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The Randeck Maar: Palaeoenvironment and habitat differentiation of a Miocene lacustrine system

M.W. Rasser [a,*], G. Bechly [a], R. Böttcher [a], M. Ebner [b], E.P.J. Heizmann [a], O. Höltke [a], C. Joachim [c], A.K. Kern [a], J. Kovar-Eder [a], J.H. Nebelsick [b], A. Roth-Nebelsick [a], R.R. Schoch [a], G. Schweigert [a], R. Ziegler [a]

[a] Staatliches Museum für Naturkunde Stuttgart, Rosenstein 1, 70191 Stuttgart, Germany
[b] Department for Geosciences, University of Tübingen, Sigwartstrasse 10, 72076 Tübingen, Germany
[c] Department of Ecology and Ecosystem Management, Technische Universität München, 85354 Freising, Germany

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ABSTRACT

The Randeck Maar in S. Germany is a well-known fossil lagerstätte with exceptionally preserved fossils, particularly insects and plants, which thrived in and around the maar lake during the Mid-Miocene Climatic Optimum (late Early/early Middle Miocene, mammal zone MN5). We provide the first critical and detailed overview of the fauna and flora with lists of 363 previously published, partially revised, and newly identified taxa. Plant remains are the most diverse group (168 taxa), followed by insects (79). The flora points towards subhumid sclerophyllous forests and mixed mesophytic forests, the former being an indication for the occurrence of seasonal drought. Three main sections can be differentiated for the habitats of the Randeck Maar lake system: (1) Deep- and open-water lake habitats with local and short-termed mass occurrences of insect larvae, amphibians, and/or gastropods, while fish is particularly scarce. The interpretation of the water chemistry is problematic because contradictive palaeoenvironmental indicators for both brackish and freshwater conditions exist. (2) Shallow parts of the lake comprise a narrow reed-belt with insects and gastropods living on the exposed plant stems as well as turtles. (3) Crater slopes and surrounding plateaus were mainly covered by subhumid sclerophyllous to mixed mesophytic forests depending on sun exposition and soil conditions. Horses and other forest-dwellers preferably lived in forested habitats while proboscideans and rhinoceratids occupied more open habitats. Our study also brings up contradictive results that cannot be untangled with the current state of knowledge and thus directions for future studies are discussed.

1. Introduction

Volcanogenic lakes offer outstanding possibilities for palaeontological research because steep crater walls and deep water prevent the system from regular mixing of water. This can cause anoxia leading to high fossil preservation potentials and an exceptional laminated palaeolimnological record (Cohen, 2003; Wuttke et al., 2010). Maar lakes have thus found remarkable scientific interest (e.g., Franzen and Michaelis, 1988; Negendank and Zolitschka, 1993). Among the best studied maar lakes are those from the Central European volcanic belt in Germany (Pirrung et al., 2001), including Eckfeld (Middle Eocene; e.g., Neuffer et al., 1994), Messel (Eocene; e.g., Franzen and Michaelis, 1988; Habersetzer and Schaal, 2004), and Enspel (Late Oligocene; e.g., Wuttke et al., 2010).

Further to the south, the Randeck Maar is of special interest because it was dated to the MN 5 mammal zone (Heizmann, 1983), which corresponds to the late Early/early Middle Miocene. This period represents a time of changing seasonality (Böhme, 2003; Harzhauser et al., 2003, 2010; Kern et al., 2011) and temperature increase, which culminated in the Mid-Miocene Climatic Optimum (MMCO; e.g. Zachos et al., 1994, 2001; Mosbrugger et al., 2005), the last time interval favourable for a thermophilous flora and fauna in Europe. Thus the numerous well-preserved fossils and associated sediments of Randeck Maar may provide deeper insights into biotic developments and interactions during this exceptional climatic period.

This paper re-evaluates published data and museum collection material of the flora and fauna thriving in and around the Miocene Randeck Maar lake and includes new material and stratigraphic logs in order to provide for the first time: (1) a detailed summary of organism groups with respect to taxonomy and palaeoecology, (2) an updated list of taxa, which may increase our knowledge of Miocene biodiversity, particularly the gamma-diversity, and (3) a reconstruction and description of the habitats in and around the lake. A detailed review of previously published studies and the taxonomic inventory is given. The results chapter comprises an evaluation of published taxa, revisions of material from older excavations housed in collections of Staatliches Museum für Naturkunde Stuttgart and University of Tübingen as well as the study of material from new excavations. Based on a compilation

* Corresponding author. Tel.: +49 711 8936 146; fax: +49 711 8936 100.
E-mail address: michael.rasser@smns-bw.de (M.W. Rasser).

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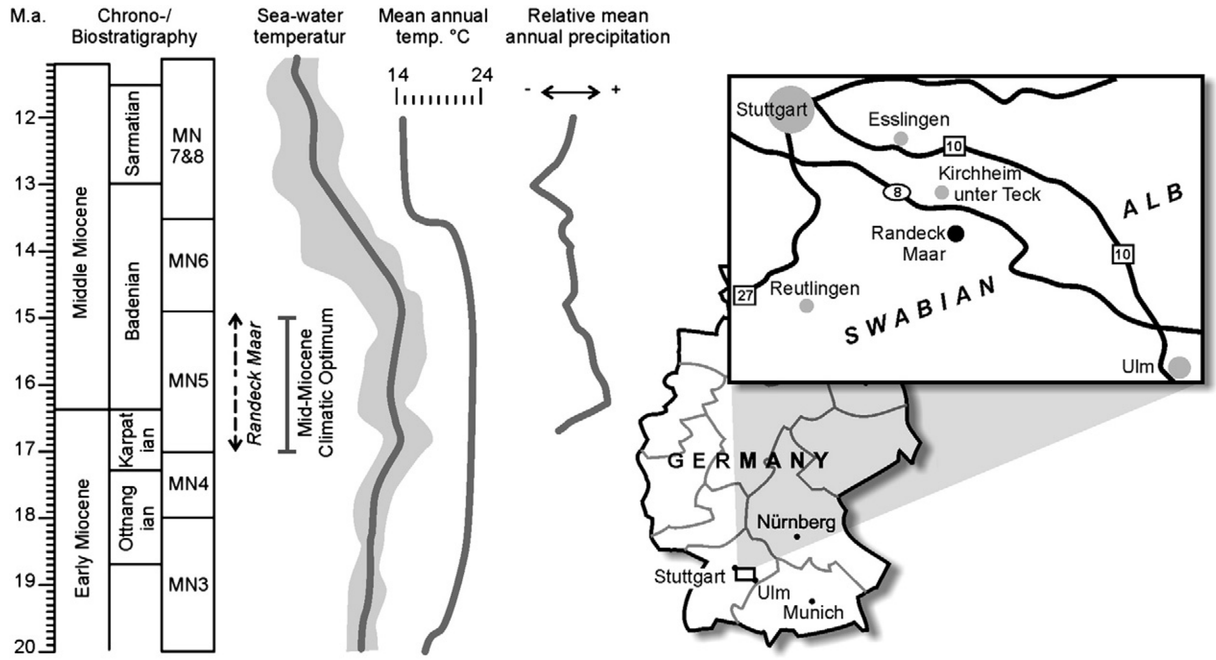


Fig. 1. Stratigraphic correlation of Randeck Maar sediments and location of Randeck Maar in southern Germany. The exact position within MN 5 is unknown. Relative changes of sea-water temperatures after Zachos et al. (2001), mean annual temperature after Böhme (2003), precipitation after Böhme et al. (2011).

of the previously published studies and new results, the palaeoenvironment of the lake system and its habitats are interpreted, including a discussion about water chemistry, palaeoclimate and comparisons with other fossil maar lakes. Finally the feasibility and direction of future studies of this exceptional fossil lagerstätte is discussed.

2. Geology

The Randeck Maar is situated in SW Germany, *c.* 9 km SSE of Kirchheim unter Teck (Fig. 1) and belongs to the Urach–Kirchheim Volcanic Field, which was active during the Early/Middle Miocene (Mäussnest, 1978; Lorenz and Zimanowski, 2000; Lutz et al., 2000). Diatrems of this volcanic field were formed by phreatomagmatic eruptions triggered by the contact between hot magma and groundwater (Lorenz, 1979). Reliable geochronological data are still scarce due to the strong weathering of the volcanic rocks (Lippolt et al., 1973; Krochert et al., 2009) and no radiometric data exist for the Randeck Maar (Schweigert, 1998). Today, the Randeck Maar represents an amphitheatre-like depression with a diameter of *c.* 1200 m, situated at the 'Albtrauf', the northern escarpment of the Upper Jurassic rocks of the Swabian Alb. Less than 60 m of lake deposits are still preserved in the centre of the maar. Calculated from the data of a drilling located in the centre of the Randeck Maar (Krautter and Schweigert, 1991) and the scattered occurrences of lacustrine limestones along the present margins, the maximum depth of the lake is estimated to have been *c.* 130 m.

It is generally assumed that the Randeck Maar was a deep lake with steep slopes (Krautter and Schweigert, 1991; Lutz et al., 2000; and discussions therein). Jankowski (1981) summarised three successive lake stages (Fig. 2). The first one represents the time directly after the formation of the maar, with reworked volcaniclastics, followed by coarse lithoclasts and clays deposited under oligotrophic conditions. The second lake stage, which Jankowski interpreted as brackish and lacustrine-eutrophic, comprises a threefold facies division consisting of bituminous laminites (Dysodil, Blätterkohle) in the central, deepest part of the basin, calcareous and marly laminites in more marginal

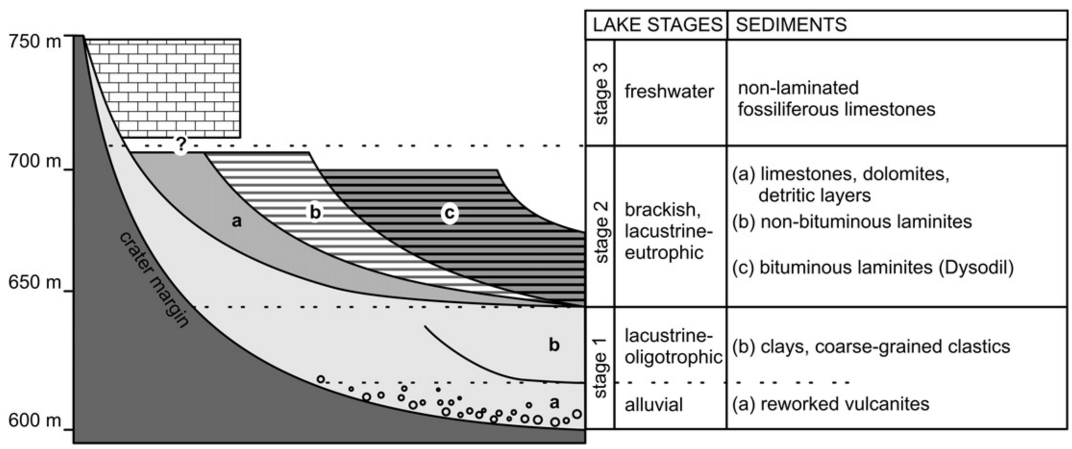


Fig. 2. Idealised cross section through the Randeck Maar and its sedimentary facies types after Jankowski (1981).

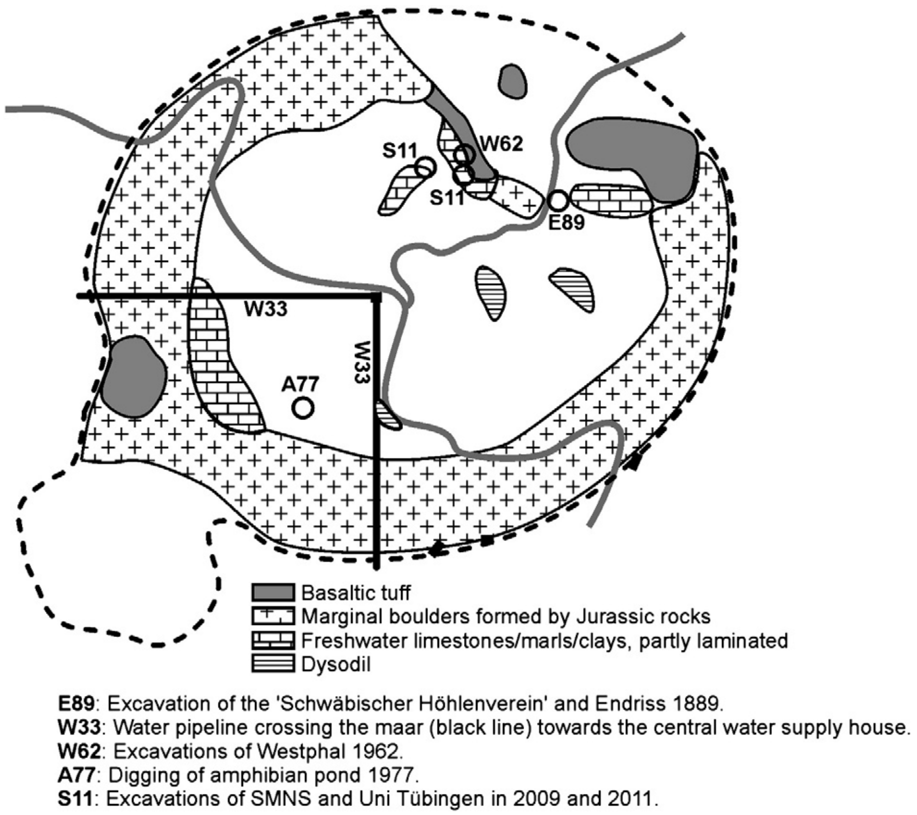


Fig. 3. Geological map of the Randeck Maar and the excavations mentioned in the text.

portions of the basin, and near-shore lake sediments such as intraclastic limestones as well as peloidal dolomites and aragonitic limestones. This last stage comprises poorly bedded freshwater limestones, sometimes with microbial build-ups. This reconstructed facies architecture (Fig. 2) is based on the occurrence of sediments in small and isolated outcrops, which is problematic, because the sediments show clear evidence of synsedimentary slumping as well as Pleistocene to recent massflows and landslides.

In terms of geomorphology, the area of the Randeck Maar lake was only slightly elevated above sea-level (e.g., Kiderlen, 1931; Roll, 1935; Heizmann et al., 2011). The area is characterised by Upper Jurassic rocks, which also represent the bed-rock of the maar. It is karstified since Paleogene times and might have comprised a topographically structured surface similar to its appearance today (Gwinner, 1968; Kuppels, 1981). Due to volcanic activity, however, the karstified landscape was at least partly smoothed by volcaniclastics.

3. Material and methods

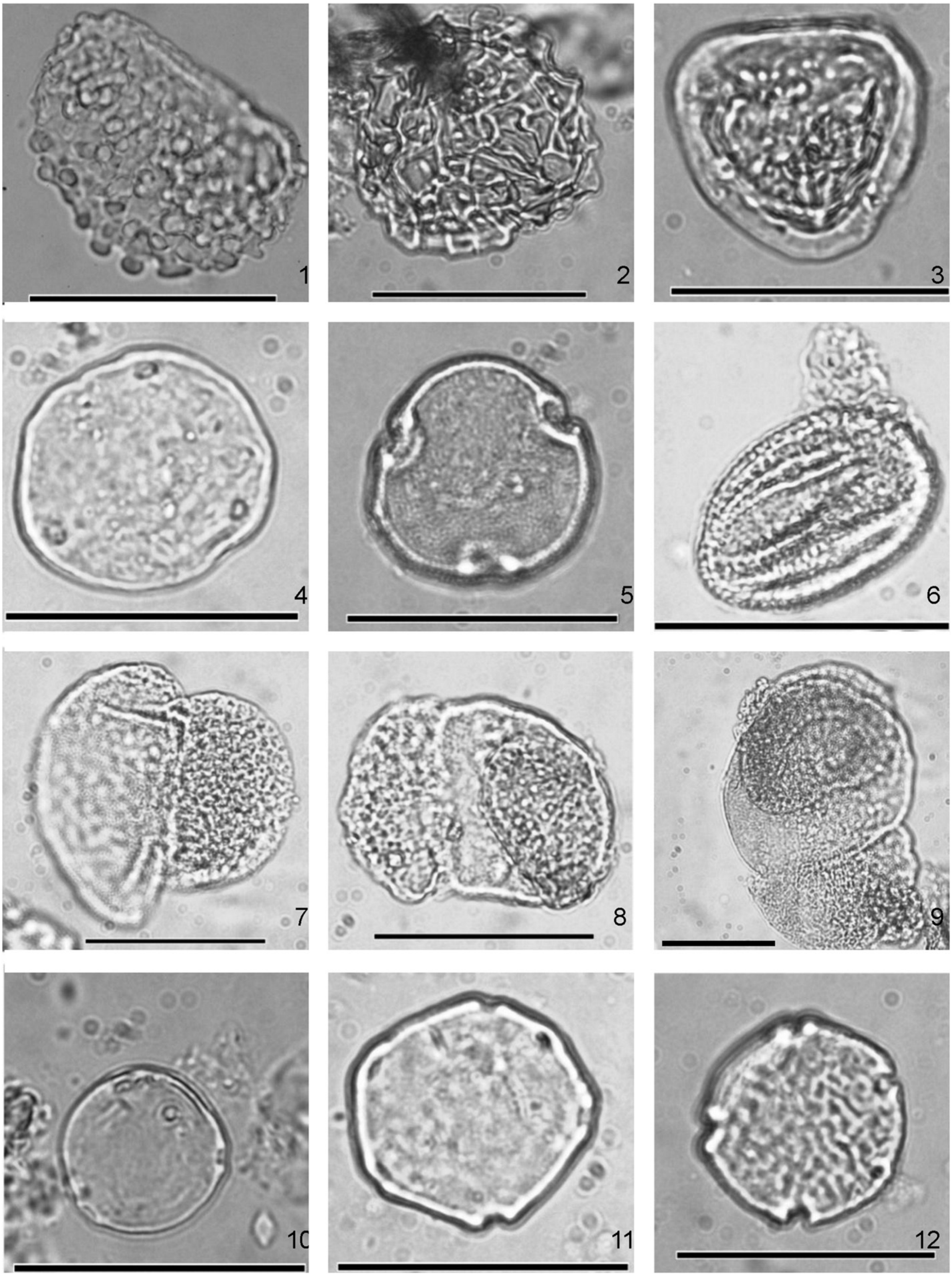
This paper combines the reassessment of (1) published data and (2) material from the collections of the Staatliches Museum für Naturkunde Stuttgart (SMNS) and the University of Tübingen, and (3) new excavations of the SMNS and University of Tübingen in 2009 and 2011 (Rasser et al., 2013). The collecting sites as well as the original position of the collection specimens in the sedimentary sequence are often unknown. Species lists for all groups are provided in the appendices. The state of knowledge differs widely for the single organism groups treated herein and a taxonomic revision was beyond the scope of this study. This is reflected in the different information given in the appendices. For better readability the authors of species are not quoted within the text but are included in the appendices.

Data for microbes, diatoms, ostracods, insects and lower vertebrates are taken from the literature. Published data were re-evaluated for the macroflora, including a rough revision. Newly acquired material was used for the study of pollen, macroflora, gastropods and small mammals. For pollen, four sediment samples were taken from the base of the section (compare Rasser et al., 2013) in a distance between 10 and 20 cm. These samples were prepared by acid hydrolysis and subsequent heavy liquid separation. Palynomorphs were analysed by an Olympus BX50 light microscope at 400× magnification, where at least 300 palynomorphs were determined. No published descriptions existed for the gastropods so far; both collection material and material from the new excavations were used for their identification. For the mammals, collection material from the SMNS and University of Tübingen was re-evaluated.

Fossils from excavations and small temporary outcrops were collected over a long period by private and institutional collectors. The most important excavations from which material is described herein are (Fig. 3): (1) Endriss, 1889 (abbreviated as E89) was an excavation by the Swabian cave society together with K.E. Endriss (1889). The author described a pit with bituminous, marly shale, which is most probably Dysodil (stage 2c in Fig. 2). (2) The construction of a water pipe in 1933 (W33) was only briefly noted by Seemann (1936). The character of the sediment is unknown. (3) In 1962, Westphal excavated a rich fauna and flora in a 2.5 m thick succession (W62 in Fig. 3) of calcareous and marly laminites and clays (Westphal, 1963), corresponding to stage

Plate I. Pollen; the scale bars equal 50 µm (all specimens: SMNSP24198). 1 *Verrucatosporites megafavus*; 2, 3, *Polypodiaceoisporites torosus*; 4, *Caryapollenites* sp.; 5, *Tilia* sp.; 6, *Araliaceoipollenites* sp.; 7., 8, *Pinus* sp.; 9, *Abies* sp.; 10, *Betula* sp.; 11, *Pterocarya* sp.; 12, *Ulmus* sp.

Plate II. Macroflora. 1, Undetermined flower remain (bar 5 mm; SMNSP24197/1); 2, *Sapindus falcifolius* sensu Rüffle (1963), probably *Ailanthus* sp. (bar 4 cm; SMNSP1600/5); 3, *Sideroxylon* (Lythraceae) (bar 1 cm; SMNSP1224/591); 3a, Detail of Fig. 3; 4, *Engelhardia macroptera* (fruit with involcrum; bar 1 cm; SMNSP24197/2); 5, *Salix* sp. fruit (bar 1 cm; SMNSP24197/3); 6, *Ruppia* sp. (bar 2 mm; SMNSP1224/146); 7, *Laurophyllum* sp. twig with leaves (SMNSP24197/4). (see on page 430)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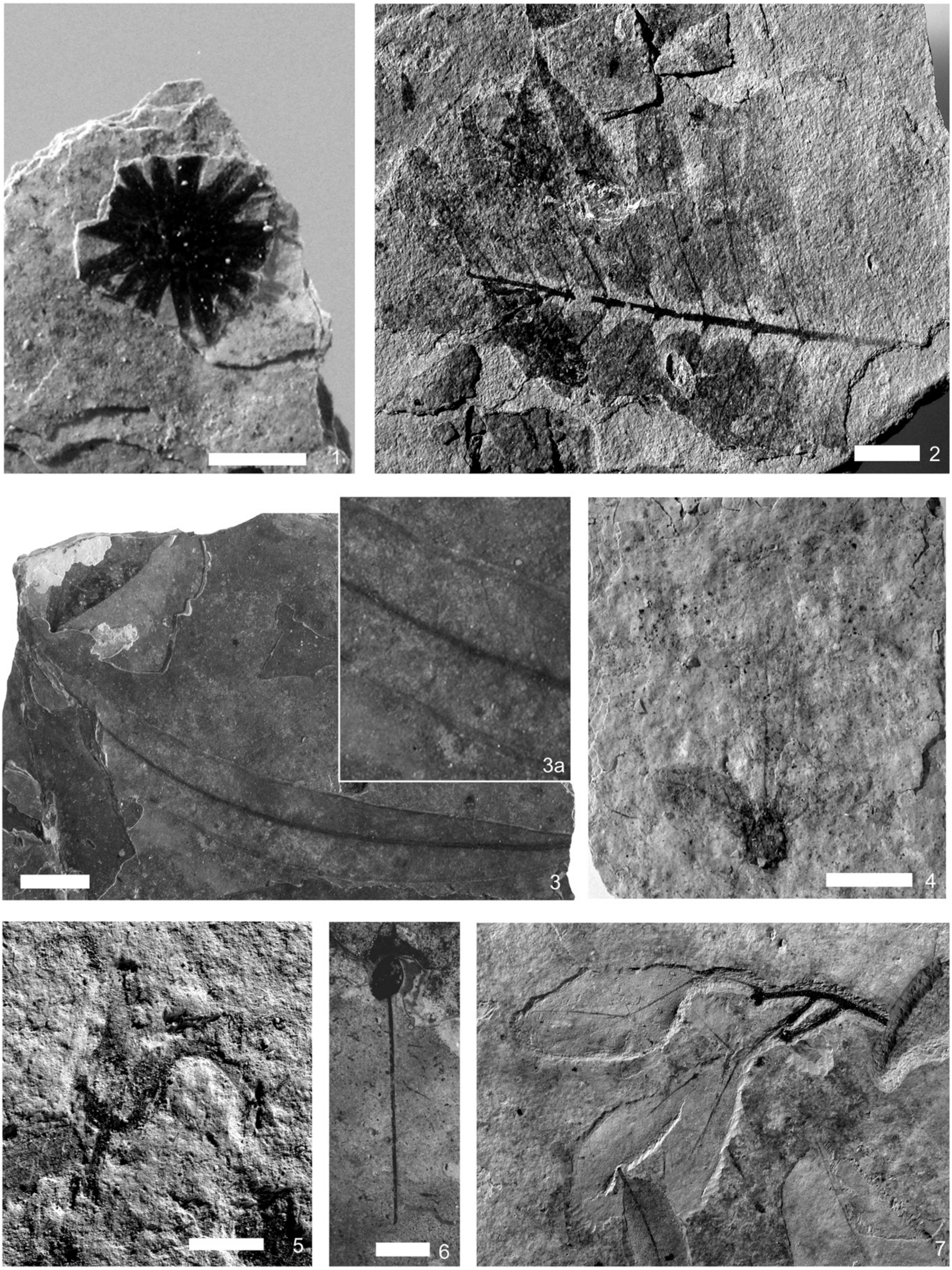


Plate II (*caption on page 428*).

2b in Fig. 2. (4) Amphibian pond 1977 (A77): During the digging of an amphibian pond for natural protection purposes, a 35 cm thick, reddish, marly layer was screen-washed providing mainly remains of small vertebrates (brief note in Heizmann, 1983). The geologic and stratigraphic position within the whole succession is unclear, but it could be part of the non-bituminous laminites (stage 2b in Fig. 2) that were found during the W62 and S11 excavations. (5) Excavations 2009 and 2011 by the SMNS and University of Tübingen (S11): the excavation in the vicinity of W62 found a 7.8 m thick section that comprised dark to light grey and brown laminates, which are composed of marlstones and clay, interrupted by a breccia rich in large vertebrate remains (Rasser et al., 2013), corresponding to stage 2b in Fig. 2.

4. Previous studies

4.1. Carbonate secreting microbes

Jankowski (1981, p. 224) mentioned small “algal” biolithes and peloids, both of which are presumably of microbial origin. These components are restricted to freshwater limestones that occur in marginal positions on top of the Randeck Maar sedimentary succession.

4.2. Diatoms

In her study about diatoms from the Nördlinger Ries, Schauderna (1983) included a list of diatoms from the Randeck Maar (Appendix A), all of which are also known from the Nördlinger Ries. She mentioned two different sampling sites with partly Dysodil-type (“papierschieferartig”) sediments. The coordinates given for the two sites might be wrong, because they point to positions that have never been described to expose lake sediments. Site 1 contains benthic diatoms pointing to increased salinity, while site 2 contains only benthic freshwater species. According to Schauderna, site 2 lies topographically higher than site 1. As discussed in the chapter on geology, however, the stratigraphic correlation of isolated outcrops is difficult due to synsedimentary and post-sedimentary mass transports.

4.3. Plants

First records of the flora from Randeck Maar were published by Endriss (1889). Süss and Mädel (1958) as well as Mädel (1960) focussed on fossil wood. Appendix C provides information on the floristic composition paralleling the records described or mentioned by different authors. The records of *Carapoxylon*, i.e. Meliaceae, *Toona*, is a subject of much controversy because other fossil records of *Toona* in Europe are restricted to the Eocene, while the flora from Randeck Maar is characteristic for the Miocene (Gregor, 1997). The latter author strongly argued for the re-deposition of Meliaceae remains (wood and fruit) from older pre-volcanic deposits.

Monographically, the flora from Randeck Maar (leaves, fruits and seeds as well as pollen) has been studied by Rüffle (1963). He determined numerous leaf taxa including cuticular structures. These slides, however, are today dried completely, biassing a taxonomical revision. Later, Gregor (1986) revised the fruit record pointing out different preservation states, i.e., compressed, partly organically preserved material and uncompressed mineralised fruits of some taxa, including the so-called *Toona*. Schweigert (1998, Fig. 22) figured a well-preserved pinnately compound leaf as *Toona*. Fossil flowers with in situ pollen were first assigned to *Gleditsia* and *Tricolporopollenites wackersdorfensis* and were later revised as the fossil genus and species *Podocarpium podocarpum* (see Plate 2, panel 1) (Liu et al., 2001).

Pollen were studied by Kottik (2002), who concentrated on a qualitative study of one sample including light and scanning electron microscopy, resulting in the identification of 50 different taxa within 24 families (Appendix C).

4.3.1. Integrated plant record (IPR) vegetation analysis and fruit ecology

Mainly based on Rüffle's monograph (1963) and Gregor's (1986) study of fructifications, Kovar-Eder and Kvaček (2007) performed an, at that time, unpublished revision of the macroflora in order to apply the Integrated Plant Record (IPR) vegetation analysis. Appendix C includes this revision and the current update.

Vegetation depends on climate and can therefore serve as a proxy for the regional climate. The IPR vegetation analysis is a semi-quantitative method which takes advantage of all plant organs preserved in the fossil record. The percentages of the broad-leaved deciduous, broad-leaved evergreen, sclerophyllous and legume-type components of zonal woody angiosperms, and the percentage of zonal herbs of all zonal taxa are calculated to assess major vegetation types (Kovar-Eder and Kvaček, 2003, 2007). The IPR vegetation analysis has successfully been applied to the fossil record of the European Miocene/Pliocene (Kovar-Eder et al., 2008; Teodoridis et al., 2009; Teodoridis, 2010; Kvaček et al., 2011). Most recently it was successfully validated by application to modern vegetation in Japan and China (Teodoridis et al., 2011).

Since differences prior to and during taphonomic processes influence the accumulation of fossil plant assemblages, sites yielding different plant organs (foliage, fruits, pollen) were essential to test the IPR vegetation analysis regarding the consistency of the results obtained from fruit, leaf and pollen assemblages. This test has been performed for several European plant sites offering comparable favourable conditions, among them the Randeck Maar (Kovar-Eder and Kvaček, 2007). The results for the Randeck Maar flora are summarised in Tables 1 and 2. Among the leaf and fruit assemblages, the SCL + LEG component surmounts 20% and in the pollen record 19%. When the results from the single organ assemblages from Randeck Maar are merged, subhumid sclerophyllous forests are the most likely vegetation type that may have surrounded this crater lake. Note that pollen data of the Randeck Maar point to more intermediate conditions than the macroflora. It may be caused by the higher probability of far-distance transport which leads to a mixture of different vegetation units and by the lower taxonomic resolution (only to the family or generic level) (Kovar-Eder and Kvaček, 2007).

More recently Palaeogene and Neogene plant assemblages (fruit, leaves, and pollen) were evaluated regarding fruiting ecology differentiating dry and fleshy animal dispersed taxa, anemochorously, autochorously, and hydrochorously dispersed taxa (Kovar-Eder et al., 2012). As a result, the distribution of fruiting types correlates well with the vegetation types depicted by the IPR vegetation analysis. Cluster analysis groups the flora of Randeck Maar together with floras that indicate subhumid sclerophyllous forests or mixed mesophytic forests.

4.4. Ostracods

Among the ostracods, Hiltermann (1980) listed *Eucypris* ? *candonaeformis*, *Candona praecox*, *Candona* sp., *C. steinheimensis*, *C. suevica*, *Cypricercus* sp., *Darwinula cylindrica* and *Metacypris rhomboidea* from the W62 excavation. No further studies concerning ostracods from the Randeck Maar have been published so far.

4.5. Insects

Insects are, besides plants, the most abundant fossil remains from the Randeck Maar site. A bibliography with a wide range of insect references was provided by Schweigert and Bechly (2001). An overview of the insect taphocoenosis was given by Ansorge and Kohnring (1995) and Joachim (2010). Altogether 15 orders have been recorded up to now. While terrestrial insects are rather diverse, aquatic insects are common but show a low diversity. Based on determinations to the ordinal level, flies and midges (Diptera) comprise 38%, ants, wasps and bees (Hymenoptera) 20%, bugs (Heteroptera) 16%, beetles (Coleoptera) 9%, aphids, leafhoppers, cicadas, etc. (Auchenorhyncha

Table 1
Zonal vegetation types as defined by percent of various components of angiosperm taxa (from Teodoridis et al., 2011).

Vegetation formation	Percentage of the BLD component of zonal woody angiosperm taxa	Percentage of the BLE component of zonal woody angiosperm taxa	Percentage of the SCL + LEG components of zonal woody angiosperm taxa	Percentage of the Zonal herb (dry + meso herb) component of zonal angiosperm taxa
Broad-leaved deciduous forests	≥0%			≤30%
Ecotone	75–80%	<30%	20%	<30%
Mixed mesophytic forests	<80%			
Ecotone		30–40%		
Broad-leaved evergreen forests		>40%	(SCL + LEG) < BLE	<25%
Subhumid sclerophyllous forests			≥20%	<30%
Xeric open woodlands		<30%	≥20%	30–40%, meso herb > dry herb up to 10% of all zonal herb
Xeric grasslands or steppe		<30%		≥40%

and Sternorhyncha) 8% and others such as Odonata, Trichoptera and Lepidoptera 9% (Joachim, 2010). Note, however, that it is particularly difficult to reconstruct insect biocoenoses from taphocoenoses, since the taphonomic processes are still poorly understood (Lutz, 1988, 1997; Lutz and Kaulfuß, 2006). Randeck Maar insects are listed in Appendix D.

4.5.1. Terrestrial insects

Midges and flies (Diptera) are the most common group among the terrestrial insects with the majority of Diptera fossils being dark-winged fungus gnats (Sciaridae, Plate 3, panel 1). Several larval and nymph stages of lower Dipterans ("Nematocera") have been found, which are discussed and listed in the section of aquatic insects due to their lifestyle and because adult fossils are rare to absent. The second most abundant group are march flies (Bibionidae; Plate 3, panel 2). In contrast to Messel, which is another famous insect site (Eocene; Wedmann et al., 2010), the predominant genus is *Plecia*, rather than *Bibio*. This difference may be explained by different climatic conditions between the Early Miocene and Middle Eocene. A significant find is that of a signal fly (Platystomatidae — *Platystoma*; Plate 3, panel 3), which is the oldest known representative of this genus. Further dipteran taxa are robber flies (Asilidae), bee flies (Bombyliidae), gall midges (Cecidomyiidae), dagger flies (Empididae), hump-backed flies (Phoridae), big-headed flies (Pipunculidae), hoverflies (Syrphidae), and crane flies (Tipulidae).

Hemiptera comprise about a quarter of the determined insects. Members of both Cicadomorpha and Fulgomorpha are present of the suborder Auchenorrhyncha, such as froghoppers (Cercopidae), cicadas (Cicadidae), Ricaniidae and leafhoppers (Cicadellidae) (Joachim, 2010). aphids (Aphididae), gall-making aphids (Pemphigidae) and jumping plant lice (Psyllidae) are recorded groups of the Sternorrhyncha (Joachim, 2010). True bugs (Heteroptera) are represented both by terrestrial taxa and by aquatic ones (see below). The terrestrial bugs include shore bugs (Saldidae), lace bugs (Tingidae), chinch or seed bugs (Lygaeidae), shield bugs (Cydnidae), and stink bugs (Pentatomidae) (Joachim, 2010; Popov, 1983).

Hymenoptera are the third most common terrestrial insect group at the Randeck Maar site, but mostly preserved in poor condition. An identification beyond the suborder Apocrita is not possible. This group was first revised by Kotthoff (2005). The most frequently represented families by specimen number are ants (Formicidae) with representatives of the genus *Lasius*, *Aneleus*, *Prenolepis* and *Camponotus*, and bees (Apidae). Among the latter, especially the genus *Apis* was extensively described by Armbruster (1938) and Zeuner and Manning (1976). Recently, Kotthoff et al. (2011) revised the honeybees from the Randeck Maar and concluded that most of the species described by former authors are most probably *Apis armbrusteri*. Joachim (2010) reported the first record of a bumble bee (Plate 3, panel 4) from the Randeck Maar site, which was recently described as *Bombus* (*Bombus*) *randeckensis* (Wappler et al., 2012). Further hymenopteran species such as Braconidae, Eucoilidae, Ichneumonidae, Mymaridae and Vespidae are represented by only a few or single specimens.

Beetles (Coleoptera) contribute only by 10% of the insects from the Randeck Maar. The most common group are leaf beetles (Chrysomelidae) and rove beetles (Staphylinidae) such as *Bembidion*/*Tachys*-related species (Schawaller, 1986). Furthermore, species of the Carabidae, Curculionidae and Chrysomelidae occur. In contrast to other localities like Rott or Enspel (Wedmann et al., 2010), the occurrence of rove beetles is higher, comprising about 15% of the beetle fossils. Albeit most of the fossils are poorly preserved, some display striking structural colours and a metallic shine (Buprestidae, Chrysomelidae; Plate 3, panel 5) (Joachim, 2010). The beetles of the families Anthicidae, Buprestidae, Cantharidae, Carabidae and Coccinellidae are only represented by very few specimens (Joachim, 2010). Furthermore, several elytra are preserved, most of them not determinable to the family level.

Thysanoptera (thrips), tiny and slender insects, are common. One family of each suborder is present: Phlaeothripidae within the Tubulifera and Thripidae within the Therebrantia (Joachim, 2010). Termites (Isoptera; Plate 3, panel 6) contribute almost 2% of the whole insect taphocoenosis (Von Rosen, 1913; Armbruster, 1941). Several species have been described, but they seem to be in need of revision (Ansorge and Kohnring, 1995).

Several other terrestrial insect orders were found at the Randeck Maar site, but with only one to nine specimens of each group. They make up less than 0.5% of the whole taphocoenosis. This is the case for barklice (Psocoptera), gryllids and tettigoniids (Orthoptera), Neuroptera represented by a mantidfly of the genus *Mantispa* and by a lacewing of

Table 2
IPR-analysis applied to the flora of the Randeck maar (Kovar-Eder and Kvaček, 2007, Tab. 3).

	Percentage of BLD of zonal taxa	Percentage of BLE of zonal taxa	Percentage of SCL + LEG of zonal taxa	Percentage of zonal herbs of all zonal taxa	Vegetation formation
Leaf	40	31	22	0	Subhumid sclerophyllous forests
Fruit	58	18	24	2	Subhumid sclerophyllous forests
Pollen	45	36	19	12	Broad-leaved evergreen forests
Leaf, fruit, pollen record	47	29	21		Subhumid sclerophyllous forests

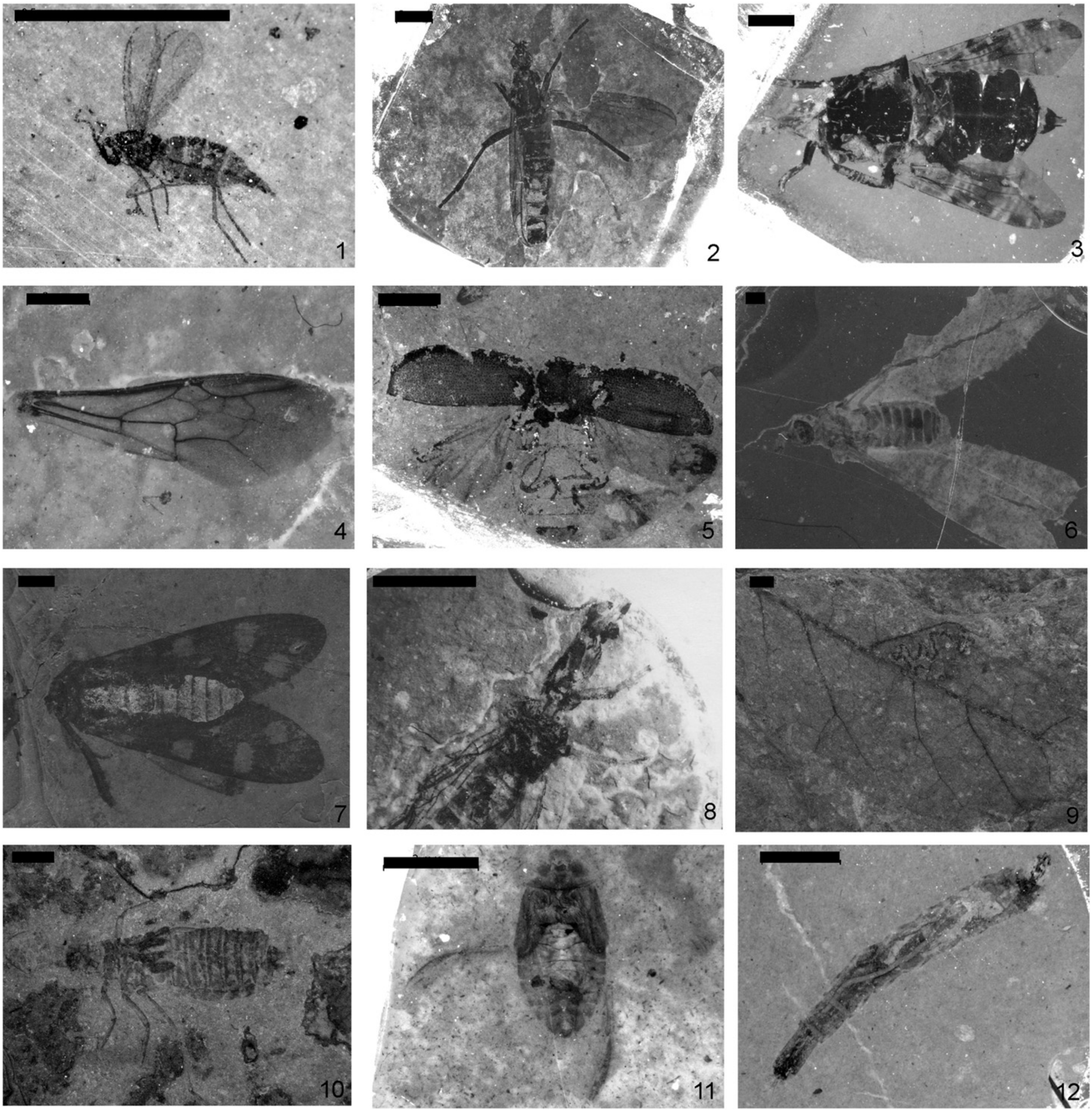


Plate III. Insects. All scale bars equal 2 mm. 1, Sciaridae (SMNS 68000/8); 2, Bibionidae (SMNS 68000/23); 3, Platystomatidae (SMNS 68000/17); 4, *Bombus* (*B.*) *randeckensis* (SMNS 68000/28); 5, Chrysomelidae (SMNS 68000/27); 6, Isoptera (SMNS 68000/21); 7, *Zygaena miocenica* (SMNS 22342); 8, Raphidioptera. The specimen from the SMNS Armbruster collection is lost and only known from this photograph by Armbruster; 9, Leaf fragment with traces of a leaf-miner fly in the upper middle part; 10, Libellulidae nymph; 11, Corixidae (SMNS 68000/31); 12, Stratiomyidae larvae (SMNS 68000/37).

the genus *Osmylus* resembling the extant European species *Osmylus fulvicephalus* (see Joachim, 2010), butterflies (Lepidoptera) such as Zygaenida (Plate 3, panel 7), scorpionflies (Mecoptera) and earwigs (Dermaptera). The sole earwig find shows only the most distal segments of the abdomen and the forceps, which is typical for this group and based on the instability of the connection of certain abdominal segments (Rust, 1999). Unfortunately, a fossil snakefly (Raphidioptera; Plate 3, panel 8), collected by Armbruster in the 1930s, is lost over the years and its only evidence are four photographs taken by Armbruster himself, which do not show genus relevant identification characteristics, but are definitely collected from the Randeck Maar site. Leaf miner trails have only been described in a few cases: One of a leaf-miner fly in an unidentified leaf (Hering, 1930) and a second one by Bleich (1988).

4.5.2. Aquatic insects

Just a few specimens of adult damselflies and dragonflies occur, but nymphal stages (Plate 3, panel 10) are abundant and even form mass occurrences (Joachim, 2010). The nymphs comprise a remarkable phenotypic variety and thus may represent different species, but this aspect has not yet been studied. Even egg-sets of damselflies were found on angiosperm leaves, which belong to the Lestidae-type and Coenagrionidae-type, resembling the extant Zygoptera families (Hellmund and Hellmund, 2002). The order Diptera is represented by larvae and pupae of the "nematoceran" families of the Chironomidae, Culicidae and Chaoboridae. In some of the fossils the syphon tube is still visible. The larvae of the family Stratiomyidae (Plate 3, panel 11) are remarkably numerous (Joachim, 2010), partly represented by the genus *Eulalia* (Hein, 1954). Besides Odonata and soldier fly nymphs, the nymphs of Corixidae (Heteroptera; Plate 3, panel 12) are the third most abundant aquatic group, but adults are absent. Other aquatic bugs are Notonectidae. Among the beetles, Dytiscidae, Dryopidae and Hydrophilidae inhabited the waters of the former lake. Mayflies (Ephemeroptera) or stoneflies (Plecoptera) are completely missing. In contrast to other palaeolakes like e.g. Enspel (Wedmann et al., 2010) or Messel (Lutz, 1987), the Randeck Maar is very poor in fossil remains of caddisflies (Trichoptera), and also portable cases have not been recorded.

4.6. Spiders

Spider remains are rare at the Randeck Maar site. Schawaller and Ono (1979) described three species from two families, wolf spiders (Lycosidae) with the new species *Lycosa miocaena* and *Lycosa lithographica* and jumping spiders (Salticidae) with the new species *Euophrys randeckensis*. Additionally, Wunderlich (1985) mentioned a new crab spider species (Thomisidae; *Palaeoxysticus extinctus*) and he further doubts that *L. miocaena* belongs to the genus *Lycosa*, but rather to *Arctosa*. At least 40 further, still unstudied specimens are stored in the SMNS Armbruster collection (Joachim, 2010). All of the described taxa from the Randeck Maar are stalking or ambush predators. None of them built webs for catching prey.

4.7. Gastropods

Only one publication of Seemann (1926) deals with gastropods, but they are only listed without further comments.

4.8. Fish

The fish fauna of Randeck Maar lake comprises only one very small species of toothcarp (killifishes, Cyprinodontiformes, Plate 5, panel 1). 20 skeletons were found in a single layer of calcareous laminated beds; three further specimens were collected close together in a silicified laminated layer. Beside these skeletons, no further remain has been found in any of the Randeck Maar deposits. It is thus assumed that both occurrences come from the same bedding plane.

The small skeletons (length up to 21 mm) show great similarities with *Prolebias malzi* from the Late Oligocene and Early Miocene of the Upper Rhinegraben area, but their otoliths point to *Prolebias weileri* from the Early Miocene (MN 4b and 5) of Switzerland and S Germany (Illerkirchberg near Ulm; Gaudant and Reichenbacher, 2002; Gaudant, 2009). Since only otoliths but no skeletons of *P. weileri* are known so far, Gaudant and Reichenbacher (2002) determined the Randeck Maar fish species as *P.* aff. *weileri.*

Recently, Costa (2012) supposed a close relationship between *Prolebias malzi* and two further fossil species to the genus *Pantanodon* (Poeciliidae, Procatopodinae). Gaudant (2013) came to the same results and, based on skeletal characters, introduced the new genus *Paralebias* for these three mentioned species and the Randeck Maar cyprinodont. While *P. malzi* nowadays belongs to this new genus, the position of *Prolebias weileri* remains uncertain due to the limited preservation of solely otoliths. According to Gaudant (2013), the Randeck Maar species is named here as *Paralebias* aff. *weileri*. *Paralebias* is a member of the subfamily Procatopodinae (family Poeciliidae, Gaudant, 2013), which are egg-laying tooth carps today living in Africa.

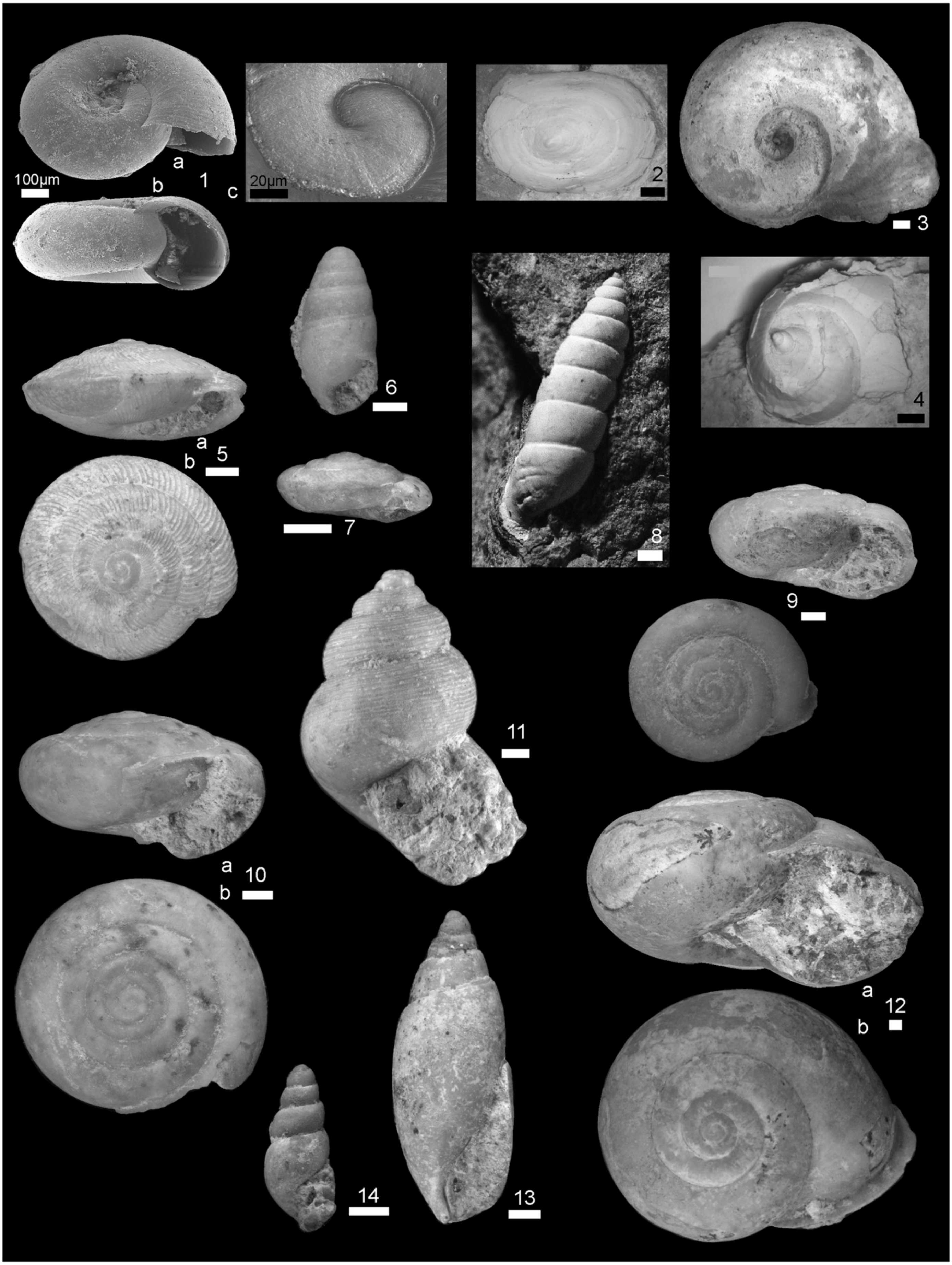
4.9. Amphibians

Amphibians are the most abundant aquatic vertebrates of the Randeck Maar, both with respect to the number of species and specimens (Appendix F). Remarkable is the high abundance of *Albanerpeton inexpectatum* (Plate 5, panel 9; around 300 cranial and postcranial bones; Böttcher, 1998; Wiechmann, 2003). The enigmatic amphibian extinct clade Albanerpetontidae is known from the Middle Jurassic to the Pliocene. In S. Germany it is known to occur from the Early Oligocene to the Early Miocene (Karpatian/Late Burdigalian, MN 5; Gardner and Böhme, 2008). Due to the fossorial life habit of albanerpetontids, in S. Germany their fossil remains are mainly found in fissure fillings, less frequently in floodplain deposits, and only once in lacustrine facies (Gardner and Böhme, 2008). This makes the occurrence of Randeck Maar exceptional. Generally, only isolated bones are known from *A. inexpectatum*. The Randeck Maar findings are restricted to the A77

Plate IV. Gastropods. Scale bars 1 mm, unless specified. 1, *Gyraulus kleini* (SMNS100789); 2, *Ferrissia deperdita* (SMNS100790); 3. *Planorbarius* cf. *mantelli* (SMNS100791); 4, *Lymnaeidae* indet. (SMNS100792); 5, *Caracollina phacoides* (SMNS100793); 6. *Cochlicopa subrimata* (SMNS100794); 7, *Discus* sp. (SMNS100795); 8, *Granaria* ?*schuebleri* (SMNS100796); 9, *Klikia coarctata* (SMNS100797); 10, *Leucochroopsis kleini* (SMNS100798); 11, *Pomatias conica* (SMNS100799); 12, *Pseudochloritis incrassata* (SMNS100800); 13, *Pseudoleacina eburnea* (SMNS100801); 14, Subulinidae indet. (SMNS100802).

Plate V. Lower vertebrates. Scale bars 1 cm, unless specified. 1, *Paralebias* aff. *weileri*, skeleton in left lateral view (SMNS 58648); 2, *Palaeopleurodeles hauffi*, probably larval stage of *Chelotriton paradoxus*, skeleton in dorsal view (SMNS 50168); 3, *Chelotriton paradoxus*, skull with cranial part of column, dorsal view (SMNS 80672); 4, *Ichthyosaura randeckensis*, skeleton in dorsal view (SMNS 95461); 5, *Palaeobatrachus hauffianus*, skeleton of tadpole, dorsal view (SMNS 80015). 6. *Palaeobatrachus hauffianus*, skeleton in dorsal view, distal parts of legs complemented (SMNS 80175); 7, Pelobatidae indet., tadpole, skeleton in dorsal view (SMNS 80211); 8, Ranidae indet., laval stage near end of metamorphosis, skeleton in dorsal view (SMNS 58655); 9, *Albanerpeton inexpectatum*, dentalia in dorsal view (SMNS 57769/1, /2); scale bar 1 mm; 10, *Diplocynodon* cf. *ungeri*, heavily crushed complete skull, (SMNS 95856); Scale bar 5 cm; 11, "*Testudo*" sp., entoplastron with right epiplastron, vetral view (96027); 12, *Chelydropsis* sp., peripheral 2 right, ventral view, area between the black lines = lateral process of the nuchal, diagnostic for the genus (SMNS 96309); 13, *Clemmydopsis* sp., right peripheral 3, ventral view (SMNS 96308); 14, *Ptychogaster* sp., left peripheral 7, ventral view (SMNS 96307). (see on page 436)

Plate VI. Small mammals. Scale bars 1 mm. 1, cf. *Allosorex gracilidens*, left m1, occlusal view (SMNS 43375 A4); 2, *Spermophilinus besanus*, right M1/2, occlusal view (SMNS 43380 G1); 3, *Palaeosciurus sutteri*, right D4/P4, occlusal view (SMNS 43380 F3); 4, *Glirulus* aff. *conjunctus*, left M1, occlusal view (SMNS 43384 P4); 5, *Bransatoglis cadeoti*, right M1, occlusal view (SMNS 43384 Q15); 6, *Glirudinus undosus*, right M1, occlusal view (SMNS 43384 Q8); 7, *Muscardinus* aff. *sansaniensis*, left M1, occlusal view (SMNS 43384 P6); 8, *Keramidomys thaleri*, left m1, occlusal view (SMNS 43382 E2); 9, *Keramidomys thaleri*, left M1/2, occlusal view (SMNS 43382 O4); 10, *Eomyops* aff. *catalaunicus*, left m1, occlusal view (SMNS 43382 E13); 11, *Eomyops* aff. *catalaunicus*, left M1/2, occlusal view (SMNS 43382 O13); 12, *Democricetodon gracilis*, left m1, occlusal view (SMNS 43383 A1); 13, *Democricetodon gracilis*, left M2, occlusal view (SMNS 43383 K1); 14, *Democricetodon mutilus*, right m1, occlusal view (SMNS 43383 B8); 15, *Democricetodon mutilus*, left M2, occlusal view (SMNS 43383 K7); 16, *Eurmyarion* cf. *weinfurteri*, right m1, occlusal view (SMNS 43383 B9); 17, *Neocometes* aff. *similis*, right m1, occlusal view (SMNS 43383 B11); 18, *Neocometes* aff. *similis*, right M1, occlusal view (SMNS 43383 H11); 19, *Anomalomys minor*, left m1, occlusal view (SMNS 43383 A13); 20, *Anomalomys minor*, left M1, occlusal view (SMNS 43383 G13); 21, *Prolagus oeningensis*, right p3, occlusal view (SMNS 43378/2). (see on page 437)



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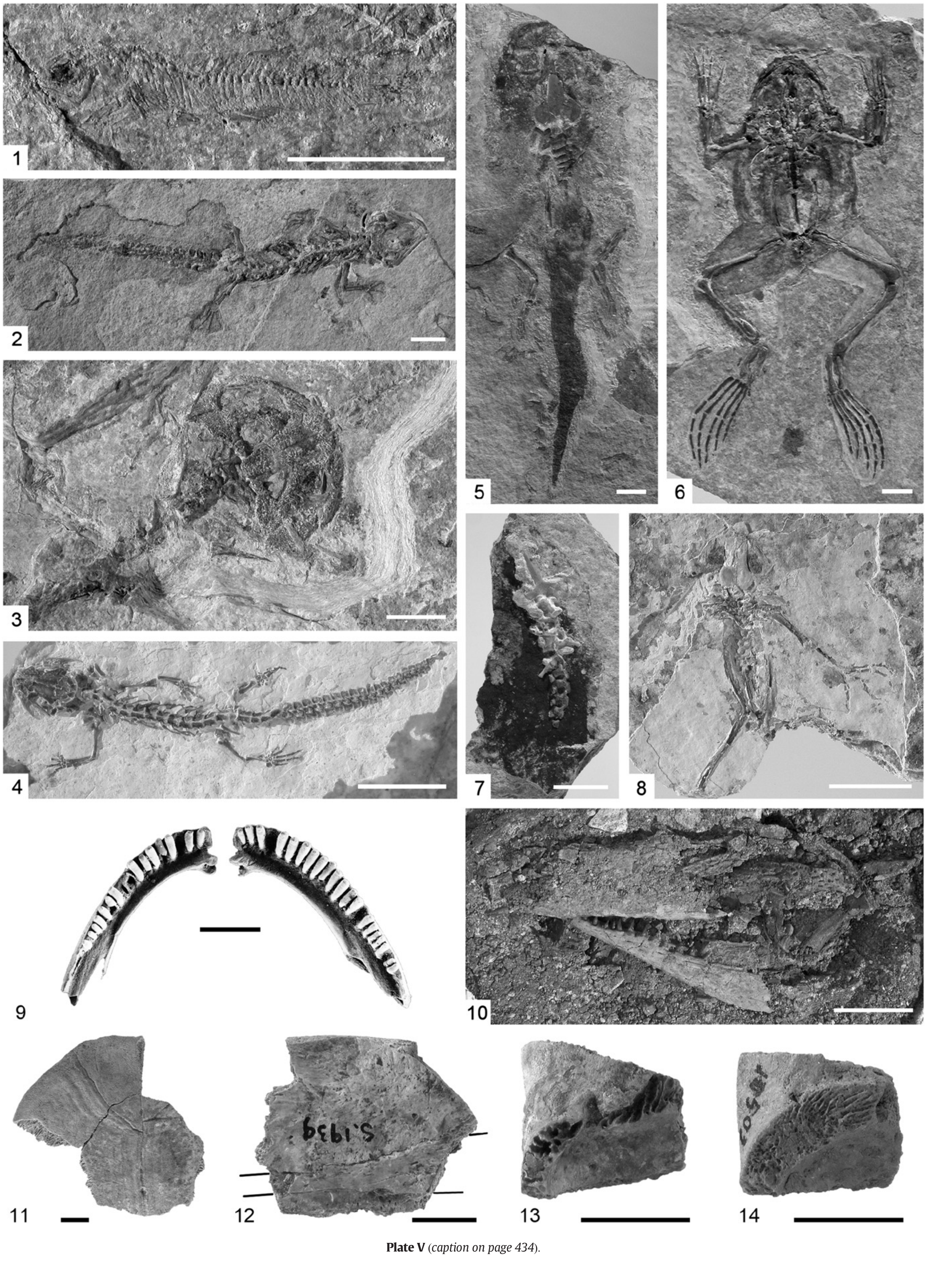

Plate V (*caption on page 434*).

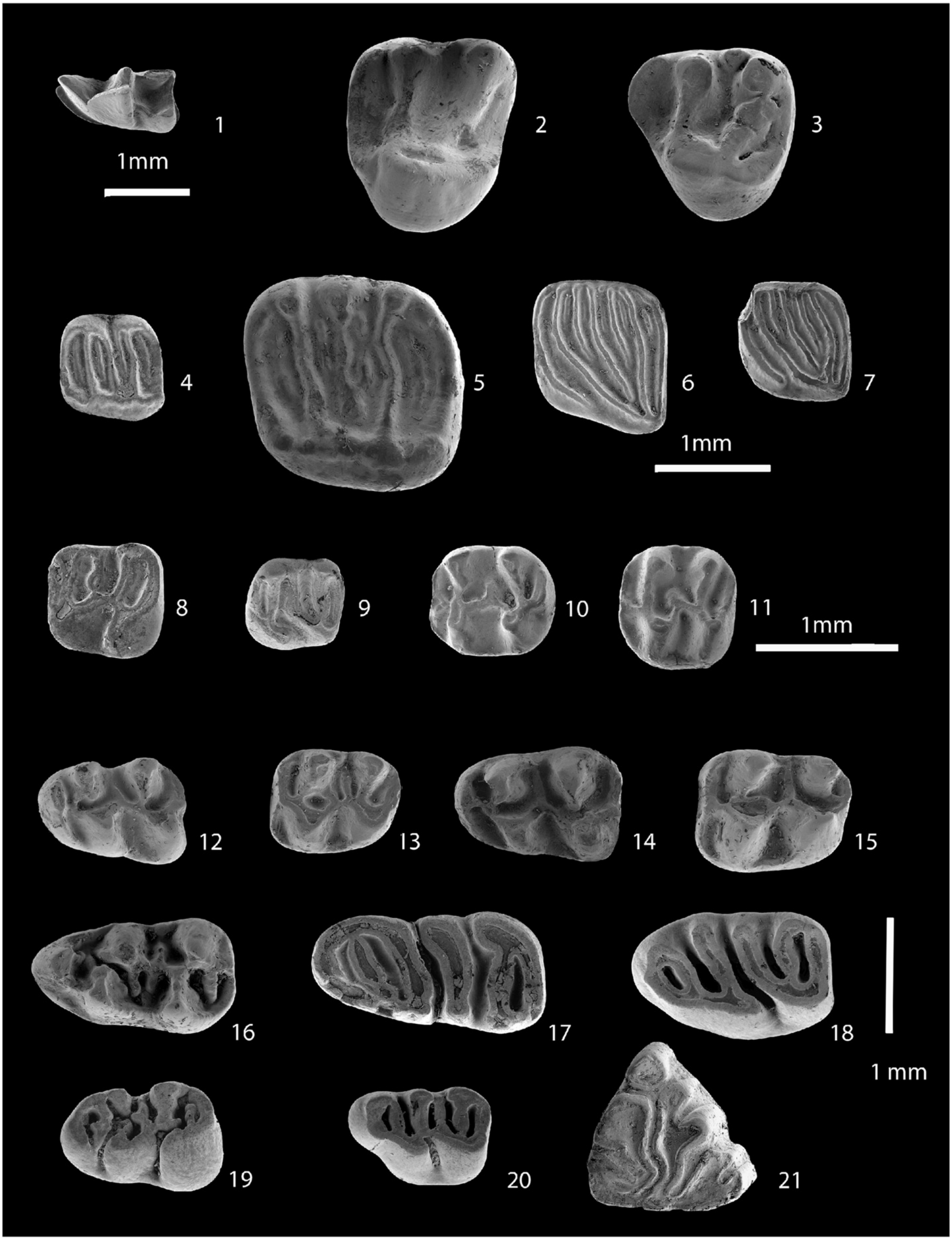

Plate VI (*caption on page 434*).

excavation. It is unclear to date, whether the albanerpetontids had an aquatic larval stage (Gardner and Böhme, 2008), but the absence of such a stage would explain its scarcity in lacustrine deposits in general and the absence in the Randeck Maar laminites (excavations W72, S11) in particular.

Urodeles are represented by several skeletons and isolated bones. The largest tailed amphibian, *Chelotriton paradoxus*, is known from Randeck Maar as both complete and partially preserved skeletons (Plate 5, panel 3). These show the characteristic features of the genus, which are: heavily ossified and strongly sculptured broad skulls, vertebrae with high neural spines capped by dermal sculptured plates, and long pointed ending ribs with tubercular processes. These findings were unknown at the time when Herre (1941) and Westphal (1977) described *Palaeopleurodeles hauffi*, which is only known from Randeck Maar (Plate 5, panel 2). Also Estes (1981) was not aware of the occurrence of *Chelotriton* at Randeck Maar, when he discussed the question whether *Palaeopleurodeles* is synonymous with *Chelotriton*.

Löffler and Westphal (1982) interpreted a new record of a small urodele as a larval *Palaeopleurodeles*. The Recent relatives of *Palaeopleurodels* and the abovementioned *Chelotriton* are the West Mediterranean Spanish ribbed newt *Pleurodeles waltl* and the SE Asian crocodile newts *Tylototriton* and *Echinotriton*. They represent the "Group II genera" or "primitive newts" of Estes (1981) and show the long and spiny ribs of the Randeck Maar urodeles. This type of ribs is unique among all urodeles. It would be very surprising, if two closely related genera with these exceptional ribs lived together in one lake during the Miocene. Due to the fact that both of the complete specimens of *Palaeopleurodeles* (holotype and SMNS 50168) have the carpalia and tarsalia unossified, while in *Chelotriton* they are ossified, the genus *Palaeopleurodeles* may represent the larval stage of *Chelotriton*.

The "Group III" genera of Estes (1981) also occur at Randeck Maar. Roček (1996) described a caudal half of a "*Triturus*-like salamandrid" and the SMNS 2009/2012 excavation yielded a perfectly preserved small skeleton, which was identified as a new species, *Ichthyosaura randeckensis* (Schoch and Rasser, 2013) shown in Plate 6, panel 4, and some fragments similar to *Lissotriton vulgaris*. In contrast to the specimen described by Roček (1960), the small skeleton shows the carpalia and tarsalia unossified, which points to a premetamorphic stage. Also the screen-washed material from the A77 excavation provided several *Lissotriton*-type bones.

The anuran fauna is dominated by *Palaeobatrachus hauffianus* (Fraas, 1909; Vergnaud-Grazzini and Hoffstetter, 1972), a species exclusively known from Randeck Maar (Plate 5, panel 6). *Palaeobatrachus* is the only genus of the anuran family Palaeobatrachidae, which became extinct in the middle Pleistocene. All species were permanent water dwellers and widespread in Central Europe during the Paleogene and Neogene (Wuttke et al., 2012). The Randeck Maar species produced gigantic tadpoles of up to 15 cm total length, which is more than double of the normal size of the larvae of *Palaeobatrachus* (Plate 5, panel 5) (Roček et al., 2006). It is suggested that highly favourable growing conditions in a warm, permanent lake with few predators led to gigantism of the tadpoles. Furthermore, fast growth and large size are defences against predation from adults of its own species (Roček et al., 2006). Additionally, larvae of Pelobatids lived in the lake (Plate 5, panel 7). Metamorphosed specimens are rarely found in lake deposits because they live terrestrially, except for the time of reproduction. Accordingly, no remains of adult specimens were found so far in the Randeck Maar. A very fragmentary ilium from the A77 excavation represents a member of the Ranidae, probably the water frog *Pelophylax* (Böhme and Ilg, 2003). Also two very small but almost completely metamorphosed skeletons are known (Plate 5, panel 8).

4.10. Reptiles

The reptile fauna is rich in species, though only isolated bones and teeth were found (Appendix F). Most of the larger remains of turtles and crocodiles were found during old excavations, while the small bones of lacertids and snakes mostly come from the A77 excavation.

Turtles are represented by *Clemmydopsis* (Plate 5, panel 13), *Chelydropsis* (Plate 5, panel 12) (Schleich, 1985; Seehuber, 1994), *Ptychogaster* (Plate 5, panel 14) and a terrestrial tortoise (Plate 5, panel 11). Remains of the latter are most frequent, but due to their very fragmentary preservation it is hardly possible to determine the genus (*Testudo* s.l. or *Paleotestudo*, Lapparent de Broin et al., 2006). The other genera are represented by only a few carapax or plastron fragments, which is insufficient for species identification. All these turtles were widely distributed in the S German Molasse Basin and its northern hinterland. "*Testudo*", *Clemmydopsis*, and *Chelydropsis* are well known, e.g., from of the Steinheim crater lake and its surroundings (MN 7), where they lived in great number (Młynarski, 1980).

Crocodile remains are very scarce with only six teeth, two small osteoderms and a small jaw fragment known. Most of the records have been found together with the remains of the other bigger vertebrates, only one small tooth originates from laminated sediments. However, during the S11 excavation a complete but heavily crushed skull with some osteoderms was recovered (Plate 5, panel 10) (Rasser, 2012, Figs. 10–11). All of the remains belong to the ubiquitous genus *Diplocynodon*, very probably the only known Middle Miocene species *D. ungeri* (Martin and Gross, 2011).

The lacertids are represented by *Chamaeleo simplex*, the type material of which comes from the A77 excavation, some jaw fragments of *Lacerta* sp., and an anguine lizard. Osteoderms of anguids are frequently found in screen washed residues (Westphal, 1963). Most of them are keeled and have an ovoid to rectangular outline, which is a morph known at least since the Eocene (Klembara and Green, 2010). In the Miocene of Europe, the anguids *Anguis*, *Ophisaurus* and *Pseudopus* are known (Klembara et al., 2010). *Anguis* has more rounded thin osteoderms without a keel, which does not fit with the Randeck Maar material. *Ophisaurus* and *Pseudopus* have different types of dentitions (Klembara, 1981). Since a few jaw fragments with teeth of both types were found, the osteoderms probably belong to *Ophisaurus* s.l. and *Pseudopus laurillardi*, which are the only known species of Early and Middle Miocene times (Klembara et al., 2010). For discussion of the *Ophisaurus* complex see Klembara and Green (2010) and Cernansky and Auge (2012).

Additionally, snake remains are documented by only a few vertebrae and teeth of a viper of the *Vipera aspis* complex, the colubrid *Texasophis* cf. *meini* and a natricid (Szyndlar and Schleich, 1993).

4.11. Birds

Bird remains are quite rare in the deposits of Randeck Maar, except for a few fragmentary bones mentioned by Westphal (1963).

4.12. Mammals

The vast majority of the small mammals was found during the A77 excavation (Appendix G). A preliminary list of the recorded taxa is published in Heizmann (1983) next to some genera mentioned in Heizmann (1998a). The first excavation that yielded some small mammals was W62. Westphal (1963) reported on five rodent teeth without precise taxonomic assignment. A partial skeleton of a bulldog bat, which is also housed at the University of Tübingen, was already discovered in 1966 close to the site of the W62 excavation, and published by Westphal (1967).

5. Results

5.1. Plants

Further taxonomic progress has been achieved and for some taxa it is even possible to ascertain that different organs derive most probably from one plant. In this context an important example is *Tremophyllum tenerrimum* (leaves) and *Embothrites borealis* (fruits), which are now *Cedrelospermum*. The fruits described as cf. *Cyclocarya cyclocarpa* by Rüffle and revised as *Pteleaecarpum europaeum* by Gregor are now considered to belong to Malvaceae s.l. *Craigia bronnii*. The leaf described as *Alangium tiliifolium* by Rüffle (1963, p. 248, Pl. 14, Fig. 15) may be regarded to derive from the same plant. Very similar leaves, described as *Dombeyopsis lobata* from the Most Basin (Bohemia) are regarded as being conspecific with *Craigia bronnii* fruits (Kvaček, 2004). For nomenclatural reasons – the different plant parts have yet never been found attached to each other – these taxa cannot be fused.

The true generic identity of *Sapindus falcifolius* (Plate 2, panel 2), which is common at Randeck Maar, is still under debate and probably different taxa are mixed here. Rüffle (1963, p. 236) does not provide information on the differences between *Sapindus* and *Ailanthus*. Winged fruits of *Ailanthus* are quite common at Randeck Maar and it cannot be excluded that foliage described as *Sapindus falcifolius* derives from *Ailanthus* as possibly does the leaf remain described by Rüffle as "Ailanthus-ähnlicher Blattrest". Schweigert (1998, Fig. 22) was inspired by the description of *Carapoxylon* by Mädel (1960) and the fruit described as *Toona* by Rüffle (1963) when he figured a well-preserved pinnately compound leaf as *Toona*. This leaf (refigured here in Plate 2, panel 2), however, matches very well *Sapindus falcifolius* as described by Rüffle (1963) and thus possibly may constitute *Ailanthus*.

During the preliminary studies for this summary it was discovered that the foliage *Sideroxylon salicites* Rüffle (1963, p. 254, Pl. 14, Figs. 1–14, Pl. 15, Figs. 9, 10, Pl. 30, Figs. 1, 2) more probably belongs to Lythraceae (possibly *Decodon* or *Microdiptera*) (see Plate 2, panel 3). Similar leaves with characteristic venation (dense secondaries, intersecondaries and intramarginal vein) and even mass-occurrences have been described recently from the Most Basin (Bohemia, Early Miocene, Kvaček and Sakala, 1999), the northwestern margin of Lake Pannon (Pellendorf, Lower Austria, Late Miocene, Kovar-Eder et al., 2002), and from the Haselbach Member (Saxony, early Oligocene, Kunzmann and Walther, 2007). This revision considerably influences the interpretation of the Randeck Maar flora because *Sideroxylon* (Sapotaceae) are trees of largely neotropical and African distribution while Lythraceae occur from the tropics to the temperate zone and comprise woody as well as non-woody representatives, many of them bound to wet habitats.

In comparison to the pollen from the Dysodil sample of Kottik (2002), the pollen from four samples of the S11 excavations are less well preserved. Though identification was limited to light microscopy, there were still 45 taxa (genera/family) detected (Appendix B). By far most abundant is *Carya*, followed by *Ulmus*, *Quercus*, *Pterocarya*, *Carpinus*, *Tilia*, *Engelhardia*, *Castanopsis*, and *Ilex*. The abundance of conifers varies between 2% and 27%; they are mainly represented by *Pinus* and *Abies*. Vines are represented by Araliaceae and sporadical presence of Vitaceae. Herbaceous taxa are mostly represented by Poaceae as well as Apiaceae and Asteraceae. Subordinate are *Sparganium* and Cyperaceae (reeds and sedges), and spores of Polypodiaceae (ferns)(Plate 1). The following taxa were found in the S11 material, but were not mentioned by Kottik (2002): the conifers *Abies* and *Picea* along with the angiosperms Apiaceae, Cyperaceae, Ericaceae, *Fagus*, *Sparganium*, *Tragopogon*. Furthermore, the following taxa were described by Kottik (2002), but are absent in the S11 material: Arecaceae, Chenopodiaceae, *Cornus*, Cupressaceae (except Taxodiaceae), *Distylium*, *Liquidambar*, *Lithocarpus*, *Sciadopitys*, *Sideroxylon*?, and *Trigonobalanopsis* as well as an additional Ulmaceae type and the spikemoss *Selaginella*.

The preliminary evaluation of the poorly preserved leaves and fruits of the S11 excavations provides evidence of *Engelhardia orsbergensis* (leaflet) (Plate 2, panel 4) and opened fruiting capsules of *Salix* (Plate 2, panel 5), which have not been reported before. *Saportaspermum* is remarkable because the specimens figured by Rüffle (1963, Pl. 1, Fig. 16, as *Pseudotsuga*) were not available for reinvestigation. Additionally, the following taxa have been identified: *Ailanthus confucii*, *Cedrelospermum* sp., *Daphnogene polymorpha*, Lauraceae gen. et sp. indet., *Engelhardia macroptera*, *Podocarpium podocarpum* (leaflet, seed-bearing pod), and *Zelkova zelkovifolia*.

Compared to other Miocene floras of S Germany and adjacent regions, the flora from Randeck Maar includes a rather high number of taxa with pinnately compound leaves: "*Acacia*" *parschlugiana* ("Unbestimmbarer, leguminosenartiger Blattrest" of Rüffle, 1963, Pl. 9, Figs. 23, 24; see Kovar-Eder et al., 2004), *Ailanthus*, *Engelhardia*, "*Juglans*" *acuminata*, *Koelreuteria*, and *Podocarpium podocarpum*. Most of them are preserved as leaves and fruits, or exceptionally even as flowers as is the case in *Podocarpium*. Remarkable is also the high number of anemochorous taxa, among them, including *Acer*, *Ailanthus*, *Craigia*, *Cedrelospermum*, *Engelhardia*, *Koelreuteria*, *Saportaspermum* (*Pseudotsuga* in Rüffle, 1963, Pl. 1, Fig. 16), and *Ulmus*. The high diversity of anemochorously dispersed plants as well as the preservation of rather numerous remains of flowers, inflorescences and even infructescences clearly indicates that wind may be regarded as essential dispersal vector causing the co-assembly of different organs of single plant taxa. In several aspects the flora from Randeck Maar shows similarities with the flora of Parschlug (Austria, Karpatian/Early Badenian; Kovar-Eder et al., 2004): (1) they share several taxa, e.g., *Ailanthus confucii*, *Cedrelospermum* sp., *Engelhardia*, *Saportaspermum*, (2) the number of anemochorous taxa is high, (3) the presence of several Fabaceae taxa, among them "*Acacia*" *parschlugiana* and *Podocarpium podocarpum*. In the Randeck Maar flora, however, oaks are rare (Rüffle, 1963, Pl. 3, Figs. 10,11), while several oak species are documented from Parschlug.

5.2. Gastropods

Aquatic gastropods are dominated by the planorbid species *Gyraulus kleini* (Plate 4, panel 1), which reveals the characteristic features of this species (Finger, 1998). It occurs randomly among the lake sediments, but can form mass occurrences along certain layers of the laminated sediments (Rasser et al., 2013). The second abundant planorbid is the limpet *Ferrissia deperdita* (Plate 4, panel 2), which differs from other limpets in size and direction of the apex (Schlickum, 1976). *Planorbarius* cf. *mantelli* (Plate 4, panel 3) is rare and its shells and particularly the apertural area are usually not preserved. One large Lymnaeida morph (Plate 4, panel 4) forms mass accumulations in certain lake sediment horizons (Rasser et al., 2013). The identification is impossible due to extreme compression and fragmentation of the large tests.

Terrestrial gastropod findings are rare in the lake sediments, their diversity, however, is much higher than that of the aquatic snails. Most shells are poorly preserved and therefore species identification is difficult. A characteristic form is the disc snail *Discus pleuradrus* (Plate 4, panel 7), which shows the typical morphology of the extant relatives of this genus. Another disc-shaped shell is *Caracollina phacodes* (Plate 4, panel 5), which reveals a flat spire and regular axial ribs. *Pseudoleacina eburnea* (Plate 4, panel 13) has a slim, fusiform shape. The last whorl is approximately two times as long as the spire. It belongs to the family Oleacinidae, which today is mainly distributed in tropical and subtropical America (Fechter and Falkner, 1989).

A tower-like shell with moderately convex, regularly growing whorls is characteristic for the family Subulinidae. The mouth is not completely preserved, but the found specimens possibly belong to *Opeas minutum*, the extant relatives of which mostly live in tropical America. Another more "tower" like species is *Cochlicopa subrimata loxostoma* (Plate 4, panel 6), which has an elongated and ovate shell, and a pear-shaped mouth. Likewise, several specimens with the outer morphology of the genus *Granaria* (Plate 4, panel 8) occur, but the preservation of the apertures is not sufficient for species identification. They resemble *G. schuebleri* (Höltke and Rasser, in press). Extant *Granaria* species thrive in open, dry, calcareous habitats (Kerney et al., 1983).

Door snails (Clausiliidae) are represented by *Triptychia* sp. The incomplete shell is composed of many whorls with axial ribs apart from the first three whorls, which are smooth and spindle-like. A fossil relative of extant *Helicodonta obvoluta*, namely *Helicodonta involuta*, was found in the collection material as well. An unambiguously determinable turbiniform genus is *Pomatias conica* (Plate 4, panel 11) with the whorl before the last one being very distinct. The protoconch is smooth but the teleconch has strong spiral ribs. The Vertiginidae are represented by the genera *Negulus* and *Columella* sp.

The largest land gastropod known from Randeck Maar is *Tropidomphalus* (*Pseudochloritis*) *incrassata* (Plate 4, panel 11) with a diameter of 24 mm. Whether *Pseudochloritis* is of subgenus or genus rank, is discussed differently. Wenz (1923) also mentioned *P. insignis*, but this material was destroyed during World War II. *T.* (*P.*) *incrassata* has a flat spira. Due to diagenesis, however, sculptures are invisible. The last whorl is convex and has a cleft-like umbilicus and a handled mouth-margin. A smaller representative of this group is *T.* (*P.*) *extincta*.

In the so-called "tuffa horizon" (as written on the collection labels), there are some shells with a *Cepaea*-type morphology. Only one specimen can be clearly identified as *C. silvana*. Another member of the Helicidae is *Klikia coarcata* (Plate 4, panel 9). It reveals a massive shell with a flat spira, regularly growing whorls and a covered umbilicus. A species with an uncertain generic attribution is "*Leucoochropsis*" *kleini* (Plate 4, panel 10), because the shell has a low spira, a sting-like umbilicus and is slightly keeled (Karpatian/Early Badenian; Moser et al., 2009). The gastropod family Vitrinidae is represented by *Vitrina* cf. *suevica*, characterised by a small spira and a large last whorl. A relatively flat spira with regularly growing whorls are characteristic for *Vallonia* cf. *subpulchella*, but the mouth is not preserved. A relative of the very common true glass snails (Zonitidae) that prefer more wet habitats is *Archaeozonites costatus*. A more uncommon gastropod is *Napaeus*, which is a new species that will be described in a separate paper by Rasser and co-authors. Further incomplete specimens possibly represent the genera *Nesovitrea*, *Aegopsis*, and *Vitrea*. All gastropods from Randeck Maar are listed in Appendix E. A detailed taxonomic study is in preparation by M. Rasser and co-authors.

5.3. Birds

A few questionable very small bones could be identified in material of the A77 excavation as well as some small feathers. During the S11 excavation an articulated distal part of a leg of a small bird has been found in the laminites (Rasser, 2012: Fig. 12). Already in 1889 (E89 excavation) an until now undetermined ulnare of a big bird was collected, probably a *Megapaloelodus* or *Palaelodus*, which are flamingo-related birds. Both are known from the Miocene lakes of Steinheim and Nördlingen (Heizmann and Hesse, 1995).

5.4. Mammals

The S11 excavation provided an almost complete skeleton of *Mormopterus* from laminitic deposits. In the residues of screen-washed sediments from this excavation, small mammal remains are scarce, but the composition roughly resembles the association of the A77 excavation. A talpid bone found in the year 2009 (S11) is an anterior phalanx of the mole *Talpa minuta*, which was a good borrower according to its humerus. *Heteroxerus*, a ground squirrel, was not recorded before. The reciprocal proportions of the hamster species *Democricetodon mutilus* (Plate 6, panels 14, 15) and *D. gracilis* (Plate 6, panel 12, 13) are also worth mentioning: In the A77 sample, *D. gracilis* is recorded roughly twice as much as *D. mutilus*. In the S11 samples the proportion is vice versa. The species list in Appendix G further includes new determinations of teeth mentioned by Westphal (1963) as well as three further rodent teeth from the Tübingen collection.

All recorded taxa are well known from sites in the S German North Alpine Foreland Basin (Rössner and Heissig, 1999). Nearly 80% of the small mammal collection belongs to rodents. The chiropteran sample includes at least seven species. The partial skeletons of *Mormopterus* are noticeable. Here *Mormopterus* is outnumbered by vespertilionds. Usually, *Mormopterus*, if recorded in a bat sample, dominates it in numbers, as demonstrated by Rachl (1983) for the Miocene chiropteran faunas of Steinberg and Goldberg in the Nördlinger Ries, or by Engesser (1972) for the late Middle Miocene Anwil fauna.

For most Miocene small mammals, their relationship to extant species is unclear. In case of the dimylids, eomyids and anomalomyids, even the families are extinct and without extant analogue.

The first large mammal were found during the E89 and WP33 excavations. A few further specimens derive from other private collections (Hölzle, Jooss, Scheer). During the A77 excavation only few large mammal specimens have been found. The same is true for the S11 campaign, but among the few specimens collected, the new find of a bovid mandible is remarkable, because it may represent a new species. The material includes 223 specimens and mainly consists of bones and bone fragments, while only a few teeth and jaw fragments are present. As among the small mammals, no articulated skeletal parts have been found.

The 15 large mammal species represent only a small part of the faunal diversity existing at that time. The Randeck Maar fauna is dominated by tragulids (chevrotain) and cervids which account for *c.* 36% of the identified specimens. Rhinos (31%; Plate 7, panel 3),

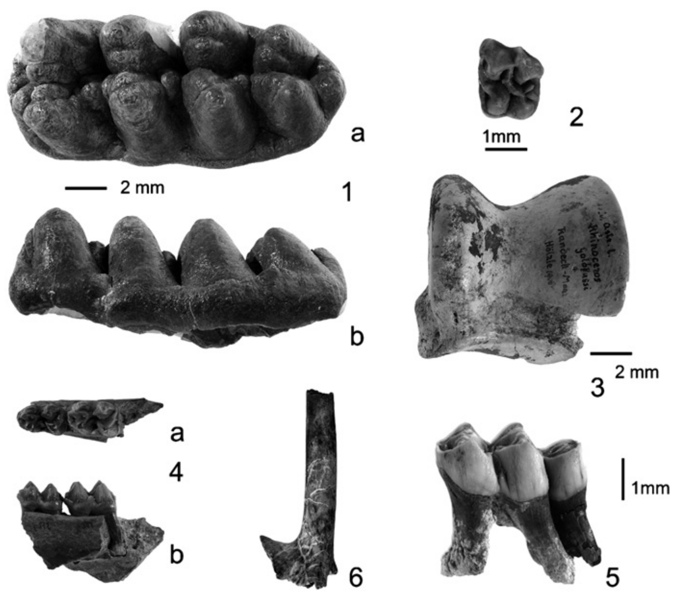

Plate V11. Large mammals. 1, *Gomphotherium angustidens*, left m3, occlusal view (SMNS 47722); 2, *Anchitherium aurelianense*, right M3, occlusal view (SMNS 10612); 3, *Brachypotherium* sp., left astragalus, dorsal view (SMNS 11630); 4, *Dorcatherium* cf. *crassum*, right dentary fragment with m1–m2, a occlusal, b. labial views (SMNS 16498); 5, *Palaeomeryx bojani*, right m3, labial view (SMNS 17420); 6, *Lagomeryx parvulus*, antler fragment, lateral view (SMNS 47723).

giraffe-like palaeomerycids (11%; Plate 7, panel 5) and the proboscidean *Gomphotherium* (9%; Plate 7, panel 1) are also well represented. There are also some carnivore bone fragments from the WP33 excavation, which might belong to one individual. They fit best to a hemicyonid and eventually represent the same taxon as an isolated m3? tooth corresponding in size and morphology to *Plithocyon stehlini*. Two mustelids (martens) differing in size are represented only by a few bones and thus cannot be determined more precisely. An edentulous mandible fragment belongs to the genus *Ursavus*. *Anchitherium* (Plate 7, panel 2), *Cainotherium*, suids and bovids are only documented by sparse findings. All forms identified to the species level are well known from numerous other localities in Central Europe (Rössner and Heissig, 1999).

5.5. Biostratigraphy

The stratigraphic correlation is mainly based on small mammals, especially on specific rodent taxa. Here only the few taxa are reviewed, which allow for a precise biostratigraphic correlation. A list of all species is given in App. 7. The best stratigraphic indicator is the eomyid *Keramidomys thaleri* (Plate 6, panel 8, 9), which is exclusively recorded from MN 5 faunas. It is known from several localities in S Germany such as Niederaichbach, Puttenhausen, Sandelzhausen, Untereichen 565 m, Oggenhausen (Abdul Aziz et al., 2008; Böttcher et al., 2009; Prieto et al., 2009). In addition, *K. thaleri* is known from Swiss faunas correlated with MN 5 (Engesser, 1990). The advanced cricetid species *Neocometes* aff. *similis* (Plate 6, panels 17, 18) also indicates an MN 5 correlation of the fauna. *Anomalomys minor* is a species recorded from many MN 5 sites (Schötz, 1980). Considering the size of the m1 and M1 teeth, the Randeck Maar fauna is close to that of Hombrechtikon in Switzerland (see Bolliger, 1992; we consider A. minutus a synonym of A. minor) and all of the teeth cover the characteristic size range of this species, which is considered another strong argument for a MN 5 correlation. Summarising the stratigraphic ranges of different mammalian taxa it can be stated with certainty that the fauna correlates with MN 5 (Fig. 1). A more precise correlation is impossible as the biostratigraphically relevant genus *Megacricetodon* was not found.

The biostratigraphic correlation is based on the sample from the excavation A77 (see Material and methods section above). Due to the uncertain position of the sample within the sedimentary framework (Fig. 2), the exact time of the beginning, the termination and the total duration of sedimentation is unknown. The species reported from the other sites are compatible with, but not sufficient for a correlation that precise.

6. Discussion

6.1. Palaeoenvironmental scenario

The environmental and habitat interpretations presented below and in Fig. 4 are based on geological features, the biological inventory of older collection material, and the most recent excavation S11. Since the position of most of the material from previous excavations within the stratigraphic sequence of the Randeck Maar is unclear, it is difficult to decide, which organisms occurred together in time and space. Therefore, our palaeoenvironmental model necessarily represents a scenario based on the current state of knowledge that may change in the future.

6.1.1. Aquatic habitats

As mentioned in the geological overview, the Randeck Maar was a typical maar lake with a restricted diameter, steep slopes and an estimated maximum water-depth of 130 m. Cohen (2003, p. 49) wrote that such crater lakes are commonly hydrologically closed basins, at least for surface flow. The deposition of sediment around the crater rim resulting from the magmatic explosion effectively seals off external drainage inputs. These factors can result in reduced mixing of different water layers and anoxia in bottom waters. Because of the most probably very restricted watershed areas, climate fluctuations may produce distinct sea-level fluctuations. Sedimentation in such crater lakes continues until the crater is filled or breached.

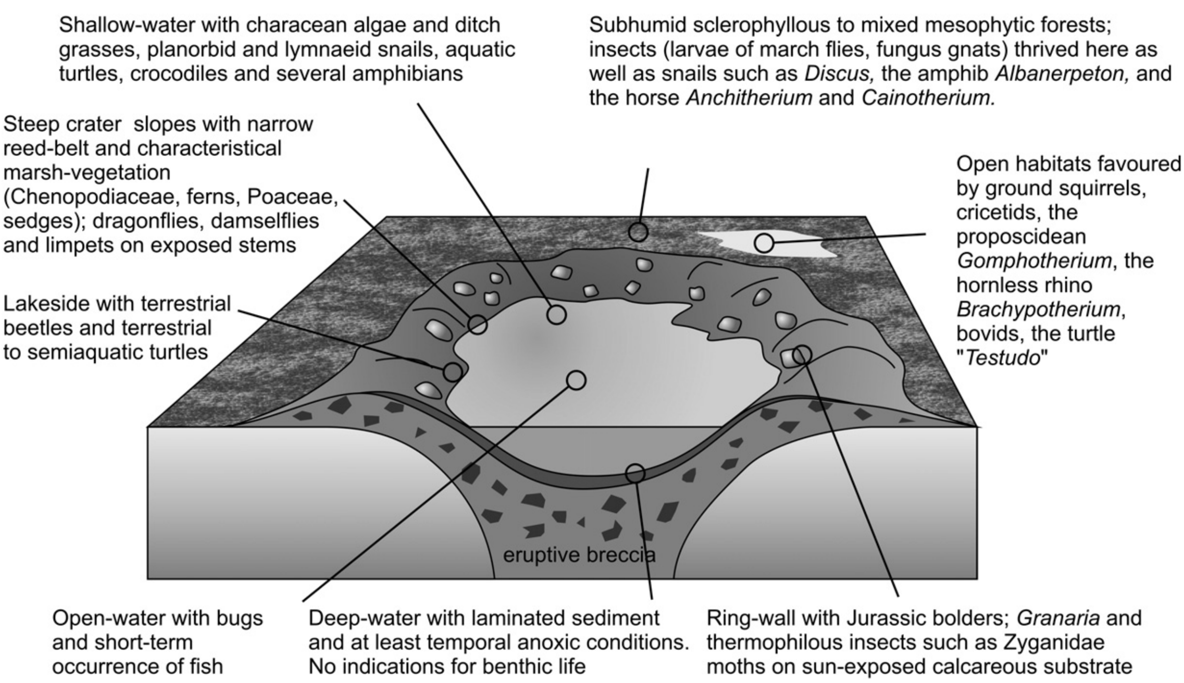

Fig. 4. Palaeoenvironmental model of the Randeck Maar lake with its habitats and selected, representative organisms.

The existence of freshwater inlets was discussed in literature (e.g., Jankowski, 1981), because its existence would critically influence the physical and chemical properties of the lake. Neither geological nor sedimentological evidence exist so far. Some insects that are typical for streams do occur, such as caddisflies and Dryopidae, but they are low in number and incomplete. Presumably they have been transported into the lake by wind or other animals.

6.1.1.1. Water chemistry. Based on geochemical evidence, Jankowski (1981) reconstructed brackish-eutrophic conditions with particularly high salinity for the deposition of most of the laminites, limestones and marls. He suggested an alkalinity that was toxic for higher developed organisms, which would explain the lack of fish for almost the whole existence of the lake. Among present-day lakes, however, the absence of fish is not unusual and not necessarily explained by water chemistry alone (Schilling et al., 2008).

Brackish water conditions are suggested by the existence of the hydrophilous plants *Ruppia* div. sp. (Plate 2, panel 6), and *Limnocarpus eseri. Ruppia* can also point to increased alkalinity (Cook, 1990). It is suggested that certain insect groups are indicative for the salinity of aquatic lake environment and so Lutz (1997) calculated a salinity of 34‰ using the percentages of Coleoptera and Hemioptera, Diptera and Hymenoptera, as well as other orders from published data. With the same equation, we calculated a salinity of 21‰ using data from the recent study of Joachim (2010). These calculations are, however, based on isolated collection material with taxa that did not necessarily co-occur, and therefore the results must be treated with caution. The turtle *Chelydropsis* probably tolerated brackish conditions, because it also occurred in the Upper Brackwassermolasse of Langenau (Heizmann, 1998b) together with brackish fish species pointing to a salinity of up to 15‰ (Reichenbacher, 1989). In the same brackish layer of Langenau, *Diplocynodon* occurs (Heizmann, 1998b), which suggests that this crocodile tolerated increased water salinity as well.

There are, however, also proxies for freshwater conditions, particularly the local mass accumulations of juvenile dragonflies of the family Libellulidae, because the majority of present-day forms avoids increased salinity, although the larvae of a few extant libellulid species (e.g. *Sympetrum sanguineum* and *Orthetrum cancellatum*) can thrive in brackish water with a salinity of up to 13‰ (rarely even 18‰). Brackish conditions are also contradicted by the occurrence of amphibians, because nearly all living amphibians need fresh water for their development. There are only very few species that tolerate slightly increased salinity (Hofrichter, 1998) and *Lissotriton vulgaris* has even been found in habitats with a salinity of up to 8‰ (Große, 2011). Since, however, a variety of amphibian species lived in the Randeck Maar lake and most of them should have reproduced in the lake, it is very unlikely that raised salinity prevailed during its whole existence.

In summary, there is good evidence for both freshwater conditions and increased salinity. This apparent contradiction could be explained by two interpretations: (1) time-equivalent habitats with both freshwater and high-salinity conditions existed adjacent to each other, or (2) the salinity has changed through time. Given the small size of the lake and the steep crater margins, the first interpretation appears to be more unlikely, while the second interpretation is also supported by the diatoms (see 4.2.): A diatom sample from the more basal parts of the succession suggests higher salinity conditions, while diatoms in a sample from the upper part indicate normal freshwater conditions.

6.1.1.2. Deep- and open-water habitats. Calcareous, marly and bituminous (Dysodil) laminites indicate a deep-water environment with at least temporal anoxic conditions. Lamination and the absence of bioturbation point to a very low hydrodynamic energy and little or almost no benthic life, which is typical for deeper environments, particularly in maar lakes. The combination of grain-size, lamination and lack of benthic life favoured partly exceptional good preservation.

The plankton may be represented by diatoms and possibly ostracods, although only benthic diatoms have been reported so far. Some bugs such as Notonectidae inhabited the lakeside and open waters.

The scarcity of fish might be caused by water chemistry, but as discussed above, this is not necessarily the only explanation. The mass-occurrence of *Paralebias* aff. *weileri* on one bedding plane indicates that it lived there at least for a short time. Other Miocene lakes of similar size without tributaries in SW Germany were colonised by at least a few fish species, which lived there for a longer period: Three species in Steinheim (Gaudant, 1989) and four in Höwenegg (Jörg, 1954; Böttcher unpublished).

6.1.1.3. Littoral and supralittoral. The plant record is indicative of shallow-water and shoreline biotopes. Characeae and *Ruppia* (ditch grasses) lived rooting in the substrate and submerged floating. *Stratiotes* (water soldiers) has roots rarely attached to the substrate. It prefers muddy, eutrophic to mesotrophic conditions (Cook, 1990). Lythraceae (?*Decodon*- or ?*Microdiptera*-like) were probably of reed-like habitus with roots and lower parts of the stem being submerged but most of the plants being erect over the water surface forming more or less extensive stands. Cyperaceae, Poaceae, Chenopodiaceae, and ferns may have grown in wet habitats at the lake margin. Considering the general maar lake topography, these shallow-water and shoreline biotopes probably were narrow. Exposed plant stems and leaves provided the ideal habitat for adult damselflies and dragonflies for foraging, mating and ovipositioning. Just like its extant representatives, the limpet *Ferrissia deperdita* inhabited these stems as well. The tremendous number of juvenile dragonflies of the family Libellulidae, whose extant representatives often prefer sundrenched waters with just a few centi- to decimetres of water-depth with soft substrate might indicate shallow-water habitats. The same habitats are preferred by Stratiomyidae (Diptera). Benthic diatoms lived in the photic portion of the littoral zone, at least in part together with ostracods.

Among the vertebrates, the turtle *Chelydropsis* was fully aquatic and lived very probably like the related extant snapping turtles on the bottom of shallower parts of the lake with abundant vegetation, like the planorbid snails *Gyraulus kleini* and *Planorbarius* cf. *mantelli*, and lymnaeid snails. This habitat was also inhabited by the crocodile *Diplocynodon* and most of the amphibians. The small turtle *Clemmydopsis* presumably lived in very shallow water as its legs are too much reduced to walk on land over longer distance or to swim in open water (Młynarski, 1980). Flamingo-related birds may have foraged on invertebrates in the shallow-water lake portions, as recently described from the Oligo-Miocene of Argentina (Melchor et al., 2012).

Most of the terrestrial beetles probably lived in the direct area of the lakeside — some as ground dwellers in the drift line and the reed belt (Carabidae, Staphylinidae) or as dwellers in the surrounding vegetation (Curculionidae, Chrysomelidae). The most common groups are leaf beetles (Chrysomelidae) and rove beetles (Staphylinidae). Some of the rove beetle species are *Bembidion*/*Tachys*-related (Schawaller, 1986), which today live in moist, near-shore habitats. Beetles of the group Staphylinidae (*Bembidio*/*Tachis*) prefer open areas with little holes and passageways, where they hunt for e.g., small gastropods (Schawaller, 1986). The terrestrial to semi-aquatic turtles *Ptychogaster* may have lived close to the shoreline as well (Młynarski, 1976).

6.1.2. Crater slopes and surrounding plateau

Due to their steepness and orientation, the crater slopes were characterised by differences in sun exposition causing differences in temperature regime and water balance (Rüffle, 1963; Schweigert, 1998; Kottik, 2002; Joachim, 2010). Fruits, leaves, and pollen complement each other. In the leaf and fruit record taxa indicating or tolerating seasonal drought are well represented. Among these are the woody taxa "*Acacia*" *parschlugiana*, *Cedrelospermum*, *Celtis*, Cupressoideae, *Engelhardia*, *Podocarpium*, *Zelkova* and *Zizyphus*. Representatives of Taxodioideae are absent both in the fruit and leaf record and extremely rare in the pollen samples. This clearly points towards the absence of swampy habitats in nearer surroundings. Further woody taxa associated are *Ailanthus*, *Daphnogene*, *Koelreuteria*, *Laurophyllum pseudoprinceps* (Plate 2, panel 7), *Magnolia*, and others.

The preferred habitat for thermophilous insects as Asilidae, Bombyliidae, Cicadidae, Zyganidae, Tettigoniidae, and Zyganidae were the drier and warmer slopes. The latter may also have lived on sun-exposed Jurassic rocks in the crater surroundings. Sun-exposed habitats were also favourable for the snail *Granaria*, who preferred calcareous substrates, and *Vallonia*, whose extant relatives thrive in open, grassy sites (Kerney et al., 1983).

Small mammal remains are usually interpreted as accumulations of regurgitation pellets of owls. The habitat of small mammals, therefore, may be assumed within the range of the predators. Some of the small mammals indicate that there were at least patches of open ground. The identified sciurids represent ground squirrels, which need open habitats, especially the xerine *Heteroxerus*. So do the cricetids with a 16% share of identified small mammals. The probosicean *Gomphotherium* and the hornless rhino *Brachypotherium* may have preferred more open environments as the turtle "*Testudo*" s.l. The Randeck bovid is rather low-crowned and may have thrived in less dense forests to open woodland.

Mixed mesophytic forests were formed mainly by deciduous trees as *Carpinus*, *Carya*, *Castanea*, *Pterocarya*, *Quercus*, *Ulmus* and *Tilia* (hornbeam, hickory, chestnut, wingnuts, oaks, elms, linden) represented in the pollen assemblages. Evergreen trees and shrubs of Rutaceae, Myrtaceae, *Ilex* (holly), Sapotaceae, Styracaceae, and Oleaceae cooccurred there. Araliaceae and Vitaceae probably constitute lianas in these forests. In these habitats insects (larvae of Bibionidae, Sciaridae, Mycetophilidae) thrived whose extant relatives favour dense vegetation, leaf litter and a high amount of humus. Phoridae and Pipunculidae prefer damp, shady habitats and rotten wood. *Albanerpeton inexpectatum* may have lived here as well, because it "preferred more stable, moist, and shaded conditions and nearby permanent water bodies of the forested karstic environment" (Gardner and Böhme, 2008). The snails *Pseudoleacina eburnean*, "*Leucochroopsis*" *kleini* and *Tropidomphalus* (*P.*) *incrassatus* are typical hygrophile wood inhabitants (Lueger, 1981; Binder, 2008). *Pomatias conica* lived under less humid conditions (Lueger, 1981). Given the ecological requirements of its extant relatives, the snail *Discus* sp. favoured humid and shady places under stones or litter (Kerney et al., 1983; Fechter and Falkner, 1989). *Helicodonta involuta* lived here on calcareous substrate along the edge of forests, just like its extant relatives (Kerney et al., 1983).

Among the small mammals, glirids, eomyids and the insectivores galericines preferred forested environments. Today, the latter are restricted to SE Asian relic areas, while they had an almost worldwide distribution during the Miocene. Therefore, it may be assumed, that the galericines inhabited a wider variety of habitats at that time. Some other insectivores such as the dimylids are restricted to forested environments (Heizmann et al., 1989; Ziegler, 1998). Among the large mammals the horse *Anchitherium aurelianense* was a typical forest dweller. *Cainotherium* and the tragulid *Dorcatherium* may have occupied different ecological niches within a forested habitat.

The rhinos *Prosantorhinus* and *Brachypotherium* are generally assumed to having lived in swampy environments in the vicinity of water, comparable to hippos, and their somewhat higher-crowned teeth indicate a certain amount of grasses in their diet. Since the Randeck Maar slopes were steep, swampy environments should, however, have been absent (and compare comments on the flora above). Consequently, the rhinos may have lived in the wider surroundings of the lake and used the lake only as a source for drinking water.

6.2. Palaeoclimate

Until now, different methods have been used to reconstruct climatic conditions for the Early/Middle Miocene of Central Europe in general and the Randeck Maar in particular. They have led to partially diverging results. Rüffle (1963) and Gregor (1986) suggested a subtropical climate with a mean annual temperature (MAT) of 15–16 °C and a rainfall of 1000–2000 mm, which was based on comparisons with the nearest living relatives of specific plant taxa. Mosbrugger et al. (2005) and Bruch et al. (2007) arrived at comparable results, using the Coexistence Approach of Mosbrugger and Utescher (1997) (MAT 15.6–16.5 °C, mean annual precipitation 1194–1356 mm, coldest month temperature 5.6–6.2 °C, warmest month temperature 26.5–27.9 °C). Note, however, that the Coexistence Approach was applied to the Randeck Maar flora based on the taxonomic resolution of Gregor (1982). Many more and partly diverging data are available now (Appendices B and C). Using thermophilic ectothermic vertebrates, Böhme (2003) suggested a dry climatic phase of up to 6 months at *c.* 16 Ma before present and an MAT of 17.4–20 or 22 °C (see also Böhme et al., 2011). Finally, the IPR vegetation analysis was applied including a taxonomic update of the plant record. The results suggest subhumid sclerophyllous forests as most likely vegetation type. This forest type characteristically develops under seasonally dry climate (Kovar-Eder and Kvaček, 2007).

Among the insects, one of the most important climate proxies are the termites (Isoptera), which are most diverse in warm to tropical areas as Australia, Africa and America. The naturally occurring northernmost representatives inhabit regions south of the 45th parallel north (Eggleton, 2000). The family of mantidflies occurs predominantly in warm climates — in Europe mainly in the Mediterranean. The few species occurring in central Europe inhabit also climatically benefited (warmer) areas (Aspöck et al., 1980). The extant representatives of the march fly genus *Plecia* are associated with tropical to warm-temperate climates (Moe and Smith, 2005). Among the backswimmers, *Anisopinae* indicate subtropical climate (Brooks, 1951) and alludes, together with the non-biting midges to warm-temperate conditions for the Randeck Maar palaeoenvironment. Several of the insect taxa of the Randeck Maar do not occur in cool-temperate Europe today. The single find of a snakefly (Raphidioptera) may be considered as conflicting evidence to a warmer climate. While Mesozoic stemgroup taxa (e.g. from Early Cretaceous Burmese amber and Brazilian Crato limestones) were adapted to tropical or sub-tropical climate, the extant crown group relatives prefer areas with cold and frosty winters (Aspöck and Aspöck, 2004). Consequently, this find does not necessarily allude to cooler climate. Wedmann et al. (2010) interpreted the occurrence of fossil bumble bees (Apidae) and the genus *Bibio* as indicative for cool climate. Even though bumble bees occur in cool regions in much higher species diversity today, there are also species that live in the Mediterranean region under warm climate, as applies for *Bibio* which occurs in regions as Tunisia, Sardinia, and Corsica (Haenni, 2009).

7. Conclusions and perspectives

Although the Randeck Maar is a locally restricted succession of lake sediments with a diameter of only *c.* 1200 m and less than 60 m of preserved sediments, it appears to comprise a complex structure with a high scientific potential on a global scale. The scientific relevance lies in the fact that the lake sediments and their fossils may provide evidence for the impact of the Mid-Miocene Climatic Optimum (MMCO) on the environment and its organisms as well as the ecological interactions between animals and/or plants. No other European locality provides such a rich insight into an ecosystem that existed during the MMCO. The sediments can be clearly dated as late Early/early Middle Miocene, Mammal Neogene zone MN 5. A more detailed dating within MN 5 is not possible with the available material.

The study is based on new excavations and re-evaluations of collection material and shows that the Randeck Maar was a typical maar lake with a rich flora and fauna. Based on all plant remains, the IPR vegetational analysis points towards subhumid sclerophyllous forests, suggesting seasonal drought. 380 taxa in all are known thus far, which are dominated by plants (168) and insects (79). The taxonomic re-evaluation combined with palaeoecological considerations allows for the reconstruction of a palaeoenvironmental model with the distinction of 1) open lake habitats, 2) littoral to supralittoral habitats, 3) crater slope with indications for more and less sun-exposed portions and 4) platform habitats. The available palaeontological proxies for water chemistry reveal indications for both freshwater conditions and raised salinity, as well as the possibility of high alkalinity.

Our results demonstrate the power of the study of a wide range of museum collection material. It does, however, also show that a lack of knowledge about the exact origin of fossils within the sedimentary succession leads to contradictive interpretations. It is, for example, not clear, whether the occurrence of both freshwater and brackish-water proxies reflects different time-equivalent environments, a large-scale trend of lake evolution, or repeated seasonal turnovers. Another contradiction is that some rhinos and other vertebrates point to the existence of swampy habitats, which is not well supported by the plant record and the geology-based assumption of a steep crater slope. Furthermore, the incomplete taxonomic knowledge of crucial fossil groups, such as diatoms, as well as the lack of sedimentological studies hinders final conclusions.

Future studies will focus on yet poorly understood organism groups that are crucial for palaeoecological and climatological questions, such as diatoms and pollen. Geochemical studies of the sediments and stable isotopes of shells and teeth will complement these interdisciplinary studies. A detailed analysis of the sedimentary sequence will help to understand the fine sediment lamination and if this was possibly caused by climatic seasonality and/or solar forcing. Further efforts for geochronological dating should be made also for this question. Drillings are required as well, because the sequence is incomplete due to landslides and outcrops are scarce. A sedimentary facies analysis can be used to construct a three-dimensional model of the different sedimentary environments.

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Appendix A. Diatoms from Schauderna (1983)

Site no. 1

Achnanthes lanceolata
Amphora szabói
Navicula halionta var. *directa*

Site no. 2

Chaetoceros sp. spores
Cymbella cistula
Cymbella cymbiformis var. *nonpunctata*
Eunotia pectinalis
Fragilaria brevistriata
Fragilaria construens
Fragilaria construens var. *venter*
Fragilaria leptostauron
Gomphonema intricatum
Navicula radiosa
Nitzschia sp.
Rhopalopia gibba
Synedra ulna
Synedra sp.

Appendix B. Pollen from the S11 excavation

Abies
Acer
Alnus
Apiaceae
Araliaceae
Arecaceae
Asteraceae
Betula
Carpinus
Carya
Castanopsis
Cupressaceae
Cyperaceae
Engelhardia
Ephedra
Ericaceae
Fagus
Ilex
Magnolia
Myrtaceae
Nyassa
Oleaceae
Picea
Pinus
Poaceae
Podocarpium
Polypodiaceae
Pterocarya
Quercus
Rutaceae
Sapotaceae
Sparganium
Styracaceae
Taxodiaceae
Tilia
Tragopogon
Ulmus
Vitaceae

Appendix C. Flora. Abbreviations: L = Leaf, F = Fruit, P = Pollen, H = Wood. (Compilation: J. Kovar-Eder, A. Roth-Nebelsick and F. Göhringer). Data from Endriss (1889), Süss and Mädel (1958), Mädel (1960), Rüffle (1963), Gregor (1986), Gregor (1997), Schweigert (1998), Kottik (2002), Kovar-Eder and Kvaček (2007), incl. updates.

	Endriss (1889)	Süß & Mädel (1958)	Mädel (1960)	Rüffle (1963)	Kvaček & Rüffle (1966)	Gregor (1986)	Gregor (1997)	Schweigert (1998)	Kottik (2002)	Kovar-Eder & Kvaček (2007) incl. current revision	S11 excavation
L				*Pteridium oeningense*		*Pteridium oeningense*		*Pteridium oeningense*		*Pteridium oeningense*	
L						*Adiantum* sp.		*Adiantum* sp.		*Adiantum* sp.	
L						cf. *Polypodium* sp.				Polypodiaceae	
L						*Lygodium* cf. *gaudinii*					
P				*Lycopodium* sp.							
P									*Selaginella* sp.	*Selaginella* sp.	
P									*Taxodiaceae*	*Cupressaceae* (Taxodiaceae)	
L				Glyptostrobus *europaeus*		*Cupressaceae*				*Cupressaceae* (*Cupressoideae*)	
F				*Cupressospermum* sp., pl. 1 fig. 17		*Cupressospermum* sp.				*Cupressospermum* sp.	
F				*Pseudotsuga* sp., pl. 1 fig. 16		*Coniferae* gen. et sp. indet.				*Saportaspermum* sp.	1x *Saportaspermum* sp.
P				*Sciadopitys*-artige Pollen							
?	*Taxodium dubium*										
P				*Pinus* sp.						*Pinus* sp.	
F						cf. *Pinus* sp.					
P									*Pinaceae*	Pinaceae	
?	*Pinus palaeostrobus*										
B				*Helobiaephyllum undulatum*						*Zizyphus zizyphoides*	
B				*Helobiaephyllum trinervium*						*Zizyphus zizyphoides*	
B				*Potamogeton* sp.							
B				*Graminophyllum ellipsoideum*							
B				*Graminophyllum amphistomatosum*						*Palmophyllum*	
B				*Graminophyllum concavum*							
F				*Panicum minutiflorum* p.p.		*Ruppia maritima-miocenica*				*Ruppia maritima-miocenica*	
F				*Panicum minutiflorum* p.p.		*Ruppia palaeomaritima*				*Ruppia palaeomaritima*	
F								*Ruppia*			
?	*Bambusium* sp.										
?	*Smilax* sp.										
?						*Limnocarpus eseri*				*Limnocarpus eseri*	
B				*Palmophyllum* sp.						*Palmophyllum* sp.ev. *Chamaerops*	
B				*Juncus* sp.							
F				*Spirematospermum wetzleri*		*Incertae sedis*				*Incertae sedis*	Incertae sedis
F						Hydrocharitaceae gen. et sp. indet.					
F						*Stratiotes* sp.				*Stratiotes* sp.	
F						Alismataceae gen. et sp. indet.					
F						Cyperaceae gen. et sp. indet.					
F				Weitere Grasreste, ? Carex							
P									Arecaceae gen. et sp. indet.	Arecaceae	
P									Poaceae gen. et sp. indet.	Poaceae	
B				*Populus balsamoides* pl. 2 fig. 12						*Populus balsamoides*	
B				*Populus balsamoides* pl. 3 fig. 1						*Populus populina*	
F				Kelchrest, pl. 15 fig. 13		*Populus* sp.				*Populus* sp.	
B				*Salix* sp.						*Salix* sp.	
L											1x *Salix* sp.
F											2x *Salix* sp.*Fruit*
B ?	*Salix varians*										
F				*Myrica praeesculenta*		*Myrica* sp.				*Dicotylophyllum* sp. (non *Myrica*!)	
B				*Juglans acuminata*						*"Juglans" acuminata*	5x *"Juglans" acuminata*
F				cf. *Cyclocarya cyclocarpa*		*Pteleaecarpum europaeum*				*Craigia bronnii*	
F				*Engelhardtia macroptera*		*Engelhardtia macroptera*				*Engelhardia macroptera*	2x *Engelhardia macroptera*
P				*Engelhardtia*-artige Pollen					*Engelhardia* sp.	*Engelhardia* sp.	
P				*Carya* sp.					*Carya* sp.	*Carya* sp.	
F						cf. *Carya vel Juglans* sp.					
P				*Pterocarya* sp.					*Pterocarya* sp.	*Pterocarya* sp.	
P				Betulaceen-artige Pollenformen							

(continued on next page)

Appendix C (*continued*)

	Endriss (1889)	Süß & Mädel (1958)	Mädel (1960)	Rüffle (1963)	Kvaček & Rüffle (1966)	Gregor (1986)	Gregor (1997)	Schweigert (1998)	Kottik (2002)	Kovar-Eder & Kvaček (2007) incl. current revision	S11 excavation
B				*Castanea atavia*						*Quercus drymeja*	
B				*Castanopsis glandulosa*							
P				Fagaceen-artige Pollen							
P									*Castanopsis* sp.	*Castanopsis* sp.	
L				*Quercus decurrens?*							
W							*Quercus* ex.gr. *kubinyi*				
L ?, P	*Quercus* sp.								*Quercus* sp.	*Quercus* sp.	
P									*Lithocarpus* sp.	*Lithocarpus* sp.	
P									*Trigonobalanopsis* sp.	*Trigonobalanopsis* sp.	
L, F	*Planera ungeri*			*Zelkova ungeri*		*Zelkova ungeri*	*Zelkova ungeri*	*Zelkova zelkovaefolia*		*Zelkova zelkovifolia*	5x *Zelkova leaf*
L, F				*Zelkova praelonga*		*Zelkova praelonga*	*Zelkova praelonga*			*Zelkova zelkovifolia*	
F				*Ulmus* cf. *protociliata*		*Ulmus* sp.				*Ulmus* sp.	1x *Ulmus* sp.
F				*Ulmus* sp. pl. 5 fig. 14		*Koelreuteria macroptera*				*Craigia bronnii*	
L				*Ulmus* sp. pl. 5 fig. 15						*Ulmus* sp.	1x *Ulmus* sp.
L ?	*Ulmus braunii*										
P									*Ulmus* sp.	*Ulmus* sp.	
L				*Celtis begonioides*			*Celtis begonioides*	*Celtis* sp.		*Celtis begonioides*	2x *Celtis* sp.
F						*Celtis* cf. *lacunosa*				*Celtis lacunosa*	
F, P						*Alnus* sp.			*Alnus* sp.	*Alnus* sp.	
P									*Betula* sp.	*Betula* sp.	
P									*Carpinus* sp.	*Carpinus* sp.	
L				*Tremophyllum tenerrimum*			*Tremophyllum tenerrimum*	*Cedrelospermum*		*Cedrelospermum ulmifolium*	3x *Cedrelospermum* sp.
P				*Ulmaceae*					*Ulmaceae*	*Ulmaceae*	
L				cf. *Broussonetia* sp.						*? Vitaceae*	
P				*Chenopodiaceen-artige Pollen*					*Chenopodiaceae*	*Chenopodiaceae*	
F				*Clematis panos*		*Cladiocarya trebovensis*				*Cladiocarya trebovensis*	
L				cf. *Magnolia attenuata*						*Magnolia* sp.	
L				Magnolienartige Blätter, pl. 7 figs. 2-3						*Magnolia* sp.	
F				*Magnolia sinuata*		Betulaceae (vel Fagaceae) gen. et sp. indet.					
F						*Magnolia* cf. *lusatica*				*Magnolia lusatica*	
L				*Laurophyllum princeps*						*Laurophyllum pseudoprinceps*	
L				*Laurus primigenia*			*Laurus primigenia*			*Laurophyllum* sp.	2x *Laurophyllum* sp.
L				*Laurus reussii*			*Laurus reussii*			*Laurophyllum* sp.	
L				*Laurus obovata*						*Laurophyllum* sp.	
L				*Laurus styracifolia*							
L				*Cinnamomophyllum polymorphum*				*Daphnogene polymorpha*		*Daphnogene polymorpha*	2x *Daphnogene* sp.
L				*Cinnamomophyllum scheuchzeri*			*Cinnamomum scheuchzeri*			*Daphnogene polymorpha*	
F				*Lauraceenartige Fruchtreste* p.p.		*Lauraceae* gen. et sp. indet.				*Lauraceae*	1x *Lauraceae fruit*
F				*Lauraceenartige Fruchtreste* p.p.		*Gleditsia knorrii*					
L, F	*Podogonium knorrii*			*Podogonium oehningense*		*Gleditsia knorrii*	*Gleditsia knorrii*	*Podocarpium podocarpum*		*Podocarpium podocarpum*	4x *Podocarpium podocarpum fruit*
L	*Podogonium lyellianum*			*Podogonium lyellianum*						*Podocarpium podocarpum*	
P							*Gleditsia lyelliana*		*Podocarpium podocarpum*	*Podocarpium podocarpum*	
L				*Gleditschia suevica*						*Podocarpium podocarpum*	
F				*Leguminocarpon bousqueti*		*Leguminocarpon bousqueti*				*Leguminocarpon bousqueti*	
F						*Leguminocarpum* div. sp.					
L				*Caesalpinites salteri*						legume-type	
L				*Leguminosenartiger Blattrest*				*Acacia parschlugiana*		*"Acacia" parschlugiana*	
F				*Fagara europaea*					*Rutaceae gen. et sp. indet.*	*Ailanthus* sp.	2x *Ailanthus* sp.
L				*Atalantia miocenica*						legume-type	
P									Rutaceae	Rutaceae	
F				*Ailanthus confucii*		*Ailanthus confucii*	*Ailanthus confucii*			*Ailanthus confucii*	
L				*Ailanthus-ähnlicher Blattrest*						*Ailanthus* sp.	
L				*Simarubaceophyllum picrasmoides*				*Koelreuteria*		*Koelreuteria* sp.	1x *Koelreuteria* sp.
F				*Toona seemannii*		*? Toona seemanni*	*Toona seemanni* problematic record			*? Toona seemanni*	
L								*Toona*		*Ailanthus* sp.	
L				*Rhus pyrrhae*						*Vitaceae*	
L				*Rhus pteleaefolia*						*Dicotylophyllum* sp.	
F				*Embothrites borealis*		*Embothrites borealis*	*Cedrelospermum aquense*	*Cedrelospermum*		*Cedrelospermum aquense*	
P				*Ilex*-artige Pollen					*Ilex* sp.	*Ilex* sp.	
L				*Acer integrilobum*			*Acer integrilobum*			*Acer integrilobum*	
L, F, P				*Acer* sp.		*Acer* div. sp.			*Acer* sp.	*Acer* sp.	3x *Acer fruit*

Appendix C (*continued*)

	Endriss (1889)	Süß & Mädel (1958)	Mädel (1960)	Rüffle (1963)	Kvaček & Rüffle (1966)	Gregor (1986)	Gregor (1997)	Schweigert (1998)	Kottik (2002)	Kovar-Eder & Kvaček (2007) incl. current revision	S11 excavation
L	*Acer trilobatum*										
L	*Sapindus falcifolius*			*Sapindus fa lcifolius*			*Sapindus falcifolius*			*Sapindus falcifolius*	3x *Sapindus falcifolius*
F				*Koelreuteria macroptera*		*Koelreuteria macroptera*		*Koelreuteria*		*Koelreuteria macroptera*	
L				*Berchemia parvifolia*			*Berchemia parvifolia*			*Berchemia parvifolia*	
L				*Rhamnus brevifolius*						*Berchemia parvifolia*	
L				*Rhamnus deletus*							
L				*Zizyphus tiliaefolius*						*? Zizyphus zizyphoides*	
F	*Ampelopsis ludwigii*			cf. *Ampelopsis ludwigii*		*Ampelopsis rotundatoides*				*Ampelopsis rotundatoides*	
F						Vitaceae gen. et sp. indet.					
P									*Vitaceae* gen. et sp. indet.	Vitaceae	
L				*Tetrastigmophyllum rottense*						Vitaceae	
F				*Tarrietia germanica*		*Koelreuteria macroptera*					
P				*Tilioide Pollenformen*							
P									*Tilia* sp.	*Tilia* sp.	
P									*Craigia* sp.	*Craigia* sp.	
L				*Alangium tiliaefolium*						*Dombeyopsis lobata* (leaf belonging to Craigia fruits)	
F				*Nyssa disseminata*		Incertae sedis					
F						*Nyssa ornithobroma*				*Nyssa ornithobroma*	
flower				*Nyssa-ähnlicher flowernrest*							
P				*Ericaceae*							
L				*Myrsinophyllum randeckense*	*Symplocos randeckense*					*Dicotylophyllum* sp.	
L				*Sideroxylon salicites*						Lythraceae	
P									*? Sideroxylon* sp.	*? Sideroxylon* sp.	
P				Sapotaceen-artige Pollen					Sapotaceae	Sapotaceae	
flower				*Diospyros brachysepala*		*"Cornus" brachysepala*				*Diospyros brachysepala*	
L ?	*Diospyros lancifolia*										
L				*Plumiera neriifolia*						*Dicotylophyllum* sp.	
L				*Ficus multinervis*						*Dicotylophyllum* sp.	
L				*Ficus arcinervis*						*Dicotylophyllum* sp.	
F				*Cypselites* sp.		*Cypselites* sp.(?)				*Cypselites* sp.	
P									Compositae gen. et sp. indet.	*Compositae*	
P									Caryophyllaceae gen. et sp. indet.	Caryophyllaceae	
W			*Carapoxylon fasciatum*								
W			*Carapoxylon ornatum*								
W		*Laurinoxylon seemannianum*									
F						*Schizandra moravica*				*Schizandra moravica*	
F						*Nymphaeaceae gen. indet.*					
F						cf. *Corylopsis urselensis*					
F						*Umbelliferopsis* cf. *molassicus*				*Umbelliferopsis* cf. *molassicus*	
F				unbestimmte Reste pl. 15, figs 16, 18		*Fraxinus* sp.				*indet. fruit remains*	
F						*Olea moldavica*				*Olea moldavica*	
P									*Oleaceae* gen. et sp. indet.	Oleaceae	
F						*Carpolithus* sp. *(Gordonia vel Polyspora* sp.*)*					
F						*Carpolithus* sp.					
						(Nymphaeacee)					
flower						*Antholithus* div. sp.					1x *Antholithus* sp.
flower						*Calyx* sp.					
P									*Distylium* sp.	*Distylium* sp.	
P									*Liquidambar* sp.	*Liquidambar* sp.	
P									*Ephedra* sp.	*Ephedra* sp.	
P									Styracaceae gen. et sp. indet.	Styracaceae	
P									Empetraceae gen. et sp. indet.	Empetraceae	
P									Araliaceae gen. et sp. indet.	Araliaceae	
L ?	*Ceanothus polymorphus*										
L ?	*Andromeda protogaea*										
?	*Prunus* sp.										
L ?	*Colutea antiqua*										

Appendix D. Insects with references of the first records from the Randeck Maar and their currently valid name with reference. Data from Schawaller (1986), Armbruster (1938), Kotthoff et al. (2011), Wappler et al. (2012), von Rosen (1913), Armbruster (1941), Hering (1930), Zeuner and Manning (1976)

Taxon	Randeck Maar reference	Valid name	Valid name reference
Anthicidae gen. spec.	Schawaller 1986		
Hauffapis scharmanni Armbruster	Armbruster 1938	*Apis armbrusteri* Zeuner	Kotthoff et al. 2011
Hauffapisi scheeri Armbruster	Armbruster 1938	*Apis armbrusteri* Zeuner	Kotthoff et al. 2011
Hauffapis scheuthlei Armbruster	Armbruster 1938	*Apis armbrusteri* Zeuner	Kotthoff et al. 2011
Bombus (*Bombus*) *randeckensis* Wappler	Wappler et al. 2012		
Cantharidae gen. (cf. *Cantharis*) spec.	Schawaller 1986		
Carabidae gen. (cf. *Bembidion*/*Tachys*) spec.	Schawaller 1986		
Chrysomelidae gen. (cf. *Lilioceris*/*Crioceris*, *Timarcha*, *Cassida*, and *Donacia*) spec.	Schawaller 1986		
Coccinellidae gen. spec.	Schawaller 1986		
Curculionidae gen. (cf. *Phyllobius*and *Apion*) spec.	Schawaller 1986		
Diacorixa germanica Popov	Popov 1989		
Dryopidae gen. (cf. Esolus) spec.	Schawaller 1986		
Dytiscidae gen. (cf. Agabus) spec.	Schawaller 1986		
Eutermes fraasi V. Rosen	von Rosen 1913		
Eutermes nickeli Armbruster	Armbruster 1941		
Eutermes sachtlebini Armbruster	Armbruster 1941		
Helophilus nothobombus Kotthoff & Schmid	Kotthoff & Schmid 2005		
Hydrophilidae gen.(cf. *Berosus* and *Enochrus*) spec.	Schawaller 1986		
(*Leucotermes*)? *dofleini* Armbruster	Armbruster 1941	*Reticulotermes dofleini*	Emerson 1971
Lycoria berckhemeri Armbruster	Armbruster 1938	*Sciara berckhemeri*	Evenhuis 1994
Lycoria braeuhaeuseri Armbruster	Armbruster 1938	*Sciara braeuhaeuseri*	Evenhuis 1994
Lycoria branconis Armbruster	Armbruster 1938	*Sciara branconis*	Evenhuis 1994
Lycoria deffneri Armbruster	Armbruster 1938	*Sciara deffneri*	Evenhuis 1994
Lycoria dietleni Armbruster	Armbruster 1938	*Sciara dietleni*	Evenhuis 1994
Lycoria ehrati Armbruster	Armbruster 1938	*Sciara ehrati*	Evenhuis 1994
Lycoria endrissi Armbruster	Armbruster 1938	*Sciara endrissi*	Evenhuis 1994
Lycoria fraasi Armbruster	Armbruster 1938	*Sciara fraasi*	Evenhuis 1994
Lycoria hennigi Armbruster	Armbruster 1938	*Sciara hennigi*	Evenhuis 1994
Lycoria hoelzlei Armbruster	Armbruster 1938	*Sciara hoelzlei*	Evenhuis 1994
Lycoria joossi Armbruster	Armbruster 1938	*Sciara joossi*	Evenhuis 1994
Lycoria kluepfeli Armbruster	Armbruster 1938	*Sciara kluepfeli*	Evenhuis 1994
Lycoria lengersdorfi Armbruster	Armbruster 1938	*Sciara lengersdorfi*	Evenhuis 1994
Lycoria milleri Armbruster	Armbruster 1938	*Sciara milleri*	Evenhuis 1994
Lycoria pompeckii Armbruster	Armbruster 1938	*Sciara pompeckii*	Evenhuis 1994
Lycoria quenstedti Armbruster	Armbruster 1938	*Sciara quenstedti*	Evenhuis 1994
Lycoria seemani Armbruster	Armbruster 1938	*Sciara seemani*	Evenhuis 1994
Lycoria wagneri Armbruster	Armbruster 1938	*Sciara wageri*	Evenhuis 1994
Mastotermites stuttgartensis Armbruster	Armbruster 1941	*Miotermes randeckensis* V. Rosen	Emerson 1971
Metatermites statzi Armbruster	Armbruster 1941		
Miopieris talboti Zeuner	Zeuner 1942		
Miotermes randeckensis V. Rosen	von Rosen 1913		
Calotermites (Glyptotermites) assmuthi Armbruster	Armbruster 1941		
Calotermes (Neotermites) frischi Armbruster	Armbruster 1941	*Proelectrotermes roseni* Armbruster	Emerson 1971
Calotermes (Neotermites) roseni Armbruster	Armbruster 1941	*Proelectrotermes roseni*	Emerson 1971
Odontomyia spec.	Kühbandner & Schleich 1994		
Paraleia minor Armbruster	Armbruster 1938	*Armbrusteleia minor*	Evenhuis 1994
Paraleia rhymosides Armbruster	Armbruster 1938	*Armbrusteleia rhymosides*	Evenhuis 1994
Phytomyza lethe Hering	Hering 1930		
Proallodia delopsides Armbruster	Armbruster 1938		Evenhuis 1994
Proallodia rhymosides Armbruster	Armbruster 1938		Evenhuis 1994
Proapolephthisa manotides Armbruster	Armbruster 1938		Evenhuis 1994
Prodelopsis epicyptides Armbruster	Armbruster 1938		Evenhuis 1994
Prodelopsis exechides Armbruster	Armbruster 1938		Evenhuis 1994
Prodocosia rondaniellides Armbruster	Armbruster 1938		Evenhuis 1994
Proepicypta obesa Armbruster	Armbruster 1938		Evenhuis 1994
Prohadroneura dziedzickides Armbruster	Armbruster 1938		Evenhuis 1994
Prohalictus schemppi Armbruster	Armbruster 1938	*Halictus schemppi* (Armbruster)	Zeuner & Manning 1976
Proleia landrocki Armbruster	Armbruster 1938		Evenhuis 1994
Promacrocera archaica Armbruster	Armbruster 1938	*Macrocera archaica*	Evenhuis 1994
Promycetomyia neoempherides Armbruster	Armbruster 1938		Evenhuis 1994
Pronovakia incerta Armbruster	Armbruster 1938		Evenhuis 1994
Prophronia dynatosomides Armbruster	Armbruster 1938		Evenhuis 1994
Prophthinia coelosides Armbruster	Armbruster 1938		Evenhuis 1994
Prophthinia leides Armbruster	Armbruster 1938		Evenhuis 1994
Protrichonta delopsides Armbruster	Armbruster 1938		Evenhuis 1994
Rhinotermites dzierzoni Armbruster	Armbruster 1941		
Rhinotermites kuehni Armbruster	Armbruster 1941		
Rhinotermites wasmanni Armbruster	Armbruster 1941		
Staphylinidae gen.(cf. Tachyporus) spec.	Schawa ller 1986		
Termes drabatyi Armbruster	Armbruster 1941		
Termes hauffi Armbruster	Armbruster 1941		
Termes korschefskyi Armbruster	Armbruster 1941		
Termes scheeri Armbruster	Armbruster 1941		
Termes scheuthlei Armbruster	Armbruster 1941		
Termes schleipi Armbruster	Armbruster 1941		
Termes stitzi Armbruster	Armbruster 1941		
Termes weismanni Armbruster	Armbruster 1941		
Zygaena miocenica Reiss	Reiss 1936	Naumann 1987	
Zygaenites controversus Burgeff	Burgeff 1951	Naumann 1987	

Appendix E. Aquatic and terrestrial gastropods

Archaeozonites costatus Sandberger, 1874
Caracollina phacodes (Thomae, 1845)
Cepaea silvana (Klein, 1853)
Cochlicopa subrimata loxostoma (Klein, 1853)
Columella sp.
Discus pleuradrus (Bourguignat, 1881)
Ferrissia deperdita (Desmarest 1814)
Granaria sp.
Gyraulus kleini (Gottschick & Wenz, 1916)
Helicodonta involuta (Thomae, 1845)
Klikia coarcata (Klein, 1853)
"Leucochropsis" kleini (Klein, 1847)
Lymnaeidae indet.
Napaeus sp.
Negulus cf. *suturalis*(Sandberger, 1858).
Opeas minutum (Klein, 1853)
Planorbarius cf. *mantelli* (Dunker 1848)
Pomatias conica (Klein, 1853)
Pseudoleacina eburnea (Klein, 1853)
Triptychia sp.
Tropicomphalus (*Pseudochloritis*) *extinctus* (Rambur, 1862)
Tropicomphalus (*Pseudochloritis*) *incrassata* (Klein, 1853)
Vallonia cf. *subpulchella* (Sandberger, 1874)
Vitrina cf. *suevica* Sandberger, 1874

Appendix F. List of fish, amphibian and reptile species, their occurrence in the Randeck Maar and habitat preferences

Taxon	Larger vertebrates from the 1895 to 1933 collections	Calcareous laminites	Amphibian pond 1977	Habitat				
				Full aquatic	Semiaquatic	Periaquatic	Terrestrial	
Fishes								
Prolebias aff. *weileri*von Salis,1967		x		x				
Amphibians								
Albanerpeton inexpectatum Estes and Hoffstetter, 1976			x			?	x	Subterran
Chelotriton paradoxus Pomel, 1853 (= ? *Palaeopleurodels hauffi* Herre, 1941)		x	x			x		
Lissotriton sp.		x	x			x		
Palaeobatrachus hauffianus (E. Fraas,1909)		x		x				
Eopelobates vel *Pelobates* sp.		x				x		
Ranidae gen. et sp. indet.		x	?		x			
Pelophylax sp.			x	x				
Reptiles								
Ptychogaster sp.	x					x		
Clemmydopsis sp.	x					x		
Testudo sp.	x						x	Heliophil
Chelydropsis sp.	x			x				
Diplocynodon cf. *ungeri* Prangner, 1845	x	? x	x	x				
Chamaeleo simplex Schleich,1994			x				x	Arborial
Lacerta sp.			x				x	Heliophil
Ophisaurus sp.			x				x	Heliophil
Vipera sp.			x				x	Heliophil
Texasophis cf. *meini* Rage and Holman, 1984			x				x	Heliophil
Natricinae gen. et sp. indet.			x		?	?		Heliophil
Birds								
Palaelodidae gen. et sp. indet.	x					x		
Aves gen. et sp. indet.		x	?x					

Appendix G. Small mammals from several excavations. For abbreviations see excavations. “1966” = donation to Tübingen collection according to Westphal (1963). Number = numbers of identified specimens

Taxon	A77	W62	1966	S11
Didelphimorphia Gill, 1872				
Didelphidae Gray, 1821				
Amphiperatherium frequens (V.Meyer,1846)	2			1
Erinaceomorpha Gregory, 1910				
Erinaceidae G. Fischer, 1814 5t				
Galerix cf. *symeonidisi* Doukas	3			1
Erinaceinae gen. et sp. indet.	1			
Soricomorpha Gregory, 1910				
Dimylidae Schlosser, 1887				
cf. *Plesiodimylus* sp.	2			
Soricidae G. Fischer, 1814				
Heterosoricinae gen. et sp. indet.	3			
cf. *Allosorex gracilidens* Viret & Zapfe,1952	3			
Talpidae G. Fischer, 1814				
Proscapanus sp.	10			
Talpa minuta Blainville, 1838	5			
Talpidae gen. et sp. indet.				1
Chiroptera Blumenbach, 1779				
Molossidae Gervais, 1856				
Mormopterus helveticus (Revilliod, 1920)	6		1	1
Megadermatidae Allen,1864				
cf. *Megaderma* sp.	1			
Vespertilionidae Gray, 1821				
cf. *Eptesicus campanensis* Baudelot, 1970	1			
cf. *Kerivoula murinoides* (Lartet, 1851) and/or *Eptesicus noctuloides* (Lartet, 1851)	15			2
cf. *Myotis ziegleri* Horacek, 2001	1			
cf. *Miniopterus fossilis* Zapfe, 1950	1			
Vespertilionidae gen. et sp. indet.	12			2
Rodentia Bowdich, 1821				
Sciuridae Fischer V. Waldheim, 1817				
Spermophilinus besanus Cuenca Bescós, 1988	10			1
Palaeosciurus sutteri Ziegler & Fahlbusch, 1986	8			
Heteroxerus aff. rubricati Crusafont,Villalta & Truyols, 1955				1
Sciuridae gen. et sp. indet.	2			
Gliridae Muirhead, 1819				
Glirudinus undosus Mayr, 1979	2	1		
Glis sp.	14			
Muscardinus aff. *sansaniensis* (Lartet, 1851)	1			
Glirulus aff. *conjunctus* (Mayr, 1979)	34			
Microdyromys koenigswaldi De Bruijn,1966	3			
Bransatoglis cadeoti Bulot, 1978	36			1
Eomyidae Deperet & Douxami, 1902				
Keramidomys thaleri Hugueney & Mein, 1968	77	3		
Eomyops aff. catalaunicus (Hartenberger, 1966)	5			
Cricetidae Fischer V. Waldheim, 1817				
Democricetodon gracilis Fahlbusch, 1964	20	4		4
Democricetodon mutilus Fahlbusch, 1964	12			13
Eumyarion cf. *weinfurteri* (Schaub & Zapfe,1953)	8			
Neocometes aff. *similis* Fahlbusch, 1964	10			
Anomalomyidae Schaub, 1925				
Anomalomys minor Fejfar, 1972	9			
Lagomorpha Brandt, 1855				
Ochotonidae Thomas, 1897				
Prolagus oeningensis König, 1825	2			
Total number	320	8	1	28

Appendix H. Large mammals from several excavations

Proboscidea Illliger, 1811
Gomphotheriidae Hay,1821
Gomphotherium angustidens (Cuvier 1817)
Carnivora Bowdich, 1821
Ursidae Fischer von Waldheim, 1817
Hemicyoninae Frick, 1926
cf. *Plithocyon stehlini* (Hürzeler, 1944)
Ursinae Fischer von Waldheim, 1817
Ursavus sp.
Mustelidae Fischer von Waldheim, 1817
Mustelidae indet. (2 taxa)
Perissodactyla Owen, 1848
Equidae Gray, 1821
Anchitherium aurelianense (Cuvier 1812)
Rhinocerotidae Gray, 1821
Brachypotherium sp.
Prosantorhinus sp.
Rhinocerotidae indet.
Artiodactyla Owen, 1848
Suidea Gray, 1821
Suidae indet.
Cainotheriidae Cope, 1881
Cainotherium cf. *bavaricum* Berger 1959
Tragulidae Milne-Edwards, 1864
Dorcatherium cf. *crassum* Lartet 1851
Palaeomerycidae Frick, 1937
*Palaeomeryx bojan*i v.Meyer 1834
Cervidae Gooldfuss, 1820
Heteroprox sp.
Lagomeryx parvulus Roger 1898
Bovidae Gray, 1821
Bovidae indet. (small form)

Appendix I. Contributions of the authors

Contributions of the single authors to this paper: Rasser: Field work, aquatic gastropods, palaeoenvironmental reconstructions, coordination, compilation of text; Bechly: Insects; Böttcher: Lower vertebrates in general; Ebner: Pollen; Heizmann: Large mammals; Höltke: Terrestrial gastropods; Joachim: Insects; Kern: Pollen, climate, comparisons with other maars; Kovar-Eder: Macroflora, IPR analysis; Nebelsick: Field work, compilation of text; Roth-Nebelsick: Field work, compilation of macroflora data; Schweigert: Geology; Schoch: Amphibians; Ziegler: Small mammals, biostratigraphy.

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