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Theresa Bloß, B.Sc.

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I. Abstract

Vogelherd Cave in Germany is a significant archaeological site that has been excavated since 1931, providing valuable insights into the lives of our ancient ancestors. The site has yielded a wealth of prehistoric material, including human remains from the Neolithic and the Magdalenian periods. However, numerous bone fragments remain unidentified.

To address this, I analyzed and taxonomically identified 640 morphologically non-diagnostic bone fragments from the site using Zooarchaeology by Mass Spectrometry (ZooMS), a palaeoproteomics-based method for taxonomic determination of small and fragmentary bones typically found in Palaeolithic assemblages on the basis of their collagen "fingerprint". Of the 640 bone fragments I analyzed using ZooMS, 88% were successfully classified. Especially significant was the identification of four new hominin bones, that were identified along with faunal material such as woolly mammoths and various ungulates, including cervids and equids.

One of the human bones was directly dated using radiocarbon (^{14}C) dating at 5480-5650 cal BP (= calendar years before present). While this bone falls in the Neolithic period, the age of the remaining human bones that are set to be dated soon has not yet been determined. The possibility of discovering anatomically modern human bones from the Aurignacian period is particularly exciting, as they could be among the earliest in Europe.

These results help shed light to our ancestors' cultural and biological evolution in Europe and highlight the importance of continuous research and the advancement of innovative analytical techniques in the field of human evolution.

II. Acknowledgements

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VI. List of Abbreviations and Taxon Definitions

AH	Archaeological Horizon
AMH	Anatomically Modern Humans (*Homo sapiens*)
Artiodactyla	Taxonomic order of even-toed (hooved) mammals, including cervids, bovids and suids
BP	Before Present
Carnivora	Taxonomic order of mammals that includes a diverse group of carnivorous species such as felines and canines
^{14}C	Radiocarbon dating
cal BP / ka BP	Calibrated years before present/ thousand years before present
Lagomorpha	Taxonomic order of small mammals that includes rabbits and hares
MALDI-TOF MS	Matrix-assisted laser desorption/ionization time-of-flight mass spectrometry
µCT	Micro-computed tomography
NISP	Number of identified specimens
Perissodactyla	Taxonomic order of odd-toed (hooved) mammals such as equids
Primates	Taxonomic order that includes mammals such as humans, apes and monkeys
Proboscidea	Taxonomic order of mammals that includes elephants and their extinct relatives, such as the woolly mammoth
VH	Vogelherd Cave
ZooMS	Zooarcheology by Mass Spectrometry

1. Introduction

Vogelherd Cave in Germany is an important archaeological site that has provided valuable insights into the lives of our ancient ancestors. It was first excavated in 1931 by Gustav Riek, and more recently, from 2005 to 2012, by Nicholas J. Conard.

The site is particularly noteworthy due to the wealth of archaeological material found there, dating mainly to the Pleistocene period, specifically the Aurignacian. The Aurignacian material is believed to have been crafted by early anatomically modern humans (AMH, *Homo sapiens*) who lived in the Swabian Jura region, inhabiting Vogelherd and other caves during the Pleistocene (Conard et al., 2004; Niven, 2007). However, the involvement of Neanderthals in the production of the Aurignacian artifacts can at the moment not be entirely ruled out (Conard et al., 2004; Sankararaman et al., 2012), given that both Neanderthals and AMH coexisted in Europe during the Middle to Upper Palaeolithic transition not long before the Aurignacian period (40–30 ka BP; Conard and Bolus, 2003). This complicates the understanding of the production and use of Aurignacian-age material at Vogelherd.

For a long time the remains of AMH retrieved at Vogelherd in 1931, known as the Stetten fossils, had given strong evidence to the theory that early modern humans were the sole producers of the Aurignacian artifacts, but the redating of these fossils with radiocarbon (^{14}C) methods revealed them to be much younger than previously thought, placing them into a Neolithic context and rendering them irrelevant in discussions of who were the makers of Aurignacian artifacts (Conard et al., 2004; Niven, 2007). This left the rich Aurignacian assemblage without any direct context to hominin remains and weakens arguments supporting the *Danube Corridor Hypothesis*, obscuring the general matter of the appearance of AMH in Central Europe (Conard et al., 2004; Conard and Bolus, 2003; Sala and Conard, 2016; Street et al., 2006). Recent radiocarbon analysis of two hominin bones recovered from the site revealed that they date back to the relatively young periods of the Neolithic and the Magdalenian (Wang et al., *in prep.*). The young age of these specimens indicates that they were either moved by animals or intentionally buried deep down in older layers by humans, possibly in form of a secondary burial ritual. This idea is consistent with findings from Hohlenstein-Stadel, where secondary burials at a cave site have been documented (Orschiedt, 2012). The discovery of the Magdalenian specimen from Vogelherd by Wang et al. (*in prep.*) is a significant milestone in the study of the site. It is the oldest human specimen identified from the cave to date, and it comes from a particularly interesting time in which, after a period of depopulation coinciding with the Last Glacial Maximum, Magdalenian groups spread back into central Europe (Barbieri et al., 2018).

In Swabia, almost all Palaeolithic sites are caves or rock shelters, with only a few notable exceptions (Barbieri et al., 2018). Burials at such sites were common during the Palaeolithic period, but in total, only a small number of individuals has been found up to date, especially in comparison to the period's long time span and the favorable preservation condition of sheltered sites (Orschiedt, 2012).

To obtain a more detailed picture of the occupation patterns of Vogelherd Cave, the identification and analysis of further human remains is necessary. Unfortunately, the remaining unidentified bones from the site are highly fragmented, making species determination challenging, especially when relying solely on bone morphology. However, palaeoproteomic techniques like Zooarchaeology by Mass Spectrometry (ZooMS) can accurately and precisely identify small and fragmentary bones that are otherwise difficult to identify based on morphology alone (Buckley and Collins, 2011). ZooMS is a powerful technique that uses protein mass spectrometry to identify and distinguish between different animal species based on their collagen profiles (Buckley, 2018; Buckley, Collins et al., 2009) and has proven itself to be particularly useful for identifying the small and fragmentary bones typically found in Palaeolithic assemblages (Brown et al., 2016). The primary focus of this thesis is to apply ZooMS to bone fragments recovered from Vogelherd Cave, with the key goal of identifying previously undiscovered human bones in addition to faunal remains.

Over the following sections, this thesis offers a comprehensive exploration of the Vogelherd Cave, including its location within the geographic setting of the Swabian Jura, the history of the excavations at the site, and the stratigraphic chronology, which will provide an overview of the cave and its surroundings. The zooarchaeology of the site is further examined through the presentation of faunal material previously examined by other researchers. Moreover, the human remains from the Magdalenian and Neolithic periods are thoroughly investigated, including the renowned Stetten fossils that were discovered during the 1931 excavations. This thesis will then delve into the cutting-edge ZooMS method, including an introduction to its principles, which is followed by an in-depth discussion of the specific materials and methods utilized in this particular study. Finally, the results of this research will be presented, critically evaluated, and compared to the zooarchaeological context presented earlier. Subsequently, the possible chronological origins of the hominin bones identified in this research are discussed, with consideration given to the Aurignacian, Magdalenian, and Neolithic periods in which the site and/or area was occupied. A final discussion is provided on possible future developments and the purpose of uses of ZooMS.

2. Vogelherd Cave - Site Background

2.1. Geographic Setting and Description of Vogelherd Cave

The Vogelherd Cave, located between Stetten and Bissingen in Germany (Figure 1), is one of the key Palaeolithic sites in the Swabian Alb region (Conard et al., 2003). The Swabian Alb, also known as the Swabian Jura, is Germany´s largest closed karst system and home to seven caves, including Vogelherd, that were awarded UNESCO World Heritage status in 2017 (Bertacchi et al., 2021). Palaeolithic research in the area has a long history, dating back to Oskar Fraas´ excavations in the 1860s (Conard, 2011; Conard and Bolus, 2006).

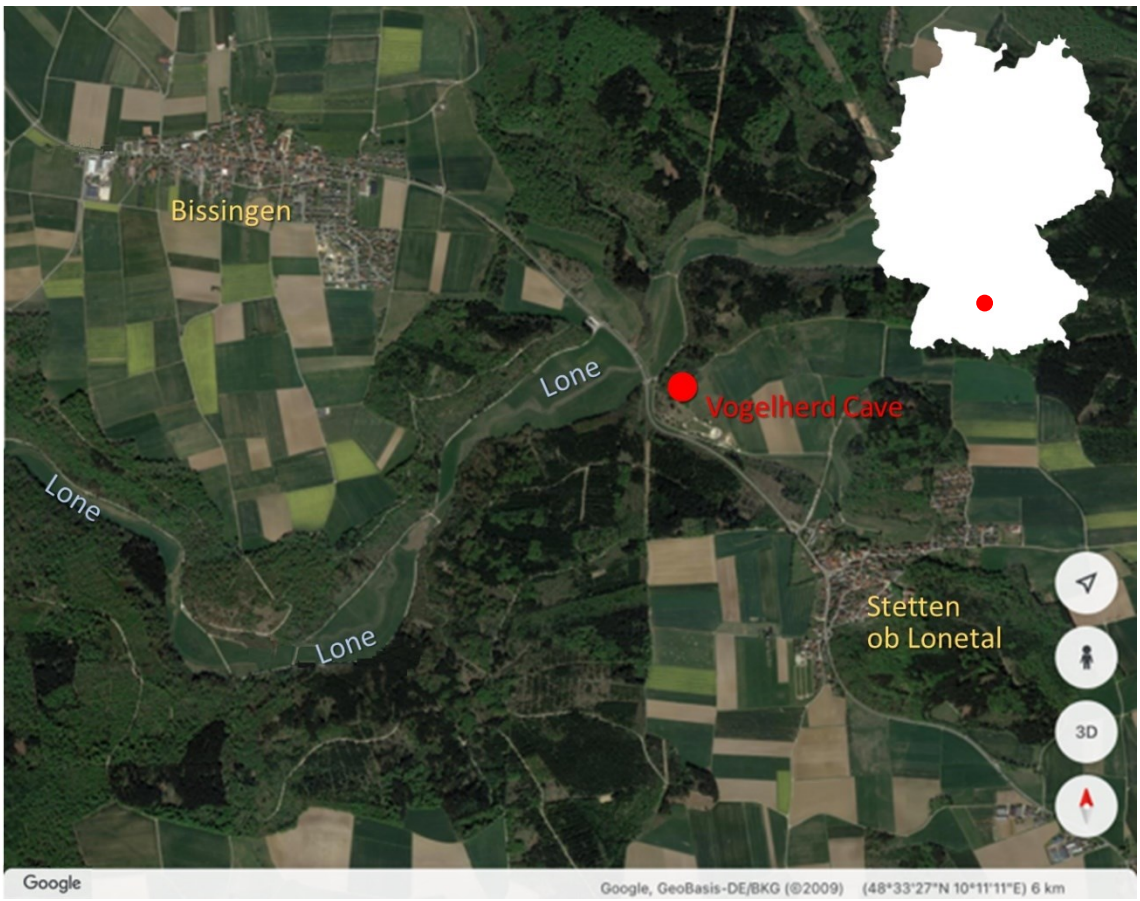

Figure 1: Geographic location of the Vogelherd Cave in the Lone Valley. (map taken from Google Earth, manipulated)

The caves in the Ach Valley and the Lone Valley are particularly interesting due to their rich archaeological record, providing evidence of prehistoric occupations spanning thousands of years in the Middle and Upper Palaeolithic (Conard, 2011; Gamble, 1979; Niven, 2007). Despite the limited number of human remains found in the caves of the Swabian Jura, researchers believe that the Middle Palaeolithic artifacts were crafted by Neanderthals and the Upper Palaeolithic artifacts by AMH, respectively, based on assumptions drawn from studies in other regions (Conard, 2011).

Moving to the Lone Valley, one of the main attractions for prehistoric groups must have been the abundance of cave shelters. Vogelherd Cave is just one of at least nine limestone caves in the area, seven of which have been found to contain Palaeolithic deposits (Abel et al., 2002; Hahn et al., 1985, cited by Niven, 2006, p. 15). However, the Lone Valley's geological and ecological diversity likely played a significant role in drawing these groups to the area as well. Bordered by two distinct ecosystems, the area offered a stark contrast between the drier plateau to the north, which may have resembled a steppe during the Pleistocene, and the vast, swampy flatlands to the south, known as *Flächenalb*, which extended all the way to the Danube River (Niven, 2006, p. 15).

Caves served as valuable shelters for prehistoric groups, and Vogelherd was no exception (Niven, 2007; Straus, 1990). The cave's location on a high limestone plateau with southern exposure and proximity to resources likely made it a desirable spot for early human settlers. In addition to providing shelter, the location of Vogelherd made it an ideal location for prehistoric groups to observe the movements of seasonally migrating mammals in the Lone Valley (Niven, 2006, p. 15; Niven, 2007; Riek, 1934). The plateau's elevation and southern exposure would have offered a strategic vantage point for observation, while the proximity to resources such as water and game would have made survival easier for these early settlers.

To the south and southwest, the Vogelherd has two main entrances (Figure 2), lying about 18 meters above the valley floor (Niven, 2007). A third entrance on the northern slope is more challenging to access (Riek, 1934, p. 7). The interior of the cave consists of passages ranging from 15 to 25 meters in length, 2 to 7 meters in width, and 2 to 3 meters in height (Niven, 2007). These dimensions made the interior spaces easy to heat with fire and ideal for the range of activities that took place during the Pleistocene (Niven, 2007).

Figure 2: Vogelherd Cave.
(credits a: Alb-Donau-Kreis Tourismus: Vogelherd; b: Reise-Zikaden: Das Innere dere Vogelherdhöhle)

According to Riek (1932), life in the Upper Palaeolithic centered mainly in the main chamber behind the southwest entrance, as well as in front of the cave. Sediments in these areas were

densely permeated with fireplaces and prehistoric artifacts, offering a glimpse into the daily lives of prehistoric groups who once inhabited the cave (Riek, 1932).

Today, Vogelherd Cave looks quite different from its appearance in the past, as it has been strongly affected by weathering processes (Niven, 2006, p. 16; Niven, 2007). Particularly the south entrance is strongly damaged (Niven, 2006, p. 16).

2.2. Excavations and Chronostratigraphy of Vogelherd Cave

Since its discovery in 1930 by Hermann Mohn, excavations led by Gustav Riek (1931) and Nicholas Conard (2005-2012) have yielded a wealth of archaeological material dating mainly to the Middle and Upper Palaeolithic periods (Conard et al., 2003). Vogelherd has been the subject of numerous studies and several have praised the site for its importance in understanding the human settlement in southwestern Germany in the Upper Palaeolithic, especially the Aurignacian period (Boger et al., 2014; Heckel et al., 2014; Niven, 2007).

2.2.1. 1931 Excavations (Gustav Riek)

In 1931, Gustav Riek and his team (Figure 3a, b) conducted a thorough excavation of the Vogelherd Cave, removing 300 m^3 of Pleistocene sediment from the cave and uncovering artifacts from the Middle and Upper Palaeolithic periods (Conard et al., 2004), as well as several human bones (Riek, 1932).

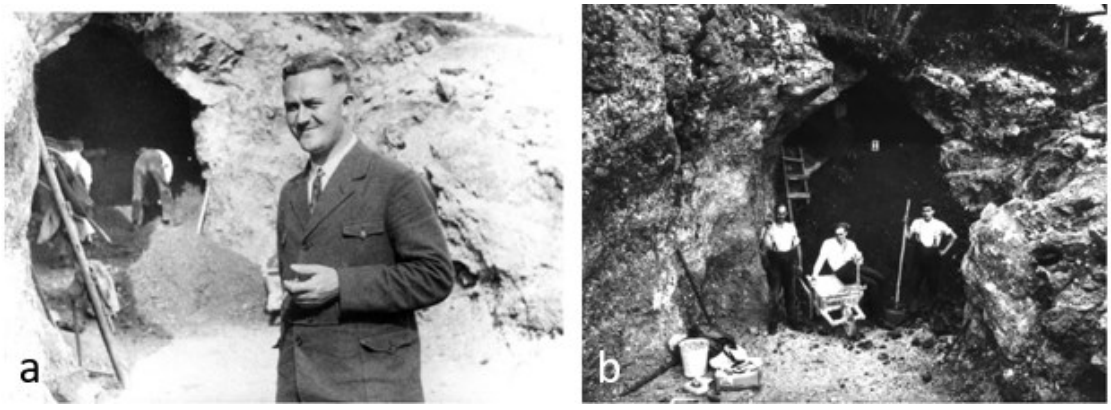

Figure 3: Excavations at Vogelherd Cave in 1931.
(a) Gustav Riek standing in front of the southwest entrance (credits: Universität Tübingen), (b) workers excavating archaeological horizon I (credits: Universität Tübingen).

Riek documented the excavation process in great detail, publishing 12 stratigraphic profiles from different areas within the cave and detailed descriptions of the sediments in his Monograph *Die Eiszeitjägerstation am Vogelherd im Lonetal* in 1934. In the 12 stratigraphic profiles, Riek recognized nine archaeological horizons (AH I-IX) (Riek, 1934, pp. 40, p. 50). Figure 4 displays a stratigraphic profile located near Vogelherd's southwest entrance, serving as a representative example.

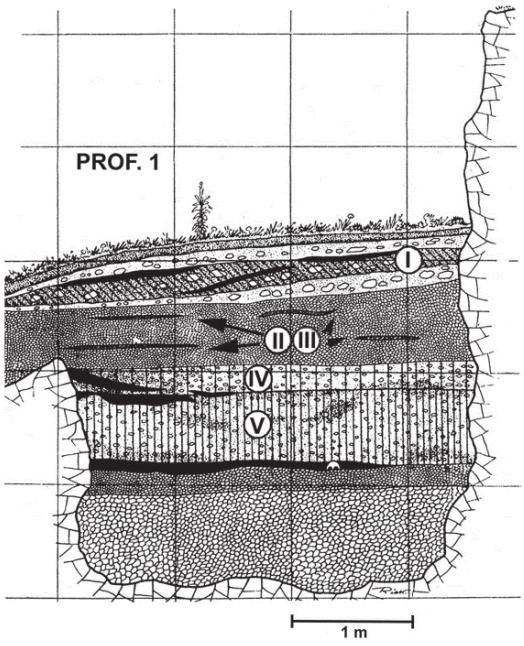

Figure 4: Stratigraphic profile 1.
Stratigraphic profile 1 shows the archaeological horizons I-V, including the location from which the Stetten 1 cranium (Homo sapiens) was retrieved from the base of the Aurignacian level V (Riek, 1934, p. 41: Fig. 3 adapted by Conard et al. 2003).

The following table (Table 1) showcases the archeological horizons documented by Riek. It is important to note that the archeological horizons were revised by Conard et al. (2003) as the designations provided by Riek are not accurate. In this thesis, the revised designations of the archeological horizons can be found in the following chapter (*2.2.2.*) in Table 2.

Table 1: Riek´s designations of the archeological horizons I-IX.

Archeological horizon (AH)	**Riek´s designation** (Riek, 1934, p. 50)
I	Neolithic (Neolithikum)
II	Magdalenian (Oberer Magdalénien)
III	Magdalenian (Unterer Magdalénien)
IV	Upper Aurignacian (Oberes Aurignacien)
V	Middle Aurignacian (Mittleres Aurignacien)
VI	Lower Aurignacian (Unteres Aurignacien)
VII	Mausterian (Moustérien)
VIII	Upper Acheulean (Jung Acheuléen)
IX	Cave floor (Höhlensohle)

Interestingly, none of the profiles documented by Riek consist of all nine archaeological horizons (Niven, 2006, p. 20).

Riek´s excavation took a total of 10 weeks to complete, during which the cave was completely emptied of its sediments (Niven, 2006 p. 6; Niven, 2007). Even though in comparison to other excavations at the time Riek´s excavation was of a high standard, the excavation protocol did not include screening and sieving of the sediments. So small finds such as lithic debitage, ivory working

debris, and bone fragments were missed (Boger et al., 2014; Conard, 2016; Niven, 2006, pp. 6). Based on the faunal remains that were reported, it is presumed that Riek and his team discarded many undiagnostic fragments that were less than 3 cm in maximum length (Niven, 2007). The discarded material, which is referred to as "*backdirt*" or "*backfill*" (Figure 23, p. 66) was deposited in front of the southwest entrance and the terrasse between the south and the southwest entrance (Schürch et al., 2020). This, of course, destroyed the stratigraphy of the layers.

2.2.2. 2005 – 2012 Excavations (Nicholas J. Conard)

The backdirt and the underlying sediments were excavated by the University of Tübingen in excavations led by Nicholas Conard (Boger et al., 2014). The team focused in particular on the backdirt in front of the south and southwest entrances of the cave, in a series of excavations between 2005 and 2012 (Boger et al., 2014; Conard et al., 2016). While Figure 5 displays the area of the re-excavation, a photograph taken during the excavations can be found in Figure 24, p. 66 in the Appendix.

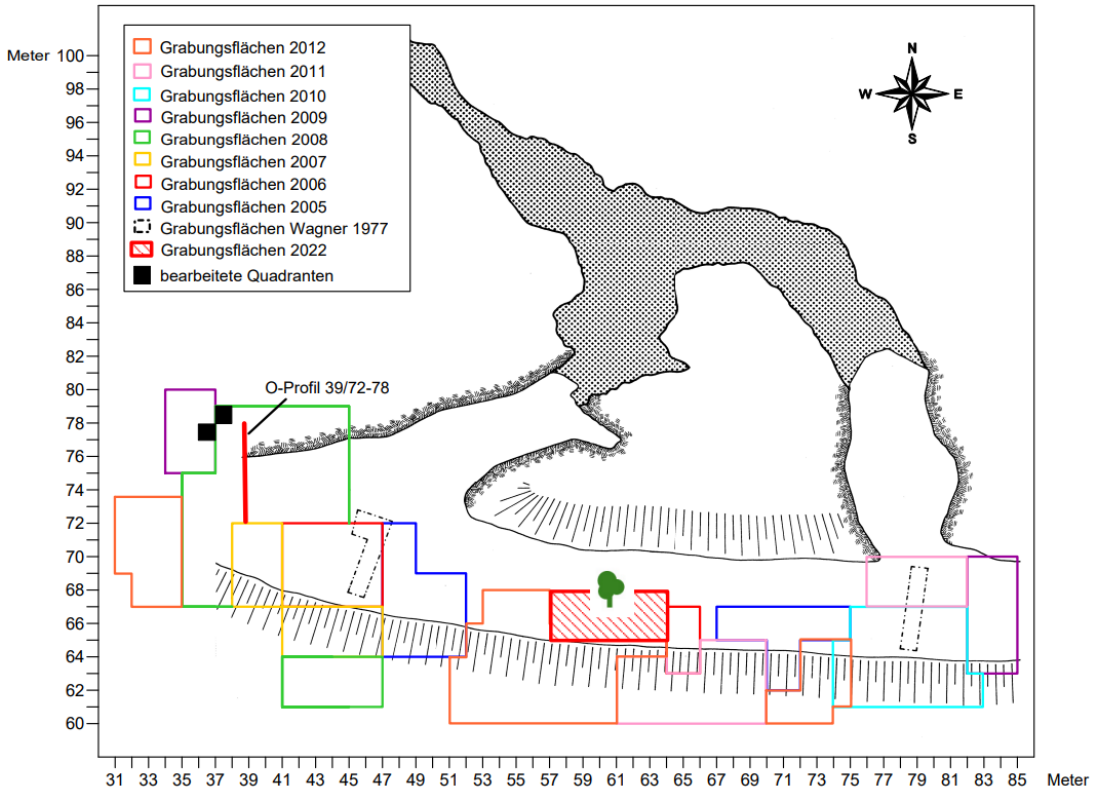

Figure 5: Areas of excavation in the backdirt at Vogelherd Cave.
The black squares show the locations from which the material analyzed in this thesis was retrieved (credits: Ältere Urgeschichte und Quartärökologie, Universität Tübingen, Alexander Janas).

As part of the re-excavations, numerous layers of sediment were recorded and documented (Figure 7). The topmost layer of the backdirt, known as HU, is a humus layer that is approximately 10 cm thick and covers the underlying sediments (Conard and Zeidi, 2011; Schürch et al., 2020).

This is not exclusively prehistoric sediment, but rather a layer of sediment that has accumulated since the 1931 excavations. The hummus is followed by a layer named HL/KS (heller Lehm, Kalkschutt) which can be described as a fine, light brown homogenous sediment mix with a high percentage of calcareous debris. This layer of about 0.5-1.2 m is the actual "backdirt", so material originally from inside Vogelherd Cave that was relocated during the 1931 excavations led by Gustav Riek (Conard and Zeidi, 2011). The HL/KS contains material from several layers of the cave, but most finds from this layer can be typologically assigned to the Aurignacian period (Conard and Zeidi, 2011; Schürch et al., 2020). Below the HL/KS lie the sediments that used to form the area in front of the cave before Riek's excavations (Boger et al., 2014). The DKS (dunkler Lehm, Kalkschutt) is a relatively thin layer of sediment that used to be the original top sediment in front of the cave before the overlay of the HL/KS. It is a dark brown, loamy layer with a high proportion of calcareous debris, that covers the intact lower layers (Boger et al., 2014; Conard and Zeidi, 2011; Schürch et al., 2020). GF/KS (gelbbrauner lösartiger Schluff, Kalkstein) and GL/GKS (gelber Lehm, grober Kalkschutt) are both yellow-brown loess-like silt with small sharp-edged and irregularly distributed limestones (Conard et al., 2010). GF/KS lies over and is, therefore, younger than GL/GKS (Conard et al., 2010). These layers are commonly referred to as the "intact layers". Although there is limited material available from these sediments, the intact layers can possibly be placed in the context of the Middle Palaeolithic period (Conard et al., 2010). Two artifacts from intact layers (Figure 6) are both Levallois offcuts (dorsal negatives arranged centripetally) and thus can be confidently placed in the Middle Palaeolithic (Conard et al., 2010; Schürch, personal correspondence). This thesis will examine the fauna of the intact layers within the framework of the Middle Palaeolithic era.

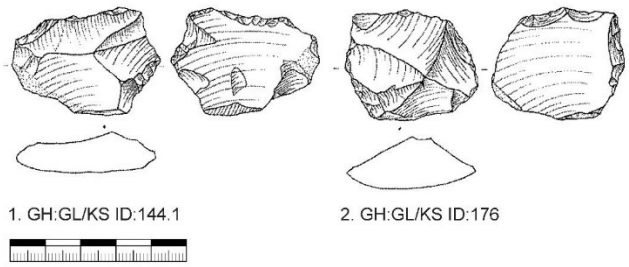

Figure 6: Middle Palaeolithic levallois offcuts from the intact layers at Vogelherd Cave. (Conard et al., 2010, adapted)

No profile was found that accurately depicts the GL/KS or GL/GKS sediments, which represent very small-scale layers. The closest profile to the area shown in Figure 7 can be seen in Figure 25 in the Appendix, but the GL/GKS is not visible there either. Based on these profiles, it can be concluded that intact layers were present beneath the HL/KS, but the amount of especially GL/GKS in the squares examined is small-scale.

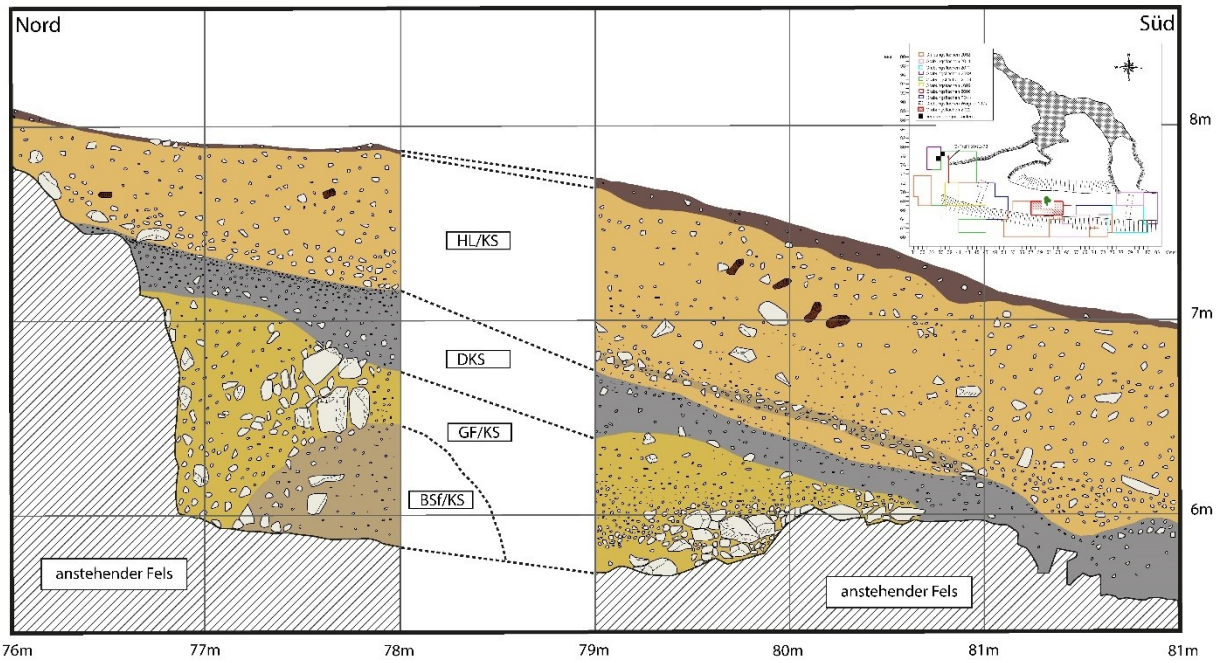

Figure 7: Excavation profile from the Vogelherd re-excavations.
This is the profile of the region where the material analyzed in this thesis study was obtained (credits: Ältere Urgeschichte und Quartärökologie, Universität Tübingen, Alexander Janas).

As noted before, Conard et al. (2003) also revised the designations of the archeological horizons Riek had documented during his excavations in 1931 (Table 2).

Table 2: The archeological horizons of Vogelherd Cave.
The middle column lists the horizons originally recognized by Riek, and the right column lists the revised layer designations.

Archeological horizon (AH)	**Riek´s designation** (Riek, 1934, p. 50)	**Revised designation** (Boger et al., 2014, Conard et al., 2003)
I	Neolithic (Neolithikum)	Neolithic
II	Magdalenian (Oberer Magdalénien)	Magdalenian
III	Magdalenian (Unterer Magdalénien)	Magdalenian
IV	Upper Aurignacian (Oberes Aurignacien)	Upper Palaeolithic (Aurignacian)
V	Middle Aurignacian (Mittleres Aurignacien)	Upper Palaeolithic (Aurignacian)
VI	Lower Aurignacian (Unteres Aurignacien)	Middle Palaeolithic (Mousterian)
VII	Mausterian (Moustérien)	Middle Palaeolithic (Mousterian)
VIII	Upper Acheulean (Jung Acheuléen)	Middle Palaeolithic
IX	Cave floor (Höhlensohle)	Middle Palaeolithic

In consideration of the revised horizon designations, the archeological horizons can be characterized as follows: The Neolithic AH I is a black-brown humus layer with yellow-white fine-grained lime (Schürch et al., 2020). This is followed by two Magdalenian layers (AH II-III) consisting mainly of yellow-white fine chipped limestone rubble. The two Aurignacian layers (AH IV-V) are of particular importance due to making up over 90% of the material found in the cave and the discovery of figurative art, organic and lithic artifacts, and morphologically identifiable remains of modern humans, (Conard et al., 2004; Niven, 2007; Riek, 1932, 1934). The Middle Palaeolithic layers (AH

VI-IX) of the Vogelherd Cave have sparse archaeological material, and Neanderthals and carnivores were likely the main occupants during this period (Boger et al., 2014). AH VI is described as small chipped limestone rubble and ochre yellow clay. AH VII and VIII consist mainly of coarse chipped limestone rubble (Boger et al., 2014). Riek (1934) classified AH IX as the "culture of the cave floor" (Riek, 1934, translated). This layer consists of ochre yellow loam and clay and is believed to date to the Marine Isotope Stage 5e, although an even older dating seems possible (Schürch et al., 2020). A crucial piece of evidence for this early chronological classification is a molar tooth of a straight-tusked elephant found in this layer, which is known to have lived during warm periods (Niven, 2006, pp. 77; Schürch et al., 2020).

Using detailed excavation methods and sieving, the new excavations revealed several thousands of bone and ivory fragments, mainly from the HL/KS layer, and the first analysis of the faunal material recovered by the team around Conard was published (Boger et al., 2014; Conard and Zeidi, 2011). However, several thousands of bone fragments that lack taxonomic determination were also collected from the backdirt and the underlying sediments.

3. Zooarchaeological Context

In 1954, palaeontologist Ulrich Lehmann published first findings on the Vogelherd faunal assemblage, including a taxonomic classification of 180 individuals (Lehmann, 1954). However, his publication lacked a clear and organized structure, making it difficult to relocate specific specimens when 50 years later Laura Niven worked on the Vogelherd material. She published a detailed summary of the faunal assemblage in her book *The Palaeolithic Occupation of Vogelherd Cave* in 2006. In her monograph, Niven (2006) discusses the identification of an impressive amount of specimens, from which over 7,000 specimens could be identified at species level (Boger et al., 2014; Niven, 2006, pp. 11, p.117). In 2014, Boger et al. published further data on the Vogelherd faunal assemblage, specifically the material recovered in the 2005-2012 excavations. These excavations added several new species to the previously known fauna of the Vogelherd site. The newly added species comprise marten (*Martes sp*.), polecat (*Mustela sp*.), European hedgehog (*Erinaceus europaeus*), and roe deer (*Capreolus capreolus*). Furthermore, the range of species has been expanded to include domestic sheep (*Ovis aries*) and goats (*Capra hircus*) that were present in the area during the Neolithic period (Boger et al., 2014).

Naihui Wang was the first to analyze material from the Vogelherd faunal assemblage (2005-2012 excavations) using ZooMS (N=240) (Wang et al., *in prep.*).

3.1. The Middle Palaeolithic / Intact Layer´s Faunal Assemblage

Four of the stratigraphic layers documented at Vogelherd Cave, namely AH VI–IX, are assigned to the Middle Palaeolithic (Conard et al., 2003; Niven, 2006, p. 77). Despite their significance in our understanding of the cave´s history, these horizons have yielded a very limited amount of archaeological material (N=544). For instance, the IX layer, which constitutes the cave floor, only produced a single molar from a straight-tusked elephant (*Elephas/Palaeoloxodon antiquus*) (Niven, 2006, pp. 78). Interestingly, the AH VII horizon (N=519), which adds the most specimens to the Middle Palaeolithic faunal assemblage, is predominantly composed of horse (*Equus ferus*) specimens. However, other animals such as rhinoceros (*Coelodonta antiquitatis*), ungulates and several carnivores are also present in this layer (Niven, 2006, p. 79). The AH VIII layer provided 18 specimens, and AH VI six specimens (Niven, 2006, pp. 78).

During the 2005-2012 re-excavations, only a small amount of archaeological material (N=210) was found in the intact layers in front of Vogelherd, making up around 12% of the material of the re-excavations. The species composition of the intact layers is similar to that found in the archaeological horizons inside the cave, with horse and woolly mammoth-sized species being the most prevalent (Boger et al., 2014). Also, the only other remain of *Elephas/Palaeoloxodon antiquus* was found in these intact layers. Signs of human exploitation, such as cutmarks were also found on some of the faunal remains retrieved from the intact layers (Boger et al., 2014).

Figure 8 displays the faunal abundance of the Middle Palaeolithic AH VI-IX and the intact layers outside the cave. The figure substantiates the impressive abundance of horses in the Middle Palaeolithic assemblage of AH VI-IX. Interestingly, though carnivores have been identified in the AH VI-IX, their abundance in the intact layers as assessed by Boger et al. (2014) is much higher. But even though these specimens were found in the intact layers, it is questionable, whether the material is originally from these sediments or may have been introduced from the overlying backfill of the 1931 excavations, which is supported by the composition of species retrieved (Boger et al., 2014).

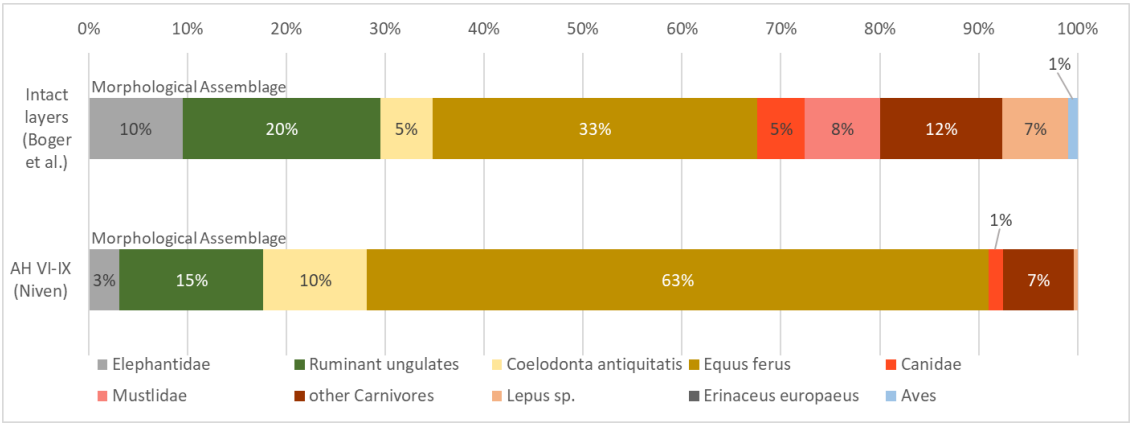

Figure 8: Faunal distribution in archaeological horizons VI-IX and the intact layers on the basis of traditional zooarchaeological analyses.
Niven (2006) documented Middle Palaeolithic archaeological horizons VI-IX (N=544) and Boger et al. (2014) reported intact layers (N=210).

Though the range of species noted by Niven (2006) and Boger et al. (2014) are similar, the distributions within the assemblage differ significantly. The findings indicate only minimal occupation of Neanderthals in the Middle Palaeolithic at Vogelherd Cave (Niven, 2006, p. 112) and also during the period of accumulation of the intact sediment layers regardless of whether this was during the Middle Palaeolithic or in parts later (Boger et al., 2014).

3.2. The Upper Palaeolithic Faunal Assemblage

While the Middle Palaeolithic horizons have provided only little amount of faunal material, the much more relevant part comes from the Upper Palaeolithic, in Niven´s analysis specifically the Aurignacian archeological horizons (AH IV-V).

The megaherbivores woolly mammoth (*Mammuthus primigenius*) and woolly rhinoceros (*Coelodonta antiquitatis*) are both well represented in the Aurignacian assemblage found at Vogelherd. Especially the woolly mammoth is numerous in comparison to other regional Palaeolithic sites, making Vogelherd one of the most significant mammoth assemblages in Central Europe (Niven, 2006, p. 193). The mammoth remains include complete teeth and bones, as well as rare deciduous tusks. Juvenile mammoths make up one-third of the assemblage, and there is evidence of exploitation, but it is unclear whether they were hunted or collected (Boger et al., 2014; Niven, 2007). Niven (2007) suggests that while mammoths may have also been used as a source of food, their primary use by the Aurignacian inhabitants of the Vogelherd Cave was for non-food subsistence needs, such as building materials and artifact production. The extent to which woolly rhinoceros were utilized by the Aurignacian inhabitants of the Vogelherd Cave for subsistence is unclear. The remains found at the site do not provide clear evidence of anthropogenic involvement, such as hunting or butchery marks (Niven, 2007). It is possible that woolly rhinoceros were also used for non-food purposes, similar to the proposed use of mammoths (Niven, 2007).

Four distinct species of cervids are known to have coexisted in the Swabian Jura, namely reindeer (*Rangifer tarandus*), red deer (*Cervus elaphus*), giant deer/Irish elk (*Megaloceros giganteus*), and roe deer (*Capreolus capreolus*) (Münzel et al., 2017). According to Niven (2007) the inhabitants of Vogelherd Cave relied heavily on the hunting and processing of these large ungulates, especially reindeer and horses, for sustenance and resource procurement. The exploitation of the cold-climate taxa reindeer (*Rangifer tarandus*) and horse (*Equus sp.*) is evident in a large number of bone remains at the site, many of which show evidence of systematic breakages, likely indicative of marrow processing activities (Niven, 2007, p. 155). Both reindeer and horse bones display cutmarks and hammerstone impact scars, indicating that these animals were hunted and butchered by the Aurignacian inhabitants of Vogelherd (Niven, 2006, p. 138). These animals provided an important source of food, including meat, marrow, and fat, as well as materials used in the creation and maintenance of tools and other artifacts (Niven, 2007). The hunting of these animals was time- and labor-intensive and was conducted primarily during warmer months, with age data indicating that reindeer were hunted during late summer and autumn, and horse hunted during summer and early autumn (Boger et al., 2014; Niven, 2006, p. 155). Niven (2006, p. 157) also implies that hunting of these species may have been carried out either by the same group hunting reindeer and horse complimentary or by different human groups occupying the cave at different times of the year. Studies also indicate the hunting of horses and reindeer during their seasonal migration, at a time when both species were in their best physical condition (Boger et al., 2014). Additionally, the horse assemblage shows signs of selective transport, possibly based on within-bone nutrients rather than economic value (Boger et al., 2014; Niven, 2007). The Irish elk, red deer, wild boar (*Sus scrofa*), and chamois (*Rupicapra rupicapra*), are represented in smaller numbers at the site and seem to have played a secondary role in human hunting activities. However, the remains of these taxa also show evidence of butchery, suggesting that they were also exploited by the Aurignacian inhabitants of Vogelherd. These taxa are primarily associated with temperate environments and may have been hunted during interstadial or milder phases of a cold stage (Niven, 2007).

Carnivores seem to have been only occasional visitors to the cave and did not inhabit it permanently, which is likely due to the intense human use of the cave during this time period (Niven, 2006, p. 187). It is unlikely that the Vogelherd served as a carnivore den regularly during the Aurignacian period, although carnivores do play a small role in the Aurignacian bone accumulation (Niven, 2006, pp. 189). The analysis of the age data of the carnivore remains discovered suggests that the majority of the remains belong to adult individuals, rather than juveniles, which aligns with the idea that the cave was not utilized as a denning site by the carnivores (Niven, 2007). However, it is worth noting that the scarcity of juvenile remains could also be a result of

preservation and collection bias rather than an absence of young individuals (Niven, 2007). Additionally, the little evidence of gnawing damage on the bones of the Aurignacian faunal assemblage overall argues against the idea that the faunal remains found at Vogelherd were carnivore prey (Niven, 2007). Only some remains of juvenile mammoth and rhinoceros bones show gnawing damage that suggests transport to the cave by bone-collecting predators such as wolves, hyaenas, or lions (Niven, 2007). The highest number of carnivore specimens comes from bears (*Ursus arctos*/ *Ursus spalaeus*). But the latter, the cave bear (*Ursus spalaeus*), which is more numerously found in the Vogelherd Aurignacian assemblage is known to live purely vegetarian (Bocherens et al., 1993; Niven, 2007). Other carnivores, such as foxes, wolverines, and wild cats, seem to have played a minor role in the Aurignacian ecosystem at Vogelherd Cave and though badgers may have been frequent visitors in the cave, their remains may be intrusive from the Holocene, as badgers tend to burrow deep into sediments (Niven, 2006, pp. 189). Note, that therefore Niven excluded all badger remains from her analysis (Boger et al., 2014). Overall, carnivores are present in the Vogelherd Aurignacian deposit, but with the exception of one fox, the other carnivore remains show no evidence of human utilization (Niven, 2006, p. 190; Niven, 2007). They seem to have been mostly background fauna or scavengers, with little to no direct involvement with human activities at the site.

The Upper Palaeolithic has also yielded a small number of hares (*Lepus sp.*) and several different types of birds at Vogelherd (Niven, 2006, p. 177). The fact that small animals such as hares and birds were found in the Aurignacian at Vogelherd is consistent with a trend of Upper Palaeolithic groups in Eurasia relying more heavily on small game for their diets during this time period (Niven, 2006, p. 180; Stiner et al., 2000). However, it is unclear if small game played a larger role in the subsistence economies at Vogelherd due to the sparse nature of the faunal remains, which could be due to taphonomic processes (Niven, 2006, p. 180). Hares were also procured in large numbers for their furs and while there is no clear evidence of this at the Swabian Jura cave faunas, there is a small trend of increasing exploitation of small game and fish during the Gravettian at Hohlenstein-Stadel (Gamble, 1979) and Geissenklösterle (Münzel and Conard, 2004), two other sites in the Swabian Jura region, indicating a similar trend in southwest Germany (Niven, 2006, p. 180).

As discussed before, Vogelherd Cave in Central Europe yielded a significant assemblage of mammoth bones. During the re-excavations Boger et al. (2014) found several more mammoth remains, making up 35% of the total HL/KS fauna (Figure 9), with 94% of the new finds being ivory fragments. They also identified additional remains of young mammoths, suggesting that the animals died in the summer, which aligns with the seasonal occupation of the site. Thus, as stated before, it is unclear whether mammoths were hunted by human groups or their remains were collected at the opportunity (Boger et al., 2014; Niven, 2007).

The analysis also proved horses to be a dominant species in the geological unit HL/KS, with a similar skeletal element distribution to the horse assemblage found in the Aurignacian (AH IV/V) deposit (Boger et al., 2014). This finding is crucial as it highlights the consistency in horse butchery and marrow extraction patterns over the time the cave was used and supports that the exploitation of horses by Palaeolithic humans was a major activity in the Palaeolithic of the Swabian Jura (Boger et al., 2014).

The total abundance of ruminant ungulates, such as Bovids, Cervids, and Suids, in the HL/KS, is 17% (Boger et al., 2014). According to Boger et al. (2014), the HL/KS reindeer remains also show similar types of butchery as seen in AH IV/V, including marrow extraction and meat removal, though the distribution of skeletal remains seems to be different (Boger et al., 2014). They also identified aurochs or bison (*Bos/Bison*), wild pig (*Sus scrofa*), red deer (*Cervus elaphus*), chamois (*Rupicapra rupicapra*), and roe deer (*Capreolus capreolus*), but all playing only a minor role in the HL/KS assemblage.

Humans seem to have used wolves for their fur, bones, and teeth, but there is little evidence of human exploitation of carnivores in general (Boger et al., 2014). The relatively low number of bears in comparison to other nearby caves may be due to human occupation of Vogelherd making it less appealing as a hibernation spot for bears (Boger et al., 2014). As Vogelherd Cave was discovered by Hermann Mohn (1931) through the burrowing activities of badgers, it does not seem surprising, that a large number of badger remains were recovered (Boger et al., 2014). However, determining whether badger remains at an archaeological site are intrusive can be difficult, so they are often excluded from analyses like the one conducted by Niven (Boger et al., 2014).

Wang analyzed additional faunal material from HL/KS using Zooarchaeology by Mass Spectrometry (Wang et al., *in prep.*). Consistent with the morphological analyses, a significant number of Elephantidae remains were identified (33%). Notably, Wang et al.´s analysis revealed a higher abundance of hare remains (10%) compared to Boger et al. (2014), who identified hare remains as accounting for 5% of the fauna.

For a better overview of the zooarchaeological context of the HL/KS and original archeological horizons II-IX, Figure 9 shows the abundance of faunal remains.

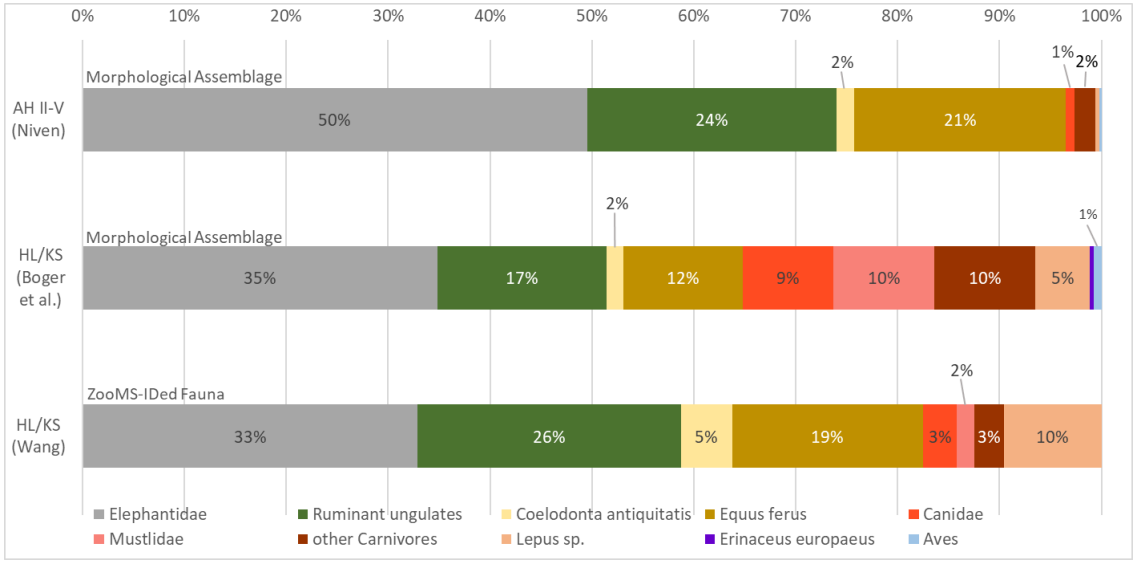

Figure 9: Faunal distribution in archaeological horizons II-V and the HL/KS sediment using both traditional methods (Niven and Boger) and ZooMS (Wang).
Faunal distribution was analyzed in AH II-V (N=7206) by Niven (2006), as well as in the HL/KS sediment by Boger et al. (2014) (N=1967) and Wang et al. (N=240[1]).

4. The Hominin fossils of Vogelherd Cave

During the 1931 excavations several human remains were found. The so-called Stetten fossils were located in the Aurignacian layers, which made them particularly interesting to Riek. Their location brought the human bones into context with the Aurignacian artifacts of the AH IV/V and gave evidence for AMH as their sole producers (Conard et al., 2004).

One of the Stetten fossils, a skull (Stetten 1, Figure 10a), was found partially encased in a strong layer of ash and resting on fine limestone debris close to the southwest entrance in the base of the "Middle Aurignacian" layer (Gieseler, 1940; Riek, 1932). Additionally, the upper jaw was found, but the cheekbones were missing (Riek, 1932). Close by, a lower jaw containing three molar teeth and belonging to the same individual (Stetten 1, Figure 10b) was found, which had also been damaged in ancient times by a knockoff of one of the Ramus mandibulae (Gieseler, 1940; Riek, 1932).

[1] Hominin specimens n=3 not included

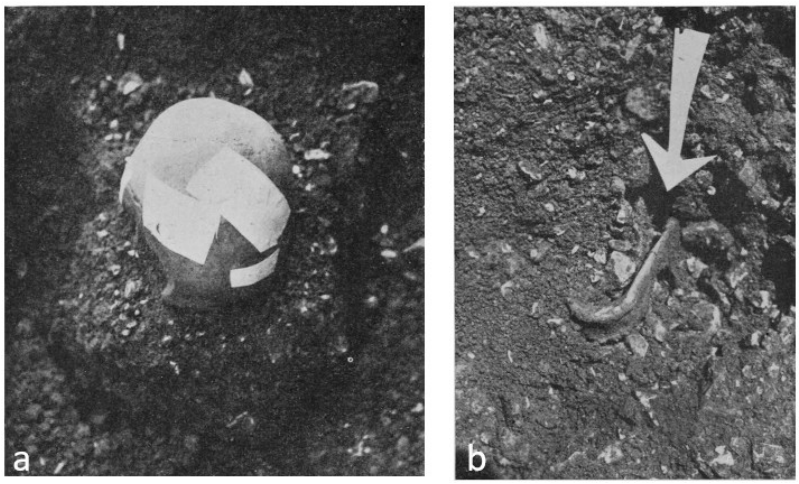

Figure 10: Stetten 1 (a) cranium and (b) mandible.
(Riek, 1932: 2+3 adapted)

Two vertebrae (Stetten 4), that were found scattered a few meters east in the same stratigraphic context are also believed to have belonged to the same individual, Stetten 1 (Gieseler, 1940; Riek, 1932). A humerus (Stetten 3), found in the central part of the cave, was initially described as being very robust and muscular by Gieseler in 1940, leading him to theorize that it could be the bone of a Neanderthal in an Aurignacian context. However, later studies using systematic morphometry disproved this theory (Churchill and Smith, 2000). The results of the study showed that based on its shape and strength measures, the specimen belongs to early modern humans and not Neanderthals (Churchill and Smith, 2000). A second cranium (Stetten 2) was found close to the south entrance of the cave, around 30 meters apart from the human remains associated with Stetten 1 (Conard et al., 2004; Gieseler, 1937). The remains are assumed to have belonged to at least 2 individuals.

Nearly 70 years after discovery, radiocarbon measurements performed directly on bone samples from Stetten 1-4 revealed that these remains are around 3,900 to 5,000 years old and therefore date to the Neolithic period (Conard et al., 2004) and not the earlier Upper Palaeolithic humans. Their age makes it certain that they originate from intrusive Neolithic burials and removes them from the context of the Aurignacian artifacts (Conard et al., 2004; Conard and Bolus, 2003).

In addition to the more famous Stetten fossils, further skeletal material was discovered at the site (Figure 11), specifically the Neolithic horizon I (Orschiedt, 1998). But as they were from such a young age, they gained less attention and popularity. The AH I individuals consist of four fragmentary crania, two maxillary and three mandibular fragments, several fragments of pelvis, several long bones, and several smaller skeletal elements of the body skeleton, such as ribs and vertebrae, though these are largely underrepresented (Orschiedt, 1998). The distribution of skeletal elements makes deposits in form of secondary burials likely (Orschiedt, 1998).

In total, there is a minimum number of six individuals represented, based on the finding of six right humeri (Orschiedt, 1998). Five of these humeri are from a Neolithic context, and the sixth could potentially be placed in a Magdalenian context (Schürch, *personal correspondence*). Unfortunately, no publications are available regarding this matter.

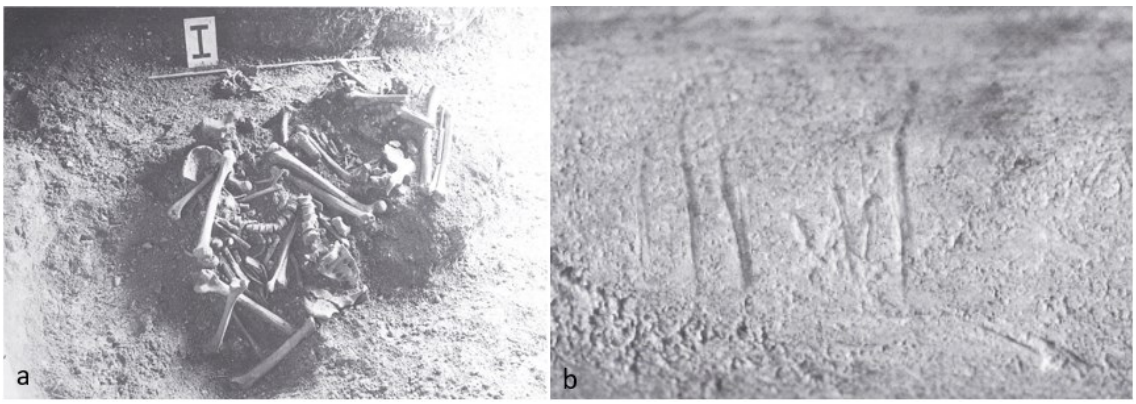

Figure 11: Human remains discovered from AH I at Vogelherd.
(a) Accumulation of human bones retrieved from the neolithic AH I (credits: G. Riek) and (b) fragment of a human ulna with cutmarks, ratio 3:1 (Orschiedt, 1998).

Several of the human remains retrieved at Vogelherd show signs of anthropogenic manipulation, such as cutmarks (Orschiedt, 1998). An example of such manipulation marks, can be seen in Figure 11b. According to Orschiedt (1998), it can be assumed that the cuts were made in an attempt to remove soft tissue remnants from the bone. Such practices were not uncommon in the Magdalenian period of Western Europe, where marks suggesting cannibalism have been found at different sites (Orschiedt, 2013; Sala and Conard, 2016).

All of the aforementioned human fossils were excavated in 1931. Of the material excavated from 2005-2012 by the Tübingen team, Wang et al. (*in prep.*) identified three human bone fragments through ZooMS. Though found in the HL/KS layer which is commonly associated with the Aurignacian and in contexts that have yielded Aurignacian beads, radiocarbon dating set one specimen into a Magdalenian context dating to approximately 16,000 years cal BP and one into a Neolithic context dating to approximately 5,000 years cal BP (Wang et al., *in prep.*). The third hominin bone could not be dated due to its small size but aDNA analyses placed it very close to the Neolithic (Wang et al., *in prep.*).

5. Material and Methods

5.1. Zooarchaeology by Mass Spectrometry

ZooMS, short for Zooarchaeology by Mass Spectrometry, is a cutting-edge palaeoproteomics method for identifying animal remains (Buckley, Whitcher Kansa et al., 2009). It specifically targets collagenous materials, such as bones, and is particularly useful for identifying remains that are otherwise difficult to classify due to fragmentation or degradation, such as those often found at Palaeolithic archeological sites (Buckley and Collins, 2011).

Proteins, such as collagen, are made up of chains of amino acids, of which there are 20 different types. These chains are called peptides. Each amino acid has a similar structure, including an alpha-carbon, a hydrogen, a carboxyl, an amino group, and a unique side chain (Hendy et al., 2020). Collagen type I is the most abundant protein found in mammals and allows for the distinction of a diverse range of mammalian groups (Buckley, Whitcher Kansa et al., 2009). The compact triple helix comprises three polypeptide alpha chains, each approximately 1,000 amino acids long (Brown et al., 2021; Henriksen and Karsdal, 2019). Typically, there are two identical alpha 1 (COL1α1) chains and a genetically distinct alpha 2 (COL1α2) chain, though this can vary in some species (Brown et al., 2021; Henriksen and Karsdal, 2019). In ZooMS, the unique peptide mass fingerprint of triple helix collagen type I is used (Buckley, 2018). The large size of collagen and its slow rate of evolution provides enough variation to differentiate between genera across the animal kingdom, but it is worth noting that the slow evolution of collagen chains means that the resolution of ZooMS is often limited to genus level (Collins et al., 2010).

Figure 12 shows the relationship between mammalian species. The closer the relationship of the species is, the more difficult an identification to species level often is. This means that the method may not be able to differentiate between closely related species or subspecies within a genus due to the limited resolution (Collins et al., 2010). Identifying similar species with identical protein sequences, for example, species within the Elephantidae, is impossible unless there is archaeological context available. Another factor to notice when using bone collagen for taxonomic identification is the process of deamidation. This is a natural degradation of the peptides, that can cause a slight shift, around 1 m/z, in the spectra (Perez Hurtado and O'Connor, 2012).

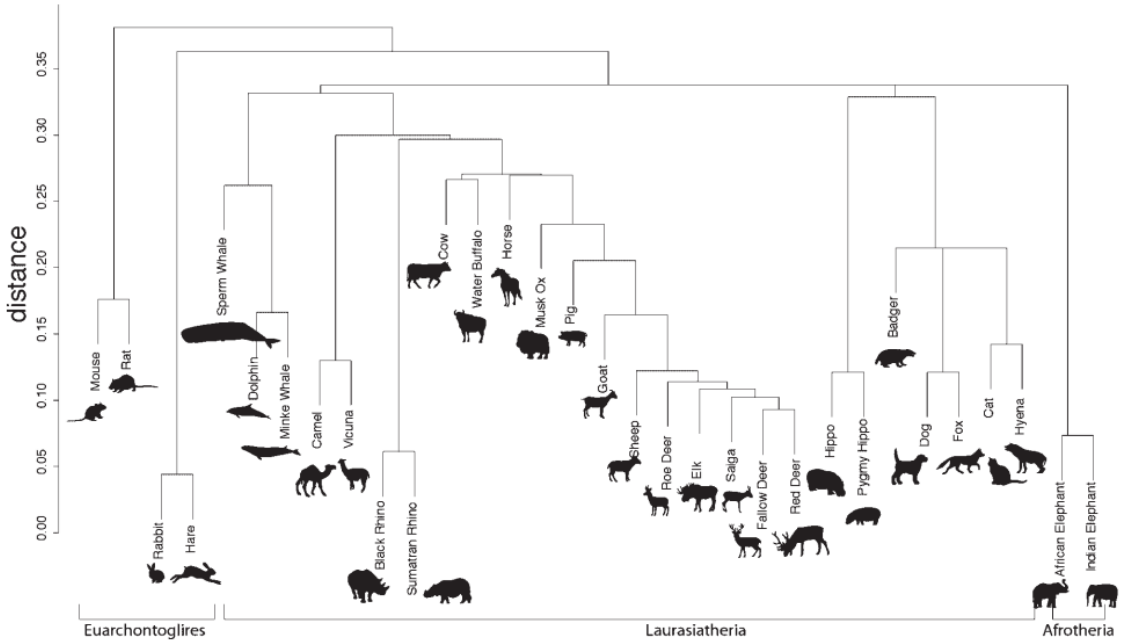

Figure 12: Dendrogram showing the relationship between mammalian species.
The dendrogram is based on the m/z values of the different species, obtained from computational analysis (Buckley, Collins et al., 2009).

The use of collagen in ZooMS has several advantages over other identification methods, such as the use of ancient DNA. Collagen degrades at a slower rate than DNA and can be sampled directly from bone, avoiding the risk of contamination during the amplification process usually carried out for DNA analysis (Buckley, Collins et al., 2009; Collins et al., 2010). Furthermore, the method is time and cost-effective, with low analytical costs per sample, making it a valuable tool within archaeological and anthropological research (Buckley, Whitcher Kansa et al., 2009; Richter et al., 2022).

The ZooMS method starts with the extraction of collagen from a sample and the digesting of the extracted collagen with a protease, typically trypsin, to create a series of collagen peptides that differ in length and mass between taxa (Buckley, 2018; Richter et al., 2022). These peptides are then acidified, purified with a C18 filter, and spotted onto a MALDI plate (Buckley et al., 2014; Richter et al., 2022). In the mass spectrometer, the matrix is excited with a laser and ionized with a +1 charge (Richter et al., 2022). The ions are then directed into a time-of-flight tube where they are separated by mass (smaller ions travel more quickly) and the resulting mass spectrum is calibrated to convert time into mass-to-charge ratios (m/z) (Buckley, 2018; Richter et al., 2022). The resulting ion spectra can be analyzed to determine the species (Buckley, Collins et al., 2009). Following Figure 13 displays the ZooMS process from the demineralization of bone material up to the final m/z spectra.

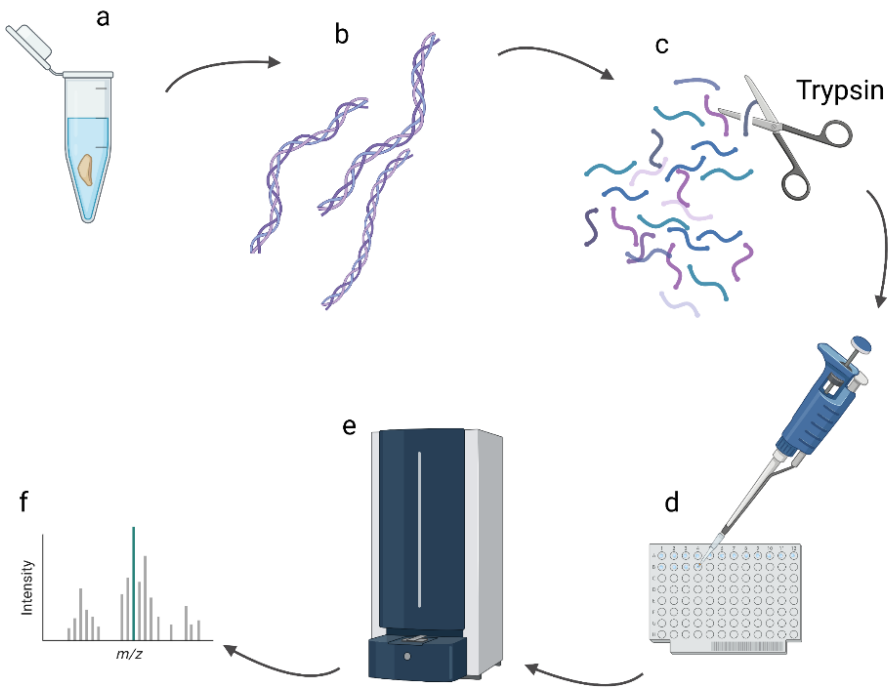

Figure 13: The ZooMS process.
(a) demineralization, (b) extracted collagen, (c) trypsin digestion, (d) spotting on target plate, (e) MALDI-TOF MS, (f) analysis of m/z peptide ratios in spectra.
(Created with BioRender.com)

The following sections will provide a more detailed explanation of the ZooMS process, as illustrated in Figure 13, with a particular emphasis on the precise treatment and handling of specimen samples carried out during this analysis.

5.2. Samples

The bone material analyzed in this Master's thesis was obtained from squares 36/77 and 37/78, which were excavated by the Universität Tübingen during the 2005-2012 re-excavations of Vogelherd. These bone fragments, ranging in size from 48-81 mg, were previously unanalyzed due to their small size or fractures, which make morphological determination difficult. To ensure a representative sample, 640 bone fragments were randomly selected for analysis from four different sediment layers: HL/KS, GF/GKS, GL/GKS, and HU. Additional information about these sediments can be found in the excavation subchapter titled *2.2.2. 2005 – 2012 Excavations (Nicholas J.* Conard).

5.3. ZooMS Sample Pretreatment

For these samples, the acid-insoluble collagen extraction method in the ZooMS protocol by Wang and Douka (2022) was used. The necessary solutions for this method include:

- 0.6 Molar (M) hydrochloric acid (HCl)

  For 1 liter, 60 µL of 10M concentrated HCl is added to 940 µL of deionized or MQ water. The solution is stored at 4°C.
- 50 milliMolar (mM) ammonium bicarbonate (NH_4HCO_3 AmBic) buffer

  For 10 ml, 39.53 mg of powdered AmBic are dissolved in 10 ml of MQ water and the pH is adjusted to 8.0 using 1M ammonium hydroxide (NH_4OH). The solution is stored at 4°C.
- 0.1M sodium hydroxide (NaOH)

  For 1 liter, 4 g of stock NaOH pellets are dissolved in 1 liter of MQ water. The solution is stored at room temperature.
- Trypsin solution (0.4 µg per µL)

  20 µg of freeze-dried stock trypsin (stored at -20°C) is resuspended in 50 µL of 50 mM Ambic.
- 5% trifluoracetic acid (TFA)

  For 100 µL, 5 µL of concentrated stock TFA is added to 95 µL of MQ water. The TFA is stored at room temperature.
- Washing solution (0.1% TFA)

  For 1 liter, 1 µL of concentrated stock TFA is added to 1 liter of MQ water. The solution is stored at room temperature.
- Conditioning solution (50:50 acetonitrile (ACN) to MQ water, 0.1% TFA)

  For 1 liter, 1 µL of concentrated stock TFA is added to a 500 µL ACN/500 µL MQ water solution. The solution is stored at room temperature.
- Matrix solution α-cyano-4-hydroxycinnamic acid (CHCA)

  10 mg stock CHCA powder is dissolved in 1 mL of conditioning solution. The solution is stored in the dark at room temperature.
- Calibration solution (for Bruker Autoflex maX LRF MALDI MS)

  ~10 mg of Bruker calibration powder are diluted with washing solution (125 µl) and stored in the fridge at 4°C in aliquots of each 10 µl. To one aliquot 15 µl of conditioning solution and 25 µl CHCA are added.

1. **Drilling:** The entire ZooMS process was conducted in the labs of the Department of Anthropology at the University of Vienna, where it began with the preparation of bone samples by drilling them to produce bone chips of 15-35 µg. The fragments were cut using a drill with a diamond-tipped saw. To avoid cross-contamination, the saw was thoroughly cleaned with a shot blaster and aluminum oxide powder between each cut. A lab coat and gloves were worn throughout all processing steps to maintain a high level of cleanliness and prevent any contamination of the samples. After drilling, the bone chips were weighed and stored in Eppendorf tubes. Each sample was assigned a unique ID, under which also the remaining bone material (not used for ZooMS) was stored.
2. **Demineralization**: The second step is the wet chemistry processing of bone samples in the wet laboratory to remove the mineral content through acid demineralization. To do this, 500 µl of 0.6 M HCL was applied to each sample, and the samples were left in the refrigerator at 4°C for 24-48 hours. After 24 hours, the samples were checked to see if they have been adequately demineralized. Demineralized samples were stored in the freezer at -20°C until further processing. Once all samples were demineralized or after a maximum of 48 hours, the samples were centrifuged at 13,000 rpm for 1 minute to separate the bone material and denser collagenous material from the acid supernatant. The remaining acid was then removed and stored in the freezer.
3. **Washing**: To restore a neutral pH, all samples were washed three times using a 50 mM ammonium bicarbonate (AmBic) solution. For each wash, 200 µl of AmBic solution was added to the samples, which were then mixed and centrifuged at 13,000 rpm for 1 minute. After centrifugation, the AmBic solution was discarded. This washing process was repeated three times for each sample to ensure a neutral pH was achieved.
4. **Gelatinization**: After the third wash, 100 µl of AmBic was added to each sample, which was then incubated in the oven for one hour at 65°C. This makes the remaining collagen soluble by turning it into gelatin. 50 µl of the gelatinized supernatant was then transferred from the Eppendorf tube to a 96-well plate and the Eppendorf tubes with the remaining bone material were stored in the freezer.
5. **Trypsin digestion**: Next, 5 µl of trypsin solution was added to each sample to initiate the digestion of the proteins. To support this process, the samples were incubated overnight at 37°C for about 12 to 18 hours. On the next day, the supernatant was acidified with 1 µl 5% TFA per sample to stop further digestion.

6. **Peptide extraction**: To extract the collagen, a C18 resin ZipTip (ThermoFisher Scientific) was used. First, the C18 filters were activated by rinsing them twice with 100 µl of conditioning solution, followed by twice with washing solution. The samples were then loaded onto the C18 filter by resuspending the sample solution 5 to 10 times. After loading, the tip was rinsed twice with washing solution. Finally, the peptide fractions were eluted by resuspending the tip 5 to 10 times in 50 µl of conditioning solution.
7. **Spotting on 384 MALDI target plate**: To prepare the matrix solution, the α-cyano-4-hydroxycinnamic acid (CHCA) was diluted 1:1 with conditioning solution (CHCA2). Next, the eluted sample fractions were mixed with the matrix solution by combining 1 µl of the fraction with 9 µl of CHCA2. The resulting mixture was spotted onto a ground steel Bruker 384 MALDI target plate in triplicate for each sample (1 - 1.2 µl of peptide fraction mixed with matrix solution). In addition, 48 spots of calibration solution (0.7 - 1 µl) were also spotted on the plate. The plate was then left to dry in the dark at room temperature.

For further details on the procedure and the solutions used, reference can be made to the acid-insoluble fraction of the ZooMS protocol by Wang and Douka (2022).

5.4. MALDI-TOF mass spectrometry

Matrix-assisted laser desorption/ionization time-of-flight mass spectrometry (MALDI-TOF-MS) is a method used to analyze fractions of digested collagen. To perform this analysis, a ground steel target plate was introduced in the MALDI spectrometer (Bruker Autoflex maX LRF MALDI MS) and all settings were adjusted for an automatic run. Initially, the B-ZooMS method was used for the first four batches of samples, but the quality of the spectra was improved after switching to the A-ZooMS method from Batch 5 onwards.

The smartbeam-II solid-state laser ionized the matrix and generated charged particles that were separated by mass and measured using a time-of-flight (TOF) mass analyzer. Spectra were acquired over a mass-to-charge ratio (m/z). The data obtained from the analysis was compatible only with Bruker software at first, and thus, to make it accessible to other software, it was converted to MZML files using R-Studio.

For some samples that showed unsatisfactory results, a second round of analysis was performed using the A-ZooMS method. Both A- and B-ZooMS methods are internally settings for the MALDI spectrometric measurements.

5.5. Data analysis methods

For species identification through ZooMS, the peptide markers detected in the samples were compared to an up-to-date reference database that is regularly updated at the University of York[2]. Table 3 shows the known peptide markers of fauna found from the German Pleistocene. The comparison of the results with the database was done with the in-house software (QuickID) developed by the Douka Lab for automatic taxonomic identification, as well as the open-source mMass software (developed by Martin Strohalm, version 6.0.2, 2005-2013) for manual analysis of the mass spectra. As each sample had been spotted and analyzed three times, the detected peptide peaks of each sample could be compared and, when possible, the possible taxa (based on their peptide markers) identified.

The data was also cross-referenced with previous morphological research on the faunal assemblage of Vogelherd Cave from Niven (2006) and Boger et al. (2014), as zooarchaeological data can give a good background on which species to expect in an assemblage (Table 3). The potential taxa were also narrowed down based on geographical information, excluding species that were not known to inhabit the Swabian Jura region during the Pleistocene, such as the Asian elephant (*Elephas maximus*), which has the same peptide markers as *Mammuthus primigenius* and *Elephas/Palaeodoxon antiquus*. Similarly, regional information was used to identify hominin remains. Since no great apes lived in Pleistocene Germany, any remains identified as Primates were designated as human (*Homo*).

[2] https://docs.google.com/spreadsheets/d/1ipm9fFFyha8IE-zRO2F5zVXIk0ldwYiWgX5pGqETzBco/edit#gid=1005946405

Table 3: Published peptide markers to the species found in zooarchaeological analyses at the Vogelherd site and in the region.

For reference, see the "ZooMS Markers: Published Data" Database (last access 03.04.2023)

Species/ Genus	COL1α1 508 - 519	COL1α2 978 - 990	COL1α2 978 - 9902	COL1α2 484 - 498	COL1α2 502 - 519	COL1α2 292 - 309	COL1α2 793 - 816	COL1α2 454 - 483	COL1α1 586 - 618	COL1α1 586 - 6182	COL1α2 757 - 789	COL1α2 757 - 7892
Bos primigenius	1105.6	1192.6	1208.6	1427.7	1580.8	1648.8	2131.1	2792.4	2853.4	2869.4	3017.4	3033.4
Canis lupus	1105.6	1210.6	1226.6	1453.7	1566.8	1609.8	2131.1	2820.4	2853.4	2869.4	2983.4	2999.4
Capra hircus	1105.6	1180.6	1196.6	1427.7	1580.8	1648.8	2131.1	2792.4	2883.4	2899.4	3077.4	3093.4
Capreolus capreolus	1105.6	1180.6	1196.6	1427.7	1550.8	1648.8	2131.1	2792.4	2883.4	2899.4	3043.4	3059.4
Cervus elaphus	1105.6	1180.6	1196.6	1427.7	1550.8	1648.8	2131.1	2792.4	2883.4	2899.4	3017.4	3033.4
Coelodonta antiquitatis	1105.6	1182.6	1453.7	1453.7	1550.8	1623.8	2145.1		2869.4	2885.4	2983.4	2999.4
Crocuta crocuta spalaea	1105.6	1207.7	1223.6	1453.7	1566.8	1639.8	2147.1	2808.4	2853.4	2869.4	2983.4	2999.4
Elephas antiquus	1105.6	1145.6	1161.6	1453.7	1579.8	1556.8	2115.1	2808.4	2853.4	2869.4	2999.4	3015.4
Equus ferus	1105.6	1182.6	1198.6	1427.7	1550.8	1649.8	2145.1	2820.4	2883.4	2899.4	2983.4	2999.4
Gulo gulo	1105.6	1219.6	1235.6	1453.7	1566.8	1609.8	2147.1	2820.4	2853.4	2869.4	2983.4	2999.4
Homo sapiens	1105.6		1235.6	1477.7	1580.8	1619.8	2115.1	2832.4	2869.4	2885.4	2957.4	2973.4
Lepus sp.	1105.6		1221.6	1453.7	1566.8/1592.8		2129.1		2883.4	2899.4	2957.4	
Lynx sp.	1105.6	1207.6	1223.6	1453.7	1566.8	1609.8	2163.1	2820.4	2853.4	2869.4	2957.4/2983.4	2999.4
Mammuthus primigenius	1105.6	1145.6	1161.6	1453.7	1579.8	1556.8	2115.1	2808.4	2853.4	2869.4	2999.4	3015.4
Martes sp.	1105.6	1219.6	1235.6	1453.7	1566.8	1609.8	2147.1	2820.4	2853.4	2869.4	2983.4	2999.4
Megaloceros giganteus	1105.6	1180.6	1196.6	1427.7	1550.8	1648.8	2131.1	2792.4	2883.4	2899.4	3017.4	3033.4
Meles meles	1105.6	1219.6	1235.6	1453.7	1566.8	1609.8	2147.1	2820.4	2853.4	2869.4	2957.4	2973.4
Mustela sp.	1105.6	1219.6	1235.6	1453.7	1566.8		2147.1	2820.4	2853.4	2869.4	2983.4	2999.4
Ovibos moschatus	1105.6	1192.6	1208.6	1427.7	1580.8	1648.8	2131.1	2792.4	2883.4	2899.4	3017.4	3033.4
Ovis aries	1105.6	1180.6	1196.6	1427.7	1580.8	1648.8	2131.1	2792.4	2883.4	2899.4	3017.4	3033.4
Panthera leo spalaea	1105.6	1207.6	1223.6	1453.7	1566.8		2147.1	2820.4	2853.4	2869.4	2983.4	2999.4
Rangifer tarandus	1105.6	1150.6	1166.6	1427.7	1580.8	1648.8	2131.1	2792.4	2883.4	2999.4	3077.4	3093.4
Rupicapra rupicapra	1105.6	1180.6	1196.6	1427.7	1580.8	1648.8	2131.1	2792.4	2883.4	2899.4	3017.4	3033.4
Sus scrofa	1105.6	1180.6	1196.6	1453.7	1550.8	1647.8	2131.1	2820.4	2883.4	2899.4	3017.4	3033.4
Ursus sp.	1105.6	1217.6	1233.6	1453.7	1566.8	1609.8	2163.1		2853.4	2869.4	2957.4	2973.4
Vulpes sp.	1105.6	1210.6	1226.6	1437.7/1453.7	1566.8	1609.8	2131.1	2820.4	2853.4	2869.4	2983.4	2999.4

As a representative example, the mass spectrum of an identified Elephantid is displayed in the figure below (Figure 14).

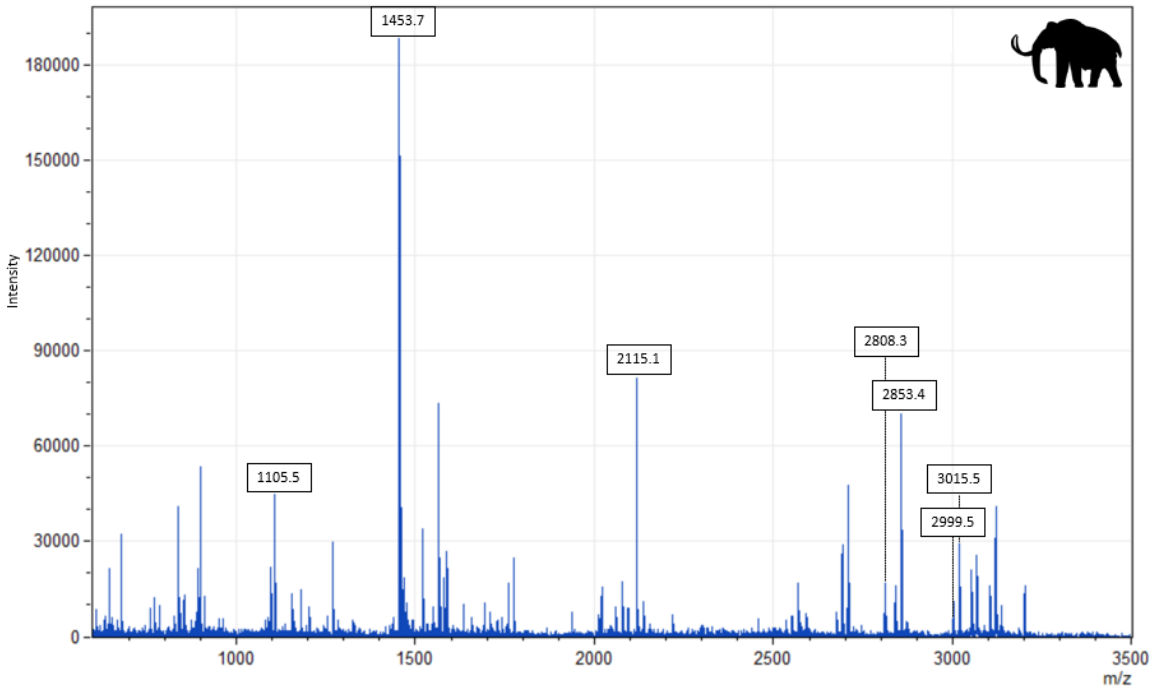

Figure 14: Mass spectrum of VH913, identified as Elephantidae.
Typical Elephantidae peptides markers are shown.
(Mammoth Silhouette sourced from PhyloPic.org, credits: Zimices (Julián Bayona))

The findings of this study were meticulously recorded and organized in Excel, where tables and figures were later generated to visualize the acquired data.

6. Results

In this study, 640 samples from the Vogelherd Cave (VH288 – VH927) were analyzed. Of these, 75 samples (12%) failed due to poor quality of their spectra, linked to bad collagen preservation. Four samples with clear spectra were assigned as "unknown". Despite good quality spectra, these four samples could not be assigned to any known taxon based on published peptide markers; they will be further analyzed in subchapter *6.7. Taxonomically unidentifiable "unknown" specimens* at the end of the results section.

Including the four unknown samples, the overall success rate of ZooMS in this study was 88% (N=565). Table 4 shows the number of failed and successfully analyzed samples. It is worth noting that in subsequent tables, the number of ZooMS-identified specimens will be abbreviated to NISP.

Table 4: Numbers and percentage of failed and successfully analyzed specimens using ZooMS. A comparison of numbers and percentages in total (all layers) and the archaeological horizons HL/KS, GF/KS, GL/GKS, and HU.

	All Layers		HL/KS		GF/KS		GL/GKS		HU	
	NISP	%	NISP	%	NISP	%	NISP	%	NISP	%
Failed samples	75	12	34	10	12	8	27	18	2	29
Successful samples (N)	565	88	295	90	141	92	124	82	5	71
Total analyzed samples	**640**	**100**	**329**	**100**	**153**	**100**	**151**	**100**	**7**	**100**

Five orders could be determined within the identified samples; these were Proboscidea, Artiodactyla, Perissodactyla, Carnivora, and Lagomorpha (based on the number of identified specimens ranked from highest to lowest) (Table 5). Additionally, four Primates classified as *Homo sapiens* were identified. These will be discussed in detail in the subchapter *6.6. Primates (ZooMS identification of Human Remains)*.

Table 5: Number and percentage of specimens per order in the archaeological horizons. The abundance of specimens per order in total (All Layers) and in the archaeological horizons HL/KS, GF/KS, GL/GKS, and HU.

	All Layers		HL/KS		GF/KS		GL/GKS		HU	
Order	NISP	%	NISP	%	NISP	%	NISP	%	NISP	%
Proboscidea	172	30	117	40	28	20	26	21	1	20
Artiodactyla	167	30	67	23	58	41	40	32	2	40
Perissodactyla	129	23	46	16	42	30	39	31	2	40
Carnivora	66	12	45	15	7	5	14	11	0	0
Lagomorpha	23	4	13	4	5	4	5	4	0	0
Primates	4	1	4	1	0	0	0	0	0	0
unknown	4	1	3	1	1	1	0	0	0	0
Total	**565**	**100**	**295**	**100**	**141**	**100**	**124**	**100**	**5**	**100**

The abundance of each order in the overall sample (Figure 15) and the archaeological horizons of interest, namely HL/KS, GF/KS, and GL/GKS (Figure 16), are displayed in the following figures.

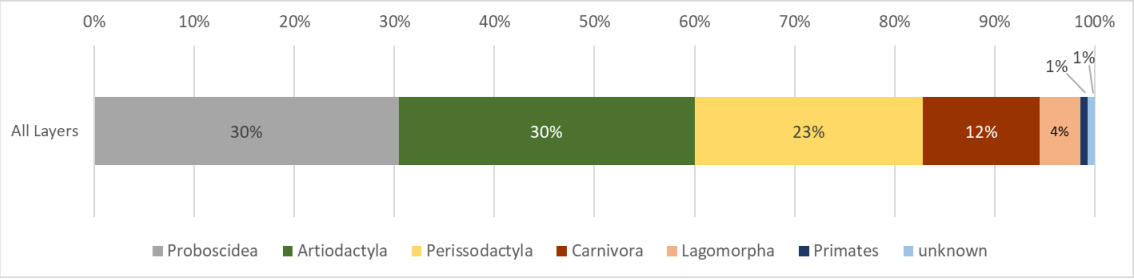

Figure 15: Distribution of the faunal orders identified in the overall analysed assemblage. ($N_{All\ Layers}$=565).

The dominance of Proboscidea in the overall sample collection can largely be attributed to the HL/KS sediment, which comprises over 50% ($N_{HL/KS}$=295) of the total samples analyzed. In the intact sediments GF/KS and GL/GKS, artiodactyls, and perissodactyls were the more common orders, as can be seen in Figure 16. Another obvious difference between the sediments was the percentage of carnivores, which was larger in the HL/KS (15%) than in the intact layers (GF/KS 5%, GL/GKS

11%). There was no variation in the percentage of Lagomorpha between the layers. The HL/KS was the only sediment in which primates (n=4) were found.

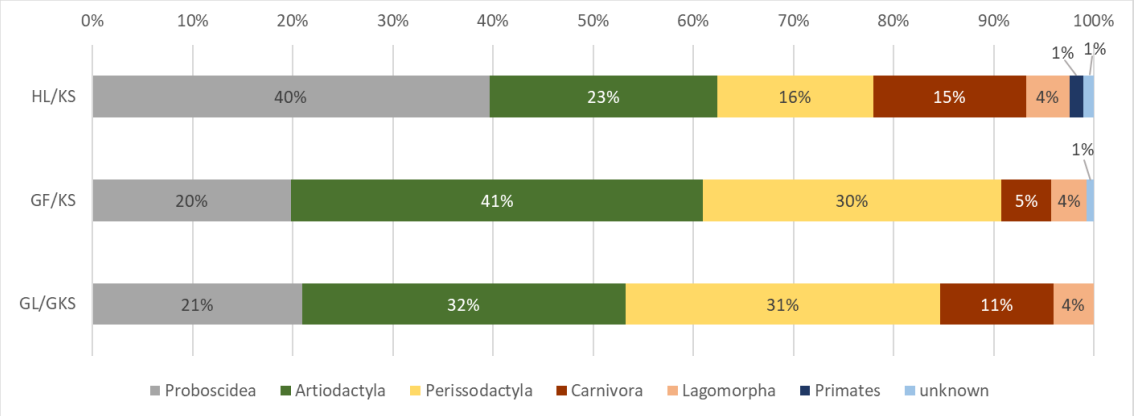

Figure 16: Distribution of the faunal orders in different archaeological horizons.
The figure shows the abundances of HL/KS (N=295), GF/KS (N=141), and GL/GKS (N=124). Based on the small number of samples provided by HU (N=5), the layer is not included in this figure.

Table 6 details further the taxonomic identification of this ZooMS work. While species-level identifications were prioritized, some samples could not be identified at this level and were instead assigned to the most specific taxon /group possible.

Table 6: Number and percentage of identified specimens.
Abundance of specimens in total (All Layers) and in the archaeological horizons HL/KS, GF/KS, GL/GKS, and HU.

	All Layers		HL/KS		GF/KS		GL/GKS		HU	
Taxon	**NISP**	**%**	**NISP**	**%**	**NISP**	**%**	**NISP**	**%**	**NISP**	**%**
Elephas/Mammuthus	172	30	117	40	28	20	26	21	1	20
Rangifer tarandus	49	9	17	6	22	16	9	7	1	20
Cervus/Capreolus/Megaloceros	63	11	32	11	6	4	24	19	1	20
Bos/Bison	40	7	8	3	30	21	2	2	0	0
Sus scrofa	2	0	2	1	0	0	0	0	0	0
Pecora (Bovidae/Cervidae)	13	2	8	3	0	0	5	4	0	0
Coelodonta antiquitatis	41	7	7	2	20	14	13	10	1	20
Equus ferus	88	16	39	13	22	16	26	21	1	20
Canis lupus	2	0	2	1	0	0	0	0	0	0
Vulpes vulpes	6	1	6	2	0	0	0	0	0	0
Canidae	2	0	1	0	1	1	0	0	0	0
Meles meles	8	1	8	3	0	0	0	0	0	0
Mustelidae	4	1	4	1	0	0	0	0	0	0
Ursus sp.	2	0	2	1	0	0	0	0	0	0
Panthera leo spalaea	1	0	1	0	0	0	0	0	0	0
Felis silvestris	2	0	2	1	0	0	0	0	0	0
Ursidae/Felidae	11	2	4	1	0	0	7	6	0	0
Felidae/Mustelidae	4	1	4	1	0	0	0	0	0	0
Hyaenidae/Mustelidae	1	0	0	0	1	1	0	0	0	0
Felidae/Hyaenidae/Mustelidae	23	4	11	4	5	4	7	6	0	0
Lepus sp.	23	4	13	4	5	4	5	4	0	0
Homo sapiens	4	1	4	1	0	0	0	0	0	0
unknown	4	1	3	1	1	1	0	0	0	0
Total	**565**	**100**	**295**	**100**	**141**	**100**	**124**	**100**	**5**	**100**

Over the following pages, the specific results of each order will be discussed.

6.1. Proboscidea

As mentioned earlier, a large proportion of the identified animal remains in this study belong to the Proboscidea, specifically the Elephantidae family, with a total of 172 specimens. In the German Pleistocene, this family is known to have consisted of two species, the woolly mammoth (*Mammuthus primigenius*) and the straight-tusked elephant (*Elephas/Palaeoloxodon antiquus*), based on morphological analysis conducted by previous researchers (for reference, see chapter *3. Zooarchaeological Context*). ZooMS cannot differentiate between the two species as they share the same peptide markers (Table 3).

As can be seen in Figure 16, the highest abundance of Elephantidae specimens can be found in the HL/KS (40%), which accounts for 117 specimens (Table 7). The abundance in the intact layers GF/KS (n=28) and GL/GKS (n=26) is similar, with Elephantids making up for approximately one-fifth of the fauna. A single Elephantidae specimen was found in the HU.

Table 7: Number of identified Proboscidea specimens.
Number of identified specimens and distribution (within the order) in the total sample (All Layers) and in the archaeological gorizons HL/KS, GF/KS, GL/GKS, and HU. As Elephas/Mammuthus are the only taxa in the Proboscidea and cannot be separated the abundance within the order is always 100%.

	All Layers		HL/KS		GF/KS		GL/GKS		HU	
Taxon	**NISP**	**%**	**NISP**	**%**	**NISP**	**%**	**NISP**	**%**	**NISP**	**%**
Elephas/Mammuthus	172	100	117	100	28	100	26	100	1	100
Total Proboscidea	**172**	**100**	**117**	**100**	**28**	**100**	**26**	**100**	**1**	**100**

6.2. Artiodactyla

The identified faunal assemblage from Vogelherd comprised 167 specimens belonging to the Artiodactyl order. Specifically, 67 samples from HL/KS, 58 from GF/KS, 40 from GL/GKS, and 2 from HU were identified (Table 8).

Of these artiodactyls, the majority were identified as belonging to the deer family ($n_{Cervidae}$=63), represented by *Cervus elaphus* (red deer), *Capreolus capreolus* (roe deer), and *Megaloceros giganteus* (Irish elk). *Rangifer tarandus* (reindeer) was also well represented by 49 specimens and Bos/Bison with 40 specimens. Interestingly, Bos/Bison are most abundant in the GF/KS, where they make up 52% of the artiodactyls. Two specimens of *Sus scrofa* (wild boar) were identified, both in the HL/KS.

Table 8: Number of identified specimens and abundance of taxa within the Artiodactyl order. Number of identified specimens and distribution (within the order) in the total sample (All Layers) and in the archaeological horizons HL/KS, GF/KS, GL/GKS, and HU.

	All Layers		HL/KS		GF/KS		GL/GKS		HU	
Taxon	**NISP**	**%**	**NISP**	**%**	**NISP**	**%**	**NISP**	**%**	**NISP**	**%**
Rangifer tarandus	49	29	17	25	22	38	9	23	1	50
Cervus/Capreolus/Megaloceros	63	38	32	48	6	10	24	60	1	50
Bos/Bison	40	24	8	12	30	52	2	5	0	0
Sus scrofa	2	1	2	3	0	0	0	0	0	0
Pecora (Bovidae/Cervidae)	13	8	8	12	0	0	5	13	0	0
Total Artiodactyla	**167**	**100**	**67**	**100**	**58**	**100**	**40**	**100**	**2**	**100**

The distinction between different Pecora taxa can be difficult, as the spectra are very similar. In total, 13 specimens (8% of artiodactyls) were assigned to "Pecora" which consists of Bovidae and Cervidae, as the result could not be further specified.

6.3. Perissodactyla

Both Equidae and Rhinocerotidae belong to the Perissodactyl order. We found 129 Perissotactyls in total; specifically 88 *Equus ferus* (horses) and 41 *Coelodonta antiquitatis* (rhinoceros) (Table 9).

Table 9: Number of identified specimens and abundance of taxa within the Perissodactyla order. Number of identified specimens and distribution (within the order) in the total sample (All Layers) and in the archaeological horizons HL/KS, GF/KS, GL/GKS, and HU.

	All Layers		HL/KS		GF/KS		GL/GKS		HU	
Taxon	**NISP**	**%**	**NISP**	**%**	**NISP**	**%**	**NISP**	**%**	**NISP**	**%**
Coelodonta antiquitatis	41	32	7	15	20	48	13	33	1	50
Equus ferus	88	68	39	85	22	52	26	67	1	50
Total Perissodactyla	**129**	**100**	**46**	**100**	**42**	**100**	**39**	**100**	**2**	**100**

When viewing the distribution of Perissodactyla taxa more closely it becomes obvious that in the HL/KS and GL/GKS horses are more abundant than rhinoceroses. Only in the GF/KS, almost half of the Perissodactyls are rhinoceroses ($n_{Coelodonta}$=20; 48%). In the HU ($n_{Perissodactyla}$=2) one horse and one rhinoceros specimen was found.

6.4. Carnivora

The order of Carnivora (N=66) contributed several species to the faunal assemblage. In total, six different species (*Canis lupus, Vulpes vulpes, Meles meles, Ursus sp., Panthera leo spalaea,* and *Felis silvestris*) were identified, though these were all found only in small numbers. Together these on species-level identified specimens make up 32% of all identified carnivores. The peptide markers of 39 specimens (59%) did not provide enough information to narrow the result down to one family. In these cases, all possible families were provided in Table 10.

Table 10: Number of identified specimens and abundance of taxa within the Carnivora order.
Number of identifiedsSpecimens and distribution (within the order) in the total sample (All Layers) and in the archaeological horizons HL/KS, GF/KS, GL/GKS, and HU.

	All Layers		HL/KS		GF/KS		GL/GKS		HU	
Taxon	**NISP**	**%**	**NISP**	**%**	**NISP**	**%**	**NISP**	**%**	**NISP**	**%**
Canis lupus	2	3	2	4	0	0	0	0	0	0
Vulpes vulpes	6	9	6	13	0	0	0	0	0	0
Canidae	2	3	1	2	1	14	0	0	0	0
Meles meles	8	12	8	18	0	0	0	0	0	0
Mustelidae	4	6	4	9	0	0	0	0	0	0
Ursus sp.	2	3	2	4	0	0	0	0	0	0
Panthera leo spalaea	1	2	1	2	0	0	0	0	0	0
Felis silvestris	2	3	2	4	0	0	0	0	0	0
Ursidae/Felidae	11	17	4	9	0	0	7	50	0	0
Felidae/Mustelidae	4	6	4	9	0	0	0	0	0	0
Hyaenidae/Mustelidae	1	2	0	0	1	14	0	0	0	0
Felidae/Hyaenidae/Mustelidae	23	35	11	24	5	71	7	50	0	0
Total Carnivora	**66**	**100**	**45**	**100**	**7**	**100**	**14**	**100**	**0**	**0**

The intact layers, GF/KS and GL/GKS together, yielded only a very small amount of carnivore specimens, making up a third of all carnivores ($n_{GF/KS + GL/GKS}$=21; 32%). The rest of the carnivores were found in the HL/KS.

6.5. Lagomorpha

Twenty-three hares (*Lepus sp.*) were identified, making up 4% of the total fauna. Interestingly, the abundance of hare is the same in all HL/KS, GF/KS, and GL/GKS (4%)(Table 6). No hare was found in HU. Table 11 shows the number of identified lagomorphs per AH.

Table 11: Number of identified Lagomorpha specimens.
Number of identified specimens and distribution (within the order) in the total sample (All Layers) and in the archaeological horizons HL/KS, GF/KS, GL/GKS, and HU. As there is only one taxon in the Lagomorpha order the abundance within the order is always 100%.

	All Layers		HL/KS		GF/KS		GL/GKS		HU	
Taxon	**NISP**	**%**	**NISP**	**%**	**NISP**	**%**	**NISP**	**%**	**NISP**	**%**
Lepus sp.	23	100	13	100	5	100	5	100	0	100
Total Lagomorpha	**23**	**100**	**13**	**100**	**5**	**100**	**5**	**100**	**0**	**100**

6.6. Primates (ZooMS identification of Human Remains)

Four human remains with the IDs VH415, VH556, VH562, and VH877 were identified in the HL/KS in this ZooMS analysis and based on the presence of distinct human peptide markers (Table 12). The human origin of these remains could be confirmed using ZooMS but exact species cannot using this method. Ancient DNA analyses is underway for these human remains. Given the layer information provided, they were all classified as *Homo sapiens*.

Table 12: Hominin peptide markers found in VH415, VH556, VH562, and VH877.

ZooMS ID	COL1a1 508 - 519	COL1a2 978 - 990	COL1a2 978 - 9902	COL1a2 484 - 498	COL1a2 502 - 519	COL1a2 292 - 309	COL1a2 793 - 816	COL1a2 454 - 483	COL1a1 586 - 618	COL1a1 586 - 6182	COL1a2 757 - 789	COL1a2 757 - 7892
VH415	1105.5			1477.7					2869.3			
VH556	1105.5			1477.7			2115.1		2869.4			
VH562	1105.5			1477.7			2115.1		2869.4			
VH877	1105.5		1235.6	1477.7	1580.7		2115.0	2833.2	2869.3	2885.3	2957.4	

VH877 had the highest quality spectrum, displaying the most hominin peptide markers. Figure 17 shows the spectrum of VH877 with its identified peptide markers.

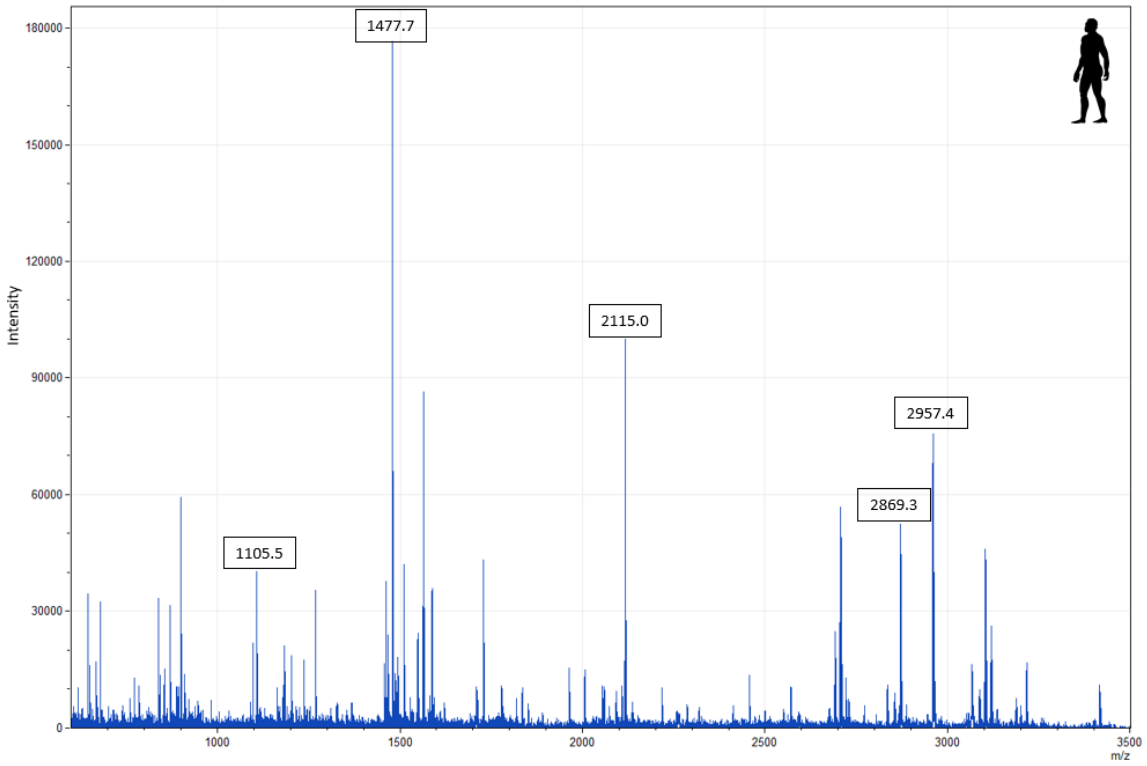

Figure 17: Mass spectrum of VH877.
The typical human peptide peaks are labeled (framed peptide marker).
(Human Silhouette sourced from PhyloPic.org, credits: T. Michael Keesey)

All mass spectra of the four identified human bones can be found in the Appendix (Figures 28-31).

The human bones have a yellowish color, with VH415 (Figure 18a) exhibiting a poorer condition and darker color compared to the other bones, which were lighter in color and less crumbly. VH415, VH556 (Figure 18b) and VH877 (Figure 18d) did not display any visible morphological features, while VH562 (Figure 18c) was sufficiently large to be identified as the left part of a human maxilla.

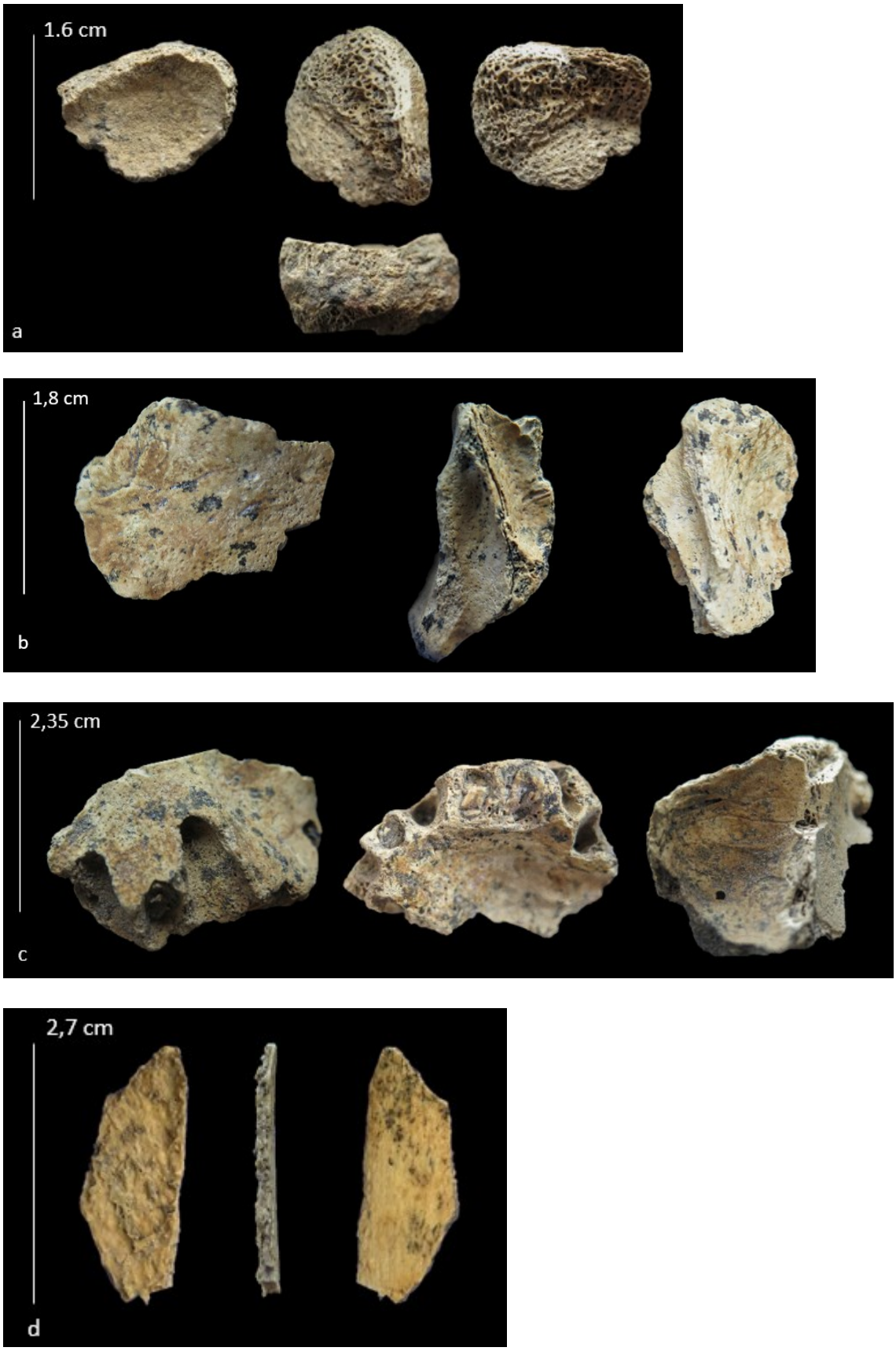

Figure 18: Photographs of the hominin bones.
(a) VH415, (b) VH556, (c) VH562 and (d) VH877.

6.6.1. µCT scanning

The hominin skeletal remains were µCT scanned to obtain detailed 3D surfaces of the bones. Martin Dockner from the University of Vienna conducted the scanning, and screenshots taken in Amira 6.5 (ThermoFisher Scientific) were used to produce the images (Figure 19). More information about the scanning procedure can be found in *Appendix 4: µCT Scanning of hominin skeletal remains*.

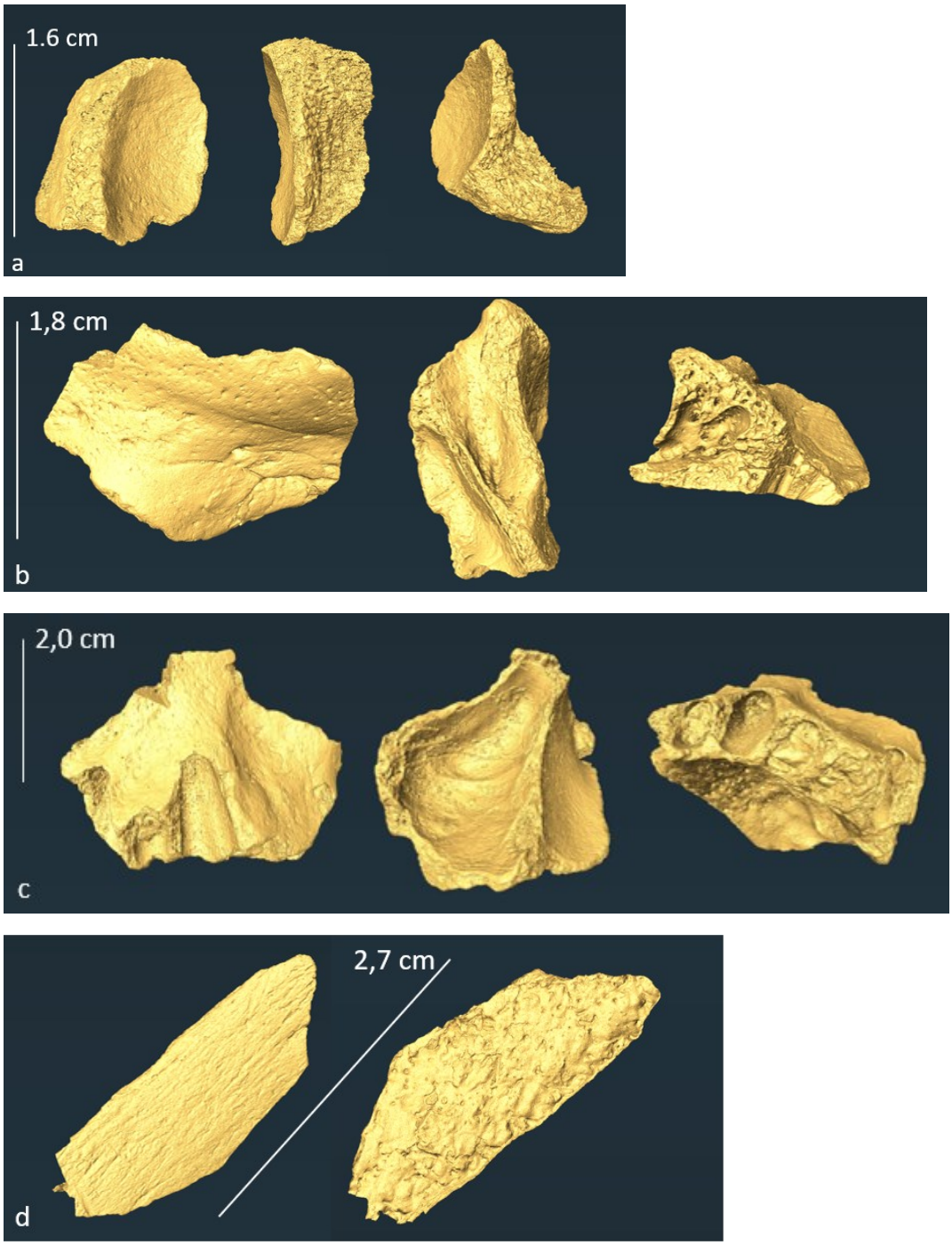

Figure 19: Screenshots of hominin specimen surfaces.
(a) VH415, (b) VH556, (c) VH562, and (d) VH877, generated in Amira 6.5.

6.6.2. Radiocarbon dating

VH562 is the only human sample from this study that has been analyzed using radiocarbon dating methods at the Higham Lab. Collagen was extracted using routine methods (Brock et al., 2010) and the precleaned gelatine was ultrafiltered prior to combustion and graphitization at the VERA laboratory in the Physics Department of the University of Vienna.

The new radiocarbon date for VH562 is VERA-7746: 4859±29 BP. When calibrated to calendar years using the IntCal2020 calibration curve the age falls at 5650-5490 cal BP or 5660-5480 cal BP (Table 13), which suggests this bone belongs to the Neolithic period. The calibrated ranges and probabilities are shown in Figure 20a, b at 2 and 3 sigma deviation.

Table 13: Confidence intervals of calibrated radiocarbon dates of VERA-7746 (VH562).

Name	Calibrated (years BP)			
	from	to	from	to
	68.3%		95.4%	
VERA-7746	5650	5490	5660	5480

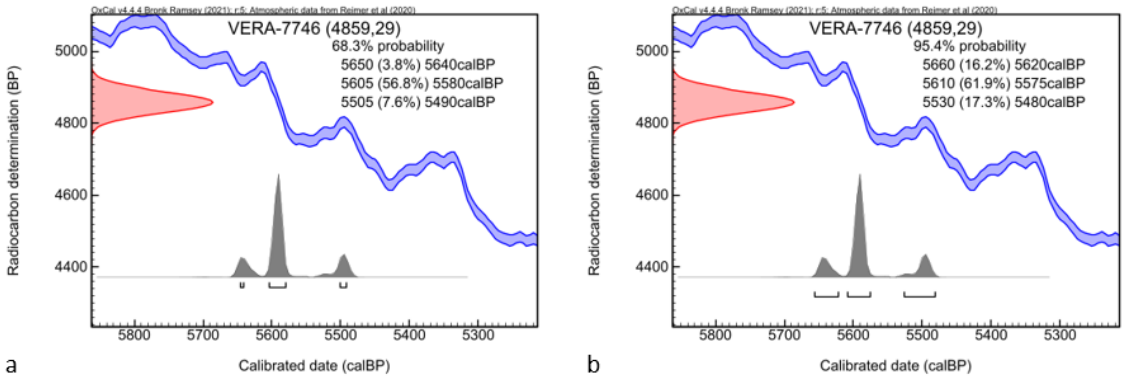

Figure 20: Radiocarbon calibration plot of VERA-7746 (VH562).
(a) 68.3% probability, (b) 95.4% probability.

6.7. Taxonomically unidentifiable "unknown" specimens

Four specimens showing decent-quality spectra did not carry peptide marker combinations that match any taxa in the published database. Certain peptide markers can be found in all of these "unknown" specimens. Based on the peptide markers (Table 14), the specimens may be birds. However, the ZooMS database is at present very limited for birds, so it is difficult to say with certainty.

Table 14: Peaks located in the spectra of the four specimens classified as "unknown".
Yellow highlights indicate shared peptide markers in at least two samples.

ID	unique peaks (m/z)	sharing peaks (m/z)													
		1095	1162	1319	1393	1459	1463	1562	1572	2133	2149	2673	2689	2777	3192
VH716	2497, 2969														
VH855	1562, 2553, 2879														
VH882	2511														
VH886	2539, 2719														

7. Discussion

7.1. Comparison of the identified fauna to zooarchaeological data

A total of 640 samples were analyzed in this study, which had an overall success rate of 88% (N=565 successful samples), a good success rate for this type of analysis. This study's taxonomic identifications are also consistent with the faunal assemblages previously identified through morphological and ZooMS studies conducted by other authors. Note, that in the following discussions of the faunal assemblage of Vogelherd, all ZooMS-identified human and "unknown" specimens identified in this study are excluded, to make the data more comparable to other studies.

Both the hominin remains and the "unknown" specimens makeup only 1% of the assemblage identified in this research, but excluding these specimens leads to slight variations in the faunal abundance when compared to the results reported in the results section of this thesis. Generally, it is also important to consider potential biases when comparing ZooMS data to morphologically analyzed bones. Specifically, certain species may be overrepresented or underrepresented due to the size or abundance of their bones or the animal size. Although small bone fragments can be analyzed through ZooMS, some of the smallest fragments are often excluded in order to preserve enough material for other types of analysis, such as aDNA or radiocarbon dating. This may impact the representation of different species in the final dataset. For example, if the remains of one woolly mammoth and one hare were fragmented into the same amount of pieces and mixed together, the larger mammoth bone fragments may be preferentially selected for ZooMS analysis due to their greater size. This could lead to an overrepresentation of mammoths in the final dataset, even if the original sample included more hare bones in terms of number. This issue of equifinality is an inherent problem with ZooMS studies. Therefore, it is important to carefully consider potential biases when interpreting ZooMS data and to account for them appropriately in comparative analyses. This, of course, is also the case in this study and the following discussion of the Vogelherd faunal assemblage.

The GL/GKS and GF/KS are both small layers that were recovered intact from below the HL/KS sediments and represent the original outside deposits of Vogelherd Cave. Since they each supplied a small number of samples to this study, they are discussed collectively, comprising 47% (N=264) of all successfully analyzed faunal specimens. In the intact layers, Artiodactyls (ruminant ungulates) constitute the highest proportion of the faunal assemblage in this study (37%), which may be potentially explainable through the before noted collection bias, as Boger et al. (2014) reported a much lower abundance (20%) (Figure 21). Conversely, horses account for a greater proportion of the faunal assemblage in the morphological analysis by Boger et al. (33%) than in this study (18%). Elephantidae comprises one-fifth of the intact layer's fauna in this study (20%), twice the

abundance reported by Boger et al. (2014). Except for one straight-tusked elephant specimen, all of the Elephantidae identified by Boger et al. (2014) are woolly mammoths, making it highly likely that elephantids in this dataset are largely mammoths. Additionally, the abundance of carnivores differs between this study and Boger et al., where authors documented a much higher abundance of carnivores (25% in total) than in this study, where only 8% of the intact layer's fauna comprise carnivores.

This is in accordance to other studies where the ZooMS-derived data identify less carnivores. This can be attributed to the fact that carnivore bones are not fragmented in the same way as prey bones are.

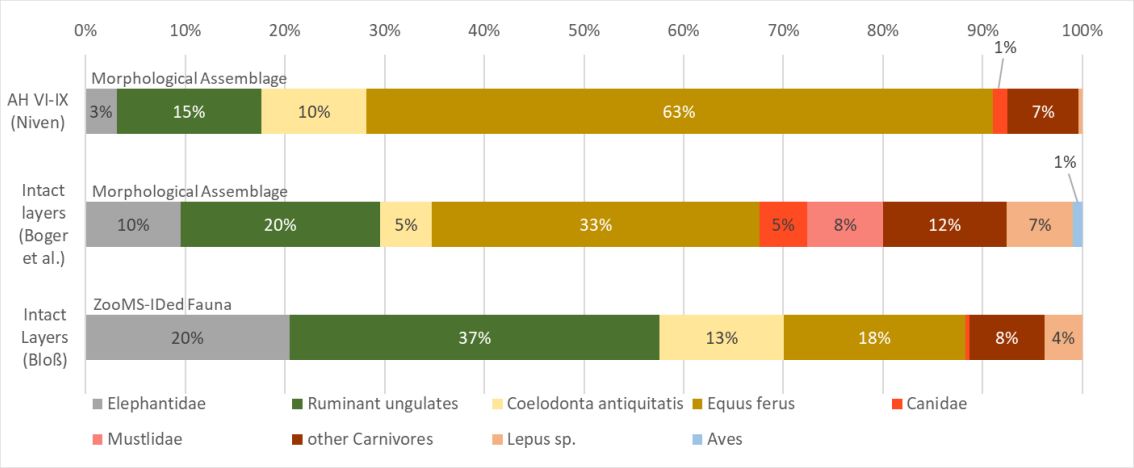

Figure 21: Faunal distribution patterns across the archaeological horizons VI-IX and the intact layers: Integration of zoo-archaeological data with new findings.
Data from archaeological horizons VI-IX (N=544) morphologically analyzed by Niven (2006) and the intact layers (N=210) morphologically analyzed by Boger et al. (2014) and ZooMS-IDed fauna of the intact layers (N=264) in this study.

In the Middle Palaeolithic horizons (AH VI-IX), Niven (2006) reported a high amount of horses (63%), which is significantly more than what the studies of the intact layers have recorded, both in the morphological and ZooMS analyses. It is also noteworthy that the abundance of Elephantidae is much lower in the AH VI-IX (3%) than in the intact layers. The high proportion of artiodactyls in this study, as well as the lower presence of horses and Elephantidae, suggests a potentially different ecological context during the time of deposition of the intact layers to the Middle Palaeolithic fauna identified by Niven. Depending on the time of material deposition, this possibly reflects changes in the environment and human activities linked to the abrupt climatic changes of Late Pleistocene and Stage 3.

The analysis of bones from the HL/KS layers, both with morphological and ZooMS identification techniques, revealed that Elephantidae played a significant role in the Upper Palaeolithic fauna at Vogelherd. The HL/KS assemblage in this study contains 41% elephant remains, which are likely to be mammoths (*Mammuthus primigenius*), as they were more common in the Vogelherd

Pleistocene fauna than the straight-tusked elephant (*Elephas/Palaeoloxodon antiquus*), of which only two specimens have been found in total, none in the HL/KS or original Upper Palaeolithic layers (Boger et al., 2014; Niven, 2006, p. 78). Although the human inhabitants of Vogelherd may have used megaherbivores for sustenance, it is more probable that they were utilized for non-food subsistence purposes (Niven, 2007). Morphological analyses of mammoth remains at Vogelherd have not shown signs of hunting, suggesting that mammoth remains were collected opportunistically, rather than through active hunting (Boger et al., 2014; Niven, 2007). This matches the phenomenon also discussed by Münzel et al. (2017), who describe a general scarcity of hunting marks on mammoth bones, especially in comparison to marks found on other species. The prevalence of *Coelodonta antiquitatis* remains at Vogelherd aligns with previous studies of the HL/KS (see Figure 22). But while rhinoceroses were present in the area, they played only a minor role in the ecosystem.

This study has also identified high abundances of ruminant ungulates (Bovidae, Cervidae, Suidae) and horses (*Equus ferus*), which was not surprising and backs previous analyses. Niven (2006, p. 138) extensively examined the impact scars and breakages on reindeer and horse remains, leading her to conclude that humans heavily relied on these animals for sustenance and resource procurement. Based on the abundance of ruminant ungulates (23%) and horses (14%), this study supports the theory of these animals being primary prey taxa at Vogelherd. Within the artiodactyls, deer (*Cervus/Capreolus/Megaloceros*) were the most abundant (48%), followed by reindeer (*Rangifer tarandus*) at 25% in the HL/KS sediment. *Sus scrofa*, represented by no more than two specimens, was found only in the HL/KS sediment, while Bos/Bison were more abundant in the intact layers than in the HL/KS.

Interestingly, this study found a much smaller abundance of carnivores in the HL/KS (15%) compared to Boger et al.'s morphological studies (29%), thus still a higher abundance than (Wang et al., *in prep.*). Specifically, the morphological analyses revealed a much higher percentage of Canidae and Mustelidae than the ZooMS analyses of both this study and the study conducted by Wang et al., *in prep.*). This raises the question of whether the analytical technique caused the deviation or if it was merely a coincidence. A close relationship of species limits the ZooMS identification accuracy (Collins et al., 2010), making it especially difficult to identify species when in addition peptide markers are missing. In several cases (n=39), even when identification as a carnivore was possible, there were not sufficient peptide markers to provide identification on family level.

When addressing hares, it is worth noting that this study, like Boger et al. (2014), identified hare remains as accounting for 5% of the fauna. However, Wang et al.´s results indicate that hares make up twice that amount (10%). This difference is most likely coincidental and it is no major deviation.

In general, the results show that hares indeed played a role in the fauna at Vogelherd Cave. This matches the idea of Upper Palaeolithic groups in Eurasia relying also on small game for their diets (Niven, 2006, p. 180; Stiner et al., 2000).

Another interesting matter is the comparison of the HL/KS faunal assemblage to that of the archeological horizons analyzed by Niven (2006). The material examined by Niven corresponds to the Upper Palaeolithic material excavated by Riek from the archeological horizons II-V in the 1931 excavations. Since the HL/KS is derived from the backdirt of the 1931 Vogelherd Cave excavation, it is expected to exhibit a similar faunal distribution to the material taken directly during the excavations. Niven's (2006) analysis of the faunal assemblage differs more from all the HL/KS findings combined than the variations among different HL/KS analyses, both morphological and ZooMS analyses (Figure 22). Notably, Niven identified the highest abundance of elephant (50%) and horse (21%) remains. But as many non-diagnostic fragments of less than 3cm were often discarded during the excavation (collection bias), this could be a contributing factor for the deviation. Interestingly, the AH VII-V analysis yielded much fewer carnivore specimens (relative to the total number of analyzed specimens) compared to all the HL/KS analyses, both morphological and ZooMS. But it is necessary to note that Niven excluded all specimens identified as badgers (*Meles meles*), as these are often intrusive in prehistoric assemblages.

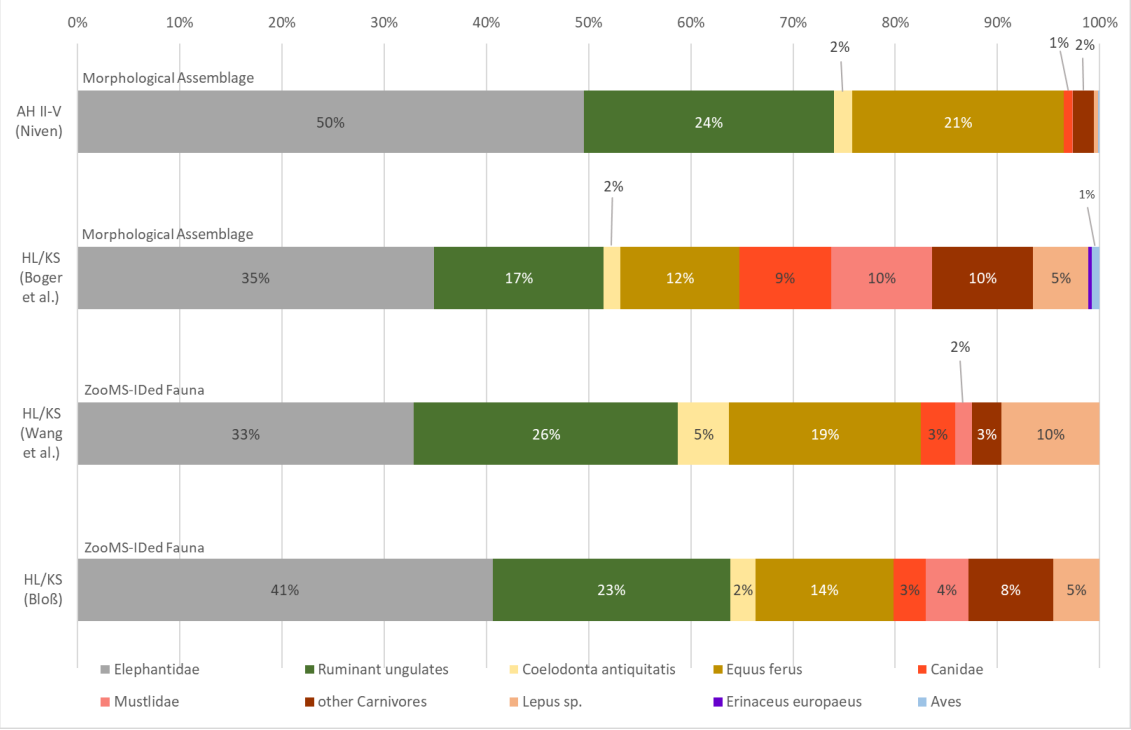

Figure 22: Faunal distribution patterns across the archaeological horizons II-V and the HL/KS sediment: Integration of zooarchaeological data with new findings.
Data from archaeological horizons II-V (N=7206) morphologically analyzed by Niven (2006) the HL/KS (N=1967) morphologically analyzed by Boger et al. (2014), the HL/KS (N=240) ZooMS-IDed by Wang et al. (in prep.) and the ZooMS-IDed HL/KS Fauna (N=288) in this study.

In conclusion, this analysis of the HL/KS sediment revealed a significant presence of Elephantidae in the fauna at Vogelherd, as well as a high abundance of ruminant ungulates and horses. These findings support the results of previous studies on the fauna of the HL/KS sediments. The HL/KS faunal assemblage exhibits notable similarities to the material uncovered from the Upper Palaeolithic archeological horizons at Vogelherd, analyzed by Niven, albeit with some variations. These similarities suggest an Upper Palaeolithic origin of the HL/KS. The data available indicates that the Pleistocene inhabitants of Vogelherd had a diverse subsistence strategy, centered around hunting and gathering, and utilizing a broad range of animal resources for sustenance, tools, and other purposes. This study offers valuable insights into the faunal assemblage of Vogelherd and advances our knowledge of human subsistence strategies during the Pleistocene.

7.2. Four new human bones - Interpretation and Implications

All four human bones identified in the analysis are from the HL/KS sediment which mainly consists of Upper Palaeolithic material (Conard and Zeidi, 2011; Schürch et al., 2020). Only one of the four human bones identified in the analysis was radiocarbon-dated (VH562) are part of this work, revealing an age of approximately 5,660-5,480 years cal BP (95.4%). This places it within a Neolithic context, which is not surprising, as all so far dated human remains from the site are relatively young and most of them are from the Neolithic era (see chapter 4).

The remaining three human bones (VH415, VH556, and VH877) will also be subjected to radiocarbon dating to provide further insights into their age and origin. Three historical contexts - the Aurignacian, the Magdalenian, and the Neolithic - are deemed plausible based on the available information regarding the history of Vogelherd Cave. Direct ^{14}C dating of the bones is necessary to confirm their age and place them in their proper historical context.

7.2.1. Aurignacian

Commencing with the earliest feasible period, humans can be placed within an Aurignacian context at the onset of the Upper Palaeolithic. If the specimens are indeed of Aurignacian age, they could be among the oldest findings of anatomically modern humans in Europe. This would lend support to the *Danube Corridor Hypothesis*, which suggests that early anatomically modern humans migrated into a depopulated central Europe along the Danube Valley during an "unfavorable climatic phase" which occurred approximately 40,000 years ago, during either the continental European equivalent of Heinrich Event 4 or the ensuing interstadial 8 (Conard and Bolus, 2006). While modern humans spread further into Europe, they coexisted with Neanderthals during what is called the “transitional period”, a timespan of approximately 2,600-5,400 years (Higham et al., 2014). This period is marked by the transition from the Middle to Upper Palaeolithic era in Europe

and later the extinction of Neanderthals amidst the changing environmental conditions of Marine Isotope Stage 3 (Conard, 2011).

The Swabian Jura is particularly interesting due to its rich archaeological record, which provides some of the earliest evidence of modern symbolic behavior in Europe. This includes the creation of art, music, and ornaments, which are documented in the Swabian Aurignacian period (Conard and Bolus, 2003). While similar evidence of jewelry production exists in East Africa and the Levant from around the same time period, the Swabian Jura stands out as the place where the earliest figurative artworks and musical instruments have been discovered (Conard and Bolus, 2003). For this period of time, especially the Vogelherd is important due to its wealth of Aurignacian assemblages (Heckel et al., 2014; Riek, 1932). Among the artifacts discovered at Vogelherd are three full ivory sculptures depicting a mammoth, a wild horse, and a cave lion, which are some of the oldest three-dimensional works of art in the world (Conard et al., 2003; Heckel et al., 2014; Riek, 1932). A picture of these artifacts can be found in Figures 26-28 in the Appendix. The archaeological context of the Aurignacian artifacts, coupled with the discovery of human bones within the same archeological horizons (namely, the Stetten fossils), has in the past led to the conclusion that anatomically modern humans were the sole producers of these artifacts (Conard et al., 2004). The Stetten fossils, which were thought to be some of the earliest anatomically modern humans in Europe, were later redated and placed into a Neolithic context (Conard et al., 2004).

However, as the HL/KS consists mostly of Upper Palaeolithic material, an Aurignacian context for specimens identified in this study is not impossible.

7.2.2. Magdalenian

The Magdalenian period is a significant cultural period of the European Upper Palaeolithic that lasted from about 20,000 years ago until the end of the Late Glacial period (Wong, 2020). In the region of the Swabian Jura, the Magdalenian era occurred much later, around 13,000 years ago, which is later than in other parts of the world (Conard et al., 2007). The area had been uninhabited during the Last Glacial Maximum, which occurred 27,200 to 23,500 years ago (Sanchez Goñi and Harrison, 2010; Svensson et al., 2006; Wong et al., 2020) and was then likely recolonized by Magdalenian hunter-gatherers from the west approximately 16,300 years ago after the ice had retreated (Taller et al., 2014; Wong et al., 2020). The Swabian Jura was resettled during the late Pleniglacial period, which was marked by cold and dry conditions. Therefore, it is unlikely that the improving climatic conditions were the main reason for the resettlement, as noted by Taller et al. (2014). Instead, these authors suggest that the resettlement was driven by population growth and the resulting need to adapt to specific environmental conditions.

An interesting matter to consider about this time is the burial practices. Although human remains from the period following the Last Glacial Maximum are rare in Europe (Orschiedt, 2013), evidence suggests that primary burials - where whole, intact bodies are buried in graves - were not the typical or predominant method of funerary practices in the past. Instead, there is a notable occurrence of deliberately treated isolated and/or fragmented human remains (Orschiedt, 2013). In Western Europe, particularly in France, Germany, Poland, and the United Kingdom, a considerable number of bones, especially cranial bones, bearing striations, and other marks of defleshing, have been discovered (Orschiedt, 2013). Moreover, in the Swabian Jura region, signs of hominin remains with indications of butchery, such as cut marks and human tooth marks, suggesting the occurrence of cannibalism (Sala and Conard, 2016).

The only hominin bone from Vogelherd, that can confidently (through radiocarbon methods) be dated into a Magdalenian context is approximately 16,000 years old, making it the oldest specimen at the site Wang et al. (*in prep.*).

7.2.3. Neolithic

The Neolithic period, also known as the New Stone Age, was a significant turning point in human history, marked by a transition from a nomadic, hunter-gatherer way of life to a more settled existence based on agriculture and animal husbandry (Miera et al., 2019; Teuber et al., 2017). This surge in human activity had unprecedented impacts on societies and the environment (Miera et al., 2019; Teuber et al., 2017; Vigne, 2011), and was closely linked to the introduction of domesticated plants and animals, which were often brought by immigrant farmers from the Near East (Tresset and Vigne, 2011). Some of these domesticates, such as sheep, goats, emmer wheat, and lentils, had no wild ancestors in Europe during the Holocene and were introduced to Southeast Europe at the onset of the Neolithic period (Tresset and Vigne, 2011). The domesticated plants and cultivated crops then spread throughout Europe, following both the Mediterranean and Danubian routes (Tresset and Vigne, 2011). As the introduction of domesticated plants and animals revolutionized human subsistence and allowed for the development of permanent settlements, housing structures were built and forests were cleared to make way for fields used for farming and grazing (Banning, 2003; Miera et al., 2019). Consequently, while the cultivation of crops allowed for a more reliable food supply, effective soil management practices became crucial for achieving high crop yields (Miera et al., 2019). Interestingly, despite these innovative developments, human remains have been discovered in caves, including at the Vogelherd, suggesting intriguing burial practices that are possible evidence of ritualistic offerings of humans, although Orschiedt (2012) acknowledges the possibility of non-ritualistic contexts for

such burials too. The human individual whose maxillary fragment was identified in this study and IDed as VH562 could be an example of either possibility.

An exact chronological classification of the yet undated human specimens identified in this study will provide further insights into human occupations, with present data already shedding light on the animal diversity at Vogelherd Cave, and therefore also the hunting and subsistence strategies of the human occupants.

7.3. Zooming into the Future: The Next Generation of ZooMS Analysis

Looking ahead, the future of ZooMS is promising. The continued development of this method, coupled with other analytical techniques such as aDNA and radiocarbon dating, will enable researchers to better understand the history of our species.

One potential concern that needs to be addressed in the future is the calibration of ZooMS datasets to make them comparable to zooarchaeological datasets. Due to the fragmentation or size of bones, there is a risk of over- or underrepresentation of certain species in the dataset, which could affect the accuracy of the results. However, this is a known issue within the ZooMS community, and researchers are actively working on developing new approaches to address this challenge. Several research groups are investigating different methods for correcting these biases and improving the accuracy of ZooMS datasets (*conference discussion*[3]).

One of the most exciting potential applications of ZooMS in the future is its ability to identify human remains in a forensic context. As demonstrated by Xu et al. (2023), ZooMS can be used in forensic investigations to reliably identify human bones from mixtures of bone fragments, providing reliable taxonomic information before expensive DNA profiling analysis is performed. This could potentially revolutionize forensic investigations by providing a faster and more cost-effective means of identifying human remains.

Furthermore, the continued development of ZooMS analysis methods will lead to even faster and more accurate identification of species. The development of a Python code for faster identification of specimens by the Douka lab at the University of Vienna (Végh and Douka, *in prep*.) is just one example of how we can expect data analysis to become more efficient in the future. Additionally, the integration of artificial intelligence and machine learning algorithms could potentially enhance the accuracy of ZooMS analysis even further, enabling researchers to identify species with even greater precision and speed.

[3] Conference "Integrating ZooMS and zooarcheology: methodological challenges and interpretive potentials", April 18-19th 2023, University of Kent, Canterbury, UK

The ZooMS method has already proven to be a valuable tool in the field of archaeological sciences, and its future applications hold great potential for enhancing our understanding of the past. As technology continues to develop, we can expect even more exciting discoveries to come to light, with big potential in shedding further light on the origins and evolution of modern humans. The future of ZooMS is full of exciting possibilities, and it will undoubtedly continue to play a significant role in our exploration of human history.

8. Conclusion

The Vogelherd Cave is a site of great importance in understanding the evolution of humans in central Europe. It has yielded valuable evidence of some of the earliest figurative art and musical instruments, as well as a wealth of zooarchaeological remains. By the application of the powerful ZooMS technique, 565 highly fragmented bone fragments were taxonomically identified in this thesis study, with results aligning with the species variation described by previous studies of the Vogelherd fauna.

The discovery of four hominin bones contributes to our understanding of the human occupations at Vogelherd. At the time of this writing, radiocarbon dating evidence is currently available for one of the four human bones (VH562), revealing an age of approximately 4900 years BP or ~5500 cal BP. This places it within a Neolithic context, which is consistent with several other human remains found at the site that have been dated so far. However, it is possible that the other three bones could date back to the Magdalenian or even the Aurignacian, which would make them some of the oldest anatomically modern human bones in Europe. Further analysis and dating of these bones will be necessary to determine their true age and historical context. Also, aDNA testing may help to determine if these bone fragments are from the same individuals as other bones identified in the past, such as the Stetten fossils.

This master's thesis successfully achieves its objective of analyzing additional bones from the site, providing valuable insights into the diversity of animal species present at Vogelherd Cave, as well as the subsistence behaviors of its human inhabitants. The identification of a wide range of animal species suggests that modern humans in the Lone Valley had a sophisticated understanding of their environment and were able to effectively exploit the resources available to them, possibly contributing to their successful adaptation and survival in the region. Additionally, this research highlights the power of ZooMS as a tool for the identification of difficult-to-identify remains and findings of this study contribute to ongoing efforts of comprehending the evolution of our species, underscoring the importance of continued research at this and other key archaeological sites.

VII. References

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VIII. Appendices

Appendix 1: Zusammenfassung (German Summary)

Die Vogelherd-Höhle ist seit den ersten Ausgrabungen im Jahr 1931 eine der bedeutendsten archäologischen Stätten in Deutschland, die wertvolle Einblicke in das Leben unserer Vorfahren gewährt. Die Stätte lieferte eine Fülle von prähistorischem Material, darunter menschliche Überreste aus dem Neolithikum und dem Magdalénien. Zahlreiche Knochenfragmente dieser Fundstätte konnten bisher jedoch nicht identifiziert werden.

Das Ziel dieser Masterarbeit war es, morphologisch nicht identifizierbare Knochenfragmente der Fundstelle durch Massenspektrometrie (ZooMS) zu analysieren, um Arten taxonomisch zu identifizieren und weitere menschliche Knochen zu finden. ZooMS ist besonders nützlich für die Analyse kleiner und fragmentarischer Knochen, die typischerweise in paläolithischen Sammlungen gefunden werden. Insgesamt wurden 640 Knochenfragmente untersucht, von denen 88% erfolgreich identifiziert werden konnten. Dabei wurden vier neue menschliche Knochen identifiziert sowie Überreste verschiedener Tierarten wie dem Wollmammut, verschiedener Huftiere und Hasen.

Ein menschlicher Knochen wurde mittels der Radiokohlenstoffdatierung (14C) direkt auf 5480-5650 cal BP (= Kalenderjahre vor der Gegenwart) datiert. Obwohl dieser Knochen aus der Jungsteinzeit stammt, ist das Alter der anderen menschlichen Knochen, die bald datiert werden sollen, noch unbekannt. Die Entdeckung von anatomisch modernen Menschenknochen aus der Aurignacien-Zeit wäre von besonderem Interesse, da sie zu den frühesten bekannten Funden dieser Art in Europa gehören würden.

Diese Ergebnisse tragen dazu bei, das Verständnis der kulturellen und biologischen Entwicklung unserer Vorfahren in Europa zu erweitern und verdeutlichen, wie bedeutend kontinuierliche Forschung und die Weiterentwicklung innovativer Analysetechniken im Bereich der menschlichen Evolution sind.

Appendix 2: Additional Figures

Figure 23: Historical photograph of the Vogelherd Cave.
The photograph showcases the backdirt produced in 1931 (credits: Universität Tübingen).

Figure 24: Photo of the re-excavation at Vogelherd Cave.
(credits: Mohsen Zeidi)

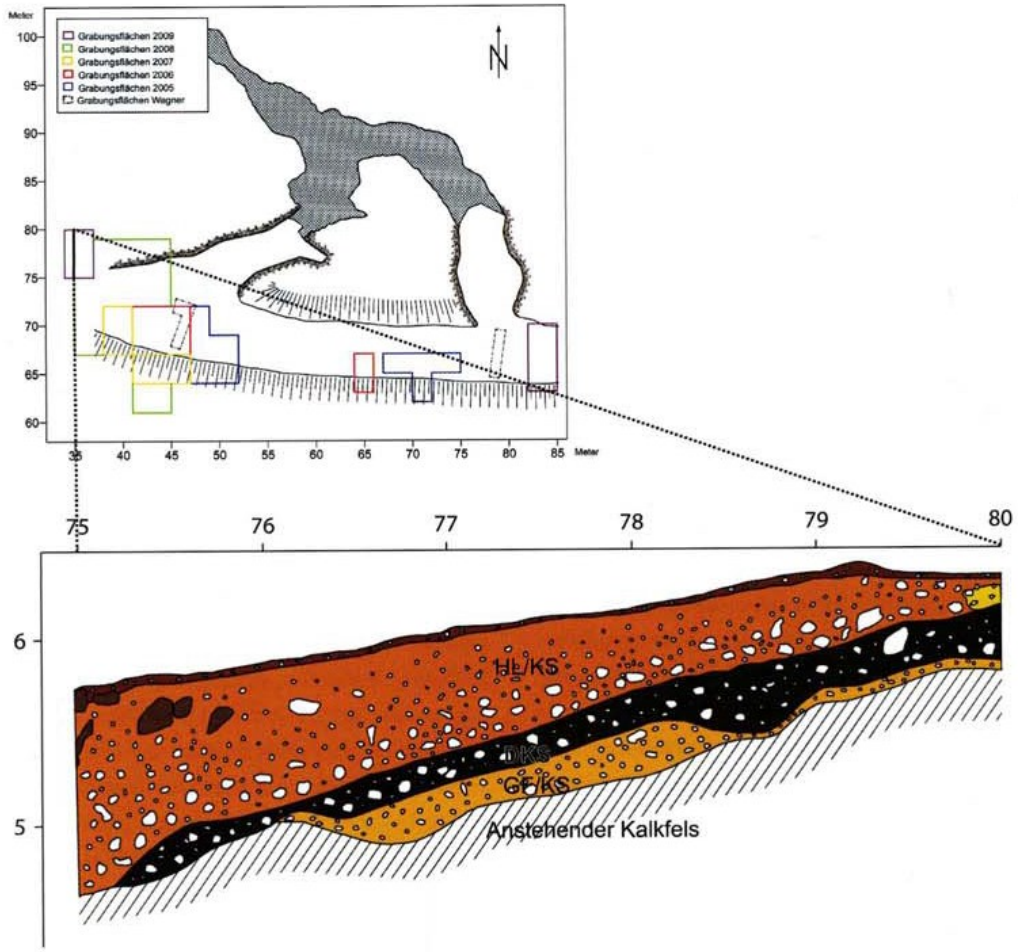

Figure 25: Areas of excavation and sediment profile from re-excavations at Vogelherd Cave.
This profile is close to the region where the material analyzed in this thesis study was obtained (Conard et al., 2010).

Figure 26: Aurignacian ivory sculpture of a wild horse.
The figure was retrieved from Vogelherd in 1931 (credits: Don Hitchcock).

Figure 27: Aurignacian ivory sculpture of a woolly mammoth.
The figure was retrieved from Vogelherd in 1931 (credits: Don Hitchcock).

Figure 28: Aurignacian ivory sculpture of a cave lion.
The figure was retrieved from Vogelherd in 1931 (credits: Don Hitchcock).

Appendix 3: Mass Spectra of hominin bones

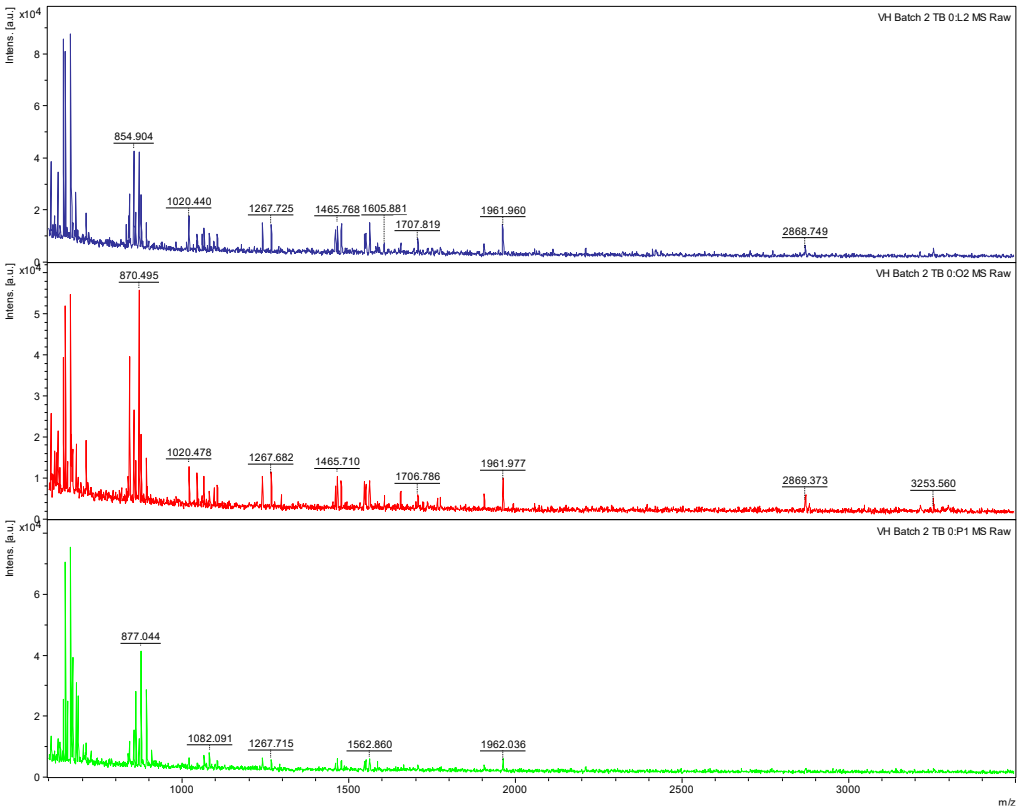

Figure 29: Mass spectrum of VH415.

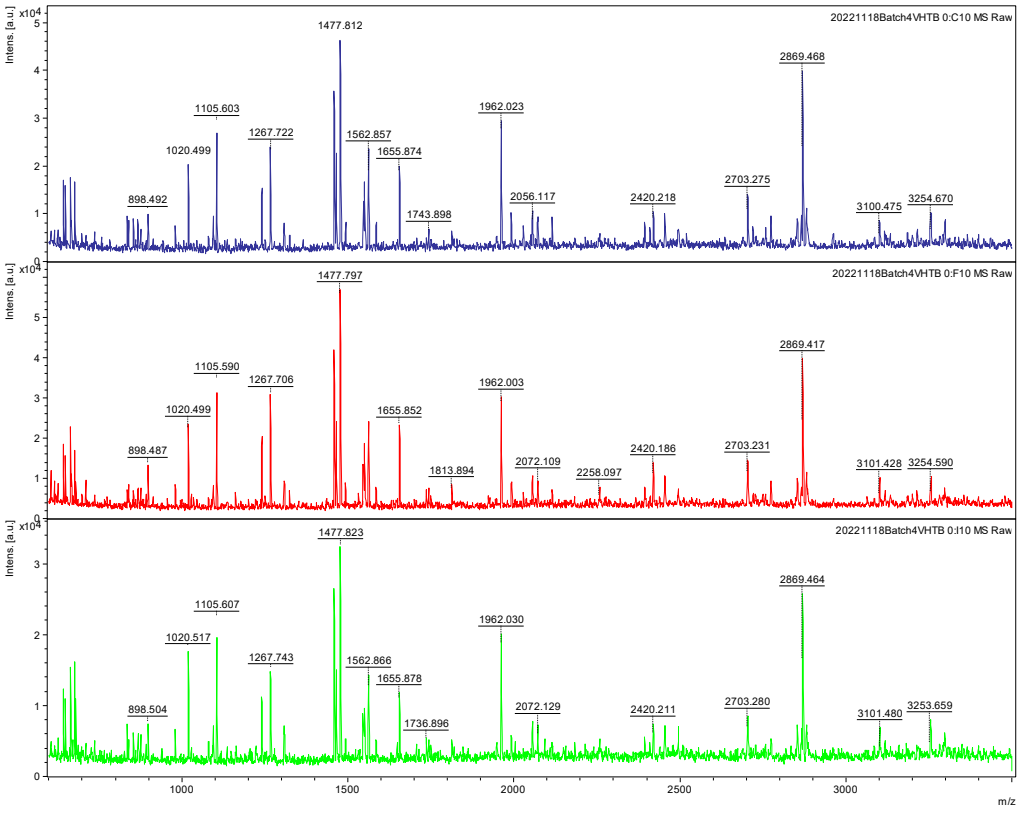

Figure 30: Mass spectrum of VH556.

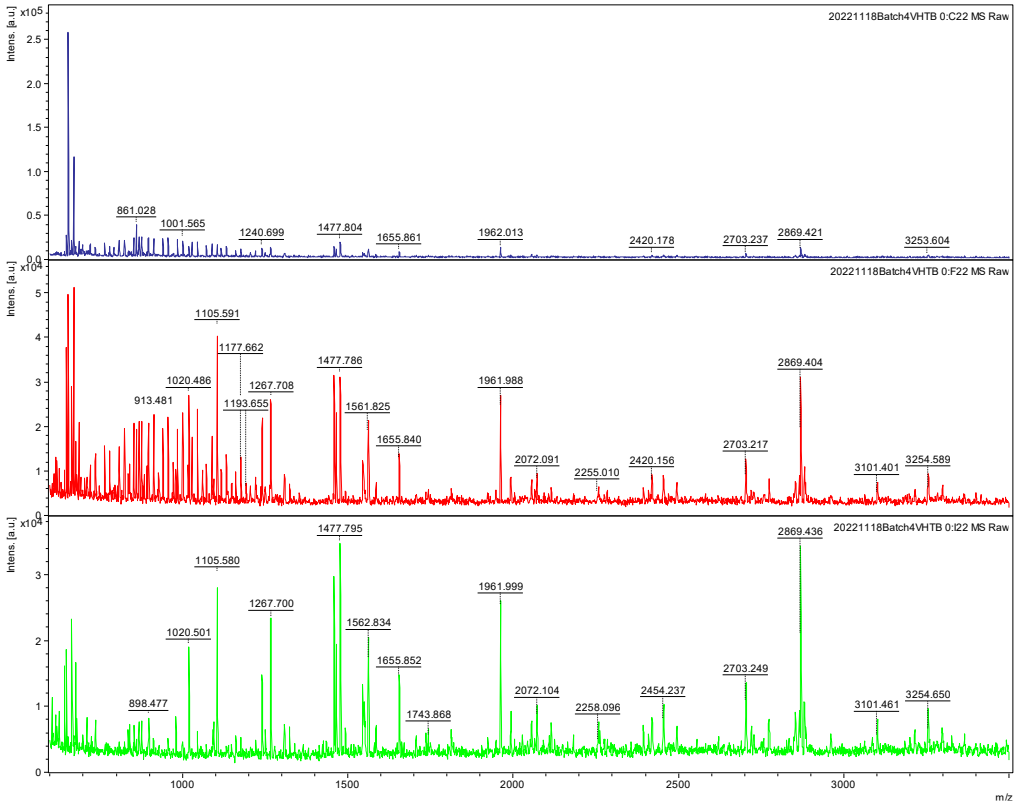

Figure 31: Mass spectrum of VH562.

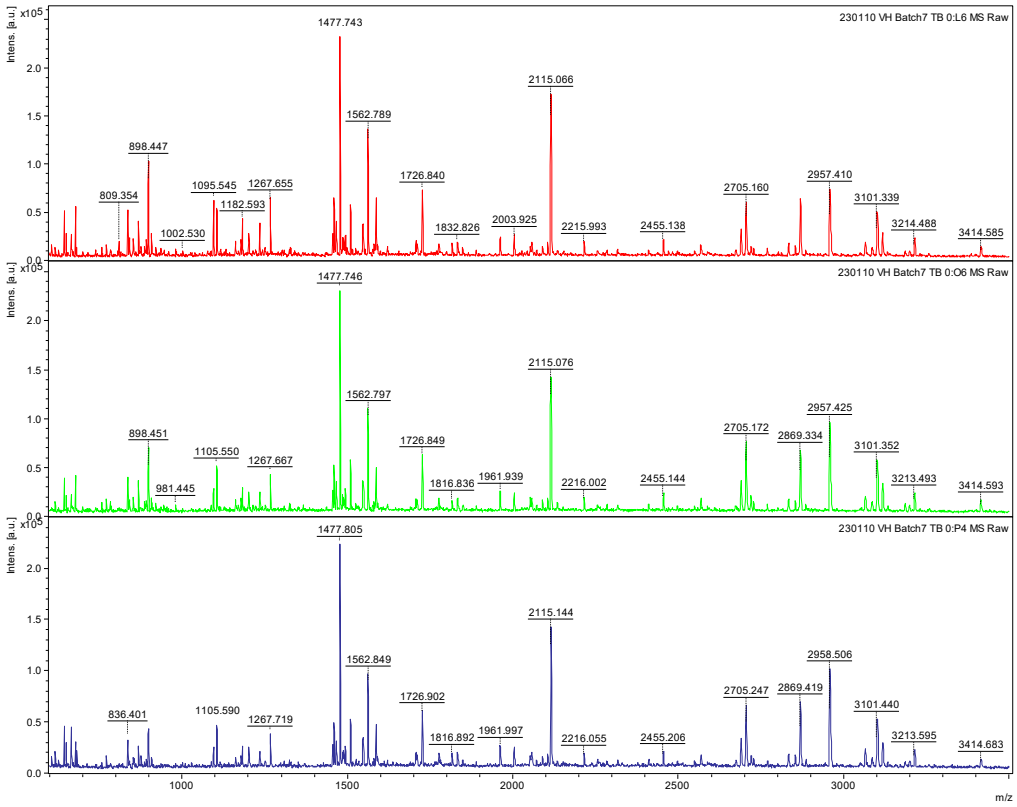

Figure 32: Mass spectrum of VH887.

Appendix 4: µCT Scanning of hominin skeletal remains

The Vogelherd human remains were scanned on January 27th, 2023 by Martin Dockner at the Core Facility for Micro-Computed Tomography at the University of Vienna (Department of Evolutionary Anthropology) with a custom-built Viscom X8060 µCT-scanner.

The following parameters were used for scanning VH415:

- 130 kV
- 160 mA
- 2801 ms exposure time
- 0,75 mm copper prefilter

The following parameters were used for scanning VH556, VH562, and VH877:

- 130 kV
- 210 mA
- 2202 ms exposure time
- 0,75 mm copper prefilter

The Raw data was obtained in form of TIFF files and then post-processed in Amira 6.5. (ThermoFisher Scientific).

Appendix 5: Raw ZooMS IDs

ID	Layer	Order	ZooMS Result
VH288	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH289	HL/KS	Carnivora	*Meles meles*
VH290	HL/KS	Carnivora	Mustelidae
VH291	HL/KS	Perissodactyla	*Equus ferus*
VH292	HL/KS	Carnivora	Felidae/Mustelidae
VH293	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH294	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH296	HL/KS	Carnivora	*Meles meles*
VH297	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH298	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH299	HL/KS	Carnivora	*Vulpes vulpes*
VH301	HL/KS	Artiodactyla	*Rangifer tarandus*
VH302	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH303	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH304	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH305	HL/KS	Carnivora	Felidae/Mustelidae
VH306	HL/KS	Lagomorpha	*Lepus sp.*
VH307	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH308	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH309	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH310	HL/KS	Carnivora	Felidae/Hyaenidae/Mustelidae
VH311	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH312	HL/KS	Carnivora	Mustelidae
VH313	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH314	HL/KS	Artiodactyla	*Rangifer tarandus*
VH315	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH316	HL/KS	Perissodactyla	*Equus ferus*
VH317	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH318	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH319	HL/KS	Perissodactyla	*Equus ferus*
VH321	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH322	HL/KS	Lagomorpha	*Lepus sp.*
VH323	HL/KS	Carnivora	Felidae/Hyaenidae/Mustelidae
VH324	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH325	HL/KS	Perissodactyla	*Equus ferus*
VH326	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH327	HL/KS	Lagomorpha	*Lepus sp.*
VH328	HL/KS	Perissodactyla	*Coelodonta antiquitatis*
VH329	HL/KS	Lagomorpha	*Lepus sp.*
VH330	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH331	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH332	HL/KS	Perissodactyla	*Equus ferus*
VH333	HL/KS	Lagomorpha	*Lepus sp.*
VH334	HL/KS	Perissodactyla	*Coelodonta antiquitatis*

VH335	HL/KS	Artiodactyla	*Cervus/Capreolus/Megaloceros*
VH336	HL/KS	Artiodactyla	*Bos/Bison*
VH337	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH338	HL/KS	Artiodactyla	*Cervus/Capreolus/Megaloceros*
VH339	HL/KS	Artiodactyla	*Cervus/Capreolus/Megaloceros*
VH340	HL/KS	Artiodactyla	*Cervus/Capreolus/Megaloceros*
VH341	HL/KS	Carnivora	Ursidae/Felidae
VH342	HL/KS	Perissodactyla	*Equus ferus*
VH344	HL/KS	Perissodactyla	*Equus ferus*
VH346	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH347	HL/KS	Artiodactyla	*Rangifer tarandus*
VH348	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH350	HL/KS	Carnivora	Felidae/Hyaenidae/Mustelidae
VH351	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH352	HL/KS	Lagomorpha	*Lepus sp.*
VH353	HL/KS	Perissodactyla	*Equus ferus*
VH354	HL/KS	Carnivora	*Panthera leo spalaea*
VH355	HL/KS	Carnivora	Felidae/Hyaenidae/Mustelidae
VH356	HL/KS	Artiodactyla	*Cervus/Capreolus/Megaloceros*
VH357	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH358	HL/KS	Perissodactyla	*Equus ferus*
VH361	HL/KS	Artiodactyla	*Sus scrofa*
VH362	HL/KS	Perissodactyla	*Equus ferus*
VH363	HL/KS	Perissodactyla	*Equus ferus*
VH364	HL/KS	Carnivora	*Canis lupus*
VH365	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH366	HL/KS	Perissodactyla	*Equus ferus*
VH367	HL/KS	Carnivora	Felidae/Hyaenidae/Mustelidae
VH368	HL/KS	Perissodactyla	*Equus ferus*
VH369	HL/KS	Artiodactyla	*Cervus/Capreolus/Megaloceros*
VH370	HL/KS	Perissodactyla	*Coelodonta antiquitatis*
VH371	HL/KS	Artiodactyla	*Rangifer tarandus*
VH372	HL/KS	Lagomorpha	*Lepus sp.*
VH373	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH374	HL/KS	Artiodactyla	*Cervus/Capreolus/Megaloceros*
VH375	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH376	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH377	HL/KS	Artiodactyla	*Cervus/Capreolus/Megaloceros*
VH378	HL/KS	Carnivora	Felidae/Hyaenidae/Mustelidae
VH379	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH381	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH382	HL/KS	Artiodactyla	*Cervus/Capreolus/Megaloceros*
VH383	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH384	HL/KS	Artiodactyla	*Cervus/Capreolus/Megaloceros*
VH387	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH389	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH390	HL/KS	Lagomorpha	*Lepus sp.*

VH391	HL/KS	Perissodactyla	*Equus ferus*
VH392	HL/KS	Carnivora	*Felis silvestris*
VH393	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH394	HL/KS	Perissodactyla	*Coelodonta antiquitatis*
VH395	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH396	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH399	HL/KS	Artiodactyla	*Cervus/Capreolus/Megaloceros*
VH400	HL/KS	Artiodactyla	*Cervus/Capreolus/Megaloceros*
VH402	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH403	HL/KS	Perissodactyla	*Equus ferus*
VH404	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH405	HL/KS	Lagomorpha	*Lepus sp.*
VH406	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH408	HL/KS	Carnivora	Ursidae/Felidae
VH409	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH410	HL/KS	Artiodactyla	*Bos/Bison*
VH411	HL/KS	Artiodactyla	*Cervus/Capreolus/Megaloceros*
VH412	HL/KS	Artiodactyla	*Cervus/Capreolus/Megaloceros*
VH413	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH414	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH415	HL/KS	Primates	***Homo sapiens***
VH416	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH417	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH418	HL/KS	Lagomorpha	*Lepus sp.*
VH419	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH420	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH421	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH422	HL/KS	Carnivora	*Vulpes vulpes*
VH423	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH424	HL/KS	Artiodactyla	*Cervus/Capreolus/Megaloceros*
VH425	HL/KS	Artiodactyla	Bovidae/Cervidae
VH426	HL/KS	Lagomorpha	*Lepus sp.*
VH428	HL/KS	Artiodactyla	*Bos/Bison*
VH429	HL/KS	Perissodactyla	*Equus ferus*
VH431	HL/KS	Perissodactyla	*Equus ferus*
VH432	HL/KS	Artiodactyla	*Cervus/Capreolus/Megaloceros*
VH434	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH436	HL/KS	Perissodactyla	*Equus ferus*
VH438	HL/KS	Artiodactyla	*Cervus/Capreolus/Megaloceros*
VH439	HL/KS	Artiodactyla	*Cervus/Capreolus/Megaloceros*
VH440	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH441	HL/KS	Artiodactyla	*Cervus/Capreolus/Megaloceros*
VH443	HL/KS	Perissodactyla	*Equus ferus*
VH444	GL/GKS	Carnivora	Ursidae/Felidae
VH445	GL/GKS	Perissodactyla	*Equus ferus*
VH446	GL/GKS	Perissodactyla	*Coelodonta antiquitatis*
VH447	GL/GKS	Proboscidea	*Elephas/Mammuthus*

VH448	GL/GKS	Perissodactyla	*Coelodonta antiquitatis*
VH449	GL/GKS	Perissodactyla	*Equus ferus*
VH450	GL/GKS	Carnivora	Ursidae/Felidae
VH451	GL/GKS	Perissodactyla	*Coelodonta antiquitatis*
VH452	GL/GKS	Artiodactyla	*Cervus/Capreolus/Megaloceros*
VH453	GL/GKS	Carnivora	Ursidae/Felidae
VH454	GL/GKS	Perissodactyla	*Coelodonta antiquitatis*
VH455	GL/GKS	Proboscidea	*Elephas/Mammuthus*
VH456	GL/GKS	Artiodactyla	*Cervus/Capreolus/Megaloceros*
VH457	GL/GKS	Artiodactyla	*Cervus/Capreolus/Megaloceros*
VH458	GL/GKS	Perissodactyla	*Equus ferus*
VH459	GL/GKS	Artiodactyla	*Cervus/Capreolus/Megaloceros*
VH460	GL/GKS	Proboscidea	*Elephas/Mammuthus*
VH461	GL/GKS	Artiodactyla	*Cervus/Capreolus/Megaloceros*
VH462	GL/GKS	Artiodactyla	*Rangifer tarandus*
VH463	GL/GKS	Proboscidea	*Elephas/Mammuthus*
VH464	GL/GKS	Artiodactyla	*Rangifer tarandus*
VH465	GL/GKS	Artiodactyla	*Bos/Bison*
VH466	GL/GKS	Artiodactyla	*Cervus/Capreolus/Megaloceros*
VH467	GL/GKS	Artiodactyla	*Rangifer tarandus*
VH468	GL/GKS	Artiodactyla	*Cervus/Capreolus/Megaloceros*
VH469	GL/GKS	Proboscidea	*Elephas/Mammuthus*
VH471	GL/GKS	Proboscidea	*Elephas/Mammuthus*
VH472	GL/GKS	Artiodactyla	*Rangifer tarandus*
VH473	GL/GKS	Artiodactyla	Bovidae/Cervidae
VH474	GL/GKS	Perissodactyla	*Equus ferus*
VH476	GL/GKS	Artiodactyla	*Cervus/Capreolus/Megaloceros*
VH477	GL/GKS	Perissodactyla	*Coelodonta antiquitatis*
VH478	GL/GKS	Perissodactyla	*Equus ferus*
VH479	GL/GKS	Proboscidea	*Elephas/Mammuthus*
VH480	GL/GKS	Proboscidea	*Elephas/Mammuthus*
VH481	GL/GKS	Proboscidea	*Elephas/Mammuthus*
VH483	GL/GKS	Proboscidea	*Elephas/Mammuthus*
VH484	GL/GKS	Proboscidea	*Elephas/Mammuthus*
VH486	GL/GKS	Perissodactyla	*Coelodonta antiquitatis*
VH487	GL/GKS	Carnivora	Felidae/Hyaenidae/Mustelidae
VH490	GL/GKS	Proboscidea	*Elephas/Mammuthus*
VH491	GL/GKS	Perissodactyla	*Coelodonta antiquitatis*
VH492	GL/GKS	Artiodactyla	*Cervus/Capreolus/Megaloceros*
VH493	GL/GKS	Artiodactyla	Bovidae/Cervidae
VH494	GL/GKS	Artiodactyla	*Cervus/Capreolus/Megaloceros*
VH495	GL/GKS	Artiodactyla	*Cervus/Capreolus/Megaloceros*
VH496	GL/GKS	Artiodactyla	*Cervus/Capreolus/Megaloceros*
VH497	GL/GKS	Proboscidea	*Elephas/Mammuthus*
VH498	GL/GKS	Artiodactyla	Bovidae/Cervidae
VH499	GL/GKS	Proboscidea	*Elephas/Mammuthus*
VH500	GL/GKS	Artiodactyla	*Cervus/Capreolus/Megaloceros*

VH501	GL/GKS	Artiodactyla	*Cervus/Capreolus/Megaloceros*
VH502	GL/GKS	Lagomorpha	*Lepus sp.*
VH503	GL/GKS	Artiodactyla	*Cervus/Capreolus/Megaloceros*
VH504	GL/GKS	Perissodactyla	*Coelodonta antiquitatis*
VH505	GL/GKS	Artiodactyla	*Cervus/Capreolus/Megaloceros*
VH506	GL/GKS	Artiodactyla	*Bos/Bison*
VH509	GL/GKS	Perissodactyla	*Coelodonta antiquitatis*
VH511	HL/KS	Perissodactyla	*Equus ferus*
VH513	HL/KS	Artiodactyla	*Cervus/Capreolus/Megaloceros*
VH514	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH515	HL/KS	Carnivora	*Canis lupus*
VH516	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH517	HL/KS	Artiodactyla	*Cervus/Capreolus/Megaloceros*
VH519	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH520	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH521	HL/KS	Artiodactyla	*Bos/Bison*
VH522	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH523	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH524	HL/KS	Carnivora	Felidae/Hyaenidae/Mustelidae
VH525	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH526	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH527	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH528	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH529	HL/KS	Carnivora	Felidae/Mustelidae
VH530	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH531	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH532	HL/KS	Perissodactyla	*Coelodonta antiquitatis*
VH533	HL/KS	Perissodactyla	*Equus ferus*
VH534	HL/KS	Artiodactyla	*Sus scrofa*
VH535	HL/KS	Artiodactyla	Bovidae/Cervidae
VH536	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH537	HL/KS	Carnivora	Felidae/Mustelidae
VH538	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH539	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH540	HL/KS	Carnivora	Felidae/Hyaenidae/Mustelidae
VH541	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH542	HL/KS	Carnivora	*Vulpes vulpes*
VH543	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH544	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH545	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH547	HL/KS	Artiodactyla	*Rangifer tarandus*
VH548	HL/KS	Artiodactyla	Bovidae/Cervidae
VH549	HL/KS	Carnivora	Felidae/Hyaenidae/Mustelidae
VH550	HL/KS	Perissodactyla	*Equus ferus*
VH551	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH552	HL/KS	Artiodactyla	*Cervus/Capreolus/Megaloceros*
VH554	HL/KS	Proboscidea	*Elephas/Mammuthus*

VH555	HL/KS	Perissodactyla	*Equus ferus*
VH556	HL/KS	Primates	***Homo sapiens***
VH557	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH558	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH559	HL/KS	Carnivora	Ursidae/Felidae
VH560	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH561	HL/KS	Carnivora	Felidae/Hyaenidae/Mustelidae
VH562	HL/KS	Primates	***Homo sapiens***
VH563	GL/GKS	Perissodactyla	*Equus ferus*
VH564	GL/GKS	Perissodactyla	*Equus ferus*
VH566	GL/GKS	Proboscidea	*Elephas/Mammuthus*
VH567	GL/GKS	Perissodactyla	*Equus ferus*
VH568	GL/GKS	Perissodactyla	*Coelodonta antiquitatis*
VH569	GL/GKS	Carnivora	Felidae/Hyaenidae/Mustelidae
VH570	GF/KS	Proboscidea	*Elephas/Mammuthus*
VH571	GF/KS	Proboscidea	*Elephas/Mammuthus*
VH572	GF/KS	Perissodactyla	*Equus ferus*
VH573	GF/KS	Artiodactyla	*Cervus/Capreolus/Megaloceros*
VH574	GF/KS	Perissodactyla	*Equus ferus*
VH576	GF/KS	Proboscidea	*Elephas/Mammuthus*
VH577	GF/KS	Artiodactyla	*Bos/Bison*
VH578	GF/KS	Lagomorpha	*Lepus sp.*
VH579	GF/KS	Carnivora	Felidae/Hyaenidae/Mustelidae
VH580	GF/KS	Perissodactyla	*Equus ferus*
VH583	GF/KS	Artiodactyla	*Bos/Bison*
VH584	GF/KS	Perissodactyla	*Equus ferus*
VH585	GF/KS	Artiodactyla	*Bos/Bison*
VH586	GF/KS	Artiodactyla	*Cervus/Capreolus/Megaloceros*
VH587	GF/KS	Perissodactyla	*Equus ferus*
VH588	GF/KS	Proboscidea	*Elephas/Mammuthus*
VH589	GF/KS	Perissodactyla	*Coelodonta antiquitatis*
VH590	GL/GKS	Proboscidea	*Elephas/Mammuthus*
VH591	GL/GKS	Proboscidea	*Elephas/Mammuthus*
VH592	GL/GKS	Proboscidea	*Elephas/Mammuthus*
VH593	GL/GKS	Perissodactyla	*Equus ferus*
VH594	GL/GKS	Artiodactyla	*Cervus/Capreolus/Megaloceros*
VH595	GL/GKS	Artiodactyla	*Cervus/Capreolus/Megaloceros*
VH596	GL/GKS	Perissodactyla	*Equus ferus*
VH598	GL/GKS	Carnivora	Felidae/Hyaenidae/Mustelidae
VH599	GL/GKS	Perissodactyla	*Equus ferus*
VH601	GL/GKS	Perissodactyla	*Coelodonta antiquitatis*
VH603	GL/GKS	Proboscidea	*Elephas/Mammuthus*
VH605	GL/GKS	Perissodactyla	*Coelodonta antiquitatis*
VH606	GL/GKS	Perissodactyla	*Equus ferus*
VH607	GL/GKS	Carnivora	Felidae/Hyaenidae/Mustelidae
VH608	GL/GKS	Carnivora	Felidae/Hyaenidae/Mustelidae
VH609	GL/GKS	Carnivora	Ursidae/Felidae

VH611	GL/GKS	Carnivora	Ursidae/Felidae
VH613	GL/GKS	Proboscidea	*Elephas/Mammuthus*
VH615	GL/GKS	Artiodactyla	*Rangifer tarandus*
VH616	GL/GKS	Carnivora	Ursidae/Felidae
VH617	GL/GKS	Carnivora	Felidae/Hyaenidae/Mustelidae
VH618	GL/GKS	Perissodactyla	*Equus ferus*
VH622	GL/GKS	Carnivora	Felidae/Hyaenidae/Mustelidae
VH623	GF/KS	Perissodactyla	*Equus ferus*
VH630	HL/KS	Carnivora	Canidae
VH631	HL/KS	Perissodactyla	*Equus ferus*
VH632	HL/KS	Artiodactyla	*Cervus/Capreolus/Megaloceros*
VH633	HL/KS	Artiodactyla	*Cervus/Capreolus/Megaloceros*
VH634	HL/KS	Artiodactyla	Bovidae/Cervidae
VH635	HL/KS	Artiodactyla	*Rangifer tarandus*
VH636	HL/KS	Carnivora	Ursidae/Felidae
VH638	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH639	GL/GKS	Perissodactyla	*Equus ferus*
VH640	GL/GKS	Perissodactyla	*Equus ferus*
VH642	GL/GKS	Carnivora	Ursidae/Felidae
VH645	GL/GKS	Artiodactyla	Bovidae/Cervidae
VH646	GL/GKS	Perissodactyla	*Equus ferus*
VH648	GF/KS	Perissodactyla	*Equus ferus*
VH649	GF/KS	Artiodactyla	*Cervus/Capreolus/Megaloceros*
VH650	GF/KS	Perissodactyla	*Coelodonta antiquitatis*
VH652	GF/KS	Perissodactyla	*Equus ferus*
VH653	GL/GKS	Perissodactyla	*Equus ferus*
VH654	GL/GKS	Artiodactyla	*Cervus/Capreolus/Megaloceros*
VH655	GL/GKS	Artiodactyla	*Cervus/Capreolus/Megaloceros*
VH656	GL/GKS	Artiodactyla	*Cervus/Capreolus/Megaloceros*
VH658	GL/GKS	Proboscidea	*Elephas/Mammuthus*
VH659	GL/GKS	Proboscidea	*Elephas/Mammuthus*
VH660	GL/GKS	Perissodactyla	*Coelodonta antiquitatis*
VH661	GL/GKS	Proboscidea	*Elephas/Mammuthus*
VH662	GL/GKS	Perissodactyla	*Equus ferus*
VH664	GL/GKS	Artiodactyla	*Rangifer tarandus*
VH665	GL/GKS	Artiodactyla	*Cervus/Capreolus/Megaloceros*
VH667	GL/GKS	Artiodactyla	Bovidae/Cervidae
VH669	GL/GKS	Artiodactyla	*Cervus/Capreolus/Megaloceros*
VH670	GL/GKS	Artiodactyla	*Cervus/Capreolus/Megaloceros*
VH672	GL/GKS	Proboscidea	*Elephas/Mammuthus*
VH673	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH674	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH675	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH676	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH677	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH678	HL/KS	Artiodactyla	*Cervus/Capreolus/Megaloceros*
VH679	HL/KS	Proboscidea	*Elephas/Mammuthus*

VH680	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH683	HL/KS	Perissodactyla	*Equus ferus*
VH684	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH685	HL/KS	Artiodactyla	*Rangifer tarandus*
VH686	HL/KS	Artiodactyla	Bovidae/Cervidae
VH687	HL/KS	Artiodactyla	Bovidae/Cervidae
VH688	HL/KS	Artiodactyla	*Bos/Bison*
VH690	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH691	HL/KS	Perissodactyla	*Equus ferus*
VH692	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH693	HL/KS	Artiodactyla	*Bos/Bison*
VH695	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH697	HL/KS	Perissodactyla	*Coelodonta antiquitatis*
VH698	HL/KS	Artiodactyla	Bovidae/Cervidae
VH699	HL/KS	Artiodactyla	*Cervus/Capreolus/Megaloceros*
VH700	HL/KS	Artiodactyla	Bovidae/Cervidae
VH701	HL/KS	Carnivora	Felidae/Hyaenidae/Mustelidae
VH702	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH703	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH704	HL/KS	Perissodactyla	*Equus ferus*
VH705	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH706	HL/KS	Artiodactyla	*Rangifer tarandus*
VH707	GF/KS	Perissodactyla	*Coelodonta antiquitatis*
VH708	GF/KS	Artiodactyla	*Rangifer tarandus*
VH709	GF/KS	Perissodactyla	*Equus ferus*
VH710	GF/KS	Perissodactyla	*Equus ferus*
VH711	GF/KS	Carnivora	Felidae/Hyaenidae/Mustelidae
VH712	GF/KS	Carnivora	Hyaenidae/Mustelidae
VH713	GF/KS	Proboscidea	*Elephas/Mammuthus*
VH714	GF/KS	Lagomorpha	*Lepus sp.*
VH715	GF/KS	Perissodactyla	*Equus ferus*
VH716	GF/KS		unknown
VH717	GF/KS	Perissodactyla	*Coelodonta antiquitatis*
VH718	GF/KS	Artiodactyla	*Bos/Bison*
VH719	GF/KS	Proboscidea	*Elephas/Mammuthus*
VH720	GF/KS	Artiodactyla	*Bos/Bison*
VH721	GF/KS	Perissodactyla	*Coelodonta antiquitatis*
VH722	GF/KS	Artiodactyla	*Bos/Bison*
VH723	GF/KS	Proboscidea	*Elephas/Mammuthus*
VH724	GF/KS	Proboscidea	*Elephas/Mammuthus*
VH725	GF/KS	Artiodactyla	*Bos/Bison*
VH726	GF/KS	Carnivora	Felidae/Hyaenidae/Mustelidae
VH727	GF/KS	Perissodactyla	*Coelodonta antiquitatis*
VH728	GF/KS	Artiodactyla	*Rangifer tarandus*
VH729	GF/KS	Perissodactyla	*Coelodonta antiquitatis*
VH730	GF/KS	Proboscidea	*Elephas/Mammuthus*
VH731	GF/KS	Perissodactyla	*Coelodonta antiquitatis*

VH732	GF/KS	Artiodactyla	*Bos/Bison*
VH733	GF/KS	Artiodactyla	*Rangifer tarandus*
VH734	GF/KS	Proboscidea	*Elephas/Mammuthus*
VH735	GF/KS	Artiodactyla	*Bos/Bison*
VH736	GF/KS	Artiodactyla	*Bos/Bison*
VH737	GF/KS	Proboscidea	*Elephas/Mammuthus*
VH738	GF/KS	Perissodactyla	*Coelodonta antiquitatis*
VH739	GF/KS	Artiodactyla	*Rangifer tarandus*
VH740	GF/KS	Artiodactyla	*Rangifer tarandus*
VH741	GF/KS	Artiodactyla	*Rangifer tarandus*
VH742	GF/KS	Perissodactyla	*Coelodonta antiquitatis*
VH743	GF/KS	Artiodactyla	*Bos/Bison*
VH744	GF/KS	Artiodactyla	*Bos/Bison*
VH745	GF/KS	Artiodactyla	*Bos/Bison*
VH746	GF/KS	Artiodactyla	*Bos/Bison*
VH747	GF/KS	Artiodactyla	*Bos/Bison*
VH748	GF/KS	Proboscidea	*Elephas/Mammuthus*
VH749	GF/KS	Perissodactyla	*Coelodonta antiquitatis*
VH750	GF/KS	Proboscidea	*Elephas/Mammuthus*
VH751	GF/KS	Artiodactyla	*Rangifer tarandus*
VH752	GF/KS	Proboscidea	*Elephas/Mammuthus*
VH753	GF/KS	Proboscidea	*Elephas/Mammuthus*
VH754	GF/KS	Proboscidea	*Elephas/Mammuthus*
VH756	GF/KS	Perissodactyla	*Coelodonta antiquitatis*
VH757	GF/KS	Perissodactyla	*Equus ferus*
VH758	GF/KS	Proboscidea	*Elephas/Mammuthus*
VH759	GF/KS	Artiodactyla	*Bos/Bison*
VH760	GF/KS	Proboscidea	*Elephas/Mammuthus*
VH761	GF/KS	Lagomorpha	*Lepus sp.*
VH763	GF/KS	Carnivora	Canidae
VH764	GF/KS	Artiodactyla	*Rangifer tarandus*
VH765	GF/KS	Perissodactyla	*Equus ferus*
VH766	GF/KS	Perissodactyla	*Equus ferus*
VH767	GF/KS	Proboscidea	*Elephas/Mammuthus*
VH768	GF/KS	Proboscidea	*Elephas/Mammuthus*
VH769	GF/KS	Artiodactyla	*Rangifer tarandus*
VH770	GF/KS	Artiodactyla	*Bos/Bison*
VH771	GF/KS	Artiodactyla	*Bos/Bison*
VH772	GF/KS	Artiodactyla	*Bos/Bison*
VH773	GF/KS	Lagomorpha	*Lepus sp.*
VH774	GF/KS	Artiodactyla	*Bos/Bison*
VH775	GF/KS	Artiodactyla	*Bos/Bison*
VH776	GF/KS	Artiodactyla	*Cervus/Capreolus/Megaloceros*
VH777	GF/KS	Artiodactyla	*Bos/Bison*
VH778	GF/KS	Perissodactyla	*Coelodonta antiquitatis*
VH779	GF/KS	Artiodactyla	*Bos/Bison*
VH780	GF/KS	Perissodactyla	*Coelodonta antiquitatis*

VH781	GF/KS	Lagomorpha	*Lepus sp.*
VH782	GF/KS	Artiodactyla	*Bos/Bison*
VH783	GF/KS	Artiodactyla	*Bos/Bison*
VH784	GF/KS	Artiodactyla	*Cervus/Capreolus/Megaloceros*
VH785	GL/GKS	Perissodactyla	*Equus ferus*
VH786	GL/GKS	Perissodactyla	*Equus ferus*
VH787	GL/GKS	Perissodactyla	*Equus ferus*
VH788	GL/GKS	Perissodactyla	*Equus ferus*
VH789	GL/GKS	Perissodactyla	*Equus ferus*
VH790	GL/GKS	Perissodactyla	*Equus ferus*
VH791	GL/GKS	Perissodactyla	*Equus ferus*
VH792	GF/KS	Perissodactyla	*Coelodonta antiquitatis*
VH793	GF/KS	Artiodactyla	*Rangifer tarandus*
VH794	GF/KS	Perissodactyla	*Coelodonta antiquitatis*
VH795	GF/KS	Artiodactyla	*Bos/Bison*
VH796	GF/KS	Perissodactyla	*Equus ferus*
VH797	GF/KS	Perissodactyla	*Coelodonta antiquitatis*
VH798	GF/KS	Perissodactyla	*Coelodonta antiquitatis*
VH799	GF/KS	Artiodactyla	*Bos/Bison*
VH800	GF/KS	Carnivora	Felidae/Hyaenidae/Mustelidae
VH801	GF/KS	Perissodactyla	*Equus ferus*
VH802	GF/KS	Perissodactyla	*Equus ferus*
VH803	GF/KS	Artiodactyla	*Bos/Bison*
VH804	GF/KS	Carnivora	Felidae/Hyaenidae/Mustelidae
VH805	GF/KS	Proboscidea	*Elephas/Mammuthus*
VH806	GF/KS	Artiodactyla	*Rangifer tarandus*
VH807	GF/KS	Perissodactyla	*Coelodonta antiquitatis*
VH808	GF/KS	Artiodactyla	*Rangifer tarandus*
VH809	GF/KS	Artiodactyla	*Rangifer tarandus*
VH810	GF/KS	Artiodactyla	*Bos/Bison*
VH811	GF/KS	Artiodactyla	*Rangifer tarandus*
VH812	GF/KS	Artiodactyla	*Rangifer tarandus*
VH813	GF/KS	Artiodactyla	*Rangifer tarandus*
VH814	GF/KS	Proboscidea	*Elephas/Mammuthus*
VH815	GF/KS	Perissodactyla	*Equus ferus*
VH816	GF/KS	Proboscidea	*Elephas/Mammuthus*
VH817	GF/KS	Artiodactyla	*Bos/Bison*
VH818	GF/KS	Artiodactyla	*Rangifer tarandus*
VH819	GF/KS	Proboscidea	*Elephas/Mammuthus*
VH820	GF/KS	Perissodactyla	*Equus ferus*
VH821	GF/KS	Artiodactyla	*Rangifer tarandus*
VH822	GF/KS	Artiodactyla	*Rangifer tarandus*
VH823	GF/KS	Perissodactyla	*Equus ferus*
VH824	GF/KS	Perissodactyla	*Coelodonta antiquitatis*
VH825	GF/KS	Perissodactyla	*Equus ferus*
VH826	GF/KS	Proboscidea	*Elephas/Mammuthus*
VH827	GF/KS	Proboscidea	*Elephas/Mammuthus*

VH828	GF/KS	Proboscidea	*Elephas/Mammuthus*
VH829	GF/KS	Perissodactyla	*Equus ferus*
VH831	HU	Perissodactyla	*Coelodonta antiquitatis*
VH832	HU	Artiodactyla	*Cervus/Capreolus/Megaloceros*
VH833	HU	Proboscidea	*Elephas/Mammuthus*
VH835	HU	Artiodactyla	*Rangifer tarandus*
VH836	HU	Perissodactyla	*Equus ferus*
VH837	GL/GKS	Artiodactyla	*Rangifer tarandus*
VH838	GL/GKS	Perissodactyla	*Equus ferus*
VH839	GL/GKS	Artiodactyla	*Rangifer tarandus*
VH840	GL/GKS	Proboscidea	*Elephas/Mammuthus*
VH841	GL/GKS	Proboscidea	*Elephas/Mammuthus*
VH842	GL/GKS	Lagomorpha	*Lepus sp.*
VH843	HL/KS	Artiodactyla	*Cervus/Capreolus/Megaloceros*
VH844	HL/KS	Carnivora	*Meles meles*
VH845	GF/KS	Proboscidea	*Elephas/Mammuthus*
VH846	GF/KS	Artiodactyla	*Cervus/Capreolus/Megaloceros*
VH847	GF/KS	Artiodactyla	*Rangifer tarandus*
VH848	GF/KS	Artiodactyla	*Rangifer tarandus*
VH849	GF/KS	Artiodactyla	*Rangifer tarandus*
VH850	HL/KS	Perissodactyla	*Equus ferus*
VH851	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH852	HL/KS	Artiodactyla	*Rangifer tarandus*
VH853	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH854	HL/KS	Carnivora	Mustelidae
VH855	HL/KS		unknown
VH856	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH857	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH858	HL/KS	Artiodactyla	*Rangifer tarandus*
VH859	HL/KS	Carnivora	*Vulpes vulpes*
VH860	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH861	HL/KS	Carnivora	Mustelidae
VH862	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH863	HL/KS	Perissodactyla	*Equus ferus*
VH864	HL/KS	Perissodactyla	*Equus ferus*
VH865	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH866	HL/KS	Artiodactyla	*Bos/Bison*
VH867	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH868	HL/KS	Carnivora	*Ursus sp.*
VH869	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH870	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH871	HL/KS	Perissodactyla	*Equus ferus*
VH872	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH873	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH874	HL/KS	Lagomorpha	*Lepus sp.*
VH875	HL/KS	Artiodactyla	*Cervus/Capreolus/Megaloceros*
VH876	HL/KS	Proboscidea	*Elephas/Mammuthus*

VH877	HL/KS	Primates	***Homo sapiens***
VH878	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH879	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH880	HL/KS	Carnivora	*Ursus sp.*
VH881	HL/KS	Carnivora	*Meles meles*
VH882	HL/KS		unknown
VH883	HL/KS	Artiodactyla	*Rangifer tarandus*
VH884	HL/KS	Perissodactyla	*Equus ferus*
VH885	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH886	HL/KS		unknown
VH887	HL/KS	Carnivora	*Meles meles*
VH888	GL/GKS	Lagomorpha	*Lepus sp.*
VH889	GL/GKS	Artiodactyla	*Rangifer tarandus*
VH890	GL/GKS	Lagomorpha	*Lepus sp.*
VH891	GL/GKS	Lagomorpha	*Lepus sp.*
VH892	HL/KS	Carnivora	*Felis silvestris*
VH893	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH894	HL/KS	Artiodactyla	*Cervus/Capreolus/Megaloceros*
VH895	HL/KS	Perissodactyla	*Coelodonta antiquitatis*
VH896	HL/KS	Artiodactyla	*Rangifer tarandus*
VH897	HL/KS	Perissodactyla	*Equus ferus*
VH898	HL/KS	Artiodactyla	*Cervus/Capreolus/Megaloceros*
VH899	HL/KS	Carnivora	*Vulpes vulpes*
VH900	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH901	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH902	HL/KS	Carnivora	*Meles meles*
VH903	HL/KS	Carnivora	*Meles meles*
VH904	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH905	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH906	HL/KS	Artiodactyla	*Rangifer tarandus*
VH907	HL/KS	Perissodactyla	*Equus ferus*
VH908	HL/KS	Artiodactyla	*Cervus/Capreolus/Megaloceros*
VH909	HL/KS	Lagomorpha	*Lepus sp.*
VH910	HL/KS	Carnivora	*Meles meles*
VH911	HL/KS	Artiodactyla	*Rangifer tarandus*
VH912	HL/KS	Perissodactyla	*Equus ferus*
VH913	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH914	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH915	HL/KS	Perissodactyla	*Equus ferus*
VH916	HL/KS	Perissodactyla	*Equus ferus*
VH917	HL/KS	Perissodactyla	*Equus ferus*
VH918	HL/KS	Artiodactyla	*Rangifer tarandus*
VH919	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH920	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH921	HL/KS	Artiodactyla	*Rangifer tarandus*
VH922	HL/KS	Proboscidea	*Elephas/Mammuthus*
VH923	HL/KS	Artiodactyla	*Rangifer tarandus*

VH924	HL/KS	Carnivora	*Vulpes vulpes*
VH925	HL/KS	Artiodactyla	*Bos/Bison*
VH926	HL/KS	Artiodactyla	*Cervus/Capreolus/Megaloceros*
VH927	HL/KS	Perissodactyla	*Equus ferus*