New Middle Miocene Ape (primates: Hylobatidae) from Ramnagar, India fills major gaps in the hominoid fossil record

Christopher C. Gilbert, Alejandra Ortiz, Kelsey D. Pugh, Christopher J. Campisano, Biren A. Patel, Ningthoujam Premjit Singh, John G. Fleagle and Rajeev Patnaik

Review timeline

Original submission:	8 February 2020
1st revised submission:	9 July 2020
2nd revised submission:	12 August 2020
Final acceptance:	13 August 2020

Note: Reports are unedited and appear as submitted by the referee. The review history appears in chronological order.

Review History

RSPB-2020-0271.R0 (Original submission)

Review form: Reviewer 1

Recommendation
Accept with minor revision (please list in comments)

Scientific importance: Is the manuscript an original and important contribution to its field?
Good

General interest: Is the paper of sufficient general interest?
Acceptable

Quality of the paper: Is the overall quality of the paper suitable?
Excellent

Is the length of the paper justified?
Yes

Should the paper be seen by a specialist statistical reviewer?
No

Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.
No

It is a condition of publication that authors make their supporting data, code and materials available - either as supplementary material or hosted in an external repository. Please rate, if applicable, the supporting data on the following criteria.

Is it accessible?
Yes

Is it clear?
Yes

Is it adequate?
Yes

Do you have any ethical concerns with this paper?
No

Comments to the Author
The manuscript by Gilbert et al describing a new catarrhine lm3 from the Siwaliks is well written, clear, and of general interest. The describe a new fossil molar from the middle Miocene and based on comparative morphology, 2D morphometric analysis of cuspal positions, and a phylogenetic anlysis, suggest that it is closely related to extant hylobatids, and name a new genus and species based on the specimen.

First off, I normally wouldn't comment on a name, but this time I can't help it "Coronapithecus" seems particularly timely given COVID 19. Personally, I don't like names based on phylogenetic hypotheses as these are often revised (e.g., Bugtilemur, Pliobates, Prohylobates, etc.). Just something to think about.

Another small point, there is no photograph of the specimen. The digital surface models are nice, but actual photographs would also be very helpful. Perhaps these could be added to figure 2.

A more important point is the lack of extant hominids in the morphometric analysis greatly weaken its effectiveness. While it does appear that extant hylobatids are morphologically distinct from the stem catarrhines sampled, it is unclear how distinctive these both are from extant hominids. Something this paper assumes, and relies on, but does not demonstrate. Samples, roughly equivalent in size to those for the hylobatids presented here, would greatly help with understanding the significance of the placement of Coronapithecus, Yuanmopithecus, and Bunopithecus.

A quick scan of the characters used in the phylogenetic analysis suggests that only 12 or 13 are available on VPL/RSP2. This suggests caution in interpreting the results.

These last 2 points taken together, in my opinion recommend greater circumspection of the results than are currently provided in the discussion. Especially given that non-cercopithecoid catarrhine molars are not particularly morphologically diagnostic in general. Especially based on single individuals. I'm not suggesting that the authors are wrong, merely the fact that one cannot be so sure given the specimen is a single, isolated tooth among a group that has been quite conservative in molar morphology.

Minor points:

Line 56, insert "right" before "lower third molar"

Line 88, change "anterior" to "mesial"

Lines 244-246, if hylobatids evolved from a form morphologically similar to dendropithecids or proconsulids, are you suggesting that dendropiths and proconsulids approximate the hominoid morphotype? Please clarify.

Lines 248-249. What does having an extensive fossil record have to do with morphological affinity? Having an extensive fossil record is related to taphonomy, paleoecology, tectonics, and the vagaries of the fossil record. I don't see what it has to do with the morphological and phylogenetic affinities of hylobatids. I suggest restructuring this sentence to clarify that these similar taxa just also happen to have an abundant fossil record. But these beg the question. To what else could they possibly show affinities? Especially since hominids were not included in the GM analysis and monkeys are pretty derived in molar morphology.

Line 251 change "more primitive dental features preserved" to "lack of dental synapomorphies with hylobatids"

Figure S2: It would be better to replace the "a", "b", etc. With taxonomic labels "VPL/RSP2", "propliopithecids", etc. So readers don't have to constantly look back and forth between the figure and the caption.

Review form: Reviewer 2

Recommendation
Major revision is needed (please make suggestions in comments)

Scientific importance: Is the manuscript an original and important contribution to its field?
Excellent

General interest: Is the paper of sufficient general interest?
Excellent

Quality of the paper: Is the overall quality of the paper suitable?
Acceptable

Is the length of the paper justified?
Yes

Should the paper be seen by a specialist statistical reviewer?
No

Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.
Yes

It is a condition of publication that authors make their supporting data, code and materials available - either as supplementary material or hosted in an external repository. Please rate, if applicable, the supporting data on the following criteria.

Is it accessible?
Yes

Is it clear?
Yes

Is it adequate?
Yes

Do you have any ethical concerns with this paper?
No

Comments to the Author

This is an important manuscript describing a new anthropoid tooth from a fossil site where few anthropoids have previously been reported. Although numerous hominoid fossils are known from other Siwaliks sites in the region, this specimen cannot be readily accommodated within any known genus. Hence, the authors propose to erect a new genus and species for this specimen, and their analyses suggest to them that the tooth represents the earliest known member of the hylobatid clade. The specimen, geological context, description/diagnosis, and some of the analyses will be very important to understanding the evolution and distribution of catarrhines in the middle Miocene. However, I have concerns regarding some components of this manuscript. These are detailed below, with additional comments in the annotated pdf. I'd be happy to review another version of this manuscript.

1. I should start by saying that I fundamentally disagree with the idea of naming a new species based on a single tooth. I do NOT disagree that this probably is a new species, and the authors are well within ICZN guidelines in naming one. My concern is that, in doing so, this isolated tooth becomes the type specimen for what is likely to be an important taxon for interpreting ape evolution. Isolated teeth make terrible type specimens, and any comparisons to this species (including future allocations from this site) would be limited to samples that contain lower m3s. Worse, the well-documented variability in this tooth position means that even those comparisons could be highly misleading.

There are many fossil sites that have large samples of anthropoid primates: Rudabanya, Paşalar, Vallès-Penedès Basin, Maboko, Songhor, Rusinga, Fayum, Lufeng, etc. Every one of these sites has individual specimens that stand out as unique within their assemblages, and that could easily form the basis for a new species. There are also many sites with only one or two anthropoid teeth that, by any reasonable estimation, differ from other known taxa. That researchers have NOT named new species in these cases speaks to the exercise of appropriate caution: both in recognizing the limits of our knowledge of variation and in creating a taxon for which there can be few meaningful comparisons. I suggest that these cautions are warranted, even at a site with only one anthropoid specimen that is geographically distant from other fossil anthropoid sites.

To be clear, I do not think this specimen does belong in any known taxon; I am convinced that it is something new, and the authors' logic in naming it is sound. I simply think that doing so is inadvisable. I also do not expect that my arguments will persuade the authors to change their minds, and I do NOT require a lengthy rebuttal to this point. The specimen is publishable even if my cautions are ignored. Ultimately, new, better-preserved specimens will someday be discovered that either supplant this one in everyone's comparative analyses, or (highly unlikely) demonstrate that this specimen is not a distinct species. In either case, basing a new species on an isolated tooth will then appear to have been overly hasty. We all field questions from students about why researchers would name a species from a holotype with little preserved anatomy. I feat thar this will become one more entry in that list, and I respect the authors too much to not point this out.

2. The generic diagnosis and description are insufficient by a wide margin to define this taxon. I do not mean insufficient according to ICZN guidelines (which require only the weakest criteria to qualify for a valid name), but insufficient to effectively allow other researchers to properly differentiate this specimen from other taxa. In particular, lumping together propliopithecids, pliopithecids, and dendropithecids – each of which is a highly variable group, and together do not constitute any set of primitive or derived m3 traits against which this specimen is compared – provides no clear differentiation from genera within these groups. Is there some reference that provides diagnostic features of the m3 in any of these families or of the three families combined? The general approach of 'here are some features in this specimen that are typically not found in these other groups' seems especially weak; likewise, saying it differs from "most" members of some higher-order taxon. Material in the supplementary document does not add much in this regard beyond what is said in the main text. There are a number of genera against which this specimen should be individually compared. Doing so will be a lengthy process and much of that material should probably go in supplementary information. Nevertheless, the authors are making extraordinary claims with substantial implications; they should provide rigorous and detailed comparisons to support those claims. In the end, with only an m3 to compare, individual comparisons cannot be too lengthy, but they should be made nonetheless.

3. Running a principal components analyses seems like a useful exploratory tool, and although the interpretation of these results seems overly confident (if each of your groups had a similar variance to the well-sampled hylobatids, would the Ramnagar tooth plot exclusively with hylobatids?) the plot supports the overall conclusions of the paper. I found the canonical variates analysis to be unconvincing and unnecessary, however. The reported cross validated results appear to be good because the data can easily classify the large sample of gibbons (in part because they are different, but also could be a function of radically different group sample sizes; see also below). Among fossils, cross validated results are only correct in 41% of cases: better than chance, but not very convincing, and apparently proconsulids cannot be correctly classified at all. Although the diagnosis was written by pooling large groups of species (e.g., propliopithecids, pliopithecids, dendropithecids), this analysis was done individually by family. If there is some hylobatid or crown hominoid aspect to m3 shape that differs from more primitive catarrhines, why not group the more primitive ones together here instead of analyzing at the family level? The results might give a sense of whether this derived/primitive distinction is valid in m3s, and if so where the Ramnagar tooth classifies. I found especially problematic that apparently group sample sizes were used to adjust the priors. To me, this is exactly the wrong way to address sample size differences. Adjusting the priors would be appropriate if, for example, all of the specimens came from a well-sampled fossil site where large numbers of fossils are typically distributed into taxa proportionately. In that case, a new fossil from that same site would most likely belong to the most abundant taxon, followed by the next most abundant, etc. The priors could be adjusted to reflect this. Here, if I understand what the authors did, the priors were adjusted based on their sample proportions, meaning that the analysis is more likely to classify unknowns into the largest sample: hylobatids. This seriously undermines the impact of classifying the Ramnagar tooth in that group. In the end, I don't think canonical variates analysis/discriminant function analysis is necessary. The PCA plot makes the intended point; trying to reinforce this with one or more more problematic analyses is counterproductive.

4. Similarly, I do not see value in running a cladistic analysis on a single tooth. I realize this practice is becoming more common (e.g., Rossie and Hill, 2018), but I find the results unconvincing. Of the 272 characters in the cladistic analysis, only 7 can be scored for the Ramnagar tooth. The literature cited by the authors to support this practice does not constitute a strong justification: one study doesn't make any recommendation on use/exclusion of missing data; one found that a single fossil taxon (of four) had identical placement relative to the other taxa regardless of whether missing data were included; one argues for including specimens with missing data but, importantly, indicates that specimens with very few preserved characters result in weak tests of character congruence. All three studies are more than 17 years old. More current literature favors the addition of more taxa/characters even when that means excessive missing data, although the justification behind this recommendation is based on overall tree topology

rather than how one OTU of interest is positioned. Nevertheless, these papers could be cited to better support the authors' methods. However, recent studies also provide rigorous assessments for the impact of the missing data. The authors should implement those assessments if they want to present a convincing argument. As with some of the multivariate analyses, I don't think a phylogenetic analysis of one tooth adds to this study. If one of the better-preserved fossil taxa were instead represented here by only an m3, would it land in the same place on the phylogenetic tree? What if a different m3 from the same taxon were used?

This research team has done great work in reviving research at a poorly sampled fossil site in a time/place that is of great importance in hominoid phylogeography. As a reward for their efforts, they've discovered an important and interesting specimen that may shed light of early crown hominoid evolution and dispersal. With an improved diagnosis and detailed comparisons to other catarrhine genera, this manuscript could have a major impact on the field. Is the specimen a hylobatid? I'm not convinced, and I suspect most readers won't be convinced by a single tooth. But it's a valid hypothesis that can be supported with evidence. Presented as such, it is worthy of publication. On the other hand, over-analyzing a single tooth to try to quash any doubt that readers might have will, in my opinion, have the opposite effect.

Decision letter (RSPB-2020-0271.R0)

13-Mar-2020

Dear Dr Gilbert:

I am writing to inform you that your manuscript RSPB-2020-0271 entitled "New Middle Miocene Ape from Ramnagar, india Fills Long-Standing Gaps in the Hominoid Fossil Record" has, in its current form, been rejected for publication in Proceedings B.

This action has been taken on the advice of referees, who have recommended that substantial revisions are necessary. With this in mind we would be happy to consider a resubmission, provided the comments of the referees are fully addressed.

However please note that this is not a provisional acceptance. As made clearer below, peer review has flagged up that more data and analysis are essential if publication is to happen.

The resubmission will be treated as a new manuscript. However, we will approach the same reviewers if they are available and it is deemed appropriate to do so by the Editor. Please note that resubmissions must be submitted within six months of the date of this email. In exceptional circumstances, extensions may be possible if agreed with the Editorial Office. Manuscripts submitted after this date will be automatically rejected.

Please find below the comments made by the referees, not including confidential reports to the Editor, which I hope you will find useful. If you do choose to resubmit your manuscript, please upload the following:

1) A 'response to referees' document including details of how you have responded to the comments, and the adjustments you have made.
2) A clean copy of the manuscript and one with 'tracked changes' indicating your 'response to referees' comments document.
3) Line numbers in your main document.

To upload a resubmitted manuscript, log into http://mc.manuscriptcentral.com/prsb and enter your Author Centre, where you will find your manuscript title listed under "Manuscripts with

Decisions." Under "Actions," click on "Create a Resubmission." Please be sure to indicate in your cover letter that it is a resubmission, and supply the previous reference number.

Sincerely,
Dr John Hutchinson, Editor
mailto: proceedingsb@royalsociety.org

Associate Editor
Board Member: 1
Comments to Author:
Thank you for your submission to Proc B.

As you will see, your paper has now been reviewed by two expert referees who have provided thorough reviews. Both referees recognise the quality and potential importance of your manuscript, but both also express important concerns that will need to be addressed in a revision.

Most notably, boosting the sample of extant hominids in the morphometric analysis and increased caution in the interpretation of the phylogenetic results are flagged up as key areas for improvement by Reviewer 1.

Reviewer 2 is even more insistent with respect to the need to increase the amount of comparative data in this manuscript in order to strengthen the scientific arguments. This referee identifies numerous well explained areas of potential improvement, and it will be critical that you carefully consider these comments before a revision might be considered acceptable for publication.

Reviewer(s)' Comments to Author:
Referee: 1

Comments to the Author(s)
The manuscript by Gilbert et al describing a new catarrhine lm3 from the Siwaliks is well written, clear, and of general interest. The describe a new fossil molar from the middle Miocene and based on comparative morphology, 2D morphometric analysis of cuspal positions, and a phylogenetic anlysis, suggest that it is closely related to extant hylobatids, and name a new genus and species based on the specimen.

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catarrhine molars are not particularly morphologically diagnostic in general. Especially based on single individuals. I'm not suggesting that the authors are wrong, merely the fact that one cannot be so sure given the specimen is a single, isolated tooth among a group that has been quite conservative in molar morphology.

Minor points:
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Lines 248-249. What does having an extensive fossil record have to do with morphological affinity? Having an extensive fossil record is related to taphonomy, paleoecology, tectonics, and the vagaries of the fossil record. I don't see what it has to do with the morphological and phylogenetic affinities of hylobatids. I suggest restructuring this sentence to clarify that these similar taxa just also happen to have an abundant fossil record. But these beg the question. To what else could they possibly show affinities? Especially since hominids were not included in the GM analysis and monkeys are pretty derived in molar morphology.

Line 251 change "more primitive dental features preserved" to "lack of dental synapomorphies with hylobatids"

Figure S2: It would be better to replace the "a", "b", etc. With taxonomic labels "VPL/RSP2", "propliopithecids", etc. So readers don't have to constantly look back and forth between the figure and the caption.

Referee: 2
Comments to the Author(s)
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1. I should start by saying that I fundamentally disagree with the idea of naming a new species based on a single tooth. I do NOT disagree that this probably is a new species, and the authors are well within ICZN guidelines in naming one. My concern is that, in doing so, this isolated tooth becomes the type specimen for what is likely to be an important taxon for interpreting ape evolution. Isolated teeth make terrible type specimens, and any comparisons to this species (including future allocations from this site) would be limited to samples that contain lower m3s. Worse, the well-documented variability in this tooth position means that even those comparisons could be highly misleading.

There are many fossil sites that have large samples of anthropoid primates: Rudabanya, Paşalar, Vallès-Penedès Basin, Maboko, Songhor, Rusinga, Fayum, Lufeng, etc. Every one of these sites has individual specimens that stand out as unique within their assemblages, and that could easily form the basis for a new species. There are also many sites with only one or two anthropoid teeth

that, by any reasonable estimation, differ from other known taxa. That researchers have NOT named new species in these cases speaks to the exercise of appropriate caution: both in recognizing the limits of our knowledge of variation and in creating a taxon for which there can be few meaningful comparisons. I suggest that these cautions are warranted, even at a site with only one anthropoid specimen that is geographically distant from other fossil anthropoid sites.

To be clear, I do not think this specimen does belong in any known taxon; I am convinced that it is something new, and the authors' logic in naming it is sound. I simply think that doing so is inadvisable. I also do not expect that my arguments will persuade the authors to change their minds, and I do NOT require a lengthy rebuttal to this point. The specimen is publishable even if my cautions are ignored. Ultimately, new, better-preserved specimens will someday be discovered that either supplant this one in everyone's comparative analyses, or (highly unlikely) demonstrate that this specimen is not a distinct species. In either case, basing a new species on an isolated tooth will then appear to have been overly hasty. We all field questions from students about why researchers would name a species from a holotype with little preserved anatomy. I feat thar this will become one more entry in that list, and I respect the authors too much to not point this out.

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3. Running a principal components analyses seems like a useful exploratory tool, and although the interpretation of these results seems overly confident (if each of your groups had a similar variance to the well-sampled hylobatids, would the Ramnagar tooth plot exclusively with hylobatids?) the plot supports the overall conclusions of the paper. I found the canonical variates analysis to be unconvincing and unnecessary, however. The reported cross validated results appear to be good because the data can easily classify the large sample of gibbons (in part because they are different, but also could be a function of radically different group sample sizes; see also below). Among fossils, cross validated results are only correct in 41% of cases: better than chance, but not very convincing, and apparently proconsulids cannot be correctly classified at all. Although the diagnosis was written by pooling large groups of species (e.g., propliopithecids, pliopithecids, dendropithecids), this analysis was done individually by family. If there is some hylobatid or crown hominoid aspect to m3 shape that differs from more primitive catarrhines, why not group the more primitive ones together here instead of analyzing at the family level? The results might give a sense of whether this derived/primitive distinction is valid in m3s, and if so where the Ramnagar tooth classifies. I found especially problematic that apparently group sample sizes were used to adjust the priors. To me, this is exactly the wrong way to address sample size differences. Adjusting the priors would be appropriate if, for example, all of the specimens came from a well-sampled fossil site where large numbers of fossils are typically distributed into taxa proportionately. In that case, a new fossil from that same site would most likely belong to the most abundant taxon, followed by the next most abundant, etc. The priors

could be adjusted to reflect this. Here, if I understand what the authors did, the priors were adjusted based on their sample proportions, meaning that the analysis is more likely to classify unknowns into the largest sample: hylobatids. This seriously undermines the impact of classifying the Ramnagar tooth in that group. In the end, I don't think canonical variates analysis/discriminant function analysis is necessary. The PCA plot makes the intended point; trying to reinforce this with one or more more problematic analyses is counterproductive.

4. Similarly, I do not see value in running a cladistic analysis on a single tooth. I realize this practice is becoming more common (e.g., Rossie and Hill, 2018), but I find the results unconvincing. Of the 272 characters in the cladistic analysis, only 7 can be scored for the Ramnagar tooth. The literature cited by the authors to support this practice does not constitute a strong justification: one study doesn't make any recommendation on use/exclusion of missing data; one found that a single fossil taxon (of four) had identical placement relative to the other taxa regardless of whether missing data were included; one argues for including specimens with missing data but, importantly, indicates that specimens with very few preserved characters result in weak tests of character congruence. All three studies are more than 17 years old. More current literature favors the addition of more taxa/characters even when that means excessive missing data, although the justification behind this recommendation is based on overall tree topology rather than how one OTU of interest is positioned. Nevertheless, these papers could be cited to better support the authors' methods. However, recent studies also provide rigorous assessments for the impact of the missing data. The authors should implement those assessments if they want to present a convincing argument. As with some of the multivariate analyses, I don't think a phylogenetic analysis of one tooth adds to this study. If one of the better-preserved fossil taxa were instead represented here by only an m3, would it land in the same place on the phylogenetic tree? What if a different m3 from the same taxon were used?

This research team has done great work in reviving research at a poorly sampled fossil site in a time/place that is of great importance in hominoid phylogeography. As a reward for their efforts, they've discovered an important and interesting specimen that may shed light of early crown hominoid evolution and dispersal. With an improved diagnosis and detailed comparisons to other catarrhine genera, this manuscript could have a major impact on the field. Is the specimen a hylobatid? I'm not convinced, and I suspect most readers won't be convinced by a single tooth. But it's a valid hypothesis that can be supported with evidence. Presented as such, it is worthy of publication. On the other hand, over-analyzing a single tooth to try to quash any doubt that readers might have will, in my opinion, have the opposite effect.

Author's Response to Decision Letter for (RSPB-2020-0271.R0)

See Appendix A.

RSPB-2020-1655.R0

Review form: Reviewer 2

Recommendation
Accept as is

Scientific importance: Is the manuscript an original and important contribution to its field?
Excellent

General interest: Is the paper of sufficient general interest?
Excellent

Quality of the paper: Is the overall quality of the paper suitable?
Excellent

Is the length of the paper justified?
Yes

Should the paper be seen by a specialist statistical reviewer?
No

Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.
No

It is a condition of publication that authors make their supporting data, code and materials available - either as supplementary material or hosted in an external repository. Please rate, if applicable, the supporting data on the following criteria.

Is it accessible?
Yes

Is it clear?
Yes

Is it adequate?
Yes

Do you have any ethical concerns with this paper?
No

Comments to the Author
I appreciate the lengths the authors have gone to in revising this manuscript. I think the result is a stronger paper. My remaining disagreements are philosophical in nature, as noted in my previous review, and should not prevent publication of this important research.

Decision letter (RSPB-2020-1655.R0)

06-Aug-2020

Dear Dr Gilbert

I am pleased to inform you that your manuscript RSPB-2020-1655 entitled "New Middle Miocene Ape from Ramnagar, india Fills Long-Standing Gaps in the Hominoid Fossil Record" has been accepted for publication in Proceedings B. Congratulations!!

The referee(s) have recommended publication, but also suggest some minor revisions to your manuscript. Therefore, I invite you to respond to the referee(s)' comments and revise your manuscript. Because the schedule for publication is very tight, it is a condition of publication that you submit the revised version of your manuscript within 7 days. If you do not think you will be able to meet this date please let us know.

To revise your manuscript, log into https://mc.manuscriptcentral.com/prsb and enter your Author Centre, where you will find your manuscript title listed under "Manuscripts with Decisions." Under "Actions," click on "Create a Revision." Your manuscript number has been appended to denote a revision. You will be unable to make your revisions on the originally submitted version of the manuscript. Instead, revise your manuscript and upload a new version through your Author Centre.

When submitting your revised manuscript, you will be able to respond to the comments made by the referee(s) and upload a file "Response to Referees". You can use this to document any changes you make to the original manuscript. We require a copy of the manuscript with revisions made since the previous version marked as 'tracked changes' to be included in the 'response to referees' document.

Before uploading your revised files please make sure that you have:

1) A text file of the manuscript (doc, txt, rtf or tex), including the references, tables (including captions) and figure captions. Please remove any tracked changes from the text before submission. PDF files are not an accepted format for the "Main Document".

2) A separate electronic file of each figure (tiff, EPS or print-quality PDF preferred). The format should be produced directly from original creation package, or original software format. PowerPoint files are not accepted.

3) Electronic supplementary material: this should be contained in a separate file and where possible, all ESM should be combined into a single file. All supplementary materials accompanying an accepted article will be treated as in their final form. They will be published alongside the paper on the journal website and posted on the online figshare repository. Files on figshare will be made available approximately one week before the accompanying article so that the supplementary material can be attributed a unique DOI.

Online supplementary material will also carry the title and description provided during submission, so please ensure these are accurate and informative. Note that the Royal Society will not edit or typeset supplementary material and it will be hosted as provided. Please ensure that the supplementary material includes the paper details (authors, title, journal name, article DOI). Your article DOI will be 10.1098/rspb.[paper ID in form xxxx.xxxx e.g. 10.1098/rspb.2016.0049].

4) A media summary: a short non-technical summary (up to 100 words) of the key findings/importance of your manuscript.

5) Data accessibility section and data citation
It is a condition of publication that data supporting your paper are made available either in the electronic supplementary material or through an appropriate repository (https://royalsociety.org/journals/authors/author-guidelines/#data).

In order to ensure effective and robust dissemination and appropriate credit to authors the dataset(s) used should be fully cited. To ensure archived data are available to readers, authors should include a 'data accessibility' section immediately after the acknowledgements section. This should list the database and accession number for all data from the article that has been made publicly available, for instance:
• DNA sequences: Genbank accessions F234391-F234402
• Phylogenetic data: TreeBASE accession number S9123
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as data, samples or models – can be accessed. This statement should be included in the data accessibility section.

If you wish to submit your data to Dryad (http://datadryad.org/) and have not already done so you can submit your data via this link http://datadryad.org/submit?journalID=RSPB&manu=(Document not available) which will take you to your unique entry in the Dryad repository. If you have already submitted your data to dryad you can make any necessary revisions to your dataset by following the above link. Please see https://royalsociety.org/journals/ethics-policies/data-sharing-mining/ for more details.

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Once again, thank you for submitting your manuscript to Proceedings B and I look forward to receiving your revision. If you have any questions at all, please do not hesitate to get in touch.

Sincerely,
Dr John Hutchinson, Editor
mailto: proceedingsb@royalsociety.org

Associate Editor
Board Member
Comments to Author:
Congratulations to the authors on a very interesting piece of work. I believe the paper is essentially ready for acceptance, although I do have a suggestion regarding the title. At present I believe the title is too general, and misses an opportunity to immediately indicate the affinities of the fossil to potential readers. Instead of only calling the fossil a 'new ape' in the title, I recommend the authors consider changing the title to:

"New Middle Miocene Ape (Primates: Stem-Hylobatidae) from Ramnagar, India Fills Major Gaps in the Hominoid Fossil Record"

I have also changed "long-standing" to "major" in the suggested title to shorten it somewhat.

Reviewer(s)' Comments to Author:

Referee: 2

Comments to the Author(s).
I appreciate the lengths the authors have gone to in revising this manuscript. I think the result is a stronger paper. My remaining disagreements are philosophical in nature, as noted in my previous review, and should not prevent publication of this important research.

Author's Response to Decision Letter for (RSPB-2020-1655.R0)

See Appendix B.

Decision letter (RSPB-2020-1655.R1)

13-Aug-2020

Dear Dr Gilbert

I am pleased to inform you that your manuscript entitled "New Middle Miocene Ape (Primates: Hylobatidae) from Ramnagar, India Fills Major Gaps in the Hominoid Fossil Record" has been accepted for publication in Proceedings B. Congratulations!!

You can expect to receive a proof of your article from our Production office in due course, please check your spam filter if you do not receive it. PLEASE NOTE: you will be given the exact page length of your paper which may be different from the estimation from Editorial and you may be asked to reduce your paper if it goes over the 10 page limit.

If you are likely to be away from e-mail contact please let us know. Due to rapid publication and an extremely tight schedule, if comments are not received, we may publish the paper as it stands.

If you have any queries regarding the production of your final article or the publication date please contact procb_proofs@royalsociety.org

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All supplementary materials accompanying an accepted article will be treated as in their final form. They will be published alongside the paper on the journal website and posted on the online figshare repository. Files on figshare will be made available approximately one week before the accompanying article so that the supplementary material can be attributed a unique DOI.

Thank you for your fine contribution. On behalf of the Editors of the Proceedings B, we look forward to your continued contributions to the Journal.

Sincerely,
Dr John Hutchinson
Editor, Proceedings B
mailto: proceedingsb@royalsociety.org

Associate Editor, Dr Daniel Field

Appendix A

Response to Reviewers

Dear Dr. Hutchinson,

Thank you to your associate editor (AE) and reviewers for the thoughtful and helpful reviews. On the following pages we provide the original comments by the AE and reviewers along with our responses to their comments in ***bold italics***.

Thanks again,

-Chris Gilbert (on behalf of all authors)

Christopher C. Gilbert, Ph. D.
Department of Anthropology
Hunter College, CUNY
New York Consortium in Evolutionary Primatology (NYCEP)
Research Associate, Division of Paleontology, American Museum of Natural History

Associate Editor
Board Member: 1
Comments to Author:
Thank you for your submission to Proc B.

As you will see, your paper has now been reviewed by two expert referees who have provided thorough reviews. Both referees recognise the quality and potential importance of your manuscript, but both also express important concerns that will need to be addressed in a revision.

Most notably, boosting the sample of extant hominids in the morphometric analysis and increased caution in the interpretation of the phylogenetic results are flagged up as key areas for improvement by Reviewer 1.

Reviewer 2 is even more insistent with respect to the need to increase the amount of comparative data in this manuscript in order to strengthen the scientific arguments. This referee identifies numerous well explained areas of potential improvement, and it will be critical that you carefully consider these comments before a revision might be considered acceptable for publication.

Reviewer(s)' Comments to Author:

Referee: 1

Comments to the Author(s)
The manuscript by Gilbert et al describing a new catarrhine lm3 from the Siwaliks is well written, clear, and of general interest. The describe a new fossil molar from the middle Miocene and based on comparative morphology, 2D morphometric analysis of cuspal positions, and a phylogenetic anlysis, suggest that it is closely related to extant hylobatids, and name a new genus and species based on the specimen.

First off, I normally wouldn't comment on a name, but this time I can't help it "Coronapithecus" seems particularly timely given COVID 19. Personally, I don't like names based on phylogenetic hypotheses as these are often revised (e.g., Bugtilemur, Pliobates, Prohylobates, etc.). Just something to think about.

Yes, this is a good point. The name was chosen and the MS written before COVID-19 was discovered and became the global menace that it now is. We recognize this and are very sensitive to it as well. We have changed the new genus name to* Kapi *in recognition of the Hindi name for "ape" in the general sense.

Another small point, there is no photograph of the specimen. The digital surface models are nice, but actual photographs would also be very helpful. Perhaps these could be added to figure 2.

We have included photographs in the Supplementary Information Figure S2. As you will see, the specimen itself is very dark, with reflective surfaces that make it not very photogenic! In any case, it is now documented, as suggested, in the comparative figure.

A more important point is the lack of extant homininds in the morphometric analysis greatly weaken its effectiveness. While it does appear that extant hylobatids are morphologically distinct from the stem catarrhines sampled, it is unclear how distinctive these both are from extant hominids. Something this paper assumes, and relies on, but does not demonstrate. Samples, roughly equivalent in size to those for the hylobatids presented here, would greatly help with understanding the significance of the placement of Coronapithecus, Yuanmopithecus, and Bunopithecus.

While we strongly feel that extant hominids are extraneous to the discussion (VPL/RSP2 is morphologically distinct from hominids in a number of ways, perhaps most importantly in its small size), we have now included as much extant hominid data as possible in the analyses as well. Unfortunately, it is impossible to collect additional data right now as many museum collections are closed, but we believe the sample sizes included are large enough to make our point (n= 10 Pongo, n=31 Gorilla, and n= 15 Pan). Results suggest that hominids largely occupy the shape space between the stem taxa and hylobatids, overlapping both groups in principal components space. Kapi falls exclusively in crown hominoid PC space and while in the area of overlap between hylobatids and some chimps, it is clearly closest to the center of the hylobatid distribution. Bunopithecus is exclusively within hylobatid PC space. Yuanmoupithecus is within the small area of overlap between hominids, hylobatids, and stem taxa, although much closer to the crown taxa. The phenetic NJ analyses confirm these observations, recovering crown hominoids, with Kapi placed as the sister taxon to hylobatids and Yuanmoupithecus as a stem hominoid.

A quick scan of the characters used in the phylogenetic analysis suggests that only 12 or 13 are available on VPL/RSP2. This suggests caution in interpreting the results.

This is a fair point, but we have to proceed with the data currently available. We have tried to be more cautious in our interpretations in the Discussion…see page 14 and thereafter. We were able to score 16 characters for Kapi. See also Supplementary Material pages 10-12

These last 2 points taken together, in my opinion recommend greater circumspection of the results than are currently provided in the discussion. Especially given that non-cercopithecoid catarrhine molars are not particularly morphologically diagnostic in general. Especially based on single individuals. I'm not suggesting that the authors are wrong, merely the fact that one cannot be so sure given the specimen is a single, isolated tooth among a group that has been quite conservative in molar morphology.

We have tried to be more cautious throughout the discussion (see page 14 and thereafter), but given that the morphometric and cladistic results both suggest that our specimen AND the widely accepted **Yuanmoupithecus** *are hominoids and/or likely stem hylobatids, we have as much confidence as one can have with the material at hand. We wish we had more specimens and more information, and we try to make this clearer throughout. However, we think the analyses presented offer strong argument for its likely affinities given the available evidence, and our analyses in fact suggest that non-cercopithecoid catarrhine specimens can be diagnosed from each other on the basis of dental features, at least in terms of many crown vs. stem specimens.*

Minor points:

Line 56, insert "right" before "lower third molar"

Changed as suggested.

Line 88, change "anterior" to "mesial"

Changed as suggested.

Lines 244-246, if hylobatids evolved from a form morphologically similar to dendropithecids or proconsulids, are you suggesting that dendropiths and proconsulids approximate the hominoid morphotype? Please clarify.

Yes and no. We are suggesting that dendropithecids (sensu lato) and proconsulids (sensu lato) may approximate the crown hominoid <u>*dental*</u> *morphotype. We have tried to be more specific about this, as suggested…see Pages 14-15. We are not suggesting that dendropithecids and proconsulids necessarily approximate the crown hominoid morphotype beyond anything other than the dentition. But since many taxa are known from only fragmentary maxilla-dental or mandibular dental remains, it is quite possible that very early stem hylobatids are represented among some of the dental material included within one of these broad radiations.*

Lines 248-249. What does having an extensive fossil record have to do with morphological affinity? Having an extensive fossil record is related to taphonomy, paleoecology, tectonics, and the vagaries of the fossil record. I don't see what it has to do with the morphological and phylogenetic affinities of hylobatids. I suggest restructuring this sentence to clarify that these similar taxa just also happen to have an abundant fossil record. But these beg the question. To what else could they possibly show affinities? Especially since hominids were not included in the GM analysis and monkeys are pretty derived in molar morphology.

We have re-written these lines, as suggested, and added hominids the analyses. Pages 14-15 now read "Judging by the affinities of both **Kapi** *and* **Yuanmoupithecus** *in our analyses, it seems most likely that hylobatids evolved from an African taxon dentally similar to dendropithecids or proconsulids, the two advanced catarrhine groups outside of crown hominoids with specimens closely approaching hylobatids in the multivariate and phylogenetic analyses. Therefore, it is entirely possible that early stem hylobatids are currently represented by some of the fossil material in the extensive East African early Miocene record, but cannot yet be distinguished based on the lack of clear hylobatid dental synapomorphies among these fragmentary taxa."*

Line 251 change "more primitive dental features preserved" to "lack of dental synapomorphies with hylobatids"

Changed as suggested.

Figure S2: It would be better to replace the "a", "b", etc. With taxonomic labels "VPL/RSP2", "propliopithecids", etc. So readers don't have to constantly look back and forth between the figure and the caption.

Changed as suggested.

Referee: 2

Comments to the Author(s)
This is an important manuscript describing a new anthropoid tooth from a fossil site where few anthropoids have previously been reported. Although numerous hominoid fossils are known from other Siwaliks sites in the region, this specimen cannot be readily accommodated within any known genus. Hence, the authors propose to erect a new genus and species for this specimen, and their analyses suggest to them that the tooth represents

the earliest known member of the hylobatid clade. The specimen, geological context, description/diagnosis, and some of the analyses will be very important to understanding the evolution and distribution of catarrhines in the middle Miocene. However, I have concerns regarding some components of this manuscript. These are detailed below, with additional comments in the annotated pdf. I'd be happy to review another version of this manuscript.

1. I should start by saying that I fundamentally disagree with the idea of naming a new species based on a single tooth. I do NOT disagree that this probably is a new species, and the authors are well within ICZN guidelines in naming one. My concern is that, in doing so, this isolated tooth becomes the type specimen for what is likely to be an important taxon for interpreting ape evolution. Isolated teeth make terrible type specimens, and any comparisons to this species (including future allocations from this site) would be limited to samples that contain lower m3s. Worse, the well-documented variability in this tooth position means that even those comparisons could be highly misleading.

There are many fossil sites that have large samples of anthropoid primates: Rudabanya, Paşalar, Vallès-Penedès Basin, Maboko, Songhor, Rusinga, Fayum, Lufeng, etc. Every one of these sites has individual specimens that stand out as unique within their assemblages, and that could easily form the basis for a new species. There are also many sites with only one or two anthropoid teeth that, by any reasonable estimation, differ from other known taxa. That researchers have NOT named new species in these cases speaks to the exercise of appropriate caution: both in recognizing the limits of our knowledge of variation and in creating a taxon for which there can be few meaningful comparisons. I suggest that these cautions are warranted, even at a site with only one anthropoid specimen that is geographically distant from other fossil anthropoid sites.

To be clear, I do not think this specimen does belong in any known taxon; I am convinced that it is something new, and the authors' logic in naming it is sound. I simply think that doing so is inadvisable. I also do not expect that my arguments will persuade the authors to change their minds, and I do NOT require a lengthy rebuttal to this point. The specimen is publishable even if my cautions are ignored. Ultimately, new, better-preserved specimens will someday be discovered that either supplant this one in everyone's comparative analyses, or (highly unlikely) demonstrate that this specimen is not a distinct species. In either case, basing a new species on an isolated tooth will then appear to have been overly hasty. We all field questions from students about why researchers would name a species from a holotype with little preserved anatomy. I feat thar this will become one more entry in that list, and I respect the authors too much to not point this out.

*We thank the reviewer for the kind comments and appreciate the sound arguments being made. We wrestled with the decision as well and we agree that a single tooth is not ideal for naming a new taxon. However, the other side of the coin is that new fossil taxa are routinely named on the basis of isolated dental material, and many examples can be found in the primate literature. For example, the earliest platyrrhine monkey, **Perupithecus**, was recently named on the basis of a single upper molar and published in **Nature**. Many early fossil euprimates have been named on the basis of a single dental specimen. Philosophically, in our opinion, if something is distinct from all other known genera and species, then it should be recognized as a new taxon. It sounds as if both reviewers, as well as ourselves, all agree that this specimen is something different than is currently known. If that were true of any living population, it would be given a new name with very little reservation. Why should it be different with the fossil record? We can also all agree that VPL/RSP2 is not an ideal type specimen, and we certainly wish we had additional material. However, there is research suggesting that anthropoid M_3s, while more variable than M_1s and M_2s, evolve more quickly, are more distinctive between closely related taxa, and are therefore perhaps more taxonomically useful than M_1s and M_2s (Mongle, 2019; this is also supported by the M_1 analysis which documents much less taxonomic separation). We hope that with additional fieldwork, we will find additional specimens. But one never knows if additional specimens will ever be found…this is the first one found in almost 100 years at Ramnagar. And by naming it, at least we all have a common name to refer to this specimen and the unique population that we all agree it most likely represents. If we do not name it, then there is no common name to refer to and the specimen becomes more likely to be lost in the shuffle. For all these reasons, we greatly appreciate the reviewers' points and agree with many of them, but in the end, we think it is better to name the taxon and offer any emended diagnoses as necessary in the future.*

2. The generic diagnosis and description are insufficient by a wide margin to define this taxon. I do not mean insufficient according to ICZN guidelines (which require only the weakest criteria to qualify for a valid name), but insufficient to effectively allow other researchers to properly differentiate this specimen from other taxa. In particular, lumping together propliopithecids, pliopithecids, and dendropithecids – each of which is a highly variable group, and together do not constitute any set of primitive or derived m3 traits against which this specimen is compared – provides no clear differentiation from genera within these groups. Is there some reference that provides diagnostic features of the m3 in any of these families or of the three families combined? The general approach of 'here are some features in this specimen that are typically not found in these other groups' seems especially weak; likewise, saying it differs from "most" members of some higher-order taxon. Material in the supplementary document does not add much in this regard beyond what is said in the main text. There are a number of genera against which this specimen should be individually compared. Doing so will be a lengthy process and much of that material should probably go in supplementary information. Nevertheless, the

authors are making extraordinary claims with substantial implications; they should provide rigorous and detailed comparisons to support those claims. In the end, with only an m3 to compare, individual comparisons cannot be too lengthy, but they should be made nonetheless.

We have greatly expanded our comparisons in the Supplementary Material (where there is more room) as suggested….please see Supplementary Material pages 12-20

3. Running a principal components analyses seems like a useful exploratory tool, and although the interpretation of these results seems overly confident (if each of your groups had a similar variance to the well-sampled hylobatids, would the Ramnagar tooth plot exclusively with hylobatids?) the plot supports the overall conclusions of the paper. I found the canonical variates analysis to be unconvincing and unnecessary, however. The reported cross validated results appear to be good because the data can easily classify the large sample of gibbons (in part because they are different, but also could be a function of radically different group sample sizes; see also below). Among fossils, cross validated results are only correct in 41% of cases: better than chance, but not very convincing, and apparently proconsulids cannot be correctly classified at all. Although the diagnosis was written by pooling large groups of species (e.g., propliopithecids, pliopithecids, dendropithecids), this analysis was done individually by family. If there is some hylobatid or crown hominoid aspect to m3 shape that differs from more primitive catarrhines, why not group the more primitive ones together here instead of analyzing at the family level? The results might give a sense of whether this derived/primitive distinction is valid in m3s, and if so where the Ramnagar tooth classifies. I found especially problematic that apparently group sample sizes were used to adjust the priors. To me, this is exactly the wrong way to address sample size differences. Adjusting the priors would be appropriate if, for example, all of the specimens came from a well-sampled fossil site where large numbers of fossils are typically distributed into taxa proportionately. In that case, a new fossil from that same site would most likely belong to the most abundant taxon, followed by the next most abundant, etc. The priors could be adjusted to reflect this. Here, if I understand what the authors did, the priors were adjusted based on their sample proportions, meaning that the analysis is more likely to classify unknowns into the largest sample: hylobatids. This seriously undermines the impact of classifying the Ramnagar tooth in that group. In the end, I don't think canonical variates analysis/discriminant function analysis is necessary. The PCA plot makes the intended point; trying to reinforce this with one or more more problematic analyses is counterproductive.

Thank you for these important points. We have first increased the sample of extant crown hominoids in the analyses by including hominids. As far as the disproportional

variance in the hylobatid sample vs. the rest of the groups, we would be more concerned about this issue if hylobatids were spanning a vast amount of PC space (particularly PC 1). And if examined at the level that the reviewer is suggesting, i.e., crown hominoids vs. likely stem hominoids/catarrhines, the difference in variance is less between these two groups and VPL/RSP2 still falls exclusively in crown hominoid space. For the DFAs, the reviewer points out a problem with taking the group sizes into account in the prior probabilities, namely that it biases the unknowns towards the larger group a priori, in this case hylobatids or crown taxa. We acknowledge the mistake, and just to be sure, we ran the original analysis assuming equal group sizes, with the results being very similar, just with lower overall classification values (86.1% correctly classified with 78.7% correct during cross-validation; VPL/RSP2 was still classified as a hylobatid with 71.1% probability, no non-hylobatids were ever misclassified as hylobatids). Regardless, the new analyses follow the reviewer's advice and more simply and conservatively present the PCA only. We agree that it makes the point and rests upon fewer a priori assumptions.

4. Similarly, I do not see value in running a cladistic analysis on a single tooth. I realize this practice is becoming more common (e.g., Rossie and Hill, 2018), but I find the results unconvincing. Of the 272 characters in the cladistic analysis, only 7 can be scored for the Ramnagar tooth. The literature cited by the authors to support this practice does not constitute a strong justification: one study doesn't make any recommendation on use/exclusion of missing data; one found that a single fossil taxon (of four) had identical placement relative to the other taxa regardless of whether missing data were included; one argues for including specimens with missing data but, importantly, indicates that specimens with very few preserved characters result in weak tests of character congruence. All three studies are more than 17 years old. More current literature favors the addition of more taxa/characters even when that means excessive missing data, although the justification behind this recommendation is based on overall tree topology rather than how one OTU of interest is positioned. Nevertheless, these papers could be cited to better support the authors' methods. However, recent studies also provide rigorous assessments for the impact of the missing data. The authors should implement those assessments if they want to present a convincing argument. As with some of the multivariate analyses, I don't think a phylogenetic analysis of one tooth adds to this study. If one of the better-preserved fossil taxa were instead represented here by only an m3, would it land in the same place on the phylogenetic tree? What if a different m3 from the same taxon were used?

Many of the citations provided are more recent than suggested, please see Refs 73-78 and now refs 90-91 in the Supplementary Material. The recent Pattinson et al. (2015) study and the recent Asher et al. (2019) and Koch and Parry (2020) papers reaffirm the older studies as well (and the older studies are still heavily cited within these newer papers…just because they are 20 years old doesn't make them any less true). The types of experiments being suggested are of course very interesting, but beyond the scope of

this paper. Overall, we appreciate the reviewer's concern that an analysis on a single tooth is not ideal. However, the cited studies, particularly the Pattinson et al. (2015) study, performed similar experiments to what the reviewer is suggesting. They found that even fragmentary specimens were likely to be placed accurately within the primate tree at broad levels, significantly greater than chance. If we were claiming detailed knowledge of the relationships within fossil and extant Hylobatidae on the basis of isolated specimens of **Yuanmoupithecus** *and* **Kapi***, we would agree that this is probably beyond the data's ability to say. We now say as much in the first 2 paragraphs of the Discussion, on pages 14-15:* **"The phylogenetic placement of these two taxa within hominoids, however, is admittedly difficult to assess in the absence of additional material."** *But to assess the phylogenetic position of fossil taxa relative to higher taxonomic groups, even fragmentary specimens can do this with accuracy (e.g., Pattinson et al., 2015). There is a higher chance of error, of course, in the absence of more data, but we feel like it's important to provide a cladistic assessment of the characters available in addition to the morphometric (largely phenetic) assessment. We note that our cladistic analysis is consistent with the morphometric NJ cluster analysis in that both* **Kapi** *and* **Yuanmoupithecus** *are both reconstructed as crown hominoids at the very least. To address the reviewers' concerns, we have further pointed out the reasonable level of uncertainty at the beginning of the Discussion (see pages 14-15), and in the Methods section of the Supplementary Material. We were able to score 16 characters for VPL/RSP2, and we wish there were additional characters to score. But nothing here is out of the ordinary for a cladistic analysis, and the taxa don't appear to be acting as wildcards. You have to go with the data that are available, even if not very complete, and studies show that adding fossil data is typically more beneficial than not. If readers choose to discount the phylogenetic analysis based on their assessment of the assumptions and data that are clearly presented, that is their choice, but we feel like the analysis should be presented. Readers and future studies should be able to evaluate the resulting tree(s) as a hypothesis given the available evidence at this time.*

This research team has done great work in reviving research at a poorly sampled fossil site in a time/place that is of great importance in hominoid phylogeography. As a reward for their efforts, they've discovered an important and interesting specimen that may shed light of early crown hominoid evolution and dispersal. With an improved diagnosis and detailed comparisons to other catarrhine genera, this manuscript could have a major impact on the field. Is the specimen a hylobatid? I'm not convinced, and I suspect most readers won't be convinced by a single tooth. But it's a valid hypothesis that can be supported with evidence. Presented as such, it is worthy of publication. On the other hand, over-analyzing a single tooth to try to quash any doubt that readers might have will, in my opinion, have the opposite effect.

Thank you again for the helpful review. We hope that you find the revised version more convincing!

We accepted all small editorial fixes that the reviewer made on the annotated PDF.

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Department of Anthropology

Response to Reviewers

Dear Dr. Hutchinson,

Thank you, again, to your associate editor (AE) and reviewers for the thoughtful and helpful reviews. On the following pages we provide the original comments by the AE and reviewers along with our responses to their comments in ***bold italics***.

Thanks again,

-Chris Gilbert (on behalf of all authors)

Christopher C. Gilbert, Ph. D.
Department of Anthropology
Hunter College, CUNY
New York Consortium in Evolutionary Primatology (NYCEP)
Research Associate, Division of Paleontology, American Museum of Natural History

Associate Editor
Board Member
Comments to Author:
Congratulations to the authors on a very interesting piece of work. I believe the paper is essentially ready for acceptance, although I do have a suggestion regarding the title. At present I believe the title is too general, and misses an opportunity to immediately indicate the affinities of the fossil to potential readers. Instead of only calling the fossil a 'new ape' in the title, I recommend the authors consider changing the title to:

"New Middle Miocene Ape (Primates: Stem-Hylobatidae) from Ramnagar, India Fills Major Gaps in the Hominoid Fossil Record"

I have also changed "long-standing" to "major" in the suggested title to shorten it somewhat.

Thank you for the kind words! We have changed the title, as suggested, to: "New Middle Miocene Ape (Primates: Hylobatidae) from Ramnagar, India Fills Major Gaps in the Hominoid Fossil Record"

Reviewer(s)' Comments to Author:

Referee: 2

Comments to the Author(s).
I appreciate the lengths the authors have gone to in revising this manuscript. I think the result is a stronger paper. My remaining disagreements are philosophical in nature, as noted in my previous review, and should not prevent publication of this important research.

Thank you, again, for the helpful review.