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Reconstructing the feeding behavior of the dwarf Sicilian hippopotamus *Hippopotamus pentlandi* and the implications for Hippopotamidae paleodiets

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Hippopotamus pentlandi, the endemic dwarf hippopotamus of Sicily, represents one of the most iconic insular large mammals of the Mediterranean Basin. Despite the abundance of fossil remains, its feeding ecology and the environmental conditions of Sicily remain poorly understood. Here, we analyze dental microwear patterns of *H. pentlandi* teeth from three fossil-rich caves (Maccagnone, San Ciro, and Cannita) to reconstruct its diet and assess potential ecological adaptations. The results indicate a significantly higher number of pits compared to both extant *H. amphibius* and extinct continental taxa (*H. antiquus*, *H. gorgops*), suggesting greater ingestion of exogenous grit. The absence of puncture pits excludes a hard fruit feeding behavior, pointing instead toward a grazing diet influenced by increased dust intake. Differences in microwear among localities may reflect variable exposure to open, arid environments across Sicily during the Middle–Late Pleistocene. These findings suggest that *H. pentlandi* maintained a grazer-like feeding ecology similar to *H. amphibius* but adapted to drier and more terrestrial conditions, highlighting the role of insularity in shaping feeding behavior and habitat preference within Mediterranean hippopotamuses.

KEYWORDS
hippopotamus, island mammals, microwear, middle Pleistocene, niche partitioning

1 Introduction

Islands represent natural laboratories for studying evolutionary and ecological dynamics, where isolation, limited resources, and environmental constraints promote unique adaptive trajectories. During the Middle and Late Pleistocene, Sicily hosted a distinctive large-mammal assemblage dominated by endemic taxa, including the dwarf hippopotamus *Hippopotamus pentlandi* and the dwarf elephant *Palaeoloxodon mnaidriensis* (Bonfiglio and Burgio, 1992; Bonfiglio et al., 2000, 2002; 2003; Mangano et al., 2020; Martino et al., 2025 and references therein). Among Mediterranean insular hippopotamuses, *H. pentlandi* is one of the best represented in the fossil record. Although the skeletal anatomy of *H. pentlandi* has been extensively described (Accordi, 1955; Capasso Barbato and Petronio, 1983; Caloi and Palombo, 1986), its feeding ecology and habitat preferences have never been quantitatively assessed. This gap in knowledge is significant, as dietary adaptations provide direct insights into the structure of past ecosystems and the evolutionary responses of megaherbivores to insular environments. Moreover, the coexistence of *H. pentlandi* with another large grazer, *P. mnaidriensis* (Mangano et al., 2020 and references therein), raises questions about potential niche partitioning, resource availability, and the composition of Pleistocene Sicilian landscapes.

Dental microwear analysis represents a powerful tool for reconstructing the dietary preferences of mammals while simultaneously offering critical information on possible paleoenvironmental conditions (Solounias and Semprebon, 2002). Despite its widespread application to Pleistocene ungulates (see Mihlbachler et al., 2016 and references therein), only one study using dental microwear texture analysis has been conducted on insular hippopotamuses (Bethune et al., 2019), whereas no study has been yet focused exclusively on *H. pentlandi* in comparison to coeval fossil hippopotamuses from the mainland.

In this study, we present the first microwear analysis of the Sicilian dwarf hippopotamus coming from three different localities of Sicily (Figure 1). By comparing *H. pentlandi* with both extant (*H. amphibius*) and extinct continental species (*H. antiquus*, *H. gorgops*), we aim to clarify its feeding behavior and evaluate its ecological role within Pleistocene Sicilian ecosystems. The results provide new insights into the paleoenvironmental conditions of the island and contribute to a broader understanding of the adaptive responses of Mediterranean megafauna to insular contexts.

2 Method

The microwear analysis used here followed the protocol established by Solounias and Semprebon (2002). In order to obtain a high-resolution silicone mold (vinylpolysiloxane) the hippopotamus tooth surfaces were firstly cleaned with acetone to eliminate possible exogenous particles. Epoxy resin was then poured into the molds to create transparent casts. The casts were examined under transmitted light with a Zeiss Stemi 2000C stereomicroscope at 35x magnification. The enamel region studied using an ocular reticle measured 0.16 mm^2. Only the casts showing a good preservation of the enamel surface were included in the dataset, whereas the casts with a poor enamel preservation or taphonomical alterations were excluded (Weber et al., 2022; Micó et al., 2024a, 2024b). Analyses primarily targeted the paracone of upper molars, but depending on the state of preservation of the teeth, other cusps/cuspids were also included in the dataset. Several studies corroborated the use of different cusps/cuspids to detect dietary habits in mammals (Merceron et al., 2016; Ramdarshan et al., 2017; Ackermans et al., 2020; Szabó and Virág, 2021; Isarankura Na Ayudhya et al., 2022). This choice is also supported by the orthal (up and down) chewing action in *H. amphibius*, which is marked by a limited degree of jaw mobility (Avedik and Clauss, 2023; Avedik et al., 2023). The classification of features followed Solounias and Semprebon (2002) and Semprebon et al. (2004). The latter authors mainly defined on the enamel surfaces two types of features: pits and scratches. Pits are characterized by a circular or sub-circular outline, while scratches are elongated features. In this study the number of pits (Npit) and scratches (Nscr) were counted on each analyzed specimen. The presence of large pits (LP = 1, the specimen exhibits four or more large pits), cross scratches (XS = 1, the specimen has four or more cross scratches), and gouges (G = 1, the specimen contains four or more gouges) was documented for all specimens. Furthermore, puncture pits (PP) and hyper-coarse scratches were also quantified. The final value reported in the study pertains to the width of the scratches (SWS), which were categorized as fine (scratch width score or SWS = 0), fine and coarse (SWS = 1), and predominantly coarse (SWS = 2) (see Rivals and Lister, 2016 and references therein).

The enamel surfaces were well-preserved for most of our sample. Three teeth were excluded due to taphonomic alterations. The complete fossil teeth analyzed in this work and ascribed to *H. pentlandi* were twenty upper molars and four lower molars. All the teeth were collected from karstic cavities, in particular seven teeth from Maccagnone, ten from Cannita and seven from San Ciro. The cusps/cuspids analyzed were six protocones, five paracones, two metacones, three metaconules, two metaconids, and two hypoconids. Four cusps were not clearly recognizable. We also included in the dataset five teeth ascribed to *H. antiquus* (Chiusi and Valdarno, Early Pleistocene) and one tooth belonging to *H. amphibius* (Africa, recent). More microwear data on teeth assigned to wild recent *H. amphibius* and fossil *H. gorgops* were derived from literature (Rivals and Lister, 2016; Uno et al., 2018; Rivals et al., 2023). All the data used in the microwear analysis are available in the Supplementary Material (S.M.1). The results of the microwear for each different group were also further tested using a two-way ANOVA (significant results with $p<0.05$) and *post-hoc* Tukey-adjusted comparisons (see Supplementary Material S.M.1). In order to ascertain the dietary categories to which the sample from Sicily was most similar, including leaf and fruit browsers as well as grazers, numbers of pits and scratches collected from existing species were incorporated into the analysis, following the methodology and the data reported by Solounias and Semprebon (2002) and Rivals et al. (2010).

FIGURE 1
(A) Sicily in Europe. **(B)** localities in the island of Sicily from where *H. pentlandi* dental material analyzed in this study was collected: Cannita, Maccagnone and San Ciro.

3 Results

The results obtained show clear differences between *H. pentlandi* (N=min-max; Nscr=15-23.5; Npit=8-52), *H. amphibius* (Nscr=17-33; Npit=7-25), *H. gorgops* (Nscr=11-19.5; Npit=6-17.5) and *H. antiquus* (Nscr=7-12.5; Npit=4.5-20) (Figure 2). The extant hippopotamus is characterized by a high Nscr, whereas this value is lower in *H. antiquus* and *H. gorgops*. All the before-mentioned species have a similar Npit. *Hippopotamus pentlandi* has a Nscr similar to the other hippopotamuses, whereas its Npit is peculiarly higher. Based on the Nscr and Npit, *H. amphibius* is characterized by a grazing diet, whereas *H. gorgops* shows more a mixed diet, with several specimens falling in the area of leaf-browsers and only a smaller number of teeth falling in the area of grazers. *Hippopotamus antiquus* specimens fall within the variability of leaf browsers, suggesting that this extinct taxa had a different diet than the extant grazer *H. amphibius*. Regarding *H. pentlandi*, its diet seems more complex than the previous taxa. Most of the specimens of the Sicilian species fall between the variability of grazers and leaf browsers, plotting in the area of fruit browsers. *Hippopotamus pentlandi* do not show puncture pits. However, the dietary pattern of *H. pentlandi* shows a peculiar high Npit in respect to mostly of the hippopotamus specimens analyzed. In particular the *H. pentlandi* from Maccagnone and Cannita show the highest Npit, whereas fewer pits are present in the sample from San Ciro. In the analyzed specimens, large pits are absent, as well as gouges, and puncture pits, whereas hyper-coarse scratches are only visible on a single specimen from Maccagnone. In most of the specimens the scratch width score is 1, and only in six teeth this value is 2. A higher value denotes a greater width of the scratches on those specimens, coming from San Ciro (four) and Maccagnone (two). The two-way ANOVA reveals a significant interaction between species and type (Nscr vs. Npit) ($F=22.475$, $p<0.001$). Although significant main effects of species ($F = 36.642$, $p=<0.001$) and type ($F = 3.955$, $p=0.0487$) are detectable, these effects must be interpreted in light of the statistically significant species-type interaction, which indicates that differences between Nscr and Npit vary among species. *Post-hoc* Tukey-adjusted comparisons reveals that mean Nscr and Npit are statistically different for *H. amphibius-H. pentlandi* and *H. antiquus-H. pentlandi*. For all the results of the *post-hoc* analyses see Supplementary Material S.M.1.

4 Discussion

4.1 Feeding habit of *Hippopotamus pentlandi*

Despite the abundance in Sicily of *Hippopotamus pentlandi*, not a lot of studies focused on the paleoecology of this species (Accordi, 1955; Caloi and Palombo, 1986). A published work based on microwear analysis through dental topography analysis (SAGA-GIS)

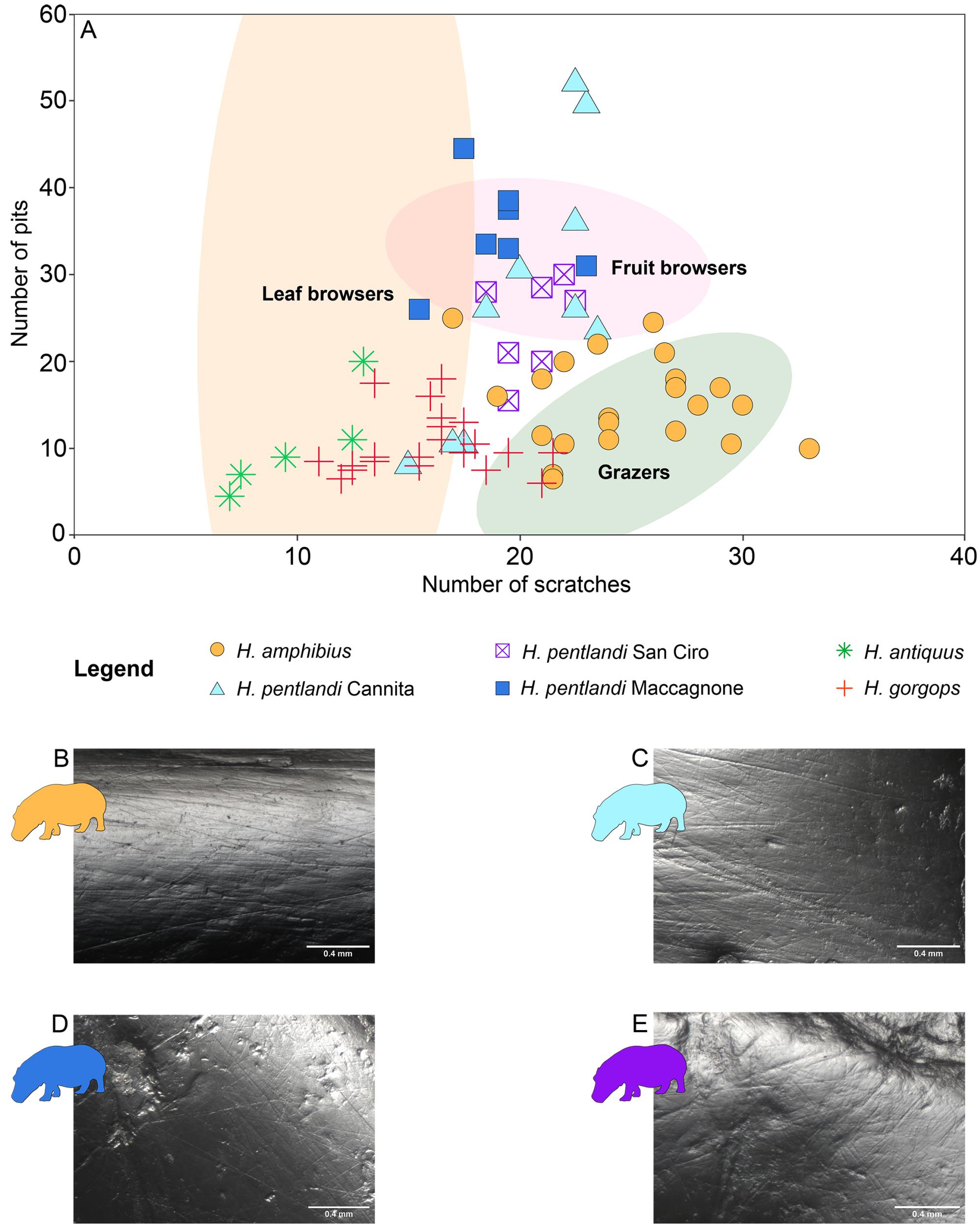

FIGURE 2
(A) scatterplot (number of scratches vs number of pits) resulted from the microwear analysis. Microphotographs of enamel surfaces of: **(B)** *H. amphibius* from Africa, MSNUP C228, M2; **(C)** *H. pentlandi* from Cannita, MGUP CNFC2, M1; **(D)** *H. pentlandi* from Maccagnone MGUP GM167, M2; and **(E)** *H. pentlandi* from San Ciro MGUP SC32, M2. Grazer, leaf browser and fruit browser areas correspond to the Gaussian confidence ellipses (p=0.95) on the centroid for the extant leaf browsers, fruit browsers and grazers from Solounias and Semprebon (2002) and Rivals et al. (2010).

and 3D surface texture analysis (3DST) performed on five different specimens of *H. pentlandi* recovered a diet similar to *H. amphibius*, with a greater dust/grit intake due to limited water sources (Bethune et al., 2019). Our study reveals that compared to fossil taxa such as *H. antiquus* and *H. gorgops*, and extant and fossil *H. amphibius*, the teeth from Sicily show a higher Npit. The high Npit in the *H. pentlandi* sample herein analyzed could be related to a higher intake of dust/grit ingested by *H. pentlandi* specimens, supporting therefore the findings of Bethune et al. (2019). However, the study conducted by Merceron et al. (2016) on small ruminants showed that grit below 100 µm don't particularly effect the dietary signal, and don't produce a higher Npit. In contrast, an exam on the microwear of guinea pigs found that grit above 95 µm does affect the microwear (Winkler et al., 2020). The results of Louail et al. (2023) further support the findings of Winkler et al. (2020), emphasizing how abundant coarse grit produces deeper, more numerous pits and more complex textures. It seems therefore plausible to relate the high Npit to a greater amount of grit ingested by *H. pentlandi*. In this scenario, *H. pentlandi* is interpreted as a grazer, similarly to *H. amphibius*, but in an environment more arid than the one typical of the extant hippopotamus. It should also be noticed that the calculus present in some of the teeth belonging to *H. pentlandi* should, in future investigations, be taken into account as it may provide more information regarding its dietary habits (de Oliveira et al., 2021 and references therein). Interestingly, *H. antiquus* is recovered as leaf browsers, suggesting it fed on less abrasive material than the extant hippopotamus, most likely on aquatic plants; a result supported by isotopes analysis (see Palmqvist et al., 2022 and references therein) and morphological characters (Made et al., 2017). *Hippopotamus gorgops* was mostly a mixed feeder foraging on both leaves and grass, as also pointed out by Uno et al. (2018), whereas *H. amphibius* is mostly recovered as grazer.

4.2 Paleoenvironmental reconstruction of Sicily

In Sicily, *H. pentlandi* is found in association with diverse fauna, including herbivores such as *P. mnaidriensis*, *Cervus elaphus siciliae*, *Dama carburangelensis*, and *Bos primigenius siciliae*, as well as several carnivorans (Bonfiglio et al., 2002; Larramendi et al., 2020; Mangano et al., 2020). Dental wear studies focused on these specific taxa have not been performed yet, however, *C. elaphus* and *D. dama* were described as mixed feeders leaning toward browsing, whereas *B. primigenius* was also a mixed feeder, but with a stronger reliance on grass (Saarinen et al., 2016). Strani et al. (2025)'s study of the microwear of *P. mnaidriensis* highlighted that this elephant was characterized by a marked prevalence of abrasive features (Strani et al., 2025), suggesting a strong reliance on grass-rich resources. This pattern has been interpreted as evidence of niche partitioning among the largest herbivores of the Sicilian Pleistocene, reducing potential trophic competition with sympatric megaherbivores. Although direct evidence of competitive interactions between *P. mnaidriensis* and *H. pentlandi* is lacking, the coexistence of two large grazing mammals on an island with limited spatial and vegetational heterogeneity makes competition for grasses and water resources a plausible scenario. The grazer-oriented diet of *P. mnaidriensis* has been linked to the expansion of open and xeric grasslands in southern Italy and Sicily during the Middle–Late Pleistocene (Strani et al., 2025). Our microwear results for *H. pentlandi* point in the same direction, and thus inhabiting frequent ingestion of exogenous grit and the use of similarly arid, dust-rich habitats. Taken together, the dietary profiles of both species suggest that Pleistocene Sicily supported a mosaic of open grasslands and sparsely-wooded areas. Our results, which point towards a drier and more open palaeoenvironment in Sicily, are in agreement with studies that link the presence of post-cranial features in *H. pentlandi* to a more terrestrial lifestyle (Caloi and Palombo, 1986). In this open environment, megaherbivores may have partitioned resources through differences in feeding height, habitat preference, or degree of selectivity. This scenario is consistent with ecological models of insular megafaunas, in which high herbivore biomass and limited habitat diversity promote divergent adaptive responses to reduce interspecific competition (Raia and Meiri, 2006).

5 Final remarks

This study provides the first detailed insight into the feeding ecology of the Sicilian dwarf hippopotamus *Hippopotamus pentlandi*. Microwear evidence reveals a grazing-oriented diet with high incidence of pits, reflecting the ingestion of exogenous grit rather than hard fruits. These results indicate that *H. pentlandi* likely inhabited more arid and open environments than those occupied by the extant *H. amphibius*. Such ecological conditions, promoted by the expansion of grasslands across Pleistocene Sicily, shaped the adaptive responses of the local megafauna. The dietary pattern of *H. pentlandi*, combined with that of the coeval *Palaeoloxodon mnaidriensis*, supports the view that the island sustained a productive and dry ecosystem. These findings contribute to understanding how insularity and climatic constraints influenced the evolution and ecological diversification of Mediterranean hippopotamuses.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author.

Ethics statement

Ethical approval was not required for the study involving animals in accordance with the local legislation and institutional requirements because it is a study on fossil material of vertebrates.

Author contributions

RM: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Validation, Visualization, Writing – original draft, Writing – review & editing. FR: Conceptualization, Data curation, Formal analysis, Methodology, Resources, Supervision, Validation, Writing – original draft, Writing – review & editing. CD: Data curation, Validation, Writing – original draft, Writing – review & editing. LP: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Writing – original draft, Writing – review & editing.

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Conflict of interest

The author(s) declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2026.1761431/full#supplementary-material

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