

Katerina Harvati and Melania Ioannidou (eds.)

Human Evolution at the CROSSROADS

TÜBINGEN
UNIVERSITY
PRESS 

Bibliografische Information der Deutschen Nationalbibliothek

Die Deutsche Nationalbibliothek verzeichnet diese Publikation in der Deutschen Nationalbibliografie, detaillierte bibliografische Daten sind im Internet über <http://dnb.de> abrufbar.



Dieses Werk ist unter einer Creative Commons Lizenz vom Typ Namensnennung - Nicht kommerziell - Keine Bearbeitungen 4.0 International zugänglich.

Um eine Kopie dieser Lizenz einzusehen, konsultieren Sie <http://creativecommons.org/licenses/by-nc-nd/4.0/legalcode> oder wenden Sie sich brieflich an: Creative Commons, Postfach 1866, Mountain View, California, 94042, USA.

Die Online-Version des vollständigen Manuskripts dieser Publikation ist auf dem Repositorium der Universität Tübingen verfügbar unter:

Die Online-Version des vollständigen Manuskripts dieser Publikation ist auf dem Repositorium der Universität Tübingen verfügbar unter:

<https://publikationen.uni-tuebingen.de/xmlui/handle/10900/163021>

<https://hdl.handle.net/10900/163021>

<https://nbn-resolving.org/urn:nbn:de:bsz:21-dspace-1630217>

Tübingen University Press 2025
Universitätsbibliothek Tübingen
Wilhelmstr. 32
72074 Tübingen
tup@ub.uni-tuebingen.de
www.tuebingen-university-press.de

ISBN (Hardcover): 978-3-98945-001-1

ISBN (PDF): 978-3-98945-002-8

Satz und Umschlaggestaltung: Cornelia True, Universität Tübingen

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).

(Vorder- und Rückseitenabbildungen von Gleiver Prieto; Copyright Katerina Harvati, Universität Tübingen)

Druck und Bindung: Druckhaus Sportflieger in der Medialis Offset GmbH

Printed in Germany

CONTENTS

1 The early record: Mygdonia and Northern Greece

Introduction to the volume

Katerina Harvati 11

1. Geometric morphometric analysis of the intermediate phalanx of

Ouranopithecus macedoniensis—a pilot study

Jana Kunze, Fotios Alexandros Karakostis, Melania Ioannidou, George D. Koufos, Katerina Harvati 21

2. Rhinocerotidae remains from the Lower Pleistocene site of Tsiotra Vryssi, Greece:

Preliminary results

Krystalia Chitoglou, Luca Pandolfi, George E. Konidaris, Dimitris S. Kostopoulos 31

3. Preliminary study of the canids from the Lower Pleistocene site of Tsiotra Vryssi

(Mygdonia basin, Greece)

Anastasia Karakosta, George E. Konidaris, Dimitris S. Kostopoulos, George D. Koufos, Katerina Harvati 37

4. The Late Villafranchian equids from the locality Tsiotra Vryssi

(Mygdonia basin, Macedonia, Greece)

Anastasia G. Gkeme, George D. Koufos, Dimitris S. Kostopoulos, Katerina Harvati 43

5. Taphonomic study of the Lower Pleistocene site of Tsiotra Vryssi

(Mygdonia basin, Greece): Preliminary results on bone modifications in equid carcasses

Anastasia Katsagoni, George E. Konidaris, Domenico Giusti, George D. Koufos,
Dimitris S. Kostopoulos, Katerina Harvati 51

6. The preliminary results of the Mygdonia basin archaeological survey project, Greece

Nicholas Thompson, Vangelis Tourloukis, Domenico Giusti, Katerina Harvati, Kostas Kotsakis 61

2 The Middle Pleistocene: archaeological and paleoenvironmental research in the Megalopolis Basin

7. Structural control, depositional environment and geo-archaeological conditions

in the Megalopolis basin, Southern Greece

Haralambos Kranis, Emmanuel Skourtsos, George Davis, Vangelis Tourloukis, Eleni Panagopoulou,
Panagiotis Karkanas, Katerina Harvati 73

8. Single-grain optical dating of sediment samples from Marathousa 1,

Southern Greece

Zenobia Jacobs, Bo Li, Kieran O’Gorman, Vangelis Tourloukis, Eleni Panagopoulou,
Panagiotis Karkanas, Katerina Harvati 77

9. Preliminary ages from cosmogenic nuclide burial dating of stratigraphy in
the Megalopolis basin

Mirjam Schaller, Todd A. Ehlers, Vangelis Tourloukis, Eleni Panagopoulou,
Panagiotis Karkanas, Katerina Harvati 85

10. An updated spatial taphonomic study of the Middle Pleistocene open-air site

of Marathousa 1 (Megalopolis basin, Greece): Preliminary results

Domenico Giusti, Vangelis Tourloukis, George E. Konidaris, Nicholas Thompson, Panagiotis Karkanas,
Eleni Panagopoulou, Katerina Harvati 95

11. First traceological study of the lithic assemblage from Marathousa 1 and contextualization of the results within the European Lower Palaeolithic Juliette Guibert–Cardin, Vangelis Tourloukis, Eleni Panagopoulou, Katerina Harvati, Elisa Nicoud, Sylvie Beyries	103
12. First stable isotope results on the ecology of the straight-tusked elephant (<i>Palaeoloxodon antiquus</i>) from the Middle Pleistocene Marathousa 1 (Peloponnese, Greece) Effrosyni Roditi, Hervé Bocherens, George E. Konidaris, Athanassios Athanassiou, Vangelis Tourloukis, Eleni Panagopoulou, Katerina Harvati	113
13. The Middle Pleistocene MIS 12 palynological record from Marathousa palaeolake in Southern Greece: Highlighting favourable conditions in Marathousa 1 (MAR-1) refugial Region during the severe glacial period Styliani Kyrikou, Elena Marinova, Ines J. E. Bludau, Panagiotis Karkanis, Eleni Panagopoulou, Vangelis Tourloukis, Annett Junginger, Katerina Harvati	123
14. Preliminary biomarker/paleoclimate reconstruction results from the Marathousa 1 Lower Paleolithic site (Megalopolis basin, Greece) Geanina-Adriana Butiseacă, Iuliana Vasilev, Vangelis Tourloukis, Annett Junginger, Andreas Mulch, Panagiotis Karkanis, Eleni Panagopoulou, Katerina Harvati	135
15. Preliminary results on the reptiles from the Middle Pleistocene of Marathousa 1, Megalopolis basin (Greece) Evangelos Vlachos, Georgios L. Georgalis, George E. Konidaris, Athanassios Athanassiou, Vangelis Tourloukis, Nicholas Thompson, Eleni Panagopoulou, Katerina Harvati	147
16. The Megalopolis Paleoenvironmental Project (MegaPal) Panagiotis Karkanis, Vangelis Tourloukis, Nicholas Thompson, Domenico Giusti, Georgia Tsartsidou, Athanassios Athanassiou, George E. Konidaris, Effrosyni Roditi, Eleni Panagopoulou, Katerina Harvati	155
17. Overview of MAR18-1A and MAR18-2A drill core analysis and chronological framework Ines J. E. Bludau, Annett Junginger, Bernd Wagner, Uwe Kirscher, Charlotte Zachow, Maria Schindler, Vangelis Tourloukis, Styliani Kyrikou, Panagiotis Karkanis, Eleni Panagopoulou, Katerina Harvati	165
18. U-series analyses of bones from Megalopolis basin sites Rainer Grün, Yuexing Feng, Jian-Xin Zhao, George E. Konidaris, Athanassios Athanassiou, Vangelis Tourloukis, Eleni Panagopoulou, Panagiotis Karkanis, Katerina Harvati	175
19. The Middle Pleistocene large mammal fauna from Kyparissia (Peloponnese, S. Greece): New collected material Athanassios Athanassiou, George E. Konidaris, Vangelis Tourloukis, Nicholas Thompson, Domenico Giusti, Eleni Panagopoulou, Panagiotis Karkanis, Katerina Harvati	187
20. Voles (Rodentia, Mammalia) as a proxy to date the site Kyparissia 4 (Megalopolis basin, Greece) Thijs van Kolfschoten, George E. Konidaris, Constantin Doukas, Athanassios Athanassiou, Vangelis Tourloukis, Eleni Panagopoulou, Panagiotis Karkanis, Katerina Harvati	197
21. Magnetostratigraphy of the Kyparissia and Choremi stratigraphic sequences (Megalopolis basin): Preliminary results Serena Perini, Giovanni Muttoni, Vangelis Tourloukis	207

22. Preliminary results on the taxonomy and paleoenvironmental analysis of the mollusc fauna from Marathousa 1, Marathousa 2 and Kyparissia 4 (Middle Pleistocene, Megalopolis basin, Greece)	
Georgia Boni, George Syrides, George E. Konidaris, Athanassios Athanassiou, Vangelis Tourloukis, Olga Koukousioura, Eleni Panagopoulou, Panagiotis Karkanas, Katerina Harvati	211
23. Ostracod contribution to the palaeoenvironmental study of Kyparissia 4 (Megalopolis basin, Greece)	
Penelope Papadopoulou, Maria Tsoni, George E. Konidaris, Vangelis Tourloukis, Eleni Panagopoulou, Panagiotis Karkanas, Katerina Harvati, George Iliopoulos	219
24. Fossil macaques (Cercopithecidae, Primates) from the Middle Pleistocene of the Megalopolis basin (Greece) with description of a new specimen from Kyparissia 4	
George E. Konidaris, Athanassios Athanassiou, Eleni Panagopoulou, Panagiotis Karkanas, Katerina Harvati	227

3 The late Middle and Late Pleistocene: results from Greece and beyond

25. A preliminary investigation of the cranial breakage patterns of the late Middle Pleistocene crania from Apidima Cave, Greece	
Judith Beier, Mirsini Kouloukoussa, Konstantinos Evangelou, Vassilis G. Gorgoulis, Joachim Wahl, Katerina Harvati	241
26. Mugharet el'Aliya: Adapting the method of surface registration to the hominin fossil record	
Carolin Röding, Chris Stringer, Rodrigo S. Lacruz, Katerina Harvati	249
27. Geoarchaeological and geochronological investigations of Palaeolithic open-air sites in Epirus, Greece	
Vangelis Tourloukis, Georgia Kourtessi-Philippakis, Panagiotis Karkanas, Sebastien Nomade, Domenico Giusti, Nicholas Thompson, Aris Varis, Annett Junginger, Miriam Schaller, Katerina Harvati	259
28. The preliminary analysis of lithic assemblages from the archaeological survey and test trench excavations at Popovo and Morfi, Greece	
Nicholas Thompson, Georgia Kourtessi-Philippakis, Domenico Giusti, Katerina Harvati, Vangelis Tourloukis	269

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

Krystalia Chitoglou^{1,*}, Luca Pandolfi², George E. Konidaris³, Dimitris S. Kostopoulos¹

¹Laboratory of Geology and Palaeontology, School of Geology, Aristotle University of Thessaloniki, Greece

²Dipartimento di Scienze Università degli Studi della Basilicata, Via dell'Ateneo Lucano, 10, 85100 Potenza, Italy

³Paleoanthropology, Institute for Archaeological Sciences and Senckenberg Centre for Human Evolution and Palaeoenvironment, Department of Geosciences, Eberhard Karls University of Tübingen, Tübingen, Germany

*krystal.chito@gmail.com

<http://dx.doi.org/10.15496/publikation-97664>

Keywords: *Stephanorhinus*; Late Villafranchian; Pleistocene; Mygdonia Basin; Greece

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. jean-vireti* 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.



<http://dx.doi.org/10.15496/publikation-97664>



K. chitoglou: <https://orcid.org/0009-0005-0009-4742>
d. s. kostopoulos: <https://orcid.org/0000-0001-5074-9050>
G. e. konidaris: <https://orcid.org/0000-0002-7041-233x>
l. pandolfi: <https://orcid.org/0000-0002-4186-4126>

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 (LGPOT).

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),

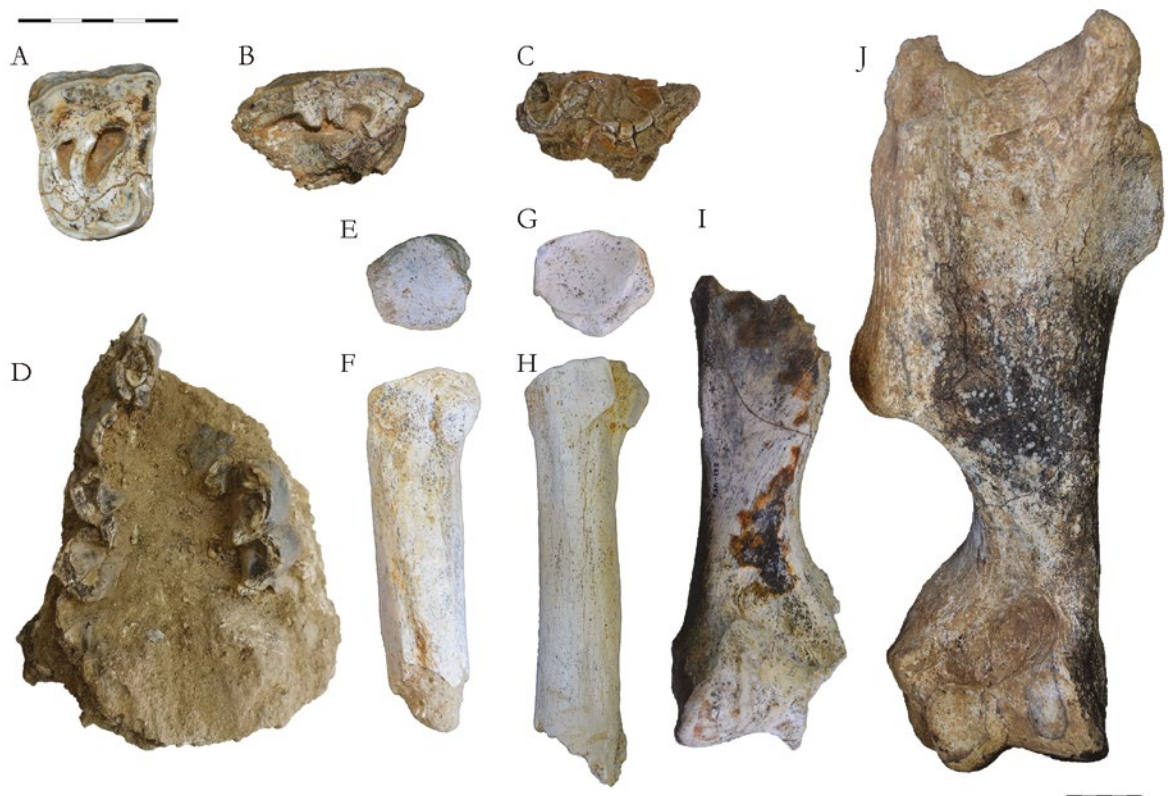


Figure 1: selected rhinocerotid material from TSR. *Stephanorhinus* sp.: a, right p4, TSR -F14-19; B, right m3, TSR -e19-10; c, right lower molar, TSR -G21-29; d, mandibular fragment preserving the left p2–p4 and right p4, TSR -d18-24. morphotype a: e–f, mtiv, TSR -F18-64a; i, humerus, TSR -133. morphotype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

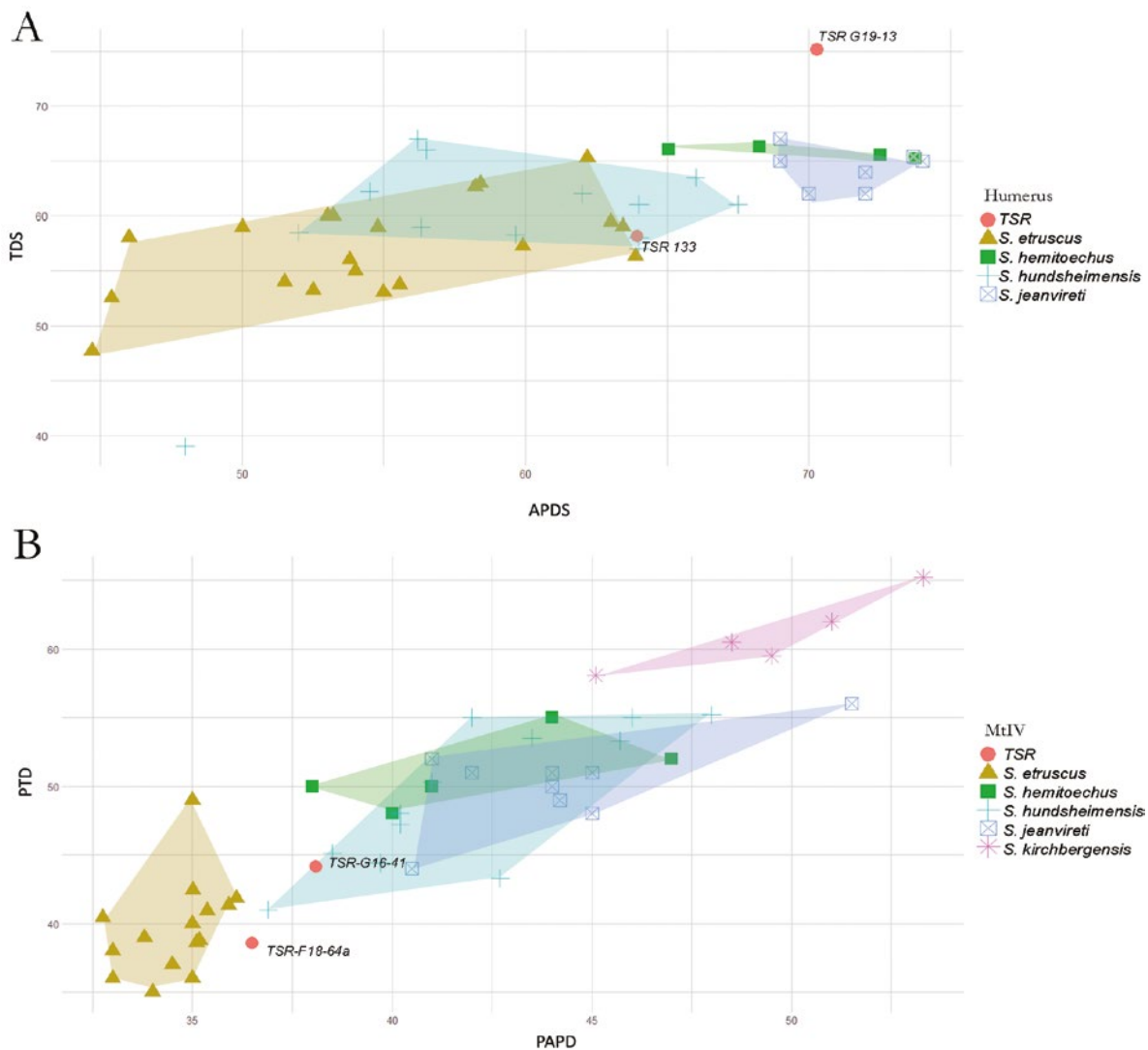


Figure 2: a: scatter plot of transversal diameter (tds) and anteroposterior diameter (apds) of the humeral diaphysis from tsiotra vryssi, morphotype a-tsr -133 and morphotype B-tsr -G19-13, in mm. data from: Guérin and Heintz (1971); Guérin (1972, 2004); mazza (1988); Fortelius et al. (1993); mazza et al. (1993); Kahlke (2001); Iacombat and moule (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); Iacombat (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 Mid-

dle 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.

ACKNOWLEDGMENTS

Excavation at TSR was supported by the ERC Consolidator Grant ERC-CoG-724703 (“CROSSROADS”) and the ERC Starting Grant ERC-StG-283503 (“PaGE”), both awarded to K.H. We also thank the two reviewers, I. Giaourtsakis and A. Athanassiou, for their useful comments.

REFERENCES

- ATHANASSIOU, A., 2011. The late Pleistocene fauna of Peneios valley (Lárisa, Thessaly, Greece): new collected material. 9th Annual Meeting of the European Association of Vertebrate Palaeontologists, Heraklion, Crete, Greece (Vol. 14).
- CIRILLI, O., Pandolfi, L. and Bernor, R.L., 2020. The Villafranchian perissodactyls of Italy: knowledge of the fossil record and future research perspectives. *Geobios*, 63, pp.1–21.
- FORTELIUS, M., Mazza, P. and Sala, B., 1993. *Stephanorhinus* (Mammalia: Rhinocerotidae) of western European Pleistocene, with a revision of *S. etruscus* (Falconer, 1868). *Palaeontographia italica*, 80(6), pp. 63–155.
- GIAOURTSAKIS, I.X., 2022. The fossil record of rhinocerotids (Mammalia: Perissodactyla: Rhinocerotidae) in Greece, in: Vlachos, E. (Ed.), in: *Fossil Vertebrates of Greece, Volume 2: Laurasiatherians, Artiodactyles, Perissodactyles, Carnivorans, and Island Endemics*. Springer, Cham, pp. 409–500.
- GUÉRIN, C., 1972. Une nouvelle espèce de rhinocéros (Mammalia, Perissodactyla) à Viallette (Haute-Loire, France) et dans d’autres gisements du Villafranchien inférieur européen: *Dicerorhinus jeanvireti* n. sp. *Travaux et Documents des Laboratoires de Géologie de la Faculté des Sciences de Lyon*, 49, pp. 53–150.
- GUÉRIN, C. 1980. Les rhinoceros (Mammalia, Perissodactyla) du Miocene terminal au Pleistocene superieur en Europe occidentale: comparaison avec les especes actuelles. *Documents du Laboratoire de Géologie de la Faculté des Sciences de Lyon*, 79, pp. 1–1182.
- GUÉRIN, C., 2004. Les rhinocéros (Mammalia, Perissodactyla) du gisement villafranchien moyen de Saint-Vallier (Drôme). *Geobios*, 37, pp. 259–278.
- GUÉRIN, C., Heintz, E., 1971. *Dicerorhinus etruscus* (Falconer, 1859), Rhinocerotidae, Mammalia, du Villafranchien de la Puebla de Valverde (Teruel, Espagne). *Bulletin du museum Nationale d’histoire Nat.*, 3.
- GUÉRIN, C., Tsoukala, E., 2013. The Tapiridae, Rhinocerotidae and Suidae (Mammalia) of the Early Villafranchian site of Milia (Grevena, Macedonia, Greece). *Geodiversitas*, 35(2), pp. 447–489.
- KAHLKE, H. D., 2001. Die Rhinocerotiden-Reste aus dem Unterpleistozän von Untermaßfeld, in: Kahlke, R.-D. (Ed.), *Das Pleistozän von Untermaßfeld bei Meiningen (Thüringen), Teil 2*. Habelt, Mainz, pp. 501–555.
- KONIDARIS, G.E., Kostopoulos, D.S., Maron, M., Schaller, M., Ehlers, T.A., Aidona, E., Marini, M., Turloukis, V., Muttoni, G., Koufos, G.D. and Harvati, K., 2021. Dating of the Lower Pleistocene vertebrate site of Tsiotra Vryssi (Mygdonia Basin, Greece): Biochronology, magnetostratigraphy, and cosmogenic radionuclides. *Quaternary*, 4(1), 1.
- LACOMBAT, F., 2005. Les rhinocéros fossiles des sites préhistoriques de l’Europe méditerranéenne et du Massif Central. *Paléontologie et implications bio-chronologiques*. BAR International Series, 1419. Oxford Archaeopress.
- LACOMBAT, F., Moullé, P.-E., 2005. Description paléontologique du *Stephanorhinus hundsheimensis* (Toula, 1902) Pléistocène Inférieur de la Tour de Grimaldi (Ligurie, Italie). *Bulletin du Musée d’Anthropologie préhistorique de Monaco*, 44, pp. 33–38.

- MAZZA, P., 1988. The Tuscan Early Pleistocene rhinoceros *Dicerorhinus etruscus*. *Palaeontographia Italica*, 75, pp. 1–87.
- MAZZA, P., Sala, B. and Fortelius, M., 1993. A small latest Villafranchian (late Early Pleistocene) rhinoceros from Pietrafitta (Perugia, Umbria, Central Italy) with notes on the Piro and Westerhoven rhinoceroses. *Palaeontographia Italica*, 80, pp. 25–50.
- MAZZA, P., Varola, A., 1999. Revision of the Middle Pleistocene rhinoceros remains from Contrada Monticelli (Castellana, Bari, Southern Italy). *II Quaternario*, 12(1), pp. 99–104.
- PANDOLFI, L., 2011. *Stephanorhinus kirchbergensis* (Jäger, 1839) from the Middle Pleistocene deposit of Riano (Rome, Central Italy). *Alpine and Mediterranean Quaternary*, 24(1), pp. 103–112.
- PANDOLFI, L., 2013. Rhinocerotidae (Mammalia, Perissodactyla) from the Middle Pleistocene site of Ponte Milvio, Central Italy. *Bollettino della Società Paleontologica Italiana*, 52, pp. 219–229.
- PANDOLFI, L. and Marra, F., 2015. Rhinocerotidae (Mammalia, Perissodactyla) from the chrono-stratigraphically constrained Pleistocene deposits of the urban area of Rome (Central Italy). *Geobios*, 48, pp. 147–167.
- PANDOLFI, L. and Tagliacozzo, A., 2015. *Stephanorhinus hemitoechus* (Mammalia, Rhinocerotidae) from the Late Pleistocene of Valle Radice (Sora, Central Italy) and re-evaluation of the morphometric variability of the species in Europe. *Geobios*, 48, pp. 169–191.
- PANDOLFI, L., Cerdeño, E., Codrea, V. and Kotsakis, T., 2017. Biogeography and chronology of the Eurasian extinct rhinoceros *Stephanorhinus etruscus* (Mammalia, Rhinocerotidae). *Comptes Rendus Palevol*, 16, pp. 762–773.
- PANDOLFI, L., Bartolini-Lucenti, S., Cirilli, O., Bukhsianidze, M., Lordkipanidze, D. and Rook, L., 2021. Paleocology, biochronology, and paleobiogeography of Eurasian Rhinocerotidae during the Early Pleistocene: The contribution of the fossil material from Dmanisi (Georgia, Southern Caucasus). *Journal of Human Evolution*, 156, p. 103013.
- SYMEONIDIS, N.K., Giaourtsakis, I.X., Seemann, R. and Giannopoulos, V.I., 2006. Aivaliki, a new locality with fossil rhinoceroses near Alistrati (Serres, Greece). *Beiträge zur Paläontologie*, 30, pp. 437–451.
- TSOUKALA, E., 2018. Rhinocerotidae from the Late Miocene and Late Pliocene of Macedonia, Greece. A revision of the Neogene–Quaternary Rhinocerotidae of Greece. *Revue de Paléobiologie*, 37, pp. 609–630.