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Manuscripts

1 **Downsizing a giant: Re-evaluating *Dreadnoughtus* body mass**

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15 **Key words:** *Dreadnoughtus*, body mass, modeling, scaling equations.

16

17 **Summary**

18 Estimates of body mass often represent the founding assumption on which

19 biomechanical and macroevolutionary hypotheses are based. Recently, a scaling

20 equation was applied to a newly discovered titanosaurian sauropod dinosaur

21 (*Dreadnoughtus*), yielding a 59,300kg body mass estimate for this animal. Herein

22 we use a modeling approach to examine the plausibility of this mass estimate for
23 *Dreadnoughtus*. We find that 59,300kg for *Dreadnoughtus* is highly implausible,
24 and demonstrate that masses above 40,000kg require high body densities and
25 expansions of soft tissue volume outside the skeleton several times greater than
26 found in living quadrupedal mammals. Similar results from a small sample of
27 other archosaurs suggests that lower-end mass estimates derived from scaling
28 equations are most plausible for *Dreadnoughtus*, based on existing volumetric
29 and density data from extant animals. Although volumetric models appear to
30 more tightly constrain dinosaur body mass there remains a clear need to further
31 support these models with more exhaustive data from living animals. The
32 relative and absolute discrepancies in mass predictions between volumetric
33 models and scaling equations also indicate a need to systematically compare
34 predictions across a wide size and taxonomic range to better inform studies of
35 dinosaur body size.

36

37 INTRODUCTION

38 Sauropod dinosaurs include the largest terrestrial animals to have ever evolved,
39 and mass properties are regarded as a crucial component of their functional,
40 behavioural, and evolutionary dynamics [1]. Recently, Lacovara et al. [2]
41 described a gigantic, near-complete titanosaurian sauropod, *Dreadnoughtus*
42 *schrani*, from Argentina. These authors used a scaling relationship between long
43 bone (femoral plus humeral) circumference and body mass [3] to derive a mass
44 estimate of 59,300kg for the holotype of *Dreadnoughtus*. This scaling equation is
45 well supported statistically in living tetrapods and to-date has been used to
46 estimate the body mass of extinct taxa to facilitate studies of physiology and

47 growth [e.g. 4] and macroevolutionary dynamics [1]. However, the mass
48 estimate seems high given that in overall skeletal proportions *Dreadnoughtus*
49 only marginally exceeds those of near-complete specimens of other sauropods
50 (e.g. *Apatosaurus*, *Giraffatitan*) whose masses have been estimated at 25-
51 35,000kg by various methods [e.g. 3, 5]. In this paper we use a digital three-
52 dimensional skeletal model and volumetric reconstructions to directly examine
53 the plausibility of the 59,300kg mass estimate for *Dreadnoughtus*, and
54 subsequently comment upon the use of scaling equations to estimate dinosaur
55 body mass.

56

57 **METHODS**

58 A digital model of the *Dreadnoughtus* skeleton from Lacovara et al. [2] was used
59 as a basis for a 3D volumetric model (Fig. 1). For comparative purposes we also
60 modeled six extant taxa (three birds, two crocodylians and one lizard) and two
61 other large sauropods using identical methods: *Giraffatitan brancai*, based on a
62 laser scan of MB (Museum für Naturkunde, Berlin, Germany) SII from our
63 previous study [5], and *Apatosaurus louisae*, based on a new 3D model of CM
64 (Carnegie Museum, USA) 3018 generated using photogrammetry [6]. Each 3D
65 skeletal model was posed in a standard 'neutral' posture, with the tail and neck
66 extending horizontally and the limbs in a fully extended, vertical position (Fig. 1).
67 Models were then divided into the following body segments: head, neck, 'trunk'
68 (thorax & limb girdles), tail, thigh, shank, foot, humerus, forearm, and hand.

69 The holotype of *Dreadnoughtus* is missing most of the cervical vertebrae,
70 as well the manus, skull and distal tip of the tail. Our convex hulling approach [5]
71 to volumetric reconstruction involves tight-fitting 3D convex polygons to each

72 body segment. As the extent of an object's convex hull is dictated solely by its
73 geometric extremes, we were able to minimise the amount of skeletal
74 reconstruction in our model (Fig. S1). For the hand and skull we used
75 photogrammetric models of these elements from *Rapetosaurus* (FMNH PR 2209),
76 another titanosaur, and re-scaled them using the reconstruction in Lacovara et
77 al. ([2], their Fig. 2). To allow convex hulling to connect the 'trunk' and neck
78 segments we duplicated the ninth cervical vertebra preserved in the specimen
79 and placed its posterior surface above the most anterior point of pectoral girdle
80 at a height consistent with the position of the preserved dorsal vertebrae. An
81 additional 10% was added to the distal tail using the reconstruction of Lacovara
82 et al. [2] as a guide (Fig. S1). In the supplementary material we provide extensive
83 sensitivity tests of our skeletal reconstruction procedure (Figs S1-S8).

84 The minimum convex hull volume for each skeletal body segment was
85 calculated using the MATLAB (www.mathworks.com) qhull command [5,7]. The
86 total minimum convex hull volume provides the minimum volume estimate for
87 each animal, and a baseline for our sensitivity analysis in which we generated
88 three further models. In the first model the minimal convex hulls were
89 geometrically expanded by 21%, following a previous study in which live body
90 mass was estimated to have been on average 21% greater than that calculated
91 from minimum convex hulls for a range of extant mammals [5]. We subsequently
92 generated a 'maximal mass model' in which the volume of the trunk segment was
93 increased by 50% and those of all other segments by 100%. Finally, we
94 expanded the minimum convex hull model of *Dreadnoughtus* by the amount
95 required to match the total body masses predicted by the scaling equation of [3].

96 For the sauropod models, body segments were given an initial density of 1000kg
97 m⁻³. Zero-density respiratory structures in the head, neck and 'trunk' segments
98 were reconstructed and the volumes of these structures subtracted from their
99 overall segment volume, as in previous volumetric studies of dinosaurs [8-10].
100 Homogeneous body densities were used for the extant taxa, based on published
101 values for crocodiles and chickens [10].

102

103 **RESULTS**

104 The convex hull volume reconstruction of *Dreadnoughtus* results in a total body
105 volume of 26.910m³ (Fig. 1a, Table 1). Expanding this minimum convex hull
106 volume by 21% raises whole-body volume to 32.534m³ (Fig.1b), while the
107 volume of our maximal model is 43.016m³ (Fig. 1c). Deducting the volume of our
108 reconstructed respiratory structures from each of these models yields total body
109 masses of 22,117kg, 27,741kg and 38,225kg for the three model iterations.

110 These data, and data from equivalent models of *Apatosaurus* and *Giraffatitan*
111 (Fig. 2a-b), are shown in Table 1, while the data from extant taxa is tabulated in
112 the supplementary information (Tables S1-6, Figs S8-9). Convex hull volumes are
113 available in the supplementary information.

114

115 **DISCUSSION AND CONCLUSIONS**

116 The mass of *Dreadnoughtus* was estimated at 59,300kg using the raw bivariate
117 predictive equation of Campione and Evans [3]. The masses of our three
118 volumetric reconstructions of *Dreadnoughtus* (Fig. 1a-c, Table 1) are equivalent
119 to 37%, 47% and 64% of the 59,300kg scaling equation mass. The 'average
120 percent prediction error' from the bi-variate equation gives a minimum mass of

121 44,095kg (5,780kg or 15% higher than our 'maximal' model) and a maximum
122 mass of 74,487kg (36,262kg or 95% higher than our 'maximal' model). The '95%
123 prediction interval' from the equation yields a range of 32,000-109,000kg for
124 *Dreadnoughtus*, which overlaps with model estimates (Fig. 2).

125 Convex hulling provides a close, objective approximation of the body
126 volume defined by a skeleton alone [5,7]. A volume 2.38 times larger than that of
127 our convex hull model is required for *Dreadnoughtus* to achieve the mean or
128 'best-estimate' scaling equation mass of 59,300kg, using our estimates for the
129 size of respiratory structures (Fig. 1d). This represents an expansion more than
130 6.5 times greater than the average value found in a sample of quadrupedal
131 mammals spanning major taxonomic groups [5]. This 2.38 times expanded
132 model (Fig. 1d) has a bulk density of 925kg m⁻³, which is higher than any
133 presently published estimate for sauropods [range 791-900kg m³; Table S7]. If
134 lower-end estimates of 800kg m⁻³ for sauropod density [8] are correct, then
135 achieving a body mass of 59,300kg for *Dreadnoughtus* would require body and
136 respiratory volumes of 74.125m³ and 14.825m³ respectively, the latter
137 representing a 310% expansion of our respiratory volumes (Fig. 1). Filling the
138 entire ribcage with a zero-density respiratory structure (Fig. S7), which is
139 obviously highly implausible, only produces a 212% increase in respiratory
140 volume. It is clear from our model that bulk densities as low or approaching
141 800kg m³ cannot be reconciled with a total body mass of 59,300kg given the
142 skeletal proportions of *Dreadnoughtus* and the space available within the ribcage
143 for low-density respiratory structures.

144 Comparison of mass predictions from volumetric reconstructions of near-
145 complete skeletons of *Apatosaurus* and *Giraffatitan* (Fig. 2) to the mean scaling

146 equation masses, produces a qualitatively similar result: scaling equation mass
147 predictions exceed those of our maximal models (Fig 2c-d). The disparity
148 between the two approaches increases further if the whole-body densities of
149 these models are set to lower-end estimates for sauropods (800kg m^{-3} [8])
150 rather than predicting density by inclusion of respiratory structures. In the case
151 of both *Apatosaurus* and *Giraffatitan* there is clear overlap between the lowest
152 scaling equation estimates and our maximal models, although as with
153 *Dreadnoughtus* there remains no overlap between the lowest scaling equation
154 masses and those derived from the upper bounds of the mammalian convex hull
155 expansion exponent (Fig. 2).

156 Convex hull volumes for extant taxa produced here required scaling
157 exponents of between 1.18-1.91 (Tables S1-6, Fig. S8-9) to reach actual
158 measured body masses, with three animals (American alligator 1.69; guineafowl
159 1.91; leghorn chicken 1.87) requiring exponents greater than that applied in our
160 'maximal' models (Fig. 1). However, increasing convex hull volume by 2.38, as
161 required for our reconstruction of *Dreadnoughtus* to reach the mean scaling
162 equation mass, results in substantial mass overestimates for all modelled extant
163 taxa (23-102% overestimates; see Tables S1-6).

164 Our analysis emphasises a number of important points that should be
165 considered in future studies. Firstly, it is vital that uncertainties and likely error
166 magnitudes are explicitly acknowledged in mass estimates derived from all
167 methods, including scaling equations. Our analysis also reveals that the higher
168 range estimates predicted by bivariate scaling equations [3] appear to be highly
169 incompatible with volumetric models that are based directly on currently
170 available volume and density data from living vertebrates ([5]; Tables S1-6).

171 Indeed, in the case of *Dreadnoughtus*, the mean, and perhaps even some lower-
172 end, scaling equation estimates appear to be implausible based on current data
173 (Figs 1-2). The high scaling equation mass for *Dreadnoughtus* also appears to
174 result in a discrepancy in relative mass predictions between the modelled
175 sauropods; our convex hull volumes (which provide a close approximation of the
176 body volume defined by the preserved skeleton) of *Apatosaurus* and *Giraffatitan*
177 represent 0.9 and 0.985 that of *Dreadnoughtus*, which appears congruent with
178 the overlap in gross linear body proportions (Fig. S11). By contrast, mean scaling
179 equation mass predictions for *Apatosaurus* and *Giraffatitan* are 0.57 and 0.70
180 that of *Dreadnoughtus* (Fig. 2). While differences in skeletal:extra-skeletal
181 dimensions should be expected [3], even in relatively closely related taxa (Tables
182 S1-6) it seems unlikely that differences in skeletal proportions of these three
183 sauropods (Figs 2 & S11) are sufficient to account for the 20-25,000kg difference
184 in body mass predicted by the scaling equation. Thus, even physiological and
185 macroevolutionary studies that use relative mass values or distribute taxa into
186 discrete mass 'categories' based on scaling equation estimates should take the
187 maximum range of values or error inherent in these equations into account.

188 Recently a similar pattern of divergence between volumetric and linear-
189 based mass estimates was found for exceptionally complete *Stegosaurus*
190 skeleton [7]. The authors attributed this discrepancy to the ontogenetic status of
191 the individual. Certain skeletal features may indicate that the *Dreadnoughtus*
192 holotype was still growing at the time of death [2]. As an organism's body
193 proportions change with age, the application of a scaling equation derived from
194 modern adult skeletons to the limb bones of a sub- or young adult may be
195 erroneous. At least some of the inconsistency we find here between mass

196 estimation techniques may therefore be due to the ontogenetic stage of the
197 specimen. Given the absence of confirmed 'adult' skeletal material for
198 *Dreadnoughtus* however, it would be challenging to account for this
199 phenomenon.

200 Estimating the mass of extinct animals is challenging [3,5,7,9-10]. By
201 directly using the determinates of mass (volume and density) and maximising
202 skeletal evidence, volumetric approaches allow inherent uncertainties in mass
203 predictions to be explicitly assessed (Figs 1-2) and plausible limits established
204 based on data and models of extant taxa. Our analysis reveals the importance of
205 extending current analyses of dinosaur body mass in two ways; first and
206 foremost by addition of further volumetric and density data on living taxa in
207 order to more tightly constrain maximum plausible values for extinct animals.
208 Second, a systematic comparison of dinosaur mass predictions from modelling
209 and scaling equations, across a wide taxonomic and size range, is needed to
210 identify and explain discrepancies between the two approaches (Fig. 2). Such a
211 study would not only lead to more informed estimates of dinosaur body mass,
212 but could also shed light on musculoskeletal adaptations for large body size in
213 different dinosaur lineages.

214

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246

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252

253 Data accessibility. Convex hull models are downloadable from Dryad (doi:XXXX).

254 Author contributions. K.T.B., S.C.R.M., C.A.B and P.L.F designed the experiments;
255 K.T.B. S.M. and P.L.F. collected the data; K.T.B., C.A.B, S.C.R.M. and S.M. analysed
256 the data; all authors contributed to the manuscript.

257

258 Conflict of interest. The authors declare that they have no competing interests.

259

260 Figure 1. *Dreadnoughtus* 3D skeletal model and the **(a)** convex hull, **(b)** plus21%,
261 **(c)** maximal and **(d)** scaling equation mass volumetric reconstructions in lateral,
262 oblique and aerial views. Black structures are respiratory volumes.

263

264

265 Figure 2. Comparison of skeletal proportions and convex hull volumes for
266 *Apatosaurus* (top), *Dreadnoughtus* (middle) and *Giraffatitan* (bottom) in **(a)**
267 dorsal and **(b)** lateral views. Comparison of mass predictions from the models in
268 this study to masses derived from the scaling equation [2], with **(c)** model mass
269 and density calculated using reconstructed zero-density respiratory structures,
270 and **(d)** density artificially set to 800 kg m^{-3} [8]. The positive error bar on our
271 maximal models represents the mass predicted by expanding convex hull
272 volumes by the highest exponent (x1.91) for mammals [5] and archosaurs to-
273 date. The 'PPE' error bars on scaling equation represent the average 'percent
274 prediction error', while '95PI' error bars represent the '95% prediction interval.'

275

276 Table 1. Mass property data for convex hull reconstructions of *Dreadnoughtus*,
277 *Apatosaurus* and *Giraffatitan*, and summary of whole-body mass data from
278 different model iterations.

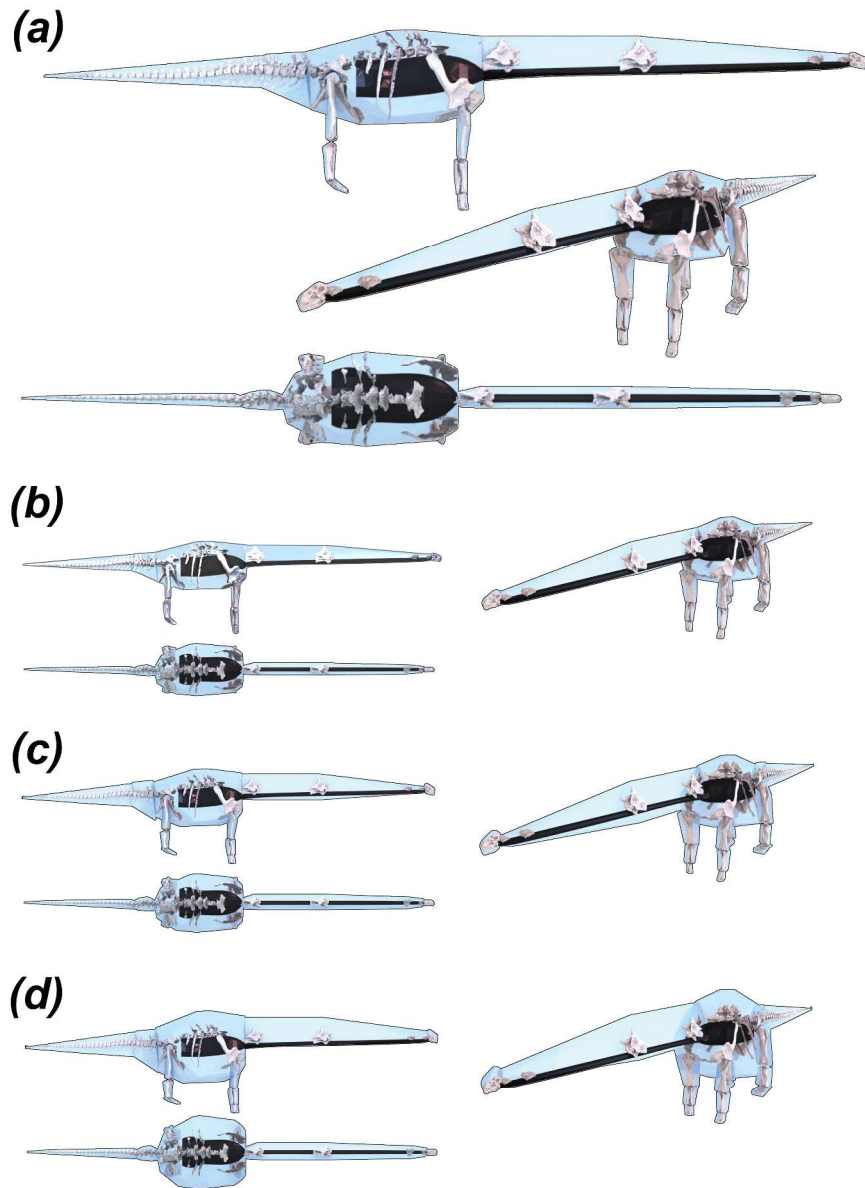
Table 1. Mass property data for convex hull reconstructions of *Droughnoughtus*, *Apatosaurus* and *Giraffatitan*, and summary of whole-body mass data from different model iterations.

Convex Hull	<i>Dreadnoughtus</i>			<i>Apatosaurus</i>			<i>Giraffatitan</i>		
	Volume (m ³)	Density (kg m ⁻³)	Mass (kg)	Volume (m ³)	Density (kg m ⁻³)	Mass (kg)	Volume (m ³)	Density (kg m ⁻³)	Mass (kg)
Body Segments									
Head	0.033	1000	33.49	0.02	1000	23.46	0.06	1000	59.45
Neck	3.110	1000	3109.99	2.62	1000	2615.16	2.46	1000	2461.00
Trunk	20.382	1000	20381.96	20.12	1000	20187.65	19.85	1000	19850.92
Tail	1.011	1000	1011.35	1.86	1000	1861.20	0.78	1000	774.76
Humerus	0.186	1000	186.08	0.23	1000	232.34	0.30	1000	298.78
Forearm	0.097	1000	97.36	0.10	1000	103.01	0.16	1000	160.67
Hand	0.024	1000	24.11	0.03	1000	25.96	0.09	1000	85.98
Humerus	0.186	1000	186.08	0.28	1000	275.31	0.30	1000	298.78
Forearm	0.097	1000	97.36	0.10	1000	103.01	0.16	1000	160.67
Hand	0.024	1000	24.11	0.03	1000	25.96	0.09	1000	85.98
Thigh	0.246	1000	246.13	0.35	1000	351.27	0.29	1000	294.19
Shank	0.110	1000	109.86	0.21	1000	208.57	0.19	1000	193.06
Foot	0.042	1000	41.91	0.08	1000	84.62	0.04	1000	35.69
Thigh	0.246	1000	246.13	0.35	1000	351.27	0.29	1000	294.19
Shank	0.110	1000	109.86	0.21	1000	208.57	0.19	1000	193.06
Foot	0.042	1000	41.91	0.08	1000	84.62	0.04	1000	35.69
Axial total	25.50	1000	24536.80	24.62	1000	24687.47	23.15	1000	23146.13
Hind limb total	0.796	1000	795.80	1.289	1000	1288.92	1.046	1000	1045.88
Fore limb total	0.614	1000	615.09	0.722	1000	722.62	1.092	1000	1090.87
Whole body	26.91	1000	25947.68	26.63	1000	26699.01	25.28	1000	25282.88
Respiratory structures									
Head	0.003	1000	3.43	0.001	1000	0.99	0.0036	1000	3.60
Neck	4.30	1000	4303.67	4.60	1000	4602.86	5.00	1000	5000.39
Trunk	0.49	1000	486.48	0.29	1000	291.95	0.33	1000	332.54

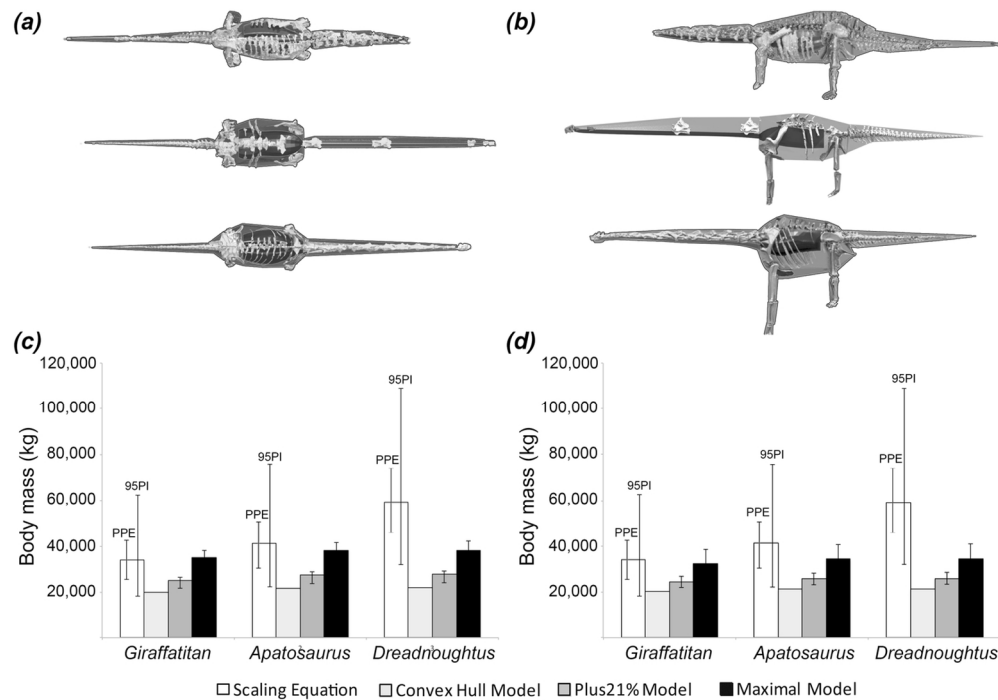
Model Iteration

Minimum									
Convex Hull	26.91	821.9	22117.98	26.63	818.8	21803.21	25.284	788.8	19946.35
Plus 21% Model	32.53	852.7	27741.68	32.26	850.5	27363.56	30.54	825.2	25204.65
Maximal Model	43.02	888.6	38224.57	43.08	886.4	38187.23	40.40	867.9	35060.42

For Review Only



Dreadnoughtus 3D skeletal model and the (a) convex hull, (b) plus21%, (c) maximal and (d) scaling equation mass volumetric reconstructions in lateral, oblique and aerial views. Black structures are respiratory volumes.
288x400mm (300 x 300 DPI)



Comparison of skeletal proportions and convex hull volumes for Apatosaurus (top), Dreadnoughtus (middle) and Giraffatitan (bottom) in (a) dorsal and (b) lateral views. Comparison of mass predictions from the models in this study to masses derived from the scaling equation [2], with (c) model mass and density calculated using reconstructed zero-density respiratory structures, and (d) density artificially set to 800 kg m⁻³ [8]. The positive error bar on our maximal models represents the mass predicted by expanding convex hull volumes by the highest exponent (x1.91) for mammals [5] and archosaurs to-date. The 'PPE' error bars on scaling equation represent the average 'percent prediction error', while '95PI' error bars represent the '95% prediction interval.'

127x90mm (300 x 300 DPI)