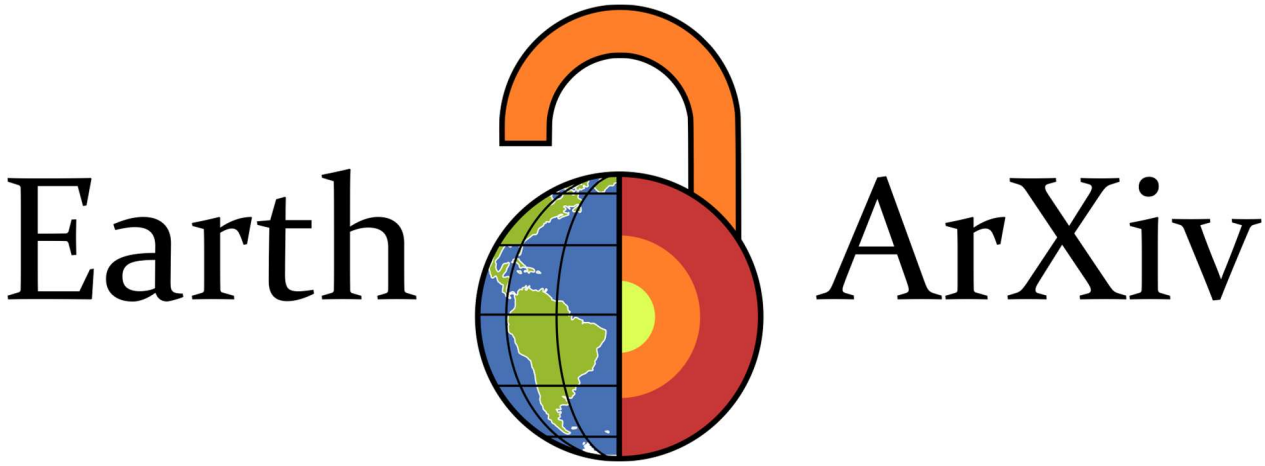

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The First Aminostratigraphies for the Quaternary of the Swiss Plateau

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Abstract. Here we develop an amino acid chronology to help establish a dated sequence for the important Early Pleistocene Höhere and Tiefere Deckenschotter morphostratigraphic units, as well as other Middle and Late Pleistocene deposits from across the Swiss Plateau. The intra-crystalline protein decomposition (IcPD) in a variety of calcium carbonate biominerals (including novel and rarely-analysed taxa) was used to develop the first aminostratigraphy for this region of central Europe. Age discrimination is possible between the Quaternary sites from the Swiss Plateau in six different biominerals: *Bithynia* opercula, shell fragments from *Fruticola*, *Arianta* and *Cepaea*, slug plates and worm granules. This chronology is compared with new and existing dating information derived from lithostratigraphy, palaeomagnetic data, biostratigraphic data (pollen, small mammals) and numerical dating methods (such as OSL/IRSL, U/Th, cosmogenic nuclides), as well as new biostratigraphic data derived from a study of Early to Late Pleistocene molluscan faunas from the Swiss Plateau. These new aminostratigraphies provide a relative chronology and give crucial new age information for a number of key sites from across the Swiss Plateau, which helps to fill major gaps in the Quaternary chronology for Switzerland.

1 Introduction

The northern Alpine Foreland region is especially propitious for the study of Pleistocene litho- bio- and climatostratigraphy due to the formation of distinct fluvioglacial gravel terraces often linked with glacial tills and much rarer interglacial sediments. This explains why the world's first ever regional Quaternary stratigraphy was attempted by Penck and Brückner (1901-1909) for the Alpine Foreland of southern Bavaria, when they named four glacial periods (Günz, Mindel, Riss and Würm). Subsequent studies have shown, however, that the Quaternary glacial history in the northern Alpine Foreland is much more complex than first thought and that significantly more glaciations have left their imprint on the landscape (Graf, 1993; Doppler et al., 2011; Ellwanger et al., 2011; Preusser et al., 2011; van Husen & Reitner, 2011; Schlüchter et al., 2021). One of the

outstanding problems that confronts any attempt at establishing a detailed regional chronology is the need to produce absolute and relative dates for the surviving deposits, which tend to be spatially separated and fragmentary due to the destructive effects of successive glacial advances. The existing chronology for the Pleistocene in Switzerland, for example, has many gaps and unknowns, especially for the Early and early Middle Pleistocene (Schlüchter et al., 2021), and similar problems exist for the chronologies of southern Germany and Austria (Doppler et al., 2011; Ellwanger et al., 2011, van Husen & Reitner, 2011). This hampers a greater understanding of the glacial and interglacial histories for the wider Alpine region.

The Quaternary archive of northern Switzerland has long been divided into four morphostratigraphic units (Graf and Burkhalter, 2016), with the highest considered to be the oldest (Fig. 1): the Höhere Deckenschotter (HDS; Higher Cover Gravels), Tiefere Deckenschotter (TDS; Lower Cover Gravels), Hochterrasse (Higher Terrace) and Niederterrasse (Lower Terrace). 'Deckenschotter' units refer to mostly fluvioglacial gravels that form a covering to low, plateau-like hills at a similar elevation range. The two Deckenschotter units documented in northern Switzerland and the neighbouring area of Baden-Württemberg, are separated by an important regional phase of incision. Four similar morphostratigraphic gravel units were documented for the Alpine Foreland of southern Bavaria by Penck and Brückner (1901-1909), who correlated them with their four named glacial periods (Günz, Mindel, Riss and Würm). Despite more recent work that has recorded the deposits of up to 16 glaciations in northern Switzerland, four of which have been linked with the formation of the HDS (Graf, 2009, Preusser et al., 2011), a modified version of the four morphostratigraphic units is still used in northern Switzerland (Graf & Burkhalter, 2016).

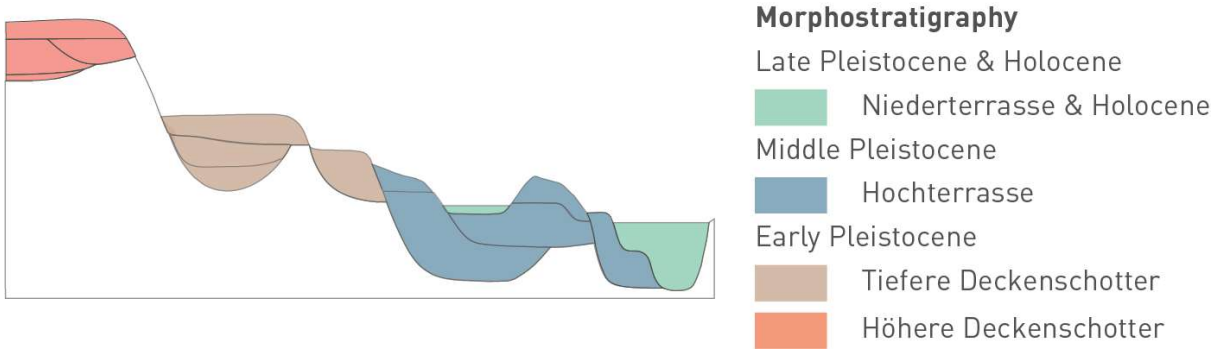


Figure 1: A simplified schematic stratigraphy for Pleistocene deposits in northern Switzerland, modified from Graf and Burkhalter (2016).

The formation of these terrace levels has been explained by progressive fluvial incision, with higher level terraces thought to reflect older base-levels, while lower terraces represent subsequent younger base-levels. The situation within areas influenced by glacial advances is complex however, as later ice advances can erode and alter previously existing sedimentary archives. Additionally, terraces can form at different levels depending on their depositional context, such as their position relative to the

ice margin. In such a setting, the correlation of sedimentary archives and determining depositional ages is essential for understanding fragmentary and complex sedimentary histories.

The sediments of the four Swiss morphostratigraphic units are mostly composed of fluvioglacial gravels and sands that are difficult to date. In deposits older than the last glacial Niederterrasse or the Middle to Late Pleistocene Hochterrasse, fine-grained deposits are uncommon and silty layers with preserved biological material are even rarer. Relatively few studies have dated sediments older than the last glaciation, with techniques including luminescence dating (OSL, IRSL), uranium-thorium dating (U/Th), cosmogenic radionuclide dating, magnetostratigraphy and biostratigraphy (Table 1 and references therein). Recent investigations using luminescence and cosmogenic dating suggest that some previously proposed ages and correlations may have to be reconsidered (e.g. Gegg et al., 2023; Dieleman et al., 2022a). Additional independent evidence for the timing of depositional archives is therefore needed to improve current understanding of Quaternary landscape evolution.

Molluscs have long been known to have biostratigraphical importance in Quaternary deposits due to the appearance and disappearance of certain marker species (cf. Meijer, 1986). Shells from Middle and Late Pleistocene deposits in Switzerland have been sporadically studied since the early twentieth century (e.g. Erni et al. 1943), but there has been a paucity of more recent work, and in many cases the material from these older studies was only partially analysed and identifications needed revision. Since 2018, the material from many of these older sites has been re-examined and revised, and new sites have been studied, several of which feature here (Thew, 2024). Moreover, when Pleistocene deposits contain biomineral remains such as mollusc shells, there is the potential to develop an aminostratigraphy for the region, using the extent of protein breakdown in certain biominerals (e.g. Abelson, 1955; Miller & Mangerud, 1985; Wehmiller et al., 2021). In this study the relative timing of several key archives from the Swiss Plateau (lowland Switzerland north of the Alps) is investigated for the first time by developing an aminostratigraphy of calcium carbonate biominerals.

Previous aminostratigraphic studies from across Europe have shown that the intra-crystalline fraction of *Bithynia* opercula exhibits closed-system behaviour (e.g. Penkman et al., 2011; Tesakov et al., 2020; Nelson et al., 2024, 2025), so their presence in some of these Swiss Plateau deposits made this material an obvious target for aminostratigraphy. Where closed-system behaviour is evident, then protein decomposition should depend solely on time and temperature (e.g. Brooks et al., 1990; Penkman et al., 2011), so within a region that has experienced the same integrated temperature history (e.g. Miller et al., 1999; Wehmiller et al., 2000), the extent of intra-crystalline protein decomposition (IcPD) provides a relative chronology. In addition, various other biominerals (aragonitic mollusc shells from *Arianta*, *Cepaea* and *Fruticola*, plus calcitic slug plates and worm granules) were present across a wider range of sites and horizons, so this study aimed to test their potential for amino acid geochronology. Chiral amino acid analyses were undertaken on bleached samples to determine the IcPD behaviour in these biominerals. The IcPD in this combination of biominerals was then used to develop the first aminostratigraphies for this region of central Europe, providing a relative chronology for several key archives from the Swiss Plateau.

2 Geological context and materials

Mollusc shells were first discovered in Deckenschotter deposits in northern Switzerland by Frei around 1910 (Frei, 1912), with 10 terrestrial species recovered from silty lenses in a series of HDS gravels at Eichbrunnen, near Freienwil, which is part of the Dürn-Gländ Plateau (Aargau). More recently, shells were discovered in 1955 by Bräm (Bräm, 1956), in a unit of silt and fine sand within a sequence of HDS gravels at Irchel Hasli at the south-eastern end of the Irchel Plateau (Zürich). Subsequent investigations of the same silty unit by Graf in 1990-92 (Graf, 1993, p.35-48) and by Bolliger et al. in 1994-95 (Bolliger et al., 1996) confirmed the frequent presence of mollusc shells, with at least 14 terrestrial and 1 aquatic species identified. Since then, shells have also been found in silty-sandy layers within fluvial gravels at the base of a HDS terrace at Albishorn-Bürglen (Gubler, 2009; Graf, 2019, p.9) and within silty deposits at the base of a TDS sequence at Hungerbol (Fig. 2), near Schienen (Baden-Württemberg; Graf, 2009, p.23-25).

An extensive survey was carried out to identify sites with mollusc shells and other suitable biominerals, which would allow an aminostratigraphic framework to be developed for the Swiss Plateau. Firstly, a literature study was conducted that focused on HDS and TDS deposits in northern Switzerland, although Hochterrasse sites were also considered. This process greatly benefited from pre-existing studies (e.g. Graf, 1993, 2009, 2019) and the explanatory guides that accompany the 1:25,000 maps of the Geological Atlas of Switzerland. As a second step, localities from northern Switzerland were assessed in the field, with still accessible sites that had previously shown a high potential being selected for re-sampling and analysis. Thirdly, the collections of the Natural History Museums in Basel, Bern and Geneva, the Paleontological Museum of the University of Zürich, the ETH Zürich and the Cantonal Museum of Geology in Lausanne were checked for suitable molluscan assemblages and/or unprocessed sediments from sites across the Swiss Plateau. Specialists likely to have amassed suitable shell material and/or sample sediments were also contacted. Finally, molluscs from sites that had been previously studied (by NT) and had independent dating evidence were also considered (such as Niederweningen, Thalgut, Abri Unterkobel and Oberbipp).

It transpired that deposits with preserved mollusc shells and other biominerals are extremely rare in HDS and TDS sequences in northern Switzerland and neighbouring areas of southern Germany. For the TDS, for example, the only locality where suitable material could be recovered was at Hungerbol, in south-central Baden-Württemberg. Most Middle and Late Pleistocene material, by contrast, has been obtained from previously collected archival samples. In all, biomineral material has been studied from deposits that cover much of the Quaternary, from HDS and TDS, through the Hochterrasse (or its temporal equivalent in the Geneva area) into the Holocene, incorporating many key interglacial and interstadial mollusc-bearing sites from across the Swiss Plateau (Fig. 2, Table 1). Detailed site information is reported in the relevant given references, while the key points are summarised here.

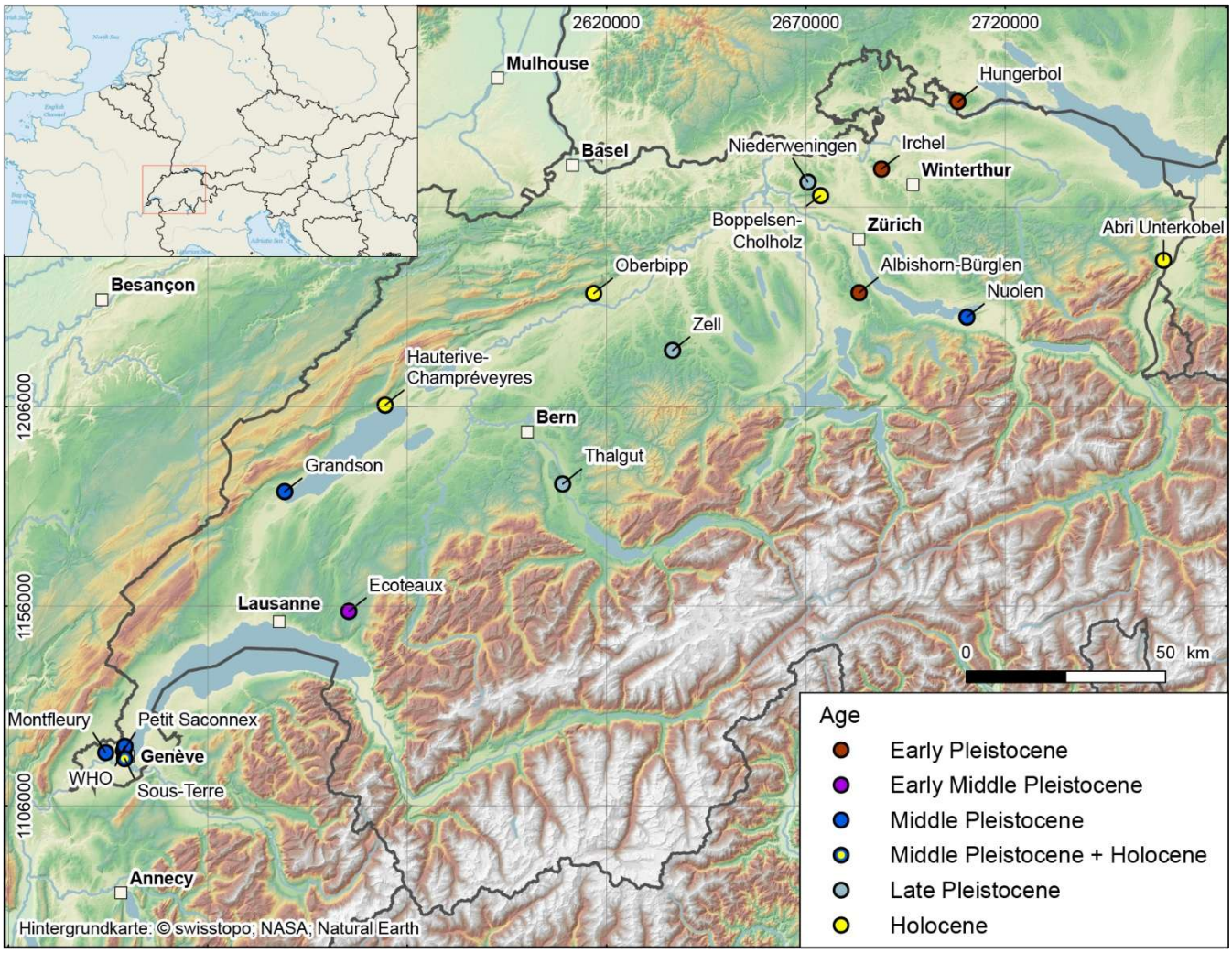


Figure 2: Location map of the Swiss Plateau with the sites mentioned in the text

2.1 Study sites and corresponding materials

2.1.1 Early Pleistocene

2.1.1.1. Irchel Plateau (Ebni, Hasli, Steig, Amselboden, Hochwacht)

The Irchel Plateau is located in north-eastern Switzerland, close to the border with southern Germany. It is a low hill of molassic marls and sandstone capped by HDS deposits. The HDS sequence includes a series of four units of massive bedded, fluvioglacial, braided-type gravels interrupted by two levels of silty deposits with preserved biological material. The lower level, below the Irchel Gravel at Ebni (Graf, 1993; Preusser et al., 201; Thew et al., 2024), consists of up to 2.5 m of fine sands and silts consistent with warm period flood plain deposits with biological material including molluscs (NEaar 13281-3), ostracods, *Chara* and earthworm granules (NEaar 13333-7).

Above the Irchel Gravel and Steig Gravel (Graf, 1993; Preusser et al., 2011), the Hasli Formation (HF) comprises up to 6.2 m of river floodplain silts and fine sands, with abundant well preserved biological material that includes small mammal teeth, molluscs (Thew et al., 2024; NEaar 13116-21; 13229-34; 13284-93), ostracods, *Chara* and earthworm granules (NEaar 13315-20; 13330-2; 13338-40). At Hochwacht and Amselboden (NEaar 14025-30; 14144-6), the base of the HF is notably coarser, with sand and fine gravel, and includes rare fragments of *Bithynia* opercula (NEaar 14141-2; 14147-8).

The small mammal assemblage from the upper part of the HF at Irchel Hasli suggests a date from c.2.1 to 1.8 Ma for the upper part of the HF (Thew et al., 2024), which corresponds to the final part of the warm stage known as the Tiglian. The molluscan faunas found within the HF at several locations include 20 species never previously recorded from Swiss Quaternary deposits, several of which are extinct. Most of these have modern or palaeo distributions that lie far to the west, south or east of the Swiss Plateau, indicating that the climate was significantly warmer than today, with hotter summers and milder winters (Thew et al., 2024, Fig. 1), in keeping with elevated global surface palaeotemperature reconstructions for the late Tiglian (Snyder, 2016). The date suggested by the small mammals is also supported by molluscan biostratigraphy, as there are several species that became extinct after the end of the Tiglian at 1.76 Ma (Thew et al., 2024; Thew, 2024). Also of note is the probable presence of *Fagus* pollen at both Hasli and Hochwacht, which became rare after the Tiglian for the rest of the Early Pleistocene (Graf, 1993, p.46; Bludau, 1995; Hahne et al., 2008; Thew et al., 2024). The lower part of the HF has a palaeomagnetic signal with reversed polarity, while the upper levels have normal polarity (Scheidt et al., 2023). When combined with the small mammal and molluscan data, this palaeomagnetic transition seems to mark the beginning of the Olduvai subchron, which took place at 1.934 Ma (Bolliger et al., 1996; Ogg, 2020; Raffi et al., 2020; Thew et al., 2024).

At Hochwacht West, the HF is succeeded by 4.2 m of bedded fluvial gravels, which c. 3 m above the HF include silty soft clasts and a large lens of silty fine sand (2.5 m across by up to 0.4 m thick), both of which contain rich molluscan faunas (NEaar 13220-2; 14019-21; 14086-8; 14135-14142; worm granules: 13307-8) typical of warm interglacial conditions (Thew et al., 2024). The molluscan faunas from this 'upper level' are very similar to those of the HF and have the same major biostratigraphic markers, as well as several new species, indicating that these faunas are of a similar late Tiglian age.
The combined evidence shows that the start of the Olduvai subchron at 1.934 Ma seems to have occurred during the upper part of the HF, while the molluscs and small mammals show that both the HF and the 'upper level' with biological remains at Hochwacht West belong to the same biostratigraphical period before the end of the Tiglian at 1.76 Ma. A continuity in the molluscan evidence throughout the HF indicates that there were no major biostratigraphic hiatuses, and that this represents a single biostratigraphic unit. Based on a combined analysis of sedimentary data, small mammal and molluscan remains and palaeomagnetic measurements, an age of 2.1-1.8 Ma was postulated by Thew et al. (2024).

The stratigraphic position of the 'Ebni silts' beneath the Irchel Gravel suggests that they predate the HF and are thus of a pre-Olduvai age (Thew et al., 2024). This is reinforced by clast petrographic data from the gravel units below and above the HF at various locations across the Irchel Plateau, which agrees with the lithostratigraphic model proposed by Graf (1993). As the

'Ebni silts' seem to coincide with an event of normal polarity (Scheidt et al., 2023), it is possible that they may correspond to a rare recording of the Feni (Réunion) Subchron, which is dated to 2.155-2.120 Ma (Raffi et al., 2020).

The gravels of the Irchel Plateau below and above the HF have also been investigated by cosmogenic dating techniques (Claude et al., 2019; Dieleman et al., 2022a). Some of the ages produced differ significantly from the age for the HF proposed above, based on the combination of the evidence from the biostratigraphy, palaeomagnetic data and the Graf (1993) lithostratigraphic model. For example, at Steig and Hasli, the Steig Gravel below the HF has been dated by the isochron-burial method to 0.9 ± 0.4 and 1.3 ± 0.1 Ma, while the Irchel Gravel below the Hasli Formation at two other sites (Hütz and Hochwacht) has isochron burial dates of 0.9 ± 0.4 and 2.6 ± 0.1 Ma (Claude et al. 2019, Dieleman et al., 2022a). These burial ages have recently been recalculated with the P-PINI code to 1.01 ± 0.82 Ma (Steig), 1.14 ± 0.15 Ma (Hasli), 2.20 ± 1.23 Ma (Hütz) and 2.63 ± 1.06 Ma (Hochwacht; Broś et al. 2025). Based solely on the cosmogenic ages, additional gravel-filled channels that cross-cut across the Irchel Plateau have been proposed to explain the apparent age contradictions, but no new evidence has so far been produced to corroborate the existence of such additional channels, while the detailed clast petrographic data seems rather to support the Graf model (Thew et al., 2024).

2.1.1.2. Albishorn-Bürglen 2 and Albishorn-Bürglen 1

This site is located in north-eastern Switzerland near the west of Lake Zürich. The molluscs of Albishorn-Bürglen 2 come from several layers of sand and sandy-silt present within up to 17 m of fluvial gravels known as the Albisboden Gravel (Graf, 2019), which form the lower part of a sequence of HDS deposits. The molluscs suggest deposition within a gravelly meandering river during an interglacial. They include most of the same biostratigraphic marker species as the Hasli Formation at Irchel, including *Clausilia stranzendorfensis* and *Cochlostoma salomoni*, suggesting an age before 1.8 Ma during the Tiglian warm stage (Thew, 2024). The basal part of the gravels, where the worm granules (NEaar 13347-9) and *Bithynia* opercula were sampled (NEaar 14613), has reversed palaeomagnetic polarity (Graf, 2019) like the lower levels of the Hasli Formation, but the polarity of the fine layers from the upper part of the gravels, where the slug plates (NEaar 14615-7) derive, has not been studied.

Above the thick Albisboden Gravel of Albishorn-Bürglen 2, are 2-6 m of fluvioglacial gravels with large boulders, followed by 9-12 m of compact ground moraine (Bürglen Till). Then, within the upper part of the same HDS sequence, are up to 1.4 m of grey-brown fairly organic sandy-silts/silts (Graf, 2019) with bands of dark blackish-brown lignite and grey tufaceous silt with molluscs that constitute Albishorn-Bürglen 1. The molluscs include a significant number of interglacial species as well as small fragments of *Bithynia* operculae (NEaar 14615-7), showing that the floodplain silts of Albishorn-Bürglen 1 represent a second warm interglacial period within this HDS sequence.

The sequence at this site therefore suggests that after the warm period represented by the fluvial gravels of Albishorn-Bürglen 2, there was an important stratigraphic break when a major advance by the Linth-Rhine Glacier led to the formation of fluvioglacial gravels and basal moraine (Bürglen Till). Then, after the interglacial period represented by the alluvial silts of Albishorn-Bürglen 1, a second glacial advance led to the deposition of another fluvioglacial gravel with intercalations of till,

named the Albiswald Gravel. The Albishorn-Bürglen 2 gravels seem to correspond to the second of the three sub-units that Graf has defined for the HDS in northern Switzerland (Graf, 2019, fig.16, p.21-23), while the succeeding deposits, including the Albishorn-Bürglen 1 silts, belong to the third sub-unit of the HDS.

The Albishorn-Bürglen 1 faunas include few of the biostratigraphical markers present at Albishorn-Bürglen 2 and the Irchel sites, but instead have four new marker species, including two (*Cochlodina fimbriata*, *Macrogastra attenuata*) that have never been found in Tiglian deposits (Thew, 2024). The molluscs from Albishorn-Bürglen 1 therefore seem to be significantly younger than those of Albishorn-Bürglen 2 and are probably post-Tiglian. Similarly, although the organic silts of Albishorn-Bürglen 1 include pollen from thermophilous tree species typical of a warm interglacial, there is no sign of *Fagus*, despite thousands of pollen grains being counted (Knipping, pers. comm. 2019). *Fagus* pollen is rather common in Tiglian contexts, but is rare in deposits dating from the remainder of the Early Pleistocene after the Tiglian (Bludau, 1995; Hahne et al., 2008), so this evidence again suggests that the Albishorn-Bürglen 1 silts are probably post-Tiglian.

At 1.76 Ma, just after the end of the Olduvai Subchron at 1.78 Ma, there was a notable cooling (after marine oxygen isotope stage [MIS] 63) that marks the transition from the Tiglian warm stage to the Eburonian cold stage in the North-West European Chronology, and denotes the transition from the older Early Pleistocene (Gelasian) to the middle Early Pleistocene (Calabrian; Westerhof et al., 2020; Cohen & Gibbard, 2022). This cooling coincided with important faunal transformations in both terrestrial and oceanic sequences, including the extinction of several key mammalian and molluscan biostratigraphic marker species. The middle Early Pleistocene incorporates two stages of the North-West European Chronology: the Eburonian cold stage from 1.76-1.49 Ma (MIS 62-50), and the Waalian warm stage from 1.49-1.22 Ma (MIS 49-37; Westerhof et al., 2020). The transition to the later Early Pleistocene at 1.22 Ma marks the start of the Menapian cold stage (MIS 36-32), which was followed by the Bavelian Complex. During the Eburonian there is clear evidence for significant glacial activity in Europe, while there appears to have been minimal glacial activity in lowland areas during the Waalian (Head & Gibbard, 2015; Thew, 2024). It therefore seems most likely that the glacial advances represented by the Bürglen Till and the Albiswald Gravel (with intercalations of till) occurred during the Eburonian, given that they also form part of the HDS terrace and immediately succeed those of Albishorn-Bürglen 2 that correspond to the late Tiglian. If true, the interglacial silts of Albishorn-Bürglen 1 would be the first site known from Switzerland with biological material dating from the middle Early Pleistocene.

2.1.1.3. Hungerbol, Germany

Hungerbol is located just inside south-western Germany, near the north-western corner of the Bodensee, within a low-lying hill capped by Quaternary sediments called the Schiener Berg. These deposits represent the morphostratigraphic unit known as the Tiefere Deckenschotter (TDS), which like the HDS is found in northern Switzerland and neighbouring areas of southern Baden-Württemberg (Graf, 2009; Preusser et al., 2011, Scheidt et al. 2023). In the traditional model, the TDS is lower than the HDS, so should be younger (Graf & Burkhalter, 2016), meaning that Hungerbol should be stratigraphically younger than Albishorn-Bürglen 1. At the base of the Hungerbol sequence are 1 to 4 m of finely bedded fluvial gravels and sands (Hungerbol

Gravel), which are succeeded by up to 2.7 m of silts and fine sands with biological material including molluscs that represents Hungerbol 2 (sampled at western end of the outcrop, NEaar 12244-50, 13327-9; 14618-9). After 0.6 m of sterile fluvial gravels there are up to 2.2 m of silts and fine sands with mollusc shells that represent Hungerbol 1 (sampled at eastern end of the outcrop, NEaar 13131-3, 13324-6). All of these sediments seem to represent floodplain deposits of the same meandering river, but while Hungerbol 2 has a fauna typical of warm interglacial conditions, the molluscs of Hungerbol 1 seem to represent a mild interstadial within the early part of the succeeding cold period. The sequence is completed by over 5 m of fluvioglacial gravels linked with a nearby ice front (Bannholz Gravel; Graf, 2009a, p.23-25). The Schiener Berg sequence is completed by up to 50 m of basal till, followed by another c. 15 m of fluvioglacial gravel, and then a further fluvioglacial unit at a somewhat lower level.

The molluscan faunas of Hungerbol 2 appear to belong within the Early Pleistocene due to the continued presence of eastern species like *Monachoides vicinus* that seem to have disappeared from the Swiss Plateau after this period, and an absence of biostratigraphic marker taxa typical for the Middle Pleistocene (Thew, 2024). The faunas are rather similar to those of Albishorn-Bürglen 1, but have two additional marker species, *Clausilia cruciata* and *Platyla polita*. The small mammal remains from Hungerbol 2 consist of teeth from two unidentified taxa of rootless Lagurids, which seem to point to a date between 1.8 and 0.8 Ma (Maul & Markova, 2007; Oldrich Fejfar, pers. comm.). When the TDS sequence from the Schiener Berg is compared with the glacial event stratigraphy for northern Europe during the Calabrian (Head & Gibbard, 2015), the most likely scenario is that the thick glacial deposits of the Schiener Berg sequence correspond to the Menapian cold stage that began around 1.22 Ma (MIS 36-32; Westerhof et al., 2020), or the succeeding Bavelian Complex, rather than the preceding Waalian warm stage. This might imply that the most likely age for the Hungerbol 2 & 1 deposits is 1.2-1.0 Ma, which belongs within the late Early Pleistocene. This is in line with a date of 1.18 ± 0.09 Ma, produced by the isochron-burial method, on the Hungerbol Gravel that underlies the silts of Hungerbol 2 & 1 (Broś et al., 2025).

2.1.2. Middle Pleistocene

The choice of sites with molluscan material that dates from the Middle and Late Pleistocene was largely governed by what was available in museum collections, although every effort has been made to have shells from as broad a temporal range as possible, as well as having sites spread across the Swiss Plateau.

2.1.2.1. Ecoteaux

Ecoteaux is a small palaeolake basin located in western Switzerland near the foot of the Alps. A core sequence (Pugin et al., 1993) shows that above the Palaeogene Molasse, the *Lower Formation* consists of 2 m of lodgement till overlain by 14 m of glaciolacustrine varved clay-silts/fine sands with drop stones, then 12 m of late glacial laminated silts and fine sands, associated with reversed palaeomagnetic polarity (likely to be late Early Pleistocene). After a hiatus, the *Upper Formation* begins with

glacial deposits associated with normal polarity (which are thus Middle Pleistocene), then 11.5 m of laminated lacustrine organic sandy-silts (Unit 7), followed by 5.5 m of silty-sands (Unit 8) with some gravel in the basal 1.3 m, with Units 7 and 8 both having wood fragments, plant remains and mollusc shells. Above another hiatus, the sequence terminates with 10 m of last glacial maximum (LGM) gravelly moraine and basal till. The analysed molluscs (NEaar 13110-2) were sampled from near the base of the lacustrine sediments at Surface Exposure B (in Pugin et al., 1993) with pollen analysis and the silty/marly nature of the sediments confirming their correlation with the lower half of Unit 7 in the core sequence.

The pollen shows that the silts of core Units 7 and 8 correspond to two interglacial warm periods separated by a colder interval (with the gravel), although the continuation of low frequencies of *Taxus*, *Abies* and *Corylus* indicates that conditions were never truly cold (Pugin et al., 1993). Although both warm periods have low frequencies of *Pterocarya*, the earlier of the two has up to 2% *Carya*, which became rare in most of Europe after the Early Pleistocene and disappeared from north of the Alps by the end of the Cromerian (end of MIS 13; Hahne et al., 2008; Orain et al., 2013; Magri et al., 2017). This indicates that both warm periods date from the early Middle Pleistocene and seem likely to represent MIS 15 and MIS 13. The largely aquatic assemblages include the extinct bivalve *Pisidium clessini*, which seems to have disappeared from Central Europe after MIS 13 and from Western Europe after MIS 7. There are also three marker taxa that appear to have first arrived in Central Europe during the Middle Pleistocene (*Acicula lineata*, *Acicula lineolata*, *Pagodulina pagodula*; Thew, 2024). As the molluscs come from the lower of the two interglacial warm deposits, this would suggest that the shells date from MIS 15. In this case, the glacial till at the base of the Upper Formation seems likely to correspond to MIS 16.

2.1.2.2. Montfleury and Sous-Terre 2

Montfleury is located to the west of Geneva, c.1.4 km to the NW of the present course of the Rhône. Two cores: Montfleury 1 (1946; Lanterno et al., 1981) and Montfleury 2 (1981/82; Wegmüller et al., 1995) were taken 115 m apart, with the molluscs coming from Montfleury 1. Above the Molasse sediments, the combined sequence from the two cores comprises: c.30 m of glaciogenic deposits (basal till, fluvioglacial, glaciolacustrine; 'Moraine basale inférieure'), indicative of full glacial conditions, followed by 1 to 1.5 m of sandy gravel, likely to correspond to late glacial conditions. Then comes up to 8 m of silty sediments with plant remains, mollusc shells (NEaar samples 12263-5) and pollen typical of a warm interglacial, termed the 'Confignon Sequence' by Wegmüller et al. (1995). This is followed by more sandy sediments, called the 'Vernier Sequence,' with molluscs and pollen indicative of much cooler conditions. Above this are silty sands with biological material typical of a warm interglacial, called the 'Montfleury Sequence' (Wegmüller et al., 1995). After a hiatus, there are thick fluvioglacial gravels (the 'Alluvion ancienne'), then another hiatus succeeded by LGM basal till.

Sous-Terre is located on the right bank of the Rhône, 5 km ESE of Montfleury and 0.5 km from where the river exits Lake Geneva. The sequence (outcrop + geotechnical cores) begins with up to 35 m of basal moraine indicative of full glacial conditions ('Moraine basale inférieure'). Above this are 1 to 2 m of grey sandy-silts capped by a thin sandy lignite, with wood fragments, plant remains and a rich molluscan fauna (Jayet and Amberger, 1969; Sous-Terre 2, the lower level of IcPD samples,

NEaar 12266-8, 13134-6, 13235-7, 13303-5, 13344-6). Above this lie 1.5 to 4 m of very compact laminated blue-grey silts with some plant material (only *Picea* needles), pollen and rare molluscs. Above a hiatus are up to 25 m of partially cemented fluvioglacial gravels with erratic blocks, known as the 'Alluvion ancienne', interpreted as corresponding to full glacial conditions. After another hiatus comes LGM basal till, then 0.7 m of grey marly silty-sand with stones and mollusc shells (Sous-Terre 1, the upper level of IcPD samples), that is early Holocene (cf. Sect. 2.1.4.1). Above this lies 1 m of late Holocene tufaceous sandy-silt with molluscs and small fragments of anthropogenic tile and brick, capped by a modern soil.

The molluscs from both the 'Confignon Sequence' at Montfleury and Sous-Terre 2 come from sandy-silt deposits linked with an active channel, almost certainly the Rhône, with Montfleury appearing to represent the edge of a palaeochannel and Sous-Terre 2 a channel margin/floodplain location. The pollen (Hofmann-Grobéty, in Jayet and Amberger, 1969; Girard, 1970; Wegmüller et al., 1995), plant remains and molluscs from these deposits are all typical of warm interglacial conditions. The pollen and molluscs from the 'Vernier Sequence' at Montfleury and the compact blue-grey silts at Sous-Terre suggest considerably cooler conditions (Reynaud, 1982 p.29; Wegmüller et al., 1995), while the silty-sands of the 'Montfleury Sequence' indicate a second interglacial period, although no molluscs have been analysed.

The pollen from the interglacial sediments at both these sites has no *Pterocarya* or grains from genera of trees/bushes that disappeared after the early Middle Pleistocene, suggesting that they probably date from the later Middle Pleistocene (Hofmann-Grobéty, in Jayet and Amberger, 1969; Girard, 1970; Wegmüller et al., 1995). The first interglacial at Montfleury has the molluscan marker species *Perforatella bidentata* that disappeared from Switzerland before the end of the Middle Pleistocene (Thew, 2024). This species is missing from the fauna of Sous-Terre 2, which instead includes the biostratigraphic marker *Clausilia rugosa antiquitatis* that seems to have disappeared after MIS 11, as well as *Aegopis klemmi* and *Zonitoides sepultus* that both became extinct after MIS 9 (Thew, 2024). The thick glacial deposits that underlie both sites correspond to the 'Moraine basale inférieure,' which is fairly widely present in the Geneva area (Moscariello et al., 1998, fig.2). This appears to represent the 'Möhlin Glaciation,' which seems to have been the most extensive in the Swiss Alpine Foreland (Preusser et al., 2011) and saw a major increase in the quantity and coarseness of debris supply into the Upper Rhine Graben north of Basel (Preusser et al., 2021). The Bünten Till at Möhlin may well represent MIS 12 (Dieleman et al., 2022b), although this age is disputed (Norgaard et al., 2023). Taken together, the evidence suggests that while the glaciogenic deposits that underlie both sites might date from MIS 12, the interglacial deposits at Sous-Terre 2 and the 'Confignon Sequence' at Montfleury are likely to represent MIS 11, the succeeding cooler deposits may well correspond to MIS 10, and the 'Montfleury Sequence' at Montfleury might correspond to MIS 9.

2.1.2.3. Nuolen/Buechberg

The site at Nuolen is found within a small plateau that forms the southern flank of the molassic hill known as the Buechberg, in north-eastern Switzerland near the foot of the Alps. This plateau, which corresponds to the Hochterrasse, is made up of thick gravel sequences with intercalated layers of marly-silt, silt and lignite. There are three levels with fine deposits, but only the

middle level has been analysed, with Nuolen 3 (NEaar samples 13128-30, 13226-8, 13309-11) coming from a western gravel quarry and Nuolen 1 (NEaar samples 13107-9) from a gravel quarry c.300 m further east. A lithostratigraphic study by Schindler (2004, p.13-31) has shown that the major stratigraphic units can be traced across most of this Hochterrasse area, meaning that correlations between the gravel quarries are plausible. The samples were taken by T. Bolliger.

The molluscan assemblages from both locations are typical of interglacial conditions, with Nuolen 1 representing the margin of a palaeochannel, while Nuolen 3 represents a marshy depression within an alluvial floodplain. The assemblages include the biostratigraphic marker *Urticicola umbrosus*, which disappeared from Central Europe before the end of the Middle Pleistocene (Thew, 2024), while a key marker species normally associated with the Eemian, *Helicodonta obvoluta*, is missing. Pollen analysis by Welten (1988, Diag.12, plus Diags. 8-11) on several profiles from nearby gravel quarries has attributed the 'lower' and 'middle' levels of marly-silt and lignite to their 'Holstein 1,' and the 'upper' level to 'Holstein 2.' These can be correlated with Interglacials 1 and 2 in the Meikirch sequence, which have been dated by OSL/IRSL to MIS 7e and 7c (Preusser et al. 2005; Railsback et al. 2015). The molluscan assemblages at Nuolen correspond to the lower of these two warm phases, so may date from MIS 7e.

2.1.2.4. Grandson

Grandson is located in western Switzerland near the south-western corner of Lake Neuchâtel. Samples were taken between 1942 and 1944 in a lignite mine located within a high lake terrace. The sequence begins with a thick layer of basal till, which is overlain by three layers of lignite alternating with marly lake silts. Above a hiatus comes up to 12 m of undated fluvioglacial gravels, then another hiatus succeeded by LGM basal till. The largely aquatic molluscan faunas come from marly-silts below the lowest lignite and between the lower and middle lignite layers. They suggest lake-levels around 50 m above today's mean level of 429 m asl. The shells analysed for IcPD (NEaar samples 12269-73) come from the upper of the two sampled levels.

The molluscs show that the sampled sediments were deposited at the edge of Lake Neuchâtel during a warm interglacial. No extinct molluscan species or varieties were present (Thew, 2024). Pollen analysis by Welten on a core taken 50-100 m to the north-west in 1982 (1988, diag.13; Jordi, 1996, fig.7) suggests that the sampled sediments correspond to their 'Holstein 1,' which can be correlated with Interglacial 1 at Meikirch that is now dated by OSL/IRSL to MIS 7e (Preusser et al., 2005). This would suggest that the molluscs may correspond to MIS 7e.

The presence of *Pterocarya* (wingnut) pollen at Grandson (up to 2%; Welten 1988, diag. 13), as well as rare grains at Buechberg near Nuolen (Welten 1988, diags. 10-11), might possibly suggest an earlier date than MIS 7, as Schlüchter et al. (2021) claim that this pollen type indicates an interglacial that is MIS 9 or older, due to its absence from Meikirch. *Pterocary*a was growing as far north as east-central Poland and Belarus during MIS 11 (Hrynowiecka and Winter 2015), and was present during MIS 9 in north-central Germany (Urban et al. 2023). Although reliable evidence for *Pterocary*a at MIS 7 sites is scarce, there are grains in a sequence at Neualbenreuth Maar in SE Germany (Stebich et al. 2020). As this pollen type is rarely frequent in later Middle Pleistocene deep core sequences in southern Europe (Magri et al., 2017), its use as a temporal marker (presence

or absence) must be viewed with caution until more research has been done for the Swiss Plateau and surrounding regions (discussed in Thew, 2024).

2.1.2.5. Petit Saconnex and World Health Organisation (WHO), Geneva

Both these sites are located within the city of Geneva, to the west of Lake Geneva, around 2 and 3 km respectively, to the north of Sous-Terre. Above the Molasse sediments, the Petit Saconnex sequence comprises up to 6 m of compact basal till, then a hiatus followed by up to 9 m of bedded grey silts and sandy-silts with molluscs and plant remains, then another hiatus succeeded by up to 8 m of partially cemented fluvioglacial sandy gravel (the 'Alluvion ancienne'), and then a final hiatus followed by LGM basal till. Of the two profiles at Petit Saconnex, the first was sampled by A. Jayet in 1961 (Jayet et al., 1961), although the shells have not been re-examined, and the second by C. Ruchat in 1994 (Thew, 2024; NEaar samples 14016-8; 14074-6). These two profiles lie 0.8 and 1.2 km to the south of the site at the World Health Organisation (WHO), where a core was taken in 1979. Molluscs were found (NEaar 14013-5; 14083-5) in 3 m of grey sandy-silts with wood fragments, similar to those at Petit Saconnex, which were underlain by 5.5 m of gravelly moraine and weathered fluvioglacial gravel and covered by 4.7 m of LGM till (Reynaud 1982). The molluscan faunas, plant remains and pollen from the two sites are very similar, being typical of an interstadial from the earlier part of a glacial period (Thew, 2024). This indicates that the silts from the two sites are probably contemporary and represent the same lithostratigraphic unit.

The fluvioglacial gravels of the 'Alluvion ancienne' that cover the mollusc-bearing silts at Petit Saconnex, as well as the interglacial levels at Sous-Terre and Montfleury, can reach up to 75 m thick in places, and have striated clasts, erratic blocks and intercalated layers of moraine, which show that they accumulated near an ice front during a full glacial period (Reynaud 1982; Arn, 1984; Maystre and Vergain, 1992). They may well date from MIS 6, as there is ample evidence that the Rhône Glacier was present in the Geneva area during this interval period (Coutterand, 2018), and there is a major erosional hiatus linked with the partial or complete removal of these gravels before the deposition of glaciogenic deposits up to 80 m thick in the Geneva area during the last glacial (Moscariello et al., 1998). The basal till beneath the silts at both Petit Saconnex and WHO seems to correspond to the 'Moraine basale inférieure,' which also underlies the sites at Sous-Terre and Montfleury. There appears to have been a major episode of erosion before the deposition of the silts at Petit Saconnex and WHO that removed the earlier sediments found at Sous-Terre, Montfleury and Confignon, which seem to date from MIS 11 to MIS 9. If this erosional event (and the silts that followed) was the precursor to the deposition of the 'Alluvion ancienne,' this might suggest that the silts at Petit Saconnex and WHO date from the early part of MIS 6. Alternatively, it is also possible that they may have accumulated during MIS 8.

2.1.3. Late Pleistocene

The Late Pleistocene sites at Zell, Thalgut and Niederweningen have deposits that seem to have accumulated during the last interglacial.

2.1.3.1. Zell

Zell is located in central Switzerland, near the north-western edge of the Alps. Molluscs from Kiesgrube (gravel quarry) Meier, south of Zell, were first studied by L. Forcart in the early 1940's (Erni et al., 1943), but most of this material seems to have been lost. The same location was resampled by A. Jayet during the mid-1940's and more recently by D. Kälin in 2019 in a profile 740 m to the SW.

The Forcart and Jayet faunas were found in an 8 m thick sequence of tufaceous silty-sands, sands and sandy fine to medium gravels that seem to be fluvial. These deposits were underlain by c. 14 m of Hochterrasse fluvioglacial gravels, and overlain by another 20 m of fluvioglacial gravels that date from the last glacial period. When D. Kälin returned to the site in 2019, he took samples in c. 7 m of silts, marly-silts and sandy-silts with molluscs (NEaar 14010-2; 14077-82), alternating with layers of fine to medium sandy gravel, which are clearly fluvial. Palynological studies together with U/Th and luminescence dating have shown that these deposits span from the start of the Eemian until the Early Würm (MIS 5e to MIS 5c; Küttel and Lotter, 1987; Wegmüller, 1996; Preusser et al., 2001; Frechen et al., 2007).

The molluscs from the Forcart and Jayet samples include a number of typical interglacial species, among which are several biostratigraphical markers that suggest an Eemian date for these faunas (Thew, 2024). These include *Acicula lineolata*, *Aegopinella nitidula*, *Aegopinella ressmanni*, *Discus perspectivus*, *Pagodulina pagodula* and *Ruthenica filograna*. The first two taxa have only ever been found at Zell, while the other four were also found at Niederweningen (Thew, 2024). When compared to the reference sequence at Niederweningen (see below), these faunas seem to correspond to a middle phase of the Eemian. Although similar, the assemblages from Zell 2019 are missing four of the marker species mentioned above, so seem to represent an earlier phase of the Eemian.

2.1.3.2. Thalgut

Thalgut is located in the Aar Valley in west-central Switzerland near the north-western edge of the Alpine massif. The site is a gravel quarry that was first studied and sampled by C. Schlüchter in 1971/72 (Schlüchter, 1976). The molluscs analysed for IcPD come from a series of up to 5 m of laminated lacustrine silts, marly-silts and sands with shells and plant remains, pollen spectra resembling the first half of the Eemian rather than MIS 7 when compared to the Meikirch sequence (Welten 1988, diags. 16, 1, 2), and OSL/IRSL dates that confirm an Eemian age (Schlüchter, 1989; Preusser and Schlüchter, 2004; Preusser et al., 2011, p.288). Among the molluscs are the interglacial markers *Aegopinella ressmanni* and *Discus perspectivus*, as well as *Pagodulina pagodula*, which may be an indicator for the Eemian in Switzerland (Thew, 2024). The fauna seems to represent the middle phase of the Eemian. The absence of several of the marker species present at the reference sequence at Niederweningen (see below), suggests that these lake deposits are missing the climax phase of the middle Eemian. The lake silts are indeed truncated, and are covered by thick gravel deposits from the last glacial period. In 1983, a core sunk beneath

the quarry floor revealed a unit of earlier lacustrine deposits c.40 m below the Eemian lake sediments (Welten, 1988), but no molluscs have been analysed from this earlier level.

The samples were taken c. 1971 and processed in two sets, in 2018 and 2021. The first (NEaar 12274-6, Thalgut 2018 in Fig. 3) consisted of *Bithynia* opercula that had been either previously extracted from the lake silts, or recovered by the sieving of 0.4 kg of unprocessed sample. Due to unexpectedly high IcPD values, a further 0.3 kg of the original sample sediment was sieved and a second series of opercula were extracted (NEaar 14071-3; Thalgut 2021 in Fig. 3).

2.1.3.3. Niederweningen

Niederweningen is located in the Wehntal Valley, in north-eastern Switzerland north of Zürich. Studies of deep cores have shown that the lower infill of the valley consists of glaciolacustrine and lacustrine silts that are dated by OSL/IRSL to MIS 6 (Anselmetti et al., 2010; Dehnert et al., 2012). After a notable hiatus, these are succeeded by the thick Lower Peat Complex, which has pollen that Welten (1988) attributed to the middle to late Eemian (MIS 5e) and the Early Würm (MIS 5d-5a). This is followed by alternating silts and thin peaty layers dated by OSL/IRSL to MIS 4 and the start of MIS 3, which are succeeded by the Upper Peat Complex that has mammoth bones and has been dated by ^{14}C and OSL/IRSL to the early-mid part of MIS 3 (Furrer et al., 2007; Hajdas et al., 2007; Preusser and Degering, 2007).

In 2015, around 0.5 m of tufaceous silts with abundant mollusc shells and thin peaty bands was discovered in construction trenches near the south-western edge of the valley, to the west of the zone where the mammoth bones were found. Coring in the same area in 2018 located 0.3 - 0.5 m of the same tufaceous deposits and confirmed that they are situated below the base of the Lower Peat and above the silts dating from MIS 6, suggesting that they are likely to be Eemian. Beneath the tufaceous silts is 0.2 - 0.4 m of blue-grey marly silts that also have frequent molluscs (Thew, 2024; Miocic et al., in review). Neither the blue-grey marly silts nor the tufaceous silts are present to the east where earlier coring and trenching took place, due to pronounced erosion at the base of the Lower Peat that seems to have occurred during the middle to late Eemian. Pollen spectra from the blue-grey marly-silts and the tufaceous silts seem to be typical for the early to middle Eemian, while the molluscan fauna is exceptionally rich, with 71 terrestrial and 23 aquatic species, many of which are typical of warm interglacial conditions. These include several biostratigraphical markers that have only ever been found in contexts linked with full interglacials in Central Europe, such as *Aegopinella ressmanni*, *Aegopis verticillus*, *Discus perspectivus* and *Pagodulina pagodula*, and two (*Daudebardia brevipes* and *Daudebardia rufa*) that seem to have first appeared in the Swiss Plateau during the Eemian (Thew, 2024). Although luminescence dating of the cored sequence was partly challenging (Preusser et al., 2023), the overall evidence seems to confirm the stratigraphical, palynological and absolute dating evidence, which suggests that these interglacial silts correspond to the Eemian. Both the pollen and the molluscs indicate that the sequence spans from the early to late Eemian, although no molluscs are preserved in the Lower Peat. The analysed biominerals (NEaar 12277-81 [15/B]; 13113-5; 13122-4; 13137-9; 13223-5; 13297-9; 13137; 13312-4 [all from 18/2 & 18/3]; 15865-7) seem to come from the early-middle (*Bithynia* opercula, slug plates) and middle (*Arianta*, *Cepaea* & *Fruticola shells*, worm granules) phases of the Eemian.

2.1.4. Holocene

To complete the series of IcPD samples from the Swiss Plateau, shell material was added from a series of Holocene sites: this includes one site where earlier deposits were already being investigated for this study (Sous-Terre 1), together with other Holocene sites from across the Swiss Plateau (Boppelsen-Cholholz, Abri Unterkobel, Oberbipp, Hauterive-Champréveyres).

2.1.4.1. Sous-Terre 1

The *Bithynia* opercula of Sous-Terre 1 (NEaar 12260-2; the upper level sampled for IcPD at this site; cf. Sect. 2.1.2.2) come from the lower part of a layer of grey marly silty-sand with some fine-medium gravel, which overlies an LGM basal till and is situated between 376.30 and 377.0 m asl, 7-8 m above the present level of the Rhône (369.30 m asl; Jayet & Amberger, 1969). The molluscan assemblage is 85% aquatic, in keeping with this sediment representing a terrace deposit, contemporary with the 10 m terrace of Lake Geneva (cf. Schoeneich, 1998). The molluscs include the pioneer forest species *Discus ruderatus*, but none of the woodland taxa that appear during the late Preboreal. By contrast, the molluscs from the upper part of this terrace deposit (not sampled for IcPD) have eight more forest species, including five that are known to have first appeared during the late Preboreal. This evidence suggests that the analysed shells date from the earlier part of the Preboreal.

2.1.4.2. Boppelsen-Cholholz

This site is located in north-eastern Switzerland and was sampled by A. Jayet in 1948 from a Höhere Deckenschotter (HDS) outcrop at Wakern, near Boppelsen (Jayet, 1949). The shells were found in 3 m of brown tufaceous sandy-silt with frequent stones, charcoal fragments and mollusc shells (NEaar 14007-9), which lay beneath 1 m of Holocene colluvium. Beneath the sampled layer was over 6 m of sterile fluvioglacial gravels and sands that correspond to the HDS. The molluscs from this site were analysed because it had long been thought that they might be contemporary with the HDS terrace. The excellent preservation of the shells and comparison with well-dated Holocene sequences elsewhere in Switzerland (Liniger and Thew, 2008, 2016; Thew 2022, 2024) indicates that the molluscan fauna appears to date from the early Boreal. The sediment in which these shells were found seems to represent the infilling of an erosional gully c. 3 m deep cut into the summit of the HDS gravels.

2.1.4.3. Abri Unterkobel, Oberriet

Abri Unterkobel is located in north-eastern Switzerland, in the Alpine Rhine Valley near the border with Austria. It is a rock-shelter with Mesolithic to Roman archaeological occupation levels (Wegmüller et al., 2013; Wegmüller 2022). The shells used for IcPD analysis (NEaar 12254-9) come from Middle Mesolithic layers dated by radiocarbon and molluscan biostratigraphy to the later Boreal (Thew, 2022). These layers include occupation material and several hearths, while overlying levels dating from the Middle Neolithic include dung from stabled sheep/goats, some of which had been burnt.

2.1.4.4. Oberbipp

Oberbipp is located in northwestern Switzerland, south of the Jura Mountains. During the excavation of a Late Neolithic dolmen in 2011/12, mollusc shells were recovered from both tufaceous sediments that lay beneath the dolmen and the infill of the burial chamber (Ramstein et al., 2020, 2022). The molluscan faunas from beneath the dolmen can be reliably attributed to the early to mid-Boreal, while the Late Neolithic deposits within the dolmen correspond to the early Subboreal (Thew, 2024). Worm granules and slug plates (NEaar 13300-2; 13341-3) come from the Boreal layer, while *Arianta*, *Fruticola* and *Cepaea* shells all come from the Late Neolithic/Subboreal level (samples NEaar 13125-7; 13140-2; 13238-40).

2.1.4.5. Hauterive-Champréveyres, Lake Neuchâtel

The *Bithynia* operculae used in this study (NEaar 12251-3) come from a late 19th century beach deposit at Hauterive-Champréveyres at the north-western margin of Lake Neuchâtel, which was sampled in 1986 prior to motorway construction. This beach was formed when the level of Lake Neuchâtel was lowered suddenly by c. 2.7 m during the late 1870's as a result of the *Premier Correction des Eaux du Jura*, causing severe erosion around the lake that at this site led to the truncation of middle Holocene lake sediments (Moulin, 1991).

2.2. Biominerals analysed

Biominerals were analysed from 31 horizons that came from the 21 sites described above. Six different types of biomineral were analysed: calcitic *Bithynia* opercula, slug plates and worm granules; and aragonitic shells from *Arianta*, *Cepaea* and *Fruticola* (Table 1). The only material for which full closed system tests and an aminostratigraphic framework had previously been developed was the *Bithynia* opercula (Penkman et al., 2013; Tesakov et al., 2020). Small-scale pilot and unpublished IcPD studies had previously been undertaken on *Arianta* and *Cepaea* shell, slug plates and worm granules, but this represents the first widespread study on these fossil materials, as well as the first IcPD data on *Fruticola* shell.

While the shell and opercula are easily identified to species level, slug plates and worm granules are more complicated. Both contain calcite, and may therefore provide a diagenetically stable biomineral for amino acid analysis. The internal shells of the family of slugs known as the Limacidae take the form of compact 'slug plates' made of calcite. The Milacidae family of slugs also have internal plates, but these are somewhat different in shape and none have been analysed for this study. Unfortunately, it is impossible to reliably identify most slug plates to species level (Kerney et al., 1980; Preece, 1998; Preece & Parfitt, 2022); taxonomic differences in proteins are likely to influence the rate of the IcPD reactions (e.g. Penkman et al., 2007; Dickinson et al., 2024), and therefore may contribute to the variability of the D/L values. Although all Limacidae are surface dwellers (South 1992), they may occasionally be found down to depths of 0.2 m (or 0.3 m for the largest species, not analysed here) if there is loose soil material or cracks and cavities at the surface, but this is unlikely to have been important for most of the sites sampled for this study as they represent accumulating river flood plain and lake margin sediments.

Certain genera of earthworms, including *Lumbricus, Aporrectodea*, *Octolasion* and *Allolobophora,* produce granules of calcium carbonate in calciferous glands and excrete them into the sediment, with *Lumbricus* being the most prolific producer

of these granules (Canti, 1998). Granules contain a high proportion of calcite (Canti, 1998; Canti and Piearce, 2003; Hodson et al., 2015). It has been proposed that proteins (along with other organic components) are incorporated into the granules during the initial precipitation of calcium carbonate as amorphous calcium carbonate (ACC) spherulites in the calciferous glands (Briones et al., 2018; Mandera et al., 2023). Organics stabilise the ACC as a milky fluid, which is then transported to the worm's oesophageal pouches where it coalesces and crystallises to form the granules (Robertson, 1936; Morgan, 1981; Gago-Duport et al., 2008).

As an excretion product (rather than the skeletal biominerals analysed for the molluscs), it should be noted that the protein control and mineral stabilities of worm granules may be more varied. There is no control by the calciferous gland of the structure of the granule, or possibly the organics incorporated. Furthermore, the chemical composition of the soil in which the worm lives will influence granule precipitation and the quantity of organic material incorporated into the crystal (Mandera et al., 2023). As such, the composition of the protein and stability of the mineral is likely to be more varied than that of skeletal biominerals. It is also currently impossible to unequivocally identify fossil worm granules to species level, which may impact on the variability of the IcPD data. The Arionidae family of slugs is also known to produce calcareous granules within their mantle that are preserved in the soil following the slug's death, but the morphology of *Arion* granules seems to be recognisably different than those excreted by earthworms (Canti, 1998) and they have not been selected in this study.

Table 1: Samples from sites across the Swiss Plateau analysed for this study, in approximate order of age (from older to younger). Morphostratigraphy where relevant: HDS: Höhere Deckenschotter, TDS: Tiefere Deckenschotter, HT: Hochterrasse, HOL: Holocene. For a qualitative assessment of the age evidence, from higher to lower probability: probable – likely – possible. Analysed materials are: *Bithynia* opercula (B), shells from *Arianta* (A), *Cepaea* (C), and *Fruticola* (F), slug plates (SP) and worm granules (WG).

Site and reference (year sampled where relevant)	**Geographical location Swiss Coordinates (LV95)**	**Morphostrati-graphic unit**	**Evidence of age (if different age interpretations, indicated by "I" and "II")**	**Analysed materials**
Irchel Plateau:			Early Pleistocene; I): older Early Pleistocene – Gelasian (lithostratigraphy, biostratigraphy; Thew et al. 2024); II): Gelasian + Calabrian (cosmogenic dating)	
Irchel Ebni (2017): 'Ebni Silts'	2687008 /1267577	basal part of HDS	I) older than Hasli Fm. based on lithostratigraphy (Graf, 1993) and clast petrography; has normal polarity (Thew et al., 2024); II) younger than Hasli Formation based on interpretation of cosmogenic dates (Dieleman et al., 2022a) If 'I' is correct, it seems to represent the first sub-unit of the HDS (cf. Graf, 2019)	SP, WG
Irchel Amselboden (2021): Hasli Fm.	2687258 /1266111	upper part of HDS	I) Hasli Formation (Fm) same age as Irchel Hasli (lithostratigraphy, molluscs; Thew et al., 2024)	B, C, F, SP
Irchel Hasli (**Bräm** 1955; Bolliger **1994/95;** Nagra **2018/19**): Hasli Fm. ***Irchel Hasli = reference site for the Hasli Fm.***	2688944 /1265570		I) Hasli Fm. 2.1-1.8 Ma (small mammals; Bolliger et al., 1996; Cuenca-Bescós, 2015; & molluscs, pollen & palaeomagnetic data; Scheidt et al., 2023; Thew et al., 2024); II) gravels beneath Hasli Fm. 1.3 ± 0.1 Ma (isochron-burial date; Dieleman et al., 2022a), recalculated by P-PINI to 1.14 ± 0.15 Ma (Broś et al. 2025)	C, F, SP, WG (Br); C, SP, WG (94/95); F, SP, WG (18/19)
Irchel Steig East (2020)	2688548 /1265629		I) Hasli Fm. same age as Irchel Hasli (molluscs, lithostratigraphy; Thew et al., 2024); II) gravels beneath Hasli Fm. 0.9 ± 0.1 Ma (isochron-burial date; Claude et al., 2019), recalculated by P-PINI to 1.01 ± 0.82 Ma (Broś et al. 2025)	A, C
Irchel Steig West (2018/19): Hasli Fm.	2688501 /1265633		I) Hasli Fm. same age as Irchel Hasli (molluscs, lithostratigraphy; Thew et al., 2024); II) same gravel unit underlying the Hasli Fm. as Steig East	SP, WG
Irchel Hochwacht East (2019): Hasli Fm.	2686077 /1268269		I) Hasli Fm. same age as Irchel Hasli (lithostratigraphy, molluscs, pollen, paleomagnetic data; Scheidt et al., 2023; Thew et al., 2024; II) gravels beneath Hasli Fm. 2.6 ± 0.1 Ma (isochron-burial date; Dieleman et al., 2022a), recalculated with P-PINI code to 2.63 ± 1.06 Ma (Broś et al. 2025)	B, C, SP, WG
Irchel Hochwacht West Hasli Fm.	2686045 /1268256		I) Hasli Fm. same age as Irchel Hasli (lithostratigraphy, molluscs; Thew et al., 2024; cf. data Hochwacht East)	A, SP

Irchel Hochwacht West Upper level: soft-clasts + sandy lens above Hasli Fm. (2019/21)		above Hasli Fm.	found 3 m above Hasli Fm. within Hochwacht Gravel, so younger but comparable warm period (molluscs; Thew et al., 2024)	C, SP
Conclusions for Hasli Fm. sites			Hasli Fm.: proposed date of c.2.1-1.8 Ma (based on small mammals, molluscs, stratigraphy & paleomagnetic data; Thew et al., 2024); seems to represent the second sub-unit of the HDS (cf. Graf 2019)	
Stratigraphy within the Hasli Fm. relative to sample position			It has been tentatively proposed that the Hasli Fm. profiles can be sub-divided into 4 parts (1-4; Thew et al. 2024 + Sup. Mat.). The analysed materials are from: Amsel (B – Part 1, C, F & SP – 2), Hoch East (B- 1 & 2; C, WG – 2, SP – 2 & 3); Hoch West (A, SP – 3); Hasli Bräm+1994/95+2018/19 (A, C, F, SP, WG – all 3); Steig East (A, C – 3); Steig West (SP, WG -3) Thus, samples from Amselboden & Hochwacht East may be older than those from Hasli (all excavations), Hochwacht West, Steig East, & Steig West	
Albishorn-Bürglen:		HDS		
Albishorn-Bürglen 2 (2017/2019): lenses in Albisboden-Gravel	2683325 /1234575	basal part of HDS	older Early Pleistocene – Gelasian; sandy-silty layers and lenses within Albisboden Gravel with molluscs of similar age to Hasli Fm.; so older than 1.8 Ma (Thew, 2024); seems to represent the second sub-unit of the HDS (Graf, 2019)	B, SP, WG
Albishorn-Bürglen 1 (2016): organic silt above Bürglen Till	2683436 /1234430	upper part of HDS	likely to be middle Early Pleistocene - Calabrian/Eburonian probably younger than 1.8 Ma (based on molluscs, Thew, 2024; pollen, pers. comm. M. Knipping, 2019; & stratigraphy, Graf 2019); seems to represent the third sub-unit of the HDS (Graf, 2019)	B
Hungerbol:		lower part of TDS	later Early Pleistocene – Calabrian/Menapian-Bavelian	
Hungerbol 2 (2016/2019) silts & fine sands	2708100 /1282505		probably 1.8/1.7 - 1.1/1.0 Ma, possibly 1.2-1.0 Ma (based on interglacial molluscs, Thew 2024; limited small mammal remains, pers. comm. O. Fejfar; Maul & Markova, 2007; & lithostratigraphy of the Schiener Berg, Graf 2009a); 1.18 ± 0.09 Ma (isochron-burial date; Broś et al., 2025) for Hungerbol Gravel that cuts into the Molasse and underlies the Hungerbol 2&1 silts & fine sand	B, A, F, SP, WG
Hungerbol 1 (2016) silts & fine sands			interstadial molluscs within succeeding cold period; Thew 2024	A, WG
Ecoteaux: lacustrine silts of Unit 7	Loc A: 2556360 /1155050 Loc B: 2555370 /1154680	independent lake basin (Rhône system)	early Middle Pleistocene (Chibanian) potentially MIS 15, because from near the base of lake deposits that include two interglacial warm periods of probable Cromerian age separated by a cold phase (MIS 15-MIS 13; based on pollen, palaeomagnetic data, lithostratigraphy, Pugin et al., 1993; and molluscs, Thew, 2024); the underlying basal till is thus likely to date from MIS 16	B
Montfleury Core 1: sandy-silts of the	2494400 /1119265	Rhône system	Middle Pleistocene (Chibanian)	F

'Confignon Sequence'			alluvial sandy-silts of the 'Confignon Sequence,' found below sands of the 'Vernier Sequence,' sandy-silts of the 'Montfleury Sequence' and gravels of the 'Alluvion-ancienne;' probably MIS 11 (based on pollen and lithostratigraphic context, Lanterno et al., 1981; Wegmüller et al., 1995; Moscariello et al., 1998; and molluscs, Thew, 2024)	
Sous-Terre 2: = lower level with samples from this site	2499175 /1117750	Rhône system	Middle Pleistocene (Chibanian) alluvial sandy-silts, below compact laminated silts and gravels of the 'Alluvion-ancienne;' probably MIS 11 (based on molluscs, Thew 2024; pollen, Girard, 1970, and lithostratigraphy, Jayet & Amberger, 1969; Moscariello et al., 1998)	A, C, F, SP, WG
Nuolen 1 + **Nuolen 3**/Buechberg from two gravel quarries, but seem to be contemporary	est. 2710160 /1228620 est. 2710370 /1228440	HT	Middle Pleistocene (Chibanian) likely MIS 7 alluvial deposits (based on correlation to nearby profiles with pollen analysis, Welten, 1988; molluscs, Thew 2024; and lithostratigraphy, Schindler, 2004, p.13-31)	B, A, C, WG
Grandson	2539300 /1184700	HT	Middle Pleistocene (Chibanian) likely MIS 7 lake terrace (based on pollen analysis, Welten, 1988; and lithostratigraphic context, Jordi, 1996, 2006)	A, B,
Petit Saconnex 1994	2498930 /1119760	Rhône system	Middle Pleistocene (Chibanian) silty sediments found beneath gravels of the 'Alluvion-ancienne;' possibly early MIS 6, or perhaps MIS 8 (based on lithostratigraphy + pollen; Jayet et al., 1961; and molluscs, 2024)	A, WG
WHO	2499230 /1120850	Rhône system	Middle Pleistocene (Chibanian) similar silty sediments to Petit Saconnex; probably same lithostratigraphic unit; possibly early MIS 6, or perhaps MIS 8 (based on lithostratigraphy + pollen, Reynaud, 1982, fig.11; and molluscs, Thew 2024)	A, SP
Zell 2019	2636552 /1220110	HT	Late Pleistocene MIS 5e to MIS 5c fluvial sediments (based on lithostratigraphic correlation to adjacent profiles with pollen analysis, + Th/U and OSL/IRSL dating (Küttel & Lotter, 1987; Wegmüller, 1996; Preusser et al., 2001; Frechen et al., 2007; and molluscs, Thew, 2024); the samples come from early Eemian layers	A, SP, WG
Thalgut 2018 & 2021	2608990 /1186615	independent lake basin (Aare system)	Late Pleistocene MIS 5e lake sediments (based on pollen analysis, Welten, 1988; OSL/IRSL dating, Preusser & Schlüchter, 2004; and molluscs, Thew, 2024); samples from early/mid Eemian layers	B
Niederweningen **2015/B** **2018/2** **2018/3**	15B: 2670409 /1262380 18/2: 2670514 /1262322 18/3: 2670428 /1262363	independent lake basin (Rhine system)	Late Pleistocene MIS 5e lake margin sediments (based on pollen analysis, molluscs and lithostratigraphic correlation to nearby profiles, Miocic et al., in review; some with pollen analysis, Welten, 1988, Drescher-Schneider et al., 2007; radiocarbon dating, Hajdas et al., 2007; and OSL/IRSL dating; Preusser & Degering, 2007; Anselmetti et al., 2010; Dehnert et al., 2012; Preusser et al., 2023); samples from early/mide Eemian (B, SP) and middle Eemian (A, C, F, WG) layers	B (15B & 18/2), SP (18/2), A, C, F, WG (18/3)
Sous-Terre 1 = upper level with samples from this site	2499175 /1117750	HOL	10 m terrace of the Rhône Early/mid Preboreal (Jayet & Amberger, 1969; based on molluscs, Thew, 2024)	B

Boppelsen-Cholholz	est. 2673650 /1258900	HOL	Early Boreal sediments (sampled by Jayet, 1949; based on molluscs, Thew, 2024); infilling an erosion feature cut into sterile HDS deposits sampled by NAGRA in 2017	A
Abri Unterkobel, Oberriet	2759659 /1242699	HOL	Later Boreal sediments inside a rock-shelter. Early Mesolithic III layer dated with archaeological material, radiocarbon and molluscs; Thew 2022; Wegmüller 2022)	A, F
Oberbipp	2616765 /1234395	HOL	Early/mid Boreal sediments beneath a Late Neolithic dolmen = early Subboreal (based on molluscs; Thew, 2024; and archaeological dating; Ramstein et al., 2022)	A, C, F, SP, WG
Hauterive-Champréveyres	2564480 /1206390	HOL	late 19th -20th century beach deposit of Lake Neuchâtel (after the historically documented "*Premier Correction des Eaux du Jura*" 1868-1891); but includes shells and opercula redeposited from earlier Holocene (Atlantic?) lake deposits (site stratigraphy in Moulin 1991); sampled 1986	B

3. Methods

All biominerals were prepared using the procedures of Penkman et al. (2008), attempting to isolate an intra-crystalline protein by oxidation, with an individual biomineral forming each sample. In brief, two subsamples were taken from each single biomineral: one fraction was directly demineralised and the free amino acids analysed (referred to as the 'free' amino acids, FAA), and the second was hydrolysed at 110°C for 24 hours to release the peptide-bound amino acids, thus yielding the 'total hydrolysable amino acid fraction' (THAA). Samples were analysed in duplicate by reverse phase high pressure liquid chromatography (RP-HPLC) using a modified method of Kaufman and Manley (1998). Standards and blanks are routinely run alongside samples each day; if their data does not fall within the expected range (2 standard deviations of >5 years worth of data), then the samples are rerun once the equipment is operating normally again. During hydrolysis, both asparagine and glutamine undergo rapid irreversible deamination to aspartic acid and glutamic acid, respectively (Hill, 1965). It is therefore not possible to distinguish between the acidic amino acids and their derivatives and they are reported together as Asx and Glx, respectively.

The D/L values of aspartic acid/asparagine, glutamic acid/glutamine, serine, alanine and valine (D/L Asx, Glx, Ser, Ala, Val) and the concentrations of Ser and Ala ([Ser]/[Ala]) were then assessed to provide an overall estimate of intra-crystalline protein decomposition (IcPD). These amino acids are the best chromatographically resolved enantiomer pairs for calcium carbonate shells in general (Powell et al., 2013), and between them also cover a wide temporal range (Penkman et al., 2011). The D/L of an amino acid will increase with increasing time, whilst the [Ser]/[Ala] value will decrease (Ala's concentration is partly contributed from the decomposition of other amino acids, notably serine and threonine). Each amino acid racemises at different rates (Asx > Ala > Glx ≈ Val), and therefore are useful over different timescales. The D/L of Ser is less useful for geochronology; the relatively fast breakdown of free Ser (which tends to be more racemised) means there is a loss of free serine as samples increase in age, resulting in a single D/L value representing more than one time-point in samples of this age (e.g. Penkman et al., 2008). However, D/L Ser is reported here as aberrant values are useful indications of contamination (e.g. Williams & Smith, 1977; Kosnik & Kaufman, 2008). Glx has an unusual pattern of racemization in the free form, due to the formation of a lactam (see Walton, 1998). As this lactam cannot be derivatised and so is unavailable for analysis, this results in relatively low precision for the FAA D/L measurements, particularly in younger samples. The IcPD of the FAA and THAA subsamples can also be used to recognise any compromised samples, as in a closed system the FAA and THAA D/Ls should be highly correlated (e.g., Preece & Penkman, 2005).

4. Results and Discussion

In Figures 3 to 9 the samples have been colour-coded according to existing evidence for the age of each site (green = Holocene; blue = Late - Mid Pleistocene [Hochterrasse or age equivalent]; olive green = late Early Pleistocene - Tiefere [Lower]

Deckenschotter; red/orange = older Early Pleistocene - Höhere [Higher] Deckenschotter). All data is reported in Supplement Table S1, and age interpretations are based on all amino acids presented.

Before this study, some pilot work had been undertaken on isolation of the intra-crystalline fraction of the non-opercula biominerals (aragonitic shells of *Fruticola fruticum, Arianta arbustorum*, *Cepaea hortensis* and calcitic slug plates and worm granules), but this represents the first comprehensive investigation of the intra-crystalline fraction in fossil specimens of these biominerals. After bleaching, an intra-crystalline fraction of amino acids was retained in each biomineral tested; if all the amino acids had been inter-crystalline, then no amino acids would have been detectable post-bleaching (Penkman et al., 2008). Whether this intra-crystalline fraction comprises a closed system can be tested through high-temperature experiments (Penkman et al., 2008; Demarchi et al., 2011), but in the absence of these, we explore the general IcPD behaviour in these fossil biominerals, and their potential for geochronology. The relative age orders proposed are based on the IcPD data, unless resolution is not possible, in which case we follow the stratigraphy in Table 1.

4.1. *Bithynia* opercula

Bithynia opercula are mineralised in the form of calcite, and this mineralogically stable form of calcium carbonate has been shown to provide a closed system repository for the intra-crystalline amino acids in opercula as old as the Eocene (Penkman et al., 2013). Most of the opercula analysed show closed system behaviour with a good correlation between the FAA and THAA fractions (Fig. 3). Only single and very small opercula fragments were obtainable from Irchel Amselboden, Albishorn-Bürglen 2 and Albishorn-Bürglen 1, resulting in very low sample concentrations that did not allow accurate D/L determination, which combined with their compositions (Fig. 4) are consistent with their being of significant age. The small fragments from Irchel Hochwacht East yielded D/L values only for Ala which is at racemic equilibrium and therefore provides only a minimum estimate of age.

Asx is one of the fastest racemizing of the amino acids discussed here (as it can racemize whilst still peptide bound), enabling good levels of resolution for younger age sites, but decreased resolution in Early and Middle Pleistocene material (e.g. Penkman et al., 2011). There are very low concentrations of Asx (a relatively unstable amino acid) in the Irchel Hochwacht East, Irchel Amselboden and Hungerbol 2 samples, so the D/L Asx is not accurately determinable. For samples where D/L Asx was accurately determined, Ecoteaux shows the highest levels of racemisation, followed by Thalgut. Nuolen, Grandson and Niederweningen show similar levels of breakdown, but lower than Thalgut. Sous-Terre 1 shows even lower Asx D/Ls. The data from Hauterive-Champréveyres was variable between samples, probably because the material is a mix of redeposited Holocene opercula and modern examples, but the opercula show the lowest levels of racemisation, indicating that this is the youngest site of the set.

Glx is one of the slower racemizing amino acids, so the level of resolution from young sites is less than that seen with faster racemizing amino acids such as Asx. For D/L Glx, where concentrations are high enough for accurate measurement, the highest levels of racemisation are observed in Hungerbol 2, with notably lower levels in Ecoteaux, and then significantly lower again for Thalgut (Fig. 3), indicating a large difference in age between these three sites. Nuolen, Grandson and Niederweningen

show even lower, but have similar Glx D/Ls to each other, while there is very little Glx racemisation in Sous-Terre 1 and Hauterive-Champréveyres (Fig. 3). This data is consistent with the Asx D/L pattern, but unlike Asx D/L, Glx is able to discriminate better between the older samples due to the slower rate of racemisation for this amino acid.

As alanine racemises at an intermediate rate, it is helpful in distinguishing ages at a range of timescales. Irchel Hochwacht East and Hungerbol 2 show the highest levels of racemisation (Fig. 3), effectively at equilibrium, and so cannot be discriminated using this amino acid. Ecoteaux opercula have slightly lower Ala D/Ls, and Thalgut significantly lower. Nuolen, Grandson and Niederweningen again show lower D/Ls, but similar to each other. Sous-Terre 1 and Hauterive-Champréveyres show the lowest levels of breakdown, consistent with their Holocene age.

Valine (Val) has extremely low rates of racemisation, and as the concentration of Val is quite low in many of these biominerals, the difficulty of measuring the D/L accurately leads to higher variability. It does, however, still prove useful for age discrimination, particularly for Early-Middle Pleistocene material. The Val D/L in the FAA and the THAA fractions support the data from the other amino acids, with Irchel Hochwacht East and Hungerbol 2 showing the highest levels of breakdown and likely to be of significant age, certainly Early Pleistocene (Fig. S1). Ecoteaux is significantly younger, in line with the site data that suggests the deposits probably date from the early Middle Pleistocene, while Thalgut is younger still. Interestingly the two sets of Thalgut samples, which show very similar data to each other, are much more degraded than expected. We do not know the full history of these samples; it is therefore possible that heating (e.g. oven drying) of the samples may have occurred before processing. We recommend that this data be treated with caution. Nuolen, Grandson and Niederweningen show low Val D/Ls, with Sous-Terre 1 and Hauterive-Champréveyres showing almost no breakdown in Val.

In summary, the opercula samples from the non-HDS sites show closed system behaviour and can therefore be used for age estimation. Assuming the same effective diagenetic temperatures experienced at all the sites, and given the temporal level of resolution possible using this biomineral, the relative age order predicted by the *Bithynia* opercula is therefore (oldest to youngest): Irchel Amselboden ≈ Albishorn-Bürglen 2 &1 ~ Irchel Hochwacht East (based on low concentrations) > Hungerbol 2 ≫ Ecoteaux ≫ Thalgut 2018 & 2021 > Nuolen 1 ≈ Grandson ≈ Niederweningen 2018/2 ≫ Sous-Terre 1 > Hauterive-Champréveyres. The very small fragments of opercula from the Höhere Deckenschotter show very high levels of degradation, greater than that observed in Early Pleistocene (Gelasian) opercula from north-western Europe (Penkman et al., 2013; Nelson et al., 2025), the Pannonian Plain (Nelson et al., 2024) and the East European Plain (Tesakov et al., 2020). While studies into calibrating the aminostratigraphies between different regions are ongoing, this supports an older Early Pleistocene (Gelasian) age for the Höhere Deckenschotter sites analysed here.

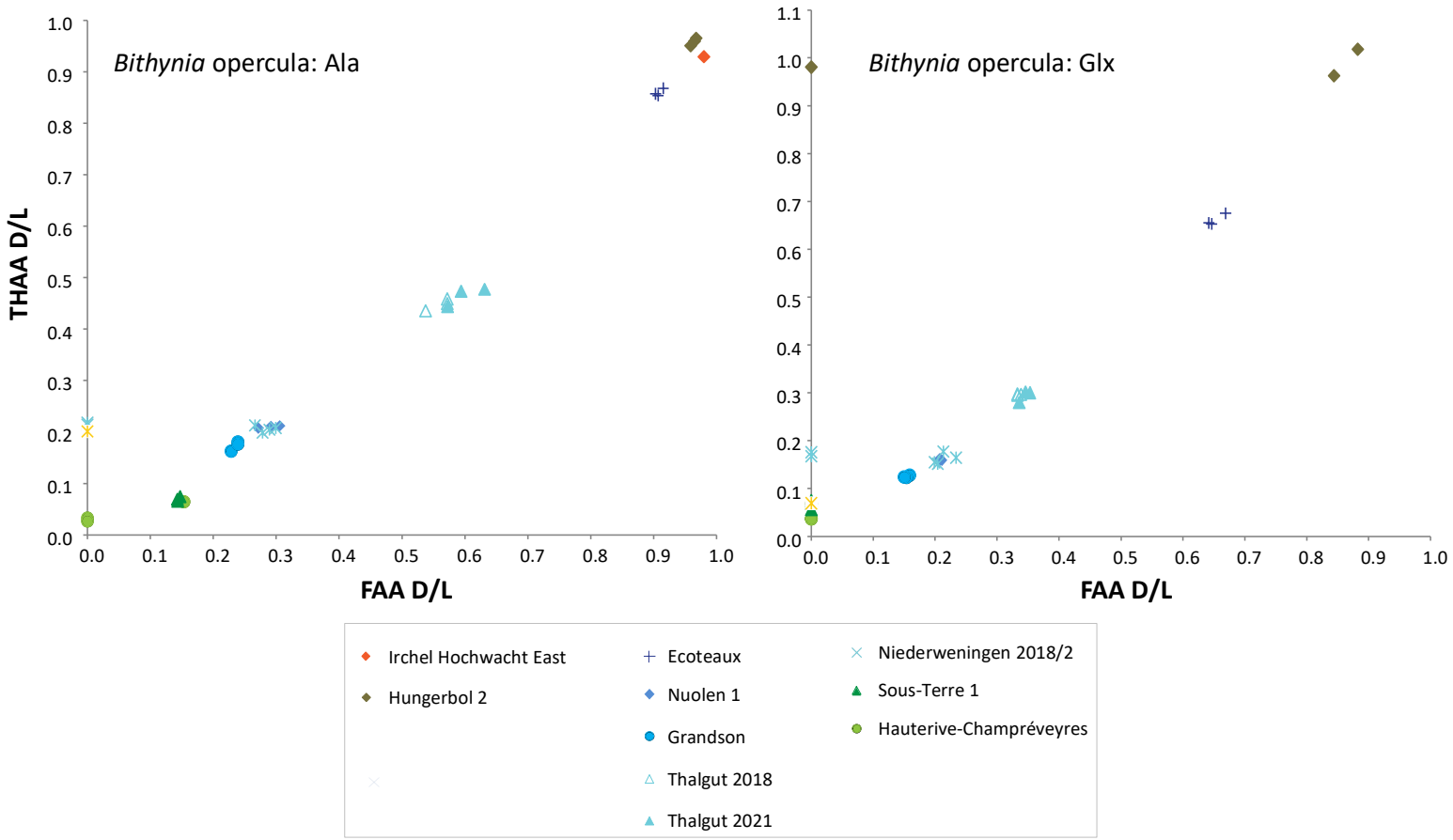


Figure 3: Means of the analytical replicates for THAA D/L vs FAA D/L for Ala (left) and Glx (right) in *Bithynia* opercula from the Swiss Plateau; green = Holocene; blue = Late - Mid Pleistocene (Hochterrasse or age equivalent); olive green = late Early Pleistocene - Tiefere (Lower) Deckenschotter; red/orange = older Early Pleistocene - Höhere (Higher) Deckenschotter. In Ala, samples from Irchel Hochwacht East and Hungerbol are both at racemic equilibrium, therefore providing only minimum estimates of age. Zero values along the x or y-axes are due to concentrations being too low to measure D/L accurately; for Hungerbol 2 this is because the amino acids are very degraded; for the younger sites at Sous-Terre 1 and Hauterive-Champréveyres, this is because so little peptide bond hydrolysis has occurred that there are very few free amino acids; for Niederweningen 2018/2, two of the opercula were too small to enable a FAA analysis. Data from Albishorn-Bürglen 2 & 1 and Irchel Amselboden are not plotted in these D/L figures as the levels of protein degradation in these samples were too high, consistent with their stratigraphic position as being the oldest in the sample set; all data is in SI.

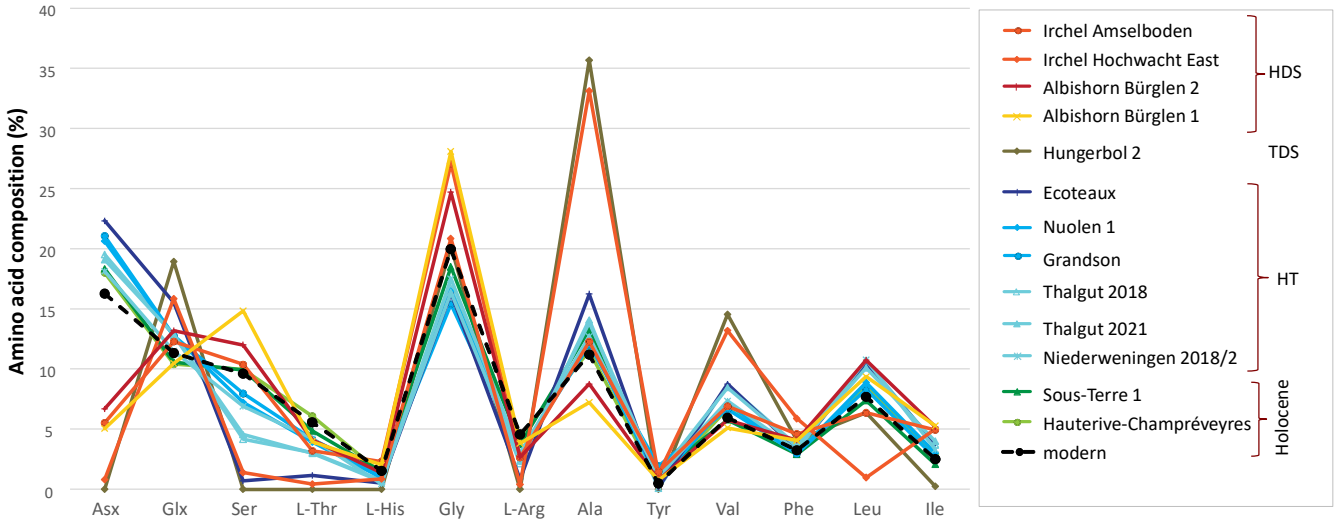


Figure 4: Means of the analytical replicates for THAA % composition in *Bithynia* opercula from the Swiss Plateau, compared to modern material from Hauterive-Champréveyres. The high levels of degradation in the HDS and TDS samples (e.g. low % Asx, higher % Glx) is consistent with significant age.

For most of the sites, this aminostratigraphy supports the age interpretation based on existing independent dating knowledge. It is no surprise, for example, to find that both recent (late 19th/20th century) *Bithynia* opercula and older (possibly Older Atlantic) redeposited opercula were present within the Hauterive-Champréveyres sample, because a major fall (2.7 m) in lake-levels in the 1870's led to significant erosion and the mixing of earlier material within the subsequent lake beach deposit.

Two sites warrant further comment: Thalgut and Niederweningen. Thalgut was expected to be Late Pleistocene in age because of OSL/IRSL dating and pollen evidence (see Sect. 2.1.3.2), so the high IcPD in the opercula from this site is unexpected. This cannot be due to sampling problems, because when C. Schlüchter studied the site in the early 1970s the only interglacial lake sediments exposed within the gravel quarry were those that have subsequently been dated to the Eemian (Welten, 1988; Schlüchter, 1989; Preusser and Schlüchter, 2004). Issues concerning heating during laboratory processing are therefore suspected, although additional analyses from material newly sieved (Thalgut 2021) from the same sediments also show high levels of IcPD (NEaar 14071-3), confirming that these high IcPD values are repeatable. It is therefore possible that historic heating of bulk sediments for drying may be responsible for these anomalous values, showing that this factor potentially needs to be considered for other archive samples.

Niederweningen seems to correspond to the Eemian (Sect. 2.1.3.3), so was expected to show lower levels of IcPD than Nuolen and Grandson, which have been correlated with MIS 7 using pollen, molluscs and stratigraphic relationships (Sect. 2.1.2.3, 2.1.2.4). More detailed interpretation may be possible by increasing the number of opercula analysed from these sites in the future. However, as the opercula were rare among the molluscan assemblages at Niederweningen (Thew, 2024), new sample sediment from this site would be required.

4.2. *Fruticola* shells

Over geological timescales, mollusc shells made of aragonite, such as those from *Fruticola*, can be more susceptible to mineral diagenesis than the more stable calcite of materials such as *Bithynia* opercula and slug plates (e.g. Land, 1967; Penkman et al., 2010, 2013). It is therefore important to identify any evidence of where mineral diagenesis has occurred, as it may compromise the age signal (Preece and Penkman, 2005). In general, there is a good correlation between FAA and THAA D/Ls (Fig. 5), which indicates closed-system behaviour. However, one of the Montfleury samples (NEaar 12264, identified in dashed red outline) shows divergence from the expected pattern in the THAA fraction, so data from this shell should be rejected due to non-closed system behaviour.

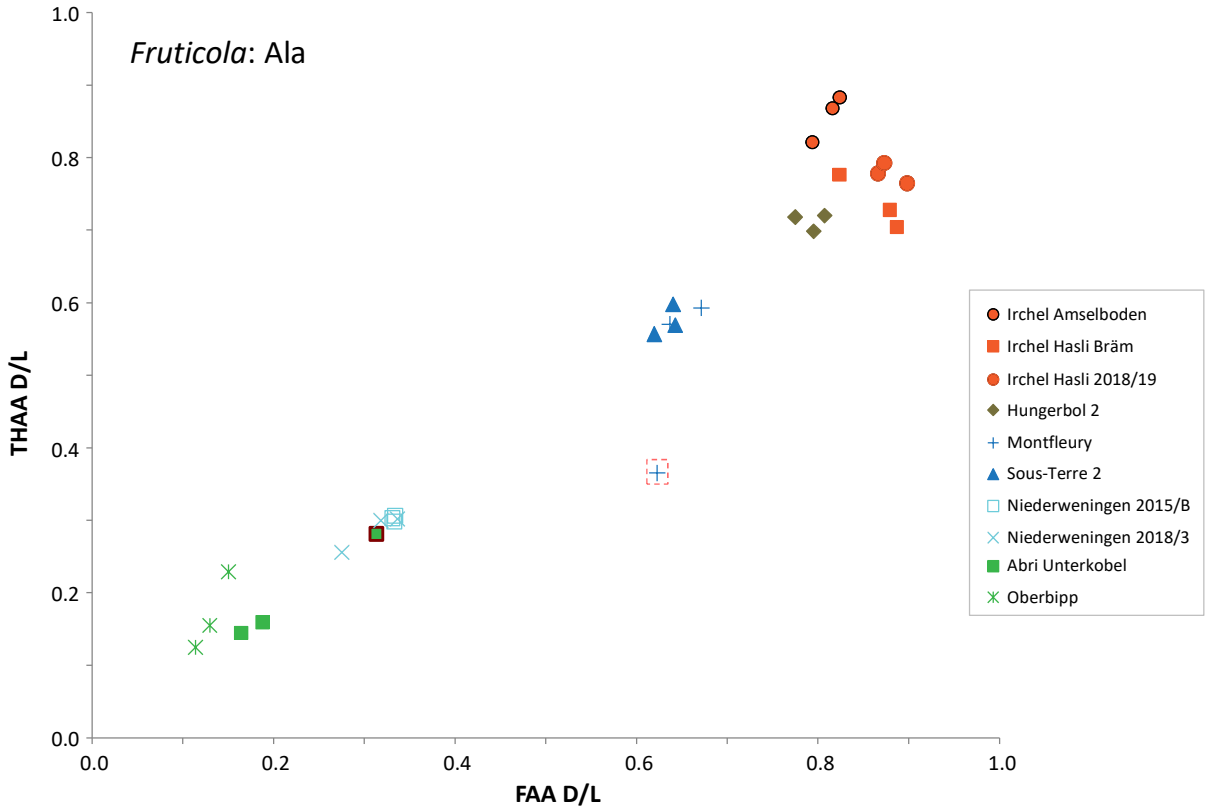


Figure 5: THAA D/L vs FAA D/L Ala in *Fruticola* shells from the Swiss Plateau. One sample from Montfleury (dashed outline in red) shows divergence from closed-system behaviour; one sample from Abri Unterkobel (dark brown solid border) shows much higher D/Ls than the other two samples, probably due to being heated (unintentionally) by proximity to a hearth.

The Irchel samples show the highest levels of racemisation of all the sites (Fig. 5 & S2). Given the limited number of samples analysed here, it is not possible to further temporally discriminate these Irchel samples based on *Fruticol*a data alone. Hungerbol 2 shows slightly lower IcPD values, consistent with an age during a later part of the Early Pleistocene and therefore younger than the Irchel sites. Montfleury and Sous-Terre 2 exhibit intermediate D/L values, similar to each other and consistent with their Middle Pleistocene age. Next lowest are Niederweningen 2015 and 2018/3, which have similar levels of IcPD to

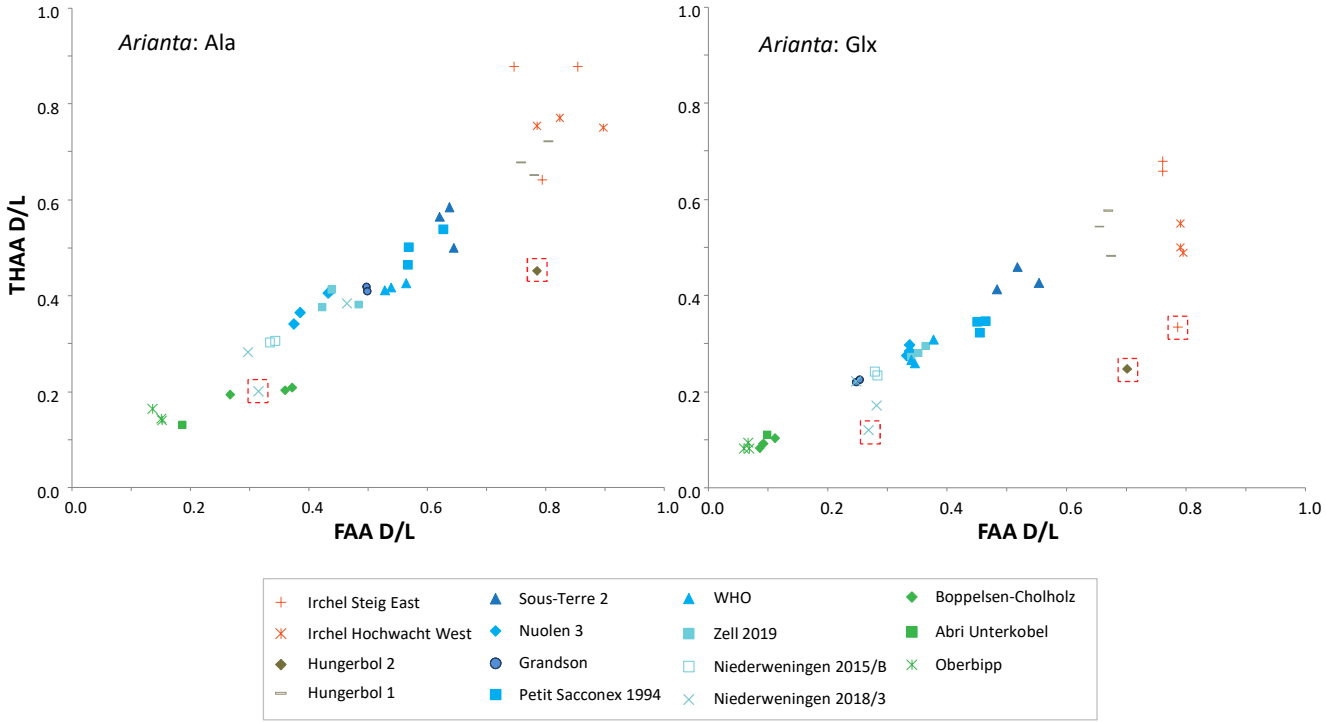
each other, consistent with their stratigraphic age attribution. Samples from Abri Unterkobel and Oberbipp show the lowest levels of breakdown, consistent with their Holocene age. There is, however, a surprisingly high level of IcPD in one of the samples from Abri Unterkobel (12259) compared with the two others (Fig. 5). This is likely to have been caused by anthropogenic heating of this shell; although none of the analysed shells from this rock-shelter site show any visible signs of burning, localised *in situ* heating of the layers occurred due to the use of hearths at regular intervals during the Mesolithic and the burning of dung accumulations during Neolithic times when the abri (shelter) was used to stable sheep and goats (Wegmüller 2022).

This first IcPD data from *Fruticola* shell indicates that for most samples this biomineral does retain closed system behaviour probably as far back as the Early Pleistocene. Assuming the same effective diagenetic temperatures experienced at all the sites, and given the temporal level of resolution possible using this biomineral, the relative age order predicted by the *Fruticola* shell is therefore (oldest to youngest): Irchel Amselboden ≥ Irchel Hasli Bräm ≈ Irchel Hasli 2018/19 > Hungerbol 2 ≫ Montfleury ≈ Sous-Terre 2 ≫ Niederweningen 2015/B ≈ Niederweningen 2018/3>> Abri Unterkobel > Oberbipp. This fits well with the hypothesised order of sites based on existing independent age data (Table 1).

4.3. *Arianta* shells

A correlation between the FAA and THAA D/Ls can be observed for *Arianta* shells (Fig. 6 & S3), which indicates potential closed-system behaviour. However, the Hungerbol 2 sample (12247; SwHAa; outlined in red) shows divergence from the expected pattern in the THAA fraction, and therefore data from this shell should be rejected. This divergence from closed system behaviour is consistent with surface alteration due to post-depositional weathering visible on the *Arianta* shells from Hungerbol 2. One sample from Irchel Steig East and two of the three Niederweningen 2018/3 samples also show IcPD patterns consistent with non-closed system behaviour (outlined in red). The values for Nuolen 3 in Ala also seem to be somewhat too low, which is also likely to have been caused by weathering as the shells showed signs of modest surface corrosion. This is likely due to diagenetic transformation of some of the fossil mineral from aragonite to calcite.

The data from Abri Unterkobel is consistent within an individual sample, but variable between samples, similar to that observed in the *Fruticola* material from this site. As there is little evidence of vertical movement or reworking of material within the rock-shelter sediments, it seems likely that differential heating has led to acceleration of the protein breakdown in two of the three shell samples. It is therefore unsurprising that the shell samples from this site show differential levels of degradation, so only the youngest ratios are likely to be representative of age.



735 **Figure 6: THAA D/L vs FAA D/L for Ala & Glx in *Arianta* shells from the Swiss Plateau. One sample from Irchel Steig East, one from Hungerbol 2, and two samples from Niederweningen 2018/3 (dashed outline in red) show divergence from closed-system behaviour. Only the unheated shells from Abri Unterkobel are shown; all data in Supplement.**

The shells from Irchel Steig East and Irchel Hochwacht West show the highest levels of protein breakdown of the non-compromised material (Fig. 6), with Hungerbol 1 samples showing somewhat less degradation. Sous-Terre 2 shows intermediate values, but higher than Petit Saconnex 1994 and WHO, which are slightly higher than Nuolen 3, Grandson and Zell 2019 which are similar to each other. Although Grandson has values that are clearly higher in Ala, in keeping with its stratigraphic position, this is not the case for Glx values, but resolution is poorer for this amino acid for Middle/Late Pleistocene-aged samples. As two of the Niederweningen 2018/3 samples show non-closed system behaviour, the age interpretation is based on the single non-compromised sample, which shows lower IcPD than the Middle Pleistocene sites and similar to Niederweningen 2015/B. Boppelsen-Cholholz, the potentially unheated sample from Abri Unterkobel, and Oberbipp show the lowest levels of IcPD, consistent with their Holocene age.

In summary, this first IcPD data from fossil *Arianta* shell indicates that for most samples, this biomineral does retain closed system behaviour as far back as the Early Pleistocene. However mineral diagenesis of the aragonitic shells compromises their IcPD signal, and so it is important to select only un-weathered shells for analysis. Assuming similar effective diagenetic temperature histories, the relative age order predicted by the *Arianta* shell is therefore (oldest to youngest): Irchel Steig East ≈ Irchel Hochwacht West > Hungerbol 1 > Sous-Terre 2 > Petit Saconnex 1994 > WHO > Grandson > Nuolen 3 ≈ Zell 2019 > Niederweningen 2015/B ≈ Niederweningen 2018/3 >> Boppelsen-Cholholz (Ala) > Abri Unterkobel > Oberbipp.

This sequence for the most part corresponds to what could be predicted from existing stratigraphic and dating evidence, with the exception of the 2019 samples from Zell, which should equate to the earlier part of the Eemian (see Sect. 2.1.3.1) and therefore would have been expected to have IcPD values similar to or marginally higher than those of Niederweningen. As there was no heating during sample preparation and there is little chance of confusion during sampling, given that the fossiliferous deposits are sandwiched between two thick units of fluvioglacial gravel, the reasons for such a discrepancy remain unclear. The values from Petit Saconnex 1994 and WHO should be rather similar as they seem to come from the same lithostratigraphic unit, although the shells from WHO are somewhat more weathered than those of Petit Saconnex. The values from both sites were expected to be younger than both Nuolen and Grandson on stratigraphic grounds, but this is not confirmed by the amino acid geochronology. The reason for this might perhaps be that the shells from both sites are somewhat older than expected, as the grey silts sampled at Petit Saconnex 1994 and WHO may possibly date from MIS 8 rather than early MIS 6.

4.4. *Cepaea* shells

In general, a correlation between the FAA and THAA D/Ls can be observed in *Cepaea* (Fig. 7 & S4), which indicates potential closed-system behaviour for this biomineral. However, there is quite a high degree of variability between samples from the same site, especially with older samples, particularly in Val. *Cepaea* has aragonitic shells, so mineral diagenesis is likely. Due to the limited dataset for this biomineral, the closed system trendline is not currently clear, so only one sample (from Irchel Steig East) has been marked as compromised. However, one sample from Sous-Terre 2, as well as samples from Irchel

Hochwacht East, Irchel Hasli 1994/95 and Irchel Steig East plot in a region below the likely trendline, so data from these samples should be treated with caution.

The shells from the Irchel Plateau show the highest levels of protein breakdown in *Cepaea* (Fig. 7). The samples from Irchel Hochwacht East, Irchel Hasli 1994/95 and Irchel Hochwacht West Upper also show very high levels of IcPD, but potential indications of non-closed system behaviour. If these Irchel Plateau samples have undergone some mineral diagenesis, then the higher IcPD values are likely to be the most useful indicator of age (Penkman et al., 2007). Despite significant variability within this group of sites, the high levels of IcPD are consistent with an Early Pleistocene age. Sous-Terre 2 shows intermediate values, with one sample potentially falling off the closed-system trendline. Nuolen 3 shows less IcPD than Sous-Terre 2, and slightly more degradation than Niederweningen 2018/3. Oberbipp has the lowest levels of IcPD, consistent with its Holocene age.

In summary, this first IcPD data from fossil *Cepaea hortensis* shell indicates that for many samples, this biomineral does retain closed system behaviour as far back as the Early Pleistocene, but mineral diagenesis of these aragonitic shells may be exhibited in some samples. Assuming the same effective diagenetic temperatures experienced at all the sites, and given the temporal resolution of this biomineral, the relative age order predicted by the *Cepaea* shell is therefore (oldest to youngest): Irchel Amselboden ≈ Irchel Hasli Bräm ≈ Irchel Hasli 1994/95 ≈ Irchel Steig East ≈ Irchel Hochwacht East ≈ Irchel Hochwacht West Upper ≫ Sous-Terre 2 ≫ Nuolen 3 > Niederweningen 2018/3 ≫ Oberbipp.

Stratigraphically, the shells from Irchel Amselboden and Irchel Hochwacht East should be slightly older than those from Irchel Hasli Bräm, Irchel Hasli 1994/95 and Irchel Steig East, whilst those from Irchel Hochwacht West Upper should be somewhat younger (Table 1), but this cannot be seen in the IcPD data, due to reduced temporal resolution at these high levels of IcPD. Interestingly, unlike the *Bithynia* opercula, the values for *Cepaea* from Niederweningen are slightly less degraded than those of Nuolen.

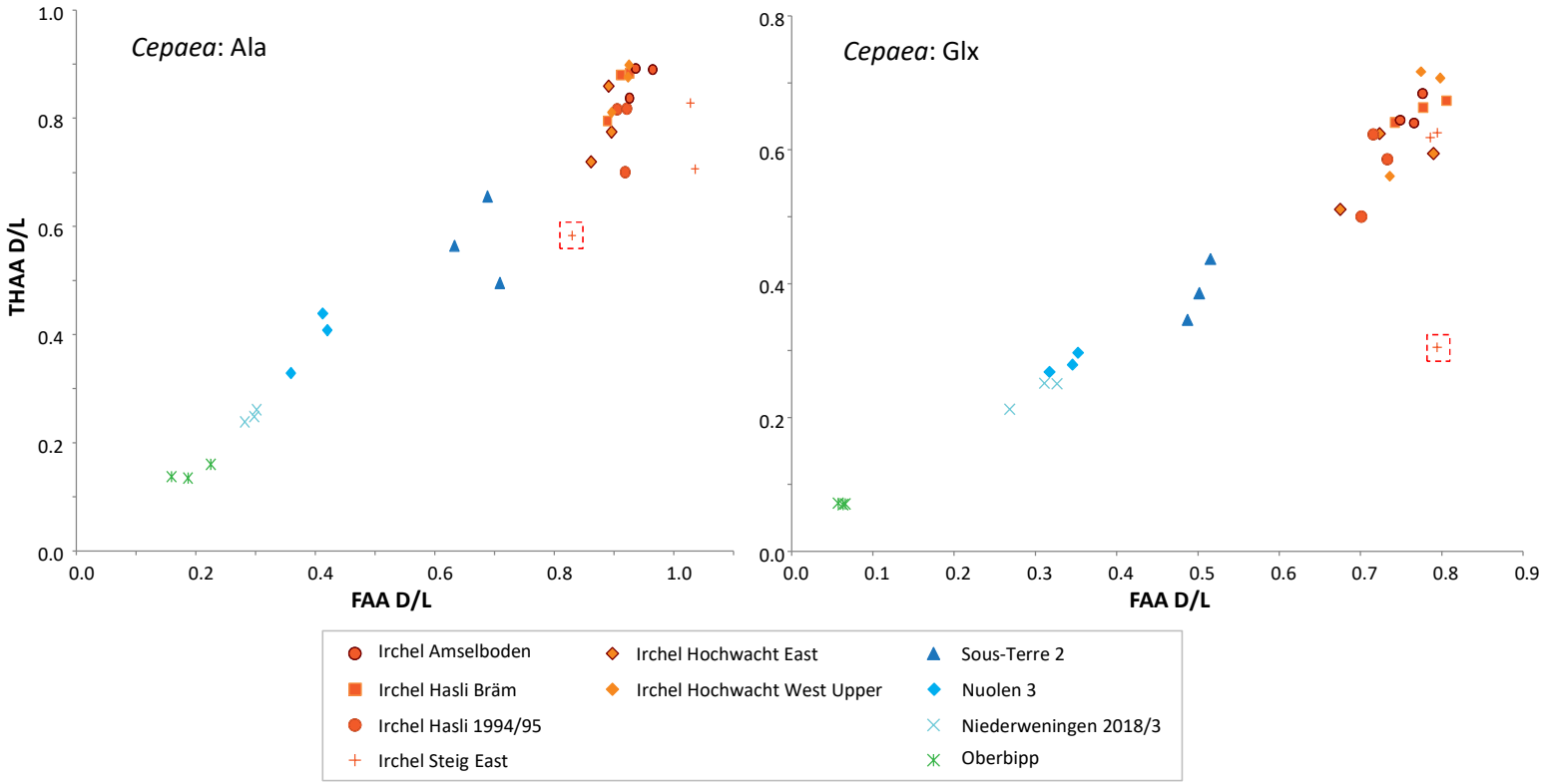


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Figure 7: THAA D/L vs FAA D/L for Ala & Glx in *Cepaea* shells from the Swiss Plateau. One sample from Irchel Steig East (dashed outline in red) shows potential divergence from closed-system behaviour.

4.5. Slug plates

Some pilot work has been undertaken on isolation of the intra-crystalline fraction of slug plates (Pope, 2010), but this represents the first wider study of the intra-crystalline fraction of fossil specimens of this biomineral. In general, a correlation between the FAA and THAA D/Ls can be observed (Fig. 8 & S5), which indicates potential closed-system behaviour for this biomineral. However, there is quite a high degree of variability between samples from the same site, especially the older samples. Both slug plates analysed from Hungerbol showed inconsistent D/L values and amino acid compositions, exhibiting non-closed system behaviour (Fig. S5).

The slug plates from Irchel Ebni show the highest levels of protein breakdown (Fig. 8), which is consistent with the proposed lithostratigraphy. The other Irchel Plateau samples also show high levels of IcPD, but interestingly the extent of racemisation in the slow-racemising amino acids is not as high as that seen from the same sites for other biominerals. This hints that the rates of the reactions in slug plates may be slower, which would result in a loss of temporal resolution, but increase the temporal range for this biomineral. The Sous-Terre 2 samples are intermediate in IcPD, with WHO showing less IcPD, followed by Zell 2019 and then Niederweningen 2018/2. The Oberbipp samples are again the lowest of the suite, consistent with their Holocene age.

In summary, this first IcPD data from fossil slug plates indicates that for most samples this biomineral does retain closed system behaviour as far back as the Early Pleistocene. The relatively high variability in some sites may be due to more than one genus being analysed. Assuming the same effective diagenetic temperatures experienced at all the sites, the relative age order predicted by the slug plates is therefore (oldest to youngest): Irchel Ebni > Irchel Hochwacht East ≥ Irchel Amselboden ≈ Irchel Hasli Bräm ≈ Irchel Hasli 1994/95 ≈ Irchel Hasli 2018/19 ≈ Irchel Steig West ≈ ≈ Irchel Hochwacht West ≈ Irchel Hochwacht West Upper ≈ Albishorn-Bürglen 2 ≫ Sous-Terre 2 > WHO > Zell 2019 > Niederweningen 2018/2 ≫ Oberbipp. The two samples from Hungerbol have divergent IcP compositions that do not permit them to be included in this proposed relative age.

Stratigraphically, the slug plates from Irchel Amselboden and Irchel Hochwacht East 16B should be slightly older than those from Irchel Hasli Bräm, Irchel Hasli 1994/95, Irchel Hasli 2018/19, Irchel Steig West, Irchel Hochwacht East 13, and Irchel Hochwacht West, while those from Irchel Hochwacht West Upper should be somewhat younger, but this cannot be seen in the IcPD data, which is likely due to a lack of temporal resolution in samples of this age. The slug plates from Albishorn-Bürglen 2 should be of a similar Early Pleistocene age to those of the Hasli Formation, which seems to be the case. Zell 2019 does seem to be younger than WHO, in keeping with the latter site being thought to be early MIS 6 or possibly older, while Zell 2019 is early Eemian, although it has IcPD slightly greater than those from Niederweningen 18/2 (which is middle Eemian), as also observed in *Arianta*.

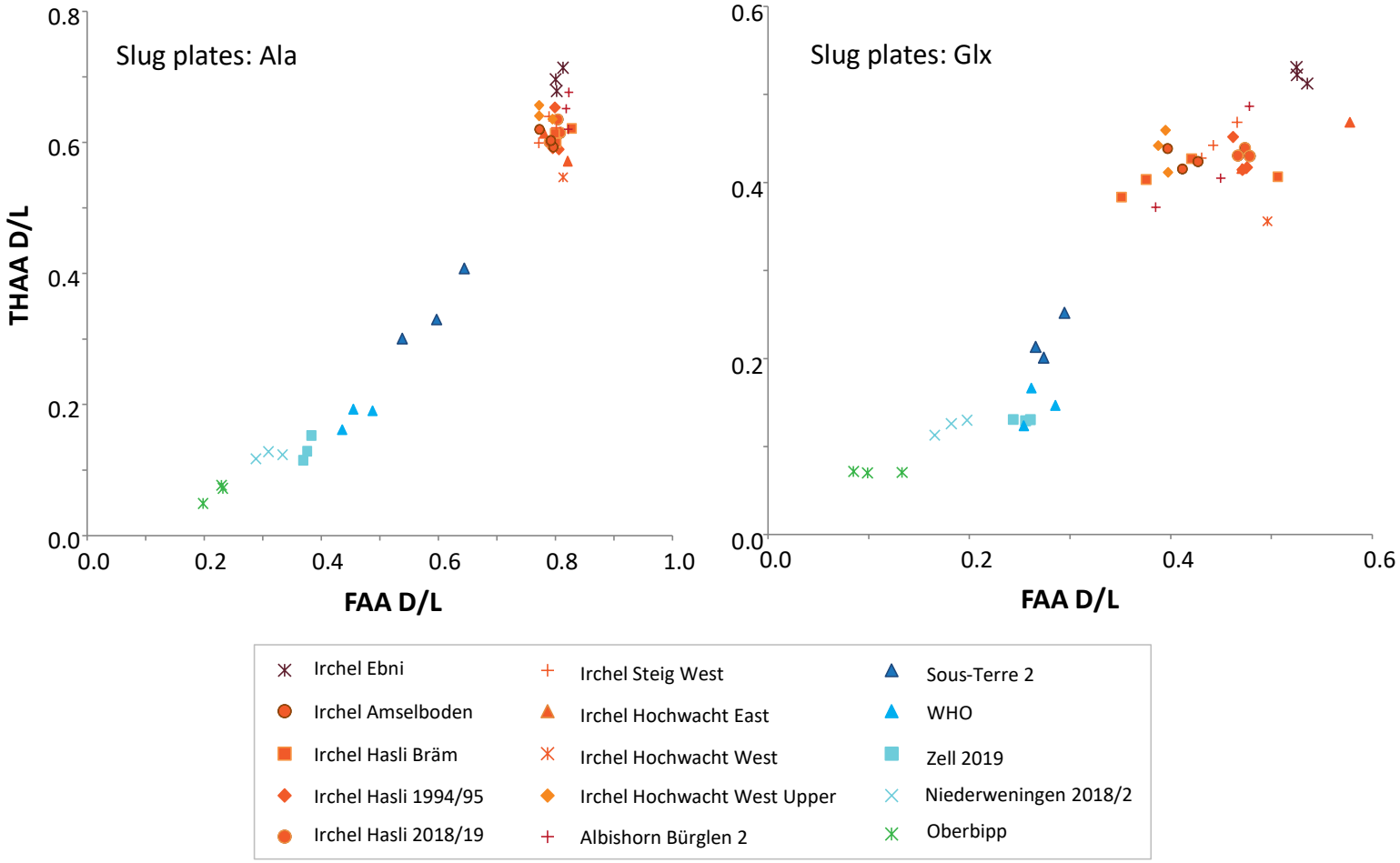


Figure 8: THAA D/L vs FAA D/L for Ala & Glx in slug plates from the Swiss Plateau.

4.6. Worm granules

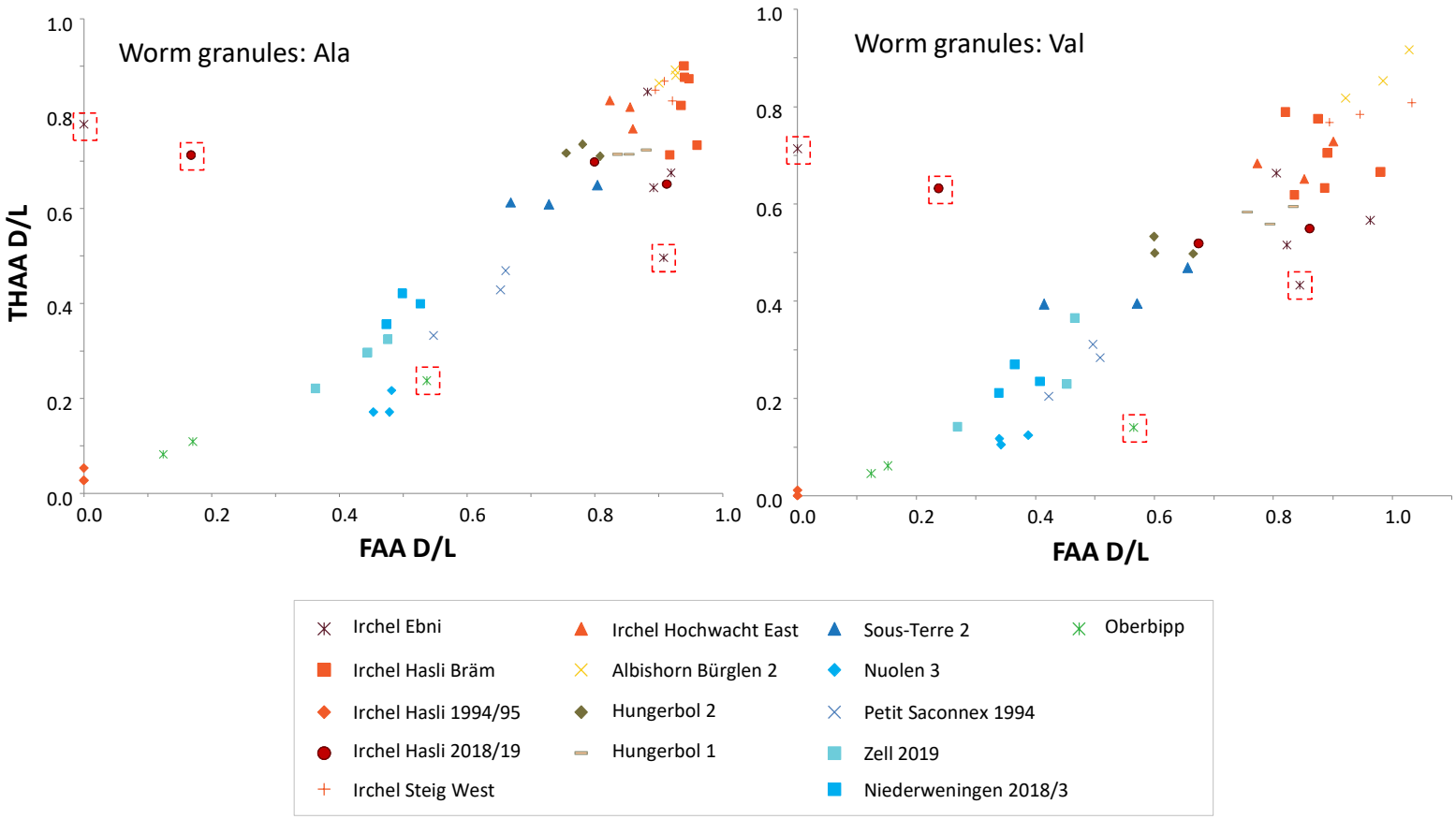
Despite the potentially confounding factors at play in worm granules (taxonomy, excretion biomineral rather than skeletal), in general there is a correlation between the FAA and THAA D/Ls (Fig. 9 & S6), which indicates potential closed-system behaviour for this biomineral. However, there tends to be a high level of variability between samples from the same site. As this is the first detailed dataset that has been collected for worm granules, it is not possible to define precisely where the closed-system trendline is likely to plot, so as yet no samples have been identified as definitely being non-closed system. However, several samples fall further away from the likely trendline for closed system behaviour, given the patterns expected based on other biomineral behaviour. These include two samples from Irchel Ebni, two samples from Irchel Hasli 2018/19, and one sample from Oberbipp. In addition, all the samples from the Early Pleistocene site Irchel Hasli 1994/95 show very low levels of IcPD, with low D/L values, high concentrations of amino acids and low levels of peptide bond hydrolysis. Given that earthworms are active within surface sediments, there is a greater potential for the intrusion of younger material when analysing this biomineral (Canti, 2007). This is certain to have been the case for the Irchel Hasli 1994/95 samples, as modern worm action was observed during excavation, and so these worm granules analysed cannot be used to constrain the age of the Pleistocene sediments at this site.

Given the high variability within sites, as well as the relatively large number of samples that are likely not to show closed system behaviour, the data from the worm granules should be interpreted with caution. However, certain age indications are still present within the worm granule dataset.

The oldest worm granules are from the Irchel sites, along with Albishorn-Bürglen 2, consistent with their Early Pleistocene age, the exception being the granules from Irchel Hasli 1994/95 that clearly represent intrusive modern elements. Those from Albishorn-Bürglen 2 display some of the greatest IcPD values, possibly due to their rapid accumulation and burial within a thick sequence of fluvial sediments, with little possibility of later intrusion or weathering. The granules from Irchel Hasli 2018/19 also show considerable variability in IcPD values, potentially indicating non-closed system behaviour and/or intrusion at some stage in the past. The granules from Hungerbol have IcPD values that are in keeping with their stratigraphic position (part of the TDS), supporting the *Fruticola* and *Arianta* datasets, so seem to date from somewhat later during the Early Pleistocene than the Irchel material. Sous-Terre 2 shows intermediate levels of IcPD, consistent with its Middle Pleistocene age, while the Petit Saconnex 1994 show incrementally lower levels of IcPD, in keeping with their stratigraphic position. Zell 2019 and Niederweningen 2018/3 samples show even lower levels of IcPD, supporting the data from the other biominerals and consistent with their Eemian age. The Nuolen 3 samples show somewhat lower than expected THAA IcPD when compared with the other biominerals from this site; without greater understanding of the closed system behaviour, this may be due to a diagenetic issue or a slightly later intrusion of younger worm granules into the Middle Pleistocene sediments. The samples from Zell 2019 are quite variable; this may have been caused by weathering, but as the deposits at Zell span from the early Eemian to the Early Würm (MIS 5e to 5c; cf. 2.1.3.2), some granules may represent later intrusions. Overall, the values for

Zell 2019 are consistent with an expected (early) Eemian age for the sampled deposits. The values for the granules from Niederweningen 18/3 are consistent with a probable middle Eemian age for these deposits. The two samples from Oberbipp that show closed system behaviour have low levels of IcPD, as expected given their Holocene age.

In summary, this first IcPD data from fossil worm granules indicates that for some samples this biomineral does retain closed system protein as far back as the Early Pleistocene. The relatively high variability in some sites may be due to multiple species being analysed, or due to a less conservative set of proteins being incorporated into the mineral due to its excretory purpose. The multi-crystalline structure of worm granules (Mandera et al., 2023) may also be more susceptible to weathering than the denser calcite of opercula and slug plates. Combined with the relatively high levels of non-closed system behaviour evident in the worm granules, and the great potential for intrusion (Canti, 2007), this preliminary dataset indicates that this biomineral may not be ideal for high resolution studies. Despite this, remarkably there remains a signal of age in the worm granule dataset. Assuming the same effective diagenetic temperatures experienced at all the sites, for sites where age interpretation is possible, the relative age order predicted by the worm granules is therefore (oldest to youngest): Irchel Ebni ≈ Irchel Hasli Bräm ≈ Irchel Hasli 2018/19 ≈ Irchel Steig West ≈ Irchel Hochwacht East ≈ Albishorn-Bürglen 2 > Hungerbol 2 ≈ Hungerbol 1 ≫ Sous-Terre 2 ≫ Petit Saconnex 1994 > Nuolen 3 ≈ Zell 2019 ≈ Niederweningen 2018/3 ≫ Oberbipp. This fits quite well with the general stratigraphic order of sites, which is a positive sign for the geochronological potential of worm granules, despite the high levels of variability observed.



875 **Figure 9: THAA D/L vs FAA D/L for Ala and Val in worm granules from the Swiss Plateau. Two samples from Irchel Ebni, one sample from Irchel Hasli 2018/19 and one sample from Oberbipp fall further from the likely trendline for closed-system behaviour (dashed outline in red). The three samples from Irchel Hasli 1994/95 appear to be modern intrusions.**

5. Conclusions: implications for AA geochronology and its contribution to the Swiss Quaternary

The amino acid data from these samples shows that age discrimination is possible between Quaternary sites from the Swiss Plateau, using this technique on six different biominerals: *Bithynia* opercula, shell fragments from *Fruticola*, *Arianta* and *Cepaea*, slug plates and worm granules. This significantly widens the types of material that can be used for amino acid geochronology, and therefore the range of palaeoenvironments that can be examined. For certain biominerals there is a clear need for additional samples per horizon to be undertaken in order to fully assess their natural variability, and hence their temporal resolution. It is hoped that by analysing more material from the same and from new sites, especially those where biomaterials are well preserved, that this pilot aminostratigraphy for the Swiss Plateau can be refined and strengthened. Despite this, there is already a considerable amount of useful age information within this pilot dataset.

A small number of samples did not show closed system behaviour, and therefore these individuals could not be used to provide age interpretations. It is also apparent that amino acid dating must be undertaken with due regard for potential anthropogenic heating of the biominerals (such as that seen at the archaeological site of Abri Unterkobel), intrusion of younger material (as seen in the worm granule dataset) and signs of significant weathering on the shells (such as that which affected the *Arianta* from Hungerbol 2). Although archive samples have produced very useful data, where possible it is preferable to analyse material from sediment with a known processing history.

The use of multiple amino acids is helpful in the generation of an overall IcPD aminostratigraphy. Interestingly the levels of temporal range and resolution differ between the biominerals, and this, combined with the lack of a single biomineral across all sites, means that a composite approach has been required in developing these aminostratigraphies for this region. In general, these pilot aminostratigraphies fit well with the pre-existing independent evidence of age for the sites.

The AA analyses strengthen the lithostratigraphic and biostratigraphic picture for the Early Pleistocene deposits from the Irchel Plateau. The Ebni silts are oldest, while the Hasli Formation (HF) deposits seem likely to represent a younger stratigraphic unit (in accord with the conclusions reached in Thew et al. 2024 (cf. Sect. 2.1.1.1)), despite some variation in IcPD values which may have been caused by mineral diagenesis in some of the aragonitic shells, probably linked with groundwater circulation in the sandier layers. The AA dataset also confirms biostratigraphic information from the molluscs that deposits sampled at Albishorn-Bürglen 2 are of a similar age to the HF. Moreover, the AA data seems to confirm existing stratigraphic and biostratigraphic evidence that material from Hungerbol 2 & 1 dates from somewhat later in the Early Pleistocene than the Irchel sites.

Ecoteaux is the first site in Switzerland to be reasonably securely attributed to the Cromerian, and the AA data strengthens this likely age estimate, with IcPD intermediate between the Early Pleistocene and Late Mid Pleistocene sites. Sous-Terre 2 and Montfleury have been shown by the AA data to be somewhat younger, providing support to lithostratigraphic and molluscan evidence for these two sites. If they are MIS 11, then these are the first that can be reliably attributed to this period in Switzerland. Petit Saconnex and WHO have a similar lithostratigraphic context and comparable molluscan assemblages,

characteristic of an interstadial within a cold period. While the AA data confirms that their relative position in a Middle Pleistocene age range, this data also suggests that both sites may be somewhat older than the expected age of early MIS 6 based on lithostratigraphic evidence, possibly of MIS 8 age. Together with the data from Sous-Terre 2 and Montfleury, this dataset provides valuable new insights into the chronology of deposits in the Geneva area.

The AA data seems to confirm a later Middle Pleistocene, possibly MIS 7, date for the high terrace of Lake Neuchâtel at Grandson, and alluvial deposits within a Hochterrasse sequence at Nuolen, both of which are linked to the Rhine system. A date of MIS 9 or older has been suggested for Grandson due to the presence of *Pterocarya* pollen (Schlüchter et al. 2021), while a few grains of *Pterocarya* pollen have also been identified from profiles near Nuolen (Welten 1988), but the AA data does not seem to support this (cf. Sect. 2.1.2.4, 2.1.2.3).

Despite strong lithostratigraphic, luminescence dating and biostratigraphic (pollen, molluscs) evidence that the palaeolake deposits at Thalgut are of Eemian age (cf. Sect. 2.1.3.2), both sets of samples of *Bithynia* opercula produced IcPD values that seem to be significantly older. The most likely scenario to explain this is that all the sample material was heated at some point post-collection, probably to dry it as was common laboratory practice. At Zell, the lithostratigraphy, dating evidence (luminescence and U/Th) and molluscan assemblages all indicate that the sampled fluvial deposits are of early-mid Eemian age (cf. Sect. 2.1.3.1). However, the AA values are somewhat variable, and seem for some materials to be slightly high. The faster rate of racemisation during warm stages (e.g. Bates, 1993; Miller et al., 1999; Penkman et al., 2013) means that the range of D/L values within an interglacial can be relatively large, with slow rates of racemisation in cold stages making it difficult to resolve the end of one interglacial from the beginning of the next in some cases. This means that until further independent evidence of age is available, we reserve judgement on the significance of these differences given the limited data set.

The material from Sous-Terre 1, Boppelsen, Oberbipp and Hauterive-Champréveyres provided some of the lowest levels of IcPD as expected, in keeping with their Holocene age. By contrast, the surprisingly high values from some of the shells from Abri Unterkobel shows the importance of taking into account any anthropogenic heating of sediments in archaeological sites when selecting samples for AA analysis.

This dataset provides the first aminostratigraphies for the Swiss Plateau and employs intra-crystalline protein decomposition (IcPD) in novel and rarely analysed biominerals (*Fruticola*, *Arianta* and *Cepaea* shell, slug plates and worm granules). Although constructing a single aminostratigraphy using several different biomineral materials is rather complex, a coherent picture has emerged that provides extremely useful age information. The conjunction of the AA geochronology with existing information, and new molluscan data (Thew, 2024), makes an important contribution to Quaternary studies in Switzerland, providing crucial new age information for a number of key sites from across the Swiss Plateau, some of which are helping to fill major gaps in the Swiss chronology.

Data availability

All amino acid data from this study is available (doi: 10.5281/zenodo.21293656) through the EQuaTE Zenodo community (https://zenodo.org/communities/equate/) and will be archived at the NOAA repository upon final publication: https://www.ncei.noaa.gov/pub/data/paleo/aar/. For the purpose of open access, a Creative Commons Attribution (CC BY) licence is applied to any Author Accepted Manuscript version arising from this submission. An early draft of this manuscript was deposited in EarthArXiv: https://doi.org/10.31223/X57700 and has been updated.

Supplement link

The link to the supplement will be included by Copernicus, if applicable: doi: 10.5281/zenodo.21293656.

Author contributions

GD led the NAGRA project studying the Deckenschotter deposits from northern Switzerland, for which the molluscan analyses and IcPD dating form a part, and helped with sampling the Irchel sites and Hungerbol. NT excavated, documented and sampled the Irchel sites and Hungerbol, collected shell material from museums, specialists and previously studied sites, analysed all the molluscan assemblages and collated stratigraphic and dating information from the studied sites; DK excavated and sampled the Irchel sites and Hungerbol and provided new shell material from Zell; MB provided valuable advice during the advancement of the project. KP led the aminostratigraphic study; ST, SP and EN undertook the laboratory analyses. All authors were involved in writing the manuscript.

Competing interests

One of the co-authors (KP) is a member of the editorial board of Geochronology.

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