



Taxonomic status, diagnosis, and paleoecological significance of the *Listriodon splendens* von Meyer, 1846

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Abstract. Lophodont Miocene suid, *Listriodon splendens* von Meyer, 1846, is a large, highly specialized lophodont suid belonging to the subfamily Listriodontinae, a group of herbivorous pigs that achieved wide geographic distribution across Eurasia and Africa during the Miocene. This species is one of the most derived members of the genus *Listriodon*, characterized by fully developed bilophodont molars, robust cranial architecture, and a robust postcranial skeleton. Its diagnostic morphology includes strongly transverse molar lophs adapted for efficient shearing of plant material, thickened frontal bones, and pronounced sexual dimorphism expressed in canine size and cranial protuberances in males. The fossil record demonstrates a broad distribution across western and central Europe, including Spain, France, Germany, Switzerland, and Austria, and extends eastward into Turkey and possibly into Kenya. Stratigraphically, its occurrence spans the middle to late Miocene (MN6-MN9), with its last confirmed European occurrence near 9.78 Ma. Functional, isotopic, and microwear evidence indicate that *L. splendens* was a specialized browser with a significant frugivorous component, inhabiting mesic woodland environments. Its extinction coincided with major climatic and vegetational shifts during the late Miocene, marking the final stage of listriodontine evolution in Europe and reflecting broader ecological restructuring of herbivore communities.

Key words: *Listriodon splendens*, Listriodontinae, suidae, Miocene, taxonomy, lophodont dentition, sexual dimorphism, paleoecology, browsing adaptation, extinction.

Aim of the study. This study aims to synthesize current knowledge concerning the taxonomic status, diagnostic morphology, phylogenetic relationships, stratigraphic distribution, and paleoecological adaptations of *Listriodon splendens*. This review clarifies its cranial, dental, and postcranial features, assesses the extent and implications of sexual dimorphism and intraspecific size variation, and evaluates its evolutionary position within Listriodontinae. Additionally, the study seeks to examine the ecological specialization of the species and its significance for understanding the evolutionary decline and extinction

of listriodontine suids in relation to environmental and climatic changes during the late Miocene.

Taxonomic status and diagnosis of *Listriodon splendens*. Lophodont Miocene suid, *Listriodon splendens* von Meyer, 1846, is a large, highly lophodont Miocene suid belonging to the subfamily Listriodontinae, a clade of “lophodont pigs” that dispersed widely across Eurasia and Africa during the early-late Miocene (van der Made 1996; van der Made & Moullé 2005; Pickford & Morales 2021; van Der Made et al 2022). Within Listriodon, *L. splendens* represents one of the most derived, fully lophodont species, characterized by strongly transverse lophs on the molars and a robust postcranial skeleton, in contrast to the more gracile Eurolistriodon, which bears elongated limb bones and a more developed canine flange (Orliac 2009; Pickford & Morales 2021). Recent systematic work confirms the distinctiveness of *L. splendens* from contemporaneous listriodonts such as *Listriodon lockharti* and from bunodont listriodontines placed in Bunolistriodon or Libycochoerus (Fortelius et al 1996; Orliac 2009; Pickford & Morales 2021).

The species has sparked taxonomic debate at the intraspecific level. A large form traditionally referred to as *L. splendens major* was described from several European localities, but the priority of the older name *trux* from La Chaux-de-Fonds suggests that *Listriodon splendens trux* may be the valid name for this large morph, and observed size bimodality may partly reflect sexual dimorphism rather than discrete subspecies (Pickford et al 2020). Despite these nomenclatural issues, *L. splendens* is consistently diagnosable by its large body size, fully lophodont cheek teeth, and cranial morphology, including thickened frontals and, in males, cranial protuberances associated with enlarged canines (Fortelius et al 1996; Pickford et al 2020; Pickford & Morales 2021).

Cranial, dental, and postcranial morphology. Cranial material from Europe and Anatolia reveals marked sexual dimorphism in *L. splendens*. Male skulls bear massive upper canines and a horn-like ossicone or frontal protuberance, as documented in the Nebisuyu skull from MN8 deposits in Turkey, interpreted as a male of the large *L. splendens* morph. This specimen shows a thickened frontal region with a horn-like process, and its dentition matches the large, fully lophodont “major” form (Pickford et al 2020). Similar cranial appendages occur on European material, and comparative cranial work on listriodonts indicates that such structures are absent or less developed in primitive Eurolistriodon and in early bunodont Listriodontinae (Orliac 2009; Pickford & Morales 2021).

Dentally, *L. splendens* is among the most lophodont of listriodonts, with upper and lower molars showing strongly developed transverse lophs (bilophodonty) and reduced cuspidal relief, an adaptation interpreted as suited to shearing leafy and soft plant matter (Hunter & Fortelius 1994; Tsubamoto et al 2017; Pickford & Morales 2021; van der Made et al 2022). Comparative microwear and facet analyses of sympatric listriodonts from Paşalar show that *Listriodon* cf. *splendens* has larger, more continuous wear facets on “phase II” surfaces than the sublophodont *Listriodon* aff. *latidens*, indicating more extensive transverse shearing and a more specialized browsing signal (Hunter & Fortelius 1994). The canines of males are particularly large and robust, and the upper central incisors may be relatively widened in some populations, paralleling the condition in related listriodont taxa (Fortelius et al 1996).

Postcranially, *L. splendens* exhibits short, robust limb bones in contrast to the elongated, gracile elements of Eurolistriodon, indicating a heavier-built animal adapted to relatively stable, perhaps forested or woodland substrates rather than cursorial locomotion in open grasslands (Pickford & Morales 2021). Postcranial material attributed to *L. cf. splendens* from Cuesta del Rey in Spain, including scapula, humerus, radius, metacarpal, and phalanges, confirms a large, stout suid with strong proximal and distal epiphyses consistent with supporting a heavy body mass (Sesé & Morales 2017).

The fossil skull of *L. splendens* demonstrates the robust morphology and derived cranial features characteristic of the species (Figure 1).



Figure 1. Fossil skull (specimen IVPP V8285) of *Listriodon splendens*. Source: Jonathan Chen, Wikimedia Commons. Licensed under Creative Commons Attribution-ShareAlike 4.0 International (CC BY-SA 4.0). <https://creativecommons.org/licenses/by-sa/4.0/>

Stratigraphic and geographic distribution. *L. splendens* is among the best-represented listriodontines in the European Neogene fossil record. Biostratigraphic syntheses place its range from MN6 to MN9, with more than 100 localities across Portugal, Spain, France, Germany, Switzerland, and Austria yielding material referable to this species (van der Made et al 2014; Pickford & Morales 2021; van der Made et al 2022). The last dated occurrence in Europe is at Can Llobateres 1 (Spain), magnetostratigraphically dated to 9.78 Ma near the end of MN9, establishing *L. splendens* as the final surviving listriodont in Europe. No younger localities have reliably produced this taxon (van der Made et al 2022).

Within Europe, *L. splendens* is abundant in sites such as Gratkorn (Austria, late Sarmatian, ca. 12.2–12.0 Ma), where associated suid material has been confidently assigned to the species on dental grounds. In the Iberian Peninsula, it occurs at numerous Aragonian and early Vallesian localities, including Castell de Barberà, where *L. splendens* co-occurs with several tetraconodontines and suines (Aiglstorfer et al 2014; van der Made et al 2014). Its absence at slightly older Vallesian sites such as Creu de Conill 20, where other suids are well represented, has been interpreted as reflecting local paleoenvironmental differences rather than large-scale biogeographic exclusion (McKenzie et al 2022).

Beyond western and central Europe, *L. splendens* extends eastward into Anatolia and possibly further into Asia. The Nebisuyu MN8 locality in the Gelibolu Peninsula of Turkey yielded a nearly complete male skull with typical *L. splendens* major dentition, extending the range of the large morph to the eastern Mediterranean (Pickford et al 2020). Additional listriodontine material from the upper Miocene of Nakali, Kenya, includes cf. *Listriodon* sp. with molar morphology comparable in size and lophodonty to *L. splendens* and *Listriodon pentapotamiae*, suggesting that a highly derived *Listriodon* lineage closely allied to *L. splendens* reached East Africa around 10 Ma (Orliac 2009; Tsubamoto et al 2017; van der Made et al 2022).

Palaeoecology and diet. Stable isotope and microwear evidence indicate that *L. splendens* was a specialized browser with a significant frugivorous component. At Gratkorn, carbon and oxygen isotope data from tooth enamel show values typical of browsing on C3 vegetation in mesic woodland settings, and *L. splendens* plots among taxa interpreted as forest-dwelling browsers. Its isotopic signature suggests a diet dominated by leaves, with a considerable input of fruits and possibly some grass, contrasting with the more root and tuber-feeding habits inferred for the sympatric suid *Parachleuastochoerus steinheimensis* (Aiglstorfer et al 2014).

Independent paleoenvironmental reconstructions support this view. In central European mid-Miocene forests such as St. Stefan (Austria, ca. 12.5 Ma), *L. splendens* is one of the most abundant large mammals. The flora there was dominated by deciduous and evergreen broad-leaved trees (*Quercus*, *Fagus*, *Castanea*, *Carya*, *Pterocarya*, *Engelhardia*, *Juglans*), with understory taxa producing sugar-rich fruits from June to December. The presence of severe dental caries in co-occurring hominoids has been linked

to high fruit consumption. Given the similar dental adaptations among late listriodontines, it is likely that *L. splendens* exploited similar fruit resources in such forested habitats (Aiglstorfer et al 2014; van der Made et al 2022).

Microwear and occlusal facet analyses from Paşalar point to differences in tooth use between lophodont *Listriodon* cf. *splendens* and sublophodont congeners. In *L. cf. splendens*, phase II facets on molars are larger and more heavily worn, consistent with powerful transverse shearing during the late closing phase, whereas *L. aff. latidens* shows a somewhat more generalized wear pattern (Hunter & Fortelius, 1994). This suggests that *L. splendens* may have been more tightly specialized on tough, fibrous foliage and pulpier plant tissues, while sharing the general browsing niche typical of listriodontines (Hunter & Fortelius 1994; Pickford & Morales 2021).

Behavioural inferences and sexual dimorphism. The combination of enlarged canines, cranial ossicones, and a robust skull roof in male *L. splendens* has prompted behavioral inferences drawn by analogy to extant suids. The Nebisuyu skull exhibits a prominent horn-like frontal protuberance interpreted as an ossicone used in head-to-head combat or display, similar to cranial appendages in modern suids such as *Phacochoerus* and *Potamochoerus* (Pickford et al 2020; Gavriloiu & Burduhos 2023; Oroian & Proorocu 2023). The marked sexual dimorphism in canine size and cranial morphology supports a social system in which male–male competition for mates was intense, likely involving physical clashes and ritualized displays (Pickford et al 2020; Pickford & Morales 2021).

Historically used size differences to define subspecies (*splendens* versus *major* or *trux*) may, in part, reflect sexual bimodality. The La Chau-de-Fonds sample includes both smaller and larger individuals within what appears to be a single morphologically coherent taxon, and current evidence suggests that the larger individuals may be males and the smaller ones females. However, the limited sample hinders firm conclusions. Nonetheless, dimorphism in cranial ornamentation and tooth size is now well documented in *L. splendens* and should be carefully considered in future systematics and paleoecological reconstructions (Pickford et al 2020; Pickford & Morales 2021).

Evolutionary context and relationships within Listriodontinae. *L. splendens* evolved within a rapidly diversifying radiation of listriodontines that underwent major dental and cranial changes between about 20 and 10 Ma. Early listriodonts were bunodont or only weakly lophodont, and phylogenetic and comparative studies indicate that the subfamily likely originated from a hyotheriid ancestor similar to *Hyotherium meisneri* (Pickford & Morales 2021; van der Made 1996; Orliac 2009). The earliest listriodontines, including *Lopholistriodon* and early *Bunolistriodon*, exhibit limited molar lophodonty and lack cranial appendages (Fortelius et al 1996; Orliac 2009).

By the middle Miocene, fully lophodont lineages such as *Listriodon* (in the strict sense) appear in Europe and western Asia, with species like *L. lockharti*, *L. latidens*, and eventually *L. splendens* representing increasingly derived stages in molar lophodonty and body size (Hunter & Fortelius 1994; Fortelius et al 1996; Pickford & Morales 2021). Phylogenetic analyses of Listriodontinae place *Listriodon*, together with *Eurolistriodon*, in a derived clade closely related to the horned *kubanochoeres*, whereas *Lopholistriodon* occupies a more basal position (van der Made 1996; Orliac 2009). The strongly lophodont, large-bodied condition of *L. splendens* thus reflects a late-stage specialization within this clade.

Biogeographically, Listriodontinae reached their maximum diversity and geographic spread during the Mid-Miocene Climatic Optimum (about 17–13.6 Ma) and subsequently declined (van der Made 1996; van der Made et al 2022). *L. splendens*, flourishing between MN6 and MN9, represents the terminal European branch of this radiation. Contemporaneous derived listriodontines in Asia, such as *L. pentapotamiae* and the later *Listriodon dukkar*, share similar dental adaptations and may form a broader lineage of large, fully lophodont browsers that persisted in the Siwaliks until about 9.8 Ma (van der Made et al 2022; Zulfiqar et al 2025). Fragmentary material from Nakali suggests that a related derived lineage dispersed into East Africa by roughly 10 Ma (van der Made 1996; Orliac 2009; Tsubamoto et al 2017).

Extinction and paleoenvironmental change. The extinction of *L. splendens* and other late listriodontines coincided with substantial environmental and floral changes across the Old World during the late Miocene. Temporal syntheses indicate that listriodontines persisted for roughly 10 million years, with their last records around 9.8 Ma in the Indian Subcontinent, 9.78 Ma in Europe (Can Llobateres 1 for *L. splendens*), and about 10 Ma in Africa (van der Made et al 2022). During this interval, global and regional climates became more seasonal, forests contracted in many regions, and open habitats with increasing bovid diversity expanded (Aiglstorfer et al 2014; van der Made et al 2022).

Van der Made and colleagues have proposed that declining atmospheric pCO₂ played a key role in this extinction. Decreasing pCO₂ is expected to lower sugar content and increase protein content in leaves and fruits, altering the nutritional profile of browse resources (van der Made et al 2022). Because listriodontines were likely foregut fermenters with lophodont dentitions adapted to processing sugar-rich leaves and fruits, they may have been disadvantaged in a world where such resources became less rewarding energetically, particularly relative to more omnivorous bunodont suids and increasingly diverse ruminants (Van der Made 1996; van der Made et al 2022).

At the local scale, paleoecological reconstructions corroborate these broader trends. At Gratkorn, niche partitioning among large herbivores shows *L. splendens* as a specialized browser with substantial fruit intake in a mesic woodland mosaic. At the same time, other suids and ruminants occupy adjacent niches (Aiglstorfer et al 2014). As environments became more open and seasonal in the late Miocene, such specialized frugivorous browsers may have faced both resource limitation and intensified competition from expanding bovid lineages and other browsers that were more flexible in their diets or better adapted to drier conditions (Aiglstorfer et al 2014; van der Made et al 2022). The disappearance of *L. splendens* thus marks not only the end of a successful listriodont lineage but also a broader restructuring of late Miocene herbivore communities across Eurasia.

Conclusions. *Listriodon splendens* is one of the most morphologically specialized and evolutionarily advanced members of Listriodontinae, characterized by fully developed lophodont dentition, a robust skeletal structure, and pronounced cranial adaptations associated with feeding and intraspecific behavior. Its diagnostic dental morphology, particularly strongly developed transverse molar lophs, indicates a high degree of dietary specialization toward browsing and frugivory in mesic woodland environments. The species exhibits marked sexual dimorphism, especially in cranial ornamentation and canine development, suggesting complex social behavior involving male competition and display. Its extensive geographic distribution across Eurasia and its possible dispersal into Africa reflect the broad ecological success of derived listriodontines during the Miocene. However, its extinction near the end of MN9 coincided with major paleoenvironmental transformations, including increased climatic seasonality and the expansion of open habitats, which likely reduced the availability of preferred browse resources and intensified ecological competition. As the terminal representative of highly specialized listriodontine suids in Europe, *L. splendens* provides critical insight into the evolutionary pathways, ecological specialization, and eventual decline of this once diverse and widespread clade.

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

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