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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 to 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 or Late Pleistocene) in Sicily, a rare case of two insular taxa evolving from the same ancestral species independently on the same island. We investigate diet-related dental wear patterns of *P. falconeri* and *P. mnaidriensis* from Sicily to test niche occupation hypotheses, comparing more spatially restricted (*P. falconeri*) to 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. *Palaeoloxodon mnaidriensis*, which coexisted with other large herbivores and carnivores, also bears 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 the *P. mnaidriensis* patterns may reflect an adaptation to a grazing diet associated with the expansion of open grasslands during the Late Pleistocene. This indicates 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 elephant.

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 it 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 with their mainland relatives (Foster 1964; Mayr 1967; Van Valen 1973; Benton *et al.* 2010; Benítez-López *et al.* 2021). Reduced predatory pressure and interspecies 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 colonized environments often leads to more

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rapid radiation and speciation compared with 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.* 2022).

Island dwarfism in 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). *Palaeoloxodon antiquus* reached Sicily at least twice during two successive colonization 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 *c.* 250 kg; Romano *et al.* 2021); 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 *c.* 1000 kg) (Ferretti 2008; Baleka *et al.* 2021; Romano *et al.* 2021).

During the first colonization event, Sicily was composed of two main islands, with the south-eastern part of Sicily possibly connected to 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 species of giant dormice, a shrew and an otter; Pavia 2008; Guglielmo & Marra 2011; Pavia & Insacco 2013). During the second colonization event Sicily was characterized 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 of the pre-existing giant dormice species and a shrew) (Bonfiglio *et al.* 2002; Marra 2009), suggesting that the islands were intermittently connected to the mainland. The presence of large carnivores in the archipelago is seen as the primary cause of the (relatively) larger size of *P. mnaidriensis*, given that a drastic reduction in size would have been a disadvantage against predation (Rozzi 2018).

From a palaeodiet viewpoint, *P. antiquus* has been found to exhibit a mixed feeding behaviour, thus possessing 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), encephalization (Larramendi & Palombo 2015), skull shape (Van Der Geer *et al.* 2018), brain size (Lyras 2018), body mass estimation (Romano *et al.* 2021), 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 hypothesize that both *P. falconeri* and *P. mnaidriensis* had a different feeding behaviour to 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 on fossil molars of *P. falconeri* and *P. mnaidriensis* from Sicilian collections.

PALAEOLOXODON FALCONERI & *P. MNAIDRIENSIS* FAUNAL COMPLEXES

The Plio-Pleistocene Quaternary fauna of Sicily is divided into Faunal Complexes (FCs) 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 became more frequent (Bonfiglio *et al.* 2002; Marra 2013).

During the early Middle Pleistocene (marine isotopic stages (MIS) 22–11; middle and late Galerian *sensu* Gliozzi *et al.* 1997), the vertebrate assemblage known as the *P. falconeri* FC was characterized 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). *Palaeoloxodon falconeri* was the largest species and no carnivorous mammal taxa are recorded, with the only exception being *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 in 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). Of the 66 species of avifauna, five are endemic to Sicily (*Cygnus equitum*, *Grus melitensis*, *Tyto mourerchauvireae*, *Athene trinacriae*, *Aegolius martae*), along with 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 characterized by a richer biodiversity (Bonfiglio *et al.* 2002), suggesting that the archipelago was connected to the Italian Peninsula by long-lasting land bridges, which enabled 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 medium-to-large sized ungulates such as boars, red and fallow deer, aurochs and bison, as well as the dwarf endemic hippopotamus *Hippopotamus pentlandi* dispersed to Sicily (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). 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). *Palaeoloxodon 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 & METHOD

The studied collection consists of 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. All fossils are stored in the Museum of Nature and Humankind of the University of Padua (Geology and Palaeontology Section; MGP), Italy. A total of 33 teeth were sufficiently preserved 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 over an individual's lifetime (Fortelius & Solounias 2000; Ackermans 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 (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).

Given that 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 colour imaging and laser confocal optical systems, the former using a white light

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

LED light source and CMOS image sensor, and the latter using 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; Appendix S1; Fig. 2). Acquisition was carried out on a plate in the central portion at ×2.5 magnification, using both laser and colour optics. For slightly larger teeth, several images were acquired with a 25% overlapping region and then combined if necessary. Using the proprietary software of the Olympus LEXT OLS4000, the 3D laser surface reconstructions were processed using a noise reduction filter to remove the spikes that may occur when measuring rough or highly reflective surfaces, which can cause detector pixel saturation 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, given that we could not 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 of 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), compared with the other two instruments, which are standard in these kinds 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

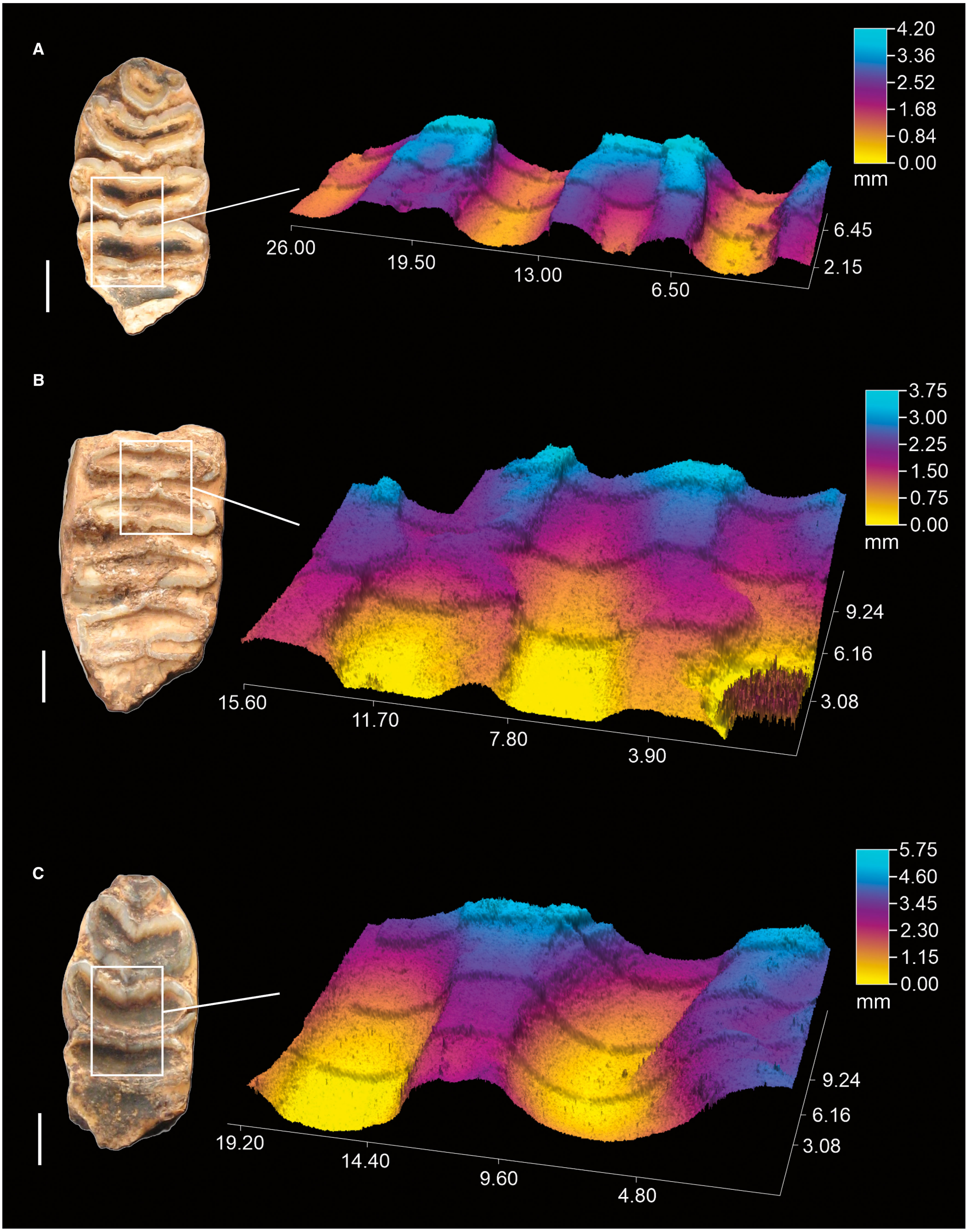

FIG. 2. Selected 3D surfaces of *P. falconeri* fossil teeth obtained with an Olympus Lext OLS4000 laser confocal microscope; false colours record differences in elevation with respect to a reference position; distances are reported in mm. A, MGP-PD 24756. B, MGP-PD 24757. C, MGP-PD 24758. Note that parallel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

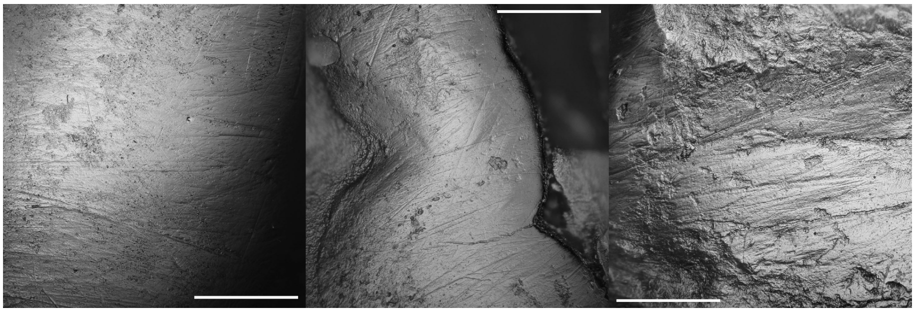

FIG. 3. Photomicrographs of enamel surfaces at ×35 magnification of selected teeth of *P. falconeri*. From left to right: specimen MGP-PD 24724 (m3), specimen MGP-PD 24731 (DP4 or M1), specimen MGP-PD 24754 (M3). Scale bars represent 500 μm.

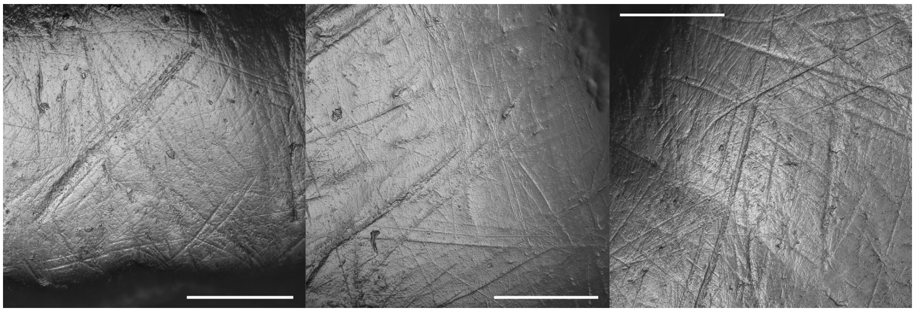

FIG. 4. Photomicrographs of enamel surfaces at ×35 magnification of selected teeth of *P. mnaidriensis*. From left to right: specimen MGP-PD 24700, (DP4 or M1), specimen MGP-PD 24693 (M3), specimen MGP-PD 24624 (m3). Scale bars represent 500 μm.

choice is based on the fact that central plates are subject to 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 (MG) to reduce interobserver error. Following Saarinen *et al.* (2015), angles were measured at the widest point of the plate, which corresponds approximately to its centre. 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 (i.e. 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 of 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 magnification, with a mounted Canon EOS 500D digital camera. Given that the lamellae are not perfectly flat, the focus stacking technique was also used to obtain a clear image of the entire surface portion. For each sample, images were taken every 5° 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, 4), discarding damaged teeth or specimens with taphonomic alterations from the analysis (King *et al.* 1999) (two molars of *P. falconeri* and eight of *P. mnaidriensis*).

Microwear data were collected using the MicroWeaR software (Strani *et al.* 2018) developed in the R environment, which enables quantification and classification of 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 used the default diameter ≤8 μm and >8 μm, respectively, and fine and coarse scratches used the default width ≤3 μm 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 (SR) to reduce interobserver error. Data were compared with those of modern taxa with known diets, including the African bush elephant (*Loxodonta africana*) and the forest elephant (*Loxodonta cyclotis*), 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* to modern diets. As independent variables, we used: (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, and raw data are given in Strani *et al.* (2025, microwear).

RESULTS

Dental mesowear

From a methodological point of view, the digital goniometer used by Saarinen *et al.* (2015) and modified as explained in Appendix S1, is the best instrument for this type of analysis in proboscidean teeth of sufficiently large size due to its low cost and time efficiency, given that measurements require only a few seconds as compared with 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 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 angle measurements taken with different instruments on the test sample (7 plates in three specimens of *P. falconeri* for the confocal microscope vs the digital profilometer, and 6 plates in four specimens of *P. mnaidriensis* for the digital goniometer vs the digital profilometer) produced consistent results (Appendix S1, fig. 2). Differences between angle measurements on the same plate (each one a mean of three measurement repeats) for the two instruments are in the 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 the *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 averaged $\delta^{13}C$ values for Asian and African mesic and xeric environments (Fig. 5). These MMAs are above the average observed in both fossil and modern proboscideans, which usually have mesowear angles narrower than 130° (Fig. 5). The *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 have much wider angles compared with 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* have a higher number of scratches than pits (*P. falconeri* average no. scratches (AS) = 31.0, average no. pits (AP) = 6.1; *P. mnaidriensis* AS = 33.3, AP = 9.3; Table 1), consistent with an abrasive diet. *Palaeoloxodon falconeri* had a scratch-dominated microwear pattern in both the Boccadifalco (AS = 25.5; percentage of specimens with between 0 and 17 scratches (%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 six individuals from Zà Minica cave having a high number of scratches (AS = 29.3) and a low percentage of specimens with between 0 and 17 scratches (16.7%). The only specimen of *P. mnaidriensis* from Puntali cave shows analogous results, with an average of 29.5 scratches being recorded on the occlusal surface. The scratches are mostly fine and mixed (*P. falconeri* scratch width score (SWS) = 0.5; *P. mnaidriensis* SWS = 0.4; overall average of all specimens regardless of provenance), with only the two individuals of *P. falconeri* from Boccadifalco cave having mostly mixed scratches (SWS = 1). Both species have microwear patterns characterized by a low number of pits (AP < 15), with *P. mnaidriensis* having a higher percentage than *P. falconeri* of individuals with more than four large pits (%LP: 41.4 vs 26.3; Table 1). The highest percentage of individuals with >4 large pits is recorded in the *P. mnaidriensis* specimens from Zà Minica cave (%LP = 50). Overall, the average number of scratches and pits is consistent with those observed in extant ungulates with a diet characterized by a high intake of abrasive items (Fig. 6). Most notably, the microwear patterns of both *P. falconeri* and *P. mnaidriensis* have significantly more scratches than that of their ancestor *P. antiquus* (Fig. 6).

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

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

DISCUSSION

Previous studies on the dietary adaptations of extinct dwarf proboscideans have focused on the island dwarf mammoth *Mammuthus exilis* (Santa Rosa Island, North America), suggesting that island conditions favoured a tendency towards a more selective, high-quality diet, given that the 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 the two Sicilian dwarf elephants would show a tendency towards a browse-rich diet similar to what has been observed in *M. exilis*, 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 identify patterns in both *P. falconeri* and *P. mnaidriensis* that 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).

Given that the microwear signal reflects the most recent meals of the animal (the so-called ‘last supper’ effect), and a

FIG. 5. Mesowear angles of *P. falconeri* (in blue) and *P. mnaidriensis* (in red) compared with those of modern species and other fossil proboscideans (data reference in SI1). Dashed lines indicate the thresholds in mesowear angle between browsing (below 106°), mixed feeding (between 106° and 117°) and grazing (above 117°). Threshold values from Saarinen & Lister (2023). *Mean based on specimens collected from different localities. *Abbreviations*: Pa, *P. antiquus*; Pf, *P. falconeri*; Pm, *P. mnaidriensis*. Boxes represent the interquartile interval (with the mean indicated); the whiskers represent the range of variation, to the exclusion of outliers (dots). Plant silhouettes from PhyloPic (https://www.phylopic.org) by T. Michael Keesey (*Brachyelytrum erectum*; CC0 1.0) and Ferran Sayol (*Fagus sylvatica*; CC0 1.0); animal silhouettes by Flavia Strani.

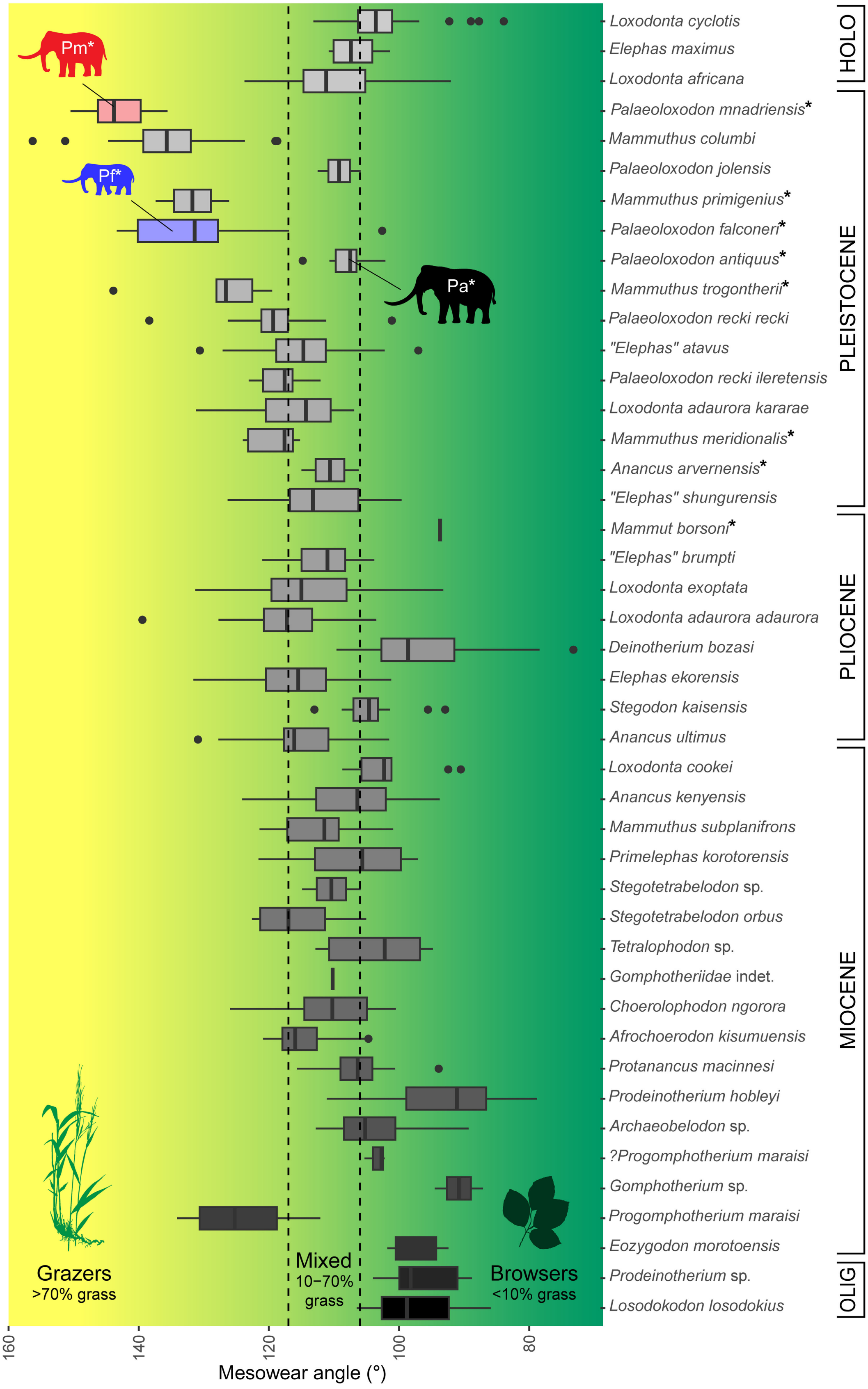
Pm*
Pf*
Pa*
Loxodonta cyclotis
Elephas maximus
Loxodonta africana
Palaeoloxodon mnadriensis*
Mammuthus columbi
Palaeoloxodon jolensis
Mammuthus primigenius*
Palaeoloxodon falconeri*
Palaeoloxodon antiquus*
Mammuthus trogontherii*
Palaeoloxodon recki recki
"Elephas" atavus
Palaeoloxodon recki ileretensis
Loxodonta adaurora kararae
Mammuthus meridionalis*
Anancus arvernensis*
"Elephas" shungurensis
Mammut borsoni*
"Elephas" brumpti
Loxodonta exoptata
Loxodonta adaurora adaurora
Deinotherium bozasi
Elephas ekorensis
Stegodon kaisensis
Anancus ultimus
Loxodonta cookei
Anancus kenyensis
Mammuthus subplanifrons
Primelephas korotorensis
Stegotetrabelodon sp.
Stegotetrabelodon orbus
Tetralophodon sp.
Gomphotheriidae indet.
Choerolophodon ngorora
Afrochoerodon kisumuensis
Protanancus macinnesi
Prodeinotherium hobleyi
Archaeobelodon sp.
?Progomphotherium maraisi
Gomphotherium sp.
Progomphotherium maraisi
Eozygodon morotoensis
Prodeinotherium sp.
Losodokodon losodokius
HOLO
PLEISTOCENE
PLIOCENE
MIOCENE
OLIG
Grazers
>70% grass
Mixed
10–70%
grass
Browsers
<10% grass
160
140
120
100
80
Mesowear angle (°)

TABLE 1. Summary of dental microwear analysis.

	Taxon		Microwear									Predicted diet	
			N	AP	AS	%LP	%0–17	SWS	%FS	%MS	%CS	Type	Type*
Total	*Palaeoloxodon falconeri*	Mean	19	6.1	31.0	26.3	15.8	0.5	52.6	42.1	5.3	Meal-to-meal mixed feeder	Grazer
		SD		2.7	11.3								
		CV		0.4	0.4								
Total	*Palaeoloxodon mnaidriensis*	Mean	29	9.3	33.3	41.4	3.4	0.4	58.6	41.4	0.0	Meal-to-meal mixed feeder	Grazer
		SD		4.4	8.5								
		CV		0.5	0.3								
Boccadifalco Cave	*Palaeoloxodon falconeri*	Mean	2	5.8	25.5	0.0	0.0	1.0	0.0	100.0	0.0	Grazer	Grazer
		SD		3.2	1.4								
		CV		0.6	0.1								
Luparello Cave	*Palaeoloxodon falconeri*	Mean	17	6.1	31.6	29.4	17.6	0.5	58.8	35.3	5.9	Meal-to-meal mixed feeder	Grazer
		SD		2.9	12.2								
		CV		0.5	0.4								
Zà Minica Cave	*Palaeoloxodon mnaidriensis*	Mean	6	9.9	29.3	50.0	16.7	0.3	66.7	33.3	0.0	Meal-to-meal mixed feeder	Mixed feeder
		SD		5.5	11.0								
		CV		0.6	0.4								
Puntali Cave	*Palaeoloxodon mnaidriensis*	Mean	1	13.5	29.5	0.0	0.0	0.0	100.0	0.0	0.0	Meal-to-meal mixed feeder	Mixed feeder
		SD		/	/								
		CV		/	/								

Abbreviations: %0–17, percentage of specimens with between 0 and 17 scratches; %CS, percentage of individuals with predominantly coarse scratches (i.e. >50% of the total); %FS, percentage of individuals with predominantly fine scratches (i.e. >50% of the total); %LP, percentage of individuals with >4 large pits; %MS, percentage of individuals with a mix of fine and coarse scratches; AP, average number of pits; AS, average number of scratches; CV, coefficient of variation; SWS, scratch width score.

*Extant seasonal and non-seasonal mixed feeders are grouped together in a single dietary category 'mixed feeders'.

grazing diet can overwrite a previous browsing microwear signal in as little as 2 weeks (Winkler *et al.* 2020), one possible explanation is that grazing was restricted to the coastal environments near the caves where these animals ultimately died. However, given that the mesowear signal represents a lifetime signal (Ackermans 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 ash produced by the volcanic activity of Mount Etna, which became active during the Middle Pleistocene (*c.* 500 ka) (Branca *et al.* 2007), could also have covered vegetation of the study area, depending on the intensity of the eruptions. A higher concentration of particles on plant parts may lead to a higher abundance of coarse features on enamel surfaces as animals chew on grit-covered 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* show 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 in Sicily during the Middle Pleistocene is supported by the associated fauna of the *P. falconeri* FC, 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 &

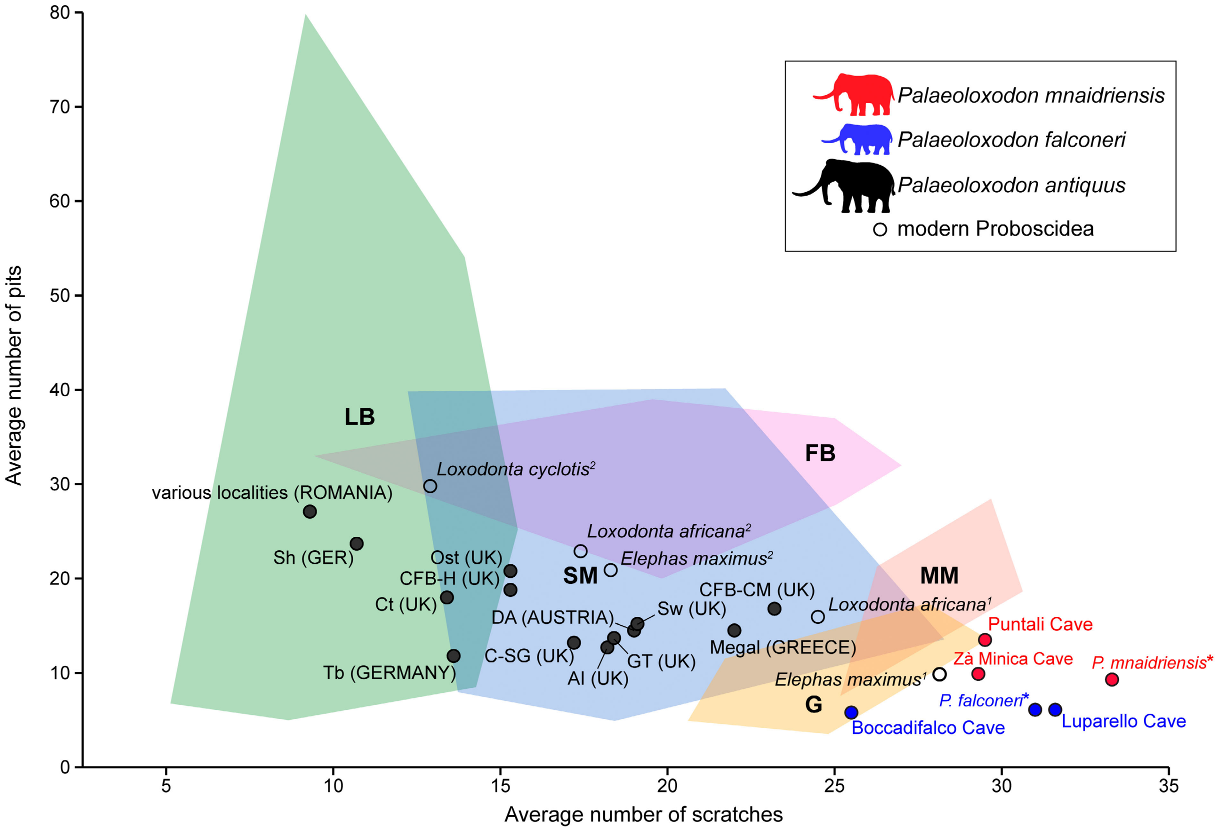

FIG. 6. Bivariate plot of the average number of pits vs the average number of scratches in *P. falconeri*, *P. mnaidriensis* (present study), *P. antiquus* (Rivals *et al.* 2019), extant proboscideans (Solounias & Semprebon 2002; Semprebon *et al.* 2016) and extant ungulates (Solounias & Semprebon 2002). *Abbreviations*: AI, Aveley & Ilford; CFB, Cromer Forest Bed; CFB-CM, CFB Cromer + Mundesley; CFB-H, CFB Happisburgh; C-SG, Crayford & Slade Green; Ct, Clacton; DA, Deutsch-Altenburg; FB, fruit browsers; G, grazers; GT, Grays Thurrock; LB, leaf browsers; Megal, Megalópolis; MM, meal-by-meal mixed feeders; Ost, Ostend (in Essex); Sh, Steinheim; SM, seasonal mixed feeders; Sw, Swanscombe; Tb, Taubach. *All specimens including those of unknown or uncertain provenance; ^{1}Solounias & Semprebon (2002); ^{2}Semprebon *et al.* (2016).

Hartley 2006). In fact, phytolith production and lignification are the known defence mechanisms that plants often rely on when exposed to prolonged and constant feeding pressure (Martínez & López-Portillo 2003; Gallardo *et al.* 2023).

Given that *P. falconeri* was the only large herbivorous mammal recorded in Sicily (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 in protective strategies even more. Extreme insular conditions, characterized by a reduced landmass with particularly scarce grass-dominated vegetation, both in terms of quantity and type (given that 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 and devote 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 characterized by a slow growth rate with marked longevity (up to *c.* 68 years) and delayed sexual maturity (*c.* 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 size throughout their ontogeny (Dmitriew 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 as a result of delayed senescence (Jordana *et al.* 2012) and to adapt to an increasingly abrasive diet (Winkler *et al.* 2013), given that they had 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 structures and a shrub-like habit on islands) may also explain the *P. falconeri* dental wear patterns, given that 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).

Palaeoloxodon 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 maximize 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 of 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 characterized by a higher degree of abrasion compared with that recorded for their mainland ancestor, the straight-tusked elephant, *P. antiquus*, which usually had 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. *Palaeoloxodon 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 the dental wear patterns of *P. mnaidriensis*, 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 rather 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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DATA ARCHIVING STATEMENT

Data for this study are available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.6djh9w1f7.

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SUPPORTING INFORMATION

Additional Supporting Information can be found online (https://doi.org/10.1002/spp2.70036):

Appendix S1. Details for dental mesowear protocols.
Appendix S2. *Palaeoloxodon falconeri* and *Palaeoloxodon mnaidriensis* faunal complexes.

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Appendix S1

Details on the dental mesowear protocols

The method of mesowear analysis introduced by Fortelius & Solounias (2000) predicts the amount of browse and grass in the diet by quantifying the occlusal relief and scoring the sharpening of the molar cusps. In its original form, as developed by Fortelius & Solounias (2000) for selenodont, lophoselenodont and trilophodont dentition (respectively of ruminants, perissodactyla and extinct mastodonts), mesowear analysis was based on a quantitative assessment of the height and profile (more or less pointy) of the cusps of molar teeth: in a low-abrasiveness diet, wear produced by tooth-on-tooth friction prevails, causing a high occlusal relief with pointed cusps, while abrasive plant material (such as grasses) causes the cusps to wear down, becoming lower and more rounded. A strictly browser diet should give a high dental relief (measured on the labial side of the upper molars and on the lingual side of the lower molars, as difference in height between the cusps' tips and the valleys' bottom) and sharp cusps' tips scored (again in labial side for the upper molars and lingual side for the lower molars) against a comparison table. In contrast, a strictly grazer diet should give a low dental relief and blunted cusps' tips, while intermediate situations should be suggestive of mixed diets (Fortelius & Solounias, 2000).

It must be noted that the mechanisms of dental wear are not fully understood. For example, it is still debated whether the high abrasiveness of a grazing diet is due to the exogenous quartz powder accidentally ingested in large quantities by animals feeding on the ground, or to the phytoliths present in the grass (Lucas & Omar, 2012). Indeed, some authors argue that the contribution of hard plant tissues mainly affects other dental wear patterns, such as microwear patterns (Van Casteren *et al.*, 2020). Nevertheless, there is ample empirical evidence that grass causes wear on dental enamel, as reflected in the mesowear signal of ungulate molars (Fortelius & Solounias, 2000). Based on all the above considerations, it is assumed that the larger the angles and the flatter the occlusal surface, the greater the presence of abrasive components in the diet (grazing diet). Conversely, the smaller the angles, the lower the presence of these elements in the diet (browsing diet).

As originally conceived, the method is not suitable for the molars of modern elephants and other elephantines because of their distinctive dental morphology and chewing motion. The scoring of the sharpness of the enamel occlusal surface is pointless, since the peculiar propalinal (antero-posterior) movement of the elephant mandible (and thus of the lower teeth on the upper teeth), rubbing the enamel plates against each other, flattens them without producing measurable facets on the occlusal surface (Saarinen *et al.*, 2015). In addition, the peculiar dental morphology, with each tooth made up of a number of transversal plates (lamellae) joined with each other by a thick layer of cementum, prevents the recording of the occlusal relief from either labial or lingual view. Saarinen *et al.* (2015) thus envisaged a new method to study dental mesowear patterns in Elephantids. It measures the angle between the bottom of the worn dentin valleys, and the peaks of the enamel ridges surrounding them at the centre of each plates that make up a tooth, following ideal tangent lines that originate at the bottom of the valley and go all the way up to the two peaks. The enamel ridges wear down more as the abrasiveness of the diet increases, resulting in reduced occlusal relief and the production of wider angles. Abrasive plant material accelerates and equalises the wear rate of enamel and dentin, resulting in a flatter occlusal relief, whereas non-abrasive (or much less abrasive) material causes deeper valleys to be carved into the softer dentin, thus resulting in a higher enamel relief.

Saarinen *at al.* (2015) use a high-precision digital goniometer with an accuracy of 0.1° (model DAF-001 from CMT Utensili) with custom modifications of the arms to be inserted inside the thin dental lamellae of Elephantids molars: two thin movable metal slats are mounted along the arms of the goniometer to elongate them proximally to the fulcrum of the instrument. The limit of this device is that the extensions of the arms must be repositioned for each single measurement. Here we propose a different customisation of the same digital goniometer (Figure 1): we applied to the instrument two steel graduated bars, welded to have the same rotation fulcrum of the goniometer's arms and mounted on metal spacers to ensure that the main part of the instrument does not touch the sample. In this way the bars can be inserted directly inside the dentine valleys, without having to be recalibrated for each measurement. It should be noted however that while this protocol removes the need to recalibrate the instrument after each use, it does not allow to measure angles with amplitude lower than 90°. Nevertheless, due to the very nature of the wear dental and tooth shape of proboscideans this is a minor issue because corners with angles <90° are not expected.

The modified digital goniometer was employed on *P. mnaidriensis* teeth, while it could not be used on the small *P. falconeri* molars as the distance between lamellae is extremely reduced and the measurement error introduced by the operator might be too high. Therefore, for *P. falconeri*, we opted to use an Olympus lextLOS4000 laser confocal microscope, with a resolution of 0.2 μm, allowing a detailed 3D reconstruction of the occlusal surface. Specifically, the accuracy for vertical measurements is 0.2+L/100 μm, where L is the length of the measured portion expressed in μm. Thus, assuming a height of 3 mm of the enamel ridges relative to the central dentin valley, we have an accuracy of 30 μm or 0.03 mm. The horizontal accuracy corresponds to 2% of the measurement taken. Acquisition was carried out at 2.5x magnification on the central portion of each plate, using both laser and color optics. Slightly larger teeth required the acquisition of several images, then combined by "photo stitching".

The confocal microscope could not be used for *P. mnaidriensis* because its teeth were too large to fit under the microscope. Thus, to test whether the measurements made with the confocal microscope in *P. falconeri* and with the digital goniometer in *P. mnaidriensis* were consistent with each other, we used a digital profilometer to repeat measurements on 3 specimens of *P. falconeri* and 4 specimens of *P. mnaidriensis*. The digital profilometer, a JR25 from NANOVEA, is able to scan and reproduce objects and surfaces in 3D, similar to a confocal microscope, using a beam of light through an optical fiber that scans the entire area of interest, achieving a resolution in the nanometer-scale, which is even higher than that of the microscope. The digital profilometer was only used on a subset of samples (Table 1) because it takes several hours to scan the relevant plate surface. In addition, unlike the confocal microscope, the profilometer does not have measurement tools integrated into the management software. It was therefore necessary to develop a multi-step protocol for measuring the angles. First, the 3D scan files (.sur format) were analysed using the image analysis software Gwyddion, rescaled using GIMP, and the angles were measured using Image J. The proposed protocols have been developed in conjunction with the Department of Mathematics and Physics of the University of Campania "Luigi Vanvitelli".

As can be seen in Figure 2 and Figure 3, a plate-by-plate comparison between measurements taken with different instruments (i.e. confocal microscope vs. digital profilometer for *P. falconeri*, and digital goniometer vs. digital profilometer for *P. mnaidriensis*) yield similar results.

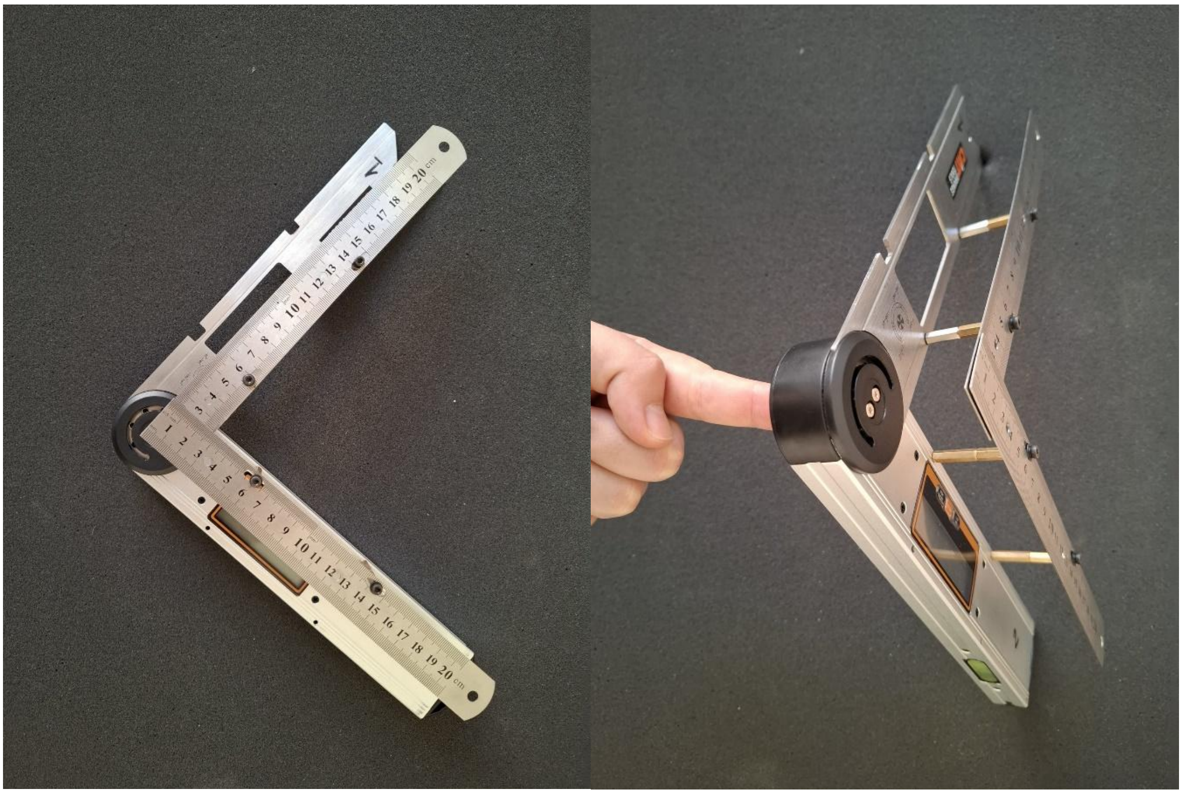

Figure 1. Digital goniometer used by Saarinen et al. (2015) with the application of two graduated bars sharing the same rotation fulcrum of the goniometer's arms.

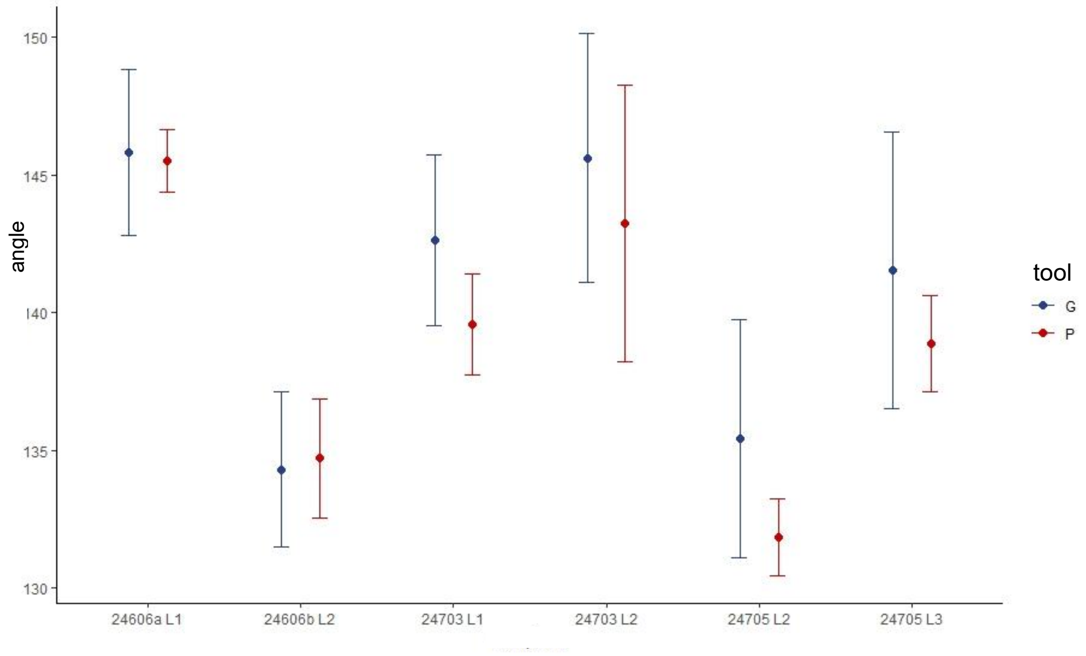

Figure 2. Plate-by-plate comparison between mesowear angles measured with the digital goniometer (G) and the digital profilometer (P) in *P. mnaidriensis*.

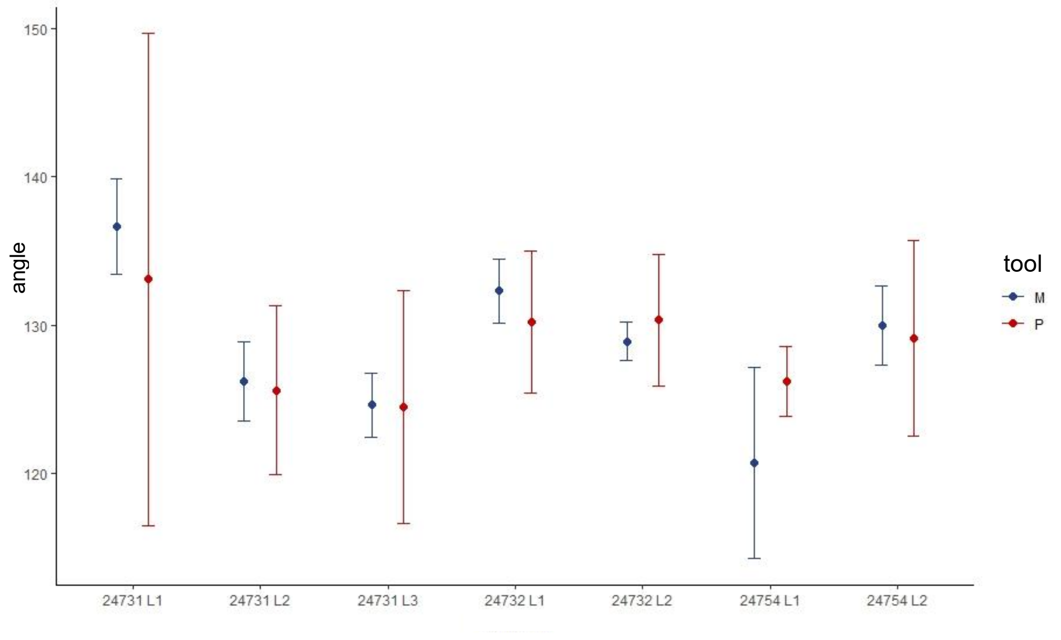

Figure 3. Plate-by-plate comparison between mesowear angles measured with the confocal microscope (M) and the digital profilometer (P) in *P. falconeri*.

Specimen	**Taxa**	**MWA**	**Tool**	**MWA**	**Tool**
MGP-PD 24731	*P. falconeri*	131.4	Confocal	136.9	Profilometer
MGP-PD 24732	*P. falconeri*	134.0	Confocal	136.7	Profilometer
MGP-PD 24733	*P. falconeri*	116.9	Confocal		
MGP-PD 24734	*P. falconeri*	141.1	Confocal		
MGP-PD 24735	*P. falconeri*	140.9	Confocal		
MGP-PD 24736	*P. falconeri*	140.2	Confocal		
MGP-PD 24737	*P. falconeri*	136.7	Confocal		
MGP-PD 24748	*P. falconeri*	128.9	Confocal		
MGP-PD 24754	*P. falconeri*	125.3	Confocal	127.6	Profilometer
MGP-PD 24756	*P. falconeri*	102.6	Confocal		
MGP-PD 24757	*P. falconeri*	143.4	Confocal		
MGP-PD 24758	*P. falconeri*	129.0	Confocal		
MGP-PD 24759	*P. falconeri*	127.8	Confocal		
MGP-PD 24606a	*P. mnaidriensis*	145.8	Goniometer		
MGP-PD 24606b	*P. mnaidriensis*	135.6	Goniometer		
MGP-PD 24615	*P. mnaidriensis*	137.4	Goniometer		
MGP-PD 24617b	*P. mnaidriensis*	150.2	Goniometer		
MGP-PD 24617a	*P. mnaidriensis*	146.4	Goniometer		
MGP-PD 24619	*P. mnaidriensis*	144.8	Goniometer		
MGP-PD 24620	*P. mnaidriensis*	139.5	Goniometer		
MGP-PD 24621	*P. mnaidriensis*	150.5	Goniometer		
MGP-PD 24693	*P. mnaidriensis*	140.5	Goniometer		
MGP-PD 24694	*P. mnaidriensis*	145.6	Goniometer		
MGP-PD 24695	*P. mnaidriensis*	146.7	Goniometer		
MGP-PD 24700	*P. mnaidriensis*	143.5	Goniometer		
MGP-PD 24701	*P. mnaidriensis*	142.9	Goniometer		
MGP-PD 24703	*P. mnaidriensis*	144.1	Goniometer		
MGP-PD 24705	*P. mnaidriensis*	137.3	Goniometer		
MGP-PD 24706	*P. mnaidriensis*	138.0	Goniometer		
MGP-PD 24709	*P. mnaidriensis*	140.4	Goniometer		
MGP-PD 24715	*P. mnaidriensis*	149.1	Goniometer		
MGP-PD 24606a	*P. mnaidriensis*	136.0	Goniometer	145.5	Profilometer

MGP-PD 24606b	*P. mnaidriensis*	120.5	Goniometer	134.7	Profilometer
MGP-PD 24615	*P. mnaidriensis*	136.0	Goniometer		
MGP-PD 24617a	*P. mnaidriensis*	135.3	Goniometer		
MGP-PD 24620	*P. mnaidriensis*	140.0	Goniometer		
MGP-PD 24693	*P. mnaidriensis*	135.7	Goniometer		
MGP-PD 24694	*P. mnaidriensis*	141.4	Goniometer		
MGP-PD 24695	*P. mnaidriensis*	142.8	Goniometer		
MGP-PD 24700	*P. mnaidriensis*	132.0	Goniometer		
MGP-PD 24701	*P. mnaidriensis*	134.5	Goniometer		
MGP-PD 24703	*P. mnaidriensis*	150.0	Goniometer	141.4	Profilometer
MGP-PD 24705	*P. mnaidriensis*	141.9	Goniometer	135.4	Profilometer
MGP-PD 24706	*P. mnaidriensis*	134.3	Goniometer		
MGP-PD 24715	*P. mnaidriensis*	139.4	Goniometer		

Table 1. Mean mesowear angles (MWA) obtained by using different tools on *P. falconeri* and *P. mnaidriensis* teeth. Only a subset of the available samples was re-measured using a profilometer.

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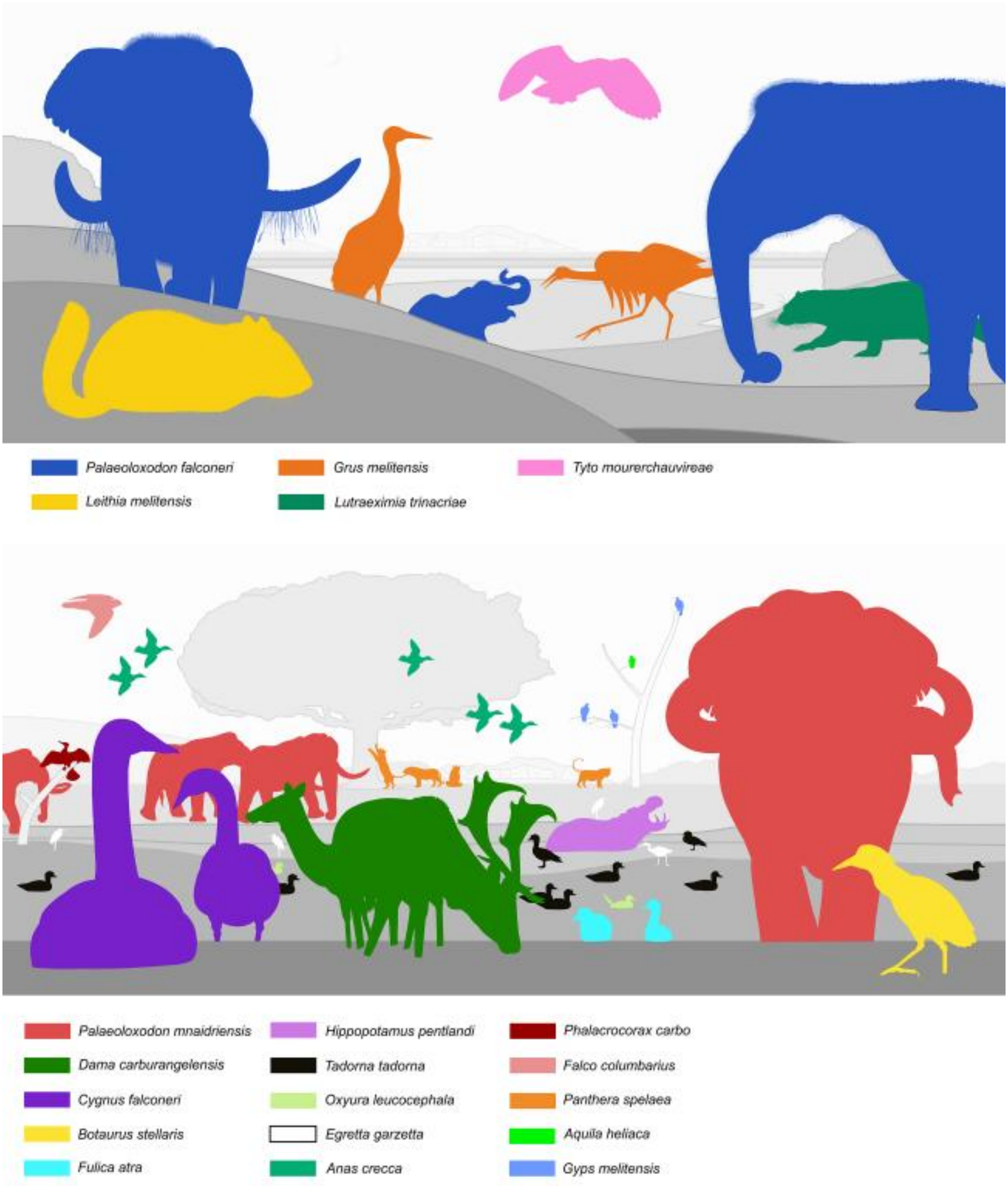
Appendix S2

Palaeoloxodon falconeri and Palaeoloxodon mnaidriensis Faunal Complexes



Schematic illustrations of the main vertebrate species of the *P. falconeri* (top) and of the *P. mnaidriensis* (bottom) Faunal Complexes. Work by Simone Zoccante.