Two Phases in the Evolution of the Body Size of Dinosaurs

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Abstract
During the Late Triassic – Jurassic phase of the evolution of dinosaurs, their mean and maximum body size increased concurrently with increasing species diversity. On the contrary, in the Cretaceous, although the number of dinosaur species increased, the body size ultimately decreased. This might have been connected with the increase of the number of land masses and the decrease of their areas in the Late Cretaceous caused by global tectonics.

Keywords: Dinosauria, Species diversity, Body size, Evolution, Global tectonics

1. Introduction
The aim of the present contribution was to recognize how the evolutionary changes of body size of dinosaurs were related to the changes of their species diversity. As yet this question was not investigated respecting the Dinosauria.

2. Material and Methods
Dinosaurs appeared in the Late Triassic Carnian Age and disappeared 164.5 million years later at the end of the Cretaceous in the Maastrichtian. I have divided this time span into 14 intervals (Table 1) of similar length. Using data from the most complete compendium of the dinosaur body masses (Paul, 2010), I computed the number of the found dinosaur species, as well as the mean and maximum body mass of those species for each interval. I have taken into consideration all the species from Paul (2010) with a known age of occurrence and estimated mass.

Different methods resulting in disparate estimates are employed to obtain body masses of dinosaur species. There is advantageous, therefore, that all the mass estimates of Paul (2010) are based on the same method: on the measure of a dinosaur volume – then converted into body mass (for the explanation of the method see Paul 1997).

There is no correlation between the number of species and the duration of an interval (r =-0.033; p (uncorrelated) = 0.91). Results of the calculations (Table 1) are plotted in the form of time series (Figure 1).

3. Results
Two distinct phases (Figure 1) may be distinguished during the evolutionary history of dinosaurs: the first – from their appearance in the Triassic till the end of the Jurassic Period (intervals 1 to 7), and the second one – in the Cretaceous (intervals 8 to 14).

In the first phase, both the time series of the species number and those for the mean and maximum body mass contain statistically significant upward trends (regression coefficients r of the series values against their observation times amount 0.834, p = 0.019; 0.855, p = 0.014 and 0.785, p = 0.036, respectively). Throughout this phase the mean and maximum body mass are strongly correlated with the species diversity (for first differences r = 0.97, p = 0.0002 and r = 0.967, p = 0.00035, respectively). This suggests that increase in body mass was driven by increasing species diversity.

During the second (Cretaceous) phase, after the extinction in the latest Jurassic, the number of species increased again showing an upward trend (r = 0.827, p = 0.021). The species increase was even almost twice as fast as in the first phase (Figure 1). However, the mean and the maximum body mass provide no statistically significant trends (r = 0.176, p= 0.705 and r = 0.68, p = 0.09, respectively), and there is no significant correlation between the mean and the maximum body mass and the specific diversity (first differences r = - 0.72, p = 0.104 and r = -
0.409, \( p = 0.419 \), respectively). Contrary to the first phase, in the second phase the dinosaurs were not consistently larger with increasing diversity.

4. Discussion

It is likely that the pattern presented in Figure 1 is at least partly caused by global tectonics. There were four continents in the Late Jurassic but already nine in the Late Cretaceous and the mean area of a continent decreased almost three times at that time in comparison with the Late Jurassic continents (Smith et al., 1994; Figure 1). This might have increased the species number of dinosaurs by increasing their provinciality (Kurten, 1969; Schopf, 1979; Dodson, 1990; Rosenzweig, 1995; Hedges et al., 1996) but simultaneously decreased their maximum and mean body mass, as the body size of big animals decreases with decreasing land area (Burness et al., 2001).

Many authors argued that in a radiating clade there is a strong correlative relation between the maximum body size and species diversity (Stanley, 1973; Gould, 1988; McShea, 1994; Trammer & Kaim, 1997; Trammer, 2002, 2005; Gillman, 2007; McClain & Boyer, 2009) such that the continuing increase in size parallels diversification. Other researches (Smith et al. 2010) did not provide support for such strong correlation. The example of dinosaurs presented herein suggests that under conditions of unconstrained diversification, the maximum body size changes with time in concert with the diversity but the size of a land area may ultimately constrain the increase of body size weakening the correlation between size and diversity.

As it is widely acknowledged, differentiated sampling intensity of various parts of the geological column may bias the results of quantitative studies based on the fossil record (e.g. Smith, 2007). The number of formations may be used as an estimate of sampling intensity related to rock availability, paleontologist interest etc. (Peters & Foote, 2001; Wang & Dodson, 2006). The number of terrestrial formations in each of the Early, Middle and Late Jurassic epochs is significantly smaller than in the Late Triassic Epoch (Peters & Foote 2001, Wang & Dodson 2006), therefore the Late Triassic – Late Jurassic increase in the species number (Figure 1) is likely to be genuine and not an artifact of sampling intensity. The number of terrestrial formations in the Late Cretaceous is greater than in the Early Cretaceous (Peters & Foote 2001, Wang & Dodson 2006), so the Cretaceous increase in the species number (Figure 1) may be spurious but the study of Wang & Dodson (2006) showed that this increase was rather genuine. The maximum size, sampled from the statistical population of differently sized objects, increases with sample size. On the contrary, the maximum size of dinosaurs decreased with the increasing number of formations and the increasing number of species in the Late Cretaceous, which suggests that this decrease may be reliable.

References


### Table 1. Species-level diversity and body size of dinosaurs in fourteen intervals of their evolutionary history.
Computed using data from Paul (2010)

<table>
<thead>
<tr>
<th>Number of interval</th>
<th>Included stages</th>
<th>Duration of interval [Ma]</th>
<th>Number of species</th>
<th>Body mass [kg]</th>
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<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>mean</td>
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<td>14</td>
<td>Maastrichtian</td>
<td>5.5</td>
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<td>Albian</td>
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<td>10</td>
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<tr>
<td>1</td>
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</table>
Figure 1. Species-level diversity and body size of dinosaurs over their history. Distribution of land masses on Earth in the Late Jurassic and in the Late Cretaceous after Smith et al. (1994) is also presented. For duration and geological age of the intervals consult Table 1. Further explanations and discussion in the text.