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Eocene sediments and a fresh to brackish water biota from the early rifting stage of the Upper Rhine Graben (west of oil field Landau, southwest Germany): implications for biostratigraphy, palaeoecology and source rock potential

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Abstract

The Eocene biota from the pre-rifting stage of the Upper Rhine Graben (southwest Germany) is, with exception of the world-famous fossil sites Messel and Bouxwiller, poorly known. While from these localities exclusively terrestrial and freshwater fossils were recovered, here we present floral and faunal assemblages from the middle Upper Rhine Graben which clearly indicate a temporarily brackish water environment and consist of a diverse palynomorph association, calcareous nannoplankton, foraminifers, ostracods and some fish and reptile remains. Based on the occurrence of *Trochastrites hohnensis,* a Lutetian age is assumed. Organic-walled dinoflagellate cysts, in particular *Phthanoperidinium comatum*, *Phthanoperidinium echinatum*, *Apectodinium homomorphum* and *Apectodinium quinquelatum*, suggest a late Ypresian to Lutetian age. The pollen and spores assemblage includes typical mid Eocene species, such as *Tegumentisporis villosoides*, *Tricolporopollenites crassostriatus* and representatives of Bombacaceae, but a late Ypresian to Priabonian age cannot be excluded. Foraminifers and ostracods do not further refine the biostratigraphical assignment. Hence, a Lutetian age is most probable. The mass occurrence of *Neocyprideis*, various foraminifer taxa and an organic-walled dinoflagellate cyst assemblage of very low diversity are indicative of a brackish water environment. Disarticulated vertebrate remains include fish teeth of Lepisosteidae, turtle plates and alligatoroid teeth of *Diplocynodon* and *Hassiacosuchus*. The present palaeogeographical scenarios do not consider a connection from the Upper Rhine Graben to the North Sea Basin, Alpine Sea/Paratethys or Paris Basin during the mid Eocene. Provided that the middle Upper Rhine Graben was land-locked and definitely not reached by a marine ingression during this time interval, we tentatively suggest that the brackish water taxa may have been accidentally introduced into a brackish inland sea by wind (anemochory), rain, highly mobile insects or vertebrates such as fish, birds and mammals (endozoochory/ectozoochory). The presumably freshwater calcareous nannoplankton species *Nannoserratolithus minutus* Martini is newly described.

Keywords Calcareous nannoplankton · Palynomorphs · Microfossils · Vertebrate remains · Palaeoecology · Organic geochemistry · Paleogene

Introduction

The almost north–south oriented Upper Rhine Graben is the central part of the intracontinental European Cenozoic Rift System which extends from the Western Mediterranean to the North Sea. The Upper Rhine Graben developed in the northwestern foreland of the Alps (Bourgeois et al. 2007). The continental rift zone is approximately 35–45 km across and ranges over 300 km from Basel in the south to Frankfurt in the north, i.e. from the Jura Mountains to the Rhenish Massif. Based on different syn-sedimentary graben subsidence rates and sediment fill various sub-grabens and -basins can be delimitated (Fig. 1). Precise levelling confirms that the fault system is still active to these days (e.g. Behrmann et al. 2003; Sissingh 2003).
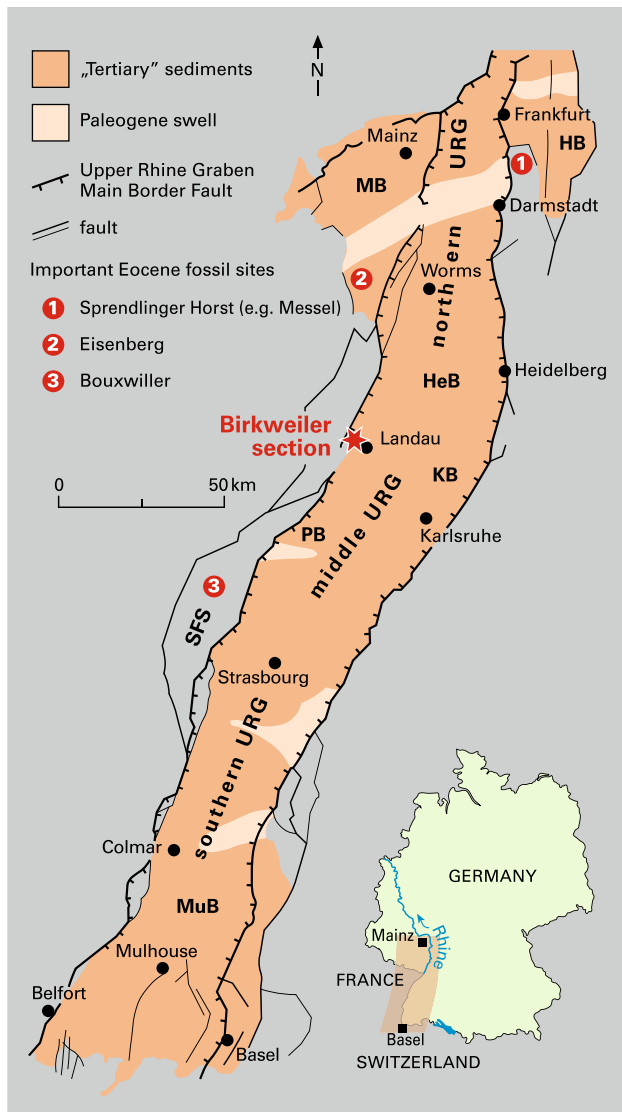
At the northern end of the graben, between Mainz and Frankfurt, the Upper Rhine Graben bifurcates into a NNE–SSW and a NW–SE striking branch. This bifurcation

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Fig. 1 Structural sketch map of the Upper Rhine Graben. *URG* Upper Rhine Graben; *MB* Mainz Basin; *HB* Hanau Basin; *HeB* Heidelberg Basin; *KB* Karlsruhe Basin; *PB* Pechelbronn Basin; *SFS* Saverne Fault System; *MuB* Mulhouse Basin. Modified after Sissingh (2006) and Grimm et al. (2011b). For detailed geological and palaeontological descriptions of important Eocene fossil sites in the middle and northern Upper Rhine Graben see e.g. Sprendlinger Horst: geological map of the area with fossil localities (Mutzl et al. 2022); geology and palaeontology (Smith et al. 2018); palynology (Thiele-Pfeiffer 1988; Lenz et al. 2007, 2011, 2015; Lenz and Wilde 2018; Moshayedi et al. 2018, 2020, 2021; Mutzl et al. 2022) – Eisenberg: description of boreholes, section in clay pit Erlenhof, lithostratigraphy (Schäfer 2000); palynology (Hottenrott 1998, 2000) – Bouxwiller and adjacent localities: lithology (Trauth et al. 1977); palaeontology (Lavoyer 2013); palynology (Schuler and Ollivier-Pierre 1981; Schuler 1990; Sittler and Ollivier-Pierre 1994)

is described as the Rhenish Triple Junction (Sissingh 2003). In the NNE–SSW branch the Upper Rhine Graben continues into several smaller Hessian grabens and basins (e.g. Wetterau Graben, Horloff-Graben, Hessen Depression

with small grabens). In the Northwest German Basin, NNE–SSW striking faults are regarded as a prolongation of the graben. The NW–SE striking graben trend includes the Neuwied Basin and the Lower Rhine Embayment which structurally extends into the Roer Valley Graben. At least parts of the European Cenozoic Rift System are pre-Mesozoic structures. They developed in ancient crustal weakness zones which probably originated from late Variscan, Permo-Carboniferous fracture systems. The Paleozoic faults were repeatedly re-activated during the Mesozoic and Cenozoic due to roughly N–S oriented, syn-collisional compression (Sissingh 2003; Allenbach and Wetzel 2006) which probably has been induced by the evolving Alpine and Pyrenean orogens (e.g. Dèzes et al. 2004).

Due to intense hydrocarbon, potash/salt, and geothermal exploration in the Upper Rhine Graben, an extensive data set comprising numerous deep wells and seismic sections has accumulated and hence, the graben has become one of the best-studied rift zones in the world. The graben is the oldest known oil province in Western Europe. Oil shows and tar sands triggered exploitation dating back to 1498 (Sittler 1972; Böcker et al. 2017). The region is still in the focus of hydrocarbon exploration as in 2003 the Römerberg oil field, one of the most significant oil reservoirs of Germany, has been discovered near Speyer during drilling of a geothermal well. Further oil fields are located e.g. near Pechelbronn, Landau and Stockstadt (Perner et al. 2018). Potash/salt exploration concentrated on the southern depocentre of the Upper Rhine Graben where in the Mulhouse Basin upper Eocene (Priabonian) to Oligocene evaporites including potash and halite were precipitated. North of this basin, near Sélestat, Strasbourg and Pechelbronn, halite and sulphate bearing successions are known from the subsurface (e.g. Cendón et al. 2008). Numerous deep geothermal boreholes have been drilled in areas of positive temperature anomalies to exploit energy from deep-seated granite and Paleozoic and Mesozoic sedimentary successions, e.g. in Landau, Soultz-sous-Forêts and Rittershoffen in eastern France (see Baillieux et al. 2013; Duringer et al. 2019; Frey et al. 2022).

The sedimentary fill of the Upper Rhine Graben reaches a maximum thickness of as much as 4000 m (Behrmann et al. 2003). The tectono-sedimentary evolution of the graben is complex. The magnitude of subsidence was different in various parts of the graben and together with climatic effects and transgressions from the Paleogene North Sea and the Alpine Molasse Basin decisive for the depositional history of the graben fill.

In the Upper Rhine Graben, the early rifting stage started in the early Eocene (Ypresian) to mid Eocene (Lutetian/Bartonian). Numerous shallow and isolated depressions, partly fault-controlled, developed separated by highs. The palaeogeographically confined depressions were filled with predominantly fluvio-lacustrine sediments. The thickness of the lowermost Schliengen Formation (Fig. 2)
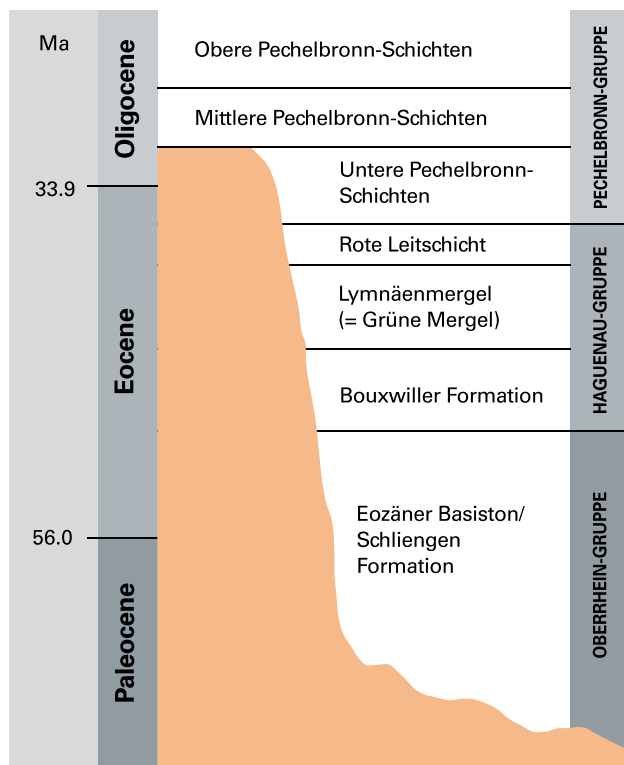
Fig. 2 Lithostratigraphy of the Paleocene to lowermost Oligocene in the middle Upper Rhine Graben. Based on Grimm et al. (2011b) and Schäfer (2013). Numerical ages (Ma) following International Chronostratigraphic Chart, 2022/10 (https://stratigraphy.org/ICSchart/ChronostratChart2022-10.pdf)

(= Siderolith-Schichten; Schäfer 2013) in the southern and middle part of the graben varies between less than a metre and up to 108 m. The formation consists of residual soils and intercalated sand horizons. As the sediments are barren with regard to non-reworked fossils, age assignment is difficult. In places they are overlain by the middle Lutetian Bouxwiller Formation (see below) (Grimm et al. 2011b). The mostly pelitic Eozäner Basiston in the middle and northern part of the Upper Rhine Graben is similar to the Schliengen Formation. The Eozäner Basiston is characterised by strong thickness variation, deposition in local depressions and the lack of time-indicative fossils. The basal variegated Eocene clays are also barren with regard to palynomorphs (e.g. Sittler 1968a). A latest Ypresian to early Lutetian age is assumed (Grimm et al. 2011b). The upper Ypresian to lower Lutetian Messel Formation (Lenz et al. 2015), world-famous for a highly diverse and exquisitely preserved flora and fauna, is mostly restricted to ancient maar lakes on the Sprendlinger Horst (e.g. maar lakes Messel and Offenthal; Smith et al. 2018; Moshayedi et al. 2020). Another biostratigraphically important site is Bouxwiller, type locality for the middle Lutetian Bouxwiller Formation which is the basal unit of the Haguenau-Gruppe. The clayey marls and limestones, deposited in small freshwater lakes, are rich in e.g. charophytes, land and freshwater snails and vertebrate remains, in particular mammal marker species (Lavoyer 2013). An intercalated thin coal seam yielded a diverse and well preserved palynomorph association (Schuler and Ollivier-Pierre 1981; Schuler 1990; Sittler and Ollivier-Pierre 1994). The middle unit of the Haguenau-Gruppe are the Grüne Mergel which are at least partially time-equivalent to the Lymnäenmergel and Landauer Mergel *sensu* Breuer and Feist (1986) (for a detailed discussion on Eocene lithostratigraphical terms in the Upper Rhine Graben see Stratigraphical synthesis). Based on charophytes and mammal remains the Grüne Mergel are dated as mid Lutetian to mid Priabonian. Deposition took place in an inland sea subdivided by highs. In the middle Upper Rhine Graben, they consist mainly of grey to greenish clays and calcareous marls. Because of the occurrence of rare organic-walled dinoflagellate cysts (dinocysts) and a low-diversity foraminiferal fauna, brief marine ingressions from the south (Schäfer 2013) or west (Grimm et al. 2011b: 59) are assumed. In the southern part thick deposits of evaporites such as anhydrite/gypsum, halite and potash give evidence of hypersaline conditions. Highest thickness values exceeding several hundred metres have been recorded from the southern and middle part of the Upper Rhine Graben (Grimm et al. 2011b). Except for a few dinocysts, foraminifers and ostracods the invertebrate fauna is dominated by land and freshwater gastropods, questionable brackish water gastropods and bivalves (e.g. Sittler 1969). A well from the Landau oilfield (Landau 117) encountered 6 m of olive grey to green grey, fossiliferous claystones and clayey marlstones. Charophytes, foraminifers, ostracods and vertebrate remains have been recovered but only the charophytes are taxonomically treated indicating a position in the Lutetian *Maedleriella embergeri* charophyte zone (Breuer and Feist 1986). Some vertebrate remains from the same core of this well have been described and figured by Weiler (1963). The Grüne Mergel are overlain by the middle Priabonian Rote Leitschicht, a distinct marker horizon. In the southern Upper Rhine Graben, a bed containing foraminifers and calcareous nannoplankton is indicative of a marine ingression (Ohmert 1993; Martini and Reichenbacher 2007). Starting with the Pechelbronn-Gruppe, i.e. in the late Priabonian, the main rifting stage commences. At the base, terrestrial, limnic, fluviatile and marine deposits were laid down but during the early Rupelian (Mittlere Pechelbronn-Schichten) the marine influence increased due to the first marine transgression from the Paleogene North Sea into the Upper Rhine Graben via the Hessian Depression. It is assumed that this resulted in a connection between the North Sea Basin and the North Alpine Molasse Basin (Sissingh 2006).

Apart from the fossil-rich Messel and Bouxwiller formations, exposed in few old pits, palaeontological data from Eocene sediments of the Upper Rhine Graben are sparse as

they are mostly overlain by a thick sedimentary succession of Oligocene to Quaternary age (e.g. Straub 1955; Wirth 1969; Breuer and Feist 1986). Fossil assemblages from the early rifting stage are particularly interesting as they are useful in unravelling complicated facies relationships such as changes in salinity, water depth and oxygen supply. In addition, some fossil groups, e.g. palynomorphs, calcareous nannoplankton, charophytes, foraminifers, ostracods and mammals, have been successfully applied to develop a biostratigraphical scheme for marine to terrestrial sediments of the Upper Rhine Graben. However, very few Eocene fossil sites yielded more than one age-indicative fossil group (e.g. wells in the Landau oil field; see Wirth 1969; Breuer and Feist 1986) which complicates biostratigraphical correlations of the oldest graben-fill sediments deposited in small and isolated depressions.

This study focuses on Eocene fossil assemblages recovered from a borehole and two temporary outcrops on the western shoulder of the middle Upper Rhine Graben which were accessible during earthworks for the bypass highway B 10 between Albersweiler and Siebeldingen, west of Landau (Fig. 3). The assemblages comprise palynomorphs, calcareous nannoplankton, foraminifers, ostracods, molluscs (Kadolsky 2015; Kadolsky and Hartkopf-Fröder, in prep.) and vertebrate

Fig. 3 Simplified map of the Birkweiler area showing outcrop localities and site of borehole B 804

remains (teleosts, reptiles, but no mammals). Overall, fossils are abundant and well preserved but apart from palynomorphs and otoliths (Bettina Reichenbacher, written communication, February 01, 2023) of low diversity. The presence of various age diagnostic and palaeoecologically significant fossil groups is exceptional for Eocene sediments in the Upper Rhine Graben. Hence, the main objectives of this interdisciplinary study are to examine the fossiliferous sediments including organic geochemical analyses and to give a comprehensive taxonomic account of the palynomorphs, calcareous nannoplankton, foraminifers, ostracods and disarticulated vertebrate skeletal remains (fish teeth, reptiles) in order to present a precise age assignment based on pollen, spores, dinocysts and calcareous nannoplankton. In particular from the palaeontological data, a palaeoenvironmental reconstruction and palaeogeographical indications will be inferred. In addition, the hydrocarbon generation potential of the studied samples is compared with the age-equivalent succession from the nearby but more graben-wards Landau oilfield region.

In the Upper Rhine Graben many lithostratigraphical units are not yet formally defined. Stratigraphical correlations are frequently hampered by the presence of various sub-basins with different subsidence, thickness variations and separate geological history (e.g. Derer 2003; Duringer et al. 2019), small-scale facies heterogeneities and complex depositional patterns due to syn-sedimentary graben tectonics and relative sea-level fluctuations (e.g. marine–brackish–freshwater; Schuler 1983; Rauscher and Schuler 1988; Rauscher et al. 1988; see also Derer 2003), different stratigraphical schemes used in France, Germany and Switzerland in former times (e.g. Pirkenseer et al. 2018), scattered and scarce fossils, the lack of state-of-the-art taxonomic research, reworking of microfossils (e.g. Pirkenseer et al. 2011) and decalcification of the host sediment, to mention but a few. Hence, numerous local lithostratigraphical terms exist. We here follow Grimm et al. (2011b) and Schäfer (2013) who summarised Paleogene/Neogene lithostratigraphical units of the Upper Rhine Graben. We refrain from translating these units into English but keep applying the original German and French terms.
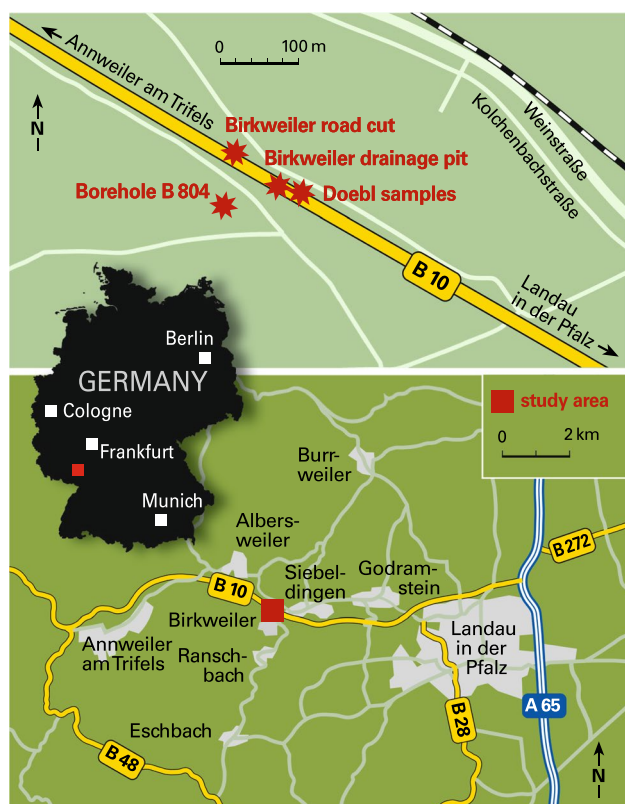
Geological setting of the Albersweiler–Siebeldingen area

The western shoulder of the Upper Rhine Graben in southern Palatinate and the northern Vosges (Fig. 1) is one of the key areas for the interpretation of the tectono-sedimentary evolution of the rift system (e.g. Illies 1963; Stapf 1988; Lopes Cardozo and Behrmann 2006). The area has been intensively studied with regard to stratigraphy, syn-rift sedimentation, structural configuration and petroleum systems because of relatively good exposures of upper Paleozoic and lower Mesozoic rocks, numerous borehole data obtained during

hydrocarbon exploration of the economically important nearby Landau oilfield (e.g. Doebl and Bader 1970; Bruss 2000; Böcker and Littke 2014, 2016; Böcker et al. 2017), some isolated Upper Triassic and Lower Jurassic outcrops (Nottmeyer 1954), and the westernmost exposures of the Mid-German Crystalline High (Reischmann and Anthes 1996; Frey et al. 2021). Stratigraphical and tectonic research resulted in several large-scale geological maps (e.g. Nottmeyer 1954; Illies 1963; Doebl and Bader 1970; Stellrecht 1971; Hartkopf 1981) which provide a detailed survey on the regional geology between Eschbach and Burrweiler.

However, the existence of numerous deep-seated landslides widespread on hill slopes formed by Triassic, Paleogene and Neogene clays and marls has been neglected or underestimated (e.g. Nottmeyer 1954) although in some areas of the Mainz Basin, where similar geological conditions are found, extensive landslides are well known. Here, landslides with a slip plane in depths of up to 25 m can cover some square kilometres (Schäfer 2012). To the north and east of Birkweiler numerous landslides have been observed, e.g. by Nottmeyer (1954) and Hartkopf (1981), but their considerable dimensions have been fully captured not until earthworks started for the bypass highway B 10 by which an entire hill slope became displaced which subsequently required large-scale stabilisation measures (Wichter et al. 1988). The reactivated fossil slip planes are up to 26 m deep, indicating massive ground movements. Following Schröder (1984) and Wichter et al. (1988), in some of the numerous boreholes Paleogene/Neogene sediments are supposed to be overlain even by dislocated Permian (Rotliegend), Upper Triassic (Keuper) and Lower Jurassic rocks. The thickness of the displaced material is claimed to reach at least 13 m (e.g. in borehole B 704; Schröder 1984: 11; Wichter et al. 1988: fig. 2). In the nearby borehole B 703 Paleogene/Neogene strata are alleged to be overlain by ca. 29 m of Lower Jurassic rocks which may be due to a landslide with the slip plane near 17 m and additional compressional tectonics. However, a re-evaluation of the microfossil assemblage of boreholes B 703 and B 704 proved a Late Triassic (Keuper) age for those strata assigned to the Paleogene/Neogene by Wichter et al. (1988: fig. 2). Probably, in these two boreholes an undisturbed succession with Keuper sedimentary rocks at the base overlain by Lower Jurassic mudstones/marlstones has been encountered. Regardless of whether displaced Lower Jurassic mudstones overlay Paleogene/Neogene ones or the Upper Triassic/Lower Jurassic succession is undisturbed, in such an extensive landslide area *in situ* and displaced material are hardly to differentiate. Particularly in shallow outcrops and boreholes with a total depth above the slip planes, displaced material cannot be identified as a result of landslide mass movements. A reliable geological map depicting those strata which are still in their original position below dislocated rock masses can hardly be constructed, particularly as the area is also characterised by

complex fault tectonics related to the western border fault of the Upper Rhine Graben. Consequently, Wichter et al. (1988) refrained from constructing a geological map in spite of having available data from 172 boreholes.

In the road cut of the bypass highway B 10 from west to east Permian (southwest of Albersweiler), Eocene (north of Birkweiler) and Lower Jurassic (west of Siebeldingen) sedimentary rocks were exposed.

To the east, the Upper Rotliegend (Permian) red beds of the Wadern Formation (Boy et al. 2012) are bordered by a major fault ("westliche Rheingrabenrandstörung" in the terminology of Stapf 1988), which roughly runs in north–south direction from west of Birkweiler through Albersweiler. The red beds are mainly composed of conglomerates and sedimentary breccias with some intercalated thin sandstone and mudstone beds. The coarse-grained facies is interpreted as alluvial fan deposits (fanglomerates) which unconformably overlay the Albersweiler gneiss complex (Reischmann and Anthes 1996).

Lower Jurassic mudstones were rather well accessible in the embankment of the ramp to the B 10 where still some small outcrops exist today. In the road cut, these mudstones were poorly exposed due to extensive landslides. The brickyard pit west of Siebeldingen was shut down years ago and when the roadworks started exposures were not accessible anymore due to recultivation. This locality was a well-known fossil site (e.g. Drexler 1958; Heidtke 2006) which yielded a diverse marine fauna including foraminifers, ostracods, molluscs and rare vertebrate remains. The Lower Jurassic sedimentary succession is composed of grey to black mudstones and marlstones. They are rich in organic matter reaching up to approx. 4.5 % TOC (total organic carbon; Böcker and Littke 2016). Thin horizons of marly limestones up to 20 cm thick and limestone concretions up to 10 cm in diameter are intercalated. The Lower Jurassic succession in the Siebeldingen area has been described in detail by Jüngst (1938) and Drexler (1958). Based on the succession in the brickyard pit west of Siebeldingen Jüngst (1938: 154) assigned the dark grey mudstones to the Lias α and lower Lias β (= Hettangian and Sinemurian) while the presence of Lias γ (Pliensbachian) was assumed to be doubtful. The occurrence of *Passaloteuthis paxillosus* (von Schlotheim, 1813) depicted in Heidtke (2006: fig. 6) clearly indicates that Pliensbachian sedimentary rocks were present in the brickyard section (Günter Schweigert, written communication, February 01, 2023).

Material

Samples were collected along the road cut of the new bypass highway B 10 north of Birkweiler (a municipality between Landau in der Pfalz and Annweiler am Trifels, southwestern

Germany) in 1980–1984 and from boreholes drilled for highway construction and landslide stabilisation (Figs. 3, 4).

Extensive earthworks were necessary as the bypass crosses an approx. 700 m long vineyard hill slope which was known to be prone to landslides since a long time (Schröder 1984; Wichter et al. 1988). During these earthworks fossiliferous Eocene sediments were exposed. Sampling concentrated on a stromatolite horizon and greenish marl horizons rich in hydrobioid gastropods as well as otoliths (Figs. 3, 4). This fossil site is hereafter named "Birkweiler road cut" (map TK 25 Sheet 6714 Edenkoben; UTM coordinates (WGS84) ca. 32U 429652 5451280; ca. R 34 29700 H 54 53022).

From this road cut Franz Doebl, then with the Wintershall AG, Betrieb Landau, sent six samples to the Geologischer Dienst Nordrhein-Westfalen, Krefeld for palynological analyses in June and July 1979. Of these a lignite sample (Fig. 3) yielded an Eocene miospore assemblage (sample no. 74933; UTM coordinates (WGS84) ca. 32U 429717 5451231; ca. R 34 29765 H 54 52973). The assemblage of a second sample (sample no. 74936, UTM coordinates (WGS84) ca. 32U 429735 5451220; ca. R 34 29783 H 54 52962) was badly preserved so that a biostratigraphical assignment was not possible. The four remaining samples proved to be barren with regard to palynomorphs.

After the beginning of the earthworks for the bypass highway B 10 north of Birkweiler new and newly reactivated landslides occurred which were tried to be stabilised by deep drainage galleries, concrete dowels, bore pile walls and rockfills. In addition, numerous exploration and inclinometer borings, some of them entirely cored, were drilled (Schröder 1984; Wichter et al. 1988). The samples were biostratigraphically investigated by Volker Sonne (then Geologisches Landesamt Rheinland-Pfalz) using foraminifers and ostracods but the results remained unpublished. This material, housed in the Landesamt für Geologie und Bergbau Rheinland-Pfalz, was available for examination. Especially important is borehole B 804 (map TK 25 Sheet 6714 Edenkoben; UTM coordinates (WGS84) 32U 429627 5451226; R 34 29675 H 54 52968; Figs. 3, 4) which yielded foraminifer, ostracod, hydrobioid and otolith assemblages. Core samples of some other boreholes (A 1–A 10) are housed in the Landesamt für Geologie und Bergbau Rheinland-Pfalz and were studied for palynology. Only samples from boreholes A 9 (map TK 25 Sheet 6714 Edenkoben; UTM coordinates (WGS84) 32U 429647 5451294; R 34 29695 H 54 53036) and A 10 (map TK 25 Sheet 6714 Edenkoben; UTM coordinates (WGS84) 32U 429704 5451191; R 34 29752 H 54 52933) yielded an Eocene palynomorph assemblage. All other samples proved either to be barren with regard to palynomorphs or to be Mesozoic in age and therefore are not considered in this study.

During the stabilisation measures, grey marls rich in hydrobioids, some other gastropod species and otoliths were collected from already excavated material of a three metres deep drainage pit right beside the highway and very close to the Birkweiler road cut locality (map TK 25 Sheet 6714 Edenkoben; UTM coordinates (WGS84) ca. 32U 429700 5451248; ca. R 34 29748 H 54 52990). As the pit was entirely boarded neither a profile could be measured nor any samples could be recovered directly from the section. Hence, samples are stratigraphically unconstrained spot samples not in stratigrapical order. Material from this site is referred to as "Birkweiler drainage pit" (Fig. 3).

Methods

Vitrinite reflectance and organic geochemistry

Vitrinite reflectance analysis was performed on six samples from the Birkweiler drainage pit and a well from the Landau oilfield following standard techniques as outlined in Böcker et al. (2017).

Three sediment samples (Albersweiler A 10, A 17 and A 19, all from the Birkweiler drainage pit) were analysed for saturated hydrocarbon distributions as described previously (Hartkopf-Fröder et al. 2007). Briefly, ground rock samples were extracted using dichloromethane containing 1 % methanol. Extract yields varied between 0.81 and 1.14 mg/g rock. The extracts were separated into compound class fractions by medium pressure liquid chromatography and the saturated hydrocarbon fractions subsequently analysed by gas chromatography and gas chromatography-mass spectrometry according to standard procedures.

Palynomorphs

Six palynological samples from the Birkweiler drainage pit were processed applying standard preparation methods, i.e. HCl-HF-HCl digestion and sieving with a 10 μm polyester fabric mesh (Ashraf and Hartkopf-Fröder 1996). Permanent strew mounts were produced with PVA as the mounting medium and Elvacite 2044™ epoxy resin as the embedding medium. Samples were analysed under a Zeiss Axioplan microscope (1000x magnification) and the software TILIA (Grimm 1993, 2004) was used for the calculation of the pollen histogram. Terrestrial pollen sums were > 250 for each sample. Dinocyst analysis was performed at 500x magnification using a Carl Zeiss Jena Jenaval microscope equipped with differential interference contrast optics. Photography was made in plain transmitted light at 1000x magnification in an Leitz Orthoplan microscope. After a first examination of an appropriate area of the slides and identification of taxa, a subsequent count of approx. 100 specimens was made, where possible. Except for sample 108581, a much higher number of specimens than counted has been observed in each sample.
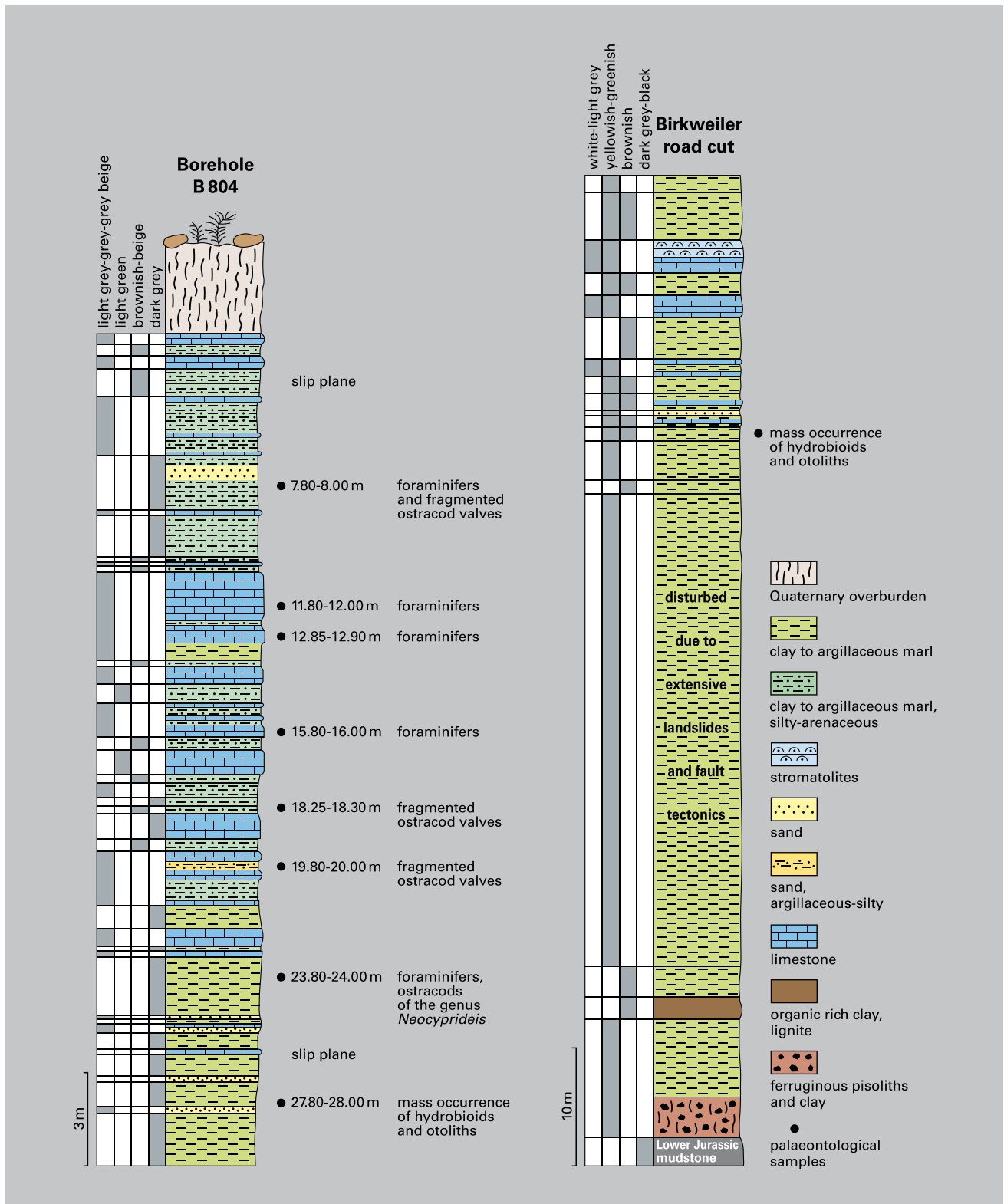
Fig. 4 Section of borehole B 804 and Birkweiler road cut. Position of slip planes in borehole B 804 following Schröder (1984). Note that lithological description for borehole B 804 is based on data provided by the drilling company
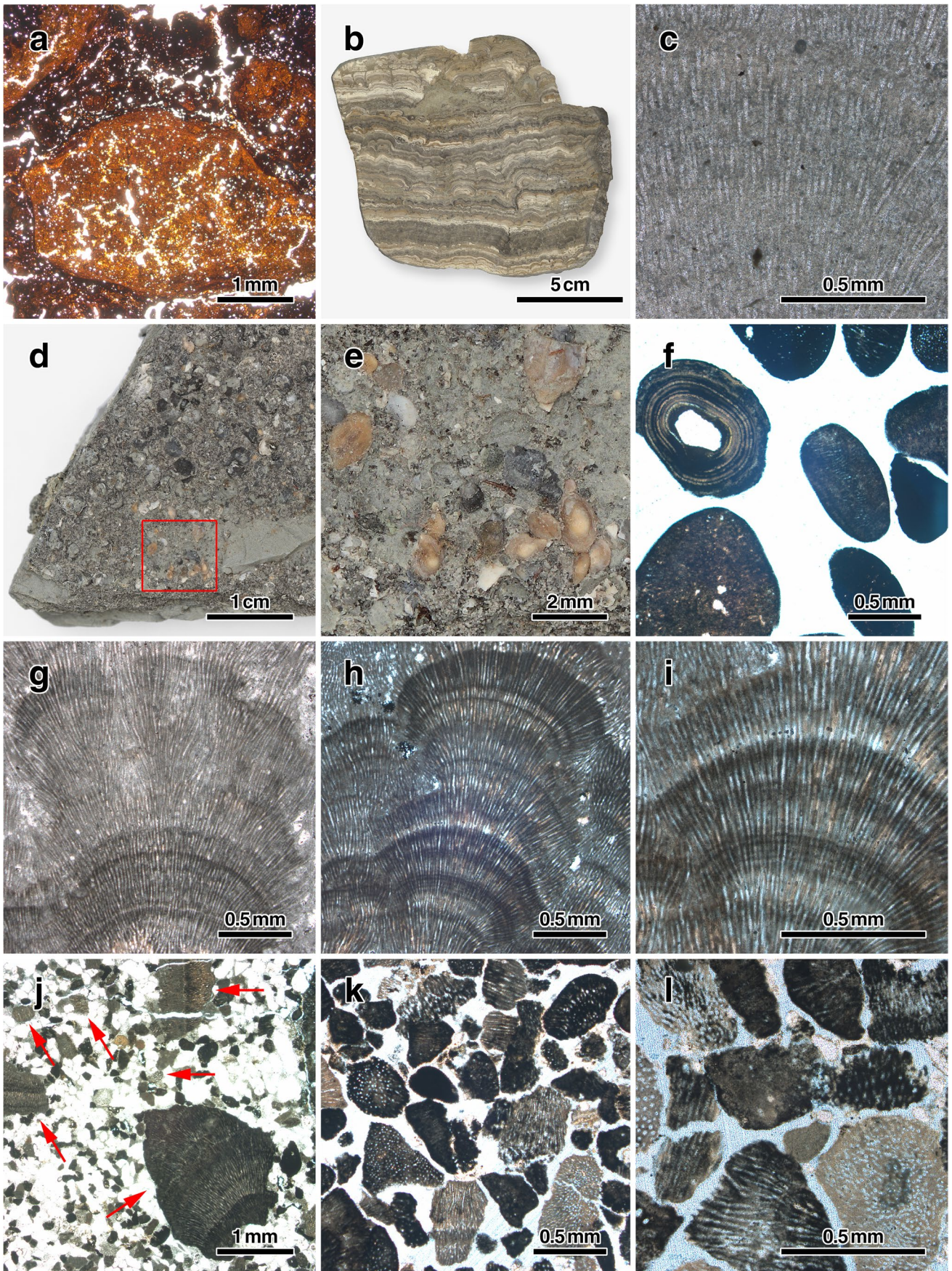
◀**Fig. 5 a** Thin section of "Bohnerz" concretions of the Schliengen Formation; Birkweiler road cut. **b** Polished section of the stromatolite horizon; Birkweiler road cut. **c** Thin section of the stromatolite horizon; Birkweiler road cut. **d** Bedding plane of grey mudstone with numerous otoliths, fragments of fish bones and gastropods; Birkweiler drainage pit. **e** Enlargement of red square in 5 d showing ten otoliths; Birkweiler drainage pit. **f** Thin section of well-rounded stromatolite fragments and a single ooid from fossil rich grey marl; Birkweiler drainage pit (thin section AW4). **g–i** Thin sections of stromatolite fragments with well-preserved outward radiating tubes and growth zonation pattern; Birkweiler drainage pit (g: thin section AZ4a, h, i: thin section AZ1). **j** Thin section of sandstone with numerous angular stromatolite fragments (red arrows); Birkweiler drainage pit (thin section AZ4a). **k, l** Thin section of indurated clastic sedimentary rock mostly composed of angular stromatolite fragments; Birkweiler drainage pit (thin section AZ4b)

Calcareous nannoplankton, foraminifers and ostracods

34 samples from the Birkweiler drainage pit were analysed for calcareous nannoplankton using smear slides, standard light microscopy and SEM techniques.

Foraminifer and ostracod samples were collected from the Birkweiler road cut, borehole B 804 and the Birkweiler drainage pit. The sediment was disaggregated by washing through a 63 μm sieve, followed by gravity separation with CCl_4 in order to enrich the microfossils from the dried residue.

Vertebrate remains

To recover molluscs (Kadolsky and Hartkopf-Fröder, in prep.), otoliths and other vertebrate remains (e.g. scales, teeth, see below), sediment from the Birkweiler drainage pit was disaggregated using 5 % hydrogen peroxide solution and washed through a 200 μm sieve. From the dried residue the fossils were handpicked. To prepare cross-sections of fish teeth single specimens were embedded in epoxy resin, ground and polished by hand. Photographs were taken using a Zeiss Axio Imager.M2m incident light microscope equipped with EC Epiplan Neofluar objectives, a HXP 120C light source and a fluorescence filter set 09 (excitation BP 450–490 nm, beam splitter FT 510 nm, emission LP 515 nm) housed in the microscopy lab of the Lehrstuhl für Geologie, Geochemie und Lagerstätten des Erdöls und der Kohle, RWTH Aachen.

Storage of material

Material used in this study is accessioned into the following collections:

- Sediment samples, thin sections, polished slabs of stromatolites: Geologischer Dienst Nordrhein-Westfalen, Krefeld; all material will be later transferred to the Landesamt für Geologie und Bergbau Rheinland-Pfalz, Mainz.

- Polished sections for vitrinite reflectance: Lehrstuhl für Geologie, Geochemie und Lagerstätten des Erdöls und der Kohle, RWTH Aachen.
- Palynological residues and slides: Geologischer Dienst Nordrhein-Westfalen, Krefeld.
- Calcareous nannoplankton: at present E. Martini's private collection; all specimens will be later transferred to the Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt/Main where the holotype of *Nannoserratolithus minutus* Martini (see below) is already housed (catalogue number SM.B 17726).
- Foraminifers, ostracods and vertebrate skeletal remains including polished sections of fish teeth: Landesamt für Geologie und Bergbau Rheinland-Pfalz, Mainz.

Results and discussion

Eocene sediments and lithostratigraphy

In the Birkweiler road cut mainly yellowish-greenish clays and marls were exposed. Marlstones, limestones and an organic matter-rich clay horizon with a thin lignite seam are intercalated (Fig. 4). West of the exposure of Lower Jurassic strata the succession starts with an approx. 3 m thick layer of light brown to white clay with numerous reddish brown to black concretions (Fig. 5 a). They consist of hematite, goethite, quartz and kaolinite ("Bohnerz") while the white clay is composed of kaolinite, quartz and goethite as shown by XRD analyses. The concretions may become so abundant that the clay only fills the space between them. The "Bohnerz" concretions and the kaolinite clay represent a residual terrestrial sediment resulting from weathering under humid, tropical-subtropical conditions since the early Eocene or even earlier. Thus, the light-coloured clay with embedded "Bohnerz" concretions is a ferruginous palaeosol characterised by a ferric to pisoplinthic horizon which developed on Lower Jurassic mudstones and corresponds to a former land surface. This unit is attributed to the Schliengen Formation (= Siderolith-Schichten) which has been recorded in the middle and southern Upper Rhine Graben and adjacent areas where residual soils accumulated in depressions on karstified Jurassic limestones (Pirkenseer et al. 2018). Typically, the clay of the Schliengen Formation consists for the most part of kaolinite (Sittler 1965, 1968b) which is not a main constituent in other stratigraphical units (Grüne Mergel to Landau Formation) of the Upper Rhine Graben (Löschan et al. 2017). A stratigraphically younger unit similar to the Schliengen Formation and consisting of clay rich in limonite concretions is well known from the Mainz Basin where these "Bohnerztone" overlay e.g. limestones and marls of the upper Oligocene (Chattian) to lower Miocene Mainz-Gruppe (Schäfer 2012).

West of the layer with numerous "Bohnerz" concretions follows a poorly exposed succession of monotonous

yellowish-greenish clays and marls. Unrecognised faulting and landslides may pretend a high thickness. Intercalated are a dark brown organic matter-rich clay horizon with a lignite seam, a very fossiliferous marl horizon (Fig. 4) and some limestone layers including a 50 cm thick stromatolite horizon (Figs. 4, 5 b, c). A sample from the lignite seam yielded an Eocene miospore assemblage (see above). Of special interest is an approx. 1.10 m thick marl layer (Fig. 4) which is extremely rich in hydrobioids (Kadolsky 2015; Kadolsky and Hartkopf-Fröder, in prep.), otoliths, vertebrate bones and teeth. The stromatolites from the Birkweiler road cut are very similar to a stromatolite horizon described by Heidtke (2006: 20, fig. 5) from the Lower Jurassic succession at the base of the brickyard pit west of Siebeldingen. In the fully marine, Lower Jurassic, organic-rich, dark grey mudstones the occurrence of stromatolites is at least unexpected. Schwarz and Griessemer (1998) reported green marls of mid Eocene age and landslides from the area of the former brickyard pit and hence, it is more likely to assume that Heidtke's stromatolite horizon is in fact part of the middle Eocene succession and not of Early Jurassic age. This assumption is also supported by the fact that from the nearby village Birkweiler a 15 cm thick stromatolite horizon embedded in light greenish grey marls has been described by Bucher (1914: 69–70) and Reis (1923: 117–120) who postulated an Oligocene or Miocene age without further substantiation. For these marls an Early Jurassic age can be excluded as such sediments are unknown from the Siebeldingen brickyard pit and adjacent Lower Jurassic outcrops. In thin sections, the microstructure (e.g. outward radiating tubes, growth zonation; see Reis 1923: pl. 3, fig. 14, pl. 4, fig. 10) of the stromatolites from the Birkweiler village and the Birkweiler road cut are very similar suggesting a widespread occurrence of the distinct stromatolite horizon(s) in that area.

Due to extensive recent and reactivated fossil landslides and complex fault tectonics in this area, it is not reasonable to assume that the entire section is undisturbed and in its original position. In addition, it even cannot be ruled out that parts of the succession include strongly weathered Upper Triassic (Keuper) clays and marls. These sediments have been encountered in boreholes along the building site of the bypass highway B 10 (Schröder 1984; Wichter et al. 1988; re-evaluation of the sediments and microfossil assemblages in boreholes B 703 and B 704 by Peter Schäfer) and are difficult to distinguish from Paleogene/Neogene sediments based on petrographical criteria alone (e.g. Nottmeyer 1954). However, the lignite seam near the base and the fossil rich layer near the top of the succession are all Eocene in age (see below). In addition, four samples from the road cut investigated by Schuler (1990) have been assigned to the middle to upper Eocene Grüne Mergel ("Marnes vertes à limnées = Salifère inférieur"; see also Châteauneuf and Ménillet 2014) and two samples rich in dinocysts to the upper

Eocene/lowermost Oligocene (Rupelian) Untere Pechelbronn-Schichten ("Couches de Pechelbronn inférieures = Sel III"; see also Duringer et al. 2019: fig. 7). From the area of the former brickyard pit near the Birkweiler road cut Schwarz and Griessemer (1998) reported Landauer Mergel *sensu* Breuer and Feist (1986) with charophytes indicative of the *Maedleriella embergeri* Zone. The recorded charophytes are clearly of Lutetian age. Additional samples from the Landauer Mergel in the Albersweiler area yielded late Eocene and perhaps even early Oligocene charophytes but no further information was provided (Schwarz and Griessemer 1998). Hence, in the Birkweiler road cut section the existence of a substantial amount of sediments other than of Eocene and early Oligocene age is rather unlikely.

The succession encountered in borehole B 804 (Fig. 4) is similar to the section in the Birkweiler road cut except that in the former limestone horizons are more abundant and dark grey sediments are more common indicating less weathered sediments. At least two slip planes have been identified in the borehole (at ca. 4 m and 26 m; Schröder 1984) and hence, the succession must be regarded as disturbed. However, the biostratigraphical data do not imply the presence of other than Eocene sediments below Quaternary overburden. Several samples of the cores from this borehole yielded foraminifer, ostracod, hydrobioid and otolith assemblages including a mass occurrence of hydrobioids and otoliths between 27.80 and 28.00 m. With regard to faunal composition this horizon is very similar to the one in the Birkweiler road cut. Due to landslides and fault tectonics these two horizons cannot be unequivocally correlated.

While in the Birkweiler road cut yellowish-greenish sediments prevail, probably indicating deep weathering enhanced by the mass movements, the marls from the Birkweiler drainage pit are predominantly light grey and medium light grey, in places medium grey and light olive grey in colour. Most of the marls lack macrofossils. However, many specimens of *Anomalorbina*?, a small-sized planorbid-like gastropod, were found on one bedding plane and specimens of the gastropod family Potamididae are concentrated in few thin layers (Kadolsky and Hartkopf-Fröder, in prep.). Some light grey, marly limestone horizons with disarticulated fish remains on the bedding planes are intercalated as well as up to few centimetres thick layers composed of marl, fine sand and masses of otoliths, hydrobioid fragments and complete hydrobioid shells (Kadolsky 2015; Kadolsky and Hartkopf-Fröder, in prep.) (Fig. 5 d, e). These layers have sharp lower and upper boundaries. After disaggregation of the sediment using 5 % hydrogen peroxide solution the resulting residue is composed of numerous hydrobioids, otoliths, stromatolite fragments, sandstone/clastic sedimentary rock fragments (Fig. 5 g–l) and very rare ooids (Fig. 5 f). In addition, rare hematite/goethite concretions ("Bohnerz"; see above) occur. By far most of the hydrobioids are broken but there are also

many complete and well-preserved shells. The gastropod assemblage is of low diversity; each shell-bearing layer is almost monospecific, with the hydrobioid *Lutetiella hartkopfi* Kadolsky, 2015 being most abundant overall. The stromatolite fragments are mainly in the grain size of medium sand to medium gravel, well rounded and with smooth and even "polished" surface (Fig. 5 f). The stromatolites are well preserved showing outward radiating tubes and growth zonation patterns (Fig. 5 g–i). Dark brown to dark grey staining of the stromatolites is likely attributed to bitumen impregnation. The sandstone also contains numerous small, angular stromatolite fragments (Fig. 5 j). Some indurated clastic sedimentary rocks are mostly composed of stromatolite fragments (Fig. 5 k, l). The small angular stromatolite fragments are probably derived from stromatolites growing right next to the depositional site while the well-rounded fragments were abraded during transport from a more distant source. In either case a high-energy event such as a storm was necessary to break up stromatolite structures. In the Birkweiler drainage pit itself no stromatolites were exposed. However, in the nearby Birkweiler road cut a 50 cm thick stromatolite horizon was encountered (Fig. 4) indicating that proper environmental conditions for stromatolite growth existed during deposition of the Eocene succession.

Based on palynomorphs and calcareous nannoplankton (see below) the investigated sediments of the Birkweiler drainage pit are assigned to the mid Eocene. However, it may be that, due to landslides, the succession in borehole B 804 and the Birkweiler road cut includes middle and upper Eocene and perhaps even lower Oligocene sediments (Schwarz and Griessemer 1998). Lithostratigraphically the succession is assigned to the Landauer Mergel *sensu* Breuer and Feist (1986), lower part of the Lymnäenmergel, Haguenau-Gruppe, an informal unit which for the first time was used by Breuer and Feist (1986: tab. 2) for a 6 m thick succession of olive grey to green grey, fossiliferous claystones and clayey marlstones in well Landau 117. Validity and range of the Haguenau-Gruppe is still under discussion (Pirkenseer et al. 2018).

Thermal maturity and organic geochemistry

In samples from the Birkweiler drainage pit most laevigate trilete spores are lemon yellow to golden yellow in colour and hence, the SCS (Spore Color Standard of Pearson 1990) is between 2 and 3 on the 11-points gradation colour chart. These values indicate an immature rank with a vitrinite reflectance between 0.3 and 0.4 % VR_r and are in good accordance with the measured vitrinite reflectance (see below; for an approximate correlation of the SCS scale and vitrinite reflectance see Marshall and Yule 1999; Hartkopf-Fröder et al. 2015). Some brown spores with SCS around 7 may be reworked.

Ichthyoliths such as the gar teeth may give some information on the thermal alteration of the sediment as they change colour from yellow to black and at very high maturity they become opaque white and finally clear and brittle (ichthyolith alteration index, IAI). Hence, with increasing maturation they follow the well-known colour path of conodonts (CAI; for more details see Hartkopf-Fröder et al. 2015). The gar teeth assemblage from Birkweiler is composed of two distinct colour populations, i.e. greyish orange to moderate yellowish brown and light grey to black. Few teeth show circular bands of both colours. Under fluorescence, most of the teeth cut and polished perpendicular to the longitudinal axis exhibit a yellow to orange fluorescence. Tooth enamel
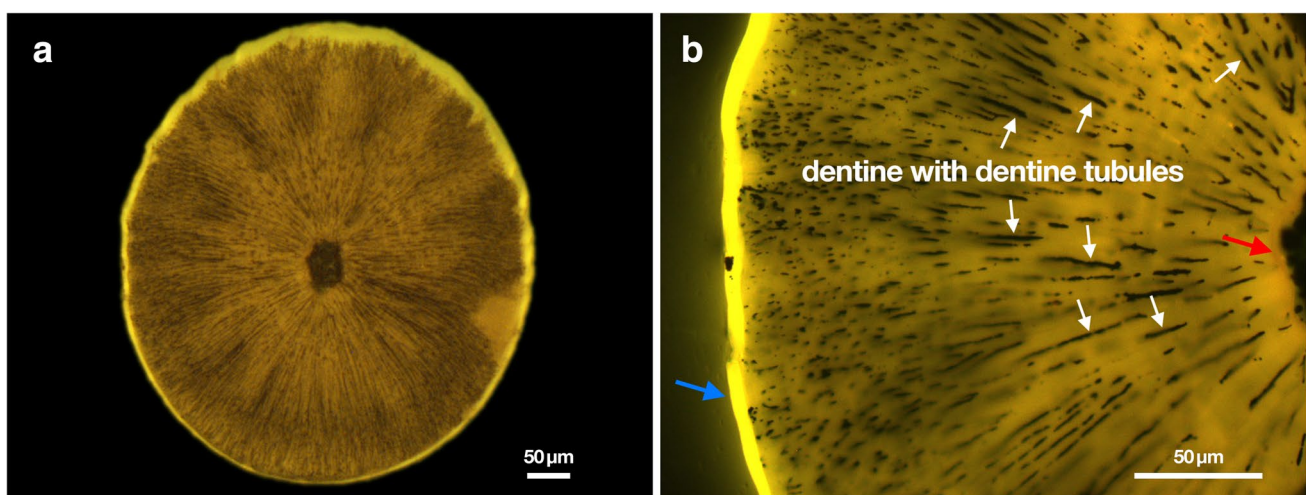
Fig. 6 a Horizontal cross-sections close to the tip of a Lepisosteidae jaw tooth showing the strongly fluorescent enamel, the radially arranged dentine tubules and the narrowed pulp cavity; Birkweiler drainage pit. **b** Same specimen as a. Strongly fluorescent enamel (blue arrow), dentine tubules (white arrows), pulp cavity (red arrow). Both photographs incident light fluorescence microscopy using a Zeiss Axio Imager.M2m, a HXP 120C light source and a fluorescence filter set 09 (excitation BP 450–490 nm, beam splitter FT 510 nm, emission LP 515 nm)

is distinguished from dentine by its stronger, bright yellow fluorescence (Fig. 6 a, b). In some teeth the inner parts of the dentine surrounding the pulp cavity exhibit a weaker fluorescence (dark brown) than in the outer parts. In one tooth no visible fluorescence of the dentine was observed but strong yellow fluorescence of the enamel. Provided that colour change of the ichthyoliths is solely controlled by maturation, the orange/brown specimens would imply a lower thermal maturity than the grey/black coloured ones. As both populations occur in the same sample reworking of those with darker colours might be assumed. While the samples from the Birkweiler drainage pit are thermally immature contemporaneous sediments from the Upper Rhine Graben fill show higher maturity (see below). The darker coloured teeth could therefore be reworked deriving from areas of higher subsidence and heat flow but this would imply, after an incipient maturation, the erosion of sediments bearing this distinct tooth type. However, this scenario is rather unlikely as it requires subsidence, thermal maturation and uplift within a short period. Irrespective of the colour all teeth are well preserved which also contradicts the assumption of reworking and transport. A more obvious explanation for the colour and fluorescence variation of the gar teeth and the occurrence of different colours and fluorescence in the very same tooth specimen takes into account that colonisation by microbes such as fungi and bacteria and subsequent degradation of organic matter causes colour change of the phosphatic fish remains (e.g. Tway et al. 1986; Koot et al. 2013). Hence, differences in colour and fluorescence of the Birkweiler ichthyoliths are here attributed rather to taphonomic processes (e.g. longer exposure times of the teeth before burial, more suitable microhabitat) than thermal alteration and reworking.

Three samples from the Birkweiler drainage pit have been analysed for source rock potential and thermal maturity (Tab. 1).

Total organic carbon (TOC) contents between 0.73 and 1.05 % and hydrogen indices (HI) between 109 and 158 mg HC/g TOC indicate poor oil generation potential and only minor gas generation potential by type III kerogens (Peters and Cassa 1994). The samples from the Birkweiler drainage pit show vitrinite reflectance values of 0.37–0.39 % VR_r indicating an immature rank. T_{max} values between 427 and 435 °C correspond to an immature to early mature rank and are in good agreement with the VR_r values (Peters et al. 2005).

From the Lymnäenmergel in wells of the Landau oil field, Teichmüller (1970, 1979), Doebl et al. (1974) and Teichmüller and Teichmüller (1981) published thermal maturity data ranging between 0.67 and 1.38 % VR_r at 1585 to 2063 m depth. Three samples from one of these wells (1902–2036 m) of the Landau oil field have been re-analysed and show considerably lower values between 0.73 and 0.81 % VR_r which is equivalent to a mid-oil window maturity (Fig. 7). However, the vitrinite reflectance

data from the Lymnäenmergel in this well are still much higher than those from the Birkweiler drainage pit. A logarithmic trend line (Fig. 7) connecting outcrop and data from the wells of the Landau oil field indicates a major subsidence and heat flow related increase in VR_r without major transient thermal effects. Maximum palaeotemperatures estimated from vitrinite reflectance data are in the range of ca. 120–130 °C (for 0.8 % VR_r) at 2000 m depth in well Landau 2 (Deming 1994).

Distribution patterns of saturated hydrocarbons in three analysed samples were similar and are exemplarily discussed for sample A 10 from the Birkweiler drainage pit (Fig. 8). In general, the distribution of hydrocarbons indicates mixed sources of the organic matter and is in agreement with low thermal maturity as assessed by Rock-Eval pyrolysis and vitrinite reflectance. n-Alkanes have been detected in the chain length range from $C_{12} - C_{33}$ and showed a bimodal distribution with maxima at C_{17} and C_{27}, respectively (Fig. 8 a). n-Alkanes in the longer chain length range ($C_{23} - C_{33}$) displayed a significant odd-over-even predominance as expressed by the Carbon Preference Index $CPI_{23–33}$ value which is a clear indication for immature terrestrial organic matter (e.g. Marynowski and Zatoń 2010). In contrast, no preference was observed for the alkane distribution around C_{17} which points to a contribution of marine organic matter. A generally similar n-alkane distribution has been reported for the Callovian (Middle Jurassic) Papartinė Formation of Lithuania (Marynowski and Zatoń 2010). In addition to n-alkanes, the isoprenoidal hydrocarbons pristane and phytane have been detected. Pristane dominated slightly over phytane as expressed by the Pr/Ph ratio which may indicate an oxic to suboxic depositional environment (Peters et al. 2005). Furthermore, the m/z 191 trace revealed the presence of a series of hopanoid hydrocarbons (Fig. 8 b) which can in principle be assigned to bacterial organic matter sources. The distribution pattern of these biomarkers was also in agreement with an immature signature of the organic matter, i.e. a significant value of the ββ/(ββ+βα+αβ) ratio indicates the presence of ββ-hopanes which disappear very early during maturation (Farrimond et al. 1998). Steranes, sterenes and steradienes were insignificant in the investigated samples.

Pollen and spores

Six samples (108575, 108579, 108581, 108585, 108586, 108590) from the Birkweiler drainage pit were investigated for pollen, spores and algae (Figs. 9, 10, 11, Electronic Supplementary Material Fig. S1 and Tabs. S1, S2). Preservation of the predominantly yellow pollen and spores is reasonable. Most pollen are compressed, sometimes crumpled and

Tab. 1 Vitrinite reflectance and Rock-Eval data of the Landauer Mergel *sensu* Breuer and Feist (1986) (= lower part of the Lymnäenmergel) from Birkweiler drainage pit and the Lymnäenmergel encountered in wells of the Landau oil field at the western Upper Rhine Graben between Birkweiler and Landau

Sample No.	Locality	Depth [m]	Stratigraphy	Lithology	Elemental analysis			Rock-Eval pyrolysis								Vitrinite reflectance		
					TOC [%]	TIC [%]	TC [%]	S1 [mg/g]	S2 [mg/g]	S3 [mg/g]	T_{max} [°C]	HI [mg HC/g TOC]	OI [mg CO_2/g TOC]	PI		VR_r [%]	N	SD
13/1261 A20-1	Birkweiler drainage pit	Outcrop	Landauer Mergel	Grey marl	1.05	0.24	1.29	0.09	1.15	0.79	427	109.0	75.1	0.07		0.37	50	0.058
13/1262 A20-2	Birkweiler drainage pit	Outcrop	Landauer Mergel	Grey marl	0.92	0.25	1.17	0.15	1.46	0.73	435	158.3	79.4	0.09		0.39	50	0.076
13/1263 A21	Birkweiler drainage pit	Outcrop	Landauer Mergel	Grey marl	0.73	2.69	3.42									0.37	31	0.065
LaX_1902	Well Landau oil field	1902	Lymnäenmergel	Marl												0.76	133	0.102
LaX_1956	Well Landau oil field	1956	Lymnäenmergel	Marl												0.73	73	0.08
LaX_2036	Well Landau oil field	2036	Lymnäenmergel	Marl												0.81	23	0.135
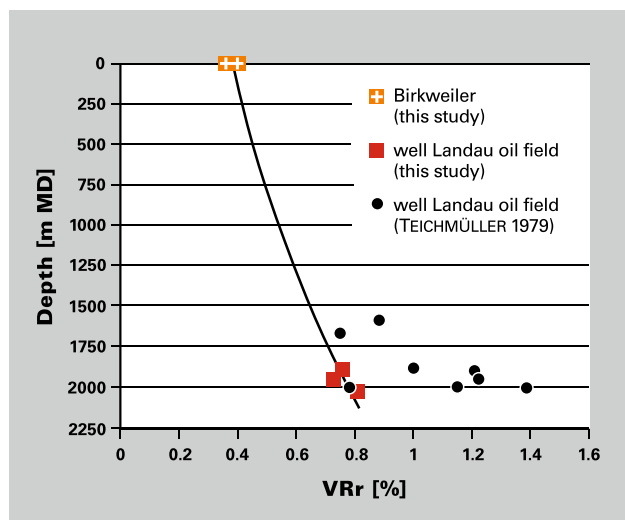
**Fig. 7** Vitrinite reflectance of the Landauer Mergel *sensu* Breuer and Feist (1986) (= lower part of the Lymnäenmergel) from Birkweiler drainage pit and the Lymnäenmergel encountered in wells of the Landau oil field at the western Upper Rhine Graben between Birkweiler and Landau. *MD* measured depth

corroded (thinning of exine) and many specimens contain black fragments, probably pyrite crystals.

The Eocene palynoflora of Germany and France has been described in detail in several comprehensive monographs (e.g. Krutzsch 1959; Châteauneuf 1980; Thiele-Pfeiffer 1988; Schuler 1990; Lenz 2000, 2005). For detailed descriptions, nomenclatural discussions and illustrations we refer to these publications.

Pollen and spores stratigraphy

Identified palynomorph taxa are listed in Electronic Supplementary Material Tab. S1. The assemblage represents a typical Eocene palynoflora of probably mid Eocene age dominated by palaeotropical elements such as *Pentapollenites* spp., *Monocolpopollenites tranquillus* (Potonié, 1934) Thomson and Pflug, 1953 ex Jansonius and Hills, 1976, *Bombacacidites* spp., *Compositoipollenites rhizophorus* (Potonié, 1934) Potonié, 1960, *Plicatopollis plicatus* (Potonié, 1934) Krutzsch, 1962 (compare Krutzsch 1967) and characterised by the absence of typical early Eocene taxa, e.g. *Thomsonipollis magnificus* (Thomson and Pflug, 1953) Krutzsch, 1960 (compare Riegel et al. 2012). Distinctive late Eocene species such as those of the palynostratigraphically important *Mediocolpopollis* Group (Krutzsch 2008; Hottenrott in Grimm et al. 2011a) were not encountered in the Birkweiler drainage pit material and *Pompeckjoidaepollenites subhercynicus* (Krutzsch, 1954) Krutzsch in Góczán, Groot, Krutzsch and Pacltová, 1967, already rare in the late Eocene (Borkener Bild, Krutzsch
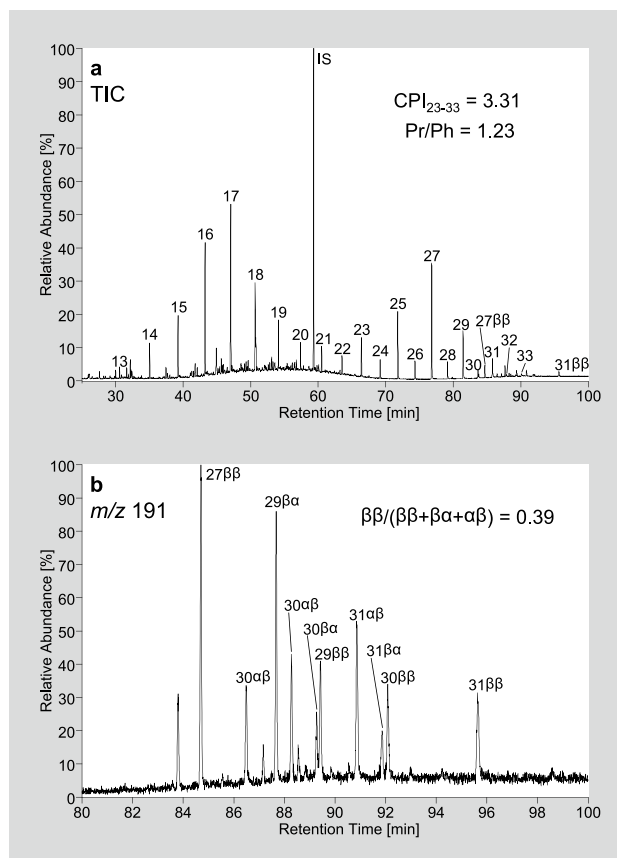
Fig. 8 a Total ion chromatogram displaying the distribution of *n*-alkanes in sample A 10, Birkweiler drainage pit; numbers on peaks indicate the number of carbon atoms in *n*-alkanes; IS, internal standard (5α-androstane); $CPI_{23–33}$, $0.5 \times ((([C_{23}]+[C_{25}]+[C_{27}]+[C_{29}]+[C_{31}]+[C_{33}])/([C_{22}]+[C_{24}]+[C_{26}]+[C_{28}]+[C_{30}]+[C_{32}]) + 0.5 \times ((([C_{23}]+[C_{25}]+[C_{27}]+[C_{29}]+[C_{31}]+[C_{33}])/([C_{24}]+[C_{26}]+[C_{28}]+[C_{30}]+[C_{32}]+[C_{34}]))$; Pr/Ph, pristane/phytane ratio. **b** Selected ion chromatogram (*m/z* 191) displaying the distribution of hopanoid hydrocarbons in sample A 10; the numbers refer to the number of carbon atoms while Greek letters indicate the configurations at carbon atoms 17 and 21 of the hopane skeleton, respectively; $\beta\beta/(\beta\beta+\beta\alpha+\alpha\beta)$, 17β,21β-hopane/ (17β,21β-hopane+17β,21α-hopane+17α,21β-hopane)

1966), is still rather common. *Plicapollis pseudoexcelsus* (Krutzsch, 1957) Krutzsch, 1961, another terminal member of the thermophile *Normapolles* Group, is typically abundant in the mid Eocene (Krutzsch 1966; Hottenrott 2002) and appears in moderate percentages (max. 5 %) at Birkweiler. *Plicatopollis plicatus*, a warmth loving species, restricted to the Eocene (Fig. 11) and especially abundant in the upper Ypresian to lower Lutetian Lower and Middle Messel Formation (Thiele-Pfeiffer 1988; Lenz et al. 2007, 2011; Lenz and Wilde 2018), appears regularly. Also typical for the mid Eocene are high percentages of *Platycaryapollenites* spp. (Juglandaceae) (Krutzsch 1992; Blumenstengel 1993; Blumenstengel et al. 1996). Especially specimens of the Bombacaceae (*Bombacacidites* spp.) and of *Tegumentisporis villosoides* (Krutzsch, 1959) Krutzsch, 1963 (e.g. sample

108579) could indicate a mid Eocene age (see Hochuli 1984, fig. 8). *T. villosoides* was known only from the Lower and Middle Messel Formation (upper Ypresian to lower Lutetian) of Messel (Thiele-Pfeiffer 1988; Lenz and Wilde 2018), the lower Eocene of Grube Prinz von Hessen (Moshayedi et al. 2018) and the middle Lutetian (Schilfkohle, late MP 13/ early MP 14 following Haubold 1989) of Geiseltal (Krutzsch 1959). Some forms, e.g. *Restioniidites minimus* (Krutzsch, 1970) Kedves, 1974 and *Ericipites callidus* (Potonié, 1931) Krutzsch, 1970, appear regularly since the Eocene (Thomson and Pflug 1953; Krutzsch 1970; Thiele-Pfeiffer 1988). While most of the time-indicative taxa of the Birkweiler drainage pit assemblage point to a mid Eocene age, few species have been reported from the late Eocene only. *Eocaenipollis* sp. 2 *sensu* Châteauneuf (1980) seems to occur only in the late Eocene (Priabonian) (Fig. 11). Originally, the species has been described from the Paris Basin where it is rare and the actual stratigraphical range may be inadequately explored so far. The same may be true for *Scabratricolporites sucii* Schuler, 1990 which has been encountered by Schuler (1990: tab. 54) in the dinocyst-rich Birkweiler assemblage assigned to the Untere Pechelbronn-Schichten (see below). In general, this species is very scarce and may be of limited stratigraphical use. The presence of *Margocolporites vanwijhei* Germeraad, Hopping and Muller, 1968 in the Birkweiler drainage pit assemblage is noteworthy. The species is well known from other Paleogene basins, e.g. Paris Basin (Châteauneuf 1980). However, in Central Europe it is a rare component. Based on the overall composition of the assemblage and the lack of the *Mediocolpopollis* Group which is a very important marker for the late Eocene we assign the Birkweiler drainage pit association to the mid Eocene. A late Eocene age is less likely.

Schuler (1990: 210–211) studied eight samples from the road cut near Birkweiler but she neither published data on the exact locality nor petrography of the sediment. Detailed palynological data were provided for five samples and two rather similar palynomorph assemblages were distinguished. Four samples yielded a palynomorph assemblage composed of angiosperm pollen, few gymnosperm pollen, trilete spores and green algae. In one sample also rare dinocysts were encountered. The palynomorph assemblage of these four samples was assigned to the Grüne Mergel ("Marnes vertes à limnées = Salifère inférieur") by Schuler (1990). Based on one sample and an additional one of which no species list is provided, a second rather similar assemblage was defined by her mostly differing in that it is rich in monospecific dinocysts (*Spinidinium*). Unfortunately, no specimens of *Spinidinium* were illustrated by Schuler (1990). Some species of *Spinidinium* resemble *Apectodinium*, but *Spinidinium* differs by having a hexa 2a plate, in contrast to the quadra 2a plate in *Apectodinium*. This distinctive feature may not always be easily observed. Most records and most species of

Spinidinium are from Cretaceous–Paleocene, but a few species of *Spinidinium* range to late Eocene (Sluijs et al. 2009).

No specimens of *Spinidinium* were encountered in the present study (see below), but monotypic *Apectodinium* was recorded in one of our samples (see Dinoflagellate cysts (dinocysts) and green algae). We suspect that Schuler's (1990) record may similarly be of monospecific *Apectodinium*, not of *Spinidinium*.

The presence of abundant dinocysts suggests a marine ingression and hence, Schuler (1990) ascribed this assemblage to the Untere Pechelbronn-Schichten ("Couches de Pechelbronn inférieures = Sel III"; see also Rauscher and Schuler 1988; Duringer et al. 2019: fig. 7). The Untere Pechelbronn-Schichten are of late Eocene/earliest Oligocene age (Grimm et al. 2011b). However, already Sittler (1969) reported dinocysts from the "Marnes calcaires grises à anhydrite et sel" which are equivalent to the Untere Grüne Mergel *sensu* Grimm et al. (2011b). With regard to the pollen and spores composition Schuler's dinocyst-rich sample differs from those assigned to the "Marnes vertes à limnées" mainly by the occurrence of *Scabratricolporites sucii* and the lack of representatives of the Bombacaceae, both being very rare in the studied samples. The assignment to the Untere Pechelbronn-Schichten by Schuler (1990) which is solely based on abundant dinocysts of only one genus, therefore, seems not to be conclusive. Unfortunately, neither geographical coordinates nor a log including the sample position were published by Schuler (1990) so that it is unknown if the two dinocyst-rich samples were collected close to those assigned to the Grüne Mergel ("Marnes vertes à limnées = Salifère inférieur") or derive from more distant localities within the course of the road cut near Birkweiler. These two samples, therefore, might come from a somewhat younger level of the Grüne Mergel (= Lymnäenmergel). Alternatively, Châteauneuf and Ménillet (2014) suggested that the *Spinidinium* dinocysts are reworked from Upper Cretaceous sediments.

Vegetation history

For a palaeoecological analysis the Restionaceae, represented by *Restioniidites hungaricus* (Kedves, 1965) Elsik, 1968, are included here to the land pollen sum (Electronic Supplementary Material Fig. S1) since modern members of the family, e.g. in southern Africa, occupy also terrestrial habitats (Moline and Linder 2005 and references therein). Krutzsch (1992) suggests that Restionaceae during the Paleogene were growing in coastal regions and even in dry habitats, e.g. on sandy substrates. However, they are often considered as representing marsh vegetation during the Eocene (see Lenz and Riegel 2001; Lenz et al. 2021). At Birkweiler *Restioniidites* spp., especially *Restioniidites hungaricus*, reaches > 25 % in three samples (108575, 108581, 108586). Sample 108586 is dominated by Restionaceae (> 65 %).

20 μm
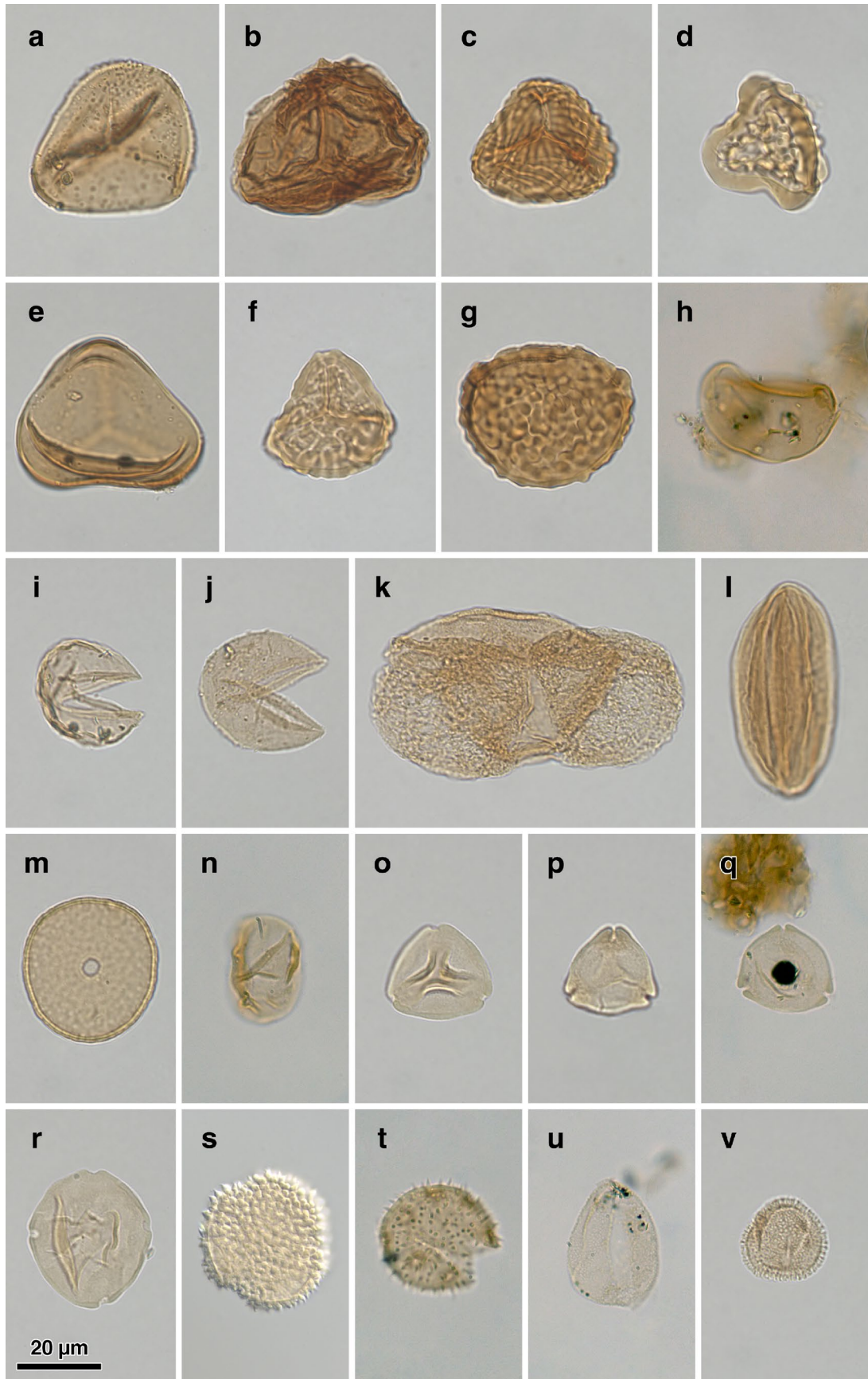
◀**Fig. 9** Miospores from Birkweiler drainage pit. **a** *Baculatisporites* sp. (slide 108590 SG 063). **b** *Retitriletes* sp. (slide 108590 SG 061). **c** *Cicatricosisporites paradorogensis* (slide 108575 SG 003). **d** *Polypodiaceoisporites* sp. (slide 108581 SG 010). **e** *Leiotriletes triangulus* (slide 108590 SG 062). **f** *Corrugatisporites multivallatus* (slide 108581 SG 007). **g** *Verrucatosporites* sp. (slide 108575 SG 022). **h** *Laevigatisporites haardti* (slide 108596). **i** *Inaperturopollenites dubius* (slide 108585 SG 021). **j** *Inaperturopollenites concedipites* (slide 108590 SG 059). **k** *Pinuspollenites labdacus* (slide 108590 SG 058). **l** *Ephedripites eocenipites* (slide 108575 SG 005). **m** *Restioniidites minimus* (slide 108575 SG 016). **n** *Graminidites* sp. (slide 108585). **o** *Platycaryapollenites lunatus* (slide 108575 SG 009). **p** *Plicapollis pseudoexcelsus* (slide 108575 SG 017). **q** *Myricipites* sp. (slide 108586, with pyrite crystal embedded in the exine). **r** *Polyatriopollenites stellatus* (slide 108575 SG 010). **s** *Compositoipollenites rhizophorus* (slide 108585 SG 032, Nomarski differential interference contrast). **t** *Malvacipollis* sp. (slide 108575). **u** *Arecipites convexus* (slide 108575). **v** *Oleoidearumpollenites microreticulatus* (slide 108575 SG 020). SG = Single Grain Mount. All photographs were taken using a 100x oil immersion objective. Slides are stored in the palynological collection of the Geological Survey North Rhine-Westphalia, Krefeld

Sparganiaceaepollenites spp. (Sparganiaceae, Typhaceae), moderately common at Birkweiler, are a typical swamp element which forms reed belts. Often Sparganiaceae appear together with Restionaceae in Eocene freshwater marshes (Lenz and Riegel 2001). *Botryococcus*, a colonial freshwater alga tolerating brackish water conditions (Guy-Ohlson 1992; Banerjee et al. 2002), is especially abundant when Restionaceae are most common, pointing to high water tables. Other algal remains, e.g. *Ovoidites* sp. (botanical affinity: Zygnemataceae; Rich et al. 1982) are rare but most of the samples contain chorate and also proximate dinocysts, which are generally more common when Restionaceae and *Botryococcus* are abundant. An exception is sample 108581, where dinocysts are extremely rare.

The most prominent arboreal elements are *Inaperturopollenites concedipites* (Wodehouse, 1933) Krutzsch, 1971 (botanical affinity: Taxodiaceae) and *I. dubius* (Potonié and Venitz, 1934) Thomsen and Pflug, 1953 (Cupressaceae) which point to locally wet conditions since many species of these families are nowadays dwellers of peat-forming swamp forests (see Schuler 1990; Lenz 2000, 2005). *Plicapollis pseudoexcelsus* and *Pompeckjoidaepollenites subhercynicus* probably belong to the Juglandaceae and are associated with both Restionaceae and Sparganiaceae. Therefore, they might be members of a marsh community, maybe growing on hammocks together with palms, as suggested at the middle Eocene site Helmstedt (Northern Germany, Lenz 2000; Lenz and Riegel 2001). On the other hand, an affinity to Rhoipteleaceae is suggested for *Plicapollis* (Krutzsch in Góczán et al. 1967; Krutzsch 1992). *Plicapollis pseudoexcelsus* and *Pompeckjoidaepollenites subhercynicus* rarely show percentages > 5 % at Birkweiler. Palm (Arecaceae) pollen, generally pointing to rather tropical, humid conditions, are regularly encountered at Birkweiler with taxa such as *Arecipites convexus* (Thiergart, 1938) Krutzsch, 1970 and *Monocolpopollenites tranquillus*, another typical Eocene element (Hottenrott 2002). *Arecipites convexus* reaches approx. 20 % in sample 108581 when also *Myricipites pseudorurensis* (Pflug in Thomson and Pflug, 1953) Grabowska and Ważyńska, 2009 (botanical affinity: Myricaceae), another element probably growing on hammocks in marsh land (Lenz and Riegel 2001), is common together with Restionaceae and *Botryococcus*. *Triatriopollenites rurensis* Pflug and Thomson in Thomson and Pflug, 1953 was also probably produced by Myricaceae and is here associated with Restionaceae. Bombacaceae (*Bombacacidites* spp.) and Icacinaceae (*Compositoipollenites rhizophorus* (Potonié, 1934) Potonié, 1960) are also considered marsh plants in the middle Eocene sediments of Helmstedt (Lenz 2000).

It is not clear, if the few pollen grains of Poaceae (*Graminidites* spp.) were produced by swamp elements of the grass family. Generally, grass pollen grains are rare until the Oligocene (Frederiksen 1985; Krutzsch 1992). Cyperaceae, also rare at Birkweiler, substitute Restionaceae as a humid element since the Oligocene (Krutzsch 1992). Direct evidence for mangrove vegetation, e.g. occurrence of *Avicennia* sp. or *Rhizophora* spp. (fossil pollen genus *Zonocostites* spp.), is missing at Birkweiler, but many Polypodiaceae, appearing at Birkweiler, might be associated with mangrove conditions. Although species of the genus *Leiotriletes* were not consistently differentiated in this study, some specimens of *Leiotriletes adriennis* (Potonié and Gelletich, 1933) Krutzsch, 1959 were identified. Some authors (e.g. Akkiraz et al. 2006) affiliate the taxon with the mangrove fern *Acrostichum* whereas others suggest a relationship to tropical *Lygodium* spp. (Schizaeaceae, see Dašková et al. 2011).

Drier, well-drained habitats are marked by the appearance of Juglandaceae (*Plicapollis pseudoexcelsus*, *Platycaryapollenites* spp.) as well as rare *Pinuspollenites* spp., e.g. *Pinuspollenites labdacus* (Potonié, 1931) Raatz, 1937 ex Potonié, 1958 and *Pinuspollenites minutus* (Zaklinskaya, 1957) Nagy, 1985 (see Châteauneuf 1980; Frederiksen 1985; Lenz et al. 2011). All those elements appear regularly, but never exceed 5 %, probably pointing to regional pollen transport from a less humid hinterland vegetation. Wilkinson et al. (1980) interpret pollen produced by Pinaceae (*Pinuspollenites* spp.) as an element of upland regions. *Tricolporopollenites parmularius* (Potonié, 1934) Krutzsch in Krutzsch, Pchalek and Spiegler, 1960, produced by Eucommiaceae, reaches up to 5 %. Today, *Eucommia ulmoides* Oliver, 1890 grows naturally in South China in hilly areas from 200 m to 1700 m above sea level where spring temperatures vary from 12.3 °C to 20.1 °C (Yu-Fei Wang et al. 2003). Pollen of a large number of paratropical trees, e.g. Sapotaceae (*Sapotaceoidaepollenites* spp., *Tetracolporopollenites* spp.), Myrtaceae (*Cupanieidites* spp.,
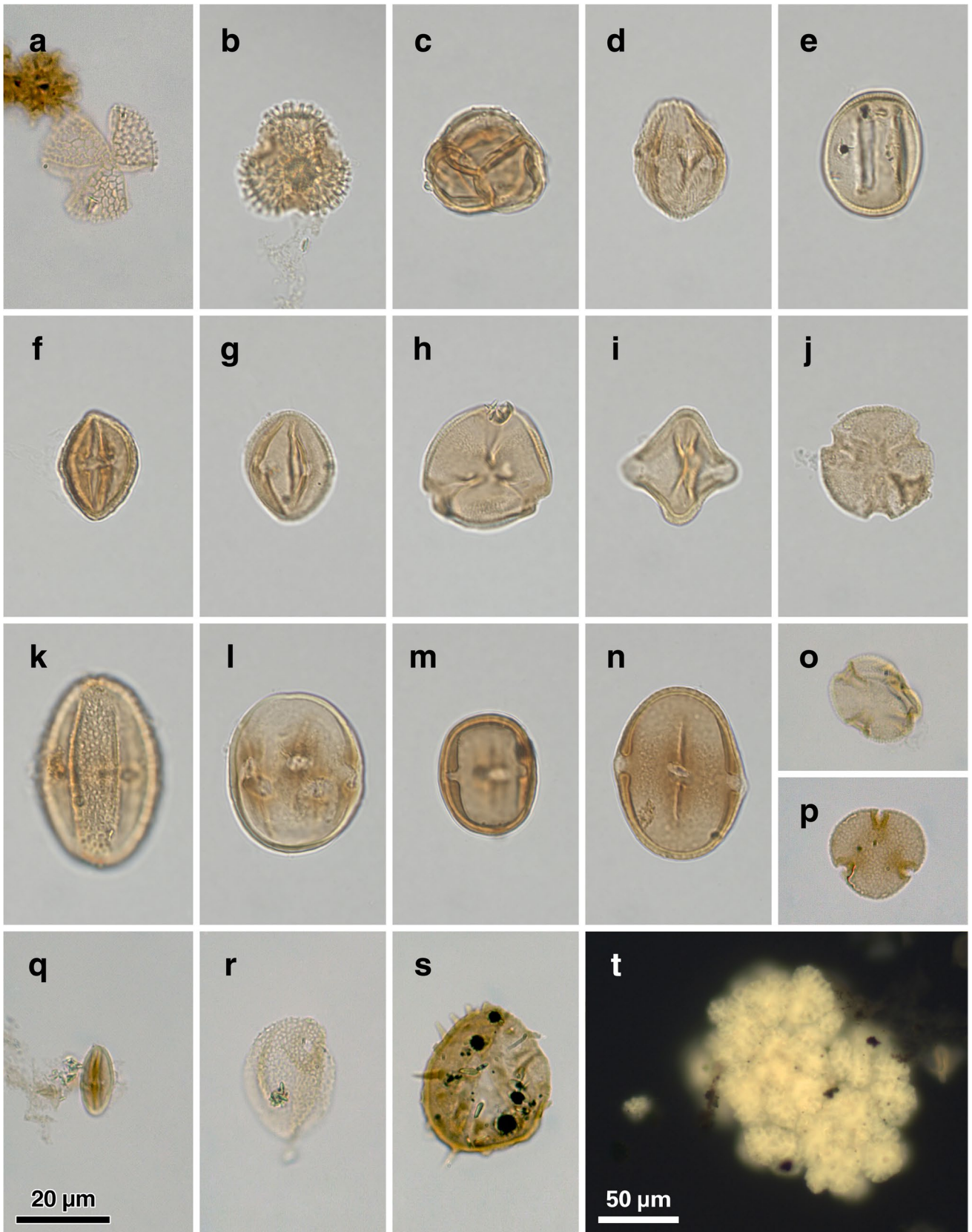
◄**Fig. 10** Miospores (**a–s**) and *Botryococcus* sp. (**t**) from Birkweiler drainage pit. **a** *Retitricolpites gracilis* (slide 108586). **b** *Ilexpollenites margaritatus* (slide 108575 SG 013). **c** *Ericipites callidus* (slide 108590 SG 065). **d** *Tricolporopollenites crassostriatus* (slide 108590 SG 036). **e** *Tricolporopollenites parmularius* (slide 108575 SG 001). **f** *Tricolporopollenites microporitus* (slide 108590 SG 034). **g** *Tricolporopollenites pseudocingulum* (slide 108575 SG 024). **h** *Scabratricolporites sucii* (slide 108585 SG 009). **i** *Pentapollenites pentangulus* (slide 108575 SG 008). **j** *Margocolporites vanwijhei* (slide 108590 SG 046). **k** *Parthenopollenites marcodurensis* (slide 108590 SG 030). **l** *Eocaenipollis* sp. 2 *sensu* Châteauneuf (1980) (slide 108575 SG 007). **m** *Tetracolporopollenites sapotoides* (slide 108590 SG 040). **n** *Sapotaceoidaepollenites obscurus* (slide 108590 SG 035). **o** *Sapotaceoidaepollenites sculptatus* (slide 108585). **p** *Bombacacidites* sp. (slide 108575). **q** *Fususpollenites fusus* (slide 108585). **r** *Sparganiaceaepollenites* sp. (slide 108585). **s** *Nupharipollis* sp. (slide 108581). **t** *Botryococcus* sp. (incident UVA–blue light fluorescence). SG = Single Grain Mount. All photographs were taken using a 100x oil immersion objective. Slides are stored in the palynological collection of the Geological Survey North Rhine-Westphalia, Krefeld

see Châteauneuf 1980), Caesalpiniaceae (*Margocolporites vanwijhei* Germeraad, Hopping and Müller, 1968*,* see Châteauneuf 1980), or *Engelhardia* (*Momipites* spp., see Lenz 2000) appear regularly. Whereas Sapotaceae, many Myrtaceae and *Engelhardia* might be indicative of wet, subtropical/tropical habitats, Caesalpiniaceae are adapted to hot climates with a distinctive season (see Brasero et al. 2009; Worobiec 2009). *Engelhardia* nowadays needs mean annual temperatures of minimally approx. 16 °C (Akkiraz et al. 2006).

Evergreen climbers were also present with taxa such as *Parthenopollenites marcodurensis* (Pflug and Thomson in Thomson and Pflug, 1953) Traverse, 1994 (botanical affinity: *Parthenocissus*, Worobiec 2009). Temperate or cosmopolitan families, e.g. Ulmaceae (*Ulmipollenites undulosus* Wolff, 1934), Ericaceae (*Ericipites* spp.) or Aquifoliaceae (*Ilexpollenites* spp.), are underrepresented at Birkweiler. Some taxa, e.g. *Eocaenipollis* sp. or *Pentapollenites pentangulus* (Pflug, 1953) Krutzsch, 1957, have a questionable botanical affinity but are characteristic for the Eocene and have a thermophilic character (Châteauneuf 1980; Schuler 1990; Lenz 2000). Gnetales are represented by few pollen grains of *Ephedripites eocenipites* (Wodehouse, 1933) Krutzsch, 1961, which is during the Eocene commonly associated with moist tropical and subtropical vegetation (Frederiksen 1985 and references therein).

Generally, a paratropical arboreal vegetation with a high quantity of wetland elements is suggested.

Schuler (1990: 210–211) identified similar pollen and spores spectra also pointing to a mid to late Eocene age. Samples were dominated by angiosperms (79–96 %) whereas pollen of Pinaceae (*Pityosporites* spp.) fluctuated between 2–11 % and Cupressaceae reached 3 % (Schuler 1990). This is in contrast to the current study where Cupressaceae and Taxodiaceae are dominant trees, clearly pointing to a massive influence of swamp forest elements (Page 1990). It is typical

that Myricaceae, a family of approximately 50 shrub and tree species often today growing near streams and in swamps (Fitzgerald 1999), are common elements in our study, but much less abundant in Schuler (1990). Schuler (1990) reports higher percentages of Flagellariaceae (*Milfordia* spp. and *Restioniidites hungaricus* in this study) only for one sample, whereas percentages of marshy elements like Restionaceae and Sparganiaceae are much more abundant in samples from the Birkweiler drainage pit. We suggest that, although both studies deal with contemporaneous deposits, Schuler (1990) investigated a palynoflora pointing to a better drained, mesic habitat. In both studies Pinaceae, as an element of the hinterland, but also Gnetales are minor constituents whereas angiosperms typical for an Eocene rainforest, e.g. belonging to Sapotaceae, the *Normapolles* Group, Bombacaceae, Icacinaceae, are detected regularly by Schuler (1990) but are more diverse in our study. Presumably, cryptogams did not play a major role in both ecosystems.

Dinoflagellate cysts (dinocysts) and green algae

The same six samples as studied for pollen and spores were investigated for dinocysts. Table S3 (Electronic Supplementary Material) presents the dinocyst taxa recorded from the Birkweiler drainage pit and Figs. 12–14 show photographs of the dinocysts. Sample 108581 is essentially barren of dinocysts with only two specimens seen. The remaining five samples are relatively rich in dinocysts. Preservation is moderate to poor.

The dinocyst assemblages are similar in all samples. Diversity is very low, with only twelve species in total recognised in the samples (Electronic Supplementary Material Tab. S3). Except for a single specimen "Unknown dinocyst species 1" the dinocysts are well known from Eocene sections outside of the Upper Rhine Graben. No reworking is observed.

In addition to dinocysts the freshwater green algae *Pediastrum* and *Botryococcus* were also recorded. *Pediastrum* is included in Electronic Supplementary Material Tab. S3. *Botryococcus* is common in all samples, but is badly preserved and was not included in the counting and is omitted from Tab. S3.

Dinocyst taxonomy notes

Taxonomy follows Fensome et al. (2019).

The genus *Apectodinium* is represented by three species, *A. homomorphum* (Deflandre and Cookson, 1955) Lentin and Williams, 1977*, A. parvum* (Alberti, 1961) Lentin and Williams, 1977 and *A. quinquelatum* (Williams and Downie, 1966) Costa and Downie, 1979, which are all intergrading in morphology (Fig. 12 a–o). Cysts with incompletely developed processes are present. Such specimens probably represent

failure to encyst completely (Denison 2021). Some other specimens of *A. quinquelatum* and *A. parvum* show a more or less clear expression of paratabulation. Such forms have previously been recorded in assemblages rich in *Apectodinium* (e.g. Châteauneuf and Gruas-Cavagnetto 1978; Heilmann-Clausen 1985). They conform with *Axiodinium tesselatum* (Châteauneuf and Gruas-Cavagnetto, 1978) Williams et al., 2015 (originally a subspecies of *A. homomorphum*) which

is here considered as an ecophenotypic variation within *Apectodinium*.

Due to the rather poor preservation, it cannot be excluded that some specimens registered here as *Apectodinium* should instead be referred to *Trivalvadinium formosum* Islam, 1983a, an ill-known taxon resembling *Apectodinium homomorphum* except for apparently having a 3I archaeopyle. 3I archaeopyles could not be identified with certainty in any specimens in the

numerical age [Ma]	59.2	56.0	47.8	37.71	33.9
Series/Epoch	Paleocene	Eocene			Oligocene
		lower	middle	upper	
Stage/Age	Thanetian	Ypresian	Lutetian/ Bartonian	Priabonian	Rupelian

Fig. 11 Stratigraphical ranges of selected pollen and spore taxa from Birkweiler drainage pit in the late Paleocene to early Oligocene of Central Europe (mainly after Lenz 2000). The assemblage suggests a mid Eocene, possibly a mid/late Eocene age. However, as the *Medio-* *colpopollis* Group is absent a late Eocene age is less likely. For discussion see text. Numerical ages (Ma) following International Chronostratigraphic Chart, 2022/10 (https://stratigraphy.org/ICSchart/ChronostratChart2022-10.pdf)

present study. *T. formosum* has previously been recorded in marginal marine–lagoonal samples rich in *Apectodinium* from the late Ypresian–Lutetian of southern England (Islam 1983a, b). As noted by Islam (1983a), the two genera are probably related and favour a brackish water environment.

Phthanoperidinium comatum (Morgenroth, 1966) Eisenack and Kjellström, 1972 includes specimens with a reduced number of very thin spines which may also be rather short (possibly due to poor preservation). However, typical cysts with more numerous spines are also present in the material (Fig. 14 c, d).

Phthanoperidinium resistente (Morgenroth, 1966) Eisenack and Kjellström, 1972 and *P. echinatum* Eaton, 1976 are morphologically intergrading (Figs. 12 r–t, 14 e, f).

Two specimens in sample 108579 are assumed to either represent *Phthanoperidinium geminatum* Bujak in Bujak et al., 1980 or *P. regale* Bujak, 1994 which only differ in the type of archaeopyle (Fig. 14 a, b). As the specimens did not reveal the archaeopyle, they are grouped together in a *Phthanoperidinium geminatum – P. regale* group. Their shared diagnostic feature is the presence of distinctive simulate zones of ornament. However, less developed simulate zones may occur in other species (Bujak et al. 1980: 74). As only two specimens have been found, the identification is somewhat uncertain.

Polysphaeridium zoharyi (Rossignol, 1962) Bujak et al., 1980, in addition to typical specimens (Fig. 13 a–c), includes cysts with very thin, almost massive processes. They are considered to represent ecophenotypic varieties.

Palaeoecology

The most striking aspect of the dinocyst assemblage from Birkweiler is the very low diversity with only twelve species present (some of which are intergrading, cf. taxonomic notes). The gonyaulacoids, a major, mainly autotroph dinoflagellate group, is only represented by *Polysphaeridium zoharyi*. The numerous absent gonyaulacoid genera are associated with a wide range of neritic settings. Normally some of these genera would be represented in any neritic assemblages, at least in very small numbers, due to mixing of motile cells or cysts by currents, storms, reworking and time averaging. The missing gonyaulacoid genera include first and foremost the widespread, common *Spiniferites* group 'generalists with open marine affinity' (Frieling and Sluijs 2018) and the *Areoligera – Glaphyrocysta* group usually assumed to have lived in more proximal environments with normal salinity waters (e.g. Frieling and Sluijs 2018). Further notable absences include among others, *Cleistosphaeridium, Operculodinium, Cordosphaeridium, Areosphaeridium* and *Thalassiphora*.

The total absence of these genera suggests that the Birkweiler site was a completely landlocked water body, a scenario which would prevent the mixing of associations.

Except for *Polysphaeridium zoharyi*, the dinocysts present at Birkweiler are peridinoids, a group which today includes many heterotrophs. The proportion of heterotrophs is likely related to the production of prey in the surface waters and thus nutrient supply (Frieling and Sluijs 2018). The dominating cysts at Birkweiler, *Apectodinium* and *Phthanoperidinium*, are commonly considered to have been heterotrophs (cf. discussions in Sluijs and Brinkhuis 2009; Frieling and Sluijs 2018). The total dominance of peridinoids thus suggests a setting enriched in food/nutrients. Further ecological signals of individual taxa are given below.

Apectodinium (Costa and Downie, 1976) Lentin and Williams, 1977

Apectodinium is abundant in all samples (20–99 %, average 56 %) (Electronic Supplementary Material Tab. S3), except for sample 108581. This genus has been known since the 1970s for its abundance at the Paleocene–Eocene transition (e.g. Downie et al. 1971; Costa and Downie 1976; Harland 1979). It was later recognised that *Apectodinium* formed strong nearly global acmes on shelves during the hot initial Eocene PETM (Paleocene–Eocene Thermal Maximum; Bujak and Brinkhuis 1998; Crouch et al. 2001; Denison 2021). Palaeoecologically, *Apectodinium* was favoured by high temperatures and does not occur in great abundance below 20 °C (Frieling et al. 2014). It also seems to be favoured by coastal proximity, increased nutrient levels and freshwater input (Sluijs and Brinkhuis 2009; Sluijs et al. 2014; Frieling and Sluijs 2018). This preference seems to agree with the fact that most acmes of *Apectodinium* (except for the worldwide distribution during the PETM) are in lagoonal or estuarine environments (see below). The PETM distribution may be linked to increased nutrient input to shelves by rivers as predicted by circulation models (cf. discussion in Sluijs et al. 2007). Heilmann-Clausen (2020) discussed post-PETM examples from the Eocene of the North Sea Basin of strong (approx. 40–99 %) local *Apectodinium* acmes developed in brackish lagoons and some other very near-shore environments, while *Apectodinium* is rare or absent in coeval offshore sediments 600–700 km away. Apparently, these strong acmes were able to pop up very locally, whenever environmental conditions were optimal.

Phthanoperidinium Drugg and Loeblich Jr., 1967

Phthanoperidinium is abundant (16–66 %, average 34 %) except for the essentially dinocyst-free sample 108581. According to Sluijs et al. (2005) and Pross and Brinkhuis (2005) abundant *Phthanoperidinium* may in some cases be tied to high productivity in relatively shallow deltaic settings. In other cases, abundant *Phthanoperidinium* may indicate offshore upwelling areas. According to Frieling and
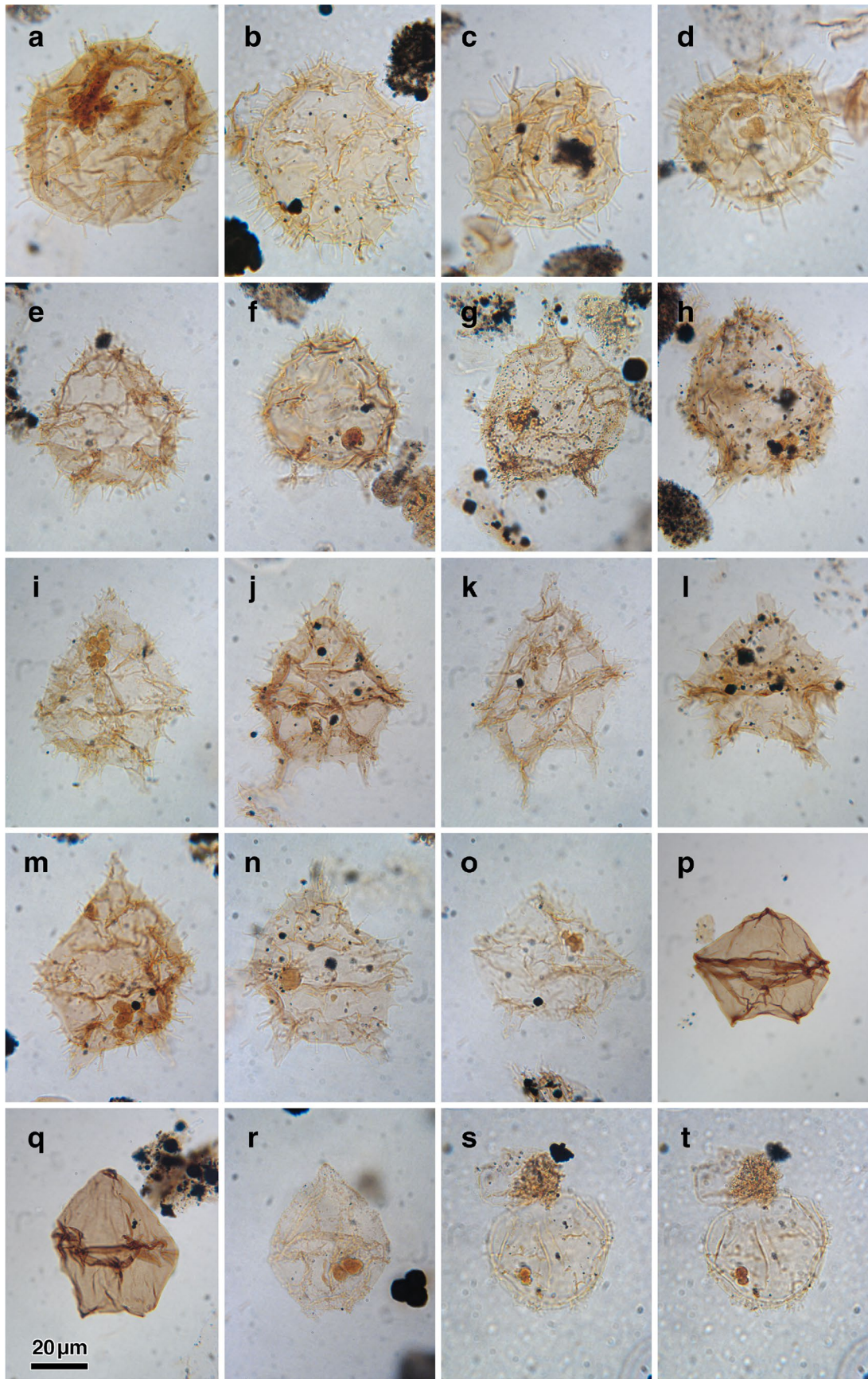
◄ **Fig. 12** Dinocysts from Birkweiler drainage pit. **a** *Apectodinium homomorphum* (slide 108590/1). **b** *Apectodinium homomorphum* (slide 108579/1). **c** *Apectodinium homomorphum* (slide 108590/1). **d** *Apectodinium homomorphum* (slide 108590/1). **e** *Apectodinium parvum – quinquelatum* transitional (slide 108575/1). **f** *Apectodinium parvum* (slide 108590/1). **g** *Apectodinium parvum* (slide 108575/1). **h** *Apectodinium parvum* (slide 108575/1). **i** *Apectodinium parvum – quinquelatum* transitional (slide 108575/1). **j** *Apectodinium quinquelatum* (slide 108586/1). **k** *Apectodinium quinquelatum* (slide 108586/1). **l** *Apectodinium quinquelatum* (slide 108586/1). **m** *Apectodinium quinquelatum* (slide 108575/1). **n** *Apectodinium quinquelatum* (slide 108586/1). **o** *Apectodinium quinquelatum* (slide 108586/1). **p** *Lejeunecysta hyalina* (slide 108579/1). **q** *Lejeunecysta hyalina* (slide 108579/1). **r** *Phthanoperidinium echinatum* (slide 108579/1). **s** *Phthanoperidinium echinatum* (slide 108579/1). **t** Same specimen as s. All photographs were taken using a 100x oil immersion objective. Slides are stored in the palynological collection of the Geological Survey North Rhine-Westphalia, Krefeld

Sluijs (2018) *Phthanoperidinium* is typically considered to be tolerant to low salinity.

Polysphaeridium zoharyi (Rossignol, 1962) Bujak et al., 1980

Polysphaeridium zoharyi is fairly common to abundant (1–19 %) in four of the five dinocyst-bearing samples. In contrast to all other species in the assemblages, *P. zoharyi* is the cyst of an extant dinoflagellate species. The motile stage of *P. zoharyi*, *Pyrodinium bahamense* Plate, 1906, mainly lives in equatorial lagoons and is tolerant to strong salinity fluctuations (e.g. Dale 1996; Pross and Brinkhuis 2005). *P. zoharyi* belongs to a group of dinocysts (epicystal Goniodomidae) which in the Paleogene have been particularly associated with seasonally elevated salinity levels (Frieling and Sluijs 2018).

Taken together, the Birkweiler dinocysts point to a completely landlocked water body with warm, nutrient-rich, brackish waters. Lagoons with fluctuating, seasonally high salinities may have been present.

The common occurrence of *Pediastrum* (14 %, cf. Electronic Supplementary Material Tab. S3) in sample 108575, and *Botryococcus* in all samples indicates significant influx of fresh water, at least temporarily.

Stratigraphical correlations and probable age

Due to the similarity of the dinocyst assemblages, the correlations and the age of the samples are discussed for all samples together.

Oldest possible age

Phthanoperidinium geminatum Bujak in Bujak et al., 1980 – *P. regale* Bujak, 1994 group

The oldest of these two species is *P. regale* with a lowest occurrence in the Norwegian-Greenland Sea near base of NP15b and near base of Chronozone C20r (Eldrett et al. 2004). The inception in Denmark is likewise in NP15 (Heilmann-Clausen and van Simaeys 2005: 195) and may be already in C21n, and thus slightly older than in the Norwegian-Greenland Sea, cf. discussion in King et al. (2016: 596). The influx of *P. regale* is a key-event defining Zone DE13 of King et al. (2016).

Relying on this group, the oldest possible age may therefore be mid Lutetian, early part of Chron C20r, or Chron C21n. It is important to note, however, that this group is only tentatively identified (cf. Dinocyst taxonomy notes).

Phthanoperidinium comatum (Morgenroth, 1966) Eisenack and Kjellström, 1972

Phthanoperidinium comatum is a well-known, distinctive dinocyst with a first occurrence in NW Europe in the late Ypresian (first occurrence in early Zone NP13, as discussed in King et al. 2016: 594). Numerous typical specimens were seen in the Birkweiler samples, and it is therefore rather certain that the samples cannot be older than early NP13.

Selenopemphix nephroides Benedek, 1972

The first occurrence of *Selenopemphix nephroides* is recorded in the North Sea Basin a little earlier than *P. comatum*, but still in the late Ypresian. It was recorded in Belgium in the Sables de Mons-en-Pévèle/Egem Member by Islam (1982), just below the lowest occurrence of the important marker *Areosphaeridium diktyoplokum* (Klumpp, 1953) Eaton, 1971, a level dated to uppermost NP12 (cf. King et al. 2016: 206). Heilmann-Clausen and Costa (1989) recorded *S. nephroides* from a similar level, just above the lowest occurrence of *A. diktyoplokum* in the Wursterheide borehole, northern Germany. However, Sluijs et al. (2009) recorded and illustrated *S. nephroides* from the PETM interval i.e. in the basal Ypresian, in the Bass River core, New Jersey. This species thus seems to have a very sporadic record, and is less reliable for dating.

Phthanoperidinium echinatum Eaton, 1976

The lowermost record of *Phthanoperidinium echinatum* is in early Ypresian in Belgium, at the base of the *Dracodinium simile* Zone (De Coninck 1991). Lowermost record in northern Germany seems to be in the mid Ypresian (Köthe 1990) and likewise in southern England (at base of the Bracklesham Beds, Eaton 1976).

Youngest possible age

Apectodinium spp.

The most dominating element in the Birkweiler assemblages is the genus *Apectodinium* with the closely related and
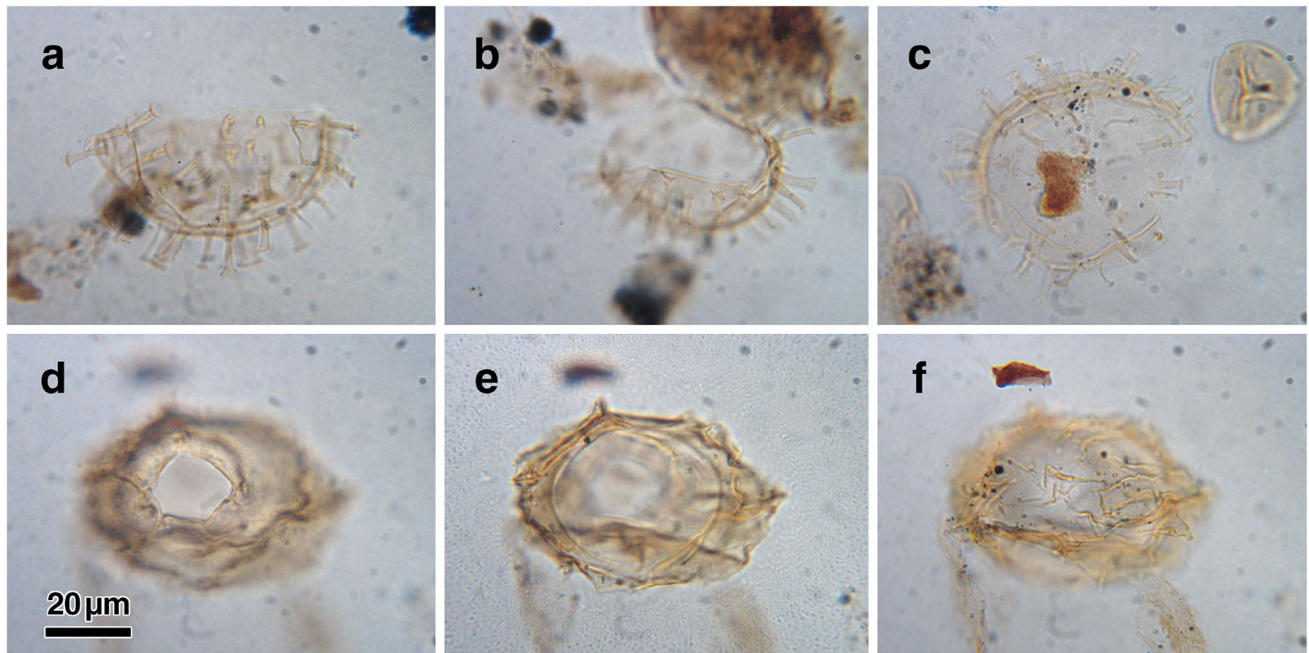
Fig. 13 Dinocysts from Birkweiler drainage pit. **a** *Polysphaeridium zoharyi* (slide 108590/1). **b** *Polysphaeridium zoharyi* (slide 108590/1). **c** *Polysphaeridium zoharyi* (slide 108590/1). **d** Unknown dinocyst sp. 1 (slide 108590/1, low focus). **e** Same specimen as d (middle focus). **f** Same specimen as d (high focus). All photographs were taken using a 100x oil immersion objective. Slides are stored in the palynological collection of the Geological Survey North Rhine-Westphalia, Krefeld

intergrading species, *A. homomorphum, A. quinquelatum* and *A. parvum*. The genus is even monotypic in sample 108586. As mentioned above, this intergrading complex is well known especially from the initial Eocene PETM interval. However, *Apectodinium* also developed strong, even monotypic, associations very locally in brackish, paralic environments in the North Sea Basin at later times during the Ypresian and Lutetian, while it is absent, or nearly so, in coeval fully marine environments (Heilmann-Clausen 2020; see Palaeoecology). This raises the question: Can this genus have survived in very marginal settings, at later Eocene times than indicated from literature? The knowledge of dinocyst assemblages in well-dated brackish lagoons through geological time is limited. Bearing this uncertainty in mind, a survey of late *Apectodinium* records in NW Europe may still yield the best available information on the youngest possible age of the Birkweiler assemblages and will therefore be presented below.

Southern England

In southern England *Apectodinium homomorphum* ranges continuously up to the top of the Barton Clay according to Costa and Downie (1976). An isolated occurrence is indicated by these authors in the middle Priabonian Middle Headon Beds, but *Apectodinium* was not recorded in the 13 samples from the Middle Headon Beds studied by the same authors, in Liengjarern et al. (1980), so the last

reliable record of *A. homomorphum* in southern England is in the late Bartonian. In a more detailed range chart of the Bartonian part of the same succession Bujak et al. (1980) indicated the top of *A. homomorphum* at a slightly lower level, in the middle of their Zone BAR-3 which is dated to the mid Bartonian (King et al. 2016: 421). No details on the abundance are given in these sources, and no other species of *Apectodinium* were recorded.

In the same area Eaton (1976) recorded sporadic *A. homomorphum* (which may include *A. quinquelatum*, by then ranked as a subspecies of *A. homomorphum*) in the Lutetian to earliest Bartonian.

Islam (1983a) recorded a strong acme of up to 40 % *A. homomorphum* (as the junior synonym *A. folliculum* Islam, 1983a) in a lower Lutetian lagoonal unit of the Earnley Formation at Bracklesham Bay. Similar observations of very abundant *A. homomorphum* were mentioned from some horizons of the upper Ypresian–Lutetian Bracklesham Beds at Alum Bay (Costa and Downie 1976). According to these authors *A. homomorphum* becomes dominant over *A. quinquelatum* in the late Ypresian and *A. quinquelatum* is only sporadically present in the Bracklesham Beds.

Northern France

In the Paris Basin Châteauneuf (1980) recorded common *A. homomorphum* in the 'Lutétien supérieur–base de l'Auversien', i.e. late Lutetian–early? Bartonian (King
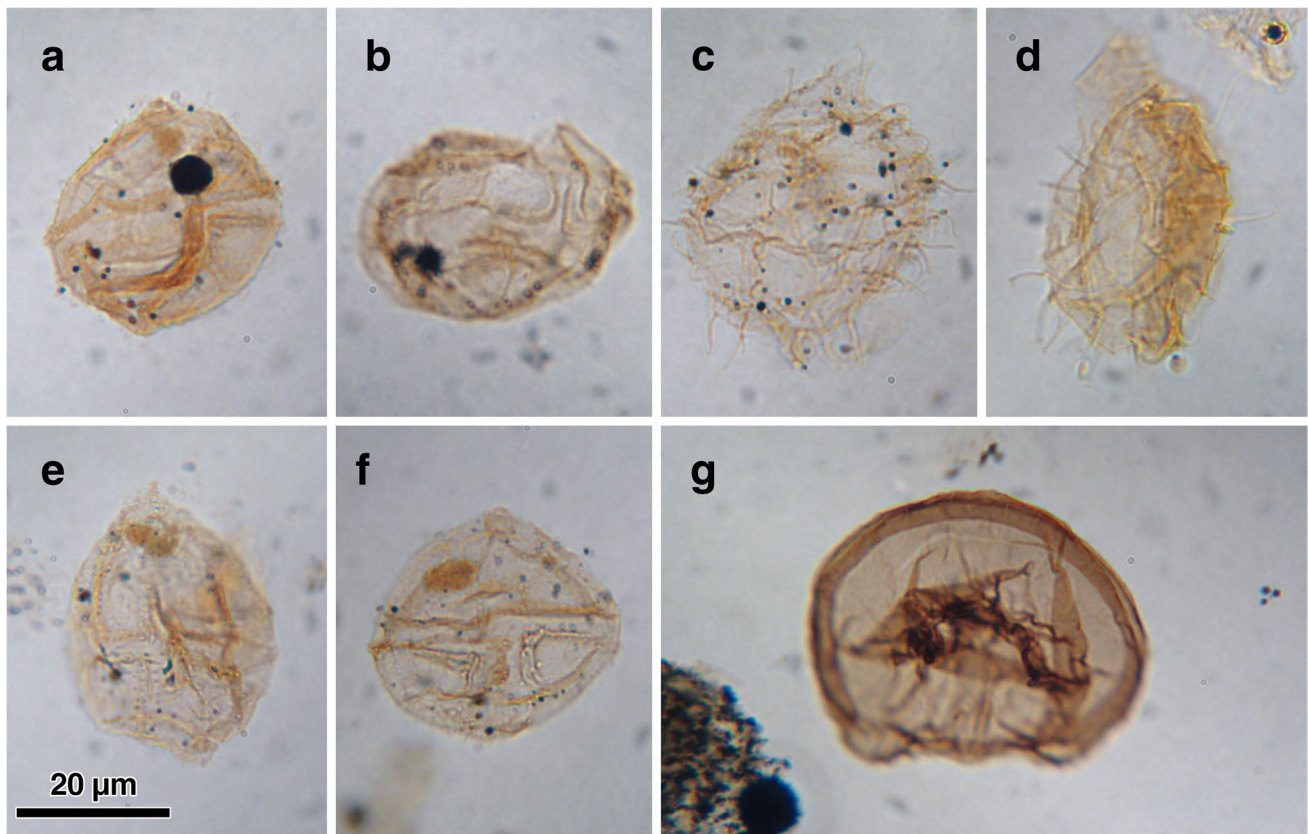
Fig. 14 Dinocysts from Birkweiler drainage pit. **a** *Phthanoperidinium geminatum – P. regale* group, uncertain identification (slide 108579/1). **b** *Phthanoperidinium geminatum – P. regale* group, uncertain identification (slide 108579/1). **c** *Phthanoperidinium comatum* (slide 108585/1). **d** *Phthanoperidinium comatum* (slide 108585/1). **e** *Phthanoperidinium resistente* (slide 108585/1). **f** *Phthanoperidinium resistente* (slide 108585/1). **g** *Selenopemphix nephroides* (slide 108579/1). All photographs were taken using a 100x oil immersion objective. Slides are stored in the palynological collection of the Geological Survey North Rhine-Westphalia, Krefeld

et al. 2016: 224). It is monotypic (90–98 %) in two samples from the basal 'Auversien' Horizon de Mont-Saint-Martin considered to be deposited in a lagoonal-continental or deltaic setting (Châteauneuf 1980: 149, 274). The Horizon de Mont-Saint-Martin is dated to the late Lutetian by King et al. (2016: 225). This is the only record of *A. homomorphum* in the mid Eocene–early Oligocene of the Paris Basin studied by Châteauneuf (1980).

No other species of *Apectodinium* were recorded by Châteauneuf (1980), except for rare *A. parvum* (as *A.* cf. *parvum*) in two sections of the lower Rupelian Marnes à Huîtres. It should be noted that, according to Châteauneuf (1980), there is no sign of reworking in these very young samples with *A. parvum*.

Northern Germany

In the Gartow borehole *A. homomorphum* is common to abundant in the middle of the mid Ypresian Subzone D8nb while it is absent above (Köthe 1990). In their integrated study of numerous other North German boreholes Köthe and Piesker (2007) indicated the tops of *A. homomorphum* and *A. quinquelatum* in Subzone D9na, which is near the Ypresian–Lutetian boundary according to King et al. (2016). No other species of *Apectodinium* ranged that high.

In the Wursterheide borehole the highest consistent occurrence of *A. homomorphum* is at 519 m in Zone D9 in which it accounts for 1–4 % of the dinocysts in several samples (Heilmann-Clausen and Costa 1989). This level is dated to late Ypresian by King et al. (2016). Sporadic and rare *A. homomorphum* continues up to 399.8 m, corresponding to early Lutetian. *A. quinquelatum* is very sporadic and rare up to earliest Lutetian.

To summarise, in northern Germany *A. homomorphum* is fairly common at a few late Ypresian levels and sporadic and rare in the early Lutetian. *A. quinquelatum* is very sporadic and rare in the earliest Lutetian.

Belgium

The Ypresian–Lutetian dinocyst succession is well known from Belgium due to several detailed studies by De Coninck (e.g. De Coninck 1976, 1977, 1985, 1991). Steurbaut et al. (2015) analysed a transitional Ypresian–Lutetian section in the Zemst Borehole for calcareous nannofossils, foraminifers and dinocysts. They discussed in particular the youngest occurrences of *Apectodinium* based on the Zemst section and previously studied sections. The following picture emerges from their discussion: *Apectodinium* is represented only by two species, *A. homomorphum* and *A. quinquelatum*, in the late Ypresian. It is frequent to abundant from the top of the Panisel Sand Member to the top of the Merelbeke Clay Member (i.e. from latest NP12 to mid NP13), with acmes of up to 14 % and 20 % at various levels at various localities. In all Belgian sections a major decrease of *Apectodinium* is observed from base of Pittem Clay (mid NP13) and upwards, as discussed in Steurbaut et al. (2015). This may be illustrated by the middle Lutetian Sands of Lede. Here De Coninck (1985) found < 1 % *A. homomorphum* in two of the four studied samples and < 1 % *A. parvum* in a third. These rare records may possibly be reworked. On the other hand, they are rather consistent with the data from northern Germany.

Western Alpine region, NW Tethyan Realm

In Haute-Savoie, France, the highest record of *A. quinquelatum* is in the Ypresian NP11 Zone. *A. homomorphum* and *A. hyperacanthum* (Cookson and Eisenack, 1965) Lentin and Williams, 1977 occur in the Lutetian and *A. homomorphum* also in the Priabonian (isolated record) (Jan du Chêne et al. 1975). In flysch from Switzerland *A. homomorphum* and *A. quinquelatum* occur in NP13, and *A. homomorphum* also in late NP14 and NP15 (Lutetian) (Jan du Chêne 1977).

Unspecified region

Costa and Downie (1979) stated that the last surviving species of *Apectodinium* are *A. quinquelatum* and *A. homomorphum* which survived to the late Eocene and early Oligocene, respectively. No details on these young records were given, however, and they are not taken into account in the present discussion.

To summarise the data on *Apectodinium*: For *A. homomorphum* the youngest reliable records are mid or late Bartonian. For *A. quinquelatum* the last reliable occurrences are somewhere in the Lutetian.

Phthanoperidinium echinatum Eaton, 1976

The youngest consistent records of *Phthanoperidinium echinatum* are mid or late Bartonian, as outlined below.

In a study of the lower and middle Eocene in southern England Bujak et al. (1980) recorded the last occurrence of *P. echinatum* within Zone BAR-3. The zone spans Beds E and F of the Naish Member and is dated to the mid Bartonian Chron C18n and NP17 (King et al. 2016: 421, fig. 152). *P. echinatum* was not recorded in the late Eocene of the same region studied by Liengjarern et al. (1980), thus supporting a Bartonian last occurrence.

In the north German Gartow borehole, the uppermost occurrence of *P. echinatum* is near top of Zone D10 (where it is common in one sample) (Köthe 1990). This level is dated to mid Bartonian (King et al. 2016: 25), and thus roughly coeval with the findings from England.

In Belgium De Coninck (1985) recorded *P. echinatum* in all four examined samples from the middle Lutetian Sands of Lede in the Mol borehole (common, with 4 % and 6 % in two of the samples). Rare *P. echinatum* (0.1–0.3 %) were recorded in six out of eight analysed samples from the Priabonian in the Dutch Woensdrecht borehole (De Coninck 1986).

In the Belgian Kallo borehole De Coninck (1995) found rare *P. echinatum* in the three Bartonian samples, but none in the five Priabonian samples (age of samples according to King et al. 2016).

In conclusion, in Belgium–the southern Netherlands *P. echinatum* is common in parts of the Lutetian, rare but consistent in the Bartonian and rare and inconsistent in the Priabonian.

P. echinatum was not recorded in the mid and late Eocene in Denmark (Heilmann-Clausen and van Simaeys 2005), nor in the late Lutetian–Oligocene of the Paris Basin studied by Châteauneuf (1980), although this author noted (p. 145) very rare *Phthanoperidinium* cf. *echinatum* in the 'Auversien' (i.e. late Lutetian/early Bartonian). This record is not included in his distribution chart, but a rare record in a single sample from the Rupelian is shown (p. 267).

Phthanoperidinium geminatum Bujak in Bujak et al., 1980 – *P. regale* Bujak, 1994 group

In the *Phthanoperidinium geminatum – P. regale* group *P. geminatum* ranges highest. The combined evidence shows that *P. geminatum* ranges to the mid Priabonian, as outlined below.

P. geminatum was established by Bujak in Bujak et al. (1980) and according to these authors the range in southern England is from Zone BAR-1 to the top of the studied interval (top of Zone BAR-5), approximately matching the Bartonian Stage (cf. King et al. 2016).

In the southern Netherlands *P. geminatum* is present in the Woensdrecht borehole in most samples up to the middle of the Priabonian Bassevelde Sands (De Coninck 1986, 1995). Similarly, in the Belgian Kallo borehole it is present in one Bartonian sample and in two out of three samples from the Bassevelde Sands, accounting for 1 % near base of this unit (De Coninck 1995).

In Denmark *P. geminatum* is very rare in two Lutetian samples from the Kysing-4 borehole, but consistent and more common in the late Bartonian and early Priabonian Chron C17n–C17r interval. *P. geminatum* is absent above, except for a single middle Priabonian sample from Chron C16n.1n and NP19/20 (at approx. 15 m). Here it accounts for 4 % and is presumably *in situ* (dinocyst data from Heilmann-Clausen and van Simaeys 2005; calcareous nannofossil- and magnetostratigraphy from Thomsen et al. 2012).

Stratigraphical conclusion

It seems certain, that the Birkweiler samples cannot be older than late Ypresian, Zone NP13 (based on *Phthanoperidinium comatum*). The *Phthanoperidinium geminatum – P. regale* group indicates an age no older than mid Lutetian. Unfortunately, this group is only tentatively identified.

Apectodinium quinquelatum suggests that the age can be no younger than Lutetian. *Phthanoperidinium echinatum* and *Apectodinium homomorphum* both suggest a youngest possible mid or late Bartonian age.

Calcareous nannoplankton

From the Birkweiler drainage pit 34 samples (M1 through M34) were investigated for calcareous nannoplankton. Since only excavated material could be sampled, the stratigraphical succession of the samples could not be established. Eleven of these samples contained autochthonous species, and in seventeen samples reworked Jurassic nannoplankton species such as *Ellipsosphaera britannica* (Stradner, 1963), *Schizosphaerella punctulata* Deflandre, 1939, *Stephanolithion bigottii* Deflandre, 1939 and some other species of Jurassic age were noted.

Two different autochthonous nannoplankton assemblages can be distinguished:

- a monospecific *Nannoserratolithus*-Assemblage with the new species *Nannoserratolithus minutus*, which is very small and could only be identified under the SEM. It is rather common in samples M1, M7 (both lacking macrofossils), M22 (with mass occurrence of hydrobioids and otoliths), but rare to infrequent in samples M6, M10, M12 (all lacking macrofossils), M14 (with hydrobioids) and M23 (with mass occurrence of hydrobioids and otoliths).

- a *Nannoserratolithus/Trochoaster/Trochastrites*-Assemblage which is present in samples M25, M26 and M31 (all with *Anomalorbina*? and otoliths).

Three additional samples from the Hydrobioid-, *Anomalorbina*?- and Potamididae-Association (see Kadolsky and Hartkopf-Fröder, in prep.) also contain the new nannoplankton species, which is rare in the Hydrobioid-Association and infrequent to common in the other two associations. In addition to the new nannoplankton species two *Trochoaster* species and one *Trochastrites* species were found in the *Anomalorbina*? sample, comparable with the above samples M25, M26 and M31. Rare reworked nannoplankton specimens from the Jurassic were noticed in all three associations.

In total, the following four calcareous nannoplankton species are present in the Birkweiler drainage pit samples.

Family Prinsiaceae Hay and Mohler, 1967
Genus *Nannoserratolithus* Martini and Schiller, 1998
Nannoserratolithus minutus Martini new species
(Fig. 15 a–d)

Holotype: Specimen shown in Fig. 15 a, stored in Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt/Main, under catalogue number SM.B 17726.
Locus typicus: Birkweiler drainage pit, north of Birkweiler near Landau, (map TK 25 Sheet 6714 Edenkoben; UTM coordinates (WGS84) ca. 32U 429700 5451248; ca. R 34 29748 H 54 52990).
Stratum typicum: Landauer Mergel *sensu* Breuer and Feist (1986), lower part of the Lymnäenmergel, Haguenau-Gruppe, middle Eocene.
Derivatio nominis: minutus (lat.) = tiny.
Diagnosis: Very small, elliptical forms consisting of two shields, with the distal shield being slightly larger than the proximal one. Shields are built out of 10 to 17 segments, with short lateral overlaps like in tiles and tapering with an offset at their outer margins. The segments join in the central area in a slight bend. Long diameter: 2.5 to 3.5 µm. Small diameter: 2.0 to 3.0 µm.

Complete coccospheres, discovered in the *Anomalorbina*?-Association, have a diameter of 12 µm and consist of approximately 30 coccoliths.
Discussion: The new species seems to represent a freshwater form and resembles *Nannoserratolithus dissolutus* Martini and Schiller, 1998 from the lower Oligocene "G-Ton" (Maifeld Formation) of the Neuwied Basin (see Martini and Schiller 1998). However, this species is larger and has 20 to 26 segments, which do not join in the central area. From other freshwater species (see Kamptner 1930), especially *Hymenomonas krejcigrafii* Martini, 1988 from the

"Untere Hydrobienschichten" (now Wiesbaden Formation; Reichenbacher and Keller 2002) of the Mainz Basin (Martini 1988), the new species can be easily differentiated by its two shields and shallower construction.

Family Lithostromationidae Deflandre, 1959
Genus *Trochoaster* Klumpp, 1953
Trochoaster deflandrei (Stradner, 1959) Martini and Stradner, 1960
(Fig. 16 a)

1959 *Polycladolithus deflandrei* nov. cent. – Stradner, fossile Discoasteriden Österreichs II, p. 18, fig. 76.
1960 *Trochoaster deflandrei* (Stradner) – Martini and Stradner, *Nannotetraster*, p. 3, tab. 1.
1991 *Trochoaster deflandrei* (Stradner) – Martini, Endemische Vertreter *Trochoaster*, p. 169, textfig. 2

Description: 6-rayed specimens, with 3 rays 120 degrees apart in an upper level and three rays in a lower level also 120 degrees apart but with a 60 degree offset. A groove is present on the central bridge which is built by ridges between the three main grooves. Towards the outer rim additional grooves and ridges are apparent. Size: 9.0–17.0 µm.
Remarks: Originally described from a marine succession of mid Eocene age from Aragon/Mexico, this species was found in lower Oligocene marine to brackish successions in the Upper Rhine Graben and Mainz Basin (Martini and Reichenbacher 2007), and also in the Chattian of the Lower Rhine region (unpublished).

Rare to few in the *Nannoserratolithus/Trochoaster/ Trochastrites*-Assemblage.

Trochoaster simplex Klumpp, 1953
(Fig. 16 b)

1953 *Trochoaster simplex* n. sp. – Klumpp, Mikrofossilien Eozän, p. 385, textfig. 4/2, pl. 16 fig. 7.
1958 *Trochoaster simplex* Klumpp – Martini, Discoasteriden NW deutschen Eozän, p. 368, pl. 5 fig. 25 a, b.
1972 *Trochoaster simplex* Klumpp – Sherwood and Levin, Closer look at *Trochoaster simplex,* p. 593, textfig. 1.

Description: 6-rayed specimens with a central groove and three smaller grooves on the central bridge. Rays in one level and 60 degrees apart. Ridges radiate outward from the centre and extend downward into the arms. For further details see Sherwood and Levin (1972). Size: 7.5–17.0 µm.
Remarks: *Trochoaster simplex* and variants are found in the marine to brackish/limnic sediments of the Mittlere Pechelbronn-Schichten in the Upper Rhine Graben and the Mainz Basin, part of the Melania Clay in northern Hesse and in the Sieblos Formation in the Rhön Mountains (Martini

1991) as well as in the Maifeld Formation in the Neuwied Basin (Martini and Schiller 1998), all of early Oligocene age. A *Trochoaster* species also occurs in nannoplankton mass-layers in the "Untere Hydrobienschichten" (now Wiesbaden Formation; Reichenbacher and Keller 2002) of the Mainz and Hanau basins (Martini 1988), indicating a certain tolerance of decreasing salinity.

Rare to few in the *Nannoserratolithus/Trochoaster/ Trochastrites*-Assemblage.

Trochoaster sp.
(not figured)

Remarks: Within the *Nannoserratolithus/Trochoaster/ Trochastrites*-Assemblage a large number of aberrant or underdeveloped specimens of a *Trochoaster* species was found. Most seem to represent *Trochoaster simplex*, but some may also belong to *Trochoaster deflandrei*. General size and organisation of rays vary considerably and may result in 4 and up to 9 rays and irregular outline in a specimen.

Genus *Trochastrites* Stradner, 1961
Trochastrites hohnensis (Martini, 1958) Bouché, 1962
(Fig. 16 c)

1958 *Discoaster hohnensis* n. sp. – Martini, Discoasteriden NW-deutschen Eozän, p. 358, pl. 2 fig. 10 a, b.
1962 *Trochastrites hohnensis* (Martini) nov. comb. – Bouché, Nannofossiles Bassin de Paris, p. 91, pl. 4 figs. 13, 14.
1986 *Trochastrites hohnensis* (Martini) – Aubry, Paleogene nannoplankton stratigraphy, p. 294, pl. 4 fig. 24.

Description: Three-rayed form with a ridge along rays and a more or less prominent bifurcation at the ends of arms. Rays are normally 120 degrees apart, but slightly aberrant specimens are known. Some larger specimens have shallow grooves on the flat parts on both sides of the ridges. Size: 8.3–13.5 µm.
Remarks: *Trochastrites hohnensis* was first described from the marine "lower Upper Eocene" ("Unteres Ober-Eozän") from well Hohne 1001 in northern Germany, and is associated with an assemblage belonging to nannoplankton zone NP15 (Martini 1958). Later it was found also in the marine Lutetian of the Paris Basin by Bouché (1962) and associated with *Rhabdosphaera inflata* Bramlette and Sullivan, 1961 by Aubry (1986). It seems to be restricted to nannoplankton zones NP14 and NP15 of mid Eocene age. The appearance together with a presumably freshwater species and the *Trochoaster* species, which arise sometimes also as mass occurrences in brackish waters (Martini 1991; Martini and Reichenbacher 2007), indicates a certain tolerance of reduced salinity.

Rare to few in the *Nannoserratolithus/Trochoaster/ Trochastrites*-Assemblage.
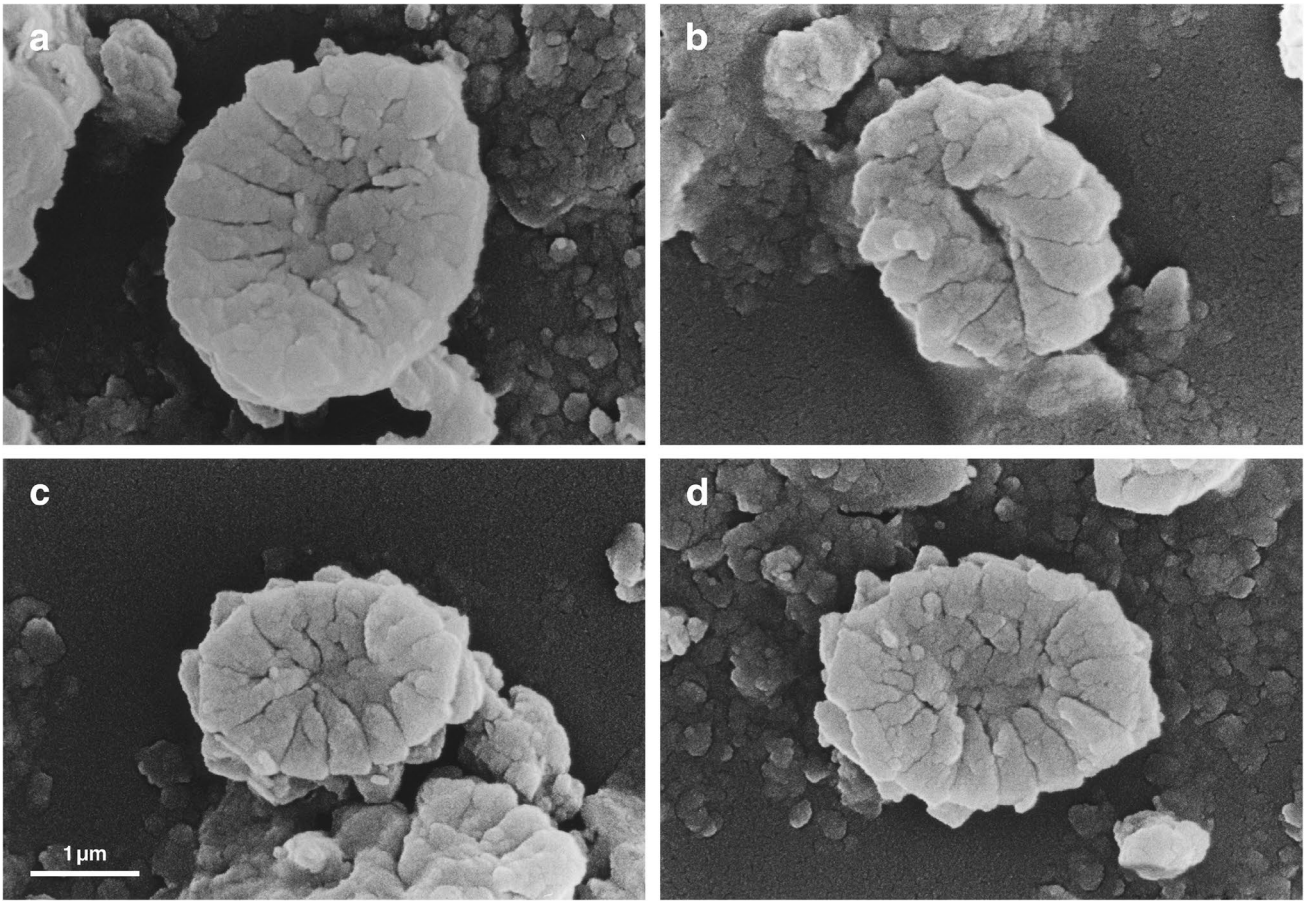
Fig. 15 Calcareous nannoplankton from Birkweiler drainage pit. *Nannoserratolithus minutus* new species Martini. Different specimens (SEM). **a** Holotype SM.B 17726. **a**, **c**, **d** proximal sides, **b** distal side; sample M1
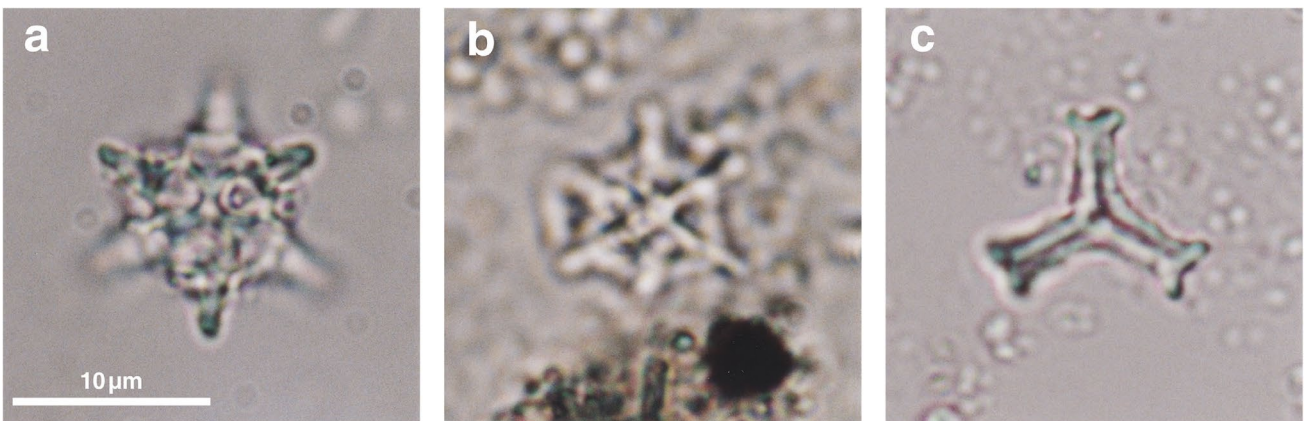
Fig. 16 Calcareous nannoplankton from Birkweiler drainage pit. Sample M25 (**a, c**), and sample from the *Anomalorbina*?-Assemblage (**b**). **a** *Trochoaster deflandrei*. **b** *Trochoaster simplex*. **c** *Trochastrites hohnensis*

The presence of only Jurassic reworked calcareous nanno-plankton besides the autochthonous species indicates a closed system without significant long-distance influences. The Jurassic material was probably derived from nearby sources. The onset of numerous reworked species from the Alpine Cretaceous and lower Paleogene occurs in the Rote Leitschicht (Couche rouge), together with the first and sudden influx of calcareous nannoplankton of late Eocene age in the southern Upper Rhine Graben (Martini and Reichenbacher 2007). Also, in the post-Eocene successions in the Upper Rhine Graben, Mainz and Hanau basins reworked nannoplankton is not restricted to Jurassic species as in the Birkweiler samples, but contains always reworked Jurassic and Cretaceous as well as Paleogene species (Martini 1990) indicating long range transport from the Alps into the Upper Rhine Graben at those times.

To get more information on the stratigraphical position of the Birkweiler sediments within the Upper Rhine Graben succession, several samples from the Lymnäenmergel (wells Landau 10, Oberweiler 1973, Freiburg 1974) were investigated together with samples from younger deposits for comparison. The Lymnäenmergel samples also contain only reworked calcareous nannoplankton of Jurassic age, but lack the new species.

The two nannoplankton assemblages from Birkweiler seem to indicate slightly different environments with regard to salinity variation. The monospecific *Nannoserratolithus*-Assemblage, probably originally representing a freshwater environment, may be followed by the *Nannoserratolithus/Trochoaster/Trochastrites*-Assemblage which is tolerant of reduced salinity and may point to a brackish water influence. A similar succession from freshwater to brackish water conditions has been reported from the lower Oligocene deposits of Sieblos/ Rhön Mountains (Martini and Rothe 1998).

Of stratigraphical importance is the presence of *Trochastrites hohnensis* in some of the Birkweiler samples. This species seems to be restricted to the mid Eocene as discussed above. Together with the allochthonous nannoplankton species of exclusively Jurassic age it indicates that the succession in the Birkweiler drainage pit belongs to the Landauer Mergel *sensu* Breuer and Feist (1986) (= lower part of the Lymnäenmergel) which are part of the Eocene Haguenau-Gruppe (Grimm et al. 2011b).

Foraminifera

Assemblages of calcareous foraminifers were found in some layers of borehole B 804 (Fig. 4), furthermore in one sample from the Birkweiler road cut and in one sample from the Birkweiler drainage pit (marls without gastropods, sample F1). The associations are of low diversity and indicate a brackish water environment of weakly increased salinity. Due to

these palaeoecological conditions the specimens usually are growth-restricted. Especially the tests from the sample of the road cut often are somewhat corroded and/or recrystal-lised. The foraminiferal assemblages include "*Rosalina*" spp., *Aubignyna*? sp., "*Nonion*" sp., *Anomalinoides* sp., *Caucasina*? *elongata* (d'Orbigny, 1846), *Caucasina*? cf. *coprolithoides* Andreae, 1884, *Turrilina* sp. and some small Miliolacea referred to as *Cycloforina*? spp. and *Quinqueloculina*? sp.

Most of the foraminifers are not age-diagnostic and hence, a specified stratigraphical assignment of the Birkweiler assemblages is not possible. The occurrence of the genus *Anomalinoides* may indicate an Eocene age as it has been described by Gebhardt et al. (2013) from middle to upper Eocene deposits at the northern Tethyan margin near Adelholzen in southeastern Bavaria (Germany). For the Upper Rhine Graben region a species of this genus was only mentioned by Doebl (1958, 1962: 385) as *Anomalina*? sp. 300. The taxon is regarded as an index fossil of the Eocene Lymnäenmergel.

"*Rosalina*" sp. A
(Fig. 17 d–g)

Test pentalobulate in outline, often with distinctly projected final chamber. Chambers arranged in one and a half whorls. All chambers visible on the spiral side. Final whorl with 5 chambers, only these chambers visible on umbilical side. Periphery rounded. Sutures somewhat depressed, slightly curved back or nearly radial. Spiral side with densely packed large pores, diameter of pores larger than the distance between the pores. Abundant but not well preserved in the sample from the road cut. Diameter of tests: 0.25–0.35 mm.

"*Rosalina*" sp. B
(Fig. 18 a, b)

Test quadrilobulate in outline. Chambers gradually increasing in size, arranged in one and a half whorls. All chambers visible on the spiral side. Final whorl with 4 chambers, only these chambers visible on umbilical side. Periphery rounded. Sutures distinctly depressed, nearly radial. Spiral side with moderately densely packed pores, diameter of pores smaller than the distance between the pores. The species occurs in some layers of borehole B 804, furthermore in the sample from the drainage pit and in the sample from the road cut. Diameter of tests: 0.20–0.23 mm.

"*Rosalina*" sp. C
(Fig. 18 d, e)

Test pentalobulate in outline. Chambers arranged in one whorl with 5 chambers. Periphery rounded. Sutures slightly depressed, nearly radial. Spiral side with wide-spaced large pores. The species occurs in some layers of borehole B 804 and in the sample from the drainage pit. Diameter of tests: 0.14–0.18 mm.

Aubignyna? sp.
(Figs. 18 i, 19 a–c)

Chambers arranged in a low trochospiral coil with 2–3 whorls in full-grown tests, but also small juvenile tests with only one and a half whorls are abundant. Final whorl with 7–8 chambers. Wall finely perforate. Sutures weakly depressed and curved back at the spiralside at least in the final whorl of full-grown tests, nearly radial in the initial whorl. Umbilical side with granules covering the umbilicus and the sutures. Last chamber somewhat inflated and strongly extended to the umbilical side. Aperture obscured by the granular deposit on the umbilical side. The species is abundant in the sample from the drainage pit, but also occurs in some samples of borehole B 804 and in the sample from the road cut. Diameter of tests: 0.11–0.34 mm.

Anomalinoides sp.
(Fig. 18 g, h)

1958 *Anomalina*? sp. 300 – Doebl, Stratigraphische und paläogeographische Ergebnisse
1962 *Anomalina*? sp. 300 – Doebl, Tertiär des Rheintalgrabens

Chambers arranged in a very low trochospiral coil with 2–3 whorls. Spiral side evolute. Final whorl with 6–9 coarsely perforated chambers. Umbilical side involute. Sutures incised, nearly radial or slightly curved back. Periphery outline lobulate or nearly rounded. Aperture a narrow slit extending from the base of the last chamber to the umbilical side. The species occurs in the sample from the road cut and in some layers of borehole B 804. Diameter of tests: 0.18–0.34 mm.

Caucasina? *elongata* (d'Orbigny, 1846)
(Fig. 19 d, f, g)

Test enlarging gradually from initial stage to final stage. Microspherical generation more or less elongated with a low trochospiral coil in initial stage. Later stage high spired with usually 3 chambers per whorl. Aperture a slit or broad oval opening at the face of the final chamber, bordered by a lip. The species occurs only in the sample of the drainage pit. Height of tests: 0.15–0.28 mm.

Caucasina? cf. *coprolithoides* (Andreae, 1884)
(Fig. 19 e)

Test more inflated. Chambers strongly increasing in size. Aperture a broad oval opening at the face of the final chamber, bordered by a lip. The species is proved only from the sample of the drainage pit. Height of figured test: 0.14 mm.

Cycloforina? sp. A
(Fig. 18 c, f)

Test quinqueloculine. Aperture circular, situated beside the penultimate chamber. No apertural tooth visible. The species is proved only from one sample of borehole B 804. Height of tests: 0.16–0.23 mm.

Cycloforina? sp. B
(Fig. 19 h)

Test quinqueloculine. Aperture circular with simple apertural tooth, situated at the distal end of the test covering parts of the penultimate chamber. The species is proved only from the sample of the drainage pit. Height of tests: 0.16–0.21 mm.

Quinqueloculina? sp.

Some small Miliolacea assigned to the genus *Quinqueloculina*? were found in some layers of borehole B 804 and in the sample from the drainage pit.

Turrilina sp.

The species only occurs in the sample from the drainage pit.

"*Nonion*" sp.

One specimen referred to as "*Nonion*" sp. was found in a sample from borehole B 804 between 7.8–8.0 m depth.

Ostracoda

Ostracods were recovered from two samples of the Birkweiler road cut of which one sample yielded a mass occurrence of the brackish water indicating ostracod genus *Neocyprideis*. Additional findings of ostracods in samples F1 and F2 from the drainage pit and in samples from borehole B 804 are rare. Some carapaces and often fragmented valves are assigned to the cypridid genus *Cypridopsis*?, which is well known from the Paleogene to the Recent. The genus usually indicates freshwater environments, but some species are tolerating also slightly increased salinities (Oertli 1963). Yet two other ostracod-species belonging to the genus *Ilyocypris*? and to the family Trachyleberididae? were found in the foraminifer yielding sample from the drainage pit (sample F1). Both species are documented only by a single carapace and no further detailed taxonomical classification is possible.
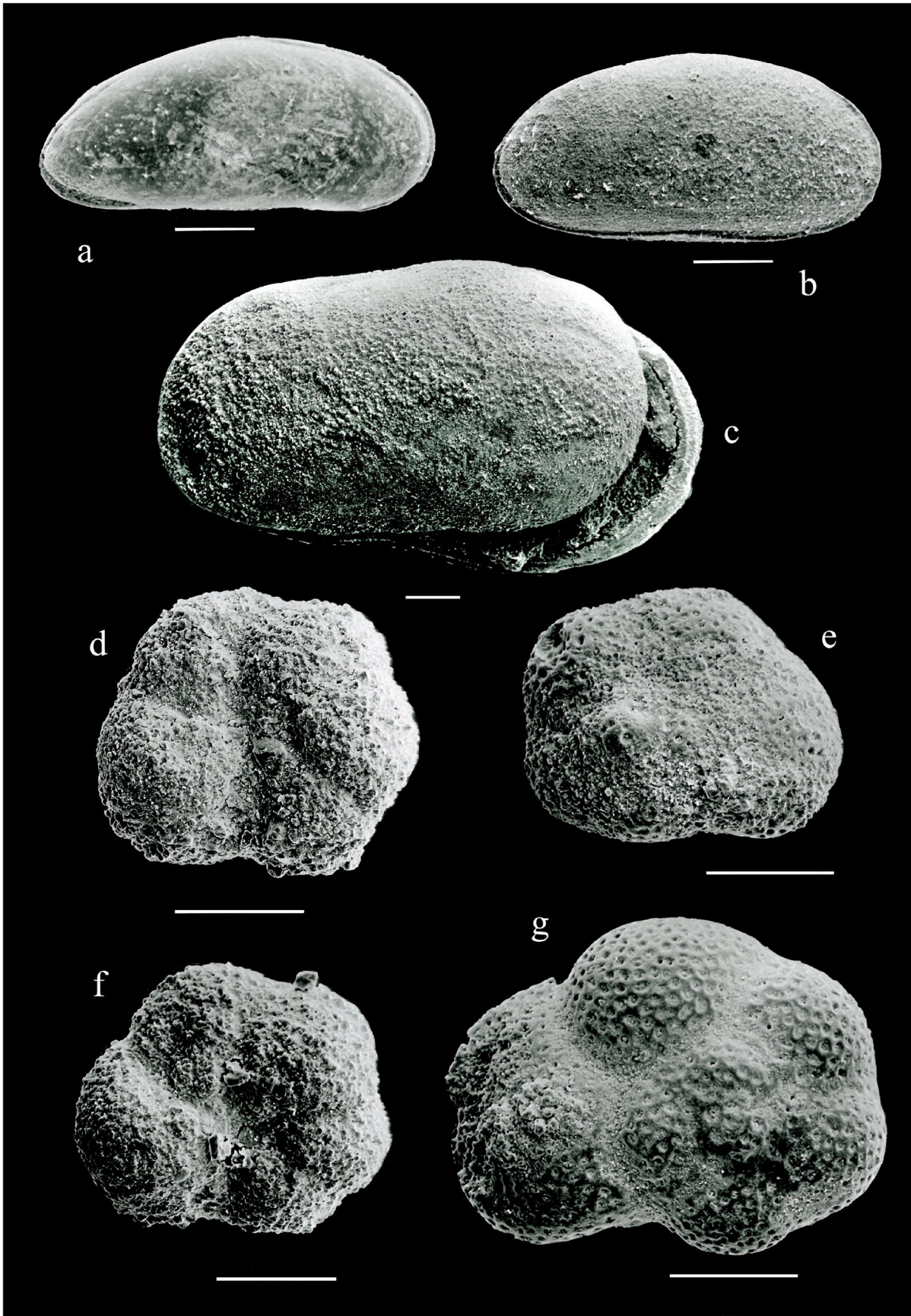
Cypridopsis? sp.
(Fig. 17 a, b)

Carapace elongated, highest in mid-length. Left valve larger than right valve. Posterior margin in lateral view somewhat narrower rounded than the anterior margin. Dorsal margin evenly curved or, especially in the right valve, very weakly angulated in mid-length. Vestibule clearly widened on the anterior margin. Fused zone on the ventral margin only widened in the anterior half of the valve. Central muscle scars could not be observed. The species occurs in one sample from the road cut and in sample F2 from the drainage pit. In the latter it is found together with the Hydrobioid-Association. Length of carapaces: 0.51–0.57 mm. Height of carapaces: 0.26–0.31 mm.

Neocyprideis sp.
(Fig. 17 c)

Unfortunately, the recovered material is not well preserved and does not allow a specific determination. Most of the specimens found are females, whose carapaces are inflated at its posterior end, which is caused by a breeding cavity developed in all species of *Neocyprideis*. Carapaces of the males are more evenly rounded in dorsal view. A comparison with Paleogene *Neocyprideis* species known from the southern North Sea Basin (see remarks) shows that *Neocyprideis* sp. resembles *Neocyprideis apostolescui* (Keij, 1957) in outline, but its dimensions (up to 0.95 mm length and 0.65 mm height measured for a female left valve) are larger. Better preserved material of *Neocyprideis* sp. is required to decide if this species belongs to the mid Eocene *N. apostolescui* – although there was no connection between the Upper Rhine Graben system and the North Sea Basin in Eocene times – or should be described as a new taxon. The species is very abundant in a sample of the road cut, rare in the foraminifer yielding sample from the drainage pit, but also occurs in one layer of borehole B 804 where one specimen could be found between 23.8 and 24.0 m depth. Length of carapaces: 0.85–0.95 mm.
**Remarks:** Keen (1990) studied the ecology and evolution of the ostracod genus *Neocyprideis* in Paleogene deposits of the southern North Sea Basin. He could recognise a phylogenetic lineage, which allows to separate four species. According to Keen (1990) the most ancestral species is the late Paleocene (Thanetian) *Neocyprideis durocortoriensis* Apostolescu, 1956. From it evolves *N. apostolescui*, known

from middle Eocene sediments, subsequently the late Eocene *Neocyprideis colwellensis* (Jones, 1857) and finally *Neocyprideis williamsoniana* (Bosquet, 1852) in the early Oligocene. The latter species is also described from lower Oligocene sediments of Turkey (Gökçen 1973). The only mention so far of a *Neocyprideis* species from the Eocene of the entire Upper Rhine Graben area including the Mainz Basin can be found in Ohmert (2014), who specified *N*. aff. *colwellensis* from the Lymnäenmergel of a core drilling near Oberweiler in the southern Upper Rhine Graben. However, this is probably not the species described here as *Neocyprideis* sp. The genus *Neocyprideis* is most common in mesohaline to polyhaline and possibly in slightly hypersaline environments. Sometimes it is found together with euhaline marine ostracods, but it is always absent in oligohaline or freshwater habitats (Keen 1977, 1990).

Vertebrate remains (fish otoliths excluded)

In addition to the very abundant fish otoliths fish remains such as scales, vertebras, spines and teeth have been found in the Birkweiler samples and in a Hydrobioid-Association from borehole B 804 (27.80–28.00 m). Especially ganoid scales (Fig. 20 a) and jaw teeth (Figs. 6 a, b, 21 a–c) of gars (Lepisosteidae) are common. The gar teeth have a striated basal part and a smooth upper part (compare Grande 2010: 74, figs. 45, 240). The enamel is thin and strongly fluorescent. Dentine tubules which start immediately below the enamel are densely distributed and radiate inwards to the pulp cavity. The diameter of the tubules does not increase towards the pulp. Close to the tip the pulp cavity is very narrow but much wider at the tooth base (Fig. 21 a). Identical teeth and one scale are described by Weiler (1963: 8, figs. 2, 3) as *Lepisosteus* sp. from olive grey to green grey, fossiliferous claystones and clayey marlstones in well Landau 117 (825–830 m, Landauer Mergel *sensu* Breuer and Feist 1986, Lutetian) and, additionally, by Weiler (1961: pl. 8, figs. 6–8, 11–14) from the "Melanienton" of Borken (see also Grande 2010: 738). The same tooth type has been reported by Lavoyer (2013: pl. 12, fig. 4) from the Mittlere Pechelbronn-Schichten of the well Preuschdorf near Pechelbronn. In the uppermost Ypresian/lower Lutetian oil shales of the Middle Messel Formation (Lenz et al. 2015) the gars are represented by *Atractosteus messelensis* Grande, 2010. Today species of the genus *Lepisosteus* are common in North and Central American lakes and rivers as well as brackish waters of estuaries and marine coastal areas (e.g. Grande 2010; Echelle and Grande 2014). Under special weather conditions mass mortalities of gars may occur and were reported from Smithers Lake, Texas, by Weigelt (1927).

Spines and soft-rays of fins as well as vertebras of unidentifiable teleosts are rare to few in the collected material. Some of the spines may belong to the perches
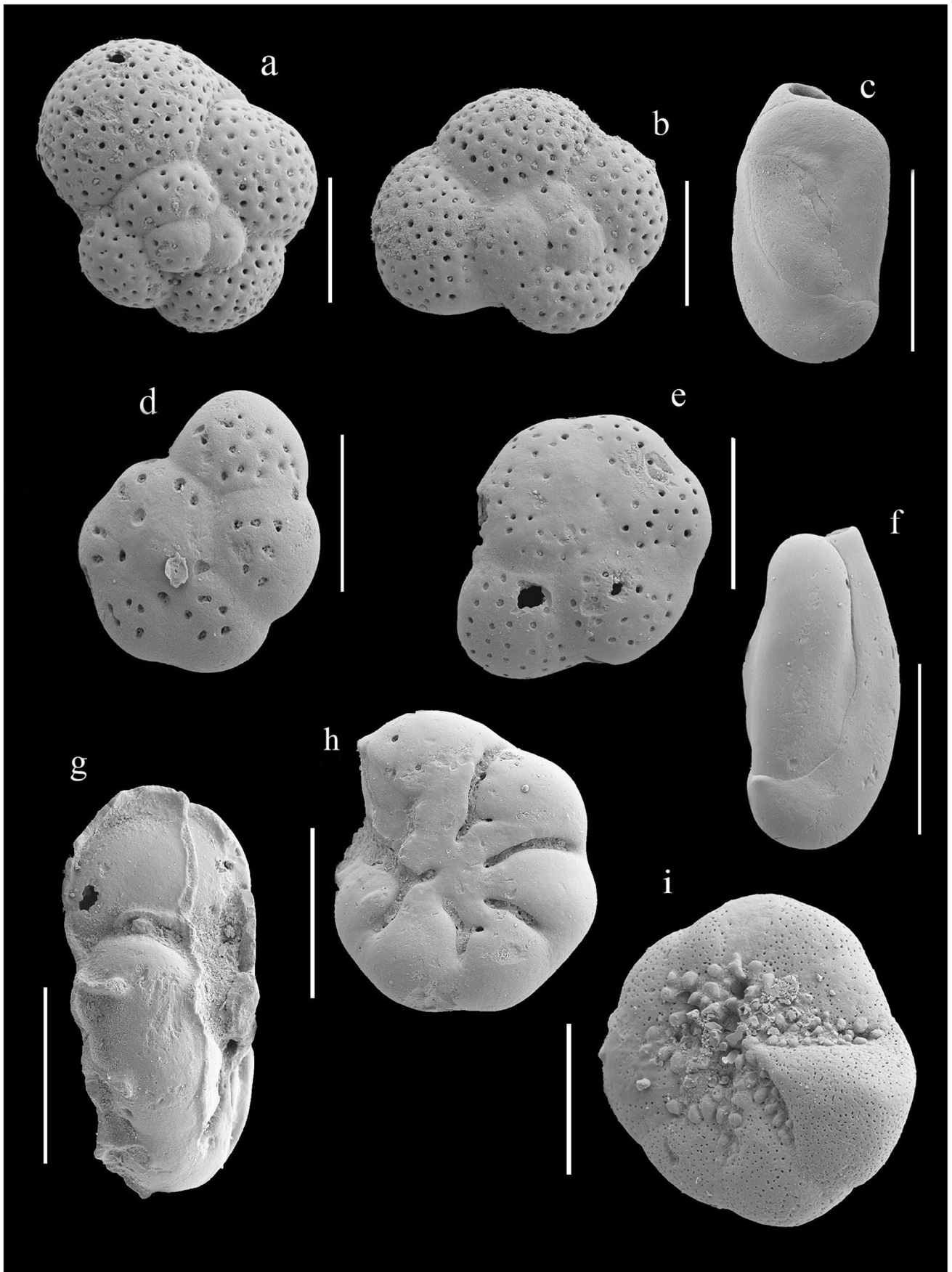
Fig. 18 Foraminifers from borehole B 804. **a**, **b** "*Rosalina*" sp. B, spiral side, 7.8–8.0 m depth. **d**, **e** "*Rosalina*" sp. C, spiral side, 7.8–8.0 m depth. **c**, **f** *Cycloforina*? sp. A, lateral view, 11.8–12.0 m depth. **g**, **h** *Anomalinoides* sp., periphery of a broken test showing part of the aperture (g); umbilical side (h), 7.8–8.0 m depth. **i** *Aubignyna*? sp., umbilical side of a juvenile test, 23.8–24.0 m depth. Scale bar: 0.1 mm

(Percidae). At present six species of five fish families are known from the classic oil shale of the Middle Messel Formation (Micklich 2018), which includes also three perches: *Palaeoperca proxima* Micklich, 1978, *Rhenanoperca minuta* Gaudant and Micklich, 1990 and *Amphiperca multiformis* Weitzel, 1933.

A sample rich in hydrobioid gastropods and otoliths from the Birkweiler road cut yielded disarticulated turtle plates, with the largest fragment measuring 17 x 25 mm. As the surface of the broken pieces are smooth and not sculptured they seem to belong to the swamp turtle *Palaeoemys* (syn. *Palaeochelys*), and not to *Allaeochelys* or *Trionyx*. Four species of turtles are known from the uppermost Ypresian/lower Lutetian Middle Messel Formation with *Palaeoemys messeliana* (Staesche, 1928) as the most common one, formerly placed in the genus *Ocadia* (see Cadena et al. 2018).

Ninety-five isolated teeth of alligatoroids were recovered from a Birkweiler road cut sample. They belong mainly to the genus *Diplocynodon*. These teeth are up to 17 mm long, are slightly bent and have weakly keeled sides (Figs. 20 b, 21 f, g). The larger ones are often split in two or more pieces. Very similar teeth were depicted by Weiler (1963: 10, fig. 10 a, b) from the Lutetian marls in borehole Landau 117 (825–830 m) and by Lavoyer (2013: pl. 13, fig. 1) from the middle Lutetian of Bouxwiller. A similar specimen (Heidtke 2006: fig. 14) is supposed to have been found in Lower Jurassic sedimentary rocks of the brickyard pit west of Siebeldingen but obviously originates from middle Eocene sediments which were exposed in the area of the former brickyard pit (Schwarz and Griessemer 1998). All material in our study was isolated from hydrobioid and otolith rich marl. The teeth are surprisingly abundant and rather well preserved. Hence, for our material reworking from Jurassic strata is excluded and the *Diplocynodon* teeth are definitely of mid Eocene age. Some sturdier and smaller teeth with more rounded tips seem to belong to the genus *Hassiacosuchus* (Fig. 21 d, e). This type was also reported from the middle Lutetian of Bouxwiller (Lavoyer 2013: pl. 13, fig. 4). Both alligatoroid genera were recorded from the uppermost Ypresian/lower Lutetian Middle Messel Formation as *Diplocynodon darwini* (Ludwig, 1877), *Diplocynodon deponiae* (Frey et al., 1987) and *Hassiacosuchus haupti* (Weitzel, 1935), formerly placed in the genus *Allognathosuchus*, together with representatives of the additional genera *Asiatosuchus*, *Boverisuchus* and *Bergisuchus* (Keller and Schaal 1988, Brochu and Miller-Camp 2018).

The above vertebrates of the Birkweiler locality are indicative of large water bodies with a well-established food chain and show some similarity regarding age and faunal composition to the latest Ypresian/early Lutetian Messel fauna (compare Smith et al. 2018).

Stratigraphical synthesis

The 3 m thick clay layer with numerous reddish brown to black concretions ("Bohnerz") at the very base of the Birkweiler road cut section did not yield any macrofossils. Hence, the depositional environment and stratigraphy is not well known. The hematite/goethite concretions and the kaolinite-rich clay are interpreted as a residual terrestrial sediment, i.e. a ferruginous palaeosol which formed under tropical-subtropical conditions (Sittler 1970). In the middle and southern Upper Rhine Graben such sediments are widespread at the base of the Paleogene succession (e.g. Doebl 1970). Usually, these residual sediments whose thickness varies between less than a metre to more than 100 m overlay karstified Jurassic limestones (Pirkenseer et al. 2018). In the Mainz Basin similar formations are of late Miocene age (Schäfer 2012). In the Birkweiler road cut the lack of any fossils in the ferruginous palaeosol hampers a bio- and chronostratigraphical assignment. The designation of the lowermost part of the Birkweiler road cut section to the Schliengen Formation is therefore solely based on petrography and its position overlying the Lower Jurassic mudstones and underlying sediments dated as Eocene.

The sediments overlying the Schliengen Formation are exceptional in that they yielded pollen and spores, dinocysts, green algae, calcareous nannoplankton, foraminifers, gastropods, ostracods and vertebrate remains, including numerous otoliths, fish teeth and scales and reptile remains.

The presence of some typical mid Eocene pollen and spores such as *Tegumentisporis villosoides*, *Tricolporopollenites crassostriatus* and representatives of Bombacaceae is significant. However, *T. villosoides* and pollen of Bombacaceae were recently identified from the upper Ypresian to lower Lutetian of Messel and the nearby locality Grube Prinz von Hessen (Lenz and Wilde 2018; Moshayedi et al. 2018) and, consequently, a late Ypresian age cannot be ruled out. Likewise, a late Eocene age is less likely due to the absence of the *Mediocolpopollis* Group which is an important marker taxon for the late Eocene in Central Europe (Krutzsch 2008; Hottenrott in Grimm et al. 2011a) although it has been reported from the mid Eocene until the beginning of the late Eocene of the Paris Basin (Schuler 1990).

Although the dinocyst diversity is very low with only twelve species recorded the assemblage constrains the age of the sediments from the Birkweiler drainage pit to not older than late Ypresian and probably not younger
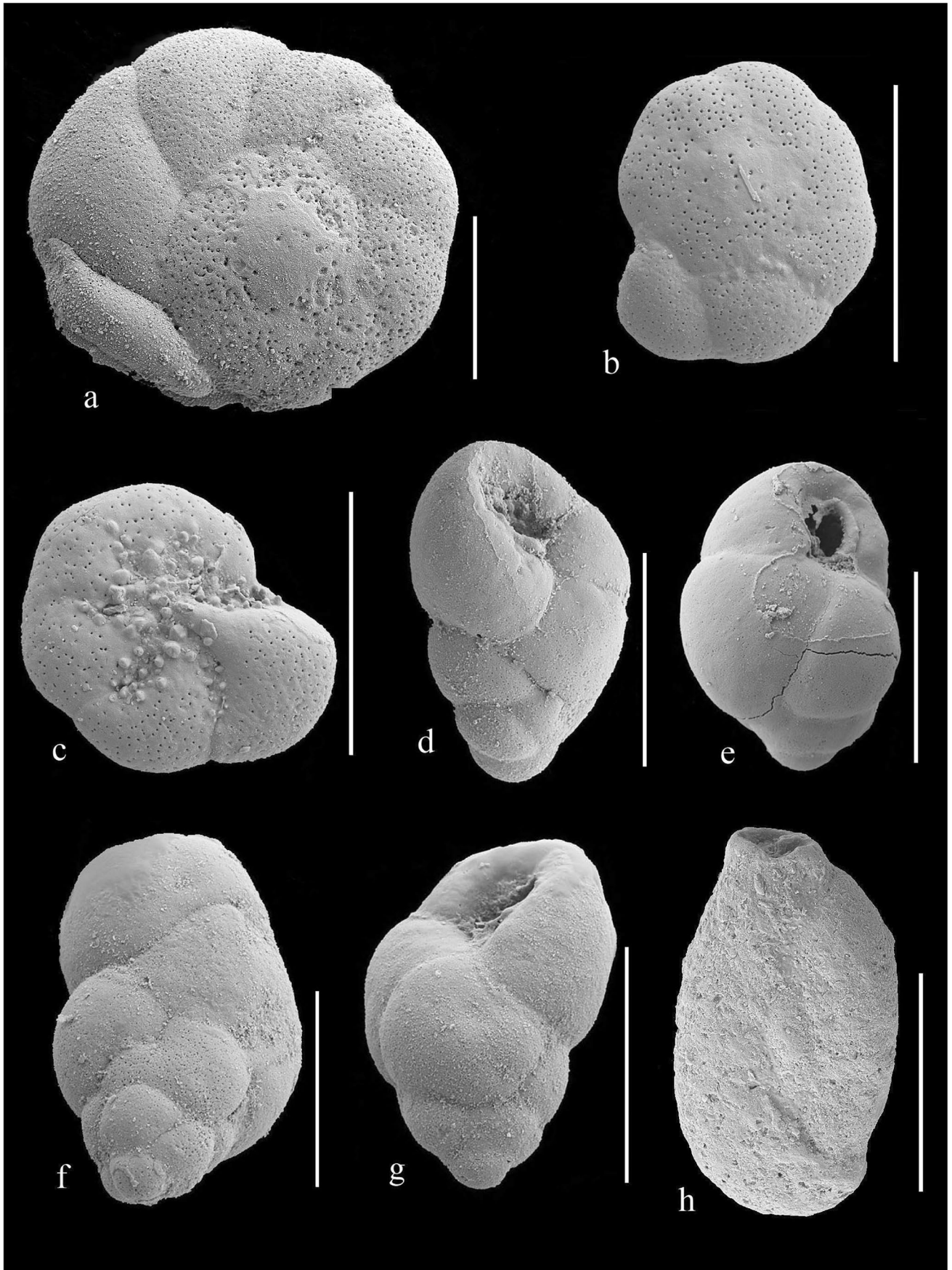
◄**Fig. 19** Foraminifers from Birkweiler drainage pit. **a–c** *Aubignyna*? sp., spiral side (a), spiral side of a juvenile test (b), umbilical side of a juvenile test (c). **d**, **f**, **g** *Caucasina*? *elongata*, juvenile megalospherical test in lateral view (d), microspherical test in oblique lateral view (f), juvenile microspherical test in lateral view (g). **e** *Caucasina*? cf. *coprolithoides*, juvenile test in lateral view. **h** *Cycloforina*? sp. B, lateral view. Scale bar: 0.1 mm

than Lutetian. The presence of numerous specimens of *Phthanoperidinium comatum* indicates that the assemblage cannot be older than early NP13 (late Ypresian). The *Phthanoperidinium geminatum – P. regale* group would restrict the oldest possible age to mid Lutetian but only two specimens were encountered so that this age assignment must be taken with some caution. The occurrence of *Apectodinium quinquelatum* suggests that the samples cannot be younger than Lutetian while *Phthanoperidinium echinatum* and *Apectodinium homomorphum* imply an age not younger than mid or late Bartonian.

Trochastrites hohnensis seems to be restricted to nannoplankton zones NP14 and NP15 (Lutetian). Foraminifers, ostracods and vertebrate remains do not further refine this biostratigraphical dating.

Based on pollen and spores, dinocysts and calcareous nannoplankton a Lutetian age is most probable though a late Ypresian to Bartonian age cannot be completely ruled out at this point.

Because of the exceptional faunal composition the lithostratigraphical assignment of the Birkweiler fossiliferous marls, organic matter-rich clays and lignite is not obvious. In the Upper Rhine Graben the Schliengen Formation is overlain by the Haguenau-Gruppe which is subdivided by Grimm et al. (2011b) from base to top into the Bouxwiller Formation, Grüne Mergel and Rote Leitschicht. The Bouxwiller Formation, only present in some isolated areas of the middle and southern Upper Rhine Graben, is well dated by charophytes and mammals and assigned to the mid Lutetian MP13b zone (Berger et al. 2005a; Lavoyer 2013). In many boreholes a gradual transition from the Siderolith "Facies" into the Grüne Mergel "Facies" has been observed (Hinsken et al. 2007). The Grüne Mergel are still an informal formation but nevertheless were differentiated into three members, the basal Untere Grüne Mergel, the Brunstatt Subformation and the *hombresi*-Mergel at the top (Grimm et al. 2011b). The application of the Grüne Mergel and the Untere Grüne Mergel may be questionable as pointed out by Kadolsky and Hartkopf-Fröder (in prep.). A widely used term in hydrocarbon exploration and basic research for middle and upper Eocene sediments in the Upper Rhine Graben is the Lymnäenmergel (e.g. Doebl 1958, 1962; Wirth 1969; Schäfer 2000, 2013). The middle Eocene basal part of the Lymnäenmergel probably includes the Landauer Mergel *sensu* Breuer and Feist (1986: fig. 2) which is an informal and poorly defined lithostratigraphical six metre thick unit composed of

a

5 mm

b

2 mm
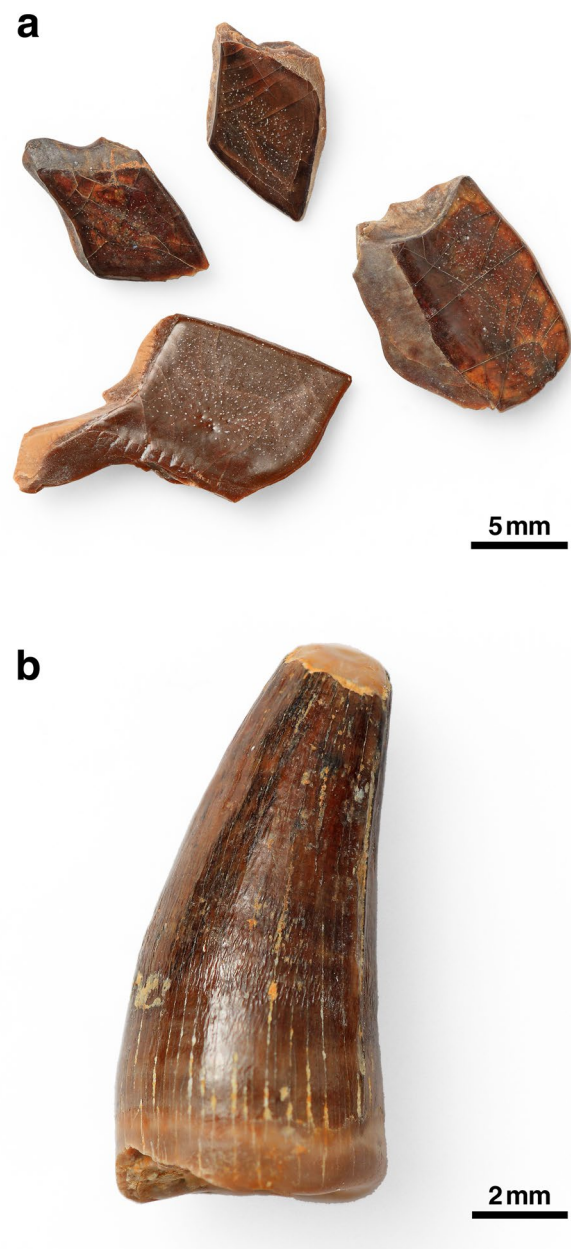
Fig. 20 Vertebrate remains from Birkweiler road cut. **a** Lepisosteidae, scales. **b** *Diplocynodon* sp. tooth

olive grey to green grey, fossiliferous claystones and clayey marlstones in well Landau 117. In this well the Landauer Mergel overlies Triassic sedimentary rocks (middle Keuper) and is overlain by the middle Rupelian Alzey Formation. Hence, the lower and the upper boundary of the Landauer Mergel are hiatuses and the entire stratigraphical range of this unit is insufficiently known. The succession in well Landau 117 includes a horizon extremely rich in gyrogonites, foraminifers, ostracods, fish and crocodylian teeth, otoliths and fragments of vertebrates (Weiler 1963; Breuer and Feist 1986). According to the charophytes the Landauer Mergel is assigned
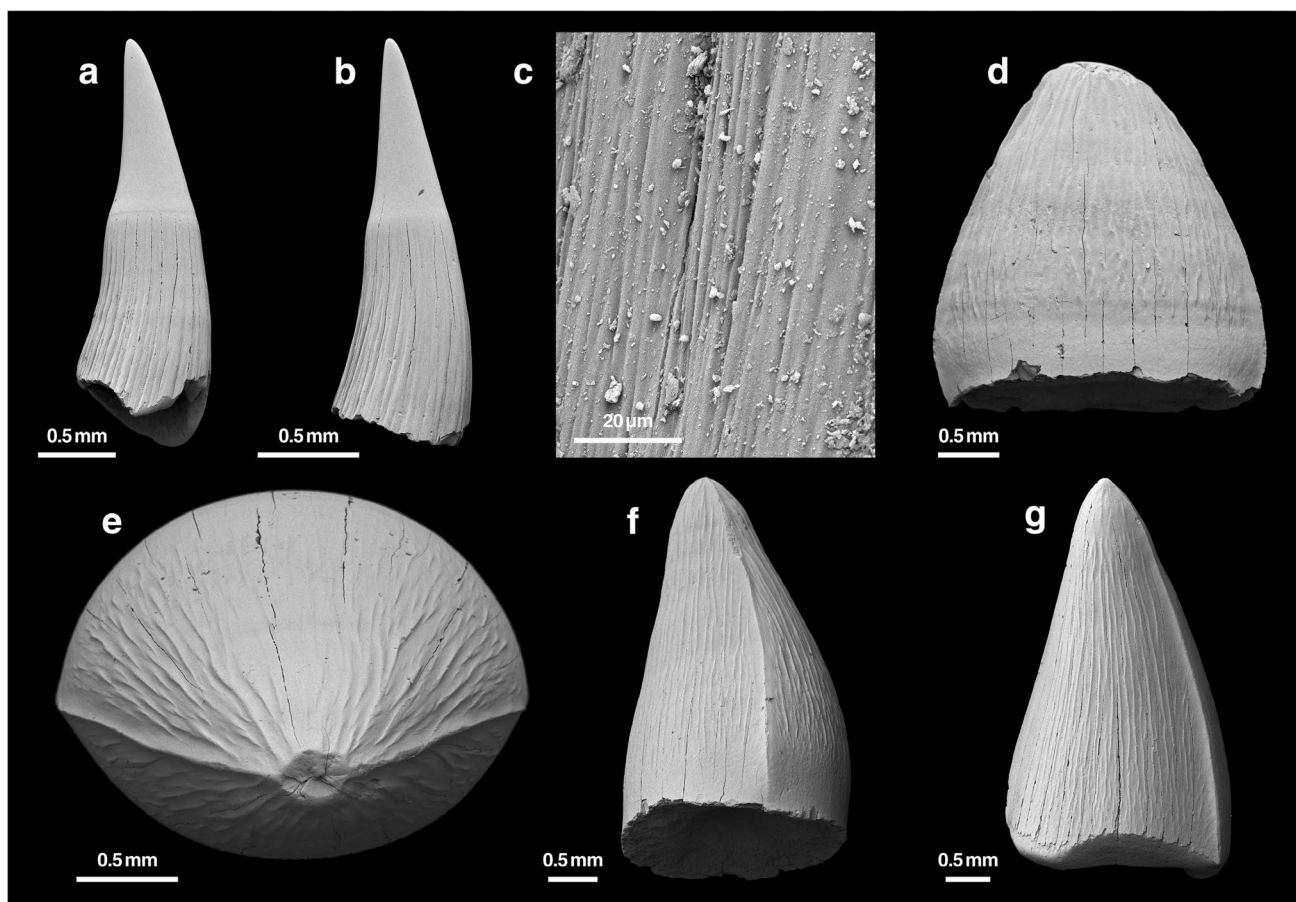
Fig. 21 Vertebrate remains from Birkweiler road cut. **a, b** Lepisosteidae, jaw teeth. **c** Lepisosteidae, jaw tooth, detail of striated basal part. **d, e** *Hassiacosuchus* sp., teeth, view at tip (e). **f, g** *Diplocynodon* sp., teeth

to the *Maedleriella embergeri* Zone (Lutetian) (Breuer and Feist 1986). Gyrogonites are absent in our samples but have been recorded by Schwarz and Griessemer (1998) from green marls temporarily exposed in the area of the former brickyard pit near the Birkweiler road cut and assigned to the Landauer Mergel. Like in well Landau 117 this assemblage is indicative of the *Maedleriella embergeri* Zone. As in the faunal list of Breuer and Feist (1986) gastropods are not mentioned they are obviously lacking in this well. However, in several wells in the Landau oil field numerous mid Eocene gastropods, ostracods, gyrogonites and fish remains, including otoliths, have been encountered (Wirth 1969). Unfortunately, no data on calcareous nannoplankton and palynomorphs are available from this succession. Despite distinct differences between the Birkweiler and the Landauer Mergel assemblages in well Landau 117 they have characteristic elements in common, i.e. a fauna clearly indicating brackish water conditions. Hence, the sediments at least from the Birkweiler drainage pit and probably also from the basal part of borehole B 804 are provisionally assigned to the Lutetian Landauer Mergel *sensu* Breuer and Feist (1986) (= lower part of the Lymnäenmergel)

until the lithostratigraphical subdivision of the Eocene succession in the Upper Rhine Graben is revised.

Palaeoecological synthesis

All fossil groups from the Birkweiler sites show very low diversity except of the pollen and spores and the moderately diverse otolith fauna (Bettina Reichenbacher, written communication, February 01, 2023) indicating an extreme environment probably due to reduced and fluctuating salinity as it is typical for marginal brackish water settings. Interestingly, all studied samples did not yield a single charophyte specimen though from the brickyard pit west of Siebeldingen Schwarz and Griessemer (1998) isolated numerous gyrogonites from green marls of Lutetian age.

The macropalaeontological data clearly indicate that at least three different gastropod associations are present in the sediments from the Birkweiler drainage pit (Kadolsky and Hartkopf-Fröder, in prep.):

- the Hydrobioid-Association, also present in the Birkweiler road cut and in borehole B 804, is characterised by mass occurrences of *Lutetiella hartkopfi* Kadolsky, 2015 associated with few other rare gastropods, abundant otoliths and the presumably freshwater calcareous nannoplankton element *Nannoserratolithus minutus* n. sp.
- the Potamididae-Association with Potamididae as the only gastropod taxon, abundant otoliths and *Nannoserratolithus minutus* n. sp.
- the *Anomalorbina*?-Association distinguished by *Anomalorbina*?, some otoliths and fish bones and the calcareous nannoplankton *Nannoserratolithus/ Trochoaster/Trochastrites*-Assemblage.

Neither the calcareous nannoplankton (except of *Nannoserratolithus minutus* n. sp.) nor the gastropod fauna from the Birkweiler drainage pit indicate a fully marine or a freshwater environment. Though some of the *Trochoaster* and *Trochastrites* species have been recorded in marine sediments they prevail in brackish water habitats in the Upper Rhine Graben, the Mainz Basin and some adjacent areas. All these species are tolerant of reduced salinity. The rare Viviparidae are the only unequivocal freshwater gastropod specimens. They occur as small fragments which are derived from a habitat different from that of the abundant *Lutetiella*. The hydrobioids and the Potamididae are all indicative of a brackish water environment (Kadolsky and Hartkopf-Fröder, in prep.). The same is true for the ostracod genus *Neocyprideis* which is extremely abundant at least in one horizon from the Birkweiler road cut. In almost all studied samples dinocysts are present but with very low diversity (only 12 species). It is noteworthy that gonyaulacoids are represented only by one species while genera typically abundant in marine environments are absent. The majority of dinocysts belong to heterotroph peridinoids such as *Apectodinium* and *Phthanoperidinium* indicating a nutrient-rich water body. Especially, the former is an opportunistic genus favoured by brackish lagoonal or estuarine to very near-shore environments. In addition, *Phthanoperidinium* and *Polysphaeridium zoharyi* are tolerant to salinity fluctuations (e.g. Sluijs and Brinkhuis 2009; Frieling and Sluijs 2018). The chlorococcalean green algae *Pediastrum* and *Botryococcus* point to freshwater input. Based on the dinocyst and green algae assemblage a completely landlocked, brackish water body with fluctuating salinity is assumed. The occurrence of foraminifers and a single microforaminiferal lining (Stancliffe 1996) suggest at least brackish conditions. A thick stromatolite horizon in the Birkweiler road cut section, similar to the Eocene/Oligocene microbial facies "biohermes" of Duringer and Gall (1994) in the southern Upper Rhine Graben, indicates a shallow water environment, possibly with temporarily dry periods.

A temporarily brackish water environment was also supposed for the Lymnäenmergel in the southwestern part of the Mainz Basin (in boreholes Ebertsheim and Lautersheim 1 near Eisenberg), where foraminifers together with gyrogonites and limnophilous ostracods have been encountered. As in borehole Lautersheim 1 the Lymnäenmergel reaches 28.4 m in thickness the northernmost Lymnäenmergel deposits with brackish influence can be expected in the Marnheim Bay *sensu* Spuhler (1937) few kilometres further north (Schäfer 2000). The moderate to high sulphur content and the maceral distribution in sapropelic coals from the Lymnäenmergel encountered in various oil wells in the central Upper Rhine Graben point to a paralic swamp, marsh or coastal plain environment (Böcker et al. 2017).

Though most recorded faunal taxa are indicative of a brackish water environment some as the alligatoroid genera *Diplocynodon* and *Hassiacosuchus* as well as the turtles have been documented in the Upper Rhine Graben exclusively from freshwater deposits.

Four species of turtles, all classified as freshwater turtles, have been reported from Messel (Cadena et al. 2018). Many modern freshwater turtles are vulnerable to increased salinity. In brackish and marine environments they become osmotically dehydrated, suffer from body mass loss and will not survive prolonged salinity exposure. However, numerous modern freshwater turtles inhabit estuarine and brackish water systems at least occasionally. In order to endure in such adverse environments freshwater turtles respond to elevated salinities by various behavioural or physiological strategies such as frequent retreats to freshwater habitats, reduction of feeding and drinking to avoid ingestion of salt water or drinking after heavy rainfalls when sea surface salinity becomes fresher. In addition, many modern freshwater turtle species are able to maintain osmoregulatory homeostasis in brackish water environments for a short time period and at least one species, the diamondback terrapin (*Malaclemys terrapin*), possesses a lachrymal gland to excrete excess salt (for detailed discussion on salinity tolerances of freshwater turtles see e.g. Bower et al. 2016; Agha et al. 2018, 2019). Reports from the fossil record of freshwater turtles found in indisputable brackish water or marine habitats seem to be rare (Agha et al. 2018). Nevertheless, it cannot be excluded that the turtles from Birkweiler were able to colonise transiently saline water habitats as long as they could temporarily move to freshwater areas.

The alligatoroid genera *Diplocynodon* and *Hassiacosuchus* are well known from Messel and Bouxwiller. Without doubt Lake Messel had no connection to brackish or marine areas. For Bouxwiller deposition in small lakes was ascertained (e.g. Grimm et al. 2011b). Recently, Lavoyer (2013)

discussed the possibility that some taxa (*Lamprothamnium*, Hydrobiidae) from Bouxwiller may be tolerant of brackish water. As there are no additional indications for a brackish water influence, e.g. dinocysts and foraminifers, and the general palaeogeographical situation excludes a link to the open sea (see below) we prefer to retain the previous model of a small, fully freshwater lake for the Bouxwiller site. Basically, modern alligators are stenohaline and largely restricted to fresh water. Contrary to crocodiles, alligators do not possess salt glands so that salinity tolerance is low which prevents long-term survival in brackish or even fully marine water bodies (Mazzotti and Dunson 1989; Taplin and Grigg 1989). Adult alligators occasionally forage in brackish water environments such as highly-productive estuaries and near coastal areas (Mazzotti and Dunson 1989) while juvenile individuals exposed to brackish water (salinity concentration 12 ‰) suffer from loss of body mass, severe dehydration and adverse effects on various physiological functions (Faulkner et al. 2018). Based on modern and fossil evidence, a permanent colonisation of the Birkweiler brackish water habitat by the alligatoroid genera *Diplocynodon* and *Hassiacosuchus* is unlikely. At best, the brackish water body was visited for occasional forays to feed on various vertebrates, e.g. fish and turtles. If this conception is correct, the alligatoroid teeth were most presumably washed from the original freshwater environment to the final site of deposition. As the teeth are extremely compact and wear-resistant they can be transported over considerable distance without exhibiting abrasion features.

The pollen and spores suggest a palaeotropical, diverse vegetation with Cupressaceae/Taxodiaceae-dominated swamp forest, probably also associated with Myricaceae, Juglandaceae, Oleaceae and Aquifoliaceae. It is interesting, that *Pentapollenites pentangulus*, a species of uncertain botanical affinity, covaries with Cupressaceae/Taxodiaceae and other wet elements. We, hence, tentatively suggest that this also biostratigraphically important species – emerging in the Paris Basin since the mid Eocene according to Châteauneuf (1980) – might also favour locally wet conditions. A rainforest with palms, Sapotaceae, Bombacaceae, Juglandaceae, Malvaceae and many other families including evergreen climbers of the Vitaceae existed close to the site. The presence of mangroves, further pointing to a brackish water influence, cannot be excluded as deduced from the occurrence of *Leiotriletes adriennis*. The latter has been associated with the mangrove fern *Acrostichum* but *Lygodium* may be an additional/alternative producer of this spore.

Provided that temperature preference of modern *Eucommia ulmoides* can be extrapolated to Eocene *Eucommia* species, the spring temperatures during deposition of the Landauer Mergel was from 13 °C to 20 °C (Yu-Fei Wang et al. 2003). The dinocyst *Apectodinium*

is very abundant and reaches 99 % in one sample. Such *Apectodinium* acmes point to a water temperature higher than 20 °C (Frieling et al. 2014). The presence of ectothermic crocodilians indicates a Mean Annual Temperature of ≥ 14.2 °C and a Coldest Month Mean temperature of ≥ 5.5 °C but alligatoroids, in particular larger individuals, seem to tolerate lower temperatures (Markwick 1998).

The high terrestrial input emphasised by type III kerogens and alkane distribution and the presence of a diverse pollen and spores assemblage including large and strongly ornamented species imply that the coast was not far from the depositional site. The lack of coarse-grained sediments in the Birkweiler sections located close to the evolving graben shoulder emphasises that subsidence was probably still negligible and that the sediments were deposited in regional shallow depressions. This is in accordance with e.g. Doebl and Bader (1970: 15, pl. A1), Sittler (1992: fig. 1), Duringer (1995: 167, 170, fig. 4) and Sissingh (1998: 261) who ascertained a negligible uplift of the graben shoulder during the mid Eocene.

Palaeogeographical implications

It is still a matter of debate if during the mid Eocene shallow marine connections existed between the Upper Rhine Graben and adjacent basins to enable migration of brackish water organisms. There is general consensus that a seaway from the northern Upper Rhine Graben to the North German-Polish Basin via the Hessen Depression or possibly also to the North Sea Basin via the Linz Passage was open not until the early Oligocene (e.g. Sissingh 2003, 2006; Ohmert 2017; Pirkenseer et al. 2018). Following the palaeogeographical reconstructions of Berger et al. (2005b) and Lavoyer (2013) the southern Upper Rhine Graben was land-locked during the mid Eocene and no marine communication established towards the North Alpine 'Pre-Molasse' Basin. This is in accordance with numerous other publications (e.g. Sissingh 1998, 2006; Dèzes et al. 2004; Pirkenseer et al. 2018). However, it must be noted that the mid Eocene palaeogeography as proposed by Sissingh (1998, 2006) is based on the assumption of a late Lutetian to Bartonian hiatus in the Upper Rhine Graben due to non-deposition and erosion as well as an age of the "*Limnaea* Marls" not older than Priabonian. More recent studies do not support such a hiatus (Hinsken et al. 2007; Lavoyer 2013) and the age of the "*Limnaea* Marls" ranges from the mid Lutetian to mid Priabonian (Grimm et al. 2011b). Following Sissingh (1998, 2003, 2006) the first marine ingression into the Upper Rhine Graben occurred during the Priabonian via the Rhône and Bresse graben systems, the Burgundy Passage and the Délemont and Laufen basins but palaeoecological, sedimentological and geochemical data may preclude such a seaway (Fontes et al. 1991). A third option, a short-term

mid Eocene marine incursion from the Paris Basin, has been suggested by Grimm et al. (2011b: 59) but a connection between the Paris Basin and the Upper Rhine Graben is not considered by e.g. Gély (2008) and Huyghe et al. (2015).

Provided that the mid Eocene Upper Rhine Graben was palaeogeographically isolated from the North German-Polish Basin, the North Sea Basin, Paris Basin and North Alpine 'Pre-Molasse' Basin colonisation of the brackish water inland sea in the Upper Rhine Graben by aquatic invertebrates was possible through passive dispersal vectors such as wind (anemochory, e.g. Rivas et al. 2019) and rain. Additionally, numerous invertebrates (e.g. flying insects) and vertebrates (e.g. aquatic birds, mud-wallowing mammals) have been empirically identified as crucial in the dispersal of viable propagules and living individuals since Darwin (1859: 385; 1882) reported on freshwater bivalves sticking to aquatic insects and birds. Thus, long-distance transport of fish eggs by water fowl or land animals has been taken into consideration by Reichenbacher et al. (2007) for the distribution of gobiid fishes from the Paratethys to the Upper Rhine Graben during the late Burdigalian. Transport can be achieved both internally (endozoochory) and externally (ectozoochory) (Bilton et al. 2001; Green and Figuerola 2005; Vanschoenwinkel et al. 2011; Coughlan et al. 2017, with further references therein). Diapausing, desiccation-resistant resting stages that adhere to plumage, bills and legs of waterbirds or the moist fur of aquatic mammals can easily be transported from one water body to another (Coughlan et al. 2015). Various studies proved that some larvae can survive out of water long enough for travel distances of 10 km and more if they are attached to waterfowl, ducks or mallards. Aquatic and semi-aquatic birds were already present during the Eocene (Mayr 2017). Various (resting) eggs can even hatch after passing the digestive tract of insects, fish (ichthyochory, Guy-Haim et al. 2017) and birds. Recently, Silva et al. (2019) and Lovas-Kiss et al. (2020) demonstrated that not only highly resistant, diapaused eggs of killifish but even the soft-membraned eggs of cyprinids survive ingestion, the acidic and anoxic environment in the digestive tract of waterbirds and egestion. Although only 0.2–1 % of the ingested eggs were found viable in the fresh faeces it is assumed that bird-mediated, internal transport of fish eggs enables the establishment of new populations in isolated, remote water bodies.

Deduced from numerous zoological studies on the dispersal of invertebrate eggs, larvae and even adult individuals via mechanisms such as anemochory, endozoochory and ectozoochory, it seems to be conclusive that a connection from the Upper Rhine Graben to adjacent marine basins was not a prerequisite to explain the presence of a brackish water fossil assemblage of low diversity. Rather, wind, rain or highly mobile animals were vectors for the dispersal of dinocysts and invertebrates which resulted in the successful establishment of

a brackish water biota in a remote water body near the western shoulder of the evolving middle Upper Rhine Graben far away from the open sea.

Conclusion

Various thermal maturity parameters, in particular Spore Color Standard, T_{max}, VR_r and biomarkers, indicate that the organic matter of the middle Eocene Landauer Mergel in the Birkweiler drainage pit site is immature and thermal maturity is distinctly lower compared to approximately time equivalent sediments in the Landau oilfield. While the Birkweiler sites are located next to the graben shoulder, this oilfield is situated more graben-wards where the overburden thickness for the Landauer Mergel is much higher (Schad 1962) and in the case of the studied samples more than 1900 m. The hydrocarbon generation potential of the Birkweiler marl samples was analysed by TOC and Rock-Eval measurements and show low values indicative of a poor generative potential. However, liptinite-rich (sapropelic) coals and organic-rich mudstones as were encountered at the base of the Birkweiler road cut section (Fig. 4) are considered as source rocks of 'high wax oils', which also contributed to the main oil fields (e.g. Landau and Römerberg). These sapropelic coals are characterised by high amounts of terrestrial organic matter. In various wells, e.g. near Speyer, about 30 km northeast of Birkweiler, they show extraordinarily high hydrocarbon potential which may be even higher than that of the Lower Jurassic Posidonia Shale (Bruss 2000; Böcker et al. 2017).

Following age indicative pollen and spores, dinocysts and calcareous nannoplankton, a Lutetian age is considered to be most probable while a late Ypresian to Bartonian age is considerably less likely.

Most of the dinocysts, calcareous nannoplankton, foraminifers, ostracods and gastropods (Kadolsky and Hartkopf-Fröder, in prep.) point to a brackish water environment. Only the Viviparidae are restricted to fresh water and were likely washed into the brackish water environment (Kadolsky and Hartkopf-Fröder, in prep.). The alligatoroids *Diplocynodon* and *Hassiacosuchus* are well known from freshwater lakes such as Messel (Brochu and Miller-Camp 2018). As for the Viviparidae remains of alligatoroids and turtles may have been displaced from their freshwater habitats into a brackish water environment. However, it cannot be excluded that alligatoroids and turtles were also able to occasionally inhabit brackish water settings. *Trochoaster* and *Trochastrites* are well known to occur in brackish water habitats in the Upper Rhine Graben. The occurrence of the ostracod *Neocyprideis* and dinocyst and foraminifer assemblages of very low diversity are all typical for brackish water habitats while unequivocal

marine indications such as diverse dinocyst or foraminifer associations are lacking. Also, the *n*-alkane distribution does not support a marine environment. A thick stromatolite horizon indicates a shallow water environment.

Fossil-rich middle Eocene sediments deposited in such an environment have rarely been reported from the Upper Rhine Graben (for examples see Kadolsky and Hartkopf-Fröder, in prep.) and the concurrent occurrence of pollen and spores, dinocysts, green algae, calcareous nannoplankton, foraminifers, gastropods, ostracods and vertebrate remains (particularly otoliths, reptiles) has been unknown so far.

The Birkweiler assemblages are similar but not identical to the one reported from the Landauer Mergel in well Landau 117 by Breuer and Feist (1986). The main differences are the lack of charophytes in the Birkweiler assemblages which, however, have been reported by Schwarz and Griessemer (1998) from a nearby site. In addition, in well Landau 117 gastropods are lacking suggesting some environmental differences between both sites. Nevertheless, the occurrence of foraminifers indicates a brackish water environment similar to Birkweiler.

The Birkweiler assemblages are the most diverse brackish water assemblages reported so far from the Eocene of the Upper Rhine Graben. The fauna flourished in a shallow brackish water inland sea with fluctuating salinity located near the western shoulder of the evolving Upper Rhine Graben. Along water bodies wetlands developed where sapropelic peat was deposited.

Regardless of whether a short-lived communication between the Upper Rhine Graben and adjoining marine basins was maintained or the Upper Rhine Graben was land-locked with no connection to any marine basin during deposition of the Birkweiler succession, brackish water organisms may have been dispersed over long distances by different vectors such as wind, rain, highly mobile insects or vertebrates. Obviously, dispersal of aquatic invertebrates by endo- and ectozoochory has so far been underestimated to conclusively explain the occurrence of Paleogene brackish water faunas in the land-locked Upper Rhine Graben.

Declarations

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