nature portfolio

Peer Review File

Denisovans from southwestern China and their subsistence strategies

Corresponding Author: Professor Hao Li

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This file contains all reviewer reports in order by version, followed by all author rebuttals in order by version.

Version 0:

Reviewer comments:

Referee #1

(Remarks to the Author)
In this manuscript, Li et al. report on Denisovan fossils and stone/bone artefacts discovered in Bianfu Cave in Yunnan, southwest China. Using uranium series and optically stimulated luminescence dating, the age of hominin activities is constrained to 190–68 ka. This interesting discovery may potentially extend the temporal and spatial distribution of Denisovans, providing new material for understanding their morphological diversity, lithic/bone technology, and survival strategies. However, the study has the following flaws:
1, Assigning artefacts to their makers—particularly to a specific hominin species—within archaeological sites is usually a challenging task that has long perplexed archaeologists and palaeoanthropologists. I note that the hominin fossils from the Bianfu Cave are found only in layers 7 and 9, whereas layers 10-12 underlying and layers 3-6 overlying them contain only artefacts and animal bone fossils. The author's assertion that layers 3-12 constitute entirely Denisovan cultural unit requires caution. In China, particularly in the southern regions, the pebble industry represented by core-flake artefacts persisted throughout most of the Pleistocene. The author's confident assertion that Denisovans exclusively occupied this site for 122 ka, in the absence of sufficient archaeological and palaeoanthropological evidence, is open to question.
2, The artefacts recovered at this site are not particularly abundant, with tools constituting a notably small proportion. Is it possible that this cave site served as a place of tool making rather than using? So, the artifact assemblage from this single site may not be representative of the real toolkit of the Denisovans (if it is).
3, The authors argue that “the inhabitants of Bianfu Cave practised specialised hunting of large-bodied prey” lacks sufficient zooarchaeological and taphonomical evidence. The fragmented animal bones discovered at the site may not be the result of hominin processing only, carnivores and rodents frequently act as transporters of cave fossil accumulations. The authors have not adequately considered this possibility.
4, The data analysis in this manuscript is flawed. In the three-dimensional geometrical morphology analysis of M2 (c and d), when conducting principal component analyses, the comparison specimens included two Denisovan teeth and three East Asian Late Middle Pleistocene Archaic Homo teeth. However, during the between-group principal component analyses, the comparison specimens comprised five East Asian Late Middle Pleistocene Archaic Homo teeth, with no Denisovan tooth sample present. The authors should provide a detailed explanation for the discrepancy in the selection of comparison specimens between the two analytical methods and include the corresponding missing specimens in both analyses.
5, The hominin dental fossils from the Bianfu Cave exhibit marked differences from known Denisovans, both in size and in the characteristics of the tooth crowns. The authors nevertheless assigned these dental remains, along with two cranial fragments and one partial radius, to the Denisovan population. Morphologically, this identification lacks sufficient evidence. Thus, palaeoproteomic evidence is crucial for allocating these hominin fossils to the Denisovan lineage. However, the protein evidence cited in this paper originates from Reference 10: Rao, H., et al. A Denisovan radius from Southwest China: ancient proteins reveal Denisovan post-cranial morphology and population dispersal. Cross citation. The authors are requested to provide detailed clarification regarding which specific hominin specimens underwent palaeoproteomic analysis and can be unequivocally identified to the Denisovans.
6, The section from lines 146-153 is a clear repeat of the content from lines 185-191.
7, In Extended Data Figure 7, P3 should be changed to P4.

(Remarks on code availability)

Referee #2

(Remarks to the Author)
Main contributions of the study:
This study presents and describes new Pleistocene human remains that the authors attribute to the Denisovan lineage — a taxon initially recognized on a genetic basis, but with largely unknown morphology. The discovery of these fossils in Yunnan Province helps to fill a gap between two regions — Tibet and Laos — which have recently yielded human remains assigned to this archaic group.
Among the seven human remains presented, the four teeth are particularly noteworthy due to their excellent state of preservation, which allowed the authors to conduct multiple descriptive and comparative analyses. The results of these analyses enhance our understanding of the morphometric variability of this taxon.
Moreover, the presence of these paleoanthropological remains within archaeological layers containing lithic and anthropogenically modified faunal material, as well as palynological archives, allowed the authors to discuss the technical behaviors, subsistence strategies, and paleoenvironmental context of the humans who occupied the site.
This study is therefore significant because it integrates multiple disciplines to document aspects of this extinct human lineage that remain poorly known: phenotype, technical behaviors, and subsistence strategies. Nevertheless, some adjustments are warranted prior to publication.
Due to our expertise, we focused mostly on the general parts of the paper, as well as the morphological analyses, and let others evaluate the dating and palynology.

Main Revisions :
• The first and main issue we identified concerns the authors' "exclusive" attribution of the archaeological sequence to Denisovans. Indeed, considering the taxonomic diversity characterizing Asia during the Late Pleistocene (H. erectus, H. sapiens, Denisovans, etc.), it seems highly imprudent to assert that the artifacts from layers 12–10, 8, and 6–3 were produced by Denisovan human groups. Furthermore, and for the same reasons regarding the known anthropological diversity in this region during the Pleistocene, we recommend that the authors exercise greater caution when claiming that Denisovans are responsible for the artifacts found in layers 7 and 9, given that the Bianfu human fossils have not undergone a detailed taphonomic and spatial study aimed at documenting the origin of their accumulation within these layers. Consequently, while assuming that the presence of these human remains in the cave does indeed have an anthropogenic origin, the authors should keep in mind that we are currently unable to rule out the hypothesis that other hominins, such as late H. erectus or H. sapiens, may have been responsible for the accumulation of Denisovan bodies or body parts in the cave. In other words, we believe it is necessary to question whether the individuals discovered at Bianfu were indeed the producers and hunters responsible for the accumulation of anthropogenically modified material at the site. We also feel that the authors need to provide more details on the taphonomy of the faunal assemblage, showing whether the main agent of accumulation were hominins or carnivores.
We acknowledge that, given the discoveries and results obtained, the most parsimonious hypothesis remains the Denisovan attribution to the artifacts in layers 7 and 9; however, it would be appropriate to emphasize that alternative possibilities exist and to introduce more conditional language in statements regarding these associations.
Moreover, we consider that the chronological range indicated by the authors for the Denisovan occupations is excessively broad given the different results obtained (Bayesian analysis, Line 130-131: 167-161 ka and 142-134 ka) and our previous remarks. Therefore, we recommend that the authors reconsider the article's title.

• Connected to this previous issue: the authors analyze the faunal and lithic material from Layers 3-12 together, despite these layers spanning up to 120 ka in time. We assume this is due to small sample sizes in some of the layers, not allowing reliable statistical analyses. Despite this, we think that it is necessary to present separate analyses for each layer, and only analyze them as one assemblage if it could be shown that there are no technological (and faunal) differences between the different horizons.

• In the analyses of EDJ morphology, a much smaller sample was used than in the metrical analyses of crown size and the comparative morphological analyses. Especially missing from the EDJ analyses are samples of earlier Neanderthals (e.g. Sima de los Huesos) and European Middle Pleistocene material (especially Mauer, as the holotype of H. heidelbergensis). Similarly, both the fossil and recent H. sapiens comparative sample is very small – especially the latter should be expanded significantly.

• Regarding the section describing the human remains, age-at-death estimates for the fossils are needed. Please at least provide them in the Supplementary Information.

• The section presenting the anthropogenically modified material lacks one or two sentences discussing the density and concentration of the remains across the different levels of the stratigraphic sequence.

• A correction needs to be made in at least one sentence of the section dealing with traces of anthropogenic origin recorded on the faunal remains (details are provided in the comments on the document).

• In the Supplementary Information, the section entitled "Technological behavior at Bianfu Cave" contains a lot of information

(pages 30 and 31) without bibliographic references. Please provide the appropriate references.

Various smaller issues:

Line 138-139: why is the lateralization of the teeth not reported here?

Line 151: this wording is not really appropriate: 'later Homo' includes Neanderthals, and Neanderthal lower P4s frequently exhibit asymmetric crown outlines.

Line 175-76: "with a protruded distolingual corner" and "non-buccally extended talonid of P4" are the same trait, aren't they?

Line 223: "knapping scars" these are usually referred to as percussion scars or notches

Line 254: "long term occupations" – isn't the density/amount of lithic material pretty limited for assumed long term occupations? Less than 1500 lithics would not be seen as indicative of long term or intense occupation in Europe or Northern Asia
Line 277: some more references to bone tool use in archaic humans would make sense here, e.g. Soressi et al., 2013; Tartar and Costamagno, 2016; Baumann et al., 2020, 2023

Line 384: Reference 47 is all messed up.

Fig 1c: the orientation of this images is unclear, is it a top-down (zenithal) view or a frontal view? Furthermore, a scale bar is missing. I also don't understand what the North arrow, with 330degrees is supposed to mean.

Fig 3, Line 428: "show the pulp cavity. " – there is no pulp cavity in sight anywhere

Supplementary info:

Line 444: italicize H. erectus

Line 452: italicize Homo

Line 503: italicize Australopithecus

Line 512: "only present in 90.5% of early Neanderthals" – present in 9 out of 10 is very frequent, not "only"

(Remarks on code availability)

Referee #3

(Remarks to the Author)
I co-reviewed this manuscript with one of the reviewers who provided the listed reports.

(Remarks on code availability)

Referee #4

(Remarks to the Author)
The manuscript presents a systematic excavation and study of the Bianfu Cave site. Through comprehensive analyses in chronology, lithic assemblage , human skeletal remains, faunal composition, and palynology, it provides a holistic understanding of the living environment, lithic technology, and hunting strategies of the Denisovans at this in-situ burial site. Morphologically, dental morphology of the Bianfu Cave hominins supports their attribution to a distinct Denisovan group, deepening our knowledge of Denisovan morphological characteristics. Moreover, the geographical location of Bianfu Cave significantly expands the known distribution range of Denisovans in Asia. This study represents a breakthrough discovery with important implications for Denisovan research. I recommend its publication in Nature. However, before publication, I have several comments and suggestions:

Comments and Suggestions:
1.Based on the OSL and U-series ages alongside the stratigraphic sequence, there appears to be a hiatus of approximately 50 ka between Layers 4 and 5, with Layer 4 itself being only 4–10 cm thick. The Bayesian model merely minimizes this gap within a plausible range. Therefore, human occupation at Bianfu Cave was likely discontinuous.
2.Human fossils are found in the cultural layers of Layers 7 and 9, all attributed to Denisovans in this study. Given the relatively continuous chronology from Layer 12 to Layer 5, these layers can be considered Denisovan cultural layers. However, with a 50 ka hiatus between Layers 4 and 5, and with only lithic remains in Layers 3 and 4 dating to around 70 ka,

can the human presence in Layers 3 and 4 be definitively identified as Denisovan?
3.Was the environment that supported large mammals and was suitable for human hunting a conifer-dominated forest environment or a forest-steppe environment? In other words, was the primary setting for the life of the Bianfu Cave humans a forest environment or a forest-steppe habitats?
4.Since the study offers a systematic investigation of the Denisovan site at Bianfu Cave, the authors should provide a comprehensive schematic diagram that visually integrates key elements such as the local geomorphology, vegetation types, faunal composition, lithic (and bone) technology, and the Denisovan population. This would be a distinctive highlight, as such integrated representation has never been achieved for previous Denisovan sites.

Minor Issues:
5.Fig. 1b: The distance scale bar is not clear in the transparent parts. River labels should be in italics and aligned along the river direction. Fig. 1c: Add a scale bar at the cave entrance location.
6.Fig. 2 (right panel): In the distribution probability plot for unmodeled ages, visually distinguish between OSL and U-series dates. Although they are labeled differently on the left, a visual distinction on the right would be more immediate. Also, please ensure the stratigraphic legend icons at the bottom of the figure are of consistent size.
7.Supplementary Materials: please provide a broader-view photograph to show the geomorphological context around Bianfu Cave. The current photos make it difficult to discern the site's topographic setting—particularly the view from the cave entrance: is the area open or steeply sloped? Is there an forest-steppe landscape?
8.The OSL age for the Layer 10 is about 40 ka younger than the U-series age for the Layer 9. While it is understandable that the OSL age might be underestimated (and the U-series date for Layer 9 appears reliable), please explain such a significant underestimation in the OSL dating.
9.What is the approximate spatial extent of human activity within the Bianfu Cave? This does not seem to be described in the manuscript.

(Remarks on code availability)

Referee #5

(Remarks to the Author)
A. This paper is a straightforward site report of a newly excavated site in China containing Denisovan fossils and associated archaeological materials spanning over 100 thousand years. (B) This new discovery is clearly an important one, albeit from a site that has been disturbed by quarrying activities, and it is of interest to a wide scientific audience. The stated purpose of the paper is to show Denisovans thriving in a mild and stable environment (compared with Baishiya Karst Cave on the Tibetan Plateau) for a long time.

C. The pollen data show a forested environment with adjacent open areas, while the fauna are quite diverse, including species as diverse as bears and rhinos. The time interval contains most of MIS 6 through MIS 4, thus two very cold stages, as well as the variable MIS 5. How exactly local environments are responding to the global climate changes is not articulated very well here, and how exactly the archaeological evidence articulates with these changes is also not that well developed (presumably because a lot of the paper is dedicated to the chronology).

F. I suggest the following changes in order to make this a better and more convincing article that goes beyond a mere description of data:

1. Add a summary chart not unlike Fig. 2 from the main article, but that, instead of focusing on the Bayesian analysis, juxtaposes the sequence of ages with marine isotope curves, speleothem records, environmental magnetism, pollen, artefact density, and any other summary data that shows the exact environmental context of the human occupation.
2. Provide a more explicit engagement with the notion of continuity and the intensity of occupation, as well as the potential site function. Here, I stress the importance of explaining the uneven spread of the lithics across different levels and the correlation of different types of lithics with the faunal assemblage.
3. Related to 2., the fauna seem to be dominated by low-utility anatomical parts, which the authors (in the supplementary file) attribute to the smashing of the long bones for marrow extraction. Since Marean and Kim's seminal paper in 1998, these claims are made based on long bone refittings, whereas here this is simply asserted. It is true that cut marks are present on some of the bones, but the faunal analysis does not go into what kind of carcass processing took place at the site. I suggest adding information about the location and distribution of cut marks and an interpretation of what this says about carcass processing at the site.
4. Introduce a spatial analysis or at least explain how the site was used at different times during its long occupation. It is unlikely that people would have used it in exactly the same way over more than 100 thousand years. While I understand that the available deposits are not the ideal ones because the quarrying activity has destroyed the likely better areas at the entrance, it is still important to understand how the cave might have been used by hominins at different times during its occupation history.

H. Finally, I suggest a thorough English grammar and spelling check, especially for the Supplementary Information file, which is very long and contains many mistakes (e.g., noun-verb agreements, etc.). This should be relatively easy to fix.

(Remarks on code availability)
There is no code, but there is raw data. I did not try to replicate their statistics by running my own code.

Version 1:

Reviewer comments:

Referee #1

(Remarks to the Author)
The authors have made impressive progress in responding to the reviewers' comments - most notably by increasing new zooarchaeological and taphonomic data that significantly enrich the archaeological interpretation of the site. Nevertheless, several key points require further clarification or revision to ensure the conclusions are fully supported by the evidence.

The argument for assigning the entire stratigraphic sequence (Layers 3-12) solely to Denisovans rests largely on the claim of "technological continuity" across these layers. However, the statistical analysis used to support this assertion was conducted exclusively on cores and flakes specifically from Layers 3, 7, and 9 (see SI-D, lines 641-652). Crucially, retouched tools-the most informative component for inferring cultural affiliation and behavioral continuity-are exceedingly scarce: only five were recovered from Layer 9 and seven from Layer 7. Such minimal sample sizes preclude robust statistical comparison. While tool types - including notches, denticulates, and scrapers - do appear broadly consistent across layers, this observation remains qualitative and visually based. My question is whether these stone tools can also be included in the statistical analysis?

The lithic assemblage is described as "expedient", and as one reviewer noted, the suggestion has been made that the site saw more tool manufacture than tool use. In reply, it is pointed out that heavy quarry damage makes it difficult to judge spatial patterning. But if the excavated area is only a small residual remnant, how can one be sure that this assemblage of stone artifacts captures the full range of Denisovan technological behavior at this site? The very low proportion of retouched pieces (34 out of 1,366) and the high share of cortical flakes (52.6%) strongly indicate that primary core reduction and raw material testing were the main activities carried out at the site. This observation is both valid and important. Rather than presenting the Bianfu Cave lithic assemblage as a complete toolkit, it is more methodologically sound and convincing to frame it as reflecting a narrower set of activities - for example, initial core reduction and expedient, on-site tool manufacture for butchery.

The raw materials are reported to originate from the Yinhe River, located approximately 2 km from the site. However, it remains unclear whether a systematic geological or archaeological survey was conducted to verify this provenance. If such a survey was undertaken, its methodology and results should be explicitly presented; if not, the claim should be appropriately qualified. Similarly, the cortex coverage data presented in Supplementary Figure 25 are reported solely as percentages, without raw data. Including these data would enable readers to better assess the degree of reduction intensity and evaluate the representative of the sample.

The Bianfu Cave teeth are acknowledged to show a mix of traits, sharing features with Denisovans and with other archaic hominins, such as those from Hualongdong. The attribution to Denisovans relies mainly on paleoproteomic evidence from a study (Rao et al.) that is still under review. However, the proteomic analysis receives only a very brief summary (in lines 222-225. More detail is required on which specimens were analyzed (the P4 and one M2) and the key peptide sequences that support the identification. Without this information, the morphological argument remains vague, and readers are forced to accept the Denisovan classification largely based on trust in unpublished work.

Age estimates for the teeth are now provided in the Supplementary Information-C (SI-C), but they are based on dental developmental standards derived exclusively from modern human populations. Given that these standards may not be directly applicable to Middle Pleistocene archaic hominins - whose growth and development could differ significantly - their use requires explicit justification. In the absence of such validation, the potential limitations and uncertainties in the age estimates should be pointed out.

The cranial remains consist of parietal fragments with thicknesses of 7.6 mm and 10 mm, respectively. Unfortunately, the manuscript does not place these measurements within the broader comparative framework - neither other known Denisovan cranial specimens (if has) nor relative to contemporaneous East Asian archaic hominins. Such comparisons may significantly strengthen palaeoanthropological understanding of the findings. Similarly, the radius is described as exhibiting a "medially facing radial tuberosity" - previously documented in late Neanderthals. If possible, a brief discussion of functional implications of this trait, particularly in light of emerging evidence on Denisovan anatomy and ecology, would enrich our knowledge on this species.

A more complete analysis of skeletal part representation has now been included (SI-F, Supplementary Table 25), noting that appendicular elements appear over - represented once bone fragments assigned to size classes are counted. However, the earlier taxon - identified sample showed a "head-and-foot-dominated" pattern. This mismatch calls for a clearer explanation: is it simply that teeth and mandibles are easier to identify than postcranial pieces, or does it point to a real taphonomic bias? In addition, more detail on cut-mark location and orientation would help support the "carcass defleshing" interpretation (SI-F, line 1280). A table or figure laying out cut-mark distribution by skeletal element would be welcome.

Several bone tools are described, including retouchers and intermediate pieces. The functional interpretation of these tools relies largely on macroscopic inspection. It is noted that “further quantitative usewear analyses will be required” (SID, lines 871-872). Given the importance of these objects for understanding Denisovan behavior, the usewear analysis is suggested to be included.

The conclusion that hominins were the primary bone-accumulating agents rests largely on the relative abundance of anthropogenic traces - specifically cut marks and percussion marks - compared to modifications attributable to carnivores or rodents (SI-F, lines 1266-1298). However, the overall frequency of these human-induced marks remains low: cut marks occur on just 1.2% of the analyzed specimens. While this pattern is consistent with hominin involvement in carcass processing, it does not preclude a meaningful contribution from other taphonomic agents - including carnivore activity, natural mortality, or post-depositional processes. Moreover, as the text itself notes, poor bone surface preservation could also explain the low modification rates. A more measured handling of the taphonomic data’s limits would be appropriate.

A Bayesian model now places a gap of 26.7-51.1 ka between Layers 5 and 4. This is a significant stratigraphic break. Does this break mark a period of no site occupation, or could it result from erosion or a pause in deposition? If the site was indeed unoccupied during this interval, the previous claim of "long-term" occupation becomes much harder to sustain. Therefore, it remains necessary to clarify whether the occupation at the site was continuous, or instead consisted of separate, repeated visits separated by long intervals of abandonment.

Several references in the supplementary information appear incomplete or are formatted incorrectly (e.g., references 67-75 in SI-D). All references need to be checked carefully for accuracy and consistency.

Some details that need to be revised in the manuscript are as follows：
1, In line 468. Fig.1.a, missing a scale bar; Fig.1.d, the depth should be in centimeters, not meters.
2, In line 509. The scale bars in Fig.3 are not clear. It’s difficult for readers to determine which samples are indicated by two liner scales. It would be better to indicate it somewhere. Additionally, in Fig.3. a,b,c,d,e., it would be better to indicate the anatomically left or right sides of the teeth and the radius, this would be more accessible for readers who are not anatomists.
3, The scale bars in Fig.4. is still unclear. Authors may indicate which bar is match to the stone artifacts, for example.
4, In Fig.4.a, it seems that 465 is not a core of unifacial flaking.
5, There are many places where the confusion between “artifact” and “artefact” in the manuscript.
6, In the “Methods，Excavation” section, the description is confusing. It states earlier that "T2 is a 3*10 m unit located in the central part of the slope", but the following paragraph says "T2. The minimum excavation area at T2 is approximately 7 m² (Layer 12), and the maximum is approximately 11 m² (Layers 7 and 8).". I think the readers can't possibly understand what you are saying?
7, In the “Extended Data Fig.3.”, the anatomically position of YHB2890 and YHB3075 are incomplete.
8，In the “Extended Data Fig.4.”, why were Cave I2 of Bianfu and Cave P4 of Bianfu not given serial numbers?
9, In the “Extended Data Fig.8.”, there is overlap between a-g and e-o, is h-o?
10, In the “Extended Data Fig.9. and Fig.10”, the using of “a,b,c” or “a-c” should be consistent in the manuscript.

(Remarks on code availability)

Referee #2

(Remarks to the Author)
I am grateful to the authors for addressing our comments in so much detail, it's especially nice to have the more detailed zooarchaeological and bone tool analyses, and everything separated out by layer. This will be a good resource for future comparisons as well.
I feel the paper is ready for publication, but I found a few very minor issues:

Line 150: human -> humans
Line 340: Denisovans -> Denisovans'

Caption of Extended Data Fig. 4: " The hominin incisors and premolars unearthed from the Bianfu Cave. " - there's only one incisor and one premolar, so they should be in singular

(Remarks on code availability)

Referee #4

(Remarks to the Author)
The authors have taken my previous comments seriously and have addressed them thoroughly. In particular, Fig. 2 has been substantially improved. it is now both more informative and visually effective, and I am satisfied with the revisions made.

Based on the Quaternary stratigraphic and chronological framework, as well as the reconstructed climatic and environmental background, I consider the findings to be robust and well supported. The conclusions drawn by the authors are scientifically sound and appropriately cautious. Overall, I am pleased with the revised manuscript and recommend it for publication.

(Remarks on code availability)

Referee #5

(Remarks to the Author)
The revised manuscript significantly improves upon the original submission and I recommend it for publication. I particularly appreciate the inclusion of a chart correlating the site's chronology and paleoenvironmental proxies for the region, as well as the detailed explanation of the taphonomy and zooarchaeology of the site. I also agree that the new title more honestly reflects the conclusions that can be drawn from the available data. Last, but not least, I can confirm that the lithic analysis results are reproducible, as attested by the attached R code.

(Remarks on code availability)
I can confirm that the lithic analysis results are reproducible, as attested by the attached R code.

Version 2:

Reviewer comments:

Referee #1

(Remarks to the Author)
The authors have provided satisfactory responses and revisions to our comments. I believe that the current version of the manuscript is perfect in terms of stratigraphy, chronology, Paleolithic archaeology, zooarchaeology, and paleoanthropology. The analyzed materials, methods, and data all have high credibility. All the research details support a reliable conclusion. I strongly recommend that this manuscript be published in the Nature.

(Remarks on code availability)

Referees' comments:

Referee #1 (Remarks to the Author):

In this manuscript, Li et al. report on Denisovan fossils and stone/bone artefacts discovered in Bianfu Cave in Yunnan, southwest China. Using uranium series and optically stimulated luminescence dating, the age of hominin activities is constrained to 190–68 ka. This interesting discovery may potentially extend the temporal and spatial distribution of Denisovans, providing new material for understanding their morphological diversity, lithic/bone technology, and survival strategies.

We thank the reviewer for his/her positive assessment of our study and for the constructive comments made below. We are providing a point-by-point response to the issues raised and explaining the changes introduced to our manuscript to address them.

However, the study has the following flaws:

1, Assigning artefacts to their makers—particularly to a specific hominin species—within archaeological sites is usually a challenging task that has long perplexed archaeologists and palaeoanthropologists. I note that the hominin fossils from the Bianfu Cave are found only in layers 7 and 9, whereas layers 10-12 underlying and layers 3-6 overlying them contain only artefacts and animal bone fossils. The author's assertion that layers 3-12 constitute entirely Denisovan cultural unit requires caution. In China, particularly in the southern regions, the pebble industry represented by core-flake artefacts persisted throughout most of the Pleistocene. The author's confident assertion that Denisovans exclusively occupied this site for 122 ka, in the absence of sufficient archaeological and palaeoanthropological evidence, is open to question.

Reply: We thank the reviewer for the comment. Regarding the statement that all layers belong to Denisovans, we have revised the phrasing to adopt a more conservative and cautious approach (see lines 66-67 and in the main text). In addition, as suggested by another reviewer, we have now modified the title of the paper to highlight the layers (7 and 9) yielding Denisovans fossils (see lines 3 and 4 in main text). For the other layers included in the sequence, we conducted further analyses of stone artefacts and animal bones and carried comparisons with layers 7 and 9. For stone artefacts, in SI-D, we added information on the technological attributes of lithics by stratum to illustrate technological continuity (subjected to statistical testing; see lines 251-253 in the main text, lines 641-652 in SI, and the newly added Supplementary Figures 21-22). For resource exploitation behaviour reflected in animal fossils, we added faunal composition, mortality profile, and skeleton elements representation by stratum and by chronological range (considering the limited number of specimens in certain layers) (See the newly added SI-F for detailed information). Our results show there are no substantial variations in lithic technology and animal exploitation patterns throughout the cultural sequence, which may likely indicate the continuity in subsistence strategy. Owing to the association of a particular hominin type in layers 7 and 9, and given this cultural continuity, the most parsimonious hypothesis would be that Denisovans are the likely hominin responsible for the accumulation of the cultural remains found at the site, please see lines 304-312 in the main text and lines 1287-1298 in SI-F for detailed information. We agree, however, that this hypothesis remains an open question at Bianfu Cave and, more broadly in southwestern China, that will require further testing with the discovery of new stratified sites.

2, The artefacts recovered at this site are not particularly abundant, with tools constituting a notably small proportion. Is it possible that this cave site served as a place of tool making rather than using? So, the artifact assemblage from this single site may not be representative of the real toolkit of the Denisovans (if it is).

Reply: We thank the reviewer for the comment. The site has suffered severe overall damage, particularly at the main entrance area that has been entirely destroyed by quarrying activity. The cave roof has also been destroyed, as shown in the revised Figure 1 and Extended Data Figure 1 in the main text. The extensive destruction of an area likely occupied by hominins during the Pleistocene makes it difficult to assess the spatial distribution of the activities within the site (see however our response below to a similar issue raised by Reviewer #5), and thus, to test whether the lithic assemblage can reliably reflect the function of the site. That said, the evidence from the faunal assemblage shows diverse anthropogenic traces, e.g., fresh fractures, percussion scars, notches associated with marrow extraction, and cut marks, indicating that hominins not only processed and consumed meat and grease resources on site, but also manufactured and utilized lithic tools at the locality. We have added this point in the main text, please see lines 265-271 on page 8. Notably, despite the limited surface area available for excavation, which has direct implications on the size of the assemblage, we quantitatively highlight consistent technological features across the whole sequence (see lines 641-652 in SI and the newly added Supplementary Figures 21 and 22). These features strongly suggest a cultural continuity over a long period of time. Given this context and the association of anthropological and cultural remains within layers 7 and 9, Bianfu Cave provides a new perspective on how lithic technology was integrated within the subsistence strategy of Denisovans. It also provides a reliable baseline from which future studies will be able to further refine our understanding of how it relates to specific local environments and how it compares with technological and behavioural variations that are yet to be documented across the regions occupied by this species. We have modified our Discussion (see lines 336-341 in the main text) to reflect this exciting prospect for future research.

3, The authors argue that “the inhabitants of Bianfu Cave practised specialised hunting of large-bodied prey” lacks sufficient zooarchaeological and taphonomical evidence. The fragmented animal bones discovered at the site may not be the result of hominin processing only, carnivores and rodents frequently act as transporters of cave fossil accumulations. The authors have not adequately considered this possibility.

Reply: We thank the reviewer for this comment, which was also raised by other reviewers. In the revised version of the SI, we have added a substantial quantity of zooarchaeological and taphonomic data to address the issues that were raised (see SI-F and newly added Supplementary Figures 40-43 and Supplementary Tables 24-29). In the revised SI, we have separated the pollen (SI-E) and the faunal assemblage (SI-F), including taphonomic analysis in the latter. In SI-F, we provide data broken down by layers on the species represented, their mortality and skeletal representation profiles as well as a comprehensive report on the bone surface modifications recorded on the assemblage. We also introduce, in the main text, a summary of this updated information in the paragraph that originally presented data on the faunal remains (lines 263-271). At the end of our point-by-point responses to the reviewers, we provide a detailed synthesis of the zooarchaeological and taphonomic study that is now introduced in the revised version of our manuscript. In response to the reviewer’s comment above, we now

demonstrate lower proportions of carnivore and rodent modifications relative to anthropogenic modifications. On this basis, we would suggest that hominins were likely the primary agents for the accumulation of the faunal assemblage, thus reinforcing our original interpretation.

4, The data analysis in this manuscript is flawed. In the three-dimensional geometrical morphology analysis of M2 (c and d), when conducting principal component analyses, the comparison specimens included two Denisovan teeth and three East Asian Late Middle Pleistocene Archaic Homo teeth. However, during the between-group principal component analyses, the comparison specimens comprised five East Asian Late Middle Pleistocene Archaic Homo teeth, with no Denisovan tooth sample present. The authors should provide a detailed explanation for the discrepancy in the selection of comparison specimens between the two analytical methods and include the corresponding missing specimens in both analyses.
Reply: Thanks for pointing this out. In the PCA analysis, we kept the original membership for each taxonomic group to catch as much variability as possible. However, bgPCA requires more specimens for each group, and therefore, we combined the East Asian late Middle Pleistocene archaic *Homo* and Denisovan during this analysis. We updated the label to illustrate this in the revised Extended Data Figure 5.

5, The hominin dental fossils from the Bianfu Cave exhibit marked differences from known Denisovans, both in size and in the characteristics of the tooth crowns. The authors nevertheless assigned these dental remains, along with two cranial fragments and one partial radius, to the Denisovan population. Morphologically, this identification lacks sufficient evidence. Thus, palaeoproteomic evidence is crucial for allocating these hominin fossils to the Denisovan lineage. However, the protein evidence cited in this paper originates from Reference 10: Rao, H., et al. A Denisovan radius from Southwest China: ancient proteins reveal Denisovan post-cranial morphology and population dispersal. Cross citation. The authors are requested to provide detailed clarification regarding which specific hominin specimens underwent palaeoproteomic analysis and can be unequivocally identified to the Denisovans.
Reply: Many thanks for your comment. The Bianfu teeth do display notable morphological differences compared to those of known Denisovans, although their M2 specimens most closely resemble those of Denisovans and late Middle Pleistocene archaic *Homo* from East Asia (also thought to represent Denisovans). Our attribution of the Bianfu teeth to Denisovans was primarily based on proteomic evidence from a radius and a parietal bone recovered from the same stratigraphic layer. To further confirm that the Bianfu teeth themselves belong to Denisovans, we conducted additional proteomic analyses on the P4 and one of the M2s. The results confirm that these teeth, like the radius and parietal, are of Denisovan origin. These new findings have been incorporated into another manuscript (Rao et al., Nature, under review) and are briefly summarized here, please see lines 222-225 in the main text for the complemented ancient proteomic information.

6, The section from lines 146-153 is a clear repeat of the content from lines 185-191.
Reply: Thank you for pointing this out. We have removed lines 185-191 from the new manuscript, see page 6 (lines 215-221) in the main text.

7, In Extended Data Figure 7, P3 should be changed to P4.

Reply: Thank you for pointing out this error, and it has been corrected. Please see the revised Extended Data Figure 7.

Referee #2 (Remarks to the Author):

Main contributions of the study:

This study presents and describes new Pleistocene human remains that the authors attribute to the Denisovan lineage — a taxon initially recognized on a genetic basis, but with largely unknown morphology. The discovery of these fossils in Yunnan Province helps to fill a gap between two regions — Tibet and Laos — which have recently yielded human remains assigned to this archaic group. Among the seven human remains presented, the four teeth are particularly noteworthy due to their excellent state of preservation, which allowed the authors to conduct multiple descriptive and comparative analyses. The results of these analyses enhance our understanding of the morphometric variability of this taxon. Moreover, the presence of these paleoanthropological remains within archaeological layers containing lithic and anthropogenically modified faunal material, as well as palynological archives, allowed the authors to discuss the technical behaviors, subsistence strategies, and paleoenvironmental context of the humans who occupied the site. This study is therefore significant because it integrates multiple disciplines to document aspects of this extinct human lineage that remain poorly known: phenotype, technical behaviors, and subsistence strategies.

Reply: We thank the reviewers (#2 and #3) for their positive assessments of our study and for the constructive comments made below. We are providing a point-by-point response to the issues raised and explaining the changes introduced to our manuscript to address them.

Nevertheless, some adjustments are warranted prior to publication. Due to our expertise, we focused mostly on the general parts of the paper, as well as the morphological analyses, and let others evaluate the dating and palynology.

Main Revisions:

• The first and main issue we identified concerns the authors' "exclusive" attribution of the archaeological sequence to Denisovans. Indeed, considering the taxonomic diversity characterizing Asia during the Late Pleistocene (H. erectus, H. sapiens, Denisovans, etc.), it seems highly imprudent to assert that the artifacts from layers 12–10, 8, and 6–3 were produced by Denisovan human groups. Furthermore, and for the same reasons regarding the known anthropological diversity in this region during the Pleistocene, we recommend that the authors exercise greater caution when claiming that Denisovans are responsible for the artifacts found in layers 7 and 9, given that the Bianfu human fossils have not undergone a detailed taphonomic and spatial study aimed at documenting the origin of their accumulation within these layers.

Reply: As mentioned above for a similar comment from Reviewer #1, we have modified the text to leave open the question related to the hominin species responsible for the accumulation of the assemblage from layers other than 7 and 9. We suggest, however, that the continuity we document both in the technology, lithic and osseous, and in faunal exploitation strategies, converges in favour of a parsimonious hypothesis of an authorship by a single hominin species. Similarly, for layers 7 and 9, it is worth noting that, until now, no reliable evidence for the occupation of the region by *H. erectus* or *H. sapiens* has been published for the time span

attested at Bianfu Cave. While we agree this could be possible in the future, the restricted area of the excavation and proximity of the human, other faunal, and cultural remains, and the similar taphonomic history shared by the human and other faunal remains argue in favour of our parsimonious hypothesis. As mentioned in our response to Reviewer #1, we have revised our main text (please see line 66 and lines 308-312), and SI-C (lines 370-376) for the taphonomy of human remains, to err on the side of caution.

Consequently, while assuming that the presence of these human remains in the cave does indeed have an anthropogenic origin, the authors should keep in mind that we are currently unable to rule out the hypothesis that other hominins, such as late H. erectus or H. sapiens, may have been responsible for the accumulation of Denisovan bodies or body parts in the cave. In other words, we believe it is necessary to question whether the individuals discovered at Bianfu were indeed the producers and hunters responsible for the accumulation of anthropogenically modified material at the site. We also feel that the authors need to provide more details on the taphonomy of the faunal assemblage, showing whether the main agent of accumulation were hominins or carnivores. We acknowledge that, given the discoveries and results obtained, the most parsimonious hypothesis remains the Denisovan attribution to the artifacts in layers 7 and 9; however, it would be appropriate to emphasize that alternative possibilities exist and to introduce more conditional language in statements regarding these associations.
Reply: The new taphonomic analysis now included in SI-F makes a strong case that hominins are the primary agent responsible for the accumulation of the faunal assemblage throughout the sequence (SI Table 29). As mentioned above, the lack of reliable evidence for the occupation of the region by *H. erectus* or *H. sapiens* in Yunnan during that time span makes it difficult to argue for interspecific competition with the Denisovan individuals represented at Bianfu Cave. We are aware of the reports of late *H. erectus* in South-east Asian Pacific Islands during that time period, and of the reported early Late Pleistocene *H. sapiens* fossils in South China, although the chronology of the sites that yielded these latter evidence remains a debated topic. We have made changes in the text, by using a more conservative language, to leave open the possibility that these species may have contributed to the accumulation of the bone assemblage. While further research may later complexify the evolutionary history of our lineage in the region, we believe we require more data to suggest that Denisovan bodies or body parts at Bianfu Cave were accumulated by another human species.

Moreover, we consider that the chronological range indicated by the authors for the Denisovan occupations is excessively broad given the different results obtained (Bayesian analysis, Line 130-131: 167-161 ka and 142-134 ka) and our previous remarks. Therefore, we recommend that the authors reconsider the article's title.
Reply: We thank the reviewers to point out this issue. We have also modified the title to fit the reality of the age of layers yielding hominin fossils. The new title (see lines 3 and 4 in the main text) now reads: "Denisovans from southwestern China and their subsistence strategies".

• Connected to this previous issue: the authors analyze the faunal and lithic material from Layers 3-12 together, despite these layers spanning up to 120 ka in time. We assume this is due to small sample sizes in some of the layers, not allowing reliable statistical analyses. Despite this, we think

that it is necessary to present separate analyses for each layer, and only analyze them as one assemblage if it could be shown that there are no technological (and faunal) differences between the different horizons.

Reply: We appreciate the reviewer's raising of this critical issue. We have now separated the lithics and faunal materials by layer and conducted the statistical analyses to demonstrate whether technological and faunal differences exist between layers. When sample size was too small to produce robust statistical tests, we combined layers belonging to the same chronological ranges, based on the Bayesian age modelling results. Together, this approach yielded results that support our interpretation according to which no significant differences on both lithic and faunal assemblages can be detected among layers (SI-D lines 641-652 and SI-F lines 1287-1298, new Supplementary Figures 21-22, 44 and Tables 17, 25).

• In the analyses of EDJ morphology, a much smaller sample was used than in the metrical analyses of crown size and the comparative morphological analyses. Especially missing from the EDJ analyses are samples of earlier Neanderthals (e.g. Sima de los Huesos) and European Middle Pleistocene material (especially Mauer, as the holotype of H. heidelbergensis). Similarly, both the fossil and recent H. sapiens comparative sample is very small – especially the latter should be expanded significantly.

Reply: Many thanks for this advice. Due to permitting restrictions, we were unable to include teeth from Sima and *H. heidelbergensis* in this study. Nevertheless, as recommended by the reviewers, we have expanded our sample by incorporating an additional 16 P_4s and 20 M_2s into the analyses. The 16 P_4s comprise three teeth from Jebel Irhoud, three of African fossil *Homo sapiens*, and ten of East Asian Holocene individuals. The 20 M_2s include two teeth of Montmaurin, three of Jebel Irhoud, seven of African fossil H. sapiens, and eight of East Asian Holocene specimens. Please see the revised Extended Data Figure 6.

• Regarding the section describing the human remains, age-at-death estimates for the fossils are needed. Please at least provide them in the Supplementary Information.

Reply: Many thanks for this advice, we have illustrated the age at death for each specimen from Bianfu Cave in the revised SI-C (lines 381-383, 410-412, 471-473 and 482-485).

• The section presenting the anthropogenically modified material lacks one or two sentences discussing the density and concentration of the remains across the different levels of the stratigraphic sequence.

Reply: We appreciate the reviewer for making this pertinent suggestion. We now provide detailed sample size by layers for both the lithic (SI-D, Supplementary Table 17) and faunal (SI-F) assemblages as well as a joint-table with the density values per layer (Supplementary Table 24, see also the revised Figure 2d in the main text) as requested. We have also added a sentence in our discussion (lines 313-316) to highlight how this data informs us on the intensity of occupation through time.

• A correction needs to be made in at least one sentence of the section dealing with traces of anthropogenic origin recorded on the faunal remains (details are provided in the comments on the document).

Reply: We thank the reviewers for pointing out this issue. We have now added one sentence to demonstrate this point, please see lines 269-271 in the main text.

• In the Supplementary Information, the section entitled "Technological behavior at Bianfu Cave" contains a lot of information (pages 30 and 31) without bibliographic references. Please provide the appropriate references.
Reply: We appreciate the reviewer for pointing out this issue. We have added the relevant literature, please see pages 34 and 35 in the revised SI-D.

Various smaller issues:
Line 138-139: why is the lateralization of the teeth not reported here?
Reply: We have added the lateralization of the teeth in the new manuscript, see line 166 in the main text.

Line 151: this wording is not really appropriate: 'later Homo' includes Neanderthals, and Neanderthal lower P4s frequently exhibit asymmetric crown outlines.
Reply: We completely agree with this. We kept "later *Homo*" and removed "symmetric crown outline of P_4". See lines 179-180 in the main text.

Line 175-76: "with a protruded distolingual corner" and "non-buccally extended talonid of P4" are the same trait, aren't they?
Reply: We agree on this, and have removed the "non-buccally extended talonid of P_4" from the new manuscript, please see line 206 in the main text.

Line 223: "knapping scars" these are usually referred to as percussion scars or notches
Reply: We agree on this, and have replaced the "knapping scars" to "percussion scars and notches", please see lines 265 and 266 in the main text.

Line 254: "long term occupations" – isn't the density/amount of lithic material pretty limited for assumed long term occupations? Less than 1500 lithics would not be seen as indicative of long term or intense occupation in Europe or Northern Asia
Reply: We thank the reviewer to raise this issue. We acknowledge that, due to the extensive destruction by quarrying activities, it is difficult for us to appreciate the core of activities implemented at the site by the hominins. Our original use of the expression long-term occupations was meant to convey repeated occupations, irrespective of the length of each one, over an extended period from MIS 6 to MIS 4. We have modified the sentence to prevent the ambiguity on the point we wished to convey, please see lines 298, 321, 366 and the modified title (lines 3 and 4) in the main text.

Line 277: some more references to bone tool use in archaic humans would make sense here, e.g. Soressi et al., 2013; Tartar and Costamagno, 2016; Baumann et al., 2020, 2023
Reply: We thank the reviewer for these reference suggestions which were included in a previous version of the manuscript but later removed owing to the limitations on the number of references indicated in the Authors guidelines. We are now referring the reader to the SI-D where

we provide a more detailed literature review, please see references 67-75 in SI-Supplementary References.

Line 384: Reference 47 is all messed up.
Reply: Done.

Fig 1c: the orientation of this images is unclear, is it a top-down (zenithal) view or a frontal view? Furthermore, a scale bar is missing. I also don't understand what the North arrow, with 330degrees is supposed to mean.
Reply: The map has been revised with a new Figure 1c to provide a clearer view of the cave. Additionally, the north arrow was adjusted and a scale bar was added as requested.

Fig 3, Line 428: "show the pulp cavity. " – there is no pulp cavity in sight anywhere
Reply: We have removed the "show the pulp cavity" from the new manuscript, see lines 547 in the main text.

Supplementary info:
Line 444: italicize H. erectus
Reply: Modified, see line 499 in SI-C.

Line 452: italicize Homo
Reply: Modified, see line 506 in SI-C.

Line 503: italicize Australopithecus
Reply: Modified,see line 558 in SI-C.

Line 512: "only present in 90.5% of early Neanderthals" – present in 9 out of 10 is very frequent, not "only"
Reply: We have removed the "only" from the new manuscript, see line 568 in SI-C.

Referee #3 (Remarks to the Author):
I co-reviewed this manuscript with one of the reviewers who provided the listed reports.
Reply: We thank Reviewer #3 for contributing feedback alongside Reviewer #2. We provided a point-by-point response to all issues and comments raised by our generous colleagues.

Referee #4 (Remarks to the Author):
The manuscript presents a systematic excavation and study of the Bianfu Cave site. Through comprehensive analyses in chronology, lithic assemblage, human skeletal remains, faunal composition, and palynology, it provides a holistic understanding of the living environment, lithic technology, and hunting strategies of the Denisovans at this in-situ burial site. Morphologically, dental morphology of the Bianfu Cave hominins supports their attribution to a distinct Denisovan group, deepening our knowledge of Denisovan morphological characteristics. Moreover, the

geographical location of Bianfu Cave significantly expands the known distribution range of Denisovans in Asia. This study represents a breakthrough discovery with important implications for Denisovan research. I recommend its publication in Nature.

Reply: We thank the reviewer for his/her positive assessments of our study and for the constructive comments made below. We are providing a point-by-point response to the issues raised and explaining the changes introduced to our manuscript to address them.

However, before publication, I have several comments and suggestions:

Comments and Suggestions:

1.Based on the OSL and U-series ages alongside the stratigraphic sequence, there appears to be a hiatus of approximately 50 ka between Layers 4 and 5, with Layer 4 itself being only 4–10 cm thick. The Bayesian model merely minimizes this gap within a plausible range. Therefore, human occupation at Bianfu Cave was likely discontinuous.

Reply: We thank the reviewer to point out this critical issue. Hiatus is commonly seen in cave sediments, which could result from erosion (e.g., by small-scale rills during raining seasons) or bioturbation activities in the cave. Unfortunately, given the limited excavation area left intact from the quarrying destruction and the lateral variation of the deposits, the spatial resolution of our sampling is relatively coarse and, hence, does not allow us to assess whether such a hiatus is widespread across the entire cave or is simply a localized feature that happened to be captured by our samples. For this reason, we cannot exclude the possibility of a discontinuous occupation between layer 4 and 5. However, since absence of evidence is not necessary the evidence of absence, neither can we rule out the possibility that human occupation was continuous. We now provide a discussion of such hiatus in the main text (lines 148-151, and lines 155-157). We have also added an interval in the Bayesian model to estimate the time length of this gap (see the revised Figure 2b). Our modified model produced indistinguishable results as the previous one, and the hiatus was modelled to last between 26,700–51,100 years (95% probability).

2. Human fossils are found in the cultural layers of Layers 7 and 9, all attributed to Denisovans in this study. Given the relatively continuous chronology from Layer 12 to Layer 5, these layers can be considered Denisovan cultural layers. However, with a 50 ka hiatus between Layers 4 and 5, and with only lithic remains in Layers 3 and 4 dating to around 70 ka, can the human presence in Layers 3 and 4 be definitively identified as Denisovan?

Reply: We thank the reviewer for pointing out the hiatus in chronology. Similarly to comments made by Reviewers #1, #2, and #3, we modified the text to adopt a more conservative language and stress that, considering the lithic and faunal data, the most parsimonious hypothesis for now would be to assign Denisovans as the possible agent for the accumulation of the cultural assemblages from layers 3 and 4 (see lines 66 and 67, 304-312 in the main text). This hypothesis is support by (1) the direct association of human and cultural remains in layers 7 and 9 and, (2) the clear continuity highlighted throughout the sequence by our quantitative comparison of the lithic and fauna assemblages.

3.Was the environment that supported large mammals and was suitable for human hunting a conifer-dominated forest environment or a forest-steppe environment? In other words, was the primary setting for the life of the Bianfu Cave humans a forest environment or a forest-steppe

habitats?

Reply: Data from pollen analysis, alongside the animal species represented in the faunal assemblage, and new information on the density of lithic and faunal remains provided in the updated version of the main text (see lines 157-159, 313-316) and SI-D, together suggest that the occupation of the site occurred when the surrounding environment was characterized by a cold-temperate evergreen conifer forest, and later, in layer 3, by a cool-temperate steppe. This is fully coherent with the dating results which suggest ages contemporaneous to MIS 6 and 4. Keeping in mind the topography in the vicinity of the site, we do not rule out likely variations in vertical distribution of vegetation types, which would have offered the occupant with a diversity of landscapes to could carry their hunting activities (lines 157-161, 320 and 321 in the main text). This diversity appears corroborated by the species represented in the faunal assemblages. For instance, *Cervus (Sika) nippon* inhabits forest edges and mountain grasslands. *Cervus elaphus* prefers coniferous forests and open alpine meadows. *Bos (Bibos) gaurus* likes forest edges, sparse forests, or grasslands. *Bubalus* sp. prefers lowland forests, wetlands, and swamps. *Rhinoceros sinensis* prefers open grasslands, savannas, shrub areas, or swamps. *Capra* sp. mainly inhabits mountain, rocky terrain, open grassland or meadow. *Crocuta crocuta ultima* prefers open grasslands. *Sus* sp. prefers forest or forest edge in mountain areas. The continuous presence throughout the sequence of species that prefers such a variety of landscapes suggests more a mosaic rather than a clear-cut distinction between forest environment or forest-steppe habitat. We have updated our main text (lines 313-325) to reflect the variations through time and the potential effect of topography in the distribution of the plant and faunal resources.

4.Since the study offers a systematic investigation of the Denisovan site at Bianfu Cave, the authors should provide a comprehensive schematic diagram that visually integrates key elements such as the local geomorphology, vegetation types, faunal composition, lithic (and bone) technology, and the Denisovan population. This would be a distinctive highlight, as such integrated representation has never been achieved for previous Denisovan sites.

Reply: We thank the reviewer for this interesting suggestion on how to improve the visual representation of our data. We have modified Figure 2 by incorporating information on vegetation types, faunal composition, lithic and bone technologies, the presence of lithics, animal bones and Denisovans across different stratigraphic layers. In addition, as suggested by Reviewer #5, we have also added climate change curves derived from deep-sea oxygen isotopes and stalagmites in the revised Figure 2 to provide a more comprehensive and integrated snapshot. Regarding the local geomorphology, we have now provided an aerial photo to vividly display the geomorphology surrounding the site, please see the revised Extended Data Figure 1a.

Minor Issues:

5.Fig. 1b: The distance scale bar is not clear in the transparent parts. River labels should be in italics and aligned along the river direction. Fig. 1c: Add a scale bar at the cave entrance location.

Reply: Thanks for pointing out these issues, we have now modified Figure 1 based on these valuable suggestions.

6.Fig. 2 (right panel): In the distribution probability plot for unmodeled ages, visually distinguish between OSL and U-series dates. Although they are labeled differently on the left, a visual

distinction on the right would be more immediate. Also, please ensure the stratigraphic legend icons at the bottom of the figure are of consistent size.

Reply: Thanks for pointing out these issues. Figure 2 has been revised according to the suggestions. Different colours have been used to distinguish the results from the two independent dating methods, and the size of the legend has been standardized.

7.Supplementary Materials: please provide a broader-view photograph to show the geomorphological context around Bianfu Cave. The current photos make it difficult to discern the site's topographic setting—particularly the view from the cave entrance: is the area open or steeply sloped? Is there an forest-steppe landscape?

Reply: A new aerial photo has been added, showcasing the broader topographical context surrounding the site. The cave entrance was completely damaged by quarrying activities. However, local villagers' descriptions suggest the original entrance was situated towards a naturally carved gully locally known as Xianrendong Gully. Therefore, the area in front of the cave is a relatively steeply slope, as shown in the aerial photo (see the revised Extended Data Figure 1a). The landscape surrounding the cave is nowadays dominated by coniferous forest vegetation (see the revised Extended Data Figure 1a). We now add a sentence in the main text to introduce the geomorphological context of the site, please see lines 123-125 in the main text.

8.The OSL age for the Layer 10 is about 40 ka younger than the U-series age for the Layer 9. While it is understandable that the OSL age might be underestimated (and the U-series date for Layer 9 appears reliable), please explain such a significant underestimation in the OSL dating.

Reply: We have provided the explanation that the age estimate of sample is considered unreliable because it was collected near the disturbed slope of the profile. It could be either its stratigraphic affinity is unreliable, or the gamma dose rate is incorrectly assessed since its 30-cm gamma field was destroyed. Irrespective of the underlying reason, this age was identified as an outlier and was not included in the Bayesian model for the occupation of the site. Please see lines 305-308 in SI-B for an added explanation.

9.What is the approximate spatial extent of human activity within the Bianfu Cave? This does not seem to be described in the manuscript.

Reply: We thank the reviewer for pointing out this issue. Unfortunately, since most of the cave has been severely destroyed by quarrying, it is difficult to accurately estimate the area and spatial distribution of human activity at the site. Estimates of the distance separating the cave entrance and the excavated area suggest that human activities extended fairly deeply in the cave. We prefer to err on the side of caution on this topic given that quarrying activities prevented us to conduct a reliable geomorphological study of the cavity.

Referee #5 (Remarks to the Author):

A. This paper is a straightforward site report of a newly excavated site in China containing Denisovan fossils and associated archaeological materials spanning over 100 thousand years. (B) This new discovery is clearly an important one, albeit from a site that has been disturbed by quarrying activities, and it is of interest to a wide scientific audience. The stated purpose of the

paper is to show Denisovans thriving in a mild and stable environment (compared with Baishiya Karst Cave on the Tibetan Plateau) for a long time.

Reply: We thank the reviewer for his/her positive assessments of our study and for the constructive comments made below. We are providing a point-by-point response to the issues raised and explaining the changes introduced to our manuscript to address them.

C. The pollen data show a forested environment with adjacent open areas, while the fauna are quite diverse, including species as diverse as bears and rhinos. The time interval contains most of MIS 6 through MIS 4, thus two very cold stages, as well as the variable MIS 5. How exactly local environments are responding to the global climate changes is not articulated very well here, and how exactly the archaeological evidence articulates with these changes is also not that well developed (presumably because a lot of the paper is dedicated to the chronology).

Reply: We thank the reviewer for his/her recommendation to better integrate the different proxies we present in the manuscript and to put them in the greater perspective of global climate changes. In the revised version of the manuscript, we introduce some changes in the main text (lines 159-162, 313-325), to highlight that the trend observed in the pollen record matches the global climate changes, and that local variations in topography likely affected the distribution of plant and animal species exploited by the hominins that occupied the site. Interestingly, for layer 3, which corresponds to the harsher climate of MIS4, we observe an increase in lithic and faunal remain density but no particular changes in technology nor a broadening of the faunal spectrum at the site (see lines 304-325 in the main text). While this pattern argues in favour of a continuity in subsistence strategy through time, it remains difficult, owing to the destruction of the archaeological record by quarrying activities, to establish whether the increase in artefact density represents a change in the frequency or the duration of occupations or in the size of the groups that visited the Bianfu Cave.

F. I suggest the following changes in order to make this a better and more convincing article that goes beyond a mere description of data:

1. Add a summary chart not unlike Fig. 2 from the main article, but that, instead of focusing on the Bayesian analysis, juxtaposes the sequence of ages with marine isotope curves, speleothem records, environmental magnetism, pollen, artefact density, and any other summary data that shows the exact environmental context of the human occupation.

Reply: Figure 2 has been revised and enhanced as suggested here and by Reviewer #4. It now incorporates the information on global and regional climatic curves, pollen, species identified in the archaeological layers, and artefactual and faunal density per layer.

2. Provide a more explicit engagement with the notion of continuity and the intensity of occupation, as well as the potential site function. Here, I stress the importance of explaining the uneven spread of the lithics across different levels and the correlation of different types of lithics with the faunal assemblage.

Reply: In relation to our answer provided in point C, we introduced changes in the main text (lines 263-271, 313-316) and SI-D and SI-F to better integrate the potential site function and variations we observe in the density of the lithic and faunal material relative to the technological and zooarchaeological data (see also the added Supplementary Figure 44 and Supplementary

Tables 17 and 24). Interestingly, for layer 3, which corresponds to the harsher climate of MIS4, we observe an increase in lithic and faunal remain density but no particular changes in technology nor a broadening of the faunal spectrum at the site. While this pattern argues in favour of a continuity in the subsistence strategy through time, it remains difficult, owing to the destruction of the archaeological record by quarrying activities, to establish whether the increase in artefact density represents a change in the frequency or the duration of occupation or in the size of the groups that exploited the Bianfu Cave. With regards to the associations between lithic tool types and faunal species, the limited typological diversity and the sample size per tool type make it difficult to reveal significant correlations with the faunal assemblage. Nonetheless, the occupants of Bianfu Cave relied on a flexible toolkit throughout the sequence, processing and consuming diverse medium and large mammal resources on site and using the cave as a place for lithic knapping, tool use (e.g., cut marks on bones), and resource consumption (see lines 263-28 in the main text and a "*detailed response on the zooarchaeological and taphonomic analysis"* below).

3. Related to 2., the fauna seem to be dominated by low-utility anatomical parts, which the authors (in the supplementary file) attribute to the smashing of the long bones for marrow extraction. Since Marean and Kim's seminal paper in 1998, these claims are made based on long bone refittings, whereas here this is simply asserted. It is true that cut marks are present on some of the bones, but the faunal analysis does not go into what kind of carcass processing took place at the site. I suggest adding information about the location and distribution of cut marks and an interpretation of what this says about carcass processing at the site.

Reply: We thank the reviewer for his/her comment, which was also raised by other reviewers. Originally, the complete zooarchaeological and taphonomic analysis was planned to be the topic of another manuscript, and thus, we had limited the data to the taxinomically identifiable specimens, which explain the over-representation of low-utility parts. In the revised version of the SI, we have added a substantial quantity of zooarchaeological and taphonomic data to address the issues. In the SI, we have separated the analyses of pollen (SI-E) and fauna (SI-F), including taphonomy. In the latter, we provide data broken down by layers (or chronological time span when sample size was insufficient) on the species represented, their mortality and skeletal representation profiles as well as a comprehensive report on the bone surface modifications recorded on the assemblage (see also the added Supplementary Tables 24-29). We also introduce, in the main text, a summary of this updated information in the paragraph that originally presented data on the faunal remains (lines 263-271). At the end of our point-by-point responses to the reviewers, we provide a detailed synthesis of the zooarchaeological and taphonomic study that is now introduced in the revised version of our manuscript (pages 25 and 26 in the Methods part of the main text, and SI-F). Together, and to answer directly to the reviewer's comment above, the new data we present on skeletal representation significantly increase the number of appendicular, high-utility, body parts. We also now provide a detailed report on the frequency and location of cut marks and percussion notches by skeletal element and layers to support our interpretations on the nature of the carcass processing activities that took place at the site (see the added Supplementary Table 29).

4. Introduce a spatial analysis or at least explain how the site was used at different times during its long occupation. It is unlikely that people would have used it in exactly the same way over

more than 100 thousand years. While I understand that the available deposits are not the ideal ones because the quarrying activity has destroyed the likely better areas at the entrance, it is still important to understand how the cave might have been used by hominins at different times during its occupation history.

Reply: In the new version of our SI, we provide a new figure (Supplementary Figure 44) that includes heat maps for both the lithic and the faunal assemblages for the layers, i.e., 3, 7, 9, 11 and 12, that have yielded a sufficient number of specimens for analysis. Despite small shifts of the concentrations along a NW and SE cline between layers 11 and 12 on the one hand and layers 7 and 3 on the other, these figures must be interpreted with caution given the limited excavated area at Bianfu Cave, i.e., ranging from approximately 7 m^2 at the bottom of the sequence to approximately 9 m^2 on the top, the likely destruction of most of the site by quarrying activities, the small size of the lithic toolkit, i.e., only 30 retouched tools for the whole sequence, and the frequency of each tool type per layer. Considering these biases, we believe best to err on the side of caution and limit our interpretation on possible variation in the site's occupation history.

H. Finally, I suggest a thorough English grammar and spelling check, especially for the Supplementary Information file, which is very long and contains many mistakes (e.g., noun-verb agreements, etc.). This should be relatively easy to fix.

Reply: We have thoroughly revised the main text and SI to ensure the quality of the English.

Referee #5 (Remarks on code availability):

There is no code, but there is raw data. I did not try to replicate their statistics by running my own code.

Reply: We now provide the code used in our study (please see our online link: https://doi.org/10.17605/OSF.IO/PFWNR) to facilitate replication by reviewers and readers.

Detailed response on the zooarchaeological and taphonomic analysis

Originally, the complete zooarchaeological and taphonomic analysis was planned to be the topic of another manuscript, and thus, we had limited the data to the taxinomically identifiable specimens, which explain the over-representation of low-utility parts. Following the comments of the reviewers, we have significantly expanded the zooarchaeological and taphonomic data presented in the text. This data is now presented in a separate section of the SI (SI-F). Below, we present a detailed description of the information we present and how it is used to respond to the issues raised by the reviewers. These issues concerned 1. the species and element as well as the mortality profile by layer; 2. the identification of the major agent(s) responsible for the accumulation of the faunal assemblage at the site; and, 3. the anthropogenic bone surface modifications and how they can inform us on the carcass processing at the site. We leave out the question raised by Reviewer #5 on the spatial distribution of the faunal remains as it was already answered above and a new figure is introduced in the new version of our manuscript to address this issue (see above).

Sampling strategy

A total of 64,378 faunal remains were found at Bianfu Cave. We provide a breakdown of their

length for each layer to allow the reviewers to appreciate the fragmentation of the faunal remains throughout the sequence. Considering that a significant amount bears recent fractures as they were recovered from brescia, we decided to focus our analysis on the specimens previously reported in the SI (Supplementary Table 23 of the original manuscript), and to add all faunal fragments measuring 5 cm or more in length. Our zooarchaeological and taphonomic assessment therefore includes a total of 7323 fragments.

Species and element identification, skeletal representation and mortality profile

Taxonomic and element identification was achieved via comparisons with the reference collection curated at the Yunan Provincial Institute of Archaeology and atlases of comparative anatomy (Pales et al., 1971; O'Connor, 2000; Reitz & Wing, 2008; France, 2017). The landmark-based approach proposed by Morin et al. (2019) was also used to assign smaller fragments to specific genera or species, and elements. When taxonomic identification wasn't possible, the fragments were attributed to a mammal size class following the method developed by Bunn (1982) and improved for periglacial environments by Discamps (2011). Skeletal representation is reported by element (Costamagno et al., 2002) . MNI for the most represented taxon was calculated using dental remains and taking into account the sequence of tooth loss and eruption. Mortality profiles for the dominant herbivore species, i.e., those with a sufficient MNI, were established based on dental wear of the third molar in adults and the fourth deciduous premolar for young individuals (e.g., Klein et al., 1981; Burke, 1992; Azorit et al., 2002; Jones & Sadler, 2012; Bowen et al., 2016) as these elements were most informative and comparable across species. Proportions of diaphyseal versus epiphyseal fragments were also calculated (Supplementary Table 25).

Bone breakage and surface modifications

The fracture planes on the fragments were described following the criteria developed by Villa and Mahieu (1991). Percussion scars and notches likely resulting from the breakage of long bones to access the marrow were recorded following the nomenclature developed by Vettese and collaborators (2021). Weathering stages were recorded based on the work of Behrensmeyer (1978) while rounding followed the stages defined by Cáceres (2002). A preliminary assessment of the preservation of the intact cortical surface was done by identifying areas covered by concretions or affected by exfoliation and rounding. Surfaces were then inspected to distinguish between anthropogenic and non-anthropogenic processes based on criteria available in the literature (Lyman, 1994; Fernández-Jalvo & Andrews, 2016). A particular focus was given to linear marks, e.g., trampling marks and cut marks, as well as bone surface modifications induced by carnivores (Selvaggio & Wilder, 2001; Pobiner, 2008; Andrés et al., 2012; Brugal & Jean-Baptiste, 2024) and rodents (Fernández-Jalvo & Andrews, 2016; Pei, 1940). Whenever possible, the location and orientation of cut marks was recorded to establish the most likely carcass processing activity taking place at the site (Marean & Kim, 1998).

Point-by-point responses to the issues raised by the reviewers

1. *Species, elements and mortality profile by layers:* In SI-F, we now provide the information on the species and elements by layer. For the mortality profiles, we include ternary diagrams plotting the proportion of juvenile, prime and old individuals for the layers that provided

sufficient sample size to make reliable inferences. Overall, we observe a relatively stable pattern emerging where prime adults dominate the assemblage throughout the sequence (Supplementary Figure 43). Likewise, appendicular bones are over-represented in most layers when animal size classes and taxonomically identifiable bones are considered together (Supplementary Table 25).

2. *Major agent(s) responsible for the accumulation of the faunal assemblage:* We now report the relative frequencies of bone surface modifications attributed to carnivores, rodents, and hominins for each layer (Supplementary Table 29). Our results support the interpretation of a primary accumulation by humans, which is supported by an over-representation of appendicular portions, the high fragmentation of long bones while fresh, the presence of epiphyses with seldom evidence of carnivore modifications, and the presence of cut marks (see below). The traces by carnivores are relatively marginal, and rodent modifications, mainly induced by porcupine, were likewise identified on some specimens totalling less than 1% of the sampled assemblage.

3. *Anatomical representation and evidence for carcass processing:* We provide a detailed synthesis on the anthropogenic modifications recorded on the Bianfu assemblage by layer (Supplementary Table 29), and include photographs of selected specimens to illustrate our observations (Supplementary Figure 41). Keeping in mind (1) the differential attrition of some elements relative to others, (2) the high fragmentation of the faunal assemblage, and (3) the limited legibility of a majority of specimens covered by concretions, ferro-manganese deposits or affected by abrasive taphonomic processes, anthropogenic modifications related to carcass processing were mainly observed on long bones. The frequency and main orientation for the cut marks suggest butchery activity involving the removal of muscle tissues rather than skinning or sinew extraction. Numerous specimens preserve percussion scars and notches attesting for the breakage of fresh long bones to access marrow, which implies the consumption of bone grease at the site, a pattern widely documented at contemporaneous Eurasian sites (e.g., Chevillard et al., 2022). Together, this pattern suggests the medium and large sized mammals were targeted for the exploitation of high-utility body parts, in spite of the numerous cranial elements found at the site and which are known to preserve better during the fossilisation process.

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Referee #1 (Remarks to the Author):

The authors have made impressive progress in responding to the reviewers' comments - most notably by increasing new zooarchaeological and taphonomic data that significantly enrich the archaeological interpretation of the site. Nevertheless, several key points require further clarification or revision to ensure the conclusions are fully supported by the evidence.

Reply: We appreciate the reviewer's positive recognition of our revisions, as well as the further constructive suggestions. We have now thoroughly revised the manuscript in response to all the valuable comments listed below.

The argument for assigning the entire stratigraphic sequence (Layers 3-12) solely to Denisovans rests largely on the claim of "technological continuity" across these layers. However, the statistical analysis used to support this assertion was conducted exclusively on cores and flakes specifically from Layers 3, 7, and 9 (see SI-D, lines 641-652). Crucially, retouched tools-the most informative component for inferring cultural affiliation and behavioral continuity-are exceedingly scarce: only five were recovered from Layer 9 and seven from Layer 7. Such minimal sample sizes preclude robust statistical comparison. While tool types - including notches, denticulates, and scrapers - do appear broadly consistent across layers, this observation remains qualitative and visually based. My question is whether these stone tools can also be included in the statistical analysis?

Reply: We thank the reviewer for this important comment. We agree that the sample of formally retouched tools is too small to support a meaningful statistical comparison. With only five retouched tools from Layer 9 and seven from Layer 7, any statistical test would have very limited power and would not provide robust evidence for or against technological continuity. For this reason, our original assessment of the retouched tool assemblage relied on technological comparison rather than statistical inference.

To make this assessment more explicit, we have now added a new supplementary table (SI Table 18) summarizing the principal technological characteristics of the formally retouched tools from Layers 3, 7 and 9, including blank type, retouch direction, number of retouched edges, number of retouch scar layers, and retouch scar counts. These data reveal the same predominance of flake blanks, unifacial retouch on a single edge, and low retouch intensity across the three assemblages, providing additional support for technological continuity. The revised text (page 29 of SI-D) and SI Table 18 have been added accordingly.

The lithic assemblage is described as "expedient", and as one reviewer noted, the suggestion has been made that the site saw more tool manufacture than tool use. In reply, it is pointed out that heavy quarry damage makes it difficult to judge spatial patterning. But if the excavated area is only a small residual remnant, how can one be sure that this assemblage of stone artifacts captures the full range of Denisovan technological behavior at this site? The very low proportion of retouched pieces (34 out of 1,366) and the high share of cortical flakes (52.6%) strongly indicate that primary core reduction and raw material testing were the main activities carried out at the site.

This observation is both valid and important. Rather than presenting the Bianfu Cave lithic assemblage as a complete toolkit, it is more methodologically sound and convincing to frame it as reflecting a narrower set of activities - for example, initial core reduction and expedient, on-site tool manufacture for butchery.

Reply: We thank the reviewer for this constructive comment. We agree that the excavated area represents only a small remnant of the original site and therefore cannot be assumed to capture the full range of Denisovan technological behaviours. More generally, archaeological assemblages often reflect specific activities rather than complete technological systems. We have therefore revised the text to avoid presenting the Bianfu Cave lithic assemblage as a comprehensive toolkit. Instead, we now interpret it more cautiously as documenting a technological system centred on expedient core reduction, on-site production of simple flake tools, and their immediate use, likely in conjunction with carcass processing and other subsistence-related activities. We believe this revised interpretation is better supported by the composition of the assemblage, including the predominance of cortical flakes and the low proportion of formally retouched tools, while remaining fully consistent with our broader conclusions concerning Denisovan technological organisation. The corresponding revision has been made in SI-D (page 33).

The raw materials are reported to originate from the Yinhe River, located approximately 2 km from the site. However, it remains unclear whether a systematic geological or archaeological survey was conducted to verify this provenance. If such a survey was undertaken, its methodology and results should be explicitly presented; if not, the claim should be appropriately qualified. Similarly, the cortex coverage data presented in Supplementary Figure 25 are reported solely as percentages, without raw data. Including these data would enable readers to better assess the degree of reduction intensity and evaluate the representative of the sample.

Reply: We thank the reviewer for raising these important points. Concerning raw material provenance, we conducted a systematic geological survey of the Yinhe River during the excavation to document the availability and relative abundance of potential knappable raw materials. We have now expanded the description of this survey in the revised main text (pages 6-7) and SI-D (page 28), and added a new Supplementary Figure 20 illustrating the surveyed riverbed, representative sampling locations, and the relative frequencies of the different rock types recorded. These new data provide the empirical basis for identifying the Yinhe River as the principal source of the lithic raw materials recovered at Bianfu Cave.

Regarding cortex coverage, the raw data for every analysed specimen were already provided in the online Excel dataset accompanying the manuscript, which was originally prepared to ensure full reproducibility of the statistical analyses conducted in R. To make these data more readily accessible, we now explicitly refer readers to this dataset in the caption of Supplementary Figure 27. This revision makes the underlying data easier to locate and allows readers to independently evaluate cortex coverage, reduction intensity, and sample representativeness.

The Bianfu Cave teeth are acknowledged to show a mix of traits, sharing features with Denisovans and with other archaic hominins, such as those from Hualongdong. The attribution to Denisovans relies mainly on paleoproteomic evidence from a study (Rao et al.) that is still under review. However, the proteomic analysis receives only a very brief summary (in lines 222-225. More detail is required on which specimens were analyzed (the P4 and one M2) and the key peptide sequences that support the identification. Without this information, the morphological argument remains vague, and readers are forced to accept the Denisovan classification largely based on trust in unpublished work.

Reply: The reviewer is completely correct about this. The attribution of Bianfu teeth to Denisovans mainly relies on the unique mutations of Denisovans. All five specimens (the tooth YHB3518, the tooth YHB3075, the parietal BFD767, the parietal BFD769, and the radius BFD771) carry a Denisovan diagnostic marker in the collagen α-2(I) chain (COL1A2 R996K). This information is presented in a separate study by Rao et al., which is currently accepted in principle. Accordingly, we have revised the relevant sentence on page 3 of the main text to read: "Palaeoproteomic analyses of five hominin specimens (one P_3, one M_2, two parietal bones, and radius) assign them to Denisovans", and have referred readers to Rao et al. for the complete analytical procedures and proteomic dataset. It should also be noted that in the geometric morphometric analyses of the EDJ of M_2s, which are provided in the present study, the two specimens from Bianfu Cave differ from the morphology of *H. erectus*, Neanderthals and *H. sapiens*, and are closest to the Denisovan specimens from Baishiya and Tam Ngu Hao 2, as well as to the Hualongdong teeth that possibly represent early Denisovans. These results based on morphology are thus consistent with those obtained with molecular analyses.

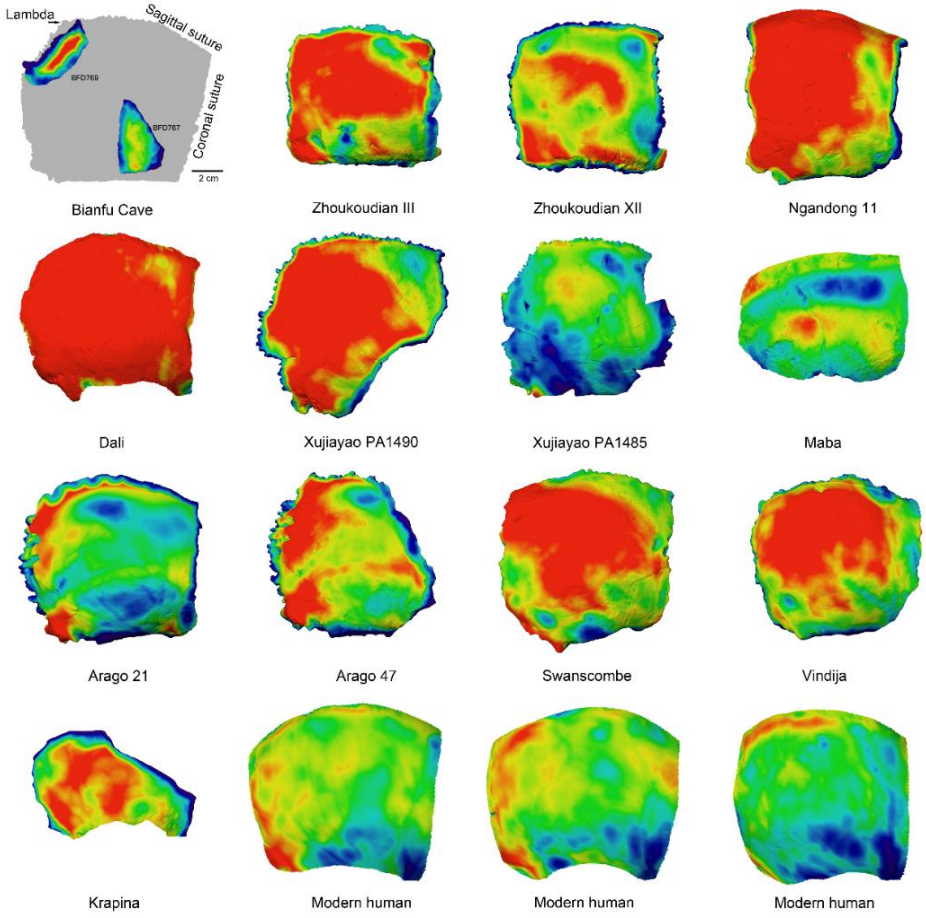
Age estimates for the teeth are now provided in the Supplementary Information-C (SI-C), but they are based on dental developmental standards derived exclusively from modern human populations. Given that these standards may not be directly applicable to Middle Pleistocene archaic hominins - whose growth and development could differ significantly - their use requires explicit justification. In the absence of such validation, the potential limitations and uncertainties in the age estimates should be pointed out.

Reply: We thank the reviewer for this important comment and agree that dental developmental standards derived from modern humans may not be directly applicable to Middle Pleistocene archaic hominins. Unfortunately, in the absence of associated deciduous teeth or first permanent molars preserving birth-related developmental markers, it is not currently possible to estimate the age at death of the Bianfu individuals using taxon-specific developmental criteria. We therefore relied on modern human standards as the best available comparative framework.

To justify this approach, we now refer to previous work showing that the dental developmental pattern of the Middle Pleistocene Xujiayao hominins is broadly comparable to that of modern humans (Xing et al., 2019). Xujiayao represents an appropriate comparative sample because these East Asian archaic hominins are chronologically close to, and share several morphological characteristics with, the Bianfu specimens (Xing et al., 2015; Wu et al., 2024; Shao et al., 2026). At the same

time, we now explicitly acknowledge in the revised text that the estimated ages should be regarded as approximate and that additional data on Denisovan dental growth and development will be required to validate this assumption. These clarifications have been added to SI-C (pages 18-19).

The cranial remains consist of parietal fragments with thicknesses of 7.6 mm and 10 mm, respectively. Unfortunately, the manuscript does not place these measurements within the broader comparative framework - neither other known Denisovan cranial specimens (if has) nor relative to contemporaneous East Asian archaic hominins. Such comparisons may significantly strengthen palaeoanthropological understanding of the findings. Similarly, the radius is described as exhibiting a "medially facing radial tuberosity" - previously documented in late Neanderthals. If possible, a brief discussion of functional implications of this trait, particularly in light of emerging evidence on Denisovan anatomy and ecology, would enrich our knowledge on this species.
Reply: We thank the reviewer for this valuable suggestion. The comparisons of Bianfu Cave parietal bones and radius with other specimens (especially the contemporaneous East Asian archaic *Homo*) were presented in details in Rao et al. (which has been accepted in principle) and briefly introduced here (see Extended Data Fig. 8 and Supplementary Table 1). We have also expanded the discussion of the medially facing radial tuberosity. The revised main text (page 6) now explains that a more posterior displacement of the radial tuberosity increases the moment arm of *M. biceps brachii* during forearm supination (Trinkaus & Churchill, 1988).



Extended Data Fig. 8. The vault thickness of the two parietal fragments from Bianfu Cave (BFD767 and BFD769) and the comparative samples, including Asian late *H. erectus* (Zhoukoudian and Ngandong), East Asian late Middle Pleistocene archaic *Homo* (Dali, Xujiayao, and Maba), *H. heidelbergensis* (Arago and Swanscombe), Neanderthals (Vindija and Krapina), and recent modern humans.

Supplementary Table 1. The bone thickness of parietal at the eminence for different comparative specimens.

Taxonomy	Bone thickness range at the parietal eminence (in mm)	Data source
Zhoukoudian *H. erectus* (n=8)	5–16	References [28]
East Asian late Middle Pleistocene archaic *Homo* (n=6)	6–12.6	References [29-31]
H. neanderthalensis (n=32)	5–17	References [32]
H. heidelbergensis (n=9)	6.5–11.5	References [32,33]
Early modern human (n=33)	3.5–12	References [32,34-37]

A more complete analysis of skeletal part representation has now been included (SI-F, Supplementary Table 25), noting that appendicular elements appear over - represented once bone fragments assigned to size classes are counted. However, the earlier taxon - identified sample showed a “head-and-foot-dominated” pattern. This mismatch calls for a clearer explanation: is it simply that teeth and mandibles are easier to identify than postcranial pieces, or does it point to a real taphonomic bias? In addition, more detail on cut-mark location and orientation would help support the “carcass defleshing” interpretation (SI-F, line 1280). A table or figure laying out cut-mark distribution by skeletal element would be welcome.

Reply: We thank the reviewer for this helpful comment. The apparent discrepancy between the previously reported "head-and-foot-dominated" pattern and the more complete skeletal-part representation results primarily from differences in taxonomic identifiability rather than from a genuine taphonomic pattern. The earlier analysis was based only on taxonomically identified remains, which are disproportionately represented by teeth, mandibles, antlers and epiphyseal fragments because these elements preserve diagnostic morphological features. In contrast, the expanded analysis now includes the numerous shaft fragments that cannot be confidently assigned to species but can be identified as long-bone elements. Many of these fragments exhibit fresh fracture surfaces and percussion notches consistent with marrow extraction. We have clarified this point in the revised SI-F (page 46).

We also agree that a more detailed presentation of the cut-mark evidence strengthens the interpretation of carcass processing. We have therefore revised the relevant section of SI-F (page 50) and added a new Supplementary Figure 44 summarizing cut-mark distribution by skeletal element, anatomical location, orientation and length. The new synthesis shows that oblique cut marks predominate on long-bone fragments, whereas transverse marks are less frequent and parallel marks are rare, a distribution consistent with defleshing activities documented in experimental and archaeological assemblages.

Several bone tools are described, including retouchers and intermediate pieces. The functional interpretation of these tools relies largely on macroscopic inspection. It is noted that "further quantitative use- wear analyses will be required" (SI- D, lines 871-872). Given the importance of these objects for understanding Denisovan behavior, the use- wear analysis is suggested to be included.

Reply: We thank the reviewer for this important suggestion and agree that use-wear analysis can provide valuable information on the function of bone tools. In the present assemblage, however, the situation differs between the retouchers and the remaining modified bone artefacts. The identification of the retouchers is based on well-established macroscopic diagnostic criteria that have been extensively validated through experimental and archaeological studies. Consequently, additional high-magnification use-wear analysis is unlikely to alter their functional interpretation.

In contrast, the functions of the four non-retoucher bone tools remain uncertain, and these are the specimens for which we considered further use-wear analyses desirable. Unfortunately, bone surface preservation constraints (decalcification and concretions) of these artefacts severely limits such analyses. Under these conditions, high-resolution microwear observations cannot be conducted reliably. We therefore consider a cautious macroscopic assessment to be the most appropriate interpretation at present, while explicitly acknowledging that future discoveries of better-preserved specimens may permit more detailed functional analyses. We have clarified this point in the revised SI-D (page 38).

The conclusion that hominins were the primary bone-accumulating agents rests largely on the relative abundance of anthropogenic traces - specifically cut marks and percussion marks - compared to modifications attributable to carnivores or rodents (SI-F, lines 1266-1298). However, the overall frequency of these human-induced marks remains low: cut marks occur on just 1.2% of the analyzed specimens. While this pattern is consistent with hominin involvement in carcass processing, it does not preclude a meaningful contribution from other taphonomic agents - including carnivore activity, natural mortality, or post-depositional processes. Moreover, as the text itself notes, poor bone surface preservation could also explain the low modification rates. A more measured handling of the taphonomic data's limits would be appropriate.

Reply: We agree that the relatively low frequency of anthropogenic surface modifications, together with the variable preservation of bone surfaces, requires a cautious interpretation of the taphonomic evidence. We have therefore revised the text of SI-F (pages 49–51) to moderate our wording and to integrate the different zooarchaeological and taphonomic observations that collectively support our interpretation.

Rather than relying solely on cut-mark frequencies, our interpretation is now based on the convergence of several independent observations. First, anthropogenic modifications (cut marks, percussion marks, percussion scars and pits) occur on 7.53% of the analysed specimens, whereas carnivore- and rodent-induced modifications occur on only 1.3%. Second, the mortality profiles of the dominant herbivore taxa are

dominated by prime-age adults, a pattern more consistent with selective hunting by hominins than with carnivore accumulations. Third, although trampling marks indicate some post-depositional disturbance within the cave, the absence of abrasion and extensive rounding suggests that the assemblage has not undergone significant transport. We also now explicitly acknowledge that poor cortical preservation probably resulted in an underestimation of surface modifications and that contributions from other accumulating and modifying agents cannot be entirely excluded (pages 49–51 in SI-F).

A Bayesian model now places a gap of 26.7-51.1 ka between Layers 5 and 4. This is a significant stratigraphic break. Does this break mark a period of no site occupation, or could it result from erosion or a pause in deposition? If the site was indeed unoccupied during this interval, the previous claim of "long-term" occupation becomes much harder to sustain. Therefore, it remains necessary to clarify whether the occupation at the site was continuous, or instead consisted of separate, repeated visits separated by long intervals of abandonment.

Reply: We thank the reviewer for raising this critical chronological issue. We agree that the Bayesian model identifies a substantial sedimentation hiatus of approximately 27–51 kyr between Layers 5 and 4, and that its implications for site occupation should be discussed more explicitly. At present, however, the nature of this hiatus remains uncertain. It could reflect a genuine interruption in hominin occupation, an erosional episode that removed part of the sequence, or a prolonged period of reduced or absent sediment accumulation. The available evidence does not allow us to distinguish confidently between these alternatives.

We have therefore revised the main text (page 4) to explicitly acknowledge this uncertainty. The revised text now states that we cannot infer hominin presence at the site during the interval between the end of Layer 5 (130–107 ka) and the beginning of Layer 4 (86–72 ka). Consequently, rather than implying continuous occupation, we now interpret the Bianfu sequence as documenting repeated Denisovan occupations spanning more than 100,000 years, while recognising that these occupations may have been separated by periods during which the site was either abandoned or not preserved in the archaeological record.

Several references in the supplementary information appear incomplete or are formatted incorrectly (e.g., references 67-75 in SI-D). All references need to be checked carefully for accuracy and consistency.

Reply: All references in the main text and SI have been carefully verified for accuracy and consistency.

Some details that need to be revised in the manuscript are as follows：

1, In line 468. Fig.1.a, missing a scale bar; Fig.1.d, the depth should be in centimeters, not meters.

Reply: Thanks for pointing out these issues. Fig. 1 has been revised accordingly.

2, In line 509. The scale bars in Fig.3 are not clear. It’s difficult for readers to determine

which samples are indicated by two liner scales. It would be better to indicate it somewhere. Additionally, in Fig.3. a,b,c,d,e., it would be better to indicate the anatomically left or right sides of the teeth and the radius, this would be more accessible for readers who are not anatomists.
Reply: Thanks for this suggestion. We have added "Upper scale bar: teeth; lower scale bar: radius and parietal bones" into the legend to specify which samples were indicated by two linear scales. We also have indicated the anatomically left or right sides of the teeth and the radius in the new legend of Fig. 3.

3, The scale bars in Fig.4. is still unclear. Authors may indicate which bar is match to the stone artifacts, for example.
Reply: We have added the following note to the legend of Fig. 4 to clarify the scale-to-specimen correspondence: "Vertical scale bar: stone artefacts; horizontal scale bars: each corresponds to a separate bone tool."

4, In Fig.4.a, it seems that 465 is not a core of unifacial flaking.
Reply: Thanks for pointing out this. The core in Fig. 4a is defined as unifacial, as only two small removals occur on the opposite face, well within the scope of unifacial flaking. This has been clarified in the revised Fig. 4 legend.

5, There are many places where the confusion between "artifact" and "artefact" in the manuscript.
Reply: We thank the reviewer for catching this inconsistency. We have now carefully reviewed the entire manuscript and standardized the spelling throughout.

6, In the "Methods，Excavation" section, the description is confusing. It states earlier that "T2 is a 3*10 m unit located in the central part of the slope", but the following paragraph says "T2. The minimum excavation area at T2 is approximately 7 m² (Layer 12), and the maximum is approximately 11 m² (Layers 7 and 8).". I think the readers can't possibly understand what you are saying?
Reply: We thank the reviewer for highlighting this confusing description. The relevant text has been revised (page 17 in the "Method" section) to clarify that T2 is a 2×6 m unit located on the central part of the slope, encompassing a small portion of the cave wall.

7, In the "Extended Data Fig.3.", the anatomically position of YHB2890 and YHB3075 are incomplete.
Reply: Thanks for pointing this out. We have added the anatomical position (left or right) into the new legend.

8，In the "Extended Data Fig.4.", why were Cave I2 of Bianfu and Cave P4 of Bianfu not given serial numbers?
Reply: Thanks for pointing this out. The serial numbers for these two teeth have been added into the new legend.

9, In the “Extended Data Fig.8.”, there is overlap between a-g and e-o, is h-o?
Reply: Thanks for pointing this out. The “e-o” has been revised to “h-o” in the new legend.

10, In the “Extended Data Fig.9. and Fig.10”, the using of “a,b,c” or “a-c” should be consistent in the manuscript.
Reply: Thanks for pointing this out. The labels “a,b,c” have been revised to “a-c” in the legends of both figures to ensure consistency with the other figure legends.

Referee #2 (Remarks to the Author):
I am grateful to the authors for addressing our comments in so much detail, it's especially nice to have the more detailed zooarchaeological and bone tool analyses, and everything separated out by layer. This will be a good resource for future comparisons as well.
I feel the paper is ready for publication, but I found a few very minor issues:
Line 150: human -> humans
Line 340: Denisovans -> Denisovans'
Caption of Extended Data Fig. 4: " The hominin incisors and premolars unearthed from the Bianfu Cave. " - there's only one incisor and one premolar, so they should be in singular.
Reply: We are truly grateful for the reviewer’s thoughtful and encouraging assessment of our revisions. We have also carefully addressed the few minor points raised.

Referee #4 (Remarks to the Author):
The authors have taken my previous comments seriously and have addressed them thoroughly. In particular, Fig. 2 has been substantially improved. it is now both more informative and visually effective, and I am satisfied with the revisions made. Based on the Quaternary stratigraphic and chronological framework, as well as the reconstructed climatic and environmental background, I consider the findings to be robust and well supported. The conclusions drawn by the authors are scientifically sound and appropriately cautious. Overall, I am pleased with the revised manuscript and recommend it for publication.
Reply: We are truly grateful for the reviewer’s thoughtful and encouraging assessment of our revisions. We also greatly appreciate the reviewer’s confidence in the paper’s readiness for publication.

Referee #5 (Remarks to the Author):
The revised manuscript significantly improves upon the original submission and I recommend it for publication. I particularly appreciate the inclusion of a chart correlating the site’s chronology and paleoenvironmental proxies for the region, as well

as the detailed explanation of the taphonomy and zooarchaeology of the site. I also agree that the new title more honestly reflects the conclusions that can be drawn from the available data. Last, but not least, I can confirm that the lithic analysis results are reproducible, as attested by the attached R code.

Referee #5 (Remarks on code availability):

I can confirm that the lithic analysis results are reproducible, as attested by the attached R code.

Reply: We are truly grateful for the reviewer's thoughtful and encouraging assessment, endorsement of the new title, and confidence in the manuscript's readiness for publication.

Referees' comments:

Referee #1 (Remarks to the Author):

The authors have provided satisfactory responses and revisions to our comments. I believe that the current version of the manuscript is perfect in terms of stratigraphy, chronology, Paleolithic archaeology, zooarchaeology, and paleoanthropology. The analyzed materials, methods, and data all have high credibility. All the research details support a reliable conclusion. I strongly recommend that this manuscript be published in the Nature.

Response: We are truly grateful for the reviewer's thoughtful and encouraging assessment of our revisions. We also greatly appreciate the reviewer's confidence in the paper's readiness for publication.