

1 **Plant use and local vegetation patterns during the second**
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4 **half of the Late Pleistocene in southwestern Germany**
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Abstract

In light of recent discoveries of early figurative art in Paleolithic sites of southwestern Germany, gaining an improved understanding of biological, cultural and social development of these hunter-gatherer populations under past environmental conditions is essential. The analysis of botanical micro- and macrofossils from the Hohle Fels Cave contributes to the limited floral record from this region. These data suggest generally open vegetation, with the presence of wood near Hohle Fels, as indicated by pollen, phytoliths and evidence from wood charcoal throughout the whole sequence of occupation.

The Aurignacian horizons (early Upper Paleolithic, starting around 44,200 cal yr BP) correlate with prevailing shrub tundra. Few arboreal pollen in the transitional section from the Aurignacien to the Gravettian horizons (middle Upper Paleolithic, until ca. 32 cal yr BP) support the model of an interglacial tundra with a mosaic of cold steppe elements and some patches of woody species. In the Gravettian the macrobotanical and the palynological record indicate colder climatic conditions and a generally reduced presence of wood patches.

Few seed remains, mostly of the Asteraceae and Poaceae families suggest the use of these plants. The collection of bearberry (*Arctostaphylos* sp.) for specific purposes is indicated by large amounts of bark fragments.

Keywords: Upper Paleolithic, Central Europe, pollen, plant macrofossils, phytoliths

Introduction

Information on vegetation development and the landscape potential for early hunter-gatherers in southwestern Germany in the last third of MIS-3 (60-26/24 ka cal yr BP) is relatively limited, not least, because this sequence is generally underrepresented in the geological record of the region (Habbe et al. 2007). Climate fluctuations occurred frequently

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though show potential to have created variable resource situations in the inhabited regions such as the cave sites of Hohle Fels and Geißenklösterle (Schelklingen, N48°22', E9°44', Kr. Ulm, 534m asl). From the earliest Aurignacien at Hohle Fels dating around 44,200 cal yr BP (Conard 2009), until the end of the Gravettian (ca. 32,000 cal yr BP) at least 6 DO (Dansgaard-Oeschger) events are documented in global paleoclimate proxy records, whose reconstructed temperature for Greenland suggest a rapid mean annual surface air temperature rise of up to 15°C within a few decades (Van Meerbeeck et al. 2008). If such fluctuations have similarly affected southwestern Germany they could have had considerable impact on the regional flora and fauna, human subsistence behavior and thus human socio-cultural development.

Inferred biomes for Europe indicate temperate grasslands together with a forest component during the warm intervals of MIS-3, while during the cold intervals steppic conditions prevailed. Recent models discuss the climatic timberline for boreal forest between N48°-50° during early MIS-3 (Van Meerbeeck et al. 2011). This suggests that the vegetation of this karstic region of SW Germany was particular sensitive to climate fluctuations. Several studies indicate steep N-S vegetational gradients during interstadials in western and central Europe (Huijzer and Vandenberghe 1998; Fletcher et al. 2010). As these models take relatively large geographic areas into account, living conditions at Hohle Fels must be reconstructed by direct empirical studies. Important questions we aim to contribute to are thus: (1) How do the cave sites of southwestern Germany, and particularly Hohle Fels, fit into the generally accepted models and vegetation patterns?; (2) What kinds of habitats were available to the hunter-gatherers at the site of Hohle Fels throughout time?; (3) Which plant resources did they use?; (4) Did changes in vegetation affect human subsistence?

Site location and chronology of Hohle Fels

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3 The cave site of Hohle Fels in the Swabian Jura of southwest Germany (48.379250N,
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5 9.755528E, 534m asl) is well-known for its stratigraphic sequence and for exposing numerous
6
7 examples of Upper Paleolithic artistic expression (Conard and Floss 2000; Conard 2003;
8
9 Conard 2009; fig. 1). The sequence covers the later MIS-3 and the following LGM (MIS-2)
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11 until the end of the Pleistocene (ca. 44,200-14,700 ka cal yr BP). While geological
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13 observations and archaeological excavations in the region have been carried out beginning
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15 with Oscar Fraas in the 1860s, the geomorphology and landscape history of the Ach Valley
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17 region have been investigated mainly since the 1970s. The current river drainage system
18
19 formed during the Riss Glacial and subsequently the general form of the landscape has been
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21 stable (Wagner 1979). Nonetheless during the Upper Paleolithic the valley plain was probably
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23 several meters lower than today, creating a reduced floodplain and a more diversified relief
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25 than today. Hahn (1988) assumes that the relief was advantageous for hunting tactics, because
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27 escape chances for game were restricted by steep slopes.
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34 The cave deposits preserved artefacts of the Middle Paleolithic (>44 ka cal yr BP), the
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36 earlier (44,200-34,280 cal yr BP), middle (34,400-32,000 cal yr BP) and later Upper
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38 Paleolithic (16,700-14,700 cal yr BP) techno-complexes. Here we often use the
39
40 archaeological terms Aurignacian, Gravettian, and Magdalenian to refer to these periods and
41
42 note a radical depopulation of the region during the LGM (Conard et al. 2012).
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46 The archaeological techno-complexes consist of different geological horizons (GH).
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48 Five main GHs are differentiated in the Aurignacian (GH 8, GH 7, GH 6b and lower and
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50 upper GH 6a) with most of the remains deriving from GH 6b and 7 (Conard et al. 2003;
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52 Conard and Bolus 2003; Conard and Malina 2006; Conard and Bolus 2012). A phase with a
53
54 lower find density marks the transition between the Aurignacian and the Gravettian (GH 5
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56 and GH 3d). Three Gravettian horizons are distinguished (GH 3cf, 3c and 3b), which
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1 contained a large number of finds (Conard et al. 2001). Erosion influenced the deposits from
2 the end of the Gravettian to the Magdalenian and a gap in the sedimentation between these
3 cultural units is a result of it (Conard and Malina 2011 and 2012). Although the Magdalenian
4 horizons are partially disturbed by erosion, they preserved abundant lithic and organic
5 artifacts and document far reaching social and economic contacts.
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11 Cave sediments and site genesis have been investigated by Miller (2009).

12 Geoarchaeology and micromorphology of the different geological horizons provide an insight
13 into a complex depositional history with numerous chemical and mechanical transformation
14 processes, and simultaneously indicate trends of local environmental conditions during the
15 phases of sedimentation. Miller found micromorphological indication of increasingly colder
16 conditions in the form of frost-related features and decreasing degree of phosphatization
17 during continuous deposition of the geological horizon 8 which corresponds to the early
18 Aurignacian. GH 6 throughout GH 3db show according to the micromorphological record a
19 warmer environment and higher moisture compared to the previous horizon. The horizons
20 corresponding to the Gravettian occupation indicate a trend towards colder conditions, with a
21 sedimentation hiatus between GH 3c and GH 3b. It is also important to note for
22 methodological reasons, that no fire places have been found, and that all carbonized plant
23 materials derive from dumping spread over the cave floor (Miller 2009).
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44 In relation with particular aspects of site characteristics and origin of samples from
45 different excavation years, the categories of paleobotanical data from Hohle Fels are
46 unequally represented over the stratigraphic sequence. While palynological data are only
47 available for geological horizons 5-3b, which covers the Aurignacien/Gravettian transition
48 (35,000-33,700 cal yr BP), including the Gravettian techno-complex (34,400-32,000 cal yr
49 BP), the macrofossils and phytoliths derive from geological horizons 8-3a covering the early
50 Aurignacian throughout the Magdalenian sequences.
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Methods

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3 Excavations at Hohle Fels started in 1870 and were continued with many long
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5 interruptions throughout the following decades. Systematic palaeobotanical sampling has
6
7 been conducted since 1995. One of the reasons for the late interest in plant remains was the
8
9 common knowledge on their generally low recovery from cave sites in Central Europe due to
10
11 taphonomic reasons (Mason 2002). Additionally, the general isolation of cave sediments from
12
13 geomorphological processes in the landscape and the small size of the area of sedimentation –
14
15 roughly 500m² in the main hall of the cave - limits the number of biotopes which may be
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17 represented in such sediments (Frenzel 1983).
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22 Limited possibilities for systematic botanical sampling due to the nature of the cave
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24 sediments, which are composed of high amounts of limestone, create a high complexity for
25
26 the interpretation of the botanical records at Hohle Fels. Nevertheless the high-precision
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28 excavation and measurements of the coordinates of each single find, such as artifacts and
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30 wood charcoal by using a total station, enable a detailed analysis of their origin and
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32 association with other finds (fig. 2). In addition to this, more than 80 radiocarbon dates mostly
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34 on bone, but also on charcoal have been acquired from all the archaeological horizons (tab. 1),
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36 allowing a relatively precise dating of the different botanical samples (Conard and Bolus
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38 2003; Conard and Bolus 2008; Conard 2009).
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Pollen analysis

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49 For this study 12 samples from a 96 cm column within an east-west profile (Qu 69)
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51 were taken and analyzed for pollen in 1995 (fig. 3). The samples were prepared following the
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53 standard technique of Faegri et al. (1989). Preservation of the pollen grains was poor which
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55 partially complicated identification. Volumes of single pollen samples were not measured,
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57 because all the samples were equally treated (same number of sub-samples, same size of glass
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1 slides for counting). The individual samples contained between 66 and 509 pollen grains. The
2 pollen sum was calculated considering all terrestrial pollen taxa (arboreal pollen (AP) + non
3 arboreal pollen (NAP)) except for Cichorioideae (subfamily of the daisy family) and Poaceae
4 (grasses) which were excluded from the pollen sum for methodological reasons (see below)
5 and to enhance visibility of changes in the other pollen types. The percentage values of the
6 different taxa were calculated based on this sum. The results were plotted with TGView
7 ver.2.0.2 (Grimm 2004).
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17 As sedimentation genesis in archaeological sites and in cave sites in particular differ
18 strongly from palaeoclimate archives such as lakes and marine basins, diverse processes
19 during sedimentation which reduce and transform the pollen spectra in cave sites have been
20 discussed in the literature. Taphonomic research, for example, revealed that sedimentation
21 conditions are more favorable in the entrance area, and become worse with thinning layers in
22 the inner part of the caves (Müller 1979). Experimental research also demonstrated that feces
23 may play a role in the introduction of pollen into the cave, as e.g. dominating Poaceae pollen
24 in a context of deposition of ruminant coprolites (Müller 1979). Similar studies exist on
25 human feces (Bryant 1969). The composition of coprolites, however, reflects the biotopes of
26 the particular creatures in case they were deposited simultaneously with the sediments
27 (Carrion et al. 2001). As is typical in the Swabian Jura, cave bears often used the caves as a
28 den. Their feces were also deposited in the Hohle Fels site (Münzel and Conard 2004; Miller
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(Bottema 1975) to re-deposition of pollen-enriched dust (Navarro et al. 2000).

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However, when account is taken of the specific taphonomy of cave sediments, they can throw light on paleoenvironmental conditions especially when studied in multidisciplinary context (Carrion et al. 1999; Mercuri 2008; Navarro et al. 2001).

Botanical macrofossils and phytoliths

Clayey sediments and high corrosion of botanical macrofossils are typical for central European cave sites and can be considered at least partially to be responsible for low concentrations of plant remains. Preservation conditions for Paleolithic botanical macrofossils in cave sites may be good, if biomineralization turned the seeds into objects with higher resistance to microbial and physical activity in the sediments (Pons 1969), or if they are located in geographic areas with arid climatic conditions (Hillman 1989; Mead et al. 1986; Davis et al. 1985). Because such conditions are generally rare or absent in central European cave sites the widespread argument of nearly exclusively meat-oriented hunter-gatherer populations evolved some decades ago, but has meanwhile been disputed through ethnographic comparison and archaeobotanical research (cf. Zvelebil and Rowley-Conwy 1984; Owen 1996; Mason 2002). Soft tissue, probably representing the bulk of plant resources used for dietary purpose, is rarely identified (Hather 1991), because too little basic research on identification methods has been conducted.

Botanical macrofossils at Hohle Fels have been extracted by flotation and wet sieving since 1996. For this study 50 samples (70 kg of sediment) have been analyzed, of which only 27 contained plant remains. This low yield is characteristic for the general preservation conditions for botanical remains from central European cave sites. Among these, 9 samples derive from Aurignacian horizons, 11 from Gravettian and 5 from Magdalenian horizons. Two samples are from mixed horizons of Gravettian/Magdalenian origin. Due to the strong adhesiveness of the clay sediment particles, extraction of plant remains for this study was

1 carried out in a two-step procedure, starting with flotation of the sediment. The remaining
2 loamy concretions were soaked for several days in water and polycarboxylates (detergent) in a
3
4 second step to help dissolve the loam and to enhance the number of extracted objects during
5
6 subsequent wet sieving. Calcareous coating of some Aurignacian macrofossils enhanced their
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8 preservation, but had to be removed with dilute hydrochloric acid before identification, which
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10 in consequence often led to further destruction. Some of the highly damaged objects could
11
12 only be identified by applying SEM. For the identification of the seed remains Jensen (1998)
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14 was a valuable source of references. We used the herbarium of the Department of Botany at
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16 the University of Tübingen for identifying the bark fragments and the reference collection in
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18 the archaeobotanical laboratory of the University of Tübingen for studying seed and charcoal
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20 remains.
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26 Wood charcoal from flotation and wet sieved samples was generally highly
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28 fragmented and contained mainly pieces below 3mm in length. This high level of
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30 fragmentation particularly affected the Aurignacian horizons, leading to underrepresentation
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32 of fragile species like *Pinus* sp.. Some charcoal from the flotation samples could therefore
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34 only be identified using thin-sections following Schweingruber (1990).
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37 We solved this problem by focusing on singular charcoal pieces recovered in situ during
38
39 excavation. These handpicked charcoals were precisely documented in their location, making
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41 post-excavation fragmentation identifiable. Therefore we are able to exclude that post-
42
43 excavation fragmentation entered the data tables (fig. 2). Proportions based on weight are
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45 principally equal to those based on counts (Chabal 1990, 1992), therefore we counted our
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47 charcoal objects. The majority of the 448 samples derive from the Aurignacian horizons, thus
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49 complementing the pollen data which represents mainly the Gravettian horizons. From the
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51 Aurignacian-Gravettian transitional horizon 20 samples could be analyzed, while only 16
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53 samples belonged to Gravettian and 101 to the Magdalenian horizons. The wood charcoal was
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55 subsequently identified by incident light microscopy.
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Subsamples for phytolith analysis, 40g of sediment each, were taken from 10 sediment samples, with most of them deriving from early and Gravettian horizons. Dr. A. Golyeva (Institute of Geography, Russian Academy of Sciences in Moscow) treated the samples for 60 minutes with hydrogen peroxide (30%) for disintegration of the sediment. The sand and clay fractions were separated from biomorphic objects by centrifugation (10 min with 1000 r/min) in a solution of cadmium and potassium iodide. Biomorphic objects on the surface were decanted and treated with water for another 5 min. by 1500 r/s in the centrifuge. Dr. A. Golyeva investigated the heavier fraction which was enriched in biomorphic objects under the microscope (250-350x magnification).

Results

Palynology at Hohle Fels

Geological horizons sampled for pollen data at Hohle Fels comprise horizons 5-3b, covering an absolute time range between 35,000 – 32,000 cal yr BP and represent mostly the Gravettian techno-complex, including the transition from the Aurignacian to the Gravettian (fig. 4). This sequence is simultaneous to two global climate fluctuations (DO 6 and 5).

Arboreal pollen occurs only as singular counts. However, in most of the samples more than 20 different pollen taxa are found, indicating sufficiently good preservation for analyzing general changes in the palynological assemblage (Moore et al. 1991). In two cases the pollen sum was below 100, which restricts statistical validity of these two pollen assemblages.

However, as this was the case at the transition from GH 3d to 3c, which is marked by a horizon of burnt bones (GH 3cf) and represents a sediment layer with a strong fire impact, it is important to include the data for demonstrating the horizon-specific preservation conditions (Schiegl et al. 2003, Miller 2009).

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In the lower most spectrum corresponding to GH5, the high relative abundance of Cichorioideae could be partially or wholly a taphonomic bias. This is supported by the comparatively low diversity of pollen taxa in this level. From GH 3d only one pollen sample is available for analysis. Arboreal pollen is tentatively better represented in the lower section (GH 5-3c). GH 3c is represented by a sequence of five pollen samples with almost no arboreal and increased *Artemisia* (sagebrush) pollen indicative of dry steppe environments, a result of cooling processes. Some mesic elements, like *Thalictrum* (meadow-rue) and *Limonium* (statice), are however also present. Generally the palynological composition of the samples found throughout the phases of GH3cf-3b is rather uniform. An even cooler-drier sequence which is not represented by pollen would have started around 31 cal yr BP.

Wood charcoal

The wood charcoal assemblage, in contrast to the pollen core, covers the full archaeological sequence, starting in the early Aurignacian (GH 8 and 7) up to the Magdalenian (GH 3a) horizons (fig. 5). With only six species the diversity in woody vegetation at Hohle Fels can be considered low in relation to Holocene sites (Kreuz 2008). However, as concerns the geographical region and chronology the wood charcoal assemblage is rich (Damblon and Haesaerts 2002).

Large fenestriform pits in the *Pinus* specimens make the identification as *Pinus sylvestris* (scots pine) likely (Schweingruber 1990), although *Pinus mugo* (dwarf mountain pine) would also be a probable candidate. Throughout the sequence numerous *Pinus* sp. fragments show compression (fig. 6f). This feature is known to occur when a pronounced curvature or stem lean that may have been caused by wind, snow, landslide or light acts on the plant (Westing 1965). A number of objects have been identified as *Populus/Salix* which may in fact represent *Salix* sp. Due to poor preservation of these charcoal fragments, it was

1 impossible to investigate the rays in tangential section. Other wood taxa represented in low
2 numbers were *Alnus* sp., *Betula* sp., and *Fagus* sp., the latter as an intrusion of Holocene
3 origin due to a long-term exposed profile, as has been shown by AMS dating ($2,110 \pm 40$
4 uncal BP).
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9 In comparison to anthracological research at the nearby Geißenklösterle Cave covering
10 the same technological sequence, and where numerous records of modern wood have been
11 recovered (Tegel unpublished data), the charcoal remains from Hohle Fels indicate that
12 modern intrusion was rare in this site. This enables a consideration of the chronological
13 dynamics in the charcoal assemblage from Hohle Fels (fig.5).
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21 The samples from the Aurignacian horizons were numerous enough to consider the
22 different geological horizons separately. The earlier Aurignacian horizons (GH 8 and 7) are
23 strongly dominated by *Pinus* sp., followed by a peak of *Salix* sp. in the later Aurignacian
24 horizons (GH 6). The abundance of *Populus/Salix* is elevated from the upper Aurignacian
25 onwards. Another increase in *Pinus* sp. can be observed at the transition from the
26 Aurignacian to the Gravettian horizons (GH 5-3d), while in the Gravettian (GH 3b-3c) *Salix*
27 sp. (*Populus/Salix*) is again dominant. In the Magdalenian horizons (GH 1-3a), *Salix* sp.
28 (*Populus/Salix*) and *Pinus* sp. are about equally present.
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45 **Other vegetative plant remains, seeds and phytoliths**

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47 Vegetative plant remains and seeds were only found in low numbers in the cave
48 sediments of Hohle Fels (tab. 2). Corrosion in these finds was high and complicated
49 identification.
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54 The concentration of macrofossils in the 29 samples analyzed was lowest in the Gravettian
55 horizons and highest in the Magdalenian.
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2 Among the most frequent finds of the Aurignacian and Gravettian horizons were bark
3 fragments, which have been identified as *Arctostaphylos* sp. (bearberry). These have been
4 identified using comparative bark morphology on different shrub species from tundra habitats
5 available in the Herbarium Tubingense. They account for 68% of the macrofossils in the
6 Aurignacian horizons, for 33% of the finds of the Gravettian horizons and occur only
7 occasionally in the Magdalenian samples. Buds and seeds of an unidentified Brassicaceae
8 species occur only in the Gravettian horizons. Culm fragments and seeds of grasses have been
9 identified from the Magdalenian, Asteraceae species and *Helianthemum* sp. from the
10 Aurignacien and Gravettian horizons (fig. 6a-e).
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22 Ten of the samples, mostly from Gravettian horizons, have been analyzed for
23 phytoliths. Only those from the Magdalenian contained phytoliths, however, in all samples
24 cellular tissue could be identified. In the samples of GH 6 woody and herbaceous detritus
25 indicating decomposition of wood and herbs have been found in situ. In GH 3 beside plant
26 tissue there were also amorphous, decomposed products of faunal origin, either from feces or
27 from animal carcasses which may relate to the large number of cave bear bone finds. The
28 horizon at the transition to the Magdalenian also contained Poaceae-type phytoliths indicating
29 that this plant group has been introduced into the cave, either as components of animal
30 coprolites or for other purposes by humans. The Magdalenian horizons contain phytoliths of
31 the dicotyledon and bryophyte type, and beside this detritus from decayed wood.
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46 Overall, an interesting side result of phytolith analysis was that wood was deposited
47 inside the cave throughout the whole sequence, indicated by the continuous presence of
48 cellular tissue.
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Discussion

Climate, environmental dynamics and human adaptations at Hohle Fels

Interpreting the botanical data at Hohle Fels

While contamination and skewed representation of taxa may be particularly relevant for the pollen record at Hohle Fels, they probably played only a minor role for the wood charcoal. Two intrusive charcoal fragments of *Fagus* have been found in Aurignacian deposits. One of them has been dated to the late Holocene (tab.1). Besides this, palynological research at other locations has indicated that *Fagus* dispersed into southern Germany only relatively late and only reached higher amounts between 7,000-6,000 BP (Gliemeroth 1995).

There is relatively little direct evidence on vegetation development during the Pleistocene of southwestern Germany. Inferences on the position of single, stadial refugia of taxa are mainly drawn from indirect hints derived from knowledge of late glacial and Holocene migration of woody species or from reviews on earlier research in northern or central Germany (cf. Huijzer and Vandenberghe 1998; Behre 1989; Behre and van der Plicht 1992). Thus the botanical data from Hohle Fels provides some important information on the local environment. Although humans are largely responsible for the transport of plant remains into the cave, we consider this data to be informative on the environment.

Palaeolithic hunter and gatherers collected plants for a relatively limited number of purposes, such as food, fuel, bedding and other constructive activities. We argue that wood was collected for fuel, mainly in the form of small branches rather than tall trees. Wood was surely a limited resource which has been exploited to the limits of availability. Therefore, the identified wood pieces probably reflect availability, rather than human choice within a broad range of plentiful woodland resources. In other words, within a landscape that can be assumed to have been relatively treeless, natural availability of woody species and human preferences

1 should have created a very similar spectrum of taxa. An additional argument in this line is the
2 contextual situation in the cave, where no fire places have so far been excavated. All the
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4 remains from the excavation trenches derive from dumping (Miller 2009), i.e. the main areas
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6 of activity may well have been either in the front of the cave or in the adjacent hall, while the
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8 excavated area was used for dumping all sorts of material no longer useful for the occupants
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10 of the cave. We may therefore assume relatively uniform source deposits, compared to the
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12 hypothetical study of the original undisturbed features. The deposits were in most cases
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14 dominated by mixed accumulations of ashes from multiple occupations that incorporated
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16 numerous cycles of seasonal activities. This generally qualifies botanical macrofossils for
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18 exploring diachronic change (Hillman in Moore et al. 2000).
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23 We argue further, for the reasons outlined above, that the Paleolithic botanical macrofossils
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25 provide information on the environment as well as on human subsistence. The need for local
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27 evidence of past vegetation elements is supported by problems in applying uniformitarian
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29 principles. Huntley et al. (2003) argue that interpretations cannot be based upon the present
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31 vegetation as increasing evidence shows that vegetation units have existed in the past, under
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33 environmental conditions without any extensive modern analog.
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39 It has been assumed that there was no reforestation during the numerous interstadials
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41 which divide the Pleniglacial. This, however, does not mean that there were no woody species
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43 (Lang 1994; Fletcher et al. 2010), as is indicated at Hohle Fels by the presence of arboreal
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45 pollen, the wood phytoliths and charcoal.
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48 Because our paleobotanical data is not equally available for all the techno-complexes we
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50 discuss our results for the Aurignacian mainly based on macrobotanical remains, and for the
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52 Aurignacian/Gravettian transition as well as the Gravettian additionally from a palynological
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54 perspective (fig. 7).
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Aurignacian (44,200-34,280 cal yr BP)

The Aurignacian geological horizons which are subdivided in an earlier (GH 8 and 7) and a later sequence (GH 6), show a clear dominance of pine wood in the earlier horizons and a strongly increased presence of willow in the later GH 6. This trend shortly reverses in the transitional Aurignacian/Gravettian phase.

Due to the very limited number of seeds there is no statistically significant difference throughout the Aurignacian and transitional Aurignacian/Gravettian horizons for this category of botanical remains.

Possible habitats of the wood species represented at Hohle Fels are more informative than their ecology. The probable species *Pinus sylvestris* and *Pinus mugo*, both are associated with sufficient moisture availability (Šibík et al. 2008; Heuertz et al. 2010), and are present in biomes varying from taiga to forest-steppe (Tarasov et al. 2000). In terms of vegetation types the question of the existence of dwarf vs. tall trees is relevant. *Salix arctica* (arctic willow) or *Salix reticulata* (net-leaved willow) were probably present, since there are some fragments with widespread, small vessels and indication for small diameters. However, a large proportion of the *Salix* sp. fragments show densely packed vessels in transversal view, which is atypical for *Salix arctica*. Modern habitats of *Salix reticulata* are thin soils on snow-covered, moist and stony slopes (Kershaw et al. 1998). Behre (1989) has argued that the greater part of the Middle Pleniglacial was relatively mild with more or less closed tundra vegetation in edaphically favorable locations. Our findings suggest that such environments were present in the area around Hohle Fels. The large number of *Salix* species in the northern temperate zone, covering a wide range of different habitats, hinders further ecological reconstruction. *Alnus* sp. and *Betula* sp. both grow on damp to fresh soils (Gale and Cutler 2000). *Betula* sp. is also present from around 35 ka cal yr BP at Hohle Fels, first in the charcoal assemblage and later on in the pollen spectrum. Although the few records of *Betula* sp. in the charcoal record

1 cannot definitely be ascribed to either dwarf or tall trees, it seems plausible that a dwarf form,
2 such as *Betula nana*, may be represented. Numerous macroremains from other locations
3
4 demonstrate that *Betula nana* was distributed in the final Pleniglacial and early Late Glacial
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6 before the reforestation of central Europe (Lang 1994; Müller 2003; Sirocko 2009).
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9 In all, the species composition of the charcoal record resembles a tundra with some
10
11 boreal elements in a probable form of conifer groups during the Aurignacian. Later in the
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13 sequence the charcoal assemblage includes deciduous components, notably *Salix* sp., and with
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15 lower amounts *Betula* sp. and *Alnus* sp.. Considering the rodent fauna during the Aurignacian
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17 sequence, tundra components are more numerous than boreal species with a strong increase in
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19 tundra elements in GH 6b, indicating that tundra may have been more significant than boreal
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21 elements (Ziegler in press). The presence of burnt bones supports the argument that wood
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23 may have been scarce and bone was used as a fuel source in the later Aurignacian horizons
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25 (Conard et al. 2012).
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29 The differences between the earlier and the later Aurignacian charcoal composition may be
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31 explained by increasingly cooler conditions throughout the Aurignacian. This is partially
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33 consistent with the micromorphological record from Hohle Fels which documents colder
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35 conditions in GH 7 in contrast to GH 8 (Miller 2009).
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41 Sediment studies at Pleniglacial sites in the east Carpathian region showed a number
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43 of climate fluctuations relevant to other Central European locations. Haesaerts et al. (2003)
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45 found for the period between 50-33 ka BP three interstadial events grading from boreal
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47 climate to more continental conditions, which stands in contrast to the multiproxy research of
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49 Huijzer and Vandenberghe (1998). The latter found that the long sequence of the Aurignacian
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51 seems to include shifting climate conditions with stronger temperature amplitude than today
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53 in the beginning, and increasingly warmer winters at the end of the Aurignacian. Their
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55 analysis is based on a large number of regional biotic and abiotic data from 268 pleniglacial
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57 sites and resulted in a reconstruction of mean temperature and prevailing climate gradient.
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1 Starting at about 42 ka BP Huijzer and Vandenberghe (1998) found a higher annual
2 amplitude in temperature for the cold interval between 41-38 ka BP with higher temperatures
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4 of the warmest month and lower temperatures of the coldest month compared to the
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6 traditional Moershoofd (50–43 ka BP) and Hengelo (39–37 ka BP) interstadials. This also
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8 correlates the cold and dry interval around 40 ka BP reconstructed for Les Échets and La
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10 Grande Pile (Woillard 1978; Guiot et al. 1993). The mean temperature of the warmest month
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12 at this time based on the multiproxy record Huijzer and Vandenberghe (1998) has been
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14 calculated to 10-11°C, mean temperature of the coldest month has been calculated between -
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16 27 to -20°C. The southern boundary of continuous permafrost was situated in northernmost
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18 Germany with only seasonally frozen ground at about N°49 – ca. 60km north of Hohle Fels,
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20 which is critical to the understanding of the general living conditions in and around the Ach
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22 Valley. Mammalian evidence from Denmark and UK agree with the cold conditions
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24 prevailing during the 41–38 ka BP interval through finds of *Mammuthus primigenius* (woolly
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26 mammoth) (Huijzer and Vandenberghe 1998). Mammoth has also been identified in large
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28 numbers together with reindeer and equids during this phase at the cave sites in southwestern
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30 Germany, including Hohle Fels (Münzel and Conard 2004).
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39 Despite chronological uncertainties for a pollen record from Rösbach/Leimen, near
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41 Mannheim (Küttel et al. 1986), Huijzer and Vandenberghe (1998) link this record to the
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43 interval between 36-32 ka BP and suggest by the presence of *Hippophaë rhamnoides* (sea
44
45 buckthorn) relatively high temperature of the warmest month, i.e. higher than 11.5°C. The
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47 mean temperature of the coldest month was estimated between -20°C and -12°C (Huijzer and
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49 Vandenberghe 1998), which would mean considerably warmer winters, and slightly warmer
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51 summers than before, and would chronologically include the transition from the Aurignacian
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53 to the Gravettian at Hohle Fels.
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Aurignacian/Gravettian transition and Gravettian (35-32,000 cal yr BP)

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3 Considering the different biotopes reflected in the pollen diagram from Hohle Fels, the
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5 lack of arboreal pollen support the model of interglacial tundra vegetation with a mosaic of
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7 cold steppe elements and some patches of woody species (fig. 4). The general outline of the
8
9 vegetation seems to correlate the description of the later phases of the Pleniglacial by Frenzel
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11 (1983). The prevailing low pollen sums should not exclusively be considered to reflect
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13 taphonomic conditions near the Hohle Fels, but also as a sign of decreasing bioproduction as
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15 typical for cooler growing conditions (Frenzel 1983).
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20 The pollen sequence at Hohle Fels falls partially into the Denekamp interstadial of
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22 northern Germany and seems to reflect what has been described by Frenzel (1983) and Lang
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24 (1994) as increasingly cooler interstadials and stadials towards the LGM (MIS-2). Behre
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26 (1989) stated that the Denekamp interstadial represented only slight amelioration of the
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28 climate which facilitated the formation of shrub tundra, which may correspond to increased
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30 *Salix* sp. records from GH 6 onwards, and is reflected in the rodent fauna primarily
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32 specialized on tundra habitats (Ziegler in press).
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37 Charcoal records available for identification were below 100 fragments from the
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39 Aurignacian/Gravettian transition (GH 5/3d) and the Gravettian horizons (GH 3c/3b), thus we
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41 do not consider them fully representative for these periods (Asouti and Austin 2005). On the
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43 other hand, the low number of charcoal pieces from the transitional period may be a result of
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45 reduced occupation (Conard et al. 2012), while low numbers of charcoal material in the
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47 Gravettian horizons may be an indication of colder climatic conditions and a generally
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49 reduced presence of woody vegetation, which is also supported by a strong increase in burnt
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51 bone providing an alternative source of fuel (Miller 2009). In the pollen data both of these
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53 aspects are supported by increasing *Artemisa* sp. (lower samples of GH 3c). Similar
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55 vegetation conditions are indicated by several minor peaks of arboreal pollen in the La
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1 Grande Pile record between ca. 36-30 ka BP. There a subsequently strong decrease of
2 arboreal pollen indicates decreasing temperatures (Woillard 1978).
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7 The Füramoos pollen profile is the only MIS-3 record in relatively close vicinity to
8 Hohle Fels. There is, however, a hiatus at Füramoos between 40-14 ka BP (Müller et al. 2003),
9 thus throughout the Aurignacian and Gravettian horizons from Hohle Fels. Palynological
10 results there indicate an increase of *Betula* and *Pinus* percentages already at the Middle/Upper
11 Paleolithic transition. The starting sequence of botanical data at Hohle Fels seems to represent
12 a continuation of this process. Considering absolute pollen numbers, an increase of arboreal
13 pollen as visible at Les Échets (Wohlfahrt et al. 2008) is not detectable at Hohle Fels which
14 may be due to the position of Les Échets further south, roughly 200 km, but also to the
15 specific nature of the pollen record genesis at Hohle Fels.
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29 The avian fauna from Hohle Fels does not show significant differences between the
30 Aurignacian and the Gravettian assemblages (Krönneck in press). The small mammal fauna in
31 contrast indicates that the Gravettian is characterized by continuous cooling with increasing
32 tundra components to up to 72%, and a complete disappearance of boreal indicators towards
33 the end of the Gravettian (Ziegler in press). GH 5 has been micromorphologically interpreted
34 to show a warmer environment and higher moisture compared to the following horizons. A
35 cold fluctuation may have triggered the appearance of *Artemisia* sp.. Together with
36 *Helianthemum* sp., recorded with a seed in GH 3c, the genera are considered as heliophytic
37 and typical for the Denekamp interstadial, indicating the openness of the vegetation (Behre
38 1989). The micromorphological interpretation of the horizons corresponding to the Gravettian
39 occupation (GH 3c-3b) is a trend towards colder conditions which corresponds the cold
40 fluctuation after DO 6. Increased *Salix* sp. charcoal may be in relation to this cold fluctuation.
41 After GH 3b follows an occupation hiatus at Hohle Fels correlating the longest and coldest
42 stadial between 25-15 ka BP.
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The Magdalenian (16,700-14,700 cal yr BP)

The Magdalenian horizons from which wood charcoal, some seeds and bark fragments of *Arctostaphylos* sp. were identified, comprise several subhorizons of GH 3a and 1.

Cryo- and bioturbation have been documented in these horizons by micromorphological means (Miller 2009). However, the large majority of the artifacts and charcoal fragments are consistent with a Magdalenian period date. Within the charcoal remains from Hohle Fels, pine and willow are about equally present.

Subsistence conditions at Hohle Fels and the use of plant resources

The most abundant vegetative plant remains at Hohle Fels are *Arctostaphylos* sp. (bearberry) bark fragments. The taxon is a dwarf shrub of the northern hemisphere (Lang 1994) and is particularly frequent in areas with coniferous forest or pine steppe forest. It however also occurs above the tree-line as an element of tall forbs (Kühn et al. 2002). Open habitats are also preferred by *Helianthemum* sp. (rockrose), which is represented with one seed in the Gravettian horizon (GH 3c).

Both, fruits and leaves of bearberry are of technical and medicinal use. They are ethnographically reported for their use in leather tanning and as diuretika, and have been found at archaeological sites (Peacock 2002; Lepofsky 2002). Although it cannot be excluded that bearberry shrub was collected together with dwarf birch and willow as fuel, the relatively low wood productivity of dwarf shrubs render an interpretation for other purposes likely.

The seeds of Poaceae as basic steppe components were probably introduced into the cave by humans. The Poaceae were also represented by stalk fragments and phytoliths, all together mostly from the upper horizons (Gravettian/Magdalenian) of the cave stratigraphy.

1 *Cirsium*-type seeds of the Asteraceae family have been found in the transitional horizon from
2 the Aurignacian to the Gravettian. Many species of the genus occur in open habitats. *Cirsium*
3
4 sp. is ethnobotanically of diverse, including medical use, and has been also recorded for Dolni
5
6 Vestonice (Mason et al. 1994).
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9 Entomogameous taxa, such as the Asteraceae, generally have lower pollen production, thus
10
11 are usually underrepresented in normal pollen precipitation, and may have directly been
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13 introduced into caves together with the plants. This has also been suggested through the
14
15 analysis of human coprolites from Mammoth Cave (Kentucky) where Bryant (1969) suggests
16
17 the use of Asteraceae/Cichoriaceae, Liliaceae and Chenopodiaceae for human diet. However,
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19 cases where Asteraceae pollen in cave sites appears in large numbers have also been related to
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21 the activities of digger bee (Bottema 1975).
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26 The family of the Brassicaceae seems to have been of some importance as a dietary
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28 supplement. A probable seed of *Rorippa* sp. (cress), and one of *Draba nemorosa* type
29
30 (woodland draba) have been found in Gravettian horizons. While cress prefers habitats along
31
32 river banks, draba occurs in open drier habitats sometimes at the edge of woods. The
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34 Brassicaceae contain various substances, including vitamins, particularly if consumed fresh,
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36 but also glucosinolates providing these plants their specific acrid collard taste. Including the
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38 pollen spectrum into the list of potentially available food plants (cf. Hillman 1989), there are a
39
40 number of additional taxa whose leaves (e.g. Cichoriaceae) and roots or tubers (e.g. Apiaceae,
41
42 Cyperaceae, Liliaceae) may have been used by the ancient humans. Soft tissues have however
43
44 not been discovered from Hohle Fels which we ascribe to taphonomic reasons that also led to
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46 highly corroded and fragmented seed remains that occur in very low find densities.
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53 The chemical components of the botanical taxa from Hohle Fels imply an important
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55 role of micronutrients and vitamins in the human diet, while meat was probably a major
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57 macronutrient source (Münzel and Conard 2004; Conard and Malina 2006; Conard 2011). In
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59 contrast to sites in temperate regions, no staple plant foods have been found at Hohle Fels.
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1 This reflects the fact that botanical taxa with large seeds and fruits, such as acorn and hazelnut,
2 were not part of the natural vegetation around Hohle Fels during the Upper Palaeolithic. This
3 observation is in line with plant-animal subsistence ratios in modern hunter-gatherer diets,
4 indicating decreasing mean subsistence dependence on gathered plant foods from roughly
5 50% at latitudes between 11°-40° from the equator, to almost 0% of plant foods at >60°
6 (figure 2D and table 2 in Cordain et al. 2000). This suggests a link between cooler
7 temperatures and higher macronutrient input from fished and hunted animal food, which is
8 also related to decreased availability of plant foods in the higher latitudes. According to
9 Cordain et al. (2000) the dependence of modern hunter-gatherers on gathered plant foods in
10 tundra environments is between 6-15%, while it is up to 55% in grassland ecosystems.
11 The bio-production for grass and forest steppe has been estimated to 10-15 tons annually per
12 hectare (Frenzel 1983). Such calculations show a high degree of deviation from the mean bio-
13 production, thus nutritional value for animals is difficult to assess. Theoretical wildlife density
14 following a decreasing climate trend may be comparable to modern “natural” forest habitats
15 in central Europe. In comparison with the expectable density of human population there
16 should have been plentiful game during the periods considered here.

17 A number of factors may be responsible for the reduced variety of plant food at Hohle
18 Fels. Beside the site-specific post-depositional taphonomy, the generally low availability of
19 plant resources should have reduced the chances of deposition of plant material, particularly
20 in the cold season. The time of death of young animals indicates the use of the cave in the
21 winter season (Münzel 2001) which would partially explain the scarcity of the botanical
22 remains. The mode of food preparation, for example consumption of raw plants, would have
23 left no trace in the archaeological record. The general problem of the direct evidence of plant
24 food could not be resolved at Hohle Fels, as in contrast to some other Palaeolithic sites,
25 neither human feces with preserved plant tissue nor teeth wearing phytolith remains have been
26 discovered.

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As concerns the perception of climate fluctuations by Paleolithic humans, which also affects subsistence strategies, it would be very helpful to know precisely how climatic fluctuations changed the landscape and the availability of resources. Particularly the DO short-term fluctuations likely confronted ancient humans with pronounced environmental change, particularly at the frontier of the tree-line as at Hohle Fels. Recent paleoclimatological work provides some results helpful for answering such questions. The nature of MIS-3 stadial-interstadial transitions in Europe, exemplified by combining palaeoclimate and/or paleobotanical reconstructions and climate models for the GS15/GI14 time interval (56-48 ka BP) provide some relevant results for southwest Germany (Van Meerbeeck et al. 2011). According to these results, the tree line with forest/shrub tundra during the moderate state of the interstadial is right in our geographic area of consideration, making it highly sensitive even to minor climate fluctuations. According to Van Meerbeeck et al. (2011), climatic limitation of tree growth during early-MIS-3 stadials and interstadials deduced from pollen records shows no evidence of tree growth in Europe during stadials. The authors also argue that forests were probably restricted to latitudes south of 50°N during interstadials. As most of the records from Hohle Fels are from the earlier and middle MIS-3 intervals, the validity of these results for later intervals is difficult to assess. Bearing in mind that a general cooling trend throughout the MIS-3 towards the LGM (MIS-2) is superimposed on the stadial-interstadial fluctuations, it may well be that interpretations for the earlier intervals do not apply to our chronological sequence, although the sparse presence of wood taxa in the interstadial sequence reflected in the data from Hohle Fels implies the validity of the results for the earlier MIS-3 intervals. In such case, the subsistence conditions in habitats sensitive to ecological change require highly adaptive flexibility from human groups on one hand, but on the other also provide a potentially broader spectrum of subsistence resources for these groups due to geographically bordering ecotopes. The range of macrobotanical species

1 from Hohlefels that are not among the plants widely used today suggest that the inhabitants of
2 the site possessed a broad knowledge of useful plants.
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7 **Conclusions**

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10 The botanical data from Hohle Fels provides some important information on the local
11 environment and patterns of plant subsistence during the Upper Paleolithic in southwestern
12 Germany. Botanical remains from the site reflect the subsistence strategy throughout the
13 complete sequence of occupation, and document the broad knowledge of plant use in these
14 hunter-gatherer communities. The edible plants preserved at Hohle Fels are no staple food,
15 but represent important sources of micronutrients.
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24 The validity of the botanical micro- and macrofossils as environmental indicators is justified
25 through the multidisciplinary approach (pollen, phytoliths, wood charcoal, seed remains), and
26 the generally reduced density of vegetation cover in the mid-latitudes during the late
27 Pleistocene, equalizing the natural availability of resources and the exploitation spectrum.
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35 The Aurignacian geological horizons show a clear dominance of pine wood in the
36 earlier horizons and a strongly increased presence of willow charcoal at the end of this
37 sequence (GH 6). The increased *Salix* sp. records correlate with prevailing shrub tundra, while
38 increased *Pinus* sp. in the earlier part of the sequence may be related to tundra with boreal
39 elements. However, including the rodent fauna into these considerations, tundra elements
40 seem to prevail. These differences may be explained by increasingly cooler conditions
41 throughout the Aurignacian. This seems at least partially confirmed by the
42 micromorphological record from Hohle Fels (comparing GH 8 and 7), and is in agreement
43 with sediment studies in the east Carpathian region. These results, however, stand in contrast
44 to multiproxy research on central European sites. The latter research argues for increasingly
45 warmer winters and summers towards the end of this sequence. However, GH 6 and the
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1 following transitional horizon GH 5 have been micromorphologically interpreted as warmer
2 and moister than the previous horizons, which shows the difficulties of integrating the local
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4 into the supra-regional evidence, particularly when taking into account that the
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6 micromorphological evidence reflects a long-term development while the botanical data may
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8 be seasonal or discontinuous.
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11 The presence of wood at Hohle Fels throughout the occupation sequence is indicated
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13 by pollen, phytoliths and the direct evidence of charcoal. Few arboreal pollen in the
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15 transitional section from the Aurignacian to the Gravettian reflect an interglacial tundra
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17 vegetation with a mosaic of cold steppe elements and some patches of woody species. Only
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19 the lower deposits of the Gravettian (GH 3cf) document a short sequence dominated by boreal
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21 rodents, which may reflect the previous interstadial conditions. In contrast, the
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23 macrobotanical record of low numbers of charcoal predominantly composed of *Salix* sp. in
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25 the Gravettian horizons, which may be indicative of colder climatic conditions and a generally
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27 reduced presence of woody vegetation. In the pollen data both of these aspects are supported
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29 by increasing *Artemisa* sp. in the later horizons (GH 3c). Towards the end of the Gravettian
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31 sequence the rodents indicate cooling with increasing tundra components and a complete
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33 disappearance of boreal indicators.
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41 Our data from the archaeological site of Hohle Fels generate the first diachronic
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43 reconstruction of available plant resources during the Late Pleistocene in a previously
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45 underinvestigated region of southwestern Germany. While the record from Hohle Fels, like
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47 that from most caves, is somewhat spotty and discontinuous our data provide a direct link
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49 between human behavior and past environmental and ecological conditions.
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Captions

1 Fig. 1 Map showing centers of early art object finds with one center located in the Ach
2 Valley around the site of Vogelherd; Detail map shows Middle and Upper Paleolithic sites in
3 the Ach and Lone valley. 1 Kogelstein, 2 Hohle Fels, 3 Geißenklösterle, 4 Sirgenstein, 5
4 Brillenhöhle, 6 Große Grotte, 7 Haldenstein, 8 Bockstein, 9 Hohlenstein, 10 Vogelherd
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10 (background map from Rau et al., 2009)

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14 Fig. 2 Projection of different finds at Hohle Fels, (a) 3D distribution of identified wood
15 charcoal (large bubbles) and other finds (dots) in the different techno-complexes; Note that
16 the distribution of charcoal is relatively even for both Aurignacien phases and at least partially
17 also for the Magdalenien layer, while there are only few finds in concentrations for Gravettian
18 layer and the transitional phase from the Aurignacian to the Gravettian, (b) horizontal
19 distribution of wood charcoal from the Lower Aurignacian (GH 7 and 8)
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31 Fig. 3 East-West-Profile and position of the pollen column (P1-P12) and indication of
32 geological horizons (GH in white letters)
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39 Fig. 4 Percentage pollen data from GH 5-3b at Hohle Fels. For position of the pollen samples
40 see fig. 3. Pollen sum was calculated on the basis of arboreal (AP) and non-arboreal pollen
41 (NAP). The percentage values of the different taxa were calculated based on this sum. Note
42 that Poaceae and Cichorioideae are excluded from the pollen sum.
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51 Fig. 5 Wood charcoal percentages in the different geological horizons GH 8-1 and rough
52 radiocarbon chronology; Z: absolute numbers of records per GH (GH - geological horizons)
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58 Fig. 6 Plant macrofossils from Hohle Fels: (a) Poaceae grain fragment, (b) Poaceae culm
59 fragment, (c) Asteraceae, (d) *Helianthemum* sp., (e) *Arctostaphylos* sp. bark fragment, (f)
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1 *Pinus* sp. compression wood; (g) and (h) *Salix* spp. (note the difference in vessel density and
2 small diameters)
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7 Fig. 7 Botanical remains from Hohle Fels, showing percentages of wood charcoal, presence of
8 other plant macrofossils, pollen percentages (Poaceae and Cichorioideae calculated by
9 excluding them from the pollen sum), and interpretation of habitats derived from the rodent
10 fauna of Geißenkösterle (after Ziegler in press). GHs are the geological horizons at Hohle Fels.
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17 NGRIP data from North Greenland Ice Core Project members (2004)
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Figure 1
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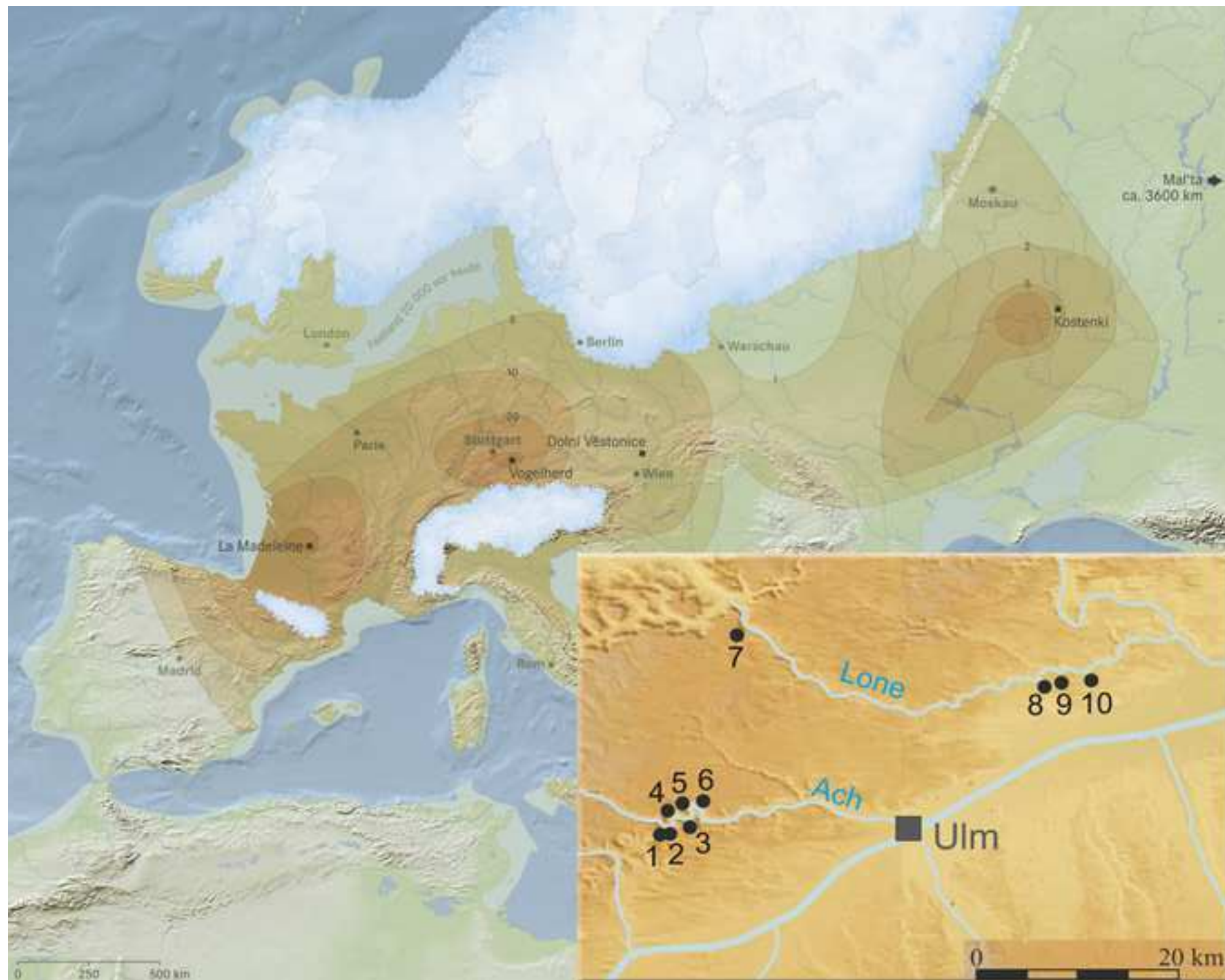


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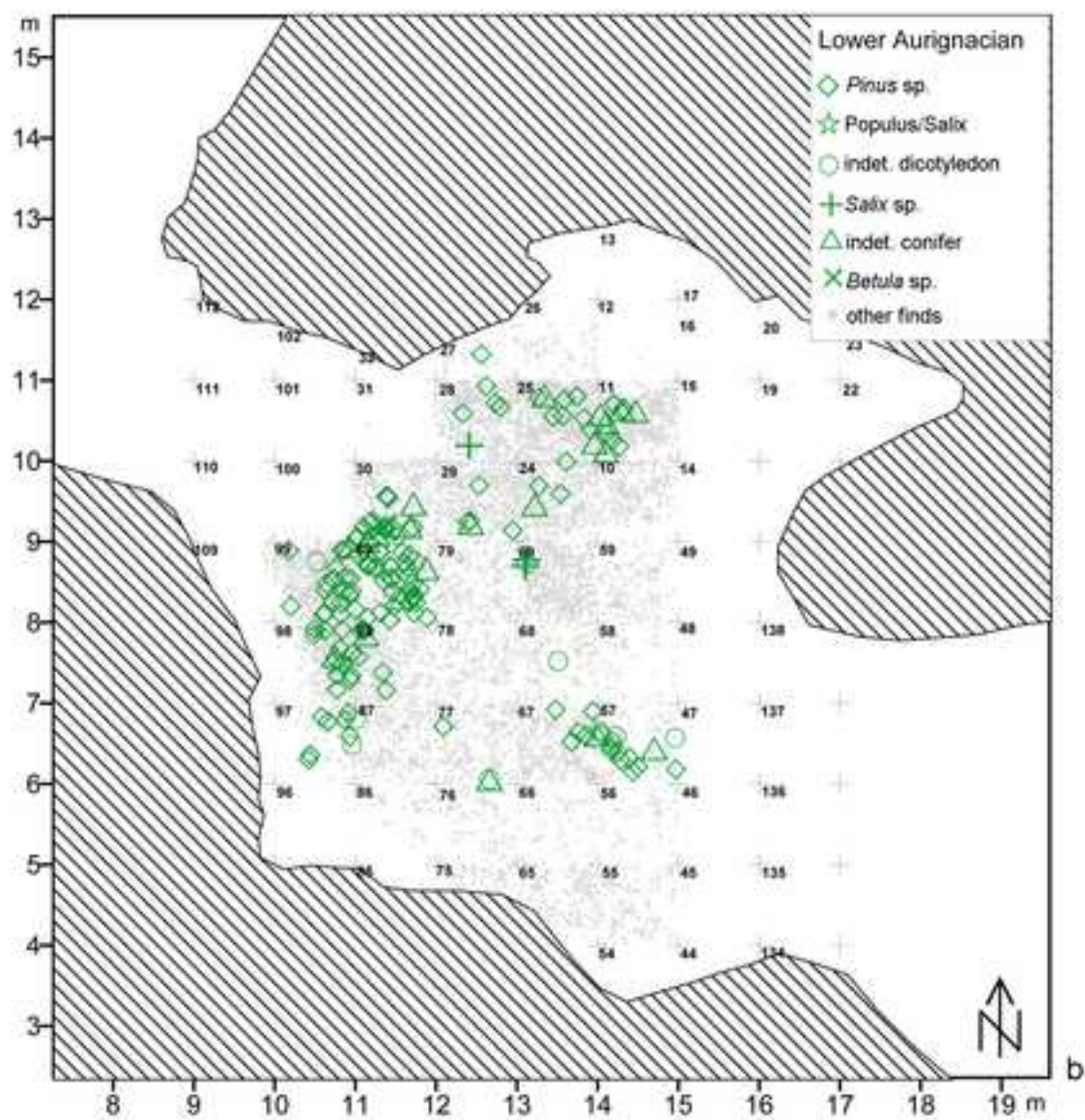
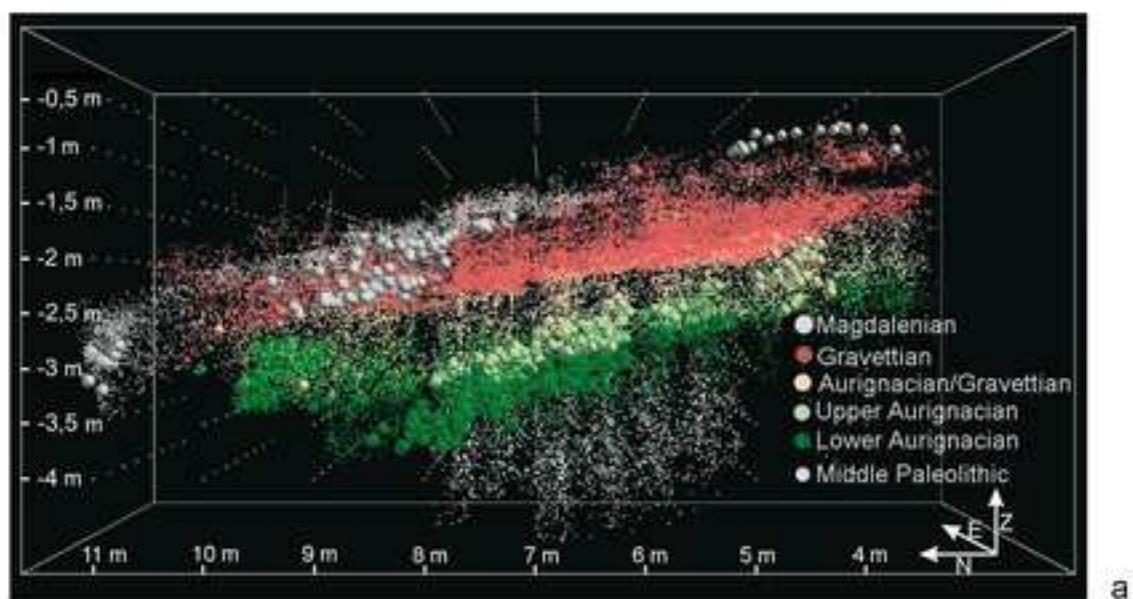


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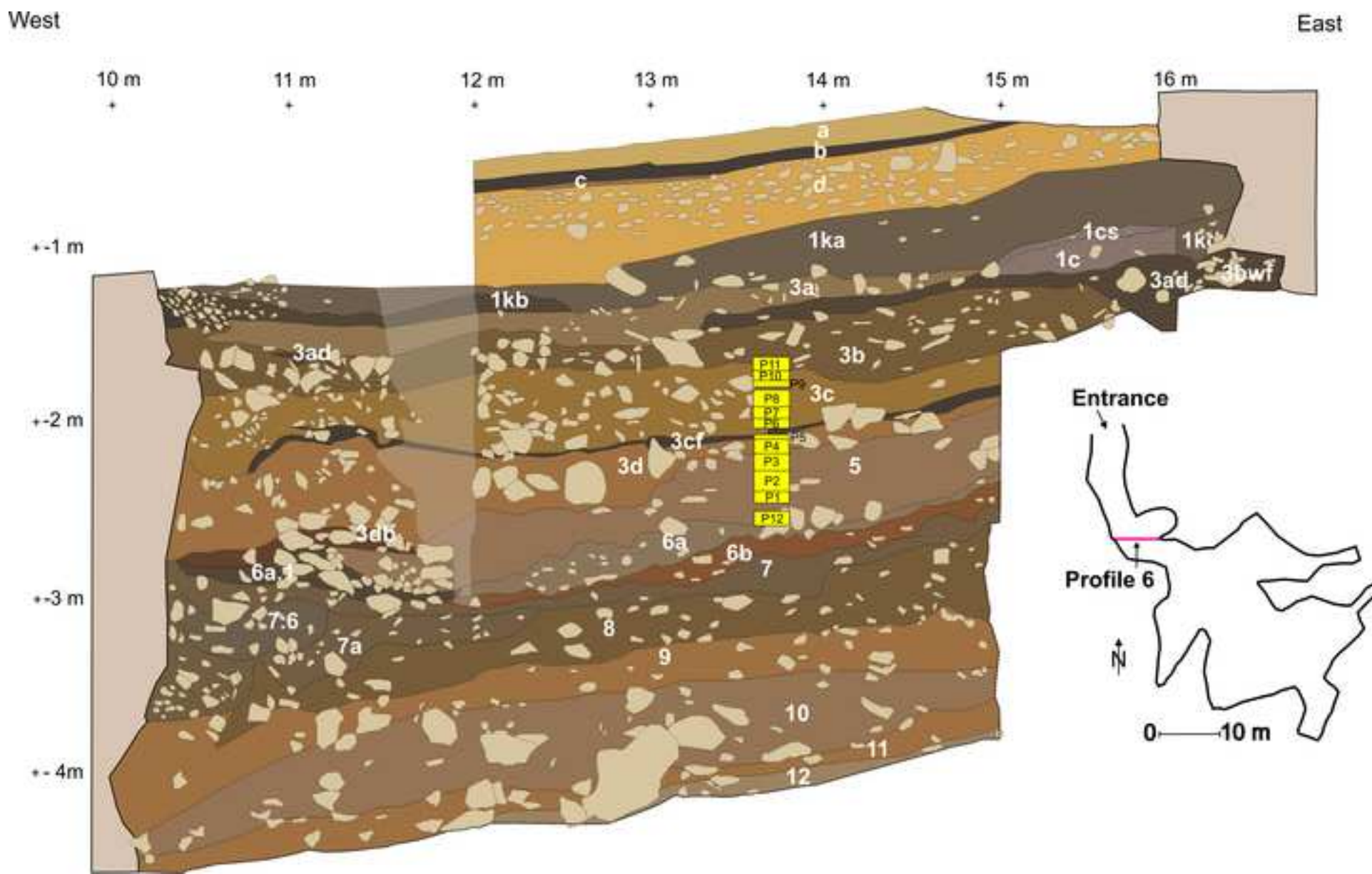


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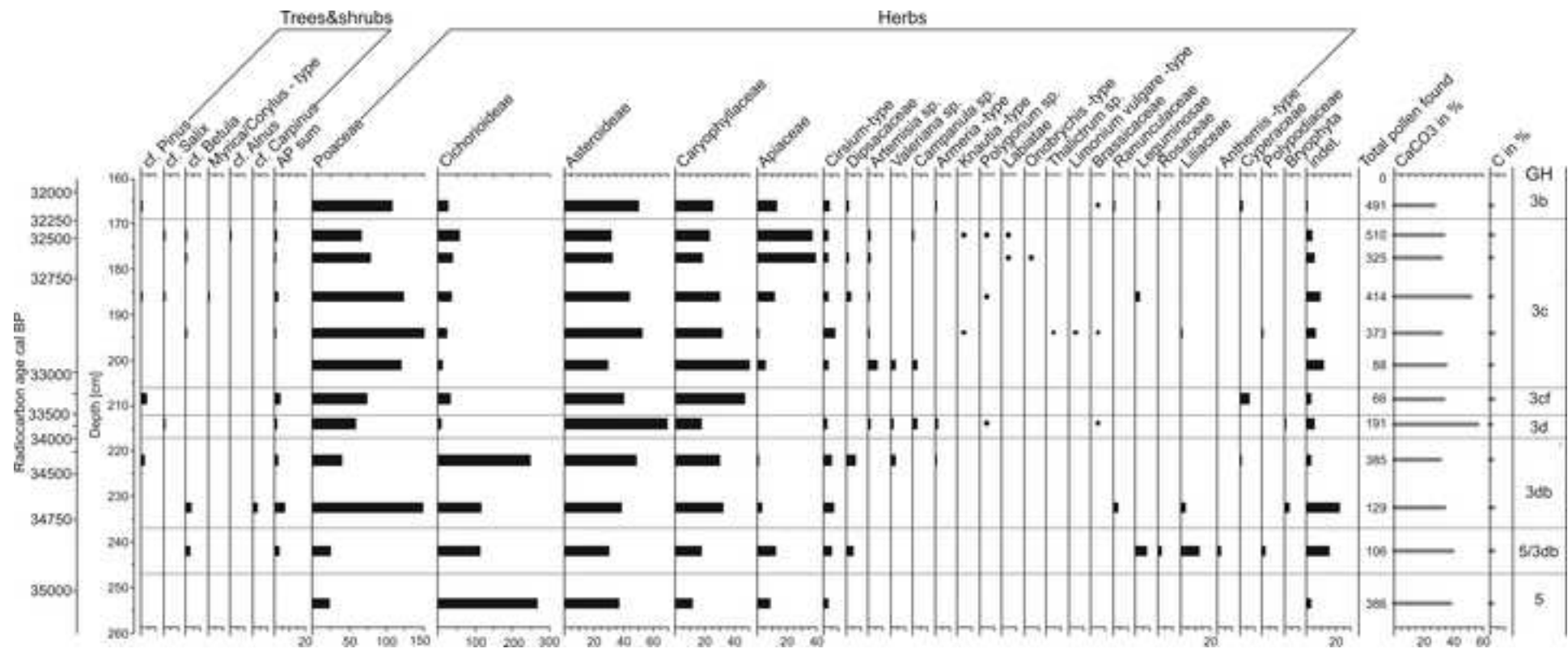


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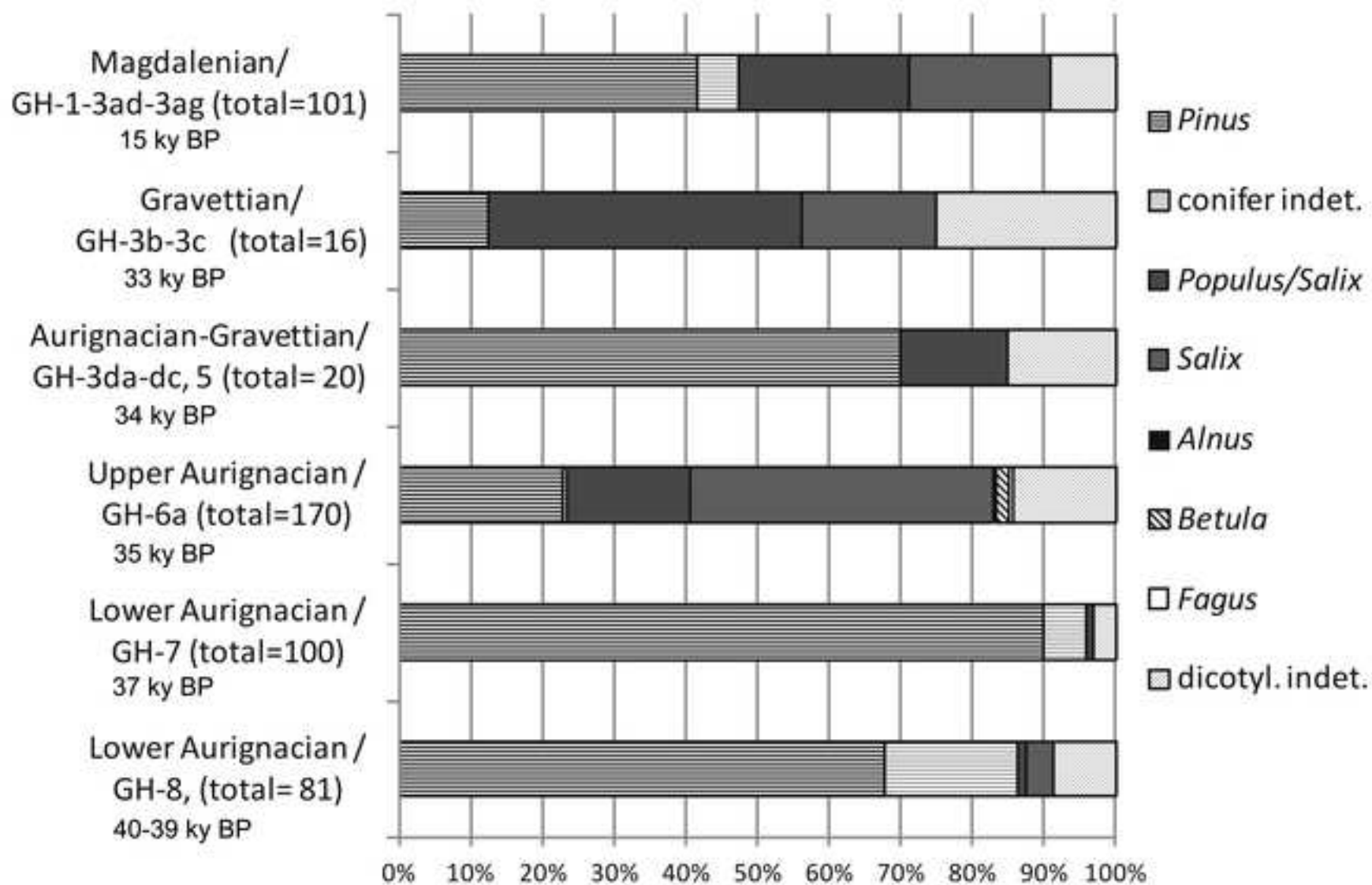


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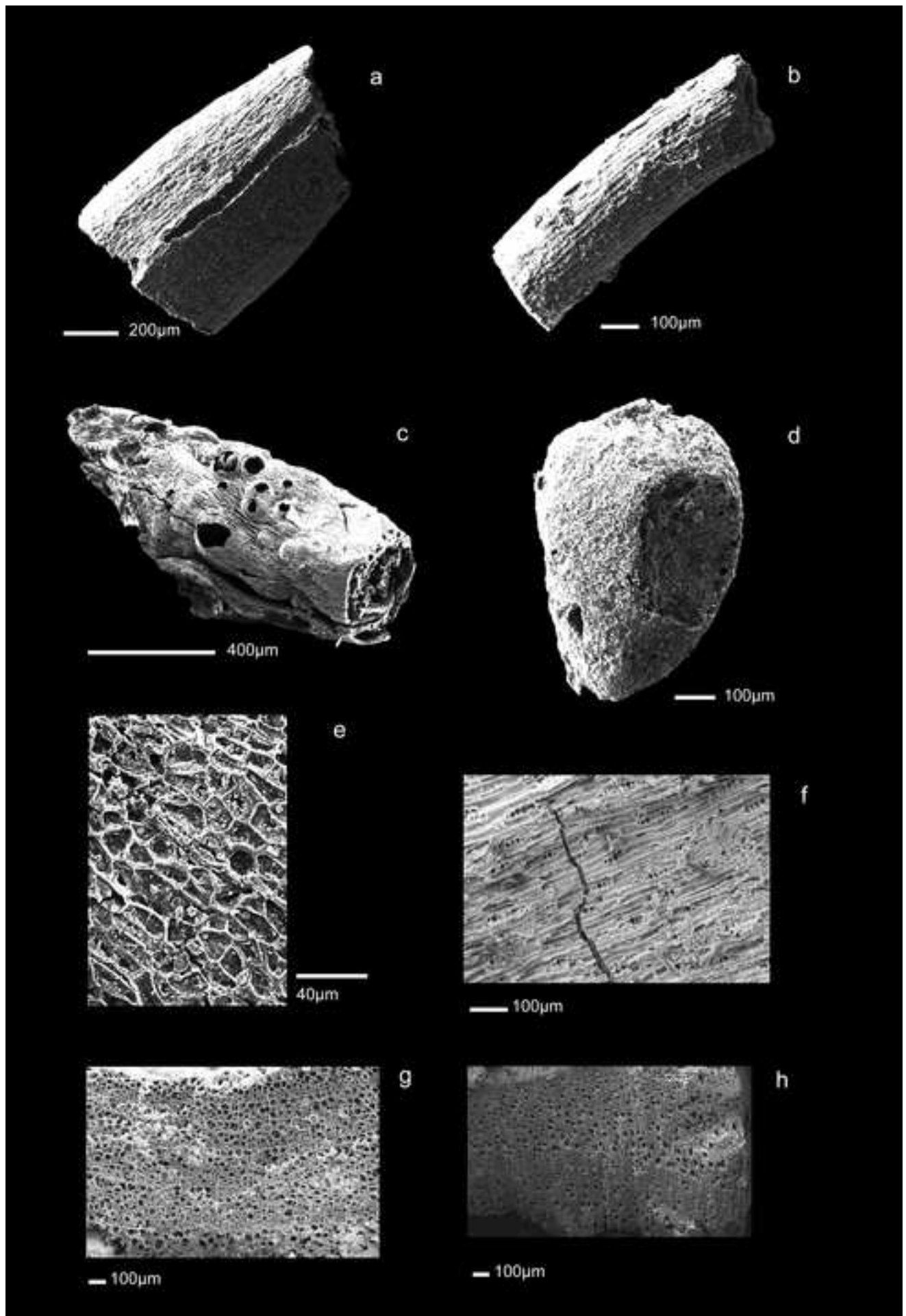


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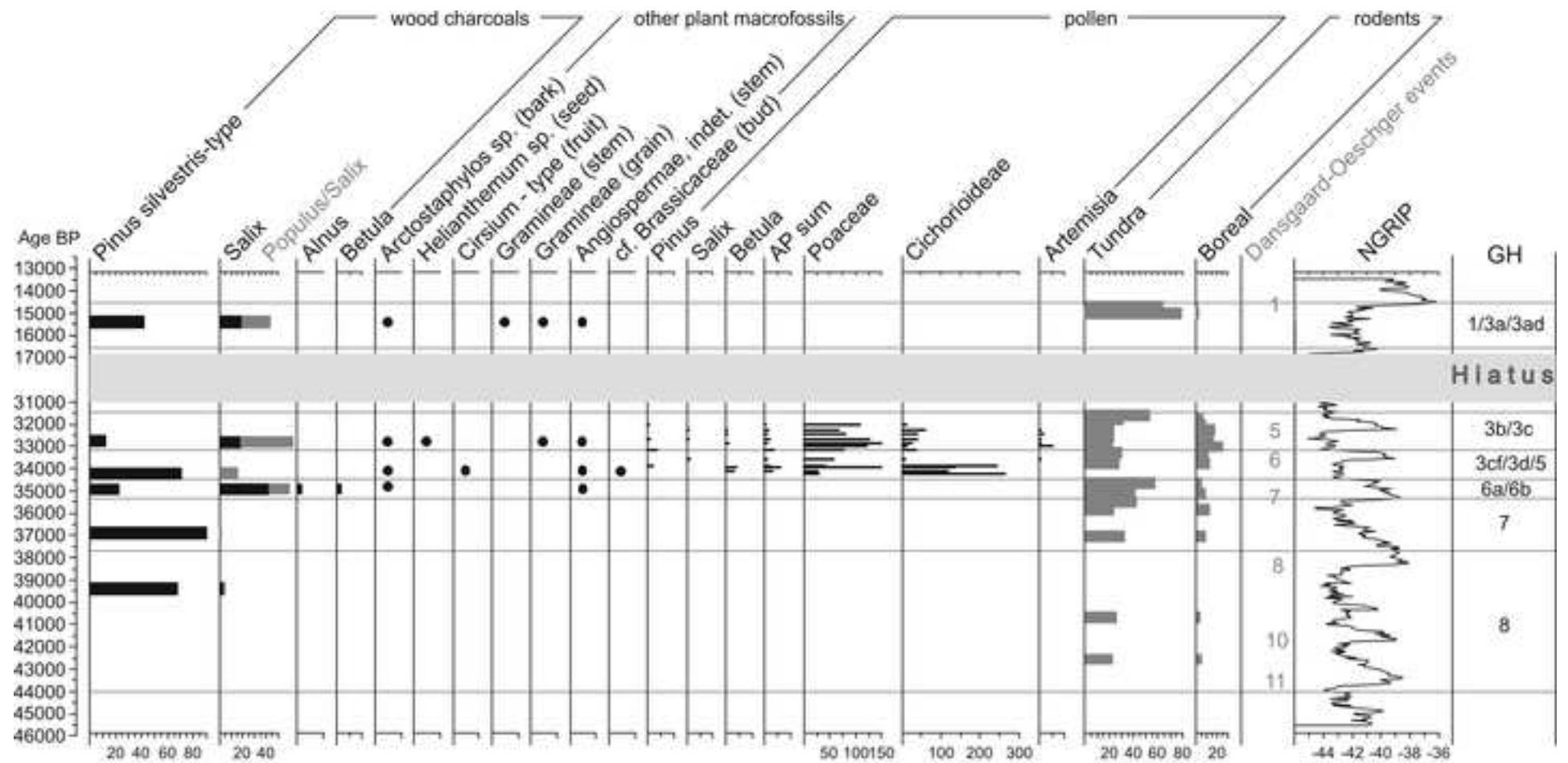


Table 1

Lab ID	GH	AH	Material	Date BP	$\delta^{13}\text{C}$	Calibrated age range (68,2 % prob.)		Cultural group	First publication
						from	to		
OxA-4979	6	III	<i>Salix</i>	27,600 ± 800	-24.7	32,580	30,960	Aurignacian	Housley et al. 1997
KIA 18875	6a	IIIa	<i>Fagus</i>	2,110 ± 40	-24.09	2,140	2,010	Modern intrusive	
KIA 18877	6a	IIIa	<i>Pinus</i>	30,170 + 250/-240	-26.48	34,440	33,980	Aurignacian	Conard 2003
KIA 18876	6a	IIIa	<i>Pinus</i>	31,010 + 600/-560	-24.95	35,570	34,400	Aurignacian	Conard 2003
KIA 18878	6b	IIIb	<i>Pinus</i>	29,780 + 330/-310	-26.06	34,190	33,640	Aurignacian	Conard 2003
OxA-4980	7	IV	<i>Salix & Betula</i>	28,750 ± 750	-25.6	33,600	31,910	Aurignacian	Housley et al. 1997
KIA 18879	7	IV	Unidentified Charcoal	31,160 + 1530/-1280	-30.07	37,260	33,760	Aurignacian	Conard 2003
OxA-19860	7b	Vb	<i>Pinus</i>	31,290 ± 180	-24.63	35,380	34,940	Aurignacian	Conard 2009
KIA 18880	8	Vb	<i>Pinus</i>	34,190 + 340/-330	-26.55	39,090	38,360	Aurignacian	Conard 2003

Table 1 AMS radiocarbon dates on charcoal from Aurignacian deposits of Hohle Fels. The *Fagus* from GH 6a represents a modern intrusion. KIA (Kiel, Leibniz-Labor für Altersbestimmung, Germany), OxA (Oxford Radiocarbon Accelerator Unit, England). Calibrated Data with calibration curve IntCal13 using OxCal 4.2.

	Aurignacian	Gravettian	Magdalenian
	GH 8-6a	GH 3c-b	GH 3a-1
<i>Arctostaphylos</i> sp. (bark fragments)	71	13	1
<i>Helianthemum</i> sp. (seed)	0	1	0
Poaceae (culm)	0	0	3
Poaceae (seeds)	0	0	1
Asteraceae (<i>Cirsium</i> - type)	1	1	0
cf. <i>Rorippa</i> sp.	0	1	0
cf. Brassicaceae (<i>Draba nemorosa</i> - type)	0	1	0
cf. Brassicaceae indet.	3	1	0
Dicotyledonae indet.	23	18	12

Table 2 Seeds and vegetative plant remains in the different cultural units