

Peer Review Information

Journal: Nature Ecology & Evolution

Manuscript Title: Sex differences in the pelvis did not evolve de novo in modern humans

Corresponding author name(s): Barbara Fischer

Editorial Notes:

Reviewer Comments & Decisions:

Decision Letter, initial version:
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1st December 2020

*Please ensure you delete the link to your author homepage in this e-mail if you wish to forward it to your co-authors.

Dear Dr Fischer,

Your manuscript entitled "Sex differences in the pelvis did not evolve de novo in modern humans. A facilitated variation hypothesis" has now been seen by three reviewers, whose comments are attached. The reviewers have raised a number of concerns which will need to be addressed before we can offer publication in Nature Ecology & Evolution. We will therefore need to see your responses to the criticisms raised and to some editorial concerns, along with a revised manuscript, before we can reach a final decision regarding publication.

We therefore invite you to revise your manuscript taking into account all reviewer and editor comments. Please highlight all changes in the manuscript text file [OPTIONAL: in Microsoft Word format].

We are committed to providing a fair and constructive peer-review process. Do not hesitate to contact us if there are specific requests from the reviewers that you believe are technically impossible or unlikely to yield a meaningful outcome.

When revising your manuscript:

* Include a "Response to reviewers" document detailing, point-by-point, how you addressed each reviewer comment. If no action was taken to address a point, you must provide a compelling argument. This response will be sent back to the reviewers along with the revised manuscript.

* If you have not done so already please begin to revise your manuscript so that it conforms to our Article format instructions at <http://www.nature.com/natecolevol/info/final-submission>. Refer also to any guidelines provided in this letter.

* Include a revised version of any required reporting checklist. It will be available to referees (and, potentially, statisticians) to aid in their evaluation if the manuscript goes back for peer review. A revised checklist is essential for re-review of the paper.

Please use the link below to submit your revised manuscript and related files:

[REDACTED]

Note: This URL links to your confidential home page and associated information about manuscripts you may have submitted, or that you are reviewing for us. If you wish to forward this email to co-authors, please delete the link to your homepage.

We hope to receive your revised manuscript within four to eight weeks. If you cannot send it within this time, please let us know. We will be happy to consider your revision so long as nothing similar has been accepted for publication at Nature Ecology & Evolution or published elsewhere.

Nature Ecology & Evolution is committed to improving transparency in authorship. As part of our efforts in this direction, we are now requesting that all authors identified as 'corresponding author' on published papers create and link their Open Researcher and Contributor Identifier (ORCID) with their account on the Manuscript Tracking System (MTS), prior to acceptance. ORCID helps the scientific community achieve unambiguous attribution of all scholarly contributions. You can create and link your ORCID from the home page of the MTS by clicking on 'Modify my Springer Nature account'. For more information please visit www.springernature.com/orcid.

Please do not hesitate to contact me if you have any questions or would like to discuss these revisions further.

We look forward to seeing the revised manuscript and thank you for the opportunity to review your work.

[REDACTED]

Reviewer expertise:

all reviewers have expertise in hominin pelvic evolution

Reviewers' comments:

Reviewer #1 (Remarks to the Author):

Comments by Philipp Gunz

It was a real pleasure to read the paper “Sex differences in the pelvis did not evolve de novo in modern humans” by Barbara Fischer and colleagues.

The authors present an elegant study design, and a well-structured argument that relevant aspects of pelvic sexual dimorphism are shared between chimpanzees and humans. Overall, I think the manuscript is of outstanding quality, and I only have fairly minor suggestions for changes and modifications.

Abstract: “... which likely enables the rapid increase in human brain size”: I found the word “enabled” in the second half a bit misleading, especially in light of the arguments about the importance of energetics for the evolution of hominin brain growth and parturition. As an easy fix I suggest switching “facilitated” and “enabled”, i.e. to change the sentence to: “... the evolution of the pattern of pelvic dimorphism ENABLED rapid evolutionary change of the magnitude of sexual dimorphism, which IN TURN FACILITATED the rapid increase in HOMININ brain size.”

Page 3, Line 3: Many authors would argue that bipedalism already evolved in the late Miocene. Also: I don't think the evolution of bipedalism and the encephalisation should be described as “events” — please reword to clarify that these are processes.

Page 3, line 7: Regarding “Lucy” being a male individual. It is true the papers cited here have made this argument more than 22 years ago, however, I am not aware of anyone in 2020 making a similar claim.

Throughout the text and in Figures 3 and 5: For some reason the terms “ultramale” and “ultrafemale” make me cringe (sounds a bit like Leni Riefenstahl). I suggest rewording and using a term like “exaggerated female”.

Page 8, line 15f: It may be worth mentioning that inlet size is not the only birth-relevant dimension in the pelvis. E.g., there is an entire body of literature about the evolution of rational birth.

Page 8, line 23: I suggest replacing “modern human evolution” with “hominin evolution”.

I suggest streamlining Introduction and Discussion. For example, the argument about the Virginia opossum appears in the Introduction and the Discussion and feels a bit redundant.

Page 10, line 11f: I must admit I don't share the author's confidence regarding the vestigial pattern. Are you saying that, e.g., some ancestor of the Virginia opossum gave birth to much larger offspring? I am not much of a marsupial expert, but I find this questionable.

Paper worth citing: Hirata et al. (2011): Mechanism of birth in chimpanzees: Humans are not unique among primates

Reviewer #2 (Remarks to the Author):

Thank you very much for inviting me to revise this manuscript. In this study, Fisher and colleagues assess the topic of sexual dimorphism in humans and chimpanzees, which is of interest not only for knowing more about these species but also for understanding the evolution of pelvic sexual dimorphism along the human lineage. Sexual dimorphism in non-human primates have been assessed using traditional methods based on angles, distances, ratios, etc. Comparison of humans and chimpanzees have been also evaluated, but this work uses 3D geometric morphometrics to assess this topic for the first time, and I personally think that 3D assessment of pelvic morphology is the best way to do it.

I have minor suggestions that I hope help improving the manuscript. I recommend acceptance of the manuscript after addressing the following comments:

Minor comments

Page 3, lines 5-7. The authors mention the conflict of sexing Lucy in previous works, but they do not explain why sexing Lucy (and other Australopithecus such as Sts 14) are difficult to be sexed compared to other Homo specimens.

Page 3, line 12. I encourage the authors to read the PhD thesis by Dr. Natalie Laudicina where she goes beyond landmarks and suggests that childbirth may not be more difficult in humans than in other primates, including chimpanzees.

Page 3, lines 20-21. True, but apart, sexual size dimorphism in chimpanzees is only moderate.

Page 4, Figure 1. The landmarks and semilandmarks located in the sacrum are confusing, as there seem to be 5 points in the human sacrum (apart from the point in the promontory and the point in the caudal tip of the sacrum) but 6 points in the chimpanzee sacrum. This is related to the fact that the authors explain how they mirror the left side hipbone to obtain the right side hipbone but they do not explain how they obtained the sacral landmarks in the midsagittal plane. In addition, humans and chimpanzees have different sacral vertebral number, so how did the authors deal with this lack of serial homology in their landmark configuration?

Page 4, Caption to Figure 1. Do the authors mean 109 3D “landmarks and semilandmarks”? If so, would it be useful to use colours to differentiate between landmarks and curve semilandmarks?

Page 4, Figure 2. Did the authors manually draw these vectors? Or are these vectors statistical vectors? If the latter, please, explain how you calculated them. Overall, it is not clear for me how these vectors were calculated (are they allometric vectors from the allometric regression of Fig. S2?)

Page 5, lines 21-23. Are these Procrustes distances reflected somewhere in the manuscript? They should be accessible for the readership.

Page 8, lines 15-17. Are these inlet sizes reflected somewhere in the manuscript?

Page 8, lines 25. Indeed, it is not that surprising. Previous research on covariation within and between elements of the trunk in humans and chimpanzees also suggest similar patterns but different magnitude of integration (see Middleton, 2015; Torres-Tamayo et al. 2020). Although the present work does not evaluate integration but pelvis morphological variation due to sexual dimorphism, I would be happy to see these findings somehow discussed in the light of the works by Middleton, 2015 and Torres-Tamayo et al. 2020.

Middleton, E. R. (2015). Ecogeographic influences on trunk modularity in recent humans. (Ph.D. Dissertation). New York University

Torres-Tamayo, N., Martelli, S., Schlager, S., García-Martínez, D., Sanchis-Gimeno, J. A., Mata-Escolano, F., ... & Bastir, M. (2020). Assessing thoraco-pelvic covariation in Homo sapiens and Pan troglodytes: A 3D geometric morphometric approach. American Journal of Physical Anthropology, 173(3), 514-534.

Page 12, first paragraph.

1) The manuscript lacks information about sample collection. The specimens collected from CARTA were CT scanned and (if I am correct and these specimens are those from the Primate Foundation of

Arizona) these bones are disarticulated. The same applies to the 4 specimens collected at the NMW. Given that the authors are assessing pelvis in anatomical connection, they should explain how they articulated the bones: did they physically articulate the pelvic bones like Ward et al. 2018 (Ward, C. V., Maddux, S. D., & Middleton, E. R. (2018). Three-dimensional anatomy of the anthropoid bony pelvis. *American Journal of Physical Anthropology*, 166(1), 3-25) did and after this, did the authors scan the resulting articulated pelvis? Or did the authors scan the disarticulated pelvic bones and then, did they virtually articulate them to obtain an articulated 3D pelvis?

2) A table indicating age, sex, institution and ID of each specimen (specially of chimpanzees, maybe in Supplementary Information) would be useful for the readership to help identify the specimens in CARTA and KUPRI.

Page 12, line 27: Sorry, but I do not understand what the authors mean by the information within the parentheses.

Typos

Page 3, line 5: Please, replace AL 288-1 by A.L. 288-1

Page 6, caption to Figure 3, line 10. Please, remove the parenthesis after "interpolation".

Page 12, line 17: Please, remove capital letters in Generalized and Analysis. Only Procrustes must be capitalized.

Data sharing

I am quite familiar with the Open Science Framework repository, where the authors hosted their code and data. If I am correct (and sorry if I am not), the authors only uploaded the txt file "Read me" with information about the data and code, but I cannot see the data and code in the repository.

Lastly, my apologies if I am missing something or if any of my comments is redundant or senseless.

I can see the name of the authors so it is fair that they can see my name too. For that reason, and according to the policy of Nature Ecology and Evolution to promote a transparent peer review, below I sign my report to the authors.

Nicole Torres-Tamayo

Reviewer #3 (Remarks to the Author):

This is an insightful paper, addressing the important question of why sex differences in the pelvis (which run in the opposite direction to sex differences in body size in most mammals) exist even when selection pressures from obstetrics are very low. As the paper points out, Schultz and many who followed him found a correlation across primates between the intensity of selection (measured by the relative size of the neonatal head and the maternal pelvic inlet) and the degree of pelvic sexual dimorphism in a species. This has been explained as the result of selection on females to enlarge the birth canal to accommodate a tight fitting fetal head. This may be true but as the authors of this paper point out, it doesn't explain why species that have very small newborns also have the same pattern (but not the same magnitude) of pelvic sexual dimorphism. They suggest that the potential for pelvic sexual dimorphism is the primitive condition (for mammals?) and that it is turned up in magnitude by obstetric selection such as that seen in the human lineage as a result of encephalization. Do the authors propose that the primitive condition was characterized by similar obstetric selection? I don't think that there is much evidence for that, although it could be true. The point that pelvic sex differences did not evolve de novo in modern humans is an important one.

One might look at other sex differences (besides size differences in the pelvis) such as those features pointed out by Phenice (Phenice, T. W. (1969). A newly developed visual method of sexing the os pubis. *American Journal of Physical Anthropology*, 30(2), 297-301.) as reliable indicators of sex in

humans to see when those appear in the human fossil record.

Lori Hager examined this very question in her (unpublished) doctoral dissertation: Hager LD (1989) The Evolution of Sex Differences in the Hominid Bony Pelvis. Ph. D. thesis, University of California, Berkeley.

See also: Hager, L. D. (1996). Sex differences in the sciatic notch of great apes and modern humans. American Journal of Physical Anthropology 99(2), 287-300.

*****END*****

Author Rebuttal to Initial comments

Response to the Reviewer's comments

"Sex differences in the pelvis did not evolve de novo in modern humans. A facilitated variation hypothesis" by Fischer, Grunstra, Zaffarini and Mitteroecker

Many thanks for the helpful comments on our manuscript. We adapted the manuscript and supplementary material accordingly. All authors have seen and approved the resubmission.

Kind regards,

Barbara Fischer

Reviewer #1 (Remarks to the Author):

Comments by Philipp Gunz

It was a real pleasure to read the paper "Sex differences in the pelvis did not evolve de novo in modern humans" by Barbara Fischer and colleagues.

Thank you!

Abstract: "... which likely enables the rapid increase in human brain size": I found the word "enabled" in the second half a bit misleading, especially in light of the arguments about the importance of energetics for the evolution of hominin brain growth and parturition. As an easy fix I suggest switching "facilitated" and "enabled", i.e. to change the sentence to: "... the evolution of the pattern of pelvic dimorphism ENABLED rapid evolutionary change of the magnitude of sexual dimorphism, which IN TURN FACILITATED the rapid increase in HOMININ brain size."

Corrected as suggested.

Page 3, Line 3: Many authors would argue that bipedalism already evolved in the late Miocene. Also: I don't think the evolution of bipedalism and the encephalisation should be described as "events" — please reword to clarify that these are processes.

Reworded as suggested.

Page 3, line 7: Regarding "Lucy" being a male individual. It is true the papers cited here have made this argument more than 22 years ago, however, I am not aware of anyone in 2020 making a similar claim.

We clarified this sentence.

Throughout the text and in Figures 3 and 5: For some reason the terms "ultramale" and "ultrafemale" make me cringe (sounds a bit like Leni Riefenstahl). I suggest rewording and using a term like "exaggerated female".

Reworded as suggested.

Page 8, line 15f: It may be worth mentioning that inlet size is not the only birth-relevant dimension in the pelvis. E.g., there is an entire body of literature about the evolution of rational birth.

Amended accordingly.

Page 8, line 23: I suggest replacing “modern human evolution” with “hominin evolution”.

Done.

I suggest streamlining Introduction and Discussion. For example, the argument about the Virginia opossum appears in the Introduction and the Discussion and feels a bit redundant.

We now mention the Virginia opossum only in the Introduction. We have not removed our mention of marsupials in the Discussion entirely, because they serve as an important example for our argument about how the pattern of pelvic sex differences is likely vestigial in some lineages.

Page 10, line 11f: I must admit I don't share the author's confidence regarding the vestigial pattern. Are you saying that, e.g., some ancestor of the Virginia opossum gave birth to much larger offspring? I am not much of a marsupial expert, but I find this questionable.

Indeed, we suggest that a sexually dimorphic pelvis was present already in early mammals or even earlier and therefore constitutes the ancestral condition among therian mammals (marsupials and placentals), with a likely origin in early amniotes (reptiles, birds, and mammals). Sexually dimorphic pelves are abundant across mammal species, and the sexually dimorphic features of these pelves are often strikingly similar. As we pointed out in the manuscript, even some marsupial species who give birth to tiny neonates share similar sexually dimorphic features. We propose that a sexually dimorphic pelvis is a vestigial trait in obstetrically unconstrained mammals such as marsupials. The assumption of an amniote origin does not require marsupial ancestors to have given birth to much larger neonates, because pelvic sex dimorphism may always have been vestigial among marsupials. The assumption of a (therian) mammalian origin does not require marsupial ancestors to have given birth to much larger neonates either, because only two extant viviparous mammalian lineages exist (marsupials and placentals), on the basis of which it is not possible to determine the ancestral state. In other words, it is not known whether extant marsupials represent the plesiomorphic therian condition. Nonetheless, we suspect that the origin of pelvic sex differences is older and predates the origin of viviparity in therian mammals given that some reptiles and birds appear to show a similar pattern of pelvic sexual dimorphism as well. We have made this clearer in our revision, see page 6 lines 27-33 and page 7 lines 1-22.

Paper worth citing: Hirata et al. (2011): Mechanism of birth in chimpanzees: Humans are not unique among primates

Thank you! We are now citing Hirata et al. on page 3, line 9.

Reviewer #2 (Remarks to the Author):

Page 3, lines 5-7. The authors mention the conflict of sexing Lucy in previous works, but they do not explain why sexing Lucy (and other Australopithecus such as Sts 14) are difficult to be sexed compared to other Homo specimens.

Australopith pelvic remains tend to be fewer than some Homo species, e.g. H. neanderthalensis, which hampers an understanding of the variation and thus the detection of sex-specific phenotypic features, which are most useful for sex estimation. Australopith pelvic morphology and body form was more different from modern humans than later Homo and so the well-known dimorphic shape features in living modern humans cannot be as readily applied to sex australopith remains. There are thus no reference samples with known sex, based on which australopith remains can be reliably sexed.

Page 3, line 12. I encourage the authors to read the PhD thesis by Dr. Natalie Laudicina where she goes beyond landmarks and suggests that childbirth may not be more difficult in humans than in other primates, including chimpanzees.

We have read Dr. Laudicina's work. However, Hirata et al. (2011) filmed vaginal birth in chimpanzees, and found that birth is a very quick process in this species, supporting our statement. Indeed, we are not aware of any empirical evidence that would contradict this statement. This is rather expected given that there is more space in the birth canal for a fetus in chimpanzees compared to humans. However, we slightly expanded on our text, to give a balanced account of the similarities and differences between human and chimpanzee births see page 3, lines 6-12.

Page 3, lines 20-21. True, but apart, sexual size dimorphism in chimpanzees is only moderate.

We agree with Reviewer 2. This is simply a general statement about great apes, as in some species size differences are more pronounced.

Page 4, Figure 1. The landmarks and semilandmarks located in the sacrum are confusing, as there seem to be 5 points in the human sacrum (apart from the point in the promontory and the point in the caudal tip of the sacrum) but 6 points in the chimpanzee sacrum. This is related to the fact that the authors explain how they mirror the left side hipbone to obtain the right side hipbone but they do not explain how they obtained the sacral landmarks in the midsagittal plane. In addition, humans and chimpanzees have different sacral vertebral number, so how did the authors deal with this lack of serial homology in their landmark configuration?

Reynolds et al. (1982), who collected the human data, physically articulated the sacrum with the left coxal bone and then measured 3D landmarks with a Hewlett Packard digitizer. Landmarks on the midline of the sacrum were measured directly, not mirrored. We added this information to the manuscript see page 9, lines 15-19.

In both humans and chimpanzees, 6 points are located on the anterior midline of the sacrum between Promontorium and Caudion. We dealt with different numbers of sacral vertebrae by collecting fixed landmarks down to the 4th transverse line in all individuals, independent of additional sacral vertebrae. Then, as the final landmark along the sacral midline, Caudion as the most caudal tip of the sacrum was measured. The 8 points along the midline of the sacrum are (definitions from Reynolds et al. 1982):

- *Promontorium: Most anterior point of the promontorium in the median-sagittal level*
- *S1 Center: point in the middle between the promontorium and first sacral segment point in the median-sagittal level*
- *1st Segment Union Point: point at the first transverse line in the median-sagittal level*
- *2nd Segment Union Point: point at the second transverse line in the median-sagittal level*
- *Inflexion: This point is located at the intersection of the longest perpendiculars from the extreme anterior ends of the sacrum. Inflexion is a geometric point which uses S1 at the proximal end and Caudion at the distal end*
- *3rd Segment Union Point: point at the third transverse line in the median-sagittal level*
- *4th Segment Union Point: Point at the fourth transverse line in the median-sagittal level*
- *Caudion: Point at the fac. sacrococcygea of the sacrum at the anterior margin in the median-sagittal level*

In the human pelvis in Fig. 1, the first segment union point is in fact there but it is not visible because of the curvature of the sacrum. In the new version of Fig. 1 it is visible because we made the surface model semi-transparent. We also added a list of landmarks to the online repository where the data and code for this study are openly accessible.

Page 4, Caption to Figure 1. Do the authors mean 109 3D “landmarks and semilandmarks”? If so, would it be useful to use colours to differentiate between landmarks and curve semilandmarks?

We adapted the figure legend as suggested and are now showing the semilandmarks in a different colour. We also made the surface model semi-transparent (see new Figure 1).

Page 4, Figure 2. Did the authors manually draw these vectors? Or are these vectors statistical vectors? If the latter, please, explain how you calculated them. Overall, it is not clear for me how these vectors were calculated (are they allometric vectors from the allometric regression of Fig. S2?)

These vectors were calculated, not hand-drawn. They are allometry vectors from a regression of pelvis shape on centroid size, pooled across sexes, and separately for each species. To visualize these regression vectors together with the shape data, we projected them onto the PC1-2 and PC2-3 planes, respectively, by orthogonal projection. Then we superimposed them on the respective sex means, to show them together with these means.

We are now explaining this in more detail in the paper see page 10, lines 10-15. We adapted the figure legend for more clarity and refer to Fig. S1 and to the methods part in the legend of Fig. 2 for details on how the vectors are computed.

Page 5, lines 21-23. Are these Procrustes distances reflected somewhere in the manuscript? They should be accessible for the readership.

The absolute values of the Procrustes distances do not have any transferable meaning as they are a function of landmark number and landmark location. They are only informative relative to each other, as they are based on the same landmark set. Therefore, we chose to present %-difference between Procrustes distances instead of absolute values.

Page 8, lines 15-17. Are these inlet sizes reflected somewhere in the manuscript?

We added a figure for the distribution of inlet size in humans and chimpanzees to the supplement (Fig. S3).

Page 8, lines 25. Indeed, it is not that surprising. Previous research on covariation within and between elements of the trunk in humans and chimpanzees also suggest similar patterns but different magnitude of integration (see Middleton, 2015; Torres-Tamayo et al. 2020). Although the present work does not evaluate integration but pelvis morphological variation due to sexual dimorphism, I would be happy to see these findings somehow discussed in the light of the works by Middleton, 2015 and Torres-Tamayo et al. 2020.

Middleton, E. R. (2015). Ecogeographic influences on trunk modularity in recent humans. (Ph.D. Dissertation). New York University

Torres-Tamayo, N., Martelli, S., Schlager, S., García-Martínez, D., Sanchis-Gimeno, J. A., Mata-Escolano, F., ... & Bastir, M. (2020). Assessing thoraco-pelvic covariation in *Homo sapiens* and *Pan troglodytes*: A 3D geometric morphometric approach. *American Journal of Physical Anthropology*, 173(3), 514-534.

We followed the suggestion of the reviewer and mention both in the Introduction and Discussion that body proportions are correlated with pelvic form in humans (page 3, lines 13-15; page 7, lines 29-31). We included several new references demonstrating these associations, including Middleton 2015, Torres-Tamayo et al. 2020, and Torres-Tamayo et al. 2018.

1) The manuscript lacks information about sample collection. The specimens collected from CARTA were CT scanned and (if I am correct and these specimens are those from the Primate Foundation of Arizona) these bones are disarticulated. The same applies to the 4 specimens collected at the NMW. Given that the authors are assessing pelvis in anatomical connection, they should explain how they articulated the bones: did they physically articulate the pelvic bones like Ward et al. 2018 (Ward, C. V., Maddux, S. D., & Middleton, E. R. (2018). Three-dimensional anatomy of the anthropoid bony pelvis. *American Journal of Physical Anthropology*, 166(1), 3-25) did and after this, did the authors scan the resulting articulated pelvis? Or did the authors scan the disarticulated pelvic bones and then, did they virtually articulate them to obtain an articulated 3D pelvis?

The specimens that we obtained electronically from CARTA were available as surface models of individual bones, while the KUPRI specimens were articulated pelvises segmented from whole body CT scans. The specimens from NHM were surface scans of individual pelvic bones. The CARTA and NHM disarticulated specimens were digitally recomposed using the software Geomagic. We added this information to the methods section (page 9, lines 7-13).

2) A table indicating age, sex, institution and ID of each specimen (specially of chimpanzees, maybe in Supplementary Information) would be useful for the readership to help identify the specimens in CARTA and KUPRI.

We added a table of chimpanzee specimens measured for this study to the online supplement (Table S1).

Page 12, line 27: Sorry, but I do not understand what the authors mean by the information within the parentheses.

As indicated in the text, this is the source of the pelvis model which we used for the visualization of our human data, www.turbosquid.com, product ID 710664, Oormi Creations. Turbosquid is a commercial website where 3D models can be purchased. We acquired a human pelvis surface model, measured our landmark set on it, and then used it for visualizing our dataset by warping it to the target landmark configurations. We specified this a bit more in the text (page 9 line 32 – page 10 line 1).

Typos

Page 3, line 5: Please, replace AL 288-1 by A.L. 288-1

Page 6, caption to Figure 3, line 10. Please, remove the parenthesis after “interpolation”.

Page 12, line 17: Please, remove capital letters in Generalized and Analysis. Only Procrustes must be capitalized.

Corrected as suggested.

Data sharing

I am quite familiar with the Open Science Framework repository, where the authors hosted their code and data. If I am correct (and sorry if I am not), the authors only uploaded the txt file “Read me” with information about the data and code, but I cannot see the data and code in the repository.

Indeed, all data and code were available in the online repository. Reviewer 2 must unfortunately have overlooked this. We placed it in a folder named “data and code for review”. As Reviewer 2 was able to see the readme file, the link we shared was apparently correct. One can access this folder by clicking on its name. It is shown right above the readme file.

Reviewer #3 (Remarks to the Author):

This is an insightful paper, addressing the important question of why sex differences in the pelvis (which run in the opposite direction to sex differences in body size in most mammals) exist even when selection pressures from obstetrics are very low.

Thank you!

They suggest that the potential for pelvic sexual dimorphism is the primitive condition (for mammals?) and that it is turned up in magnitude by obstetric selection such as that seen in the human lineage as a result of encephalization. Do the authors propose that the primitive condition was characterized by similar obstetric selection? I don't think that there is much evidence for that, although it could be true.

Indeed, we propose that a sexually dimorphic pelvis was present already in early mammals and therefore constitutes the ancestral condition. Sexually dimorphic pelves are abundant across mammal species, and the sexually dimorphic features of these pelves are often strikingly similar in their patterns. Surprisingly, even some bird and reptile pelves share the same sexually dimorphic pelvic features. We therefore suggest that these patterns initially evolved in response to obstetric selection, either to enable birth of large offspring in early mammals or potentially even earlier, to facilitate oviposition in amniotes. Just as live offspring, eggs need to be able to pass through the birth canal without breaking. We aim to empirically test this hypothesis in our future research. We clarified this argument in the discussion (page 7, lines 7-11).

The point that pelvic sex differences did not evolve de novo in modern humans is an important one. One might look at other sex differences (besides size differences in the pelvis) such as those features pointed out by Phenice (Phenice, T. W. (1969). A newly developed visual method of sexing the os pubis. *American Journal of Physical Anthropology*, 30(2), 297-301.) as reliable indicators of sex in humans to see when those appear in the human fossil record. Lori Hager examined this very question in her (unpublished) doctoral dissertation: Hager LD (1989) *The Evolution of Sex Differences in the Hominid Bony Pelvis*. Ph. D. thesis, University of California, Berkeley. See also: Hager, L. D. (1996). Sex differences in the sciatic notch of great apes and modern humans. *American Journal of Physical Anthropology* 99(2), 287-300.

Thank you for pointing out these interesting references. Indeed, Hager's work (1996) is very relevant for this study and her results are in line with ours. She found that human sex differences in the sciatic notch – in human females it is wide and shallow, while males it is narrow and deep – are also present in other great apes. We now cite the suggested reference by Hager (1996) in the Introduction and Discussion (page 2, line 8; page 6, lines 18).

Decision Letter, first revision:

Our ref: NATECOLEVOL-201011831A

26th January 2021

Dear Dr. Fischer,

Thank you for submitting your revised manuscript "Sex differences in the pelvis did not evolve de novo in modern humans. A facilitated variation hypothesis" (NATECOLEVOL-201011831A). It has now been seen by the original referees and their comments are below. The reviewers find that the paper has improved in revision, and therefore we'll be happy in principle to publish it in Nature Ecology & Evolution, pending minor revisions to satisfy the referees' final requests and to comply with our editorial and formatting guidelines.

We are now performing detailed checks on your paper and will send you a checklist detailing our editorial and formatting requirements in about a week. Please do not upload the final materials and make any revisions until you receive this additional information from us.

Thank you again for your interest in Nature Ecology & Evolution Please do not hesitate to contact me if you have any questions.

[REDACTED]

My pronouns: she/her

Reviewer #1 (Remarks to the Author):

Many thanks for the careful revisions. I feel the authors have addressed all my concerns. Congratulations on an outstanding piece of scholarship—I look forward to seeing it in print.

I only have a few small recommendations for the supplementary data.

I applaud the authors' decision to make the data and Mathematica code available. With a few tiny changes, this resource will likely be even more useful to other researchers.

Some of the filenames are in German (ohnesteissbeinv3.obj) ... I suggest renaming these files.

I suggest creating one single streamlined analysis file in Mathematica. Please also add a comment that one needs to run the notebook with the extra functions first.

Rather than hard-coding the absolute file path (/Users/barbaraf/Work/Science Projects/Evolution of Childbirth/Chimpanzees/data/data_tidy/humanchimplmdatabiometricdata.m) it would be more elegant to copy all files into one directory and use a solution like:

```
path=NotebookDirectory[]
Get[FileNames["humanchimplmdatabiometricdata.m", path, 2]]
```

Reviewer #2 (Remarks to the Author):

I am quite happy with this revised version of the manuscript. The authors addressed all my suggestions and concerns, so I recommend acceptance of the manuscript.

Nicole Torres-Tamayo

Reviewer #3 (Remarks to the Author):

The manuscript is significantly improved by revision following the three reviews. I recommend publication

One point to note: Line 69-72 – Hirata and colleagues showed that chimpanzees may give birth occiput anterior (which was previously thought to be unique to humans) but they did not show that chimpanzees have a birth mechanism like the one typical of humans in which the head enters the pelvic inlet facing transversely and then rotates as it passes to the midplane and outlet. So it not correct that “chimpanzee fetuses also appear to rotate during parturition, similar to humans”. The do at least sometimes rotate, but not particularly in the way that humans generally do. Melissa Stoller showed in her dissertation that monkeys also may rotate during birth, but again not in the same way as humans and they emerge in a facial presentation (Stoller, M.K., 1996. The obstetric pelvis and mechanism of labor in nonhuman primates. Dissertation, University of Chicago)

Our ref: NATECOLEVOL-201011831A

2nd February 2021

Dear Dr. Fischer,

Thank you for your patience as we've prepared the guidelines for final submission of your Nature Ecology & Evolution manuscript, "Sex differences in the pelvis did not evolve de novo in modern humans. A facilitated variation hypothesis" (NATECOLEVOL-201011831A). Please carefully follow the step-by-step instructions provided in the personalised checklist attached, to ensure that your revised manuscript can be swiftly handed over to our production team.

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In recognition of the time and expertise our reviewers provide to Nature Ecology & Evolution's editorial process, we would like to formally acknowledge their contribution to the external peer review of your manuscript entitled "Sex differences in the pelvis did not evolve de novo in modern humans. A facilitated variation hypothesis". On a trial basis for those reviewers who give their assent, we will be publishing their names alongside the published article. We will not be publishing any of the submitted peer review comments.

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If you have any further questions, please feel free to contact me.

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Reviewer #1:

Remarks to the Author:

Many thanks for the careful revisions. I feel the authors have addressed all my concerns. Congratulations on an outstanding piece of scholarship—I look forward to seeing it in print.

I only have a few small recommendations for the supplementary data.

I applaud the authors' decision to make the data and Mathematica code available. With a few tiny changes, this resource will likely be even more useful to other researchers.

Some of the filenames are in German (ohnesteissbeinv3.obj) ... I suggest renaming these files.

I suggest creating one single streamlined analysis file in Mathematica. Please also add a comment that one needs to run the notebook with the extra functions first.

Rather than hard-coding the absolute file path (/Users/barbaraf/Work/Science Projects/Evolution of

Childbirth/Chimpanzees/data/data_tidy/humanchimplmdatabiometricdata.m) it would be more elegant to copy all files into one directory and use a solution like:

```
path=NotebookDirectory[]
Get[FileNames["humanchimplmdatabiometricdata.m", path, 2]]
```

Reviewer #2:

Remarks to the Author:

I am quite happy with this revised version of the manuscript. The authors addressed all my suggestions and concerns, so I recommend acceptance of the manuscript.

Nicole Torres-Tamayo

Reviewer #3:

Remarks to the Author:

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Manuscript: NATECOLEVOL-201011831A

Author: Barbara Fischer

Article type: Article

Title:

To comply with our house style, we will need to drop the subtitle from the existing title. I suggest you change to **'Sex differences in the pelvis did not evolve de novo in modern humans.'**

Abstract:

It is commonly assumed that the strong sexual dimorphism of the human pelvis evolved for delivering the relatively large human foetuses. Here we compare pelvic sex differences across modern humans and chimpanzees using a comprehensive geometric morphometric approach. Even though the magnitude of sex differences in pelvis shape was two times larger in humans than in chimpanzees, we found that the pattern is almost identical in the two species. We conclude that this pattern of pelvic sex differences did not evolve de novo in modern humans and must have been present in the common ancestor of humans and chimpanzees, and thus also the extinct *Homo* species. We further suggest that this shared pattern was already present in early mammals and propose a hypothesis of facilitated variation as an explanation: the conserved mammalian endocrine system strongly constrains the evolution of the pattern of pelvic differences but enables rapid evolutionary change of the magnitude of sexual dimorphism, which in turn facilitated the rapid increase in hominin brain size.

Your paper will be accompanied by the editor's summary and subject terms below. Please let us know if there are any inaccuracies.

Editor's Summary:

"Comparing pelvic sex differences across modern humans and chimpanzees reveals a similar pattern despite differences in magnitude of pelvis shape dimorphism, suggesting that this pattern did not evolve de novo in modern humans but was present in the last common ancestor of humans and chimpanzees".

Proposed Subject Terms:

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Term 2:	Evolutionary developmental biology
Term 3:	Evolutionary theory
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- ☐ Competing Interests Statement
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- ☐ Tables
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- ☐ Please remove footnotes within the manuscript and integrate them into the main text.

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Methods

References

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Author Rebuttal, first revision:

"Sex differences in the pelvis did not evolve de novo in modern humans" by Fischer, Grunstra, Zaffarini and Mitteroecker

Response to reviewers, second resubmission**Comments by Reviewer 1**

Many thanks for the careful revisions. I feel the authors have addressed all my concerns. Congratulations on an outstanding piece of scholarship—I look forward to seeing it in print.

Thank you!

I only have a few small recommendations for the supplementary data. I applaud the authors' decision to make the data and Mathematica code available. With a few tiny changes, this resource will likely be even more useful to other researchers. Some of the filenames are in German (ohnesteissbeinv3.obj) ... I suggest renaming these files.

We changed the filenames as suggested.

I suggest creating one single streamlined analysis file in Mathematica. Please also add a comment that one needs to run the notebook with the extra functions first.

The visualisation part of the analysis is computationally expensive while the other parts are not. We therefore believe that it makes sense to keep these code sections apart in separate notebooks, as this allows for more convenient execution of the code in meaningful pieces. However, we edited the file containing the morphometric functions and removed all functions that are not

used in the subsequent analysis. We also integrated the sliding landmark algorithm into the same functions file. As suggested, we added a note that the notebook that defines the functions needs to be run first.

Rather than hard-coding the absolute file path (/Users/barbaraf/Work/Science Projects/Evolution of Childbirth/Chimpanzees/data/data_tidy/humanchimplmdatabiometricdata.m) it would be more elegant to copy all files into one directory and use a solution like:

```
path=NotebookDirectory[]
```

```
Get[FileNames["humanchimplmdatabiometricdata.m", path, 2]]
```

Thank you for this suggestion, which we were happy to follow. We made all file paths relative to the new directory “code and data”, which makes the code portable. We kept the sub-structure of the folders within this directory, as we believe that they help with the overview over all contained files (3 subfolders: code, data, data for visualisation and supplement).

Comments by Reviewer 2

I am quite happy with this revised version of the manuscript. The authors addressed all my suggestions and concerns, so I recommend acceptance of the manuscript.

Thank you!

Comments by Reviewer 3

The manuscript is significantly improved by revision following the three reviews. I recommend publication

Thank you!

One point to note: Line 69-72 – Hirata and colleagues showed that chimpanzees may give birth occiput anterior (which was previously thought to be unique to humans) but they did not show that chimpanzees have a birth mechanism like the one typical of humans in which the head enters the pelvic inlet facing transversely and then rotates as it passes to the midplane and outlet. So it not correct that “chimpanzee fetuses also appear to rotate during parturition, similar to humans”. They do at least sometimes rotate, but not particularly in the way that humans generally do. Melissa Stoller showed in her dissertation that monkeys also may rotate during birth, but again not in the same way as humans and they emerge in a facial presentation (Stoller, M.K., 1996. The obstetric pelvis and mechanism of labor in nonhuman primates. Dissertation, University of Chicago)

Following the reviewer's suggestion, we now state clearly that fetal rotation during birth in chimpanzees is similar in certain aspects but not identical to that in humans (page 3, lines 6-7).

Final Decision Letter:

24th February 2021

Dear Dr Fischer,

We are pleased to inform you that your Article entitled "Sex differences in the pelvis did not evolve de novo in modern humans", has now been accepted for publication in Nature Ecology & Evolution.

Before your manuscript is typeset, we will edit the text to ensure it is intelligible to our wide readership and conforms to house style. We look particularly carefully at the titles of all papers to ensure that they are relatively brief and understandable.

The subeditor may send you the edited text for your approval. Once your manuscript is typeset you will receive a link to your electronic proof via email, with a request to make any corrections within 48 hours. If you have queries at any point during the production process then please contact the production team at rjsproduction@springernature.com. Once your paper has been scheduled for online publication, the Nature press office will be in touch to confirm the details.

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