

Reassessing the phylogeny of Quaternary Eurasian Rhinocerotidae

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Received 17 October 2022; Revised 23 November 2022; Accepted 7 December 2022

ABSTRACT: The phylogenetic relationships within Eurasian Quaternary rhinoceroses is reassessed for the first time by means of Bayesian analysis. The results show *Stephanorhinus* as a monophyletic clade, with *Pliorhinus* as a sister taxon and *Coelodonta* as their closest relative. A new scenario on the origin, evolution and paleobiogeography of Quaternary rhinoceroses is therefore provided. *Stephanorhinus* originated in the Mediterranean Basin, dispersing towards Eastern Eurasia during the Early Pleistocene and leading to *S. kirchbergensis*. *S. hemitoechus* probably originated in Europe. © 2023 The Authors *Journal of Quaternary Science* Published by John Wiley & Sons Ltd.

KEYWORDS: Eurasia; evolution; phylogeny; Quaternary; Rhinocerotidae

Introduction

The phylogeny of European Quaternary Rhinocerotidae has been a matter of discussion for decades (Supporting Information SOM S1). Despite the long story of the research on this group, Quaternary rhinoceroses are still poorly understood, and a consensus on validity and relationships among the different species seems still far from being reached. In 1942, Kretzoi established the genus *Stephanorhinus* for some Plio-Pleistocene extinct rhinoceroses, but this name was only adopted 30 years after Kretzoi's paper (SOM S1). Guérin (1980) rejected this name and ascribed the European Pleistocene rhinoceroses (except the woolly rhino) to the genus *Dicerorhinus* and then to a new subgenus, and later genus, *Brandtorhinus*. According to Guérin, the morphological features listed by Kretzoi (1942) were not exclusive to *Stephanorhinus*. In 1993, Fortelius *et al.* proposed *Brandtorhinus* as a junior synonym of *Stephanorhinus*, and referred the European species *Dicerorhinus jeanvireti*, *Rhinoceros etruscus*, *R. hundsheimensis* (= *D. etruscus brachycephalus* in partim), *R. hemitoechus* and *R. kirchbergensis* (= *D. mercki* in partim) to the genus *Stephanorhinus*.

During recent decades, a few attempts have been made to investigate the phylogeny and taxonomy of this emblematic group, but without claiming new hypotheses or depicting new evolutionary frameworks (SOM S1).

Here, the first comprehensive phylogeny of the extinct European Quaternary rhinoceroses is provided along with its paleobiogeographical implications.

Methods and material

This study includes late Neogene, Quaternary and extant Rhinocerotidae from Eurasia that are known from cranial and postcranial material (SOM S2).

The matrix includes 284 characters: 278 from Antoine (2002) with some emendation by Antoine *et al.*, (2022), plus 279–284 from Deng *et al.* (2011) and Uzunidis *et al.* (2022) (SOM S3). The character states for *Stephanorhinus* species, and other Eurasian taxa, are coded through direct observa-

tions (SOM S2), whilst those of other taxa are from Pandolfi *et al.* (2021a) and Uzunidis *et al.* (2022). The analysis follows the protocol adopted in Uzunidis *et al.* (2022). The outgroup includes four taxa, *Tapirus terrestris*, *Hyrachyus eximius*, *Trigonias osborni* and *Ronzotherium filholi*, and the ingroup includes 30 taxa (SOM S4). Due to the great number of convergent characters within Rhinocerotina, the analysis does not include the extant representatives of African species, *Ceratotherium simum* and *Diceros bicornis*, to focus on Eurasian species only. The Bayesian analysis is performed in MrBayes v3.2.7 (Ronquist *et al.*, 2012) and follows the protocol adopted by Parry *et al.* (2021) (SOM S3). Parsimony-uninformative characters (autapomorphies) are included in the analysis; *Tapirus terrestris* is considered as a outgroup; additive characters are considered as in parsimonious analysis. The relationships between *Rhinoceros*, *Dicerorhinus sumatrensis*, *Coelodonta antiquitatis* and *Stephanorhinus kirchbergensis* are partially constrained according to the results obtained by Liu *et al.*, (2021). The fossil record is calibrated considering Heissig (1999), Guérin (1980), Fortelius *et al.* (1993), Antoine (2002), Deng *et al.* (2011), Antoine *et al.*, (2022), Pandolfi *et al.* (2021a, 2021b) and Uzunidis *et al.* (2022).

Results

Three most-parsimonious trees are retrieved from the parsimonious analysis (SOM S5). The trees differ in the relationship among *Dicerorhinus* species, *D. sumatrensis*, *D. fusuiensis* and *D. gwebinensis*, thus resulting in a polytomy in the consensus tree shown in Fig. 1 (tree length = 1358 steps, consistency index = 0.274, homoplasy index = 0.726). In the consensus tree, the Rhinocerotini clade (node 1) is composed of Rhinocerotina and Teleoceratina. Two major clades are present within Rhinocerotina (node 2): one including the South Asian taxa and *Lartetotherium* and *Gaindatherium* (node 3) and the other including the Northern Eurasian species (node 4). Within node 4, the first dichotomy isolated *Dihoplus schleiermacheri* and the second one isolated 'Di.' *pikermiensis*. A large clade (node 5) is composed of Plio-Pleistocene species belonging to *Pliorhinus*, *Coelodonta* and *Stephanorhinus*. *Pliorhinus* and *Coelodonta* are sister taxa (node 6), and this clade is supported by seven

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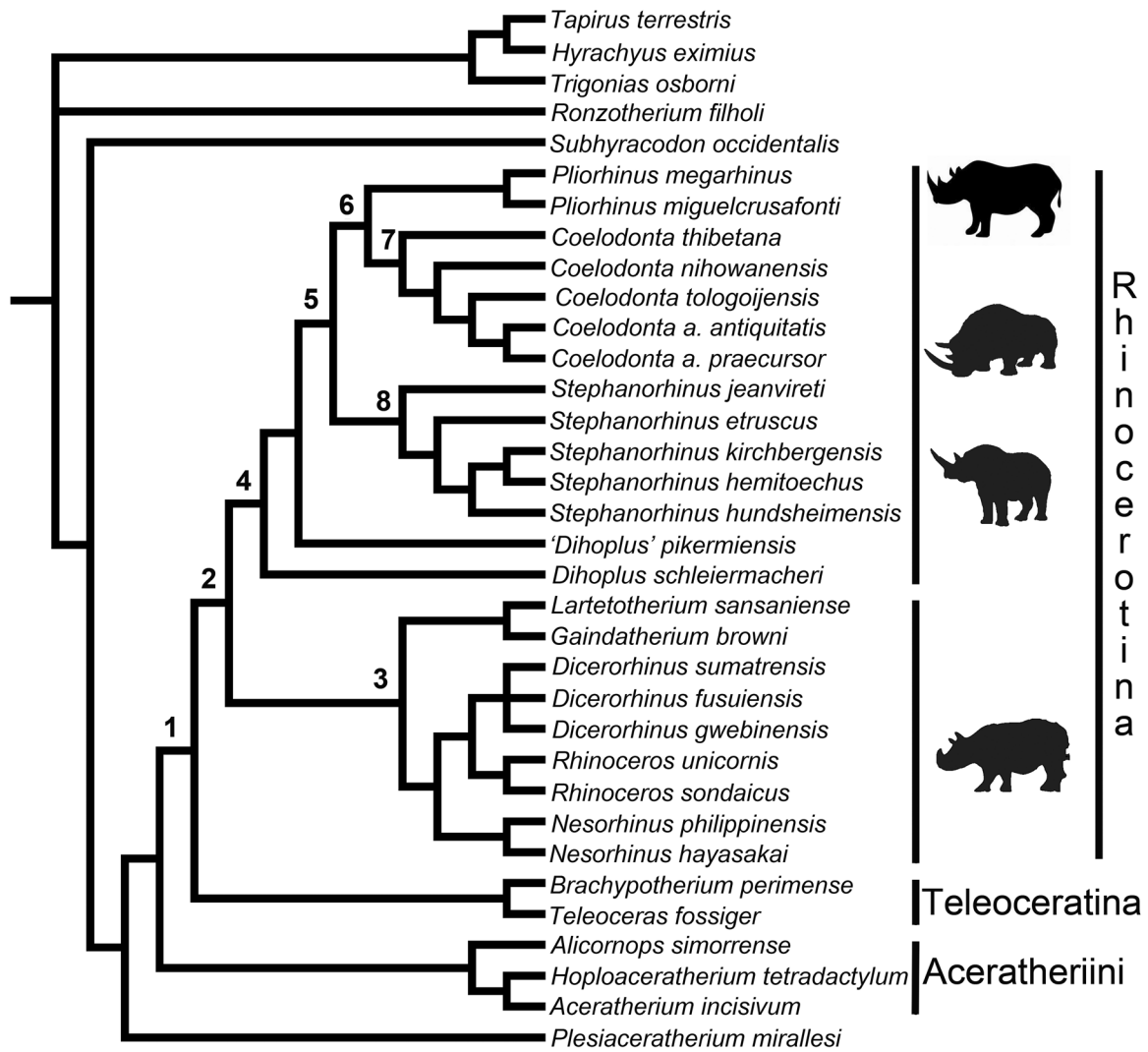


Figure 1. Consensus tree obtained with the parsimonious analysis of 284 characters and 34 species. Numbers on nodes represent: 1, Rhinocerotini; 2, Rhinocerotina; 3, *Lartetotherium*, *Gaindatherium* and the South East Asian clade; 4, Northern Eurasian species; 5, clade of Northern Eurasian Plio-Pleistocene species; 6, *Pliorhinus*–*Coelodonta* clade; 7, *Coelodonta* clade; 8, *Stephanorhinus* clade.

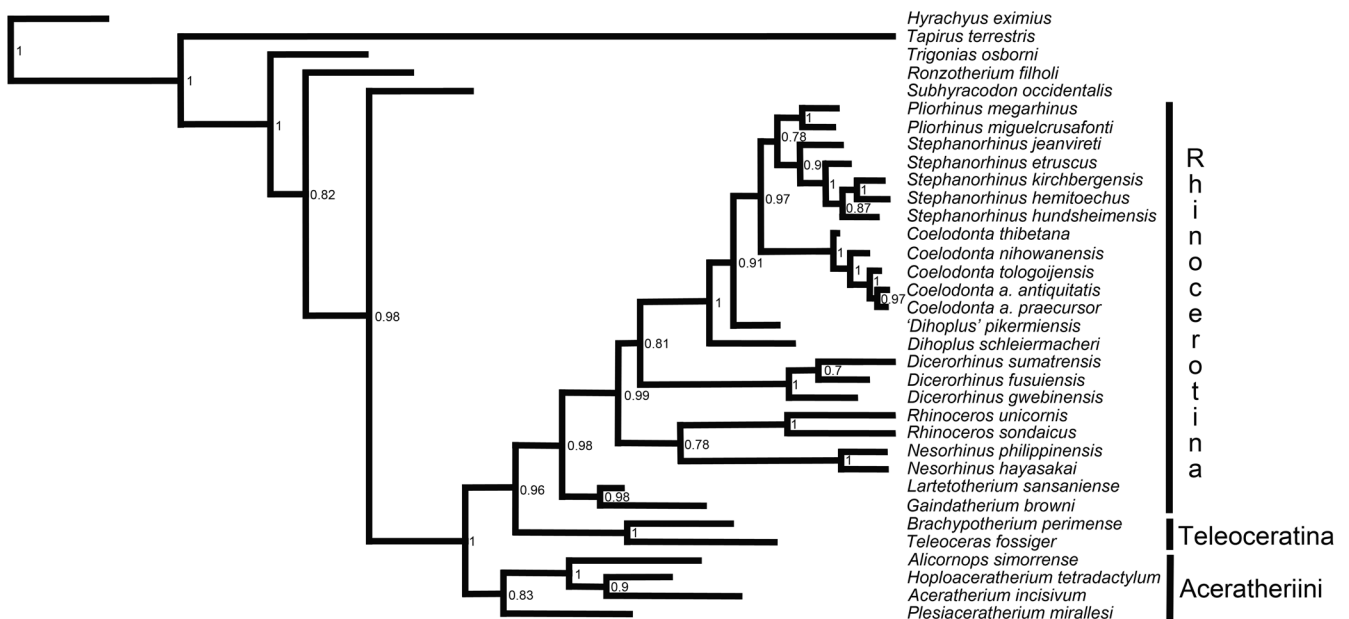


Figure 2. Time-calibrated phylogenetic inference from Bayesian analysis of the character matrix in SOM S4. Numbers at nodes represent probabilities for analysis.

unambiguous synapomorphies. The relationships within *Coelodonta* (node 7) are the same as highlighted by Uzunidis *et al.* (2022) and this clade is supported by a bootstrap value of 100 (SOM S6). The *Stephanorhinus* clade (node 8) is supported by seven unambiguous synapomorphies. Within *Stephanorhinus*, the first branch isolated *S. jeanvireti* and the second one *S. etruscus*. The third branch isolated *S. hundsheimensis*, whilst *S. kirchbergensis* and *S. hemitoechus* are sister taxa. The clade composed of *S. etruscus*, *S. hundsheimensis*, *S. hemitoechus* and *S. kirchbergensis* is supported by 12 unambiguous synapomorphies and by a bootstrap value of 82. The apomorphy list of the nodes in the consensus tree is reported in SOM S7. For the Bayesian analysis, the topology of the highest posterior probability, shown in Fig. 2, is relatively similar to the consensus tree. Within the Eurasian fossil species, three main clades are recognized and strongly supported, *Coelodonta* ($p = 1$), *Pliorhinus* ($p = 1$) and *Stephanorhinus* ($p = 0.96$). The main difference between the two trees is in the position of the *Pliorhinus* clade, which results in a sister-taxon relationship with the *Stephanorhinus* clade in the Bayesian analysis. The node supporting this relationship has a $p = 0.78$.

Discussion and conclusion

A phylogenetic analysis of Eurasian Neogene and Quaternary rhinoceroses, inclusive of *Stephanorhinus* species, is presented here. The analysis includes the most complete and well-preserved material presently available for the considered species and aims to reconstruct the relationships within *Stephanorhinus* and its relatives, i.e. *Dihoplus*, *Pliorhinus* and *Coelodonta*. The results support the monophyly of *Stephanorhinus*, including the latest Pliocene and Pleistocene representatives. The Bayesian analysis suggests a close relationship between *Pliorhinus* and *Stephanorhinus* in agreement with the available fossil records of the considered species. *Pliorhinus* probably originated in East Eurasia and dispersed towards Western Eurasia with *P. megarhinus*, at the end of the Miocene (Pandolfi *et al.*, 2015). No *Stephanorhinus* records are currently known from Eastern Eurasian during the Neogene. *Stephanorhinus* (Fig. 3) originated in Europe from early Pliocene *Pliorhinus* representatives that gave rise to *S. jeanvireti* during the latest Pliocene (Guérin, 1980). The low support of the node including the latest Pliocene *S. jeanvireti* is probably due to the high rate of convergences with the species belonging to *Pliorhinus*. In the parsimonious analysis, node 8 (Fig. 1) is supported by seven synapomorphic features, whilst the Pleistocene species of the genus *Stephanorhinus* cluster together and are strongly supported in both analyses, being also defined by 13 synapomorphies (SOM S7). According to the available fossil record, *Stephanorhinus* reached the Eastern area of Eurasia only during the Early Pleistocene (Tong, 2012; Pandolfi *et al.*, 2021b). *S. etruscus* represents the early divergent Pleistocene rhinoceros within *Stephanorhinus*, and *S. hundsheimensis* is a sister taxon to *S. kirchbergensis*–*S. hemitoechus* (Fig. 3). The latter relationship is particularly intriguing if considering the c. 1.8 Ma record of *Stephanorhinus* from Dmanisi that yielded cranial remains assigned as morphotypes or species closely related to these taxa (Pandolfi *et al.*, 2021b). *S. kirchbergensis* has its oldest record in China (Tong, 2012), but it cannot be excluded that several Early Pleistocene remains assigned to this taxon could instead be referred to *S. hundsheimensis*, being represented by scanty or fragmented specimens. *S. kirchbergensis* is certainly documented in China starting from the latest Early to early Middle Pleistocene, as testified by several well-preserved cranial remains (Tong, 2012). *S. hemitoechus*, never recorded outside

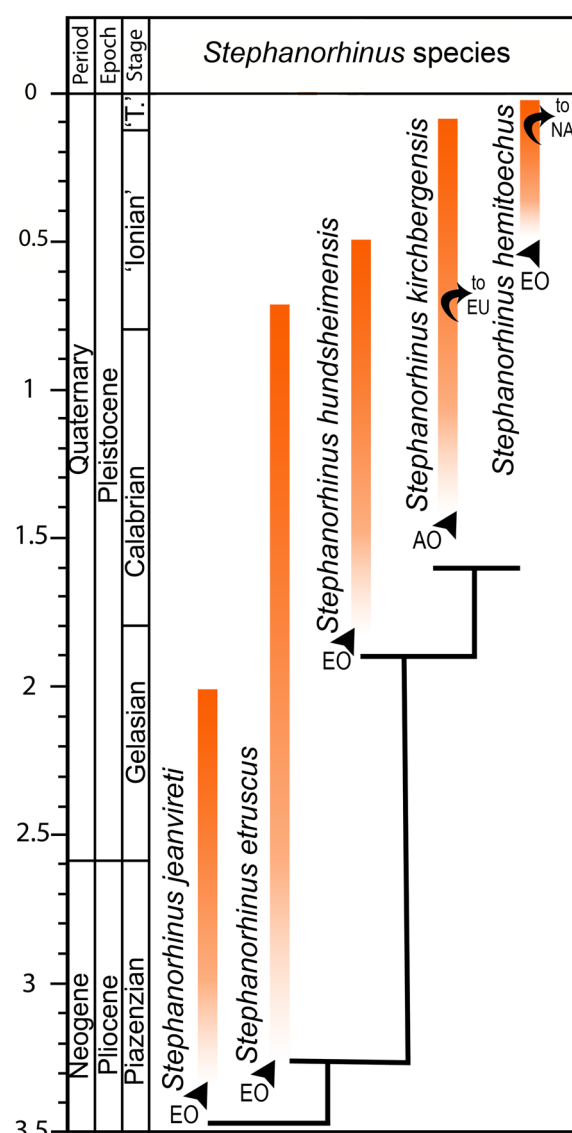


Figure 3. Time-calibrated phylogeny of Eurasian fossil species of *Stephanorhinus*. EO = European origin; AO = Asian origin; EU = Europe; NA = North Africa. Arrows indicate dispersal events. [Color figure can be viewed at wileyonlinelibrary.com]

the Mediterranean area (Guérin, 1980; Fortelius *et al.*, 1993), probably originated in Europe, representing an evolution *in loco* of rhinoceros populations towards a specialization of a grass-dominated mixed feeder habit (Pandolfi *et al.*, 2021b).

The present results show a new evolutionary framework within the Quaternary Eurasian rhinoceroses and suggest an alternative scenario with respect to previous published hypotheses. The analysis supports a close relationship between *Stephanorhinus* and *Pliorhinus*, the monophyly of *Stephanorhinus* and suggests a close relationship among the Middle Pleistocene species. Although further studies are needed to understand the origin of some species and further material would be helpful to provide a more detailed analysis, this work provides the first evidence of a complex relationship within the Quaternary rhinoceroses and sheds some insight on such iconic taxa.

Competing interests

The author declares that there are no competing interests.

Acknowledgements. This research received support from the SYNTHESYS Project <http://www.synthesys.info/>, which is financed by

European Community Research Infrastructure Action under the FP7 'Capacities' Programme: AT-TAF-2550, DE-TAF-3049, GB-TAF-2825, HU-TAF-3593, ES-TAF-2997.

Data availability statement

The data that supports the findings of this study are available in the supplementary material of this article

Author contributions—Luca Pandolfi: Conceptualization; Investigation; Funding acquisition; Writing - original draft; Methodology; Validation; Visualization; Writing - review & editing; Software; Formal analysis; Data curation; Supervision; Resources; Project administration.

Supporting information

Additional supporting information can be found in the online version of this article.

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