



## Systematics, paleoecology, and evolutionary significance of *Hippopotamodon antiquus* within the Late Miocene Suidae

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**Abstract.** The reconstruction of suid taxonomy and phylogeny relies heavily on fossil evidence, which documents the extensive evolutionary history of the family beyond its limited modern diversity. This mini-review examines the role of fossil taxa in suine systematics, with a particular focus on *Hippopotamodon antiquus*, a large tetraconodontine suid widely distributed in the Late Miocene of southeastern Europe and the eastern Mediterranean. The taxonomic history of *H. antiquus* has been complicated by fragmentary material and morphological overlap with other large suids, but recent revisions have refined its diagnosis based on dental and postcranial characteristics. The species is characterized by massive bunodont dentition, robust cranial architecture, and heavily built postcranial elements, indicating a large-bodied, graviportal omnivorous-herbivorous lifestyle. Biochronological data place *H. antiquus* primarily within Vallesian faunas (ca. 9.6-9.4 Ma), where it occurs in association with woodland-adapted mammalian assemblages. Paleoecological evidence suggests that it inhabited humid, forest-savanna mosaic environments, exploiting a broad dietary niche. Phylogenetically, *H. antiquus* represents a derived member of the Eurasian tetraconodontine radiation and occupies a key position in understanding late Miocene suid diversification and biogeographic connectivity across the Aegean region. This synthesis highlights the importance of integrating fossil data in reconstructing suid evolutionary history and clarifying the ecological roles of extinct large-bodied suines.

**Key Words:** biochronology, eastern Mediterranean, fossil mammals, *Hippopotamodon antiquus*, Late Miocene, paleoecology, phylogeny, suid evolution, Suidae, taxonomy, Tetraconodontinae, Vallesian.

**Introduction.** The reconstruction of suid (Suidae) taxonomy and phylogeny critically depends on the integration of fossil evidence, as extant diversity represents only a small and derived fraction of a much broader evolutionary history (Raza et al 2023; Pacheco-Scarpitta 2025). The family Suidae originated at least as early as the Oligocene in Asia and subsequently diversified extensively across Afro-Eurasia, producing numerous extinct lineages with a wide range of ecological adaptations (Balint et al 2024). Consequently, modern suine taxonomy cannot be fully understood without reference to these fossil taxa, which document transitional morphologies, ancestral character states, and extinct branches of the phylogenetic tree.

Fossil suids are particularly important for clarifying systematic relationships because morphological convergence - especially in dental structures - has historically led to taxonomic confusion and misclassification among both fossil and extant forms (Pickford 2011). The inclusion of fossil taxa allows researchers to break up long branches in phylogenetic reconstructions, identify homologous versus convergent traits, and calibrate divergence times using stratigraphic data. In modern evolutionary frameworks, fossils are indispensable for time-calibrated phylogenies, providing the only direct evidence for the temporal dimension of lineage diversification.

Several fossil taxa illustrate the central role of paleontological data in suid systematics. For instance, *Sus arvernensis* represents one of the earliest well-defined members of the genus *Sus* in Eurasia and is widely regarded as close to the ancestry of multiple extinct and extant suine lineages, making it crucial for understanding the origin of modern pigs (Iannucci et al 2024). Similarly, the extinct genus *Kolpochoerus* provides key insights into African suid evolution, showing morphological affinities with modern genera such as forest hogs and warthogs and documenting diversification during the Plio-Pleistocene (Gavriloaie & Burduhos 2023; Gavriloaie & Petrescu-Mag 2023; Pickford & Chaïd-Saoudi 2024).

Other important fossil groups include members of the subfamily Tetraconodontinae, an extinct lineage of suids distributed in Africa and Asia, which exhibit distinct dental and cranial adaptations and help elucidate early diversification patterns within the family (Alba et al 2025). Miocene taxa such as *Propotamochoerus* and related forms further contribute to reconstructing the early radiation of Suinae and the ecological contexts in which modern suids evolved (Iannucci & Begun 2022).

In addition, the integration of fossil and extant material within unified taxonomic frameworks has proven essential for achieving consistency in classification. Comparative studies that analyze both fossil and living species using the same morphological criteria demonstrate that only through such integration can a coherent and evolutionarily meaningful taxonomy be established (Hardjasasmita 1987).

Fossil suids are not merely supplementary data but constitute a fundamental component of suine systematics. They provide critical information on ancestral morphologies, evolutionary transitions, and temporal frameworks, enabling a more robust and accurate reconstruction of the taxonomy and phylogeny of modern pig species.

The aim of this study is to synthesize current knowledge on the taxonomy, morphology, paleoecology, and evolutionary context of *Hippopotamodon antiquus* (Kaup, 1833) in order to clarify its role within Late Miocene suid diversification and Eurasian faunal dynamics.

**Taxonomic history and diagnosis of *Hippopotamodon antiquus*.** *H. antiquus* is a large suine artiodactyl of the tribe Tetraconodontini, widespread in late Miocene deposits of Europe and the Eastern Mediterranean. Its taxonomy has long been complicated by the fragmentary nature of type material, overlapping size ranges with other large suines (notably *Microstonyx* and some metridiochoerines) (van der Made & Hussain 1989; Harris & Liu 2007; Pickford 2016), and historical use of a broad "*H. antiquus*" concept for diverse late Miocene forms. Recent systematic work on upper Miocene artiodactyl assemblages in the eastern Mediterranean, including Küçükçekmece West and East (European Turkey), has refined the diagnosis of *H. antiquus* and clarified its separation from other suids in Vallesian faunas (Kostopoulos & Sen 2016). At Küçükçekmece West, *H. antiquus* is documented by isolated cheek teeth and postcranial elements, notably robust lower premolars (p2-p3) and a large magnum, which together indicate a very large, heavily built suid (Kostopoulos & Sen 2016; Kostopoulos & Sylvestrou 2021). The teeth show stout, bunodont cusps and strong basal cingula, with dimensions exceeding those of sympatric medium-sized suids and approaching the upper size range of European Miocene suines (Kostopoulos & Sen 2016).

Cranial and more complete mandibular material from other late Miocene localities (synthesized in broader suoid systematic revisions) depict *H. antiquus* as a very large, short-faced suid with extremely robust zygomatic arches, a deep rostrum, and greatly developed canines, especially in males, indicating strong sexual dimorphism and intraspecific competition similar to that in other large Miocene and Plio-Pleistocene suids (Kostopoulos & Sen 2016). The lower premolars are relatively shortened and broadened, with complex accessory cusps, and the molars are massive, with low crowns and expanded talonids, consistent with highly abrasive but still predominantly bunodont mastication (Bernor & Fessaha 2000). The genus is thus differentiated from more cursorial, slender snouted tetraconodonts and from the highly specialized, horned kubanochoeres by its combination of extreme robusticity, large size and conservative bunodonty (Kostopoulos & Sen 2016).

**Stratigraphic range and geographic distribution.** *H. antiquus* is characteristic of late Miocene (mainly Vallesian) faunas of southeastern Europe and adjacent Anatolia. The record at Küçükçekmece West, dated biochronologically to about 9.6-9.4 Ma, provides a key age anchor for the species (Liu et al 2005; Kostopoulos & Sen 2016). The artiodactyl association, dominated by the tragulid *Dorcatherium* and giraffids such as *Palaeogiraffa*, constrains the assemblage to the early Vallesian and demonstrates that *H. antiquus* was already established in the eastern Mediterranean at this time (Kostopoulos & Sen 2016). Comparable large *Hippopotamodon* material is known from other Vallesian and early Turolian localities in the Balkans and Anatolia, although detailed modern revisions remain incomplete; most authors regard *H. antiquus* as a broadly distributed large suid taxon in the circum-Aegean region during the late Miocene, with possible westward extensions into central Europe. The rarity of complete individuals and the frequent use of open nomenclature (*H. antiquus*) reflect persistent taxonomic uncertainty at species level in many assemblages (Kostopoulos & Sen 2016).

**Associated faunal assemblages and paleoenvironment.** The paleoecology of *H. antiquus* is best inferred from its occurrence within multi-taxon artiodactyl communities. At Küçükçekmece, *H. antiquus* co-occurs with a rich assemblage including *Dorcatherium maliki*, *Palaeotragus*, *Palaeogiraffa pamiri*, *Bohlinia* cf. *attica*, several bovids and gazelles, within deposits interpreted as Vallesian in age (Kostopoulos & Sen 2016). The dominance of *Dorcatherium*, a small tragulid associated with dense woodland and forest understorey, and of the medium-sized giraffid *Palaeogiraffa*, together with the presence of large browsing giraffids and a diverse bovid fauna, indicates predominantly wooded conditions with local open patches rather than extensive grasslands (Kostopoulos & Sen 2016).

In this ecological framework, *H. antiquus* likely occupied the role of a large, omnivorous-herbivorous suid exploiting a mixture of browse, fruits, roots and some grasses in forest-savanna mosaics along riverine and lakeshore environments. Its great body size and powerful jaws suggest the capacity to process tough, fibrous plant material and possibly to scavenge or predate opportunistically on small vertebrates, paralleling the ecological breadth of modern large suids but at larger body mass. The presence of robust limb elements such as the magnum, and the overall rarity of cursorial specializations, are consistent with a graviportal, relatively slow-moving animal adapted to soft, vegetated substrates and riparian settings.

**Functional morphology and biology.** Although postcranial remains of *H. antiquus* are still few, the available material and comparisons with other large suids indicate a strongly built skeleton supporting a massive trunk and large head (Figure 1). The magnum from Küçükçekmece shows enlarged articular surfaces for metacarpals, reflecting substantial weight bearing and a powerful forelimb adapted to rooting and possibly to intraspecific combat (Kostopoulos & Sen 2016). Short, broad premolars and low-crowned molars with expanded occlusal surfaces point to heavy occlusal loading and a grinding masticatory regime; wear patterns in comparable large suids suggest extensive mastication of coarse vegetation and perhaps grit-rich diets in floodplain environments.

Cranial reconstructions based on related *Hippopotamodon* and other tetraconodonts suggest that males bore enormous, laterally projecting canines used for display and combat, while females possessed smaller but still robust tusks. Such sexual dimorphism implies a polygynous social structure with intense male-male competition, probably in riverine territories or around key resource patches. The combination of large size, robust limbs and semi-aquatic or at least water-associated habitats is convergent in several large late Miocene suines and reflects a general trend toward exploitation of productive, wet lowland ecosystems.



Figure 1. Skull of *H. antiquus*

(source: <https://age-of-mammals.ucoz.ru/index/gippopotamodony/0-2311>).

**Phylogenetic relationships and evolutionary context.** *H. antiquus* is part of the Eurasian tetraconodontine radiation that includes genera such as *Microstonyx* and some African metridiochoerines. Systematic revisions of late Miocene suids consistently place *Hippopotamodon* among the most derived and largest suines of the European record, evolving from smaller, more generalized tetraconodont ancestors during the middle to late Miocene, in parallel with the diversification of ruminant lineages in increasingly seasonal but still wooded environments. The occurrence of *H. antiquus* at Küçükçekmece alongside a bovid and giraffid assemblage with strong Anatolian and southern Balkan affinities highlights faunal connections across the Aegean region and supports a biogeographic scenario of repeated dispersals between Anatolia and southeastern Europe during the Vallesian (Kostopoulos & Sen 2016).

Within this framework, *H. antiquus* represents a high-biomass, large suid niche that may have been ecologically analogous to later Pliocene-Pleistocene large hippopotamids and suids in Eurasia and Africa, although still fully artiodactyl and not closely related to *Hippopotamus*. Its eventual disappearance from the fossil record coincides with the late Miocene-early Pliocene restructuring of Eurasian faunas, with the expansion of more advanced suids and the rise of highly efficient large ruminants in open habitats, which likely outcompeted *Hippopotamodon* in many regions as climates became cooler and more seasonal.

**Conclusions.** *Hippopotamodon antiquus* is a key element of late Miocene suid diversity in the eastern Mediterranean, characterized by very large body size, robust bunodont dentition and heavily built postcranial elements. Refined biochronological and paleoenvironmental data from Vallesian assemblages such as Küçükçekmece West place this taxon in wooded, water-rich landscapes at about 9.6-9.4 Ma and emphasize its role as a dominant large omnivorous-herbivorous suid in forest-savanna mosaics. Ongoing revisions of Miocene suid systematics and additional material from Anatolia and the Balkans will further clarify its phylogenetic relationships, geographic range and evolutionary fate within the broader context of Eurasian late Neogene mammal communities.

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

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