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Feeding strategies of the Pleistocene insular dwarf elephants *Palaeoloxodon falconeri* and *Palaeoloxodon mnaidriensis* from Sicily (Italy)

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Abstract

The fossil record of the Mediterranean islands attests several cases of insular dwarfism. The extinct large-sized straight-tusked elephant *Palaeoloxodon antiquus* underwent this process at least twice during the Pleistocene, resulting in the evolution of *Palaeoloxodon falconeri* (early Middle Pleistocene) and *Palaeoloxodon mnaidriensis* (late Middle Pleistocene/Late Pleistocene) in Sicily, a rare case of two insular taxa evolving from the same ancestral species independently on the same island and subsequently. We investigate diet-related dental wear patterns of *P. falconeri* and *P. mnaidriensis* from Sicily to test hypotheses on their niche occupation in more spatially restricted (*P. falconeri*) versus a more widely distributed, mainland-like (*P. mnaidriensis*) insular contexts. Although *P. falconeri* did not compete with other herbivorous mammals and could have exploited the most nutritious and palatable resources as a browser, dental meso- and microwear patterns suggest a high degree of dietary

abrasion. *P. mnaidriensis*, which coexisted with other large herbivores and carnivores, also displays dental meso- and microwear patterns indicative of a high intake of abrasive items. A scenario of insular woodiness (i.e., increased woodiness in insular plants), combined with intense exploitation of the limited vegetation due to the absence of predatory pressure, may explain the abrasive dental wear patterns of *P. falconeri*. The high degree of abrasion observed in *P. mnaidriensis* patterns may reflect an adaptation to a grazing diet associated with the expansion of open grasslands during the Late Pleistocene. Our results show that the dwarf elephants of Sicily developed similar dietary adaptations, albeit in response to different ecological conditions.

Key words: island rule, Quaternary, Sicily, dental mesowear, dental microwear, insular dwarf elephants.

INTRODUCTION

Islands represent the best natural laboratories to investigate how species adapt and evolve in a confined habitat with limited resources. The "island rule" or Foster's rule (Foster, 1964) is a widely studied phenomenon in evolutionary biology and refers to the tendency of small vertebrate taxa to increase in body size (insular gigantism) and large-sized taxa to decrease in size (insular dwarfism) compared to their mainland relatives (Foster, 1964; Mayr, 1967; Van Valen, 1973; Benton *et al*., 2010; Benítez-López *et al*., 2021). Reduced predatory pressure and interspecific competition coupled with limited availability of food resources and land area, are the main drivers of body size change in insular species (Foster, 1964, Rozzi, 2018; Ponti *et al.*, 2023). Moreover, the lack of competition in newly colonised environments often leads to more rapid radiation and speciation compared to mainland biota (Losos & Ricklefs, 2009).

Examples of island gigantism and dwarfism are well documented in fossil mammals (Brown *et al*., 2004; Mazza & Rustioni, 2008), particularly in Mediterranean islands, which played a key role as refugia and radiation hotspots during Quaternary glacial and interglacial phases (Palombo *et al*., 2012; Bover *et al*., 2019; Lyras *et al*., 2021).

Island dwarfism within the proboscideans is one of the best-known cases of these phenomena from Mediterranean localities (Athanassiou *et al.*, 2019, Palombo *et al.*, 2020). The large-sized, straight-tusked elephant *Palaeoloxodon antiquus* (up to 4 m in height at the withers), a

Quaternary megaherbivore that was widespread in Europe during the Middle and Late Pleistocene, is considered to be the ancestor of the two insular dwarf species *Palaeoloxodon falconeri* and *Palaeoloxodon mnaidriensis* from Sicily and Malta (Palombo, 2003; Palombo & Ferretti, 2005; Herridge, 2010; Baleka *et al*., 2021). *P. antiquus* reached Sicily at least twice during two successive colonisation events (Palombo & Ferretti, 2005): the first, during the early Middle Pleistocene, resulted in the evolution of *P. falconeri*, the smallest of all fossil dwarf elephants (only 1 m at the withers and an estimated weight of ~250 kg; Romano *et al*., 2019); the second event, during the late Middle Pleistocene, resulted in the evolution of *P. mnaidriensis*, which was considerably smaller than *P. antiquus* but larger than *P. falconeri* (around 2 m at the withers, with an estimated weight of ~1000 kg) (Ferretti, 2008; Romano *et al*., 2019; Baleka *et al*., 2021).

During the first colonisation event, Sicily was composed of two main islands, with the south-eastern part of Sicily possibly connected with Malta and isolated from the mainland (Bonfiglio *et al*., 2002). The vertebrate fossil record of this phase suggests a high level of endemism, with the absence of large carnivores and with *P. falconeri* being the only recorded large herbivorous mammal (the only other recorded mammals on the island being three giant dormice, a shrew, and an otter; Pavia, 2008; Guglielmo & Marra, 2011; Pavia and Insacco, 2013). During the second colonisation event, Sicily was characterised by a more heterogeneous vertebrate fauna, also including other middle and large-sized herbivorous (*Hippopotamus pentlandi*, *Cervus elaphus*, *Dama dama*, *Bos primigenius*, *Bison priscus*) and predacious (*Ursus arctos*, *Canis lupus*, *Panthera spelaea*, *Crocuta crocuta*) mammals, together with small mammals (two surviving giant dormice and a shrew) (Bonfiglio *et al*., 2002; Marra, 2009), suggesting that the islands were intermittently connected with the mainland. The presence of large carnivores in the archipelago is reckoned as the primary cause of the (relatively) larger size of *P. mnaidriensis*, as a drastic reduction in size would have been a disadvantage against predation (Rozzi, 2018).

From a palaeodietary viewpoint, *P. antiquus* has been found to exhibit a mixed feeding behaviour, thus displaying a certain degree of dietary plasticity depending on the environmental context (Palombo *et al*., 2005; Rivals *et al*., 2019; Briatico & Bocherens, 2023; Roditi *et al*., 2024), with a more grass-rich mixed diet recorded in southern Europe in both open (Megalópolis, La Polledrara; Greek and Italian peninsulas) and mosaic landscapes (Casal de' Pazzi; Italian Peninsula) (Palombo *et al*., 2005; Briatico & Bocherens, 2023; Roditi *et al*.,

2024). Dental microwear patterns compatible with a browsing behaviour are recorded in specimens from Eastern and Central Europe (Rivals *et al*., 2019).

With regard to *P. falconeri* and *P. mnaidriensis*, several studies have been conducted on these proboscidean species, focusing on skeletal morphology (Ferretti, 2008), encephalisation (Larramendi & Palombo, 2015), skull shape (Van Der Geer *et al*., 2018), brain size (Lyras, 2018), body mass estimation (Romano *et al*., 2019), ancient DNA (Baleka *et al.*, 2021), and bone and dental histology (Köhler *et al*., 2021), but relatively little is known about their palaeoecology, and no data are currently available on the feeding behaviour of either *P. falconeri* or *P. mnaidriensis*.

Here, we analyse the diets of both dwarf elephants, to investigate the evolutionary response of the *Palaeoloxodon* lineage in terms of dietary adaptations to insularity. Specifically, we hypothesise that both *P. falconeri* and *P. mnaidriensis* displayed a different feeding behaviour than their ancestor in response to a marked reduction in body size and resource availability. A lower body mass, and therefore reduced food intake, would have allowed for a more selective, high-quality diet, which would have been advantageous in habitats with reduced resource availability. In this scenario, we would expect to detect a shift towards a browsing or browse-rich diet in both species, particularly in *P. falconeri*, which did not have to compete with other herbivorous mammals for palatable plant resources. To test this hypothesis, we investigated the food-related dental micro- and mesowear patterns of *P. falconeri* and *P. mnaidriensis* fossil molars from Sicilian collections.

P. falconeri and P. mnaidriensis Faunal Complexes

The Plio-Pleistocene Quaternary fauna of Sicily is divided into Faunal Complexes (FC) that describe the palaeogeographic evolution of the islands, recording a trend from a high level of endemism during the early Middle Pleistocene to a lower endemism level during the Late Pleistocene, up to the Last Glacial Maximum, when faunal exchanges with the southern Italian Peninsula become more frequent (Bonfiglio *et al*., 2002; Marra, 2013).

During the early Middle Pleistocene (MIS 22–11; middle and late Galerian sensu Gliozzi *et al*., 1997), the vertebrate assemblage known as the *P. falconeri* FC was characterised by a marked endemism and a poor biodiversity, thus suggesting that taxa reached Sicily through a single

dispersion event (Bonfiglio *et al*., 2002) (Appendix S2). *P. falconeri* was the largest species and no carnivorous mammal taxa are recorded, with the only exception of *Lutraeximia trinacriae*, a fish-eating otter (Burgio & Fiore, 1988; Cherin *et al*., 2016) and *Vulpes* sp. The *P. falconeri* FC is recorded in both Sicilian and Maltese terrestrial successions, indicating that Sicily included several connected islands that remained isolated from the mainland for most of the early Middle Pleistocene (Bonfiglio *et al*., 2002; Pavia & Insacco, 2013). Other examples of insular gigantism among fossil mammals include the giant endemic shrew *Crocidura esuae* and three species of giant dormouse (Bonfiglio *et al*., 2002). Endemism is also observed in the herpetofauna with the insular giant Sicilian-Maltese lizard *Lacerta siculomelitensis* (Bonfiglio *et al*., 2002; Guglielmo & Marra, 2011; Marra, 2013). Among the 66 species of the avifauna, five are endemic to Sicily (*Cygnus equitum*, *Grus melitensis*, *Tyto mourerchauvireae*, *Athene trinacriae*, *Aegolius martae* and a still undescribed, small-sized Corvidae) (Bonfiglio *et al*., 2002; Pavia, 2008; Pavia & Insacco, 2013).

During the late Middle Pleistocene (MIS 10–4) and Late Pleistocene (MIS 3–2) (respectively, early-middle Aurelian and late Aurelian), faunal assemblages known as the *P. mnaidriensis* FC and the Pianetti–San Teodoro FC were characterised by a richer biodiversity (Bonfiglio *et al*., 2002), suggesting that the archipelago was connected to the Italian Peninsula by long-lasting land bridges, which allowed the dispersion of several newcomer taxa into Sicily, now comprising a larger land mass due to Last Glacial Period glacio-eustatics. *Palaeoloxodon mnaidriensis* replaced *P. falconeri* and the occurrence of medium-to-large sized ungulates such as boars, red and fallow deer, aurochs, and bisons, as well as the dwarf endemic hippopotamus *Hippopotamus pentlandi* (Bonfiglio *et al*., 2002; Guglielmo & Marra; 2011; Marra 2013) (Appendix S2),. Contrary to the *P. falconeri* FC, the assemblage also includes middle- to large-sized carnivores such as bears, wolves, cave lions, and cave hyaenas (Bonfiglio *et al*., 2002; Guglielmo & Marra, 2011; 2013). Among the 50 bird taxa recorded, only two are endemic (*Grus melitensis* surviving from the previous FC and the giant swan *Cygnus falconeri*, often misattributed to the *P. falconeri* FC) (Pavia, 2001). The Pianetti–San Teodoro FC is similar to the *P. mnaidriensis* FC except for the occurrence of equids (*Equus hydruntinus*) and the extinction of dwarf hippopotamus, endemic dormice, and *Crocidura esuae* (Bonfiglio *et al*., 2002). *P. mnaidriensis* disappeared during the Last Glacial Maximum (Palombo et al., 2020), a phase when the mammalian faunal composition becomes very similar to that recorded in the southern Italian Peninsula (Castello FC) (Bonfiglio *et al*., 2002).

MATERIAL AND METHOD

The studied collection comprises fossil material coming from four caves in north-west Sicily (Fig. 1). Fossils of *P. falconeri* were recovered from Zà Minica and Puntali caves, while material of *P. mnaidriensis* either was unearthed from Boccadifalco and Luparello caves (Fig. 1) or is of uncertain provenance but has been recovered in the same area (see SI1, 2). All fossils are stored in the Museum of Nature and Humankind of the University of Padua (Geology and Palaeontology Section). A total of 33 teeth were preserved well enough to be studied for the mesowear analysis (13 of *P. falconeri* and 20 of *P. mnaidriensis*) and 48 for the microwear analysis (19 of *P. falconeri* and 29 of *P. mnaidriensis*).

Dental mesowear

Mesowear analysis evaluates the combined effect of friction (tooth-on-tooth wear) and abrasion (food-on-tooth wear) on tooth morphology. This analysis provides information on the animal's diet over the long term (years) and, thus, an estimation of the tooth wear experienced by individuals over their lifetime (Fortelius & Solounias, 2000; Ackermans *et al*., 2020). The method used here was developed by Saarinen *et al.* (2015) for elephantid molars and quantifies the occlusal relief by measuring the angles formed by the two enamel walls with respect to the bottom of the intermediate dentine valley: a high (browser-like) relief produces a more closed angle, while a low (grazer-like) relief produces a more open angle (details in on-line Appendix S1).

Measurements taken on *P. mnaidriensis* teeth (N = 31) were performed using a digital goniometer with an accuracy of 0.1° (as in Saarinen *et al.*, 2015), model DAF-001 from CMT Utensili. However, the base of the instrument was too large to fit inside the plates, a problem already encountered by Saarinen *et al.* (2015). It was therefore necessary to modify the goniometer by attaching two thin metal extensions to the arms, so that they shared the goniometer's rotational fulcrum and, unlike the different type of extensions introduced by Saarinen *et al.* (2015), did not need to be repositioned for each measurement (Appendix S1 - fig. 1).

Since the molars of *P. falconeri* (N = 13) are too small to be measured with this instrument, they were scanned with an Olympus LEXT OLS4000 laser scanning confocal microscope, coupling color imaging and laser confocal optical systems, the first with a white light LED light source and CMOS image sensor, whereas the second with a 405 nm laser diode light source and a high-sensitivity photomultiplier. This enabled the acquisition of 3D morphometric models of the occlusal surface at very high resolution (0.2 μm) (details in Appendix S1 - fig. 2). Acquisition was carried out on a plate in the central portion at 2.5x magnification, using both laser and color optics. For slightly larger teeth, several images were acquired with a 25% overlapping region and then combined together if necessary. Using the proprietary software Lext (Olympus), the 3D laser surface reconstructions were processed using a noise reduction filter to remove spikes, that may occur when measuring rough or highly reflective surfaces and causing the detector pixels saturations or extremely low signal detection, respectively. On the 3D surfaces, virtual cross-sections of the plates were analysed and angles were directly measured on the extracted profiles. Scan results were exported in CSV format to allow their use in spreadsheets.

To test whether the measurements made with the digital goniometer in *P. mnaidriensis* and with the confocal microscope in *P. falconeri* were consistent with each other, since we couldn't fit the large teeth of the former under the microscope, we used a third instrument, a digital profilometer, JR25 from NANOVEA, to repeat measurements on a subset of samples. The choice of not measuring all the specimens of the two species with this instrument was motivated by the fact that its use is somewhat impractical (long operating times of several hours for a single profile acquisition, followed by a multi-step protocol for extracting the angles, as detailed in Appendix S1), when compared with the other two instruments, which are standard in these kind of studies.

Following Saarinen *et al.* (2015) and Saarinen & Lister (2016), measurements were performed on the three central plates of each tooth, when possible. Teeth with a lower number of well-preserved plates with at least one central plate were also analysed. Teeth without plates in suitable condition, i.e., with all plates damaged or not fully erupted, were discarded. For teeth with an even number of plates, the protocol required the use of two plates posterior to the centre, and one anterior plate; this choice is based on the fact that central plates are subject to a medium-wear and are likely to record the signal more evenly than anterior plates (typically very worn) or posterior plates (not yet fully emerged) (Saarinen *et al.*, 2015).

All measurements were taken by a single operator (M.G.) to reduce interobserver error. Following Saarinen *et al.*, (2015), angles were measured at the widest point of the plate, which corresponds approximately to its center. For each plate, the angle measurement was repeated three times around the widest point to reduce errors related to cracks or imperfections in the tooth, which can be particularly influential in microscopy and profilometer measurements, given the level of magnification (even a small point groove could affect the measurement). The average of the three measurements for each plate was used to calculate the mesowear angle of each tooth, which is the average of the angles measured on all its plates. Raw data in Strani et al. (2025, mesowear).

Dental microwear

For the analysis of dental microwear, we followed the protocol proposed by Solounias & Semprebon (2002). The occlusal surfaces of the teeth were cleaned with acetone and then with alcohol (95%). The surfaces were moulded with high-resolution silicone (vinyl polysiloxane) and casts were made with clear epoxy resin. The casts were examined under incident light using a Nikon Eclipse ME600 stereomicroscope at 35× mounted with a Canon EOS 500D digital camera. As the lamellae are not perfectly flat, the focus staking technique was also used to obtain a clear image of the entire surface portion. For each sample, images were taken every 5 degrees of progressive focus (from the top to the base of the selected enamel band) and merged using the Helicon Focus software. For each sample, we photographed the central lamellae and selected enamel bands with preserved diet-related microwear patterns (Figs. 3 and 4), discarding damaged teeth or specimens with taphonomic alterations (King *et al*., 1999) (2 molars of *P. falconeri* and 8 of *P. mnaidriensis* were discarded from this analysis).

Microwear data were collected using the MicroWeaR software (Strani *et al*., 2018) developed in R environment, which allows to quantify and classify microwear marks in a semi-automatic way. We quantified all categories of microwear features in a standard square area of 0.16 mm^2 and features were automatically divided into scratches and pits based on length/width ratio (≤4 for pit and >4 for scratch as proposed by Ungar, 1995). For each of these two categories, different subcategories based on the diameter (for pits) and width (for scratches) were also automatically recorded: small and large pits (by default diameter ≤8 and >8 μm, respectively), and fine and coarse scratches (by default the width ≤3 and >3 μm, respectively). We also carried

out the microwear analysis in two different 0.16 mm^2 study areas for each specimen and then we calculated the average to reduce count errors (Solounias & Semprebon, 2002). All data were collected by a single operator (S.R.) to reduce interobserver errors. Data were compared with those of modern taxa with known diets including the African bush (*Loxodonta africana*) and the forest (*Loxodonta cyclotis*) elephants and the Asian elephant (*Elephas maximus*) (Solounias & Semprebon, 2002; Semprebon *et al*., 2016). Results were also compared with available data for *P. antiquus* from different European localities (Rivals *et al*., 2019). Discriminant analysis was used to assign the microwear patterns of *P. falconeri* and *P. mnaidriensis* into modern diets. As independent variables, we include (1) average number of pits, (2) average number of scratches, (3) percentage of individuals with predominantly fine scratches, (4) percentage of individuals with predominantly coarse scratches, (5) percentage of individuals with a mixture of fine and coarse scratches, and (6) percentage of individuals with >4 large pits (modified from Solounias & Semprebon, 2002). Analyses were performed with IBM SPSS Statistics 24. Raw data in Strani et al. (2025, microwear).

RESULTS

Dental mesowear

From a methodological point of view, the digital goniometer employed by Saarinen *et al.* (2015), and modified as explained in Appendix S1, is the best instrument for this kind of analysis in proboscidean teeth of sufficiently large size, thanks to its low cost and time efficiency, as measurements require just a few seconds, as compared to the long acquisition times of the other two instruments. However, the confocal microscope is necessary for the small teeth of *P. falconeri* for which the measurement error introduced by the manual positioning of the goniometer arms would be too large. The profilometer would be a solution applicable to elephant teeth of any size, but it requires an extremely long acquisition time and a multi-step protocol to process the data.

The angular measurements taken with different instruments on the test sample (7 plates in three specimens of *P. falconeri* with the confocal microscope vs. the digital profilometer, and 6 plates in four specimens of *P. mnaidriensis* with the digital goniometer vs. the digital profilometer)

yielded consistent results (see Fig. 2 in SI3). Differences between angle measurements on the same plate (each one a mean of three measurement replicas) with the two instruments are in range of 0.1-2.7% of the mean angle (but for a single case with a difference of 4.5%), and in all cases the difference is smaller than the 95% confidence interval of each mean angle.

According to the dental mesowear analysis performed on the largest available dataset for each species (i.e., measurements taken at the centre of the plates with the confocal microscope in *P. falconeri*, and with the digital goniometer in *P. mnaidriensis*), both dwarf elephants have a wide angle between the dentin valleys and the enamel ridges, with a mean mesowear angle (MMA) of 143.3° for *P. mnaidriensis* and 130.2° for *P. falconeri* (Fig. 5), suggesting a high level of abrasion in the diet of both species. When compared with data from other fossil and modern proboscideans (from Saarinen *et al.* [2015] and Saarinen & Lister [2023]), both *P. falconeri* and *P. mnaidriensis* MMAs fall within the range of a C4 plant-grass-dominated/grazing diet following the C3/C4 dietary spectrum proposed by Saarinen *et al.* (2015) which is based on $\delta^{13}C$ averaged values for Asian and African mesic and xeric environments (Fig. 5). These values are above the average observed in both fossil and modern proboscideans which usually display mesowear angles narrower than 130° (Fig. 5). *P. falconeri* and *P. mnaidriensis* MMAs are in fact closer to those recorded in molars of Late Pleistocene grazing mammoths such as the woolly mammoth *Mammuthus primigenius* (MMA = 131.8°) or the North American *Mammuthus columbi* (MMA = 135.5°) (Mead *et al.*, 1986; Gillette & Madsen, 1993; Saarinen & Lister, 2016) (Fig. 5). Both *P. falconeri* and *P. mnaidriensis* also display much wider angles compared to their mainland ancestor *P. antiquus* for which narrower angles (MMA = 108.1°) have been recorded in molars from British Middle and Late Pleistocene localities (Saarinen & Lister, 2016) (Fig. 5).

Dental microwear

Both *P. falconeri* and *P. mnaidriensis* display a higher number of scratches than pits (*P. falconeri* AS = 31.0, AP = 6.1; *P. mnaidriensis* AS = 33.3, AP = 9.3; Table 1), consistent with an abrasive diet. *Palaeoloxodon falconeri* shows a scratch-dominated microwear pattern in both Boccadifalco (AS = 25.5; 0-17% = 0) and Luparello (AS = 31.6; %0-17 = 17.6) caves. A similar pattern is observed for the few *P. mnaidriensis* teeth of known provenance, with the 6 individuals from Zà Minica cave displaying a high number of scratches (AS = 29.3) and a low

311 percentage of specimens with between 0 and 17 scratches (0-17% = 16.7). The only specimen
312 of *P. mnaidriensis* from Puntali cave shows analogous results, with an average of 29.5 scratches
313 being recorded on the occlusal surface. The scratches are mostly fine and mixed (*P. falconeri*
314 SWS = 0.5; *P. mnaidriensis* SWS = 0.4; total average), with only the two individuals of *P.*
315 *falconeri* from Boccadifalco cave showing mostly mixed scratches (SWS = 1). Both species
316 display microwear patterns characterised by a low number of pits (AP < 15), with *P.*
317 *mnaidriensis* having a higher percentage of large pits than *P. falconeri* (%LP = 41.4 vs %LP =
318 26.3; Table 1). The highest percentage of individuals with >4 large pits is recorded in the *P.*
319 *mnaidriensis* specimens from Zà Minica cave (%LP = 50). Overall, the average number of
320 scratches and pits is consistent with those observed in extant ungulates with a diet characterised
321 by a high intake of abrasive items (Fig. 6). Most notably, both *P. falconeri* and *P. mnaidriensis*
322 display significantly more scratch-dominated microwear patterns than their ancestor *P.*
323 *antiquus* (Fig. 6).

324 Discriminant analysis using all available quantitative and qualitative microwear variables (see
325 Material and Methods) classifies both *P. falconeri* and *P. mnaidriensis* (total mean, including
326 all specimens even those of unknown or uncertain provenance) as meal-by-meal mixed feeders
327 (70.2% correctly classified modern taxa, 57.4% in cross-validation; Table 1). Meal-by-meal
328 mixed feeders are virtually indistinguishable from grazers in terms of average number of
329 scratches but differ in average number of pits (lower in grazers) and scratch texture (finer in
330 meal-by-meal mixed feeders) (Solounias & Semprebon, 2002). The result of this discriminant
331 analysis may be due to the low percentage of coarse scratches observed in both species (<6%;
332 Table 1). Indeed, when the extant meal-by-meal mixed feeders are grouped together in a single
333 dietary category with seasonal mixed feeders, which are also characterised by the presence of
334 finer scratches, both dwarf elephants are classified as grazers (76.6% correctly classified
335 modern taxa, 61.7% in cross-validation; Table 1).

336 If only fossil specimens from known localities are considered, *P. mnaidriensis* from Zà Minica
337 cave and the single individual from Puntali cave are classified as mixed feeders (Table 1). The
338 two individuals of *P. falconeri* from Boccadifalco cave are instead classified as grazers
339 (whether or not seasonal and non-seasonal mixed feeders are grouped together), while the
340 specimens from Luparello cave are classified as either meal-by-meal mixed feeders or grazers
341 (Table 1).

DISCUSSION

Previous studies on the dietary adaptations of extinct dwarf proboscideans have focused on the insular dwarf mammoth *Mammuthus exilis* (Santa Rosa Island, North America), suggesting that insular conditions favoured a tendency towards a more selective, high-quality diet, as its dental microwear patterns are consistent with a browse-rich feeding behaviour, in contrast to the more generalist/grass-dominated diet of its mainland ancestor *Mammuthus columbi* (Semprebon *et al*., 2016). This dietary shift has been interpreted as a consequence of both reduced body size and reduced competition with other herbivorous taxa for access to high-quality, more palatable plant resources (i.e., leaves, forbs and fruits), which are easier to digest and richer in nutrients than ligneous or fibre-rich parts (Demment & Van Soest, 1985; Semprebon *et al*., 2016) or grasses (Hunt *et al.*, 2008).

It would therefore be expected that both Sicilian dwarf elephants would show a similar tendency, especially in the case of *P. falconeri*, which underwent a process of considerable body size reduction and lived in habitats virtually free from predatory pressure and competition with other herbivorous taxa (Bonfiglio *et al.*, 2002). However, dental meso- and microwear analyses record patterns in both *P. falconeri* and *P. mnaidriensis* are compatible with highly abrasive diets, consistent with what is observed in modern grazers or fossil mainland proboscideans with a grazing diet. The degree of abrasion recorded in both species is even more pronounced than that reported in the literature for their mainland ancestor *P. antiquus* (Fig. 6) (Palombo *et al*., 2005; Rivals *et al*., 2019).

Since the microwear signal reflects the last meals of the animal (the so called “last supper” effect), and a grazing diet can overwrite a previous browsing microwear signal in as little as two weeks (Winkler *et al*., 2020), one possible explanation is that grazing was restricted to the coastal environments near the caves where these animals ultimately perished. However, since the mesowear signal is influenced by the diet over the last years of an animal’s life (Ackermans *et al*., 2020), this unexpected result cannot be attributed solely to seasonal dietary changes. Instead, it must reflect the species’ typical diet, requiring an alternative explanation.

On islands, windy conditions may lead to a higher concentration of mineral particles on grass and leaves, similar to what is observed in arid environments (Van Der Geer, 2014). Moreover, the ashes produced by volcanic activities of Mount Etna, which volcanism began during the

Middle Pleistocene (~ 500 ka) (Branca *et al.* 2007), could also have covered vegetation of the study area depending on the intensity of the eruptions. Higher concentration of particles on plant parts may lead to a higher abundance of coarse features on enamel surfaces as animals chew on grit-infested vegetation, resulting in grazing microwear patterns that can mask the true diet of the species (Williams & Kay, 2001; Solounias & Semprebon, 2002; Kaiser & Rössner, 2007). However, both *P. falconeri* and *P. mnaidriensis* display an abundance of finer scratches and few (mostly small) pits (Table 1), which are not compatible with the so-called "dirty" feeding behaviour, suggesting that the heavily scratched enamel surfaces are not the result of ingestion of plant parts covered with salt or sand, but of a grass-rich diet.

The presence of open landscapes inSicily during the Middle Pleistocene is supported by the associated fauna of the *P. falconeri* Faunal Complex, such as the occurrence of the little bustard *Tetrax tetrax* (Bonfiglio *et al*., 2002), a grassland bird, and by the proposed herbivory of the giant dormouse *Leithia melitensis* (Hennekam *et al*., 2020).

Herbaceous plants (e.g., *Poaceae*) contain abundant phytoliths, amorphous silica deposits that enhance structural strength while also deterring herbivory by reducing digestibility (Hunt *et al*., 2008). The production of phytoliths increases under high herbivore pressure (Massey & Hartley, 2006). In fact, phytolith production and lignification are known defence mechanisms that plants often rely on when exposed to prolonged and constant feeding pressure (Martínez & López-Portillo, 2003; Gallardo *et al*., 2023).

As *P. falconeri* was the only large herbivorous mammal recorded inSicily, with no known predators, it had free access to all available vegetation, which probably had a major impact on the already stressed island flora, causing plants to invest even more in protective strategies. Extreme insular conditions, characterised by a reduced landmass with particularly scarce grass-dominated vegetation, both in terms of quantity and type (as island plant species diversity is influenced by island size; Kohn & Walsh, 1994) and high herbivory pressure, may thus explain the abrasive diet of *P. falconeri*, with the dwarf elephant having to adapt to a low-quality, fibre-based diet that devotes most of its resources to subsistence. This scenario is supported by palaeohistological analysis of *P. falconeri* material from Spinagallo Cave (Sicily), suggesting that this species was characterised by a slow growth-rate with marked longevity (up to ~68 years) and delayed sexual maturity (~15 years) (Köhler *et al*., 2021), In life-history theory, a

reduction in growth-rate is generally associated with low resource availability, with organisms retaining small body sizes throughout their ontogeny (Dimitriew, 2011).

A similar condition has also been observed in the dwarf insular fossil bovids of the genus *Myotragus* from the Balearic Islands, which developed increasingly high-crowned teeth both as a result of delayed senescence (Jordana *et al*., 2012) and to adapt to an increasingly abrasive diet (Winkler *et al*., 2013) as they displayed dental wear patterns compatible with either a grazing diet (in *M. pepgonellae*, *M. kopperi*, and *M. batei*) or with a browsing diet characterized by an unusually high content of abrasives (in *M. balearicus*, the terminal species of the *Myotragus* lineage) (Jordana *et al*., 2012).

Insular secondary woodiness, (i.e., plants developing more lignin-rich portions and shrub-like habit on islands) may also explain *P. falconeri* dental wear patterns, as this phenomenon of plant insularity has been correlated with the lack of large herbivores, increased aridity and island isolation on continental islands (Zizka *et al.*, 2022).

P. mnaidriensis lived in a less isolated, more mainland-like biota that included other potential competitors and predators, and was still a relatively large animal even if smaller than *P. antiquus*. Pollen data from deposits in northeastern Sicily (San Teodoro Cave) point to the occurrence of steppe-like landscapes with refugia of temperate or Mediterranean vegetation during the Late Pleistocene (Yll *et al*., 2006). In this case, grazing may be the result of a niche partitioning mechanism to avoid competition with other large herbivores and maximise the use of readily available grasses to maintain a relatively large body mass, rather than a consequence of extremely scarce resource availability.

CONCLUSION

Dental meso- and microwear analyses on Sicilian dwarf elephants shed light on the dietary adaptations of two key insular species of the Mediterranean Pleistocene. Diet-related dental meso- and microwear patterns of both *P. falconeri* and *P. mnaidriensis* are consistent with a diet characterised by a higher degree of abrasion compared to that recorded for their mainland ancestor, the straight-tusked elephant, *P. antiquus*, which usually displayed a mixed diet. Despite body-size reduction, which would have allowed for lower food intake and thus a diet

based on the selection of easier-to-digest soft plant parts, a high-fibre grazing diet is observed in both species.

The abrasion-dominated dental microwear patterns of *P. falconeri* might be linked to extreme insular conditions with limited vegetation coupled with high herbivory pressure. *P. falconeri* was in fact the only large herbivorous mammal recorded in Sicily during the Middle Pleistocene with no known predators, thus it exerted a major and constant feeding pressure on the island vegetation which in turn led to plants adopting defensive mechanisms, such as overproduction of phytoliths and lignification, resulting in the "over-scratched" signal recorded by the microwear analysis. Insular secondary woodiness may also explain the patterns recorded in this species, although no evidence of this phenomenon is currently available for the Middle Pleistocene vegetation of Sicily.

The high degree of abrasion recorded in *P. mnaidriensis* dental wear patterns, which lived in a less isolated, more mainland-like context and coexisted with other herbivorous mammals, may instead not be a result of overpressure on vegetation but of an adaptation to the spread of open grasslands in the southern Italian Peninsula during the late Middle and Late Pleistocene glacial periods.

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463

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476

477 SUPPORTING INFORMATION

478 **Appendix S1.** Details for dental mesowear protocols.

479 **Appendix S2.** *Palaeoloxodon falconeri* and *Palaeoloxodon mnaidriensis* faunal complexes

480

481 DATA ARCHIVING STATEMENT

482 Data for this study are available in the Dryad Digital Repository: DOI:
483 10.5061/dryad.6djh9w1f7 [please note that the data for this paper are not yet published and this
484 temporary link should not be shared without the express permission of the author]

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Figure captions

Figure 1. Geographical location of the caves from where the *P. falconeri* and *P. mnaidriensis* material was collected (maps edited from https://d-maps.com).

Figure 2. Selected 3D surfaces of *P. falconeri* fossil teeth obtained with Olympus Lext OLS4000 laser confocal microscope; false colors record differences in elevation with respect to a reference position; distances are reported in mm. A: MGP-PD 24756; B: MGP-PD 24757; C: MGP-PD 24758. Note that parallel darker bands are unavoidable artefacts due to multiple images stitching; however, these were accurately avoided when extracting the cross-section profiles for angles measurements. Scale bar: 1 cm.

Figure 3. Photomicrographs of enamel surfaces at 35× magnification of selected teeth of *P. falconeri*. From left to right: specimen MGP-PD 24724 (m3), specimen MGP-PD 24731 (DP4 or M1), specimen MGP-PD 24754 (M3). Scale bar: 500 μm.

Figure 4. Photomicrographs of enamel surfaces at 35× magnification of selected teeth of *P. mnaidriensis*. From left to right: specimen MGP-PD 24700, (DP4 or M1), specimen MGP-PD 24693 (M3), specimen MGP-PD 24624 (m3). Scale bar: 500 μm.

Figure 5. Mesowear angles of *P. falconeri* (in blue) and *P. mnaidriensis* (in red) compared to those of modern species and other fossil proboscideans (data reference in SI1). Dashed lines indicate the threshold between browsing (below 106°), mixed feeding (between 106° and 117°) and grazing (above 117°) mesowear angle values. Threshold values from Saarinen and Lister (2023). Pa: *P. antiquus*; Pf: *P. falconeri*; Pm: *P. mnaidriensis*. Boxes represent the interquartile interval, with mean (transverse line); vertical lines are ranges of variation, to the exclusion of outliers (dots). Plants' silhouettes from PhyloPic (http://phylopic.org) by T. Michael Keesey (Public Domain) and Ferran Sayol (Public Domain), animals' silhouettes by Flavia Strani.

Figure 6. Bivariate plot of the average number of pits versus average number of scratches in extant ungulates (data modified from Solounias & Semprebon, 2002) and extant and fossil proboscideans (data from Semprebon *et al,,* 2016 and Rivals *et al.,* 2019). Abbreviations: LB; leaf browsers; FB; fruit browsers; SM; seasonal mixed feeders; MM; meal-by-meal mixed feeders; G; grazers. AI; Aveley & Ilford. CFB-CM; CFB - Cromer + Mundesley. CFB-H; CFB – Happisburgh. Ct; Clacton. C-SG; Crayford & Slade Green. DA; Deutsch-Altenburg. GT; Grays Thurrock. Megal; Megalópolis. Ost; Ostend. Sh; Steinheim. Sw; Swanscombe. Tb; Taubach. *= all specimens including those of unknown or uncertain provenance. [1]= Solounias & Semprebon (2002). [2]= Semprebon *et al*, (2016).

Table caption

Table 1. Summary of dental microwear analysis. Abbreviations: average number of pits (AP); average number of scratches (AS); percentage of individuals with >4 large pits (%Lp); scratches width score (SWS); percentage of specimens with between 0 and 17 scratches (%0–17); percentage of individuals with predominantly fine scratches (%FS); percentage of individuals with a mix of fine and coarse scratches (%MS); percentage of individuals with predominantly coarse scratches (%CS); standard deviation (SD); coefficient of variation (CV). *Extant

764 seasonal and non-seasonal mixed feeders are grouped together in a single dietary category
765 “mixed feeders”.