Who peeled the bones? An actualistic and taphonomic study of axial elements from the Toll Cave Level 4, Barcelona, Spain

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Abstract

Equifinality constitutes a challenge when interpreting agency in archaeological sites. The fact that a specific type of damage frequently cannot be linked to a single actor, behavior, or ecological context, handicaps correct interpretations of site formation processes. Actualistic studies have been used to address this type of problem by creating models and analogies to infer the processes that occurred in the past and explain the formation processes of fossil faunas found at archaeological sites. Here, we apply this approach using observational data from Arilla et al. (2014) describing the consumption of ungulate carcasses by wild brown bears (*Ursus arctos arctos*). We focus on a specific type of damage, peeling, which was observed to be one of the most significant modifications of axial skeletal elements of carcasses eaten by bears. This fact was especially relevant because the peeling damage was initially attributed to the feeding activities of primates (humans and chimpanzees—*Pan troglodytes*) and only anecdotally to other taphonomic agents. The observational data are then applied to Level 4 of Toll Cave (Moià, Barcelona, Spain), dated to >49,000 ^{14}C BP, which has been interpreted to be a hibernation lair with significant activity by carnivores and sporadic human presence. Rib and vertebral peeling have also been identified at

Level 4 bone assemblage, casting doubt on the agent responsible for this damage (effector) in the cave. The aim of our study is to address the equifinality problems that involve peeling as a taphonomical signature in archaeological sites, taking the Pleistocene site of Toll Cave as a case study.

Keywords: Actualism; Bear; Pleistocene; Taphonomy; Peeling; Axial bones; Ribs; Toll Cave

1. Introduction

From their supposedly intentionally arranged bones (e.g., Bergounioux, 1958) to their depiction in some of the world's earliest artwork (e.g., Chauvet et al., 1996; Clottes, 2003), ursids, especially cave bears (including the chronospecies *Ursus deningeri* and *U. spelaeus*), have historically played some role in behavioral interpretations of early Eurasian hominins. Indeed, "[s]*cenarios of Neandertal* [*Homo neanderthalensis*] *'cave bear cults', and forced eviction by spear point of giant bears from cave men's homes, continue to hold tremendous popular appeal*" (Stiner, 1998a: 303). Beyond specific research on extinct ursid craniodental functional morphology (e.g., Sacco and Van Valkenburgh, 2004; Figueirido et al., 2009), occlusal dental microwear (e.g., Pinto Llona and Andrews, 2001; Pinto Llona, 2006, 2013; Peigné et al, 2009; Donohue et al., 2013; Münzel et al., 2014; Jones and DeSantis, 2016; Pappa et al., 2019; Peigné and Merceron, 2019; Ramírez-Pedraza et al. in press) and isotope analyses of bulk bone and dental collagen (e.g., Bocherens et al., 1990, 1994, 1997, 2004, 2006, 2014; Fernández-Mosquera, 1998; Fernández-Mosquera et al., 2001; Vila Taboada et al., 1999, 2001; Bocherens 2002, 2003, 2004, 2015, 2019; Richards et al., 2008; Blant et al., 2010; Grandal-d'Anglade et al., 2011, 2019; Münzel et al., 2011, 2014; Pérez-Rama et al., 2011; Horacek et al., 2012; Pacher et al., 2012; Robu et al., 2013, 2017; Trinkaus and Richards, 2013; Krajcarz et al., 2016; Ramírez-Pedraza et al., 2019), most osteological studies of assemblages containing bear remains since the "taphonomic revolution" spearheaded by Binford (1981) and Brain (1981) fall into two main categories: (1) those concerned with assessing the extent to which large ursids were responsible for modifying potential archaeological faunas (e.g., Gargett, 1996; Stiner et al., 1996; Stiner, 1998a, 1988b) or creating purported artifacts (e.g., d'Errico, 1998; d'Errico et al., 1998a,b) and (2) those concerned with the characterization of ursid foraging (e.g., to what extent were prehistoric bears cannibalistic or scavengers) (e.g., Pinto Llona and Andrews, 2002, 2004; Lolliot and Philippe, 2004; Pinto Llona et al., 2005; Quilès et al., 2006; Rabal-Garcés et al., 2012).

These studies were valuable, having shed light on bear paleoecology and behavior. Unfortunately, they were also comparative in nature. Here, we use the term "comparative" as it is defined by Klein and Cruz-Uribe (1984). For Klein and Cruz-Uribe (and like-minded researchers), the comparative approach to faunal analysis involves making controlled comparisons of different paleontological faunas (or within a single paleontological fauna). In other words, interpretations are based on the comparison of one (or more) unknown(s) to another unknown—that is, there are many unknown variables when interpreting taphonomic data.

In contrast, fewer studies concerned with bone modification by ursids have employed an explicitly actualistic approach (e.g., Haynes 1980, 1982, 1983; Domínguez-Rodrigo and Piqueras, 2003, Saladié et al., 2013; Sala and Arsuaga, 2013; Arilla et al., 2014). In our opinion, this alternative type of research has an important advantage over comparatively based approaches because, in contrast to comparative studies, actualistic studies rely on direct observations in the modern world to document the chain of causal relationships between taphonomic actors (in these cases, bears), their actions (feeding), effectors (teeth) and effects (damage to bones) (e.g., Gifford-Gonzalez, 1991). The results of actualistic studies (of known origin) are then effectively used to interpret paleontological or archaeological faunas of unknown origins.

Actualistic studies, which are currently carried out by paleontologically and archaeologically minded researchers, fall into two major categories: naturalistic and experimental. Necessarily, many naturalistic studies are actually quasi-actualistic. Marean (1995: 66), describing this type of modern research as "comparative" (not to be confused with "comparative" in the sense defined by Klein and Cruz-Uribe, 1984), provides an example of its shortcomings compared to the most rigorously conducted actualistic studies, in which each step of the causal chain is observed: "*suppose we take five hyena dens excavated in the last 30 years, study them, and arrived at inferred linkages between trace* [effect] *and actor* [hyena] *with the goal of developing methods to recognize fossil hyena dens…The linkage between trace and actor is inferred: no one actually saw all the bones being accumulated by hyenas. This inference, then, becomes the bridging argument used to identify fossil assemblages as hyena dens*". In the strictest sense, Marean (1995)'s implicit incertitude about these types of quasi-actualistic datasets is legitimate. That admitted, we still believe that quasi-actualistic data can be employed—preferably along with those derived from authentic actualistic studies—to accurately interpret fossil faunas. In many cases, the desired causal chains are all but established in quasi-actualistic datasets, including especially in the body of zooarchaeologically oriented work on modern hyena den assemblages, alluded to by Marean (1995).

Probably more serious than the complexities associated with naturalistic actualistic (NA) approaches are those associated with experimental actualistic (EA) approaches. The way in which a carcass is modified by a consumer/taphonomic agent is contingent on a host of variables, including (but not limited to) the number of consumers involved in feeding, the physical condition and relative hunger of that/those consumer(s), the size of the carcass that is being eaten, and the relative completeness and condition of the carcass (e.g., whole vs partial or disarticulated; fresh versus putrid). Most experimental actualistic studies in paleoanthropology have been conducted on captive or semi-captive taphonomic agents. By their nature, captive studies are highly artificial, skewing the variables mentioned above even more severely than what would be observed under natural conditions. Additionally, it often appears that captive animals suffer more acutely from boredom or behavioral disturbances (e.g., stereotypes) than do wild variants. In the context of bone modification studies, the differential degrees of boredom experienced by captive and wild carcass consumers might underlie the more intense chewing damage evinced on bone samples damaged by the former group compared to that generated by the latter (e.g., Haynes, 1982; Sala and Arsuaga, 2013; Arilla et al., 2014).

Indeed, Gidna et al. (2013: 1903) emphasize the importance of "*environmental contexts to understand[ing] carnivore [i.e., taphonomic agent] behavior and their resulting bone modification patterns*," concluding that "*analogical models based on experiments carried out with captive carnivores may be biased and inadequate as proxies for wild carnivore bone modification behaviors.*" To this point, the contrast between bone modification patterns induced by captive (Saladié et al., 2013) and wild (Sala and Arsuaga, 2013) brown bears (*U. arctos*) is especially instructive. Damage produced by captive subjects is much more intense than that caused by wild bears. The bone damage induced by captive bears is comparable to that created by durophagous mammalian carnivores, such as spotted hyenas (*Crocuta crocuta*)—generating fractures on dense cortical bone, eliminating the epiphyses of long limb bones, and imparting a high density of tooth marks on bones, as well as tooth-marking a large total number of individual bones (Saladié et al., 2013). In addition to the possibility that the differential degree of boredom might be responsible for the contrast between bone samples modified by captive and wild bears, we also note that all extant ursids are omnivorous. Accordingly, their respective dependence on—and interest in—meat and plant foods varies between species, particular populations of various species, and seasons, among other factors (e.g., Purroy and Clevenger, 1991; Mattson, 1997).

To date, studies on the Sima de los Huesos fauna (Sierra de Atapuerca, Spain) represent the only application of the growing body of actualistically based research on ursids to the interpretation of the formation of a fossil assemblage (Sala, 2012; Sala et al., 2014). Other studies, such as that by Fourvel et al. (2014), employ actualistically derived data but utilize those data selectively, still taking a largely comparative approach—in this case, to ascertain whether accumulations of modified cave bear bones were created by bears themselves (cannibalism) or by other large, sympatric carnivorous predators and scavengers (see also, Diedrich, 2009, 2012). In this study, we first present NA data on modifications induced by wild Eurasian brown bears (*U. a. arctos*) on the bones of various ungulate carcasses and then apply our results to the interpretation of the Level 4 (MIS 3) fauna from Toll Cave (Barcelona, Spain) —the formation of this assemblage is hypothesized to be the result of ursid hibernation activities, with very minor input from hominins (Rosell et al., 2014, 2017; Ramírez-Pedraza et al., 2019). In addition, the Level 4 fauna includes 33 rib specimens (10 from *U. spelaeus*) and 7 vertebral specimens (6 from *U. spelaeus*) that display peeling damage. Peeling damage—where strips of cortex have been removed from a bone's surface—can occur on any category of bone but is prominently observed on the ribs of animals that were consumed by modern humans (*H. sapiens*) or chimpanzees (*Pan troglodytes*) (e.g., White, 1992; Pickering and Wallis, 1997; Fernández-Jalvo and Andrews, 2011; Pickering et al. 2013), bears (*U. a. arctos*) (Arilla et al., 2014; Rosell et al., 2019), and sporadically foxes (*Vulpes vulpes*) (Arilla et al., 2019). In contrast, peeling has not been observed on rib specimens in several (actualistically derived) faunas created by non-primate taphonomic agents, including spotted hyenas (*Cr. crocuta*), wolves (*Canis lupus lupus*), domestic dogs (*Ca. l. familiaris*), African hunting dogs (*Lycaon pictus*), and leopards (*Panthera pardus*) (Pickering et al., 2013). Pickering et al. (2013) never claimed that rib peeling was exclusively attributable to the actions of primates, but these researchers did conclude that this type of damage is rare enough in non-primate produced faunas and common enough in human-produced ones that it "*appear[s] to be diagnostic of hominoid/hominin behavior*," especially when observed in association with other human-produced damage, like stone tool butchery marks.

In this actualistically based context, it is tempting to implicate hominins for the production of peeled bear ribs (and vertebrae) from Level 4 of Toll Cave, especially given the trace evidence of hominin presence in the level. Extending this allegation leads to the tantalizing, but not novel (e.g., Bächler, 1928, 1940; Gabori-Csánk, 1968), hypothesis that Neandertals killed, butchered and ate (probably hibernating) cave bears. This hypothesis will be proven false if the following are demonstrated: (1) that extant *U. a. arctos* is suitable for modelling the taphonomic potential of extinct cave bears (see Materials and Methods) and (2) that *U. a. arctos* is capable of creating—and naturally does create—rib and vertebral peeling that is identical and occurs at comparable frequencies to that produced by the actions of primate taphonomic agents. The demonstration of these points, combined with the otherwise low-level cultural and archaeological imprint of hominins in Level 4, could effectively exclude the possibility that Neandertals were significant taphonomic actors during the accumulation of the Level 4 fauna, as well as weaken the support of a broader Neandertal bear-hunting hypothesis.

2. Materials and Methods

2.1. Archaeo-paleontological sample: Toll Cave Level 4 fauna

Toll Cave is in the proximity of Moià, a town located 50 km north of Barcelona (Spain). Toll Cave is part of the Coves del Toll karstic system, which comprises several galleries that are >2 km in length and at an elevation of 760 m a.s.l. The South Gallery, situated in the entrance of Toll Cave, houses a Late Pleistocene to Holocene sedimentary sequence, ~9 m in depth, of considerable archaeo-paleontological significance that was partially excavated in the 1950s and 1970s. The previous excavations consisted of a succession of stratigraphic pits made at regular intervals along the entirety of the South and East Galleries. Pits A and B occupied the entire entrance area. The other pits (until Pit Z) had smaller dimensions (between 4 and 2 m^2). These excavations revealed a stratigraphic sequence dominated by a succession of sands and clays of fluvial origin, which demonstrate the significant relationship between the cave and the hydric system of the zone (the "Bassot and Mal" Torrents). Several occupations from the Bronze Age and Neolithic were identified at Level 1 (Bergadà and Serrat, 2001). Level 2, composed of thick sands and small limestone gravels, corresponds to an erosive period, probably related to the later Pleistocene or the early Holocene. No archaeo-paleontological remains were recovered in this layer. Level 3 and Level 4 have a similar composition, a combination of carbonated and red clays. Building on previous research in the area (Serra-Ràfols et al., 1957), we have focused our recent work on the upper strata of the sequence (Bergadà and Serrat, 2001), with Level 4 as the deepest unit excavated to date, revealing a surface area of more than 20 m^2. Biochronological results (Fernández-García and López-García, 2013) place Level 4 in the Late Pleistocene (MIS 3). More recently, some samples were sent for AMS dating, which showed that Level 3 ranges between 46,660 and 45,900 cal BP at 68.2% probability and that Level 4 is outside the ^{14}C range (>49,000 ^{14}C BP). Only one bone of a large-sized mammal was dated earlier, at max 49,860 cal BP at 68.2% probability (Ramírez-Pedraza et al., 2019).

The South Gallery from Toll Cave was interpreted by the first researchers as a hibernation place for cave bears because of the high number of remains attributed to *Ursus spelaeus* (Serra-Ràfols et al., 1957). This interpretation was maintained in subsequent studies, which determined that the main function of the cave during the formation of Level 4 was as a hibernation den for cave bears, which engaged in both cannibalism and the scavenging of other bear carcasses. The cave, however, was also used by other large carnivores, as is demonstrated by fossil remains of hyenas, lions, and wolves. Some remains of herbivores (mainly horses, aurochs, and red deer) seem to have been transported into the cave by these non-human predators that probably also scavenged the pre-existent faunal set (bears carcasses) (Rosell et al., 2014; Ramírez-Pedraza et al., 2019). Human presence is attested by a few lithic tools [a flake of chert, a discoid core, a flake and three fragments of limestone, and two fragments of quartz; Picin et al. (2020)] and 17 cut-marked bone specimens (including 10 from *U. spelaeus* and 7 from other variously sized animals).

The taphonomic study of Toll Cave Level 4 presented here included the observation of bone surface damage generated by both non-human and human agents on faunal specimens recovered in fieldwork seasons between 2010 and 2013. Our results focus solely on the axial skeletal elements –ribs and vertebrae [sacrum and sternum included], because our aim here was to ascertain the responsible agent that produced the rib and vertebral peeling. A total of 1491 fossil specimens were analyzed, of which 370 belonged to the axial skeleton (see section 3.1 for details). Identification was guided by standard zooarchaeological and taphonomic criteria and methods (e.g., Maguire et al., 1980; Binford, 1981; Brain, 1981; Shipman and Rose, 1983; Blumenschine et al., 1996; Lyman, 2008). All bone specimens were examined under a stereomicroscope using magnifications up to 110x. Selected bone specimens were also analyzed using an analytical FEI QUANTA 600 Environmental Scanning Electron Microscope (ESEM) and a KH-8700 3D digital microscope. Different types of cut marks were detected, and characteristics, such as location on the bone surface and morphology, were taken into account to associate the damage with specific butchery activities (e.g., Shipman and Rose, 1983; Lyman, 2008). The presence/absence of anthropogenic bone breakage was also registered (e.g., Pickering and Egeland, 2006; Capaldo and Blumenschine, 1994; White, 1992; Pickering et al., 2013). We identified carnivore damage using the criteria described by Maguire et al. (1980), Binford (1981), and Blumenschine and Selvaggio (1988) and compared this damage with published arguments regarding the revision of the criteria for distinguishing between tooth-marks and other alterations (Blumenschine et al., 2007; Galán et al., 2009).

2.2. Is *U. arctos* a reliable referent for inferring the taphonomic potential of *U. spelaeus*?

Ursus arctos has a broad global distribution, including parts of Europe, Asia, and North America, but it occupies relatively small, discontinuous ranges (McLellan et al., 2008). Numerous behavioral observations and isotopic studies agree that *U. arctos* is omnivorous. It is not our intent to review these studies here. Rather, our aim is to establish that, with regard to bone-modifying potential, extant *U. arctos* can serve as an effective referent for extinct *U. spelaeus*. In their study of extant ursid craniodental functional morphology, Sacco and Van Valkenburgh (2004: 41) diagnosed *U. arctos* as a trophic carnivore (in addition to its taxonomic classification as a member of the Order Carnivora), "*distinguished by, among other features, molar size reduction, flexible mandibles and, most surprisingly, relatively small carnassial blades*". This means that extant brown bears lack the "*well-developed craniodental adaptations that enhance muscle leverage and dental function*" and instead seem to exploit the "*disparity in body size between* [themselves] *and their* [smaller] *preferred prey…* [by relying] *on muscular strength to process kills…*" (Sacco and Van Valkenburgh, 2004: 49).

Extinct *U. spelaeus* was, on average, only slightly larger than *U. arctos* (Christiansen, 1999). However, there are significant differences between the species in other morphological details. Most apparent among these differences is the retention of a "typical" ursid dental formula in *U. arctos* of 3.1.4.2/3.1.4.3, whereas most known *U. spelaeus* skulls that retain full dentitions show a formula of 3.1.1.2/3.1.1.3 (but see, Nagel et al., 2005). Typically, cave bear skulls (unlike those of extant brown bears) also display a "domed" frontal region in profile, as well as broad, prominent sites for the attachment of large temporal and masseter muscles (e.g., Kurtén, 1976; Grandal-d'Anglade and López González, 2005). The "dry skull" method of bite force analysis confirmed what was inferred from consideration of the robust construction and conspicuous muscle attachment sites of cave bear skulls—that this extinct species had a lower bite force in the upper carnassials than large cats (similar to that of the giant panda) and a higher bite force than polar bear, consistent with a primarily herbivorous diet (Grandal-d'Anglade, 2010). A geometric morphometric analysis of the cave bear skull (van Heteren et al., 2014; see also, Mazza et al., 1995; Mattson, 1998) agrees with this dietary conclusion. Similarly, the majority of isotopic studies of central and western European cave bear fossils show that *U. spelaeus* $\delta^{15}N$ values plot the same as or lower than the values yielded by strict herbivore fossils recovered from the same sites (e.g., Bocherens et al., 1994, 2004). In the case of Toll Cave, the stable isotopes analysis shows that the diet of *U*. *spelaeus* is similar to its diets at other European sites of the Late Pleistocene with only some differences in the $\delta^{13}C$ values, which are probably related to the local vegetal landscape at different altitudes. However, the tooth microwear patterns of the cave bear from the same site are like those of extant omnivorous and carnivorous ursid species, suggesting dietary flexibility and abilities to shift toward a more omnivorous diet (Ramírez-Pedraza et al., 2019).

We do not think that apparent morphological and trophic differences between *U. arctos* and *U. spelaeus* listed above disqualify the former as a suitable referent for modelling the taphonomic potential of the latter. First, the isotopic analysis of Late Pleistocene cave bears remains from Peştera cu Oase (Romania) revealed that that these individuals were omnivorous (Richards et al., 2008; see also, Hilderbrand et al., 1996) and were likely to have at least occasionally consumed the flesh of conspecifics (Quilès et al., 2006). Second, the results of a recent occlusal microwear analysis of cave bear teeth from northern Spain indicated that they are "*consistent with* [damage patterns resulting from] *bone consumption*" (Pinto Llona, 2013: 49). Finally, Mazza et al. (1995) demonstrated that extant brown bears and extinct cave bears share similar origins and insertions of their chewing musculature onto the skull. As a result, it is reasonable to conclude that the two taxa exert(ed) masticatory forces along comparable planes, with an emphasis on vertical loading of food items.

In summary, *U. arctos* is obviously not an exact match for its prehistoric congener *U. spelaeus*. But, based on both phylogenetic proximity and functional morphological continuities, the former provides the most reasonable extant referent for modelling the taphonomic potential of the latter.

An interesting issue of discussion is the apparent common wintering context in the cases of cannibalistic scavenging identified for cave bear fossils (Kurtén, 1976) because such scenarios do not seem to be the norm in brown bears (see, for example, García Vázquez, 2015; Grandal et al., 2019). Starvation was probably the main cause of death for bears, especially for cubs, older bears, and/or those that failed to store sufficient reserves of energy before the onset of winter (e.g., Rogers, 1981, 1987; Stiner, 1998a; Rabal-Garcés et al., 2012). The key point here is that cave bears could have hibernated together with other conspecifics, which would have allowed them access to the carcasses of individuals that did not survive the lethargy process. This hypothesis could explain the Pleistocene deposits with high rates of individuals and gnawing damage by bears and/or other large carnivores (e.g., Stiner, 1998a; Pinto Llona and Andrews, 2002, 2004; Pinto Llona et al., 2005; Rabal-Garcés et al., 2012). Moreover, the time factor related to the formation of bone assemblages cannot be forgotten because a slow sedimentation rate could have led to a significant accumulation of cave bear specimens that *a priori* could be misinterpreted as synchronous. Linked to this, it is also worth highlighting the existence of large numbers of beds or *bauges* on the same cave floors, as if several individuals had co-hibernated in a kind of "collective dormitory" (e.g., Philippe and Fosse, 2003; Quilés et al., 2006). Although it is not easy to demonstrate at the archaeological level whether several individuals simultaneously inhabited the cave, some studies based on mitochondrial DNA (mDNA) and isotopic values ($\delta^{13}C$ and $\delta^{15}N$) suggest that cave bears "*formed stable maternal social groups, at least for the purpose of hibernation*" (Grandal et al., 2019: 436; see also Fortes et al., 2016). This behavior seems to not be present in brown bears –either in fossils or in present day samples– as they are mostly solitary, and therefore, having access to the carcasses of their dead conspecifics should not be considered as a regular occurrence in their behavior (e.g., García Vázquez, 2015; Grandal et al., 2019). Nevertheless, evidence of the re-use of winter beds, as well as groups of beds on small, rocky, and inaccessible areas, has been observed in current brown bears in the Cantabrian and Pyrenees mountains (Naves and Palomero, 1993; Fosse et al., 2004; Palomero et al., 2011). From a taphonomical approach, cannibalistic scavenging in caves or karstic traps might reproduce a similar or equivalent context as that observed in open-air areas because complete carcasses are available. In these cases, the consumption sequences might follow standard patterns and/or leave specific damage on bones (likely with varied intensity, depending, for example, on the season or predation pressure in the environment), which we have explored in our observational series with Pyrenean *U. a. arctos* and applied to the karstic context of Level 4 of Toll Cave.

2.3. Modern naturalistic actualistic samples

2.3.1. Modern brown bears, the Spanish Pyrenees

During our naturalistic observations in the field, the controlled population of brown bears in the Catalan Pyrenees, Spain, was composed of 25–30 individuals, half males and half females. The largest individual was a male called Pyros, aged 25, weighing between 230 and 270 kg, depending on the season. These specimens came from Eastern Europe, mainly from Slovenia, and were stepwise reintroduced into this area in 1996 through a project known as "Life Project". This project was initiated after an agreement between the European Union and the Governments of France, Catalonia, and Aragon. The main aim was to recover endangered wildlife in the Pyrenees, focused mainly on the brown bear and bearded vulture. Our work, conducted from 2010 to 2013, on this reintroduced population was facilitated by and carried out in collaboration with a bear monitoring team from the Conselh Generau Val d'Aran (Aran Valley's Council) and DAAM (Department of agriculture, livestock, fish, food and environment of the Catalan Government) of the Generalitat de Catalunya, funded by the Ministry of Agriculture, Food and Environment of the Spanish Government.

Photo- and video-traps were used to collect observational data on the consumption of 17 complete ungulate carcasses (1 *Equus caballus*, 1 *Bos taurus*, 4 *Cervus elaphus*, 1 *Capra hircus*, 3 *Capreolus capreolus*, and 7 *Ovis aries*) by at least 6 different free-ranging bears. Table 1 summarizes the taxonomic distribution, broad ontogenetic developmental stage (i.e., infant, juvenile, adult), and the number and type of bears that fed on any individual carcass [for more details, see Arilla et al. (2014)].

We considered the ungulate carcass weight when conducting our analysis. The carcass sample was divided into three size categories: large (300–1000 kg; *Bos* and *Equus*; individuals=2), medium-sized (100–300 kg; *Cervus*; individuals=4), and small (<100 kg; *Capreolus*, *Capra*, *Ovis*; individuals=11). For each carcass, we also generated taphonomic data to complement the feeding observational data. Using the phototraps, we were able to monitor each carcass until we determined that the bears had lost interest in feeding on it further (lack of revisits) (see details in

Arilla et al., 2014; Table 1). We subjected each bone specimen to stereomicroscopic, ESEM, and 3D digital microscope analyses identical to those described above for the archaeological bone specimens from Level 4 of Toll Cave.

2.3.2. Modern humans and captive chimpanzees

Two samples of ungulate ribs modified by the feeding activities of modern human pastoralists (Khoikhoi, Namibia) served as additional actualistic datasets to which the modern brown bear and Toll Cave Level 4 bear rib specimens were compared. Peeling data from captive chimpanzees (USA) were also collected but not used in our statistical analysis because no combination of bone modifications was provided –alterations were listed and described individually (Pickering and Wallis, 1997; see section 2.4). These modern primate-derived samples have been studied previously, with many associated publications; they were selected for this study because of their high incidences of rib peeling damage (Brain, 1981; Pickering and Wallis, 1997; Fernández-Jalvo and Andrews, 2011; Pickering et al., 2013). In summary, the finding of these studies that is the most relevant to the present study was the identification and definition of three distinct rib peeling "types" that can result from the feeding activities of highly manipulative primate consumers of ungulate carcasses.

2.3.3. Types of axial element peeling

White (1992) was the first author to describe classic peeling: "*with classic peeling, layer(s) of lamella(e) is/are missing in strip(s) from the rib's dorsal, ventral or both cortices…Classic peeling can occur at various points along a rib's length but is commonly observed at the sternal terminations of short fragments of the vertebral ends of ribs*" (Pickering et al., 2013: 291). "*With general peeling, an area of the whole dorsal or ventral cortex of a rib is peeled backed for some length, revealing the internal trabeculae of the rib*" (Pickering et al., 2013: 1299). Incipient peeling is related to the "bent rib ends," described by Fernández-Jalvo and Andrews (2011); it is "*a type of peeling where a strip(s) of lamaella(e) is/are only partially peeled back against the rib shaft, not fully removed from the specimen*" (Pickering et al., 2013: 1300). Pickering et al. (2013) proposed that incipient peeling is more a function of the simple splitting apart of the dorsal and ventral cortices in ribs once they become frayed by chewing or breaking back. Thus, unlike classic and general peeling, incipient peeling is more a consequence of the intrinsic physical properties of an affected rib than of any taphonomic force(s) applied to it. For this reason, we provide data on incipient peeling separately in this study and exclude incidences of this type of alteration from our statistical analyses and discussion in order to focus solely on classic and general peeling, from here lumped together as simply peeling.

2.4. Statistical analysis

Given that bones modified by bears have no human-imparted marks, we carried out the human-bear comparative analysis excluding combinations of factors in variables that included cut marks. If we include cut marks, the bone assemblages, which exhibit peeling by both agents, can be clearly separated with almost 100% accuracy. By excluding cut marks, we used the combination of categories indicated in the first part of Table 2—namely, no modification, fractures, peeling, tooth marks, fractures plus peeling, and combinations of tooth marks with fractures or peeling or the three modifications (fractures, peeling, tooth marks) occurring together on the same bone. With these bone surface modifications (and their combinations), we start from the assumption that an array of traits helps in the identification of a taphonomic agent.

Although the human assemblage was composed of small carcasses exclusively, the actualistic assemblage included bones from large, medium-sized, and small carcasses. For this reason, we created two general agency categories (humans and bears) and four analytical categories (humans and bears feeding on small, medium-sized, and large carcasses). Because our statistical analysis was based on damage combinations, data from captive chimpanzees were excluded.

Data were analyzed combining three different types of tests. First, a combination of the Chi-square test and Fisher test was used. The Fisher test was used because it is recommended for contingency tables that have missing data and fields where n<10. For the Fisher test, a simulation of p-values was performed using a Monte Carlo method, as recommended for contingency tables larger than 2x2. Default simulation consisted of the conditional on the rows and the marginal on the columns, provided the marginals were positive (Patefield, 1981). A total of 1–7 simulations were carried out.

As a complement, a bootstrapped correspondence analysis (CA) was performed on the contingency table. This was done using R´s "cabootcrs" library. This library creates a CA where variable levels appear in Euclidean space in a double graph: one for columns and another for rows.

In each case, elliptical 95% confidence regions for column and row points indicate the similarities of variable categories.

3. Results

3.1. Toll Cave Level 4 fauna

Level 4 includes 1491 fossil remains (seasons 2010–2013), with 604 of these specimens being identified to the species level (40.51%). The faunal assemblage includes 13 taxa and 35 individuals (Table 3). The minimal number of individuals (MNI) was calculated primarily from dental pieces. Cave bear (*Ursus spelaeus*) was the main taxon, representing almost 90% of the identified specimens (NISP=524 of 604 or 86.75%; MNI=19 of 35 or 54.29%). The remaining species were represented by few remains (NISP<18) and one or two individuals. Spotted hyena (*Crocuta crocuta*, NISP=2, MNI=2) and small-sized carnivores, such as fox (*Vulpes vulpes*, NISP=3, MNI=1) and wildcat (*Felis silvestris*, NISP=2, MNI=1), were also present, together with some ungulates, such as horse (*Equus ferus*, NISP=13, MNI=2), red deer (*Cervus elaphus*; NISP=10, MNI=2), auroch (cf. *Bos primigenius*; NISP=6, MNI=1), roe deer (*Capreolus* cf. *capreolus*; NISP=9, MNI=1), and rhinoceros (*Stephanorhinus* sp., NISP=3, MNI=1). In addition, we recovered 18 bone fragments belonging to two individuals of Leporidae, and four that were attributed to one unidentified bird. Although the results for the estimated age at death of the individuals suggest the presence of all age groups, with a predominance of adults (MNI=17 of a total of 35 specimens; 48.6%), infantile animals were present in high proportions (MNI=11; 31.43%). The minimum number of elements (MNE) was 534, and this was primarily represented by ribs (*n*=136), phalanges (*n*=68), vertebrae (*n*=55), and mandibles (*n*=52). Axial bones account for 35.8% of the anatomical profile. In contrast, scapulae (*n*=3) and radii (*n*=5) were the least represented, mainly in bears, followed by humeri (*n*=9), ulnae (*n*=10), femuri (*n*=10), and tibiae (*n*=11).

We detected cut marks (Table 4; Figure 1) and identified incisions on 17 faunal specimens (1.34%, with respect to total number of bone fragments; teeth excluded). Few skeletal elements of the carcasses exhibited cut marks, with 11 occurring on ribs (64.71%). Among the recovered remains according to species and body size classes, bears (NSP=10 of 524 bear bones recovered; 1.91%) displayed the highest proportions of cut-marked bones. We documented several activities on the basis of the morphology, placement, and distribution of cut marks over the bone surface: we detected skinning on one phalanx two of a bear digit, defleshing on 10 bone fragments (five ribs—

vertebral side, one vertebra, three metadiaphyses/shafts of long bones, and one flat bone fragment), and visceral removal on six sternal sides of ribs (four belonging to bears, one to a medium-sized animal, and one to a small-sized animal). We did not identify any anthropogenic bone breakage in the form of percussion notches (evidence of marrow extraction) at Level 4.

We registered tooth-marks and structural damage on 279 bone remains (21.88%, teeth excluded; Figure 2): *Ursus spelaeus* (*n*=94), *Bos primigenius* (*n*=2), *Capreolus* cf. *capreolus* (*n*=5), unidentified carnivore (*n*=1), *Cervus elaphus* (*n*=2), *Equus ferus* (*n*=1), Leporidae (*n*=4), large-size (*n*=57), medium-size (*n*=53), small-size (*n*=54), and unidentified bones (*n*=6). With regard to skeletal elements, ribs (*n*=78), unidentifiable long bone shaft fragments (*n*=49), vertebrae (*n*=26), and flat bones (*n*=25) constituted 63.8% of the alterations (axial bones accounted for 37.3%). Pits and scores were the most common tooth marks, with 84 and 44 remains, respectively. Pits located on cancellous tissue did not exceed 8.1 mm in length and 7.9 mm in breadth, and those placed on dense cortical bone ranged from 1.7 to 7.8 mm in length and from 1.2 to 6.5 mm in breadth. We also documented carnivore breakage in the form of crenulated edges (*n*=78), crushing (*n*=3), fractures and longitudinal cracks (*n*=44), and diaphyseal cylinders (*n*=7). We also registered other alterations, such as pitting (*n*=19), digestion (*n*=21), furrowing (*n*=21), and scooping-out (*n*=12).

In addition, we identified peeling on ribs (*n*=33) and the transverse and spinous process of vertebrae (*n*=7) (Figure 3). We primarily registered peeling on the ends of ribs (*n*=28; 11 of bear), although we also located five uneven surfaces with stepped layers of lamellae on the necks of ribs belonging to bears (*n*=3) and to large (*n*=1)- and small (*n*=1)-sized animals. It is important to note that these specimens attributed to body size categories might correspond to adult (large size) and young (medium and small sizes) bears, but the lack of taxonomical requirements prevented us from making a more accurate attribution. Classic peeling was the most represented type, although incipient peeling was also present on ribs in the form of crushed and cracked edges with a fringed appearance (fraying). This type was often combined with bent ends, which leave a curved shape. Vertebrae showed peeled surfaces on transverse processes and, in the case of two atlases of bear, on the area situated between the anterior tubercle and the transverse process. Damage located on transverse processes was observed at their ends, independent of side and surface. Altogether, 10.81% of axial bones recovered at Level 4 show peeled areas (NSP=40 of 370 axial fragments). In addition, one scapula of a large-sized animal displayed peeling on the infraspinous fossa (caudal angle), together with three flat bone fragments of medium and small sizes (Table 5).

3.2. Modern brown bears, the Spanish Pyrenees

3.2.1 Behavioral observations

From the data collected in images, the consumption process seems to begin at the lower belly, and during this action, the bears use their forepaws continuously to break the ribs and more easily access the viscera contained in the thoracic cavity. Only in a case involving a large-sized carcass (cow) and a large bear did this process begin at different parts of the skeleton, including the neck, abdomen, and lower belly. Damage to ribs seems to occur from three movements, which are not exclusive of each other (Figure 4): (1) the bear steps on top of the ungulate ribcage and presses until fracturing it, (2) the bear opens the ribcage, expanding the ribs with its forepaws, and (3) the bear bites the ends of the ribs and breaks them with sudden and abrupt head movements, using its forepaws top help. During this process, a large portion of the vertebrae (both transverse and spinous processes) can also be affected.

As Sala and Arsuaga (2013) observed, the transport of carcasses was rare. The absence of the regular movement over a long distance of the carcasses may be related to two main phenomena, apart from the possible detection of human elements nearby (smells and infrared cameras): (1) bears are generally solitary animals and do not compete with members of their pack to access the best parts of carcasses, unlike what occurs among the social carnivores that usually follow an hierarchical order during the dividing up of the carcass (Pinto Llona et al., 2005), and (2) currently, there is virtually no predation pressure in the Pyrenees for bears, and the consumption of a carcass (especially in cases of scavenging) extends in time beyond what would be natural in a context with a higher rate of competition.

After the consumption of the viscera, a slight interest in fat was also documented. This interest manifested as the furrowing and crushing of the proximal epiphysis of the humerus, femur and tibia, distal femur, and some vertebrae bodies. These changes were also observed by Sala and Arsuaga (2013) on the same skeletal parts. No regular access to marrow was observed, and therefore, the breakage of long bones and/or presence of shaft-cylinders were not documented. These data contrast with those reported by Lolliot and Phillipe (2004) at Balme à Collomb (Savoie, France), where large numbers of broken femurs were detected (56.6%). Occasionally, fractures on the spinal column were observed on the lumbar vertebrae to access the spinal marrow. There was a similar action on the cervical vertebrae when bears separated the skull from the axial skeleton for the same reason (access the spinal marrow). Thereafter, the bears seemed to stop accessing the carrion between a period covering 1 week and less than 2 months depending on the season and age of the bear (see Table 1).

The majority of the damaged carcasses were in spring and summer, and we observed no modifications in animals in autumn and winter (Arilla et al., 2014). Perhaps because the Pyrenean forest is so rich with vegetable food resources (including fruits, nuts, and mushrooms) in the autumn and because brown bears hibernate through winter, the consumption of large vertebrate carrion peaks in spring (Braña et al., 1988; Clevenger and Purroy, 1991; Clevenger et al., 1992, 1997; Naves et al., 2006). The Pyrenean forest provides a high diversity and quantity of vegetable resources in autumn, which might satisfy the nutritional requirements of these animals, and therefore, it is possible that carrion is often rejected, at least during the period that relates to the present study.

Most of the carcasses consumed by bears were characterized by the preservation of the skeleton in an anatomical or semi-anatomical position. Nevertheless, the action of small scavengers (e.g., foxes, martens, vultures, bearded vultures) or other natural processes (e.g., water flow) caused the spread of some bones within a rate of 50 up to 250 m^2 [Observations (OBs) 4, 5, 6, 7, and 17; Arilla et al. (2014)].

3.2.2. Peeling (and associated damage) on axial bones

We recovered 646 bones belonging to the axial region in our observational series (61% of expected bones): 68 of large size (23 ribs, 45 vertebrae), 166 of medium size (77 ribs and 89 vertebrae), and 412 of small size (187 ribs and 225 vertebrae) (Table 6). We identified damage produced by brown bears on 459 axial bones, accounting for 71.05% of recovered specimens (Figure 5). The data showed that the bulk of bone modifications clustered on lumbar vertebrae (80 of 86 recovered had alterations), yielding percentages between 91.8% in small and 100% in large ungulates. Thoracic vertebrae showed high damage values in large animals (86.36%; *n*=19 damaged of 22 recovered bones) as did the cervical vertebrae in medium-sized ungulates (85.71%;

n=18 of 21 recovered). With regard to ribs, 73.17% (*n*=210 of 287) displayed alterations, with higher slightly percentages in the large-sized category (78.26%). Caudal vertebrae showed the lowest values, with only one damaged specimen. All the sacra of large- and medium-sized ungulates were damaged. Five sacra of small-sized mammals showed alterations (62.5%) (Table 6).

Transversal fractures were the most common alteration observed in the actualistic samples (*n*=214; 33.13%). Among broken axial bones, lumbar vertebrae showed the highest proportions, with 100% (*n*=6) of recovered items damaged for the large-sized category and 68.42% (*n*=13) of recovered items damaged for the medium-sized category. We usually observed transversal fractures on the distal part of the spinous and transverse processes. In contrast, longitudinal cracks and furrowing on vertebral bodies were less well represented in the samples, with 11 (1.7%) and 19 (2.94%) modified items, respectively. Tooth-marked (pits, punctures, and scores) bones composed 22.14% of the recovered axial specimens (*n*=143). After fractures, tooth-marking corresponded to the most common type of documented damage, followed by peeling (*n*=132; 20.43%). Pits and scores were primarily located on the sacra of small-sized (*n*=5; 62.5%) and on the mid-distal shaft of ribs of large-sized (*n*=13; 56.52%) animals. In contrast, we registered no tooth-marks on the sacra of large- and medium-sized animals. We detected crenulated edges on 6.35% of recovered bones (*n*=41). These alterations were mainly located on the spinous process of vertebrae (*n*=22; 78.57%). We also observed crushing on 103 remains (33.13%), and this was primarily located on the sacra and cervical vertebrae of medium-sized animals, with percentages between 66.67% (*n*=2) and 52.38% (*n*=11). This modification was scarcely present on the body of thoracic vertebrae (*n*=4; 4.76%) and was absent from the caudal vertebrae and sacrum of large-sized animals (Table 7).

Classic and incipient peeling was identified on 132 specimens (20.43% of axial bones recovered; Figure 6). We observed classic peeling on 74 bones, primarily on lumbar vertebrae (*n*=31; 36.05%). These elements showed ragged and uneven surfaces, with stepped layers of lamellae on the transverse process in 96.77% (*n*=30) of the recovered lumbar vertebrae. Although we observed peeled areas on the vertebral and sternal surfaces of transverse processes, 90.32% (*n*=28) were registered on the vertebral side. We observed only one case of classic peeling on the spinous process (3.23%) and three on the sternal surface (9.68%) in small-sized animals. On the contrary, thoracic vertebrae exhibited damage on the spinous process (*n*=10; 83.33%). As for the ribs, those attributed to small-sized animals showed the highest percentages (*n*=22; 11.76%). We detected this type of modification on both vertebral and sternal surfaces in a more balanced manner than we observed in the previous cases. Despite this, the vertebral surface showed the highest proportion, with 80% of peeled ribs. This damage was primarily detected between the middle region and the end of ribs (*n*=27; 90%); only two specimens showed peeled areas on the neck zone. Regarding incipient peeling, 58 bones exhibited this damage. We identified incipient peeling on the ribs of medium- and small-sized ungulates, with percentages between 23.38% (*n*=18) and 17.11% (*n*=32), and on the lumbar vertebrae of small-sized animals, with a percentage of 11.48% (*n*=7). This type of alteration was absent on cervical and caudal vertebrae, as well as on the sacrum and sternum, and it was practically absent on thoracic vertebrae (only one specimen showed incipient peeling on the spinous process; 0.95%). Incipient peeling was predominantly in the areas located between the mid-shaft and end of ribs (*n*=48; 96%) and on the vertebral surface (*n*=41; 82%); only two ribs (4%) showed peeled areas on the necks, and nine showed them on sternal surfaces (18%). Peeled areas in lumbar vertebrae were detected on the transverse process. Although we detected this damage on both vertebral and sternal surfaces, the damage was predominantly located on the vertebral sides (*n*=5; 71.43%). Peeled bones also showed some associated bone alterations (*n*=39; 29.32%), such as crenulated edges on the distal shaft of ribs (*n*=2); transversal fractures on mid-shafts, distal ends, and to a lesser extent, necks of ribs (*n*=7); transversal fractures on the spinous process of thoracic vertebrae (*n*=1) and on the spinous, transverse, and mammillary processes of lumbar vertebrae (*n*=12); crushing on the head and distal shafts of ribs (*n*=4) and on the spinous processes of lumbar vertebrae (*n*=2); longitudinal cracks on distal shafts of ribs (*n*=3); and furrowing on the body of one thoracic vertebra (Table 8).

Peeling induced by brown bears was not only documented on axial bones; two scapulae of *Capra hircus* also showed this alteration on the proximal and distal parts of the spinous process. Both specimens showed associated damage, in the form of crushing and one with a crenulated edge, on their infraspinous fossa.

3.3. Modern humans and captive chimpanzees

3.3.1 Modern humans

Although the two samples generated by the Khoikhoi modern human pastoralists and compiled by Brain (1981) have been analyzed by several researchers (Pickering and Wallis, 1997; Fernández-

Jalvo and Andrews, 2011; Pickering et al., 2013), here, we used the data from the study by Pickering et al. (2013), which are the most exhaustive. This work includes 29 ribs from Soutrivier Valley and 163 from Gobabeb. All of them correspond to goat (*Capra hircus*) and, therefore, to small-sized ungulates. Most of them display different types of damage (only five from Gobabeb were left intact after the processing and consumption of the carcasses). The most common type of damage was generated by tool use. Therefore, the number of cut-marked bones (isolated cut marks or in association with other modifications) is high (120 cut-marked ribs *vs* 72 no-cut-marked ribs). More than 76% of the ribs show transverse fractures (alone or with other types of damage). Moreover, the authors noted the presence of tooth marks in 108 of the cases (56.25%).

Regarding classic/general peeling, this modification was observed in 129 cases, which represents 67.19% of the ribs. Peeling was always observed in association with other modifications; thus, there were no ribs that exclusively showed peeling. The most common types of damage were peeled ribs with tooth marks and fractures, both with cut marks (30.2% of the peeled bones) and without cut marks (27.1%). Cut-marked ribs with peeling and transverse fractures were also common (20.9%). The other combinations were less frequent. Most of the peeling was produced on the sternal side of the ribs (68.1%). Nevertheless, the vertebral side was also affected (31.9%). At this point, caution is warranted, and it is important to consider whether tool use could have affected other taphonomic modifications like peeling.

3.3.2 Chimpanzees

Bone damage caused by chimpanzees was studied by Pickering and Wallis (1997). These authors used four captive groups of chimpanzees: one from the Tulsa Zoo in Oklahoma and three from the Southwest Foundation for Biomedical Research (SFBR) in San Antonio, Texas. All of these groups were stocked with partially disarticulated limb bones of goats and several ribs of cattle, except one of the groups from the SFBR received only limb bones of goats. Classic/general peeling was observed only on ribs (n = 13; which represents 18.05% of the ribs), mostly in addition to shallow tooth marks.

Plummer and Stanford (2000) also detected peeling generated by chimpanzees from the Gombe National Park (Tanzania). This study consisted of a taphonomic analysis of the recovered remains of five red colobuses (*Colobus badius*) that were captured and consumed by these chimpanzees.

The authors observed peeling in 2 of the 28 ribs recovered. Unfortunately, the authors provided few details about this specific modification. Something similar was observed by Pobiner et al. (2007) with chimpanzees from Ngogo (Kibale National Park, Uganda). In this case, the authors analyzed 455 remains of 65 red colobuses resulting from 57 hunting episodes. Among these remains, the authors recovered 59 ribs. Although the damage to these bones was significant (including fraying and bend ends), the authors noted only one case of classic/general peeling (1.7%).

3.4. Correspondence analysis (CA)

A Chi-square (X-squared=205.2597, df=21, p-value<2.2e-16) test revealed significant differences among the combinations of categories of both variables (type of agent and type of combination of modifications). A Fisher test with p-simulated values yielded a similar result (p-value<2.2e-07). These results indicated that at the assemblage level, the modifications of bone caused by chewing by humans and bears could be well discriminated.

The bootstrapped CA revealed that the total amount of inertia explained by the two-dimension solution was 99.52. Of this, the first dimension alone accounted for as much as 88.68% of the inertia. The most important category combinations for the first dimension for rows were fracture+peeling and tooth mark+fracture+peeling. The combinations that contributed most to the second dimension of rows were tooth marks and peeling independently. For columns, all the bear subsamples contributed similarly on the first dimension and only slightly differently on the second dimensions, where modifications by bears on large carcasses were significantly different from those created by bears on medium-sized and small carcasses (Table 2).

As shown in Figure 7-left, there was no difference in the modifications of small- and medium-sized carcasses by bears; in contrast, both categories differed from the large carcasses, as both had higher frequencies of tooth marks and of tooth marks combined with fractures. Both the number of bone fragments with peeling alone and the number with fractures alone seemed to be larger in bear-modified carcasses than in human-modified carcasses. A clear result was found with the Khoikhoi sample when fractures were combined with peeling and with tooth marks. Humans generated more bones with fractures combined with peeling and tooth marks than bears. As shown in Figure 7-right, the bones bearing tooth marks and peeling were the most ambiguous for differentiating bears from humans. In contrast, the higher incidences of peeling associated with fractures and the combination of fractures and tooth marks led to better discrimination and occurred much more frequently in human-chewed assemblages. This is further reinforced by the fact that the only overlap that occurred (when excluding the tooth mark-peeling combination) was in the frequency of tooth marks that were documented alone. The confidence ellipse was too large for tooth marks alone, probably because the number of specimens in which tooth marks were documented not in combination with other categories was extremely small in both the human and bear subsamples.

Interesting results were obtained when archaeological data were incorporated. Figure 8 shows that the bone alterations associated with peeling on the ribs in the Toll assemblage are closer to those naturally modified by bears (NA study) than to those modified by the Khoikhoi. Three clearly differentiated groups can be identified in Figure 8-left. The first group corresponds to our NA study, which was influenced by isolated fractures and a combination of fractures and tooth marks. The second group corresponds to the data from the Toll Cave assemblage, where isolated peeling, isolated tooth marks, and the absence of modifications played a decisive role. Specifically, it was the inertia generated by the variable "isolated peeling" that produced a slight overlap between the two groups, especially between the peeling generated by bears in the NA study on large-sized ungulates and the peeling documented on the bears' own bones from Toll Cave. The third group is formed by sets generated by the Khoikhoi, which move significantly away from the other two and in which a combination of fractures, tooth marks, and peeling seemed to be the variable that exerted the greatest influence. On the other hand, Figure 8-right shows the considerable influence that the agents as variables have on the modifications. In this case, the isolated peeling was close to the NA study and the data from Toll Cave. However, peeling combined with tooth marks was located between the Khoikhoi variable and the different variables of the NA study, while the combination of fractures and peeling, greatly influenced by the Khoikhoi, had little relevance to the group of variables for Toll Cave.

4. Discussion and Conclusions

The application of the methods and techniques of modern taphonomy has revealed the important complexity of the trophic dynamics generated around the carcass(es) of bears that died during the hibernation process, which has led to important debates regarding both the actors that intervened and the effects they caused (e.g., Diedrich, 2009, 2012; Fourvel et al., 2014). These carcasses represented a relatively accessible source of resources for many carnivores (including the bears themselves). In addition, carcasses located in caves, under conditions of constant temperature and humidity, could preserve these nutrients for scavengers for a long time, as observed by Brain (1981) in relation to South African caves. This researcher noticed the interest of hyenas in the carcasses of animals that had been dead for several years inside the caves, and this could be equally applicable to the caves of the Palearctic zone throughout the Pleistocene. Therefore, much of the taphonomic complexity observed could derive from the possible intervention of several different actors on the same carcass over relatively separate periods of time. Such taphonomic complexity would increase considerably in places where the hibernation process of bears would have alternated with the presence of the dens, shelters, or breeding places of other carnivores. This alternating sequence would lead to an overlapping of events (or palimpsests, to use the term of Binford, 1981) and to a significant dispersal of the remains, accompanied by a greater diversity of bone surface modifications.

Visits by human groups, although occasional, should also be taken into consideration. Based on the presence of cut marks, the anthropogenic exploitation of the carcasses of bears that died while hibernating has been suggested in several Middle Paleolithic sites such as Font de Gaume III and Regourdou in France (Armand et al., 2003, 2004; Cavanhié, 2009-10) or Nietoperzowa in Poland (Wojtal et al., 2015). These sites are characterized by a low or moderate anthropic impact, as was also seen in our study case. A small amount of physical evidence has been recovered at Level 4 of Toll Cave (17 cut-marked bones, 10 of them corresponding to bears, and 9 lithic tools), but this is sufficient to make some important inferences about the Neandertal use of bear carcasses at the site. Eight of the ten cut marks on bears are located on the ventral side of the ribs, suggesting recurring evisceration processes and, therefore, primary and relatively immediate access to the animals. Taking into account that evisceration is a butchery activity that usually leaves very few cut marks on bones (stone tools are not always used for this activity), it may tentatively be inferred to be a regular action of human groups when they obtained these resources from the sites mentioned above. The butchery activities would mainly be related to the first stages of carcass processing, such as skinning, removing the viscera, and preparing certain anatomical units for transport to the sites of consumption. The unselected elements would consequently remain exposed to other scavengers. From this perspective, no significant differences can be seen when comparing this scenario with other sites interpreted as natural karstic traps, where human groups took advantage of fallen ungulate carcasses (see examples in Brugal and Jaubert, 1991; Rosell, 1998; Huguet et al., 1999; Brugal et al., 2006). These latter sites are characterized by low anthropic impact, as defined by little evidence of butchery activities (<3% of cut-marked bones) with significant anatomical biases toward the axial elements (60–75% correspond to the ribs and vertebrae). The absence of limbs is usually associated with anthropic transport to sites of intended for consumption. The action of carnivores is also abundant in these places (>20%), both through their primary access to some of the fallen carcasses and by their scavenging of remains abandoned by previous biological agents, including human groups. It should be noted that the action of these animals could also have caused the disappearance of some elements, but the general tendency would be consumption at the place of procurement, as evidenced by the high proportion of damage detected on the bones.

The study of peeling may be another option to consider when assessing the interventions of the different agents and their degree of intensity on the Toll Cave faunal assemblage and, by extension, on those of other European sites with similar dynamics. Here, we addressed this specific aspect of bone damage to deepen our understanding of the bending fractures inflicted by bears and by humans on the ribs of whole carcasses and their possible similarities and differences. The peeling damage, and the frequency with which it appeared, was one of the most notable and surprising findings of our NA study (Arilla et al., 2014; Rosell et al., 2019a, 2019b). Our experimental results have not allowed us to differentiate the peeling carried out by bears from that produced by humans when considering only the morphological criteria and considering the peeling as the sole modification (Rosell et al., 2019a). However, a statistical analysis based on a combination of damage provided interesting data for differentiation. The results from the CAs indicate a strong dependence of human-induced peeling (Khoikhoi) with other modifications, mainly tooth marks, while bear-induced peeling appears usually isolated or associated with fractures. Thus, the peeled ribs from Toll Cave are closer to those from our NA studies and, therefore, can mostly be associated with bear activities. From these data, the most reasonable inference is the "regular" scavenging by bears of the carcasses of their dead congeners in Toll Cave, with all the implications this entails regarding our knowledge of the behavior of these extinct animals. For instance, one of these implications is that the regular encountering of other bear carcasses by cave bears supports the frequency of cannibalism among these animals, as has been suggested by other researchers (e.g., Pinto Llona and Andrews, 2002, 2004; Lolliot and Philippe, 2004; Pinto Llona et al., 2005; Quilès et al., 2006; Rabal-Garcés et al., 2012). Among current bears, this disproportionate interest in meat occurs only immediately after hibernation, and it is progressively lost as the year progresses and the diversity of products of plant origins increases (e.g., Palomero et al., 2011; Rabal-Garcés et al., 2012; Arilla et al., 2014). This phenomenon, together with the significant absence of the transport of carcasses or of parts of them to dens or shelters (Sala and Arsuaga, 2013), suggests, in the Toll case, that scavenging activity occurred after hibernation.

The intervention of bears in the cave does not exclude the possibility that other agents, such as human groups, would also have carried out actions aimed at obtaining or exploiting carcasses. In fact, both cut marks and a small set of lithic tools support there was anthropogenic access to these resources, as discussed above. The peeling generated by humans usually occurs during the final process of consumption, as an activity related to fracturing bones and directly obtaining their internal resources. Human consumption of some specific parts at the site of hunting has been observed from an ethnoarchaeological perspective, such as among the Kua, who consume organs and long-bone marrows (Bartram, 1993), although this phenomenon rarely affects the ribs. Peeling by humans seems to occur mostly during the final stages of processing in the sites of consumption—consequently, it would not be frequent modification in the procurement places (or kill sites) of the carcasses. The case of the Khoikhoi (and other pastoral groups) is not comparable, as the animals consumed were mainly domestic (goats) and the slaughter and consumption sites were usually the same (e.g., Brain, 1981). In the case of bears, Arilla et al. (2014) observed a special interest for the rib cages, not only when the carcass was fresh but also when it was exposed for some time. The fracturing of the ribs by flexion and/or pressure using the forepaws and sometimes the mouth is consistently practiced according to practically all neotaphonomic observations documented by photo- and video-traps. This indicates that the peeling produced by bears in Toll Cave should not be considered exclusive to primary and immediate access, as it could also occur during later scavenging processes (and even on thoracic cages abandoned previously by humans).

Another important aspect to consider is the body size of the animals. In the case of bears, peeling is observed mainly on the ribs of small-sized animals (<100 kg) but also in animals of medium

(100–300 kg) and large sizes (>300 kg). However, the only animals consumed by the Khoikhoi were goats and therefore of small size. Statistical analyses did not indicate an important influence of this variable in distinguishing between bear- and human-induced peeling; however, whether human groups can inflict this type of modification on large- and medium-sized animals, in non-induced or induced contexts, has yet to be considered. It would also be interesting to identify the types of alterations that are associated with peeling to enable statistical analyses similar to those shown in this work.

Hunting and the cave bear cult have been a matter of controversy since the beginning of systematic cave research in the early 19th century. Some authors have proposed the idea that these carnivores were hunted and used for their symbolic significance, while others have advocated natural deaths in contexts where occasional anthropic intrusions also existed (e.g., Fedele, 1968; Jéquier, 1975; Tillet, 1997; Tillet and Bernard-Guelle, 1998; Fosse et al., 2002; Auguste, 2003; Bona et al., 2007; Cvetkovic and Dimitrijevic, 2014; Bocherens et al., 2014; Fourvel et al., 2014). The methods of hunting and of obtaining bear resources have long been debated (e.g., Binford, 2002; Fosse et al., 2002), although current evidence attests to the processing of the carcasses of these animals since the late Lower Pleistocene, as in the case of Gran Dolina in Spain (Saladié et al., 2011). Such activities have also been detected in sites such as Boxgrove in the UK (Smith, 2012, 2013) and the Caune de l'Arago in France (Quilés, 2003) and determined to have occurred during the Middle Pleistocene. Notably, the regular occurrence of multiple examples of brown bears at the Biache-Saint-Vaast site, dated to MIS 7, has been interpreted to be the result of the hunting activities of human groups who inhabited that territory (Auguste, 1991, 1992, 1995). From this time on, signs of the exploitation of these animals became increasingly common during the Middle Paleolithic, especially evidence such as cut marks on the bones. Neandertal use of bears has been described in several European sites, including the Arcy-sur-Cure (David and Poulain, 1990), Grotte des Cèdres (Bez, 1995), Prélétang (Tillet and Bernard-Guelle, 1996; Tillet, 2002), Le Portel (Gardeisen, 1999), and those already named above such as Font de Gaume III and Regourdou (Armand et al., 2003, 2004; Cavanhié, 2009-10) in France. Other examples come from Goyet and Scladina Cave in Belgium (Germonpré and Sablin, 2001; Abrams et al., 2014), Grotta dei Moscerini, Sant Agostino (Stiner, 1994), Badalucco, Madonna dell' Arma, Caverna delle Fate, Ciota Ciara, Arma delle Manie (Quilés, 2003; Valensi and Psathi, 2004), Rio Secco and Fumane Cave (Romandini et al., 2018) in Italy, Bockstein (Kitagawa et al., 2012), Taubach (Bratlund, 1999a, b), GeissenKlösterle, Kogelstein, and Grosse Grotte (Münzel and Conard, 2004) in Germany, Salzofen Cave in Austria (Armand et al., 2004), Divje Babe in Slovenia (Turk et al., 1997, 2018), Érd in Hungary (Daschekc, 2014), Pesturina in Serbia (Majkić et al., 2018), and Nietoperzowa in Poland (Wojtal et al., 2015). The case of Hayonim Cave is also notable, as it is located in Israel (Stiner, 2005). Grayson and Delpech (2003) and Torres et al. (2007) suggest that the expansion of human populations during the Upper Paleolithic considerably multiplied the contacts between bears and humans. The hunting of these animals then began to leave stronger or more direct evidence, as is the case at the Aurignacian site in the Potocka Zijalka Cave in Slovenia, where a hole in the scapula of a cave bear has been interpreted as produced by the impact from a projectile (Rabeder et al., 2004). Moreover, a flint projectile tip embedded in the transverse process of a cave bear vertebra was found at the Gravettian site of Höhle Fels in Germany, which together with a large number of cut marks on different individuals was interpreted to have resulted from human hunting activities (Münzel et al., 2001; Münzel, 2004; Münzel and Conard, 2004; Wojtal et al., 2015).

In summary, the study presented here demonstrates how NA approaches carried out with wild animals and without any human interference (induction) that would disturb their natural behavior are not only informative regarding taphonomic activities (feeding) and their effects (bone damage) but also help resolve interpretative issues at archaeological sites. The statistical analyses based on combinations of bone damage has allowed us to propose that the association of peeling with other alterations on the ribs from Toll Cave Level 4 is more similar to that observed in the assemblages naturally modified by bears than to that observed in humans. Accordingly, it has been possible to infer that bears regularly scavenged the carcasses of their dead congeners in the cave and, thereby, to propose behavioral patterns for these extinct carnivores.

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Captions

Figure 1. Cut marks on level 4 faunal assemblage from Toll Cave: A, C-D) ventral surface of bear ribs; B) ventral surface of a medium-sized animal rib.

Figure 2. Carnivore-induced damage on bear bones from Toll Cave Level 4: A) cranium; B,D) ulna; C) femur; E) tibia; F) rib; G) femur; H) fibula.

Figure 3. Peeling on axial bones from Toll Cave Level 4: A) large-sized animal rib; B) medium-sized animal rib; C, J, M) bear atlas; D) flat (vrt/rb) bone of large-sized animal; E,F-I,K) bear rib; L) bear dorsal vertebra.

Figure 4. Examples of bear movements around the carcass resulting in peeling damage on axial regions: A1-3) bear pressing on the ungulate ribcage until fracturing it; B1-3) bear opening the ribcage by expanding the ribs using its forepaws; C1-3) bear biting several points on the ribs and breaking them with sudden head movements with help of its forepaws (e.g., C3).

Figure 5. Damage produced by brown bears on axial bones during actualistic series: A) red deer vertebra (OB 6); B) red deer rib 5 (OB 15); C) roe deer vertebrae (OB 3); D) goat rib (OB 12); E) red deer rib 5 (OB 15); F) red deer rib 6 (OB 15); G) sheep rib (OB 10); H) red deer rib 6 (OB 15); I) red deer 11 (OB 16); J,K) sheep ribs (OBs 10, 14); L) red deer atlas (OB 4); M) sheep rib (OB 9); N) red deer rib 6 (OB 15); O) sheep sacrum (OB 14); P,Q) sheep vertebrae (OB 10); R) red deer rib 2 (OB 15); S) red deer rib 7 (OB 15).

Figure 6. Classic and incipient peeling produced by brown bears on axial bones during actualistic series: A) sternal end of a roe deer rib (OB 2); B) transverse process of a roe deer vertebra (OB 2); C) red deer rib 11 (OB 16); D) transverse process of a sheep vertebra (OB 8); E) spinous process of a sheep vertebra (OB 17); F) sheep rib (OB 9); G) sheep rib (OB 10); H) sheep rib 1 (OB 17); I) spinous process of a sheep vertebra (OB 17); J,K, M-O) transverse process of goat vertebrae (OB 12); L,P) spinous process of a sheep vertebra (OB 17); Q,R) spinous process of a sheep vertebra (OB 11); S) bent ends and fraying on ribs of red deer (OBs 4,16), roe deer (OBs 2,5), sheep and goat (OB 12).

Figure 7. Correspondence Analysis (CA) of damaged (peeling and associated alterations) ungulate ribs by brown bears and Khoikhoi people. Naturalistic actualistic (NA) data with brown bears were taken from Arilla et al. (2014) and Rosell et al. (2019) –new specific data on peeled ribs are also included in this study– and the Khoikhoi sample from Pickering et al. (2013).

Figure 8. CA of damaged (peeling and associated alterations) ribs from actualistic approaches (brown bears and Khoikhoi people) and Toll Cave Level 4 faunal assemblage. NA data were taken from Arilla et al. (2014), Rosell et al. (2019) and Pickering et al. (2013).

Figure 1

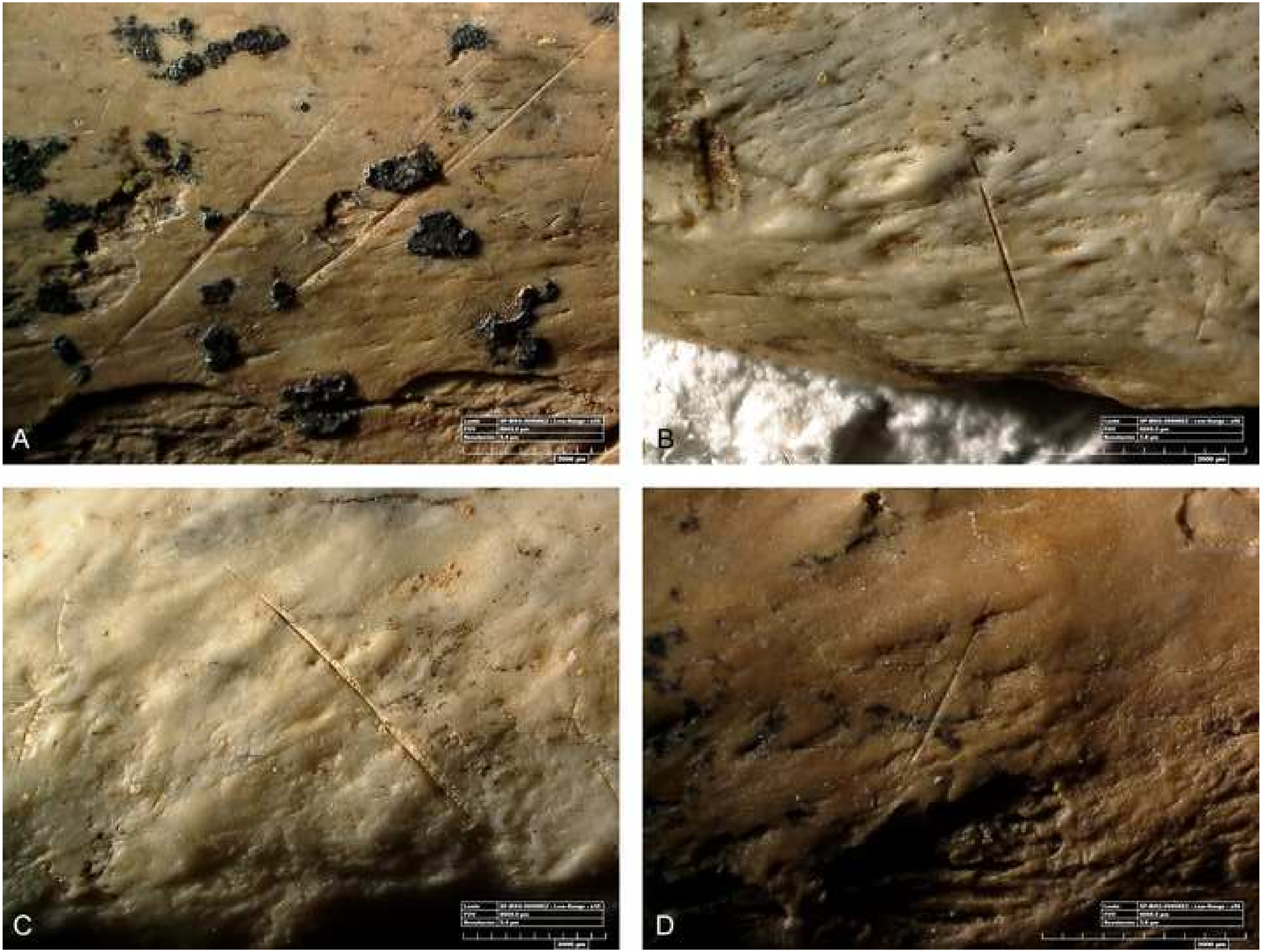


Figure 2


A
A1
A1
5 cm
B
5 cm
B1
B1
C
C1
C1
C2
3 cm
C2
D
3 cm
E
E1
2 cm
E1
F
F1
2 cm
F1
G
G1
1 cm
G1
H
H1
H1
2 cm

Figure 3


A
1 cm
B
1 cm
C
C1
2 cm
C1
D
2 cm
E
2 cm
F1
F1
2 cm
F
G
2 cm
H
H1
H1
2 cm
I
1 cm
J
J1
2 cm
J1
K
2 cm
L
L1
L1
2 cm
M
2 cm

Figure 4


A.1
HCO ScoutGuard
4.17.2010 20:54:04
A.2
HCO ScoutGuard
4.18.2010 18:48:42
A.3
HCO ScoutGuard
4.18.2010 18:49:03
B.1
HCO ScoutGuard
4.18.2010 18:49:40
B.2
HCO ScoutGuard
4.18.2010 18:49:43
B.3
HCO ScoutGuard
4.18.2010 18:54:06
C.1
HCO ScoutGuard
4.13.2010 8:51:40
C.2
HCO ScoutGuard
4.18.2010 18:45:55
C.3


A
1 cm
B
1 cm
C
1 cm
D
1 cm
E
1 cm
F
1 cm
G
G1
G1
1 cm
H
1 cm
I
1 cm
J
1 cm
K
1 cm
L
1 cm
M
1 cm
N
2 cm
O
2 cm
P
1 cm
Q
1 cm
R
1 cm
S
1 cm

Figure 6

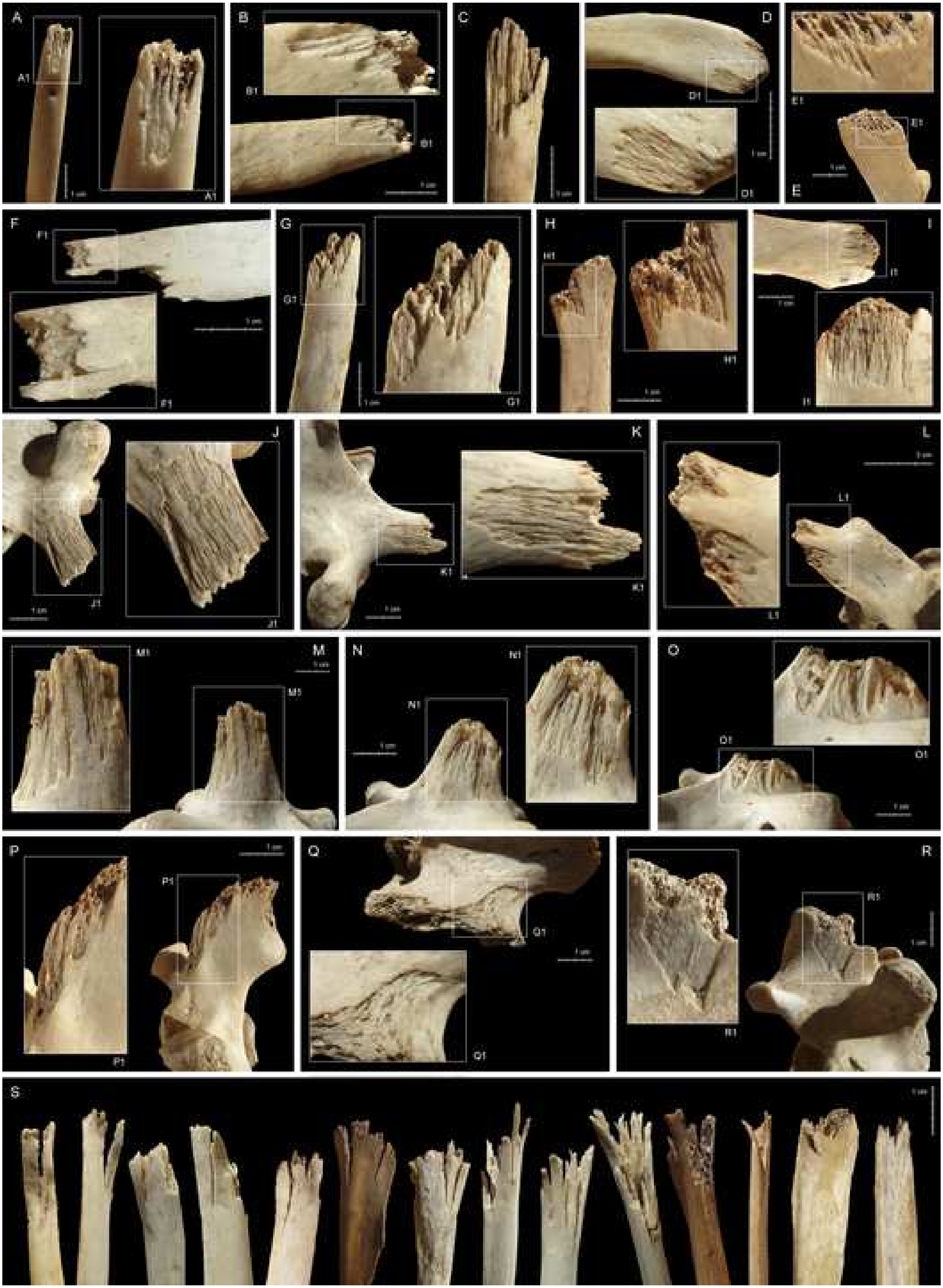

A
A1
A1
1 cm
B
B1
B1
1 cm
C
1 cm
D
D1
D1
1 cm
E
E1
E1
1 cm
F
F1
F1
1 cm
G
G1
G1
1 cm
H
H1
H1
1 cm
I
I1
I1
1 cm
J
J1
J1
1 cm
K
K1
K1
1 cm
L
L1
L1
1 cm
M
M1
M1
1 cm
N
N1
N1
1 cm
O
O1
O1
1 cm
P
P1
P1
1 cm
Q
Q1
Q1
1 cm
R
R1
R1
1 cm
S
1 cm

Figure 7

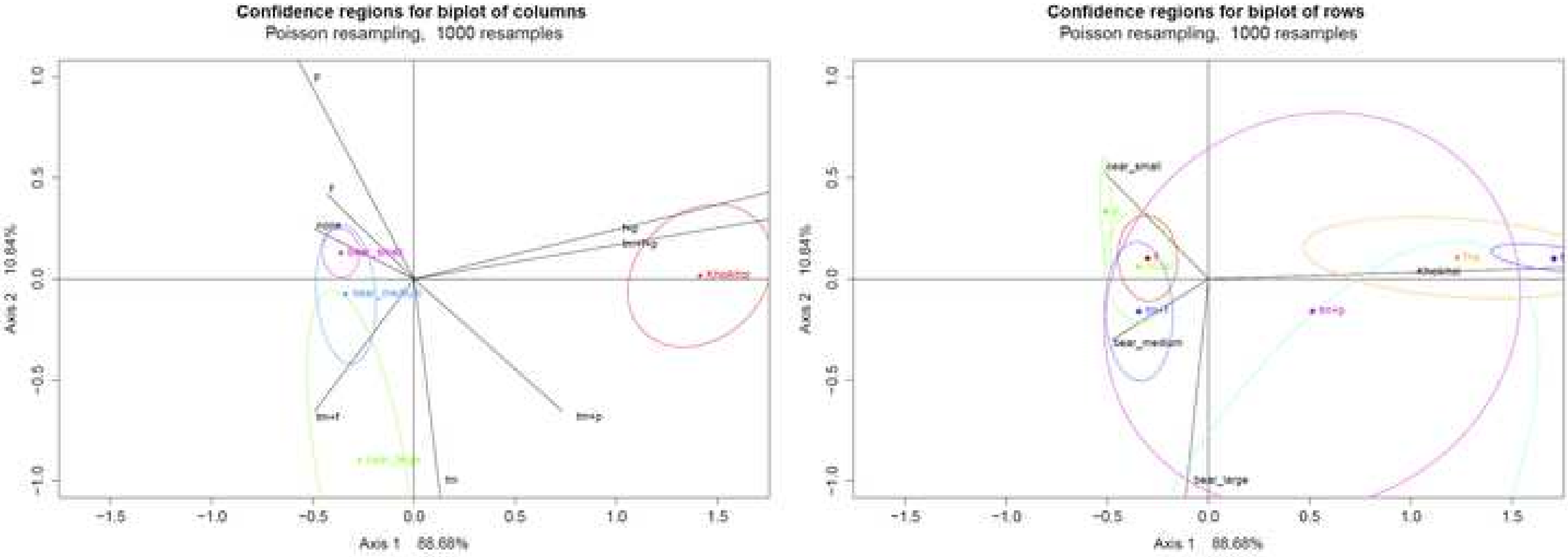
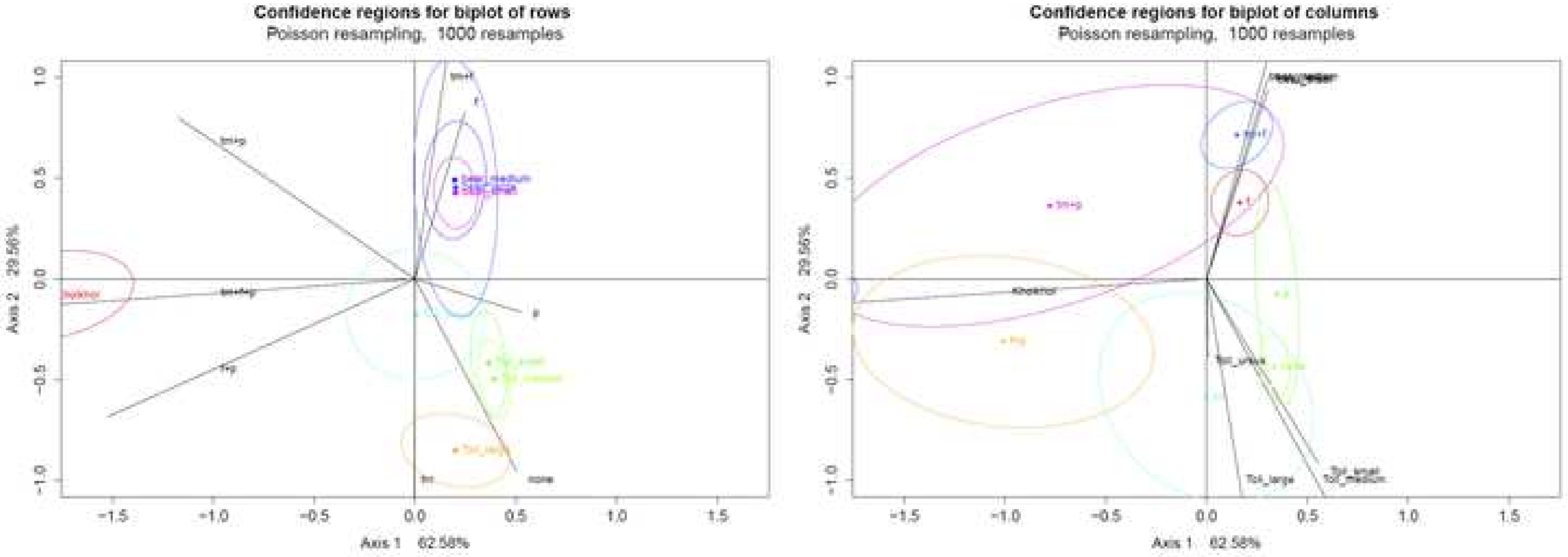

Confidence regions for biplot of columns
Poisson resampling, 1000 resamples
Axis 1 88.68%
Axis 2 10.84%
-1.5
-1.0
-0.5
0.0
0.5
1.0
1.5
p
f
none
Sear_short
Sear_medium
fm+f
Sear_large
fm
fm+p
fsg
fm+fsg
Khokhar
Confidence regions for biplot of rows
Poisson resampling, 1000 resamples
Axis 1 88.68%
Axis 2 10.84%
sear_small
Sear_medium
Sear_large
Khokhar
fm+f
fm+p
f
fsg

Figure 8



Confidence regions for biplot of rows

Poisson resampling, 1000 resamples

Confidence regions for biplot of columns

Poisson resampling, 1000 resamples

Table 1

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Table

Table 1_R1.doc

Table 2

Table 3

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Table 4

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Table 5

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Table 6

Table 7

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Table 8

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Table 8_R1.doc