$

The coefficient of correlation (r) equals 0.877 and is significant at $P < 0.001$; the 95% confidence interval of the slope = 0.488 ± 0.097 and that of the intercept = 1.23 ± 0.06. The relationship is plotted in Fig. 1.

Two pairs of relative diversity and size data (open circles in Fig. 1; underlined in Table 1) were excluded from the regression as more or less atypical and as lying beyond the subset of more evenly distributed points. These data points represent the Eocene part of the mammalian radiation. The values for size are disproportionally high compared to diversity here. This may reflect a taphonomic loss of species, sampling bias (as large fossils are easier

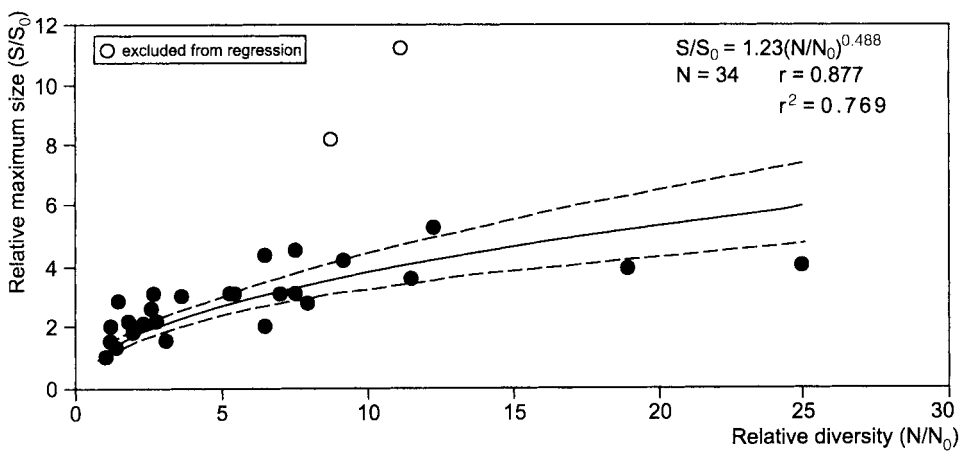

Fig. 1. Relative maximum body size of radiating clades as a function of relative diversity. Dashed lines enclose 95% confidence interval around the regression line. At point $N/N_0 = 1$, $S/S_0 = 1$, eight points overlap. For raw data, consult Table 1.

to find than small ones) or exceptionally high rates of increase in maximum body size due to the origin and the early evolution of cetaceans.

The regression line calculated with all available data included observations eliminated in the earlier calculation (1) – equals $S/S_0 = 1.21(N/N_0)^{0.549}$ – and its parameters do not differ significantly from the parameters of the first regression line (1) based on a Student's *t*-test. I prefer the first regression line (1), however, because its slope (= 0.488) is more consistent with the slope (= 0.498) of the regression line obtained during the test (see below).

TEST FOR THE FORMULA

I propose the following independent test to verify whether the formula in equation (1) displays predictive power. The test applies to systematic groups (Table 2) that are still in the midst of their adaptative radiation (representatives of the Modern Evolutionary Fauna of Sepkoski, 1981).

Knowing the length of the first fossil species of a given taxon (S_0), and knowing the number of species in the taxon today (N), I calculated (Table 2) its expected extant maximum size (S) using equation (1). I also calculated 95% confidence limits (in this case, a kind of 'prediction limits') for each expected maximum size (Fig. 2). I later compared the expected maximum size with the actual one. As most actual size values occur within the confidence limits of the expected size values for the studied taxa (Fig. 2), the formula appears to work well. Some points representing the actual maximum size values, however, lie outside the confidence limits of the predicted sizes (Fig. 2). This pertains to marine mammals that are too big and to echinoids and bony fishes that are too small. Perhaps natural selection accelerated the increase in size of marine mammals, but held it back in the case of echinoids and fishes.

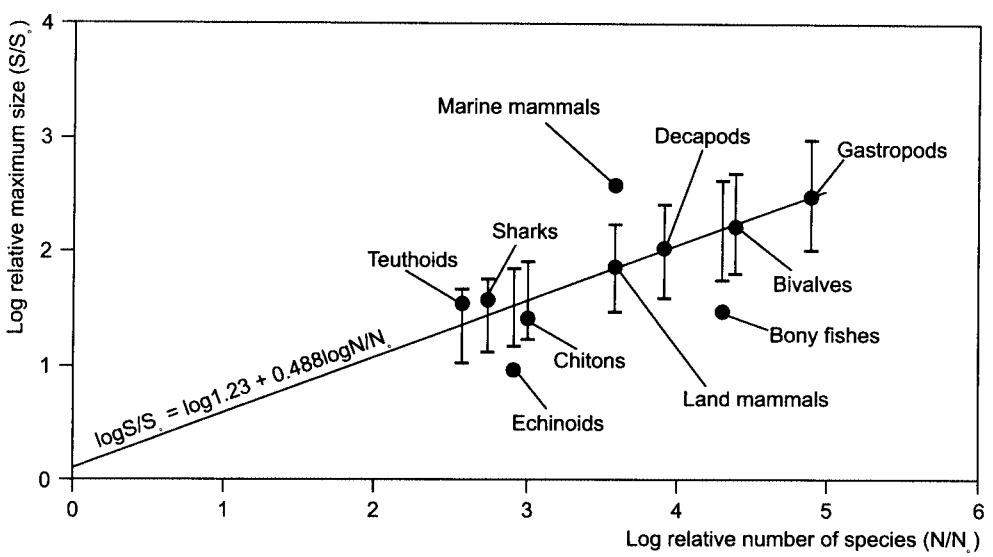

Fig. 2. Test for equation (1). Actual values of relative maximum body size (S/S_0) of some living taxa (solid dots) fit well in the main with the regression line $(S/S_0) = 1.23(N/N_0)^{0.488}$ deduced from the fossil record. Vertical lines show 95% confidence limits of predicted (today's) values of size.

Table 2. Test for equation (1)

	Body length of first species (S_0) [cm]	Initial number of species (N_0) assuming monophyly	Number of living species (N)	Maximum body length today (S) [cm]	
				Expected	Actual
Bivalvia	1	1	25 000	$S = 1.23N^{0.488}$ 172	*Tridacna gigas* 170
Gastropoda	1	1	80 000	$S = 1.23N^{0.488}$ 304	*Syrinx aruanus* coiled 80, after uncoiling 305
Polyplacophora	1	1	1 000	$S = 1.23N^{0.488}$ 36	*Amicula stelleri* 26
Teuthoidea	45	1	375	$S = 45(1.23N^{0.488})$ 998	*Architeuthis princeps* 1600
Decapoda (Arthropoda)	3.5	1	8 500	$S = 3.5(1.23N^{0.488})$ 356	*Macrocheira kaemperi* 380
Echinoidea	3.25	1	850	$S = 3.25(1.23N^{0.488})$ 107	*Paracentrotus* sp. 30
Chondrichtyes	45	1	550	$S = 45(1.23N^{0.488})$ 1203	Whale shark 1700
Osteichtyes	20	1	20 000	$S = 20(1.23N^{0.488})$ 3089	*Acipenser transmontanus* 600
Mammalia	8	1	4 000	$S = 8(1.23N^{0.488})$ 563	Land mammals: African elephant 600 Marine mammals: blue whale 3000

Note: Expected (calculated) and actual (today's) maximum sizes of some living invertebrate and vertebrate groups. As the biggest extant gastropod *Syrinx aruanus* is spirally coiled but the first Cambrian snail was not, I show not only the length of coiled *S. aruanus* but its length after uncoiling and laying end-to-end as well. Animal lengths after Abbott (1968), Abbott and Dance (1990), Benton (1997), Cox *et al.* (1969), Durham *et al.* (1966), Glaessner (1969), Knight *et al.* (1960) and Naef (1922).

The regression line resulting from the regression analysis of the actual data from Table 2 equals $S/S_0 = 1.03(N/N_0)^{0.498}$, a very similar result to the earlier regression (1) deduced from the fossil record (Table 1). According to a Student's t-test, there is no significant difference between the slopes of the two regression lines.

DISCUSSION

The formula in (1) is a kind of allometric equation that is so common in ecology, which relates biological forms and processes to body size (see Peters, 1983). Such a pattern suggests a universal link between allometry and the evolution of body size (for other such links, see Demetrius, 2000). Although the data set is not very large, conclusions can be drawn regarding the general importance of the evolution of body size.

The relation found may be universal, as it concerns a whole spectrum of organisms of strikingly different morphological complexity and ecology: from unicellular, marine, planktonic foraminiferans to the land vertebrates. The pattern appears to be universal irrespective of the kinds of mechanisms that have driven the size increase. The mechanisms varied from diffusion in the case of pelycosaurs and Neogene foraminiferans to directional forces operating on Paleogene foraminiferans and mammals (Alroy, 1998; Trammer and Kaim, 1999).

Relative diversity and relative maximum size are shown to increase at different rates: relative diversity grows more quickly than relative maximum size (body length). At the beginning of a radiation, when diversity is low, maximum body size increases more in relation to diversity than later in the radiation when diversity is higher (Fig. 1). In other words, diversity-specific rate of growth of maximum size declines as maximum size increases – bigger maximum increases less than the smaller one – according to the re-formed (both sides divided by N/N_0) version of the equation presented earlier:

$$(S/S_0)/(N/N_0) = 1.23(N/N_0)^{-0.512} \quad (2)$$

It is perhaps the case that not only do such physiological and ecological parameters as specific metabolic rate, mortality rate and population density decline with body size, but that the rate of evolutionary size increase declines with size as well. Moreover, Alroy (1998) found that, among mammals, the rate of evolutionary size increase is less at large sizes than in the middle of the size range, and Trammer and Kaim (1999) noted that the rate of evolutionary increase of the minimum size in a clade is usually greater than the rate of increase of the maximum.

The allometric relation introduced here may also help to explain the widely held view that, for many clades, the rate of morphological evolution is highest when the clade is young but drops markedly with time (see Stanley, 1979).

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