



Paleoecology, biochronology, and paleobiogeography of Eurasian Rhinocerotidae during the Early Pleistocene: The contribution of the fossil material from Dmanisi (Georgia, Southern Caucasus)

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ABSTRACT

Rhinocerotidae represents a common element in the Eurasian Pleistocene faunas. Origin, dispersal route, and biochronology of several species are still poorly understood due to gaps in the fossil record, in particular from central Eurasia. A remarkable collection of rhinoceros remains was recovered from the Early Pleistocene site of Dmanisi (Georgia). This collection is unique for the Early Pleistocene Rhinocerotidae records due to its abundance in remains, its age (ca 1.8 Ma) and geographic position (between Eastern and Western Eurasia). Two crania, which display some different morphological traits, are assigned to two different morphotypes and investigated by means of geometric morphometrics using landmarks and semilandmarks. Shapes in lateral and dorsal views of different Rhinocerotini species are compared with the studied crania to infer paleoecological information. The shape in the lateral view reflects ecological niche, in particular feeding type from browsing to grazing, and it also represent taxonomic discrimination. Morphotypes 1 and 2 from Dmanisi fall in two different clusters, corresponding to two different species, notably in lateral view. The results suggest a niche partitioning during the Early Pleistocene of Dmanisi between a browse-dominated and a grass-dominated mixed feeders, or possibly the presence of two ecomorphotypes of the same species. A comprehensive update of the Early Pleistocene occurrences of Eurasian Rhinocerotidae is reported in the discussion on the paleoecology of the extinct Northern Eurasian rhinocerotines.

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1. Introduction

Rhinocerotidae represents a group of large mammals that first occurred during the latest Eocene in North America and later in Eurasia and Africa (Guérin, 1980; Prothero et al., 1986; Antoine, 2002). Among this family, the Rhinocerotina clade, composed by the five extant species and their closest relatives, dispersed through Eurasia and Africa and adapted to different feeding habits, surviving to the extinction and decline of several other groups during the Mio-Pliocene transition such as elasmotheres, brachypotheres, and aceratheres (Guérin, 1980; Heissig, 1996; Antoine, 2002; Geraads,

2010). Among Rhinocerotina, the extinct Northern Eurasian clade (*Stephanorhinus* and *Coelodonta*) reached a high diversity of species and feeding strategies during the Pleistocene, being represented by browser, mixed feeder, and grazer species (Zeuner, 1934; Loose, 1975; Guérin, 1980; Pandolfi and Maiorino, 2016). This group of rhinoceroses has been the subject of several studies over the past decades. Many of these studies were mainly focused on Western European specimens (Cerdeño, 1993; Fortelius et al., 1993; Kahlke, 2001; Lacombat, 2005; van der Made, 2010; Kahlke and Kaiser, 2011; Pandolfi and Tagliacozzo, 2015; Pandolfi et al., 2017, 2019; Rivals and Lister, 2016; Cirilli et al., 2020; Stefaniak et al., in press) with very few articles devoted to Eastern Asian taxa (e.g., Tong, 2012). The temporal and spatial distribution and ecology of Pleistocene rhinoceros species are poorly documented or studied in

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some geographic areas such as Anatolia, Caucasus, and the Near East (Fig. 1), despite the important role that these areas had in the faunal exchange across the Old World, within Eurasia as well as between Eurasia and Africa.

The hominid site of Dmanisi (Georgia), which provides more than 200 specimens referable to the family Rhinocerotidae, is among the Early Pleistocene key localities that might grant a better understanding of the dispersal and evolution of Northern Eurasian species. The archeological site of Dmanisi is located in South Caucasus, on a wedge-like promontory at the confluence of the Pina-sauri and Mashavera rivers, and has been excavated since 1983. The site is dated to 1.85–1.77 Ma by a combination of $^{40}\text{Ar}/^{39}\text{Ar}$ ages, paleomagnetism and biozonation, and yielded a remarkable collection of hominin fossils as well as small and large mammal

remains (Gabunia et al., 2000; Ferring et al., 2011; Lordkipanidze et al., 2013; Cappellini et al., 2019).

Part of the Rhinocerotidae specimens collected at Dmanisi were included in a systematic study by Vekua (1995) and assigned to *Dicerorhinus etruscus etruscus*. The Dmanisi rhinoceros material has been later referred to *Stephanorhinus etruscus*, *Stephanorhinus hundsheimensis*, and *Stephanorhinus ex gr. etruscus-hundsheimensis* (Pandolfi et al., 2017; Krijgsman et al., 2019; Cappellini et al., 2019). However, the rhinoceros specimens collected at Dmanisi remain largely unpublished and the whole collection has to be described in a detailed systematic study.

Here we analyze two crania from the Early Pleistocene of Dmanisi by means of geometric morphometrics to detect morphological traits to infer paleoecology and to discuss about

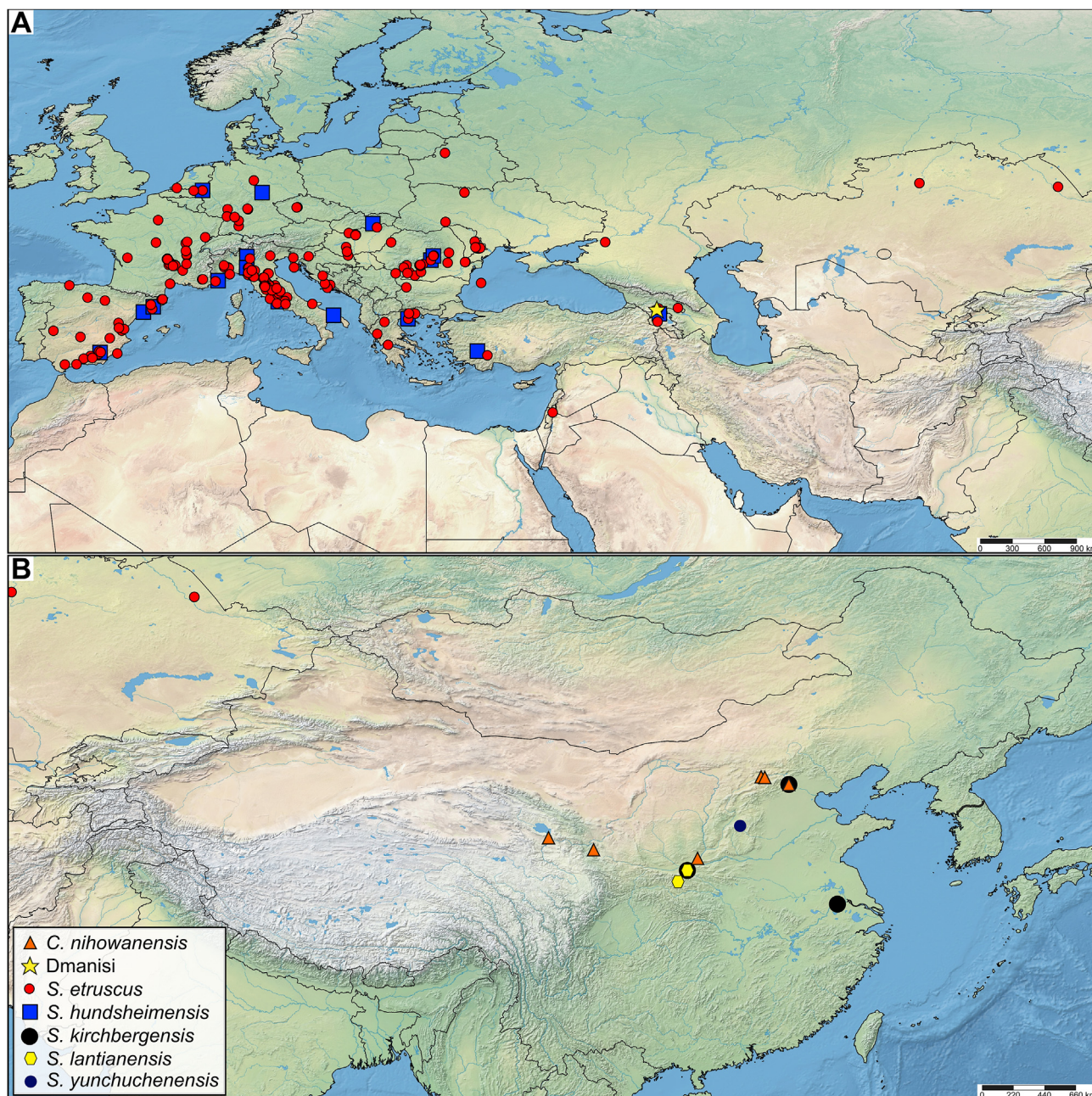


Figure 1. Early Pleistocene records of Northern Eurasian *Stephanorhinus* and *Coelodonta* (after Geraads et al., 2020).

temporal and spatial distribution within the framework of Northern Eurasian Rhinocerotidae.

2. Materials and methods

The Rhinocerotidae material from Dmanisi is curated by the S. Janashia Museum of Georgia, Georgian National Museum, Tbilisi, Georgia (GNM). The material here considered includes two almost complete adult crania: Dm63/64.2.b1y.60 and D3270.

2.1. Comparative material

The specimens from Dmanisi were compared with the Eurasian rhinoceros species referred to the genera *Stephanorhinus* and *Coelodonta* (Supplementary Online Material [SOM] Table S1). Anatomical terminology follows the established protocol by Antoine (2002) and Antoine et al. (2010).

To conduct the geometric morphometric analyses, we collected images of rhinoceros crania, in lateral view ($n = 72$) and in dorsal view ($n = 54$). The data set (revised and updated after Pandolfi and Maiorino, 2016) includes the extant species *Diceros rhinus sumatrensis* and five extinct Northern Eurasian taxa (*S. etruscus*, *S. hundsheimensis*, *Stephanorhinus kirchbergensis*, *Stephanorhinus hemitoechus*, and *Coelodonta antiquitatis*). The specimen list is reported in the SOM Table S1. To investigate shape changes within the same lineage, the sample includes phylogenetically related taxa from the Eurasian Pleistocene (see Pandolfi and Maiorino, 2016).

2.2. Methods

Taking into account the preservation of the investigated crania and the ecological-aims of the analysis, 10 landmarks and 28 semilandmarks were digitized in two dimensions on each cranium in lateral view (Fig. 2A), and 6 landmarks were placed on each cranium in dorsal view (Fig. 2B), using the software tpsDig2 v. 2.17 (Rohlf, 2013). Because the specimens from Dmanisi are partially damaged and do not preserve the complete tooth rows, we excluded from the landmark configuration several points detectable on the zygomatic arches, maxillae and basicrania. Each specimen was scaled using scale bars. We digitized semilandmarks along the dorsal profile of the cranium. Semilandmarks are used to capture morphological information of outlines assumed to be homologous among specimens (Bookstein et al., 2002; Perez et al., 2006). We performed a Generalized Procrustes analysis (GPA; Bookstein, 1991) in R Environment (R Core Team, 2019), using the 'procSym' function in Morpho R package v. 2.0.3 (Schlager, 2013). GPA was used to analyze shape among specimens in the cranial samples. Centroid size (Bookstein, 1986) represents the individual size of specimens and its variation among the considered taxa is shown by boxplots.

Principal component analysis (PCA) on the Procrustes shape variables was performed to identify the orthogonal axes of maximal variation in the data set. A cluster analysis, based on unweighted pair group method with arithmetic mean (UPGMA), was performed on the averaged Procrustes distances of the two data sets to assess similarities between taxa. We used the 'adonis' function from vegan R package v. 2.5–7 (Oksanen et al., 2020) and the 'mycca' function from deformetrics R package v. 0.99 (Piras et al., 2017) to test the presence of allometry in cranial shape variation and therefore the relationship between Procrustes coordinates and centroid size (CS).

3. Results

3.1. Brief morphological description of the crania

We provisionally refer the two Dmanisi crania as Morphotype 1 (D3270) and Morphotype 2 (Dm63/64.2.b1y.60) in the morphological description and in the geometric morphometric analyses.

The two crania collected at Dmanisi lack the zygomatic arches, the palatine area, and the maxillae at the level of the molar row (Fig. 3; SOM Figs. S1 and S2). The two crania preserve the neurocranial portion, the dorsal side of the cranium, and the nasals. Both crania are dolichocephalic and display a concave dorsal profile with evident horn bosses, a partially ossified nasal septum and a ventrally closed auditory pseudomeatus.

Morphotype 1 (Fig. 3D) shows a weak lateral apophysis on the nasals. The rear border of the nasal notch is at the level of the mid of P⁴. The occipital face is rather straight on both crania, but in Morphotype 1, the occipital condyles are more downward inclined. The nuchal crest is more robust in Morphotype 1 than in Morphotype 2. The preorbital constriction is wide. In occipital view, the Morphotype 1 has a rectangular occipital face, with the width at mastoid close to that of the nuchal crest. Furthermore, the cranium shows a straight nuchal crest from the occipital view.

Morphotype 2 (Fig. 3H) does not exhibit a lateral apophysis on the nasals. The rear border of the nasal notch is at the level of mid of P³. The nuchal crest is less robust than Morphotype 1. In dorsal view, the posterior border of the nuchal crest is concave in both the crania, but in Morphotype 2 the external sides are more expanded. The frontal-parietal crests are well separated in both crania (SOM Fig. S1). Morphotype 2 shows a narrower preorbital constriction. In occipital view, the occipital contour is trapezoidal, wider at the mastoids. Furthermore, Morphotype 2 shows a concave dorsal profile of the nuchal crest in occipital view.

The two crania only preserve the premolar row: P², P³, and P⁴ are present (SOM Fig. S2). The ectoloph profile of the premolars on Morphotype 1 is wavy, with evident paracone fold, mesostyle fold, and metacone fold; parastyle and metastyle are long in particular on P⁴. Furthermore, a reduced lingual cingulum is present on the teeth at the entrance of the mediusinus. On Morphotype 2, the ectoloph profile is slightly convex, with a shallow paracone fold and the absence of mesostyle and metacone fold. Parastyle and mesostyle are very short. The teeth, in particular P⁴, are lower crowned than in Morphotype 1 (SOM Fig. S2).

3.2. Brief comparisons

The Morphotype 1 (cranium D3270) is rather long with narrow nuchal crest (length nasal-nuchal crest = 715 mm; length nasal-occipital condyles = 655 mm; height occipital face = 143.31 mm; transverse diameter of the nuchal crest = 129.09 mm; transverse diameter of the mastoids = 184 mm), while Morphotype 2 (cranium Dm63/64.2.b1y.60) is shorter than the other and displays a wider occipital face (length nasal-nuchal crest = 697.73 mm; length nasal-occipital condyles = 647.15 mm; height occipital face = 150.95 mm; transverse diameter of the nuchal crest = 150.76 mm; transverse diameter of the mastoids = 218.20 mm). The crania from Dmanisi are different from the typical *S. etruscus* from Upper Valdarno (Fig. 3F; SOM Figs. S1 and S2), which is characterized by smaller size, lower occipital face, and a rather straight dorsal profile of the cranium. The typical material of *Stephanorhinus hundsheimensis* (Fig. 3E), which is Middle Pleistocene in age, displays a bell-shape occipital face, with a convex dorsal profile of the nuchal crest (in occipital view), and a forward inclined occipital face. Compared with *S. kirchbergensis* (Fig. 3G), both crania from Dmanisi have a length nasal-nuchal

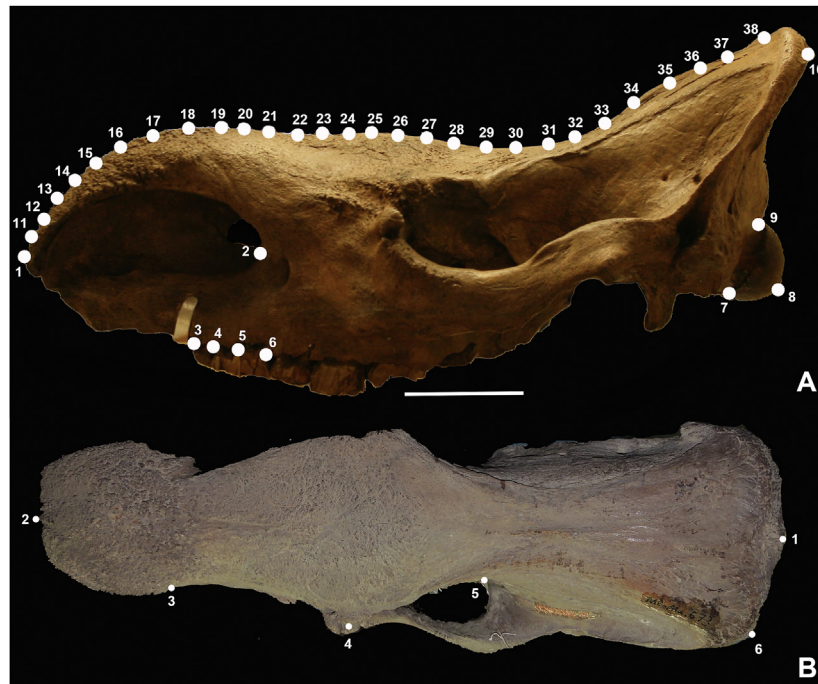


Figure 2. Landmark configuration on cranium in lateral (A) and dorsal (B) views. A: 1, anterior tip of the nasals; 2, rear tip of the nasal notch; 3, anterior border of P^2 (at the base of the crown); 4, P^2/P^3 transition (at the base of the crown); 5, P^3/P^4 transition (at the base of the crown); 6, posterior border of P^4 (at the base of the crown); 7, basal border of the occipital condyles; 8, posterior tip of the occipital condyle; 9, dorsal border of the occipital condyle; 10, posterior tip of the nuchal crest; 11–38 semilandmarks. B: 1, posterior tip of the nuchal crest; 2, anterior tip of the nasals; 3, contact between the nasal rugosity and the lateral border of the cranium; 4, lateral tip of the frontals; 5, postorbital constriction; 6, maximal convexity at the lateral border of the nuchal crest. Scale bar equals 10 cm.

crest greater than the length of nasal-occipital condyles and a higher and straight occipital face. In Middle Pleistocene *S. hemitoechus* (Fig. 3C), the nuchal crest overhangs the occipital condyles, and the occipital face is mainly backward inclined. *Stephanorhinus lantianensis* displays narrower nasals, a shorter nuchal crest, and a lower occipital face. *Coelodonta* spp. differs from the studied crania by having a totally ossified nasal septum, more concave dorsal profile at the frontal-parietal bones, more massive neurocranium with more developed nuchal crest, thicker enamel and more hypsodont teeth.

The teeth of Morphotype 2 (Dm63/64.2.b1y.60) share some common characters with *S. etruscus* and *S. hundsheimensis* (e.g., lingual cingulum, weak paracone fold, brachydont tooth) while the teeth of Morphotype 1 (D3270) displays some features that are not recorded in the observed samples referable to the two above-mentioned taxa (e.g., wavy ectoloph with metacone, mesostyle and paracone folds, long metastyle and parastyle) (SOM Fig. S2).

3.3. Geometric morphometric analyses in lateral view

The first 8 principal components of the PCA explain the 95% of total shape variance. Figure 4A plots PC1 (52.62% of the total shape variance) and PC2 (15.9% of the total shape variance), whereas Figure 4B shows the relationship between PC1 and PC3 (10.87% of the total shape variance). The SOM Figure S3 shows the 3D plot with the relationship between PC1, PC2, and PC3. Negative PC1 values are associated with a cranium showing short nasals, a pre-molar row posteriorly placed (rear border of the nasal notch at the level of P^2) and with the nuchal crest which does not overhang the occipital condyle. This morphology is typical of *D. sumatrensis*, a browser species. Positive PC1 values are associated with a *S. hemitoechus*-like cranium, with long nasals, rear border of the nasal notch between P^3 and P^4 , and a posteriorly forwarded nuchal

crest. Positive PC2 values characterize crania with the rear border of the nasal notch at the level of P^3 , anterior border of the nasals bended downwards, and nuchal crest overhanging the occipital condyle. Negative PC2 values characterize crania with the rear border of the nasal notch between P^3 and P^4 , with high nasal horn boss, and with the nuchal crest not bended posteriorly. In positive PC3 values, the nasals are short, the occipital face is high, and the frontal boss is low, while in negative PC3 the occipital face is low, the frontal horn boss is high, and the nasals are long. As for the entire cranial shape, *D. sumatrensis* is well differentiated from *Coelodonta* spp. and *Stephanorhinus* spp. at negative PC1 values. *Coelodonta* spp. is differentiated from *Stephanorhinus* spp. at positive PC2 values. Within *Stephanorhinus*, *S. hemitoechus* is differentiated from *S. kirchbergensis* at positive PC2 values, while *S. etruscus* and *S. hundsheimensis* occupy a similar position in the morphospace. Dmanisi Morphotype 1 is close to *S. hemitoechus* shape space in PC1-PC2 plot (Fig. 4A), but it is between the shape spaces of *S. hundsheimensis* and *S. hemitoechus* in the 3D plot considering the three PCs (SOM Fig. S3). The Morphotype 2 is close to the shape spaces occupied by *S. kirchbergensis* and *S. hundsheimensis* and falls within the shape space occupied by *S. etruscus* for PC1-PC2 plot (Fig. 4A) and for PC1-PC2-PC3 plot (SOM Fig. S3). The pairwise multivariate analysis of variance (MANOVA) performed on shape data (SOM Table S2) confirms the morphological differences between *D. sumatrensis*, *Coelodonta* and *Stephanorhinus*. The shape, in lateral view, is correlated with size ('adonis', $R^2 = 0.26$, p -value = 0.001; 'mycca', $R^2 = 0.26$, p -value = 0.001; SOM Fig. S4). Notably, low CS values correspond a *D. sumatrensis*-like shape (browser), whereas high CS values correspond a *S. hemitoechus*-*C. antiquitatis*-like shape (grazer). Boxplot (Fig. 5) shows the CS values of the cranium in lateral view for each considered taxon; the values of the Dmanisi' crania fall within the ranges of *C. antiquitatis*, *S. kirchbergensis*, and *S. hemitoechus*, being on average larger than

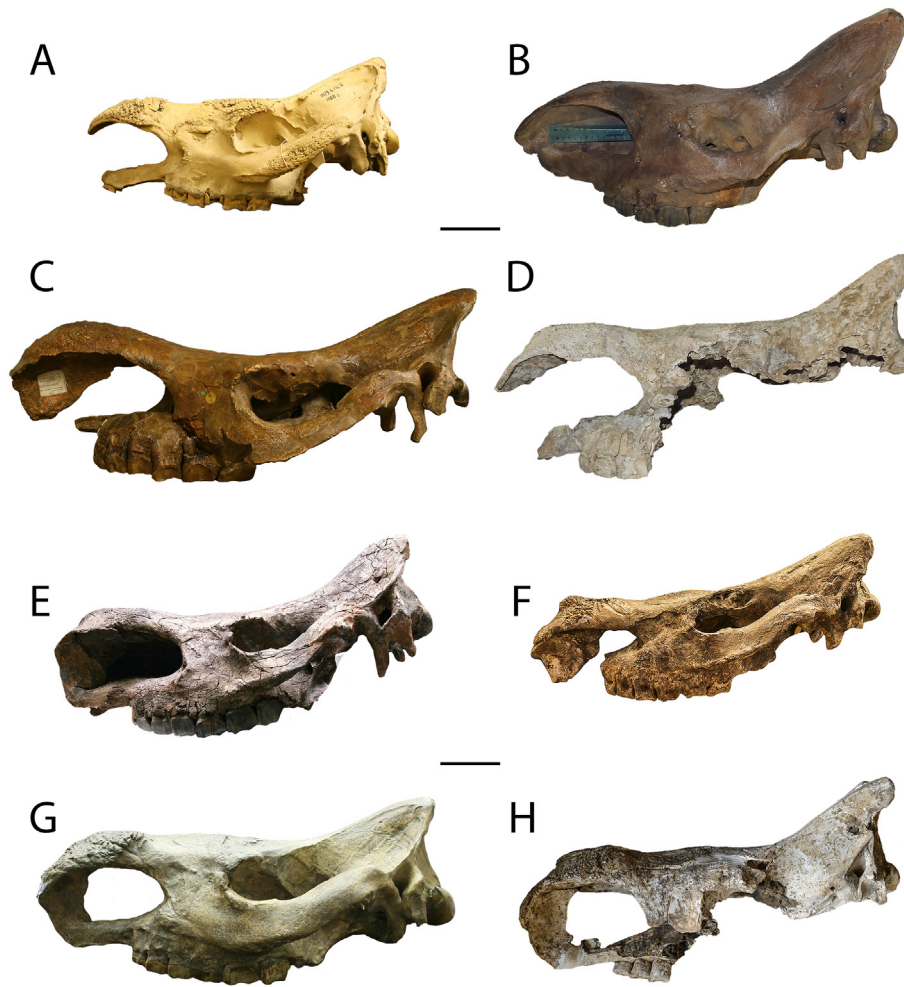


Figure 3. Comparison between the rhinocerotine crania included in this work. A, *Dicerorhinus sumatrensis* (NHMUK 1879-6-14-2); B, *Coelodonta antiquitatis* (NHMUK no code North Sea); C, *Stephanorhinus hemitoechus* (NHMUK 45 205); D, Dmanisi Morphotype 1 (GNM Dm63/64.2.b1y.60); E, *Stephanorhinus hundsheimensis* (MPP no code); F, *Stephanorhinus etruscus* (IGF 756); G, *Stephanorhinus kirchbergensis* (SMNK PAL4254); H, Dmanisi Morphotype 2 (GNM D3270). Scale bar equals 10 cm.

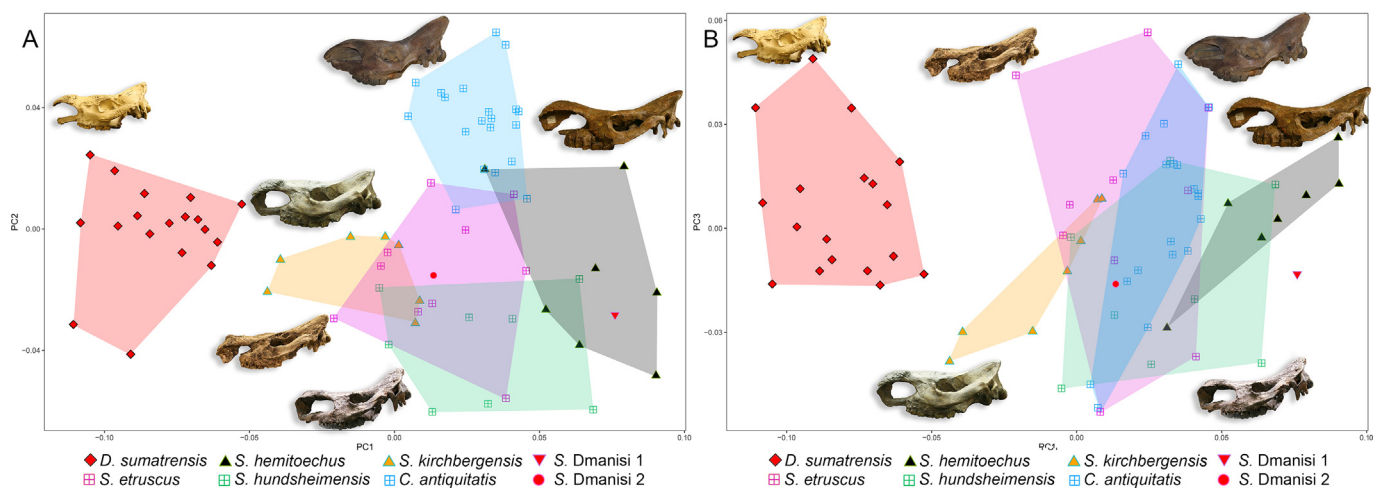


Figure 4. Principal components (PC) scatterplots between PC1 and PC2 (A) and between PC2 and PC3 (B) of the rhinocerotine and Dmanisi crania in lateral view.

D. sumatrensis, *S. etruscus*, and *S. hundsheimensis*. Eventually, the UPGMA dendrogram of morphological similarities (performed on the per-species averaged cranial shape data) of cranial shape in

lateral view (Fig. 6) shows that Morphotype 1 is closer to the mean shape of *S. hemitoechus*, whereas Morphotype 2 is close to the mean shape of *S. kirchbergensis*. *D. sumatrensis* is separated from

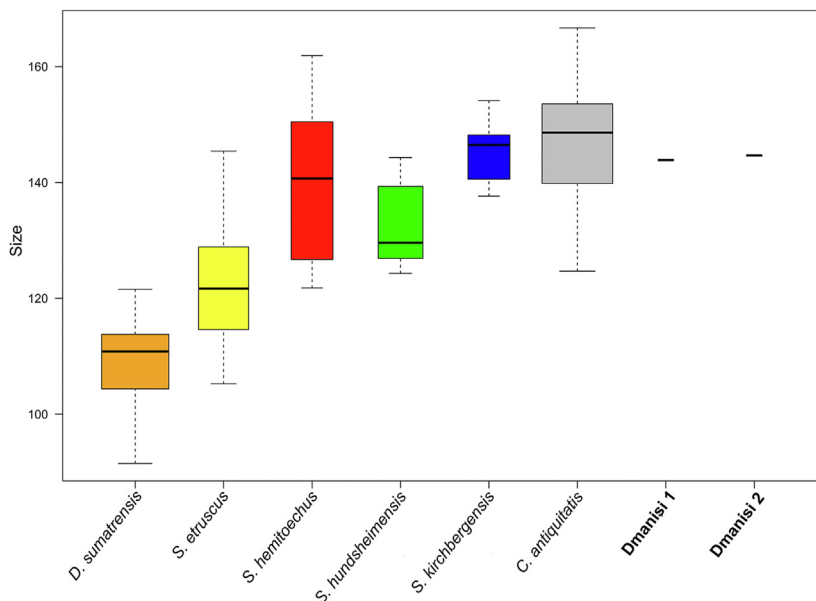


Figure 5. Box plots of size variation (centroid size) of crania (lateral) of the Eurasian rhinocerotines and the Morphotypes from Dmanisi.

Coelodonta spp. and *Stephanorhinus* spp., while *S. etruscus* and *S. hundsheimensis* show similar shapes. The shape area occupied by these last two taxa is wide and partially overlapped, being greatly dispersed along PC axes.

3.4. Geometric morphometric analyses in dorsal view

The first 8 principal components of PCA explain the 100% of total shape variance. Figure 7A shows the relationship between PC1 (49.67% of the total shape variance) and PC2 (22.5% of the total shape variance) whilst Figure 7B plots PC1 and PC3 (10.03% of the total shape variance). The SOM Figure S5 shows the 3D plot with

the relationship between PC1, PC2 and PC3. Crania with a slightly convex posterior border of the nuchal crest and a narrow post-orbital constriction are associated with negative values of PC1, whereas positive values of PC1 cluster cranium with a rather straight posterior border of the nuchal crest and a less narrow postorbital constriction. In positive PC2 values, the nuchal crest is narrow, and the frontals are wide, whereas negative PC2 values characterize the cranium with a wider nuchal crest and narrower frontals. Positive PC3 values cluster smaller crania while negative PC3 values wider. *D. sumatrensis* is well differentiated from *Coelodonta* spp. and *Stephanorhinus* spp. at positive PC1 values and negative PC2 values. *Coelodonta* is quite similar to *S. hemitoechus*

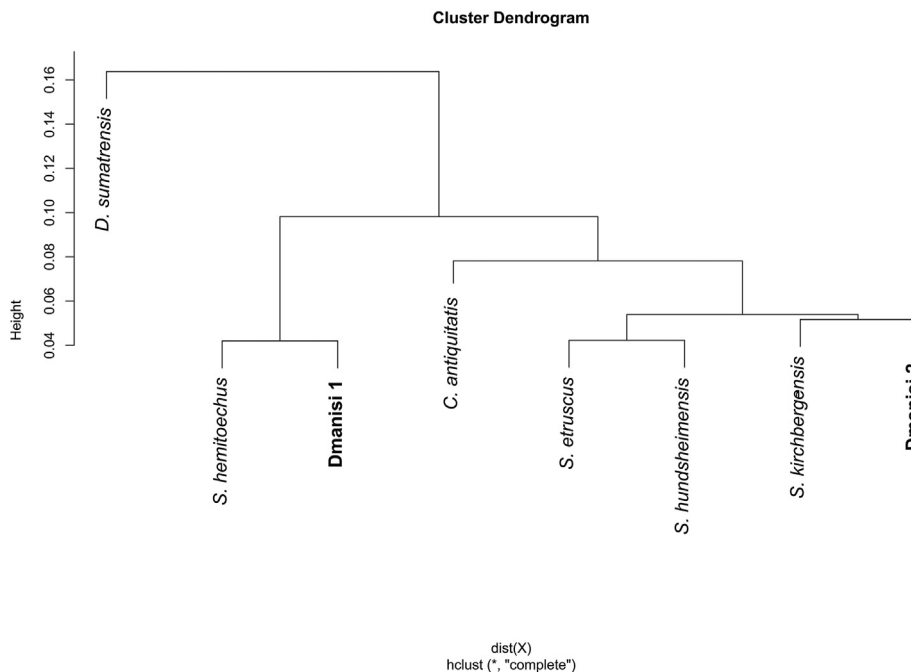


Figure 6. Dendrogram resulting from a cluster analysis based on unweighted pair group method with arithmetic mean (UPGMA) of crania in lateral view.

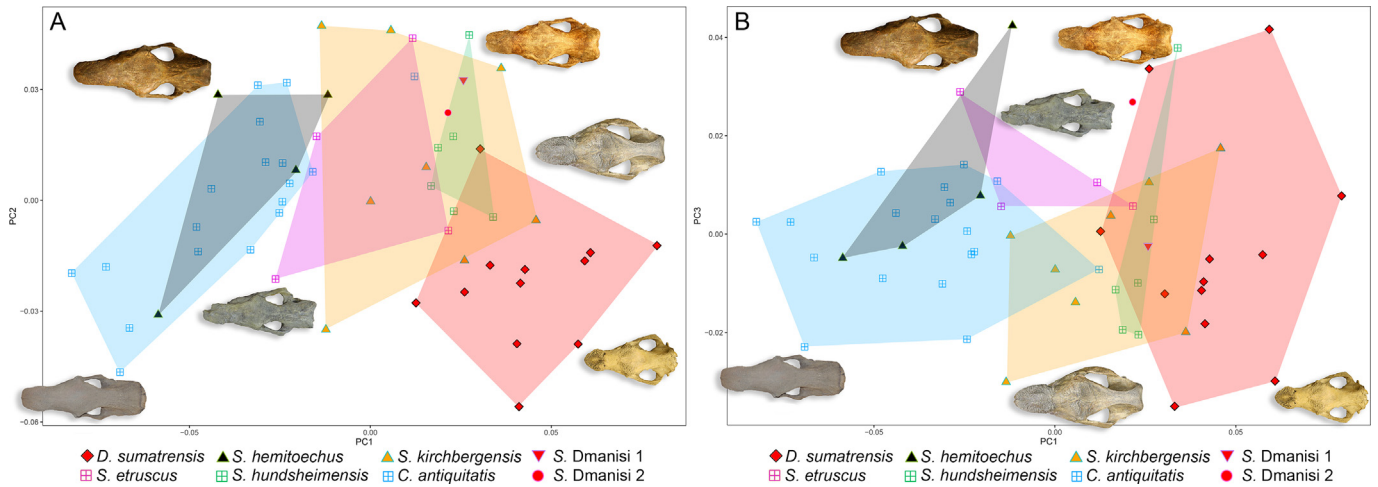


Figure 7. Scatterplots between PC1 and PC2 (A) and between PC2 and PC3 (B) of the rhinocerotine and Dmanisi crania in dorsal view.

but differentiated from the other *Stephanorhinus* spp. The Dmanisi morphotypes are close to *S. etruscus* and to *S. kirchbergensis* for PC1 and PC2. The Morphotype 2 falls within the shape space occupied by *S. kirchbergensis*, *S. hundsheimensis*, and *S. etruscus*. The pairwise MANOVA performed on shape data (SOM Table S3) confirms the shape differences among *D. sumatrensis*, *Coelodonta* spp., and *Stephanorhinus* spp. *Coelodonta* and *S. hemitoechus* are statistically different from the other taxa. The shape, in dorsal view, is correlated with size ('adonis', $R^2 = 0.104$, p -value = 0.001; 'mycca', $R^2 = 0.104$, p -value = 0.001; SOM Fig. S6). Similarly to the results obtained for the lateral view, low CS values correspond a *D. sumatrensis*-like shape, while high CS values correspond a *S. hemitoechus*-*C. antiquitatis*-like shape. Boxplot (Fig. 8) shows the CS values for the analyses of the cranium in dorsal view for each considered taxon; the CS values of the two morphotypes from Dmanisi are relatively different between them and respectively fall within the ranges of *Coelodonta* and *Stephanorhinus* spp. The UPGMA dendrogram of morphological similarities (performed on the per-species averaged cranial shape data) of cranial shape in

dorsal view (Fig. 9) shows that the Morphotype 1 from Dmanisi is close to Morphotype 2 and both are related to the *S. etruscus*-*S. hundsheimensis*-*S. kirchbergensis* group rather than *S. hemitoechus*-*C. antiquitatis* cluster.

4. Discussion

4.1. Sexual dimorphism or different taxa?

The morphological differences detected on the two crania from Dmanisi raised some doubts concerning the presence of sexual dimorphism rather than the occurrence of two taxa.

Extant rhinoceroses exhibit different degrees and traits of sexual dimorphism. Groves (1982) reported a bimodal distribution for the width of the nasals in *Rhinoceros unicornis*, and an average higher value of occipital height and mastoid width in males. Females of *Rhinoceros sondaicus* are larger than males (Guérin, 1980; Groves, 1982) but they display a large overlap in nasal width, despite males have a well-developed horn and females a little developed or

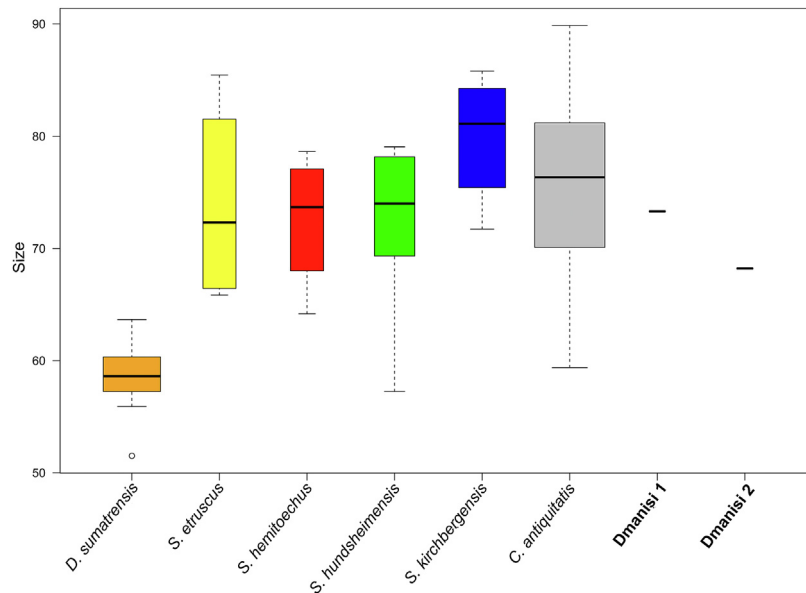


Figure 8. Size variation (centroid size) of crania (dorsal) of the Eurasian rhinocerotines and the Morphotypes from Dmanisi.

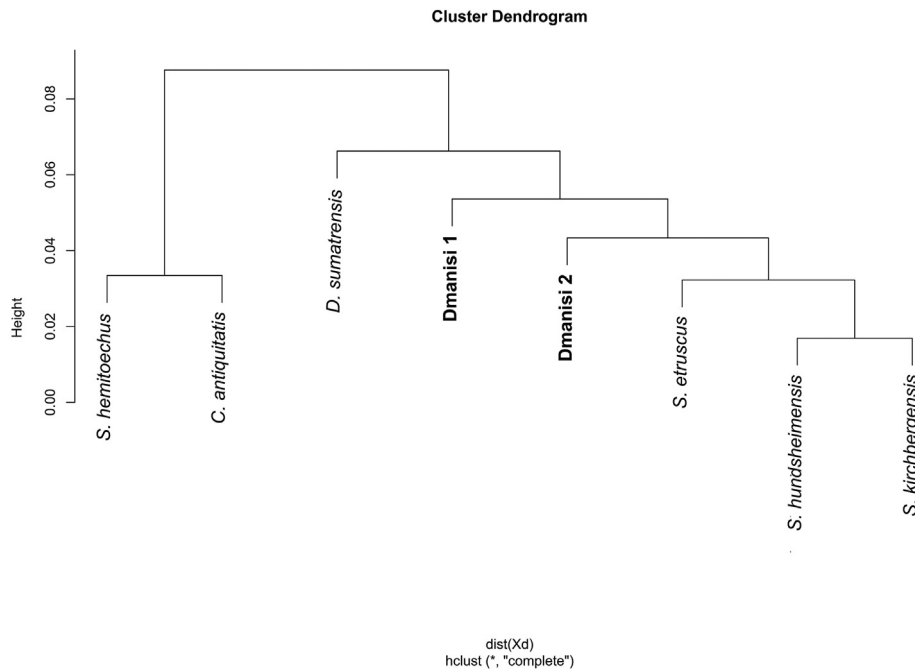


Figure 9. Dendrogram resulting from a cluster analysis based on unweighted pair group method with arithmetic mean (UPGMA) of crania in dorsal view.

absent nasal horn (Pocock, 1946; Groves, 1982). According to Pocock (1946) and Groves (1982), nasal width differs in males and female of *D. sumatrensis*, at least in the mainland and Sumatran forms but not in the Bornean subspecies (cf. Groves, 1982). Furthermore, wild Sumatran rhinoceros males are proportionally larger than females (Groves, 1982). This is partially supported by the results observed in the SOM Figure S4; although crania of extant taxa sometimes lack information about sex and it is not possible to statistically test their differences, it can be noticed that some males specimens (i.e., NHMUK 1952-4-1-2, 1921-2-8-2) have higher CS values with respect to females (i.e., NHMUK, 1921-2-8-4, 72-12-31). Anyway, two distinct groups are not detectable. Owen-Smith (1988) pointed out that *Ceratotherium simum* (the white rhino) is sexually dimorphic in body size and horn size whereas *Diceros bicornis* (the black rhino) is monomorphic. According to Rachlow and Berger (1995), adult males of white rhino have larger horn bases than adult females.

Although documented in extinct Miocene Eurasian rhinocerotids, elasmothers, and aceratheres (Deng, 2001, 2005; Lu et al., 2020), sexual dimorphism has been poorly investigated or understood in the Plio-Pleistocene Northern Eurasian rhinocerotines.

In 1955, Thenius (1955) suggested that the presence or absence of ossified nasal septum could be regarded as a case of sexual dimorphism and that the ossification of the septum was the response to the weight of the nasal horn (larger in males than in females). He suggested that males of *S. etruscus* were characterized by a partially ossified nasal septum, while females were characterized by absence or poorly developed nasal septum. Loose (1975) argued against this hypothesis and also claimed that, for the extant African species, the variability of nasal horns is so large that it is impossible to correlate its development with the sex of the animal. Furthermore, Loose (1975) reported that he was not able to find any sex characters in the cranium of the African species and *D. sumatrensis*. Borsuk-Białynicka (1973) suggested that some of the craniometric characters of *C. antiquitatis* display an undoubted, not always, distinct bimodality. This concerns the width of occiput (measured above the external acoustic meatus = width at the mastoids), maximum length, the orbit-nuchal crest and orbit-nasal

notch lengths and the width of cranium in the region of zygomatic arches. The sexual dimorphism on this species, however, is partial; its ranges for males and females overlap to a considerable extent, which slightly obliterates the bimodal character of the distribution (Borsuk-Białynicka, 1973). Nothing has been done on *Stephanorhinus* although a few old articles reported a distinction on males and females, probably on the basis of the nasal width (Azzaroli, 1962). Here, a relationship between shape and size, similarly to *D. sumatrensis*, seems to be partially observable in *S. etruscus*, even if there is no certainty that this correlation can be related with sexual dimorphism rather than geographic variability; this topic needs to be detailed investigated pending the availability of a larger sample size. The width of the nasal (WN) on the crania from Dmanisi differs of only ca. 10.5 mm (D3270 WN = 146 mm; Dm63/64.2.b1y.60 WN = 135.50 mm), too low to eventually distinguish between a male and a female. Borsuk-Białynicka (1973) assigned long crania with wide occiput at the mastoid and wide zygomatic arches to males. The longer cranium from Dmanisi (D3270) is characterized by a narrower and lower occiput in respect to the other. Difference in shape morphology of the occiput has been normally indicated as diagnostic for Pleistocene and extant species (Azzaroli, 1962; Loose, 1975; Guérin, 1980; van der Made, 2010; Pandolfi et al., 2013) and, at present knowledge, we suggest that the morphological differences detected on the two Dmanisi' crania cannot be linked with a sexual dimorphism. Tooth morphologies are normally useful to discriminate among some Pleistocene species (e.g., *S. kirchbergensis*, *S. hemitoechus*, *Coelodonta* spp.), but not (or partially) for some others (*S. etruscus*, *S. hundsheimensis*). The systematic attribution of the late Early Pleistocene Eurasian rhinoceroses is strongly debated and, pending the description of all the remains collected at Dmanisi, we provisionally referred the studied specimens as *S. ex gr. etruscus-hundsheimensis*.

4.2. Paleocology and ecomorphotypes

The head posture and the shape of the occipital area have been used in the past to infer the feeding habits of extant and fossil rhinoceroses (Zeuner, 1934; Loose, 1975; Bales, 1996; van der Made,

2010). A number of recent ecological studies centered on the orientation of the semicircular canal in the inner ear to reconstruct the head posture and infer dietary habit in ungulates (Schellhorn, 2018; Benoit et al., 2020). Although it seems that the inner ear in extant Rhinocerotidae provides information on the usual head postures linked to feeding preferences (Schellhorn, 2018), some doubts on the validity of this correlation were also raised (Benoit et al., 2020). Zeuner (1934) suggested that different angles between the occiput and the palate can be related with a browser or grazer habit. In particular, the author reported a small angle in grazers, such as *C. simum*, and a larger angle in browsers, such as *Rhinoceros sondaicus*. Loose (1975) underlined these characters in Pleistocene fossil rhinoceroses and concluded that *S. hemitoechus* is apparently the only exclusively grazing species while the Zeuner's measurements of *Coelodonta* suggest no adaptation to grazing. Bales (1996) analyzed the head shape variation in extant rhinos by means of two-dimensional geometric morphometrics, suggesting a relationship between feeding adaptations and cranial shape. Grazer species are characterized by a backward oriented occipital face with an elongated nuchal crest (that overhangs the occipital condyles), while browsers have different head posture with a forward inclined occipital face. Recent studies suggested that *C. antiquitatis* was mainly a grazer, although, at different times of the year and depending on the region, its diet was also supplemented by leaves of shrubs and trees while *S. kirchbergensis* was a flexible browser (Stefaniak et al., in press). The browser habit of *S. etruscus* seems to be confirmed by mesowear and microwear analyses (Rivals and Lister, 2016) performed on specimens from the Red Crag Nodule Bed (latest Pliocene ca 3–2.5 Ma) and East Runton (ca 1.8 Ma). Yet, the Red Crag Nodule Bed specimens most probably represent a distinct species close to '*S. miguelcrusafonti*' rather than *S. etruscus*. Kahlke and Kaiser (2011), conducting a mesowear analysis on teeth from two Middle Pleistocene German localities, highlighted that *S. hundsheimensis* was the most ecologically flexible rhinoceros of the Palaearctic Plio-Pleistocene. In early Middle Pleistocene of England (Pakefield and Boxgrove), *S. hundsheimensis* has higher mesowear scores than *S. etruscus* suggesting that the Hundsheim rhinos was restricted to the mixed-feeding ecospace, varying from browse-dominated to graze-dominated mixed feeding. According to Rivals and Lister (2016), *S. kirchbergensis* had browser traits and it was adapted to feed on leaves from trees or shrubs and also included fruits and seeds in its diet, whilst mesowear and microwear patterns indicated *S. hemitoechus* as grazer or mixed-feeder with an adaptation to more open environments in respect to *S. etruscus* and *S. hundsheimensis*. In addition to Rivals and Lister (2016), Rivals and Ziegler (2018) confirmed the browsing diets for *S. kirchbergensis* and grazing traits for *S. hemitoechus* based on mesowear and microwear from two Middle Pleistocene sites in Germany (Heppenloch and Steinheim). Plant remains on teeth and mesowear analyses of *S. kirchbergensis* also supported it was a browser species (van der Made and Grube, 2010; Saarinen et al., 2016) or was a mixed feeder (Kirillova et al., 2017), with a diet consisting of herbaceous leaf and woody plants. A certain degree of flexibility (in diet and environment) both in *S. kirchbergensis* and *S. hemitoechus* have been reported by some scholars, with tendency to be respectively a browse-dominated mixed feeder and a grass-dominated mixed feeder (Hernesniemi et al., 2011; van Asperen and Kahlke, 2015; Saarinen et al., 2016; Rivals and Lister, 2016). The position of the cranial shape within the morphospace here reported would reflect these differences in feeding strategy among the Pleistocene Northern Eurasian rhinoceroses. *S. kirchbergensis* is placed between *D. sumatrensis* and *S. etruscus* suggesting crania

have a browser-type shape. *S. hundsheimensis* and *S. etruscus* have an intermediate position between *S. kirchbergensis* and *S. hemitoechus* and partially overlap. The different position in morpho-space of Morphotypes 1 and 2 from Dmanisi would suggest the presence of two different feeding strategy, a browse-dominated and a grass-dominated mixed feeder, and therefore a niche partitioning of the Dmanisi rhinoceroses or possibly the presence of two ecomorphotypes of the same species. The cranial shape in extant rhinoceroses can be indeed affected by changes in dietary habit during the life span of the animal, as demonstrated in captive individuals of Asian species from zoos (Groves, 1982). In respect to the wild counterpart, captive *R. unicornis* crania are generally characterized by smaller size, and proportionally broader zygomatic arches, higher occiput, and broader mastoids. These abnormalities could be related with the captive condition, being the animals fed from a trough on the floor (Groves, 1982). In particular, the development of rugosities on the zygomatic arches would be related to excessive use of masseters (probably to cope with some unaccustomed dietary staple according to Groves, 1982). A similar condition seems to be present in *R. sondaicus*, while *D. sumatrensis* appears to have been affected by captivity in different ways (Groves, 1982): evidently affected, with a narrow occiput probably due to positioning of the feeding troughs (2 observations); unaffected (2 observations); and probably adversely affected (1 observation). Accordingly, different environmental pressures, such as climatic oscillations, could affect feeding conditions and influence some cranial features thus resulting in different morphs of the same species. The few available data on rhinoceroses, anyway, do not highlight changes in the main tooth morphologies between wild and captive specimens thus suggesting they can be, at present, retained as differences at specific level. Considering the morphological differences of the premolars between the two crania from Dmanisi, they could not be considered as ecomorphotypes of the same species even if this hypothesis cannot be completely ruled out. A comprehensive study on changes in cranial shape within the same species during climatic oscillations or different environmental conditions has to be yet performed and discussed under the light of both on extant and extinct rhinoceros cranial variability.

The paleoclimatic and paleoenvironmental data from the site of Dmanisi highlighted an environment similar to African savannah (Messenger et al., 2010b) or Mediterranean-type climate (Blain et al., 2014) around 1.77 Ma. Notably, paleobotanical studies (pollens, phytoliths, fruits) suggested a composite temperate ecosystem with dominant grasses and an increase in aridity contemporaneous with the human presence (Messenger et al., 2008, 2010a, b). Small mammals (rodents) and herpetofauna suggested warm and arid conditions in the site, with open and dry environments and some open woodlands and bushy areas (Agustí and Lordkipanidze, 2011; Blain et al. 2014; Cappellini et al., 2019), while large mammals suggest a mosaic-like landscape with remarkable differences in humidity and the presence of forested areas (suggested by the abundance of cervids) (Cappellini et al., 2019). Accordingly, the environmental reconstruction at Dmanisi, with the presence of a dominant open environment and forested or open woodland areas, would support the presence of two different feeding habits or two ecomorphs and a possible niche partitioning in Rhinocerotidae.

Niche partitioning among rhinoceroses also occurs nowadays in extant African and Asian species. In Africa, the true grazer *C. simum* co-occur with the browser species *D. bicornis* since the Early Pleistocene (Geraads, 2010); similarly, in South East Asia, *R. unicornis* co-occurred with *R. sondaicus* during the Pleistocene (Antoine, 2012). In the case of co-occurrence of two browsing

species such as *D. sumatrensis* and *R. sondaicus*, competitive interactions are avoided by using different habitats (Groves and Kurt, 1972; Groves and Leslie, 2011).

4.3. The Early Pleistocene record of Northern Eurasia: the state of the art and the implication of the Dmanisi findings

The presence of at least six species during the Early Pleistocene is well-documented in Northern Eurasia: *S. etruscus* (Falconer, 1868), *S. hundsheimensis* (Toula, 1902), *Stephanorhinus yunchuchenensis* (Chow, 1963), *S. lantianensis* (Hu and Qi, 1978), *S. kirchbergensis* (Jäger, 1839), and *Coelodonta nihowanensis* (Kahlke, 1969).

S. etruscus occurs for the first time in Europe during the latest Pliocene, being represented by a few remains close in size and morphology to Upper Valdarno specimens and then smaller than *Stephanorhinus jeanvireti* generally reported from latest Pliocene/earliest Pleistocene sites and recently documented in a younger locality (Guérin, 1980; Mazza, 1988; Cerdeño, 1993; Pandolfi and Marra, 2015; Pandolfi et al., 2015, 2017, 2019; Cirilli et al., 2020). The origin of *S. etruscus* is still poorly understood, but in recent cladistic analyses, it is placed in a sister-taxon relationship with “*Dihoplus*” *pikermiensis* (Antoine and Saraç, 2005). Pandolfi and Marra (2015) and Pandolfi et al. (2015, 2017) suggested that *S. etruscus* was the sole rhinoceros’ species in Western Europe from ca 2.5 Ma to ca 1.2 Ma. *S. etruscus* has been reported in around 200 localities, of which 66 in Italy, 33 in France, and 24 in Spain, confirming its role as one of the most abundant species during the Pleistocene of Eurasia (Fig. 10; Geraads et al., 2020). Furthermore, *S. etruscus* persisted in central Italy and Spain until the end of the Early Pleistocene (Cerdeño, 1993; van der Made, 2010; Pandolfi and Marra, 2015; Pandolfi et al., 2017). The presence of the Etruscan rhino during that time in Spain is here confirmed at Huéscar-1,

Granada Province, around 0.8 Ma (Cerdeño, 1993; van der Made, 2010; Ros-Montoya et al., 2012; Pandolfi et al., 2017), based on direct observations of material housed at MNCN (LP) and the revision of the specimens published by Santafé and Casanovas (1987) as *Dicerohinus etruscus brachycephalus*.

The first occurrence of *S. hundsheimensis* in the Iberian Peninsula was previously placed at ca. 1.6 Ma, in the site of Venta Micena (Orce; Santafé and Casanovas, 1987; Ros-Montoya et al., 2012; Madurell-Malapeira et al., 2014), but the morphological and morphometric features of the specimens from Venta Micena suggest instead an attribution to *S. etruscus* (see Cerdeño, 1993; van der Made, 2010; Pandolfi and Erten, 2017). *S. hundsheimensis* was also reported at Barranco León 5 and Fuente Nueva 3, in the Guadix-Baza basin (dated between 1.4 and 1.3 Ma) by Lacombe (2010). The latter author also suggested that the specimens from both localities are similar to the specimens identified at Pietrafitta (Perugia, central Italy), which are undoubtedly morphologically and morphometrically similar to *S. etruscus* (van der Made, 2010; Pandolfi and Petronio, 2011; Pandolfi et al., 2017; Cirilli et al., 2020), except for a skeleton of one individual which displays some differences with *S. etruscus*, being more similar to *S. hundsheimensis* (see discussion in Cirilli et al., 2020). *S. hundsheimensis* is correctly reported in the Vallès-Penedès Basin (ca. 1.2–0.78 Ma; Madurell-Malapeira et al., 2010, 2014), at Untermaassfeld (ca. 1.1 Ma; Kahlke, 2001), in the Mygdonia Basin at Platanochori-1 and possibly Apollonia (latest Villafranchian, ca. 1.2 Ma) (Konidaris et al., 2015) and in Italy at Lefte (ca. 1.1 Ma; Pandolfi and Erten, 2017). Few and scanty remains collected at Gombasek (Slovakia, latest Early–early Middle Pleistocene) resemble *S. hundsheimensis* whilst in Romania, the species is recorded in some latest Early Pleistocene localities (Betfia V, Budesti, Feldioara-Cetate; Pandolfi et al., 2017; Pandolfi and Erten, 2017). Accordingly, *S. etruscus* and *S. hundsheimensis* were both present in Europe during the latest Early Pleistocene

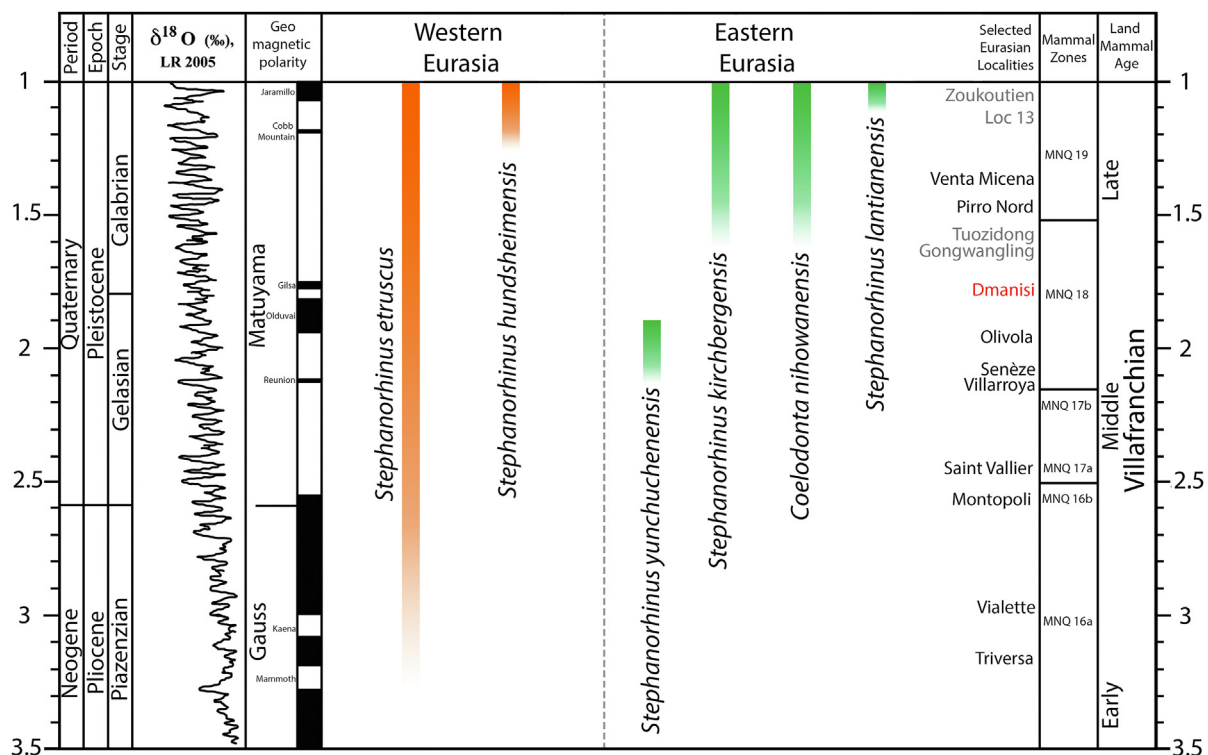


Figure 10. Chronological distribution of Northern Eurasian rhinocerotines during the Early Pleistocene (after Tong, 2012; Pandolfi et al., 2017; Pandolfi and Erten, 2017; Geraads et al., 2020).

(Fig. 10) but probably they occupied different habitats, being documented in different localities (Fig. 1).

At the present, *S. yunchuchenensis* is recorded only in one locality in Yushe Basin (Shanxi Province, Early Pleistocene), even if the exact location is uncertain; the age is estimated on regional geological information (Tong, 2012). Anyway, the morphology of the cranium and teeth referred to this species, closely resembles *S. kirchbergensis* (as also noted by Chow, 1963). The expanded nasal bones are similar in shape and size to that observed in *S. kirchbergensis* cranium SMNS 6617.2.12.67.3 and can be regarded as a sexual dimorphic trait. Accordingly, the Chinese species is here considered as a junior synonym of the Merck' rhino.

S. lantianensis was established on an almost complete cranium of an old individual; the species was at first documented at Gongwangling (Lantian Country, Shaanxi Province) with a late Early Pleistocene age (ca. 1.15 Ma; recently re-dated at 1.6 Ma: Zhu et al., 2015). A *Dicerorhinus* sp., possibly *S. lantianensis*, is reported at Longgupo by Liu et al. (2015).

S. kirchbergensis is recorded earlier in East Asia than in Western Europe. The species has been reported in Early Pleistocene localities of China such as Gongwangling (latest Early Pleistocene: Liu et al., 2015) and Zhoukoudian Loc. 13 (Early/Middle Pleistocene boundary: Tong, 2012). Recently a juvenile right maxilla from Tuozidong cave deposits (ca 1.6 Ma: Dong et al., 2013) has been assigned to this species.

The grazer *C. nihowanensis* also occurred during the Early Pleistocene (Deng et al., 2011; Tong and Wang, 2014) but its records are confined to the eastern area of China. It co-occurs in Nihewan Basin with *S. kirchbergensis* (Tong and Wang, 2014; Geraads et al., 2020), thus providing the evidence of a niche partitioning during the Early Pleistocene.

The scanty record from Kazakhstan and neighbor areas during the considered time span does not allow to depict a clear framework of the species there represented (even if dubitatively assigned as *S. etruscus*; Geraads et al., 2020 and reference therein) or to detect a niche partitioning among the rhinoceros species (at present no localities with more than one species are documented: Fig. 1). The Dmanisi record would be the evidence of a complex association and niche partitioning in Eurasian stephanorhine rhinoceroses during the Early Pleistocene. Furthermore, the morphological differences between the studied crania and the typical Pleistocene Western Eurasian taxa would suggest a deep revision of the late Early Pleistocene rhinoceroses doubtfully assigned alternatively as *S. etruscus* or *S. hundsheimensis* or closely related forms and provide the evidence of the importance of a deep systematic study of the Dmanisi' remains.

5. Conclusions

Large terrestrial mammals' adaptations to different environments correspond to the variation of different food item they can eat, and therefore in variation of cranial morphologies. In rhinoceroses these variations can be detected on teeth and head posture, and different lineages evolved convergent traits, in particular to feed on grasses. Rhinoceros teeth morphologies are strongly influenced by the wear stage and several features change with the age of the animal; it is therefore difficult to investigate and compare quantitatively the different shapes considering the teeth only. It would be instead possible to detect feeding strategies by investigating the cranial shape within the same lineage. The rhinoceros records from Dmanisi offer the opportunity to test this hypothesis, as two crania referable to *Stephanorhinus* come from this site. The crania display some morphological differences that at present cannot be linked with intraspecific variability and sexual dimorphism. Although a detailed study on the cranial shape of

Pleistocene rhinoceroses through time and space as well as on ontogenetic patterns is needed, the recent evidence on feeding habits agrees with the position of the crania here studied within the morphospace allowing to infer the presence of two different feeding types or ecomorphotypes at Dmanisi. A similar condition, even if testified among extant taxa, is not documented in Europe during the Early Pleistocene, being that area occupied alternatively by *S. etruscus* (a browser) and *S. hundsheimensis* (highly flexible feeder) but is instead present in Eastern Asia. The coexistence of two morphotypes at Dmanisi fits well with the patchy environments that characterize the Dmanisi site at 1.85–1.77 Ma.

Author contributions

LP and LR conceived the paper; D.L. and M.B. provided the Dmanisi material; LP and LR collected the data on Dmanisi rhinoceroses; LP collected the data set, performed the analyses and the comparisons, revised the rhinoceros occurrences; LP wrote the paper with the contributions from SBL, OC, MB, DL, LR; LP, SBL, OC, MD, DL, LR discussed the results.

Competing interest

The authors declare no conflict of interest.

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Supplementary Online Material

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