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Diversity, population structure and palaeoecology of the Pleistocene large cervids from the Padang Highlands, Sumatra

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Abstract

This chapter deals with the dentognathic remains of the Late Pleistocene large cervids from the Padang Highlands caves in Sumatra. We used linear and geometric morphometric techniques to investigate variation, taxonomic position and body size trends in a dataset of upper and lower molars. Dental mesowear was used to assess dietary preference in a subsample. The results suggest the Padang Highlands cervids belonged to multiple populations of an early stock of *Rusa* deer the size of sambar (*Rusa unicolor*), but morphologically reminiscent of Javan rusa (*Rusa timorensis*). The *Rusa* sp. of Sumatra was reconstructed as a mixed feeder with an increase in the grazing component with age.

Keywords: Cervidae, *Rusa*, taxonomy, Sundaland, morphometrics, mesowear

Abstrak

Bab ini membahas sisa-sisa dentognatik (rahang dan gigi) Cervidae berukuran besar yang berasal dari umur Pleistosen Akhir, yang ditemukan di gua-gua Dataran Tinggi Padang di Sumatra. Kami menggunakan teknik morfometrik linier dan geometris untuk menyelidiki variasi, posisi taksonomi, dan kecenderungan ukuran tubuh dalam kumpulan data geraham atas dan bawah. *Mesowear* gigi digunakan untuk menilai preferensi diet dalam sub-sampel. Hasil penelitian menunjukkan bahwa Cervidae Dataran Tinggi Padang termasuk dalam beberapa populasi dari stok awal jenis *Rusa* seukuran sambar (*Rusa unicolor*), tetapi secara morfologi menyerupai rusa Jawa (*Rusa timorensis*). *Rusa* sp. dari Sumatra direkonstruksi sebagai pemakan tumbuhan campuran, dengan peningkatan komponen merumput seiring bertambahnya usia.

Kata kunci: Cervidae, *Rusa*, taksonomi, Sundaland, morfometrik, *mesowear*

Introduction

Although Eugène Dubois has primarily been credited with the discovery of *Homo erectus* in Java (Dubois 1894; de Vos 2004), another, sometimes-neglected, accomplishment of his was the meticulous collection of large numbers of vertebrate fossils found in association with those hominin remains. These collections have allowed several generations of researchers to develop a more detailed understanding of the biostratigraphy of Java (de Vos 1985, 1996; van den Bergh et al. 2001; von Koenigswald 1933, 1934, 1935) and the palaeobiology of several mammalian groups (Badoux 1959; Hardjasmita 1987; Hooijer 1958, 1960). However, a large part of Dubois' collection was discovered not on Java but during his preceding 1887–90 stay on Sumatra (de Vos 2004). The fossils he found there can mostly be traced to three karstic limestone caves in the Padang Highlands: the Jambu and Sibrambang caves, close to Tapisello, and the recently rediscovered Lida Ajer Cave near Pajakombo (de Vos 1983; Westaway et al. 2017). While the geological context of Lida Ajer is better understood, movements inside that cave may have redeposited the fossils (Louys et al. 2017), and it is not possible to reassign the finds from Lida Ajer to specific stratigraphic layers (Westaway et al. 2017). At present, very little is known about the geology and taphonomy of Jambu and Sibrambang (Wirkner and Hertler 2019). Therefore, temporal, spatial and altitudinal relationships within these three caves' individual fossil assemblages are unclear.

Although, due to porcupine gnawing (Bacon et al. 2015), the material from these sites consists almost exclusively of teeth, a wide range of mammals are represented (de Vos 1983). The faunal spectrum appears to be primarily composed of extant taxa and suggests the presence of closed forest (Bacon et al. 2015; de Vos 1983; Louys 2007). As a consequence, earlier researchers have generally considered the fossils to be of Holocene age (Dubois 1891; Hooijer 1960, 1962) and of limited relevance to questions of human evolution and palaeobiogeography. This assumption was later amended by de Vos (1983), who suggested that the Sumatran material is of early Late Pleistocene age and probably correlates with the Punung faunal stage of Java, a notion later confirmed by chronometric studies (Chapter 5, this volume; Skelton 1985; Westaway et al. 2007, 2017). Several absolute dates have been obtained for Lida Ajer (73–63 ka; Westaway et al. 2017), Sibrambang (80–60 ka; Bacon et al. 2015) and Jambu (>70 ka; Bacon et al. 2015; Skelton 1985), and today little doubt is left about their ages being Pleistocene. Nevertheless, a more recent study (Chapter 5, this volume) suggests that the individual cave assemblages may represent a mix of fossils with different ages, ranging widely between the Middle and Late Pleistocene. That being said, there is no doubt that our increased understanding of the chronology, in addition to the rediscovery of two Pleistocene *Homo sapiens* teeth in the Lida Ajer assemblage (Westaway et al. 2017) has reignited interest in Dubois' Sumatran collections.

Despite having attracted less attention than the Javan fossil record, the material from the Padang Highlands caves has been examined in several studies (Hooijer 1948, 1960, 1962). Although part of the ungulate fauna was described by Hooijer (1958), the Cervidae have only recently become the focus of more detailed study (Gruwier et al. 2015; Wirkner and Hertler 2019). In part, the omission of this family can be explained by the complexity of cervid evolution in the wider Indomalayan region (e.g. Heckeberg 2020). Most of the known Pleistocene taxa have been described from material found in Java, but the identification of individual fossils from that island remains problematic because the original descriptions have often been based on isolated teeth or antler fragments (Dubois 1891, 1908; Martin 1886; von Koenigswald 1933, 1934). In the absence of a comprehensive synthesis of the Javan cervids, it remains challenging to consider the position of the Sumatran fossils within a wider evolutionary framework for the region.

Regardless of these drawbacks, deer form a large and important component of the Lida Ajer, Jambu and Sibrambang assemblages. In the Dubois collection, of the approximately 10,000 remains from the three cave sites, about 24% are currently catalogued as cervid. More than half of these are of a small type identified as Indian muntjac (*Muntiacus* sp.) (de Vos 1983). Most of the other fossils belong to one or more larger forms, typically placed within the genus *Rusa* (de Vos 1983; Gruwier et al. 2015). The taxonomic status of these large deer, and whether one or multiple species are present, remains uncertain. Previous morphometric analyses have, nevertheless, suggested a close relationship between some of the large deer fossils and *Rusa unicolor*, *Rusa timorensis*, or *Cervus kendengensis*, a Javan species from the Pleistocene that is often considered a member of the genus *Rusa* (Gruwier et al. 2015).

In addition to contributing to our understanding of cervid evolution, the Sumatran fossils are also significant in that they represent a valuable resource that gives ecological context to the early presence of hominins in Southeast Asia. Irrespective of their taxonomic status, new methods—such as ecomorphological analysis, community structure analysis, dental wear studies and biomolecular analyses—make fossil deer remains useful for palaeoenvironmental reconstruction (Amano et al. 2016; Curran 2012; Li et al. 2017; Louys 2012). During the last few years, the Sumatran cervids have been included in broader palaeoecological studies of the region (Bacon et al. 2015; Louys 2007, 2012; Louys and Meijaard 2010), stable isotope analyses (Janssen 2017; Janssen et al. 2016) and mesowear studies (Wirkner and Hertler 2019). However, no study is currently available that deals specifically with the larger deer or that summarises the results of earlier work on them.

In this chapter, we examine the taxonomic status, population structure and ecology of the large cervids from the Padang Highlands using a multiproxy approach. To assess diversity and taxonomic status in the assemblage, we used a comparative morphometric approach on a number of extant and fossil deer molars. Dental measurements were also used to explore the sample for body size trends, sexual size dimorphism, and their potential ecological implications. Dental mesowear analysis on upper and lower molars was used to evaluate aspects of dietary ecology.

Materials

For our linear morphometric analyses, we used length and width measurements of 116 lower third molars of fossil *Rusa* sp. from Sumatra. The measurements were taken at Naturalis Biodiversity Center in Leiden. Five of the specimens could be specifically traced to Sibrambang cave, while the others came from Padang Highlands caves, most probably from either Jambu, Lida Ajer or Sibrambang. Our comparative sample consisted of 223 molars of extant species, primarily collected at the Natural History Museum, London; the Muséum National d'Histoire Naturelle, Paris; the National Museum of Scotland, Edinburgh; Naturalis Biodiversity Center, Leiden; the Royal Belgian Institute of Natural Sciences, Brussels; Natuurhistorisch Museum Rotterdam; Ghent University Museum; and the archaeozoology labs of the University of Lille and the Center for Artefact Research, Mechelen. (See Table 6.1; see doi.org/10.5281/zenodo.5876370 for the supplementary data.) A limited number of measurements were taken from the literature (Dong and Chen 2015; Sykes et al. 2011 and supplementary data therein).

Standardised photographs of a smaller number ($n = 43$) of upper third molars were taken at the same institutions for geometric morphometric (GMM) analysis (Table 6.1). This included eight fossil *Rusa* sp. specimens from the Padang Highlands collection at Naturalis Biodiversity Center and 35 specimens belonging to five extant species of the genus *Rusa*. Pathological teeth and specimens with

a severe degree of attrition were excluded to avoid complicating the placement of the landmarks. When possible, right upper molars were selected, but in a few cases left ones were included by digitally mirroring them in tpsDig 2.16 (Rohlf 2004).

Table 6.1: Numbers of upper molars (m3 sup) and lower third molars (m3 inf) used in linear and geometric morphometric (GMM) analysis, calculation of body mass (see Figure 6.4) and sex determination.

Taxon	Number of specimens	
	Linear morphometric analysis (m3 inf)	GMM analysis (m3 sup)
<i>Rusa</i> sp. (Padang Highlands fossils)	116 ^a	8
<i>Rusa unicolor</i> (sambar)	30	12
<i>Rusa timorensis</i> (Javan rusa)	20	10
<i>Rusa alfredi</i> (Prince Alfred's deer)	4	2
<i>Rusa marianna</i> (Philippine deer)	5	1
<i>Cervus kendengensis</i> (Javan fossils)	28	10
<i>Cervus elaphus</i> (red deer)	16	—
<i>Rucervus eldii</i> (Eld's deer)	12	—
<i>Rucervus duvaucelii</i> (swamp deer)	7	—
<i>Axis axis</i> (spotted deer)	71 ^b	—
<i>Axis porcinus</i> (hog deer)	24	—
<i>Axis kuhlii</i> (Bawean deer)	2	—
<i>Dama dama</i> (fallow deer)	32	—
Total	367	43

^a Includes five specimens specifically from Sibrambang.

^b Includes 27 specimens of one population of *A. axis* from Kanha National Park, India.

Source: Authors' data.

After excluding a number of specimens that were insufficiently preserved, a sample of 27 upper and lower molars from the Padang Highlands was retained for mesowear analysis. Because both anterior and posterior cusps were assessed, this corresponded to 39 usable cusps (see Table 6.2). We included first, second and third molars, but in several instances the rank was unclear, and specimens were designated as upper molars (M1/2/3 sup) or lower first or second molars (m1/2 inf). As with the teeth used in our morphometric analyses, most of the material could be assigned only broadly to the Padang Highlands caves, not to a specific site. In only five cases could the provenance be traced to Sibrambang cave.

Table 6.2: Materials used for tooth age estimation, individual dental age stage, mesowear analysis, body mass estimation and sex determination.

Fossil site	Tooth position	Wear stage: number of teeth / usable cusps						
		Total	0	1	2	3	4	5
Padang Highlands	M1/2/3 sup	20/28	—	3/5	10/14	5/6	2/3	—
	m1/2 inf	1/1	—	—	—	—	1/1	—
	m3 inf	1/2	1/2	—	—	—	—	—
Sibrambang	m3 inf	5/8	—	—	2/4	2/3	1/1	—

Note: The numbers of teeth and cusps are sorted by fossil site, tooth position and wear stage.

Source: Authors' data.

Methods

Linear and GMM analyses were used to explore diversity and taxonomy in our dataset of fossil teeth. First, a linear morphometric analysis was conducted on a sample of lower third molars from the Padang Highlands caves, in comparison with a series of extant Southeast Asian species and a sample of *Cervus kendengensis* specimens from the Pleistocene of Java. Length (Dap) and width (Dt) measurements were taken following Heintz (1970) and plotted on an XY-graph using PAST 2.17b (Hammer et al. 2001). Statistical significance ($p < 0.05$) of between-group differences was tested using multivariate analysis of variance (MANOVA) followed by Mann-Whitney pairwise comparisons. Holm-Bonferroni corrected p -values were used to minimise the family-wise error rate (Holm 1979).

For the lower third molars used in our morphometric analyses (Table 6.1), and for the smaller, more diverse sample of upper and lower molars subsequently used for mesowear analysis (Table 6.2), body mass and sex were assessed. We reconstructed total body mass using regressions on linear dimensions, based on Janis (1990) (Table 6.3). Length (Dap), width (Dt) and surface area (Dap \times Dt) were used as variables. To assess the precision of the estimate, we used the correlation coefficient for each of the regressions provided by Janis (1990), as well as the per cent standard error of the estimate (%SEE in Table 6.3) and the per cent prediction error (%PE). These values show that, despite the robust correlation coefficient, the standard error of the estimate and the prediction error are high in all of the equations. The regression gives values that indicate a range rather than an absolute value. The reason for this is that body mass is not a constant but varies with sex, age and other life history traits. In order to control for the effects of age, we used only permanent molars belonging to adult individuals. Furthermore, Janis's (1990) method accounts for the effects of sex by using a comparative dataset for body size based on males only. Although this leads to reconstructed values that overestimate body mass in female individuals, it is a useful approach in taxa with high sexual dimorphism such as cervids, because values based on an unsexed regression sample would result in averaged body masses, which do not represent either sex. Taking these potentially confounding factors into account, we used an average of the predicted body mass calculated for each of the three variables for further analysis.

Table 6.3: Regressions applied on upper and lower molars to calculate body mass and sex.

Regression used for body mass reconstruction per element	Slope	Intercept	R ²	% SEE	% PE	Source
m3 inf length	3.143	0.799	0.957	27.4	19.1	Janis (1990)
m3 inf width	3.000	1.877	0.880	49.6	35.9	Janis (1990)
m3 inf area	1.561	1.346	0.953	28.8	19.9	Janis (1990)
M3 sup length	3.281	1.073	0.959	26.8	18.3	Janis (1990)
M3 sup width	3.286	1.375	0.921	38.7	23.8	Janis (1990)
M3 sup area	1.651	1.214	0.954	28.2	19.2	Janis (1990)
Female body mass inferred from male body mass in <i>Rusa</i> sp.	0.577	8.036	0.805	—	—	Data from Nowak (1999), A.T. Smith and Xie (2008), Francis (2008)

% SEE: per cent standard error of the estimate.

% PE: per cent prediction error.

Note: Where the rank of a molar (i.e. whether it was a first or second molar) was unclear, we considered the tooth a second molar for the purposes of the regressions.

Source: Authors' data based on regressions by Janis (1990), Francis (2008), Nowak (1999) and A.T. Smith and Xie (2008).

The calculated body masses were then used to predict sex for each specimen. This was done by considering the largest individual in the sample as male and inferring maximum body mass for the largest female by a regression based on published pairs of male and female body masses from recent representatives of the genus *Rusa* (Francis 2008; Nowak 1999; Smith A.T. and Xie 2008). Specimens with values below the maximum female body mass were considered female.

As it was unclear whether the Padang Highlands fossils represent one or multiple species, we conducted disparity analyses on the fossil molar dataset in comparison with a number of extant cervid species. To accomplish this, we took two approaches to test if the magnitude of variance was significantly larger in *Rusa* sp. than is normally expected in related species or populations. In our first approach, we calculated the standard deviation (SD) of the regressions of the linear data against body mass and expressed it as a percentage of body mass (% SD). As an additional coherence test, this value was then compared to the maximum prediction error of the regression. If % SD was lower than the maximum prediction error, this indicated that the value was coherent and not confounded by additional sources of variation.

Our second method to assess disparity in the samples consisted of conducting a series of pairwise Levene's tests (Cardini et al. 2007; Hallgrímsson et al. 2006) directly on tooth length (Dap) and on tooth surface area (Dap × Dt). Levene's *F* compares the within-group variance between different populations by calculating the deviation of each specimen from the group mean (Cardini et al. 2007). These deviations are then compared between different groups via MANOVA (Cardini et al. 2007). An *F*-statistic is used to test the null hypothesis that two compared groups are randomly drawn from the combined set of mean deviations (Hallgrímsson et al. 2006). If the (Holm-Bonferroni corrected) *p*-values are below the α -value ($p < 0.05$), the difference in variance between populations is not expected to be equal.

As a complementary technique to explore morphological variation, we conducted a GMM analysis on a small sample of upper third molars of fossil *Rusa* sp. from Sumatra, fossil *Cervus kendengensis* from Java and four extant *Rusa* species (Table 6.1). GMM not only allows for the exclusion of isometric size effects from the dataset (Zelditch et al. 2004) but also has the advantage of picking up subtle morphological differences and has already proven to be a powerful method for studying phenotypic diversity in artiodactyls (Brophy et al. 2014; Cucchi et al. 2009; Evin et al. 2013). The GMM model used here consisted of an improved version of an earlier model by Gruwier et al. (2015), where shape was defined by placing a number of homologous landmarks at discrete anatomical loci along the outline of the third molar (Gruwier et al. 2015; Zelditch et al. 2004). Standardised photographs were taken of the occlusal surface, using the protocol described in Gruwier et al. (2015). After placing eight type I and type II landmarks (Baab et al. 2012) on the outline of each tooth using tpsDig 2.16 (Rohlf 2004) (see Figure 6.1), the Cartesian coordinate data were extracted and further analysed in PAST 2.17b (Hammer et al. 2001). Here, we used a generalised Procrustes superimposition to scale, rotate and translate the objects, to exclude all information irrelevant to shape (Walker 2000). As this translation results in a projection of the data in a Euclidean space tangential to the Procrustes shape space (Viscosi and Cardini 2011), we tested the accuracy of this approximation with tpsSmall 1.20 (Rohlf 2003).

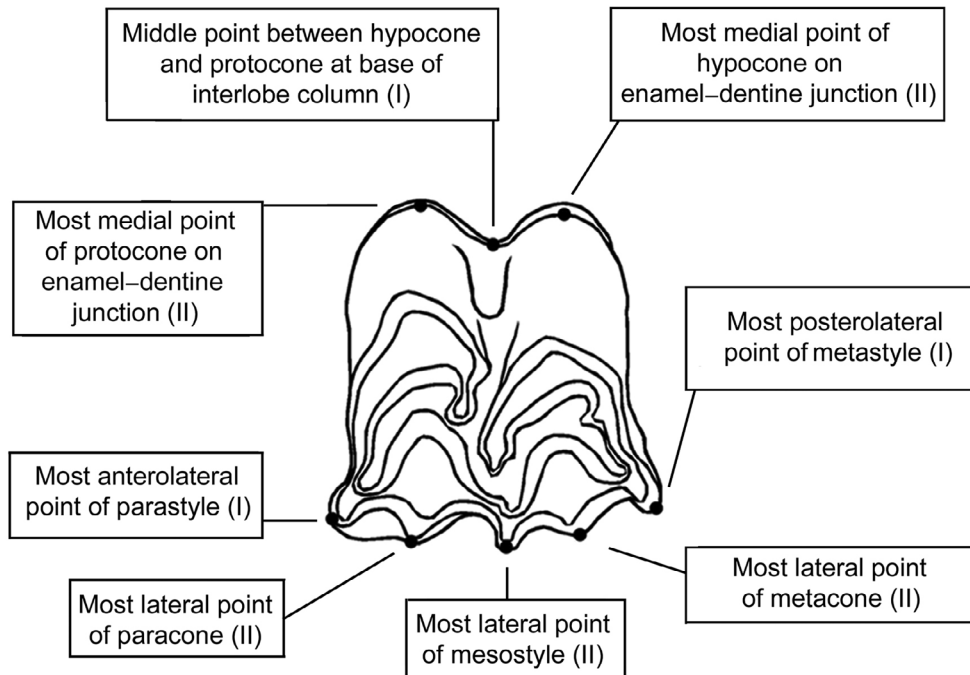


Figure 6.1: Landmarks recorded on the upper third molar, with illustration of the occlusal surface and description of landmark location and type.

(I) Type I landmark.

(II) Type II landmark.

Source: Image by the authors.

To explore morphological variation in the Procrustes-transformed coordinate data, we first conducted a between-groups principal component analysis (PCA). In this approach, eigenvectors are derived from the variance-covariance matrix of the group means instead of the individual specimens, which has the advantages that the original Procrustes distances in shape space are preserved and differences between populations are emphasised (Seetah et al. 2012). We used a non-parametric MANOVA, followed by Mann-Whitney pairwise comparisons, on the relevant principal component scores to assess the statistical significance ($p < 0.05$) of the cluster separations (Gruwier and Kovarovic 2021; Hou et al. 2021; Marramà and Kriwet 2017; Polly et al. 2013; Schutz et al. 2009). A permutational test was selected because the assumptions required for parametric testing are not necessarily met by data that results from GMM analysis (Cardini et al. 2015; Gruwier and Kovarovic 2021; Lopez-Lazaro et al. 2018). The number of relevant components retained for analysis was indicated by a scree plot of the eigenvalue distribution (Jackson 1993). Shape changes along the axes of variation were visualised with thin-plate spline deformation grids.

To further assess the relationship between different members of the genus *Rusa*, and to maximise between-group variation, a canonical variates analysis was run on a subsample including *R. unicolor*, *R. timorensis*, *C. kendengensis* and fossil *Rusa* sp. from Sumatra. As with the PCA, the significance ($p < 0.05$) of between-group differences was tested using a non-parametric MANOVA with associated pairwise comparisons. This was conducted on the first two axes, which together explained the majority of the variation. The Holm-Bonferroni procedure was used as a multiple correction technique (Holm 1979). Reclassification rates with jackknifed cross-validation were provided for the different assigned groups.

Finally, dental mesowear analysis was used to explore the dietary ecology of the cervids from the Padang Highlands. In this method, gross patterns of molar wear are categorised by assessing tooth cusp shape and relief, as these aspects are indicative of the abrasiveness of consumed dietary plant matter (Fortelius and Solounias 2000). Consequently, mesowear analysis can be used as a proxy for vegetation structure and to help infer palaeoenvironmental conditions. In this study, we recorded the mesowear signal on the buccal side of the upper molars and on the lingual side of the lower molars, from a series of digital photographs of the teeth. We used a ruler-based mesowear II approach that distinguishes seven mesowear stages (MWS) and combines cusp shape and relief into a single value (Ackermans 2020). This digital ruminant ruler is superimposed on the photographs of the molars and scored according to a protocol developed by Wirkner and Hertler (2019). In this model, MWS 0, 2, 4 and 6 correspond to specific combinations of mesowear variables, while MWS 1, 3 and 5 represent intermediate stages. On the ruminant ruler, a low score (MWS 0) indicates a browsing diet, while a high score (MWS 3 or higher) signifies a grazing diet with soft to increasingly dry grasses. The intermediate stages (MWS 1 and 2) are indicative of mixed diets with either a browsing or a grazing component (Wirkner and Hertler 2019).

To account for the potential effect of age in the mesowear analysis, molars were assigned to different tooth age classes. Based on photographs of the occlusal surface, wear stages were recorded according to Wirkner and Hertler's (2019) protocol. This tooth age reflects the degree of wear, but not necessarily the absolute age of an individual. In part this is because molars at different positions in the tooth row are subject to different rates of wear (Wirkner and Hertler 2019). To convert the wear stages of molar cusps of different rank to usable ontogenetic categories, we translated the wear stages into the individual dental age stages (IDAS) of Anders et al. (2011:547), adapted by Wirkner and Hertler (2019). Six age categories are identified in this scheme: 'prenatal' (0), 'infant' (1), 'juvenile' (2), 'adult' (3), 'late adult' (4) and 'senile' (5). Except for the lower third molars, we designated every tooth as a second molar, which is the standard tooth position in Fortelius and Solounias' (2000) mesowear method. Body masses were calculated using the regressions provided by Janis (1990), which are shown in Table 6.3, and the boundary value that was calculated for the whole *Rusa* dataset was used to delineate the presumably male portion of the sample from the potentially female specimens.

Results

When plotting the length and width measurements of the lower third molar of seven extant Southeast Asian species, Pleistocene *Cervus kendengensis*, and *Rusa* sp. from the Padang Highlands, there was visual separation between several groups (see Figure 6.2). A MANOVA confirmed that overall group differences were significant ($p < 0.01$). Associated pairwise comparisons indicated that most between-group differences were significant (Table 6.4). Members of the genus *Axis* gave lower scores than members of the genera *Rusa* and *Rucervus*. *Rusa unicolor* was the largest species and gave higher scores than the other extant species, except for *Rucervus duvaucelii*, whose score did not differ significantly from that of *Rusa unicolor* ($p = 1$). *Rusa timorensis* and *Cervus kendengensis* were significantly smaller than *Rusa unicolor* ($p < 0.01$) and *Rucervus duvaucelii* ($p < 0.01$). The fossil *Rusa* specimens from the Padang Highlands were visually of the same size as *Rusa unicolor*, but the MANOVA suggested that this group was significantly different from all the other groups ($p < 0.01$).

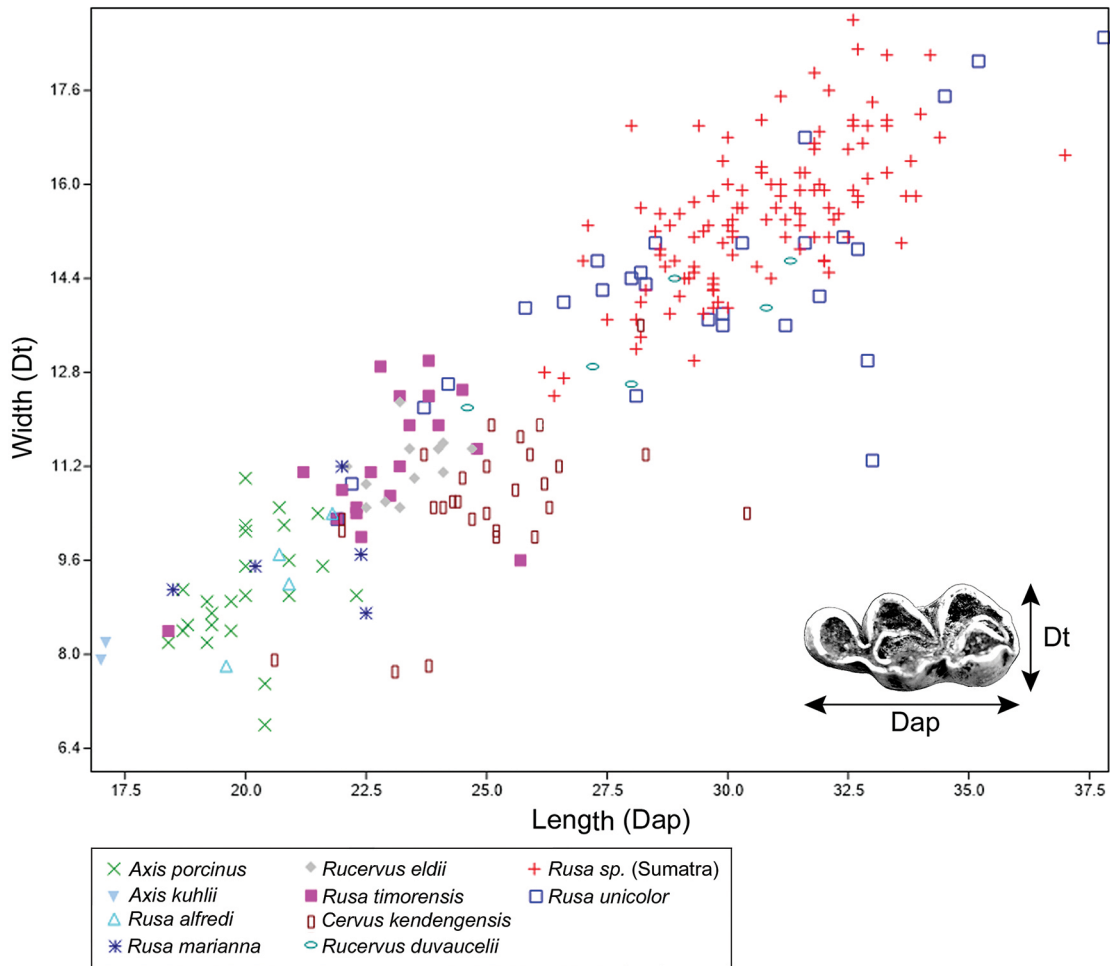


Figure 6.2: Length (Dap) and width (Dt) measurements of Padang Highlands *Rusa* sp., Pleistocene *Cervus kendengensis* and extant Southeast Asian Cervini.

Source: Image by the authors.

Table 6.4. Holm-Bonferroni corrected *p*-values of pairwise comparisons of a multivariate analysis of variance on length (Dap) and width (Dt) measurements of lower third molars.

Taxon	<i>Rusa unicolor</i>	<i>Rusa timorensis</i>	<i>Axis porcinus</i>	<i>Rusa</i> sp. (Padang)	<i>Rucervus alfredi</i>	<i>Rusa eldii</i>	<i>Axis kuhlii</i>	<i>Rucervus duvaucelii</i>	<i>Rusa marianna</i>
<i>R. timorensis</i>	<0.01*	—	—	—	—	—	—	—	—
<i>A. porcinus</i>	<0.01*	<0.01*	—	—	—	—	—	—	—
<i>R. sp.</i> (Padang fossils)	<0.01*	<0.01*	<0.01*	—	—	—	—	—	—
<i>R. alfredi</i>	<0.01*	1	1	<0.01*	—	—	—	—	—
<i>R. eldii</i>	<0.01*	1	<0.01*	<0.01*	1	—	—	—	—
<i>A. kuhlii</i>	<0.01*	0.18	1	<0.01*	1	0.43	—	—	—
<i>R. duvaucelii</i>	1	<0.01*	<0.01*	<0.01*	<0.01*	0.05*	0.11	—	—
<i>R. marianna</i>	<0.01*	1	1	<0.01*	1	1	0.23	0.05*	—
<i>C. kendengensis</i>	<0.01*	<0.01*	<0.01*	<0.01*	0.12	0.02*	<0.01*	<0.01*	0.05*

* Significant values ($p \leq 0.05$).

Source: Authors' data.

Levene's test on lower third molar length and surface area gave insight into the intraspecific variation of seven different taxa (see Table 6.5 and Figure 6.3). In these results, F -values significantly deviating from 1 indicate a difference between the two groups' variances. This showed that, as far as molar length and surface area were concerned, intraspecific variability was unequal among the species. The species of the genera *Axis* and *Dama* demonstrated a relatively low variance, and the difference between these taxa was not significant (as shown in Table 6.5). However, when *C. elaphus*, and especially *R. unicolor*, were compared with the other species, Levene's F was in most cases significantly different from 1, suggesting that the variance of *C. elaphus* and *R. unicolor* was higher (Table 6.5). *R. timorensis* had a significantly lower variance in length than *R. unicolor*, but this was similar to that of the *Axis* species. In the *Rusa* fossils from the Padang Highlands, the variance was similar to that in *R. timorensis* and, especially, *C. elaphus*, lower than in *R. unicolor*, and higher than in the genera *Axis* and *Dama* (Table 6.5, Figure 6.3).

Table 6.5: Results of Levene's tests on tooth length (Dap) and surface area (Dap × Dt).

Taxa	Length (Dap)			Surface area (Dap × Dt)		
	Levene's F	p	R2	Levene's F	p	R2
<i>A. axis</i> × <i>Rusa</i> sp. ^a	13.44	<0.01*	0.06	12.97	<0.01*	0.06
<i>A. axis</i> × <i>Axis porcinus</i>	2.62	0.7	0.02	6.09	0.16	0.06
<i>A. axis</i> × <i>Rusa unicolor</i>	67.33	<0.01*	0.40	18.30	<0.01*	0.15
<i>A. axis</i> × <i>Rusa timorensis</i>	0.01	1	0.01	0.11	1	0.01
<i>A. axis</i> × <i>Dama dama</i>	0.10	1	0.01	11.37	0.01*	0.11
<i>A. axis</i> × <i>Cervus elaphus</i>	8.99	0.04*	0.09	5.39	0.18	0.05
<i>A. porcinus</i> × <i>R. sp.</i> ^a	12.77	<0.01*	0.09	13.31	<0.01*	0.08
<i>A. porcinus</i> × <i>R. unicolor</i>	29.60	<0.01*	0.37	11.27	<0.01*	0.18
<i>A. porcinus</i> × <i>R. timorensis</i>	1.33	1	0.03	3.17	0.49	0.07
<i>A. porcinus</i> × <i>D. dama</i>	1.33	1	0.02	1.73	0.77	0.03
<i>A. porcinus</i> × <i>C. elaphus</i>	6.59	0.14	0.14	9.64	0.03*	0.20
<i>R. unicolor</i> × <i>R. sp.</i> ^a	60.99	<0.01*	0.30	5.65	0.17	0.03
<i>R. unicolor</i> × <i>R. timorensis</i>	20.50	<0.01*	0.31	6.17	0.16	0.11
<i>R. unicolor</i> × <i>D. dama</i>	32.36	<0.01*	0.36	12.24	0.12	0.20
<i>R. unicolor</i> × <i>C. elaphus</i>	6.59	0.14	0.13	1.53	0.77	0.03
<i>R. timorensis</i> × <i>R. sp.</i> ^a	4.02	0.36	0.02	4.96	0.19	0.03
<i>R. timorensis</i> × <i>C. elaphus</i>	2.84	0.7	0.07	2.92	0.49	0.07
<i>D. dama</i> × <i>R. sp.</i> ^a	8.07	<0.01*	0.05	16.63	<0.01*	0.10
<i>D. dama</i> × <i>C. elaphus</i>	5.21	0.24	0.10	11.88	0.02*	0.24
<i>C. elaphus</i> × <i>R. sp.</i> ^a	1.75	0.93	0.01	0.01	1	0.01

* Significant values ($p < 0.05$).

^a Padang Highlands fossils.

Source: Authors' data.

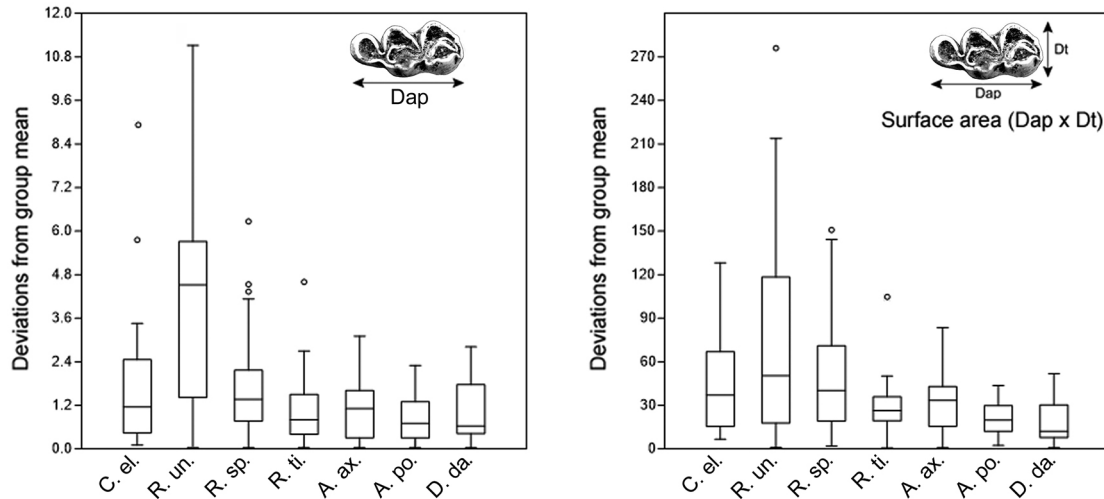


Figure 6.3: Box plots of deviations from group mean per species, for lower third molar length and surface area.

Note: C. el = *Cervus elaphus*, R. un = *Rusa unicolor*, R. sp. = *Rusa* sp. (Padang), R. ti = *Rusa timorensis*, A. ax = *Axis axis*, A. po = *Axis porcinus*, D. da = *Dama dama*.

Source: Authors' data.

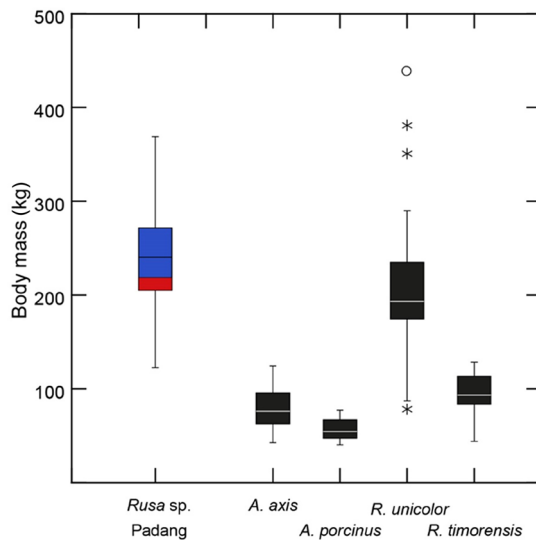


Figure 6.4: Reconstructed body masses of the *Rusa* species from the Padang Highlands compared to a sample of recent species, namely *Axis axis*, *Axis porcinus*, *Rusa unicolor* and *Rusa timorensis*.

Source: Authors' data.

We then calculated body masses for fossil *Rusa* sp. from the Padang Highlands based on teeth ($n = 134$), and for a subsample of four recent species ($n = 167$, Table 6.1) for comparative purposes (see Figure 6.4). The average body mass in the fossil *Rusa* sample was 241 ± 54 kg. Absolute values corresponded to recent representatives of *R. unicolor* rather than of the smaller *Axis* species or the endemic *R. timorensis* from Java. Individual body masses in the fossil *Rusa* sample ranged from 123 kg to 369 kg. The range covered by the values matched the corresponding range in the *R. unicolor* sample better than that in any other species included in our comparative sample. *R. timorensis* was substantially smaller.

Along with geographical range, another source of variability in a sample of body masses is sex, particularly in species with a high degree of sexual dimorphism. We assessed sex-specific body masses in our dataset by inferring a boundary value for female body masses from the largest individual body mass occurring in the sample (438 kg). This boundary value was 221 kg. Assuming all specimens displaying body masses with a higher value represent males, and all individuals with a lower body mass represent females, our dataset included 85 male and 52 female individuals.

For the GMM analysis, we first established that the projection of the shape coordinates in tangent shape space was adequate for further analysis (slope = 0.998, $p = 1$). A PCA on the Procrustes residuals of the Padang Highlands molars and of molars from five extant members of the genus *Rusa* revealed substantial shape variation (see Figure 6.5). As indicated by a plot of the eigenvalue distribution (see the supplementary data at doi.org/10.5281/zenodo.5876370), the first two components, which explained 90.4% of the variation, were retained as relevant. The thin-plate spline deformation grids revealed that the shape changes along the first axis were mainly expressed as a difference in relief between the parastyle, paracone, metastyle and metacone and a difference in medio-lateral depth (see Figures 6.1 and 6.5). The second axis showed that there was variation in the relief between the base of the interlobe column and the hypocone and protocone, a difference in antero-posterior length of the medial relative to the lateral side, and a variation in the more or less medial position of the parastyle and metastyle relative to the paracone, mesostyle and metacone. The scatter plot (Figure 6.5) revealed a substantial overlap in shape between the Sumatran fossils and *R. unicolor*, *R. timorensis* and *C. kendengensis*. *R. marianna* and *R. alfredi* were well separated, especially on PC1, and indicated the presence of a different morphology in each of these island forms. Pairwise comparisons following a MANOVA on the relevant components (PC1 and PC2, $p < 0.01$) confirmed that *Cervus kendengensis*, *R. timorensis*, *R. unicolor* and the Padang Highlands fossil *Rusa* sp. were not significantly different from each other (see Table 6.6). Despite their visual separation, *R. alfredi* and *R. marianna* did not significantly differ from the other species after multiple corrections (see Table 6.6).

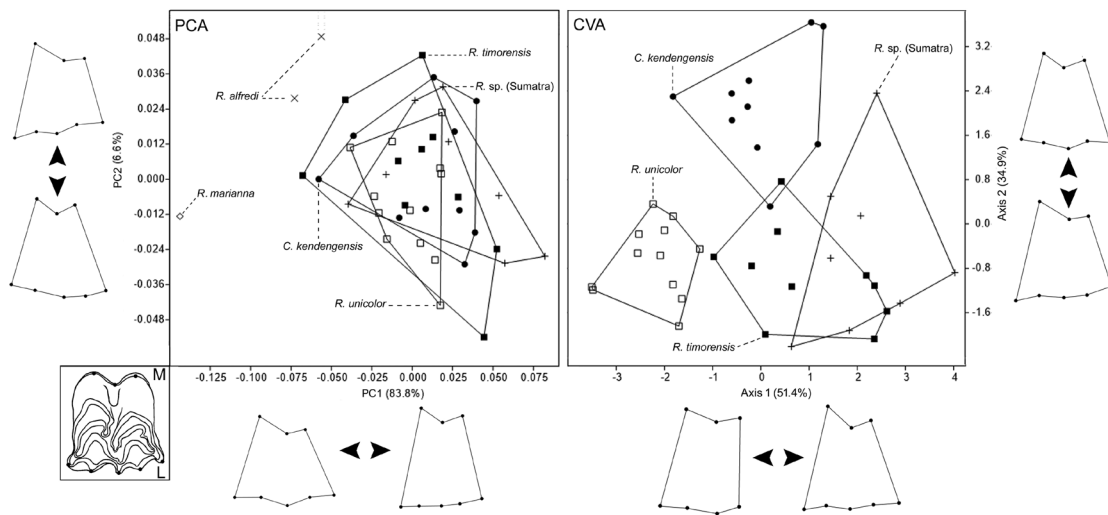


Figure 6.5: Principal component analysis and canonical variates analysis on *Rusa* sp. from the Padang Highlands and several species of the genus *Rusa* and the fossil *Cervus kendengensis* from Java.

Note: Shape changes along the axes are visualised with thin-plate spline deformation grids showing hypothetical extreme values at the end of each axis.

PC = principal component; CV = canonical variate.

L = lateral; M = medial.

R. = *Rusa*; *C.* = *Cervus*.

Source: Image by the authors.

Table 6.6: Pairwise comparisons of a multivariate analysis of variance (MANOVA) on the first two axes of the principal component analysis (PCA) and canonical variates analysis (CVA) on members of the genus *Rusa* and the closely related *Cervus kendungensis*, and reclassification rates with jackknifed cross-validation for the CVA.

MANOVA PCA					
Taxon	<i>R. timorensis</i>	<i>R. unicolor</i>	<i>R. sp. (Padang)</i>	<i>C. kendungensis</i>	<i>R. alfredi</i>
<i>R. unicolor</i>	0.150	—	—	—	—
<i>R. sp. (Padang)</i>	0.168	0.190	—	—	—
<i>C. kendungensis</i>	0.168	0.198	1	—	—
<i>R. alfredi</i>	0.168	0.248	1	1	—
<i>R. marianna</i>	0.176	0.742	1	1	1

MANOVA CVA					
Taxon	<i>R. timorensis</i>	<i>R. unicolor</i>	<i>R. sp. (Padang)</i>		
<i>R. unicolor</i>	<0.01*	—	—		
<i>R. sp. (Padang)</i>	0.13	<0.01*	—		
<i>C. kendungensis</i>	<0.01*	<0.01*	<0.01*		

Reclassification rates CVA					
Taxon	<i>R. timorensis</i>	<i>R. unicolor</i>	<i>R. sp. (Padang)</i>	<i>C. kendungensis</i>	Correct %
<i>R. timorensis</i>	3	3	4	0	30
<i>R. unicolor</i>	2	10	0	0	83
<i>R. sp. (Padang)</i>	3	1	2	2	25
<i>C. kendungensis</i>	1	2	1	6	60

Note: Numbers represent p-values. * Significant value ($p \leq 0.05$).

R. = *Rusa*; C. = *Cervus*. Padang = Padang Highlands fossils.

Source: Authors' data.

To obtain a better understanding of the relationship between the Padang Highlands fossils and *C. kendungensis*, *R. unicolor* and *R. timorensis*, a CVA was run on a subsample that included only these species. A scatter plot of the first two axes revealed a better visual separation for these groups than the PCA. (Both the CVA and the PCA scatter plots are shown in Figure 6.5). The Padang Highlands specimens overlapped mostly with *R. timorensis* and were well separated from *R. unicolor* on the first axis. The extinct *C. kendungensis* from Java gave similar scores on the first axis as *R. timorensis* and *Rusa* sp. (Padang) but gave higher scores on the second axis than the other three forms. A MANOVA on the first two axes (see Table 6.6) showed that these differences were significant ($p < 0.01$), with pairwise comparisons indicating that only the difference between *R. timorensis* and *Rusa* sp. (Padang) was not significant ($p = 0.13$). In general, this was confirmed by the reclassification rates for the CVA (also shown in Table 6.6). Of the *R. unicolor* specimens, 83.3% were correctly reclassified with jackknifed cross-validation, suggesting an idiosyncratic shape for this group. *R. timorensis* and *Rusa* sp. (Padang) showed lower reclassification rates (respectively 30% and 25%), but the majority (66%) of the specimens in either of those two groups were reclassified correctly or as part of the other group. Morphologically, these between-group differences were expressed as a less medially extended protocone and a more laterally placed metacone and metastyle, relative to the parastyle and paracone, in specimens with a low score on the first axis (*R. unicolor*). Specimens with a higher score on this axis (*R. timorensis*, *C. kendungensis* and *Rusa* sp. [Padang]) had a more medially extended

protocone and a more medially placed metacone and metastyle. Variation along the second axis was mainly expressed as a less laterally extended parastyle in specimens with a high score (*C. kendengensis*).

For the mesowear analysis, we first assigned teeth to different age classes. The analysed teeth ranged from MWS 2 to MWS 4. In IDAS terms, the sample comprised juvenile (IDAS 2), adult (IDAS 3) and late adult (IDAS 4) individuals. IDAS 3 was represented by the most specimens (over 60%), while the number of IDAS 2 and IDAS 4 specimens was almost even (see Figure 6.6). Our initial sample of teeth included 54 cusps from 27 teeth that each had at least one intact cusp. Because they were damaged, 15 cusps were excluded. Hence, 39 cusps were usable for further analysis (see Table 6.2). Body masses in this sample varied between 123 kg and 292 kg. The range of variability was thus smaller than in the extended sample of *Rusa* sp. The average body mass was 210 ± 44 kg. According to the higher boundary value obtained from the lower-molar dataset, 8 of the specimens represented male individuals and 19 represented females.

Our results illustrated an increase in the range of the mesowear score from juvenile to adult. As the box plots (see Figure 6.6) show, the greatest range occurred in IDAS 3 and the smallest range in IDAS 4. While IDAS 2 and IDAS 3 included cusps at MWS 0, the minimum MWS of IDAS 4 was 1. IDAS 3 had the highest maximum MWS (3.5), while IDAS 2 had the lowest maximum MWS (2.5). The interquartile ranges of the MWS of IDAS 3 and IDAS 4 were identical, while IDAS 2's was smaller. The median MWS of IDAS 3 was higher than that of IDAS 2.

There was also a rise in the mean MWS as IDAS increased: from 1.4 ± 0.8 at IDAS 2 through 1.9 ± 0.9 at IDAS 3 to 2.1 ± 0.8 at IDAS 4 (see Figure 6.6). Therefore, the examined *Rusa* sp. from the Padang Highlands was classified as a mixed feeder at all three examined IDASs. However, there was an increase in the grazing component during ontogeny, resulting in a shift from the browsing side of the spectrum (at IDAS 2) to the grazing one (at IDAS 4).

Discussion

When considering the results of the dietary analysis (see Figure 6.6), we noted that our data showed a Gaussian age distribution. This was to be expected, as the adult stage covers the longest period of an individual's life history (Anders et al. 2011). Therefore, in a naturally accumulated population, most teeth are expected to be at this age stage. The mesowear analysis shows a mixed-feeder signal in all the represented age stages. Enamel stable isotope data published by Janssen et al. (2016), which was collected on a different series of Padang Highlands *Rusa*, showed a predominantly C_3 signal that frequently had $\delta^{13}C$ lower than -12 permil (Janssen et al. 2016 and supplementary data

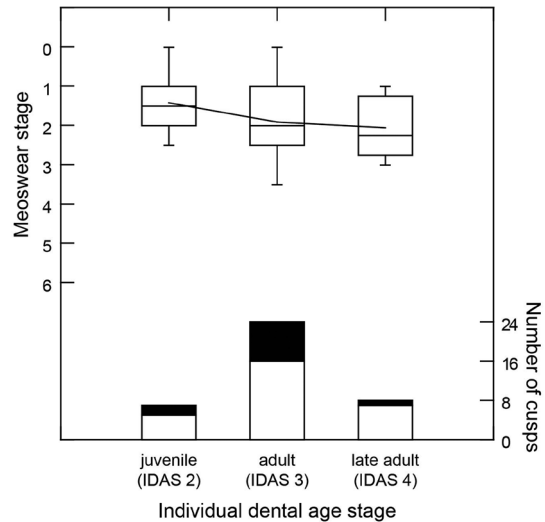


Figure 6.6: Mesowear signal of *Rusa* sp. (Padang Highlands fossils) at different individual dental age stages (IDAS).

Note: The line on the box plot shows the arithmetic mean. The bar chart shows the sample sizes; black = male; white = female. IDASs not represented in the sample are not shown.

Source: Image by the authors.

therein). Integrating these data with our mesowear results indicates that fossil *Rusa* sp. primarily fed on C_3 plants with mildly abrasive components. This is not surprising when we consider that during the Late Pleistocene, the Padang Highlands were probably covered by lowlands rainforest with patches of montane and limestone rainforest (Backer and Bakhuizen van den Brink 1980; Whitten et al. 2000); this environment would have contained plant materials matching the indicated characteristics, such as leaves from trees, shrubs and bushes, or along the rivers, ferns and bamboo leaves. The mesowear signals obtained in the present study did not indicate a diet consisting of dry grasses. However, two cervid teeth in the enamel isotope study displayed a clear C_4 signal (Janssen et al. 2016 and supplementary data therein). Possible candidates for herbaceous plants that follow a C_4 metabolism and that are available in higher densities but generate a mixed-feeder mesowear signal are *Amaranthus viridis* or *Portulaca* sp. (Maria Adelia Widijanto pers. comm. 2021). Unfortunately, none of the teeth examined in our sample were included in the study by Janssen et al. (2016), precluding direct comparison of data about individual molars.

The specimens in our sample evidenced an increasingly variable diet throughout the individual's lifespan (Figure 6.6). Our age-specific datasets indicated a mixed diet with a slight shift from a stronger browsing component to a stronger grazing component with increasing age. This mixed-feeder signal does not necessarily indicate an uninterrupted mixed diet, because a mixed diet may also result from seasonal shifts in vegetation (Rivals et al. 2011; Wirkner and Hertler 2019). However, in extant *Rusa* species (i.e. *R. timorensis* and *R. unicolor*), the juvenile stage persists for a maximum of only 1.2 years, whereas the adult stage has a duration of several years (Tacutu et al. 2018) and thus includes multiple seasons during which the mesowear signal can accumulate. Adults are therefore expected to exhibit a more varied diet than younger individuals. If animals consume a more resistive diet during the dry season, the mesowear signal from older individuals will reflect this seasonal shift. An increase in the grazing component of the signal may thus result from seasonally changing food resources. Yet the isotope data provided by Janssen et al. (2016) did not indicate seasonally varying diets. Moreover, present representatives of the genus *Rusa* are known to be extremely opportunistic feeders (Hedges et al. 2015; Timmins et al. 2015). Such an opportunistic diet will also lead to increasingly variable mesowear signals, obscuring any seasonal variations.

Extant *R. timorensis* and *R. unicolor* live in flexible, temporal groups (Hedges et al. 2015; Leslie 2011; Timmins et al. 2015) containing a higher number of individuals during peak mating season. The herds generally segregate by sexes and combine during the mating season only. This results in a strong numerical bias towards female individuals (Leslie 2011; Timmins et al. 2015). Although in the small subsample studied in our mesowear analysis, such a female-biased ratio is present (19 females to 8 males in our sample), this is unlikely to reflect an ecological pattern, as the precise geographic origin and geological context of our subsample are unknown and may cover a period of several thousand years or more. This is confirmed by our wider analysis of body mass dimorphism in a dataset of lower third molars. Here, the sex ratio reverses to 52 females and 85 males and does not contradict a scenario with several populations of *Rusa* in various seasons.

Besides providing indications regarding sexual dimorphism, the results of the body mass analyses were also informative about the taxonomic status and diversity of our sample of deer fossils. The body mass data indicate that the variability in the fossil dataset is relatively high compared with that of several medium-sized cervids (*Axis axis*, *A. porcinus* and *R. timorensis*), and is closer to that of *R. unicolor*. However, *R. unicolor* is a widely distributed species with a geographic range that extends across large parts of South and Southeast Asia (Timmins et al. 2015). Our sample of this species ($n = 25$) included specimens from across this range and from islands as well as continental

ecosystems. The variability in this extant sample was relatively large for a single species: the sample included specimens of exceptionally heavy body mass (438, 381 and 351 kg) as well as individuals of lower than average body mass (78 kg).

Overall, the data indicated that the fossil *Rusa* sp. sample included specimens of a single species, but from various populations, corresponding to a dataset of mixed geological, chronological and/or spatial provenance. This is in line with our unbalanced male–female body mass ratio, which also may suggest the presence of more than one population.

Levene's test on tooth length and surface area further supports these interpretations, showing differences in the variance of several cervid species, but without indicating variance in the fossils beyond that expected at the species level (Figure 6.3, Table 6.4). In fact, the Sumatran fossil sample showed a relatively high degree of variation, somewhat lower than that of extant *R. unicolor*. With a variance similar to that of *Cervus elaphus*, also a wide-ranging species with several distinct subspecies and populations (Geist 1998), *Rusa* sp. fossils probably represented multiple populations of a single species.

If we assume that only one species is represented in the fossil dataset, that species' taxonomic status remains to be determined. The results shown in our plot of molar length and width (Figure 6.2) support the conclusion by earlier researchers that the large Padang Highlands cervids were similar to members of *Rusa*, especially *R. unicolor* (de Vos 1983; Gruwier et al. 2015). Their conclusion was, however, based on the assumption that tooth size can be used as a reliable indicator of taxonomic affinity. This assumption is only partially supported by our GMM analysis (see Figure 6.4 and Table 6.5). The PCA of the upper third molars supports the hypothesis that *Rusa* sp. was related to *Cervus kendengensis*, *R. unicolor* and *R. timorensis*, but the CVA provided deeper insight into the relationship between these four species. It showed that, after the removal of isometric size effects, the *Rusa* sp. molars had a greater morphological similarity to the *R. timorensis* and *C. kendengensis* molars than to those of *R. unicolor*. The *R. timorensis* molars were particularly similar to the Padang Highlands molars. If we accept that the observed phenotypic variation is phylogenetically driven, the possibility that the Sumatran fossils belonged to a large type of *Rusa timorensis*, or a related form, must be considered.

Although *R. unicolor* is currently the only large cervid species living on Sumatra (Francis 2008; Geist 1998), the notion that this may not necessarily have been the case during the Late Pleistocene is supported by palaeontological evidence from the region. Certain taxa, such as orangutans (*Pongo* spp.), tapirs (*Tapirus indicus*) and tigers (*Panthera tigris*), are known to have been more widely distributed across the Sundanese islands before the Holocene (Earl of Cranbrook and Piper 2009; Piper et al. 2007; van den Bergh et al. 2001). This is also seen in the Padang Highlands assemblages, in which the remains of leopard (*Panthera pardus*) (de Vos 1983), banteng (*Bos sondaicus*) (Hooijer 1958) and long-nosed monkey (*Nasalis* sp.) (Smith et al. 2021) represent taxa that are currently absent from Sumatra but are still found on either Java or Borneo. It is conceivable that *R. timorensis*, a species currently endemic to Java and Bali (Martins et al. 2017), previously had a wider distribution across Sundaland. The large size of the Padang Highlands teeth does not contradict such an interpretation. Several Sundanese taxa, such as *Pongo*, *Muntiacus* and *Bubalus bubalis*, are known to have been substantially larger than their extant conspecifics during the Late Pleistocene (Hooijer 1948, 1958; Medway 1964).

Perhaps the most tantalising evidence to support our hypothesis that *Rusa timorensis*, or a closely related form, may previously have been part of the Sumatran fauna comes from a recent genetic study of the genus *Rusa* by Martins et al. (2017). Although these authors confirmed the validity of the species *R. timorensis* and *R. unicolor*, they found clear evidence for introgression between Javan *R. timorensis* populations and Sumatran *R. unicolor* (Martins et al. 2017). This would suggest that during glacial stages, when the Sunda Shelf emerged, isolated *Rusa* populations on Java and Sumatra were connected and thus hybridised in a contact region (Martins et al. 2017). During the Late Pleistocene, this was by no means an exceptional condition, as for 60% of the last 150,000 years, sea-levels were at least 30 m below the current level, low enough for the narrow Sunda Strait to emerge between the two islands (Voris 2000). Although some palaeoenvironmental reconstructions suggest that the Padang Highlands assemblages accumulated during an interglacial stage (de Vos 1983, but see Chapter 5, this volume), it seems likely that the fossil *Rusa* deer were part of an early stock that was connected to Javan *Rusa* populations at intermittent intervals. Probably the *R. unicolor* populations currently present on Sumatra result mostly from a later dispersal event that brought their ancestors from the mainland (Martins et al. 2017). Whether the early stock consisted of a large *Rusa timorensis*, an extinct form or perhaps a *Rusa timorensis* x *Rusa unicolor* hybrid cannot be inferred from our data with any confidence. In this context, it is worth mentioning that when hybridisation does occur between the two species, individuals reach sizes more like that of *R. unicolor* (Forsyth et al. 2015; van Mourik and Schurig 1985). Whether this would result in large deer with *R. timorensis*-like dental traits in the palaeontological record is unclear. Nevertheless, our data suggest a complex evolutionary history of the genus *Rusa* in Southeast Asia.

Conclusion

Our study demonstrates the use of a multiproxy approach to reconstruct the characteristics of an extinct taxon. In summary, we conclude that the large cervid remains from the Padang Highlands belonged to a large *Rusa* deer, of a different type than extant *R. unicolor* from Sumatra, with morphological traits reminiscent of *R. timorensis*. *Rusa* sp. was reconstructed as a mixed feeder during all ontogenetic stages, and, based on comparison with published carbon isotope data, must have relied on a diet consisting mainly of trees, shrubs and bushes as well as ferns and bamboo leaves.

In the future, more extensive GMM and palaeogenomic analyses of Pleistocene deer could shed further light on the evolutionary history of the genus *Rusa*. Such studies would, ideally, be part of a wider revision of the cervid fossil record from the Sundaic region, including fossils of *R. timorensis* from Java. Additional palaeoecological analyses, such as dental microwear analysis or stable isotope analysis, would complement our mesowear analysis and provide further details about the dietary ecology of the Padang Highlands cervids.

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