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1 **Journal of Anatomy - Evolutionary Morphology**

2 **Body cavity volume reconstruction in terrestrial tetrapods**

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17

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22

Abstract

23 **Abstract**

24 Although it is generally assumed that herbivores have more voluminous body cavities

25 due to larger digestive tracts required for the digestion of plant fiber, this concept has not

26 been addressed quantitatively. We estimated the volume of the torso in 126 terrestrial

27 tetrapods (synapsids including basal synapsids and mammals, and diapsids including

28 birds, non-avian dinosaurs and reptiles) classified as either herbivore or carnivore in

29 digital models of mounted skeletons, using the convex hull method. The difference in

30 relative torso volume between diet types was significant in mammals, where herbivores

31 relative torso volumes about two times larger than that of carnivores, supporting the

32 general hypothesis. However, this effect was not evident in diapsids. This may either

33 reflect the difficulty to reliably reconstruct mounted skeletons in non-avian dinosaurs, or

34 a fundamental difference in the *bauplan* of different groups of tetrapods, for example due

35 to differences in respiratory anatomy. Evidently, the condition in mammals should not be

36 automatically assumed in other, including more basal, tetrapod lineages. In both

37 synapsids and diapsids, large animals showed a high degree of divergence with respect to

38 the proportion of their convex hull directly supported by bone, with animals like

39 elephants or *Triceratops* having a low proportion, and animals such as rhinoceros having

40 a high proportion of bony support. The relevance of this difference remains to be further

41 investigated.

42

43 Key words: photogrammetry; anatomy; ribcage; digestive tract; herbivory; carnivory

44

45 **Introduction**

46 Tetrapods have diversified into an enormous variety of body forms that display
47 convergent evolution at various levels of organismal design. For example, the
48 gastrointestinal tract (GIT) is adapted in size and shape to an animal's diet (Cuvier and
49 Duméril, 1838, Treves, 1886). In broad terms, the diets of herbivorous animals are less
50 easily digested than those of carnivores, and require both the presence of a large number
51 symbiotic gut microbes and time for these microbes to perform their digestive function
52 (Stevens and Hume, 1998). Therefore, in order to accommodate this large microbiome,
53 and to delay digesta passage, the GIT of herbivores are typically considered to be
54 particularly long and/or voluminous (Cuvier and Duméril, 1838, Orr, 1976).

55 Differences in the length of the intestinal tract according to diet have been
56 repeatedly shown for fish (Wagner et al., 2009, Karachle and Stergiou, 2010), lizards
57 (O'Grady et al., 2005) and in other animal lineages such as invertebrates (Griffen and
58 Mosblack, 2011), but not convincingly in birds (DeGolier et al., 1999, Lavin et al., 2008).
59 In mammals, similar evidence is questionable and mostly limited to small body sizes
60 (Barry, 1977, Wang et al., 2003). Chivers and Hladik (1980) calculated lower volumes of
61 the combined stomach, caecum and colon (from linear GIT dimensions) for mammalian
62 carnivores as compared to herbivores of similar cubic body length, and Schiek and Millar
63 (1985) found more GIT tissue mass in herbivorous than carnivorous small mammals up
64 to about 1 kg. However, Starck (1982) doubted that trophic groups can really be
65 distinguished by the length of their intestinal tracts, and Lavin et al. (2008) did not detect
66 a difference in the small intestinal length or volume in small mammals of different diet
67 types. A major difficulty in such comparisons may be that the most relevant

68 characteristic, a measure of gut fill, is available for a large number of herbivore species
69 (Clauss et al., 2013) because their digestive tract usually always contains a relatively
70 constant amount of digesta, but is not similarly available for carnivores where gut
71 contents may vary enormously (Potgieter and Davies-Mostert, 2012).

72 Nevertheless, a voluminous torso that can host a voluminous GIT is considered a
73 prerequisite for high-fiber herbivory (Hotton III et al., 1997), and the appearance of the
74 torso - as judged from articulated skeletons or the shape of ribs - is considered an
75 indication for a diet type in fossil and extant tetrapods (Hotton III et al., 1997, Sues and
76 Reisz, 1998, Reisz and Sues, 2000), including hominids (Bryant, 1915, Aiello and
77 Wheeler, 1995). However, quantitative tests of this concept are lacking. In this
78 manuscript, we intended to test whether the volume of the body cavity (coelomic or the
79 combination of thorax and abdomen), as reconstructed from mounted skeletons of various
80 terrestrial tetrapods, differs systematically with the diet typically ascribed to these
81 species. We hypothesized herbivores to have larger body cavities for a given body size
82 than carnivores. Additionally, we expected that among herbivorous non-avian dinosaurs,
83 species without adaptations for ingesta particle size comminution (such as a grinding
84 mastication or a gizzard) should have more voluminous body cavities than species with
85 such adaptations, because a voluminous gut and the corresponding long digesta retention
86 times can compensate for a lack of particle size reduction (Clauss et al., 2009, Hummel
87 and Clauss, 2011).

88

89 **Methods**

90 We compiled a dataset of digital 3D models of 11 mounted mammal skeletons available
91 from Sellers et al. (2012), from 19 previously performed scans (Gunga et al., 1999,
92 Gunga et al., 2007, Gunga et al., 2008, Stoinski et al., 2011), and additionally from our
93 own reconstruction of 96 specimens based on photogrammetry. If, for a species available
94 from Sellers et al. (2012) we also had a skeleton model of our own, we used our own
95 model. All skeletal material was photographed with permission of the respective museum
96 or institution. Although rarely discussed in detail (Bates et al., 2009b, Hutchinson et al.,
97 2011, Sellers et al., 2012, Brassey and Sellers, 2014), a typical issue in dealing with
98 mounted skeletons is the quality of the mount; whenever discussed, the positioning of the
99 ribs and the intervertebral spaces are among the characteristics considered particularly
100 critical. Because for our study, the torso was the main target, we did not focus on the
101 quality of other mounted parts (such as the neck, head, or tail). For the torso, we only
102 chose mounts in which the ribs were in a fixed position (as opposed to 'dangling loosely'),
103 where the rib cage did not have a 'compressed' appearance (such as in mounts where the
104 osseous ventral ends of the ribs appeared too close to allow for a cartilaginous part or a
105 sternum), and where the articular facets of the ribs and the thoracic vertebrae apposed
106 each other. This resulted in 126 digital skeletons of tetrapods including 86 synapsids (10
107 'mammal-like reptiles' or basal synapsids and 76 fossil and extant mammals), 38 diapsids
108 (6 extant birds, 27 non-avian dinosaurs, 5 fossil and extant reptiles), and two amphibians.
109 Of these, 31 were categorized as carnivores and 95 as herbivores (Table S1).

110 For reconstruction from multiple images, we first made a series of overlapping
111 photographs from a large number of positions in a circle around the specimen. The
112 images were acquired with a Canon 600D DSLR camera, in most of the cases mounted

113 on a tripod. For the majority of reconstructions we used an image resolution of 2592 x
114 1728 pixels, because we found this quality to be sufficient for our purposes. The 3D
115 models were computed from these image sequences using publicly available structure-
116 from-motion software Visual SFM (Wu, 2007, Wu et al., 2011, Wu, 2012) and Bundler
117 (Snavely et al., 2006), and multiview stereo software PMVS2 (Furukawa and Ponce,
118 2010). The resulting reconstructions (Fig. 1A) were then scaled to true size. For this
119 purpose, we measured several distances on the skeletal specimens or its location (such as
120 the length of boards on which specimens were mounted), identified them in the point
121 cloud and scaled the reconstruction accordingly. We cleaned the point clouds from the
122 background, from supporting structures (such as poles on which bones were mounted)
123 that would interfere with the reconstruction of the convex hull of the torso, and
124 reconstruction artefacts (Fig. 1B). The 3D reconstructions used from previous sources
125 resembled, in their state, those produced during the present study at this stage.

126 From this stage onwards, the workflow was identical for 3D reconstructions from
127 previous sources and the ones generated for the present study. Side views of all 3D
128 reconstructions used in this study are given as Fig. S1-S5 in the online supplement, and
129 the original 3D reconstructions can be accessed at Morphobank (www.morphobank.org,
130 Project P2404). The torsos were segmented out using open source software Meshlab
131 (Cignoni et al., 2008). In doing so, care was taken to remove from torsos all aspects that
132 do not contribute to the volume of the body cavity, such as the spinal processes of the
133 vertebrae. Then, the volumes of convex hulls (Sellers et al., 2012, Brassey and Sellers,
134 2014) (Fig. 1C) of the torsos were calculated using Point Cloud Library (Aldoma et al.,
135 2012). Five torsos that were reconstructed mainly from one side were digitally mirrored

136 (indicated in Table S1). In eight cases, the convex hull of the torso was not plausible and
137 included additional space, for example lateral to the ribcage; in these cases, the torso was
138 digitally cut into two parts (typically at the level of the last rib) and the convex hull
139 calculated for each part, and the resulting individual volumes added together (specimens
140 indicated in Table S1).

141 In comparative analyses, it is necessary to correct for body size. Typically, this is
142 done using body mass (Peters, 1983, Calder, 1996, Sibly et al., 2012), and alternatives are
143 mostly only resorted to if body mass itself is not available. Body mass measure were not
144 available for the specimens from which the skeletons for the present study had been
145 taken, and therefore, a skeletal proxy for body mass had to be found. However, also
146 methodological considerations argue against using body mass in this case: The volume of
147 the torso represents a major proportion of overall body mass, and therefore, differences in
148 torso volume most certainly are reflected in body mass differences already. 'Correcting'
149 for body mass (rather than for body size) would hence most likely diminish any potential
150 trophic signal. On the other hand, body mass itself might serve as a proxy for body cavity
151 volume when compared to another size proxy. Please refer to the online supplement for a
152 more detailed discussion and a demonstration of this concept in Tables S3 and S4.
153 Because body mass itself is not a useful proxy for the question of our study, mass
154 reconstructions from convex hull volumes of the complete skeletons were not considered
155 a valid option. Given the nature of our data, the most promising candidate was femur
156 length (Campione and Evans, 2012). The femur length was calculated as the length of the
157 bounding box of the thighbone (Fig. 1D). For this, we aligned the bone to the axis using
158 principal component analysis (Jolliffe, 2002). The first principal axis, which is the axis of

159 the largest variation of the data, for the thighbone usually corresponds to the main
160 direction in which the bone is elongated.

161 As a proxy for the proportion of the convex hull of the abdominal cavity that was
162 not ‘supported’ by bony structures (i.e., a proxy for how much of the abdominal wall
163 reconstructed as the convex hull spanned ‘open distances’ in the mounted skeleton), we
164 calculated the ‘free-hull ratio’. We sampled 8000 evenly distributed points (with constant
165 distance between the points for a given skeleton) on the convex hull, labeled every
166 sample of it as ‘supported’ or ‘non-supported’ (purple and green dots, respectively, in
167 Fig. 1E), and calculated the ratio of the number of ‘non-supported’ points to the number
168 of all points. Labels were ascribed by the following procedure. For each 3D point on the
169 skeleton we determined the closest point on the convex hull and marked all sampled
170 points within a certain distance of it as ‘supported’. This distance had to be adapted to the
171 size of the animal; we took 3% of the diagonal of the bounding box of the total animal
172 model as determined by principal component analysis (Jolliffe, 2002). We used the
173 region growing method from Point Cloud Library (Aldoma et al., 2012) to cluster the
174 points with the same labels together. We took the largest cluster of ‘non-supported’
175 points, which usually corresponded to the area of the abdominal wall (and discarded the
176 cases when it did not). A higher ‘free-hull ratio’ indicates that a larger proportion of the
177 body cavity is delineated by soft tissue (i.e., the abdominal wall).

178 Species were classified as herbivores or carnivores (thus omitting more subtle
179 categories such as omnivores) based on the main category of diet items, using a variety of
180 sources (Walls, 1981, Losos and Greene, 1988, Rand et al., 1990, Weishampel et al.,
181 1990, Reisz and Sues, 2000, Reisz, 2006, Wilman et al., 2014), including the

182 Paleobiology Database (www.paleobiodb.org). Herbivorous dinosaurs were classified as
183 chewers or non-chewers following Weishampel et al. (1990) and considering sauropods
184 as neither chewing nor grinding ingesta in a gizzard (Wings and Sander, 2007;
185 classifications in Table S1).

186 We analyzed the influence of diet on the volume of the torso or the free-hull ratio as
187 related to femur length, accounting for phylogeny based on a tree constructed from
188 literature data (the basic topology of tetrapod groups is based on tree of life project
189 (Maddison and Schulz, 2007) supplemented with specific references). See the online
190 supplement for a detailed description of the phylogenetic tree.

191 Data were evaluated as

$$192 \quad \text{Torso volume (cm}^3\text{)} = a \text{ (factor) Femur length}^b$$

193 and

$$194 \quad \text{Free-hull ratio} = a \text{ (factor) Femur length}^b$$

195 using log-transformed data and diet type (carnivore or herbivore), chewing type (in
196 non-avian dinosaur herbivores: chewers and non-chewers) or various taxonomic factors
197 in addition, as indicated in Table 1 and 2. When using an additional factor, first a model
198 that included the femur length-factor interaction was used; if the interaction was not
199 significant, the same model without the interaction was used. For example, if the (factor)
200 term was coded, for diet, as carnivore = 0 and herbivore = 1, then the resulting factor
201 estimate z can be translated into 'herbivores have a z times larger torso volume than
202 carnivores'. To account for the phylogenetic non-independence of data, analyses were
203 performed using Phylogenetic Generalized Least Squares (PGLS). The phylogenetic
204 signal (λ) was estimated using maximum likelihood (Revell, 2010). λ can vary between 0

205 (no phylogenetic signal) and 1 (strong phylogenetic signal; similarity among species
206 scales in proportion to their shared evolutionary time), i.e. we assumed Pagel's correlation
207 structure (Pagel, 1999, Freckleton et al., 2002). Statistical tests were performed using the
208 package CAPER (Orme et al., 2010) in R 2.15.0 (Team, 2011). Results of analyses with
209 Ordinary Least Squares (OLS), i.e. without accounting for the phylogenetic structure of
210 the data, using the package nlme (Pinheiro et al., 2011), are also reported. Note that for
211 some analyses that specifically address a question linked to phylogeny, such as the
212 question whether basal synapsids differ from all other groups, analyses that 'correct' for
213 the phylogenetic relationships cannot provide a relevant answer. The significance level
214 was set to 0.05. Based on the general geometric relationship between a length and a
215 volume measure, we expected torso volumes to scale approximately with femur length to
216 the cubic power (length³).

217

218 **Results**

219 Generally, torso volume scaled to femur length at an exponent that included the cubic
220 power (i.e., femur length^{3.0}) in the 95% confidence interval, as expected for a geometric
221 scaling of a volume-distance relationship (Table 1). This overall scaling did not differ
222 between synapsids and diapsids (Table 1). However, the basal synapsids had torso
223 volumes about 3.5 times larger than all the other clades (Table 1, Fig. 2A).

224 In the overall dataset, diet had a significant effect on the torso volume, with
225 herbivores having about 1.5 times larger torso volumes than carnivores (Table 1). This
226 was due to a clear effect of diet in mammals - the largest clade in our dataset. In
227 mammals, herbivores again had about 1.5 times larger torso volumes than carnivores

228 (Table 1, Fig. 2A). We did not have a sufficient number of basal synapsids to test for a
229 difference between diet types and the visual pattern does not suggest a clear distinction
230 between carnivores and herbivores in this group (Fig. 2A).

231 In contrast to mammals, there was no significant effect of diet on torso volume in
232 all diapsids or in non-avian dinosaurs only (Table 1, Fig. 2B). We did not have a
233 sufficient number of birds or reptiles to test for a difference between diet types in these
234 diapsid clades; the visual patterns, however, did not suggest a clear distinction between
235 carnivores and herbivores in these groups, nor in non-avian dinosaurs (Fig. 2B). Among
236 herbivorous non-avian dinosaurs, there was no difference in relative torso volume
237 between species with or without a grinding mastication (Table 1, as exemplified by the
238 non-chewers *Giraffatitan*, *Stegosaurus* and *Euoplocephalus* compared to the chewer
239 *Iguanodon* in Fig. 2B).

240 The relationship of the free hull ratio and femur length was generally negative,
241 indicating that larger animals had a lower proportion of their body cavity delineated by
242 soft tissue (Table 2). This was evident in both synapsids (Fig. 3A) and diapsids (Fig. 3B).
243 Diet did not have an effect on this relationship (Table 2). Variation in the free hull ratio
244 increased with body size (Fig. 3AB), some animals having a low contribution of bony
245 support to the delineation of the body cavity (such as proboscideans amongst mammals in
246 Fig. 3A or *Triceratops* among non-avian dinosaurs in Fig. 3B), and some animals with a
247 ribcage nearly delineating the complete ventral body cavity (such as giraffe or rhinoceros
248 among mammals in Fig. 3A or *Diplodocus* among non-avian dinosaurs in Fig. 3B).

249

250 **Discussion**

251 The hypothesis that herbivores have more voluminous body cavities than carnivores was
252 confirmed for the mammals in our dataset. However, no diet effect was detected in
253 diapsids and non-avian dinosaurs. Considering the overrepresentation of mammals in our
254 dataset, and in particular the low number of birds, reptiles and carnivorous non-avian
255 dinosaurs, this finding may be due to a restricted sample size, and should be considered
256 explorative for these groups. In this respect, we hope that making our digital skeletons
257 accessible at Morphobank will facilitate similar tests with increased sample sizes as more
258 digital skeletons become available. However, individual findings, such as a particularly
259 large body cavity in a carnivorous varanid (Fig. 2B), possibly indicate that the diet effect
260 observed in mammals need not necessarily be reflected in other groups.

261 Several important methodological constraints of our study need to be mentioned.
262 The use of femur length as a proxy for body size might not be considered ideal, also
263 because measurements were not taken on the original skeletons but, to grant consistency
264 across all 3D models used, on the digitally isolated 3D reconstruction of the femur.
265 Inaccurate measurements, such as underestimation of femur length due to overlap of
266 other skeletal structures such as the acetabulum, may evidently occur. Yet, the question
267 about a more suitable proxy than femur length is difficult to answer. As stated in the
268 methods, because the torso volume represents a major proportion of overall body mass, it
269 appears probable that differences in the torso volume-femur length relationship should be
270 mirrored in the body mass-femur length relationship. See the online supplement for an
271 explorative analysis suggesting support for this hypothesis (using literature body mass
272 data in connection with our own measurements). An even more important constraint of
273 studies such as ours is the quality of the skeletal mounts used (Bates et al., 2009b,

274 Hutchinson et al., 2011, Sellers et al., 2012, Brassey and Sellers, 2014, Claessens, 2015).
275 Incorrect reconstructions of rib shape and rib position, exacerbated by a lack of
276 conservation of cartilaginous components of the torso (such as costal and sternal cartilage
277 and intervertebral disks) or small osseous structures (such as components of the pectoral
278 girdle), will greatly influence any measurements derived from skeletal mounts, and are
279 the more likely to occur the less familiar a curator is with the species in question.
280 Inherently, this means that fossil specimens underlie a greater uncertainty in this respect
281 than representatives of extant species. Ultimately, concurrent measurements of gut tissue,
282 gut content and body mass as well as body cavity volume in healthy, non-fasted animals
283 will be required to empirically prove the assumption that extant herbivores carry more
284 weight at similar body size than extant carnivores.

285 The absence of a diet effect in non-avian dinosaurs could on the one hand reflect
286 these difficulties in correctly reconstructing skeletal appearance in fossil organisms, in
287 particular the rib cage (Bates et al., 2009a, Claessens, 2015). On the other hand, the
288 absence of a clear diet signal in diapsids could be linked to the *bauplan* heterogeneity
289 within lineages (e.g., bipedal vs. quadrupedal, which in non-avian dinosaurs mostly
290 mirrors the herbivore/carnivore dichotomy); or due to an ectothermic or mesothermic
291 metabolism in reptiles and (some) non-avian dinosaurs (Grady et al., 2014, Werner and
292 Griebeler, 2014) that did not exert a similar selective pressure on optimal body design as
293 endothermy. Heterogeneity might even have occurred on the level of metabolism
294 between dinosaur lineages. Additionally, the respiratory system of diapsids with its
295 heterogenous lung, pneumatized bones and space occupied by variable coelomic air sacs,
296 and unidirectional air flow (O'Connor and Claessens, 2005, Perry et al., 2011, Farmer,

297 2015) may exert additional selective pressures on the shape of the torso (Claessens, 2015)
298 that are not yet fully understood. A specific prediction about a difference in the body
299 cavity volume between herbivorous non-avian dinosaurs with and without adaptations for
300 ingesta particle size reduction (Hummel and Clauss, 2011, Clauss et al., 2013) could also
301 not be confirmed in the present study.

302 In contrast, the general concept of larger body cavity volumes that accommodate
303 larger guts in herbivores is supported for mammals. Reasons for the distinct diet
304 difference in mammals may be the large sample size, the large number of extant
305 specimens (in which constructing correct skeletal mounts may be easier), and the fact that
306 mounts of fossil forms can be more easily constructed with extant species as reference
307 guidelines. Additionally, the high overall mammalian level of metabolism and efficient
308 cursoriality, which might have led to an evolutionary arms race of predators and prey
309 (Lovegrove, 2001) that represented a high level of selective pressure for an optimized
310 torso volume, may be responsible for the clearer separation of diet types. Given that basal
311 synapsids had relatively higher torso volumes than mammals, one could hypothesize an
312 evolutionary optimization or 'escalation' (Vermeij, 1987, 2013) of the body shape in the
313 synapsid lineage.

314 In developing evolutionary arms race scenarios, such as between predators and
315 prey, the effects of differences in body shape with their effect on the center of gravity
316 (Bates et al., 2009b, Bates et al., 2016), differences in the weight of digestive organ tissue
317 (Schiek and Millar, 1985), and especially the effects of putative differences in the weight
318 of digestive tract contents (Müller et al., 2013) should be considered, which may lead to
319 different non-muscle:muscle ratios in predators and prey. In the context of changes within

320 lineages, such as changes in insular forms in the absence of predators, estimating body
321 cavity dimensions from carefully reconstructed mounted skeletons may provide
322 additional evidence to understand constraints of vertebrate *bauplan* evolution.

323 In our dataset, diapsids and synapsids shared the characteristic of an increasing
324 divergence in the 'free hull ratio' with increasing body size. Some species had a high, and
325 some had a low proportion of the body cavity delineated by soft tissue only. Such
326 differences may be linked to differences in cursoriality (Bramble, 1987), where a more
327 rigid torso (with a lower 'free-hull ratio') may be a prerequisite for galloping. For
328 example, considering the debate about the locomotion capabilities of *Triceratops*
329 (Thulborn, 1982, Paul and Christiansen, 2000), the similarity of *Triceratops* to
330 proboscideans (which do not gallop) with respect to an abdominal cavity with particularly
331 little bony support might represent an additional argument against galloping in the former
332 group. Differences in the 'free hull ratio' may also be related to the degree that the gut can
333 accommodate increasing intake levels by distension without compromising digesta
334 retention times (Clauss et al., 2007).

335 Examples such as the proboscideans and the proboscis monkey (*Nasalis larvatus*)
336 in Fig. 2A emphasize a limitation of the convex hull method that may arguably even lead
337 to an underestimation of the real difference between herbivores and carnivores: the part
338 of the convex hull that is not supported by bony structures, and hence is estimated as a
339 relatively straight line, might in reality be a bulging abdominal wall. Whereas in
340 carnivores, the rib cage may usually represent the most ventral part of the torso contour,
341 this lowest point is typically not marked by the rib cage in herbivores, but is positioned
342 posterior to it and marked by the soft-tissue abdominal wall (Starck, 1982). The

343 reconstruction of this soft tissue border is particularly difficult from mounted skeletons
344 (Bates et al., 2009b). In the proboscis monkey, with its typical bulging belly (Harding,
345 2015), it seems even as if a reduction in the extent of the rib cage facilitates the extreme
346 expansion of the abdominal cavity - an effect not reflected in the convex hull estimate of
347 the torso in this species. Correspondingly, in our dataset, the proboscis monkey
348 represented an outlier as the mammalian herbivore with the smallest relative torso
349 volume (Fig. 2A). For a more realistic approximation of the total body cavity volumes,
350 more comprehensive studies that include 3D reconstructions of taxidermic specimens or
351 live animals at various stages of food intake levels may be required. To our knowledge,
352 no systematic investigations on these different *bauplan* strategies exist. In theory, animals
353 could evolve a voluminous body cavity either by soft tissue expansion, by a deepening
354 and broadening of their ribcage and corresponding pelvic structures, or by a combination
355 of both.

356 In conclusion, differences in the body cavity volume exist between herbivores and
357 carnivores exist in mammals that most likely reflect differences in the digestive anatomy
358 and physiology between these groups (Stevens and Hume, 1998). The apparent decrease
359 in body cavity volume from basal synapsids to mammals possibly represents an example
360 of evolutionary optimization. In the comparison of dinosaurs with mammals, in addition
361 to questions about the reliability of skeletal reconstructions, our preliminary findings may
362 hint at fundamental *bauplan* differences linked to the different lung anatomy between
363 synapsids and diapsids, due to different levels of metabolism leading to differences in the
364 distinction in digestive anatomy between trophic guilds, or other hitherto unknown
365 factors.

366

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381

382 **Data accessibility**

383 The online supplement contains images of all skeletons used in this study with their
384 calculated convex hulls, all original measurements and species characteristics, three
385 outliers not considered in the final dataset, and details on the construction of the
386 phylogenetic tree. The Phylogenetic tree as Mesquite (nexus) file (129Tetrapods.nex) as
387 well as all digital 3D skeleton reconstructions are deposited (full skeleton, isolated femur,
388 isolated torso, torso convex hull, mirrored torso where applicable) in Morphobank Project
389 P2404. Reviewers/Editors, please login at <http://www.morphobank.org> using as email
390 address the project number "P2404" and as password "SNS533" to access the nexus file
391 and the .ply files. Download the .ply files and open in Meshlab (freely available at
392 <http://meshlab.sourceforge.net/>); if you open the whole skeleton and the hull at the same
393 time, you can see the reconstructed torso hull and the skeleton together.

394

395 **Authors contributions**

396 MC, OH, PMS designed the study. IN, MC, BH acquired the data, HCG provided
397 additional data, IN processed the data, IN, DF, JK, MC prepared the torsos, IN, DF, JK
398 took the digital measurements, CM collated the phylogenetic tree, CM and MC analyzed
399 the resulting measurements. MC, IN, CM prepared the first draft of the manuscript that
400 then received input from all co-authors.

401

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578

579 **Table 1.** Results of statistical analyses according to Torso volume= *a* (factor) Femur length^{*b*} (and the
 580 corresponding factor*Femur length interaction) in Ordinary Least Squares (OLS) and Phylogenetic
 581 Generalized Least Squares (PGLS)

Stats	λ	A (95%CI)	p	b (95%CI)	p	factor[#] (95%CI)	p	interaction[†] p
OLS	(0)	2.23 (1.38, 3.59)	0.001	All specimens (n=126) 2.97 (2.84, 3.11)		-	-	-
PGLS	0.906**	5.20 (2.47, 10.93)	<0.001	3.04 (2.88, 3.21)	<0.001	-	-	-
OLS	(0)	1.75 (0.97, 3.16)	0.067	3.01 (2.86, 3.15)	<0.001	<i>Synapsid/Diapsid</i> 1.21 (0.92, 1.60)		0.178 n.s.
PGLS	0.904**	7.59 (2.94, 19.61)	<0.001	3.03 (2.87, 3.20)	<0.001	0.70 (0.41, 1.22)	0.215	n.s.
OLS	(0)	1.70 (1.13, 2.57)	0.013	3.02 (2.90, 3.13)	<0.001	<i>Basal synapsid</i> 3.64 (2.52, 5.26)		<0.001 n.s.
PGLS	0.907**	5.29 (2.51, 11.17)	<0.001	3.04 (2.87, 3.21)	<0.001	0.81 (0.47, 1.40)	0.449	n.s.
OLS	(0)	1.94 (1.21, 3.09)	0.007	2.92 (2.78, 3.05)	<0.001	<i>Diet</i> 1.57 (1.19, 2.08)		0.002 n.s.
PGLS	0.872**	4.81 (2.39, 9.66)	<0.001	3.01 (2.84, 3.17)	<0.001	1.48 (1.13, 1.95)	0.005	n.s.
OLS	(0)	2.38 (0.92, 6.16)	0.085	<i>All carnivores (n=31)</i> 2.85 (2.55, 3.15)		-	-	-
PGLS	0.922*	8.93 (2.66, 29.95)	0.001	2.79 (2.45, 3.13)	<0.001	-	-	-
OLS	(0)	2.83 (1.64, 4.90)	<0.001	<i>All herbivores (n=95)</i> 2.94 (2.79, 3.08)		-	-	-
PGLS	0.918**	5.74 (2.58, 12.74)	<0.001	3.06 (2.88, 3.25)	<0.001	-	-	-
OLS	(0)	1.71 (0.89, 3.28)	0.112	Synapsids (n=86) 3.07 (2.87, 3.26)		-	-	-
PGLS	0.926**	4.47 (2.14, 9.34)	<0.001	3.13 (2.93, 3.33)	<0.001	-	-	-
OLS	(0)	1.35 (0.78, 2.33)	0.285	3.09 (2.93, 3.26)	<0.001	<i>Basal synapsid</i> 3.45 (2.34, 5.08)		<0.001 n.s.
PGLS	0.920**	1.68 (0.32, 8.73)	0.539	3.13 (2.93, 3.33)	<0.001	2.66 (0.61, 11.66)	0.199	n.s.
OLS	(0)	1.51 (0.81, 2.81)	0.202	2.98 (2.79, 3.18)	<0.001	<i>Diet</i> 1.72 (1.23, 2.40)		0.002 n.s.
PGLS	0.926**	13.12 (4.10, 42.02)	<0.001	2.73 (2.35, 3.10)	<0.001	0.31 (0.09, 1.14)	0.082	0.028
OLS	(0)	0.31 (0.01, 7.79)	0.499	Basal synapsids (n=10) 3.96 (2.94, 4.98)		-	-	-
PGLS	0	0.50 (0.02, 12.99)	0.685	3.83 (2.77, 4.89)	<0.001	-	-	-

582 (ctd.)

Stats	λ	A (95%CI)	p	b (95%CI)	p	factor [#] (95%CI)	p	interaction [†] p
Mammals (n=76)								
OLS	(0)	1.45 (0.84, 2.50)	0.189	3.07 (2.91, 3.24)	<0.001	-	-	-
PGLS	0.703**	1.44 (0.72, 2.88)	0.300	3.07 (2.90, 3.24)	<0.001	-	-	-
Diet								
OLS	(0)	1.12 (0.70, 1.81)	0.640	2.98 (2.84, 3.12)	<0.001	2.08 (1.58, 2.73)	<0.001	n.s.
PGLS	0.476	1.19 (0.63, 2.24)	0.598	3.02 (2.86, 3.19)	<0.001	1.56 (1.06, 2.29)	0.027	n.s.
Mammal carnivores (n=18)								
OLS	(0)	1.93 (0.89, 4.19)	0.117	2.79 (2.53, 3.05)	<0.001	-	-	-
PGLS	0	1.91 (0.88, 4.17)	0.122	2.80 (2.54, 3.05)	<0.001	-	-	-
Mammal herbivores (n=58)								
OLS	(0)	1.95 (1.09, 3.49)	0.028	3.03 (2.86, 3.20)	<0.001	-	-	-
PGLS	0.755	1.25 (0.55, 2.83)	0.592	3.15 (2.95, 3.35)	<0.001	-	-	-
Diapsids (n=38)								
OLS	(0)	2.01 (0.95, 4.23)	0.075	2.96 (2.78, 3.15)	<0.001	-	-	-
PGLS	0	2.88 (1.24, 6.69)	0.019	2.88 (2.68, 3.09)	0.127	-	-	-
Diet								
OLS	(0)	1.84 (0.85, 3.97)	0.131	2.94 (2.75, 3.13)	<0.001	1.25 (0.78, 2.03)	0.363	n.s.
PGLS	0	2.32 (0.95, 5.67)	0.074	2.87 (2.66, 3.07)	<0.001	1.42 (0.84, 2.38)	0.197	n.s.
Diapsid carnivores (n=8)								
OLS	(0)	2.18 (0.53, 8.99)	0.324	2.89 (2.50, 3.29)	<0.001	-	-	-
PGLS	1***	1.72 (0.43, 6.79)	0.471	3.01 (2.66, 3.37)	<0.001	-	-	-
Diapsid herbivores (n=30)								
OLS	(0)	2.12 (0.84, 5.39)	0.124	2.96 (2.74, 3.18)	<0.001	-	-	-
PGLS	0	3.31 (1.21, 9.09)	0.027	2.86 (2.62, 3.11)	<0.001	-	-	-
Non-avian dinosaurs (n=27)								
OLS	(0)	2.87 (0.67, 12.30)	0.168	2.89 (2.56, 3.21)	<0.001	-	-	-
PGLS	0.651**	2.05 (0.54, 7.83)	0.303	2.96 (2.65, 3.27)	<0.001	-	-	-
Diet								
OLS	(0)	2.15 (0.47, 9.84)	0.333	2.89 (2.57, 3.21)	<0.001	1.37 (0.81, 2.31)	0.248	n.s.
PGLS	0.604	1.43 (0.32, 6.49)	0.647	2.97 (2.66, 3.29)	<0.001	1.40 (0.74, 2.66)	0.317	n.s.
Non-avian dinosaur herbivores (n=23)								
OLS	(0)	3.19 (0.68, 14.86)	0.155	2.87 (2.53, 3.22)	<0.001	-	-	-
PGLS	0.639	2.00 (0.47, 8.45)	0.358	2.97 (2.64, 3.31)	<0.001	-	-	-
Chewer								
OLS	(0)	2.87 (0.63, 13.05)	0.189	2.84 (2.50, 3.18)	<0.001	1.39 (0.87, 2.23)	0.187	n.s.
PGLS	0.649	2.14 (0.31, 14.61)	0.445	2.97 (2.60, 3.34)	<0.001	0.96 (0.45, 2.02)	0.907	n.s.

583 Torso volume in cm³, Femur length in cm584 * λ significantly different from 0, ** λ significantly different from 0 and 1, *** λ not significantly different from 0 and 1

585 #factor coding: Diet (carnivore = 0, herbivore = 1), Synapsid/Diapsid (diapsid = 0, Synapsid = 1), Basal synapsid (no basal synapsid =

586 0, basal synapsid = 1), Chewer (chewer = 0, nonchewer = 1)

587 †models were calculated with interaction term first; if this was not significant, the model was again calculated without the interaction

588 term; estimates for the factor in this table always represent the models where either the interaction was significant or excluded

589 **Table 2.** Results of statistical analyses according to Free-hull ratio = a (factor) Femur length^b (and the
 590 corresponding factor*Femur length interaction) in Ordinary Least Squares (OLS) and Phylogenetic
 591 Generalized Least Squares (PGLS)

Stats	λ	A (95%CI)	p	b (95%CI)	p	factor [#] (95%CI)	p	interaction [†] p
All specimens (n=126)								
OLS	(0)	0.37 (0.29, 0.48)	<0.001	-0.19 (-0.26, -0.11)	<0.001	-	-	-
PGLS	0.693**	0.32 (0.21, 0.49)	<0.001	-0.17 (-0.27, -0.06)	0.002	-	-	-
<i>Synapsid/Diapsid</i>								
OLS	(0)	0.38 (0.27, 0.52)	<0.001	-0.19 (-0.27, -0.11)	<0.001	0.99 (0.85, 1.15)	0.891	n.s.
PGLS	0.687**	0.28 (0.16, 0.47)	<0.001	-0.16 (-0.27, -0.06)	0.003	1.16 (0.84, 1.61)	0.373	n.s.
<i>Basal synapsid</i>								
OLS	(0)	0.39 (0.30, 0.50)	<0.001	-0.19 (-0.27, -0.12)	<0.001	0.85 (0.67, 1.08)	0.182	n.s.
PGLS	0.694**	0.32 (0.21, 0.49)	<0.001	-0.17 (-0.27, -0.06)	0.002	1.02 (0.72, 1.44)	0.929	n.s.
<i>Diet</i>								
OLS	(0)	0.37 (0.28, 0.48)	<0.001	-0.19 (-0.27, -0.12)	<0.001	1.05 (0.90, 1.23)	0.527	n.s.
PGLS	0.709**	0.31 (0.21, 0.47)	<0.001	-0.18 (-0.29, -0.08)	0.001	1.18 (0.99, 1.41)	0.066	n.s.
<i>All carnivores (n=31)</i>								
OLS	(0)	0.28 (0.19, 0.43)	<0.001	-0.11 (-0.24, 0.02)	0.112	-	-	-
PGLS	1.000*	0.22 (0.12, 0.40)	<0.001	-0.08 (-0.23, 0.07)	0.290	-	-	-
<i>All herbivores (n=95)</i>								
OLS	(0)	0.43 (0.30, 0.59)	<0.001	-0.22 (-0.31, -0.13)	<0.001	-	-	-
PGLS	0.511**	0.39 (0.25, 0.59)	<0.001	-0.22 (-0.33, -0.10)	<0.001	-	-	-
Synapsids (n=86)								
OLS	(0)	0.41 (0.29, 0.59)	<0.001	-0.22 (-0.32, -0.11)	<0.001	-	-	-
PGLS	0.882**	0.19 (0.11, 0.33)	<0.001	-0.17 (-0.31, -0.02)	0.028	-	-	-
<i>Basal synapsid</i>								
OLS	(0)	0.43 (0.30, 0.61)	<0.001	-0.22 (-0.33, -0.12)	<0.001	0.83 (0.65, 1.06)	0.140	n.s.
PGLS	0.796**	0.28 (0.11, 0.74)	0.012	-0.21 (-0.36, -0.06)	0.006	0.19 (0.04, 0.90)	0.040	0.031
<i>Diet</i>								
OLS	(0)	0.41 (0.29, 0.59)	<0.001	-0.22 (-0.33, -0.11)	<0.001	1.02 (0.84, 1.22)	0.876	n.s.
PGLS	0.826**	0.20 (0.12, 0.33)	<0.001	-0.21 (-0.35, -0.07)	0.005	1.33 (1.08, 1.64)	0.010	n.s.
Basal synapsids (n=10)								
OLS	(0)	0.09 (0.01, 0.81)	0.064	0.22 (-0.48, 0.91)	0.563	-	-	-
PGLS	0***	0.04 (0.00, 0.44)	0.031	0.46 (-0.34, 1.26)	0.292	-	-	-

592 (ctd.)

Stats	λ	A		b		factor [#]		interaction [†]
		(95%CI)	p	(95%CI)	p	(95%CI)	p	p
Mammals (n=76)								
OLS	(0)	0.45	<0.001	-0.23	<0.001	-	-	-
		(0.31, 0.63)		(-0.34, -0.13)				
PGLS	0.180	0.46	<0.001	-0.22	<0.001	-	-	-
		(0.31, 0.67)		(-0.33, -0.11)				
Diet								
OLS	(0)	0.46	<0.001	-0.23	<0.001	0.93	0.509	n.s.
		(0.32, 0.65)		(-0.33, -0.12)		(0.76, 1.14)		
PGLS	0.171	0.47	<0.001	-0.22	<0.001	0.96	0.756	n.s.
		(0.31, 0.70)		(-0.33, -0.10)		(0.76, 1.22)		
Mammal carnivores (n=18)								
OLS	(0)	0.31	<0.001	-0.09	0.146	-	-	-
		(0.22, 0.43)		(-0.21, 0.03)				
PGLS	0.709***	0.32	<0.001	-0.11	0.084	-	-	-
		(0.22, 0.46)		(-0.23, 0.01)				
Mammal herbivores (n=58)								
OLS	(0)	0.48	0.031	-0.26	<0.001	-	-	-
		(0.31, 0.77)		(-0.40, -0.13)				
PGLS	0.147	0.53	0.015	-0.26	0.001	-	-	-
		(0.32, 0.87)		(-0.40, -0.12)				
Diapsids (n=38)								
OLS	(0)	0.31	<0.001	-0.14	0.029	-	-	-
		(0.19, 0.50)		(-0.26, -0.02)				
PGLS	0.609**	0.30	<0.001	-0.17	0.036	-	-	-
		(0.16, 0.54)		(-0.33, -0.02)				
Diet								
OLS	(0)	0.28	<0.001	-0.16	0.015	1.24	0.186	n.s.
		(0.17, 0.47)		(-0.28, -0.04)		(0.91, 1.68)		
PGLS	0.600**	0.29	0.001	-0.17	0.039	1.03	0.866	n.s.
		(0.15, 0.58)		(-0.33, -0.01)		(0.72, 1.48)		
Diapsid carnivores (n=8)								
OLS	(0)	0.20	0.002	-0.06	0.503	-	-	-
		(0.11, 0.37)		(-0.23, 0.11)				
PGLS	0.613***	0.21	0.003	-0.08	0.369	-	-	-
		(0.11, 0.38)		(-0.24, 0.08)				
Diapsid herbivores (n=30)								
OLS	(0)	0.41	0.010	-0.20	0.015	-	-	-
		(0.22, 0.77)		(-0.35, -0.05)				
PGLS	0.633**	0.35	0.010	-0.20	0.050	-	-	-
		(0.16, 0.73)		(-0.38, -0.01)				
Non-avian dinosaurs (n=27)								
OLS	(0)	1.57	0.391	-0.49	<0.001	-	-	-
		(0.57, 4.34)		(-0.72, -0.27)				
PGLS	0.764*	0.39	0.161	-0.24	0.127	-	-	-
		(0.11, 1.39)		(-0.53, 0.06)				
Diet								
OLS	(0)	1.38	0.562	-0.49	<0.001	1.15	0.464	n.s.
		(0.47, 4.07)		(-0.72, -0.26)		(0.79, 1.67)		
PGLS	0.766*	0.48	0.338	-0.25	0.122	0.84	0.621	n.s.
		(0.11, 2.10)		(-0.55, 0.05)		(0.43, 1.66)		
Non-avian dinosaur herbivores (n=23)								
OLS	(0)	1.70	0.355	-0.51	0.001	-	-	-
		(0.57, 5.08)		(-0.75, -0.26)				
PGLS	0.857*	0.44	0.264	-0.27	0.122	-	-	-
		(0.11, 1.79)		(-0.60, 0.06)				
Chewer								
OLS	(0)	1.92	0.212	-0.47	0.001	0.68	0.025	n.s.
		(0.71, 5.18)		(-0.69, -0.25)		(0.50, 0.93)		
PGLS	0.713***	0.93	0.938	-0.35	0.063	0.64	0.233	n.s.
		(0.15, 5.70)		(-0.69, 0.00)		(0.31, 1.30)		

593 Free-hull ratio represents the proportion of the convex hull reconstruction of the torso not immediately supported by bone; Femur
594 length in cm

595 * λ significantly different from 0, ** λ significantly different from 0 and 1, *** λ not significantly different from 0 and 1

596 [#]factor coding: Diet (carnivore = 0, herbivore = 1), Synapsid/Diapsid (diapsid = 0, Synapsid = 1), Basal synapsid (no basal synapsid =
597 0, basal synapsid = 1), Chewer (chewer = 0, nonchewer = 1)

598 [†]models were calculated with interaction term first; if this was not significant, the model was again calculated without the interaction
599 term; estimates for the factor in this table always represent the models where either the interaction was significant or excluded

600 **Figure legends**

601 **Figure 1.** Illustration of the image processing for *Hexaprotodon liberiensis*. The raw data
602 (A) was scaled, cleaned of background and supporting structures (B). The torso was
603 isolated, removing structures that would influence the convex hull in a way not
604 corresponding to the actual body cavity, e.g. the spinal processes. Then the convex hull
605 was calculated (C). Note the absence of ribs in the area where they had been covered by
606 the scapula. Finally, the femur was isolated (D) to measure its length. The convex hull
607 was later divided (E) into parts that are supported by bone (red dots) and parts that are not
608 (green dots), to estimate the 'free-hull ratio'.

609

610 **Figure 2.** Relationship between the femur length (as proxy for body size) and the
611 reconstructed volume of the body cavity in (A) synapsids and (B) diapsids. Closed
612 symbols and full regression lines (cf. Table 1) indicate herbivores (except for the
613 Amphibia), open symbols and dotted line indicate carnivores. Skeletal models with the
614 estimated convex hull of the torso depicted include (A, from left to right) *Lycaenops*,
615 *Moschops*, *Nasalis*, *Panthera leo*, *Bos gaurus*, (B, from left to right:) *Varanus*,
616 *Euoplocephalus*, *Giraffatitan*, *Stegosaurus*, *Iguanodon*. Regression lines in (A) for
617 mammals, in (B) for all diapsids.

618

619 **Figure 3.** Relationship between the femur length (as proxy for body size) and the
620 proportion of the torso not supported by bone ('free-hull ratio') in (A) synapsids and (B)
621 diapsids. Closed symbols and full regression lines (cf. Table 2) indicate herbivores
622 (except for the Amphibia), open symbols and dotted lines indicate carnivores. Skeletal
623 models with the estimated convex hull of the torso depicted include (A, from top to
624 bottom) *Mammutus*, *Elephas*, *Giraffa*, *Diceros*, (B top to bottom:) *Triceratops*,
625 *Atlasaurus*, *Diplodocus*. Regression lines in (A) for mammals, in (B) for all diapsids.