

# The Rauenberg fossil Lagerstätte (Baden-Württemberg, Germany): A window into early Oligocene marine and coastal ecosystems of Central Europe



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## ARTICLE INFO

### Article history:

Received 10 June 2016

Received in revised form 27 September 2016

Accepted 5 October 2016

Available online 7 October 2016

### Keywords:

Oligocene

Rupelian

Bodenheim Formation

Taxonomic diversity

Paleoecology

Fossil lagerstätte

## ABSTRACT

The Oligocene was a period of profound climatic and biotic changes, coinciding with a shift from a mostly ice-free warmhouse world at the Eocene-Oligocene boundary to a globally cooler, more seasonal climate. The Rauenberg locality (Baden-Württemberg, Germany) is one of the most significant early Oligocene fossil assemblages in Europe, containing both marine and terrestrial elements of fauna and flora. Preservation is often superb and comprises complete and articulated skeletons with soft tissue preservation. The diverse assemblage provides critical insights into the paleoenvironment of the Upper Rhine Valley. We reassess diversity at the locality, resulting in a list of 302 taxa found at the site, 207 of which are marine (52% of taxa represented by macrofossils). The rest are interpreted as originating from the coastal environment. Molluscan, echinoderm, and plant macrofossil diversity are assessed here for the first time. Based on these new results, we interpret Rauenberg as representing a fully marine assemblage deposited in a moderately shallow, low-energy tropical-subtropical environment. Productivity was high, and seafloor anoxia was intermittently developed. There is no evidence for long-term brackish influence or mangrove swamps, and no direct evidence for the development of seagrass meadows. On land, warm, frost-free conditions permitted the development of prevailingly evergreen sclerophyllous broad-leaved forests along with pine and palm-rich coastal forests on sandy soils. The marine invertebrate fauna shows more northerly affinities, whereas the vertebrate fauna is distinctly Paratethyan.

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## 1. Introduction

The Oligocene was a period of profound climatic changes. Its beginning, the Eocene-Oligocene boundary, marked the transition from a mostly ice-free warmhouse world to an interval of globally cooler climate and Antarctic ice-sheet formation (Coxall et al., 2005; Miller et al., 1998; Pusz et al., 2011; Zachos et al., 2008). Oligocene climate at middle and higher latitudes particularly differed from conditions during the Eocene by increasing seasonality, i.e. the development of cool winter seasons (Roth-Nebelsick et al., 2014). Fossil remains reflect this trend. Oligocene fossil plant assemblages, for example, show increasing invasion of arctotertiary floristic elements (Kvaček and Walther, 2001), and a turnover occurred within the terrestrial vertebrate community ("Grande Coupure") (Delfino et al., 2003; Stehlin, 1910).

The clay pit "Unterfeld" at Rauenberg (Baden-Württemberg, Germany) contains one of the most significant early Oligocene fossil assemblages in Europe, and is an important locality for reconstructing early Oligocene floral and faunal diversity. Although fossils, especially those of fishes, have been known for a long time, scientific excavations at the site were intensified after the discovery of the first Old World fossils of modern-type hummingbirds (Mayr, 2004a). Preservation is often superb and comprises complete and articulated skeletons with soft tissues preserved. The Rauenberg site contains both marine and terrestrial elements of the fauna and flora. The diverse assemblage provides critical insights into the paleoenvironment of the Upper Rhine Valley and is of particular significance, because it preserves marine and terrestrial organisms across a broad taxonomic spectrum. As such, the Rauenberg site adds to an understanding of early Oligocene ecosystems in Central Europe. Located at a slightly lower latitude than its current location (paleolatitude 43.74°N, 12.81°E, Paleobiology Database rotation file: Wright et al. (2013); current: 49.27°N, 8.67°E), the locality lies in a region potentially more heavily influenced by sea level dynamics and tectonic evolution than latitudinally-driven climatic zonation. However, this is controversial and remains to be rigorously examined in a cohesive framework. In the past, independent studies have attempted to

reconstruct the paleoenvironment and sedimentation regime of this locality using various techniques (e.g., micro- and macropaleontology, stratigraphy and geochemistry), resulting in inconclusive and partially contradictory interpretations. Here, we present new data and synthesize existing results to generate a more complete picture of a marine and coastal paleoenvironment in the early Oligocene of Germany. We provide a summary of the taxonomic diversity at the Rauenberg locality based on reexamination of previously collected but as-yet undescribed material, and also reassess the published literature in order to compile an up-to-date list of taxa from the locality. Some groups, such as plankton, fishes, and birds, are already well-known from Rauenberg (see Section 5 for details); others, such as plants and macroinvertebrates, have never been studied in detail. The synthesis of information from these different groups provides a wealth of new information for paleoenvironmental reconstruction.

## 2. Geology

The geology of the Paleogene clay pits on the eastern edge of the Upper Rhine Graben, mined since the beginning of the 19th century, has been studied by Wagner-Klett (1919), Weiler (1931, 1966), Sittler (1967), Doebl (1976), Schweizer (1982), Weiss (1988), Trunkó and Munk (1998), and Grimm et al. (2002).

### 2.1. Tectonic setting

The former clay pits of Unterfeld, Frauenweiler-Wiesen, and Rohrlach (Fig. 1A, B), referred to hereafter as the Rauenberg clay pits, or simply Rauenberg, are located in the Upper Rhine Graben (Oberrheingraben: Fig. 1D), a region that underwent complex development during the Tertiary. The main rifting phase began in the Oligocene, with continuing northbound thrust of the Alps and the Pyrenees (Dür and Grimm, 2011). Perpendicular to the compression narrowing the graben in a NNE-SSW direction, there was east-west- to WNW-ESE-oriented crustal strain and spacious trench formation. Subsidence of the

Upper Rhine Graben took place between two principal, approximately parallel, faults; subsidence was more or less constant at 4.5 km, with an opening 4–7 km wide (Dürr and Grimm, 2011). The Mainz, Hanau, and Neuwied Basins began to form during these main rifting stages.

The main rifting phase ended in the later Rupelian–Chattian. It was a time of large-scale restructuring in the area of the western Mediterranean, and the main compression shifted south and east (Dürr and Grimm, 2011). In the late Oligocene, strong subsidence of the central Heidelberg–Mannheim Trench began, while subsidence of the marginal plates (Mainz Basin, southern Taunus foothills, Hanau Basin) stopped and the southern Rhenish Slate Mountains gradually rose. The Upper Rhine Graben briefly formed a dextral shear zone in a NE–SW-directed compressive stress field, in which the Heidelberg–Mannheim Graben subsided as a right-lateral transtensional basin (Schumacher, 2002; Villemain and Bergerat, 1987). Today, the Paleogene of Rot-Malsch, on the eastern edge of the Upper Rhine Graben, forms a tectonic fold ridge which is subdivided by numerous step faults (Barth, 1970; Wagner-Klett, 1919).

## 2.2. Lithology

During the second and third Rupelian transgressions (sensu Hardenbol et al., 1998), marine to brackish sediments were deposited in the area of the northern Upper Rhine Graben. These sediments, described as the Graue Schichtenfolge (Doebl, 1967, 1970) or the Froidefontaine Subgroup (Grimm et al., 2011; Grimm, 2005), are differentiated into clayey basinal facies with pelagic faunal elements and sandy-gravelly coastal facies (Fig. 1E).

The Froidefontaine Subgroup extends throughout the Upper Rhine Graben and neighboring areas. It overlies the deposits of the Pechelbronn Group or encroaches on pre-Tertiary subsurface, and is overlain by the colorful, sandy marls of the Niederroedern Formation (Grimm et al., 2011). In the central southern Upper Rhine Graben, the Froidefontaine Subgroup is usually around several hundred meters thick. In the northern Upper Rhine Graben, the thickness in the central trench decreases to <150 m.

The Froidefontaine Subgroup is a marine-brackish sequence consisting of an alternation of bituminous, dark grey to light grey greenish mudstones, clay marls and siltstones with locally fine sandstones which interfinger at the borders with the coastal sands and gravels of the Alzey Formation. A lithologic subdivision into the Alzey Formation (= Meeressand), Bodenheim Formation (= Rupelton with Foraminiferenmergel, Fischschiefer and Upper Rupelton), Meletta Beds and Cyrenenmergel is possible.

The deposits of the Bodenheim Formation document the second Rupelian transgression (Hardenbol et al., 1998) in the Upper Rhine area. The Bodenheim Formation consists of grey to blackish-brown finely bedded to laminated clays, calcareous clays, and clay marls, which can be subdivided into the Wallau, Hochberg, and Rosenberg Members (Grimm et al., 2011). In the central and southern part of the Upper Rhine Graben, e.g., near Wiesloch, sporadically turbiditic calcareous sandstone were occasionally deposited. In addition, fine sand beds, layers with bioturbation, and a layer with concretions (the so-called “Lower Geode horizon” of Trunkó and Munk (1998)) are differentiated.

The section in the clay pit was described in detail by Grimm et al. (2002) (Fig. 1C). In the Rauenberg clay pits, the Wallau and Hochberg Members of the Bodenheim Formation are present. The sediments in the clay pit consist of clay- to siltstones, which vary in consolidation and generally show clear bedding and lamination. The subdivision of

the profile may be caused by changes in particle size, carbonate content, color, or alternation between laminated and unstratified beds. Lamination is attributable to different causes: most lamination is caused by changes in particle size due to rhythmic sedimentological events, but also infrequently by arrhythmic events. Other laminae, such as calcareous mud layers or calcareous sand layers (“Kalkhaut” of Trunkó and Munk (1998)) are common and consist of organic layers of mass occurrences of calcareous nannoplankton. Trunkó and Munk (1998) identify two thin horizons with concretions in the pit, described as the Lower and Upper Geode horizons. The concretions are isolated or fused together, consisting of medium grey, weathered yellowish ochre dolomitic mudstone containing fossil remains. The concretions show polychaete burrows and are developed early in diagenesis (Grimm et al., 2002).

The carbonate content in the profile is very irregular, but up to 95–100% originates from calcareous microfossil remains (calcareous nannoplankton and foraminifera). The dolomite content varies between 1 and about 87 wt% (Grimm et al., 2002).

The color varies from light grey to dark grey based on minor variations in organic carbon content (TOC). The TOC content in the examined clay pit is 4.8–5.4 wt% (uncorrected, Grimm et al. (2002)).

The dark bituminous shales contain abundant pyrite, marcasite, and other metal sulfides. The majority of the metal sulfides consist of pyrite in the form of small cubes and blooms. Marcasite occurs in the form of spheres, aggregates and fillings of burrows (Trunkó and Munk, 1998). Phosphatic skeletal grains (fish remains, teeth, and coprolites) are common and of black-brown color. The clay mineral illite dominates, followed by kaolinite and chlorite. Secondary gypsum crystals are also present (Weber, 1951).

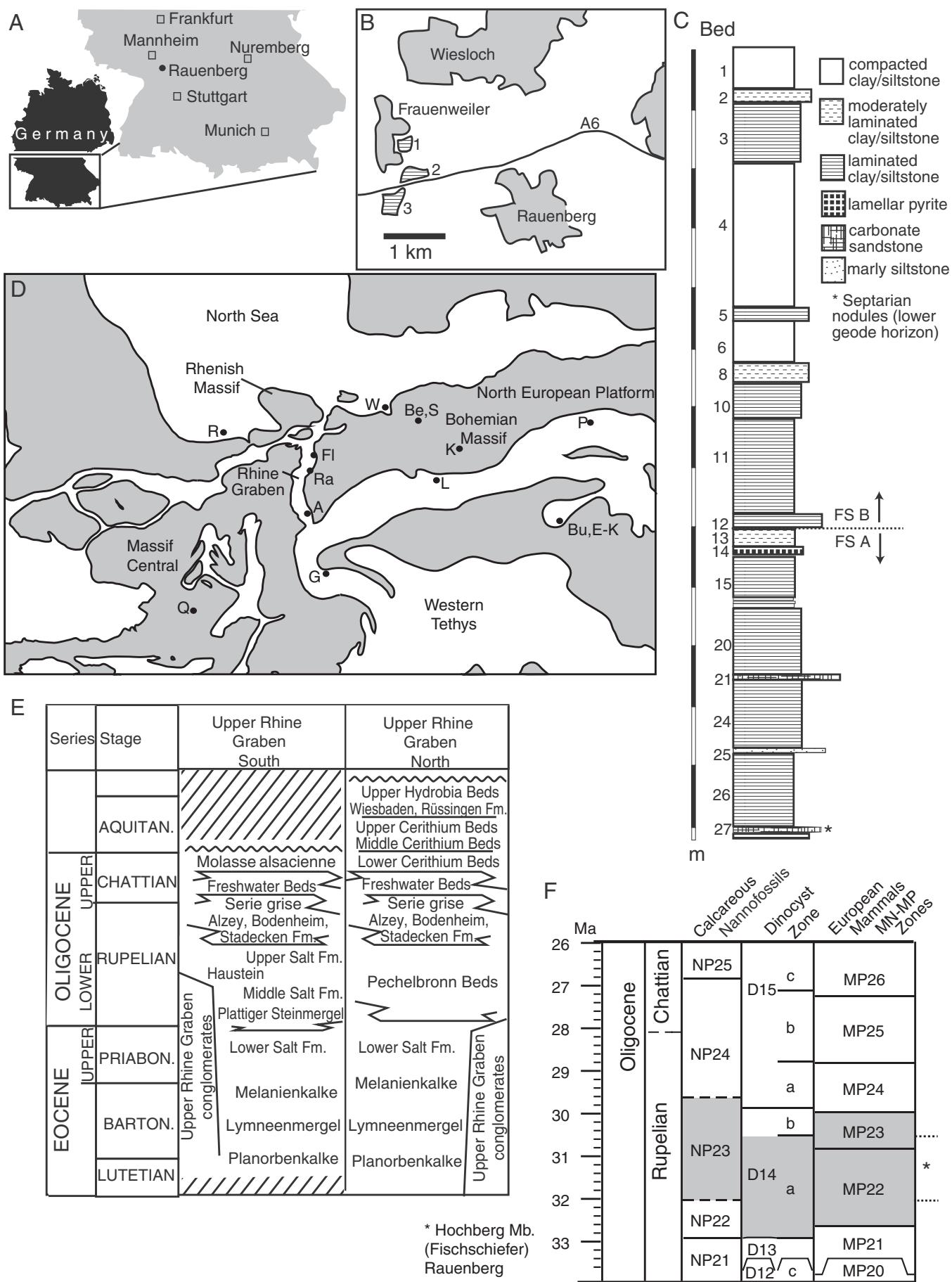
## 3. Biostratigraphy

Among the calcareous nannoplankton, the occurrence of *Transversopontis pygmaea* indicates an Oligocene age between NP 23 and NP 24 (after Köthe, 1986). The section comprising the Hochberg Member is correlated to NP 23 (after Martini, 1971; modified from Müller, 1978): from the last occurrence of *Reticulofenestra umbilica* to the first occurrence of *Cyclicargolithus abisectus* and/or *Helicosphaera recta*. Consistent with the calcareous nannoplankton, dinoflagellate cysts in the sediments can be placed in the Subzone D 14 a (lower Oligocene, Rupelian). This subzone is marked from the first occurrence of *Chiropertidium galea* to the last occurrence of *Enneadocysta pectiniformis*. Corresponding well with the microfossils, the mammalian creodont genus *Apteroodon* is associated with MP 22–MP 23 (Frey et al., 2010) (Fig. 1F).

The foraminiferal association is also typical of the Rupelian. Characteristic and frequent forms are *Cyclammina placenta*, *Bathysiphon tauriensis*, *Stilostomella ewaldi* and *Bolivina beyrichii*. It is possible to subdivide the Hochberg Member at Rauenberg into the foram-rich Fischschiefer A and the foram-poor Fischschiefer B (Grimm, 1991, 1994). Fischschiefer B cannot be further subdivided, however Fischschiefer (=FS) A shows mass occurrences of *Bolivina beyrichii* and *Stilostomella ewaldi* (Beds 19–13: Fig. 1C), which correspond to the *Bolivina beyrichii*–*Stilostomella ewaldi* Abundance Zone (after Grimm, 2002) and FS 2 and FS 3 (after Grimm, 1991, 1994). The division between Fischschiefer parts A and B does not correspond to a shift in dinoflagellate cysts or other microflora.

Some of the calcareous nannoplankton have been reworked from older Eocene, Cretaceous, or Jurassic strata. Reworking cannot be identified based on the state of preservation, but is indicated by the presence

**Fig. 1.** Locality and stratigraphy. A, Location of Rauenberg, Baden-Württemberg, Germany. B, Location of the clay pits referred to in the text relative to the city of Rauenberg. 1–Rohrlach, 2–Frauenweiler-Wiesen, 3–Unterfeld. C, Stratigraphic section from the Hochberg Member, Unterfeld clay pit. Parts B and C redrawn from Grimm et al. (2002). D, Early Oligocene (Rupelian) paleogeography of Europe, showing important Oligocene localities discussed in the text. Map modified from Meulenkamp et al. (2000) based on Spiegel et al. (2007). E, Lithostratigraphy of the Upper Rhine Graben, modified after Rasser et al. (2008). F, Estimated biostratigraphic age of the Hochberg Member (Fischschiefer); produced with TSCreator (<http://tscreator.org>). Abbreviations. A, Allschwil, Switzerland; Be,S, Bechlejovice and Seifhengersdorf; Bu,E-K, Budapest and Eger-Kiseged, Hungary; FS A, Fischschiefer A; FS B, Fischschiefer B; Fl, Flörsheim, Mainz Basin; G, Canton Glarus, Switzerland; Ra, Rauenberg; K, Kundratice; L, Linz, Austria; P, southern Poland; Q, Phosphorites du Quercy; R, Rupel, Belgium; W, Weissensteiner Basin, Germany.



of calcareous nannoplankton from NP 11–NP 12. Reworked dinocysts were recovered from Eocene, but not Cretaceous, species.

#### 4. Materials and methods

Macrofossils occur mainly as scattered remains in the sediment at the Rauenberg locality. Consequently, many years of intensive excavations, mainly by private collectors but more recently by the Staatliches Museum für Naturkunde Karlsruhe (SMNK), were necessary to assemble the collections at the Hessisches Landesmuseum Darmstadt (HLMD), Institut für Geowissenschaften Universität Heidelberg (GEOW), SMNK, and the Staatliches Museum für Naturkunde Stuttgart (SMNS) on which this study is based. Fossil plant material has also been studied from the collection of the Naturmuseum Augsburg. The material was collected by many different individuals over many years, and so stratigraphic information is for the most part lacking, making it impossible to assess potential changes at the site over time.

The collection of fossil plant material at the SMNS comprises >600 specimens; that of the SMNK has approximately 300, and that of the Naturmuseum Augsburg >200 specimens. Unfortunately, the private collectors focused on well-preserved plant material, largely neglecting strongly fragmented material and small remains. Consequently, such material has only been sampled since 2007 when J. Kovar-Eder contacted the collectors.

Leaves are preserved as carbonized compressions suitable for cuticular analysis (Figs. 2–3). The material collected prior to 2007 was usually coated with a varnish, which hampers cuticle studies. Cuticle preparations have been performed from >280 specimens, however, of which almost 200 were successful. Cuticles of some taxa are well preserved, however most are heavily infected by fungi (Fig. 3).

The fossil insects from Rauenberg are generally poorly preserved as a very thin and brittle coaly film that is, in many specimens, fragmented into tiny rectangular blocks like a mosaic (Suppl. Fig. 1B), most likely due to unsuitable preparation and storage. Many specimens have been coated with cellulose varnish, which further deteriorated the visibility of the fossils.

#### 5. Systematic overview

For a complete list of taxa recovered, refer to Appendix A. The following sections are intended as a brief overview.

##### 5.1. Plankton and benthic foraminifera

Calcareous nannoplankton and dinoflagellate cysts from the Rauenberg clay pit were investigated by Grimm et al. (2002); foraminifera have also been studied (Grimm et al., 2002; Weiss, 1988). The taxonomic diversity of the calcareous nannoplankton flora is low. Dinoflagellate cysts are common in the investigated section. Planktonic foraminifera are rare; only one short planktonic bloom occurs over the studied interval. Foram diversity is typical for a Rupelian benthic fauna, with low numbers of species but some species occurring at high abundance. Other calcareous microfossils such as calcispheres, interpreted as crustacean eggs (described as *Orbulina bituminosa*: Grimm and Grimm (1996)) and tintinnids (*Pseudarcella rhumbeleri*) are found in such high abundance that they exceed forams in some layers (Grimm et al., 2002).

#### 5.2. Macroflora and pollen

Plant macrofossils are abundant at the Rauenberg locality and comprise not only leaves and, more rarely, fructifications of the terrestrial flora, but also marine algae (Fig. 2). A brief overview of plant macrofossils with several ambiguous determinations was provided by Winterscheid and Gregor (2008) (Suppl. Table 1). Sittler (1965) provided a synthetic list of pollen and spores from the Hochberg Member in the Alsace region of the Upper Rhine Graben based on drill cores, and Pross et al. (1998) later studied the palynomorphs from the Mainz Basin (Middle Rupelton, NP 23, drill core Bodenheim), but the palynomorphs from the Rauenberg section have not been studied. The macroscopic remains (leaves and fruits) have recently been evaluated (Kovar-Eder, in press).

##### 5.2.1. Aquatic plants

Thalli of at least three different marine algae can be distinguished, probably belonging to the Phaeophyceae and/or Rhodophyceae (e.g., Fig. 2A). One of them bears aerocysts as in, for instance, the modern genus *Cystoseira*. Fragments of monocotyledons that might be interpreted as reeds, sedges or seagrasses (all monocotyledons) are extremely rare. Remains of reeds and reed-like plants such as sedges or seagrasses were not identified; those remains preliminarily identified as “reeds” by Micklich and Hildebrandt (2010) may represent algae or fragmentary palm (*Phoenicites*), cycad, or conifer remains.

##### 5.2.2. Land plants (macrofossil record)

The land plant record is diverse. 66 species have been identified, including 14 new species, some of them of cryptic systematic affinity (Suppl. Table 2; Kovar-Eder, in press). At the family level, Lauraceae are most diverse, represented by at least nine species, and at the generic level *Pinus* is most diverse (6 species represented by fascicles, 2 species by cones: e.g., Fig. 2B). At the species level, *Platanus neptuni* is by far the most common element (Figs. 2E, 3B) followed by *Daphnogene cinnamomifolia* (Figs. 2L, 3C). Some species are documented by several remains, such as *Laurophyllo pseudoprinceps* (Figs. 2K, 3D), *Tetraclinis salicornioides* (Fig. 2C), and the palms *Palmacites lamanonis* (Fig. 2N) and *Sabalites major*. Other species are represented by few specimens. These include *Betula*, *Carya*, *Comptonia diffiformis* (Fig. 2G), *Craigia*, *Distylium* sp., *Engelhardia* (Fig. 2I), *Eotrigonobalanus furcinervis haselbachensis*, *Hydrangea*, *Laurus abchasica*, *Myrica* div. sp. (Figs. 2F, 3F), *Phoenicites* sp. (Figs. 2O, 3H), Arecaceae (? Calamoideae), *Populus germanica*, *Sloanea olmediaefolia* (Figs. 2J, 3G), *S. artocarpites*, *Symplocos volkeri* (Figs. 2M, 3E), *Ceratozamia floersheimensis* (Figs. 2D, 3A), *Doliostrobus taxiformis*, *Sequoia abietina*, *Taxodium* sp., and fern frond fragments such as *Lygodium kaulfussii*, among others.

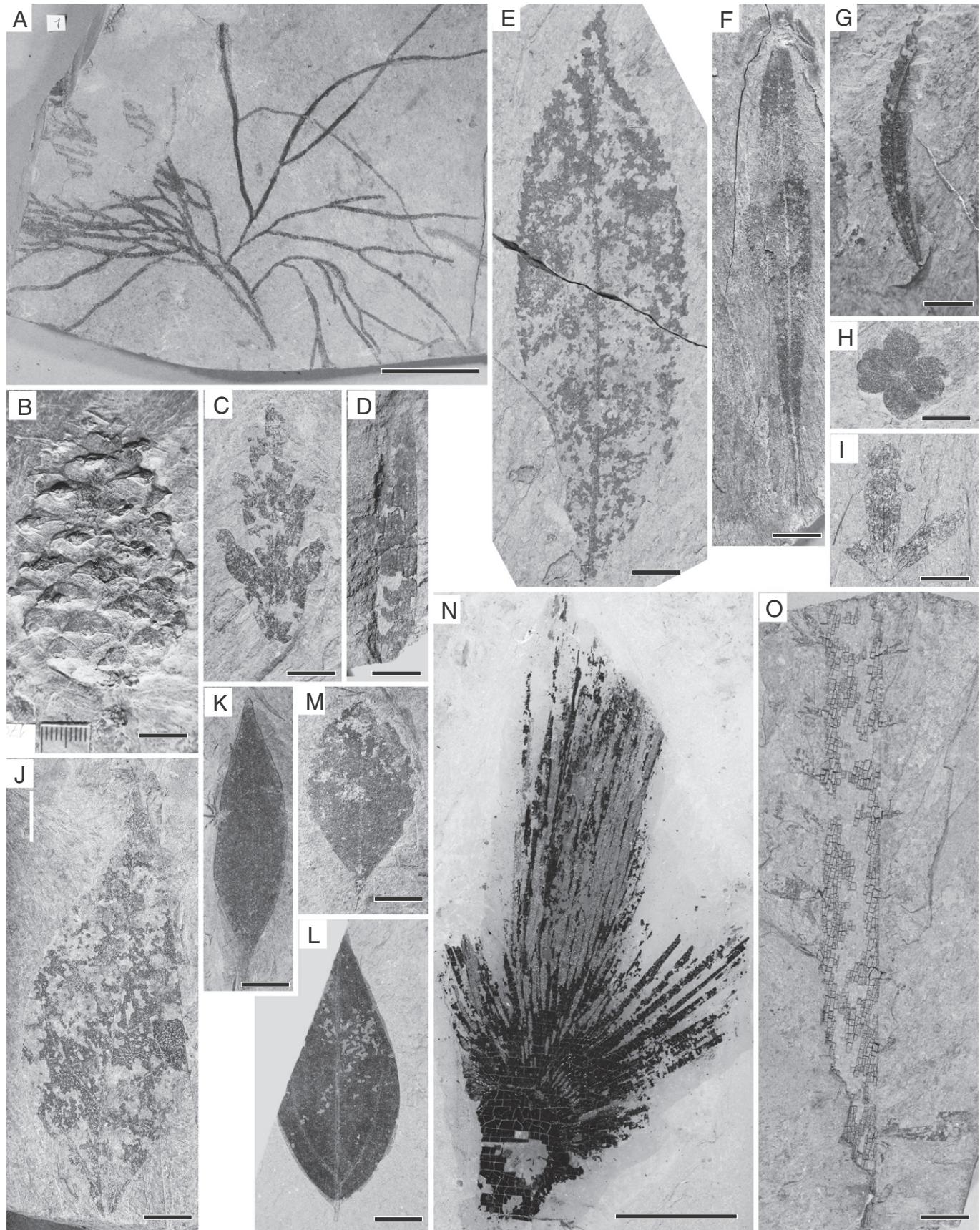
Approximately 35% of all terrestrial taxa were presumably tall trees or trees and around the same percentage encompasses taxa that were likely small trees or shrubs (Suppl. Table 2). Roughly 13% of plant species represent lianas or climbers. Taxa with anemophilous and zoophilous pollen dispersal are almost equally represented (~40%). In the fruit vector, zochorous dispersal (~41%) appears slightly more abundant than anemochorous dispersal (37%); additionally 13% of species probably had a dyschorous or autochorous fruit vector.

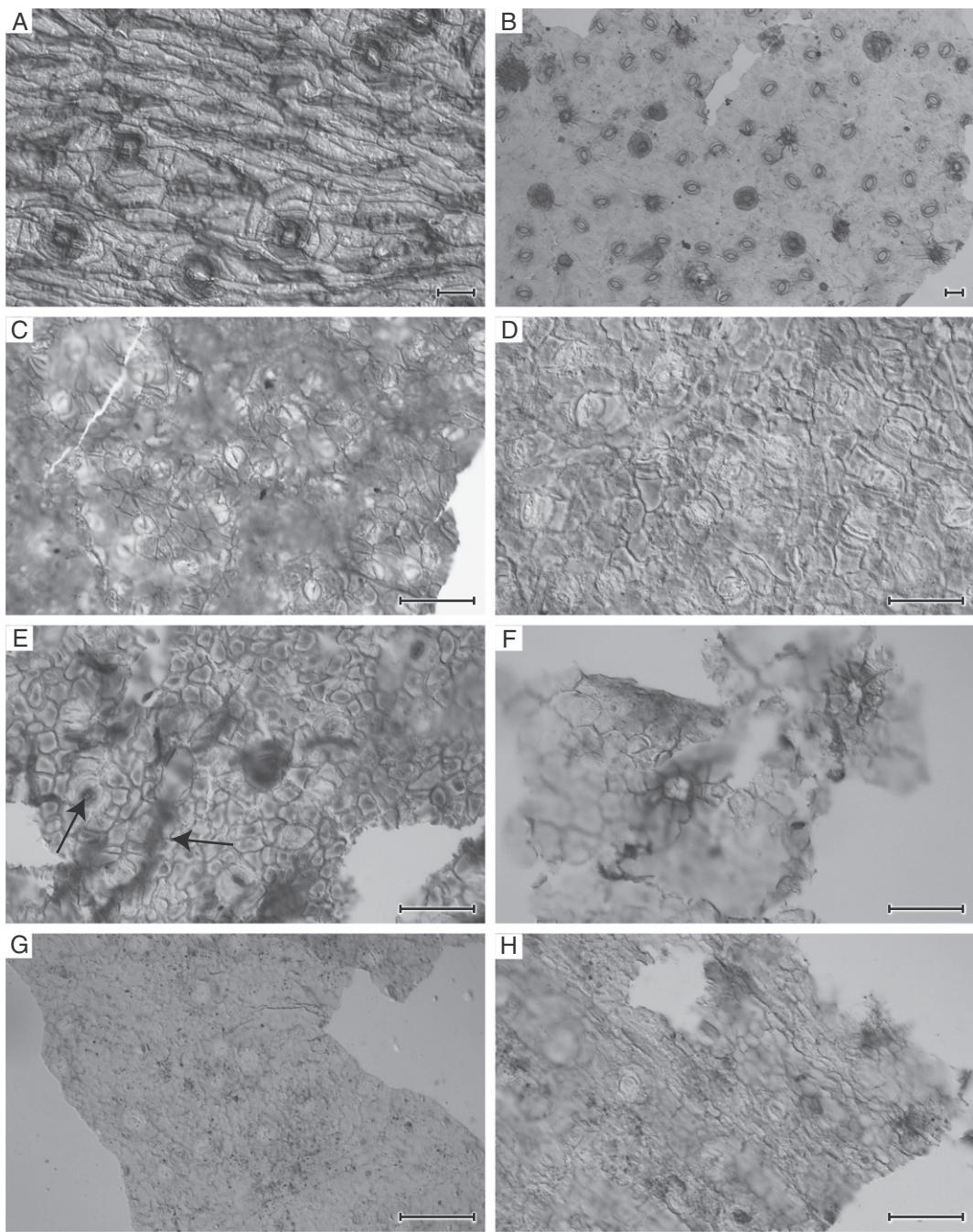
More than 60% of the woody angiosperm species were probably evergreen, bearing either entire-margined (Lauraceae) or minutely toothed leaves (*Distylium*, *Engelhardia*, *Myrica*, *Sloanea*, *Symplocos*). Less than 20% of woody angiosperms were likely deciduous and for 10–15% it remains ambiguous whether they shed their leaves regularly.

**Fig. 2.** Plant macrofossils from Rauenberg; all specimens figured are housed at the SMNS. A, Algae gen et sp. indet., slender linear thallus, several times forked; P 1952/1; B, *Pinus* (*Pinus*) cf. *thomasiana* (Goeppert) Reichenbach, cone, P 1952/176; C, *Tetraclinis salicornioides* (Unger 1841) Kvaček 1989, branched twig with cupressoid foliage, P 1952/118; D, *Ceratozamia floersheimensis* (Engelhardt) Kvaček, leaf fragment with parallel running venation, P 1952/456; E, *Platanus neptuni* (Ettingshausen) Büžek, Holý and Kvaček, P 1952/32; F, *Myrica longifolia* Unger, P 1952/50; G, *Comptonia diffiformis* (Sternberg) Berry, P 1952/166; H, *Hydrangea microcalyx* Sieber, calyx of a flower, P 1952/145; I, *Engelhardia macroptera* (Brongniart) Unger, involucrum of a fruit, P 1952/154; J, *Sloanea olmediaefolia* (Unger) Kvaček and Hably, P 1952/340; K, *Laurophyllo pseudoprinceps* Weyland and Kilpper, P 1952/48; L, *Daphnogene cinnamomifolia* (Brongniart) Unger, P 1953/7; M, *Symplocos volkeri* Kvaček, P 1952/65; N, *Palmacites lamanonis* Brongniart, P 1952/113; O, *Phoenicites* sp., rhachis of a pinnate leaf showing the attachment of the pinnae, P 1952/12. Scale = 20 mm (A), 10 mm (B, D–M, O), 5 mm (C), and 50 mm (N).

Taphonomic bias is suggested by the low representation of Fagaceae (a single specimen of *Eotrigonobalanus furcinervis haselbachensis*), since 8 types of Fagaceae pollen (17% of recovered pollen) have been reported

from more westerly localities in the Rhine Graben (Sittler, 1965). Deciduous woody angiosperms are not diverse and, with the exception of *Platanus neptuni*, are mainly represented by fructifications (*Betula*





**Fig. 3.** Leaf cuticle preparations from the Rauenberg locality. A, *Ceratozamia floersheimensis* (Engelhardt) Kvaček, stomata-bearing cuticle and short, strongly cutinized cells arranged in short rows; this structure excludes the reed or sedge-like nature of these remains (compare A–D), P 1952/456/2; B, *Platanus neptuni* (Ettingshausen) Büžek, Holý and Kvaček, stomata-bearing abaxial cuticle with peltate trichomes, P 1952/32/1; C, *Daphnogene cinnamomifolia* (Brongniart) Unger, stomata-bearing abaxial cuticle, P 1952/76/2; D, *Laurophylllum pseudoprinceps* Weyland and Kilpper, stomata-bearing abaxial cuticle, P 1953/48/2; E, *Symplocos volkeri* Kvaček, stomata-bearing abaxial cuticle, fungal infection via stoma (arrow) and hyphae, P 1952/65/1; F, *Myrica longifolia* Unger, tetracellular trichome bases, P 1952/50/1; G, *Sloanea olmediaefolia* (Unger) Kvaček and Hably, abaxial cuticle, stomata characteristically faint, P 1952/340/1; H, *Phoenicites* sp. brachyparacytic stomata with parallel orientation, P 1952/12/1. Scale bar = 50 µm.

*dryadum*, *Carya quadrangula*, *Craigia bronii*) or calyx remains (*Hydrangea microcalyx*) (Fig. 2H).

Especially noteworthy is the occurrence of *Ceratozamia floersheimensis* (Zamiaceae) (Fig. 2D, 3A). This cycad is known from Flörsheim (Fig. 1D), an important early Oligocene locality in the Mainz Basin (2 fragments), Rauenberg (1), Budapest (1), and Tribolje (1) (formerly Trifail, Slovenia). The first report of *Ceratozamia* was from Flörsheim (Kvaček, 2002), where it was originally described as *Iris floersheimensis* by Engelhardt (1911). In the Cenozoic, cycads were already relicts in the European flora.

Another important finding is *Laurus abchasica*, a Lauraceae species commonly occurring as an accessory element in late Oligocene and especially early to middle Miocene floras of Central Europe. Along with a record from Flörsheim (one fragment: Kvaček (2004)), the three fragments from Rauenberg are the oldest reported records of *L. abchasica*.

*Sloanea artocarpites* (Elaeocarpaceae) has been recognized unambiguously from Flörsheim (Kvaček et al., 2001). *Sloanea olmediaefolia* is very abundant in the Tard Clay (Hungary) while *S. artocarpites* is also known from Northern Bohemia (České Středohoří Mountains). All

these records derive from the Oligocene. The most similar living relatives are restricted to subtropical regions in eastern China.

In general, the flora from Rauenberg has closer affinity to the Oligocene and even Miocene record of Europe than that of the Eocene.

### 5.3. Macroinvertebrates

#### 5.3.1. Mollusca

Our study provides the first survey of gastropods and bivalves from the Rauenberg locality. The studied material comes from various historical and modern excavations, and since the stratigraphic origin of the material from within the Rauenberg succession is usually unknown it is difficult to interpret which of the described benthic invertebrate taxa occurred together and therefore might have formed benthic communities. The molluscan fauna of the Bodenheim and Alzey Formations has been little-studied in the Rhine Valley, but is well-known from neighboring localities in Germany (e.g., Mainz Basin), Belgium, and the Netherlands (e.g., Boekschoten, 1963; Glibert, 1957a, 1957b; Marquet, 2010; Neuffer, 1973, 1984; Sanderberger, 1858–1863; van den Bosch et al., 1975). However, few works compare all these localities, which might have resulted in an inflation of synonymous names.

The gastropod assemblage (entirely epi- or infaunal) is very unusual: of the seven identified genus- or species-level taxa, five are from predatory families. Of the remaining two, the aporhaid *Drepanocheilus*

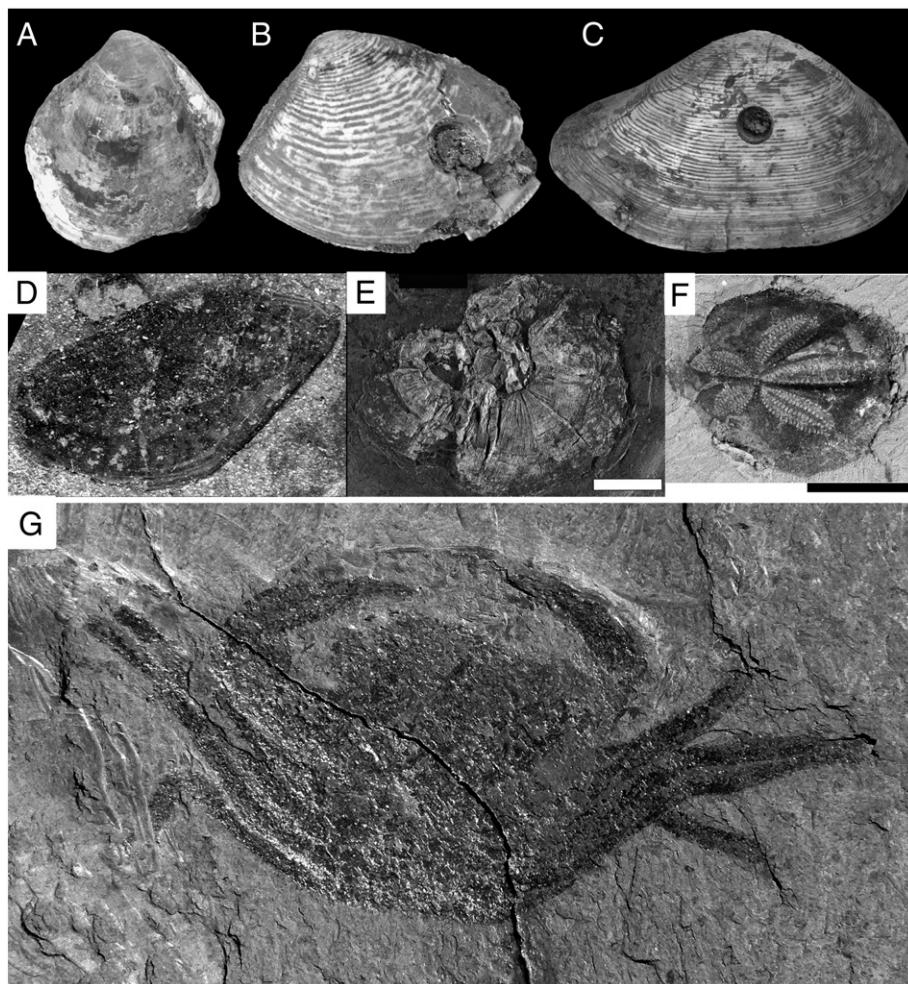
cf. *D. speciosus* is considered a semi-infaunal detritivore (Roy, 1994; Saul and Squires, 2015) and the batillariid *Granulolabium plicatum*? either an epifaunal grazer or a deposit feeder (Ozawa et al., 2009).

Muricids and naticids are predators, and the holes they bore in the shells of their molluscan prey are well-documented in the fossil record (e.g., Bromley, 1981; Fretter and Graham, 1962; Zonneveld and Gingras, 2014). Both groups are present in the Rauenberg deposits, represented by *Muricopsis* sp. (Muricidae) and *Euspira* cf. *E. micromphalus* (Naticidae). The Fasciolariidae (represented by *Streptochetus* sp.) are also malacophagous (also feeding on polychaetes), but feed by wedging open the valves of bivalves or the operculum of snails (Modica and Holford, 2010; Wells, 1958) and therefore leave no trace fossils.

Cassidae (represented by *Galeodea depressa*) are known predators of echinoderms (especially sea urchins), leaving boreholes in the tests (Hughes and Hughes, 1981).

Epitoniids (possibly represented by *Opalia*? sp.) feed on corals and sea anemones (Kokshoorn et al., 2007; Robertson, 1963); however there are no fossils of cnidarians known from Rauenberg.

Of the ten bivalve species, only two (*Chama weinheimensis* and *Isognomon* sp.) are from epifaunal families; the rest are infaunal and include some possible deep infaunal representatives (*Panopea*? sp. and *Pholadomya weissi*?). Seven species are from families of suspension-feeding habits; nuculids (represented by *Nucula duchasteli*; Fig. 4B) might be either suspension-feeders or deposit-feeders, and yoldiids



**Fig. 4.** Marine macroinvertebrates from Rauenberg. A, *Thyasira benedeni*; SMNK-PAL 7585, shell length 10.4 mm. B, *Nucula duchasteli*, with borehole (ichnospecies *Sedilichnus paraboloides*); SMNK-PAL 7343, shell length 13.8 mm. C, *Portlandia deshayesiana*, with borehole (ichnospecies *Sedilichnus paraboloides*); SMNK-PAL 7585, shell length 19.9 mm. D, Operculum of a neogastropod (likely Muricoidea), embedded in the rock matrix; SMNK-PAL 8058, greater length 11.9 mm. E, A balanid colony consisting of two individuals with broken shell showing the internal shell structure (SMNK PAL 7352); scale bar = 10 mm. F, The irregular sea-urchin *Ova* sp. (SMNK PAL 7796); scale bar = 10 mm. G, *Coeloma taunicum* (v. Meyer, 1862), SMNS 106866. Total width of specimen including pereiopods = 100 mm.

(*Portlandia deshayesiana*; Fig. 4C) are deposit-feeders. The family Thyasiridae (represented by *Thyasira benedeni*; Fig. 4A) has species with and without chemosymbiotic sulfide-oxidizing bacteria (Dufour, 2005; Rozemarijn et al., 2011; Southward, 1986). Symbiont-bearing thyasirid species tend to be larger and to live in shallower waters than species lacking symbionts (Dufour, 2005). The fossil species *T. michelotti*, from the Austrian Miocene (Badenian), was considered to be chemoautotrophic by Zuschin et al. (2001). In Rauenberg, *T. benedeni* occurs exclusively in life position in the pyrite horizon (i.e., in sulfide-rich sediments, Bed 9, Fig. 1C); this suggests chemosymbiosis, as this species is known from pyrite-bearing horizons in other localities (e.g., Boekschoten, 1963).

Overall, the most abundant mollusks are the gastropods *Streptochetus* sp. and *Drepanocheilus* cf. *D. speciosus* and the bivalves *Thyasira benedeni* (Fig. 4A), *Nucula duchasteli* (Fig. 4B) and *Portlandia deshayesiana* (Fig. 4C).

### 5.3.2. Echinodermata

Only one species of irregular sea urchin was found (Fig. 4F), represented by 26 specimens in the SMNK collections. They are mostly fragmented and deformed by sediment pressure and therefore identification is difficult. The general morphology and the presence of two goniopores suggests, however, referral to *Ova* (Spatangoida, Schizasteridae).

### 5.3.3. Crustacea

Decapod crustaceans from Rauenberg are very rare, represented only by a few poorly preserved, undescribed specimens of the crab *Coeloma taunicum* (Brachyura: Gonoplacoidea; Fig. 4G). This species was widespread in the Rupelian seaway of the Upper Rhine Graben and is also known from clayey deposits of Central Germany (Freess, 1992; Polkowsky, 2005; von Fritsch, 1870). The extreme flattening of the specimens of *C. taunicum* from Rauenberg and the absence of the pleon in ventral view indicates that these fossils do not represent carcasses but moults. It is likely that preservation biases or low benthic oxygen levels are responsible for the absence of other decapods such as shrimps and squat lobsters which would otherwise be expected in this type of environment. From elsewhere in the region (Dämmelwald I and II and Dammstücke clay pits northeast of Wiesloch), Wagner-Klett (1919) described additional crustaceans. Reappraisal of these remains suggests that, in addition to *C. taunicum*, ghost shrimps (Callianassidae gen. et sp. indet.), and the lobster *Hoploparia klebsi* (Noetling) were present. *Hoploparia klebsi* is widely distributed in Oligocene sediments from Northern Germany.

Barnacles are also known from Rauenberg. They are represented by shells of two unattached individuals in the SMNK collection (Fig. 4E). Two further individuals attached to the entoplastron of a cheloniid turtle were figured by Alexander and Frey (2010). The shape of the shells is most similar to the genus *Protochelonibia*, which is thus far the oldest representative of the extant sea-turtle fouling Chelonibiidae (Cirripedia: Balanomorpha; Harzhauser et al. (2011)). The SMNS collection additionally houses an unattached colony of an unidentified smaller type of barnacle as well as four samples with poorly preserved shells of goose barnacles (Pedunculata).

### 5.3.4. Insecta

A relatively rich assemblage of fossil insects is known from Rauenberg (Fig. 5; Suppl. Fig. 1), however the material is largely undescribed, aside from the work of Monninger and Frey (2010) and a brief mention in recent newspaper reports (Anonymous, 2014; Ott, 2014). 340 specimens were examined from the SMNK and SMNS collections as part of the current study (Appendix B). Although many of these were collected by private individuals, most notably H. and A. Oechsler, it is important to note that the collection does not seem to be affected by collection bias, as every item remotely resembling a fossil was collected and preserved. Only very few of the fossil insect specimens are

associated with stratigraphic data. However, anecdotal information provided by the fossil collectors suggests that insects are mostly found in the upper beds.

With few exceptions (i.e., cicada, SMNS 112 and jewel beetle, SMNS 140; Fig. 5A,D) there are no details preserved in the fossil insects from Rauenberg, apart from a shadowy outline of the insect body. Some of the better-preserved specimens include a few larger beetles (Fig. 5C,H) and beetle elytra (Fig. 5E), a butterfly (Fig. 5J), and a complete fossil damselfly (Fig. 5F).

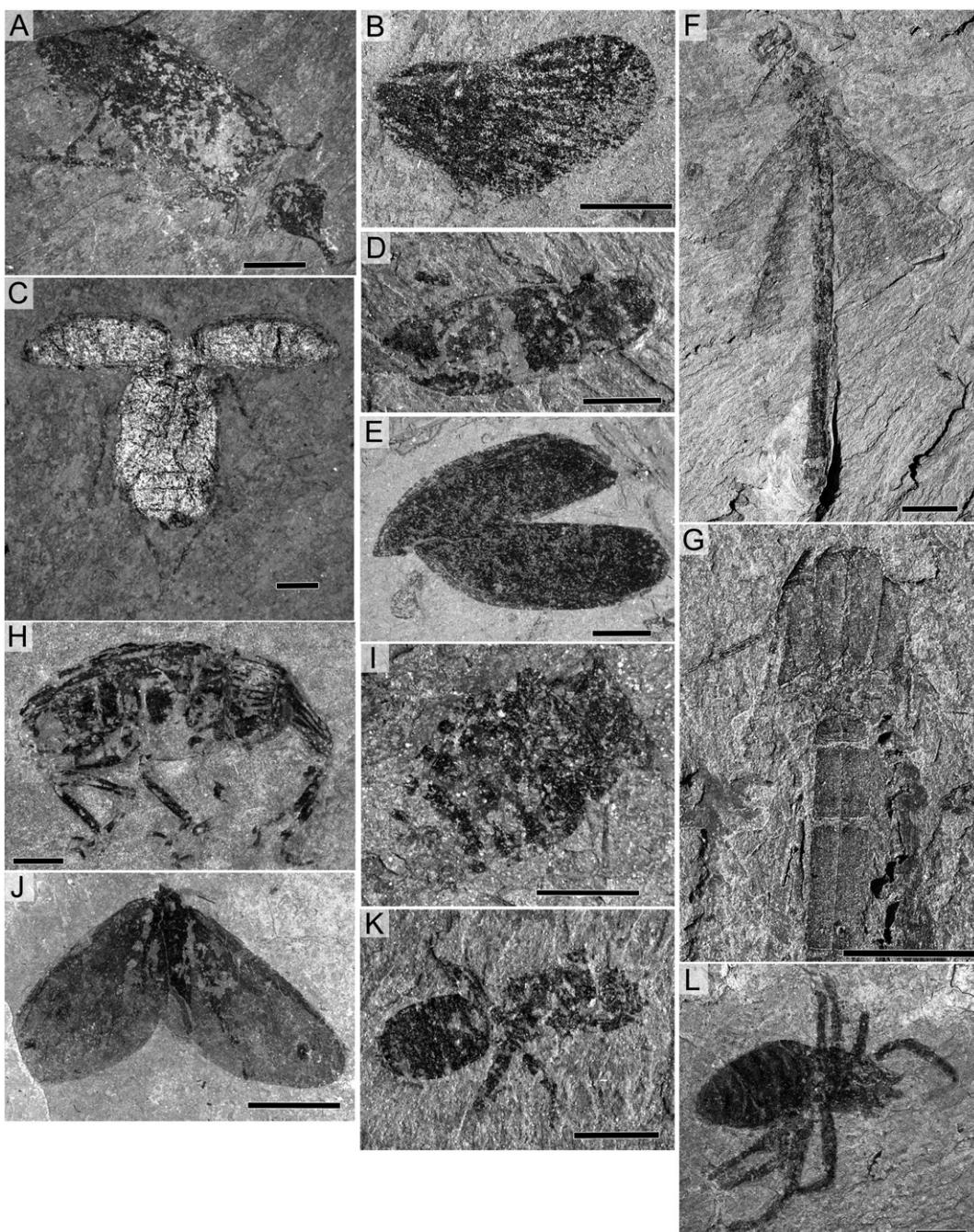
Among the 340 fossil insects in the studied collections, 122 specimens (36%) are indeterminate insects. Among the remaining 218 specimens, representatives of 8 insect orders (Odonata, Orthoptera, Auchenorrhyncha, Heteroptera, Hymenoptera, Coleoptera, Diptera and Lepidoptera) could be recognized. The record of the superorder Amphiesmenoptera by Monninger and Frey (2010) was confirmed as Lepidoptera-Geometridae. Family-level determination was only possible for 33 specimens, representing 11 families or superfamilies (Calopterygidae, Carabidae, Staphylinidae, Elateridae/-oidea, Buprestidae, Cerambycidae, Curculionidae/-oidea, Pentatomidae/-oidea (Fig. 5I), Formicidae (Fig. 5K), Bibionidae, and Geometridae). Of the 218 specimens that could be determined to order-level, the vast majority (154 specimens: 71%) are Coleoptera. Nine specimens representing larvae or pupae have also been recovered.

In the SMNK collection, there are four specimens of the order Odonata that can be attributed to the suborder Zygoptera (Fig. 5F,G). Even though few details of the wing venation are preserved, all specimens except SMNK-PAL-8379 can be determined to family level as Calopterygidae based on the complete interpleural suture (Asahina, 1957) of the very robust pterothorax (Fig. 5G), which is otherwise only known from the exclusively Neotropical family Polythoridae. Similar size indicates that all four specimens could represent the same taxon (Suppl. Table 3). At least one specimen (SMNK-PAL-8088, and probably SMNK-PAL-8379) is a female, as the ovipositor pouch is visible on the abdomen. Because calopterygids oviposit into submerged aquatic vegetation, it can be presumed that these specimens are all females that drowned during misguided oviposition attempts on the ocean.

Otherwise, most of the insects are terrestrial pterygotes that were probably transported by wind into the marine environment. The large percentage of complete insects (ca. 75% complete vs. 25% fragments or isolated elytra), including delicate insects such as Diptera and Hymenoptera, suggests that the animals drowned and rapidly sank to the bottom. Beetles probably had a longer drifting time because of air trapped beneath the elytra. During decomposition of the animals, the elytra became detached (Fig. 5E). A strange phenomenon is the preservation of both elytra together without any other remains of the body in 10 of the fossil beetles. The lack of damage to the elytra excludes the possibility that this fragmentary preservation is due to predation. The most likely explanation is incomplete decay, where the elytra have been detached from the thorax but remained in connection to each other.

### 5.3.5. Arachnida

There are only three terrestrial arthropods from Rauenberg that are not pterygote insects. All three are arachnids; myriapods are absent. We also discovered a large arachnid (SMNK-PAL-7798) originally misidentified as a beetle. This specimen is about 23 mm long with seven of eight legs preserved, segmented opisthosoma, half-ovoid prosoma/carapax, long pedipalps (1 preserved) with two elongate basal segments, and apparently orthognathous chelicerae (Fig. 5L). At first glance, it resembles a spider of the suborder Mesothelae; however, the shape of the prosoma/carapax, the pattern of segmentation of the opisthosoma, and the broad connection between these two tagmata refute an attribution to Araneae. This specimen most likely represents a poorly preserved and partly decayed scorpion lacking the tail and the pincers (chelae) (P. Selden pers. comm., 2015).



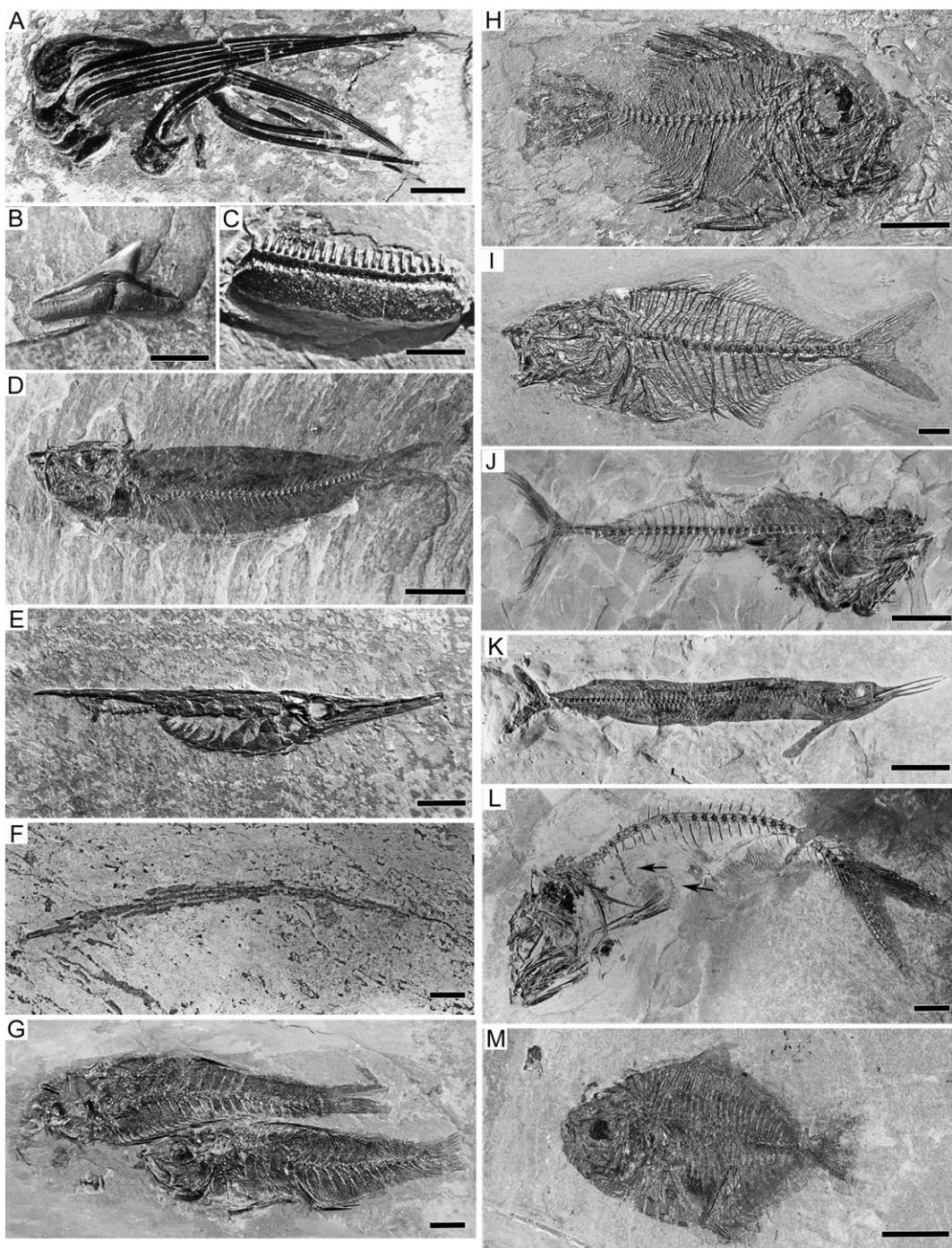
**Fig. 5.** Fossil insects from the Oligocene of Rauenberg. A, Auchenorrhyncha, SMNS 112, the only insect from this locality with faintly preserved wing venation. B, Auchenorrhyncha, wing, SMNK-PAL-unnumbered. C, Coleoptera, SMNS 39b (the fossil is black, the reflection is due to coating with cellulose varnish). D, Coleoptera, Buprestidae, SMNS 140. E, Coleoptera, Carabidae, SMNS 4. F, Odonata, Zygoptera, SMNK-PAL-8379. G, Odonata, Zygoptera, Calopterygidae, SMNK-PAL-8089 (note the complete interpleural suture). H, Coleoptera, Curculionidae, SMNK-PAL-6565. I, Heteroptera, Pentatomidae, SMNS 21. J, Lepidoptera, Geometridae (note the small eyespot on distal part of wing), specimen is prepared by transfer to resin, SMNK-PAL-6572. K, Hymenoptera, Formicidae, SMNS 161. L, Arachnida, Scorpiones?, SMNK-PAL-7798. Scale parts A–G, I, L = 5 mm; part J = 10 mm, parts H,K = 2 mm.

#### 5.4. Vertebrates

##### 5.4.1. Chondrichthyes and Actinopterygii

Fish remains (Figs. 6–7) are the dominant faunal elements of the Rauenberg clay pits, both in the field and in museum collections (Micklich and Hildebrandt, 2010; K. Eck, pers. observ.). Fishes from Rauenberg were first mentioned in the literature by Wagner-Klett (1919) and later revised by Weiler (1931), who identified a total of 19 taxa. In a subsequent publication, Weiler (1966) emphasized the general significance of this fish fauna for paleobiological reconstruction and paleogeography. He recognized a total of 31 fish taxa, with

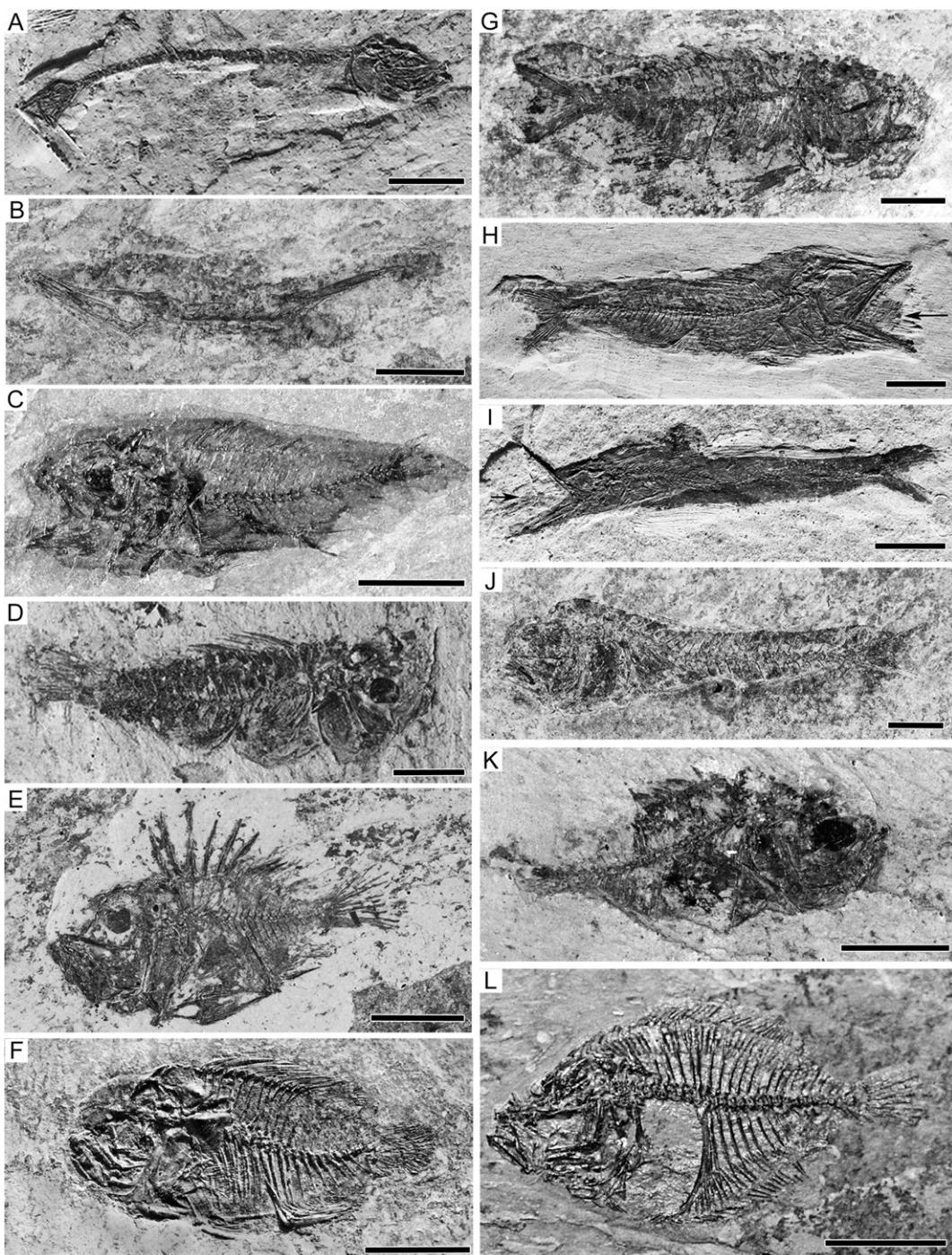
slight taxonomic deviations from his earlier publication. However, according to the maps from these publications, these authors referred to records from the ancient Dämmelwald I and II and Dammstücke clay pits NE of Wiesloch (Wagner-Klett, 1919), and the Rohrlach and Frauenweiler-Wiesen clay pits east of the small village of Frauenweiler, now a suburb of Rauenberg (Micklich and Hildebrandt, 2005; Weiler, 1966) (Fig. 1B). The Unterfeld clay pit was first mentioned as a fossil fish locality by Eikamp (1983), but without any faunistic details. A detailed synopsis of the fishes from this locality was published by Micklich and Parin (1996), who distinguished 52 distinct taxa, and was updated by Micklich (1998), who corrected some errors and briefly



**Fig. 6.** Typical fishes and fish remains from the Rupelian of Rauenberg. A, Basking shark, *Keasius parvus* (HLMD-SMFF 32), bundle of gill rakers from filtering apparatus; B, Requiem shark, *Physogaleus latus*, lower lateral tooth in lingual view (HLMD-WT 705); C, Eagle ray, *Myliobatidae* indet. aff. “*Myliobatus*” var. *oligocaena*, symphysal tooth (HLMD-WT 707); D, Herring, “*Sardinella*” *sardinines* (HLMD-SMFF 667); E, Shrimpfish, *Aeoliscus heinrichi* (HLMD-WT 861); F, Pipefish, *Doryrhamphus* sp. (HLMD-SMFF 7); G, Pair of sea bass, *Oliganodon budensis* (HLMD-SMFF 15a); H, Bigeye, *Priacanthus spinosus* (HLMD-WT 687); I, Jack, *Archaeus glarisanus* (HLMD-WT 37); J, Bonito, *Sarda brachycephala* (HLMD-WT 41); K, Billfish, *Palaeorhynchus* cf. *P. glarisanus* (HLMD-SMFF 27); L, Stromateid-like fish, *Propercina* sp., arrows indicate the vertebral column of prey fish in the gut (HLMD-SMFF 23); M, Stromateid-like fish, *Pinichthys pulcher* (HLMD-WT 29). Scale bars A–C, F–G = 5 mm, scale bars D–E, H–I, L–M = 10 mm, scale bars J–K = 50 mm.

characterized some new faunal elements. The number of teleosts recognized from the locality was further increased by Micklich and Hildebrandt (2010), who included 72 taxa in their paleobiological analyses. The chondrichthyan fauna was revised by Hovestadt et al. (2010). The updated faunal list reflecting ongoing study of the material now comprises 74 discrete taxa (Appendix A; Suppl. Table 4). It must to be stressed that this synopsis is a snapshot, as several of the listed taxa are only preliminary identifications and are in need of detailed revision.

Recently, several taxonomic revisions of the Rauenberg fishes have been undertaken. The shark *Triakis kelleri* was described by Hovestadt and Hovestadt-Euler (2002) from the Unterfeld clay pit, and *Carcharhias gustrowensis* is also present at this locality, although most records are from younger (Chattian) localities (Hovestadt and Hovestadt-Euler, 2010). The record of an almost-complete juvenile basking shark (Hovestadt and Hovestadt-Euler, 2012) is also of striking importance, as little is known concerning the spawning behavior and presumed



**Fig. 7.** Early juvenile stages of fishes from the Oligocene of Rauenberg. A, Herring, cf. "Sardinella" sardinites (HLMD-WT 764); B, Shrimpfish, *Aeoliscus heinrichi* (HLMD-WT 937); C, Scorpionfish, cf. *Sebastes* sp. (HLMD-SMFF 93b); D, Seabass, cf. *Oliganodon budensis* (HLMD-WT 200); E, Bigeye, *Priacanthus spinosus* (HLMD-WT 361); F, Butterflyfish *tholichthys* larval stage (HLMD-WT 410a); G, Jack, cf. *Archaeus glarisianus* (HLMD-WT 815); H, Spanish mackerel, *Scomberomorus* cf. *S. lingulatus*, arrow indicates prey fish in mouth (HLMD-WT 803b); I, Billfish, *Palaeorhynchus glarisianus*, arrow indicates prey fish in mouth (HLMD-WT 807); J, Stromateid-like fish, *Propercarina* sp. (HLMD-WT 224); K, Stromateid-like fish, *Pinichthys pulcher* (HLMD-WT 224); L, Flatfish, *Oligoscoptthalmus weissi* (HLMD-WT 254). Scale bars = 5 mm.

nursery grounds of these sharks (McCandless et al., 2007). *Weissobatis*, an eagle ray, was described as coming from the lower parts of the Meletta Beds (Hovestadt and Hovestadt-Euler, 1999). If so, this would be one of the youngest vertebrate fossils from the locality. It is significant for myliobatid systematics and phylogenetic relationships. Among the Syngnathoidei (revised by Parin and Micklich, 1996a; Parin and Micklich, 1996b), *Frauenweilerstomus synarcialis*, a genus and species which is not rare but is exclusively reported from Rauenberg, is particularly noteworthy. *Aeoliscus distinctus* is also only

known from Rauenberg. In addition, the presence of the syngnathids *Microphis* and *Nerophis* extend the stratigraphic range of these taxa from essentially Recent (*Microphis*: Serravallian-Langhian (Bachmayer, 1980); *Nerophis*: early Miocene (Sergienko, 1971)) into the Paleogene. *Musculopedunculus* (Parin and Astakhov, 2007) is of special interest as it represents a new family of the Trichiuroidae, and *Oligoremora rhenana*, a new genus and species of Echeneidae, has recently been described which, based on meristic data, most closely resembles representatives of the extant genus *Remora* (Micklich et al. 2016). The presence

of tholichthys larvae (Fig. 7F) represents the oldest record of butterflyfishes worldwide (Micklich et al., 2009). Interestingly, and in contrast to their great rarity in extant tropical plankton and midwater trawl samples – according to Leis (1989), they have a mean frequency of 0.09% of all larvae captured – two additional records were found in 2012 (N. Micklich, pers. observ.).

As previously suggested (Micklich, 1998, 2005), some of the taxa listed in Appendix A may be “waste-basket” taxa comprising more than one nominal genus and/or species. Others remain undescribed. The total diversity of the fish fauna is therefore undoubtedly greater than the current state of the art. For instance, a new lophiid genus and species is recognized, closely related to the extant *Sladenia* and the fossil *Caruso* (G. Carnevale, pers. comm.). Ongoing study of *Propercarina* (Figs. 6L, 7J) indicates that the Rauenberg material differs from the other known species and may represent a new species (T. Přikryl, pers. comm., N. Micklich, pers. observ.), and a similar situation exists concerning the presumed *Leiognathoides* (A. Bannikov, Y. Yamamoto, pers. comm., N. Micklich, pers. observ.). However, the largest ongoing work is a revision of the scombrids (K. Monsch, pers. comm., N. Micklich, pers. observ.), including documentation of material in existing collections and detailed systematic revision of selected taxa. Currently, about 30 genera and species can be distinguished (K. Monsch, pers. comm.). Some of them, e.g., those resembling *Diplospinus* and *Neopinnula*, were previously known exclusively from extant representatives. Others (e.g., *Abadzekhia*) were

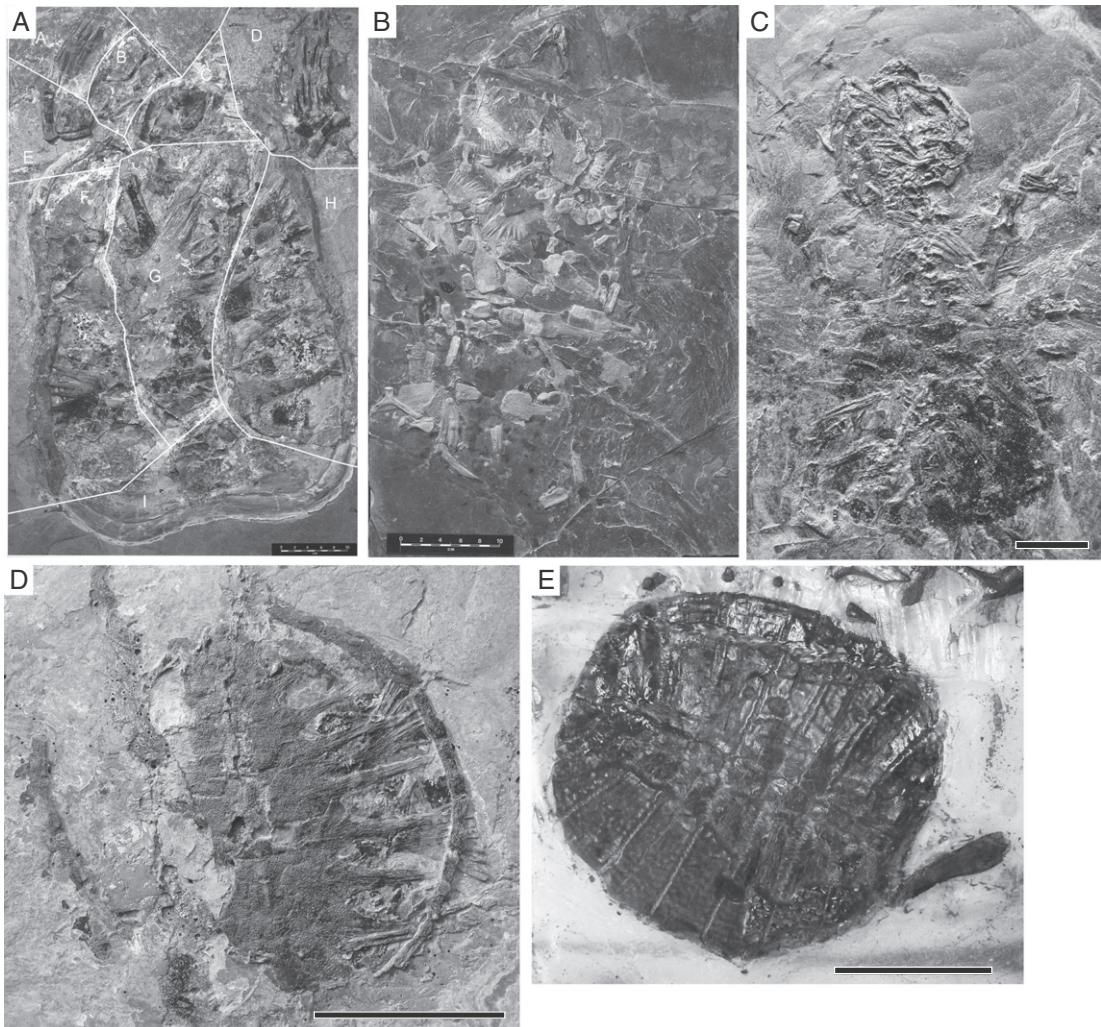
only known from localities in the eastern Paratethys, and more are completely new and as yet undescribed.

The fish fauna is typically Cenozoic, specifically Rupelian. Aside from the presumed sphyraenids, no actinopterygian species range extends earlier than the Paleocene (Suppl. Fig. 2). About 40 are more or less restricted to the Rupelian or slightly younger layers, and 11 species are known exclusively from Rauenberg. This number will increase following reevaluation of some of the groups discussed above (e.g., Lophiidae, Scombroidei), as well as those specimens currently identified only to genus or family. 14 taxa are also known from extant forms. For at least six of them, the records from Rauenberg extend their stratigraphical range from (almost) Recent into the lower Oligocene.

#### 5.4.2. Reptilia

In the mudstones of the clay pits around Rauenberg, turtles are rare. Due to their predominantly fragmentary nature, little work has been undertaken on this clade. Only 19 specimens are known to date. There are two near-complete skeletons and four fragments at the SMNK, two partial skeletons and 10 fragments at the HLMD, one isolated humerus at the GEOW, and seven specimens at the SMNS. Of these, only the more complete material housed at the SMNK has been described (Alexander and Frey, 2010).

Marine turtles or Chelonioidae comprise three families: Cheloniidae, Protostegidae, and Dermochelyidae. The bulk of the marine turtles from



**Fig. 8.** Cheloniid Turtles from Rauenberg. A, an almost-complete cheloniid SMNK-PAL 6608; note the plates were reassembled incorrectly (plate borders are marked in white); B, a disarticulated cheloniid SMNK-PAL 6609; C, a juvenile cheloniid including skull and forelimbs SMNS 87449/26; D, a juvenile cheloniid carapace SMNS 80738/2; E, carapace referable to Trionychidae (SMNS 96919). Photos parts A, B courtesy of Griener; used with permission. Scale = 1 cm (C) and 5 cm (D, E).

Rauenberg, including the material previously described by Alexander and Frey (2010), are referred to Cheloniidae despite having a wide range of body sizes (Fig. 8A–D). The Karlsruhe specimens (SMNK-PAL 6608, SMNK-PAL 6609; Fig. 8A–B) are poorly preserved, permitting identification only to family level. Within the Stuttgart sample, the better articulated specimens closely resemble “*Chelonia*” *gwinneri*, particularly a large adult (SMNS 80529/1); SMNK-PAL 6608 is also similar to “*Chelonia*” *gwinneri* (Alexander and Frey, 2010). The Rauenberg material highlights problems with the assignment of juvenile cheloniid specimens to species. For instance, SMNK-PAL 6609 strongly resembles *Glarichelys knorri*, however, the secondary transversal and longitudinal sections of the neuralia are more similar to the late Miocene taxa “*Euclastes*” *melii* and *Procolpochelys grandaeva* (Alexander and Frey, 2010). At present, *Glarichelys knorri* is based exclusively on juvenile specimens.

The nine cheloniid specimens studied here fall into a wide size range and most probably form an ontogenetic series. Further studies are required to (1) test this hypothesis and (2) address the question of whether the single Rauenberg taxon is distinct from “*Chelonia*” *gwinneri* and *Glarichelys knorri*.

In addition, a single specimen (SMNS 96919; Fig. 8E) of soft-shelled turtle (Trionychidae) is reported here for the first time, and bears a close resemblance to *Trionyx (Platypeltis) posterus*. Extant trionychid turtles preferentially inhabit freshwater but also occur in brackish water, sometimes with surprisingly high salt concentrations (Ernst et al., 2000). However, they have been reported to temporarily invade marine habitats (Das, 2008; Shanas et al., 2012). The presence of a trionychid at Rauenberg may indicate the presence of a nearby freshwater source, such as a river mouth. Trionychid and cheloniid turtles are uninformative climatic indicators because of their wide temperature tolerance. A number of extant trionychids occur at high latitudes (45°) and hibernate (e.g., Harding, 1997; Reese et al., 2003). Cheloniid sea turtles also occasionally invade subpolar waters (e.g., Bustard, 1972; Carr, 1952).

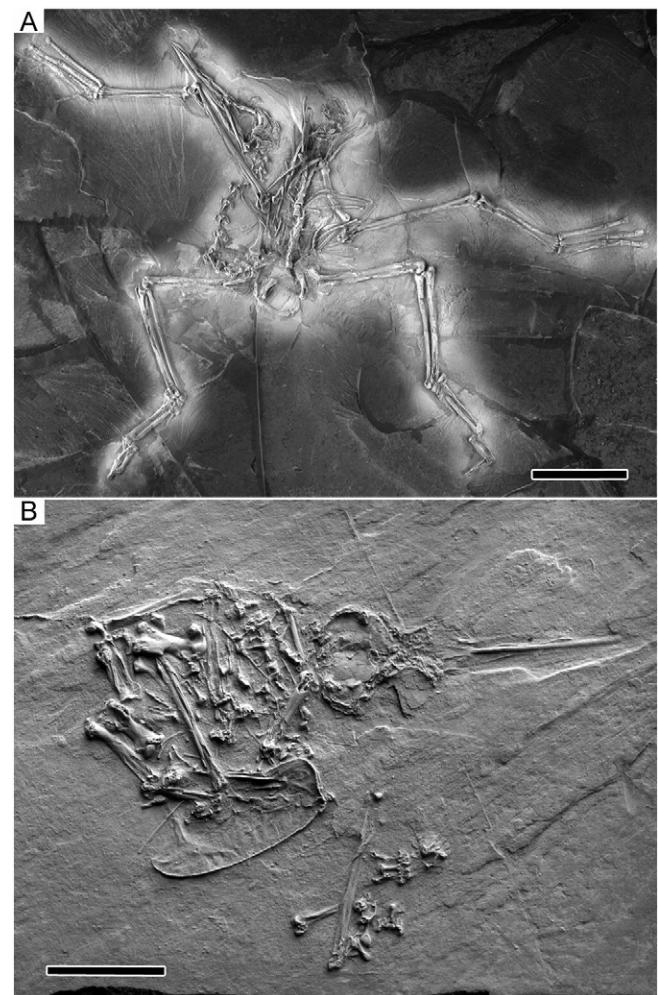
#### 5.4.3. Aves

Rauenberg is one of the most significant localities for early Oligocene fossil birds in Europe, being among the few sites that yield well-preserved partial skeletons rather than isolated bones. The most abundant birds from Rauenberg are procellariiforms of the taxon *Rupelornis* (Diomedoididae), of which several partial and complete skeletons are known (Mayr, 2009a; Mayr et al., 2002; Mayr and Smith, 2012) (Fig. 9A). Two species appear to have coexisted, whose taxonomic status is in need of revision. One is likely to be conspecific with *R. definitus* from the Rupelian of Belgium, whereas the other probably belongs to a *Rupelornis* species that was first described from the early Oligocene of France. Diomedoidid procellariiforms had a wide distribution in the early Oligocene epicontinental seas of Europe and the Near East, having been reported from localities in Belgium, France, Switzerland, Poland, and Iran (Mayr, 2009b).

Another aquatic bird from Rauenberg is the loon *Colymboides? metzleri* (Gaviiformes) (Mayr, 2004b). This species is known from a single skeleton and seems to be closely related to a loon species from the Rupelian of Belgium (Mayr, 2009c; Mayr and Smith, 2013).

Altogether, six species of landbirds are known from Rauenberg, all of which provide significant insights in the evolution of their respective groups. Today, the nectarivorous hummingbirds (Trochilidae) only occur in the New World. At the time of their description, specimens of *Eurotrochilus inexpectatus* from Rauenberg represented the earliest fossil records of hummingbirds (Mayr, 2004a, 2007; Mayr and Micklich, 2010) (Fig. 9B). Closely related species are now known from the early Oligocene of the Luberon area in France and from the Rupelian of Poland (Mayr, 2009b).

Two further landbirds from Rauenberg that closely resemble related species from the early Oligocene of the Luberon area include a *Primotrogon*-like trogon (Trogoniformes), which is known from a partial wing (Mayr, 2005a), and *Turnipax oechslerorum*, a stem group



**Fig. 9.** Articulated and associated avian remains from Rauenberg. A, *Rupelornis* cf. *brodkorbi* (Procellariiformes: Diomedoididae; SMNK-PAL 3812); B, *Eurotrochilus inexpectatus* (Apodiformes, Trochilidae: SMNK-PAL 5591). Scale = 5 cm (A) and 1 cm (B).

representative of buttonquails (Turnicidae) known from a single specimen (Mayr, 2009b; Mayr and Knopf, 2007a). Trogons have a pantropical distribution and include insectivorous and frugivorous species. They excavate nest cavities in tree trunks and therefore occur in forested areas and open woodlands. Buttonquails are an Old World group of small charadriiform birds, which today occur in arid semi-deserts, but *Turnipax* exhibits a much more primitive morphology than its extant relatives and its ecological preferences may have differed.

A stem group representative of mousebirds (Coliiformes), *Oligocolius brevitarsus*, is represented by a dissociated partial skeleton (Mayr, 2000). The Rauenberg fossil was the first record of the distinctive taxon *Oligocolius*, which appears to have been adapted to a more aerial way of life than its extant African relatives. A second more recently described species of the taxon from the late Oligocene of Germany (Mayr, 2013) is associated with preserved stomach contents, indicating that *Oligocolius* was a specialized frugivore.

Two partial skeletons of a tody, *Palaeotodus itardiensis* (Todidae; (Mayr and Knopf, 2007b; Mayr and Micklich, 2010), have also been recovered. Todies are very small alcediniform birds, which have a relict extant distribution on the West Indian islands. *Palaeotodus itardiensis* was originally described from late Eocene and early Oligocene localities of the Quercy fissure fillings in France (Mayr, 2009b).

One of the oldest representatives of the Pici, the clade including woodpeckers and allies, is known from Rauenberg: *Rupelramphastoides knopfi*. This species is one of the smallest known representatives of the clade (Mayr, 2005b, 2006). *Rupelramphastoides* does not exhibit any of

the specialized dietary or locomotory adaptations found in its extant relatives.

Rauenberg also yielded fossils of a passerine bird, *Wieslochia weissi* (Mayr and Manegold, 2004, 2006). At the time of its description, it was the oldest European fossil occurrence of Passeriformes, the most species-rich clade of extant birds, which includes more than half of all extant avian species, although in the past years equally old fossils have been described from the early Oligocene of Poland (Bocheński et al., 2011, 2013). *Wieslochia weissi* is among the earliest well-represented fossil passerines.

#### 5.4.4. Mammalia

Mammalian remains from Rauenberg are extremely rare, with very few specimens known. These include a creodont carnivore (Frey et al., 2010), as well as undescribed sirenian material (Dugongidae) and a bat.

The dugongid remains consist of a nearly-complete specimen at the HLMD (Schögl and Micklich, 2012), an isolated forelimb at the SMNS, and skull and rib fragments at GEOW, and have been referred to the early Oligocene species "*Halitherium cf. schinzi*" based on the occurrence of this taxon in other early Oligocene coastal deposits from Central Europe, especially Germany (e.g., Domning and Pervesler, 2001; Kaup, 1838; Voss, 2008).

The chiropteran specimen housed at the SMNS consists of a partial skeleton preserved as part and counterpart, including a left dentary and a right maxillary fragment. There are no accessory cuspules on the lingual talon of the upper molars, and so a referral to *Leuconoe* can be ruled out. The specimen is most consistent with the vespertilionid *Myotis horaceki* from the late Oligocene of Germany (Ziegler, 2000, 2003). A second nearly-complete specimen is housed in the Castle of Bruchsal Museum, but was not available for study.

The creodont *Apterodon rauenbergensis* consists of a mandibular fragment. Other European taxa referred to this genus have been recovered from the Rupelian fissure fillings of the Quercy Phosphorites and the Mainz and Weissenster Basins. This is the first terrestrial mammal reported from Rauenberg.

## 6. Discussion

### 6.1. Biotic interactions and soft-tissue preservation

There are several bivalves in the Rauenberg material (<10% of the total sample) bearing boreholes attributable to the ichnospecies *Sedilichnus paraboloides* (Fig. 4B–C). Recent representatives of both Naticidae and Muricidae are known to create holes comparable to *S. paraboloides* (Zonneveld and Gingras, 2014), suggesting that gastropods from these families are responsible for these traces. There are no traces of predation on Rauenberg echinoderms, in spite of the presence of Cassidae (Gastropoda), perhaps not surprisingly since echinoderms are represented only by burrowing spatangoids.

Many vertebrate fossils from Rauenberg are exceptionally preserved, capturing ecological interactions and soft-tissue details rarely available for fossil taxa. The fishes are particularly informative. Among the sharks, *Carcarhias gustrowensis* is known from a pregnant female containing eight embryos in the reproductive tract (Hovestadt and Hovestadt-Euler, 2010), while the holotype of *Triakis kelleri* is preserved as the stomach contents of a carcharhinid shark (Hovestadt and Hovestadt-Euler, 2002). One specimen of the bird *Rupelornis* is preserved with two shark teeth that probably stuck in the soft tissue of the carcass and either indicate direct predation or scavenging (Mayr et al., 2002).

Many of the teleost fishes also preserve gastrointestinal contents. All macroscopic gut contents identified preserve the remains of other fishes. Piscivorous fishes in the assemblage include the aulostomids *Frauenweilerstomus* and *Aulostomus*, as well as *Palaeogadus*, *Palaeorhynchus* (Fig. 7I), *Propercaria* sp. (Fig. 6L), trichiurids, scombrids (e.g., *Sarda*, *Scomberomorus*; Fig. 7H) and carangids (e.g., *Seriola*,

*Archaeus*). Some of the smallest scombrids (30 mm in total length) preserve other fishes in the digestive tract. Particularly noteworthy is a number of specimens of *Archaeus* (7 individuals) preserved with *Oliganodon* partially swallowed, emphasizing that these two common genera encountered each other fairly often and were not spatially or temporally segregated. A specimen of *Carcarhias gustrowensis* is interpreted as having myliobatid and chimaeroid spines embedded in the jaw cartilages (Hovestadt and Hovestadt-Euler, 2010). In addition to gastric contents, a single specimen of *Lepidopus*, as well as several scombrids, have phosphatic cololites (intestinal casts) preserved in the posterior abdominal region; these occasionally contain externally visible fish scales (e.g., SMNS 87457/297).

Stomach contents consisting of a large mass of fish bones are preserved in the fossil loon *Colymboides? metzleri* (Mayr, 2004b), and the holotype of the turnicid *Turnipax oechslerorum* contains gastroliths (Mayr and Knopf, 2007a). A cheloniid turtle also preserves unidentified intestinal contents (Alexander and Frey, 2010).

One of the cheloniids shows evidence of colonization by balanomorph barnacles during its lifetime (Alexander and Frey, 2010). Barnacles are filter-feeders that are attached to a hard substrate, which can be either rocks or larger animals. The isolated specimens either fell off a dead turtle, a marine mammal, such as the dugongid "*Halitherium cf. schinzi*", or driftwood in the case of the goose barnacles. The barnacles attached to the turtle carapace represent the oldest record of sea-turtle fouling balanids in the fossil record, a biological interaction that has otherwise only been recorded from the Miocene (Harzhauser et al., 2011; Hayashi et al., 2013).

The leaf remains are often strongly infected by fungi. The cuticles show both hyphae and fructifications. Often the stomata are masked by fungi that obviously invaded the leaves (Fig. 3E). Fungal infection and growth started shortly prior to or after abscission, during the transport of the leaf but prior to deposition.

Several of the fishes preserve color patterns (e.g., *Microcanthus* sp.; Micklich and Parin, 1996), and even more common is preservation of retinal pigments (Figs. 6M, 7C–E, K). Some of the keratin plates in both the SMNK cheloniids are preserved as a bacterial crust (see Martill, 1987; Wuttke, 1996). Except for those of the procellariiform *Rupelornis*, most bird skeletons are strongly dissociated, which is especially true for small land birds. Although soft-tissue preservation appears to be rare, a specimen of *Rupelornis* (SMNS 85947/1) shows preservation of feathers; an isolated feather is also known (SMNS unnumbered).

### 6.2. Paleobiogeography

#### 6.2.1. Marine

Numerous authors have postulated a marine connection during the Rupelian between the Paleogene North Sea and the Paratethys to the South via the Upper Rhine Graben (but see Berger, 1996, who questioned the existence of a southern connection). The southern connection is hypothesized to have passed through either the Bresse and Rhône Valleys and the Raurachian Depression (Doebl and Teichmüller, 1979; Sittler, 1992; Weiler, 1952, 1956) or via a narrow straight along the uplifting Alps (Büchi, 1983; Spiegel et al., 2007). Berger et al. (2005a, 2005b) identified three transgressive events during the Rupelian and did not exclude the existence of a marine connection between the North Sea, the Upper Rhine Graben, and the Paratethys during the deposition of the Hochberg Member (nannoplankton zones NP 21–23) (Fig. 1D). Based on the lateral continuity of the Froidefontaine Subgroup, Sissingh (2003) also concluded an intermittent North-South marine connection existed during the Rupelian, via the Hessian Depression to the North. The existence of a North-South marine connection during the early Oligocene has been supported based on calcareous nannoplankton (Martini, 1982; Martini and Müller, 1971), fossil fishes (Micklich, 1998), and sedimentological markers (Kuhlemann and Kempf, 2002).

Consistent with a connection to the North Sea, the calcareous nanno-plankton flora corresponds to the Zone NP 23 of Northern Germany, but in the Rauenberg section *Reticulofenestra dictyoda* and *R. scissura* are less abundant. The foraminiferal fauna agrees with the fauna in the Hochberg Member of the Bodenheim Formation of the Mainz Basin. The dinoflagellate *Tectatodinium pellitum* is also found in the Bodenheim (Hochberg and Rosenberg Members), Alzey, and Stadecken Formations of the Mainz Basin (Pross, 1997).

The molluscan species and genera identified at Rauenberg are all known from coeval and neighboring deposits in Germany (Mainz Basin) and Belgium (e.g., Marquet, 2010; Neuffer, 1973, 1984). The molluscan fauna of Rauenberg appears to be much less diverse than those of coeval localities, however this may be biased by the small number of specimens recovered.

The paleobiogeography of the fish fauna of the Wiesloch-Rauenberg Tertiary block was first considered by Weiler (1931). More modern revisions suggest that, aside from some northern elements, the Rauenberg fish fauna is very similar to that of localities in the eastern Paratethys (Micklich and Parin, 1996; Pharisat and Micklich, 1998). Centriscids generally are typical for the Red Sea and Indo-Pacific; *Leiognathoides* ["*Equula*"] *altapinna* is described from the lower Oligocene (Rupelian) of Allschwil in Switzerland (Weiler in Hess and Weiler, 1955), as well as from the lower Oligocene of the North Caucasus (Bannikov and Parin, 1997); *Anenchelum angustum*, *Palaeorhynchus glarisanus* and *P. zitteli* are reported from the lower Oligocene of Canton Glarus, Switzerland (Furrer and Leu, 1998; Monsch and Bannikov, 2012); *Syngnathus incompletus*, *Repropca sabbai*, *Propercaria rebeli*, and *P. pietschmanni* are known from the Rupelian of Sulsănești-Muscel in the Romanian Carpathians (Bannikov, 1991; Cosmovici, 1887; Příkryl et al., 2014). *Oligosphenopsis gracilis*, *Abadzhekia marinae*, *A. tarletskovi*, *Auxides cernegurae*, *Pinichthys pulcher*, and *Rybapina caucasica* are typical elements of the upper Eocene (Kuma Horizon), the lower Oligocene (Psheka Horizon), as well as for the Chattian of the northern Lower Caucasus (Bannikov, 1988, 1995; Bannikov and Parin, 1997; Monsch and Bannikov, 2012).

As with the fishes, the cheloniids show paratethyan affinities: "*Chelonia*" *ginneri* is known only from the Upper Rhine Graben locality of Flörsheim (Wegner, 1918), whereas *Glarichelys knorri* is known from Glarus, Switzerland and several localities in the Eastern Paratethys (Winnica, Ukraine; Caspian Sea region: Aslanova et al., 1979; Gray, 1831, Mlynarsky, 1959).

Based on foraminiferal assemblages, Grimm (1994) suggested a N-S-directed current system predominated in the Upper Rhine Valley marine strait during deposition of the Hochberg Member. The originally northerly current switched to a southerly current during the later Rupelian, concurrent with deposition of the Meletta Beds (Grimm, 1994; Spiegel et al., 2007). This north to south current direction is consistent with the North Sea affinities of the plankton in the Hochberg Member. An ecological filter at the southern opening has also been invoked to explain the discrepancy between the invertebrate and vertebrate faunas (Spiegel et al., 2007).

## 6.2.2. Terrestrial

Several Oligocene floras are known from marine deposits along the western and southern coasts of ancient Europe (Fig. 1D). In the Rhine Graben, the flora of Flörsheim (Mainz Basin), also dated to NP 23, has been recently revised (Kvaček, 2004). The flora of Rauenberg closely resembles that of Flörsheim, both with regard to the depositional facies, floristic composition and the fact that numerous species are known from only one or few specimens (Suppl. Tables 1–2). The most remarkable similarities are the presence of the cycad *Ceratozamia floersheimensis*, *Sloanea*, and the thus-far oldest occurrences of *Laurus abchasica* and fan and feather palms in both assemblages. Deciduous woody taxa are diverse neither in Flörsheim nor in Rauenberg, but in the former locality single leaves document the presence of *Carpinus*, *Ostrya*, and *Rosa*, while in the latter these have not been detected.

Only a single leaf of probable Betulaceae affinity and a winged fruit of *Betula* are documented. While nearly absent from Rauenberg, three species of Fagaceae are recorded from Flörsheim, among which *Trigonobalanopsis rhamnoides* is rather common. The differences between the sites may partly be related to more favorable depositional conditions for terrestrial plants in Flörsheim than in Rauenberg. It is remarkable, however, that palm remains are more diverse and abundant in Rauenberg than in Flörsheim. At each site, numerous cryptic taxa occur. The plant assemblage of Flörsheim is classified to the floristic complex Nerchau-Flörsheim (Kvaček and Walther, 2001).

Along the northern Paratethys coast, the upper part of the Tard Clay Formation, mainly the sites Budapest and Eger-Kisege, Hungary (Hably, 1992; Kvaček and Hably, 1998), are also dated to NP 23. This material is less suitable for cuticle studies than that of Rauenberg or Flörsheim, which impairs comparisons. Rauenberg (and Flörsheim) share the occurrence of *Ceratozamia floersheimensis*, *Daphnogene*, *Engelhardia*, *Laurophyllo*, *Platanus neptuni*, *Sloanea*, and the conifers *Pinus*, *Taxodium*, and *Tetraclinis salicornioides*, as well as the extremely low diversity of deciduous woody angiosperms, with the flora of the Tard Clay. Rauenberg and the flora from the Tard Clay Formation share rare records of *Craigia* fructifications. Rauenberg differs from the Hungarian flora among others by the presence, diversity (5 species), and abundance of palm leaf fragments as well as by the absence of taxa characteristic of Eocene and early Oligocene floras such as *Chamaecyparisites hardtii*.

Further east, the plant assemblage from the surroundings of Linz, Austria (Kovar, 1982), recently dated to the earliest Miocene (Aquitanian: Grunert et al., 2010), shares several taxa with Rauenberg, such as Lauraceae (*Daphnogene*, *Laurophyllo pseudoprinceps*, *L. acutimontanum*), *Platanus neptuni*, *Engelhardia*, *Pinus*, *Tetraclinis salicornioides*, and *Taxodium*. Furthermore, an as-yet undescribed feather palm also from the area of Linz and now stored in the collections of the Vienna Natural History Museum indicates similarities to the flora from Rauenberg (J. Kovar-Eder pers. observ.). The Linz flora differs from that of Rauenberg in the presence of several Fagaceae species (deciduous and evergreen) and rather common twig fragments of the conifer *Cunninghamia*. Fan palms are present from Linz but their remains are rare. Though deciduous woody angiosperms from Linz are neither common nor diverse and, moreover, poorly preserved, *Acer*, *?Alnus*, *Fagus*, *Ulmus*, and *?Zelkova* are documented, unlike at the Rauenberg locality.

The rich early Oligocene record from Northern Bohemia and northeastern parts of Germany includes lowland assemblages often connected to lignite formation, e.g., Haselbach-Serie, Weissenster Basin near Leipzig (Mai and Walther, 1978), and volcanic environments, e.g., Kudratice (Kvaček and Walther, 1998), Bechlejovice (Kvaček and Walther, 2004), Seifhennersdorf (Walther and Kvaček, 2007). The lowland record primarily reflects a wide range of wetland environments ranging from fluvial to swampy habitats, while the plant assemblages, especially from maar deposits, provide insights into the mesophytic (i.e., zonal) vegetation. The much higher diversity of deciduous taxa in the record of Northern Bohemia and adjacent regions is remarkable in comparison to the flora of Rauenberg and other fossil plant sites in Hungary and Austria along the southern and western coasts of ancient Europe. This phenomenon may be partially related to differences in depositional processes, i.e., longer transport possibly connected to higher water energy may be assumed for the plant remains in marine deposits. Nevertheless, differences between the fossil floras from the Rhine Graben and the northern Paratethys region on the one hand and from North Bohemia and northeastern parts of Germany on the other hand are consistent. This implies not only a north-south vegetational gradient (Boreal Province versus Paratethys Province), but the strong floristic affinities of the floras from the Rhine Graben and those from the Paratethys compared to the sites in Bohemia and northeastern Germany also indicate a gradient from more continental regions to environments close to marine coasts along the Paratethys and Rhine Graben seas.

As with the flora, the avifauna shows affinities to coeval coastal localities. The procclariiform *Rupelornis* is known from contemporaneous Rupelian localities in Belgium and from the early Oligocene of France, and appears to have been an abundant seabird in the epicontinental seas covering Europe in the early Oligocene. *Colymboides? metzleri* was likewise reported from the early Oligocene Rupelian stratotype in Belgium (Mayr and Smith, 2013). The landbird faunas are similar to Rupelian sites in Poland, which also yielded *Eurotrochilus* fossils and passerines.

### 6.3. Paleoenvironmental reconstruction

#### 6.3.1. Marine environment

**6.3.1.1. Salinity.** Many sources of evidence support fully marine salinity levels at Rauenberg during deposition of the Hochberg Member. Following Martini (1978: 160), the calcareous nannoplankton *Reticulofenstra dictyoda* is found only in sediments deposited under fully marine conditions, but small specimens of *Reticulofenstra* are also found in layers with reduced salinity. All molluscan species recovered were fully marine. Species that could tolerate reduced salinity (e.g., Neuffer, 1984) have not been recovered. Likewise, echinids can only live under normal saline conditions (e.g., Prothero, 2013). According to the life habits of adult individuals of extant comparative species, all fish taxa from Rauenberg are found in fully marine habitats (Suppl. Fig. 3A). Due mainly to different drift times, Lutz (1997) suggested that the taphocoenosis of terrestrial insects in marine sediments can be a good indication for salinity, and proposed an index using the relative frequencies of the delicate Diptera + Hymenoptera (DH), robust Coleoptera + Heteroptera (CH), and other orders (AO). The respective values for the Rauenberg locality (N.ges. = 221 = 100%; DH = 30 = 13.6%; CH = 179 = 81%; AO = 12 = 5.4%) result in a calculated salinity of S = 0.7%, similar to the present-day Baltic Sea [formula:  $S = (100 - y_{DH} - y_{CH}) * 1.304\% = y_{AO} * 1.304\%$ ]. While this value may not be very reliable, mainly because of the large percentage of undeterminable insects, the result does cast some doubt on the general applicability of the formula.

Following deposition of the Hochberg Member, fully marine conditions are hypothesized to have persisted during the early deposition of the Meletta Beds, followed by increasing brackish influence (Sissingh, 1998).

**6.3.1.2. Water temperature.** As with salinity, an interpretation of subtropical-tropical conditions during the Rupelian is well-supported for Rauenberg. The dinoflagellate *Tectatodinium pellitum* – a neritic species – indicates warm water conditions (after Head and Nøhr-Hansen, 1999). Among the gastropods, both aporhaid and batillariids also prefer warm-temperate to tropical waters (Ozawa et al., 2009; Saul and Squires, 2015). Most extant comparative fish taxa occur in subtropical and/or tropical regions and seas (Micklich and Hildebrandt, 2010; Micklich and Parin, 1996) (Suppl. Fig. 3B). Very few of the taxa from the Unterfeld clay pit indicate colder waters. Exceptions include cods of the genus *Palaeogadus* and left and righteye flounders of the genera *Oligoscophthalmus* and *Oligoleuronectes*. A few others (e.g., ponyfishes of the genus *Leiognathoides*) may represent tropical conditions. Consistent with the other groups, chelonids (Mrosovsky, 1980) and sirenians (Domning, 2001) spend most of their life in tropical and subtropical climatic zones. Isotopic analysis indicates water temperatures of ~13.6 °C winter/17.3 °C summer at 30–40 m depth for the Mainz Basin, 65 km to the north (Walliser et al., 2015).

**6.3.1.3. Depth.** Unlike temperature and salinity, interpretations of water depth at Rauenberg are widely variable. Based on the high percentage of juvenile forms as well as on the excellent preservation of the fishes, Weiler (1966) assumed that the fish fauna of the Wiesloch-Rauenberg Tertiary block was indicative of a shallow, nutrient-rich bay, not far from the shoreline. This hypothesis was accepted in several more recent

publications (Micklich, 2005; Micklich and Hildebrandt, 2010; Micklich et al., 2009). However, Grimm et al. (2002), based on the presence of certain benthic forams, concluded that the fossil-bearing sediments must have been deposited at the bottom of an approximately 200 m-deep marginal basin of the Rhine Graben sea, which was separated from the main seaway by a submarine ridge. Micklich and Hildebrandt (2010) favored the idea of upward transport of the forams (e.g., by upwelling waters) over the downward transport of the fishes because the excellent preservation of many fish specimens excludes long-distance transport from coastal waters into distal deeper ones. The fish fauna lacks typical mesopelagic forms like bristlemouths (Gonostomatidae), lanternfishes (Myctophidae), lightfishes (Phosichthyidae) and marine hatchetfishes (Sternoptychidae), all of which are well-represented in other fossil fish associations of similar age (e.g., Gregová, 2013). Although to be used with caution (for discussion, see Micklich and Hildebrandt, 2010), a comparison with presumably related extant taxa shows that the majority (over 80%) of the Rauenberg forms are indicative of shallow water depths (<50 m). Only a few (~30%) entered depths below 200 m (Suppl. Fig. 3C). Of the latter, some extant representatives (e.g., Gempylidae, Trichiuridae) also approach the surface waters, either occasionally, during their diurnal migration at night, or with upwelling waters (e.g., Nakamura and Parin, 1993). Basking sharks (Fig. 6A) also cruise in shallow coastal waters during springtime. With a presumed relationship to the extant *Sladenia*, the new lophiid genus and species is one of the few taxa which may indicate a depth below 900 m. However, it is also related to the genus *Caruso* from the Eocene of Monte Bolca in northern Italy (Carnevale and Pietsch, 2012), which represents a shallow lagoonal environment (G. Carnevale, pers. comm.). In contrast, halfbeaks of the genus *Hemiramphus*, pipefishes of the genera *Syngnathus* and *Microphis*, and shrimpfishes of the genus *Aeoliscus* (Fig. 6E) occur almost exclusively in superficial water layers, and the tholichthys larvae of butterflyfishes (Fig. 7F) are neritic or oceanic and occur in the uppermost water layers, probably in the neuston (Leis, 1989). The vast majority of the Unterfeld clay pit fish fauna – almost 90% according to excavations conducted in 2009 (Micklich and Hildebrandt, 2010) – consists of small herrings and shrimpfishes, whose extant relatives inhabit shallow waters. In addition, as already pointed out by Weiler (1966), the Rauenberg teleostean fauna is dominated by postlarval, early juvenile and juvenile forms (Fig. 7). Most often, these stages are characterized by lifestyles which differ from those of the adults. Shallow water habitats like seagrass meadows, mangrove swamps, coastal lagoons and estuaries, as well as intertidal zones are well known as nursery grounds for a large variety of fish species, even pelagic species and those inhabiting deeper waters as adults (e.g., Cocheret de la Mornière et al., 2002; Fujii and Noguchi, 1993; Griffiths, 2002; Honda et al., 2013; Hutchings et al., 2002; Laegdsgaard and Johnson, 2001; Sinović et al., 2004). Juvenile stages of Scombridae, Trichiuridae, and Stromateidae are also known from trawling samples in harbor areas (e.g., Charleston Harbor; N. Micklich, pers. observ.). Also, it is important to note the presence of pregnant sharks, which also prefer coastal waters as nursery grounds (McCandless et al., 2007). One individual has been reported by Hovestadt and Hovestadt-Euler (2010), and a second specimen is under preparation at the HLMD (N. Micklich, pers. observ.). These observations are strong arguments for a shallower water habitat rather than for a deeper basin. A minimum water depth below fair weather wave base (~20 m) is supported based on the development of a dysaerobic-exaerobic benthic environment and indicators of a low-energy sedimentary regime (see below). However, the strong dominance of beetles is typical of insect taphocoenoses from deeper water deposits (Lutz, 1997; Wedmann et al., 2009). In addition, sedimentological parameters such as the presence of a distal turbidite in Bed 21 and dolomite rhombs, which form during early diagenesis in water deeper than 100 m in almost every bed, suggest depths greater than ~80 m.

According to the life habits of adults of extant comparative species, most fishes (about 30%) show affinities for reef environments, however

almost 39% have a pelagic lifestyle. Although this was certainly different for post-settlement larvae and juveniles, it nevertheless may indicate an offshore connection. This appears to be substantiated by the presence of tholichthys larvae (these larvae increase in abundance from nearshore to offshore in the Hawaiian Islands (Leis, 1989)) and of some larger individuals of pelagic sharks and scombrids. However, the larvae may not have actively entered the area from offshore, but could have been occasionally washed in by currents or during storms. The sharks and scombrids may either have been washed in as carcasses, or actively entered the area in search of nursery grounds or prey (Weiler, 1966).

The lack of any identifiable aquatic insects (with the exception of the four damselflies) and aquatic insect larva (contra Micklich and Hildebrandt (2010)) suggests that the marine environment was sufficiently distant from the shore that no such insects could be washed in via fluvial sources (in contrast to Frey et al. (2010), who hypothesized that the sediments were deposited in the immediate vicinity of the shoreline close to a river mouth based on the recovery of the terrestrial mammal *Apterodon*). The occurrence of cerambycid and buprestid beetles could indicate that the distance to the shore was not too great, as these families are rarely recorded as flying at high altitudes or over the open sea (Rust, 1999: 274); however only four specimens were recovered. Likewise the possible insect larvae (9 specimens) and three arachnids would exclude aerial transportation and suggest a closer distance to the shore, although rafting on plants remains a possibility.

**6.3.1.4. Productivity.** Blooms of calcareous nannoplankton, mainly of smaller calcareous nannoplankton, occur in the section. Thin calcareous layers are formed biogenetically during mass occurrences of calcareous nannoplankton and benthic foraminifera due to episodic plankton blooms. The benthic foraminifera show the same blooms as the calcareous nannoplankton. Mass layers of the foram *Stilostomella ewaldi* occur on the top of the calcareous laminae because mass occurrences of benthic foraminifera are slightly delayed relative to phytoplankton blooms. Such a concentration of planktonic material is typical for larger estuaries and upwelling zones. In the Upper Rhine Graben, an inland sea, these blooms were probably caused by the appearance of nitrogen (ammonia, nitrite and nitrate) and phosphorus, the latter due to remineralization of organic matter (Grimm et al., 2002).

**6.3.1.5. Substrate (benthos).** We divided the foraminifera into four ecological groups, following Jones and Charnock (1985). Forams which lived semi-infaunally to infaunally are most abundant, free-living epibenthic forms typical of a soft-bottom association are also present. Fixosessile forams are rare because of the lack of hard ground. Both the wedge-shaped irregular echinoids (*Ova* sp.) and the crab *Coeloma* are adapted for burrowing in soft sediment (McNamara and Philip, 1980), which is in agreement with the clayey substrate at the locality. Aporrhaid and batillariid gastropods are also most commonly found on fine-grained sandy mudflats on continental margins (Ozawa et al., 2009; Saul and Squires, 2015). The long spines projecting from the aperture of aporrhais are considered an adaptation to avoid sinking in soft sediment (Gründel et al., 2009).

The good preservation of the coccospheres indicates a lack of bottom currents. A large portion of the bivalves (over 80%) are preserved in life position, as are the echinids, which is another indication of a very calm sedimentary environment with little bioturbation. Taphonomy of the cheloniids suggests in situ decay and disarticulation, and also implies a calm environment with low rates of sedimentation.

Due to a highly specialized diet, the presence of the sirenian "*Halitherium*" is an indirect but highly suggestive indicator of seagrass meadows in the region (Reich et al., 2015; Vélez-Juarbe, 2014). However, given the rarity of sirenian remains and the absence of seagrass macrofossils, these may have been located adjacent to the Rauenberg locality, or "*Halitherium*" had a less restrictive diet than assumed elsewhere.

**6.3.1.6. Oxygen (benthos).** The dinoflagellate *Thalassiphora pelagica* is found in large quantities in the section, indicating poorly oxygenated bottom water (after Pross, 1997). Some of the foram species (*Bolivina beyrichii*, *Bathisyphon tauriensis*, *Cyclammina placenta*, *Stilostomella ewaldi*), the possibly chemoautotrophic bivalve *Thyasira benedeni*, as well as preservation of organic matter in the cheloniids are also indicative of low (dysaerobic to ex aerobic) oxygen conditions. However, endobenthic species are present at relatively high abundance among the bivalves and echinoderms, suggesting long-term oxic conditions for the beds in which they occur. In addition, almost 30% of the fishes are demersal, supporting at least periodic oxygenation of bottom waters. Examples include the eagle ray *Weissobatis*, and the flatfishes *Oligoscophthalmus* (Fig. 7L) and *Oligopleuronectes* (Hovestadt et al., 2010; Sakamoto et al., 2003, 2004). *Deutschschenechelys*, referred to Moringuidae (spaghetti eels), shows morphological traits which indicate a burrowing way of life (Prokofiev, 2012).

### 6.3.2. Terrestrial conditions

**6.3.2.1. Climate.** Numerous plant taxa, such as *Ceratozamia floersheimensis*, Lauraceae, *Sloanea*, and various palms, indicate a largely frost-free temperature regime and warm climatic conditions. The flora of Rauenberg yields many small-leaved taxa (prevailing leaf size class microphyll, i.e., 2.25–20.25 cm<sup>2</sup>) which raises the question of seasonality in precipitation. Climate is estimated based on the closest modern analog for the flora of Rauenberg, which is the southern portion of the modern distribution of evergreen sclerophyllous broad-leaved forests (sensu Wang, 1961) in SE-Asia and on the climatic requirements of the most similar living relatives of taxa such as *Ceratozamia*, *Craigia*, *Platanus neptuni*, and *Sloanea* (Kovar-Eder, in press). The climate may have been comparable to conditions in SE-Asia and North America around 20°N latitude today, and is estimated as follows: mean annual temperature 19–24 °C, mean annual precipitation 1300–1700 mm, mean temperature of the warmest month 28–29 °C, mean temperature of the coldest month 8–14 °C, mean precipitation of the wettest month >230 mm, that of the driest month 18–38 mm, with the warm period being wetter than the cold one. These data indicate seasonality in temperature and precipitation. In other words, the climate estimates correspond to a Cfa climate with tendencies towards a relatively dry season in winter (Cw climate) (transient to tropical monsoon (Am) or tropical winter-dry (Af) climate sensu Köppen, 1936, Peel et al., 2007). Rare and rather small remains of charcoal indicate wildfires probably caused by lightning. It is impossible to estimate frequency or magnitude of such events from these minor remains.

These results differ from those derived for the flora of Flörsheim (mean annual temperatures of 16–18 °C, mean coldest month temperature 6–10 °C, mean warmest month temperature 25–28 °C, mean sum of annual precipitation 1000–1300 mm: Pross et al., 1998). The considerable discrepancies in the estimates may result from the fact that the estimates for Flörsheim are mainly based on the pollen record, which does not allow for a taxonomic resolution below the family or genus level.

Pross and Schmiedl (2002) interpreted changes in the dinoflagellate cysts assemblage as resulting from a long-term paleoenvironmental change from drier to more humid conditions during the deposition of the Fischschiefer. At present, a lack of stratigraphic control prevents our addressing this possibility.

**6.3.2.2. Terrestrial environment.** We include the palynological results of Sittler (1965), since this remains the only available study of pollen from the Hochberg Member. However, these results derive from cores from the Rhine Graben to the west of Rauenberg and no modern revision has been attempted.

The land plants from Rauenberg represent an allochthonous assemblage. The plant material was transported prior to fossilization, as

indicated by fragmentation and fungal degradation, as well as by the fact that predominantly robust plant parts are preserved and numerous taxa are documented by few or single remains. Most likely only a very limited percentage of the source flora is preserved, which hampers attempts to reconstruct the coastal paleoenvironment.

The presence and relative high diversity of *Pinus* (6 species by brachyblasts, 2 by cones), palms (5), and Myricaceae (4) in the macrofossil record may indicate a forest community (coastal pine forests) that possibly developed on sandy soils near the coast. The pollen record includes *Pinus* (2 types, together making up 8.5%) and Myricaceae (4 types), but no palm pollen. *Daphnogene cinnamomifolia* and/or *Laurophylloides pseudoprinceps* possibly also occurred in this community. *Platanus neptuni* may have grown in diverse habitats both zonal and azonal, including coastal environments as well as along streams and on river banks. Along with the robustness of its foliage, this may explain its dominance in the plant assemblage of Rauenberg (Suppl. Table 2). *Carya* and *Populus* may also have been elements of riparian habitats. Pollen of *Betula*, *Pterocarya*, and *Ulmus* indicate a higher diversity of deciduous taxa than the macrofossil record.

We suspect that the majority of the Lauraceae, Ceratozamia, *Craigia*, *Distylium*, *Hydrangea*, *Sloanea*, *Symplocos*, *Engelhardia*, and others (macrofossil record) and *Carpinus*, *Liquidambar*, and *Ulmus* (pollen record) represent mesophytic forests, i.e. zonal vegetation. For species such as, e.g., *Daphnogene cinnamomifolia* or *Laurophylloides pseudoprinceps*, as well as species of *Craigia*, *Myrica*, *Betula*, *Carpinus*, *Engelhardia*, *Liquidambar*, *Pterocarya*, and *Ulmus*, we assume rather wide ecological tolerance, so that they were not necessarily bound to a specific habitat but may have flourished in diverse environments. Both the macrofossil and pollen record lack evidence of nearby swampy environments, including mangroves. In these forests, the number of evergreen woody taxa distinctly exceeded that of deciduous ones. Zoophilous woody angiosperms provided food mainly for insects, and flowering plants with endozoochorous as well as dyschorous fruit vectors offered a diversified diet for the terrestrial fauna (Suppl. Table 2). The Integrated Plant Record Vegetation Analysis (Kovar-Eder et al., 2008), outecology of most similar living relatives as well as the sociological analysis indicates evergreen sclerophyllous broad-leaved forests sensu Wang (1961) as the most likely zonal vegetation type (Kovar-Eder, in press).

Most of the landbirds from Rauenberg are small arboreal birds, consistent with the interpretation of a forested coastal environment. Only one presumed predominantly terrestrial taxon has been found, the buttonquail *Turnipax*, which is likely to have been a granivorous bird. Idiornithidae, extinct relatives of the South American seriemas which are very abundant in early Oligocene localities of the Quercy fissure fillings in France, are notably absent from Rauenberg (Mayr, 2009b). These terrestrial birds are assumed to have been denizens of open areas, and their absence in Rauenberg can be attributed to the absence of suitable open habitats. Among the insects, the absence of Blattodea and Neuroptera, as well as the rarity of Orthoptera and Auchenorrhyncha weakly supports the interpretation of a warm-temperate and humid forest rather than an arid savannah habitat near the coast. However, no proxies for warm climate (e.g., Mantodea or Isoptera) could be identified among the entomofauna, with a putative earlier record of Mantodea (Monninger and Frey, 2010) having been misidentified.

Based on its elongated bill and presumed hovering capabilities, the hummingbird *Eurotrochilus* was probably nectarivorous, like its extant relatives. The presence of this taxon in Rauenberg implies the occurrence of ornithophilous plants that evolved bird-pollinating morphologies (see Suppl. Table 2). *Oligocolius* was frugivorous, and the trogon and the piciform *Rupelramphastoides* were either insectivorous and/or frugivorous. The presence of these taxa, as well as hummingbirds, is consistent with the interpretation of relatively mild winters, although we cannot exclude the possibility that these birds may have been migratory.

## 7. Conclusions

Although the Rupelian assemblage from Rauenberg is composed predominantly of marine taxa, 95 of 302 taxa currently identified from the locality are terrestrial (31% total, or 48% of taxa represented by macrofossils). Based on new results, we interpret Rauenberg as a fully marine locality, deposited in a moderately shallow, low-energy tropical-subtropical environment. Productivity was high, and seafloor anoxia was intermittently developed. There is no evidence for long-term brackish influence or mangrove swamps, and no direct evidence for the development of seagrass meadows. On land, warm, frost-free but winter-dry conditions permitted the development of prevailingly evergreen sclerophyllous broad-leaved forests and near-coastal pine and palm-rich forests on sandy soils. The marine invertebrate fauna shows more northerly affinities, whereas the vertebrate fauna is distinctly Paratethyan. The Rauenberg locality thus provides a detailed snapshot of Rupelian marine and terrestrial diversity and paleoenvironments spanning a period of rapid environmental change. Comprehensive faunal lists, such as the one presented here, provide important baseline data for further comparisons of diversity or ecological structure between localities from different time slices, as well as between coeval localities from different latitudes or environments.

In spite of exceptional preservation allowing detailed insights into e.g., trophic relationships, some questions remain unanswered. Available material suffers from sampling bias: historical collections focused on spectacular and decorative fossils and as such certain paleoecologically important groups may be absent or, at minimum, underrepresented. A lack of stratigraphic control does not allow an assessment of changing conditions at the locality, for instance involving faunal change through time, the existence of temporary brackish conditions or the relative predominance of oxic vs. anoxic benthic conditions. In addition, the amount of absolute time, and hence changes in sedimentation rate, encompassed by the locality is unknown. New bed-by-bed excavations at the locality, initiated in 2014, promise to address these issues. During the first year of the project >5400 specimens were collected, and accessioning and preparation are ongoing.

## Acknowledgements

Thanks to the Klaus Tschira Stiftung and the municipality of Rauenberg, who financially and logically supported our work at the Unterfeld clay pit. S. Staudt, K.-L. Metzger, and many unnamed student assistants helped with excavations, and H. and A. Oechsler collected a significant amount of material. Thanks to M. Keller and C. Knopf for donation of fossils, K. Weiß for the preparation of some bird specimens, W. Munk (SMNK) for information about the insect material preserved at SMNK, M.C. Grimm for discussion, A. Köthe and T. Schindler for collaboration on micropaleontology, and L. Hetterscheid (WUR) for help in tracking down old literature. Thanks to A. F. Bannikov (Paleontological Institute of the Russian Academy of Sciences, Moscow), G. Carnevale (Dipartimento di Scienze della Terra, Università degli Studi di Torino), and K. A. Monsch (Naturalis, Leiden) for valuable comments regarding the fish fauna. We are indebted to J. Dunlop (MNB) and P. Selden (Univ. Kansas) for information on one arachnid specimen, and to J. Skartveit (NLA Høgskolen, Bergen) for determination of the bibionid dipteres. Thanks to M. Harzhauser and A. Kroh (Vienna) for discussions about balanids and echinoderms. R.B.S. was supported by a doctoral grant from CNPq (Conselho Nacional de Desenvolvimento Científico e Tecnológico, Brazil) (process #245575/2012-0). This paper is dedicated to the late Frank Broghammer (former mayor of Rauenberg) and Klaus Tschira (founder of the Klaus Tschira Foundation GmbH). Without their help and engagement the Unterfeld excavations would not have been possible. M. Voss and an anonymous reviewer provided comments that improved the manuscript.

## Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.palaeo.2016.10.002>.

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