

# Palaeoecological Reconstruction of Serows and Gorals (Bovidae: Caprinae) from the Pleistocene of Thailand using Dental Mesowear and Hypsodonty: Implications for Species Conservation

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## ABSTRACT

Two species in the subfamily Caprinae, the Sumatran serow *Capricornis sumatraensis* and Chinese goral *Naemorhedus griseus* are currently distributed in Thailand and listed as vulnerable species. The Himalayan goral *N. goral* has no dispersion in Thailand, whereas fossil evidence shows the coexistence of all three species during the Pleistocene. However, the diet and habitat preferences of the Pleistocene *C. sumatraensis* remain disputed and the information on those of the Pleistocene gorals is limited. To clarify the points, the mesowear analysis in combination with measurements of hypsodonty indices were performed on these three caprine taxa. Molar samples were collected from four palaeontological fossil sites (Pha Bong, Khok Sung, Tham Wiman Nakin and Tham Lod Rockshelter), covering a time span from the Middle to Late Pleistocene, and from extant individuals. The mesowear results combined with the hypsodonty index suggest that the Pleistocene populations were likely to be mixed feeders, while the extant *C. sumatraensis* shows more browsing signals. In agreement with the previous carbon isotope data of tooth enamel, the present study supports the idea that the Pleistocene caprine populations underwent drastic changes in diet and habitat use between the Pleistocene and the present day, possibly driven by the climate change and anthropogenic disturbances since the beginning of the Holocene. In order to protect the extant wildlife populations, the potential restoration of habitats and conservation plan for native caprines are necessary.

**Keywords:** Tooth wear, Diet, Habitat, Ruminantia, Quaternary, Southeast Asia.

## INTRODUCTION

Serows (*Capricornis*) and gorals (*Naemorhedus*) are members of the ungulate family Bovidae, subfamily Caprinae. Two species of extant caprines, *C. sumatraensis* (Sumatran serows) and *N. griseus* (Chinese gorals) are common in Thailand (Duckworth *et al.*, 2008a; Duckworth *et al.*, 2008b). *C. sumatraensis* is distributed in southern, western and northern parts of Thailand, Malaysia and Indonesia (Chairat, 2007; Duckworth *et al.*, 2008b; Nakhasathein, 2017). *N. griseus* is found in western and northern regions of Thailand, Myanmar and India (Duckworth *et al.*, 2008a; Buranapim *et al.*, 2014; Safoowong, 2015). *C. sumatraensis* nowadays

inhabits steep and stony hills at elevations of 200–3,000 m above sea level (Wilson and Mittermeier, 2011), while *N. griseus* lives at a narrower range of elevations of 1,400–1,929 m above sea level (Chaiyarat *et al.*, 1999). However, the existence of fossil *N. goral* (Himalayan gorals) as well as *C. sumatraensis* and *N. griseus* has been documented in lowland areas of Thailand during the Pleistocene (Tougaard, 1998; Tougaard, 2001; Shoocongdej *et al.*, 2007; Bocherens *et al.*, 2017; Wattanapituksakul *et al.*, 2018; Suraprasit *et al.*, 2020). *N. goral* is nowadays found from Bhutan, India, and Pakistan (Duckworth and MacKinnon, 2008; Giri *et al.*, 2011; Bhattacharya *et al.*, 2012), in rugged areas and evergreen forests near cliffs at altitudes between 900 and 4,000 m (Duckworth

and MacKinnon, 2008; Bhattacharya *et al.*, 2012), but became extirpated from Thailand, probably after the Late Pleistocene (Suraprasit *et al.*, 2020; Suraprasit *et al.*, 2021a). Therefore, the local extinction of *N. goral* in Thailand might have been related to environmental, ecological, and climatic changes in the region during the Late Quaternary.

There are several effective methods used in studies of ungulate palaeoecology, such as stable carbon isotope ( $\delta^{13}\text{C}$ ) and dental wear investigations, sedimentological analyses, palynological reconstructions and ecomorphological indicators (Croft *et al.*, 2018). However, information on optimal diets and habitats for the Pleistocene caprines in Thailand has been only obtained from the stable carbon isotope studies (Suraprasit *et al.*, 2020). In principle,  $\delta^{13}\text{C}$  extracted from tooth enamel of fossils reflects the types of plants on which ungulates have foraged:  $\text{C}_3$ ,  $\text{C}_4$ , mixed  $\text{C}_3/\text{C}_4$ , or CAM plants (*e.g.*, Cerling and Harris, 1999; MacFadden *et al.*, 1999; Kohn and Cerling, 2002). Consumption of  $\text{C}_3$  plants refers to dwelling in closed habitats such as woodlands and open to deep forests, whereas the dietary intake of  $\text{C}_4$  plants reflects open habitats such as grasslands (*e.g.*, Cerling and Harris, 1999; MacFadden *et al.*, 1999; Kohn and Cerling, 2002). The  $\delta^{13}\text{C}$  of tooth enamel fossils from the Middle Pleistocene sites of Pha Bong and Tham Wiman Nakin revealed that *C. sumatraensis* was a  $\text{C}_4$  grazer associated with open grasslands (Bocherens *et al.*, 2017; Pushkina *et al.*, 2010). In contrast, *C. sumatraensis* from the late Middle Pleistocene of Khok Sung (northeastern Thailand) and the Late Pleistocene of Nam Lot (northern Laos) was considered to be a  $\text{C}_3$  browser related to close habitats (Bacon *et al.*, 2018b; Suraprasit *et al.*, 2018; Suraprasit *et al.*, 2020). The results of Suraprasit *et al.* (2020) showed that the Pleistocene *C. sumatraensis* from Tham Lod Rockshelter had a wide range of diets (pure  $\text{C}_3$  to  $\text{C}_4$  plants) living in a variety of habitats between closed and open environments. The Late Pleistocene *C. sumatraensis* from Boh Dambang, Cambodia, was either a pure  $\text{C}_3$  browser or  $\text{C}_4$  grazer (Bacon *et al.*, 2018a). In gorals, the  $\delta^{13}\text{C}$  results showed that Pleistocene gorals foraged on either pure  $\text{C}_4$  or mixed  $\text{C}_3/\text{C}_4$  plants (Suraprasit *et al.*, 2020). Concerning the extant populations, *C. sumatraensis* was recognized as a  $\text{C}_3$  browser (Pushkina *et al.*, 2010; Suraprasit *et al.*, 2020). Based on only the carbon isotope analysis by Suraprasit *et al.* (2020), one specimen of extant *N. griseus* suggested its consumption of mixed  $\text{C}_3/\text{C}_4$  plants, whereas the extant *N. goral* consumed pure  $\text{C}_3$  or mixed  $\text{C}_3/\text{C}_4$  plants. As mentioned above, it seems that the diet and habitat preferences of Pleistocene *C. sumatraensis* were flexible and also different from those of extant

populations, and the information on those of gorals remains limited. Such points need further clarification using other ecological approaches.

Mesowear is one of the potential methods to define an animal's dietary adaptation on the basis that each animal possesses characteristics of dental attrition and abrasion due to different lifelong feeding habits through space and time. This accurate and non-laborious method has been originally developed for ungulates (*e.g.*, Fortelius and Solounias, 2000; Kaiser *et al.*, 2013) and has been then applied to other mammalian groups (*e.g.*, Ulbricht *et al.*, 2015; DeSantis *et al.*, 2018). The mesowear examines the relative contribution of tooth wear from attrition (tooth-to-tooth contact) and abrasion (tooth-to-food contact) on the enamel of occlusal surfaces (Fortelius and Solounias, 2000). It is well-known that grasses have a high silica content and are well-adapted to grow in open landscapes adhered by soil and grit. Thus, grazers and species living in open habitats possess more abrasive wear due to grass consumption, resulting in lower reliefs and blunt cusps (Damuth and Janis, 2011; Kubo and Yamada, 2014). In contrast, tooth wear from attrition that is derived from low abrasive foods such as leaves, twigs or fruits results in high occlusal reliefs and sharp cusps for browsers.

Alternatively, hypsodonty (relative increase in the height of a cheek tooth) is considered to be one of the morphological predictors in ungulates' diets reflecting overall average wear rates (Janis, 1988; Fortelius and Solounias, 2000). It represents an adaptation to tooth wear effected by both intrinsic properties of the ingested food and extrinsic habitat factors (Damuth and Janis, 2011; Kaiser *et al.*, 2013). The hypsodonty index (HI) is calculated by the ratio of the crown height of the m3 to its width (Janis, 1988). According to Hofmann (1989), feeding habits inferred from the HI can be divided into three categories: browsers, grazers, and mixed feeders. Browsers generally have brachydont dentition with low HI, but grazers possess high-crowned teeth with high HI. Mixed feeders have a HI value intermediate between the two groups. It is noted that the resolution of the mesowear method increased when it was used in combination with the HI (Fortelius and Solounias, 2000; Kaiser *et al.*, 2013). Consequently, the HI has been included into the palaeoecological analysis and is often used as additional data associated with the mesowear variables.

In this study, we perform the mesowear and HI analyses of Pleistocene and extant caprines from Thailand. The obtained information on diet and feeding habits of caprines is discussed with that achieved by other

approaches. The dietary adaptation can contribute to a better understanding of the adaptive radiation of the three caprine species from Thailand during the Pleistocene to today. It may also clue up the causes of extirpation of *N. goral* from Thailand and guide the conservation plan for native caprines in the future.

## METHODOLOGY

### Specimen Collection

Sixty-three fossils of *C. sumatraensis* (n = 19), *N. griseus* (n = 22) and *N. goral* (n = 22) were collected from four palaeontological and archaeological sites in Thailand: Pha Bong, Khok Sung, Tham Wiman Nakin, and Tham Lod Rockshelter, covering a time span from the Middle Pleistocene to the Late Pleistocene (Fig. 1). Data from thirty adult specimens of extant *C. sumatraensis* (n = 22), *N. griseus* (n = 4), and *N. goral* (n = 4) were recovered

from six collections in Thailand and one collection in Germany: Khao Nang Ram Wildlife Research Center, Uthai Thani (KNR); Om Koi Wildlife Breeding Center, Chiang Mai (OK); Natural History Museum of Chulalongkorn University, Bangkok (CUMNH); Zoological Museum of Kasetsart University, Bangkok (ZMKU); Forestry Museum of Kasetsart University, Bangkok (FMKU); Thailand Natural History Museum, National Science Museum, Pathum Thani (THNHM) and Zoologische Staatssammlung München, Munich, Germany (ZSM). All extant specimens are the animals that died during the 20th century (1900AD to 2000AD). Juveniles and senescent adults were excluded from this study. This research was approved for the use of wild specimens by the Department of National Park, Wildlife and Plant Conservation, Thailand (Permission number 0907.4/6178). The sources and number of specimens in this study are shown in Table 1.

**Table 1.** General information of four palaeontological sites and seven collections from museums and wildlife sanctuaries in this study.

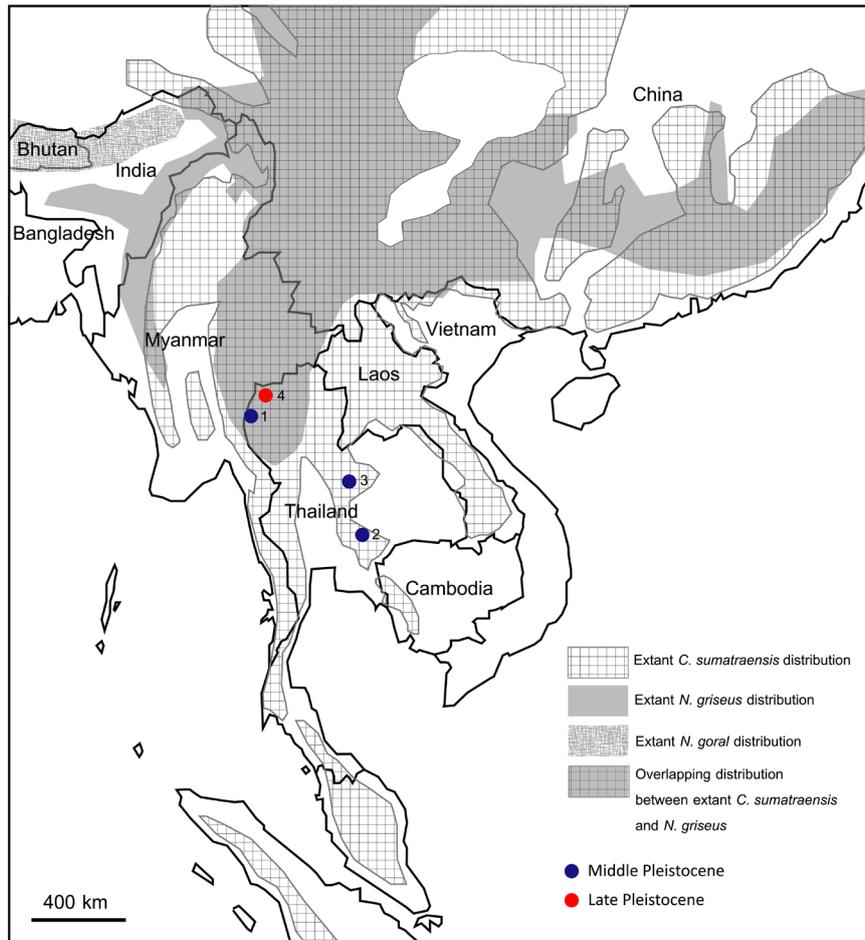
Localities	Ages	Elevation above sea level (m)	Taxa and number of fossils	References
Pha Bong	400-200 ka, late Middle Pleistocene	280	<i>N. goral</i> (n = 10)	Bocherens <i>et al.</i> , 2017
Khok Sung	217 or 130 ka, late Middle Pleistocene	150	<i>C. sumatraensis</i> (n = 2)	Suraprasit <i>et al.</i> , 2015, 2016; Duval <i>et al.</i> , 2019
Tham Wiman Nakin	>169 ka, late Middle Pleistocene	500	<i>C. sumatraensis</i> (n = 10) <i>N. goral</i> (n = 4)	Esposito <i>et al.</i> , 1998, 2002; Tougard, 1998, 2001; Suraprasit <i>et al.</i> , 2021a
Tham Lod Rockshelter	32-12 ka, late Late Pleistocene	640	<i>C. sumatraensis</i> (n = 7) <i>N. griseus</i> (n = 22) <i>N. goral</i> (n = 8)	Shoocongdej <i>et al.</i> , 2007; Marwick and Gagan, 2011; Wattanapitaksakul <i>et al.</i> , 2018; Suraprasit <i>et al.</i> , 2021b
CUMNH	present	-	<i>C. sumatraensis</i> (n = 3)	
THNHM	present	-	<i>C. sumatraensis</i> (n = 7)	
KNR	present	200-1,000	<i>C. sumatraensis</i> (n = 5)	Nakhasathien, 2017
OK	present	1,400-1,929	<i>N. griseus</i> (n = 3)	Chaiyarat <i>et al.</i> , 1999
ZMKU	present	-	<i>C. sumatraensis</i> (n = 3)	
FMKU	present	-	<i>C. sumatraensis</i> (n = 2)	
ZSM	present	-	<i>C. sumatraensis</i> (n = 2) <i>N. griseus</i> (n = 1) <i>N. goral</i> (n = 4)	

**Abbreviations:** Khao Nang Ram Wildlife Research Center (KNR), Om Koi Wildlife Breeding Center (OK), Natural History Museum of Chulalongkorn University (CUMNH), Zoological Museum of Kasetsart University (ZMKU), Forestry Museum of Kasetsart University (FMKU), Thailand Natural History Museum, National Science Museum (THNHM) and Zoologische Staatssammlung München (ZSM), Germany.

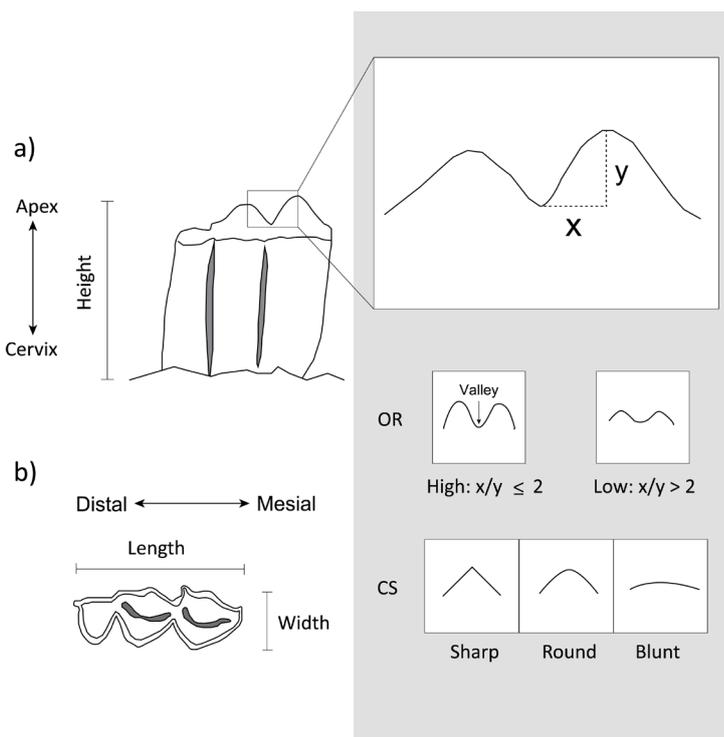
### Mesowear Analysis

The mesowear method treats molars as two variables: the occlusal relief (OR) and cusp shape (CS), which are observed on the cutting edge of either the paracone cusp of M2 (upper) or the protoconid cusp of m2 (lower). Only the sharper one (paracone or protoconid) was scored (Fortelius and Solounias, 2000). Unworn and

heavily-worn teeth as well as those with broken cusps were excluded from the analysis. The molars were photographed with a mirrorless digital camera (Fujifilm X-A2). The OR was classified as high or low, depending on the distance from the valley to the highest cusp (Fig. 2a). The height of cusps was calculated using the ImageJ program (v. 1.51k) after transferring digital photos from



**Figure 1.** The distribution of Pleistocene and extant caprines in Southeast Asia, eastern region of South Asia, and South China. The locations of fossil sites studied in Thailand are shown: 1 = Pha Bong, Mae Hong Son; 2 = Khok Sung, Nakhon Ratchasima; 3 = Tham Wiman Nakin, Chaiyaphum; and 4 = Tham Lod Rockshelter, Mae Hong Son. Extant populations of *C. sumatraensis* and *N. griseus* have an overlapping distribution at the northern part of Thailand, Myanmar, and China. The figure is modified after Suraprasit *et al.* (2020).



**Figure 2.** Measurements of the m3. a) crown height and mesowear analysis following Merceron *et al.* (2007); b) crown width and length.

the camera. The OR was used in the analysis as a percent of high occlusal relief (perH). The CS was recorded by characterizing the shape of a cusp apex as sharp, round, or blunt (Fig. 2a). The teeth were observed with the naked eye or a hand lens at 10X magnification. The CS was then calculated into percentages: a percentage of sharp CS (perS), a percentage of round CS (perR) and a percentage of blunt CS (perB). A mean of each percentage was calculated for each species, separately between the Pleistocene and extant populations.

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### Hypsodonty Index (HI)

The length, width, and height of the m3 crown were measured using a digital caliper (precision of 0.01 mm) (Fig. 2). The HI was calculated from the height of m3 divided by its width (Janis, 1988; Damuth and Janis, 2011). The value of each species was presented as the mean  $\pm$  standard error (SE), using SPSS 22.0. As most of the teeth of extant specimens (in this study) have not fully erupted yet and remain embedded in the jaw bone, the measurement of the actual height of m3 might be underestimated. Hypsodonty is interpreted as a species-specific adaptation and also carries phylogenetic effects. There is little evidence that hypsodonty is reversed in a

lineage once attained and varying degrees of HI within a species have rarely been documented (Damuth and Janis, 2011; Kaiser *et al.*, 2013). Thus, in the present study, the HI for each species was calculated based on the Pleistocene isolated teeth, which allow more accurate height measurements of dental crowns than the incompletely erupted teeth of extant individuals. Following Janis (1988), the HI was employed to divide the molars into four categories: HI < 1.5 for brachyodont; 1.5 < HI < 3.0 for mesodont; 3.0 < HI < 4.5 for hypsodont; HI > 4.5 for highly hypsodont. To explore trends of diet preferences of the caprines, scatterplots of the HI and mesowear variables (using R 4.0.1) were used to observe relationships between data from this study and from Fortelius and Solounias (2000) that showed obvious trends related to ungulate diets.

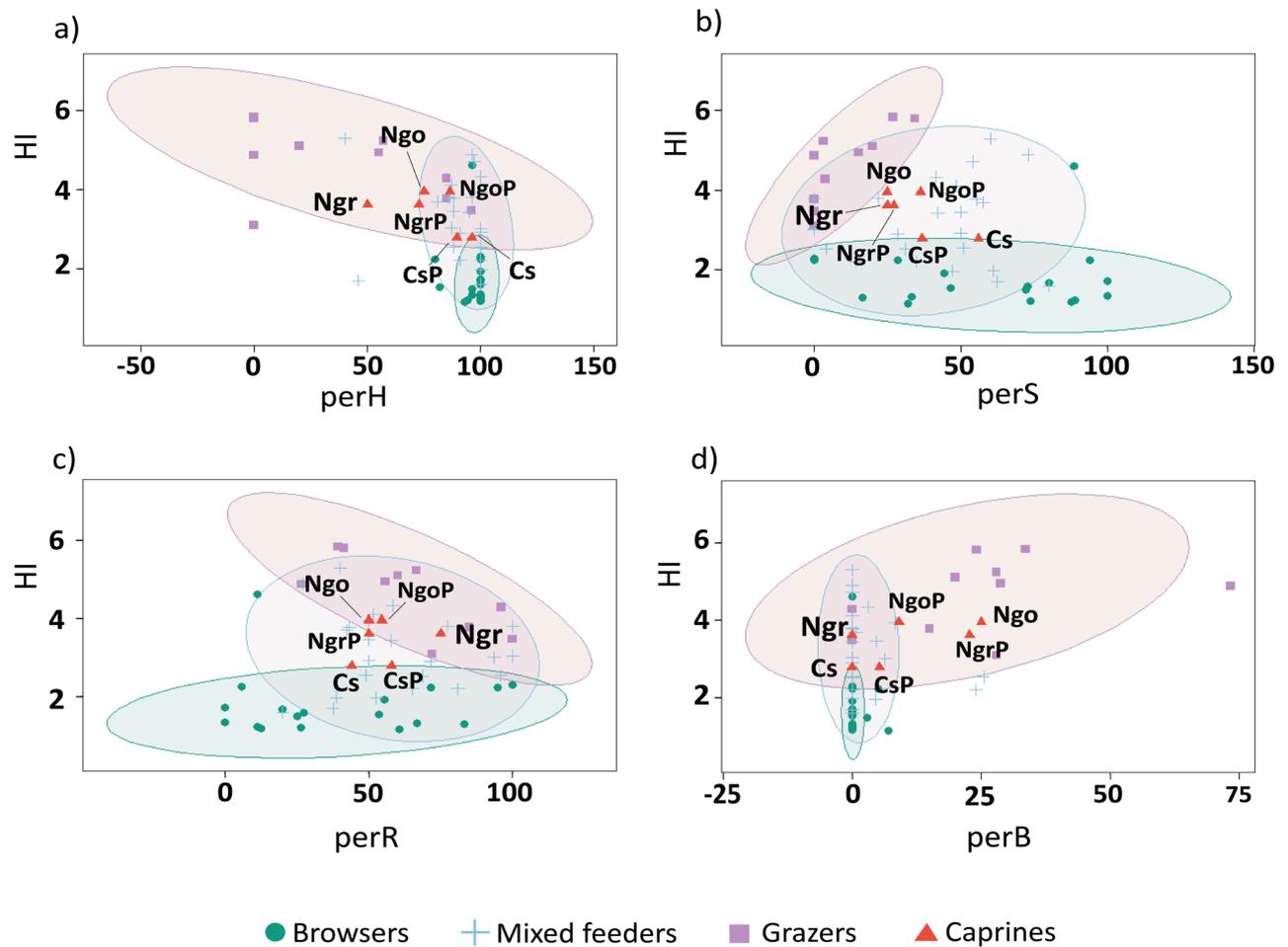
## RESULTS

Results of the HI and mesowear analysis were shown in Table 2. Within the Pleistocene populations, *N. goral* had the highest HI of 3.95 and *C. sumatraensis* had the lowest HI of 2.77. Concerning the mesowear results, overall, the Pleistocene caprines tended to have higher percentages of perR (round cusp) and perB (blunt cusp) than the extant species of which the blunt cusps were not observed (0%) in both *C. sumatraensis* and *N. griseus*. Among the extant species, *C. sumatraensis* had higher percentages of perH (high occlusal relief) and perS (sharp cusp), and lower percentages of perR and perB than the two species of *Naemorhedus*. In scatterplots that showed the correlation between HI and mesowear variables (Fig. 3), the Pleistocene caprines were most apt

**Table 2.** Results of hypsodonty index (HI) and mesowear analysis. The HI of extant caprine species was obtained from those of the Pleistocene fossil specimens.

Species	n	HI	Mesowear			
			perH	perS	perR	perB
Pleistocene						
<i>C. sumatraensis</i>	19	2.77 $\pm$ 0.30	89.47	36.84	57.89	5.26
<i>N. griseus</i>	22	3.61 $\pm$ 0.37	72.72	27.27	50.00	22.73
<i>N. goral</i>	22	3.95 $\pm$ 0.28	86.36	36.36	54.55	9.09
Extant						
<i>C. sumatraensis</i>	22	2.77	96.00	56.00	44.00	0
<i>N. griseus</i>	4	3.61	50.00	25.00	75.00	0
<i>N. goral</i>	4	3.95	75.00	25.00	50.00	25.00

Abbreviations: perH = a percent of high OR, perS = a percent of sharp CS, perR = a percent of round CS and perB = a percent of blunt CS.



**Figure 3.** Scatter plots of HI with a) percentage of high OR (perH), b) percentage of sharp CS, c) percentage of round CS (perR) and d) percentage of blunt CS (perB) of Pleistocene and extant caprines. The comparative dataset of extant ungulates follows Fortelius and Solounias (2000). Abbreviations: Cs = extant *C. sumatraensis*, CsP = Pleistocene *C. sumatraensis*, Ngr = extant *N. griseus*, NgrP = Pleistocene *N. griseus*, Ngo = extant *N. goral*, and NgoP = Pleistocene *N. goral*.

to fall within 95% confidence ellipse for mixed feeders. The extant caprines also tended to be incorporated into the group of mixed feeders, although *C. sumatraensis*, in comparison with the Pleistocene population, showed a remarkable shift into the overlap area together with other browsers.

## DISCUSSION

Hypsodonty is an adaptation to endure tooth wear, associated with diets and habitats in ungulates (Mihlbachler *et al.*, 2010; Damuth and Janis, 2011; Fraser and Theodor, 2011). Feedings on plants with a large amount of silica such as grasses or diets mixed up with grits can generate high stress abrasion, imposing an evolutionary selection for the high-crowned molars to resist a high wear rate (Heywood, 2010). In contrast, low stress abrasion is produced during chewing soft diets such as leaves or fruits, hence retaining brachydonty in a lineage. Generally, grazers have highly hypsodont

teeth, while browsers possess brachydont appearances. Mixed feeders have often hypsodont teeth (Damuth and Janis, 2011). Mesodont, an intermediate condition, is possibly seen in browsers and mixed feeders. Based on the results of this study, the HI of Pleistocene caprines falls within the range of hypsodonty for both species of *Naemorhedus* or high-degree mesodonty for *C. sumatraensis*, suggesting an evolutionary trend towards mixed-feeding habits. It is noteworthy that the HI of Pleistocene *N. goral* is similar to previous data from extant populations (HI = 4.03) (Mendoza and Palmqvist, 2008), whereas the HI of Pleistocene *C. sumatraensis* is distinctly lower from that of extant species (HI = 3.93) reported by Janis (1988). Compared to that in *C. sumatraensis*, the higher degree of hypsodonty in both species of *Naemorhedus* suggests an adaptation for being more specialized in grass consumption, which is congruent with previously analyzed isotope data (Suraprasit *et al.*, 2020).

Concerning the mesowear analysis, occlusal relief and cusp shape were diagnosed due to their expressions of tooth wear rate on the entire occlusal surface affected by attrition-abrasion contact. Browsing causes less intensive tooth wear, resulting in a higher occlusal relief and a sharper cusp than grazing. The results showed that the Pleistocene caprines were likely to have higher percentages of round and blunt cusps than the extant ones. Among the extant species, the degree of tooth wear was lower in *C. sumatraensis* in accordance with its high occlusal relief and sharp cusp. Although both Pleistocene and extant caprines are included in the group of mixed feeders as examined by the mesowear variables combined with the HI, the extant *C. sumatraensis* obviously exhibits a close link with the browser category. It implies that the Pleistocene populations of these three caprine species were likely to be mixed feeders but the extant *C. sumatraensis* possibly consumes relatively more browse material. Our findings of the Pleistocene caprines are congruent with the carbon isotope studies of Bacon *et al.* (2018a) and Suraprasit *et al.* (2020). For the extant species, the results of *C. sumatraensis* are similar to those of previous isotope studies (Pushkina *et al.*, 2010; Suraprasit *et al.*, 2020) and analyses of feces, stomach contents and nibble traces (Chairat, 2007; Junshum *et al.*, 2010; Nakhasathein, 2017). The information on the two extant species of *Naemorhedus* seems to corroborate evidence from analyses of fecal pellets and from field surveys (Chaiyarat *et al.*, 1999; Ilyas and Khan, 2004; Juniad *et al.*, 2012). It was reported that constituent elements in feces of *N. goral* (from India) and *N. griseus* were a mixture of grasses and dicotyledonous herbage plants, the former of which was proportionally higher, suggesting the state of grass-dominated mixed feeders.

Differences in feeding habits of *C. sumatraensis*, from the Pleistocene mixed feeders to extant browsers, could support ecological changes through time. During the Pleistocene, the palaeoenvironments in Thailand corresponded mostly to a forest-grassland mosaic (Morley, 1991; White *et al.*, 2004; Pushkina *et al.*, 2010; Bocherens *et al.*, 2017; Suraprasit *et al.*, 2018, 2019, 2021b). Mixed feeders resided in intermediate habitats and possibly utilized food resources in both of more closed and open landscapes. Due to the decline of grasslands caused by the warmer and more humid climate during the Pleistocene-Holocene boundary (Louys and Robert, 2020; Suraprasit *et al.*, 2020), the Sumatran serow has turned its feeding habits into a browsing signal related to more closed habitats.

From other viewpoints, excessive habitat degradation for agriculture and illegal harvest induced by anthropogenic

activities could have detrimental consequences on the decreased number of extant caprine populations (Wattanapituksakul *et al.*, 2018; Suraprasit *et al.*, 2020). Based on the accumulation of bones and the faunal evidence in Tham Lod Rockshelter, early modern humans hunted these caprine species for resources (Wattanapituksakul *et al.*, 2018). It is congruent with the fact that the extant caprine populations currently occupy restricted areas on forested mountains at high altitudes as safe places from poaching (Wilson and Mittermeier, 2011). Consequently, the abrupt decrease in extant caprine populations, including the local extinction of *N. goral* in Thailand, is possibly caused by the reduction of open grasslands driven by the climate change during the Pleistocene-Holocene transition and by the negative effects of continual anthropogenic disturbances from the past until now. An earnest environmental management incorporated with educating people is of necessity for balancing sustainable exploitation and habitat conservation to ensure the long-term survival of these caprine populations.

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#### REFERENCES

- Bacon, A. M., P. Düringer, K. Westaway, R. Joannea-Boyau, J. Zhao, N. Bourgon, E. Dufour, S. Pheng, S. Tep, J.L. Ponche, L. Barnes, A. Blin, E. Patole-Edoumba and F. Demeter. 2018a. Testing the savannah corridor hypothesis during MIS2: the Boh Dambang hyena site in southern Cambodia. *Quaternary International* 464: 417-439.
- Bacon, A.M., N. Bourgon, E. Dufour, C. Zanolli, P. Düringer, J. L. Ponche, P.O. Antoine, L. Shackelford, N.T.M. Huong, T. Sayavonkhamdy, E. Patole-

- Edoumba and F. Demeter. 2018b. Nam Lot (MIS 5) and Duoi U'Oi (MIS 4) Southeast Asian sites revisited: Zooarchaeological and isotopic evidences. *Palaeogeography, Palaeoclimatology, Palaeoecology* 512: 132-144.
- Bhattacharya, T., T. Bashir, K. Poudyal, S. Sathyakumar and G.K. Saha. 2012. Distribution, occupancy and activity patterns of goral (*Nemorhaedus goral*) and serow (*Capricornis thar*) in Khangchendzonga Biosphere Reserve, Sikkim, India. *Mammal. Mammal Study* 37: 173-181.
- Bocherens, H., F. Schrenk, Y. Chaimanee, O. Kullmer, D. Mörike, D. Pushkina, and J.-J. Jaeger. 2017. Flexibility of diet and habitat in Pleistocene South Asian mammals: implications for the fate of the giant fossil ape *Gigantopithecus*. *Quaternary International* 434: 148-155.
- Buranapim, N., N. Sitasuwan, A. Kongprempoon, K. Korkusol, B. Siriaroonrat and S. Kamolnorrath. 2014. Reintroduction and behavioral observations of Chinese gorals (*Naemorhedus griseus*) in natural conditions. *The Thai Journal of Veterinary Medicine* 44: 75-83.
- Cerling, T.E. and J.M. Harris. 1999. Carbon isotope fractionation between diet and bioapatite in ungulate mammals and implications for ecological and paleoecological studies. *Oecologia* 120: 347-363.
- Chairat, R. 2007. *Habitat and Distribution of Serow (Capricornis sumatraensis) in Phu Khieo Wildlife Sanctuary, Chaiyaphum Province*. Phukhieo –EU Project. Department of National Parks, Wildlife and Plant Conservation, Bangkok, Thailand.
- Chaiyarat, R., W. Laohajinda, U. Kutintara and J. Nabhitabhata. 1999. Ecology of the goral (*Naemorhedus goral*) in Om Koi wildlife sanctuary, Thailand. *Natural History Bulletin of the Siam Society* 47: 191-205.
- Croft, D.A., D.F. Su and S.W. Simpson. 2018. *Methods in paleoecology*. Springer, Switzerland. 410 pp.
- Damuth, J. and C. Janis. 2011. On the relationship between hypsodonty and feeding ecology in ungulate mammals, and its utility in palaeoecology. *Biological reviews* 86: 733-758.
- DeSantis, L.R.G, J. Alexander, E.M. Biedron, P.S. Johnson, A.S. Frank, J.M. Martin and L. Williams. 2018. Effects of climate on dental mesowear of extant koalas and two broadly distributed kangaroos throughout their geographic range. *PLOS ONE* 13: e0201962.
- Duckworth, J.W. and J. MacKinnon. 2008. *Naemorhedus goral*. The IUCN Red List of Threatened Species 2008. Available: www.iucnredlist.org. [online] Assessed June 6, 2019.
- Duckworth, J.W., R. Steinmetz and R. Chaiyarat. 2008a. *Naemorhedus griseus*. The IUCN Red List of Threatened Species 2008. Available: www.iucnredlist.org. [online] Assessed June 6, 2019.
- Duckworth, J.W., R. Steinmetz and J. MacKinnon. 2008b. *Capricornis sumatraensis*. The IUCN Red List of Threatened Species 2008. Available: www.iucnredlist.org. [online] Assessed June 6, 2019.
- Duval, M., F. Fang, K. Suraprasit, J.J. Jaeger, M. Benammi, Y. Chaimanee, J.I. Cibana and R. Grün. 2019. Direct ESR dating of the Pleistocene vertebrate assemblage from Khok Sung locality, Nakhon Ratchasima Province, Northeast Thailand. *Palaeontologia Electronica* 22:1-25.
- Esposito, M., Y. Chaimanee, J.J. Jaeger. and J.L. Reys. 1998. Datation des concrétions carbonatées de la Grotte du Serpent (Thaïlande) par la méthode Th/U. *Comptes Rendus de l'Académie des Sciences* 326: 603-608.
- Esposito, M., J.L. Reys, Y. Chaimanee and J.J. Jaeger. 2002. U-series Dating of Fossil Teeth and Carbonates from Snake Cave, Thailand. *Journal of Archaeological Science* 29: 341-349.
- Fraser, D. and J.M. Theodor. 2011. Comparing ungulate dietary proxies using discriminant function analysis. *Journal of Morphology* 272: 1513-1526.
- Fortelius, M. and N. Solounias. 2000. Functional characterization of ungulate molars using the abrasion-attrition wear gradient: a new method for reconstructing paleodiets. *American Museum Novitates* 3301: 1-36.
- Giri, S., A. Aryal, R.K. Koirala, B. Adhikari and D. Raubenheimer. 2011. Feeding Ecology and Distribution of Himalayan Serow (*Capricornis thar*) in Annapurna Conservation Area, Nepal. *World Journal of Zoology* 6: 80-85.
- Heywood, J. J. N. 2010. Explaining patterns in modern ruminant diversity: contingency or constraint? *Biological Journal of the Linnean Society* 99: 657-672.
- Hofmann, R.R. 1989. Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. *Oecologia* 78: 443-457.
- Ilyas, O. and J.A. Khan. 2004. Food habits of barking deer (*Muntiacus muntjak*) and goral (*Naemorhedus goral*) in Binsar Wildlife Sanctuary, India. *Mammalia* 67: 521-532.
- Janis, C.M. 1988. An estimation of tooth volume and hypsodonty indices in ungulate mammals, and the correlation of these factors with dietary preference. *Mémoires du Muséum national d'Histoire naturelle Série C* 53: 367-387.
- Junaid, M., F. Ahmad, R.C. Saxena and S.K. Bansal. 2012. Botanical composition determination of goral

- Naemorhedus goral* (Artiodactyla: Bovidae): goral rescue centre, Pahalgam, Jammu & Kashmir, India. *The European Zoological Journal* 1: 99-104.
- Junshum, P., A. Joomwong and S. Kamtubtim. 2010. A survey and estimate density of serow in Khao Somphot non-hunting area, Lopburi province. Thepsatri Rajabhat University, Thailand.
- Kaiser, T.M., D.W.H. Muller, M. Fortelius, E. Schulz, D. Codron and M. Clauss. 2013. Hypsodonty and tooth facet development in relation to diet and habitat in herbivorous ungulates: implications for understanding tooth wear. *Mammal Reviews* 43: 34-46.
- Kohn, M.J. and T.E. Cerling. 2002. Stable isotope compositions of biological apatite. *Reviews in Mineralogy and Geochemistry* 48: 455-488.
- Kubo, M.O. and E. Yamada. 2014. The inter-relationship between dietary and environmental properties and tooth wear: comparisons of mesowear, molar wear rate, and hypsodonty index of extant Sika Deer populations. *PLOS ONE* 9: e90745.
- Louys, J. and P. Robert. 2020. Environmental drivers of megafauna and hominin extinction in Southeast Asia. *Nature* 586: 402-406.
- MacFadden, B.J., T.E. Cerling, J.M. Harris and J. Prado. 1999. Ancient latitudinal gradients of C<sub>3</sub>/C<sub>4</sub> grasses interpreted from stable isotopes of New World Pleistocene horse (*Equus*) teeth. *Global Ecology and Biogeography* 8: 137-149.
- Marwick, B. and M.K. Gagan. 2011. Late Pleistocene monsoon variability in northwest Thailand: an oxygen isotope sequence from the bivalve *Margaritanopsis laosensis* excavated in Mae Hong Son province. *Quaternary Science Reviews* 30: 3088-3098.
- Mendoza, M and Palmqvist, P. 2008. Hypsodonty in ungulates: an adaptation for grass consumption or for foraging in open habitat? *Journal of Zoology* 274: 134-142.
- Merceron, G., E. Schulz, L. Kordos and T.M. Kaiser. 2007. Palaeoenvironment of *Dryopithecus brancoi* at Rudabanya, Hungary: evidence from dental meso- and micro-wear analyses of large vegetarian mammals. *Journal of Human Evolution* 53: 331-349.
- Mihlbachler, M.C., F. Rivals, N. Solounias and G.M. Semprebon. 2010. Dietary change and evolution of horses in North America. *Science* 331: 1178-1181.
- Morley, R.J. 1991. Tertiary stratigraphic palynology in Southeast Asia: current status and new directions. *Bulletin of the Geological Society of Malaysia* 28: 1-36.
- Nakhasathien, S. 2017. *The serow in Thailand: distribution, habitats and some behaviors* (in Thai). Seub Nakhasathien foundation, Nonthaburi, Thailand. 44 pp.
- Pushkina, D., H. Bocherens, Y. Chaimanee and J.J. Jaeger. 2010. Stable carbon isotope reconstructions of diet and paleoenvironment from the late Middle Pleistocene snake cave in Northeastern Thailand. *Naturwissenschaften* 97: 299-309.
- Safoowong M. 2015. Population, Distribution and Habitat of Goral in Protected area. *Wildlife Progress* 15: 167-185.
- Shoocongdej, R., N. Phumijumngong, K. Chintakanon, N. Pureepatpong, U. Hoontrakul and C. Treerayapiwat. 2007. *Final report of Highland Archaeology Project in Pang Mapha District, Mae Hong Son Province Phase 2. Vol. 2*. Bangkok: Thailand Research Fund (TRF).
- Suraprasit, K., J.J. Jaeger, Y. Chaimanee, M. Benammi, O. Chavasseau, C. Yamee, P. Tian and S. Panha. 2015. A complete skull of *Crocota crocota ultima* indicates a late Middle Pleistocene age for the Khok Sung (northeastern Thailand) vertebrate fauna. *Quaternary International* 374: 34-45.
- Suraprasit, J.J. Jaeger, Y. Chaimanee, O. Chavasseau, C. Yamee, P. Tian and S. Panha. 2016. The Middle Pleistocene vertebrate fauna from Khok Sung (Nakhon Ratchasima, Thailand): biochronological and paleobiogeographical implications. *ZooKeys* 613: 1-157.
- Suraprasit, K., H. Bocherens, Y. Chaimanee, S. Panha and J.J. Jaeger. 2018. Late Middle Pleistocene ecology and climate in Northeastern Thailand inferred from the stable isotope analysis of Khok Sung herbivore tooth enamel and the land mammal cenogram. *Quaternary Science Reviews* 193: 24-42.
- Suraprasit, K., S. Jongautchariyakul, C. Yamee, C. Pothichaiya and H. Bocherens. 2019. New fossil and isotope evidence for the Pleistocene zoogeographic transition and hypothesized savanna corridor in peninsular Thailand. *Quaternary Science Reviews* 221: 105861.
- Suraprasit, K., J.J. Jaeger, R. Shoocongdej, Y. Chaimanee, A. Wattanapituksakul and H. Bocherens. 2020. Long-term isotope evidence on the diet and habitat breath of Pleistocene to Holocene caprines in Thailand: implications for the extirpation and conservation of Himalayan gorals. *Frontiers in Ecology and Evolution* 8: 1-16.
- Suraprasit, K., J.J. Jaeger, Y. Chaimanee and C. Sutcharit. 2021a. Taxonomic reassessment of large mammals from the Pleistocene *Homo*-bearing site of Tham Wiman Nakin (Northeast Thailand): relevance for faunal patterns in mainland Southeast Asia. *Quaternary International* 603: 90-112.
- Suraprasit, K., R. Shoocongdej, K. Chintakanon and H. Bocherens. 2021b. Late Pleistocene human paleoecology in the highland savanna ecosystem

- of mainland Southeast Asia. *Scientific Reports* 11: 16756.
- Tougaard, C. 1998. *Les faunes de grands mammifères du Pléistocène moyen terminal de Thaïlande dans leur cadre phylogénétique, paléoécologique et biochronologique*. PhD thesis. France (Montpellier): University of Montpellier II.
- Tougaard, C. 2001. Biogeography and migration routes of large mammal faunas in South–East Asia during the Late Middle Pleistocene: focus on the fossil and extant faunas from Thailand. *Palaeogeography Palaeoclimatology Palaeoecology* 168: 337–358.
- Ulbricht, A., C.M. Lutz and E. Schulz. 2015. Can mesowear analysis be applied to small mammals? A pilot-study on leporines and murines. *Mammalian Biology* 80: 14-20.
- Wattanapituksakul, A., A. Filoux, A. Amphansri and S. Tumpeesuwan. 2018. Late Pleistocene Caprinae assemblages of Tham Lod Rockshelter (Mae Hong Son province, Northwest Thailand). *Quaternary International* 493: 212-226.
- White, J.C., D. Penny, L. Kealhofer and B. Maloney. 2004. Vegetation changes from the late Pleistocene through the Holocene from three areas of archaeological significance in Thailand. *Quaternary International* 113: 111-132.
- Wilson, D.E. and Mittermeier, R.A. 2011. *Handbook of the mammals of the world. Vol. 2. Hoofed mammals*. Lynx editions, Barcelona.

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