Faunal evidence for a difference in clothing use between Neanderthals and early modern humans in Europe

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Abstract

In this paper we report a study designed to shed light on the possibility that clothing differences played a role in the replacement of the Neanderthals by early modern humans. There is general agreement that early modern humans in Europe utilized specialized cold weather clothing, but the nature of the clothing used by Neanderthals is debated. Some researchers contend that they did not use clothes. Others argue that they were limited to cape-like clothing. Still others aver that their clothing was not substantively different in terms of thermal effectiveness from that of early modern humans. To test between these hypotheses, we employed a novel line of evidence—the bones of animals whose skins may have been made into clothing. We used an ethnographic database to identify mammalian families that were used to create cold weather clothing in the recent past. We then compared the frequency of occurrence of these families in European archaeological deposits associated with early modern humans and Neanderthals. We obtained two main results. One is that mammalian families used for cold weather clothing occur in both early modern human- and Neanderthal-associated strata. The other is that three of the families—leporids, canids, and mustelids—occur more frequently in early modern human strata than in Neanderthal strata. There is reason to believe that the greater frequency of canid and mustelid remains in early modern human strata reflects the use of fur trim on fitted garments. Thus, these findings are most consistent with the hypothesis that Neanderthals employed only cape-like clothing while early modern humans used specialized cold weather clothing. We end by discussing the implications of this hypothesis for the debate about the replacement of the Neanderthals by early modern humans.

Key words: Neanderthals; early modern humans; Oxygen Isotope Stage 3; specialized cold weather clothing; Mustelidae; Canidae; Mousterian; Aurignacian; Gravettian

Introduction

Recently significant progress has been made in our understanding of early modern human origins. For several decades there was debate about the nature of the appearance of early modern humans outside of Africa. Some argued that *Homo sapiens* originated in Africa around 200,000 years ago (kya) and then spread throughout the rest of the world, replacing or absorbing regional groups of non-modern hominins as they went (Stringer 2002). Others asserted that *H. sapiens* evolved in different regions from different groups of non-modern hominins over the course of the last two million years (Wolpoff et al. 2000). This dispute has been resolved in the last few years, as a result of new fossil discoveries and the development of novel methods (e.g. ancient DNA) (Collard and Dembo 2013). Today, there is widespread agreement that *H. sapiens* originated in Africa about 200 kya and migrated into the other regions of the world 100,000-150,000 years later (Cartmill and Smith 2009; Klein 2009). Even those researchers who were once the main proponents of the multiregional evolution model now accept that migration from Africa within the last 100,000 years played an important role in the appearance of *H. sapiens* outside of Africa (Wolpoff et al. 2004). Now that the out of Africa versus multiregional evolution debate has been resolved in favour of the former model, attention has shifted to elucidating the details of the process by which the migrating early modern humans replaced the various regional groups of non-modern hominins.

In western Eurasia, the non-modern hominins replaced by the migrating early modern humans were the Neanderthals. Neanderthals were close relatives of early modern humans—so close in fact that the two species seem to have been able to interbreed (e.g. Green et al. 2010; Fu et al. 2014). They had brains that were similar in size to those of *Homo sapiens*, a long, low cranial vault with pronounced brow-ridges, and a large, prognathic face (Cartmill and Smith 2009). Neanderthals were stocky. Their average body mass and stature have been estimated as 72 kg and 161-165 cm, respectively (Ruff et al. 1997; Feldesman et al. 1990). They also had relatively short forearms and lower legs (Ruff 1993, Holliday 1997). The size and shape of the Neanderthal body are widely accepted to be adaptations to glacial conditions (Ruff 1993, Holliday 1997). Neanderthals lived in small, dispersed groups, and specialized in hunting large game (Stiner 2001; Stiner et al. 2009). They made sophisticated stone tools, but evidence from several sites indicates that their use of fire was restricted to warm periods, which suggests they may not have been able to create fire at will but only take advantage of naturally occurring fires (Sandgathe et al. 2011). Additionally, they did not build structures or utilize symbols on a regular basis (Klein 2003). Genetic and morphological data suggest Neanderthals were a distinct species by at least 200 kya (Cartmill and Smith, 2009). Modern humans joined Neanderthals in Europe ca. 42 kya, during Oxygen Isotope Stage 3 (OIS3) (Stringer 2006). Within a few thousand years, the Neanderthals had disappeared. Current evidence indicates they went extinct 30-24 kya (Klein 2003; Finlayson et al., 2008). With regard to geographic range, the Neanderthals were a western Eurasian species. Their fossilized remains have been found from Wales in the north to Israel in the south, and from Portugal in the west to Central Asia in the east (Klein 2003; Krause et al. 2007). So far, no Neanderthal fossils have been found in Africa, South Asia, or East Asia.

Why early modern humans were able to replace Neanderthals is contested. Some researchers argue that early modern humans out-competed Neanderthals because they were able to exploit more resilient and reliable resources, such as rabbits, fish, and plants that require processing to eat (Stiner 2001; Mellars 2004; Stiner and Kuhn 2006, Richards and Trinkaus, 2009). Others aver that Neanderthals did not disappear as a consequence of competition with early modern humans. According to Stewart (2007), for example, the fact that Neanderthals died out in Europe at the same time as two “interglacial survivors,” the straight-tusked elephant (*Elephas antiquus*) and Merck’s rhino (*Stephanorhinus kirchbergensis*), indicates that, contrary to the current consensus, Neanderthals were warm adapted rather than cold adapted. The corollary of this, Stewart contends, is that Neanderthals went extinct because they were unable to cope with the substantial decrease in temperature associated with OIS3. Finlayson (2004, 2009) and Jiménez-Espejo et al. (2007) have also argued that the Neanderthals were driven to extinction by the effects of climate change rather than competition with early modern humans. Still others have proposed that a combination of competition with early modern humans and the effects of climate change were responsible for the Neanderthals’ disappearance (Stringer et al. 2003). These researchers suggest that during OIS3, rapid climatic fluctuations destabilized the environment, and the combined stress of an unstable resource base and the arrival of new competitors drove the Neanderthals to extinction.

The study reported here was designed to shed light on the possibility that differences in clothing played a role in the replacement of Neanderthals by early modern humans. Jim O’Connell was, we believe, the first person to suggest such might be the case. Jim put forward this idea in his 2006 contribution to the modern human origins debate, “How did modern humans displace Neanderthals? Insights from hunter-gatherer ethnography and archaeology” (O’Connell, 2006). Jim’s thesis in this paper was that the replacement of the Neanderthals by early modern humans may have been an episode of competitive exclusion in which differences in diet breadth were crucial. He argued that early modern humans had a broader diet than the Neanderthals, and went on to suggest that this would have allowed them to occupy a wider array of habitats than the Neanderthals. As a result of this, he continued, early modern humans eventually would have driven the Neanderthals from their former range. While discussing the archaeological evidence that supports this scenario, Jim highlighted a critical prerequisite for early modern humans to have been able to occupy a wider range of habitats than Neanderthals—namely that they would have had to invest more heavily in technologies for coping with cold conditions (e.g. hearths, shelter, and clothing) than Neanderthals. The idea that clothing played an important role in the replacement of the Neanderthals by early modern humans was subsequently elaborated by Gilligan (2007) and Wales (2012).

The impact of differences in Neanderthal and early modern human clothing could have been substantial. As is well known, prolonged exposure to cold in the absence of adequate clothing can lead to frostbite and hypothermia, and eventually, death. At the extreme, then, differences in clothing could have had an impact on the health and perhaps even the survivorship of Neanderthals compared to early modern humans. Even if this were not the case, the impact of clothing differences could still have been considerable. For example, given the need to avoid frostbite and hypothermia, such differences could have influenced the length of the daily “time window” for foraging, and limited the latitude and elevation at which foraging was possible, which in turn could have affected daily foraging return rates. Differences in clothing may have affected daily foraging return rates in other ways too. Ethnographic work indicates that insufficiently warm clothing can hinder hunting tactics involving long periods of inactivity, such as ambush hunting (Stenton 1991). Therefore, clothing differences could have impacted the effectiveness of foraging, resulting in a difference in daily foraging return rates. This in turn could have led to a difference in calorie intake and, ultimately, inter-birth interval (Froehle and Churchill 2009). Thus, even if differences in clothing did not affect health and survivorship directly, they could have played a role in the replacement event via their impact on reproductive rate and demography.

Currently, it is unclear whether there was a difference in early modern human and Neanderthal clothing. There is general agreement that as early modern humans moved into glacial Europe, they would have adopted highly insulative specialized cold weather clothing systems, involving multiple fitted garments made from well-tanned, pliable hides[1]. This is based, in part, on the recovery of bone needles at early modern human sites in Africa and Eurasia (Backwell et al. 2008, Hoffecker 2005a). In Africa, a bone needle-like implement has been recovered from deposits dating to ca. 61 kya at the site of Sibudu, South Africa (Backwell et al. 2008). The oldest eyed bone needles from Eurasia date to 37-40 kya and are generally accepted to be associated with modern humans (Golovanova et al. 2010a, 2010b). There is also evidence that modern humans regularly processed hides. Ethnographic and archaeological data indicate that lithic endscrapers are specialized tools for intensive hide scraping (e.g. Hayden 1990, Jefferies 1990; Shott and Weedman 2007; Loebel 2013), and endscrapers are common in early modern human sites in Eurasia. Additional support for the hypothesis that early modern humans used specialized

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[1] At the moment, there is no generally accepted terminology for discussing craft-produced clothing. For example, Hayden (1990) suggested a tripartite classification of basic capes, improved capes, and luxury garments, while Gilligan (2007) distinguished between “simple clothing” and “complex clothing”. We are not content with either of these schemes. Accordingly, we have elected to use the terms “cape-like clothing” and “specialized cold weather clothing” to refer to the two types of ensemble that have so far featured in the debate about Neanderthal and early modern human clothing use. We believe the meaning of “cape-like clothing” should be self-evident. The term “cold weather clothing” is often used by researchers who work on clothing performance to refer to ensembles of garments that are designed to protect against extremely cold environments such as the Arctic and high mountains (e.g. Oakes et al., 1995). We added “specialized” to make it even clearer that the garments are specifically designed for cold weather.

cold weather clothing is provided by ca. 24,000 year old carved ivory figurines from Russia that appear to depict individuals wearing fur parkas (Hoffecker 2005a).

In contrast, the nature of the clothing used by Neanderthals is debated. Some researchers have suggested Neanderthals did not use clothing. Kittler et al. (2003), for example, used molecular techniques to investigate the divergence between human head and body lice. They reasoned that this divergence would have occurred after hominins began to wear clothes and therefore dating it should provide a *terminus post quem* for the origin of clothing. They also reasoned that the genetic diversity of body lice from different regions should be informative about the origin of the use of clothing. Kittler et al. found that head and body lice diverged about 72,000 ±42,000 years ago, which postdates the first appearance of early modern humans. They also found much greater genetic diversity among African body lice than among body lice from other regions. Kittler et al. concluded from these findings that the use of clothing likely originated with early modern humans in Africa, and that archaic hominins like the Neanderthals probably did not use clothing. The following year Kittler et al. (2004) reported a revised date of 107 kya for the origin of body lice. Kittler et al.'s (2003, 2004) basic finding—that clothing use first developed among early modern humans living in Africa—was subsequently replicated using more sophisticated techniques by Toups et al. (2011).

Other researchers have argued that Neanderthals used clothing but did not employ garments of the same thermal effectiveness as early modern humans (Hayden, 1990, 1993; Gilligan, 2007; Wales, 2012). Drawing on ethnographic data, Hayden (1990, 1993) argued that specialized cold weather clothing was not a requirement among many historic groups living in temperate regions. Rather, it was mainly a status marker and its production depended on resource abundance. Because he could identify no evidence for true resource abundance in the Middle Palaeolithic, he suggested that Neanderthals likely used only cape-like clothing. Subsequently, Gilligan (2007) argued that the Neanderthals probably relied on cape-like clothing rather than specialized cold weather clothing because no needles and few precision cutting tools have been recovered from Neanderthal sites. Wales (2012) has also argued that Neanderthal clothing would have been less thermally effective than that of early modern humans. He modeled climate conditions at early modern human and Neanderthal sites in Europe, and found that early modern human sites were frequently in areas that would have required them to cover 80-90% of their bodies, whereas Neanderthal sites were located in areas that would have required only 70-80% of the body to be covered. Wales concluded from this that while early modern humans would often have needed to employ specialized cold weather clothing, Neanderthals would rarely have needed to do more than drape themselves with the fur of a large-bodied animal.

Still other researchers have suggested that the clothing of the Neanderthals would have been similar in terms of thermal effectiveness to the clothing used by early modern humans. White (2006) is one such researcher. Focusing on the situation in Britain, he argued that the low temperatures during OIS3 would have required Neanderthals to wear tailored fur clothing. He also argued that cape-like clothing would not have been an option because it would have impeded arm movements. Sørenson (2009) is another proponent of the hypothesis that Neanderthal clothing would have been similar to that of modern humans. He modeled Neanderthal energetics with different amounts of clothing, and concluded that Neanderthals living in northern Europe would have had to cover all but small portions of their bodies with fitted clothing as early as 125 kya, long before the start of OIS3. According to Sørenson, the absence of bone needles at Neanderthal sites does not mean they only employed cape-like clothing. He suggested that Neanderthals would have been able to make fitted clothing using what he describes as “awl-like points” and “knife-like blades” to cut strips of skin and join skins together (p. 2203).

In our study, we focused on a line of evidence that so far has received relatively little attention in the debate about the possibility of a difference in the clothing of early modern humans and Neanderthals—the bones of animals whose skins may have been used to produce clothing (see White [2006] for a rare exception). The study had three parts. First, we identified mammalian families that were present in Europe during OIS3. This was accomplished with the aid of the Stage 3 Project Faunal Database, which records the presence of mammal species at 493 European archaeological and palaeontological sites dated to 60-20 kya. Next, we identified which mammalian families were used to manufacture cold weather clothing by recent mid-to-high latitude small-scale societies. This was achieved with the assistance of a large ethnographic database. In the last part of the study, we returned to the Stage 3 Project Faunal Database. We targeted families that the second part of the study indicated were used in cold weather clothing, and tested for significant differences in the frequencies of their remains in Neanderthal- and early modern human-associated strata. We focused on the 333 strata in the Stage 3 Faunal Database that contain Mousterian, Aurignacian, or Gravettian artefacts. Neanderthals are widely accepted to have manufactured the Mousterian, while early modern humans are generally thought to have produced the Aurignacian and Gravettian (e.g. van Andel and Davies 2003; O'Connell, 2006). The Mousterian, which is often treated as synonymous with the Middle Palaeolithic period, emerged ca. 250 kya and disappeared around 40 kya (Adler et al., 2014; Richter, 2011). The Aurignacian appeared around 42 kya and is the first industry in Europe uniquely associated with early modern humans (Douka et al. 2014). The Gravettian overlapped with the end of the Aurignacian and lasted until around 24 kya (Hoffecker 2005b). Thus, together, the Aurignacian and Gravettian cover the period of coexistence between Neanderthals and early modern humans.

Materials and Methods

The study had three parts. First, we identified mammalian taxa that were present in Europe during OIS3, using the Stage 3 Project Faunal Database (http://www.esc.cam.ac.uk/research/research-groups/research-projects/stage-three-project/stage-three-project-database-downloads). The Stage 3 Project Faunal Database contains data from most of the archaeological sites from Europe that have yielded mammalian faunal remains and been radiometrically dated to 60-20 kya, as well as a number of European palaeontological sites that fall in the same time range (Stewart et al. 2003). OIS3 began ca. 60 kya and ended ca. 24 kya. However, the members of the Stage 3 Project elected to include sites up to and including 20 kya in the database in order to incorporate the start of the LGM, which began ca. 21 kya (van Andel 2003). For the purposes of the Stage 3 Project, the geographic extent of Europe was defined as the western Palaearctic, bordered by the Atlantic to the West, the Mediterranean to the South, the Arctic Ocean to the North, and the 40ºE longitude line to the East (van Andel and Davies 2003). Mammalian taxa are recorded as present/absent in the strata included in the database.

In the second part of the study, we searched the electronic version of the eHRAF World Cultures Database (http://hraf.yale.edu/online-databases/ehraf-world-cultures/) for mentions of the use of the mammals in cold weather clothing produced by recent non-industrial groups from mid-to-high latitudes. The eHRAF World Cultures Database is a cross-cultural database that contains information on numerous aspects of the cultural and social lives of a worldwide sample of 258 ethnographic groups. In searching the eHRAF World Cultures Database, common names were used rather than formal taxonomic names. The common names were taken from *Walker's Mammals of the World* (Nowak 1999). We focused on the family level because the common names of many taxa are not unique to a single genus or species (e.g. "fox" can refer to the *Vulpes* genus or the *Alopex* genus), and because several taxa that have been recovered from archaeological strata that date to OIS3 are now extinct and therefore cannot be utilized by recent human groups. Focusing on the family level allowed extinct taxa to be included in the analysis, because extinct species and genera could be categorized as members of extant families that are used for clothing by recent groups. Because the goal of the analyses was to identify taxa used in traditional, craft-produced cold weather clothing, we did not include groups such as African Americans, Arab Americans and Cuban Americans (deemed "Regional and Ethnic Cultures" by the eHRAF World Cultures Database) or results for clothing suspected to have been mass-produced. Disregarding "Regional and Ethnic Cultures" left a total of 237 groups. Of these 237 groups, 133 come from mid-to-high latitudes, and 104 come from tropical latitudes. We defined "mid-to-high" latitude groups as those whose territories are north of or encompass the Tropic of Cancer, or south of or encompass the Tropic of Capricorn. The geographic territories of the groups were taken from the Human Relations Area Files, and latitudes from Stanford (2003). Any item of clothing described as warm or for winter or cold weather use was deemed to be "cold weather clothing". Repeated mentions of the use of a taxon for a particular type of clothing by a single group were not counted. For example, if multiple ethnographies noted that the Chukchee used reindeer hides to make winter parkas, only one use was counted.

Lastly, we returned to the Stage 3 Project Faunal Database to test for differences between Neanderthals and early modern humans in their exploitation of fauna suitable for producing cold weather clothing. Specifically, we tested for differences in the frequency of the remains of mammalian families that the second step of the study indicated were used to produce cold weather clothing in ethnographic contexts. We compared early modern human-associated Aurignacian/Gravettian strata with Neanderthal-associated Mousterian strata, focusing on families that were often used for cold weather clothing in the ethnographic sample. We defined "often" as ≥1% of ethnographic uses. We did not include so-called "transitional" industries such as the Chatelperronian because of the ongoing debate about their validity as cultural entities and their association with Neanderthals versus early modern humans (e.g. Bar-Yosef and Bordes 2010).

In selecting strata, we limited the date range to 60-20 uncal kya, so that outliers were not included. Only strata that contain faunal data and were clearly linked with the Mousterian, Aurignacian, or Gravettian were included. Potentially mixed strata were not included. Duplicate entries for a stratum were consolidated. If strata names given by the original monograph and the database's editorial notes were contradictory, the stratum name from the original monograph was used. If the editorial notes gave additional stratigraphic information that did not contradict the original monograph, the editorial notes were used to distinguish strata. If strata were not named in the database but were associated with different industries (e.g. one unnamed Aurignacian stratum and one unnamed Mousterian stratum from the same site), both strata were included. Unnamed strata associated with the same industry at a single site that were only differentiated by elevation were consolidated. If an entry indicated that it represented more than one stratum (e.g. "stratum 10-11"), and the strata in question were already represented in the dataset, the multi-strata data were consolidated with the existing strata (e.g. "stratum 10-11" was consolidated with "stratum 10" and "stratum 11"). However, if one of the strata was not already represented, the multi-strata data were kept as a distinct data point (e.g. if "stratum 2-9" was present as well as "strata 5" and "strata 6," then "stratum 2-9" was kept as a distinct stratum). At some sites, only descriptions were given as strata names. In these cases, strata with similar names were consolidated. As a rule, the strata nomenclature listed in the database was trusted, unless strata names obviously did not in fact refer to strata. For example, at Sunghir, a number of burials were listed as strata, but dating reports (Dobrovolskaya et al. 2012) state that the burials come from the main Gravettian occupation. So, faunal data from the "burial layers" were consolidated with the

Gravettian stratum data. Of the 333 strata that were included in the analysis, 96 were Mousterian, 132 Aurignacian, and 105 Gravettian.

To test for differences in the frequency of the remains of cold weather clothing families between Aurignacian/Gravettian strata and Mousterian strata, we used the chi-squared test. Because we effectively conducted multiple unplanned tests, we used Benjamini and Hochberg's (1995) method of significance-level correction.

Results

The remains of members of 24 mammalian families are recorded in the Stage 3 Project Faunal Database. These families are listed in the Appendix.

Table 1 summarizes the results of our search of the eHRAF World Cultures Database. Details of animals used to make cold weather clothing were available for 77 of the 133 mid-to-high latitude societies included in the search. In total, there were 238 distinct cold weather clothing uses of the mammalian families represented in the Stage 3 Project Faunal Database. Cervidae was the most commonly utilized family; members of the deer family accounted for 32% of the cold weather clothing uses. After Cervidae, the next most commonly used families were Bovidae (16%), Mustelidae (14%), Leporidae (10%), Canidae (10%), Ursidae (6%), Sciuridae (4%), Castoridae (4%), and Felidae (2%). None of the other 15 families comprised more than 1% of cold weather clothing uses. Hereinafter, we will refer to the nine families that comprised 2% or more of the uses as "cold weather clothing families."

TABLE 1 ABOUT HERE

The remains of cold weather clothing families occur in both Mousterian strata and Aurignacian/Gravettian strata (Table 2). However, the frequencies differ, and for some families the difference is statistically significant. When the numbers of Mousterian and Aurignacian/Gravettian strata containing the remains of the nine cold weather clothing families are compared with the chi-squared test, three families are significantly more frequent in Aurignacian/Gravettian strata than in Mousterian strata: Canidae (p=0.000), Leporidae (p=0.000), and Mustelidae (p=0.000) (Table 2). In contrast, none of the cold weather clothing families is significantly more frequent in Mousterian strata than in Aurignacian/Gravettian strata. Thus, cold weather clothing families occur in both early modern human-associated strata and Neanderthal-associated strata, but some families are found more frequently in the former than in the latter.

TABLE 2 ABOUT HERE

Discussion

Potentially, these results have important implications for the debate about clothing use by Neanderthals and early modern humans, but there are some complications that need to be evaluated before the implications are clear. One is that the Stage 3 Faunal Database only records the presence/absence of taxa rather than the actual number of specimens recovered per taxon. This is potentially problematic because it means that one specimen of a taxon in a stratum was given the same weight as, say, 100 specimens of the same taxon in another stratum, in the analyses. Thus, in principle, the analyses could have obscured a numerical dominance of cold weather clothing specimens in Mousterian strata. It is surprisingly difficult to evaluate this possibility. Values for Number of Individual Specimens (NISP) and Minimum Number of Individuals (MNI) have been published for remarkably few Mousterian, Aurignacian, and Gravettian sites. However, data for a small but balanced sample of sites with published NISP values (15 Mousterian and 15 Aurignacian/Gravettian sites) suggests that this concern can be discounted. Canids, leporids, and mustelids consistently represent a higher percentage of the NISPs at the Aurignacian/Gravettian sites that at the Mousterian sites (Table 3).

TABLE 3 ABOUT HERE

A second problematic issue is that certain Late Pleistocene mammals (e.g. bears, hyenas) can be expected to have utilized some of the same caves and rock shelters as Neanderthals and early modern humans, and therefore some of the bones found in the focal strata are likely to have been introduced as a result of the activities of such species. It is possible, therefore, that the difference in the representation of cold weather clothing families in Mousterian strata and Aurignacian/Gravettian strata has nothing to do with the actions of Neanderthals and early modern humans. However, it is unlikely that the activities of cave-using species explain the higher frequency of canid, leporid, and mustelid remains in Aurignacian/Gravettian strata. Not only is the proportion of Aurignacian/Gravettian strata that are from caves and rock shelters lower than the proportion of Mousterian strata that are from such sites (Table 4), but also the proportion of Aurignacian/Gravettian cave/rock shelter strata that contain canids, leporids, and mustelids is lower than the proportion of Mousterian cave/rock shelter strata that contain canids, leporids, and mustelids (Table 5).

TABLES 4 AND 5 ABOUT HERE

Differential availability of species is a third concern. In principle, the difference in the representation of cold weather clothing families in Mousterian strata and Aurignacian/Gravettian strata could be due to early modern humans having greater access to members of those families rather than because they targeted them more often. This also seems unlikely. The three key families—canids, leporids, and mustelids—are ubiquitous in Europe and were likely so throughout the Late Pleistocene (Nowak 1999). Temporal proximity to the Last Glacial Maximum does not explain the higher frequency of canids, leporids, and mustelids in early modern human strata either. To investigate this possibility, we removed the Gravettian strata from the dataset and re-ran the comparison. The results did not change. Canid, leporid, and mustelid remains were significantly more frequent in Aurignacian strata than in Mousterian strata (Table 6). This indicates that the difference in behaviour between Neanderthals and early modern humans was present in the earliest phase of early modern human colonization of Europe and does not reflect a greater availability of cold weather clothing families closer to the Last Glacial Maximum.

TABLE 6 ABOUT HERE

The final concern is that the pattern is real but is a consequence of differences in diet rather than differences in clothing production and use, i.e. canids, leporids, and mustelids do occur more frequently in Aurignacian/Gravettian strata than in Mousterian strata because early modern humans were hunting them more often than were Neanderthals, but early modern humans were hunting them for food rather than for producing cold weather clothing. This possibility is more difficult to evaluate, not just because taxa can be hunted for both meat and fur, but also because humans vary so widely in terms of the things they are willing to eat. Nevertheless, we think it is unlikely that the difference in the representation of cold weather clothing families in Mousterian and Aurignacian/Gravettian strata is solely due to differences in dietary preferences. The higher frequency of Leporidae is probably due in part to early modern humans hunting them for food, but that is unlikely to be the case for Mustelidae and Canidae. A search of the eHRAF World Cultures Database indicated that no canid or mustelid genus was recorded as being used for food more than 11 times, which suggests that mustelids and canids are rarely eaten by humans living at mid to high latitudes. The corollary of this is that the greater frequency of mustelids and canids in Aurignacian/Gravettian strata is unlikely to be a consequence of these families having been hunted for food more often by early modern humans than by Neanderthals. Instead, the difference seems likely to be a consequence of a greater use of mustelid and canid pelts for cold weather clothing by early modern humans.

Given that none of the main potential criticisms of our results withstands scrutiny, we can now consider their implications for the debate about clothing use by Neanderthals and early modern humans. To reiterate, there is general agreement that early modern humans in Europe utilized specialized cold weather clothing, but the nature of the clothing used by Neanderthals is disputed. Some researchers contend that they did not use clothes (e.g. Kittler et al., 2003; Toups et al., 2011). Others argue that they were limited to ineffective, cape-like clothing (Gilligan, 2007; Wales, 2012). Still others aver that their clothing was not substantively different in terms of thermal effectiveness from that of early modern humans (Sørenson, 2009; White, 2006). Thus, currently there are three hypotheses with respect to differences in clothing use between Neanderthals and early modern humans: 1) the Neanderthals did not use clothes at all, while early modern humans employed specialized cold weather clothing; 2) the Neanderthals employed only cape-like clothing, which was of limited thermal effectiveness, while early modern humans used specialized cold weather clothing; and 3) the Neanderthals used specialized cold weather clothing just like early modern humans.

Our first finding—that the remains of cold weather clothing families occur in both early modern human-associated strata and Neanderthal-associated strata—is not consistent with all of the hypotheses. Given that, as we explained earlier, we can be reasonably confident that the canid and mustelid remains are more likely to be indicators of clothing use than they are of dietary behaviour, an implication of their occurrence in both early modern human strata and Neanderthal strata (Table 2) is that both Neanderthals and early modern humans used clothing. This conflicts with the hypothesis that Neanderthals did not use clothes at all, while early modern humans employed specialized cold weather clothing. In contrast, it is in line with the hypothesis that the Neanderthals employed only cape-like clothing while early modern humans used specialized cold weather clothing. It is also in line with the hypothesis that the Neanderthals used specialized cold weather clothing just like early modern humans.

Our second finding—that the remains of leporids, mustelids, and canids occur significantly more often in early modern human-associated strata than in Neanderthal-associated strata—is easier to reconcile with one of the remaining hypotheses than with the other. The higher frequency of leporids, mustelids, and canids in early modern human strata is difficult to square with the hypothesis that the Neanderthals used specialized cold weather clothing just like early modern humans. It might have been possible if some of the other cold weather clothing families occurred more frequently in Neanderthal strata than in early modern human strata. If that had been the case, it might have been possible to argue that the skins of the cold weather clothing families in question do not differ substantively in terms of thermal effectiveness from those of leporids, canids, and mustelids, and that Neanderthals and early modern humans simply chose to use different species to produce their cold weather clothing. However, given that none of the cold weather families is more common in Neanderthal-associated strata than in early modern human-associated strata, the "adaptively neutral choice" explanation is not viable. Instead, the higher frequency of leporids, mustelids, and canids in early modern human strata suggests that the clothing of early modern humans was different from that of the Neanderthals and involved the use of more fur, which would have made it more thermally effective. Thus, our results run counter to the idea that the Neanderthals used specialized cold weather clothing just like early modern humans.

By way of contrast, the higher frequency of leporids, mustelids, and canids in early modern human strata than in Neanderthal strata is consistent with the hypothesis that the Neanderthals employed only cape-like clothing while early modern humans used specialized cold weather clothing. All we need to assume is that the early modern humans' clothing required more skins of leporids, mustelids, and canids than did the cape-like clothing of the Neanderthals. This assumption is supported by the ethnographic record, which indicates that fur trim was a key feature of the specialized cold weather clothing developed by a number of groups living in the Arctic, and that mustelid and canid pelts were favoured for such trim (Bogoraz-Tan 1909; Pryde 1972; Oakes et al., 1995, Cotel et al. 2004). Research carried out to shed light on this preference suggests that mustelid and canid fur makes excellent trim because its mixture of long and short hairs slows the velocity of air in the "boundary layer" at the edges of clothing, where skin is exposed, and therefore reduces heat loss (Oakes et al., 1995; Cotel et al. 2004). In addition, mustelid and canid fur sheds ice and frost easily (Oakes et al., 1995; Cotel et al. 2004). These observations suggest that the higher frequency of mustelid and canid remains in early modern human strata could well be a consequence of early modern humans adding fur trim to certain items of clothing to make them more thermally effective.

To shed further light on this possibility, we compared the number of wolverine (*Gulo gulo*) specimens in the Aurignacian/Gravettian and Mousterian strata represented in the Stage 3 Project Faunal Database. We focused on wolverines for three reasons. First, wolverine fur was widely used as ruffs on parkas and other garments by recent sub-Arctic and Arctic groups (Oakes et al., 1995). Second, work on the protection against adverse weather conditions offered by different furs indicates that wolverine fur is the best natural fur to use as a parka ruff (Oakes et al., 1995; Cotel et al. 2004; Mizell et al. 1965). It provides excellent protection from the wind, sheds hoarfrost particularly well, and is extremely durable (Oakes et al., 1995, Cotel et al. 2004; Itkonen 1962). Lastly, contemporary trapping organizations advise that wolverine pelts are ill suited for the construction of the bodies and arms of coats because the fur is too long and the leather too heavy (e.g. http://www.montanatrappers.org/furbearers/wolverine.htm#). Together, these observations suggest that the presence of wolverine in an archaeological deposit indicates the production and use of parkas with fur ruffs.

We found a substantial disparity in the number of wolverine remains in Aurignacian/Gravettian and Mousterian strata. There are 56 wolverine remains in the 237 Aurignacian/Gravettian strata, but not a single wolverine specimen in any of the 96 Mousterian strata. Given that there is reason to think wolverine remains indicate the use of parkas with fur ruffs, the presence of wolverine bones in numerous Aurignacian/Gravettian strata and their complete absence in Mousterian strata supports the idea that early modern humans added fur trim to their clothing to make them more thermally effective, while Neanderthals did not. This is consistent with the hypothesis that the Neanderthals employed only cape-like clothing while early modern humans used specialized cold weather clothing.

Our study highlights another line of evidence that supports the hypothesis that Neanderthals used cape-like clothing while early modern humans used specialized cold weather clothing. The hypothesis is now supported by modeling work that indicates Neanderthals could not have survived during the cold periods of OIS3 without some form of clothing (Aiello and Wheeler, 2003; Wales, 2012); by the occurrence of bone needles in early modern human-associated strata but not in Neanderthal-associated strata (Hoffecker 2005a; Golovanova et al. 2010a, 2010b); and by differences in the frequency of the remains of mammals that are known to be useful for making cold weather clothing in Neanderthal-associated and early modern human-associated strata. None of these lines of evidence is conclusive, but we believe that collectively they make a good case for favouring the hypothesis that Neanderthals used cape-like clothing while early modern humans used specialized cold weather clothing over its competitors.

There may in fact be another line of evidence that supports the hypothesis that Neanderthals used cape-like clothing while early modern humans used specialized cold weather clothing. The thermal effectiveness of hide clothing is affected by the nature and degree of processing of the hide. Pliable hide is much warmer than stiff hide, because it can be made to conform to the body. Thus, evidence for hide processing in Neanderthal strata versus early modern human strata is potentially informative about the thermal effectiveness of their clothing. There is a clear difference between Neanderthals and early modern humans with regard to the best-known hide processing tool—the endscraper. As we explained earlier, there is good evidence that endscrapers were specialized hide processing tools (e.g. Hayden 1990; Jefferies 1990; Shott and Weedman 2007; Loebel 2013). Endscrapers typically occur in high frequencies in early modern human sites in Europe, but they are almost non-existent in Neanderthal sites (Hayden 1990; Mellars 1995). This difference could be taken to indicate that Neanderthals did not use clothing at all. However, there are two reasons to think that this interpretation is incorrect. First, use-wear studies indicate that Neanderthals employed other types of stone tools for hide processing (e.g., Beyries 1988; Anderson-Gerfaud 1990; Hayden 1990). Hide processing made up a small percentage of the tasks identified in these studies, but the percentage was not negligible. In addition, Soressi and colleagues (2013) have recently reported the discovery of bone *lissoirs* that were used for hide processing at two Middle Palaeolithic sites in Europe. Together, these observations suggest that Neanderthals engaged in hide processing on a regular basis, but not with the same frequency as early modern humans. This, we contend, is the pattern predicted by the hypothesis that Neanderthals used cape-like clothing while early modern humans used specialized cold weather clothing. So, it appears that the hypothesis is actually supported by four lines of evidence.

If the Neanderthals only had cape-like clothing while the early modern humans had specialized cold weather clothing, there are implications for the replacement of the Neanderthals by early modern humans. As explained earlier, it is generally agreed that the Neanderthals' stout body and relatively short limbs are adaptations to glacial conditions (Feldesman et al. 1990, Ruff 1993). In contrast, the bodies of early modern humans appear to have been adapted for tropical conditions (Ruff 1993). Thus, the implications depend on the advantage of early modern human clothing over Neanderthal clothing compared to the advantage of Neanderthal physiology over early modern human physiology. If early modern human clothing conferred a small advantage relative to the advantage conferred by Neanderthal physiology, then early modern humans' clothing may have simply helped level the playing field in relation to Neanderthal physiology, allowing them to cope with cold temperatures as well as Neanderthals could. Alternatively, if the advantage conferred by early modern human clothing was large compared to the advantage conferred by Neanderthal physiology, then early modern humans' clothing could have helped them outcompete Neanderthals. There are at least two reasons for favouring the second of these scenarios. One is that energetic modeling work suggests the lower critical temperature and minimum sustainable ambient temperature for Neanderthals would have been only 1 to 2.5 °C below those for early modern humans (Aiello and Wheeler 2003), which suggests that the advantages conferred by Neanderthal physiology were relatively small. The other is that there is evidence that early modern humans were able to withstand more adverse conditions than Neanderthals. Their cold period occupations extend further north than do those of Neanderthals (van Andel et al. 2003), and attempts to reconstruct climatic conditions at archaeological sites dating to OIS 3 indicate that, on average, early modern human-associated sites experienced higher wind chill than Neanderthal-associated sites (Aiello and Wheeler 2003). This implies that, with respect to cold stress, early modern humans' physiological disadvantages were outweighed by their technological advantages. There is reason therefore to believe that the difference in clothing helped early modern humans successfully compete with Neanderthals for territory and resources.

Why there was a difference in the clothing used by Neanderthals and early modern humans is unclear. There appear to be two possibilities. One is that the Neanderthals were insufficiently intelligent to create garments of the same thermal effectiveness as those used by early modern humans. Klein (2009) has argued that early modern humans were able to "wield culture more effectively" (p. 1526) than Neanderthals due to a change in their brain function ca. 50 kya. According to Klein, this change enhanced the ability of early modern humans to communicate symbolically and allowed them to produce tools from a wider range of materials. It is feasible that the manufacture of specialized cold weather clothing is another consequence of the putative change in brain function. The other possibility is that cultural factors explain the difference in clothing. Recent history demonstrates that differences in cognitive ability are not needed for one hominin population to expand at the expense of another, or for one hominin population to cope with a deteriorating climate while another does not—cultural factors are sufficient. Cultural innovations enabled early farmers to expand into areas of Europe already occupied by hunter-gatherer groups, and cultural factors explain why the Greenland Norse died out while the Inuit Greenlanders expanded their territory during the Little Ice Age (Henrich 2010). Thus, it is feasible that the difference in clothing was a consequence of differences in cultural trajectories, combined with social and/or linguistic impediments to cultural transmission from early modern humans to Neanderthals. For example, it is possible that the Neanderthals' failure to develop more thermally effective clothing relates to the procurement of pelts. Trapping appears to be required for successful hunting of mustelids and canids (Holliday 1998). Thus, it could be that Neanderthals failed to develop as thermally effective clothing as early modern humans because their trapping technology was less productive than that developed by early modern humans, as Holliday and Churchill (2006) have suggested. Determining which, if any, of these hypotheses is correct will require further empirical research.

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Table 1. Frequency of use of mammalian families for cold-weather clothing by recent mid-to-high latitude small-scale groups. Data from eHRAF. Only families that make up ≥1% of uses are listed. See text for further details.

Family	#	%
Cervidae	77	32
Bovidae	39	16
Mustelidae	34	14
Leporidae	24	10
Canidae	24	10
Ursidae	14	6
Sciuridae	10	4
Castoridae	10	4
Felidae	5	2
Other families	1	0
Total	238	

Table 2. Results of chi-squared tests comparing frequencies of remains of cold-weather clothing families in Mousterian and Aurignacian/Gravettian strata. Data from the Stage 3 Project Mammalian Fauna Database. P-values based on the chi-squared test. Because we effectively conducted multiple unplanned tests, we used Benjamini and Hochberg's (1995) method of significance-level correction. The corrected significance level was = 0.017.

Family	**% Moust**	**% Au/Gr**	**p-value**
Bovidae	91	84	0.096
Canidae	51	78	0.000***
Castoridae	7	9	0.559
Cervidae	92	95	0.188
Felidae	44	40	0.492
Leporidae	23	55	0.000***
Mustelidae	20	42	0.000***
Sciuridae	18	18	0.998
Ursidae	54	45	0.136

Table 3. Comparison of Number of Individual Specimens (NISP) for canids, leporids, and mustelids at Mousterian sites vs Aurignacian/Gravettian sites. All = All non-microfauna. % = Total NISP of Focal taxon as a percentage of total non-microfauna NISP.

Site	Country	Canid	Leporid	Mustelid	All	Source of data
Mousterian sites						
Lynford	UK	7	0	0	1363	Schreve (2006)
Geissenklosterle	Germany	45	8	0	764	Kitagawa et al. (2012)
Hohle Fels	Germany	9	1	0	659	Kitagawa et al. (2012)
Hohlenstein-Stadel	Germany	401	4	0	7245	Kitagawa et al. (2012)
Bockstein	Germany	58	7	0	1208	Kitagawa et al. (2012)
Vogelherd	Germany	8	2	0	543	Kitagawa et al. (2012)
Saint-Cesaire	France	10	3	0	1544	Morin 2012
Pech-de-l'Azé IV	France	3	0	0	1003	Dennis Sandgathe
Roc de Marsal	France	12	0	0	2019	Dennis Sandgathe
La Quina	France	16	0	1	5396	Debénath and Jelinek (1998)
Mujina Pecina	Croatia	5	22	4	272	Miracle (2005)
Frechet	France	19	9	1	810	Mourre et al. (2008)
Pech-de-l'Azé I	France	2	2	2	813	Soressi et al. (2008)
Grotte Tournal	France	31	34	0	1644	Boyle (1998)
Jonzac	France	0	0	0	788	Dennis Sandgathe
	Total	**626**	**92**	**8**	**26071**	
	%	**2.40**	**0.35**	**0.03**		
Aurignacian/Gravettian sites						
Abri Pataud	France	82	5	0	4040	Bouchud (1975)
Roc de Combe	France	51	20	22	1694	Soulier and Mallye (2012)
Saint-Cesaire	France	53	5	6	5038	Morin (2012)
La Solutre	France	25	35	0	3586	Bemilli and Bayles 2009
Geissenklosterle	Germany	373	449	1	7046	Kitagawa et al. 2012
Hohle Fels	Germany	166	526	1	5163	Kitagawa et al. 2012
Hohlensten-Stadel	Germany	254	22	0	2423	Kitagawa et al. 2012
Bockstein	Germany	28	19	0	366	Kitagawa et al. 2012

Vogelherd	Germany	58	27	0	4617	Kitagawa et al. 2012
Abri Castanet	France	36	30	0	1384	Castel 2011
Buran Kaya III	Ukraine	620	290	10	2156	Crepin et al. 2014
Milovice G	Czech Republic	18	28	4	1326	Svoboda et al. 2005
Willendorf I	Austria	71	9	0	224	Musil 2003
Willendorf II	Austria	104	4	2	294	Musil 2003
Maisieres-Canal	Belgium	64	151	1	352	Gautier 1979
	Total	**2003**	**1620**	**47**	**39709**	
	%	**5.04**	**4.08**	**0.12**		

Table 4. Frequencies of Mousterian and Aurignacian/Gravettian strata from caves/rock shelters versus open-air sites.

	Mousterian		Aurignacian/Gravettian	
	#	%	#	%
Caves/rock shelters	83	86	174	73
Open-air sites	13	14	63	27
Total	96		237	

Table 5. Frequencies of strata containing potential cave-dwelling taxa from caves/rock shelters versus open-air sites. Potential cave-dwelling taxa = leporids, canids, mustelids, ursids, sciurids, and felids. Covered = cave/rock shelter strata. Open = open-air strata.

	Mousterian		**Aurignacian/Gravettian**	
	Covered	**Open**	**Covered**	**Open**
All	63 (90%)	7 (10%)	151 (72%)	60 (28%)
Leporids	17 (77%)	5 (23%)	82 (63%)	48 (37%)
Mustelids	14 (74%)	5 (26%)	54 (55%)	45 (45%)
Canids	44 (90%)	5 (10%)	127 (68%)	59 (32%)

Table 6. Results of chi-squared tests comparing frequencies of remains of cold-weather clothing families in Mousterian and Aurignacian strata. P-values based on the chi-squared test. Because we effectively conducted multiple unplanned tests, we used Benjamini and Hochberg's (1995) method of significance-level correction. The corrected significance level was = 0.017.

Family	**% Mousterian**	**% Aurignacian**	**p-value**
Bovidae	91	87	0.411
Canidae	51	82	0.000***
Castoridae	7	3	0.242[1]
Cervidae	92	97	0.077
Felidae	44	38	0.372
Leporidae	23	42	0.003***
Mustelidae	20	40	0.001***
Sciuridae	18	25	0.189
Ursidae	54	48	0.397

[1] Yates' continuity correction was applied for expected values of <5

Appendix. Mammalian taxa represented in the Stage 3 Project Faunal Database

Family	**Taxon**	**Common name(s) (45)**
Bovidae	*Bos primigenius*	Auroch
	Bos sp.	Auroch, cattle, kouprey, banteng, gaur, seladang, yak
	Bison sp./*B. priscus*	Bison, wisent, buffalo
	Capra sp.	Goat, ibex, tur, markhor
	Capra ibex	Ibex
	Capra pyrenaica	Spanish ibex
	Ovis sp.	Sheep, mouflon, urial, argali
	Ovibos moschatus	Musk ox
	Saiga tartarica	Saiga antelope, saiga
	Undifferentiated bovids	
Canidae	*Canis lupus*	Wolf
	Cuon sp.	Dholes
	Vulpes vulpes	Red fox
	Vulpes corzac	Corsac fox
	Alopex lagopus	Arctic fox
Castoridae	*Castor fiber*	Beaver
Cercopithecidae	*Macaca sylvana/sylvanus*	Macaque, barbary ape
Cervidae	*Dama dama*	Fallow deer
	Megaloceros sp./*Megaloceros giganteus*	Giant deer
	Alces alces	Elk, moose
	Cervus elaphus	Red deer, wapiti, elk
	Rangifer tarandus	Reindeer, caribou
	Capreolus capreolus	Roe deer
	Rupicapra rupicapra	Chamois
Dipodidae	*Sicista* sp.	Birch mice

	Sicista subtilis	Southern birch mouse
	Sicista betulina	Northern birch mouse
	Allactaga sp	Jerboas
	Alactagulus sp.	Jerboas, little earth hares
Elephantidae	*Mammuthus primigenius*	Mammoth, woolly mammoth
	Elephas (*Palaeoloxodon*) *antiquus*/*Elephas* (*Palaeoloxodonta*) sp.	Straight-tusked elephants
Equidae	*Equus hydruntinus*	Steppe ass
	Equus hemionus	Hemione, kulan, onager
	Equus cabalus	Wild horse
	Equus sp.	Horse, kiang, zebra, quagga, ass, burro, donkey, hemione, kulan, onager
	Equus asinus	Ass, burro, donkey
	Equus latipes	Extinct horse
Erinaceidae	*Erinaceus* sp.	Eurasian hedgehogs
	Erinaceus europea	Hedgehog
Felidae	*Panthera* sp.	Big cats
	Panthera leo	Lion
	Panthera spealea	Cave lion
	Panthera pardus	Leopard
	Felis sylvestris	Wild cat
	Lynx lynx/Felis lynx/Felis sp.	Lynx
	Lynx/Felis pardina	Pardel lynx, Spanish lynx
	Lynx sp.	Undifferentiated lynxes
Hyaenidae	*Crocuta crocuta*/*Hyaena spelaea*	Spotted hy(a)ena, striped hy(a)ena
Hystricidae	*Hystrix cristata*/*vinogradovi*	Porcupine, Old World porcupine
Leporidae	*Oryctolagus cuniculus*	Rabbit
	Lepus sp.	Hares, jack rabbits
	Lepus europaeus/*capensis*	Brown hare

	Lepus timidus	Mountain hare
	Lepus tolai	Tolai hare
Muridae	*Apodemus* sp.	Old World mice
	Apodemus flavicollis	Yellow-necked mouse
	Apodemus sylvaticus	Wood mouse
	Cricetus cricetus	Common hamster
	Cricetus sp.	Hamsters
	Cricetulus migratorius	Grey hamster
	Mesocricetus sp.	Golden hamster
	Allocricetus bursae	Extinct hamster
	Arvicola sapidus	Southern water vole
	Arvicola terrestris	Northern water vole
	Arvicola sp.	Water vole
	Pliomys lenki	Extinct vole
	Pliomys sp.	Extinct voles
	Ptericola (*Pitymys*) *fatioi* (subgenus of *Microtus*)	No common name found
	Ptericola (*Pitymys*) *duodecimcostatus*	No common name found
	Ptericola (*Pitymys*) *subterraneneus*	No common name found
	Pericola (*Pitymys*) *savii*	No common name found
	Ptericola (*Pitymys*) sp.	No common name found
	Microtus brecciensis/carbrera	No common name found
	Microtus afghanus	No common name found
	Microtus hyperboreus	No common name found
	Microtus arvalis	Common vole, vole
	Microtus agrestis	Field vole
	Microtus gregalis	Vole, meadow mouse
	Microtus nivalis	Snow vole
	Microtus oeconomus/raticeps	Northern vole
	Microtus sp.	Undifferentiated voles, meadow mice

	Clethrionomys glareolus	Bank vole
	Clethrionomys rutilus	Ruddy vole
	Clethrionomys rufocanus	Grey sided vole
	Clethrionomys sp.	Red backed mice
	Lemmus sp.	Lemmings
	Lemmus lemmus	Norway lemming
	Dicrostonyx torquatus	Collared lemming
	Lagurus lagurus	Steppe lemming
	Eolagurus luteus	No common name found
	Myopus schisticolor	Wood lemming
	Spalax sp.	Mole-rats
	Ellobius sp.	Mole-voles, mole-lemmings
Mustelidae	*Meles meles*	Badger
	Mustela minuta	Least weasel
	Mustela erminea	Stoat, ermine
	Mustela nivalis	Weasel
	Mustela sp.	Mink, ferret, weasel, stoat, ermine, polecat
	Putorius/Mustela putorius	Polecat
	Putorius putorius robusta/Mustela eversmanni	Large polecat, steppe polecat
	Martes sp.	Marten, fisher, sable
	Gulo gulo	Wolverine
	Lutra lutra	Otter
Myoxidae	*Myoxus/Glis glis*	Edible doremouse, fat doremouse
	Muscardinus avellanarius	Doremouse, hazel mouse
	Eliomys quercinus	Garden doremouse
Ochotonidae	*Ochotona pusilla*	Pika, mouse hare, coney
Rhinocerotidae	*Dicerorhinus/Stephanorhinus mercki/kirckbergensis*	Extinct rhino
	Dicerorhinus/Stephanorhinus hemitoechus	Extinct rhino

	Dicerorhinus/Stephanorhinus sp.	Hairy rhino, Sumatran rhino
	Coelodonta antiquitatis	Woolly rhino
Soricidae	*Crocidura* sp. group	White toothed shrews
	Sorex "araneaus" group	Common shrews
	Sorex minutus	Pigmy shrew
	Sorex minutissimus	Least shrew
	Sorex sp.	Long-tailed shrews
	Neomys sp.	Water shrews
Sciuridae	*Pteromys* sp.	Flying squirrels
	Marmota primigenia	Extinct marmot
	Marmota bobak	No common name found
	Marmota sp.	Marmot, woodchuck, groundhog
	Marmota marmota	Alpine marmot
	Spermophilus major/Citellus superciliosus	No common name found
	Spermophilus sp.	Ground squirrels, susliks
	Sciurus vulgaris	Red squirrel
Suidae	*Sus scrofa*	Wild boar, wild pig, pig
Talpidae	*Talpa* sp.	Old World moles
	Talpa europea	Mole
	Desmana sp.	Desmans
Ursidae	*Ursus arctos*	Brown bear, grizzly, grizzly bear
	Ursus sp.	Bears
	Ursus spelaea	Cave bear
Vespertilionidae	*Plecotus auritus*	Old World long-eared bat