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

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

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Introduction

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

History of G. sivalensis fossil discovery

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

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

Geographic and stratigraphic distribution of fossils

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

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

Size estimates

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

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

Materials & Methods

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

Studied material and dimensions measured

The only vertebra measured was the holotype, specimen nr OR39747, a cervical vertebra (Figure 2). Falconer & Cautley (1843) presented an extensive description of this specimen. A caudal fragment of a 'fourth' cervical no OR39748 (Lydekker, 1885a), also described as a second cervical by Falconer, 1845), as well as a caudal part of a 'third' cervical no OR39746 (Lydekker, 1885a) that have also been assigned to *G. sivalensis* were missing from the Siwalik collection in 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.

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

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

Ontogenetic data were obtained from previous studies by the authors (Mitchell, van Sittert & Skinner, 2009; van Sittert, Skinner & Mitchell, 2010, 2014), whilst interspecific regression equations were sourced from previously published work (Anderson, Hall-Martin & Russell, 1985; Roth, 1990; Scott, 1990). Due to the finding that body mass predictions from dental dimensions can be problematic and that post cranial dimensions are probably better predictors (Damuth, 1990; Fortelius, 1990; Janis, 1990), we did not consider the tooth dimensions available (Supplementary table 1) as predictors for body mass in the present study.

Statistical analysis

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

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

((Observed value – predicted value)/predicted value) x 100

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

Results

Characteristics of fossil specimens

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

Dimensions measured

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

Predictions based on vertebra OR39747

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

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

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

Predictions based on long bone dimensions

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

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

Discussion

Vertebral identity of OR39747

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

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

Ontogenetic and interspecific scaling models

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

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

Neck length and reaching height

Badlangana, Adams & Manger (2009) presented interspecific predictions for vertebral neck length based on vertebral body length. Using their data, we could estimate *G. sivalensis* C2-C7 vertebral neck length as 1150 mm, slightly shorter (45 mm or 4%) than our ontogenetic data. There are therefore reasonable grounds to believe that our estimated neck length based on ontogenetic data is valid, or at least close to interspecific curves. Further support can be seen in where the *G. camelopardalis* ontogenetic curve gives appropriate predictions for vertebral neck length in both the *G. camelopardalis* and okapi ontogenetic series Figure 6.

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

Body mass

The body mass predictions for *G. sivalensis* using available specimens and allometric equations are extremely wide (Figure 5). This could mean, firstly, that some specimens may have been incorrectly assigned to *G. sivalensis*. Secondly, that not all allometric equations are equally suitable for body mass predictions. Thirdly, that not all bone types are equally suitable for body mass predictions; femurs and humeri are, for example, generally more suitable for this purpose than more distal bones, while it is unusual to use vertebrae as proxies for body mass. Indeed, vertebrae are not ideal candidates as body mass predictors. The vertebral body length, especially in the cervical area, may be influenced by other factors as body mass such as the number of vertebrae that is possible in a region (compare reptiles and mammals), the lifestyle of the species, the morphology of the animal and the use of neck. Nevertheless, because OR39747 is the holotype, it was inevitable to use it as a proxy for body mass before we could determine which fossil specimens was correctly assigned to *G. sivalensis*. In order to find which vertebral dimensions are robust enough to predict body mass in taxonomic closely related animals, we compared body mass prediction errors predictions in giraffes and okapis. We found the caudal extremity's dorsoventral diameter the most robust, which gives a prediction error of 17% and 25% in okapis and giraffes respectively (Figure 7). Vertebral cross sectional properties are better indicators of the stresses and strains in the vertebral column and by implication the body mass of the animal, although these relationships are complex and incompletely understood (Slijper, 1946). The caudal dorsoventral vertebral height predicts a body mass of 390kg in *G. sivalensis*. Unfortunately there aren't any published interspecific regression equations using vertebral dimensions for the prediction of body mass in ungulates that the authors are aware of, making the *G. camelopardalis* ontogenetic regression of body mass to caudal vertebral body height the best candidate for giraffinae currently at hand. Interestingly however, when we calculate the average body mass prediction from the remaining vertebral regression equations (C3 vertebral body length, cranial height, cranial width and caudal width), a fairly similar result is obtained - 368kg. The only body mass prediction to fall outside the 95% confidence interval (373kg±119kg) based on all vertebral dimensions (including caudal vertebral height) is vertebral body length, predicting a mass of 575kg. If one argues that, compared to vertebral body length, the cross sectional measurement is an inadequate proxy for body mass in this case, it would mean that either the animal had a relatively thin neck with a proportionally (to body mass) stockier body than extant giraffes. Alternatively, if cross sectional measurements overestimates body mass it could mean that the animal had a thick neck with a proportionately smaller body than extant giraffes. The former scenario would be more plausible biomechanically, indicating that if cross sectional measurements are inadequate, an underestimation of body mass would be more likely. If one argues that neck length is an inadequate proxy in this case, it could mean that the *G.* sivalensis is either proportionately more slender or stockier than similar weight giraffes. An underestimation of body mass based on vertebral length would mean that *G. sivalensis* was more bulky relative to modern giraffes, however, that would also invalidate the cross sectional vertebral measurements unless the animal had a relatively thin neck with a bulky body. If vertebral body length overestimates body mass in this case it would mean a relatively longer neck with a slender body.

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

Interestingly, this body mass is about 150kg higher than would be indicated by a *G. camelopardalis* of similar neck length, 342kg more than the mass predicted from OR39747 cross sectional properties. This could mean that either the humeral fossil specimens were incorrectly assigned to *G. sivalensis*, that *G. sivalensis* had a relatively stockier body and thinner neck than *G. sivalensis* or that the holotype vertebra came from a female animal and that the humeral specimens came from large males.

Outlier long bone predictions

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

Conclusions

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

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1

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

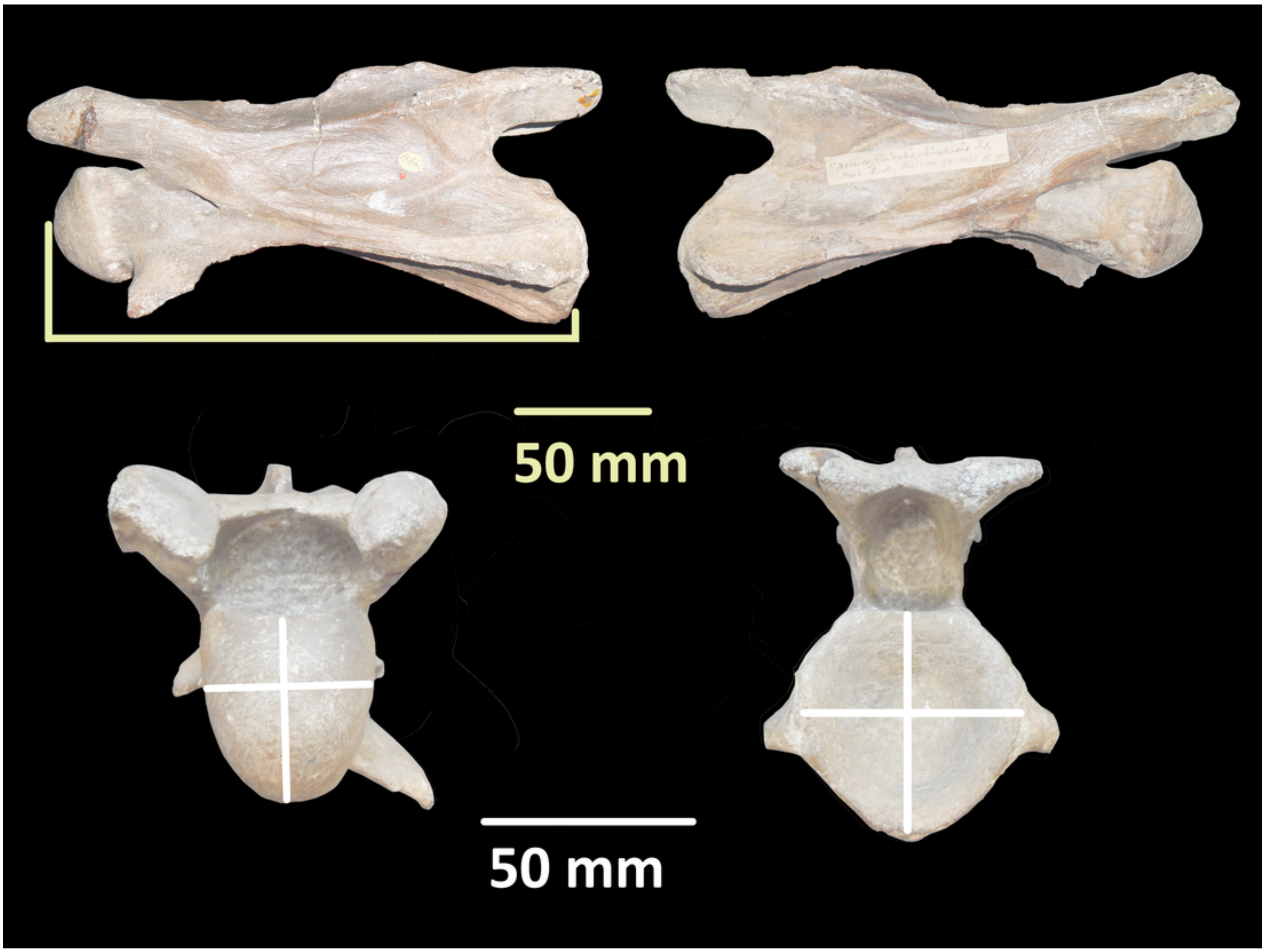
The marker indicates the location of the Shivalik Fossil Park in the Siwalik hills, a subhimalayan mountain range. This is most probably the area 'west to the river Jumna' (currently Yamuna river) that Falconer and Cautley (1843) referred to. Map data: AutoNavi, Google.


Almaty
Алматы
Bishkek
Бишкек
Tashkent
Kyrgyzstan
XINJIANG
Tajikistan
Kabul
کابل
Islamabad
اسلام آباد
JAMMU AND
KASHMIR
Lahore
لاہور
Faisalabad
فیصل آباد
Ludhiana
Multan
ملتان
Pakistan
PUNJAB
UTTARAKHAND
TIBET
HARYANA
New Delhi
UTTAR
PRADESH
Nepal
Kathmandu
काठमाडौं
SIKKIM
Jaipur
RAJASTHAN
Agra
Lucknow
Hyderabad
حیدرآباد
BIHAR
Patna
MADHYA
PRADESH
JHARKHAND
GUJARAT
Ahmedabad
Rajkot
Indore
India
WEST BENGAL
CHHATTISGARH
Surat
Nagpur
ODISHA
Nashik
MAHARASHTRA
Mumbai
TELANGANA
Visakhapatnam
Hyderabad
GOA
ANDHRA
PRADESH
KARNATAKA
Chennai
Bengaluru
Map data ©2015 AutoNavi, Google

2

Giraffa sivalensis holotype, specimen OR39747.

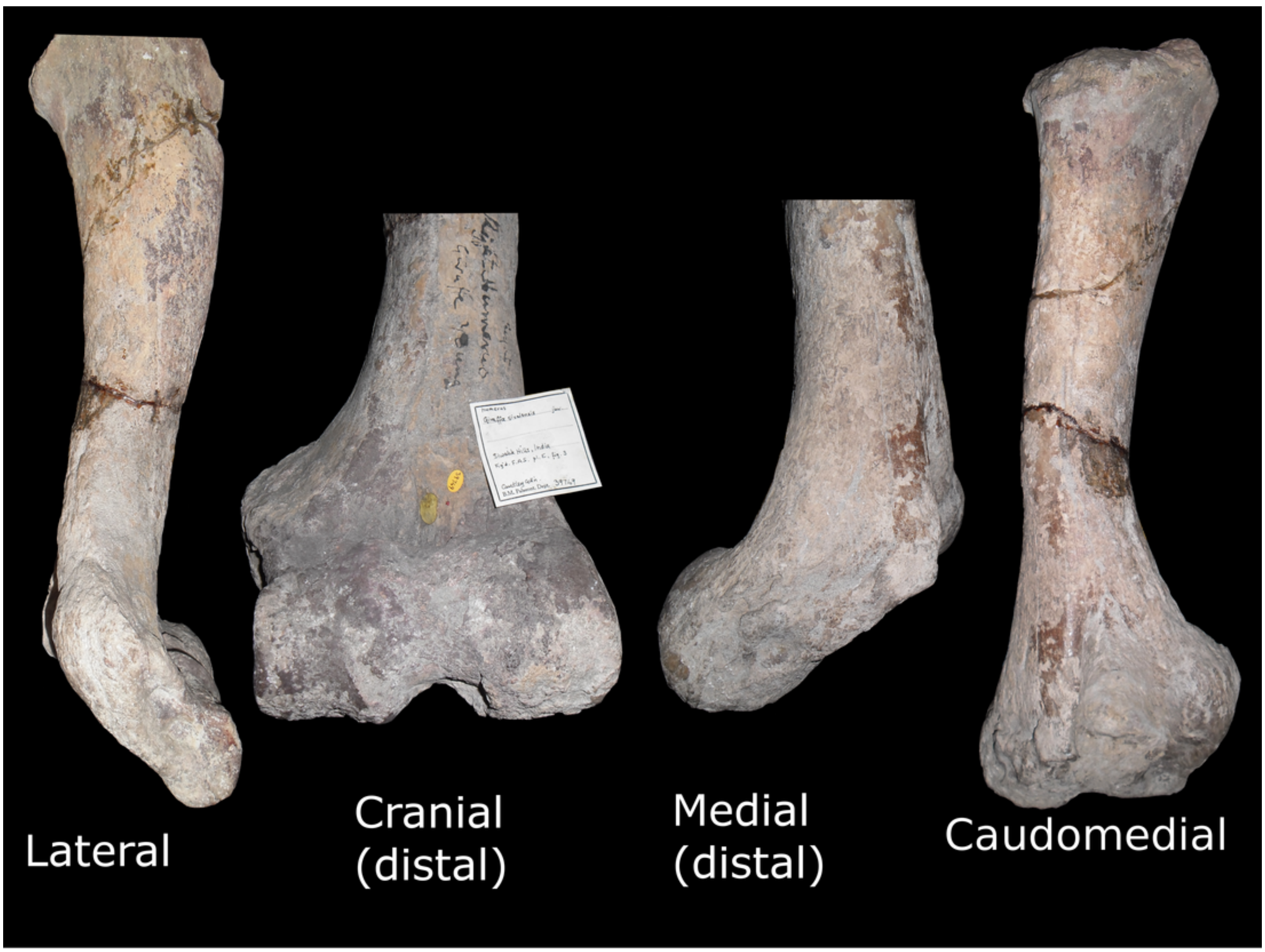
Presented,from left to right, in left lateral, right lateral, cranial and caudal views.



3

Specimen OR39749.

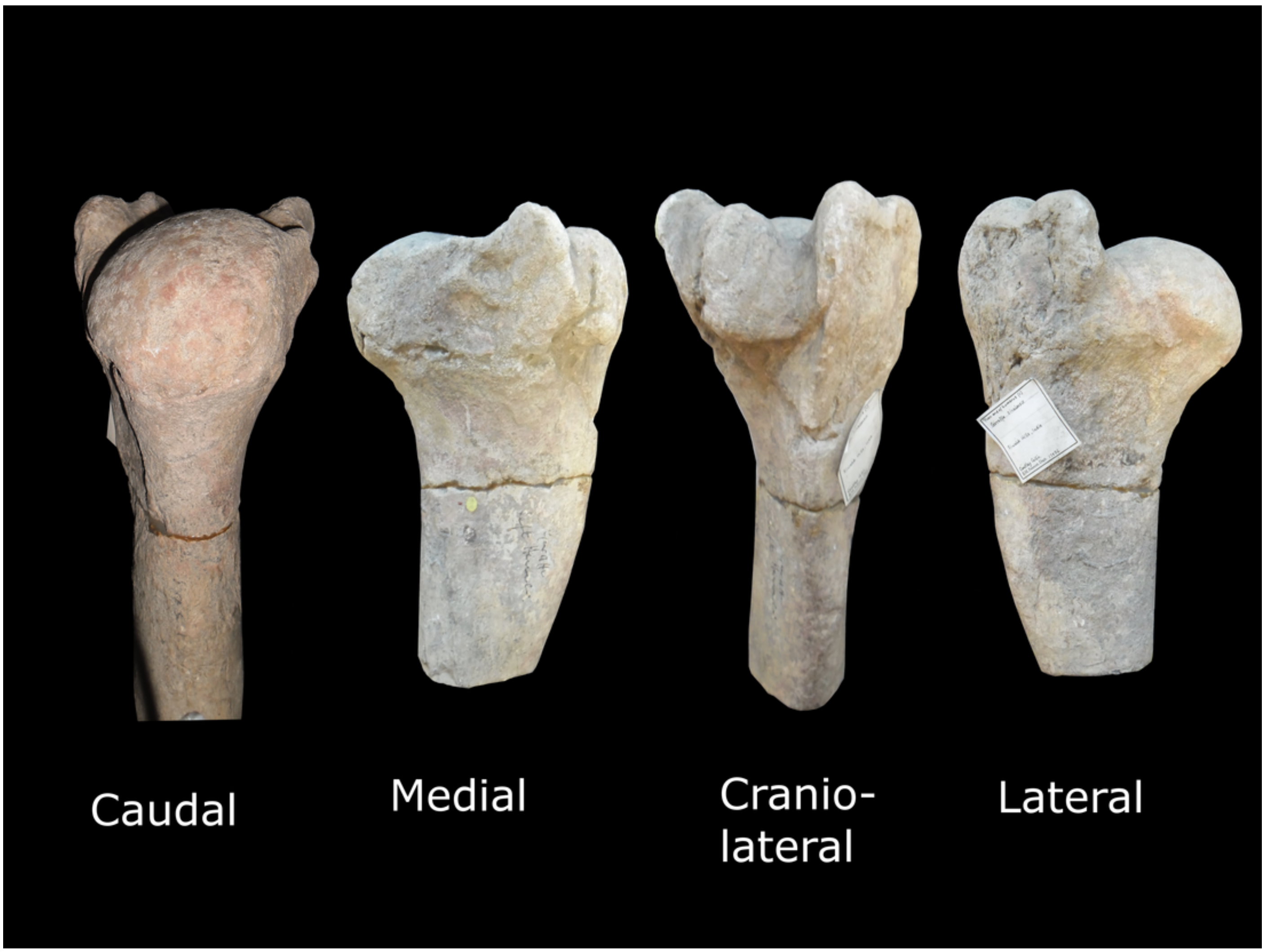
This image represents different views of a right humerus that has been assigned to *G. sivalensis*. The image is not to scale, and where only distal parts of the bone are shown, has been enlarged relative to images of the specimen *in toto*.



4

Specimen OR17136.

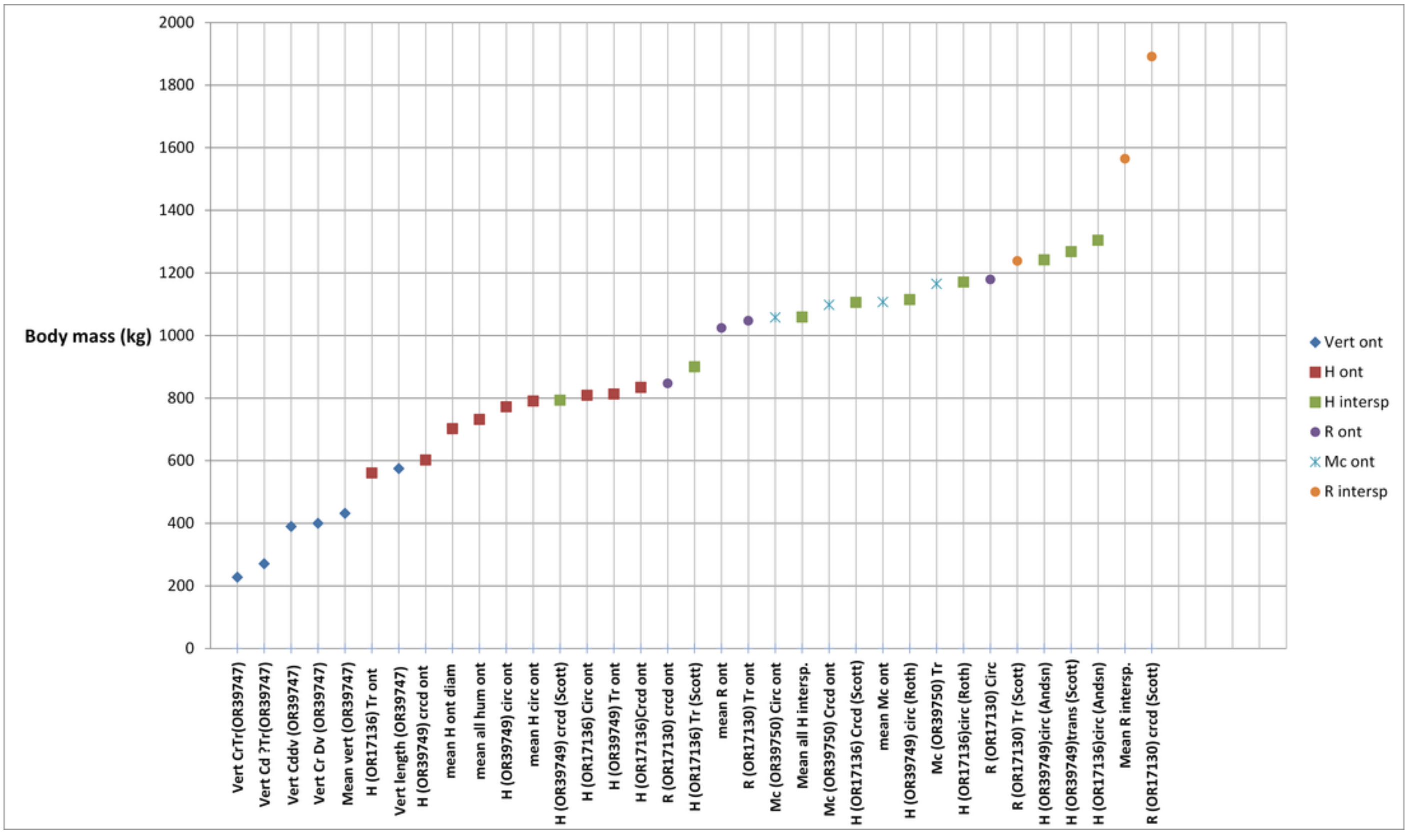
This represents different views of the proximal part of a left humerus that has been assigned to *G. sivalensis*. Not too scale.



5

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

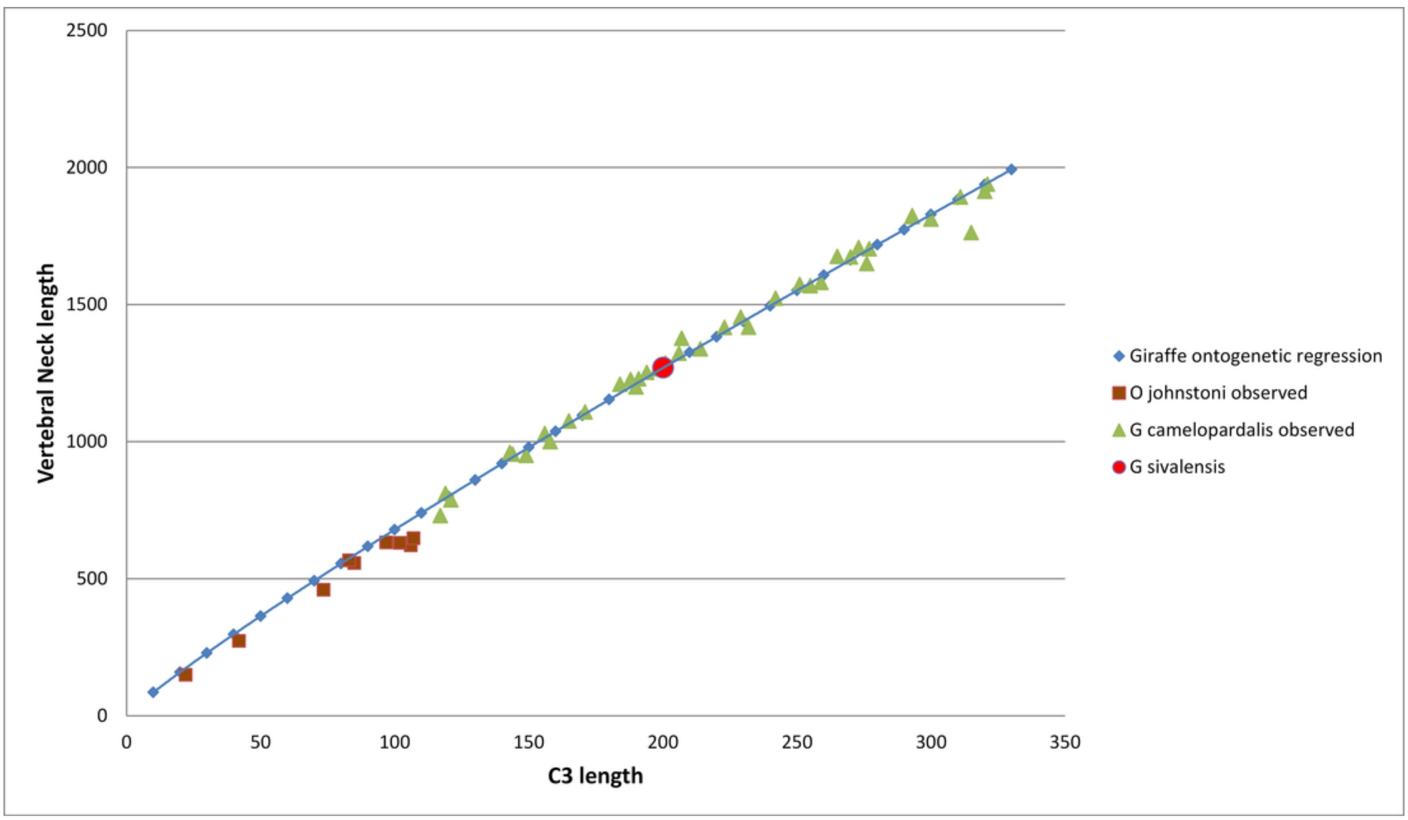
The labels are divided into predictions from vertebral dimensions (diamond shapes), humeral dimensions (Squares), radial dimensions (circles) and metacarpal dimensions (crosses). The humeral and radial dimensions are further subdivided into those originating from ontogenetic allometric equations (red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


Body mass (kg)
2000
1800
1600
1400
1200
1000
800
600
400
200
0
Vert ont
H ont
H intersp
R ont
Mc ont
R intersp
Vert CrTr(OR39747)
Vert Cd ?Tr(OR39747)
Vert Cddv (OR39747)
Vert Cr Dv (OR39747)
Mean vert (OR39747)
H (OR17136) Tr ont
Vert length (OR39747)
H (OR39749) crcd ont
mean H ont diam
mean all hum ont
H (OR39749) circ ont
mean H circ ont
H (OR39749) crcd (Scott)
H (OR17136) Circ ont
H (OR39749) Tr ont
H (OR17136)Crcd ont
R (OR17130) crcd ont
H (OR17136) Tr (Scott)
mean R ont
R (OR17130) Tr ont
Mc (OR39750) Circ ont
Mean all H intersp.
Mc (OR39750) Crcd ont
H (OR17136) Crcd (Scott)
mean Mc ont
H (OR39749) circ (Roth)
Mc (OR39750) Tr
H (OR17136)circ (Roth)
R (OR17130) Circ
R (OR17130) Tr (Scott)
H (OR39749)circ (Andsn)
H (OR39749)trans (Scott)
H (OR17136)circ (Andsn)
Mean R intersp.
R (OR17130) crcd (Scott)

6

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

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



7

The body mass prediction errors (absolute values) associated with various dimensions in *O. johnstoni* and *G. 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 likely to be in *G. sivalensis* as well. No other dimension or regression line gives prediction errors below 20% for both species. Nevertheless, vertebral caudal dorsoventral diameter does 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%, and those markers lying on this line actually indicate prediction errors higher than 100%. Abbreviations: Oj, *Okapia johnstoni*; Gc, *Giraffa camelopardalis*; P.E, prediction error; other abbreviations as for Figure 2.

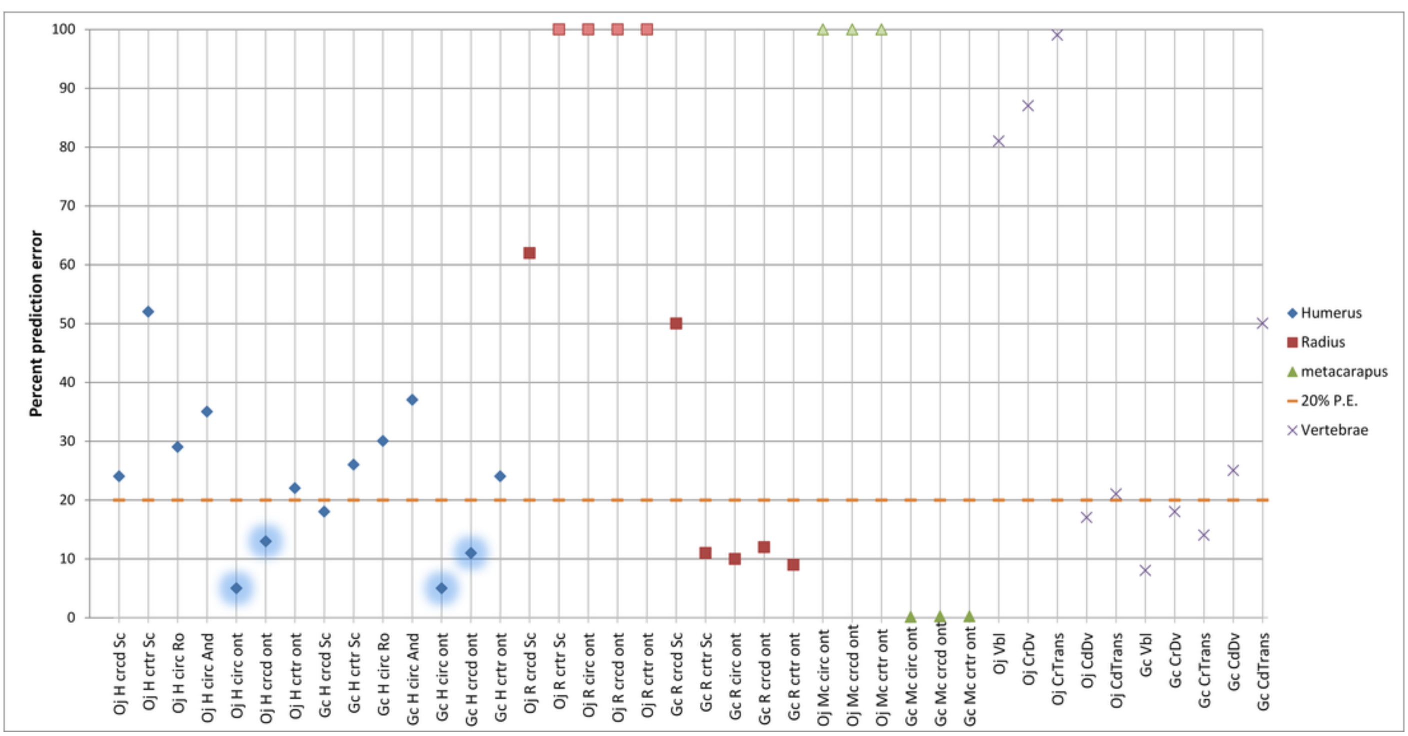


Table 1 (on next page)

Dimensions of the *G sivalensis* holotype

Comparison of the present study's measurements with that of Falconer and Cautley (1843). Dimensions for the *G sivalensis* holotype; a well preserved C3 cervical vertebra (specimen OR39747). All values in mm. Nomenclature is based on the Nomina Anatomica Veterinaria (International Committee on & Veterinary Gross Anatomical Nomenclature, 2012)

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, from the most cranial curvature of the cranial extremity to the most caudal part of the caudal extremity	Length of the body of the vertebrae between articulating heads	200.2 ± 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	

Table 2(on next page)

(on next page)

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

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

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. OR39749 is marked as a juvenile.

Table 3(on next page)

Okapi dimensions data

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

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

***Abbreviations:* DMNH, Ditsong National Museum of Natural History (Formerly Transvaal Museum); MNHN, Museum National d'Histoire Naturelle; SM, Senckenberg Museum; 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.**

Table 4(on next page)

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

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

2

Table 5(on next page)

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

Independent(x) variable	Model sample	Model r2	Allometric equation	Body mass prediction
OR39747 (C3) vertebral body length	G camelopardalis ontogenetic data	0.91	y = 0.022 .x^1.919	575
OR39747 (C3) cr dv		0.77	y = 0.0023.x^3.21	400
OR39747 (C3) cr lat		0.84	y= 0.0054.x^2.967	228
OR39747 (C3) cd dv		0.69	y= 0.0048.x^2.847	390
OR39747 (C3) cd lat		0.64	y= 0.0227.x^2.360	271
Average of vertebral dimensions				373
OR39747 (C5) vertebral body length	G camelopardalis ontogenetic data			
OR39747 (C5) cr dv				
OR39747 (C5) cr lat				
OR39747 (C5) cd dv				
OR39747 (C5) cd lat				
Humerus midshaft circumference (OR17136)	G camelopardalis ontogenetic data	0.98	y = 8.96*10-4 x2.55	809
Humerus midshaft circumference (OR39749)	G camelopardalis ontogenetic data			772
average of humeral circumferences				791
Humerus midshaft craniocaudal diameter (OR17136)	G camelopardalis ontogenetic data	0.98	y = 3.59*10-2 x2.32	834
Humerus midshaft craniocaudal diameter (OR39749)	G camelopardalis ontogenetic data		y = 3.59*10-2 x2.32	602
Humerus midshaft transverse diameter (OR17136)	G camelopardalis ontogenetic data	0.96	y = 2.00*10-2 x2.53	561
Humerus midshaft transverse diameter (OR39749)	G camelopardalis ontogenetic data		y = 2.00*10-2 x2.53	813
average humeral cr cd and transverse				703
all humeral ontogenetic average				732
Radius midshaft circumference (OR17130)	G camelopardalis ontogenetic data	0.99	y = 1.65*10-4 x2.93	1179
Radius midshaft craniocaudal diameter (OR17130)	G camelopardalis ontogenetic data	0.98	y = 2.89*10-3 x3.19	847
Radius midshaft transverse diameter (OR17130)	G camelopardalis ontogenetic data	0.99	y = 1.18*10-2 x2.67	1047
radius average				1024
Metacarpal midshaft circumference (OR39750)	G camelopardalis ontogenetic data	0.96	y = 4.70*10-5 x3.24	1058
Metacarpal midshaft craniocaudal diameter (OR39750)	G camelopardalis ontogenetic data	0.97	y = 1.59*10-3 x3.40	1098
Metacarpal midshaft transverse diameter (OR39750)	G camelopardalis ontogenetic data	0.98	y = 6.71*10-3 x2.95	1165
average metacarpus				1107
Humerus midshaft craniocaudal diameter (OR17136)	Artiodactyl interspecific allometry (Scott, 1990)	0.94	y =7.63 x 2.455	1106
Humerus midshaft craniocaudal diameter (OR39749)				793
Humerus midshaft transverse diameter (OR17136)	Artiodactyl static interspecific (Scott, 1990)	0.95	y =12.4 x2.46	900
Humerus midshaft transverse diameter (OR39749)				1268

Humerus midshaft circumference (OR17136)	Various mammalian taxa (Roth 1990)	0.99	y = 9.45*10^-4 x2.61	1170
Humerus midshaft circumference (OR39749)				1115
Humerus midshaft circumference (OR17136)	Various mammalian taxa (Anderson et al 1985)	0.99	0.0009*x^2.6392	1304.165927
Humerus midshaft circumference (OR39749)				1241.389631
all humeral interspecific average				1059
Radius midshaft craniocaudal diameter (OR 17130)	Artiodactyl static allometry (Scott, 1990)	0.93	y =29.2x2.51	1891
Radius midshaft transverse diameter (OR 17130)	Artiodactyl static allometry (Scott, 1990)	0.91	y = 8.19 x2.555	1238
radial interspecific average				1565

2