

The Hasli Formation of the Irchel Plateau – A key record for older Early Pleistocene interglacial sediments in northern Switzerland

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ABSTRACT

In the Alpine region of Central Europe, terrestrial Early Pleistocene deposits with preserved faunal and botanical remains are rare. The predominantly gravelly Höhere Deckenschotter (HDS) deposits of northern Switzerland and adjoining south-western Germany are considered the oldest Quaternary sediments in the northern Alpine Foreland, linked with the first extensive Quaternary Alpine glaciations.

This multidisciplinary study investigates the Hasli Formation (HF), a unique silty unit with well-preserved biological remains within an HDS sequence at the Irchel Plateau north of Zürich, providing new climatic and environmental data for these exceptional deposits, as well as crucial information about their age. Systematic mapping of the HF, in addition to the underlying and covering gravel units, has been coupled with sedimentary logging and biostratigraphic analysis at several sites. The HF is present over an area c.4 by up to 1.4 km, and where studied is 1.6–6.2 m thick. The sediments and biological material are indicative of overbank deposits accumulating within the damp floodplain of a large meandering river.

The recovered small mammal remains are from eight arvicolid species or genera, including *Mimomys pliocenicus*, *M. reidi/tigliensis* and *Clethrionomys cf. kretzoi*, which became extinct c.1.8 Ma, and *Pliomys episcopolis/simplicior*, which first appeared c.2 Ma ago. The over 75k identified molluscs, include c.72k coming from 89 terrestrial species and over 3k from 28 aquatic taxa. The molluscan faunas from all locations where the HF has been studied share important biostratigraphic marker species, and indicate analogous climatic and environmental conditions. The marker species include several that became extinct during the Early Pleistocene, of which *Clausilia stranzendorfensis* and *Cochlostoma salomoni*, present throughout the HF, are the most important as they disappeared c.1.8 Ma. Many marker species have modern or palaeo-distributions that lie far to the west, south and east of the Swiss Plateau, showing that the climate was much warmer than today, typical for the Tiglian warm stage. The alluvial floodplain was covered by rather dense, mature woodland.

Amino acid (AA) analysis shows that molluscan remains from the HF are among the oldest of the Quaternary shell material studied from across the Swiss Plateau. Palaeomagnetic data shows a change from reversed to normal polarity within the upper part of the HF. When combined, the small mammal and molluscan remains, palaeomagnetic measurements, AA geochronology and sedimentary data, suggest an age of 2.1–1.8 Ma for the HF. Recently produced cosmogenic dates bracket the age of the HDS gravels beneath the HF to depositional periods between 2.6 and 0.9 Ma, with the youngest ages being in disagreement with our findings. The abundance and diversity of the molluscs from the Irchel Plateau, with several rare extinct species, together with a notable small mammal assemblage, make this a key palaeontological site and an important reference point for European Quaternary biostratigraphy.

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1. Introduction

Terrestrial archives of Early Pleistocene deposits are rather rare in the Alpine region of Central Europe and are often difficult to date, which explains why current understanding of Early Pleistocene landscape evolution in this area is limited. Even scarcer are deposits of this age with well-preserved faunal and botanical remains that can provide biochronological age data, as well as valuable insights into their environmental and climatic contexts.

The deposits of the ‘Höhere Deckenschotter’ (HDS, ‘Higher Cover Gravels’) in northern Switzerland have long been thought to be the oldest Quaternary sediments in the western Alpine Foreland (Graf, 1993). They mostly consist of fluvio-glacial gravels, with intercalated glaciogenic sediments in places. These gravels directly overlie Neogene Molassic or Mesozoic bedrock and are normally preserved as localised relics on the top of low hills. The bedrock topography at several sites indicates that they accumulated within broad, incised channels (Frei, 1912; Gubler, 2009; Graf, 2019).

The HDS forms the highest of four distinct morphostratigraphic units that are present at different altitudes in northern and central Switzerland (Fig. 1), with the other three being the ‘Tiefere Deckenschotter’ (TDS, ‘Lower Cover Gravels’), the ‘Hochterrasse’ (‘High Terrace’) and the ‘Niederterrasse’ (‘Lower Terrace’). Of the two Deckenschotter units recorded in northern Switzerland and the neighbouring area of south-western Germany, the higher HDS is considered to be older than the lower TDS (e.g. Müller et al., 2002), with the two being separated by a significant phase of incision. These four morphostratigraphic units of largely gravelly sediments were originally defined for the Alpine Foreland of southern Germany by Penck and Brückner (1901–1909), who correlated them with four named glacial periods (Günz, Mindel, Riss and Würm). During the second half of the 20th century, however, it became increasingly evident that Quaternary glacial history in this area is much more complex (Schlüchter, 1988; Graf, 1993; Schlüchter and Kelly, 2000). The deposits of up to 16 glaciations have now been recorded from northern Switzerland, of which four have been linked with the formation of the HDS (Graf, 2009; Preusser et al., 2011; Graf and Burkhalter, 2016).

Since the late 20th century, the HDS deposits have been assigned to

the older Early Pleistocene (Gelasian), based mainly on small mammal remains found at Irchel Hasli, north of Zürich (Bolliger et al., 1996), but recent cosmogenic dates (Akçar et al., 2014; Claude et al., 2019; Knudsen et al., 2020; Dieleman et al., 2022) have suggested significantly younger ages that correspond to the middle (1.8–1.2 Ma; Santerian + Emilian Stages of the Calabrian) or later Early Pleistocene (1.2–0.77 Ma; Sicilian Stage of the Calabrian). So far, the divergence between these age estimations remains unresolved. This has stimulated a comprehensive search within HDS sequences for rare fine-grained sediments with biological remains, which although thought to represent interglacial deposits (Graf, 1993) have never been examined in detail until now.

This study investigates HDS deposits from the Irchel Plateau (Fig. 2), where they are rather well exposed and include a unique body of silty sediments that has been named the ‘Hasli Formation’ (HF; Preusser et al., 2011). It was within the HF that small mammal remains were discovered at Irchel Hasli that could be attributed to biozone MN17 of the European small mammal chronology, which dates between 2.6 and 1.8 Ma (Bolliger et al., 1996). Although this silty unit has exceptional preservation for a range of faunal remains, including small mammals and molluscs, it has never been systematically studied. This exceptional setting has permitted a multidisciplinary approach that provides new insights into one of the earliest periods of the Swiss Quaternary, including the climatic, environmental and sedimentary contexts for these deposits, as well as crucial information about their age.

A first systematic mapping of the extent, thickness and altitude of the HF is coupled with detailed sedimentary logging and biostratigraphic analysis at several key sites, giving a reliable lateral overview for much of the Irchel Plateau. Both old and new profiles through the HF have been systematically sampled to recover biological material. Although the main focus is upon the HF, this study also considers the underlying and covering gravelly sediments, using topographical mapping and clast petrographic analysis to give a more complete overview of the geometry, extent and stratigraphic relationships of the various gravel units that make up the HDS of the Irchel Plateau.

2. Geological setting and research background

The Irchel Plateau, located in northern Switzerland (Fig. 2), is formed of mid-Miocene Upper Freshwater Molasse that is overlain above an erosive contact by up to 50 m of HDS deposits, forming a hill that rises to c.350 m above the level of the Rhine. The HDS deposits extend for c.4 km, by up to c.1.4 km wide, with the base dipping from 655 to 660 m asl (above sea-level) at Hasli in the SE to c.625 m asl at Hochwacht in the NW.

Until the mid-20th Century, research on the HDS sediments of the Irchel Plateau was restricted to a study of the gravel units (Frei, 1912; Bendel, 1923; Weber, 1928, 1934). In 1955, H. Bräm discovered faunal remains (molluscs, worm granules) in a silty bed within the HDS at Irchel (Bräm, 1956), and all his material was subsequently stored at the Palaeontological Museum of Zurich (PIMUZ). In 1993, as part of a study of the Deckenschotter deposits of northern Switzerland, H.R. Graf published a thorough investigation of the stratigraphy and deposits of the Irchel Plateau, which included a first detailed description from several sites of the silty unit sampled by Bräm, and documented finds of molluscs, ostracods and *Chara* (Graf, 1993). In 1994, T. Bolliger discovered arvicolid teeth among the Bräm material that were of obvious importance for Quaternary biostratigraphy. After relocating where Bräm had found these teeth, he and D. Kälin undertook an excavation at Hasli in 1994–1995. All the recovered arvicolid teeth were published in Bolliger et al. (1996). A subsequent re-examination of the material by G. Cuenca-Bescós (2015) has narrowed the probable biostratigraphic age.

Graf (1993, in Preusser et al., 2011) distinguished five units within the HDS deposits of the Irchel Plateau (Fig. 3A). Four of these are gravels that possess significantly different clast petrographies (cf. 4.2), but are all thought to have originated from the Walensee-Rhine catchment. The oldest of these, the Langacher Gravel, is up to 6 m thick and directly

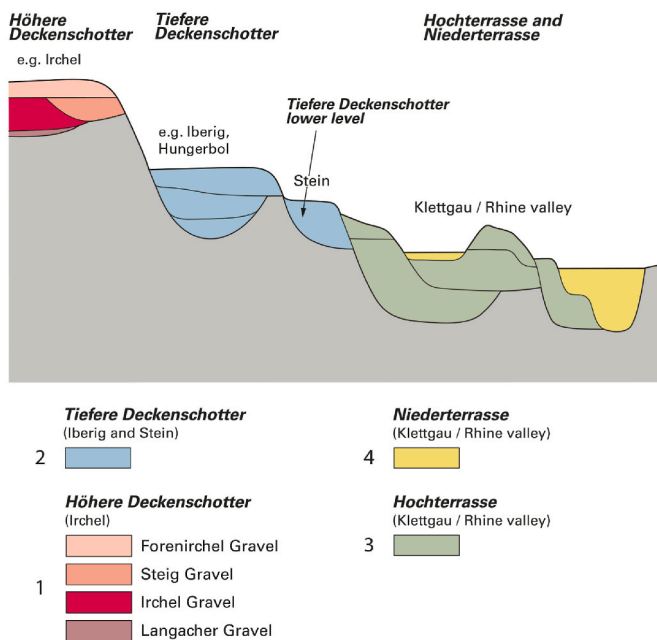


Fig. 1. A simplified schematic lithostratigraphy for Pleistocene deposits in northern Switzerland, from oldest (1) to youngest (4). Modified from Graf and Burkhalter (2016).

overlies the Molasse, but is only of limited extent due to subsequent erosion. This unit is succeeded at Irchel Ebni by a locally restricted series of up to 2.5 m of probable warm period fine sandy gravels, sands and overbank silts with calcareous nodules, here named the ‘Ebni silts.’ Above an erosive contact, there follows up to 25 m of the Irchel Gravel, which is present across most of the Irchel Plateau except for the SE where it is truncated by the Steig Gravel. The Irchel and Steig Gravels are overlain by the silts and fine sands of the Hasli Formation (HF), which Graf (1993) interpreted as warm period alluvial overbank sediments (Fig. 3A). Finally, the HF is overlain by the Forenirchel Gravel, which as will be shown below (cf. 4.4), seems to comprise several different deposits with a yet to be clarified stratigraphy, so the term ‘Forenirchel Gravel complex’ is used here.

This stratigraphic model has been challenged by Claude et al. (2019) and by Dieleman et al. (2022), who propose different stratigraphies with additional gravel-filled channels (Fig. 3B) to explain apparent age discrepancies between cosmogenic ages when placed within the lithostratigraphic units proposed by Graf (1993).

The dominant horizontal bedding structures within the gravel units of the HDS at Irchel is typical for cold-climate gravelly braided rivers (Miall, 1977, 2006; Gibbard and Lewin, 2002). Evidence for a direct glacier presence has not been found, but proximity to a glacier front is shown by boulders up to 1.5 m at the base of the Irchel Gravel at Strengelbrunnen, and over 1 m at the base of the Langacher Gravel at Ebni and within the Steig Gravel at Hasli (Graf, 1993). Clast morphometric analysis at several outcrops has also been used to confirm a

fluvioglacial origin for the Langacher, Irchel and Steig Gravels (Dieleman et al., 2022).

Basal tills and other glaciogenic sediments are clearly present within HDS sequences closer to the Alps at Uetliberg (Heim, 1891; Frei, 1912; Bolliger, 1999; Graf, 2019) and at Albishorn (Gubler, 2009; Graf, 2019). These form part of the third of three sub-units proposed for the HDS in northern Switzerland by Graf (2019, Fig. 16). Glaciogenic layers and glacial boulder lag deposits are also present within the third sub-unit of the HDS at Altberg, Wildstock and Egg, proving that glacier advances beyond the Alpine Massif to similar points to those reached during the Middle and Late Pleistocene, had already taken place during the Early Pleistocene (Graf, 1993; Preusser et al., 2011).

3. Methods used to study the Irchel plateau

3.1. Field methods

Graf (1993) documented the HF at six locations along the south-western edge of the Irchel Plateau (Fig. 2, Table 1). Four of these have been re-excavated (Hasli, Steig, Amselboden and Hochwacht), and three new sites have been discovered along the north-eastern edge of the Plateau (Schaffhuser, Wilemerirchel and Rütelbuck). At the four study sites, trenches were cut by hand using several terraces, making sure that the whole sequence was visible and that all weathered material was removed to reveal fresh sediment free from contamination. The profile at Steig East was partially excavated by a mechanical digger, as was the

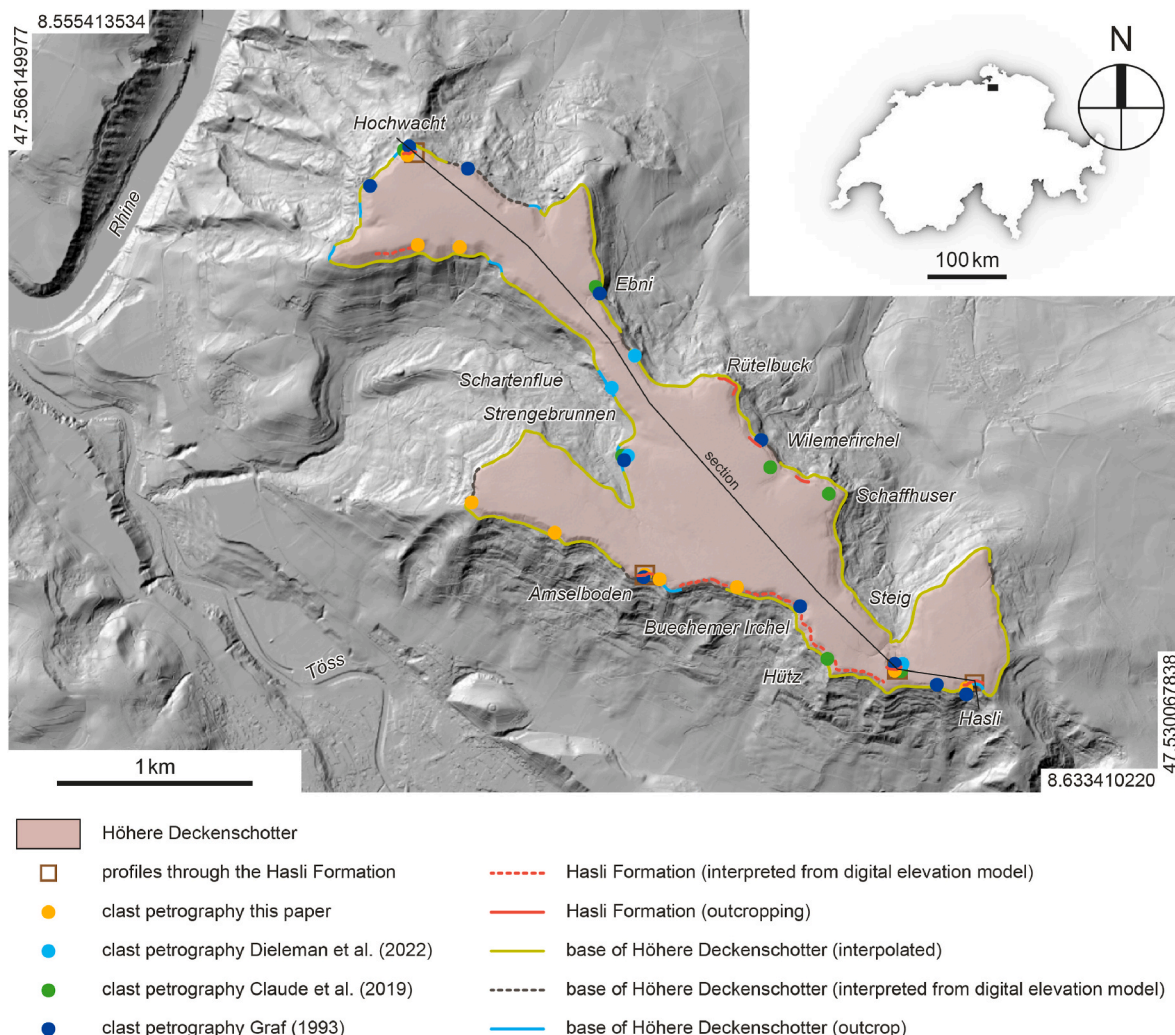


Fig. 2. Map showing the distribution of Höhere Deckenschotter (HDS) deposits across the Irchel Plateau. Studied profiles are marked with a square.

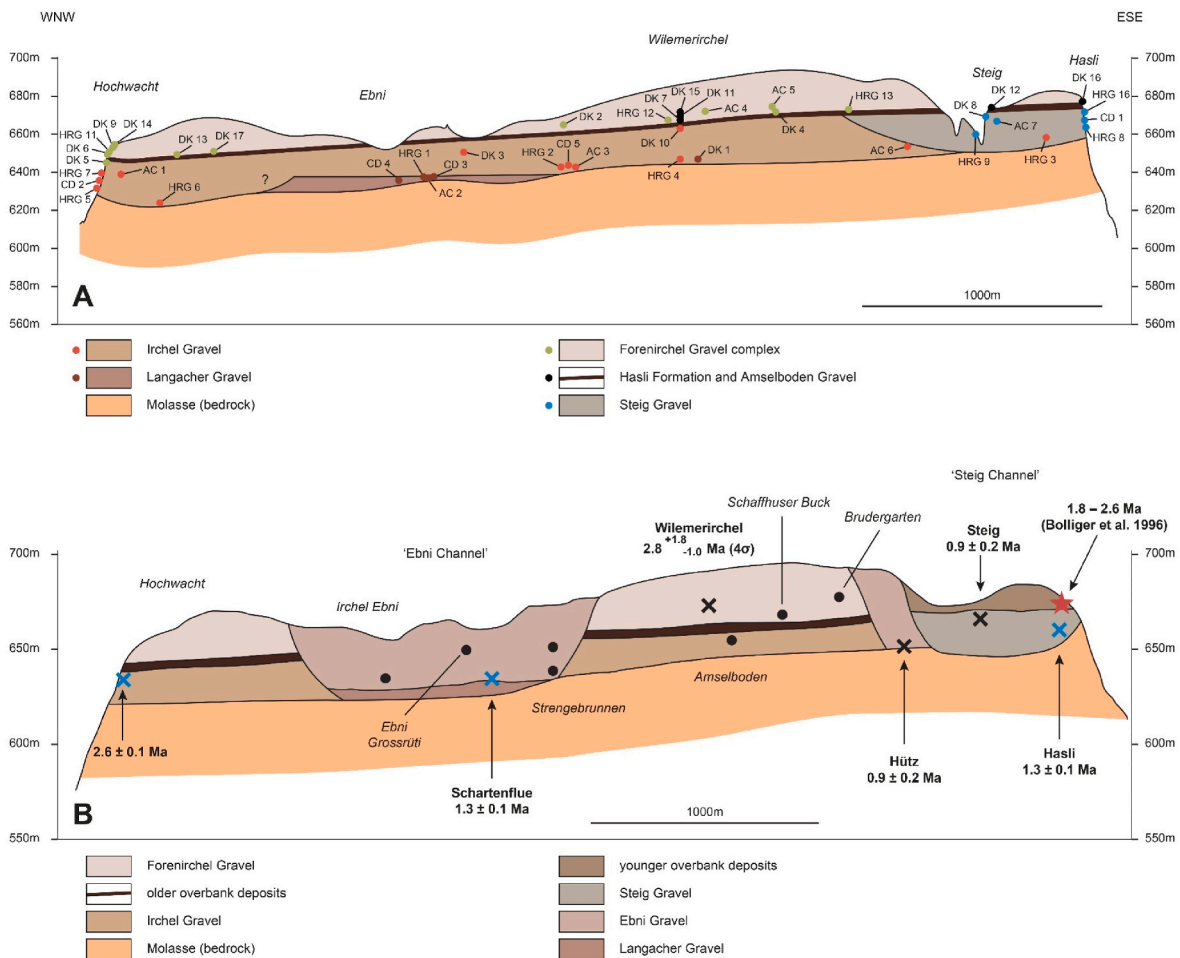


Fig. 3. Cross sections through the Irchel Plateau showing the different gravel units and the position of the Hasli Formation (trace of Section A shown in Fig. 2). Section A: according to Graf (1993), Preusser et al., (2011), and this study; Section B: according to Dieleman et al., (2022), overbank deposits related according to Dieleman pers. comm. 2023. Samples for clast petrography - HRG: Graf (1993), AC: Claude et al., (2019), CD: Dieleman et al., (2022), DK: this study (cf. data in SM Tables S1a–S1c). Black crosses = cosmogenic dates from Claude et al., (2019), blue crosses = dates from Dieleman et al., (2022), black dots = CD clast petrography samples.

profile through stratigraphically lower silty sediments at Ebni. At both Hochwacht and Steig, two profiles were investigated that were around 45 m apart. After cleaning, the sediments were documented in detail and sampled. Comprehensive series of samples between 1.5 and 7.0 kg were taken for molluscan analysis, while larger samples of 10–26 kg were taken from selected layers to recover small mammal remains. Samples were taken according to lithological boundaries, with a typical sampling interval of 10–30 cm depending upon whether the sediments looked favourable for molluscs and other remains. Where processing of the smaller samples revealed promising small mammal material, return visits were made to take new large samples. Small samples (0.1–0.2 kg) were also taken for pollen analysis in organic layers and in grey silty layers with minimal weathering, while samples for palaeomagnetic study were taken from the same profiles in 2016–18. At Ebni, a column of bulk samples between 2.0 and 22.0 kg was taken in 2017, together with smaller samples for pollen and palaeomagnetic analyses.

The extent and lateral continuity of the HF between the study trenches was mapped in the field, assisted by high-resolution digital elevation models (Swisstopo DTM-AV). The coordinates and altitude of the base of the HF were precisely measured at five sites across the Plateau by Koch & Partner (Laufenburg) using GNSS measurements in combination with photogrammetric evaluation methods.

3.2. Clast petrographic analyses

To better constrain the stratigraphic relationships between the gravel units underlying and overlying the HF, clast petrographic analyses were undertaken at 17 sites across the Irchel Plateau (Figs. 2 and 3). Samples of 100 clasts 2–6 cm across were examined from each site. The clasts were washed, broken, tested with hydrochloric acid (3.2%), examined with a magnifying glass and classified. Six main rock classes were employed: limestone, dolomite, radiolarite/chert, sandstone, quartzite/vein quartz, and crystalline rocks.

The new results were compared with those of 13 clast samples from Graf (1993, n = 200), 7 from Claude et al. (2019, n = 250) and 5 from Dieleman et al. (2022, n = 251–279). This gives a total of 42 analyses, with 7391 examined clasts (SM Tables S1a–S1c). Although the rock classes used were slightly different, they could nevertheless be aggregated into comparable groups.

3.3. Biological methods

3.3.1. Small mammals

Bulk sediment samples of 10–26 kg were taken from selected layers in most profiles and wet sieved to recover small mammal remains. By contrast, c.800 kg was wet sieved during the 1994–95 excavation at Hasli (Bolliger et al., 1996), from the equivalent of Layer 12 in the present study (both excavations were made by D. Kälin and T. Bolliger).

Table 1

Studied outcrops with the Hasli Formation (SE to NW) within the HDS of the Irchel Plateau (SM = Supplementary Material). Sites with no bibliographic reference are newly discovered.

Site	Coordinates [°] (WGS84 ~ETRS89); altitude: m asl (base of HF)	References	Drawn profile
Hasli	8.619890124/47.534838816; 675.0	Graf (1993), p. 41, Bolliger et al., (1996)	Fig. 5
^a Steig WestSteig East	8.614020045/47.535465189 8.614643371/47.535422885; 669.7	Graf (1993), p. 41	SM Fig. S1D Fig. 6
Buechener Irchel	8.606111757/47.538846230	Graf (1993), p. 41	
Schaffhuser	8.608065146/47.544313332		
^b Wilemerirchel	8.605822276/47.545622194		
Rütelbuck	8.602493269/47.548902774; 659.5		
Amselboden	8.597607722/47.539930022; 663.5	Graf (1993), p. 41	SM Fig. S1C
Forenirchel	8.596176187/47.540070258	Graf (1993), p. 40	
Hochwacht West East	8.581913696/47.559379541 8.582341341/47.559492252; 647.4	Graf (1993), p. 40	SM Fig. S1A Fig. 7

Sites in **bold** have been investigated in detail during this study. The coordinates and altitudes (base of the HF) of the 5 measured points have an accuracy of 2–5 cm.

^a “Schottergrube” in Graf (1993), “gravel pit near Steig” in Akçar et al., (2014), “Steig” in this paper.

^b Investigated in detail during 2021–22, but not included with the study profiles discussed here because the base of the HF was not reached.

3.3.2. Molluscs

The 99 samples of 1.5–7 kg taken for molluscan analysis (totalling >375 kg) from the four principal sites, as well as 5 bulk samples from Wilemerirchel (total 113 kg), were washed through a series of sieves (smallest 0.3 mm). After drying, the residues were sorted in their entirety to extract molluscs, as well as other biological material like bone fragments, earthworm granules, bird eggshell, plant remains, ostracods and *Chara*. The totality of the shell material was then identified to species level with the help of a personal reference collection (held by N. Thew), shells lent by the Natural History Museum in Bern and reference works such as Ložek (1964) and Frank (2006). After identification, the shell fragments were quantified for the majority of samples, with MNI (minimum number of individuals) values listed for each site by sample and by species in results tables (SM Tables S2b and S2c). The counts have not been adjusted for sample weight, but a ‘total molluscs per kilo of sediment’ value shows molluscan abundances for the layers. For some samples with very abundant molluscs, frequency estimates are given instead of absolute counts. To facilitate interpretation, the taxa have been placed in one of fifteen ecological groups for both terrestrial and aquatic habitats (Fig. 10; SM Tables S2a and S2d), defined according to published ecological data (Favre, 1927; Boycott, 1934, 1936; Ellis, 1962; Puisségur, 1976; Mouthon, 1980; Kerney et al., 1983; Turner et al., 1998; Kerney, 1999; Glöer, 2002, Glöer, 2020; Welter-Schultes, 2012) and personal field observations. Malacozones have been defined (SM Tables S2b and S2c) based upon the presence and abundance of biostratigraphic marker species, significant changes in the frequencies of more common taxa and the proportional representation of the ecological groups. Further subdivisions into subzones represent finer differences between the assemblages.

3.4. Amino acid (AA) geochronology

This approach uses chiral amino acid analysis of biominerals (such as mollusc shells) to determine intra-crystalline protein decomposition (IcPD) behaviour. Where closed-system behaviour occurs, protein decomposition should depend solely on time and temperature (e.g. Penkman et al., 2011, 2013), so the degree of IcPD can provide a relative chronology. Several different biomineral materials have been analysed from a number of sites across the Swiss Plateau, spanning from the Early Pleistocene to the Holocene, in order to construct an aminostratigraphy that can help to date the Deckenschotter deposits. These materials included calcitic opercula from the water snail *Bithynia tentaculata*, slug plates and earthworm granules, plus aragonitic shell fragments from the large terrestrial snails *Arianta arbustorum*, *Cepaea hortensis* and *Fruticola fruticum*. Such a range of materials was used because the various sites rarely have more than a few of each type. The methods used and all analytical results from the Swiss sites are fully discussed in Penkman et al. (2024). Here we focus on the results from the slug plates coming

from the Irchel Plateau and a few other sites across the Swiss Plateau.

3.5. Magnetostratigraphy

As part of an extensive palaeomagnetic study of Deckenschotter deposits in northern Switzerland, samples were taken within the HF at Hochwacht East, Steig West and Hasli, as well as from the ‘Ebni silts’. A detailed description of all field and laboratory methods is given in Scheidt et al. (2023a). From the field samples taken at these four sites, 67 lab samples were prepared and subjected to demagnetisation procedures in order to determine their characteristic remanent magnetisation (ChRM). Strict selection criteria were applied to ensure that the ChRM of the lab samples represents detrital or post-detrital remanent magnetisation generated by the geomagnetic field during or shortly after sediment accumulation. This selection process reduced the data set to the results from just 23 lab samples. These were recovered from five depth levels at Hochwacht East (7 samples), one level from Steig West (1 sample), seven levels from Hasli (7 samples) and four levels from Ebni (8 samples).

4. Results for the stratigraphy and sedimentology of the HDS sequence at Irchel

4.1. Outcrops and spatial extent of the HF and other silty levels with biological material

In most locations, the HF is present in steep, hard-to-access terrain above near-vertical cliffs formed by the underlying cemented Irchel or Steig Gravels. Natural outcrops of the HF are relatively rare due to its modest thickness, low resistance to weathering and attractiveness for vegetation. Where visible, the HF is mainly formed of silt and fine sand, as confirmed by the detailed logs for the study profiles (cf. 4.3). The marked change from weathering-resistant gravels beneath the HF to the easily-eroded silts of this unit, produces a well-defined geomorphological marker horizon that can be reliably traced for much of the length of the Irchel Plateau (Figs. 2, 3A and 4). While the study profiles and new outcrops give precise indications for the position and thickness of the HF (Table 1), the presence of this unit is also marked by a modest but noticeable flattening in the terrain that is usually covered by redeposited slope material. In some locations cemented layers at the base of the overlying ‘Forenirchel Gravel complex’ are also clearly visible in both the field and in the digital terrain model, allowing the probable summit of the HF to also be recognised. An extrapolation of the altitude of the HF from the various outcrops suggests that the presence of this unit is affected by surface topography, as in places it has been lost due to subsequent surficial erosion (Fig. 3A). No outcrops of the HF could be found in the Schartenflue-Ebni area, for example, where there is a depression in the Plateau surface.

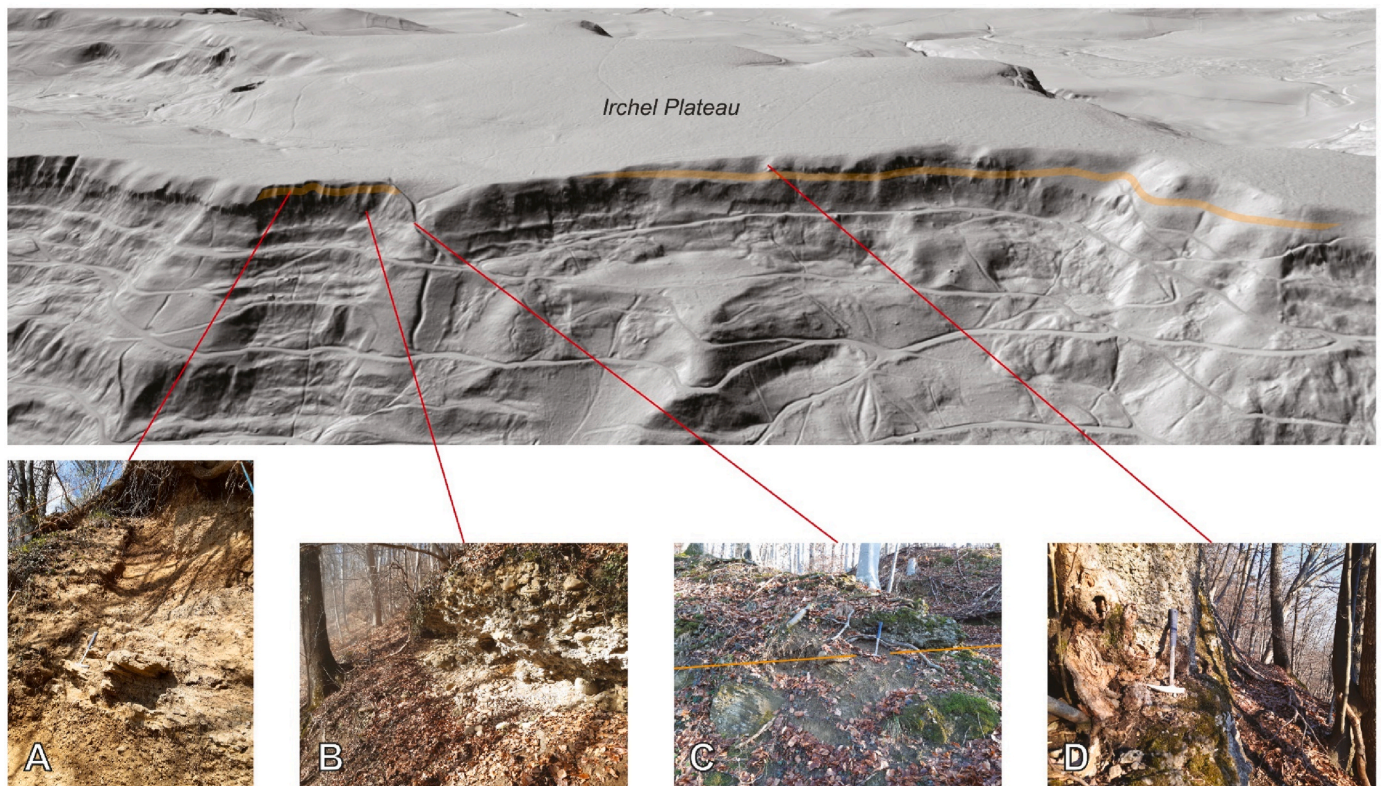


Fig. 4. A 3-dimensional view of the south-eastern part of the Irchel Plateau (high-resolution digital terrain model, ©Federal Office of Topography, swisstopo), showing outcrops and the assumed position of the Hasli Formation (HF). A: Amselboden profile through the HF; B: near the base of the Irchel Gravel; C: contact Massasse/HDS Irchel Gravel; D: 'Forenirchel Gravel complex.'

At Hasli, located at the SE point of the Irchel Plateau, the HF overlies the Steig Gravel at 675.0 m asl, while at Hochwacht East, at the NW corner of the Plateau, the HF overlies the Irchel Gravel at 647.4 m asl. The base of the HF thus dips at a gradient of c.7 ‰ from the SE to the NW and runs more or less parallel to the base of the HDS.

The 'Ebni silts' first described by Graf (1993), have so far only been found at this location. They represent the lowest level with biological material found at the Irchel Plateau. Apart from these silts and the HF, a third, 'upper level' with silty sediments and biological remains has been newly discovered within the HDS at Hochwacht West (cf. 4.3.6), c.3 m above the HF within fluvial gravels attributed to the 'Forenirchel Gravel complex' by Graf (1993). In addition to a lens of silty fine sand (2.5 m wide by up to 0.4 m thick) with abundant well-preserved molluscs, the summit of the gravels that underlay this sandy lens included silty soft clasts up to 0.35 m across that also contained abundant molluscs.

4.2. Clast petrography of the gravel units bounding the HF

A reappraisal of all the new and published clast petrographic data seems to confirm the validity of the four petrographic gravel types proposed by Graf (1993). The first gravel type, with the highest proportion of crystalline clasts, corresponds to the Langacher Gravel, while the second type, with somewhat lower crystalline values, represents the Irchel Gravel. The third type, with a high-dolomite content, some crystalline clasts and a relatively low limestone content, corresponds to the Steig Gravel. The fourth type, with a very low crystalline content and high proportion of limestone, characterises the 'Forenirchel Gravel complex'. Despite somewhat different methodologies (Graf, 1993; Claude et al., 2019; Dieleman et al., 2022, this paper), the four data sets are remarkably congruent relative to their apparent stratigraphic position (SM Tables S1a–S1c). The stratigraphic expression of these four types of gravel clast petrography (Fig. 3A) can be fully explained within

the relatively simple model proposed by Graf (1993; Fig. 23). Based on clast petrographic data alone, there appears to be no necessity to propose the more complex geometries postulated by Claude et al. (2019) and Dieleman et al. (2022).

Furthermore, there seems to be a lithostratigraphic succession between the gravel types, with the proportion of crystalline clasts decreasing markedly from the base of the HDS (Langacher and Irchel Gravels) towards the top ('Forenirchel Gravel complex'), while the proportion of limestone increases significantly. Notably, all but one of the samples with a petrographic signature typical for the 'Forenirchel Gravel complex' overlie the HF, while the other sample (DK 5) lies immediately below the HF.

In addition, there is a newly identified gravel type, the 'Amselboden Gravel', which exists as a gravel unit several metres thick in the Amselboden profile, a gravel up to 0.6 m thick at Steig West (Fig. 6C) and a 0.2 m layer at Hasli. This gravel is dominated by friable, often highly weathered sandstones, while calcareous clasts are completely absent (SM Table S1c). It is typically rather silty, matrix-supported and has no dominant clast orientation. At Amselboden and Hasli it forms near horizontal layers, while at Steig West it is present within an erosion channel (Fig. 6C). Nevertheless, in all three profiles the Amselboden Gravel is found immediately above the HF and accumulation seems to have been rather rapid, possibly due to mass movement within the river valley. It is thus notably different from the other gravel types, which are mostly clast-supported, rather coarse sandy fluvio-glacial gravels, with a great variety of Alpine clasts (with frequent limestones) that tend to be horizontal or imbricated. The petrographic signature of the Amselboden Gravel, with weathered sandstones, no limestones, and the presence of soft-clasts of probable diamicton, suggests that this gravelly material may have been redeposited from pre-existing gravel bodies upstream that had already been subject to strong weathering.

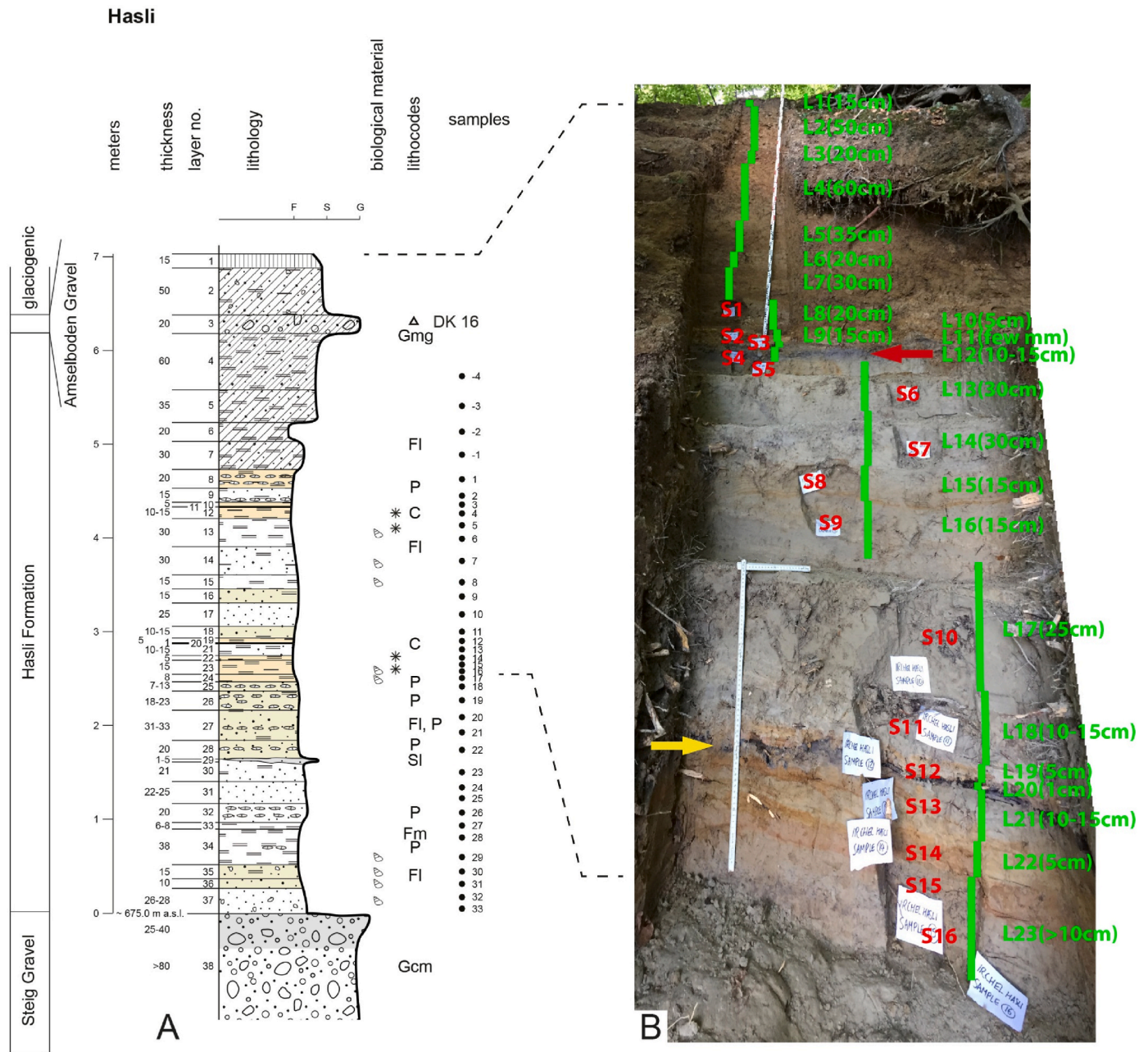


Fig. 5. Profile Hasli, the type locality for the Hasli Formation. A: lithostratigraphic profile with layer numbers. B: photo documentation of the upper part of the profile, with layer numbers and sampling points for biological material indicated. Red arrow = dark grey clayey-silts with small mammal remains (Layer 12); yellow arrow = lower lignite horizon. For lithostratigraphic key see Fig. 6.

4.3. Lithostratigraphy and sedimentology of the HF

Six profiles through the HF were recorded in detail at four locations (Fig. 2). Short descriptions of the sediments in these profiles are given below, which are restricted to layers that clearly belong within the HDS. Overlying, possibly Middle Pleistocene, glaciogenic sediments are not described. Lithofacies codes are according to Miall (1977, 2006).

4.3.1. Hasli (Fig. 5)

The 6.2 m of HF observed at Hasli is the longest and most complete sequence through this unit, making it the type profile. The HF begins above the strongly cemented summit of the Steig Gravel with silty fine sand with some pebbles (Layer 37). Above this are 2.2 m (up to Layer 25) of thinly interbedded grey/olive-grey silts and fine sands (reddened by Fe in places) with intermittent bands of calcareous nodules, followed by

0.4 m of grey silt with clay, and capped by 1 cm of black finely laminated lignite (Layer 20). Above this are 1 m of grey thinly interbedded silts and fine sands with calcareous nodules (stained by Fe in places), followed by 0.3 m of grey silt with clay, then 0.10–0.15 m of dark grey clayey silt with small mammal remains, capped by 3–5 mm of black finely laminated lignite (Layer 11). Above this are 0.4 m of olive-grey clayey silts, then 1.45 m of olive-grey/olive-brown sandy silts with intense iron staining. This is covered by 0.2 m of strongly weathered fine-medium matrix-supported gravel with frequent clasts of decomposed sandstone with no preferred orientation, which corresponds to the Amselboden Gravel. Molluscs are found in most layers, from the base of the profile up to c.4.75 m (Layers 37–8). The most important small mammal remains were found in Layer 12, 4.2–4.35 m from the base and 2.0–1.85 m from the top of the HF.

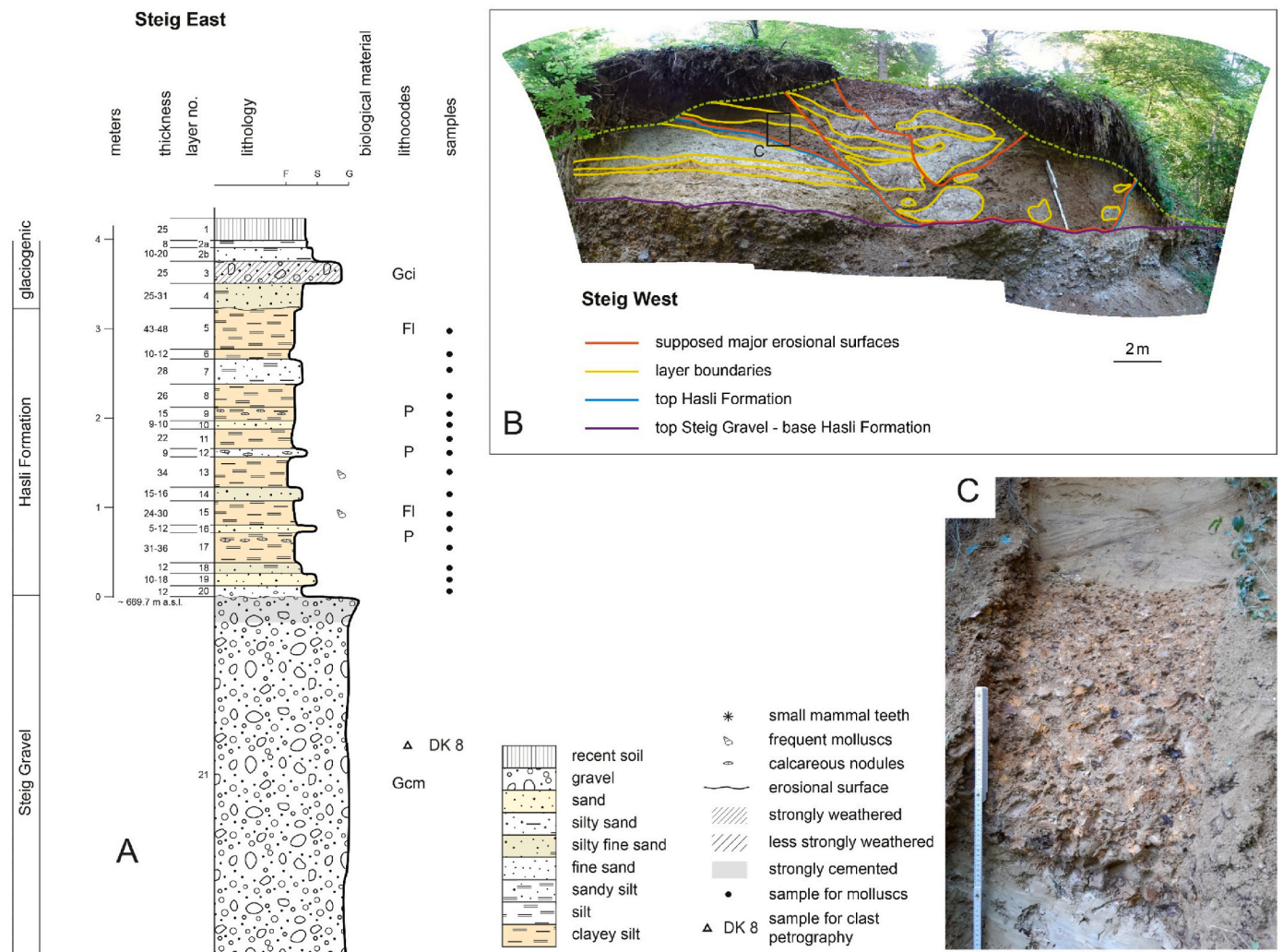


Fig. 6. A: Profile Steig East; B: Profile Steig West. A and B are c.45 m apart. In both profiles, the dolomite-rich Steig Gravel underlies the Hasli Formation. C: Amselboden Gravel at Steig West, overlying the eroded summit of the HF within a multiphase channel, seen at the centre and right in B. C corresponds to the drawn profile seen in Fig. 12.

4.3.2. Steig East (Fig. 6A)

The 8 m profile includes 3.25 m of HF. Above the strongly cemented summit of the Steig Gravel, the HF begins with 2 m of grey/olive-grey thinly interbedded silts and fine sands with calcareous nodules in places, interrupted by two layers (17 and 15) of clayey silt. Above this are 1.25 m of darkish olive-grey/grey clayey-silts and silts. There are molluscs up to 2.15 m in the profile (Layer 9), which are especially abundant in Layers 15 and 13. The upper part of the HF and any subsequent sediments (Amselboden Gravel or ‘Forenirchel Gravel complex’) seem to be missing due to later erosion.

4.3.3. Steig West (SM Fig. S1D and 6B)

The c.7 m profile lies c.45 m west of Steig East and includes a channel cut into the HF. The up to 2.15 m of HF sediments begin above the strongly cemented summit of the Steig Gravel with 0.45 m of grey to reddish-grey thinly interbedded silts and fine sands, with three cemented sand layers and intense iron staining in places (Layer 2). This is followed by 0.2 m of reddish-yellow-brown clayey-silts, then up to 0.9 m of grey/light grey silty fine sand and clayey-silt with calcareous nodules and abundant molluscs (Layers 4 to 6), and then up to 0.6 m of olive-grey/brownish-grey clayey-silt with very few shells. These silts are truncated by a sharp erosion surface that represents the edge of a small channel, followed by up to 0.6 m of very sandy, matrix-supported fine-medium gravel with frequent clasts of decomposed sandstone, the

Amselboden Gravel (Layer 9; Fig. 6C), which in the centre of the channel is mixed with angular soft clasts of collapsed grey HF silt up to 1 m across. Above this comes c.1 m of fine-medium sand with a few bands of fine gravel (Layers 10–14). In the centre of the channel these layers are represented by thin layers of sandy fine-medium gravel with soft clasts of collapsed HF silt up to 2 m across, and are capped by 0.55 m of sandy fine-medium gravel, then up to 0.15 m of grey silt (Layers 15–16). The upper 0.8–1 m of the profile was obscured by recent material.

The erosion surface that truncates the upper part of the HF and is followed by the Amselboden Gravel, forms the eastern edge of a channel c.11 m wide by c.3 m deep (Fig. 6B), which in its deepest part (4 m wide) is incised until the summit of the Steig Gravel. The channel has a complex infill sequence, with several layers of very sandy gravel together with large angular soft-clasts of collapsed silty bank material from the HF, indicating very rapid accumulation. There seem to have been at least three erosional events with m-scale down-cutting, each followed by rapid deposition of sandy gravel and blocks of collapsed HF bank material. The morphology (low width: depth ratio) of this channel is typical for a meandering river (Bravard and Petit, 1997), while its small size and rapid infilling suggests that it may have been an erosional overspill channel for major flooding events from a larger river that lay nearby to the west.

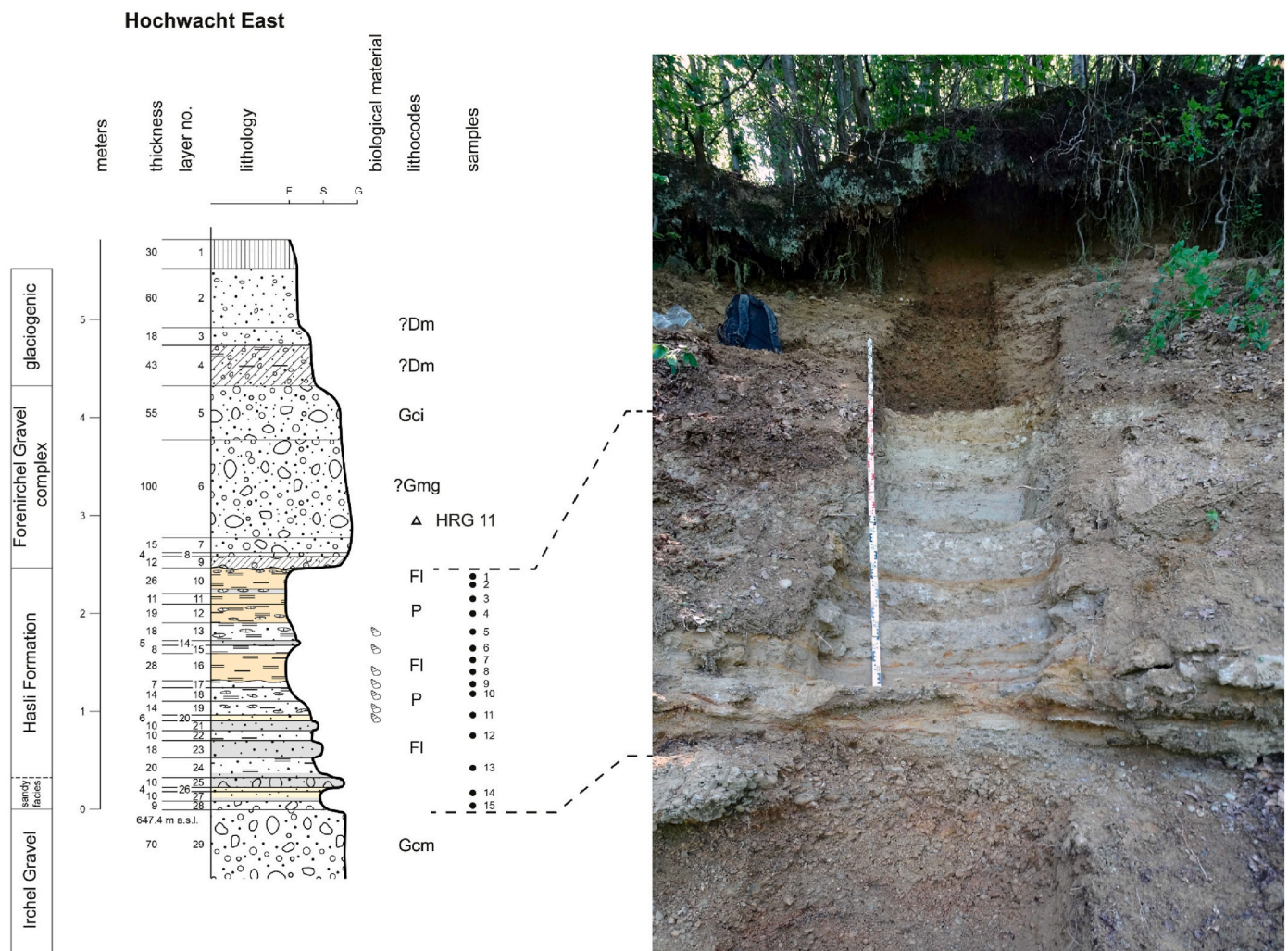


Fig. 7. Profile Hochwacht East. For lithostratigraphic key see Fig. 6.

4.3.4. Amselboden (SM Fig. S1C)

This c.7 m profile includes 1.6–2 m of HF. This begins above the Irchel Gravel with up to 0.2 m of very sandy fine gravel (Layer 1b), followed by c.1 m of cemented sandy layers alternating with olive-grey sandy-silts, all of which correspond to the sandy facies of the HF, dip towards the west and may represent the edge of an active channel. Above this comes 0.25–0.65 m of grey horizontally-bedded silt, then 0.35 m of olive-grey sandy-silt, both with frequent calcareous nodules and abundant molluscs. All these layers have molluscs. Above a sharp erosion surface comes 0.3–0.6 m of olive-brown matrix-supported strongly weathered fine-medium silty gravel with no preferred clast orientation and frequent clasts of decomposed sandstone, then 0.3–0.55 m of sterile sand with rilling erosion (to 0.3 m deep) at base and summit, followed by 0.6 m of analogous, strongly weathered fine-medium silty gravel. Above this comes 1 m of similar but only moderately weathered olive-grey fine-coarse silty gravel, with a soft-clast >0.7 m across of brownish-grey sandy-silt with pebbles that seems to be diamicton. All three gravel layers correspond to the Amselboden Gravel. Above c.0.1 m of sterile laminated silt comes >1.35 m of olive-grey-brown moderately weathered matrix-supported gravel that is sandier and has frequent sub-horizontal or imbricated clasts, but which from clast petrography seems also to represent the Amselboden Gravel. The upper c.5 m of this profile is covered by slope debris. Thus, although the HF in the Amselboden profile has been significantly truncated by subsequent erosion, it is the only study sequence where the Amselboden Gravel is well-developed.

4.3.5. Hochwacht East (Fig. 7)

The c.7 m profile includes 2.5 m of HF. This begins above the Irchel Gravel with up to 0.18 m of very sandy fine gravel (Layer 28), followed by c.0.25 m of olive-grey alternating sands, cemented sands and sandy fine-medium gravel, with cross-bedding structures (Layers 27–25). These four layers, which correspond to the sandy facies of the HF, dip towards the west and may represent the edge of an active channel. This is followed by c.0.6 m of grey/reddish grey alternating thin beds of horizontally-bedded silty-sand and cemented sand. Above this comes c.1 m of grey thinly interbedded sandy-silts and silty fine sands with frequent calcareous nodules and abundant molluscs (Layers 20–13), then 0.6 m of light olive-grey clayey-silts with some calcareous nodules but few molluscs. Above a sharp erosion surface comes 1.9 m of rather finely bedded olive-grey/olive-brown sandy gravels that dip towards the west and have mostly horizontal or imbricated clasts, of which the lowest 0.2 m are stained reddish by Fe or black by Mn. These fluvial gravels were attributed to the basal part of the ‘Forenirchel Gravel complex’ by Graf (1993).

4.3.6. Hochwacht West (SM Fig. S1A)

The c.7 m profile lies c.45 m west of Hochwacht East. The c.1.8 m of HF begins above the Irchel Gravel with c.0.6 m of brownish-grey/olive-grey silty fine-medium sand with some fine gravel, and then 0.3–0.4 m of grey/darkish olive-grey sandy-silt and silty fine sand with some calcareous nodules and abundant molluscs (Layers 5 to 7). This is followed by c.0.85 m of grey/olive-grey silts and clay-silts with fairly

frequent calcareous nodules but few molluscs. Above a sharp erosion surface comes c.4.2 m of rather finely bedded olive-grey/olive-brown sandy gravels, largely clast-supported, which dip towards the west and have mostly horizontal or imbricated clasts. Around 3 m above the base of these gravels is a lens, 2.5 m wide by up to 0.4 m thick, of olive-grey/grey silty fine sand with abundant molluscs. The summit of the gravels that underlie the sand lens has several silty soft clasts up to 0.35 m across that also have abundant molluscs. These two deposits represent the 'upper level' with biological material.

At Hochwacht West, like Hochwacht East, the HF is overlain by gravels that Graf (1993) attributed to the 'Forenirchel Gravel complex'. The presence of soft clasts and a sand lens with abundant warm interglacial molluscs, however, indicates that the up to c.4.2 m of rather finely bedded fluvial gravels are different from the subsequent fluvio-glacial gravels of the 'Forenirchel Gravel complex' and may be labelled the 'Hochwacht Gravel'. Although their clast petrography (samples DK6, DK9 and DK14) is very similar to the typical 'Forenirchel Gravel complex', an analysis by Graf (1993, Sample 11, Fig. 22) shows a flow direction (SSW-NNE) at 90° to the fluvio-glacial gravels of the 'Forenirchel Gravel complex' (ESE-WNW) further to the SE in the Irchel Plateau.

4.4. Summary for the sedimentology of the HF

Overall, the HF is characterised by grey to olive-grey (beige when weathered) thinly interbedded silts and fine sands with fairly frequent erosion surfaces. It has a sheet-like depositional geometry with a preserved thickness of 1.6–6.2 m and a spatial extension of at least 2 km (Hasli - Rütelbuck), but more probably c.4 km (Hasli - Hochwacht), by up to c.1.4 km wide (Forenirchel - Rütelbuck), typical for the alluvial overbank deposits of a large lowland meandering river (Platt and Keller, 1992; Miall, 2006). At the base of the HF at Hochwacht and Amselboden are beds of sandy fine gravel and sand that represent the sandy facies of the HF, as they have warm period terrestrial and aquatic molluscs. These slope downwards towards the west, so may represent the eastern edge of an active channel due to their dip and relative coarseness. If correct, this would indicate that the bed deposits of the meandering river that formed the HF probably consisted of gravels and sands and is likely to have flowed to the west of the Irchel Plateau. The frequent occurrence of irregular calcareous nodules, also at Ebni, seems to indicate circulating groundwater and a fluctuating near-surface water-table during a period of warm interglacial climate (Precece et al., 2007).

Internally, the sediments appear to be organised in vertical aggradation cycles in the form of fining-upward sequences, with sandier deposits at the base of each cycle succeeded by siltier sediments and then silts with clay. These cycles are best developed at Hasli, which is the longest profile, with four cycles of fairly regular thickness (1.20, 1.70, 1.45 and 1.85 m), two of which are capped by thin lignite layers indicating that sedimentation had almost ceased. As floodplain conditions became drier, accelerated pedogenesis at the end of all four cycles led to the mobilisation of Fe and Mn and the dissolution of mollusc shells, leading to differential preservation among the molluscan assemblages (cf. 5.2, Fig. 10). These four cycles allowed the sequence at Hasli to be divided into four stratigraphic 'Parts,' which reflect changes in both the sediments and the molluscan assemblages (cf. Fig. 10 and Table 2). There is also a clear trend for fining-upwards through the HF as a whole, with the sediments of Parts 1 and 2 being significantly sandier than those of Parts 3 and 4. Similar though not necessarily time-equivalent sedimentary cycles could be recognised in the profiles at Hochwacht and Steig, which also allowed their sequences to be sub-divided into 'Parts,' although at Hochwacht there seems to have been greater erosion at the floodplain surface during the accumulation of the HF.

The basal contact of the HF above the underlying gravels is sharp but not necessarily erosional, whereas the upper boundary of the HF always appears to be erosional and is succeeded by different sedimentary units. These include fluvio-glacial gravels of the 'Forenirchel Gravel complex' at Schaffhuser, Wilemerirchel and Rütelbuck, the Amselboden Gravel at

Amselboden, Steig West and Hasli, and the Hochwacht Gravel at Hochwacht (cf. Table 1). At Wilemerirchel the surface of the underlying Irchel Gravel can be seen to rise somewhat towards the SE, while the base of the overlying 'Forenirchel Gravel complex' descends towards the NW, causing the HF to wedge out in both directions, although the HF is observable again further to the SE and NW.

5. Results for the faunal and botanical remains

5.1. Small mammals

Despite a comprehensive sampling campaign, identifiable small mammal remains have only been found in Layer 12 at Hasli, in the upper levels of the HF, although tooth fragments were also found in Layers 23, 22 and 13. Frequent fragments in the upper part of the HF at Wilemerirchel seem once to have been from complete teeth, before post-depositional shattering. The remains from Layer 12 mostly consist of fragments from isolated teeth (Fig. 8). Although the interior dentine from the teeth has largely been lost, the exterior enamel is in most cases extremely well preserved. Interior dentine is commonly dissolved by humic acids in damp and marshy ground, so as Layer 12 was partially decalcified, with most mollusc shells being lost, it is unsurprising that only the enamel wall of the teeth is generally preserved.

Most of the teeth found in Hasli Layer 12 are from arvicoline, a subfamily of cricetids that includes voles and lemmings. Altogether, Layer 12 has yielded 15 complete teeth and around 80 larger identifiable fragments, producing the following faunal list:

Mimomys pliocaenicus Forsyth Major, 1902.

Mimomys reidi Hinton, 1910 or *Mimomys tigliensis* Tesakov (1998).

Mimomys sp.

Pliomys episcopalis Méhely, 1914 or *Pliomys simplicior* Kretzoi, 1956.

Clethrionomys cf. *kretzoi* (Kowalski, 1958).

Borsodia sp.

Lagurodon sp.

Lemmus sp.

Apodemus cf. *sylvaticus* (Linnaeus, 1758).

The identification criteria and measurements for the more complete teeth are given in detail in Cuenca-Bescós (2015). The final list is similar to the one in Bolliger et al. (1996), although the murid species *Apodemus* cf. *sylvaticus* and *Clethrionomys* cf. *kretzoi* are new additions. Another small difference concerns the genus *Pliomys*, with *P. episcopalis/simplicior* being preferred to *P. cf. episcopalis*. The assemblage includes rooted teeth from large and small *Mimomys* taxa, but lacks the rootless arvicoline genus *Allophaiomys* (*Microtus*) that first appeared in Central Europe during the Olduvai Subchron, shortly before 1.8 Ma (Maul and Markova, 2007). Rooted arvicoline species are the ancestors of rootless arvicoline taxa that have constantly growing cheek teeth, and their presence indicates an age early within the Early Pleistocene (as defined since 2009; Fejfar and Heinrich, 1990; Fejfar et al., 1997; Rekovets and Kovalchuk, 2017).

5.2. Terrestrial and aquatic molluscs

Molluscs have been recovered from all six of the profiles excavated through the HF at Hasli, Steig, Amselboden and Hochwacht in 2018–21, as well as from a newer profile at Wilemerirchel (2021–23) and from those sampled by previous researchers at Hasli (Bräm, 1956; Bolliger et al., 1996), Forenirchel and Hochwacht NE (Graf, 1993). Although preservation is variable, identification to species level has been possible for most levels at all of these sites (SM Tables S2b, S2c1, S2c2). The molluscan remains from the stratigraphically lower silts at Ebni are poorly preserved and dominated by slug plates, which are far more resistant to physical erosion and chemical weathering as they are formed of denser calcite rather than the more porous aragonite of mollusc shells. By contrast, the molluscs from the 'upper level' at Hochwacht West are rather well preserved and exceptionally diverse.

Table 2
Important molluscan species for biostratigraphy and climate from the Irchel Plateau sites. Based upon new analyses from Switzerland and a comprehensive literature review of Western and Central European sites (Theew, 2024).

Terrestrial Molluscan species (never before found in CH [Switzerland] unless marked with *; extinct †)	Period when last present in the Swiss Plateau	Biostratigraphic details	Modern or palaeo-distribution relative to CH	Climate status	Hasli (Pt = Part)				Steig East & West				Wilemer-irchel	Foren-irchel (Graf, 1993)	Amselboden		Hochwacht East & West				Hochwacht 'Upper level'
					Pt 1	Pt 2	Pt 3	Pt 4	Pt 1	Pt 2	Pt 3	Pt 4			Pt 1	Pt 2	Pt 1	Pt 2	Pt 3	Pt 4	
<i>Aegopinella ressmanni</i>	Eemian	still living, absent from CH after Eemian	E	Int	x	x	x	x		x	x		x		x	x	x	x	x	x	x
<i>Discus perspectivus</i> *	Interglacial		E	Int									x			x					
<i>Urticicola umbrosus</i>	later Middle Pleistocene 0.48–0.13 Ma	still living, absent from CH after MIS 7	E, NE	Int	x	x	x	x		x					x	x					
<i>Clausilia pumila</i>		still living, absent from CH after MIS 11 or MIS 9	E, NE																		x
<i>Perforatella bidentata</i> *			E, NE		x	x	x	x		x							x	x	x		x
<i>Clausilia rugosa antiquitatis</i> †		globally extinct after MIS 11	C. Europe	Int	x	x	x	x		x					x	x					
<i>Neostyriaca corynodes ornata</i> †	Early Pleistocene or early Middle Pleistocene	globally extinct after MIS 13	E		x					x			x		x	x					x
<i>Causa holosericea</i> *	before 0.48 Ma	still living, never before identified from pre-Holocene strata in CH	S, SE, E	Int ws																	x
<i>Ciliella ciliata</i> *		still living, never before identified in CH north of the Alps	S, SW, SE	Int ws									x								x
<i>Oxychilus clarus</i> *			S, SE	Int ws											x						x
<i>Monachoides vicinus Trochulus filicinus</i>	later Early Pleistocene (EP3) 1.2–0.77 Ma	still living, probably absent from CH after EP3	E SE	Int ws Int ws	x	x	x	x		x	x		x	x	x	x	x	x	x	x	x
<i>Azeca goodalli</i>	middle Early Pleistocene	still living, possibly absent from CH after EP1 or EP2	NW, W, SW	Int mw	x	x	x	x		x	x		x			x	x	x	x	x	x
<i>Cepaea nemoralis Trochulus leucozonus</i>	(EP2)		W, SW	Int mw									x			x	x	x	x		x
<i>Retinella elephantium</i> †	1.78–1.2 Ma	globally extinct after MIS 11, possibly absent from CH after EP1 or EP2	W, SW	Int mw												x	x	x	x		x
<i>Acicula parcelineata Poireria dilatata dilatata Spermodea lamellata</i>	older Early Pleistocene (EP1)	still living, probably absent from CH after EP1	E S	Int vws Int vws									x			x	x	x	x		x
<i>Serrulella</i> sp. †	2.6–1.78 Ma	globally extinct after EP3, probably absent from CH after EP1	NW, W	Int mw			x								x			x	x		
			S, E	Int ws									x				x				

(continued on next page)

Table 2 (continued)

Terrestrial Molluscan species (never before found in CH [Switzerland] unless marked with *; extinct †)	Period when last present in the Swiss Plateau	Biostratigraphic details	Modern or palaeo-distribution relative to CH	Climate status	Hasli (Pt = Part)				Steig East & West				Wilemer-irchel	Foren-irchel (Graf, 1993)	Amselboden				Hochwacht East & West				Hochwacht 'Upper level'			
					Pt 1	Pt 2	Pt 3	Pt 4	Pt 1	Pt 2	Pt 3	Pt 4			Pt 1	Pt 2	Pt 3	Pt 4	Pt 1	Pt 2	Pt 3	Pt 4				
<i>Archaeogopsis (Retinella) acutus</i> †		globally extinct after EP2, probably absent from CH after EP1	SE, E	Int ws				x					x			x	x	x	x	x	x					x
<i>Macrogastrea sessenheimensis</i> †			E	Int ws	x	x	x					x														x
<i>Oxychilus steiningeri</i> †			E	Int ws																						x
<i>Clausilia stranzendorfensis</i> †		globally extinct after EP1	E	Int ws	x	x	x																			x
<i>Cochlostoma salomoni</i> †			W, SW	Int mw	x	x	x	x				x														x
<i>Neostyriaca dehmi</i> †			C. Europe	Int																						x
<i>Triptychia new sp.</i> †			S, E	Int								x														x

Climate key: Int = Interglacial indicator species; Int ws = with notably warm summers; Int vws = with very warm summers; Int mw = with very mild winters. Species in bold = principal biostratigraphic marker species for the older Early Pleistocene in Central Europe. The older Early Pleistocene (2.6–1.78 Ma) = Gelasian; middle Early Pleistocene (1.78–1.2 Ma) = Satermanian + Emilian Stages of the Calabrian; later Early Pleistocene (1.2–0.77 Ma) = Sicilian Stage of the Calabrian.

For all sites sampled between 1955 and 2023 from the three levels with biological material at the Irchel Plateau, a minimum number of c.75,280 individuals have been identified, which include c.71,890 terrestrial molluscs (95.5%) coming from 89 species and c.3390 aquatic molluscs (4.5%) from 28 taxa (SM Tables S2b, S2c1, S2c2). Of these, the 'Ebni silts' produced just 180 individuals from 3 terrestrial taxa coming from 6 samples, the HF has yielded 83 terrestrial and 27 aquatic species from 104 samples, while the 'upper level' from Hochwacht West has produced 72 terrestrial and 18 aquatic taxa from just 4 samples (1 from a soft clast, 3 from the sandy lens). Taken as a whole, this represents an exceptional assemblage for Switzerland, as it matches those from the most important sites for molluscan palaeontology known from the Early Pleistocene in Central, Western and Eastern Europe. Of the five principal sites studied from the HF, Hochwacht has the most diverse faunas for both terrestrial (71 species) and aquatic molluscs (19 taxa), while Hasli has 69 terrestrial species and 15 aquatic taxa (including the Bräm material), Amselboden has 58 terrestrial and 11 aquatic species, Wilemerirchel has 56 terrestrial and 4 aquatic species, and Steig has just 52 terrestrial taxa but 16 aquatic species.

These rich molluscan assemblages provide important information about the three levels with biological material, including their age (cf. 8.1.3), the climate during their accumulation (cf. 8.2), local terrestrial environments within the floodplain (cf. 8.3) and the sedimentary environments in which the deposits accumulated (cf. 8.4).

The faunas from the five principal sites where the HF was sampled, in addition to the shells recovered by Graf (1993, p. 41) at Forenirchel, share a number of important biostratigraphic marker species (Fig. 9, Table 2, SM Fig. S2), as well as indicating very similar climatic and environmental conditions. This strongly suggests that the investigated HF sediments from all these sites belong to the same stratigraphic unit, and that they were all more or less contemporary. Variations in species representation between the profiles seem to have been due to modest differences in the local terrestrial floodplain environment, as well as to taphonomic processes linked with sedimentation within a complex floodplain setting.

All but one of the important molluscan biostratigraphic marker species (Fig. 9, Table 2, SM Fig. S2) have never previously been found in Switzerland and many are rare for Central Europe, meaning that the Irchel sites are of major palaeontological importance. These include several that became extinct during the Early Pleistocene, such as *Archaeogopsis acutus*, *Clausilia stranzendorfensis*, *Cochlostoma salomoni*, *Macrogastrea sessenheimensis*, *Neostyriaca dehmi*, *Serrulella* sp. and *Triptychia new sp.* (Thew, 2024). The specimens of *Clausilia stranzendorfensis* found at the Irchel sites appear to correspond to a variety first illustrated by Frank (2006, Plate XXXI), which seems to have been present from the Late Pliocene until the older Early Pleistocene at Stranzendorf in NE Austria before going extinct. The new species of *Triptychia*, found only at Wilemerirchel, is an exceptional discovery. It is the first time that *Triptychia* has been found in Early Pleistocene deposits, as this genus was previously thought to have completely disappeared at the end of the Pliocene.

The 'upper level' at Hochwacht has most of the major biostratigraphical marker species present in the HF (Fig. 9, Table 2, SM Fig. S2), indicating that these faunas are of a similar age. Nevertheless, the presence of five new terrestrial taxa not found in the HF, including *Clausilia pumila* and the extinct *Oxychilus steiningeri* (only previously found at Deutsch-Altenburg, NE Austria; Frank, 2006), may be linked with the slightly younger stratigraphic position of the 'upper level' (Thew, 2024).

As mentioned above (cf. 4.4), the sequence at Hasli could be divided into four stratigraphic 'Parts' based on sedimentary evidence, together with notable changes in the molluscan faunas, while those at Steig, Hochwacht and Amselboden could also be sub-divided (Table 2, SM Tables S2b, S2c1, S2c2). These changes are illustrated in Fig. 10 for Hasli and Hochwacht East, the only profiles where quantitative data is available for all samples. Although the 'Parts' from these sites may not

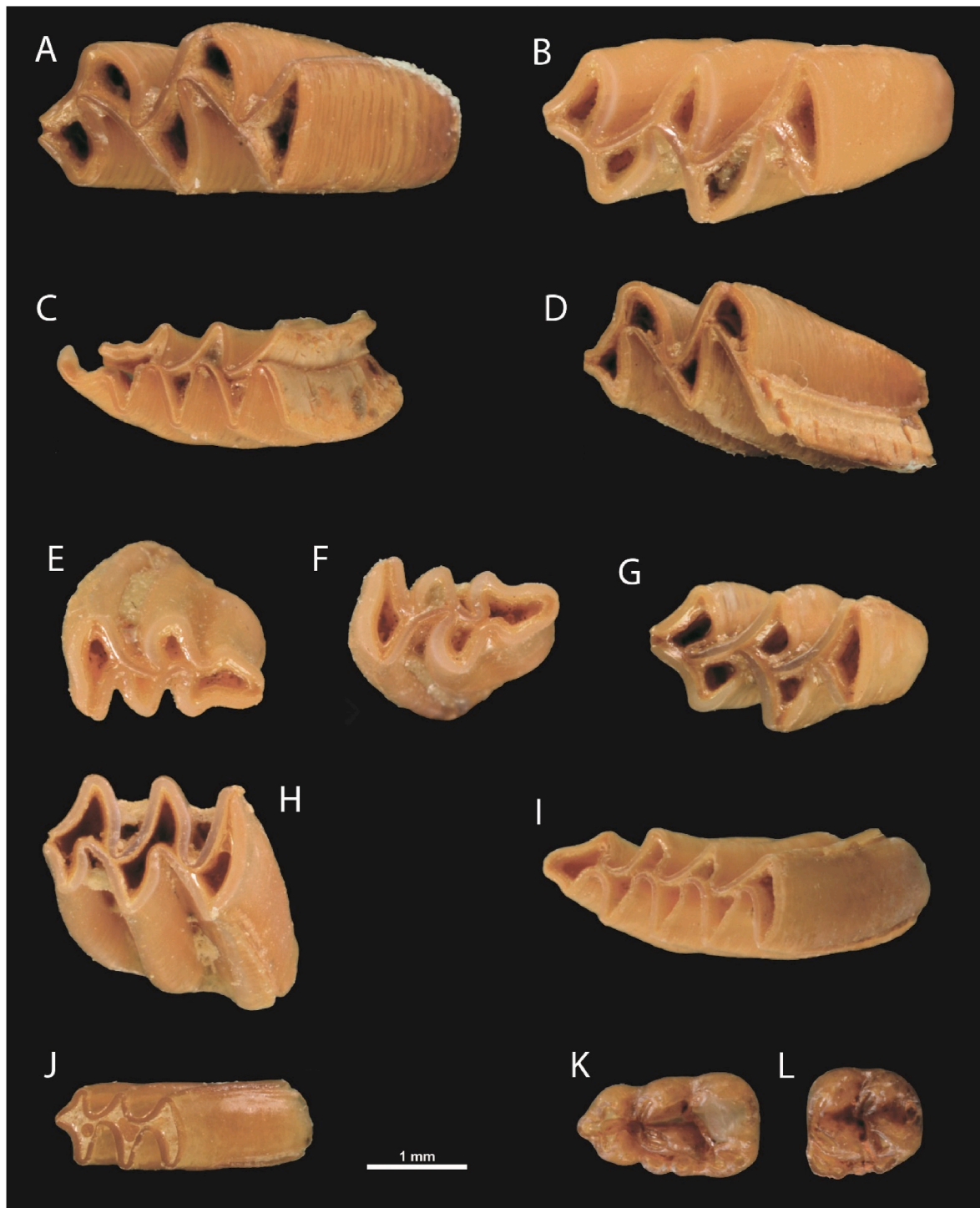


Fig. 8. The most important rodent molars from Hasli Layer 12 in occlusal view: A. *Mimomys pliocaenicus* (M^1 sin.), B. *Mimomys pliocaenicus* (M^1 dext.), C. *Mimomys reidi/tigliensis* (m_1 dext.), D. *Mimomys* sp. (half upper molar), E. *Mimomys reidi* (M^3 sin.), F. *Mimomys reidi* (M^3 dext.), G. *Mimomys reidi* (M^1 sin.), H. *Borsodia* sp. (M^1 dext.), I. *Pliomys episcopal/simplicior* (m_1 dext.), J. *Clethrionomys* cf. *kretzoi* (m_3 dext.), K. *Apodemus* cf. *sylvaticus*, (m_1 sin.), L. *Apodemus* cf. *sylvaticus*, (m_2 sin.).

necessarily be time-equivalent, forest species increased and became more diverse during Part 2 at all four locations, with a rise in Group 1 taxa showing that the forest became more developed and had greater numbers of large mature trees. At Hasli, Hochwacht and Steig, Part 3 is marked by significant increases in open ground and marsh molluscs, while the proportion of forest species declined and shell preservation is distinctly better due to wetter conditions. At Hasli and Steig West there were also significant increases in aquatic molluscs. At all three sites Part 4a shows a sharp decline in molluscan numbers, while shell preservation

is much poorer (SM Tables S2b, S2c1, S2c2).

5.3. Pollen and charcoal

Relatively little pollen work has been done on the deposits of the Irchel Plateau, largely because test samples have proved to be disappointing (K. Bieri in Graf, 1993, this study). At Hasli, seven samples from the HF have yielded assemblages with rather poorly preserved pollen (SM Table S3). Part 2 of the Hasli sequence has *Pinus*, *Picea* and low

frequencies of *Acer*, *Alnus*, *Betula*, cf. *Castanea*, *Corylus*, *Fagus*, *Quercus* and *Tilia*, suggesting mixed coniferous and deciduous woodland during a period of warm interglacial climate. By contrast, Part 3 only has pollen from *Picea* and *Pinus*, plus some *Abies* and *Quercus*, which may suggest that the forest had become less diverse and more coniferous, possibly due to somewhat damper and cooler conditions although differential preservation may have influenced the spectra. At Hochwacht East, 9 samples from the HF (K. Bieri in Graf, 1993, p. 46) produced poor assemblages that include a significant proportion of *Fagus*, together with *Picea*, a little *Fraxinus* and some herbaceous pollen, although the *Fagus* may largely represent modern contamination as it is mostly well preserved and especially common in the upper two samples. Poor assemblages from Ebni include some *Pinus*, *Picea*, *Fagus* and herbaceous pollen, possibly suggesting a local environment with mixed woodland during a period of warm climate.

Although charcoal and mineral (Fe) encrusted wood fragments were regularly noted within the bulk samples taken from the HF (SM Tables S2b, S2c1, S2c2), these were very rarely large enough to be studied. Their regular presence is in keeping with the molluscan and pollen evidence for the presence of a floodplain forest.

5.4. Earthworm granules

Earthworm granules are common in many samples from the 'Ebni silts', the HF and the 'upper level' at Hochwacht (SM Tables S2b S2c1, S2c2). During their life-time worms excrete large numbers of multicrystalline calcitic granules from their calciferous glands, mostly in the upper 20 cm of a soil profile (Canti, 1998). From their size and morphology, the Irchel granules seem to have been produced by *Lumbricus* species, especially *L. terrestris* (Bräm, 1956; Canti and Pearce, 2003; Canti, 2007). *L. terrestris* thrives in fairly damp loamy soils where the pH is neutral or alkaline, there is surface leaf litter (Canti, 2007) and the climate is relatively mild (Tiunov et al., 2006).

5.5. Ostracods

Ostracods have been found in samples from the 'Ebni silts', the HF (especially the lower levels at Hasli and Steig) and rarely in the sand lens of the 'upper level' at Hochwacht (SM Tables S2b, S2c1, S2c2). No new identifications have been made, but morphological variations show that the valves probably come from several different species. The valves from two ostracod taxa previously identified from Ebni (*Candona angulata*, *Cytherissa lacustris*) are typical of fairly calm, mineral-rich waters (Graf, 1993, p. 36).

5.6. Chara

Low frequencies of *Chara* oogonia have been found in the 'Ebni silts' and in the HF at Hasli and Amselboden (SM Tables S2b, S2c1, S2c2). The *Chara* from Amselboden are *Chara vulgaris* (P.-O. Mojon pers. comm. 2023), a polymorphic species that lives in a wide variety of aquatic habitats including rivers, but avoids locations with energetic water movement. Present since the Miocene (e.g. Casanovas-Vilar et al., 2022), *C. vulgaris* requires fairly temperate conditions, so becomes rare beyond 60°N in Europe and reaches a maximum of 63.5°N in Sweden (GBIF Secretariat, 2023).

6. Results for the amino acid geochronology

The molluscan remains from the HF have produced some of the highest ICPD values of all the Quaternary molluscan material analysed for amino acid geochronology from sites across the Swiss Plateau (Fig. 11; Penkman et al., 2024), showing that they are among the oldest. All the non-Irchel sites in Fig. 11 are also discussed in Thew (2024). Allowing for mineral diagenetic issues linked with differential weathering of some of the aragonitic shell material (which tends to reduce

THAA D/L values, making the affected shells appear to be younger if only THAA is considered; Penkman et al., 2007), the samples from the different profiles through the HF have similar ICPD values. This indicates that they are of comparable relative ages within the temporal levels of resolution for the technique, which is consistent with the interpretation that they come from the same lithostratigraphic unit. Slug plates from the 'upper level' at Hochwacht also have analogous values to those of the HF, confirming that they are of a similar age. The 'Ebni silts' seem to be slightly older than the HF, in line with their lithostratigraphic position.

7. Results for the magnetostratigraphy

Mineral magnetic analysis of the samples reveals that their magnetic mineralogy is composed of common detrital ferrimagnetic minerals, such as pure or cation-substituted magnetite, maghemite and members of the titanomagnetite and ilmenohematite solid solution series. In addition, there are considerable amounts of largely detrital haematite and some occurrences of secondary goethite. The identification of detrital minerals serves to verify the primary character of the polarity of the geomagnetic field determined for the samples.

The 23 accepted samples show both normal and reversed ChRM directions (Figs. 12 and 13A). As the palaeomagnetic results and their interpretation are fully discussed in Scheidt et al. (2023a), only a brief overview is provided here. At Hochwacht East all but the uppermost sample have reversed polarity. Four of the seven samples also have secondary magnetisation oriented roughly antiparallel to the ChRM, but only the reversed overprint of the topmost sample with normal ChRM is important for the chronostratigraphic interpretation of the results. The single sample from Steig West comes from the lower part of the HF and carries a reversed signal with a normal overprint. The demagnetisation data from the Hasli samples is particularly difficult to interpret in terms of magnetic polarity stratigraphy. The blocking temperatures indicate a large variation in the magnetic mineral composition, probably due to a variable intensity of diagenetic overprinting and the formation of secondary minerals. Overall, there appear to have been rather large diagenetic changes in the magnetic mineral composition, so the primary (detrital) nature of some components is not always certain. The seven accepted samples show a sequence of polarities from bottom to top of: reversed (1 sample) – normal (1) – reversed (2) – normal (3 samples; Fig. 13A). Yet such a sequence of polarity changes seems to be unrealistic, as it implies several subchrons represented within just a few metres of alluvial overbank sediment, so one or more samples may have given false results. The single lower sample with normal polarity could perhaps be discarded as it is crossed by a redox front that may have erased the primary magnetisation. Alternatively, the two samples with reversed ChRM directly above could perhaps be excluded, as they have high levels of goethite and may therefore have acquired pervasive secondary magnetisation. Overall, it is not evident whether the single normal or the two reversed samples provide false results, but what is clear is that the HF at Hasli shows a polarity change from reversed (base) to normal (top) within the upper part of the profile.

Finally, the eight samples obtained from the 'Ebni silts' show exclusively normal ChRM, without any signs of antiparallel secondary magnetisation.

8. Discussion and interpretation

8.1. The ages of the Hasli Formation and the 'Ebni silts'

8.1.1. Correlating the Hasli Formation between the various Irchel sites

Before any age can be proposed for the HF, it is important to note that the available evidence from this multidisciplinary investigation shows that the HF deposits from the study sites all share a high degree of similarity in terms of their sediments, biological material, palaeomagnetic data and ICPD values. This strongly supports a correlation

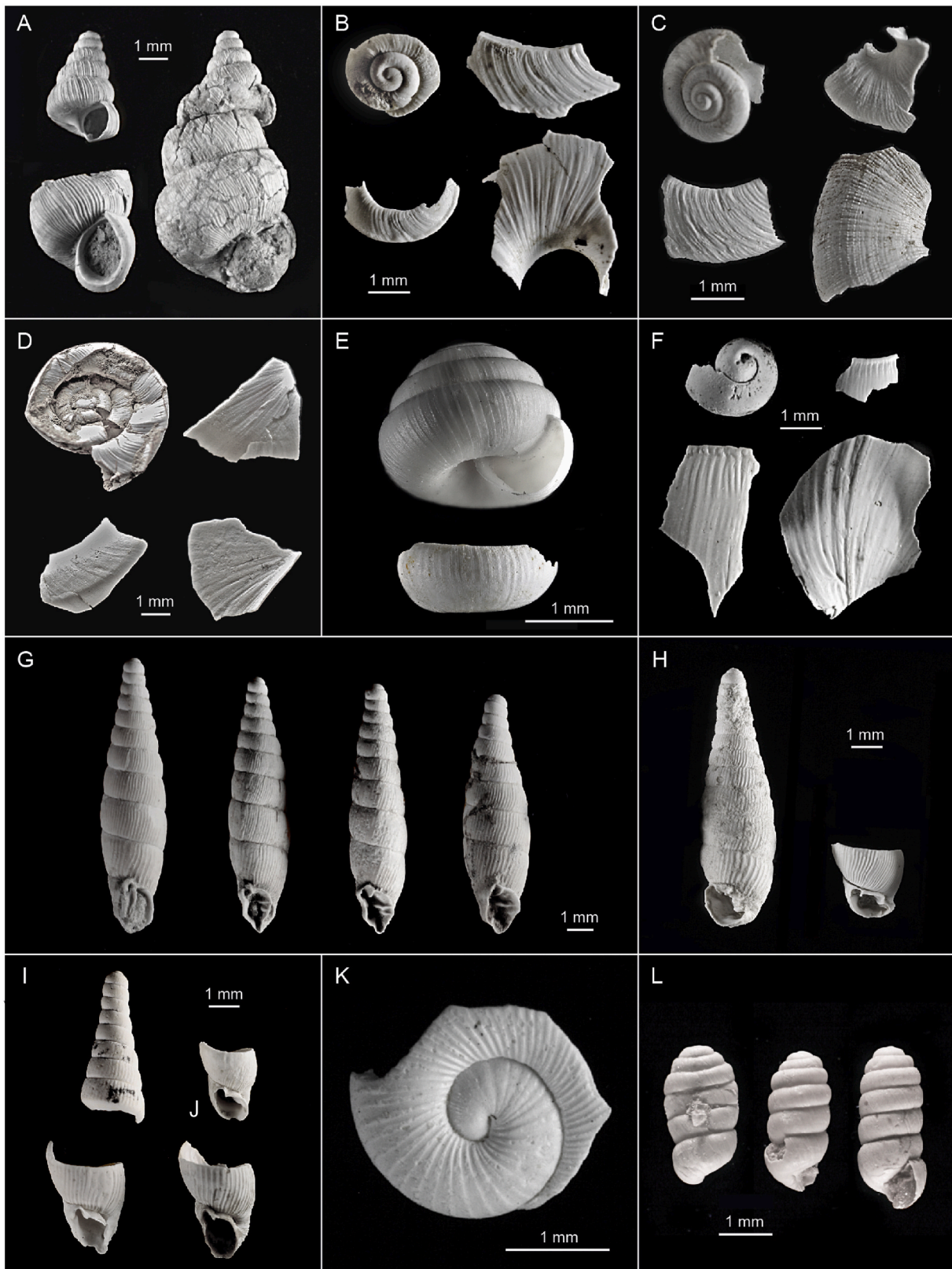


Fig. 9. Several of the most important molluscan species from the Irchel Plateau sites: A. *Cochlostoma salomoni*, B. *Archaeogopsis acutus*, C. *Retinella elephantium*, D. *Monachoides vicinus*, E. *Spermodea lamellata**, F. *Poiretia dilatata dilatata*, G. *Clausilia stranzendorfensis*, H. *Macrogastra sessenheimensis*, I. *Neostyriaca corynodes ornatula*[°] + J. (top right) *Neostyriaca dehmi*, K. *Oxychilus steingeri*, L. *Columella columella*. *Holocene reference shell from UK; [°]N. *corynodes ornatula* shells from Hungerbol (TDS deposits).

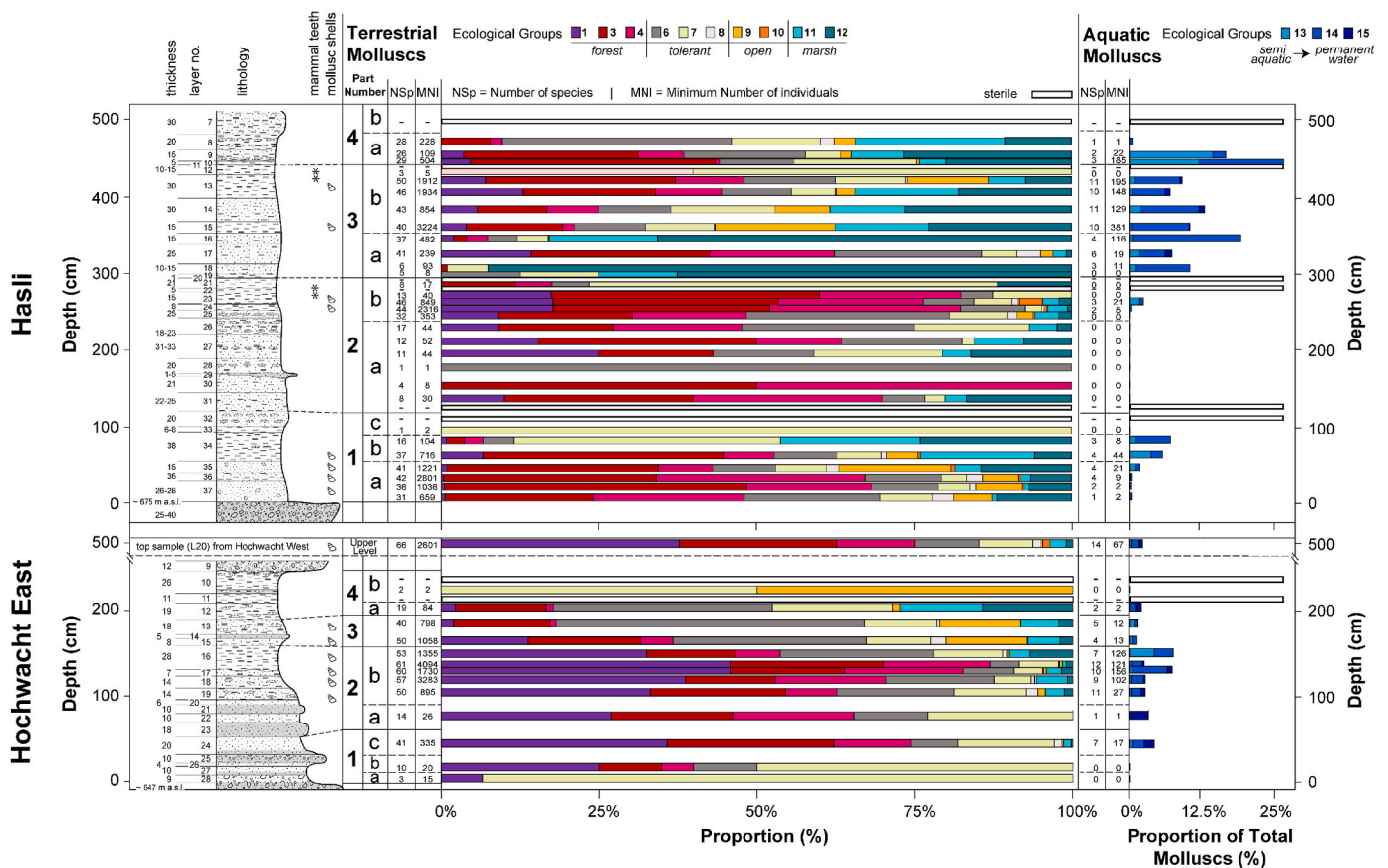


Fig. 10. Composition of the molluscan faunas in the Hasli and Hochwacht East profiles, showing variations in forest, tolerant, open ground and marsh species, as well as aquatic molluscs, in addition to molluscan frequencies and the number of species.

between them and confirms that they belong to the same lithological unit, as proposed by Graf (1993), which seems to extend across much of the Irchel Plateau. By contrast, the ‘Ebni silts’ clearly correspond to a separate earlier level, while the sandy-silts of the ‘upper level’ with biological material discovered at Hochwacht West are somewhat younger, supported by their stratigraphic position.

8.1.2. Small mammals

The presence of the index species *Mimomys pliocaenicus* and *M. reidi/tigliensis* is the main reason that the fauna from the upper levels of the HF at Hasli could be attributed by Bolliger et al. (1996) to biozone MN17 of the small mammal chronology for West-Central Europe (Mein, 1975), which dates from the older Early Pleistocene (Gelasian) between 2.6 and 1.8 Ma (Fig. 14). This age estimate is based on FAD (First Appearance Datum) and LAD (Last Appearance Datum) information from a significant number of Early Pleistocene sites, including locations with numerical dates (Table 3). *Mimomys pliocaenicus*, which is normally accompanied by a similar suite of species, was widespread across much of Europe during the older Early Pleistocene, and in Central Europe seems to have an LAD of c.1.8 Ma, like *Clethrionomys cf. kretzoi* (Table 3; Maul and Markova, 2007). Of equal importance is the presence of *Pliomys episcopalisp/simplicior*, which seems to have first appeared in Central Europe during the Olduvai Subchron (Maul and Markova, 2007) after 1.934 Ma (Raffi et al., 2020). From these elements, it appears that the small mammal assemblage from the upper levels of the HF at Hasli probably dates from c.2.0–1.8 Ma.

There is no evidence for the diachronic appearance of the key species referred to above, a phenomenon known to occur in vertebrate and invertebrate biostratigraphy (Lister, 1992, van der Meulen et al., 2011). The numerical ages for the Western, Central and Eastern European

occurrences of *Mimomys pliocaenicus*, for example, indicate no significant variation (Table 3). Indeed, there seem to be only modest differences for the FAD and LAD of most arvicoline taxa between Central and Eastern Europe during the Pleistocene (Maul and Markova, 2007; Tesakov et al., 2019; Krokmal et al., 2021; 2023).

8.1.3. Terrestrial and aquatic molluscs

The molluscan biostratigraphic marker species present in the HF include several that are extinct. These include *Clausilia stranzendorfensis*, *Cochlostoma salomoni*, *Neostyriaca dehmi* and *Triptychia new sp.*, which probably went extinct around 1.8 Ma, *Macrogastra sessenheimensis*, which disappeared between 1.5 and 1.3 Ma, plus *Archaegopis acutus* and *Serrulella sp.*, which died out around 1.2 Ma (Fig. 9, Table 2, SM Fig. S2; Thew, 2024). The East-Central European species *C. stranzendorfensis* and the Western European taxon *C. salomoni* represent two of the most important molluscan biostratigraphical markers for the older Early Pleistocene in Central Europe (Thew, 2024). Their presence throughout the HF strongly suggests that this unit accumulated before c.1.8 Ma. The ‘upper level’ at Hochwacht, which is separated from the HF by 3 m of fluvial gravel so is slightly younger, has most of the same major marker species as the HF, including *C. stranzendorfensis* and *C. salomoni*, showing that the fauna is of a similar age (Thew, 2024). It also has several additional taxa, including *Oxychilus steiningeri*, which seems to have become extinct around 1.2 Ma (cf. Frank, 2006).

8.1.4. Pollen

The presence of *Fagus* (beech) pollen at Hasli and possibly at Hochwacht is important, although the grains at the latter site may largely derive from contamination during sampling (SM Table S3). Pollen from this tree species was relatively well represented during the Tiglian, but

Table 3
Compilation of key sites from West-Central Europe with small mammal remains of MN17 age.

Locality	Country	References	Age (Ma)	Dating Method
Puebla de Valverde	Spain	Sinusía et al. (2004)	between Feni and Olduvai	M
Sidestrand*	United Kingdom	Maher and Hallam (2005), Preece et al., (2020)	normal polarity, pre-Olduvai	M
Russel-Egypte*	The Netherlands	Tesakov (1998) Westerhoff et al. (1998)		
Maalbeek Un 2*				
Tegelen				
Zuurland-2 Core*	The Netherlands	van Kolfschoten (1988), Preece et al. (2020)		
Roca-Neyra	France	Nomade et al. (2014)	2.60 ± 0.02 final MN16b	Ar/Ar, M
Chillac	France	Azzaroli et al. (1988), Nomade et al. (2014), Paquette et al. (2021)	2.34 ± 0.08 ^a (above fauna) 2.285 ± 0.046 ^b	^a Ar/Ar ^b U/Pb
Blassac	France	Paquette et al. (2021)	Matuyama pre-Olduvai 2.14 ± 0.12 ^a , 1.946 ± 0.029 ^b	M ^a K/Ar ^b U/Pb
Mont Coupet*	France	Paquette et al. (2021)	2.274 ± 0.032 ^b 2.14 ± 0.18 ^a (above fauna)	M ^b U/Pb ^a Ar/Ar
Senèze*	France	Delson et al. (2006), Nomade et al. (2014) Paquette et al. (2021)	2.176 ± 0.032 ^a , 2.132 ± 0.042 ^a , 2.104 ± 0.050 ^a , 2.100 ± 0.029 ^b ; Matuyama between Feni and Olduvai	M ^a Ar/Ar ^b U/Pb
St. Vallier*/***	France	Guérin et al. (2004)		M
Uhlenberg*	Germany	Ellwanger et al. (1994), Strattnr and Rolf (1995)	normal polarity, Olduvai Subchron	M
Stranzendorf G*	Austria	Rabeder (1981), Frank and Rabeder (1997a)	Matuyama, below possible. Feni Subchron, so pre 2.1 Ma	M
Deutsch-Altenburg 3, 10*	Austria	Rabeder (1981), Frank and Rabeder (1997c)		
Castelfranco di Sopra**	Italy	Masini and Torre (1990), Kotsakis et al. (2003)		
Coste San Giacomo*	Italy	Bellucci et al. (2014), Bona et al. (2015)	around 2.1 Ma, Matuyama pre-Olduvai Subchron	M

M = Magnetostratigraphy; Ar/Ar = Ar^{40}/Ar^{39} ; U/Pb = U^{238}/Pb^{206} ; * small mammal fauna with *Mimomys pliocaenicus*; ** type locality for *Mimomys pliocaenicus*; *** reference locality for MN17.

became rare during the remainder of the Early Pleistocene (Bludau, 1995; Hahne et al., 2008). *Fagus* then seems to have reappeared during the early Middle Pleistocene, being present, for example, in profiles within the Upper Rhine Graben near Heidelberg (Knipping, 2008).

8.1.5. Palaeomagnetic data

The palaeomagnetic data from Hochwacht East and Hasli indicates that a change from reversed to normal polarity occurred somewhere within the upper part of the HF (Fig. 12; Scheidt et al., 2023a). The reversed overprint of the topmost sample at Hochwacht East requires that this transition corresponds to the onset of one of the normal subchrons within the Matuyama Chron. Based on palaeomagnetic evidence alone, this transition probably represents the start of the Olduvai or Jaramillo Subchrons, as these lasted significantly longer and are thus more likely to have been preserved in continental sedimentary archives than the shorter-lived Feni and Cobb Mountain Subchrons (Fig. 13B). The similarity of the polarity sequences at Hochwacht East and Hasli is consistent with sedimentary and biological evidence that accumulation of HF sediments at these sites was more or less synchronous. The single sample with reversed polarity from the base of the HF at Steig West accords with the lower part of the sequences from the two other sites.

The data from the 'Ebni silts' reveals remanence acquisition during a time of normal polarity, which based solely on palaeomagnetic evidence could represent the Gauss Chron, subchrons of the Matuyama Chron or the Brunhes Chron. Additional sources of evidence are therefore required to decide which of these scenarios is most likely (Scheidt et al., 2023a).

8.1.6. Combining the new dating evidence for the Hasli Formation

The palaeomagnetic data clearly shows that there was a transition from reversed to normal polarity within the upper part of the HF, which

represents the onset of a subchron within the Matuyama Chron. When the small mammal, molluscan and AA data is taken into account, this transition seems very likely to represent the onset of the Olduvai Subchron at 1.934 Ma (Ogg, 2020; Raffi et al., 2020), which lies within the Tiglian warm stage. The molluscan evidence also indicates that the HF represents a period that for the most part had a notably warm and rather stable climate (cf. 8.2), in keeping with isotopic values for the Tiglian in the MIS curve (Lisiecki and Raymo, 2005). The small mammal and molluscan biostratigraphical age datasets for the HF are constrained by well-established regional biostratigraphic frameworks from across Europe that have been verified by numerical and palaeomagnetic dating (cf. 8.1.2, 8.5, Table 3).

The 'upper level' with warm stage biological material at Hochwacht West lies above the HF, separated by c.3 m of gravel, but seems to belong within the same biostratigraphical period (cf. 5.2), so must also date from before the termination of the Tiglian warm period at 1.76 Ma (end of MIS 63; Channell et al., 2020; Westerhoff et al., 2020; Cohen and Gibbard, 2022). This implies that the end of the HF is likely to date from around 1.8 Ma or not long before.

A continuity of the molluscan evidence throughout the studied sedimentary sequences (cf. 5.2) indicates that there were no major biostratigraphy hiatuses within the HF. The most complete sequence of HF sediments from all the study sites is at Hasli, where the start of the Olduvai Subchron at 1.934 Ma lies within the upper part of the HF. If it can be assumed that sedimentary accumulation was fairly constant from this point until the end of the HF (at around or not long before 1.8 Ma), extrapolating rates of sedimentation for the lower part of the sequence before the palaeomagnetic transition would seem to imply that the HF probably began to accumulate before 2.0 Ma. A more accurate age estimate for the HF may therefore be 2.1–1.8 Ma, with the 'upper level' dating from c.1.8 Ma.

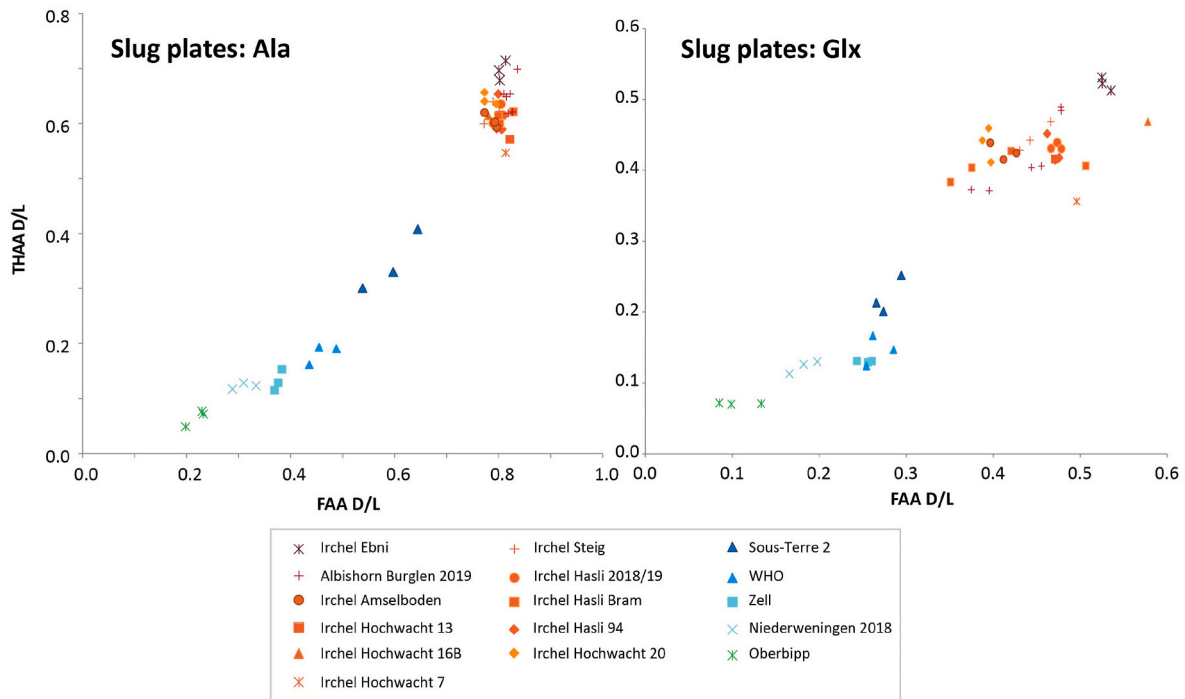


Fig. 11. FAA versus THAA D/L for Ala (left) and the slower racemising amino acid Glx (right), for individual samples of slug plates from investigated sites across the Swiss Plateau.

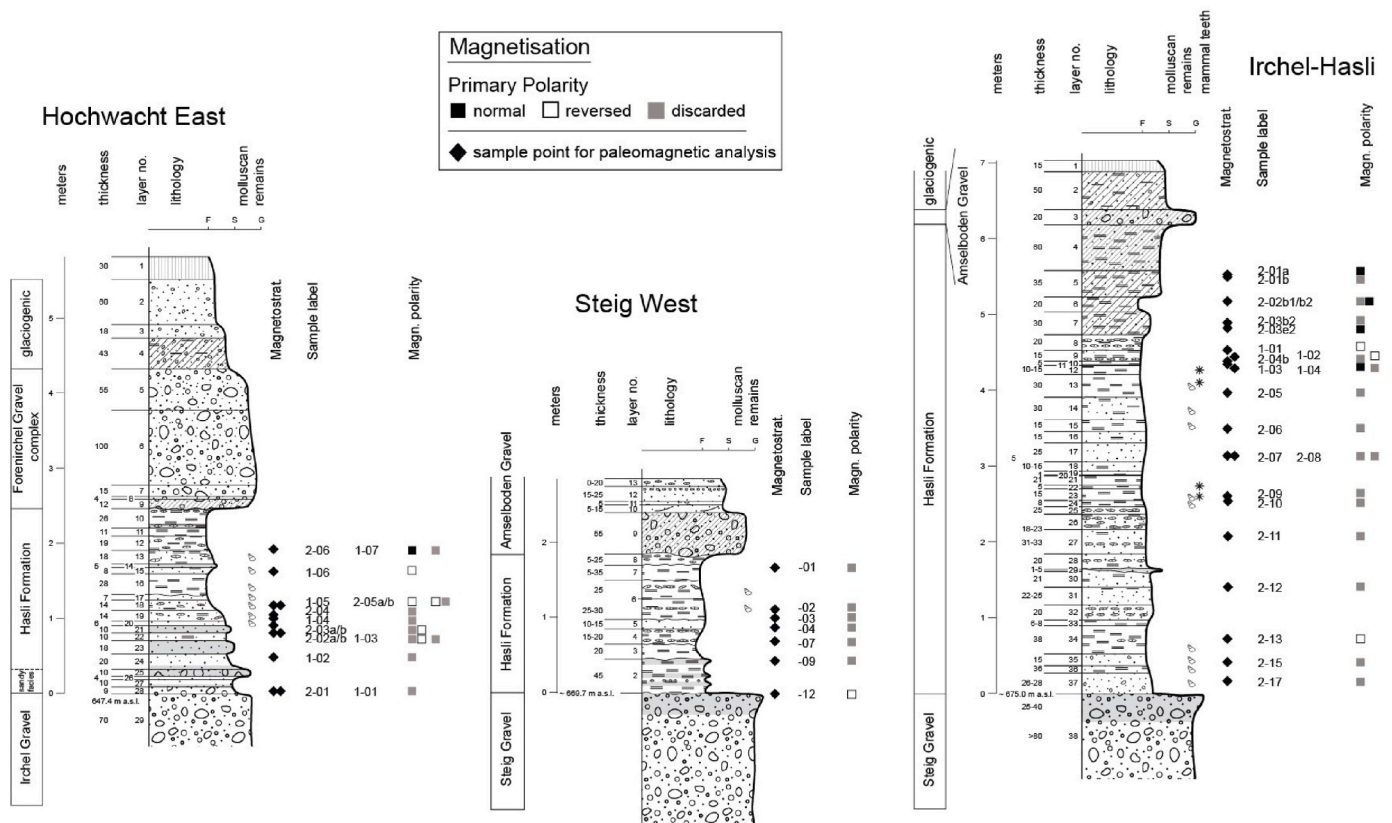


Fig. 12. Results of the palaeomagnetic analysis plotted against the study profiles from the Irchel Plateau.

8.1.7. Comparison with ages proposed by cosmogenic nuclide dating

The age of 2.1–1.8 Ma proposed for the HF based on a combination of the biological remains, palaeomagnetic and AA data, the sediments and the lithostratigraphy of the Irchel Plateau, is at odds with the ages for the

HDS gravels from the Plateau produced by cosmogenic dating techniques. When compared with the stratigraphic model (Fig. 3A) proposed by Graf (1993), the ages produced by the isochron-burial (IB) and depth-profile (DP) dating techniques include: $1.3 \pm 0.1 \text{ Ma}^\circ$ (IB) for the

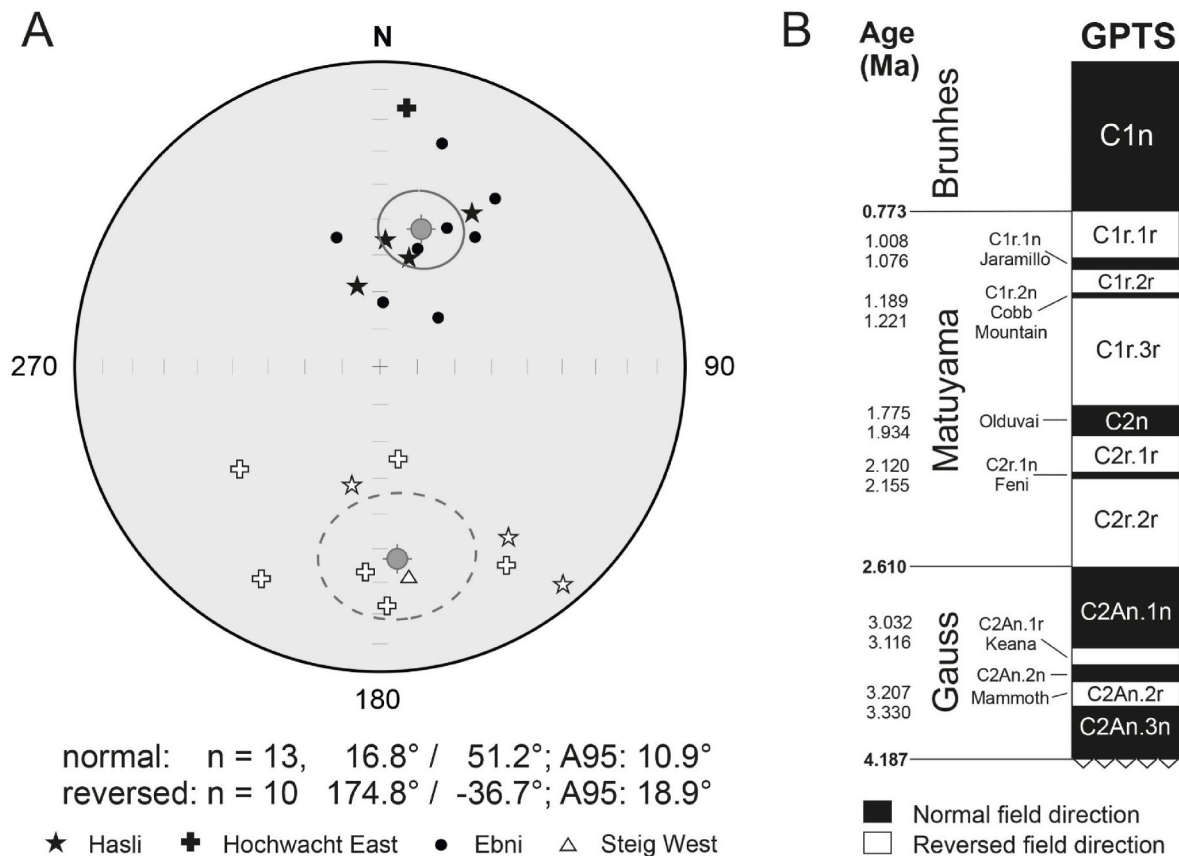


Fig. 13. A: ChRM distribution of discrete samples from Hasli, Hochwacht East, Ebni and Steig West in Lambert projection. The symbols indicate upward (open) and downward (filled) directions for the ChRM vectors; upward = negative inclination, downward = positive inclination. The mean directions for normal and reversed samples are shown with a 95% confidence cone in grey. B: Geomagnetic polarity changes from the Late Pliocene to the Middle Pleistocene (Astronomically Tuned Neogene Time Scale ATNTS2020; Raffi et al., 2020).

Langacher Gravel at Schartenflue; $2.6 \pm 0.1^\circ$ (IB) and $0.9 \pm 0.4^*$ (IB) recalculated to $1.51 \pm 0.47 \text{ Ma}^+$ (P-PINI) for the Irchel Gravel at Hochwacht and Hütz; $0.4^{+1.7}_{-0.2}$ (DP), $0.9 \pm 0.4^*$ (IB) and $1.3 \pm 0.1 \text{ Ma}^\circ$ (IB) for the Steig Gravel at Steig and Hasli, all from beneath the HF; as well as $2.8^{+1.8}_{-1.0} \text{ Ma}^*$ (DP) for the ‘Forenirchel Gravel complex’ above the HF at Wilemerirchel (Claude et al., 2019*, Knudsen et al., 2020+, Dieleman et al., 2022*). DP ages for Early to Middle Pleistocene deposits seem to be unreliable, however, due to deposits rapidly reaching nuclide steady-state conditions when linked with relatively high erosion rates (Grischott et al., 2020). Moreover, significant contradictions remain for the IB dates, both with the estimated age for the HF proposed above and between the dates themselves if they are placed within the stratigraphic model proposed by Graf (1993).

To resolve these apparent contradictions between the dates, new stratigraphic models have been proposed in which additional gravel-filled channels cross-cut the Irchel Plateau, and the HF is either present only at the south-eastern tip of the Plateau (Claude et al., 2019) or occurs in geographically interrupted segments across the Plateau (Fig. 3B; Dieleman et al., 2022). The occurrence of higher-order cut-and-fill architecture within the HDS sequence has already been proposed for the Steig area by Graf (1993), based on gravel petrography and clast orientation, but no new evidence has so far been produced to demonstrate the existence of any additional channels (at Schartenflue-Ebni for example), apart from the cosmogenic dates themselves. By contrast, detailed mapping has shown that the HF can be reliably traced for long stretches along the edge of the Irchel Plateau, although in places such as Schartenflue-Ebni it seems to have been subsequently lost to surficial erosion. The simple stratigraphic model (Fig. 3A) proposed by Graf (1993) appears to be closest to reality, as it

accords better with the clast petrography, mapping data and field observations, as well as the biological data for the HF discussed above, which indicate lateral continuity and the presence of the HF across much of the Irchel Plateau. Moreover, as the petrographic succession between the gravel types (cf. 4.2) seems likely to reflect a progressive change in the main source area for the gravel clasts, this change may well have been irreversible and thus favour the simple stratigraphic model.

The significant differences between the ages proposed by this multidisciplinary study and by cosmogenic dating are difficult to reconcile. Both biostratigraphic (Fejfar et al., 1997; Maul and Markova, 2007; Cuenca-Bescós et al., 2010) and cosmogenic dating techniques (Granger, 2006, 2014) have been successfully used for previous studies, but both also have their inherent problems. Reworking of biological material is a potential shortcoming of biostratigraphy, for example, although this can be discounted for the delicate remains found within the HF. Moreover, biostratigraphy is a relative dating method where independent numerical age controls may only be available for sites some distance away (cf. 8.5). On the other hand, the cosmogenic isochron burial method relies on a set of samples with differing inherited nuclide concentrations, which when plotted can generate a viable age. It requires knowledge about the production ratio between the measured nuclides, which may vary significantly according to the depth at which samples acquired their nuclide concentration. This is especially true for fluvio-glacial gravels, which are intrinsically problematic for the assumptions involved with this method as their provenance implies sample clasts that were eroded from below a glacier where nuclide production (i.e. their acquired concentration) is very low (Granger, 2014; Knudsen et al., 2020). This problem has recently been addressed by a ‘source-to-sink’ modelling approach (P-PINI) that has been applied

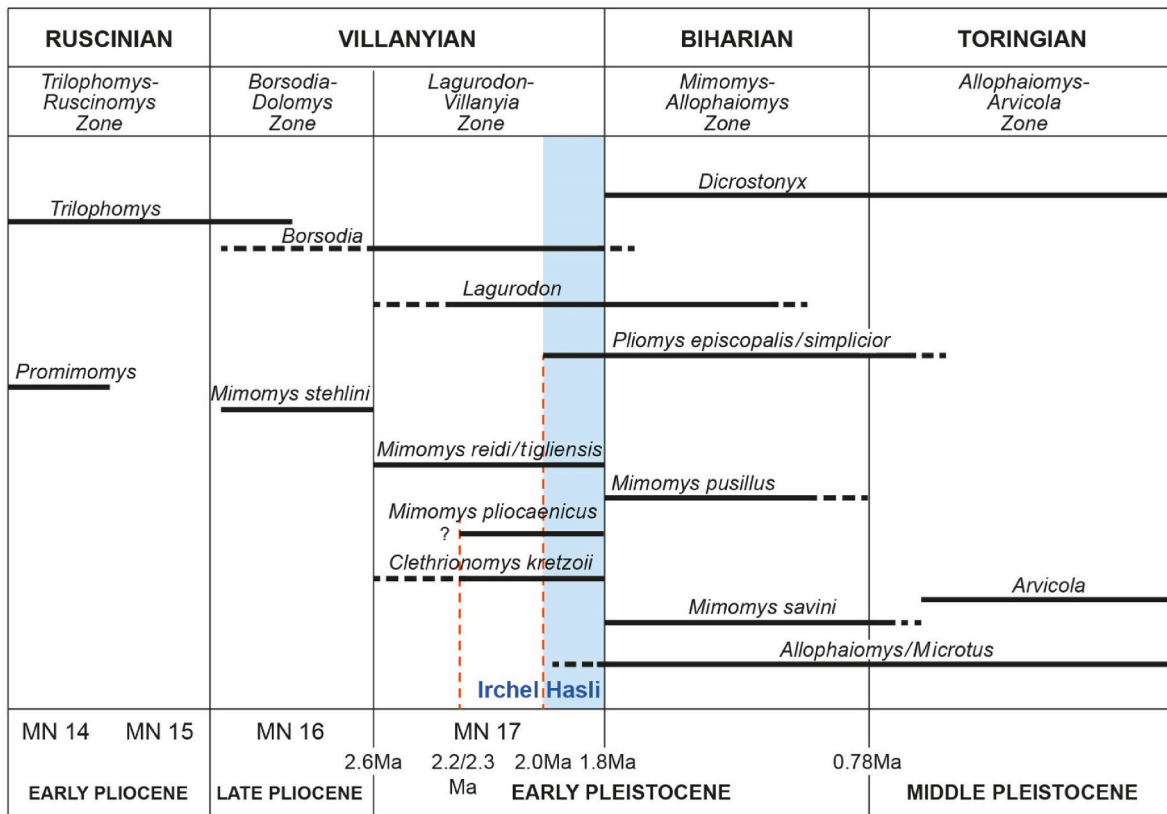


Fig. 14. Time chart for selected small mammal genera/taxa in Central Europe, including the key marker species present at Hasli (based on Fejfar et al., 1997, 2011; Frank et al., 1997; Maul and Markova, 2007).

to the measured nuclide records of samples from northern Switzerland (Knudsen et al., 2020; Nørgaard et al., 2023). At present, however, the highly complex isochron burial and P-PINI techniques allow dating measurements to produce significantly different age results when they are recalculated (e.g. Claude et al., 2019; Knudsen et al., 2020; Dieleman et al., 2022). A thorough uncertainty estimate that considers all estimations and calculations would therefore be extremely helpful for future discussions, as some of the apparent age contradictions may fall within a larger uncertainty bracket. It may also be useful to apply additional dating methods to stratigraphic sequences with cosmogenic ages. For now, however, the age contradiction at Irchel remains, although new samples, outcrops or methods may help to resolve this dilemma in future.

In Dieleman et al. (2022) it was argued that the small mammal teeth from Hasli may have been reworked, possibly inside a soft-clast. The fragile prismatic teeth from the arvicolids at Hasli, however, have exterior enamel that is fresh, and shows no signs of discolouration, alteration or physical abrasion, making direct fluvial reworking highly unlikely (Fig. 8). Moreover, the great majority of molluscs and ostracods from the same deposits are well-preserved and include shells and valves from small, fragile species, showing that most biological material is contemporary with the HF sediments. In addition, the molluscan faunas from Hasli are very similar to those from the HF profiles at Hochwacht, Steig, Amselboden and Wilemerirchel, making reworking even more unlikely. Finally, the small mammal teeth were all found within Layer 12 at Hasli, which is part of an in-situ sequence of 6.2 m of HF overbank sediments (Fig. 5B).

8.1.8. The age of the ‘Ebni silts’

The ‘Ebni silts’ are both underlain and succeeded by thick units of fluvio-glacial gravel within an HDS sequence. These gravels have individual lag boulders over 1 m across (cf. 2) that appear to have been

transported a considerable distance from the Alps into the Alpine foreland by extensive glaciers. Fluvial sediments within the Upper Rhine Graben near Heidelberg have shown that while the Late Pliocene was associated with very warm conditions and significant surface stability, the older Early Pleistocene saw a major increase in detrital sedimentation due to intervals with a notably cooler, moister and less stable climate linked with greater glacial activity in the Alps (Gabriel et al., 2013; Scheidt et al., 2015, 2020). As the HDS fluvio-glacial gravels at Irchel were also connected to the Rhine system, it seems highly likely that they also date from the Early Pleistocene. It is thus improbable that the normal polarity found in the ‘Ebni silts’ accumulated during the Gauss Chron, as this corresponds to the Late Pliocene. Nevertheless, if the lithostratigraphic model proposed by Graf (1993; Fig. 3A) is correct, then the ‘Ebni silts’ are older than the HF, in keeping with the AA results, and are thus of a pre-Olduvai age.

Biological material, calcareous nodules and the overbank nature of the sediments suggest that the ‘Ebni silts’ correspond to a warm period. As the silts seem from stratigraphic and clast petrographic data to pre-date both the Irchel Gravel and the HF, and the HF appears to include the onset of the Olduvai Subchron, the ‘Ebni silts’ may include a rare recording of the Feni (Réunion) Subchron, which is dated to 2.155–2.120 Ma (Fig. 13B; Raffi et al., 2020). Until now it has mostly been found in volcanic rocks or deep ocean cores and has seldom been documented in continental sediments (Channell et al., 2020). Although the preservation and recording of this relatively brief event within alluvial sediments might seem unlikely, there are other examples where the Feni Subchron may also have been found, such as in southern England (Preece et al., 2020), central France (Nomade et al., 2014; Paquette et al., 2021), east-central Spain (Sinusia et al., 2004), eastern Austria (Fink, 1979) and north-west Italy (Monesi et al., 2016). Thus, the combined evidence from the Irchel sequence seems to leave open the possibility that the ‘Ebni silts’ may correspond to the Feni Subchron.

8.2. Climate

Within the HDS of the Irchel Plateau there are three different levels with silty sediments that have yielded biological material. At Ebni, the lowest level, the presence of biological remains (molluscs, worm granules, ostracods and *Chara*) together with abundant calcareous nodules, within overbank deposits, indicates that the 'Ebni silts' probably accumulated within the floodplain of a meandering river during a period of warm climate.

The molluscan faunas from the HF include many taxa typical of warm interglacial conditions (Fig. 9, Table 2, SM Fig. S2, SM Tables S2b, S2c1, S2c2). The geographical distributions of these species show that while a number have modern or palaeo-distributions located in Central Europe, six have distributions that lie much further to the west and/or south-west of the Swiss Plateau (*Cochlostoma salomoni*, *Retinella elephantium*, *Spermodea lamellata*), four have distributions that lie to the south or far to the south (*Poiretia dilatata dilatata*), fourteen have distributions that lie to the east or far to the east (*Acicula parcelineata*, *Archaeogypsis acutus*, *Clausilia stranzendorfensis*, *Monachoides vicinus*, *Serrulella* sp.), and three have distributions that lie to the south-east, including the Alpine region (*Trochulus filicinus*, *T. leucozonus*). Importantly, all of the taxa with modern or palaeo-distributions that lie far from the Swiss Plateau have never previously been identified from Swiss Quaternary deposits. This evidence seems to suggest that the climate contemporary with the accumulation of the HF was on the whole significantly warmer than today, with species possessing distributions that lie far to the south or east indicating higher summer temperatures, while taxa with distributions that lie far to the west imply milder winters. Similarly, the pollen from Hasli includes several thermophilous tree species indicative of warm interglacial conditions. This picture is in good agreement with global surface palaeotemperature reconstructions, which indicate a significantly warmer climate during the older Early Pleistocene (Gelasian) before c.1.8 Ma (Snyder, 2016). There seems to have been a notable cooling around 1.76 Ma that marks the transition from the Tiglian warm stage to the Eburonian cold stage in the North-West European Chronology, and coincides with the boundary from the Gelasian to the Calabrian Stage at 1.8 Ma (Gibbard and Head, 2020). This cooling event saw important faunal changes in both terrestrial and oceanic sequences across the Northern Hemisphere, including the extinction of several key marker species at the Villanyian/Biharian transition in the European small mammal chronology (Fig. 14).

There is also molluscan evidence for climatic variation during the accumulation of the HF. The upper levels of Part 2 at Hasli and Hochwacht, for example, appear to have been particularly warm and dry (Fig. 10). By contrast, Part 3 in the sequences from Hasli, Hochwacht and Steig seems to have been somewhat cooler and wetter, which led to increases in open ground and marsh molluscs, while forest and shade-loving taxa declined, and allowed the shells to be better preserved due to wetter conditions and reduced pedogenesis. This interval also saw the appearance at Hochwacht of the cold-tolerant pioneer *Columella columella* (Fig. 9, SM Table S2c2), which is normally associated with cold-period assemblages and lives today above 1000 m in the Alps and in the far north of Europe (Turner et al., 1998; Welter-Schultes, 2012). Similarly, the presence of *Lemmus* sp. among the small mammal assemblage from near the end of Part 3 at Hasli may also point to cooler conditions, as the species from this genus are typically found in moist, rather open habitats in colder regions (Macdonald, 1984). Conditions may therefore have been somewhat cooler and damper at this time, although forest molluscs continued to be rather diverse at all three sites.

The well-preserved and diverse molluscan faunas from the 'upper level' at Hochwacht West indicate a densely forested floodplain environment with interglacial conditions that were equally as clement as those for the HF, with warmer summers and milder winters than today.

8.3. Local terrestrial paleoenvironment

The molluscan sequences through the HF at all the study sites reflect biosuccessional processes within an interglacial floodplain forest, coupled with changes in the local floodplain environment due to flooding activity. Evidence for pedological processes (Fe and Mn) together with calcareous nodules and marsh molluscs, show that at certain times and locations the floodplain surface was only moderately damp, while at others it was rather wet and marshy.

The overall impression given by the molluscan faunas from Hasli is for a fairly rapid progression from moderately open, mixed coniferous and deciduous forest (Part 1), to rather dense, mature, more deciduous woodland with large trees and a rich understory of tall herbs, shrubs and young trees (Part 2; Fig. 10, SM Tables S2b, S2c1, S2c2). The pollen from Hasli includes a variety of deciduous and coniferous tree species (SM Table S3), and although the spectra are dominated by conifers, this may largely be due to preservational conditions. As the environment became notably damper during Part 3 of the sequence (Fig. 10), this coincided with an opening out of the forest, with fewer large trees and some loss of woodland species. The small mammal fauna from near the end of Part 3 at Hasli indicates rather open marshy ground (*Lemmus* sp.), bordered by fairly open woodland (*Apodemus* cf. *sylvaticus* and *Clethrionomys* cf. *kretzoi*), as groups typical of denser forest like Sciurini (tree squirrels) and Gliridae (dormice) are missing (Macdonald, 1984), although caution is required when comparing fossil taxa with the ecology of nearest living relatives.

The molluscan faunas from Hochwacht, Amselboden and Wilemerirchel show a more rapid progression towards rather dense, mature, primarily deciduous woodland with large trees, although at Hochwacht, like Hasli, there are signs later in the sequence for a significant opening out of the forest linked with damper conditions (Fig. 10; SM Tables S2b, S2c1, S2c2). By contrast, the faunas from Steig suggest that the local environment was significantly more open throughout the sequence, with fairly open woodland, abundant tall herbs and patches of more open ground, due to damper floodplain conditions.

8.4. Sedimentary environments

The poor molluscan assemblage from the 'Ebni silts' consists mainly of slug plates, together with shells from two marsh species (SM Table S2b). These, along with the silty nature of the sediments and the presence of ostracod valves, *Chara* and calcareous nodules, all point to accumulation within a damp floodplain subject to flooding events, not far from the active channel of a meandering river.

The HF is characterised by thinly interbedded grey/olive-grey silts and fine sands with fairly frequent erosion surfaces, together with the regular presence of varying quantities of aquatic and marsh molluscs, ostracods and *Chara*, and a dominant component of non-marsh terrestrial molluscs, with worm granules, some charcoal and small mammal remains (SM Tables S2b, S2c1, S2c2). This is consistent with the accumulation of overbank sediments within the floodplain of a lowland-type meandering river, which formed part of the Rhine system (Graf, 1993). Proximity to the active channel seems to have influenced how sandy the sediments were and the balance between sedimentation and erosion within the HF, with erosion appearing to have been more severe at Hochwacht but less important at Hasli. There is sedimentary and molluscan evidence within the sequence at Hasli for four depositional cycles, which allows the sequence to be divided into four stratigraphic 'Parts' (Fig. 10, cf. 4.4). The sequences at Hochwacht and Steig have similar although not necessarily time-equivalent sedimentary cycles, which also permit them to be sub-divided into 'Parts.' Vertical and horizontal differences in sedimentation may reflect a composite structure for the HF, linked to variations in discharge and sediment supply, and to depositional differences across the floodplain (Nanson and Croke, 1992; Miall, 2006). Sandy and gravelly sediments at the base of the HF at Hochwacht and Amselboden may represent the eastern edge of an

active channel that used to flow to the west of the Irchel Plateau. The presence of three small aquatic gastropod species that live in permanent subterranean waters or in freshwater springs (SM Figs. S2.21–S2.23), two of which are unidentified and may well be extinct, suggests that spring-fed streams may have been entering the floodplain from surfaces of higher ground nearby.

For the ‘upper level’ at Hochwacht West, the molluscs from the silty soft-clasts indicate that these represent flood silts, while the sandy lens has aquatic molluscs that suggest accumulation within a quieter stretch of a gravelly meandering river (SM Table S2c2). The c.4.2 m thick series of fluvial gravels that surround the soft clasts and the sand lens have been labelled the Hochwacht Gravel because of their important biological content. They seem likely to represent the gravelly and sandy bed of a meandering river that may well have been the same river that formed the HF. Further fieldwork and better documentation of their bedding structures is required to reliably separate the Hochwacht Gravel from the massively-bedded, sterile fluvio-glacial gravels of the subsequent ‘Forenirchel Gravel complex’ and the matrix-supported deposits of the Amselboden Gravel.

8.5. Comparisons with other key Early Pleistocene sites in Europe

HDS sites in Switzerland and southern Germany that have fine-grained deposits with preserved biological remains are rare. These include up to 17 m of HDS fluvial gravels at Albishorn-Bürglen (Graf, 2019) that have sporadic sandy and silty layers with molluscs. The rather diverse faunas include 58 terrestrial and 10 aquatic species, including most of the same biostratigraphic marker taxa present in the HF, such as *Archaeogopsis acutus*, *Clausilia stranzendorfensis*, *Cochlostoma salomoni*, *Macrogastra sessenheimensis* and *Poiretia dilatata dilatata* (Thew, 2024). In a gravel quarry at Eichbrunnen, near Freienwil (AG) at the edge of the Dürn-Gländ Plateau, a silty layer up to 0.6 m thick within HDS gravels yielded a molluscan fauna that seems to include *Cochlostoma salomoni*, suggesting an assemblage of a similar age to the HF (Frei, 1912, p. 24–26, reinterpreted in Thew, 2024).

There are few Early Pleistocene sites across Western, Central and Eastern Europe that have a similar richness in faunal remains as the HF. To the east in NE Austria, the key sites are Stranzendorf, Krems and Deutsch-Altenburg. Stranzendorf has a sequence of loessic silts with palaeosols that span from the Late Pliocene to the older Early Pleistocene, between c.3.2 and c.1.8 Ma, with rich assemblages of terrestrial molluscs (c.90 taxa) and mammals (Frank and Rabeder, 1997b). Krems-Schießstätte has similar deposits with varied assemblages of terrestrial molluscs (c.70 taxa) and small mammals, which date from c.1.9 to c.0.5 Ma (Frank and Rabeder, 1997a). Both sites have detailed palaeomagnetic sequences. Deutsch-Altenburg has a series of more than 50 fissure fillings discovered during quarrying at the Pfaffenberg. Despite doubts that may sometimes apply to the stratigraphic integrity of karstic fissure fillings, both the mammals and terrestrial molluscs show no signs of mixing and seem to represent sealed assemblages that formed fairly rapidly at intervals between the Late Pliocene and the early Middle Pleistocene, although no shells were preserved before c.2 Ma (Frank and Rabeder, 1997c). These three sites are important as they show that *Clausilia stranzendorfensis*, a key molluscan marker species for the HF, was present until c.1.8 Ma at Stranzendorf, but was absent from later levels at the other two sites (Frank, 2006). The small mammal faunas include similar species to those at Hasli, including *Mimomys pliocaenicus*, *M. reidi*, and *Pliomys episcopolis/simplicior* (Table 3).

The most important site in southern Germany is Uhlenberg in SW Bavaria, which has fairly rich assemblages of molluscs (50 terrestrial, 29 aquatic taxa) and small mammals that can be attributed to biozone MN17. The deposits have normal palaeomagnetic polarity, so seem to date from the Olduvai Subchron (Dehm, 1979; Rähle, 1995; Strattner and Rolf, 1995). This site has several of the same molluscan and small mammal marker species as the HF, including *Cochlostoma salomoni*, *Neostyriaca dehmi* and *Macrogastra sessenheimensis* (Rähle, 1995;

Nordsieck, 2007), plus *Mimomys pliocaenicus*, *M. reidi* and *Pliomys episcopolis* (Ellwanger et al., 1994, Table 3). Several other sites in the same area have significant molluscan assemblages of a similar age that are also analogous to those from the HF (Rähle and Bibus, 1992). Important older Early Pleistocene small mammal assemblages comparable to the Hasli fauna have also been found at Neuleiningen (Maul, 1996) and Schernfeld (Carls and Rabeder, 1988), although they lack independent dating.

In France, there are Late Pliocene sites with rich molluscan assemblages at Cessey-Sur-Tille and Sessenheim, with the former also having frequent small mammals (Chaline and Michaux, 1974; Puisségur, 1976; Schlickum and Geissert, 1980), but there are few older Early Pleistocene sites with preserved molluscs. By contrast, there are several well-dated sites from this period that have small mammal faunas analogous to those from the HF, including Mont Coupet and Senèze with dates from 2.3 to 2.1 Ma (Table 3; Heintz et al., 1974; Pastre et al., 2015; Paquette et al., 2021), as well as undated sites with comparable faunas, such as Montoussé 5 (Clot et al., 1976a, 1976b) and Saint-Vallier (Guérin et al., 2004). More recent deposits with small mammal remains at the Grotte du Vallonnet have an absolute date of c.1.4 Ma (Paunesco, 2002).

The Netherlands has very rich sites for small mammal and molluscan remains, such as the Maalbeek Pit and the Russel-Tiglia-Egypte Pit at Tegelen (Freudenthal et al., 1976; Tesakov, 1998; Westerhoff et al., 1998, van den Hoek Ostende and de Vos, 2006), with the former thought to date from c.2.4–2.2 Ma and the latter to c.2.0–1.8 Ma (van Kolfschoten, 2001). There is also a sequence of deposits rich in small mammal and molluscan remains in the Zuurland-2 Core at Brielle, which covers much of the Tiglian (c.2.4 to 1.8 Ma) and significant parts of the middle to later Early Pleistocene (Meijer, 1988; van Kolfschoten, 1988; 2001; van Kolfschoten et al., 2018; Preece et al., 2020). Both sites have some of the same molluscan and small mammal marker species as the HF, including *Cochlostoma salomoni*, *Mimomys pliocaenicus* and *M. reidi* (Table 3). A series of small mammal faunas from a core at Moriaan-shoofd covers much of the older Early Pleistocene (Slupik et al., 2013; Mayhew et al., 2014), while mammal remains and molluscs from the site at Bavel date from the later Early Pleistocene (Spaink, 1968, van Kolfschoten, Masini and Torre, 1990).

South of Switzerland in Italy, the small mammals from the Early Pleistocene follow a similar chronological pattern to those of Central Europe, including sites with palaeomagnetic data which show that *Mimomys pliocaenicus* disappeared around 1.8 Ma (Kotsakis et al., 2003; Masini and Sala, 2007, 2011; Bona et al., 2015). Most locations with terrestrial molluscs, however, have somewhat different faunas from those in Central Europe (Esu and Girotti, 1991; Gliozzi et al., 1997; Petronio et al., 2002; Esu and Ciangherotti, 2004).

9. Summary and conclusions

From 1.6 to 6.2 m of HF sediments have been exposed at 9 different sites within HDS deposits across the Irchel Plateau, and at 4 of these the HF has been excavated, documented and sampled in 6 profiles. In general, the HF occurs at 20–25 m above the base of the HDS, overlying the often strongly cemented summit of the Irchel and Steig Gravels. The grey to olive-grey silts and fine sands of the HF, with calcareous nodules, aquatic and marsh molluscs, ostracods and *Chara*, together with a dominant component of non-marsh terrestrial molluscs, worm granules, charcoal and small mammal remains, is indicative of overbank sediments accumulating within the damp floodplain of a lowland-type meandering river. This is in good agreement with field mapping and high-resolution digital terrain analysis, which indicate that originally the HF probably represented a continuous layer for the length and much of the width of the Irchel Plateau, although in places it appears to have been lost to subsequent surficial erosion. It also seems possible that the HF did not accumulate or was notably thinner in parts of the Irchel Plateau where the summit of the underlying gravels may have risen significantly above the surface of the former flood plain. The rich

terrestrial molluscan faunas indicate a significantly warmer climate than today, with rather dense, mature, deciduous and coniferous woodland with large trees, in accord with the pollen evidence.

The small mammal remains and molluscs, in conjunction with palaeomagnetic data, AA geochronology, sedimentary data and lithostratigraphy, suggest an age of 2.1–1.8 Ma for the HF. An ‘upper level’ of silty sediments and biological remains is of a very similar age to the HF although slightly younger, possibly around 1.8 Ma. The ‘Ebni silts’ seem to be somewhat older, and may correspond to the Feni Subchron dated to 2.155–2.120 Ma. These suggested ages are significantly older than several cosmogenic dates recently produced for the Irchel Plateau and other HDS sequences in northern Switzerland. While the apparent age divergence cannot be resolved here, the biological dataset from this study links the HF at Irchel to a well-established, partially dated regional biostratigraphic framework, which offers great potential for emerging dating methods to robustly test this framework in future. The abundance and diversity of the molluscs from the Irchel Plateau, with several rare extinct species, together with a significant small mammal assemblage, make this one of the key palaeontological and stratigraphic sites in Europe and an important reference point for European Quaternary biostratigraphy.

Author contributions

The excavation, documentation, sampling and stratigraphic analysis of the Irchel sites was undertaken by G. Deplazes, D. Kälin, N. Thew and M. Buechi. G. Cuenca-Bescós took additional samples for small mammals. The molluscs were studied by N. Thew, pollen was analysed by M. Knipping, while small mammal remains were prepared by D. Kälin, and identified by G. Cuenca-Bescós, aided by I. Urresti, who also undertook an extensive literature review. Petrographic analyses were by D. Kälin, the palaeomagnetic study was by S. Scheidt and AA geochronology by K. Penkman. F. Maier supported the data visualisations. All authors contributed to finalising the manuscript. The project was planned and coordinated by G. Deplazes.

Dedication

This paper is dedicated to Prof. Dr. Oldřich Fejfar† (1931–2023), Faculty of Natural Sciences, Charles University Prague, Czech Republic, for his pioneering work with Holarctic Neogene and Plio-Pleistocene small mammal palaeontology and biostratigraphy. Without his identification of the Arvicolid teeth recovered at Irchel Hasli by Bräm in 1955, plus Bolliger and Kälin in 1994–5, the present project would never have been conceived.

Data availability

The palaeomagnetic data is available in Scheidt et al., (2023b), while a comprehensive molluscan data set can be consulted in Thew (2024). The amino acid data will be deposited with NOAA upon publication. The authors have applied a Creative Commons Attribution (CC BY) licence to any Author Accepted Manuscript version arising from this submission.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Nigel Thew reports financial support was provided by National Cooperative for the Disposal of Radioactive Waste. Daniel Kälin reports financial support was provided by National Cooperative for the Disposal of Radioactive Waste.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.quascirev.2024.108550>.

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