Highlights

- New and comprehensive dental microwear database for modern Ursidae is presented
- Talonid area of m1 is most effective in the differentiation of ursid ecospaces
- Dietary ecospaces were established for the extant species
- Dietary differences can be traced also in brown bears from different latitudes
- The ecospace and palaeodietary niche were established for the fossil Grays bears, UK

The bear necessities: a new dental microwear database for the interpretation of palaeodiet in fossil Ursidae

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Keywords: *Ursus*, teeth, microwear, palaeodiet, interglacial, Britain.

Abstract

This study presents a new database of dental microwear features for extant bear species, which is used to interpret palaeodiet in brown bear (*Ursus arctos*) from the late Middle Pleistocene site of Grays Thurrock, U.K. Applying light stereomicroscopy techniques in dental microwear analysis, we highlight, for the first time, that the talonid area of the first lower molar (m1) in extant ursids is most effective in the differentiation of dietary ecospaces. Extant bear species can be separated into different parts of a dietary ecospace revealing microwear features that mirror their dietary preferences. Of particular note is the differentation of ecospaces within modern brown bear populations from different geographical regions and the potential for identifying seasonal variation in diet. The results demonstrate that the diet of the late Middle Pleistocene brown bear from the interglacial site of Grays Thurrock was closely comparable to that of the modern *U. arctos* from northern Europe, the American black bear (*Ursus americanus*), and the sun bear (*Helarctos malayanus*). This suggests the dietary importance of fibrous food, as well as soft fruits and invertebrates and a small vertebrate component. This finding is in agreement with climatic conditions and habitats inferred for the MIS 9 interglacial. The creation and testing of a dental microwear database for all modern bear species provides a foundation for subsequent application to other extinct Pleistocene bear populations.

1. Introduction

The rapid climatic fluctuations of the Pleistocene produced major changes in the palaeobiogeography and community structure of European mammalian populations, as a result of repeated environmental and vegetation changes (e.g. Barnosky et al., 2004; Hofreiter and Stewart, 2009; Stuart and Lister, 2007; Kahlke et al., 2011; Stuart and Lister, 2012). Large carnivores are of particular relevance to our understanding of the impact of these changes on the contemporary fauna, since (1) they are extremely diverse in terms of the adaptations of individual guild members to a particular environment and mode of life and (2) they demonstrate contrasting feeding strategies. This can be exemplified by the Ursidae since bears were one of the most common elements of the Pleistocene large mammal guild and demonstrate some of the most remarkable dietary flexibility of any of the large carnivores.

1.1. Dietary flexibility in modern Ursidae

The Family Ursidae is today widely distributed and is represented by eight species, each adapted to a particular environment and mode of life (Fig. 1). According to morphological and molecular data (Krause et al., 2008), five extant genera are recognized: *Melursus*, *Ursus*, *Helarctos*, *Tremarctos* and *Ailuropoda*. Three extant species, the polar bear *Ursus maritimus*, giant panda *Ailuropoda melanoleuca* and sloth bear *Melursus ursinus* have highly specialised diets, representing hypercarnivory, herbivory and insectivory/frugivory respectively (Joshi et al., 1997; Derocher et al., 2002; Macdonald, 2009) (Fig. 1).

However, many bear species are omnivorous and can adjust their diet according to food availability in different habitats. The most extreme example of behavioural flexibility in the Ursidae is that of the brown bear *Ursus arctos*, which not only occupies a wider range of habitats in the Palearctic (except Africa) and Nearctic, but also demonstrates greater dietary variability than any other species of bear (McLellan et al., 2008; Bojarska and Selva, 2011) (Fig. 1). Furthermore, in arctic and alpine regions, modern brown bears exhibit dietary extremes characterised by large volumes of meat (including large concentrations of spawning salmon) and roots (Mattson, 1998). The more carnivorous tendency in North American brown bears differentiates them from, and reduces potential dietary overlap with, another bear species on the same continent, namely the black bear *Ursus americanus*. The black bear is generally referred to as omnivorous, with a diet that varies slightly seasonally and regionally (Bennett et al., 1943; Garshelis et al., 2008a; Macdonald, 2009; Frary et al., 2011) but apparently consumes more plant and fruit matter (soft mast) than salmon (Fortin et al., 2007) (Fig. 1). Another important example of adaptability to diverse environments and different dietary preferences within the brown bear is the fact that northern European brown bear are more carnivorous than their southern counterparts, based on the proportion of ungulates in their diet during all seasons (except during winter hibernation) (Persson et al., 2001; Bojarska and Selva, 2011) (Fig. 1). In contrast to the more carnivorous northern European brown bears, populations found in the deciduous and mixed forests of continental central and eastern Europe (e.g. the Dinaric and Carpathian mountain ranges) exploit a large variety of soft mast, such as fleshy fruits, together with hard mast items (i.e. fruits and seeds with a hard outer covering or exocarp, nuts and acorns and pine seeds) (Bojarska and Selva, 2011). The brown bears of Greece represent the most southerly distribution in Europe of the species (Karamanlidis et al., 2015), with green vegetation and soft mast comprising the predominant foods consumed (Giannakos, 1997; Vlachos et al., 2000).

It is hypothesised that modern bear species should serve as appropriate analogues when reconstructing the palaeodiet and palaeoecology of Pleistocene bear species during both cold- and temperate-climate periods. This is because their diet should vary predictably between greater and lesser amounts of meat to non-meat input, and between greater and lesser amounts of hard to the soft mast, dependent on climate, environment, and species.

1.2. Palaeodiet of the Ursidae

Although the complexities of individual ecosystems and the dietary flexibility of the Ursidae (despite their carnivorous morphological features) can make interpretation of their feeding ecology difficult (Robbins et al., 2004; Sacco and Van Valkenburgh, 2006), the availability of innovative techniques such as isotopic and microwear analyses has made it possible to explore palaeoecology and palaeodiet even in extinct species. Isotopic proxies reveal information on both palaeodiet of bears and palaeoenvironment (e.g. Bocherens et al., 1994; Hilderbrand et al., 1996; Reinhard et al., 1996; Stiner et al., 1998; Bocherens et al., 2004; Richards et al., 2008; Bocherens et al., 2011; Dotsika et al., 2011; Naito et al., 2016; Krajcarz et al., 2016; Grandal d'Anglade et al., 2018). Particular attention has been given to cave bear assemblages from different sites since aspects of their palaeoecology have been much debated (e.g. Bocherens et al., 1990, 1994; 2004; 2011; Fernández Mosquera et al., 2001; Münzel et al., 2011; Pacher et al., 2012; Krajcarz et al., 2016; Bocherens, 2018).

For example, cave bears *Ursus spelaeus*, were a herbivorous species (echoing earlier inferences made on the morphology of the cranium and dentition; Kurtén, 1968) with a diet based mainly on C3 plants (Bocherens et al., 1994; Fernández Mosquera et al., 2001 ; Münzel et al., 2011). Bocherens et al. (2011) suggested ecological differentiation between two genetically distinct cave bear species, *Ursus eremus* and *Ursus ingressus*, as well as *U. arctos* from Austria. Both cave bear species were exclusively herbivorous but apparently consumed different plant types, whereas brown bears also included some animal protein in their diet. Krajcarz et al. (2016) carried out a comprehensive study on $\delta^{13}C$ and $\delta^{15}N$ values of *U. spelaeus* from European sites with assemblages dated to Marine Oxygen Isotope Stage (MIS) 3, in order to identify latitudinal, longitudinal or altitudinal patterns. They demonstrated that there is isotopic homogeneity between the cave bears from Central-Eastern Europe and those from Central, Western and Southern Europe. They suggested that this may reflect, either, the climatic and vegetation homogeneity of ecosystem, which is in contradiction to palaeoclimatic data, or may be typical for cave bears, due to their low ecological flexibility. In addition, the authors also reported correlation with respect to altitude, for example altitudinal gradient -0.0013‰/m of

$\delta^{15}N$ values was seen in most samples except at two Romanian sites and an increasing altitudinal gradient was visible in several groups of sites in $\delta^{13}C$ values (0.0006‰/m internal gradient of $\delta^{13}C$ values). All analysed cave bears appeared to be herbivores with low $\delta^{15}N$ values, with the exception of those from the two Romanian sites (Pestera cu Oase and Ursilor) that show higher than expected $\delta^{15}N$ values. Krajcarz et al. (2016) attributed these outliers to probably local phenomena (as yet undetermined), since no underlying geographical factors could be identified. More recently, Bocherens (2018) undertook similar stable isotope analyses on more than 300 cave bear bones from all over Europe and confirmed that all populations, including those from Romania, presented values overlapping with herbivores and not with carnivores.

Stable isotope studies of fossil brown bears have consistently identified differences in diet compared to cave bears, largely through their enhanced consumption of animal protein (e.g. Bocherens et al., 1997; Stiner et al., 1998; Bocherens et al., 2011). In addition, dietary adaptations are equally influenced by competition with other species (Münzel et al., 2011; Bocherens, 2015). Analysis of North American short-faced bear *Arctodus simus* remains has revealed that these bears were hyper-carnivorous and consumed meat such as reindeer and muskoxen (Bocherens, 2015). The $\delta^{15}N$ values for most *U. arctos* prior to 20 ka in Beringia are subdued compared to those of *A. simus*, suggesting that the former was out-competed for meat resources by the latter and forced to adopt a more herbivorous diet, a pattern that is reversed from 20 ka onwards, after the extinction of *A. simus* (Barnes et al., 2002; Bocherens, 2015).

1.3. Dental Microwear Analysis

Dental Microwear Analysis (DMA) is another technique by which an animal's palaeoecological niche can be elucidated. Taking into account factors such as facet type and tooth type (Ungar, 2015), observations of dental microwear patterns in living mammals have revealed that these patterns renew every few days or weeks in life, so at the point of death, the marks recorded will illustrate the final weeks of diet of the animal (Grine, 1986). Using the analysis of dental micro-abrasion or microwear, a number of previous studies have used the dietary patterns in specimens of extant species in order to reconstruct both palaeodiet in their fossil relatives and to explore palaeoenvironmental change (e.g. Walker et al., 1978; Solounias et al., 1988; Solounias and Semprebon, 2002; Rivals and Deniaux, 2003; Merceron et al., 2004a; b; 2005a; b; Semprebon and Rivals, 2006; Semprebon and Rivals, 2007; Rivals and Athanassiou, 2008; Semprebon and Rivals, 2010; Medin et al., 2015).

In terms of application to mammals, DMA has been successfully applied to primates (e.g. Grine, 1981; Teaford and Walker, 1984; Grine, 1986; Ungar, 1998; Semprebon et al., 2004; Ungar and Lucas, 2010) and to a wide variety of herbivores (e.g. Rivals & Lister, 2016), including ungulates (e.g. Merceron et al., 2005a; Rivals et al., 2007; Rivals and Semprebon, 2011) and proboscideans (e.g. Green et al., 2005; Palombo et al., 2005; Todd et al., 2007; Rivals et al., 2010; Rivals et al., 2012; Rivals and Lister, 2016). The technique has also been applied to living and fossil carnivores (e.g. Van Valkenburgh et al., 1990; Anyonge, 1996; Dewar, 2004; Goillot et al., 2009; Stynder et al., 2012; DeSantis et al., 2012; Bastl et al., 2012). For example, Dewar (2004) examined the palaeodiet of fossil miacids, condylarths, creodonts and other fossil carnivores by applying the low magnification stereomicrowear technique (after Solounias and Semprebon, 2002) and comparing the data with those generated from a sample of extant *Ursus*, *Canis*, *Lycaon*, *Otocyon*, *Urocyon* and *Ailuropoda* genera. He focused on examination of the M1 (first upper molar) and particularly on the paracone, concluding that pits distinguished the consumption of meat better than scratches. Goillot et al. (2009) applied microwear analysis on both slicing and grinding facets of M1 and m1 teeth of carnivores, modifying the Solounias and Semprebon (2002) low–magnification method and analysing the surfaces through an image software package developed by Merceron et al. (2004a; 2005b). More specifically, Goillot et al. (2009) used some extant species from the following carnivore families: Ursidae, Ailuridae, Hyaenidae, Mustelidae, Eupleridae, Herpestidae, Felidae, Procyonidae and Canidae in order to explore the dietary habits of the extinct amphicyonid, *Amphicyon major*. These authors agreed that microwear analysis using optical stereomicroscopy could be applied to most carnivores and in particular, they highlighted the importance of the slicing facet of the carnassial teeth in facilitating palaeodietary interpretation. They concluded that the microwear features on the slicing area of *A. major* carnassials suggested an omnivorous diet, although one with strong meat-eating tendencies, suggesting affinities with the diet of the modern red fox (*Vulpes vulpes*). *A. major* also possessed a high number of scratches and many broad pits, indicating that it consumed a significant proportion of plants and hard items (Goillot et al., 2009). Bastl et al. (2012) also applied the low magnification microwear technique (after Solounias and Semprebon, 2002), using an extant sample of carnivores (Hyaenidae, Felidae, Canidae, Viverridae, and Nandiniidae) with different dietary habits in order to elucidate the microwear patterns for bone/meat, meat/bone, meat, mixed carnivorous (meat/plant matter) and fruit-based diets, before comparing these against a fossil hyaenodont. Based on their microwear observations and enamel microstructure results, *Hyaenodon* teeth were judged to exhibit heavy gouging and extensive pitting and scratching of the enamel, indicating the consumption of tough foods such as bone. Analogies were drawn with the features on the teeth of extant striped hyaena (*Hyaena hyaena*) and spotted hyaena (*Crocuta crocuta*), thereby implying similar dietary behaviour (Bastl et al., 2012).

1.4. DMA in Ursidae

Despite the potential of the technique for establishing the palaeodietary ecology of fossil mammals and consequently shedding light on Pleistocene palaeoenvironments, few studies to date have focused on Ursidae (Pinto-Llona and Andrews, 2001; Pinto-Llona, 2006; Peigné et al., 2009; Donohue et al., 2013; Pinto-Llona, 2013; Münzel et al., 2014; Jones and DeSantis, 2016; Medin et al., 2017; Peigné and Merceron, 2018) and little has therefore been known of diet-related impacts on the enamel of bears. Pinto-Llona and Andrews (2001) were the first to study enamel wear patterns in the Ursidae and compared modes and degrees of tooth wear between brown and cave bears from northern Spain in order to establish whether cave bears were consuming (plant) foods with a high grit content. Both macroscopic and microscopic observations were made, and although the methodology is not very clear regarding the microscopic parts, the authors concluded that the cave bears from this geographical region did not ingest gritty foods. Later, Pinto-Llona (2006) further developed the methodology regarding the microwear features on *U. arctos* and *U. spelaeus*, by analysing two facets on the m1, the distal facet of the protoconid and the lingual facet of the hypoconid, using SEM, before digitising the features and analysing the images using bespoke microwear software (after Ungar et al., 1991). According to this study, cave bears possessed the highest proportion of pits relative to scratches in both facets and the greatest density of microwear features. In contrast, brown bears had a large concentration of scratches on both facets, which was interpreted as the result of grass consumption (Pinto-Llona, 2006). Moreover, Pinto-

Llona (2006) suggested that the preferred orientation in microwear features seen in cave bears (which interestingly is not replicated in brown bears) is a function of both the chewing dynamic and nature of the food consumed. Later studies by Peigné et al. (2009) and Goillot et al. (2009) demonstrated that low-magnification microwear studies could be applied to recent and fossil specimens. Peigné et al. (2009) concentrated on the labial facet of the paraconid of the m1 and the conclusion was drawn that cave bears from Goyet in Belgium, had an omnivorous diet, since they presented an intermediate number of small and large pits, revealing a different pattern to both piscivores and herbivores. However, these conclusions must be treated as tentative as these investigations were hampered by the use of modern databases that excluded some of the most common bear species, namely *U. arctos*, *U. americanus* and *U. thibetanus*.

Donohue et al. (2013) were the first to apply dental microwear texture analysis (DMTA) on ursids. DMTA relies on a combination of scanning confocal profilometry and scale-sensitive fractal analysis (SSFA) and the terminology, therefore, differs from that of the stereomicrowear methods (Scott et al., 2006). This approach recognises that teeth function on multiple levels and therefore, that microwear surface textures are likely to be sensitive to scale (Ungar, 2015 and references therein). SSFA is based on the idea that the apparent length, area, and volume of a rough surface will change according to the scale of observations, so surfaces may appear smooth at a coarse scale and rough with increasing fine resolution (Ungar, 2015). Area-scale fractal complexity (Asfc) and length-scale anisotropy of relief (epLsar) are the two of the basic terms that are used to calculate DMTA. According to Ungar (2015), heavily pitted surfaces tend to have higher Asfc values than those dominated by uniform-sized scratches, while a surface dominated by striations aligned in the same direction has a higher epLsar value than one dominated by pits or one with scratches lacking a preferred orientation. Donohue et al. (2013), although they included black bear in their reference database, also excluded *U. arctos* and *U. thibetanus*, again limiting the full potential of their study. More recently, Jones and DeSantis (2016) applied DMTA to examine microwear of cave bear from various countries including Germany, France, Czech Republic and Italy, but no details are given on the precise origin or stratigraphic age of these specimens. The authors used the Donohue et al. (2013) database and added some extant *U. arctos* specimens. Their results suggested that the cave bear diet was very diverse, similar to that of other ursids and only distinguishable from the diet of *U. maritimus*.

Münzel et al. (2014) and Medin et al. (2017) applied both stable isotope and the low magnification microwear technique in their exploration of the palaeoecology of different cave bear species. Münzel et al. (2014) studied material from two sites in the Swabian Jura (SW Germany) Geißenklösterle and Hohle Fels (with *U. spelaeus* and *U. ingressus*) and two sites from the Totes Gebirge (Austria), Gamssulzen (with *U. ingressus*) and Ramesch (with *U. eremus*). These authors concluded that cave bears demonstrated considerable dietary flexibility, based on the different proportions of pits to scratches observed, but again, the relatively modest size of their modern reference dataset (albeit containing a wider range of species than in previous studies) did not allow full exploration of the full range of palaeodietary diversity. Medin et al., (2017) applied DMA and isotopes on *Ursus etruscus*, specimens from Orce sites in Andalusia, southern Spain, concluding that these early Pleistocene bears were all omnivores and with results from one site (Venta Micena), implying a significant contribution of fish in the diet.

Finally, Peigné and Merceron (2018) employed DMTA on cave bears from Goyet in Belgium using 13 specimens from Peigné et al. (2009) and the database of Jones and DeSantis (2016) with five modern bear species. Peigné and Merceron (2018) observed significantly low surface complexity (Asfc) in the cave bears when compared with *T. ornatus*, *U. americanus* and *U. maritimus* and intermediate values for anisotropy (epLsar) similar with those of most modern bears. According to the authors, the low Asfc values are indicative of the exclusion of hard and brittle foods from the diet of these cave bears, at least before their dormancy period. Hence, their main conclusion was that during the pre-dormancy period, the Goyet bears show dietary flexibility.

1.5. Aims and objectives

In this study, we present, for the first time, a comprehensive reference database of microwear signatures in modern bear teeth, representing not only the eight extant species with different known diets but also including brown bears from different latitudes. In order to establish the most appropriate tooth area and effective differentiation of species ecospaces, microwear features were observed on both the trigonid and talonid areas of the same molars. The reference database is then compared directly with the evidence from fossil brown bear specimens from the late Middle Pleistocene interglacial site of Grays Thurrock, Essex, in order to elucidate palaeodiet in these, the first representatives of the species, in the U.K.

2. Geological setting of the fossil site

One of the best preserved late Middle Pleistocene mammalian assemblages in the U.K. is that from Grays Thurrock (henceforth referred to as Grays) in Essex, located 32 km to the east of London on the north bank of the River Thames (Lat.

51.478387, Long. 0.326346; Fig. 2). The Grays deposits have been assigned to the Corbets Tey Gravel Formation (Bridgland, 1994), laterally equivalent to the Lynch Hill Gravel Formation of the Middle Thames and to the Barling-Dammer Wick Gravel Formation of eastern Essex (Bridgland, 1994). Reinterpretation of the lower Thames terrace sequence by Bridgland (1994), supported by biostratigraphical analysis of the mammalian assemblage by Schreve (2001), aminostratigraphy (Penkman et al., 2011) and absolute dating (Bridgland et al., 2013), has correlated the temperate, fossiliferous sediments within the Corbets Tey Formation, and hence the Grays deposit, with Marine Oxygen Isotope Stage (MIS) 9 of the deep sea record, a post-Hoxnian 'intra-Saalian' interglacial, 337-300,000 ka, and the second of four post-Anglian interglacials indicated within the Lower Thames sequence.

During the 19th century, a variety of very well-preserved fossil mammalian remains were collected during the extraction of clay ("brickearth") from three main pits at the Grays site. The stratigraphy and the sediments of the site were first examined by Morris (1836) with most of the remains collected between 1845 and 1850 and today housed in the Natural History Museum (London). The fossiliferous beds comprised laminated clays with sand and gravel layers, overlain by a shell bed (Schreve, 1997) (Fig. 2). A complete study of the assemblage was carried out by Schreve (1997) who identified over 1500 specimens from 27 mammalian taxa and assigned the assemblage to the Purfleet Mammal Assemblage-Zone, correlated with MIS 9 (Schreve, 2001). The key mammalian faunal taxa listed in Schreve (2001). One of the principal features of MIS 9 in Britain is the replacement of *U. spelaeus* by *U. arctos*, which seemingly became the dominant large carnivore at this time (Schreve, 2001). The presence of hominins at the site is also attested to by butchery marks on many of the mammal bones (e.g. on *U. arctos* metatarsals, NHMUK PV OR21290)

(Schreve, 2001; Schreve and Currant, 2003). A predominance of woodland species indicates fully temperate environmental conditions (Schreve, 1997). Beetle assemblages from other MIS 9 sites indicate that the climate was warmer than today with mean summer temperatures between 16 and 17°C and winter temperatures between -11 and +13°C (Coope, 2010).

3. Materials and methods

A reference database of 110 extant bear specimens used in this study (Pappa, 2016) is shown in Table 1. Only wild-caught, provenanced and aged adult specimens were used, to cover all eight extant species, as well as (for *U. arctos*) a geographical range including Greece, central Europe, northern Europe, Russia and America (USA) – Alaska and Canada (see File S.1.1 supplemental material and method and Table S.1). Eleven specimens of fossil *U. arctos* from Grays Thurrock were obtained from the Natural History Museum in London (with the following registration numbers: NHMUK PV OR 20260; NHMUK PV M 95990; NHMUK PV M 95989; NHMUK PV OR 22030; NHMUK PV OR 22029 two specimens; NHMUK PV M 96013; NHMUK PV M 96012; NHMUK PV M 96011; NHMUK PV M 95998; NHMUK PV M 96010) (see Table S.1). Different factors such as the type of teeth, the type of facet and the wear stage must always be taken into account before the analysis as they may have an influence on the microwear patterns (Ungar, 2015).

In this study, in each collection examined, the first lower molars (m1, carnassials) with an occlusal surface wear indicative of prime adults (categories IV, V, VI and VII of Stiner, 1998) were selected. This tooth is ideal for study since it combines areas both for crushing food (talonid) and for slicing (trigonid with protoconid and paraconid cusps) (Fig. 3). On all specimens from extant species, microwear analysis was conducted on both the slicing and the grinding area, with the purpose of revealing potential differentiation on the microwear pattern of each area. In addition, we focused on the non-facet surfaces of the enamel (Fig. 3), since these have previously proved to be more informative than the facet surface in bears (e.g. Münzel et al., 2014) and in other taxa such as primates (Ungar and Teaford, 1996).

Where fossil m1 specimens from the Grays site were unavailable or poorly preserved, the upper fourth premolar (P4) and/or the upper first molar (M1) were used as an alternative, since Xafis et al. (2017) have demonstrated that this does not influence the microwear signal obtained. Microscopic enamel microwear features were assessed via standard light stereomicroscopy (after Solounias and Semprebon, 2002) (see File S.1.2 – supplementary material). This involved counting of the number of scratches and pits and observation of additional variables, such as small and large pits, gouges, punctures, fine coarse and hypercoarse scratches and presence or absence of cross scratches (see File S.1.3 – supplementary material).

Bivariate plots and Principal Component Analyses (PCA) were used to reconstruct the different dietary ecospaces that each extant bear species occupies and to explore dietary variability *between* species and *within* brown bear groups from different geographical regions. Subsequently, the microwear results of fossil *U. arctos* from Grays were compared with those from the modern reference database in order to establish palaeodietary traits in this particular population. ANOVA and Tukey's post-hoc test for honest significant differences were calculated using PAST software (Hammer et al., 2001) (see File S.1.4 supplementary material).

4. Results

4.1. Grinding (talonid) and slicing (trigonid) areas in extant Ursidae

Table 1 shows the total number of individuals from each extant species and the number of specimens for which the grinding (talonid) and slicing (trigonid) areas were analysed. These are shown against the results from both areas, including mean, standard deviation and 95% confidence interval for both pits and scratches. All sampled specimens and their microwear features are listed in details in Table S.1.

Comparison of microwear features for both the grinding and slicing surfaces respectively plotted as bivariate graphs (Fig. 4A, B) revealed that the patterns based on observations of the grinding area are more distinct, allowing clearer differentiation of the diets and species (Fig. 4A). There is a clear separation on the grinding area between the bamboo eater *A. melanoleuca* and the hyper-carnivorous *U. maritimus*, with the former having the highest average number of pits and intermediate values for average number of scratches (Fig. 4A). The same graph reveals a further distinction between species with differing diets since the insectivorous *M. ursinus* exhibits a relatively high average number of pits and the smallest average number of scratches compared to both *U. maritimus* and the insectivorous/frugivorous *H. malayanus*, the latter having an intermediate average number of pits and scratches.

Additionally, all *U. arctos* groups are distinguished from the other species and occupy the right-hand sector of the graph, in which the total number of average values for scratches is higher than for all other species (Fig. 4A). Even within the *U. arctos* group, it is tentatively suggested that separation between individuals from different geographical regions may exist. *U. arctos* from central Europe (n= 10) have the highest average number of pits, *U. arctos* from Russia (n= 23) and northern Europe have intermediate values, whereas *U. arctos* from Greece (n= 4) have the lowest average number of pits. In contrast, the omnivorous *U. americanus* (n= 9) plots in the left-hand sector of the graph and is clearly differentiated from the *U. arctos* group including those from USA and Alaska (n= 8), having a smaller average number of scratches and an intermediate average number of pits (Fig. 4A).

In carnivores, pits rather than scratches have been described as the most dietary-diagnostic features (Bastl et al., 2012). Thus, the total number of large pits versus small pits was plotted in Fig. 4C for the grinding area. The results reveal that *U. arctos* from Greece has the lowest number of small pits, but a relatively high number of large pits, which clearly differentiate it from the other *U. arctos* groups from different geographical regions. In contrast, *U. arctos* from central Europe possess a relatively small number of large pits and an intermediate number of small pits, again differentiating them from *U. arctos* from northern Europe (n= 9), which has the highest number of large pits and small pits (Fig. 4C). Regarding the *U. arctos* from Russia, although there is an overlap of some individuals with *U. arctos* from both northern and central Europe, most have a relatively high number of large pits, closer to the ecospace occupied by *U. arctos* from Greece. *A. melanoleuca* (n= 4) is readily distinguished from the other species and displays the highest number of small pits in any of the species observed. In contrast, most individuals of *U. maritimus* (n= 14) have a lower number of large pits and an intermediate number of small pits (Fig. 4C).

4.2 Statistical tests

To establish which microwear variables are significant in the differentiation of extant species, analysis of variance (ANOVA) statistical tests were performed, together with Tukey's pairwise comparison tests, for measurements of all microwear features made on both the grinding and slicing areas from all species. The p-values for all microwear features reveal significant ($p<0.05$) differences between the groups on the grinding area (Table 2), while the p-values for the following microwear features: scratches, pits, fine scratches, coarse scratches, large pits, small pits and puncture pits reveal significant ($p<0.05$) differences between groups on the slicing area (Table 3).

This means that between any one pair of bear species, there is a significant difference in at least one of the above features. Two features, the scratch width score and the observation of cross-scratches (absence or presence) were excluded from this test as most values were very similar between species. The statistical tests confirm that observations on the grinding surface reveal clearer (i.e. more significant) differentiation between species for most microwear features, and also more significant pairwise differences than for observations on the slicing area.

4.3. Principal Component Analysis (PCA) of extant ursid species

Fig. 5A and 5B show the distribution of extant species through a PCA and the different dietary ecospaces. Nine independent variables (see also caption Fig. 5) of dental microwear were used, representing eight extant bear species including *U. arctos* from five different geographical regions (Greece, Kamchatka-Russia, Central Europe, North Europe and USA). Table 4 summarises the PCA with the values for each component.

On the grinding area, PC1 explains 41.78% of variance and PC2 accounts for 20.99% (Fig. 5A), while on the slicing area, PC1 explains 36.88% and PC2 for 26.25% of variance (Fig. 5B). On both the grinding and slicing areas, PC1 is heavily influenced by a positive association with the number of puncture pits (NpP) and by a negative association with the scratch width score (SWS) (Fig. 5A and B). Although Fig. 5B reveals differentiation between some of the extant species such as *U. arctos* from Greece, *U. maritimus* and *A. melanoleuca*, all of which have clear microwear patterns, there are significant overlaps between the other species. In contrast, the ecospaces on the grinding area are more distinct (Fig. 5A).

On the grinding area (Fig. 5A), the *A. melanoleuca* ecospace is distinguished from other species by having a high number of small pits, absence of coarse scratches and the highest number of fine scratches. These scratches have the same orientation (Fig. 6A). The hyper-carnivorous *U. maritimus* is equally clearly separated from other species by having the highest scratch width score, as well as an absence of puncture pits (Fig. 5A). It is also the only species to reveal the presence of hyper-coarse scratches (Fig. 6B). Unfortunately, the ecospace of the insectivorous *M. ursinus* and the frugivore/omnivore *T. ornatus* are not very well defined (Fig. 5A). The former is plotted across a wide range on the PCA graph while the latter, with only one individual, lies within the identified ecospace of *M. ursinus*. In the case of *M. ursinus* most probably this is a result of the small number of individuals sampled (n=4). In addition, the wide distribution of *M. ursinus* suggests that the diets of these individuals were quite variable from one to another. Nevertheless, both species are clearly separated from the ecospace of both polar bear and panda. *M. ursinus* also overlaps with areas of the *U. americanus*, *H. malayanus* and *U.arctos* (Russia) ecospaces (Fig. 5A). Most of the sloth bear specimens are characterised by a high number of pits, a small number of scratches and a moderate to high percentage of puncture pits (Fig. 6C).

At the other end of the microwear spectrum (i.e. on the central and right-hand side of the plot in Fig. 5A) and determined by the positive association with the number of puncture pits (Npp), lie most of the omnivorous species. However, some of these species also have individuals that occupy the left-hand side of the microwear spectrum and not unexpectedly, there is an overlap between species. More specifically, the ecospace of *U. arctos* from northern Europe can be differentiated from *U. arctos* from central Europe by an intermediate number of pits, the smallest number of scratches compared to the other *U. arctos* specimens and the smallest percentage of puncture pits (Fig. 5A and 6D). On the other hand, *U. arctos* from central Europe similar to *U. arctos* from Russia show the highest percentage of pits, as well as puncture pits, gouges, and large pits and there is an overlap on their ecospaces (Fig. 5A, 6E and 6G). Both *U. arctos* from Russia and central Europe have also a similar number of gouges compared to other species. Furthermore, the former occupies a wide range on the graph, most likely suggesting that diet is variable from one individual to another (Fig. 5A). Interestingly, *U. arctos* from Greece do not overlap or even plot close to *U. arctos* from northern Europe or to any other species. In contrast the group from Greece occupies a separate ecospace on the left-hand side of the PCA plot (Fig. 5A). The microwear features from this group show the lowest number of pits amongst any of the bears, with a relatively high scratches width score and coarse scratches. Unexpectedly, given its omnivorous diet, *U. thibetanus* is also clearly differentiated from the ecospace of the other omnivorous species and is relatively close to the microwear spectrum of *U. maritimus* (Fig. 5A). *U. thibetanus* displays the lowest percentage of puncture pits compared to the other omnivorous species and has the highest scratch width score after *U. maritimus*, resulting in a rather coarse enamel surface.

As may be anticipated, there is overlap between the dietary ecospaces of *U. americanus* and *U. arctos* from the USA, since both species are omnivorous and occupy more or less the same ecological zones, but there are also some differences between individuals (Fig. 5A). The microwear features from these groups show an intermediate number of pits, the black bear having a higher percentage of puncture pits than most of the North American *U. arctos* but smallest compared to other brown bear species, while the North American brown bear, in contrast, has a higher percentage of coarse scratches, small pits and fine scratches on most individuals. It is worth mentioning that the dietary ecospaces of both *U. americanus* and North American *U. arctos* are clearly separated and are different from those of *U. arctos* from central Europe. Most individuals of *U. arctos* from northern Europe overlap with individuals of *U. americanus* species (Fig. 5A).

The insectivore/frugivore *H. malayanus* similar to *U. arctos* from Russia, plots across a wide area of the graph and its ecospace overlaps with more than one group from the other species (Fig. 5A). This implies that diet is quite variable from one individual to another and may also reflect local dietary adaptability across geographical regions and seasons. However the majority of *H. malayanus* individuals plot very close to the ecospaces of *U. americanus*, *U. arctos* from North America and *U. arctos* from northern Europe, showing very similar microwear features such as a relatively high percentage of fine scratches, small pits and small percentage of puncture pits (Fig. 6F).

In summary, the PCA results on the grinding area (Fig. 5A) reveal more clearly the ecospace of each bear species than those on the slicing area (Fig. 5B). Microwear differences in the grinding area of the m1s in extant ursids, therefore, correlate well with observed differences in their modern diets and highlight the considerable potential for employing the method with respect to the dietary preferences of extinct bears.

4.4. Fossil U. arctos *from Grays (MIS 9)*

Only the grinding (talonid) area was used for the analysis of fossil *U. arctos* from Grays since this has been demonstrated to render the clearest separation into dietary ecospace. *U. arctos* from Grays lie close to the modern *U. arctos* group, occupying the right-hand sector of the bivariate graph in Fig. 4D, which describes a higher mean number of scratches. The Grays *U. arctos* have an intermediate mean number of pits and a relatively high mean number of scratches and occupy a position between *U. arctos* from central Europe and those from the USA, although they have a smaller mean value for pits than the former and a higher mean value than the latter (Fig. 4D). In addition, *U. arctos* from Grays possess a lower mean value for scratches when compared with *U. arctos* from the USA, overlapping *U. arctos* from both Russia and northern Europe (Fig. 4D.). Fig. 4C compares *U. arctos* from Grays with the extant bear database regarding the total number of large pits versus small pits. Most *U. arctos* individuals from Grays have an intermediate to high number of small pits and an intermediate number of large pits and plot very close to some *U. arctos* individuals from central Europe, northern Europe, and Russia (Fig. 4C). Table 5 shows a statistical summary of eight microwear features for *U. arctos* from Grays. The ANOVA and Tukey's HSD test results for Grays bears in comparison with extant species on the grinding area are described in File S.2.

The PCA graph for the Grays bear specimens shows the results of observations of the grinding surfaces of specimens in comparison with the modern database of bears (Fig. 7). The first axis (PC1) accounts for 40.59% of the total variance and the second (PC2) for 20.78%. Most of the *U. arctos* specimens from Grays occupy part of the central area of the graph, overlapping predominantly with the dietary ecospace of *U. arctos* from northern Europe (Fig. 7). Moreover, as with both *U. arctos* from northern Europe and from Grays, there is noticeable overlap with the dietary ecospace of *U. americanus* and *U. arctos* from the USA. Additionally, the position of *U. arctos* from Grays is clearly separated from that of the hypercarnivore *U. maritimus* and from the herbivore *A. melanoleuca.* This position reveals that most of the Grays bears (9 out of 11 individuals) possess a small percentage of puncture pits compared to other *U. arctos* group but display an intermediate percentage for most other variables.

5. Discussion

5.1. Extant Ursidae microwear database

This study has presented a comprehensive database that demonstrates for the first time that microwear analysis can be applied successfully to most Ursidae, in order to reveal both *inter*-specific differentiation and *intra*-specific variation (the latter seen in *U. arctos* from different geographical regions and seasons). However, it is critical that the interpretation of diet using dental microwear in bears considers carefully the complexities of the enamel structure, tooth morphology and the wear stage present and/or the surface selected, since all of these may influence subsequent analysis (Pappa, 2016).

Dental microwear differences on the grinding surface of bear enamel proved to be notably clearer and revealed more distinctly the ecospace of each species than the results on the slicing area. Donohue et al. (2013) reported that the shearing facet of the m1 does not reflect the known dietary differences of modern bears and further suggested the use of the m2 hypoconulid area as a better proxy for diet. However, it is not clear why these authors did not instead focus on the talonid area of the m1, which is used for crushing food instead of slicing. It has been repeatedly demonstrated that ursids often use their forelimbs to stabilise food items while grabbing, tearing, or cracking food with their carnassials (e.g. Davis, 1964; Ewer, 1973; Peyton, 1980), which may explain why dental microwear on the trigonid area of the m1 in bears does not correlate as clearly with diet. In contrast, the ecospace of each extant bear species in this study is revealed very clearly using the talonid area in both bivariate (Fig. 4) and PCA (Figs. 5 and 6) plots. Table 6 presents a summary of the key microwear features identified in each extant species in this study.

A. melanoleuca has a highly specialised diet consisting mainly of bamboo (e.g. Davis, 1964), which is convincingly captured in the microwear data of this study, particularly by the presence of the highest number of fine scratches (usually with the same orientation) (see Table 6). It has been proposed from studies on herbivore species that there is an association between wide (coarse) scratches and diets rich in large phytoliths with C4 open ground grasses and between narrower (fine) scratches with smaller C3 woodland grasses (Solounias and Semprebon, 2002; Merceron et al., 2004a; b; Semprebon et al., 2004; Merceron et al., 2005a). Bamboo, a member of the Family Poaceae, is a monocotyledonous flowering C3 grass plant (Yeoh et al., 1981), which serves to explain the high number of fine scratches and the absence of coarse features seen in the enamel surfaces of *A. melanoleuca* (also consistent with the results from microwear texture analyses by Donohue et al. (2013) and optical stereomicroscopic microwear studies by Goillot et al. (2009) and Peigné et al. (2009), although these last also reported infrequent pitting, which contrasts with the high number of small pits found during this study.

U. maritimus diets are also well predicted by the microwear feature data. This species has a highly specialised hypercarnivorous diet, preying almost exclusively on seals (e.g. Rugh and Shelden, 1993; Derocher et al., 2002) but with occasional fish, sea birds and their eggs and carrion (Ewer, 1973), even some berries during summer months (Derocher et al., 2002). This is the only species to display hypercoarse scratches (Table 6), which are a reflection of both diet and the extreme Arctic environment in which it lives. It is also worth mentioning that few scratches and a moderate number of pits have been previously reported for meat eaters (Goillot et al., 2009), while Van Valkenburg et al. (1990) demonstrated that flesh consumers that avoid any bone consumption (such as cheetahs) possess few pits but an abundance of narrow scratches. Furthermore, the size and also proportion of broad scratches found on meat eaters by Goillot et al. (2009) has been proposed to be a consequence of contact with the bone surface during consumption. Contrary to the results presented here, the microwear texture analysis on polar bear specimens undertaken by Donohue et al. (2013) reported high Asfc values (i.e. heavily pitted), similar to *U. americanus*. These authors proposed that this is due to either consumption of bone or freshwater fish and berries during summer, a rather unexpected conclusion for an animal that is a well established hypercarnivore.

The third extant species among the Ursidae that has a highly specialised diet is *M. ursinus*, which consumes mainly invertebrates (insects, e.g. termites and ants) and occasionally fruit (Joshi et al., 1997), inhabiting lowland ecosystems including wet or dry tropical forests, savannas, scrublands and grassland (Garshelis et al., 2008b and references therein). The ecospace and the microwear features (Table 6) of the insectivorous *M. ursinus* in this study suggest that the diet of these individuals was variable, albeit indicating the presence of a considerable amount of abrasive or hard food in their diets. Both shells and arthropods have been shown to cause abrasive microwear patterns (Joshi et al., 1997).

Since most of the remaining bear species studied are generalists and consume a wide variety of foods, it is unsurprising that some overlap between dietary ecospaces were noted. However, this study has revealed additional striking differences between them regarding their microwear patterns.

U. arctos from northern Europe (classed as "soft mast" feeders) show microwear features (few puncture pits and gouges and intermediate numbers of scratches and pits) that reflect their mixed diet (Table 6) of soft mast plants/fruits with few or no seeds (e.g. apples, berries, mushrooms), forb species native to cool temperate environments (e.g. aspen, coltsfoot, bishop's weed and dandelion) and mammals (e.g. domestic cow and pig, moose, wild boar). Northern European bears have a more carnivorous input (flesh/meat but avoiding bone) compared to their southern counterparts (e.g. Persson et al., 2001; Vulla et al., 2009; Bojarka and Selva, 2011) and can be differentiated in the microwear data of this study from *U. arctos* from the brown bears of the deciduous and mixed forests of continental central Europe. The latter consume hard mast items (i.e. fruits and seeds with a hard outer covering or exocarp, nuts and acorns and pine seeds), the last being dominant in the diet (Bojarska and Selva, 2011), as well as a large variety of soft mast, such as fleshy fruits. *U. arctos* populations from central Europe accordingly show heavily pitted enamel surfaces compared with both *U. arctos* from northern Europe and with the rest of the omnivorous species (Table 6). This diet is well described by the microwear features identified here and accords well with the picture of hard and abrasive fruits with seeds or potential bone contact in their diet (e.g. Semprebon et al., 2004; Bastl et al., 2012).

It is worth mentioning that the dietary composition of brown bears also varies between seasons and so, for example, *U. arctos* from central Europe in spring and summer feeds on plant matter markedly more often than in other seasonal periods, while during autumn, cranberries and ash berries are favoured (Sidorovich, 2006).

Vulla et al. (2009) noted seasonal variation in European brown bear diet, with consumption during autumn dominated by carbohydrate-rich plants (berries, cereals, fruits and hard mast), with minimal animal-food items. In contrast, in spring and summer, bears preferred protein-rich food items such as animals and insects, as well as plants and forbs. Hence, the season of death parameter of the wild modern bear specimens included in this study should be considered as this might explain the breadth of some brown bear ecospaces. Unfortunately, this information is not always available in museum collections but should be incorporated into future analyses of modern analogue material wherever possible.

Although the predominant food of *U. thibetanus* is also "hard mast", similar to *U. arctos* from central Europe, some differences are to be expected in the items that these animals consume, since they inhabit different ecological zones, with the former occupying a variety of forest habitats, including coniferous, temperate broad-leaved, subtropical and tropical zones (Garshelis and Steinmetz, 2008; Macdonald, 2009). *U. thibetanus* diet shows high seasonal variability, incorporating leaves, shoots, insects, a variety of fruits and only in some areas, animal protein (Huygens et al., 2003; Garshelis and Steinmetz, 2008; Koike et al., 2012). The Asian black bear individuals from this study are clearly differentiated not only from the other omnivorous species but also from the other "hard mast" eater (*U. arctos* from central Europe) (Table 6). These individuals have been able to exploit different food resources resulting in a rather coarse enamel surface (Table 6). Such patterns have been identified before by Bastl (2012) as a result either from the crushing of shells or other hard food including bone.

The Russian brown bear population inhabits the whole forest zone (known as the 'Beringian' forest-tundra) and has been also observed in the tundra zone

(Bergman, 1936; Kistchinkski, 1972; McLellan et al., 2008; Macdonald, 2009). Russian brown bears consume predominantly fish and other vertebrates, supplemented by fleshy fruits and nuts, depending on the season (e.g. Bergman, 1936; Krechmar, 1995; Bojarska and Selva, 2011). In summer, plants, ants and other insects, squirrels, hares, marine mammals and salmon are most regularly consumed, whereas in autumn, pine nuts and berries, especially those of *Vaccineum*, *Empetrum*, *Sorbaria*, *Lonicera*, *Padus* and *Crataegus* and above all, the seeds of *Pinus pumila* cones (Kistchinski, 1972) are favoured. The ecospace and the microwear features (see Table 6) of the *U. arctos* from Kamchatka in this study equally reflect dietary variability, most probably due to the different season of death. Hence, some of the individuals record ingestion of hard and abrasive fruits with seeds or potential bone contact in their diet (see Semprebon et al., 2004; Bastl et al., 2012), whereas others, with few pits and narrow scratches, show features consistent with those of flesh eaters (Van Valkenburg et al., 1990).

The predominant food of the brown bear group from Greece is “soft mast”. These bears consume wheat, the fruit of *Prunus*, acorns, ants and diverse understory plants (Giannakos, 1997; Vlachos et al., 2000; Paralikidis et al., 2010). These individuals reveal striated rather than pitted facets in the microwear features, which have been attributed to the ingestion of softer foods such as fruits and immature leaves in other taxa (Grine, 1981; 1986). Nevertheless, the microwear features and the ecospace from this group do not correlate well with those of other “soft mast” feeders in this study (notably northern European brown bears and North American black bears), perhaps a function of the small number of individuals analysed from Greece.

U. americanus populations extend across North America from Canada to Mexico (Dobey et al., 2005; Garshelis et al., 2008a; Frary et al., 2011) and broadly overlap in range with the North American brown bear. Black bear is a primarily temperate and boreal forest species (Garshelis et al., 2008a) and the predominant food type of the species is soft mast (Cottam et al., 1939; Hilderbrand et al., 1999; Fortin et al., 2007). In spring, these bears consume new plant growth and occasionally vertebrate carcasses, during summer, herbaceous material and fruits are the primary food items and in autumn, they feed mostly on berries and mast (Larivière, 2001). This omnivorous diet is reflected in the microwear features (Table 6), which show similarities to the other ”soft mast” feeders in this study and clearly differ from the ”hard mast” consumers. Most individuals reveal small round pits, which have been linked with the plucking of soft food items (Mainland, 2003; Merceron et al., 2004a).The diet of North American brown bear is very similar to that of black bears but with more carnivorous tendencies (Mowat and Heard, 2006; Fortin et al., 2007). Salmon and terrestrial prey such as caribou and moose, when they are abundant, form large part of their diet (Mowat and Heard, 2006). Again, this preference is obvious on the microwear pattern and ecospace identified for the majority of the North American brown bear individuals in this study.

Finally, the insectivore/frugivore *H. malayanus* of Southeast Asia found chiefly in tropical rain forest environments (encompassing a great variety of forest types), although some groups have also been observed in ecosystems that have a long dry season (Fredriksson *et al*., 2008). The ecospace and the microwear patterns (Table 6) observed from this species in the present study is in good agreement with the established diet of this species, which includes insects such as bees, ants and beetles but also soft mast (Augeri, 2005; Fredriksson et al., 2006).

5.2. Fossil U. arctos *microwear compared to extant database*

The position occupied by the brown bears from Grays Thurrock in dietary ecospace suggests that these individuals shared many similarities in the diet with modern *U. arctos* from northern Europe, *U. americanus,* and *H. malayanus* (Fig. 6 L). The predominant food item for both *U. arctos* from northern Europe and *U. americanus* is soft mast (Mattson, 1998; Bojarska and Selva, 2011), and for *H. malayanus,* it is invertebrates (insects), followed by soft mast (Fredriksson et al., 2006). Hence, it can be suggested on the basis of the dental microwear results that the Grays bears predominantly consumed fibrous food as well as soft fruits and invertebrates, together with a modest vertebrate component. In Britain, the interglacial episode correlated with MIS 9 (Bridgland et al., 2001; Schreve et al., 2002; Green et al., 2006; Roe et al., 2009) provided a range of medium to large-sized herbivore prey, such as wild horse, red deer, roe deer, fallow deer, elk, giant deer and aurochs, as well as megaherbivores such as narrow-nosed rhinoceros and straight-tusked elephant. At the same time, diversity in the carnivore guild had declined since the early Middle Pleistocene, with only *C. lupus*, *V. vulpes*, *C. crocuta,* and rare *P. leo* noted (Schreve, 1997). This may have presented *U. arctos* with additional opportunities to include meat in its diet through its own predatory activity, although carrion could also be consumed.

However, the predominant signature in the diet of soft mast and invertebrates correlates particularly well with the evidence from this interglacial for notably warm climatic conditions, leading to a diversity of plant and insect resources. Sites in Britain attributed to this temperate episode are characterized by widespread deciduous woodland, dominated by *Quercus, Tilia,* and *Ulmus,* with *Fraxinus* and *Alnus* in damper areas, and *Salix* and *Corylus avellana* forming the shrub layer (eg. Green et al., 2006). Many of these trees and shrubs produce soft mast in the form of buds and catkins in spring that form an essential part of the modern brown bear diet (Nowak, 1999). Soft, fleshy fruits were supplied by taxa such as *Prunus*, *Pyracantha clactonensis, Cornus sanguinea, Rubus, Vitis,* and *Hypericum*, with abundant edible meadowland, aquatic and riparian plants are also reported (Bridgland et al., 2001; Green et al., 2006; Roe et al., 2009).

The MIS 9 interglacial in Britain is also noted as an exceptionally warm period, with mean summer temperatures higher than the present day. Palaeotemperature reconstructions, based on Mutual Climatic Range analysis of coleopteran assemblages from MIS 9 sites in Britain, record minimum July temperatures of between 17°C and 19°C in southern England, with the best-constrained January temperatures ranging from -4°C to +1°C (eg. Green et al., 2006). This places MIS 9 on a par with the Last Interglacial (MIS 5e), in terms of its overall warmth during the summer months in particular (Candy et al., 2010). This favourable environment allowed a proliferation of invertebrate taxa to flourish, with some of the overall highest diversity noted for an interglacial, for example in the coleopteran assemblage from the site of Hackney Downs in London, 38km distant from the site of Grays, where 253 taxa have been identified (Green et al., 2006). As with the palaeobotanical evidence, this again underlines the availability of abundant insect resources for brown bear populations during this interglacial.

6. Conclusions

- This study is the first to develop and validate a robust database of dental microwear features for extant Ursidae.
- Within the m1, the talonid area is confirmed as the most effective in the differentiation of ursid dietary ecospaces.

- The dietary ecospaces of specialists, *U. maritimus* and *A. melanoleuca*, can be clearly differentiated from those of omnivorous species.
- Some dietary variability is also suggested amongst the generalist species and between *U. arctos* from different geographical regions, although overlaps are noted.
- Where broad dietary ecospaces are observed (e.g. *U. arctos* from Russia, *H. malayanus*), this is interpreted as individual variability, perhaps reflecting local dietary adaptability across geographical regions and seasons.
- Palaeodietary reconstruction of *U. arctos* from Middle Pleistocene interglacial deposits at Grays, UK reveals that fibrous food as well as soft fruits and invertebrates, together with a modest vertebrate component, was consumed. The potential now exists for the dental microwear technique to be more widely applied to reconstruct palaeodiet in other extinct ursids.

Acknowledgments

We thank Royal Holloway University of London and the Institut Català de Paleoecologia Humana i Evolució Social in Tarragona, who kindly provided material, room and utilities for the study. We are grateful to Frank Zachos (Natural History Museum of Vienna), Alexander Bibl (Natural History Museum of Vienna), Celine Bens (Natural History Museum of Paris), Géraldine Veron (Natural History Museum of Paris), Christian Funk (Natural History Museum of Berlin), Andy Currant (Natural History Museum of London), Pip Brewer (Natural History Museum of London), Emma Bernard (Natural History Museum of London); Christos Vlachos (Aristotle University of Thessaloniki in Greece) who gave access to the collections. Chris Collins (Natural History Museum of London), Efstratia Verveniotou (Natural History

Museum of London) and Adrian Palmer (Royal Holloway University of London) helped with the laboratory work. We thank, Ioanna Varsou who helped with the design of the figures. We thank the anonymous reviewers and the editor for making constructive comments, which improved this paper. Florent Rivals received the financial support of the *Ministerio de Ciencia, Innovación y Universidades* grant HAR2016-76760-C3-1-P and the *Generalitat de Catalunya*, AGAUR agency, 2017-SGR-836 Research Group. Spyridoula Pappa was part-funded by a Royal Holloway studentship.

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Captions Figures and Tables

Figure 1. Dietary groupings of the key food items consumed by each extant bear species, including their dietary regimes (with symbols) and their geographical distribution. Soft* mast: fibres food, including leaves and fruits with no seeds. Hard** mast: berries and fruits with seeds as well as nuts. References: 1) Rugh and Shelden, 1993; 2) Derocher et al., 2002; 3) Mattson, 1998; 4) Fortin et al., 2007; 5) Bojarska and Selva, 2012; 6) Mowat and Heard, 2006; 7) Bergman, 1936; 8) Kistchinski, 1972; 9) Krechmar, 1995; 10) Elgmork and Kaasa, 1992; 11) Persson et al., 2001; 12) Vulla et al., 2009; 13) Rigg and Gorman, 2005; 14) Vlachos et al., 2000; 15) Paralikidis et

al., 2010; 16) Cottam et al., 1939; 17) Bennett et al., 1943; 18) Hilderbrand et al., 1999; 19) Huygens et al., 2003; 20) Peyton, 1980; 21) Joshi et al., 1997; 22) Bargali et al., 2004; 23) Ramesh et al., 2009; 24) Davis, 1964; 25) Augeri, 2005 and 26) Fredriksson et al., 2006. References for maps from top to bottom: Wiig et al., 2015; McLellan et al., 2008; Garshelis et al., 2008a; Garshelis and Steinmetz, 2008 Goldstein et al., 2008; Garshelis et al., 2008b; Lü et al., 2008; Fredriksson et al., 2008.

Figure 2. A. The marine oxygen isotope stratigraphy as a climatic yardstick (modified from Walker and Lowe, 2007), even numbers reflect interglacials. B. Map of Britain with Grays Thurrock Geographic location. C. Map of the Thurrock area, showing the Grays pits and the geological deposits (modified from Bridgland, 1994).

Figure 3. A. Tooth morphology of first lower carnassials (m1). *U. arctos* Specimen from natural History Museum, Life Sciences department with the following registration number: 52.1575. B. Same specimen buccal side showing with black ellipses the areas that observations were focused. C. Photomicrograph of *U. maritimus* specimen from Natural History Museum of Vienna, registration number 14657, at x25 magnification with facet and non-facet enamel surfaces and scale bar 0.5mm.

Figure 4. Bivariate plots for extant species and for bears from Grays (MIS 9), U. K. A. Extant species - Analysis on grinding (talonid) area (average number of pits versus scratches). B. Extant species - Analysis on slicing (trigonid) area (average number of pits versus scratches). C. Plot of raw data of the total number of large versus small

pits for extant bear database and bears from Grays in comparison with them. D. Plot of average number of pits versus scratches for bears from Grays in comparison with the extant bear database. Error bars represent the standard deviation of pits and scratches.

Figure 5. PCA plots (component 1 versus 2) showing comparative distribution of microwear features of extant bear species. A. Grinding (talonid) area. B. Slicing (trigonid) area. For details of symbols, see key. Symbols of variables (microwear features) as follow: NS: number of scratches; NP: number of pits; NfineS: number of fine scratches; NcoarseS: number of coarse scratches; NLP: number of large pits; NsP: number of small pits; Ngouge: number of gouges; Npp: number of puncture pits; SWS: score of wide scratches.

Figure 6. Photomicrographs of selected extant bear species and extinct *Ursus arctos* from Grays, tooth enamel surface at 35 times magnification and bar scales 0.4mm. A. *Ailuropoda melanoleuca* (specimen from Berlin Natural History Museum, Life Sciences department, number 17246) with the highest number of fine scratches and small pits and with scratches that have the same orientation. B. *Ursus maritimus* (specimen from Vienna Natural History Museum, Life Sciences department, number 14657) with the highest scratches width score of any extant bear species and with absence of puncture pits. C. *Melursus ursinus* (specimen from Berlin Natural History Museum, Life Sciences department, number 56748) with small number of scratches and moderate percentage of puncture pits. D. *Ursus arctos* from northern Europe (specimen from Berlin Natural History Museum, Life Sciences department, number

93300) with intermediate number of scratches and pits. E. *Ursus arctos* from central Europe (specimen from Vienna Natural History Museum, Life Sciences department, number 67916) with the highest percentage in comparison to other U. arctos of pits, puncture pits, gouges and large pits. F. *Helarctos malayanus* (specimen from Berlin Natural History Museum, Life Sciences department, number 28472) with relatively high percentage of fine scratches and small pits. G. *Ursus arctos* from Russia (specimen from Vienna Natural History Museum, Life Sciences department, number 40633) with low to high percentage of puncture pits and gouges and relatively high number of large pits. H. *Ursus arctos* from Grays (specimen from London Natural History Museum, Life Sciences department, number OR 22030) with a small percentage of puncture pits compared to other *Ursus arctos* group.

Figure 7. PCA grinding (talonid) area showing comparative distribution of microwear features of the extinct Ursus arctos from Grays (shaded polygon showing ecospace), in comparison with extant bear species. For details of extant species symbols, see Fig. 5 key. Symbols of variables (microwear features), same as see Fig. 5, see caption details.

Table 1. Extant bear species, additional information such as mean, standard deviation (SD) and 95% confidence interval (CL) for each species are presented for both grinding (talonid) and slicing (trigonid) area.

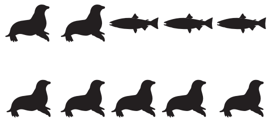
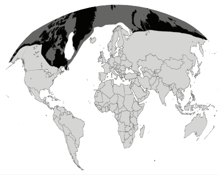
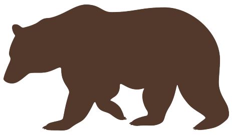
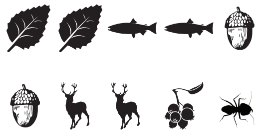
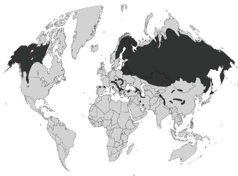
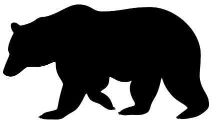
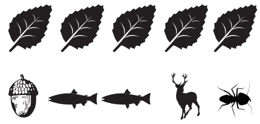
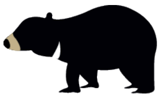
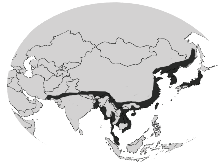
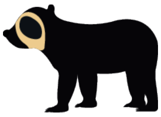
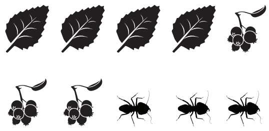
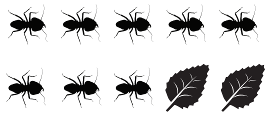
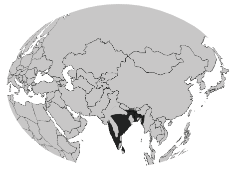
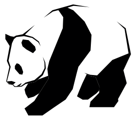
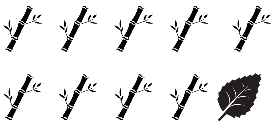
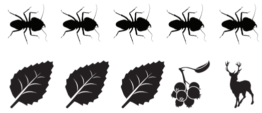
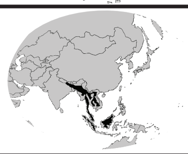
Table 2. ANOVA and Tukey’s HSD test results for extant species on the grinding area. Summary of the results from all features that were measured in each species, compared and tested between and within groups. Abbreviations as follows: Sum of sqrs is the sum of squares due to features; df is the degree of freedom in the features; Mean sqrs is the mean sum of squares due to features; F is the F-statistic and p is the p-value. Pair – wise comparison = Values below the diagonal are the results of Tukey’s method and those above are the p-values (significant comparisons are in bold). **1:** *Ailuropoda melanoleuca* (n = 4); **2:** *Helarctos malayanus* (n =17); **3:** *Melursus ursinus* (n= 4); **4:** *Ursus americanus* (n= 9); **5:** *Ursus maritimus* (n= 14); **6:** *Ursus thibetanus* (n= 6); **7:** *Ursus arctos,* Greece (n= 4); **8:** *Ursus arctos,* Central Europe (n= 10); **9:** *Ursus arctos*, USA (n= 8); **10:** *Ursus arctos*, Russia (n= 23); **11:** *Ursus arctos*, North Europe (n = 9).

Table 3. ANOVA and Tukey’s HSD test results for extant species in the **slicing** area. Summary of the results from all features that were measured in each species, compared and tested between and within groups. Abbreviations as follows: Sum of sqrs is the sum of squares due to features; df is the degree of freedom in the features; Mean sqrs is the mean sum of squares due to features; F is the *F*-statistic and p is the p-value. Pair – wise comparison = Values below the diagonal are the results of Tukey’s method and those above are the p-values (significant comparisons are in bold). **1:** *Ailuropoda melanoleuca* (n= 3); **2:** *Helarctos malayanus* (n= 11); **3:** *Melursus ursinus* (n= 4); **4:** *Ursus americanus* (n= 9); **5:** *Ursus maritimus* (n= 14); **6:** *Ursus thibetanus* (n= 4); **7:** *Ursus arctos*, Greece (n= 4); **8:** *Ursus arctos*, Central Europe (n= 8); **9:** *Ursus arctos*, USA (n= 3); **10:** *Ursus arctos*, Russia (n= 21).

Table 4. Extant species, analysis on the grinding (talonid) and slicing (trigonid) area. Summary of Principal Component Analysis (PCA).

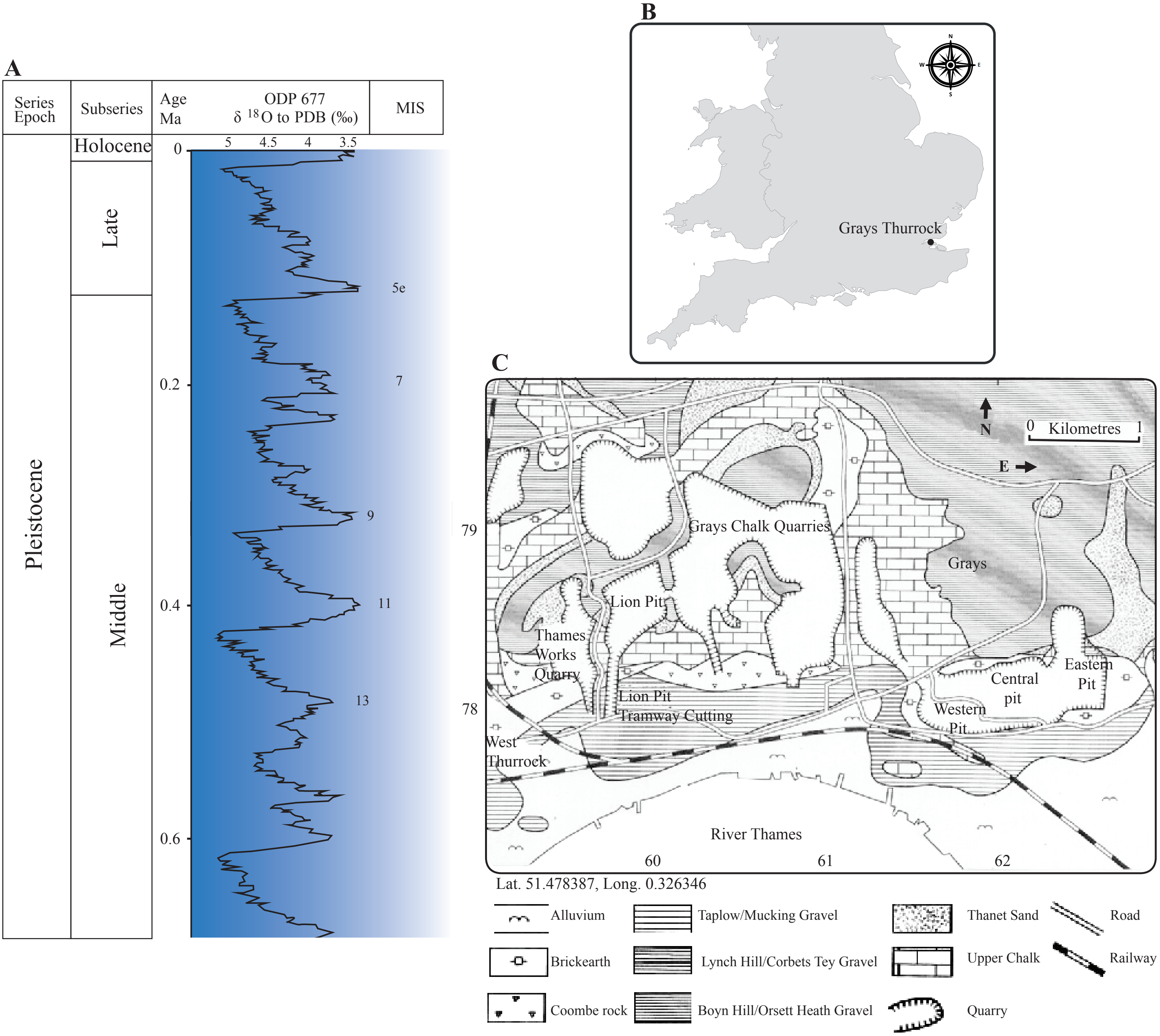
Table. 5. Grays Thurrock (MIS 9), UK (n: 11) statistical summary of eight microwear features. Mean, standard deviation (SD), 95% confidence interval (CL), 1st and 3rd quartile, minimum (min), maximum (max) and median values are given.

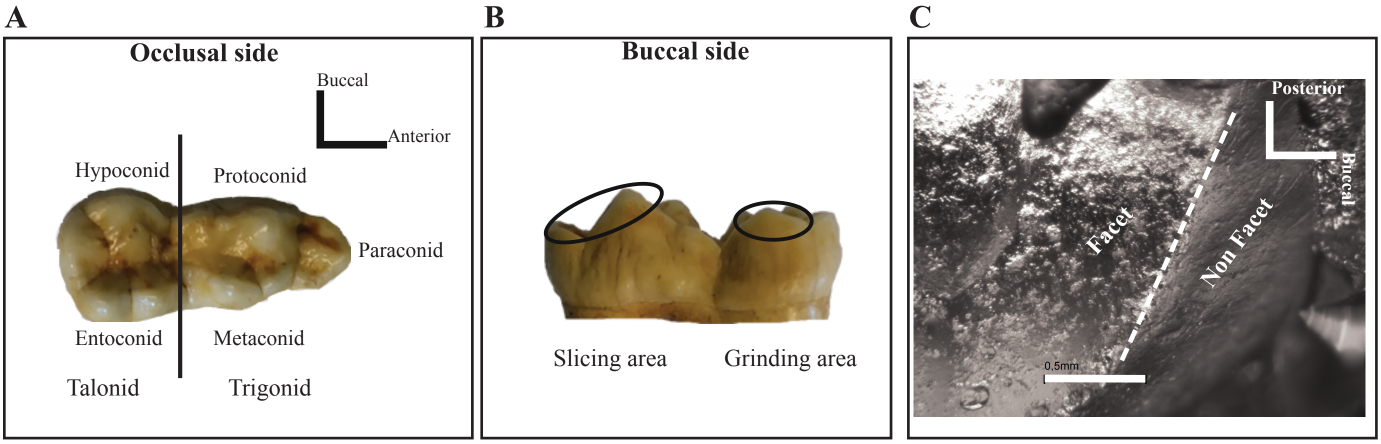
Table 6. Summary of key microwear characteristics identified in each extant species in this study.

Bear Species	Dietary grouping Term-Group	Dietary Regimes Most consumed food items	Geographical distribution
 *Ursus maritimus*	**Hypercarnivore** Vertebrates (1, 2)		
 *Ursus arctos*	**Omnivore** USA- Vertebrates (3, 4, 5, 6) Russia- Vertebrates (5, 7, 8, 9) North Europe- Soft* mast (5, 10, 11, 12) Central Europe- Hard** mast (5, 13) Greece- Soft* mast (5, 14, 15)		
 *Ursus americanus*	**Omnivore** Soft* mast (3, 4, 16, 17, 18)		
 *Ursus thibetanus*	**Omnivore** Hard** mast (3, 19)		
 *Tremarctos ornatus*	**Omnivore** Soft* mast (20)		
 *Melursus ursinus*	**Insectivore** Invertebrates (21, 22, 23)		
 *Ailuropoda melanoleuca*	**Herbivore** Foliage (3, 24)		
 *Helarctos malayanus*	**Omnivore** Invertebrates (25, 26)		

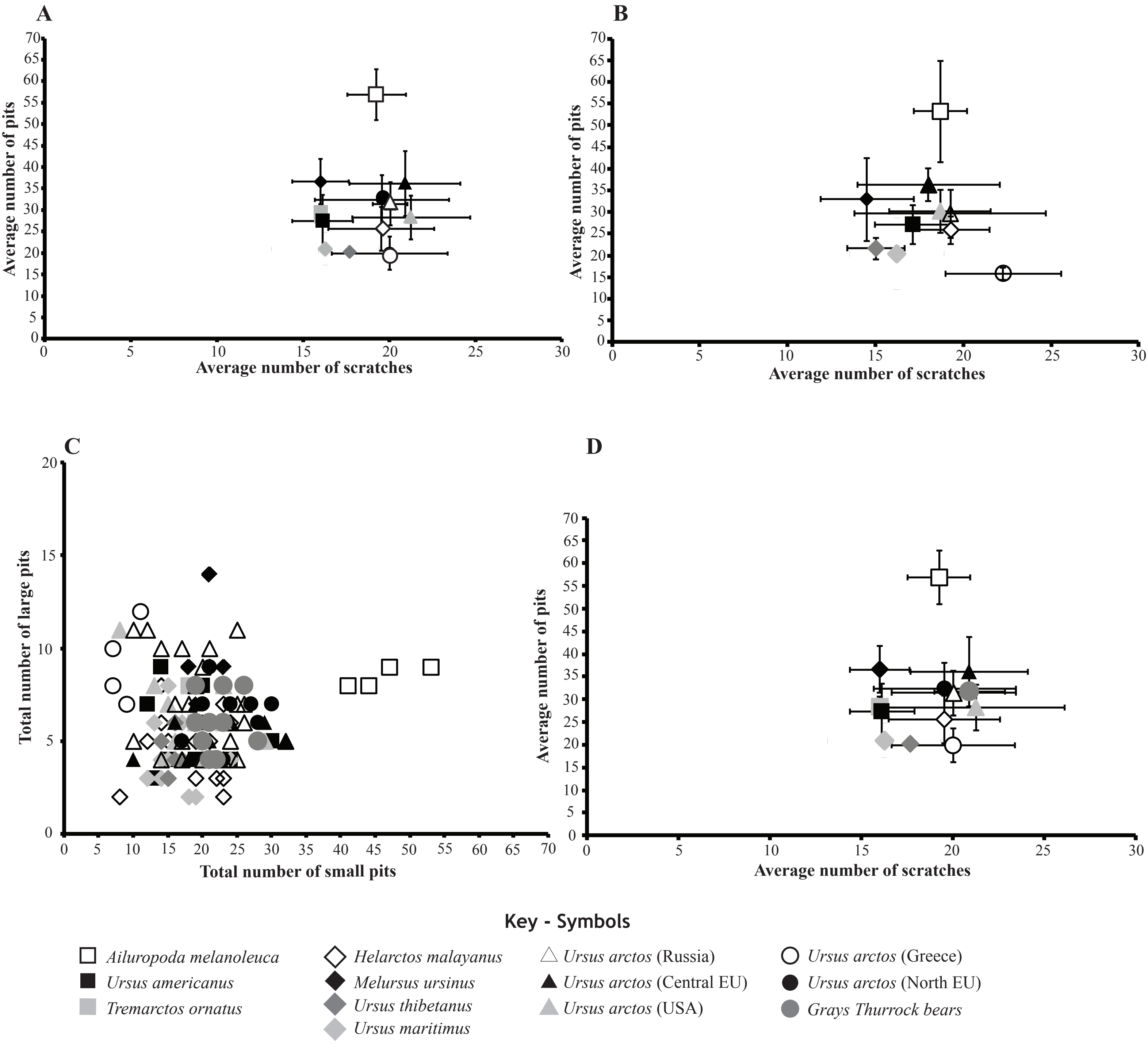
Soft* mast — Hard** mast — Hard** mast — Vertebrates, seals

Invertebrates — Vertebrates, flesh — Vertebrates, fish — Foliage, bamboo


A
Series Epoch
Subseries
Age Ma
ODP 677
δ 18O to PDB (‰)
MIS
Pleistocene
Holocene
Late
Middle
0
0.2
0.4
0.6
5
4.5
4
3.5
5e
7
9
11
13
B
Grays Thurrock
C
N
E
0 Kilometres 1
Grays Chalk Quarries
Grays
Lion Pit
Thames Works Quarry
Lion Pit Tramway Cutting
Central pit
Eastern Pit
Western Pit
West Thurrock
River Thames
79
78
60
61
62
Lat. 51.478387, Long. 0.326346
Alluvium
Taplow/Mucking Gravel
Thanet Sand
Road
Brickearth
Lynch Hill/Corbets Tey Gravel
Upper Chalk
Railway
Coombe rock
Boyn Hill/Orsett Heath Gravel
Quarry

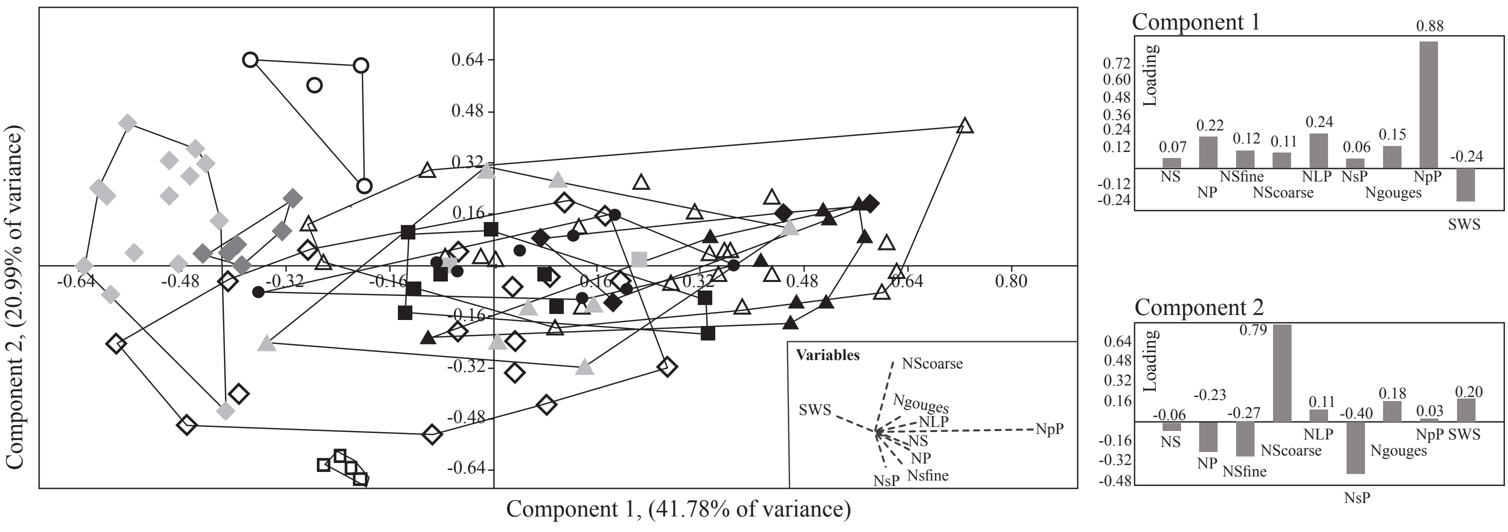


A
Occlusal side
Buccal
Anterior
Hypoconid
Protoconid
Paraconid
Entoconid
Metaconid
Talonid
Trigonid
B
Buccal side
Slicing area
Grinding area
C
Posterior
Buccal
Facet
Non Facet
0,5mm

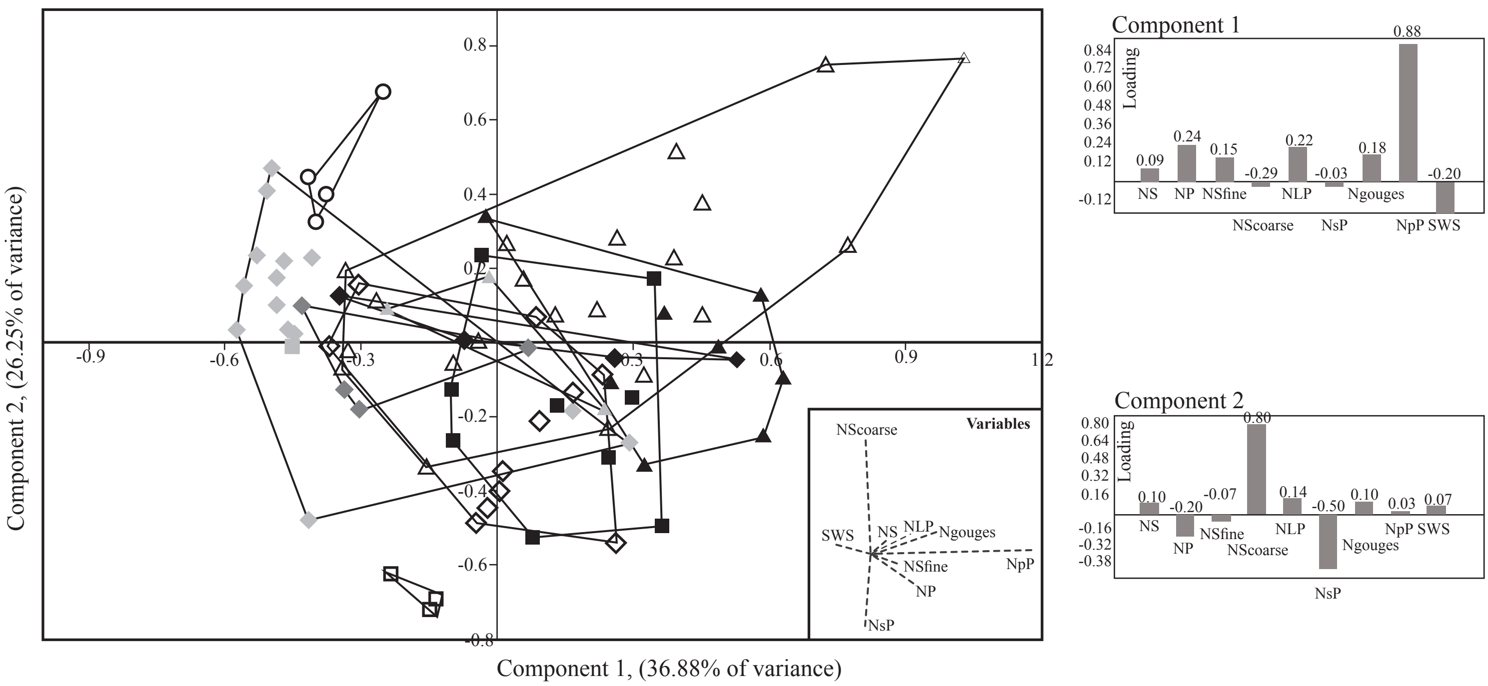


A
Average number of pits
Average number of scratches
B
Average number of pits
Average number of scratches
C
Total number of large pits
Total number of small pits
D
Average number of pits
Average number of scratches
Key - Symbols
Ailuropoda melanoleuca
Ursus americanus
Tremarctos ornatus
Helarctos malayanus
Melursus ursinus
Ursus thibetanus
Ursus maritimus
Ursus arctos (Russia)
Ursus arctos (Central EU)
Ursus arctos (USA)
Ursus arctos (Greece)
Ursus arctos (North EU)
Grays Thurrock bears

A



B



Key - Symbols

Ailuropoda melanoleuca
Ursus americanus
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Helarctos malayanus
Melursus ursinus
Ursus thibetanus
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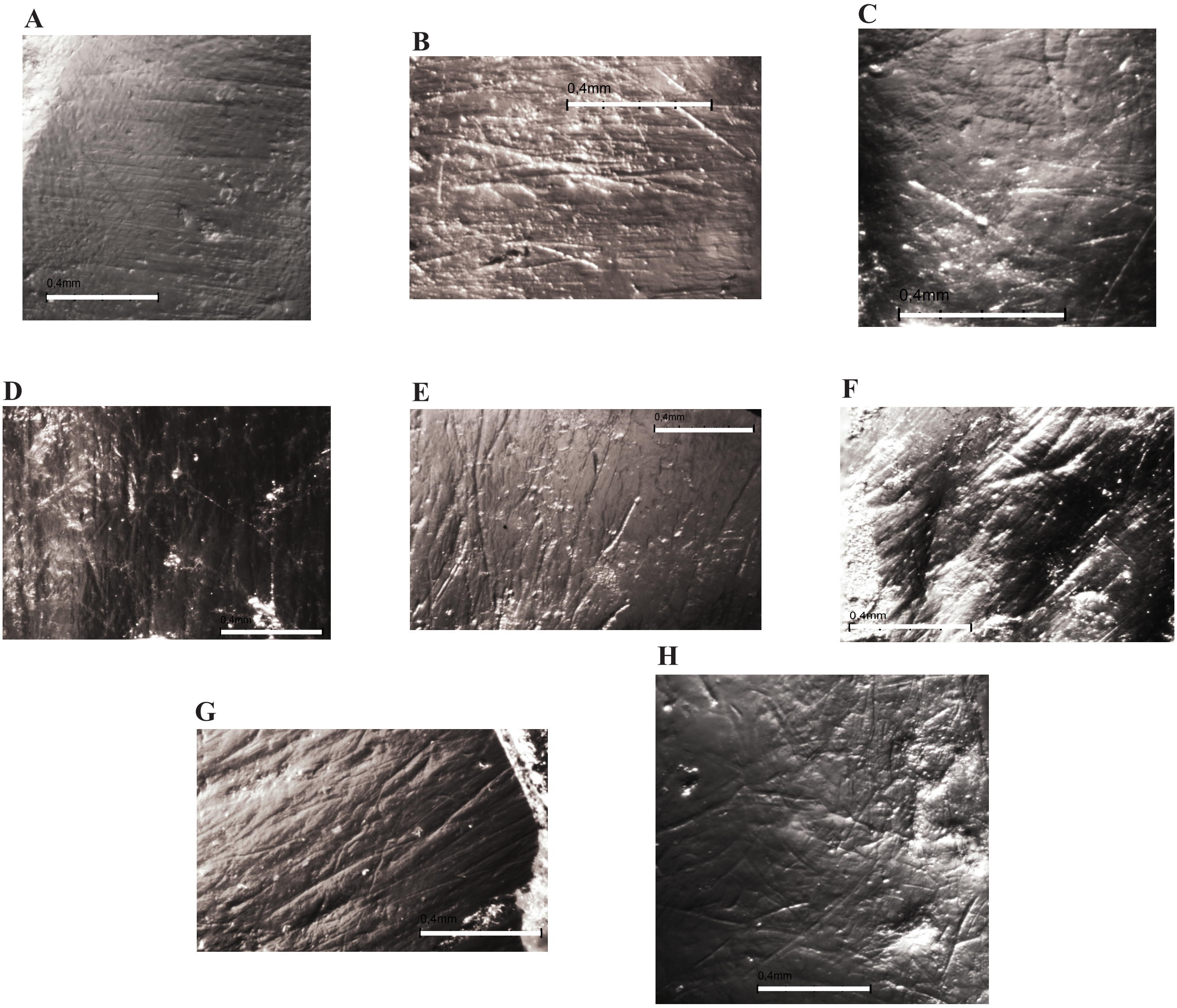
Ursus arctos (Russia)
Ursus arctos (Central EU)
Ursus arctos (USA)
Ursus arctos (Greece)
Ursus arctos (North EU)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B
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C
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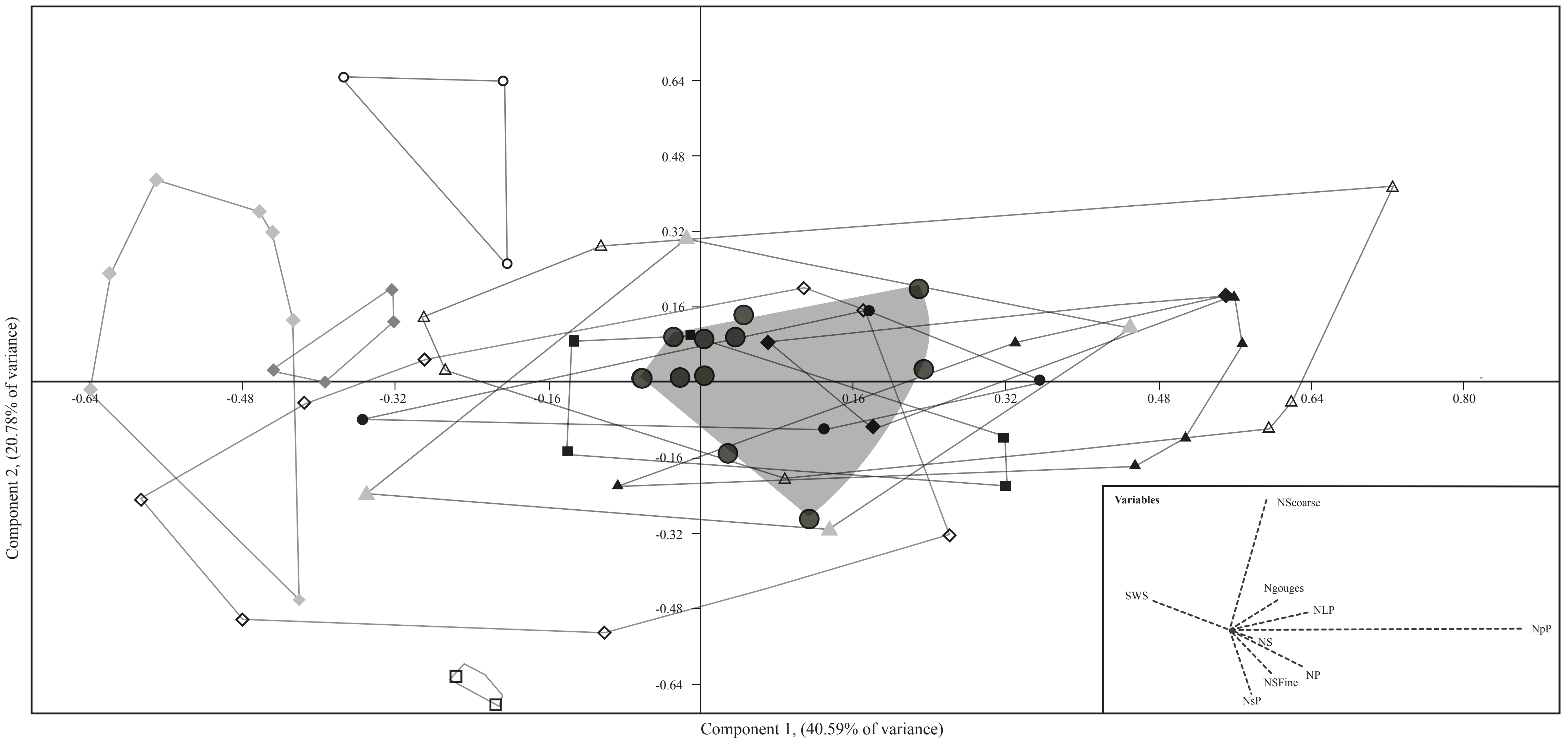
D
0,4mm
E
0,4mm
F
0,4mm
G
0,4mm
H
0,4mm



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0.32
0.16
-0.16
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-0.64
-0.64
-0.48
-0.32
-0.16
0.16
0.32
0.48
0.64
0.80
Component 2, (20.78% of variance)
Component 1, (40.59% of variance)
Variables
NScoarse
Ngouges
SWS
NLP
NpP
NS
NP
NSFine
NsP

Tables

Table 1

			Pits		Scratches	
Species	**Observations on grinding (G) or slicing (S)**	**n**	**Mean; SD**	**95% CL**	**Mean; SD**	**95% CL**
Ailuropoda melanoleuca	G	4	57.0; ±5.9	5.8	19.3; ±1.7	1.7
	S	3	53.3; ±11.7	13.3	18.7; ±1.53	1.7
Helarctos malayanus	G	17	25.7; ±5.2	2.5	19.5; ±3.1	1.5
	S	12	26.0; ±3.2	1.8	19.3; ±2.2	1.2
Melursus ursinus	G	4	36.8; ±5.3	5.1	16.0; ±1.6	1.6
	S	4	33.0; ±9.6	9.4	14.5; ±2.6	2.61
Ursus americanus	G	9	27.4; ±6.1	4.0	16.1; ±1.8	1.2
	S	9	27.2; ±4.5	2.95	17.1; ±2.15	1.4
Ursus maritimus	G	14	20.9; ±3.8	2.0	16.3; ±3.1	1.6
	S	14	20.4; ±8.2	4.3	16.2; ±2.7	1.4
Ursus thibetanus	G	6	20.3; ±1.4	1.1	17.7; ±1.8	1.4
	S	4	21.75; ±2.5	2.45	15.0; ±1.6	1.6
***Ursus arctos* (Greece)**	G	4	20.0; ±3.8	3.8	20.0; ±3.4	3.3
	S	4	16.0; ±1.4	1.4	22.25; ±3.3	3.24
***Ursus arctos* (Central Europe)**	G	10	36.2; ±7.6	4.7	20.9; ±3.2	2.0
	S	8	36.4; ±3.8	2.6	18.0; ±4.0	2.8
***Ursus arctos* (USA)**	G	8	28.4; ±5.1	3.5	21.3; ±4.8	3.3
	S	3	30.3; ±4.9	5.6	18.7; ±2.9	3.3
***Ursus arctos* (Russia)**	G	23	31.5; ±5	2.0	20.0; ±3.4	1.4
	S	21	29.8; ±5.6	2.4	19.2; ±5.45	2.3
***Ursus arctos* (North Europe)**	G	9	32.4; ±5.7	3.8	19.6; ±3.9	2.6

Table 2

Number of Scratches – ANOVA results:

Source	Sum of sqrs	df	Mean sqrs	F=ratio	p
Between groups:	338.21	10	33.8	3.275	**0.001** ***
Within groups:	1001.64	97	10.3		

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**
1		1	0.7075	0.7489	0.8085	0.9974	1	0.9963	0.9836	1	1
2	0.2326		0.5961	0.641	0.7099	0.9904	1	0.9993	0.9949	1	1
3	2.705	2.938		1	1	0.996	0.4069	0.1438	0.0871	0.391	0.585
4	2.613	2.845	0.09248		1	0.9978	0.45	0.1669	0.1027	0.433	0.631
5	2.467	2.7	0.2378	0.1453		0.9992	0.5202	0.2086	0.1317	0.503	0.7
6	1.318	1.55	1.387	1.295	1.149		0.952	0.7139	0.574	0.946	1
7	0.6243	0.3917	3.329	3.237	3.092	1.942		1	0.9997	1	1
8	1.373	1.141	4.078	3.986	3.841	2.691	0.7491		1	1	0.9
9	1.665	1.432	4.37	4.277	4.132	2.983	1.04	0.2913		1	0.9
10	0.6604	0.4279	3.366	3.273	3.128	1.978	0.0362	0.7129	1.004		1
11	0.2543	0.0218	2.959	2.867	2.722	1.572	0.3699	1.119	1.41	0.406	

Number of Pits – ANOVA results:

Source	Sum of sqrs	df	Mean sqrs	F=ratio	P
Between groups:	6036.54	10	603.6	21.91	**< 0.0001** ****

Within groups:	2672.2	97	27.5		

	1	2	3	4	5	6	7	8	9	10	11
1		**0.0002**	**0.0001**	**0.0001**	**0.0001**	**0.0002**	**0.0002**	**0.0001**	**0.0002**	**0.0001**	**0.0001**
2	15.95		**0.006**	0.9999	0.8209	0.6924	0.6109	**0.01164**	0.9966	0.583	0.360
3	10.32	5.628		**0.0428**	**0.00018**	**0.0002**	**0.0002**	1	0.1044	0.726	0.898
4	15.06	0.886	4.742		0.4109	0.2832	0.2235	0.07352	1	0.926	0.776
5	18.38	2.434	8.062	3.32		1	1	**0.0002**	0.2231	**0.01**	**0.0034**
6	18.69	2.738	8.366	3.624	0.3033		1	**0.0002**	0.1393	**0.005**	**0.0016**
7	18.85	2.908	8.536	3.794	0.4732	0.1699		**0.0002**	0.1044	**0.003**	**0.0011**
8	10.6	5.348	0.2803	4.462	7.782	8.086	8.255		0.1665	0.839	0.957
9	14.59	1.36	4.268	0.4742	3.795	4.098	4.268	3.988		0.988	0.9272
10	12.98	2.964	2.664	2.078	5.398	5.702	5.871	2.384	1.604		1
11	12.51	3.434	2.194	2.548	5.868	6.172	6.342	1.914	2.074	0.47	

Number of Fine Scratches – ANOVA results:

Source	Sum of sqrs	df	Mean sqrs	F=ratio	P
Between groups:	604.91	10	60.5	5.295	**< 0.0001 ******
Within groups:	1108.05	97	11.4		

	1	2	3	4	5	6	7	8	9	10	11
1		0.9905	**0.01836**	0.06763	**0.00072**	0.1934	**0.0281**	0.9961	1	0.834	0.688
2	1.548		0.294	0.586	**0.02613**	0.8532	0.3759	1	1	1	0.9988
3	5.144	3.596		1	0.9961	0.9983	1	0.2349	0.0899	0.69	0.835
4	4.506	2.959	0.6375		0.9377	1	1	0.5056	0.25	0.92	0.976
5	6.529	4.981	1.385	2.022		0.7378	0.9888	**0.01836**	**0.0047**	0.132	0.228
6	3.891	2.343	1.253	0.6155	2.638		0.9996	0.7933	0.5163	0.993	0.9992
7	4.946	3.398	0.1978	0.4396	1.583	1.055		0.3075	0.1268	0.777	0.897
8	1.385	0.1629	3.759	3.121	5.144	2.506	3.561		1	1	0.997
9	0.7914	0.7565	4.353	3.715	5.737	3.1	4.155	0.5935		0.987	0.9497
10	2.4	0.8521	2.744	2.106	4.129	1.491	2.546	1.015	1.609		1
11	2.748	1.2	2.396	1.759	3.781	1.143	2.198	1.363	1.956	0.348	

Number of Coarse Scratches – ANOVA results:

Source	Sum of sqrs	df	Mean sqrs	F=ratio	P
Between groups:	81.97	9	9.1	5.962	< 0.0001 ****
Within groups:	140.55	92	1.5		

	2	3	4	5	6	7	8	9	10	11
2		0.9273	1	0.7778	0.8797	**0.0002**	0.8308	0.9921	0.3958	0.445
3	1.966		0.9833	1	1	**0.0002**	1	1	0.9957	0.998
4	0.4057	1.56		0.9114	0.9646	**0.0002**	0.941	0.9995	0.5886	0.641
5	2.441	0.4753	2.035		1	**0.0002**	1	0.9992	0.9999	1
6	2.153	0.1872	1.747	0.288		**0.0002**	1	0.9999	0.9987	1
7	10.39	8.425	9.985	7.95	8.238		**0.0002**	**0.000159**	**0.0002**	**0.0002**
8	2.303	0.337	1.897	0.1383	0.1498	8.088		0.9998	0.9996	1
9	1.404	0.5617	0.9985	1.037	0.7489	8.987	0.8987		0.9484	0.965
10	3.26	1.294	2.855	0.819	1.107	7.131	0.9573	1.856		1
11	3.152	1.186	2.746	0.7105	0.9985	7.239	0.8488	1.747	0.1085	

Number of Large Pits – ANOVA results:

Source	Sum of sqrs	df	Mean sqrs	F=ratio	P
Between groups:	213.62	10	21.4	5.225	< 0.0001 ****
Within groups:	396.57	97	4.1		

	1	2	3	4	5	6	7	8	9	10	11
1		0.071	0.9844	0.1526	**0.01322**	**0.0132**	0.9998	0.1387	0.8624	0.934	0.701
2	4.474		**0.0018**	1	1	1	**0.0089**	1	0.9072	0.822	0.976
3	1.654	6.128		**0.0051**	**0.00034**	**0.0003**	1	**0.0045**	0.1716	0.257	0.087
4	4.042	0.432	5.695		0.9984	0.9984	**0.0233**	1	0.9786	0.942	0.997
5	5.291	0.817	6.945	1.249		1	**0.0013**	0.9989	0.5771	0.444	0.766
6	5.291	0.817	6.945	1.249	0		**0.0013**	0.9989	0.5771	0.444	0.7662

7	0.9921	5.466	0.6614	5.034	6.283	6.283		**0.0205**	0.4171	0.549	0.251
8	4.101	0.373	5.754	0.05879	1.191	1.191	5.093		0.9728	0.93	0.996
9	2.315	2.159	3.968	1.727	2.976	2.976	3.307	1.786		1	1
10	2.042	2.432	3.695	2	3.25	3.25	3.034	2.059	0.2732		1
11	2.719	1.755	4.373	1.323	2.572	2.572	3.711	1.382	0.4042	0.677	

Number of Small Pits – ANOVA results:

Source	Sum of sqrs	df	Mean sqrs	F=ratio	P
Between groups:	3844.29	10	384.4	14.62	0.0001 ****
Within groups:	2550.71	97	26.3		

	1	2	3	4	5	6	7	8	9	10	11
1		**0.0002**	**0.0001**	**0.0001**	**0.0001**	**0.0002**	**0.0002**	**0.0001**	**0.0002**	**0.0002**	**0.00017**
2	14.46		0.9999	1	0.9988	0.9834	**0.0151**	0.9278	1	1	0.7935
3	13.56	0.8974		1	0.9203	0.7694	**0.0018**	0.999	0.9998	1	0.987
4	14.21	0.2455	0.652		0.9942	0.9566	**0.0087**	0.9684	1	1	0.879
5	15.67	1.208	2.105	1.453		1	0.1572	0.4303	0.9993	0.964	0.2506
6	16.13	1.667	2.564	1.912	0.4595		0.3062	0.242	0.9886	0.861	0.123
7	19.69	5.231	6.129	5.477	4.024	3.564		**0.0002**	**0.0181**	**0.003**	**0.0002**
8	12.39	2.071	1.174	1.826	3.279	3.738	7.302		0.9091	0.995	1
9	14.54	0.0805	0.978	0.326	1.127	1.586	5.151	2.152		1	0.7602
10	13.81	0.6537	0.2438	0.4082	1.861	2.321	5.885	1.417	0.7342		0.9651
11	11.95	2.506	1.608	2.26	3.713	4.173	7.737	0.4347	2.586	1.852	

Number of Gouges – ANOVA results:

Source	Sum of sqrs	df	Mean sqrs	F=ratio	P
Between groups:	55.52	8	6.9	16.1	0.0001 ****
Within groups:	37.07	86	0.4		

	2	3	5	6	7	8	9	10	11
2		**0.0001**	1	0.9882	**0.0001**	**0.0001**	1	1	1
3	9.788		**0.0001**	**0.0001**	0.8575	0.9563	**0.0001**	**0.0001**	**0.0001**
5	0.4425	10.23		0.9355	**0.0001**	**0.0001**	0.9998	0.9959	1
6	1.363	8.425	1.805		**0.0009**	**0.0004**	0.998	1	0.9958
7	7.682	2.106	8.124	6.319		1	**0.0002**	**0.0002**	**0.0002**
8	8.103	1.685	8.546	6.74	0.4213		**0.0001**	**0.0002**	**0.0001**
9	0.3097	9.478	0.7522	1.053	7.372	7.793		1	1
10	0.7219	9.066	1.164	0.641	6.96	7.381	0.4121		1
11	0.1927	9.595	0.6352	1.17	7.489	7.91	0.117	0.5291	

Number of Puncture Pits – ANOVA results:

Source	Sum of sqrs	df	Mean sqrs	F=ratio	P
Between groups:	341.681	8	42.7	10.76	0.0001 ****
Within groups:	357.229	90	3.9		

	2	3	4	5	7	8	9	10	11
2		0.4418	0.9929	0.4996	0.6223	**0.0037**	1	0.1639	0.9998
3	3.052		0.9388	**0.0019**	**0.00344**	0.6343	0.736	0.9998	0.8012
4	1.263	1.789		0.08772	0.1351	0.056	1	0.6795	1
5	2.928	5.98	4.191		1	**0.0001**	0.2396	**0.0003**	0.1907
7	2.673	5.725	3.936	0.2556		**0.0001**	0.334	**0.0006**	0.273
8	5.699	2.648	4.437	8.628	8.372		**0.0153**	0.9186	**0.0215**
9	0.6267	2.425	0.6361	3.555	3.3	5.073		0.3812	1
10	3.814	0.7622	2.551	6.742	6.487	1.885	3.187		0.4527
11	0.7857	2.266	0.477	3.714	3.459	4.914	0.159	3.028	

Table 3

Number of Scratches – ANOVA results:

Source	Sum of sqrs	df	Mean sqrs	F=ratio	P
Between groups:	261.63	9	29.1	2.131	0.04 *
Within groups:	968.32	71	13.6		

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
1		1	0.7025	0.9995	0.9844	0.8306	0.8487	1	1	1
2	0.3802		0.522	0.9937	0.936	0.672	0.9455	0.9999	1	1
3	2.614	2.994		0.9763	0.9989	1	**0.03122**	0.8656	0.7025	0.5324
4	0.976	1.356	1.638		1	0.9947	0.4148	1	0.9995	0.9944
5	1.539	1.919	1.076	0.5627		0.9999	0.203	0.9985	0.9844	0.9402
6	2.3	2.681	0.3137	1.325	0.7618		0.05717	0.9429	0.8306	0.682
7	2.248	1.868	4.862	3.224	3.787	4.549		0.6786	0.8487	0.9416
8	0.4183	0.7985	2.196	0.5577	1.12	1.882	2.666		1	0.9999
9	0	0.3802	2.614	0.976	1.539	2.3	2.248	0.4183		1
10	0.3585	0.02173	2.973	1.334	1.897	2.659	1.89	0.7768	0.3585	

Number of Pits – ANOVA results:

Source	Sum of sqrs	df	Mean sqrs	F=ratio	P
Between groups:	4267.41	9	474.2	13.56	< 0.0001 ****
Within groups:	2482.54	71	34.9		

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
1		**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.001**	**0.0002**	**0.0002**
2	10.71		0.6428	1	0.8608	0.9735	0.1668	0.1325	0.97	0.9885
3	7.967	2.743		0.8434	**0.026**	0.07388	**0.00061**	0.9947	0.9992	0.9962
4	10.23	0.4789	2.264		0.6676	0.8812	0.07533	0.2681	0.9972	0.9994
5	12.92	2.211	4.954	2.69		1	0.9689	**0.0014**	0.1692	0.2345
6	12.38	1.665	4.408	2.144	0.5458		0.8471	**0.0048**	0.3544	0.4535
7	14.63	3.918	6.661	4.397	1.707	2.253		**0.0002**	**0.0062**	**0.010**
8	6.645	4.065	1.322	3.586	6.276	5.731	7.984		0.806	0.7128
9	9.012	1.698	1.045	1.219	3.909	3.363	5.616	2.367		1
10	9.236	1.474	1.269	0.9951	3.685	3.139	5.392	2.591	0.2239	

Number of Fine Scratches – ANOVA results:

Source	Sum of sqrs	df	Mean sqrs	F=ratio	P
Between groups:	366.65	9	40.7	3.639	0.001 ***
Within groups:	806.05	72	11.2		

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
1		0.9988	**0.0056**	0.6291	**0.0098**	0.2701	0.5736	0.4104	0.518	0.5281
2	1.092		0.0551	0.972	0.0862	0.7577	0.9573	0.8821	0.9377	0.9416
3	5.659	4.567		0.5736	1	0.8995	0.6291	0.7835	0.6834	0.6737
4	2.772	1.68	2.887		0.691	0.9999	1	1	1	1
5	5.411	4.319	0.2475	2.64		0.9517	0.7423	0.8713	0.7901	0.7817
6	3.58	2.488	2.079	0.8084	1.831		1	1	1	1
7	2.887	1.795	2.772	0.1155	2.524	0.6929		1	1	1
8	3.233	2.142	2.425	0.4619	2.178	0.3464	0.3464		1	1
9	3.003	1.911	2.656	0.231	2.409	0.5774	0.1155	0.231		1
10	2.982	1.89	2.677	0.21	2.43	0.5984	0.09448	0.252	0.021	

Number of Coarse Scratches – ANOVA results:

Source	Sum of sqrs	df	Mean sqrs	F=ratio	P
Between groups:	134.34	8	16.8	5.228	< 0.0001 ****
Within groups:	221.62	69	3.2		

	2	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
2		0.7199	1	0.835	0.9998	**0.00017**	0.7199	0.509	0.2432
3	2.461		0.8569	1	0.9547	**0.01691**	1	1	0.9973
4	0.3555	2.106		0.9328	1	**0.00023**	0.8569	0.6769	0.3782
5	2.171	0.2901	1.816		0.9856	**0.00908**	1	0.9998	0.9866
6	0.7691	1.692	0.4136	1.402		**0.00042**	0.9547	0.8445	0.5682
7	7.537	5.076	7.181	5.366	6.768		**0.01691**	**0.04176**	0.13
8	2.461	0	2.106	0.2901	1.692	5.076		1	0.9973
9	2.912	0.4512	2.557	0.7412	2.143	4.625	0.4512		0.9999
10	3.557	1.096	3.201	1.386	2.788	3.98	1.096	0.6446	

Number of Large Pits – ANOVA results:

Source	Sum of sqrs	df	Mean sqrs	F=ratio	P
Between groups:	175.7	9	19.5	2.093	0.04 *
Within groups:	662.4	71	9.3		

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
1		0.6135	0.9813	0.4244	0.4108	0.473	0.473	0.6544	0.9963	1
2	2.804		0.9971	1	1	1	1	1	0.9843	0.8985
3	1.58	1.224		0.9777	0.9748	0.9859	0.9859	0.9984	1	0.9998
4	3.203	0.3984	1.622		1	1	1	1	0.9321	0.7608
5	3.233	0.4285	1.653	0.0301		1	1	1	0.9258	0.7481
6	3.097	0.2931	1.517	0.1054	0.1355		1	1	0.9513	0.8031
7	3.097	0.2931	1.517	0.1054	0.1355	0		1	0.9513	0.8031
8	2.718	0.0862	1.138	0.4846	0.5147	0.3793	0.3793		0.9895	0.9198
9	1.264	1.54	0.3161	1.939	1.969	1.833	1.833	1.454		1
10	0.7224	2.082	0.8579	2.48	2.51	2.375	2.375	1.996	0.5418	

Number of Small Pits – ANOVA results:

Source	Sum of sqrs	df	Mean square	F=ratio	P
Between groups:	2791.07	9	310.1	9.655	< 0.0001 ****
Within groups:	2280.51	71	32.1		

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
1		**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**
2	10.59		0.9923	1	0.9916	0.9888	0.378	0.9388	0.9999	1
3	9.199	1.394		0.9974	0.614	0.5859	**0.04281**	1	1	0.8903
4	10.4	0.19	1.204		0.9797	0.9743	0.3007	0.968	1	0.9997
5	12	1.41	2.803	1.6		1	0.94	0.3752	0.8674	1
6	12.06	1.468	2.862	1.658	0.0584		0.9503	0.3504	0.8486	0.9999
7	13.9	3.308	4.701	3.498	1.898	1.84		**0.01513**	0.1277	0.7137
8	8.688	1.905	0.511	1.715	3.314	3.373	5.213		0.9985	0.6984
9	9.812	0.7805	0.6132	0.5905	2.19	2.249	4.088	1.124		0.987
10	11.31	0.7185	2.112	0.9085	0.6911	0.7495	2.589	2.623	1.499	

Number of Puncture Pits – ANOVA results:

Source	Sum of sqrs	df	Mean sqrs	F=ratio	P
Between groups:	212.82	7	30.4	4.521	<0.001 ***
Within groups:	443.85	66	6.7		

	2	**3**	**4**	**5**	**6**	**8**	**9**	**10**
2		0.9903	0.9874	0.9521	0.9667	0.1969	1	0.88
3	1.183		1	0.524	0.5725	0.6843	0.9929	0.9996
4	1.237	0.05357		0.499	0.5473	0.7081	0.9905	0.9998
5	1.572	2.755	2.809		1	**0.01151**	0.9422	0.2349
6	1.468	2.652	2.705	0.1033		**0.01431**	0.9589	0.2692
8	3.594	2.411	2.357	5.166	5.062		0.2138	0.9288
9	0.0584	1.125	1.179	1.63	1.527	3.536		0.8962
10	1.895	0.7117	0.6582	3.467	3.363	1.699	1.837	

Table 4

Facet	Axis/PC	Eigen value	% Complete variance
Grinding	1	0.12	41.78
	2	0.06	20.99
	3	0.03	11.59
	4	0.02	8.15
	5	0.02	6.77
	6	0.02	6.16
	7	0.01	4.22
	8	0.00	0.23
	9	0.00	0.11
Slicing			
	1	0.1350	36.88
	2	0.0961	26.25
	3	0.0427	11.66
	4	0.0402	10.98
	5	0.0232	6.33
	6	0.0151	4.12
	7	0.0115	3.14
	8	0.0019	0.52
	9	0.0004	0.12

Table 5

Microwear features (variables)	Mean ± SD	95% CL	1st Quartile	min	median	max	3rd quartile
Pits	31.82; ± 3.22	1.90	29	29	32	37	33.5
Scratches	20.91; ±1.92	1.13	19.5	18	21	24	22.5
Fine Scratches	17.18; ±1.66	0.98	16	15	18	20	18
Coarse Scratches	3.73; ±1.10	0.65	3	2	4	5	4.5
Large Pits	5.91; ±1.51	0.89	5	4	6	8	7
Small Pits	22; ±2.86	1.69	20	19	21	28	23
Gouges	1.54; ±0.82	0.48	1	0	2	3	2
Punctures	2.36; ±0.67	0.39	2	2	2	4	2.5

Table 6

Species	Dietary grouping (see also Fig. 1)	Microwear characteristics (from this study)
A. melanoleuca	Foliage-Herbivore	The highest number of fine scratches and small pits. The highest average number of pits. Most scratches have the same orientation. Absence of coarse scratches.
U. maritimus	Vertebrates-Hypercarnivore	Few scratches. Small number of pits. The highest scratches width score of any extant bear species. Absence of puncture pits. Presence of hypercoarse scratches.
U. thibetanus	Hard mast-Omnivore	High scratches width score (2nd after *U. maritimus*). The lowest percentage of puncture pits in comparison with the other extant species. The smallest average number of pits and an intermediate average number of scratches.
M. ursinus	Invertebrates-Insectivore	High number of pits. Small number of scratches. Moderate percentage of puncture pits.
H. malayanus	Invertebrates-Omnivore	Relatively high percentage of fine scratches. Relatively high percentage of small pits. Relatively small average number of pits and intermediate to high average number of scratches. Small percentage of puncture pits.
U. americanus	Soft mast-Omnivore	Intermediate percentage of fine scratches. Intermediate number of pits. Higher percentage of puncture pits than *U. arctos* from USA. Small average number of scratches.
U. arctos, USA	Vertebrates-Omnivore	Intermediate number of pits. Small percentage of puncture pits in comparison with the other *U. arctos* species. Higher percentage of coarse scratches than *U. americanus.* Smaller percentage of pits than *U. americanus.* The highest average number of scratches.
U. arctos, Russia	Vertebrates-Omnivore	Low to high percentage of puncture pits and gouges. Relatively high number of large pits. Small number of scratches. Intermediate values of average number of pits.
U. arctos, North Europe	Soft mast-Omnivore	Small percentage of puncture pits and gouges. Intermediate number of scratches. Intermediate to high number of pits.
U. arctos, central Europe	Hard mast-Omnivore	The highest percentage in comparison to other *U. arctos* of: Pits; Puncture pits; Gouges and Large pits.
U. arctos, Greece	Soft mast-Omnivore	The lowest percentage of pits and of puncture pits in comparison to the other omnivorous species. Intermediate scratches width score. High coarse scratches. Relatively high average number of scratches.

File S.1. Supplementary material (Material and Method)

S.1.1. Material

The reference bears for this study were selected from eight different museum and university collections around Europe including the Natural History Museum in Vienna, Austria, the Natural History Museum in Paris, France (Department of Comparative Anatomy), the Natural History Museum in Berlin, Germany, the Aristotle University of Thessaloniki (Geology Department) and Aristotle University of Thessaloniki (Laboratory of Wildlife and freshwater Fisheries of the School of Forestry and Natural Environment), Greece (see also Table S. 1). A set of 168 specimens was initially collected. After exclusion of specimens with obvious *post mortem* damage, pathologies or poor preservation, 110 samples from modern bears were ultimately included in the microwear analysis of this study. All modern samples were examined both on the grinding (talonid) and the slicing (trigonid) area hence, Table S.1. and Table S.2. show the complete list of the material and their raw microwear features results.

These include *A. melanoleuca* (n: 4), *H. malayanus* (n: 17), *M. ursinus* (n: 4), *T. ornatus* (n: 2), *U. americanus* (n: 9), *U. maritimus* (n: 14), *U. thibetanus* (n: 6). *U. arctos*, Greece (n: 4); *U. arctos*, central Europe (n: 10); *U. arctos*, USA (n: 8 [4 specimens from Alaska]); *U. arctos*, Russia (n: 10) and *U. arctos*, northern Europe (n: 9).

Microwear observations were calibrated against the known diets of modern bears from extensive published research (e.g. Davis, 1964; Joshi *et al*., 1997; Mattson, 1998; Hilderbrand *et al*., 1999; Derocher *et al*., 2002; Augeri, 2005; Bojarska and Selva, 2012) and the bear species organised into dietary groups (see also Fig 1 main text).

S.1.2. Methodology

Enamel microwear features were evaluated via standard light stereomicroscopy at low magnification (x35) to quantify microwear features on high-resolution epoxy casts of teeth, following the cleaning, moulding, casting and examination protocol developed by Solounias and Semprebon (2002) and Semprebon *et al*., (2004). The following steps were completed:

a) The occlusal surface of each specimen was first carefully cleaned with a cotton stick using acetone to remove any consolidants or varnish from the occlusal surface of the tooth (Fig. S.1 A).

b) The surface was then cleaned with a cotton swab and 96% alcohol to remove the acetone residues that can be left on the surface (Fig. S.1 A).

c) Once dry, the moulding substance, a high-resolution dental silicone suitable for microwear analysis (President Plus Regular Body; Coltene whaledent, REF. 4627) (Goodall *et al*., 2015), was applied with a gun (mixed with the hardener in its single-use tip), directly onto the tooth (Fig. S.1 B).

d) Once the silicone was completely dry, which required a waiting time of 5 to 10 minutes in order to ensure the best moulding results, a wall of Lab Putty (President fast Coltene whaledent; REF. 4632) was formed around the mould (Fig. S.1 C).

e) Subsequently, this mould was further processed at the lab (Department of Geography, Royal Holloway University of London [RHUL]) by being filled with clear epoxy resin (Fig. S.1 D, E & F). After 24 hours, the resin was hard enough to remove the tooth casts from the moulds.

The resin casts were then examined under a light microscope. Those with bad preservation or other taphonomical marks (including any marks produced by excavation process, storage in the collection and, more rarely, by the cleaning procedure) were excluded from the subsequent analysis. The specimens were studied both in the Geography Department of Royal Holloway University of London (RHUL) with an Olympus SZ51 with WHSZ 10x –H/22 stereomicroscope at x35 magnification and at the Institut Català de Paleoecologia Humana i Evolució Social (IPHES) in Spain, using a Zeiss Stemi 2000C stereomicroscope at x35 magnification (Fig. S.1 G). The use of a different brand of stereomicroscope does not influence the results (F. Rivals, pers. comm.). External (and where required, internal) lights on the microscopes were used to reveal the microfeatures on the enamel surface of the samples. Microwear features were quantified in a square area of 0.16 mm^2 by using an ocular reticle (Fig. S.1 H).

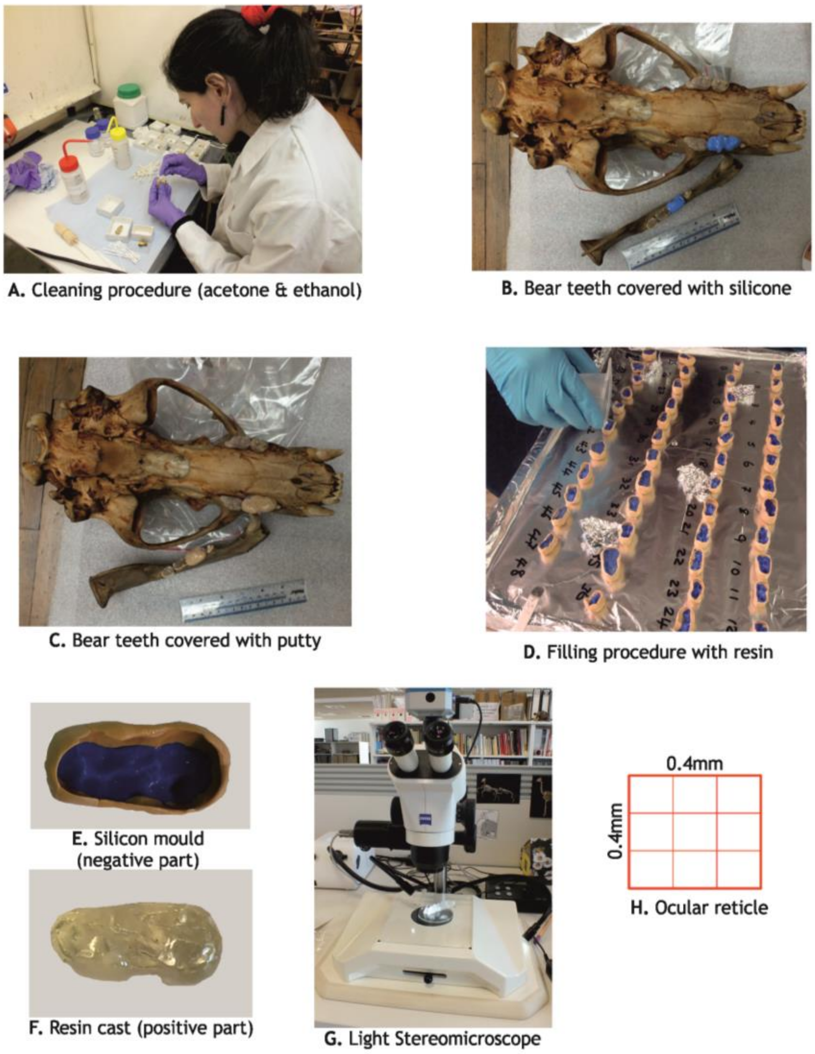

Figure S.1. Dental Microwear Analysis procedure. **A**. Cleaning process of teeth surface with acetone and then with 96% alcohol. **B.** Teeth of a bear skull covered with silicone. **C.** Bear teeth covered with putty. **D.** Filling procedure with clear epoxy resin in the laboratory. **E.** Silicone mould (negative part). **F.** Resin cast (positive part) **G**. Zeiss Stemi 2000C stereomicroscope. **H**. An ocular reticle with a square area of 0.16 mm^2 used in the quantification of the microwear features.

S.1.3. Description of microscopic scars

The microscopic scars that appear on the tooth are variable and before starting the analysis, it is important to differentiate and to categorise these features. Solounias and Hayek (1993) first instituted a set of categories regarding microwear features. Later Solounias and Semprebon (2002) introduced four more variables, in addition to the traditionally-counted number of scratch scars (elongated microfeatures with straight parallel sides) and pits scars (circular or sub-circular microfeatures with approximately similar widths and lengths), namely the classification of pits as small or large and scratches as fine and coarse. Subsequently, Semprebon *et al*. (2004) added new type of scratches and pits in terms of their texture, describing both “hypercoarse” scratches and “puncture” pits.

This study follows the classification of microwear features based on Solounias and Semprebon (2002) and Semprebon *et al*. (2004). Hence, the following features were identified on bear samples, reflecting the masticatory actions of the animals involved:

1. Pits are microwear features that are circular or subcircular in outline. Pits can be separated into the following categories:

- **Small pits**. These are bright white in colour under the microscope and have a very regular appearance with sharp, distinct and circular borders (Fig. S.2 A and B).

- **Large pits**. These are deeper than the small pits and dark in colour. They are at least double the size of the small pits and often have somewhat less regular outlines, albeit retaining a circular form (Fig. S.2 A).

2. Gouges (G) are microfeatures that are both larger and deeper than large pits and with irregular edges. Usually the surface of enamel has the appearance of being “chipped” away (Fig. S.2 A).

3. Punctures (P) vary in size; they can be as small as small pits but can also be much larger. The key to their identification is their depth, since they are very deep (usually deepest at their centre) and symmetrical, with regular margins, (Fig. S.2 A).

4. Scratches (S) are elongated microwear features that are straight and have parallel sides. Scratches can be divided into the following categories:

- Fine scratches, which are narrow and relatively shallow (Fig. S.2 B).
- Coarse scratches, which are wider and relatively deep, usually with a high refractivity (Fig. S.2 B) (after Semprebon *et al*. [2004]).
- Hypercoarse scratches, which are wider than coarse scratches and with a dark colour (Fig. S.2 B) (after Semprebon *et al*. [2004]).
- Cross scratches, which are oriented more-or-less perpendicular to the majority of scratches on the enamel surface.

5. A **Scratch Width Score** (SWS) is assigned, depending on the level of scratches observed. A score of zero (0) is given when only fine scratches are present, one (1) when there is a mixture of fine and coarse scratches on the surface, two (2) when predominantly coarse scratches are present and three (3) when the surface has also hypercoarse scratches.

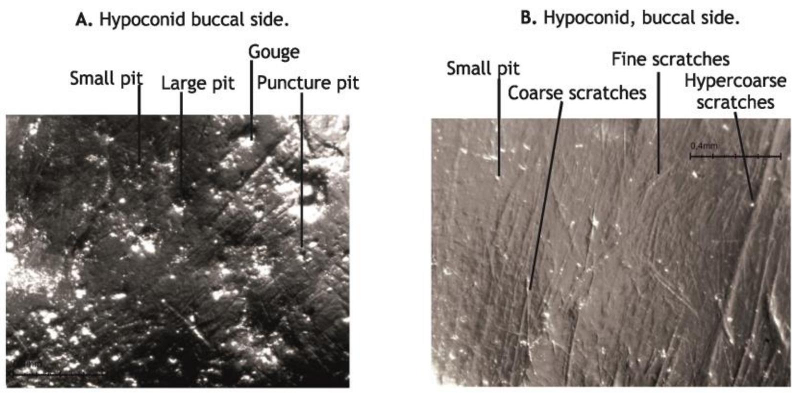

Figure S.2. Microwear features observed on m1 samples (buccal side of hypoconid) (Natural History Museum of Vienna specimen number A. 40633 and B. 40640) under stereolight-microscope with x35 magnification including all the different features observed on bear samples.

S.1.4. Statistical methods used for DMA

All data for the DMA were collected in Excel, before application of both Excel and PAST statistical packages.

Regarding the extant species (which form the main comparative database of this study), statistical analysis was completed for both the slicing and grinding areas in all samples. The data were first examined using bivariate graphs.

In order to explore which microwear traits best differentiate the species, an Analysis of Variance (ANOVA) with a Tukey’s pairwise test were used for the observations on both the grinding and slicing areas.

A Principal Components Analysis (PCA) was employed to identify any groupings emerging from individual scores from both grinding and slicing areas. Nine different variables were examined. Statistical analysis of extinct bear samples included bivariate comparison as well as PCA.

File S.2. ANOVA and Tukey's HSD test results for Grays bears in comparison with extant species

To understand better which microwear traits differentiate the extinct species from Britain, analysis of variance (ANOVA) statistical tests were performed, along with Tukey's pairwise comparison tests. Table 1 presents the ANOVA tests for all extant species and extinct species from Britain using the grinding area of the m1. These revealed significant ($p<0.05$) differences for the following microwear features: scratches, pits, fine scratches, coarse scratches, large pits, small pits and puncture pits. This means that there any pair of bear species displays a significant difference in at least of the above features. Two variables, the scratches width score and the presence/absence of cross scratches were excluded from the analyses since little variation was observed between species.

The significant differences (p-values) between species as revealed by the Tukey's pairwise tests are highlighted in pink in Tables 1. With respect to the number of gouges present, as expected, none of the bear species differs significantly. However, all the other microwear features show significant differences between bear species. Thus, from these tables it is clear that there is a very good separation between species on almost all the microwear features. This is especially relevant for pits, coarse scratches and small pits, which possess the biggest number of pairwise bear species where the p-value shows significant differences (Table 1).

Table 1. ANOVA and Tukey's HSD test results for Grays *U. arctos* species from Britain and extant species on the **grinding** area. A summary is given of the results from all the different features that were measured in each species and compared and tested between and within groups. Abbreviations as follows: Sum of sqrs is the sum of squares due to features; df is the degree of freedom in the features; Mean sqrs is the mean sum of squares duet to features; F is the *F*-statistic and p is the p-value. Pair – wise comparison = Values below the diagonal are the results of Tukey's method and those above are the p-values (significant comparisons are in bold). **1:** *Ailuropoda melanoleuca* (n: 3); **2:** *Helarctos malayanus* (n: 11); **3:** *Melursus ursinus* (n: 4); **4:** *Ursus americanus* (n: 9); **5:** *Ursus maritimus* (n: 14); **6:** *Ursus thibetanus* (n: 4); **7:** *Ursus arctos*, Greece (n: 4); **8:** *Ursus arctos*, Central Europe (n: 8); **9:** *Ursus arctos*, USA (n: 3); **10:** *Ursus arctos*, Russia (n: 21); **11:** *Ursus arctos*, North Europe (n: 9); **12:** Grays *Ursus arctos* (MIS 9) *Ursus arctos* (n: 10).

Number of Scratches – ANOVA results:

Source	Sum of sqrs	df	Mean square	F=ratio	p
Between groups:	376.0	11	34.18	3.5	0.0003 (???)
Within groups:	1038.6	107	9.71		

	1	2	3	4	5	6	7	8	9	10	11	12
1	-	1	0.691	0.736	0.800	0.998	1	0.997	0.985	1	1	0.997
2	0.244	-	0.572	0.620	0.693	0.992	1	1	0.996	1	1	1
3	2.832	3.075	-	1	1	0.997	0.374	0.118	0.067	0.357	0.560	0.116
4	2.735	2.978	0.097	-	1	0.998	0.418	0.139	0.081	0.400	0.608	0.137
5	2.583	2.826	0.249	0.152	-	0.999	0.491	0.178	0.107	0.473	0.683	0.175
6	1.38	1.623	1.452	1.355	1.203	-	0.953	0.698	0.548	0.947	0.991	0.694
7	0.654	0.41	3.485	3.388	3.236	2.033	-	1	1	1	1	1
8	1.438	1.194	4.269	4.173	4.02	2.817	0.784	-	1	1	1	1
9	1.743	1.499	4.574	4.478	4.325	3.122	1.089	0.305	-	1	0.996	1
10	0.691	0.448	3.523	3.426	3.274	2.071	0.038	0.746	1.051	-	1	1
11	0.266	0.023	3.098	3.001	2.849	1.646	0.387	1.171	1.476	0.425	-	1
12	1.446	1.202	4.277	4.181	4.028	2.825	0.792	0.008	0.297	0.754	1.179	-

Number of Pits – ANOVA results:

Source	Sum of sqrs	df	Mean square	F=ratio	p
Between groups:	6101.9	11	554.72	21.4	< 0.0001 ****
Within groups:	2775.8	107	25.94		

	1	2	3	4	5	6	7	8	9	10	11	12
1	-	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**
2	16.68	-	**0.004**	1	0.814	0.676	0.589	**0.007**	0.997	0.559	0.328	0.481
3	10.79	5.886	-	**0.031**	**0.000**	**0.000**	**0.000**	1	0.083	0.712	0.897	0.781
4	15.75	0.927	4.959	-	0.379	0.251	0.193	0.056	1	0.927	0.766	0.887
5	19.22	2.546	8.432	3.473	-	1	1	**0.000**	0.193	**0.007**	**0.002**	**0.004**
6	19.54	2.863	8.749	3.79	0.317	-	1	**0.000**	0.114	**0.003**	**0.001**	**0.002**
7	19.72	3.041	8.927	3.968	0.495	0.178	-	**0.000**	0.083	**0.002**	**0.001**	**0.001**
8	11.09	5.593	0.293	4.666	8.139	8.456	8.634	-	0.139	0.834	0.958	0.886
9	15.26	1.423	4.463	0.496	3.969	4.286	4.463	4.17	-	0.989	0.928	0.978
10	13.58	3.1	2.786	2.173	5.646	5.963	6.141	2.493	1.677	-	1	1
11	13.09	3.591	2.295	2.665	6.137	6.455	6.632	2.002	2.169	0.492	-	1
12	13.42	3.258	2.628	2.331	5.804	6.121	6.299	2.335	1.835	0.158	0.334	-

Number of Fine Scratches – ANOVA results:

Source	Sum of sqrs	df	Mean square	F=ratio	p
Between groups:	633.8	11	57.62	5.4	< 0.0001 ****
Within groups:	1135.7	107	10.61		

	1	2	3	4	5	6	7	8	9	10	11	12
1	-	0.991	**0.011**	**0.048**	**0.000**	0.157	**0.018**	0.997	1	0.822	0.662	0.986
2	1.63	-	0.252	0.552	**0.017**	0.843	0.333	1	1	1	0.999	1
3	5.416	3.786	-	1	0.997	0.999	1	0.196	0.066	0.663	0.823	0.287
4	4.745	3.115	0.671	-	0.936	1	1	0.467	0.210	0.917	0.976	0.598
5	6.874	5.244	1.458	2.129	-	0.716	0.990	**0.011**	**0.003**	0.103	0.189	**0.020**
6	4.097	2.467	1.319	0.648	2.777	-	1	0.777	0.478	0.994	0.999	0.874
7	5.208	3.578	0.208	0.463	1.666	1.111	-	0.266	0.098	0.759	0.892	0.374
8	1.458	0.172	3.958	3.287	5.416	2.639	3.749	-	1	1	0.997	1
9	0.833	0.797	4.583	3.911	6.041	3.263	4.374	0.625	-	0.988	0.949	1

10	2.527	0.897	2.889	2.218	4.347	1.57	2.681	1.069	1.694	-	1	1
11	2.893	1.263	2.523	1.852	3.981	1.204	2.314	1.435	2.06	0.366	-	1
12	1.723	0.094	3.693	3.021	5.151	2.373	3.484	0.265	0.89	0.804	1.17	-

Number of Coarse Scratches – ANOVA results:

Source	Sum of sqrs	df	Mean square	F=ratio	p
Between groups:	83.0	10	8.30	5.5	< 0.0001 ****
Within groups:	152.7	102	1.50		

Pair – wise comparison = Values below the diagonal are the results of Tukey's method and those above are the p-values (significant comparisons are in bold). **2:** *H. malayanus* (n: 11); **3:** *M. ursinus* (n: 4); **4:** *U. americanus* (n: 9); **5:** *U. maritimus* (n: 14); **6:** *U. thibetanus* (n: 4); **7:** *U. arctos*, Greece (n: 4); **8:** *U. arctos*, Central Europe (n: 8); **9:** *U. arctos*, USA (n: 3); **10:** *U. arctos*, Russia (n: 21); **11:** *U. arctos*, North Europe (n: 9); **12:** Grays Thurrock (MIS 9) *U. arctos* (n: 10).

	2	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
2	-	0.940	1	0.796	0.895	**0.000**	0.848	0.995	0.402	0.454	0.510
3	2.013	-	0.988	1	1	**0.000**	1	1	0.997	0.999	1
4	0.415	1.598	-	0.925	0.973	**0.000**	0.952	1	0.603	0.657	0.712
5	2.5	0.487	2.085	-	1	**0.000**	1	1	1	1	1
6	2.205	0.192	1.79	0.295	-	**0.000**	1	1	0.999	1	1
7	10.64	8.628	10.23	8.141	8.436	-	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**
8	2.358	0.345	1.943	0.142	0.153	8.283	-	1	1	1	1
9	1.438	0.575	1.023	1.062	0.767	9.203	0.920	-	0.959	0.973	0.983
10	3.339	1.325	2.923	0.839	1.134	7.303	0.980	1.901	-	1	1
11	3.228	1.214	2.812	0.728	1.023	7.414	0.869	1.79	0.111	-	1
12	3.111	1.098	2.696	0.611	0.906	7.53	0.753	1.673	0.227	0.116	-

Number of Large Pits – ANOVA results:

Source	Sum of sqrs	df	Mean square	F=ratio	p
Between groups:	214.1	11	19.46	5.0	< 0.0001 ****
Within groups:	419.5	107	3.92		

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
1	-	0.060	0.987	0.135	**0.010**	**0.010**	1	0.122	0.866	0.939	0.697	0.344
2	4.637	-	**0.001**	1	1	1	**0.006**	1	0.912	0.824	0.979	1
3	1.714	6.351	-	**0.004**	**0.000**	**0.000**	1	**0.003**	0.153	0.237	0.073	**0.016**
4	4.189	0.448	5.903	-	0.999	0.999	**0.018**	1	0.982	0.947	0.998	1
5	5.484	0.847	7.198	1.295	-	1	**0.001**	0.999	0.567	0.428	0.766	0.968
6	5.484	0.847	7.198	1.295	0	-	**0.001**	0.999	0.567	0.428	0.766	0.968
7	1.028	5.665	0.686	5.217	6.512	6.512	-	**0.015**	0.400	0.537	0.231	0.067
8	4.25	0.387	5.964	0.061	1.234	1.234	5.278	-	0.976	0.935	0.997	1
9	2.399	2.238	4.113	1.79	3.085	3.085	3.427	1.851	-	1	1	1
10	2.116	2.521	3.83	2.073	3.368	3.368	3.144	2.134	0.283	-	1	0.997
11	2.818	1.819	4.532	1.371	2.666	2.666	3.846	1.432	0.419	0.702	-	1
12	3.552	1.085	5.266	0.637	1.932	1.932	4.58	0.698	1.153	1.436	0.734	-

Number of Small Pits – ANOVA results:

Source	Sum of sqrs	df	Mean square	F=ratio	p
Between groups:	3891.2	11	353.74	14.4	< 0.0001 ****
Within groups:	2632.7	107	24.60		

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
1	-	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**
2	15.17	-	1	1	0.999	0.985	**0.009**	0.927	1	1	0.781	0.971
3	14.23	0.942	-	1	0.919	0.755	**0.001**	0.999	1	1	0.989	1
4	14.91	0.258	0.684	-	0.995	0.957	**0.005**	0.970	1	1	0.875	0.991
5	16.44	1.267	2.209	1.524	-	1	0.128	0.394	1	0.965	0.215	0.526
6	16.92	1.749	2.691	2.007	0.482	-	0.269	0.207	0.990	0.854	0.097	0.305
7	20.66	5.489	6.43	5.746	4.222	3.74	-	**0.000**	**0.012**	**0.002**	**0.000**	**0.000**
8	13	2.173	1.231	1.915	3.44	3.922	7.661	-	0.907	0.996	1	1
9	15.25	0.085	1.026	0.342	1.182	1.665	5.404	2.257	-	1	0.745	0.961
10	14.48	0.686	0.256	0.428	1.953	2.435	6.174	1.487	0.770	-	0.966	0.999

11	12.54	2.629	1.687	2.371	3.896	4.378	8.117	0.456	2.713	1.943	-	1
12	13.27	1.899	0.958	1.642	3.166	3.648	7.388	0.274	1.984	1.213	0.730	-

Number of Gouges – ANOVA results:

Source	Sum of sqrs	df	Mean square	F=ratio	p
Between groups:	5.5	3	1.82	3.5	0.03
Within groups:	11.5	22	0.52		

	3	**7**	**8**	**12**
3	-	0.664	1	0.129
7	1.624	-	0.664	0.664
8	0	1.624	-	0.129
12	3.249	1.624	3.249	-

Number of Puncture Pits – ANOVA results

Source	Sum of sqrs	df	Mean square	F=ratio	p
Between groups:	141.0	7	20.15	5.27	< 0.0001 ****
Within groups:	317.3	83	3.823		

	2	**3**	**4**	**8**	**9**	**10**	**11**	**12**
2	-	0.3	0.979	**0.001**	0.992	0.294	0.999	1
3	3.269	-	0.875	0.485	0.810	1	0.677	0.459
4	1.353	1.916	-	**0.025**	1	0.870	1	0.997
8	6.105	2.836	4.753	-	**0.017**	0.492	**0.0083**	**0.003**
9	1.161	2.108	0.192	4.944	-	0.804	1	0.999
10	3.286	0.017	1.933	2.82	2.125	-	0.669	0.451
11	0.842	2.427	0.511	5.264	0.319	2.444	-	1
12	0.377	2.892	0.976	5.728	0.784	2.909	0.465	-

Table S.1.

Table S.1. Microwear features raw results for extant and extinct bear species on the **grinding area**. Abbreviations for museums: NHMV: the Natural History Museum in Vienna, Austria; NHMP: the Natural History Museum in Paris, France (Department of Comparative Anatomy); ZMB: the Natural History Museum in Berlin, Germany; AUThG: the Aristotle University of Thessaloniki (Geology Department), Greece; AUThW: Aristotle University of Thessaloniki (Laboratory of Wildlife and freshwater Fisheries of the School of Forestry and Natural Environment), Greece and NHMUK PV M or OR: the Natural History Museum in London (Earth Sciences Department), UK. Abbreviations for features: S: Scratches; P: Pits; Fs: Fine scratches; Cs: Coarse scratches; SWS: Scratches width score; Lp: Large pits; Sp: Small pits; G: gouges; Pp: puncture pits and XS: cross scratches present (1) or absent (0). Wear of Stage after Stiner (1998).

Specimen number	Taxon – Origin	Tooth, Side, sex	S	P	Fs	Cs	SWS	Lp	Sp	G	Pp	XS	Wear of Stage
ZMB MAM 17246	*A. melanoleuca*	m1, Right, Female	21	62	21	0	0	9	53	0	0	0	V
ZMB MAM 17246	*A. melanoleuca*	m1, Right	17	61	17	0	0	8	44	0	0	0	V
ZMB MAM 17542	*A. melanoleuca*	m1, Left	19	56	19	0	0	9	47	0	0	0	VI
ZMB MAM 85761	*A. melanoleuca*	m1, Left	20	49	20	0	0	8	41	0	0	0	VI
NHMP 1899-193	*H. malayanus*	m1, Right	22	10	21	1	1	2	8	0	0	1	VI
NHMP 1913-505	*H. malayanus*	m1, Left	22	28	21	1	1	6	19	0	3	1	V
NHMP 1913-72	*H. malayanus*	m1, Left	26	30	25	1	1	4	24	0	2	1	V
NHMP 1932-3197	*H. malayanus*	m1, Left	19	25	19	0	0	2	23	0	0	0	VI
NHMP 1901.652	*H. malayanus*	m1, Right	21	28	19	2	1	3	22	0	3	1	VI
NHMP 1919-62	*H. malayanus*	m1, Left	17	27	16	1	1	8	14	0	5	1	IV
NHMP A2132	*H. malayanus*	m1, Left	19	20	17	2	1	5	12	0	3	1	V
NHMP 1971-188	*H. malayanus*	m1, Right	19	22	16	3	1	3	19	0	0	1	VI
ZMB MAM 17531	*H. malayanus*, Thailand	m1, Right, Male	17	24	16	1	1	5	19	0	0	1	V
ZMB MAM 17245	*H. malayanus*, Borneo	m1, Right	26	29	22	4	1	3	23	0	3	1	V
ZMB MAM 105707	*H. malayanus*, Thailand	m1, Left	19	28	15	4	1	5	21	0	2	1	V
ZMB MAM 28472	*H. malayanus*, Sumatra	m1, Left	17	32	15	2	1	6	24	0	2	1	IV
ZMB MAM 17533	*H. malayanus*, Thailand	m1, Right, Female	18	23	17	1	1	6	14	0	3	1	V
ZMB MAM 17533	*H. malayanus*, Thailand	m1, Right, Female	15	26	13	2	1	8	14	1	4	1	V
ZMB MAM 34002	*H. malayanus*, Thailand	m1, Right, Female	20	30	15	5	1	9	21	0	3	1	VI

ZMB MAM 85771	*H. malayanus*, Sumatra	m1, Left	17	25	13	4	1	5	15	2	3	1	V
ZMB MAM 17532	*H. malayanus*, Thailand	m1, Right	18	30	14	4	1	7	23	0	0	1	V
NHMP 1883-59	*M. ursinus*	m1, Right	14	37	12	2	1	9	23	2	3	1	V
ZMB MAM 44144	*M. ursinus*, Kaulas, India	m1, Right, Female	16	34	12	4	1	7	19	2	6	1	V
ZMB MAM 56748	*M. ursinus*, Japan	m1, Left	18	32	15	3	1	9	18	3	2	1	V
ZMB MAM 44743	*M. ursinus*, Kaulas, India	m1, Right, Male	16	44	12	4	1	14	21	3	6	1	IV
NHMP 1848-369	*T. ornatus*	m1, Right	16	27	13	3	1	6	19	0	2	0	V
ZMB MAM 6121	*T. ornatus*, Venezouela	m1, Right	16	30	13	3	1	8	18	0	4	0	VI
NHMV 63555	*U. americanus*, Alaska	m1, Left	15	29	12	3	1	3	24	0	2	1	V
NHMV 64947	*U. americanus*, Alaska	m1, Right	14	20	11	3	1	4	13	0	3	1	V
NHMV 8269	*U. americanus*, Alaska	m1, Right, Male	18	36	16	2	1	7	24	0	5	1	IV
NHMV 8273	*U. americanus*, Alaska	m1, Left, Female	16	22	14	2	1	8	12	0	2	1	IV
NHMV 8271	*U. americanus*, Alaska	m1, Right, Female	17	28	14	3	1	5	20	0	3	1	IV
NHMV 8270	*U. americanus*, Alaska	m1, Left, Male	17	37	14	3	1	4	30	0	3	1	IV
NHMV 8272	*U. americanus*, Alaska	m1, Left, Male	15	25	13	2	1	4	19	0	2	1	IV
NHMV 8274	*U. americanus*, Alaska	m1, Right, Male	19	29	17	2	1	9	15	0	5	1	V
NHMV 8275	*U. americanus*, Alaska	m1, Left, Female	14	21	11	3	1	5	14	0	2	1	V
NHMV 7140	*U. maritimus*	m1, Left, Female	14	29	14	0	0	4	24	1	0	0	V
NHMV 13176	*U. maritimus*	m1, Right	18	23	12	2	3	6	16	0	1	0	IV
NHMV 7150	*U. maritimus*	m1, Left, Female	19	23	13	2	3	2	18	0	0	0	IV
NHMV 7139	*U. maritimus*	m1, Left, Male	14	21	8	2	3	2	19	0	0	0	IV
NHMV 7149	*U. maritimus*	m1, Right, Male	12	17	8	3	3	3	14	0	0	0	V

NHMV 7141	*U. maritimus*	m1, Left	19	23	16	3	3	8	15	0	0	0	IV
NHMV 7148	*U. maritimus*	m1, Left, Female	14	15	9	3	3	3	12	0	0	0	IV
NHMV 7143	*U. maritimus*	m1, Left, Female	16	22	10	4	3	6	16	0	0	0	V
NHMV 14657	*U. maritimus*	m1, Left	16	25	9	6	3	5	20	0	0	0	IV
NHMV 7794	*U. maritimus*	m1, Right	15	19	11	3	3	6	13	0	0	1	V
NHMV 7144	*U. maritimus*	m1, Left	19	23	11	5	3	6	17	0	0	0	IV
NHMV 7142	*U. maritimus*	m1, Righ, Female t	17	18	12	2	3	4	14	0	0	0	IV
NHMV 7147	*U. maritimus*	m1, Left	23	16	16	5	3	4	14	0	0	1	IV
NHMV 7138	*U. maritimus*	m1, Righ, Female t	12	19	5	5	3	4	15	0	0	0	V
NHMP 2006-415	*U. thibetanus*	m1, Right	17	20	14	3	1	4	16	0	0	0	V
ZMB MAM 56747	*U. thibetanus*, Japan	m1, Right	20	22	16	4	1	6	16	0	0	0	IV
ZMB MAM 69401	*U. thibetanus*, Japan	m1, Right	15	20	12	3	1	5	14	1	0	0	V
ZMB MAM 24592	*U. thibetanus*, Thibet	m1, Left	17	18	14	3	1	3	15	0	0	1	V
ZMB MAM 69400	*U. thibetanus*, Japan	m1, Right	19	21	15	4	1	5	14	2	0	1	V
ZMB MAM 69396	*U. thibetanus*, Thibet	m1, Right	18	21	15	3	1	4	17	0	0	1	V
AUThG 1	*U. arctos*, Greece	m1, Left	22	25	18	4	1	12	11	2	0	1	V
AUThG 1	*U. arctos*, Greece	m1, Right	21	17	14	7	1	8	7	2	0	1	V
AUThW 2	*U. arctos*, Greece	m1, Left	15	17	6	9	1	7	9	1	0	1	V
AUThW 3	*U. arctos*, Greece	m1, Left	22	21	14	8	1	10	7	3	1	1	V
NHMV 52	*U. arctos*, Slovakia, central EU	m1, Right	17	27	14	3	1	4	10	3	10	1	V
NHMV 21491	*U. arctos*, Ukraine, central EU	m1, Left	16	29	13	3	1	6	16	2	5	1	VI
NHMV 51	*U. arctos*, Slovakia, central EU	m1, Left	21	45	18	3	1	5	32	2	6	1	V
NHMV 7146	*U. arctos*, central EU	m1, Left	23	44	18	5	1	6	29	2	7	1	V
NHMV 67919	*U. arctos*, Romania, central EU	m1, Right	23	39	18	5	1	6	24	3	6	1	V
NHMV 4220	*U. arctos* (Europe)	m1, Right, Female	24	46	21	3	1	5	32	3	6	1	VI
NHMV 7396	*U. arctos*, Bosnia, central EU	m1, Right	21	39	16	5	1	6	24	3	6	1	V
NHMV 55276	*U. arctos*, Bulgaria, central EU	m1, Right, Male	20	34	18	2	1	7	19	1	7	1	VI
NHMV 67301	*U. arctos*, Slovenia, central EU	m1, Left	18	34	15	3	1	5	21	2	6	1	IV

NHMV 46465	*U. arctos*, Romania, central EU	m1, Left	26	25	24	2	1	4	18	0	2	1	VI
NHMV 7793	*U. arctos*, Canada, N. America	m1, Right	13	28	11	2	1	11	8	2	7	1	VI
ZMB MAM 87110	*U. arctos*, America	m1, Right	16	25	11	5	1	7	15	0	3	1	V
ZMB MAM 87110	*U. arctos*, America	m1, Right	22	23	16	6	1	8	13	0	2	1	V
ZMB MAM 43592	*U. arctos*, Middle Creek, USA	m1, Left, Male	25	37	23	2	1	5	29	0	3	1	V
ZMB MAM 37701	*U. arctos*, Alaska, N. America	m1, Left, Female	26	25	24	2	1	4	20	0	0	1	V
ZMB MAM 43593	*U. arctos*, Alaska, N. America	m1, Left, Female	26	32	23	3	1	6	23	0	3	1	V
ZMB MAM 87132	*U. arctos*, Alaska	m1, Right	23	33	21	2	1	8	23	0	2	1	V
ZMB MAM 69342	*U. arctos*, Alaska, N. America	m1, Right	19	24	17	2	1	5	16	0	3	1	V
NHMV 40624	*U. arctos*, Kamtchatka, Russia	m1, Left	14	35	12	2	1	6	26	0	3	1	IV
NHMV 40633	*U. arctos*, Kamtchatka, Russia	m1, Left	19	40	15	4	1	11	25	0	4	1	V
NHMV 40635	*U. arctos*, Kamtchatka, Russia	m1, Right	19	32	15	4	1	6	24	0	2	1	IV
NHMV 40608	*U. arctos*, Kamtchatka, Russia	m1, Left	27	30	23	4	1	4	14	1	11	1	IV
NHMV 40607	*U. arctos*, Kamtchatka, Russia	m1, Right	25	34	21	4	1	5	24	0	5	1	V
NHMV 40613	*U. arctos*, Kamtchatka, Russia	m1, Left	20	29	17	3	1	4	20	0	5	1	VI
NHMV 40625	*U. arctos*, Kamtchatka, Russia	m1, Right	21	30	18	3	1	10	14	1	5	1	V
NHMV 40616	*U. arctos*, Kamtchatka, Russia	m1, Left	22	29	19	3	1	5	17	0	7	1	IV
NHMV 40628	*U. arctos*, Kamtchatka, Russia	m1, Left	24	36	21	3	1	10	17	0	9	1	IV
NHMV 40615	*U. arctos*, Kamtchatka, Russia	m1, Right	18	29	14	4	1	11	12	0	6	1	IV
NHMV 40611	*U. arctos*, Kamtchatka, Russia	m1, Left	24	30	20	4	3	7	16	3	4	1	IV
NHMV 40645	*U. arctos*, Kamtchatka, Russia	m1, Left	19	29	15	4	1	4	23	0	2	1	VI
NHMV 40640	*U. arctos*, Kamtchatka, Russia	m1, Right	19	34	13	6	1	4	25	0	5	1	V
NHMV 40636	*U. arctos*, Kamtchatka, Russia	m1, Right	17	25	15	2	1	4	17	0	4	1	IV

NHMV 40630	*U. arctos*, Kamtchatka, Russia	m1, Right	18	35	14	4	1	7	26	0	2	1	IV
NHMV 40609	*U. arctos*, Kamtchatka, Russia	m1, Right	19	27	16	2	1	8	19	1	6	1	V
NHMV 40648	*U. arctos*, Kamtchatka, Russia	m1, Left	18	28	14	4	1	7	18	0	3	1	IV
NHMV 40634	*U. arctos*, Kamtchatka, Russia	m1, Left	26	39	23	3	1	10	21	0	8	1	IV
NHMV 40643	*U. arctos*, Kamtchatka, Russia	m1, Left	21	18	16	5	1	5	10	1	2	1	IV
NHMV 40605	*U. arctos*, Kamtchatka, Russia	m1, Right	19	33	13	7	1	11	10	1	12	1	V
NHMV 40626	*U. arctos*, Kamtchatka, Russia	m1, Right	21	37	16	5	1	5	32	0	0	1	IV
NHMV 40642	*U. arctos*, Kamtchatka, Russia	m1, Right	14	29	10	4	1	9	20	0	0	1	V
NHMV 40638	*U. arctos*, Kamtchatka, Russia	m1, Right	17	37	13	4	1	7	25	0	5	1	V
ZMB MAM 14425	*U. arctos*, Lithuania, N. Europe	m1, Left	28	32	23	5	1	7	24	0	2	1	IV
ZMB MAM 14414	*U. arctos*, Lithuania, N. Europe	m1, Left	16	30	12	4	1	7	20	0	3	1	V
ZMB MAM 14423	*U. arctos*, Lithuania, N. Europe	m1, Left	24	41	20	4	1	7	30	1	3	1	V
ZMB MAM 14422	*U. arctos*, Lithuania, N. Europe	m1, Right	18	28	15	3	1	4	23	0	1	1	V
ZMB MAM 14404	*U. arctos*, Lithuania, N. Europe	m1, Left	17	38	14	3	1	6	28	1	3	1	IV
ZMB MAM 14408	*U. arctos*, Lithuania, N. Europe	m1, Right	18	24	15	3	1	5	17	0	2	1	V
ZMB MAM 14403	*U. arctos*, Lithuania, N. Europe	m1, Right	17	28	14	3	1	6	20	0	2	1	V
ZMB MAM 14402	*U. arctos*, Lithuania, N. Europe	m1, Right	19	39	15	4	1	7	27	0	5	1	V
ZMB MAM 93300	*U. arctos*, Lithuania, N. Europe	m1, Left	19	32	14	5	1	9	21	0	3	1	V
NHMUK PV OR 20260	*U. arctos*, extinct Grays Thurrock, UK – no stratigraphy	m1, Left	24	29	20	4	1	5	20	0	4	1	V
NHMUK PV M 95990	*U. arctos*, extinct Grays Thurrock, UK – Corbets Tey Gravel Formation	m1, Left	23	32	18	5	1	8	19	2	3	1	VIII
NHMUK PV M 95989	*U. arctos*, extinct Grays Thurrock, UK – Corbets Tey Gravel Formation	m1, Left	20	29	16	4	1	4	21	2	2	1	VI
NHMUK PV OR 22030	*U. arctos*, extinct Grays Thurrock, UK – Corbets Tey Gravel Formation	m1, Right, Female	23	32	18	5	1	6	23	1	2	1	VI
NHMUK PV OR 22029	*U. arctos*, extinct Grays Thurrock, UK – Corbets Tey Gravel Formation	m1, Left, Male	20	37	15	5	1	8	26	1	2	1	VIII

NHMUK PV OR 22029	*U. arctos*, extinct Grays Thurrock, UK – Corbets Tey Gravel Formation	m1, Left, Male	22	29	18	4	1	4	22	1	2	1	VIII
NHMUK PV M 96013	*U. arctos*, extinct Grays Thurrock, UK – Corbets Tey Gravel Formation	m1, Left	19	32	15	4	1	6	21	3	2	1	V
NHMUK PV M 96012	*U. arctos*, extinct Grays Thurrock, UK – Corbets Tey Gravel Formation	m1, Right	18	35	16	2	1	8	23	2	2	1	VIII
NHMUK PV M 96011	*U. arctos*, extinct Grays Thurrock, UK – Corbets Tey Gravel Formation	m1, Left	19	29	16	3	1	5	20	2	2	1	VII
NHMUK PV M 95998	*U. arctos*, extinct Grays Thurrock, UK – Corbets Tey Gravel Formation	M1, Left	21	37	19	2	1	5	28	1	3	1	VI
NHMUK PV M 96010	*U. arctos*, extinct Grays Thurrock, UK – Corbets Tey Gravel Formation	M1, Right	21	29	18	3	1	6	19	2	2	1	VII

Table S.2.

Table S.2. Microwear features raw results for extant bear species on the **slicing area**. Abbreviations for museums as following: NHMV: the Natural History Museum in Vienna, Austria; NHMP: the Natural History Museum in Paris, France (Department of Comparative Anatomy); ZMB: the Natural History Museum in Berlin, Germany; AUThG: the Aristotle University of Thessaloniki (Geology Department), Greece and AUThW: Aristotle University of Thessaloniki (Laboratory of Wildlife and freshwater Fisheries of the School of Forestry and Natural Environment), Greece. Abbreviations for Features: S: Scratches; P: Pits; Fs: Fine scratches; Cs: Coarse scratches; SWS: Scratches width score; Lp: Large pits; Sp: Small pits; G: gouges and Pp: puncture pits. Wear of Stage after Stiner, 1998.

Specimen number	Taxon – Origin	Tooth, Side, Sex	S	P	Fs	Cs	SWS	Lp	Sp	G	Pp	XS	Wear of Stage
ZMB MAM 17246	*A. melanoleuca*	m1, Right, Female	17	62	17	0	0	11	51	0	0	0	V
ZMB MAM 17542	*A. melanoleuca*	m1, Left	20	58	20	0	0	11	47	0	0	0	VI
ZMB MAM 85761	*A. melanoleuca*	m1, Left	19	40	19	0	0	6	34	0	0	0	VI
NHMP 1899-193	*H. malayanus*	m1, Right	21	25	20	1	1	5	18	0	2	1	VI
NHMP 1913-505	*H. malayanus*	m1, Left	20	26	19	1	1	4	20	0	2	1	V
NHMP 1913-72	*H. malayanus*	m1, Left	19	34	18	1	1	5	25	0	4	1	V
NHMP 1932-3197	*H. malayanus*	m1, Left	19	26	17	2	1	8	15	0	3	1	VI
NHMP 1901.652	*H. malayanus*	m1, Right	20	29	17	3	1	5	20	0	4	1	VI
NHMP 1919-62	*H. malayanus*	m1, Left	22	22	22	0	0	7	13	0	2	1	IV
NHMP A2132	*H. malayanus*	m1, Left	19	25	18	1	1	7	16	0	2	1	V
ZMB MAM 17245	*H. malayanus*,Borneo	m1, Right	16	25	12	4	1	4	21	0	0	0	V
ZMB MAM 105707	*H. malayanus*,Thailand	m1, Left	19	25	17	2	1	4	18	0	3	1	V
ZMB MAM 34002	*H. malayanus*,Thailand	m1, Right, Female	22	23	18	4	1	4	16	0	3	1	VI
ZMB MAM 85771	*H. malayanus*, Sumatra	m1, Left	15	26	10	5	1	9	17	0	0	1	V
NHMP 1883-59	*M. ursinus*	m1, Right	16	44	11	5	1	4	34	2	4	1	V
ZMB MAM 44144	*M. ursinus*, Kaulas, India	m1, Right, Female	14	25	9	5	1	6	18	0	1	1	V
ZMB MAM 56748	*M. ursinus*, Japan	m1, Left	17	38	14	3	1	11	19	1	7	1	V
ZMB MAM 44143	*M. ursinus*, Kaulas, India	m1, Right	11	25	8	3	1	8	15	0	2	1	IV
ZMB MAM 6121	*T. ornatus*, Venezouela	m1, Right	13	17	10	3	1	3	14	0	0	0	VI
NHMV 63555	*U. americanus*, Alaska	m1, Left	13	29	13	0	0	4	22	0	3	1	V
NHMV 64947	*U. americanus*, Alaska	m1, Right	20	25	14	6	1	7	16	0	2	1	V
NHMV 8269	*U. americanus*, Alaska	m1, Right, Male	18	32	15	3	1	4	23	0	5	1	IV
NHMV 8273	*U. americanus*, Alaska	m1, Left, Female	15	30	14	1	1	4	20	0	6	1	IV
NHMV 8271	*U. americanus*, Alaska	m1, Right, Female	18	34	16	2	1	5	25	0	4	1	IV
NHMV 8270	*U. americanus*, Alaska	m1, Left, Male	18	25	16	2	1	3	20	0	2	1	IV
NHMV 8272	*U. americanus*, Alaska	m1, Left, Male	16	26	14	2	1	7	16	0	3	1	IV

NHMV 8274	*U. americanus*, Alaska	m1, Right, Male	19	25	15	4	1	8	12	0	5	1	V
NHMV 8275	*U. americanus*, Alaska	m1, Left, Female	17	19	15	2	1	4	13	0	2	1	V
NHMV 7140	*U. maritimus*	m1, Left, Female	13	29	10	1	3	6	23	0	0	0	V
NHMV 13176	*U. maritimus*	m1, Right	19	23	13	1	3	6	11	0	6	0	IV
NHMV 7150	*U. maritimus*	m1, Left, Female	18	15	12	3	3	2	13	0	0	0	IV
NHMV 7139	*U. maritimus*	m1, Left, Male	15	16	9	4	3	3	13	0	0	1	IV
NHMV 7149	*U. maritimus*	m1, Right, Male	19	16	13	4	3	5	11	0	0	0	V
NHMV 7148	*U. maritimus*	m1, Left, Female	15	19	10	5	1	2	17	0	0	0	IV
NHMV 7143	*U. maritimus*	m1, Left, Female	20	15	13	7	3	4	11	0	0	0	V
NHMV 14657	*U. maritimus*	m1, Left	14	21	10	3	3	6	15	0	0	0	IV
NHMV 7145	*U. maritimus*	m1, Left	12	44	9	3	1	10	31	0	3	0	IV
NHMV 7794	*U. maritimus*	m1, Right	15	13	8	5	3	7	6	0	0	0	V
NHMV 7144	*U. maritimus*	m1, Left	13	19	6	5	3	5	14	0	0	1	IV
NHMV 7142	*U. maritimus*	m1, Right, Female	18	23	11	5	3	8	15	0	0	0	IV
NHMV 7147	*U. maritimus*	m1, Left	19	12	15	4	1	2	10	0	0	1	IV
NHMV 7138	U. maritimus	m1, Right, Female	17	20	13	3	3	5	15	0	0	1	V
NHMP 2006-415-	U. thibetanus	m1, Right	17	22	19	3	1	4	14	1	3	0	V
ZMB MAM 69401	*U. thibetanus*, Japan	m1, Right	15	19	11	4	1	3	13	0	0	0	V
ZMB MAM 69400	*U. thibetanus*, Japan	m1, Right	13	21	11	2	1	7	14	0	0	1	V
ZMB MAM 69396	*U. thibetanus*, Thibet	m1, Right	15	25	13	2	1	7	17	1	0	1	V
AUThG 1	*U. arctos*, Greece	m1, Left	27	16	19	8	1	4	12	0	0	1	V
AUThW 2	*U. arctos*, Greece	m1, Left	20	14	13	7	1	4	9	1	0	1	V
AUThW 3	*U. arctos*, Greece	m1, Left	22	17	13	9	1	9	6	2	0	1	V
AUThW 5	*U. arctos*, Greece	m1, Right	20	17	13	7	1	4	13	0	0	1	V
NHMV 21491	*U. arctos*, Ukraine, central EU	m1, Left	21	32	19	2	1	2	24	0	6	1	VI
NHMV 51	*U. arctos*, Slovakia, central EU	m1, Left	15	41	12	3	1	5	24	3	9	1	V
NHMV 7146	*U. arctos*, central EU	m1, Left	15	31	7	8	1	11	18	0	2	0	V
NHMV 67919	*U. arctos*, Romania, central EU	m1, Right	17	35	13	4	1	7	20	4	4	1	V
NHMV 4220	*U. arctos* (Europe)	m1, Right, Female	15	35	12	3	1	7	23	1	4	1	VI
NHMV 7396	*U. arctos*, Bosnia, central EU	m1, Right	14	41	12	2	1	5	25	3	8	1	V
NHMV 55276	*U. arctos*, Bulgaria, central EU	m1, Right	23	37	18	5	1	6	21	3	7	1	VI
NHMV 67301	*U. arctos*, Slovenia, central EU	m1, Left	24	39	19	5	1	3	27	1	8	1	IV
NHMV 7793	*U. arctos*, Canada, N. America	m1, Right	17	28	15	2	1	6	17	1	4	1	VI
ZMB MAM 87110	*U. arctos*, America	m1, Right	22	36	16	6	1	8	27	0	1	1	V
ZMB MAM 43594	*U. arctos*, Canada, N. America	m1, Left	17	27	12	5	1	9	16	0	2	1	V

NHMV 40650	*U. arctos*, Kamtchatka, Russia	m1, Left	17	29	13	4	1	6	21	0	2	1	V
NHMV 40624	*U. arctos*, Kamtchatka, Russia	m1, Left	19	25	15	4	1	9	15	0	1	1	IV
NHMV 40633	*U. arctos*, Kamtchatka, Russia	m1, Left	16	35	12	4	1	11	18	0	6	1	V
NHMV 40635	*U. arctos*, Kamtchatka, Russia	m1, Right	17	31	12	5	1	6	21	0	4	0	IV
NHMV 40608	*U. arctos*, Kamtchatka, Russia	m1, Left	20	36	17	3	1	10	22	0	4	1	IV
NHMV 40607	*U. arctos*, Kamtchatka, Russia	m1, Right	24	24	18	6	1	6	10	2	6	1	V
NHMV 40613	*U. arctos*, Kamtchatka, Russia	m1, Left	15	39	13	2	1	10	24	2	3	0	VI
NHMV 40616	*U. arctos*, Kamtchatka, Russia	m1, Left	18	20	13	5	1	5	10	0	5	1	IV
NHMV 40649	*U. arctos*, Kamtchatka, Russia	m1, Left	24	39	20	4	1	19	9	1	10	1	VI
NHMV 40628	*U. arctos*, Kamtchatka, Russia	m1, Left	34	26	26	8	1	12	3	1	10	1	IV
NHMV 40615	*U. arctos*, Kamtchatka, Russia	m1, Right	15	19	11	4	1	8	11	0	0	1	IV
NHMV 40611	*U. arctos*, Kamtchatka, Russia	m1, Left	23	27	18	5	1	6	14	2	5	1	IV
NHMV 40645	*U. arctos*, Kamtchatka, Russia	m1, Left	15	30	11	4	1	4	24	0	2	1	VI
NHMV 40640	*U. arctos*, Kamtchatka, Russia	m1, Right	16	29	12	4	1	5	23	0	1	1	V
NHMV 40636	*U. arctos*, Kamtchatka, Russia	m1, Right	18	30	14	4	1	4	26	0	0	1	IV
NHMV 40630	*U. arctos*, Kamtchatka, Russia	m1, Right	15	28	9	6	1	5	19	1	3	1	IV
NHMV 40609	*U. arctos*, Kamtchatka, Russia	m1, Right	14	29	12	2	1	2	24	0	2	1	V
NHMV 40644	*U. arctos*, Kamtchatka, Russia	m1, Right	14	28	11	5	1	14	12	0	2	1	VI
NHMV 40634	*U. arctos*, Kamtchatka, Russia	m1, Left	28	38	22	6	1	18	2	2	16	1	IV
NHMV 40605	*U. arctos*, Kamtchatka, Russia	m1, Right	27	34	15	12	1	8	18	4	4	1	V
NHMV 40626	*U. arctos*, Kamtchatka, Russia	m1, Right	15	29	11	4	1	8	17	1	3	1	IV