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Journal Article**Author(s):**

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Publication date:

2024-12-01

Permanent link:

<https://doi.org/10.3929/ethz-b-000696311>

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Originally published in:

Palaeogeography, Palaeoclimatology, Palaeoecology 655, <https://doi.org/10.1016/j.palaeo.2024.112504>



A Bajocian event of global coral reef growth: Record from northern Switzerland

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ARTICLE INFO

Editor: Professor L Angiolini

Keywords:

Coral reef
Jurassic
Switzerland
Mesophotic
Palynology
Palaeoecology

ABSTRACT

Following the extinction event at the Triassic – Jurassic boundary and during the Pliensbachian – Toarcian events, coral reef builders were severely affected, and the number of reef domains during the early Middle Jurassic was at an all-time low. However, new and updated data seem to show that corals were more widespread than previously thought, particularly during the Bajocian (170–168 Ma), but biostratigraphic markers are lacking to constrain the precise timing of reef evolution of this interval. A recently discovered 40 m-thick carbonate unit in northern Switzerland, on the northern Tethys margin, documents this rapid growth. Two cores from this unit display a reef with a high number of specimen but a low coral diversity, dated as Bajocian, which likely grew at a considerable water depth (upper limit of the mesophotic zone or 20–30 m). Additionally, it developed on top of clay mineral-rich accumulation characterised by low relief. Twelve different coral genera were identified, with a strong predominance of *Periseris*, *Isastrea*, *Thamnasteria* and *Dendraraea*. In the absence of other biostratigraphic markers, palynomorphs were used to provide accurate dating, which shows that palynology is a powerful tool for dating reef deposits. The results show reef growth during the early Bajocian, in the Sauzei and Humphriesianum ammonite zones, based on the palynological data, yielding similar ages to other Bajocian reef localities in the Eastern Paris Basin in France and Luxembourg dated simultaneously. These results indicate that the Middle Jurassic and more specifically the last two ammonite zones of the early Bajocian were periods suitable for coral reef builders, and that global regrowth of coral reefs occurred more rapidly than expected. A new Bajocian reef distribution is presented, showing no reefs at latitudes below 15°. This distribution pattern is probably due to the fact that water temperature was too elevated (> 25 °C) towards the equator for corals, which prevented reef growth. This would tend to favour a scenario in which the global climate, in particular temperature, is a determining factor for coral reef growth.

1. Introduction

On a global scale, the Middle Jurassic (Aalenian, Bajocian, Bathonian, Callovian) is currently considered to be unfavourable for coral reef growth and to a lesser extent, to level-bottom coral assemblages. At that time, most reef builders and corals in particular were still recovering from the devastating climate-induced crisis of the Early Jurassic (Pliensbachian, Toarcian) (Krencker et al., 2020). Global warming, a global perturbation of the carbon cycle and increased continental

weathering produced one of the most intense extinction events for corals (Vasseur et al., 2021). Indeed, the number of reefs established in the early Middle Jurassic is one of the lowest recorded during the entire Mesozoic (Kiessling et al., 1999; Leinfelder et al., 2002). In comparison, the Late Jurassic (Oxfordian–Kimmeridgian) is much better known for having a higher number of reefs (Kiessling et al., 1999, 2009). Based on these observations, it seemed clear that the Middle Jurassic was not yet an opportune time for coral reef development, probably due to profound and persistent changes in the environment and ecosystem structure.

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<https://doi.org/10.1016/j.palaeo.2024.112504>

Received 27 December 2023; Received in revised form 28 August 2024; Accepted 10 September 2024

Available online 13 September 2024

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However, based on literature studies and a modern re-evaluation of previously dated reefs, it is possible to show a significantly higher number of Bajocian sites. The outcome can be attributed to the application of advanced dating techniques and a fresh assessment of reef ecology conducted at different periods, such as ongoing research by Degiacomi A. (personal communication) at the Gisliflue in the Jura Mountains or by Lathuilière et al. (2023). These new assessments have extended the geographical area covered by reefs during the Bajocian. The differentiation of Bajocian and Bathonian reefs and the differentiation of reefs built by other organisms (bivalves, sponges) has also improved the assessment of early Middle Jurassic reef systems. Several coral genera are not recorded before the Bathonian: *Dendrostroma*, *Bracthelia*, *Hexaflos*, *Ceratocoenia*, *Polymorphostrea*, *Kobyia*, *Semeloseria*, *Bathycoenia*, *Ovalostrea*, *Polystylidium*, *Solenocoenia*, *Keriophyllia*, *Sakalavastraea* (for a detailed compendium see Lathuilière and Huang (in press)). The coral assemblages of the Bajocian and Bathonian also differ significantly. A better documented site is that in Kachchh in India where *Microsolena* and *Montivaltia* are abundant (Fürsich et al., 1994). Other sites are not so well documented by quantitative approaches but provide comparable approximations (e.g. Alloiteau, 1958 for Madagascar, Beauvais, 1972, Lathuilière and Michel, 2019 for France, Negus and Beauvais, 1975 for England, Draganescu and Beauvais, 1985 for Romania, Pandey et al., 2000 for Jordan). Most Bajocian localities are distributed along a hypothetical palaeogeographical belt on the northern margin of the Tethys. The number of reefs and their presence in a pattern is probably indicative of a global coral reef event during the early Bajocian, not fully explored yet, with substantially greater production of carbonate by reef builders and more rapid recovery of these organisms in the Tethyan realm and across the globe. We use one of these recently discovered Bajocian reefs, identified in northern Switzerland, as an example to highlight this trend during the Bajocian. The discovery of a new Bajocian coral reef in northern Switzerland does not come as a complete surprise, as Bajocian reefs have already been described in the same region (Aargau region) by Wullschlegel (1966) and were mainly present around this latitude during the Bajocian, forming a large platform over today's France and Luxembourg (Purser, 1975; Durllet and Thierry, 2000; Guillocheau et al., 2002). The Bajocian reefs are, however, not widespread in Switzerland and in general in basins east to the Paris Basin. While the development of the central part of the Eastern Paris Basin and French Jura is stratigraphically well constrained and detailed (Contini, 1970; Sadki and Weis, 2023), little is known about the biostratigraphic frame of the eastern part closer to the deeper settings of the Tethys, corresponding today to Switzerland (Gonzalez and Wetzel, 1996). The establishment of a precise biostratigraphy with robust dating is necessary to establish the possibility of a global reef event during the Bajocian. Here we present new data, collected from two cores drilled in a palaeohigh revealed by seismic exploration with a good level of coral preservation, a lithostratigraphic description and additional data on microfacies and biostratigraphy. This reef was discovered within the framework of the "Sachplan Geologische Tiefenlager" (SGT, Sectoral Plan for Deep Geological Repositories) by the National Cooperative for the Disposal of Radioactive Waste (Nagra). Three siting regions in northern Switzerland are investigated as potential deep geological repositories for radioactive waste. The host rock (Opalinus Clay) and its confining stratigraphic units are being explored by deep drilling and 3D seismic analysis. In the Nördlich Lägern study area, 2D seismic data have already revealed a rounded palaeohigh in the Middle Jurassic upper confining units of the Opalinus Clay (Madritsch et al., 2013; Meier and Deplazes, 2014) and was later confirmed by 3D seismic data. The Nagra boreholes Bülach-1-1 and Stadel-3-1 drilled within this palaeohigh show well preserved corals (macro- and micro-morphologies but no aragonitic microstructures), dated to the Bajocian. This new unit is informally named «Herrenwis Unit» after the location name "Herrenwis", where it was drilled for the first time in borehole Bülach-1-1. Since the reef interval in both cores cannot be dated otherwise due to the lack of ammonites, the use of well-calibrated

palynostratigraphy was crucial and allowed for accurate dating of the reef interval using the standard biochronological scales established in Cariou and Hantzpergue (1997) and Ogg et al. (2016). Additional palynostratigraphic analyses were performed on sequences including similar coral reefs in France to explore the power and efficiency of the methodology. The findings from Switzerland and France are used to re-evaluate similar coral reefs that have been insufficiently dated so far, in order to assess the number and extent of Bajocian coral reefs at the global scale.

2. Geological setting and palaeogeography

2.1. Geological context

The two studied cores were drilled approximately 20 km north of the city of Zurich close to Bülach and Stadel in northern Switzerland (Fig. 1A). The drilling sites are located on the Molasse Plateau (Eastern Molasse Basin) in the eastern part of the Tabular Jura. A series of normal and thrust faults with a NEE - SWW orientation are located to the north and south of the study area (Madritsch et al., 2013; Madritsch et al., 2018) (Figs. 1B).

The formations in the area are mainly Quaternary and Cenozoic series, with Jurassic rocks outcropping a few kilometres to the west (Fig. 2).

Seismic data (Meier and Deplazes, 2014; Nagra, 2019) have revealed a large seismofacies body (originally called "Schwellenzone", German for "sill zone") in the centre of the Nördlich Lägern area, east of the Weiach-1 borehole and around the Bülach-1-1 and Stadel-3-1 boreholes (Fig. 3). With the findings of Bülach-1-1 and Stadel-3-1 this seismofacies body is called an "isolated carbonate unit" (Fig. 1B). Its northern and western boundary can be mapped well, whereas its southern and eastern boundary are uncertain due to tectonic influence in the south and limitation of the 3D-geophysical survey area. The two deep boreholes in the "isolated carbonate unit" have revealed a coral reef facies that was previously unknown and therefore given the new informal name «Herrenwis Unit». The coral facies are underlain by the Wedelsandstein Formation and partly by the «Humphriesoolith Formation».

This study was conducted on samples acquired from the two boreholes Bülach-1-1 Stadel-3-1. The boreholes are approximately 2.7 km apart (Figs. 2 and 3). In the search for potential outcrop analogues for the «Herrenwis Unit», the regions of Lorraine and Burgundy in France seemed the most appropriate. The choice of the east of France is based on the fact that during the Middle Jurassic, much of central Europe was covered by a shallow epicontinental sea, which facilitated the development of a vast carbonate platform east of the Paris Basin during the Middle Jurassic (Gonzalez and Wetzel, 1996; Wetzel et al., 2013). This expansive platform extended over Eastern France, Luxembourg and parts of Germany and began to form during the Bajocian, progressively advancing northwards (Burgundy to Lorraine) and eastwards, as described by Gonzalez and Wetzel (1996). Bajocian reefs largely covered significant parts of Burgundy and Lorraine, making this region a good target in the search for potential analogues to the «Herrenwis Unit». Notable sites include the Rumelange quarry (Lathuilière et al., 2003; Fayard et al., 2005), Malancourt-la-Montagne quarry (Durand et al., 1989; Geister and Lathuilière, 1991), Pouillenay quarry (Rat and Amiot, 1979) and the Vauchignon cliff (Durllet et al., 2001; Brigaud et al., 2009) and extend from the border between France and Luxembourg to the east of Lyon (France), some 400 km from North to South.

2.2. Palaeogeographical context

During the Middle Jurassic, most of the present European landmass was covered by a large, warm, shallow epicontinental sea, which resulted in the deposition of carbonate and siliciclastic sediments from Portugal to Norway (Fig. 4A). At the same time, crustal extension due to the break-up of the supercontinent Pangea created a series of horsts and

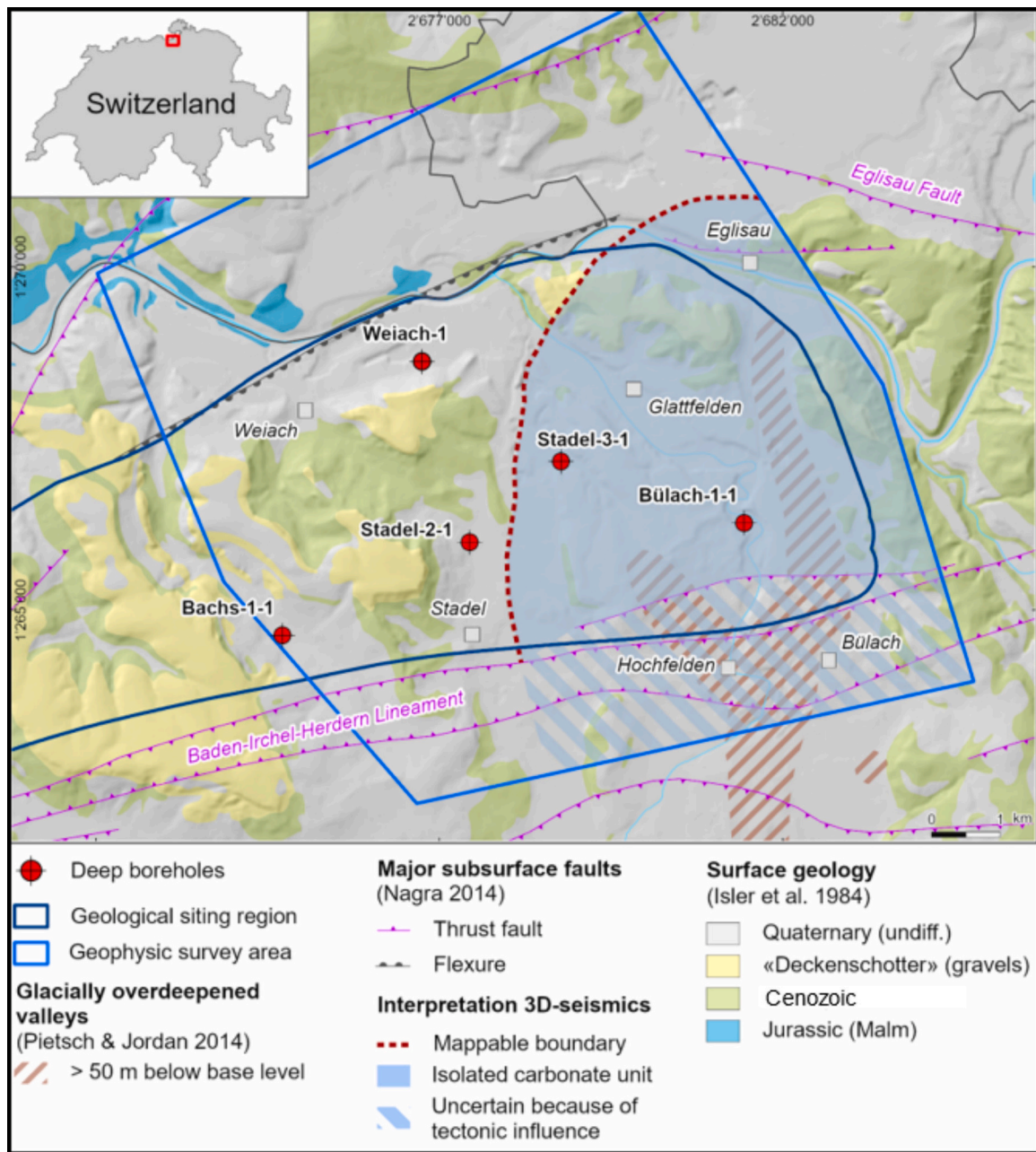


Fig. 1. Overview of the Nördlich Lägern and well sites. The Bülach-1-1 (BUL1-1) and Stadel-3-1 (STA3-1) wells are drilled in the seismic anomaly (in blue). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

grabens in Europe. This caused the subsidence of Europe by rifting and created accommodation for the deposition of sediments (Callomon, 2003). The Swiss Plateau was part of the mid-European epicontinental Basin; bordered to the west by the Burgundy Platform (eastern Paris Basin) and to the south by some landforms (Alemannic Land, Trümpy, 1980) and the Tethys Ocean (Fig. 4B). The Middle Jurassic deposits of the Swiss Plateau consist mainly of claystone, argillaceous or sandy marl and oolitic, iron-oolitic and bioclastic limestone with shallowing-upwards successions (Burkhalter, 1995; Gonzalez and Wetzel, 1996). The slow rise in sea level and steady subsidence in this region allowed a large input of sediments, with oolitic carbonates in shallow settings in the west, while marly to argillaceous sediments were deposited in basinal settings further east (Gonzalez and Wetzel, 1996).

3. Material and Methods

3.1. Coral identification

Coral identification was carried out at the Nagra core repository in Mellingen (Aargau, Switzerland) on cores from the Bülach-1-1 and Stadel-3-1 boreholes. The core from the Bülach-1-1 borehole was previously cut into slabs and fixed into casts with resin (Kaehr and Gysi, 2021). The core from the Stadel-3-1 borehole was cut into 1 m segments approximately. Corals were identified directly on the cores following the taxonomic criteria established by Lathuilière (2000a, 2000b). The corals were divided and counted by one metre segments at a time. A total of 720 individual corals were identified with a hand lens in the Bülach-1-1 core and 796 in the Stadel-3-1 core, mostly to genus level. Local polishing and hydrochloric acid (HCl, 10 %) were used to remove scratches to better assess the internal structures of the corals.

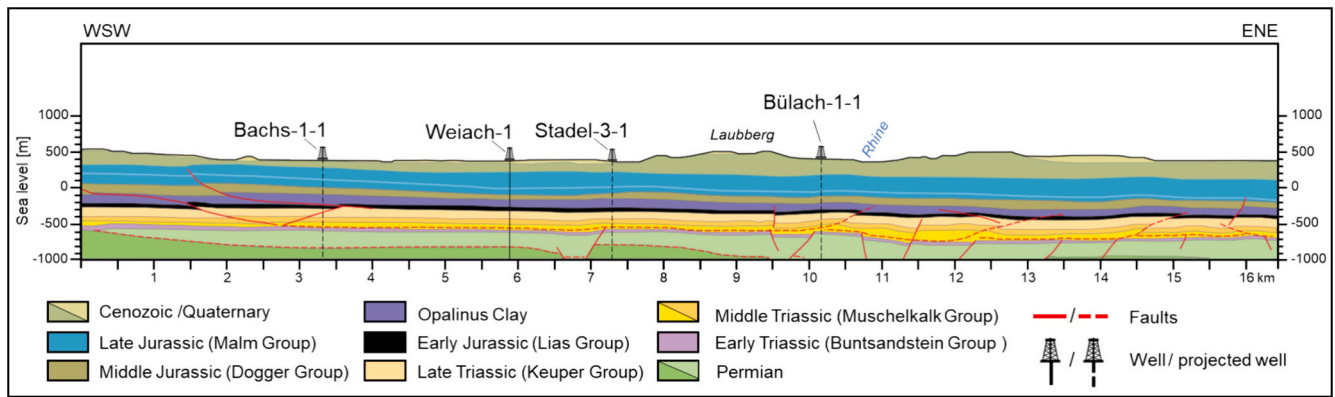


Fig. 2. Profile line of the Nördlich Lägern siting region, passing by the Weiach-1 well (modified from Nagra, 2014). The Bachs-1-1, Stadel-3-1 and Bülach-1-1 wells are projected on the profile line.

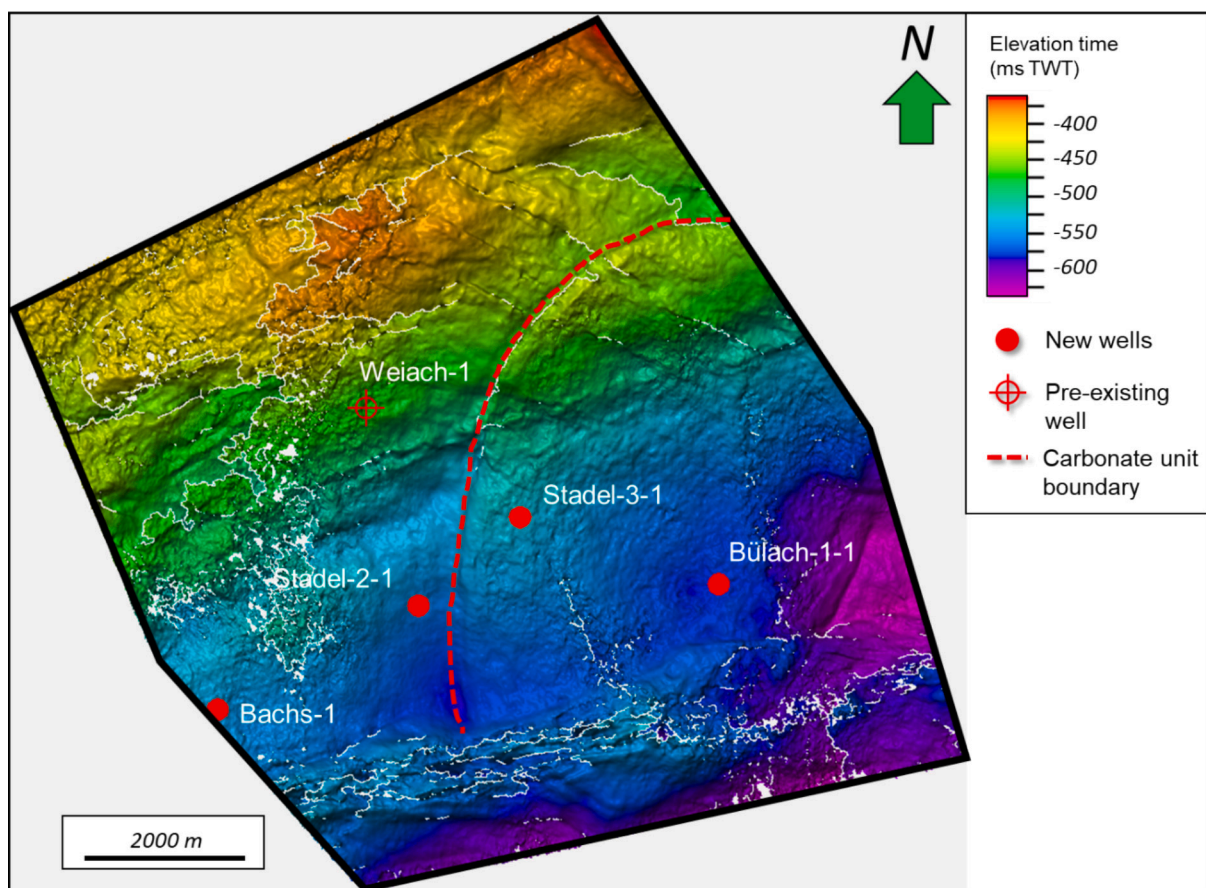


Fig. 3. Subcrop map (Top reflection of the «Herrenwis Unit») of the geophysical survey area acquired in the Nördlich Lägern siting region, with core locations.

3.2. Thin section preparation and petrography

Forty-two thin sections (19 from Bülach-1-1 well, 23 from the Stadel-3-1 well) were used to investigate whether the coral-rich layer represents an in-place coral reef and to study the associated microfacies. All thin sections were cut on the side of the core so that the long side was parallel to the direction of coring and thus covered as much of the stratigraphy as possible. Seven thin sections (BUL1-1-860.36 to BUL1-1-812.08 in Wohlwend et al., 2021) of limestone lithologies from the Bülach-1-1 well, with a standard length of 4 cm, were prepared at the University of Basel, which were stained on the left half using the technique of Dickson (1965) for better identification of the carbonate

minerals calcite, Fe-calcite and Fe-dolomite. The samples with high porosity were also impregnated with a blue epoxy resin prior to thin section preparation to estimate their porosity percentage. The other thirty-five thin sections (named AR-1 to AR-29, including duplicates) were prepared at the University of Geneva. Here no size standard was applied to better account for the size of the samples and no staining was used.

3.3. Sample preparation for palynology

The processing of the rock samples for palynological analyses (19 samples from Bülach-1-1, 17 from Stadel-3-1, 3 samples from

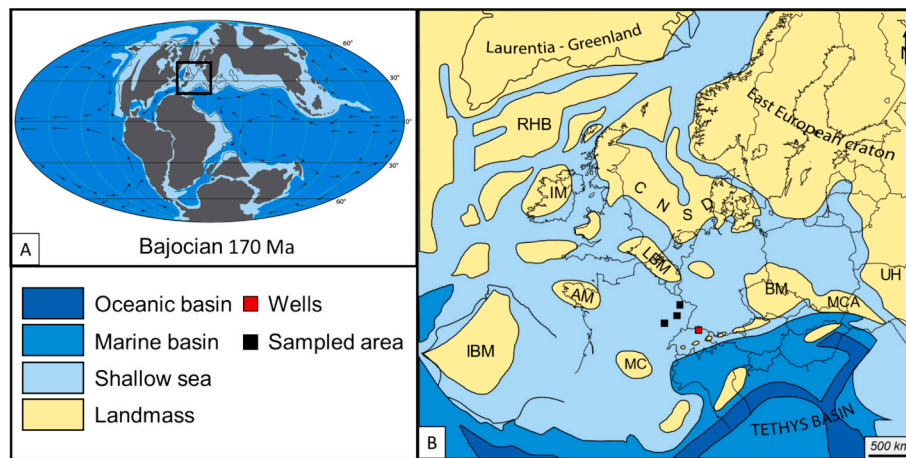


Fig. 4. A World palaeogeographical map of the Bajocian (Middle Jurassic) (modified from [Kiessling et al., 1999](#)); B Palaeogeographical map of Europe in the Middle Jurassic (modified from [Ziegler, 1990](#)), Principal landmasses in Europe: AM Armorican Massif, BM Bohemian Massif, CNSD Central North Sea Dome, IBM Iberian Meseta, IM Irish Massif, LBM London-Brabant Massif, MC Massif Central, MCA Meta-Carpathian Arc, UH Ukrainian High.

Malancourt-La-Montagne, 4 samples from Bainville-sur-Madon, 1 sample from Pouillenay) was carried out by PLS Palynological Laboratory Services Ltd. (Holyhead, Anglesey, UK). The treatment followed the standard protocol ([Wood et al., 1996](#)) using concentrated HCl and concentrated HF, followed by a short oxidation with HNO₃ and, if necessary, ultrasonic treatment. The residues are sieved to a mesh size of 15 µm. The sieved residues were mounted on microscope slides and analysed by transmitted light microscopy. Two consecutive counts were carried out as part of the quantitative microscopic analysis. In the first count, 200 grains of all palynomorphs were counted and the number of dinoflagellate cysts noted. In a second count, only dinoflagellate cysts were counted until a total of 100 cysts were reached. The slide

remainder was checked for additional uncounted species. The range charts with the total number of dinoflagellate cysts counted in the 19 samples from Bülach-1-1 and the 17 from Stadel-3-1 are shown in the Supplementary Material. The question mark after the genus name indicates uncertainty as to the correct taxonomic assignment of the species to the genus. For the total range charts of the palynomorphs, reference is made to the corresponding Nagra reports on the individual boreholes ([Wohlwend et al., 2021, 2022](#)).

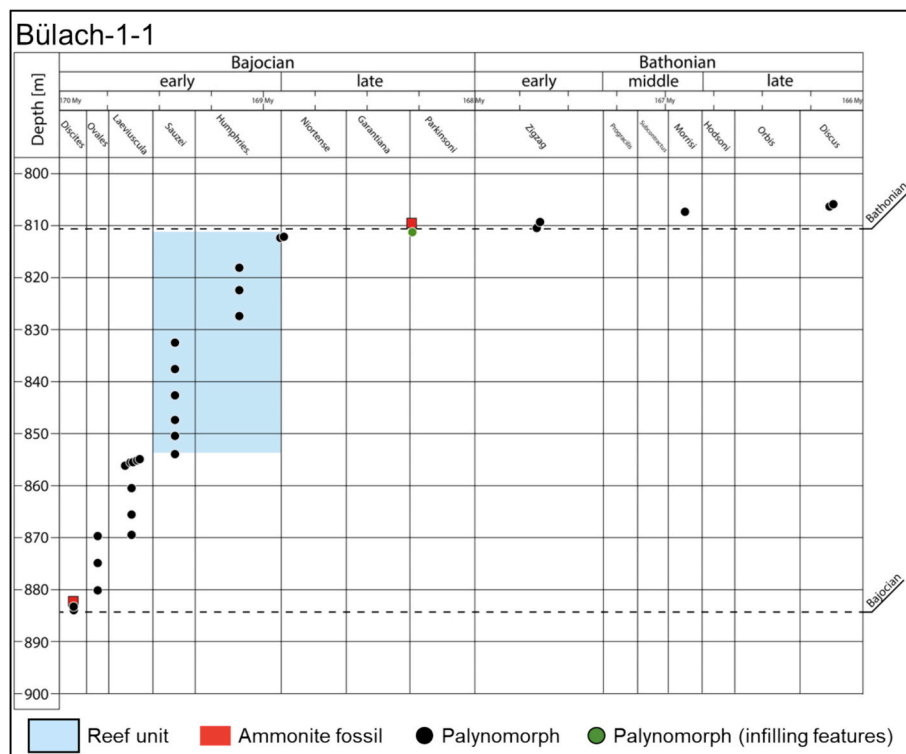


Fig. 5. Palynomorph and ammonite biostratigraphic data plotted by depth and age, Bajocian and Bathonian of the Bülach-1-1 well ([Wohlwend et al., 2021](#)). Infilling features are samples taken from sediment filled with greyish-green claystone and bioclastic sediment, likely representing later infill into coral porosity and cavities. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4. Results

4.1. Biostratigraphy

In Bülach-1-1, the top of the reef unit shows palynomorphs encompassing different ammonite zones at the same depth on the cores (Humphriesianum, Niortense). Few ammonites were found, but their preservation prevented reliable identification (Fig. 5).

4.1.1. Ammonite biostratigraphy

The macrofossils and especially the ammonites are very rare in the two cores from the analysed successions and thus allow only an incomplete biostratigraphic dating. In Bülach-1-1 a total of three ammonites were identified within the Bajocian section (Wohlwend et al., 2021). One ammonite is a questionable *Hyperlioceras?* sp. at a depth of 882.71 m from the underlying Wedelsandstein Formation which is most probably from the Discites Zone, an unpreparable ammonite fragment found within the reef unit from 852.11 m, and a *Pseudogartiana* sp. ranging from the Garantiana Zone to the early Parkinsoni Zone, located at 812.03 m, just lying on the iron-rich facies (hardground) at the top of the «Herrenwis Unit».

In Stadel-3-1 only one truncated ammonite was found in the close vicinity of the «Herrenwis Unit» (Wohlwend et al., 2022). It is a *Pseudoperisphinctidae*, found at 701.64 m, which cannot be further identified and probably indicates a Bathonian age.

4.1.2. Palynomorphs biostratigraphy

Most of the samples studied yielded good palynological residues with rich and diverse palynoflora. Palynomorph preservation is good throughout the section studied. The palynomorph assemblages are mainly composed of dinoflagellate cysts, pollen and spores. In Bülach-1-1, a total of 41 distinct levels were dated by palynomorphs (Wohlwend et al., 2021) from which 19 levels with a rich dinoflagellate cyst fauna are presented in this study. In Stadel-3-1, a total of 40 different levels were dated (Wohlwend et al., 2022) from which 17 levels are presented in this study. Both detailed dinoflagellate cyst range charts are presented in the Supplementary Material.

4.1.2.1. Bülach-1-1. In the Bülach-1-1 core 19 samples (Fig. 5) have been analysed from the described interval. Two samples have been collected from the Wedelsandstein Formation (856.09 m and 855.56 m), four samples are coming from the «Humphriesioolith Formation» (855.47 m to 853.99 m), 11 samples cover the «Herrenwis Unit» (850.27 m to 812.05 m) and two additional samples were collected from the overlying strata (812.01 m and 810.58 m). The stratigraphic succession can be grouped into five palynological sample intervals based on the palynomorphs.

In the first palynological sample interval, eight samples were collected within the depth range of 869.64 m to 854.98 m. Only the upper five samples between 856.09 m and 854.98 m are shown in the Supplementary Material with the complete range charts. They all belong to the underlying formations of the «Herrenwis Unit». These samples exhibit distinct dinoflagellate cyst assemblages. Notable species include *Cavatodissiliodinium hansgochti* Feist-Burkhardt and Monteil, 2001, *Durotrigia daveyi* Bailey, 1987 and *Durotrigia* spp., which consistently occur throughout the samples. *Durotrigia daveyi* becomes particularly abundant in the upper portion of the interval. *Batiacasphaera* spp. are abundant and very diverse, showing a wide variety of wall structures and surface ornamentation. Additionally, two unique dinoflagellate cyst species, *Bradleyella* sp. 1 and *Gresslyodinium mirabile* Below, 1990, are recorded with multiple specimens in the upper part of the interval. *Bradleyella* sp. 1 closely resembles, or possibly conspecific with, *Bradleyella adela* Fenton, 1980, a rare species previously described from the Bajocian of the UK (Fenton et al., 1980). *Gresslyodinium mirabile*, a species with striking ornamentation and distinct morphology, has not

been reported in the literature since its initial description by Below (1990). The defined interval extends from the first occurrence of *Batiacasphaera laevigata* (Smelror 1988b) to the first occurrence of *Kallosphaeridium hypornatum* Praus, 1989 in the higher interval (sample 853.99 m). The First Appearance Datum (FAD) of *Batiacasphaera laevigata* is in the Laeviuscula Zone, while the FAD of *Kallosphaeridium hypornatum* (sample above) is in the Sauzei Zone (Praus, 1989). Therefore, the interval is dated to the Laeviuscula Zone.

The second palynological sample interval contains the six samples from 853.99 m to 832.36 m. The lowermost sample at 853.99 m still belongs to the underlying «Humphriesioolith Formation», but all samples taken above it come from the lower part of the «Herrenwis Unit». The assemblages in the lower part of the palynological sample interval show similarities to those observed below. However, the upper part of the interval exhibits lower species richness and diversity, with the topmost sample yielding very little palynological residue. *Kallosphaeridium hypornatum* has its first (questionable) occurrence at the base of the interval and appears intermittently throughout and above the interval. *Evansia? Spongogranulata* Below, 1990 is also present intermittently, with its last occurrence in the sample just above the top of the interval (sample 827.38 m). Notable last occurrences within this interval include *Cavatodissiliodinium hansgochti*, *Dissiliodinium giganteum* Feist-Burkhardt, 1990, and consistent *Mancodinium semitabulatum* Morgenroth, 1970. There is also an unusual occurrence of a few single specimens of *Phallocysta* spp. and *Phallocysta eumekes* Dörhöfer and Davies, 1980 in the upper part of the interval. The defined interval spans from the first questionable occurrence of *Kallosphaeridium hypornatum* in the Sauzei Zone to the first occurrence of *Acanthaulax crista* (Wetzel, 1967a), *Cavatodissiliodinium* sp. 1, sp. 2, sp. 3, *Durotrigia filapicata* (Gocht, 1970a), *Phallocysta thomasii* Smelror, 1991 and *Wanaea* sp. 1 in the interval above which were so far considered to have their FADs in the Humphriesianum Zone. Therefore, the interval is interpreted to be Sauzei Zone.

The third palynological sample interval contains the three samples 827.38 m, 822.35 m and 818.03 m. The lowest sample at 827.38 m is characterised by numerous first occurrences: *Acanthaulax crista*, *Cavatodissiliodinium* sp. 1, sp. 2 and sp. 3, *Durotrigia filapicata*, *Phallocysta thomasii*, *Valensiella/ Ellipsoidictyum* spp. (questionable) and *Wanaea* sp. 1 all having their FADs in the Humphriesianum Zone. The samples 822.35 m and 818.03 m exhibit similarities to the sample at 827.38 m but lack the presence of *Phallocysta thomasii*. Notably, the two samples include the first occurrences of *Atopodinium* sp. 1, *Meiourogonaulax* sp. 2, questionable *Nannoceratopsis spiculata* Stover, 1966, *Rhynchodiniopsis?* sp. 1 and *Wanaea* sp. 2, all having their FAD within the Humphriesianum Zone. The range of *Phallocysta thomasii* is considered to be restricted to the Romani and Humphriesianum subzones of the Humphriesianum Zone. *Evansia? Spongogranulata* was so far considered to have its LAD in the Sauzei Zone, but its range may reach into the early Humphriesianum Zone. The sample interval is dated from the Humphriesianum Zone with the sample 827.38 m dating to the Romani and Humphriesianum subzones of the Humphriesianum Zone.

The sample taken at 813.27 m yielded very little residue with only a few single grains. An age assignment is therefore not possible.

The fourth palynological sample interval contains the two samples 812.19 m and 812.05 m. The assemblages are characterised by numerous first occurrences. In the basal sample, these include *Aldorfia aldorfensis* (Gocht, 1970) (questionable), *Batiacasphaera* sp. 1, *Ctenodinium* spp. (questionable), *Gonyaulacysta pectiniger* (Gocht, 1970b), *Korystocysta gochti* (Sarjeant, 1976), *Meiourogonaulax valensii* Sarjeant, 1966, *Nannoceratopsis spiculata* and *Rhynchodiniopsis? Regalis* (Gocht, 1970b). In the second sample, the first occurrences include *Atopodinium polygonale* (Beju, 1983), *Ctenodinium continuum* Gocht, 1970b (questionable), *Endoscrinium asymmetricum* Riding, 1987a, *Gongyodinium hocneratum* Fenton, 1980 and *Valvaeodinium spinosum* Fenton, 1980. The species *Durotrigia daveyi* is common in both samples, and the top of its acme is in the upper sample of this interval. Last occurrence in this

interval has also *Nannoceratopsis gracilis* s.l. [Alberti, 1961](#). The FADs of the first occurring species are in the Blagdeni Subzone of the Humphriesianum Zone (*Aldorfia aldorfensis* and *Rhynchodiniopsis? regalis*), the Niortense Zone (*Atopodinium polygonale*, *Ctenidodinium continuum*, *Korystocysta gochtii*, *Gonyaulacysta pectinifera*, *Valvae-odinium spinosum*) and higher within Niortense Zone (*Endoscrinium asymmetricum*, *Ctenidodinium ornatum* ([Eisenack, 1935](#)), *Gonylodinium hocneratum*). The LAD of *Nannoceratopsis gracilis* s.l. is in the Niortense Zone. The LAD of consistently occurring *Durotrigia daveyi* is considered to be in the Humphriesianum Zone, but the species may reach up to the Garantiana Zone. The dinoflagellate cyst taxa indicate an age corresponding to the Niortense Zone. The concurrent common occurrence of *Durotrigia daveyi*, however, indicates a mixture with a slightly older palynoflora that corresponds to the latest Humphriesianum Zone (Blagdeni Subzone) in age.

The fifth palynological sample interval is represented by a single sample at 812.01 m, collected directly above the hardground and therefore from the base of the overlying formation. The assemblage in this sample reveals several first occurrences, including *Ctenidodinium sellwoodii* ([Sarjeant, 1975](#)) group, *Gonyaulacysta eisenackii* ([Deflandre, 1939](#)) (questionable), *Sirmiodiniopsis* sp., and *Valvae-odinium vermicylindratum* [Below, 1987](#), among others. Notable last occurrences include *Acanthaulax crispa*, *Durotrigia daveyi*, and *Meiourogonaulax valensii*. The FAD of the *Ctenidodinium sellwoodii* group corresponds to the Garantiana Zone, while the FADs of *Gonyaulacysta eisenackii* and *Sirmiodinium* sp. align with the Parkinsoni Zone. The LAD of *Durotrigia daveyi* is within the Garantiana Zone, and that of *Acanthaulax crispa* falls within the Parkinsoni Zone. The sample is dated as Garantiana to Parkinsoni Zone.

4.1.2.2. Stadel-3-1. In the Stadel-3-1 core 17 samples ([Fig. 6](#)) have been analysed from the interval described. The lowermost sample has been collected from the uppermost part of the Wedelsandstein Formation (742.33 m), the following 14 samples cover the «Herrenwis Unit» (741.99 m to 701.66 m) and additional two sample were collected from

the overlying strata (701.64 m and 701.38 m). The stratigraphic succession can be grouped into five palynological sample intervals based on the palynomorphs, whereby four samples (720.09 m, 703.71 m, 701.79 m and 701.66 m) were specifically collected to constrain the possible age of infilling of younger sediment.

In the first palynological sample interval, three samples were collected, ranging in depth from 760.65 m to 742.33 m. Only the uppermost sample at 742.33 m is shown in the Supplementary Material with the complete range chart. The assemblages in this interval exhibit the first appearances of *Batiacasphaera laevigata*, *Cavatodissiliodinium hansgochtii*, and *Durotrigia daveyi* at the base. *Dissiliodinium giganteum* is commonly observed and can be abundant. *Bradleyella adela* is recorded in the topmost sample, while *Nannoceratopsis dictyambonis* [Riding, 1984a](#) shows its last occurrence within this interval. The interval is defined by the FADs of *Batiacasphaera laevigata* and *Cavatodissiliodinium hansgochtii* at the base, which are in the Laeviuscula Zone, continuing until the FAD of *Kallosphaeridium hypornatum* in the interval above, which is in the Sauzei Zone. Therefore, the interval is dated Laeviuscula Zone.

The second palynological sample interval contains the five samples spanning depths from 741.99 m to 736.02 m. The assemblages within this interval exhibit similarities to those observed below, but they also reveal the first occurrence of *Kallosphaeridium hypornatum*. *Hystriodinium* sp. is observed for the last time in the sample at 741.41 m. The interval is defined from the first occurrence of *Kallosphaeridium hypornatum*, which lies in the Sauzei Zone, to the first occurrence of the questionable *Phallocysta thomasi* in the interval above, which would be in the Humphriesianum Zone. Therefore, the interval is dated Sauzei Zone.

The third palynological sample interval contains the two samples taken at depths 729.98 m and 727.06 m. Within this interval, the assemblages reveal the first occurrences of the questionable *Phallocysta thomasi* and questionable *Durotrigia filapicata*. The last occurrences include the questionable *Cavatodissiliodinium hansgochtii*, *Dissiliodinium*

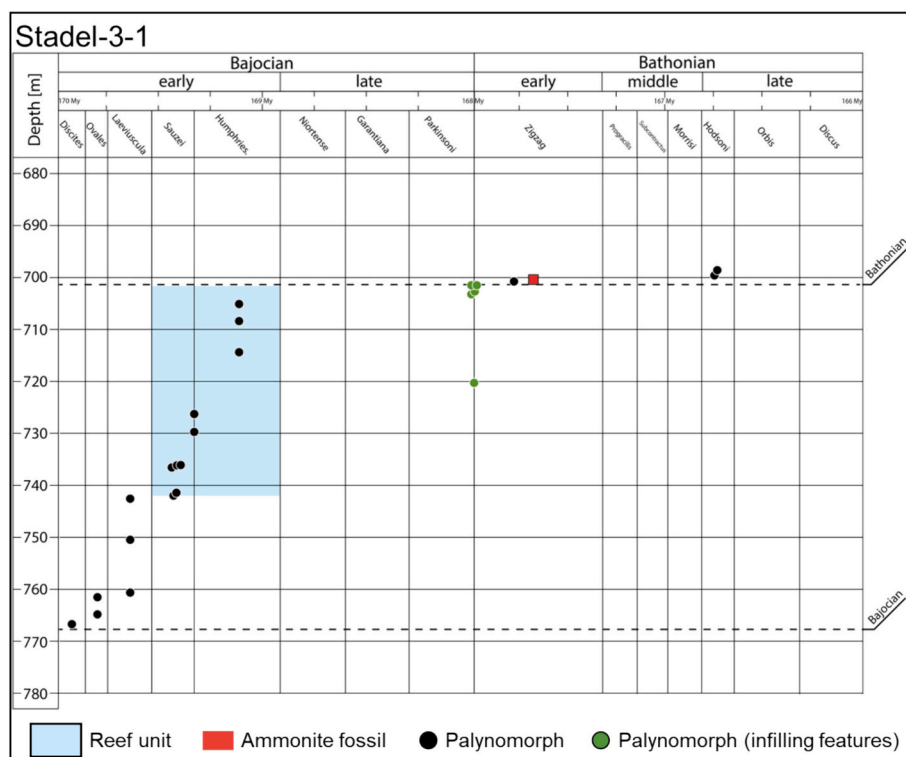


Fig. 6. Palynomorph and ammonite biostratigraphic data plotted by depth and age, Bajocian and Bathonian of the Stadel-3-1 well ([Wohlwend et al., 2022](#)). Infilling features are samples taken from sediment filled with greyish-green claystone and bioclastic sediment, likely representing later infill into coral porosity and cavities. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

giganteum, and *Moesiodinium raileanui* Antonescu, 1974 at the base, as well as *Evansia? spongogranulata* at the top of the interval. The interval is defined by the first appearance of the questionable *Phallocysta thomasi* and extends to the last occurrence of *Evansia? spongogranulata*. The LADs of *Cavatodissiliodinium hansgochti*, *Dissiliodinium giganteum*, *Evansia? spongogranulata*, and *Moesiodinium raileanui* all fall within the Sauzei Zone. The range of *Phallocysta thomasi* is considered to be limited to the Romani and Humphriesianum subzones within the Humphriesianum Zone. The FAD of *Durotrigia filapicata* is within the Humphriesianum Zone. Based on the co-occurrence of these taxa, the interval is interpreted Sauzei to Humphriesianum Zone.

The fourth palynological sample interval contains the three samples ranging from 714.37 m to 705.02 m. Within this interval, the dinoflagellate cyst assemblages include *Acanthaulax crispera*, *Batiacasphaera* spp., *B. laevigata*, *Dissiliodinium* spp., *Durotrigia daveyi*, *Gongylocladus erymnoteichon* Fenton, 1980, *Kallosphaeridium hypornatum*, *Nannoceratopsis gracilis* s.l., and *Valensiella/Ellipsoidictyum* spp. *Cavatodissiliodinium* sp. 3 is recorded in the sample at 714.37 m, while “*Hypolytodinium*” sp. and *Mancodinium semitabulatum* are recorded in the sample at 708.23 m. The interval is defined by the occurrence of *Acanthaulax crispera*, which has its FAD in the Humphriesianum Zone, and extends to the last occurrence of *Mancodinium semitabulatum*, having the LAD also in the Humphriesianum Zone. The range of “*Hypolytodinium*” sp. is considered to be limited to the Romani and Humphriesianum subzones of the Humphriesianum Zone. The sample interval is therefore interpreted as Humphriesianum Zone.

The fifth palynological sample interval contains the three samples ranging from 701.79 m to 701.64 m and therefore covers the stratigraphic top of the «Herrenwis Unit» into the above following strata and in addition also the sample collected at 703.71 m from a greenish slightly bioclastic sedimentary cavity filling. The composition of the dinoflagellate cyst assemblages in these samples is very different to that below. Assemblages are rich and diverse. Taxa recorded regularly in these assemblages include *Acanthaulax crispera*, *Atopodinium polygonale*, *Ctenidodinium* spp., *Ct. continuum*, *Ct. sellwoodii* group, *Durotrigia daveyi*, *Gongylocladus hocneratum*, *Korystocysta gochti*, *Meiourogonyaulax valensii*, *Nannoceratopsis spiculata*, *Orobodinium* spp., *O. automobile*, *Rhynchodiniopsis? regalis*, *Sirmiodiniopsis* sp. in Feist-Burkhardt and Wille (1992) and *Valvaedinium spinosum*. In all four samples of the interval there are some unexpected occurrences that conflict with the age suggested by the majority of taxa. These are *Dissiliodinium giganteum* and *Hystrichodinium? sp.* in the sample at 703.71 m, questionable *Ctenidodinium combazii* Dupin, 1968 at 703.71 m and 701.79 m, *Cavatodissiliodinium* spp., *Lithodinia* spp. and *Tubotuberella dangeardii* (Sarjeant, 1968) at 701.79 m, *Nannoceratopsis plegas plegas* Drugg, 1978 at 701.66 m, and *Nannoceratopsis gracilis* s.l. at 701.64 m. Based on the majority of taxa recorded, the assemblages in this interval correspond best to the Parkinsoni Zone, as *Orobodinium automobile* Gocht and Wille, 1990 and *Sirmiodiniopsis* sp. have their FADs in the Parkinsoni Zone and *Acanthaulax crispera* has its LAD also in the Parkinsoni Zone. Conflicting with this age assignment are the odd occurrences of taxa with an FAD in the Zigzag Zone (*Ctenidodinium combazii*, *Lithodinia* spp., *Tubotuberella dangeardii*) and of taxa with their main distribution or LADs in the early Bajocian (*Dissiliodinium giganteum*, *Cavatodissiliodinium* spp., *Hystrichodinium? sp.*, *Nannoceratopsis gracilis* s.l., *Nannoceratopsis plegas plegas*). Therefore, the samples in this interval are interpreted Parkinsoni to Zigzag Zone, with some early Bajocian.

The last sample documented here belongs to a greyish-green claystone observed between corals at 720.09 m. The assemblage is very different to the samples collected below and above with a mixture of dinoflagellate cysts of different age. The recorded dinoflagellate cysts include i.a. *Acanthaulax crispera*, *Cavatodissiliodinium* spp., *Ctenidodinium continuum*, *Ct. sellwoodii* group, *Dissiliodinium* spp., *Endoscrinium asymmetricum*, *Gonyaulacysta eisenackii*, *G. pectiniger*, *Korystocysta gochti*, *Mancodinium semitabulatum*, *Meiourogonyaulax valensii*, *Nannoceratopsis spiculata*, *Orobodinium* spp., *Sirmiodiniopsis* sp. of Feist-Burkhardt and

Wille (1992), *Valensiella/Ellipsoidictyum* spp. and *Valvaedinium spinosum*. The different assemblage of the sample makes it difficult to give a constrained age. There are a few specimens of taxa that are restricted to the early Bajocian, but most taxa recorded are typical for a late Bajocian or somewhat younger age, with some of them having a LAD in the early Bathonian Zigzag Zone. Typical for the early Bajocian are *Cavatodissiliodinium* spp. and *Mancodinium semitabulatum*, the latter having a LAD in the Humphriesianum Zone. Taxa with an FAD in the Humphriesianum Zone, but also common later in the late Bajocian are *Acanthaulax crispera*, *Meiourogonyaulax valensii*, *Nannoceratopsis spiculata* and *Valensiella/Ellipsoidictyum* spp. Taxa with a FAD in the Niortense Zone are *Ctenidodinium continuum*, *Endoscrinium asymmetricum*, *Gonyaulacysta pectiniger*, *Korystocysta gochti* and *Valvaedinium spinosum*. The taxa *Orobodinium* spp., *Gonyaulacysta eisenackii* and *Sirmiodiniopsis* sp. have their FADs in the Parkinsoni Zone. The LAD of *Acanthaulax crispera* is in the Parkinsoni Zone, and that of *Meiourogonyaulax valensii* and *Sirmiodiniopsis* sp. are in the Zigzag Zone. The sample is interpreted to range from possibly Humphriesianum Zone to Zigzag Zone, with most constituents indicating Parkinsoni Zone.

In Stadel-3-1, the palynological association shows a development of the reef unit occurring mainly in the same time zone as in Büllach-1-1 (Sauzei / Humphriesianum zones) but with some uncertainties in identification on some levels (Fig. 6). Palynomorphs from an interval belonging to younger ammonite zones (Garantiana, Parkinsoni) were identified below palynomorphs typical for the older Humphriesianum zone. A single ammonite fragment was found near the reef unit, in the Aalenian section (776.94 m - Bradfordensis Zone).

Incidentally, the «Herrenwis Unit» appears to have developed mainly during the early Bajocian (Propinquans respectively Sauzei and Humphriesianum zones, according to the biochronological scale of Cariou and Hantzpergue, 1997 and Dietze et al., 2011).

4.1.2.3. Palynological results from the quarries from France. From three well known Bajocian sites from Burgundy and Lorraine in Eastern France, eight additional palynological samples have been collected: One sample was collected from the quarry of Pouillenay (47°29'47.0"N / 4°28'26.0"E) from the coral boundstone facies of the Calcaire à entroques Formation (POU1). Four samples were collected from the quarry of Bainville-sur-Madon (BAI: 48°35'58.9"N / 6°04'31.6"E) whereby the lower two of them (BAI1 and BAI2) were collected 25 cm and 50 cm above the onset of the Calcaire à polypiers inférieur Formation. The third sample (BAI3) was collected from the “Lucinenbank” (after Klüpfel, 1919) and the fourth was collected slightly above the Calcaire à polypiers supérieur Formation. The three samples from the old quarry of Malancourt-la-Montagne (49°13'27.9"N / 6°04'15.3"E) were collected also at the onset of the coral facies of the Calcaire à polypiers inférieur Formation. The lowest one (MAL1) within the first corals, the second one (MAL2) from a claystone layer 30 cm higher and the third one (MAL3) within the first thicker corals (0.8 m above MAL1). Out of the eight samples, five yielded good palynological residues. The other three samples (POU1, BAI3 and MAL3) did not yield enough palynomorphs to allow a palynostratigraphic age assignment. In all samples, preservation of the palynomorphs is good.

4.1.2.4. Quarry of Bainville-sur-Madon. The palynomorph assemblages in the samples BAI1 and BAI2 from the onset of the coral facies (base of Calcaire à polypiers inférieur Formation) are rich. The dinoflagellate cyst assemblages are of relatively low diversity and are composed primarily of taxa belonging the family Gonyaulacaceae. These are superabundant *Batiacasphaera* spp., *Dissiliodinium* spp., common to abundant *Durotrigia* spp., questionable *D. filapicata*, questionable *Gongylocladus erymnoteichon*, *Kallosphaeridium* spp. and questionable *K. hypornatum*. Other taxa recorded are *Nannoceratopsis* spp., *N. gracilis* s.l., *Phallocysta thomasi*, *Valvaedinium* spp., *V. sphaerichinatum* and *V. vermipellitum* Below, 1987b. The two samples are defined by the occurrence of

Phallocysta thomasii, which is considered to be restricted to the Romani and Humphriesianum subzones of the Humphriesianum Zone. The FAD of *Durotrigia filapicata* is in the Humphriesianum Zone. Therefore, the two samples are dated Romani to Humphriesianum Subzones of the Humphriesianum Zone.

The sample BAI4, which was most probably collected slightly above the top of the Calcaire à polypiers supérieur Formation, documents an assemblage clearly varying from the two lower ones. The sample includes *Acanthaulax crista*, *Atopodinium polygonale*, *Batiacasphaera* sp. 1, *Carpathodinium predae* Drugg, 1978, *Durotrigia daveyi*, *Endoscrinium* spp., *Meiourogonyaulax valensii*, *Nannoceratopsis spiculata*, *Rhynchodiniopsis? regalis*, *Rhynchodiniopsis? sp. 1* of Feist-Burkhardt and Götz (2016), *Valensiella/Ellipsoidictyum* spp., and *Valvaeodinium spinosum*. There are no representatives of the genus *Ctenodinium* recorded. The sample is defined by the occurrences of *Carpathodinium predae*, *Endoscrinium* spp., *Rhynchodiniopsis? regalis* and *Valvaeodinium spinosum*, having their FADs all in the Niortense Zone, and the common occurrence of *Durotrigia daveyi* and that of *Rhynchodiniopsis? sp. 1*. The LAD of *Durotrigia daveyi* is in the Garantiana Zone. *Rhynchodiniopsis? sp. 1* is a precursor form of *Rhynchodiniopsis? regalis* and has its main distribution in the latest part of the Humphriesianum Zone and in the Niortense Zone, before it is replaced by *Rhynchodiniopsis? regalis* proper, presumably in the Niortense Zone. Therefore, this sample is interpreted to belong to the Niortense Zone.

4.1.2.5. Quarry of Malancourt-la-Montagne. The palynomorph assemblages in the samples MAL1 and MAL2 are rich. The dinoflagellate cyst assemblages are of relatively low diversity and are composed primarily of taxa belonging to the family Gonyaulacaceae. These are superabundant *Batiacasphaera* spp., *B. laevigata*, *Dissiliodinium* spp., common to superabundant *Durotrigia* spp., questionable *D. filapicata*, questionable *Gonyodinium erymnoteichon* and *Kallosphaeridium hypornatum*. Other taxa recorded are *Kalyptea stegasta* (Sarjeant, 1961a), questionable *Mancodinium semitabulatum*, *Nannoceratopsis* spp., *N. gracilis* s.l., *Phallocysta thomasii*, *Valvaeodinium* spp. and *V. sphaerechinatum* Below, 1987b. The two samples are defined by the occurrence of *Phallocysta thomasii*, which is considered to be restricted to the Romani and Humphriesianum subzones of the Humphriesianum Zone.

4.2. Coral reef description and composition

4.2.1. Evidence of in-situ coral growth

The corals in both studied cores show distinctive characteristics typical of in situ growth. The large majority of corals in both cores of Bülach-1-1 and Stadel-3-1 are upright and in growth position, stacked on top of other (Fig. 7). In the case of remobilisation or gravity flows, one would expect the corals to have a range of different growth orientations and be placed in random positions (Perry, 2005). This is not the case in both studied cores. The corals show virtually no fragmentation. The samples displaying breakage often show fractures on the curved ends of the corals, indicating these are fractures related to pressure from above, postdating the time of growth. Some corals show typical growth characteristics that cannot be maintained with displacement, such as branching corals still in living position and corals growing directly on top of another. Most corals do not display signs of deterioration synonymous with transport such as fractures, cracks and erosion (Perry, 2005). However, some corals in the cores do show some features of displacement, like tilting to the side. Overall, structures testifying to significant transport and reworking remain subordinate. They are rather due to natural breakage of dead or damaged coral in the reef.

4.2.2. Drill core description and microfacies

The core description follows the classification of growth fabrics of Insalaco (1998) for scleractinian reefs. The facies are differentiated in the cores by the dominant kind of growth fabric. Matrices of boundstone and non bioconstructed carbonates are described with usual textural terms of Dunham (1962) completed by the descriptive terms of Embry and Klovan (1971) namely floatstone and rudstone. For the description of coral colonies, we used the terms massive when corallites are laterally united (Alloiteau, 1957), platy when they expand mostly laterally, patchoid when single corallites occur at the tip of each branch, and ramose when branches are made of numerous corallites.

4.2.2.1. Four lithofacies have been recognised. Lithofacies F1: skeletal rudstone and grainstone (Fig. 8).

The main component consists of skeletal fragments of diverse organisms including bivalves, echinoderms (mostly crinoids), gastropods, corals and a rich association of benthic foraminifera. Microbial crusts



Fig. 7. Features indicative of in-situ coral reef growth and polarity interpretation: **A** *Periseris* (2) growing on a *Thamnasteria* (1); **B** Weight fracture on coral extremities (arrow); **C** *Thecosmilia* in growth position; **D** Vermiform borings within the *Periseris* (1) skeleton. The boring organism penetrated downward from the upper surface. Branch of vertically growing *Thecosmilia* (2). Vesicular dissepiment with a convex upward shape demonstrating the growth polarity (3). *Gastrochaenolites* boring (4) made by a bivalve that penetrated from the lower face of the coral, free when the larva settled. The cavity shows a geopetal structure that indicates a normal polarity.

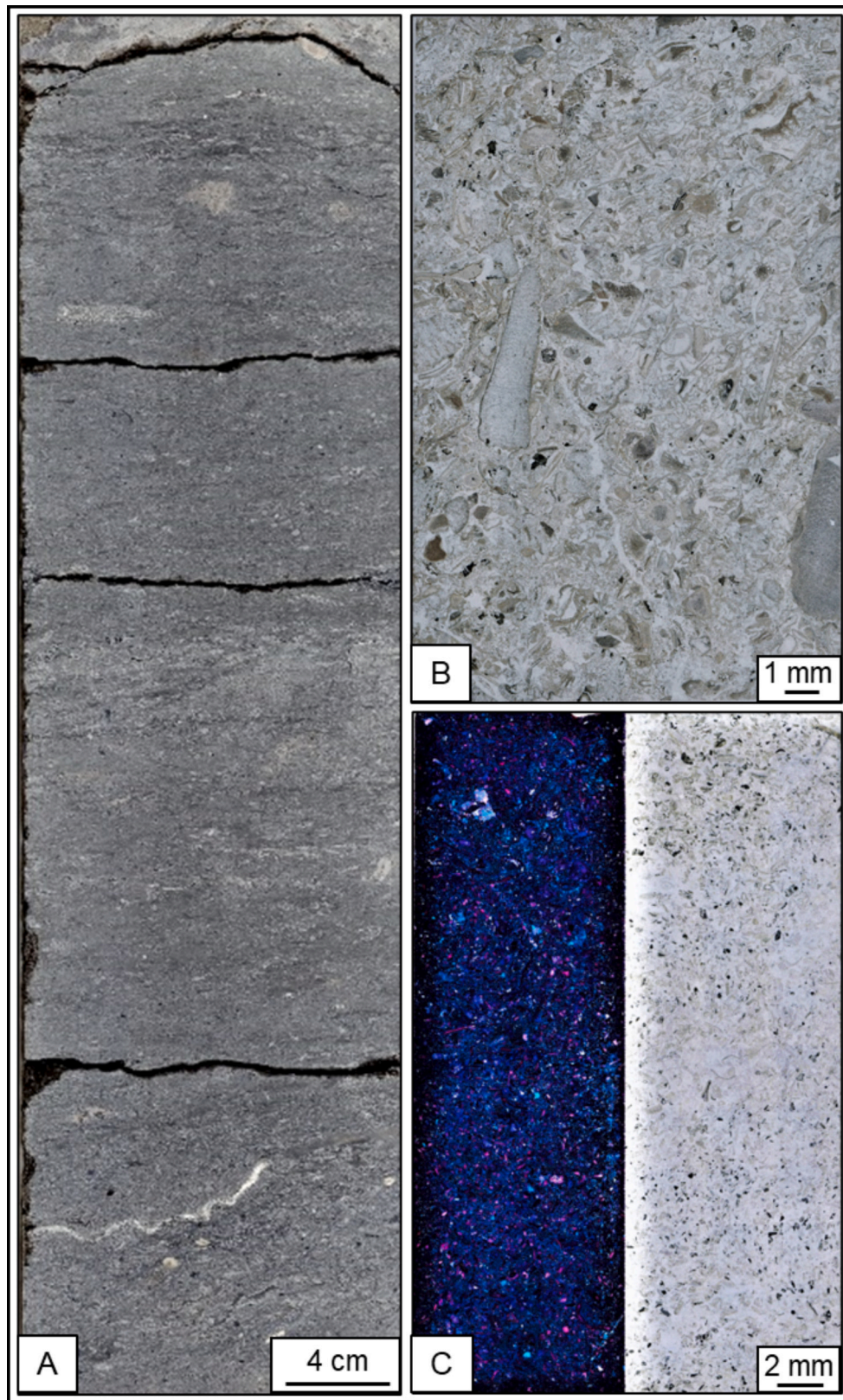


Fig. 8. Facies 1 skeletal rudstone and grainstone: **A** Bioclastic limestone (Bülach-1-1 core); **B** Rudstone composed of coral fragments, bivalve shells, echinoderm fragment (thin section Stadel-3-1); **C** grainstone composed mainly of echinoderm fragments, bivalves, rich in foraminifera (thin section Bülach-1-1).

are absent throughout this facies.

Lithofacies F2: coral platestone (Fig. 9).

The facies consist of platestone with well-preserved corals (*Isastrea*, *Periseris*, *Thamnasteria*). Bioerosion on the coral skeleton is widespread. The matrix consists mostly of wackestone, only locally mudstone. The

components in the matrix consist of encrusting serpulids, echinoids, sponge spicules, coral fragments and echinoid spines. Bioerosion affects both the upper and the lower surfaces (Fig. 9). The porosity commonly displays geopetal sediment infills.

Lithofacies F3: coral pillarstone (sparse) (Fig. 10).

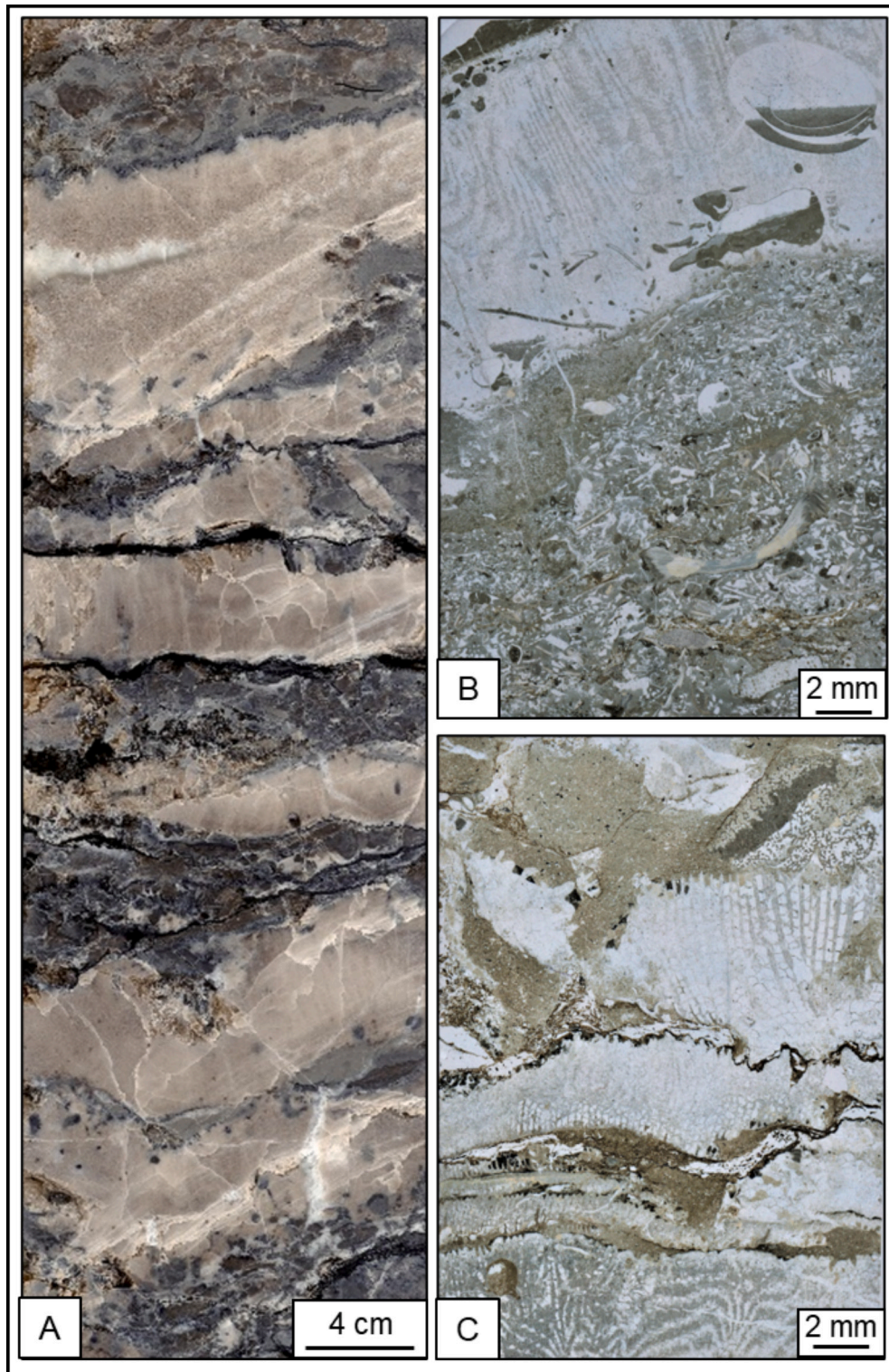


Fig. 9. Facies 2 coral platestone: **A** Growth dominated by platy coral colonies (Bülach-1-1 core) with bioerosion visible on the upper and lower surfaces; **B** Platestone composed of a massive bioeroded (*Gastrochaenolites*) platy coral colony (*Periseris*) with geopetal structures highlighting the polarity, with a wackestone matrix (thin section Stadel-3-1); **C** Platestone composed of several platy coral colonies (*Thamnasteria*, *Isastrea*, encrusted by a sponge) growing in close succession, with a mudstone matrix (thin section Bülach-1-1).

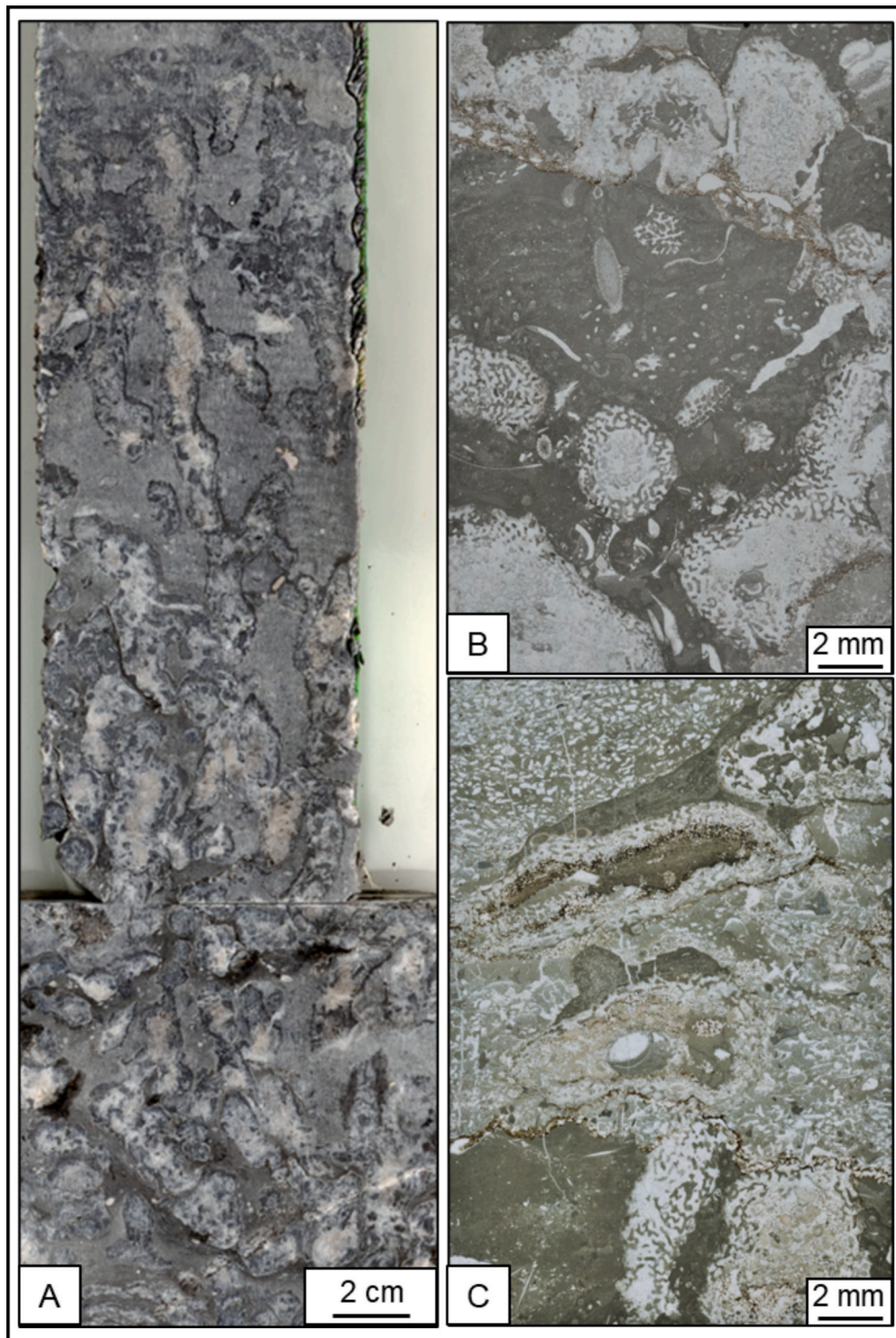


Fig. 10. Facies 3 coral sparse pillarstone: **A** Growth dominated by branching coral colonies (*Dendraraea* in growth position) growing vertically (Bülach-1-1 core); **B** Pillarstone composed of branching coral colonies (*Dendraraea*), with a mudstone matrix containing sponges and echinoderms (thin section Bülach-1-1); **C** Pillarstone composed of branching coral colonies (*Dendraraea*), with a wackestone matrix rich in coral fragments (thin section Stadel-3-1).

The facies is characterised by upward growing corals (*Dendraraea*, *Thecosmilia*). Some of the corals are slightly tilted. Some corals show bioerosion features. The matrix consists of mudstone or wackestone with serpulids, well-preserved echinoids, bivalves, sponges and crinoid fragments. The framework is more filled with sediment than corals, and the corals are widely apart and not densely packed, making more of a sparse pillarstone.

Lithofacies F4: skeletal rudstone with ferruginous crust (Fig. 11).

A ferruginous layer occurs at the top of the reef units and consists of an iron-rich crust with an accumulation of fossil fragments such as echinoderms (crinoids, sea-urchin spines) and bivalves, along with marl extraclasts.

Based on these results, a facies distribution along the sections of the «Herrenwis Unit» was compiled for the Bülach-1-1 and Stadel-3-1 cores (Fig. 12). The «Herrenwis Unit» is 41.90 m thick in the Bülach-1-1 well. The «Herrenwis Unit» in the Bülach-1-1 core begins at 853.94 m on a

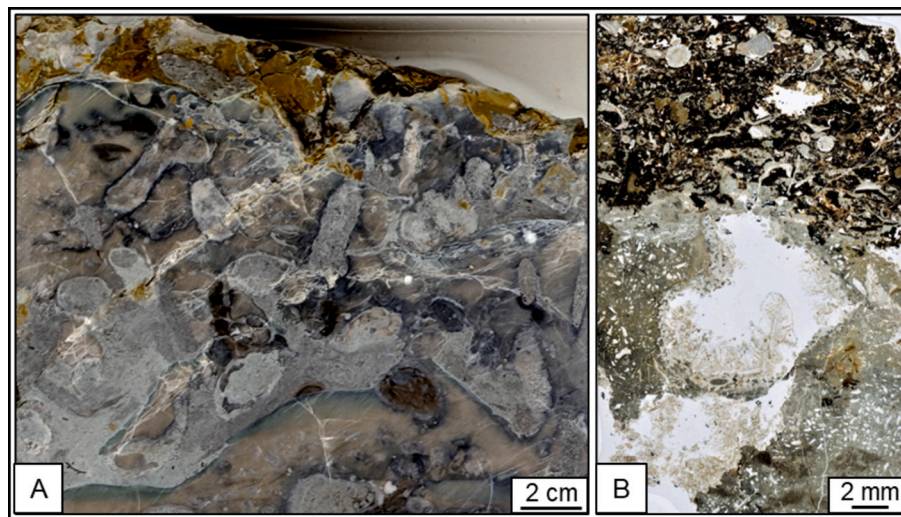


Fig. 11. Facies 4 Ferruginous crust: **A** summit facies within the coral reef unit at both well sites displaying an iron-rich crust rich in fossil fragments (wackestone) (Bülach-1-1 core); **B** Iron-rich crust rich in crinoid fragments, echinoderms fragments and spines, branching coral showing dissolution in a matrix rich in coral fragments (thin section Stadel-3-1).

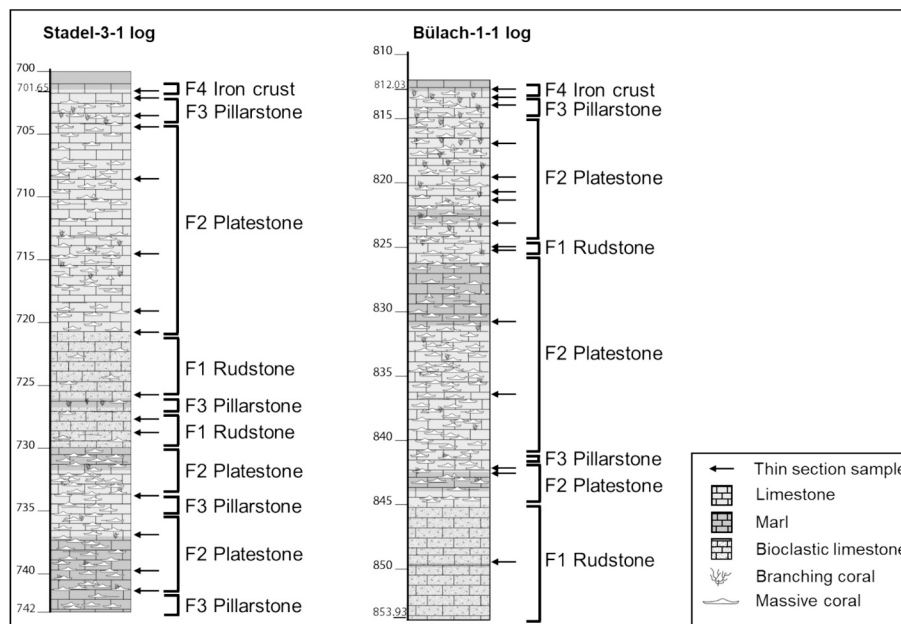


Fig. 12. Facies distribution of the «Herrenwis Unit» based on the descriptive classification of [Insalaco \(1998\)](#) along the wells of Bülach-1-1 and Stadel-3-1.

thin interval with iron-oooids, which belongs to the «Humphriesoolith Formation». The lowest part consists of 10 m of a rudstone facies F1 (bioclastic limestone) where no coral in growth position is observed. The coral-bearing section is mostly composed of the platestone facies F2 (27.00 m in total). The top shows a shift towards a pillarstone facies F3 at 815.00 m with a strong proportion of *Dendraraea* (3.30 m in total) before the reef unit is covered by an iron-rich facies F4 (Fig. 12). The top of the reef is visible at 812.03 m in the core. The «Herrenwis Unit» is 40.35 m thick in the Stadel-3-1 well. The «Herrenwis Unit» in the Stadel-3-1 core begins at 742.00 m immediately on the top of the Wedelsandstein Formation with autochthonous growth facies, with a succession of platestone F2 (26.00 m in total) and pillarstone facies F3 (7.00 m in total). The middle of the unit shifts to a rudstone facies F1 (8.00 m in total) with little corals growing during this interval. The upper part of the unit is dominated by a platestone facies F2, while the top of the reef shows the same facies succession than in Bülach-1-1 with a shift to a

pillarstone facies F3 cut by an iron-rich layer F4 (Fig. 12), visible at 701.65 m.

4.2.3. Coral diversity

Thirteen coral genera including an unidentified genus of the family Polystyliidiidae, all belonging to the order Scleractinia, were identified in the Bülach-1-1 and Stadel-3-1 cores (Fig. 13).

Five of the thirteen genera identified represent 700 of the 720 individual specimens that were identified in the Bülach-1-1 core, and 759 of the 796 individual specimens in the Stadel-3-1 core, or more than 95 % of the total coral population in the two studied cores (Fig. 14). Most genera correspond to a single species.

4.2.3.1. Bülach-1-1 core. Nine different coral genera were identified in this core (Fig. 15). The diversity of the coral population along the Bülach-1-1 core shows an increase from 840.00 m to 837.00 m. A

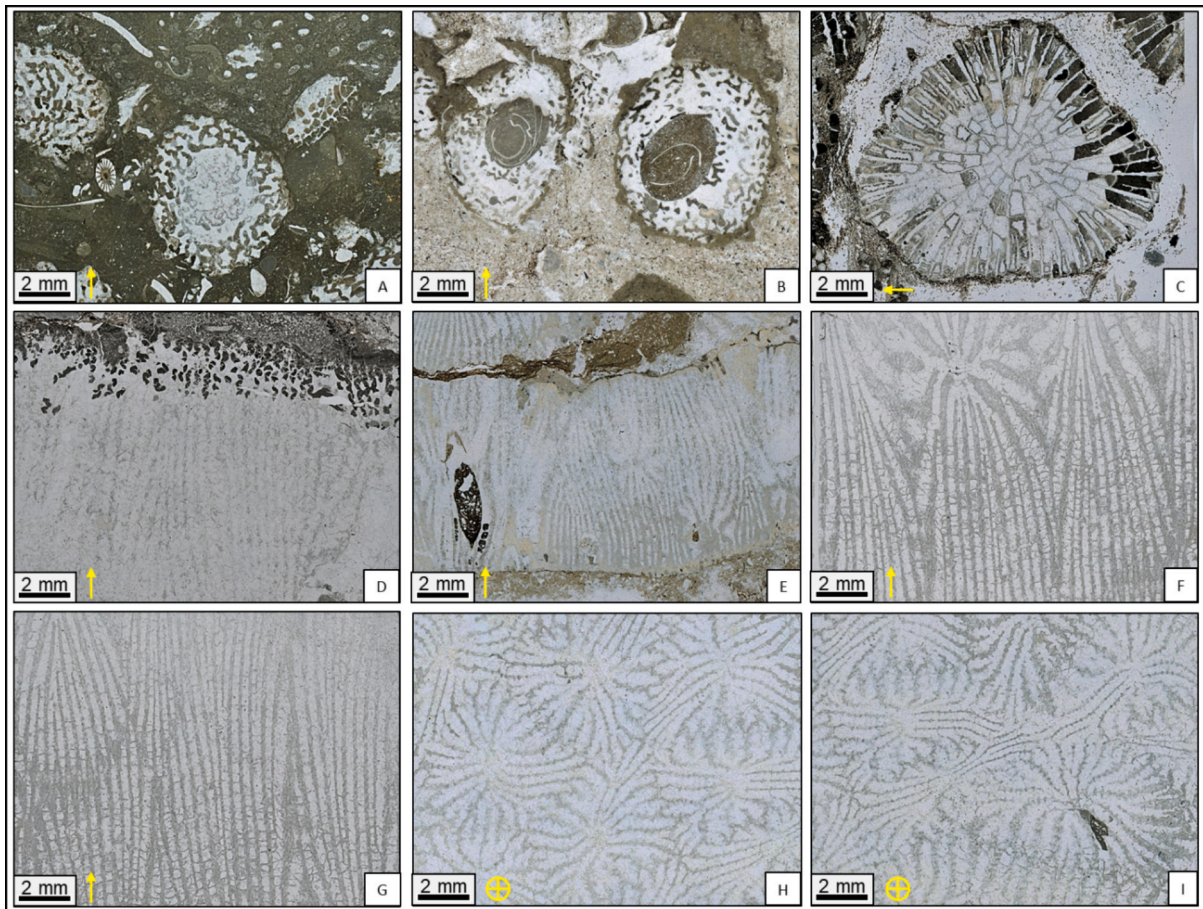


Fig. 13. Main coral taxa of the Bajocian from the «Herrenwis Unit» (Bülach-1-1 and Stadel-3-1 cores): **A** (BUL1–1812.81 m), **B** (BUL1–1836.78 m) Ramose *Dendraraea*, transversal view of branches in thin section; **C** (BUL1–1842.39 m) Phaceloid *Thecosmilia*, transversal view in thin section; **D** (BUL1–1820.82 m) Massive dish-shape *Periseris*, longitudinal view in thin section; **E** (BUL1–1825.55 m) Massive dish-shape *Thamnasteria*, longitudinal view in thin section; **F** (BUL1–1825.58 m), **G** (BUL1–1825.58 m) Massive cerioid *Isastrea*, oblique view in thin section; **H** (BUL1–1816.25 m), **I** (BUL1–1816.25 m) Cerio-meandroid *Isastrea*, transversal view in thin section.

significant decrease in diversity can be observed from 836.00 m to 829.00 m where only one genus is present (*Periseris*), this trend persists up to 826.00 m. The coral diversity starts to increase again from 825.00 m up to the top of the reef (812.03 m), where the highest generic diversity can be observed (7 different genera) before a clear end of the coral facies («Herrenwis Unit»). *Isastrea* and *Thamnasteria* are found almost all along the core in significant numbers (11 to 20 per metre). *Periseris* is the third most present genus, in slightly lower numbers (mainly 1 to 10 colonies). *Dendraraea* shows a strong increase in numbers in the last 5 m of the reef unit.

Only fragments of coral were observed in the lowest part of the «Herrenwis Unit», from 853.93 m to 845.00 m. This section is mainly composed of bioclastic limestone (grainstone), rich in crinoid fragments. The total coral population shows a slow decrease from 837.00 m to 828.00 m (30 colonies to 5) and an increase from 827.00 m to 812.00 m (5 to 35). The *Periseris* population shows a large increase in absolute abundance from 833.00 m to 829.00 m (2–3 colonies to 20), and a smaller one from 824.00 m to 820.00 m (8 to 13). The *Thamnasteria* population is relatively low in number in the lower half of the reef unit (845.00 m to 830.00 m) and shows a steady increase in the upper half (0–2 to 8–10). The *Isastrea* population shows higher numbers in the lower half (8 to 18) and a sharp decrease in the upper half (2 to 10). The *Dendraraea* population shows low abundance in most of the reef and a strong increase (0 to 25) in the last meters of the reef unit (816.00 m to 812.00 m). *Thecosmilia* population shows a peak of more than 30 individuals at the beginning of the reef and is rare in the rest of the coral

limestone. At the top of the reef unit, all coral genera except *Dendraraea* show a declining trend, with *Dendraraea* showing a strong increase in numbers.

4.2.3.2. Stadel-3-1 core. Twelve different coral genera were identified in this core (Fig. 16). *Periseris* was identified throughout the reef interval, *Isastrea* and *Thamnasteria* in more than 80 % of the core length. They constitute a major part of the reef diversity in this core. *Thecosmilia* can be identified exclusively in the lower third of the core, *Dendraraea* exclusively in the upper third of the core. An interval where only *Periseris* and some *Thamnasteria* are present can be observed from 727.00 m to 723.00 m. Never more than five genera are identified on the same segment (see methods).

The total coral population in Stadel-3-1 shows a three-part trend. The first part (742.00 m to 723.00 m) shows a population ranging from 5 colonies to 20, with two peaks at 48 and 30 colonies, linked to a notable increase in the population of *Isastrea* and *Thecosmilia* for the former and a notable increase in the population of *Periseris* for the latter. From 722.00 m to 710.00 m, the total population increases significantly, from 15 to 60 colonies. The total population then gradually decreases from 710.00 m to 701.00 m (from more than 50 to 2), with all coral genera showing such a pattern at the top of the core. The *Periseris* population is globally present along the core, with strong variations in numbers. The highest densities of colonies can be observed in the lower third of the core, from 742.00 m to 728.00 m (3 to 17). It shows a notable decrease from 712.00 m to 701.00 m (15 to 2). The *Thamnasteria* population

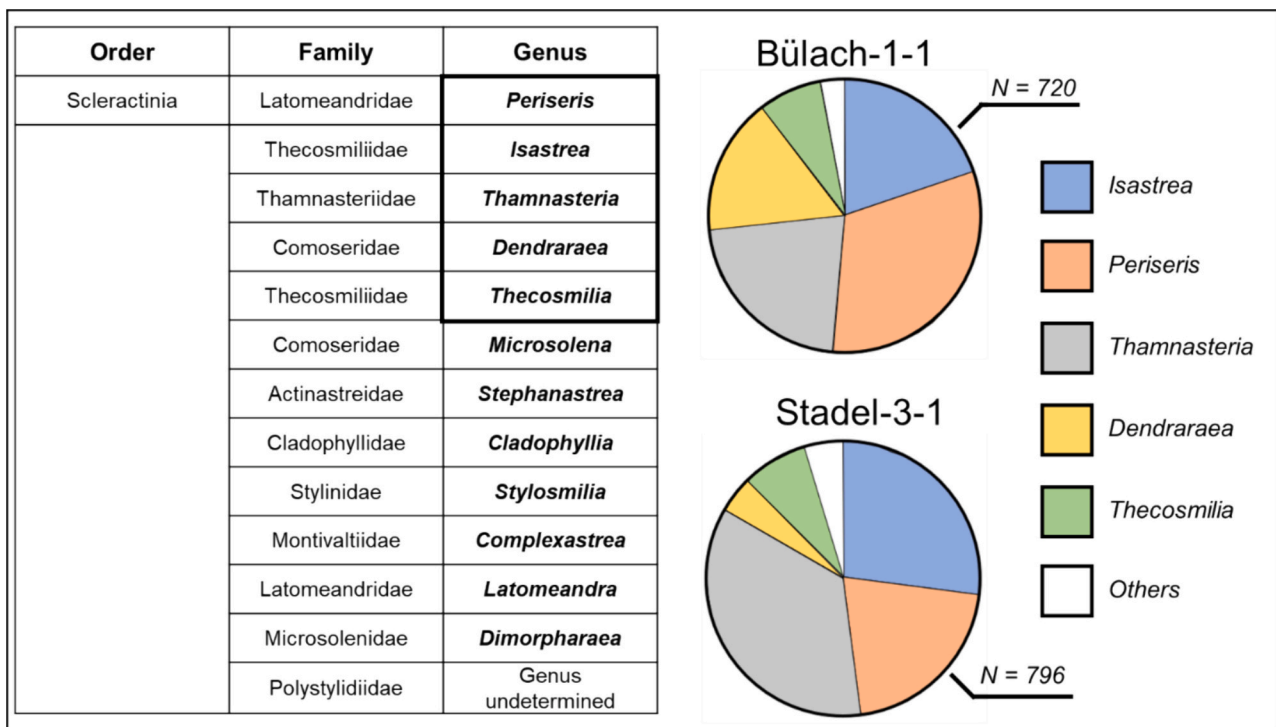


Fig. 14. List of identified coral genera in the Bülach-1-1 and Stadel-3-1 cores. Thirteen coral genera belonging to the Scleractinia Order, were identified. Five out of the twelve distinguished and counted genera represent respectively 700 of the 720 individual specimens that were identified in the Bülach-1-1 core, and 759 of the 796 individual specimens in the Stadel-3-1 core, making up to 95 % of the total coral population in the two studied cores.

shows low numbers (1 to 10) from 742.00 m to 717.00 m, with a large increase from 716.00 m to 710.00 m (9 to 46). A sharp decrease follows from 710.00 m to 701.00 m. The *Isastrea* population shows low numbers (1–10) with a large increase around 720.00 m (more than 20). A notable decrease follows from 714.00 m to 701.00 m (from more than 20 to 3). The *Dendraraea* population shows an irregular pattern throughout the upper part, with few colonies appearing from 716.00 m to 711.00 m. A strong peak appears just at the top of the core (703.00 m). *Thecosmilia* population appears only in the lower half of the reef unit, showing a strong peak around 735.00 m (more than 15).

5. Discussion

5.1. Environmental constraints and biostratigraphic framework for Bajocian coral reefs

5.1.1. Reef scarcity and recovery challenges during the early Jurassic

The entire Early Jurassic was not favourable for reef development in general and coral reefs in particular, mainly due to the aftermath of the Triassic-Jurassic mass extinction event (Tanner et al., 2004; Lathuilière and Marchal, 2009; Kiessling, 2011; Boivin, 2019) and its dramatic effects on marine faunal diversity. The number of reported coral reef-bearing localities is low, as coral reef builders have suffered high extinction rates related to global warming and drowning of platforms (Kiessling et al., 2007). Reef-building organisms also suffered from severe crises during the Early Jurassic, notably near the Pliensbachian/Toarcian boundary and the subsequent Toarcian Oceanic Anoxic Event (T-OAE) (Vasseur et al., 2021), an event linked to volcanism in the Karoo-Ferrar large igneous province (Moulin et al., 2011). Extinction events due to global warming and intense continental weathering at the Pliensbachian-Toarcian boundary and during the subsequent T-OAE may be linked as the cause of the demise of the shallow-water carbonate platform of the South-Western Tethys (Brame et al., 2019; Krencker et al., 2020). Traditionally, the Early Jurassic reflects a reef gap, with a scarcity of coral reefs significantly replaced by bivalve reefs and a

narrow geographical distribution, with coral reefs located mainly in the westernmost and southern Tethys (Lathuilière and Marchal, 2009). The Middle Jurassic shows a similar pattern, with coral reefs still struggling to recover after the crisis events at the onset of the Jurassic. Based on the database on Phanerozoic reefs of Kiessling et al. (1999), seven reef building “cycles” were identified. Although part of the Late Triassic – Late Jurassic “cycle”, in contrast to the Oxfordian-Kimmeridgian reef event, the Bajocian has a low number of reef localities, consistent with the conclusions drawn above on crisis events.

5.1.2. Biostratigraphic constraints on the age of the reef facies

The palynological analyses of the cores from Bülach-1-1 and Stadel-3-1 prove that the first corals and bioclastic limestone and thus also the base of the «Herrenwis Unit» falls in the Sauzei Zone. In Bülach-1-1, almost the lower half of the succession was deposited during the Sauzei Zone (up to sample 832.36 m). In Stadel-3-1 the lower third is of the same age. The upper part was then deposited during the Humphriesianum Zone in both cores.

The end of the reef facies and thus also the end of the «Herrenwis Unit» is somewhat more difficult to interpret, as the samples collected in both cores near the top contain dinoflagellate assemblages with a mixture of different ages. In Bülach-1-1, the uppermost two samples at 812.19 m and 812.05 m show several FADs of the first occurring species, which are in the Blagdeni Subzone of the Humphriesianum Zone (*Aldorfia aldorfensis* and *Rhynchodiniopsis? regalis*), the Niortense Zone (*Atopodinium polygonale*, *Ctenidodinium continuum*, *Korystocysta gochtii*, *Gonyaulacysta pectinifera*, *Valvaedinium spinosum*) and higher within Niortense Zone (*Endoscrinium asymmetricum*, *Ctenidodinium ornatum*, *Gonylodinium hocneratum*). Branching corals in the uppermost 10 to 20 cm in the core (Fig. 11A and B) show some dissolution features. The sediment that was later infilled into these vugs contained a dinoflagellate assemblage indicative of the Niortense Zone. However, the coral facies most likely contains a palynoflora corresponding in age to the Humphriesianum Zone (possibly Blagdeni Subzone).

With the data from Bülach-1-1 some more samples have been

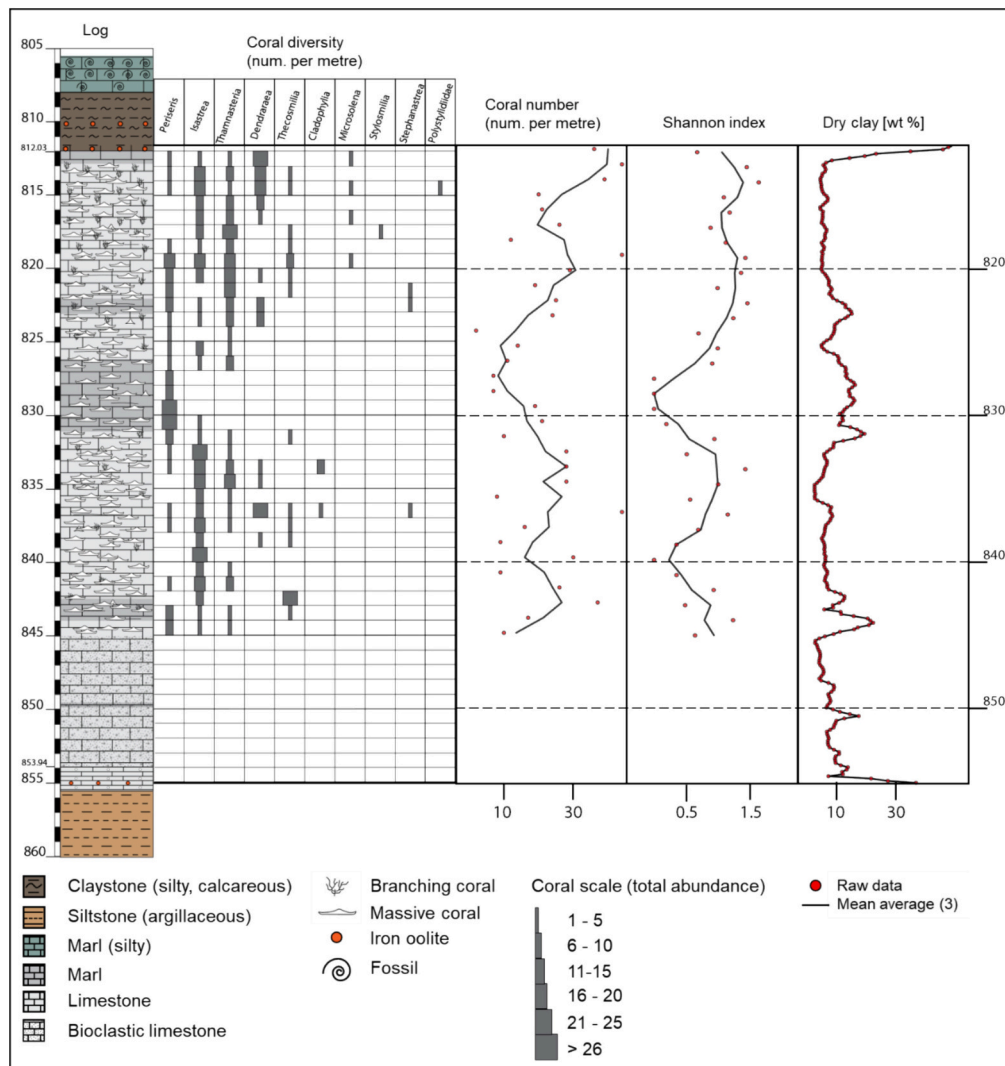


Fig. 15. Diversity of the coral populations in Bülach-1-1 borehole. Dry Clay in weight percentage from MultiMin (Marnat and Becker, 2021).

collected in Stadel-3-1 to assess the age of younger sediment infillings (720.09 m, 703.71 m, 701.79 m and 701.66 m). The assemblages of these four samples display a similar mixture of different ages as in Bülach-1-1. The greyish-green claystone at 720.09 m, as well as the greenish slightly bioclastic sediment at 703.71 m most probably represent both a later infill of sediment into the coral interparticular porosity and/or cavities. The sample at 720.09 m is interpreted to range from possibly Humphriesianum Zone to Zigzag Zone, with most constituents indicating the Parkinsoni Zone, which would result in an infilling during the Parkinsoni and Zigzag zones. The sample 703.71 m, for example, contains among others *Dissilodinium giganteum* and *Hystrichodinium?* sp. indicating an early Bajocian age as well as a questionable *Ctenidodinium combazii* with its FAD in the Zigzag Zone. The next higher sample at 701.79 m (a greyish, slightly bioclastic marl) again appears to fill a cavity, which may have been formed by dissolution processes of former corals. The sample shows even a more diverse assemblage with *Cavatodissilodinium* spp., *Lithodinia* spp. and *Tubotuberella dangeardii* with a FAD in the Zigzag Zone. The top sample at 701.66 m, containing the limonitic stromatolitic crust at the top of the succession, shows again a dinoflagellate cyst assemblage with the main distribution or LADs in the early Bajocian (*Nannoceratopsis plegas plegas*).

The deposition of the upper part of the coral limestone seems to have taken place during the Humphriesianum Zone. The end of coral growth was in the Humphriesianum Zone. There is no documented younger age

from the coral limestone succession. Nothing was subsequently deposited on the reef over a longer period, which is documented by the limonitic stromatolitic crust or hardground. The sample collected from cavities between corals and possibly in previously dissolved corals at the top document unexpected dinoflagellate cysts. Therefore, several infillings seem to occur during the Niortense Zone (Bülach-1-1) and Parkinsoni and Zigzag zones with reworking of older sediments mainly from the Parkinsoni Zone as well as from early Bajocian (Stadel-3-1). Sedimentation on top of the reef body («Herrenwis Unit») probably resumes in the Garantiana Zone to early Parkinsoni Zone in Bülach-1-1 (*Pseudogarantiana* sp. directly on the hardground at 812.03 m; Wohlwend et al., 2021) and certainly during the Zigzag Zone in Stadel-3-1 (palynological sample at 701.38 m). However, the 8 cm thick bed (701.63–701.55 m) with calcitic and limonitic iron-oids between the top of the reef facies and the sample at 701.38 m was not dated (Wohlwend et al., 2022). Therefore, a similar age as in Bülach-1-1 is very likely.

5.1.3. New reef distribution during the Bajocian

The hypothesis of a global reef demise event during the Bajocian requires precise dating to establish the temporal framework within which the reefs developed. The palynostatigraphy was crucial for dating and allowed a precise dating of the reef interval using the bio-chronological standard scales established in Cariou and Hantzpergue

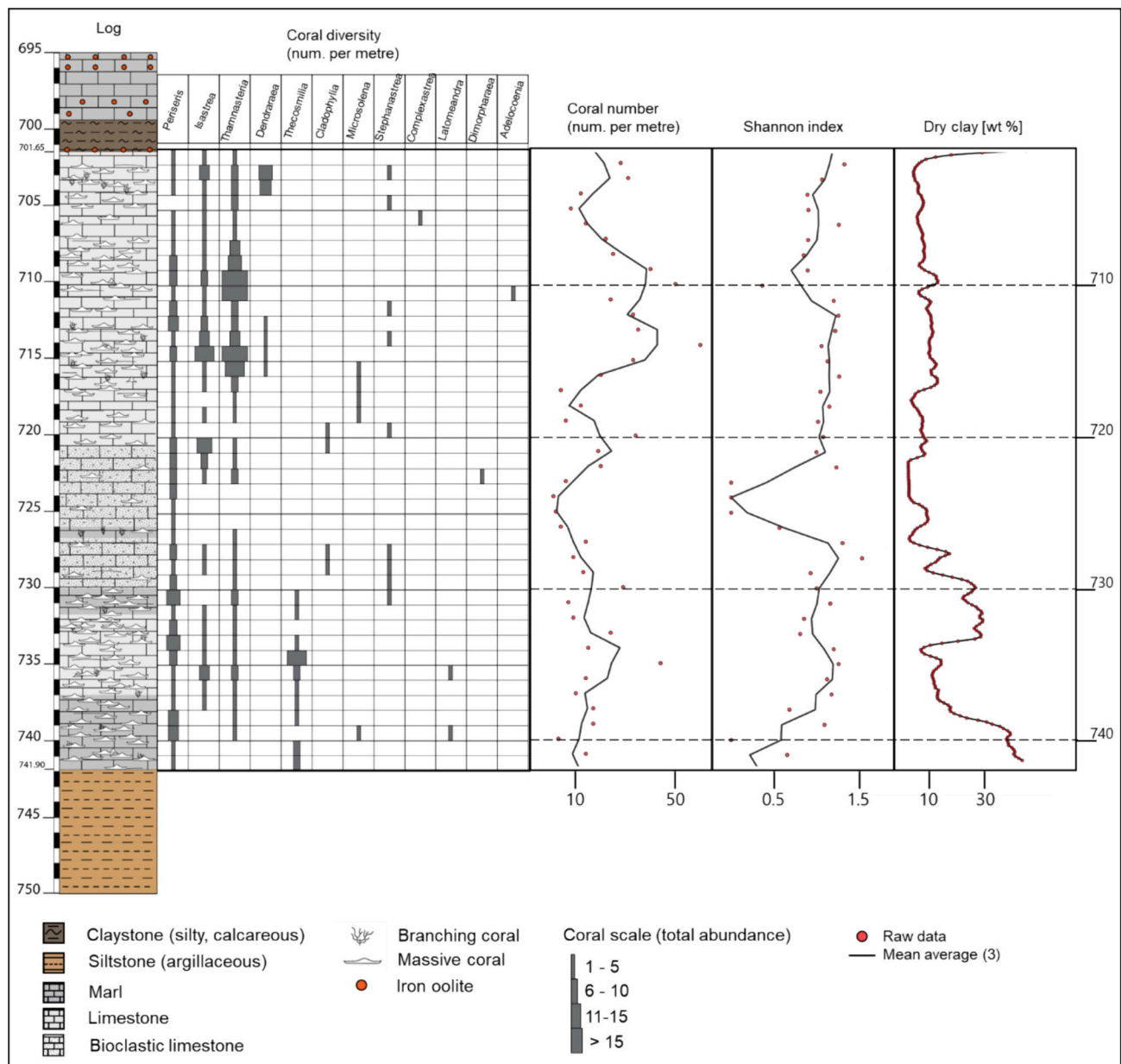


Fig. 16. Diversity of the coral Population in Stadel-3-1 borehole. Dry Clay in weight percentage from MultiMin (Marnat and Becker, 2022).

(1997) (Figs. 5 and 6). The same method has been used in several known Bajocian sites in Eastern France (Burgundy and Lorraine) for this study, including the quarries of Pouillenay, Bainville-sur-Madon and Malancourt-la-Montagne (Fig. 17). These quarries are part of the Eastern Paris Basin Platform, which was extensively developed during the Bajocian. The samples from analogues in France were taken from the Calcaire à Polypiers Formation. This unit is well developed in France, expands over Burgundy and Lorraine and is dated in many sites (Piuz, 2004) from the Sauzei to the Humphriesianum ammonite zones (Durllet and Thierry, 2000; Piuz, 2004). This unit is therefore an excellent benchmark for the comparison of palynological data from the early Bajocian. The palynological assemblages from the «Herrenwis Unit» and from the quarries sampled in France show very strong similarities and can all be dated to the Sauzei to Humphriesianum ammonite zones (early Bajocian) (Fig. 17). The new palynological results from France are in agreement with the recent re-assessment of ammonite biostratigraphy in Luxembourg (Sadki and Weis, 2023). The result also provides strong evidence that parts of the Eastern Paris Basin Platform and the patch

reefs of Switzerland share the same time frame and may be related to the same reef building event. The coral beds reported by Schmidill (1951) in Southern Germany belong to the same palaeogeographical unit. It is also worth noticing that several Bajocian sites in France and England exhibit an abrupt break in sedimentation, referred to as the Vesulian Transgression or Unconformity (Arkell, 1933; Durllet and Thierry, 2000). This event corresponds to a rapid marine transgression within shallow carbonate systems, leading to a distinct erosive surface extensively affected by bioerosion. Notably, this seems to be a shared feature with the reef of the «Herrenwis Unit» and could serve as an additional argument for correlation.

Initially restricted to the western and southern part of the Tethys (Morocco, France), new localities in the more eastern part of the Tethyan realm have been identified, namely in Slovakia (Ivanova et al., 2019; Lathuilière et al., 2023). They were initially considered Oxfordian (Morycowa and Misik, 2005). Pandey and Fürsich (2006) also described Bajocian reefs in the same stratigraphic interval in Iran. Unpublished work also suggests a more extensive development of Bajocian reefs in

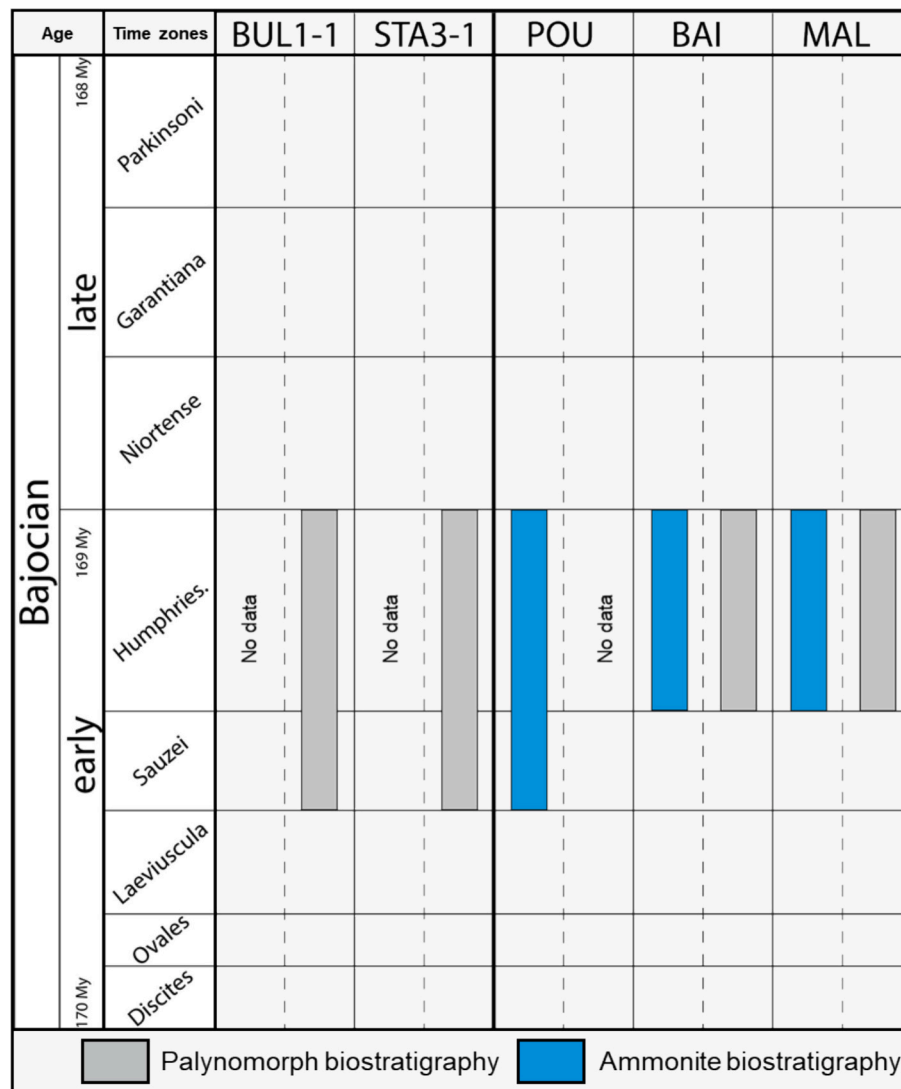


Fig. 17. Comparison of biostratigraphic data of Bajocian reefs from northern Switzerland (BUL1-1: Bülach-1-1 well, STA3-1: Stadel-3-1 well) and from France (POU: Pouillenay quarry, BAI: Bainville-sur-Madon quarry, MAL: Malancourt quarry). Ammonites and palynology dating establish a shared timeframe of reef growth for the «Herrenwis Unit» (Switzerland) and the Calcaire à polypier Formation from the Eastern Paris Basin platform. Zonation established for Western Europe, modified from Cariou and Hantzpergue (1997).

Croatia (personal communications, Turnšek) and in Romania (unpublished field data from B. Lathuilière and I. Lazar). On the Western American shelf, Bajocian reefs are described in Chile (Prinz, 1991) and Argentina (Morsch, 1996). The coral reefs in these localities show strong similarities to those of the «Herrenwis Unit» in composition (Table 1). However, the age of most occurrences is not defined at the resolution of an ammonite zone. Therefore, these coral reefs are not always clearly identified as being of Bajocian age. For example, the Middle Jurassic reefs of Morocco that are so common and prominent in Middle and High Atlas were considered late Bajocian (Sadki and Sha, 2018) and have been reassigned to the early Bajocian (Danisch et al., 2021). The present study makes the case that if palynology is used to accurately date coral reefs, as done here, the coral reefs currently assigned to the interval Bajocian-Bathonian in the various databases could be mostly of early Bajocian in age. This would lead to the conclusion that coral reefs were more widespread than previously thought during the Bajocian (geographical distribution from Leinfelder et al., 2002). This reveals a new map of the early Middle Jurassic where coral reefs are no longer restricted by the more favourable conditions of the Western Tethys but were able to thrive in other locations (Fig. 18). Therefore, the early Bajocian represents a more significant step in the recovery of coral reefs

than previously thought (Leinfelder et al., 1994; Kiessling et al., 1999).

In Kiessling et al. (2002), notable coral reefs are absent in Eastern Tethys prior to the Oxfordian. This is mirrored in the low number of reef domains in Leinfelder et al. (2002). The thick coral-bearing Bajocian series from the East of France (Lorraine), Luxembourg and South of Germany combined with a palaeogeographical expansion not recorded since the Hettangian tends to highlight the fact that the Bajocian was indeed more favourable for coral reef constructors and the stage of a global coral reef growth event.

Even with a higher number of reefs and a greater volume, Bajocian coral reefs are still somewhat geographically constrained and isolated, despite the availability of shallow seas and shelves (Lathuilière and Marchal, 2009). Their palaeogeographical distribution shows positions mainly around the 30°N and 30°S for Bajocian reefs in almost all sites (Fig. 18): for the Western Tethys France (Geister and Lathuilière, 1991; Lathuilière, 2000a, 2000b), Switzerland (Wullschleger, 1966), Luxembourg (Fayard et al., 2005), Germany (Schmidtill, 1951), Croatia (Turnšek, personal communication), Romania (unpublished data) and Slovakia (Ivanova et al., 2019; Lathuilière et al., 2023), for the Eastern Tethys Iran (Pandey and Fürsich, 2006), Tadjikistan (Bazarov et al., 1976 uncertain dating), for the Western Pacific shelf, Idaho (Stanley and

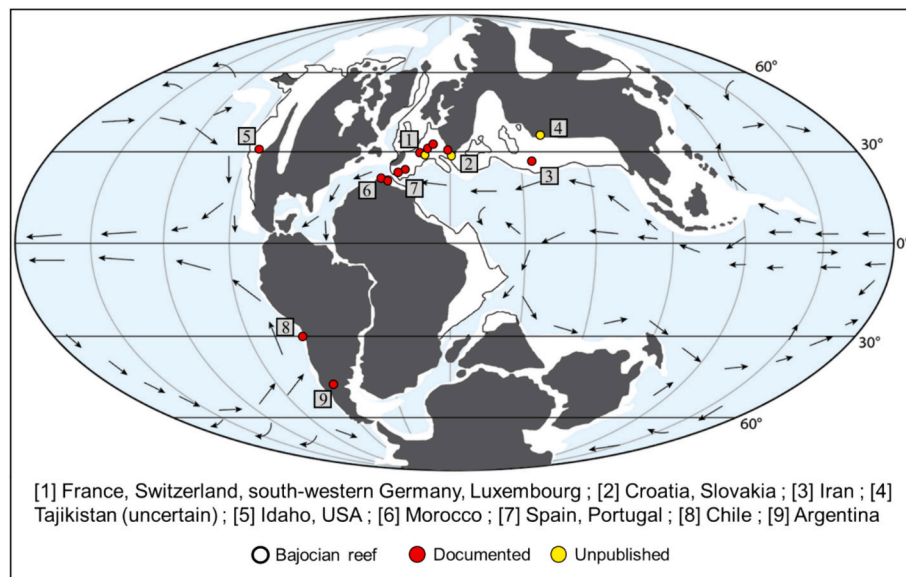


Fig. 18. Distribution of Bajocian reef (modified from Leinfelder et al., 2002).

Beauvais, 1990), Argentina (Morsch, 1996) and Chile (Prinz, 1986, 1991), for the Southern Tethys Spain (Reolid, 2009), Portugal (Borges et al., 2011) and Morocco (Dresnay, 1971; Stanley, 1981; Ait Addi, 2015). For Morocco, according to the biostratigraphic re-assignment made by Danisch et al. (2021), the part of the very numerous Bajocian reefs that belong to the early Bajocian still needs to be studied.

Most of the reefs developed at higher latitudes than one would normally expect, essentially creating a gap along the palaeoequator, even with adequate opportunities of settlement on the eastern African coast and in Indonesia (Leinfelder et al., 2002; Lathuilière and Marchal, 2009). The observed distribution pattern suggests that during the Bajocian, the environmental conditions in low latitudes were not conducive to reef growth. As a result, coral populations may have been forced to migrate towards colder waters at higher latitudes (Retallack, 2001; Beerling, 2002; Hautmann, 2004; Michel et al., 2019). The abnormal distribution pattern observed could potentially be attributed to low-latitude water temperatures that were too high ($> 25\text{ }^{\circ}\text{C}$) to support reef growth (Alberti et al., 2017, 2020). This explanation aligns with the climatic events that occurred during the Triassic-Jurassic Boundary, and in the Early Jurassic (Tanner et al., 2004; Gretz et al., 2013; Boivin, 2019; Krencker et al., 2020). It aligns also with the recent evidence of communities dominated by stromatoporoids in Middle Jurassic equatorial warm waters (Leshno et al., 2023).

5.2. Coral reef growth and palaeoecology

5.2.1. Palaeoecology and palaeoenvironment

5.2.1.1. Encrusters and microbialites. The faunal assemblage in both cores exhibits similarities, with numerous reef-associated organisms such as gastropods, echinoderms, and bivalves observed throughout the reef (Fagerstrom, 1987; Harriott and Banks, 2002). These organisms, which include grazers and suspension feeders, are typically associated with reefs due to their reliance on the substrate, shelter, and food provided by the reef structure. Most corals in the sampled cores, particularly *Perisera*, *Thamasteria*, and *Isastrea*, display various types of borings, including *Gastrochaenolites*, *Entobia*, and *Trypanites* (Fig. 9). The presence of borings on both the top and less exposed underside surfaces of the corals suggests that there was space between the corals and their sediment substrate during growth. This implies a slow sedimentation rate (Jones and Hunter, 1991; Olivier et al., 2006), allowing space for organisms like sponges, bivalves, and echinoderms to access and bore

into the coral skeleton. The correlation between the scarcity of bivalve borings and the abundance of phototrophic organisms, suggesting that the pronounced borings observed in the coral cores may be attributed to a deeper, less illuminated environment, where suspended sediment and/or plankton reduced light penetration (Dupraz and Strasser, 2002). These organisms typically exhibit higher tolerance to environmental variations compared to corals and can thrive in mesotrophic to oligotrophic conditions (Geister and Lathuilière, 1991; Insalaco et al., 1997).

Microbialites in coral reefs are organosedimentary deposits formed through microbial activity, involving the interaction of microbial communities with the surrounding environment. They consist of layers of sediment and carbonate minerals precipitated and cemented by the metabolic activities of microbes such as bacteria and algae (Burne and Moore, 1987; Dupraz et al., 2011). In reef ecosystems, microbialite formation is often associated with extremely low sedimentation rates (Dromart, 1992; Leinfelder et al., 1993). Microbialites can appear as encrustations on coral surfaces, within the reef matrix, or as distinct structures separate from the coral framework. They commonly exhibit laminated or clotted textures, with varying compositions based on environmental conditions (Land and Moore, 1980; Montaggioni and Camoin, 1993; Webb et al., 1997; Camoin et al., 1999; Olivier et al., 2006; Westphal et al., 2010).

While microbial encrustation was common in the Upper Jurassic reefs (Leinfelder and Schmid, 2000), fewer examples are reported from the Middle Jurassic (Lathuilière, 1982; Durlet et al., 2001; Lathuilière et al., 2023) with, however, some locations showing very extensive encrustation of the coral reef (Olivier et al., 2006). In the Bülach-1-1 core, microbialites are found encrusting all coral surfaces, while in the Stadel-3-1 core, only a few corals show encrustation, primarily on the upper surfaces (Figs. 9 to 11). The microbial crust in Bülach-1-1 is thin ($< 1\text{ cm}$), smooth, and compact with a micritic texture, indicating a relatively undeveloped microbial crust compared to other Jurassic reefs (Riding, 2000; Mei, 2007). This limited development of microbial crust could be attributed to environmental factors such as sediment input or light availability. The lower microbialite coverage and extensive boring observed in both cores suggest that the conditions were not optimal for the development of a thick microbial crust (Camoin et al., 2006; Westphal et al., 2010). The differences in microbialite coverage between the cores may reflect variations in sedimentation rates, light availability (depth, turbidity), and position within the reef system (Olivier et al., 2004). The microbial encrustation, being thin and sporadic, indicates that conditions such as reduced luminosity or high sedimentation rates

might have limited microbialite growth (Schmid, 1996; Olivier et al., 2003). This combination of factors, including carbonate and clay mineral input, suggests a complex interplay of conditions affecting microbial growth during the reef's development.

During the initial stages of reef growth, consisting of coral colonies and an associated fauna (bivalves and echinoderms), there seemed to be a simultaneous occurrence of the first phase of development and the initiation of a second phase. This second phase was characterised by the formation of millimetric-thick microbialite crusts. The progression of the second phase, marked by the development of these crusts, probably took place concurrently with the ongoing activities of the first phase. Eventually, sediment encroached, filling in part of the residual porosity. The influx of sediment, especially siliciclastic input, occurred after the growth of corals and the formation of the microbialite crust.

5.2.2. Reef development

The coral reefs from the Bülach-1-1 and Stadel-3-1 boreholes show lower coral diversity compared to modern or Upper Jurassic reefs (Dupraz and Strasser, 1999; Martin-Garin et al., 2012) and are comparable to Bajocian reefs reported elsewhere (Lathuilière, 2000a, 2000b). The faunal composition in these reefs matches Lower Bajocian reefs observed in France (Lorraine) and Luxembourg (Lathuilière, 2000b). Specifically, Bülach-1-1 contains nine different genera, while Stadel-3-1 has twelve, with five genera constituting over 90 % of the corals (Fig. 14). This is significantly lower diversity compared to Oxfordian reefs, where over twenty genera co-exist in a single locality (Martin-Garin et al., 2012). A notable triad of abundant massive coral genera, including *Periseris*, *Isastrea*, and *Thamnasteria*, is characteristic of the Bajocian (Lathuilière, 2000b).

The coral assemblage's composition is closely linked to environmental conditions such as water temperature, depth, light availability, and sediment input (Kiessling et al., 2011; Martin-Garin et al., 2012). Analysis using diversity indexes (Shannon index) reveals two significant decreases in coral diversity at specific depths: 840.00 m and 831.00 m in Bülach-1-1, and 738.00 m and 726.00 m in Stadel-3-1. These decreases correlate with an increase in clay mineral content (831.00 m in Bülach-1-1 and 733.00 m in Stadel-3-1), indicating that increased sediment load affects coral distribution and ecology (Stoddart, 1969; Bull, 1982; Done, 1982; Babcock and Smith, 2000; Fabricius, 2005). The resulting dominance of *Periseris* and the decline of other coral populations suggest that certain environmental conditions, such as higher clay content, significantly impact coral communities.

Most corals in the cores are massive and display a plate-like, flat morphology. This development of massive corals, as opposed to branching forms, is driven by environmental patterns and moderate sedimentation rates (Geister and Lathuilière, 1991; Rice and Hunter, 1992; Leinfelder, 1994; Lathuilière, 2000b; Schmid et al., 2001). In contrast, mesotrophic and mesophotic environments are typically associated with microsolenid-rich coral communities in the Oxfordian (Insalaco, 1996; Leinfelder et al., 1996; Nose and Leinfelder, 1997; Dupraz and Strasser, 2002). This assumption is mainly based on functional morphologic analyses of pennular corals (Lathuilière and Gill, 1995; Gill et al., 2004) and their comparison to similar recent corals of the genus *Leptoseris* described by Schlichter (1991). Although *Microsolenidae* (now named for priority reasons *Comoseridae*, Fromentel de, 1861 in place of *Microsolenidae*, Duncan (1884)) were less common during the Middle Jurassic, the increase of pennular coral *Periseris* could however indicate higher nutrient content due to increased clay sedimentation.

Coral shapes in the Bülach-1-1 and Stadel-3-1 cores, primarily flat and plate-like, suggest adaptation to conditions with lower light availability or deeper waters (Barnes, 1973; Graus and Macintyre, 1976; Leinfelder, 1996; Buddemeier and Smith, 1999; Anthony et al., 2005). During the Jurassic, scleractinian corals were already able to perform photosynthesis due to their likely symbiotic association with zooxanthellae algae, enabling them to harness sunlight to synthesize their own

organic matter (Leinfelder, 2001; Gill et al., 2004). This observation is consistent with recent reefs where platy corals dominate below 30 m (Goreau and Wells, 1967; Zlatarski and Martinez Estalella, 1982), indicating that Bajocian reefs likely developed at depths no shallower than 20 m. The presence of *Dendraraea* at the top of the reef in Bülach-1-1 could signify shallowing or increased sediment influx (Lathuilière, 2000b). This hypothesis aligns with the zonation of *Dendraraea* in Oxfordian reefs (Lathuilière et al., 2005; 2021) and with modern reef succession patterns where lamellar colonies precede branching types (James, 1984; Tucker et al., 1990).

5.2.3. Bajocian reefs in Switzerland

Bajocian coral reefs in Switzerland have been neglected since the early work of Koby (1889). Few examples have been documented (Wullschleger, 1966; Gonzalez and Wetzel, 1996) and the reefs in Switzerland are less imposing than the thick series in Burgundy (Durllet et al., 2001), Lorraine or Luxembourg (Geister and Lathuilière, 1991; Lathuilière et al., 2003), but they are worth noting as they are able to push the limit of the coral reef builders' realm to a time when it is supposed to be much less extensive. During the Middle Jurassic, the study area (northern Switzerland) was an epicontinental sea but closer to the Tethys realm (Gonzalez and Wetzel, 1996). Consequently, most of the lithological series from this time are rich in siliciclastics, a sign of the slightly deeper setting and the influx and sedimentation of terrigenous material towards basins, both of which are detrimental to coral growth. The reef development in this region is not yet well established, probably more sporadic, more related to local palaeo-highs and not in extensive formations resulting from the progradation of wide platforms along the northern Tethyan margin. Indeed, the reefs of the «Herrenwis Unit» can be linked to similar reefs in the same areas. The Gisliflue Reef, 30 km to the southwest, is a reef of similar thickness and composition (Wullschleger, 1966; Gonzalez and Wetzel, 1996). The coral assemblage shows some similarities to the reefs studied from the Bülach-1-1 and Stadel-3-1 cores and compares well to Bajocian reefs in terms of ecology (Degiacomi A., personal communication). Poorly documented archives from pre-Second World War drilling campaigns in the German region of Jestetten, 15 km north of the studied location, also indicate the presence of a 40-m thick coral unit (Franz, 2022). However, coral units are not known from outcrops east of the Gisliflue Reef. This suggests that a number of small patch reefs have probably flourished in neighbouring regions of Switzerland and Southern Germany during the Bajocian. According to the classification of Kiessling et al. (1999), this region of Switzerland should count as a significant new Phanerozoic reef domain.

6. Conclusion

Two new deep boreholes have revealed the presence of a Bajocian reef at the edge of the Northern Alpine Molasse Basin in northern Switzerland. They both show a newly discovered stratigraphic succession («Herrenwis Unit») and display the presence of a forty-metres thick coral reef.

Precise dating of the cores with palynological assemblages has established an early Bajocian age for these reefs, in the Sauzei to Humphriesianum ammonite zones. The same assemblages and time zones were determined from samples from known Bajocian reefs located in eastern France (Burgundy and Lorraine) and show persuasively that the reefs from the «Herrenwis Unit» and the Eastern Paris Basin are contemporaneous. They also share similar coral and faunal diversity.

A low diversity of coral fauna composed mainly of massive forms (*Periseris*, *Isastrea*, *Thamnasteria*) is predominant throughout the reef in both cores. Branching forms (*Dendraraea*, *Thecosmilia*) are also present and co-occur with the massive forms. Massive corals are almost exclusively platy and developed preferably horizontally as it is well known in Recent mesophotic reefs. The corals show signature bioerosion in both cores and all surfaces are affected, indicating the corals grew freely before the residual cavities were filled with sediment.

The associated fauna is mainly composed of bivalves, sponges and echinoderms. Microbialite crusts have developed in both cores but are much more present in Bülach-1-1 than in Stadel-3-1. The microbialites are not well developed and occur as thin crusts (0–1 cm). This could be because of an environment rich in clay minerals, which hinders microbial activity, strong encrusting organism activity (oysters), or that the corals were buried before the crust could grow further.

The coral reef probably consists of isolated patch reefs that developed under non-ideal conditions (slightly mesotrophic), at a less optimal depth (mesophotic, more than 20 m) and with clay mineral and nutrient inputs. At least two noticeable decreases in diversity in the coral population can be highlighted in the two cores with diversity indices. One of the events can clearly be correlated to an increase in clay mineral content and resulted in only a single coral species remaining, while all others could not withstand the change in environmental conditions. Decrease in diversity, increase in clay minerals and increase in nutrients could all be linked to a single causal climatic origin. The occurrence of the second event can be attributed to the deposition of bioclastic limestone, which is formed by the accumulation of skeletal fragments transported to this site through marine currents and covering the reef bodies.

New reef data, reassessment of known reefs and the differentiation of Bajocian and Bathonian reefs show that significantly more coral reefs than estimated encountered favourable conditions to grow and develop during the end of the early Bajocian. This result indicates that the conditions for extensive reef growth were ripe at the end of the early Bajocian. As the same genera were already present at the beginning of the Bajocian and even more diverse in the Bathonian, we discard the hypothesis of coral population more resilient to harmful environmental conditions. Even with the new Bajocian reef distribution presented in this study, no reefs are reported from latitudes lower than 15°, with most known reefs located closer to 30°. This distribution pattern happened most likely because the temperature was too high towards the Equator, preventing reef growth. This would tend to favour a scenario in which the global climate, in particular temperature, is decisive in coral reef growth.

CRediT authorship contribution statement

Arnaud Ruchat: Writing – original draft, Methodology, Investigation, Data curation, Conceptualization. **Bernard Lathuilière:** Writing – review & editing, Supervision, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Stephan Wohlwend:** Writing – review & editing, Supervision, Methodology, Data curation, Conceptualization. **Gaudenz Deplazes:** Writing – review & editing, Validation, Supervision, Funding acquisition, Conceptualization. **Gregor P. Eberli:** Writing – review & editing, Supervision, Methodology, Formal analysis, Data curation, Conceptualization. **Susanne Feist-Burkhardt:** Methodology, Formal analysis, Data curation. **Elias Samankassou:** Writing – review & editing, Visualization, Validation, Supervision, Funding acquisition.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Arnaud Ruchat reports financial support was provided by National Co-operative for the Disposal of Radioactive Waste. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The data that has been used is confidential.

Acknowledgements

We are grateful to the National Cooperative for the Disposal of Radioactive Waste (Nagra) for funding this project, giving access to the material and providing unpublished data. We thank the two anonymous reviewers and the journal's editor, Lucia Angiolini, for their insightful comments and advice, which improved the clarity and quality of the initial manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.palaeo.2024.112504>.

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