SEM pollen analysis of Miocene deposits of Entrischenbrunn (Bavaria, Germany) reveal considerable amounts of pollen of subhumid and sclerophyllous together with azonal water plants reflecting the vegetation mosaic of a braided river system

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ABSTRACT

The 1 m thick intercalated marly sediments of Entrischenbrunn represent a floodplain pond within a braided fluvial system of late Langhian age. The organic rich upper part of the marls that are characterized by the presence of numerous plant macrofossils, are investigated for palynomorphs with SEM. The results reveal that many typical azonal broad leaved forest elements were present (e.g., *Fraxinus* and *Liquidambar*) and some of the common macrofossils, such as *Hemitrapa, Podocarpium*, *Platanus* sp., *Quercus* spp. etc. However, because of non-resistant pollen walls, the two dominant components of the macroflora, *Daphnogene* and *Populus* are not represented in the palynoflora. In contrast, plants not known from macrofossils or rare for this locality are present: several aquatic plants (e.g., *Callitriche* sp., *Ludwigia* sp.*, Decodon* sp.), and a large portion of more subhumid and sclerophyllous plants such as *Celtis* "*tournefortii*-type", two *Ephedra* spp., two *Erica* spp. affiliable with Mediterranean species, *Quercus* sp. section Ilex, a Sapoteae, *Sideroxylon* sp., *Rehderodendron* sp., *Ulmus* sp. section Foliaceae *Zelkova* "*abelicea/serrata*-type", and *Ziziphus* "*mucronata/mauritania/jujube*-type", whereas *Diospyros* sp. and cf. *Royena* sp. can be interpreted to present humid to subhumid conditions. The reasons for this mixture might be threefold: 1. localized well-drained substrates and water loss on particularly pebbly, gravelly and sandy deposits of the braided river system or 2. presence of a geographically controlled localized lower humidity in that area, or 3. because of a generally drier period within the Middle Miocene.

1. Methodology

Of the ca. one metre thick lacustrine succession only three fine-grained, organic rich and marly clay samples of the lacustrine deposit were suitable for pollen analysis. The samples were washed and dried, powdered by hand using a mortar and pistil. The powder was treated in the classical way with HCl and HF with a following acetolysis to reduce organic material such as wood and other palynodebris, and to deepen the color of the palynomorphs. The resulting extract was mixed with glycerol and stored in small glass vials. Small drops of the extract were transferred onto glass slides, evenly spread to count and search for pollen. After screening 10 slides per sample a plateau and the saturation of diversity was reached. The pollen grains were then mounted with the help of a micro-manipulator (fine hair glued to a preparation needle) to clean drops of glycerol onto another glass slide and photographed with a Nikon Eclipse 80 microscope and ProgRes digital camera. After photographing, the pollen grains were again transferred with a micro-manipulator onto SEM stubs, washed with alcohol and then sputtered with gold. SEM investigation was done with a FEI Inspect S 5001. The stubs are stored under the inventory number IPUW7843_1 to IPUW7843–10 in the Department of Paleontology, University Vienna.

2. Introduction

2.1. Geological and stratigraphical background

The gravel and sand pit Entrischenbrunn near (Pfaffenhofen, (Bavaria, Germany 48.4854, 11.5409) consists of gravel, sands and intercalated marls of Middle Miocene age (Figs. 1, 2). The sediment succession is situated within the Upper Freshwater Molasse (OSM) between two marker horizons: the so called Brock-Horizon (Ries crater material) below, at the base of the sand pit, and 14.6 Myr old bentonites above,

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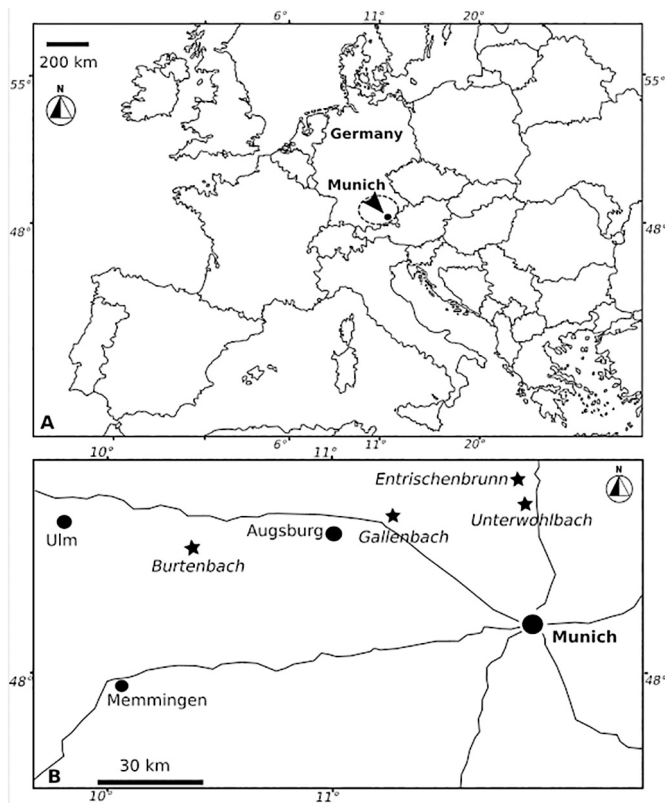*E-mail address:* christa.hofmann@univie.ac.at (C.-C. Hofmann).

Fig. 1. Sketch map of **A.** Europe and **B.** the Upper Fresh Water Molasse area between Augsburg and Munich showing the Entrischenbrunn locality and as well the localities used in the discussion.

which were dated by Rocholl et al. (2018b) and crop out in the nearby pit of Unterwohlbach. For the Brock Horizon currently differing magneto-stratigraphic results indicate ranges ages of 14,8 and14.9
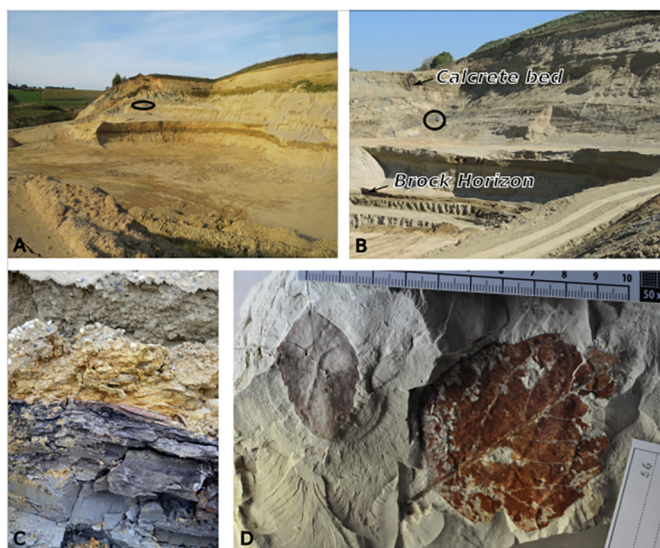

Fig. 2. Outcrop conditions of the Entrischenbrunn gravel pit **A.** view from far away, the ellipse encircling a palaeobotanist working at the ca. 1 m thick lens of marly clays of the sampling spot. **B.** Closer view of the gravel pit with the sampling position marked by a circle and the underlying Brock Horizon and an overlying calcrete bed that witnesses periodical desiccation. **C.** Close up of the sampled horizon with a sharp contrast between the organic rich marl and the sandy, gravelly fluvial deposits. The close up comprises less than 40 cm, photo courtesy of A. Groeger. **D.** abundant macrofloral elements comprising various *Populus mutabilis* Heer.

million years, respectively (Rocholl et al., 2018a, 2018b; Schmieder et al., 2018a, 2018b). However, based on small mammal stratigraphy, a cyclical subdivision of the Middle Miocene Upper Freshwater Molasse prepared by Fiest (1986; 1994) and later published by Heissig (2006), allows to narrow down the age of the Entrischenbrunn deposits to an interval between 14.9 to 14.7 million years (Fiest, pers. communication). The fossil leaf layer represent his OSM 8, which belongs to the "Middle Series" (= Mittlere Serie) of Dehm (1955), which should not be confused with the carpologically based OSM-phytozonation of Gregor (1982a). von Webenau (1995) renamed it to KZK (Karpozönosenkomplex) and additionally introduced his PZK (Phyllozönosenkomplex), a zonation based on the leaf taphocoenosises. Consequently, the locality represents the end or a succeeding period of the ca. 17 to 15 my old Mid-Miocene Climate Optimum (ends at 14.7 Ma after Holbourn et al., 2014) and is older than the Middle Miocene Climate Transition (Kovar-Eder and Teodoridis, 2018). According to current research by Fiest (Fiest, pers. communication) the deposits originate from a Middle Miocene braided river system that drained the North Alpine Foreland Basin (NAFB) towards the Rhone valley to the west, discharging its water load into the Mediterranean sea (Harzhauser et al., 2005). Since the flow direction matched the strike direction of molasse sediments, the lateral extension of this river system is either eroded (to the north) or covered by younger sediments (to the south). Only palynological research allows an insight into peripheral vegetation and environmental conditions of this basin.

In the gravel pit of Entrischenbrunn a one meter thick lens of lacustrine marl is wedged into the alternations of gravel and sands. This sequence is interpreted as deposit of a floodplain pond (Schmitt and Butzmann, 1997) and terminates with a several centimeters thick organic rich layer resulting from the siltation phase (Fig. 2). The sample with the best preserved pollen assemblage presented here originates from the organic rich layer, while the underlying limnic marls proved to be almost sterile in pollen, due to bad preservation (see below Results). About 10 m below, the Brock Horizon currently crops out in the deepest part of the pit. It contains up to 1 m large boulders, which are interpreted as ejected material from a meteorite impact in the Nördlinger Ries 80 km to Northwest (Sachse et al., unpublished data).

2.2. Macrofossil content

For more than 25 years fossils have been recovered from the Entrischenbrunn gravel pit near Pfaffenhofen north of Freising (Schmitt and Butzmann, 1997, Wallner and Gregor, 2011; Sautner and Werner, 2019; Fig. 1) and a new and particularly rich leaf flora has been collected (Table 1; Sachse et al., unpublished data). Despite of a rich macrofossil record for the Upper Freshwater Molasse (Obere Süßwassermolasse = OSM; e.g. Gregor, 1982a, 1982b; Gregor, 2011a, 2011b; Gregor and Sachse, 2016; Gregor et al., 2012; Jung, 1984, 1986, Knobloch, 1986, 1988; Sachse, 2018, 2022), palynological research is rare (e.g., Seitner, 1987; Gregor et al., 1989; Zetter and Ferguson, 2001: only *Trapa* pollen; some unpublished reports by Meier, NLFB-Hannover) and limited mostly to light microscopy based identifications with doubtful or ambiguous results.

The macrofossils of the investigated deposits of the NAFB usually reflect humid plant communities of a mostly azonal plant belt of a vast flood plain system (see Gregor, 2011b). However, a special feature of the leaf flora (Fig. 2; Sachse et al., unpublished data) of the Entrischenbrunn site is the absolute dominance of *Populus mutabilis* Heer, whose extant counterpart *P. euphratica* Olivier grows alongside ephemeral river beds from Central Asia to Northern Africa, as well as narrow-leaved sun leaves of *Daphnogene polymorpha* forma *bilinica* (Unger) Sitár et Kvaček (Sachse et al., unpublished data). Besides, other oaks (*Quercus drymeja* Unger) and xerophytic members of buckthorn and spindle tree families (Rhamnaceae and Celastraceae), which usually are only sporadically detected in the NAFB floras, are present

Table 1
Summarized macroflora based on Sachse et al. (unpublished data).

Family	Taxa
Aristolochiaceae	*Aristolochia colchica*
? Ephedraceae	? *Ephedra sotzkiana*
Lauraceae	*Daphnogene polymorpha, Laurophyllum pseudoprinceps, L.* Spp.
Smilacaceae	*Smilax* sp. "*Sagittifera*"-morphotype,? *S. miohavanensis*
Poales indet.	*Monocotyledonae* fam. gen. et sp. indet
Typhaceae	*Typha latissima*
Cyperaceae	*Rhizocaulon hambachense,*? *Carex* sp.
Poaceae	*Phragmites oeningensis*
Berberidaceae	*Mahonia heterophylla*
Ranunculaceae	*Clematis csabae*
Platanaceae	*Platanus leucophylla, P. lineariloba*
Buxaceae	*Buxus pliocenica*
Altingiaceae	*Liquidambar europaea*
Hamamelidaceae	"*Parrotia*"*pristina*
Vitaceae	*Tetrastigmophyllum betulaeforme, T. hungaricum, Vitis vitifolia*
Fabaceae	*Podocarpium podocarpum, Pueraria maxima, Gleditsia allemanica, Cassiophyllum berenices, "Acacia"oeningensis, "Caesalpinia"falconeri, "Glycyrrhiza"*aff. *deperdita, Leguminosites undulatus, "Robinia" regeli "Omphalobium"relictum,*
Rosaceeae	cf. *Rosa* sp., aff. *R. palustris* fos, "*Crataegus*"*longepetiolata, Sibiraea rottensis*
Rhamnaceae	*Berchemia multinervis, B. parvifolia, Frangula palaeofrangula, Ziziphus protolotus, Paliurus tiliifolius*
Cannabaceae	*Celtis japeti*
Ulmaceae	cf. *Cedrelospermum ulmifolium, Ulmus pyramidalis, U. minuta, U. braunii*
Fagaceae	*Trigonobalanopsis rhammnoides* vel *Castanopsis* sp. vel *Lithocarpus* sp., *Quercus drymeja, Q. mediterranea, Q. neriifolia*
Myricaceae	*Myrica lignitum, M.* cf. *macrodontata*
Juglandaceae	*Juglans acuminata*
Celastraceae	*Celastrus moravicus, Celastrophyllum cuneifolium*
Salicaceae	*Populus mutabilis, P. balsamoides, P. latior, Salix* sps.
Lythraceae	*Decodon gibbosus*
Anarcadiaceae	*Pistacia miolentiscus*
Myrtaceae	*Dicotylophyllum apollinis (Myrtus)*
? Adoxaceae	? *Viburnum* sp. vel *Sambucus* sp.
? Sapindaceae	"*Sapindus*"*cupanioides, S. falcifolius*
Rutaceae	*Zanthoxylon europaeum*
Simaroubaceae	*Ailanthus* cf. *ailanthifolia*
Thymelaeaceae	*Daphne aquitanica*
Polygonaceae	*Reynoutria paleojaponica*
? Sapotaceae	*Sapotacites minor*
? Ebenaceae	"*Diospyros*"*pannonica*"
Theaceae	*Ternstroemites pereger*
Symplocaceae	*Symplocos* sp.
Styracaceae	*Styrax burdigalensis,?Rehderodendron* sp.
Ericaceae	aff. *Vaccinium* sp.
Santalaceae	*Viscum morlotii*
Oleaceae	*Fraxinus inaequalis, F. grossedentata, Phillyrea pschechensis*
incertae sedis	"*Cedrela*"*sarmatica, "Myrica"oehningensis, "Neritinium"majus, "Rhus"pyrrhae, "Quercus"cruciata, "Viburnum"atlanticum, Dicotylophyllum* sps.

(Table 1). Probably a minor part of the macro flora from Entrischenbrunn originates from the zonal vegetation, that is interpreted as subhumid sclerophyllous forests (ShSF). This vegetation type was identified by Kovar-Eder and Teodoridis (2018) in 27 other Miocene localities from Central Europe. By using the Intergrated Plant Record method (Kovar-Eder and Kvaček, 2007) they suggested therefore that the ShSf was the most likely predominant zonal vegetation in Central Europe. The term ShSf combines characteristic leaf morphological and climatological features of a specific geographical area and is introduced by Kovar-Eder et al., 2008 for describing the corresponding zonal vegetation type. Sclerophylly describes a particular leaf morphological pattern of plants living in warm and dry climates, such as hard, leathery leaves stiffened with sclerenchyma and woody tissue and short distances between leaf nodes. These adaptions were developed to prevent moisture loss. Subhumid conditions are characterized by reduced humidity, that restrains the growth of trees. Such plant associations with small sclerophyllous and legume-like leaves exceeds 20% of the woody taxa.

To get a better understanding of the varying macrofossil results of the different localities in the Upper Freshwater Molasse (Sachse, 2022; Sachse and Schmitt, 2016; Sachse et al., unpublished data; Schmitt and Butzmann, 1997), and to get an estimation how much of the plants were either humid or subhumid/sclerophyllous, we focus here on palynologically investigated samples from Entrischenbrunn. The routine application of scanning electron microscopy helped to discriminate various taxa and allowed an approximation of their climatic and edaphic requirements.

3. Results

Of three samples from the lacustrine and floodplain deposits of Entrischenbrunn only the organic rich one is relatively diverse in pollen taxa (Table 2), the other two marl samples display very few broken bisaccates (*Pinus* spp.), fragments of algal cysts and unidentifiable material, despite thorough screening and represent only a part of the microflora of Entrischenbrunn: *Populus* and Lauraceae pollen usually has weak and non-resistant wall structures and are rarely preserved in fossil sediments, both were not found, despite the presence of many *Populus mutabilis* and *Daphnogene* Unger spp. Macrofossils. Unsurprisingly, the most common macrofloral elements such as the fruits of *Podocarpium podocarpum* (A. Braun) Herendeen and *Hemitrapa heissigii* Gregor are richly represented by their pollen counterparts (*Tricolporopollenites wackersdorfensis* Thiele-Pfeiffer and *Sporotrapoidites erdtmani* (Nagy) Nagy, respectively), and other macroflora elements are reflected in the pollen flora as well (Table 2). Generally, this heterogeneous assemblage reflects also the preservational and /or taphonomical conditions of the sediments (lacustrine marls), as only a few samples are suitable for palynology and therefore can only represent a part of the entire Entrischenbrunn microflora. However, there are some interesting features: Of 68 taxa, eight are water plants or plants growing near water, 17 are warmth loving plants that are interpreted to grow in drier habitats and/or under seasonally drier conditions (subhumid and/or sclerophyllous) or humid to subhumid conditions, two taxa are somewhat ambiguous, five are Pinaceae from the hinterland, five are undetermined, and the rest (approximately the half) is represented by typical azonal elements.

3.1. Description of selected pollen taxa and their affiliation with extant taxa and distribution today

The distribution of the modern equivalents (=extant most similar looking taxa under LM and SEM) of the fossil pollen taxa of subhumid and sclerophyllous plants from Entrischenbrunn (genus, genus section = similar to the section of the genus, and species-type = the most similar looking species) were summarized with the help of plants of the world online (POWO). Extant taxa are taken from "World checklist of selected plants" Royal Botanical Gardens, Kew (http://wcsp.science.kew.org), from www.tropicos.org., from the African plant database (www.ville-ge.ch/musinfo/bd/cjb/africa/) (version 3.4.0) and from Flora of China (www.efloras.org) and GBIF database (www.gbif.org.). The climatic ranges are given in the Koeppen-Geiger classification (updated by Kottek et al., 2006; Rubel et al., 2017) and the complete information is summarized in Table 3. Pollen terminology is based on Halbritter et al. (2018).

3.1.1. Subhumid and sclerophyllous elements (Plates I–III)
The elements described here in more detail comprises two *Ephedra* spp. with Mediterranean affinities, a non aquatic Poaceae gen. indet. with "avena" ornamentation, *Ulmus* sp. section Foliaceae, *Zelkova* "*abelicea/serrata*-type", *Celtis* "*tournefortii*-type", *Quercus* sp., section Ilex, *Ziziphus* "*mucronata/mauritana/jujuba*-type", *Sideroxylon* sp., an indetermined Sapotae, *Rehderodendron* sp., *Phillyrea* sp., and *Chenopodium* sp. Two Ebenaceae, cf. *Royena* and *Diospyros* sp. have today a pantropical distribution, but also species adapted to drier climates and might represent plants cooping with humid to subhumid

Table 2

Presence of pollen of the organic rich marly clay sample and probable macrofossil equivalents.

Family	Genus/taxon	N	Counts	Peculiar	Macro fossils
Pteridaceae	*Pteris-like*		1		/
Ephedraceae	*Ephedra*	2	3		*? Ephedra sotzkiana*
Pinaceae	*Pinus diploxylon*		6		/
	Pinus haploxylon		82		/
	Picea		1		/
	Abies		1		/
	Cathaya		6		/
	bisacc indet.		2		/
Cupressaceae	*Taxodium /Glyptostrobus*		18		/
Typhaceae	*Typha/Sparganium*		1		*Typha latissima*
Poaceae	gen. Indet	3	6		gen. indet.; *Phragmites oeningensis*
Buxaceae	*Buxus*		2		*Buxus pliocenica*
Platanaceae	*Platanus*		14		*P. leucophylla, P.lineariloba*
Altingiaceae	*Liquidambar*		5		/
Hamamelidaceae	gen. Indet		1		"*Parrotia*"pristina
Vitaceae	*Parthenocissus/Ampelopsis*		2		*Tetrastigmophyllum hungaricum, T. betulaeforme*
	?Vitis		5		*Vitis vitifolia*
Salicaceae	*Salix*		14		*Salix* (various taxa)
Fabaceae	*T. wackersdorfensis*		37	Tetrads	*Podocarpium podocarpum*
Ulmaceae	*Cedrelospermum-like*		36		cf. *Cedrelospermum ulmifolium*
	Ulmus	2	31		*Ulmus* sp. (5 taxa)
	Zelkova		7		/
	Celtis		19		*C. japeti, pirskenbergensis*
Rhamnaceae	*Ziziphus*		8		*?Ziziphus protolotus* Unger
Fagaceae	*Fagus*		9		/
	Quercus	?4	34		various *Quercus taxa*
	Castaneoideae		4		*Trigono vel Lithocarpus*
Juglandaceae	*Juglans*		5		*Juglans acuminata*
	Pterocarya		4		/
	Carya		11		/
	Engelhardioide		4		/
Myricaceae	*Myrica*		11		*Morella lignitum*
Betulaceae	*Alnus*		3		/
	Betula		4		/
Myrtaceae	*?Myrtus*		1		*Dicotylophyllum appolinis* (*?Myrtus*)
Onagraceae	*Ludwigia*		3		/
Lythraceae	cf. *Lythrum*		13	Lumps	/
	Decodon		21		*Decodon gibbosus*
	Sporotrapoidites heissigii		93	Tetrads	*Hemitrapa heissigii*
Malvaceae	*Tilia*		1		/
Chenopodiaceae	cf. *Chenopodium*		4		/
Cornales	*Nyssa-like*		1		/
Ericaceae	*Erica*	2	7		Ericaceae gen. et sp. indet
Styracaceae	*Rehderodendron*		13		cf. *Rehderodendron* vel Rhamnaceae
Sapotaceae	*Sideroxylon*		9	Lumps	*Sapotacites minor*
	Sapotae		2		/
Ebenaceae	*Diospyros*		1		*Diospyros pannonica*
	cf. *Royena*		1		/
?Cyrillaceae	gen. Indet		4		/
Plantaginaceae	*Callitriche*		15	Lumps	/
Oleaceae	*Fraxinus*		22		*Fraxinus inaequalis*
	Phillyrea		7		*Phillyrea pschechensis*
Aquifoliaceae	*Ilex*		1		/
Lamiaceae	*Lycopus/Mentha*		1		/
Adoxaceae	*Viburnum*		1		*? Viburnum* sp. vel *Sambucus* sp.
extinct unknown	*Operculumpollis*		1		/
indet	varia	5	13		/
sum			632		

conditions. The pollen assemblage contains also Pinaceae (*Pinus* diploxylon-type, *Picea, Abies*, and *Cathaya*), and pollen assignable to *Buxus* sp. (see Table 2) that are interpreted to have grown further away in the hinterland area because no corresponding macrofossils of the latter ones have been found so far in these deposits.

Gymnosperms
GNETALES Luerssen
EPHEDRACEAE Dumortier
Ephedra Linné
Ephedra sp. 1 (Plate I, 1–3)
Description LM: Ellipsoidal pollen grain, elongated elliptic outline in equatorial view; polyplicate, with ca. six plicae, equatorial axis ca. 45 μm, polar axis ca. 16.5 μm (N = 2; P/E ratio = 2.7); pollen wall thickness ca. 0.8–1.2 μm; tectate, psilate. SEM: Grooves ("pseudosulci") between plicae display first and second order branching (terminology after (Bolinder et al., 2016)); ektexine tectate, covered entirely a with faint criss-cross micro-rugulate pattern.

Remarks: Pollen of the genus *Ephedra* are described in the pollen literatureas morpho genus *Ephedripites* Bolchovitina & Potonié emend. Krutzsch. Our pollen type looks like a derived, anemophilous *Ephedra* type and resembles somewhat the Asian species *E. equesitina* Bunge and *Ephedra distachya* Linné (compare Bolinder et al., 2016, fig. 6C and 6L). The faint fine criss-cross micro-rugulate pattern visible under SEM resembles the ektexine ornamentation that can be found on pollen of *Ginkgo* Linné and other fossil *Ephedripites* pollen (Hofmann et al.,

Table 3

Summary of the pollen of subhumid to humid and sclerophyllous plants, their most similar looking modern equivalents and their habitats and the Köppen-Geiger climate classification (for explanation see Kottek et al., 2006). Abbreviations SDF = seasonal drier forest, MDF-Shr = Mediterranean drier forest and shrubland, St = steppe, ERF = ephemeral riverine forest, DGL-S = dry grassland and savannah, DD = dry open and disturbed substrate, SHF = seasonal humid evergreen forest, HF = humid forest.

Family	Partly humid to subhumid and sclerophyllous pollen taxa	Most similar looking modern equivalent (genus, species)	Habitat	Koeppen-Geiger Climate classification
Ephedraceae	*Ephedra* sp. 1	*E. equisetina*	St	BSh BWk Csa Dfa Dfb Dwb Dwd
		E. distachya	St MDF-Shr	BSh BWk Csa Csb
	Ephedra sp.2	*E. foemina*	St	BSh BWk Csa Dwb
		E. trifurcata	St	BWh BWk BSk Csa
Poaceae	gen. indet.	*Dactylis glomerata*	DGL-S St	Am Aw BSh BSk BWh Cfa Cfb Csa Csb Cwa Cwb Dfb Dfc Dfa Dwb
		Hyparrhenia hirta	DGL St DD	BSh BSk BWh Csa Csb Cwa Cwb
		Catapodium rigidum	DGL DD St	BSh BSk Cfb Csa Csb Dfa Dfb
		Cutandia maritima	MDF-Shr DGL St	BSh BSk BWh Cfb Csa Csb Cwa Cwb
		Poa compressa	DGL DD St	BSh BSk BWh Cfa CfaCsa Csb Cwa Cwb
		Agropyrum cristatum	DGL St	BSh BSk BWh Cfb Csa, Csb Cwa Cwb Dfa Dfc Dwb
		Tricholaena teneriffae	DGL DD St	Aw BSh BSk BWh Csa Csb Cwa Cwb
Rhamnaceae	*Ziziphus*	*Z. mucronata*	SDF-S ERF	Aw BSh BSk BWk Cfa Cfb Cwa Cwb
		Z. mauritania	HF SDF-S ERF	Aw Am BSh BWh Cwa Cwb
		Z. jujuba	SDF-S ERF MDF-Shr	Cfa Cfb Cwa Cwb Dwa Dwb Dwc
Ulmaceae	*Ulmus*	*U. minor*	BLF-MDF St	BSh BSk BWh Cfa Cfb Csa Csb
		U. pumila	ST SDF ERF	BWh BWk Cfa Cwa Cwb Dwa Dwb
		U. castaneifolia	HF SDF	Cfa Cwb Cwb
		U. chenmoui	HF SDF	Cfa Cwa Aw Am
		U. szechuanica	HF SDF	Cfa Cwa Cwb
		U. davidiana	HF SDF	Am Aw Cfa Cwa Dwa Dwb Dfc
		U. prunifolia	HF SDF	Cfa Cwa Cwb
		U. microcarpa	HF SDF	BWk BSk Dwc
		U. changi	HF SDF	Cfa Cfb Cwa
	Zelkova	*Z. abelicea*	MDF-Shr	Csa Csb
		Z. serrata	SDF	Aw Cfa Cfb Cwa Dfa
Cannabaceae	*Celtis*	*C. tournefortii* type	SDF MMF	BSh BSk BWh Cfa Cfb Csa Csb
Amaranthaceae	cf. *Chenopodium*	*C. acuminatum*	DGL DD	Am Aw BSk BWh BWk Dwa Dwc Cfa Cwa
		C. ficifolium	DGL DD	Aw BSh BWk BWh Cfb Csa Csb Cwa Dwa
		C album	DGL DD	Aw BSh BWk BWh Cfa Cfb Csa Csb Cwa Dfb Dfc Dwa Dwc
		C glaucum = Oxybasis glauca	DGL DD	Aw BSh BWk BWh Cfa Cfb Csa Csb Cwa Dfb Dfc Dwa Dwc
Fagaceae	*Quercus* sect. Ilex	*Q. coccifera*	MDF-Shr	BSh BWh Cfa Csa Csb
		Q. zingiana	MMF	Am Aw Cfa Cfb Cwa
Sapotaceae	Sapotae	*Mimusops*	HF BLF SDF	Aw Af Am BSh BWh Cfa Cfb Cwa Cwb Csa
		Madhuca	HF BLF SDF	Aw Af Am As BSh Cfa Cwa Cwb
		Manilcara	HF BLF SDF	Aw Af Am Cfa Cfb Cwa BSh BWh Bsk
	Sideroxylon	*S. celastrinum*	SHF BLF	Af Aw Am BSh BSk Cfa
		S. ibarrae	SHF	Am Aw Cwa Cfb
		S. jabilla	SHF	Am Aw
		S. mascatense	SDF	Aw BSh BWh Cfa Cwa
		S. occidentale	SHF SDF	Am Aw BSh BSk BWh Cfa
		S. reclinatum	BLF	Cfa
		S. salicifolium	SDF SHF	Am Aw BSh BWh Csa Csc
		S saxorum	SHF BLF SDF	Af Am Aw BSk Cfa Cwa Cwb
		S wightianum	SHF SDF	Am Aw Cfa Cwa Cwb
		S. spinosus = Argania spinosa	SDF	Am Aw BSk BWh BWk Cfa Cwa Dwa
Styracaceae	*Rehderodendron*	*R. macrocarpum*	SDF	Cwa Cwb
		R microcarpum	SDF	Cwa Cwb
		R. kwantungense	HF SDF	Cwa Cfa
Ebenaceae	*Royenia*	*R. fischeri*	SDF ERF	Aw BSh Cwa Cwb
		R. loureiriana	DD Shr	Aw BSh Cwa
		R. austroafricana = pubescens	SDF?	BWh BWk BSh Cfa, Cfb, Csb Cwb
	Diospyros	sp.	HF BLF SDF	all C and A climates
Ericaceae	*Erica* sp.1	*E. scoparia*	MDF-Shr	Csa Csb BSh Cfa Cfb
	Erica sp. 2	*E. arborea*	MDF-Shr	Csa Csb Cfb BSh BSk BWh Aw
		E. bergiana	MDF-Shr	BSh BSk Cfa Csa Csb
Oleaceae	*Phillyrea*	*P. latifolia*	MDF-Shr	Csa Csb BSh BSk Cfa Cfb

2022). Most of the *Ephedra* taxa are sclerophyllous and thrive in arid to semi-arid areas on rocky or sandy ground.

Ephedra sp. 2 (Plate I, 4–6)
Description LM: Ellipsoidal pollen grain, elongated elliptic outline in equatorial view; polyplicate, with ca. twelve plicae, equatorial axis ca. 34.6 μm, polar axis ca. 14 μm (P/E ratio = 2.47); pollen wall thickness ca. 0.8 to 1 μm; psilate. SEM: Grooves ("pseudosulci") between plicae are straight to slightly undulating without first and second order branching (terminology after Bolinder et al., 2016; ektexine tectate, smooth to very faintly micro-rugulate.

Remarks: This pollen taxon looks more like the ancestral pollen type of *Ephedra* in Bolinder et al. (2015, 2016), comprising extant *E. foemina* Forsskål and *E. trifurca* Torrey ex. S.Watson in Bolinder et al. (2015, fig. 1 A and fig. 1 E, respectively). These taxa have been observed to behave more entomophilous than the more derived wind pollinated ones (see *Ephedra* sp. 1; Bolinder et al., 2015, 2016). The modern, generally entomophilous *Ephedra* also are sclerophyllous and thrive also under arid to semi-arid conditions.

Remarks to the two Ephedra sp.: Two *Ephedra* pollen taxa have been described with LM and SEM from the mid-Miocene Randecker Maar by Kottik (2002, pl. 2 figs. 8–10 and 11–13, respectively) that have
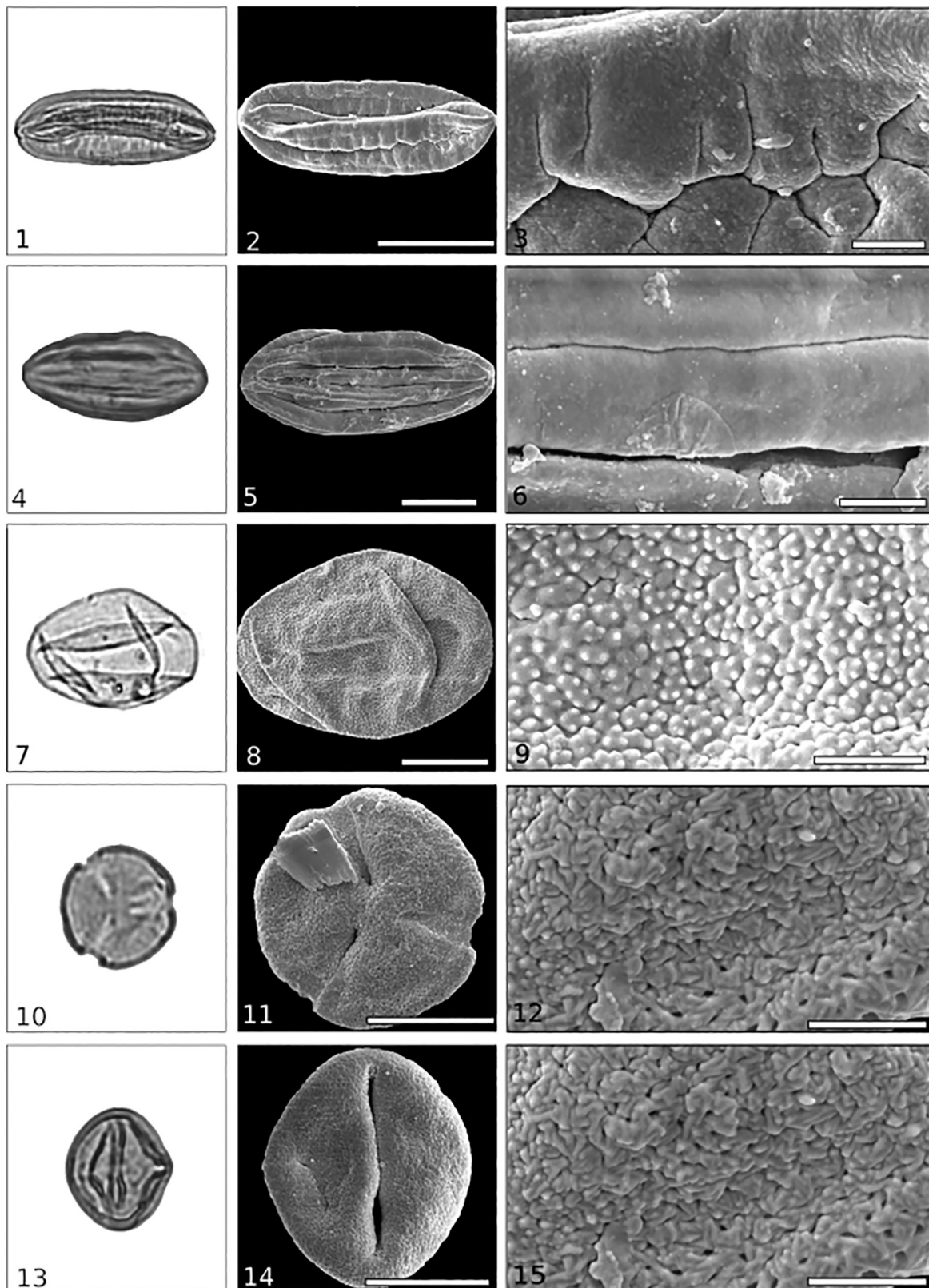
Plate I. Subhumid and sclerophyllous elements from Entrischenbrunn. **1–3.** *Ephedra* sp. 1, **1.** LM images, **2.** SEM overview image and **3.** SEM detail. **4–6.** *Ephedra* sp. 2, **4.** LM image, **5.** SEM overview, **6.** SEM detail. **7–9.** Poaceae with "avena" ornamentation, **7.** LM image, **8.** SEM overview, **9.** SEM detail. **10–15.** *Ziziphus* "*mucronata/mauritania/jujuba*-type", **10–12.** In polar view, **13–15.** equatorial view, **10.** and **13.** LM images, **11** and **14.** SEM overviews, **12.** and **15.** SEM details. LM images × 1000, bar in SEM overview 10 μm, bar in SEM detail 2 μm.
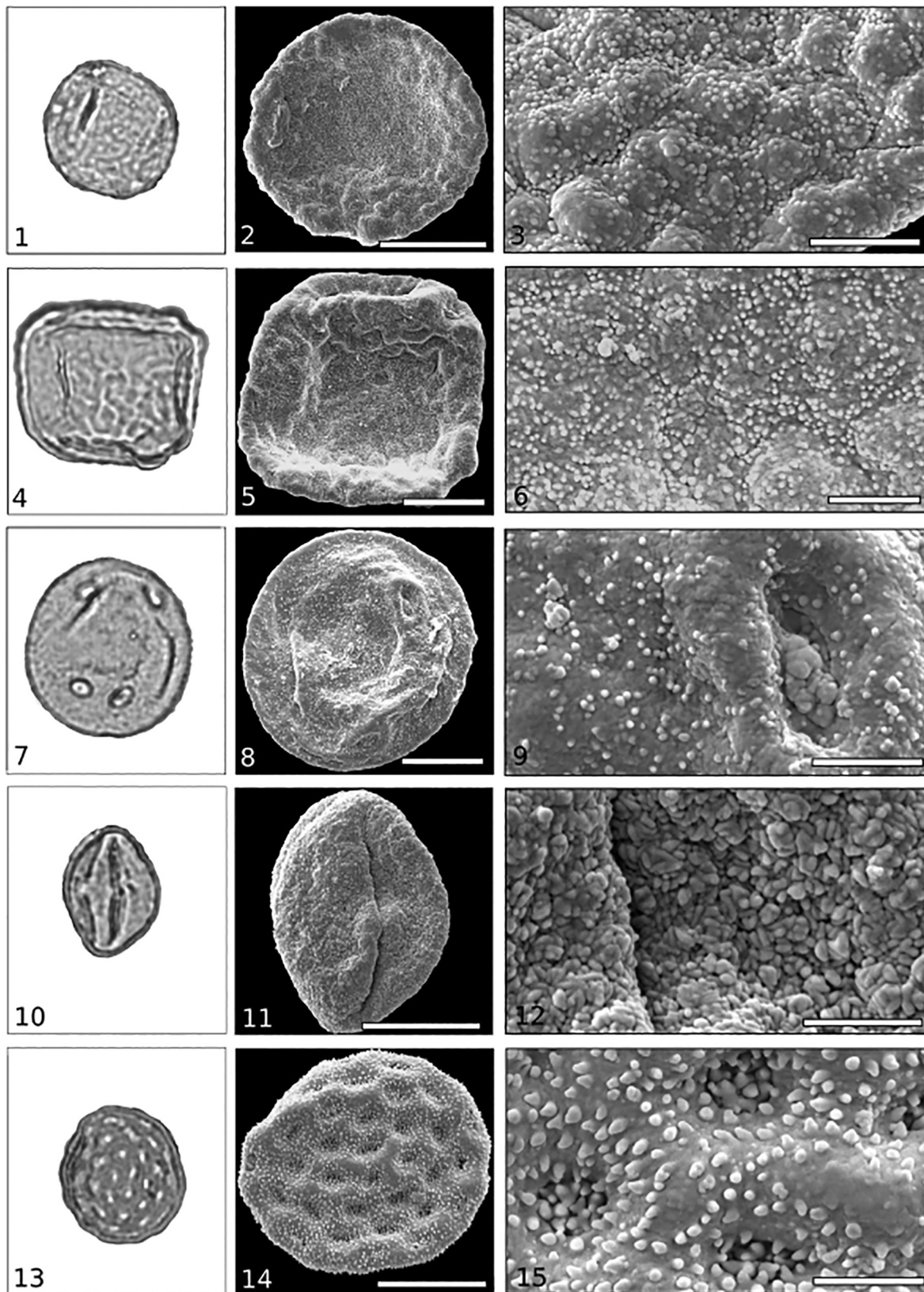
Plate II. Subhumid and sclerophyllous elements from Entrischenbrunn. **1–3.** *Ulmus* sp. section Foliaceae, **1.** LM images, **2.** SEM overview image and **4.** SEM detail. **4–6.** *Zelkova "abelicea/serrata*-type", **4.** LM image, **5.** SEM overview, **6.** SEM detail. **7–9.** *Celtis "tournefortii*-type", **7.** LM image, **8.** SEM overview, **9.** SEM detail. **10–12.** *Quercus* sp. section Ilex, **10.** LM image, **11.** SEM overview, **12.** SEM details. **13–15.** *Chenopodium* sp., **13.** LM image, **14.** SEM overview, **15.** SEM detail. LM images × 1000, bar in SEM overview 10 μm, bar in SEM detail 2 μm.
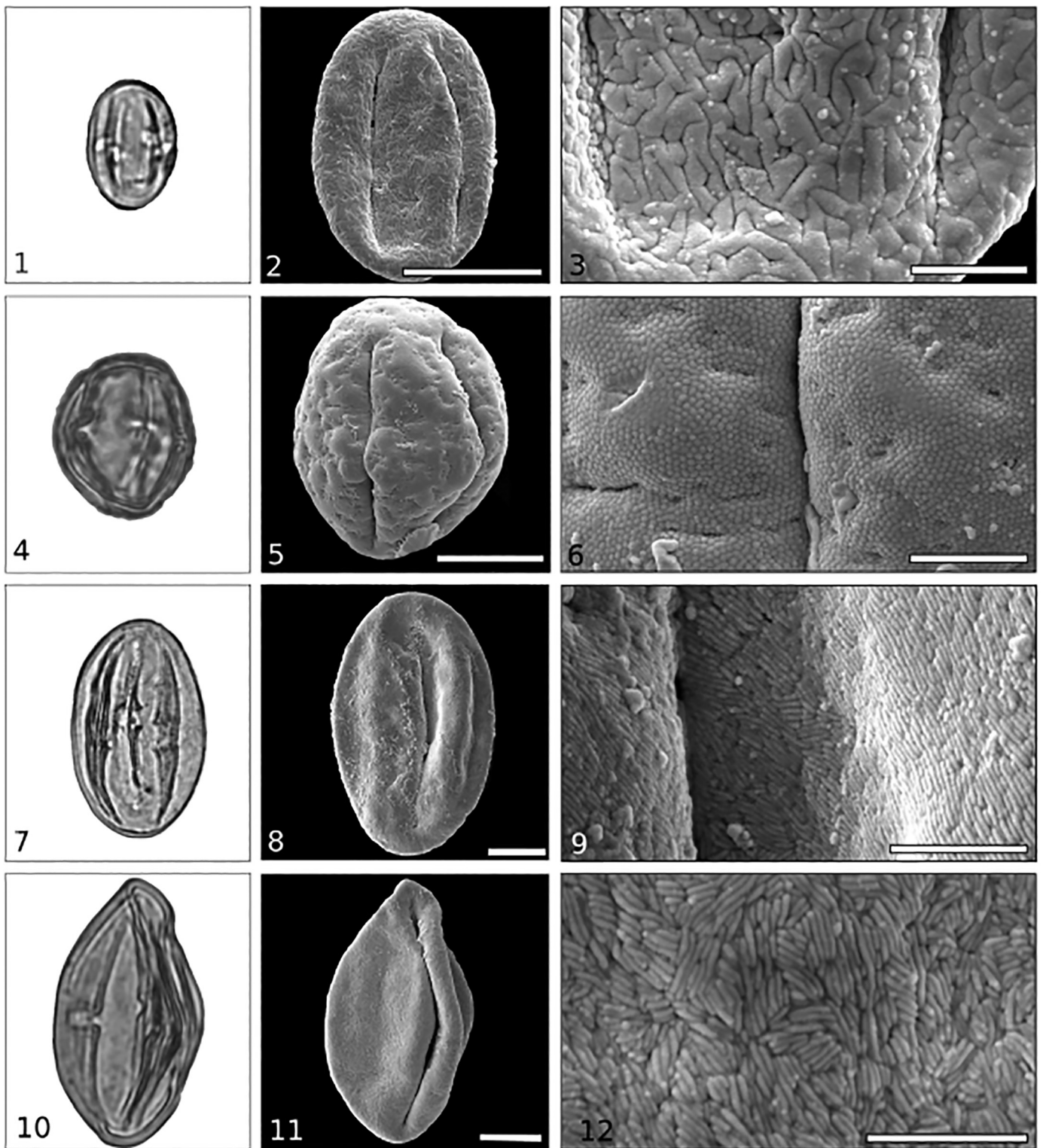
Plate III. Subhumid and sclerophyllous elements from Entrischenbrunn. **1–3.** *Sideroxylon* sp., **1.** LM images, **2.** SEM overview image and **3.** SEM detail. **4–6.** Sapotae, **4.** LM image, **5.** SEM overview, **6.** SEM detail. **7–9.** cf. *Royenia*, **7.** LM image, **8.** SEM overview, **9.** SEM detail. **10–12.** *Diospyros* sp., **10.** LM image, **11.** SEM overview, **12.** SEM details. LM images × 1000, bar in SEM overview 10 μm, bar in SEM detail 2 μm.

roughly the same dimensions as the two taxa described here, but they are not the same, because both display as much as the double amount of plicae, the same applies to the one *Ephedra* grain described bei Thiele Pfeiffer (1980, pl. 7 figs. 10, 11). There are some twig fragments from Entrischenbrunn that might belong to *Ephedra sotzkiana* (Unger) Schimper.

Angiosperms
POALES Small
POACEAE (R. BR.) Barnhart
Poaceae with "avena-type" tectum ornamentation (sensu Beug et al., 2004, considering LM images investigation; Mander and Punyasena, 2015 considering SEM investigation) (Plate I, 7–9).

Description LM: Monoporate, prolate to spheroidal pollen grain, elliptical to sub-circular in equatorial view, deflated and folded; polar axes range from ca. 32.1 to 38 μm and equatorial axes ca. from 28.2 μm (folded specimen) to 35.2 μm (n = 3); wall thickness ca. 0.7 to 0.9 μm; annulus is relatively shallow and has a diameter of ca. 4.6 to 5 μm, pore diameter ca. 1.5 to 1.8 μm; scabrate. SEM: The tectum surface is areolate, with supratectal blunt micro-echini or micro-gemmae, areolae are polygonal and angular, generally much smaller than 1 μm in diameter (ca. 0.3 to 0.7 μm across), ca. 0.2 μm high and are covered with two (generally three to five) occasionally up to ten micro-echini.

Remarks: Considering size and shape, pore and annulus diameters, and tectum ornamentation a literature search was undertaken, to get the most similar looking grass pollen to compare with (Andersen and Bertelsen, 1972 with 12 species, SEM images; Ater, 1986 with one species LM and SEM images; Beug, 2004 with over 100 species, measurements and LM images; Köhler and Lange, 1979 with 12 species, SEM images; Mander and Punyasena, 2015, with six species: tectum detail SEM images; Mander et al., 2014 with twelve species: tectum detail SEM images; Nunes Morgado et al., 2015 with 45 species, LM and SEM images; Page, 1978 with 35 species and few SEM images and measurements; https://www.paldat.org/search/taxonomic with 64 species LM and SEM images, and coarsely measured dimensions; Perveen and Quaiser, 2012 with 55 species, measurements and few SEM images; Reille, 1992 with 32 species, LM images and scale bars; Reille, 1995 with 40 species, LM images and scale bars; Reille, 1998 with 102 species, LM images and scale bars). This literature data base includes more than 400 grass species, and the information was combined when possible and revealed that only a handful of extant taxa that resemble our fossil taxon: Best fit is the cosmopolitan *Dactylis glomerata* Linné mentioned in Beug (2004, page 90) with "avena-type ornamentation and is well illustrated in Halbritter and Heigl (2021, SEM images), Mander et al. (2014, SEM image fig. 1–92), Nunes Morgado et al. (2015, fig. 2 14 A, B, LM and SEM images), and Reille (1992, page 404, LM image). Second best fits are *Hyparrhenia hirta* (Linné) Stapf in Halbritter and Weis (2015, SEM images), in Reille (1995, page 86, LM images) and measurements in Perveen and Quaiser (2012), however they mentioned a very protruding annulus, which is not seen in Halbritter and Weis (2016). Then comes *Catapodium rigidum* (Linné) C.E. Hubb in Halbritter (2019) and *Cutandia maritima* (Linné) Barbey in Halbritter (2016a, SEM images). Other taxa resemble to a lesser extent, such as *Poa compressa* Linné, that has a reminiscent tectum ornamentation (Halbritter, 2016b, SEM images), but is clearly spheroidal and has a considerably smaller diameter (Reille, 1998 page 203). There are other grass species that fit size or shape, however, there is no information about detailed tectum ornamentation such as in *Tricholaena teneriffae* (Linné f.) Link and *Agropyrum cristatum* (Linné) Gaertner. It is remarkable that all the similar looking grass taxa are not aquatic grasses, such as *Phragmites* Adanson and *Phalaris* Linné etc. and that certain climates are preferred. Mostly C climates, for example the Mediterranean to seasonal climates and very often the dry conditions.

ROSALES Perleb
RHAMNACEAE Jussieu
Paliurae
Ziziphus Miller
Ziziphus "mucronata/mauritania/jujuba-type" (Plate I, 10–15)
Description LM: Spheroidal to subprolate pollen grain, with a circular outline in polar view (fossilized and compressed) and an elliptic to rhombic outline in equatorial view; tricolporate, colpi ca. 10.9 to 15.1 μm long, pori lalongate to circular ca. 1 μm high and up to 3.8 mm wide; polar axis ca.19.6 μm and equatorial axes ca. 14.9 to 17.2 μm (N = 2); wall thickness ca. 1 μm. SEM: ektexine is tectate, perforate, micro-rugulate, whereas micro-rugulae are arranged in an irregular criss-cross pattern. Perforations and striae increase in size in the mesocolpium areas producing a micro-striato-reticulate pattern; visible colpus membrane micro-verrucate.

Remarks: The aperture configuration and ektexine ornamentation resemble some Rhamnaceae, such as *Ziziphus* in Perveen and Quaiser (2005, e.g. *Z. nummularia* (Burman f.) Wight et Arnott fig. 1A–C) and in Schirarend and Köhler (1993, fig. 8 I, 8M *Z. mauritania* Lamarck and *Z. mucronata* Willdenow SEM images, respectively). In particular the small-scaled exine ornamentation of *Z. mucronata* and *Z. jujuba* Miller in Miyoshi et al. (2011) fit perfectly. There are some minor resemblances with *Paliurus* Tournefort ex Miller species depicted by Schirarend (1996, e.g. *P. ramosissimus* (Loureiro) Poiret figs. 34–45) and Schirarend and Köhler (1993, fig. 8 B–D *P. hemsleyanus* Rehder ex Schirarend & Olabi, LM images), however the criss-cross striation of the tectum of *Paliurus* taxa is considerably larger scaled than on our taxon. Pollen of *Ziziphus* and *Paliurus* of the Rhamnaceae have been summarized by Schirarend and Köhler (1993) as *Lasiodiscus*-type, however *Lasiodiscus* and *Ziziphus* differ in detailed ornamentation under SEM (compare Schirarend and Köhler, 1993). Our pollen resembles slightly the morpho taxon *Rhamnaceaepollenites* Thiele-Pfeiffer (Thiele-Pfeiffer, 1980, *R. triquetrus* Thiele-Pfeiffer pl. 9, figs. 12–17). The subhumid *Ziziphus mucronata* and subhumid to humid *Z. mauritania* today live in the savannah biome of western subtropical Africa along ephemeral rivers ("rivieres") under pronounced seasonal conditions and southern Eurasia (Irak to India to south China). *Z. jujuba* on the other hand can grow in humidity (Cfa climate) but prefers more drier conditions (Table 3). The two most similar looking taxa and *Z. mauritania* belong to the Old World clade of Paliurae (Islam and Simmons, 2006). Two small sclerophyllous leaves of *Ziziphus protolotus* Unger probably correspond to this pollen type and can be interpreted as a thorny scrub or little trees growing on dry stands like sand bars.

ULMACEAE Mirbel
Ulmus Linné
Ulmus sp.-section Foliaceae (Plate II, 1–3)
Description LM: Oblate pollen grain, circular to slightly pentangular outline in polar view; always pentaporate; equatorial diameter range from 21.7.8 to 29.8 μm (N = 4); wall thickness ca. 0.9 to 1.38 μm, sexine thicker than nexine, particularly at the aperture areas; tectate, verrucate. SEM: Verrucae are of 1 to 1.5 μm in diameter, generally shallow, and densely covered with micro-gemmae.

Remarks: Pollen of this type is known under the fossil taxon *Polyporopollenites verrucatus* sps. *major* and sps. *minor* Thiele-Pfeiffer (Thiele-Pfeiffer, 1980, p. 129–130, pl. 8 figs. 24–27, 28–31, respectively) and after comparison with various extant Ulmaceae (LM) was interpreted to belong to *Zelkova* Spach. However, this pollen type generally resembles extant Ulmaceae pollen, including *Zelkova*, described and depicted in Stafford (1995 pls. 3–12, LM and SEM images) and particularly there is also a strong resemblance to *Ulmus minor* Miller in Stockmarr (1974, pl. 1 fig. 3, pl. 2 fig. 3 and 3a, pl. 3 fig. 3 and 3a; SEM images), but less so in Stafford (1995, pl. 9 figs. 1–5) and Beug (2004, pl. 105 fig. 25, LM image). The small size fits also *Ulmus pumila* Linné and *U. castaneifolia* Hemsley in Li et al. (2011, pl. 1138, figs. 1–4, pl. 1140 figs. 1–4, SEM images). These three most similar looking *Ulmus* species belong to *Ulmus* section Foliaceae (including six other *Ulmus* species: *U. changi* W.C. Cheng, *U. chenmoui* W.C. Cheng, *U. davidiana* Planchon, *U. microcarpa* L.K. Fu, *U. prunifolia* W.C. Cheng, and *U. szechuanica* W.P. Fang, see Whittemore et al., 2021; Table 3) and can be interpreted to belong to the stem lineage of this section (compare Whittemore et al., 2021, fig. 2). Pollen morphologies of the other taxa in section Foliaceae are not available except for *U. davidiana*, which pollen are slightly larger, tetra- to pentaporate and rugulate to verrucate (Li et al., 2011, pl. 1137, fig. 1–4; Moon et al., 2015, table 2). Most *Ulmus* species belong to broad-leaved deciduous forests and of these many grow adjacent to riverine environments or under generally more humid conditions (e.g., of section Foliaceae *U. castaneifolia*, *U. chenmoui*, *U. changi*; *U. davidiana, U. szechuanica*), but can cope with dry winters (Cwa and Cwb climates; Table 3). However, a few species are also adapted to much drier conditions and are characteristic

elements along ephemeral river courses in steppe environments with-standing colder climates, such as *Ulmus minor, U. microcarpa* and *U. pumila* (Table 3) in Siberia, Mongolian and Tarim desserts (Fu et al., 2003, Solla et al., 2005; Wang, 1961). A few elm leaves representing several species have been identified: for example the small sized leaves of *U. minuta* Göppert sensu Knobloch (1969) and *U. braunii* Heer correspond to the extant drought tolerant *U. minor* and *U. parvifolia* Jacquin, respectively. On the other side longer leaves are usually assigned to *U. pyramidalis* Goeppert as elements of rather humid hard wood forest associations.

Zelkova Spach

Zelkova "abelicea/serrata-type" (Plate II, 4–6)

Description LM: Oblate to sub-oblate pollen grain, quadrangular outline in polar view; tetraporate; equatorial diameter range from 30.8 to 35.1 μm (N = 2); wall thickness ca. 1.4 to 1.6 μm, thinned in the polar areas, sexine thicker than nexine and thickened around the aperture areas; tectate, verrucate to rugulate. SEM: Rugulae and verrucae are relatively shallow and densely covered with micro-gemmae.

Remarks: The differentiation of pollen of *Zelkova* and *Ulmus* has been demonstrated by Morita et al. (1998). Pollen morphology of several *Zelkova* species has been described, measured and partly depicted by Nakagawa et al. (1998, *Z. sicula* DiPasquale, G.Garfi et P.Quézel, pls. 1–3 and *Z. carpinifolia* (Pallas) Dippel pl. 4; LM images), and individual species of *Zelkova* have been depicted in Stafford (1995, tetraporate *Zelkova albelicea* (Lamarck) Boissier pl. 13 figs. 1–6, pl. 14 figs. 1–6, LM and SEM images), Li et al. (2011, *Zelkova serrata* (Thunberg) Makino pl. 1134 figs. 1–4, SEM images), and Morita et al. (1998, pentaporate *Zelkova serrata* figs. 4, 11, 12 LM and SEM). Our pollen taxon is very reminiscent in size, apertural configuration, the pronounced tectum rugulate ornamentation and density of supratectal gemmae to *Z. abelicea* and *Z. serrata*. Pollen of *Zelkova sicula* and *Z. carpinifolia* are considerably larger than *Z. abelicea*, whereas *Z. sicula* is also generally pentaporate (occasionally hexaporate) and much less rugulate (Nakagawa et al., 1998, Table 2, pls. 1–3). In Europe, fossils of *Zelkova* are known since the Eocene (Mai, 1995) and today two species are known from the Mediterranean: *Z. sicula* from Sicily and *Z. abelicea* from Crete both are sub-humid to sclerophyllous (Csa, Csb) elements, whereas *Z. serrata* occurs in warm temperate to tropical and partly seasonally controlled China, Korea, Japan and Taiwan (Table 3). The macrofossils of Entrischenbrunn comprise no *Zelkova* leaves and this genus is considered rare in the Middle Miocene Molasse (Sachse et al., unpublished data).

CANNABACEAE Martynov

Celtis Linné

Celtis "tournefortii-type" (Plate II 7–9)

Description LM: Oblate (fossilized compressed state) pollen grain, circular outline in oblique polar view; always tetraporate; equatorial diameters range from 25.2 to 28 μm (N = 2); wall thickness ca. 0.8–1 μm; tectate, scabrate. SEM: ektexine is undulated to very faintly shallowly rugulate to verrucate, very faintly fossulate to perforate and irregularly covered with micro-gemmae.

Remarks: Extant pollen grains of *Celtis* have been depicted by Staffort (1995 pls. 1, 2), and the tetraporate condition and small size are well comparable to pollen of the extant *Celtis tournefortii* Lamarck (Zarafshar et al., 2010, fig. 1, page 148; Shahbaz and Sharif, 2017, fig. 7C–F), an Eurasian subhumid *Celtis* species that inhabits steppe and dry forests in Mediterranean climate zones (Table 3; Roloff and Bärtels, 2008), like the other western Eurasian *Celtis* species, *C. australis* Linné and *C. occidentalis* Linné (Browics and Zielinski, 1982). After Mai (1995), the macrofossil *Celtis trachytica* Ettingshausen is closely related to the extant *C. tournefortii* and may be a witness of the "Mediterransindische Refugialflora" of Schwarz (1938); Mai, 1995, page 282) that comprised also elements, such as *Quercus ilex* Linné, *Argania* Roemer et Schultes (= *Sideroxylon* Linné) and also *Ephedra, Ziziphus* and *Styrax* Linné. After Kovar-Eder et al. (2004) *C. trachytica* is a later

synonym of *C. japeti* Unger, which is part of the Entrischenbrunn macrofossil assemblage.

FAGALES Engler
FAGACEAE Dumortier
Quercus Linné

Quercus sp. section Ilex (Plate II, 10–12)

Description LM: Prolate pollen grain with a rhombic outline in equatorial view; tricolporate with a lalongate porus ca. 2.5 to 3 μm wide and 2 μm high; polar axis ca. 21 mm, equatorial axis ca. 15.5 μm; wall thickness ca. 1.1 μm; scabrate. SEM: The tectum surface is undulating and composed of short, sometimes fused, irregularly oriented microrugulae, the micro-rulae are between 0.2 and 0.3 μm long and less than 1 μm wide; in the equator area the sexine is protruding over the endoaperture, thus building a bridge structure.

Remarks: The fossil pollen grain resembles to some extent Oligocene *Quercus* pollen from Central Europe (Denk et al., 2012: *Quercus* infrageneric group Ilex on pl. 3, 1–3), considering size and aperture configuration, but not as much in its short micro-rugulate ornamentation. There are similarities in the tectum ornamentation of fossil *Quercus* grains from China (Liu et al., 2007: morphotaxon 4 on pl. 2 figs. 1–2, pl. 3 figs. 1–6), however our pollen is much smaller and has a different shape. Also there are similarities in the tectum ornamentation of Holocene *Quercus* from the Japan Sea (Tekleva et al., 2014, *Quercus* group 5 on fig. 5), but our pollen is tricolporate and much smaller. The tectum ornamentation of our fossil pollen with short micro-rugulae is somehow reminiscent of extant *Quercus* from *Q.* sectionIlex and to a lesser extent *Q.* sectionCyclobalanopsis (Denk and Grimm, 2009, fig. 1 A–H, fig. 4 A–E; Denk and Tekleva, 2014, *Q.* section Ilex figs. 7–10, to some extent comparable are *Q. coccifera* Linné and *Q. kingiana* Craib fig. 8L, fig. 9L, respectively). The same applies to a lesser extant to *Quercus* taxa in the *Q.* section Cyclobalanopsis (Makino et al., 2009, *Q. gilva* Blume pl. 6 figs. 1–3, 6, 11, 16 and *Q. glauca* Thunberg pl. 8 figs. 1–4, 6, 7). The most similar modern taxa are subhumid zonal elements from the Mediterranean or montane areas in temperate to subtropical Asia, and their climatic requirements are in Table 3. This pollen type might be associated with leaf fossil *Quercus drymeja* Unger of Entrischenbrunn, which also belongs to section Ilex, but should be treated as morphotype complex, instead of a well defined fossil species (Denk et al., 2017).

CARYOPHYLLALES Jussieu Ex Berchtold & J.Presl
AMARANTHACEAE Jussieu
Chenopodium Linné

cf. *Chenopodium* sp. (Plate II, 13–15)

Description LM: Spheroidal pollen grain with circular outline in all views; pantoporate ca. 68 pori (size range between 1.2 to 1.4 μm) evenly distributed over the pollen surface; diameter ca. 20 to 22.2 μm; wall thickness ca. 1 to 1.2 μm with the sexine probably as thick as nexine; tectate, scabrate. SEM: The ektexine is covered regularly and densely by micro-echini and the operculi of the pori are covered densely by micro-echini (width of base ca. 0.25 μm and length ranging from 0.3 to 0.4 μm).

Remarks: Pollen of Amaranthaceae genera look very similar, and therefore it is difficult to assign fossil pollen grains to a genus (Borsch, 1998; Borsch et al., 2018). Our pollen has many similarities (size, pore- number and -size, size and density of echini) to *Chenopodium*. There are in size, pore number, pore diameter and tectum ornamentation some resemblances to *Chenopodium acuminatum* Willdenow described and depicted in Chung and Lee (1995, figs. 13, 14, SEM images), *C. ficifolium* Smith in Hamdi et al. (2009, fig. 3 e, f), *C. album* Linné (Perveen and Quaiser, 2012 fig. 2 c, d), *C. glaucum* Linnè (Halbritter, 2016c); because fossil *Chenopodium* seeds have been encountered in the sediments of the Randecker Maar (Gregor, 1982a) we tentatively assign our pollen grain to the genus *Chenopodium*. *Chenopodium* is generally a plant of drier, often haline habitats with ephemeral or seasonal rainfall (Table 3; Kühn et al., 1993). This taxon

is distributed on gravelly banks and wastelands from South Siberia to Mongolia, Korea and temperate China to Europe.

ERICALES Dumortier
SAPOTACEAE Jussieu
SAPOTOIDAE Miller
Sideroxylon Linné
Sideroxylon sp. (Plate III, 1–3)
Description LM: Prolate pollen grain, elliptic outline in equatorial view; tetracolporate, colpi length is ca. two thirds of the polar axis, endoaperture more-or-less circular; polar axis ca. 19.5 μm, equatorial axis ca. 13 μm; wall thickness ca. 0.7 to 0.9 μm; tectate. SEM: ektexine displays irregularly arranged rugulae and fossulae, the rugulae are ca. 0.3 to 0.6 μm wide and ca. 0.7 to 3.5 μm long, irregularly shaped, often splitting or fusing and are composed of densely packed micro-verrucae (approximately <0.1 μm in diameter); the visible colpus membrane is micro-verrucate.

Remarks: This pollen type, that occasionally occurs in tiny lumps, has similarities with several extant *Sideroxylon* pollen depicted in Harley (1991a), e.g., *S. wightianum* Hooker et Arnott fig. 13G; *S. celastrinum* (Kunth) T.D.Pennington fig. 24 A-D; *S. ibbarae* (Lundell) T.D. Pennington fig. 24 E; *S. confertum* C. Wright fig. 24 H-K; *S. jubilla* (Ekman ex Urb.) T.D. Pennington fig. 24M, N; *S. occidentale* (Ekman ex Urb.) T.D. Pennington fig. 25 A–D; *S. spinosum* (=*Argania spinosa*) (Linné) Skeels fig. 25J, K, LM and SEM images). Very similar pollen grains were shown in Kottik (2002, pl. 10 figs. 16–18, LM and SEM images), and in Thiele-Pfeiffer (1980, pl. 17 figs. 34–37, LM images). Many of these extant taxa are sub-humid in warm temperate to subtropical seasonal climate (Table 3). The macroflora of Entrischenbrunn comprises some sclerophyllous leaves assigned to *Sapotacites minor* (Unger) Heer and probably belong to *Bumelia* (=*Sideroxylon*) or *Mimusops* (Sachse et al., unpublished data).

SAPOTEAE Eaton
Sapoteae "*Mimusops*/*Manilkara*/*Madhuca*-type" (Plate III, 4–6)
Description LM: Prolate to sub-prolate pollen grain, elliptic to slightly rhombic outline in equatorial view; tetracolporate, colpi length is ca. 17.9 μm, endoporus seems to be compressed and is lalongate (ca. 1.5 μm high and 4.5 μm wide), costae visible polar axis ca. 24.4 μm and equatorial axis ca. 20 μm; wall thickness ca. 1.4 μm with the sexine as thick as to thicker than the nexine; tectate. SEM: The tectum surface is undulating and locally perforate to fossulate, the ektexine is composed of densely and regularly arranged, circular micro-verrucae (approximately > than 0.2 μm).

Remarks: Harley (1990, 1991a, 1991b) studied the morphology of Sapotaceae pollen and separated the family into major pollen groups (on the basis of apertural configuration, colpus length, tectum ornamentation, presence or absence of continuous endexinous thickening in the equatorial region). Our pollen type resembles various taxa of extant *Mimusops* Linné, *Manilkara* Adanson, *Madhuca* Hamilton Ex J.F. Gmelin and to a much lesser extant *Palaquium* Blanco taxa of the Sapoteae either on LM images or SEM images in Harley (1991b, fig. 5 A–C, F, fig. 6 A, D–F, LM, fig. 7F, fig. 9 D, F, G, K, fig. 10 E, F, fig. 14 A, D–F, L, fig. 25N, P). No modern equivalent resemble our fossil pollen in all characters considering overall shape and size, aperture configuration, wall thickness, and micro-ornamentation under SEM, and the pollen of extant taxa are much larger. Other fossil pollen resembling our pollen somehow are known from the Eocene of Germany and Austria (Hofmann, 2018, fig. 6 D–F and G–I, respectively), and from the Miocene of Germany and Austria (Draxler and Zetter, 1991, pl. 3, figs. 1–3; Hofmann and Lichtenwagner, 2020, fig. 3D–F; Kmenta, 2011, pl. 15, figs. 4–14; Kottik, 2002, pl. 10, figs. 8–15; Meller et al., 1999, pl. 5, figs. 1–3) and from Turkey (Bouchal et al., 2017, pl. 11, figs. 8–10) but cannot be unambiguously affiliated to a single genus. The climate ranges from seasonal tropical to seasonal dry climates in the Old World and New World tropics (Table 3). The sclerophyllous character of the possbile

counterparts in the leaf record (see above) might indicate a subhumid to humid stand.

EBENACEAE Gücke
Royena Linné
cf. *Royena* sp. (Plate III, 7–9)
Description LM: Prolate pollen grain, elliptic outline in equatorial view, more-or-less lobate in polar view; tricolporate, colpi length ca. 24.4 μm, endoapertures lalongate to circular (ca. 3.8 μm high and ca. 4.2 μm wide), costae visible; polar diameter ca. 44.4 μm, equatorial diameter ca. 27.8 μm; wall thickness ca. 1.1 to 1.3 μm; tectate scabrate. SEM: ektexine is regularly, finely striate, faintly perforate, striae (ca. 0.1 μm wide and ca. 1 to 2 μm long) running more-or-less parallel to the polar axis in the mesocolpium area but can change perpendicularly direction at the margo.

Remarks: The overall shape, aperture configuration and ektexine ornamentation is characteristic for many *Diospyros* Linné and *Royena* taxa (e.g., Erdtman, 1969; Geeraerts et al., 2009; Grygorieva et al., 2013, Morton, 1994; Morton and Kincaid, 1995), but this is a quite large specimen and only a few species investigated by Geeraerts et al. (2009), five of 62: *D. crassiflora* Hiern, *D. lotus* Linné, *D. outbatchensis* Kostermans, *D. virginiana* Linné, table 1 and *D. fischeri* Gürcke; size measurements page 339) are in this size range. However, *D. crassiflora* and *D. lotus* have much longer colpi and conspicuous perforations in the mesocolpi areas, and *D. virginiana* has a micro-rugulate ornamentation and as well longer colpi. Of Indian *Diospyros* species (Tissot et al., 1994, pl. 21 lower half) only *D. bourdilloni* Brandis has comparable large pollen, but is also characterized by very long colpi and conspicuous fossulae and perforations in the mesocolpium area. The LM image of this taxon resembles *D. mespiliformis* Hochstetter ex A. DeCandolle in Gosling et al. (2013, pl. XLIII figs. 1–3), but this species is considerably smaller. The colpi length, size and ektexine ornamentation of this fossil pollen type resembles most closely *Royena fischeri* Gürke (former = *Diospyros fischeri* in Geeraerts et al., 2009, fig. 2L, page 342) and *R. loureiroana* G. Don (Geeraerts et al., 2009, page 342), both species display the exceptionally long striae, whereas the latter is slightly smaller and have been shown to belong to the phylogenetic subgroup 1 together with R. *austro-africana* De Winter (=*D. pubescens* Person) in Geeraerts et al. (2009, page 342, fig. 5).

Diospyros Linné
Diospyros sp. (Plate III, 10–12)
Description LM: Prolate pollen grain, elliptic outline in equatorial view, more-or-less lobate (fossilized state) in polar view; tricolporate, colpi are very long (ca. 35.2 μm) reaching the poles, endoapertures lalongate (ca. 1.3 μm high and ca. 3.3 μm wide), costae visible; polar diameter ca. 42.2 μm, equatorial diameter ca. 23.7 μm; wall thickness ca. 1 to 1.2 μm; tectate scabrate. SEM: ektexine is regularly, finely striate, faintly perforate, striae (ca. 0.08 μm wide and ca. 0.3 to 0.7 μm long) are arranged in sets of four to eight and these sets are arranged at angles to each other.

Remarks: The LM image resembles African *Diospyros abyssinica* Hiern in size, apertures and pollen wall thickness (Gosling et al., 2013, pl. XCIII figs. 1–4), however, the size of *D. abyssinica* in Geeraerts et al. (2009, tables 1, 2) is much smaller and the ornamentation is more micro-rugulate. The large size and long colpi resemble *D. crassiflora*, *D. lotus* and *D. bourdilloni* but the ektexine ornamentation of *D. crassiflora* is more coarsely rugulate (Geeraerts et al., 2009, fig. 2J) and in *D. lotus* and *D. bourdilloni* conspicuously perforate in the mesocolpi. The ektexine ornamentation of our pollen type resembles to some extent *Diospyros batocana* Hiern in Geeraerts et al. (2009, fig. 2G), but this species is considerably smaller and has a subspheroidal shape.

Remarks to cf. Royena sp. and Diospyros sp.: *Diospyros* is a large pan-tropical genus with 500–600 species (Duangjai et al., 2009) living in A

and C climates of Köppen-Geiger, whereas *Royena* is a small genus (ca. 20 species) from southern Africa (Duangjai et al., 2009) living in C and B climates with several species cooping with drier conditions (e.g. *Royena fischeri, R. loureiroana, R. austroafricana, Diospyros batocana, D. lotus, D. mespiliformis, D. oubatchensis*) and many of these taxa are characterized by exceptionally large pollen grains. The distinction of the two genera on the basis of pollen morphology is difficult (Geeraerts et al., 2009; Morton and Kincaid, 1995), and pollen morphological studies cover only a tenth of the species (e.g., Erdtman, 1969; Geeraerts et al., 2009; Gosling et al., 2013; Grygorieva et al., 2013; Morton, 1994; Morton and Kincaid, 1995; Tissot et al., 1994). The reason we refer the first Ebenaceae as "cf. *Royena*" is because of the striking similarity to *Royena fischeri* and *R. loureiroana*. The large size of both fossil pollen taxa can be also observed in a *Diospyros* pollen from the middle Miocene of Denmark described by Bouchal and Denk (2021; postulated climate Cfa, Cwb) and is a common character in dispersed fossil *Diospyros* pollen (see Bouchal and Denk, 2021 for more information). The LM images from Denmark look similar to our *Diospyros* pollen but the ektexine under SEM has very conspicuous perforations and fossulae. Nevertheless, it has been also shown that many extant *Diospyros* species evolved later than the middle Miocene (Linan et al., 2019, fig. 2), and consequently the fossil pollen might be assigned to the roots of modern clades but not to species. In the macroflora a leaf probably belonging to Ebenaceae: "*Diospyros*" *pannonica* Ettingshausen is present.

ERICACEAE Jussieu
Erica Linné
Erica "scoparia-type" (Plate IV, 1–3)

Description LM: Tetrahedral tetrad, quadrangular to circular outline in basal view; tricolporoidate/tricolporate; tetrad size ca. 24.5 × 24.7 to 26.6 × 30 μm (N = 4); wall thickness ca. 1.2–1.4 μm with the sexine as thick as to thicker than nexine; tectate, scabrate to verrucate. SEM: ektexine is rugulate, verrucate to micro-verrucate, fossulate; sizes of rugulae increase at the polar areas and the towards the margos, whereas the verrucae and micro-verrucae are located in the mesocolpium areas, rugulae and verrucae are regularly and densely covered with micro-echini.

Remarks: This pollen type resembles *Erica scoparia* Linné in Foss and Doyle (1988, fig. 12 A–E) and also *E. arborea* Linné (Halbritter and Heigl, 2020b), which are both common in the (Table 3) of Portugal, Spain and on the Macaronesian islands west of Portugal and of northern Africa, both do also occur in France and in Italy in temperate and humid conditions, on acidic rocky soils. Their leaves are considered as sclerophyllous.

Erica "arborea-type" (Plate IV, 4–6)

Description LM: Tetrahedral tetrad, triangular to circular outline in apical view; tricolporoidate/tricolporate; tetrad size ca. 23.3 × 24.1; wall thickness ca. 1.1 μm with the sexine thicker than nexine; tectate, scabrate to verrucate. SEM: ektexine is micro-verrucate, sizes of micro-verrucae (ca. 0.2 to 0.7 μm in diameter) and increase in size slightly towards the margos, micro-verrucae are regularly and densely covered with shallow micro-gemmae.

Remarks: This pollen type resembles *Erica arborea* in Halbritter (2020) and *E. bergiana* Linné in Halbritter and Buchner (2016) and Miocene *Erica* pollen from Austria (Hofmann and Lichtenwagner, 2020, fig. 2 J–L). After McGuire and Kron (2005) *E. arborea* is interpreted to be the closest relative of all the south African Erica taxa, such as *E. bergiana*. *E. arborea* and *E. bergiana* are sclerophyllous shrubs that thrive under Mediterranean conditions (winter rain, dry summer; Table 3) in the Mediterranean region and in South Africa, respectively, but have their outliers as well in temperate regions (see above).

STYRACACEAE A. DeCandolle et Sprengler
Rehderodendron Hu
Rehderodendron sp. (Plate IV 7–9)

Description LM: Prolate pollen grain, elliptic to slightly rhombic outline in equatorial outline; tricolporate, colpi reaching the polar areas,

endoapertures lalongate, rectangular (ca. 2.2 to 2.8 μm high and ca. 3.5 to 4 μm wide), costae visible; polar diameter ranging from 32.1 to 35.1 μm, equatorial axis from 20.2 to 23.8 μm (N = 3); wall thickness ca. 0.9 to 1.1 μm; tectate, scabrate. SEM: ektexine is rugulate to micro-rugulate (rugulae ca. 0.8 μm to 1 μm wide and up to 2.5 μm long), fossulate and rarely perforate; rugulae are ornamented with perpendicularly to diagonally arranged conspicuous striae giving an impression of a twisted rope-like pattern; area of the endoaperture can display a bridge structure (two of three cases); colpus margin can be perpendicularly striated.

Remarks: Extant *Rehderodendron* pollen have been described and depicted by Morton and Dickison (1992, pl. 1, figs. 2K, 4N).Very comparable pollen types have been encountered in several Miocene German localities (Kottik, 2002, pl. 10, figs. 4–7 as Styracaceae; Vomela, 2016 pl. 31, figs. 1–9 as *Rehderodendron*) and in Austria (Hofmann et al., 2002, pl. 4 figs. 7–9 as *Rehderodendron*; Hofmann and Lichtenwagner, 2020, fig. 2 G–H as *Rehderodendron*). This *Rehderodendron* pollen resembles pollen of extant *R. kwantungense* Chun, *R. microcarpum* K.M.Feng ex. T.L.Ming and *R. macrocarpum* Hu (Hofmann and Zhao, n.d.) that grow under Cwa and Cwb conditions in China, Vietnam and Myanmar (Table 3). Some leaf fossils of Entrischenbrunn resemble those of the family Styracaceae, but they can not be reliably attributed, because they lack clear morphological characters.

LAMIALES Bromhead
OLEACEAE Hoffmannsegg et Link
Phillyrea Linné
Phillyrea sp. (Plate IV 10–12)

Description LM: Spheroidal to sub-spheroidal pollen grain, circular in equatorial view; tricolpate; polar diameter ca. 21.3 μm, equatorial diameter ca. 21.1 μm; wall thickness ca. 1.5 to 1.6 μm with the sexine thicker than the nexine; semitectate, reticulate. SEM: The extexine is coarse reticulate, heterobrochate, brochi irregularly shaped; muri are simplicolumellate, ca. 0.5 to 0.8 μm wide and display regular, perpendicular striation; columellae are not abundant (ca. four to five per brochus) and 0.5 to 0.7 μm high, visible foot layer is smooth.

Remarks: This pollen type fits in size, aperture configuration and ektexine sculpture and ornamentation of the muri pollen of *Phillyrea* in Halbritter (2016c), *P. angustifolia* Linné; 2016d, *P. vilmoriniana* Boissier et Balansa ex. Boissier), Halbritter and Weis (2016), *P. latifolia* Linné), and Sachse (2001), pl. 8 figs. 5–9 *P. angustifolia*), and to a much lesser extent *Chionanthus* Linné in Guo et al. (1994, fig. 1 and pl. 1 fig. 2A–D) and Miyoshi et al. (2011, *Chionanthus retusus* Lindley et Paxton plate 208 figs. 4–7 and *C. ramiflorus* Roxburgh plate 208 figs. 8–11; SEM images), because all *Chionanthus* display smooth muri. Our pollen type resembles mostly *P. latifolia* that today thrives in the Mediterranean (Table 3). *Phillyrea* like pollen have been reported from the middle Miocene by Bouchal et al. (2017, Yatagan lignite mine, Turkey) and from Grímsson et al. (2020, Lavanttal, Austria) and a single leaf of *P. pschechensis* Kutuzkina has been discovered from Entrischenbrunn (Sachse et al., unpublished data).

3.1.2. Aquatic plants

There are eight aquatic plants or plants growing near water (Table 2, Plates V, VI), these are amongst others *Ludwigia sp., Sporotrapoidites erdtmanii (Trapa*-like), pollen of Lythraceae gen. indet., *Decodon* sp., *Callitriche* sp. and *Lycopus/Mentha*-type pollen.

MYRTALES Reichenbach
ONAGRACEAE Jussieu
Ludwigia Linné
Ludwigia sp. (Plate V, 1–3)

Description LM: Oblate to sub-spheroidal pollen grain, triangular to circular outline in polar view, tricolporate with strongly protruding short ectoapertures (diameter 14.6 to 18.7 μm); equatorial diameters range from 37 to 56.9 μm (N = 2); wall thickness ca. 1.5 to 1.6 μm with the sexine as thick as to thicker than nexine; tectate, scabrate
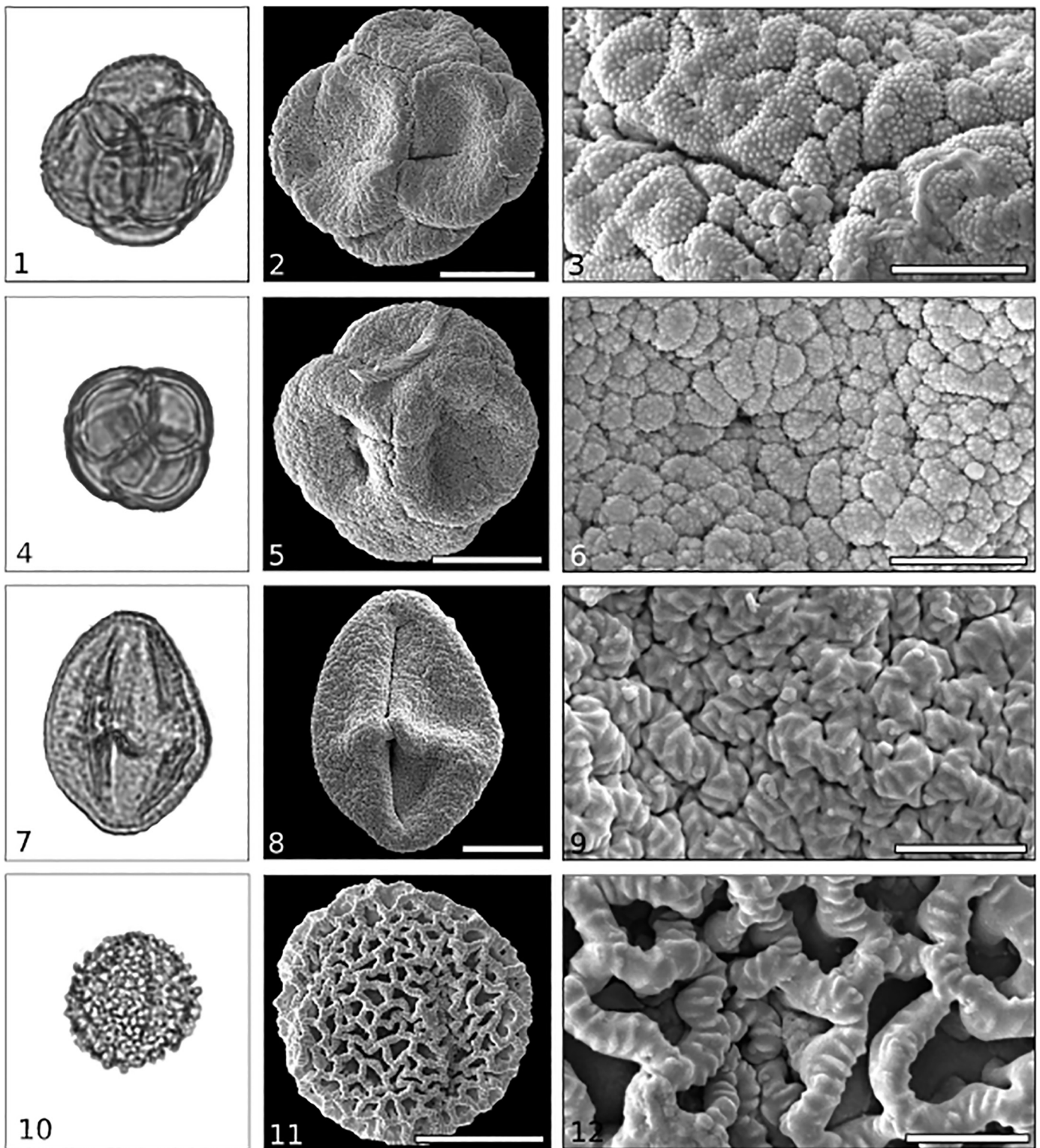
Plate IV. Subhumid and sclerophyllous elements from Entrischenbrunn. **1–3.** *Erica* sp. 1, **1.** LM images, **2.** SEM overview image and **3.** SEM detail. **4–6.** *Erica* sp. 2, **4.** LM image, **5.** SEM overview, **6.** SEM detail. **7–9.** *Rehderodendron* sp., **7.** LM image, **8.** SEM overview, **9.** SEM detail. **10–12.** *Phillyrea* sp., **10.** LM image, **11.** SEM overview, **12.** SEM details. LM images × 1000, bar in SEM overview 10 μm, bar in SEM detail 2 μm.

with viscin threads visible. SEM: ektexine is irregularly densely micro-rugulate to micro-verrucate, whereas the pori display more micro-rugulae and the poles are mixed micro-rugulate and micro-verrucate; viscin threads are smooth.

Remarks: This pollen type is known as fossil genus *Corsinipollenites* Nakoman and resembles *C. oculusnoctis* (Tiergarth) Nakoman ssp.

oculusnoctis Krutzsch in Krutzsch (1968, pl. 1 figs. 1, 2; LM images) and in Thiele-Pfeiffer (1980, pl. 9 fig. 30, LM images), which was interpreted by both authors to belong to the Oenotheraceae family (= Onagraceae). This pollen type resembles some extant *Ludwigia* taxa in Praglowski et al. (1983), particularly the ektexine ornamentation *L. nervosa* (Poiret) *H. hara* fig. 7J–L and *L. hyssoppifolia* (G. Don) Exell
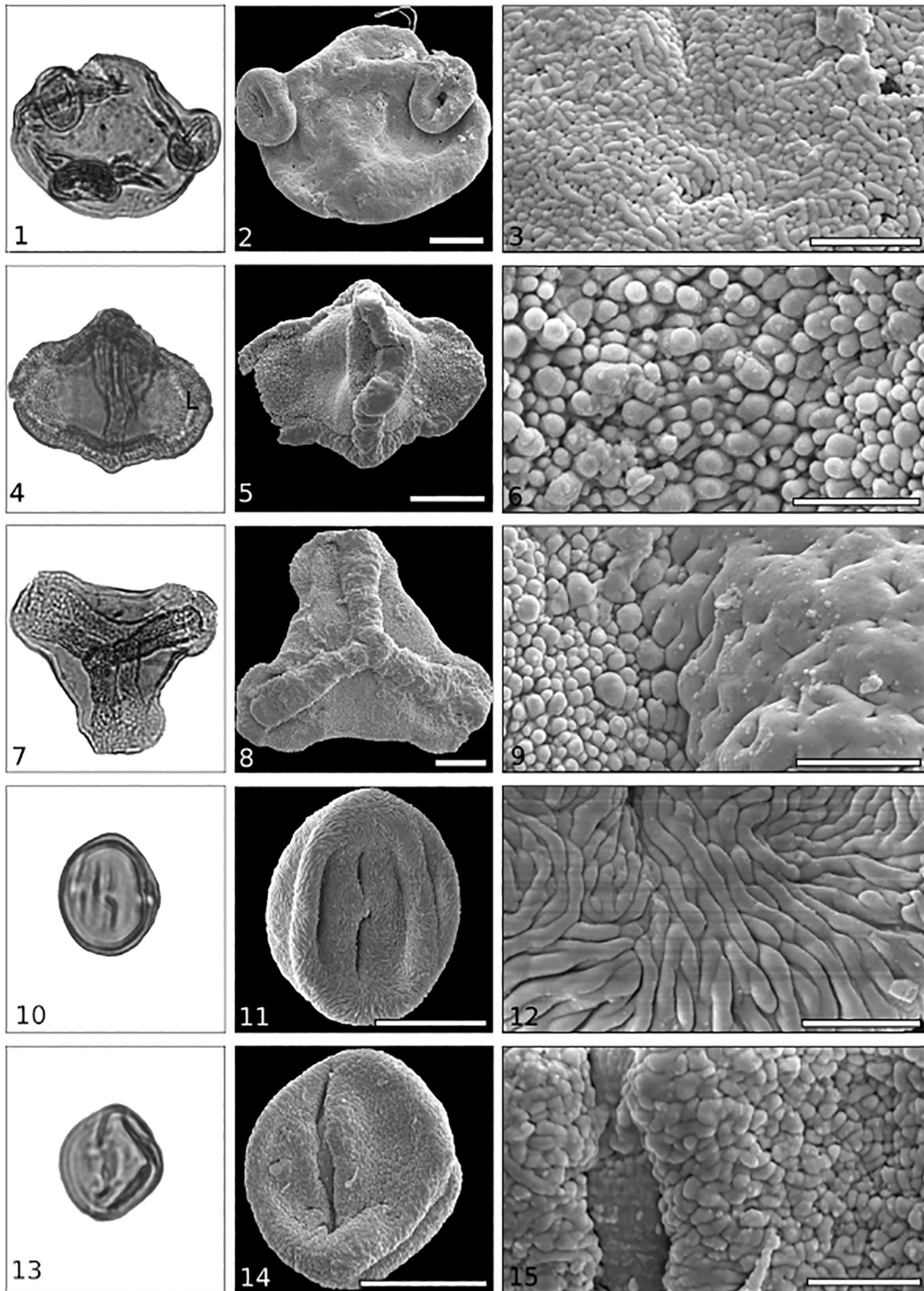
Plate V. Aquatic elements from Entrischenbrunn. **1–3.** *Ludwigia* sp., **1.** LM images, **2.** SEM overview image and **3.** SEM detail. **4–9.** *Sporotrapoidites erdtmanii*, **4–6.** equatorial view, **7–9.** polar view. **4.** and **7.** LM images, **5.** and **8.** SEM overviews, **6.** and **9.** SEM details. **10–12.** Lythraceae gen. indet., **10.** LM image, **11.** SEM overview, **12.** SEM details. **13–15.** *Decodon* sp., **13.** LM image, **14.** SEM overview, **15.** SEM detail. LM images × 1000, bar in SEM overview 10 μm, bar in SEM detail 2 μm.
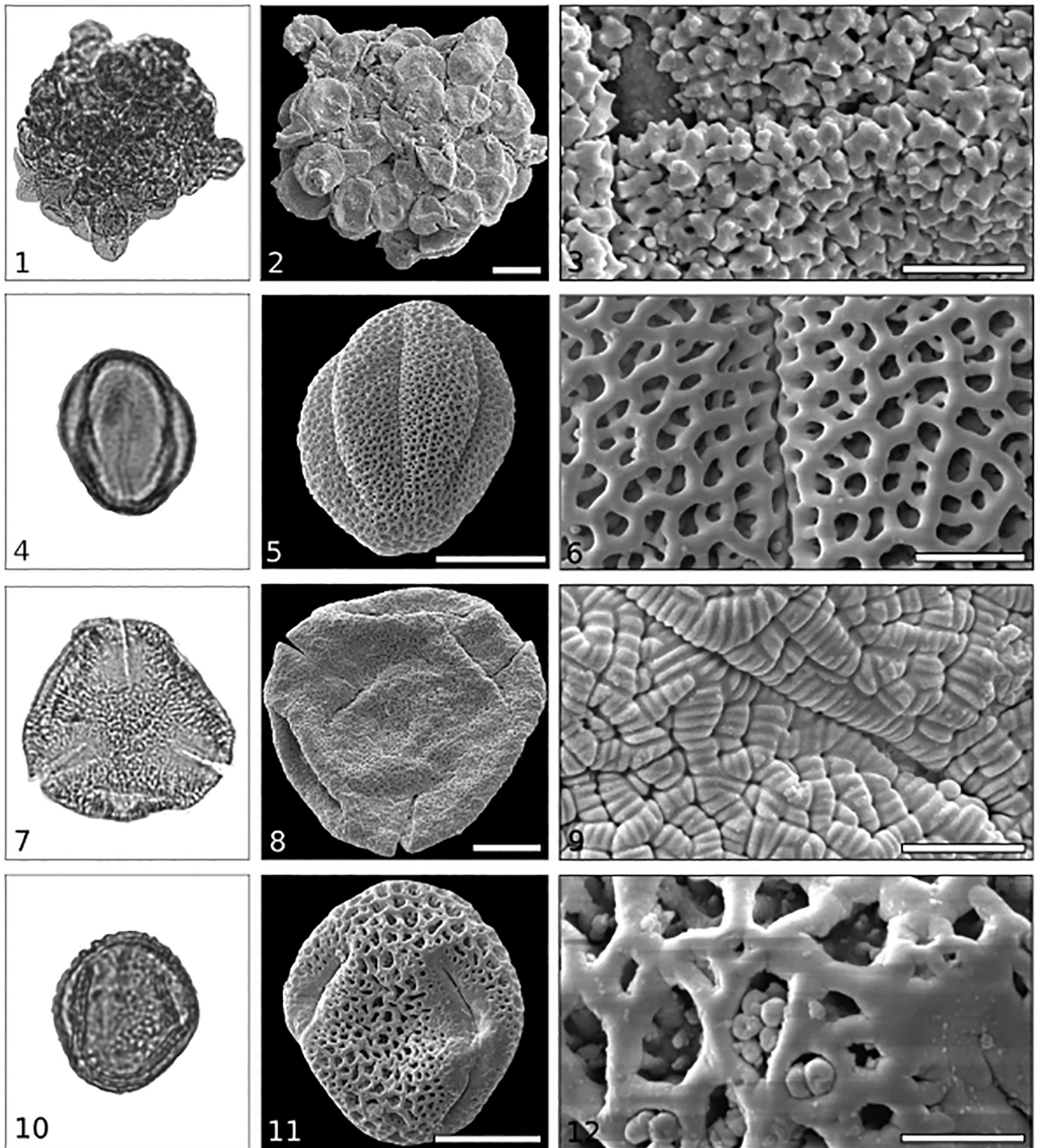
Plate VI. Aquatic and ambiguous elements from Entrischenbrunn. **1–6.** Aquatic elements, **7–12.** Ambiguous elements. **1–3.** *Callitriche* sp., **1.** LM images, **2.** SEM overview image and **3.** SEM detail. **4–6.** "*Lycopus/Mentha*-type", **4.** LM image, **5.** SEM overview, **6.** SEM detail. **7–9.** *Tricolporopollenites wackersdorfensis*, **7.** LM image, **8.** SEM overview, **9.** SEM detail. **10–12.** *Viburnum* sp., **10.** LM image, **11.** SEM overview, **12.** SEM details. LM images × 1000, bar in SEM overview 10 μm, bar in SEM detail 2 μm.

fig. 10 H) and fossil *Ludwigia* sp. 1 from the Miocene of China in Grímsson et al. (2012b, figs. 4–7).

LYTHRACEAE J.St.-Hilaire
Extinct *Sporotrapoidites erdtmanii* (Nagy) Nagy (Plate V, 4–9)

Description LM: Spheroidal to sub-spheroidal pollen grain, triangular outline in polar view, elliptic to rhombic in equatorial view; tricolp(or)ate with very protruding, swollen ectoapertures, whereas the outer pollen wall produce a thick meridional crest around the pollen body in equatorial view and a cross-like feature in polar view; polar diameter

ranges from 33.1 to 38.5 µm (N = 5) and equatorial diameter from 33.8 to 50.1 µm (N = 4), wall thickness ca. 2.5 to 2.7 µm, sexine thicker than nexine; tectate, scabrate, perforate. SEM: ektexine is densely micro-verrucate (sizes from 0.2 to 0.9 µm) in the mesocolpium areas, the thickened tectate areas running from the ectoapertures to the poles are tectate, perforate to fossulate and ca. 4.7 to 5.8 µm wide and ca. 2 to 4 µm high.

Remarks: Zetter and Ferguson (2001) described several types of *Sporotrapoidites* pollen from Cenozoic sediments with the help LM and SEM images, and depicted the morphological variety of *S. erdtmannii* (Zetter and Ferguson, 2001, pl. 1 figs. 1–22), a species that is characterized by having the smallest pollen grains in this genus. Our pollen from Entrischenbrunn display exactly the same outlook and variation. *S. erdtmannii* is interpreted to represent the pollen of *Hemitrapa* Miki (Miki, 1959; Mohr, 1983). The nuts of *Hemitrapa* are locally concentrated in the outcrop indicating, that this area of the lake was probably populated by a floating carpet.

LYTHRACEAE gen. indet. (Plate V, 10–12)

Description LM: Spheroidal to subprolate pollen grain, elliptical to circular in equatorial view, circular to lobate in the polar view; tricolporate with short colpi (ca. 10.7 µm in length) and more-or-less circular pori (ca. 0.8 to 1 µm in diameter), short pseudocolpi and not very prominent meridional ridges; polar axes ca. 19.9 to 21.5 µm and equatorial axes ca. 17.9 to 20.3 µm (N = 3), wall thickness ca. 0.8 to 1 µm, slightly thickened at the poles, sexine thicker than nexine. SEM: ektexine is tectate, striate to micro-verrucate, striae are ca. 0.25 to 0.4 µm wide and range in length between 0.4 to 5 µm, the longer striae tend to split or fuse and the longest striae are in the polar areas and shortest in the areas of the pseudocolpi; occasionally visible colpus membrane is micro-verrucate.

Remarks: Our pollen type resembles slightly the fossil Lythraceae gen. Indet in Hofmann et al. (2002, pl. 3 figs. 9–11) and to some extant *Lythrum* species, for example *L. borysthenicum* (Schrank) Litvinov and *L. salicaria* Linné (Booi et al., 2003, pls. 1, 2 and pls. 8–10, respectively), and to an ever lesser extant *L. alatum* Pursh and *L. curtisii* Fernald in Grímsson et al. (2011, pl. 2 figs. A–F and G–J, respectively), however all extant *Lythrum* taxa have much longer striae and distinctly verrucate colpi and pseudocolpi. There are also some few reminiscences with "*Decodon* morpho type 5" in Grímsson et al. (2012b, pl. 3 figs. G–I, but not J–L). One could speculate that our pollen (plus eventually morpho type 5 in Grímsson et al., 2012a) might be the pollen equivalent of the extinct diaspore morpho taxon *Microdiptera* Chandler which has been interpreted to be closely related to *Decodon* by Matthews and Ovenden (1990). *Microdiptera* often co-occurs with diaspores of *Decodon* in the same habitat (see summary in Graham, 2013).

Decodon J.F. Gemelin

Decodon sp. (Plate V,13–15)

Description LM: Spheroidal to subprolate pollen grain, elliptical to circular in equatorial view, circular to slightly triangular in the polar view; tricolporate with long colpi (ca. 13.3 µm in length) and circular pori (ca. 0.8 µm in diameter), polar axes ca. 19 to 19.3 µm and equatorial axes ca. 17 to 17.2 µm (N = 2), wall thickness ca. 0.8 µm. SEM: ektexine is tectate, micro-verrucate to micro-rugulate, micro-verrucae are ca. 0.2 to 0.5 µm in diameter and sometimes elongated, the micro-verrucae are larger in size and more elongated towards the polar area; occasionally visible colpus membrane is very faintly micro-verrucate.

Remarks: Our pollen resembles very closely *Decodon* sp. 2 in Hofmann et al. (2002, pl. 3 figs. 6–8, LM and SEM images) from the Karpatium of the Korneuburger Basin (Austria) and *Tricolporopollenites* sp. 6 in Thiele-Pfeiffer (1980, pl. 17 figs. 21–23), the latter has been interpreted to belong to the Lythraceae (e.g. *Ammania* Linné) by Thiele-Pfeiffer (1980). Pollen of fossil *Decodon* from the northern

hemisphere have been thoroughly investigated with LM and SEM by Grímsson et al. (2012a) and at least six pollen morphotypes could be distinguished from the from the middle Eocene to the late Miocene. *Decodon* sp. 2 from Hofmann et al. (2002) is represented as "*Decodon* morphotype 4" in Grímsson et al. (2012b). The extant *Decodon verticillatus* (Linné) Elliott is the only representative of this genus today and is a typical wetland plant thriving near water and in marshes in the eastern part of North America (Tiner, 1993), and comparable wetland habitats have been inferred for the fossil *Decodon* taxa by Graham (2013), Grímsson et al. (2012a), and Matthews and Ovenden (1990). Several leaf fossils affiliated with *Decodon* are present and are interpreted to part of the reed belt surrounding the lake/pond.

LAMIALES Bromhead
PLANTAGINACEAE Jussieu
Callitriche Linné
Callitriche sp. (Plate VI, 1–3)

Description LM: Lump of spheroidal to sub-spheroidal pollen grains, circular outline in all views; inaperturate or tricolpate?, apertures badly visible; diameters range from 11.7 to 18.4 µm; tectate, scabrate. SEM: ektexine is perforate to fossulate, irregularly micro-echinate, the bases of micro-echini are often fused to produce a somewhat micro-reticulate structure, generally five micro-echini produce a set; presumable apertures are slit-like; visible foot layer is smooth.

Remarks: This pollen type occurs in a large lump and the uncertainty of the apertural configuration and the semitectate exine structure resembles somehow amphibious *Callitriche* taxa (see Cooper et al., 2000, f.e. *C. cribosa* Schotsman figs. 33–36). *Callitriche* is an aquatic plant of temperate regions of the northern hemisphere.

LAMIACEAE Martinov
"*Lycopus*/*Mentha*-type" (Plate VI, 4–6)

Description LM: Spheroidal to subprolate pollen grain, with an elliptical to circular outline in equatorial view and circular outline in polar view; hexacolpate with ca. 15 to 17 µm long colpi; polar axis ca. 23.6 µm long and equatorial axis ca. 19.9 µm long; semitectate, micro-reticulate. SEM: Semitectate, micro-reticulate, incompletely bireticulate, with with brochi sizes ranging from 0.3 µm to 1 µm, larger brochi display a bireticulate pattern and increase in size towards the mesocolpium and polar areas; muri are smooth, ca. 0.3 µm wide and simplicolumellate.

Remarks: This pollen taxon resembles *Lycopus* Linné (e.g. *L. europaeus* Linné in Halbritter and Ulrich, 2016a), *Lycopus* spp. in Moon and Hong (2003), figs. 1–30), *Lycopus lucidus* Turczaninow ex. Bentham in Miyoshi et al. (2011, pl. 229, figs. 1–3), and *Mentha* Linné (e.g., *M. arvensis* Linné in Ulrich, 2016; *M. longifolia* (Linné) Hudson in Halbritter and Ulrich, 2016b) and to a much lesser extant *Origanum vulgare* Linné (Halbritter et al., 2020), because the latter displays free standing columellae in the brochi. *Lycopus* is growing in damp places near water.

3.1.3. Ambiguous pollen taxa

Two floral elements (Plate VI, 7–12) are either plants with pollen which cannot be securely affiliated with one species or a specific climatic condition: The first is *Tricolporopollenites wackersdorfensis* (macrofossil equivalent *Podocarpium*), that has been observed in many localities as macrofossil (leaves and fruits) and suggested to grow under various different climate conditions (Kovar-Eder et al., 2004). The second is *Viburnum* sp. which resembles closely deciduous *V. opulus* (humid temperate), but also evergreen *V. tinus* and *V. davidii* (mediterranean to seasonal subtropical climate requirements). The matter is complicated by the fact that the macrofossil of "*Viburnum atlanticum*" (Table 2) is not comparable to *V. opulus*. Another leaf fragments is somehow comparable to *V. lantana* but also to *Sambucus nigra*. The second is

FABALES Bromhead
FABACEAE Lindley
Extinct: *Tricolporopollenites wackersdorfensis* Thiele-Pfeiffer (Plate VI, 7–9)

Description LM: Oblate pollen grain, triangular to slightly circular outline in polar view; tricolporate; equatorial diameter ranging from 37 to 41.4 μm (N = 3); wall thickness ca. 1.4 to 1.5 μm, with the sexine as thick as to thicker than nexine; tectate, micro-reticulate. SEM: Tectate, perforate, micro-rugulate to rugulate and fossulate, micro-rugulae and rugulae are irregularly, densely arranged and are perpendicularly, finely grooved.

Remarks: This pollen is common and was recognized by Mohr and Gregor (1984) as pollen generation of *Podocarpium podocarpum*, formerly known as *Gleditsia knorri* (Heer) Gregor. Thiele-Pfeiffer (1980) described this taxon from the Miocene brown coal deposits near Wackersdorf (Bavaria, Germany). Another name for this pollen is *Fupingopollenites* G.W. Liu occurring from Oligocene to mid-Miocene Chinese strata (Gregor, 1986; Kovar-Eder et al., 2004; Liu et al., 2001). Macrofossils of *Podocarpium* are mostly found in wide range of humid to subhumid habitats including alluvial, and mixed mesophytic forests (e.g. Kovar-Eder et al., 2004; Rasser et al., 2013). Since the corresponding leaflets and pods of *Podocarpium podocarpum* (A. Braun) Herendeen have been frequently found in Entrischenbrunn it is very likely that the mother plants grew next to the depositional site.

DIPSACALES Berchthold & J.Presl
ADOXACEAE E. Meyer
Viburnum Linné
Viburnum sp. (Plate VI, 10–12)

Description LM: Prolate to sub-prolate pollen grain, elliptic to slightly rhombic in equatorial view; tricolporate, colpi reach the polar areas, endoaperture lalongate; polar axis ca. 25.7 μm, equatorial axis ca. 23.2 μm; wall thickness ca. 1.4 to 1.6 μm with the sexine thicker than the nexine; semitectate, reticulate. SEM: Extexine is reticulate, heterobrochate, foveolate to perforate brochi decrease in size towards the margos; brochi are irregularly angular to circular, with sizes between 1 to 1.8 μm in diameter and filled with free standing columellae; muri are simplicolumellate, smooth, ca. 0.3 to 0.4 μm wide and stand on ca. 0.5 to 0.8 high, densely spaced columellae; margos are tectate, smooth and foveolate to perforate.

Remarks: This pollen type has resemblances to *Viburnum* species with a tectate margo, particularly *V. opulus* Linné (section Opulus; Halbritter and Heigl, 2020a; Miyoshi et al., 2011, pl. 248 figs. 7–9), *V. tinus* Linné and *V. davidii* Franchet (both section Tinus; Halbritter and Heigl, 2020b; Donoghue, 1984, pl. 3 C and D, E, respectively). Whilst *V. opulus* is growing under temperate climates and likes humid/damp areas near water the two evergreen *Viburnum* of the section Tinus prefer either Mediterranean conditions (*V. tinus*) to warm temperate conditions (*V. davidii*, eflora of China).

3.1.4. Broad leaved forest elements

Most pollen taxa of the pollen assemblage are belonging to azonal plants (Plate VII, 1–9), they represent the typical Miocene humid elements such as *Parthenosissus/Ampelopsis*-type, *Liquidambar* sp., *Ulmus* spp., *Fraxinus* sp. etc. (see Table 2).

SAXIFRAGALES Berchthold & J.Presl
ALTINGIACEAE Horaninow
Liquidambar Linné
Liquidambar sp. (Plate VII, 1–3)

Description LM: Spheroidal pollen grain, circular to slightly elliptic outline in all views; pantoporate, porus diameter range from 4.5 to 5.6 μm, pori evenly distributed on the pollen surface; general diameter of pollen grain ca. 35 to 37 μm; wall thickness ca. 1.2 to1.3 μm, nexine thinner than the sexine; tectate, scabrate. SEM: ektexine perforate, foveolate, tectum surface covered with more-or-less regularly spaced supra-tectal micro-echini/gemmae; pori are circular to elliptic, porus membranes covered with loosely arranged, irregularly shaped angular verrucae of 1 μm or > 1 μm, with scattered supra-tectal micro-echini, porus margins smooth to slightly irregularly.

Remarks: Comparable extant *Liquidambar* taxa (including *Altingia* Noronha) are shown by Bogle and Philbrick (1980), Fujiki and Ozawa (2007), and Ickert-Bond and Wen (2006). Some *Liquidambar* and former *Altingia* species display both more elliptical or circular pores and frizzy or smooth porus margins. This pollen type has been frequently found in Miocene strata of Europe (ranging from Oligocene to Pleistocene; Krutzsch, 1957, 1966) and published under the fossil taxon name *Periporopollenites stigmosus* (Potonié) Thomson et Pflug. Pollen of Altingiaceae are known since the Mastrichtian (Hofmann et al., 2011) from Siberia. *Liquidambar* is an azonal element along rivers in swamps and floodplains (Mai, 1995).

VITALES Jussieu ex Berchtold et J.Presl
VITACEAE Jussieu
cf. *Parthenocissus/Ampelopsis*-type (Plate VII, 4–6)

Description LM: Prolate pollen grain, elliptic outline in equatorial view; tricolporate, colpi reaching the polar areas, pori circular; polar axis ca. 37.2 to 37.6 μm, equatorial axis ca. 24 to 25.1 μm (N = 2); wall thickness ca. 1.7–1.9 μm, sexine much thicker than nexine; semitectate, reticulate, tectate margo. SEM: Reticulate, heterobrochate, perforate to foveolate at the margo; muri smooth, simplicolumellate.

Remarks: This pollen type is summarized under the fossil genus *Tricolporopollenites macrodurensis* Thomson et Pflug and might represent similar looking Vitaceae pollen grains of the genera *Parthenocissus* Planchon, *Ampelopsis* Michaux, *Cissus* Linné and *Cayratia* Jussieu (see Thiele-Pfeiffer, 1980). Our pollen grains have strong resemblances to either *Parthenocissus* (e.g., Miyoshi et al., 2011, pl. 147 figs. 13–16) and *Ampelopsis* (Perveen and Qaiser, 2008, fig. 1A–B). *Parthenocissus* and *Ampelopsis* are typical climbers at forest margins. This pollen type assignable to *Parthenocissus/Ampelopsis* could be associated with the fossil leaves of *Tetrastigmophyllum hungaricum* Andreánszky from Entrischenbrunn. Such leaves are generally are compared with leaves of *Parthenocissus*, *Cayratia* or *Tetrastigma* (Miquel) Planchon.

LAMIALES Bromhead
OLEACEAE Hoffmannsegg et Link
Fraxinus Linné
Fraxinus sp. (Plate VII, 7–9)

Description LM: Sub-spheroidal pollen grain, circular to triangular in polar view; tricolpate; equatorial diameter ca. 15.2 to 19.4 μm, polar diameter 18.3 to 19.4 μm (N = 4); wall thickness ca. 1.4 μm with the sexine thicker than nexine; semitectate, reticulate. SEM: ektexine is reticulate, heterobrochate, brochi irregularly shaped and about 1 to 1.8 μm in diameter and decrease towards the colpi; muri are simplicolumellate and 0.4 to 0.8 μm wide and display either perpendicular striate ornamentation or irregularly distributed micro-gemmae, columellae are 0.25 to 0.3 μm high and highest in the mesocolpium; visible colpus membrane micro-verrucate.

Remarks: This pollen type fits in size, aperture configuration and ektexine sculpture and ornamentation of the muri pollen of extant *Fraxinus* in Guo et al. (1994, fig. 1 and pl. 2 fig. 6 a–d to 8 a–d), in Sachse (2001), pl. 8 figs. 10–13) and Diethard & Heigl (2016, *F. excelsior* Linné). Two species of fossil *Fraxinus* leaves are present in Entrischenbrunn: *F. grossedentata* Laurent and *F. inaequalis* Heer.

4. Discussion

4.1. Overlap of macro and microflora

The here presented palynological results complement and corroborate partly the macrofossil findings of Schmitt and Butzmann (1997), Wallner and Gregor (2011) and Sachse et al. (unpublished data), and
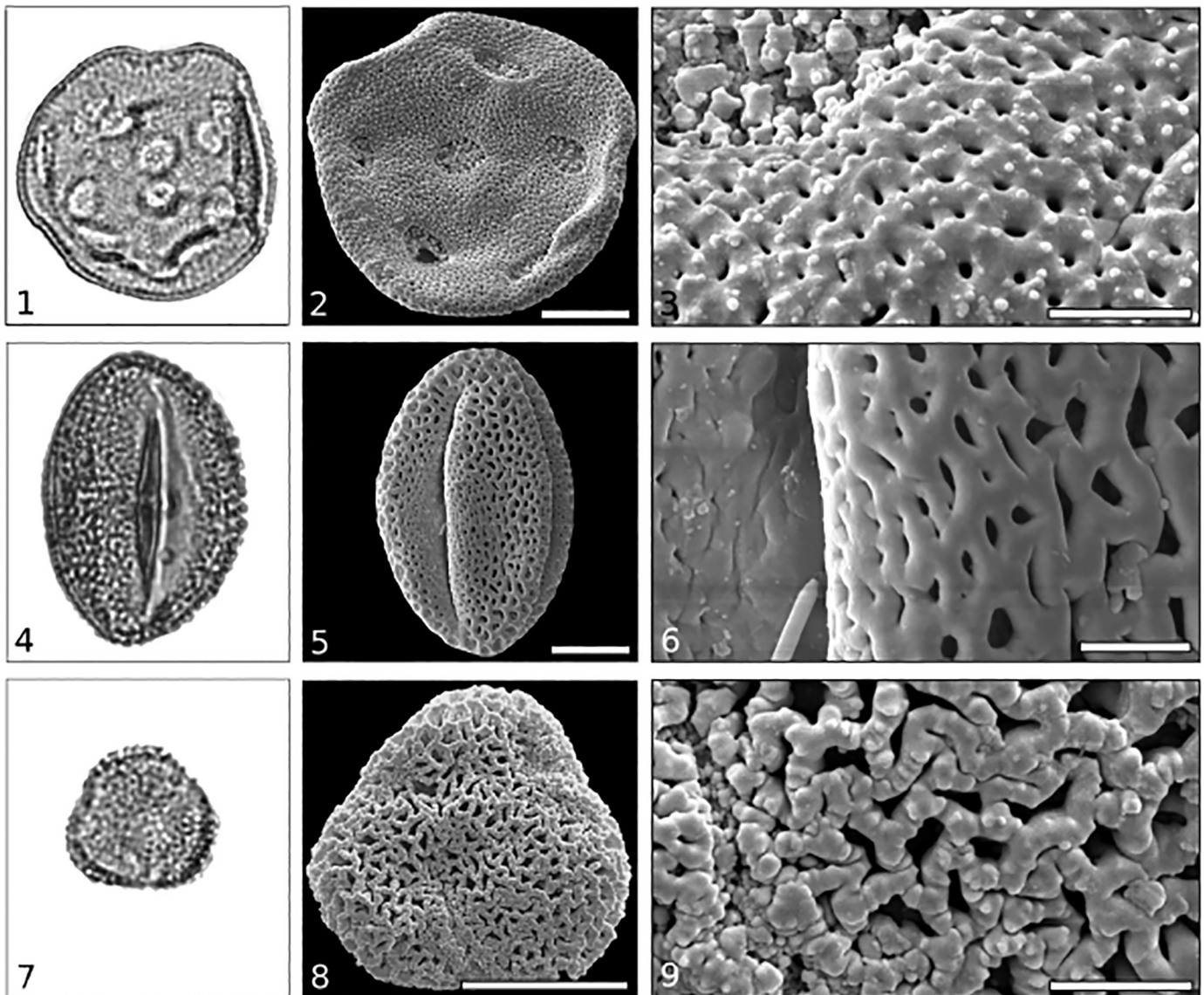
Plate VII. Classical azonal elements from Entrischenbrunn. **1–3.** *Liquidambar* sp., **1.** LM images, **2.** SEM overview image and **3.** SEM detail. **4–6.** "*Parthenocissus/Ampelopsis*-type", **4.** LM image, **5.** SEM overview, **6.** SEM detail. **7–9.** *Fraxinus* sp., **7.** LM image, **8.** SEM overview, **9.** SEM detail. LM images × 1000, bar in SEM overview 10 μm, bar in SEM detail 2 μm.

therefore facilitates an environmental, vegetational reconstruction and an approximation of how locally restricted the growing conditions were for this site (Table 3). There are taxonomic overlaps of some taxa that are not treated in this paper: The second Poaceae pollen taxon is spheroidal and around 20 to 24 μm in diameter and might be well associated with a rhizome fragment has been determined as"*Phragmites*"*oeningensis* Al. Braun, however, it might represent another reed or drier azonal element. The few *Typha* pollen encountered can be associated with sprout fragments of *Typha latissima* Al. Braun and indicating that it was a minor element of the reed belt. Both taxa are more-or-less autochthonous. Numerous pollen of *Platanus* sp. represent a part of the adjacent probably dense alluvial forest, since several leaves and even some fragments of bark of *Platanus* have been found which were presumably washed into the depositional site. The cf. *Vitis* sp. pollen could be probably associated with a single occurrence of a leaf of *Vitis vitifolia* (A. Braun) Proch. et Bužek. *Salix* sp. pollen is mirrored by a variety of leaf forms belonging to several species of *Salix* that occurred along the fluvial channels. The palynological record of conifers is especially interesting, since so far no findings of leaves, cones or seeds are

reported from the Bavarian Middle Miocene NAFB (e.g. Meller and Gregor, 2001).

4.2. Mismatches between palynoflora and macroflora

Particularly rare pollen of *Abies* sp. and *Picea* sp. (Table 2) may indicate a probably already existing alpine belt of the arising Eastern Alp mountain ranges positioned ca. 150 km to the south, where a growing proportion of montane coniferous elements in palynological samples are reported from the Middle Miocene onward by Jiménez-Moreno et al. (2008). At that time an Alpine montane forest was fully established more further away in the Swiss Central Alps, which had already exceeded modern altitudes (Krsnik et al., 2020). Pollen of *Cathaya* sp. generally is associated with mixed mesophytic or evergreen forests, the low numbers of *Cathaya* pollen might confirm that such forests on fertile soil were located far beyond the active river system. The genus *Pinus* includes a broad spectrum of ecological preferences, but its pollen grains are usually only assigned to two form types due to limited taxonomical characteristics. The *Pinus* haploxylon-type is generally assigned to pines of the Subgenus Strobus (e.g. Gernandt et al., 2005). Its species

include a wide range of ecological preferences as dry sand bars or peats. We interpret the high amount of this pollen type in Entrischenbrunn as indication that the mother plants grow not too far, but outside of the active river system, because no macrofossils within the whole braided river system of the OSM have been reported yet. Less pollen refer to the *Pinus* diploxlon-type (Subgenus Pinus) which derive from various species (e.g. Gernandt et al., 2005). They can therefore not be interpreted in terms of ecological preferences and might be transported in from far distance. In contrast Cupressaceae pollen referred to Taxodioideae (*Taxodium* or *Glyptostrobus*) show a clear ecological signal, although they are difficult to distinguish and therefore usually grouped together (e.g. Grímsson et al., 2011). As these taxa are present in high amounts, their mother plants probably grew in swamp forests not to far from the depositional site, where silting up had already progressed. Also the rare trilete *Pteris*-like fern spores, which can not be reliably attributed to the generic level, could come from such wet habitats like bogs, peats or river edges, but also drier places.

Nearly 75% of the counted individual leaf fossils (Sachse et al., unpublished data) originate from trees lacking fossilizable pollen, i.e. Lauraceae (mainly *Daphnogene* Unger) and *Populus* and emphazise a large mismatch between findings of fossil leaf flora and palynofloras. On the other hand, pollen of water plants (e.g., *Ludwigia* sp., *Decodon* sp., *Callitriche* sp.), herbs and shrubs (e.g., *Lycopus*/*Mentha*-type, cf. *Chenopodium* sp., *Ephedra* spp.) or trees from nearby (cf. Cupressaceae/Taxodioideae, *Fraxinus* sp., *Liquidambar* sp., *Juglans* sp., *Carya* sp., *Pterocarya* sp.) or from more distant stands (e.g., Pinaceae species, *Rehderodendron* sp., *Diospyros* sp., *Sideroxylon* sp.) are generally not represented in the macrofossil record but reflect a mosaic distribution of varying hydrological controlled vegetation types.

4.3. The presence of subhumid and sclerophyllous elements

The pollen assemblage of Entrischenbrunn reveals an interesting mixture of Miocene classic azonal plants (e.g., Fagaceae, Juglandaceae, Ulmaceae, Salicaceae), water plants and helophytes and a considerate proportion of shrubs and woody plants that can thrive under drier and subhumid conditions and are more sclerophyllous.

4.3.1. Pollen

There are several possibilities that some plants preserved as pollen in Entrischenbrunn show signals of either (humid)-subhumid conditions or are sclerophyllous plants. Both types can be either influenced by either seasonally drier phases in the year or grow on local drier areas within the azonal (wide and spacious braided river system) and/or zonal vegetation (abandoned braided river system, hinterland) that are only partly reflected in the macroflora, because pollen are transported much further from their mother plants than leaves. The Köppen signatures of these plants and their most similar looking modern equivalents are summarized in Table 3 and are generally characterized by A (tropical) and C (warm) climates, however when considering precipitation they show a somewhat "Mediterranean" Csa, Csb climate (dry summers: e.g., *Erica* spp.; *Ephedra* spp., *Zelkova* "abelicea/serrata-type", *Quercus* sect, Ilex) and also subhumid Cwa and BSh climates (e.g., *Ephedra* spp., *Ziziphus* "mucronata/mauritania/jujuba-type", *Celtis* "tournefortii-type" etc. see Table 3) are represented. This kind of composition is not surprising, since such "Köppen"-based analysis is orientated on the current ecological adaptions to present atmospheric circulation patterns, whereas the Middle Miocene lacks a strong latitudinal temperature gradient, probably resulting in a circulation pattern consisting of just one – weaker – atmospheric cell instead of three as today (Langford and Lewis, 2009). Additionally, the lack of cold winters resulted in a much more extended growing season, so that the seasonal timing – winter or summer – of arid phases had less effect on the vegetation than the severity and length of such intervals. Also the plants ability of evolutionary adaptions to seasonal changes in precipitation should be taken into consideration. However, a recent analysis of

Langhian palaeosoil carbonates from Switzerland hinted temporal water stress during summer times, accompanied by high precipitation (Methner et al., 2020), which possibly would result in a combination of Cw and Cs-climates.

4.3.2. Macroflora

Only less than half of the pollen taxa are typical azonal riparian woody broad-leaved plants (see Table 2), which is not unusual when looking at recently published palynological investigations of middle Miocene sediments routinely using LM in combination of SEM (e.g., Kottik, 2002; Grímsson et al., 2011, 2015, 2016, 2020; Bouchal et al., 2016, 2017, 2018). This "drier plants signal" in the palynoflora is also corroborated by some taxa of the macrofossils found in Entrischenbrunn (Table 1): dominance by *Populus mutabilis* Heer, numerous taxa of legume-like foliage and fruits, *Crataegus*, various Rhamnaceae, *Ulmus braunii* Heer, *Quercus drymeja* Unger, *Q. mediterranea* Unger, *Q. neriifolia* (Al. Braun), Celastraceae and Simaroubaceae (compare also middle Miocene localities summarized in Kovar-Eder and Teodoridis, 2018) and the presence of numerous small-sized sun leaves of *Daphnogene* indicate a rather open forest vegetation. This partly corroborates the results of Kovar-Eder and Teodoridis (2018). They suggested, based on the Integrated Plant Record analysis (Kovar-Eder et al., 2008) using over 30 fossil floras (including Entrischenbrunn), that the zonal vegetation of the Paratethys and the Molasse of the Alps should be characterized as more subhumid and sclerophyllous zonal vegetation during the middle Miocene (ShSF of Kovar-Eder and Teodoridis, 2018), stating that the drier period was in the whole area and not only locally. This is in some agreement with the reconstructed precipitation curves of Böhme et al. (2011), where the late Langhian was interpreted to represent a "relatively drier" period than the early Langhian and the Tortonian.

4.3.3. An approximation to reconstruct edaphic and climatic conditions

The question, if the "drier plant signal" of pollen and macro flora in Entrischenbrunn witness a more subhumid and sclerophyllous azonal vegetation sensu Kovar-Eder and Teodoridis (2018), a drier period during the Langhian (Böhme et al., 2011), or a local phenomenon cannot be answered here completely. There might be a few reasons for the latter:

A braided river system covering laterally a wide area is characterized by a mosaic pattern of various azonal groundwater-bound vegetation types with different humidity requirements over a microrelief of sandy and gravelly and fine-grained substrate. For example an open vegetation with subhumid and sclerophyllous plants (such as *Ephedra* spp., *Erica* spp., *Quercus* sp. section Ilex, grasses) might have grown away from the active river channels on the pebbly or sandy bars of an abandoned channel or even adjacent to the braid plain, where the groundwater level was lower than in the hydrological active area. The Ebenaceae, Sapotaceae, *Rehderodendron* sp., *Ziziphus* "mucronata/mauritania/jujuba-typ"e, *Celtis* "tournefortii-type" and *Ulmus* sp. section Foliaceae could have grown along an ephemeral channels (only water during flooding events) representing subhumid to humid stands, depending on the water discharge and groundwater level in the active braid plan or along the abandoned braid plain (subhumid). The humidity loving plants were distributed along the active channels (such as *Platanus* sp., *Ulmus* sp., *Liquidambar* sp.), water saturated the fine-grained flood plains (e.g., Taxodioideae) and flood plain ponds (e.g., *Decodon* sp., *Callitriche*, *Mentha*/*Lycopus*-type). This mosaic distribution might have been accentuated by autocyclic changes of channels characteristic of a highly dynamic braided river system where with phases of silting up, during local channel abandonment, and phases of flooding and erosion of channels and flood plains during high water discharges, switched laterally over wider areas. If these autocycles can be explained by small-scale climatic oscillations like in the Dinarides lakes of Bosnia and Herzegovina (Jiménez-Moreno and Mandic, 2020) cannot be answered here.

Changes of the atmospheric circulation pattern, for example, might have created a rain shadow area, due to framing by surrounding mountain chains. The presence of mountain elements (e.g., Pinacaee) witnesses already uplifted areas in the South.

The true answer will lie in more detailed sedimentological work and mapping (e.g. Fiest, 1994; Fiest unpublished data). Additionally, a large number of sand and gravel pits contain fossil plant assemblages and fossils in numerous collections are waiting for discovery or (re-)investigation. In such way a high potential for high resolution of spatial and temporal palaeo-vegetation mapping could allow closer insights into Middle Miocene environmental changes. However, there are some clues to follow already now and we focus here on localities, which contain also macro-palaeobotanical results:

1. Positioned 6 km to the south, in the upper part of OSM 9 of Fiest (1994), the slightly younger fossil locality Unterwohlbach (see Fig. 1) yields a smaller portion of drier elements in the macro flora (Gregor and Schmitt, 2016; Sachse and Schmitt, 2016, Sachse et al., unpublished data), however, the pollen content has not been investigated yet. We assume, that this locality could indicate either the transition to the so called wetter climate period of a Milankovich driven humid interval of the Middle Miocene Thermal Maximum (Böhme et al., 2011), or a more wetter palaeo-hydrological position in the drainage system. It possibly was located closer to an active river channel and thus closer to the ground water level resulting in a more waterlogged locality with its corresponding vegetation. This would explain that leaves of *Platanus* sp. and *Populus balsamoides* Goeppert from humid stands could accumulate temporarily in laterally restricted in high concentrations in the Entrischenbrunn pond, indicating an inflow from a neighboring humid vegetation further away. (Sachse et al., unpublished data).

2. The alluvial forest flora of Gallenbach near Augsburg (see Fig. 1) is slightly younger (i.e. lower part of OSM 9, Fiest, 1994; Fiest, pers. communication) and yields a very similar macrofloral composition and therefore also similar ecological signals. Although studied by Seitner (1987) only with light microscopy, the overall palynological composition shows a dominance of *Pinus* sp., *Cathaya* sp., Taxodioieae, and some *Myrica* sp. pollen as swamp elements, alluvial forests with high percentages of *Ulmus* and *Podocarpium*, some Juglandaceae, *Alnus* sp., as well as lake and lake margin facies dominated by *Hemitrapa*, Nymphaeaceae, some *Potamogeton* sp., and significant numbers of Cyperaceae, Poaceae, *Sparganium/Typha*-type. Also dry stands with *Ephedra*, *Buxus*, Poaceae and some pollen of a distant mesophytic forest (*Quercus* spp., *Symplocos* sp., Araliaceae, *Engelhardia* sp., and Castaneoideae) are recorded. Additionally, the rough description of the macroflora by Schmid and Gregor (1983) indicates a close match with *Hemitrapa*, *Populus mutabilis*, *Daphnogene* sp. and *Ulmus* sp. as dominant elements, but should be investigated in much greater detail.

3. Additionally, the Early Langhian flora of Burtenbach yields elements from all of these facies units mentioned above, even with a wider taxonomic spectrum (Seitner, 1987), which can be probably explained by its stratigraphic position within the Middle Miocene Climate Optimum (MMCO). Unfortunately, many of these taxa were not identified to genus level. However, elements from drier habitats and poplars from alluvial forests are much less present in the flora (Sachse, 2022). Instead *Podocarpium podocarpum* and *Daphnogene eibandii* Sachse (Sachse, 2022) are major elements of a local pond vegetation, indicating a higher water supply.

For the reasons given above, such ecological variety might be due to different climate signals derived from those localities. However, for the moment, climate variations caused by Milankovich cycles could hardly be reliably detected in a braided river system due to the lack of fine stratigraphic and continuous resolution. An improved stratigraphic resolution in future might lead to a better understanding spatial and temporal variation in the Molasse flora of this time.

For the Entrischenbrunn locality, which was situated in a large scale braided river system we can up to know conclude, that the various

hydrological controlled substrates and (e.g., pebbly and sandy bars, silty and clayey floodplains and floodplain ponds, natural levees, abandoned and flooded channels etc) gave rise to a very complex diversity of plants ranging from water plants, to swamp elements, plants along channels to plants from different well-drained substrates with a distinct dry or sclerophyllous appearance.

5. Conclusions

The middle Miocene locality of Entrischenbrunn is characterized by a high proportion of subhumid and sclerophyllous pollen of plants such as two *Ephedra* spp., two *Erica* spp. with affinities to modern Mediterranean species, *Ziziphus*"mucronata/mauritania/jujuba-type", *Diospyros*, cf. *Royena*, *Celtis*-"tournefortii-type", *Sideroxylon* etc. These pollen and *Populus mutabilis*, small-sized *Daphnogene* spp., and *Quercus drymeja*, etc. witness drier conditions ((reduced humidity), either climatically or locally controlled (e.g., edaphic conditions of a braided fluvial river system, autocyclic changes). Current level of knowledge makes it difficult to fully explain why the palynoflora of Entrischenbrunn (and probably the Gallenbach palynoflora) is deviating from previously published palyno- and macrofloras. However, for the OSM, a detailed analysis of the complex vegetational structure and the taxonomical composition can be only achieved by combining SEM/LM-palynological and macrofossil investigations and sedimentological mapping. The OSM with its many sand pits with improving stratigraphical resolution might offer a high potential for a palaeo-vegational mapping in space and time. Regarding the present climatic changes towards conditions resembling the Miocene ones, more intensive research provides not only a better understanding of regional Miocene environmental and climatic changes, but also might help us to answer questions concerning regional landscape management in near future.

Data availability

All data is available in this manuscript

Declaration of Competing Interest

We have no conflict of interest, with any person.

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