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Human Evolution at the CROSSROADS

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Umschlagbild: Artistic depiction of the interdisciplinary, multiproxy paleoenvironmental reconstruction of the Marathousa 1 site (Megalopolis, Greece), illustrating its role as a glacial refugium, investigated during CROSSROADS. All fauna depicted was recovered in excavation, while hominin presence is inferred by lithic artifacts. The vegetation is based on plant macrofossils, diatoms, pollen and stable isotope analysis of animal bones from the site. The wooden spear depicted is based on the Middle Pleistocene spears found in Schöningen (Germany).
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CONTENTS

2 RHINOCEROTIDAE REMAINS FROM THE LOWER PLEISTOCENE SITE OF TSIOTRA VRYSSI, GREECE: PRELIMINARY RESULTS

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2.1 INTRODUCTION

Pleistocene rhinocerotids are poorly investigated in Greece, compared to the Miocene ones. The limited systematic studies, as well as the scanty and fragmentary material allow only partial classifications, frequently at the genus level, i.e., *Stephanorhinus* sp. Based on the recent review by Giaourtsakis (2022), during the Pleistocene, rhinocerotids were represented by two genera in Greece; *Coelodonta* and *Stephanorhinus*. The most common representative of the genus Stephanorhinus is *S. etruscus*, which has been reported more or less certainly from the Early Pleistocene (middle Villafranchian to Epivillafranchian) faunas of Kalamoto 1 and 2, Krimni, Livakos, Molykrio, Psychiko, Richea, Aivaliki, Tourkovounia 3-5 and Vatera DS. The Middle–Late Pleistocene species, *S. hemitoechus*, is recorded in the localities of Penios and Petralona (Athanassiou, 2011; Symeonidis et al., 2006; Tsoukala, 2018; Giaourtsakis, 2022), whereas *S. jeanvireti* is present in some Pliocene localities, such as Angelochori, Milia and Saint George Priporos (Guérin and Tsoukala, 2013; Tsoukala, 2018).

This contribution presents the preliminary results of the study of the Rhinocerotidae remains from the fossiliferous site of Tsiotra Vryssi (TSR) in the Mygdonia Basin (Northern Greece). The site, discovered in 2014, belongs to the upper parts of the Gerakarou Formation and yielded a late Villafranchian vertebrate fauna dated between 1.78 Ma and ~1.5 Ma (Konidaris et al., 2021). Among the mammalian remains, Rhinocerotidae are represented by numerous specimens, and their study aims to contribute to the taxonomy of the Greek Pleistocene rhinoceroses as well as to the biochronological and biogeographical distribution of the genus *Stephanorhinus* in Europe.

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2.1.1. MATERIALS AND METHODS

The TSR Rhinocerotidae assemblage includes 61 dental and postcranial specimens, the most complete of which are preliminarily presented here. No adequately preserved or informative cranial specimens have been discovered so far. The specimens were measured using a digital caliper based on a combination of methods proposed by Guérin (1980), Mazza (1988), Fortelius et al. (1993) and Lacombat (2005). The material was compared morphologically and metrically with known Eurasian *Stephanorhinus* specimens based both on direct observations and on published literature. The TSR material is stored at the Museum of Geology, Palaeontology and Palaeoanthropology of the Aristotle University of Thessaloniki (LGPUT).

2.1.2. SYSTEMATIC PALEONTOLOGY

The morphological and metrical comparison of TSR rhinoceros remains points to the distinction of two taxa.

Cranial, dental and fragmented material (Fig. 1 A–D) (n=41 specimens) were ascribed to *Stephanorhinus* sp., because of their poor preservation and/or the advanced stage of dental wear that resulted in lacking distinctive characters. Yet, lower teeth can be distinguished in two groups according to their size. The same applies to the vertebrae and the fragmentary postcranial material, where no confident attribution at specific level is possible.

The rest of the material is attributed to two morphotypes, A and B. Smaller in size specimens, referred to the Morphotype A (n=13 specimens),

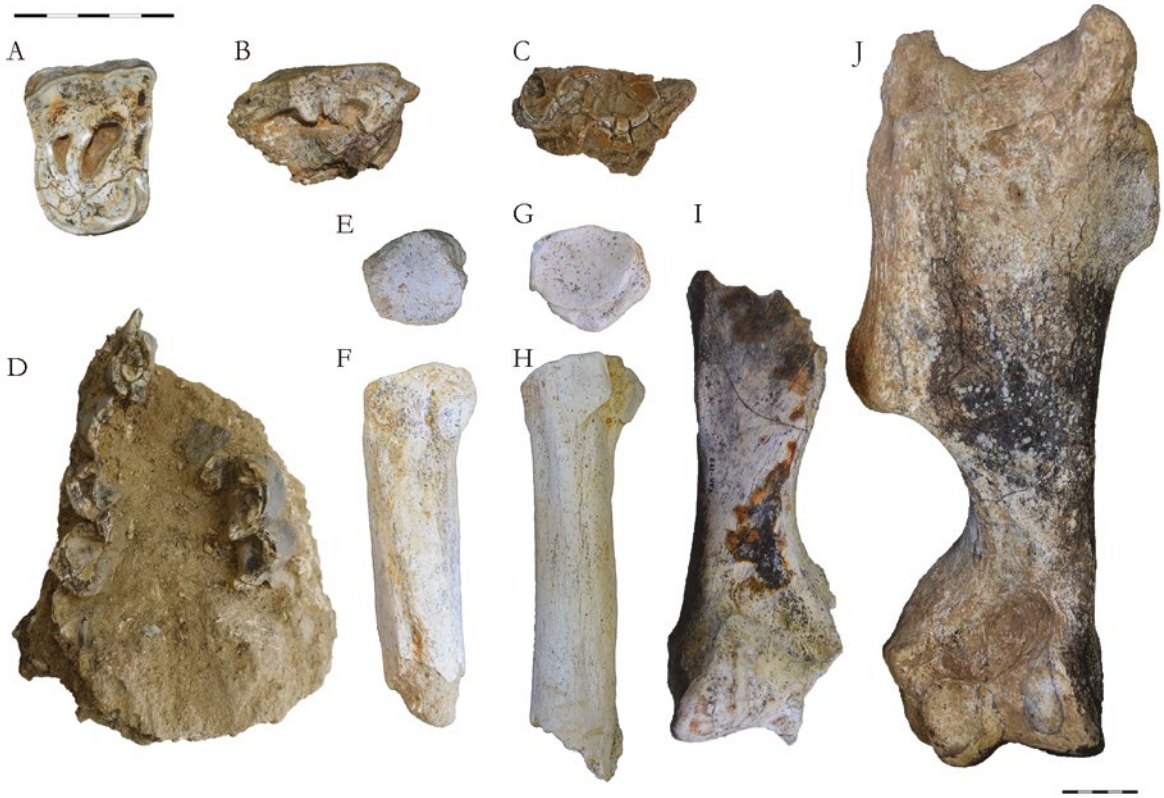

Figure 1: selected rhinocerotid material from tsr. *Stephanorhinus* sp.: a, right p4. tsr-F14-19; B, right m3, tsr-e19-10; c, right lower molar, tsr-G21-29; d. mandibular fragment preserving the left p2–p4 and right p4, tsr-d18-24. morphotype a: e–F, mtiv, tsr-F18-64a; i, humerus, tsr-133. morphotype B: G–H, mtiv, tsr-G16-41; and J, humerus, tsr-G19-13. –l eft scale bar for a–H and right for iJ, 50 mm.

are the distal part of a left humerus TSR-133 (Fig. 1I); a proximal part of a left ulna, TSR-G21-73; two proximal parts of left radii, TSR-G21-72 and TSR-C17-7; a tibia, TSR-50; and the articulated tarsals and metatarsals TSR-F18-64 (Fig. 1 E–F). Specimens larger in size, ascribed to the Morphotype B (n=7 specimens), include a complete right humerus, TSR-G19-13 (Fig. 1J); a proximal epiphysis of a left fourth metacarpal (McIV), TSR-F18-64; an almost complete femur, TSR-F18-56; femoral diaphyses TSR-G20-50, TSR-D16-27 and TSR-F22-3; and a fourth metatarsal (MtIV), TSR-G16-41 (Fig. 1G–H).

The two morphotypes can be clearly distinguished based on the biometrical comparison of the humeri, (Fig. 2A), where TSR-133 falls close to the range of the small-sized rhinoceros *S. etruscus*, whereas TSR-G19-13 is much larger, greater than

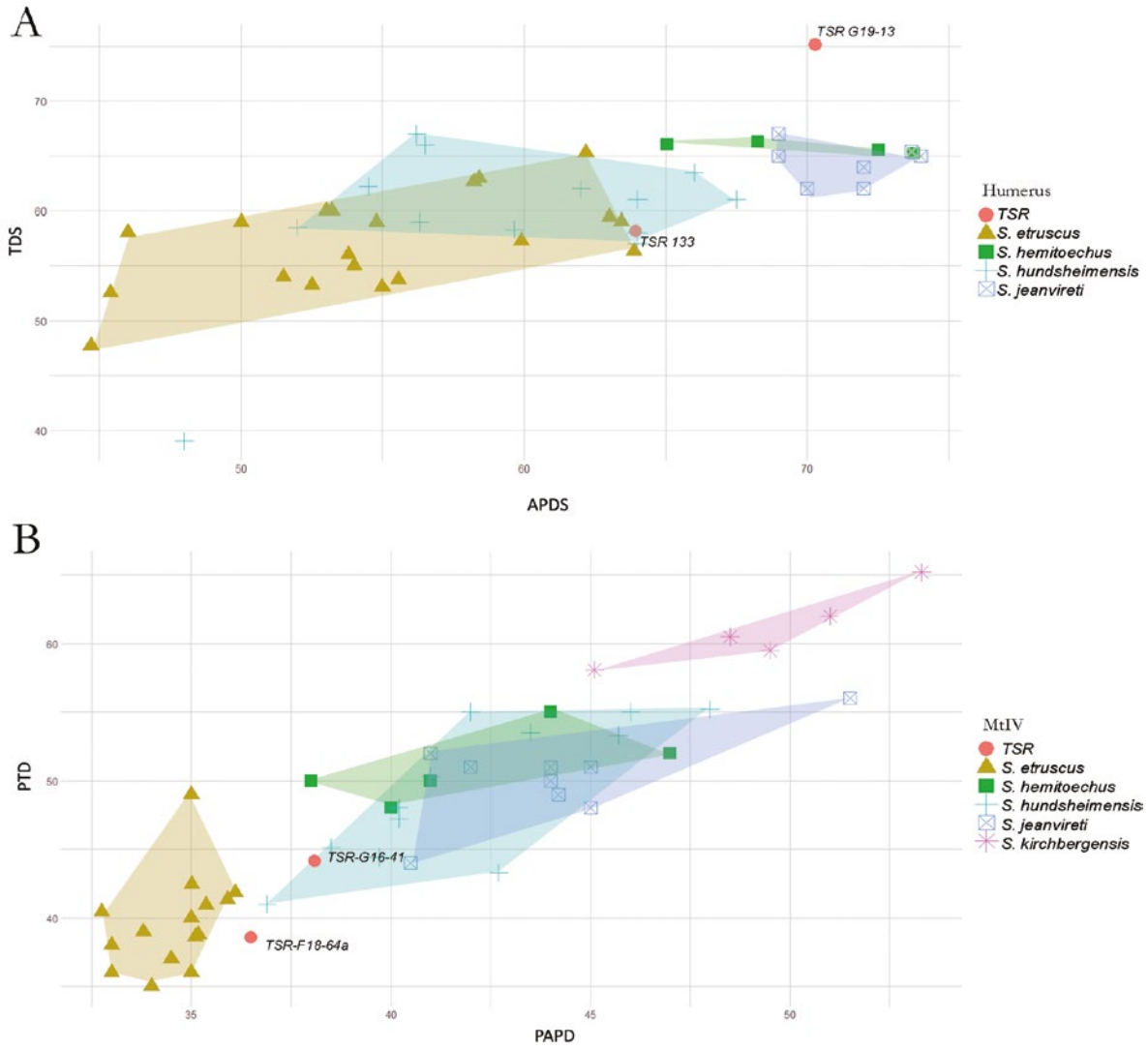

Figure 2: a: scatter plot of transversal diameter (tds) and anteroposterior diameter (apds) of the humeral diaphysis from tsiotra vryssi, morphotype a -tsr -133 and morphotype B-tsr -G19-13, in mm. data from: Guérin and Heintz (1971); Guérin (1972, 2004); mazza (1988); Fortelius et al. (1993); mazza et al. (1993); Kahlke (2001); l acombat and moulle (2005); pandolfi (2011); pandolfi and tagliacozzo (2015); pandolfi et al. (2017). B: scatter plot of the proximal transversal diameter (ptd) and proximal anteroposterior diameter (papd) of mtiv specimens from tsiotra vryssi, morphotype a -tsr -F18-64a, morphotype B-tsr -G16-41, in mm. data from Guérin (1972); mazza (1988); Fortelius et al. (1993); Kahlke (2001); l acombat (2005); Guérin and tsoukala (2013); pandolfi et al. (2017).

S. hemitoechus and *S. jeanvireti.* However, diaphyseal *Stephanorhinus* measurements show remarkable intraspecific variability, also affected by the ontogenetic age of the individual. Therefore, future analyses will focus on the articular surfaces of the distal epiphysis. Regardless of the poor preservation of TSR-133, which preserves only the medial part of the distal epiphysis and part of the diaphysis, these two specimens differ in morphological features as well. TSR-133 has a much slenderer diaphysis and a flatter medial part of the proximal border of the trochlear medial lip than TSR-G19-13. Accordingly, metrical and morphological distinction is evident in the two preserved MtIV: the much larger TSR-G16-41 and the smaller TSR-F18-56a. The scatter plot of the transversal diameter of the proximal epiphysis against its anteroposterior diameter shows that TSR-G16-41 falls into the range of *S. hundsheimensis,* whereas the specimen TSR-F18-64a is close to the range of *S. etruscus* (Fig. 2B). Additionally, the MtIV TSR-G16-41 differs from TSR-F18-64a in the more transversally elongated proximal articular surface in proximal view. In medial view, the anterior articular surface for the MtIII of TSR-F18-64a has a round shape, whereas the same surface in TSR-G16-41 has almost double the size and is square-shaped. Furthermore, in the same view, the posterior articular surface in TSR-G16-41 is in contact with the lateral tuberosity, resulting in a posterior extension.

2.1.3. DISCUSSION AND CONCLUSIONS

Morphological and biometrical comparisons of the TSR rhinocerotid material with Eurasian specimens indicate the presence of two morphotypes, likely representing two distinct species of *Stephanorhinus.* The co-existence of two or more *Stephanorhinus* species at the same locality has already been documented elsewhere, e.g., at the late Middle Pleistocene site of Ponte Molle (Italy) where the probable mixed-feeder *S.* cf. *hemitoechus* coexisted with the browser *S. kirchbergensis* (Pandolfi, 2013; Pandolfi and Marra, 2015) or the fauna of Montopoli (Italy), at the Plio-Pleistocene boundary, where the browsers *S. etruscus* and *S. jeanvireti* co-occurred (Pandolfi, 2013). *Stephanorhinus etruscus* and *S. hundsheimensis* are also documented as probably coexisting in the late Early Pleistocene fauna of Pietrafitta (Italy), but the material may come from different fossiliferous levels (Cirilli et al., 2020), and in the Middle Pleistocene site of Castellana (Italy) where reworking of the material is, however, mentioned (Mazza and Varola, 1999).

The presence of two morphotypes in a single site has also been reported at Dmanisi (Georgia), where this co-existence was interpreted as either a niche partitioning between rhinoceroses with different feeding habits (browse-dominated and grass-dominated mixed feeders) or as the occurrence of two ecomorphotypes of the same rhinoceros' species (Pandolfi et al., 2021). In the latter hypothesis, the TSR rhinocerotid may represent a single species, which differentiated from the typical *S. etruscus,* perhaps showing affinities towards *S. hundsheimensis,* or as a transitional local population.

Further material and thorough study of the TSR rhinoceroses will possibly allow the confirmation of the coexistence of two species during the late Early Pleistocene in Eurasia. Furthermore, in combination with their taxonomic identification at the species level, this will probably lead to significant conclusions regarding the chrono-spatial distribution of European rhinoceroses during the Early Pleistocene.

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