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

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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, metacarpi 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.

Introduction

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.

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. Lydekker,

19   (1885a) however 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 a 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**)**.

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*.

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.

Materials and Methods

Studied material and dimensions measured

All postcranial specimens assigned to *G. sivalensis* that were available at the Natural History

Museum in London were studied. From these specimens, body and neck size estimates were

calculated using giraffe ontogenetic or available interspecific allometric equations. The only

vertebra measured was the holotype, specimen OR39747, which is a cervical vertebra. Falconer

and Cautley (1843) presented an extensive description of this specimen. A caudal fragment of a

'fourth' cervical OR39748 (Lydekker, 1885a), also described as a second cervical by Falconer

(1845), as well as a caudal part of a 'third' cervical OR39746 (Lydekker, 1885a) that were

assigned to *G. sivalensis* were missing from the Siwalik collection at the Natural History

Museum. Dimensions were measured with a vernier calliper and included: vertebral body length,

cranial vertebral body height, cranial vertebral body width, caudal vertebral body height, caudal

vertebral body width and spinous process length (Figure 2).

Additional postcranial specimens assigned to *G. sivalensis* held at the Natural History Museum

include fragments of two humeri (OR39749 and OR17136; Figure 3 and Figure 4 respectively), a

fragment of a radius/ulna (OR17130) and various fragments of metacarpi and phalanges. All

metacarpal specimens except OR39750 were avoided due to the unclear numbering of specimens

and deformation of the fossils. Measurements of the long bones included length, midshaft

circumference and midshaft diameter in craniocaudal and transverse planes. The length and

circumference measurements were done with a measuring tape, while the cross sectional

diameters were done with a vernier calliper.

78   Because there is no complete *G. sivalensis* skeleton its shape needs to be inferred as analogous to

79   the only other extant *Giraffa: G. camelopardalis*. One of the methods of inferring body size from

80   a model animal or animals requires that regression equations in the form $y=mx^b$ (Huxley, 1932)

81   be constructed. These regression equations can be based on data from different species

82   (interspecific allometry), within the growth phase of a single animal (ontogenetic allometry) or

83   amongst adult animals of different size but within the same species (static allometry). We

84   applied ontogenetic as well as interspecific allometric equations to predict body mass in this

85   case.

86

87   Ontogenetic data were obtained from previous studies by the authors (Mitchell, van Sittert &

88   Skinner, 2009; van Sittert, Skinner & Mitchell, 2010, 2015). These data were used to construct

89   allometric equations to describe body mass or body dimensions. The dimensions used from

90   ontogenetic vertebral data is summarised in Table 2. Interspecific regression equations were

91   sourced from previously published work (Anderson, Hall-Martin & Russell, 1985; Roth, 1990;

92   Scott, 1990; Campione & Evans, 2012). The dimensions measured for the long bone ontogenetic

93   data are summarised in Table 3

94

95   There are inherent problems associated with using dental measurements as body size predictors,

96   especially when only a single tooth is used (Damuth, 1990; Fortelius, 1990; Janis, 1990).

97   Nevertheless, we have estimated size from teeth originally measured by Falconer & Cautley

98   (1843), even though these teeth were initially assigned to a new species *G. affinis,* a species that

99   was eventually abandoned (Lydekker, 1883). Uncertainty regarding these teeth specimens

100   persisted until recent times (Spamer, Daeschler & Vostreys-Shapiro, 1995). Teeth specimens

101 described by authors other than Falconer and Cautley which are noted in Supplementary Table 1

102 were not evaluated further as there was either uncertainty regarding the authors' species

103 association (Lydekker, 1876), or the teeth specimens were not necessarily collected in the

104 vicinity (or in the correct stratigraphical layer) of fossils described by Falconer and Cautley

105 (Lydekker, 1878), or because certain specimens were deciduous. Table 4 presents dental

106 specimens as well as dimensions as measured by Falconer and Cautley (1843). Body masses

107 were estimated from regression equations established by Damuth (1990).

108

109 *Statistical analyses*

110 Allometric equations were generated from bivariate data through ordinary least squares

111 regression. To facilitate this, measurements were logarithmically transformed to base *e* prior to

112 analyses. According to Warton et al. (2006), ordinary least squares regression is appropriate

113 when one wishes to predict y from x, even when x contains measurement error, as long as the

114 results are interpreted in the context of 'predicting y from x measured with error'. It is worth

115 noting that there is controversy regarding the practice of logarithmically transforming data in

116 scaling studies (Packard, Boardman & Birchard, 2009, 2010; Cawley & Janacek, 2010; Packard,

117 2013). The main argument is whether error becomes larger as body mass increases

118 (multiplicative error), in which case logarithmic transformation is appropriate, or whether there

119 is no correlation between error and body mass, in which case logarithmic transformation is not

120 appropriate (Glazier, 2013). The debate is ongoing and will not be reviewed here. In this study

121 we selected the method of log-transformation of data as it enables more convenient comparison

122 among similar datasets.

123 Because body dimensions (especially body masses) can be predicted by different equations and

124 by different fossil specimens, the predictions need to be validated. If regression equations had

125 reasonable power in estimating body mass in both extant *Giraffids* (*G. camelopardalis* and

126 *O. johnstoni*), then they were regarded as robust enough to extrapolate to *G. sivalensis* as well.

127 Therefore, dimensions of 10 okapi skeletons were recorded in addition to data obtained from

128 *G. camelopardalis*. The okapi skeletons were housed in various museums and were recorded as

129 the opportunities presented themselves (Table 5). Adult okapi specimens were assumed to have

130 weighed 250 kg, with a range of 200 kg to 300 kg (Lindsey & Bennett, 1999; Stuart & Stuart,

131 2006). The mature okapi specimens were identified both through additional data associated with

132 each museum specimen as well as by the degree of fusion of the epiphyses. The robustness of

133 giraffe ontogenetic as well as interspecific equations to predict body mass in both adult giraffes

134 and adult okapis correctly were assessed through the percent prediction error, calculated

135 according to Smith (1984) and van Valkenburgh (1990):

136

137 ((Observed value-Predicted value)/ Predicted value) x 100

138

139 *Assumptions made*

140 One of the major assumptions of this study is that *G. sivalensis* dimensions can be modelled

141 from *G. camelopardalis* ontogeny. Although it is unusual to model an animal from the ontogeny

142 of a different species it is not unique (an example is Roth, 1990). In assigning the holotype to a

143 specific vertebra, we also assumed that there would be broad similarity in shape between the

144 cervical vertebrae of *G. sivalensis* and *G. camelopardalis*. Falconer and Cautley (1843)

145 illustrated this assumption to be the case for many but not all features of the holotype vertebra.

146   Another assumption was that the specimens used came from the same *Giraffa* species. We tried

147   to use only those specimens that were clearly attributable to the Plio-Pleistocene and to the

148   vicinity of the holotype discovery (Figure 1), to limit possible confusion with other *Giraffa*

149   species like *G. punjabiensis*. However, in some instances these criteria were not clear due to the

150   lack of other samples or information, as in the discussion of vertebrae OR39746 and OR39748.

151   Lastly, in terms of estimating body proportions in adult animals based on vertebral length,

152   similarity in shape to *G. camelopardalis* was assumed.

Results

Dimensions measured

The OR39747 and long bone dimensions measured are summarised in Table 2 and Table 3

respectively, and where applicable the dimensions contain the equivalent measured values

according to Falconer and Cautley (1843). Except for the cranial vertebral body height, our

measurements on OR39747 are within 1% to 5% of that reported by Falconer and Cautley

(1843). Dimensions measured from okapi skeletons are presented in Table 5. Table 5 also

contains predictions and prediction errors for okapi vertebral neck length based on *G.*

camelopardalis ontogenetic data.

Predictions based on vertebra OR39747

Based on *G. camelopardalis* ontogenetic data, the average of dorsal and ventral neck length

including soft tissue in *G. sivalensis* was 1467 mm ($y = 1.55\ x^{0.859}$), the vertebral neck length

excluding soft tissue was 1270 mm ($y = 10.66\ x^{0.902}$) and the foreleg (hoof to withers) height in

the living *G. sivalensis* adult was 2540 mm ($y = 7.61x^{0.663}$, Table 6). This would mean that the

reaching height of *G. sivalensis* was around 3.9m.

The different vertebral dimensions predict the body mass to be within a range of 228 kg to 575

kg, with an average of 373 kg (Table 7, 95% Confidence interval (CI) ±168 kg). We identified

which of these dimensions could predict body mass accurately across species by calculating

prediction errors when applying the *G. camelopardalis* regression equations to both extant

giraffes and okapis. Naturally, because the predictions were done using *G. camelopardalis*

ontogenetic allometry, the *G. camelopardalis* prediction errors were lowest (8% to 50%).

176 Predictions for okapi body mass, however, ranged from 17% to 99%. The only variable which

177 provided relatively low body mass prediction errors in both okapi (17%) and *G. camelopardalis*

178 (25%) was the caudal vertebral body dorsoventral height. This dimension predicts a body mass

179 of 390 kg in *G. sivalensis* if we consider OR39747 as a third cervical. If OR39747 was

180 considered a fourth or fifth cervical, body mass predictions will be 274 kg ($y= 0.0011*x^{3.128}$) or

181 187 kg ($y = 0.0004*x^{3.285}$) respectively (Table 7).

182

183 *Predictions based on long bone dimensions*

184 All of the *G. sivalensis* long bone specimens available at the Natural History Museum were

185 incomplete proximally and/or distally. It was clear, nevertheless, that the bones had a similar

186 slender appearance of extant giraffes and were elongated. Humeral specimen OR39749 was

187 almost complete except for the proximal metaphysis, which has clearly broken off at the physeal

188 line of a subadult animal. Regarding the radius/ulna specimen, the bones' fusion at the midshaft

189 was not complete as in modern giraffes, where the two bones are indistinguishable at midshaft in

190 adults. The metacarpus specimen included in the study had the same caudal 'columns' or caudal

191 groove as those evident in the extant giraffe (Solounias, 1999; van Schalkwyk, 2004; van

192 Schalkwyk, Skinner & Mitchell, 2004) as well as in those of the okapi (own observation).

193

194 As no bones were complete length wise, bone length could not be used as a predictor for body

195 mass which, in any case, has been as shown to be a poor estimator of body mass in other taxa

196 (Scott, 1990). Based on circumferences of the humeri (OR39749 and OR17136) and using *G.*

197 *camelopardalis* ontogenetic data these specimens may have belonged to animals with body

198 weight in the range of 770 kg to 810 kg. An extant giraffe of this body mass would have a

199   humerus length of about 477 mm to 484 mm ($y=63.2*Body\ mass^{0.304}$), which is just slightly

200   longer than the 453 mm measured on OR39749 that lacked a distal metaphysis. The predictors

201   based on radial and metacarpal cross sectional dimensions offered much higher body mass

202   estimates, with averages of 1024 kg and 1107 kg respectively. In addition to employing

203   ontogenetic data to generate allometric equations, we also referred to previously published

204   interspecific studies (Anderson, Hall-Martin & Russell, 1985; Roth, 1990; Scott, 1990;

205   Campione & Evans, 2012). Interspecific equations tended to predict heavier body masses than

206   ontogenetic equations, especially so in the distal long bone samples.

207

208   *Predictions based on dental dimensions*

209   Four molars and two premolars were used for size predictions (Table 4), using equations

210   developed by Damuth (1990). Body mass predictions based on tooth length (average = 577 kg,

211   standard deviation = 155 kg) tended to be smaller than the predictions based on tooth width

212   (average = 881 kg, standard deviation = 188 kg, $t(27) = 4.83, p <0.01$). Predictions from molar

213   length dimensions also tended to be lower than those from premolar lengths (average from molar

214   lengths = 473 kg, average from premolar lengths = 682 kg, $t(9) = -3.12, p <0.05$).

215

216 **Discussion**

217 *Vertebral identity of OR39747*

218 The anatomical identity of OR39747 was disputed by Lydekker (1885a). He showed that

219 Falconer was in a habit of not counting the atlas and axis as cervical vertebrae – which often

220 meant that the start of the numbering of vertebra commenced at the third or occasionally the

221 second postcranial vertebra. Mammalian C3 to C5 forms a repetitive series and often does not

222 have the distinguishing characteristics present in the other cervical vertebrae (Solounias, 1999).

223 It is therefore indeed challenging to assign OR39747 to a specific vertebra. However, if we

224 assume approximate similarity in shape between *G. sivalensis* and *G. camelopardalis* vertebrae,

225 there are clues in the extent to which the cranial articular processes (*Proc. articularis cranialis)*

226 extend beyond the body or centrum of the vertebra (*Corpus vertebrae*). In the *G. camelopardalis*

227 C3, this process extends well beyond the cranial extremity of the vertebral body, but ends before

228 or approximately at the same dorsoventral plane as the vertebral body in C4 and C5. Judging

229 then by the extent of the articular processes of OR39747, it is a third, fourth or fifth cervical in

230 decreasing order of likelihood. Falconer was therefore correct in assigning this vertebra as a third

231 cervical, albeit fortuitously so.

232

233 *Ontogenetic and interspecific scaling models*

234 It is unusual although not unique to use ontogenetic allometry to predict an extinct animal's size.

235 For instance, Roth (1990) proposed that smaller animals of a species with distinctive

236 morphologies (be they juvenile or adult) may still be better analogues than other taxa, at least in

237 some aspects. We believe that this view is warranted in the current study as no extant species has

238 such an extreme shape as *G. camelopardalis.* Predicting fossil masses from interspecific

239   equations are further complicated by the decision of which taxa to include in regressions. For

240   example, it is not clear whether predictions generated from interspecific allometric data are more

241   accurate when based on closely related taxa with similar locomotor habits (Runestad, 1994;

242   Janis, Theodor & Boisvert, 2002) or when using a wider sampling base (De Esteban-Trivigno,

243   Mendoza & De Renzi, 2008). Other factors that may influence precision of body mass

244   predictions in interspecific studies are body mass estimations (instead of body mass

245   measurements), small intrataxa sample sizes, and overrepresentation of animals of one sex or of

246   exaggerated proportions. To overcome these problems, we investigated which ontogenetic

247   scaling parameters, if any, might be suitable and robust enough for predictions amongst extant

248   giraffidae. It is possible that giraffe ontogenetic equations are also acceptable for comparison not

249   just amongst the giraffidae but amongst, for example, extant camelids with similar gaits.

250   However, okapis were considered as an adequate reference in this case as they are closest to

251   giraffes phylogenetically and because the ontogenetic scaling of their long bones scales

252   differently to other cetartiodactyla (Kilbourne & Makovicky, 2012).

253   Ontogenetic scaling and interspecific scaling exponents are generally not interchangeable

254   (Gould, 1966; Pélabon et al., 2013); in this case it is dependent on the assumption that *G.*

255   *sivalensis* had a similar body plan as juvenile extant giraffes. We thus found it appropriate,

256   where possible, to test both ontogenetic and interspecific curves to infer proportions of

257   *G. sivalensis*, but realised that neither of these methods may be appropriate for each and every

258   dimensions measured.

259

260   *Neck length and reaching height*

261   Badlangana, Adams & Manger (2009) presented interspecific predictions for vertebral neck

262   length based on vertebral body length. Using their data (presented in Table 1 of Badlangana,

263   Adams & Manger, 2009), we could estimate *G. sivalensis* C2-C7 vertebral neck length as 1150

264   mm (Table 6), slightly shorter (45 mm or 4%) than vertebral neck length calculated from our

265   ontogenetic data. There are therefore reasonable grounds to believe that our estimated neck

266   length based on ontogenetic data is valid, or at least close to interspecific curves. Further support

267   for this rationale can be seen where the *G. camelopardalis* ontogenetic curve gives appropriate

268   predictions for vertebral neck length in both the extant giraffe and okapi (Figure 5). Extant adult

269   giraffes have an average external neck length of about 2013 mm in males (1000 kg and above)

270   and 1832 mm in females (800 kg and above) (Mitchell, van Sittert & Skinner, 2009). Assuming

271   the same body plan for *G. sivalensis* as for *G. camelopardalis*, then *G. sivalensis* had around 350

272   mm (20%) to 550 mm (27%) shorter necks than modern giraffes, depending on whether

273   OR39747 came from a female or male animal. This is a slightly longer neck length than Falconer

274   & Cautley's (1843) estimated neck length for *G. sivalensis,* which is approximately a third

275   shorter than extant giraffes.

276

277   ***Body mass***

278   The body mass predictions for *G. sivalensis* are wide (Figure 6). Possible reasons for the large

279   range of predictions are that certain fossils were erroneously attributed to *G. sivalensis* and/or

280   that certain specimens and allometric equations are inadequate for body mass predictions. Before

281   decisions could be made regarding the validity of attributing a fossil to *G. sivalensis*, we

282   ascertained the equations that were robust enough to predict body mass accurately across species.

283

284 *Vertebra OR39747 body mass estimates*

285 It is unconventional to use vertebrae as proxies for body mass, although due to the lack of other

286 samples it has been done before (see for instance Taylor, 2007; Taylor & Naish, 2007). As

287 OR39747 is the holotype, it necessitates that body mass estimates are made from it if other

288 *Giraffa spp.* specimens are to be attributed to it. Although vertebral body length has higher R^2

289 values than cross sectional vertebral properties (Table 7, van Sittert, Skinner & Mitchell, 2010),

290 cross sectional properties are still preferable predictors of body mass in this case. The first reason

291 is that R^2 value is inferior to percent prediction error (%PE) and percent standard error of the

292 estimate when assessing reliability of body mass predictions through regressions (Smith, 1984).

293 Secondly, vertebral cross sectional properties are subjected to the stresses and strains within the

294 neck (Slijper, 1946) and therefore are a much better indicator of head and neck mass and by

295 implication body mass. Conversely, vertebral body length is influenced by factors other than

296 body mass such as the number of vertebrae in an anatomical area (compare birds and mammals'

297 cervical region) or the lifestyle of the animal. We found caudal vertebral height (dorsoventral

298 diameter) to have the lowest %PE (25% and 17%) when predicting body mass in both extant

299 giraffes and okapis respectively (Table 7, Figure 7), and therefore considered this dimension to

300 be most robust for body mass predictions across giraffids. There are no other published

301 interspecific regression equations using vertebral dimensions for the prediction of body mass in

302 ungulates of which we are aware. The caudal vertebral height predicts a body mass of 390 kg in

303 *G. sivalensis*. Interestingly, the average body mass prediction from the remaining vertebral

304 regression equations (C3 vertebral body length, cranial height, cranial width and caudal width,

305 Table 7) is fairly similar - 368 kg. The only body mass prediction to fall outside the 95%

306   confidence interval based on all vertebral dimensions including vertebral height (373 kg ± 119

307   kg) is vertebral body length, predicting a mass of 575 kg.

308   Nevertheless, the body mass prediction from caudal vertebral height could be either an over or

309   underestimate. Considering it as an overestimate would mean that this animal had a relatively

310   heavy neck and head complex but a slender or lightweight body. This is unlikely as a larger head

311   and neck complex is unsupportable unless accompanied by a larger total body size (Taylor &

312   Wedel, 2013). Conversely an underestimate would mean a slender neck and head complex but a

313   relatively stocky body. This is a more plausible scenario and if indeed it is the case, it might

314   explain the discrepancy between vertebral and dental body mass predictions when compared to

315   those of limb bones.

316

317   *Limb bone body mass estimates*

318   Interspecific long bone cross sectional properties, although probably more closely related to

319   body mass than any other variable, have nevertheless been found to be poor predictors of body

320   mass in giraffes and in some cases, okapis (McMahon, 1975; Anderson, Hall-Martin & Russell,

321   1985; Scott, 1990; Janis, Theodor & Boisvert, 2002), although it should be noted that a recent

322   interspecific study has shown giraffes to be more amenable to interspecific equation predictions

323   (Campione & Evans, 2012). Similarly, we found higher prediction errors with interspecific

324   equations compared to *G. camelopardalis* ontogenetic curves, with a 5% prediction error based

325   on humeral ontogenetic data (Figure 7). Errors were inflated when using more distal bones.

326   Therefore, the most appropriate long bone variable useful for *G. sivalensis* body mass

327   determination is very likely humeral cross sectional properties, using our ontogenetic *G.*

328   *camelopardalis* sample.

329

330   The average body mass estimated from humeral ontogenetic analysis is 732 kg. Interestingly,

331   this body mass is about 150 kg more than would be indicated by a *G. camelopardalis* of similar

332   neck length, and 342 kg more than the mass predicted from OR39747 cross sectional properties.

333   This could mean that either the humeral fossil specimens were incorrectly assigned to *G.*

334   *sivalensis,* that *G. sivalensis* had a relatively stockier body and thinner neck than *G.*

335   *camelopardalis* or that the holotype vertebra came from a female and the humeral specimens

336   from large males.

337   Unfortunately, none of the other long bone dimensions seem to be reliable predictors of body

338   mass across extant giraffids. The best non-humerus candidate using interspecific scaling seems

339   to be the radius transverse diameter with a 43% and 11% prediction error in okapis and giraffes

340   respectively. This dimension predicts that the specimen belonged to an animal of approximately

341   1238 kg, which suggests this animal might have been heavier than *G. sivalensis*. There are no

342   interspecific equations for metacarpi that we could find, and therefore we could only rely on

343   ontogenetic equations. Yet, similar to the radial prediction, the metacarpal transverse diameter

344   predicts a body mass of 1165 with around 20% prediction error. The inflated prediction errors

345   could be because humeri and femora are generally more suitable for body mass predictions than

346   more distal bones, especially in giraffes (McMahon, 1975). It is also possible that the fossil long

347   bones were incorrectly assigned to *G. sivalensis* and perhaps belonged to another similar species

348   existing at the same time and location.

349

350   *Dental body mass estimates*

351 There have been numerous dental specimens ascribed to *G. sivalensis* (Supplementary Table 1).

352 Unfortunately, not all of these specimens are from the same locality and are probably from

353 different stratigraphic zones. Subsequently, there appeared to be uncertainty regarding the

354 correct species allocation of these fossils (see especially Lydekker, 1876). A discussion on the

355 morphology and correct species classification of teeth specimens assigned to *G. sivalensis* were

356 not considered as part of this study, and we therefore used only those teeth mentioned by

357 Falconer and Cautley (1843). These specimens were originally assigned to the species *G. affinis* -

358 a classification later abandoned by Falconer himself and also disputed by Lydekker (1883), who

359 re-assigned the fossils to *G. sivalensis*. As the specimens originated from the same area and

360 strata as the holotype OR39747, which is the Pliocene of the Siwaliks (Lydekker, 1885a), we

361 believe it reasonable to consider them as truly *G. sivalensis* teeth until further evidence emerges.

362

363 Molar length measurements are more reliable indicators of body mass than molar width or area

364 (Damuth, 1990; Fortelius, 1990; Janis, 1990). Furthermore, Janis (1990) found that premolar row

365 length are poorer correlates than molar row length. Molar lengths predict an animal within the

366 range of 288 kg to 673 kg, which is similar to OR39747's caudal vertebral height body mass

367 prediction of 390 kg.

368

369 *Combined size estimates*

370 Lydekker's (1885a) suggestion that OR39747 belonged to a small individual could have meant

371 that the animal was still immature, that the animal was a relatively small individual of the species

372 or that the species itself was small within the genus. It is unlikely that Lydekker meant an

373 immature animal as the fusion of the epiphyses to the body of the vertebra is complete and clear

374 definitions of bony ridges and muscular depressions indicate a mature animal (Falconer &

375 Cautley, 1843). Lydekker might have based his idea of a small individual on two larger vertebrae

376 assigned to *G. sivalensis* - a proximal part of a 'third' and distal part of a 'fourth' cervical,

377 OR39746 and OR39748 respectively (Lydekker, 1885a, Table S1). Unfortunately, these

378 vertebrae were not locatable within the Siwalik collection at the time of this study (Personal

379 communication, P Brewer, Curator of fossil mammals, Natural History Museum, 2013), and we

380 subsequently could not measure them. Nevertheless, Falconer (1845) reported OR39748 to be

381 2.1 inch (53.3 mm) in height and width at the caudal extremity, which is only 0.2 mm greater and

382 0.1 mm less than our respective measurements of OR39747 (Table 2). Based on ontogenetic

383 allometry for caudal vertebral body height, OR39748 came from an animal weighing 394 kg or

384 277 kg, depending on whether it was a C3 or C4 vertebra respectively (Table 7). The animal

385 from which the holotype vertebrae originated was therefore also not relatively small compared to

386 the size estimated from specimen OR39748. It is possible though, especially considering body

387 mass estimates from the humerus, that there might have been sexual size dimorphism present in

388 *G. sivalensis*. If that is indeed the case, OR39747 and OR39748 would have been females about

389 half the size of fully grown male animals, a possibility also supported by the fossil teeth

390 considered in body mass estimates.

391

392 **Conclusion**

393 Our considered opinion is that the *G. sivalensis,* from which the holotype cervical vertebra

394 originated weighed approximately 400 kg, had a neck length of about 1.47 m and a reaching

395 height of 3.9 m. There is a possibility that it displayed sexual dimorphism, in which case male

396 animals would have been a little less than twice the size of females and both would have had a

397   similar morphology. If sexual dimorphism was not present and all bones were correctly

398   attributed to this species, then the animal had a slender neck with a relatively stocky body, a

399   shape that is not unrealistic to imagine.

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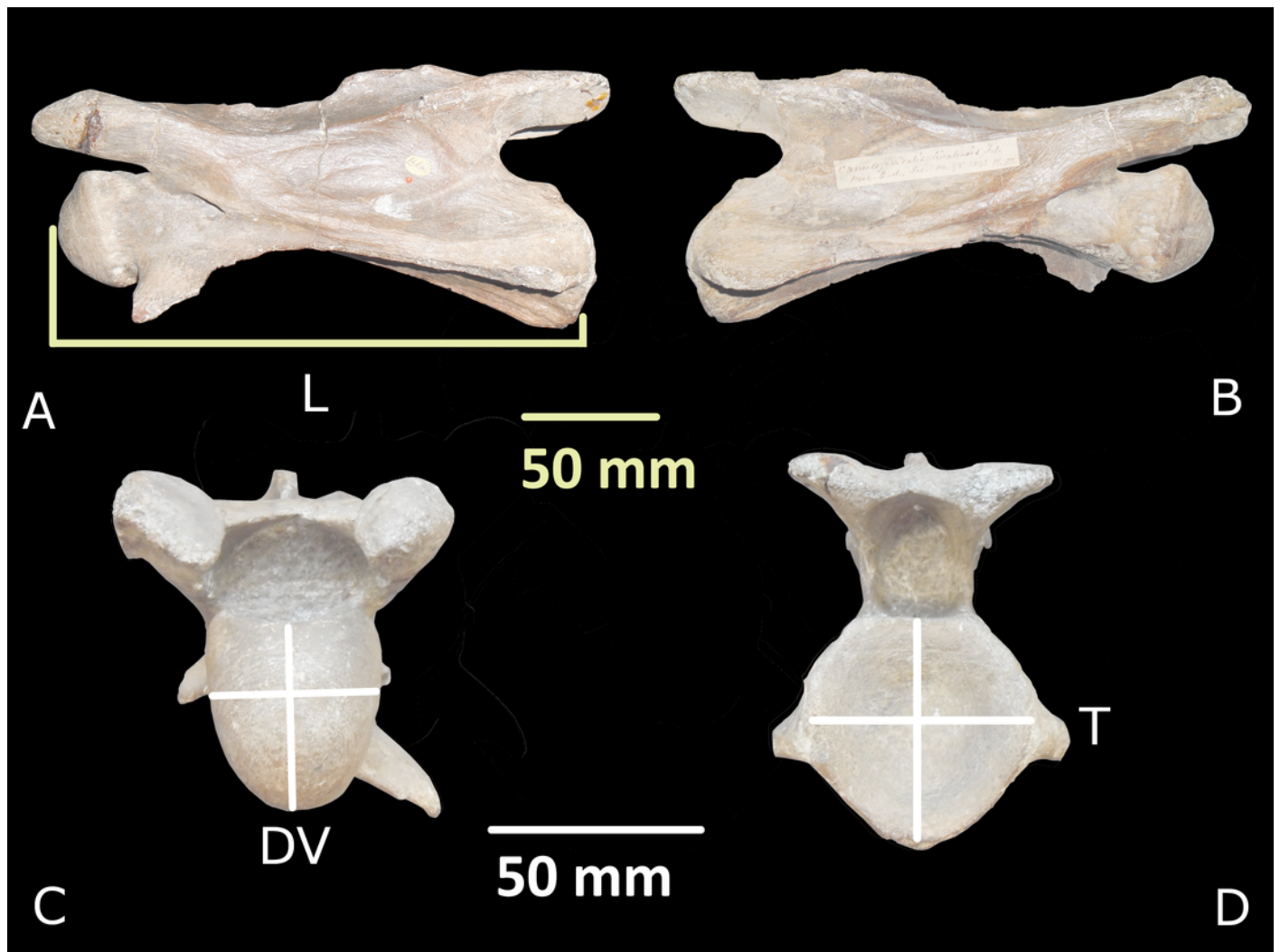
531

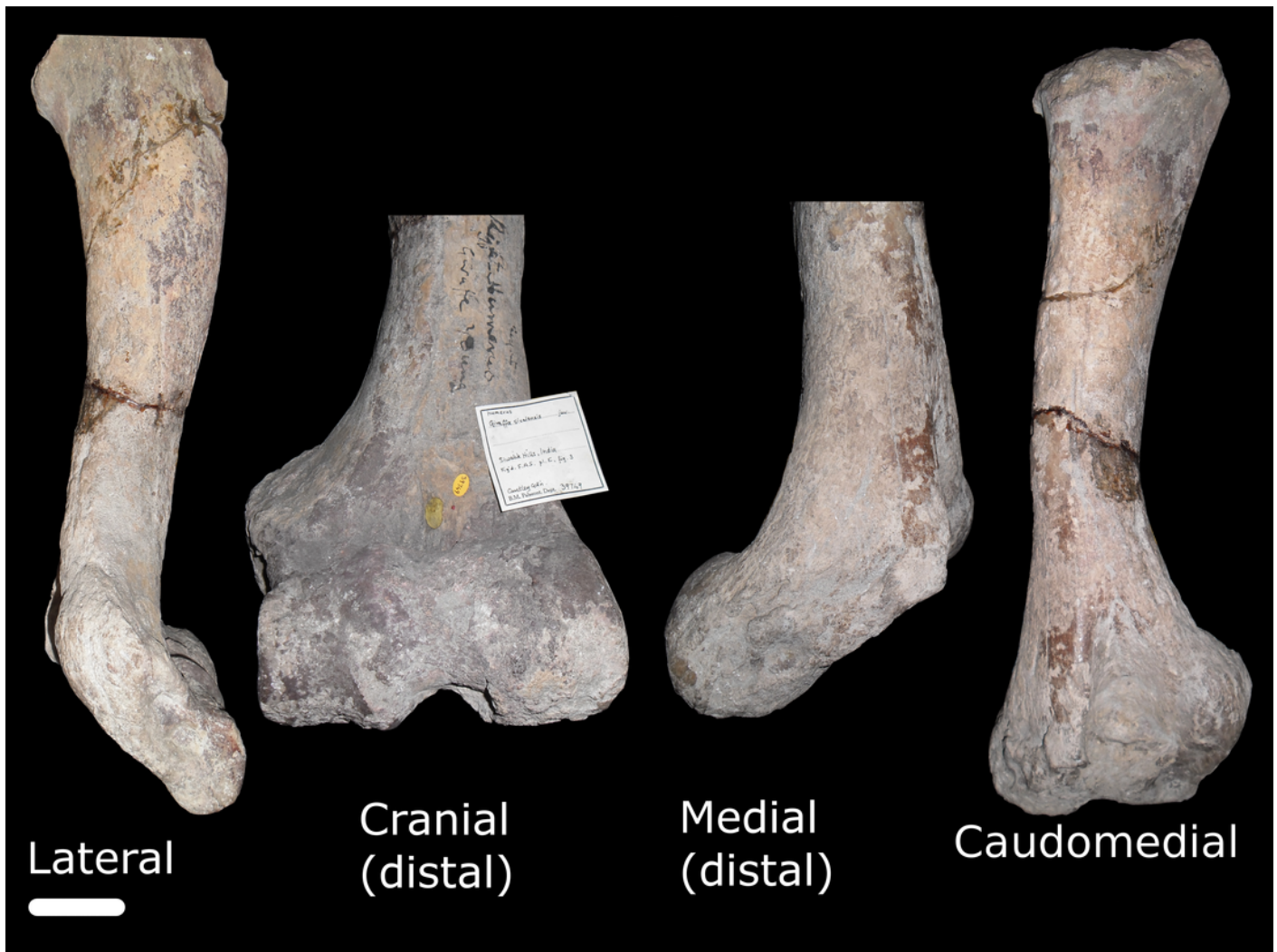
1

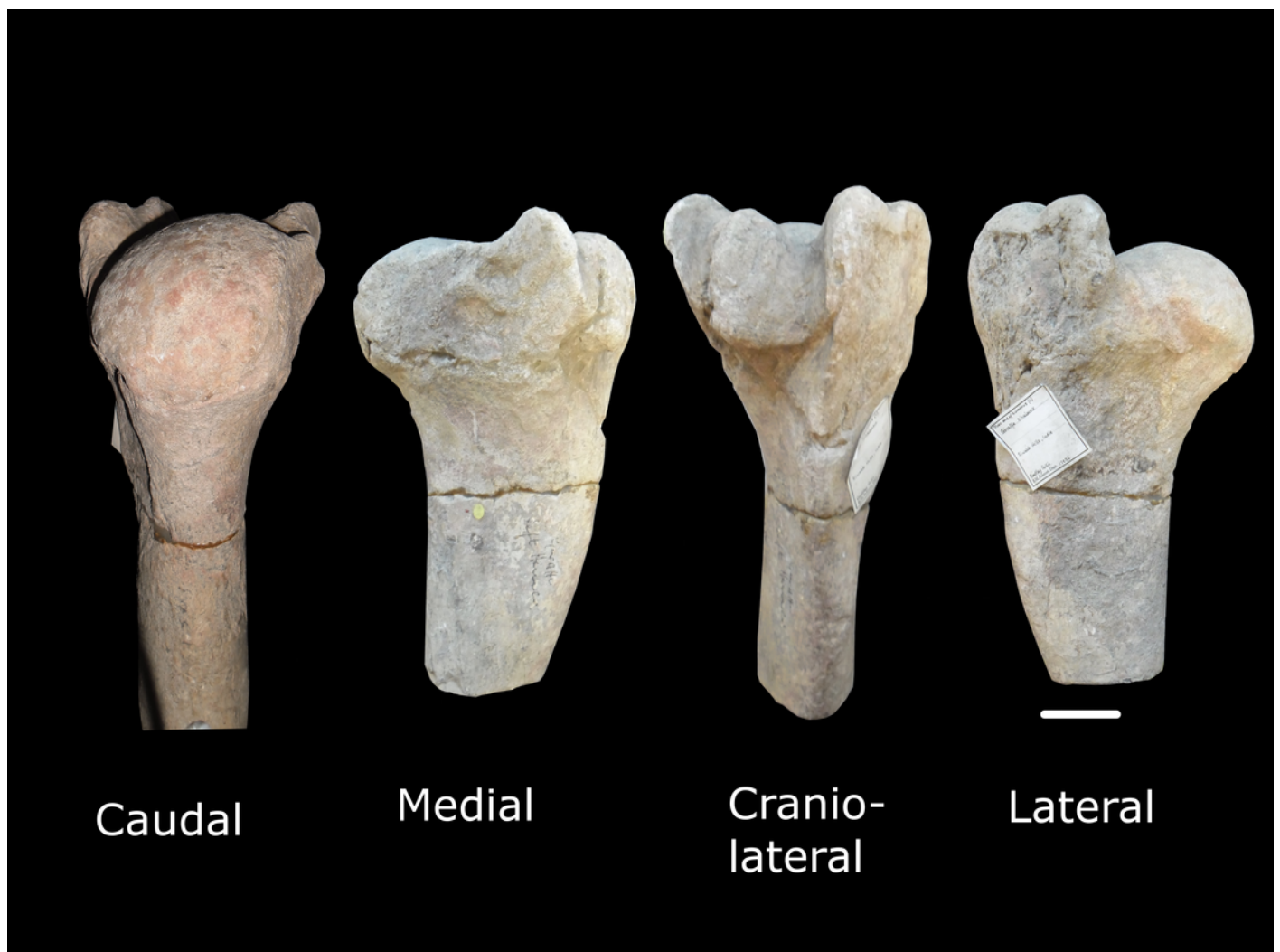
A map indicating the probable vicinity of *G. sivalensis* fossil discoveries.

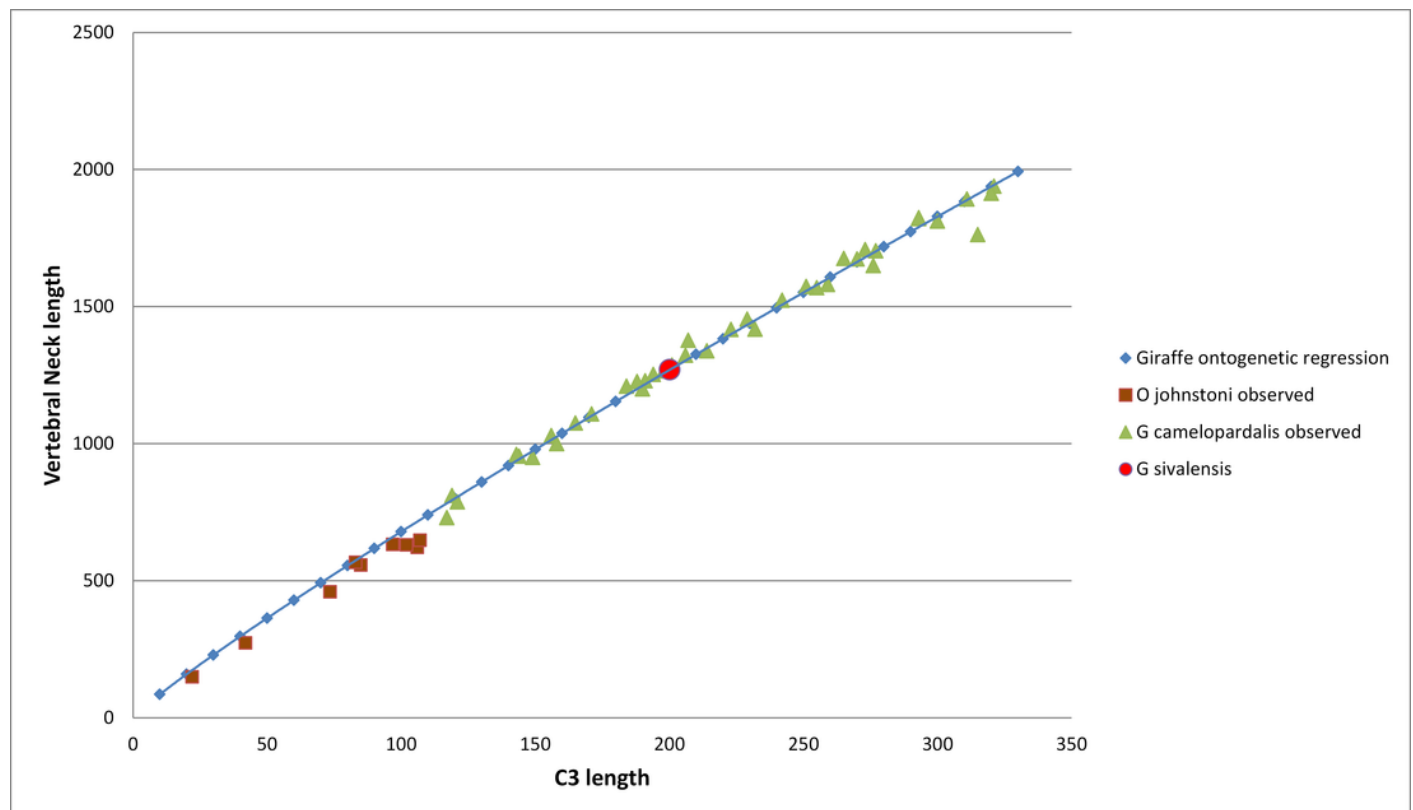
The marker indicates the location of the Shivalik Fossil Park in the Siwalik Hills, a subHimalayan mountain range. This is most probably the area 'west to the river Jumna' (currently Yamuna River) to which Falconer and Cautley (1843) referred. Map data: AutoNavi, Google.

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.

Specimen OR39749.

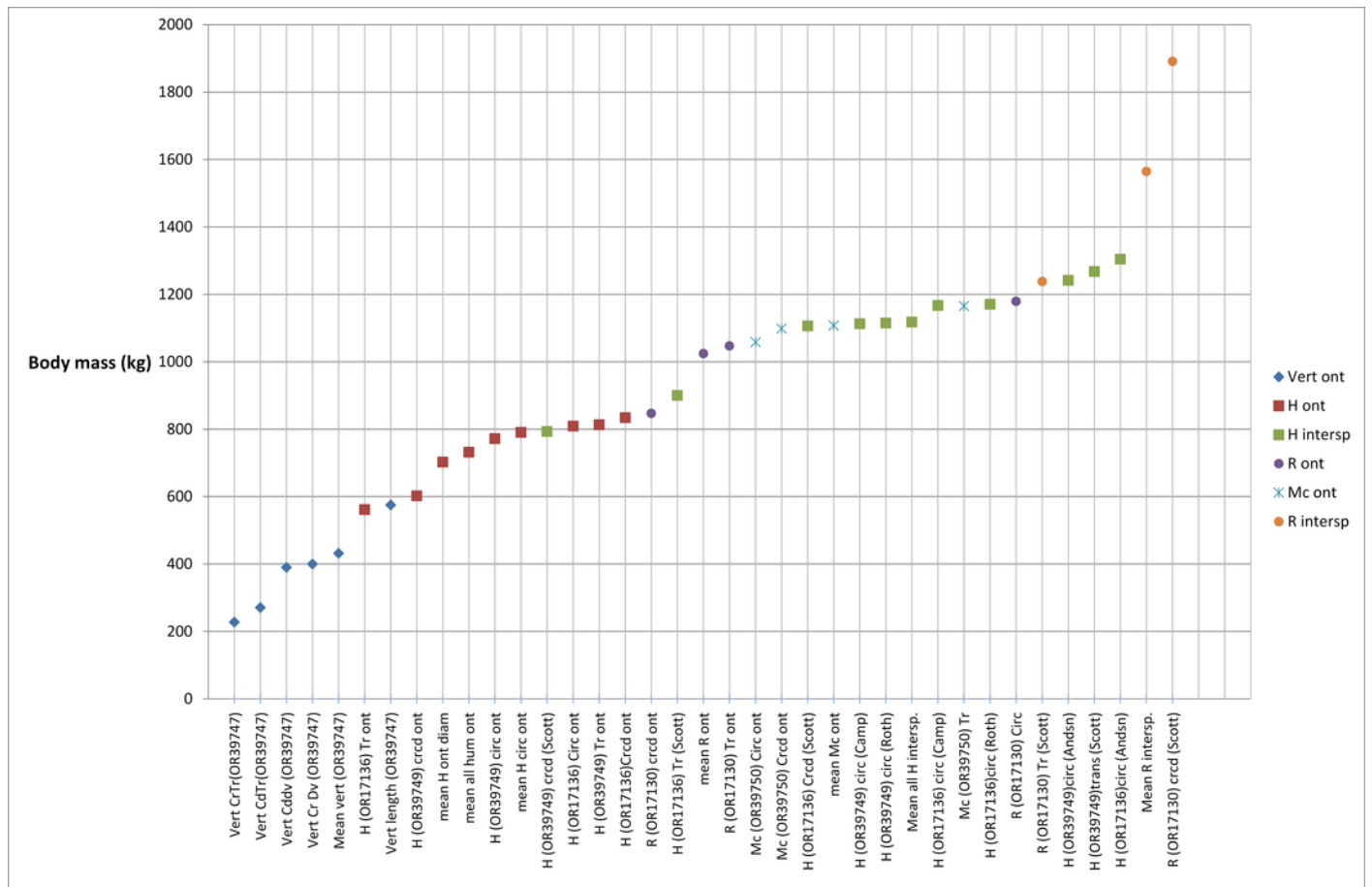
This image represents different views of a right humerus that has been assigned to *G. sivalensis.* The different views are not to scale; where only distal parts of the bone are shown, these have been enlarged relative to images of the specimen in toto. The scale bar indicates 50 mm and pertains to the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

Specimen OR17136.

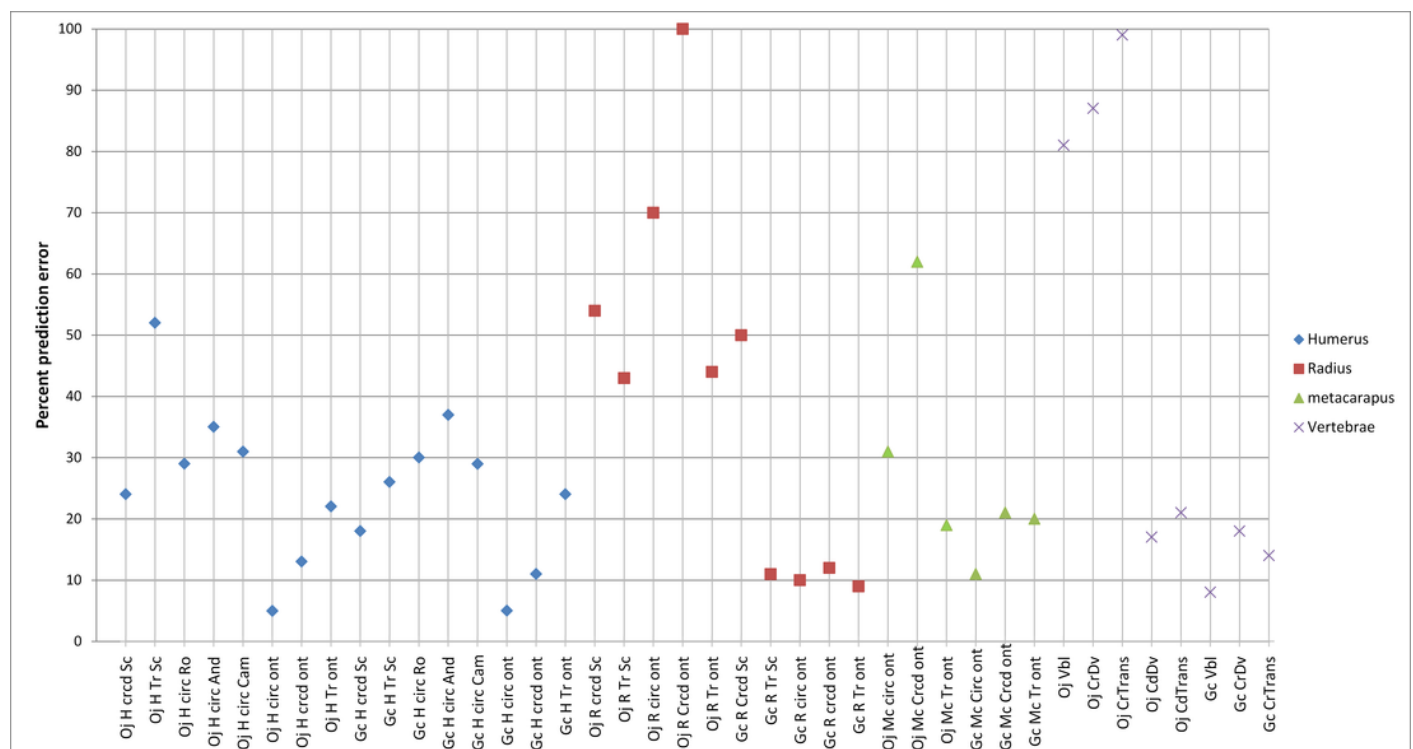
This represents different views of the proximal part of a left humerus that has been assigned to *G. sivalensis*. The scale bar indicates 50 mm and pertains to the lateral view only as the different views are not drawn to scale.

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.

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 zygoapohyses 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 *G. camelopardalis.* 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 *G. affinis*. Lydekker (1876) however refuted this species and proposed that it in actual fact *G. sivalensis*.
Larger than extant giraffes with smaller teeth than extant giraffes.	Mitchell & Skinner, 2003	Review of literature.

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)

Dimension and description	Falconer & Cautley (1843)'s terminology	Present study's measurement (± 95% confidence interval for three measurements) (mm)	Falconer & Cautley (1843) measurement (mm)
Vertebral body length: Longitudinal axis of the vertebral body (*Corpus vertebrae*), from the most cranial curvature of the cranial extremity (*Extremitas cranialis [Caput vertebrae]*) to the most caudal part of the caudal extremity (*Extremitas caudalis [Fossa vertebrae]*)	Length of the body of the vertebrae between articulating heads.	200.2 ± 0.7	198.1
Cranial vertebral body height: Greatest dorsoventral height of cranial extremity.	Vertical height articulating head?	42.9 ± 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±2.8	35.6
Caudal Vertebral body height: Greatest dorsoventral height of caudal extremity.	Vertical diameter, articular cup, posterior end	53.1±0.3	50.8
Caudal vertebral body width: Greatest transverse width of caudal extremity.	Transverse diameter, articular cup, posterior end	53.4±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±2.6	

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.

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								

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

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	$38.02 \times TUMW^{2.77}$ (all ungulates)	752 kg
				$32.36 \times TUMW^{2.87}$ (all selenodonts)	945kg
				$17.78 \times TUMW^{2.97}$ (selenodont browsers)	718 kg
			Greatest with of penultimate molar = 1.45 in = 36.83 mm	$32.36 \times SUMW^{2.78}$ (all ungulates)	731 kg
				$22.91 \times SUMW^{2.96}$ (all selenodonts)	991 kg
				$12.02 \times SUMW^{3.08}$ (selondont 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.	$19.50 \times TUML^{2.81}$ (all ungulates)	288 kg
				$8.71 \times TUML^{3.12}$ (all selenodonts)	372 kg
				$6.31 \times TUML^{3.29}$ (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	$38.02 \times TUMW^{2.77}$ (all ungulates)	752 kg

Fossil specimens	Museum no	References to specimen	Dimensions	Relevant regression equation (reference)	Body mass prediction
			surface.		
				32.36 x TUMW$^{2.87}$ (all selenodonts)	915 kg
				17.78 x 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 xTLML$^{2.99}$ (all ungulates)	489 kg
				3.24 x TLML$^{3.19}$ (all selenodonts)	533 kg
				2.24 x TLML$^{3.35}$ (selenodont browsers)	673 kg
			Average of length measurements (SD)		**565 (96) kg**
			Greatest width = 1.0 in = 25.4 mm	109.64xTLMW$^{2.73}$ (all ungulates)	750 kg
				77.62 x TLMW$^{2.93}$ (all selenodonts)	1014 kg
				64.56x 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	79.43xTLPL$^{2.76}$ (all ungulates)	599 kg
				61.66xTLPL$^{2.92}$ (all selenodonts)	780 kg
				20.42x TLPL$^{3.19}$ (selenodont browsers)	618 kg
			Average of length measurements (SD)		**666 (99) kg**
			Width = 0.9 in = 22.86 mm	524.81xTLPW$^{2.45}$ (all ungulates)	1121 kg
				524.81x TLPW$^{2.53}$ (all selenodonts)	1440 kg
				398.11x 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	169.82xSUPL$^{2.51}$ (all ungulates)	570 kg

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

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.

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		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	$PVNL=10.65*C3VBL^{0.902}$	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				

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

Dimension predicted for *G. sivalensis* (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	*G. camelopardalis* 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	*G. camelopardalis* ontogenetic data	$y = 9.708x^{\wedge 0.908}$ $CI = 0.881 - 0.936$ $R^2 = 0.99$	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	*G. camelopardalis* 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	*G. camelopardalis* 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	*G. camelopardalis* 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	*G. camelopardalis* 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	*G. camelopardalis* 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	*G. camelopardalis* ontogenetic data	$y = 7.600x^{0.742}$ $CI = 0.678-0.806$ $R^2 = 0.95$	3880 mm

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

SD = Standard deviation. PE = Prediction Error

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 *G. camelopardalis* data)	Body mass confidence intervals in kg (based on prediction errors when applied to *O. johnstoni* data)
OR39747 (C3) vertebral body length	*G. camelopardalis* ontogenetic data	0.91	$y = 0.022*x^{1.919}$	575	8% PE (529-612)	81% PE (109-1041)
OR39747 (C3) cr dv	*G. camelopardalis* ontogenetic data	0.77	$y = 0.0023*x^{3.21}$	400	18% PE (328-472)	87% PE (52-748)
OR39747 (C3) cr lat	*G. camelopardalis* ontogenetic data	0.84	$y= 0.0054*x^{2.967}$	228	14% PE (196-260)	99% PE (2-454)
OR39747 (C3) cd dv	*G. camelopardalis* ontogenetic data	0.69	$y= 0.0048*x^{2.847}$	390	25% PE (293-487)	17% PE (323-456)
OR39747 (C3) cd lat	*G. camelopardalis* 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	*G. camelopardalis* ontogenetic data	0.69	$y= 0.0048*x^{2.847}$	394	25% PE (296-493)	17% PE (327-462)
OR39747 (C4) cd dv	*G. camelopardalis* ontogenetic data	0.69	$y= 0.0011*x^{3.128}$	274		
OR39747 (C5) cd dv	*G. camelopardalis* ontogenetic data	0.69	$Y = 0.0004*x^{3.285}$	187		
Humerus midshaft circumference (OR17136)	*G. camelopardalis* 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)	*G. camelopardalis* ontogenetic data			772	5% PE (732-812)	5%PE (731-813)
average of humeral circumferences (SD)				791 (26)		
Humerus midshaft craniocaudal diameter (OR17136)	*G. camelopardalis* 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)	*G. camelopardalis* ontogenetic data		$y = 3.59*10-2 x^{2.32}$	602	11% PE (537-667)	13%PE (522-682)
Humerus midshaft transverse diameter (OR17136)	*G. camelopardalis* 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)	*G. camelopardalis* 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)	*G. camelopardalis* ontogenetic data	0.99	$y = 1.65*10\text{-}4\ x^{2.93}$	1179	10%PE (1064-1294)	31%PE (726-1390)
Radius midshaft craniocaudal diameter (OR17130)	*G. camelopardalis* ontogenetic data	0.98	$y = 2.89*10\text{-}3\ x^{3.19}$	847	12%PE (746-948)	62%PE (416-1780)
Radius midshaft transverse diameter (OR17130)	*G. camelopardalis* ontogenetic data	0.99	$y = 1.18*10\text{-}2\ x^{2.67}$	1047	9%PE (948-1146)	19%PE (943-1387)
Radius ontogenetic average (SD)				1024 (167)		
Metacarpal midshaft circumference (OR39750)	*G. camelopardalis* ontogenetic data	0.96	$y = 4.70*10\text{-}5\ x^{3.24}$	1058	11%PE (942-1174)	31%PE (726-1390)
Metacarpal midshaft craniocaudal diameter (OR39750)	*G. camelopardalis* ontogenetic data	0.97	$y = 1.59*10\text{-}3\ x^{3.40}$	1098	21%PE (867-1329)	62%PE (416-1780)
Metacarpal midshaft transverse diameter (OR39750)	*G. camelopardalis* ontogenetic data	0.98	$y = 6.71*10\text{-}3\ x^{2.95}$	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)		