



Taxonomy, biochronology, and paleobiogeography of *Propotamochoerus provincialis* in the Late Miocene of Western Eurasia

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Abstract. *Propotamochoerus provincialis* represents the last European occurrence of the genus *Propotamochoerus* and a key taxon for understanding suid evolution and dispersal during the Late Miocene. Historically, its taxonomy and stratigraphic range were obscured by mixed type material, leading to erroneous interpretations of its persistence into the Pleistocene. Recent revisions have clarified its diagnosis and restricted its temporal range to the Turolian-Ruscinian interval (MN13-MN14). This review synthesizes current knowledge on the species' taxonomy, morphology, stratigraphy, geographic distribution, and phylogenetic relationships. Morphologically, *P. provincialis* is distinguished by robust bunodont dentition, reduced anterior premolars, and cranial features indicative of a generalized omnivorous lifestyle. Biochronologically, it serves as an important marker for the latest Miocene-earliest Pliocene transition in the Euro-Mediterranean region. Paleobiogeographic evidence supports a diachronous westward dispersal from the Balkans into central and western Europe, facilitated by changing paleogeographic conditions. The species occupied a range of humid, mosaic environments and exhibited ecological flexibility prior to its extinction, likely linked to environmental changes and the arrival of the genus *Sus*. Overall, *P. provincialis* represents a terminal element of a widespread Eurasian radiation and provides critical insights into late Neogene faunal dynamics.

Key Words: biochronology, dispersal, Eurasia, Late Miocene, Messinian, paleobiogeography, paleoecology, *Propotamochoerus provincialis*, Ruscinian, Suidae, taxonomy, Turolian.

Aim of the study. The aim of this study is to synthesize and clarify the taxonomy, stratigraphic range, paleobiogeography, and evolutionary significance of *Propotamochoerus provincialis* within the context of Late Miocene suid diversification in western Eurasia.

Taxonomic history and diagnosis of *Propotamochoerus provincialis*. *Propotamochoerus provincialis* is a late Miocene suid belonging to the tribe Dicoryphochoerini within Suinae and represents the latest European member of the genus *Propotamochoerus* (Gallai & Rook 2006; Gallai 2007; Gallai & Rook 2011; Iannucci et al 2021). Historically, the taxonomy and temporal range of *P. provincialis* were confused because the type series from Montpellier was shown to be an admixture of material referable both to *P. provincialis* and to the much younger *Sus strozzi*, obscuring the diagnosis and suggesting an unrealistically long stratigraphic range into the Pliocene-Pleistocene (Iannucci et al 2021). Recent revision of the Montpellier material and comparison with large late Miocene and early Pliocene samples from Europe have provided an emended diagnosis and clarified the status of *P. provincialis* as the Turolian-Ruscinian representative of *Propotamochoerus* in western Eurasia (Geraads et al 2008; Iannucci et al 2021).

Morphologically, *P. provincialis* is a medium- to large-sized suid, larger than *P. palaeochoerus* and the Balkan species *P. aegaeus*, but smaller than Asian forms such as *P. hyotherioides* (Geraads et al 2008; Iannucci et al 2021; Iannucci & Begun 2022; Lazaridis et al 2022). Diagnostic features include relatively robust cheek teeth, with molars that are less elongated than in *P. hysudricus* and *P. hyotherioides*, and a reduced, often single-rooted P1 that may be vestigial and closely approximated to the canine and P2 (Geraads et al 2008). In contrast to *P. palaeochoerus*, the parietal ridges are more widely spaced and the skull profile is more or less straight dorsally (Van der Made et al 1999). On the lower dentition, p3 tends to be relatively broad and P4 less elongated than in earlier *Propotamochoerus* species, while M3 may show a moderately developed third lobe, but without the prominent hexaconid typical of some Asian taxa (Van der Made et al 1999; Geraads et al 2008). These characters, together with metric differences quantified in multivariate analyses, distinguish *P. provincialis* from Vallesian *P. palaeochoerus*, the peri-Balkan *P. aegaeus* and Asian congeners (Van der Made et al 1999; Geraads et al 2008; Iannucci et al 2021; Iannucci & Begun 2022; Lazaridis et al 2022).

Stratigraphic range and biochronological significance. Early interpretations placed *P. provincialis* from the latest Miocene into the middle Pleistocene because of misidentified *S. strozii* remains within the type series (Iannucci et al 2021; Dăescu et al 2025). A comprehensive reassessment of the Casino Basin material (Tuscany) and the Montpellier sample demonstrates that all securely identified European *Propotamochoerus* from the late Turolian belong to *P. provincialis* and that the species does not extend beyond the Turolian-Ruscinian transition, roughly MN13-MN14 (Iannucci et al 2021). This reassignment removes evidence for survival of *Propotamochoerus* into the later Pliocene and restores the classical view that *Sus* dispersed into Europe during the early Pliocene and replaced other suids (Balint et al 2024) without overlap with *P. provincialis* (Iannucci et al 2021).

Independent Italian and Balkan records support this refined chronology. At Monticino Quarry (Brisighella, northern Apennines), dental and postcranial remains referred to *P. provincialis* occur in a latest Messinian (MN13) assemblage, confirming the presence of the species in the very latest Miocene of the northern Apennines (Gallai & Rook 2011). In Sicily, reappraisal of the rich Gravitelli fauna shows that abundant suid material, long known only from early 20th-century descriptions, is referable to *P. provincialis* and occurs stratigraphically below the pre-evaporitic Tripoli Formation dated at about 7 Ma, implying a late Tortonian or earliest Messinian age (MN11-MN12) (Iannucci 2024). This makes Gravitelli the earliest Italian record of *P. provincialis* and documents an early phase of its westward dispersal into the central Mediterranean (Iannucci 2024).

These data, combined with Balkan occurrences, indicate a diachronous spread of *P. provincialis* in western Eurasia. The genus *Propotamochoerus* appears first in the Balkans around 8.3 Ma, reaches Sicily before 7 Ma, and is documented in the Iberian Peninsula by about 6.2 Ma (Iannucci 2024). Within this pattern, *P. provincialis* marks the late Turolian suid assemblages and serves as a valuable biochronological indicator for the latest Miocene-earliest Pliocene transition in the Euro-Mediterranean region (Gallai & Rook 2011; Iannucci et al 2021; Iannucci 2024).

Geographic distribution and paleobiogeography. *P. provincialis* is known from multiple late Miocene localities across western and central Europe, including the classic Montpellier area in southern France, sites in Italy such as the Casino Basin, Monticino Quarry and Gravitelli, and occurrences in the Balkans and Iberian Peninsula (Geraads et al 2008; Gallai & Rook 2011; Iannucci et al 2021; Iannucci 2024). The Casino Basin fauna, which includes *P. provincialis* in association with *Mesopithecus pentelicus*, *Tapirus arvernensis* and a late Messinian hippopotamid, records a latest Messinian continental assemblage in Tuscany and indicates faunal exchanges between the Iberian Peninsula and the central Mediterranean (Iannucci et al 2021; Martino et al 2024).

The detailed revision of Gravitelli shows that the suid assemblage is entirely European in character, with no African suid taxa present; *P. provincialis* occurs together with typical European mammals and only the hippopotamid represents an immigrant of African ancestry (Iannucci 2024; Martino et al 2024). The presence of *P. provincialis* at

Gravitelli before 7 Ma implies that emergent landmasses connected Sicily to the European mainland earlier than previously thought and supports a model of stepwise westward dispersal of Turolian faunas through the Aegean and central Mediterranean corridors (Iannucci 2024). Iberian records dated to around 6.2 Ma represent the final stage of this westward expansion (Iannucci 2024).

Beyond Europe, the genus *Propotamochoerus* is widespread in Asia, with *P. hysudricus* in the Siwaliks and *P. hyotherioides* and *P. wui* in China, but these taxa occupy earlier and partly overlapping intervals and represent distinct phylogenetic branches (Hou et al 2019; Aslam et al 2021). The European late Turolian *P. provincialis* has been interpreted as part of a western Eurasian lineage derived from earlier forms with affinities to *P. hysudricus* or *P. hyotherioides* that dispersed from Asia into Europe in the middle-late Miocene, subsequently differentiating regionally (Van der Made et al 1999; Geraads et al 2008; Iannucci et al 2021; Iannucci & Begun 2022).

Morphology, functional anatomy and biology. The dentition of *P. provincialis* is bunodont, with relatively low-crowned molars and well-developed basal pillars, consistent with generalized omnivorous or mixed-feeding habits typical of suids (Geraads et al 2008; Gallai & Rook 2011; Iannucci et al 2021). Cheek teeth are robust, with conspicuous cusps and cingula, but lack the strong hypsodonty or complex lophodont patterns typical of highly specialized grazers, suggesting a diet including leaves, fruits, roots and possibly some grass, in mosaic woodland-open habitats (Gallai & Rook 2011; Iannucci et al 2021; Iannucci & Begun 2022).

Knowledge of the postcranial skeleton of *Propotamochoerus* has historically been limited. The Monticino Quarry assemblage provides one of the first detailed descriptions of postcranial elements securely attributed to *P. provincialis*, including an astragalus, cuboid, navicular and a distal phalanx (Gallai & Rook 2011). These elements show a morphology broadly comparable to that of the extant wild boar *Sus scrofa*, indicating that postcranial anatomy within Suidae is relatively conservative and that *P. provincialis* likely had a “boar-like” locomotor pattern adapted to cursorial to semi-cursorial movement in varied terrain (Gallai & Rook 2011). The combination of medium-large body size and conservative postcranial morphology suggests ecological flexibility, but probably with a preference for habitats offering both cover and access to water, consistent with the environments reconstructed for late Miocene European basins (Gallai & Rook 2011; Iannucci & Begun 2022; Iannucci 2024).

Cranially, *P. provincialis* shares with other *Propotamochoerus* species a relatively elongate snout (Figure 1) and moderately developed canines in males, reflecting intraspecific competition and display typical of suids, but lacks the extreme cranial specializations seen in large, horned Miocene suids such as *Kubanochoerus* (Van der Made et al 1999; Geraads et al 2008; Iannucci et al 2021).



Figure 1. Skull of *Propotamochoerus provincialis* found in Musaitu ravine (Source: https://commons.wikimedia.org/wiki/File:MNEIN_Moldova).

The reduced P1 and trend toward simplification of anterior dentition may correlate with changes in foraging behavior and selection on rooting and cropping strategies compared with earlier *Propotamochoerus* species (Van der Made et al 1999; Geraads et al 2008).

Relationships within *Propotamochoerus* and Suinae. Within *Propotamochoerus*, at least five species are widely recognized: *P. hyotherioides*, *P. hysudricus*, *P. palaeochoerus*, *P. provincialis* and *P. wui*, with additional regional forms such as *P. aegaeus* now formally validated for the peri-Balkan Turolian record (Van der Made et al 1999; Geraads et al 2008; Hou et al 2019; Aslam et al 2021; Iannucci et al 2021; Lazaridis et al 2022). *P. palaeochoerus* characterizes Vallesian and early Turolian European faunas (MN9-MN10) and is replaced in later Turolian assemblages by a different *Propotamochoerus* form, now interpreted as *P. provincialis* rather than an Asian taxon (Van der Made et al 1999; Geraads et al 2008; Iannucci et al 2021; Iannucci & Begun 2022). Balkan and Aegean material previously attributed to Asian *P. hysudricus* or *P. hyotherioides* has been reassigned to *P. aegaeus*, a species intermediate in size and morphology between *P. palaeochoerus* and *P. provincialis* but distinct from both (Van der Made et al 1999; Geraads et al 2008; Iannucci et al 2021; Iannucci & Begun 2022; Lazaridis et al 2022).

Asian *P. hysudricus* from the Siwaliks is a moderate-sized suid with relatively large cheek teeth, elongated M1 and characteristic basal pillars, interpreted as derived from *Hyotherium* and representing a key stock within Suinae that gave rise to several later lineages including *Potamochoerus*, *Sus*, *Microstonyx* and related genera (Aslam et al 2019, 2021). Chinese *P. hyotherioides* and *P. wui* form separate branches within the genus and display their own regional specializations in premolar and molar morphology (Hou et al 2019). In this broader phylogenetic context, *P. provincialis* represents the terminal European element of a *Propotamochoerus* radiation that diversified across Eurasia during the late Miocene and was ultimately replaced by *Sus* and other more derived suids in the Pliocene (Van der Made et al 1999; Pickford 2013; Iannucci et al 2021).

At a higher taxonomic level, *Propotamochoerus* is considered close to *Palaeochoerus* and early suines and is part of an ancestral stock from which several major suid lineages emerged. Work on Siwalik *Propotamochoerus* emphasizes its proximity to *Palaeochoerus* and its role as a precursor of later Suinae, with ancient propotamochoeroid lineages giving rise to *Potamochoerus* and *Sus* in one branch and to *Microstonyx*, *Hippopotamodon* and related taxa in another (Aslam et al 2019, 2021; Petrescu-Mag et al 2025). In Africa, Pliocene metridiochoerines and phacochoerines appear to have descended from a "*Postpotamochoerus provincialis*"-like ancestor that entered Africa from Europe after the arrival of *Dasychoerus* (*Sus*)-like suids, linking *P. provincialis* to the origins of several African suid clades (Pickford 2013).

Paleoecology and faunal context. The paleoecology of *P. provincialis* can be inferred from its anatomy and from associated faunal and sedimentary evidence. In the Casino Basin, *P. provincialis* occurs in latest Messinian deposits together with mesopithecids, tapirs and hippopotamids within fluvio-lacustrine successions, indicating humid, freshwater-rich environments and vegetational mosaics with woodland elements (Iannucci et al 2021; Martino et al 2024). The Gravitelli fauna, now dated to late Tortonian-earliest Messinian, similarly comprises a largely European assemblage including *P. provincialis* and an endemic hippopotamid, suggesting insular or peri-insular conditions with persistent freshwater systems and sufficient vegetational resources for medium-to-large omnivores and herbivores (Iannucci 2024).

At Monticino Quarry, the presence of *P. provincialis* in association with a diverse Messinian vertebrate assemblage in gypsum karst fissure fills reflects terrestrial habitats along the margins of evaporitic basins, with local freshwater and vegetational refugia during the Messinian Salinity Crisis (Gallai & Rook 2011; Martino et al 2024). Across these localities, *P. provincialis* appears as a versatile suid thriving in a range of late Miocene landscapes, from coastal basins to intramontane depressions, provided that woodland cover, rootable soils and permanent or seasonal water sources were available. Its extinction around the Turolian-Ruscinian transition coincides with major environmental reorganization

at the end of the Messinian Salinity Crisis and with the arrival and radiation of *Sus*, a more generalized and eventually dominant Eurasian suid, which likely intensified dietary and habitat competition (Gallai & Rook 2011; Pickford 2013; Iannucci et al 2021; Iannucci 2024).

Conclusions. *Propotamochoerus provincialis* is now recognized as the characteristic late Turolian-earliest Ruscinian suid of western Eurasia, with a clarified diagnosis and stratigraphic range restricted to approximately MN13-MN14. Its medium-large body size, bunodont dentition and conservative postcranial morphology indicate a generalized, wild-boar-like omnivore inhabiting humid, structurally complex landscapes around the Mediterranean. Detailed regional studies in Italy, the Balkans and western Europe have resolved long-standing taxonomic and chronological problems, shown that *P. provincialis* dispersed diachronously from the Balkans into the central and western Mediterranean, and positioned the species within a broader Eurasian radiation of *Propotamochoerus* that bridges early suines and later lineages such as *Sus* and African Pliocene-Pleistocene suids.

Conflict of interest. The authors declare that there is no conflict of interest.

References

- Aslam S., Khan A. M., Ahmad R. M., Iqbal A., Akhtar M., 2019 Systematic study of the new remains of *Propotamochoerus hysundricus* (Suidae, Mammalia) from the Late Miocene-Early Pliocene Middle Siwaliks (Pakistan). In: Paleobiodiversity and tectono-sedimentary records in the Mediterranean Tethys and related eastern areas. Boughdiri M., Bádenas B., Selden P., Jaillard E., Bengtson P., Granier B. (eds), Springer, Cham, pp. 61-63.
- Aslam S., Khan A. M., Ahmad R. M., Iqbal A., Waseem M. T., 2021 Systematic study of the new remains of *Propotamochoerus hysudricus* (Suidae, Mammalia) from the Late Miocene-Early Pliocene of Middle Siwaliks (Pakistan). *Arabian Journal of Geosciences* 14:73.
- Balint C., Papuc T., Coroian C., Bordea D., Oroian C., Bora F. D., Popescu M., Petrescu-Mag I. V., 2024 Molecular data in suid systematics and phylogeny: utility and limitations. *Porc Res* 14(1):56-61.
- Dăescu A. M., Popescu M., Coroian C. O., Bora F. D., Petrescu-Mag I. V., 2025 *Sus strozzii* Gray, 1821 and the early evolution of Eurasian pigs: zoological insights from a key fossil porcine. *Porc Res* 15(1):17-21.
- Gallai G., 2007 [Systematics, paleoecology, paleogeography of Italian fossil Suidae]. *Paleo Italia* 17:17-22. [in Italian]
- Gallai G., Rook L., 2006 *Propotamochoerus* sp. (Suidae, Mammalia) from the late Miocene of Gravitelli (Messina, Sicily, Italy) rediscovered. *Rivista Italiana di Paleontologia e Stratigrafia* 112(2):317-321.
- Gallai G., Rook L., 2011 *Propotamochoerus provincialis* (Gervais, 1859) (Suidae, Mammalia) from the latest Miocene (late Messinian; MN13) of Monticino Quarry (Brisighella, Emilia-Romagna, Italy). *Bollettino della Società Paleontologica Italiana* 50(1):29-34.
- Geraads D., Spassov N., Garevski R., 2008 New specimens of *Propotamochoerus* (Suidae, Mammalia) from the late Miocene of the Balkans. *Neues Jahrbuch Fur Geologie Und Palaontologie-Abhandlungen* 248(1):103-113.
- Hou S., Su D. F., Kelley J., Deng T., Jablonski N. G., Flynn L. J., Ji X., Cao J., Yang X., 2019 New fossil suid specimens from the terminal Miocene hominoid locality of Shuitangba, Zhaotong, Yunnan Province, China. *Journal of Mammalian Evolution* 26(4):557-571.
- Iannucci A., 2024 A reappraisal of the lost suids from the Late Miocene of Gravitelli (Sicily, Italy) and paleobiogeographical implications. *Palaeoworld* 33(2):469-491.
- Iannucci A., Begun D. R., 2022 Suidae (Mammalia, Artiodactyla) from the late Miocene hominoid locality of Alsótelekes (Hungary). *Geobios* 71:39-49.

- Iannucci A., Cherin M., Sorbelli L., Sardella R., 2021 Suidae transition at the Miocene-Pliocene boundary: a reassessment of the taxonomy and chronology of *Propotamochoerus provincialis*. *Journal of Mammalian Evolution* 28:323-335.
- Lazaridis G., Tsoukala E., Kostopoulos D. S., 2022 Validation of a prematurely abolished new *Propotamochoerus* Pilgrim, 1925 species (Mammalia, Suidae) from SE Mediterranean. *Comptes Rendus Palevol* 21(26):531-549.
- Martino R., Rook L., Mateus O., Pandolfi L., 2024 The Late Miocene hippopotamid, *Archaeopotamus pantanellii* nov. comb., from the Casino Basin (Tuscany, Italy): paleobiogeographic implications. *Historical Biology* 36(4):891-904.
- Petrescu-Mag I. V., Bora F. D., Popescu M., Oroian C., Daescu A. M., 2025 Taxonomic status, diagnosis, and evolutionary significance of the *Microstonyx major* (Gervais, 1848-1852). *Porc Res* 15(1):29-34.
- Pickford M., 2013 The diversity, age, biogeographic and phylogenetic relationships of Plio-Pleistocene suids from Kromdraai, South Africa. *Annals of the Ditsong National Museum of Natural History* 3(1):11-32.
- Van der Made J., Krakhmalnaya T., Kubiak H., 1999 The pig *Propotamochoerus palaeochoerus* from the upper Miocene of Grytsiv, Ukraine. *Estudios Geológicos* 55: 283-292.
- ***https://commons.wikimedia.org/wiki/File:MNEIN_Moldova_-_Skull_of_Propotamochoerus_provincialis_-_found_in_Musaitu_ravine.jpg. Accessed: November, 2025.

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