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RESEARCH

On the Exploitation and Significance of Bivalve Shells at the Magdalenian Site of Petersfels (Southwestern Germany) Using an Integrated Approach

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Abstract
Marine shells and freshwater mollusks serve as valuable proxies for understanding cultural and environmental interactions in human history. They provide insights into past activities, exchange networks, and ecological dynamics. The site of Petersfels in Germany, rich in modified shells, offers a unique opportunity to investigate the significance of mollusk shells for the Magdalenian of central Europe. This study presents findings from our investigation of the nearly complete collection of bivalve shells recovered from the site, including 84 *Glycymeris* sp. specimens, 2 *Gryphaea arcuata*, 2 *Polymesoda* sp., and a fragment of an *Ostrea* sp. By applying qualitative and quantitative methods accompanied by a comprehensive experimental program, we sought to (1) uncover the origins and selection of the bivalves, (2) discuss modifications of shells made by anthropogenic and natural agents, and (3) elucidate aspects of their functions and symbolism. Our findings reveal that the bivalve shells were modified into ornaments. Despite taphonomic alterations affecting surface traces, we observed signs of modification such as flat facets featuring parallel striations produced by abrasion, signs of prolonged use and reuse, and a perforation technique consistent with sawing. Double-perforated shells indicate a willingness to reuse them after the first perforation wears down. The two fossil specimens of *Gryphaea arcuata* and the fragment of an oyster were instead perforated by drilling. The entire sample showed rounded and smooth perforations and evidence of plastic deformations, hinge thinning, and worn facets resulting from extended use. The evidence of reusing shells and their extended lifespan highlights their significance in the symbolic and artistic expressions of the Magdalenian groups, reflecting the complex social and symbolic communication among these prehistoric communities.

Keywords Bivalve shells · Ornaments · Magdalenian · Petersfels · Use-wear analysis · Multivariate statistical analysis

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Introduction

Mollusk shells derived from marine or freshwater environments, fossilized or natural, have been collected and utilized since the earliest stages of human history (Bar-Yosef, 2005; Joordens et al., 2015; Baysal, 2019).

The earliest archaeological evidence suggests that mollusks primarily served as a food source (Marean et al., 2007) before mollusk shells were adapted into tools by early hominins, although the transition may have co-occurred. An engraved shell tool discovered at Trinil (Java, Indonesia), dated to at least 400,000 years ago, was associated with *Homo erectus* and accompanied by evidence of freshwater shellfish consumption (Joordens et al., 2015). The exploitation of aquatic resources likely played an essential role in the nutritional advancements necessary for the development of the uniquely large and complex human brain, highlighting the importance of diverse food sources in human evolution (Broadhurst et al., 1998; Klein & Bird, 2016; Parkington, 2010; Will et al., 2022).

The varied shapes, colors, and textures of mollusk shells, along with their practicality, quickly captured the attention of humans, leading them to collect and utilize these natural resources for functional purposes (Zilhão et al., 2010; Hoffman et al., 2018). At the Mousterian level L in Grotta del Cavallo, Italy, fragments of *Callista chione* were knapped and modified using Quina technology, demonstrating the Neanderthals' capacity to adapt to diverse environmental conditions (Romagnoli et al., 2016). This innovative behavior has also been identified at multiple Paleolithic sites along the Mediterranean coast (Douka, 2011; Douka & Spinapolice, 2012). Evidence from sites such as Blombos Cave in South Africa (Henshilwood & Dubreuil, 2011) and Upper Paleolithic locations in Europe (de Beaune, 1987; Conard, 2003; Vanhaeren & Lozouet, 2014; Zilhão et al., 2010) indicates that shells also served as containers for mixing pigments.

The emergence of *Homo sapiens* in Africa (Hublin et al., 2017) marked a pivotal moment when shells began to acquire new significance as a means of self-expression and a way to convey individuality. This behavior has come to be regarded as a defining characteristic of modern human behavior (Kuhn & Stiner, 2006; Bednarik, 2008; Cattelain, 2012; Bar-Yosef Mayer, 2020). Evidence indicates that the intentional selection and collection of marine mollusk shells for non-utilitarian purposes first occurred at Misliya Cave in Israel and Pinnacle Point in South Africa, dating back to between 240,000 and 160,000 years ago and around 160,000 years ago, respectively (Bar-Yosef Mayer, 2020; Jerardino & Marean, 2010).

In contrast, modified shells featuring one or more perforations have been discovered in Middle Paleolithic and Middle Stone Age sites throughout the Levant and in North and South Africa. These artifacts date back approximately 140,000 to 70,000 years ago, coinciding with the emergence of anatomically modern humans in Africa and their subsequent migration into Europe (Bar-Yosef Mayer & Hayes, 1989; d'Errico et al., 2005; Bar-Yosef Mayer, 2005; Bouzouggar et al., 2007; d'Errico et al., 2009, 2008; Bar-Yosef Mayer et al., 2009; Zilhão et al., 2010; Henshilwood & Dubreuil, 2011; Vanhaeren et al., 2013; d'Errico et al., 2015; d'Errico & Beckwell, 2016; Hoffmann et al., 2018; Steele et al., 2019; Ekshtain et al., 2019; Sehasseh et al., 2021).

Since the Upper Paleolithic, humans have increasingly utilized marine shells, diversifying the forms and species employed (*e.g.*, Taborin, 1993; Stiner, 1999; Henshilwood & Dubreuil, 2011; Vanhaeren & d'Errico, 2006; Stiner et al., 2013; Vanhaeren et al., 2019). Nevertheless, archaeological research has historically given little attention to personal ornaments, particularly in the early to mid-twentieth century (Abadía & Nowell, 2015; Erlandson, 2001; Baysal, 2019). However, with the advent of the *châine opératoire* concept in the study of lithic technology, scholars have begun to explore prehistoric ornaments from new perspectives, investigating their technological, symbolic, evolutionary, and cognitive dimensions (Abadía & Nowell, 2015).

The way humans create and utilize ornamental objects is intricately linked to the properties of the raw materials. Factors such as texture, shape, and hardness significantly influence the workability of these materials, subsequently determining the gestures and techniques required for modification. Some shells have natural shapes that are inherently suitable for use without modification. In contrast, others may have inspired our ancestors to adopt them as pendants in their earliest stages, mainly due to the presence of natural perforations (Bar-Yosef Mayer et al., 2020).

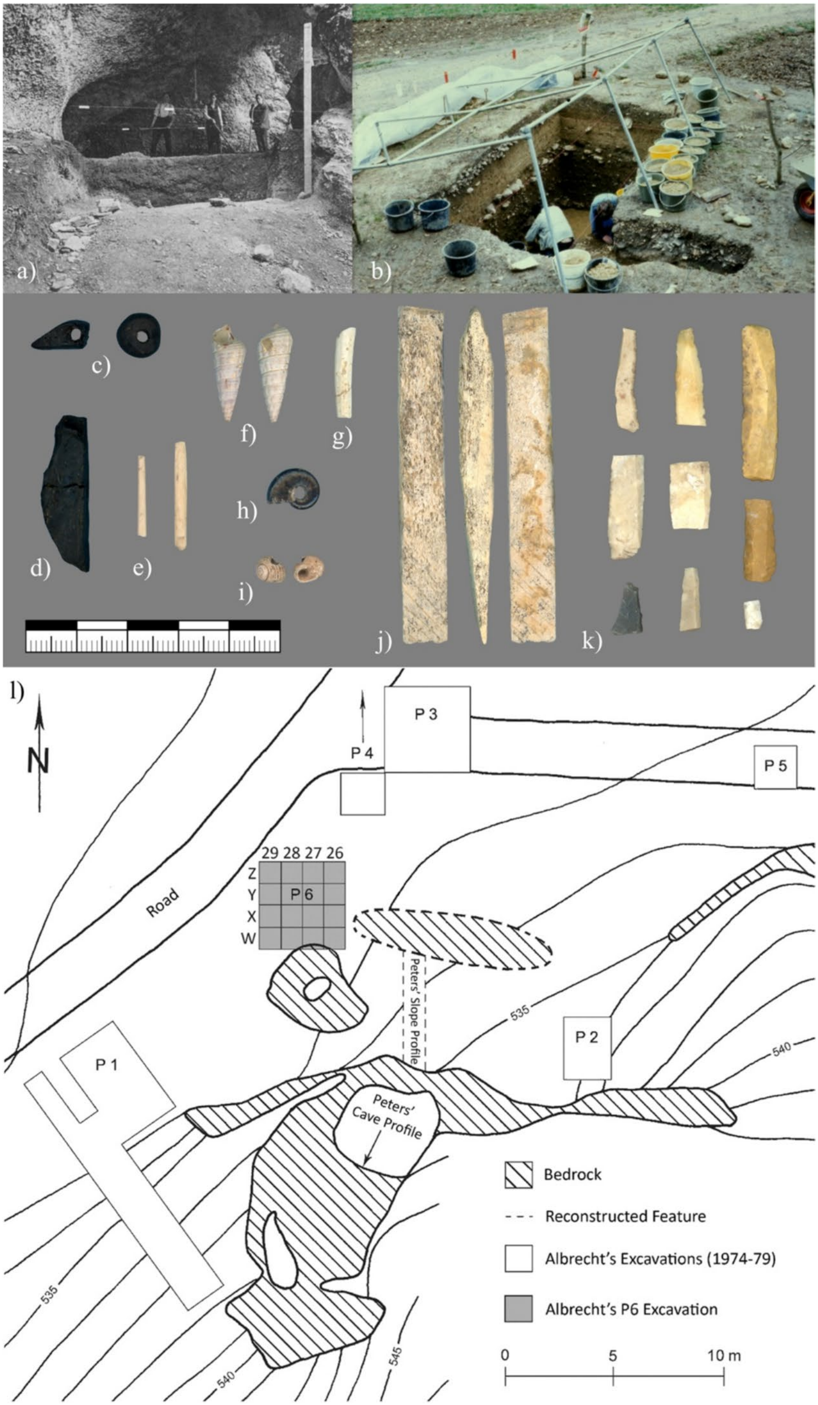
Hominis frequently utilized various shell species, including *Tritia* sp*., Columbella rustica, Mitrella scripta, Dentalium* sp., *and Glycymeris* sp., (*e.g.*, Vanhaeren & d'Errico, 2001; Tátá et al., 2014; Arrighi et al., 2020; Soler-Mayor et al., 2025). Among these, *Tritia* sp. and *Columbella rustica* have particularly attracted considerable scholarly interest (*e.g.*, Vanhaeren et al., 2006; Cristiani et al., 2020; Hoareau, & Beyries, 2022; d'Errico et al., 2005, 2009, 2015; Pescaux, 2017; Bar-Yosef Mayer, 2015; Bosch et al., 2023; Gazzo et al., 2025). Although bivalve shells like *Glycymeris* and *Veneridae* were prevalent during prehistoric times, there is a scarcity of comprehensive archaeological case studies focused on their methods of perforation and suspension (but see Taborin, 1993; d'Errico et al., 1993; Cabral & Monteiro-Rodrigues, 2015; Wei et al., 2016; Bar-Yosef Mayer et al., 2020; Schürch et al., 2021). Given the influence of bivalve species and shell morphology on perforation methods, a reference collection is crucial before analyzing and interpreting archaeological samples.

This study aims to establish a comprehensive reference collection of perforated bivalve shells, particularly those of *Glycymeris*, to investigate the variations in technological and use-wear traces resulting from different perforation techniques and binding methods over a controlled period. The findings from this experimentation will serve as a benchmark for examining a significant assemblage of bivalve shells discovered at the Magdalenian site of Petersfels in Southern Germany. The significance of these bivalve shells at Petersfels extends beyond their practical applications; they also held considerable cultural and symbolic value. By understanding how these shells were exploited and processed, we can gain valuable insights into the practices, cultural traditions, and interactions of the Magdalenian in Central Europe during the late Upper Paleolithic.

Fig. 1 Petersfels excavation and artifacts from different campaigns: **a** excavation in the Petersfels Cave between 1927 and 1928 (Photo: Peters, 1930), **b** excavation outside of the cave in trench P3 in 1975 (Photo: G. Albrecht), **c** jet pendants, **d** half-finished and broken female jet figurine, **e** needle fragments, **f** *Granulolabium plicatum*, **h** fossile ammonite, **i** *Homalopoma sanguineum*, **j** Point with double beveled base, **k** backed bladelets, **l** map of formal excavation (Photos: Q. Schäfer, B. Schürch; site plan modified after: McCartin et al., 2023 and Pfeifer, 2016)

Personal Ornaments in the Magdalenian and the Case Study of Petersfels

Petersfels was first excavated in 1927 by Eduard Peters, with the excavation continuing until 1932 (Fig. 1a). Unfortunately, much of his documentation was lost or destroyed during World War II. The best sources regarding the excavation can be found in Peters' publications (Peters, 1930, 1932) as well as in the critical examination conducted by Mauser (Mauser, 1970). Peters focused his efforts on the cave and parts of the terrace. Within the cave, he excavated in 5 cm spits (Mauser, 1970) and did not sieve the sediments; instead, he spread them out on a large canvas (Segeltuchplane) to uncover smaller artifacts (Albrecht, 1979; Albrecht & Hahn, 1991). The backdirt from Peters' excavations was later investigated by Albrecht (Albrecht & Hahn, 1991; Albrecht, 1974, 1979), who also excavated 22 square meters in various areas around the cave from 1974 to 1979 (Fig. 1b and l; Albrecht, 1979; Albrecht & Hahn, 1991). Additional excavations were conducted at the site by Schiele in the 1960 s and by Reinerth in the 1970 s (Albrecht et al., 1994). The overwhelming majority of artifacts from all excavations can be attributed to the Magdalenian (Albrecht, 1979; Albrecht & Hahn, 1991; Albrecht et al., 1994; Mauser, 1970; Peters, 1932). While artifacts from a Holocene context are also present, they are notably less abundant (Albrecht et al., 1994). Not all excavations at the site have been thoroughly analyzed in conjunction, prompting Albrecht and Hahn to project the total number of artifacts. They estimated that the site likely produced around 60,000 backed bladelets along with 9,000 needles and needle fragments (Figs. 1e, k). By focusing on these two categories of artifacts, it becomes evident that Petersfels stands out as one of the most significant Magdalenian sites in Europe (Mauser, 1970). The conventional radiocarbon dates from Albrecht's excavations indicate that the Magdalenian at this site spans from 16,000 to 13,500 calibrated years before the present (Jaguttis-Emden, 1983). Additionally, it is important to mention the female figurines of the Gönnerdesdorf type (Bosinski & Fischer, 1974), made from jet and suitable for use as pendants (Figs. 1c-d; Albrecht, 1979), as well as the extensive assemblage of antler and bone artifacts (Fig. 1j, Pfeifer, 2016). Other personal ornaments from Petersfels include a large variety of perforated animal teeth, perforated disks, fossil shark teeth, perforated stone, and one ochre pendant (Mauser, 1970; Peters, 1930; Wolf, 2019). Especially the use of jet (Peschaux & Ligouis, 2023; Wolf, 2019) and the increased number of personal ornaments made from mollusk shells (Rähle, 1983, 1994) are typical of the Magdalenian in Southern Germany (Figs. 1c,f-i), as well as the low frequency of ivory as a raw material for personal ornaments (Münzel et al., 2017; Wolf, 2015, 2019; Dutkiewicz et al., 2018), which was preferred during the Aurignacian and Gravettian periods (Wolf, 2019).


a)
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Peters' Slope Profile
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P 2
540
P 1
Peters' Cave Profile
Bedrock
Reconstructed Feature
Albrecht's Excavations (1974-79)
Albrecht's P6 Excavation
535
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The malacofaunal assemblage from Petersfels consists of a minimum of 248 shells of different types: bivalves, gastropods, scaphoids, and ammonites and other fossils from Jurassic formations. Previous studies of the shells from Petersfels were primarily conducted by Rähle (Rähle, 1983, 1994), with more recent analyses carried out by Eriksen (Eriksen, 2002) and Schürch (Schürch et al., 2023). These analyses demonstrated the abundance of shells in the Petersfels assemblage. Rähle (1994) presented 108 shells of 15 species, Eriksen (2002) presented 248 shells of 22 species, and Schürch et al., (2023) presented and analyzed 113 *Glycymeris* shells from Petersfels (the numbers vary depending on which excavation campaigns and species are included in the analyses).

In this project, we focus on the bivalves, because the site is rich in this class of shells.

According to our knowledge and based on the published literature, a minimum of 120 complete and fragmented bivalve shells have been found at the site. Due to the research history, the bivalves recovered at Petersfels originated from various excavations and are housed in different museums, thus limiting access to some specimens for microscopical analysis at the Material Cultural Laboratory (hereafter MCL) at the University of Tübingen. The bivalves addressed in this study represent the shells available to the authors at the current state of the analysis. Six *Glycymeris* from the Schiele excavation stored at the Pfahlbaumuseum Unteruhldingen and 8 *Glycymeris* from the Peters excavation housed at the Landesmuseum Karlsruhe were not studied and were not analyzed in detail.

Materials and Methods

In 2023, Schürch & colleagues (2023) published the findings of a taxonomical assessment and biometric analysis of 113 *Glycymeris* shells from Petersfels. This analysis included measurements of length, width, thickness, weight, state of preservation, presence, and type of perforation, and macroscopically visible red pigment traces. Additionally, a smaller sample of 12 complete and fragmented *Glycymeris* shells was examined as part of a pilot microscopic investigation into production and use-related traces. The promising preliminary results and the integrity of the specimens motivated us to expand the sample size and plan a more detailed functional and biometric analysis supported by a comprehensive experimental reference collection.

This study encompasses a microscopic examination of the remaining portion of the sample, incorporating an additional three bivalve species discovered at the site. The sample presented includes 84 complete and fragmented bivalves belonging to the species *Glycymeris* sp., two complete *Polymesoda subarata subarata,* two complete *Gryphaea arcuata*, and one fragment of *Ostrea* sp., for a total of 89 specimens (Fig. 2). The shells studied all come from the Peters excavation (Peters, 1930, 1932; Rähle, 1983, 1994) and are stored and curated at the Archaeological Hegau-Museum in Singen. All shells mentioned in the text are identified by their ID number.

In this study, we focus on interpreting microscopic evidence that may indicate the production method for the shell perforations found at Petersfels and assessing

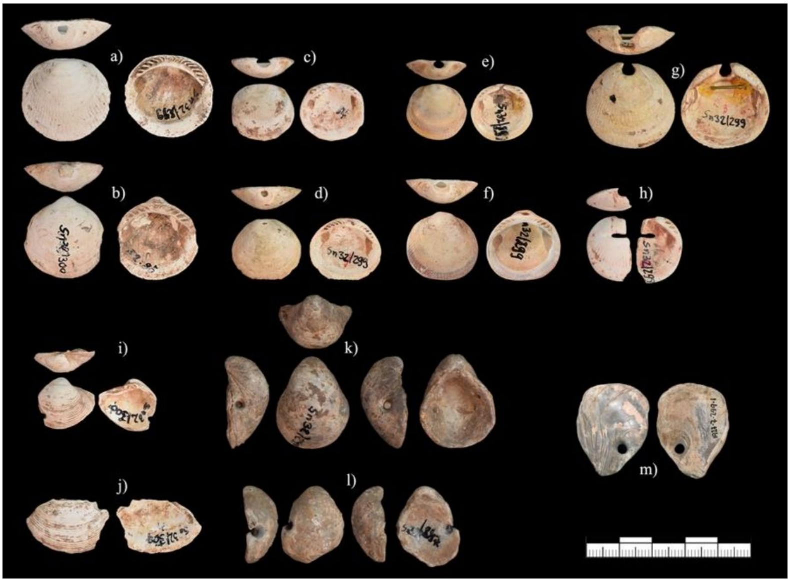

Fig. 2 Overview of a selection of analyzed shells and indication of their state of preservation. **a**–**h**) *Glycymeris* sp.: **a**–**b** fossil or poor surface preservation; **c**–**d**, **g**), **h**) intermediate surface preservation; **e**–**f**) fresh with decent surface preservation; **a**, **c**–**f** single perforation; **g**, **h** double perforation, **b** not perforated); **i**, **j** *Polymesoda subarata subarata*: **i** not perforated, **j** likely perforated. but not preserved); **k**, **l**. *Gryphaea arcuata* **k** double perforated, **l** single perforation; **m** *Ostrea* sp. (ID's: **a**) 40, **b**) 60, **c**) 106, **d**) 108, **e**) 53, **f**) 46, **g**) 56, **h**) 114, **i**) 116, **j**) 112, **k**) 128, **l**) 127, **m**) **1**; Photos: B. Schürch)

whether these shells were ultimately utilized as adornments. Most *Glycymeris* specimens are intact, consisting of 42 complete or worn (semi-complete) perforations and 17 non-perforated shells, while 22 have broken holes. Fragments without perforations ($n=3$), like pieces of the rim or valve, were counted but not analyzed microscopically.

The shells were comprehensively analyzed using qualitative and quantitative approaches. We incorporated metrical, statistical, technological, and functional analyses along with a comprehensive experimental program to investigate their production, function, and statistical relationships.

We employed a rigorous analytical approach to determine the origin of the perforations in the Petersfels *Glycymeris* shells, whether they were caused by abrasion or occurred naturally. We conducted a comprehensive 2D shape outline analysis complemented by metric measurements and multivariate statistical methods. We utilized a Hirox HRX-01 3D digital microscope set at a consistent ×20 magnification to record the length, width, area, and perimeter of the perforations. This enabled us to capture both experimentally abraded perforations and intact or nearly complete archaeological ones. Additionally, we included a set of modern shells with naturally occurring perforations to compare and analyze metric and shape variations among the three groups.

For the shape analysis, we applied Elliptic Fourier Analysis (EFA; Rohlf, 1990) to the 2D outlines of the perforations extracted from high-resolution images using

DiaOutline software (Wishkerman & Hamilton, 2018). The raw 2D coordinates were processed and analyzed in R (Posit Team, 2023; R Core Team, 2023) using the *Momocs* package (Bonhomme et al., 2014), following standard procedures in the field (Falcucci et al., 2024; Leplongeon et al., 2020; Matzig et al., 2021). Before EFA, we standardized the outlines by centering, scaling, and rotating them. EFA was performed with harmonics capturing 99.9% of cumulative harmonic power ($n=41$). Subsequently, we conducted Principal Component Analysis (PCA) to explore shape variability across the dataset, categorizing perforations into archaeological ($n=46$), experimental ($n=40$), and natural ($n=31$) groups. The group of archaeological perforations includes three *Glycymeris (*ID 13, 17, 25*)* with complete holes, which were previously microscopically studied and published in Schürch et al. (2023); these are not listed in this study. Natural perforations were all recorded at the umbo and caused by marine abrasion, while experimental perforations were all made by abrasion.

To investigate the relationship between size and shape, we conducted an additional PCA using the main Principal Components (PCs) derived from the 2DGM analysis ($n=3$), along with area (in mm2) and diameter (in mm) measurements obtained from the 3D digital microscope. We used the *FactoMineR* (Lê et al., 2008) and *factoextra* (Kassambara & Mundt, 2020) packages to accomplish this. Finally, we conducted disparity tests (Guillerme, 2018) to quantify morphological and metric variations across archaeological, experimental, and natural perforations, bootstrapping the PCA data 1000 times as per Matzig et al. (2021). The dataset, R script, and the 2D coordinates of the perforations are available in the associated Zenodo repository (Venditti et al., 2025).

Subsequently, we examined the specimens under microscopes to identify any traces associated with their production and use. We followed the protocol established by Schürch *et al*. (2023).

For macro-scale observations, we looked for signs of rounding, abrasion, pitting, scarring, and plastic deformations using an Olympus SZX7 microscope, which offers magnification from 8×to 56×with 10×eyepieces and a LED ring light source. Additionally, we utilized the Hirox HRX-01 digital microscope, which covers a magnification range of 20×to 2,500x. Microscale observations, including polish, abrasion, striations, grooves, and pitting, were conducted using an Olympus BX53M metallographic microscope operating in reflected light, paired with×10 eyepieces and×5,×10,×20, and×50 objectives. The characterization of macro and microscopic wear attributes relies on the wear patterns observed on chipped (Van Gijn, 1990) and macro lithic tools (Adams et al., 2009). Other researchers have also adopted this framework for analyzing microwear on shell (Lammers-Keijsers, 2008; Bar-Yosef Mayer et al., 2020).

The archaeological material was tested against a reference collection of naturally and anthropically perforated bivalves (*Glycymeris glycymeris*) sourced from modern thanatocoenoses along the Mediterranean coasts (fresh mollusks) and from the Mainz Basin (fossil *Glycymeris subterebratularis* (planicostalis)). The shell species and shell preservation were identified with the assistance of malacologist R. Janssen, using the reference collection from the malacological comparison collection at the Senckenberg Institute in Frankfurt. We also utilized the reference collection of fossil bivalve shells from the Mainz Basin and fresh bivalve shells from the Mediterranean, housed at the MCL at the University of Tübingen. Additionally, we reviewed the literature on fossil and modern specimens of *Glycymeris* (Taborin, 1993; Schäfer, 2012; Nolf & Swinnen, 2013).

Given that most of the Petersfels sample consisted of *Glycymeris* shells, our experiments focused solely on this group of bivalves. The experimental program outlined here builds upon and enhances the preliminary results discussed by Schürch et al. (2023) which also included pieces from the Albrecht excavation (Albrecht, 1979). Further comparisons were conducted with the existing published literature on the production and use of bodily ornaments, mainly focusing on bivalves (Taborin, 1993; d'Errico et al., 1993; Berganza et al., 2012; Wei et al., 2016; Pescaux, 2017; Falci et al., 2019; Laporte et al., 2021; Gazzo et al., 2025). The microscopic analysis of experimental and archaeological materials, as well as the execution of the experiments, was conducted at the MCL of the University of Tübingen.

The Experimental Program

Analyzing shells presents challenges when investigating wear traces. The intricate lamellar microstructure of shells varies by type, and their shiny, reflective, and naturally polished surfaces can complicate trace observation under microscopic lenses (Cuenca-Solana et al., 2017). Furthermore, throughout their lives, shells undergo various taphonomic processes during deposition and post-archaeological recovery. Modifications such as perforation, biodegradation, concretion, abrasion, and fragmentation can impact the shells' integrity, potentially mimicking or obscuring genuine wear traces (Cabral & Martins, 2016; Driscoll, 1967). In addition, the development and analysis of manufacture and use-related traces are influenced by many factors, including production techniques, duration of use, patterns of wear, and the types of binding materials employed.

These factors often interact in complex ways, complicating the analytical processes and interpretations. Understanding these interrelated factors is crucial for comprehensively assessing the artifacts in question. Thus, distinguishing between natural and anthropogenic evidence is essential to interpret the archaeological material accurately. This necessitates a comprehensive reference collection and a multifaceted experimental approach.

The supplementary information details the experimental protocol, and below, we present a summary of the key findings.

Results of the Experimentation

The findings from our extensive experimental program have demonstrated that *Glycymeris* shells can be effortlessly transformed into decorative pieces, such as pendants, or integrated into clothing as embellishments. Abrasion is the most effective and rapid method for creating a perforation in this shell type. Fresh specimens can be processed in just a few minutes, while shells with natural perforations can be used without modification. Abrasion-based perforation leaves distinctive and

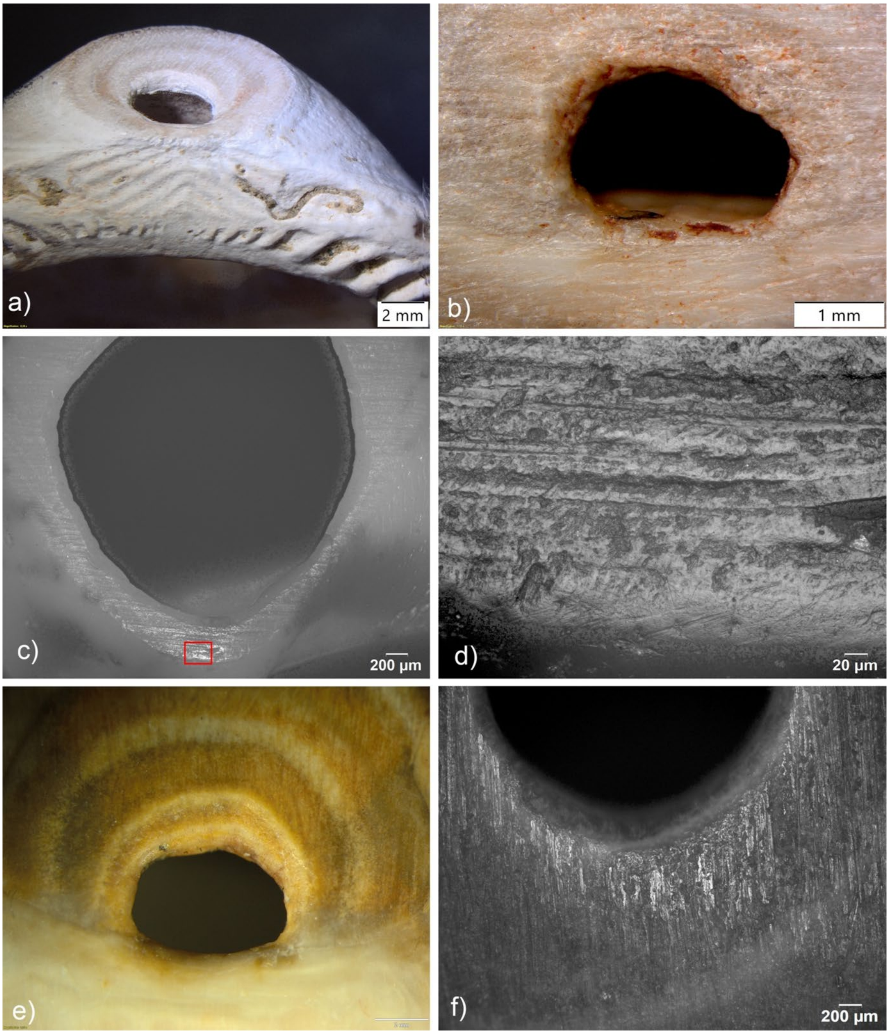

Fig. 3 Major production and use-related traces observed on the experimental *Glycymeris*. **a** shell 170, a flat 90 degree facet on the umbo with parallel striations due to abrasion on a coarse grain size sandstone; **b** shell ID 167, smoothing and rounding of the hole after rotating a leather strand with ochre for 60 min (see Fig. S12 for comparison with the pre-use picture); **c** Exp #151, use-related polish to the attachment area near the hinge on a shell worn as an earring that is loosely tied and assembled with another shell using sinew strings treated with fat; **d** close-up of red box in **c**) showing the polished hinge with striations; **e** Exp #165, smoothing and rounding, along with the onset of plastic deformation at the bottom of the hole on a *Glycymeris* shell, sewn with a tanned leather string to a leather skirt for 245 h (see Fig. S12 for comparison with the pre-use picture); **f** shell ID 184; overlap between manufacturing traces caused by abrasion on a medium grain size sandstone and use traces from continuously rubbing inside and outside a leather strand in the perforation (Micrographs: F. Venditti)

recognizable marks, featuring a flat facet with parallel striations on the umbo (Figs. 3a,b; S1a-d; S2e-f). Although sawing and drilling techniques are also effective for bivalves, achieving perforation requires specialized tools—such as a sharp blade, a pointed tool, or a drill—and demands more energy and time, particularly for fossil specimens (Figs. S1e and S2a).

Wearing the shells results in characteristic macro and microwear patterns in the attachment area (Figs. S6, S7, S8). Wear, such as polishing and striations, occurs due to the friction caused by the strings passing through the perforation. Several factors influence the development and distribution of string wear on the shells, including the positioning of the strings, the tension applied through the hole, whether the shells are freely assembled or static, their weight, and the thickness and material composition of the strings used. We observed the following: (1) macroscopic rounding, smoothing, and widening of the perforations (Figs. 3b, e and S3); (2) the formation of polish and micro rounding and smoothing in the attachment area (Figs. 3c, d, f and S4); (3) the presence of striations on the smoothest aspect of the polish (Fig. 3d); (4) plastic deformations (Fig. 3e); and (5) an overlap between technological and use-wear traces (Figs. 3f and S5). The erasure and superimposition of manufacturing and use traces are evident on shells perforated by abrasion, where the use-related polish displays a linear topography reflecting the striations of the abrasive sandstone (Fig. 3f).

In our replicative experiments, we observed that the duration of wear impacts polish development; however, it is not the only factor influencing this process. Notably, shells arranged together and subjected to the same treatment for the same period showed different levels of use-wear. This variation complicates the reconstruction of attachment systems and the interpretation of a collection of shells as parts of a single bodily ornament (*e.g.*, necklace, bracelet, anklet), especially in archaeological contexts. Different levels of use-wear on elements of the same ornament were also noted by Falci & colleagues (2019), who studied microwear on various bodily ornaments from ethnographic collections.

Results

Glycymeris

Origin and Taphonomy

A re-examination of the shells has revealed significant alterations in the *Glycymeris* assemblage. In some instances, poor surface preservation hindered accurate classification into specific groups (fossil or fresh specimens) and made species identification impossible. However, we identified a predominance of fresh or semi-fresh specimens, although fossil ones are also present. In Fig. 2, (a) and (b) depict fossil or poorly preserved *Glycymeris* examples, (c) and (d) represent intermediate examples, and (e) and (f) are recent specimens. We observed pre-depositional alterations on fresh shells caused by marine abrasion, resulting in the smoothing and rounding of natural surface patterns, particularly around the valve's perimeter and hinge (Fig. 4a). Additionally, bioerosion from drilling

Fig. 4 Pre- and post-depositional modification on *Glycymeris* from Petersfels. **a** rounding of the shell's outline (shell 61); **b** predator drilling (shell 109); **c–d** erosion on fossil *Glycymeris* (shells 99 and 63); **e** scratched flat faceted umbo (shell 49) (Micrographs: F. Venditti)

predators was noted on one shell (Fig. 4b). Fossil specimens showed decalcification, resulting in the loss of their original pigmentation and natural surface patterns, which gave the valve a dull appearance (Figs. 4c–d). Furthermore, post-depositional alterations, such as fragmentation and mechanical or chemical modifications, have undoubtedly impacted the *Glycymeris* assemblage after their abandonment. This is supported by the limited presence of microwear observed, despite evidence of prolonged use. However, tracing the underlying taphonomic processes is challenging, given the difficulty in accurately assigning most shells to their excavation locations (trenches and pits inside or outside the cave and backdirt).

Alongside the taphonomic alterations, 22 shells in the museum collections exhibited traces of modern glue inside their perforations, which resulted from mounting them in the museum and interfered with observation at high magnification.

Regarding the provenance of the *Glycymeris*, it is likely that the recent specimens originated from the Mediterranean or Atlantic sea, approximately 380 km away. In contrast, the fossil specimens can be found in the Mainz basin (*e.g.*, *Granulolabium plicatum* or *Polymesoda subarata subarata*, as shown in Fig. 1f and Fig. 2i–j), with a minimum transport distance of about 230 km.

Technological and Morphometric Analysis

We categorized the 84 Glycymeris shells analyzed into five groups based on their integrity (Table 1).

- Group 1 consists of entire or fragments of shells with preserved perforations ($N=35$)
- Group 2 includes complete shells with worn perforations at the lower part of the holes adjacent to the hinge ($N=7$)
- Group 3 encompasses shell fragments that have broken holes ($N=22$)
- Group 4 consists of complete shells that show no modifications ($N=17$)
- Group 5 includes fragments of valves or rims ($N=3$).

Except for 11 shells deemed non-diagnostic for microscopic analysis, all shells in groups 1, 2, 3, and 4 were examined at low and high magnifications, while group 5 was not investigated microscopically.

Overall, the perforations in the sample display a consistent outline. They are predominantly characterized by symmetric holes that are either subcircular or elliptical. The interior and exterior walls of the perforations are regular and smooth (Fig. 5a, b).

In Schürch et al. (2023), the authors presented six perforated shells with no visible macro or microscopic wear on the umbo, such as flat facets, conical sections, or drilling traces. When viewed in the sagittal plane, these shells maintain the natural convexity of the umbo in the upper part of the perforation. In this study, we identified an additional five perforated shells that share the same characteristics: they have smooth, subcircular perforations with regular walls and show no evidence of anthropogenic modifications at either macro or micro scales (Fig. 5a, b).

Instead, most of the analyzed shells—specifically, 41 specimens—shared a notable characteristic: a relatively flat, 90-degree facet at the umbo (Fig. 5c). Four specimens exhibited visible parallel striations on their facets (Fig. 5d–g). Notably, shells numbered 52 and 83 displayed identical trace patterns (Figs. 5d-e). Our observations revealed flat facets at the umbo, accompanied by bands of varying widths and depths, long and short parallel striations oriented obliquely or perpendicularly to the longitudinal axis of the shells. In both instances, the linear features were

Table 1 List of *Glycymeris* shells analyzed in this study, along with related documentation of the perforations

Progressive number	ID	Shell's species and state of preservation	Integrity	Alteration	Perforations	Macrowear on perforation	Microwear on perforation
1	40	*Glycymeris* fossil	Complete	Rounding, discoloration	Single, intact	90-degrees flat facet, deformations and thinning of the lower rim, rounded walls, possibly drilling traces	/
2	41	*Glycymeris* fossil	Complete	Rounding, discoloration	Not-perforated	/	/
3	42	*Glycymeris* ?	Complete	Rounding, discoloration	Not-perforated	/	/
4	43	*Glycymeris* fossil	Complete	Rounding, discoloration	Not-perforated	/	/
5	44	*Glycymeris* ?	Complete	Rounding, discoloration	Single, intact	90-degrees flat facet, rounding	/
6	45	*Glycymeris* fresh	Complete	Rounding, discoloration	Single, intact	/	/
7	46	*Glycymeris* fresh	Complete		Single, intact	90-degrees flat facet, deformations and thinning of the lower rim, rounding of the inner walls	Use-related polish inner rim, patchy polish with striations
8	47	*Glycymeris* ?	Complete	Rounding, discoloration, corrosion	Not-perforated	/	/
9	48	*Glycymeris* ?	Complete	Rounding, discoloration,	Single, intact	90-degrees flat facet, rounding of the inner walls	/

Table 1 (continued)

Progressive number	ID	Shell's species and state of preservation	Integrity	Alteration	Perforations	Macrowear on perforation	Microwear on perforation
10	49	*Glycymeris* fresh	Complete	Rounding, discoloration, striations	Single, intact	90-degrees flat polished facet, smoothing and rounding of the inner walls, deformation of the lower rim	Weak polish on the rim
11	50	*Glycymeris* ?	Complete	rounding, discoloration	Single, intact	90-degrees flat facet, rounding of the walls	/
12	51	*Glycymeris* fresh	Complete	Rounding, discoloration	Single, intact	90-degrees flat facet, rounding and smoothing of the walls, deformation of the lower rim	/
13	52	*Glycymeris* fresh	Complete	Rounding	Single, intact	90-degrees flat facet with oblique striations, hollowed facet on the inner wall, off-set deformation of the lower rim	Polished rim with striations
14	53	*Glycymeris* fresh	Complete	Rounding	Single, worn out	90-degrees flat polished facet with oblique striations,	Striations, polished inner rim
15	54	*Glycymeris* fresh	Complete	Rounding,	Single, intact	90-degrees flat facet	/
16	55	*Glycymeris* fresh	Complete	Rounding, shiny valve	Single, broken	90-degrees flat facet, smoothing and rounding of the inner walls,	Striations
17	56	*Glycymeris* ?	Complete	Rounding, discoloration	Double, worn out	/	/

Table 1 (continued)

Progressive number	ID	Shell's species and state of preservation	Integrity	Alteration	Perforations	Macrowear on perforation	Microwear on perforation
18	57	*Glycymeris* fossil	Complete	Rounding, discoloration, eroded umbo	Not-perforated	/	/
19	58	*Glycymeris* ?	Complete	Rounding, discoloration,	Single, intact	90-degrees flat facet, hollowed facet on the lower rim	/
20	60	*Glycymeris* ?	Complete	Rounding, discoloration	Not-perforated	/	/
21	61	*Glycymeris* ?	Fragment	Rounding, discoloration	Single, broken	/	/
22	62	*Glycymeris* ?	Complete	Rounding, discoloration	Single, intact	90-degrees flat facet, smoothing and rounding of the inner walls, deformation and polished lower rim	/
23	63	*Glycymeris* ?	Complete	Rounding, discoloration, eroded umbo	Not-perforated	/	/
24	64	*Glycymeris?*	Complete	Rounding, discoloration,	Not-perforated	/	/
25	65	*Glycymeris* ?	Complete	Rounding, discoloration	Single, intact	90-degrees flat facet, rounding of the inner walls	/
26	66	*Glycymeris* fresh	Complete	Rounding, discoloration	Single, intact	90-degrees flat facet, rounding of the inner walls	
27	67	*Glycymeris*?	Complete	Rounding, discoloration	Single, worn out	90-degrees flat facet, slight rounding of the inner walls	/

Table 1 (continued)

Progressive number	ID	Shell's species and state of preservation	Integrity	Alteration	Perforations	Macrowear on perforation	Microwear on perforation
28	68	*Glycymeris* ?	Complete	Rounding, discoloration	Single, intact	90-degrees flat facet, slightly deformed toward the rim	Parch of use-related polish on the rim
29	69	*Glycymeris* fresh	Complete	Rounding, less discoloration	Single, intact	90-degrees flat facet, smoothing and rounding of the inner lower rim,	Polish and striations on the facet
30	70	*Glycymeris* fresh	Complete	Rounding, discoloration	Single, intact	90-degrees flat facet, rounding of the inner lower wall,	/
31	71	*Glycymeris* ?	Complete	Rounding, discoloration	Single, worn out	90-degrees flat facet	/
32	72	*Glycymeris* ?	Fragment	Rounding, discoloration	Single, broken	/	/
33	73	*Glycymeris* fresh	Complete	Rounding, discoloration	Single, intact	90-degrees flat facet, smoothing and rounding of the inner lower wall, deformations and thinning of the lower rim	/
34	74	*Glycymeris* fresh	Complete	Rounding, discoloration	Single, broken	90-degrees flat facet	/
35	75	*Glycymeris* fresh	Complete	Rounding, discoloration, exfoliation	Single, worn out	/ likely natural perforation	/
36	76	*Glycymeris* fresh	Complete	Rounding, discoloration	Not-perforated	/	/
37	77	*Glycymeris* ?	Complete	Rounding, discoloration	Single, intact	90-degrees flat facet, smoothing and rounding of the inner lower rim	/

Table 1 (continued)

Progressive number	ID	Shell's species and state of preservation	Integrity	Alteration	Perforations	Macrowear on perforation	Microwear on perforation
38	78	*Glycymeris* ?	Complete	Rounding, discoloration	Not-perforated	/	/
39	79	*Glycymeris*?	Complete	Rounding, discoloration	Single, broken	/	/
40	80	*Glycymeris* ?	Complete	Rounding, discoloration	Not-perforated	/	/
41	81	*Glycymeris* ?	Complete	Rounding, discoloration	Single, intact	90-degrees flat facet, smoothing and rounding of the inner lower rim	/
42	82	*Glycymeris* ?	Complete	Rounding, discoloration	Not-perforated	/	/
43	83	*Glycymeris* fresh	Complete	Rounding, discoloration	Single, intact	90-degrees flat facet with oblique striations, rounding of the walls	Use-related patch of polish on the facet
44	84	*Glycymeris* ?	Complete	Rounding, discoloration	Not-perforated	/	/
45	85	*Glycymeris* ?	Complete	Rounding, discoloration	Not-perforated	/	/
46	86	*Glycymeris* fresh	Complete	Rounding, less discoloration	Single, intact	90-degrees flat facet	/
47	87	*Glycymeris* ?	Complete	Rounding, discoloration	Single, intact	90-degrees flat facet, rounding and smoothing of the inner walls, extreme thinning of the rim	/

Table 1 (continued)

Progressive number	ID	Shell's species and state of preservation	Integrity	Alteration	Perforations	Macrowear on perforation	Microwear on perforation
48	88	*Glycymeris* ?	Complete	Rounding, discoloration	Single, intact	90-degrees flat facet, rounding and smoothing of the inner walls, deformation of the lower rim	/
49	89	*Glycymeris* ?	Complete	Rounding, discoloration	Single, intact	90-degrees flat facet, rounding and smoothing of the inner walls, deformation of the lower rim	/
50	90	*Glycymeris* ?	Complete	Rounding, discoloration	Single, broken	90-degrees flat facet	/
51	91	*Glycymeris* ?	Complete	Rounding, discoloration	Not-perforated	/	/
52	92	*Glycymeris* ?	Complete	Rounding, discoloration	Single, broken	/ likely natural perforation	/
53	93	*Glycymeris* fresh	Complete	Rounding, discoloration	Single, intact	90-degrees flat facet, rounding and smoothing of the inner walls, slight deformation of the lower rim	
54	94	*Glycymeris* fresh	Complete	Rounding, discoloration	Single, intact	rounding and smoothing of the inner walls, deformations and thinning of the lower rim likely natural perforation	/

Table 1 (continued)

Progressive number	ID	Shell's species and state of preservation	Integrity	Alteration	Perforations	Macrowear on perforation	Microwear on perforation
55	95	*Glycymeris* fresh	Complete	Rounding, discoloration	Single, intact	90-degrees flat facet, rounding and deformation of the lower rim	/
56	96	*Glycymeris* ?	Complete	Rounding, discoloration	Single, worn out	90-degrees flat facet, rounding	/
57	97	*Glycymeris* ?	Complete	Rounding, discoloration	Single, worn out	Rounding likely natural perforation	/
58	98	*Glycymeris* fresh	Complete	Rounding, discoloration	Single, intact	90-degrees flat facet, rounding	Patches of polish around the perforation on the facet
59	99	*Glycymeris* ?	Complete	Rounding, discoloration	Single, broken	Likely natural perforation /	/
60	100	*Glycymeris* ?	Complete	Rounding, discoloration, encrustation	Single, broken	/	/
61	101	*Glycymeris* fresh	Complete	Rounding, less discoloration	Single, intact	90-degrees flat facet, rounding	/
62	102	*Glycymeris* ?	Complete	Rounding, discoloration	Single, intact	90-degrees flat facet, rounding and smoothing of the inner walls, deformations and thinning of the lower rim	/
63	103	*Glycymeris* fresh	Complete	Rounding, discoloration	Single, broken	Thinning of the rim	/

Table 1 (continued)

Progressive number	ID	Shell's species and state of preservation	Integrity	Alteration	Perforations	Macrowear on perforation	Microwear on perforation
64	104	*Glycymeris* fresh	Complete	Rounding, discoloration	Single, intact	90-degrees flat facet, rounding and smoothing of the inner walls, extreme thinning of the rim	Tiny polish on the rim
65	105	*Glycymeris* ?	Complete	Rounding, discoloration	Not-perforated	/	/
66	106	*Glycymeris* fresh	Complete	Rounding, discoloration	Single, broken	90-degrees flat facet	Weak sheen around the perforation
67	107	*Glycymeris* ?	Complete	Rounding, discoloration	Single, intact	90-degrees flat facet, rounding, slight deformation inner lower rim	/
68	108	*Glycymeris* fresh	Complete	Rounding, discoloration	Single, intact	90-degrees flat facet, rounding, deformation inner lower rim	/
69	109	*Glycymeris* ?	Fragment	Rounding, discoloration	Double, broken (one is natural)	/	/
70	110	*Glycymeris* ?	Fragment of valve	Rounding, discoloration	Single, broken	/	/
71	111	*Glycymeris* ?	Fragment of valve	Rounding, discoloration	Single, broken	/	/
72	113	*Glycymeris* ?	Fragment of valve	Rounding, discoloration	Single, intact	90-degrees flat facet, rounding	/
73	114	*Glycymeris* ?	Fragment	Rounding, discoloration	Single, broken	(1) indeterminable; (2) sawing	/
74	115	*Glycymeris* ?	Fragment	Rounding, discoloration	Single, broken	/	/

Table 1 (continued)

Progressive number	ID	Shell's species and state of preservation	Integrity	Alteration	Perforations	Macrowear on perforation	Microwear on perforation
75	117	*Glycymeris* ?	Fragment	Rounding, discoloration	Single, broken	/	/
76	118	*Glycymeris* ?	Fragment	Rounding, discoloration	Single, broken	/	/
77	119	*Glycymeris* ?	Fragment	Rounding, discoloration	Single, broken	/	/
78	120	*Glycymeris* ?	Fragment	Rounding, discoloration	Not-perforated	/	/
79	121	*Glycymeris* ?	Fragment of valve	Rounding, discoloration	/	/	/
80	122	*Glycymeris* ?	Fragment of valve with rim	Rounding, discoloration	/	/	/
81	123	*Glycymeris* ?	Fragment	Rounding, discoloration	Single, broken	/	/
82	124	*Glycymeris* ?	Fragment	Rounding, discoloration	Single, broken	/	/
83	125	*Glycymeris* ?	Fragment	Rounding, discoloration	Single, broken	/	/
84	129	*Glycymeris* ?	Fragment of rim	Rounding	/	/	/

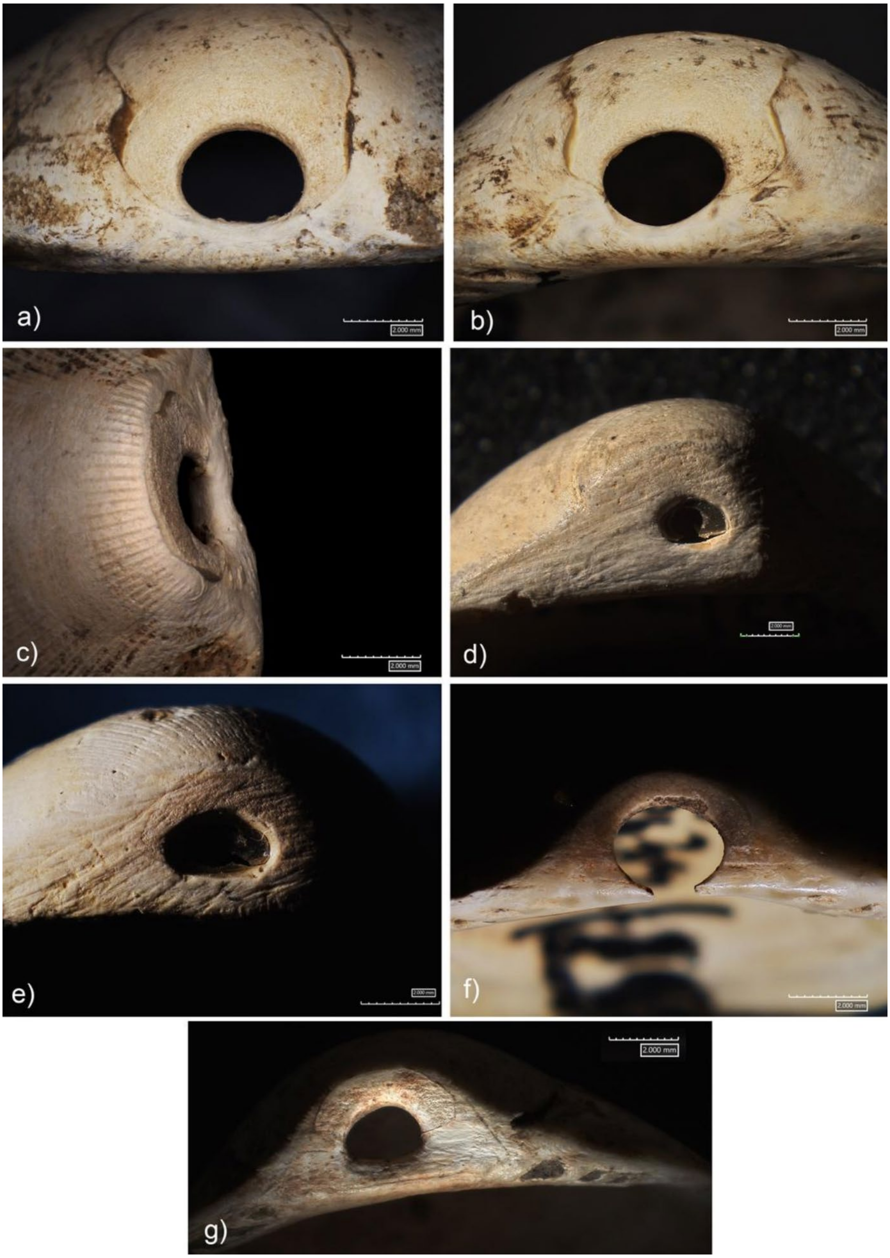

Fig. 5 Perforated *Glycymeris* from Petersfels. **a**–**b** perforated *Glycymeris* ID 113 and 94 showing any sign of human modification; **c** perforated *Glycymeris* exhibiting a flat 90 degree on the umbo; **d**–**e** perforated *Glycymeris* ID 52 and 83 showing bands of wide, long and short parallel striations oriented obliquely to the longitudinal axis of the shells; **f**–**g** perforated *Glycymeris* ID 53 and 13 showing bands of long and thin parallel striations oriented perpendicular to the longitudinal axis of the shells. (Micrographs: F. Venditti)

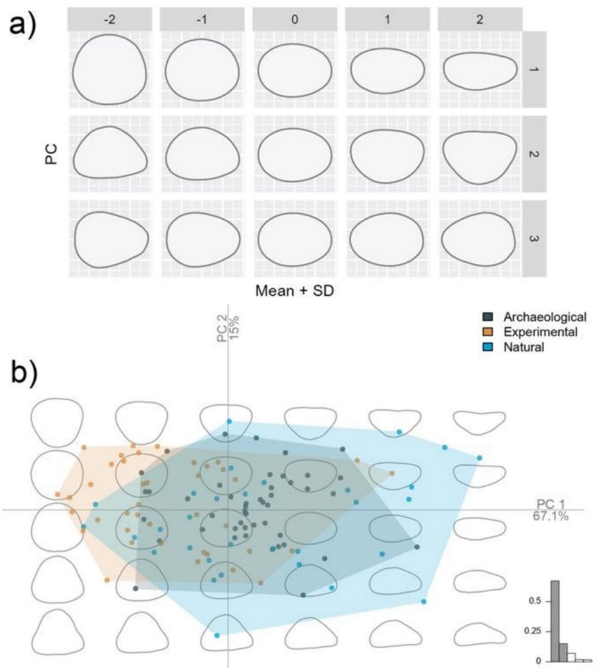

Fig. 6 Results of the 2-Dimensional Geometric Morphometrics analysis (2DGM) of the shell's perforation performed in *Momocs*. **a** Shape variation across the first three principal components (PCs), with SD referring to standard deviation; **b** Principal Component Analysis (PCA) bivariate plot of the first two PCs (PC1 vs. PC2). The figure also illustrates the shape variability of the perforations across these two axes

asymmetrical around the umbo, extending predominantly to one side, suggesting a tendency toward leftward movement during the abrasion process that created the perforation.

As demonstrated in our experiments and supported by published reference collections (*e.g.*, Berganza et al., 2012; Taborin, 1993; Wei et al., 2016), these technological signatures result from abrading the umbo against an abrasive surface, such as sandstone or harder rocks, through a to-and-fro motion. This technique typically produces striations on the facet that indicate the direction of the motion. The depth and spacing of the striations and grooves on shells 52 and 83 imply the use of coarse rocks, whereas a fine to medium rock texture results in closer and narrower striations, as observed in shells 53 and 1080. The latter two specimens (53 and 13) exhibit long, thin, and fine linear features on the umbo, close to the hinge, which are accentuated by the color contrast between the natural surface and the reddish pigmentation spread across the umbo (Fig. 5f–g).

The morphometric analysis of the perforations reveals distinct patterns. The first three PCs from the PCA of the perforation outlines explain 89.2% of the variance in the dataset (Fig. S9). PC1 primarily captures the transition from oval to more elliptical shapes, reflecting the relationship between the maximum length and width of the perforations (Fig. 6a). PC2 and PC3 describe the symmetry of the perforations: PC2 captures distal–proximal asymmetry, while PC3

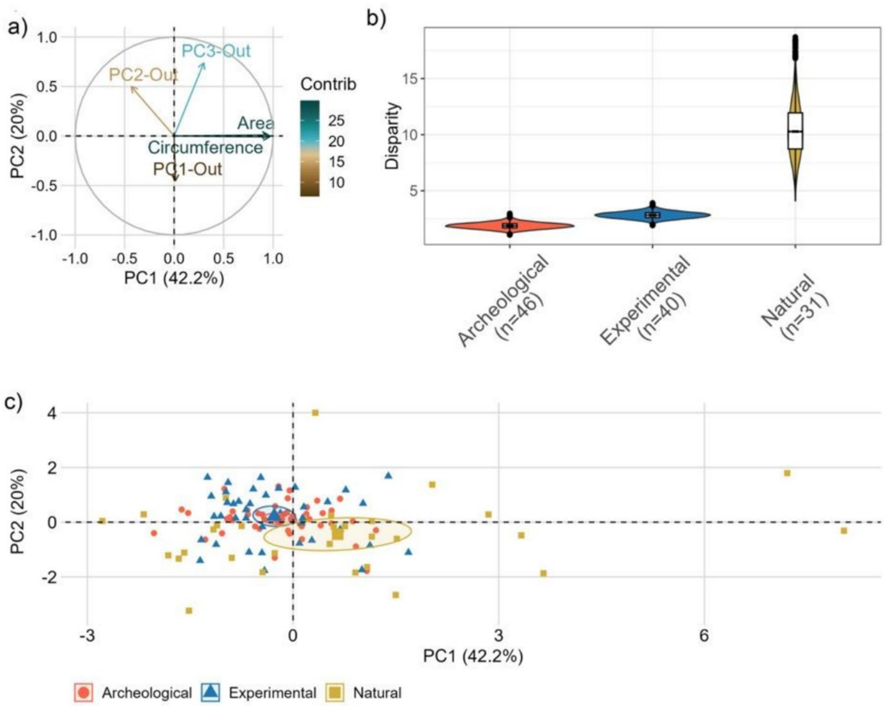

Fig. 7 Results of the PCA on shape and metric data. **a** Contribution of the quantitative variables to the first and second components. PC1-Out, PC2-Out, and PC3-Out represent the PC scores from the shape outline analysis; **b** Boxplots visualizing the sum of variance (disparity) for the perforation groups studied; **c** PC1 to PC2 biplot displaying the distribution of the perforations, categorized by archaeological, experimental, and natural groups. For details on the color, please refer to the legend

captures lateral left–right asymmetry. Spearman's rank correlation analyses were performed to evaluate potential allometric signals for PC1, PC2, and PC3 using circumference measurements. The correlations with PC1 (rho = 0.0202, $p = 0.8$) and PC3 (rho = 0.1125, $p = 0.2$) are weak and non-significant, while the correlation with PC2 shows a moderate, statistically significant negative allometric signal (rho = −0.252, $p < 0.01$).

Mean shape comparisons reveal that archaeological perforations tend to have a more elliptical shape than experimental abrasion ones (Fig. S10). The PCA plot shows significant overlap among the three groups, with however a notable increase in morphological similarity observed in the archaeological specimens (Fig. 6b). Since shape data alone did not fully capture the variability within the dataset, we performed a second PCA combining the first three PCs from the outline analysis with metric data. Interestingly, the circumference and area exhibit higher values and greater dispersion among the natural perforations (Fig. S11a-b).

The first four PCs from this second PCA explain 98.8% of the variance, with PC1 (42.2% of variance) being strongly correlated with the circumference and area of the perforations (Fig. 7a). The morphological parameters derived from the previous

2DGM analysis are mostly correlated with PC2 (20% of variance). Specifically, the elongation of the perforations (represented by PC1 in the 2DGM) is negatively correlated with PC2, while the values associated with proximal–distal and lateral asymmetries (PC2 and PC3 in the 2DGM analysis) show positive correlations with PC2, contributing significantly to this dimension.

The PCA biplot demonstrates marked differences between natural and archaeological/experimental perforations. The mean and confidence intervals of the latter two groups fall on the negative axis of PC1 and the positive axis of PC2, contrasting sharply with the natural perforations (Fig. 7c). The confidence ellipse and high dispersion of data points in the natural perforation group further emphasize the increased variability in both size and shape for these specimens. Based on the first four PCs of the combined shape and size PCA, disparity analysis effectively illustrates within-group variances, with statistically significant pairwise differences as indicated by the Wilcoxon signed-rank test. Natural perforations show a substantially higher sum of variance compared to both archaeological and experimental specimens (Fig. 7b). Overall, these results strongly suggest that the perforations on the *Glycymeris*, characterized by flat surfaces and an absence of striations, were likely anthropogenically modified by abrasion.

Use-wear Analysis

Several shells showed localized wear, which we interpret as a sign of extended suspension. Among the 42 specimens with complete or semi-complete perforations, we observed the following: (a) round and smooth inner walls of the perforations; (b) a widening of the perforation at its base (Figs. 8a–b); (c) plastic deformations appearing as a hollowed facet with smooth contours localized in the inner wall adjacent to the hinge (Fig. 8c–e); and (d) deformations and thinning of the hinge (Fig. 8g-i). The shape analysis confirms these observations, as the archaeological specimens are more frequently characterized by a marked proximal deformation and asymmetry, as captured by PC2, compared to the natural perforations.

In two instances (specimens 102 and 94), the facet shows a symmetrical alignment with the deformation observed on the hinge, which appears thinned and C-shaped (Fig. 8h–i). In contrast, specimens 46 and 104 exhibited significant thinning of the shell hinge without an associated inner facet. However, the perforations demonstrate a use-related widening in the area adjacent to the hinge (Fig. 8g). The combination of hinge thinning with either inner facets or hole deformation suggests that these features resulted from use rather than taphonomic processes. While all inner perforations are rounded and smooth, specimen 62 is notable for having the smoothest and most rounded inner surface at the bottom of the perforation (Fig. 8f).

Furthermore, all shells categorized as group 2, consisting of 7 specimens, are marked by worn perforations in the lower section of the hole (Fig. 9). The missing part lacks the sharp edges typical of modern fractures while displaying thinned and rounded extremities, occasionally ending in pointed, rounded tips (Fig. 9a–c).

Two specimens with double perforations likely suggest extended use. Shell 56 has an initial perforation on the umbo that became worn over time, leading to a subsequent perforation just above it. This shell was likely discarded after the lower part

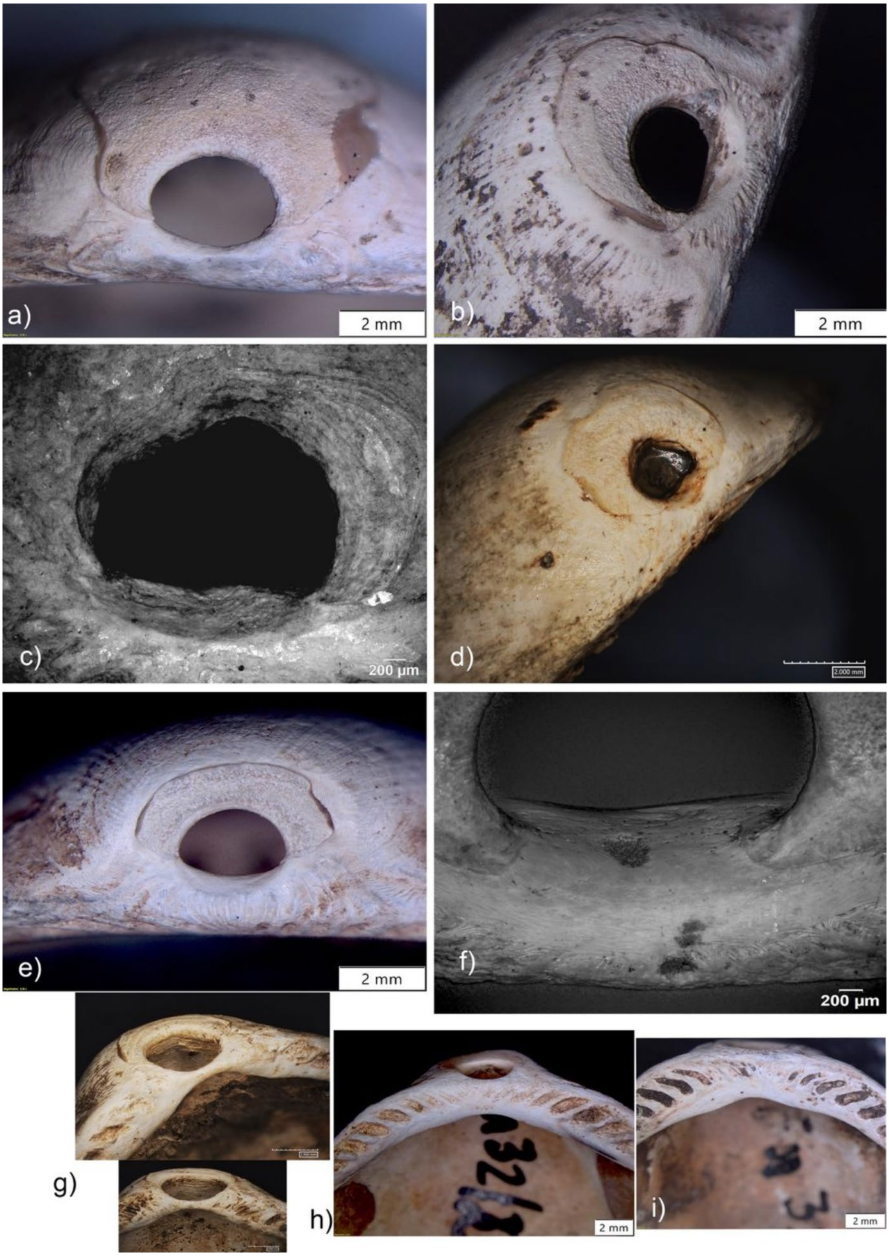

Fig. 8 Perforated *Glycymeris* from Petersfels with evidence of prolonged use. **a**–**b** widening of the perforation at its base (shells 73 and 102); **c**–**e** plastic deformations at the base of perforations (shells 98, 108, 88); **f** extreme smoothing of the inner surface of perforation (shell 62); **g** extreme thinning of the hinge (shells 104 and 87); **h**-**i** symmetrical thinning of the hinge (shells 46 and 102). (Micrographs: F. Venditti)

Fig. 9 Perforated *Glycymeris* from Petersfels with worn perforations in the lower section of the hole, adjacent to the hinge. **a**–**c** thinned and rounded extremities, ending in pointed, rounded tips (shells 96, 67, 71); **d**–**e** double perforated shells (shells 56 and 114), **f** close-up of the sawing mark on shell 114 (Micrographs: F. Venditti)

of the perforation broke again next to the top of the initial hole (Fig. 9d). Shell 114 is a shell fragment that preserves part of two distinct perforations. The first perforation on the umbo seems to have formed through abrasion, although there is no clear evidence of striations or a flat facet surrounding the hole. The second perforation, located in the middle of the valve, has a longitudinal shape with a V-shaped cross-section. As shown in our reference collection (see SI and Fig. S2a), this perforation matches the characteristics of those made by sawing with a sharp flint tool (Fig. 9e–f).

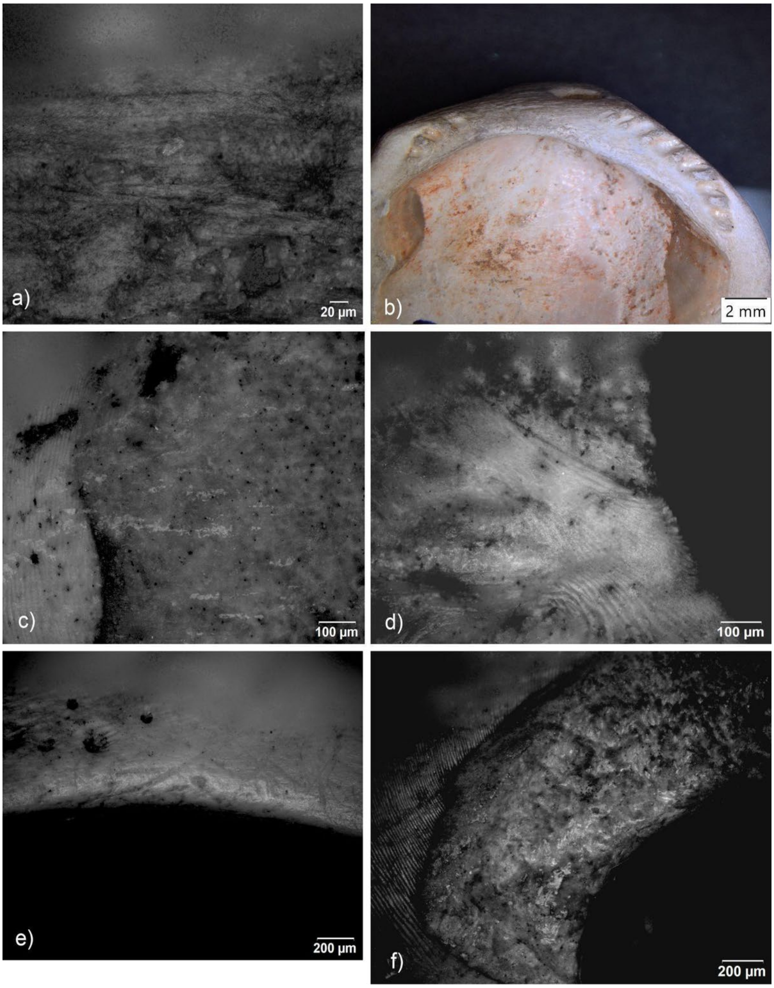

Fig. 10 Perforated *Glycymeris* from Petersfels exhibiting microwear. **a**–**b** shell 52 showing an off-centered deformed hinge and a polish along the hinge, **c**–**d** shell 69 with production and use-related polish; **e**–**f** shell 46 showing a developed polish on the inner left wall of perforation; **f** shell 83 displaying a polish on the facet of the perforation (Micrographs: F. Venditti)

The previously discussed macroscopic wear does not correlate with the microscopic scale. Evidence of technological wear, along with use-related polish or striations, is limited and mainly identifiable in small patches on the micro-surface of the shells. In specimens 52 and 69, use-related polishes overlap with technological striations resulting from abrasion (Fig. 10). Shell 52 exhibits a sinuous polish that has developed along the hinge, which appears rounded and smooth (Fig. 10a). The hinge shows some thinning and is slightly off-center to the left, likely due to usage (Fig. 10b). Shell 69 displays striations that have flattened from use (Fig. 10c), accompanied by a rough polish that extends around the circumference of the hole,

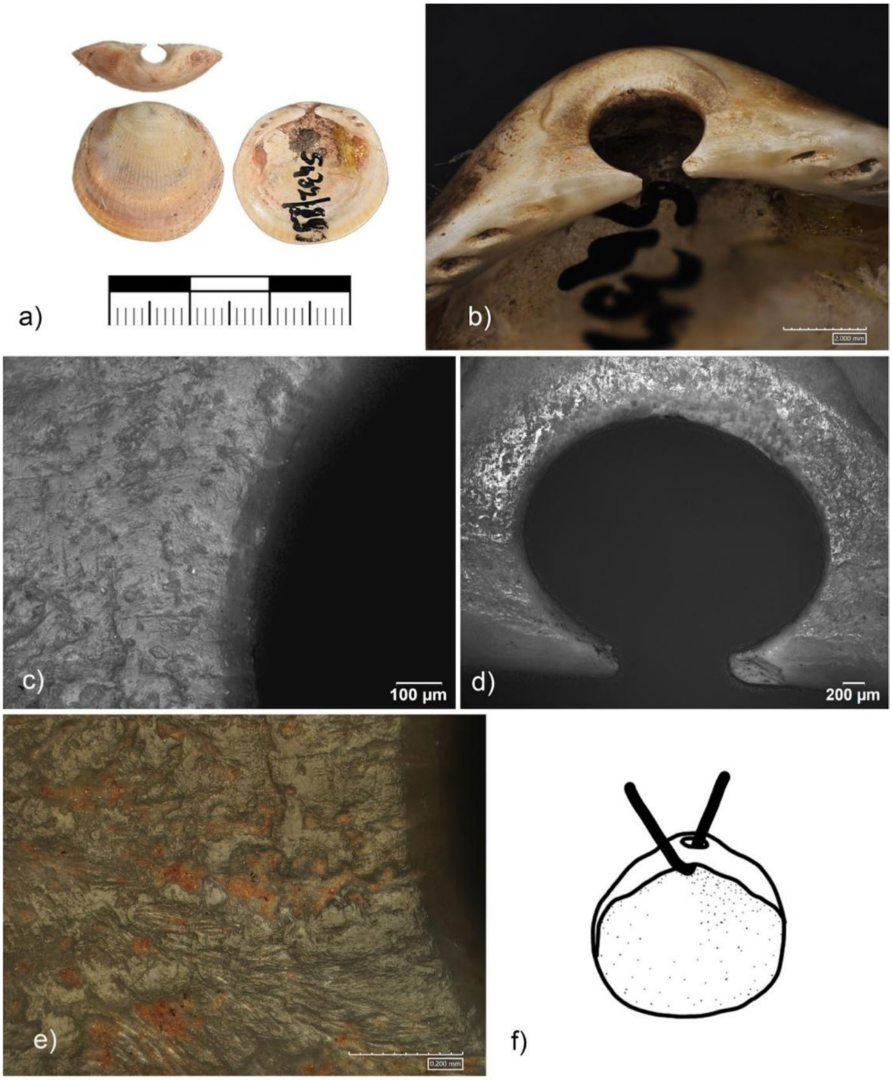

Fig. 11 Perforated *Glycymeris* 53 compelling evidence of prolonged use. **a** front and back view of *Glycymeris* 53; **b** worn out perforation made by abrasion; **c** close-up of the polished facet exhibiting narrow striations; **d** polished flat facet; **e** close-up of the polished facet with ochre residues; **f** reconstructive hypothesis of the *Glycymeris* suspension mode (Micrographs: F. Venditti, Drawing: B. Schürch)

possibly produced by contact with hide (Fig. 10d). Specimen 46 features a thinned and polished hinge, with remnants of technological wear visible along the upper circumference of the hole, along with a diffused sheen (Fig. 10e). Shell 83 has developed a smooth and flat polish on the left flat facet of the perforation (Fig. 10f). In contrast, technological striations are clearly visible at low magnification but only faintly discernible on a micro-scale.

Glycymeris 53 is a fresh shell with better preservation. It provides compelling evidence of prolonged use (Fig. 11a). A bright, domed polish extends uniformly around the facet of the perforation, showcasing a few long, slender striations that run perpendicular to the shell's axis (Fig. 11c–d). The polished surface is distinctly recognizable compared to the natural texture of the shell, especially where a small fracture, which occurred *ab antiquo*, has exposed part of the upper area surrounding the perforation. The polish likely formed after repeated contact against a surface during use. This perforation also exhibits a notable degree of rounding and a worn hinge caused by the friction with the string (Fig. 11b,f). Additionally, the facet at the umbo is covered with a red, powdery pigmentation that appears embedded in the shell's surface texture (Fig. 11e).

We documented 34 shells that exhibited traces of red coloration on both the inner and outer valves, as well as around the edges of the perforations. In the study by Schürch et al. (2023), three *Glycymeris* from Petersfels, which exhibited abundant red residues across their valves, were analyzed using Energy Dispersive X-ray analysis (EDX). The high iron content of these residues identifies them as ochre.

Other Bivalve Shells

Among the five non-*Glycymeris* shells, the two *Polymesoda subarata subarata* specimens (one complete and one rim fragment) show no perforations. In contrast, the *Ostrea* sp. fragment and the two *Gryphaea arcuata* are perforated (Table 2).

The oyster's valve fragment features a single round perforation with smooth internal walls. Concentric striations are evident at macro and micro scales, particularly on the inner valve, where three deep semi-circular grooves radiate outward from the perforation. Inside the perforation, we observed a transition from rough to smooth polish along the external rim of the hole.

The two *Gryphaea arcuata* are fossil specimens from the Lias α (or lowest Lower Jurassic or in German Unterer Unterjura, distance to the nearest outcrops of the Lias α from Petersfels is roughly 20 km), exhibiting well-preserved, albeit rounded, surfaces. They provide valuable insights into their production and usage. Specimen 127 is a fragment of a valve with a single broken perforation. This perforation is round, with smooth inner walls and a biconical shape. It was created by drilling with a pointed lithic tool in a bidirectional motion. Drilling striations are visible within the hole at both low and high magnifications, appearing as two thin, elongated circular grooves (Fig. 12g). The perforation wall expands toward the center of the valve, where we observed an extensive transition from rough to smooth use-related polish, accompanied by isolated parallel thin micro striations.

Specimen 128 features two symmetrical perforations on each side of the valve (Fig. 13a). These round perforations have smooth inner walls and a conical shape, indicating that they were created by drilling from the exterior toward the interior of the valve (Fig. 13d). The shell exhibits two perforations that create circular grooves along the inner walls. On a macro scale, we observed symmetrical deformations in the upper ring of the perforations, extending toward the shell's rim (Fig. 13b, c).

Table 2 List of other bivalve shells analyzed in this study, along with related documentation of the perforations

Progressive number	ID	Shell's species and state of preservation	Integrity	Alteration	Perforations	Macrowear on perforation	Microwear on perforation
1	116	*Polymesoda*fossil Complete		Rounding, discoloration	Not-perforated	/	/
2	112	*Polymesoda* fossil Frag. of rim		/	/	/	/
3	127	*Gryphaea arcuata* fossil Fragment		Rounding	Single, broken	Rounding and smoothing, biconical drilling traces	Diffuse polish inside the rim
4	128	*Gryphaea arcuata* fossil Complete		Rounding	Double, intact	Rounding and smoothing, unifacial drilling traces	/
5	130	*Ostrea* fossil Fragment		Rounding	Single, intact	Rounding and smoothing, biconical drilling traces	Patches of polish inside the rim

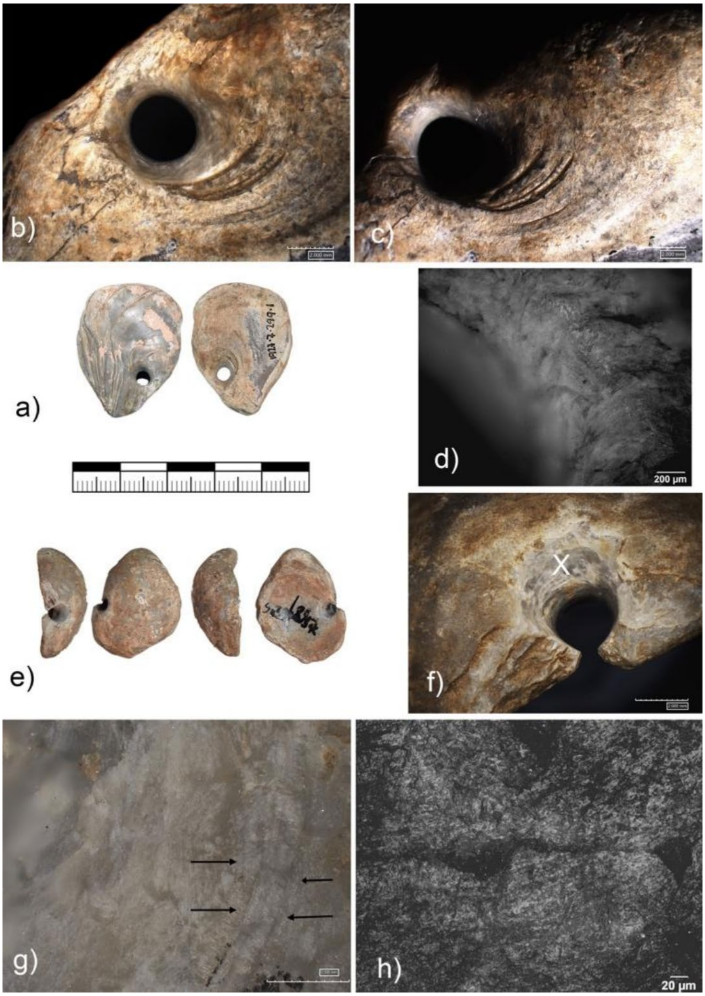

Fig. 12 Perforated *Ostrea* sp. and *Griphea arcuata* from Petersfels. **a** Front and back view of the *Ostrea* sp.; **b** overview of the perforation with smooth internal walls; **c** deep semi-circular grooves; **d** polish along the external rim of the hole; **e** front and back view of the *Griphea arcuata* 127; **f** smooth and rounded inner wall of the perforation; **g** close-up of the concentric drilling striations; **h** close-up of the polished inner wall of the perforation. The white cross designates the location of the polished area (Micrographs: F. Venditti)

This observation suggests that the valve may have been secured or sewn with a thread passing through the interior to showcase the front (Fig. 13f). One of the perforations exhibited a rough and sinuous polish. At the same time, the other showed a localized rough polish on the upper inner ring of the hole (Fig. 13e).

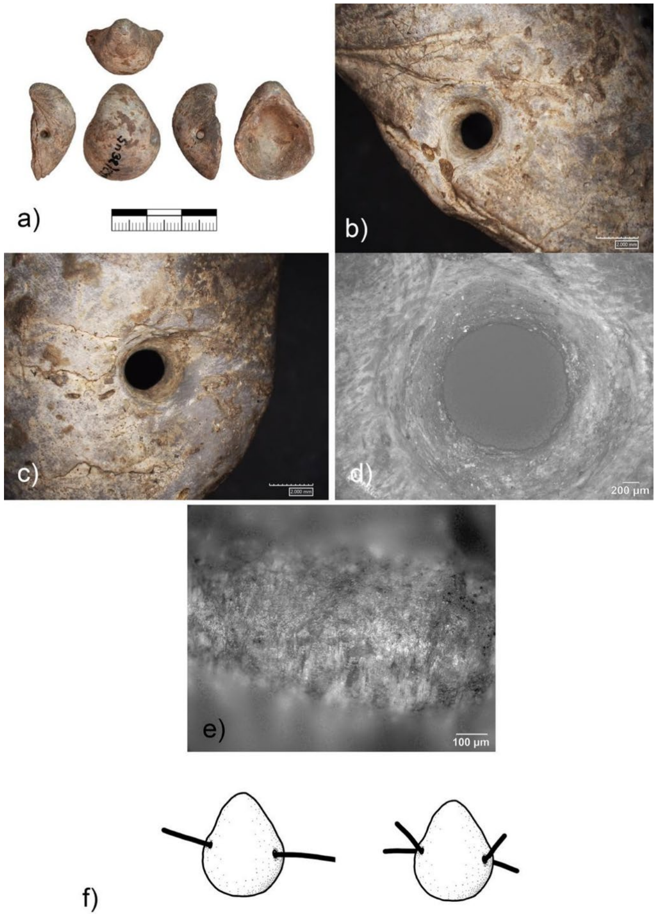

Fig. 13 Perforated *Griphea arcuata* from Petersfels. **a** Front and back view of *Griphea arcuata* ID 128; **b–c** symmetrical perforations exhibiting symmetrical deformations in the upper ring of the perforations, extending toward the shell's rim; **d** round perforation made by drilling; **e** close-up of the polish on the upper inner ring of the hole; **f** reconstructive hypothesis of the shell's suspension mode (Micrographs: F. Venditti, Drawings: B. Schürch)

Discussion

The large variety of perforated and non-perforated shells (Eriksen, 2002; Rähle, 1983, 1994) in different shapes, colors, and species discovered at Petersfels highlights the critical role shells play in shaping the cultural identity of these human groups.

Our thorough analysis of bivalves at Petersfels has shown that these shells were intentionally collected, modified, and used as suspended ornaments.

One key question when examining perforated shells is whether the perforations are of anthropogenic or natural origin. The Petersfels assemblage demonstrates that distinguishing between naturally occurring and culturally modified shells can be challenging.

Relying solely on optical microscopic observations proved insufficient to address this research question for all *Glycymeris* analyzed in this study. Integrating geometric morphometrics with statistical analysis offers a robust framework for exploring the variability among experimental, natural, and archaeological perforated shells. This approach enabled us to quantify and analyze morphological variability, providing deeper insights into the processes influencing shell production and usage across different settings. Four *Glycymeris* shells—three from this study and one previously reported in Schürch et al., (2023)—were perforated by abrasion against an abrasive rock. These shells exhibit two key diagnostic signs of abrasion: the flattening of the umbo and the presence of bundles of parallel striations (SI, and d'Errico et al., 1993; Taborin, 1993; Wei et al., 2016). We expected to find more *Glycymeris* shells with this combination of characteristic wear patterns; however, most samples displayed flat facets without any discernible striae. One possible explanation for this could be the poor preservation state of many shells, with striations obscured by taphonomic alterations affecting the periostracum of the umbo. This is exemplified by specimen 49, which reveals a flat umbo with linear scratches resulting from taphonomic modifications (Fig. 4e). These alterations have compromised the integrity of the periostracum, consequently exposing its porous and brittle texture. Notably, *Glycymeris* 53, which shows the most evident macro and micro traces, is a fresh specimen with better-preserved surfaces. The absence of technological traces also characterizes the valve of *Glycymeris* 114, which was sawn using a sharp lithic tool to create the longitudinal perforation. However, no traces in the form of incisions or striations were noted either macroscopically or microscopically, as shown in the comparative images of sawing traces on shells (see SI and Peresani et al., 2019, Fig. 6). Additionally, our analysis uncovered an unexpected discrepancy between the prominent macro traces and the limited microwear observed on the shells, a phenomenon attributed to shell alteration.

Except for *Glycymeris* 53, which displayed extensive macro and micro traces indicative of prolonged use, the other *Glycymeris* only showed isolated patches of polish. Nevertheless, they exhibited rounded and smooth perforations, as well as evidence of plastic deformation, hinge thinning, and worn facets, all resulting from extended use.

The absence of striations made it difficult to interpret the Petersfels shells as having been perforated by abrasion confidently. However, a substantial body of evidence supports this hypothesis.

Based on our observations of many naturally perforated bivalves, only one shell exhibited a highly circumscribed flat facet around the hole. In all other cases, the umbo consistently retains its convex shape around the hole, a characteristic further supported by comparisons with naturally perforated bivalves documented in the scientific literature (Bar-Yosef Mayer et al., 2009; Cabral & Martins, 2016; Wei et al., 2016; Light, 2017; Laporte et al., 2021; Schürch et al., 2021; Rigaud et al., 2022). Natural perforations exhibit high internal variance in shape and size, contrasting the uniformity observed in the archaeological perforations at Petersfels. While shape outline analysis alone revealed significant overlap among the three compared groups (*i.e.*, archaeological, experimental, and natural), combining shape and size data indicated that archaeological perforations are closer to experimentally abraded perforations than to naturally occurring ones. We are aware that the sizes and shapes of archaeological perforations are also the result of use and perhaps taphonomic processes. However, the marked overlap between archaeological and experimental data suggests that taphonomic and use-related processes did not cause substantial later changes to these perforations.

In addition, the recovery of 17 unmodified *Glycymeris* suggests that these shells were initially collected without holes at the umbo, possibly intended for later modification (Fig. 4d). Overall, while the combined evidence suggests that most of the perforations were likely anthropogenic, we do not rule out the possibility that, in some cases, shells with natural perforations were selected and transported to the site, as attested by a small group of perforated shells that showed no signs of human modification.

Our investigation revealed that the *Glycymeris* shells were collected for display purposes. By analyzing the distribution pattern of macro traces, we could reconstruct the arrangement of the mollusks. It appeared that they had either been hung or sewn onto clothing or headgear, with a thread running along the hinge of the shells (Fig. 11f). Observations of plastic deformations, polishes, and worn hinges provide strong evidence of significant wear on the hinge (see also the *Glycymeris* from Hohle Fels in Schürch et al., 2023, p. 146). Another indication that the shells were worn and displayed to others is the presence of a red colorant identified as ochre on 34 specimens. As noted in Schürch et al., 2023, the ochre adheres firmly to the shell surface, and in some specimens, it is covered by patches of sediment that show no traces of ochre. This suggests that the shells were intentionally colored with a red pigment or stained through contact with ochre-dyed materials rather than being colored by the sediment itself. Furthermore, if the ochre originated after deposition, we would expect to find a greater number of shells exhibiting red stains.

Comparing *Glycymeris* with the two *Gryphaea arcuata* and *Ostrea* has revealed distinct technological and use-wear features. The non-*Glycymeris* shells show clear evidence of perforation through drilling, and the presence of use-related polish on the inner walls of these perforations indicates their intended use as adornments. Notably, the symmetrical deformations observed on the double-perforated *Gryphaea* offer valuable insights into the mode of wear on the valve.

It is important to note that different shell species exhibit distinct methods for creating perforations. Our experimental replication has shown that abrasion is the most efficient and rapid technique for producing perforations in *Glycymeris,* as confirmed by other studies (Taborin, 1993; d'Errico et al., 1993; Light, 2017, and references therein). In contrast, alternative methods such as picking or drilling prove ineffective due to the positioning of the hole, as the umbo is the shell valve's most prominent convex area. However, abrasion may not be suitable for all types of shells, particularly those featuring flat valve regions.

The Role of Glycymeris at Petersfels

The significance of *Glycymeris* shells for the Magdalenian groups at Petersfels is highlighted by the considerable distances required to gather them. Whether these mollusk shells were obtained through established exchange networks among regional groups or collected during specialized expeditions to their natural sources remains uncertain. Petersfels is strategically located in the Bruder Valley, between the Danube and Rhine river systems. Following Maier's regional grouping in the Magdalenian (Maier, 2015), the site lies between the two lithic raw material procurement areas of the Circum-Jurassic and the Danube groups. According to a recent study (Schürch et al., 2025), the two regions also exhibit connections in raw material exchange. Petersfels may have functioned as a critical nexus for exchanging resources, goods, and ideas among various groups traversing the valley, thereby playing a pivotal role in the socio-cultural dynamics of the Magdalenian groups in the region. According to this scenario, the deliberate gathering of shells would indicate the extensive networks established by the site's inhabitants (Schürch et al., 2021, 2023), and Petersfels would be key to our understanding of connectivity and networks in the Magdalenian of Central Europe.

Due to their lightweight and small size, *Glycymeris* shells and most other shell species are particularly suitable for transport over long distances, and their collection may have been integrated into other economic activities, such as hunting (Binford, 1979; Eriksen, 2002). If we assume that the *Glycymeris* were transported from the Mediterranean or Atlantic Ocean, the Magdalenian would have to travel approximately 380 km as the crow flies to gather fresh specimens and 230 km to collect fossil shells from the Mainz basin. These distances may have been duplicated if we assume that Magdalenian groups did not cross the Alps but instead navigated around them.

Given these considerations, it seems more likely that the shells were obtained through extensive networks established by the site's inhabitants with nearby groups rather than through direct sourcing (Schürch et al., 2021, 2023; Álvarez-Fernandez, 2001; 2009). However, in either of the two scenarios, the care and effort invested in collecting, perforating, and using these shells emphasize their significance beyond mere decoration and highlight the role of personal ornaments in translating a cultural signal into cultural geography (Vanhaeren & d'Errico, 2006).

During the Magdalenian, prehistoric communities engaged in extensive contact, fostering a unified cultural expression. The presence of various Mediterranean and Atlantic mollusk species, including *Homalopoma sanguineum, Tritia neritea, Littorina obtusata, Nucella lapillus, and Dentalium* sp., at Late Glacial sites along the Rhine-Rhone axis—such as Petersfels, Hohle Fels, Andernach-Martinsberg-2, Munzingen, Kohlerhöhle, Monruz, Grotte de la Passagère, Abri des Pecheurs, and Canecaude I—indicates a well-established network of contact among Magdalenian groups inhabiting central western Europe (Álvarez-Fernandez, 2001; 2009; Eriksen, 2002).

The evidence of exchange networks is further reinforced by the use of jet to create female figurines in a similar style at both Neuchâtel and Petersfels, along with the extensive utilization of *Glycymeris* among thousands of shell species by Magdalenian groups in Germany and Switzerland (Eriksen, 2002; Wolf, 2019).

The importance of shells for Upper Paleolithic groups is also demonstrated by their desire to create replicas of shells using various materials. Albrecht (1979) identified a jet pendant that he interpreted as a shell replica (Albrecht, 1979, Plate 40). Other examples of shell replicas come from the Aurignacian of La Souquette (O'Hara et al., 2015). The technological and social practice of replicating objects using raw materials different from the originals is part of the Upper Paleolithic cultural tradition. This is further evidenced by the discovery of ivory and bone beads shaped like vestigial canines of red deer at various Upper Paleolithic sites across Eurasia (Kölbl & Conard, 2003; Alvarez-Fernandez & Jöris, 2008; Tejero et al., 2021).

Conclusion

The utilization of mollusk shells represents a significant aspect of the symbolic material culture and artistic expressions of Magdalenian groups (Álvarez-Fernandez, 2001; Pescaux, 2017). Notably, fossil or recent *Glycymeris* shells were among the most commonly used species during the Magdalenian, along with various mollusks and ornaments made from jet, which served as favored ornamental materials (Eriksen, 2002; Kölbl & Conard, 2003; Pescaux, 2017; Álvarez-Fernandez, 2009; Wolf, 2019).

Petersfels is regarded as a pivotal site in Central Europe for the study of ornamentation due to the abundance of beads and pendants crafted from materials such as teeth, bone, ivory, shells, and jet (Álvarez-Fernandez, 2009). Our microscopic analysis has revealed that the bivalve shells were deliberately perforated and transformed into ornaments. The localized rounding and smoothing, plastic deformations of holes and hinges, and signs of polishing suggest they were used over an extended period. While these shells served to embellish clothing and personal items, their significance went beyond mere aesthetics. They likely held symbolic value related to status, group identity, social interactions, or even religious beliefs.

In conclusion, our study of bivalves has provided insights into the techno-cultural and economic practices, as well as the symbolic and aesthetic expressions of the Petersfels people. This was made possible through a multidisciplinary methodological approach that allowed us to establish a reference for macro and micro traces linked to the production of perforations and the use of shells as ornaments. Geometric morphometrics and statistical analysis complemented and integrated the findings from the microscopic observations, providing a deeper insight into the variability reflected in the various investigated perforations. Ultimately, the microwear analysis revealed methods of production and use of the bivalve shells. By utilizing these advanced methodologies, we enhanced the interpretation of the archaeological bivalve shells, resulting in a more nuanced understanding of past cultural practices and environmental interactions at Petersfels.

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Author Contribution F.V: conceptualization, data curation, formal analysis, investigation, methodology, project administration, visualization, and writing original draft preparation, review and editing; A.F.: formal analysis, investigation, methodology, visualization, writing -review and editing; B.S: conceptualization, project administration, visualization, and writing, -original draft and writing -review and editing.

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Data Availability We performed data manipulation, visualization, and statistical analysis in R v.4.3.1 and RStudio, utilizing several packages. The analyzed dataset is available in the associated research compendium on Zenodo (Venditti *et al*., 2025): https://doi.org/10.5281/zenodo.15391823. The Zenodo repository includes the R script used for the geometric morphometrics and statistical analyses, along with the raw outline 2D coordinates.

Declarations

Competing interests The authors declare no competing interests.

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