



## Taxonomic status, diagnosis, and evolutionary significance of the *Microstonyx major* (Gervais, 1848-1852)

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**Abstract.** Late Miocene suine, *Microstonyx major* (Gervais, 1848-1852) is a large extinct suid widely distributed across Eurasia during the late Miocene (Turolian, MN11–13) and represents one of the most characteristic suine taxa of this interval. It is taxonomically assigned to the subfamily Suinae. It is distinguished from other contemporaneous suids by a combination of reduced and relatively slender premolars, enlarged and morphologically complex molars, and characteristic cranial proportions, including a markedly elongated rostrum. Comparative morphological and metric analyses demonstrate pronounced intraspecific polymorphism, including strong sexual dimorphism and geographic variation in premolar reduction, which historically led to the erection of multiple nominal taxa later synonymized with *M. major*. Fossil evidence documents a broad geographic distribution extending from southeastern Europe and Anatolia, including important assemblages in Greece, Bulgaria, and Turkey, to eastern Asia, particularly China, and the Siwalik region of Pakistan. Phylogenetic analyses consistently place *M. major* as the earliest divergent member of the crown group Suinae, underscoring its importance for understanding the origin and early diversification of modern pig lineages. Functional and ecological interpretations of cranial and dental morphology indicate adaptation to intensive rooting and omnivorous feeding strategies, particularly in mesic and mosaic environments. Its broad stratigraphic range, morphological variability, and evolutionary trends make *M. major* a key biochronological marker and an essential taxon for reconstructing late Miocene paleoecological dynamics and suid evolutionary history.

**Key Words:** *Microstonyx major*, Suidae, Suinae, Late Miocene, Turolian, Eurasia, taxonomy, phylogeny, craniodental morphology, paleoecology, biochronology.

**Aim of the study.** This study aims to synthesize current knowledge regarding the taxonomic position, diagnostic morphology, phylogenetic relationships, geographic distribution, and paleoecological significance of Late Miocene suine, *Microstonyx major* (Gervais, 1848-1852), based on published fossil evidence and systematic revisions. Particular emphasis is placed on clarifying its diagnostic craniodental features, evaluating

the extent and implications of its intraspecific variability, and assessing its phylogenetic placement within crown Suinae. Additionally, this review seeks to highlight the biochronological and paleoenvironmental importance of the species, as well as its role in reconstructing dispersal patterns and evolutionary processes among late Miocene Eurasian suids.

**Taxonomic position and diagnosis of *Microstonyx major*.** *Microstonyx major* (Gervais, 1848–1852) is a large extinct suid widely distributed in the late Miocene (Turolian, MN11–13) of Eurasia and regarded as one of the characteristic elements of upper Miocene mammal faunas in southeastern Europe and western Asia (Van der Made & Hussain 1989; Kostopoulos et al 2001; Kostopoulos 2005; Van der Made et al 2013). It belongs to the subfamily Suinae within Suidae. It is usually distinguished from other late Miocene suines such as *Propotamochoerus*, *Hippopotamodon*, and *Molarochoerus* by its relatively slender and reduced premolars, enlarged and complex molars, and particular proportions of the skull and mandible (Liu et al 2004; Kostopoulos 2005; Van der Made et al 2013; Hou et al 2018).

Comparisons of multiple Eurasian populations show that *M. major* is a markedly polymorphic species, with strong sexual size dimorphism in cranial dimensions and variability in premolar reduction patterns (Kostopoulos et al 2001; Liu et al 2004; Kostopoulos 2005). This polymorphism initially led to the erection of several nominal taxa, such as *Hippopotamodon sivalense* and *Dicoryphochoerus titanoides*, which detailed revisions have subsumed under *M. major*, making the latter a broadly defined, long-ranging species (Van der Made & Hussain 1989; Kostopoulos 2005). In craniodental morphology, *M. major* differs from *Propotamochoerus* by less molarized fourth premolars (P4, p4) and distinctive m3/M3 structure, and from *Molarochoerus* by the latter's extreme premolar molarization, supporting the separation of these genera within Suinae (Gallai & Rook 2006; Hou et al 2018).

Phylogenetically, recent analyses of living and fossil suines place *M. major* as the earliest divergent member of the crown-Suinae clade, basal to the lineages leading to African suids (*Kolpochoerus*, *Metridiochoerus*, *Phacochoerus*) and Eurasian *Sus*, highlighting its importance for understanding the early evolution of modern pigs (Cherin et al 2018). Independent evidence from the Siwalik record suggests that *M. major*, together with *Hippopotamodon* and *Jhelumia*, arose from a *Propotamochoerus*-like ancestor within an ancient propotamochoeroid stock that also gave rise to *Potamochoerus* and *Sus* (Aslam et al 2021).

**Geographic and stratigraphic distribution.** The fossil record of *M. major* spans much of western and central Eurasia during the late Miocene (Bernor & Fessaha 2000; Pickford et al 2004; Liu et al 2005; Sylvestrou & Kostopoulos 2009). In southeastern Europe and Anatolia, the species is common in Turolian faunas (MN11–13), with rich material known from Greece, Bulgaria, and central Turkey (Kostopoulos et al 2001; Kostopoulos 2005; Van der Made et al 2013). The Akkasdağı locality in central Anatolia, dated to MN12, has yielded at least ten individuals, including juveniles and a nearly complete skull, representing a medium sized population with an elongated skull and moderately reduced premolars (Kostopoulos 2005).

In the Hayranlı–Haliminhani area (Sivas Basin, central Anatolia), *M. major* is documented from the Derindere Member of the İncesu Formation at localities 58-HAY-2 and 58-HAY-19. Detailed study of these assemblages, combined with biostratigraphic correlations, indicates that they belong to the lower part of MN11 rather than MN12, demonstrating an earlier occurrence of *M. major* in Anatolia than previously recognized. This reassignment is based partly on incisor morphology, which in 58-HAY-2 appears close to a morphological transition interpreted as an adaptation to intensified rooting, dated between about 8.7 and 8.12 Ma (Van der Made et al 2013).

To the east, large cranial remains from the Hezheng area of northern China confirm the presence of *M. major* in the late Miocene "Red Clay" Hipparion fauna (Liu et al 2004). These Chinese fossils represent a relatively small-sized eastern population with a reduced premolar row and marked sexual bimodality in size, suggesting both geographic structuring

and a degree of ecological specialization compared with western populations (Liu et al 2004). Combined with evidence from the Siwaliks of Pakistan, where *M. major* occurs in the Nagri Formation and shares species and genera with European faunas, this distribution indicates strong faunal interchange between western Eurasia and northern South Asia during the late Miocene (Van der Made & Hussain 1989; Liu et al 2004; Aslam et al 2021).



Figure 1. Geographic distribution of *Microstonyx major* during the Late Miocene (Turolian MN11–13).

**Intraspecific variability and subspecific groups.** Detailed metric and morphological analyses of southeastern European and Anatolian material have revealed significant geographic and temporal structuring in *M. major*. A study of Bulgarian Turolian localities (MN11–13), together with Greek material, supports the recognition of at least three morphometric groups that may correspond to subspecies or chronomorphs. The earliest group (MN11–12) comprises small-sized forms with relatively elongated premolar rows and small third molars; these populations, represented for example at Perivolaki, Kerassia, and Vathylakkos, likely represent a distinct small-medium subspecific lineage related to the Maragha suid of Iran (MN11) (Kostopoulos et al 2001).

A second group (MN12–13) includes medium sized individuals attributed to *M. major* erymanthius. In contrast, a third group, *M. major*, characterizes the latest Turolian (MN13) and is generally larger, with further premolar reduction and molar row shortening (Kostopoulos et al 2001). The last two groups appear closely related to one another and to the latest Vallesian *M. major* from Nikiti (end of MN10), suggesting a coherent evolutionary trend from earlier, small-bodied and relatively premolar-rich forms toward larger, long-skulled forms with reduced premolars (Kostopoulos et al 2001; Kostopoulos 2005). Statistical comparisons with northern Chinese material indicate that *M. major* as a whole was highly polymorphic, with regional differences in body size and premolar reduction but a shared pattern of allometric growth that distinguishes it from *Hippopotamodon*, whose relatively stout premolars reflect a different allometric trajectory (Liu et al 2004). This suite of traits reinforces the recognition of *M. major* as a single, variable species across its wide range, rather than a complex of closely related but distinct taxa (Van der Made & Hussain 1989; Kostopoulos et al 2001; Liu et al 2004; Kostopoulos 2005).

**Functional morphology and ecology.** Functional interpretations of the craniodental anatomy of *M. major* point to a suid adapted to intensive rooting and to exploiting relatively soft, probably mesic, substrates and plant resources. The species is characterized by large, bunodont molars with well-developed cusps and complex enamel topography suited to crushing and grinding, consistent with an omnivorous diet dominated by fibrous plant material and underground storage organs (Kostopoulos et al 2001; Kostopoulos 2005; Van der Made et al 2013).

A key feature is the evolutionary change in lower incisor morphology documented in the Hayranlı-Halimani assemblages. *M. major* shows a trend toward more procumbent, enlarged incisors with modified occlusal surfaces, interpreted as a further adaptation to rooting behavior. The timing of this incisor transformation, constrained to a relatively brief interval between about 8.7 and 8.12 Ma, suggests a rapid evolutionary response to environmental change, possibly reflecting a shift to more seasonal or closed habitats where digging for below-ground resources became increasingly important (Van der Made et al 2013).

Skull proportions from Akkasdağı and other MN12 localities indicate a strongly elongated rostrum relative to the braincase, combined with moderate premolar reduction (Kostopoulos 2005). This cranial elongation appears to be associated with the terminal phase of the species' ecological range, implying that late Turolian populations of *M. major* may have specialized toward particular foraging strategies or habitat types before their extinction (Kostopoulos 2005). Postcranial remains, although less frequently described, are consistent with an animal of substantial body size and robust build, suitable for ranging widely and exploiting a variety of habitats, from open woodlands to more humid, forest-bordered environments (Kostopoulos et al 2001; Liu et al 2004; Kostopoulos 2005).

Comparisons with coeval suids reinforce this ecological inference. In northern China, the presence of *M. major* in the Red Clay faunas, which represent a later and more humid phase of the regional late Miocene, indicates that the genus preferred or at least persisted best in relatively humid conditions, in contrast to drier, more open paleoenvironments where other suids dominated (Liu et al 2004). Similarly, in Anatolia and southeastern Europe, *M. major* is part of faunal assemblages interpreted as wooded or mosaic habitats rather than pure open steppe (Kostopoulos et al 2001; Kostopoulos 2005; Van der Made et al 2013).

**Evolutionary relationships within suinae.** The evolutionary history of *M. major* must be viewed against the broader diversification of Suinae in the late Miocene. Detailed revision of Siwalik suids shows that *Propotamochoerus hysudricus*, a medium sized species with enlarged cheek teeth and elongated m1, is a key representative of an ancestral propotamochoeroid stock that gave rise to several major lineages (Aslam et al 2021). One branch led to *Potamochoerus* and *Sus*, another to *Hippohyus* and *Sivahyus*, and a third to *M. major*, *Hippopotamodon*, and *Jhelumia* (Aslam et al 2021). This scenario is consistent with more recent cladistic analyses that recover *M. major* as the basalmost member of a monophyletic Suinae, branching off before the divergence of African and Eurasian modern pig lineages (Cherin et al 2018; Aslam et al 2021).

The early separation of *M. major* suggests that it retained a mosaic of plesiomorphic and derived traits. On one hand, its general cranial and dental pattern links it to more primitive Miocene suines such as *Palaeochoerus* and *Hyotherium* via *Propotamochoerus*; on the other hand, its degree of premolar reduction, molar enlargement, and cranial elongation anticipates character states later seen in *Sus* and some verrucosic pigs (Cherin et al 2018; Aslam et al 2021). This intermediate status makes *M. major* an important taxon for calibrating rates and pathways of craniodental evolution in Suinae, especially the transition from generalized browsing-omnivory to more specialized rooting and mixed feeding typical of many modern pigs.

Biogeographically, the presence of *M. major* in both western Eurasia and northern China, combined with shared taxa between Indian and Eurasian faunas, implies substantial faunal interchange across the Eurasian landmass in the late Miocene (Van der Made & Hussain 1989; Liu et al 2004; Aslam et al 2021). The distinct suid assemblage of northern China, in which *M. major* co-occurs with other derived suines, marks a biogeographic

province connected to western Eurasia yet isolated from southern China and the Indian subcontinent, underscoring the role of climatic and topographic barriers in structuring late Miocene mammalian dispersals (Liu et al 2004).

**Paleoenvironmental and biochronological significance.** Because of its broad distribution, stratigraphic range, and well-documented morphological evolution, *M. major* serves as a valuable biochronological and paleoenvironmental indicator in late Miocene deposits. Subtle changes in tooth proportions, incisor morphology, and skull elongation help refine local biozonations within the Turolian (MN11–13), particularly in southeastern Europe and Anatolia (Kostopoulos et al 2001; Kostopoulos 2005; Van der Made et al 2013). For example, the recognition that the Hayranlı–Halimani suid assemblages belong to the lower part of MN11 rather than MN12 rests in part on the transitional state of incisor morphology, interpreted as lying close to the onset of enhanced rooting adaptation (Van der Made et al 2013).

In central Anatolia, the Akkasdağı population corresponds to late middle Turolian (MN12) and shares a suite of characters, medium size, elongated skull, moderate premolar reduction, with other MN12 populations, recording a phase near the end of the species' ecological range (Kostopoulos 2005). In the Balkans, differentiation among the three *M. major* groups provides additional resolution for correlating localities across Greece and Bulgaria and for tracking faunal changes through the Turolian, including shifts in community composition toward more open or more humid habitats (Kostopoulos et al 2001).

In northern China, the restriction of *M. major* to the later, more humid Red Clay faunas links its occurrence to a specific climatic phase. It supports paleoenvironmental reconstructions of increased humidity in the late Miocene of the Hezheng area (Liu et al 2004). Thus, beyond its taxonomic interest, *M. major* integrates information across morphology, biogeography and stratigraphy, contributing to a more nuanced understanding of late Miocene ecosystem dynamics and the evolutionary history of Suidae in Eurasia (Van der Made & Hussain 1989; Kostopoulos et al 2001; Liu et al 2004; Kostopoulos 2005; Van der Made et al 2013; Cherin et al 2018; Aslam et al 2021).

**Conclusions.** *Microstonyx major* represents a distinct and evolutionarily significant member of Suinae, characterized by a unique combination of reduced premolars, enlarged bunodont molars, and elongated cranial morphology. Despite marked polymorphism, including geographic variation and sexual dimorphism, available morphological and metric evidence support its recognition as a single, widely distributed species rather than a complex of multiple closely related taxa. Phylogenetically, its basal position within the crown-group Suinae underscores its importance for understanding the early evolutionary divergence of modern pig lineages. Its extensive geographic range across Eurasia and its presence in multiple well-dated Turolian faunas demonstrate substantial faunal interchange during the late Miocene. Functional adaptations, particularly in incisor and molar morphology, indicate ecological specialization toward intensive rooting and omnivorous feeding in mesic and mosaic environments. Furthermore, its well-documented evolutionary trends and stratigraphic distribution make *M. major* a valuable biochronological and paleoenvironmental indicator, contributing significantly to the reconstruction of late Miocene ecosystem dynamics and the evolutionary history of Eurasian Suidae.

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

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Received: 18 October 2025. Accepted: 22 November 2025. Published online: 30 December 2025.

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How to cite this article:

Petrescu-Mag I. V., Bora F. D., Popescu M., Oroian C., Dăescu A. M., 2025 Taxonomic status, diagnosis, and evolutionary significance of the *Microstonyx major* (Gervais, 1848-1852). *Porc Res* 15(1):29-34.