**Rebuttal letter**

Dear Prof John Hutchinson

We are appreciative of the swift, positive and constructive manner in which this manuscript was reviewed. Most of the reviewers’ concerns were valid ones, and have addressed each of the concerns below. The manuscript has been extensively revised and we believe this offers a much improved version. We hope that you and the reviewers will agree, and subsequently find it suitable for publication in PeerJ.

Sincerely,

SJ van Sittert

G Mitchell

**Reviewer 1**

We thank reviewer 1 for the willingness and openness to supply the comments un-anonymously.

**On basic reporting**

In general we have expanded on the analyses and data reported.

**On experimental design**

*Discussion needed of why ontogenetic regression data are appropriate for okapi.*

It is possible that giraffe ontogenetic equations are also acceptable to use in, for example, bovids or camelids. However, interspecific regression equations predict both giraffes and okapis poorly (Scott, 1990). Similarly, okapi long bones scale as an exception to cetartiodactyls during ontogeny (Kilbourne & Makovicky, 2012). Nevertheless, the question we wanted to answer was not which genus scales most similarly to giraffes. We wished to find out if we could validate the use of giraffe ontogenetic regression equations in another smaller giraffid, like the okapi. In other words, are some of the giraffe ontogenetic regression equations robust enough to be used interspecifically among giraffids? We appreciated the suggestion of using camelids in addition to okapis. However, although such a study would be interesting, we feel that expanding the study design to the other families in order to find out which ones are most appropriate is the topic of another paper altogether. Thank you for the reference to Janis, Theodor & Boisvert (2002).

**Validity of the findings**

*Suggestion of using dental predictors*

Initially, we decided to exclude dental measurements because of the inherent problems associated with them as body mass predictors (Damuth, 1990; Janis, 1990). In addition, as the focus of this study was post cranial dimensions we did not measure these specimens ourselves. Nevertheless, as the use of fossil teeth specimens were suggested by both reviewer 1 and reviewer 2 and we agree that it will complement the paper, we have included a section estimating body mass from fossil teeth specimens reported by Falconer & Cautley (1843)

**Comments for the author**

*Grammatical and style inconsistencies*

We thank the referee for taking the additional time to highlight grammatical and style inconsistencies.

**Abstract: (Southern Asia or southern Asia):** We maintained Southern Asia as it designates a region and should therefore be capitalised.

**Lines 100 -102 (Roth’s statement):** We do not disagree with Roth, and have removed the sentence.

**Line 114 (dental dimensions):** The use of dental dimensions was discussed above.

**Line 173 (physeal):** This word refers to the physeal line (*Linea physialis*) which denotes the physeal cartilage (*Cartilago physialis*)*,* the site where longitudinal bone growth and ossification occurs.

**Line 266 (nonsensical sentence):** We have rewritten this sentence to clarify the statement.

**Reviewer 2**

**Comments to the author**

*Implications of body weight (“The size is so similar to that of a small giraffe that it really makes no difference what the actual weight prediction is”).*

Compared to other much larger megafauna, we agree that the difference in body weight between *G. sivalensis* and *G. camelopardalis* does not seem great. Nevertheless, there is indeed a big difference in height (in terms of mammals) between extant giraffes and *G. sivalensis -* about 3.8 m in *G. sivalensis* compared to around 5 m in *G. camelopardalis* (Skinner & Chimimba, 2005). Additional height has major influences on a mammal’s anatomy and physiology (Harrison, 1980; Mitchell & Skinner, 1993, 2003, 2011; Endo et al., 1997; Mitchell, van Sittert & Skinner, 2009a,b). Therefore, in terms of ‘elongated’ species like giraffes, there can indeed be significant differences in physiology even when there is not a ‘huge’ difference in body mass.

*Assumption that fossil specimens came from same individual and horizon*

We do not agree with the reviewer that we *assumed* that that “these bones found so long ago come from the same individual and the same horizon” or that they “belong to one individual” or that we “assume that the specimens all belong to the same species”. We explicitly stated:

* Introduction
	+ “The references to these fossil specimens are extensive, incomplete and confusing”
	+ “…controversy even exists regarding the prevalence of giraffids within the Siwaliks”
	+ “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”
* Discussion:
	+ “This could mean, firstly, that some specimens may have been incorrectly assigned to *G sivalensis*”
	+ “This could mean that either the humeral fossil specimens were incorrectly assigned to *G sivalensis*… or that the holotype vertebra came from a female animal and that the humeral specimens came from large males”
	+ “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 … and confirmation as (to) which fossil species they belonged to will have to wait until more complete skeletal finds are made”
* Conclusion
	+ “… or even another *Giraffa* species living at the same time.”

Nevertheless, we assumed the reviewer perhaps wanted more explicit statement to this effect in the introduction, which we have done.

*Assumption that ‘specimens all belong to the same species’*

See above. Although we agree that there were more than one giraffid species known per location, there are only three known to occur in the Pinjor zone during the late Pliocene early Pleistocene - *Giraffa sivalensis* and *Sivatherium giganteum* and *Bramatherium geraadsi* (Bhatti, 2004).

*“If these are indeed all from one taxon, why does it have to have the proportions of a modern giraffe?”*

We were fully aware of this problem, and therefore stated that our height estimates came with the assumption that *G. sivalensis* had similar body proportions as an equivalent weight *G. cameloparadalis*. It is not perfect, but it is what we can work with until further specimens are discovered. All long bones used had a similar slenderness to them as modern giraffes, and we believe that our assumption is not without merit.

*Dentition as predictors of size*

Dentition as a predictor of body size has inherent problems (Damuth, 1990; Fortelius, 1990). However, we agree that there is enough reason to include some body mass estimates from them, which we have done.

*Ontogenetic sampling, data and interspecific application thereof*

Indeed, ontogenetic allometric data are very much underrepresented in the literature relative to interspecific data. As we have mentioned in the manuscript, it is also uncommon to use ontogenetic curves for interspecific predictions (but note that it is by no means unique, as reviewer 3 has also pointed out - see Roth (1990). We have made it clear that there is enough reason to attempt it in this case, the major one being that extant giraffids fit interspecific curves poorly (Scott, 1990). In addition, we believe our study design and results validate our decision to do so, especially referring to Figure 6 and Figure 7.

*Is the holotype Giraffa?*

That the holotype has been classified as a *Giraffa* has to date not been disputed. The reasons for assigning the holotype as a *Giraffa spp.* was already extensively discussed by Falconer & Cautley (1843), as pointed out in the manuscript.

**Miscellaneous comments:**

Note: There were discrepancies in line numbers as given in the full downloadable reviewing manuscript and the FINAL\_MANUSCRIPT.DOCX file. In reviewer 2’s case we referred to the numbers as in the FINAL\_MANUSCRIPT.DOCX file, as they correspond to the comments made.

**196-205:**

We are not sure what the reviewer meant by “Ontogenetic data ontogenetic sample for allometric equation and ontogenetic equations”, and therefore cannot address this comment.

**241-254:**

We are not sure what the reviewer meant by “allometric problem - what problem explain” or to which “allometric problem” the reviewer is referring to. Subsequently, we cannot address this concern.

**261-264 (“interspecific curves – what is this?”):**

By interspecific curves we mean regression equations that are constructed from data of animals of different species but of similar/ equivalent life stage, usually adults. We consider this terminology as quite clear within the field of allometry (a simple Google search will produce a number of results with the same term), and subsequently did not deem it necessary to expand on this explanation.

**312 (conflicting data on size):**

Line 311 to 313 reads: “If one argues that, compared to vertebral body length, the cross sectional measurement is an inadequate proxy for body mass in this case…” It is not clear what the reviewer wanted us to address here, and we therefore could not address this concern.

**(“Capitalize Siwalik Hills”):**

We have capitalized Siwalik Hills throughout the text, thank you for this pointing this out.

**Lines 35-36 - 50 -51 (“confusing re-write and explain better.”):**

The lines in question read as follows (from line 34):

“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.”

We presume the confusion regards the citations mentioned. Keep in mind that many of Falconer’s original papers were also compiled in the Fauna Antiqua Sivalensis by Murchison, and so might have two reference sources. In addition to the Fauna Antiqua Sivalensis which was published in (1868), Murchison also published a set of descriptions of Falconer’s plates (many of which were unpublished) in (1867). We have included this explanation in the introduction.

**(line 49-51):**

“Regarding sub-Himalayan giraffes for instance, controversy even exists regarding the prevalence of giraffids with the Siwaliks (compare Lydekker, 1883; Aleem Ahmed Khan 1991 and Bhatti, 2004).”

We are not sure what the reviewer finds confusing here. We have addressed another comment with regard to Line 50 below, and we hope it will clarify any confusion.

**48 (“*G. attica* and *G. vetusta* are a very arcane names – remove from your list – these are *Bohlinia attica* now and hence not *Giraffa*”)**

Regarding the usage of older terms like *G attica* and *G vetusta*, it was stated that ‘subsequently species ….have been proposed, not all of which are generally accepted’. Nevertheless, we have removed these terms to avoid confusion.

**48-49 (“It seems like you are conducting a quick systematic revision. This is a rather involved task. You cannot say all these names can be or may be sivalensis. I would add a clarification that you are speculating here.”)**

We are not conducting a systematic revision here. The point we were trying to make was that subsequent to the *G. sivalensis* holotype discovery, other (possible) extinct *Giraffa* species have been discovered. We are in no way speculating that other extinct *Giraffa spp* are actually *G. sivalensis*.

**50 (“there is no controversy as to the prevalence of giraffids in the Siwaliks – be precise.”)**

The main controversy related to a statements by Lydekker ({{1876}}, p.104 and 105), where he was struck by the rarity of *Giraffa* teeth amongst the ruminants. The reviewer is however correct, there is *currently* no controversy regarding the prevalence of *Giraffa* fossils in the Siwaliks. We have deleted this sentence.

**Line 65 (“what is 0.6 million year? Write a number”):**

0.6 million years is 600 000 years. We do not think this is ambiguous. In fact, the number as written comes from the first sentence of Nanda’s abstract in Quaternary International: “Pinjor Mammalian Fauna, ranging in age from 2.58 to 0.6Ma, is the youngest fauna of the Siwalik Group.”

**Line 75 (“or distinct genera – very unclear – what do you mean?”):**

We do not think this is unclear. However, we have rewritten the first sentence of that paragraph and believe that it reads much better.

**Line 95 (“The Natural History Museum”):**

We are not sure if the reviewer’s suggestion of “The Natural History Museum” is correct here. As an example, look at this phrase at the bottom of the home page of the Natural History Museum’s website (http://www.nhm.ac.uk/): “The Trustees of the Natural History Museum, London”. We therefore left the sentence as is.

**Line 149-157 (“very minor need to mention these observations”):**

We agree, and have subsequently shortened this paragraph.

**151 (“British museum is that of archaeology in London – and Museum should be: The Natural History Museum”):**

Thank you for this comment; we have corrected the museum name.

**256 (“giraffines this is vague – do you mean Giraffinae?”)**

We agree, and following a similar query from reviewer 3, have abandoned the use of Giraffinae altogether in this manuscript.

**“Sir Cautley – when a person has died we remove titles – unless you are writing a historical type of text”**

We have removed the title.

**218 (“processus articularis cranialis is the only anatomical term you use. Why so fancy with this there are dozens of other characters on vertebrae that you ignore.”)**

In the very same sentence reference is also made to the ‘*Corpus vertebrae’*. However, we have subsequently included Latin names for the anatomical references mentioned in Table 2 (revised draft) as well.

**231(“vertebrae (plural)”**

Corrected to the plural.

**(“Capitalize: (island) - Perim Island”)**

We have corrected the capitalisation throughout.

**Reviewer 3**

**Basic reporting**

*Confidence intervals*

We have included confidence intervals for *G. sivalensis* body size and shape estimates. We appreciate the idea of including allometric equations next to the estimates and have done so throughout the text, except in the abstract.

*Statement of assumptions*

We agree that assumptions made would be clearer if a section is specifically devoted to them, and have followed the reviewer’s suggestion in this regard.

**Experimental design**

We have included the equations from Campione & Evans (2012). Thank you for this suggestion.

**Validity of the findings**

We have expanded on the controversy regarding the size estimate from OR39747 in the introduction, and have brought up the issue again in the discussion. We have also added a table describing these differences.

**Specific comments to the author**

**31. (Ambiguous taxonomy):**

We have rewritten the sentence to remove the ambiguity.

**84. (Size controversy):**

Issue addressed as described above.

**91. (Dimensions):**

We have included dimensions measured in the relevant figure.

**93. (Size controversy):**

Issue addressed as described above.

**110. (Champione and Evans):**

We have included data from Champione and Evans.

**116. (Scaling controversy):**

We are aware of the controversy. Initially we felt it would distract from the paper to mention this. However, we agree that there might be merit to do so and have briefly covered the main issues.

**124. (Okapi systematics):**

We thank the reviewer for bringing this to our attention. We based our original assignment of okapis to Giraffinae on a classification by Geraads (1986). However, we have abandoned the use of Giraffinae altogether in this manuscript.

**133. (The 20% cut off):**

We based predictions errors below 20% relatively low in a similar way as did Biknevicius (1999) on his study on armoured and unarmoured mammals. We have however removed this arbitrary cut-off point and considered only those estimates with the lowest prediction errors.

**136. (Confidence intervals for estimations):**

We have included confidence intervals in to the estimated parameters. However, 95% percent confidence intervals for the slope were extremely wide, despite high R2 values. For example, 95% confidence intervals for body mass based on the 95% confidence interval for the slope (1.715-2.124) provided body masses of 195 to 1699kg. We thought a better indication of body mass error was the percentage prediction error of the equation to the body estimate.

**138-146. (Paragraph on geology of holotype):**

This section was merely to provide background information on the holotype specimen which might be used in future to pinpoint its location and relate further specimens to the holotype. The background information was also provided as there did seem to be some confusion in the literature. However, we agree that the paragraph is too long and looks out of place and have subsequently shortened it and moved it to the introduction.

**152. (Table 3 allometric equations):**

We have included the allometric equation used to predict neck length (Table 5 in the revised manuscript).

**154. (Reference to allometric scaling relationship):**

We included a reference to the ontogenetic data mentioned.

**157. (Uncertain wording):**

We have rewritten this sentence.

**160. (Refer to Table 5):**

We have referred to the relevant Table in this sentence.

**176. (Metapodial ‘columns’):**

The ‘columns’ refers to the caudal groove of the metapodial bones. It was indeed described in the given reference by (van Schalkwyk, Skinner & Mitchell, 2004): “…the metacarpal shape, which was anteriorly cylindrical, had a posterior concavity that is more marked in giraffes than in buffaloes. Figures 7 & 8 illustrate these differences”, although it was not called ‘columns’ as such. We have however included van Schalkwyk et al's (2004) paper, van Schalkwyk's (2004) thesis and Solounias' (2007) work to avoid confusion in references.

**180. (17130 vs 17136):**

This was an error which we have now corrected. It should have read: “…of humeri OR39749 and OR17136.”

**182. (Reference to scaling equation):**

We have included an allometric equation.

**192. (Size dispute):**

We agree and have highlighted the dispute in the introduction.

**213-218. (Data not supporting conclusion):**

We feel that if the holotype isn’t much smaller than comparable vertebral specimens, it does lend evidence against the animal from which the holotype came being a small animal, relatively speaking. However, we agree that the section needs to be rewritten and have done so.

Although the correlation coefficients of vertebral length to body mass is much better than vertebral width to body mass, vertebral length unfortunately does not hold out well when used across species. Additionally and perhaps more importantly, R2 values are not good indicators of the predictive strength of equation - percent prediction error and percent standard error of the estimate is (Smith, 1984; van Valkenburgh, 1990). We have included an explanation to this effect in the manuscript.

**220. (Uniqueness of method):**

We agree and have referenced Roth’s paper.

**226. (Validity of recent interspecific studies):**

We have incorporated Campione & Evans' (2012) work into the interspecific studies mentioned.

**254. (Missing word):**

Corrected

**273. (Cross sectional properties):**

Clarified that cross sectional properties are preferable to length measurements.

**280. (Reference to Table 5):**

Referred to the appropriate table

**284 - 296. (Clarification of section):**

We agree and have rewritten and clarified the section.

**309. (Size of individual):**

Agreed, we have incorporated this fact in the discussion.

**432. (Misspelled references):**

Corrected.

References

Bhatti ZH. 2004. Taxonomy, evolutionary history and biogeography of the Siwalik giraffids. PhD Thesis. Lahore: University of the Punjab.

Biknevicius AR. 1999. Body mass estimation in armoured mammals: cautions and encouragements for the use of parameters from the appendicular skeleton. *Journal of Zoology* 248:179–187.

Campione NE, Evans DC. 2012. A universal scaling relationship between body mass and proximal limb bone dimensions in quadrupedal terrestrial tetrapods. *BMC Biology* 10:60.

Damuth J. 1990. Problems in estimating body masses of archaic ungulates using dental measurements. In: *Body Size in Mammalian Paleobiology: Estimation and Biological Implications*. Cambridge: Cambridge University Press, 229–253.

Endo H, Yamagiwa D, Fujisawa M, Kimura J, Kurohmaru M, Hayashi Y. 1997. Modified neck muscular system of the giraffe (Giraffa camelopardalis). *Annals of Anatomy-Anatomischer Anzeiger* 179:481–485.

Falconer H, Cautley PT. 1843. On some fossil remains of Anoplotherium and Giraffe, from the Sewalik Hills, in the north of India. *Proceedings of the Geological Society of London* 4:235–249.

Falconer H, Murchison C. 1867. *Description of the plates of the Fauna Antiqua Sivalensis*. London : R. Hardwicke.

Fortelius M. 1990. Problems with sing fossil teeth to estimate body sizes of extinct mammals. In: Damuth J, MacFadden BJ eds. *Body Size in Mammalian Paleobiology: Estimation and Biological Implications*. Cambridge: Cambridge University Press.

Geraads D. 1986. Remarques sur la systématique et la phylogénie des Giraffidae (Artiodactyla, Mammalia). *Geobios* 19:465–477.

Harrison DFN. 1980. Biomechanics of the giraffe larynx and trachea. *Acta Oto-Laryngologica* 89:258–264.

Janis CM. 1990. Correlation of cranial and dental variables with body size in ungulates and macropodoids. In: *Body size in mammalian paleobiology: estimation and biological implications*. Cambridge: Cambridge University Press,.

Janis CM, Theodor JM, Boisvert B. 2002. Locomotor evolution in camels revisited: a quantitative analysis of pedal anatomy and the acquisition of the pacing gait. *Journal of vertebrate paleontology* 22:110–121.

Kilbourne BM, Makovicky PJ. 2012. Postnatal long bone growth in terrestrial placental mammals: Allometry, life history, and organismal traits. *Journal of Morphology* 273:1111–1126.

Mitchell G, van Sittert SJ, Skinner JD. 2009a. The structure and function of giraffe jugular vein valves. *South African Journal of Wildlife Research* 39:175–180.

Mitchell G, van Sittert SJ, Skinner JD. 2009b. Sexual selection is not the origin of long necks in giraffes. *Journal of Zoology (London)* 278:281–286.

Mitchell G, Skinner JD. 1993. How giraffe adapt to their extraordinary shape. *Transactions of the Royal Society of South Africa* 48:207–218.

Mitchell G, Skinner JD. 2003. On the origin, evolution and phylogeny of giraffes Giraffa camelopardalis. *Transactions of the Royal Society of South Africa* 58:51–73.

Mitchell G, Skinner JD. 2011. Lung volumes in giraffes, Giraffa camelopardalis. *Comparative biochemistry and physiology. Part A, Molecular & integrative physiology* 158:72–78.

Murchison C. (ed.) 1868. *Palæontological Memoirs and Notes of the Late Hugh Falconer: With a Biographical Sketch of the Author*. London: R. Hardwicke.

Roth VL. 1990. Insular dwarf elephants: a case study in body mass estimation and ecological inference. In: Damuth JD, MacFadden BJ eds. *Body Size in Mammalian Paleobiology: Estimation and Biological Implications*. Cambridge: Cambridge University Press, 151–179.

Van Schalkwyk OL. 2004. Bone density and calcium and phosphorous content of the giraffe (*Giraffa camelopardalis*) and African buffalo (*Syncerus caffer*) skeletons. Pretoria: University of Pretoria.

Van Schalkwyk OL, Skinner JD, Mitchell G. 2004. A comparison of the bone density and morphology of giraffe (*Giraffa camelopardalis*) and buffalo (*Syncerus caffer*) skeletons. *Journal of zoology* 264:307–315.

Scott K. 1990. Postcranial dimensions of ungulates as predictors of body mass. In: Damuth J, MacFadden BJ eds. *Body size in mammalian paleobiology*. Cambridge: Cambridge University Press,.

Skinner JD, Chimimba CT. 2005. Family Giraffidae Gray 1821. In: The mammals of the Southern African Subregion. Cambridge: Cambridge University Press, 616–620.

Smith RJ. 1984. Allometric scaling in comparative biology: problems of concept and method. *American Journal of Physiology-Regulatory, Integrative and Comparative Physiology* 246:R152–R160.

Solounias N. 2007. Family Giraffidae. In: Prothero DR, Foss SE eds. *The Evolution of Artiodactyls*. Baltimore: Johns Hopkins University Press,.

Van Valkenburgh B. 1990. Skeletal and dental predictors of body mass in carnivores. In: *Body size in mammalian paleobiology*. Cambridge: Cambridge University Press,.