Confirmed archaeological evidence of water deer in Vietnam: relics of the Pleistocene or a shifting baseline?

C. M. Stimpson, S. O'Donnell, N. T. M. Huong, R. Holmes, B. Utting, T. Kahlert and R. J. Rabett

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Revised submission: 2 June 2021
Final acceptance: 7 June 2021

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

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Review History

RSOS-210529.R0 (Original submission)

Review form: Reviewer 1

Is the manuscript scientifically sound in its present form?
Yes

Are the interpretations and conclusions justified by the results?
Yes

Is the language acceptable?
Yes

Do you have any ethical concerns with this paper?
No

Have you any concerns about statistical analyses in this paper?
No
Recommendation?
Accept with minor revision (please list in comments)

Comments to the Author(s)
Stimpson et al. have presented new specimens from Hang Thung Binh 1 cave, Vietnam, which can be attributed to the water deer, Hydropotes inermis. These novel late Pleistocene occurrences of this species represent the southern-most extent of the range, both extant and fossil, and this represents an important contribution to our knowledge of the biogeography of this taxon. The authors have made adequate comparisons to extant cervoids from the region and have provided a cogent argument for why these specimens represent water deer. The Quaternary fossil record of Southeast Asia remains largely understudied compared to East Africa or North America, and this study provides another piece of the puzzle of how extant mammal communities in the region have evolved.

I thought the study was very interesting, since not much is known about fossil water deer. It’s great to see some basic taxonomic work from this region, couched within the larger topic of shifting baselines and Quaternary extinctions and extirpations. I thought the morphological and statistical analyses were quite sufficient to determine whether the specimens under investigation were in fact water deer. My biggest concern was with the structure of the discussion. It was a little hard to follow, and did not seem, to me at least, to flow well in an “answering research questions” framework. This is not to say that the discussion needs a re-write, but I would say that a re-structuring would benefit the reader.

For example, lines 378-380 seem to present a good question that can be addressed with your new data, and so do lines 412-414. I think leading with what you found, i.e., Vietnamese water deer in the latest Pleistocene, and how that can inform the idea of shifting baselines or Quaternary extinctions/extirpations would provide a more impactful discussion. It would also harken back to your introduction where you introduce these ideas at the beginning. Your discussion about the changing floral regimes through the late Pleistocene and Holocene could follow, providing supporting arguments for why the water deer are found in their extant range. While reading the paper, it wasn’t really clear to me how the climatic changes that occurred regionally, i.e. Heinrich event 1, etc, were related to the patterns of vegetation change, and therefore the water deer. It might be worth simplifying that section and making it more streamlined.

I also think the manuscript would benefit from a discussion about Quaternary extinctions in the region, and importantly faunal persistence, range shifts, and metapopulation dynamics. What you have seems to be a relict Pleistocene population that got extirpated. There’s a lot of exciting research coming out of the region such as the giant muntjac that you described from Northern Vietnam, the work Sam Turvey has done on population collapses in muntjac, and the new species of gibbon from China. It would help show that there is still much to be learnt from Pleistocene and Holocene records from this part of the world. Moreover, it would be hugely beneficial to see what other species in the region show similar patterns. I know off-hand that all three species of asian rhinos were once more widely distributed through South Asian, Southern China, and Southeast Asia, but are now relegated to isolated pockets.

Ending with your conservation and re-introduction message would in my mind be a good way to wrap up this fascinating story. Overall, I think this is a great paper. I had additional minor edits, that I have included in the attached pdf (Appendix A).
Review form: Reviewer 2

Is the manuscript scientifically sound in its present form?
Yes

Are the interpretations and conclusions justified by the results?
Yes

Is the language acceptable?
Yes

Do you have any ethical concerns with this paper?
No

Have you any concerns about statistical analyses in this paper?
No

Recommendation?
Accept with minor revision (please list in comments)

Comments to the Author(s)

Dear authors,

I have read your manuscript, titled "Confirmed archaeological evidence of water deer in Vietnam: relics of the Pleistocene or a shifting baseline?", on evidence of the first Vietnamese Hydropotes population with much interest and pleasure. This is a clearly written transdisciplinary manuscript based on a careful conducted study what not only bridges fields palaeontology/archaeology (past) and conservational biology (present and future) in a model manner, but also guides to future management of conservational measures for Vulnerable species and hints to the mandatory consideration of the big picture as a necessity for reasonable procedures. On the other hand, it provides as well valuable additional information to mammal zooarchaeologists and palaeontologist on the fossil record of Hydropotes inermis and its ancient habitat. Your methodology is rigorous and the conclusions are fully supported by the data. I congratulate on the comparative morphology of the teeth among Pecora, which is really not an easy task, but you managed that with bravery.

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Decision letter (RSOS-210529.R0)

We hope you are keeping well at this difficult and unusual time. We continue to value your support of the journal in these challenging circumstances. If Royal Society Open Science can assist you at all, please don’t hesitate to let us know at the email address below.

Dear Dr Stimpson

On behalf of the Editors, we are pleased to inform you that your Manuscript RSOS-210529 "Confirmed archaeological evidence of water deer in Vietnam: relics of the Pleistocene or a shifting baseline?" has been accepted for publication in Royal Society Open Science subject to minor revision in accordance with the referees’ reports. Please find the referees’ comments along with any feedback from the Editors below my signature.

We invite you to respond to the comments and revise your manuscript. Below the referees’ and Editors’ comments (where applicable) we provide additional requirements. Final acceptance of your manuscript is dependent on these requirements being met. We provide guidance below to help you prepare your revision.

Please submit your revised manuscript and required files (see below) no later than 7 days from today’s (ie 26-May-2021) date. Note: the ScholarOne system will ‘lock’ if submission of the revision is attempted 7 or more days after the deadline. If you do not think you will be able to meet this deadline please contact the editorial office immediately.

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Thank you for submitting your manuscript to Royal Society Open Science and we look forward to receiving your revision. If you have any questions at all, please do not hesitate to get in touch.

Kind regards,
Royal Society Open Science Editorial Office
Royal Society Open Science
openscience@royalsociety.org

on behalf of Dr Emily Lindsey (Associate Editor) and Pete Smith (Subject Editor)
openscience@royalsociety.org

Associate Editor Comments to Author (Dr Emily Lindsey):
Associate Editor: 1
Comments to the Author:
The article was reviewed by two experts, both of whom noted the interest and value of the article and recommended publishing with minor revisions. The two main concerns the reviewers raised that should be addressed for publication were:
1. A more well-developed description of the tooth morphology, and ensuring accuracy and consistency with the diagnostic references.
2. A restructuring of the discussion for clarity and highlighting the importance of the presented study for broader research and conservation-related questions.

Both reviewers also made substantive in-line comments in the manuscript .pdf’s that the authors should address as well.

Congratulations on a well-received article! I look forward to the revised submission.

Reviewer comments to Author:
Reviewer: 1

Comments to the Author(s)
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Reviewer: 2
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===PREPARING YOUR MANUSCRIPT===

Your revised paper should include the changes requested by the referees and Editors of your manuscript. You should provide two versions of this manuscript and both versions must be provided in an editable format:
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a 'clean' version of the new manuscript that incorporates the changes made, but does not highlight them. This version will be used for typesetting.
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At Step 7 'Review & submit', you must view the PDF proof of the manuscript before you will be able to submit the revision. Note: if any parts of the electronic submission form have not been completed, these will be noted by red message boxes.

Author's Response to Decision Letter for (RSOS-210529.R0)

See Appendices D & E.

Decision letter (RSOS-210529.R1)

We hope you are keeping well at this difficult and unusual time. We continue to value your support of the journal in these challenging circumstances. If Royal Society Open Science can assist you at all, please don't hesitate to let us know at the email address below.

Dear Dr Stimpson,

I am pleased to inform you that your manuscript entitled "Confirmed archaeological evidence of water deer in Vietnam: relics of the Pleistocene or a shifting baseline?" is now accepted for publication in Royal Society Open Science.

If you have not already done so, please remember to make any data sets or code libraries 'live' prior to publication, and update any links as needed when you receive a proof to check - for instance, from a private 'for review' URL to a publicly accessible 'for publication' URL. It is good practice to also add data sets, code and other digital materials to your reference list.
You can expect to receive a proof of your article in the near future. Please contact the editorial office (openscience@royalsociety.org) and the production office (openscience_proofs@royalsociety.org) to let us know if you are likely to be away from e-mail contact -- if you are going to be away, please nominate a co-author (if available) to manage the proofing process, and ensure they are copied into your email to the journal. Due to rapid publication and an extremely tight schedule, if comments are not received, your paper may experience a delay in publication.

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On behalf of the Editors of Royal Society Open Science, thank you for your support of the journal and we look forward to your continued contributions to Royal Society Open Science.

Kind regards,
Royal Society Open Science Editorial Office
Royal Society Open Science
openscience@royalsociety.org

on behalf of Dr Emily Lindsey (Associate Editor) and Pete Smith (Subject Editor)
openscience@royalsociety.org

Associate Editor Comments to Author (Dr Emily Lindsey):
Associate Editor: 1
Comments to the Author:
(There are no comments.)

Reviewer comments to Author:

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### Appendix A

#### ROYAL SOCIETY OPEN SCIENCE

**Confirmed archaeological evidence of water deer in Vietnam: relics of the Pleistocene or a shifting baseline?**

| Journal: | *Royal Society Open Science* |
|----------|-----------------------------|
| Manuscript ID | RSOS-210529 |
| Article Type: | Research |
| Date Submitted by the Author: | 28-Mar-2021 |
| Complete List of Authors: | Stimpson, Christopher; Queen's University Belfast School of Natural And Built Environment; Oxford University Museum of Natural History O'Donnell, Shawn; Queen's University Belfast, School of Natural and Built Environment Mai Huong, Nguyen Thi; Vietnam Academy of Social Sciences, Institute of Archaeology Holmes, Rachael; University of Leicester, School of Geography, Geology and the Environment Utting, Benjamin; University of Cambridge, Archaeology Kahlert, Thorsten; Queen's University Belfast Rabet, Ryan; Queen's University Belfast |
| Subject: | taxonomy and systematics < BIOLOGY, palaeontology < BIOLOGY, environmental science < BIOLOGY |
| Keywords: | water deer, Hydropotes inermis, zooarchaeology, Vietnam, Pleistocene |
| Subject Category: | Ecology, Conservation, and Global Change Biology |

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*Does your article include research that required ethical approval or permits?:*
This article does not present research with ethical considerations

*Statement (if applicable):*
CUST_IF_YES_ETHICS :No data available.

**Data**

*It is a condition of publication that data, code and materials supporting your paper are made publicly available. Does your paper present new data?:*
Yes

*Statement (if applicable):*
The datasets supporting this article have been uploaded as electronic supplementary material.

**Conflict of interest**

I/We declare we have no competing interests

*Statement (if applicable):*
CUST_STATE_CONFLICT :No data available.

**Authors’ contributions**

This paper has multiple authors and our individual contributions were as below

*Statement (if applicable):*
CMS and RR conceived the study; CMS conducted analyses and identification and drafted the manuscript with contributions from all authors; CMS, RH and BU conducted the review of Quaternary records of *Hydropotes inermis*; CMS and BU performed statistical tests; TK translated German language source material; CMS, BU, RR, TK, carried out excavation, site analysis and recording; SO and NTMH produced the paleoenvironmental synthesis. All authors revised the manuscript and gave final approval for publication.
Confirmed archaeological evidence of water deer in Vietnam: relics of the Pleistocene or a shifting baseline?

C.M. Stimpson\textsuperscript{1,2}, S. O’Donnell\textsuperscript{1} N.T.M. Huong\textsuperscript{3} R. Holmes\textsuperscript{4}, B. Utting\textsuperscript{5}, T. Kahlert\textsuperscript{1} and R.J. Rabett\textsuperscript{1}

\textsuperscript{1}School of Natural & Built Environment, Queen’s University Belfast, Elmwood Avenue, Belfast BT7 1NN, UK.
\textsuperscript{2}Oxford University Museum of Natural History, Parks Road, Oxford, OX1 3PW, UK.
\textsuperscript{3}Vietnam Academy of Social Sciences, Institute of Archaeology, 61 Phan Chu Trinh Str., Hoan Kiem, Hanoi, Vietnam.
\textsuperscript{4}School of Geography, Geology and the Environment, University of Leicester, University Road, LE1 7RH, UK
\textsuperscript{5}Department of Archaeology, University of Cambridge, Downing Street, Cambridge CB2 3DZ, UK

Author for correspondence:
Christopher M. Stimpson
Email: c.stimpson@qub.ac.uk

Abstract
Studies of archaeological and palaeontological bone assemblages increasingly show that the historical distributions of many mammal species are unrepresentative of their longer-term geographical ranges in the Quaternary. Consequently, the geographical and ecological scope of potential conservation efforts may be comparatively narrow. Here we consider a case in point, the water deer \textit{Hydropotes inermis}, which has historical native distributions in eastern China and the Korean peninsula.

We present morphological and metric criteria for the taxonomic diagnosis of mandibles and maxillary canine fragments from Hang Thung Binh 1 cave in Tràng An World Heritage Site, which confirm the prehistoric presence of water deer in Vietnam. Dated to between 13,000 and 16,000 years before present, the specimens are further evidence of a wider Quaternary distribution for these Vulnerable cervids, are valuable additions to a sparse Pleistocene fossil record and confirm water deer as a component of the Upper Pleistocene fauna of northern Vietnam. We also examine the environmental context of the water deer of Tràng An before considering if the new finds represent relics of an Upper Pleistocene population, or are an early indication of an unrecognised southerly distribution with possible implications for the conservation of the species in the future.

Keywords: water deer, \textit{Hydropotes inermis}, zooarchaeology, Vietnam, Pleistocene

1. Introduction
The last 2.58 million years, the Quaternary period, saw the rise of our own species and the evolution of a modern mammal fauna [1]. Now, as the mechanisms, scale and rapidity of recent human impact on ecosystems worldwide have no geological analogue, efforts to characterise the “Anthropocene” are gaining impetus [2-3] and the global biodiversity crisis becomes increasingly acute [4-6]. With mammal populations in decline, the necessity and utility of longer-term Quaternary records to provide “pre-Anthropocene” insights into populations, diversity and geographical range is being demonstrated [6-11]. The principal warrant of this longer-term perspective is that baselines for quantification and description (e.g. species inventories, geographic range, habitat requirements etc.) are set in the context of
recent, ecological timescales (typically < 100 years), where populations may have already experienced degradation through human activities (e.g. direct exploitation, habitat modification) for millennia [6, 11-12].

A dilemma of this “shifting baseline syndrome” [13-14] is that if by the time records began species distributions were already unrepresentative of much of the Quaternary, how effective are conservation measures likely to be in the context of degraded habitats and range [15]? In this paper we consider a case-in-point, the water deer, *Hydropotes inermis* (Swinhoe, 1870). We present new archaeological evidence that confirms the presence of this small cervid, which has experienced pronounced recent declines in geographical range and numbers [16-18], in prehistoric Vietnam.

Water deer are currently found in eastern China and the west of the Korean peninsula (figure 1). A comprehensive review of their biology, life and natural history can be found in Schilling and Rössner [18]. In brief, this species is a small bodied, chestnut-coloured, solitary deer (Cervidae), which stands approximately 0.5 m tall at the shoulder and weighs up to 15 kg. Uniquely in the Cervidae, the males do not develop antlers but instead are characterised by long maxillary canine teeth: the current balance of evidence suggests that antler loss was secondary [18]. Water deer are almost entirely solitary beyond the rut, unlike most deer species, and thus are more akin to musk deer (Moschidae) and chevrotains (Tragulidae).

Though understudied, the water deer is a potentially important model organism to investigate the evolution of the Cervidae generally and antlers, specifically [17-19].

Two subspecies have been recognized: the Chinese water deer *H. inermis inermis* (Swinhoe, 1870) and the Korean water deer *H. inermis argyropus* (Heude, 1884) although their validity has been questioned on molecular and morphological grounds [19, 21-22]. Accurate estimates of current numbers of Asian water deer are difficult to determine although the species is in decline and is classified as Vulnerable by the IUCN [16]. Chinese populations have recently experienced steep declines in numbers and a reduction in geographical range and are now present in isolated fragments in the eastern Yangtze Basin and the Zhoushan Islands (figure 1). Hunting pressure and loss of habitat are reported to be the principal causes of this decline [23].

In North Korea, water deer are presently distributed along the west coast (figure 1) and are believed to be present in most of South Korea where, in some areas, the animals are sufficiently numerous to conflict with agricultural interests [24-25]. Water deer have been the subject of re-introduction and release efforts in China and the Koreas in the twentieth and twenty first centuries [21, 25-26]. Translocated populations in the United Kingdom and France (source populations first introduced in 1900 and 1970, respectively) now account for approximately 40% of the global population [17]. Within the United Kingdom, their distribution is limited to the Midlands and East Anglia and restricted by suitable habitat availability [27]. A population was also intentionally translocated to the north-east of the Korean Peninsula by the North Korean government in the 1960’s [21] and has since potentially expanded their range into the Khasanskiy district of Russia. There is currently not enough evidence to determine whether the Russian populations are transient, or stable and reproducing [28].

Historical records indicate that water deer ranged over eastern China and were found between Liaoning in the north and Guangdong in the south, as far as the lower Yangtze basin, as well as central and southern Korean peninsula [25, 30] (figure 1). Bones and teeth of water deer recovered from Holocene-age (11.65 thousand years before present [BP] to recent [31], where “present” is held at 1950) archaeological sites in the region [11, 32-36] indicate an even
wider former geographical distribution; as far west as eastern Tibet (Xizang), as far as Inner Mongolia in the north, to the east of the Korean Peninsula and into southern China (Figure 1). Notably, recent archaeological investigations of four Iron Age sites (1300-400 years BP) have also produced evidence of water deer in central Taiwan [32]. While not all archaeological sites represent contemporaneous records, these data indicate that the water deer now occupies less than ten percent of its former maximum Holocene range [11].

Earlier, Quaternary records of water deer from the Pleistocene (2.58 million to 11.65 thousand years before present [37]) are scarce and the accuracy of some fossils identifications have been queried [cf. 50 and 51]. Six Middle Pleistocene (770,000 to 126,000 years BP) fossil sites have yielded records across southern, central, and northern China. Remarkably, records also include finds from Tarumi NT cave in western Japan where skeletal remains referred to “Hydropotes cf. inermis” were recovered with a fauna that contained both exotic and extinct forms [44]. Upper Pleistocene (126,000 to 11,650 years BP) records are limited to four sites in central China and one site in the north, near the Korean Peninsula (Figure 1).

There are no recent, historical or confirmed archaeological records of water deer in Vietnam. The possibility of the prehistoric presence of the species was raised in a preliminary list of identified Upper Pleistocene animal bone in 2009 [52]. The remains that were recovered by a joint Vietnamese-Bulgarian project during investigations of Mai Da Dieu (a rock shelter approximately 30 km to the south of Tràng An, the focus of the present study) in the late 20th century. The list included “Chinese water deer, Hydropotes inermis (Swinhoe, 1870)”. No figures, stratigraphic provenance, or data, however, were provided and the author points out that “these taxonomic attributions are provisional, pending additional study” [52: 207]. More recently, a collection of palaeontological fossil teeth in 2020, also in northern Vietnam, from the Upper Pleistocene cave site of Lang Trang (80,000 to 100,000 years BP) included a single lower fourth premolar attributed to H. inermis [53].

Here, we present confirmed archaeological evidence of the prehistoric presence of water deer from the Tràng An Landscape Complex World Heritage Site (hereafter “Tràng An”). The dental remains of a minimum of two individuals were recovered from late Upper Pleistocene archaeological deposits in the cave site of Hang Thung Binh 1. We present the stratigraphic and chronological context of the new specimens and the morphological and metric criteria used for taxonomic diagnosis. We then synthesise the available evidence for the environmental context of the Upper Pleistocene water deer of Tràng An. We conclude considering if the new finds reflected different climatic conditions and are relics of the Pleistocene, or these records are an early indication of an unrecognised southerly distribution and hence a shifted baseline, with possible implications for the conservation of the species in the future.

2.1 Location

The Tràng An karst landscape and environs are located in Ninh Binh Province, Northern Vietnam (see [9, 54-57] for detailed descriptions). Hang Thung Binh 1 (TB1) is one of six caves within an isolated limestone hill of the same name, in the northwest corner of the Tràng An core zone, 1.5 km west of the main massif set within cultivated alluvial plains (Figure 2). TB1 is a small two-chambered, east-facing cave (20° 15’ 41.8” N; 105° 51’ 53.1” E; Figure 2) situated 27 m asl and currently overlooks cultivated fields towards the north-west margin of the main massif. TB1 was investigated archaeologically in 2012 by the Vietnamese Institute of Archaeology (VIA), Hanoi [58] and by the SUNDASIA project from 2017 [57]. The SUNDASIA
project excavated two trenches and the specimens reported here (table 1; figure 3) were recovered during excavations in the second trench, which was opened in the front of the main chamber (figure 2).

2.2 Stratigraphic and chronological context

In Trench 2, an area of approximately 5.5 m² was excavated to an average depth of 1.60 m below the current cave floor. The trench yielded a sequence covering the 20th century to over 18,000 years BP (figure 2). The cervid specimens were recovered from an aceramic, shell-rich (predominantly Cyclophorous spp.), midden deposit, contexts (F907) to (F9015), which comprised of occasional stone tools, numerous fragments of animal bone and frequent charcoal fragments. Context (F907) was also notable for the presence of an inhumation [57] dating to around the Pleistocene-Holocene transition and recovered between 27.27 and 27.03 m asl (figure 2).

Two cervid mandible fragments (TB1-F908.2-SF40 and TB1-F912-SF42, hereafter “SF40” and “SF42”, respectively) and two fragments of maxillary canines (TB1-F912-SF43 and TB1-F912-SF44, hereafter “SF43” and “SF44”, respectively) were recovered from the midden layers underlying the inhumation. SF 40 was recovered at 26.95 m asl on 17th November 2018. SF 42, SF 43 and SF44 were recovered together six days later in close proximity in the same area, 0.1 m deeper in the sequence at 26.85 m asl (figure 2). There was no indication of significant reworking or discernible signs of bioturbation or disturbance to the deposits that would suggest that the specimens were intrusive or ex situ. From context, the specimens most likely represent the remains of animals exploited as food.

Direct dating was not attempted as previous efforts to radiocarbon date archaeological bone from TB1 and other project sites had consistently failed due to lack of collagen content [57]. Chronological context is provided by six radiocarbon dates from charcoal recovered from the stratigraphic sequence (figure 2; table S2). These dates were obtained via accelerator mass spectrometry at the AMS 14Chrono Centre facility at Queen’s University Belfast. They were calibrated with calib 8.2 [59] using the Intcal. 20 calibration curve [60]. Calibrated radiocarbon dates are shown here as two sigma ranges as “cal. BP” (“calibrated years before present”). Calibrated dates from the sequence are in superposition and indicate that the midden deposits accumulated between the end of the Last Glacial Maximum (26.5 to 19 cal. BP; [61]) and the early Holocene. The available dates effectively bracket the specimens reported here to between 13,000 and 16,000 cal. BP.

3. Materials and Methods

Identification of the specimens (table 1) was made as part of ongoing analysis of the vertebrate remains recovered from Tràng An by the SUNDASIA project. The analysis was carried out in the UK at the Oxford University Museum of Natural History with the permission of the Tràng An Management Board and Ninh Binh Peoples Committee. The specimens are to be stored and curated by the Tràng An Management Board in Ninh Binh upon completion of the project.

The specimens were identified by morphological and metric comparisons to museum specimens and morphometric data. Modern comparative specimens were consulted at the Oxford University Museum of Natural History (OUMNH) and previous observations and measurements at the Natural History Museum, UK (Stimpson, unpublished data) and American Museum of Natural History (Utting, unpublished data) were employed. Comparative descriptions and dental metric data were also compiled from the literature [9,
Dental measurements are shown and defined in table 2. All measurements collected in this study were taken with dial callipers to the nearest 0.01 mm.

Statistical tests were also performed to compare dental metrics of the archaeological specimens with museum specimens and published sources. Univariate normative comparisons were performed with a modified t-test [72-74] with step-down correction to control familywise false-positive error rate in multiple comparisons [75]. The tests were performed using the E-clip Multivariate and Univariate Normative Comparisons online platform [76]. Tests were run with a chosen alpha of 0.05. This approach assumes normality in the normative (comparative) samples. Comparative data sets were examined for departures from normality (Shapiro Wilk W) using the functions in PAST 3.20 [77]. Output of statistical tests is shown in table 3.

4. Results
4.1 Description
SF40 is a fragment of a right mandibular body (maximum length of specimen = 78.88 mm) with a complete toothrow, p2 to m3 (figure 3). The specimen was recovered in two pieces and was conserved and then refitted - the break is located anterior of the m2. Approximately 80% of the mandibular body is preserved although the ventral surface has suffered some damage. Most of the diastema is absent, as are the incisors and ascending ramus. Sediment (and a small fragment of shell on the labial side of the body, between the alveoli of the m2 and m3) has formed a hard crust through calcium carbonate deposition and is adhered to much of the specimen, particularly around the base of the teeth. After limited cleaning by hand, the morphology of the upper crowns and occlusal surfaces was clear.

The dentition is adult but is unworn. Individual dental age stage (IDAS) is early IDAS 3 based on eruption and wear to the molars [78]. The p4 is “molarised” in that, in terms of gross morphology, this tooth comprises of two distinct lobes. The anterior lobe is broad, whereas the posterior lobe is compressed and elongate in the labial-lingual direction with well-developed posterolingual and posterolabial conids. The anterior and mesolingual conids are fused, forming a contiguous structure, which enclose an anterior fossette. The lingual edges of the metaconids of the molars are simple, with single shallow folds. Weakly developed anterior cingulids are present on the m1 and m2. A small, slender anterior ectostylid is present on the m3 (figure 4).

SF42 is a small fragment (maximum length of specimen = 32 mm) of the dorsal surface of the body of a right mandible (figure 3). The ventral side is broken away. Two complete, unworn teeth, p4 and m1, are preserved in situ and appear slightly larger and more robust than those in SF40. A portion of the alveolus for the m2 is also preserved. As in SF40, the p4 is also “molarised” (figure 4), with an elongate posterior lobe and well-developed posterolingual and posterolabial conids. A weakly-developed anterior cingulid and a weakly-developed and elongate (in the labial-lingual direction) ectostylid is present on the m1. The lingual edge of the metaconids lack complex folds or crenulations.

SF43 is a left maxillary canine (maximum length of specimen = 51.20 mm; figure 3). The specimen was recovered in two pieces and refitted. The closed root and majority of crown are preserved, although the crown is chipped and broken at the tip (figure 4). The tooth curves posteriorly. The lateral surface of the crown is concave. The medial surface is relatively flat.

SF44 is the broken tip of a left maxillary canine (maximum length of specimen = 17.92 mm; figure 3). As with SF43, SF44 is convex on the lateral side and flattened on the medial.
4.2 Diagnosis

Absolute size of specimens, tooth dimensions and morphology all indicate small ruminant: either a species of the Cervidae or Moschidae. The relatively long, posteriorly curved canine with a closed root also indicates the so-called “fanged” deer or musk deer.

The fourth lower premolars are present in both mandible fragments and are “molarised”. While Hooijer [51] describes one exceptional specimen of \textit{M. muntjak vaginalis} (AMNH 43056), where the anterior and mesolingual conids meet (but are not fused), this character discounts \textit{Muntiacus} [19, 51, 80] and indicates three candidate taxa: \textit{Moschus} spp., \textit{H. inermis} and \textit{Elaphodus cephalophus} (figure 4; for \textit{Moschus} spp., \textit{M. moschiferus} is figured).

The smallest of the three taxa, the musk deer - \textit{Moschus} spp. - are not true cervids and are classified in a separate family, Moschidae. Musk deer are currently distributed from the Himalayas to North East Asia, with up to seven extant species [81]. The smallest species, \textit{Moschus berezovskii} (Flerov, 1928; extant body weight 6-9 kg), the “dwarf” or “forest musk deer”, ranges into South China and marginally into north Vietnam, where it has been reported in karst habitats. The much-reduced Vietnamese populations were, until recently, thought to be Siberian musk deer, \textit{M. moschiferus} [82].

\textit{Moschus} is indicated against here by the relatively simple lingual outline of the molars in SF40 and SF42. Specifically, “double-folded” lingual margins of the metaconids are key diagnostic characters of \textit{Moschus} [63,80] and are absent in the archaeological material (figure 4). Furthermore, anterior cingulids and mesostylids are relatively well developed in comparative specimens from the genus in comparison to the archaeological material. Conversely, posterolingual and posterolabial conids were well developed on the p4 in the available reference material.

Univariate comparison of dental measurements from extant and Pleistocene \textit{M. moschiferus} with the archaeological specimens, found measures to be statistically significantly larger in the archaeological specimens (table 3). Although statistical comparison was not possible due to lack of a sufficient sample size, the width of canine SF43 was greater and the overall tooth approximately 30% larger than that of the comparative material for \textit{Moschus}.

The largest of the three potential taxa, the tufted deer, \textit{E. cephalophus}, (17-30kg) is currently found in southern China, with historical records from eastern Myanmar [83]. In terms of gross size and morphology, the mandibles and teeth of extant tufted deer appear larger and more robust than the TB1 material (figure 4). Relatively well developed ectostylids are apparent on the molars. If present, anterior cingula are very weak: they are more commonly absent in comparative material for \textit{E. cephalophus}. The posterolabial and posterolingual conids of the p4 are not as developed as in the archaeological specimens, but there is a relatively deep fold in the lingual wall between the anterior stylid and anterior conid, which is absent in the p4 of SF40 and SF42. These characters are also consistent in large Pleistocene specimens of the genus figured in [51]. The maxillary canine in \textit{E. cephalophus} appears shorter, but much more robust than in SF43.

Toothrow length and p4 length of SF40 was found to be statistically significantly smaller than comparative data for extant tufted deer. No statistically significant difference was found in p4 length between SF42 and comparative data, however, and it is likely that individual tooth length may not be the most sensitive measure to discriminate between \textit{Hydropotes} and \textit{Elaphodus}. Comparisons of m3 lengths of Upper Pleistocene \textit{E. cephalophus} [70] suggest that this metric is statistically significantly larger than SF40 (table 3).
In terms of morphology, the archaeological specimens most closely match the available comparative material for water deer, *H. inermis*. The molarised p4 in *H. inermis* has an elongate posterior lobe and well-developed posterolinguinal and posterolabial conids as in both archaeological specimens (figure 4; see also [19] for the potential diagnostic significance of posterolabial conids). Weakly developed anterior cingulids are present on the molars of available comparative material. The lingual walls of the metaconids are relatively simple (i.e., lack complex folds), as in the archaeological specimens, a key character to distinguish *Hydropotes* from *Moschus* [63, 80].

While both archaeological mandibles and their teeth appear marginally larger and more robust in comparison to extant reference material for *Hydropotes*, the dental metrics of the archaeological specimens are within the ranges of equivalent available data for extant specimens (figure 4). No statistically significant differences were found in lower tooth rows lengths or premolar row lengths between SF40 and comparative data for *H. inermis*. No differences were found between p4 lengths in SF40 and SF42 or available comparative data. No significant difference was found in canine width between SF43 and comparative data for *H. inermis* (table 3).

Confirmed Pleistocene records for *H. inermis* are scarce, as are Pleistocene age dental data (with the exception of the p4 from Lang Trang, below). It was not possible to locate a data set to investigate the possibility of larger Pleistocene body size in the region [e.g. 51, 84]. It was possible, however, to re-run the tests with the stated hypothesis that metrics from the TB1 specimens are statistically significantly larger than the available extant/Holocene data. In the case of this 1-tailed test, toothrow length of SF40 was found to be statistically significantly larger than the Holocene dataset; with \( p = 0.047 \), however, this result is marginal (table 3). Conversely, premolar row length in SF40 was not found to be statistically significantly larger than the available comparative data. For SF42, length of p4 was not found to be statistically significantly larger the comparative data set. Finally, canine width in SF43 was not found to be statistically significantly larger than comparative data (table 3). The dimensions of the *H. inermis* specimen from Lang Trang (PIN 579/20; \( L = 11.5 \) mm; \( W = 8.1 \) mm [53]), however, suggest that the fourth premolar is relatively large in comparison to data from Holocene animals. Length was found to be statistically significantly different from Holocene comparatives and when the Upper Pleistocene specimens from TB1 are included (table 3). While the p4 figured in [53] is worn, which can potentially affect measurements of teeth to a degree [84], these data suggest that the specimen from Lang Trang reflects an earlier, larger-toothed and/or larger-bodied form.

In summary, morphological and metric characters indicate that the TB1 specimens are attributable to *Hydropotes*. There are no compelling grounds to suggest a larger, Pleistocene subspecies and no reason (geographical or otherwise) for proposing a separate species. The specimens from TB1 are referred to *H. inermis*. The identified remains derive from at least two individuals. The size of the canine fragments indicate the finds include male animals [cf. 62].

5. Discussion

The remains of water deer from TB1 confirms the prehistoric presence of the species in northern Vietnam. The specimens, dating to between 13,000- and 16,000-years BP, are valuable contributions to the sparse Pleistocene record for the species and are, at present, the most recent records in Vietnam. These new finds, however, raise questions.

Firstly, what were climatic and environmental conditions around TB1 between 13,000- and 16,000-years BP? This was a period of significant global climatic instability [85].
also an important question as Upper Pleistocene zooarchaeological evidence from cave sites within Tràng An indicate a focus on the exploitation of forest-adapted taxa from the karst [56,86]. The position of TB1 in a “satellite” hill overlooking the plain to the west of the karst, however, is likely to be pertinent (figure 2).

Observations of extant animals indicate that, while interlinked forest patches are a significant factor that can mediate localised abundance [24], water deer tend to be a lowland species with a preference for more open, marginal and riparian habitats. These habitats include reed-beds and tall, damp and undisturbed grasslands, with forbs and woody plants such as species of Asteraceae, Leguminosae and Fagaceae as favoured food plants [87-89]. Were similar habitats present on the plain outside the cave, or were the Upper Pleistocene water deer of TB1 living in different conditions? Palaeoenvironmental data for the last deglaciation in Northern Vietnam are sparse although records clearly show that rapid climatic fluctuations were experienced during this period [90]. Inferences for the period between 16,000 to 13,000 years BP for the Tràng An karst and the intervening plains, can be synthesised from a combination of proxies at various spatial scales.

Two archaeological cave sites have yielded relevant records for this time period: a multi-proxy record from Hang Trong in the interior of the Tràng An karst [56] and the pollen and spore record from Con Moong Cave [91], just over 20 km to the west of Tràng An. Proxy data from these sites included charcoal from Dipterocarpaceae, Leguminosae and Sapotaceae; pollen from euphorbs and mimosoid legumes; and stably more negative δ13C values (c. -30‰) of n-alkanes and n-alkanoic acids preserved in sedimentary organic carbon, indicative of forest plants using the C3 photosynthetic pathway [56] and arboreal pollen assemblages comprising forest taxa adapted to cool, moist environments, such as Castanea, Castanopsis (Fagaceae), Betula (Betulaceae), Juglans, Engelhardia and Platycarya (Juglandaceae) [91]. These data suggest that that limestone karsts on the southern margin of the Song Hong delta remained forested throughout the last deglaciation. Further, these areas likely acted as forest refugia during stadials and times of rapid climatic changes and supported upland vegetation typical of higher elevations today alongside lowland taxa of tropical lineages.

For the alluvial and coastal plains, basal units of two boreholes drilled into fluvio-deltaic deposits along the course of the Song Hong, east of Tràng An, yielded radiocarbon ages of 15,000-13,000 cal. BP [92-93] as well as palaeoenvironmental proxies in the form of palynological assemblages and sedimentological structures [94]. Facies 1.1 of the ND-1 core, located approximately 30 km ENE from Tràng An, produced two radiocarbon ages of 15,000 and 14,800 cal. BP [91]. The lithology of this unit was upward-fining and consisted of cross-bedded fluvial sands, and interlaminated muds and organic sediments interpreted as lateral accretion within a river meander, as well as channel fill. Pollen preservation was relatively poor but contained grains of conifers (Cryptomeria; Taxodioidaeae; Pinus), upland broadleaf taxa (e.g., Quercus) and various temperate riparian elements [94].

Further downstream, near to the modern delta front and about 70 km east from Tràng An, Unit 1 of the NP core sits underlies a radiocarbon age of around 12,000 cal. BP [93]. The silts of this unit yielded pollen assemblages comprising grasses (Poaceae), sedges (Cyperaceae), willow (Salix), oak (Quercus) and chinquapin (Castanopsis). These assemblages suggest a floodplain environment with scattered freshwater marsh, with the pollen from temperate broadleaf elements likely transported to the site fluvially from the surrounding uplands. Given the depths of these basal units, the riparian, floodplain and marsh environments they represent occurred within the ancient valley incised by the Song Hong during times of lower sea level in the Upper Pleistocene. It is a reasonable proposition then,
that the plain outside TB1 carried a seaward-draining watercourse that flowed through a similar mosaic of alluvial environments, which incorporated more open wetland habitats, surrounded by upland and limestone forests on the karst. These data suggest that similar or preferred habitats of extant water deer were present in the Upper Pleistocene on the plains around TB1 and that cooler, but not necessarily drier, conditions prevailed.

This leads to the question: are the Tràng An specimens relicts of cooler Pleistocene conditions or are the new finds an early indication of a previously unrealised, more recent presence in Vietnam? More practically, could archaeological evidence warrant a potential case for (re)introduction into Tràng An? Reintroduction campaigns are, in practice, complex and necessarily must navigate a series of ethical, economic, sociological, and ecological factors. Thorough consideration of the potential risks to the environment and livelihoods is required and must be balanced against potential benefits of ecosystem services and ecotourism, in addition to the welfare of reintroduced populations. It is beyond the scope of the present paper to discuss these issues in detail and we consider the current evidence as a hypothetical case.

Currently, only two other sites in Vietnam, Mai Da Dieu and Lang Trang, have yielded possible evidence of water deer; specimens from the former remain unconfirmed. Both these sites are in northern Vietnam and are Upper Pleistocene in age. It is not possible to determine any directly associated radiocarbon dates with the unconfirmed Mai Da Dieu material, but dates given in the 2009 publication [52] suggest a post-LGM context and a broadly similar age to the TB1 specimens. The tooth reported from Lang Trang is older and currently dated to between 80,000-100,000 years BP [53]. The Pleistocene distribution of a species is not typically perceived as a justification for designating it as “native” within the modern area. Firstly, potential source populations for reintroductions may derive from a different genetic population of the species. In this case, however, concerns about differing genetic lineages may perhaps be allayed by the questionable subspecific status of extant water deer. Secondly, given the climatic and environmental change that occurred during the Pleistocene-Holocene transition, Pleistocene populations may have been adapted to and reliant upon different conditions than the Holocene [15].

Water deer are today regarded as a temperate species (e.g. [89, 95]) and extant and Quaternary records of water deer do tend towards temperate latitudes (figure 1). As we have seen, available proxies indicate that the Upper Pleistocene landscapes of Tràng An reflected cooler conditions than the sub-tropical climate of the Holocene. Regional palaeoenvironmental proxies also indicate that a drier and cooler climate at the beginning of the Holocene, following the Younger Dryas stadial, which saw reduced temperature and precipitation approximately 12,900 to 11,700 years BP. While water deer may have persisted into the early Holocene, increasing temperature and humidity and the establishment of subtropical climate and environmental change [96] may have precluded the persistence of populations of water deer in Northern Vietnam.

This argument, at least in part, would be an artefact of the shifting baseline syndrome. The historical distribution of water deer in China, and the recent finds in Taiwan [30, 32] present a significant challenge to this simplistic climatic and environmental narrative. Historical records place water deer at sub-tropical latitudes in China until recently, in the 20th century. In addition to the identified archaeological material, historical documents indicate that water deer were, until relatively recently, common and widespread in Taiwan until extirpation in the 19th century [32].
In practical terms, only confirmed and reliably dated specimens would provide unequivocal evidence of populations surviving into the Holocene. A search for potential specimens from Holocene age archaeological sites in Vietnam, either in archives or during future investigations would be worthwhile, as would a review of potential documentary evidence. A comprehensive assessment would also require other factors such as hunting by humans, or competitive exclusion by other species to be considered, but there are currently no clear climatic or environmental factors that would have been a definitive barrier to the survival of water deer into the Holocene in northern Vietnam.

6. Conclusion

Newly identified fossils from the archaeological cave site of Hang Thung Binh 1 in the Tràng An World Heritage Landscape Complex Site confirm the presence of water deer, *H. inermis*, in northern Vietnam in the Upper Pleistocene. The new specimens are further evidence of a wider Quaternary distribution for these Vulnerable, globally declining cervids, are valuable additions to a sparse Pleistocene fossil record and confirm water deer as a component of the Upper Pleistocene fauna of northern Vietnam.

Current archaeological and palaeontological evidence for the presence of water deer in the country is extremely sparse and restricted to the Upper Pleistocene. While water deer are today associated with temperate latitudes, a brief survey of the known historical distribution and recent archaeological evidence indicates that the species has been capable of surviving in sub-tropical climates and habitats. The possibility that water deer survived into the Holocene in northern Vietnam is a hypothesis to be tested.

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Data accessibility. The datasets supporting this article have been uploaded as electronic supplementary material.

Author contributions. CMS and RR conceived the study; CMS conducted analyses and identification and drafted the manuscript with contributions from all authors; CMS, RH and BU conducted the review of Quaternary records of *Hydropotes inermis*; CMS and BU performed statistical tests; TK translated German language source material; CMS, BU, RR, TK, carried out excavation, site analysis and recording; SO and NTMH produced the paleoenvironmental synthesis. All authors revised the manuscript and gave final approval for publication.

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160x113mm (200 x 200 DPI)
Figure 2. Hang Thung Binh 1. (a) Tràng An karst in plan, with location of Hang Thung Binh 1 (TB1 – red triangle) (b) looking north across the coastal plain, towards isolated hill containing TB1 (red triangle) with the Tràng An karst to the east and pagoda complex in the background (original photograph: TK) (c) TB1 in plan showing location of trenches and section D (d) representative west-facing section, showing calibrated radiocarbon dates (cal. BP) and find levels of Hydropotes inermis specimens SF40, SF42, SF43 and SF44. Levels are metres above sea level.

248x240mm (200 x 200 DPI)
Figure 3. Upper Pleistocene specimens of Hydropotes inermis recovered from the Hang Thung Binh 1 archaeological cave site in the Tràng An World Heritage Area, Ninh Binh, Northern Vietnam. SF40 right mandible with toothrow, p2-m3, (a) labial side (b) lingual side and (c) occlusal surface of teeth. SF42 right mandibular fragment with p4 and m1 in situ, (d) labial side I lingual side and (f) occlusal surface of teeth. SF43 left maxillary canine (g) lateral and (h) medial aspects. SF44 left maxillary canine tip (i) lateral and (j) medial aspects. Scale = 20 mm.

162x107mm (300 x 300 DPI)
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139x164mm (200 x 200 DPI)
Table 1 Provenance and description of identified specimens of *Hydropotes inermis* from the Hang Thung Binh 1 archaeological cave site in the Tràng An World Heritage Landscape Complex Site, Ninh Binh, Northern Vietnam.

| Site | Trench | Grid sq. | Context | SF no. | Description                                      |
|------|--------|----------|---------|--------|--------------------------------------------------|
| TB1  | 2      | TR2EE    | F908.2  | 40     | right mandibular body and complete toothrow p2-m3 |
| TB1  | 2      | MS-E     | F912    | 42     | right mandible fragment with p4 and m1           |
| TB1  | 2      | MS-E     | F912    | 43     | left maxillary canine with root and crown.       |
| TB1  | 2      | MS-E     | F912    | 44     | fragment of left maxillary canine - tip of crown |
Table 2 Measurements of three *Hydropotes inermis* specimens from the archaeological cave site of Hang Thung Binh (TB1) in the Tràng An World Heritage Area, Ninh Binh, Northern Vietnam. All measurements are in mm. C – maxillary canine; p – mandibular premolar; m – mandibular molar; L – length (anterior-posterior); W – width (labial-lingual); p2-p4 – mandibular premolar row length; m1-m3 – mandibular molar row length; p2-m3 – mandibular toothrow length.

| tooth/toothrow | dimension | SF40 | SF42 | SF43 |
|----------------|-----------|------|------|------|
| C              | W         |      |      |      |
| p2             | L         | 6.56 | /    | /    |
|                | W         | 3.19 | /    | /    |
| p3             | L         | 8.2  | /    | /    |
|                | W         | 5.36 | /    | /    |
| p4             | L         | 8.64 | 9.44 | /    |
|                | W         | 5.86 | 6.24 | /    |
| m1             | L         | 9.82 | 9.8  | /    |
|                | W         | 7.2  | 7.38 | /    |
| m2             | L         | 11   | /    | /    |
|                | W         | 7.11 | /    | /    |
| m3             | L         | 13.8 | /    | /    |
|                | W         | 6.68 | /    | /    |
| p2-p4          | L         | 24.2 | /    | /    |
| m1-m3          | L         | 34.45| /    | /    |
| p2-m3          | L         | 57.96| /    | /    |
Table 3 Summary of statistical output for tests of normality (Shapiro Wilk W) and univariate normative comparisons (modified t-test) of specimens from Tràng An and Lang Trang with comparative data (tables S3-S5). Significant results are shown in bold. Taxon data sets: 1 Holocene; 2 Pleistocene and Holocene; 3 Upper Pleistocene

| Spec | Measure | Taxon     | n  | W     | p (norm.) | hyp  | sig  | diff  | mod. t | p   |
|------|---------|-----------|----|-------|-----------|------|------|-------|--------|-----|
| SF40 | L p2-m3 | H. inermis | 28 | 0.9398| 0.1093    | 2-tailed | N    | 1.778 | 1.747  | 0.084  |
| SF40 | L p2-m3 | E. cephalophus | 17 | 0.9215| 0.1566    | 1-tailed (smaller) | Y    | -1.972 | -1.916  | 0.034  |
| SF40 | L p2-m3 | M. moschiferus | 10 | 0.9287| 0.4353    | 1-tailed (larger) | Y    | 5.025  | 4.791  | <0.001  |
| SF40 | L p2-p4 | H. inermis | 24 | 0.9297| 0.09588   | 2-tailed | N    | 0.78  | 0.765  | 0.454  |
| SF40 | L p4    | E. cephalophus | 7 | 0.9312| 0.5611    | 1-tailed (smaller) | Y    | -3.539 | -3.31  | 0.008  |
| SF40 | L p4    | H. inermis | 7  | 0.9457| 0.6902    | 2-tailed | N    | 0.261 | 0.244  | 0.826  |
| SF42 | L p4    | H. inermis | 7  | 0.9457| 0.6902    | 2-tailed | N    | 1.384 | 1.295  | 0.23   |
| SF42 | L p4    | E. cephalophus | 7 | 0.9312| 0.5611    | 1-tailed (smaller) | N    | -0.545 | -0.51  | 0.294  |
| SF42 | L p4    | M. moschiferus | 7 | 0.9261| 0.518     | 1-tailed (larger) | Y    | 6.326  | 5.917  | <0.001  |
| SF43 | Cw      | H. inermis | 8  | 0.9184| 0.4174    | 2-tailed | N    | -0.061 | -0.058 | 0.943  |
| SF40 | L p2-m3 | H. inermis | 28 | 0.9398| 0.1093    | 1-tailed (larger) | Y    | 1.778  | 1.747  | 0.047  |
| SF40 | L p2-p4 | H. inermis | 24 | 0.9297| 0.09588   | 1-tailed (larger) | N    | 0.78  | 0.765  | 0.224  |
| SF42 | L p4    | H. inermis | 7  | 0.9457| 0.6902    | 1-tailed | N    | 1.384 | 1.295  | 0.118  |
| SF43 | Cw      | H. inermis | 8  | 0.9184| 0.4174    | 2-tailed | N    | -0.061 | -0.058 | > 0.9  |
| SF40 | L m3    | E. cephalophus | 24 | 0.9499| 0.2696    | 1-tailed | Y    | -4.038 | -3.957 | <0.001  |
| PIN  | L p4    | H. inermis | 7  | 0.9457| 0.6902    | 2-tailed | Y    | 4.276  | 4      | <0.001  |
| PIN  | L p4    | H. inermis | 9  | 0.9318| 0.4983    | 2-tailed | Y    | 4.177  | 3.963  | 0.01   |

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Appendix B

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The Morphology of the Lower Fourth Premolar as a Taxonomic Character in the Ruminantia (Mammalia: Artiodactyla), and the Systematic Position of Triceromeryx
Author(s): Christine M. Janis and Adrian Lister
Source: Journal of Paleontology, Vol. 59, No. 2 (Mar., 1985), pp. 405-410
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ABSTRACT—The morphology of the lower fourth premolar has been used as a taxonomic indicator in the pecoran fossil record, for example to separate cervid species, and to differentiate giraffids from cervoids. We demonstrate considerable inter- and intraspecific variation in cervoid and bovid P4 morphology, and show in particular that the typical giraffid type of P4, with suppression of the central connection between labial and lingual walls, appears among living and fossil cervoids, and very exceptionally among bovids. This character of the premolar dentition has been used to unite the lower Miocene pecoran genus Triceromeryx, known from a single incomplete individual from Spain, with the Giraffidae, although it was originally united with the Dromomerycidae on the basis of the possession of an occipital horn. We conclude that the known material of Triceromeryx is insufficient to assign this genus firmly to any known pecoran family, and that it should remain for the time being as Pecora incertae sedis.

INTRODUCTION

The primitive dental condition for the suborder Ruminantia (Mammalia, Artiodactyla) is for simple sectorial premolars, and this condition is seen today in living mouse-deer (infraorder Tragulina). However, in the infraorder Pecora the more derived condition of submolariform premolars is seen in the earliest and most primitive members (Webb and Taylor, 1980). Within different pecoran lineages the premolars have apparently become more molariform in independent fashions. Both the pattern of molarization, and the details of the manner in which these teeth have become complicated, have been given much significance in attempts to determine the taxonomic interrelationships within ruminant artiodactyls (e.g., Loomis, 1925; Hamilton, 1973).

Information gleaned from premolar morphology has been of particular importance in assigning fossil taxa to the appropriate lineage, and lower premolar morphology has been particularly useful as lower dentitions are more abundant in the fossil record than are upper ones. Firstly, several workers have used lower premolars as a basis for identifying giraffoids in the fossil record (e.g., Colbert, 1936; Churcher, 1970; Hamilton, 1978a). They pointed out that there is a characteristic difference in the formation of the anterior part of the lower fourth premolar (P4) which distinguishes giraffes from other ruminants that molarize this premolar. Whereas in cervids and bovids the lingual wall is connected to the labial wall by a transverse crest [the "central transverse crest" of Hamilton (1978a)] (Figure 1.2–1.6), in giraffes this crest is suppressed (Figure 1.7).

Secondly, the composition of the lingual wall itself, and in particular the degree to which the paraconid and metaconid contribute to it, has been used as a taxonomic character to separate genera and species within the Cervidae and Bovidae (e.g., Azzaroli, 1953; Gentry and Gentry, 1978).

It is our contention that the morphology of the anterior part of the lower fourth premolar is much more variable than has hitherto been realized, especially among cervoids. While a particular pattern may be the general condition for each of the various pecoran lineages, the amount of individual variation is such that this character cannot be used in isolation to assign a single fossil specimen to a particular lineage. This problem was foreseen to some extent by Hamilton (1978b) when he recognized that the living cervid genus Rangifer possesses a "giraffe" type of lower fourth premolar. The same is true also of Alces. These two genera in fact
have a greater degree of molarization of the premolar row than most other cervids. Our concern in this paper is to demonstrate the variability of P₄ form within and between other cervoid, and bovid, lineages, and to relate this to the assignment of the problematical pecoran *Triceromeryx pachecoi*, known from a single incomplete specimen from the lower Miocene of Spain (Crusafont Pairó, 1952).

### MATERIALS AND METHODS

Populations of living and fossil pecorans were examined for variation in P₄ morphology from the following institutions: the British Museum (Natural History), London, England; the Naturhistorisches Museum, Mainz, Germany; the Forschungsinstitut Senckenberg, Frankfurt, Germany; the Frick Collection, American Museum of Natural History, New York, U.S.A.; the Museum of Comparative Zoology, Harvard University, U.S.A.; the National Museum of Kenya, Nairobi, Kenya; the Transvaal Museum, Pretoria, South Africa; the Cape Town Museum, South Africa.

### RESULTS

The results for cervid pecorans are summarized in Table 1; cf. Figure 1. Considerable variation in P₄ form is apparent between and even within species, both living and fossil. The anterior part of the lingual wall may be absent (Figure 1.2), or formed by the metaconid (Figure 1.3), or by the paraconid (Figure 1.4), and in some cases a typically “giraffid” condition is seen, with suppression of the central transverse crest (Figure 1.7). In some individuals of the type shown in Figure 1.3 and 1.4, the paraconid and metaconid may fuse, especially lower in the crown, to form a continuous structure, as in Figure 1.5. The same fusion may occur in the “giraffid” type; that shown in Figure 1.7 is in the fused state.

Particularly interesting variability is seen in the dromomerycid *Dromomeryx whitfordi* from the middle Miocene of North America, in which three forms of molarization (types 3, 4 and 7) occur within a single population. There is also evidence that the frequencies of the variants within a species can change markedly, as shown by the figures for two different populations of *Cervus elaphus*.

For the Bovidae, we have examined a total of about 400 specimens from 33 living species, covering all of the African and Indian tribes. The species studied are listed in Table 2. Considerable variation was again seen in the development of the metaconid and paraconid. The most frequent pattern among these bovid tribes is that of Figure 1.6, where the metaconid tends to fuse to the entoconid rather than to the paraconid. However, P₄'s of types 2–4 are also occasionally observed (see also Gentry, 1978, fig. 27.1). In addition, P₄ type 5, with paraconid and metaconid joined to form a continuous anterolingual wall even high in the crown, has been observed as a variant within certain species of the tribes Cephalophini, Reduncini, Alcelaphini, Tragelaphini and Bovini (see Table 2). We have not to date observed this condition in any specimen of bovids from the tribes Neotragini, Gazellini or Hippotragini, although our sample sizes for some species are small (see Table 2). The distribution of this form of P₄ amongst the bovid tribes revealed by these results broadly corresponds to that given by Gentry (1978). However its occurrence, even
in those tribes where it is found, is not constant either between or within species.

The highest frequency of $P_4$ type 5 is among the Tragelaphini. In one specimen of Tragelaphus angasi observed, there was also complete suppression of the central transverse crest to produce a quasi-giraffid morphology (Figure 1.7). This is the only bovid specimen observed to show this condition.

Our giraffid sample was not as extensive as that for cervoids and bovids, owing to the relative scarcity of these animals in museum collections. However, we have never observed variation from the giraffid form of $P_4$ (Figure 1.7) in any skull examined, amounting to 35 specimens of Giraffa camelopardis, plus several of Okapia johnstoni, from museums in Europe, Africa and North America.

**DISCUSSION**

The results presented here show, firstly, that in species-level cervoid taxonomy it is unwise to assume that the $P_4$ morphology found in a given population of a certain species is a constant, taxonomically valid feature of that species. This is evident from the intra- and interpopulation variation seen in Cervus elaphus. Thus, to take a single example, the poor development of the metaconid noted in small samples of middle Pleistocene Megaceros species from England (Azzaroli, 1953), need not be diagnostic. We have not assessed in detail the relative contributions of intra- and interspecific variation in bovid $P_4$'s, but our results suggest that caution is advisable in bovid species-level taxonomy also.

Secondly, on the level of distinguishing the bovid tribes, it would seem that the presence of paraconid-metaconid fusion in $P_4$ type 3, 4 or 5, indistinguishable because of advanced stage of wear, number of individuals examined. Percentages: percentages of specimens in each sample showing each type of $P_4$. Note: in the Capreolus specimens scored as type 7, the central transverse crest varies from being absent to being weakly developed, but never joins the metaconid.

**Table 1** — Cervoid specimens examined. Institutions: BMNH, British Museum (Natural History); AMNH, American Museum of Natural History; MCZ, Museum of Comparative Zoology; NHM, Naturhistorisches Museum; NMN, National Museum of Kenya, Nairobi; CTM, Cape Town Museum; TM, Transvaal Museum. 1 to 7: types of $P_4$ pattern as in Figure 1. 3(−5): showing type 3, or type 5 where it is clear that this is a fused or advanced-wear stage of 3. 4(−5): showing type 4 or type 5 where it is clear that this is a fused or advanced-wear stage of 4. 3/4/5: $P_4$ type 3, 4 or 5, indistinguishable because of advanced stage of wear. N: number of individuals examined.
Table 2—Bovid specimens examined. : occurrence within a species, but not necessarily in all individuals. Other symbols and abbreviations as in Table 1.

| Tribe      | Species                  | Institutions | N  | Occurrence of P₄ type 5 | Occurrence of P₄ type 7 |
|------------|--------------------------|--------------|----|------------------------|------------------------|
| Boselaphini| Boselaphus tragocamelus | BMNH, CTM    | 14 | -                      | -                      |
| Tragelaphini| Tragelaphus scriptus     | BMNH, CTM, TM| 24 | -                      | -                      |
|            | Tragelaphus angasi       | CTM          | 6  | +                      | +                      |
|            | Tragelaphus strepsiceros | CTM, TM      | 17 | +                      | +                      |
|            | Boocercus eurycerus      | NMN          | 1  | +                      | -                      |
|            | Taurotragus oryx         | NMN, CTM, TM | 12 | +                      | -                      |
| Cephalophini| Cephalophus caerules     | BMNH         | 15 | -                      | -                      |
|            | Cephalophus monticola    | NMN          | 6  | -                      | -                      |
|            | Sylvicapra grimmia       | NMN, CTM     | 28 | +                      | -                      |
| Bovini     | Syncerus caffer          | CTM, TM      | 11 | +                      | -                      |
| Neotragini | Neotragus moschatus      | NMN          | 7  | -                      | -                      |
|            | Ourebia ourebi           | CTM          | 2  | -                      | -                      |
|            | Oreotragus oreotragus    | CTM, TM      | 6  | -                      | -                      |
|            | Raphicerus melanotis     | CTM          | 10 | -                      | -                      |
|            | Raphicerus campestris    | CTM          | 17 | -                      | -                      |
|            | Madoqua kirkii           | NMN          | 3  | -                      | -                      |
| Reduncini  | Redunca arundinum        | BMNH, CTM, TM| 32 | -                      | -                      |
|            | Redunca fulvorufula      | CTM, TM      | 17 | -                      | -                      |
|            | Pelea capreolus          | CTM, TM      | 6  | +                      | -                      |
|            | Kobus ellipsiprymnus     | NMN, CTM, TM | 15 | +                      | -                      |
| Gazellini  | Gazella thomsoni         | BMNH         | 30 | -                      | -                      |
| (Antilopini)| Litocranius walleri     | BMNH, NMN   | 16 | -                      | -                      |
|            | Ammodorcas clarkei       | BMNH         | 3  | -                      | -                      |
|            | Antidorcas marsupialis   | CTM          | 10 | -                      | -                      |
| Hippotragini| Hippotragus niger        | CTM, TM      | 11 | -                      | -                      |
|            | Hippotragus equinus      | TM           | 2  | -                      | -                      |
|            | Oryx gazella             | CTM, TM      | 10 | -                      | -                      |
| Alcelaphini| Aepyceros melampus       | BMNH, CTM, TM| 17 | +                      | -                      |
| (sensu Vrba)| Beatragus hunteri       | BMNH         | 6  | -                      | -                      |
|            | Alcelaphus buselaphus    | NMN, CTM, TM | 18 | -                      | -                      |
|            | Damaliscus lunatus       | NMN, CTM, TM | 12 | -                      | -                      |
|            | Connochaetes taurinus    | NMN, CTM, TM | 20 | +                      | -                      |

in some cervid genera (Rangifer, Alces), and as a frequent variant in a number of other cervid species and in Dromomeryx among the dromomerycids, and even as a rare variant in at least one species of Bovidae, we conclude that this character cannot be used in isolation to assign a single fossil specimen to the family Giraffidae, as has been the case with Triceromeryx pachecoi (Churcher, 1970; Hamilton, 1978a).

Triceromeryx was originally assigned to the Dromomerycidae on the basis of possessing a forked occipital horn in addition to simple supra-orbital horns (Crusafont-Pairó, 1952), as a simple occipital horn was also present in the dromomerycid subfamily Craniocerotinae (Frick, 1937), despite the fact that Triceromeryx was found in Spain and all known dromomerycids were exclusively North American. The taxonomic affinities of the dromomerycids are uncertain, and thus Triceromeryx has been given significance as a possible clue to their origin and affinities, notwithstanding the very limited amount of material assignable to this genus. Dromomerycids are often lumped together with the paleomerycids, the so-called “basal” Eurasian pecoran group (e.g., Stirton, 1944; Romer, 1966). However, whereas the Old World “paleomerycids” can be shown to be a polyphyletic assemblage, with most members assignable to the Giraffidae (Hamilton, 1978b) or the Moschidae (Webb and Taylor, 1980), it seems likely that the Dromomerycidae are a monophyletic group, radiating in North America from an immigrant Eurasian pecoran in the lower Miocene (see Janis, 1982). They are variously claimed to be cervoids (e.g., Frick, 1937) or giraffoids (e.g., Stirton, 1944; Crusafont Pairó, 1952) as they share
with giraffes the elongation of the occipital region and the possession of a simple, unbranching, nondeciduous ossicone that was apparently covered with skin rather than keratin (the condition in bovids). However, dromomerycids possess the derived cervoid characters of a closed metatarsal gulley (see Leinders, 1979) and a double lacrymal orifice (see Leinders and Heintz, 1980), and do not share the giraffe autapomorphy of a bilobed lower canine (see Hamilton, 1978a). It seems likely that they are a cervoid family, and that their superficial resemblances to giraffes are convergences, resulting from a similar feeding behavior of high-level browsing (Janis, 1982).

Triceromeryx was assigned to the Giraffidae by both Churcher (1970) and Hamilton (1978a) primarily on the basis of the form of the $P_4$. Both authors refer to the post-cranial material of Triceromeryx as "paleotragine-like," and Crusafont Pairó (1952) noted that various details of the limbs, especially of the carpus and radius, were more similar to primitive giraffids such as Palaeotragus than to cervids or Palaeomeryx. However, cervid limb morphology seems to represent a derived condition for pecorans (Leinders, 1979), and the taxonomic affinities of the genus Palaeomeryx are uncertain (Hamilton, 1978a, 1978b). In the absence of a detailed evaluation of which pecoran limb characteristics are primitive and which are derived, direct comparison of Triceromeryx with Palaeotragus in this manner is meaningless, as both may merely represent the retention of the shared primitive condition. (It is unfortunate that the distal end of the metatarsus of Triceromeryx is lacking, so it is impossible to determine whether or not it had a cervoid type of closed gulley. Also lacking is the anterior end of the lower jaw, so it cannot be determined if it shared the giraffe character of a bilobed canine.)

It may well be the case that Triceromeryx is an aberrant giraffid, especially as no other Old World material assignable to dromomerycids has as yet been identified. However, as the only positive character linking Triceromeryx with giraffes is the form of the $P_4$, and this type of $P_4$ can be seen among both cervids and dromomerycids, it seems to us that there is insufficient evidence from the material available at present firmly to unite this animal with any known pecoran family.

The lower Miocene Old World ruminants are poorly known, and clear characters that would unite them with various pecoran or traguloid families are not as yet determined (though see Webb and Taylor, 1980, for hornless ruminants). The ubiquitous Miocene genus Palaeomeryx, originally assigned to the Giraffidae by Ginsburg and Heitz (1966) on the basis of associated ossicone material, has been shown by Hamilton (1978a, 1978b) to lack derived giraffid characters. He classified the genus as Pecora incertae sedis, along with certain other Miocene "palaomerycids" such as Propalaeoryx and Prolibytherium. We suggest that until more material of Triceromeryx is discovered, and until a full review is undertaken of primitive and derived character states in Miocene pecorans, Triceromeryx would also be best considered as Pecora incertae sedis rather than assigned either to the Giraffidae or the Dromomerycidae.

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Confirmed archaeological evidence of water deer in Vietnam: relics of the Pleistocene or a shifting baseline?

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Statement (if applicable):
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CMS and RR conceived the study; CMS conducted analyses and identification and drafted the manuscript with contributions from all authors; CMS, RH and BU conducted the review of Quaternary records of Hydropotes inermis; CMS and BU performed statistical tests; TK translated German language source material; CMS, BU, RR, TK, carried out excavation, site analysis and recording; SO and NTMH produced the paleoenvironmental synthesis. All authors revised the manuscript and gave final approval for publication.
Confirmed archaeological evidence of water deer in Vietnam: relics of the Pleistocene or a shifting baseline?

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Abstract
Studies of archaeological and palaeontological bone assemblages increasingly show that the historical distributions of many mammal species are unrepresentative of their longer-term geographical ranges in the Quaternary. Consequently, the geographical and ecological scope of potential conservation efforts may be comparatively narrow. Here we consider a case in point, the water deer *Hydropotes inermis*, which has historical native distributions in eastern China and the Korean peninsula.

We present morphological and metric criteria for the taxonomic diagnosis of mandibles and maxillary canine fragments from Hang Thung Binh 1 cave in Tràng An World Heritage Site, which confirm the prehistoric presence of water deer in Vietnam. Dated to between 13,000 and 16,000 years before present, the specimens are further evidence of a wider Quaternary distribution for these Vulnerable cervids, are valuable additions to a sparse Pleistocene fossil record and confirm water deer as a component of the Upper Pleistocene fauna of northern Vietnam. We also examine the environmental context of the water deer of Tràng An before considering if the new finds represent relics of an Upper Pleistocene population, or are an early indication of an unrecognised southerly distribution with possible implications for the conservation of the species in the future.

Keywords: water deer, *Hydropotes inermis*, zooarchaeology, Vietnam, Pleistocene

1. Introduction
The last 2.58 million years, the Quaternary period, saw the rise of our own species and the evolution of a modern mammal fauna [1]. Now, as the mechanisms, scale and rapidity of recent human impact on ecosystems worldwide have no geological analogue, efforts to characterise the “Anthropocene” are gaining impetus [2-3] and the global biodiversity crisis becomes increasingly acute [4-6]. With mammal populations in decline, the necessity and utility of longer-term Quaternary records to provide “pre-Anthropocene” insights into populations, diversity and geographical range is being demonstrated [6-11]. The principal warrant of this longer-term perspective is that baselines for quantification and description (e.g. species inventories, geographic range, habitat requirements etc.) are set in the context of
recent, ecological timescales (typically < 100 years), where populations may have already experienced degradation through human activities (e.g. direct exploitation, habitat modification) for millennia [6, 11-12].

A dilemma of this “shifting baseline syndrome” [13-14] is that if by the time records began species distributions were already unrepresentative of much of the Quaternary, how effective are conservation measures likely to be in the context of degraded habitats and range [15]? In this paper we consider a case-in-point, the water deer, *Hydropotes inermis* (Swinhoe, 1870). We present new archaeological evidence that confirms the presence of this small cervid, which has experienced pronounced recent declines in geographical range and numbers [16-18], in prehistoric Vietnam.

Water deer are currently found in eastern China and the west of the Korean peninsula (figure 1). A comprehensive review of their biology, life and natural history can be found in Schilling and Rössner [18]. In brief, this species is a small bodied, chestnut-coloured, solitary deer (Cervidae), which stands approximately 0.5 m tall at the shoulder and weighs up to 15 kg. Uniquely in the Cervidae, the males do not develop antlers but instead are characterised by long maxillary canine teeth: the current balance of evidence suggests that antler loss was secondary [18]. Water deer are almost entirely solitary beyond the rut, unlike most deer species, and thus are more akin to musk deer (Moschidae) and chevrotains (Tragulidae).

Though understudied, the water deer is a potentially important model organism to investigate the evolution of the Cervidae generally and antlers, specifically [17-19].

Two subspecies have been recognized: the Chinese water deer *H. inermis inermis* (Swinhoe, 1870) and the Korean water deer *H. inermis argyropus* (Heude, 1884) although their validity has been questioned on molecular and morphological grounds [19, 21-22]. Accurate estimates of current numbers of Asian water deer are difficult to determine although the species is in decline and is classified as Vulnerable by the IUCN [16]. Chinese populations have recently experienced steep declines in numbers and a reduction in geographical range and are now present in isolated fragments in the eastern Yangtze Basin and the Zhoushan Islands (figure 1). Hunting pressure and loss of habitat are reported to be the principal causes of this decline [23].

In North Korea, water deer are presently distributed along the west coast (figure 1) and are believed to be present in most of South Korea where, in some areas, the animals are sufficiently numerous to conflict with agricultural interests [24-25]. Water deer have been the subject of re-introduction and release efforts in China and the Koreas in the twentieth and twenty first centuries [21, 25-26]. Translocated populations in the United Kingdom and France (source populations first introduced in 1900 and 1970, respectively) now account for approximately 40% of the global population [17]. Within the United Kingdom, their distribution is limited to the Midlands and East Anglia and restricted by suitable habitat availability [27]. A population was also intentionally translocated to the north-east of the Korean Peninsula by the North Korean government in the 1960’s [21] and has since potentially expanded their range into the Khasanskiy district of Russia. There is currently not enough evidence to determine whether the Russian populations are transient, or stable and reproducing [28].

Historical records indicate that water deer ranged over eastern China and were found between Liaoning in the north and Guangdong in the south, as far as the lower Yangtze basin, as well as central and southern Korean peninsula [25, 30] (figure 1). Bones and teeth of water deer recovered from Holocene-age (11.65 thousand years before present [BP] to recent [31], where “present” is held at 1950) archaeological sites in the region [11, 32-36] indicate an even
wider former geographical distribution; as far west as eastern Tibet (Xizang), as far as Inner Mongolia in the north, to the east of the Korean Peninsula and into southern China (Figure 1). Notably, recent archaeological investigations of four Iron Age sites (1300-400 years BP) have also produced evidence of water deer in central Taiwan [32]. While not all archaeological sites represent contemporaneous records, these data indicate that the water deer now occupies less than ten percent of its’ former maximum Holocene range [11].

Earlier, Quaternary records of water deer from the Pleistocene (2.58 million to 11.65 thousand years before present [37]) are scarce and the accuracy of some fossils identifications have been queried [cf. 50 and 51]. Six Middle Pleistocene (770,000 to 126,000 years BP) fossil sites have yielded records across southern, central, and northern China. Remarkably, records also include finds from Tarumi NT cave in western Japan where skeletal remains referred to “Hydropotes cf. inermis” were recovered with a fauna that contained both exotic and extinct forms [44]. Upper Pleistocene (126,000 to 11,650 years BP) records are limited to four sites in central China and one site in the north, near the Korean Peninsula (Figure 1).

There are no recent, historical or confirmed archaeological records of water deer in Vietnam. The possibility of the prehistoric presence of the species was raised in a preliminary list of identified Upper Pleistocene animal bone in 2009 [52]. The remains that were recovered by a joint Vietnamese-Bulgarian project during investigations of Mai Da Dieu (a rock shelter approximately 30 km to the south of Tràng An, the focus of the present study) in the late 20th century. The list included “Chinese water deer, Hydropotes inermis (Swinhoe, 1870)”. No figures, stratigraphic provenance, or data, however, were provided and the author points out that “these taxonomic attributions are provisional, pending additional study” [52: 207]. More recently, a collection of palaeontological fossil teeth in 2020, also in northern Vietnam, from the Upper Pleistocene cave site of Lang Trang (80,000 to 100,000 years BP) included a single lower fourth premolar attributed to H. inermis [53].

Here, we present confirmed archaeological evidence of the prehistoric presence of water deer from the Tràng An Landscape Complex World Heritage Site (hereafter “Tràng An”). The dental remains of a minimum of two individuals were recovered from late Upper Pleistocene archaeological deposits in the cave site of Hang Thung Binh 1. We present the stratigraphic and chronological context of the new specimens and the morphological and metric criteria used for taxonomic diagnosis. We then synthesise the available evidence for the environmental context of the Upper Pleistocene water deer of Tràng An. We conclude considering if new finds reflected different climatic conditions and are relics of the Pleistocene, or these records are an early indication of an unrecognised southerly distribution and hence a shifted baseline, with possible implications for the conservation of the species in the future.

2.1 Location

The Tràng An karst landscape and environs are located in Ninh Binh Province, Northern Vietnam (see [9, 54-57] for detailed descriptions). Hang Thung Binh 1 (TB1) is one of six caves within an isolated limestone hill of the same name, in the northwest corner of the Tràng An core zone, 1.5 km west of the main massif set within cultivated alluvial plains (Figure 2). TB1 is a small two-chambered, east-facing cave (20° 15’ 41.8” N; 105° 51’ 53.1” E; Figure 2) situated 27 m asl and currently overlooks cultivated fields towards the north-west margin of the main massif. TB1 was investigated archaeologically in 2012 by the Vietnamese Institute of Archaeology (VIA), Hanoi [58] and by the SUNDASIA project from 2017 [57]. The SUNDASIA
project excavated two trenches and the specimens reported here (table 1; figure 3) were recovered during excavations in the second trench, which was opened in the front of the main chamber (figure 2).

2.2 Stratigraphic and chronological context
In Trench 2, an area of approximately 5.5 m² was excavated to an average depth of 1.60 m below the current cave floor. The trench yielded a sequence covering the 20th century to over 18,000 years BP (figure 2). The cervid specimens were recovered from an aceramic, shell-rich (predominantly Cyclophorous spp.), midden deposit, contexts (F907) to (F9015), which comprised of occasional stone tools, numerous fragments of animal bone and frequent charcoal fragments. Context (F907) was also notable for the presence of an inhumation [57] dating to around the Pleistocene-Holocene transition and recovered between 27.27 and 27.03 m asl (figure 2).

Two cervid mandible fragments (TB1-F908.2-SF40 and TB1-F912-SF42, hereafter “SF40” and “SF42”, respectively) and two fragments of maxillary canines (TB1-F912-SF43 and TB1-F912-SF44, hereafter “SF43” and “SF44”, respectively) were recovered from the midden layers underlying the inhumation. SF 40 was recovered at 26.95 m asl on 17th November 2018. SF 42, SF 43 and SF44 were recovered together six days later in close proximity in the same area, 0.1 m deeper in the sequence at 26.85 m asl (figure 2). There was no indication of significant reworking or discernible signs of bioturbation or disturbance to the deposits that would suggest that the specimens were intrusive or ex situ. From context, the specimens most likely represent the remains of animals exploited as food.

Direct dating was not attempted as previous efforts to radiocarbon date archaeological bone from TB1 and other project sites had consistently failed due to lack of collagen content [57]. Chronological context is provided by six radiocarbon dates from charcoal recovered from the stratigraphic sequence (figure 2; table S2). These dates were obtained via accelerator mass spectrometry at the AMS 14Chrono Centre facility at Queen’s University Belfast. They were calibrated with calib 8.2 [59] using the Intcal. 20 calibration curve [60]. Calibrated radiocarbon dates are shown here as two sigma ranges as “cal. BP” (“calibrated years before present”). Calibrated dates from the sequence are in superposition and indicate that the midden deposits accumulated between the end of the Last Glacial Maximum (26.5 to 19 cal. BP; [61]) and the early Holocene. The available dates effectively bracket the specimens reported here to between 13,000 and 16,000 cal. BP.

3. Materials and Methods
Identification of the specimens (table 1) was made as part of ongoing analysis of the vertebrate remains recovered from Tràng An by the SUNDASIA project. The analysis was carried out in the UK at the Oxford University Museum of Natural History with the permission of the Tràng An Management Board and Ninh Binh Peoples Committee. The specimens are to be stored and curated by the Tràng An Management Board in Ninh Binh upon completion of the project.

The specimens were identified by morphological and metric comparisons to museum specimens and morphometric data. Modern comparative specimens were consulted at the Oxford University Museum of Natural History (OUMNH) and previous observations and measurements at the Natural History Museum, UK (Stimpson, unpublished data) and American Museum of Natural History (Utting, unpublished data) were employed. Comparative descriptions and dental metric data were also compiled from the literature [9,
Dental measurements are shown and defined in Table 2. All measurements collected in this study were taken with dial callipers to the nearest 0.01 mm.

Statistical tests were also performed to compare dental metrics of the archaeological specimens with museum specimens and published sources. Univariate normative comparisons were performed with a modified *t*-test [72-74] with step-down correction to control familywise false-positive error rate in multiple comparisons [75]. The tests were performed using the E-clip Multivariate and Univariate Normative Comparisons online platform [76]. Tests were run with a chosen alpha of 0.05. This approach assumes normality in the normative (comparative) samples. Comparative data sets were examined for departures from normality (Shapiro Wilk W) using the functions in PAST 3.20 [77]. Output of statistical tests is shown in Table 3.

4. Results

4.1 Description

SF40 is a fragment of a right mandibular body (maximum length of specimen = 78.88 mm) with a complete toothrow, p2 to m3 (Figure 3). The specimen was recovered in two pieces and was conserved and then refitted - the break is located anterior of the m2. Approximately 80% of the mandibular body is preserved although the central surface has suffered some damage. Most of the diastema is absent, as are the incisors and ascending ramus. Sediment (and a small fragment of shell on the labial side of the body, between the alveoli of the m2 and m3) has formed a hard crust through calcium carbonate deposition and is adhered to much of the specimen, particularly around the base of the teeth. After limited cleaning by hand, the morphology of the upper crowns and occlusal surfaces was clear.

The dentition is adult but is unworn. Individual dental age stage (IDAS) is early IDAS 3 based on eruption and wear to the molars [78]. The p4 is “molarised” in that, in terms of gross morphology, this tooth comprises of two distinct lobes. The anterior lobe is broad, whereas the posterior lobe is compressed and elongate in the labial-lingual direction with well-developed posterolingual and posterolabial conids. The anterior and mesolingual conids are united, forming a contiguous structure, which enclose an anterior fossette. The lingual edges of the metacnidos of the molars are simple, with single shallow folds. Weakly developed anterior cingulids are present on the m1 and m2. A small, slender anterior ectostylid is present on the m3 (Figure 4).

SF42 is a small fragment (maximum length of specimen = 32 mm) of the dorsal surface of the body of a right mandible (Figure 3). The ventral side is broken away. Two complete, unworn teeth, p4 and m1, are preserved in situ and appear slightly larger and more robust than those in SF40. A portion of the alveolus for the m2 is also preserved. As in SF40, the p4 is also “molarised” (Figure 4), with an elongate posterior lobe and well-developed posterolingual and posterolabial conids. A weakly-developed anterior cingulid and a weakly-developed elongate (in the labial-lingual direction) ectostylid is present on the m1. The lingual edge of the metacnidos lack complex folds or crenulations.

SF43 is a left maxillary canine (maximum length of specimen = 51.20 mm; Figure 3). The specimen was recovered in two pieces and refitted. The closed root and majority of crown are preserved although the crown is chipped and broken at the tip (Figure 4). The tooth curves posteriorly. The lateral surface of the crown is concave. The medial surface is relatively flat.

SF44 is the broken tip of a left maxillary canine (maximum length of specimen = 17.92 mm; Figure 3). As with SF43, SF44 is convex on the lateral side and flattened on the medial.
**4.2 Diagnosis**

Absolute size of specimens, tooth dimensions and morphology all indicate small ruminant: either a species of the Cervidae or Moschidae. The relatively long, posteriorly curved canine with a closed root also indicates the so-called “fanged” deer or musk deer. The fourth lower premolars are present in both mandible fragments and are “molarised”. While Hooijer [51] describes one exceptional specimen of *M. muntjak vaginalis* (AMNH 43056), where the anterior and mesolingual conids meet (but are not fused), this character discounts *Muntiacus* [19, 51, 80] and indicates three candidate taxa: *Moschus* spp., *H. inermis* and *Elaphodus cephalophus* (figure 4; for *Moschus* spp., *M. moschiferus* is figured).

The smallest of the three taxa, the musk deer - *Moschus* spp. - are not true cervids and are classified in a separate family, Moschidae. Musk deer are currently distributed from the Himalayas to North East Asia, with up to seven extant species [81]. The smallest species, *M. berezovskii* (Flerov, 1928; extant body weight 6-9 kg), the “dwarf” or “forest musk deer”, ranges into South China and marginally into north Vietnam, where it has been reported in karst habitats. The much-reduced Vietnamese populations were, until recently, thought to be Siberian musk deer, *M. moschiferus* [82].

*Moschus* is indicated against here by the relatively simple lingual outline of the molars in SF40 and SF42. Specifically, “double-folded” lingual margins of the metaconids are key diagnostic characters of *Moschus* [63,80] and are absent in the archaeological material (figure 4). Furthermore, anterior cingulids and mesostylids are relatively well developed in comparative specimens from the genus in comparison to the archaeological material. Conversely, posterolingual and posterolabial conids were well developed on the p4 in the available reference material.

Univariate comparison of dental measurements from extant and Pleistocene *M. moschiferus* with the archaeological specimens, found measures to be statistically significantly larger in the archaeological specimens (table 3). Although statistical comparison was not possible due to lack of a sufficient sample size, the width of canine SF43 was greater and the overall tooth approximately 30% larger than that of the comparative material for *Moschus*.

The largest of the three potential taxa, the tufted deer, *E. cephalophus*, (17-30kg) is currently found in southern China, with historical records from eastern Myanmar [83]. In terms of gross size and morphology, the mandibles and teeth of extant tufted deer appear larger and more robust than the TB1 material (figure 4). Relatively well developed ectostylids are apparent on the molars. If present, anterior cingula are very weak: they are more commonly absent in comparative material for *E. cephalophus*. The posterolabial and posterolingual conids of p4 are not as developed as in the archaeological specimens, but there is a relatively deep fold in the lingual wall between the anterior stylid and anterior conid, which is absent in the p4 of SF40 and SF42. These characters are also consistent in large Pleistocene specimens of the genus figured in [51]. The maxillary canine in *E. cephalophus* appears shorter, but much more robust than in SF43.

Toothrow length and p4 length of SF40 was found to be statistically significantly smaller than comparative data for extant tufted deer. No statistically significant difference was found in p4 length between SF42 and comparative data, however, and it is likely that individual tooth length may not be the most sensitive measure to discriminate between *Hydropotes* and *Elaphodus*. Comparisons of m3 lengths of Upper Pleistocene *E. cephalophus* [70] suggest that this metric is statistically significantly larger than SF40 (table 3).
In terms of morphology, the archaeological specimens most closely match the available comparative material for water deer, *H. inermis*. The molarised p4 in *H. inermis* has an elongate posterior lobe and well-developed posterolingual and posterolabial conids as in both archaeological specimens (figure 4; see also [19] for the potential diagnostic significance of posterolabial conids). Weakly developed anterior cingulids are present on the molars of available comparative material. The lingual walls of the metaconids are relatively simple (i.e., lack complex folds), as in the archaeological specimens, a key character to distinguish *Hydropotes* from *Moschus* [63,80].

While both archaeological mandibles and their teeth appear marginally larger and more robust in comparison to extant reference material for *Hydropotes*, the dental metrics of the archaeological specimens are within the ranges of equivalent available data for extant specimens (figure 4). No statistically significant differences were found in lower tooth rows lengths or premolar row lengths between SF40 and comparative data for *H. inermis*. No differences were found between p4 lengths in SF40 and SF42 or available comparative data. No significant difference was found in canine width between SF43 and comparative data for *H. inermis* (table 3).

Confirmed Pleistocene records for *H. inermis* are scarce, as are Pleistocene age dental data (with the exception of the p4 from Lang Trang, below). It was not possible to locate a data set to investigate the possibility of larger Pleistocene body size in the region [e.g. 51,84]. It was possible, however, to re-run the tests with the stated hypothesis that metrics from the TB1 specimens are statistically significantly larger than the available extant/Holocene data. In the case of this 1-tailed test, toothrow length of SF40 was found to be statistically significantly larger than the Holocene dataset; with \( p = 0.047 \), however, this result is marginal (table 3). Conversely, premolar row length in SF40 was not found to be statistically significantly larger than the available comparative data. For SF42, length of p4 was not found to be statistically significantly larger the comparative data set. Finally, canine width in SF43 was not found to be statistically significantly larger than comparative data (table 3). The dimensions of the *H. inermis* specimen from Lang Trang (PIN 579/20; L = 11.5 mm; W = 8.1 mm [53]), however, suggest that the fourth premolar is relatively large in comparison to data from Holocene animals. Length was found to be statistically significantly different from Holocene comparatives and when the Upper Pleistocene specimens from TB1 are included (table 3). While the p4 figured in [53] is worn, which can potentially affect measurements of teeth to a degree [84], these data suggest that the specimen from Lang Trang reflects an earlier, larger-toothed and/or larger-bodied form.

In summary, morphological and metric characters indicate that the TB1 specimens are attributable to *Hydropotes*. There are no compelling grounds to suggest a larger, Pleistocene subspecies and no reason (geographical or otherwise) for proposing a separate species. The specimens from TB1 are referred to *H. inermis*. The identified remains derive from at least two individuals. The size of the canine fragments indicate the finds include male animals [cf. 62].

5. Discussion

The remains of water deer from TB1 confirms the prehistoric presence of the species in northern Vietnam. The specimens, dating to between 13,000- and 16,000-years BP, are valuable contributions to the sparse Pleistocene record for the species and are, at present, the most recent records in Vietnam. These new finds, however, raise questions.

Firstly, what were climatic and environmental conditions around TB1 between 13,000- and 16,000-years BP? This was a period of significant global climatic instability [85]. This is
also an important question as Upper Pleistocene zooarchaeological evidence from cave sites within Tràng An indicate a focus on the exploitation of forest-adapted taxa from the karst [56,86]. The position of TB1 in a “satellite” hill overlooking the plain to the west of the karst, however, is likely to be pertinent (figure 2).

Observations of extant animals indicate that, while interlinked forest patches are a significant factor that can mediate localised abundance [24], water deer tend to be a lowland species with a preference for more open, marginal and riparian habitats. These habitats include reed-beds and tall, damp and undisturbed grasslands, with forbs and woody plants such as species of Asteraceae, Leguminosae and Fagaceae as favoured food plants [87-89]. Were similar habitats present on the plain outside the cave, or were the Upper Pleistocene water deer of TB1 living in different conditions? Palaeoenvironmental data for the last deglaciation in Northern Vietnam are sparse although records clearly show that rapid climatic fluctuations were experienced during this period [90]. Inferences for the period between 16,000 to 13,000 years BP for the Tràng An karst and the intervening plains, can be synthesised from a combination of proxies at various spatial scales.

Two archaeological cave sites have yielded relevant records for this time period: a multi-proxy record from Hang Trong in the interior of the Tràng An karst [56] and the pollen and spore record from Con Moong Cave [91], just over 20 km to the west of Tràng An. Proxy data from these sites included charcoal from Dipterocarpaceae, Leguminosae and Sapotaceae; pollen from euphorbs and mimosoid legumes; and stably more negative $\delta^{13}$C values (c. -30‰) of n-alkanes and n-alkanoic acids preserved in sedimentary organic carbon, indicative of forest plants using the C$_3$ photosynthetic pathway [56] and arboreal pollen assemblages comprising forest taxa adapted to cool, moist environments, such as *Castanea*, *Castanopsis*, *Betula* (Betulaceae), *Juglans*, *Engelhardia* and *Platycarya* (Juglandaceae) [91]. These data suggest that limestone karsts on the southern margin of the Song Hong delta remained forested throughout the last deglaciation. Further, these areas likely acted as forest refugia during stadials and times of rapid climatic changes and supported upland vegetation typical of higher elevations today alongside lowland taxa of tropical lineages.

For the alluvial and coastal plains, basal units of two boreholes drilled into fluviodeltaic deposits along the course of the Song Hong, east of Tràng An, yielded radiocarbon ages of 15,000-13,000 cal. BP [92-93] as well as palaeoenvironmental proxies in the form of palynological assemblages and sedimentological structures [94]. Facies 1.1 of the ND-1 core, located approximately 30 km ENE from Tràng An, produced two radiocarbon ages of 15,000 and 14,800 cal. BP [91]. The lithology of this unit was upward-fining and consisted of cross-bedded fluvial sands, and interlaminated muds and organic sediments interpreted as lateral accretion within a river meander, as well as channel fill. Pollen preservation was relatively poor but contained grains of conifers (*Cryptomeria*; Taxodioidae; *Pinus*), upland broadleaf taxa (e.g., *Quercus*) and various temperate riparian elements [94].

Further downstream, near to the modern delta front and about 70 km east from Tràng An, Unit 1 of the NP core sits underlies a radiocarbon age of around 12,000 cal. BP [93]. The silts of this unit yielded pollen assemblages comprising grasses (Poaceae), sedges (Cyperaceae), willow (*Salix*), oak (*Quercus*) and chinquapin (*Castanopsis*). These assemblages suggest a floodplain environment with scattered freshwater marsh, with the pollen from temperate broadleaf elements likely transported to the site fluvially from the surrounding uplands. Given the depths of these basal units, the riparian, floodplain and marsh environments they represent occurred within the ancient valley incised by the Song Hong during times of lower sea level in the Upper Pleistocene. It is a reasonable proposition then,
that the plain outside TB1 carried a seaward-draining watercourse that flowed through a similar mosaic of alluvial environments, which incorporated more open wetland habitats, surrounded by upland and limestone forests on the karst. These data suggest that similar or preferred habitats of extant water deer were present in the Upper Pleistocene on the plains around TB1 and that cooler, but not necessarily drier, conditions prevailed.

This leads to the question: are the Tràng An specimens relicts of cooler Pleistocene conditions or are the new finds an early indication of a previously unrealised, more recent presence in Vietnam? More practically, could archaeological evidence warrant a potential case for (re)introduction into Tràng An? Reintroduction campaigns are, in practice, complex and necessarily must navigate a series of ethical, economic, sociological, and ecological factors. Thorough consideration of the potential risks to the environment and livelihoods is required and must be balanced against potential benefits of ecosystem services and ecotourism, in addition to the welfare of reintroduced populations. It is beyond the scope of the present paper to discuss these issues in detail and we consider the current evidence as a hypothetical case.

Currently, only two other sites in Vietnam, Mai Da Dieu and Lang Trang, have yielded possible evidence of water deer; specimens from the former remain unconfirmed. Both these sites are in northern Vietnam and are Upper Pleistocene in age. It is not possible to determine any directly associated radiocarbon dates with the unconfirmed Mai Da Dieu material, but dates given in the 2009 publication [52] suggest a post-LGM context and a broadly similar age to the TB1 specimens. The tooth reported from Lang Trang is older and currently dated to between 80,000-100,000 years BP [53]. The Pleistocene distribution of a species is not typically perceived as a justification for designating it as “native” within the modern area. Firstly, potential source populations for reintroductions may derive from a different genetic population of the species. In this case, however, concerns about differing genetic lineages may perhaps be allayed by the questionable subspecific status of extant water deer. Secondly, given the climatic and environmental change that occurred during the Pleistocene-Holocene transition, Pleistocene populations may have been adapted to and reliant upon different conditions than the Holocene [15].

Water deer are today regarded as a temperate species (e.g. [89, 95]) and extant and Quaternary records of water deer do tend towards temperate latitudes (figure 1). As we have seen, available proxies indicate that the Upper Pleistocene landscapes of Tràng An reflected cooler conditions than the sub-tropical climate of the Holocene. Regional palaeoenvironmental proxies also indicate that a drier and cooler climate at the beginning of the Holocene, following the Younger Dryas stadial, which saw reduced temperature and precipitation approximately 12,900 to 11,700 years BP. While water deer may have persisted into the early Holocene, increasing temperature and humidity and the establishment of subtropical climate and environmental change [96] may have precluded the persistence of populations of water deer in Northern Vietnam.

This argument, at least in part, would be an artefact of the shifting baseline syndrome. The historical distribution of water deer in China, and the recent finds in Taiwan [30, 32] present a significant challenge to this simplistic climatic and environmental narrative. Historical records place water deer at sub-tropical latitudes in China until recently, in the 20th century. In addition to the identified archaeological material, historical documents indicate that water deer were, until relatively recently, common and widespread in Taiwan until extirpation in the 19th century [32].
In practical terms, only confirmed and reliably dated specimens would provide unequivocal evidence of populations surviving into the Holocene. A search for potential specimens from Holocene age archaeological sites in Vietnam, either in archives or during future investigations would be worthwhile, as would a review of potential documentary evidence. A comprehensive assessment would also require other factors such as hunting by humans, or competitive exclusion by other species to be considered, but there are currently no clear climatic or environmental factors that would have been a definitive barrier to the survival of water deer into the Holocene in northern Vietnam.

6. Conclusion

Newly identified fossils from the archaeological cave site of Hang Thung Binh 1 in the Tràng An World Heritage Landscape Complex Site confirm the presence of water deer, *H. inermis*, in northern Vietnam in the Upper Pleistocene. The new specimens are further evidence of a wider Quaternary distribution for these Vulnerable, globally declining cervids, are valuable additions to a sparse Pleistocene fossil record and confirm water deer as a component of the Upper Pleistocene fauna of northern Vietnam.

Current archaeological and palaeontological evidence for the presence of water deer in the country is extremely sparse and restricted to the Upper Pleistocene. While water deer are today associated with temperate latitudes, a brief survey of the known historical distribution and recent archaeological evidence indicates that the species has been capable of surviving in sub-tropical climates and habitats. The possibility that water deer survived into the Holocene in northern Vietnam is a hypothesis to be tested.

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Data accessibility. The datasets supporting this article have been uploaded as electronic supplementary material.

Author contributions. CMS and RR conceived the study; CMS conducted analyses and identification and drafted the manuscript with contributions from all authors; CMS, RH and BU conducted the review of Quaternary records of *Hydropotes inermis*; CMS and BU performed statistical tests; TK translated German language source material; CMS, BU, RR, TK, carried out excavation, site analysis and recording; SO and NTMH produced the paleoenvironmental synthesis. All authors revised the manuscript and gave final approval for publication.

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248x240mm (200 x 200 DPI)
Figure 3. Upper Pleistocene specimens of Hydropotes inermis recovered from the Hang Thung Binh 1 archaeological cave site in the Tràng An World Heritage Area, Ninh Binh, Northern Vietnam. SF40 right mandible with toothrow, p2-m3, (a) labial side (b) lingual side (c) occlusal surface of teeth. SF42 right mandibular fragment with p4 and m1 in situ, (d) labial side (e) lingual side and (f) occlusal surface of teeth. SF43 left maxillary canine (g) lateral and (h) medial aspects. SF44 left maxillary canine tip (i) lateral and (j) medial aspects. Scale = 20 mm.

162x107mm (300 x 300 DPI)

https://mc.manuscriptcentral.com/rsos
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139x164mm (200 x 200 DPI)
Table 1 Provenance and description of identified specimens of *Hydropotes inermis* from the Hang Thung Binh 1 archaeological cave site in the Tràng An World Heritage Landscape Complex Site, Ninh Binh, Northern Vietnam.

| Site | Trench | Grid sq. | Context | SF no. | Description                                      |
|------|--------|----------|---------|--------|--------------------------------------------------|
| TB1  | 2      | TR2EE    | F908.2  | 40     | right mandibular body and complete toothrow p2-m3 |
| TB1  | 2      | MS-E     | F912    | 42     | right mandible fragment with p4 and m1           |
| TB1  | 2      | MS-E     | F912    | 43     | left maxillary canine with root and crown.       |
| TB1  | 2      | MS-E     | F912    | 44     | fragment of left maxillary canine - tip of crown |
Table 2 Measurements of three *Hydropotes inermis* specimens from the archaeological cave site of Hang Thung Binh (TB1) in the Tràng An World Heritage Area, Ninh Binh, Northern Vietnam. All measurements are in mm. C – maxillary canine; p – mandibular premolar; m – mandibular molar; L – length (anterior-posterior); W – width (labial-lingual); p2-p4 – mandibular premolar row length; m1-m3 – mandibular molar row length; p2-m3 – mandibular toothrow length.

| tooth/toothrow | dimension | SF40 | SF42 | SF43 |
|----------------|-----------|------|------|------|
| C              | W         | /    | /    | 10.98|
| p2             | L         | 6.56 | /    | /    |
|                | W         | 3.19 | /    | /    |
| p3             | L         | 8.2  | /    | /    |
|                | W         | 5.36 | /    | /    |
| p4             | L         | 8.64 | 9.44 | /    |
|                | W         | 5.86 | 6.24 | /    |
| m1             | L         | 9.82 | 9.8  | /    |
|                | W         | 7.2  | 7.38 | /    |
| m2             | L         | 11   | /    | /    |
|                | W         | 7.11 | /    | /    |
| m3             | L         | 13.8 | /    | /    |
|                | W         | 6.68 | /    | /    |
| p2-p4          | L         | 24.2 | /    | /    |
| m1-m3          | L         | 34.45| /    | /    |
| p2-m3          | L         | 57.96| /    | /    |
Table 3 Summary of statistical output for tests of normality (Shapiro Wilk W) and univariate normative comparisons (modified t-test) of specimens from Tràng An and Lang Trang with comparative data (tables S3-S5). Significant results are shown in bold. Taxon data sets: ^1 Holocene; ^2 Pleistocene and Holocene; ^3 Upper Pleistocene

| Spec | Measure | Taxon     | n  | W       | p (norm.) | hyp    | sig  | diff | mod. t | p    |
|------|---------|-----------|----|---------|-----------|--------|------|------|--------|------|
| SF40 | L p2-m3 | *H. inermis* ^1 | 28 | 0.9398  | 0.1093    | 2-tailed | N    | 1.778 | 1.747  | 0.084 |
| SF40 | L p2-m3 | *E. cephalophus* ^1 | 17 | 0.9215  | 0.1566    | 1-tailed (smaller) | Y    | -1.972 | -1.916  | 0.034 |
| SF40 | L p2-m3 | *M. moschiferus* ^1 | 10 | 0.9287  | 0.4353    | 1-tailed (larger) | Y    | 5.025  | 4.791  | <0.001 |
| SF40 | L p2-p4 | *H. inermis* ^1 | 24 | 0.9297  | 0.09588   | 2-tailed | N    | 0.78  | 0.765  | 0.454 |
| SF40 | L p4    | *E. cephalophus* ^1 | 7  | 0.9312  | 0.5611    | 1-tailed (smaller) | Y    | -3.539 | -3.31  | 0.008 |
| SF40 | L p4    | *H. inermis* ^1 | 7  | 0.9457  | 0.6902    | 2-tailed | N    | 0.261 | 0.244  | 0.826 |
| SF42 | L p4    | *H. inermis* ^1 | 7  | 0.9457  | 0.6902    | 2-tailed | N    | 1.384 | 1.295  | 0.23  |
| SF42 | L p4    | *E. cephalophus* ^1 | 7  | 0.9312  | 0.5611    | 1-tailed (smaller) | N    | -0.545 | -0.51  | 0.294 |
| SF42 | L p4    | *M. moschiferus* ^1 | 7  | 0.9261  | 0.518     | 1-tailed (larger) | Y    | 6.326  | 5.917  | <0.001 |
| SF43 | Cw      | *H. inermis* ^1 | 8  | 0.9184  | 0.4174    | 2-tailed | N    | -0.061 | -0.058 | 0.943 |
| SF40 | L p2-m3 | *H. inermis* ^1 | 28 | 0.9398  | 0.1093    | 1-tailed (larger) | Y    | 1.778  | 1.747  | 0.047 |
| SF40 | L p2-p4 | *H. inermis* ^1 | 24 | 0.9297  | 0.09588   | 1-tailed | N    | 0.78  | 0.765  | 0.224 |
| SF42 | L p4    | *H. inermis* ^1 | 7  | 0.9457  | 0.6902    | 1-tailed | N    | 1.384 | 1.295  | 0.118 |
| SF43 | Cw      | *H. inermis* ^1 | 8  | 0.9184  | 0.4174    | 2-tailed | N    | -0.061 | -0.058 | > 0.9 |
| SF40 | L p4    | *E. cephalophus* ^1 | 24 | 0.9499  | 0.2696    | 1-tailed | Y    | -4.038 | -3.957 | <0.001 |
| PIN  | 5792/20 | L p4      | *H. inermis* ^1 | 7  | 0.9457  | 0.6902    | 2-tailed | Y    | 4.276  | 4      | <0.001 |
| PIN  | 5792/20 | L p4      | *H. inermis* ^1 | 9  | 0.9318  | 0.4983    | 2-tailed | Y    | 4.177  | 3.963  | 0.01  |
Appendix D

Dear Dr Lindsey,

Re: RSOS-210529 Stimpson et al. Confirmed archaeological evidence of water deer in Vietnam: relics of the Pleistocene or a shifting baseline?

Pleased find enclosed details of the revisions to our manuscript, as requested. We would like to express our thanks to the editors and expert reviewers for their time, constructive criticism and encouraging comments. We feel that the article has benefited and improved as a result of their input and by addressing their comments. We have amended the Acknowledgements: “We thank two anonymous reviewers for their encouraging comments and constructive criticism, which improved the content and structure of the manuscript.”

Here, we address the main points that you raise, followed by the point-by-point responses to each reviewer’s comments.

MAIN POINTS

Associate Editor Comments to Author (Dr Emily Lindsey):

Comments to the Author:
The article was reviewed by two experts, both of whom noted the interest and value of the article and recommended publishing with minor revisions. The two main concerns the reviewers raised that should be addressed for publication were:

1. A more well-developed description of the tooth morphology, and ensuring accuracy and consistency with the diagnostic references.
2. A restructuring of the discussion for clarity and highlighting the importance of the presented study for broader research and conservation-related questions.

1. We have expanded descriptions of lower toothrows, with greater coverage of p2 and p3 and lower molars. Dental terminology has also been reviewed throughout and modified, where necessary, as directed by the reviewer. Figure 4 has been revised, accordingly and Figure 3 has been amended to include occlusal details of the archaeological specimens at greater magnification. Full details are provided in the point-by-point responses to reviewer 2.

2. We have restructured the discussion to follow the recommendations of the reviewer 1, below. For the sake of transparency, text that has been added or removed as part of the restructure has been highlighted. Full details are provided in the point-by-point responses to reviewer 1.

Reviewer 1

“My biggest concern was with the structure of the discussion. It was a little hard to follow, and did not seem, to me at least, to flow well in an “answering research questions” framework. This is not to say that the discussion needs a re-write, but I would say that a re-structuring would benefit the reader. For example, lines 378-380 seem to present a good question that can be addressed with your new data, and so do lines 412-414. I think leading with what you found, i.e., Vietnamese water deer in the latest Pleistocene, and how that can inform the idea of shifting baselines or Quaternary extinctions/extirpations would provide a more impactful discussion. It would also harken back to your introduction where you introduce these ideas at the beginning. Your discussion about the changing floral regimes through the late Pleistocene and Holocene could follow, providing supporting arguments for why the water deer are found in their extant range. While reading the paper, it wasn’t really clear to
me how the climatic changes that occurred regionally, i.e. Heinrich event 1, etc, were related to the patterns of vegetation change, and therefore the water deer. It might be worth simplifying that section and making it more streamlined.

Agreed. As a summary, the discussion was restructured as follows:

Significance of Upper Pleistocene Vietnamese water deer – relics, or longer term, previously unrealized population? (and the significance of regional records on range collapse, etc.)

Are the the finds a case for reintroduction? Current records in Vietnam - Pleistocene sites in the Northern Vietnam only- genetic and environmental issues for using Pleistocene records as a basis to propose reintroductions. Environmental context of the water deer of Trang An.

Current evidence indicates cooler (but not necessarily drier) conditions (current available date range potentially incorporates stadial and interstadial conditions)—consistent with modern temperate distribution. Therefore, water deer restricted to temperate climes and restricted to Pleistocene in Vietnam? Sub-tropical records as an example of shifting baselines, which challenge this neat but overly simplistic narrative.

Finally, only confirmed, securely dated records from Vietnam would provide unequivocal evidence of a Holocene population.

I also think the manuscript would benefit from a discussion about Quaternary extinctions in the region, and importantly faunal persistence, range shifts, and metapopulation dynamics. What you have seems to be a relict Pleistocene population that got extirpated. There’s a lot of exciting research coming out of the region such as the giant muntjac that you described from Northern Vietnam, the work Sam Turvey has done on population collapses in muntjacs, and the new species of gibbon from China. It would help show that there is still much to be learnt from Pleistocene and Holocene records from this part of the world. Moreover, it would be hugely beneficial to see what other species in the region show similar patterns. I know off-hand that all three species of asian rhinos were once more widely distributed through South Asian, Southern China, and Southeast Asia, but are now relegated to isolated pockets. Ending with your conservation and reintroduction message would in my mind be a good way to wrap up this fascinating story.”

Agreed, but these issues are discussed and cited in the Introduction as the context for the current research. They are, however, recalled in the discussion with the additional text:

Page 8 Line 338 (“Changed” pdf) “But what does these new records from Tràng An represent? Are they simply relics of the Pleistocene or are the new finds an early indication of a previously unrealised, more recent presence in Vietnam and hence, a shifted baseline? This would not be without precedent. Work on later Quaternary palaeontological and zooarchaeological assemblages has highlighted the vulnerability and scale of range collapse of other mammalian herbivores in East and Southeast Asia [e.g. 10,11].”

Reviewer 1 point-by-point responses

| Original | “Changed” |
|----------|-----------|
| Page/Line | Page/Line | Comment/Revision |
| 1/31 | 1/30 | “It would be good to include your main conclusions here that follow from your analyses of the paleoenvironment.” |

Response
"We also examine the environmental context of the water deer of Tràng An before considering if the new finds represent relics of an Upper Pleistocene population, or are an early indication of an unrecognised southerly distribution with possible implications for the conservation of the species in the future."

Replaced with

"Palaeoenvironmental proxies suggest that the Tràng An water deer occupied cooler, but not necessarily drier, conditions than today. We consider if the specimens represent extirpated Pleistocene populations or indicate a previously unrecognised, longer-standing southerly distribution with possible implications for the conservation of the species in the future."

4/106

Comment/Revision

"Please specify what you mean by exotic"

3/101

Response

"both exotic and extinct forms" replaced with "extinct forms and taxa previously unrecorded from Japan"

6/245

Comment/Revision

This section can be removed or integrated into the discussion

6/248

Response

Text removed:
Musk deer are currently distributed from the Himalayas to North East Asia, with up to seven extant species [81]. The smallest species, M. berezovskii (Flerov, 1928; extant body weight 6-9 kg), the "dwarf" or "forest musk deer", ranges into South China and marginally into north Vietnam, where it has been reported in karst habitats. The much-reduced Vietnamese populations were, until recently, thought to be Siberian musk deer, M. moschiferus [82].

References updated from [81] onward

Comment/Revision

6/258

I know what you’re trying to say here with statistically significant, but you can remove the term statistically especially since you are referring to Table 3, which has p-values. It reads a lot better when you remove the term statistically

Response

"statistically" removed throughout section 4.2 where it is used in this context except from 7/316, where it is stated in a hypothesis

Comment/Revision

See R1 main point on restructuring the Discussion

9/373

Response

Text removed (redundant) to accommodate restructuring:
"What do we know of the climatic and environmental conditions around TB1 between 13,000- and 16,000-years BP? There is an important environmental question here, as Upper Pleistocene zooarchaeological evidence from cave sites within the Tràng An karst indicate a particular focus on the exploitation of forest-adapted taxa from the karst by humans [56,84]. The position of TB1
in a “satellite” hill overlooking the plain to the west of the karst “proper”, however, is likely to be pertinent (figure 2)."

| Page | Comment/Revision |
|------|------------------|
| 7/325 | It might be worth giving examples of the climatic instability you are talking about |
| 8/338 | Here again, it would be worth talking a bit more about these climatic fluctuations. |

**Response**

To address these points, the following text and reference was added as part of the restructured Discussion:

“Global climates experienced significant instability between 13,000- and 16,000-years BP [87], which encompassed the glacial conditions of Heinrich Stadial 1 followed by the shift to the relatively brief period of warm and wet conditions of the Bolling-Allerod Interstadial. Chinese speleothem records indicate that this shift occurred in the region towards the end of the more recent radiocarbon date range for the water deer of TB1, between approximately 14,700 and 13,000 years BP [88]. While it is not possible, at present, to state with certainty if the Tràng An specimens derived from stadial or (at the latter end of the current date range) interstadial conditions, or a transitional period between the two, palaeoenvironmental inferences for the Tràng An karst and the intervening plains can be synthesised from a combination of proxies at various spatial scales.”

Additional reference:
88. Zhang H, Ait Brahim Y, Li H, Zhao J, Kathayat G, Tian Y, Baker J, Wang J, Zhang F, Ning Y, Edwards RL. 2019 The Asian summer monsoon: Teleconnections and forcing mechanisms—A review from Chinese speleothem δ18O records. Quaternary 2, 26. (doi: 10.3390/quat2030026)

| Page | Comment/Revision |
|------|------------------|
| 9/392 | I would cite the authors here instead of calling the article “the 2009 publication”. Or, rephrase the sentence to indicate that in 2009, new dates suggest a post-LGM context |

**Response**

“in the 2009 publication” replaced with “by Popov”

**Reviewer 2**

“In my eyes the manuscript is almost ready for publication and has major importance to science in the framework described above. The only criticism I come up with concerns the description of the tooth crown morphology. Although the p4 represents a key tooth for species identification, p2 and p3 hold cervid specific differences from Moschus, but aren’t described, and m1 to m3 are almost not described. This would be important to future work searching for more Hydroptes material in archives and excavations. Please see more detailed comments in the annotated manuscript itself.”
We have expanded descriptions of lower toothrows, with greater coverage of p2, p3 and lower molars. Full details are provided in the point-by-point responses, below.

Moreover, you say that you have used Bärmann & Rössner (2011) as the source for tooth crown element nomenclature, what is only true in part. Some elements are differently named than in B & R and do not even follow the principles given there. Hence, either please adapt or clarify in the text that B & R has been used as a basis for your modifications.

Agreed, upon review there are cases where the terminology from older source material (e.g Colbert and Hooijer) has been incorrectly retained. Dental terminology has been reviewed throughout and modified, where necessary, as directed by R2. Full details are provided in the point-by-point responses, below.

The molarisation of p4s is a commonly known phenomenon in mammal odontology and mammal palaeontology what has not to be put in quotation marks. Please see for example Janis and Lister (1985) (attached).

“molarised” is replaced with molarised, throughout.

However, although homology of crown elements in non-molarised and molarised is not evidenced in the fossil record by step by step transition states, there are ideas / hypotheses on what element in a non-molarised p4 is homologous to an element in a molarised p4. As to cervids I have provided more details in the annotated manuscript.

Last but not least, as tooth morphology is so crucial in that paper, higher magnified occlusal views are recommended."

Macro shots of the occlusal surfaces of SF40 and SF42 have been added to figure 3. Figure 4 has also been revised, showing toothrows at greater magnification and amended with more details of molarised and non-molarised p4s.

Reviewer 2 - point-by-point responses

| Original | Changed |
|----------|---------|
| Page/Line | Page/Line | Comment/Revision |
| 1/21 | Wouldn’t “inappropriately” the more appropriate word instead of “comparatively”? | Response |
| 2/51 | Comment/Revision | begin? |
| 2/49 | Response | Changed to “begin” |
| 3/127 | Comment/Revision | reflected |
| 3/120 | Response | Changed to “reflect” |
| 3/127 | Comment/Revision | addition for more specification: “ecological adaptations under different” |
| 3/120 | Response | “reflected different climatic conditions” revised to “reflect different ecological adaptations under different climatic conditions” |
I see differences to Bärmann & Rössner (e.g. in Fig 4, anterior stylid of Bärmann & Rössner became anterior conid and mesolingual conid in B & R became anterior stylid and internal and external postmetacristid in B & R became double fold) and suggest that you either adapt or say that you have modified from Bärmann & Rössner.

Agreed, upon review there are deviations from Bärmann & Rössner, which retain the nomenclature from earlier, source material. These deviations have been revised and are shown on a point-by-point basis, below. Figure 4 has also been amended and revised, accordingly.

Not true! The dentition is medium worn to slightly worn; even the p2 is slightly worn.

"but is unworn" deleted

Quotation marks removed from molarised, here and throughout. Figure 4 is updated.

Please add "alike the corresponding molars"

"alike the corresponding molars" added

revised to:

"the posterior lobe is compressed in the anterior-posterior direction. A well-developed posterior stylid extends lingually from the posterolabial conid."
| Page | Text |
|------|------|
| 5/214 and 5/226 | Homology of structures in non-molarized and molarized premolars is still debated, but from my experience I would say that this is a mesolingual conid, isolated from the transverse crest and shifted a bit anteriorwards, with anterolingual and posterolingual cristid, positioned lingual of the anterior valley. There is no anterior conid. The posterolabial cristid is reduced so that the posterior elements are disconnected from the anterior elements. |
| 5/202 | **Response**  
Deleted: “The anterior and mesolingual conids are fused, forming a contiguous structure, which enclose an anterior fossette.”  
As per R2’s concerns, this statement uses inconsistent terminology and is revised:  
“The anterior lobe is relatively broad and consists of the mesolingual conid and anterolingual and posterolingual cristids detached from the transverse crest, shifted to the anterior and positioned to the lingual side of the anterior valley, which recalls an anterior fossa. A deep valley incises the labial side of the tooth at the location of the posterolabial cristid, which demarcates the anterior and posterior lobes. The posterior lobe is compressed in the anterior-posterior direction. A well-developed posterior stylid extends to the lingual side from the posterolabial conid.” |
| 5/216 | **Comment/Revision**  
What are “lingual edges of the metaconids” (this is not a term from Bärmann & Rössner)? Postmetacristid and premetacristid? |
| 5/215 | **Response**  
Agreed, this recalls the older, source material and does not follow Bärmann & Rössner. Revised to “external postmetacristids” throughout e.g.  
The molars lack external postmetacristids.  
“there is no external postmetacristid” |
| 5/216 | **Comment/Revision**  
This is rather little information on differences in the molars especially the grade of prominence of lingual stylids and columns of metaconid and entoconid. Furthermore, how and if cristids connect to one another. Moreover, the the back fossa of the m3 differs in arrangement. And, I am missing details on differences in p2 and p3. Moschus has rather roundish p2 and p3 whereas the cervids have longish triangular ones. |
| 5/200 | **Response**  
Agreed, coverage is biased towards the p4. The following text has been revise (for nomenclature) with additions:  
 Added:  
SF40  
“The p2 and p3 are relatively elongate and triangular in outline.” |
“The anterior and posterior lobes of the molars are broadly equal in size and shape, with triangular cusps. The adjoining edge of the posterior lobe is offset, labial of the metastylid; the preentocristid abuts the internal postprotocristid of the anterior lobe, next to the posterior margin of the anterior fossa. Except for a pointed mesostylid on the m2, which extends lingually and curves posteriorly, the lingual stylids are not well developed. Rounded mesostylids and entostylids are more prominent on the m1 and m3. The molars lack external postmetacristids. On the labial side, weakly developed anterior cingulids are present on the m1 and m2. A small, slender anterior ectostylid is present on the m3, which has a rounded hypoconulid and an isolated back fossa (figure 4).”

SF42

“As in SF40, the p4 is also molarised, with an elongate posterior lobe and well-developed stylid on the posterolabial conid. A weakly-developed anterior cingulid and a weakly-developed and compressed (in the anterior-posterior direction) ectostylid is present on the m1. As for SF40, the joining edge of the posterior lobe is offset, labially. The lingual stylids are weakly developed and there is no external postmetacristid (figure 4).”

In the comparison with Moschus

“Moschus is indicated against for SF40 by rather rounded, rectangular p2 and p3, compared to the relatively elongate and triangular equivalents in the archaeological specimen. Characteristics of the molars of Moschus also contrast with those of SF40 and SF42. Firstly, the lingual outlines of the molars in SF40 and SF42 are relatively simple and lack external postmetacristids. Well developed external postmetacristids are key diagnostic characters of Moschus [63,80] (figure 4). Secondly, anterior cingulids and mesostylids are relatively well developed and prominent in comparative specimens from the genus Moschus, unlike the archaeological specimens. Thirdly, the location where the posterior lobe of the molars joins their anterior counterpart is much less offset and much more “in line”, lingually, with the location of the metastylid. Finally, the margins of the labial conids are rather angular, with shallow indents in the cristids, compared to the archaeological specimens, which are more rounded and lack indentations.”

In the comparison with E. cephalophus

“Unlike the archaeological material, the posterior columns of the molars (entoconid and hypoconid) appear slightly compressed in comparison to the anterior columns (metaconid and protoconid) with relatively well developed ectostylids between them. Furthermore, mesostylids appear well developed in comparison to metastylid and entostylid.”

In the comparison with Hydropotes
"As a rule, metastylids were most prominent of the lingual stylids but prominent mesostylids were found to be variably present. In all cases, however, lingual stylids were not as well developed as in Moschus. The lingual edges of the molars are relatively simple and lack external postmetacristids, as in the archaeological specimens, a key character to distinguish Hydropotes from Moschus [63,80]. The location of where the posterior lobe joins the anterior lobe of the molars is offset labially, as in the archaeological specimens.

5/221 Comment/Revision
the teeth are even medium worn!

5/220 Response
"unworn" deleted

5/225 Comment/Revision
compressed

5/224 Response
"elongated" replaced with "compressed"

5/225 Comment/Revision
anterior-posterior

5/224 Response
"Labial-lingual" replaced by "anterior-posterior"

5/230 Comment/Revision
What about the anterior view? Those elongated ruminant canines are specific in anterior view as well.

5/230 Response
Added: "From the anterior aspect, the crown flares slightly to the lateral side and is relatively straight with a slight, sinuous line."

Figure 3 has been amended and includes anterior and posterior views of SF43

5/230 Comment/Revision
Please add "in lateral view"

6/232 Response
"in lateral view" added

5/230 Comment/Revision
Hmm, strange normally they are convex, may be drop shaped in diameter. Are you sure you haven't mixed up convex with concave?

6/232 Response
Thank you! A clumsy error. Revised to: "convex"

5/232 Comment/Revision
Ahhh, please see my comment two lines above: Iguess there you have mixed up convex with concave.

6/235 Comment/Revision
Agreed, as above

6/235 Comment/Revision
Please add "a"

6/238 Response
"a" added

6/235 Comment/Revision
please add "mesodont"

6/238 Response
| Page | Comment/Revision | Response |
|------|------------------|----------|
| 6/236 | I don't think this sentence is necessary. | Deleted “The relatively long, posteriorly curved canine with a closed root also indicates the so-called “fanged” deer or musk deer.” |
| 6/240 | As for 5/214 | Deleted: where the anterior and mesolingual conids meet (but are not fused) replaced with “anterolingual cristid of the mesolingual conid adjoins the anterior conid to encircle the anterior valley (but are not fused)” |
| 6/251 | As for 5/216 | “double-folded” lingual margins of the metaconids” Replaced by “well developed external postmetacristids” |
| 6/269 | Do you mean that the anterolingual cristid of the mesolingual conid and the anterior stylid limit a short valley? | “fold in the lingual wall between the anterior stylid and anterior conid, which is absent in” Replaced by “There is a relatively wide valley in the lingual wall between the anterolingual cristid of the mesolingual conid and an anterior stylid not present in SF40 and SF42 (figure 4).” |
| 7/281 | compressed | |
| 7/290 | “elongate” replaced with “compressed” | |
| 7/283 | Comparison with the anterior lobe of the p4 is missing. | |
| 9/292 | Added “The metaconid of the anterior lobe is isolated from the transverse crest and shifted anteriorly to the lingual side of the anterior valley. The labial side of the tooth is deeply incised at the location of the posterolabial cristid.” | |
| 8/327 | by | This sentence has been removed as a result of restructuring the Discussion (see R1 – main points) |
| 8/348 | Are those deep rooting trees? I guess in karst plants have to root deep to get enough water. | |
| Page | Section | Comment/Revision | Response |
|------|---------|-----------------|----------|
| 9/396 | Response | All those taxa are wind pollinated, so it is possible those grains could have come from forests on valley floors rather than, or in addition to, the karst limestone. To reflect this “and intervening valleys” is included: “These data suggest that limestone karsts and intervening valleys on the southern margin of the Song Hong delta remained forested throughout the last deglaciation.” | |
| 9/392 | Comment/Revision | **Last Glacial Maximum** | |
| 8/353 | Response | “LGM” replaced with “Last Glacial Maximum” | |
| Figure 2 (a) | Comment/Revision | Numbers are hard to see, should be improved | |
| Figure 2 (d) | Comment/Revision | Not indicated in legend | Numbers made more visible |
| Figure 3 | Comment/Revision | Not indicated in legend | The limestone is indicated, but the basal rock in the figure lacks grey shading, as per the legend and higher in the sequence – this is corrected. |
| Figure 3 caption (e) | | | “I” replaced by “(e)”: note, caption revised with updated figure. |
| Table 2 | Comment/Revision | Why don’t you give canin measurements? This would be important for future studies. | Agreed, but our specimens were not complete. We provide measurements in the description and include available comparative data in the supplementary files. |
| | | Why don’t you give length as well? Both measurements would be more indicative. | We now include a length measurement for SF43, with the caveat it is broken. The table caption is updated accordingly. |
Dear Dr Lindsey,

Re: RSOS-210529 Stimpson et al. Confirmed archaeological evidence of water deer in Vietnam: relics of the Pleistocene or a shifting baseline?

We would like to express our thanks to the editors and expert reviewers for their time, constructive criticism and encouraging comments. We feel that the article has benefited and improved as a result of their input and by addressing their comments. (This is reflected in an addition to the Acknowledgements: “We thank two anonymous reviewers for their encouraging comments and constructive criticism, which improved the content and structure of the manuscript.”)

Here, we address the main points that you raise, followed by the point-by-point responses to each reviewer’s comments.

**MAIN POINTS**

**Associate Editor Comments to Author (Dr Emily Lindsey):**

**Associate Editor: 1**

Comments to the Author:

The article was reviewed by two experts, both of whom noted the interest and value of the article and recommended publishing with minor revisions. The two main concerns the reviewers raised that should be addressed for publication were:

1. A more well-developed description of the tooth morphology, and ensuring accuracy and consistency with the diagnostic references.
2. A restructuring of the discussion for clarity and highlighting the importance of the presented study for broader research and conservation-related questions.

1. We have expanded descriptions of lower toothrow, with greater coverage of p2 and p3 and lower molars. Dental terminology has also been reviewed throughout and modified, where necessary, as directed by the reviewer. Figure 4 has been revised, accordingly and Figure 3 has been amended to include occlusal details of the archaeological specimens at greater magnification. Full details are provided in the point-by-point responses to reviewer 2.

2. We have restructured the discussion to follow the recommendations of the reviewer 1, below. For the sake of transparency, text that has been added or removed as part of the restructure has been highlighted. Full details are provided in the point-by-point responses to reviewer 1.

**Reviewer 1**

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patterns of vegetation change, and therefore the water deer. It might be worth simplifying that section and making it more streamlined.

Agreed. As a summary, the discussion was restructured as follows:

Significance of Upper Pleistocene Vietnamese water deer – relics, or longer term, previously unrealized population? (and the significance of regional records on range collapse, etc.)

Are the finds a case for reintroduction? Current records in Vietnam - Pleistocene sites in the Northern Vietnam only- genetic and environmental issues for using Pleistocene records as a basis to propose reintroductions. Environmental context of the water deer of Trang An.

Current evidence indicates cooler (but not necessarily drier) conditions (current available date range potentially incorporates stadial and interstadial conditions)– consistent with modern temperate distribution. Therefore, water deer restricted to temperate climes and restricted to Pleistocene in Vietnam? Sub-tropical records as an example of shifting baselines, which challenge this neat but overly simplistic narrative.

Finally, only confirmed, securely dated records from Vietnam would provide unequivocal evidence of a Holocene population.

I also think the manuscript would benefit from a discussion about Quaternary extinctions in the region, and importantly faunal persistence, range shifts, and metapopulation dynamics. What you have seems to be a relict Pleistocene population that got extirpated. There’s a lot of exciting research coming out of the region such as the giant muntjac that you described from Northern Vietnam, the work Sam Turvey has done on population collapses in muntjac, and the new species of gibbon from China. It would help show that there is still much to be learnt from Pleistocene and Holocene records from this part of the world. Moreover, it would be hugely beneficial to see what other species in the region show similar patterns. I know off-hand that all three species of asian rhinos were once more widely distributed through South Asian, Southern China, and Southeast Asia, but are now relegated to isolated pockets. Ending with your conservation and re-introduction message would in my mind be a good way to wrap up this fascinating story.”

Agreed, but these issues are discussed and cited in the Introduction as the context for the current research. They are, however, recalled in the discussion with the additional text:

“But what does these new records from Tràng An represent? Are they simply relicts of the Pleistocene or are the new finds an early indication of a previously unrealised, more recent presence in Vietnam and hence, a shifted baseline? This would not be without precedent. Work on later Quaternary palaeontological and zooarchaeological assemblages has highlighted the vulnerability and scale of range collapse of other mammalian herbivores in East and Southeast Asia [e.g. 10,11].”

Reviewer 1 point-by-point responses

| Original Page/Line | “Changed” Page/Line | Comment/Revision |
|-------------------|---------------------|------------------|
| 1/31              | “It would be good to include your main conclusions here that follow from your analyses of the paleoenvironment.” |
| Response          | “We also examine the environmental context of the water deer of Tràng An before considering if the new finds represent relics of an Upper Pleistocene population, or are an early indication of an” |
unrecognised southerly distribution with possible implications for the conservation of the species in the future."

Replaced with

“Palaeoenvironmental proxies suggest that the Tràng An water deer occupied cooler, but not necessarily drier, conditions than today. We consider if the specimens represent extirpated Pleistocene populations or indicate a previously unrecognised, longer-standing southerly distribution with possible implications for the conservation of the species in the future.”

| Comment/Revision |
|------------------|
| 4/106 | “Please specify what you mean by exotic” |
| Response | “both exotic and extinct forms” replaced with “extinct forms and taxa previously unrecorded from Japan” |

| 6/245 | This section can be removed or integrated into the discussion |
| Response | Text removed:
Musk deer are currently distributed from the Himalayas to North East Asia, with up to seven extant species [81]. The smallest species, M. berezovskii (Flerov, 1928; extant body weight 6-9 kg), the “dwarf” or “forest musk deer”, ranges into South China and marginally into north Vietnam, where it has been reported in karst habitats. The much-reduced Vietnamese populations were, until recently, thought to be Siberian musk deer, M. moschiferus [82].

References updated from [81] onward |

| 6/258 | I know what you’re trying to say here with statistically significant, but you can remove the term statistically especially since you are referring to Table 3, which has p-values. It reads a lot better when you remove the term statistically |
| Response | “statistically” removed throughout section 4.2 where it is used in this context except from line 290, where it is stated in a hypothesis |

| 7/325 | It might be worth giving examples of the climatic instability you are talking about |
| Comment/Revision | |

| 8/338 | Here again, it would be worth talking a bit more about these climatic fluctuations. |
| Response | The following text and reference was added as part of the restructured Discussion:

“Global climates experience significant instability between 13,000- and 16,000-years BP [87], which encompassed the glacial conditions of Heinrich Stadial 1 followed by the shift to the relatively brief
period of warm and wet conditions of the Bolling-Allerod Interstadial. Chinese speleothem records indicate a regional shift between approximately 14,700 and 13,000 years BP [88].”

This potential significance of this shift is also highlighted:
“Given the range that is encompassed by the available radiocarbon dates, it is not possible to state if the specimens of Tràng An specimens derived from stadial or interstadial conditions for certain, but the available proxies data suggest that similar or preferred habitats of extant water deer were present in the Upper Pleistocene on the plains around TB1, which reflected cooler, but not necessarily drier, conditions than the sub-tropical climate of the Holocene.”

Comment/Revision

9/392

I would cite the authors here instead of calling the article “the 2009 publication”. Or, rephrase the sentence to indicate that in 2009, new dates suggest a post-LGM context.

Response

“in the 2009 publication” replaced with “by Popov”

Reviewer 2

“In my eyes the manuscript is almost ready for publication and has major importance to science in the framework described above. The only criticism I come up with concerns the description of the tooth crown morphology. Although the p4 represents a key tooth for species identification, p2 and p3 hold cervid specific differences from Moschus, but aren’t described, and m1 to m3 are almost not described. This would be important to future work searching for more Hydropotes material in archives and excavations. Please see more detailed comments in the annotated manuscript itself.

We have expanded descriptions of lower toothrows, with greater coverage of p2, p3 and lower molars. Full details are provided in the point-by-point responses, below.

Moreover, you say that you have used Bärmann & Rössner (2011) as the source for tooth crown element nomenclature, what is only true in part. Some elements are differently named than in B & R and do not even follow the principles given there. Hence, either please adapt or clarify in the text that B & R has been used as a basis for your modifications.

Agreed, upon review there are cases where the terminology from older source material (e.g Colbert and Hooijer) has been incorrectly retained. Dental terminology has been reviewed throughout and modified, where necessary, as directed by R2. Full details are provided in the point-by-point responses, below.

The molarisation of p4 is a commonly known phenomenon in mammal odontology and mammal palaeontology what has not to be put in quotation marks. Please see for example Janis and Lister (1985) (attached).

“molarised” is replaced with molarised, throughout

However, although homology of crown elements in non-molarised and molarised is not evidenced in the fossil record by step by step transition states, there are ideas / hypotheses on what element in a non-molarised p4 is homologous to an element in a molarised p4. As to cervids I have provided more details in the annotated manuscript.
Last but not least, as tooth morphology is so crucial in that paper, higher magnified occlusal views are recommended."

Macro shots of the occlusal surfaces of SF40 and SF42 have been added to figure 3. Figure 4 has also been revised, showing toothrows at greater magnification and amended with more details of molarised and non-molarised p4s.

Reviewer 2 - point-by-point responses

| Original Page/Line | Revised Page/Line | Comment/Revision |
|--------------------|-------------------|------------------|
| 1/21               |                   | Wouldn't "inappropriately" the more appropriate word instead of "comparatively"? |
|                    | Response          |                   |
|                    |                   | Agreed. Revised to: “inappropriately” |
| 2/51               |                   | begin? |
|                    | Response          |                   |
|                    |                   | Changed to “begin” |
| 3/127              |                   | reflected |
|                    | Response          |                   |
|                    |                   | Changed to “reflect” |
| 3/127              |                   | addition for more specification: “ecological adaptations under different” |
|                    | Response          |                   |
|                    |                   | “reflected different climatic conditions” revised to “reflect different ecological adaptations under different climatic conditions” |
| 3/128              |                   | please add “if” |
|                    | Response          |                   |
|                    |                   | “if” added |
| 4/149              |                   | are composed of? |
|                    | Response          |                   |
|                    |                   | “comprised” changed to “composed” |
| 5/186              |                   | I see differences to Bärmann & Rössner (e.g. in Fig 4 anterior stylid of Bärmann & Rössner became anterior conid and mesiolingual conid in B & R became anterior stylid and internal and external postmetacristid in B & R became double fold) and suggest that you either adapt or say that you have modified from Bärmann & Rössner |
|                    | Response          |                   |
|                    |                   | Agreed, upon review there are deviations from Bärmann & Rössner, which retain the nomenclature from earlier, source material. These deviations have been revised and are shown on a point-by-point basis, below (from Page 5, line 214 onwards). Figure 4 has also been amended and revised, accordingly. |
| 5/205              |                   | Comment/Revision |

| **5/210** | **Not true! The dentition is medium worn to slightly worn; even the p2 is slightly worn.** |
|-----------|----------------------------------------------------------------------------------|
| **Response** | **“but is unworn” deleted** |

| **5/211** | **you do not have to put that word in quotation marks as it is a common term in odontology** |
|-----------|----------------------------------------------------------------------------------|
| **Response** | **Quotation marks removed from molarised, here and throughout. Figure 4 is updated.** |

| **5/212** | **Please add “alike the corresponding molars”** |
|-----------|----------------------------------------------------------------------------------|
| **Response** | **“alike the corresponding molars” added** |

| **5/213** | **and elongate in the labial-lingual direction** |
|-----------|----------------------------------------------------------------------------------|
| **Response** | **revised to:** |

| **5/214 and 5/226** | **homology of structures in non-molarized and molarized premolars is still debated, but from my experience I would say that this is a mesolingual conid, isolated from the transverse crest and shifted a bit anteriorwards, with anterolingual and posterolingual cristid, positioned lingual of the anterior valley. There is no anterior conid. The posterolingual cristid is reduced so that the posterior elements are disconnected from the anterior elements.** |
|-------------------|-------------------------------------------------------------------------------------------------------------------|
| **Response** | **Deleted: “The anterior and mesolingual conids are fused, forming a contiguous structure, which enclose an anterior fossette.”** |

As per R2’s concerns, this statement uses inconsistent terminology and is revised:

“The anterior lobe is relatively broad and consists of the mesolingual conid and antero- and posterolingual cristids detached from the transverse crest, shifted to the anterior and positioned to the lingual side of the anterior valley, which recalls an anterior fossa. A deep valley incises the labial side of the tooth at the location of the posterolingual cristid, which demarcates the anterior and posterior lobes. The posterior lobe is compressed in the anterior-posterior direction. A well-developed posterior stylid extends to the lingual side from the posterolingual conid.”
Comment/Revision

5/216

What are "lingual edges of the metaconids" (this is not a term from Bärmann & Rössner)? Postmetacristid and premetacristid?

Response

Agreed, this recalls the older, source material and does not follow Bärmann & Rössner. Revised to:

The molars lack external postmetacristids.

Comment/Revision

5/216

This is rather little information on differences in the molars especially the grade of prominence of lingual stylids and columns of metaconid and entoconid. Furthermore, how and if cristids connect to one another. Moreover, the the back fossa of the m3 differs in arrangement. And, I am missing details on differences in p2 and p3. Moschus has rather roundish p2 and p3 whereas the cervids have longish triangular ones.

Response

Agreed, coverage is biased towards the p4. The following text has been added:

Added:

SF40

“The p2 and p3 are relatively elongate and triangular in outline.”

“The anterior and posterior lobes of the molars are broadly equal in size and shape, with triangular cusps. The adjoining edge of the posterior lobe is offset, labial of the metastylid; the preentocristid abuts the internal postprotocristid of the anterior lobe, next to the posterior margin of the anterior fossa. The lingual edges of the molars are relatively simple. Except for a pointed mesostylid on the m2, which extends lingually and curves posteriorly, the lingual stylids are not well developed. Rounded mesostylids and entostylids are more prominent on the m1 and m3. The molars lack external postmetacristids. On the labial side, weakly developed anterior cingulids are present on the m1 and m2. A small, slender anterior ectostylid is present on the m3, which has a rounded hypoconulid and entoconulid and an isolated back fossa (figure 4).”

SF42

“As in SF40, the p4 is also molarised, with an elongate posterior lobe and well-developed stylid on the posteroabial conid. A weakly-developed anterior cingulid and a weakly-developed and compressed (in the anterior-posterior direction) ectostylid is present on the m1. As for SF40, the joining edge of the posterior lobe is offset, labially. The lingual stylids are weakly developed and there is no external postmetacristid (figure 4).”

In the comparison with Moschus

“Moschus is indicated against for SF40 by rather rounded, rectangular p2 and p3, compared to the relatively elongate and
triangular equivalents in the archaeological specimen. Characteristics of the molars of Moschus also contrast with those of SF40 and SF42. Firstly, the lingual outlines of the molars in SF40 and SF42 are relatively simple and lack external postmetacristids. Well developed external postmetacristids are key diagnostic characters of Moschus [63, 80] (figure 4). Secondly, anterior cingulids and mesostylids are relatively well developed and prominent in comparative specimens from the genus Moschus, unlike the archaeological specimens. Thirdly, the location where the posterior lobe of the molars joins their anterior counterpart is much less offset and much more “in line”, lingually, with the location of the metastylid. Finally, the labial margins of the labial conids are rather angular, with shallow indents in the cristids, compared to the archaeological specimens, which are more rounded and lack indentations.”

In the comparison with E. cephalophus
“Unlike the archaeological material, the posterior columns of the molars (entoconid and hypoconid) appear slightly compressed in comparison to the anterior columns (metaconid and protoconid) with relatively well developed ectostylids between them. Furthermore, mesostylids appear well developed in comparison to metastylid and entostylid.”

In the comparison with Moschus
“more rectangular, rounded p2 and p3 in musk deer and”

In the comparison with Hydropotes
“As a rule, metastylids were most prominent of the lingual stylids but prominent mesostylids were found to be variably present. In all cases, however, lingual stylids were not as well developed or as robust as in Moschus. The lingual edges of the molars are relatively simple and lack external postmetacristids, as in the archaeological specimens, a key character to distinguish Hydropotes from Moschus [63, 80]. The location of where the posterior lobe joins the anterior lobe of the molars is offset labially, as in the archaeological specimens.

5/221 Comment/Revision
the teeth are even medium worn!
Response
“, unworn” deleted

5/225 Comment/Revision
compressed
Response
“elongated” replaced with “compressed”

5/225 Comment/Revision
anterior-posterior
Response
“Labial-lingual” replaced by “anterior-posterior”

Comment/Revision
| 5/230 | What about the anterior view? Those elongated ruminant canines are specific in anterior view as well. |
|-------|------------------------------------------------------------------------------------------------------------------|
|       | **Response**                                                                                                           |
|       | Added: “The anterior aspect of the crown flares slightly to the lateral side and is relatively straight, with a slight, sinuous line. “ |
|       | **Figure 3** has been amended and includes anterior and posterior views of SF43 |
| 5/230 | **Comment/Revision**                                                                                                    |
| 5/230 | Please add "in lateral view"                                                                                           |
|       | **Response**                                                                                                           |
|       | “in lateral view” added                                                                                               |
| 5/230 | **Comment/Revision**                                                                                                    |
|       | Hmm, strange normally they are convex, may be drop shaped in diameter. Are you sure you haven't mixed up convex with concave? |
|       | **Response**                                                                                                           |
|       | Thank you! A clumsy error. Revised to: "convex"                                                                       |
| 5/232 | **Comment/Revision**                                                                                                    |
|       | Ahhh, please see my comment two lines above: I guess there you have mixed up convex with concave.                     |
|       | **Response**                                                                                                           |
|       | Agreed, as above                                                                                                       |
| 6/235 | **Comment/Revision**                                                                                                    |
|       | Please add "a"                                                                                                         |
|       | **Response**                                                                                                           |
|       | “a” added                                                                                                              |
| 6/235 | **Comment/Revision**                                                                                                    |
|       | please add "mesodont"                                                                                                  |
|       | **Response**                                                                                                           |
|       | “mesodont” added                                                                                                       |
| 6/236 | **Comment/Revision**                                                                                                    |
|       | I don't think this sentence is necessary.                                                                             |
|       | **Response**                                                                                                           |
|       | Deleted “The relatively long, posteriorly curved canine with a closed root also indicates the so-called “fanged” deer or musk deer.” |
| 6/240 | **Comment/Revision**                                                                                                    |
|       | As for 5/214                                                                                                          |
|       | **Response**                                                                                                           |
|       | Deleted: where the anterior and mesolingual conids meet (but are not fused) replaced with “anterolingual cristid of the mesolingual conid adjoins the anterior conid to encircle the anterior valley (but are not fused)” |
| 6/251 | **Comment/Revision**                                                                                                    |
|       | As for 5/216                                                                                                          |
|       | **Response**                                                                                                           |
|       | “double-folded” lingual margins of the metaconids”                                                                     |
|       | Replaced by “well developed external postmetacristids”                                                                 |
|       | **Comment/Revision**                                                                                                    |
| Page | Comment/Revision |
|------|------------------|
| 6/269 | Do you mean that the anterolingual cristid of the mesolingual conid and the anterior stylid limit a short valley? |
| **Response** | |
| | “fold in the lingual wall between the anterior stylid and anterior conid, which is absent in” |
| | Replaced by |
| | “there is a relatively wide valley in the lingual wall between the anterolingual cristid of the mesolingual conid and an anterior stylid not present in SF40 and SF42 (figure 4).” |
| 7/281 | compressed |
| **Response** | |
| | “elongate” replaced with “compressed” |
| 7/283 | Comparison with the anterior lobe of the p4 is missing. |
| **Response** | |
| | Added “The metaconid of the anterior lobe is isolated from the transverse crest and shifted anteriorly to the lingual side of the anterior valley. The labial side of the tooth is deeply incised at the location of the posterolabial cristid.” |
| 8/327 | by |
| **Response** | |
| | This sentence has been removed as a result of the restructured of Discussion. |
| 8/348 | Are those deep rooting trees? I guess in karst plants have to root deep to get enough water. |
| **Response** | |
| | All those taxa are wind pollinated, so it is possible those grains could have come from forests on valley floors rather than, or in addition to, the karst limestone. To reflect this “and intervening valleys” is included: “These data suggest that limestone karsts and intervening valleys on the southern margin of the Song Hong delta remained forested throughout the last deglaciation.” |
| 9/392 | Last Glacial Maximum |
| **Response** | |
| | “LGM” replaced with “Last Glacial Maximum” |
| Figure 2 | |
| (a) | numbers are hard to see, should be improved |
| **Response** | |
| | Numbers made more visible |
| Figure 2 | |
| (d) | Not indicated in legend |
| **Response** | |
The limestone is indicated, but the basal rock in the figure lacks grey shading, as per the legend and higher in the sequence – this is corrected.

**Comment/Revision**

**Figure 3**

As p4 morphology plays a crucial role in identification, additional figures of the occlusal surface of both p4s with a higher magnification were eligible.

**Response**

Higher magnification images of the details of the occlusal surface of teeth have been added to figures 3 and 4.

**Figure 3 caption**

**Comment/Revision**

(e)

**Response**

"I" replaced by "(e)": note, caption revised with updated figure.

**Comment/Revision**

Why don't you give canin measurments? This would be important for future studies.

**Response**

Agreed, but our specimens were not complete. We provide measurements in the description and include available comparative data in the supplementary files.

**Comment/Revision**

**Table 2**

Why don't you give length as well? Both measurements would be more indicative.

**Response**

We now include a length measurement for SF43, with the caveat it is broken. The table caption is updated accordingly.