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 (Tougard, 1998; Tougard, 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 (δ^{13}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, δ^{13}C extracted from tooth enamel of fossils reflects the types of plants on which ungulates have foraged: C_3, C_4, mixed C_3/C_4, or CAM plants (*e.g*., Cerling and Harris, 1999; MacFadden *et al*., 1999; Kohn and Cerling, 2002). Consumption of C_3 plants refers to dwelling in closed habitats such as woodlands and open to deep forests, whereas the dietary intake of C_4 plants reflects open habitats such as grasslands (*e.g*., Cerling and Harris, 1999; MacFadden *et al*., 1999; Kohn and Cerling, 2002). The δ^{13}C of tooth enamel fossils from the Middle Pleistocene sites of Pha Bong and Tham Wiman Nakin revealed that *C. sumatraensis* was a 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 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 C_3 to 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 C_3 browser or C_4 grazer (Bacon *et al*., 2018a). In gorals, the δ^{13}C results showed that Pleistocene gorals foraged on either pure C_4 or mixed C_3/C_4 plants (Suraprasit *et al*., 2020). Concerning the extant populations, *C. sumatraensis* was recognized as a 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 C_3/C_4 plants, whereas the extant *N. goral* consumed pure C_3 or mixed C_3/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	*N. goral* (n = 10)	Bocherens *et al.*, 2017
Khok Sung	217 or 130 ka, late Middle Pleistocene	150	*C. sumatraensis* (n = 2)	Suraprasit *et al.*, 2015, 2016; Duval *et al.*, 2019
Tham Wiman Nakin	>169 ka, late Middle Pleistocene	500	*C. sumatraensis* (n = 10) *N. goral* (n = 4)	Esposito *et al.*, 1998, 2002; Tougard, 1998, 2001; Suraprasit *et al.*, 2021a
Tham Lod Rockshelter	32–12 ka, late Late Pleistocene	640	*C. sumatraensis* (n = 7) *N. griseus* (n = 22) *N. goral* (n = 8)	Shoocongdej *et al.*, 2007; Marwick and Gagan, 2011; Wattanapituksakul *et al.*, 2018; Suraprasit *et al.*, 2021b
CUMNH	present	-	*C. sumatraensis* (n = 3)	
THNHM	present	-	*C. sumatraensis* (n = 7)	
KNR	present	200–1,000	*C. sumatraensis* (n = 5)	Nakhasathien, 2017
OK	present	1,400–1,929	*N. griseus* (n = 3)	Chaiyarat *et al.*, 1999
ZMKU	present	-	*C. sumatraensis* (n = 3)	
FMKU	present	-	*C. sumatraensis* (n = 2)	
ZSM	present	-	*C. sumatraensis* (n = 2) *N. griseus* (n = 1) *N. goral* (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
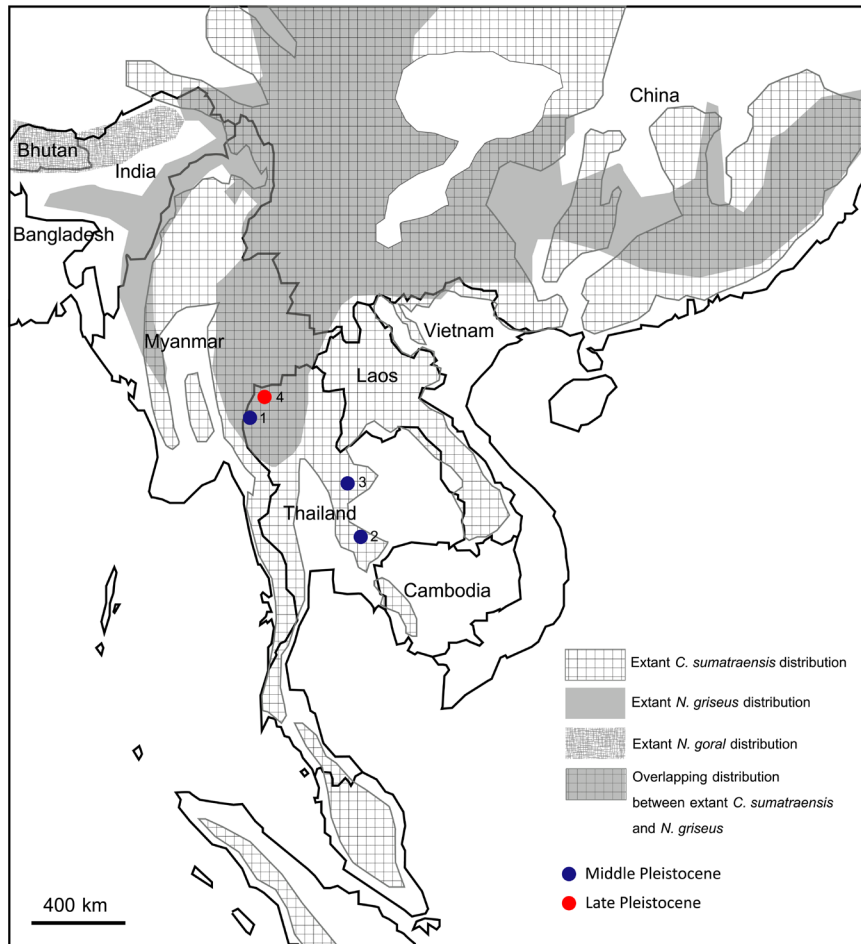
Figure 1. The distribution of Pleistocene and extant caprines in Southeast Asia, eastern region of South Asia, and South China. The locations of fossil sites studied in Thailand are shown: 1 = Pha Bong, Mae Hong Son; 2 = Khok Sung, Nakhon Ratchasima; 3 = Tham Wiman Nakin, Chaiyaphum; and 4 = Tham Lod 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).
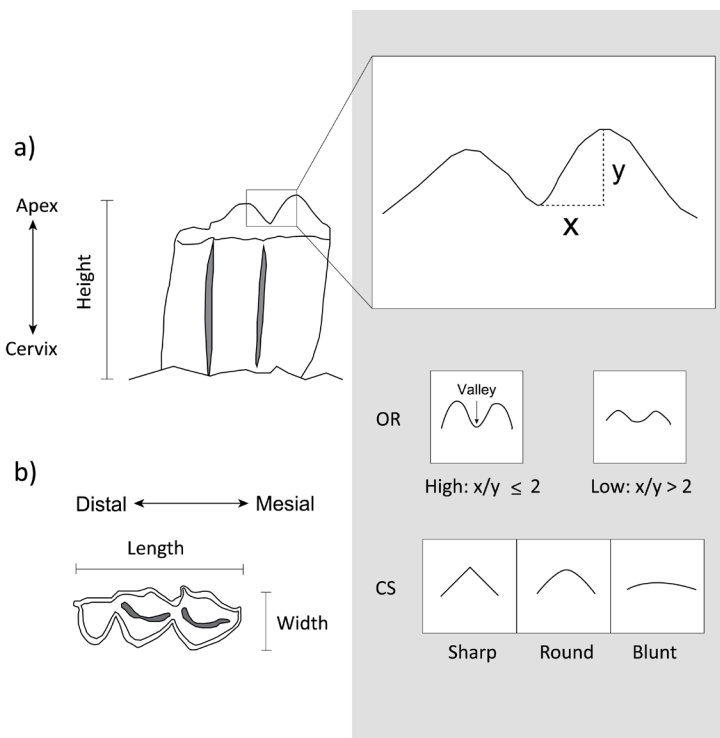

Figure 2. Measurements of the m3. a) crown height and mesowear analysis following Merceron *et al*. (2007); b) crown width and length.

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.

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 ± 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 brachydont; 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 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.

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						
C. sumatraensis	19	2.77 ± 0.30	89.47	36.84	57.89	5.26
N. griseus	22	3.61 ± 0.37	72.72	27.27	50.00	22.73
N. goral	22	3.95 ± 0.28	86.36	36.36	54.55	9.09
Extant						
C. sumatraensis	22	2.77	96.00	56.00	44.00	0
N. griseus	4	3.61	50.00	25.00	75.00	0
N. goral	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.
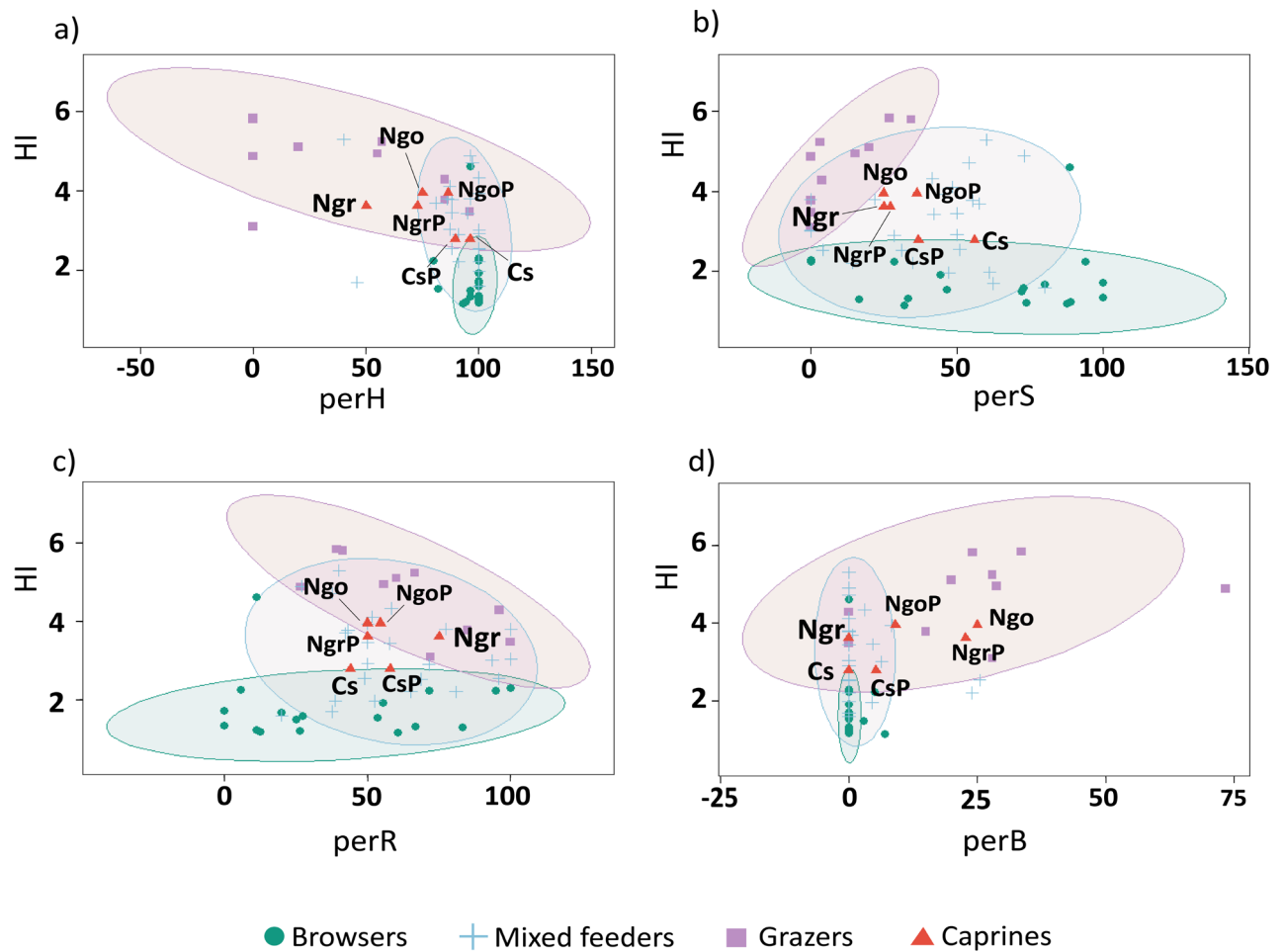
Figure 3. Scatter plots of HI with a) percentage of high OR (perH), b) percentage of sharp CS, c) percentage of round CS (perR) and d) percentage of blunt CS (perB) of Pleistocene and extant caprines. The comparative dataset of extant ungulates follows Fortelius and Solounias (2000). Abbreviations: Cs = extant *C. sumatraensis*, CsP = Pleistocene *C. sumatraensis*, Ngr = extant *N. griseus*, NgrP = Pleistocene *N. griseus*, Ngo = extant *N. goral*, and NgoP = Pleistocene *N. goral*.

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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