

On reconstructing *Giraffa sivalensis*, an extinct giraffid from the Siwalik hills, India

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Giraffa sivalensis was probably the last species of the genus to occur in Southern Asia. The holotype, a single cervical vertebra of uncertain anatomical position, was discovered in the upper Siwalik deposits of India, placing the occurrence of this animal during the Plio-Pleistocene. No estimates of its body mass have been ~~made yet~~^{published}. Here we estimated neck length, leg length and body mass from available postcranial fossil specimens, which included a complete cervical vertebra (established as a third cervical, C3), fragments of two humeri, a radius/ulna and various metacarpi. Body size and body shape estimates were based on *Giraffa camelopardalis* ontogenetic allometry and, where available, interspecific allometry. *G. sivalensis* had an average neck length of approximately 147 cm and a total reaching height of 388 cm. However, we found that different dimensions, equations, and fossil measurements gave wide prediction ranges for body mass (C3 dimensions predicted 228kg-575kg; humerus dimensions predicted 561kg-1304kg; radius dimensions predicted 847kg-1891kg and metacarpus dimensions predicted 1058kg-1165kg). To determine which estimations were most reliable, we evaluated which equations predicted body mass with the smallest errors in two different sized extant giraffines (giraffes and okapis). It was found that vertebral dimensions were accurate for neck length characteristics, but less so for body mass estimates. The most appropriate predictor for body mass was humeral circumference using *G. camelopardalis* ontogenetic data, which estimated a body mass of 790kg. The most appropriate vertebral predictor for body mass was caudal dorsoventral vertebral body height which, ~~when~~^{the} using the holotype, estimated a body mass of around 400kg. This could indicate sexual dimorphism, a stockier body in *G. sivalensis* compared to *G. camelopardalis*, or even that another *Giraffa* species existed during the same period.

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29

30 Introduction

31 *G. sivalensis* (Falconer & Cautley, 1843) is the longest established ^{species of} extinct giraffe, yet neither a
32 complete skull nor specimens directly related to the holotype vertebra have been found ~~yet~~ (Matthew,
33 1929). Notwithstanding this, many fossil specimens have been assigned as belonging to (or not
34 belonging to) this species, without adequate consideration of its size estimates (Table S1). In addition,
35 many of these specimens have only been described in the Fauna Antiqua Sivalensis (Falconer &
36 Murchison, 1867), of which many of the plates (notably from plate E) have never been published.

37 *History of G. sivalensis fossil discovery*

38 In 1838 Sir Proby Cautley briefly described the discovery of a remarkable vertebra in the Siwalik hills
39 in India. He alluded to it as belonging to the giraffe genus – a significant statement, because up until
40 that time, no ~~other~~ fossil *Giraffa* species were known. Falconer and Cautley (1843) subsequently
41 named the species ‘*Camelopardalis sivalensis*’ and assigned the fossil, which was to become the
42 holotype, as a third cervical vertebra. Based on the dimensions, Falconer and Cautley predicted the
43 animal to be about a third as long as extant giraffes.

44 Since Cautley’s discovery other *Giraffa*-like fossils have also been found in Asia, Europe and Africa.
45 The references to these fossil specimens are extensive, incomplete and confusing (Table S1 contains all
46 the references to *G. sivalensis* fossil specimens). Subsequently species like *G. attica*, *G. priscilla*, *G.*
47 *vetusta*, *G. jumae*, *G. stillei*, *G. gracilis*, *G. pygmaea* and *G. punjabiensis* have been proposed, not all
48 of which are generally accepted. Regarding sub-Himalayan giraffes for instance, controversy even
49 exists regarding the prevalence of giraffids within the Siwaliks (compare Lydekker, 1883; Aleem
50 Ahmed Khan, 1991 and Bhatti, 2004). Falconer (1868) summarised the giraffid fossils kept in the
51 Asiatic museum of the Bengal and those discovered on Perim island (Falconer, 1845) as well as plates
52 figuring some of the more important finds (Falconer & Murchison, 1867). Later, Lydekker would also
53 publish notes on fossil giraffids (1876, 1878, 1883) including their accompanying stratigraphy in the
54 Siwaliks. Lydekker also summarised all the giraffid specimens contained in the British and Indian
55 museum (Lydekker, 1885a,b), and renamed the genus *Camelopardalis* to *Giraffa*. Pilgrim reviewed all
56 the fossil Giraffidae of India in 1911. Notably, he made a distinction between the *Giraffa* species
57 discovered in the middle Siwaliks (*G. punjabiensis*) and that from the upper Siwaliks (*G. sivalensis*).

58 *Geographic and stratigraphic distribution of fossils*

59 Matthew (1929) placed the upper Siwalik deposits, where *G. sivalensis* fossils and nearly all Siwalik
60 fauna discovered by early writers such as Falconer have been found, as part of the Pinjor zone (see also
61 Gaur, Vasishat & Chopra, 1985; Aleem Ahmed Khan, 1991; Nanda, 2002, 2008; Bhatti, 2004). The
62 Pinjor zone dates to about 2.58 to 0.6 million years ago, placing fauna discovered in this site during the
63 late Pliocene/ early Pleistocene (Nanda, 2008).

64 The site of discovery of the holotype for *G. sivalensis* is given by Falconer and Cautley (1843) only as
65 in ‘the Sewalik range to the west of the river Jumna’ (currently the Yamuna river). Spamer, Daeschler
66 & Vostreys-Shapiro (1995) described the locality as ‘Siwalik hills, near Hardwar, Uttar Pradesh’. This
67 is however unlikely as Hardwar is east of the Yamuna river. We therefore believe the locality was
68 probably in the vicinity of the current Shivalik fossil park, Saketi, Himachal Pradesh, India (Figure 1)

69 *Size estimates*

70 The problem with assigning closely related fossil specimens to similar or distinct genera, especially in
71 the case of *G. sivalensis*, is that size estimates of the animal based on the holotype are often inadequate.
72 What was inferred about the size of *G. sivalensis* for example, is that was about ‘one third shorter’ with
73 a neck about ‘one tenth more slender’ as extant giraffes (Falconer & Cautley, 1843), that it was about
74 the same size as modern giraffes (Bhatti, 2004) or even that certain diameter measurements of the
75 holotype were larger than extant giraffes (Lydekker, 1876).

76 In this paper we attempt to summarise and clarify the relevant information about *G. sivalensis* and its
77 remains. In addition, we will discuss size and shape estimates for this animal.

78

79 **Materials & Methods**

80 All postcranial specimens assigned to *G. sivalensis* which were available in the Natural History
81 Museum, London, were studied. From these specimens body and neck size estimates were calculated
82 using giraffe ontogenetic or available interspecific allometric equations.

83 *Studied material and dimensions measured*

84 The only vertebra measured was the holotype, specimen **nr** OR39747, a cervical vertebra (Figure 2).
85 Falconer & Cautley (1843) presented an extensive description of this specimen. A caudal fragment of a
86 ‘fourth’ cervical **no** OR39748 (Lydekker, 1885a), also described as a second cervical by Falconer,
87 1845), as well as a caudal part of a ‘third’ cervical **no** OR39746 (Lydekker, 1885a) that have also been
88 assigned to *G. sivalensis* were missing from the Siwalik collection in the Natural History museum.
89 Dimensions were measured with a vernier calliper and included: vertebral body length, cranial
90 vertebral body height, cranial vertebral body width, caudal vertebral body height, caudal vertebral body
91 width and spinous process length.

92 Additional postcranial specimens assigned to *G. sivalensis* held at the Natural History Museum include
93 fragments of two humeri (OR39749, OR17136; Figure 3 and Figure 4 respectively), a fragment of a
94 radius/ulna (OR17130) and various fragments of metacarpal and phalanges (Lydekker, 1885a). Certain
95 of the metacarpal specimens were avoided in this study due to the unclear numbering of specimens and
96 deformation of the fossils. Subsequently only metacarpal specimen number OR39750 was deemed
97 usable. Measurements of long bones included length, circumference, cranio-caudal diameter and
98 medio-lateral diameter. The length and circumference measurements were done with a measuring tape,
99 while the cross sectional diameters were done with a vernier calliper.

100 According to Roth (1990), estimation of body characteristics (especially body mass) from a fossil
101 requires either a reconstruction of the animal based on a nearly complete skeleton, a model animal
102 inferred to be the same size and shape or a group of broadly analogous animal forms. In order to
103 predict body characteristics of a fossil from a model animal or group of animals, one can use regression
104 equations of the form $y=mx^b$ (Huxley, 1932). These regression equations can be based on data from
105 different species (interspecific allometry), within the growth phase of a single animal (ontogenetic
106 allometry) or amongst adult animals of different size but within the same species (static allometry). We
107 applied both ontogenetic as well as interspecific allometric equations to predict body mass in this case.

Since you did not do this (not having the data), I assume you disagree with Roth - should either say you didn't because you don't have the data, or explain why Roth is wrong, or omit this sentence.

108 Ontogenetic data were obtained from previous studies by the authors (Mitchell, van Sittert & Skinner,
 109 2009; van Sittert, Skinner & Mitchell, 2010, 2014), whilst interspecific regression equations were
 110 sourced from previously published work (Anderson, Hall-Martin & Russell, 1985; Roth, 1990; Scott,
 111 1990). Due to the finding that body mass predictions from dental dimensions can be problematic and
 112 that post cranial dimensions are probably better predictors (Damuth, 1990; Fortelius, 1990; Janis,
 113 1990), we did not consider the tooth dimensions available (Supplementary table 1) as predictors for
 114 body mass in the present study. Why not? It's true these papers suggest that postcranial dimensions are better estimators, but
 even so the dental equations still have very high r^2 and are reasonable predictors, especially if
 you use tooth lengths (not area) and a phylogenetically & functionally limited equation (such as
 all ruminant or all selenodont). I think including a dental prediction would give a better ability to
 compare your range of estimates to other size estimates for other fossil mammals, since dental
 data are so much more likely to be preserved.

115 *Statistical analysis*

116 Allometric equations were generated from bivariate data through ordinary least squares regression. To
 117 facilitate this, measurements were logarithmically transformed to base e prior to analysis. According to
 118 Warton et al. (2006), ordinary least squares regression is appropriate when one wishes to predict y
 119 from x , even when x contains measurement error, as long as the results are interpreted in the context of
 120 'predicting y from x measured with error'.

121 Because conflicting body dimensions (especially body masses) are often predicted by the different
 122 equations and by different fossil specimens, the predictions needed to be validated. If regression
 123 equations had reasonable predicting power in both of the extant species within the subfamily Giraffinae
 124 (*G. camelopardalis* and *Okapia johnstoni*), it was regarded as robust enough to extrapolate to *G.*
 125 *sivalensis* as well. Therefore, dimensions of 10 okapi skeletons were recorded in addition to the
 126 recorded *G. camelopardalis* data. The skeletons were housed in various museums and were recorded as
 127 opportunity presented itself. Where only adult specimens were used, adult okapi specimens were
 128 assumed to have weighed 250 kg, with a range of 200 – 300 kg (20% error) (Lindsey & Bennett, 1999;
 129 Stuart & Stuart, 2006). Prediction power of giraffe ontogenetic equations and interspecific equations on
 130 giraffe and okapi body masses were assessed through the percent prediction error, calculated as (van
 131 Valkenburgh, 1990):

$$132 \text{ ((Observed value – predicted value)/predicted value) x 100}$$

133 Prediction errors around 20% or less were considered as have adequate predicting power and
 134 robusticity within the size ranges of okapis and giraffes within the Giraffinae.

135

136 Results

137 *Characteristics of fossil specimens*

138 Matthew (1929) noted that *G. sivalensis* fossils are composed of soft, light, sandy matrix. Furthermore,
139 that ‘it is significant that most of the modern types... are in this type (*white fossilisation*) of
140 preservation’. The specimens observed by the authors at the British museum were, however, dark in
141 colour and not ‘soft fossil’. In fact, it agrees more with Falconer & Cautley's (1843) description of
142 ‘hard fossil’: “...acquires as specific hardness, or tinge of iron, with increased specific gravity”. The
143 ‘hard fossil’ type occurs when sandstone (as opposed to clay) is the matrix, and agrees with Cautley's
144 1838 original description noting that the type specimen was cleared out of a block of sandstone, as well
145 as Falconer and Cautley’s (1843) observation that the ‘smaller species of giraffe’ consists of ‘hard
146 fossil’.

147 *Dimensions measured*

148 The OR39747 and long bone dimensions measured are summarised in Table 1 and Table 2
149 respectively, and where applicable contains the equivalent measured values according to Falconer and
150 Cautley (1843). Except for the cranial vertebral body height, dimensions measured on OR39747 by the
151 authors are within 1% to 5% to that reported by Falconer and Cautley. Applicable data taken from the
152 measurements of okapi specimens are presented in Table 3.

153 *Predictions based on vertebra OR39747*

154 Based on *G. camelopardalis* ontogenetic data, *G. sivalensis* neck length (i.e. the average of dorsal and
155 ventral neck lengths) was 1467 mm in the live animal (i.e. skeletal including soft tissue length, Table
156 4). Based on skeletal tissue only, excluding soft tissue, the neck length is around 1270-1280~~mm~~. Using
157 the same ontogenetic data, we could estimate the foreleg (hoof to withers height, including soft tissue)
158 as 2540 mm, assuming that this animal had the same proportions as a growing giraffe. This would
159 mean that the reaching height of *G. sivalensis* was around 3.9~~m~~.

160 The different vertebral dimensions taken predict the body mass to be within a range of 228 to 575 kg,
161 with an average of 432 kg. By looking at the prediction error expected for each variable used in the
162 predictions, we may ascertain which predictions are more reliable across species. Naturally, because
163 the predictions were done using giraffe ontogenetic allometry, the giraffe predictions errors are lowest

164 (8% to 50%). Predictions for okapi body mass, however, range from 17% to 99%. The only variable
165 which gave relatively low prediction errors in both okapi (17%) and giraffe (25%) was caudal vertebral
166 body dorsoventral height. This dimension predicts a body mass of 390 kg if we consider OR39747 as a
167 third cervical (if it was considered a fourth or fifth cervical, body mass predictions will be 274 kg or
168 187 kg respectively.

169 *Predictions based on long bone dimensions*

170 All of the *G. sivalensis* long bone specimens available at the Natural History Museum were incomplete
171 proximally and / or distally. It was clear nevertheless, that the bones had the same slender appearance
172 of extant giraffes and were elongated. Humeral specimen OR 39749 was almost complete except for
173 the proximal metaphysis, which has clearly broken off at the **physeal** line of a subadult animal. is this a real word? shouldn't it be epiphyseal?
174 Regarding the radius/ulna specimen, the bones' fusion at the midshaft was not complete as in modern
175 giraffes, where the two bones are indistinguishable at midshaft in adults. The metacarpus specimen
176 included had the same caudal 'columns' as that described in the extant giraffe (van Schalkwyk, Skinner
177 & Mitchell, 2004), as well as that seen in *Okapia johnstoni* (own observation).

178 As no bones were complete length wise, bone length could not be used as a predictor for body mass,
179 which, in any case, is not a good estimator for body mass in other taxa (Scott, 1990). Based on
180 circumferences of humeri OR39749 and OR17130 and using *G. camelopardalis* ontogenetic data these
181 specimens may have belonged to animals in the range of around 770 kg to 810 kg. An extant giraffe of
182 this body mass would have a humerus length of about 475 mm to 485 mm, which is just slightly longer
183 than the 453 mm measured on OR39749 (which lacked only a distal metaphysis). The predictors based
184 on radial and metacarpal cross sectional dimensions gave much higher body mass estimates - averages
185 of 1024 kg and 1107 kg respectively (Table 5). In addition to our extant giraffe ontogenetic sample for
186 allometric equation generation, we also employed interspecific equations from previous studies
187 (Anderson, Hall-Martin & Russell, 1985; Roth, 1990; Scott, 1990). Interspecific equations tended to
188 predict heavier body masses than ontogenetic equations, especially so in the distal long bone samples.

189

190 **Discussion**191 *Vertebral identity of OR39747*

192 The anatomical identity of OR39747 was disputed by Lydekker (1885a), when he suggested that the
193 vertebra was probably a fifth cervical vertebra of a ‘very small individual’. Lydekker based his
194 suggestion on the observation that Falconer was in a habit of not counting the atlas and occasionally
195 the axis as cervicals, and started numbering the cervicals at the second or third vertebra. Mammalian
196 C3 to C5 vertebrae forms a repetitive series and often does not have the distinguishing characteristics
197 present in the other cervical vertebrae (Solounias, 1999). It is therefore indeed challenging to assign
198 OR39747 to a specific vertebral number. If we assume approximate similarity in shape between *G.*
199 *sivalensis* and *G. camelopardalis* vertebrae, however, there are clues in the extent to which the cranial
200 articular processes (*Proc. Articularis cranialis*) extend beyond the body or centrum of the vertebra
201 (*Corpus vertebrae*). In the *G. camelopardalis* C3 this process extends well beyond the cranial
202 extremity of the vertebral body, but ends before or approximately at the same dorsoventral plane as the
203 vertebral body in C4 and C5. Judging by the extent of the articular processes of OR39747 ~~then~~, it is a
204 third, fourth and fifth cervical in decreasing order of likelihood. Falconer was therefore correct in
205 assigning this vertebra as a third cervical, albeit fortuitously so.

206 Lydekker’s (1885a) suggestion of a very small individual could not have implied an immature animal,
207 as the fusion of the epiphysis to the body of the vertebra is complete and the clear definitions of bony
208 ridges and muscular depressions point to a mature animal. Lydekker thus probably based his idea of a
209 small individual on two larger *G. sivalensis* vertebrae (a proximal part of a ‘third’ (OR39746) and
210 distal part of a ‘fourth’ cervical (OR39748), as mentioned in his catalogue of the Natural History
211 Museum (1885a, Table S1). These two vertebra were however not locatable within the Siwalik
212 collection at the time of this study (P Brewer, Curator of fossil mammals, NHM, personal
213 communication, 2013). Nevertheless, Falconer (1845) reported OR39748 to be 2.1 inch (53.3 mm) in
214 width and height at the caudal extremity, which is only 0.2 mm greater than our measurement of
215 OR39747’s caudal extremity. Based on our allometric equations this does not indicate that OR39747
216 came from a ‘very small’ individual. Indeed, OR39748 will have weighed 394/kg or 277/kg if it was a
217 C3 or C4 respectively. Rather, it may merely be an indication of confusion regarding the identity of
218 serial cervical vertebrae or might also be related to sexual size dimorphism amongst adults.

219 *Ontogenetic and interspecific scaling models*

220 The method employed here is unique in that it uses ontogenetic allometry to predict an adult animal's
221 size. We believe that, in this case, it is warranted because of the unique shape of giraffines. In order to
222 describe life history traits and morphologies from fossil specimens, it is customary to find associated
223 characters in fossil and extant specimens and extrapolate fossil traits and morphologies accordingly
224 (Runestad, 1994). However, no extant species has such an extreme shape as *G. camelopardalis*, and the
225 only other extant giraffid is the okapi. Indeed, interspecific allometric equations predict extant giraffids
226 poorly (McMahon, 1975; Scott, 1990). It is also uncertain what to consider as 'suitable' extant taxa; for
227 example, it is not clear whether predictions generated from interspecific allometric data are more
228 accurate when based on closely related taxa with similar locomotor habits (Runestad, 1994), or when
229 using a wider sampling base (De Esteban-Trivigno, Mendoza & De Renzi, 2008). Other difficulties
230 associated with available interspecific allometric equations include body mass estimations (instead of
231 body mass measurements), small intrataxa sample sizes and over-representation of animals of one sex
232 or of exaggerated proportions.

233 To overcome this problem, we investigated which ontogenetic scaling parameters, if any, might be
234 suitable for predictions within giraffines. Similarly, Roth (1990) proposed that smaller animals of a
235 species with distinctive morphologies (be they juvenile or adult) may still be better analogues than
236 other taxa, at least in some aspects. Nevertheless, we remained cognisant of the fact ontogenetic
237 scaling and interspecific scaling exponents are generally not interchangeable (Gould, 1966; Pélabon et
238 al., 2013); in this case it is dependent on the assumption that *G. sivalensis* had a similar body plan as
239 juvenile extant giraffes. We thus found it appropriate, where possible, to make use of both ontogenetic
240 and interspecific curves to infer proportions of *G. sivalensis*, but realise that neither of these methods
241 may be appropriate for each and every dimension predicted.

242 *Neck length and reaching height*

243 Badlangana, Adams & Manger (2009) presented interspecific predictions for vertebral neck length
244 based on vertebral body length. Using their data, we could estimate *G. sivalensis* C2-C7 vertebral neck
245 length as 1150 mm, slightly shorter (45 mm or 4%) than our ontogenetic data. There are therefore
246 reasonable grounds to believe that our estimated neck length based on ontogenetic data is valid, or at
247 least close to interspecific curves. Further support can be seen in where the *G. camelopardalis*

248 ontogenetic curve gives appropriate predictions for vertebral neck length in both the *G. camelopardalis*
249 and okapi ontogenetic series Figure 6.

250 Extant adult giraffes have an average external neck length of about 2013 mm (males 1000 kg and
251 above) and 1832 mm (females 800 kg and above) (Mitchell, van Sittert & Skinner, 2009). Assuming
252 the same body plan for *G. sivalensis* as for *G. camelopardalis*, then *G. sivalensis* had around 350 mm
253 (20%) to 550 mm (27%) shorter necks than modern giraffes, depending if the OR39747 vertebra were
254 from a male or female animal. This close to Falconer and Cautley's (1843) estimated neck length for
255 *G. sivalensis* being around a 'third' shorter neck than extant giraffes. Our proposed reaching height of
256 3.9m in the animal from whence OR39747 comes with reservation as it assumes that *G. sivalensis* and
257 *G. camelopardalis* had similar body proportions.

258 *Body mass*

259 The body mass predictions for *G. sivalensis* using available specimens and allometric equations are
260 extremely wide (Figure 5). This could mean, firstly, that some specimens may have been incorrectly
261 assigned to *G. sivalensis*. Secondly, that not all allometric equations are equally suitable for body mass
262 predictions. Thirdly, that not all bone types are equally suitable for body mass predictions; femurs and
263 humeri are, for example, generally more suitable for this purpose than more distal bones, while it is
264 unusual to use vertebrae as proxies for body mass. Indeed, vertebrae are not ideal candidates as body
265 mass predictors. The vertebral body length, especially in the cervical area, may be influenced by other
266 factors as body mass such as the number of vertebrae that is possible in a region (compare reptiles and
267 mammals), the lifestyle of the species, the morphology of the animal and the use of neck. Nevertheless,
268 because OR39747 is the holotype, it was inevitable to use it as a proxy for body mass before we could
269 determine which fossil specimens were correctly assigned to *G. sivalensis*. In order to find which
270 vertebral dimensions are robust enough to predict body mass in phylogenetically taxonomic closely related animals, we
271 compared body mass prediction errors predictions in giraffes and okapis. We found the caudal
272 extremity's dorsoventral diameter to be the most robust, which gives a prediction error of 17% and 25% in
273 okapis and giraffes respectively (Figure 7). Vertebral cross sectional properties are better indicators of
274 the stresses and strains in the vertebral column and by implication the body mass of the animal,
275 although these relationships are complex and incompletely understood (Slijper, 1946). The caudal
276 dorsoventral vertebral height predicts a body mass of 390 kg in *G. sivalensis*. Unfortunately there aren't
277 any published interspecific regression equations using vertebral dimensions for the prediction of body

278 mass in ungulates that the authors are aware of, making the *G. camelopardalis* ontogenetic regression
 279 of body mass to caudal vertebral body height the best candidate for giraffinae currently at hand.
 280 Interestingly however, when we calculate the average body mass prediction from the remaining
 281 vertebral regression equations (C3 vertebral body length, cranial height, cranial width and caudal
 282 width), a fairly similar result is obtained - 368 kg. The only body mass prediction to fall outside the
 283 95% confidence interval (373 kg ± 119 kg) based on all vertebral dimensions (including caudal vertebral
 284 height) is vertebral body length, predicting a mass of 575 kg. If one argues that, compared to vertebral
 285 body length, the cross sectional measurement is an inadequate proxy for body mass in this case, it
 286 would mean that either the animal had a relatively thin neck with a proportionally (to body mass)
 287 stockier body than extant giraffes. Alternatively, if cross sectional measurements overestimates body
 288 mass it could mean that the animal had a thick neck with a proportionately smaller body than extant
 289 giraffes. The former scenario would be more plausible biomechanically, indicating that if cross
 290 sectional measurements are inadequate, an underestimation of body mass would be more likely. If one
 291 argues that neck length is an inadequate proxy in this case, it could mean that the *G. sivalensis* is either
 292 proportionately more slender or stockier than similar weight giraffes. An underestimation of body mass
 293 based on vertebral length would mean that *G. sivalensis* was more bulky relative to modern giraffes,
 294 however, that would also invalidate the cross sectional vertebral measurements unless the animal had a
 295 relatively thin neck with a bulky body. If vertebral body length overestimates body mass in this case it
 296 would mean a relatively longer neck with a slender body.

297 Interspecific long bone cross sectional properties, although probably more closely related to body mass
 298 than any other variable, have nevertheless been found ^{to be} as poor predictors of body mass in giraffes and
 299 okapis (Anderson, Hall-Martin & Russell, 1985; Roth, 1990; Scott, 1990). We derived similar
 300 conclusions from our results. Ontogenetic curves do however give more acceptable prediction errors of
 301 5% for both giraffes and okapis (Figure 7). Errors ^{were} ~~got~~ inflated when using more distal bones. We
 302 conclude ~~in this regard~~ that the most appropriate long bone variable useful for *G. sivalensis* body mass
 303 determination is very likely humeral cross sectional properties, based on our ontogenetic *G.*
 304 *camelopardalis* sample. The average humeral ontogenetic body mass estimate is 732 kg.

305 Interestingly, this body mass is about 150 kg higher than would be indicated by a *G. camelopardalis* of
 306 similar neck length, 342 kg more than the mass predicted from OR39747 cross sectional properties.
 307 This could mean that either the humeral fossil specimens were incorrectly assigned to *G. sivalensis*,

308 that *G. sivalensis* had a relatively stockier body and thinner neck than *G. sivalensis* or that the holotype
309 vertebra came from a female animal and that the humeral specimens came from large males.

310 *Outlier long bone predictions*

311 Unfortunately, none of the other long bone dimensions seem to be reliable predictors of body mass
312 across giraffine body sizes. The best candidate, with around 50-60% prediction error, seems to be
313 ~~be consistent - you used cranio-caudal earlier, and craniocaudal in the tables~~ radius cranio-caudal diameter, using Scott's interspecific equation. This dimension predicts the
314 specimen belongs to an animal of around 1800 kg, which, even acknowledging a 50% prediction error,
315 seems inappropriate for *G. sivalensis*. We therefore suggest that the radial specimens were incorrectly
316 assigned to *G. sivalensis* and perhaps belong to another giraffid. Giraffid metacarpal specimens
317 unfortunately are not nearly amenable to body mass predictions in either giraffes or okapis, using any
318 allometric equation currently available, and confirmation as which fossil species they belonged to will
319 have to wait until more complete skeletal finds are made.

320 Conclusions

321 We have proposed a body mass of around 400 kg for *G. sivalensis* based, unconventionally, on cervical
322 vertebral dimensions and ontogenetic *Giraffa* data. The humeral limb bones predicted a mass of around
323 800 kg however, which could indicate sexual dimorphism, a more stocky body form or even another
324 *Giraffa* species living at the same time. We argued that the holotype is a third cervical vertebra and not
325 a fifth cervical. *G. sivalensis* had a neck length of about 1470 mm in the live animal and, assuming
326 similar neck length to limb length proportions as extant giraffes, had a reaching height of 3.9m.

327

328 Acknowledgements

329 We thank Virgini Volpato and Katrin Krohman for assistance at the Senckenberg museum, Frankfurt,
330 Emma Bernard for assistance at the Natural History Museum, London, Tarik Afoukati from the
331 Muséum national d'Histoire naturelle, Paris and the Ditsong Museum of Natural History, Pretoria,
332 South Africa. Ms Marie Watson at the Centre for Veterinary Wildlife Studies for her general
333 administrative assistance in the planning of travel to relevant institutions. The late Prof John Skinner's
334 support was instrumental in the completion of this study.

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- 438

1

Map indicating the probable vicinity of *G. sivalensis* fossil discoveries.

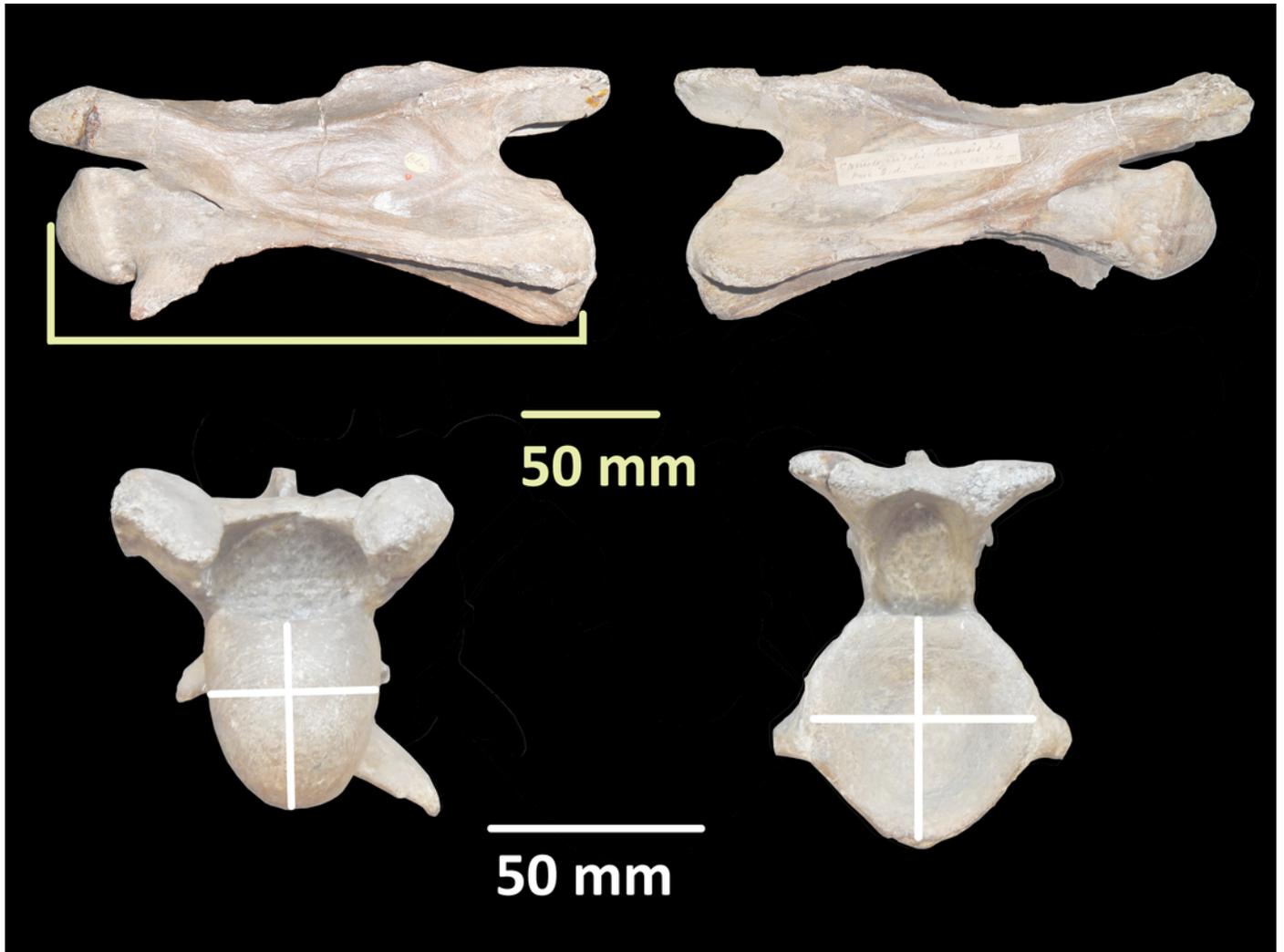
The marker indicates the location of the Shivalik Fossil Park in the Siwalik hills, a sub^Hhimalayan mountain range. This is most probably the area 'west to the river Jumna' (currently Yamuna river) that Falconer and Cautley (1843) referred to. Map data: AutoNavi, Google.



2

Giraffa sivalensis holotype, specimen OR39747.

Presented, from left to right, in left lateral, right lateral, cranial and caudal views.

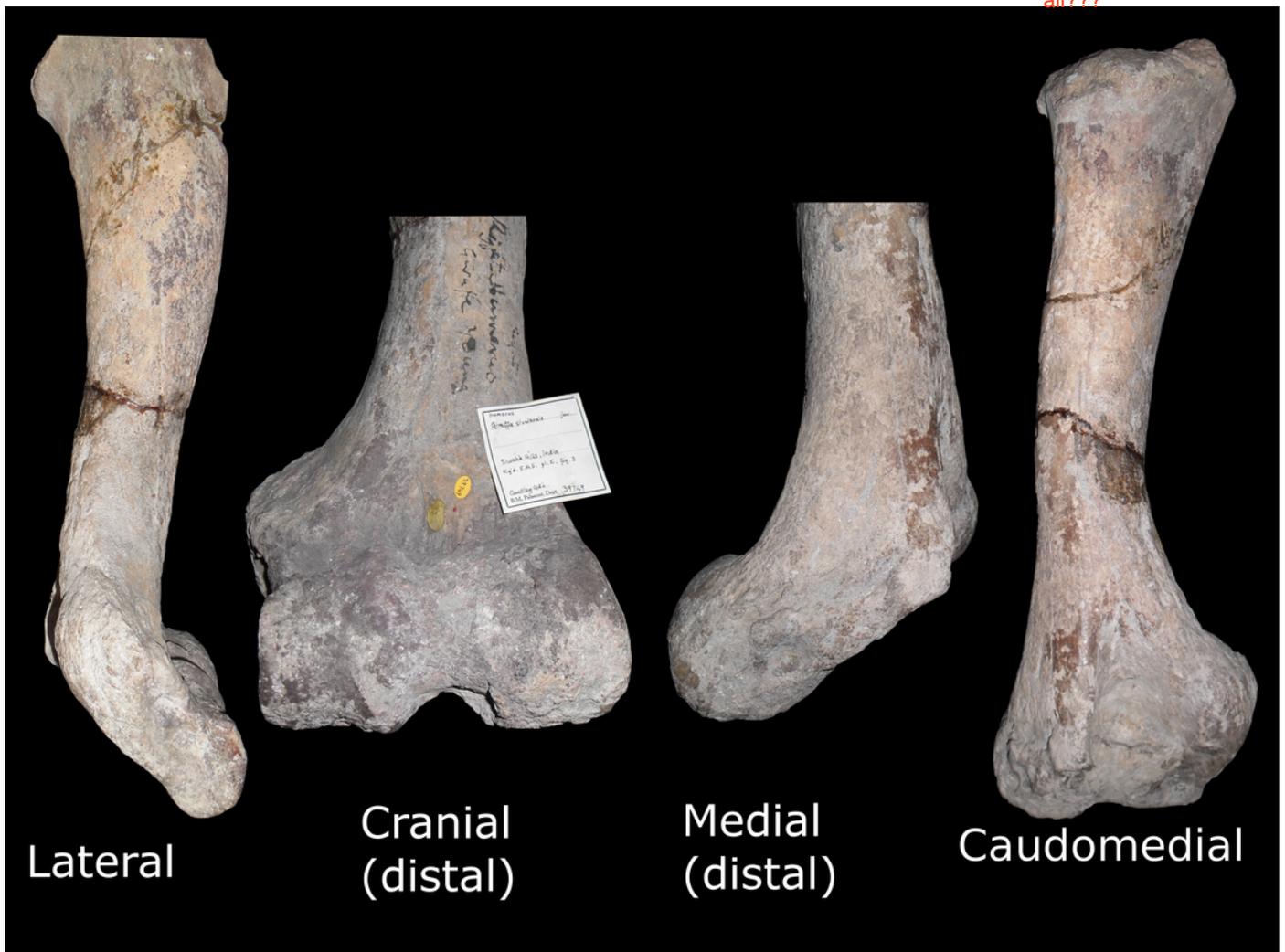


3

Specimen OR39749.

This image represents different views of a right humerus that has been assigned to *G. sivalensis*. The image is not to scale, and where only distal parts of the bone are shown, has been enlarged relative to images of the specimen *in toto*.

Even if not to
scale, why no
scale bars or
indication of size at
all???

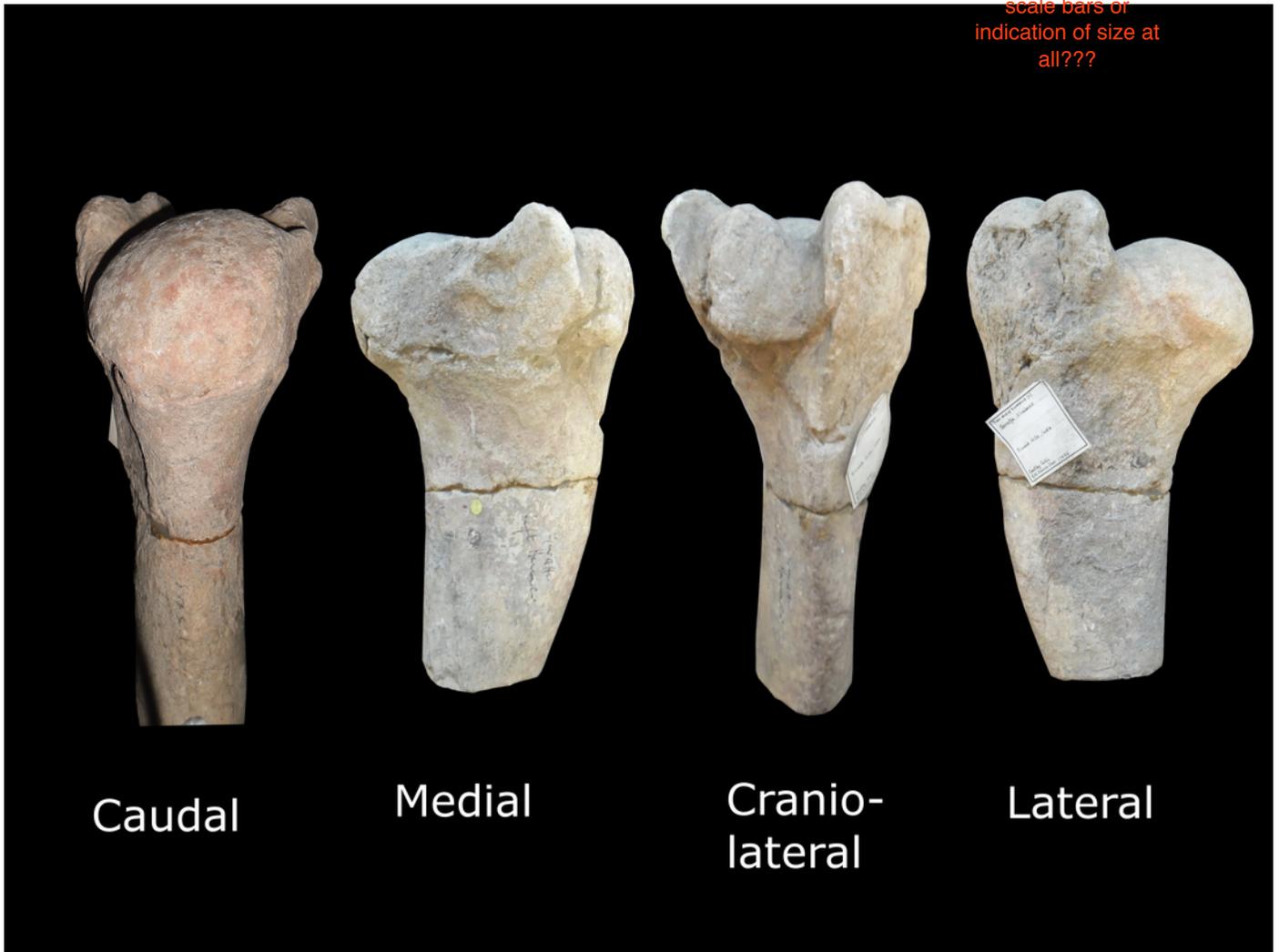


4

Specimen OR17136.

This represents different views of the proximal part of a left humerus that has been assigned to *G. sivalensis*. Not to scale.

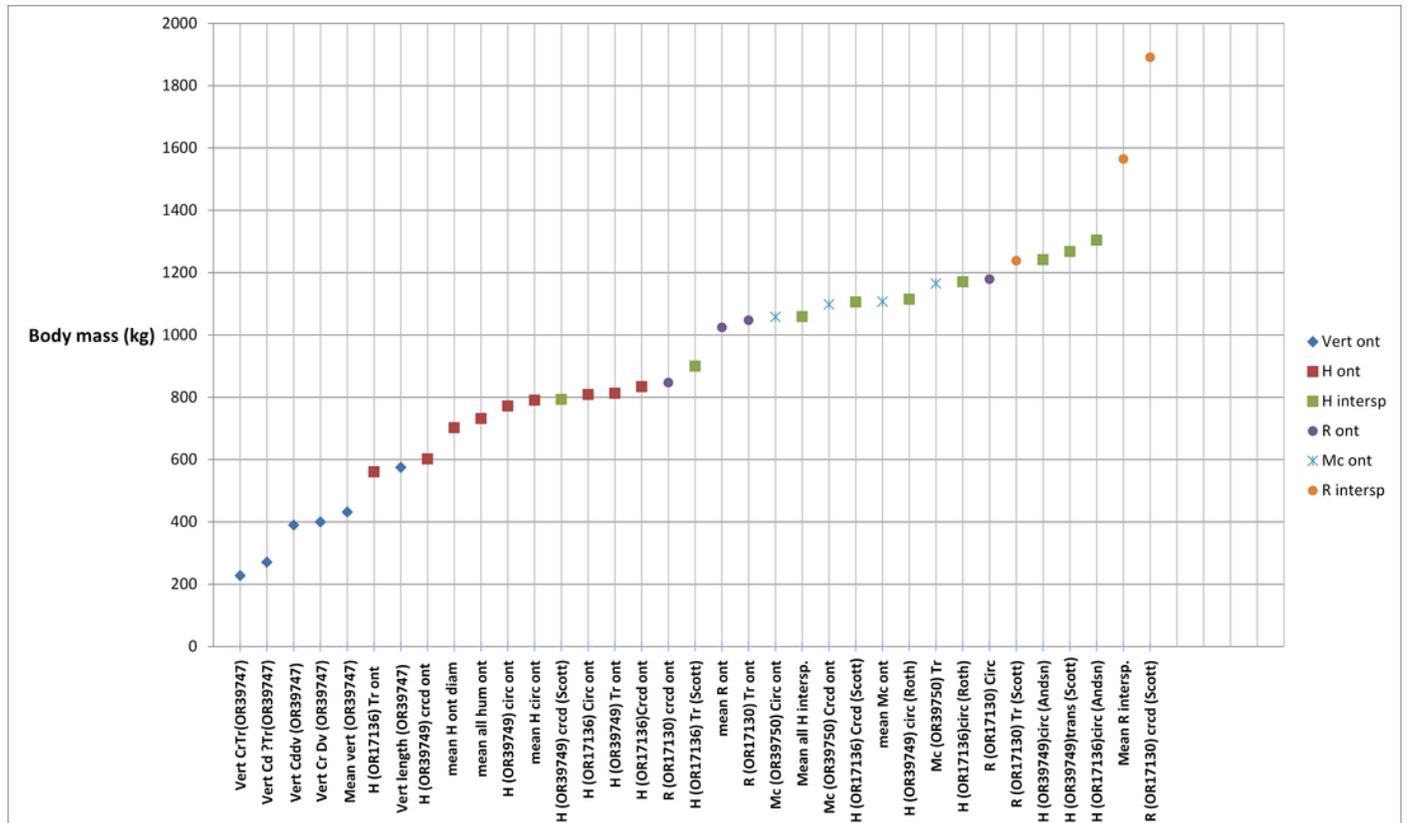
Even if not to scale, why no scale bars or indication of size at all???



5

Body mass predictions for *G. sivalensis* based on various fossil specimens.

The labels are divided into predictions from vertebral dimensions (diamond shapes), humeral dimensions (Squares), radial dimensions (circles) and metacarpal dimensions (crosses). The humeral and radial dimensions are further subdivided into those originating from ontogenetic allometric equations (red and purple, respectively) and those from interspecific equations (green and orange, respectively). Shapes that are drawn larger denote mean values of a group. Note that the interspecific predictions generally give higher estimates of body mass than predictions based on ontogenetic data. Furthermore the distal bones tend to predict higher values than the humeral predictions. Vertebral predictions give the lowest body mass estimates. Abbreviations: Vert, Vertebral body; H, humerus; R, Radius; Mc, Metacarpus; Cr, cranial; Cd, Caudal; CrTr, cranial transverse dimension; CrDv, cranial dorsoventral diameter; CdTr, caudal transverse diameter; Cddv, Caudal dorsoventral diameter; CrCd, craniocaudal midshaft diameter; Tr, transverse midshaft diameter; Circ, midshaft circumference; ont, ontogenetic sample; inters, interspecific sample; Sc, (Scott, 1990); Ro, (Roth, 1990); An, (Anderson, Hall-Martin & Russell, 1985).



6

The relationship between neck length and C3 vertebral length throughout ontogeny in giraffes and okapis.

A regression line is based on the giraffe ontogenetic series and extrapolated to the okapi range. The use of a regression line for ontogenetic and phylogenetic allometry seems to be appropriate in this case, supporting the use of a giraffe ontogenetic regression line to predict a neck length value for *G. sivalensis*.

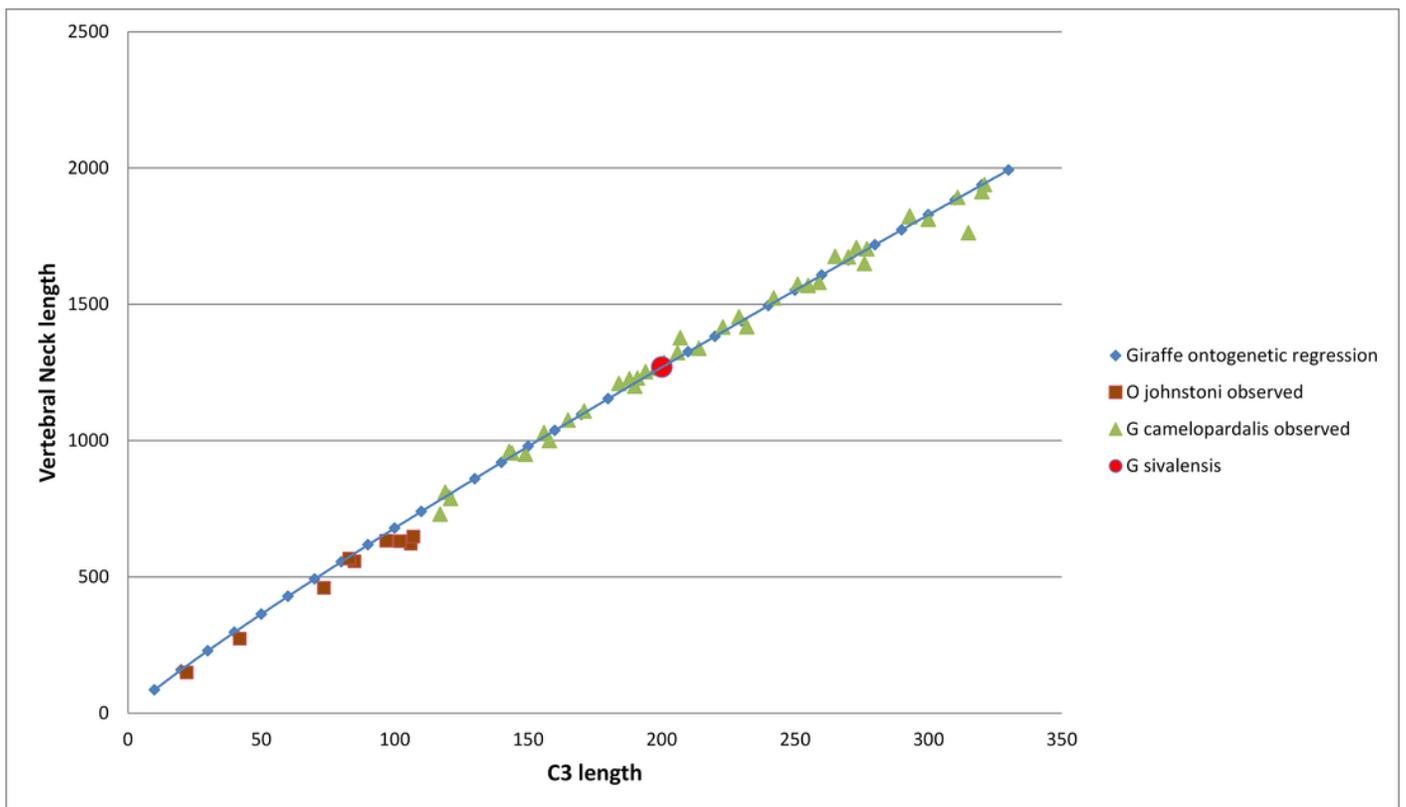


Table 1 (on next page)

Dimensions of the *G sivalensis* holotype

Comparison of the present study's measurements with that of Falconer and Cautley (1843).

Dimensions for the *G sivalensis* holotype; a well preserved C3 cervical vertebra (specimen OR39747). All values in mm. Nomenclature is based on the Nomina Anatomica Veterinaria (International Committee on & Veterinary Gross Anatomical Nomenclature, 2012)

2

Dimension and description	Falconer & Cautley (1843)'s terminology	Present study's measurement (\pm 95% confidence interval for three measurements) (mm)	Falconer & Cautley (1843) measurement (mm)
Vertebral body length: Longitudinal axis of the vertebral body, from the most cranial curvature of the cranial extremity to the most caudal part of the caudal extremity	Length of the body of the vertebrae between articulating heads	200.2 \pm 0.7	198.1
Cranial vertebral body height: Greatest dorsoventral height of cranial extremity	Vertical height articulating head?	42.9 \pm 1.4	25.4
	Antero-posterior diameter articulating head?		48.3
Cranial vertebral body width: Greatest transverse width of cranial extremity	Greatest diameter at articulating head	36.2 \pm 2.8	35.6
Caudal Vertebral body height: Greatest dorsoventral height of caudal extremity	Vertical diameter, articular cup, posterior end	53.1 \pm 0.3	50.8
Caudal vertebral body width: Greatest transverse width of caudal extremity	Transverse diameter, articular cup, posterior end	53.4 \pm 0.3	50.8
Spinous process length: From roof of the vertebral foramen to the highest point of the spinous process, perpendicular to the long axis of the vertebral body		21.8 \pm 2.6	

3

Table 2 (on next page)

Dimensions for long bone specimens marked as belonging to *G. sivalensis*. All values in mm.

Specimen no	HL	HCirc	HCr	HTr	RL	RCirc	RCr	RTr	McL	MCirc	McCr	McTr
OR39750*									389	186	53	60
OR17130†					220	217	53	71				
OR39749‡	453	212	66	66								
OR17136*	279	216	76	57								

- 2 *Abbreviations:* H, Humerus; R, Radius; Mc, Metacarpus; L, Length; Circ, midshaft circumference; Cr,
3 midshaft Craniocaudal diameter; Tr, midshaft transverse diameter. * distal proportion lacking. † only
4 diaphysis. ‡ proximal metaphysis missing. OR39749 is marked as a juvenile.

Table 3 (on next page)

Okapi dimensions data

The studied okapi specimens and their dimensions used in determining the appropriateness of allometric equations in determining body size and shape estimates in *G. sivalensis*.

Specimen no	Museum	OTVL	ONL	ONL-1	OTL	OFL	OHL	N:FL	PNL	%PE
az2348	DMNH	1259	557	522	702	932	971	0.60	586	0.05
az2440	DMNH	1392	567	531	825				574	0.01
1973-178	MNHN	722	273	260	449	752	797	0.36	310	0.14
1961-131	MNHN	400	149	137	252	553	605	0.27	174	0.17
1984-56	MNHN		459	428					514	0.12
1996-102	MNHN	1529	632	600	897	1018	1007	0.62	660	0.04
27194	SM	1442	621	589	821	1018	991	0.61	715	0.15
73224	SM	1521	647	613	874	993	994	0.65	722	0.12
56346	SM	1458	630	599	828	998	985	0.63	691	0.10
92290	SM			142		534	553			

2 **Abbreviations:** DMNH, Ditsong National Museum of Natural History (Formerly Transvaal Museum); MNHN, Museum National
3 d'Histoire Naturelle; SM, Senckenberg Museum; OTVL, observed total vertebral length; ONL, observed neck length; ONL-1,
4 observed neck length minus C1; OTL, observed trunk length; OFL, observed front limb long bone lengths; OHL, observed hind
5 limb long bone lengths; N:FL, neck length to foreleg length ratio; PNL, predicted neck length; % PE, percent prediction error for
6 vertebral length based on giraffe ontogenetic allometry.

7

Table 4(on next page)

Power functions, their origin and predicted values for linear dimensions of *G. sivalensis*.

Dimension predicted for <i>G sivalensis</i> (dependant (y) variable)	Prediction based on (independent (x) variable)	Equation generated from	Equation	Prediction
Vertebral neck length (C1 to C7)	OR39747 (C3) vertebral body length	<i>G camelopardalis</i> ontogenetic data	$y = 10.66 x^{0.902}$	1270 mm
Vertebral neck length (C2 to C7)	OR39747 (C3) vertebral body length	<i>G camelopardalis</i> ontogenetic data	$y = 9.708x^{0.908}$	1195 mm
Vertebral neck length (C2 to C7)	OR39747 (C3) vertebral body length	Various ungulates, data from (Badlangana, Adams & Manger, 2009)	$y = 5.023 x^{1.03}$	1150 mm
Dorsal neck length (occipital crest to withers)	OR39747 (C3) vertebral body length	<i>G camelopardalis</i> ontogenetic data	$y = 1.694 x^{0.820}$	1321 mm
Ventral neck length (angle of jaw to acromion)	OR39747 (C3) vertebral body length	<i>G camelopardalis</i> ontogenetic data	$y = 1.442 x^{0.890}$	1608 mm
Average neck length (of dorsal and ventral neck length)	OR39747 (C3) vertebral body length	<i>G camelopardalis</i> ontogenetic data	$y = 1.55 x^{0.859}$	1467 mm
Front leg length (humerus+ radius+ metacarpus long bones)	OR39747 (C3) vertebral body length	<i>G camelopardalis</i> ontogenetic data	$y = 70.2x^{0.598}$	1668 mm
Foreleg withers height	OR39747 (C3) vertebral body length	<i>G camelopardalis</i> ontogenetic data	$y = 4.90x^{0.7455}$	2540 mm
Approximate reaching height	OR39747 (C3) vertebral body length	<i>G camelopardalis</i> ontogenetic data	$y = 7.600x^{0.742}$	3880 mm

2

Table 5 (on next page)

Functions for the prediction of body mass based on various *G. sivalensis* specimens.

Independent(x) variable	Model sample	Model r2	Allometric equation	Body mass prediction
OR39747 (C3) vertebral body length	G camelopardalis ontogenetic data	0.91	$y = 0.022 \cdot x^{1.919}$	575
OR39747 (C3) cr dv		0.77	$y = 0.0023 \cdot x^{3.21}$	400
OR39747 (C3) cr lat		0.84	$y = 0.0054 \cdot x^{2.967}$	228
OR39747 (C3) cd dv		0.69	$y = 0.0048 \cdot x^{2.847}$	390
OR39747 (C3) cd lat		0.64	$y = 0.0227 \cdot x^{2.360}$	271
Average of vertebral dimensions				373
OR39747 (C5) vertebral body length	G camelopardalis ontogenetic data			
OR39747 (C5) cr dv				
OR39747 (C5) cr lat				
OR39747 (C5) cd dv				
OR39747 (C5) cd lat				
Humerus midshaft circumference (OR17136)	G camelopardalis ontogenetic data	0.98	$y = 8.96 \cdot 10^{-4} \cdot x^{2.55}$	809
Humerus midshaft circumference (OR39749)	G camelopardalis ontogenetic data			772
average of humeral circumferences				791
Humerus midshaft craniocaudal diameter (OR17136)	G camelopardalis ontogenetic data	0.98	$y = 3.59 \cdot 10^{-2} \cdot x^{2.32}$	834
Humerus midshaft craniocaudal diameter (OR39749)	G camelopardalis ontogenetic data		$y = 3.59 \cdot 10^{-2} \cdot x^{2.32}$	602
Humerus midshaft transverse diameter (OR17136)	G camelopardalis ontogenetic data	0.96	$y = 2.00 \cdot 10^{-2} \cdot x^{2.53}$	561
Humerus midshaft transverse diameter (OR39749)	G camelopardalis ontogenetic data		$y = 2.00 \cdot 10^{-2} \cdot x^{2.53}$	813
average humeral cr cd and transverse				703
all humeral ontogenetic average				732
Radius midshaft circumference (OR17130)	G camelopardalis ontogenetic data	0.99	$y = 1.65 \cdot 10^{-4} \cdot x^{2.93}$	1179
Radius midshaft craniocaudal diameter (OR17130)	G camelopardalis ontogenetic data	0.98	$y = 2.89 \cdot 10^{-3} \cdot x^{3.19}$	847
Radius midshaft transverse diameter (OR17130)	G camelopardalis ontogenetic data	0.99	$y = 1.18 \cdot 10^{-2} \cdot x^{2.67}$	1047
radius average				1024
Metacarpal midshaft circumference (OR39750)	G camelopardalis ontogenetic data	0.96	$y = 4.70 \cdot 10^{-5} \cdot x^{3.24}$	1058
Metacarpal midshaft craniocaudal diameter (OR39750)	G camelopardalis ontogenetic data	0.97	$y = 1.59 \cdot 10^{-3} \cdot x^{3.40}$	1098
Metacarpal midshaft transverse diameter (OR39750)	G camelopardalis ontogenetic data	0.98	$y = 6.71 \cdot 10^{-3} \cdot x^{2.95}$	1165
average metacarpus				1107
Humerus midshaft craniocaudal diameter (OR17136)	Artiodactyl interspecific allometry (Scott, 1990)	0.94	$y = 7.63 \cdot x^{2.455}$	1106
Humerus midshaft craniocaudal diameter (OR39749)				793
Humerus midshaft transverse diameter (OR17136)	Artiodactyl static interspecific (Scott, 1990)	0.95	$y = 12.4 \cdot x^{2.46}$	900
Humerus midshaft transverse diameter (OR39749)				1268

Humerus midshaft circumference (OR17136)	Various mammalian taxa (Roth 1990)	0.99	$y = 9.45 \cdot 10^{-4} x^{2.61}$	1170
Humerus midshaft circumference (OR39749)				1115
Humerus midshaft circumference (OR17136)	Various mammalian taxa (Anderson et al 1985)	0.99	$0.0009 \cdot x^{2.6392}$	1304.165927
Humerus midshaft circumference (OR39749)				1241.389631
all humeral interspecific average				1059
Radius midshaft craniocaudal diameter (OR 17130)	Artiodactyl static allometry (Scott, 1990)	0.93	$y = 29.2 x^{2.51}$	1891
Radius midshaft transverse diameter (OR 17130)	Artiodactyl static allometry (Scott, 1990)	0.91	$y = 8.19 x^{2.555}$	1238
radial interspecific average				1565

2