A 41,500 year-old decorated ivory pendant from Stajnia Cave (Poland)

Sahra Talamo1,2,*, Wioletta Nowaczewska3, Andrea Picin1,2, Antonino Vazzana4, Marcin Binkowski5, Marjolein D. Bosch1,6,7,8, Silvia Ceratillo2, Marcin Diakowski9, Helen Fewlass3, Adrian Marciszak10, Dragana Paleček3, Michael P. Richards11, Christina M. Ryder12, Virginie Sinet-Mathiot1, Geoff M. Smith1, Paweł Socha10, Matt Sponheimer1,12,13, Krzysztof Stefaniak2, Michael P. Richards11, Andrzej Wiśniewski9, Marcin Żarski15, Stefano Benazzi4,1, Adam Nadachowski16 & Jean-Jacques Hublin1,17

Evidence of mobiliary art and body augmentation are associated with the cultural innovations introduced by *Homo sapiens* at the beginning of the Upper Paleolithic. Here, we report the discovery of the oldest known human-modified punctate ornament, a decorated ivory pendant from the Paleolithic layers at Stajnia Cave in Poland. We describe the features of this unique piece, as well as the stratigraphic context and the details of its chronometric dating. The Stajnia Cave plate is a personal ‘jewellery’ object that was created 41,500 calendar years ago (directly radiocarbon dated). It is the oldest known of its kind in Eurasia and it establishes a new starting date for a tradition directly connected to the spread of modern *Homo sapiens* in Europe.

The emergence of decoration and adornment of the human body is considered one of the earliest manifestations of symbolic behavior, marking the beginning of ethnolinguistic identity and social complexity in human evolution1,4. Timing when and where personal ornaments appeared in the archaeological record are important for reconstructing the trajectories of abstract thinking of archaic humans and understanding how figurative representations varied through time1,4. In Europe, the oldest evidence of body adornment is documented at ~46 ka BP in the Initial Upper Paleolithic layers of Bacho Kiro where several carnivore teeth were worked into pendants3,4. A successive technical advancement is recorded in the Early Aurignacian (~40 ka BP) when mammoth ivory started to be manipulated for the production of pendants and mobiliary arts5–7. Within these novel accessories, a new type of decoration—the alignment of punctuations—emerged on some ornaments in south-western France8, and figurines in Swabian Jura (Germany)9. Thus far, most of these iconic adornments were recovered during older excavations, with less recognition of site formation histories and post-depositional disturbance. Hence, their chronological attribution is based only on the stratigraphic context rather than direct dating. Recent chronometric programs on sites in Swabian Jura10 yielded contradictory results corroborating the inaccurate provenience of the samples collected during previous fieldwork. This situation makes the reconstruction of the emergence

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1Department of Human Evolution, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, 04103 Leipzig, Germany. 2Department of Chemistry G. Ciamicin, University of Bologna, Via Selmi 2, 40126 Bologna, Italy. 3Department of Human Biology, University of Wrocław, ul. Przybylszewskiego 63, 51-148 Wrocław, Poland. 4Department of Cultural Heritage, University of Bologna, Via degli Ariani 1, 48121 Ravenna, Italy. 5X-Ray Microtomography Lab, Department of Biomedical Computer Systems, Institute of Computer Science, Faculty of Computer and Materials Science, University of Silesia, Będzisza 39, 41-200 Sosnowiec, Poland. 6Vienna Institute for Archaeological Science, University of Vienna, Franz-Klein-Gasse 1, 1190 Vienna, Austria. 7Turkana Basin Institute Ltd, Turkana, Kenya. 8Turkana Basin Institute, Stony Brook University, N-507 Social and Behavioural Sciences, NY 11794-4364 Stony Brook, USA. 9Department of Stone Age Archaeology, Institute of Archeology, University of Wrocław, Szewska 48, 50-139, Wrocław, Poland. 10Department of Paleozoology, University of Wrocław, Sienkiewicza 21, 50-335 Wrocław, Poland. 11Department of Archaeology, Simon Fraser University, Burnaby, BC V5A, 156, Canada. 12Department of Anthropology, University of Colorado Boulder, Boulder, CO 80309, USA. 13Centre for the Exploration of the Deep Human Journey, University of the Witwatersrand, Johannesburg, Gauteng, South Africa. 14Evolutionary Genomics Section, Globe Institute, University of Copenhagen, Copenhagen, Denmark. 15Polish Geological Institute-National Research Institute, Rakowiecka 4, 00-975 Warsaw, Poland. 16Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Sławkowska 17, 016 Kraków, Poland. 17Collège de France, 11 Place Marcellin Berthelot, 75005 Paris, France. *email: sahra.talamo@unibo.it
The Stajnia Cave is a natural shelter located on the northern side of the Kraków-Częstochowa Upland in southern Poland (50° 36′ 58″ N, 19° 29′ 04″ E) (Fig. 1a). The site was investigated between 2006 and 2010 exposing a stratigraphic sequence of seven units (from G at the bottom (MIS 5c), to A (MIS 1) at the top) (Supplementary Sect. 1 and Fig. S1). During the excavations, a series of Neanderthal remains were found within a large collection of bones of Late Pleistocene steppe-tundra species, and Middle and Upper Paleolithic artefacts (see Supplementary Sects. 1 to 4). In 2010, two fragments of an ornate ivory pendant (S-22222 + S-23100) were discovered in layer D1 (Figs. 1b,c, and 2). In addition, an awl fragment (S-12160) was identified among the bone fragments from layer D1 (Fig. 3). A recent reassessment of the archaeological record of Stajnia Cave reveals that post-depositional frost disturbances and modern distortions displaced artefacts and human remains between layers. Since most of the lithics collected in layer D1 are associated with the Central and Eastern European Micoquian and very few are classified as Upper Paleolithic (Supplementary Figs. S3 and S4), the accurate cultural attribution of the pendant and the awl required direct radiocarbon dating. In order to minimise the amount of material exposed to destructive analysis, the most recent methodological advancements in $^{14}$C were followed.
Results

The pendant and the awl. The pendant is characterised by an oval shape with rounded margins, two drilled holes and decoration consisting of patterns of sequential punctures. The largest piece of the pendant is 4.5 cm long and 1.5 cm wide while the thickness varies between 0.36 and 0.39 cm. The reconstructed width of the complete artefact is shown in Fig. 2. There is one fully preserved perforation visible on the largest piece (hole 1 in Fig. 2) located close to the centre of the reconstructed artefact, near its upper edge. Another hole (hole 2
in Fig. 2), initially located near the opposite edge of the artefact, is partly preserved. The diameter of the fully preserved hole 1 is 2.3 mm and the original diameter of the partly preserved hole 2 was probably the same. The dorsal surface of the object is ornamented with at least 50 punctures creating an irregular looping curve (Fig. 1c). The ornamentation is partly destroyed by exfoliation which occurred close to the hole 1 (Figs. 1c, 2d). Besides this exfoliation, longitudinal cracks are also visible on the surface of the object.

Scanning electron microscopy (SEM) was conducted to verify the artefactual character of the observed features and to identify the technology used for their manufacture. The SEM analysis (Fig. 2b–e,g) indicates that the dorsal surface of the pendant does not present clear traces of intentional preparation preceding the creation of the punctures. The ventral puncture, however, presents traces of smoothing (Fig. 2g) which are linear and parallel to the longest axis of the artefact. The V-shaped cross-sections of the marks suggest the use of a flint artefact (Fig. 2b,g), and the differences in depth and width of the striations may be explained by the irregular edge of the applied stone tool17. Hole 1 and hole 2 were artificially manufactured by drilling from both sides which were not thinned previously, resulting in a biconical shape in cross-section (Fig. 2f). Most of the punctures are similar in terms of their outlines and cross-sections (Fig. 2c,e), which makes it highly probable that they all were made with the same tool—possibly in a relatively short time18. Punctures located directly below the fully preserved hole 1 display a slightly different morphology with less defined edges (Fig. 2a). The possibility that these punctures were made at a different time than the others cannot be excluded, however, gradual tool wear or a changed position of the tool are more parsimonious.

The maximum length of the awl is 68.33 mm (Fig. 3). Several wear facets are visible along the awl surface, and the basal cross-sections (5.8 × 3.4 mm) is flattened (Fig. 3). On the bottom side, there is a smoothed surface with round pronounced edges and flattening spike. The top side is more concave, and towards the tip, an extremely smooth facet is responsible for further refining. The lateral sides of the spike are rounded and polished. At c. 38.18 mm from the spike, the awl becomes basally thicker. Clear evidence of bone working is shown at the bottom facet, which has sharp edges towards both sides and the round spike show evidence of wear signs, indicating that an extensive use before discarding (Fig. 3).

Zooarchaeology by mass spectrometry (ZooMS) analysis reveals the pendant to be made from mammoth ivory and the awl from a horse bone (Supplementary Sect. 5).

The dating. Bones and ivory are the most suitable and well-established osseous materials to attempt radiocarbon dating15,19,20. The presence of collagen in the pendant (R-EVA 2651) and awl (R-EVA 2650) were tested using the near-infrared (NIR) analysis before sampling for radiocarbon dating. The results indicate that both specimens are well preserved and predicted yields 5.30 ± 1.52% (Pendant) and 8.04 ± 1.43% (Awl) weight collagen (Supplementary Fig. S6), which align closely with the collagen yields obtained following extraction (Table 1).
Collagen was extracted from both specimens at the Max Planck Institute for Evolutionary Anthropology (MPI-EVA) in Leipzig, Germany. The collagen from the pendant and the awl was radiocarbon dated twice with a ThermoFinnigan Flash EA coupled to a Delta V isotope ratio mass spectrometer. The bones with human modifications are indicated by an asterisk in the MPI Lab Code. Results are rounded to the nearest 10 years.

Table 1. The results of AMS radiocarbon dating and OSL from Stajnia. For 20 samples, stable isotopic analysis was evaluated at MPI-EVA, Leipzig (Lab Code S-EVA), using a ThermoFinnigan Flash EA coupled to a Delta V isotope ratio mass spectrometer. The bones with human modifications are indicated by an asterisk in the MPI Lab Code. Results are rounded to the nearest 10 years.

| MPI lab code | Level | Square | Submitter no | Species | Start mass (mg) | mg of collagen | Collagen % | C:N | Lab code | 14C Age BP | Err 1σ | CalBP 68.3% From-To | CalBP 95.4% From-To | References |
|--------------|-------|--------|---------------|---------|----------------|--------------|------------|-----|----------|------------|--------|-------------------|-------------------|------------|
| D1           | 1D    | D-1160 |               | Equid    | 108.9          | 27.3          | 8.0        | 3.3 | ETH-99041.1 | 37,903     | 267    | 40,500            | 42,700            | This paper |
| D1           | 3D    | D-2499 |               | UNG-unguiculata | 654.6       | 46.8          | 7.1        | 3.3 | ETH-19852   | > 49,000   |        |                   |                   | This paper |
| D1           | 7D    | D-949  |               | UNG-unguiculata | 626.3       | 57.5          | 5.9        | 3.2 | ETH-19863   | > 49,000   |        |                   |                   | This paper |
| E2           | 5E    | E-1704 |               | Mammoth   | 606.3          | 25.2          | 4.2        | 3.3 | ETH-19847.1 | > 50,000   |        |                   |                   | This paper |
| E2           | 1D    | E-1128 |               | Equid     | 652            | 74.2          | 11.7       | 3.2 | ETH-19870   | > 49,000   |        |                   |                   | This paper |
| E2           |       |        |               |          | UNG-unguiculata |             |            |     | ETH-20091.2 | > 45,600   | 1800   |                   |                   | This paper |
| E2           | 3D    | E-2363 |               | UNG-unguiculata | 552.3       | 55.3          | 2.4        | 3.3 | ETH-19858   | > 49,000   |        |                   |                   | This paper |
| E2           | 11F   | E-1272 |               | Equid     | 678.6          | 75.3          | 11.1       | 3.3 | ETH-19871   | > 49,000   |        |                   |                   | This paper |
| E2           | 11F   | E-1132 |               | UNG-unguiculata | 498.6       | 89.1          | 14.6       | 3.3 | ETH-19869   | > 49,000   |        |                   |                   | This paper |
| E2           | 4D    | E-2562 |               | UNG-unguiculata | 821.1       | 85.9          | 10.1       | 3.3 | ETH-19856   | > 49,000   |        |                   |                   | This paper |

| MPI lab code | Level | Square | Submitter no | Species | Start mass (mg) | mg of collagen | Collagen % | C:N | Lab code | 14C Age BP | Err 1σ | CalBP 68.3% From-To | CalBP 95.4% From-To | References |
|--------------|-------|--------|---------------|---------|----------------|--------------|------------|-----|----------|------------|--------|-------------------|-------------------|------------|
| C18          | 9E    | C-1320 |               | Mammoth   | 625.8          | 17.3          | 3.0        | 3.3 | ETH-11448.1 | > 50,000   |        |                   |                   | This paper |
| C18          | 10E   | C-1320 |               | UNG-unguiculata | 498          | 35.3          | 2.3        | 3.3 | ETH-19870   | 40,000    | 420    |                   |                   | This paper |
| C18          |       |        |               |          | Mammoth        |             |            |     | ETH-11448.1 | > 50,000   |        |                   |                   | This paper |
| C18          | 6E    | C-2782 |               | UNG-unguiculata | 809.9       | 62.0          | 4.7        | 3.3 | ETH-19851   | 36,080    | 460    | 41,150            | 40,740            | This paper |
| C18          | 7D    | C-1434 |               | UNG-unguiculata | 498          | 35.3          | 2.3        | 3.3 | ETH-19870   | 40,000    | 420    |                   |                   | This paper |
| C18          | 10E   | C-1320 |               | UNG-unguiculata | 498          | 35.3          | 2.3        | 3.3 | ETH-19870   | 40,000    | 420    |                   |                   | This paper |
| C18          | 5E    | C-2477 |               | UNG-unguiculata | 809.9       | 62.0          | 4.7        | 3.3 | ETH-19851   | 36,080    | 460    | 41,150            | 40,740            | This paper |
| C18          | 10E   | C-1320 |               | UNG-unguiculata | 498          | 35.3          | 2.3        | 3.3 | ETH-19870   | 40,000    | 420    |                   |                   | This paper |
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We then constructed a Bayesian chronological model using the software OxCal 4.4.23 and the new IntCal20 curve24 to refine the calibrations of the radiocarbon dates of Stajnia Cave. The calibrated dates (un-modelled in
Table 1) and the modelled ages obtained are shown in Supplementary Table S5 and Fig. S7. We did not include dates > 49,000 BP in the model. As is evident from Supplementary Fig. S7, the lowermost layers of the cave (layers E, D3 and D2) extend beyond the range of the radiocarbon method. Five further dates in layer D1 and one date in layer C18 are also > 49,000 BP, even though these layers contain Upper Paleolithic artefacts. This demonstrates the poor agreement between the high-resolution 14C dates and the poor resolution of the stratigraphy at the site, resulting in a model agreement index of 34.5% with four outliers (higher than 20%) out of 14 modelled samples. This situation implies that the awl and the pendant (32% and 21% outlier probability respectively), found in layer D1, have likely moved between layers and probably originate from layer C19 rather than layer D1. This hypothesis is corroborated by the radiocarbon age of two bones from layer C19 that have similar chronological ranges to the awl and pendant (Table 1). The sample R-EVA 739 (MAMS-19851: 36,080 ± 460 BP) also shows anthropogenic modifications suggesting a close association between the human settlement of the cave and the ivory pendant.

**Discussion**

The direct radiocarbon date makes the Stajnia ornate pendant (41,730–41,340 cal BP (68.3%)) the earliest punctate ivory object known to date to the Early Upper Palaeolithic record in Eurasia (Fig. 4b, Table 1). Although the Aurignacian settlement at Stajnia Cave was ephemeral (Supplementary Sect. 4), the direct radiocarbon dates on the pendant and the awl establish that the dispersal of these elaborate and highly manufactured objects, as
forms of cultural innovation with highly symbolic values by Homo sapiens, was established by around 42,000 cal BP. The radiocarbon dating on other ivory fragments reveals the transport on-site of mammoth tusks since the Middle Paleolithic (Table 1), but only during the Early Aurignacian, this raw material was worked for the production of mobile art.

We consider the possibility that the age of the pendant itself is much older than the decoration carved upon it to be unlikely given the experimental and chronological data presented here. The direct ages of the two precious objects correspond to the chronological range of layer C19 suggesting a short-term occupation at the site during the Aurignacian rather than a chronological coincidence.

Although permafrost may allow perfect preservation of mammoth tusks in open-air sites for millennia, these conditions are absent during MIS 3 and MIS 2 in southern Poland24. This evidence implies that over thousands of years the mammoth tusk was likely subjected to taphonomic processes causing progressive deterioration of the ivory. As shown in our replicative experiment (see Supplementary Sect. 8), using a subfossil and desiccated tusk fragment in middle/poor condition would have been unworkable for shaping and decorating an ornament alike the one found in Stajnia. Therefore, we assume that the shaping and punctate decoration was made on a mammoth tusk in fresh condition corroborating the age of ~ 41,500 cal BP.

Determining precisely when the punctate ornaments emerged in Eurasia required comparison with the other archaeological sites where this artistic pattern was found (Fig. 4). At Geißenklosterle Cave (Germany), punctuations were identified in horizon IIb (an ivory anthropomorph shows a regular punctate decoration on the backside) ranging between 40,280–38,800 cal BP (68.3%) (new modelled calibrated ranges with IntCal20 in Supplementary Sect. 7, and in Supplementary Tables S6, S7 and S14). In France, the use of the punctate motif emerged during the Early Aurignacian at Tuto de Camalhot (40,790–30,830 cal BP (68.3%), new modelled calibrated ranges with IntCal20 in Supplementary Sect. 7, and in Supplementary Tables S11 and S14) and only during a later phase in several sites located in the Castel-Merle Valley18 ranging between 39,800 and 36,240 cal BP (68.3%) (new modelled calibrated ranges with IntCal20 in Supplementary Sect. 7, and Supplementary Tables S8–S10 and S14). However, our model output reveals a low agreement index and poor stratigraphic integrity for Vogelherd Cave. At Tuto de Camalhot Cave, the boundaries obtained from the Bayesian model should be considered ‘hypothetical’ because they are based on two bones without any stratigraphic information. Further east, patterns of sequential punctures on ivory pendants were made during the EUP in the Russian Plains26,29. Thus far, this evidence reveals a broad geographical distribution of punctate graphic representation (Fig. 4a), and it shows that in Eurasia, the punctate decoration of the pendant at Stajnia Cave predates other instances of this type of ornamentation activity by 2000 years (Fig. 4b and Supplementary Table S14).

A deeper examination of the beginning of the diffusion of mobile art and body augmentation in Eurasia shows some chronological uncertainties (Supplementary Sect. 7). While at Sungir, the direct dates on the buried individuals25 give a precise indication of the age of the ivory beads, at Yana post-depositional processes (e.g., col-luviation, solifluction, or ice drift)26 could have displaced some pendants from their original position. In Europe, apart from Geißenklosterle, all the personal ornaments were discovered during excavations carried out in the late 19th and the early twentieth century and are associated only indirectly with the Early or Recent Aurignacian (SI Sect. 7). At Geißenklosterle, the chronology is well established for the different Aurignacian levels25 (new ranges with IntCal20 in Supplementary Sect. 7 and Supplementary Table S6). In contrast, the low chronological resolution of the other Early Upper Paleolithic sites impedes a clear understanding of the diachronic development of Aurignacian artistic expression. This situation is mainly due to the poorly constrained 14C dating resolution caused by questionable stratigraphic contexts at the sites10 (Supplementary Sect. 7). In the light of the Stajnia pendant, the model that the Swabian Jura was the centre of the diffusion of artistic innovations (Kulturpumpe hypothesis)16 needs further examination.

Summary and conclusion. The punctate decorative motif is one of the artistic innovations that developed during the Early Aurignacian128 in Europe and the EUP in the Russian Plains26,29. Thus far, these marks on mobile objects have been interpreted as hunting tallies, arithmetic counting systems, or lunar notation18, whereas others have suggested aesthetic purposes7. The looping curve represented on the Stajnia pendant is similar to the chronological range of layer C19 suggesting a short-term occupation at the site during the Aurignacian rather than a chronological coincidence.

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The age of ~41,500 cal BP of the decorated ivory pendant from Stajnia Cave underlines the importance of directly dating mobiliary art to solve the intriguing puzzle of the emergence of symbolic behaviour and modern cognition in human evolution.

Materials and methods

Radiocarbon dating. A total of 20 animal bone samples, including the pendant and the awl, were selected for radiocarbon dating. The collagen was extracted at the Department of Human Evolution, Max Planck Institute for Evolutionary Anthropology (MPI-EVA) in Leipzig (Germany) following the procedures in Talamo and Richards15 and Fewlass, et al.15 (MPI-Code: R-EVA).

The outer surface of the samples are first cleaned by a shot blaster and then 500 mg of the whole bones and c. 350 mg of the pendant and the awl were sampled. The samples are then decalcified in 0.5 M HCl until no CO₂ effervescence is observed. 0.1 M NaOH is added for 30 min to remove humics. The NaOH step is followed by a final 0.5 M HCl step for 15 min. The resulting solid is gelatinised following Longin41 at pH 3 in a heater block at 75 °C for 20 h. The gelatin is then filtered in an Eze-Filter” (Elkay Laboratory Products (UK) Ltd.) to remove small (> 80 µm) particles. The gelatin is then ultrafiltered with Sartorius ”VivaspinTurbo” ultrafilters (30 kDa MWCO)32. Prior to use, the filter is cleaned to remove carbon containing humectants33. The samples are lyophilised for 48 h. To supervise possible contamination introduced during the pretreatment stage, a pretreated 14C-free bone sample was used, kindly provided by the Oxford Radiocarbon Accelerator Unit (ORAU). Prior to sending the samples to the Mannheim facility for AMS dating (laboratory code MAMS)34, the collagen yield, C:N ratios, together with isotopic values are evaluated in order to understand the preservation of the collagen.

All the samples pretreated at the MPI-EVA passed the evaluation criteria (bones with > 1% weight collagen and C:N ratios in the range 2.9–3.641) for good quality collagen (Table 1). The collagen of the pendant and the awl was split into two parts, one was sent to Mannheim AMS and the second one to the ETH Zürich (laboratory code, ETH), where the collagen extracts were graphitised using the AGE III36 and dated using the MICADAS34,37. The AMS measurements of the collagen backgrounds which were used in the age correction of all samples were highly reproducible within and between each magazine (~ 500 mg bone extractions: 2016 mean F14 C = 0.00168, s.d. = 0.00018; 2018 mean F14 C = 0.00220, s.d. = 0.00025). Due to the high reproducibility of the background measurements, extended measurement time, high rate of transmission and the use of the R Combine of two separate dates, both the pendant and the awl, in Oxcal, we were able to reach exceptional levels of precision. An additional 1‰ was added to the error calculation of the samples, as per standard practice.

Archaeological methods. The excavation was laid out using a 1×1 m grid system. The sedimentary sequence was excavated according to the natural stratigraphy. The position of the archaeological finds was recorded using a 3D coordinates system (see38,39). The excavated sediments were sieved using 2 mm and 4 mm mesh screens. The floated materials were separated for the recovery of micromammals, shattered bone fragments, lithic chips, and charcoal.

Stajnia pendant analyses. Organic materials such as antler, bone and ivory can be distinguished by their micromorphological structure. In worked and especially polished objects, raw material identification is not always straightforward. Raw material identification of the Stajnia pendant was carried out by evaluating the broken edges and the exfoliated surface of the object around one of the perforations where the internal structure of the organic material was exposed. Mammoth tusk consists of a series of cones that are sequentially formed in the pulp cavity. These cones are made up of stacked dentine plates that, on macroscopic inspection, appear as milk-white homogeneous fibrous bands (e.g.40,41). Within these bands, microscopic canals 2 µm in diameter radiate outward from the pulp cavity42. These canals or dentinal tubules, in turn, are surrounded by collagen fibrils that coil up along the tubules42. The different orientations of the stacked radially distributed layers form the genus-specific distinctive patterns called ‘Schreger lines’ (see42 and references therein), which can be observed in transverse sections of larger tusk fragments. In this study, the material identification was based on the examination of the morphological features such as dentinal tubules and microlamiae that were visible on the broken edges of the object as well as on the exfoliated surface near one of the perforations (Fig. 2). The Stajnia pendant was analysed microscopically with a stereoscopic Olympus SZX9 microscope (magnification 6,3–57 ×) and metallographic microscope Nikon ECLIPSE LV100 (magnification 50–500 ×) at the Laboratory for Archaeological Conservation and Archaeometry Institute of Archaeology Wrocław University. The high-magnification photographs were made with Environmental Scanning Electron Microscope Philips XL 30 ESEM/ TMP at the Laboratory Scanning Microscopy (SEM)—Department of Geochemistry, Mineralogy and Petrology University of Silesia in Sosnowiec. The SEM analysis was used to examine the structure (including the analysis of the topography) of the surface of the object.

Virtual restoration of the Stajnia pendant. High-resolution µCT images of the two plaque fragments (S22222 and S23100) were obtained with an X-ray micro-computed tomography (XMT) scanner using the following scan parameters: voltage equal to 100 kV, currently equal to 0.062 mA, 1.0 mm AI filter, the reconstructed volume contains 1500 × 1500 × 1600 voxels. The data were segmented, and a three-dimentional isosurface of the external structure of the finds was created using Avizo Lite 2019.1 software (Thermo Fisher Scientific, Waltham, Massachusetts, USA)35,44. The 3D digital models obtained were then uploaded in Geomagic Design X (3D Systems, Rock Hill, South Carolina, USA) to carry out the optimisation of the surfaces (this process consists of cleaning and correcting defects to create fully closed surfaces)44. Subsequently, we proceeded with the virtual restoration of
the Stajnia plaque. First, we proceeded with the interactive alignment of the two parts of the plaque, using the recognisable contact points as a reference. After obtaining an optimal alignment, the two fragments were joined, and the integration of the missing parts which formed cavities between the two original finds was carried out. Lastly, the photographic texture was applied using MeshLab 2020.03 software.

**NIR spectroscopy.** Bone/ivory samples were scanned using a fiber-optic reflectance probe attached to a LabSpec 4 NIR spectrometer (Malvern Panalytical) with a spectral range of 350 nm to 2500 nm. A Savitzky-Golay transformation (derivative order = 2; polynomial order = 3; smoothing points = 31) was performed to correct for additive and multiplicative effects in the spectral data using Unscreamer X software (Camo Analytics). Partial least squares regression of data (wavelengths 1685–1740 nm and 2000–2300 nm) from specimens with known collagen yields was used to create a model predicting collagen content. The resulting 3-factor model was used to predict % collagen in the unknown specimens. Because the model suggested collagen preservation in the specimens was very good (> 5% collagen yield) for samples of this antiquity, we were able to minimise the destruction of samples for subsequent analysis.

**ZooMS.** Zooarchaeology by mass spectrometry (ZooMS) analyses tissues rich in collagen type I and uses protein amino acid sequence variation to provide a taxonomic identification. Both samples R-EVA 2650 (the awl) and R-EVA 2651 (the pendant) were analysed following ZooMS protocols which have been previously described in detail. Collagen extracted for the radiocarbon dating process was used for ZooMS analysis. Each collagen sample was incubated into 100 µl of 50 mM of ammonium bicarbonate (Ambic) at 65 °C for 1 h, and 50 µl of the resulting supernatant was digested using trypsin (Promega) at 37 °C overnight. Samples were subsequently acidified using 1µl of 20% TFA, and peptide extracts were cleaned on C18 ZipTips (Thermo Scientific). Each sample was spotted in triplicate on a MALDI Bruker plate with the addition of α-Cyano-4-hydroxyxynamic acid matrix. MALDI-TOF–MS analysis was conducted at the Fraunhofer IZI (Leipzig, Germany), using an autoflex speed LRF MALDI-TOF (Bruker) in reflector mode, positive polarity, matrix suppression up to 590 Da and collected in the mass-to-range 700–3500 m/z. Triplicates were then merged for each sample, and taxonomic identifications were made through peptide marker mass identification in comparison to a database of peptide marker series for medium to larger sized mammalian species.

Received: 30 June 2021; Accepted: 22 October 2021
Published online: 25 November 2021

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Acknowledgements
The excavation at Stajnia Cave and studies of the finds were supported by the Ministry of Culture and National Heritage grant no. 02350/11/FPK/NID, the International Visegrad Fund grant no. 21010125, Voivodship Inspector of Monuments in Katowice grant no. 117/11, Szczecin University, Polish Geological Institute-National Research Institute, grant no. 61.3608.1302.00.0, University of Wrocław, University of Silesia, Institute of Systematics and Evolution of Animals Polish Academy of Sciences. We are indebted to L. Rådström, J. Wawrzyniuk, M. M. Socha, and S. Steinberger for technical assistance. We are grateful to L. Rädisch, S. Steinberger, and M. Steinberger for criticism and discussions.

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...and others.
family, owner of the land, and the "Elementarz" Foundation for their support during the fieldwork. F. Welker has received funding from the European Research Council (ERC) under the European Union's Horizon 2020 research and innovation programme (grant agreement No. 948365). S. Benazzi has received funding from the European Research Council (ERC) under the European Union's Horizon 2020 research and innovation programme (grant agreement No. 724046 – SUCCESS, http://www.erc-success.eu/). A. Picin is supported by the Max Planck Society and the German Research Foundation (DFG grant n° 429271700—STONE). This project is funded by Max Planck Society and the European Research Council under the European Union's Horizon 2020 Research and Innovation Programme (grant agreement No. 803147 RESOLUTION, https://site.unibo.it/resolution-erc/en).

Author contributions
S.T. WN. and A.N.conceived the project; S.T., W.N., A.P., M.B., S.C., M.D., H.F., A.M., M.D. B., D.P., M.P.R., C.M.R., V.S-M., G.M.S., P.S., M.S.K.S., A.V., F.W., H.W., A.W., M.Z., S.B., A.N., J-J. H., performed research; S.T., A.P., W.N., M.B., M.D.B., S.C., M.D., H.F., A.M., D.P., M.P.R., C.M.R., V.S-M., G.M.S., P.S., M.S., K.S., A.V., F.W., H.W., A.W., M.Z., S.B., A.N., J-J. H. analysed all archaeological data; S.T. and A.P. wrote the paper with the collaboration of all the co-authors.

Funding
Open Access funding enabled and organized by Projekt DEAL.

Competing interests
The authors declare no competing interests.

Additional information
Supplementary Information The online version contains supplementary material available at https://doi.org/10.1038/s41598-021-01221-6.

Correspondence and requests for materials should be addressed to S.T.

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