Glycymeris molluscs in the context of the Upper Palaeolithic of Southwestern Germany

Glycymeris-Mollusken im Kontext des Jungpaläolithikums Südwestdeutschlands

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Abstract - Vogelherd and Petersfels are two of the richest central European Palaeolithic sites from the Aurignacian and Magdalenian periods. Vogelherd is known for its figurative art, flutes and ornaments made of ivory, while Petersfels is known for its complex ornament assemblage, especially the female figurines made of jet. Both sites yielded *Glycymeris* molluscs, which can provide unique information on the mobility and social behaviour of groups from the Upper Palaeolithic of southern Germany. In this paper, we examine the *Glycymeris* finds from southern Germany and place them in a broader European context by summarising the finds from Belgium, Switzerland, France, and Italy. *Glycymeris* are one of the most common bivalve species in the Upper Palaeolithic of Central Europe and are found from the Aurignacian until the Magdalenian. The analyses presented here constitute a functional analysis of *Glycymeris* and an interpretation of their significance in terms of long-distance connections. Finally, we address use-traces and residues left on the *Glycymeris* and put forward various hypotheses for future investigation.

Zusammenfassung - *Der Vogelherd und Petersfels sind zwei der reichsten Fundstellen Zentraleuropas aus dem Aurignacien bzw. dem Magdalénien. Der Vogelherd ist für seine Kleinkunstwerke, Flöten und Schmuck aus Elfenbein bekannt. Der Petersfels ist für sein komplexes Schmuckinventar, insbesondere für die Frauenfiguren aus Gagat, bekannt. Aus beiden Fundstellen sind Glycymeris Mollusken vorhanden. Diese können uns einzigartige Informationen zur Mobilität und zum sozialen Verhalten der Gruppen aus dem Jungpaläolithikums Süddeutschlands liefern. Im vorliegenden Beitrag untersuchen wir die Glycymeris Funde aus Süddeutschland und betten diese in einen europäischen Kontext ein in dem wir die Funde aus Belgien, der Schweiz, Frankreich und Italien zusammenfassen. Glycymeris sind eine der häufigsten Muschelarten im Kontext des Jungpaläolithikums Zentraleuropas und finden sich durchgehend vom Aurignacien bis zum Magdalénien. Die hier vorgestellten Analysen erlauben eine funktionelle Ansprache der Glycymeris und eine Interpretation in Bezug auf Fernverbindungen. Schließlich befassen wir uns mit den Gebrauchsspuren und Residuen an den Glycymeris und stellen verschiedene Hypothesen auf, die in Zukunft weiter untersucht werden sollen.*

Keywords - Molluscs, Upper Palaeolithic, Aurignacian, Vogelherd, Magdalenian, Petersfels
Mollusken, Jungpaläolithikum, Aurignacien, Vogelherd, Magdalénien, Petersfels

Introduction

Molluscs are a unique archaeological resource, which allow archaeologists to reconstruct both long-distance connections and elements of group behaviour, features that are quite difficult to assess with other artefact categories (Rivière 1878-1887; Taborin 1993a; Stiner 1999; Álvarez-Fernández 2001; Eriksen 2002; Álvarez-Fernandez 2010; Colonese et al. 2011; Stiner et al. 2013; Maier 2015; Kandel et al. 2018). Their initial appearance at archaeological sites dates to the Middle Stone Age in Africa and Middle Palaeolithic in Europe, where they were used as a dietary resource, tools, and personal ornaments (Henshilwood et al. 2004; d'Errico et al. 2005; Vanhaeren et al. 2006; Bouzouggar et al. 2007; d'Errico et al. 2008; Bar-Yosef Mayer et al. 2009; Eiwanger et al. 2012; Vanhaeren et al. 2013; Bar-Yosef Mayer 2014; Romagnoli et al. 2016). With the onset of the Upper Palaeolithic in Europe, groups began to use molluscs as ornaments more frequently (Taborin 1993a; Vanhaeren & d'Errico 2006; Peresani et al. 2019).

The genus *Glycymeris* stands out among the different mollusc species exploited by humans during the course of their evolution. The archaeological record is rich in examples of *Glycymeris* shells used in different ways and for different purposes. One of these usages is the utilisation of *Glycymeris*

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as containers, suggested by the recovery of pigments within the shells (Beaune 1987; Floss & Conard 2001; Conard 2003; Vanhaeren & Lozouet 2014). One of the most unambiguous examples of the use of shells as containers comes from Blombos in South Africa (Henshilwood et al. 2011). There, a *Haliotis midae* mollusc was found in association with a toolkit consisting of a grindstone, a piece of ochre, charcoal, bone and a hammerstone. The shell was probably used to hold the colouring materials and to mix them.

Glycymeris shells were also modified and used as tools. In the Upper Palaeolithic, there are examples from the Gravettian (Cuenca-Solana et al. 2013) and the Aurignacian (Douka 2011). There are further examples from the Middle Palaeolithic (Douka & Spinapolice 2012; Romagnoli et al. 2016; Villa et al. 2020), during which molluscs were often worked in a similar way to stone artefacts.

More common was the use of *Glycymeris* as adornments. In this case, shells exhibit a perforation that indicates that they were worn as personal ornaments. One of the main questions concerning the use of shells as a decoration is the origin of perforations, i.e., whether the molluscs were perforated by humans or were naturally perforated and later collected. There are various ways in which natural perforation can occur (Light 2017, Table 20.1.), and there have been multiple attempts to compare natural with experimental perforations (D'Errico et al. 1993; Taborin 1993b; Bar-Yosef Mayer et al. 2009; Cabral & Martins 2016; Light 2017). Regardless, in both cases, natural and man-made perforations could be assigned a cultural meaning (Light 2017), especially when sites are very far away from the coast or the geological outcrop. In central Europe, there are many examples of the use of molluscs for personal ornamentation (e.g.: Kölbl & Conard 2003; Vanhaeren & d'Errico 2006; Bar-Yosef Mayer et al. 2009; Stiner et al. 2013; Bar-Yosef Mayer et al. 2020; Sehasseh et al. 2021).

This paper presents an overview on the *Glycymeris* from Upper Palaeolithic sites in Southern Germany with a focus on the sites Vogelherd and Petersfels (Fig. 1), which are among the richest sites in central Europe. We also present *Glycymeris* from other sites (Hohle Fels, Geißenklösterle, Brillenhöhle and Gnirshöhle), where we had the opportunity to study these shells. These sites are not as rich in *Glycymeris* finds and therefore only complement the main part of the study. We also present a catalogue of Upper Palaeolithic sites from parts of Europe to provide a

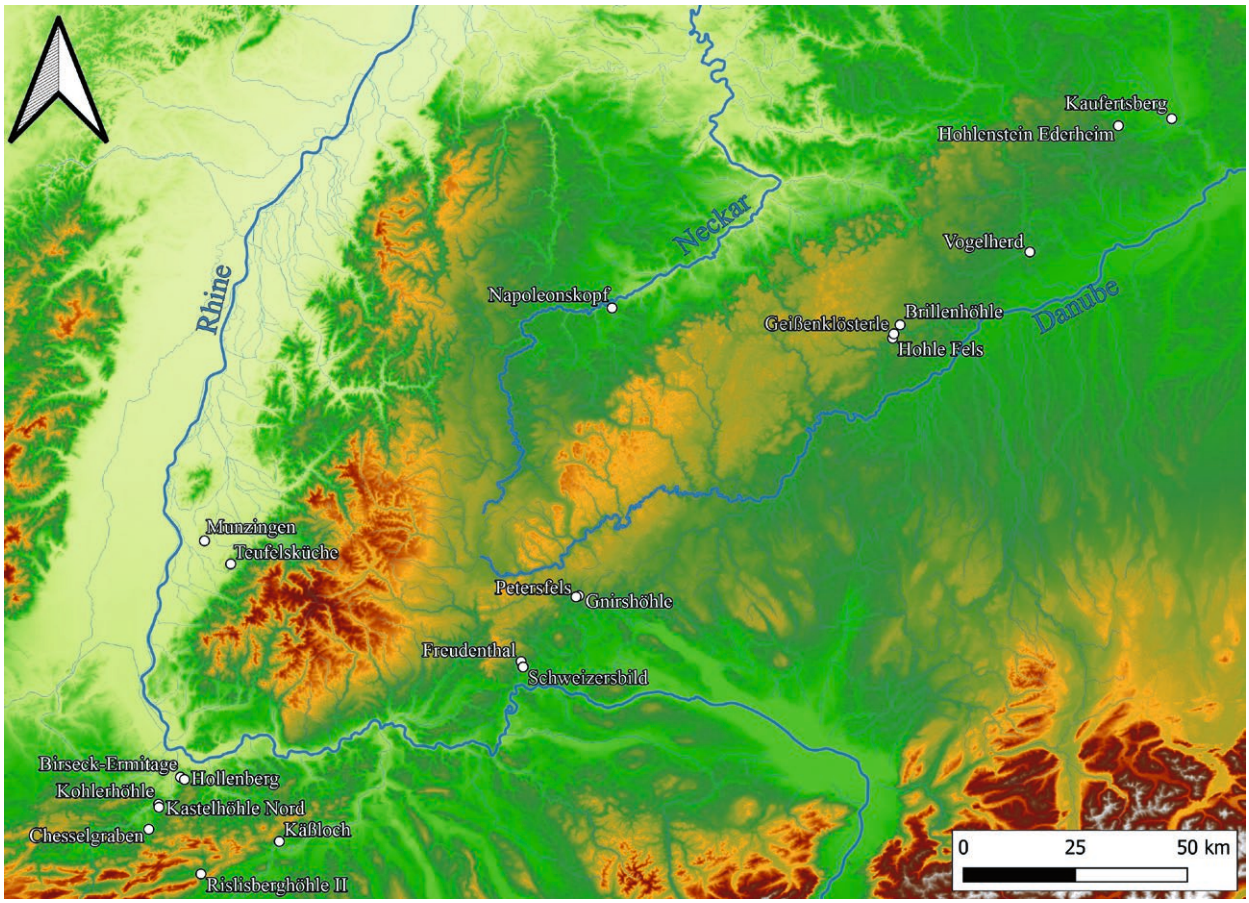

Fig. 1. Map of archaeological sites with *Glycymeris* from southwestern Germany and Switzerland. (Background map: © European Union, Copernicus Land Monitoring Service 2021, European Environment Agency (EEA)).

Abb. 1. *Karte der archäologischen Fundstellen mit Glycymeris aus Südwest-Deutschland und der Schweiz. (Hintergrundkarte: © European Union, Copernicus Land Monitoring Service 2021, European Environment Agency (EEA)).*

broader overview of the genus. The origin of *Glycymeris* was determined for those specimens from Vogelherd and Petersfels. Previously, the function of *Glycymeris* in southern Germany has not been sufficiently discussed. Therefore, the aim of this paper is to bridge this gap and discuss the data available to come to a more profound statement about the use of these shells. This is accomplished further by a preliminary microwear analysis of the *Glycymeris*.

The site of Vogelherd

Vogelherd Cave is located in the Lone Valley near the town of Niederstotzingen. The site was excavated by Gustav Riek, a prehistorian from Tübingen, in 1931 (Riek 1932, 1934) (Fig. 2). In just three months, Riek and four workers excavated the site almost completely. The backdirt, or rather the sediments of the excavation, was dumped directly in front of the two entrances of the cave (Burkert 1991; Conard & Malina 2006). Riek described nine archaeological layers (Riek 1934; Burkert 1991; Schürch et al. 2021); some of these can be considered as thick anthropogenic horizons with high find density, especially the two Aurignacian layers IV and V. The rest of the layers were found in different geological layers (I, II, III, VI, VII, VIII, IX). Riek attributed Layer I to the Neolithic, which consists of a black-brown humus layer with small, embedded limestone debris. Layers II and III were attributed to the Magdalenian by Riek and are both embedded in one geological horizon, which is described as yellow-white fine limestone debris. Layers VI, VII, VIII, and IX were attributed to the Middle Palaeolithic. Riek´s cultural attribution does not always correspond to the current chronological attribution of the layers. This is currently being investigated in a dissertation work (Schürch in prep.), as it is already clear that this classification needs revision, given evidence of mixing between the layers. However, this ongoing investigation, which will be carried out based on both the ^{14}C data (Hahn 1977; Burkert 1991; Conard 2002; Conard & Bolus 2008; Bolus 2011) and the stone artefacts, would go beyond the extent of this paper. The finds presented here are from Layer V (the lower Aurignacian layer) and layer HL/KS (*heller Lehm/Kalkschutt*; pale clay/limestone debris) of the backdirt excavations (Fig. 3) (see below).

The bivalves from Vogelherd layer V (Riek 1934, Fig. XXIX, 13, 16, 17) have received little attention since their discovery in 1931 (Riek 1934, 223; Hahn 1977, 286; Schürch et al. 2021) (Fig. 4). These molluscs are considered to be of Aurignacian age, because the ^{14}C dates of layer V fall between 42,000 and 36,000 calBP (Hahn 1977; Burkert 1991; Conard 2002; Conard & Bolus 2003; Teyssandier et al. 2006; Conard & Bolus 2008; Bolus 2011) and the typological attribution of layer V (Riek 1934; Hahn 1977). The dating of mixed bone samples (Hahn 1977, 1993) and the human skeletal remains from the Neolithic secondary burials from layer V (Conard et al. 2004) are not included in age determination of layer V.

There is also a fragment of a cephalopod from layer V (Riek 1934, Table XXIX.14; Dutkiewicz 2018: 268), a fossil ammonite fragment with seven parallel notches (Dutkiewicz 2018) (Fig. 4:13). Besides the molluscs from layer V, there is one mollusc fragment from layer IV (Fig. 4:12); which was depicted and described by Riek as a stone artefact (Riek 1934, Table XXIII.16). Layer IV can mainly be interpreted as Aurignacian, but the ^{14}C dates and the ongoing research on the stone artefacts also shows a small Gravettian component.

Other molluscs come from the re-excavations conducted between 2005 and 2012 by Conard and a team from the University of Tübingen (Conard 2013; Conard & Zeidi 2014; Conard 2016) (Fig. 2). The excavations concentrated on the backdirt from Riek's excavation that was deposited between the southwestern and the southern entrance of the cave. A total area of 108 m^2, which represents the

Fig. 2. Vogelherd. Left: Backdirt of the 1931 excavation of Riek in front of the southwestern entrance of Vogelherd. (Photo: Riek 1931); Right: Excavation of the backdirt from 1931 in 2008 in front of the southwestern entrance. (Photo: University Tübingen).

Abb. 2. *Vogelherd. links: Abraumhalde der Grabung von Riek 1931 vor dem südwestlichen Eingang des Vogelherds (Foto: Riek 1931), rechts: Ausgrabung der Abraumhalde von 1931 im Jahr 2008 vor dem südwestlichen Eingang (Foto: Universität Tübingen).*

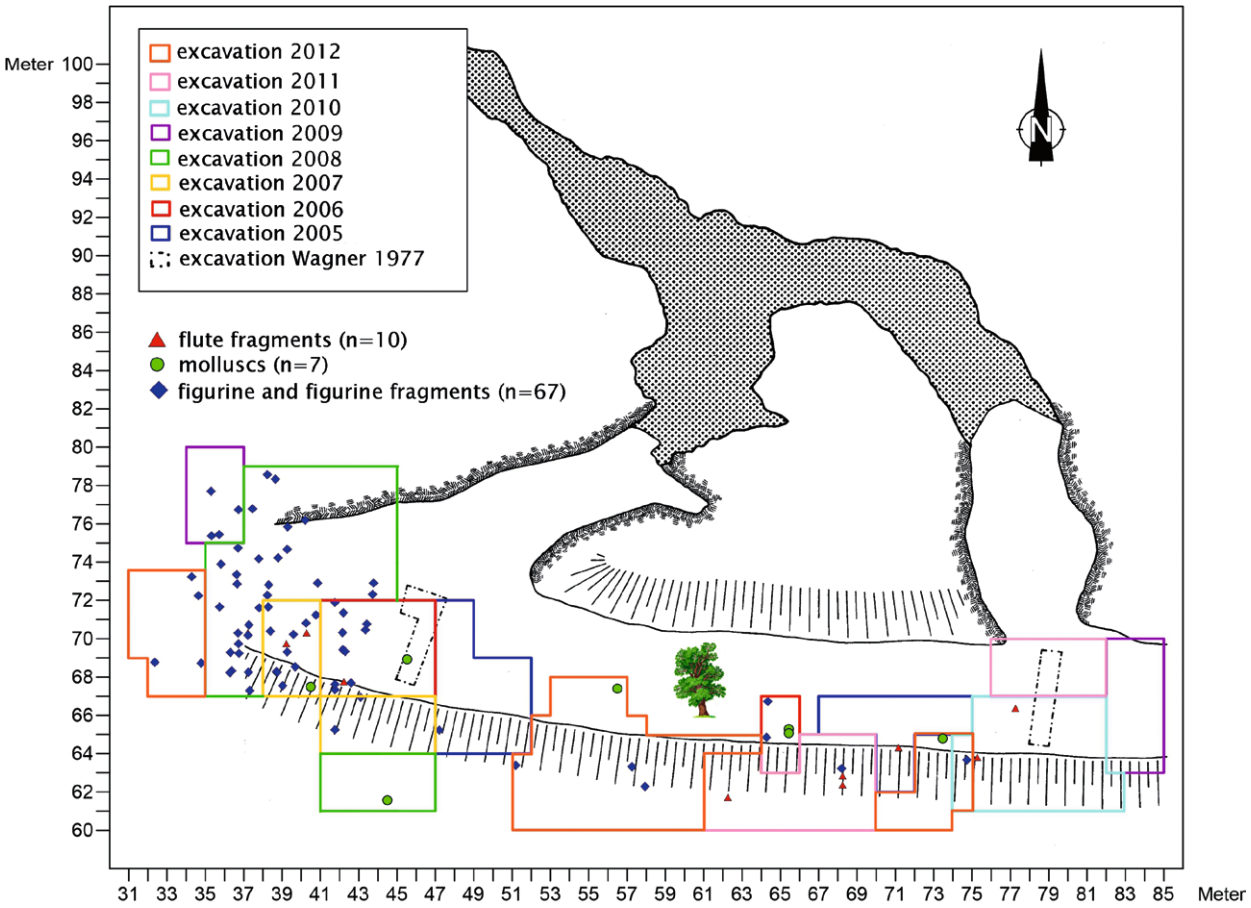

Fig. 3. Vogelherd. Plan of the re-excavations at Vogelherd and the distribution of the molluscs, flute fragments and figurines (modified after Conard 2016).

Abb. 3. *Vogelherd. Plan der Nachgrabungen am Vogelherd und die Verteilung der Mollusken, Flötenfragmente und Figurinen (modifiziert nach Conard 2016).*

majority of the backdirt from the 1931 excavation, was excavated between 2005 and 2012 (Fig. 3) (Conard 2016). In contrast to the excavation of the backdirt by E. Wagner in 1977 that did not yield any finds (Wagner 1979, 1981), the excavations by Conard showed that the sediments of the backdirt were still very rich in finds, including such noteworthy artefacts as the ivory figurines and the flute fragments (Conard et al. 2009; Dutkiewicz 2021). The sediment from the Riek excavation was redeposited and, as a result, the stratigraphy is not intact. The backdirt was either dug down to the surface of the slope, which was visible on the dark humus layer, or down to the bedrock (Conard & Malina 2006; Schürch et al. 2021). The main layer of the backdirt is geological layer HL/KS (Schürch et al. 2021).

The *Glycymeris* from the re-excavation all derive from the HL/KS layer. It is characterised by light brown sediment with a high amount of limestone debris, and the assemblage is mainly composed of Aurignacian finds. This is supported by the presence of *fossiles directeurs* from the Aurignacian. Among them are double perforated beads (Wolf 2015), split-based points (Kitagawa & Conard 2020), and typical Aurignacian stone artefacts (Schürch in prep.). When assessing the age of the *Glycymeris* finds, various factors must be considered. Although most of the finds from the re-excavation are from the Aurignacian, this cannot be supported with absolute numbers yet. Therefore, a clear assignment of the *Glycymeris* from the re-excavation to the Aurignacian is not possible. Nevertheless, the state of preservation of the *Glycymeris* from both excavations and the similar size of the pieces would suggest a classification to the Aurignacian.

Besides the *Glycymeris* molluscs, there is one additional mollusc of the family Veneridae (Schürch et al. 2021) found in the backdirt of Vogelherd Cave. It was found by a private collector and is part of the collection 'Scheer' stored in the Württembergisches Landesmuseum in Stuttgart (Wagner 1981).

The site of Petersfels

Petersfels is located in the Bruder Valley near the town of Engen. The site was excavated for the first time in 1927 by Eduard Peters (Peters 1930, 1932) (Fig. 5), who continued with two additional campaigns in 1928 and 1932. Peters excavated both the cave as well as parts of the terrace and the slope, discovering a red-yellow layer with limestone plaques, which plays an important

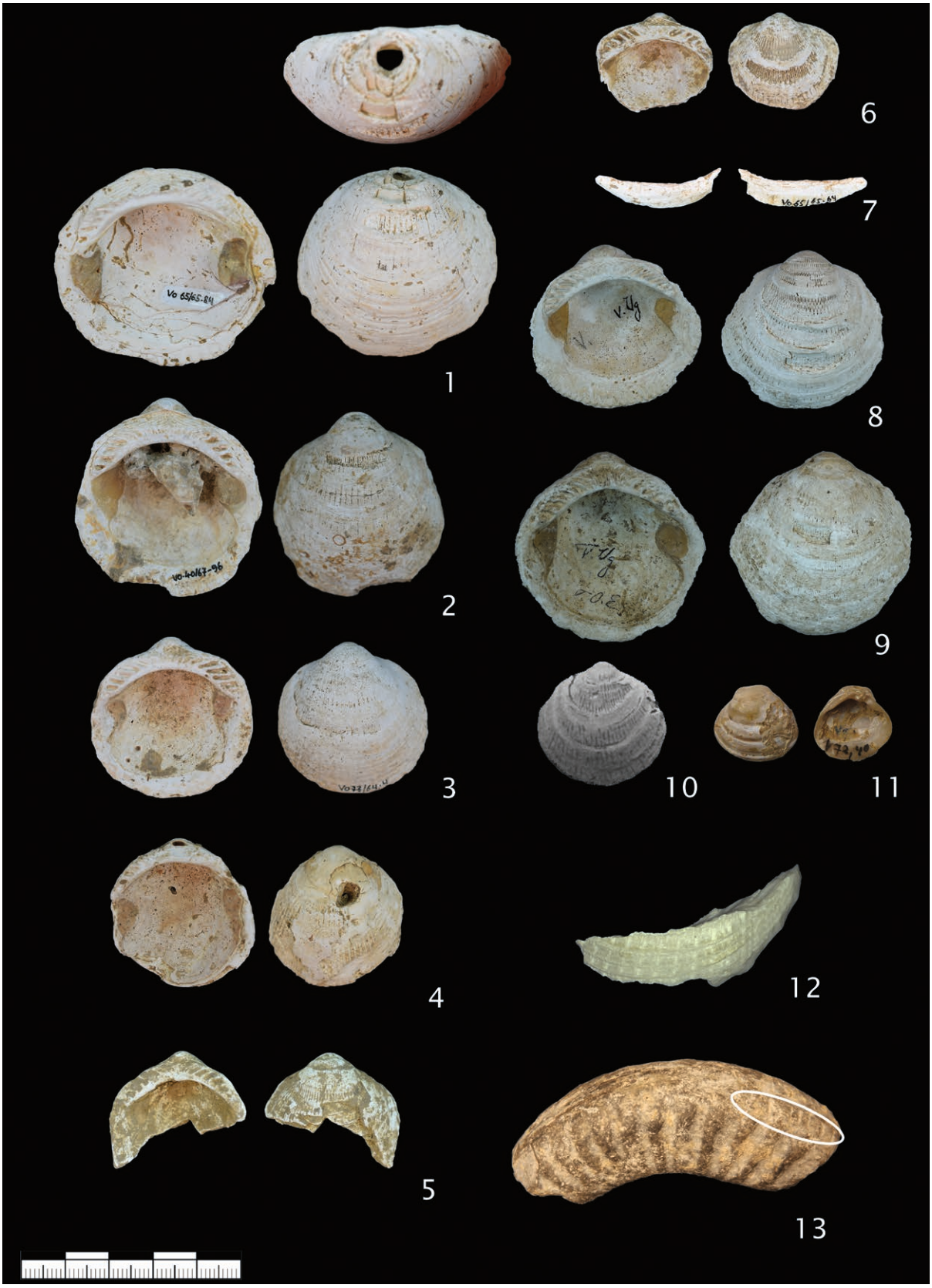

Fig. 4. Molluscs from Vogelherd: 1–7) Fossil *Glycymeris* from the re-excavations by the University of Tübingen (Photos: B. Schürch); 1 and 4) Perforated *Glycymeris*; 8–10) *Glycymeris* from the 1931 excavation, layer V (Photos: B. Schürch and Riek 1934); 11) Veneridae (Scheer Collection, WLM, Photo: Landesmuseum Württemberg, Jörg Götze); 12) Bivalve fragment from Layer IV (Photo: B. Schürch); 13) Jurassic (Lias) ammonite with seven parallel notches from layer V (notches circled in white; Photo: ©URMU, Hannes Wiedmann).

Abb. 4. *Mollusken aus dem Vogelherd: 1.–7. Fossile Glycymeris aus den Nachgrabungen der Universität Tübingen (Fotos: B. Schürch). 1. und 4. Durchlochte Glycymeris; 8.–10. Glycymeris aus der Grabung 1931, Schicht V (Foto: B. Schürch und Riek 1934); 11. Veneridae (Sammlung Scheer, WLM, Foto: Landesmuseum Württemberg, Jörg Götze) 12. Fragment einer zweischaligen Muschel aus Schicht IV (Foto: Schürch); 13. Ammonit aus dem Jura (Lias) mit sieben parallelen Kerben aus Schicht V (Kerben sind auf der rechten Seite des Stückes sichtbar und in weiß umkreist; Foto: Urgeschichtliches Museum/URMU).*

Fig. 5. Petersfels. Left: excavation in the cave of Petersfels between 1927 and 1928 (Photo: Peters 1930, Tab. I); right: excavation in trench P3 in 1975 outside of the cave (Photo: G. Albrecht).

Abb. 5. *Petersfels. links: Ausgrabung in der Petersfelshöhle zwischen 1927 und 1928 (Foto: Peters 1930, Tafel I), rechts: Ausgrabung im Graben P3 im Jahr 1975 außerhalb des Petersfels (Foto: G. Albrecht).*

role in the analysis of pigment residues. Later on in the 1960s, Hermann Schiele conducted new excavations, which were followed by Hans Reinerth in the 1970s, who made several trenches with a mechanical excavator (Albrecht & Hahn 1991; Pfeifer 2016). From 1974-1979, the University of Tübingen excavated at the site for four campaigns under the direction of Gerd Albrecht (Albrecht 1979, 1983, 1983) (Fig. 5).

The majority of the finds from Petersfels date to the Magdalenian, which is also shown by the ^{14}C data. Petersfels and the nearby site of Gnirshöhle have almost exclusively yielded finds from the Magdalenian (Fig. 6). The ^{14}C data from Petersfels and Gnirshöhle have been summarised by Albrecht et al. (2019) and Pfeifer (2016). The Petersfels ^{14}C dates from Albrecht's excavation fall between 16,000 and 14,500 calBP and the dates from Gnirshöhle fall between 16,000 and 15,000 calBP (Albrecht et al. 2019). The *Glycymeris* from Petersfels presented in this study come from the excavations of Peters, Schiele and Albrecht. The results presented here are limited to the *Glycymeris* finds, as the remaining mollusc assemblage has already been studied (Rähle 1983; Eriksen 2002).

Glycymeris shells: an overview

The two basic types of molluscs at the archaeological sites in southern Germany are gastropods and bivalves (Sommerville et al. 2017). *Glycymeris* are bivalves and they consist of two separate valves,

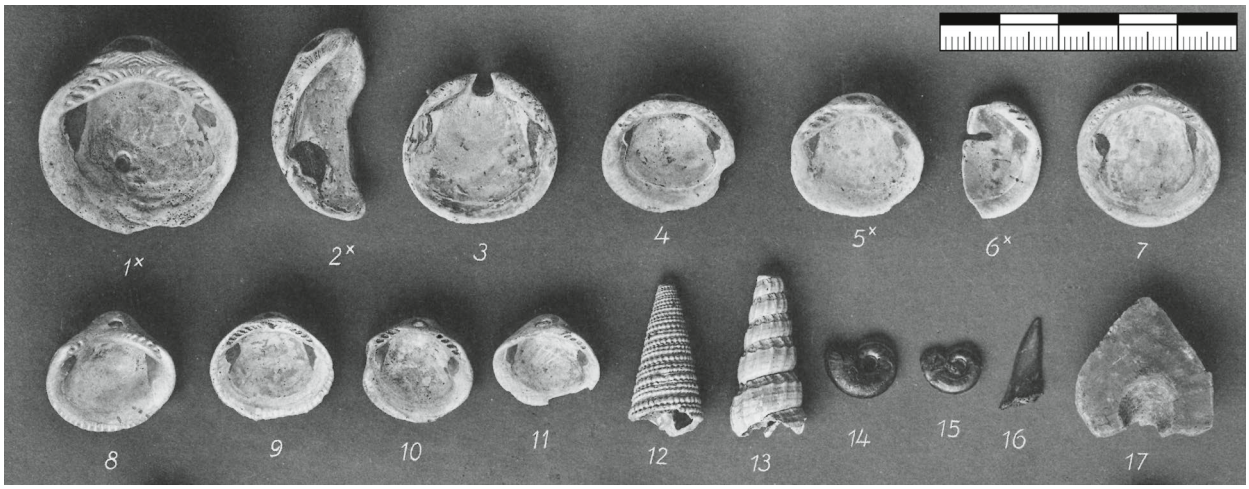

Fig. 6. Part of plate XXI from Peters 1930 (scale added later): 1-11) *Glycymeris*; 12-13) gastropods; 14-15) fossil ammonites; 16) fossil shark tooth; 17) calcite crystal. The numbers marked with an X were found on the terrace outside the cave. No. 3 and 6 correspond to the two pieces (1 and 2) of figure 11.

Abb. 6. *Ausschnitt der Tafel XXI aus Peters 1930 (Maßstab nachträglich eingefügt): 1-11 Glycymeris, 12-13 Gastropoden 14-15 fossile Ammoniten, 16 fossiler Haizahn, 17 Kalkspatkrystall. Die Nummern die mit einem X markiert sind wurden im Vorplatzbereich und daher außerhalb der Höhle gefunden. Nr. 3 und 6 entsprechen den beiden Stücken (1 und 2) von Abbildung 11.*

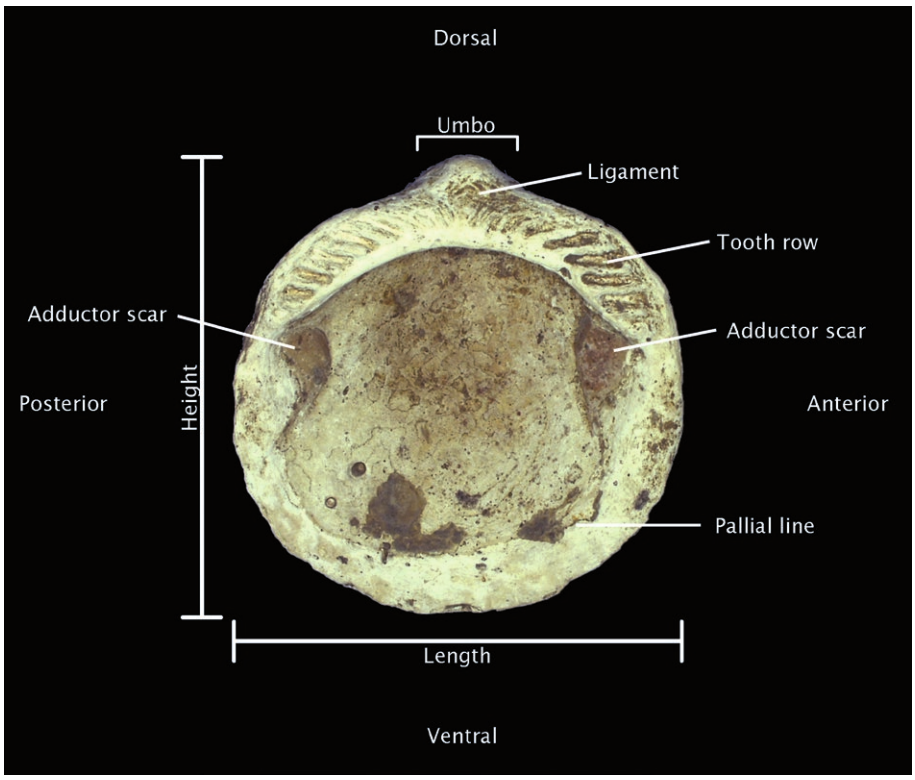

Fig. 7. Main features of *Glycymeris* and measurements used in this study. (Photo: B. Schürch).
Abb. 7. *Hauptmerkmale von Glycymeris und verwendete Messungen. (Foto: B. Schürch).*

which articulate about a hinge (Fig. 7) (Sommerville et al. 2017). The *Glycymeris* belong to the family Glycymerididae, and other common names include dog cockles and bittersweet clam in English (Light 2017) and *Samtmuschel* in German (Linné 1758; Deshayes 1839; Schürch et al. 2021). *Glycymeris* live in soft sediments and feed by filtering water (Sommerville et al. 2017).

The two valves of the genus *Glycymeris* are approximately equilateral in shape, and in the closed state, the two halves fit together without any gap. The umbo of the bivalves is arranged perpendicular to the body axis or slightly curved forward. The firm ligament connecting the moving parts of the shell sits dorsal in front of and behind, or just in front of, the umbo. The edge of the valves is curved and shows numerous teeth perpendicular or oblique to the edge, depending on the species (Nolf & Swinnen 2013). Two sphincters of approximately equal size are present. The shell is relatively thick. The outer shells show radial and/or margin-parallel ridges, but *Glycymeris* species with nearly smooth shells also exist. *Glycymeris* often possess a natural, light reddish-brown colouration inside the shell (Nolf & Swinnen 2013). *Glycymeris* live worldwide, but preferentially in warmer seas. Nowadays, different species of *Glycymeris* live in the Atlantic and the Mediterranean (Nolf & Swinnen 2013). Fossil *Glycymeris* can be found in various deposits of Tertiary age including the Mainz Basin, the Parisian Tertiary, and the Belgian Tertiary (Rähle 1994).

Materials and Methods

A total of 131 *Glycymeris* was included in the analysis. Of these pieces, 115 come from Petersfels, ten from Vogelherd, three from Hohle Fels, one from Geißenklösterle, one from Brillenhöhle, and one from Gnirshöhle. The Vogelherd *Glycymeris* likely come from the Aurignacian and the *Glycymeris* from Petersfels are of Magdalenian age. The *Glycymeris* from Geißenklösterle and Brillenhöhle and one of the *Glycymeris* from Hohle Fels can be attributed to the Gravettian. The two other *Glycymeris* from Hohle Fels and one *Glycymeris* from Gnirshöhle can be attributed to the Magdalenian. We provided a more detailed chronological framework (see above) for the sites of Vogelherd and Petersfels, being the two main sites discussed in this study. The chronological attribution of the *Glycymeris* from sites not investigated in this study can be found in SI Tab. 1.

The determination of the origin of the *Glycymeris* from Vogelherd and Petersfels was carried out by geologist Olaf Höltke at the State Museum of Natural History in Stuttgart. A large comparative collection from various fossil outcrops can be accessed there. In addition, supplementary literature was consulted for the determination of the *Glycymeris* (Nolf & Swinnen 2013).

The whole sample was first scrutinized by BS and SW. All data on the *Glycymeris* were entered into an Access database (SI Tab. 1), which included the molluscs from Petersfels, Vogelherd, Hohle

Fels, Geißenklösterle, Gnirshöhle, and Brillenhöhle (N = 131). For these pieces, the length, width, thickness, weight, state of preservation, presence of perforation, presence and type of perforation (shallow, deep, incised), and the presence of macroscopically visible red pigment traces were recorded. For this purpose, a Keyence VHX-500 F Digital Microscope equipped with an Olympus KL 1600 LED lamp was used. Photos were taken using a Hirox HRX-01 digital microscope covering a magnification range of 20x-2,500x available at the Material Culture Laboratory at University of Tübingen. In addition, a database of sites that have yielded *Glycymeris* finds from the Palaeolithic was also created, including sites from Germany, Switzerland, Belgium, Italy, and France. Previous analyses have shown that there are long-distance connections from southwestern Germany to these regions (e.g., Eriksen 2002; Maier 2015).

With the aim of testing the potential of the full sample for a future in-depth microwear analysis, we carried out a preliminary microscopic investigation of a restricted subsample of complete and fragmented perforated *Glycymeris* shells from Petersfels, Vogelherd and Hohle Fels sites (N = 15). The subsample was selected without applying any specific criterion and it represents all shells available at the time of the analysis at the Department of Early Prehistory and Quaternary Ecology (University of Tübingen). The analysis was useful for assessing the state of preservation and evaluating the interpretive potential of the archaeological assemblage in terms of macro and micro techno-functional traces. In this study, we paid particular attention for signs of human intervention around the perforations (namely on the umbo region) that could attest man-made rather than natural modifications. The archaeological and experimental results arising from this preliminary examination will serve as a basis for a future comprehensive analysis aimed at investigating not only the production, but also the function of *Glycymeris* shells from the aforementioned archaeological sites.

The subsample for microwear analysis included one perforated complete specimen from Hohle Fels, twelve complete and fragmented specimens from Petersfels, and two complete specimens from Vogelherd. Both fresh and fossil molluscs were included, with a higher number of fossil specimens. The specimens were individually stored in plastic boxes and analysed at the Material Culture Laboratory at the University of Tübingen.

Microwear analysis was carried out combining the low and high-power approach, which is a well-established methodology commonly used in techno-functional studies (Tringham et al. 1974; Keeley 1980; Odell & Odell-Vereecken 1980; van Gijn 1990; Rots 2010; van Gijn 2010). An Olympus SZX7 microscope with magnification ranging from 8x to 56x and equipped with a LED ring light source was used for macro scale observations (e.g., rounding, abrasion, pitting, scarring, plastic deformations). An Olympus BX53M metallographic microscope working in reflecting light and equipped with 10x eyepieces and 5x, 10x, 20x and 50x objectives was used for recording micro wear evidence such as polish, abrasion, striations and grooves. Wear traces on the archaeological materials were interpreted by comparison with a set of experiments explicitly performed for this case-study and aimed at testing different perforation techniques on modern *Glycymeris* shells. Additional comparisons were based on the available published literature on techno-functional studies on bivalve shells (e.g., D'Errico et al. 1993; Taborin 1993a; Cabral & Rodrigues 2015; Cabral & Martins 2016; Wei et al. 2016; Bar-Yosef Mayer et al. 2020; Mărgărit et al. 2020).

Since several specimens, notably from Petersfels, exhibited presence of red pigmentations spread all over the surface of shells, we performed a SEM-EDX analysis in order to investigate the elemental compositions of those deposits. We analysed two shells from Vogelherd, nine shells from Petersfels, and two shells Hohle Fels. A small amount of the reddish deposit was scratched off the shells and deposited onto a standard SEM carbon adhesive. The extracted residue was then examined using the secondary electron (SE) and the backscattered electron (BSE) detector. While with the former we obtained topographical and textural traits of the residue, with the latter we obtained elemental information through grey-scale images according to the atomic number (Pedergnana & Ollé 2018).

Experimental reference collection

The aim of this experimentation has been to test the techniques used in prehistory for perforating *Glycymeris* shells and recording macro and microscopic technological traces associated to each technique. The final goal was to build a reference collection of perforated *Glycymeris* shells to serve as a comparison for interpreting the archaeological material.

Beside anthropogenic perforations, we particularly ensured that naturally perforated *Glycymeris* shells were also analysed. Shells from thanatocoenoses assemblages often display natural perforations on the umbo. The archaeological record indicates that the collection of naturally perforated shell was a common behaviour among our ancestors during prehistoric times (e.g., Bar-Yosef Mayer et al. 2020). Since natural perforations may mimic anthropogenic modifications, their correct identification is thus crucial for reliably interpreting the archaeological assemblage.

Based on the evidence from the archaeological sample, we built a preliminary reference collection of perforated *Glycymeris* shells testing three different techniques: 1) abrasion, 2) drilling, and 3) sawing (Fig. 8). We tested both fresh and fossil *Glycymeris* shells. Two fresh shells and two fossil shells were used to test each technique for a total of 12 specimens. The specimens were collected from thanatocoenoses assemblages

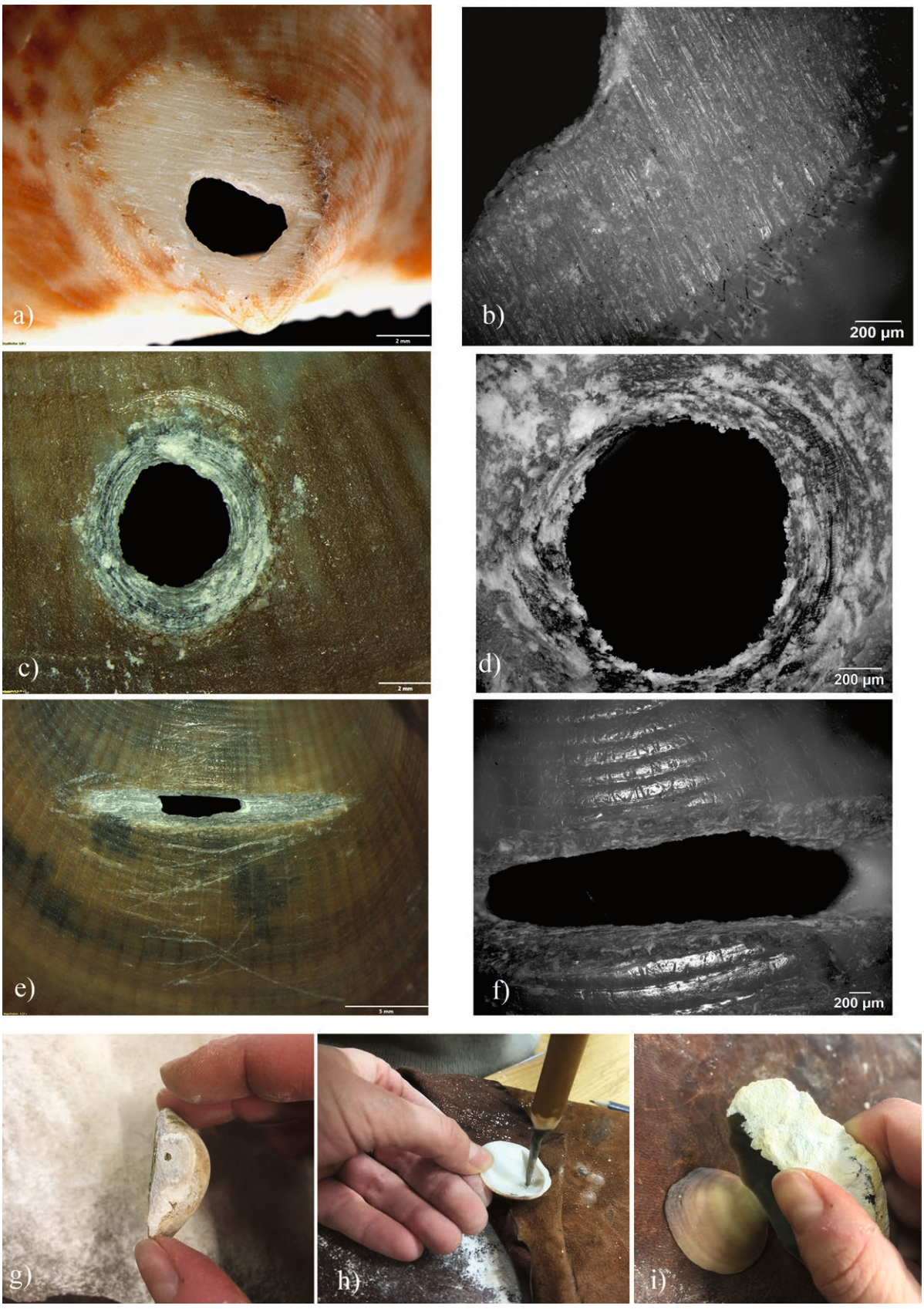

Fig. 8. Experimental Perforations: a-b) Macro and micro traces of perforation by abrasion on a fresh shell; c-d) Macro and micro traces of perforation by drilling; e-f) Macro and micro traces of perforation by sawing. Experimental perforation made by rotating a pointed stone tool; g-i) Different moments of the experimental activity. Magnification: a) 10x; b) 100x; c) 16x; d) 100x; e) 8x; f) 100x. (Photos: F. Venditti).

Abb. 8. *Experimentelle Durchlochungen. a-b) Makro- und Mikrospuren der Durchlochung durch Abrieb an einer rezenten Muschel, c-d) Makro- und Mikrospuren der Durchbohrung durch Bohren; e-f) Makro- und Mikrospuren der Durchbohrung durch Sägen. Experimentelle Durchlochung durch Rotation eines spitzen Steinwerkzeugs, g-i) verschiedene Momentaufnahmen der experimentellen Aktivität. Vergrößerung: a) 10x; b) 100x; c) 16x; d) 100x; e) 8x; f) 100x. (Fotos: F. Venditti).*

in Italy (along the Tyrrhenian beaches) and Germany (fossil shell midden in the Mainz Basin). The experiments were performed by FV along with skilled and unskilled students exploring prehistoric techniques for perforating bivalve shells in the framework of the BA/MA class "Experimenting Ornaments in the Paleolithic" at University of Tübingen.

- **Abrasion**
  Abrasion was performed by rubbing the most prominent umbo region against a medium-grained sandstone (Fig. 8: g). The shells were held between the thumb and the index finger, and back and forth movements were performed perpendicular to the bivalve axis until opening a hole. On average, less than 1 minute is necessary for making a complete perforation on fresh shells, while the thicker and harder umbo region of fossil specimens required between three and five minutes.
  Diagnostic features for this technique on both fresh and fossil shells are: 1) the creation of a flattened surface in place of the prominent convex umbo and 2) subparallel narrow striations on top of the flat facet following the kinetics of the to-and-fro motion (Fig. 8: a-b). The striations reflect the size of the grains composing the sandstone. The morphology of the perforation is circular with regular or sub-regular outlines, depending on the inclination of the shell on the sandstone during rubbing. At high magnification, a slight jagged internal contour was also observed. It is possible to regularise the hole by rotating a pointed lithic tool inside the preformation. However, we did not consider this variable in our experimental protocol.
- **Drilling**
  Drilling was performed by using a bow drill equipped with a flint drill bit. Rotation by drilling was performed unifacially but testing both faces (from the outside to the inside or from the inside to the outside) (Fig. 8: h). The perforation resulted in a conical hole with circular and regular or slightly jagged contours exhibiting concentric drilling striations on the interior walls (Fig. 8: c-d). The perforations were performed a few millimetres below the umbo due to the impossibility of executing the hole at the umbo using this technique. At low magnification, we noticed macro detachments around the perforation on the opposite shell's valve where the perforation was initiated (e.g. on the ventral face in the case the perforation was initiated on the dorsal one). As an alternative, a handle drill was also tested, but we found that the use of the bow drill allowed for better control of the rotary motion and faster attainment of a symmetric hole (5 min for a fresh shell and 15 min for a fossil shell).
- **Sawing**
  Sawing was performed by applying back-and-forth bidirectional movements with a sharp unretouched stone tool (Fig. 8: i). Sawing produced a characteristic long and deep groove. In the middle of this groove, a split-like elongated hole opened-up with sub-regular contours (Fig. 8: e-f). Only five minutes are required for perforating fresh shells with this technique while we needed three times as much time for achieving a perforation on fossil shells, characterized by massive and thick valves. We performed the perforations a few millimetres below the umbo toward the middle of the dorsal valve, where this kind of perforation was observed on the Petersfels assemblage. We recorded random shallow incisions below the groove produced by accidental contact of the lithic tool with the dorsal face of the shell during the activity (Fig. 8: e). This perforation is very diagnostic and is easily recognizable even with the naked eye and cannot be confused with taphonomic traces when observed on the archaeological material.
- **Final remarks**
  As a general rule, we observed that perforations on fresh shells are achievable after a few seconds or minutes (depending on the technique used), while fossil specimens require at least twice the time (e.g., sawing). However, we must bear in mind that time required to achieve a complete perforation also depends on the size of the shell, the force applied, the speed of the to-and-fro motion, and the type of sandstone used. However, we noticed that abrasion is the quickest and most efficient technique for perforating *Glycymeris* shells. This technique is easy to perform and does not require any specific expertise nor toolkit, allowing the attainment of round and regular holes with little effort.
  All three techniques tested in this experimental trial showed technological macro and micro traces characteristic of the motions and activities performed, with striations being the most diagnostic ones. Despite that, shells can often exhibit natural perforations on the umbo or on the dorsal or ventral face which can mimic those made by humans. Shell valves are subjected to several taphonomic processes before and after their collection by humans (Gutiérrez-Zugasti 2009; Cuenca-Solana et al. 2017). Abrasion is the main cause of natural perforations in shells and is the result of the combined smoothing action of the water and sand. The umbo is the area most affected by abrasion because it is the most prominent one and, therefore, most subjected to mechanical stresses. The natural abrasion starts by creating a flat and round surface on top of the umbo (Fig. 9: a), which gradually becomes larger until thinning the umbo and creating a hole. Natural holes produced by abrasion show both rounded and regular contours (Fig. 9: b-c) but also irregular morphologies (Fig. 9: d), depending on the abrasive processes to which they have been exposed (Fig. 9). The morphology of the natural hole may thus resemble the anthropogenic perforation by abrasion, but in the former, striations are absent, as well as the flat facet surrounding the perforation. Indeed, as shown in figure 9 (b), natural

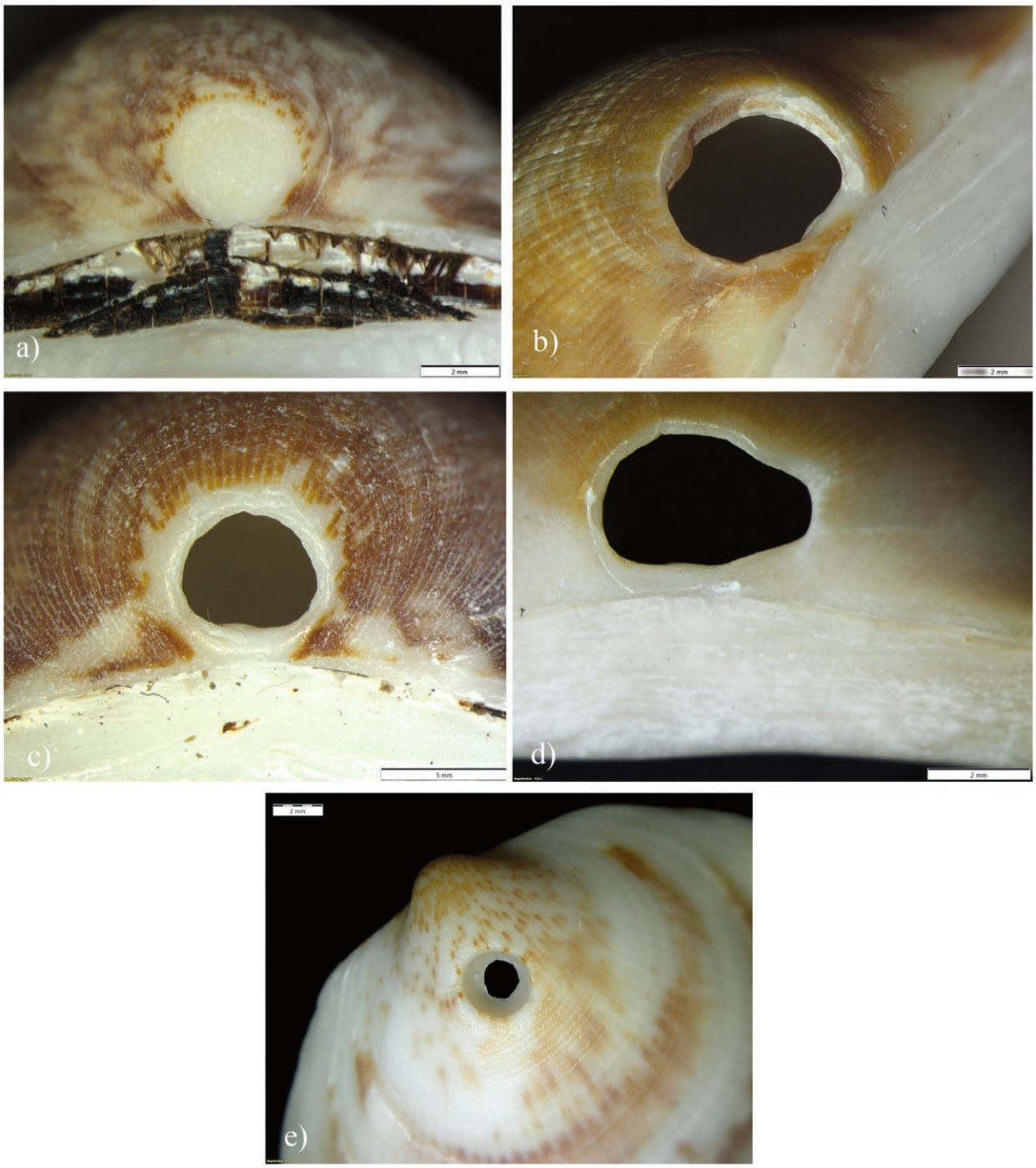

Fig. 9. Natural perforations on modern *Glycymeris* shells made by abrasion (a-d) and predators (e). Magnification: a) 50x; b) 25x; c) 32x; d) 16x; e) 8x). (Photos: F. Venditti).

Abb. 9. *Natürliche Durchlochungen auf rezenten Glycymeris-Schalen durch Abrieb (a-d) und Raubtiere (e). Vergrößerung: a) 50x, b) 25x, c) 32x, d) 16x, e) 8x). (Fotos: F. Venditti).*

holes maintain the convexity of the umbo around the perforation, a feature not observable on anthropogenic perforation made by abrasion.

Natural perforations can also be derived from the activity of marine predators trying to obtain calcium carbonate or to access the mollusc for nutritional purposes. In this case, these conical holes can resemble those performed by drilling, but they lack the typical concentric drilling striations observable at low and high magnifications (Fig. 9: e).

Results

Origin

The analysed *Glycymeris* from sites in southern Germany originate from two different provenance areas. At Vogelherd, the assemblage is almost exclusively made up of fossil molluscs from the Mainz Basin (Fig. 4). In this area, there are outcrops in the Alzey region that originate from the Upper Marine Molasse, dating to the Miocene at 23-25 million years ago.

Here, fossil shells were already accessible in the Pleistocene, and *Glycymeris* shells can also be found in the Gravettian sites of Sprendlingen and Mainz Linsenberg in the Mainz Basin (Neeb & Schmitdgen 1921/24; Bosinski et al. 1985; Bosinski 2008). We assume an origin from the Mainz Basin, which is based on geographical proximity to the sites of interest. However, an origin from the more distant Belgian and Parisian Tertiary is also possible. An origin from the Erminger Turitellenplatte, an outcrop located in southern Germany, can be excluded due to the poor preservation and inaccessibility (Höltke 2009). The pieces from this deposit occur in a breccia and were only accessible during modern construction work.

The mollusc fragment from layer IV is sub-recent, not fossil, and, therefore, does not come from the Mainz Basin (Fig. 4: 12). The Venus bivalve from Vogelherd could only be assessed based on a photo; therefore, a determination of species and origin was not possible. The ammonite from layer V originates from the lower Jurassic layer of the Swabian Jura (Dutkiewicz 2018) (Fig. 4: 13).

The *Glycymeris* from Petersfels are partly fossil and partly sub-recent (Fig. 6). Due to inaccessibility, only a portion of the Petersfels assemblage could be analysed. The fossil *Glycymeris* from Petersfels originate from the Mainz basin, and the sub-recent *Glycymeris* originate from the Mediterranean. Our determinations are consistent with previous analyses of molluscs from the site (Eriksen 2002), which suggest origins of the entire mollusc assemblage in the Mediterranean (380 km distance), the Atlantic (800 km distance), the Paris Basin (350 km distance), the Mainz Basin (240 km distance), the Steinheim Basin (130 km distance), the Kirchberg strata near Illerkirchberg (100 km distance), and the Swabian Jura (surrounding the site) (Rähle 1983, 1994; Eriksen 2002).

Size

One of the striking features of *Glycymeris* molluscs is the size of the pieces (Fig. 10). Here, there are differences between the *Glycymeris* from Vogelherd and the pieces from Petersfels, Hohle Fels, Geißenklösterle and Brillenhöhle. The complete specimens from Vogelherd (N = 6) have an average height of 38.68 mm (median = 39.24, standard deviation = 5.17) and an average length of 39.38 mm (median = 38.00, standard deviation = 5.03). The complete pieces from Petersfels (N = 70), Hohle Fels (N = 2), Geißenklösterle (N = 1) and Brillenhöhle (N = 1) have an average height of 20.35 mm (median = 20.23, standard deviation = 2.59) and an average length of 21.71 mm (median = 21.70, standard deviation n= 2.71). The perforated molluscs were also included in this group.

Colouring residues

Possible ochre remains on the *Glycymeris* are macroscopically recognizable in pieces from Vogelherd, Petersfels and Hohle Fels. The EDX was able to detect iron in five of the 13 molluscs tested (Fig. 11; for a detailed overview see the supplementary material). In addition to the iron component, calcium, which is found in the calcite of the mollusc shells, was also detected. Without further analysis of the cave sediments, however, evidence of ochre in the shells cannot be established without a doubt. Especially in Petersfels, the evidence of ochre is problematic, as Peters noted a red-coloured layer ("Rote Kulturschicht")

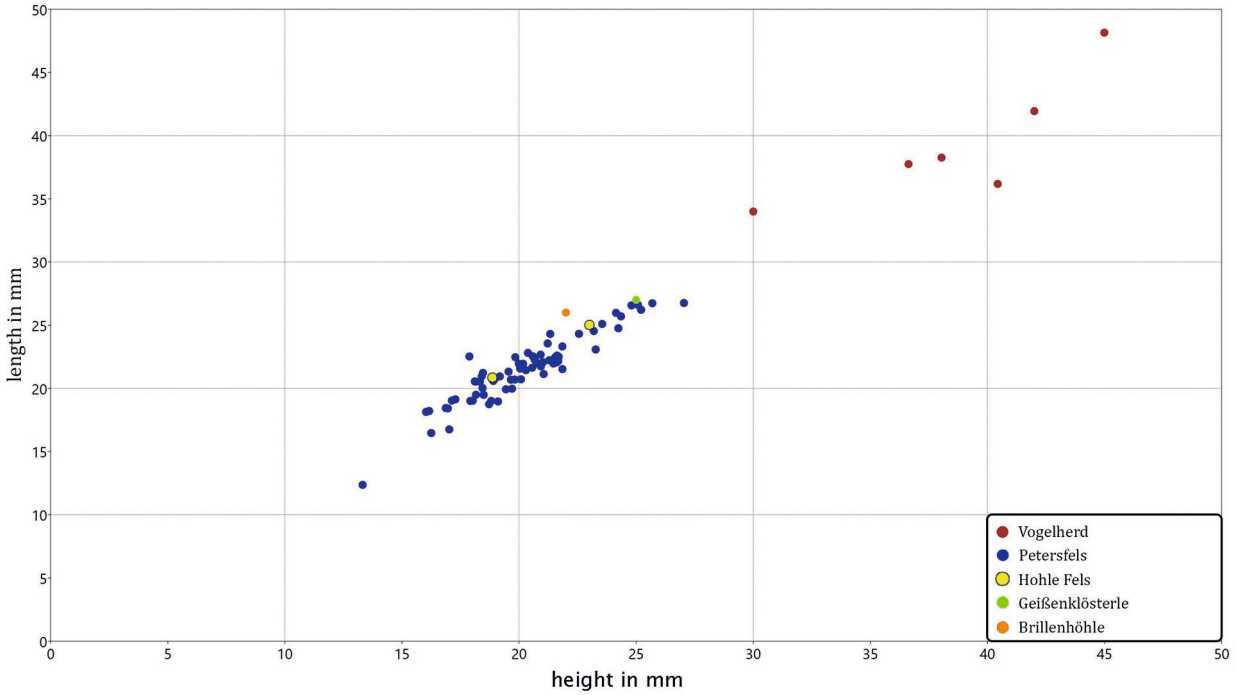

Fig. 10. Size distribution of the recorded *Glycymeris* finds from southwestern Germany.
Abb. 10. *Größenverteilung der aufgenommenen Glycymeris Funde aus Südwestdeutschland.*

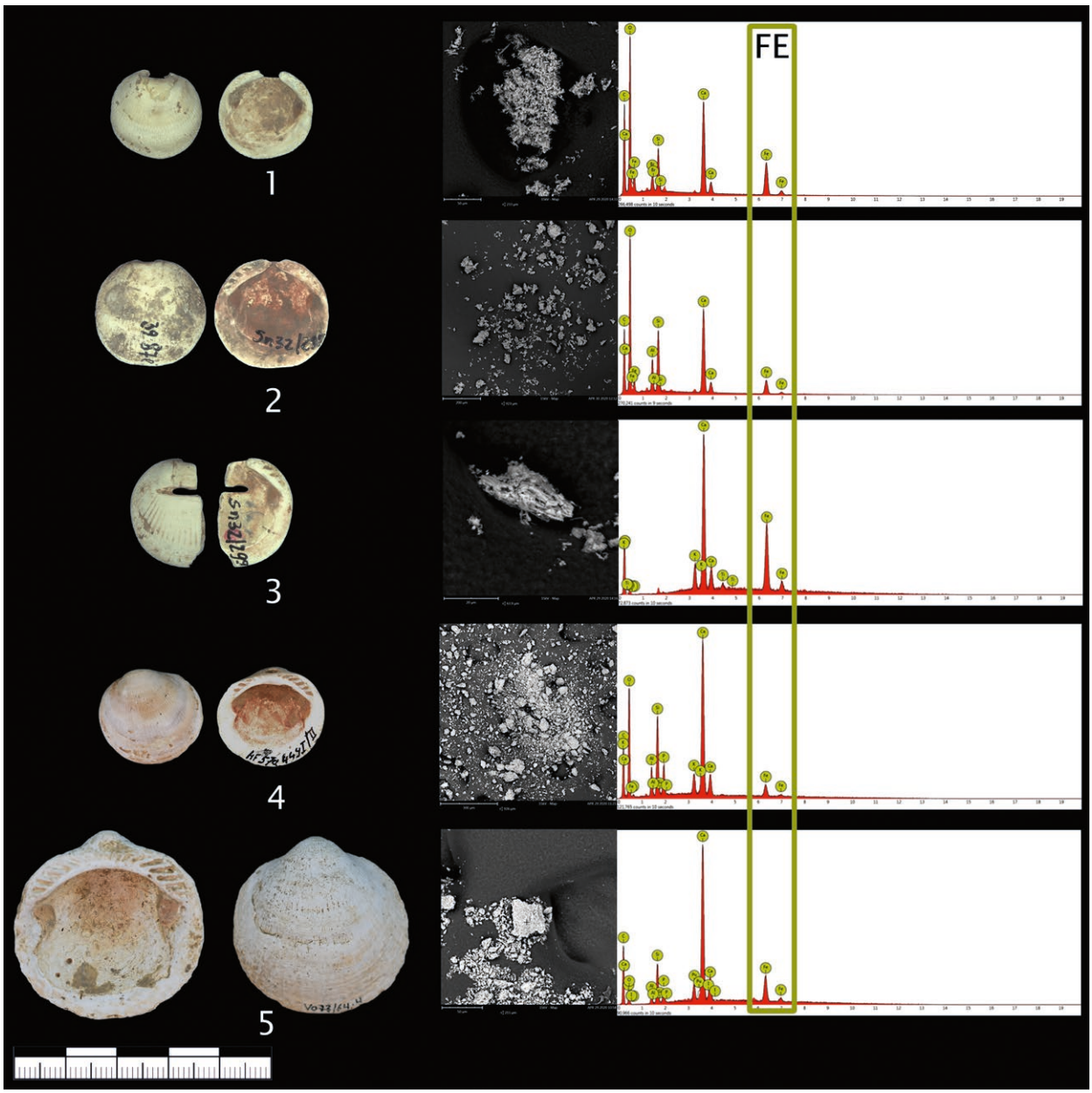

Fig. 11. *Glycymeris* from Petersfels, Hohle Fels and Vogelherd: 1. Petersfels (Nr. 39); 2. Petersfels (Nr. 59); 3. Petersfels (Nr. 114); 4. Hohle Fels (HF 57a, 449); and 5. Vogelherd (73/64 4), SEM micrograph of the sample powder (middle) and EDX spectrum (right). The iron component in the EDX spectrum is highlighted by the green box and the label FE (= iron) for better visibility. The exact composition of the spectra can be found in the SI Figs. 1-5. (Photos: B. Schürch, T. Miranda).

Abb. 11. *Glycymeris aus Petersfels, Hohle Fels und Vogelherd: 1. Petersfels (Nr. 39), 2. Petersfels (Nr. 59), 3. Petersfels (Nr. 114), 4. Hohle Fels (HF 57a, 449) und Vogelherd (73/64 4), SEM-Aufnahme des Probenpulvers (Mitte) und EDX-Spektrum (rechts). Die Eisenkomponente im EDX-Spektrum ist zur besseren Sichtbarkeit durch einen grünen Kasten und die Beschriftung FE (= Eisen) hervorgehoben. Die genaue Zusammensetzung der Spektren ist dem Anhang zu entnehmen (SI Abb. 1-5) (Fotos: B. Schürch, T. Miranda).*

in the cave (Peters 1930, 1932; Mauser 1970). The red colouration of this layer may have also influenced the residues observed on the *Glycymeris*. Despite that, microscopic observations on two specimens (one from Hohle Fels and one from Petersfels) demonstrate that the ochre was intentionally spread on the inner valve by humans rather than resulting from taphonomic processes. As shown in figure 13 (d) the red colourant is embedded in the microtopography of the shells and, more importantly, brownish sediment particles cover the layer of ochre, testifying their later deposition. However, the examples examined also show that there are very different amounts of ochre deposits in the shells. Some *Glycymeris* show a very thin reddish layer, while others have a thicker layer.

Archaeological perforations

A total of 107 out of 131 *Glycymeris* showed clear and distinct perforations on the umbo. The remaining pieces were severely damaged on the umbo region. Therefore, a reliable characterization was not possible (Tab. 1). As already discussed above, a crucial aspect when

Archaeological site	*Glycymeris* (N = 131)	Perforated (of 107 possible)	Double perforated	Perforation at Umbo	Perforation at bulge
Petersfels	115	83	2	81	2
Vogelherd	10	2	-	2	-
Hohle Fels	3	3	-	3	-
Geißenklösterle	1	1	-	1	-
Brillenhöhle	1	1	-	1	-
Gnirshöhle	1	-	-	-	-

Tab. 1. *Glycymeris* molluscs of the analysed archaeological sites. Perforation presence, location and type.
Tab. 1. *Glycymeris Mollusken der untersuchten archäologischen Fundstellen. Durchlochung, Lage und Art der Durchlochung.*

studying perforated shells concerns the interpretation of the nature of perforations. The adoption of microscopic techniques for the investigation of microwear is a valid approach for shedding light on the real origin of these perforations. The results of a preliminary microwear study are reported below.

Preliminary results of the microwear analysis

We considered the sample of 15 specimens suitable for carrying out a microwear analysis. However, we observed that the *Glycymeris* fossil shells from Vogelherd exhibited weathered surfaces that contributed to the loss of material on the dorsal face of the valve (e.g., exfoliation probably occurred during diagenesis) (Fig. 4: 1 & 2), while fossil specimens from Petersfels displayed better preserved surfaces, although a medium to high degree of rounding was observed, especially along the margins. Despite that, the hinge teeth and the serration along the ventral valve margins were nearly always well-recognizable in all specimens, a sign that the shells have undergone only moderate abrasive action.

Out of the 15 *Glycymeris* shells analysed for microwear traces in this study, five display complete morphologies and perforations, while one specimen is a proximal shell fragment preserving its complete hole. In addition, seven shell fragments exhibit incomplete perforations while two others represent small fragments of a valve.

Because of the state of preservation of the two Vogelherd shells, we observed no reliable technological traces on the umbo around the perforations.

Concerning the incomplete perforations from Petersfels, six shells show elliptical holes with smoothed regular walls and no evidence of anthropic modifications at a macro or micro scale. In particular, the umbo lacks the typical flat facet, while it retains its natural convexity. We thus interpreted these holes as produced by natural abrasion (Fig. 12).

On the remaining sample from Petersfels, out of the four complete and almost complete perforations, one shell suggests the presence of technological traces produced during the manufacture of the hole (Fig. 13: a). The view in profile of the umbo shows a perfectly flattened surface, suggesting it was made by rubbing the umbo against an abrasive surface (Fig. 13: b). At a macroscopic level, we recorded striations below and around the perforation running parallel to the longitudinal axis of the shell (Fig. 13: c). Linear features are highlighted by the colouring contrast between the natural surface (white in colouration) and the reddish pigmentation on the umbo region, confirmed to be pigment by the EDX analysis (see SI. 4). Indeed, a well-recognizable layer of red pigment is spread on the ventral side of the shell, while on the dorsal side slight red shades suggest its ancient presence. At higher magnification, a localised polish exhibiting linear features testifies to the longitudinal contact with a hard material such as a sandstone used during the abrasive process.

We recorded a similar combination of linear traces, flat perforation, and red stains on the complete *Glycymeris* valve from Hohle Fels (Fig. 13: e). Additionally, on this specimen, the shell portion below the perforation shows a bright, rounded, and polished area characterized by a smooth polish with wide long isolated parallel striations (Fig. 13: f-g). The polish is most likely the result of repetitive friction with threads and clothes during use, suggesting that the shell was suspended on the body or sewn on clothes. This is also supported by the presence of volume deformations that might have been triggered by string tension (Fig. 13: h). We noted a similar volume deformation in the same area on a shell from Petersfels, which displays a complete perforation without any sign of technological traces. Use-related traces will be further tested in future experiments aimed at investigating the use of *Glycymeris* shells and the development of wear traces corresponding to various modes of adornment.

Finally, remarkable is the presence of three specimens from Petersfels with double perforations. One of the shells has a perforation (Fig. 14: a-c) on the umbo and a second perforation directly above it. Both perforations are broken off or worn. A second *Glycymeris* from Petersfels (Fig. 14: d) is also double perforated, bearing one perforation on the umbo and one longitudinal perforation on the bulge. The second perforation was most likely produced by sawing the dorsal side of the shell with a sharp cutting tool, as shown by the typical sawing mark (see Fig. 8: e for comparison). Another double perforated *Glycymeris* (Fig. 14: g) has one perforation on the umbo and a smaller perforation on the bulge. In this case, the small perforation is natural and probably from a Clionaidae

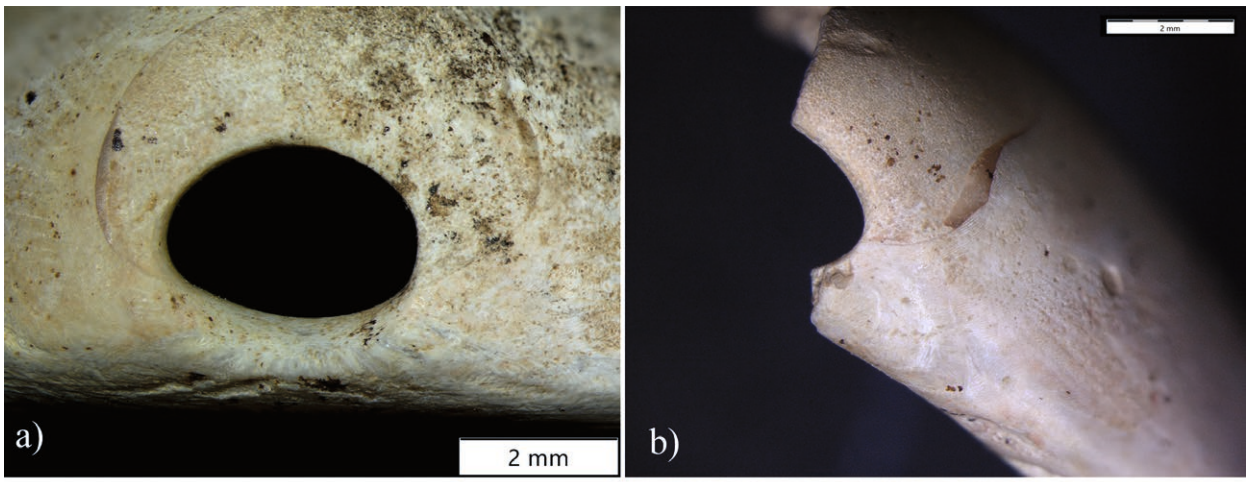

Fig. 12. Two archaeological *Glycymeris* shells from Petersfels (specimens No. 158 and No. 997S): a) complete perforation from specimens No. 158 (magnification 20x) and b) a fragmented perforation from specimen No. 997S interpreted as naturally holed (magnification 16x). (Photos: F. Venditti).

Abb. 12. *Zwei archäologische Glycymeris-Muscheln aus Petersfels (Fundnummer Nr. 158 und Nr. 997S): a) eine vollständige Durchlochung der Muschel 158 (Vergrößerung 20x) und b) eine fragmentierte Durchlochung der Muschel (Nr. 997S), die als natürlich durchlocht interpretiert wird (Vergrößerung 16x). (Fotos: F. Venditti).*

sponge (boring sponge) or a snail (Fig. 14: h). These three specimens were not part of the 15 shells subjected to microscopic examination because they were not available at time of the analysis. However, future microwear analysis is planned for these specimens in order to shed light on their production and use.

Discussion

We identified the Mainz basin as provenance of the *Glycymeris* from Vogelherd Cave. Hence, we reconstruct a long-distance connection to the Mainz Basin during the Aurignacian at Vogelherd, a distance of about 200 km. We cannot determine if the fossil molluscs were objects of bartering or if they were passed on by multiple regional groups. Furthermore, a direct acquisition of the molluscs cannot be proven. In any case, the molluscs found their way to the Swabian Jura. Other long-distance connections are revealed based on lithic raw material analyses. For example, one possible connection to the Aurignacian of Vogelherd is retraced to Bavaria, a distance of about 120 km, which is reconstructed based on the presence of Tabular Jurassic chert (Burkert & Floss 2005; Chang 2015; Herkert et al. 2015). While connections like this along the Danube certainly existed (e.g. Floss et al. 2015), evidence from this study on the *Glycymeris* show a long-distance connection northward from the Swabian Jura to the Mainz Basin.

The hints to long-distance connections during the Swabian Aurignacian are sparse. One example is Baltic flint from Hohlenstein-Stadel in the Lone Valley which represents a long-distance connection of several hundred kilometres to the north (Burkert & Floss 2005). There are also similarities concerning the raw material use of shale for personal ornaments of Bockstein-Törle in Baden-Württemberg and Wildscheuer Cave in Hessen, as well as the similar ivory raw forms for ornaments from Lommersum and Bockstein-Törle (Wolf et al. 2013; Wolf 2015). The form of the basket-shaped beads which is known from Hohle Fels Cave is also documented in Belgium at Spy (Otte 1979; Vanhaeren & d'Errico 2006). Fragments of ivory points with a flat-oval shaped cross-section and rounded edges are also found at Hohle Fels, Wildscheuer, and Spy (Otte 1979; Conard & Malina 2007). These are possible hints of a long-distance connection to the northwest. Another connection can be drawn from the Lias ammonite from layer V of Vogelherd (Dutkiewicz 2018), which probably originates from the northern margin of the Swabian Jura, a distance of about 30 km. There, the layers of the lower Jurassic are accessible.

Concerning the molluscs, there are various differences between the *Glycymeris* assemblages of Vogelherd and the other *Glycymeris* of the subsequent archaeological cultures. The observed size difference between *Glycymeris* from Vogelherd and all other sites in southwestern Germany may indicate a specific use for the respective artefacts. For example, the *Glycymeris* shells from Vogelherd are, on average, almost twice as large as the pieces from Petersfels, Hohle Fels, Geißenklösterle, Brillenhöhle, and Gnirshöhle. This difference in size and the rarity of perforations at Vogelherd could indicate a different use and function.

The preliminary results obtained from the microwear analysis of the *Glycymeris* from Vogelherd, Hohle Fels, and Petersfels have highlighted the potential in terms of microwear analysis, especially at Petersfels. Here, technological traces showed that at least two different techniques were used for perforating the shells: abrasion against a sandstone and sawing with a lithic tool. Shells with natural perforations

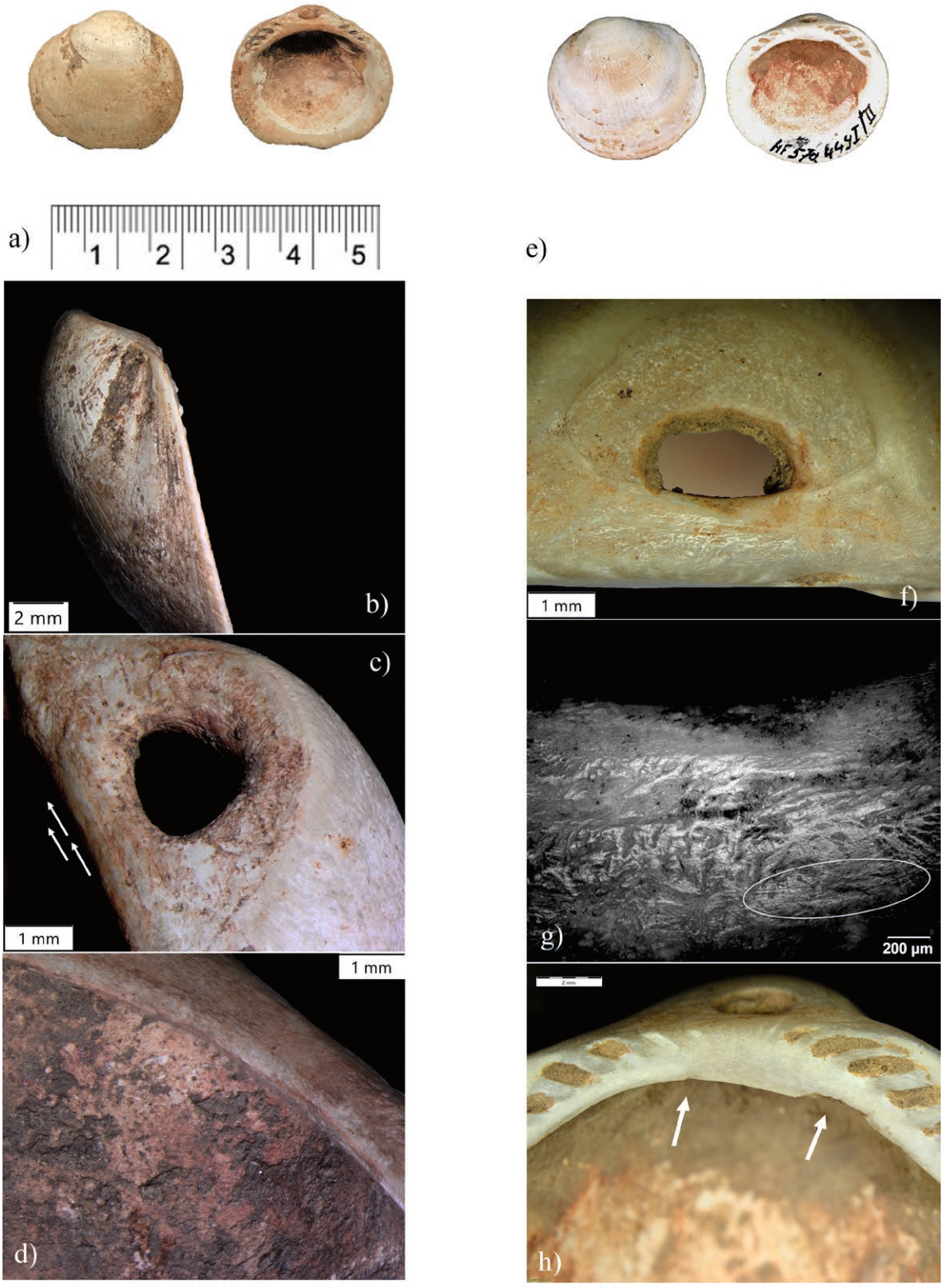

Fig. 13. Archaeological *Glycymeris* shells and related wear traces: a) Dorsal and ventral view of *Glycymeris* from Petersfels (No. 1086); b) View in profile showing the flat facet due to perforation by abrasion (magnification 8x); c) Parallel grooves below the perforation resulting from abrasion (magnification 25x); d) Layer of pigment spread inside the inner valve. Notice that the brownish sediment particles overlaps the reddish valve surface (magnification 25x); e) Dorsal and ventral view of *Glycymeris* shell from the Gravettian of Hohle Fels (layer:3b/II unit:57a Nr.:499); f) Highly polished area developed below the perforation (square in white, magnification 25x); g) Close up of the polish and striation (circled in white, 10x); h) Volume deformations on the ligament area (magnification 12.5x). (Photos: F. Venditti).

Abb. 13. *Archäologische Glycymeris Mollusken und zugehörige Abnutzungsspuren. a) Glycymeris aus dem Petersfels (Nr. 1086), b) Profilansicht der Molluske mit der flachen Durchlochung (Vergrößerung 8x) , c) parallele Rillen unter der Durchlochung (Vergrößerung 25x), d) Ockerschicht im inneren der Muschel, e) Glycymeris Molluske aus dem Hohle Fels (Schicht:3b/II Unit:57a Nr.:499 I), f) stark polierter Bereich der sich unter der Durchlochung ausgebildet hat (weißer Kasten, Vergrößerung 25x), g) Nahaufnahme der Politur und der Rillen (umkreist in weiß, 10x), h) Volumenverformung im Bereich der Ligamente (Vergrößerung 12,5x). (Fotos: F. Venditti).*

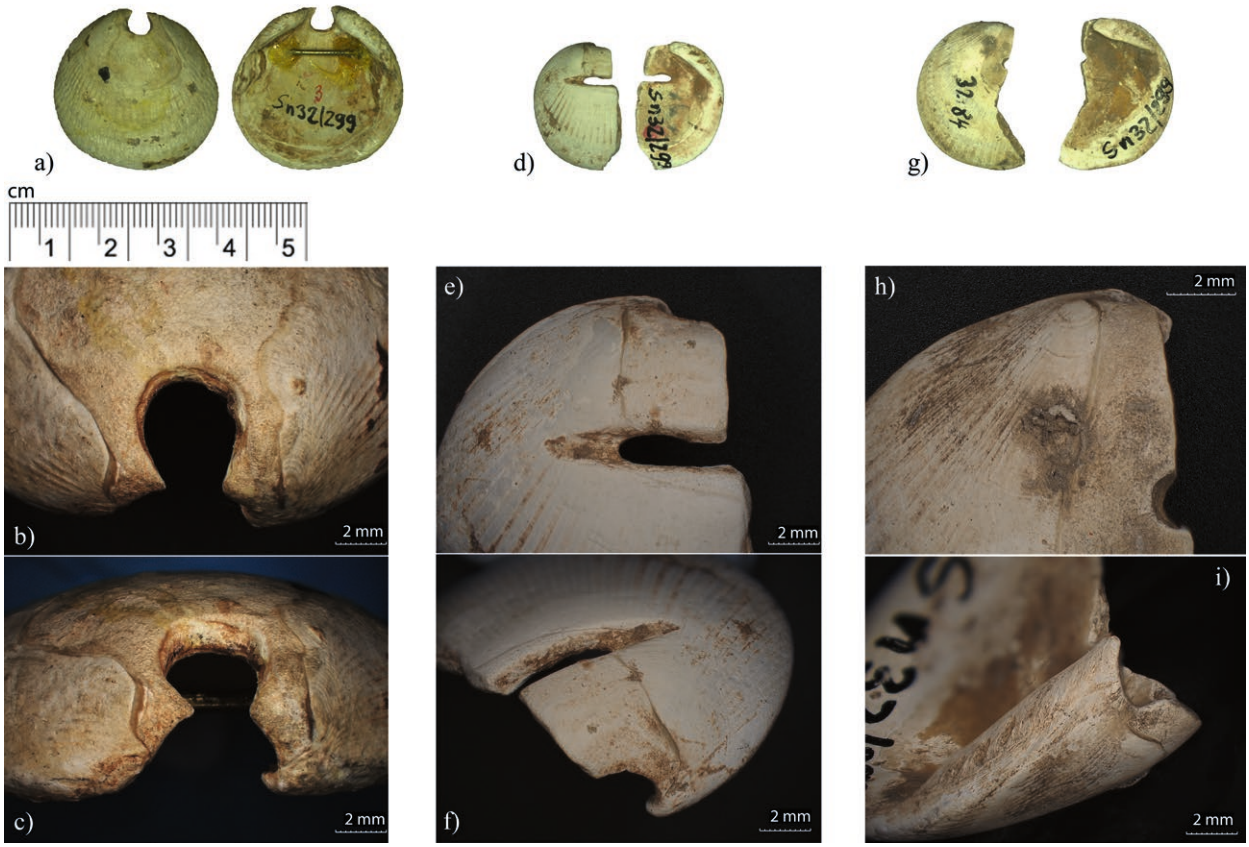

Fig. 14. Perforated molluscs from Petersfels: a) Double perforated *Glycymeris* (No. 56); b) One perforation directly above this perforation (magnification 20x); c) One perforation on the umbo and (magnification 20x). d) Double perforated *Glycymeris* (No. 114); e) One perforation was made longitudinally on the bulge (magnification 20x); f) One perforation is on the umbo (magnification 20x). Traces of pigment are visible in the depressions and on the inside. g) Double-perforated *Glycymeris* (No. 109); h) One natural perforation on the bulge (magnification 30x); i) One perforation on the umbo (magnification 20x). (Photo: B. Schürch; F. Venditti).

Abb. 14. *Durchlochte Mollusken aus dem Petersfels: a) Doppelt durchlochte Glycymeris, b) eine direkt oberhalb dieser Durchlochung (Nr. 56) (Vergrößerung 20x) und c) eine Durchlochung am Umbo (Vergrößerung 20x) d) Doppelt durchlochte Glycymeris (Nr. 114) e) eine Durchlochung ist am Umbo (Vergrößerung 20x) und f) eine Durchlochung wurde längs auf der Aufwölbung angebracht (Vergrößerung 20x). In den Vertiefungen und auf der Innenseite sind Ockerspuren sichtbar. g) doppelt durchlochte Glycymeris (Nr. 109), h) eine natürliche Durchlochung auf der Aufwölbung (Vergrößerung 30x) und i) eine Durchlochung am Umbo (Vergrößerung 20x). (Foto: B. Schürch; F. Venditti).*

were also collected by the inhabitants of Petersfels, as testified by the perforated specimens without technological traces. In addition, the presence of a second perforation, after the first wore and broke, testifies to the prolonged use of shells and the desire to extend their life. The use of pigments may indicate that the shells were worn and displayed to others.

The positive results from this pilot study encourage further analysis of the whole assemblage of *Glycymeris* shells recovered at Petersfels. We plan to perform more comprehensive experiments to test the manufacture and use of these shells as ornaments and to shed light on their greater role within the Magdalenian groups of southwestern Germany.

Colouring residues within the molluscs will also play an important role for the interpretation of future experiments. Ochre was discovered in all sites presented here. At some sites, like Vogelherd or the Aurignacian layers of Hohle Fels, ochre is present but did not have a significant influence on the colour of the layers, instead being used to colour personal ornaments made from mammoth ivory (Velliky et al. 2021). The molluscs from Vogelherd, Petersfels, and Hohle Fels, which were investigated with SEM, also bear traces of iron. As it is no longer possible to examine the sediment in the immediate vicinity of the molluscs, it is thus not possible to prove the origin of the pigment traces beyond doubt. However, ochre remains can also be found at some sites that Taborin (1993a) examined. She reconstructs their mode of adornment based on burials preserving various molluscs (Taborin 1993a: 307). When considering her work, there are three possibilities for the formation of the ochre residues: colouring of the pieces by the surrounding sediment, use of the shells as containers, or adhesion of the ochre traces by wearing the molluscs on clothing/hair that was dyed with ochre. The presence of perforations on some of the Vogelherd pieces provide an opportunity to assess these possible scenarios. The origin of the pigment on non-perforated pieces can only be explained by their use as containers or by the colouring of the sediment. The perforated shells are not ideally suited for use as

containers and could be coloured by the sediment or via use as personal ornaments.

At Petersfels, the excavator Peters notes a red-yellow layer with limestone plaques at a depth of 115 cm (Peters 1930). This layer had a thickness between 30 cm and 40 cm. Peters (1930: 18) described this deposit as one layer, but he was careful with his description and was aware of the incompleteness of the excavation. Mauser (1970: 16) examined sediment samples that Peters left for further analysis and described them as heterogeneous, but all samples still show the red colour. Mauser stated that the red-yellow deposit cannot be one layer but the result of different settlements in and near the cave site. According to him, the Magdalenian hunter-gatherers used ochre frequently. That is why the powder was found throughout the whole stratigraphic sequence in his point of view. Additionally, he analysed the artefacts of Peters excavations and found different styles that likely belong to different temporal occasions. Therefore, he rejected the claim that the "cultural layer", defined by Peters, represents a single cultural event. In any case, the use of colourants is obvious – it is not a natural occurrence inside the cave, but anthropogenic. This means that the molluscs could have been coloured by the layer itself and/or directly by the inhabitants of the site. In the case of intentional colouration, it is unfortunately not possible to differentiate between shells that were coloured while being used as a container and shells that were coloured for aesthetic purposes. Additionally, pigments were likely not used as an abrasive powder while grinding to produce holes, as powder is present on both the interior and exterior surfaces. However, in some cases, the presence of anthropogenic colourants is still confirmed, due to the adherence of sediment overlying the red colouration. Given this evidence, it is clear that the purpose of ochre in these contexts is multi-faceted (see Wolf et al. 2018). Concerning our study, the use of pigments for the treatment of *Glycymeris* may indicate that the shells were worn and displayed to others.

For Petersfels, further statements of long-distance connections are possible. The presence of fossil *Glycymeris* forms a connection to the Mainz Basin, which is about 240 km away from the site. The sub-recent *Glycymeris* from the Mediterranean are about 380 km away from Petersfels. If we assume that the Magdalenian groups did not pass the Alps as a barrier that required circumvention, this extends the distance to almost 600 km. In addition to the long-distance connections that can be reconstructed based on *Glycymeris*, there are also other long-distance connections that were made using other molluscs to the Mediterranean region, the Atlantic, the Paris Basin, the Mainz Basin, the Steinheim Basin, the Kirchberg strata, and the Swabian Jura (Rähle 1983; Eriksen 2002). The lithic raw material used at Petersfels also shows a connection to the German and French Jura (Danube and Circum-Jurassic Group) (Maier 2015). The use of *Glycymeris* is common during the Magdalenian (see SI Tab. 1), especially in southwestern Germany and Switzerland (Eriksen 2002; Floss 2019). The people in this region were in close contact and shared the same cultural expressions. This is also supported by the use of jet for female figurines of the same style at Neuchâtel (Switzerland) and Petersfels. These particular artefacts could represent an exchange between groups or individuals or be the result from the groups' mutual influence on each other. The use of this one specific form between two sites hints at the idea that this form was of particular importance. Considering Mauser's interpretation that Petersfels was inhabited during several different phases during the Magdalenian (Mauser 1970), the *Glycymeris* can be seen as a stable form in this cultural frame.

Conclusion

The investigation of the *Glycymeris* from Vogelherd and Petersfels has shown that there are long-distance connections in the early and late Upper Palaeolithic of southern Germany, which can otherwise only rarely be reconstructed. Even if not all pieces can be attributed to a specific use, different possibilities of use could be discussed. With the extension of our microwear analysis in the future we will be able to present further results on the *Glycymeris* and other mollusc species and their use.

When all *Glycymeris* finds from the Upper Palaeolithic of Europe (Germany, Belgium, Switzerland, France, and Italy) are summarised (Fig. 15), the broad geographic and temporal span of this species becomes clear. Sites with *Glycymeris* are found in the Aurignacian (N = 12), the Gravettian (N = 10), the Solutrean (N = 6), and the Magdalenian (N = 80). As the number of *Glycymeris* dramatically increases during the Magdalenian throughout Central Europe, it is likely that the occurrence of this mollusc underlies an element of common culture during this period. Compared to the use of mammoth ivory during the Aurignacian and the Gravettian, the Magdalenian constitutes a clear change in raw material preference towards the use of jet and molluscs (Wolf 2019), although ivory was still available (Veil 1982). For the latter, the *Glycymeris* were the most important type. This is probably the result of the movement of people with different cultural backgrounds into Central Europe after the second cold maximum of the last Ice Age (e.g., Taller 2014; Maier 2015). According to genetic analysis, these people came from the Near East (Posth et al. 2016) and, according to archaeological studies, also from Western Europe (e.g. Bocquet-Appel & Demars 2000; summarised in Taller 2014; Wolf 2019).

For the most part, *Glycymeris* are described as ornamental objects, as many bear signs of perforation and use. One example being Petersfels, the richest known Magdalenian site in Central Europe, which exhibits raw materials for ornament production, parts

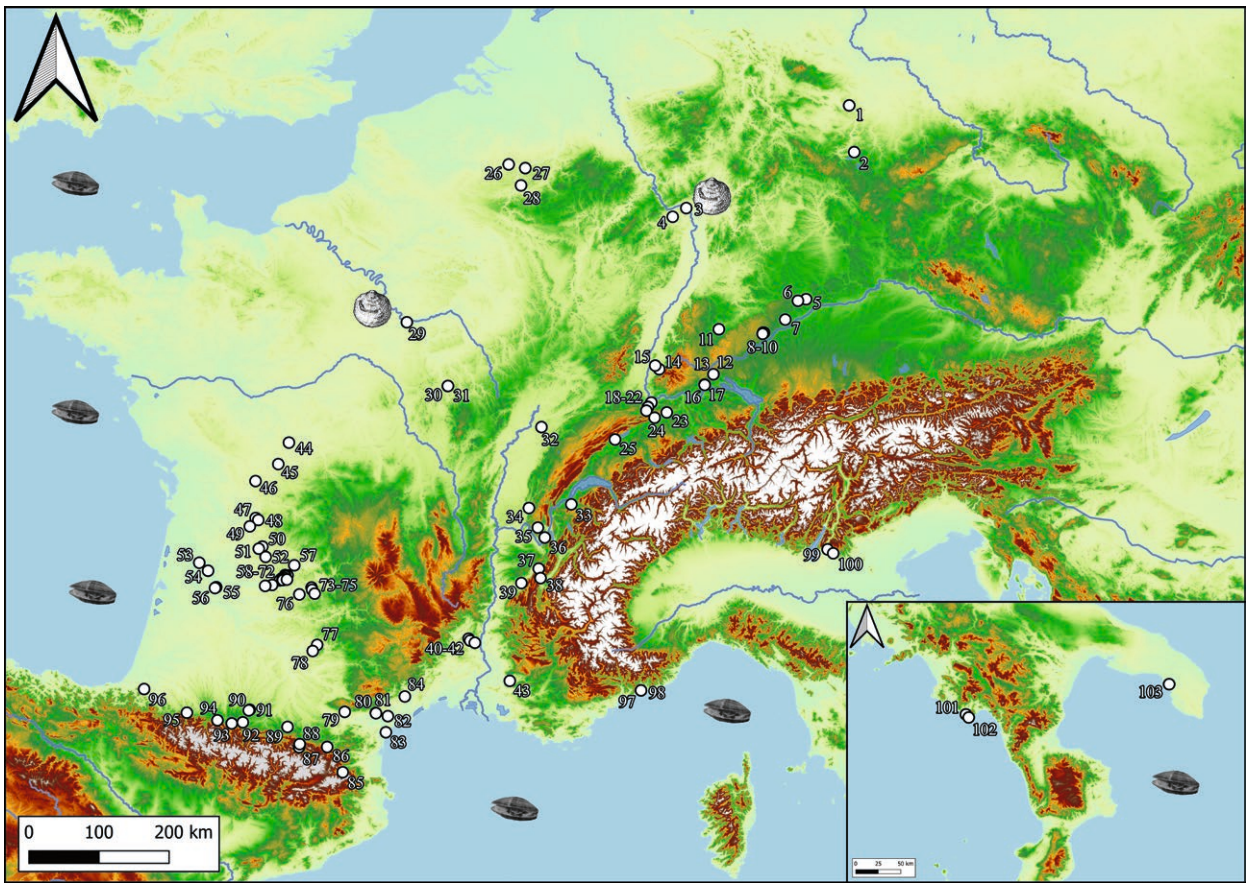

Fig. 15. Upper Palaeolithic sites with *Glycymeris* from Germany, Switzerland, Belgium, France, and Italy. The fossil deposits of *Glycymeris* in the Mainz and Paris basins are marked with a bivalve half. *Glycymeris* live in the Mediterranean as well as in the Atlantic, which are marked with living shells. For site codes, see table SI 1 (Background map: © European Union, Copernicus Land Monitoring Service 2021, European Environment Agency (EEA)). The majority of the listed sites from France are based on Taborin 1993a. The primary literature and the number of *Glycymeris* from these sites were not double checked in the course of this work; the corresponding references and the number of pieces can be taken from Taborin 1993a.

Abb. 15. *Jungpaläolithische Fundstellen mit Glycymeris aus Deutschland, Schweiz, Belgien, Frankreich und Italien. Die fossilen Lagerstätten der Glycymeris im Mainzer und Pariser Becken sind mit einer Muschelhälfte gekennzeichnet. Glycymeris leben sowohl im Mittelmeer als auch im Atlantik, dies ist mit zweiklappigen Muscheln gekennzeichnet. Fundstellencodes sind Tabelle SI 1 zu entnehmen (Hintergrundkarte: © European Union, Copernicus Land Monitoring Service 2021, European Environment Agency (EEA)). Der Großteil der aufgeführten Fundstellen aus Frankreich stammt aus Taborin 1993a. Die Primärliteratur und die Anzahl der Glycymeris zu diesen Fundstellen wurde im Zuge dieser Arbeit nicht überprüft, entsprechende Verweise und die Anzahl der Stücke sind Taborin 1993a zu entnehmen.*

of the production sequences, and used ornaments. The presence of anthropogenically modified *Glycymeris* during the entirety of the Upper Palaeolithic sequence highlights the importance and significance of this category of artefacts.

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Number (on map)	Site	Country	Number of Glycymeris	Technocomplex	References
1	Nebra	Germany	1?	Magdalenian	Maier 2015; Mania 1999
2	Kniegrotte	Germany	3	Magdalenian	Höck 2000; Maier 2015
3	Mainz-Linsenberg	Germany	1	Gravettian	Neeb & Schmitdgen 1921/24
4	Sprendlingen	Germany	9	Gravettian	Bosinski et al. 1985
5	Kaufertsberg	Germany	1	Magdalenian	Kaulich 1983
6	Hohlenstein Ederheim	Germany	2	Magdalenian	Narr 1965
7	Vogelherd	Germany	10	Aurignacian	Riek 1934; Wagner 1981; Schürch et al. 2021
8	Brillenhöhle	Germany	1	Gravettian	Otte 1981
9	Geißenklösterle	Germany	1	Gravettian	Kölbl 2003
10	Hohle Fels	Germany	2 + 1	Gravettian+Magdalenian	Rähle 1994; Kölbl 2003; Schürch 2021
11	Napoleonskopf, Bad Niedernau	Germany	1	Magdalenian	Paradeis 1907; Mauser 1976; Kölbl 2003
12	Gnirshöhle	Germany	1	Magdalenian	Albrecht et al. 1977; Schürch 2021
13	Petersfels	Germany	113	Magdalenian	Rähle 1994; Schürch 2021
14	Teufelsküche	Germany	3	Magdalenian	Zotz 1928
15	Munzingen	Germany	1	Magdalenian	Padtberg 1925; Albrecht 1981
16	Freudenthal	Switzerland	1	Magdalenian	Eriksen 2002; Karsten 1874
17	Schweizersbild	Switzerland	5	Magdalenian	Eriksen 2002; Nüesch 1896
18	Hollenberg	Switzerland	20	Magdalenian	Eriksen 2002; Stampfli 1981; Sedlmeier 1988
19	Birseck-Ermitage	Switzerland	1	Magdalenian	Sarasin 1918; Sedlmeier 1988
20	Kohlerhöhle	Switzerland	18	Magdalenian	Eriksen 2002; Lüdin 1938; Sedlmeier 1988
21	Kastelhöhle Nord	Switzerland	10	Magdalenian	Eriksen 2002, Sedlmeier 1988
22	Chesselgraben	Switzerland	1	Magdalenian	Eriksen 2002; Sedlmeier 1988
23	Käßloch	Switzerland	2	Magdalenian	Eriksen 2002; Stampfli 1981; Sedlmeier 1988
24	Rislisberghöhle II	Switzerland	1	Magdalenian	Eriksen 2002, Sedlmeier 1988
25	Monruz	Switzerland	7	Magdalenian	Eriksen 2002, Affolter et al. 1994
26	Grotte de Spy	Belgium	3	Gravettian	Lejeune 1987; Otte 1979
27	Goyet 3	Belgium	1	Magdalenian	Maier 2015
28	Trou de Chaleux	Belgium	1?	Magdalenian	Álvarez Fernandez 2010
29	Pincevent	France	1	Magdalenian	Vanhaeren & Lozouet 2014
30	Arcy sur Cure, Le Fees	France	2	Gravettian	Taborin 1993a; Bailloud 1955
31	Arcy sur Cure, Trilobite	France	3	Aurignacian+Magdalenian	Taborin 1993a; Bailloud 1955
32	Trou de la Mere Clochette	France	1	Aurignacian	Taborin 1993a; Bailloud 1955
33	Veyrier	France	15	Magdalenian	Taborin 1993a
34	Lag de Baille	France	1	Magdalenian	Taborin 1993a
35	Les Hoteaux	France	2	Magdalenian	Taborin 1993a

Appendix 1. Overview of Upper Palaeolithic sites with *Glycymeris* from Germany, Switzerland, Belgium, France, and Italy with numbers of *Glycymeris* and the associated technocomplexes. For some of the sites it was not possible to make a precise statement on the number of *Glycymeris*. These are marked with a "?". For some of the sites only the presence of *Glycymeris* is known. These are marked with an "X". (The majority of the listed sites from France are based on Taborin 1993a. The primary literature and the number of *Glycymeris* from these sites were not double checked in the course of this work; the corresponding references and the number of pieces can be taken from Taborin 1993a).

***Appendix 1.** Übersicht zu den jungpaläolithischen Fundstellen mit Glycymeris aus Deutschland, Schweiz, Belgien, Frankreich und Italien mit Anzahlen der Glycymeris und den zugehörigen Technokomplexen. Für einige der Fundstellen konnte keine genaue Aussage zur Anzahl der Glycymeris gemacht werden, diese sind mit einem „?" gekennzeichnet. Zu einigen der Fundstellen ist nur das Vorhandensein von Glycymeris bekannt diese sind mit einem „X" markiert. (Der Großteil der aufgeführten Fundstellen aus Frankreich stammt aus Taborin 1993a. Die Primärliteratur und die Anzahl der Glycymeris zu diesen Fundstellen wurde im Zuge dieser Arbeit nicht überprüft, entsprechende Verweise und die Anzahl der Stücke sind Taborin 1993a zu entnehmen).*

Number (on map)	Site	Country	Number of Glycymeris	Technocomplex	References
36	Pierre-Chatel les Romains	France	4	Magdalenian	Taborin 1993a
37	Grotte a Bibi	France	1	Magdalenian	Taborin 1993a
38	Balme de Glos	France	X	Magdalenian	Taborin 1993a
39	Calvaire	France	1	Magdalenian	Taborin 1993a
40	Le Colombier	France	1	Magdalenian	Taborin 1993a
41	Oullins	France	1	Magdalenian	Taborin 1993a
42	Figuier	France	X + 19	Aurignacian + Magdalenian	Vanhaeren 2006, Taborin 1933a
43	Soubeyras	France	1	Magdalenian	Taborin 1993a
44	Angle sur Anglin	France	2	Magdalenian	Taborin 1993a
45	La Marche	France	1	Magdalenian	Taborin 1993a
46	Le Chaffaud	France	2	Magdalenian	Taborin 1993a
47	Le Placard	France	54	Solutrean+Magdalenian	Taborin 1993a
48	Montgaudier	France	4	Magdalenian	Taborin 1993a
49	Roc de Sers	France	1	Solutrean	Taborin 1993a
50	Fourneau du Diable	France	1	Solutrean	Taborin 1993a
51	Rochereil	France	2	Magdalenian	Taborin 1993a
52	Raymonden-Chancelade	France	7	Magdalenian	Taborin 1993a
53	Roc de Marcamps	France	12	Magdalenian	Taborin 1993a
54	St-Germain la Riviere	France	1	Magdalenian	Taborin 1993a
55	Fontarnaud	France	2	Magdalenian	Taborin 1993a
56	Faustin	France	13	Magdalenian	Taborin 1993a
57	Badegoule	France	7	Solutrean+Magdalenian	Taborin 1993a
58	Labattut	France	2	Solutrean	Taborin 1993a
59	Longueroche	France	2	Magdalenian	Taborin 1993a
60	Le Ruth-Pages	France	1	Gravettian	Taborin 1993a
61	La Madeleine	France	6	Magdalenian	Taborin 1993a
62	Villepin	France	1	Magdalenian	Taborin 1993a
63	Laugerie-Basse	France	6	Magdalenian	Taborin 1993a
64	Laugerie Haute Est	France	3	Magdalenian	Taborin 1993a
65	Lartet	France	2	Aurignacian	Taborin 1993a
66	Roc-St-Cirq	France	1	Magdalenian	Taborin 1993a
67	Chateau des Eyzies	France	X	Magdalenian	Taborin 1993a
68	Chez-Galou	France	X	Magdalenian	Taborin 1993a
69	Cap Blanc	France	X	Magdalenian	Taborin 1993a
70	Lestruque	France	7	Magdalenian	Taborin 1993a
71	Le Soucy	France	4	Magdalenian	Taborin 1993a
72	Grotte de la Roche	France	3	Magdalenian	Taborin 1993a
73	Crozo Bastido	France	1	Magdalenian	Taborin 1993a

Appendix 1. Overview of Upper Palaeolithic sites with *Glycymeris* from Germany, Switzerland, Belgium, France, and Italy with numbers of *Glycymeris* and the associated technocomplexes. For some of the sites it was not possible to make a precise statement on the number of *Glycymeris*. These are marked with a "?". For some of the sites only the presence of *Glycymeris* is known. These are marked with an "X". (The majority of the listed sites from France are based on Taborin 1993a. The primary literature and the number of *Glycymeris* from these sites were not double checked in the course of this work; the corresponding references and the number of pieces can be taken from Taborin 1993a). (continued)

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Number (on map)	Site	Country	Number of Glycymeris	Technocomplex	References
74	Combe-Cullier	France	2	Magdalenian	Taborin 1993a
75	Murat	France	1	Magdalenian	Taborin 1993a
76	Roc de Combe	France	2	Gravettian	Taborin 1993a
77	Fontalès	France	6	Magdalenian	Taborin 1993a
78	Bruniquel	France	3	Magdalenian	Taborin 1993a
79	Canecaude	France	2	Magdalenian	Taborin 1993a
80	Tournal	France	2	Magdalenian	Taborin 1993a
81	Bize petite Grotte	France	1	Magdalenian	Taborin 1993a
82	Régismont	France	X	Aurignacian	Vanhaeren 2006
83	La Crouzade	France	2	Magdalenian	Taborin 1993a
84	Rothschild	France	1	Aurignacian	Taborin 1993a
85	Embulla	France	1	Solutrean	Taborin 1993a
86	Cauna de Bel Vis	France	4	Magdalenian	Taborin 1993a
87	La Vache C1+C2	France	3	Magdalenian	Taborin 1993a
88	Rhodes II	France	1	Magdalenian	Taborin 1993a
89	Mas D´Azil	France	12	Magdalenian	Taborin 1993a
90	Les Rideaux	France	1	Magdalenian	Taborin 1993a
91	Les Scilles	France	3	Magdalenian	Taborin 1993a
92	Gourdan	France	3	Magdalenian	Taborin 1993a
93	Lortet	France	21	Magdalenian	Taborin 1993a
94	Aurensan	France	3	Magdalenian	Taborin 1993a
95	Arudy-Espelugue	France	2	Magdalenian	Taborin 1993a
96	Isturitz I + V	France	1 + 13	Aurignacian+Magdalenian	Taborin 1993a
97	Grotte des Enfants	Italy	X	Aurignacian	Vanhaeren 2006
98	Riparo Mochi	Italy	X	Aurignacian	Vanhaeren 2006; Stiner 1999
99	Fumane	Italy	42	Aurignacian	Peresani et al. 2019
100	Riparo Tagliente	Italy	3	Epigravettian	Fontana et al. 2009
101	Cala	Italy	X	Aurignacian	Vanhaeren 2006
102	Grotta della Serratura	Italy	14	Gravettian	Martini et al. 2003
103	Cavallo	Italy	X	Aurignacian	Vanhaeren 2006

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Appendix 1. *Übersicht zu den jungpaläolithischen Fundstellen mit Glycymeris aus Deutschland, Schweiz, Belgien, Frankreich und Italien mit Anzahlen der Glycymeris und den zugehörigen Technokomplexen. Für einige der Fundstellen konnte keine genaue Aussage zur Anzahl der Glycymeris gemacht werden, diese sind mit einem „?" gekennzeichnet. Zu einigen der Fundstellen ist nur das Vorhandensein von Glycymeris bekannt diese sind mit einem „X" markiert. (Der Großteil der aufgeführten Fundstellen aus Frankreich stammt aus Taborin 1993a. Die Primärliteratur und die Anzahl der Glycymeris zu diesen Fundstellen wurde im Zuge dieser Arbeit nicht überprüft, entsprechende Verweise und die Anzahl der Stücke sind Taborin 1993a zu entnehmen). (Fortsetzung)*

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