PALAEOECOLOGICAL INVESTIGATIONS ON PLIO-PLEISTOCENE EUROPEAN RHINOCEROSES (GENUS *STEPHANORHINUS*): POWDER X-RAY DIFFRACTION, CARBON ISOTOPE GEOCHEMISTRY, TOOTH WEAR ANALYSES AND BIOMETRY

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INTRODUCTION

The PhD project aims to a palaeoecological investigation based on classical palaeontological morphobiometry, supported by geochemical and X-ray diffraction analyses, focusing on four rhinoceros species of the European Plio-Pleistocene genus *Stephanorhinus*: *S. megarhinus* (Pliocene), *S. elatus* (Late Pliocene), *S. etruscus* (Early Pleistocene) and *S. hundsheimensis* (late Early-Middle Pleistocene).

S. megarhinus (de Christol, 1834) is a slender and large sized rhinoceros with brachyodont teeth from the Pliocene deposits of Europe and is morphologically relatively similar to the Late Pliocene *S. elatus* (Croizet & Jobert, 1828), that is slightly smaller in size. *S. etruscus* (Falconer, 1868) is a small browsing rhinoceros characteristic of the Early Pleistocene deposits of Western Europe. Unfortunately, very little is known about the ecology of these ancient rhinoceros species because the previous works, in many cases quite old, reported just morphological descriptions (*e.g.*, Azzaroli, 1962; Guérin, 1972, 1980, 1982; Mazza, 1988; Pandolfi, 2013).

From the late Early to the Middle Pleistocene the species *S. hundsheimensis* (Toula, 1902) is recorded in the whole Europe, it is a generalist species and thus it deserves more attention on its diet and adaptive possibilities. Moreover *S. hundsheimensis* represents an interesting case study to test the size and proportions variations along its chronological and geographical range. Fortelius *et al.* (1993) and Lacombat (2006, 2009) record a noticeable dimensional variation through time with a smaller-sized form from the Upper Villafranchian and a larger one from the Galerian. Furthermore, a huge geographic variability is known among coeval populations in both morphology and size, with the latter increasing from low to high latitudes (Lacombat, 2009; Ballatore & Breda, 2013). For these reasons, *S. hundsheimensis* is very important to evaluate the adaptive meaning of these size changes against the changing climatic and environmental parameters in Quaternary rhinoceros.

In the Middle Pleistocene, other two species of the genus *Stephanorhinus* were present (but they are not included in PhD research project): *S. hemitoechus* (Falconer, 1868), known as "the steppe rhinoceros", a robust medium-large sized rhinoceros on the most grazer side of the *Stephanorhinus* browser-grazer spectrum, and the larger *S. kirchbergensis* (Jäger, 1839), known as "the forest rhinoceros", that shows the highest specialization in browsing.

Using rhinoceroses as working taxon is useful due to their extremely rich record in the Plio-Pleistocene deposits, since the taxon was one of the most abundant in the herbivorous communities, then macromammals lead information at a regional geographic scale, that is essential in order to reconstruct evolutionary dynamics at macroregional level (Europe). Moreover, these forms show close relation to the modern rhinoceroses so a strict comparison is possible. Finally the selected time span is useful due to the richness in the fossil record and to the fine stratigraphic resolution that allows testing evolutionary issues.

PALAEOECOLOGICAL INVESTIGATIONS

The ecological investigations should bring to a better understanding of the evolutionary history of the genus *Stephanorhinus* in relation to the changing environmental conditions. The four species on the focus of our research show a wide degree of adaptability to different environmental contexts from wet woodland to dry

steppe and, considering the strong climatic variations occurred during the time range of their existence, the investigation of their palaeoecology (size variation, diet adaptation, niche partitioning) is of paramount interest to shed light on the evolution of natural systems in the past. This concentrates in particular on the diet through an interdisciplinary approach.

Carbon isotope and paired powder X-ray diffraction (XRPD) analysis, are useful mineralogical techniques available for palaeontological research, and the interdisciplinary approach includes mesowear analysis, 3D microwear texture analysis and morphology-biometry, which are among the most innovative palaeoecological techniques. They lead to the acquisition of new information on the animals' life condition, on the competition with other taxa, and on the climatic variation and consequent adaptive processes, they can provide a better knowledge of the environmental condition in the past. In particular, the investigated time span, from the Late Pliocene to the Middle Pleistocene, is a period characterized by strong climatic fluctuations that became more and more severe in the Middle Pleistocene, forcing the latest *S. hundsheimensis* populations to drastic adaptations before they become extinct.

Among the investigated species, *S. megarhinus* (Pliocene), *S. elatus* (Late Pliocene), *S. etruscus* (Early Pleistocene) and *S. hundsheimensis* (Middle Pleistocene), only the last one has already been palaeoecologically investigated, therefore our work aims to provide the first palaeoecological analysis of the earlier species and add some information on the variability of *S. hundsheimensis*.

PALAEOECOLOGICAL INFERENCES FROM CARBON ISOTOPE ANALYSIS

For the carbon isotope analysis, we collected rhinoceroses' samples from the Pliocene to the Middle Pleistocene. Since bone and dentine are poorly crystalline tissues, recrystallization could have occurred during fossilization processes, so we used powder XRPD analyses to assess the validity of the isotopic signal. As a result the crystal size increases in relation to the increasing *c/a* ratio, therefore it is correlated with the carbonate substitution: Type B structural carbonate inclusion, replacing for bone phosphate, leads to the increase of *c* and to a decrease of *a* cell parameters (Michel *et al*., 1995). Since crystal size is a good predictor in estimating the biogenic signal retention, we can exclude the samples with high crystallinity.

Concerning the dietary information derived from the carbon isotope analysis, C4 plants have a less negative $\delta^{13}C$ value than C3 (Bender, 1971; Smith & Epstein, 1971), we gained that the rhinoceroses *S. hundsheimensis* and *S. kirchbergensis* from Mosbach2 showed the same $\delta^{13}C$ value, comparable with the modern *Rhinoceros unicornis*. These isotopic results are in good agreement with the mesowear data that indicate flexible diet including hard food with soft leaves, as a generalist subsistence strategy (for the species *S. hundsheimensis*, Kahlke & Kaiser, 2011; for the species *S. kirchbergensis*; Van Asperen & Kahlke, 2015). The samples from the earlier localities of Senèze, Vialette, and Montpellier have a high crystallinity so the isotopic signal is not valid.

PALAEOECOLOGICAL INFERENCES FROM DENTAL ANALYSES

Since the ecology of the species *S. megarhinus* (Pliocene), *S. elatus* (Late Pliocene), and *S. etruscus* (Early Pleistocene), has not been previously investigated in the literature (only the Middle Pleistocene species have been object of previous studies), and since the isotopic signal is not valid in these earlier species, we approached the study of their ecology through the analysis of their teeth at different levels: morphology-biometry, mesowear, and 3D dental texture microwear analyses.

The mesowear and 3D-DMTA analyses show the three species had a similar diet. Despite the climatic fluctuations from the Pliocene to the Early Pleistocene, the European rhinoceroses do not change their dietary habit and the mesowear score places these fossil species between the browsers modern species, *D. sumatrensis* and *R. sondaicus*, and the mixed feeder, *R. unicornis*, so they were not pure browsers but neither as generalists as the Pleistocene *S. hundsheimensis* (which is closer to *R. unicornis* by the previous geochemical results).

This correspondence in the diet habit gains particular interest when the differences in size are considered. The three species are indeed quite distinct: *S. etruscus* has a clearly smaller size range, with proportions similar to *S. elatus*; *S. elatus* and *S. megarhinus* have a bigger size with wide overlapping, but they differ in the proportions: *S. megarhinus* has longer proximal bones and shortened metapodials (in particular in the posterior limb), as expected from its heavier body mass (*S. megarhinus* reaches the biggest size).

The teeth biometry clearly separates the bigger rhinoceros from Montpellier from those from Vialette and Senèze (the teeth of the two more recent populations are not distinguishable by size) but such a difference is simply related to the single palaeopopulations investigated and cannot be extended to the three species since there is an high inter-specific size range for each tooth. This confirms how the influence of local environmental conditions affects the size variation and, as a consequence, the high phenotypical plasticity observed in these species. The differences observed in the body size are not correlated to any difference in the dietary habit, so other evolutionary factors and more complex processes of adaptation should explain size and body mass diversity. This is not surprising for rhinoceroses, among which *S. hundsheimensis* had been recognized by several author (Fortelius *et al*., 1993; Mazza, 1993; Mazza *et al*., 1993; Lacombat, 2005, 2006; Kahlke & Kaiser, 2011; Ballatore & Breda, 2013) as an extremely flexible species, characterized by high adaptability and plasticity. Given its wide recorded size range, we studied in detail its biometry in order to gain a better clarification of its evolutionary pathways.

EVOLUTIONARY REMARKS ON *S. HUNDSHEIMENSIS* THROUGH SIZE VARIABILITY ANALYSIS

The size of *S. hundsheimensis* is extremely variable and size variability is not simply related either to a general chronological trend of size increase (with two different forms) or to a latitudinal gradient: the distinction of two different size groups as claimed by Lacombat (2005, 2009) and Fortelius *et al*. (1993) is not supported. Although a very small form of the species is present in some localities of the Early Pleistocene (Pietrafitta, Soleilhac and Saint-Prest), the coeval rhinoceros from Untermassfeld clearly shows a wide size range encompassing the "small-form" and the "large-form". Since these small *S. hundsheimensis* fall in the range of *S. etruscus*, a detailed morphological comparison among these two species is desirable prior to conclude something about the origin of *S. hundsheimensis* and its relation to *S. etruscus*. The chronologically important remains from Pietrafitta, need an extended revision since just few of them were available for this research.

The populations of *S. hundsheimensis* from continental Europe underwent a general trend of size increase through time from the Early Pleistocene locality of Untermassfeld to those of the early Middle Pleistocene of Voigtstedt and Süssenborn, then, in the Middle Pleistocene, the size decreased in Central Germany (Mauer and Mosbach2), while it remained unvaried in the southern region of Hundsheim (Austria). This highlights the main influence of local environmental factors driving the evolution of this flexible species.

In Britain the *S. hundsheimensis* populations seem not to vary with time but their body size is reduced in comparison to coeval continental populations. The persisting size through time might indicate more constant climatic conditions thanks to the mitigating effect of the sea while the size reduction could tentatively be explained by a mild insularism process. Interestingly, our previous results, given by dental size comparison (Ballatore & Breda, 2013), show a slightly larger size for the British teeth when compared with the coeval teeth from Isernia, so a different scaling of teeth and postcranials could be suggested, with British postcranials smaller but teeth larger than the coeval continental sample. The great size variability of the species is in good agreement with the ecological plasticity proved at Süssenborn and Voigtstedt (Kahlke & Kaiser, 2011) and further ecological research, regarding mesowear analysis of Mosbach2, Mauer and British localities, would give interesting information. Therefore the size variability, the ubiquity and longevity of the species are well congruent with the ecological plasticity that characterizes it.

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