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Combined LM and SEM study of the middle Miocene (Sarmatian) palynoflora from the Lavanttal Basin, Austria: part IV. Magnoliophyta 2 – Fagales to Rosales

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Abstract
An ongoing investigation of the middle Miocene (Sarmatian) palynoflora from the Lavanttal Basin continues to show that it contains an extremely rich assemblage of angiosperm taxa. The Fagales to Rosales pollen record documented here contains 34 different taxa belonging to the Betulaceae (*Alnus, Betula, Carpinus, Corylus, Ostrya*), Fagaceae (*Castanea, Fagus, Quercus* Groups Cerris, Ilex, Cyclobalanopsis, Quercus/Lobatae), Juglandaceae (Engelhardioideae, *Carya, Juglans, Pterocarya*), Myricaceae (*Morrella vel Myrica*), Cannabaceae (*Celtis*), Elaeagnaceae (*Elaeagnus*), Rhamnaceae, Rosaceae (*Prunus*) and Ulmaceae (*Cedrelospermum, Ulmus, Zelkova*). Two of the pollen types represent extinct genera, *Trigonobalanopsis* and *Cedrelospermum*, and are also reported for the first time from the Lavanttal Basin along with pollen of Rhamnaceae and *Prunus*. The different types of *Quercus* pollen are now affiliated with Groups Cerris, Cyclobalanopsis, Ilex and Quercus/Lobatae based on sculpturing elements observed using scanning electron microscopy (SEM). Köppen signatures of potential modern analogues of the fossil Fagales and Rosales suggest a subtropical (*Cfa, Cwa*) climate at lower elevation and subsequent subtropical to temperate climate with altitudinal succession (*Cfa* → *Cfb*/*Dfa*→ *Dfb; Cwa* → *Cwb* → *Dwb*) in the Lavanttal area during accumulation of the palynoflora. Most of the fossil taxa have potential modern analogues that can be grouped as nemoral and/or merido-nemoral vegetation elements, and the diversity of Fagales indicates a varying landscape with a high variety of niches.

Keywords: *angiosperms, Cenozoic, Carinthia, fossil pollen, eudicots, palaeovegetation*

This contribution is the fourth part of a series of papers (Grímsson & Zetter 2011; Grímsson et al. 2011, 2015a) on the middle Miocene (Sarmatian) palynoflora from the Lavanttal Basin, Austria. It completes the record of an important subclade of the fabid (rosid I) clade within the rosids: the nitrogen-fixing clade. The nitrogen-fixing clade includes four angiosperm orders (APG 2009): Fabales, Rosales, Cucurbitales and Fagales. The Fabales have already been covered in the third part (Grímsson et al. 2015a). No member of Cucurbitales has been found in the Lavanttal assemblage. Hence, this paper will cover the remaining members of the nitrogen-fixing clade, palynomorphs that can be assigned to either the Fagales or Rosales. In total, eight families, 16 extant and two extinct genera, and a total of 34 pollen taxa are covered in the current study. Members of the Fagales can be particularly informative for palaeoclimatic and ecological conditions. Hence, we used the recently proposed 'Köppen signatures' (Denk et al. 2013), which aim at characterising the general climatic niche of an extant or extinct taxon. The 'Köppen signature' of a taxon describes in which general climate zones (using the Köppen-system) the taxon can be found today (e.g. *Cfa-Cfb*; warm temperate, fully humid climates

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with warm to hot summers), or thrived in the past. By summarising the 'Köppen signatures' of all elements in a palaeoflora, general climatic trends can be identified (e.g. locally delayed Miocene cooling in the northern North Atlantic; see Denk et al. 2013). In most cases, this involves choosing modern analogues to represent fossil taxa. However, it is (theoretically) possible to score a fossil taxon decoupled from modern analogues based on available secondary evidence. Using 'Köppen signatures' already established for a number of modern species, which are potential modern analogues of the Lavanttal taxa and including a substantial number of species so far not covered, we draw preliminary conclusions about the climate and ecology of the Lavanttal flora (a final, comprehensive assessment will be done in the final series contribution).

Material and methods

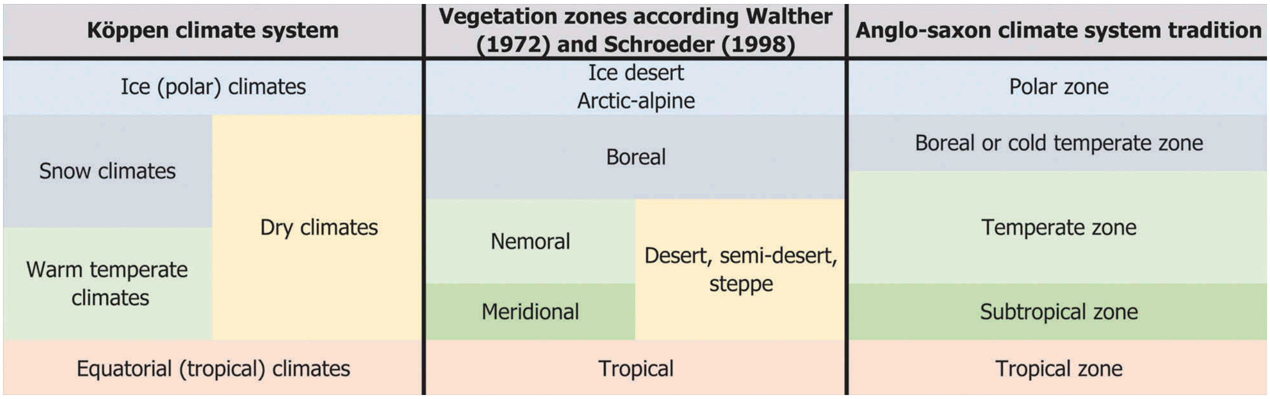
For a detailed account on the geographical position, geology and age of the Lavanttal Basin and its surroundings, sedimentology, palaeoenvironment, preservation of organic matter, sediment sampling and methods used for studying the palynomorphs, see Grímsson et al. (2011). For descriptions of ginkgophytes and gnetophytes and their ecological implication as well as fossil records, see Grímsson et al. (2011). For corresponding information on the conifer pollen from the Lavanttal Basin, see Grímsson and Zetter (2011), and for information on pollen of the Magnoliales to Fabales, see Grímsson et al. (2015a).

Nomenclatural conventions for climate and vegetation zones

We apply three nomenclatural conventions/systems that serve different aspects of climate and vegetation (Figure 1): (a) the Köppen climate system, which distinguishes climate zones by certain abiotic parameters or combinations thereof (see Kottek et al. 2006) and represents them in a three letter code referring to the general climate types (first letter), the seasonal distribution of precipitation (second letter) and the seasonal distribution or general level of warmth (third letter; Table I). (b) The general categorisation of vegetation zones according to Walter (1973) and Schroeder (1998), distinguishing five major latitudinal-altitudinal vegetation belts on the Northern Hemisphere: the tropical zone, the meridional zone, the nemoral zone, the boreal zone and the artic-alpine zone, and the commonly used terminology for latitudinal climate belts in Anglo-saxon literature, which recognises a subtropical climate zone in addition to the tropical, temperate and polar zones. Figure 1 shows (roughly) the correlation of the different concepts.

Climatic and ecological categorisation of modern species used as modern analogues for determined fossil pollen taxa

We used the recently proposed 'Köppen signatures' (Denk et al. 2013) to summarise the climatic niche occupied by potential modern analogues (species groups, genera) of the determined pollen taxa as provided in the ClimGrim database and updated for not yet covered species. We further categorised the modern species, the group of potential modern analogues, as vegetation elements ('generalists', 'meridio-nemoral', 'nemoral', 'boreal', 'arctic-alpine'; Figure 2; see Denk et al. 2013) and include three new categories (based on Schroeder 1998; see Velitzelos et al. 2014, table 23) to accommodate species with hygric and thermic preferences (availability of water and warmth) not covered by the data set used by Denk et al. (2013): (i) 'tropical' – species restricted to tropical *A*-climates;



Köppen climate system		Vegetation zones according Walther (1972) and Schroeder (1998)		Anglo-saxon climate system tradition
Ice (polar) climates		Ice desert Arctic-alpine		Polar zone
Snow climates	Dry climates	Boreal		Boreal or cold temperate zone
Warm temperate climates		Nemoral	Desert, semi-desert, steppe	Temperate zone
		Meridional		Subtropical zone
Equatorial (tropical) climates		Tropical		Tropical zone

Figure 1. Generalised climate and vegetation systems for the Northern Hemisphere used in this study. Shown is how the Köppen climate system and its Anglo-Saxon modification correlates with the vegetation zones used by Walther (1973) and Schroeder (1998), in order to establish synonymy of terminologies.

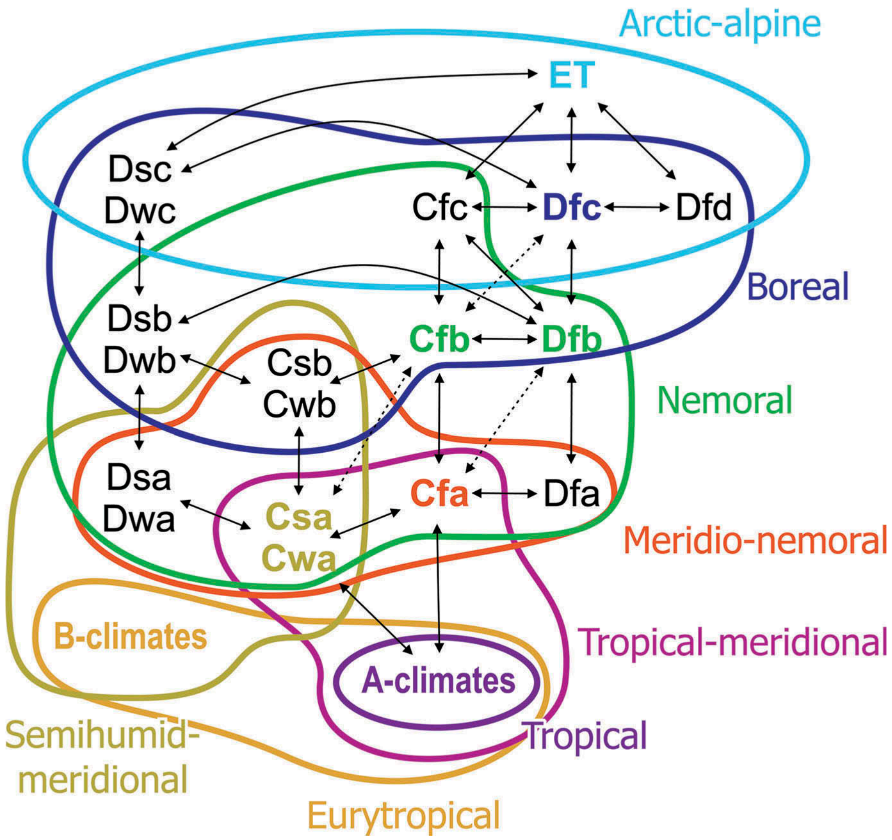


Figure 2. Circumscription of vegetation elements by Köppen climate types ('Köppen signatures'), introducing four new categories (scheme modified after Denk et al. 2013).

(ii) 'tropical-meridional' – species occurring in tropical *A*-climates and *Cw*-(*Cfa*-)climates; (iii) 'semihumid-meridional' – species occurring in winter- and/or summer-dry warm temperate climates mostly (*Cw*-, *Cs*-climates) but not tropical *A*-climates or fully humid warm temperate *Cf*-climates; (iv) 'eurytropical' – species restricted to dry climates (*B*-climates). Figure 2 shows the updated concept (modified after Denk et al. 2013). Extracted data from the updated ClimGrim database v. 0.2.1 (http://www.palaeogrimm.org/data) is provided in File S1 in the electronic supplement.

Systematic palaeontology

All descriptions of angiosperm pollen presented here include the most diagnostic features observed both in light microscopy (LM) and scaning electron microscopy (SEM). The pollen terminology follows mostly Punt et al. (2007) and Hesse et al. (2009). The classification and author names of orders and families follow APG III (2009). Families and genera are arranged in alphabetical order. When present, *incertae sedis* taxa are listed at the end of each larger taxonomic group.

Table I. Explanation of the three letter code used in the Köppen climate classification.

First letter: general climate type	Second letter: seasonal distribution of precipitation	Third letter: seasonal distribution of warmth (*C*-, *D*-climates); general level of warmth (*B*-, *E*-climates)
A = equatorial climates	***f*** = fully humid ***m*** = monsoonal ***s*** = summer-dry (rare) ***w*** = winter-dry	[not applicable]
B = dry climates	***S*** = steppe climate ***W*** = desert climate	***k*** = cold ***h*** = hot
C = warm temperate climates	***f*** = fully humid ***s*** = summer-dry ***w*** = winter-dry	***a*** = hot summer ***b*** = warm summer ***c*** = cool [short] summer
D = snow climates	***f*** = fully humid ***s*** = summer-dry ***w*** = winter-dry	***a*** = hot summer ***b*** = warm summer ***c*** = cool [short] summer ***d*** = cold [essentially no] summer
E = polar climates	***T*** = tundra climate ***F*** = frost climate	

Note: See Kottek et al. (2006) for quantitative definition of categories.

Fabids
Order Fagales Engl.
Family Betulaceae Gray
Subfamily Betuloideae Arn.

Genus Alnus *Mill.*

Alnus *sp. 1 (Subgenus* Alnus *vel* Clethropsis)
(Figure 3A–C)

Description. — Pollen, monad, oblate, outline pentangular to quadrangular in polar view, elliptic in equatorial view; polar axis 16–19 µm long in LM, equatorial diameter 20–27 µm wide in LM, 18–24 µm wide in SEM; stephanoporate (4–5), pori verstibulate, annulate, meridionally elongated, arci distinct, connecting apertures; exine 0.9–1.2 µm thick, nexine thinner or as thick as sexine, sexine thickened around pori; tectate; sculpturing psilate to scabrate in LM, rugulate to microrugulate in SEM, rugulae with a microechinate suprasculpture, rugulae narrow and of low relief, sculpture elements less conspicuous on arci (SEM).

Remarks. — Pollen morphology (LM, SEM) and partly the ultrastructure (SEM) of Betulaceae has been described in detail by Chen (1991) and Blackmore et al. (2003). The pollen morphology (LM and SEM) of all subgenera of *Alnus*, including pollen from most of the extant *Alnus* species has been documented by Huang (1972), Lieux (1980), Chen (1991), Jones et al. (1995), Wang et al. (1995), Fritz and Allesch (1999), Perveen and Qaiser (1999), Blackmore et al. (2003), Beug (2004), Fujiki and Ozawa (2007), Li et al. (2011a), May (2011), Miyoshi et al. (2011), Leopold et al. (2012), May and Lacourse (2012) and Liu et al. (2014). Fossil pollen showing LM-based morphological affinities to pollen of modern *Alnus* have commonly been assigned to the pollen form-genera *Alnipollenites* (e.g. Potonié 1931; Stuchlik et al. 2009; Zetter et al. 2011) and *Polyvestibulopollenites* (e.g. Thomson & Pflug 1953; Stuchlik et al. 2009). Assignment of individual fossils to one of the (two or) three modern subgenera *Alnus, Clethropsis, Alnobetula* (Furlow 1979; Leopold et al. 2012) is, however, difficult. Only the subgenus *Alnobetula* is somewhat distinct by the frequency of polar arci (common in the two Asian species *A. sieboldiana* Matsum. and *A. firma* Siebold et Zucc.) and by having a dominant pore number of ≥ 5. Species of subgenera *Alnus* and *Chletropsis* are dominantly four- or five-pored. Distinctness in pollen is corroborated by other characteristics of *Alnus* species. Extant species of subgenus *Alnobetula* differ from those of the other two subgenera in a number of vegetative characteristics (Murai 1964; Furlow 1979; Chen & Li 2004) and nuclear ITS data (Navarro et al. 2003; Chen & Li 2004), whereas the sister subgenera *Alnus* and *Chlethropsis* show large morphological overlap despite their genetic distinctness.

Fossil record. — The oldest fossil records of *Alnus* are of Paleocene to (early) Eocene age from North America, the Russian Far East, China and Japan (e.g. Budantsev 1982; Zetter et al. 2011; Liu et al. 2014). The earliest megafossils in western North America are *A. parviflora* (Berry) Wolfe et Wehr from the early Eocene McAbee flora (*c.* 52 Ma) of British Columbia, Canada (Dillhoff et al. 2005), and about co-eval localities such as Republic, Washington (state), USA (Wolfe & Wehr 1987), where they are represented by very common foliage and the typical pistillate (female) 'cones' (woody catkins) associated with *Alnus* pollen and various Alnus pollen catkins ('cones'). The early middle Eocene *A. clarnoensis* X.Y.Liu, Manchester et J.H.Jin (Liu et al. 2014), considered by the authors to represent subgenus *Alnus*, is based on associated leaves, staminate inflorescences with *in situ* pollen, and woody, fruiting infructescences found in the Clarno Formation (central Oregon, USA). From the Eocene onwards isolated organs of *Alnus* (leaves, catkins with or without *in situ* pollen, dispersed pollen) have been commonly reported in palaeofloras of North America (e.g. Wolfe 1966; Meyer & Manchester 1997; Liu et al. 2014), Europe (from mid-Oligocene onwards; e.g. Mai 1987; Mai & Walther 1991; Dašková 2008; Denk et al. 2011) and across Asia (e.g. Chung & Huang 1972; Budantsev 1982; Liu 1996). Only by the Pleistocene has *Alnus* pollen been reported in the (northern) Andes of South America, which still host a species of *Alnus, A. acuminata* Kunth. Due to common convergence in preservable traits, individual fossils (isolated organs) are difficult to assign to distinct intrageneric lineages within *Alnus* (Liu et al. 2014). A recent molecular dating suggests that the modern species of genus *Alnus* did not diverge prior to the mid-Miocene (Grimm & Renner 2013). Based on this study, all fossil species assigned to *Alnus* older than the Miocene may represent ancestral or extinct lineages within the genus. Earlier dating studies (e.g. Forest et al. 2005) produced even younger crown ages. Liu et al. (2014) described *A. clarnoensis* on a combination of leaves, infructescences (woody catkins) and staminate inflorescences with *in situ* pollen, and considered it as a member of subgenus *Alnus*. This led them to the conclusion that the subgenera were already established in the Eocene. In fact, due to data availability, the five included species in the final dating run by Grimm and Renner (2013) only included members of a

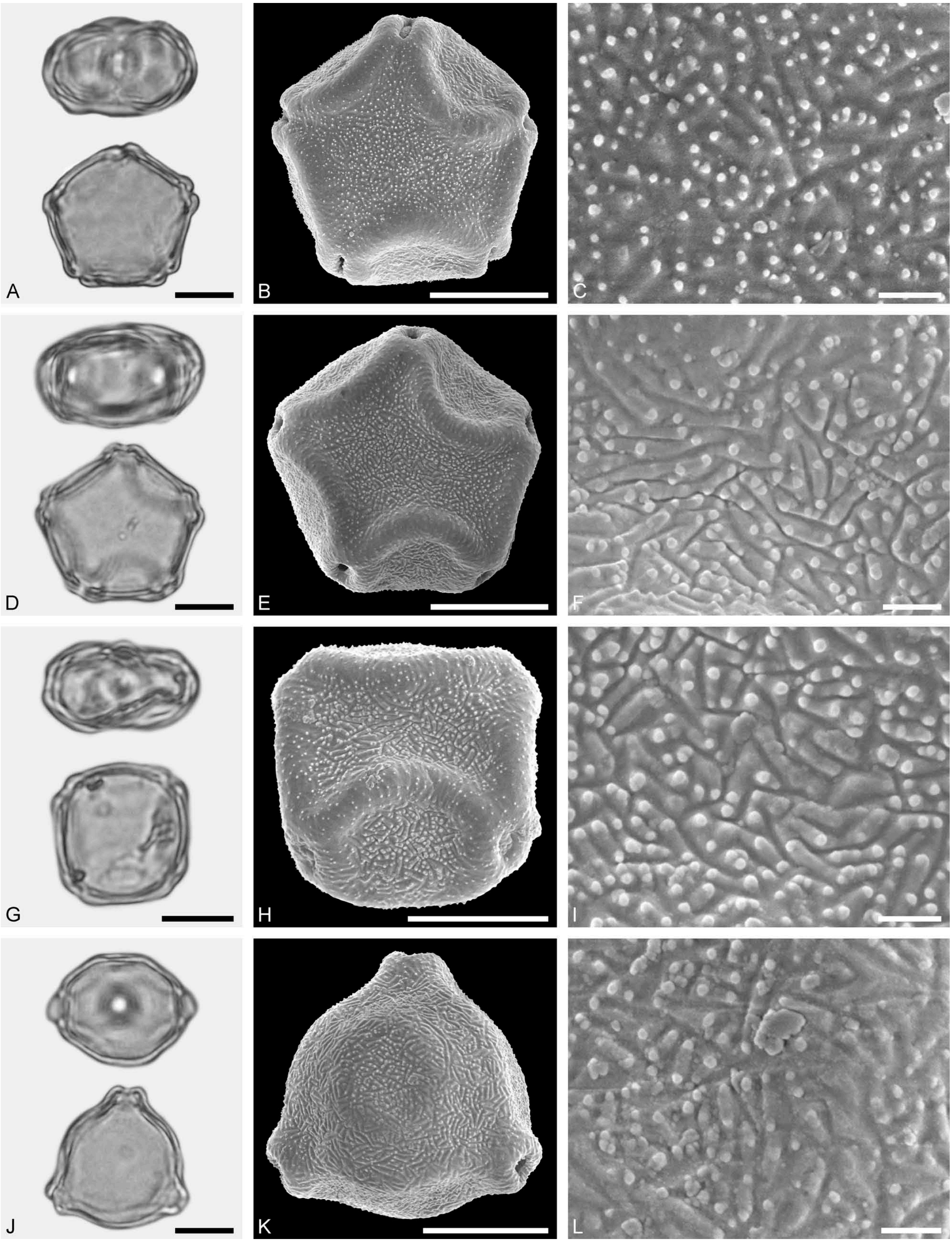


Figure 3. LM (**A, D, G, J**) and SEM (**B, C, E, F, H, I, K, L**) micrographs of dispersed fossil Betulaceae pollen. **A–C.** *Alnus* sp. 1, close-up of polar area. **D–F.** *Alnus* sp. 2 with five pori, close-up of polar area. **G–I.** *Alnus* sp. 2, grain with four pori, close-up of polar area. **J–L.** *Betula* sp. 1, close-up of polar area. Scale bars – 10 µm (A, B, D, E, G, H, J, K), 1 µm (C, F, I, L).

clade corresponding to subgenus *Alnus*. The data set did include *A. nepalensis* D.Don, a species originally assigned to the subgenus *Clethropsis* but nesting within the subgenus *Alnus* clade according to molecular data (e.g. Chen & Li 2004; Grimm & Renner 2013), a position further supported by overall pollen features (Leopold et al. 2012). Hence, the molecular estimates only give an estimate for crown group radiation within this subgenus, but not the genus itself, which would resolve the potential conflict between the finding of *Alnus clarnoensis* (Liu et al. 2014) and the *c.* 15 Ma younger crown group divergence estimates (Grimm & Renner 2013). In addition, all highlighted diagnostic characters are also found in at least one of the three species of subgenus *Chletropsis sensu stricto* (Leopold et al. 2012; Liu et al. 2014, table 2), which is resolved as the sister clade of subgenus *Alnus* in available molecular phylogenies (Navarro et al. 2003; Chen & Li 2004) and morphologically overlapping with the latter.

Ecological implications. — Up to 35 *Alnus* species can be grouped into three subgenera, which, based on ITS data, largely group according to the morphological-systematic concepts of Murai (1964) and Furlow (1979): the subgenera *Alnus* and *Clethropsis* are resolved as sister clades, and the subgenus *Alnobetula* as the first diverging lineage. *Alnus* occurs usually as an azonal element accompanying water bodies, alongside streams, on riverbanks, typically in forested areas (e.g. Li & Skvortsov 1999; Denk et al. 2001). With about 25 species, the subgenus *Alnus* is the most diverse lineage and the most widespread. *Alnus acuminata* extends into the mid- to high-altitudinal forest belts (1400–3100 m above sea level [a.s.l.] of the Andes in South America (until south Argentina), whereas *Alnus hirsuta* (Spach) Rupr. is found in the northern parts of eastern Eurasia (Siberia to northeast China, Korea, Russian Far East and Japan) at elevations of 700 to 1500 m (Li & Skvortsov 1999; see Grimm & Renner 2013, file S4, for a compilation of geographic, altitudinal and climate distribution of Betulaceae genera and commonly accepted species). With up to ten species, the subgenus *Alnobetula* is less diverse than the subgenus *Alnus*, and, except for *A. alnobetula* (Erh.) K.Koch (incl. *Alnus viridis* [Chaix.] DC.), which has adapted to the subarctic climate conditions, is exclusively found in the temperate zone of northeast Asia. The two Asian species of the subgenus *Clethropsis* occur in montane forests of the foothills of the Himalayas and on Taiwan between sea-level and 2900 m a.s.l. (Li & Skvortsov 1999), whereas their North American relative has a scattered distribution in mild temperate lowlands of eastern United States (south-central Oklahoma, southern Delaware and south-eastern Maine).

The genus is widespread in the extra-tropical part of the Northern Hemisphere (per-humid or seasonally dry climates; *BS-*, *C-*, *D*-climates) showing no clear preference for a certain climate (Grimm & Renner 2013, file S4) or vegetation zone (Schroeder 1998). Individual species of *Alnus* can be categorised as generalists, semihumid-meridional, meridio-nemoral, nemoral, boreal, or arctic-alpine elements (File S1). Based on the modern distribution of the subgenera *Alnus* and *Clethropsis*, the trees producing the fossil *Alnus* pollen from the Lavanttal Basin could have been elements of various habitats such as swamp and riparian forests (levee and back-swamp forests), but also as accessory element in the hinterland montane forests.

Alnus *sp. 2 (subgenus* Alnus *vel* Clethropsis)
(Figure 3D–I)

Description. — Pollen, monad, oblate, outline pentangular to quadrangular in polar view, elliptic in equatorial view; polar axis 12–19 µm long in LM, equatorial diameter 21–29 µm wide in LM, 19–24 µm in SEM; stephanoporate (4–5), pori verstibulate, annulate, meridionally elongated, arci distinct, connecting apertures; exine 0.7–1.0 µm thick (LM), nexine thinner or as thick as sexine, sexine thickened around pori; tectate; sculpturing psilate to scabrate in LM, rugulate to microrugulate in SEM, rugulae with a microechinate suprasculpture, rugulae wide and of high relief, sculpture elements less conspicuous on arci (SEM).

Remarks. — Rugulae are broader, more conspicuous and of higher relief and the microechini are also much larger than in *Alnus* sp. 1.

Genus Betula *L.*

Betula *sp. 1*
(Figures 3J–L, 4A–C)

Description. — Pollen, monad, oblate, outline convex triangular in polar view, elliptic in equatorial view; polar axis 18–20 µm long in LM, equatorial diameter 23–26 µm wide in LM, 21–23 µm wide in SEM; triporate, pori verstibulate, annulate; exine 0.8–1.1 µm thick (LM), nexine thinner than sexine, circular thickening of nexine in polar areas; tectate; sculpturing psilate to scabrate in LM, rugulate to microrugulate in SEM, rugulae with a microechinate suprasculpture, rugulae wide and of high relief (SEM).

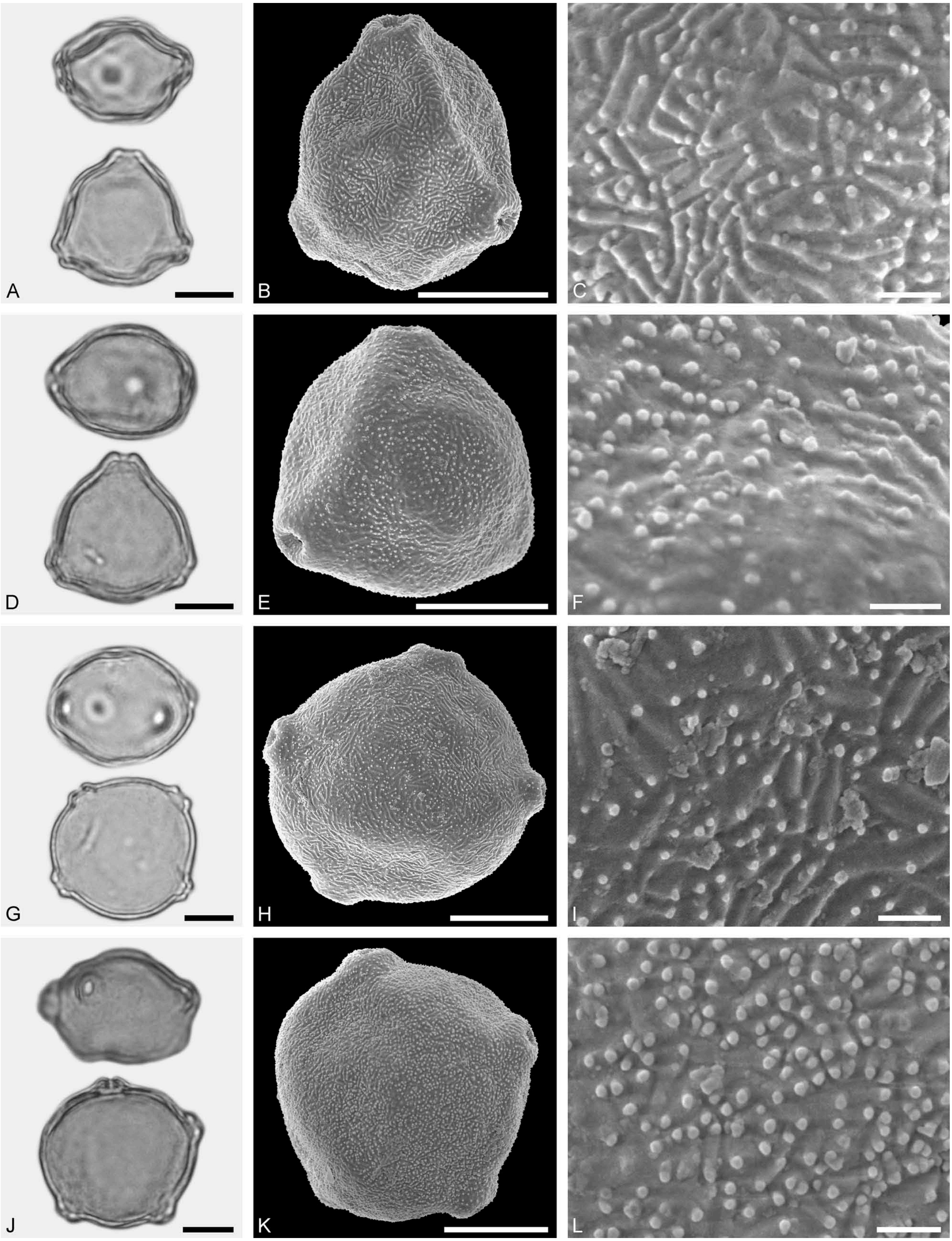


Figure 4. LM (**A, D, G, J**) and SEM (**B, C, E, F, H, I, K, L**) micrographs of dispersed fossil Betulaceae pollen. **A–C.** *Betula* sp. 1, close-up of polar area. **D–F.** *Betula* sp. 2, close-up of polar area. **G–I.** *Carpinus* sp. 1, close-up of polar area. **J–L.** *Carpinus* sp. 2, close-up of polar area. Scale bars – 10 µm (A, B, D, E, G, H, J, K), 1 µm (C, F, I, L).

Remarks. — The pollen morphology (LM and SEM) of many extant *Betula* species has been presented by Birks (1968), Lieux (1980), Zavada and Dilcher (1986), Chen (1991), Jones et al. (1995), Wang et al. (1995), Mäkelä (1996), Fritz and Allesch (1999), Blackmore et al. (2003), Wei (2003), Beug (2004), Clegg et al. (2005), Karlsdóttir et al. (2007, 2008), Li et al. (2011a), Miyoshi et al. (2011) and Lin et al. (2013). The pollen ultrastructure (SEM, transmission electron microscopy [TEM]) of *Betula* has been described and figured by Zavada and Dilcher (1986), Pehlivan (1987) and Blackmore et al. (2003). Fossil pollen showing LM-based morphological affinities to pollen of modern *Betula* have commonly been assigned to the pollen form-genus *Betulapollenites* (e.g. Potonié 1960; Stuchlik et al. 2009).

Fossil record. — The fossil record of *Betula* parallels the one of its putative sister genus *Alnus*, both regarding its spatial and temporal distribution (e.g. Mai 1995). As with *Alnus*, the oldest fossil with unambiguous affinities to *Betula, B. leopoldae* P.R. Crane et Stockey (foliage, aments and associated *Betula* pollen), has been reported from the Eocene McAbee flora of western North America (Dillhoff et al. 2005) predating earliest unambiguous records in western Eurasia and East Asia (mostly pollen, but also nuts and bracts, *B. longisquamosa* Mädler, and infructescences, e.g. Zastawniak and Walther 1998, late Miocene, Poland). *Betula* macrofossils and microfossils are common elements in numerous post-Eocene temperate fossil floras. *Alnus* and *Betula* are commonly found in the same assemblages; this is why Mai (1981b) placed them in the same group ('group 1') of arcto-tertiary elements.

Ecological implications. — The Kew Checklist for Betulaceae lists 90 accepted species of *Betula* (see Grimm & Renner 2013, file S4). In both altitudinal and latitudinal distribution, *Betula* exceeds other genera of Fagales (Li & Skvortsov 1999; Thompson et al. 1999b, 2006; Fang et al. 2009; Grimm & Renner 2013). In contrast to other genera of the Betulaceae, a large number of *Betula* species have been described from the cold-temperate to arctic regions of the Northern Hemisphere such as northern North America (10 spp.) and Siberia (13 spp.) and the mountainous, central part of Asia (about 25 spp.). In comparison, 19 species are known from China and 14 from Korea and Japan. Six species occur in Europe, four in south-western Asia, and ten in North America outside the subarctic region. Some species thrive at sea-level, while others are pure montane taxa (e.g. Furlow 1997; Li & Skvortsov 1999). Other species prefer temperate to subarctic swamps and bogs (e.g. North American *B. pumila* L. and the East Asian *B. fructicosa* Pall). The most temperature tolerant species are *B. humilis* Schrank, *B. nana* L. (arctic and high mountains of Eurasia; Meusel et al. 1965; IOPI 1996–2007) and *B. neoalaskana* Sarg. (Russian Far East to northern North America; Furlow 1997; Thompson et al. 2006).

Species of *Betula* are (co-)dominant elements of boreal northern hemispheric forests thriving in warm temperate or snow climates with relatively to very short (cold) summers (*Cfc-, Dfb-, Dfc-, Dfd*-climates), but are frequently found also in nemoral habitats such as temperate broad-leaved forests, open woods and thickets (Furlow 1997; Li & Skvortsov 1999) and associated climate zones (snow to warm temperate climates, fully humid or winter-dry with warm to hot summers: *Cwa, Cwb, Cfa, Cfb, Dfb, Dwa, Dwb*). A few species (*B. alnoides* Buch.-Ham. ex D.Don, *B. cylindrostachya* Lindl. ex Wall., *B. jinpingensis* P.C.Li, *B. luminifera* H.J.P.Winkel) can be found in distinctly subtropical settings (*Cwa-, Cfa*-climates) in the Himalayan foothills (mostly below 2000 m a.s.l.) and south-western China (Li & Skvortsov 1999; Shaw et al. 2014a). Most species of *Betula* can be categorised as nemoral or boreal elements, but a few represent semihumid-meridional, meridio-nemoral, and arctic-alpine elements (File S1). Thus, the occurrence of *Betula* can be taken as an indication of forested habitats of various temperature regimes, but excludes tropical (*A*-climates) and desert/steppe climates (*B*-climates) and habitats.

Betula *sp. 2*
(Figure 4D–F)

Description. — Pollen, monad, oblate, outline convex triangular in polar view, elliptic in equatorial view; polar axis 20–22 µm long in LM, equatorial diameter 25–27 µm wide in LM, 20–22 µm wide in SEM; triporate, pori verstibulate, annulate; exine 1.0–1.2 µm thick (LM), nexine thinner than sexine, circular thickening of nexine in polar areas; tectate; sculpturing psilate to scabrate in LM, rugulate to microrugulate in SEM, rugulae with a microechinate suprasculpture, rugulae wide and of low relief (SEM).

Remarks. — The sculpture elements (rugulae) are much less conspicuous in *Betula* sp. 2 than in *Betula* sp. 1, and they are also wider apart and shorter.

Subfamily Coryloideae Hook.f.

Genus Carpinus *L.*

Carpinus *sp. 1*
(Figure 4G–I)

Description. — Pollen, monad, oblate, outline convex quadrangular in polar view, elliptic in equatorial view; polar axis 23–25 µm long in LM, equatorial diameter 30–32 µm wide in LM, 28–30 µm wide in SEM; stephanoporate (4), pori annulate; exine 0.8–1.0 µm thick (LM), nexine thinner than sexine; tectate; sculpturing psilate to scabrate in LM, rugulate in SEM, rugulae with a microechinate suprasculpture, rugulae long and conspicuous, widely spaced (SEM).

Remarks. — The pollen morphology (LM and SEM) of *Carpinus* has been documented by Huang (1972), Lieux (1980), Chen (1991), Jones et al. (1995), Wang et al. (1995), Fritz and Allesch (1999), Blackmore et al. (2003), Beug (2004), Akhondnezhad et al. (2011), Li et al. (2011a) and Miyoshi et al. (2011). The pollen ultrastructure (TEM) of *Carpinus* has been described and figured by Pehlivan (1987). Fossil pollen showing LM-based morphological affinities to pollen of modern *Carpinus* have commonly been assigned to the pollen form-genera *Carpinuspollenites* (e.g. Thiergart 1937; Stuchlik et al. 2009) and *Carpinipites* (e.g. Srivastava 1966; Stuchlik et al. 2009). Of the four extant genera in the Coryloideae, three (*Ostrya, Ostryopsis* and *Corylus*) have predominantly three-porate pollen in contrast to *Carpinus*, which are usually four-porate. According to plastid or combined plastid-nuclear phylogenies, *Carpinus* is nested in *Ostrya* (e.g. Yoo & Wen 2002, 2007; Grimm & Renner 2013); hence, the four-porate pollen can be seen as an apomorphy of *Carpinus* within the coryloid subclade of Betulaceae.

Fossil record. — The earliest fossils with affinities to Coryloideae (including the modern genera *Carpinus, Corylus, Ostrya* and *Ostryopsis*) are *Palaeocarpinus* from the Paleocene of north-western China and North Dakota (Manchester & Guo 1996; Manchester et al. 2004). Earliest fossils that can be reliably assigned to the modern *Carpinus* (and *Corylus*, see later) are fruits that have been described from the Republic flora of the latest early Eocene of Washington (state), north-western North America (*C. perryae* Pigg, Manchester et Wehr; Pigg et al. 2003). In Eurasia, the genus can be traced back to the late Eocene of Japan (Tanai 1972; Uemura & Tanai 1993), and the latest Eocene/earliest Oligocene of Europe based on macrofossils and pollen (Berger 1953; Mai 1995; Stuchlik et al. 2009). *Carpinus* has a continuous fruit record in the Neogene of Poland (middle Miocene onwards), studied in detail and compared to extant species of North America, western Eurasia and East Asia (morphology and anatomy) by Jentys-Szaferowa (1975). Apparently, species with similarity to modern North American (fruits, leaves), western Eurasian and East Asian morphotypes co-existed in the Miocene and Pliocene of Europe (Jentys-Szaferowa 1975; Mai 1995).

Ecological implications. — *Carpinus* is a widespread, northern hemispheric genus with *c.* 39 species. Two species, *C. caroliniana* Walter and *C. tropicalis* (Donn. Sm.) Lundell, occur in eastern North America and Mesoamerica, respectively, two in western Eurasia. The genus is most diverse in East Asia (*c.* 34 species). In China, species of *Carpinus* grow at altitudes between 200 and 2900 m, in subtropical to temperate forests of hilly/mountainous regions, on mountain slopes and in valleys. Most of the species diversity is concentrated in the subtropical broad-leaved forests of south-western China (Sichuan, Yunnan, Guangxi and Guizhou provinces); six species have ranges including or limited to subtropical and temperate regions of Korea and Japan. *Carpinus londoniana* H. J.P.Winkl. extends into north Vietnam (Ohwi 1965; Li & Skvortsov 1999); *C. faginea* Lindl. has a distribution restricted to western and central part of the Himalayas. The most widespread species is *C. viminea* Wall. ex Lindl. (Himalayas to Korea and Vietnam). In the Himalayas, *Carpinus* is found at moderately high altitudes of up to 2800 m (Nepal) and at 2700–3300 m (Meusel et al. 1965). The western Eurasian species *C. betulus* L. extends from France (up to 1000 m a.s.l. in the Alps) and southernmost Sweden (Scania) to Iran. In the south-eastern part of its range, it co-occurs with the second western Eurasian species, *C. orientalis* Mill. (Meusel et al. 1965). The North American *C. caroliniana* is limited to the nemoral zone (see Walter 1973; Schroeder 1998) of the eastern part of the United States (excluding southern Louisiana to Georgia) into southernmost Canada, where it grows as an understory tree in moist habitats lowland deciduous forest and at altitudes below 300 m (Furlow 1997). Its Mesoamerican counterpart *C. tropicalis,* occurring from northern Mexico to Costa Rica, can be the dominant tree in the montane cloud forests along streams in canyons (Stritch 2014).

In general, *Carpinus* prefers warm temperate climates with sufficient rain during growing season (*Cf*-, *Cw*-climates), with only one species, *C. orientalis* extending locally (Albania, western Greece; Adana, Osmaniye and Hatay provinces, south-eastern Turkey) into summer-dry climates of the Mediterranean (Browics & Zieliński 1982). Together with *Corylus, Carpinus* is an indicator for well-drained, mixed mesophytic broad-leaved forests of the humid warm temperate zone (nemoral zone; Walter 1973; Schroeder 1998). Species of *Carpinus* can be categorised as semihumid-meridional, meridio-nemoral and/or nemoral elements (File

S1). Since all modern species prefer moist habitats, it is likely that the *Carpinus* pollen from the Lavanttal basin originated from trees growing either in lowland levee or riparian forests or along streams and rivulets in mountain valleys and adjacent slopes.

Carpinus *sp. 2*
(Figures 4J–L, 5A–C)

Description. — Pollen, monad, oblate, outline convex quadrangular in polar view, elliptic in equatorial view; polar axis 22–25 µm long in LM, equatorial diameter 31–33 µm wide in LM, 28–30 µm wide in SEM; stephanoporate (4), pori annulate; exine 0.9–1.1 µm thick, nexine thinner than sexine; tectate; sculpturing psilate to scabrate in LM, rugulate in SEM, rugulae with a microechinate suprasculpture, rugulae short and inconspicuous, closely packed (SEM).

Remarks. — Rugulae are much shorter, less conspicuous, more closely packed, and with a much higher number of microechini than in *Carpinus* sp. 1.

Genus Corylus *L.*

Corylus *sp.*
(Figure 5D–F)

Description. — Pollen, monad, oblate, outline convex triangular in polar view, elliptic in equatorial view; polar axis 19–21 µm long in LM, equatorial diameter 24–26 µm wide in LM, 23–25 µm wide in SEM; triporate, pori small, circular; exine 0.8–0.9 µm thick (LM), nexine thinner than sexine; tectate; sculpturing psilate to scabrate in LM, microrugulate in SEM, rugulae with a microechinate suprasculpture, high density of microechinate per rugulae (SEM).

Remarks. — The pollen morphology (LM and SEM) of *Corylus* has been documented by Chen (1991), Fritz and Allesch (1999), Blackmore et al. (2003), Wei (2003), Beug (2004), Wang et al. (1995), Li et al. (2011a), Miyoshi et al. (2011) and Nikolaieva et al. (2014). The pollen ultrastructure (SEM, TEM) of *Corylus* has been described and figured by Pehlivan (1987) and Blackmore et al. (2003). Fossil pollen showing LM-based morphological affinities to pollen of modern *Corylus* have commonly been assigned to the pollen form-species *Triporopollenites coryloides* H.Pflug (e.g. Thomson & Pflug 1953; Stuchlik et al. 2009).

Fossil record. — The early macrofossil record of the Coryleae has been summarised by Crane (1989) and Pigg et al. (2003). The earliest macrofossils that can be reliably assigned to *Corylus* are infructescences with nuts, *C. johnsonii* Pigg, Manchester et Wehr, from the middle Eocene of Republic, Washington. These fossil fruits are considered most similar to several modern Chinese species (Pigg et al. 2003). Older coryloid records from the Paleocene of western North America (Montana), Greenland and England are of uncertain generic affinity (Pigg et al. 2003). *Corylus* apparently did not reach Europe before the late Oligocene after the closure of the Turgai (Mai 1995). In his overview of arcto-tertiary elements, Mai (1995) noted that the genus was also present in the Paleocene of East Asia, but this has yet to be confirmed. Late Cretaceous and Paleogene pollen that has occasionally been assigned to *Corylus* (e.g. Muller 1981) may in fact belong to extinct, ancestral lineages of Coryleae (especially *Palaeocarpinus*), the clade comprising *Corylus, Carpinus, Ostrya* and *Ostryopsis* (Pigg et al. 2003; Zetter et al. 2011). Unambiguous *Corylus* pollen can only be determined by a combination of LM and SEM, and so far, is unknown from Central European sediments older than the Miocene (R. Zetter, pers. observation through *c.* 40 years of work on fossil pollen material form all over Europe).

Ecological implications. — *Corylus* consists of *c.* 16 species with a disjunct distribution in the Northern Hemisphere (Li & Skvortsov 1999; Whitcher & Wen 2001). Ten species occur in East Asia, four are found in western Eurasia, and two in North America. Widespread species are common pioneer trees; *Corylus* species are common accessory and shrubby elements of broad-leaved dry to mesic forests (Coladonato 1993, Fryer 2007). The East Asian species are found in temperate broad-leaved forest, one species, however, *C. heterophylla* Fisch. ex Trautv., extends into eastern Mongolia, south-eastern Siberia, and the southern Russian Far East. In China, the species occur at mid- to high-altitudes (400–3000 m) in montane areas, preferring forested valleys and mountain slopes (Li & Skvortsov 1999). Three of the four western Eurasian species are restricted to south-eastern Europe and the Euxinian, Colchic and Hyrcanian regions south of the Black Sea, in the Caucasus and adjacent areas of northern Iran (Browics & Zieliński 1982). The most widespread western Eurasian species, *C. avellana* L., the common hazelnut, is widely cultivated but also naturally found throughout temperate zone of western Eurasia with a range extending from the Iberian Peninsula to southern Scotland, southern Scandinavia (up to 600 m a.s.l. in southern Norway) and into the European part of Russia, the Black Sea region, the Caucasus and south-eastern Turkey and adjacent

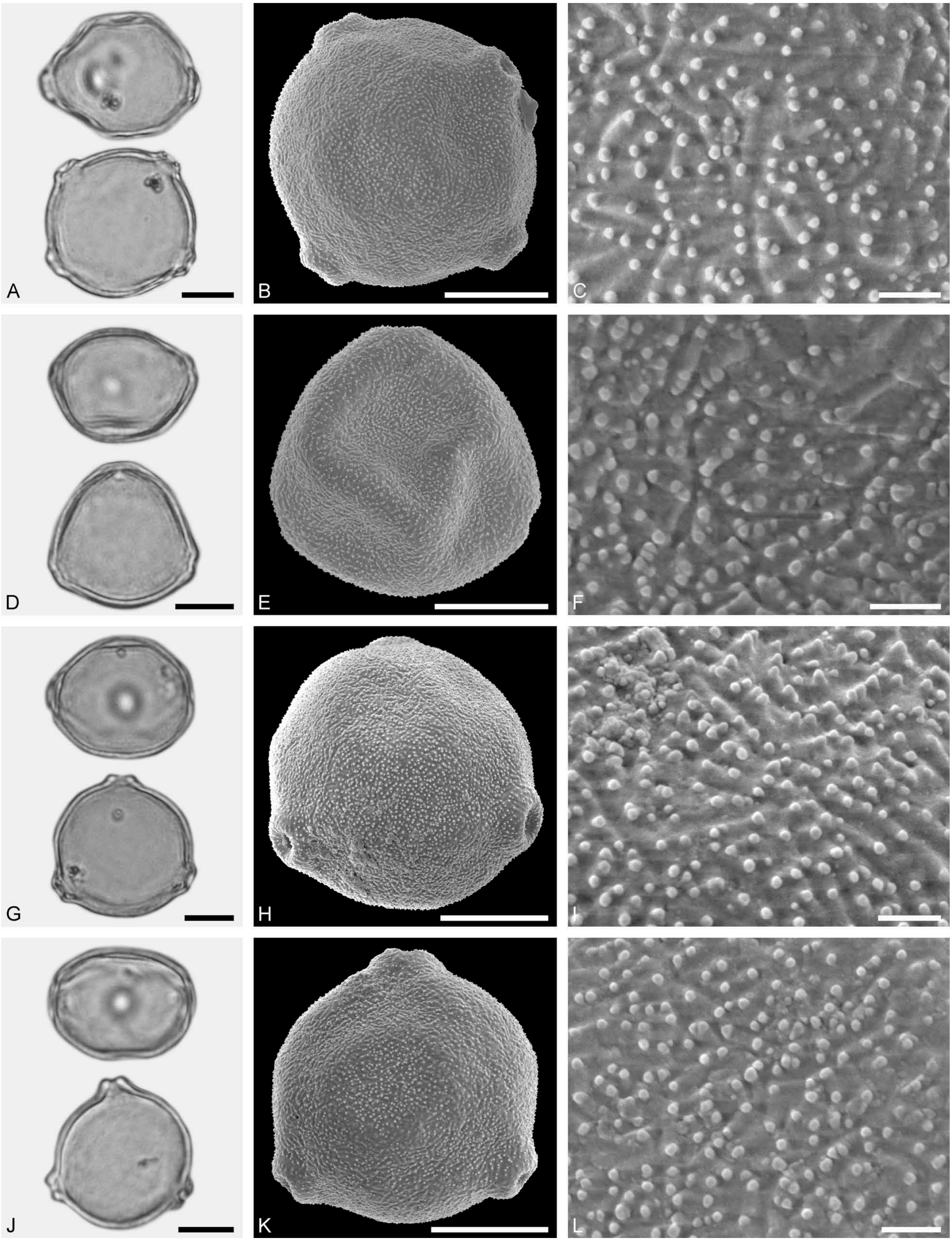


Figure 5. LM (**A, D, G, J**) and SEM (**B, C, E, F, H, I, K, L**) micrographs of dispersed fossil Betulaceae pollen. **A–C.** *Carpinus* sp. 2, close-up of polar area. **D–F.** *Corylus* sp., close-up of polar area. **G–L.** *Ostrya* sp., close-ups of polar area. Scale bars – 10 μm (A, B, D, E, G, H, J, K), 1 μm (C, F, I, L).

Iran/Iraq. In the Alps, it reaches up to the subalpine zone (Meusel et al. 1965). The two North American species, *C. americana* Walter and *C. cornuta* Marshall, are found in eastern North America in moist to dry, open woods and thickets, including disturbed areas, up to 750 m a.s.l. Both species can be considered as weeds, sometimes as pests in managed forests (Furlow 1997). In the Pacific states (California to British Columbia), *Corylus cornuta* prefers rocky slopes.

Corylus is typical for the nemoral zone (Schroeder 1998), with a climate preference for warm temperate, fully humid climates with warm summers (*Cfb*; see Grimm & Renner 2013, file S4). Most species have a range covering also *Cwb*- or *Dfb*-climates (warm temperate to snow climates with sufficient precipitation during growing season and warm summers). Species of *Corylus* can hence be categorised as nemoral elements (File S1). Based on the characteristic occurrence of the genus in its disjunct areas in North America, western Eurasia and East Asia, we figure that *Corylus* has grown in the understory of mixed broad-leaved deciduous forests or at margins of beech-dominated forests surrounding the wetland basin.

Genus Ostrya *Scop.*

Ostrya *sp.*
(Figure 5G–L)

Description. — Pollen, monad, oblate, outline convex triangular in polar view, elliptic in equatorial view; polar axis 21–25 µm long in LM, equatorial diameter 27–30 µm wide in LM, 24–27 µm wide in SEM; triporate, pori annulate; exine 1.0–1.2 µm thick (LM), nexine thinner than sexine; tectate; sculpturing psilate to scabrate in LM, microrugulate to rugulate in SEM, rugulae with a microechinate suprasculpture, rugulae of low relief, microechinii conspicuous and of high density (SEM).

Remarks. — Pollen of extant *Ostrya* has been described and figured using LM and SEM by Lieux (1980), Accorsi et al. (1991), Chen (1991), Jones et al. (1995), Wang et al. (1995), Fritz and Allesch (1999), Blackmore et al. (2003), Beug (2004), Li et al. (2011a) and Miyoshi et al. (2011). The ultrastructure (TEM) of *Ostrya* pollen has been documented by Pehlivan (1987). Fossil pollen showing LM-based morphological affinities to pollen of modern *Ostrya* have commonly been assigned to the pollen form-genus *Ostryoipollenites* (e.g. Potonié 1960; Stuchlik et al. 2009). Whereas pollen of the closely related *Carpinus* is usually four-porate, pollen of species of *Ostrya* are usually three-porate as the pollen in their more distant relatives *Ostryopsis* and *Corylus* (e.g. Chen 1991). According to plastid or combined plastid-nuclear phylogenies, *Ostrya* is paraphyletic to *Carpinus* (e.g. Yoo & Wen 2002, 2007; Grimm & Renner 2013). Hence, the three-porate situation may be plesiomorphic within the *Carpinus-Ostrya*(*-Ostryopsis*) lineage, and the pollen could possibly also represent an extinct or ancestral taxon predating the formation of *Carpinus* as a distinct lineage.

Fossil record. — Reports of fossil *Ostrya* are scarcer than of other extant Coryloideae. The earliest unequivocal fossil record of *Ostrya* in North America is *O. oregoniana* Chaney fruits and leaves from the earliest Oligocene Bridge Creek flora of John Day Formation, Oregon, western North America (*c.* 33 Ma; Meyer & Manchester 1997), where it occurred until the middle Miocene, and has a continuous record in eastern North America until present times (e.g. Graham 1999; Manchester 1999). In Europe, *Ostrya* is known from the lower Oligocene (diagnostic involucres surrounding the nutlets; Mai 1995; Kvaček & Walther 1998) and Pliocene (fruits; Jentys-Szaferowa 1975). The earliest East Asian records (involucres, fruits, wood) are from the Miocene of Japan (e.g. Tanai 1961, 1972) and China (WGCPC 1978).

Ecological implications. — *Ostrya* is composed of *c.* nine tree species with a northern hemispheric distribution. Five are growing in East Asia and three in North America. The only western Eurasian species, *O. carpinifolia* Scop., ranges from south-central and south-eastern Europe via Turkey (Taurus Mountains) to the Caucasus and into Lebanon (e.g. Browics & Zieliński 1982). It prefers shrubby, sunny hillsides, is often found on dry, rocky slopes (on limestone), and is an important element of deciduous forests and scrubs and open coniferous woodland (Shaw et al. 2014b). The subtropical Chinese species, found in mixed forests at altitudes of 200–1300 m (Li & Skvortsov 1999) have fairly restricted distributions (Fang et al. 2009). The two other East Asian species have a distinctly temperate distribution. *Ostrya japonica* Sarg. is found in temperate forests, ranging from north-central China via Korea to Japan (Ohwi 1965; Li & Skvortsov 1999). *Ostrya yunnanensis* W.K.Hu has only been reported from the Luquan Xian Mountain in Yunnan, where it grows in moist forest at an elevation of 2600 m a.s.l. *Ostrya virginiana* (Mill.) K.Koch is the most widespread among the North American species, with a continuous distribution area in eastern North America and numerous disjunct occurrences throughout Mesoamerica (*O. virginiana guatemalensis* (H.Winkl.)

E.Murray; IOPI 1996–2007). In the United States and Canada, it occurs throughout the lowlands (0–300 m a.s.l.) on moist to dry slopes and ridges, and occasionally on moist, well-drained flood plains. The other two species, *O. knowtonii* Sarg. and *O. chisosensis* Correll have a restricted, scattered distribution in Utah, Arizona, New Mexico and the Texan-Mexican borderlands (along the Rio Grande) along rivulets and rocky slopes in moist canyons at 1200–2300 m a.s.l. (Furlow 1997).

Generally restricted to the subtropical belt of the Northern Hemisphere (Browics & Zieliński 1982; Furlow 1997; Li & Skvortsov 1999), a few species of *Ostrya* appear to be adapted to climates and habitats with substantial draught during growing season (*Cs*- and *BS*-climates) such as *O. carpinifolia* in the Mediterranean and *O. chisosensis* growing in southwest Texas along the Rio Grande (Mexican-Texan border). All others prefer climates with sufficient or excess precipitation in summer (*Cf*-climates in North America and western Eurasia; *Cf*- and *Cw*-climates in East Asia). All species of *Ostrya* except for the East Asian *O. trichocarpa* D.Fang et Y.S.Wang (semihumid-meridional element) and the North American *O. chisosensis* (eurytropical element) can be categorised as meridio-nemoral or nemoral elements (File S1). With respect to the habitat ranges of extant *Ostrya*, the fossil pollen may have either produced by trees thriving in mixed deciduous broad-leaved and coniferous hinterland forests (dry or sun-exposed hillsides, mountains; in analogy to the habitats of the Eurasian species) or in lowland riparian and floodplain forests (in analogy to the *O. virginiana*-habitat).

Family Fagaceae Dumort.

Genus Castanea *Mill.*

Castanea *sp.*
(Figure 6A–C)

Description. — Pollen, monad, prolate, outline lobate in polar view, elliptic in equatorial view; polar axis 13–15 µm long in LM, 11–13 µm long in SEM, equatorial diameter 8–10 µm wide in LM, 6–8 µm wide in SEM; tricolporate, pori lalongate, colpi long; exine 0.8–1.0 µm thick (LM), nexine thinner than sexine; tectate; sculpturing psilate in LM, rugulate, fossulate, perforate in SEM.

Remarks. — The pollen morphology (LM and SEM) and ultrastructure (SEM) of Castaneoideae pollen has been thoroughly documented by Crepet and Daghlian (1980), Miyoshi (1982), Praglowski (1984), Wang and Pu (2004), Li et al. (2011a) and Miyoshi et al. (2011). The pollen of *Castanea, Castanopsis, Chrysolepis, Lithocarpus* and *Notholithocarpus* are very similar in size and shape. Using LM only, they are indistinguishable at the generic level. Pollen of *Castanopsis* and *Lithocarpus*/*Notholithocarpus* commonly overlap in size and shape and arrangement of sculpturing elements seen under SEM, and cannot be distinguished. *Castanea*-type pollen appears to be generally smaller and narrower than pollen of the other genera. Under the SEM the rugulate sculpturing is flattened and smoother (fused) in appearance (e.g. Praglowski 1984). Fossil pollen showing LM-based morphological affinities to pollen of modern *Castanea* has commonly been assigned to the pollen form-genus *Cupuliferoipollenites* (e.g. Potonié 1960; Stuchlik et al. 2014).

Fossil record. — According to the summary of Mai (1995), *Castanea* has its earliest occurrence in the Paleocene of North America and Eocene of East Asia. In Europe and West Asia, it is recorded from the Oligocene onwards. To date, the earliest reliable Castaneoideae fossils are staminate catkins (inflorescences), *Castaneoidea puryearensis* Crepet et Daghlian, with *in situ* Castaneoideae-type pollen from the middle Eocene of Tennessee, south-eastern United States (Crepet & Daghlian 1980). The early Cainozoic macrofossil record of *Castanea* or *Castanea*-like leaf fossils is not convincing because of the overlapping features in leaf morphology within several genera of Fagaceae. This has only been partly resolved using epidermal anatomy from both North American (Jones & Dilcher 1988) and European (Kvaček & Walther 2010) leaf fossils. Based on cuticle features, Jones and Dilcher (1988) described *Castaneophyllum tenesseense* (Berry) Jones et Dilcher from the Eocene of Tennessee (south-eastern United States), and Kvaček and Walther (2010) described two different European *Castaneophyllum* leaf types affiliated with *Castanea* from the late Eocene of Czech Republic (*Castaneophyllum venosum* [Rossm.] Erw.Knobloch et Kvaček), and from the early Oligocene of Slovenia, Germany and Czech Republic (*Castaneophyllum lonchitiforme* Kvaček et H.Walther). Unequivocal records of *Castanea* leaves with cuticle features and fruits are known mostly from the Miocene in Europe (e.g. Mai 1995). The fossil pollen records of Castaneoideae-type pollen based on LM studies date back to the Upper Cretaceous (e.g. Muller 1981). Since pollen of the different genera within the subfamily Castaneoideae cannot be differentiated using LM only, and in most cases not even using SEM, it unclear when the first real *Castanea*-type pollen occur. Dispersed fossil *Castanea*-type pollen has been described using combined LM and SEM by

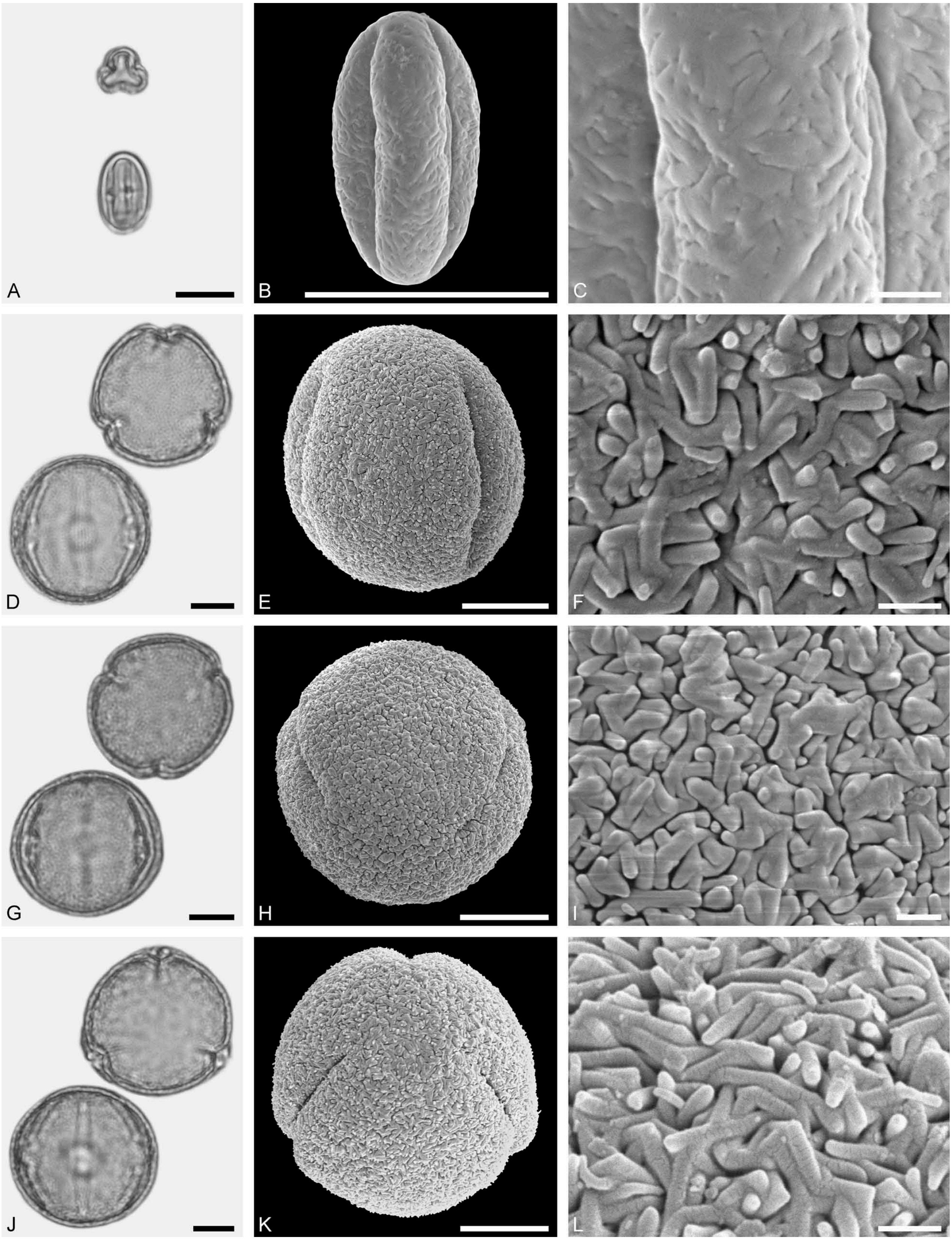


Figure 6. LM (**A, D, G, J**) and SEM (**B, C, E, F, H, I, K, L**) micrographs of dispersed fossil Fagaceae pollen. **A–C.** *Castanea* sp., close-up of central mesocolpium. **D–L.** *Fagus* sp., close-ups of mesocolpium (**F, I**) and polar area (**L**). Scale bars – 10 μm (A, B, D, E, G, H, J, K), 1 μm (C, F, I, L).

Bouchal et al. (2014) from the late Eocene of Colorado, USA.

Ecological implications. — *Castanea* is a small genus with *c.* eight extant species with a wide (disjunct) distribution in the temperate zone of the Northern Hemisphere, occurring in North America, eastern and western Asia, and southern Europe. Four species are native to East Asia, *C. crenata* Siebold et Zucc., *C. henryi* (Skan) Rehder et Wilson, *C. mollissima* Blume and *C. seguinii* Dode. The American chestnuts, *C. dentata* (Marshall) Borkh., *C. ozarkensis* Ashe and *C. pumila* Mill. are all native to south-eastern North America. The European chestnut, *C. sativa* Mill. is native to southern Europe and western Asia (e.g. Nixon 1997; Huang et al. 1999; Dane et al. 2003). The Asian *Castanea* species in China (Korea, Japan) are known to thrive in mixed mesophytic forests, especially on mountain slopes, ranging from sea level to an altitude of 2800 m (Huang et al. 1999). The American *C. dentata* and *C. ozarkensis* are growing in rich deciduous forests and mixed forests, occurring at an altitude between 0 and 1200 m. *Castanea pumila* occurs in forests and open woods, forest understory, dry sandy and wet sandy barrens, at an altitude of 0 to 1000 m (Nixon 1997).

Six of the about eight species of *Castanea* can be categorised as nemoral elements following the definition of Denk et al. (2013), and two (*C. ozarkensis*, a North American endemic with very restricted distribution; *C. pumila*) as meridio-nemoral (File S1). Kvaček and Walther (2010) noted that the early Eocene and Oligocene *Castaneophyllum* species (affiliated with *Castanea*) were deciduous trees adapted to warm temperate conditions that occurred within subtropical evergreen forests and mixed mesophytic forests.

Genus Fagus *L.*

Subgenus Fagus

Fagus *sp.*

(Figure 6D–L)

Description. — Pollen, monad, spheroidal, outline circular in polar and equatorial views; polar axis 33–35 µm long in LM, 30–33 µm long in LM, equatorial diameter 31–36 µm wide in LM, 28–31 µm wide in SEM; tricolporate, colpi narrow, nexine thickened around pori; exine 1.0–1.3 µm thick (LM), nexine thinner than sexine; tectate; sculpturing scabrate in LM, rugulate, fossulate in SEM, rugulae often diverging and protruding (SEM).

Remarks. — The pollen morphology (LM and SEM) of *Fagus* has been described and figured in detail by Crepet and Daghlian (1980), Miyoshi (1982), Saito (1992), Denk (2003), Wang and Pu (2004), Li et al. (2011a) and Miyoshi et al. (2011). The ultrastructure (TEM) of *Fagus* pollen has been studied by Crepet and Daghlian (1980), Praglowski (1982) and Wang and Pu (2004). The pollen morphology of extant *Fagus* pollen is very similar to that observed in fossil grains. Pollen from species of the subgenus *Engleriana* according to Shen (1992; *F. engleriana* Seemen, *F. japonica* Maxim., *F. okamotoi* C.F.Shen) are slightly different to those of the subgenus *Fagus* (all other species), they usually have a narrower colpi that reaches to the poles, and also the pollen grains are generally smaller than those of subgenus *Fagus* (Praglowski 1982; Denk 2003). *Fagus* pollen grains commonly occur in the Lavanttal samples and show a remarkable high variability in size, form and sculpturing under SEM. The same phenomenon has been documented for other palaeopalynofloras and material from extant *Fagus* flowers (e.g. Grímsson et al. 2015b). The size of the fossil *Fagus* pollen grains from the Lavanttal Basin and the arrangement of their colpi suggest that they belong to the subgenus *Fagus*. Fossil pollen showing LM-based morphological affinities to pollen of modern *Fagus* have commonly been assigned to the pollen form-genus *Faguspollenites* (e.g. Raatz 1937; Stuchlik et al. 2014).

Fossil record. — *Fagus* has an extremely well documented Cainozoic fossil record extending back to the Eocene (e.g. Tralau 1962; Zetter 1984: Kvaček & Walther 1991; Denk & Meller 2001; Denk 2004; Manchester & Dillhoff 2004; Grímsson & Denk 2005). The fossil record and biogeographic history of *Fagus* was recently summarised by Denk and Grimm (2009a). The earliest *Fagus* records (cupules, fruits, foliage, pollen) to date are from the late early Eocene of British Columbia, western Canada (*F. langevinii* Manchester et Dillhoff; Manchester & Dillhoff 2004; for age determination see Denk & Dillhoff 2005), and Washington, north-western United States (Republic locality; S.R. Manchester, pers. communication, 2015). Various additional *Fagus* macrofossils and pollen have been documented from the middle Eocene of Vancouver Island (western Canada), Axel Heiberg Island (north-eastern Canada) and western Greenland (e.g. McIntyre 1991; Richter & LePage 2005; Mindell et al. 2009; Grímsson et al. 2015b). The oldest Asian *Fagus* fossils to date were found in the Russian Far East and north-eastern China and are of middle to late Eocene age (e.g. Denk & Grimm 2009a). The fossil record of *Fagus* further indicates that this genus dispersed from

East Asia into Europe during the early Oligocene following the closure of the Turgai Seaway. In the Miocene, *Fagus* is found throughout the Northern Hemisphere (Denk & Grimm 2009a).

Dispersed fossil *Fagus* pollen studied using combined LM and SEM has been reported from the late early Eocene of British Columbia (Manchester & Dillhoff 2004), the middle Eocene of West Greenland (Grímsson et al. 2015b), the early Oligocene of Germany (Denk et al. 2012) and the late Miocene of Japan (Saito 1992).

Ecological implications. — *Fagus* is a small tree genus consisting of two distinct putative subgenera, subgenus *Fagus* (seven species) and subgenus *Engleriana* (three species) with a northern hemispheric distribution (Shen 1992; Denk 2003; Denk et al. 2005). *Fagus* is an important component of mixed broad-leaved evergreen-deciduous forest in North America and East Asia, and it is the most prominent broad-leaved forest tree in Europe and western Asia (Zhou & Li 1994; Peters 1997).

Fagus is one of the most ecologically and climatically indicative tree genera of the temperate zones of the Northern Hemisphere (Köppen 1936; Peters 1997; Grimm & Denk 2012); all three widespread and common species or species-complexes, *F. grandifolia* Ehrh. in eastern North America (northern Mexico to southern Canada), *F. sylvatica* L. (*s.l.*) in western Eurasia (northern Spain to northern Iran) and *F. crenata* Blume in Japan (Ryushu to southern islands, Hokkaido) can be (single-)dominant elements of mesic forests (e.g. Maycock 1994) within the warm temperate to snow climates with warm summers and ample precipitation throughout the year (*Cfb-*, *Dfb*-climates). In the warmer, subtropical *Cfa*-climates, *Fagus* becomes an accessory element (Maycock 1994). The genus *Fagus* shows also a strong correlation between altitudinal and latitudinal distribution (Maycock 1994; Cao 1995; Grimm & Denk 2012), and appears to be entirely absent from the summer-rain, winter-dry monsoon climates of East Asia in contrast to other Fagaceae genera such as *Quercus, Castanopsis* (sister genus of *Castanea*) and *Lithocarpus*. All *c.* nine species of *Fagus* can be categorised as nemoral elements (File S1; see Grimm & Denk 2012).

Genus Quercus *L.*

Quercus *sp. 1 (*Quercus *Group Cerris)*
(Figure 7A–I)

Description. — Pollen, monad, prolate, outline lobate in polar view, elliptic in equatorial view; polar axis 27–34 μm long in LM, 25–33 μm long in SEM, equatorial diameter 23–27 μm wide in LM, 20–26 μm wide in SEM; tricolporoidate; exine 0.9–1.2 μm thick (LM), nexine thinner than sexine; tectate; sculpturing scabrate in LM, microrugulate, perforate in SEM, rugulae forming irregularly distributed and protruding agglomerates (SEM).

Remarks. — The pollen morphology (LM and SEM) of *Quercus* Group Cerris has been presented by Miyoshi (1982), Wei (2003), Wang and Pu (2004), Denk and Grimm (2009b), Makino et al. (2009), Li et al. (2011a) and Miyoshi et al. (2011). The ultrastructure of this group has been documented by Wang and Pu (2004) and Denk and Tekleva (2014). Fossil pollen showing LM-based morphological affinities to pollen of modern *Quercus* have commonly been assigned to the pollen form-genus *Quercoidites* (e.g. Potonié 1960; Stuchlik et al. 2009).

Fossil record. — The rich fossil record of *Quercus* is in dire need of revision, partly because the systematic concepts that have been used are to some degree outdated, partly because of the many morphological convergences observed in the genus (Denk & Grimm 2010). The most diagnostic feature to distinguish major oak lineages in the fossil record is the sculpturing of pollen seen under SEM (Denk & Grimm 2009b). In this respect, the oldest unambiguous fossil record of *Quercus* Group Cerris (according to Denk & Grimm 2010) is pollen from the Oligocene–Miocene boundary of central Europe (Kmenta 2011). Further well-documented pollen records are from the early and middle Miocene and Pliocene of Central Europe (Ferguson et al. 1998; Van der Burgh & Zetter 1998; Hofmann et al. 2002) and the Miocene of eastern China (Liu et al. 2007) until the Holocene of the Sea of Japan (Tekleva et al. 2014). Macrofossils that have traditionally been linked to the section/subgenus *Cerris* may be of different systematic affinities. Modern types of Group Cerris (very similar or identical to extant species) start to occur in the Pliocene of the Eastern Mediterranean at regional scales (Velitzelos et al. 2014).

Ecological implications. — Group Cerris is one of the least-diverse lineages of oaks; nevertheless, its about ten species are ecologically relatively diverse. In contrast to their evergreen sister lineages Group Ilex and Group Cyclobalanopsis, most species are essentially deciduous, however they are relatively tolerant against summer draught except for the East Asian species. Species like *Quercus suber* L., the cork oak, and *Q. ithaburensis* Decne. (incl. *Q. macrolepis* Kotschy, the Valonia oak) are particularly adapted to the summer dry climates of the Mediterranean (e.g. Ne'Eman 1993; Petroselli et al. 2013), and widely

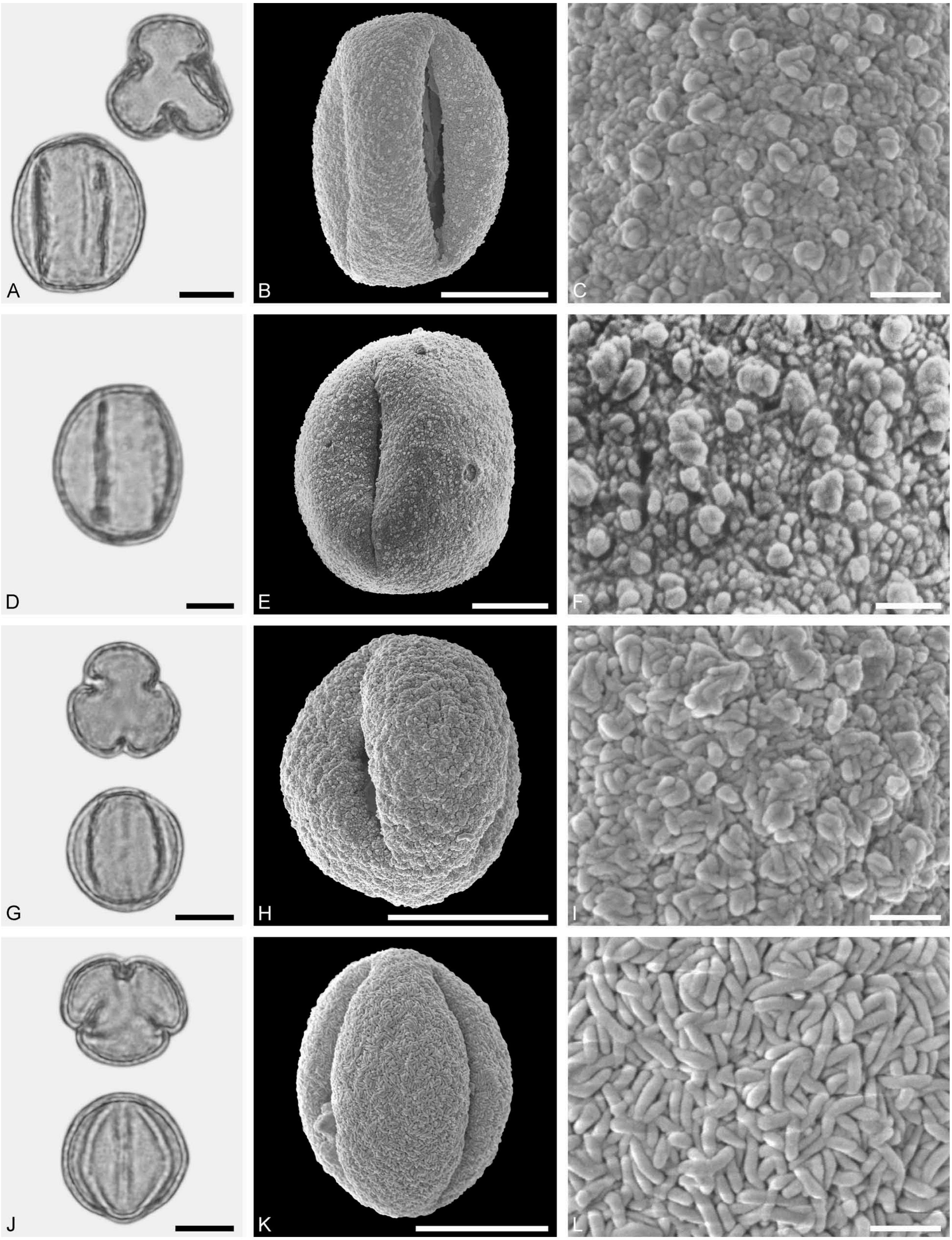


Figure 7. LM (**A, D, G, J**) and SEM (**B, C, E, F, H, I, K, L**) micrographs of dispersed fossil Fagaceae pollen. **A–I.** *Quercus* sp. 1 (*Quercus* Group Cerris), close-ups of central mesocolpium. **J–L.** *Quercus* sp. 2 (*Quercus* Group Ilex), close-up of mesocolpium. Scale bars – 10 µm (A, B, D, E, G, H, J, K), 1 µm (C, F, I, L).

cultivated. Other species such as *Q. cerris* L. can be found in dry and mesic forests of the Mediterranean region and have been successfully introduced e.g. to the British Islands, where they naturalised (Stace 1997). *Quercus libani* Oliv. and *Q. brantii* Lindl. are typical elements across the entire range of the Taurus and Zagros Mountains, where they thrive in cultivated lands and montane forests alike (south-eastern Turkey, northern Iraq, south-western Iran; Browics & Zieliński 1982). In contrast to their western Eurasian counterparts, the East Asian species prefer fully humid, mild climate conditions and can be found in mixed mesophytic, subtropical to temperate forests of China and Japan (Huang et al. 1999).

The three East Asian and two of the western Eurasian species of *Quercus* Group Cerris can be categorised as meridio-nemoral and nemoral elements; the remaining five western Eurasian species with a combined range from the eastern Mediterranean to the Levant and eastern Iran as semihumid-meridional (File S1).

Quercus *sp. 2 (*Quercus *Group Ilex)*
(Figure 7J–L)

Description. — Pollen, monad, prolate to spheroidal, outline lobate in polar view, elliptic in equatorial view; polar axis 22–24 µm long in LM, 19–21 µm long in SEM, equatorial diameter 20–22 µm wide in LM, 16–18 µm wide in SEM; tricolporate; exine 0.9–1.0 µm thick (LM), nexine thinner than sexine; tectate; sculpturing scabrate in LM, rugulate to microrugulate, perforate in SEM, rugulae partly interwoven (SEM).

Remarks. — The pollen morphology (LM and SEM) of *Quercus* Group Ilex has been presented by Miyoshi (1982), Wei (2003), Wang and Pu (2004), Denk and Grimm (2009b), Fujiki and Ozawa (2007), Makino et al. (2009), Li et al. (2011a), Miyoshi et al. (2011) and Denk and Tekleva (2014). The pollen ultrastructure of this group has been documented by Wang and Pu (2004) and Denk and Tekleva (2014).

Fossil record. — Because of its generally plesiomorphic type (Denk & Grimm 2009b), pollen of *Quercus* Group Ilex cannot be as straightforwardly identified as pollen of the other intrageneric groups of oaks. Nevertheless, due to a recent study covering all species of Group Ilex and focussing in particular on intragroup/intraspecies variation (Denk & Tekleva 2014), it is possible to identify types that are indistinguishable from pollen of modern species of Group Ilex. The oldest records of Group Ilex are from the early Oligocene of Central Europe (Denk et al. 2012), whereas similar but older pollen from western Greenland represents an extinct lineage of *Quercus*/Fagaceae (Grímsson et al. 2015b). In western Eurasia, Group Ilex becomes most diverse in the Miocene of the eastern Mediterranean, where macrofossil remains with affinity to either the western Eurasian *Q. ilex* L. as well as several East Asian species of Group Ilex are abundant and collectively addressed as *Q. drymeja* Unger and *Q. mediterranea* Unger (electronic supplement to Denk et al. 2014; Velitzelos et al. 2014). Pollen of Group Ilex has also been documented for the Miocene of eastern China (Liu et al. 2007), the Pleistocene and Holocene of Japan (Nakagawa et al. 1996; Tekleva et al. 2014) and from the Miocene onwards in Central Europe (Ferguson et al. 1998; Van der Burgh & Zetter 1998; Hofmann et al. 2002)

Ecological implications. — Traditionally, members of this group have been considered to indicate seasonal, subtropical conditions with pronounced phases of draught ('subxerophytic'; e.g. Kovar-Eder et al. 2004) probably because of the distribution of *Quercus ilex* and *Q. coccifera* L. in the Mediterranean region and the fact that all species are evergreen (e.g. Axelrod 1983). However, only three (*Q. aucherii* Jaub. et Spach, endemic to southwest Turkey; *Q. alnifolia* Poech, endemic to Cyprus; *Q. coccifera*, widespread in the Mediterranean) of the four western Eurasian species are limited to summery-dry, Mediterranean climates (*Csa, Csb*). The most widespread species, *Q. ilex*, extends its range into fully humid, mostly subtropical habitats (e.g. Petroselli et al. 2013), profiting from global warming trends (Delzon et al. 2013) and is a common element in various habitats of the Mediterranean region including dry and mesic forests.

The same holds for the western Asian and East Asian members of the group which have a distribution spanning from the southern flanks of the Himalayas, where they can locally occur until nearly 4000 m a.s.l. (Bisht et al. 2013), via the southern half of China (Huang et al. 1999), into low- to mid-altitudes of southern and central Japan (southern islands, Hokkaido; Ohwi 1965) where they grow usually in montane, mixed mesophytic and subalpine forests under climates with moderate to high summer precipitation (*Cfa-*, *Cfb-*, *Cwa-*, *Cwb-*, *Dwa-*, *Dwb*-climates). As exemplarily illustrated in the Miocene of western Turkey, the fossil members of this group thrived in a similar environment (Denk et al. 2014). Overall, most species of Group Ilex can be categorised as nemoral elements, but also include meridio-nemoral (*Q. ilex*) and semihumid-meridional taxa (File S1).

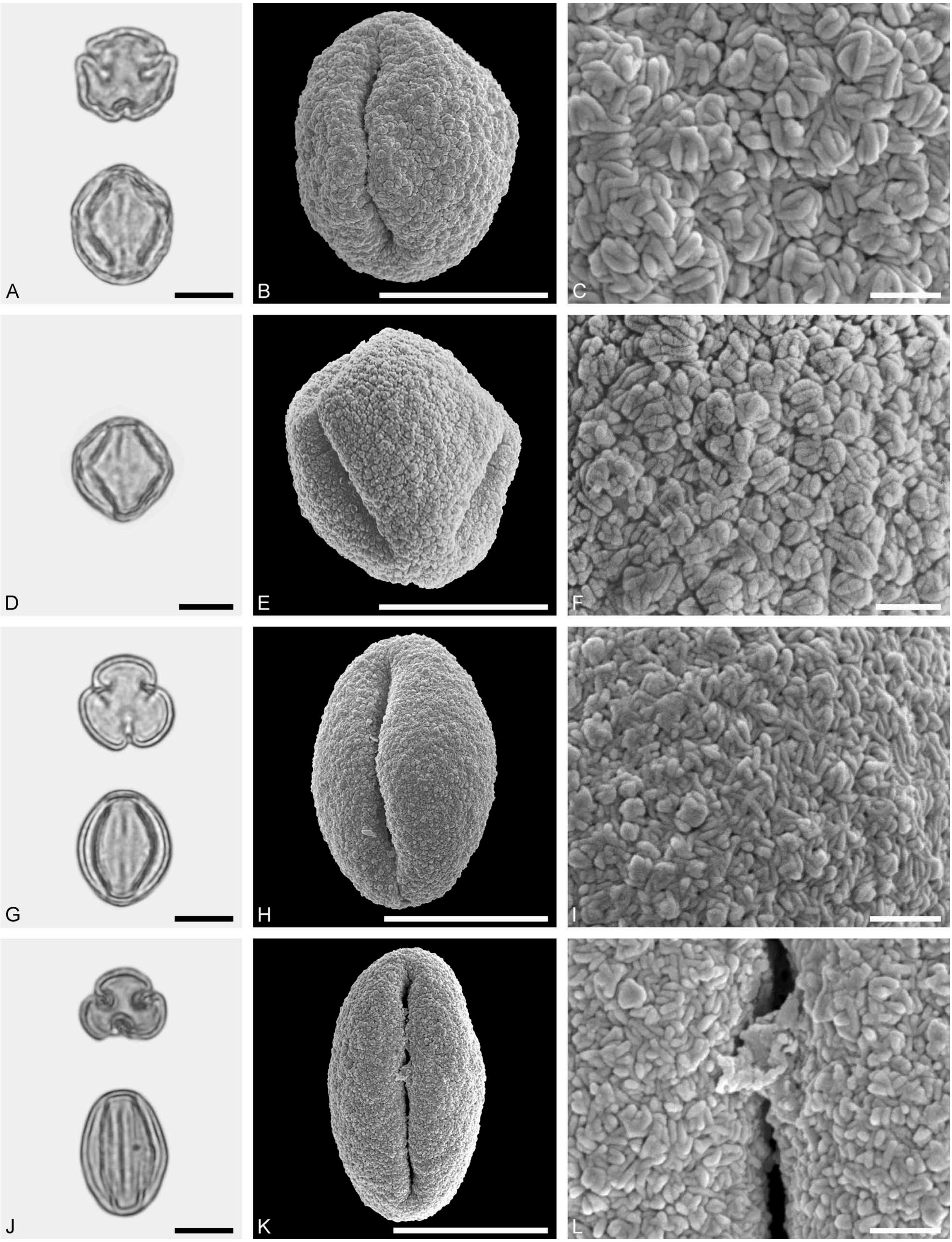


Figure 8. LM (**A, D, G, J**) and SEM (**B, C, E, F, H, I, K, L**) micrographs of dispersed fossil Fagaceae pollen. **A–F.** *Quercus* sp. 3 (*Quercus* Group Ilex), close-ups of central mesocolpium. **G–L.** *Quercus* sp. 4 (*Quercus* Group Ilex), close-ups of mesocolpium (**I**) and area around colpus (**L**). Scale bars – 10 μm (A, B, D, E, G, H, J, K), 1 μm (C, F, I, L).

Quercus *sp. 3 (*Quercus *Group Ilex)*
(Figure 8A–F)

Description. — Pollen, monad, prolate to spheroidal, outline circular to lobate in polar view, elliptic in equatorial view; polar axis 18–21 µm long in LM, 16–18 µm long in SEM, equatorial diameter 17–19 µm wide in LM, 13–15 µm wide in SEM; tricolporate; exine 0.8–1.0 µm thick (LM), nexine thinner than sexine; tectate; sculpturing scabrate in LM, microrugulate in SEM, microrugulae clustered, clusters densely packed (SEM).

Remarks. — The rugulae in *Quercus* sp. 2 are much longer than the rugulae in *Quercus* sp. 3. The rugulae in *Quercus* sp. 2 are forming a single layer, but are clustered in *Quercus* sp. 2 and the clusters are showing different relief.

Quercus *sp. 4 (*Quercus *Group Ilex)*
(Figure 8G–L)

Description. — Pollen, monad, prolate, outline lobate in polar view, elliptic in equatorial view; polar axis 20–23 µm long in LM, 17–19 µm long in SEM, equatorial diameter 14–16 µm wide in LM, 11–13 µm wide in SEM; tricolporate, pori small, indistinct; exine 0.8–1.0 µm thick (LM), nexine thinner than sexine; tectate; sculpturing psilate in LM, microrugulate, perforate in SEM, microrugulate sometimes forming clusters, cluster irregularly distributed (SEM).

Remarks. — The rugulae in *Quercus* sp. 2 are much longer than the rugulae in *Quercus* sp. 4. The rugulae in *Quercus* sp. 2 are forming a single layer, but are partly clustered in *Quercus* sp. 4, and the clusters are showing different relief. *Quercus* sp. 3 shows clear pori (LM) that are not visible in *Quercus* sp. 4. The rugulae of *Quercus* sp. 4 are much shorter and narrower than the rugulae in *Quercus* sp. 3. The clusters in *Quercus* sp. 4 are also fewer, smaller and wider apart than observed in *Quercus* sp. 3.

Quercus *sp. 5 (aff.* Quercus *Group Cyclobalanopsis)*
(Figure 10D–F)

Description. — Pollen, monad, prolate, outline lobate in polar view, elliptic in equatorial view; polar axis 20–22 µm long in LM, 19–21 µm long in SEM, equatorial diameter 12–14 µm wide in LM, 12–14 µm wide in SEM; tricolporate; exine 0.6–0.7 µm thick (LM), nexine thinner than sexine; tectate; sculpturing psilate in LM, rugulate, perforate, fossulate in SEM, rugulae with a microechinate suprasculpture (SEM).

Remarks. — Pollen morphology (LM and SEM) of *Quercus* Group Cyclobalanopsis has been described by Miyoshi (1982), Wei (2003), Wang and Pu (2004), Fujiki and Ozawa (2007), Denk and Grimm (2009b), Makino et al. (2009), Li et al. (2011a) and Miyoshi et al. (2011). The pollen ultrastructure (TEM) of this group has been presented by Wang and Pu (2004) and Denk and Tekleva (2014).

Fossil record. — A cupule likely representing *Quercus* Group Cyclobalanopsis and associated with *Quercus* acorns of unknown affinity has been found in the nuts beds of the middle Eocene Clarno Formation of western North America (Manchester 1994), and represents the oldest record of this otherwise purely East Asian clade of oaks. Oldest records in East Asia date to the late Eocene of Japan (leaves and fruits; Huzioka & Takahashi 1970), and have been occasionally reported from the Oligocene onwards in Chinese and Japanese macrofossil assemblages (e.g. Ishida 1970; Manning 1978; Yabe 2008). The only pollen grains so far documented using SEM were from the Pleistocene of Nepal (Nakagawa et al. 1996) and, possibly, Miocene of eastern China (Liu et al. 2007). The Lavanttal pollen would represent the first Eurasian record of Group Cyclobalanopsis outside its modern distribution range, indicating that this today (tropical-)subtropical East Asian oak lineage extended into Europe in the middle to late Miocene. With respect to all currently available data on oaks, such an extension of the range appears unlikely, and it cannot be entirely ruled out that the pollen is underdeveloped pollen of a red oak (Group Lobatae; Solomon 1983).

Ecological implications. — Members of the Group Cyclobalanopsis are usually found in the subtropical (meridional) regions of East Asia with hot summers and sufficient or excess precipitation during growing season (see Fang et al. 2009). Their main habitats are wet, mixed or broad-leaved evergreen forests, in lowlands, valleys and on mountain slopes; several species are also found in montane, nemoral mixed-mesophytic forests, including mountain tops, at altitudes of up to 2800 m (Huang et al. 1999). Most species of Group Cyclobalanopsis can be categorised as semihumid-meridional or meridio-nemoral elements (File S1). If oaks with affinities to Group Cyclobalanopsis thrived in Lavanttal, they would be indicative of wet, subtropical conditions in the lowlands, where they formed part of mixed evergreen-deciduous forests as today found in southern China.

Quercus *sp. 6 (*Quercus *Group Quercus/Lobatae)*
(Figure 9A–L)

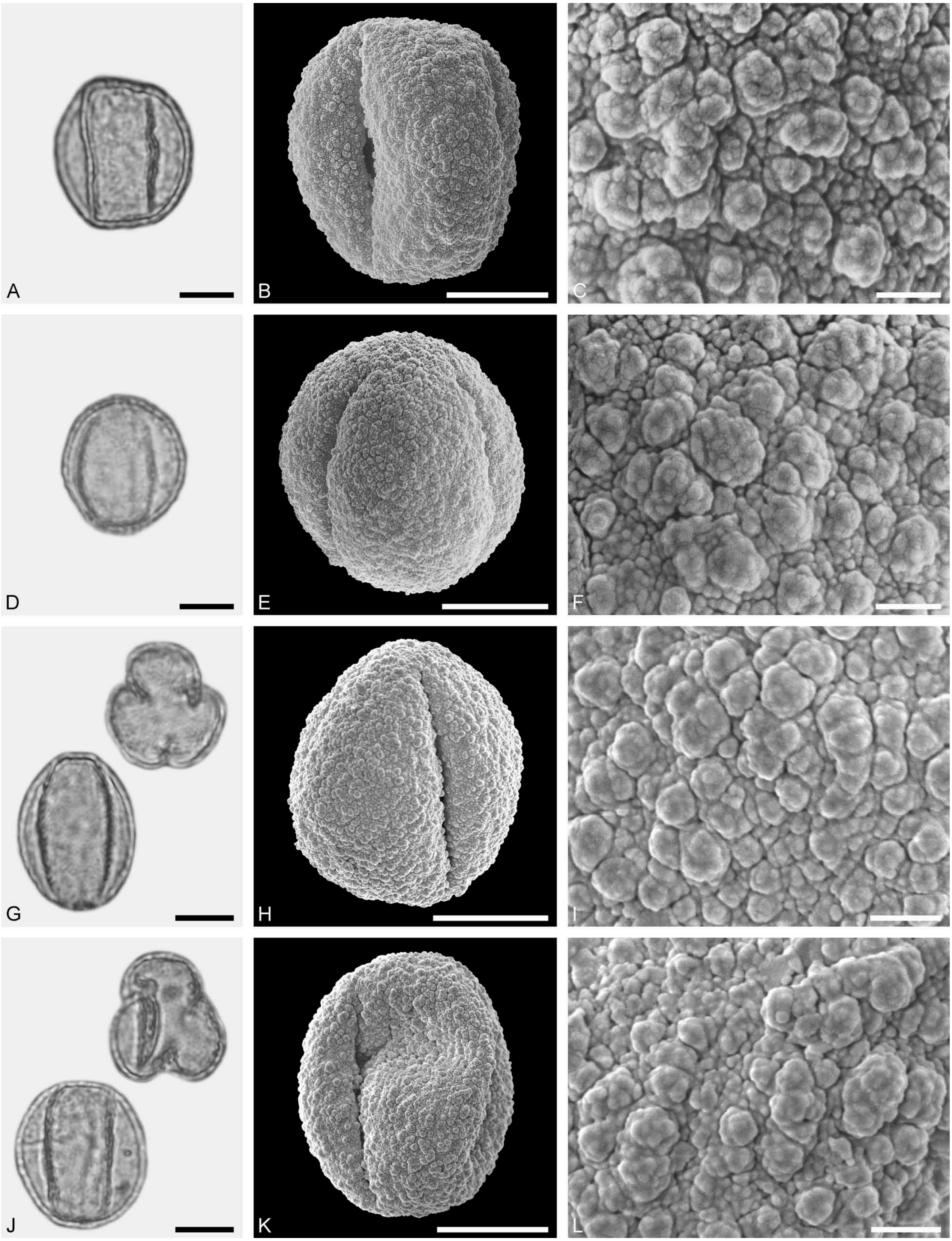


Figure 9. LM (**A, D, G, J**) and SEM (**B, C, E, F, H, I, K, L**) micrographs of dispersed fossil Fagaceae pollen. **A–L.** *Quercus* sp. 6 (*Quercus* Group Quercus/Lobatae), close-ups of central mesocolpium. Scale bars – 10 µm (A, B, D, E, G, H, J, K), 1 µm (C, F, I, L).

Description. — Pollen, monad, prolate, outline lobate in polar view, elliptic in equatorial view; polar axis 25–28 µm long in LM, 23–27 µm long in SEM, equatorial diameter 19–25 µm wide in LM, 18–24 µm wide in SEM; tricolporoidate; exine 0.9–1.2 µm thick (LM), nexine thinner than sexine; tectate; sculpturing scabrate in LM, microverrucate, perforate in SEM, microverrucae often fused to form large agglomerates of different shape, microverrucae with a granulate suprasculpture (SEM).

Remarks. — Pollen morphology (LM and SEM) of *Quercus* Group Quercus/Lobatae has been described and figured by Crepet and Daghlian (1980), Lieux (1980), Miyoshi (1982), Jones et al. (1995), Wei (2003), Wang and Pu (2004), Denk and Grimm (2009b), Makino et al. (2009), Li et al. (2011a) and Miyoshi et al. (2011). The pollen ultrastructure (TEM) of these groups has been documented by Crepet and Daghlian (1980) and Denk and Tekleva (2014).

Fossil record. — Oldest fossils that can be unambiguously linked to either Group Quercus, the ‘white oaks’, and/or Group Lobatae, the ‘red oaks’, are fossil pollen reported from the middle Eocene of Axel-Heiberg Island, Arctic Archipelago, north-eastern Canada (McIntyre 1991) and western Greenland (Grímsson et al. 2015b); and subsequently (Eocene–Oligocene boundary) from the eastern foothills of the Rocky Mountains (Bouchal et al. 2014) and the early Oligocene of Central Europe (Denk et al. 2012). Seeds with basal abortive ovules, today only found in the northern hemispheric Group Quercus and the exclusively Eurasian Groups Cerris and Ilex, have been reported from the middle Miocene of Washington, north-western United States (Borgardt & Pigg 1999), in association with potential white oak foliage. Four of the eight *Quercus* pollen morphotaxa figured by Liu et al. (2007) from the Miocene of China are representing this lineage and this pollen type has also been found in Holocene of the Sea of Japan (Tekleva et al. 2014). Pollen of this lineage has also been reported from the middle to late Miocene of Iceland, indicating episodic migration of oaks across the North Atlantic Land Bridge (Denk et al. 2010, 2011).

Ecological implications. — Both groups of oaks are ecologically and taxonomically highly diverse in North America (*c.* 200 species) including evergreen species adapted to diverse habitats (such as chaparral, wood steppe, humid-subtropical forests) as well as deciduous species populating mesic to dry subtropical to boreal forests (e.g. Nixon 1997), including such dominated by or including beech trees (*Fagus*; e.g. Maycock 1994). Particularly in Group Lobatae, species are found that thrive along river beds and in back-swamp forests (Nixon 1997). In the south-western part of the United States and across Mexico, white and red oaks are found in distinctly dry (semi-arid) settings (e.g. Baja California, lee-ward parts of the Sierra Madre). Red and white oaks are co-dominant in several North American vegetation zones such as the Oak-Hickory and Oak-Chestnut regions (southern United States) and the Oak-Pine Region (south-eastern United States) and Oak-Chestnut Region (Atlantic coast states; Maycock 1994) In Eurasia, Group Lobatae is extinct (see Denk et al. 2012), and Group Quercus is limited to deciduous species of temperate (nemoral to boreal) forests (Schroeder 1998). About five species can be found in East Asia, the most widespread being *Quercus mongolica* Fischer ex Ledeb., which ranges from Siberia and Mongolia to Japan, Sakhalin and the Kuril Islands. In China, the species are restricted to mixed mesophytic deciduous forests at 0–2700 m a.s.l. (Huang et al. 1999).

Although the Eurasian species of Group Quercus are typically found in fully humid warm-temperate to snow climates (*Cfa*, *Cfb*, *Dfb*), similar to *Fagus* and *Corylus*, they include a few species in western Eurasia that have adapted to summer-dry Mediterranean and near-steppe climate conditions (*Cs*- and *BS*-climates; e.g. subsection Galliferae; Tschan & Denk 2012). The northern limit of white oaks in North America and Eurasia marks the boundary between snow climates with warm summers (*Dfb*) and cool (short) summers (*Dfc*). Species of Groups Quercus and Lobatae can be categorised as tropical-meridional, eurytropical, semihumid-meridional, meridio-nemoral, nemoral or boreal elements (File S1). Given the high variation of habitats and climate conditions covered by individual members of *Quercus* Groups Quercus and Lobatae, particular in North America, no discrete conclusions can be drawn on their role in the Lavanttal biota at this point.

Quercus *sp. 7 (*Quercus *Group Quercus/Lobatae)* (Figure 10A–C)

Description. — Pollen, monad, prolate, outline lobate in polar view, elliptic in equatorial view; polar axis 32–34 µm long in LM, 31–33 µm long in SEM, equatorial diameter 26–28 µm wide in LM, 22–24 µm wide in SEM; tricolporoidate; exine 1.1–1.3 µm thick (LM), nexine thinner than sexine; tectate; sculpturing scabrate in LM, microverrucate in SEM, microverrucae often forming small rounded clusters, clusters irregularly distributed (SEM).

Remarks. — *Quercus* sp. 7 has a clear poroid (LM) germination area that is not observed in *Quercus* sp. 6. The fused microverrucae in *Quercus* sp. 6 form

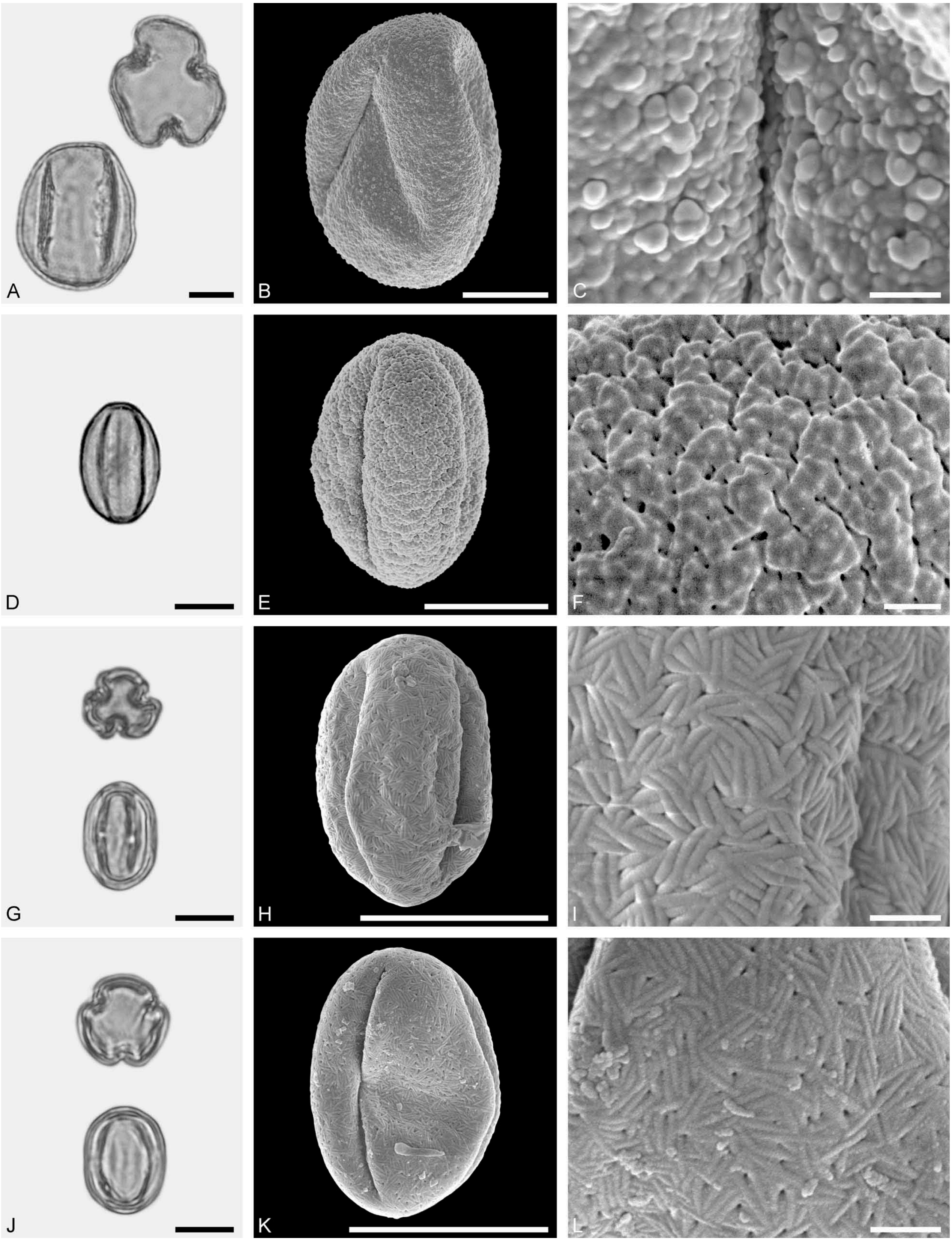


Figure 10. LM (**A, D, G, J**) and SEM (**B, C, E, F, H, I, K, L**) micrographs of dispersed fossil Fagaceae pollen. **A–C.** *Quercus* sp. 7 (*Quercus* Group Quercus/Lobatae), close-ups of area around colpi. **D–F.** *Quercus* sp. 5 (aff. *Quercus* Group Cyclobalanopsis), close-up of mesocolpium. **G–L**. *Trigonobalanopsis* sp., close-up of mesocolpium. Scale bars – 10 µm (A, B, D, E, G, H, J, K), 1 µm (C, F, I, L).

large agglomerates that are not comparable to the small ones observed in *Quercus* sp. 7. The agglomerates in *Quercus* sp. 7 do not show the granulate suprasculpture observed in *Quercus* sp. 6.

Genus Trigonobalanopsis *Kvaček et H. Walther (extinct)*

Trigonobalanopsis *sp.*
(Figure 10G–L)

Description. — Pollen, monad, prolate, outline lobate in polar view, elliptic in equatorial view; polar axis 16–21 µm long in LM, 13–18 µm long in SEM, equatorial diameter 11–16 µm wide in LM, 9–12 µm wide in SEM; tricolporate, colpi long; exine 0.7–1.1 µm thick (LM), nexine as thick or slightly thicker than sexine; tectate; sculpturing psilate in LM, rugulate to microrugulate, perforate in SEM, parallel rugulae forming irregularly arranged groups, rugulae segmented (SEM).

Remarks. — Fossil pollen showing LM-based morphological affinities to pollen of the extinct *Trigonobalanopsis* have sometimes been assigned to the pollen form-species *Cupuliferoipollenites oviformis* (Potonié) Potonié ex Potonié (e.g. Stuchlik et al. 2014).

Fossil record. — *Trigonobalanopsis* fossils (leaves, cupules, fruits) are numerous in the European late Cainozoic record. *Trigonobalanopsis exacantha* (Mai) Kvaček et H.Walther cupules/fruits have been documented from the Miocene of Germany and the Czech Republic (e.g. Kvaček & Walther 1988). Leaves of *T. rhamnoides* (Rossm.) Kvaček et H. Walther have been documented from the late Eocene of the Czech Republic, the Oligocene of Germany, the Miocene of Poland, Germany, Austria and the Czech Republic (e.g. Kvaček & Walther 1988, 1989). Pollen assigned to *T. schmidtii* H.Walther et Zetter has been described from laminar surface of fossil *T. rhamnoides* leaves from the Miocene of Germany (Walther & Zetter 1993). Dispersed *Trigonobalanopsis* pollen has been described, using combined LM and SEM, from the early Oligocene of Germany (Denk et al. 2012), the early Miocene of Austria (Meller et al. 1999) and the late Miocene of Iceland (Denk et al. 2011).

Ecological implications. — Mai (1995) and Meller et al. (1999) listed *Trigonobalanopsis* in several Eocene to Miocene floras in Europe, in association with predominately subtropical as well as distinctly temperate elements. In the Oligocene of Central Europe, *Trigonobalanopsis* is found part of a flora that supposedly thrived in a humid, warm temperate climate (Denk et al. 2012). In Iceland, pollen of *Trigonobalanopsis* is found in the 10 Ma (in a similar setting) and 4.2–3.8 Ma floras (after substantial local cooling; Denk et al. 2011, 2013). More precise ecological and climatic preferences of this extinct Fagaceae have yet to be established.

Family Juglandaceae DC. ex Perleb
Subfamily Engelhardioideae Iljinsk.

Engelhardioideae gen. et sp. indet.
(Figure 11A–L)

Description. — Pollen, monad (rarely in tetrads), oblate, outline convex triangular in polar view, elliptic in equatorial view; polar axis 17–19 µm long in LM, equatorial diameter 23–27 µm wide in LM, 18–26 µm wide in SEM; triporate; exine 0.8–1.1 µm thick, nexine thinner than sexine; tectate; sculpturing psilate to scabrate in LM, microechinate in SEM, microechini at regular interval, microstriate to microrugulate pattern radiating from base of echini (SEM).

Remarks. — The subfamily Engelhardioideae includes four well-defined extant genera that are supported by both molecular and morphological data; *Alfaroa, Alfaropsis, Engelhardia* (often misspelled as '*Engelhardtia*'; see Dilmy 1955) and *Oreomunnea* (e.g. Manchester 1987b; Manos & Stone 2001; Manos et al. 2007; Zhang et al. 2013). The most comprehensive work on Juglandaceae pollen including species representing every extant genera of the family is that of Stone and Broome (1971, 1975). Pollen of *Rhoiptelea*, a genus recently transferred into the family (APG 2009: subfamily Rhoipteleoideae), has also been studied in detail by Skarpy et al. (2009). *Alfaroa, Alfaropsis* (as *Engelhardia roxburghiana* Wall.), *Engelhardia* and *Oreomunnea* pollen has been studied and figured using LM, SEM and TEM by Whitehead (1965) and Stone and Broome (1975). Fossil pollen showing LM-based morphological affinities to pollen of modern Engelhardioideae have commonly been assigned to the pollen form-genus *Momipites* (e.g. Nichols 1973; Stuchlik et al. 2009). Based on the morphology of the pollen from the Lavanttal Basin, in comparison to pollen from extent genera of Engelhardioideae, it could be affiliated with *Alfaroa, Engelhardia* or *Oreomunnea*. Based on the complete fossil record of Engelhardioideae detailed most recently by Manchester (1987b), the pollen probably originates from either *Oreomunnea* or *Engelhardia*, but is more likely affiliated with *Oreomunnea* since it has a much richer and widespread European macrofossil record during the Miocene than *Engelhardia*.

Fossil record. — Engelhardioideae have a rich and well-documented fossil record in the Cainozoic of

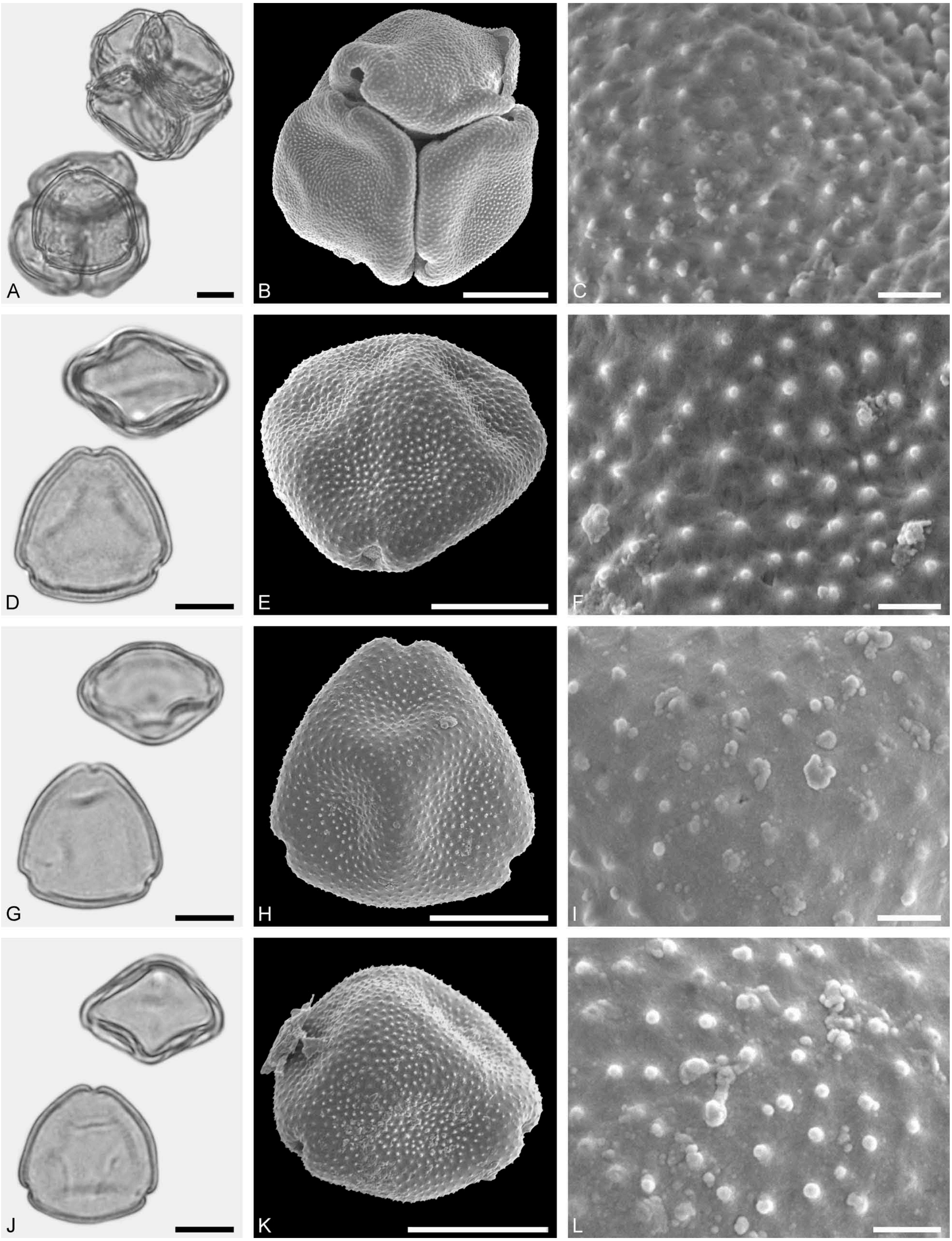


Figure 11. LM (**A, D, G, J**) and SEM (**B, C, E, F, H, I, K, L**) micrographs of dispersed fossil Juglandaceae pollen. **A–L.** Engelhardioideae gen. et sp. indet. (*Alfaroa* vel *Engelhardia* vel *Oreomunnea*), pollen in tetrad (**A**), single grains (**D, G, J**), close-ups of polar area. Scale bars – 10 µm (A, B, D, E, G, H, J, K), 1 µm (C, F, I, L).

the Northern Hemisphere composed of fruits, leaves, wood, catkins and *in situ* and dispersed pollen (see partly table 4 in Manchester 1987b). Pollen of the Engelhardioideae-type has been reported from the Upper Cretaceous and Paleocene of North America and the Paleocene of Europe (e.g. Muller 1981; Manchester 1989b). Based on correlation with macrofossils, all Engelhardioideae pollen records prior to the Eocene are questioned by Manchester (1987b, 1989b) and considered to represent extinct lineages that have not reached the level of extant genera. Engelhardioideae-type catkins/inflorescences (*Eokachyra aeolius* Crepet, Dilcher et Potter; *Eoengelhardia puryearensis* Crepet, Daghlian et Zavada) with *in situ* pollen characteristic for the subfamily have been described from the middle Eocene of Tennessee, east south-central United States (Crepet et al. 1975, 1980). Different Engelhardioideae-type fruits, *Palaeocarya puryearensis* (Berry) Manchester and *Paraengelhardtia eocenica* Berry, have been reported from the same locality (e.g. Manchester 1987b, 1989b). The earliest records of Engelhardioideae-type wood (*Engelhardioxylon nutbedensis* Manchester; *E. texana* Manchester) come also from North America, i.e. the middle Eocene of south-central and north-western United States (Manchester 1983). Wood of Engelhardioideae has also been recorded from the late Eocene of Europe (*E. macrocrystallosum* H.Gottwald; Gottwald 1992), and from the Oligocene of the Russian Far East (*E. mameticum* Blokh. et Snezhk.; Blokhina et al. 2002; Blokhina 2004, 2007). Fossil Engelhardioideae fruits are considered the most reliable and easily affiliated organs of the subfamily.

According to Manchester (1987b), *Alfaroa*-type fruits are not known from the fossil record, but *Oreomunnea*-like (*Palaeocarya* sect. *Palaeocarya*) and *Alfaropsis*-/*Engelhardia*-like (*Palaeocarya* sect. *Monocosta*) types of fruits are numerous throughout the Cainozoic of North America and Eurasia. Approximately eight different fruit species, four occurring in the middle to late Eocene of the United States (California, Oregon, Kentucky, Tennessee, Washington), one from the Oligocene (Oregon) and one from the Miocene (Idaho) of the United States, one from the Miocene of East Asia (Japan, Korea), and one ranging from the middle Eocene to Pliocene of Europe, have been affiliated with *Oreomunnea* and assigned to sect. *Palaeocarya* (e.g. Jähnichen et al. 1977, 1984; Tanai & Uemura 1983; Manchester 1987b). Fossils of sect. *Monocosta* are rare in the fossil record and only three species, two from the Eocene of the United States (Mississippi, Utah), and one from the late Oligocene of Europe (France), have been affiliated with *Alfaropsis*/*Engelhardia* and assigned to this section (e.g. Jähnichen et al. 1977; Manchester 1987b). Newly described fruit fossils (*Oreomunnea grahamii* Manchester et Herrera) from the early Miocene of Panama represent the earliest macrofossil record of *Oreomunnea* (Herrera et al. 2014). *Alfaropsis*/*Engelhardia*-type leaves are hard to identify because of convergences with leaves of other genera/families and their record is minute and unreliable (e.g. Manchester 1987b). Fossil *Oreomunnea*/*Alfaroa*-like leaflets are frequent in the Cainozoic record of Europe (Kvaček 1972; Jähnichen et al. 1977; 1984; Jähnichen 1991) and south-eastern United States (Dilcher & Manchester 1986). These have mostly been assigned to two species, *Oreoroa orsbergensis* (Wessel et Weber) Dilcher et Manchester, from the middle Eocene to late Miocene of Europe, and *Oreoroa claibornensis* Dilcher et Manchester, from the middle Eocene of east south-central United States (Dilcher & Manchester 1986).

Ecological implications. — The genera of Engelhardioideae are all relatively small, *Alfaroa* comprises five species, *Alfaropsis* is composed of only a single species, *Engelhardia* includes *c.* six species, and *Oreomunnea* has two species (e.g. Manning 1966, 1978; Stone 1968, 1977, 2010; Lu et al. 1999). *Oreomunnea* and *Alfaroa* occur in the Americas, *Alfaropsis* and *Engelhardia* in East Asia. In the Americas, *Oreomunnea* has a more restricted distribution than *Alfaroa. Oreomunnea mexicana* (Standl.) J.-F.Leroy ranges from southern Mexico to Costa Rica, occurring at altitudes of 600 to 1900 m (Stone 1977). *Oreomunnea pterocarpa* Oerst. is endemic to Costa Rica, growing at altitude of 200 to 1500 m. This species is mostly restricted to the rainforests of the Cartago Province, where it is a typical canopy tree at mid-elevation sites where the annual rainfall approaches 7000 mm/yr (Stone 1977). *Alfaroa* has a wider distribution occurring from Mexico to Columbia and the West Indies. *Alfaroa costaricensis* Standl. is occurring in Mexico, Guatemala, Costa Rica and Panama, growing at altitude of 600 to 3200 m (Stone 1977). *Alfaroa guatemalensis* (Standl.) L.O.Williams et Ant. Molina is endemic to Guatemala; there it occurs at altitude of 1200 to 2200 m and is often growing on rich volcanic soil in the mountain forests (Stone 2010). *Alfaroa manningii* J.León is endemic to Costa Rica, growing at altitude of 300 to 1300 m in the premontane rainforest (Stone 1977). *Alfaroa mexicana* D.E.Stone is occurring in Mexico and Mesoamerica, and can be found in rich deciduous forests at altitudes of 730 to 1700 m (Stone 1968). *Alfaroa williamsii* Ant.Molina is occurring in Mesoamerica and Colombia, growing at an altitude of 1100 to 2300 m.

In conclusion, both *Alfaroa* and *Oreomunnea* thrive in wet habitats under subtropical to tropical climates

(*A*-, *Cwa*-, *Cfa*-climates). In Asia, *Engelhardia* has a wide distribution ranging from India over eastern Asia and into Melanesia (*A*-climates, hot *Cwa*-climates; e.g. Manning 1966, 1978; Lu et al. 1999). In China, the three *Engelhardia* species, *E. hainanensis* P.Y. Chen, *E. serrata* Blume and *E. spicata* Blume, occur in rich valley forests and/or on mountain slopes, and depending on the species can be found from sea level to an altitude of 2100 m (Lu et al. 1999). *Alfaropsis* has a more discontinuous distribution occurring in hilly and mountain regions of eastern Pakistan, southern China, Taiwan, Vietnam, Sumatra and Borneo. *Alfaropsis roxburgiana* (Wall.) Iljinsk., the sole species of the genus, occurs in mixed broad-leaved and/or evergreen forest in China at an altitude of 200 to 1500 m (e.g. Manning 1966, 1978; Lu et al. 1999). Except for *Alfaropsis*, all other modern members of Engelhardioideae have a restricted distribution with focus on the tropical-subtropical climate zones (*A*-climates, and warmest variants of *Cwa*-/*Cfa*-climates). Species of *Alfaroa* and *Oreomunnea* occur in the premontane rainforests of Central America (tropical *A*-climates) as well as in the succeeding temperate virgin and cloud forests at elevations of up to 1700 m in (southern) Mexico and 2200 m in Costa Rica (*Cfa*-, *Cwb*-climates; Stone 1977, 2010) and could be categorised as tropical-meridional or meridio-nemoral elements (File S1).

The distribution in the past was, however, much less restricted (Kvaček 2007, addressed as '*Engelhardia*'), and fossils with affinities to Engelhardioideae are frequently found in association with fully temperate elements indicating that they were more tolerant regarding temperature regimes than their modern relatives (e.g. Kvaček 2007). Also, Manchester (1987b) concluded that based on the diversity of Engelhardioideae from the middle Eocene of North America, that included different species of *Palaeocarya*, and also *Paleooreomunnea* and *Paraengelhardtia*, suggested a primary radiation of this group under a subtropical climate. In conclusion, fossil Engelhardioideae should be scored as (*A*+)*Cfa*+*Cfb*+*Cwa* +*Cwb* taxa regarding their 'Köppen signature'; and possibly included also nemoral elements following the definition of Denk et al. (2013).

Subfamily Juglandoideae Eaton

Genus Carya *Nutt.*

Carya *sp.*
(Figure 12A–L)

Description. — Pollen, monad (rarely tetrads), oblate, outline convex triangular in polar view, elliptic in equatorial view; polar axis 28–33 µm long in LM, equatorial diameter 41–49 µm wide in LM, 41–44 µm wide in SEM; triporate, one or more pori subequatorially positioned; exine 1.3–1.8 µm thick (LM), nexine thinner than sexine, exine thinner in distal central polar area, thinning circular in outline; tectate; sculpturing scabrate in LM, microechinate in SEM, microechini at regular interval, microstriate to microrugulate pattern radiating from base of echini (SEM).

Remarks. — The subfamily Juglandoideae includes five well-defined extant genera that are supported by both molecular and morphological data: *Carya* (incl. *Annamocarya*), *Juglans* and *Pterocarya*; and the monotypic *Cyclocarya* and *Platycarya* (e.g. Manchester 1987b; Manos & Stone 2001; Manos et al. 2007; Zhang et al. 2013). Pollen morphology (LM and SEM) and ultrastructure (TEM) of *Carya* has been presented in detail by Stone and Broome (1975). Pollen of various extant *Carya* species has also been studied (LM, SEM, rarely TEM) by Stone (1963), Whitehead (1963, 1965), Stone et al. (1964), Lieux (1980), Liu (1987), Jones et al. (1995), Wang et al. (1995), Fritz and Allesch (1999), Beug (2004), Li et al. (2011a) and Miyoshi et al. (2011). Fossil pollen showing LM-based morphological affinities to pollen of modern *Carya* have commonly been assigned to the pollen form-genus *Caryapollenites* (e.g. Krutzsch 1961; Stuchlik et al. 2009).

Fossil record. — *Carya* has a fairly rich fossil record in the Cainozoic of the Northern Hemisphere composed of fruits, leaves, wood, catkins and *in situ* and dispersed pollen (see table 5 in Manchester 1987b). *Carya*-like pollen is known from several localities from the late Paleocene of North America and Europe (e.g. Muller 1981; Manchester 1987b, 1989b; Zetter et al. 2011). It has been pointed out that these pollen grains are smaller than pollen of extant *Carya* and evidence from the fruit record also indicates that the modern *Carya* had not yet diverged. Fossil pollen comparable to pollen of extant *Carya*, in both size and morphology, is first known from the Eocene and/or Oligocene of North America, Europe and western Siberia, and from the middle Miocene of eastern Asia. The pollen record further suggests that *Carya* thrived in Europe until the late Pleistocene (e.g. Muller 1981; Manchester 1987b, 1989b).

The fossil record of *Carya* fruits has been summarised and revised by Mai (1981a) and Manchester (1987b). These studies acknowledge 14 species from the late Eocene to late Pliocene of Europe, two species from the Oligocene and Miocene of western Siberia, one from the Miocene of China, four from the Miocene and Pliocene of Japan, and two species from the early Oligocene and Miocene of the Unites

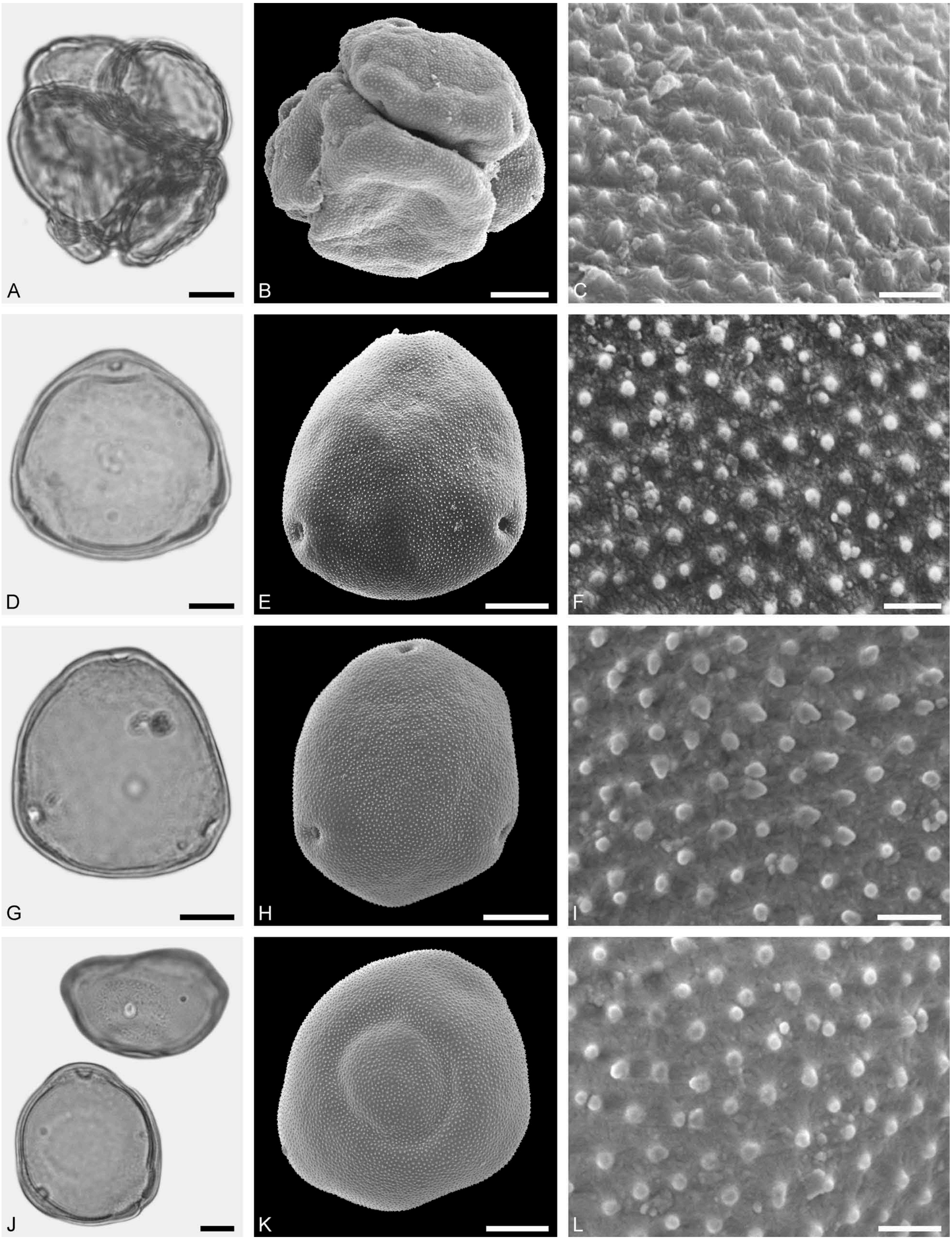


Figure 12. LM (**A, D, G, J**) and SEM (**B, C, E, F, H, I, K, L**) micrographs of dispersed fossil Juglandaceae pollen. **A–L.** *Carya* sp., pollen in tetrad (**A**), single grains (**D, G, J**), close-ups of polar area. Scale bars - 10 µm (A, B, D, E, G, H, J, K), 1 µm (C, F, I, L).

States (Mai 1981a; Manchester 1987b). *Carya* catkins/inflorescences (*C. florissantensis* Manchester) with *in situ Carya*-type pollen have been described from the early Oligocene of Colorado, USA (Manchester 1987b). Fossil wood affiliated with *Carya* is rare, but has been documented from the late Cainozoic of Europe and Japan. These include *Eucaryoxylon crystallophorum* W. R. Müller-Stoll et E. Mädel from the Miocene of Hungary (Müller-Stoll & Mädel 1960), *E. moenanum* W. R. Müller-Stoll et E. Mädel-Angeliewa from the late Pliocene of Germany (Müller-Stoll & Mädel-Angeliewa 1983) and *C. protojaponica* Watari from the Miocene of Japan (Watari 1952). There are numerous findings of fossil *Carya* leaves/leaflets from the Cainozoic of North America and Eurasia, but *Carya* leaves are hard to identify with certainty because of the overlap with leaves/leaflets of *Cyclocarya, Juglans* and *Pterocarya*. In his monograph on fossil Juglandaceae, Manchester (1987b) does not revise the leaf record of *Carya* or *Carya*-like fossils, but names five species based on leaf material, which he considered representing extant *Carya*. These include *C. sessilis* MacGinite from the Eocene of California (USA; MacGinite 1941), *C. cashmanensis* Wolfe and *C. pugetensis* Wolfe from the Eocene of Washington (USA; Wolfe 1968), *C. libbeyi* (Lesq.) MacGinite from the early Oligocene of Colorado (Unites States; MacGinite 1953) and *C. serraefolia* (Göpp.) Kräusel from the late Oligocene and Miocene of the Czech Republic (Europe; Knobloch 1961; Bůžek 1971). Fossil *Carya* leaves/leaflets have also been described from East Asia (e.g. Tanai 1992). It has been hypothesised that *Carya* originated in North America during the early Paleocene and dispersed into Europe during late Paleocene or early Eocene time over the North Atlantic Land Bridge and probably dispersed further into Asia following the closure of the Turgai Seaway in the early Oligocene (Zhang et al. 2013). The two major clades within *Carya*, corresponding to the extant lineages of eastern Asia and eastern North America, are thought to have split latest in the Miocene (Zhang et al. 2013).

Ecological implications. — *Carya* is composed of *c.* 15 tree species showing a disjunct distribution in subtropical to mild temperate areas of eastern North America (11 native species; Stone 1997) and eastern Asia (four native species; Lu et al. 1999). *Carya* is considered a monophyletic genus composing two well supported clades that correspond to the eastern Asian group and the eastern North American group (e.g. Zhang et al. 2013). The species ranging in habitat from temperate mixed mesophytic forests to mountain rain forests (Stone 1997; Lu et al. 1999). The climatic and ecological niche of East Asian and North American *Carya* is relatively equivalent, the distribution focus lies in the subtropical, warm temperate climates with hot summers with sufficient precipitation during growing season (*Cfa, Cwa*), and most species thriving close to water bodies and floodplains (Stone 1997; Lu et al. 1999). Most species can be categorised as meridio-nemoral elements (File S1). In the Lavanttal, *Carya* may have thrived in a habitat similar to its modern representatives in the south-eastern quarter of the United States, as part of thermophilic wetland forest.

Genus Juglans *L.*

Juglans *sp.*
(Figure 13A–L)

Description. — Pollen, monad, oblate, heteropolar, outline circular to polygonal in polar and equatorial view; polar axis 30–35 µm long in LM, equatorial diameter 36–43 µm wide in LM, 33–40 µm wide in SEM; stephanoporate (10–12), often 1–3 pori positioned outside the equator on the distal polar side, pori annulate; exine 1.0–1.3 µm thick, nexine thinner than sexine; tectate; sculpturing scabrate in LM, microechinate in SEM, microechini numerous and at regular interval, microstriate to microrugulate pattern circling the base of echini (SEM).

Remarks. — The LM and SEM based pollen morphology of many *Juglans* species has been investigated by Stone et al. (1964), Whitehead (1965), Ueno (1967), Huang (1972), Stone and Broome (1975), Lieux (1980), Jones et al. (1995), Fritz and Allesch (1999), Wei (2003), Beug (2004), Mert (2010), Li et al. (2011a) and Miyoshi et al. (2011). The pollen ultrastructure (TEM) of *Juglans* has been presented by Stone et al. (1964), and Stone and Broome (1975). Fossil pollen showing LM-based morphological affinities to pollen of modern *Juglans* have commonly been assigned to the pollen form-genus *Juglanspollenites* (e.g. Raatz 1937; Stuchlik et al. 2009).

Fossil record. — *Juglans* has a rich fossil record in the Cainozoic of the Northern Hemisphere composed mostly of fruits and dispersed pollen, but also leaves (see partly table 6 in Manchester 1987b). The LM-based pollen record of the genus has been summarised by Muller (1981) and Manchester (1987b, 1989b). The earliest pollen records of *Juglans* are from the Eocene of North America, but pollen of this genus first became widespread in North America and Eurasia during the Oligocene and Miocene. The fossil fruit record of *Juglans* is extensive with numerous North American and Eurasian records extending back to the Eocene.

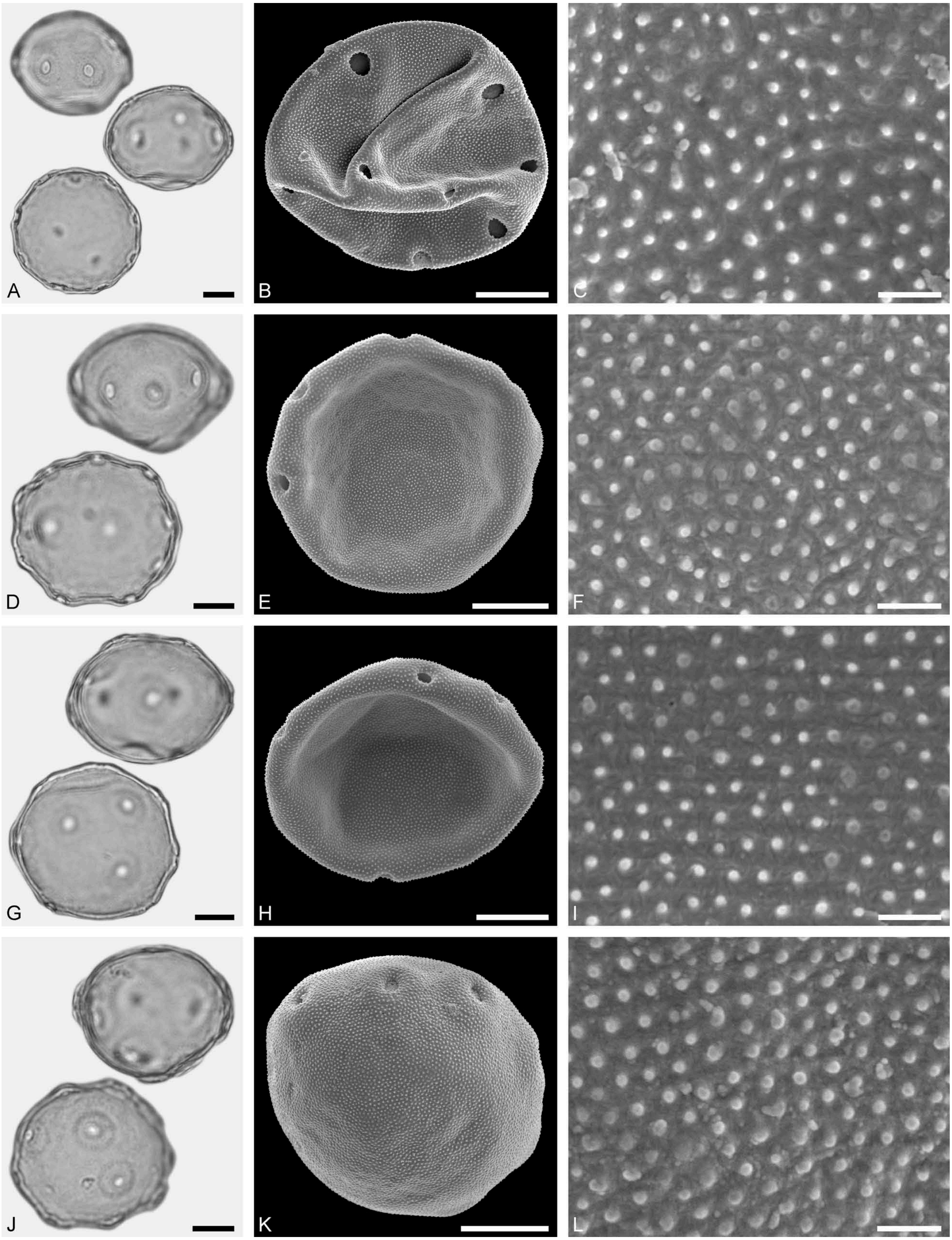


Figure 13. LM (**A, D, G, J**) and SEM (**B, C, E, F, H, I, K, L**) micrographs of dispersed fossil Juglandaceae pollen. **A–L.** *Juglans* sp., pollen with varying number of pori (**A, D, G, J**), close-ups of distal polar area (**C, L**), and proximal polar area (**F, I**). Scale bars – 10 μm (A, B, D, E, G, H, J, K), 1 μm (C, F, I, L).

Juglans fruits of sect. *Rhysocaryon* (black walnuts) include among others *J. clarnensis* Scott from the middle Eocene of Oregon (north-western United States), *J. calvertiana* Berry from the Miocene of Maryland and Virginia (north-eastern United States), *J. nevadensis* Berry from the Miocene of Nevada (south-western United States), *J. siouxensis* (Barbour) Berry from the Miocene of Nebraska (mid-western United States) and *J. linkii* Brown from the late Miocene/early Pliocene of north-western Ecuador that is the only megafossil of *Juglans* recorded from South America (Manchester 1987b). *Juglans* fruits of section *Cardiocaryon* (butternuts) include among others *J. lacunosa* Manchester from the early to middle Oligocene of Washington, *J. tephrodes* Unger from the middle/late Oligocene to Pliocene of Europe, *J. megacinerea* Miki ex Chaney from the Miocene to Pleistocene of Japan, *J. siberica* P.I.Dorof. from the Miocene western Siberia, *J. eocinerea* L.V.Hills, Klovan et A.R.Sweet from the Miocene of Banks Island in Arctic Canada (e.g. Kirchheimer 1957; Hills et al. 1974; Nirei 1975; Manchester 1987b).

There are many reports of fossil *Juglans* leaves/leaflets from the Cainozoic of North America and Eurasia, but *Juglans* leaves are hard to identify with certainty because of overlap with leaves/leaflets of *Carya, Cyclocarya* and *Pterocarya*. According to Manchester (1987b), the leaf/leaflet record of *Juglans* needs to be revised.

Ecological implications. — *Juglans* is the largest genus within the Juglandaceae, composed of *c.* 21 species, occurring in eastern and western North America, Central America, the West Indies and western South America, across Asia and south-eastern Europe (Manning 1978; Stanford et al. 2000). The genus is divided into four sections. Section *Cardiocaryon* includes three species, *J. mandshurica* Maxim., occurring in China, Taiwan and Korea; *J. sigillata* Dode, occurring in China and Korea; and *J. ailantifolia* Carrière, occurring in Japan. Section *Dioscaryon* includes only a single species, *J. regia* L., ranging from south-eastern Europe over to Iran and the Himalayas and into China. Section *Rhysocaryon* includes 16 species, all occurring in the Americas and the West Indies. Section *Trachycaryon* has only a single species, *J. cinerea* L., occurring in the eastern United States.

The genus shows a wide range of habitats, occurring in various different forest types, thriving in temperate to tropical climates (e.g. Manning 1978; Stone 1997; Lu et al. 1999; Stanford et al. 2000). Species of *Juglans* can be addressed as semihumid-meridional, meridio-nemoral or nemoral elements (File S1). The plants producing *Juglans* pollen could have been part of various lowland to mid-altitude habitats at Lavanttal, but are overall indicative of a climate characterised by a pronounced summer.

Genus Pterocarya *Kunth.*

Pterocarya *sp.*
(Figure 14A–L)

Description. — Pollen, monad, oblate, sometimes heteropolar, outline polygonal in polar view, elliptic in equatorial view; polar axis 18–31 µm long in LM, equatorial diameter 29–43 µm wide in LM, 27–39 µm wide in SEM; stephanoporate (5–8); sometimes one pori positioned outside the equator on the distal polar side, pori annulate; exine 0.9–1.3 µm thick, nexine thinner than sexine; tectate; sculpturing scabrate in LM, microechinate in SEM, microechini at regular interval, microstriate to microrugulate pattern radiating from base of echini, pattern inconspicuous (SEM).

Remarks. — pollen has been studied and figured using LM, SEM and TEM by Stone and Broome (1975). Several other researchers have also investigated and figured LM and SEM based micrographs showing *Pterocarya* pollen from different extant species, e.g. Whitehead (1965), Liu (1987), Wang et al. (1995), Fritz and Allesch (1999), Beug (2004), Li et al. (2011a) and Miyoshi et al. (2011). Fossil pollen showing LM-based morphological affinities to pollen of modern *Pterocarya* hase commonly been assigned to the pollen form-genus *Polyatriopollenites* (e.g. Pflug 1953; Stuchlik et al. 2009).

Fossil record. — The macrofossil record of *Pterocarya* has been summarised by Kirchheimer (1957) and Manchester (1987b). The LM-based palynological record of *Pterocarya* and *Pterocarya*-like pollen has been summarised by Muller (1981) and Manchester (1987b, 1989b). *Pterocarya*-like pollen has been documented from the uppermost Cretaceous of Russia and North America, but as pointed out by Manchester (1987b, 1989b), these grains are much smaller than pollen of extant *Pterocarya* and have only been studied using LM; all these records are considered doubtful and need further validation. The first *Pterocarya*-like pollen grains corresponding to pollen of extant *Pterocarya* are from the Paleocene of the Russian Far East and the United States; the oldest European record is from early Eocene. By the late Eocene, *Pterocarya* pollen are documented from most areas of the Northern Hemisphere, but come much more abundant in the Oligocene and Miocene (e.g. Muller 1981; Manchester 1987b).

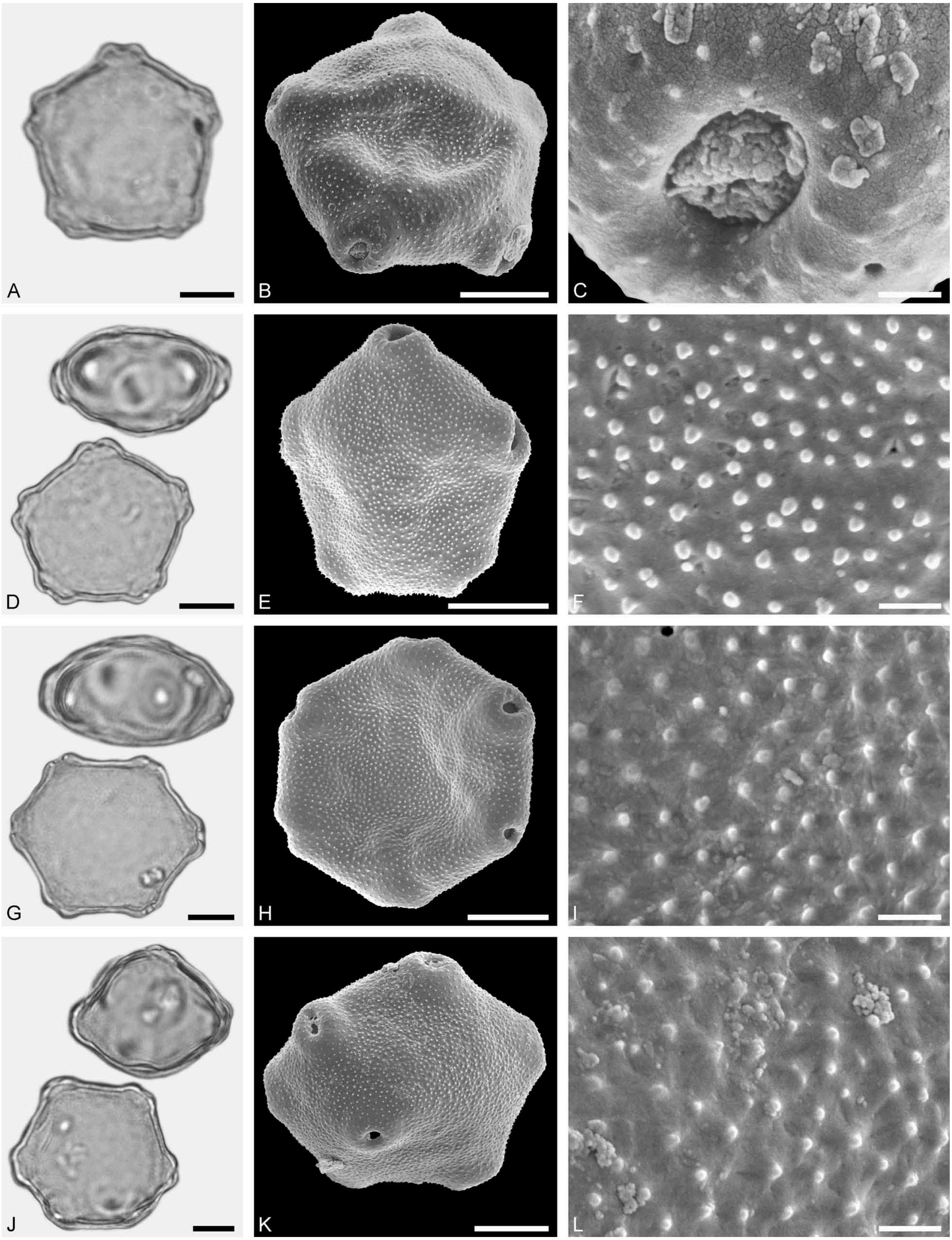


Figure 14. LM (**A, D, G, J**) and SEM (**B, C, E, F, H, I, K, L**) micrographs of dispersed fossil Juglandaceae pollen. **A–L.** *Pterocarya* sp., pollen with varying number of pori (**A, D, G, J**), close-ups of aperture membrane (**C**), distal polar area (**E, L**), and proximal polar area (**J**). Scale bars – 10 µm (A, B, D, E, G, H, J, K), 1 µm (C, F, I, L).

Pterocarya fruits are well-documented from the Cainozoic of the Northern Hemisphere, with the earliest fruit, *P. macginitti* Manchester et Dilcher, occurring in the middle Eocene of Wyoming, USA (Manchester & Dilcher 1982). Additional North American species based on fruits include *P. occidentalis* Manchester from the Oligocene of California (western United States), *P. eomacroptera* Manchester and *P. smiley* Manchester from the Miocene of Idaho (north-western United States; Manchester 1987b). The European record of *Pterocarya* fruits has been summarised by Kirchheimer (1957), suggesting that several species were present during the late Cainozoic in this part of the world. *Pterocarya* fruits have also been described from the Miocene of Iceland (Denk et al. 2011). According to Manchester (1987b), the European *Pterocarya* fruit record needs to be revised. Various different *Pterocarya* fruits have also been described from the Oligocene and Miocene of Asia (e.g. Manchester 1987b). The earliest *Pterocarya* fruits are from the middle Eocene of North America and during the Oligocene the genus dispersed across North America, Europe and Asia, as documented by fossil fruits, dispersed pollen and leaves. During the Miocene it had a wide distribution across most of the Northern Hemisphere.

Ecological implications. — *Pterocarya* is a small genus composing only six species of deciduous trees, five are native to East Asia and one occurs mainly in the Caucasus region (e.g. Manning 1978; Lu et al. 1999; Denk et al. 2001). The five East Asian species, *P. hupehensis* Skan, *P. macroptera* Batalin, *P. rhoifolia* Siebold et Zucc., *P. stenoptera* C.DC., *P. tonkinensis* Dode, distributed in China, Korea and Japan, occur mostly in moist forests, in lowlands, valleys or on mountain slopes. They often grow along riverbanks or streams and, depending on the species and the geographical region, ranging from sea level to an altitude of 3500 m (Lu et al. 1999). *Pterocarya fraxinifolia* (Poir.) Spach has a restricted distribution confined to the Caucasus region and Asia Minor, occurring mostly in the Hyrcanian mixed forests along the seashores of the Black and Caspian Seas at an altitude below 1000 m. Typically found in lowland riparian forests and on mountain slopes in rich mixed broadleaved deciduous forests, it occurs also at an altitude up to 1700 m in the Zagros Mountains of Iran (e.g. Akhani & Salimian 2003; Sheykholislami & Ahmadi 2009). Most East Asian species of the genus have also a (very) restricted distribution. The two species with non-restricted distributions (*P. rhoifolia, P. stenoptera*) are nemoral elements (File S1). Based on the modern habitat of *Pterocarya*, it is likely that the fossil *Pterocarya* pollen from the Lavanttal Basin originate from trees growing in and around the lowland or the surrounding hillsides and mountain slopes, especially along the banks of streams and rivers running into the basin.

Family Myricaceae A.Rich. ex Kunth

*Myricaceae gen. et spec. indet. (*Morella *vel* Myrica) (Figure 15A–F)

Description. — Pollen, monad, oblate, outline convex triangular in polar view, elliptic in equatorial view; polar axis 19–21 µm long in LM, equatorial diameter 22–24 µm wide in LM, 20–23 µm wide in SEM; triporate, exine protruding in areas of apertures; exine 0.9–1.0 µm thick (LM), nexine thinner than sexine; tectate; sculpturing scabrate in LM, microechinate, perforate in SEM, numerous perforations in-between microechini.

Remarks. — Pollen morphology (LM and SEM) and ultrastructure (TEM) of all four Myricaceae genera have been studied by Sundberg (1985). Numerous other pollen studies include LM and SEM documentation of all *Myrica* and most *Morella* species (e.g. Huang 1972; Lieux 1980; Jones et al. 1995; Wang et al. 1995; Fritz & Allesch 1999; Punt et al. 2002; Beug 2004; Fujiki et al. 2005; Fujiki & Ozawa 2007; Li et al. 2011a; Miyoshi et al. 2011). Based on these studies, the distinctive feature of Myricaceae pollen is the so-called '*Myrica*' type aperture. In the vicinity of the pores, the nexine is lacking and the sexine is thickened forming an annulus (Sundberg 1985). Pollen in Myricaceae is rather homogeneous and only the pollen of *Canacomyrica* and *Comptonia* are distinctive (Sundberg 1985). Pollen of the two extant *Myrica* species and the *c.* 47 *Morella* species overlap both in LM morphology and SEM sculpturing and cannot be set apart. The fossil Myricaceae type pollen from Lavanttal could therefore originate from plants belonging to *Myrica* or *Morella*.

Fossil pollen showing LM-based morphological affinities to pollen of modern *Morella* and *Myrica* has commonly been assigned to the pollen form-genus *Myricipites* -(e.g. Wodehouse 1933; Stuchlik et al. 2009).

Fossil record. — Myricaceae comprise four genera, the monotypic *Comptonia* and *Canacomyrica*, the small *Myrica* (two species) and *Morella* with *c.* 47 species (e.g. Wilbur 1994; Huguet et al. 2005; Herbert 2005a, 2005b; Herbert et al. 2006). With the exception of *Comptonia* and *Canacomyrica*, most Myricaceae species have traditionally been assigned to *Myrica*. Pollen affiliated to Myricaceae has been documented from the Late Cretaceous of North

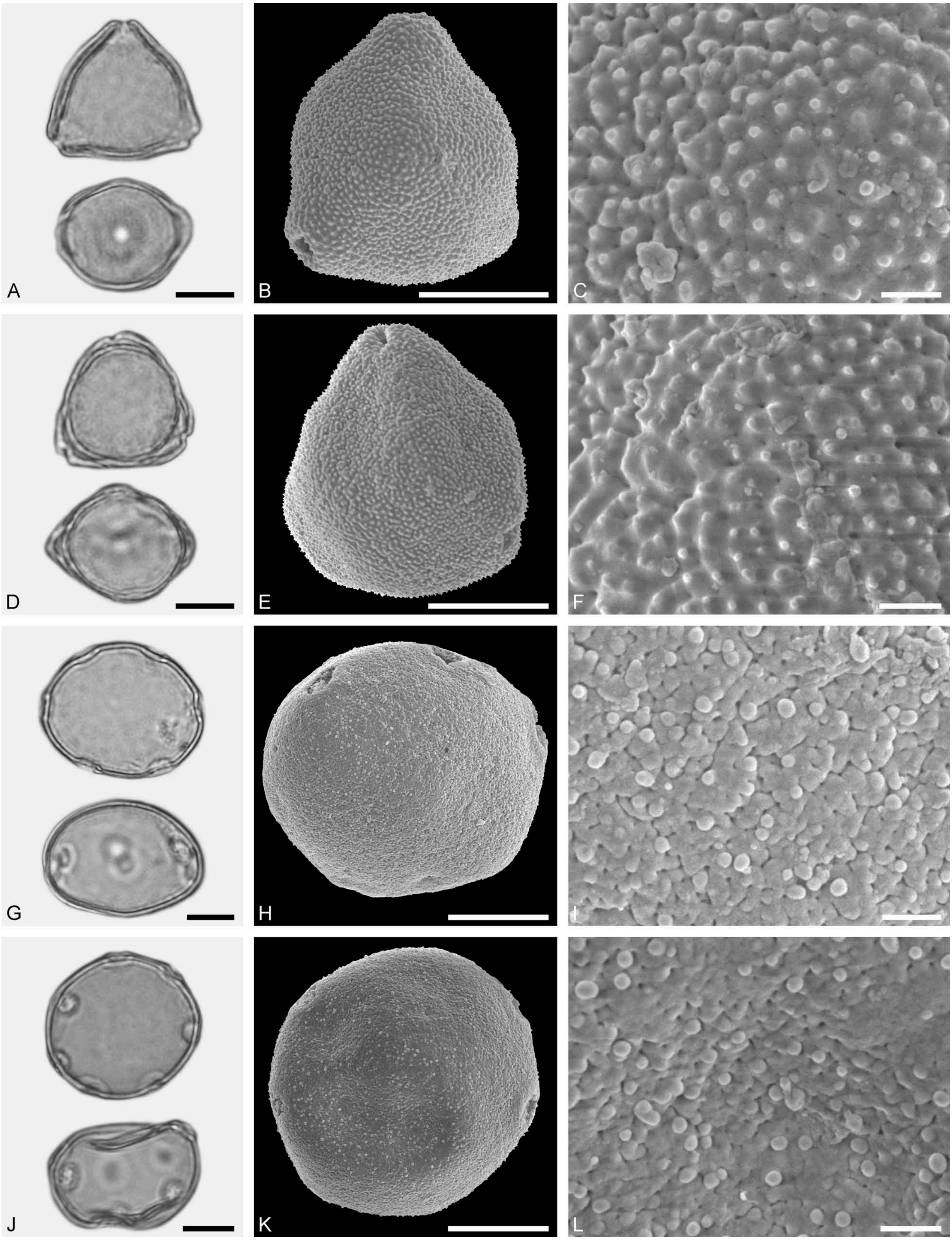


Figure 15. LM (**A, D, G, J**) and SEM (**B, C, E, F, H, I, K, L**) micrographs of dispersed fossil Myricaceae and Cannabaceae pollen. **A–F.** Myricaceae gen. et spec. indet. (*Morella* vel *Myrica*), close-ups of polar area. **G–L.** *Celtis* sp. 1, close-ups of polar area. Scale bars – 10 μm (A, B, D, E, G, H, J, K), 1 μm (C, F, I, L).

America and the Paleocene of Eurasia, becoming more abundant during the Eocene and Oligocene of Europe. This type of pollen is also very frequent in Miocene sediments of Europe (e.g. Muller 1981). The nomenclatural problems associated with *Myrica* versus *Morella* (see later) have resulted in a confusing fossil record of the two genera. Even though leaves of *Myrica* (sunken stomata) can be distinguished from those of *Morella*, and the structure of their fruits are also distinguishable, most authors have assigned *Morella* fossils to *Myrica* (see Herbert 2005b). According to Mai (1995), *Myrica* (*s.l.*, incl. *Morella*) has an Eocene to Miocene fossil record in Europe. For an accurate circumscription of the fossil record of these two genera previous documentations including leaf fossils and carpological fossils needs to be revised.

Ecological implications. — There are clear differences between the two deciduous species, the cold-tolerant *Myrica gale* L. found in warm temperate and snow climates with warm and cold summers (*Cfb-*, *Cfc-*, *Dfb-*, *Dfc*-climates) and the summer-draught tolerant, temperate *Myrica hartwegii* S.Watson (mostly *Csb*-climates), and the remaining predominately subtropical to tropical – thriving in the equatorial *A*-climates and warm temperate *Cfa-*, *Cwa-*, *Csa*-climates – evergreen species that are now all included in the genus *Morella* (cf. Huguet et al. 2005; Herbert 2005a, 2005b). The two *Myrica* species are deciduous shrubs with dry fruits adapted for dispersal by water. *Myrica hartwegii* is endemic to the northern and central Sierra Nevada of California, where it occurs along the borders of streams at elevation of 250 to 1800 m (Bornstein 1997). *Myrica gale* is widespread and has an almost circum-boreal distribution. Depending on the geographical region, it extends from sea level to *c.* 700 m a.s. l. It is a lowland wetland plant occurring along streams and lake margins, in ponds and bogs, wet heaths and fens, in marshes and sea lochs, and it is abundant in swampy environments (e.g. Bornstein 1997; Skene et al. 2000).

Morella comprises evergreen shrubs and small trees producing papillose fleshy fruits that are dispersed mostly by birds (Herbert 2005b). The shrubs or small trees are found in many habitats growing from sea level to *c.* 3000 m a.s.l., occurring in lowland valley forests as well as mountain slope forests. The plants are part of various different forest types, occurring in mixed evergreen conifer and broad-leaved forests, mixed deciduous-evergreen broad-leaved forests and evergreen broad-leaved forests (e.g. Bornstein 1997; Lu & Bornstein 1999). Most of the *Morella* species are, however, growing in wetland habitats, thriving near streams and rivers, in coastal swamps and marshes, around lakes margins, in bogs and around ponds or in wet meadows.

The two species of *Myrica* could be addressed as boreal and semihumid-meridional elements (File S1), whereas species of *Morella* could be categorised as tropical-meridional, semihumid-meridional, meridio-nemoral, or nemoral. Nevertheless, both *Myrica* and *Morella* require wetland habitats or sufficient inflow of water through their substrate; hence a similar habitat is suggested for the plants producing the fossil pollen from Lavanttal.

Order Rosales Bercht. et J.Presl
Family Cannabaceae Martynov

Genus Celtis *L.*

Celtis *sp. 1*
(Figure 15G–L)

Description. — Pollen, monad, spheroidal to oblate, outline circular to elliptic in polar view, elliptic in equatorial view; polar axis 21–25 μm long in LM, equatorial diameter 30–35 μm wide in LM, 27–30 μm wide in SEM; stephanoporate (5–9), pori sometimes subequatorially positioned, circular to elliptic, sexine slightly thickened around pori; exine 0.9–1.1 μm thick (LM), nexine thinner than sexine; tectate; sculpturing psilate in LM, microrugulate, perforate, fossulate, microechinate in SEM, microechini irregularly distributed, apex of microechini blunt, pori membrane microrugulate, microechinate (SEM).

Remarks. — The pollen morphology and ultrastructure of Cannabaceae has been studied in detail by Zavada (1983) and Takahashi (1989). *Celtis* pollen from numerous North American, European, African and Asian species have been investigated and figured using both LM and SEM, and sometimes TEM, by Huang (1972), Zavada (1983), Zavada and Dilcher (1986), Takahashi (1989), Lieux (1980), Jones et al. (1995), Stafford (1995), Beug (2004), Sattarian et al. (2006), Zarafshar et al. (2010), Li et al. (2011a) and Miyoshi et al. (2011). Fossil pollen showing LM-based morphological affinities to pollen of modern *Celtis* have commonly been assigned to the pollen form-genus *Celtipollenites* (Nagy 1969; Stuchlik et al. 2009).

Fossil record. — The macrofossils record of *Celtis* dates back to the Paleocene of the Americas and East Asia with leaves and fruits of *C. aspera* (Newb.) Manchester, Akhmetiev et Kodrul, early Paleocene of western North America, eastern China and the Russian Far East, and endocarps from the late Paleocene of Brazil. Earliest macrofossil records in Europe are from the Eocene (see Manchester et al. 2002). The genus becomes a relatively common element of fossil assemblages (leaves, endocarps, flowers) in the Miocene of Europe (e.g. in Austria, Meller 1998, 2011; Kovar-Eder et al. 2004; Gross et al. 2014). Since the endocarps of *Celtis* have a high content of biogenic carbonate (e.g. Wang et al. 1997), they have a high preservation potential and can be found in vertebrate-bearing sediments lacking other plant remains (e.g. Gregor 1986). Fossil records from Africa are rare but endocarps have been reported from the Miocene of Kenya (Chesters 1957) and Pliocene hominid sites (Bonnefille 2010).

Ecological implications. — *Celtis* is widely distributed in tropical and temperate regions of the Northern and Southern Hemisphere and comprises *c.* 60 species (Sherman-Broyles et al. 1997; Fu et al. 2003). The six North American species can be divided into two ecological groups. The eastern North American *C. laevigata* Willd., *C. occidentalis* L. and *C. tenuifolia* Nutt. occur along streams, in flood plains, forested hillsides and woodlands at low elevations, essentially in warm temperate, fully humid climates with hot summers (*Cfa*). *Celtis lindheimeri* Engelm. ex K. Koch, *C. pallida* Torr. (ranging from southernmost United States to northern Argentina) and *C. reticulata* Torr. occur in warm semi-dry to desert conditions, in canyons, on mesas, along washes, in brushland and grassland, often preferring hard, rocky substrate, occurring at altitudes of up to 2300 m (Sherman-Broyles et al. 1997). The four western Eurasian species are found in the meridional zone (see Schroeder 1998), the two widespread species *C. australis* L. and *C. occidentalis* L. in both dry and humid habitats (e.g. Meusel et al. 1965; Browics & Zieliński 1982). The 11 species of *Celtis* occurring in China are typically found in tropical monsoon rain forests (and extending into south Asia, southeast Asia and Australasia) and subtropical and mixed mesophytic forests from sea level up to 2400 m (Fu et al. 2003). In Africa, *Celtis* is part of several semi-humid to humid vegetation types such as the tropical and subtropical broad-leaved forests of eastern Guinea, Nigeria and Cameroon and the semi-deciduous forests of central and western Africa (e.g. Fayolle et al. 2014; Miller & Gosling 2014).

Most northern hemispheric species of *Celtis* can be categorised as meridio-nemoral or nemoral elements, three as tropical-meridional or tropical, and two as eurytropical (restricted to dry climates). In the light of the Fagales diversity, it can be assumed that the *Celtis* pollen found in the Lavanttal Basin originate from trees with similar habitat preferences as the modern eastern North American and East Asian species, thriving in the lowland wetlands and surrounding hillside mixed broad-leaved deciduous and evergreen forests.

Celtis *sp. 2*
(Figure 16A–C)

Description. — Pollen, monad, spheroidal to oblate, outline circular to elliptic in polar view, elliptic in equatorial view; polar axis 21–23 µm long in LM, equatorial diameter 22–24 µm wide in LM, 20–22 µm wide in SEM; triporate, pori circular, sexine slightly thickened around pori; exine 0.9–1.1 µm thick (LM), nexine thinner than sexine; tectate; sculpturing psilate in LM, microechinate, perforate in SEM, microechini irregularly distributed, pori membrane microechinate (SEM).

Remarks. — The main difference between *Celtis* sp. 1 and *Celtis* sp. 2 is that the former is characterised by 5–9 pori that are sometimes at irregular intervals, but *Celtis* sp. 2 is triporate. The sculpturing (SEM) in *Celtis* sp. 1 is characterised by numerous perforations and fossulae, but these are only rarely occurring in *Celtis* sp. 2.

Cannabaceae gen. et spec. indet.
(Figure 16D–F)

Description. — Pollen, monad, spheroidal to oblate, outline elliptic in polar and equatorial views; polar axis 21–23 µm long in LM, equatorial diameter 23–25 µm wide in LM, 22–24 µm wide in SEM; diporate, pori circular, sexine thickened around pori, pori annulate; exine 0.8–0.9 µm thick (LM), nexine thinner than sexine; tectate; sculpturing psilate in LM, microechinate, granulate, perforate in SEM, microechini irregularly distributed (SEM).

Remarks. — Since we cannot affiliate this pollen type with any particular genus in the Cannabaceae, we refrain from drawing any further interpretation based on this pollen type.

Family Elaeagnaceae Juss.

Genus Elaeagnus *L.*

Elaeagnus *sp.*
(Figure 16G–L)

Description. — Pollen, monad, oblate, heteropolar, outline triangular in polar view, elliptic in equatorial view; equatorial diameter 27–52 µm wide in LM, 26–47 µm wide in SEM; tricolporate, colpi short, widening towards distal ends; exine 1.2–2.4 thick (LM), nexine thinner than sexine, sexine protruding

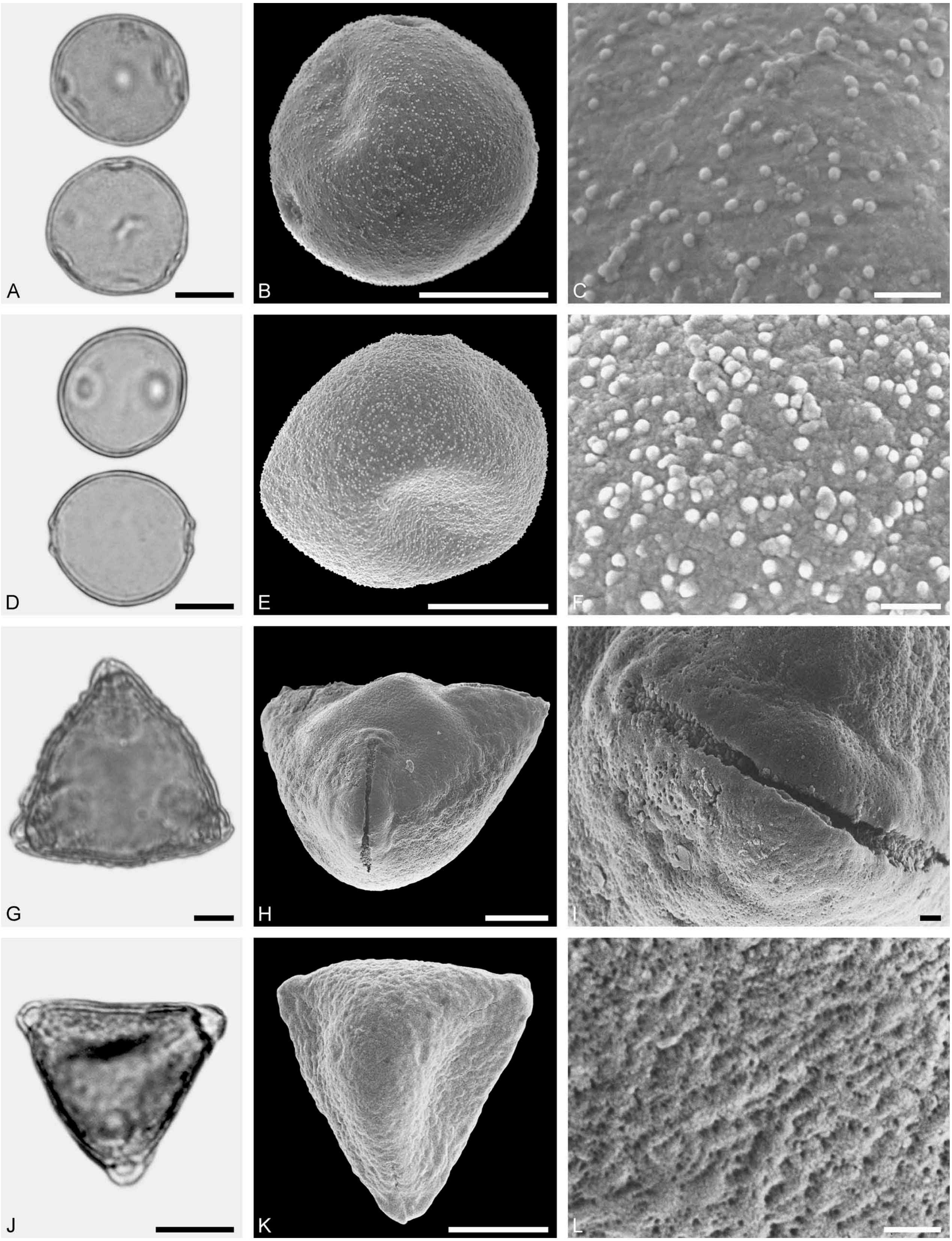


Figure 16. LM (**A, D, G, J**) and SEM (**B, C, E, F, H, I, K, L**) micrographs of dispersed fossil Cannabaceae and Elaeagnaceae pollen. **A–C.** *Celtis* sp. 2, close-up of polar area. **D–F.** Cannabaceae gen. et spec. indet., close-up of polar area. **G–L.** *Elaeagnus* sp., close-ups of area around colpus (**I**), and mesocolpium (**L**). Scale bars – 10 µm (A, B, D, E, G, H, J, K), 1 µm (C, F, I, L).

around pori forming an atrium, area around colpi also protruding; tectate; sculpturing scabrate in LM, microrugulate, granulate, perforate in LM, colpus membrane microverrucate (SEM).

Remarks. — We were unable to find any comprehensive comparative palynological study of extant Elaeagnaceae/*Elaeagnus* species. Pollen from individual *Elaeagnus* species have been documented using LM and SEM by several authors (e.g. Huang 1972; Wang et al. 1995; Beug 2004; Fujiki & Ozawa 2007; Li et al. 2011a; Miyoshi et al. 2011). The fossil pollen grains from Lavanttal are comparable to extant pollen of *E. glabra* Thunb. as figured by Fujiki and Ozawa (2007) and Miyoshi et al. (2011). Fossil pollen showing LM-based morphological affinities to pollen of modern *Elaeagnus* have commonly been assigned to the pollen form-species *Slovakipollis elaeagnoides* Krutzsch (Krutzsch 1962; Stuchlik et al. 2014).

Fossil record. — The pollen and macrofossil record of Eleagnaceae/*Elaeagnus* was briefly mentioned by Friis et al. (2011) and recently summarised by Su et al. (2014). According to these authors, the Late Cretaceous and Paleogene pollen records of Elaeagnaceae and/or *Elaeagnus* are all uncertain and need to be studied in more detail. The only reliable macrofossil records of *Elaeagnus* are wood remains (*E. semiannulipora* Watari) from the early Miocene of Japan (Watari 1952), leaves (*E. tibetensis* T.Su et Z.K.Zhou) from the late Miocene of eastern Tibet (Su et al. 2014) and a flower (*E. orchidioides* [Straus] H.J.Gregor) from the Pliocene of Germany (Gregor & Mai 1984). In Europe, comparable *Elaeagnus*-type pollen grains have been reported from the Miocene of Poland (Stuchlik et al. 2014), Germany (Krutzsch 1962; Thiele-Pfeiffer 1980) and Austria (Zetter 1988).

Ecological implications. — *Elaeagnus* comprises *c.* 70–90 species of shrubs, sometimes climbing, or small trees, deciduous or evergreen, native to North America, Eurasia and north-eastern Australia. The dominant part of the species is native to the Qinghai-Tibet Plateau and surrounding regions (Qin & Gilbert 2007; Sun & Lin 2010; Su et al. 2014). In China, *Elaeagnus* thrives in various temperate to subtropical forest types. It can be found along streams and small rivers and lakes; it grows in open areas, in thickets and bushland, and in open woodlands as well as in dense forests. *Elaeagnus* is found in valley forests and on hills, forested mountain slopes and mountains, and it occurs at elevation ranging from sea level to *c.* 2800 m a.s.l. (Qin & Gilbert 2007; Sun & Lin 2010).

Most species of *Elaeagnus* can be categorised as meridio-nemoral or nemoral elements, few species are distinct in being restricted to seasonally (*Cwa*; semihumid-meridional: e.g. *E. conferta* Roxb., *E. gonyanthes* Benth.) or generally dry climates (*B*-climates; eurytropical elements; e.g. *E. angustifolia* L., *E. oxycarpa* Schltdl.; File S1). Because of the vast range of habitats of extant *Elaeagnus*, it is hard to pinpoint where the plants that produced the fossil pollen were growing during accumulation of the sediments. Based on the fossil pollen and their affiliation to *E. glabra* Thunb., it is possible that they originate from evergreen shrubs that were growing along highland and mountain streams within the dense mixed forests surrounding the lowland wetland basins.

Family Rhamnaceae Juss.

Rhamnaceae gen. et spec. indet.
(Figure 17A–C)

Description. — Pollen, monad, oblate, outline convex-triangular in polar view, elliptic in equatorial view; polar axis 17–18 µm long in LM, equatorial diameter 21–23 µm wide in LM, 17–18 µm wide in SEM; tricolporate, colpi conspicuous (deep, SEM), sexine protruding in area of colpi, margins of endopori thickened in corners where crossing colpi (LM); exine 1.3–1.4 µm thick (LM), nexine as thick as sexine; tectate; sculpturing reticulate in LM, microreticulate to reticulate in SEM, muri high and psilate, muri fused along colpi forming a margo, lumina varying in size and outline, often elongated (SEM).

Remarks. — The pollen morphology (LM and SEM) of Rhamnaceae has been presented among others by Zhang and Chen (1986, 1992), Schirarend and Köhler (1993), Schirarend (1996), Punt et al. (2003) and Perveen and Qaiser (2005). The general morphology of the Lavanttal pollen clearly fits this family (form, outline, arrangement of colpi/pori, thickenings, margo, etc.). The fossil pollen is mostly similar to pollen from extant species of *Paliurus, Ziziphus* and *Rhamnus*, but we are unable to affiliate this pollen type to a particular genus with any certainty based on the SEM sculpturing. Despite the apparent number of studies on pollen of extant Rhamnaceae, only a fraction of the *c.* 900 species have been published. More comparable material showing pollen of extant taxa is needed to reliably affiliate this pollen type with a particular extant genus. Fossil pollen showing LM-based morphological affinities to pollen of modern Rhamnaceae have commonly been assigned to the pollen form-genus *Rhamnaceaepollenites* (Thiele-Pfeiffer 1980; Stuchlik et al. 2014).

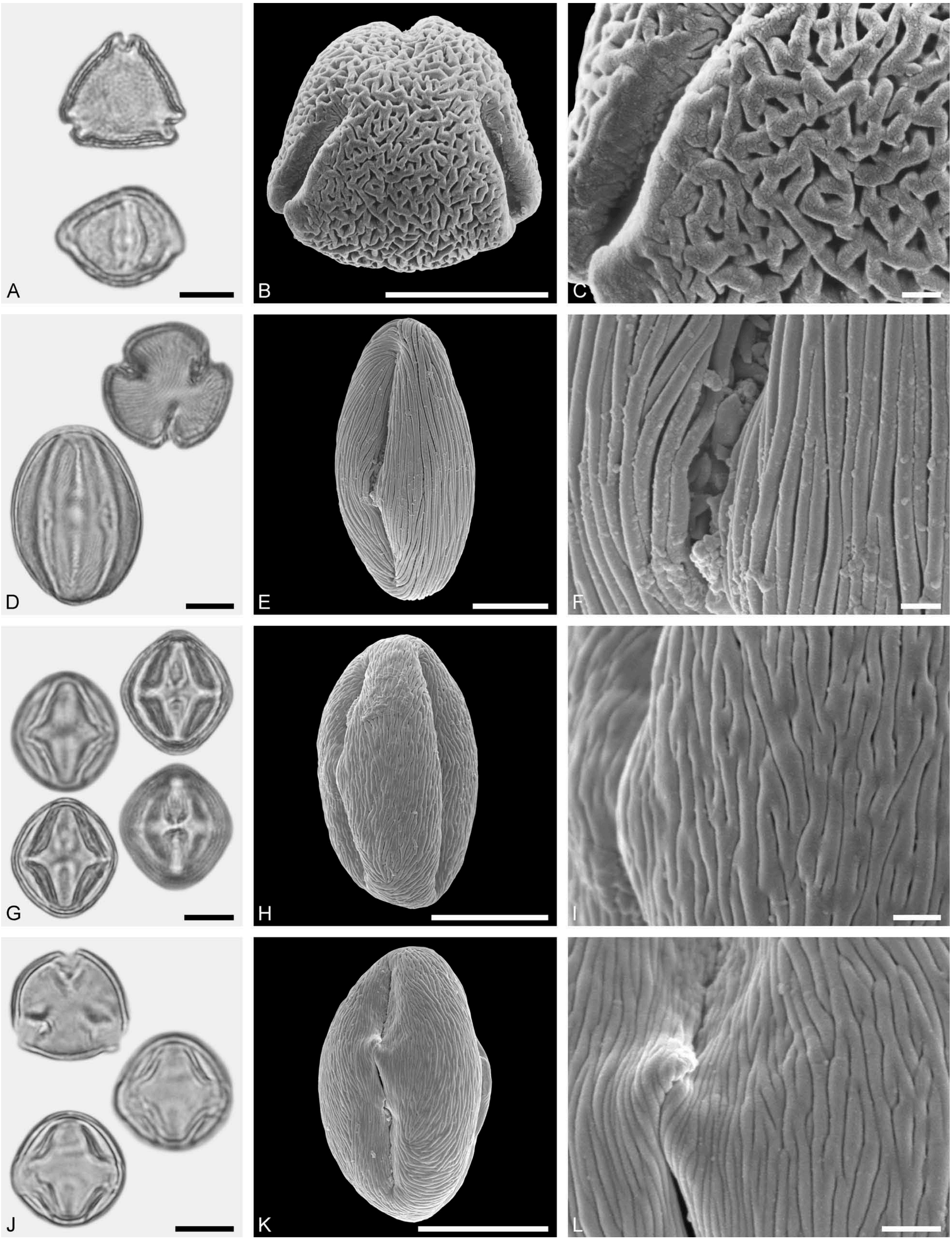


Figure 17. LM (**A, D, G, J**) and SEM (**B, C, E, F, H, I, K, L**) micrographs of dispersed fossil Rhamnaceae and Rosaceae pollen. **A–C.** Rhamnaceae gen. et spec. indet., close-up of area around colpus and mesocolpium. **D–F.** *Prunus* sp. 1, close-up of colpus membrane and area around colpus. **G–L.** *Prunus* sp. 2, close-ups of mesocolpium (**I**), and the sexine bridge arching over pori (**L**). Scale bars – 10 µm (A, B, D, E, G, H, J, K), 1 µm (C, F, I, L).

Fossil record. — The biogeographic history and fossil record of the family has been discussed by Richardson et al. (2000b, 2004), Burge and Manchester (2008; genus *Paliurus*) and Friis et al. (2011). Based on these authors, only a single reliable record dates back to the Late Cretaceous, a flower, *Coahuilanthus belinda* Calvillo-Canadell et Cevallos-Ferriz from Mexico (Calvillo-Canadell & Cevallos-Ferriz 2007). No reliable records of Rhamnaceae are known from the Paleocene. Various fossil *Paliurus* fruits occur from the middle Eocene to late Miocene in North America, the late Eocene to Pleistocene in Asia, and from the Oligocene to Pliocene in Europe (e.g. Burge & Manchester 2008). The fossil pollen record of Rhamnaceae was last summarised by Muller (1981), showing that pollen of this type occurs in Oligocene and younger sediments.

Ecological implications. — The Rhamnaceae are a moderately large family composed of 50 genera and *c.* 900 species of shrubs, trees, climbers and one herb. The family has a cosmopolitan distribution and is occurring mostly in warm temperate to tropical environments (Richardson et al. 2000a, 2000b; Chen & Schirarend 2007). Since we are unable to affiliate the fossil pollen with any certainty to a particular genus, we refrain from giving any detailed assumptions on the ecology/habit of the plant that produced this pollen. Based on the similarities of the fossil pollen to those of extant *Paliurus*, *Ziziphus* and *Rhamnus*, it is, however, likely that it represents an evergreen or deciduous shrub or small tree growing in the understory, or in marginal sheltered areas, possibly along small streams, in the dense mixed hillside forests surrounding the wetland basin.

Family Rosaceae Juss.

Genus Prunus *L.*

Prunus *sp. 1*
(Figure 17D–F)

Description. — Pollen, monad, prolate, outline lobate in polar view, elliptic in equatorial view; polar axis 37–38 µm long in LM, 38–39 µm long in SEM, equatorial diameter 27–28 µm wide in LM, 19–20 µm wide in SEM; tricolporate, colpi long, endopori circular, margin of endopori slightly thickened, endopori not wider than the width of colpi; exine 1.1–1.3 µm thick (LM), nexine thinner than sexine; tectate; sculpturing striate in LM and SEM, striae long, extending between polar areas, rarely dividing, striae 0.5–0.6 µm wide, sexine partly arching over pori forming a bridge, colpus membrane microechinate (SEM).

Remarks. — The Rosaceae include about 90 genera and *c.* 3000 species; recent phylogenetic studies recognise three subfamilies: Rosoideae, Dryadoideae and Spiraeoideae. The subfamily Spiraeoideae includes the tribe Amygdaleae, which comprises the genus *Prunus* (Potter et al. 2007). The basic pollen morphology of all three rosaceous subfamilies (see Potter et al. 2007) and many genera/species of the tribes and subtribes within Rosaceae have been studied to some extent. Pollen types of the subfamily Rosoideae have been studied using mostly LM and SEM by Huang (1972), Hebda et al. (1988a, 1988b), Hebda and Chinnappa (1990), Jones et al. (1995), Wang et al. (1995), Beug (2004), Tahir (2005), Fujiki and Ozawa (2007), Chung et al. (2010), Li et al. (2011a), Miyoshi et al. (2011), Wrońska-Pilarek (2011), Wrońska-Pilarek and Jagodziński (2011), Wrońska-Pilarek et al. (2012), Perveen and Qaiser (2014) and Faghir et al. (2015). The subfamily Dryadoideae has been studied by Hebda et al. (1988b) and Beug (2004). The pollen of the subfamily Spiraeoideae has been studied by Huang (1972), Hebda et al. (1988a, 1988b), Jones et al. (1995), Wang et al. (1995), Beug (2004), Bednorz et al. (2005), Dönmez (2008), Joneghani (2008), Sorkheh et al. (2008), Vafadar et al. (2010), Zamani et al. (2010), Li et al. (2011a), Miyoshi et al. (2011), Geraci et al. (2012), Ćalić et al. (2013), Shi et al. (2013) and Perveen and Qaiser (2014). Based on these studies, the Rosaceae pollen grains from Lavanttal can be affiliated with *Prunus*.

Rosaceae pollen grains are rarely correctly identified/affiliated in LM-based palaeopalynological studies. They have sometimes been misidentified as Cyrillaceae and/or Clethraceae, or simply overlooked. Some fossil pollen showing LM-based morphological affinities to pollen of modern Rosaceae has been assigned to different form-species under the pollen form-genus *Tricolporopollenites* (e.g. Thomson & Pflug 1953; Stuchlik et al. 2014).

Fossil record. — The Rosaceae have an extensive Cainozoic fossil record starting in the early Eocene composed of leaves, endocarps, fruits, wood, flowers and pollen (LM), that has been summarised by Kirchheimer (1973), Muller (1981), Mai (1984, 1995), Manchester (1999), Zhichen et al. (2004), DeVore and Pigg (2007), Friis et al. (2011), Benedict et al. (2011), Li et al. (2011a) and Liu et al. (2013). *Prunus* has been reported from the Eocene onwards of North America, Asia and Europe. In Asia, *Prunus wutuensis* Y.Li, Thierry Sm., Chang-Jiang Liu, N.Awasthi, Jian Yang, Yu-Fei Wang et Cheng-Sen Li endocarps have been documented from the early Eocene Wutu Formation of Wutu, Shandong Province, east China (Li et al. 2011b). *Prunus*-type of wood has been described from the Oligocene to Miocene of Japan (Suzuki 1984; Takahashi & Suzuki 1988) and several different *Prunus* endocarp types are known from the late Miocene to Pliocene of Japan (Miki 1936, 1938; Tanai & Onoe 1961). In North America, flowers, fruits and *in situ* pollen of *P. cathybrownae* J.C.Benedict, DeVore et Pigg have been described from the latest early Eocene (*c.* 49.4 Ma) Republic Flora of north-eastern Washington State (USA; Benedict et al. 2011). *Prunus*-type leaves are also frequent in the Republic Flora (DeVore & Pigg 2007). *Prunus* endocarps are known from the Eocene Princeton Chert of British Columbia (Canada; Cevallos-Ferriz & Stockey 1991) and the Clarno Nut Beds of Oregon (USA; *P. weinsteinii* Manchester, *P. olsonii* Manchester; Manchester 1994). *Prunus*-type of wood has been reported from the Princeton Chert, the Clarno Nut Beds and from the Eocene of Yellowstone National Park, Wyoming (USA; Wheeler et al. 1978; Cevallos-Ferriz & Stockey 1990; Wheeler & Manchester 2002). In Europe, fossil *Prunus* endocarps are frequent components of fruit and seed floras and are known from the Eocene onwards. At least 23 different *Prunus* species have been described based on endocarps from the Eocene to Pliocene fossil record of Europe (e.g. Kirchheimer 1973; Mai 1984, 1995). Fossil *Prunus*-type of pollen has been described using SEM from the middle Miocene of Iceland (Denk et al. 2011).

Ecological implications. — *Prunus* consists of *c.* 200 species growing mostly in the temperate parts of the Northern Hemisphere, but with many representatives in tropical and subtropical regions (e.g. Yü et al. 1986; Lee & Wen 2001; Gu & Bartholomew 2003; Mabberley 2008). Native *Prunus* shrubs and trees in China and East Asia thrive at elevations between 200–3800 m a.s.l. and occur in various temperate to subtropical and sometimes tropical forest types, including deciduous broad-leaved, evergreen broad-leaved, mixed deciduous and evergreen broad-leaved, and mixed broad-leaved conifer forests. They grow in sparse forests or at forests margins, in thickets and scrub vegetation and in dense forests, and are often found along stream sides in valleys or on gravely slopes in forested areas (Yü et al. 1986; Gu & Bartholomew 2003; Wen & Shi 2012). In North and Central America, the native, arborescent *P. serotina* Ehrh. is widely distributed within the Deciduous Forest Region of eastern United States and Canada, ranging south from Nova Scotia and New Brunswick to Florida, and west to the Lake Superior, Minnesota, South Dakota, eastern Nebraska, eastern Kansas, eastern Oklahoma and eastern Texas. It also has disjunct populations in Arizona and New Mexico as well as in Mexico and Guatemala (McVaugh 1951). Depending on the geographical region, *P. serotina* occurs from sea-level to mountain tops at elevations of *c.* 2000 m a.s.l. It grows in thickets, sparse woodlands, at forest margins and in dense forests, it is also growing on lowland floodplains, in canyons and along mountain sides and on high summits (McVaugh 1951).

Distribution data available for 12 species of *Prunus* reflect the climate variance of the genus, covering most subtypes of warm temperate and snow climates, and including species that can be categorised as generalist, meridio-nemoral, nemoral and boreal elements (File S1). Based on the habitat range of extant *Prunus*, the pollen from Lavanttal could have originated from trees/shrubs growing along streams in the lowland wetlands or on the floodplain. The *Prunus* plants could also have been part of the dense mixed forests surrounding the lowland and reaching into the highland and mountains.

Prunus sp. 2
(Figure 17G–L)

Description. — Pollen, monad, prolate to spheroidal, outline circular to convex-triangular in polar view, elliptic in equatorial view; polar axis 19–24 µm long in LM, 20–24 µm long in SEM, equatorial diameter 19–22 µm wide in LM, 13–15 µm wide in SEM; tricolporate, endopori lalongate, margins of endopori perpendicular to polar axis slightly thickened; exine 0.8–1.1 µm thick (LM), nexine thinner than sexine, sexine protruding around pori; tectate; sculpturing psilate to weakly striate in LM, striate in SEM, striae longitudinally arranged, often merging and diverging, striae variable in thickness, narrowing towards colpi, sexine arching over pori forming a distinct bridge (SEM).

Remarks. — *Prunus* sp. 1 is much larger than *Prunus* sp. 2. The latter also show a more distinct bridge over the pori (LM). The striae in *Prunus* sp. 1 are much longer and straighter than the striae observed in *Prunus* sp. 2. The striae in *Prunus* sp. 2 are merging and diverging more often than in *Prunus* sp. 1.

Family Ulmaceae Mirb.

Genus Cedrelospermum *Saporta (extinct)*

Cedrelospermum *sp.*
(Figure 18A–L)

Description. — Pollen, monad, oblate, outline quadrangular to hexagonal in polar view, elliptic in equatorial view; polar axis 17–22 µm long in LM, equatorial diameter 24–36 µm wide in LM, 24–32 µm wide in SEM; stephano-(4–6)porate, sex-

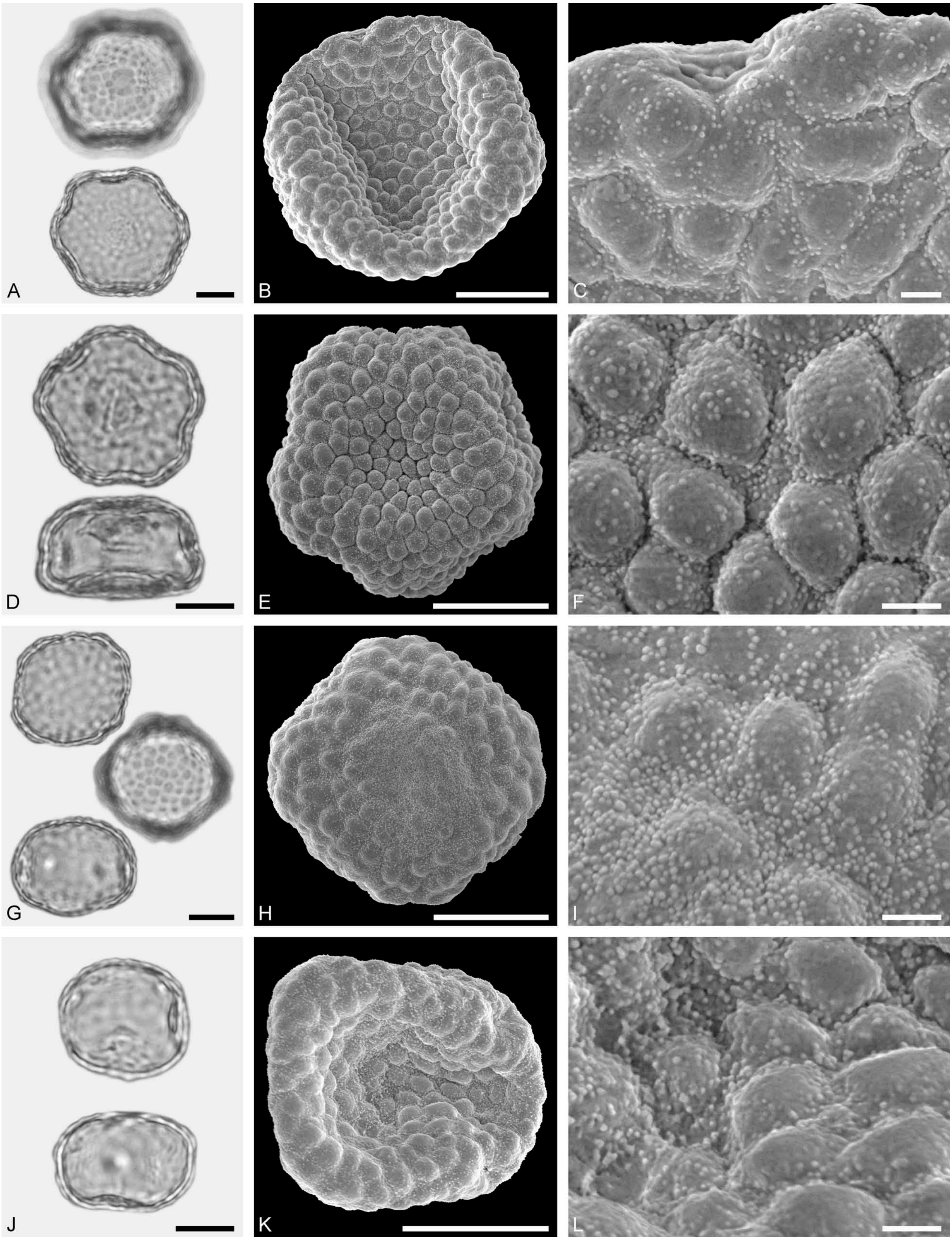


Figure 18. LM (**A, D, G, J**) and SEM (**B, C, E, F, H, I, K, L**) micrographs of dispersed fossil Ulmaceae pollen. **A–L.** *Cedrelospermum* sp., pollen with varying number of pori (**A, D, G, J**), close-ups of area around porus (**C**), distal polar area (**I**), and proximal polar area (**L**). Scale bars – 10 µm (A, B, D, E, G, H, J, K), 1 µm (C, F, I, L).

ine slightly protruding in area of endopori; exine 1.5–2.6 µm thick, nexine thinner than sexine, sexing slightly thicken around endopori, nexine thinner in distal polar area; tectate; sculpturing verrucate in LM, verrucate, microechinate in SEM, verrucate similar in size, mostly closely space, microechini numerous, occurring on both verrucate and in-between (SEM).

Remarks. — This genus is diagnosed on the basis of fruits (e.g. Manchester 1987a, 1989a; Hably & Thiébaut 2002). *In situ* pollen from staminate flowers of *Cedrelospermum* attached to leaves and fruits have been described from the middle Eocene Parachute Creek Member of the Green River Formation (Manchester 1989b). Dispersed fossil pollen showing LM-based morphological affinities to pollen of the extinct *Cedrelospermum* have been assigned to the pollen form-species *Polyporopollenites verrucatus* Thiele-Pfeiffer (Thiele-Pfeiffer 1980) and the form-genus *Ulmipollenites* (e.g. Wolff 1934; Stuchlik et al. 2009).

Fossil record. — *Cedrelospermum* leaves and fruits have been documented from the Eocene to Miocene of Europe. The oldest European records are from the middle Eocene of Germany (Wilde & Manchester 2003) and Hungary (Erdei & Rákosi 2009). The middle Miocene fruits from Romania (Paraschiv 2008) and the pollen from the Lavanttal Basin are thus far the youngest records in Europe. In North America, *Cedrelospermum* has been documented from the middle Eocene to Oligocene, whereas records from southern Mexico are of uncertain age, but probably not older than Oligocene and younger than Pleistocene (Magallón-Puebla & Cevallos-Ferriz 1994). The distribution of the genus is strictly restricted to these two areas.

Manchester and Tiffney (2001) have discussed the phylogeography of Ulmaceae, based on morphological phylogenetic analyses, and regarded *Cedrelospermum* as a link between the southern (*Phyllostylon, Ampelocera*) and northern genera (*Ulmus, Zelkova, Hemiptelea*). In Austria, fruits of *C. aquense* (Saporta) Saporta are documented from the early to middle Miocene Styrian sites Leoben and Schönegg (Hably & Thiébaut 2002) and the early Oligocene Tyrolian site Häring. For the early/middle Miocene fruits from Leoben, Schönegg and Parschlug (Styria), the binomen *C. stiriacum* (Ettingshausen) Kovar-Eder et Kvaček (Kovar-Eder et al., 2004) has been established, because Kovar-Eder et al. (2004) regarded the Miocene records as clearly distinguishable from the Paleogene records. Leaves of *C. flichei* (Saporta) Hably et M.Thiébaut are described from Häring and the nearby locality Duxer Köpfl (Butzmann et al. 2009), those of *C. ulmifolium* (Unger) Kovar-Eder et Kvaček from Parschlug and Weingraben (Burgenland; Jechorek & Kovar-Eder 2004).

Ecological implications. — *Cedrelospermum* fossils have been found in several Eocene to Miocene floras in association with numerous tropical to temperate elements (e.g. Rüffle 1963; Mai 1995; Manchester 1999; Meller et al. 1999; Hably & Thiébaut 2002; Kovar-Eder et al. 2004; Collinson et al. 2012). Mai (1995) regarded the species as a pioneer element in open habitats. The probable ecology of *Cedrelospermum* is still not known. For instance, various interpretations have been provided for the *Cedrelospermum*-rich Céreste Flora (France, Oligocene): swamp forest (Théobald 1937), seasonal climate with mainly open, herbaceous vegetation (Lutz 1984) and unknown palaeoecology (Hably & Thiébaut 2002). In the Eocene of Messel, *Cedrelospermum* is found in association with a very rich carpoflora including numerous (humid) tropical-subtropical elements (Collinson et al. 2012).

The association of *Cedrelospermum* with a highly diverse Fagales flora including many meridio-nemoral and nemoral elements that are not tolerating summer-draught (such as *Corylus, Fagus*; restricted to *Cfa-*, *Cfb-*, *Dfb*-climates) or have only recently adapted to such situations (*Quercus* Group Ilex; mostly *Cfa-*, *Cwa-*, *Cwb*-climates) at the Lavanttal locality, is in agreement with the hypothesis of Gregor (1986; *Cfa*-climate) for the Parschlug flora (Austria, Miocene). Notably, the only evergreen species of the widespread and diverse genus *Ulmus* is restricted to low and mid-altitudes of the Himalayas and montane regions of southern China, where it thrives in a subtropical, monsoonal *Cwa*-climate, with high summer precipitation (see later). We assume that the Lavanttal *Cedrelospermum* thrived in similar habitats: humid, mixed broad-leaved and evergreen lowland forests.

Genus Ulmus *L.*

Ulmus *sp. 1*
(Figure 19A–L, 20A–F)

Description. — Pollen, monad, oblate, outline quadrangular to hexagonal in polar view, elliptic in equatorial view; polar axis 20–24 µm long in LM, equatorial diameter 26–31 µm wide in LM, 25–28 µm wide in SEM; stephano-(4–6)porate, sexine slightly protruding in area of endopori; exine 1.0–1.4 µm thick, nexine thinner than sexine, sexing slightly thicken around endopori, nexine thinner in distal polar area; tectate; sculpturing rugulate in LM, rugulate, microechinate, perforate in SEM, rugulae 1.0–1.2 µm wide, rugulae often fused and surrounding depressions (SEM).

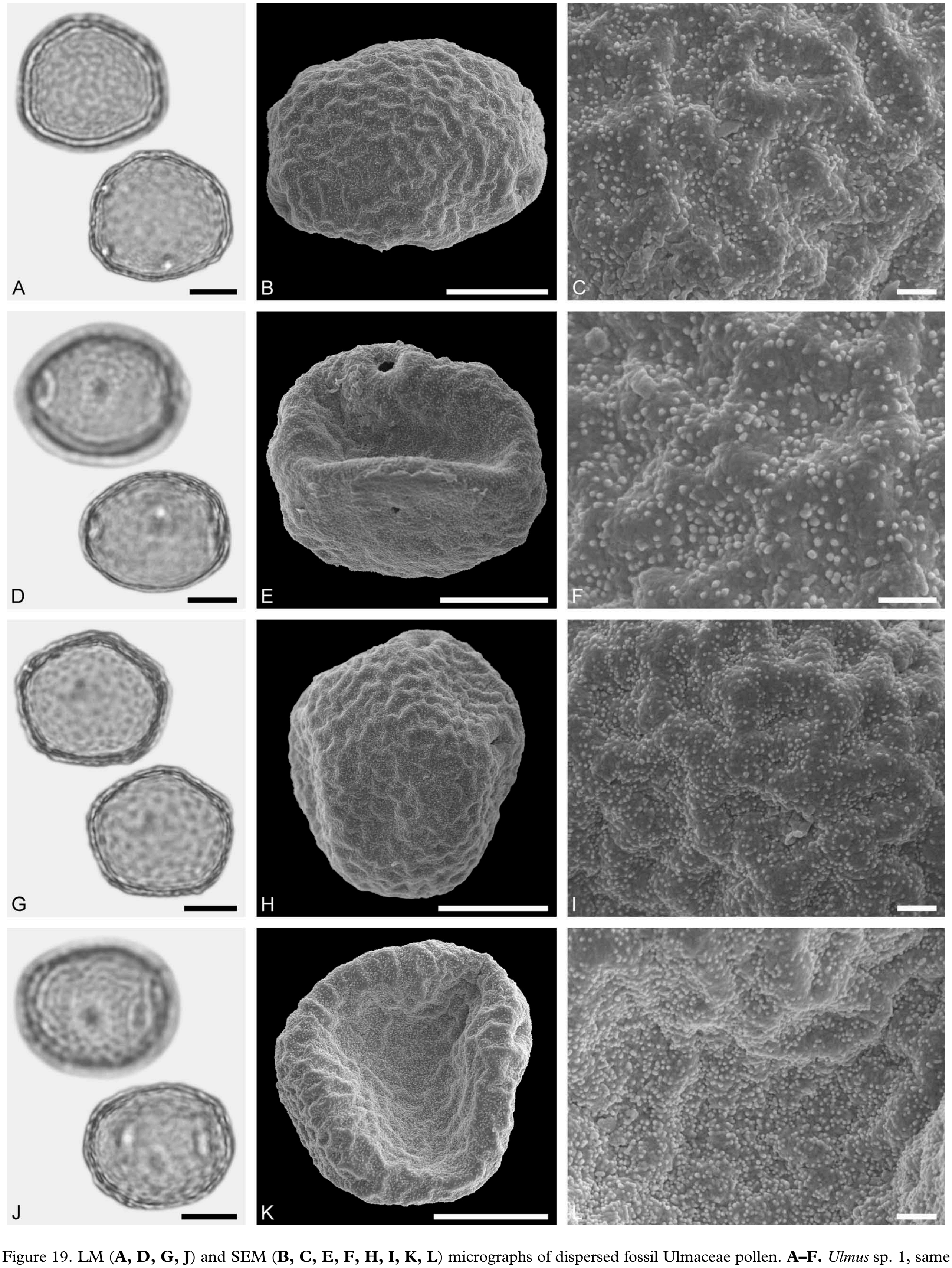


Figure 19. LM (**A, D, G, J**) and SEM (**B, C, E, F, H, I, K, L**) micrographs of dispersed fossil Ulmaceae pollen. **A–F.** *Ulmus* sp. 1, same grain with six pori, distal side of grain (**B, C**), and proximal side of grain (**E, F**). **G–L.** *Ulmus* sp. 1, same grain with five pori, distal side of grain (**B, C**), and proximal side of grain (**E, F**). Scale bars – 10 μm (A, B, D, E, G, H, J, K), 1 μm (C, F, I, L).

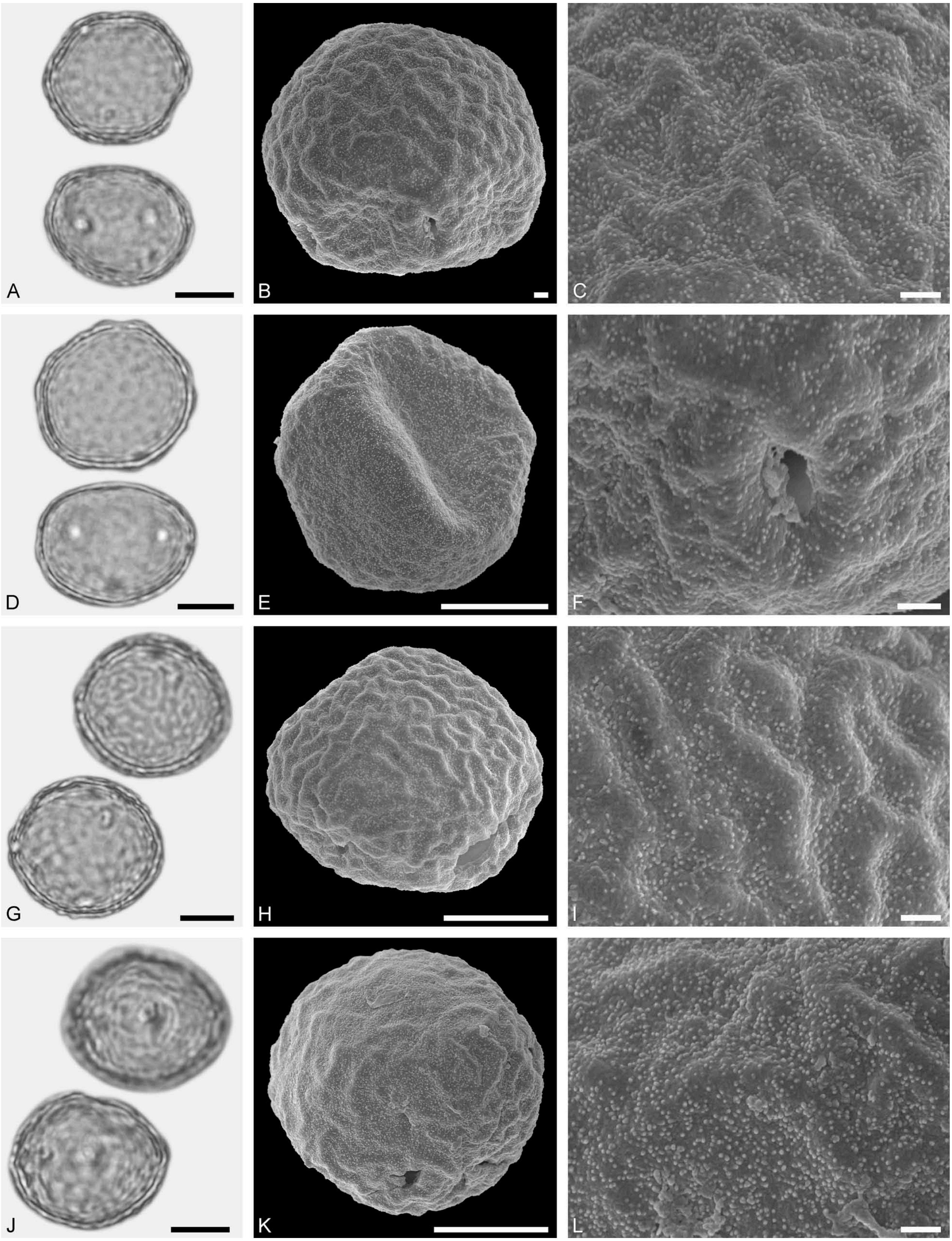


Figure 20. LM (**A, D, G, J**) and SEM (**B, C, E, F, H, I, K, L**) micrographs of dispersed fossil Ulmaceae pollen. **A–F.** *Ulmus* sp. 1, same grain with five pori, distal side of grain (**B, C**), and proximal side of grain (**E**), close-up (**F**) showing porus. **G–L.** *Ulmus* sp. 2, same grain, distal side of grain (**H, I**), and proximal side of grain (**K, L**). Scale bars – 10 µm (A, B, D, E, G, H, J, K), 1 µm (C, F, I, L).

Remarks. — The pollen morphology and ultrastructure of extant Ulmaceae has been studied in detail by Zavada (1983) and Takahashi (1989). Pollen from various extant North American and Eurasian *Ulmus* species has been studied and figured using LM, SEM and sometimes TEM by Huang (1972), Zavada (1983), Zavada and Dilcher (1986), Takahashi (1989), Lieux (1980), Xin et al. (1993), Jones et al. (1995), Stafford (1995), Wang et al. (1995), Morita et al. (1998), Beug (2004), Li et al. (2011a) and Miyoshi et al. (2011). For characters on how to distinguish between *Ulmus* and *Zelkova* pollen, see Morita et al. (1998), amongst others. Fossil pollen showing LM-based morphological affinities to pollen of modern *Ulmus* has commonly been assigned to the pollen form-genus *Ulmipollenites* (e.g. Wolff 1934; Stuchlik et al. 2009).

Fossil record. — The early *Ulmus*-like fossil record of the Paleocene-Eocene has been summarised by Denk and Dillhoff (2005). Some of the best preserved early fossils are associated and attached fruits and leaves of *U. okanaganensis* Denk et Dillhoff from the early Eocene McAbee and co-eval floras of British Columbia, western North America (Denk & Dillhoff 2005). The Eocene to Oligocene fossil record of *Ulmus* has been summarised by Manchester (1989c) suggesting that unambiguous *Ulmus* remains are not found in Eurasia before the Oligocene. *Ulmus* is very abundant in European Miocene leaf assemblages (Mai 1995; Meller & Hably 2014), and fruits have been found from the late early/early middle Miocene Parschlug site (Kovar-Eder et al. 2004). From the Lavanttal Basin, Berger (1955) mentioned *Ulmus* leaves from Messensach (early middle Miocene) and St Stefan (late middle Miocene).

Ecological implications. — *Ulmus* is a large and widespread northern hemispheric genus and common element of broad-leaved deciduous forests of the temperate zone with a preference for warm temperate climates with warm or hot summers and sufficient precipitation during growing season (*Cfa-*, *Cfb-*, *Cwa-*, *Cwb*-climates). Some species are tolerant against generally low temperatures, e.g. *U. glaucescens* Franch., *U. pumila* L., *U. laciniata* Mayr, extending into regions with snow climates and short (cold) summers (Fu et al. 2003; Fang et al. 2009); one widespread species, *U. minor* Mill. extends into summer-dry climates (*Csa, Csb*).

The mainly deciduous trees, rarely shrubs, occur in different forest types. About 35 to 45 species are described, with a centre of distribution in central and northern Asia (Todzia & Panero 1998). In China, 21 species are known, 14 of them are endemic (Fu et al. 2003), the others are also growing in Russia, Korea and Japan. The trees occur in lowland, subtropical mixed evergreen broad-leaved forests at 200–900 m a.s.l. and in montane mixed mesophytic forests at 700–1800 (–2900) m a.s.l. Most species occur along river banks and mountain ravines, in wetlands near streams, on mountain slopes, and often on limestone. The only evergreen species, *Ulmus lanceifolia* Roxb., is growing between 300–1500 m a.sl., in some provinces in China and also in Bhutan, India, Thailand and Vietnam (Fu et al. 2003). In North America, about ten species are native, also in southern Mexico (Todzia & Panero 1998), but none in western North America. In the south-eastern United States, they are growing in different types of woodland habitats, in floodplains and lowland woodlands as well as in upland forests, along banks of streams, and in wet to moist rich woodlands (Godfrey & Wooten 1981). *Ulmus* is often growing on limestone and may occur up to 900 m a.s.l. (Sherman-Broyles et al. 1997). In riparian forests, *Ulmus* prefers nutrient-rich and alkaline soil (Mai 1995), but may tolerate poor soil conditions (Elias 1980). *Ulmus* species can be categorised as generalists, semihumid-meridional (*U. lanceifolia*), meridio-nemoral, nemoral and boreal (*U. laciniata*) elements (File S1). At Lavanttal, *Ulmus* may have been part of the riparian forests, growing close to lakes and along rivers/streams and reaching into the (mesic) slope forests surrounding the basin.

Ulmus *sp. 2*
(Figure 20G–L, 21A–F)

Description. — Pollen, monad, oblate, outline quadrangular to hexagonal in polar view, elliptic in equatorial view; polar axis 20–25 µm long in LM, equatorial diameter 27–33 µm wide in LM, 25–29 µm wide in SEM; stephano-(4–6)porate; exine 0.8–1.1 µm thick, nexine thinner than sexine, sexing slightly thicken around endopori, nexine thinner in distal polar area; tectate; sculpturing rugulate in LM, rugulate, microechinate in SEM, rugulae 0.8–0.9 µm wide, rugulae often running parallel, flanked by elongated depressions (SEM).

Remarks. — In *Ulmus* sp. 1, the rugulae are fused and surrounding depressions (LM and SEM), but in *Ulmus* sp. 2, the rugulae are running parallel and flanked by elongated depressions.

Genus Zelkova *Spach*

Zelkova *sp.*
(Figure 21G–L, 22A–L)

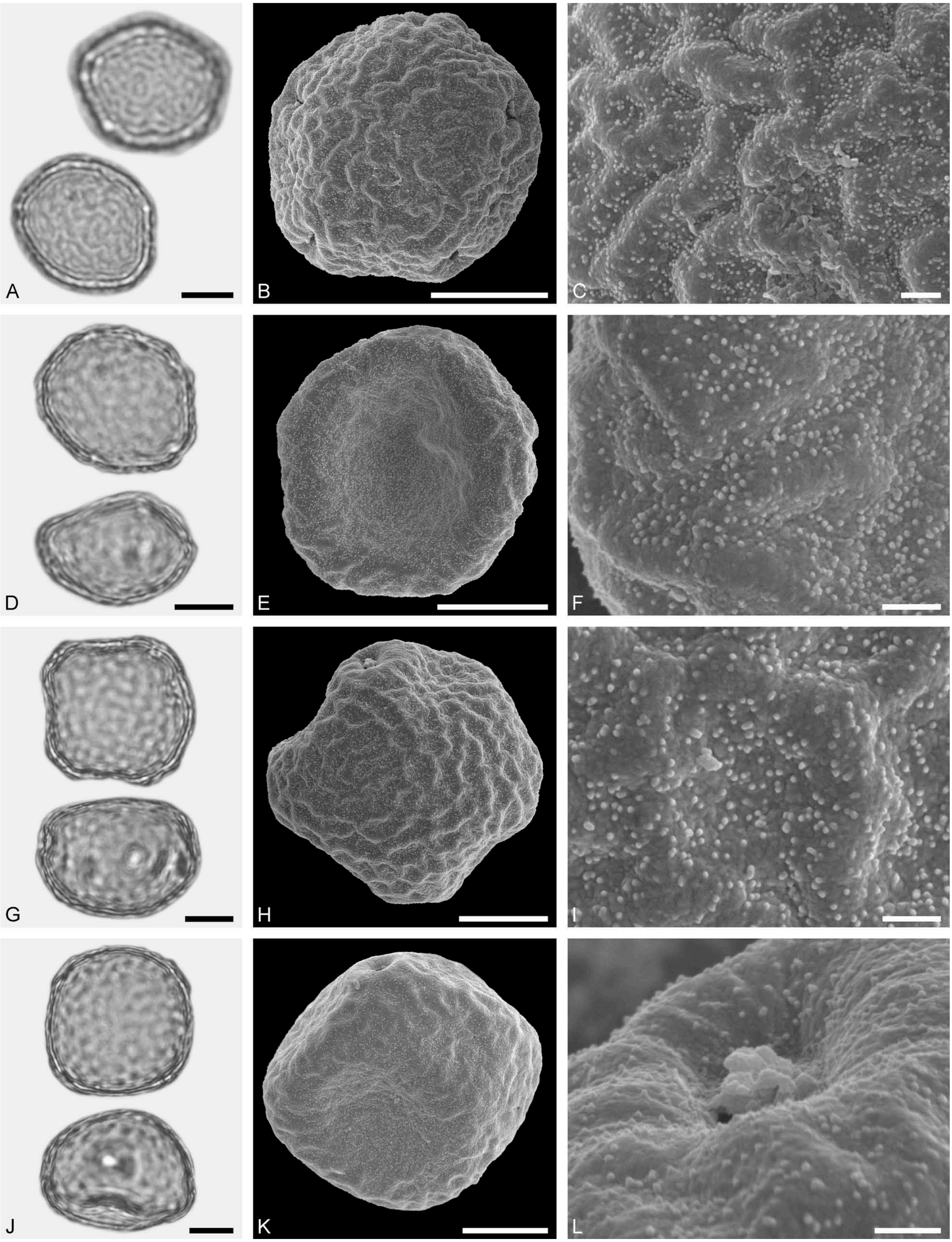


Figure 21. LM (**A, D, G, J**) and SEM (**B, C, E, F, H, I, K, L**) micrographs of dispersed fossil Ulmaceae pollen. **A–F.** *Ulmus* sp. 2, same grain with five pori, distal side of grain (**B, C**), and proximal side of grain (**E, F**). **G–I.** *Zelkova* sp., grain with four pori, distal side (**H, I**). **J-L.** *Zelkova* sp., grain with four pori, proximal side of grain (**K**), close-up of pori showing membrane (**L**). Scale bars – 10 μm (A, B, D, E, G, H, J, K), 1 μm (C, F, I, L).

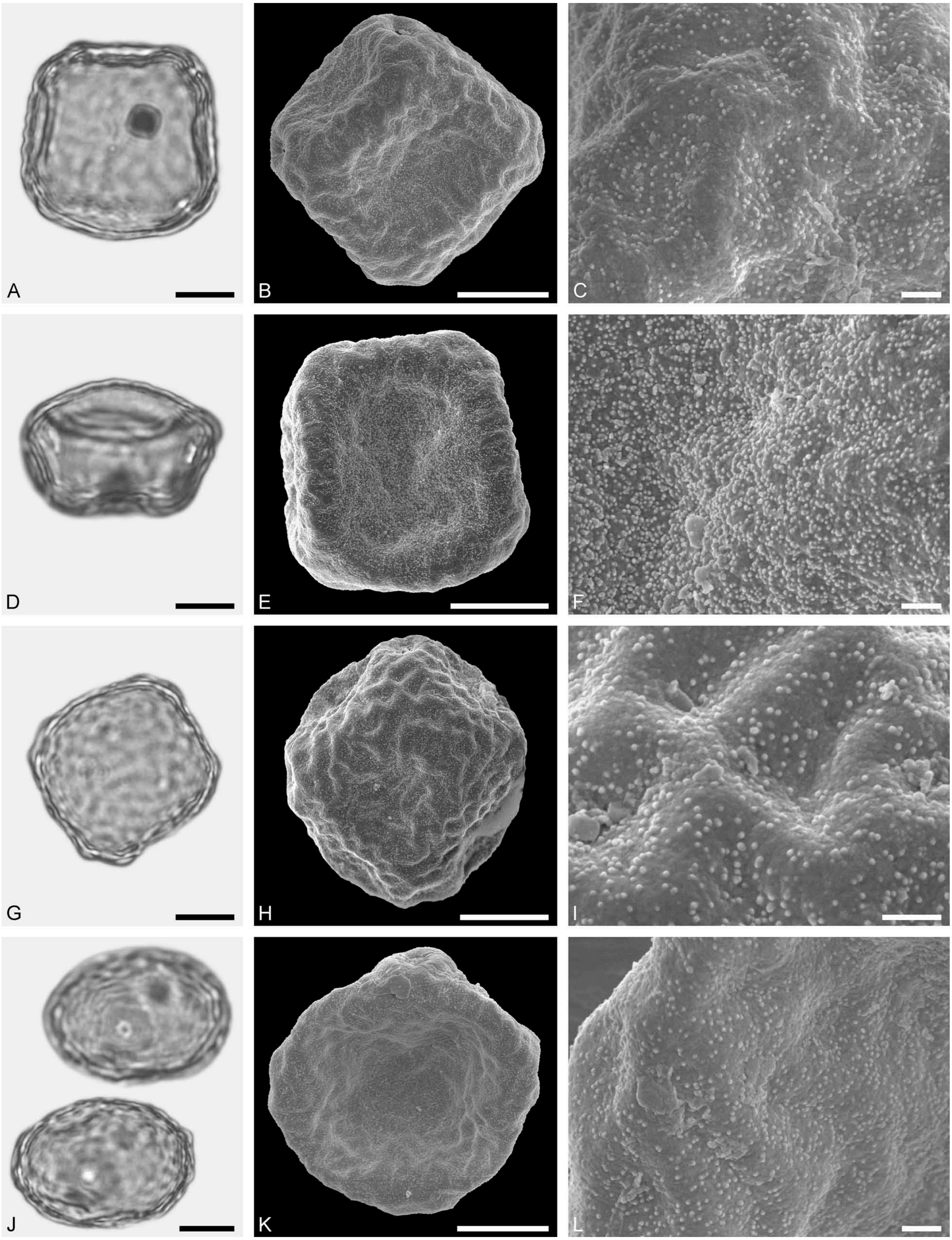


Figure 22. LM (**A, D, G, J**) and SEM (**B, C, E, F, H, I, K, L**) micrographs of dispersed fossil Ulmaceae pollen. **A–F.** *Zelkova* sp., same grain with four pori, distal side of grain (**B, C**), and proximal side of grain (**E, F**). **G–L.** *Zelkova* sp., same grain with four pori, distal side (**H, I**), and proximal side (**K, L**). Scale bars – 10 μm (A, B, D, E, G, H, J, K), 1 μm (C, F, I, L).

Description. — Pollen, monad, oblate, outline quadrangular to hexagonal in polar view, elliptic in equatorial view; polar axis 23–26 µm long in LM, equatorial diameter 31–36 µm wide in LM, 30–32 µm wide in SEM; stephano-(4–6) porate; exine 1.2–1.7 µm thick, nexine thinner than sexine, sexing slightly thicken around endopori, nexine thinner in distal polar area; tectate; sculpturing rugulate in LM, rugulate, microechinate in SEM, rugulae 1.0–1.2 µm wide, rugulae often fused and surrounding depressions (SEM).

Remarks. — *Zelkova* pollen from all of the six extant western and east Asian and Mediterranean species has been described and figured based on LM and/or SEM investigations by Huang (1972), Takahashi (1989), Stafford (1995), Morita et al. (1998), Nakagawa et al. (1998), Li et al. (2011a) and Miyoshi et al. (2011). Studies on the ultrastructure (TEM) of *Zelkova* pollen are rare (e.g. Takahashi 1989). Fossil pollen showing LM-based morphological affinities to pollen of modern *Zelkova* has commonly been assigned to the pollen form-genus *Zelkovaepollenites* (e.g. Nagy 1969; Stuchlik et al. 2009).

Fossil record. — *Zelkova* was widely distributed in the Northern Hemisphere during Paleogene and Neogene times (Wang et al. 2001; Denk & Grimm 2005). In North America, *Zelkova* leaves have been described from the late Paleocene/early Eocene and fruits have been documented from Oligocene sites (Burnham 1986; Manchester 1989c). Denk and Grimm (2005) concluded – based on molecular, morphological and fossil evidence – that the genus originated in the northern Pacific region and migrated towards Europe in the late Oligocene after the closure of the Turgai Strait. In Eurasia, the genus has a solid fossil record from the Eocene onwards (Mai 1995; Lui et al. 1996) and has been documented from the late Pliocene of the Netherlands and the Eemian interglacial period in south-eastern Europe (Lang 1994). *Zelkova* leaves are widespread in the Eurasian leaf fossil record and typically addressed as *Z. zelkovifolia* (Unger) Bůžek et Kotl., e.g. late Oligocene of Rott, Germany, middle Miocene of Parschlug, Austria, late Miocene of Vegora, Greece, and Pliocene of Mogi, Japan (see Denk & Grimm 2005, table 7). From the Lavanttal Basin, *Zelkova* leaves have been mentioned by Berger (1955) from the Ölbach locality and from Schönweg by Hofmann (1929; as '*Planera ungeri* Kovats').

Ecological implications. — Today, *Zelkova* is represented in the Northern Hemisphere by three species in East Asia (two widespread, one highly restricted), one in the Caucasus-Hyrcanian area, one in Crete and one in Sicily. The latter can be regarded as relict trees, which survived the Quaternary glaciations in the eastern Mediterranean area (e.g. Wang et al. 2001; Christe et al. 2014). The trees are up to 30–60 m high or are of shrubby growth in unfavourable conditions (dry stands). In China, *Zelkova* occurs between 200 to 2500 m a.s.l. in valleys along streams (Fu et al. 2003) within the mixed northern hardwood forests, the deciduous broad-leaved forests, and as minor element also within the mixed mesophytic forests (Wang 1961). In central Japan, *Zelkova serrata* (Thunb.) Makino is one of the few tall tree species that are found in forests dominated by *Fagus*. Along river valleys on unstable ground, *Z. serrata* is found within mixed evergreen broad-leaved forests typically associated with *Acer* (Miyawaki & Suzuki 1980). *Zelkova carpinifolia* (Pall.) K.Koch occurs in the Hyrcanian forests and the Caucasus; typical habitats are the lowland forests south of the Caspian Sea in an essentially fully humid, warm temperate climate (*Cfa, Cfb*) associated with mainly deciduous elements and some evergreen shrubs or lianas (e.g. Akhani et al. 2010) and somewhat drier stands in Georgia (periphery of the Colchic area and eastern central Georgia) associated with evergreen species and mean annual precipitation of > 1000 mm/yr (Denk et al. 2001). Akhani et al. (2010) stress the lack or only short dry period and that the mean temperature of the coldest month is above 0 °C. In the summer-dry Mediterranean climates, *Z. abelicea* (Lam.) Boiss. is restricted to the relatively humid mountains of Crete, where it grows on limestone and thrives in the vicinity of dolines (sinkholes in karst areas) acting as natural water reservoirs (Søndergaard & Egli 2006), whereas the population of the Sicilian endemic *Z. sicula* Di Pasquale, Garfi et Quézel is threatened by annihilation.

Despite their restricted distribution at present, the four putative relict species (three in western Eurasia and *Zelkova sinica* C.K.Schneid. in China) share the distinct preference for warm temperate climates with the two relatively wide spread species in East Asia (*Z. schneideriana* Hand.-Mazz., southern and central China; *Z. ser-*

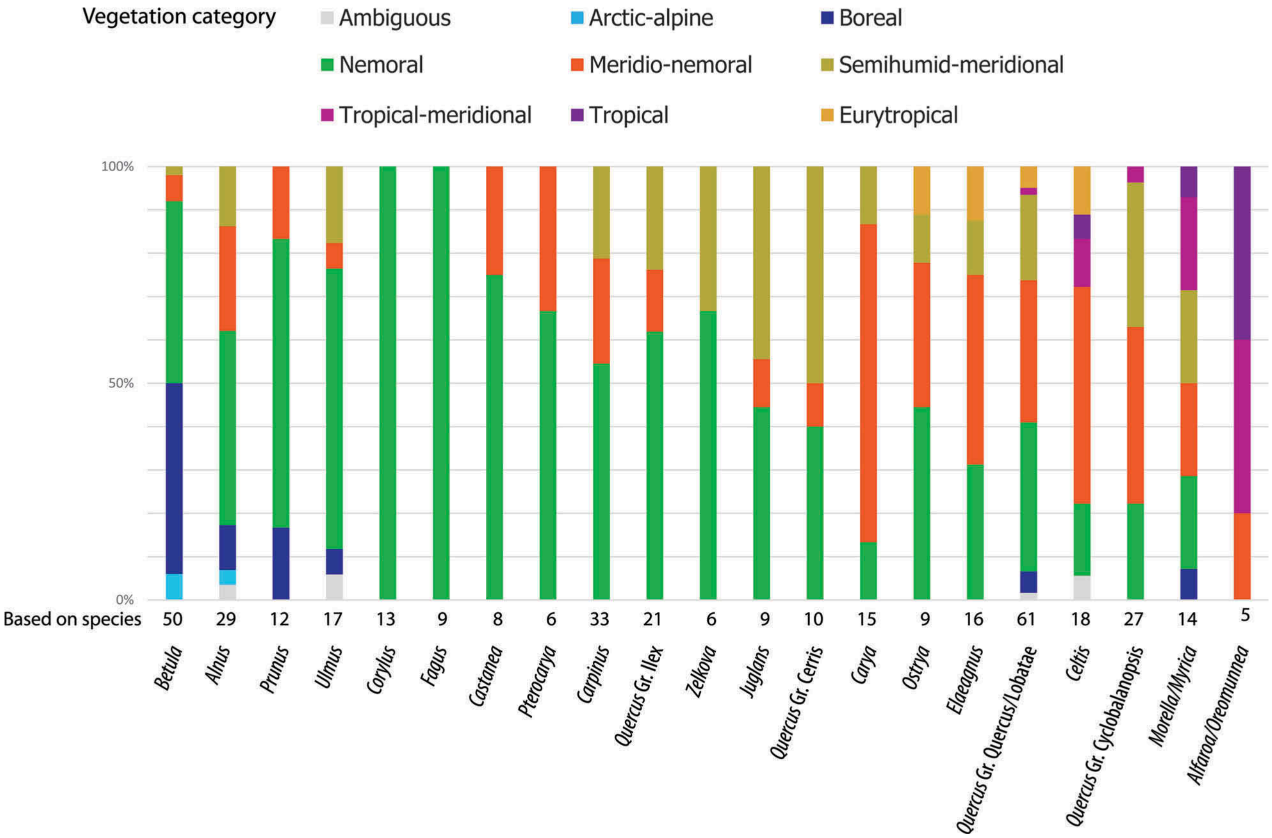


Figure 23. Köppen signatures of potential modern analogues of Fagales and Rosales lineages found at the Lavanttal site. The bar chart shows the proportion of extant species part of the modern genus/lineage categorised for generalised climate-vegetation types (see Denk et al. 2013; see Material and Methods section). Generalists – no distinct climatic preference; arctic-alpine elements – occurring in tundra (*ET*) and adjacent climates; boreal elements – preference for *D*-climates, occurring in climates with cold and short summers but not *ET* climates; nemoral elements – preference for warm temperate and/or snow climates with warm summers (*Cfb, Cwb, Csb, Dfb, Dwb, Dsb*); meridio-nemoral elements – preference for warm temperate climates with hot, but not warm, summers (*Cfa*- and *Cwa*-climates); semihumid-meridional elements – preference for semihumid warm temperate climates with hot (and warm) summers; tropical-meridional – preference for tropical (*A*-climates) and warm temperate climates with hot but not warm summers; tropical – species restricted to tropical (*A*-climates); eurytropical – preference for non-tropical climates with summer draught and generally dry climates (*B*- and *Cs*-climates).

rata, China to Kuril Islands; e.g. Fu et al. 2003; Kvavadze & Connor 2005). Overall, species of *Zelkova* can be categorised as semihumid-meridional, meridio-nemoral, and nemoral elements (File S1).

Discussion

Occurrence and identification of angiosperm pollen

Most of the angiosperm pollen types described here represent genera producing very distinct pollen; pollen types that are usually identifiable using LM. These include commonly reported Miocene elements in European palynofloras such as *Alnus, Betula, Fagus, Quercus, Carya, Juglans* and *Pterocarya*. Most of the families (Betulaceae, Fagaceae, Juglandaceae, Myricaceae, Ulmaceae) and genera dealt with here were previously mentioned by Klaus (1984). Pollen of the families Rosaceae (*Prunus*) and Rhamnaceae have not been reported before, and additional pollen types affiliated with previously identified families like the Betulaceae, Fagaceae and Ulmaceae/Cannabaceae are also presented for the first time (Table II). Since Klaus (1984) made most of his investigations using only LM, we are sometimes not sure if the pollen, we describe/figure, represent the same taxon as mentioned in the study by Klaus (Table II).

Even though many of the pollen types represent commonly reported elements, the individual taxa

Table II. Angiosperm pollen described in this study in comparison to Klaus (1984).

This study	Klaus (1984)
Alnus sp. 1 (Subgenus *Alnus* vel *Clethropsis)*	*Alnus* Form A
Alnus sp. 2 (Subgenus *Alnus* vel *Clethropsis)*	?*Alnus* Form B
Betula sp. 1	*Betula*
Betula sp. 2	x
Carpinus sp. 1	?*Carpinus*
Carpinus sp. 2	?*Carpinus*
Corylus sp.	?*Corylus* (not figured)
Ostrya sp.	*Ostrya*
Castanea sp.	*Castanea*
Fagus sp.	*Fagus* cf. *mexicana*, *Fagus longipetiolata*, *Fagus* Form A, *Fagus* Form B
Quercus sp. 1 (*Quercus* Group Cerris)	?*Quercus* Form A, ?*Quercus* Form C, ?*Quercus* Form E
Quercus sp. 2 (*Quercus* Group Ilex)	x
Quercus sp. 3 (*Quercus* Group Ilex)	x
Quercus sp. 4 (*Quercus* Group Ilex)	?*Quercoidites microhenrici*, ?*Quercus* Form B
Quercus sp. 5 (*Quercus* ?Group Cyclobalanopsis)	x
Quercus sp. 6 (*Quercus* Group Quercus/Lobatae)	?*Quercus* Form D, ?*Quercus* Form E, ?*Quercus* Form F
Quercus sp. 7 (*Quercus* Group Quercus/Lobatae)	?*Quercus* Form D, ?*Quercus* Form F
Trigonobalanopsis sp.	x
Engelhardioideae gen. et sp. indet. (*Alfaroa* vel *Engelhardia* vel *Oreomunnea*)	*Engelhardia* (*Oreomunnea*)
Carya sp.	*Carya*
Juglans sp.	*Juglans*
Pterocarya sp.	*Pterocarya*
Myricaceae gen. et spec. indet. (*Morella* vel *Myrica*)	?*Myrica*
Celtis sp. 1	*Juglanspollenites verus*
Celtis sp. 2	*Celtis*
Cannabaceae gen. et spec. indet.	x
Elaeagnus sp.	?*Elaeagnus* (not figured)
Rhamnaceae gen. et spec. indet. 1	x
Prunus sp. 1	x
Prunus sp. 2	x
Cedrelospermum sp.	*Planera aquatica*
Ulmus sp. 1	*Ulmus laevis*
Ulmus sp. 2	x
Zelkova sp.	*Zelkova*

Note: Question marks indicate when we are uncertain if the LM based description and/or micrographs by Klaus (1984) correspond to our pollen types.

(pollen types) described in this paper rarely make up more than 0.5% of the entire palynomorph spectrum (F. Grímsson, pers. observation based on four years of studying this sample). Of the taxa described here, pollen of *Fagus* is by far the most common type encountered and appears in various, albeit non-specific (hence all addressed as *Fagus* sp.) forms and shapes. The rarest pollen grains are those of *Corylus*, *Castanea*, *Quercus* sp. 2, *Quercus* sp. 5, *Quercus* sp. 7, Cannabaceae gen. et spec. indet., *Elaeagnus*, Rhamnaceae gen. et spec. indet., *Prunus* sp. 1 and *Prunus* sp. 2.

Palaeoecological interpretations and palaeoenvironmental reconstructions – preliminary results

Previous accounts on the middle Miocene (Sarmatian) palynoflora from the Lavanttal Basin (Grímsson et al. 2011, 2015a; Grímsson & Zetter 2011) have shown that spores and pollen accumulated in a freshwater environment. Species richness and habitat of possible modern analogues suggests that the spores and pollen originate from plants growing directly within the lowland wetland and are reflecting various units of the autochthonous vegetation, and also the allochthonous vegetation surrounding the main basin. Many of the previously described spores and pollen were dispersed by plants occupying various microsites within the lowland wetland forest (lake margins, along rivers, swamps, on levees, hammocks, floodplains, etc.) or at its periphery. These include *Carex*, *Cercidiphyllum*, *Dryopteris*, *Ephedra*, *Ginkgo*, *Glyptostrobus*, *Larix*, *Liquidambar*, *Lycopodium*, *Magnolia*, *Osmunda*, *Parthenocissus*, *Picea*, *Pinus*, *Platanus*, *Ranunculaceae*, *Salix*, *Sciadopitys*, *Selaginella*, *Sequoia*, *Sparganium*, *Sphagnum*, *Typha* and *Vitis*. Based on the ecological preferences of potential modern analogues a large part of the pollen was apparently dispersed by plants thriving in different habitats of the surrounding lowland, highland or mountain forests. These include *Abies*, *Buxus*, *Cathaya*, *Cedrus*, *Cercidiphyllum*, *Cryptomeria*, *Daphnyphyllum*, *Distylium*, *Fortunearia*, *Ginkgo*, *Keteleeria*, *Larix*, *Lycopodium*, *Parrotia*, *Parthenocissus*, *Picea*, *Pinus*, *Pteris*, *Sequoia*, *Trochodendron*, *Tsuga* and *Vitis*.

The angiosperm pollen presented here may also originate from plants that could have thrived in various habitats and vegetation units of the lowland, hinterland, and surrounding highland and mountains. *Alnus*, *Betula*, *Carpinus*, *Carya*, *Cedrelospermum*, *Celtis*, *Elaeagnus*, *Juglans*, *Myrica*/*Morella*, *Ostrya*, *Prunus*, *Pterocarya*, *Quercus* Group Quercus/Lobatae, *Trigonobalanopsis* and *Ulmus* were most likely growing in the lowland wetland forests (mixed evergreen/deciduous broad-leaved/conifer forests), some in swampy areas, or around lake margins and along streams and rivers, or on floodplains and on levees, and growing mostly in riparian forests and mesophytic forests bordering the basin. Some of these plants (*Prunus*, *Betula*, *Pterocarya*, *Myrica*/*Morella*, *Elaeagnus*) were probably also growing along streams reaching into the surrounding highland and/or mountains. *Corylus*, *Quercus* Group Cyclobalanopsis, *Zelkova*, Engelhardioidea and Rhamnaceae were most likely growing in lowland/hinterland forests outside the wetlands, along the periphery of the wetland basin reaching into hillside forests surrounding the basin. *Castanea* and *Quercus* Group Cerris and Group Ilex were probably confined to the mixed hillside and mountain forest at some distance from the main accumulating area.

Based on the climatic preferences, expressed by their 'Köppen signatures', which the Fagales and Rosales lineages present at the Lavanttal site (Figure 23; Table III), tropical (*A*-)climates and climates with pronounced (summer) draught (*B*-, *Cs*-, *Ds*-climates) can be ruled out for this timescale and region. The same holds for boreal climates with short but humid summers (*Cfc, Dfc, Dfd, Dwc*). Especially the diversity of Fagales, including genera that are today composed predominately or exclusively of nemoral and meridio-nemoral elements (Figure 23), points to climate conditions not unlike

Table III. Summarised 'Köppen signatures' for Fagales and Rosales of Lavanttal.

Pollen taxon/taxa		Köppen signature	Indicative of
B	*Alnus* sp. 1/2	***Cfa***, *Cfb, Cwa, Cwb, Csa, Csb, Dfa, Dfb, Dfc, Dwa, Dwb, Dwc, Dsb, Dsc, ET*	Warm temperate, snow and polar climates
B	*Betula* sp. 1/2	***Cfa***, *Cfb, Cfc, Cwa, Cwb, Dfa, Dfb, Dfc, Dfd, Dwa, Dwb, Dwc, Dsb, Dsc, ET*	Non-tropical (non-equatorial) and non-Mediterranean-type (*Cs*) climates
B	*Carpinus* sp. 1/2	***Cfa***, *Cfb, Cwa, Cwb, Csa, Dwa, Dwb, Dfa, Dfb*	Warm temperate and snow climates; humid and semihumid
B	*Corylus* sp.	***Cfa***, *Cfb, Cwb, Dfa, Dfb, Dwa, Dwb, Dsb*	Warm temperate or snow climates with humid and warm to hot summers
B	*Ostrya* sp.	*B*, ***Cfa***, *Cfb, Cwa, Cwb, Csa, Dfa, Dfb*	Non-tropical climates with warm to hot summers
F	*Castanea* sp.	***Cfa***, *Cfb, Cwb, Dwa* (*Csa, Csb*)[a]	Essentially warm temperate climates with humid and warm to hot summers
F	*Fagus* sp.	***Cfa***, *Cfb, Dfb*	Humid, warm temperate to snow climates with warm to hot summers
F	*Quercus* sp. 1 (Group Cerris)	***Cfa***, *Cfb, Csa, Csb, Dsa, Dsb*	Fully humid or summer-dry warm temperate climates, or snow climates with warm to hot and dry summers
F	*Quercus* sp. 2–4 (Group Ilex)	***Cfa***, *Cwa, Cwb*	Warm temperate climates with humid, warm to hot summers
F	*Quercus* sp. 5 (Group Cyclobalanopsis)	*A*, ***Cfa***, *Cwa, Cwb*	Tropical or warm temperate climates with predominately hot and humid summers
F	*Quercus* sp. 6/7 (Group Quercus/ Group Lobatae)	*B*, ***Cfa***, *Cfb, Cwa, Cwb, Csa, Csb, Dfa, Dfb*	Non-tropical climates with warm to hot summers
J	*Carya* sp.	***Cfa***, *Cfb, Cwa, Dfa, Dfb*	Warm temperate and snow climates with humid and warm to hot summers
J	Engelhardioideae	*A*, ***Cfa***, *Cfb, Cwa, Cwb*	Tropical or warm temperate climates with humid and warm to hot summers
J	*Juglans* sp.	***Cfa***, *Cfb, Cwa, Cwb, Csa, Csb, Dfa, Dfb, Dwb*	Warm temperate or snow climates with warm to hot summers
J	*Pterocarya*	***Cfa***, *Cfb, Cwa, Cwb, Dfa, Dfb, Dwa*	Warm temperate or snow climates with humid and warm to hot summers
M	*Morella* vel *Myrica*	*A*, ***Cfa***, *Cfb, Cwa, Cwb, Csa, Csb*[b]	Tropical or warm temperate climates[b]
C	*Celtis* sp. 1/2	*A, B*, ***Cfa***, *Cfb, Cwa, Cwb, Dfa, Dwa, Dwb, Csa*	Tropical climates, warm temperate climates with warm to hot summers, (semi-)arid climates
E	*Elaeagnus* sp.	*B*, ***Cfa***, *Cfb, Cwa, Cwb*	Temperate humid, semihumid or arid climates
R	*Prunus* sp. 1/2	***Cfa***, *Cfb, Cwa, Cwb, Csb, Dfa, Dfb, Dfc, Dwb*	Warm temperate and snow climates with warm to hot summers
U	*Ulmus* sp. 1/2	*B*, ***Cfa***, *Cfb, Cwa, Cwb, Csa, Csb, Dfa, Dfb, Dfc, Dwa, Dwb, Dwc*	Non-tropical and non-polar climates
U	*Zelkova* sp.	***Cfa***, *Cfb, Cwa, Cwb, Csa, Csb, Dfb*	Warm temperate and snow climates with warm to hot summers

Note: B, Betulaceae; F, Fagaceae; J, Juglandaceae; M, Myricacea; C, Cannabaceae; E, Elaeagnaceae; R, Rosaceae; U, Ulmaceae.

[a] The only species extending into *Csa*-, *Csb*-climates is the widely cultivated *Castanea sativa*.

[b] Not including the boreal *Myrica gale*.

those found today in the lowlands and adjacent mountain regions of the (south-)eastern United States, the humid-meridional region of western Eurasia (e.g. northern Italy, Black Sea region, western Caucasus), central and southern China, or Honshu (Japan). These regions are characterised by subtropical conditions at lower elevations (*Cfa*-, *Cwa*-climates) and subsequent altitudinal successions: *Cfa* → *Cfb*/*Dfa* → *Dfb* in eastern United States, western Eurasia, central China and Japan, or *Cwa* → *Cwb* → *Dwb* in southern China (the same situation can be found in the southern foothills of the Himalayas). The climax vegetation in these areas are mixed mesophytic forests and various forms of the 'Laurisilva' (mixed evergreen/deciduous broad-leaved forests), forest types characteristic for the humid and semi-humid, summer-rain areas of the meridional and nemoral zone (Walter 1973; Schroeder 1998; see Velitzelos et al. 2014, table 23). Dominant and common genera in these forests are the various members of the northern hemispheric Fagales, which are represented by 23 different lineages at the Lavanttal site. The most important taxa for palaeovegetation and climate reconstruction are *Fagus*, a genus with a relatively narrow climatic and ecological niche and one of the most dominant genera in mixed mesophytic forests of North America, China and Japan (Maycock 1994; Cao 1995; Peters 1997), and *Quercus* Group Ilex, a co-dominant group in the East Asian monsoon influenced, winter-dry or fully humid southern foothills of the Himalayas and montane regions of south-western and central China (Huang et al. 1999; see also distribution maps in Fang et al. 2009). Equally informative is *Corylus*, with a similar ecological and climatic niche as *Fagus*, and the co-occurrence of *Carya*, *Juglans*, *Pterocarya* and Engelhardioideae, pinpointing towards rich mixed evergreen-broad leaved forests as today only found in south-western China (Fang et al. 2009) and the warm subtropical parts of the south-eastern United States (see distribution maps in Thompson et al. 1999a, 1999b, 2001; eFloras 2008). The high Fagales diversity further indicates a varying landscape with a relatively high variety of niches including riparian, dry and mesic forests (Table IV; showing habitat preferences of the potential modern analogues of the Lavanttal Fagales and Rosales).

The angiosperm taxa described here as well as spores and pollen previously mentioned by Grímsson et al. (2011), 2015a) and Grímsson and Zetter (2011) represent only a part of the well preserved and species rich palynoflora from the phosphoritic nodules of the Lavanttal Basin. Additional angiosperm pollen types will be described in following contributions. Fully detailed interpretation of the palaeovegetation, ecology and climate awaits further notice until all the angiosperm pollen have been described.

Table IV. Preferred general forest types of extant species of genera represented among the Lavanttal Fagales and Rosales.

	RF	MF	DF
Morella vel *Myrica*	x		x
Zelkova	x		x
Pterocarya	x		
Alnus	x	x	
Betula	x	x	
Carpinus		x	
Castanea		x	
Quercus Group Cyclobalanopsis		x	
Engelhardioideae		x	x
Ostrya		x	x
Quercus Group Cerris		x	x
Quercus Group Ilex		x	x
Querucs Group Quercus/Lobatae		x	x
Carya	x	x	x
Celtis	x	x	x
Elaeagnus	x	x	x
Juglans	x	x	x
Prunus	x	x	x
Ulmus	x	x	x
Cedrelospermum †	?	?	?
Trigonobalanopsis †	?	?	?

Note: RF, riparian forest; MF, mesic forest; DF, dry forest.

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Supplemental data

Supplemental data for this article can be accessed here.

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