\$ SUPER

Contents lists available at ScienceDirect

Quaternary Science Reviews

journal homepage: www.elsevier.com/locate/quascirev





The 'La Celle interglacial': a key-record of MIS 11c palaeoenvironments and palaeoclimate in NW Europe

N. Limondin-Lozouet ^{a,*}, J. Dabkowski ^a, P. Antoine ^a, J.J. Bahain ^b, P. Voinchet ^b, K.E.H. Penkman ^c, D. White ^c, M.C. Jolly-Saad ^d, P. Auguste ^e, B. Ghaleb ^f

- a Laboratoire de Géographie Physique, UMR 8591 CNRS-Université Paris1 Panthéon-Sorbonne-Paris Est Créteil, 2 rue Henri Dunant, 94320, Thiais, France
- ^b Histoire naturelle des humanités préhistoriques UMR 7194 MNHN-CNRS-UPVD, 75013, Paris, France
- ^c BioArCh, Dept of Chemistry, University of York, York, YO10 5DD, United Kingdom
- ^d Centre de géomorphologie et palynologie Henri Elhaï, UMR 7041 CNRS-Université Paris Nanterre, 92000, Nanterre, France
- e Evo-Eco-Paléo, UMR 8198 CNRS-Université de Lille, 59000, Lille, France
- f GEOTOP, Université du Québec à Montréal, PO box 8888, Sta. Downtown area, Montréal, PQ.H3C 3P8, Canada

ARTICLE INFO

Keywords: Middle Pleistocene Interglacial dynamics Bioproxies Geochemistry Land snails Leaf imprints Tufa

ABSTRACT

The La Celle calcareous tufa formation, located in the Seine valley (Paris Basin, France) provides an exceptional stratigraphic record (9 m thick), yielding a wide variety of palaeontological remains (molluscs, leaf prints, ostracods, mammals) as well as geochemical data allowing a detailed reconstruction of the environmental and climatic dynamics during the Marine Isotope Stage (MIS) 11c interglacial. The chronological assignment of the site is particularly well constrained by a number of methods (U-series, electron spin resonance, thermoluminescence). This review synthesises previously published data as well as new research on the formation of the deposit (stratigraphy, micromorphology), amino-acid geochronology, palaeobotany, and compares these results with those of European palynological references. Several important markers of the continental environments during MIS 11c are identified. The malacological succession is of particular importance for reconstructing the vegetation dynamics, reflecting the expansion of forest biotopes and their subsequent degradation and is closely linked to geochemical analyses, providing a reliable framework for the associated climatic conditions. The La Celle sequence yields the only complete record for the development of the "Lyrodiscus fauna", a characteristic biostratigraphic signature of MIS 11c in NW Europe. The long molluscan succession of La Celle is the relevant reference for the integration of shorter regional malacological series into the environmental dynamics of the interglacial. The occurrence of several Mediterranean trees, and mammal remains of Hippopotamus and Macaca are registered during the climatic optimum revealed by geochemistry. Together with isotopic data this set of thermophilic bioproxies indicates the warmest and wettest conditions ever recorded for late Middle Pleistocene interglacials in the region. Comparison of the reconstructed palaeoenvironmental and climatic succession with the nearest long pollen series demonstrates that the La Celle tufa deposit records almost the entire interglacial. Therefore, the "La Celle Interglacial" is proposed as a major reference for understanding the evolution of the MIS 11c continental landscapes and biodiversity in northwestern Europe.

1. Introduction

Recent investigations have highlighted the importance of high resolution terrestrial records for a better understanding of palaeoenvironmental and palaeoclimatic dynamics during interglacial periods (Past Interglacials Working Group of PAGES, 2016;

Kleinen et al., 2014). In northern Europe, long continental interglacial successions are mostly preserved in lacustrine contexts. However, in the westernmost part of this territory where such sequences are rare, tufa formations have yielded valuable archives of temperate periods in fluvial environments (Pentecost, 1995, 2005; Antoine et al., 2007, 2024). Moreover, calcareous tufas appear to be the only deposits

E-mail addresses: nicole.limondin@lgp.cnrs.fr (N. Limondin-Lozouet), julie.dabkowski@lgp.cnrs.fr (J. Dabkowski), pierre.antoine@lgp.cnrs.fr (P. Antoine), bahain@mnhn.fr (J.J. Bahain), Pvoinch@mnhn.fr (P. Voinchet), kirsty.penkman@york.ac.uk (K.E.H. Penkman), dustin.white@york.ac.uk (D. White), saad.marie-claude@orange.fr (M.C. Jolly-Saad), Patrick.Auguste@univ-lille1.fr (P. Auguste), ghaleb.bassam@uqam.ca (B. Ghaleb).

https://doi.org/10.1016/j.quascirev.2025.109667

 $^{^{\}ast}$ Corresponding author.

recording the interglacial optima (Antoine and Limondin-Lozouet, 2004), and several studies confirm the importance of these formations to define a reference record of Pleistocene interglacial dynamics (Antoine et al., 2007; Preece et al., 2007; Ortiz et al., 2009; Pazzaglia et al., 2013; Limondin-Lozouet and Preece, 2014). Tufas usually fossilise in situ abundant and diverse fossil groups (Preece, 1991; Capezzuoli et al., 2014; Dabkowski, 2014) and are suitable archives of geochemical information from which palaeoclimatic conditions can be inferred (Andrews, 2006; Dabkowski et al., 2011). Finally, they can be directly and precisely dated by radiometric methods (radiocarbon and U-series), and additional dating can be achieved on their organic and archaeological contents (Bahain et al., 2022; Granai and Wackenheim, 2022; Horvatinčić et al., 2000). Among north-west European Pleistocene tufas, MIS 11c is the best-represented interglacial, with seven sites dated to this complex warm period (Fig. 1). These deposits do not usually exceed 1–3 m in height, while the La Celle tufa is almost 9 m thick. It therefore provides a remarkable opportunity to reconstruct a detailed succession of the interglacial palaeoenvironmental evolution allowing robust comparison with regional and global palaeoclimatic parameters.

The site of La Celle was discovered at the end of the 19th century and recognized as a unique record of an ancient temperate period through its malacological and floral fossils (Tournouër, 1874, 1877; Saporta de, 1874). At the same time, about thirty Acheulean handaxes were collected from several archaeological horizons located in the middle part of the tufa sequence (Collin et al., 1895). In the 1960s new stratigraphic observations at La Celle, together with investigations on fluvial terraces of the Seine valley, allowed attribution of the formation to the MIS 11 interglacial (formerly Mindel-Riss in Bourdier, 1969; Rousseau, 1992; Lautridou et al., 1999). Studies on this important site were reassessed at the beginning of the 2000s using a multidisciplinary approach including stratigraphical data, dating, geochemical analyses and palaeontological remains, based on both the revision of ancient collections and new sampling (Limondin-Lozouet et al., 2006). Preliminary results

highlighted the important palaeoenvironmental potential of the site and led to the discovery of traces of an Acheulean occupation during the forest optimum (Limondin-Lozouet et al., 2010). Several publications have previously focused on either the palaeobotanical, malacological, archaeological or geochemical investigation at La Celle (Jolly-Saad et al., 2007; Limondin-Lozouet et al., 2010, 2015, 2020; Dabkowski et al., 2011, 2012) but a large amount of data remained unpublished, including stratigraphic and micromorphological observations, dating from amino acid geochronology, etc. Moreover, although the previous studies demonstrated the richness and the importance of the site for the detailed understanding of environments and climate prevailing during MIS 11c, a complete data synthesis formally establishing La Celle as one of the best-documented and longest reference records for this period in Northwest Europe was needed.

This paper thus combines, for the first time, all data collected at La Celle since the investigations were relaunched in the early 2000s; already published studies are enriched by new data that have not been previously available in the scientific literature (Table 1). This review leads to an improved understanding of the whole sequence and original data interpretations and discussions, most notably a detailed step-by-step reconstruction of the tufa development. The palaeoenvironmental and palaeoclimatic reconstructions inferred from the La Celle record are discussed and compared in the frame of North-West European continental references for MIS 11c.

2. Geomorphology, stratigraphical framework and new micromorphological data

The La Celle tufa (Lat $48^{\circ}23$ N; Long $2^{\circ}50$ E) is located on the right-hand valley slope of the Seine river, 2.5 km upstream from its confluence with the Loing River and 90 km upstream from Paris. It is located on a middle fluvial terrace of the Seine, the basal contact of which is approximately 15 m above the modern floodplain, and at a relative

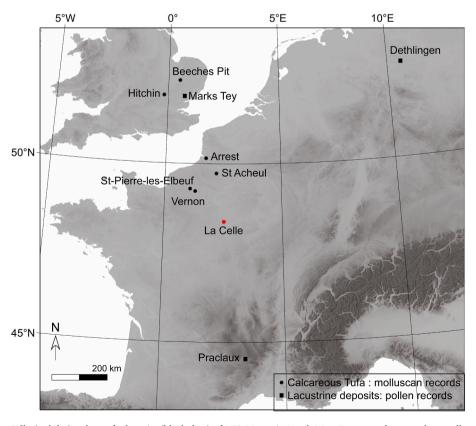


Fig. 1. Location map of La Celle (red dot), other tufa deposits (black dots) of MIS 11 age in North-West Europe and nearest long pollen sequences (black squares) discussed in the text. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 1Summary table of previously published studies on the La Celle site and unpublished data presented in this article.

Methods	Published data	This paper
Stratigraphy	Pits S1 to S5/Long profile (Limondin-Lozouet et al., 2006, 2010)	Profile S2 (SM1) and step- by-step reconstruction of the tufa development (Fig. 11)
Micromorphology	Partly available in a PhD thesis (Dabkowski et al., 2011)	Complete data (Fig. 9 + SM2)
Dating	U series on indurated tufa samples and U series combined with electron spin resonance (ESR) on horse tooth, ESR on sand grains, thermoluminescence (TL) on burnt flint (Bahain et al., 2010; Voinchet et al., 2015)	AAR (Table 3, Fig. 5 and SM4)
Malacology	Detailed analyses, especially in a European palaeogeographical perspective (Limondin-Lozouet et al., 2006, 2010, 2020)	Comparison with long pollens series (Fig. 13)
Large mammals	Identification and preliminary discussion (Auguste <i>in</i> Limondin-Lozouet et al., 2006; Auguste, 2009)	Comparison with European data
Palaeobotany	Revision of Munier-Chalmas collection-Jussieu University (Jolly-Saad et al., 2007)	Revision of samples from MNHN Geological Dept. and <i>Musée de Nemours</i> (Fig. 8)
Geochemistry	Stable isotopes, Mg/Ca and Sr/Ca ratios from the sampling column G1 (Dabkowski et al., 2011, 2012)	

altitude of about +25 m above the maximum incision of the present-day valley. An important part of the tufa deposit, which may have initially covered an area of about 12.5 ha with a variable thickness of 8–15 m (Tournouër, 1877), was destroyed by the exploitation of the quarry in the 19th century. At present, only two areas of intact tufa remain: in the eastern part of the site under the cemetery, where the deposit is therefore inaccessible, and along the western boundary of the former quarry face, where the most recent investigations were carried out in the 20th

century (Bourdier, 1961, 1969) and then by our team from 2003 (Fig. 2). At this time, the stratigraphy was first observed from limited profiles excavated for malacological sampling. Three of these (S1, S5 and S2; Fig. 2) on the western side of the former quarry showed that the tufa was preserved over a thickness of at least 9 m along the slope (Limondin-Lozouet et al., 2006). A series of boreholes drilled into and around the top of the formation then demonstrated the maximum extent of the tufa to west (Fig. 2). Finally, a main section of 35 m in total was created, allowing precise correlation of the sedimentary units, new sampling and a better reconstruction of the formation dynamics (Figs. 2 and 3 and Supplementary Material – SM – 1).

2.1. General overview of the stratigraphy

The largest area excavated in La Celle corresponds to the already well-published "Long Section" (Fig. 3; Limondin-Lozouet et al., 2010, 2020; Dabkowski et al., 2012), which extends 27 m laterally along the slope, and the adjacent 8 m-long "Profile S2", which shows most of the stratigraphic units described in the "Long Section", but along an almost perpendicular section (SM1). The detailed unit-by-unit description is provided in SM1 to complement the general overview of the stratigraphy below.

Upslope at the NE end of the "Long Section" (Fig. 3), the tufa lays directly on the altered calcareous Eocene bedrock (unit 17), while downslope, it overlies sandy to silty deposits from the uppermost part of the fluvial terrace (units 16 and 15). The first tufa deposits (units 14 to 11) are coarse to sandy-silty with detrital material including abundant broken shells and bones, quartz, indurated limestone blocks, etc., especially in units 14 and 13. Unit 10 is a silty tufa including *in situ* bioconstructions and large fragments of tufa forming a barrage-like mound, associated upslope with the sandy-silty deposits with indurated 10 cm blocks of tufa and the fine sandy to granular tufa from units 9 and 8, respectively. The upper part of those three units is eroded by a discontinuous level of large limestone and tufa blocks (NB3) and overlaid by unit 7.

Unit 7 comprises charcoals, abundant mollusc shells and fragments of tufa, some showing evidence of heating. This unit has developed as an upbuilding humic soil in which colluvial sedimentation, pedogenesis and bioturbation are contemporaneous (Limondin-Lozouet et al., 2010).

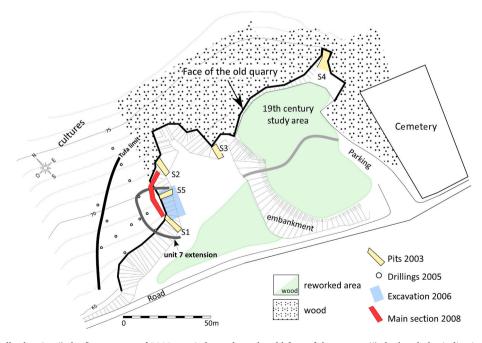


Fig. 2. Site map of La Celle showing i) the first surveys of 2003, carried out along the old face of the quarry, ii) the boreholes indicating the maximum westward extent of the tufa and iii) the main section cut along the slope.

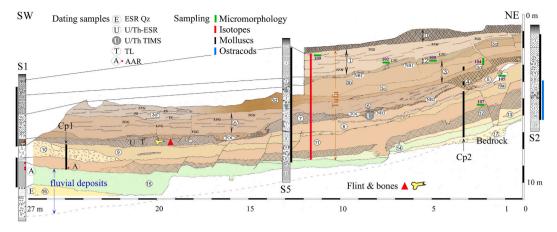


Fig. 3. Stratigraphy of the tufa deposit at La Celle with sampling location. Profiles created in 2003 are plotted against the "Long Section" excavated in 2008. Detailed description of units is given in SM1.

It includes large mammal remains and lithic artefacts attributed to the Acheulean culture (Limondin-Lozouet et al., 2010). Unit 7 is then eroded by a second, continuous, level of blocks (NB2), locally associated with channelized structures (Fig. 3) infilled by oncolithic granular tufa (facies TOC).

The relationship of units 5 and 4 to the rest of the stratigraphy remains unclear if only the 'Long Section' is considered. Indeed, the whole tufa mass has been affected upslope by a network of reverse faults caused by differential compaction processes and a rotational downslope sliding of the tufa mass linked to post depositional periglacial processes (Fig. 3). However, observations from "Profile S2" (SM1), together with the comparison of the malacological assemblages from sampling columns S5 and Cp2 (Fig. 3), suggest that unit 4 is actually contemporaneous with unit 7, and that unit 5 is the continuation of unit 8 (Limondin-Lozouet et al., 2020).

Few detrital elements are preserved in the following tufa unit 6. Both units 6 and 3 are locally laminated, with alternation of granular to sandy tufa, especially in subunits 6' and 3d' downslope (Fig. 3). A last block level (NB1) is associated with unit 2, which is eroded at its top. The uppermost unit 1 is a finer facies (TFH) with discontinuous layers of sandy-granular tufa with oncolith (TGS) and, mainly at its base, indurated tufa with leaf imprints (Fig. 3).

2.2. Micromorphology and microalgae determination

To complement field observations, a micromorphological study was carried out at La Celle on 12 thin sections of undisturbed blocks extracted from the 'Long Section' (7 blocks) and the adjacent 'profile S2' (Fig. 3 and SM1). Tufa deposits are mainly related to the activity of cyanobacteria and microalgae, which can be taxonomically determined from the crystal morphology (Freytet, 1997). As part of a detailed description of all thin sections, 'morphotaxa' identification is provided in SM2. Fossil 'morphotaxa' can be assigned to one or more modern microalgae based on comparisons of calcite organisation in modern contexts where the latter have been biologically identified (Freytet, 1997, 1998). Features that then provide key-information on palae-oecological and palaeoenvironmental conditions (Fig. 4) are summarised here.

At La Celle, micromorphological forms assigned to algal 'morphotaxa' *Broutinella* sp./*Plaziatella* sp. associated with *Koeniguerella sequanensis* predominate. The occurrence of *Koeniguerella sequanensis* is noteworthy (Fig. 4: A), as its holotype was defined at La Celle (*Sequana* is the Latin name for the Seine river; Freytet, 1997). However, the equivalence of this fossil taxon with modern green algae or certain cyanobacteria (blue-green algae) is uncertain (Freytet, 1997), so no reliable palaeoecological interpretation can be made based on its

presence. On the other hand, Broutinella sp./Plaziatella sp. (Fig. 4: B & B') are clearly associated to some modern cyanobacteria (Freytet, 1998) indicating the effective presence of water (i.e. water level between 0.5 and 30 cm) in an environment where mosses are excluded (Pentecost and Riding, 1986). Broutinella sp./Plaziatella sp. are specifically observed in the units at the base of the sequence with facies poor in detrital elements (units 13 to 11) and in unit 1 (Fig. 3). Additionally, all tufa units contain Wallnerella fascinans bioconstructions (Fig. 4: C, C' & D), which are known to result from the intensive diagenesis of Oocardium crystals (Freytet, 1998). This green alga appears to be more abundant in dynamic currents, especially in regions where summer temperatures exceed 25 °C (Pentecost, 1991). In unit 3, W. fascinans is associated to Sarfatigirella aquavivae (Fig. 4: E), a morphotaxa whose holotype has also been defined at La Celle (Freytet, 1998). Its morphology is similar to that of the modern brown algae Vaucheria, which develops under relatively high hydrodynamic conditions.

In the La Celle thin sections, bioconstructions are observed both *in situ* and as part of the detrital content of some tufa units (specifically units 3d, 3c, 2, and 1; SM2). However, rounded to sub-rounded quartz grains dominate the detrital content, with fragmented shells and bones also observed (Fig. 4: F & F'; and Fig. S1: B, C & C' in SM2). The latter are particularly abundant in unit 7, which has a specific micromorphological facies with a micritic matrix likely to comprise carbonated ashes (Fig. 4: F & F'). The detrital content also includes burnt elements and, locally, abundant earthworm biospheroids (Fig. S1: B in SM2). Altered bioconstructed fragments are generally difficult to identify and are enclosed in a dense micritic to macrosparitic matrix (Fig. S1: A & A' in SM2).

In summary, from the bottom to the top of the sequence, the microfacies observed at La Celle provide palaeoenvironmental information: the constructed facies of unit 13c were built in a relatively large (cyanobacteria Broutinella sp./Plaziatella sp.) and (W. fascinans) water body. These structures were then dismantled, reworked and deposited nearby (few detrital elements, few fragmented bioconstructions and shells) by waters with similar dynamics (units 13a and 12a). During deposition of unit 13a, the slope was not yet stabilised (presence of limestone fragments from the substratum among the clasts). In situ constructions indicating relatively deep and dynamic waters are again preserved (unit 11). The alternation of facies, constructed in situ and then reworked, related to the same fossil algae, actually reflects the spatial variations of the same environment during units 13 to 11, characterised by a fairly high-water level and a relatively intense flow. During the development of unit 7, slight colluviation mixed detrital elements (bone fragments, detrital minerals including quartz) with the tufa and carbonated ashes, which give this unit its characteristic grey colour. According to microscopic observations, the stream was more

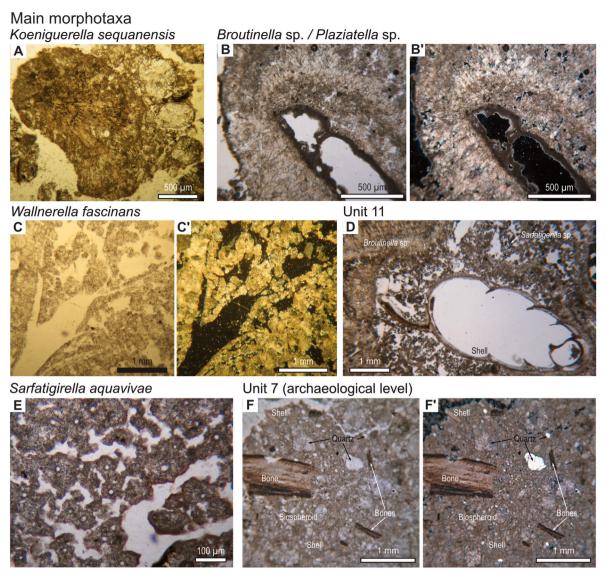


Fig. 4. Photographs in thin section of typical morphotaxa and tufa facies observed at La Celle. Scales are given for each of them. A. fragments of Koeniguerella sequanensis bioconstructions from unit 7 in plane-polarised light (PP); B&B'. Broutinella sp./Plaziatella sp. from unit 11 encrusting a vegetation pseudomorph, in PP (B) and crossed-polarised (XP) light (B'); C&C'. Wallnerella fascinans from unit 1 encrusting a root pseudomorph in PP (C) and XP (C'); D. gastropod shell encrusted by Broutinella sp. from unit 11 (PP), fragment of bioconstruction by Sarfatigirella aquavivae are also visible while sparse in this unit; E. Sarfatigirella aquavivae bioconstruction from unit 3d (PP); F&F'. Unit 7 (archaeological level), with abundant detrital material including quartz, shell and bone fragments, as well as biospheroid, in calcitic matrice identified as carbonated ashes, in PP (F) and XP (F'). More details are provided in SM2.

dynamic during the deposition of units 3 and 2 (abundant detrital elements including quartz and *Sarfatigirella aquavivae*). During the deposition of unit 1, the intensity of the current decreased (reduction in the proportion of detrital elements), but remained significant (diffuse oblique laminations, *W. fascinans*). Unit 1 is also deposited in relatively deep water (cyanobacteria *Broutinella* sp./*Plaziatella* sp.). Spring inputs appear to be abundant throughout the sequence, but are more dynamic in units 3 and 2. The almost constant presence of *Wallnerella fascinans* also indicates relatively warm summers during MIS 11.

3. Geochronology

To ensure a robust geochronological control, five independent dating methods have been applied at La Celle: U-series on indurated tufa samples and U-series combined with electron spin resonance (ESR) on horse tooth enamel, ESR on quartz grains, thermoluminescence (TL) on burnt archaeological flint and amino acid geochronology (AAG) on mollusc opercula (SM3: Tables S1–S6). A summary of previous

geochronological results is presented below (Table 2), while data from the AAG analyses is new.

3.1. U-series

U-series analyses were performed on La Celle indurated tufa samples by two different analytical techniques: alpha (α) spectrometry, HNHP, MNHN, Paris and TIMS, GEOTOP, UQAM, Montreal. If the α spectrometry analysis cannot allow an age calculation due to the limit of the method (>350 ka, SM3: Table S1), the TIMS analyses permit the dating of the La Celle samples, providing consistent ages of 387.5 (+88.8/48.1) ka and 388.4 (+51/-34) ka (Table 2 and SM3: Table S2).

3.2. Combined ESR/U-series and quartz-ESR

ESR/U series and ESR dating methods were also applied on La Celle samples, on quartz grains extracted from fluvial sediments of unit 16 located downslope beneath the tufa and on horse tooth from unit 7

Table 2
Geochronological dates from La Celle deposits (IPH-MNHN: Institut de Paléontologie Humaine, Muséum National d'Histoire Naturelle, Paris, France; Nottingham: Quaternary TL surveys Nottingham, UK; Geotop: Université du Québec à Montréal, Canada).

Profile	Unit	Material	Method	Result	Laboratory
S4	Upper part of the tufa	Indurated tufa	U-series α spectrometry	> 350 ka	HNHP - MNHN
S4	Upper part of the tufa	Indurated tufa	U-series TIMS	387.5 (+88.8/-48.1) ka	GEOTOP - UQAM
Main section	NB3: block layer	Indurated tufa	U-series TIMS	388.4 (+51/-34) ka	GEOTOP - UQAM
Main section	7: fine grey tufa	Heated flint	TL	$418\pm48~\mathrm{ka}$	Nottingham
Main section	7: fine grey tufa	Horse tooth	ESR/U-series	$424\pm38~\mathrm{ka}$	HNHP - MNHN
Main section	16: fluvial sand	Quartz grains	ESR	$452\pm60~\mathrm{ka}$	HNHP - MNHN

respectively (Bahain et al., 2010; Voinchet et al., 2015). The ESR age obtained on the fluvial sands (452 \pm 60 ka, MIS11/12, SM3: Table S3) is in agreement with the position of the deposit in the fluvial system. The ESR/U-series age of 424 \pm 38 ka (SM3: Table S4) is consistent with this result and with the U-series TIMS ages of indurated tufa samples.

3.3. Thermoluminescence

Heating tests were performed on a burnt flint from the archaeological set discovered in level 7 indicating that the artifact was heated to 350–400 °C in prehistoric times (Mercier *in* Limondin-Lozouet et al., 2010). Dating TL measurements on this sample at Nottingham (SM3: Table S5) provided an age of 418 \pm 48 ka very similar to the date obtained on the horse tooth from the same level.

3.4. Amino-acid geochronology

The intra-crystalline protein decomposition (IcPD) in several individual samples of *Bithynia tentaculata* opercula were analysed from four samples in La Celle (Table 3 and SM4). This aquatic gastropod is found primarily at the top of the fluvial series in unit 15, a fine silty deposit (Fig. 3: Profile S1, malacological samples 1; 2006.11; 2006.14), or immediately above at the base of the overlying tufa layer unit 11 (Fig. 3: Profile Cp1, malacological sample 1). According to stratigraphy and the molluscan succession, these samples correspond to the beginning of the interglacial period (Limondin-Lozouet et al., 2020).

All samples were processed using the methods of Penkman et al. (2008, 2011). In brief, individual *Bithynia* opercula were cleaned, powdered and bleached (to isolate the intra-crystalline fraction) and the free amino acids (FAA), and total hydrolysable amino acid (THAA) fractions analysed by reverse phase high pressure liquid chromatography (RP-HPLC) alongside standards and blanks. The concentration, composition and D/L values of aspartic acid/asparagine (Asx), glutamic acid/glutamine (Glx), serine (Ser), alanine (Ala) and valine (Val) as well as the [Ser]/[Ala] value were then assessed to provide an overall estimate of intra-crystalline protein decomposition (IcPD); as each amino acid racemises at different rates, they are useful over different time-scales. All of the samples from La Celle (Fig. 5) showed closed system behaviour (Preece and Penkman, 2005; Kosnik et al., 2008).

When compared to other sites in the same river basin and region, the La Celle samples have higher levels of IcPD than samples from the MIS 9 sample from Soucy (Chaussé et al., 2004; Antoine et al., 2007), and

Table 3AAR samples analysed from La Celle.

NEaar no.	Sample name	Horizon	Material	n
4575–8	FLC1Bto1-4	Profile S1, M1, unit 15	B. tentaculata opercula	4
9934–6	FLCM1Bto1-3	Profile Cp1, M1, unit 11	B. tentaculata opercula	3
9937–9	FLCM11Bto1- 3	Profile S1 2006, M11, unit 15	B. tentaculata opercula	3
9940–2	FLCM14Bto1-3	Profile S1 2006, M14, unit 15	B. tentaculata opercula	3

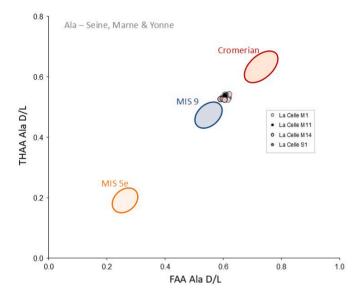


Fig. 5. FAA vs THAA D/L for alanine from the intra-crystalline fraction of individual *Bithynia* opercula from La Celle, compared to other sites from the Seine, Yonne and Marne terraces; the ellipses encompass the range of their D/L data.

lower levels than the likely Cromerian-aged material from Joinville-le-Pont and Bois de l'Epinette (Schlickum, 1974). Although the comparator dataset is relatively limited, this supports a correlation with MIS 11. The levels of IcPD are considerably higher than for British material of this age (Penkman et al., 2013), consistent with the higher mean annual temperatures and lower latitude (SM4).

The diverse suite of techniques and material dated at La Celle provides a mean age of ~400 ka and gives strong confidence to the attribution of the deposit to the MIS 11c interglacial. Geochronological dating is in good agreement with geological arguments related to the position of the site in the River Seine terrace system (Lautridou et al., 1999; Antoine et al., 2007), and in regard to the other main fluvial systems of the Paris Basin such as the Somme (Antoine et al., 2007, 2019) and the Yonne (Chaussé et al., 2004). They are also consistent with the occurrence of the "Lyrodiscus fauna", a malacological assemblage typical of MIS 11 tufas in northwestern Europe (Rousseau et al., 1992; Limondin-Lozouet, 2017), and reinforce the chronological value of this important biostratigraphic marker.

4. Palaeoenvironmental data

La Celle is already renowned for its remarkable palaeontological content, especially its molluscs and botanical imprints (Table 1).Molluscs are the sole fossil group to be present in the whole sedimentary sequence, as high calcareous content favoured both development of snail populations and subsequent shell preservation (Preece, 1991). Slow accumulation of tufa fossilized *in situ* communities providing the opportunity of a detailed reconstruction of local environments as well as

a general indication about the regional climate. There is thus a very rich mollusc record at La Celle, already extensively published (Limondin-Lozouet et al., 2006, 2010, 2020) and summarised below. The second important fossil group is represented by leaf and fruit impressions, recovered during quarry works in the 19th century. The revision of the collection curated at Sorbonne Université (Paris) has led to a publication (Jolly-Saad et al., 2007), and additional data are provided by samples from the Muséum National d'Histoire Naturelle (Paris) and the Musée de Nemours that have been recovered more recently (Table 1): those results are summarised thereafter. This palae-oenvironmental framework is enhanced by more discrete data from large mammal remains found in the archaeological level, and the study of ostracod assemblages recovered in the basal part of the formation.

4.1. Mollusca

At La Celle, malacological analyses were based on revision of old collections and new study of 120 samples distributed in five profiles which have yielded 42,074 individuals belonging to 103 taxa, 94 of which were assigned to species. The complete set of malacological data and associated analyses were presented in a previous paper (Limondin-Lozouet et al., 2020). The exceptional thickness of the La Celle formation allows observation of the spread and development of the so-called "Lyrodiscus fauna" (Fig. 6), recognized as a biochronological reference of MIS 11 tufas in Northwest Europe (Rousseau et al., 1992; Limondin-Lozouet and Antoine, 2006; Limondin-Lozouet, 2017). This assemblage is characteristic of a peculiar humid forest environment, hosting several taxa now extinct or out of their modern range originating



Fig. 6. Selected shells representative of the Lyrodiscus fauna from La Celle. 1 Retinella (Lyrodiscus) elephantium (Bourguignat, 1869)†, 2 Aegopis acieformis (Klein, 1846)†, 3 Aegopinella bourdieri Rousseau & Puissegur, 1989†, 4 Belgrandia marginata (Michaud, 1831), 5 Cochlostoma septemspirale (Razoumovsky, 1789), 6 Clausilia pumila (Pfeiffer, 1828), 7 Macrogastra ventricosa (Draparnaud, 1801), 8 Clausilia dubia Draparnaud, 1805, 9 Ruthenica filograna (Rossmässler, 1836), 10 Perforatella bidentata (Gmelin, 1791), 11 Spermodea lamellata (Jeffreys, 1830), 12 Hygromia limbata (Draparnaud, 1805), 13 Discus ruderatus (Hartmann, 1821), 14 Platyla polita (Hartmann, 1840), 15 Platyla similis (Reinhardt, 1880), 16 Bradybaena chouquetiana (Tournouer, 1877)†, 17 Ena montana (Draparnaud, 1801). Species 1, 2, 3 and 16 are extinct, the other taxa are now absent in the Paris Basin and most have current central or southern European ranges.

from central and southern Europe. The malacological succession of La Celle is divided into 4 biozones, illustrating the main stages of environmental change throughout the stratigraphy (Table 4; Fig. 7). The first zone corresponds to assemblages recovered in alluvial silty deposits underlying the tufa; they are composed of ecologically tolerant pioneer species reflecting a marshy grassland. Within the tufa deposit, the following two biozones (zones 2 and 3) are characterized by increasing diversity of shade-loving species, demonstrating the progressive development of forest cover until a maximum phase in the middle part of the deposit. During this episode, the shift between the two Discus species is particularly noteworthy (Table 4). Currently D. ruderatus has a boreo-alpine distribution and lives mainly in birch and coniferous woods, while D. rotundatus is widespread over temperate Europe but does not reach the northernmost areas of Scandinavia and lives in woods and shady places (Kerney et al., 1983; Welter-Schultès, 2012). In North-West European Quaternary successions, D. ruderatus characterizes the earliest stages of pioneer birch and coniferous forest environments and disappear or is outnumbered by D. rotundatus when deciduous woodlands develop (e.g. Preece and Day, 1994; Limondin-Lozouet and Preece, 2014; Granai, 2021). In the uppermost tufa level mollusc assemblages of zone 4 reveal a marked forest decline. In addition, a correspondence analysis was conducted classifying molluscan faunas within five ecological groups (ecozones) named A to E (Table 4; Fig. 7), based on the extent of vegetation cover and soil moisture conditions. The open wet land category (A) coincides with zone 1 characterized by a marshy grassland. The open forest landscapes (B) develop just after and are similar to those of the decreasing tree cover at the top of the series (zones 2a, top of 3b and 4); both episodes are characterized by the presence of hygrophilous snails. Groups C and D correspond to the increasing extension of the dense forest cover towards a closed canopy (zones 2b, 2c and 3a). Finally group E contains diversified forest assemblages but with less populated communities suggesting the thinning of the tree cover (zone 3b).

The synthetic diagram (Fig. 7) shows the occurrence of forest species that are the most characteristic element of environmental changes during interglacials. At La Celle this group is particularly rich and diverse and includes many allochthonous or extinct species. The high sedimentation rate that characterizes the La Celle tufa deposit allows a detailed reconstruction of the successive arrivals of these most ecologically sensitive species and to reconstruct the establishment of the

Lyrodiscus fauna. The order of appearance of these species depends on their ecological tolerance, with the most specialized arriving last, and follows a geographical logic corresponding to the distance from the refuge areas. The first forest colonizers are species with a current northern and western European distribution. Gradually, species of central European origin reach the area, while southern taxa only arrive during the maximum extension of the forest cover. This succession highlights two main recolonization routes of forest malacological species from the western (Iberian Peninsula) and central European (Carpathian) refuges while the Mediterranean area plays a secondary role (Limondin-Lozouet et al., 2020). The Lyrodiscus assemblage becomes established at the end of the forest expansion phase (zone 2c) and persists throughout the forest optimum (zone 3).

4.2. Flora

Recent investigations did not yield new discoveries of leaf imprints but an important collection was recovered at the end of the 19th century from the deposits in the eastern part of the quarry (Munier-Chalmas collection housed at the Sorbonne Université in Paris). The earliest lists of vegetation macrofossils from La Celle (Saporta de, 1874, 1876; Capdeville, 1959) have been updated after revision of the Sorbonne Université collection by Jolly-Saad et al. (2007) who discussed misinterpretations and proposed several new taxa identifications. In this last study 24 taxa have been described, to which should be added 5 species reported by the former authors whose determination is not doubtful, suggesting that their absence is due to losses when the collection was moved (Table 5). Since then a few samples from La Celle were identified in the Geological department of the Muséum National d'Histoire Naturelle in Paris, confirming the occurrence of Scolopendrium officinale and Pinus sp. cones in the deposit (Fig. 8). The flora is composed by a typical thermophilic calcicole group (Quercus, Viburnum lantana, Ligustrum vulgare, Evonymus europaeus, Cornus sp., Prunus sp.) and many taxa related to wet conditions (Acer pseudoplatanus, Fagus sylvatica, Salix group). Most noteworthy is the occurrence of several trees which, without human intervention, would be absent from the area today and which have a Mediterranean affinity (Ficus carica, Celtis australis, Buxus sempervirens). Compared to the current regional vegetation, the flora recorded at La Celle is much more diverse.

No precise stratigraphical allocation is attached to the leaf samples in

Table 4
Summary description of La Celle mollusc zones. Complete data set and analyses available in Limondin-Lozouet et al. (2020).

Units	Biozones	Molluscan assemblage	Interpretation	Ecozones	Interpretation
Sandy tufa: 1	4 forest decline	Dominant hygrophilous open-ground taxa (O. elegans, Succinella oblonga, T. hispidus, V. costata) strict forest snails disappear, most tolerant shade-demanding taxa (Aegopinella nitidula, V. crystallina, Arianta arbustorum) and wet woodland species (S. lamellata, O. navarricus, Perforatella bidentata)	Open wet with wooded spots	В	wet open soil and clear wood
Tufa: 7 to 2	3 forest b	Forest snails diversity maintained but numbers tend to decrease, expansion of some open environment taxa (<i>Pupilla muscorum</i> , <i>T. hispidus</i> , <i>V. costata</i>)	Dense forest and open spots	E	clearest forest
	a	Forest snails 50–70 %, maximum diversity, intolerant species (Ruthenica filograna, Pomatias elegans, Cochlostoma septemspirale, Sphyradium doliolum, Pagodulina pagodula, Aegopis acieformis, Platyla similis)	Closed canopy with full Lyrodiscus fauna	D	closed forest
Silt: 13 and Tufa: 12 to 8	2 forest c expansion	Forest snails up to 30-46 %, species of moist closed canopy (Retinella elephantium, Balea heydeni, Platyla polita, Fruticicola fruticum, Aegopinella pura, Helicodonta obvoluta, Oxychilus navarricus)	Development of humid forest with <i>Lyrodiscus</i> fauna	С	well drained soil, closed forest
	t	Forest snails more than 20 % of total landsnails, <i>Discus rotundatus</i> outnumbers <i>D. ruderatus</i> , diversification of Clausiliidae (<i>Clausilia dubia</i> , <i>C. pumila</i> , <i>Macrogastra ventricosa</i> , <i>Cochlodina laminata</i>)	Spread of deciduous forest		
	a	Appearance of tolerant forest snails <10 % of total land snails (<i>Discus ruderatus</i> , Vitrea crystallina, Clausilia bidentata, Ena montana, Spermodea lamellata, Zonitoides excavatus)	Spread of pioneer forest	В	wet open soil and clear wood
Basal silts: 15, 14	1 wet grassland	Tolerant species (Cochlicopa lubrica, Vallonia pulchella, Trochulus hispidus, Nesovitrea hammonis, Punctum pygmaeum, Euconulus fulvus) and hygrophilous snails (Oxyloma elegans, Zonitoides nitidus, Vertigo antivertigo) including some boreo-alpine taxa (Vertigo genesii, V. geyeri, Columella columella)	Marshy grassland, pioneer fauna with some glacial relics	A	open and wet environment

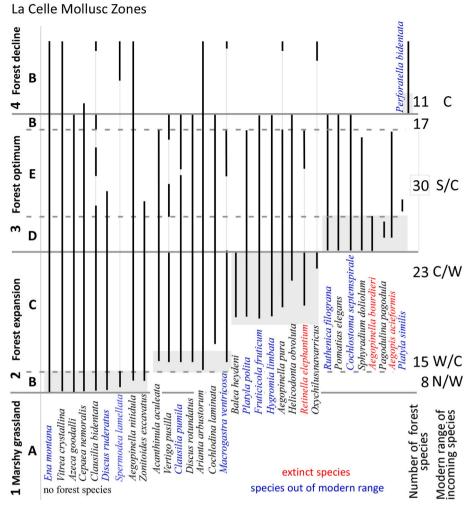


Fig. 7. Succession of forest land snails in the La Celle tufa formation. 1–4: biozones based on appearance/extinction and acme development of critical species. A–E: ecological zones reflecting categories of environment according to density of vegetation cover and soil humidity. For complete data set and analyses see Limondin-Lozouet et al. (2020). Modern European ranges: North (N), West (W), Centre (C), South (S).

the collection. However, indications from early studies (Munier-Chalmas, 1903; Jodot, 1907) show abundant remains of mesophilous taxa (*Pinus, Betula, Salix, Populus*) in the lowest part of the tufa, and the presence of most thermophilic trees (*Ficus, Buxus*) from the middle part of the formation and in the uppermost indurated beds. This stratigraphic distribution of plant taxa suggests the evolution of climatic parameters toward milder conditions from the base to the middle part of the tufa deposit.

4.3. Mammals

The earliest studies reported four taxa from the lower part of the tufa, Sus, Meles, Castor and Cervus (Tournouër, 1877). Excavations in 2006 yielded 57 bone fragments in unit 7 belonging to five taxa associated with Acheulean lithic industry (Limondin-Lozouet et al., 2006, 2010, 2015). Most abundant bone remains belong to Cervus elaphus and Equus sp. (Fig. 9, photographs 3 to 8). The horse is similar to caballine equids described by Eisenmann (1991) from British sites such as Hoxne, Clacton and Swanscombe, all three attributed to the Hoxnian (MIS 11) interglacial (Schreve et al., 2007; Auguste, 2009). Two species, Macaca sylvanus and Hippopotamus cf. amphibius, are represented by a single remain, a tooth and a metatarsal respectively (Limondin-Lozouet et al., 2006) (Fig. 9, photographs 1 and 2 respectively). The report of Macaca is the first in the north of France. In Europe, macaque fossils are never common but, according to modelling of their past distribution, La Celle

is in an area highly favourable to their survival (Elton and O'Regan, 2014). During MIS 11 in Northern Europe, the species is known in Great Britain at Swanscombe and Hoxne (Schreve, 2001; Ashton et al., 2008) and in Germany at Bilzingsleben II (Fischer et al., 1991). At La Celle, the discovery of thermophilous floral remains, including fossilized figs (Fig. 8G), in the middle part of the deposit is consistent with the occurrence of Macaca known as a consumer of fruits, flowers and leaves (Elton and O'Regan, 2014). The presence of Hippopotamus at La Celle is the first occurrence of the genus to be securely dated to the MIS 11 interglacial in northwestern Europe. In the same area Hippopotamus is recorded in MIS 7 deposits at Montières in the Somme valley and Moru in the Oise valley and thus appears as a regular component of Middle Pleistocene interglacial faunas (Auguste, 2009). The general morphology and dimensions of the metatarsal from La Celle are similar to those of the extant H. amphibius, but due to the lack of cranial material, the species identification remains tentative. According to Mecozzi et al. (2023), the first dispersal of H. amphibius in Europe took place from 560/460 ka, and if so, the specimen from La Celle could document the migration of the species towards northern latitude during MIS 11. For other authors, however, this hypothesis is still under debate and requires further data on securely identified cranial remains (Martino et al., 2024a; and b). Elsewhere in North West Europe H. amphibius is recorded only during the Late Pleistocene in Eemian deposits of the Rhine and Thames valleys (Kolfschoten van, 2000; Schreve et al., 2007). Its absence from the contemporary site of Caours in the Somme basin (Antoine et al., 2024) is probably related to the small size of the Scardon River, as the *Hippopotamus* semi-aquatic lifestyle requires significant bodies of water (Auguste, 2009; Martino et al., 2024a). A fifth taxa is represented by the lower canine of a small carnivore which is not sufficiently diagnostic to allow a taxonomic attribution. This mammal assemblage indicates a mixed environment including open areas and dense woodlands that developed under fully temperate climatic conditions.

4.4. Ostracods

Ostracod faunas were studied in detail from profile S2, present mainly in units 14 to 12 (Carbonel in Limondin-Lozouet et al., 2006). La Celle ostracod faunas are characteristic of cold waters, rich in calcium and of a relatively high energy stream environment becoming calmer at the top. Two trends can be observed. The first concerns the stygophilic species: Cavernocypris subterranea, which dominates at the bottom (units 14 and 13), is then gradually replaced by *Potamocypris zschokkei*, a more tolerant species in unit 12. The other trend relates to the Pseudocandona taxa, where P. compressa is replaced by P. albicans, the latter being less rheophilic than the former. This reinforces what was shown by the source species, i.e. a slightly more turbulent environment at the base of the succession than at the top. The distribution of the ostracod faunas is clearly correlated with the development of wet, even swampy environments, highlighted by the mollusc faunas in zones 1 and 2a (Table 4). They disappear when the forest biotopes become denser and the soils less waterlogged. At the base of the tufa formation, the species are cold stenotherms, due to their very close association with phreatic water.

5. Palaeoclimatic data

As continental carbonates precipitating at ambient temperature, calcareous tufas have supported geochemical analyses for palaeoclimatic reconstructions since the 1980s, particularly through oxygen and carbon stable isotopes (calcite δ^{18} O and δ^{13} C; see Andrews, 2006 and references within). Together with the Eemian tufa in Caours (Somme valley, France), La Celle has been the first Pleistocene site where such proxies were investigated. The strong relevance of $\delta^{18}O$ and δ¹³C in tufas as palaeoclimatic proxies during past interglacials, as already known for the Holocene, has been demonstrated thanks to comparisons with the robust, strictly parallel and independent palaeoenvironmental record provided by mollusc assemblages (Dabkowski et al., 2011). Variations in tufa δ^{18} O are mainly induced by changes in the mean annual atmospheric temperature while the $\delta^{13}C$ is a proxy of moisture conditions, especially related to the vegetation and soil type/abundance. At La Celle, complementary information on the rainfall amount was provided by the Mg/Ca and Sr/Ca ratios, showing a strong correlation with the δ^{13} C (Dabkowski et al., 2012).

The isotope records (Fig. 10), especially the $\delta^{18}O$, show stepped curves that reflect hiatuses at the boundaries between units 7 and 6, then between units 2 and 1. Two climatic features are noteworthy: i) the strong, warm and wet, optimum characterised by high $\delta^{18}O$ and low $\delta^{13}C$ values, and coinciding with U7, and ii) the cooler but very humid episode in the upper part of the tufa (U1, Fig. 10; Dabkowski et al., 2012). The lowest $\delta^{13}C$ values are recorded in unit 1, suggesting that the conditions were even wetter than during the optimum. Comparison with geochemical data from the Holocene tufa of Saint-Germain-le-Vasson

Table 5

Taxonomic inventory of La Celle flora specimens. Collections: Paris Sorbonne Université (PSU), Muséum National d'Histoire Naturelle, Paris (MNHN), Musée de la Préhistoire de Nemours (MPN). Species in grey have not been recognized in recent revisions.

Collections	PSU, MNHN, MPN				PSU	MNHN	MPN
Authors	SAPORTA 1876	MUNIER- CHALMAS 1903	JODOT 1907	CAPDEVILLE 1959	JOLLY-SAAD et al. 2007	JOLLY-SAAD 2021	JOLLY-SAAD 2022
Bryophytes	x	x	Х	х	х	х	
Hépathiques		x				х	
Osmunda regalis L.				х			
Phragmites sp.				х			
Monocotyledons unidentified				х		х	
Scolopendrium officinale Sw.	x		х	х		x	
Pinus austriaca Hôss		x	х	х			
Pinus sp.						x	
Acer pseudoplatanus L.	x	x	х	х	х		х
Acer sp.					Х	x	
Alnus glutinosa L.						×	
Betula pubescens Ehrh.				х		x	
Betula sp.		x	х		х		
Buxus sempervirens L.	x	x	х	х	Х	x	
Celtis australis L.					Х		
Cercis siliquastrum L.	x		х	х			
Clematis vitalba L.	x		х	х		х	
Cornus sp.					Х	x	
Corylus avellana L.	x		х	х	Х	×	
Euonymus latifolius Scop.	х		х	х	Х		
Euonymus europaeus L.					х	х	
Fagus sylvatica L.					Х	Х	
Ficus carica L.	х	х	х	х	х	Х	
Fraxinus excelsior L.	х		х	x			

Hedera helix L.								
Laurus nobilis L. X	Hedera helix L.	Х		Х	Х	Х	Х	
Laurus nobilis var. canariensis Webb. X X X X Parietaria officinalis L. aff. P. erecta X X X X Mert. & Koch X <td< td=""><td>Laurus canariensis Webb.</td><td></td><td></td><td>Х</td><td>Х</td><td></td><td></td><td></td></td<>	Laurus canariensis Webb.			Х	Х			
Ligustrum vulgare L.	Laurus nobilis L.		х	х				
Parietaria officinalis L. aff. P. erecta Mert. & Koch Mert.	Laurus nobilis var. canariensis Webb.	Х						
Mert. & Koch X X X Populus canescens Smith X X X Populus tremula L. X X X Prunus Insititia L. X X X Prunus malaheb L. X X X Prunus spinosa L. X X X Salix cf. S. caprea L. X X X Salix cf. S. caprea L. X X X X Salix cinerea L. X X X X X Salix cinerea L. X X X X X X Salix cinerea L. X X X X X	Ligustrum vulgare L.					х	Х	
Populus cf. P. nigra L. X X X Populus tremula L. X X X Prunus institita L. X X X Prunus malaheb L. X X X Prunus spinosa L. X X X Prunus spinosa L. X X X Prunus sp. X X X Salix cf. S. caprea L. X X X Salix f. S. caprea L. X X X Salix cf. S. caprea L. X X X Salix cf. S. caprea L. X X X Salix cf. S. caprea L. X X X Salix fragilist. X X X X Salix fragilist. X X X X					х			
Populus tremula L. X X Prunus institita L. X X Prunus malaheb L. X X Prunus padus L. X X Prunus spinosa L. X X Prunus sp. X X Quercus sp. X X Salix cf. S. caprea L. X X Salix f. S. caprea L. X X Salix increa L. X X Salix fragilist. X X Salix incana Schrank X X Salix incana Schrank X X Salix spens L. X X Salix sp. X X Salix sp. X X Sambucus ebulus L. X X Sambucus nigra L. X X Viburnum lantana L. X X Viburnum tinus L. X X Unidentified sp. 2 X X Apiaceae seeds X X	Populus canescens Smith	Х		х	Х			
Prunus malaheb L. X	Populus cf. P. nigra L.				Х	×		
Prunus malaheb L. X X X X Prunus padus L. X X X X Prunus spinosa L. X X X X Prunus sp. X X X X X Quercus sp. X	Populus tremula L.				Х		х	
Prunus padus L. X X Prunus spinosa L. X X Prunus sp. X X Quercus sp. X X Salix cf. S. caprea L. X X Salix cf. S. alba L. X X Salix cinerea L. X X X Salix fragilist. X X X Salix incana Schrank X X X Salix repens L. X X X Salix sp. X X X Sambucus ebulus L. X X X Sambucus nigra L. X X X Ulmus campestris L. X X X Viburnum lantana L. X X X Viburnum tinus L. X X X Unidentified sp. 1 X X Apiaceae seeds X X X	Prunus insititia L.				Х			
Prunus spinosa L. X X Prunus sp. X X Quercus sp. X X Salix cf. S. caprea L. X X Salix cinerea L. X X X Salix cinerea L. X X X X Salix fragilist. X X X X Salix incana Schrank X X X X Salix repens L. X X X X Salix sp. X X X X Sambucus ebulus L. X X X X Sambucus nigra L. X X X X Ulmus campestris L. X X X X Viburnum lantana L. X X X X Viburnum tinus L. X X X Apiaceae seeds X X X	Prunus malaheb L.	Х		х				
Prunus sp. X X Quercus sp. X X X Salix cf. S. caprea L. X X X X Salix cinerea L. X X X X X X Salix fragilist. X	Prunus padus L.				Х			
Quercus sp. X X X Salix cf. S. caprea L. X X X X Salix cf. S. alba L. X <	Prunus spinosa L.				Х	x		
Salix cf. S. caprea L. X X X Salix cf. S. alba L. X X X X Salix cinerea L. X X X X X Salix fragilist. X X X X X Salix incana Schrank X X X X X Salix repens L. X X X X X Salix sp. X X X X X Sambucus ebulus L. X X X X X Sambucus nigra L. X X X X X X Ulmus campestris L. X <td< td=""><td>Prunus sp.</td><td></td><td></td><td></td><td></td><td>x</td><td></td><td></td></td<>	Prunus sp.					x		
Salix cf. S. alba L. X	Quercus sp.					x	х	
Salix cinerea L. X	Salix cf. S. caprea L.					x	Х	x
Salix fragilisL. X	Salix cf. S. alba L.					x		
Salix incana Schrank X X X Salix repens L. X X X Salix cf. S. viminalis L. X X X Salix sp. X X X Sambucus ebulus L. X X X Sambucus nigra L. X X X Ulmus campestris L. X X X Viburnum lantana L. X X X Unidentified sp. 1 X X X Unidentified sp. 2 X X X Apiaceae seeds X X X	Salix cinerea L.	х		х	Х	x	х	x
Salix repens L. X Salix cf. S. viminalis L. X Salix sp. X Sambucus ebulus L. X Sambucus nigra L. X Ulmus campestris L. X Viburnum lantana L. X Viburnum tinus L. X Unidentified sp. 1 X Unidentified sp. 2 X Apiaceae seeds X	Salix fragilisL.	х		х	Х	x		
Salix cf. S. viminalis L. X X Salix sp. X X Sambucus ebulus L. X X Sambucus nigra L. X X Ulmus campestris L. X X Viburnum lantana L. X X Viburnum tinus L. X X Unidentified sp. 1 X X Unidentified sp. 2 X X Apiaceae seeds X X	Salix incana Schrank				Х	x	х	x
Salix sp. X X Sambucus ebulus L. X X Sambucus nigra L. X X Ulmus campestris L. X X Viburnum lantana L. X X Viburnum tinus L. X X Unidentified sp. 1 X X Unidentified sp. 2 X X Apiaceae seeds X X	Salix repens L.				х			
Sambucus ebulus L. X Y	Salix cf. S. viminalis L.					x		
Sambucus nigra L. X X Ulmus campestris L. X X Viburnum lantana L. X X Viburnum tinus L. X X Unidentified sp. 1 X X Unidentified sp. 2 X X Apiaceae seeds X X	Salix sp.		x				х	
Ulmus campestris L. X X Viburnum lantana L. X X Viburnum tinus L. X X Unidentified sp. 1 X X Unidentified sp. 2 X X Apiaceae seeds X X	Sambucus ebulus L.	Х		х				
Viburnum lantana L. X X Viburnum tinus L. X Image: Control of the control	Sambucus nigra L.				Х	×		
Viburnum tinus L. X Unidentified sp. 1 X Unidentified sp. 2 X Apiaceae seeds X	Ulmus campestris L.				Х			
Unidentified sp. 1 X Unidentified sp. 2 X Apiaceae seeds X	Viburnum lantana L.					Х	х	
Unidentified sp. 2 X Apiaceae seeds X	Viburnum tinus L.	х						
Apiaceae seeds X	Unidentified sp. 1						Х	
	Unidentified sp. 2						х	
Unidentified seed X	Apiaceae seeds						Х	
	Unidentified seed						х	

(Normandy, France) demonstrates that, in northern France, the MIS 11c was warmer and especially wetter than the present interglacial (Dabkowski and Limondin-Lozouet, 2022).

6. Data synthesis: depositional history and palaeoenvironmental reconstruction

The diverse and rich palaeontological, micromorphological and geochemical data has been combined to reconstruct the dynamics of tufa development and the related palaeoenvironmental and palaeoclimatic conditions. This can be summarised in six main steps (labelled A to F), leading to the stratigraphic succession observed at the location of the La Celle "Long Section", as shown in Fig. 10.

Step A – At La Celle, the earliest Quaternary sediments overlying the erosion step in the limestone bedrock are represented by a thick body (>1.5m in S1) of coarse fluvial gravels interbedded with sand lenses (unit 16). These deposits are typical of high-energy braided river systems deposited in periglacial environments. They are connected to full glacial periods and commonly form the main body of the alluvial terraces in northern France valleys (ie. Somme, Seine, Yonne, etc.; Antoine et al., 2000, 2007). They are overlaid by laminated greenish calcareous silt (unit 15) characterising flood plain overbank sediments. These deposits were formed during flooding events of a single channel meandering system as demonstrated for the bottom valley sequences

formed during the Weichselian-Holocene cycle. They represent early interglacial conditions in the climatically-driven system of the fluvial terraces in the Paris Basin (Antoine et al., 2007). The ESR dating on quartz from unit 16 (Fig. 3 and Table 2) is consistent with an assignment to the MIS 12/11 transition. Additionally, the deposition of the silty unit 15 in the Paleo-Seine floodplain is contemporaneous with the onset of tufa at La Celle (units 14 and 13). Tufa precipitation requires both that temperatures and especially humidity have increased (Pentecost, 1995, 2005; Dabkowski and Beaumont, 2024) and that springs have begun to supply carbonate-rich waters on the slope, as emphasized by the occurrence of cold stenotherm ostracod species related with phreatic waters (Fig. 11: Step A). Units 15 (fluvial silt) and 14 (tufa) both host malacological assemblages assigned to zone 1, i.e. to a pioneer fauna characteristic of a marshy grassland. The following tufa unit 13 records the spread of Discus ruderatus and the associated pioneer coniferous forest (mollusc zone 2a; Table 4). In early studies beds of Pinus cones are reported in the basal part of the tufa about 2 m above the fluvial gravel (Munier-Chalmas, 1903; Jodot, 1907). Parallel, unit 14 provides the earliest geochemical data on tufa calcite for the sequence. It suggests that climatic conditions were still relatively cool and dry compared to those recorded next (Fig. 10; Dabkowski et al., 2012). Unit 13 is not preserved at the sampling location for geochemistry (Fig. 3).

Step \underline{B} – In the field, the first tufa units 14 to 11 show strong similarities. The last three have been observed in thin section: the

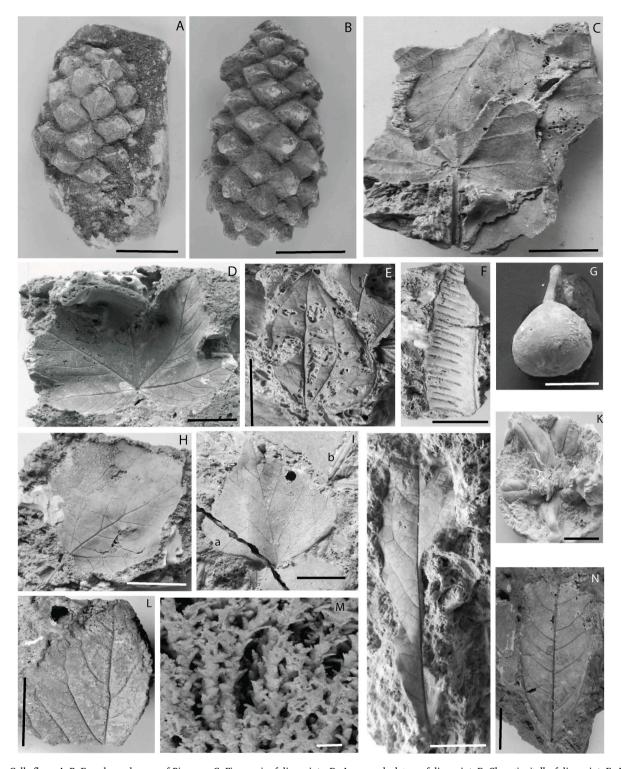


Fig. 8. La Celle flora: A–B: Female seed cones of *Pinus* sp.; C: *Ficus carica* foliar prints; D: *Acer pseudoplatanus* foliar print; E: *Clematis vitalba* foliar print; F: *Asplenium scolopendrium* foliar print with sporangia. G: *Ficus carica* fruit molding. H: *Populus tremula* foliar print; I: (a) *Betula pubescens*, (b) *Salix incana* foliar prints; J: unidentified taxa, leaf print; K: *Buxus sempervirens* stem molding with leaves and one flower or fruit in the central part of the molding; L: *Viburnum lantana* leaf print; M: Bryophytic facies; N: unidentified taxa. Scale bars: A-B, D, E, F, H, I, K, L: 2 cm; G, N: 1.5 cm; M: 1 cm. Photographs from Munier-Chalmas collection, Geological Department of the Muséum National d'Histoire Naturelle, Paris (MNHN).

predominance of indurated facies, mainly constructed by *Broutinella* sp./ *Plaziatella* sp. (Fig. 4B and B'), suggests that the water depth was between 0.5 and 30 cm while the fossil algae *Wallnerella fascinans* also indicates a lively flow (SM2; Freytet, 1998, 1997). The succession of *in situ* indurated facies and partly reworked fragments of incrusted vegetation corresponds to lateral variations of the same tufa environment

from upslope springs (Fig. 11: Step B). In unit 13, detrital elements including quartz, broken shells and bones, and fragments of limestone from the substratum are still present, which confirm that the slope was not completely stabilised when tufa started forming at La Celle (previous Step A). On the other hand, only few detrital elements are preserved in units 12 and 11, as vegetation developed. This is strongly consistent with

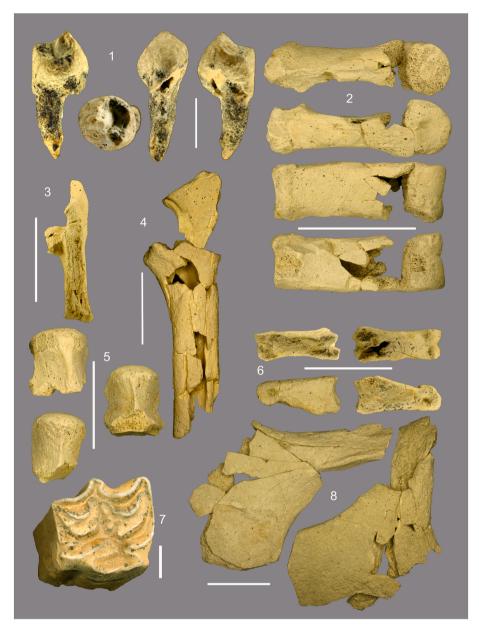


Fig. 9. La Celle mammal fauna from Unit 7. 1 Macaca sylvanus left upper fourth premolar, scale 5 mm; 2 Hippopotamus cf. incognitus left metatarsal IV, scale 5 cm; Cervus elaphus: 3 calcaneus, 4 right radio-ulna, 5 thoracic vertebrae, 6 proximal phalanx, scale 5 cm; Equus sp. type Hoxne: 7 tooth, scale 1 cm, 8 coxal, scale 5 cm.

the disappearance of ostracod faunas and the spread of *Discus rotundatus*, characteristic of deciduous forests in those units (mollusc zone 2b; Table 4), contemporaneously with the increase of humidity conditions as recorded by the δ^{13} C decrease in unit 12 (Fig. 10; Dabkowski et al., 2012).

The geometry and facies of the following units 10 to 8 are typical of barrage systems developed in moderate stream flow, downslope from the feeding spring (Fig. 11: Step B): unit 10, made of indurated tufa edifices built *in situ*, is associated with coarse deposits including large fragments of tufa and, locally, *in situ* bioconstructions within a sandygranular tufaceous sediment in units 9 and 8. No micromorphological observations are reported from these units on the "Long Section". Mollusc assemblages indicate a moist closed forest, characterised by the settlement of the *Lyrodiscus* fauna (mollusc zone 2c; Table 4). According to geochemical data, temperate and moist conditions are already settled at the top of unit 12, but increasing temperature and humidity (i.e. decreasing δ^{18} O and increasing δ^{13} C, respectively) are observed again in unit 8, leading to the climatic optimum recorded in the following unit 7

(Fig. 10).

Steps C & D - Level NB3 made of an accumulation of reworked tufa blocks testifies to a major episode of colluvial deposition caused by an event of opening up of the landscape (Fig. 11: Step C). This level also contains burnt fragments of flint and tufa. Unit 7 is not so coarse-grained (granular) but still contains burnt elements and ashes identified under the microscope, which give it its grey colour. The presence of detrital minerals from the slope and abundant shells and bone fragments (Fig. 4: F&F') testify to less extensive colluvial dynamics, reflecting the reestablishment of vegetation (Fig. 11: Step D). Springs were still active during the development of this unit, contributing to the precipitation of an abundant micritic matrix. As for the palaeoenvironmental and palaeoclimatic markers, they record optimal interglacial conditions. The maximal diversity and number of forest snails are reached in unit 7 (mollusc zone 3a; Table 4), while geochemical data indicate maximal mean annual temperatures (maximal δ^{18} O values) and wet conditions associated with particularly intense rainfall (Fig. 10; Dabkowski et al., 2012). The landscape opening at a time when it was not expected

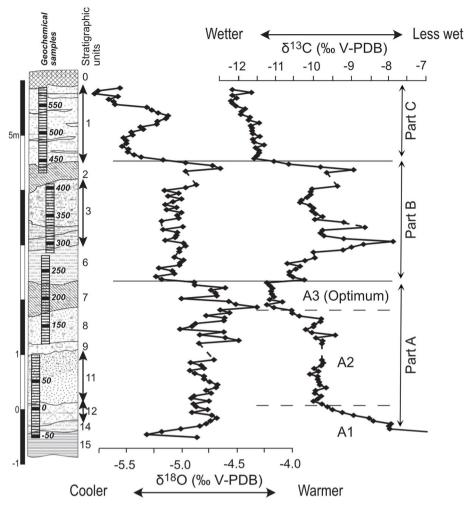


Fig. 10. Summarised tufa calcite isotopic data from 'La Celle-Sampling column G1' (modified after Dabkowski et al., 2012). The stratigraphical sequence is shown on the left with position of the samples (n = 113). The left curve is $\delta^{18}O$ and the right $\delta^{13}C$. In unit 7, the $\delta^{18}O$ maximum and strong $\delta^{13}C$ minimum correspond to the optimum.

(during the climatic optimum), together with the presence of burnt elements and ashes in block level NB3 and unit 7 show the occurrence of at least one fire event on the slope, already discussed by Limondin-Lozouet et al. (2010). The archaeological level excavated at the base of this unit is therefore contemporaneous with the climatic optimum of MIS 11c and the local fire episode (Fig. 11: Step C) as attested by the presence of a heated flint artifact that has been TL-dated. The remains of mammals found are also characteristic of particularly warm and humid conditions, especially those of *Macaca* and *Hippopotamus*. Early studies indicate beds of *Acer*, *Buxus* and *Ficus* imprints in the middle part of the deposit between 5 and 6 m above the fluvial gravels (Munier-Chalmas, 1903; Jodot, 1907). The wealth of information provided by the various disciplines is illustrated in a reconstruction of the Seine valley during this phase of the interglacial period (Fig. 12).

The upper part of unit 7 is eroded by a second block level (NB 2). However, it contains little or no burnt elements, and the overlying unit 6 is not as grey in colour as unit 7. Therefore, the possibility of a fire episode here cannot be supported by field observations. However, the transition between units 7 and 6 corresponds to a marked change in both the palaeoenvironmental and palaeoclimatic records, indicating a sedimentary hiatus. The number and diversity of forest mollusc shells decrease although the assemblage remains clearly dominated by forest taxa (mollusc zone 3b; Table 4). The stable isotope curves show abrupt, step-like variations at the transition between units 7 and 6 (Fig. 10) toward cooler and less humid conditions. This could be

contemporaneous with a regional episode of forest regression as discussed by Dabkowski et al. (2012) and in the following section 7.

Step E - The tufa formation resumes with the deposition of unit 6, which contains only a few detrital elements that form greyish layers, testifying to the re-establishment of vegetation. Further down the slope, the overlying unit 7 is locally eroded by oncolith channels (TOC; Fig. 3). Sub-unit 6' then consists of alternating granular and fine sandy layers, laminated, indicating moderate spring activity. Unit 3 is then dominated by sandy-granular deposits containing detrital material reworked from the slope and lenses of sandy tufa. These field observations are therefore indicative of a system of small channels running down the slope (Fig. 11: Step E). In thin sections (SM2), detrital elements (quartz, shell fragments) are abundant and bioconstructions are present in the form of highly fragmented pieces. Only small structures attributed to Sarfatigirella aquavivae and Wallnerella fascinans have been locally observed in situ. These two fossil taxa, especially S. aquavivae (Fig. 4E), indicate highly dynamic conditions and therefore active springs, in agreement with field observations.

However, geochemical data indicate reduced moisture conditions, particularly in Unit 3, which may be associated with a change in vegetation and soil type/abundance (Fig. 10). Indeed, the mollusc fauna in zone 3b is characterised by a diversified forest fauna, but with a reduced number of shells and peaks in the number of open ground species, suggesting a reduction in forest cover. In particular, a marked decrease in deciduous forest species is recorded at the end of this malacological

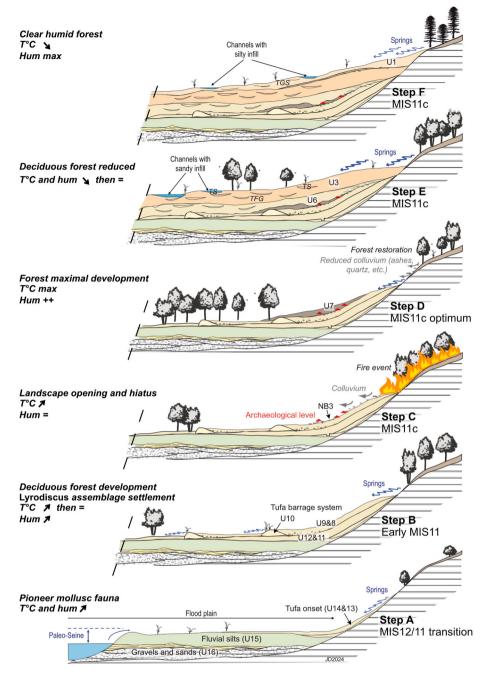


Fig. 11. Palaeoenvironmental reconstruction of the La Celle tufa edification.

zone in Unit 2 (Table 4). This is consistent with the cooler temperatures recorded by stable oxygen isotopes since the base of Unit 6 (Fig. 10), marking the end of the climatic optimum.

The transition between units 2 and 1 is marked by a new hiatus observed in the field and in abrupt changes in both the palae-oenvironmental and palaeoclimatic records (Table 4 and Fig. 10). Similarly to the earlier hiatus observed between Unit 7 and 6, it could be related to important regional environmental changes, discussed further by Dabkowski et al. (2012) and in the next section.

<u>Step F</u> – The smaller grain size of unit 1 indicates less-dynamic conditions than those of units 6, 3, and 2. Microscopic observations support this interpretation, as detrital elements are less abundant. However, the presence of the fossil species *Wallnerella fascinans* is still significant (Fig. 4C and C'). The other identified taxa (cyanobacteria *Broutinella* sp./*Plaziatella* sp.) indicate relatively deep water (SM2). A

laminated structure is observed both in thin sections and in the field, suggesting small, divagating channels with fine fill (Fig. 11: Step F). Unit 1 is contemporaneous with mollusc zone 4, which indicates a reduction in forest cover, although patches of wet woodland persist in an open, humid environment (Table 4). These data are consistent with the record of minimum temperatures and particularly humid conditions in Unit 1, as indicated by the lowest δ^{13} C and δ^{18} O values, respectively (Fig. 10).

Finally, the top of the tufa formation was probably eroded as soon as the next glaciation (MIS 10) began, as the next alluvial terrace had been incised, and then during the following climatic cycles, until it reached its present configuration.

7. Discussion

The long sequence of La Celle is the key-reference for aligning shorter



Fig. 12. Landscape reconstruction at La Celle during the interglacial optimum. Drawing B. Clarys.

regional malacological series with a similar assemblage into the environmental dynamics of the MIS 11 interglacial, as it is a unique record of the emergence, development and disappearance of the *Lyrodiscus* fauna. Comparison of malacological data from Northwestern European MIS 11 tufas with the La Celle succession demonstrates that other shorter sequences from England and France (Fig. 1) yield faunas matching those of La Celle zones 2c and 3, indicating the maximum extension of the forest cover and corresponding to the appearance and development of the *Lyrodiscus* assemblage (Limondin-Lozouet et al., 2020). Dating from Saint Pierre lès Elbeuf (Cliquet et al., 2009; Voinchet et al., 2015), Vernon (Lécolle et al., 1990), Saint-Acheul (Limondin-Lozouet and Antoine, 2006) and Beeches Pit (Preece et al., 2007; Voinchet et al.; 2015) are consistent with those of La Celle and strengthen the correlation of the *Lyrodiscus* fauna occurrence with MIS 11c.

La Celle is thus the longest MIS 11c tufa sequence preserved until now in North-West Europe and the only one showing the complete development of mollusc faunas reflecting expansion of forest biotopes. Vegetation reconstruction inferred from malacological data is corroborated by numerous leaf imprint occurrences and reinforced by the presence of thermophiles mammal species. Moreover, these palaeontological datasets are closely linked to geochemical analyses providing a reliable framework of associated climatic conditions and the reconstructed environmental succession. The La Celle results are a model for regional sequences and can be compared to other long records at a wider European scale.

8. The MIS 11 interglacial palaeoenvironmental dynamics and climatic variability ${\bf r}$

The La Celle data can be compared to other regional MIS 11c pollen records from Marks Tey in Great Britain (Turner, 1970), Dethlingen in Germany (Koutsodendris et al., 2010) and Praclaux in South-eastern France (Reille et al., 2000) (Fig. 13). The first biostratigraphic zone at La Celle is characterized by a pioneer fauna of open wet ground that is very similar in composition to the earliest Lateglacial Weichselian assemblages recovered in the area (Limondin-Lozouet, 2011) and corresponding in palynological records to an interstadial vegetation cover with Salix, Betula and Pinus (Antoine et al., 2000; Pastre et al., 2003). In the following zone 2a, forest snails appear and particularly Discus ruderatus, a species emblematic of pioneer coniferous forests. This succession can be compared with the pre-temperate phase (zone Ho I) at Marks Tey and zones 1 and 2 at Praclaux, both palynological records showing a boreal forest dominated by Pinus, Betula evolving to a temperate forest with open areas at Praclaux. Moreover, early studies

undertaken at La Celle report the presence of abundant cones of *Pinus* in the basal tufa layers (Limondin-Lozouet et al., 2010) that may correspond to this earliest phase of forest development.

Subsequently *Discus rotundatus* appears and outnumbers *D. ruderatus* (Fig. 7 and Table 4) This Discus succession has been identified as a classical marker of the spread of deciduous forest in interglacial successions of Northwestern Europe (Preece and Day, 1994; Preece and Bridgland, 1999; Meyrick, 2001; Limondin-Lozouet and Preece, 2014). The important increase of forest species including those forming the Lyrodiscus assemblage indicates the development of the forest cover until a closed canopy. This succession from zones 2b to 3a at La Celle correlates with an isotopic record showing increasing humidity and temperature ending in an optimum phase (Fig. 13: Part A). That stage can be compared with the early temperate and mesocratic phases at Mark Teys and Dethlingen and with zones 3 to 5 at Praclaux. All palynological successions indicate the development of temperate forest and increasing humidity marked by the occurrence of Taxus. Sustained mild climate is highlighted at Praclaux while zone VII at Dethlingen corresponds to the maximum occurrence of forest temperate taxa. Indurated tufa beds yielding imprint leaves of thermophilic taxa Buxus and Ficus, were observed in the middle part of La Celle tufa (Limondin-Lozouet et al., 2010).

During most of zone 3b at La Celle, the diversity of forest snail species is persistent, but their individual occurrences are discontinuous and the abundance of their populations is decreasing. At the top of zone 3b most of the species composing the Lyrodiscus fauna vanish. This distribution suggests progressive openings of the forest cover. Isotopic data indicate less temperate conditions and unstable humidity with dry episodes which correspond to punctual development of open ground snails (Pupilla muscorum, Vallonia costata) (Limondin-Lozouet et al., 2020). This episode can be compared with the late temperate and oligocratic phases at Marks Tey and Dethlingen, which show a progressive decline in temperate forests, replaced by grassland communities. Similarly, zones 6 to 8 at Praclaux show a phase of temperate forest followed by a decrease of temperate taxa to the expanse of coniferous (Pinus, Picea) and cooler climatic conditions. In all pollen sequences, this last stage corresponding to cooler climatic conditions is characterised by the presence of Pterocarya.

The interglacial forest dynamics is marked by several disruptions. At Dethlingen two peaks of *Pinus* are registered, the most important occurs in the upper part of the mesocratic phase (zone VIII) and has been interpreted as a climatic oscillation named OHO (Older Holsteinian Oscillation) which is comparable to the Holocene 8.2 ka climatic event (Koutsodendris et al., 2012). The second *Pinus* peak (zone XI) occurs in

the middle of the oligocratic phase. These events are hardly visible in the Praclaux succession which is consistent with previous observations pointing to the absence of the OHO in European palaeoclimate records between 45° and 50° latitude North (Koutsodendris et al., 2012). In the Marks Tey succession the top part of the early temperate phase (zone Ho IIc) is affected by an episode of decline in some temperate trees and increasing herbaceous pollen associated to fire evidence revealed by abundant charcoal fragments (Turner, 1970). Later on, this event, named the NAP phase, has been correlated with an abrupt climatic oscillation recorded in the North Atlantic cores and compared to the OHO event in terms of their position in the vegetation history (Tye et al., 2016; Candy et al., 2021).

At La Celle three hiatuses occur during the forest expansion (Fig. 13). The first is recorded at the transition between zones 2 and 3 (i.e. at the base of the unit 7), where the forest reaches its maximum development and is related to a fire event evidenced by a colluvial deposit (level NB3), and the presence of charcoals, ashes as well as burn flint (Fig. 11: Step C). This event is in the same position as the NAP phase of Marks Tey within the vegetation dynamics (Fig. 13). A similar event was recorded at Hoxne and led to the suggestion that major fires may have affected the vegetation over a wide area of southern East Anglia (Turner, 1970). In this context, the La Celle data would allow this interpretation to be extended to the regions on the other side of the Channel, although further observations are mandatory to confirm this hypothesis. Because of the hiatus created by the fire event, the La Celle isotopic archives contain no evidence linking this event to a cold climate oscillation, as it has been argued for the Marks Tey NAP phase based on a correlation between the site's tephra and North Atlantic ice cores (Candy et al., 2021). The other hiatuses of La Celle are situated at the base and top of zone 3b. They have been tentatively linked to episodes of forest regression (Dabkowski et al., 2012). However, the local or regional impact of these events remains difficult to determine.

The top part of the La Celle succession (zone 4) is characterized by a dramatic impoverishment of the forest snail community. Remaining species in this category are the most ecologically tolerant together with a

few wet woodland species, both showing declining populations. Dominant snails during this episode are hygrophilous and open ground taxa (Table 4). These data are consistent with geochemical record indicating the coolest and wettest conditions of the sequence. This phase can be compared with post temperate and telocratic phases at Marks Tey and Dethlingen marked by the domination of boreal trees and the development of open grassland vegetation. At Praclaux the top zone 9 is characterized by a boreal forest and the increase in NAP communities.

To sum up, the palaeoenvironmental reconstruction deduced from the malacofauna of La Celle shows a regular development of forest habitats, with an optimal phase in the middle part of the deposit, followed by a gradual regression of wooded areas in the second part of the tufa formation and ending with the opening of the landscape in the upper level. It appears consistent with vegetation dynamics reconstructed from long continental pollen records supporting correlation of the La Celle interglacial with MIS 11c.

8.1. Chronological position of La Celle interglacial within MIS 11c

Peculiarity of duration, climatic parameters and rhythm of sea level rise of MIS 11c has been extensively exposed and discussed in recent years, providing a number of interpretations related to the impact of global parameters on the structure of this long interglacial and discussing the response and timing of continental biocenoses (e.g. Rousseau, 2003; Tzedakis et al., 2022). The scheme of terrestrial palaeoenvironments appears consistent in the southern part of Europe (Oliveira et al., 2016; Desprat et al., 2017; Kousis et al., 2018) but diverse variations are observed in the northernmost part of the continent producing a mosaic of regional responses during the first part of the interglacial (Tzedakis et al., 2022), and even suggestions of delayed growth of temperate forest at some locations north of 50° (Koutsodendris et al., 2010, 2012). In this context the chronological representativeness of the La Celle sequence that exhibits three hiatuses and is very probably eroded in its upper part has to be questioned. Multiple dates unambiguously place La Celle within the interval of MIS 11c as defined by the chronological frame of

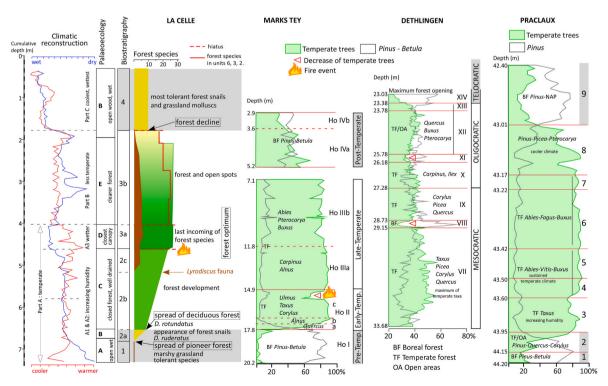


Fig. 13. La Celle schematic vegetational development based on molluscan data and climatic episodes inferred from the geochemical record of tufa calcite compared with pollen tree development at Marks Tey (Turner, 1970), Dethlingen (Koutsodendris et al., 2010) and Praclaux (Reille et al., 2000) during MIS 11c. Grey areas highlight earliest and latest parts of the interglacial.

SPECMAP (Imbrie et al., 1984: 423-395 ka BP), the benthic LR04 stack (Lisiecki and Raymo, 2005: 428-397 ka) and that proposed by Tzedakis et al. (2022: 426-396 ka), but the wide margins of error in the absolute dating (Table 2) make it impossible to use them to estimate the precise duration covered by the tufa deposit. However, the evolution of both biological and climatic proxies provide relevant information.

Dispersion of land snails might occasionally be due to animal transportation (Wada et al., 2011) but is mainly linked to the spread of vegetation on which gastropods depend (Cameron, 2016). Thus, the presence of the *Lyrodiscus* fauna on both sides of the Channel would have been hardly possible without a land connection. As it is now widely conceived that the Dover Straight was definitely opened during MIS 12 by a catastrophic overflow of the glacial lake confined in the southern North Sea (Gibbard, 1995; Gupta et al., 2007), the connexion between the malacological faunas would have been only possible during the earliest stages of the MIS 11 interglacial. This hypothesis is in accordance with the reconstructions of Termination V showing a slow rise of sea-level that took some 20 ka to reach its maximum allowing persistence of land bridges during the early part of MIS 11c (Rohling et al., 2010; Tzedakis et al., 2022).

The La Celle succession provides a unique record of the emergence, development and disappearance of the *Lyrodiscus* fauna and creates a framework to position shorter British sequences during the phase of maximum forest extension (Limondin-Lozouet et al., 2020), as supported by the interpretation of key site datasets (Kerney, 1959; Preece et al., 2007; Sherriff et al., 2021). This implies that the dispersion of this peculiar assemblage toward westernmost territories of south-east England must have begun during the first part of MIS 11c when low sea level allowed maintenance of a land connection. The basal part of La Celle tufa recording the emergence of the *Lyrodiscus* fauna was therefore most likely formed during the first part of the interglacial.

The episode of pronounced closed canopy and the thermal optimum are clearly synchronous according to consistent palaeontological and geochemical data (zone 3a and part A3, respectively; Fig. 13). Comparable malacological signatures and associated interglacial geochemical values have been reported in the UK from Beeches Pit (Preece et al., 2007) and Hitchin (Kerney, 1959; Sherriff et al., 2021). At both sites, the data have been interpreted in a similar way and correlated with the Ho III palynological zone of the Hoxnian succession and paralleled with the maximum temperature of the EPICA record (Sherriff et al., 2021). In the palynological succession of Marks Tey zone Ho III and associated isotopic values correspond to the late Hoxnian 'warmth' of the second part of the interglacial, posterior to the NAP cold event dated around 415 ka by tephrochronology, and compared with the late MIS 11c warmth of the Atlantic records (Tye et al., 2016; Candy et al., 2021). The detailed La Celle malacological model allows the UK occurrences of the Lyrodiscus fauna to be placed on the boundary of zones 3a-3b (Limondin-Lozouet et al., 2020). If all correlations are correct, it suggests that the second half of the La Celle sequence is to be placed in the second part of the interglacial.

Comparison with the pollen records indicates that the La Celle succession covers most of the MIS 11c. This interpretation is strengthened by the high level of biodiversity observed at the site which far exceeds that of any other interglacial series from the late Middle Pleistocene to the Holocene (Jolly-Saad et al., 2007; Limondin-Lozouet and Preece, 2014; Limondin-Lozouet et al., 2020). For example, at La Celle, the mollusc fauna is represented by 103 taxa, 94 of which are identified to the species level; by comparison, the Eemian tufa at Caours yields 80 taxa including 71 species, while the proportion for the Holocene tufa at Saint-Germain le Vasson are 61 taxa including 51 species identifications (Antoine et al., 2024; Limondin-Lozouet and Preece, 2004). At the European scale, molluscan diversity appears to have been markedly higher during the interglacial stages of the late Middle and Late Pleistocene than during the Holocene, with sites attributed to MIS 11 representing the richest assemblages (Limondin-Lozouet and Preece, 2014). Although climatic parameters are lacking for most continental sequences, studies

of tufas from northern France indicate that La Celle MIS 11 climate was wetter and warmer than the Holocene and MIS 5e (Dabkowski and Limondin-Lozouet, 2022). These conditions certainly had a decisive impact on the development of mollusc biodiversity and associated vegetation. Additional palaeoclimatic data from continental archives are therefore required to clarify the relationships between climatic regimes and biotic communities. It should also be noted that high biodiversity has been reported at several MIS 11c sites across Europe (Ložek, 2000; Rousseau, 2003; Preece et al., 2007; Mania, 2024) and interpreted by the authors as highlighting the exceptional duration of this interglacial period, which played a major role in the development of diverse fauna and flora assemblages expanding from central and southern European refugia.

9. Conclusion

Due to its high sedimentation rate, well preserved stratigraphic sequence, palaeontological richness, geochemical data and particularly well constrained chronology, the La Celle tufa is an outstanding sequence for reconstructing climatic and palaeoenvironmental conditions of MIS 11c in NW Europe.

Specifically, it provides a great diversity of land snails and the reference for the Lyrodiscus fauna development, allowing the position of other sites with this assemblage composition within the MIS 11c chronology. The unusual mixture of central and southern European elements has allowed discussion of migration routes and location of major refuges in the Carpathians and the Iberian Peninsula (Limondin-Lozouet et al., 2020). La Celle also records one of the richest macrofloral assemblages and the first occurrence of Hippopotamus in NW Europe (and the first Macaca in northern France) during MIS 11c. Additionally, it is the longest MIS 11c climatic record based on tufa geochemistry which has served as a reference site for comparing climatic intensity of past interglacials (Dabkowski and Limondin-Lozouet, 2022). Comparison of vegetation dynamics with long NW European pollen records is strongly consistent and demonstrates the contemporaneity of La Celle with almost the entire MIS 11c interglacial. Therefore, the "La Celle Interglacial" is proposed as a major reference for this period in Northwestern Europe.

Authors contributions

Nicole Limondin-Lozouet: Project coordination, Malacological analysis, General interpretation, Manuscript draft. Julie Dabkowski: Stratigraphy, micromorphology, Geochemistry analysis, General interpretation, Manuscript draft. Pierre Antoine: Stratigraphy, Geomorphology. Jean-Jacques Bahain: U-Th dating. Pierre Voinchet: ESR dating. Kirsty Penkman: Amino Acid analysis and interpretation. Dustin White: Amino Acid analysis and interpretation. Marie-Claude Jolly-Saad: leaf imprints identification and interpretation. Patrick Auguste: mammals identification. Bassam Ghaleb: U-Th TIMS dating.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

Research was funded by the CNRS (Project SITEP-ECLIPSE) and the ANR (Project Neandroots). We are indebted to Pierre Lozouet (Muséum National d'Histoire Naturelle de Paris) for photographs of shells and mammal remains. Field work and preservation of the site received support from local authorities Mairie de Vernou-La-Celle and CG Seine-et-Marne. Amino acid analyses were part of the EQuaTe project that has received funding from the European Research Council (ERC) under the

European Union's Horizon 2020 research and innovation programme (grant agreement No. 865222). Thanks to Sheila Taylor & Kirsty High for technical support in the lab. We thank the reviewers for their constructive comments.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.guascirev.2025.109667.

Data availability

For the purpose of open access, the authors have applied a Creative Commons Attribution (CC BY) licence to any Author Accepted Manuscript version arising from this submission. All amino acid data from this study will be made available through the NOAA repository upon publication: https://www.ncei.noaa.gov/pub/data/paleo/aar/.

References

- Andrews, J.E., 2006. Paleoclimatic records from stable isotopes in riverine tufas: synthesis and review. Earth Sci. Rev. 17, 85–104. https://doi.org/10.1016/j.earscirev.2005.08.002.
- Antoine, P., Fagnart, J.P., Limondin-Lozouet, N., Munaut, A.V., 2000. Le tardiglaciaire du bassin de la Somme: éléments de synthèse et nouvelles données. Quaternaire 11, 85–98. https://doi.org/10.3406/quate.2000.1658.
- Antoine, P., Limondin-Lozouet, N., 2004. Identification of MIS 11 interglacial tufa deposit in the Somme valley (France): new results from the Saint-Acheul fluvial sequence. Quaternaire 15, 41–52. https://doi.org/10.3406/quate.2004.1753.
- Antoine, P., Limondin-Lozouet, N., Chaussé, C., Lautridou, J.P., Pastre, J.F., Auguste, P., Bahain, J.J., Falguères, C., Galehb, B., 2007. Pleistocene fluvial terraces from northern France (Seine, Yonne, Somme): synthesis, and new results from interglacial deposits. Quat. Sci. Rev. 26, 2701–2723. https://doi.org/10.1016/j.guascirev.2006.01.036.
- Antoine, P., Limondin-Lozouet, N., Dabkowski, J., Bahain, J.J., Galehb, B., Reyss, J.L., Auguste, P., Sévêque, N., Jamet, G., Jolly-Saad, M.C., Gauthier, A., Lebreton, L., Locht, J.L., 2024. Last interglacial in Western Europe: 20 years of multidisciplinary research on the Eemian (MIS 5e) calcareous tufa sequence at Caours (Somme basin, France) a review. Boreas 53, 297–346. https://doi.org/10.1111/bor.12654.
- Antoine, P., Moncel, M.-H., Locht, J.-L., Bahain, J.J., Voinchet, P., Hérisson, D., Hurel, A., 2019. The earliest record of Acheulean Human occupation from Northern Europe and the rediscovery of the Moulin Quignon site. Nat. Sci. Rep 9, 13091. https://www.nature.com/articles/s41598-019-49400-w.
- Ashton, N., Lewis, S.G., Parfitt, S.A., Penkman, K.E.H., Coope, G.R., 2008. New evidence for complex climate change in MIS 11 from Hoxne, Suffolk, UK. Quat. Sci. Rev. 27, 652–668. https://doi.org/10.1016/j.quascirev.2008.01.003.
- Auguste, P., 2009. Evolution des peuplements mammaliens en Europe du Nord-Ouest durant le Pléistocène moyen et supérieur. Le cas de la France septentrionale. Quaternaire 20, 527–550. https://doi.org/10.4000/quaternaire.5361.
- Bahain, J.J., Falguères, C., Dolo, J.M., Antoine, P., Auguste, P., Limondin-Lozouet, N., Locht, J.L., Tuffreau, A., Tissoux, H., Farkh, S., 2010. ESR/U-series dating of teeth recovered from well-stratigraphically age-controlled sequences from Northern France. Quat. Geochronol. 5, 371–375. https://doi.org/10.1016/j.quageo.2009.02.007.
- Bahain, J.J., Farkh, S., Falguères, C., Shao, Q., Voinchet, P., Ghaleb, B., Hérisson, D., Locht, J.L., Limondin-Lozouet, N., Auguste, P., Gauthier, A., Dabkowski, J., Deschodt, L., Antoine, P., 2022. ESR/U-series dating Eemian human occupations of Northern France. Quat. Geochronol. 71, 101305. https://doi.org/10.1016/j.quageo.2022.101305.
- Bourdier, F., 1961. Sur l'âge des tufs de la Celle-sur-Seine. Bull. Assoc. Nat. Vallee Loing Massif Fontainebleau 37, 42–43.
- Bourdier, F., 1969. Etude comparée des dépôts quaternaires des bassins de la Seine et de la Somme. Bull. Inf. Geol. Bassin Paris 21, 169–231.
- Cameron, R., 2016. Slugs and Snails. William Collins, Baydon.
- Candy, I., Tye, G.J., Coxon, P., Hardiman, M., Matthews, I., Palmer, A., 2021. A tephrabased correlation of marine and terrestrial records of MIS 11c from Britain and the North Atlantic. J. Quat. Sci. 36, 1149–1161. https://doi.org/10.1002/jqs.3367.
- Capdeville, J., 1959. Résumé: etude paléobotanique du tuf de la Celle-sous-Moret (Seineet-Marne). Bulletin de l'Association des Naturalistes de la vallée du Loing 35 (55–60), 116–117, 75-76; 97-99.
- Capezzuoli, E., Gandin, A., Pedley, M., 2014. Decoding tufa and travertin (fresh water carbonates) in the sedimentary record: the state of the art. Sedimentology 61, 1–21. https://doi.org/10.1111/sed.12075.
- Chaussé, C., Voinchet, P., Bahain, J.J., Connet, N., Lhomme, V., Limondin-Lozouet, N., 2004. Middle and upper Pleistocene evolution of the river Yonne valley (France). First results. Quaternaire 15, 53–64. https://doi.org/10.3406/quate.2004.1754.
- Cliquet, D., Lautridou, J.P., Antoine, P., Lamothe, M., Leroyer, M., Limondin-Lozouet, N., Mercier, N., 2009. Les quatre loess anciens de Saint-Pierre-lès-Elbeuf (Normandie, France): nouvelles données archéologiques, géochronologiques et paléontologiques. Quaternaire 20, 321–343. https://doi.org/10.4000/quaternaire.5234.

- Collin, E., Reynier, P., de Mortillet, A., 1895. Découverte de silex taillés dans les tufs de la Celle-sous-Moret. Revue Mensuelle de l'Ecole d'Anthropologie 5, 318–322.
- Dabkowski, J., 2014. High potential of calcareous tufas for integrative multidisciplinary studies and prospects for archaeology in Europe. J. Archaeol. Sci. 52, 72–83. https://doi.org/10.1016/j.jas.2014.07.013.
- Dabkowski, J., Limondin-Lozouet, N., Antoine, P., Marca-Bell, A., Andrews, J., 2011.

 Enregistrement des variations climatiques au cours des interglaciaires d'après l'étude des isotopes stables de la calcite de tufs calcaires pléistocènes du nord de la France: exemple des séquences de Caours (SIM 5e; Somme) et de La Celle-sur-Seine (SIM 11; Seine-et-Marne). Quaternaire 22, 275–283. https://doi.org/10.4000/quaternaire.6010.
- Dabkowski, J., Limondin-Lozouet, N., Antoine, P., Andrews, J., Marca-Bell, A., 2012. Climatic variations in MIS 11 recorded by stable isotopes and trace elements in a French tufa (La Celle, Seine valley). J. Quat. Sci. 27, 790–799. https://doi.org/ 10.1002/jps.2567.
- Dabkowski, J., Limondin-Lozouet, N., 2022. Comparison of temperature and humidity during MIS 11 and MIS 5e interglacials with the Holocene using stable isotopes in tufa deposits from Northern France. Quat. Res. 107, 147–158. https://doi.org/ 10.1017/qua.2021.66.
- Dabkowski, J., Beaumont, L., 2024. Rise and decline of Holocene tufas across Europe: exploring east/west and north/south similarities and differences in the climatic and anthropogenic impacts on their development. J. Quat. Sci. 39, 960–971. https://doi.org/10.1002/jgs.3637.
- Desprat, S., Oliveira, D., Naughton, F., Sanchez Goñi, M.F., 2017. L'étude du pollen des séquences sédimentaires marines pour la compréhension du climat : l'exemple des périodes chaudes passées. Quaternaire 28, 259–269. https://doi.org/10.4000/ quaternaire.8102.
- Eisenmann, V., 1991. Les chevaux quaternaires européens (Mammalia, Perissodactyla). Taille, typologie, biostratigraphie et taxonomie. Geobios 24, 747–759.
- Elton, S., O'Regan, H.J., 2014. Macaques at the margins: the biogeography and extinction of *Macaca sylvanus* in Europe. Quat. Sci. Rev. 96, 117–130. https://doi. org/10.1016/j.quascirev.2014.04.025.
- Fischer, K., Guenther, E.W., Heinrich, W.D., Mania, D., Musil, R., Nötzold, T., 1991. Bilzingsleben IV. *Homo Erectus* Seine Kultur Und Seine Umwet, 44. Veröffenlichungen Lan-desmuseum für Vorgeschichte Halle, Berlin.
- Freytet, P., 1997. Non marine Permian to Holocene algae from France and adjacent country. Part 1. Annales de Paléontologie (Vert-Invert) 83, 289–332.
- Freytet, P., 1998. Non marine Permian to Holocene algae from France and adjacent country. Part 2. Annales de Paléontologie (Vert-Invert) 84, 3–51.
- Gibbard, P.L., 1995. The formation of the Strait of Dover. Geological Society 96, 15–26. https://doi.org/10.1144/GSL.SP.1995.096.01.03. London, Special Publications.
- Granai, S., 2021. Récentes investigations malacologiques holocènes en Champagne (France): repères malacostratigraphiques, remarques biogéographiques et anthropisation des versants. Quaternaire 32, 11–27. https://doi.org/10.4000/ quaternaire.14999.
- Granai, S., Wackenheim, Q., 2022. La datation radiocarbone sur coquilles de mollusques continentaux: quelles limites et quels usages. In: Lachenal, T., Marcigny, C., Milcent, P.Y., Mordant, C., Peake, R., Talon, M. (Eds.), Mesurer Le Temps De L'Âge Du Bronze. Actes De La Journée Thématique De L'Aprab, 6 Mars 2020, pp. 21–33. Gupta, S., Collier, J.S., Palmer-Felgate, A., Potter, G., 2007. Catastrophic flooding origin
- Gupta, S., Collier, J.S., Palmer-Felgate, A., Potter, G., 2007. Catastrophic flooding origi of shelf valley systems in the English Channel. Nature 448, 342–345. https://doi. org/10.1038/nature06018.
- Horvatinčić, N., Čalić, R., Geyh, M.A., 2000. Interglacial growth of tufa in Croatia. Quat. Res. 53, 185–1985. https://doi.org/10.1006/qres.1999.2094.
- Imbrie, J., Hays, J.D., Martinson, D.G., Mc Intyre, A., Mix, A.C., Morley, J.J., Pisias, N.G.,
 Prell, W.L., Shackleton, N.J., 1984. The orbital theory of Pleistocene climate: support from a revised chronology of the marine d18O record. In: Berger, A.L., Imbrie, J.,
 Hays, J., Kukla, G., Saltzman, B. (Eds.), Milankovitch and Climate, Part I. Reidel Publ. Company, Dordrecht, pp. 269–305.
- Jodot, P., 1907. Excursion aux carrières de tufs quaternaires de la Celle-sous-Moret (Seine-et-Marne). Bulletin de la Société des Naturalistes Parisiens 4, 1–12.
- Jolly-Saad, M.C., Dupéron, M., Dupéron, J., 2007. Nouvelle étude des empreintes foliaires des tufs holsteiniens de La Celle-sous-Moret (Seine-et-Marne). Palaeontographica B 276, 145–160.
- Kerney, M.P., 1959. An interglacial tufa near Hitchin, Hertfordshire. Proc. Geol. Assoc. 70, 322–337.
- Kerney, M.P., Cameron, R.A.D., Jungbluth, J.H., 1983. Die Landschnecken Nord-und Mitteleuropas. Paul Parey, Hamburg.
- Kleinen, T., Hildebrandt, S., Prange, M., Rachmayani, R., Müller, S., Bezrukova, E., Brovkin, V., Tarasov, P.E., 2014. The climate and vegetation of Marine Isotope Stage 11 – model results and proxy-based reconstructions at global and regional scale. Quat. Int. 348, 247–265. https://doi.org/10.1016/j.quaint.2013.12.028.
- Kolfschoten van, T., 2000. The Eemian mammal fauna of Central Europe. Neth. J. Geosci. 79, 269–281. https://doi.org/10.1017/S0016774600021752.
- Kosnik, M.A., Kaufman, D.S., Hua, Q., 2008. Identifying outliers and assessing the accuracy of amino acid racemization measurements for geochronology: I. Age calibration curves. Quat. Geochronol. 3, 308–317. https://doi.org/10.1016/j. quageo.2008.04.002.
- Kousis, I., Koutsodendris, A., Peyron, O., Leicher, N., Francke, A., Wagner, B., Giacco, B., Knipping, M., Pross, J., 2018. Centennial-scale vegetation dynamics and climate variability in SE Europe during Marine Isotope Stage 11 based on pollen record from Lake Ohrid. Quat. Sci. Rev. 190, 20–38. https://doi.org/10.1016/j. quascirev.2018.04.014.
- Koutsodendris, A., Müller, U.C., Pross, J., Brauer, A., Kotthoff, U., Lotter, A.F., 2010. Vegetation dynamics and climate variability during the Holsteinian interglacial

- based on a pollen record from Dethlingen (northern Germany). Quat. Sci. Rev. 29, 3298–3307. https://doi.org/10.1016/j.quascirev.2010.07.024.
- Koutsodendris, A., Pross, J., Müller, U.C., Brauer, A., Fletcher, W.J., Külh, N., Kirilova, E., Verhagen, F.T.M., Lücke, A., Lotter, A.F., 2012. A short-term climate oscillation during the Holsteinian interglacial (MIS 11c): an analogy to the 8.2 ka climatic event? Global Planet. Change 92–93, 224–235. https://doi.org/10.1016/j.gloplacha.2012.05.011.
- Lautridou, J.P., Auffret, J.P., Baltzer, A., Clet, M., Lécolle, F., Lefebvre, D., Lericolais, G., Roblin-Jouve, A., Balescu, S., Carpentier, G., Descombes, J.C., Occhietti, S., Rousseau, D.D., 1999. Le fleuve Seine, le fleuve Manche. Bull. Soc. Geol. Fr. 170, 545–558.
- Lécolle, F., Rousseau, D.-D., Lautridou, J.P., Puisségur, J.J., 1990. Le tuf de Vernon : nouvelles données (stratigraphie, paléoclimatologie, datations, corrélations). Bulletin du Centre de Géomorphologie du CNRS, Caen 38, 131–149.
- Limondin-Lozouet, N., 2011. Successions malacologiques à la charnière Glaciaire/ Interglaciaire: du modèle Tardiglaciaire-Holocène aux transitions du Pléistocène. Quaternaire 22, 211–220. https://doi.org/10.4000/quaternaire.5971.
- Limondin-Lozouet, N., 2017. "L'assemblage à *Lyrodiscus*", marqueur paléoenvironnemental et biostratigraphique des formations du SIM 11 en Europe du Nord-Ouest. Quaternaire 28, 231–238. https://doi.org/10.4000/quaternaire.8135.
- Limondin-Lozouet, N., Preece, R.C., 2004. Molluscan successions from the Holocene tufa of st-germain-le-vasson in Normandy, France. J. Quat. Sci. 19, 55–71. https://doi. org/10.1002/jqs.812.
- Limondin-Lozouet, N., Antoine, P., 2006. A new Lyrodiscus (Mollusca, Gastropoda) assemblage at Saint-Acheul (Somme Valley): reappraisal of Stage 11 malacofaunas from Northern France. Boreas 35, 622–633. https://doi.org/10.1111/j.1502-3885.2006.tb01168.x.
- Limondin-Lozouet, N., Preece, R.C., 2014. Quaternary perspectives on the diversity of land snail assemblages from NW Europe. J. Molluscan Stud. 80, 224–237. https:// doi.org/10.1093/mollus/eyu047.
- Limondin-Lozouet, N., Antoine, P., Auguste, P., Bahain, J.J., Carbonel, P., Chaussé, C., Connet, N., Dupéron, J., Dupéron, M., Falguères, C., Freytet, P., Ghaleb, B., Jolly-Saad, M.C., Lhomme, V., Lozouet, P., Mercier, N., Pastre, J.F., Voinchet, P., 2006. Le tuf calcaire de La Celle-sur-Seine (Seine et Marne): nouvelles données sur un site clé du stade 11 dans le Nord de la France. Quaternaire 17, 5–29. https://doi.org/10.4000/quaternaire.722.
- Limondin-Lozouet, N., Nicoud, E., Antoine, P., Auguste, P., Bahain, J.J., Dabkowski, J., Dupéron, J., Dupéron, M., Falguères, C., Ghaleb, B., Jolly-Saad, M.C., Mercier, N., 2010. Oldest evidence of Acheulean occupation in the Upper Seine valley (France) from an MIS 11 tufa at La Celle. Quat. Int. 223–224, 299–311. https://doi.org/10.1016/j.quaint.2009.10.013.
- Limondin-Lozouet, N., Antoine, P., Bahain, J.J., Cliquet, D., Coutard, S., Dabkowski, J., Ghaleb, B., Locht, J.L., Nicoud, E., Voinchet, P., 2015. Northwest European MIS 11 malacological successions: a framework for the timing of Acheulean settlements. J. Quat. Sci. 30, 702–712. https://doi.org/10.1002/jqs.2798.
- Limondin-Lozouet, N., Dabkowski, J., Antoine, P., 2020. Palaeoenvironmental dynamics of MIS 11 interglacial in northwestern Europe based on the malacological succession of La Celle (Seine Valley, France): relationship with glacial refugia and palaeobiodiversity. Palaeogeogr. Palaeoclimatol. Palaeoecol. 560, 110044. https:// doi.org/10.1016/j.nalaeo.2020.110044.
- Lisiecki, L.E., Raymo, M.E., 2005. A Pliocene-Pleistocene stack of 57 globally distributed benthic d18O records. Paleoceanography 20, PA1003. https://doi.org/10.1029/ 2004PA001071
- Ložek, V., 2000. Palaeoecology of Quaternary Mollusca. Antropozoikum 24, 35–39. Mania, D., 2024. Pleistozäne Molluskengesellschaften aus dem Saalegebiet und Harzvorland ihre Aussage zur Klima- und Umweltentwicklung. In: Landesamtes Für Denkmalpflege Und Archäologie Sachsen-Anhalt, 93. Landsmuseum für Vorgeschichte Band. Halle.
- Martino, R., Marra, F., Beccari, V., Ibanez Rios, M., Pandolfi, L., 2024a. Middle Pleistocene *Hippopotamus amphibius* (Mamma, Hippopotamidae) from southern Europe: implications for morphology, morphometry and biogeography. Quat. Sci. Rev. 331, 108613. https://doi.org/10.1016/j.guascirev.2024.108613.
- Martino, R., Marra, F., Rios, M., Pandolfi, L., 2024b. The Middle Pleistocene Hippopotamus from Malagrotta (Latium, Italy): new data and future perspectives. Quaternary 7, 13. https://doi.org/10.3390/quat7010013.
- Mecozzi, B., Iannucci, A., Mancini, M., Tentori, D., Cavasinni, C., Conti, J., Messina, M. Y., Sarra, A., Sardella, R., 2023. Reinforcing the idea of an early dispersal of *Hippopotamus amphibius* in Europe: restoration and multidisciplinary study of the skull from the Middle Pleistocene of Cava Montanari (Rome, central Italy). PLoS One 18, 11. https://doi.org/10.1371/journal.pone.0293405.
- Meyrick, R.A., 2001. The development of terrestrial mollusc faunas in the 'Rheinland region' (western Germany and Luxembourg) during the Lateglacial and Holocene. Quat. Sci. Rev. 20, 1667–1675. https://doi.org/10.1016/S0277-3791(01)00031-2.
- Munier-Chalmas, E., 1903. Notice Sur Les Travaux Scientifiques De M. Munier-Chalmas. Le Bigot. Lille.
- Oliveira, D., Desprat, S., Rodrigues, T., Naughton, F., Hodell, D., Trigo, R., Rufino, M., Lopes, C., Abrantes, F., Sanchez Goñi, M.F., 2016. The complexity of millennial-scale variability in southwestern Europe during MIS 11. Quat. Res. 86, 373–387. https:// doi.org/10.1016/j.yqres.2016.09.002.
- Ortiz, J.E., Torres, T., Delgado, A., Reyes, E., Díaz-Bautista, A., 2009. A review of the Tagus river tufa deposits (central Spain): age and palaeoenvironmental record. Quat. Sci. Rev. 28, 947–963. https://doi.org/10.1016/j.quascirev.2008.12.007.
- Past Interglacials Working Group of PAGES, 2016. Interglacials of the last 800,000 years. Rev. Geophys. 54, 162–219. https://doi.org/10.1002/2015RG000482.
- Pastre, J.F., Limondin-Lozouet, N., Leroyer, C., Ponel, P., Fontugne, M., 2003. River system evolution and environmental changes during the Lateglacial in the Paris

- Basin (France). Quat. Sci. Rev. 22, 2177–2188. https://doi.org/10.1016/S0277-3791(03)00147-1.
- Pazzaglia, F., Barchi, M.R., Buratti, N., Cherin, M., Pandolfi, L., Ricci, M., 2013.
 Pleistocene calcareous tufa from the Ellera basin (Umbria, central Italy) as a key for an integrated paleoenvironmental and tectonic reconstruction. Quat. Int. 292, 59–70. https://doi.org/10.1016/j.quaint.2012.11.020.
- Penkman, K.E.H., Kaufman, D.S., Maddy, D., Collins, M.J., 2008. Closed-system behaviour of the intra-crystalline fraction of amino acids in mollusc shells. Quat. Geochronol. 3, 2–25. https://doi.org/10.1016/j.quageo.2007.07.001.
- Penkman, K.E.H., Preece, R.C., Keen, D.H., Meijer, T., Parfitt, S.A., White, T.S., Collins, M.J., 2011. A chronological framework for the British Quaternary based on Bithynia opercula. Nature 476, 446–449. https://doi.org/10.1038/nature10305.
- Penkman, K.E.H., Preece, R.C., Bridgland, D.R., Keen, D.H., Meijer, T., Parfitt, S.A., White, T.S., Collins, M.J., 2013. An aminostratigraphy for the British Quaternary based on Bithynia opercula. Quat. Sci. Rev. 61, 111–134. https://doi.org/10.1016/j. quascirev.2012.10.046.
- Pentecost, A., 1991. A new and interesting site for the Calcite-encrusted desmid Oocardium stratum Naeg, the British Isles. Eur. J. Phycol 26, 297–301.
- Pentecost, A., 1995. The quaternary travertine deposits of Europe and Asia Minor. Quat. Sci. Rev. 14, 1005–1028. https://doi.org/10.1016/0277-3791(95)00101-8.
- Pentecost, A., 2005. Travertine. Springer-Verlag, Berlin Heidelberg.
- Pentecost, A., Riding, R., 1986. Calcification in Cyanobacteria. In: Leadbeater, B.S.C., Riding, R. (Eds.), Biomineralization in Lower Plants and Animals, Systematics Association Special, ume 30. Clarendon Press, Oxford, pp. 73–90.
- Preece, R.C., 1991. Mapping snails in time: the prospect of elucidating the historical biogeography of the European malacofauna. Proceedings of the Xth International Malacological Congress, Tübingen 1989, pp. 47–49.
- Preece, R.C., Day, S.P., 1994. Comparison of Post-glacial molluscan and vegetational successions from a radiocarbon-dated tufa sequence in Oxfordshire. J. Biogeogr. 21, 463–478. https://doi.org/10.2307/2845651.
- Preece, R.C., Bridgland, D.R., 1999. Holywell Coombe, folkestone: a 13, 000 year history of an English chalkland valley. Quat. Sci. Rev. 18, 1075–1125. https://doi.org/ 10.1016/S0277-3791(98)00066-3.
- Preece, R.C., Penkman, K.E.H., 2005. Molluscan assemblages and amino acid dating of the Lower Palaeolithic site at East Farm, Barnham, Suffolk. PGA (Proc. Geol. Assoc.) 116, 363–377. https://doi.org/10.1016/S0016-7878(05)80053-7.
- Preece, R.C., Parfitt, S.A., Bridgland, D.R., Lewis, S.G., Rowe, P.J., Atkinson, T.C., Candy, I., Debenham, N.C., Penkman, K.E.H., Rhodes, E.J., Schwennninger, J.L., Griffiths, H.I., Whittaker, J.E., Gleed-Owen, C., 2007. Terrestrial environments during MIS 11: evidence from the Palaeolithic site at West Stow, Suffolk, UK. Quat. Sci. Rev. 26, 1236–1300. https://doi.org/10.1016/j.guascirev.2006.11.016.
- Reille, M., de Beaulieu, J.L., Svobodová, H., Andrieu-Ponel, V., Goeury, C., 2000. Pollen analytical biostratigraphy of the last five climatic cycles from a long continental sequence from the Velay region (Massif Central, France). J. Quat. Sci. 15, 665–685. https://doi.org/10.1002/1099-1417(200010)15:7<665:AID-JOS560>3.3.CO:2-7.
- Rohling, E.J., Braun, K., Grant, K., Kucera, M., Roberts, A.P., Siddall, M., Trommer, G., 2010. Comparison between Holocene and Marine Isotope Stage -11 sea-level histories. Earth Planet Sci. Lett. 291, 97–105. https://doi.org/10.1016/j.epsl.2009.12.054.
- Rousseau, D.D., 1992. Is causal ecological biogeography a progressive research approach? Quat. Sci. Rev. 11, 593–601. https://doi.org/10.1016/0277-3791(92) 90016-2.
- Rousseau, D.D., Puisségur, J.J., Lécolle, F., 1992. West-European terrestrial molluscs assemblages of isotopic stage 11 (Middle Pleistocene): climatic implications. Palaeogeogr. Palaeoclimatol. Palaeoecol. 92, 15–29. https://doi.org/10.1016/0031-0182(92)90132-0.
- Rousseau, D.D., 2003. The continental record of stage 11: a review. In: Droxler, A.W., Poore, R.Z., Burckle, L.H. (Eds.), Earth's Climate Ans Orbital Eccentricity: the Marine Isotope Stage 11 Question, Geophysical Monograph Series, 137. American Geophysical Union, Washington, pp. 213–222.
- Saporta de, G., 1874. Sur l'existence constatée du figuier aux environs de Paris à l'époque quaternaire. Bulletin de la Société Géologique de France, série 3 2, 439–443.
- Saporta de, G., 1876. Sur le climat des environs de Paris à l'époque du diluvium gris, à propos de la découverte du laurier dans les tufs quaternaires de la Celle. Comptes-rendus de l'Association Française pour l'Avancement des Sciences Clermont-Ferrand 5, 640–654.
- Schlickum, W.R., 1974. Die Gattung Tanousia Servain. Arch. Molluskenkd. 104, 73-79.
- Schreve, D.C., 2001. Differentiation of the British late Middle Pleistocene interglacials: the evidence from mammalian biostratigraphy. Quat. Sci. Rev. 20 (16–17), 1693–1705. https://doi.org/10.1016/S0277-3791(01)00033-6.

 Schreve, D.C., Keen, D.H., Limondin-Lozouet, N., Auguste, P., Santisteban, J.I.,
- Schreve, D.C., Keen, D.H., Limondin-Lozouet, N., Auguste, P., Santisteban, J.I., Ubilla, M., Matoshko, A., Bridgland, D.R., Westaway, R., 2007. Progress in faunal correlation of late Cenozoic fluvial sequences 200-4: the report of the IGCP 449 Biostratigraphy subgroup. Quat. Sci. Rev. 26, 2970–2995. https://doi.org/10.1016/ i.quascirev.2007.07.021.
- Sherriff, J.E., Schreve, D.C., Candy, I., Palmer, A.P., Whie, T.S., 2021. Environments of the climatic optimum of MIS 11 in Britain: evidence from the tufa sequence at Hitchin, southeast England. J. Quat. Sci. 1–18. https://doi.org/10.1002/jqs.3303.
- Tournouër, R., 1874. Note sur les coquilles des tufs quaternaires de la Celle, près Moret (Seine-et-Marne). Bulletin de la Société Géologique de France, série 3 2, 443–452.
 Tournouër, R., 1877. Note complémentaire sur les tufs quaternaires de La Celle, près Moret (Seine-et-Marne). Bull. Soc. Geol. Fr. 646–671 série 3 t.5.
- Turner, C., 1970. The middle Pleistocene deposits at marks Tey, essex. Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci. 257 (817), 373–437.
- Tye, G.J., Sherriff, J., Candy, I., Coxon, P., Palmer, A., McClymont, E.L., Schreve, D.C., 2016. The δ^{18} O stratigraphy of the Hoxnian lacustrine sequence at Marks Tey, Essex,

- UK: implications for the climatic structure of MIS 11 in Britain. J. Quat. Sci. 31, 75-92. https://doi.org/10.1002/jqs.2840.
- Tzedakis, C.P., Hodell, D.A., Nehebass-Ahles, C., Mitsui, T., Wolff, E.W., 2022. Marine Isotope stage 11c: an unusual interglacial. Quat. Sci. Rev. 284, 107493. https://doi. org/10.1016/j.quascirev.2022.107493.
- Voinchet, P., Moreno, D., Bahain, J.J., Tissoux, H., Tombret, O., Falguères, C., Moncel, M.H., Schreve, D., Candy, I., Antoine, P., Ashton, N., Beamish, M., Cliquet, D., Despriée, J., Lewis, S., Limondin-Lozouet, N., Locht, J.L., Parfitt, S.,
- Pope, M., 2015. New chronological data (ESR and ESR/U-series) for the earliest Acheulian sites of north-western Europe. J. Quat. Sci. 30, 610–622. https://doi.org/10.1002/jqs.2814.
- Wada, S., Kawakami, K., Chiba, S., 2011. Snails can survive passage through a bird's digestive system. J. Biogeogr. 39, 69–73. https://doi.org/10.1111/j.1365-2699.2011.02559.x.
- Welter-Schultès, F.W., 2012. European Non-marine Molluscs, a Guide for Species Identification. Planet Poster Editions, Göttingen.