Grana

ISSN: 0017-3134 (Print) 1651-2049 (Online) Journal homepage: https://www.tandfonline.com/loi/sgra20

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Christa-Charlotte HofmannCHRISTA-CHARLOTTE HOFMANN & Sophie LichtenwagnerSOPHIE LICHTENWAGNER

To cite this article: Christa-Charlotte HofmannCHRISTA-CHARLOTTE HOFMANN & Sophie LichtenwagnerSOPHIE LICHTENWAGNER (2019): First palynological results of accessorial elements from the Langhian Schaßbach clay pit, Lavanttal Basin (Austria) – LM and SEM investigations of Cornales and Ericales, Grana, DOI: 10.1080/00173134.2019.1641550

To link to this article: https://doi.org/10.1080/00173134.2019.1641550

Grana, 2019
https://doi.org/10.1080/00173134.2019.1641550

First palynological results of accessorial elements from the Langhian Schaßbach clay pit, Lavanttal Basin (Austria) – LM and SEM investigations of Cornales and Ericales

CHRISTA-CHARLOTTE HOFMANN & SOPHIE LICHTENWAGNER

Department of Palaeontology, University of Vienna, Vienna, Austria

Abstract
Preliminary results of the palynoflora from the Schaßbach clay pit comprise accessorial floral elements of three Cornales and five Ericales pollen taxa that have modern living equivalents from different continents. The eight taxa are relatively rare in the palynological assemblages and are affiliated with the genera *Nyssa, Mastixia, Erica, Vitellariopsis, Rehderodendron* and *Polyspora. Nyssa* sp. resembles closely the deciduous *Nyssa sylvatica* of temperate America, the two *Erica* spp. resemble the south European tree heathers *Erica arborea* and *Erica lusitanica*, and *Vitellariopsis* sp. looks like evergreen *Vitellariopsis marginata* from subtropical southern Africa. The living equivalents of *Mastixia* spp., *Rehderodendron* sp. and *Polyspora* sp. are evergreen taxa from subtropical and tropical Asia.

Keywords: *Miocene pollen, Nyssaceae, Ericaceae, Sapotaceae, Styracaceae, Theaceae*

The Miocene sedimentary rocks of the Lavanttal Basin (Carinthia, Austria) are a mixture of freshwater and brackish to marine beds deposited between *c.* 17 to *c.* 11 myr: Deposition commenced during the early Miocene (Burdigalian) and terminated around the early late Miocene (early Tortonian; Beck-Managetta 1952; Reischenbacher & Sachsenhofer 2013). The sedimentary succession was interrupted in the upper part (middle Serravallian) and probably in the lower part (around 16 myr at the Burdigalian/lower Langhian boundary) by two unconformities (see Beck-Managetta 1952; Tollman 1985; Reischenbacher & Sachsenhofer 2013; Meller et al. 2015, figure 2). The investigated sediments were collected in the Oberaigen district, situated at the western border of the central Lavanttal, from an open pit at Schaßbach (Figure 1; see Meller et al. 2015 for comprehensive geological overview). This pit was on and off mined for clays and is now partly re-filled and naturalised. The mined sediments are interpreted to represent a part of the Langhian age Mühldorf Formation (Beck-Managetta 1952; Lippolt et al. 1975; Reischenbacher et al. 2007; Reischenbacher & Sachsenhofer 2013; Meller et al. 2015). Regular field campaigns with students from Vienna University since 2010 have yielded large numbers of plant fossils (mostly leaves, diaspores and twigs) and sediment samples for palynology from Schaßbach. The very rich macrofossil spectrum is dominated by leaves of *Platanus*, various Fagaceae (e.g. *Fagus, Quercus*) and Betulaceae (*Alnus, Betula*), *Juglans, Ulmus, Zelkova*, numerous entire margined leaves, *Glyptostrobus* twigs and cones and many more leaves and diaspores, that all await a thorough systematic treatment. The macrofossil diversity of this locality is similar to the more-or-less contemporaneous Schönweg locality in the lower Lavanttal (see Meller et al. 2015, table 1). Of the macrofossils so far studied, findings of *Ginkgo adiantoides* (Unger) Heer from Schaßbach have been published by Meller et al. (2015). Previous palynological investigations of Lavanttal material concentrated on younger, Sarmatian (Serravallian) deposits including terrestrial sediments from plant fossil-bearing localities (Klaus 1955,

Correspondence: Christa-Charlotte Hofmann, Department of Palaeontology, University of Vienna, Vienna, Austria. E-mail: *christa.hofmann@univie.ac.at*

(Received 1 March 2019; accepted 26 June 2019)

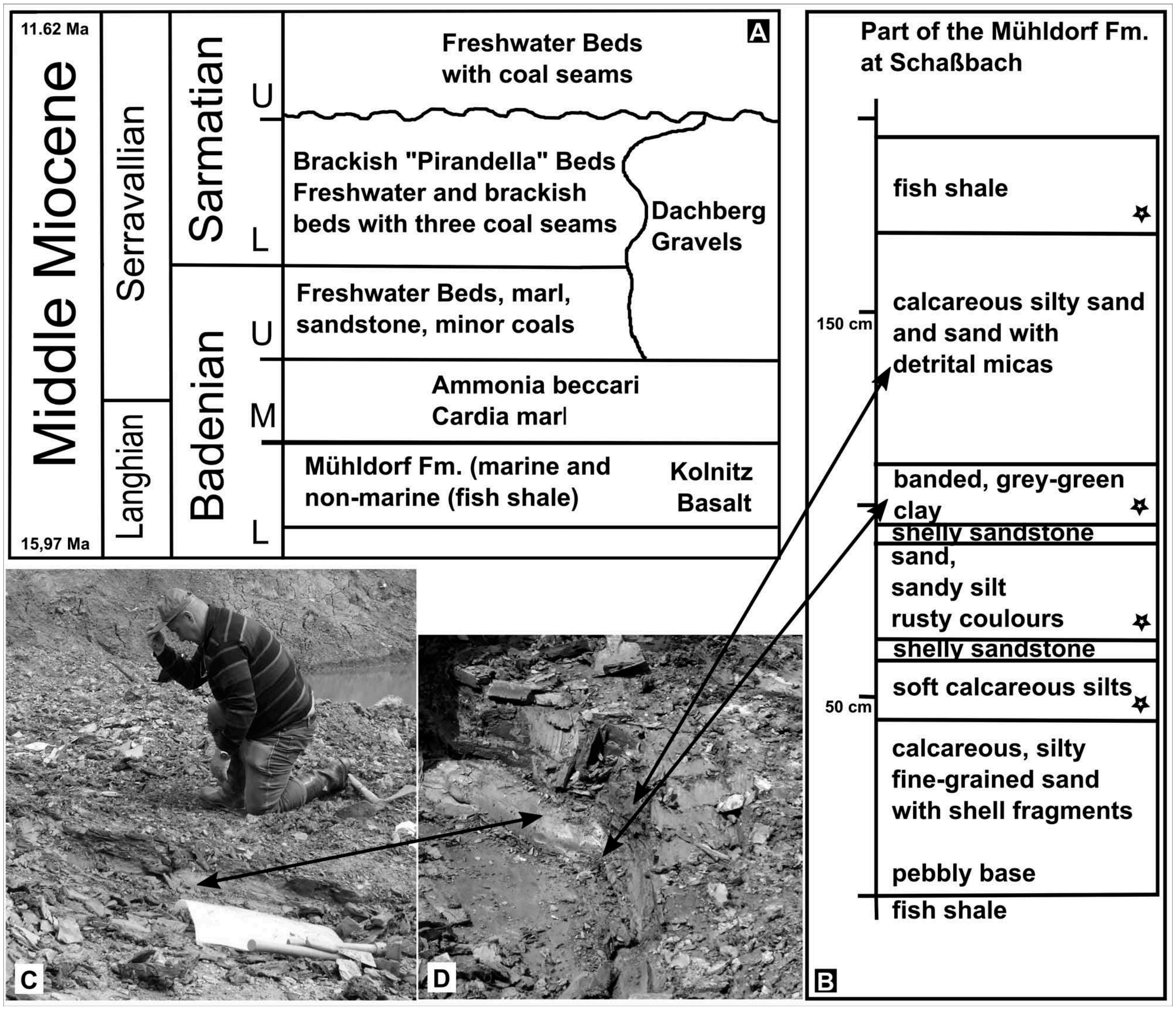

Figure 1. **A.** Stratigraphy and sediments of the investigated locality in the Lavanttal. Stratigraphic chart of the middle Miocene sediments in the Lavanttal (after Reischenbacher & Sachsenhofer 2013; Meller et al. 2015). **B.** Part of a small sedimentary profile of the lacustrine lower part of the Mühldorf Formation at the clay pit Schaßbach, district Oberaigen. The four pollen samples are indicated with an asterisk. **C.** Reinhard Zetter kneeling on the banded grey-green clay. **D.** Photograph of the of the banded grey-green clay and overlying calcareous silty sand and sand with detrital micas.

1984), and phosphorite nodules that yielded excellently preserved pollen and spores (e.g. Grímsson et al. 2011, 2015, 2016). Only four samples of the Schaßbach sediments collected for palynology had significant amounts of reasonably well-preserved pollen that comprise accessorial pollen from the orders Cornales and Ericales.

Material and methods

The four investigated sediment samples from the Schaßbach clay pit came from a *c*. 120 cm thick horizon consisting of intercalations of plant fossil-bearing silty clays, medium-grey, barren clays, and plant fossil-bearing slightly sandy silts and clays, and organic rich papery clays ('Papierschiefer' containing mostly fish remains); the sample of the latter is generally poor in palynomorphs, and palynomorph preservation in all samples is not good (Figure 1B, pollen samples are indicated by an asterisk). Sample preparation followed standard wet chemical procedures (e.g. Klaus 1987): crushed samples were boiled in hydrochloric acid (HCl) until the carbonate part was dissolved and then treated with hydrofluoric acid (HF) to dissolve the silicates (cold processing over four days). The organic remains were again boiled in HCl for 5 min, decanted and

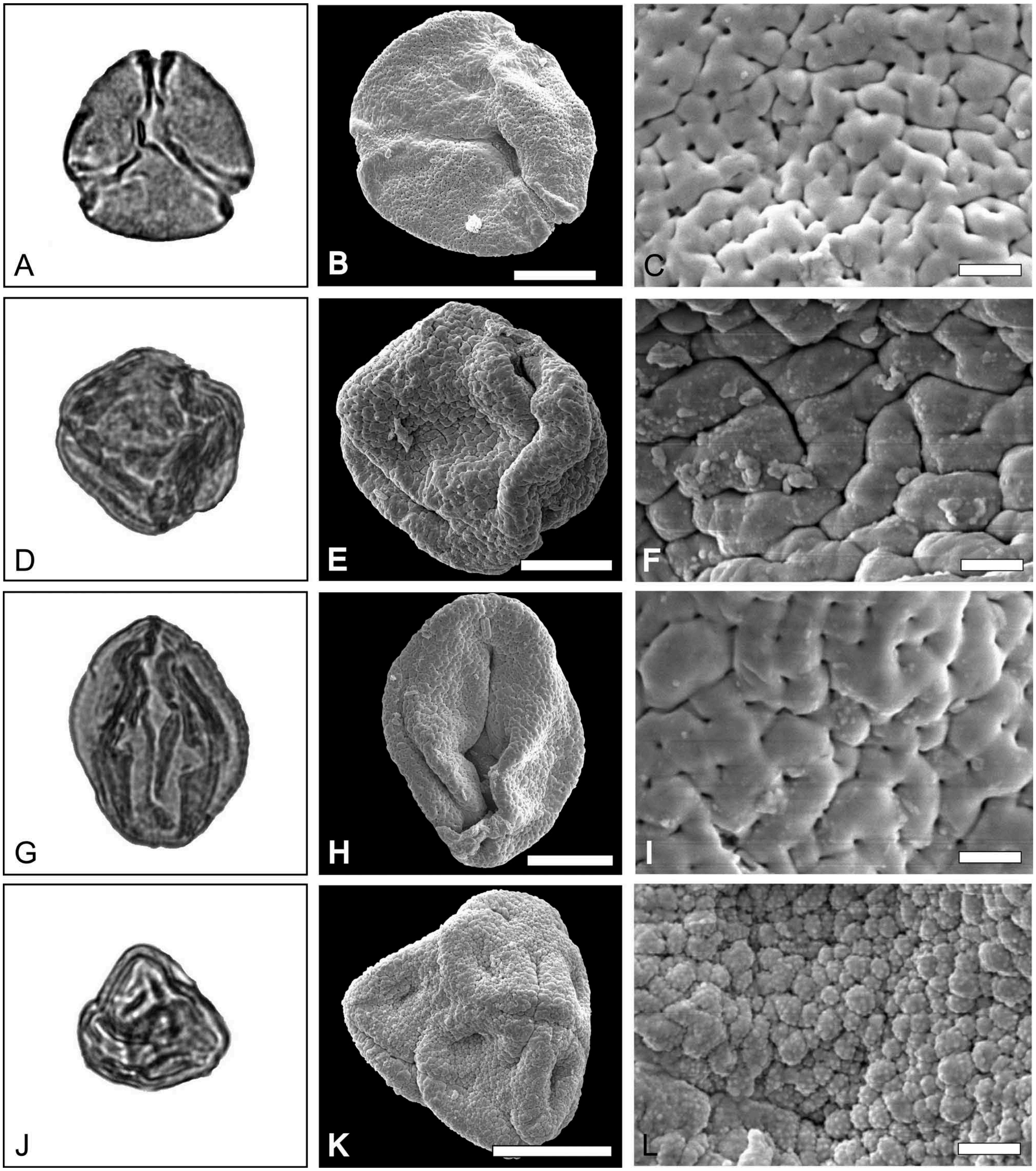

Figure 2. LM and SEM images of pollen of Cornales and Ericales. **A–C.** *Nyssa* sp. **A.** LM overview. **B.** SEM overview of the same grain as **A. C.** SEM detail of the same grain as **A. D–F.** *Mastixia* sp. 1. **D.** LM overview. **E.** SEM overview of the same grain as in **D. F.** SEM detail of the same grain as in **D. G–I.** *Mastixia* sp. 2. **G.** LM overview. **H.** SEM overview of the same grain as in **G. I.** SEM detail of the same grain as in **G. J–L.** *Erica* sp.1. **J.** LM overview. **K.** SEM overview of the same grain as in **J. L.** SEM detail of the same grain as in **J.** Scale bars – 10 μm (B, E, H, K), 2 μm (C, F, I, L).

washed several times with water, but not sieved, thus retaining palynomorphs < 10 μm in size, followed by acetolysis. The remaining residues were mixed with glycerine and stored in tightly closing glass vials. For light microscopy (LM) investigation, the pollen were isolated with a micro-manipulator from the sample smears on a glass slide into a clean drop of glycerine on a new slide and photographed with a Samsung digital camera. Afterwards, the same pollen were moved with a micro-manipulator to a scanning electron microscopy (SEM) stub and rinsed in a drop of 100% alcohol to remove the glycerine. The stubs were sputtered with gold and examined with a SEM (FEI InspectS 500). Stubs and photographs are stored in the Department of Palaeontology, University of Vienna, under inventory numbers IPUWSB7841/1/1-10 to IPUWSB7841/4/1-10.

Systematic palynology

The Schaßbach pollen assemblages are generally dominated by various taxa of the wind pollinated Pinaceae, Cupressaceae, Fagaceae, Juglandaceae, Ulmaceae and Platanaceae. In contrast, fern and moss spores are rare (seven taxa). The here presented accessorial elements of Cornales pollen comprise *Nyssa* sp. and two *Mastixia* spp. (Nyssaceae), whereas the Ericales pollen are slightly more diverse; two *Erica* spp. (Ericaceae), one *Vitellariopsis* sp. (Sapotaceae), one *Rehderodendron* sp. (Styracaceae), and one *Polyspora* sp. (Theaceae). These taxa represent only a small portion of the accessory elements of the pollen and spore flora (up to now *c.* 60 taxa) and occur in very small numbers (*N* = 1–3). In the following systematic treatment the classification follows Stevens (2001, and onwards) and pollen terminology follows Hesse et al. (2009).

Description of the pollen grains

Order Cornales Link
Family Nyssaceae Martius
Genus Nyssa Gronov. ex. L.
Nyssa sp. (Figure 2A–C)

Description LM. — Tricolporate, prolate to subspheroidal pollen grains (*N* = 3), rhombic to elliptic in equatorial view or triangular to circular in polar view in compressed state (Figure 2A); polar axes from 26.7 to 37.7 µm, equatorial axes from 21.6 to 29.2 µm; colpi 16.3 to 29.1 µm long, endoapertures slightly lalongate, rectangular to circular, *c.* 2.3 to 4.7 µm high and 3.1 to 6.2 µm wide, costae well visible; wall thickness *c.* 1–1.4 µm with the sexine as thick as to thicker than nexine; tectate, scabrate.

Description SEM. — The ectexine is tectate, fossulate, perforate, in between fossulae micro-rugulate to micro-verrucate, the margo is tectate and sparsely perforate and smooth in the equator (Figure 2B, C); micro-rugulae are irregularly shaped *c.* 0.5 µm wide and up to 1 µm long. (Figure 2C).

Comparative remarks. — Among extant species of *Nyssa*, the fossil pollen is more similar in size, apertural arrangement and ectexine ornamentation to *Nyssa sylvatica* Marsh. depicted in Göschl (Göschl 2008, plates 10–12). *Nyssa* is a flood tolerant genus disjunctly distributed in North and Central America and Asia; *Nyssa sylvatica* is a North American species. Examples of fossil *Nyssa* pollen resembling *Nyssa sylvatica* are given in Masselter (2001, plate 14, figures 4–6) and Vomela (2016, plate 28, figures 7–9).

Genus *Mastixia* Blume
Mastixia sp. 1 (Figure 2D–F)

Description LM. — Tricolporate, prolate pollen grain in equatorial view elliptic to rhombic (obliquely compressed), polar axis 30.5 µm and equatorial axis 27.9 µm (*N* = 1, Figure 1D); colpus difficult to discern *c.* 19.3 µm long and endoporus not properly visible but probably lalongate with visible costae (Figure 2D); wall thickness *c.* 1.3–1.5 µm with the sexine thicker than the nexine; tectate, scabrate.

Description SEM. — The ectexine is tectate, rugulate to verrucate, fossulate and perforate (Figure 2E), whereas the rugulae/verrucae are partly more-or-less angular or rounded, rugulae and verrucae are flat and smooth with sizes ranging between *c.* 1.5 to 3 µm in length and 0.7 to 1 µm in width and are bordered by the fossulae, fossulae and perforation are often connected (Figure 2F).

Mastixia sp. 2 (Figure 2G–I)

Description LM. — Tricolporate, prolate pollen grain in equatorial view elliptic, polar axis 30.5 µm and equatorial axis 27.9 µm (*N* = 1, Figure 2G); colpus *c.* 29.2 µm long and endoporus lalongate to elliptic, *c.* 2.7 µm high and 4.4 long, costae visible; wall thickness *c.* 1.3–1.6 µm, with the sexine thicker than the nexine; tectate, scabrate, perforate.

Description SEM. — The ectexine is tectate, perforate, fossulate and faintly rugulate, whereas the rugulae are pronounced only in the mesocolpium areas, the poles and the margo are perforate to fossulate (Figure 2H, I).

Comparative remarks. — The two *Mastixia* fossil species strongly resemble a number of extant *Mastixia* taxa described and depicted by Ferguson (1977, figures 9a–f). *Mastixia* sp. 1 is reminiscent of *Mastixia* taxa of probably early Miocene age from Wiesa (Germany) depicted in Vomela (2016, plate

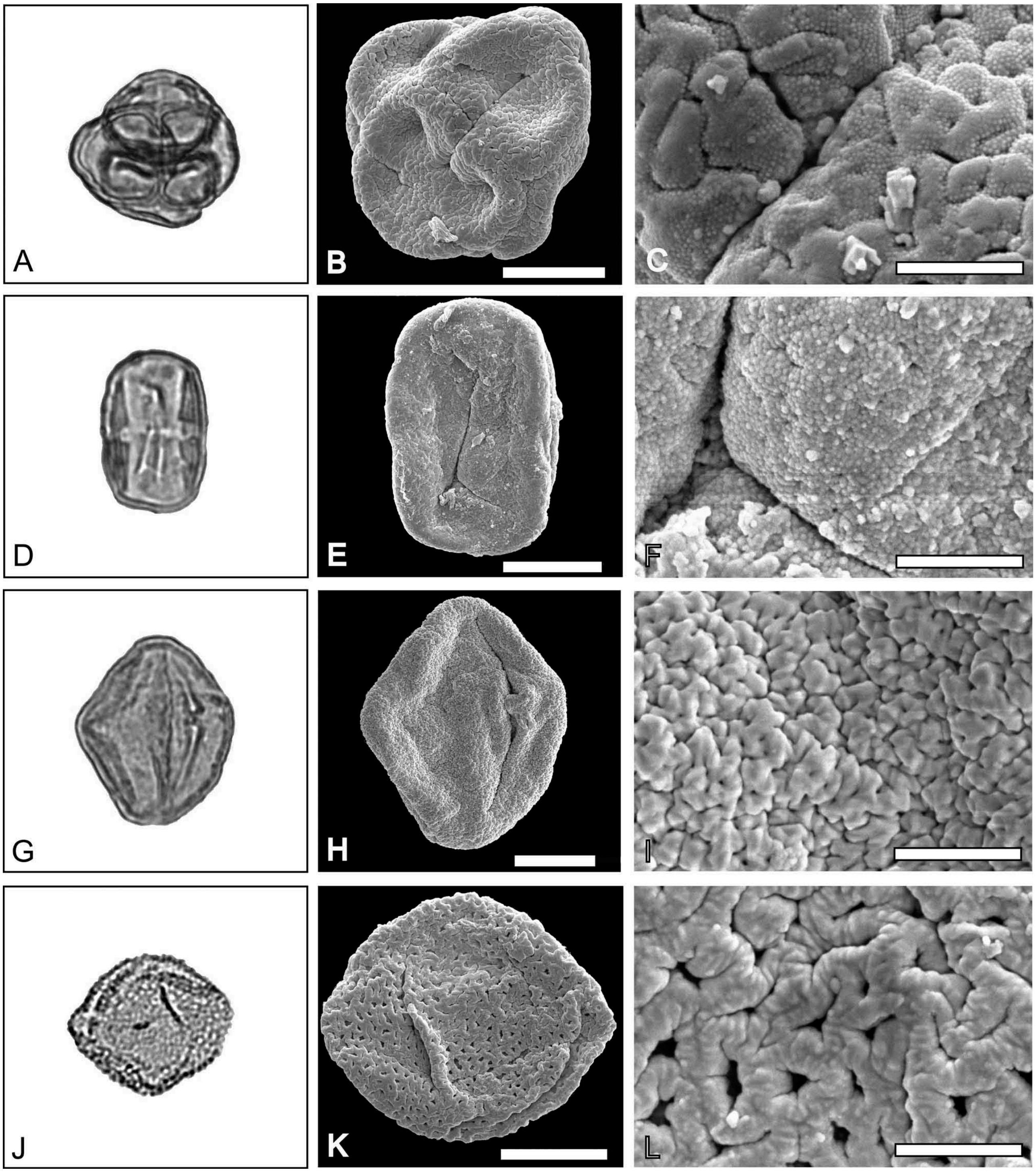

Figure 3. **A–C.** LM and SEM images of pollen of Ericales. *Erica* sp. 2. **A.** LM overview. **B.** SEM overview of the same grain as **A. C.** SEM detail of the same grain as **A. D–F.** *Vitellariopsis* sp. **D.** LM overview. **E.** SEM overview of the same grain as in **D. F.** SEM detail of the same grain as in **D. G–I.** *Rehderodendron* sp. **G.** LM overview. **H.** SEM overview of the same grain as in **G. I.** SEM detail of the same grain as in **G. J–L.** *Polyspora* sp. **J.** LM overview. **K.** SEM overview of the same grain as in **J. L.** SEM detail of the same grain as in **J.** Scale bars – 10 µm (B, E, H, K), 2 µm (C, F, I, L).

29, figures 1–6), of middle Miocene *Mastixia* sp. from Kreuzau (Germany) depicted in Ferguson et al. (1997, plate 5, figures 1–3), and of *Mastixia* sp. from the middle Miocene in the Hausruck area (Austria) in Masselter and Hofmann (2005, figures 5, 1–3); all these dispersed pollen grains resemble the extant *Mastixia cuspidata* Blume (Ferguson 1977, figure 9a, h) and *Mastixia tetrandra*

(Thwaites) C.B. Clarke in Premathilike and Nilsson (2001, figure 6D, E). *Mastixia* sp. 2 is reminiscent of Mastixiaceae gen indet. from Wiesa (Germany) depicted in Vomela (2016, plate 29, figures 10–12) and the LM image resembles more extant *Mastixia montana* (Wight ex Thwaites) C.B. Clarke Bedd. (Premathilike & Nilsson 2001, figure 6A). Manchester et al. (2009) suggested that the European fossils affiliated with *Mastixia* or 'mastixioids' might actually belong to the sister genus *Diplopanax* Handel-Mazzetti.

Ericales Dumort.
Ericaceae Juss.
Ericoideae
Ericeae DC ex Duby
Erica L.
Erica sp. 1 (Figure 2J–L)

Description *LM.* — Tetrahedral tetrad, triangular to slightly rounded outline in apical view and quadrangular to circular in basal view (Figure 2J); tetrad size 20 µm × 21 µm to 23 µm × 24 µm in diameter (*N* = 2); pollen tricolporoidate/tricolporate; wall thickness *c.* 1–1.2 µm with sexine as thick as to probably slightly thicker than nexine; tectate, scabrate.

Description SEM. — The ectexine is tectate, microverrucate to micro-rugulate/rugulate, fossulate (Fig-Figure 2K), the mesocolpium and polar areas are micro-verrucate (*c.* 0.2–0.6 µm in diameter) and the areas at the margo micro-rugulate to rugulate (rugulae *c.* 0.7–1.3 µm long and 0.8 µm wide), all microrugulae and micro-verrucae are densely covered by regularly spaced micro-echini (Figure 2L).

Erica sp. 2 (Figure 3A–C)

Description *LM.* — Tetrahedral tetrad, elliptic to slightly quadrangular in outline in basal view (Figure 2A); tetrad size 26 µm × 27.5 µm in diameter (*N* = 1); pollen tricolporoidate/tricolporate (Figure 3A); wall thickness *c.* 0.9–1.3 µm with the sexine slightly thicker than the nexine; tectate, scabrate.

Description SEM. — The ectexine in the polar areas and margos is rugulate (rugulae up to 2 µm in length and up to 1.3 µm in width; Figure 3B) and conspicuously fossulate (Figure 3B, C), the mesocolpium areas are more micro-verrucate to micro-rugulate, the micro-verrucae and micro-rugulae are more flat-topped than in *Erica* sp. 1; the entire tectum is covered densely by regularly spaced micro-echini (Figure 3C).

Comparative remarks. — Many modern *Erica* species display this distinctive ectexine pattern and are covered by regularly spaced micro-echini. But generally the tetrads of these species are double the size of the fossil tetrads described here. The only extant *Erica* taxon comparable in size is *Erica arborea* L. in Halbritter (2016, 10–25 µm in diameter) and in Sarwar and Takahashi (2014, SEM figures 1A, 2A, 2E; 27–32 µm in diameter), but the ornamentation of the micro-echini is not as pronounced as in our fossil *Erica* specimen. *Erica* sp. 1 also slightly resembles *Erica bergiana* L. (heather from the Cape flora in South Africa) in Halbritter and Buchner (2016, LM and SEM images), which also has pronounced micro-echini, and *Erica arborea* (near east, Mediterranean, north African tree heather) in Halbritter (2016, LM and SEM images) that has not so pronounced micro-echini. Eocene pollen affiliated with *Erica arborea* has been described by Hofmann (2018, figure 2A–C). *Erica* sp. 2 resembles more *Erica lusitanica* Rudolphi (Spanish and Portuguese tree heather) in Halbritter (2017) and middle Miocene *Erica* pollen from Germany (Ferguson et al. 1997, plate 4, figures 10–12).

Sapotaceae Juss.
Sapotoideae Eaton
Mimusopeae Hartog
Vitellariopsis (N.E. Br.) Aubrév.
Vitellariopsis sp. (Figure 3D–F)

Description LM. — Tetracolporate, prolate pollen grain, rounded rectangular in equatorial view; polar axis *c.* 25.5 µm and equatorial axis *c.* 16.7 µm (*N* = 1); colpus *c.* 14.8 µm long, endoaperture lalongate to circular *c.* 1.8 µm high and *c.* 2.5 µm wide (Figure 3D); wall thickness *c.* 0.9–1 µm; tectate, psilate.

Description SEM. — The extexine is tectate, microverrucate and sparsely, but regularly perforate (Figure 3E); micro-verrucae are regularly distributed, dense and evenly sized (1–1.2 µm in diameter, Figure 3F).

Comparative remarks. — The apertural configuration visible under LM and the ectexine pattern visible under SEM resemble extant Mimusopeae pollen depicted in Harley (1991, figure 6D–F, LM images of e.g. *Mimusops angel* Chiov; figure 10C–F, LM and SEM images of *Vitellariopsis marginata* (N.E, Br.) Aubrév.). Fossil pollen comparable to our *Vitellariopsis* pollen are known from the lower Eocene: e.g. Mimusopeae-type pollen from Krappfeld (Austria) and middle Eocene Mimusopeae-type pollen from

Borken (Germany), both in Hofmann (2018, figure 6D–F and G–I, respectively), from the lower Miocene of Germany in Kmenta (2011, plate 15, figures 4–14 as Sapotaceae gen. indet.; resembling *Manilkara*), in Kottik (2002, plate 10, figures 8–15 resembling *Manilkara* and *Mimusops*), from Austria, in Meller et al. (1999, plate 5, figure 1–3 as Sapotaceae gen. indet.; resembling *Manilkara*), from the middle Miocene of Austria (Draxler & Zetter 1991, plate 3, figure 1–3 as Sapotaceae-Habitus; resembling *Vitellariopsis* and *Mimusops*), from Turkey (Bouchal et al. 2017, plate 11, figures 8–10; as tribe Sapoteae with suggestions to *Mimusops*, *Payena* and *Madhuca*).

Styracaceae Dumort.
Rehderodendron Hu
Rehderodendron sp. (Figure 3G–H)

Description LM. — Tricolporate prolate to subprolate pollen grain, rhombic to elliptical in equatorial outline; polar axes range from *c.* 30.6 to 34.8 µm and equatorial axes from *c.* 24.6 to 25.4 µm ($N = 2$, Figure 3G); colpus length between *c.* 26.3 and 29.6 µm, colpus protrudes conspicuously at the endoapertures, endoapertures lalongate, more-or-less rectangular *c.* 1.4–1.7 µm high and *c.* 2.3–3.3 µm long; wall thickness *c.* 1–1.3 µm; tectate, scabrate.

Description SEM. — The ectexine is micro-rugulate to rugulate, fossulate and perforate (Figure 3H), whereas the irregularly, angular shaped micro-rugulae and rugulae (*c.* 0.5–0.8 µm wide and up to 2.5 µm long) are bordered by fossulae and perforations, the ornamentation by micro-verrucae give the impression that the micro-rugulae and rugulae are composed of even smaller tectal elements (Figure 3I).

Comparative remarks. — LM images of this pollen strongly resemble extant Styracaceae pollen described and depicted by Morton and Dickison (1992). SEM images resemble particularly *Rehderodendron macrocarpum* Hu and to a lesser extent *Sinojackia xylocarpa* Hu (Morton & Dickison 1992, plate 1, figures 2K, 4N). Lower Miocene *Rehderodendron* pollen from Austria also look similar, e.g. in Hofmann et al. (2002, plate 4, figures 7–9) and from Germany in Kottik (2002, plate 10, figures 4–7) and in Vomela (2016, plate 31, figures 1–9).

Theaceae Ker Gawler
Theeae Szyszylowicz
Polyspora Sweet
Polyspora sp. (Figure 3J–L)

Description LM. — Tricolporate, subprolate pollen grain, rhombic to elliptical in equatorial outline; polar axis 22.9 µm and equatorial axis 26.5 µm ($N = 1$, Figure 3J); colpus length *c.* 11.5 µm, endoaperture most likely lalongate *c.* 2.3 µm high and *c.* 3.8 µm wide; wall thickness *c.* 0.7–0.9 µm with the sexine thicker than the nexine; reticulate.

Description SEM. — The ectexine is semitectate, reticulate to micro-reticulate, heterobrochate; the brochi are either slit-shaped, roughly triangular or more-or-less rectangular (diameters or lengths of brochi range from 0.3 to 1.3 µm, Figure 3K, L); muri are *c.* 0.5–0.7 µm wide, flat and ornamented with grooves running perpendicular to the muri displaying a sort of coarse annelid pattern (Figure 3L); visible footlayer is smooth.

Comparative remarks. — This pollen type resembles well *Polyspora chrysandra* (Cowan) Hu ex B. Bartholomew & T.L. Ming depicted in Wei (2003, plate 27, figures 7, 8 as *Gordonia chrysandra* Cowan) and extant *Polyspora axillaris* (Roxb. ex Ker Gawl.) Sweet ex G. Don in Li et al. (2011, p. 1093 as *Gordonia axilliaris* [Roxb. ex Ker Gawl.] Endl.) and in Fendt (1996, plate 10, figures 1–7 as *Gordonia axilliaris*). However, the extant *Gordonia* pollen depicted are nearly twice the size of the fossil one. The Asian species of *Gordonia* have been transferred to the genus *Polyspora* by Bartholomew and Ming (2005), based on molecular phylogenetic work by Yang et al. (2004) and Zhang et al. (2014).

Discussion

Cornales

Today, *Nyssa* (Nyssaceae) has a disjunct distribution in the Americas (four species in the southern United States and Costa Rica) and East Asia (three species; Wang et al. 2012). However, since the late Palaeogene *Nyssa* was distributed across the entire northern hemisphere (Eyde 1997). The fossil record from this time onwards is dominated by diaspores and pollen (e.g. Kuprianova 1960, in Kazakhstan; Mai & Walther 1978, in Europe; Manchester 1994, in North America). Our *Nyssa* pollen resembles pollen of the extant North American *Nyssa sylvatica* Marsh., a tall deciduous tree with variable climatic requirements for growth. It occurs in the entire eastern part of North America (to northern Mexico in the south and to southern Ontario to the north) and inhabits moist soils of valleys and uplands up to *c.* 1200 m above sea level (a.s.l.) (Little 1996). Miocene aged diaspores of *Nyssa disseminata* (Ludw.) Kirchh. from Europe are also affiliated with *Nyssa* *sylvatica*, in contrast to Paleogene *Palaeonyssa* and *Protonyssa*, both erected by Reid and Chandler, that have been associated with *Nyssa sinensis* Oliv., and the same is true for Eocene *Nyssa* pollen from Europe and China (Hofmann et al. 2019).

Mastixia is a genus consisting of *c.* 20 species of evergreen trees inhabiting the subtropics and tropics in southeast Asia (Eyde & Qiuyun 1990). Fossil occurrences are chiefly diaspores (e.g. *Mastixiocarpum, Eomastixia*) and to a lesser degree pollen. First occurrences of *Mastixia* diaspores are known from the late Cretaceous (Knobloch & Mai 1986). However, the majority of finds are from the Eocene (e.g. Chandler 1926; Reid & Chandler 1933; Stockey et al. 1998, diaspores) and Miocene (e.g. Kirchheimer 1957; Mai 1995, diaspores); these all occur in the western part of the northern hemisphere. Pollen assigned to *Mastixia* were less commonly encountered during the Eocene (e.g. Thiele-Pfeiffer 1988: under *Tricolporopollenites satzveyensis* Pflug and *Tricolporopollenites edmundi* [R. Pot.] Thomson & Pflug), but have been more frequently described from Miocene deposits (Ferguson et al. 1997; Masselter & Hofmann 2005; Vomela 2016). Abundant occurrences of *Mastixia* in Miocene strata of Europe have been always associated with warmer periods and called 'Mastixiodeen-Floras' according to Mai (1970). Up to recently, mastixioid fossils had not been reported from Asia, however, leaves and diaspores assigned to *Mastixia* recently have been described from Miocene to Pleistocene Siwalik strata in eastern India (Khan et al. 2017).

Ericales

Erica of the Ericaceae comprises around 800 taxa occurring in Europe, North Africa and the Middle East and tropical Africa and the Cape Flora (South Africa) the latter area is known for having the highest diversity (McGuire & Kron 2005). Our two *Erica* taxa described here can be affiliated with southern European tree heathers: *Erica* sp. 1 resembles the tree heather *Erica arborea*, a taxon distributed from the Mediterranean biome in Europe and North Africa to the Ethiopian highlands and *Erica* sp. 2 resembles more closely *Erica lusitanica* (Spanish or Portuguese tree heather). However, *Erica* sp. 1 is also slightly reminiscent of the shrubby heather *Erica bergiana* from the Cape Flora. Molecular phylogenetic studies by McGuire and Kron (2005) proposed that *Erica arborea* is the sister to all the African *Erica* taxa and that the European ancestor of all African *Erica* species must have been as widespread as the extant *Erica arborea* today. We suggest that the Schaßbach *Erica* sp. 1, plus similar *Erica* pollen records from the middle Miocene in western Anatolia (Bouchal et al. 2016), lower Eocene *Erica*-type pollen from the Cobham lignite, England (Hofmann 2018), and fossil diaspores of *Erica palaeoarborea* Van der Burgh from upper Miocene strata of Germany (Van der Burgh 1987) are from the same stock as the ancestor lineage for the African *Erica* taxa and support the hypothesis of McGuire and Kron (2005) and Pirie et al. (2016) that migration and radiation through Africa to South Africa could have taken place since the middle Miocene (around 15 Ma). More information on Eocene *Erica* and Ericaceae pollen are given in Hofmann (2018).

Vitellariopsis (tribe Mimusopeae). — The Sapotaceae are a tropical to subtropical family consisting of five tribes (Pennington 1991; Swenson & Anderberg 2005). Our taxon can be affiliated with *Vitellariopsis*, which is a small genus of small trees living in southern Africa. The Mimusopeae comprise amongst others also *Mimusops* (Africa and southern Asia) and pantropical *Manilkara* (Pennington 1991). One of the oldest fossils of Sapotaceae are pollen: *Sapotaceoidaepollenites rotundus* Harris of the Upper Cretaceous (Australia; Harris 1972; Stoian 2002) might be a member of the Mimusopeae according to Harley in Armstrong (2010). After the Cretaceous, the diversity of Sapotaceae pollen during the Eocene increased tremendously. All five tribes are present in the fossil record in Europe (e.g. Harley 1991; Armstrong 2010; Hofmann 2018). The tribe Mimusopeae is known since the lower Eocene in Europe: Lower Eocene Krappfeld in Austria (Hofmann 2018), mid-Eocene from the Isle of Wight, England (Harley 1991, affiliated with the African *Tieghemella heckelii* [A. Chev] Pierre ex Dubard), and mid-Eocene Borken, Germany (Hofmann 2018, affiliation with South American *Manilkara*). However, after the global Oligocene cooling event, all Sapotaceae tribes were probably wiped out and only members of the Mimusopeae tribe (e.g. *Vitellariopsis, Mimusops* and *Manilkara*) were present in Europe during Miocene times. These genera were either more adaptable to the successively cooling temperatures or the result of long distance dispersal from, for example, Africa (Armstrong et al. 2014).

Rehderodendron of the Styracaceae is an Asian genus, with five species, of small deciduous trees that are distributed today in China, Vietnam and Myanmar (Fritsch et al. 2001). The fossil record of this genus is based mainly on diaspores and starts in the early Eocene in Europe and ends in the Pliocene (see summaries in Mai 1970; Manchester et al. 2009). Unambiguous assignation of fossil pollen to different Styracaceae genera can be only achieved by using the SEM: *Styrax* is known since the Eocene (Hofmann 2018) and *Rehderodendron* occurs relatively frequently as an accessorial element in Miocene palynofloras (e.g. Hofmann et al. 2002; Kottik 2002; Vomela 2016).

Polyspora is a monophyletic small evergreen genus of the Theaceae (five species: Bartholomew & Ming 2005); these species were previously included in *Gordonia*. However, it has been demonstrated by molecular phylogenetic analyses that the Asian members of *Gordonia* should be incorporated into the Asian monophyletic genus *Polyspora* and this genus is sister to the remaining tribe Theeae (Yang et al. 2004; Zhang et al. 2014). Additionally, the *Polyspora* pollen from Schaßbach does not show any similarities to pollen of the American *Gordonia lasianthus*. Fossil occurrences of *Polyspora* are rare: Diaspores identified as '*Gordonia*' *truncata* Chandler are known from Bartonian strata in England (Chandler 1926; Mai 1971), diaspores of *Polyspora kilpperi* Gregor have been described from Miocene browncoals in Germany (Gregor 1978), and middle Miocene '*?Gordonia oberdorfensis*' Kovar-Eder (affiliation with *Gordonia* including *Polyspora*, e.g. *Polyspora axilliaris*) leaf fossils from a seam parting of a browncoal mine in Austria have been described by Kovar-Eder and Meller (2001). However, this is the first time that pollen of *Polyspora* has been described and it fits well with the affiliation with *Polyspora axilliaris* of the fossil leaves from Oberndorf in Austria.

Conclusions

Palynological studies on macrofossil-bearing sediments complement the floral spectrum and add to the understanding of the ancient vegetation. Despite the prevalence of deciduous leaf fossils, such as *Platanus, Quercus, Fagus, Alnus, Betula*, and unidentified entire margined leaves at the Schaßbach clay pit (Austria) of Langhian age, the pollen record provides evidence of small evergreen undergrowth trees and shrubs that are no longer present in Austria. Eight accessorial pollen taxa were described and affiliated with mostly evergreen extant genera from different continents: *Nyssa* sp. (resembling deciduous American *Nyssa sylvatica*), two *Mastixia* spp. from Asia, two *Erica* spp. (one resembling the tree heather *Erica arborea* and one the tree heather *Erica lusitanica*) from southern Europe, *Vitellariopsis* sp. from southern Africa, *Rehderodendron* sp. and *Polyspora* sp. (resembling *Polyspora axilliaris*) from Asia. The last is interesting, because leaves of *Gordonia*/*Polyspora* have been previously reported from middle Miocene strata of Styria (Austria). Except for the two tree heather species, which both nowadays inhabit the Mediterranean biome, the evergreen taxa (*Mastixia* spp., *Polyspora* and *Vitellariopsis*) and the deciduous *Rehderodendron* and *Nyssa* disappeared from Austria, probably due to the subsequent cooling during the Pliocene and Pleistocene.

Acknowledgements

Numerous students of Vienna University are thanked for digging, collecting, preparing and fixating the macrofossils and pollen samples whilst partaking the summer semester field and laboratory courses of the Palaeontology Department since 2010. These field and laboratory courses were always taught by Reinhard Zetter and Ch.-Ch.H. All knowledge in palynology of Ch.-Ch.H. is based on the patient teaching of Reinhard Zetter since 1994 and she is immensely grateful for that.

Disclosure statement

No potential conflict of interest was reported by the authors.

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