

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

Sybrand J van Sittert, Graham Mitchell

Giraffa sivalensis occurred during the Plio-Pleistocene period and probably represents the terminal species of the genus in Southern Asia. The holotype is an almost perfectly preserved cervical vertebra of disputed anatomical location. Although there is also uncertainty regarding this animal's size, other specimens that have been assigned to this species include fragments of two humeri, a radius, metacarpal and teeth. Here we estimate neck length, leg length and body mass using interspecific and, unusually, ontogenetic allometry of extant giraffe skeletal parameters. The appropriateness of each equation to estimate body mass was evaluated by calculating the prediction error incurred in both extant giraffes (*G. camelopardalis*) and okapis (*Okapia johnstoni*). It followed that the equations with the lowest prediction error in both species were considered robust enough to use in *G. sivalensis*. The size of *G. sivalensis*, based on the holotype, is proposed as 400 kg (range 228 kg - 575 kg), with a neck length of approximately 147 cm and a height of 390 cm. The molar lengths of tooth specimens considered agree with this size estimate. The humerus was the most appropriate long bone to establish body mass, which estimates a heavier animal of ca 790 kg. The discrepancy with the vertebral body weight estimate might indicate sexual dimorphism. Radial and metacarpal specimens estimate *G. sivalensis* to be as heavy as extant giraffes. This may indicate that the radius and metacarpus are unsuitable for body mass predictions in *Giraffa spp.* Alternatively, certain long bones may have belonged to another long legged giraffid that occurred during the same period and locality as *G. sivalensis*. We have concluded that if sexual dimorphism was present then males would have been about twice the size of females. If sexual dimorphism was not present and all bones were correctly attributed to this species, then *G. sivalensis* had a slender neck with a relatively stocky body.

1 Introduction

2

3 *Giraffa sivalensis* (Falconer & Cautley, 1843) was the first extinct *Giraffa* species to be
4 discovered, yet neither a complete skull nor specimens related to the holotype vertebra have been
5 found. Notwithstanding this limitation, many fossil specimens have been assigned as belonging
6 to this species, without adequate consideration of its size or without explicitly citing the
7 stratigraphic horizon of discovery (Table S1). In addition, many of the discovered specimens
8 have only been described in the Fauna Antiqua Sivalensis, which is a collection of Falconer's
9 publications and unpublished notes (Murchison, 1868). Although all the plates (notably plate E)
10 within the Fauna Antiqua Sivalensis are well described (Falconer & Murchison, 1867), many of
11 them have never been published.

12

13 *History of G. sivalensis discovery*

14 In 1838 Cautley briefly described the discovery of a remarkable vertebra in the Siwalik Hills in
15 India. He believed the specimen to be very similar to that of extant giraffes - a significant
16 statement, because up until that time no other fossil *Giraffa* species were known. Falconer and
17 Cautley (1843) subsequently named the species *Camelopardalis sivalensis* and assigned the
18 fossil, which was to become the holotype (Badam, 1979), as a third cervical vertebra. However,
19 Lydekker (1885a) disputed this and proposed that the holotype was in actual fact a fifth cervical
20 vertebra of a 'very small individual'. Since Cautley's discovery, other *Giraffa*-like fossils have
21 also been found in Asia, Europe and Africa, subsequently leading to proposals for species such
22 as *G. priscilla*, *G. jumae*, *G. stillei*, *G. gracilis*, *G. pygmaea* and *G. punjabiensis*. The references

23 to these fossil specimens are extensive, incomplete and confusing as can be seen by the
24 references to *G. sivalensis* alone in Table S1.

25 *Geographic and stratigraphic distribution of fossils*

26 Matthew (1929) placed the upper Siwalik deposits, where *G. sivalensis* fossils and nearly all
27 Siwalik fauna discovered by early writers such as Falconer have been found (Lydekker, 1876), as
28 part of the Pinjor zone (Gaur, Vasishat & Chopra, 1985; Akhtar et al., 1991; Nanda, 2002, 2008;
29 Bhatti, 2004). The Pinjor zone dates to roughly 2.58 to 0.6 million years ago, placing the fauna
30 discovered in this site as originating during the late Pliocene / early Pleistocene (Nanda, 2008).
31 The site of discovery of the holotype for *G. sivalensis* was presented by Falconer and Cautley
32 (1843) only as ‘the Sewalik range to the west of the river Jumna’ (currently the Yamuna river).
33 Although Spamer, Daeschler & Vostreys-Shapiro (1995) described the locality as ‘Siwalik Hills,
34 near Hardwar, Uttar Pradesh’, this is unlikely as Hardwar is east of the Yamuna. We therefore
35 believe the locality was probably in the vicinity of the current Shivalik fossil park, Saketi,
36 Himachal Pradesh, India (Figure 1).

37

38 *Size estimates and controversy*

39 Size estimates of *G. sivalensis* have been inadequate or contradictory. For example, it has been
40 proposed that *G. sivalensis* was about ‘one third shorter’ with a neck about ‘one tenth more
41 slender’ than extant giraffes (Falconer & Cautley, 1843), and that the holotype belonged to a
42 very small individual (Lydekker, 1885a), that it had the same sized cranium as extant giraffes but
43 with a shorter neck (Lydekker, 1876), that it was a large species but smaller than extant giraffes
44 (Bhatti, 2004, p 155), that it was of comparable size to modern giraffes (Bhatti, 2004, p.255),
45 that it was larger than extant giraffes (Mitchell & Skinner, 2003) and that certain proportions of

46 the species' neck were larger than extant giraffes (Lydekker, 1876, p.105). Additional fossil
47 specimens originally thought to belong to a separate species, *G. affinis* (Falconer & Cautley,
48 1843), were subsequently shown to belong to *G. sivalensis* and are currently believed to indicate
49 a larger individual of the species (Lydekker, 1876, p.105; Bhatti, 2004, p140). Table 1
50 summarises previous size estimates for *G. sivalensis*.

51

52 In this paper we outline and clarify the relevant information about *G. sivalensis* and its remains.

53 In addition, we have made new estimates of its size and shape.

54

55 **Materials and Methods**

56 *Studied material and dimensions measured*

57 All postcranial specimens assigned to *G. sivalensis* that were available at the Natural History
58 Museum in London were studied. From these specimens, body and neck size estimates were
59 calculated using giraffe ontogenetic or available interspecific allometric equations. The only
60 vertebra measured was the holotype (OR39747, Figure 2), a cervical which had been extensively
61 described by Falconer and Cautley (1843). A caudal fragment of a ‘fourth’ cervical (OR39748;
62 Lydekker, 1885a), also described as a second cervical by Falconer (1845), as well as a caudal
63 part of a ‘third’ cervical (OR39746; Lydekker, 1885a) were missing from the Siwalik collection
64 at the Natural History Museum. Dimensions were measured with a vernier calliper and included:
65 vertebral body length, cranial vertebral body height, cranial vertebral body width, caudal
66 vertebral body height, caudal vertebral body width and spinous process length (Figure 2).

67

68 Additional postcranial specimens assigned to *G. sivalensis* held at the Natural History Museum
69 include fragments of two humeri (OR39749 and OR17136; Figure 3 and Figure 4 respectively), a
70 fragment of a radius/ulna (OR17130) and various fragments of metacarpi and phalanges. All
71 metacarpal specimens except OR39750 were avoided due to the unclear numbering of specimens
72 and deformation of the fossils. Measurements of the long bones included length, midshaft
73 circumference and midshaft diameter in craniocaudal and transverse planes. The length and
74 circumference measurements were done with a measuring tape, while the cross sectional
75 diameters were done with a vernier calliper.

76

77 Because there is no complete *G. sivalensis* skeleton its shape needs to be inferred as analogous to
78 the only other extant *Giraffa*: *G. camelopardalis*. One of the methods of inferring body size from
79 a model animal or animals requires that regression equations in the form $y=mx^b$ (Huxley, 1932)
80 be constructed. These regression equations can be based on data from different species
81 (interspecific allometry), within the growth phase of a single animal (ontogenetic allometry) or
82 amongst adult animals of different size but within the same species (static allometry). We
83 applied ontogenetic as well as interspecific allometric equations to predict body mass in this
84 case.

85

86 Ontogenetic data were obtained from previous studies by the authors (Mitchell, van Sittert &
87 Skinner, 2009; van Sittert, Skinner & Mitchell, 2010, 2015). These data were used to construct
88 allometric equations to describe body mass or body dimensions. The dimensions used from
89 ontogenetic vertebral data are summarised in Table 2. Interspecific regression equations were
90 sourced from previously published work (Anderson, Hall-Martin & Russell, 1985; Roth, 1990;
91 Scott, 1990; Campione & Evans, 2012). The dimensions measured for the long bone ontogenetic
92 data are summarised in Table 3

93

94 There are inherent problems associated with using dental measurements as body size predictors,
95 especially when only a single tooth is used (Damuth, 1990; Fortelius, 1990; Janis, 1990).
96 Nevertheless, we have estimated size from teeth originally measured by Falconer & Cautley
97 (1843), even though these teeth were initially assigned to a new species *G. affinis*, a species that
98 was eventually abandoned (Lydekker, 1883). Uncertainty regarding these teeth specimens
99 persisted until recent times (Spamer, Daeschler & Vostreys-Shapiro, 1995). Teeth specimens

100 described by authors other than Falconer and Cautley which are noted in Supplementary Table 1
101 were not evaluated further as there was either uncertainty regarding the authors' species
102 association (Lydekker, 1876), or the teeth specimens were not necessarily collected in the
103 vicinity or stratigraphical layer of fossils described by Falconer and Cautley (Lydekker, 1878), or
104 because certain specimens were deciduous. Table 4 presents dental specimens as well as
105 dimensions as measured by Falconer and Cautley (1843). Body masses were estimated from
106 regression equations established by Damuth (1990).

107

108 *Statistical analyses*

109 Allometric equations were generated from bivariate data through ordinary least squares
110 regression. To facilitate this, measurements were logarithmically transformed to base e prior to
111 analyses. According to Warton et al. (2006), ordinary least squares regression is appropriate
112 when one wishes to predict y from x , even when x contains measurement error, as long as the
113 results are interpreted in the context of 'predicting y from x measured with error'. It is worth
114 noting that there is controversy regarding the practice of logarithmically transforming data in
115 scaling studies (Packard, Boardman & Birchard, 2009, 2010; Cawley & Janacek, 2010; Packard,
116 2013). The main argument is whether error becomes larger as body mass increases
117 (multiplicative error), in which case logarithmic transformation is appropriate, or whether there
118 is no correlation between error and body mass, in which case logarithmic transformation is not
119 appropriate (Glazier, 2013). The debate is ongoing and will not be reviewed here. In this study
120 we selected the method of log-transformation of data as it enables more convenient comparison
121 among similar datasets.

122 Because body dimensions (especially body masses) can be predicted by different equations and
123 by different fossil specimens, the predictions need to be validated. If regression equations had
124 reasonable power in estimating body mass in both extant giraffids (*G. camelopardalis* and
125 *O. johnstoni*), then they were regarded as robust enough to extrapolate to *G. sivalensis* as well.
126 Therefore, dimensions of 10 okapi skeletons were recorded in addition to data obtained from
127 *G. camelopardalis*. The okapi skeletons were housed in various museums and were recorded as
128 the opportunities presented themselves (Table 5). Adult okapi specimens were assumed to have
129 weighed 250 kg, with a range of 200 kg to 300 kg (Lindsey & Bennett, 1999; Stuart & Stuart,
130 2006). The mature okapi specimens were identified through additional data associated with each
131 museum specimen as well as by the degree of fusion of the epiphyses. The robustness of giraffe
132 ontogenetic as well as interspecific equations to predict body mass in both adult giraffes and
133 adult okapis correctly were assessed through the percent prediction error, calculated according to
134 Smith (1984) and van Valkenburgh (1990):

135

136
$$\frac{((\text{Observed value} - \text{Predicted value}) / \text{Predicted value}) \times 100}{137}$$

137

138 *Assumptions made*

139 One of the major assumptions of this study is that *G. sivalensis* dimensions can be modelled
140 from *G. camelopardalis* ontogeny. Although it is unusual to model an animal from the ontogeny
141 of a different species it is not unique (an example is Roth, 1990). In assigning the holotype to a
142 specific vertebra, we also assumed that there would be broad similarity in shape between the
143 cervical vertebrae of *G. sivalensis* and *G. camelopardalis*. Falconer and Cautley (1843)
144 illustrated this assumption to be the case for many but not all features of the holotype vertebra.

145 Another assumption was that the specimens used came from the same *Giraffa* species. We tried
146 to use only those specimens that were clearly attributable to the Plio-Pleistocene and to the
147 vicinity of the holotype discovery (Figure 1), to limit possible confusion with other *Giraffa*
148 species like *G. punjabiensis*. However, in some instances these criteria were not clear due to the
149 lack of other samples or information, as in the discussion of vertebrae OR39746 and OR39748.
150 Lastly, in terms of estimating body proportions in adult animals based on vertebral length,
151 similarity in shape to *G. camelopardalis* was assumed.

152 **Results**153 *Dimensions measured*

154 The OR39747 and long bone dimensions measured are summarised in Table 2 and Table 3
155 respectively, and where applicable the dimensions contain the equivalent measured values
156 according to Falconer and Cautley (1843). Except for the cranial vertebral body height, our
157 measurements on OR39747 are within 1% to 5% of that reported by Falconer and Cautley
158 (1843). Dimensions measured from okapi skeletons are presented in Table 5. Table 5 also
159 contains predictions and prediction errors for okapi vertebral neck length based on *G.*
160 *camelopardalis* ontogenetic data.

161

162 *Predictions based on vertebra OR39747*

163 Based on *G. camelopardalis* ontogenetic data, the average of dorsal and ventral neck length
164 including soft tissue in *G. sivalensis* was 1467 mm ($y = 1.55 x^{0.859}$), the vertebral neck length
165 excluding soft tissue was 1270 mm ($y = 10.66 x^{0.902}$) and the foreleg (hoof to withers) height in
166 the living *G. sivalensis* adult was 2540 mm ($y = 7.61x^{0.663}$, Table 6). This would mean that the
167 reaching height of *G. sivalensis* was around 3.9m.

168

169 The different vertebral dimensions predict the body mass to be within a range of 228 kg to 575
170 kg, with an average of 373 kg (Table 7, 95% Confidence interval (CI) ± 168 kg). We identified
171 which of these dimensions could predict body mass accurately across species by calculating
172 prediction errors when applying the *G. camelopardalis* regression equations to both extant
173 giraffes and okapis. Naturally, because the predictions were done using *G. camelopardalis*
174 ontogenetic allometry, the *G. camelopardalis* prediction errors were lowest (8% to 50%).

175 Predictions for okapi body mass, however, ranged from 17% to 99%. The only variable which
176 provided relatively low body mass prediction errors in both okapi (17%) and *G. camelopardalis*
177 (25%) was the caudal vertebral body dorsoventral height. This dimension predicts a body mass
178 of 390 kg in *G. sivalensis* if we consider OR39747 as a third cervical. If OR39747 was
179 considered a fourth or fifth cervical, body mass predictions will be 274 kg ($y = 0.0011x^{3.128}$) or
180 187 kg ($y = 0.0004x^{3.285}$) respectively (Table 7).

181

182 *Predictions based on long bone dimensions*

183 All of the *G. sivalensis* long bone specimens available at the Natural History Museum were
184 incomplete proximally and/or distally. It was clear, nevertheless, that the bones had a similar
185 slender appearance of extant giraffes and were elongated. Humeral specimen OR39749 was
186 almost complete except for the proximal metaphysis, which has clearly broken off at the physeal
187 line of a subadult animal. Regarding the radius/ulna specimen, the bones' fusion at the midshaft
188 was not complete as in modern giraffes, where the two bones are indistinguishable at midshaft in
189 adults. The metacarpus specimen included in the study had the same caudal 'columns' or caudal
190 groove as those evident in the extant giraffe (Solounias, 1999; van Schalkwyk, 2004; van
191 Schalkwyk, Skinner & Mitchell, 2004) as well as in those of the okapi (own observation).

192

193 As no bones were complete length wise, bone length could not be used as a predictor for body
194 mass which, in any case, has been shown to be a poor estimator of body mass in other taxa
195 (Scott, 1990). Based on circumferences of the humeri (OR39749 and OR17136) and using *G.*
196 *camelopardalis* ontogenetic data these specimens may have belonged to animals with body
197 weight in the range of 770 kg to 810 kg. An extant giraffe of this body mass would have a

198 humerus length of about 477 mm to 484 mm ($y=63.2(\text{Body mass})^{0.304}$), which is just slightly
199 longer than the 453 mm measured on OR39749 that lacked a distal metaphysis. The predictors
200 based on radial and metacarpal cross sectional dimensions offered much higher body mass
201 estimates, with averages of 1024 kg and 1107 kg respectively. In addition to employing
202 ontogenetic data to generate allometric equations, we also referred to previously published
203 interspecific studies (Anderson, Hall-Martin & Russell, 1985; Roth, 1990; Scott, 1990;
204 Campione & Evans, 2012). Interspecific equations tended to predict heavier body masses than
205 ontogenetic equations, especially so in the distal long bone samples.

206

207 *Predictions based on dental dimensions*

208 Four molars and two premolars were used for size predictions (Table 4), using equations
209 developed by Damuth (1990). Body mass predictions based on tooth length (average = 577 kg,
210 standard deviation = 155 kg) tended to be smaller than the predictions based on tooth width
211 (average = 881 kg, standard deviation = 188 kg, $t_{(27)} = 4.83$, $p < 0.01$). Predictions from molar
212 length dimensions also tended to be lower than those from premolar lengths (average from molar
213 lengths = 473 kg, average from premolar lengths = 682 kg, $t_{(9)} = -3.12$, $p < 0.05$).

214

215 **Discussion**216 *Vertebral identity of OR39747*

217 The anatomical identity of OR39747 was disputed by Lydekker (1885a). He showed that
218 Falconer was in a habit of not counting the atlas and axis as cervical vertebrae – which often
219 meant that the start of the numbering of vertebra commenced at the third or occasionally the
220 second postcranial vertebra. Mammalian C3 to C5 forms a repetitive series and often does not
221 have the distinguishing characteristics present in the other cervical vertebrae (Solounias, 1999).
222 It is therefore indeed challenging to assign OR39747 to a specific vertebra. However, if we
223 assume approximate similarity in shape between *G. sivalensis* and *G. camelopardalis* vertebrae,
224 there are clues in the extent to which the cranial articular processes (*Proc. articularis cranialis*)
225 extend beyond the body or centrum of the vertebra (*Corpus vertebrae*). In the *G. camelopardalis*
226 C3, this process extends well beyond the cranial extremity of the vertebral body, but ends before
227 or approximately at the same dorsoventral plane as the vertebral body in C4 and C5. Judging
228 then by the extent of the articular processes of OR39747, it is a third, fourth or fifth cervical in
229 decreasing order of likelihood. Falconer was therefore correct in assigning this vertebra as a third
230 cervical, albeit fortuitously so.

231

232 *Ontogenetic and interspecific scaling models*

233 It is unusual although not unique to use ontogenetic allometry to predict an extinct animal's size.
234 For instance, Roth (1990) proposed that smaller animals of a species with distinctive
235 morphologies (be they juvenile or adult) may still be better analogues than other taxa, at least in
236 some aspects. We believe that this view is warranted in the current study as no extant species has
237 such an extreme shape as *G. camelopardalis*. Predicting fossil masses from interspecific

238 equations are further complicated by the decision of which taxa to include in regressions. For
239 example, it is not clear whether predictions generated from interspecific allometric data are more
240 accurate when based on closely related taxa with similar locomotor habits (Runestad, 1994;
241 Janis, Theodor & Boisvert, 2002) or when using a wider sampling base (De Esteban-Trivigno,
242 Mendoza & De Renzi, 2008). Other factors that may influence precision of body mass
243 predictions in interspecific studies are body mass estimations (instead of body mass
244 measurements), small intrataxa sample sizes, and overrepresentation of animals of one sex or of
245 exaggerated proportions. To overcome these problems, we investigated which ontogenetic
246 scaling parameters, if any, might be suitable and robust enough for predictions amongst extant
247 Giraffidae. It is possible that giraffe ontogenetic equations are also acceptable for comparison not
248 just amongst the Giraffidae but amongst, for example, extant camelids with similar gaits.
249 However, okapis were considered as an adequate reference in this case as they are closest to
250 giraffes phylogenetically and because the ontogenetic scaling of their long bones scales
251 differently to other cetartiodactyla (Kilbourne & Makovicky, 2012).
252 Ontogenetic scaling and interspecific scaling exponents are generally not interchangeable
253 (Gould, 1966; Pélabon et al., 2013); in this case it is dependent on the assumption that *G.*
254 *sivalensis* had a similar body plan as juvenile extant giraffes. We thus found it appropriate,
255 where possible, to test both ontogenetic and interspecific curves to infer proportions of
256 *G. sivalensis*, but realised that neither of these methods may be appropriate for each and every
257 dimension measured.

258

259 *Neck length and reaching height*

260 Badlangana, Adams & Manger (2009) presented interspecific predictions for vertebral neck
261 length based on vertebral body length. Using their data (presented in Table 1 of Badlangana,
262 Adams & Manger, 2009), we could estimate *G. sivalensis* C2-C7 vertebral neck length as 1150
263 mm (Table 6), slightly shorter (45 mm or 4%) than vertebral neck length calculated from our
264 ontogenetic data. There are therefore reasonable grounds to believe that our estimated neck
265 length based on ontogenetic data is valid, or at least close to interspecific curves. Further support
266 for this rationale can be seen where the *G. camelopardalis* ontogenetic curve gives appropriate
267 predictions for vertebral neck length in both the extant giraffe and okapi (Figure 5). Extant adult
268 giraffes have an average external neck length of about 2013 mm in males (1000 kg and above)
269 and 1832 mm in females (800 kg and above) (Mitchell, van Sittert & Skinner, 2009). Assuming
270 the same body plan for *G. sivalensis* as for *G. camelopardalis*, then *G. sivalensis* had around 350
271 mm (20%) to 550 mm (27%) shorter necks than modern giraffes, depending on whether
272 OR39747 came from a female or male animal. This is a slightly longer neck length than Falconer
273 & Cautley's (1843) estimated neck length for *G. sivalensis*, which is approximately a third
274 shorter than extant giraffes.

275

276 ***Body mass***

277 The body mass predictions for *G. sivalensis* are wide (Figure 6). Possible reasons for the large
278 range of predictions are that certain fossils were erroneously attributed to *G. sivalensis* and/or
279 that certain specimens and allometric equations are inadequate for body mass predictions. Before
280 decisions could be made regarding the validity of attributing a fossil to *G. sivalensis*, we
281 ascertained the equations that were robust enough to predict body mass accurately across species.

282

283 *Vertebra OR39747 body mass estimates*

284 It is unconventional to use vertebrae as proxies for body mass, although due to the lack of other
285 samples it has been done before (see for instance Taylor, 2007; Taylor & Naish, 2007). As
286 OR39747 is the holotype, it necessitates that body mass estimates are made from it if other
287 *Giraffa spp.* specimens are to be attributed to it. Although vertebral body length has higher R^2
288 values than cross sectional vertebral properties (Table 7, van Sittert, Skinner & Mitchell, 2010),
289 cross sectional properties are still preferable predictors of body mass in this case. The first reason
290 is that R^2 value is inferior to percent prediction error (%PE) and percent standard error of the
291 estimate when assessing reliability of body mass predictions through regressions (Smith, 1984).
292 Secondly, vertebral cross sectional properties are subjected to the stresses and strains within the
293 neck (Slijper, 1946) and therefore are a much better indicator of head and neck mass and by
294 implication body mass. Conversely, vertebral body length is influenced by factors other than
295 body mass such as the number of vertebrae in an anatomical area (compare birds and mammals'
296 cervical region) or the lifestyle of the animal. We found caudal vertebral height (dorsoventral
297 diameter) to have the lowest %PE (25% and 17%) when predicting body mass in both extant
298 giraffes and okapis respectively (Table 7, Figure 7), and therefore considered this dimension to
299 be most robust for body mass predictions across giraffids. There are no other published
300 interspecific regression equations using vertebral dimensions for the prediction of body mass in
301 ungulates of which we are aware. The caudal vertebral height predicts a body mass of 390 kg in
302 *G. sivalensis*. Interestingly, the average body mass prediction from the remaining vertebral
303 regression equations (C3 vertebral body length, cranial height, cranial width and caudal width,
304 Table 7) is fairly similar - 368 kg. The only body mass prediction to fall outside the 95%

305 confidence interval based on all vertebral dimensions including vertebral height (373 kg \pm 119
306 kg) is vertebral body length, predicting a mass of 575 kg.
307 Nevertheless, the body mass prediction from caudal vertebral height could be either an over or
308 underestimate. Considering it as an overestimate would mean that this animal had a relatively
309 heavy neck and head complex but a slender or lightweight body. This is unlikely as a larger head
310 and neck complex is unsupportable unless accompanied by a larger total body size (Taylor &
311 Wedel, 2013). Conversely an underestimate would mean a slender neck and head complex but a
312 relatively stocky body. This is a more plausible scenario and if indeed it is the case, it might
313 explain the discrepancy between vertebral and dental body mass predictions when compared to
314 those of limb bones.

315

316 *Limb bone body mass estimates*

317 Interspecific long bone cross sectional properties, although probably more closely related to
318 body mass than any other variable, have nevertheless been found to be poor predictors of body
319 mass in giraffes and in some cases, okapis (McMahon, 1975; Anderson, Hall-Martin & Russell,
320 1985; Scott, 1990; Janis, Theodor & Boisvert, 2002), although it should be noted that a recent
321 interspecific study has shown giraffes to be more amenable to interspecific equation predictions
322 (Campione & Evans, 2012). Similarly, we found higher prediction errors with interspecific
323 equations compared to *G. camelopardalis* ontogenetic curves, with a 5% prediction error based
324 on humeral ontogenetic data (Figure 7). Errors were inflated when using more distal bones.
325 Therefore, the most appropriate long bone variable useful for *G. sivalensis* body mass
326 determination is very likely humeral cross sectional properties, using our ontogenetic *G.*
327 *camelopardalis* sample.

328

329 The average body mass estimated from humeral ontogenetic analysis is 732 kg. Interestingly,
330 this body mass is about 150 kg more than would be indicated by a *G. camelopardalis* of similar
331 neck length, and 342 kg more than the mass predicted from OR39747 cross sectional properties.
332 This could mean that either the humeral fossil specimens were incorrectly assigned to *G.*
333 *sivalensis*, that *G. sivalensis* had a relatively stockier body and thinner neck than *G.*
334 *camelopardalis* or that the holotype vertebra came from a female and the humeral specimens
335 from large males.

336 Unfortunately, none of the other long bone dimensions seem to be reliable predictors of body
337 mass across extant giraffids. The best non-humerus candidate using interspecific scaling seems
338 to be the radius transverse diameter with a 43% and 11% prediction error in okapis and giraffes
339 respectively. This dimension predicts that the specimen belonged to an animal of approximately
340 1238 kg, which suggests this animal might have been heavier than *G. sivalensis*. There are no
341 interspecific equations for metacarpi that we could find, and therefore we could only rely on
342 ontogenetic equations. Yet, similar to the radial prediction, the metacarpal transverse diameter
343 predicts a body mass of 1165 with around 20% prediction error. The inflated prediction errors
344 could be because humeri and femora are generally more suitable for body mass predictions than
345 more distal bones, especially in giraffes (McMahon, 1975). It is also possible that the fossil long
346 bones were incorrectly assigned to *G. sivalensis* and perhaps belonged to another similar species
347 existing at the same time and location.

348

349 *Dental body mass estimates*

350 There have been numerous dental specimens ascribed to *G. sivalensis* (Supplementary Table 1).
351 Unfortunately, not all of these specimens are from the same locality and are probably from
352 different stratigraphic zones. Subsequently, there appeared to be uncertainty regarding the
353 correct species allocation of these fossils (see especially Lydekker, 1876). A discussion on the
354 morphology and correct species classification of teeth specimens assigned to *G. sivalensis* were
355 not considered as part of this study, and we therefore used only those teeth mentioned by
356 Falconer and Cautley (1843). These specimens were originally assigned to the species *G. affinis* -
357 a classification later abandoned by Falconer himself and also disputed by Lydekker (1883), who
358 re-assigned the fossils to *G. sivalensis*. As the specimens originated from the same area and
359 strata as the holotype OR39747, which is the Pliocene of the Siwaliks (Lydekker, 1885a), we
360 believe it reasonable to consider them as truly *G. sivalensis* teeth until further evidence emerges.

361

362 Molar length measurements are more reliable indicators of body mass than molar width or area
363 (Damuth, 1990; Fortelius, 1990; Janis, 1990). Furthermore, Janis (1990) found that premolar row
364 length are poorer correlates than molar row length. Molar lengths predict an animal within the
365 range of 288 kg to 673 kg, which is similar to OR39747's caudal vertebral height body mass
366 prediction of 390 kg.

367

368 *Combined size estimates*

369 Lydekker's (1885a) suggestion that OR39747 belonged to a small individual could have meant
370 that the animal was still immature, that the animal was a relatively small individual of the species
371 or that the species itself was small within the genus. It is unlikely that Lydekker meant an
372 immature animal as the fusion of the epiphyses to the body of the vertebra is complete and clear

373 definitions of bony ridges and muscular depressions indicate a mature animal (Falconer &
374 Cautley, 1843). Lydekker might have based his idea of a small individual on two larger vertebrae
375 assigned to *G. sivalensis* - a proximal part of a 'third' and distal part of a 'fourth' cervical,
376 OR39746 and OR39748 respectively (Lydekker, 1885a, Table S1). Unfortunately, these
377 vertebrae were not locatable within the Siwalik collection at the time of this study (Personal
378 communication, P Brewer, Curator of fossil mammals, Natural History Museum, 2013), and we
379 subsequently could not measure them. Nevertheless, Falconer (1845) reported OR39748 to be
380 2.1 inch (53.3 mm) in height and width at the caudal extremity, which is only 0.2 mm greater and
381 0.1 mm less than our respective measurements of OR39747 (Table 2). Based on ontogenetic
382 allometry for caudal vertebral body height, OR39748 came from an animal weighing 394 kg or
383 277 kg, depending on whether it was a C3 or C4 vertebra respectively (Table 7). The animal
384 from which the holotype vertebrae originated was therefore also not relatively small compared to
385 the size estimated from specimen OR39748. It is possible though, especially considering body
386 mass estimates from the humerus, that there might have been sexual size dimorphism present in
387 *G. sivalensis*. If that is indeed the case, OR39747 and OR39748 would have been females about
388 half the size of fully grown male animals, a possibility also supported by the fossil teeth
389 considered in body mass estimates.

390

391 **Conclusion**

392 Our considered opinion is that the *G. sivalensis*, from which the holotype cervical vertebra
393 originated weighed approximately 400 kg, had a neck length of about 1.47 m and a reaching
394 height of 3.9 m. There is a possibility that it displayed sexual dimorphism, in which case male
395 animals would have been a little less than twice the size of females and both would have had a

396 similar morphology. If sexual dimorphism was not present and all bones were correctly
397 attributed to this species, then the animal had a slender neck with a relatively stocky body, a
398 shape that is not unrealistic to imagine.

399 References:

- 400 Akhtar M, Sarwar M, Saeed M, Khan AA. 1991. Vertical distribution of Siwalik giraffids. *Acta*
401 *Scientia* 1:145–152.
- 402 Anderson JF, Hall-Martin A, Russell DA. 1985. Long-bone circumference and weight in
403 mammals, birds and dinosaurs. *Journal of Zoology* 207:53–61.
- 404 Badam GL. 1979. *Pleistocene Fauna of India with special reference to the Siwaliks*. Pune, India:
405 Deccan College Postgraduate and Research Institute.
- 406 Badlangana NL, Adams JW, Manger PR. 2009. The giraffe (*Giraffa camelopardalis*) cervical
407 vertebral column: a heuristic example in understanding evolutionary processes? *Zoological*
408 *Journal of the Linnean Society* 155:736–757.
- 409 Bhatti ZH. 2004. Taxonomy, evolutionary history and biogeography of the Siwalik giraffids.
410 PhD Thesis. Lahore: University of the Punjab.
- 411 Campione NE, Evans DC. 2012. A universal scaling relationship between body mass and
412 proximal limb bone dimensions in quadrupedal terrestrial tetrapods. *BMC Biology* 10:60.
- 413 Cautley PT. 1838. Note on a fossil ruminant genus allied to Giraffidae, in the Siwalik Hills.
414 *Journal of the Asiatic Society of Bengal* 7:658–660.
- 415 Cawley GC, Janacek GJ. 2010. On allometric equations for predicting body mass of dinosaurs.
416 *Journal of Zoology* 280:355–361.
- 417 Damuth J. 1990. Problems in estimating body masses of archaic ungulates using dental
418 measurements. In: *Body Size in Mammalian Paleobiology: Estimation and Biological*
419 *Implications*. Cambridge: Cambridge University Press, 229–253.
- 420 De Esteban-Trivigno S, Mendoza M, De Renzi M. 2008. Body mass estimation in Xenarthra: a
421 predictive equation suitable for all quadrupedal terrestrial placentals? *Journal of morphology*
422 269:1276–1293.
- 423 Falconer H. 1845. Description of some fossil remains of Dinotherium, Giraffe, and other
424 mammalia, from the Gulf of Cambay, western coast of India, chiefly from the collection
425 presented by Captain Fulljames, of the Bombay Engineers, to the Museum of the Geological
426 Society. *Quarterly Journal of the Geological Society* 1:356–372.
- 427 Falconer H. 1868. Description by Dr. Falconer of fossil remains of Giraffe in the museum of
428 Asiatic Society of Bengal. In: Murchison C ed. *Palaeontological memoirs and notes of the late*
429 *Hugh Falconer. Fauna Antiqua Sivalensis*. London: R. Hardwicke, 206–207.

- 430 Falconer H, Cautley PT. 1843. On some fossil remains of Anoplotherium and Giraffe, from the
431 Sewalik Hills, in the north of India. *Proceedings of the Geological Society of London* 4:235–249.
- 432 Falconer H, Murchison C. 1867. *Description of the plates of the Fauna Antiqua Sivalensis*.
433 London : R. Hardwicke.
- 434 Fortelius M. 1990. Problems with single fossil teeth to estimate body sizes of extinct mammals. In:
435 Damuth J, MacFadden BJ eds. *Body Size in Mammalian Paleobiology: Estimation and*
436 *Biological Implications*. Cambridge: Cambridge University Press,.
- 437 Gaur R, Vasishat N, Chopra SRK. 1985. New and some additional fossil mammals from the
438 Siwaliks exposed at Nurpur, Kangra district, H.P. *Journal of the palaeontological society of*
439 *India* 30:42–48.
- 440 Glazier DS. 2013. Log-transformation is useful for examining proportional relationships in
441 allometric scaling. *Journal of theoretical biology* 334:200–203.
- 442 Gould SJ. 1966. Allometry and size in ontogeny and phylogeny. *Biological reviews of the*
443 *Cambridge Philosophical Society* 41:587–640.
- 444 Huxley JS. 1932. *Problems of relative growth*. New York: The dial press.
- 445 International Committee on, Veterinary Gross Anatomical Nomenclature. 2012. Nomina
446 Anatomica Veterinaria (N.A.V.).
- 447 Janis CM. 1990. Correlation of cranial and dental variables with body size in ungulates and
448 macropodoids. In: *Body size in mammalian paleobiology: estimation and biological*
449 *implications*. Cambridge: Cambridge University Press,.
- 450 Janis CM, Theodor JM, Boisvert B. 2002. Locomotor evolution in camels revisited: a
451 quantitative analysis of pedal anatomy and the acquisition of the pacing gait. *Journal of*
452 *vertebrate paleontology* 22:110–121.
- 453 Kilbourne BM, Makovicky PJ. 2012. Postnatal long bone growth in terrestrial placental
454 mammals: Allometry, life history, and organismal traits. *Journal of Morphology* 273:1111–1126.
- 455 Lindsey SL, Bennett CL. 1999. *The Okapi: Mysterious Animal of Congo-Zaire*. Austin:
456 University of Texas Press.
- 457 Lydekker R. 1876. Notes on the fossil mammalian faunae of India and Burma. In: *Records of the*
458 *Geological Survey of India*. London: Trübner and Co., 86–105.
- 459 Lydekker R. 1878. Notices of Siwalik Mammals. In: *Records of the Geological Survey of India*.
460 London: Trübner and Co., 83–95.

- 461 Lydekker R. 1883. Indian Tertiary and post Tertiary vertebrata: Siwalik Camelopardalidae. In:
462 *Memoirs of the Geological survey of India: Palaeontologica Indica, Being Figures and*
463 *Descriptions of the Organic Remains Procured During the Progress of the Geological Survey of*
464 *India*. Calcutta: Geological survey of India, by order of the Governor-General of India, 99–142.
- 465 Lydekker R. 1885a. *Catalogue of fossil mammalia. Part ii. Containing the order ungulata,*
466 *suborder Artiodactyla*. London: Taylor and Francis. Printed by order of the Trustees.
- 467 Lydekker R. 1885b. *Catalogue of the remains of Siwalik Vertebrata contained in the Geological*
468 *Department of the Indian Museum, Calcutta*. Printed by the Superintendent of Government
469 Printing, India.
- 470 Matthew WD. 1929. Critical observations upon Siwalik mammals (exclusive of Proboscidea).
471 *Bulletin of the American Museum of Natural History* 56:437–560.
- 472 McMahon TA. 1975. Allometry and Biomechanics: Limb Bones in Adult Ungulates. *The*
473 *American Naturalist* 109:547–563.
- 474 Mitchell G, van Sittert SJ, Skinner JD. 2009. Sexual selection is not the origin of long necks in
475 giraffes. *Journal of Zoology (London)* 278:281–286.
- 476 Mitchell G, Skinner JD. 2003. On the origin, evolution and phylogeny of giraffes *Giraffa*
477 *camelopardalis*. *Transactions of the Royal Society of South Africa* 58:51–73.
- 478 Murchison C. (ed.) 1868. *Palæontological Memoirs and Notes of the Late Hugh Falconer: With*
479 *a Biographical Sketch of the Author*. London: R. Hardwicke.
- 480 Nanda AC. 2002. Upper Siwalik mammalian faunas of India and associated events. *Journal of*
481 *Asian Earth Sciences* 21:47–58.
- 482 Nanda AC. 2008. Comments on the Pinjor Mammalian Fauna of the Siwalik Group in relation to
483 the post-Siwalik faunas of Peninsular India and Indo-Gangetic Plain. *Quaternary International*
484 192:6–13.
- 485 Packard GC. 2013. Is logarithmic transformation necessary in allometry? *Biological Journal of*
486 *the Linnean Society* 109:476–486.
- 487 Packard GC, Boardman TJ, Birchard GF. 2009. Allometric equations for predicting body mass
488 of dinosaurs. *Journal of Zoology* 279:102–110.
- 489 Packard GC, Boardman TJ, Birchard GF. 2010. Allometric equations for predicting body mass
490 of dinosaurs: a comment on Cawley & Janacek (2010). *Journal of Zoology* 282:221–222.
- 491 Pélabon C, Bolstad GH, Egset CK, Cheverud JM, Pavlicev M, Rosenqvist G. 2013. On the
492 relationship between ontogenetic and static allometry. *The American naturalist* 181:195–212.

- 493 Roth VL. 1990. Insular dwarf elephants: a case study in body mass estimation and ecological
494 inference. In: Damuth JD, MacFadden BJ eds. *Body Size in Mammalian Paleobiology:
495 Estimation and Biological Implications*. Cambridge: Cambridge University Press, 151–179.
- 496 Runestad JA. 1994. Humeral and Femoral Diaphyseal Cross-sectional Geometry and Articular
497 Dimensions in Prosimii and Platyrrhini (primates) with Application for Reconstruction of Body
498 Mass and Locomotor Behavior in Adapidae (primates: Eocene). Johns Hopkins University.
- 499 Van Schalkwyk OL. 2004. Bone density and calcium and phosphorous content of the giraffe
500 (*Giraffa camelopardalis*) and African buffalo (*Syncerus caffer*) skeletons. Pretoria: University of
501 Pretoria.
- 502 Van Schalkwyk OL, Skinner JD, Mitchell G. 2004. A comparison of the bone density and
503 morphology of giraffe (*Giraffa camelopardalis*) and buffalo (*Syncerus caffer*) skeletons. *Journal
504 of zoology* 264:307–315.
- 505 Scott K. 1990. Postcranial dimensions of ungulates as predictors of body mass. In: Damuth J,
506 MacFadden BJ eds. *Body size in mammalian paleobiology*. Cambridge: Cambridge University
507 Press,.
- 508 Van Sittert SJ, Skinner JD, Mitchell G. 2010. From fetus to adult - an allometric analysis of the
509 giraffe vertebral column. *Journal of Experimental Zoology Part B Molecular and Developmental
510 Evolution* 314B:469–479.
- 511 Van Sittert S, Skinner J, Mitchell G. 2015. Scaling of the appendicular skeleton of the giraffe
512 (*Giraffa camelopardalis*). *Journal of Morphology* 276:503–516.
- 513 Slijper EJ. 1946. Comparative biologic-anatomical investigations on the vertebral column and
514 spinal musculature of mammals. *Verhandelingen der Koninklijke Nederlandsche Akademie van
515 Wetenschappen Afdeling Natuurkunde* 42:1–128.
- 516 Smith RJ. 1984. Allometric scaling in comparative biology: problems of concept and method.
517 *American Journal of Physiology-Regulatory, Integrative and Comparative Physiology*
518 246:R152–R160.
- 519 Solounias N. 1999. The remarkable anatomy of the giraffe's neck. *Journal of Zoology (London)*
520 247:257–268.
- 521 Spamer EE, Daeschler E, Vostreys-Shapiro LG. 1995. *A Study of Fossil Vertebrate Types in the
522 Academy of Natural Sciences of Philadelphia: Taxonomic, Systematic, and Historical
523 Perspectives*. Academy of Natural Sciences.
- 524 Stuart C, Stuart M. 2006. *Field Guide to Larger Mammals of Africa*. Cape Town: Struik
525 Publishers.

- 526 Taylor MP. 2007. Xenoposeidon week, day 4: the question everyone is asking ... how big was it?
527 Available at [http://sypow.com/2007/11/18/xenoposeidon-week-day-4-the-question-everyone-is-](http://sypow.com/2007/11/18/xenoposeidon-week-day-4-the-question-everyone-is-asking-how-big-was-it/)
528 [asking-how-big-was-it/](http://sypow.com/2007/11/18/xenoposeidon-week-day-4-the-question-everyone-is-asking-how-big-was-it/) (accessed May 27, 2015).
- 529 Taylor MP, Naish D. 2007. An Unusual New Neosauropod Dinosaur from the Lower Cretaceous
530 Hastings Beds Group of East Sussex, England. *Palaeontology* 50:1547–1564.
- 531 Taylor MP, Wedel MJ. 2013. Why sauropods had long necks; and why giraffes have short necks.
532 *PeerJ* 1:e36.
- 533 Van Valkenburgh B. 1990. Skeletal and dental predictors of body mass in carnivores. In: *Body*
534 *size in mammalian paleobiology*. Cambridge: Cambridge University Press.
- 535 Warton DI, Wright IJ, Falster DS, Westoby M. 2006. Bivariate line-fitting methods for
536 allometry. *Biological reviews of the Cambridge Philosophical Society* 81:259–291.

1

A map indicating the probable vicinity of *G. sivalensis* fossil discoveries.

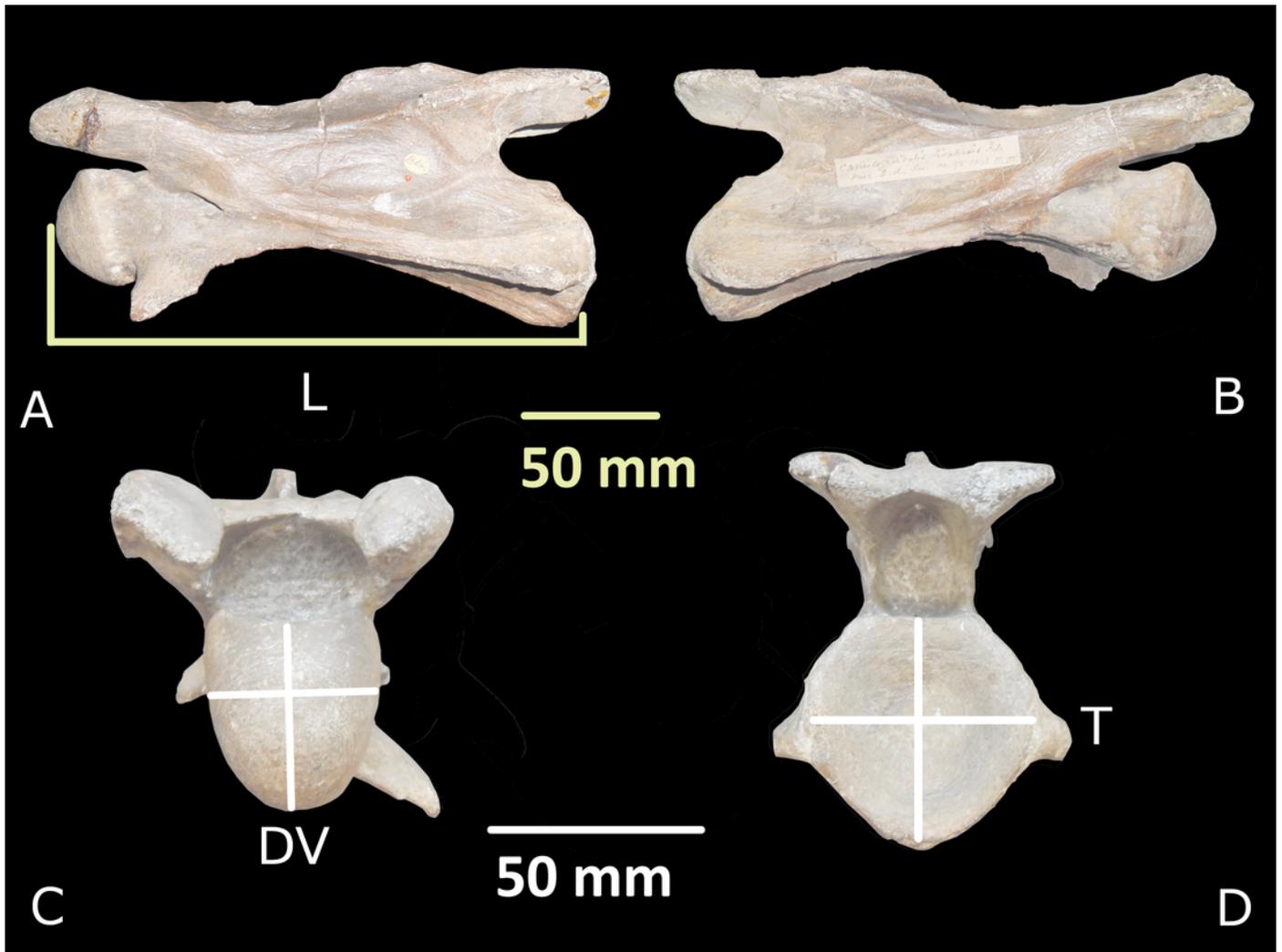
The marker indicates the location of the Shivalik Fossil Park in the Siwalik Hills, a subHimalayan mountain range. This is most probably the area 'west to the river Jumna' (currently Yamuna River) to which Falconer and Cautley (1843) referred. Map data: AutoNavi, Google.



2

Giraffa sivalensis holotype, specimen OR39747.

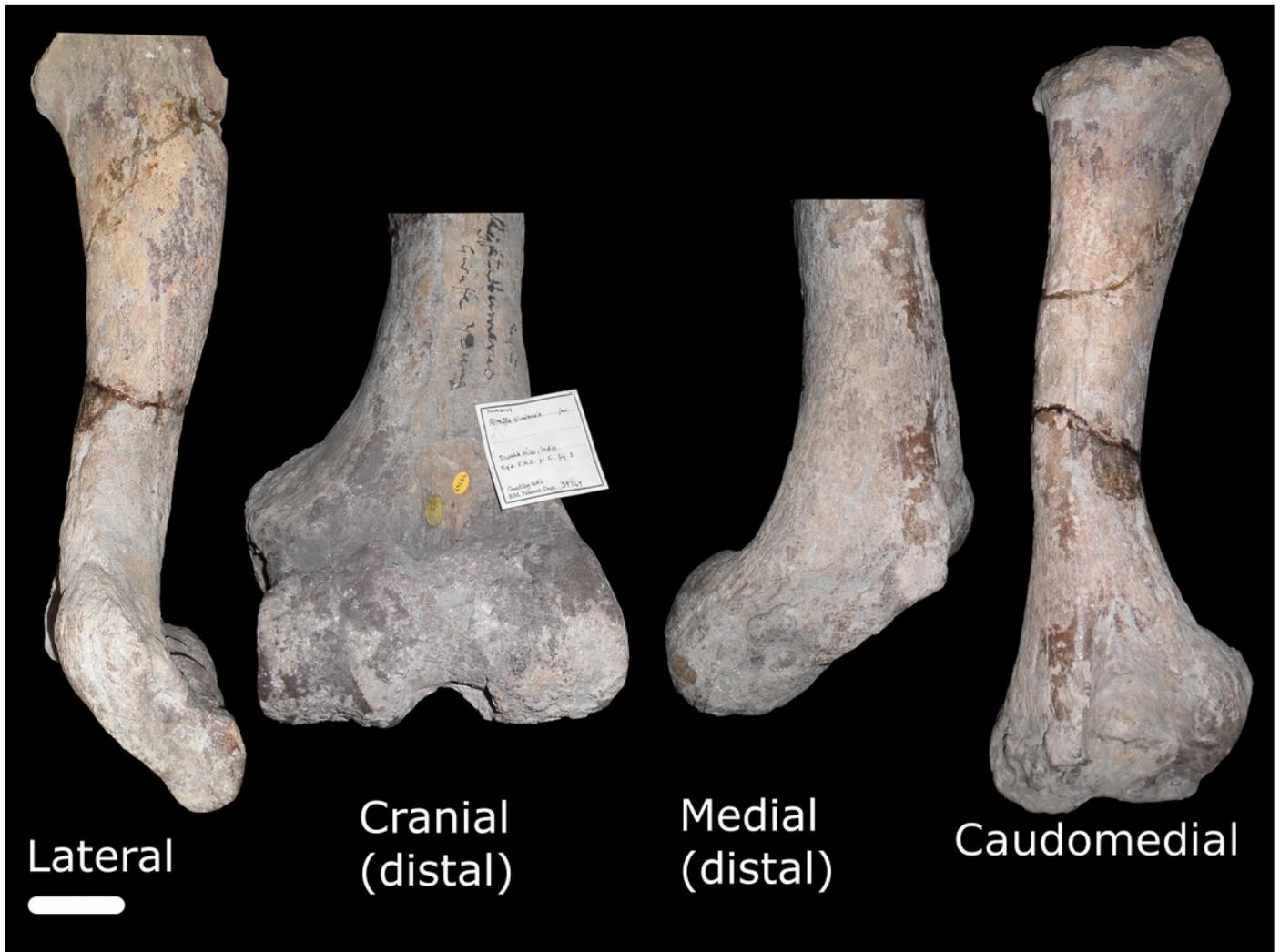
Presented, from left to right, in left lateral (A), right lateral (B), cranial (C) and caudal (D) views. On left lateral view the line indicates the landmarks for the vertebral body length (L) measurement. On cranial and caudal views the vertical lines indicate the height (dorsoventral, DV) while the horizontal lines indicate the width (transverse, T) measurements.



3

Specimen OR39749.

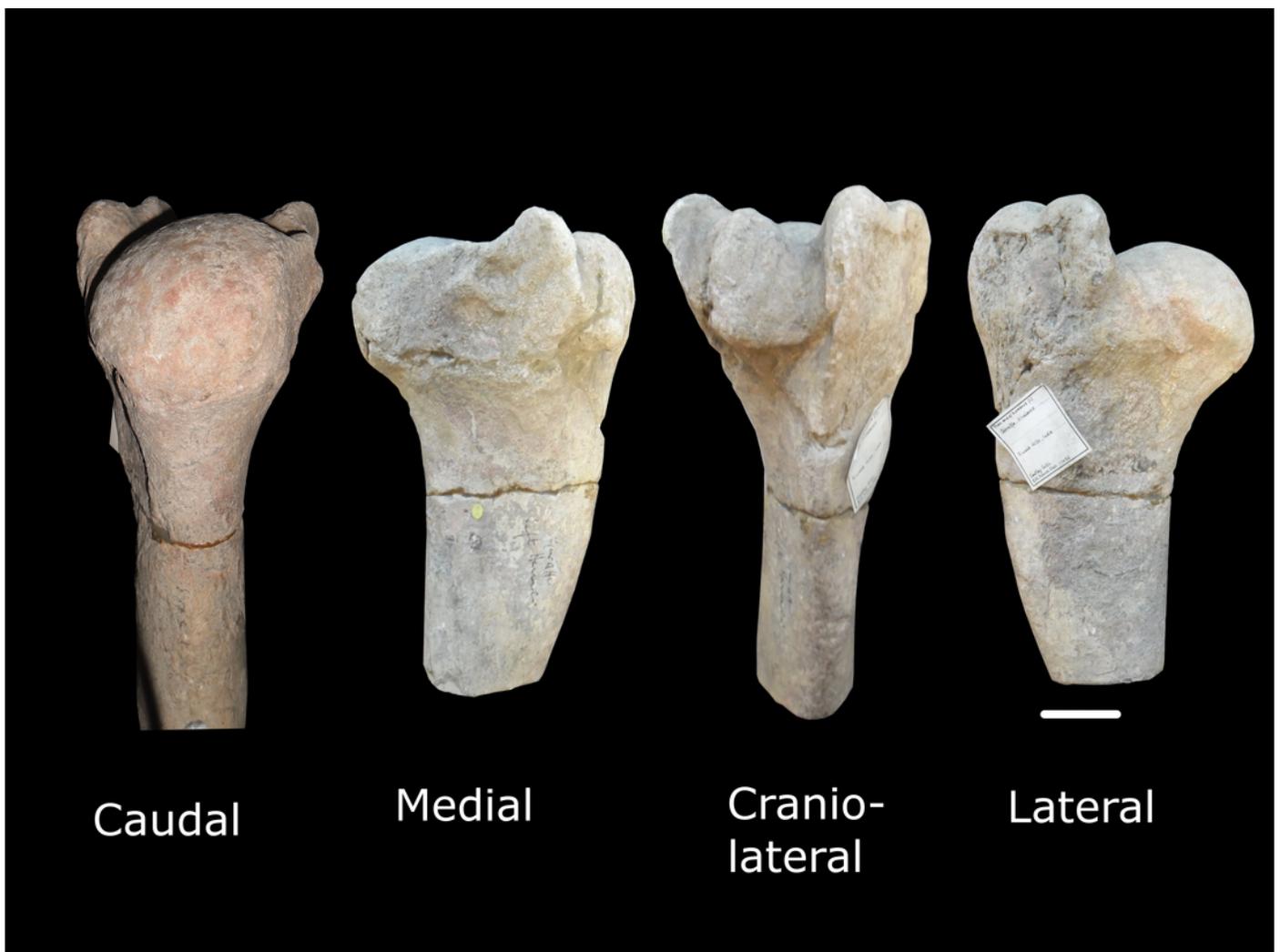
This image represents different views of a right humerus that has been assigned to *G. sivalensis*. The different views are not to scale; where only distal parts of the bone are shown, these have been enlarged relative to images of the specimen in toto. The scale bar indicates 50 mm and pertains to the lateral view only.



4

Specimen OR17136.

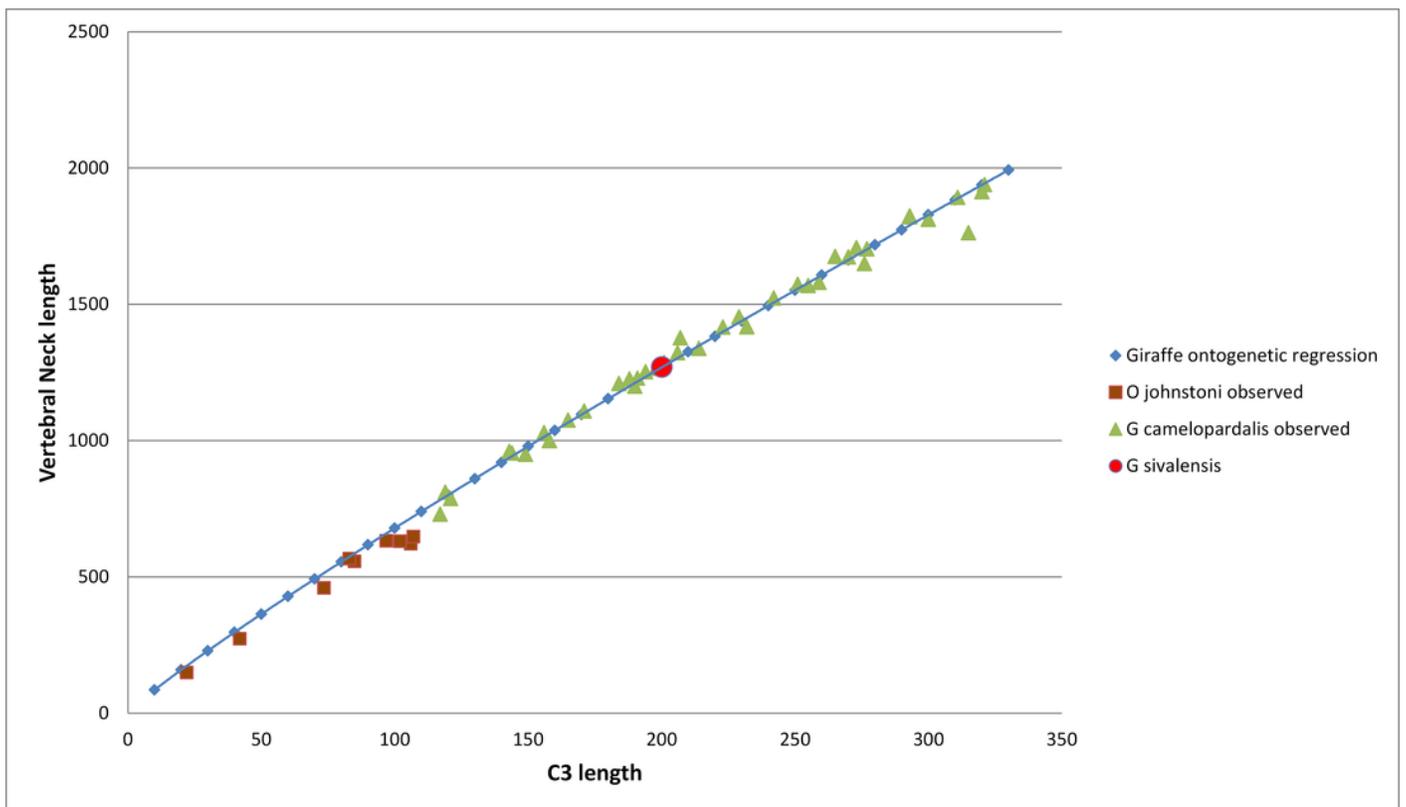
This represents different views of the proximal part of a left humerus that has been assigned to *G. sivalensis*. The scale bar indicates 50 mm and pertains to the lateral view only as the different views are not drawn to scale.



5

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

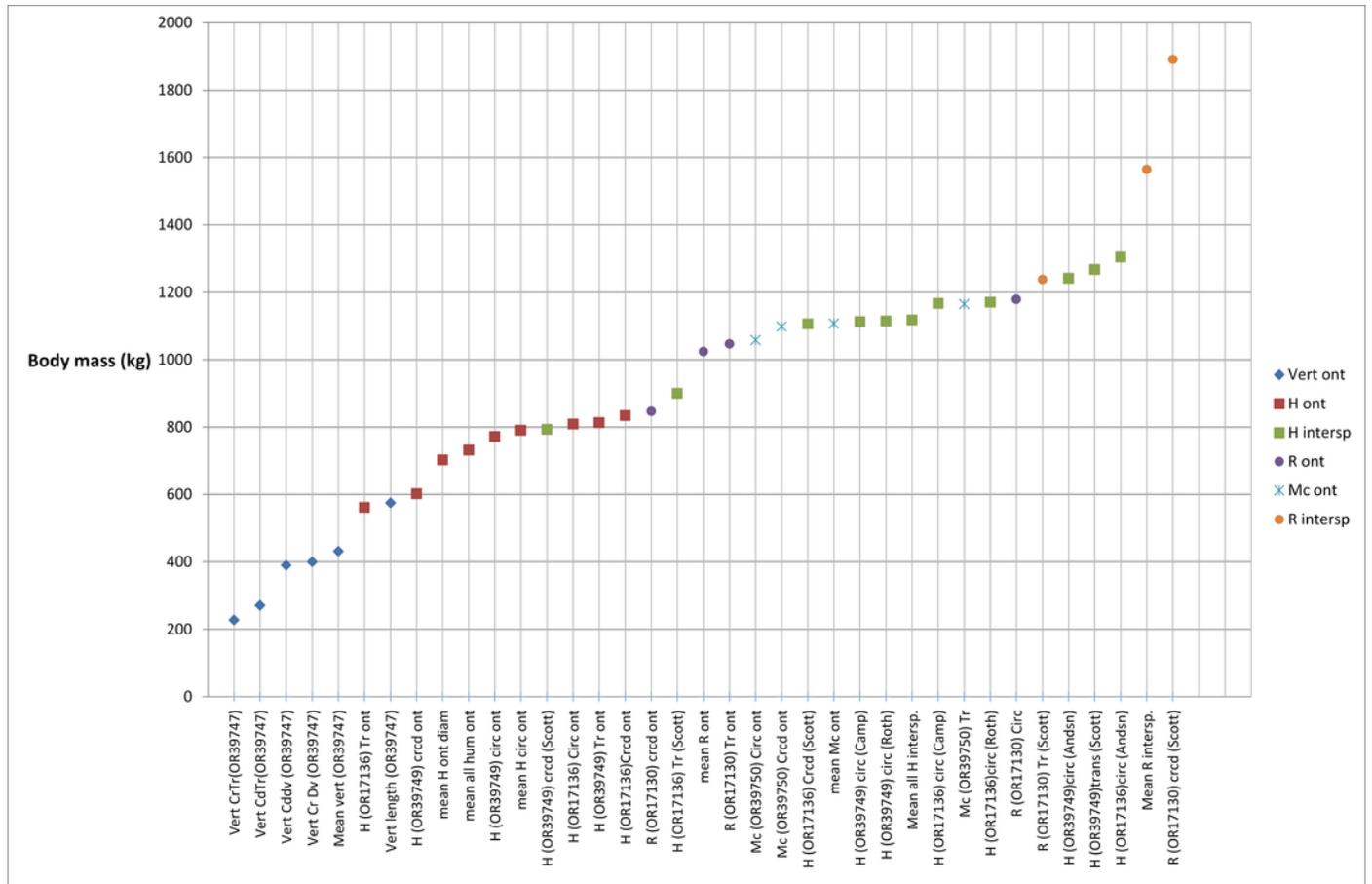
A regression line is based on the giraffe ontogenetic series and is extrapolated to the okapi range. The use of a regression line for ontogenetic and phylogenetic allometry seems to be appropriate in this case, supporting the use of a giraffe ontogenetic regression line to predict a neck length value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



6

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). Note that the interspecific predictions generally provide heavier estimates of body mass than predictions based on ontogenetic data. Furthermore, the distal bones tend to predict higher values than the proximal (humerus) bone predictions. Vertebral predictions give the lightest 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)



7

The body mass prediction errors (absolute values) associated with various dimensions in *Okapia johnstoni* and *Giraffa camelopardalis*.

Of the available regressions and variables measured, it would appear that humeral circumference and craniocaudal diameter (using *G. camelopardalis* ontogenetic regression) is best suited for body mass predictions, both in giraffes and okapis, and therefore also likely to be useful for body mass predictions in *G. sivalensis*. Vertebral caudal dorsoventral diameter represents an acceptable variable should estimates only be based on the holotype, with prediction errors of 17% and 25% in giraffes and okapis respectively. Different shapes indicate different bones used for body mass predictions. Note that for clarity of the graph, the maximum indicated prediction error is 100%. Abbreviations: Oj: *Okapia johnstoni*; Gc: *Giraffa camelopardalis*; P.E: Prediction Error; other abbreviations as listed for Figure 2.

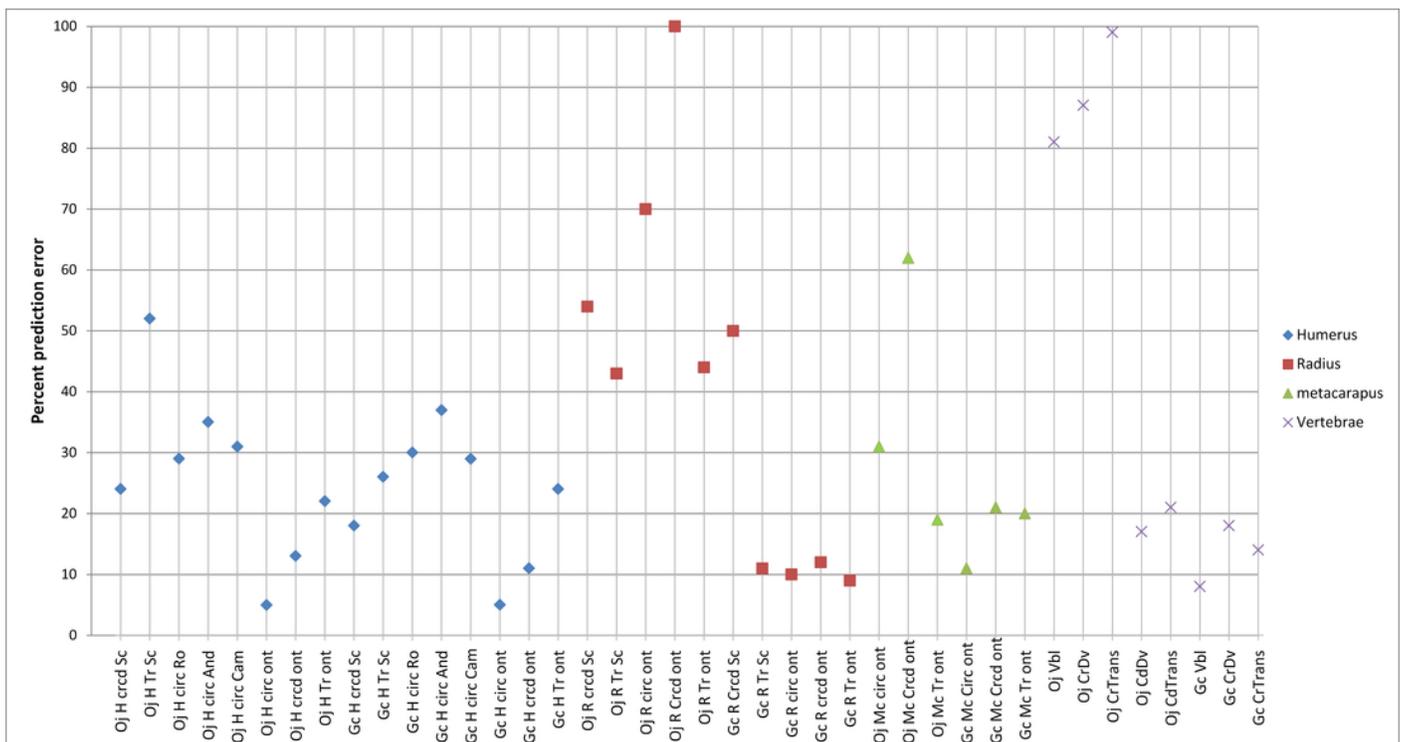


Table 1 (on next page)

Previous size estimates of *G. sivalensis*

| Size estimate | Author | Relevant specimens/ comments |
|--|---|---|
| 'One third shorter' with a neck 'one tenth more slender' as extant giraffes. | Falconer & Cautley, 1843; Lydekker, 1876 (p.105) | Holotype vertebra, OR39747 |
| Large species but smaller than extant giraffes. | Bhatti, 2004, p. 155 | No specimen referred to. |
| Of comparable size to modern giraffes. | Bhatti, 2004, p.225 | No specimen referred to. |
| Similar head size to extant giraffes but with a shorter neck. | Lydekker, 1876, p.105 | OR39747. Lydekker noted that the areas of the zygoapophyses are 'considerably larger' than in those of extant giraffes, making the neck 'at least equally strong' as that that of extant giraffes. The larger cranial and caudal articular surfaces were also noted by Falconer and Cautley (1843). |
| Similar in size to extant giraffes. | Lydekker, 1883 | Cervical vertebra similar in size as that of <i>G. camelopardalis</i> . Referring to an imperfect 'first' cervical vertebra, later catalogued as a 'third' cervical, BM39746 (Lydekker, 1885a). |
| Slightly larger than extant giraffes. | Murchison, 1868, P207 | Right humerus. Museum of the Asiatic Society of Bengal no 43, Natural History Museum no 39749. Exact form to that of extant giraffes, but a little larger (Falconer, 1868). Lydekker (1885a) however mentioned that this fossil bone originated from a 'small individual'. |
| Similar in size to extant giraffes. | Murchison, 1868, p.206 | Left radius. Asiatic Museum of Bengal no 690. Nearly equal in dimensions to existing giraffes. |
| Similar in size to extant giraffes. | Murchison, 1868, p.207 | Left metacarpus. Asiatic Museum of Bengal no 52. Of the size of existing giraffe. |
| Similar in size to extant giraffes. | Lydekker, 1885a | Phalangeals, no 17131a. Almost indistinguishable from the corresponding bones of extant giraffes. |
| Similar in size to extant female giraffes. | Falconer & Cautley, 1843 | Fragments from upper and lower jaws. Falconer originally |

| | | |
|--|--------------------------|---|
| | | ascribed these specimens to <i>G. affinis</i> . Lydekker (1876) however refuted this species and proposed that it in actual fact <i>G. sivalensis</i> . |
| Larger than extant giraffes with smaller teeth than extant giraffes. | Mitchell & Skinner, 2003 | Review of literature. |

2

Table 2 (on next page)

Dimensions for the *G. sivalensis* holotype; a well preserved third cervical vertebra (OR39747)

Falconer and Cautley's (1843) findings are also presented. All values in mm. Nomenclature is based on the Nomina Anatomica Veterinaria (International Committee on & Veterinary Gross Anatomical Nomenclature, 2012)

1

| 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 (<i>Corpus vertebrae</i>), from the most cranial curvature of the cranial extremity (<i>Extremitas cranialis [Caput vertebrae]</i>) to the most caudal part of the caudal extremity (<i>Extremitas caudalis [Fossa vertebrae]</i>) | 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 | |

2

Table 3 (on next page)

Dimensions for long bone specimens marked as belonging to *G. sivalensis*.

All values in mm. OR39749 is marked as a juvenile. Abbreviations: H: Humerus; R: Radius; Mc: Metacarpus; L: Length; Circ: Midshaft circumference; Cr: midshaft craniocaudal diameter; Tr: midshaft transverse diameter.* distal proportion lacking. † only diaphysis. ‡ proximal metaphysis missing.

1

| 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

Table 4(on next page)

Summary of fossil teeth assigned to *G. affinis* by Falconer and Cautley (1843), and subsequently assigned to *G. sivalensis*. All regressions equations were obtained from Damuth (1990).

Abbreviations: TUML: Third Upper Molar Length, TUMW: Third Upper Molar Width, SUMW: Second Upper Molar Width, TLML: Third Lower Molar Length, TLMW: Third Lower Molar Width, TLPL: Third Lower Premolar Length, TLPW: Third Lower Premolar Width, SUPL: Second Upper Premolar Length, SUPW: Second Upper Premolar Width, SD: Sample Standard Deviation

1

| Fossil specimens | Museum no | References to specimen | Dimensions | Relevant regression equation (reference) | Body mass prediction |
|--|---------------------------|--|---|---|----------------------|
| Fragment of left maxilla including two rear molars. The 'back part of the maxillary, beyond the teeth, is attached'. | 39756 a (Lydekker, 1885a) | Figured in Plate 2 fig. 3a and 3b of Falconer & Cautley, (1843). | Joint length of two back molars, maxilla = 2.5 in = 63.5mm | | |
| | | | Greatest with of last molar = 1.4 in = 35.56 mm | $38.02 \times \text{TUMW}^{2.77}$ (all ungulates) | 752 kg |
| | | | | $32.36 \times \text{TUMW}^{2.87}$ (all selenodonts) | 945kg |
| | | | | $17.78 \times \text{TUMW}^{2.97}$ (selenodont browsers) | 718 kg |
| | | | Greatest with of penultimate molar = 1.45 in = 36.83 mm | $32.36 \times \text{SUMW}^{2.78}$ (all ungulates) | 731 kg |
| | | | | $22.91 \times \text{SUMW}^{2.96}$ (all selenodonts) | 991 kg |
| | | | | $12.02 \times \text{SUMW}^{3.08}$ (selodont browsers) | 801 kg |
| | | | Average of width measurements (SD) | | 823 (117) kg |
| Rear molar of right maxilla | 39756 (Lydekker, 1885a) | Figured in Plate 2 fig. 4 of Falconer and Cautley (1843). | Length = 1.2 in = 30.48 mm * it is not sure whether this is the greatest dimensions or occlusal surface. | $19.50 \times \text{TUML}^{2.81}$ (all ungulates) | 288 kg |
| | | | | $8.71 \times \text{TUML}^{3.12}$ (all selenodonts) | 372 kg |
| | | | | $6.31 \times \text{TUML}^{3.29}$ (selenodont browsers) | 481 kg |
| | | | Average of length measurements (SD) | | 380 (97) kg |
| | | | Width = 1.4 in = 35.56 mm * it is not sure whether this is the greatest dimensions or occlusal | $38.02 \times \text{TUMW}^{2.77}$ (all ungulates) | 752 kg |

| Fossil specimens | Museum no | References to specimen | Dimensions | Relevant regression equation (reference) | Body mass prediction |
|--|----------------------------|--|--|---|----------------------|
| | | | surface. | | |
| | | | | $32.36 \times \text{TUMW}^{2.87}$ (all selenodonts) | 915 kg |
| | | | | $17.78 \times \text{TUMW}^{2.97}$ (selenodont browsers) | 718 kg |
| | | | Average of width measurements (SD) | | 795 (105) kg |
| Fragment of left mandible containing the third molar | 39755 (Lydekker, 1885a) | Figured in plate 2 figure 5a and 5b of Falconer & Cautley, (1843). | Length = 1.7 in = 43.18 mm | $6.31 \times \text{TLML}^{2.99}$ (all ungulates) | 489 kg |
| | | | | $3.24 \times \text{TLML}^{3.19}$ (all selenodonts) | 533 kg |
| | | | | $2.24 \times \text{TLML}^{3.35}$ (selenodont browsers) | 673 kg |
| | | | Average of length measurements (SD) | | 565 (96) kg |
| | | | Greatest width = 1.0 in = 25.4 mm | $109.64 \times \text{TLMW}^{2.73}$ (all ungulates) | 750 kg |
| | | | | $77.62 \times \text{TLMW}^{2.93}$ (all selenodonts) | 1014 kg |
| | | | | $64.56 \times \text{TLMW}^{2.88}$ (selenodont browsers) | 718 kg |
| | | Average of width measurements (SD) | | 827 (162) kg | |
| Third premolar of the left mandible, detached. | 39757 (Lydekker, 1885a) | Figured in Plate 2 figure 6 of Falconer & Cautley, (1843). | Length = 1.0 in = 25.4 mm | $79.43 \times \text{TLPL}^{2.76}$ (all ungulates) | 599 kg |
| | | | | $61.66 \times \text{TLPL}^{2.92}$ (all selenodonts) | 780 kg |
| | | | | $20.42 \times \text{TLPL}^{3.19}$ (selenodont browsers) | 618 kg |
| | | | Average of length measurements (SD) | | 666 (99) kg |
| | | | Width = 0.9 in = 22.86 mm | $524.81 \times \text{TLPW}^{2.45}$ (all ungulates) | 1121 kg |
| | | | | $524.81 \times \text{TLPW}^{2.53}$ (all selenodonts) | 1440 kg |
| | | | | $398.11 \times \text{TLPW}^{2.49}$ (selenodont browsers) | 964 kg |
| | | Average of width measurements (SD) | | 1175 (243) kg | |
| Second premolar of right maxilla | | Figured in Plate 2 figure 7 of Falconer & Cautley, (1843). | Length = 1.0 in = 25.4 mm | $169.82 \times \text{SUPL}^{2.51}$ (all ungulates) | 570 kg |

| Fossil specimens | Museum no | References to specimen | Dimensions | Relevant regression equation (reference) | Body mass prediction |
|------------------|-----------|------------------------|--|---|----------------------|
| | | | | $141.25 \times \text{SUPL}^{2.65}$ (all selenodonts) | 746 kg |
| | | | | $20.41 \times \text{SUPL}^{3.26}$ (selenodont browsers) | 776 kg |
| | | | Average of length measurements (SD) | | 697 (111) kg |
| | | | Width = 1.12 in = 28.45 mm | $380.19 \times \text{SUPW}^{2.3}$ (all ungulates) | 840 kg |
| | | | | $416.87 \times \text{SUPW}^{2.31}$ (all selenodonts) | 953 kg |
| | | | | $208.93 \times \text{SUPW}^{2.44}$ (selenodont browsers) | 738 kg |
| | | | Average of width measurements (SD) | | 843 (108) kg |

Table 5 (on next page)

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*.

Abbreviations: DMNH: Ditsong National Museum of Natural History (Formerly Transvaal Museum), Pretoria, South Africa; MNHN: Museum National d'Histoire Naturelle, Paris, France; SM: Senckenberg Naturmuseum, Frankfurt, Germany; OTVL: Observed Total Vertebral Length; ONL: Observed Neck Length; ONL-1: Observed Neck Length Minus C1; OTL: Observed Trunk Length; OFL: Observed Front Limb Long Bone Lengths; OHL: Observed Hind Limb Long Bone Lengths; N:FL: Neck Length to Foreleg Length ratio; PNL: Predicted Neck Length; % PE: Percent Prediction Error for vertebral length based on giraffe ontogenetic allometry.

1

| Specimen no | Museum | OTVL | OVNL | OVNL-1 | C3VBL | OFL | N:FL | PVNL | Predicted neck length regression equation | %PE |
|-------------|--------|------|------|--------|-------|------|------|------|---|------|
| az2348 | DMNH | 1259 | 557 | 522 | 85 | 932 | 0.60 | 586 | $PVNL=10.65*C3VBL^{0.902}$ | 0.05 |
| az2440 | DMNH | 1392 | 567 | 531 | 83 | | | 574 | | 0.01 |
| 1973-178 | MNHN | 722 | 273 | 260 | 42 | 752 | 0.36 | 310 | | 0.14 |
| 1961-131 | MNHN | 400 | 149 | 137 | 22.1 | 553 | 0.27 | 174 | | 0.17 |
| 1984-56 | MNHN | | 459 | 428 | 73.5 | | | 514 | | 0.12 |
| 1996-102 | MNHN | 1529 | 632 | 600 | 96.9 | 1018 | 0.62 | 660 | | 0.04 |
| 27194 | SM | 1442 | 621 | 589 | 106 | 1018 | 0.61 | 715 | | 0.15 |
| 73224 | SM | 1521 | 647 | 613 | 107 | 993 | 0.65 | 722 | | 0.12 |
| 56346 | SM | 1458 | 630 | 599 | 102 | 998 | 0.63 | 691 | | 0.10 |
| 92290 | SM | | | 142 | 22 | 534 | | | | |

2

Table 6 (on next page)

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

1

| Dimension predicted for <i>G. sivalensis</i> (dependent (y) variable) | Prediction based on (independent (x) variable) | Equation generated from | Equation, Slope Confidence interval, R ² | Prediction |
|---|--|---|--|------------|
| Vertebral neck length (C1 to C7) | OR39747 (C3) vertebral body length | <i>G. camelopardalis</i> ontogenetic data | $y = 10.66 x^{0.902}$ CI = 0.874 – 0.930 R ² = 0.99 | 1270 mm |
| Vertebral neck length (C2 to C7) | OR39747 (C3) vertebral body length | <i>G. camelopardalis</i> ontogenetic data | $y = 9.708x^{0.908}$ CI = 0.881 – 0.936 R ² = 0.99 | 1195 mm |
| Vertebral neck length (C2 to C7) | OR39747 (C3) vertebral body length | Various ungulates, data from (Badlangana, Adams & Manger, 2009) | $y = 5.023 x^{1.025}$ CI = 0.977 – 1.614 R ² = 0.99 | 1148 mm |
| Dorsal neck length (occipital crest to withers) | OR39747 (C3) vertebral body length | <i>G. camelopardalis</i> ontogenetic data | $y = 1.694 x^{0.822}$ CI = 0.716 – 0.928 R ² = 0.87 | 1321 mm |
| Ventral neck length (angle of jaw to acromion) | OR39747 (C3) vertebral body length | <i>G. camelopardalis</i> ontogenetic data | $y = 1.442 x^{0.890}$ CI = 0.765 – 1.014 R ² = 0.85 | 1608 mm |
| Average neck length (of dorsal and ventral neck length) | OR39747 (C3) vertebral body length | <i>G. camelopardalis</i> ontogenetic data | $y = 1.55 x^{0.859}$ CI = 0.767 – 0.951 R ² = 0.91 | 1467 mm |
| Front leg length (humerus+ radius+ metacarpus long bones) | OR39747 (C3) vertebral body length | <i>G. camelopardalis</i> ontogenetic data | $y = 70.2x^{0.598}$ CI = 0.332 – 0.8642 R ² = 0.87 | 1668 mm |
| Foreleg withers height | OR39747 (C3) vertebral body length | <i>G. camelopardalis</i> ontogenetic data | $y = 7.61x^{0.663}$ CI = 0.586 – 0.741 R ² = 0.92 | 2558 mm |
| Approximate reaching height (hoof to occipital crest) | OR39747 (C3) vertebral body length | <i>G. camelopardalis</i> ontogenetic data | $y = 7.600x^{0.742}$ CI = 0.678-0.806 R ² = 0.95 | 3880 mm |

2

Table 7 (on next page)

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

SD = Standard deviation. PE = Prediction Error

1

| Independent(x) variable | Model sample | Model r2 | Allometric equation | Body mass prediction (kg) | Body mass PE% confidence intervals in kg (based on prediction errors when applied to <i>G. camelopardalis</i> data) | Body mass confidence intervals in kg (based on prediction errors when applied to <i>O. johnstoni</i> data) |
|--|---|----------|-------------------------------|---------------------------|---|--|
| OR39747 (C3) vertebral body length | <i>G. camelopardalis</i> ontogenetic data | 0.91 | $y = 0.022 * x^{1.919}$ | 575 | 8% PE (529-612) | 81% PE (109-1041) |
| OR39747 (C3) cr dv | <i>G. camelopardalis</i> ontogenetic data | 0.77 | $y = 0.0023 * x^{3.21}$ | 400 | 18% PE (328-472) | 87% PE (52-748) |
| OR39747 (C3) cr lat | <i>G. camelopardalis</i> ontogenetic data | 0.84 | $y = 0.0054 * x^{2.967}$ | 228 | 14% PE (196-260) | 99% PE (2-454) |
| OR39747 (C3) cd dv | <i>G. camelopardalis</i> ontogenetic data | 0.69 | $y = 0.0048 * x^{2.847}$ | 390 | 25% PE (293-487) | 17% PE (323-456) |
| OR39747 (C3) cd lat | <i>G. camelopardalis</i> ontogenetic data | 0.57 | $y = 0.0227 * x^{2.360}$ | 271 | 50% PE (136-407) | 21% PE (214-328) |
| Average of OR39747 vertebral dimensions (SD) | | | | 373 (135) | | |
| OR39748 (C3) cd dv | <i>G. camelopardalis</i> ontogenetic data | 0.69 | $y = 0.0048 * x^{2.847}$ | 394 | 25% PE (296-493) | 17% PE (327-462) |
| OR39747 (C4) cd dv | <i>G. camelopardalis</i> ontogenetic data | 0.69 | $y = 0.0011 * x^{3.128}$ | 274 | | |
| OR39747 (C5) cd dv | <i>G. camelopardalis</i> ontogenetic data | 0.69 | $Y = 0.0004 * x^{3.285}$ | 187 | | |
| Humerus midshaft circumference (OR17136) | <i>G. camelopardalis</i> ontogenetic data | 0.98 | $y = 8.96 * 10^{-4} x^{2.55}$ | 809 | 5% PE (767-851) | 5%PE (766-852) |
| Humerus midshaft circumference (OR39749) | <i>G. camelopardalis</i> ontogenetic data | | | 772 | 5% PE (732-812) | 5%PE (731-813) |
| average of humeral circumferences (SD) | | | | 791 (26) | | |
| Humerus midshaft craniocaudal diameter (OR17136) | <i>G. camelopardalis</i> ontogenetic data | 0.98 | $y = 3.59 * 10^{-2} x^{2.32}$ | 834 | 11% PE (743-925) | 13%PE (723-945) |
| Humerus midshaft craniocaudal diameter (OR39749) | <i>G. camelopardalis</i> ontogenetic data | | $y = 3.59 * 10^{-2} x^{2.32}$ | 602 | 11% PE (537-667) | 13%PE (522-682) |
| Humerus midshaft transverse diameter (OR17136) | <i>G. camelopardalis</i> ontogenetic data | 0.96 | $y = 2.00 * 10^{-2} x^{2.53}$ | 561 | 24% PE (429-693) | 22%PE (438-684) |
| Humerus midshaft transverse diameter (OR39749) | <i>G. camelopardalis</i> ontogenetic data | | $y = 2.00 * 10^{-2} x^{2.53}$ | 813 | 24% PE (622-1004) | 22%PE (635-991) |
| Average humeral craniocaudal and transverse (SD) | | | | 703 (141) | | |
| All humeral ontogenetic average | | | | 732 (119) | | |

| | | | | | | |
|---|--|------|-------------------------------|------------|-------------------|------------------|
| (SD) | | | | | | |
| Radius midshaft circumference (OR17130) | <i>G. camelopardalis</i> ontogenetic data | 0.99 | $y = 1.65 * 10^{-4} x^{2.93}$ | 1179 | 10%PE (1064-1294) | 31%PE (726-1390) |
| Radius midshaft craniocaudal diameter (OR17130) | <i>G. camelopardalis</i> ontogenetic data | 0.98 | $y = 2.89 * 10^{-3} x^{3.19}$ | 847 | 12%PE (746-948) | 62%PE (416-1780) |
| Radius midshaft transverse diameter (OR17130) | <i>G. camelopardalis</i> ontogenetic data | 0.99 | $y = 1.18 * 10^{-2} x^{2.67}$ | 1047 | 9%PE (948-1146) | 19%PE (943-1387) |
| Radius ontogenetic average (SD) | | | | 1024 (167) | | |
| Metacarpal midshaft circumference (OR39750) | <i>G. camelopardalis</i> ontogenetic data | 0.96 | $y = 4.70 * 10^{-5} x^{3.24}$ | 1058 | 11%PE (942-1174) | 31%PE (726-1390) |
| Metacarpal midshaft craniocaudal diameter (OR39750) | <i>G. camelopardalis</i> ontogenetic data | 0.97 | $y = 1.59 * 10^{-3} x^{3.40}$ | 1098 | 21%PE (867-1329) | 62%PE (416-1780) |
| Metacarpal midshaft transverse diameter (OR39750) | <i>G. camelopardalis</i> ontogenetic data | 0.98 | $y = 6.71 * 10^{-3} x^{2.95}$ | 1165 | 20%PE (932-1398) | 19%PE (943-1387) |
| Average metacarpus | | | | 1107 (54) | | |
| Humerus midshaft craniocaudal diameter (OR17136) | Artiodactyl interspecific allometry (Scott, 1990) | 0.94 | $y = 7.63 x^{2.455}$ | 1106 | 18%PE (906-1305) | 24%PE (844-1368) |
| Humerus midshaft craniocaudal diameter (OR39749) | Artiodactyl interspecific allometry (Scott, 1990) | | | 793 | 18%PE (650-936) | 24%PE (605-981) |
| Humerus midshaft transverse diameter (OR17136) | Artiodactyl static interspecific (Scott, 1990) | 0.95 | $y = 12.4 x^{2.46}$ | 900 | 26%PE (662-1138) | 52%PE (428-1372) |
| Humerus midshaft transverse diameter (OR39749) | Artiodactyl interspecific allometry (Scott, 1990) | | | 1268 | 26%PE (822-1518) | 52% (603-1933) |
| Humerus midshaft circumference (OR17136) | Various mammalian taxa (Roth, 1990) | 0.99 | $y = 9.45 * 10^{-4} x^{2.61}$ | 1170 | 30%PE (822-1518) | 29%PE (831-1509) |
| Humerus midshaft circumference (OR39749) | Various mammalian taxa (Roth, 1990) | | | 1115 | 30%PE (784-1446) | 29%PE (792-1438) |
| Humerus midshaft circumference (OR17136) | Various mammalian taxa (Anderson, Hall-Martin & Russell, 1985) | 0.99 | $0.0009 x^{2.6392}$ | 1304 | 37%PE (819-1789) | 35%PE (842-1766) |
| Humerus midshaft circumference (OR39749) | Various mammalian taxa (Anderson, Hall-Martin & Russell, | | | 1241 | 37%PE (780-1702) | 35%PE (801-1681) |

| | | | | | | |
|--|--|------|------------------------|------------|------------------|------------------|
| | 1985) | | | | | |
| Humerus midshaft circumference (OR17136) | Ungulates (Campione & Evans, 2012) | 0.95 | $y = 1.469 x^{2.5273}$ | 1167 | 29%PE (831-1503) | 31%PE (800-1534) |
| Humerus midshaft circumference (OR39749) | Ungulates (Campione & Evans, 2012) | | | 1113 | 29%PE (792-1433) | 31%PE (763-1463) |
| All humeral interspecific average (SD) | | | | 1112 (180) | | |
| Radius midshaft craniocaudal diameter (OR 17130) | Artiodactyl static allometry (Scott, 1990) | 0.93 | $y = 29.2 x^{2.51}$ | 1891 | 50%PE 946-2837 | 54%PE 870-2911 |
| Radius midshaft transverse diameter (OR 17130) | Artiodactyl static allometry (Scott, 1990) | 0.91 | $y = 8.19 x^{2.555}$ | 1238 | 11%PE 1102-1374 | 43%PE (711-1765) |
| Radial interspecific average (SD) | | | | 1565 (462) | | |

2