Allometry of visceral organs in living amniotes and its implications for sauropod dinosaurs

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Abstract

Allometric equations are often used to extrapolate traits in animals for which only body mass estimates are known, such as dinosaurs. One important decision can be whether these equations should be based on mammal, bird, or reptile data. To address whether this choice will have a relevant influence on reconstructions, we compared allometric equations for birds and mammals from the literature to those for reptiles derived from both literature and hitherto unpublished data. Organs studied included the heart, kidneys, liver, and gut, as well as gut contents. While the available data indicates that gut content mass does not differ between the clades, the organ masses for reptiles are generally lower than those of mammals and birds. In particular, gut tissue mass is significantly lower in reptiles. When applying the results in the reconstruction of a sauropod dinosaur, the estimated volume of the coelomic cavity greatly exceeds the estimated volume of the combined organ masses, irrespective of the allometric equation used. Therefore, substantial deviation of sauropod organ allometry from that of the extant vertebrates can be allowed conceptually. Extrapolations of retention times from estimated gut contents mass and food intake do not suggest digestive constraints on sauropod dinosaur body size.
Allometry of visceral organs in living amniotes and its implications for sauropod dinosaurs

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Summary

Allometric equations are often used to extrapolate traits in animals for which only body mass estimates are known, such as dinosaurs. One important decision can be whether these equations should be based on mammal, bird, or reptile data. To address whether this choice will have a relevant influence on reconstructions, we compared allometric equations for birds and mammals from the literature to those for reptiles derived from both literature and hitherto unpublished data. Organs studied included the heart, kidneys, liver, and gut, as well as gut contents. While the available data indicates that gut content mass does not differ between the clades, the organ masses for reptiles are generally lower than those of mammals and birds. In particular, gut tissue mass is significantly lower in reptiles. When applying the results in the reconstruction of a sauropod dinosaur, the estimated volume of the coelomic cavity greatly exceeds the estimated volume of the combined organ masses, irrespective of the allometric equation used. Therefore, substantial deviation of sauropod organ allometry from that of the extant vertebrates can be allowed conceptually. Extrapolations of retention times from estimated gut contents mass and food intake do not suggest digestive constraints on sauropod dinosaur body size.

Key words: allometry, scaling, coelomic cavity, ingesta retention, digestion, gut
Body mass is generally considered the most important predictor of morphological,
physiological and ecological characteristics of animals, and a multitude of allometric
correlations between body mass and other measurements have been established in biology
(Peters 1983; Schmidt-Nielsen 1984; Calder 1996). While mostly used for the investigation of
fundamental laws determining the functions of certain animal groups, or of life in general,
allometric equations are also often used for the reconstruction of morphological, physiological
and ecological traits of animals for which only body mass but few other biological parameters
can be estimated directly. Especially in considerations about characteristics and constraints of
the extinct dinosaur megafauna, such equations have been applied (Alexander 1989;
McGowan 1989).

One interesting approach in this respect is to test whether a specific set of predictions or
estimates are really compatible with other aspects of anatomy or physiology. For example,
Seymour & Lillywhite (2000) demonstrated in model calculations that an upright posture of
the neck in sauropods is incompatible with current understanding of cardiovascular function
in vertebrates. Other examples for the use of allometry are the studies by Gunga et al. (2007;
2008), who used allometric equations on the organ size of mammals from Anderson et al.
(1979), Schmidt-Nielsen (1984) and Calder (1996) to test whether reconstructions of the body
size of a prosauropod and a sauropod, in particular the volume of the coelomic cavity of these
animals, match the calculated space requirement of the internal organs.

For such reconstructions, a concept is required: Should physiological inferences in dinosaurs
be based on mammals, birds, or reptiles, and for which parameters does the choice of extant
analogue make a difference? Dinosaurs are usually considered to have been endotherms (like
birds and mammals) rather than ectotherms (reptiles), but an „intermediate“ metabolism (Reid
1997) or even a distinct ontogenetic shift in metabolic rate has been hypothesized for them
(Sander & Clauss 2008), which might be relevant for the size of metabolic organs.
In order to test whether the available data suggested a difference or a similarity of allometric correlations between body mass (BM) and organ mass in reptiles, birds and mammals, we compared allometric equations for birds and mammals from the literature to allometric equations for reptiles derived from a collection of literature and hitherto unpublished data, and used the results for a plausibility test of a recent sauropod dinosaur reconstruction (Gunga et al. 2008) and a model calculation to assess whether digestive anatomy and physiology should be considered a limiting factor in sauropod body size.

Methods

A data collection on reptile organ mass was compiled using literature sources (Else & Hulbert 1981; Hailey 1997; Dohm et al. 1998), as well as unpublished data from personal observations (Hummel and Clauss, unpubl. data) and from three recent dissertation theses (Kopsch 2006; Eberle 2007; Schneemeier 2008). Data were available for the mass of the heart, the kidneys, the liver and the empty gastrointestinal tract (GIT). Data on lung tissue mass was not available from these studies, and we could not locate other sources that provided sufficient data for an inclusion of lung tissue in this study. Additionally, data on the wet content mass of the total GIT was compiled for herbivorous reptiles (Karasov et al. 1986; Parra 1978; Bjorndal & Bolten 1990; Foley et al. 1992; Barboza 1995; Hailey 1997; Mackie et al. 2004) and herbivorous birds (Herd & Dawson 1984; Dawson et al. 1989; Grajal 1995), and compared to the data collection for herbivorous mammals from Clauss et al. (2007a). If more than one set of data was available for a species, an average was calculated and used in the analyses, in order to avoid overrepresentation of any species. The data are given in the electronic appendix.

Organ scaling is described by the allometric equation: $Y = a \cdot BM^b$
where $Y$ is organ mass correlated with body mass (BM, masses in kg). The exponent $b$ is a scaling factor, which describes the scaling with body size. If $b = 0$, body size has no effect; if $b = 1$, $Y$ shows a linear correlation to BM.

Data on body mass and organ mass were ln-transformed: $\ln(\text{organ mass}) = \ln(a) + b \ln(\text{BM})$.

Linear regressions were calculated using SPSS 16.0 (SPSS Inc., Chicago, Illinois, USA) including the 95% confidence intervals for both $a$ and $b$. Because the original datasets of Calder (1996) were not available, we tested whether the 95% confidence intervals for $a$ and $b$ in reptiles included the values given for the respective factors and exponents for birds and mammals by this author.

**Results**

The 95% confidence interval (CI) of the allometric exponent ($b$) included 1.0 for each of the four organs tested (Tab. 1); in other words, all organs did not deviate significantly from a linear correlation with body mass. The 95% CI of the allometric exponent also included the value given by Calder (1996) for birds and mammals for the heart and kidneys (Tab. 1, Fig. 1), but not for the liver and the just not for gastrointestinal tract. The 95% CI of the intercept of the ln-transformed equation ($\ln(a)$) included values for birds and mammals in the case of the liver, indicating that irrespective of the scaling pattern with body mass, the actual mass of this organ is similar between the three vertebrate clades in the body size range studied (Tab. 1, Fig. 1c). In the case of the heart, the mammalian value for $a$ was just included in the upper 95% CI of reptiles, whereas that for birds was above the CI (Tab. 1, Fig. 1a). Similarly, the 95% CI for the intercept of the kidney included the mammalian but not the avian value (Fig. 1b).

The reptilian intercept was lower than both the mammalian and the avian value for the gastrointestinal tract. Thus, the data indicates that the GIT of reptiles, birds and mammals shows a similar scaling pattern with body mass, but, for reptiles, at a generally lower level (Fig. 1d).
A visual comparison of data on the mass of the wet contents of the whole GIT (Fig. 2) indicates that systematic differences between herbivorous reptiles, birds and mammals are unlikely. The calculated difference in the allometric exponent between reptiles and mammals (Table 1) should therefore be viewed with caution; using the calculated equation, a reptile-like herbivore would consist of nothing but gut contents at a body mass of approximately 670 kg.

Discussion

The findings of this study suggest while there appear to be no relevant differences in the allometry of the liver mass and the mass of the gastrointestinal contents, differences do exist between mammals, birds, and reptiles with respect to the allometry of heart, kidney, and the gastrointestinal tissue mass. When compared to allometric equations found by Else and Hulbert (1985) for reptiles, the animals in our study generally achieved higher organ weights for their body masses.

Given the variety of mammal, bird, and reptile species, and the limited selection of species available for the derivation of allometric equations, such results need to be considered with caution. Organ masses in reptiles as well as other clades can be influenced by sex, reproductive status and hibernation status (Telford Jr. 1970; Beuchat & Braun 1988) or food availability and quality (Relyea & Auld 2004; Naya et al. 2005; Naya & Bozinovic 2006).

However, in the collection of allometric equations of Calder (1996) which was used as reference here, there is no evident separation of data for such factors; therefore, the undifferentiated inclusion of data appeared justified for a comparison between clades here.

In correspondence with expectations linked to the differences in metabolism, with low metabolic rates in reptiles and higher rates in birds as compared to mammals (McNab 2002), the organ masses for heart and kidney showed higher values for $a$ in the same sequence.
Similarly, birds exceed mammals in the capacity and the weight of their respiratory system (Lasiewski & Calder 1971; Calder 1996; Maina 2006), but lung masses of mammals and reptiles are similar at similar body masses (Else & Hulbert 1985). The most impressive difference in organ mass between reptiles on the one hand, and mammals and birds on the other, is in the tissue of the gastrointestinal tract. Whereas the contents of the gastrointestinal tract appear to be similar in herbivorous mammals, reptiles and birds (Parra 1978; Bjorndal 1997), the endothermic clades have significantly higher gut tissue masses. Although intestinal microvilli area does probably not differ significantly between herbivorous reptiles and mammals (Ferraris et al. 1989), there is a significant difference in the intestinal surface area between the two clades, mainly due to differences in intestinal length (Karasov et al. 1985; Karasov & Diamand 1985; Karasov et al. 1986; Ferraris et al. 1989). Birds and mammals have distinctively longer small intestines than reptiles (Stevens & Hume 1995), and in birds, the muscular gizzard additionally increases gut tissue mass.

The choice of the allometric equation for the extrapolation of organ tissue masses thus can have relevance for the outcome of organismal reconstructions (Table 2). Using organ allometries for ectothermic organisms (reptiles) should yield generally lower estimates. However, when extrapolating to gigantic body masses by the use of allometric equations such as those derived in the present study, a conceptual problem arises (Table 2). Any slight differences in the allometric exponent $b$ will, at very large body masses, lead to very different results, which may, in their scope and ranking, even be different from the observed ranking (see Table 1) based on $a$. In Table 2, it can be seen that when the exact equations from Table 1 are used for the estimation of organ masses in a 38 ton dinosaur in the “allometric approach”, the derived reptile equation would lead to dramatically higher estimates for the liver mass, although reptiles would be assumed to have similar (this study) or even slightly lower liver masses than mammals (Else & Hulbert 1985). This paradoxical result is caused by
the difference in the allometric exponent $b$ (1.061 in reptiles as opposed to 0.87 in mammals).

Evidently, at extrapolations to such gigantic masses, the error in the estimation of $b$ inherent in the use of imperfect datasets is too large to yield realistic results. A potential solution to overcome this effect, especially when comparing different sets of calculations, is to assume a common exponent $b$ for all clades. In our case, where the 95% confidence interval for $b$ always included 1.0 (linearity) in the reptiles, we suggest that in the absence of information on 95% confidence intervals in birds and mammals, all correlations can be assumed to be linear. This approach leads to a consistent ranking of extrapolated organ masses according to the reptile-mammal-bird sequence that can be observed in the original equations (Table 1).

Whether we assume that a reptile (ectotherm) or mammal/bird (endotherm) equation should be used for a 38 ton-sauropod dinosaur can lead to a difference in estimated gut tissue mass of more than 1670 kg (or 4.4 % of the assumed body mass). In the case of sauropods, it has been postulated that these animals underwent an ontogenetic shift in their metabolic rate, from juvenile endotherms to adult mass-homoethersms (with low metabolic rates) (Farlow 1990; Sander & Clauss 2008), and intestinal length is usually considered to reflect metabolic rate (Williams et al. 2001). This view of sauropod metabolism would, for example, imply, due to the apparent association of intestinal length and metabolism, that the growth of intestinal tissue mass was less during ontogeny in sauropods than it is in mammals. This view would therefore justify the use of “reptile equations” for adult sauropods, thus alleviating theoretical constraints on the capacity of the coelomic cavity. Gunga et al. (2008) had already concluded that the coelomic cavity of a 38 ton-sauropod dinosaur (*Brachiosaurus brancai*), which they assumed to harbour a volume of 32 m$^3$ according to their body size reconstructions, provided more space than necessary for most of the organs of this cavity (including a proportion of the skeleton, the blood volume, and the muscle mass, but without accounting for mesenteries, coelomic fat, and reproductive organs), which they estimated at 21 m$^3$. Using our “linear”
approach and the reptile functions (Table 2), and adopting a linear approach based on the
mammal functions used by Gunga et al. (2008) for those organs which we could not include
in our study, we arrive at a volume estimate of only 17.6 m$^3$. Evidently, even when
considering that mesenteries, fat, and reproductive organs are not included in these
calculations, the current data allows for a dramatic increase in organ masses in the
reconstruction of sauropod dinosaurs. As sauropods are thought to have heterogenous (avian-
type) lungs with an airsac system (Sander & Clauss 2008), a part of the space in the coelomic
cavity was probably filled with these airsacs. In birds, the lungs and airsacs may account for
as much as 20% of the total body volume (King 1966); in the 38 ton-sauropod of Gunga et al.
(2008), with an estimated total volume of approximately 47.6 m$^3$, this would represent a total
lung and airsac volume of 9.5 m$^3$. Even if we assume that the majority of this volume was
placed within the coelomic cavity, the reconstruction would still allow for theoretical
increases in any organ masses.

Given that we must assume elevated metabolic rates in certain ontogenetic stages, and no
mastication of ingesta (Farlow 1990; Sander & Clauss 2008), the gastrointestinal contents
could be a plausible candidate for a mass above estimates based on regressions from extant
animals – to allow a thorough digestion in spite of absent food comminution and without
compromising intake (Farlow 1987; Clauss et al. 2007b). In order to roughly estimate whether
gut capacity should be considered a limiting factor in sauropods, we extrapolated the dry
matter intake for sauropods from Hummel et al. (2008) to a 38 ton-sauropod; these values are
given at four assumed levels of metabolism. Assumptions were made for a medium-quality
and a low-quality diet (with presumed apparent dry matter and energy digestibilities of 44 and
33 %, respectively); additionally, we estimated the dry matter concentration in sauropod gut
contents to be 15 %, a level similar to that of mammals (but probably lower than in reptiles,
M. Clauss, pers. obs.). Using the equation by Holleman & White (1989) that links dry matter
intake, digestibility, dry matter gut capacity, and ingesta retention time, we can estimate the
mean retention time in hypothetical sauropods of varying metabolic level (Table 3; see
electronic appendix for details). At the normal, extrapolated gut capacity, retention times are
between 4 and 8 days for a medium-quality food; a doubling of the gut content – which would
still leave about 10m$^3$ of the presumed coelomic cavity unoccupied for mesenteries, fat, and
reproductive organs – would result in retention times between 8 and 16 days. Thus, estimated
retention times fall within the range of 11 days measured in Galapagos tortoises (*Geochelone
nigra*) (Hatt et al. 2002), which – as extant reptiles – do not chew their food.

In conclusion, this study as well as that of Gunga et al. (2008) show that, from the aspect of
organismal reconstruction based on body volume and organ estimates, no restrictions are
evident in the sauropod *bauplan*; on the contrary, given our current equations for organ
allometry, the body cavity of sauropods as it reconstructed allows leeway for any adjustments
in organ size that one might deem necessary to fit their – potentially unique – lifestyle. In
particular, digestive physiology is an unlikely candidate for a potential body size limitation in
sauropods.

**Acknowledgments**

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Barboza, P. 1995 Digesta passage and functional anatomy of the digestive tract in the desert


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Table 1: Statistics of regression analysis according to the equation organ mass = $a$ BM$^b$

(masses in kg) for reptiles. Allometric organ equations for birds and mammals are from Calder (1996); data for gut contents of mammals from Clauss et al. (2007a) and for birds from Herd & Dawson (1984), Dawson et al. (1989) and Grajal (1995)

<table>
<thead>
<tr>
<th>Organ</th>
<th>Clade (species)</th>
<th>BM range (kg)</th>
<th>a</th>
<th>95% CI</th>
<th>b</th>
<th>95% CI</th>
<th>$R^2$</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Heart</td>
<td>Reptile [28]</td>
<td>0.008-1.052</td>
<td>0.005</td>
<td>0.0036-0.0070</td>
<td>1.055</td>
<td>0.929-1.181</td>
<td>0.919</td>
<td>&gt;0.001</td>
</tr>
<tr>
<td></td>
<td>Mammal</td>
<td>-</td>
<td>0.006</td>
<td>-</td>
<td>0.98</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Kidney</td>
<td>Reptile [28]</td>
<td>0.008-0.990</td>
<td>0.006</td>
<td>0.0037-0.0085</td>
<td>0.945</td>
<td>0.792-1.099</td>
<td>0.860</td>
<td>&gt;0.001</td>
</tr>
<tr>
<td></td>
<td>Mammal</td>
<td>-</td>
<td>0.007</td>
<td>-</td>
<td>0.85</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Liver</td>
<td>Reptile [29]</td>
<td>0.008-0.715</td>
<td>0.033</td>
<td>0.0219-0.0484</td>
<td>1.066</td>
<td>0.917-1.216</td>
<td>0.888</td>
<td>&gt;0.001</td>
</tr>
<tr>
<td></td>
<td>Mammal</td>
<td>-</td>
<td>0.033</td>
<td>-</td>
<td>0.87</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>GIT</td>
<td>Reptile [29]</td>
<td>0.008-1.123</td>
<td>0.031</td>
<td>0.0207-0.0458</td>
<td>1.159</td>
<td>0.997-1.321</td>
<td>0.889</td>
<td>&gt;0.001</td>
</tr>
<tr>
<td></td>
<td>Mammal [11]</td>
<td>-</td>
<td>0.075</td>
<td>-</td>
<td>0.94</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>GIT wet</td>
<td>Reptile [12]</td>
<td>0.059-3.150</td>
<td>0.080</td>
<td>0.0584-0.1104</td>
<td>1.389</td>
<td>1.195-1.583</td>
<td>0.962</td>
<td>&gt;0.001</td>
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<tr>
<td>contents</td>
<td>Mammal [71]</td>
<td>0.015-3140</td>
<td>0.107</td>
<td>0.094-0.121</td>
<td>1.062</td>
<td>1.029-1.095</td>
<td>0.983</td>
<td>&gt;0.001</td>
</tr>
<tr>
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<td>Bird [5]</td>
<td>0.712-35.330</td>
<td>0.044</td>
<td>0.000-545.1</td>
<td>1.204</td>
<td>-3.347-5.755</td>
<td>0.919</td>
<td>0.184</td>
</tr>
</tbody>
</table>

n.a. = not available
Table 2: Extrapolation of organ masses (in kg) of a hypothetical 38000 kg vertebrate (the estimated mass of *Brachiosaurus*, a sauropod dinosaur, Gunga et al. 2008) under different assumptions: “linear approach” = assuming linear scaling with body mass for all clades, i.e. $b = 1.0$, using values for $a$ from Table 1; “allometric approach” = using the exact equations as given in Table 1. Note that due to small differences in the exponent $b$, extrapolations using the exact equations will yield fundamentally different results.

<table>
<thead>
<tr>
<th></th>
<th>linear approach</th>
<th>allometric approach</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Reptile</td>
<td>Mammal</td>
</tr>
<tr>
<td>Heart</td>
<td>190</td>
<td>228</td>
</tr>
<tr>
<td>Kidney</td>
<td>228</td>
<td>266</td>
</tr>
<tr>
<td>Liver</td>
<td>1254</td>
<td>1254</td>
</tr>
<tr>
<td>GIT tissue</td>
<td>1178</td>
<td>2850</td>
</tr>
</tbody>
</table>

Table 3: Estimation of ingesta mean retention time (MRT) in a hypothetical 38000 kg vertebrate (the estimated mass of *Brachiosaurus*, a sauropod dinosaur, Gunga et al. 2008) at different levels of metabolism and hence daily food intake (for 'medium' and 'low' quality food, Hummel et al. 2008) at the extrapolated gut capacity of 610 kg dry matter (from Table 1, linear approach, assuming a dry matter concentration of 15 % in gut contents) and at a doubled gut capacity; MRT estimated according to Holleman & White (1989). DMI = dry matter intake; DFE = dry faecal excretion

<table>
<thead>
<tr>
<th>Level of metabolism</th>
<th>DMI (kg/d)</th>
<th>DFE (kg/d)</th>
<th>MRT hours (days)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Gut capacity</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>610 kg DM</td>
<td>1220 kg DM</td>
<td></td>
</tr>
<tr>
<td><strong>Medium quality food</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Reptile</td>
<td>20</td>
<td>11</td>
<td>927 (39)</td>
</tr>
<tr>
<td>Intermediate 1</td>
<td>96</td>
<td>53</td>
<td>197 (8)</td>
</tr>
<tr>
<td>Intermediate 2</td>
<td>140</td>
<td>78</td>
<td>135 (6)</td>
</tr>
<tr>
<td>Mammal</td>
<td>188</td>
<td>104</td>
<td>100 (4)</td>
</tr>
<tr>
<td><strong>Low quality food</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Reptile</td>
<td>28</td>
<td>18</td>
<td>639 (27)</td>
</tr>
<tr>
<td>Intermediate 1</td>
<td>127</td>
<td>84</td>
<td>139 (6)</td>
</tr>
<tr>
<td>Intermediate 2</td>
<td>186</td>
<td>124</td>
<td>94 (4)</td>
</tr>
<tr>
<td>Mammal</td>
<td>250</td>
<td>166</td>
<td>70 (3)</td>
</tr>
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</table>
Fig. 1. Correlations of body mass and organ mass in reptiles (diamonds, solid line), mammals (interrupted line) and birds (dotted line) for a) heart, b) kidneys, c) liver and d) gastrointestinal tissue. Reptile data from this study [see electronic appendix], mammal and bird regression lines from Calder (1996).

Fig. 2. Wet contents mass of the total gastrointestinal tract in mammals (data from Clauss et al. 2007a), birds (data from Herd & Dawson 1984, Dawson et al. 1989, Grajal 1995) and reptiles [data in electronic appendix] in relation to body mass.