THE OCCURRENCE OF POLLEN OF SCIADOPITYACEAE LUERSS. THROUGH TIME

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Abstract: Here we present LM and SEM data of pollen of extant Sciadopitys verticillata, fossil Cerebropollenites from Aptian/Albian strata (Austria, Mongolia) and Sciadopityspollenites from Campanian/Maastrichtian and Oligocene/Miocene strata (Siberia, Germany). Measurements and image comparisons show that the investigated fossil pollen taxa range from somewhat comparable to very similar to extant Sciadopitys verticillata, and that a previous affiliation of Cerebropollenites taxa with Tsuga cannot be corroborated. Additionally, it can be speculated that either the Rhaetian to Lower Cretaceous Sciadopityspollenites macroverrucosus and Cerebropollenites serratus (R. Potonie) Raatz ex R. Potonie have been affiliated with extant Sciadopitys verticillata, and should be used only when the pollen in question is undoubtedly Sciadopitys Siebold et Zucc.. This has been corroborated by investigating pollen wall ultrastructures of fossil Sciadopityspollenites and extant Sciadopitys taxa (Surova and Kvatadze 1988). For the Upper Cretaceous record also known to consist of macrofossils of Sciadopitys (Ohsawa et al. 1991, Saiki 1992; both ovulate cones), but macrofossils and pollen were much more common during the Neogene (e.g., Manum 1962, Krutzsch 1971, Boulter and Kvaček 1989, Schneider 1992, Hofmann et al. 2002, Stuchlik et al. 2002, Dolezych and Schneider 2006, Grimsson and Zetter 2011). The pollen genus Cerebropollenites occurs from the Lower Jurassic (Hettangian) to Lower Cretaceous in the northern hemisphere (e.g., Fisher and Dunay 1981, Visscher and Brugman 1981, Hemgreen et al. 1996, Larsson 2009). In later papers, Cerebropollenites pollen were analysed using TEM (e.g., Batten and Dutta 1997, Sanchez et al. 2001).

Key words: Sciadopityaceae, pollen, Cretaceous, Neogene, Cerebropollenites, Sciadopityspollenites

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Introduction

The extant umbrella pine (Sciadopitys verticillata Siebold et Zucc.) is the only member of the phylogenetically isolated Sciadopityaceae LuerSS. (Farjon 2005, Eckenwalder 2009, Earle 2021), and is an evergreen conifer tree now only present in southern and western Japan, where it is restricted to parts of southern Honshu, Shikoku, and Kyushu (Farjon 2005, Earle 2021). Here it occurs on rocky slopes in mixed middle altitude cloud forests at 500–1,200 m elevation (Farjon 2005, Eckenwalder 2009, Earle 2021). In contrast to its very restricted distribution today, its macrofossils are known from the northern hemisphere of Eurasia since the Upper Cretaceous from Japan (Saiki 1992, Uemura 1986), probably the Paleocene of Canada (Christophel 1973) and since the Eocene in Germany (Dolezych and Schneider 2006, Sadowski et al. 2016). There are even earlier occurrences affiliated to Sciadopityaceae all summarized in the family of Miroviaceae M. N. Bose et Manum, but the relationships of these fossils to Sciadopityaceae are not resolved (see below).

To reconstruct the fossil history of Sciadopityaceae, we focus here on fossil pollen genera associated with Sciadopityaceae, such as Sciadopityspollenites R. Potonie., and on the fossil pollen genus Cerebropollenites T. Nilsson, which has been compared, particularly C. macroverrucosus (Thierg.) Eberh.Schulz (synonyms of this species are also: Pollenites macroverrucosus Thierg., Tsugaepollenites mesozoicus Couper and Cerebropollenites mesozoiacus (Couper) Tage Nilsson; see Schulz 1967: 603), with extant Tsuga canadensis Carrière (Couper 1958, Nilsson 1958). The genus Sciadopityspollenites is known from the Upper Cretaceous onwards (this paper and Takahashi 1997). After Potonie (1967: 153), the species Sciadopityspollenites serratus (R. Potonie et VenitZ) Raatz ex R. Potonie has been affiliated with extant Sciadopitys verticillata, and should be used only when the pollen in question is undoubtedly Sciadopitys Siebold et Zucc.. This has been corroborated by investigating pollen wall ultrastructures of fossil Sciadopityspollenites and extant Sciadopitys taxa (Surova and Kvatadze 1988).
Dettman and Potonié (2003), and these authors also suggested affinities with *Tsuga Carrière*, or at least an old lineage leading to or an ancestral group of *Tsuga*, despite the fact that *Tsuga*-like macrofossils are known only from the Upper Cretaceous strata onwards (e.g., Kirchheimer 1934, Florin 1963, Ferguson 1967, LePage 2003). However, not everybody was convinced by this botanical affiliation: Klaus (1987: 260) describes *Tsugaepollenites mesozoicus* Couper (≡ *Cerebropollenites mesozoicus* = *C. macroverrucosus*) as a pollen with *Sciadopitys*-habit, and other scientists instead of using the pollen genus *Cerebropollenites* preferred *Sciadopityspollenites* such as: “*S. macroverrucosus*” and “*S. mesozoicus*” (Waksmundzka 1981, Ilyina 1985, Ichinnorov 2003, Kuzmichev et al. 2018), thus increasing the number of species in *Sciadopityspollenites*. To clear up these misunderstandings, this paper represents various *Cerebropollenites* and *Sciadopityspollenites* pollen grains analysed with LM and SEM from various localities and ages, and compares them with extant pollen come from Austria (Rehbreingraben Formation “Gaultflysch”; Egger and Coric 2017). The stratigraphic age of the Austrian locality, which is situated near St. Pölten (Lower Austria), has been constrained by dinoflagellate cysts (see Egger and Coric 2017: 49–51).

**Locality 1.** The Aptian to Albian coastal sediments from Austria (Rehbreingraben Formation “Gaultflysch”; Egger and Coric 2017). The stratigraphic age of the Austrian locality, which is situated near St. Pölten (Lower Austria), has been constrained by dinoflagellate cysts (see Egger and Coric 2017: 49–51).

**Locality 2.** The Aptian to Albian coal-bearing strata from Mongolia (Khovil-open pit mine) in the Khovil-Tugrug subbasin (Choir-Nyalsga basin, SE of Ulaanbaatar, central Mongolia), for which the stratigraphic range has been determined by the presence of various *Pilogisporites notensis* Cookson et M.E.Dettmann, *Osmundaditites wellmanii* Couper, *Aequiriradites spinulosus* (Cookson et M.E.Dettman) Cookson et M.E.Dettman, *Taurocuspores reducns* (Bolikh.) Stover, *Leptolepidites verrucatus* Couper, *Cicatricosisporites australiensis* R.Potónie, *Cyathidites australis* Couper, *Pinuspollenites aralis*us Bolikh., *Alisporites sp.* *Cycadopites sp.* *Araucariadites australis* Cookson, *Classopolis classoides* Pflug etc. (Hofmann et al. in prep.).

Both Aptian/Albian localities contain palynological assemblages dominated by bryophytes, fern spores and pollen of Pinaceae, Cupressaceae and Ginkgoaceae.

**Locality 3.** The Campanian/Maastrichtian strata of the Timerdayahkh Formation come from sedimentological profiles of riverbank outcrops along the Tuung River in the Vilui basin (west Siberia, Russia). Most of the samples yielded various stratigraphically valuable species of *Aquilapollenites* Rouse emend. by Srivastava and Rouse (1970), *Manicorpus N.Mchedl.* and *Azonia Samoilovitch

Material and methods

The fossil pollen grains come from four localities in total, two of Lower Cretaceous, one Upper Cretaceous, and one Oligocene/Miocene ages. The extant pollen come from Japan, collected by LJS from the Dajiwa-Gura cliff edge of the Mt. Odaigahara plateau (altitude 1,500–1,560 m), Nara Prefecture, Central Japan, in 2012.

**Locality 1.** The Aptian to Albian near coastal sediments from Austria (Rehbreingraben Formation “Gaultflysch”; Egger and Coric 2017). The stratigraphic age of the Austrian locality, which is situated near St. Pölten (Lower Austria), has been constrained by dinoflagellate cysts (see Egger and Coric 2017: 49–51).

**Locality 2.** The Aptian to Albian coal-bearing strata from Mongolia (Khovil-open pit mine) in the Khovil-Tugrug subbasin (Choir-Nyalsga basin, SE of Ulaanbaatar, central Mongolia), for which the stratigraphic range has been determined by the presence of various *Pilogisporites notensis* Cookson et M.E.Dettmann, *Osmundaditites wellmanii* Couper, *Aequiriradites spinulosus* (Cookson et M.E.Dettman) Cookson et M.E.Dettman, *Taurocuspores reducns* (Bolikh.) Stover, *Leptolepidites verrucatus* Couper, *Cicatricosisporites australiensis* R.Potónie, *Cyathidites australis* Couper, *Pinuspollenites aralis*us Bolikh., *Alisporites sp.* *Cycadopites sp.* *Araucariadites australis* Cookson, *Classopolis classoides* Pflug etc. (Hofmann et al. in prep.).

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pollen. The investigated material comprises very fine-grained to fine-grained floodplain, palaeosol, peat, lake and mud clast/drape sediments (Hofmann and Zetter 2007, 2010, Spicer et al. 2008).

**Locality 4.** The Oligocene/Miocene sedimentary succession of the Bayerhof-Maar (Bavaria, Germany) starts with a volcanic breccia, and is then filled with lake sediments that are terminated by a swampy to peaty phase (Rohrmüller 2003). The Maar is part of a Neogene volcanic zone in the still tectonically active area between the Eger rift and the Franconian line at the margin of the Bohemian mountains, and the sediments have K/Ar-age of 23.3 and 21.7 myr (Rohrmüller and Horn 2003). The microflora represents a peculiar mixture of Oligocene and Miocene elements (Sachse and Hofmann 2020).

The sedimentary rock samples were washed, dried and milled with a mortar and pestle. The resulting powder was treated with HCl, HF and subsequent acetylation to reduce silicate, carbonates, organic material such as wood and other palynodebris, and to darken the colour of the palynomorph walls. The remaining palynomorph extract was mixed with glycerine and stored in small glass vials. For investigation, a drop of extract was smeared onto a glass slide and evenly spread to search for pollen to be investigated. The investigated pollen grains then were transferred with a micro-manipulator (fine hair glued to a preparation needle) to a clean drop of glycerine on another slide and photographed. Then these pollen grains were again transferred with a micro-manipulator onto a SEM stub, washed with alcohol and then sputtered with gold. SEM investigation was done with a FEI Inspect S 5001. Pollen sacs from a small male pollen cone of *Sciadopitys verticillata* were soaked in a drop of acetylation mixture on a glass slide and manipulated with a needle to release the pollen from the sacs. The sacs in the acetylates mixture were repeatedly heated up for a few seconds over a candle flame to colour the pollen wall and drive out the cell contents. The pollen was then fished out with a micro-manipulator (hair mounted on a needle) and transferred to a clean drop of glycerol for LM photography, together with a micrometer (Nikon). After photography, the pollen was moved with a micro-manipulator to SEM stubs, like the fossil pollen. The stubs are stored under inventory numbers IPUW 3830_10a–j, 7840_20a–f, 7840_30a–f at the Institute of Palaeontology, University Vienna (IPUW).

**Systematic palaeobotany.** Measurements of extant and fossil pollen of *Sciadopityaceae* and some *Tsuga* species and measurements from the literature (Macko 1957, Couper 1958, Schulz 1967, Stuchlik et al. 2002) are summarized in Table 1, and show that the size of *Sciadopitys verticillata* pollen corresponds with sizes of all fossil *Cerebropollenites* spp. and *Sciadopityspollenites* pollen, and are considerably smaller than extant and fossil *Tsuga* pollen (Kirchheimer 1934, Ueno 1951, Ho and Sziklai 1972, Grimsson and Zetter 2011, Sachse and Hofmann 2020, Hofmann – unpublished data).
Family Sciadopityaceae

Genus Sciadopitys Siebold et Zucc., 1842

Sciadopitys verticillata Siebold et Zucc., 1842

Text-fig. 1a–i

Description. Monad pollen of spheroidal to suboblate shape, elliptical to circular in polar view and elliptical in equatorial view; equatorial diameter 41.7 to 53.3 µm (LM, N = 11) and 24.4 to 37.1 µm (SEM, N = 5); polar diameter 35.5 to 43.3 µm (LM, N = 3) and 23.8 to 24.6 µm (SEM, N = 2); wall thickness in general using LM ranges from 2.3 to 3.3 µm (N = 1), using SEM 1.7 µm (N = 1); nexine ca. 0.6 µm and sexine ca. 1.1 µm); wall thickness at the leptoma was not measurable under LM and once under SEM: nexine 0.4 µm; sexine 0.3 to 0.7 µm (if present); sculpturing verrucate and occasionally slightly rugulate, perforate to foveolate with evenly spaced supratectal echini, verrucae and rugulae are not the result of a folding sexine; leptoma area either naked or unevenly covered by angular, partly echinate micro-verrucae.

Remarks. The verrucae and rugulae are the smallest of here-investigated pollen.

Genus Cerebropollenites Tage Nilsson, 1958

Cerebropollenites thiergartii Eberh.Schulz, 1967

Text-fig. 2a–c

Occurrence. Locality 1, St. Pölten, Austria.

Description. Monad pollen of subspheroid to suboblate shape, elliptical in equatorial view; equatorial diameter ca. 55.5 µm (LM) to 48.9 µm (SEM); polar diameter ca. 40 µm (LM) to 37.6 µm (SEM, N = 1); wall thickness 2.5 to 3.1 µm; nexine thinner than sexine; sculpturing verrucate
to occasionally rugulate and perforate covered with evenly spaced supratectal echini; leptoma area either naked or unevenly covered by angular, partly echinate micro-verrucae.

**Cerebropollenites thiergartii** Eberh.Schulz, 1967

*Text-fig. 2d–f*

**Occurrence.** Locality 2, Khovil opencast mine, Mongolia.

**Description.** Monad of subspheroidal shape, circular to elliptical pollen grain in polar view, and elliptical in equatorial view; equatorial axes 42.4–48.7 µm (LM) and 33.1 to 37.4 µm (SEM), polar axis ca. 24.4 µm (SEM, N = 3); wall thickness ca. 2.2 to 2.8 µm, probably thinning towards the leptoma (thinning well visible on LM image); sculpturing verrucate to occasionally rugulate, perforate, with evenly distributed supratectal echini; leptoma partly covered with echinate micro verrucae.

Remarks. In two *C. thiergartii* specimens the verrucae are considerably smaller than in *C. macroverrucosus* (see below), and very well comparable to the ones in *Sciadopityspollenites serratus* and extant *Sciadopitys verticillata*.

**Cerebropollenites macroverrucosus** (Thierg.)

*Text-fig. 2g–i*

**Occurrence.** Locality 2, Khovil opencast mine, Mongolia.
Description. Monad of spheroidal shape; circular to subcircular in polar and equatorial view; equatorial axes 35.5 µm (LM) and 26.6 to 31 µm (SEM, N = 1); equatorial diameter ca. 31.1 (LM) and 18.3 µm; wall thickness ca. 1.8 to 2.7 µm, probably thinning towards the leptoma; sculpturing rugulate to verrucate, unevenly and faintly perforate, with loosely arranged supratectal echini; leptoma covered with smaller echinate verrucae.

Remarks. Here the rugulae and verrucae are the largest in the investigated pollen.

*Sciadopityspollenites* R.POTONIÉ, 1958
cf. *Sciadopityspollenites serratus* (R.POTONIÉ et VENITZ)
R.POTONIÉ, 1958
Text-fig. 3a–f

Occurrence. Locality 3, Vilui Basin opencast mine, Russia.

Description. Monad pollen of spheroidal to oblate shape, elliptical to circular in polar view and elliptical in equatorial view; equatorial diameter ca. 45.5 to 53.3 µm (LM) and 26.4 to 35.7 µm (SEM, N = 2); the polar diameter ca. 36.6 to 37.7 µm (LM) and 27.2 to 29 µm (SEM); wall thickness ca. 2.4 to 2.8 µm, nexine thinner than sexine; wall thickness at leptoma was not measurable under LM, but looks thinner; sculpturing verrucate, perforate covered densely with evenly spaced supratectal echini; leptoma sulcus shaped and much less ornamented.

Remarks. These specimens are very comparable with extant pollen, but have smaller and fewer perforations than the Oligocene to Miocene *Sciadopityspollenites serratus* described below.

Text-fig. 3. Upper Cretaceous to Oligocene/Miocene *Sciadopityspollenites* taxa, all scale bars in LM and SEM overview images 10 µm, scale bars in SEM detailed images 2 µm, a–f: cf. *Sciadopityspollenites serratus* from Vilui basin (Siberia), a - LM image, equatorial view, b - SEM equatorial overview with leptoma, c - detail SEM of leptoma? and echinate verrucae, d - LM image equatorial view, e - SEM of distal polar view, f - SEM detailed view of verrucate, echinate perforate sexine sculpturing; g–i: *Sciadopityspollenites serratus* from Bayerhof Maar (Germany), g - LM image of proximal polar side, h - SEM overview of distal polar side, i - SEM detail of verrucate, echinate, perforate sculpturing.
**Sciadopityspollenites serratus** (R.Potonié et Venitz)

R.Potonié, 1958

Text-fig. 3g–i

**Occurrence.** Locality 4, Bayerhof Maar, Germany.

**Description.** Monad pollen of suberoshedral to oblate shape, elliptical to circular in polar view, elliptical in equatorial view; equatorial diameter ca. 36.5–48.8 μm (LM) and 38.6 to 50.5 μm (SEM, N = 1); wall thickness ca. 1.9 to 2.2 μm; nexine thinner than sexine; wall thickness at leptoma was not measurable under LM but looks thinner; sculpturing verrucate to rugulate and faintly perforate covered with evenly spaced supratectal echini; leptoma sulcus shaped and much less ornamented (visible under LM).

**Remarks.** This pollen grain has also been displayed in Sachse and Hofmann (2020), and is more perforated than the extant specimens.

**Discussion.**

There are considerable differences in pollen sizes, depending whether one measures the pollen in glycerol or a comparable mounting medium under LM, or in a more desiccated state after washing with alcohol under SEM; the SEM measurements are always smaller (Tab. 1 and descriptions). In the older literature (e.g., Macko 1957, Couper 1958, Schulz 1967), the sizes are the result of measurements under LM, and the maximal sizes are considerably larger than the SEM sizes (compare data of Grimsson and Zetter 2011: 203). Additionally, the longer the time span whilst acetolyzing extant pollen material, the more the size decreases, and even the shape of the pollen can change. It is suggested that the individual fossilization processes (depth, temperature, pressure) have an influence on the varying sizes of fossil pollen in different localities: for example, the pollen of *Cerebropollenites macroverrucosus* and *C. thiergartii* from the opencast Khovil basin coal (Mongolia) are relatively smaller than the ones described by Schulz (1967) from Central Europe. The same is true for *C. thiergartii* from St. Pölten (Austria). Generally, when comparing pollen sizes of extant species with fossil Sciadopityaceae, the fossil ones are somewhat smaller, and overall, the pollen of Sciadopityaceae are smaller than extant and fossil *Tsuga* species (Tab. 1). This also can be said for the size of the leptoma of Sciadopityaceae and *Tsuga* on the proximal pole (Tab. 1).

All pollen investigated are characterised by more-or-less regularly distributed very small supratectal echini, these echini are quite loosely arranged on *Cerebropollenites macroverrucosus*, but densely arranged on the rest of the extant and fossil investigated pollen grains. In contrast, only one species of *Tsuga* (*T. heterophylla* Sarg.) is somewhat echinate (see Ho and Sziklai 1972: figs. 23, 24; Sachse and Hofmann 2020: pl. 2, figs. 5, 6 of fossil *Tsuga heterophylla*-type), but the echini are much larger and longer than the echini of Sciadopityaceae. The same is true for the presence of perforations of the sexine in extant (well visible) and fossil Sciadopityaceae: they are quite conspicuous (nearly foveolate in the Oligocene/Miocene *Sciadopityspollenites serratus*), fairly visible on *Cerebropollenites thiergartii*, and not so well observable on *Cerebropollenites macroverrucosus*. *Tsuga*, on the other hand, has no perforations in the sexine.

The TEM investigation of pollen walls of extant *Sciadopitys verticillata* by Kurmann (1992: fig. 2C) and Uehara and Saiki (2011: figs 12–18) show that the sculpturing of the sexine is not the result of an undulating sexine, as suggested by Batten and Dutta (1997: 35, 37), and to some degree by Shang and Zavada (2003), but a result of a continuous size increase of ectexine granules that at the end can fuse to produce a relatively unstructured layer (Uehara and Saiki 2011: 181–182). The undulating or folding sexine is a feature that can be clearly observed in extant *Tsuga canadensis* (Kurmann 1992: TEM section fig. 1d). However, in Shang and Zavada (2003: TEM sections in figs 8–11), an occasional undulating exine can be observed.

Besides the pollen record, we want to also discuss macrofossils assigned to the Sciadopityaceae, to reconstruct the biogeographical history of this family. The most common fossils are of the cladodes, although cones, seeds and wood are also preserved. In extant *Sciadopitys* these cladodes, sometimes termed “double-needles” (e.g., Eckenwalder 2009), are the photosynthetic organs, as the leaves are very reduced. They are characterised as long and thin needle-like structures with an emarginate tip and a glabrous adaxial groove, and a deep central abaxial papillate groove (Florin 1931, Eckenwalder 2009, Dörken and Stützel 2011). The stomata are within the abaxial groove, but obscured by the papillae (Farjon 2005). Additionally, there are the two vascular bundles running on either side of the median groove (Dörken and Stützel 2011).

The earliest *Sciadopitys*-like macrofossils consisting of cones and cladodes are Upper Cretaceous-aged remains from Japan (Ogura 1932, Tsukada 1963, Ohsawa et al. 1991, Saiki 1992). During the Cenozoic, these fossils (cladodes assignable to *Sciadopitys tertiaire* MENZEL, cones and wood fragments assigned to *Sciadopityoxylon wettsteinii* JURASKY) occur more frequently in Europe from the Eocene – Pliocene (Menzel 1913, Florin 1922, Jurasky 1928, Gothan 1936, Thiergart 1949, Weyland et al. 1967, Schneider 1992, 2004, 2008, Mai 1995, 1999, 2000, 2004, Figueiral et al. 1999, Philippe et al. 2002, Dolezych 2005, Dolezych and Schneider 2006, Manchester et al. 2009), with cladodes assignable to *Sciadopitys* occurring in Eocene Baltic amber (Sadowski et al. 2016). There are suggestions that *Sciadopitys* was a source plant for this amber deposit, based on chemical analyses (Wolfe et al. 2009). The incompletely preserved *Sciadopitophyllum canadense* CHRISTOPHEL is not thought to be closely related as the emarginate leaf tips and cuticular features were not preserved (Christophel 1973).

Older (Lower Jurassic to Lower Cretaceous) fossil conifer needles with a deep abaxial papillate groove had been thought to be *Sciadopitys*-like, and were described as *Sciadopitytes GÖPP. et MENGE in Halle* (1915). This was transferred to *Sciadopityoides SVESNIK., which was then subsequently split in to *Mirovia REYMAN. emend. by Bose and Manum (1991), Oswaldtheeria M.N.BOSE et MANUM, Holkopytis M.N.BOSE et MANUM and Sciadopityoides SVESNIK. emend. by Bose et Manum (1991). Species assigned to Oswaldtheeria were then transferred back to *Mirovia* following reinvestigation of the type material (Nosova and Wcislo-Luranec 2007). Now these genera...
are placed in the Miroviaceae M.N. Bose et Manum, which are distinguished from Sciadopitys by the absence of an emarginate tip and two veins (Bose and Manum 1991, Manum et al. 2000). These taxa originate from circum-Arctic localities (Halle 1915, Florin 1922, Bose 1955, Gothan and Weyland 1973, Bose and Manum 1990, 1991), Poland (Reymanówna 1985, Nosova and Wcisło-Luraniec 2007), Germany (Manum et al. 2000), Spain (Gomez 2002) and Kazakhstan (Nosova and Kiritchkova 2008). The exact relationship of the Miroviaceae to Sciadopitys remains uncertain.

If we combine the new fossil and extant pollen data and that of the macrofossils, a few points arise: if the pollen from the Lower Cretaceous localities in Europe and Asia (e.g., Cerebropollenites macroverrucosus and C. thiergartii) have putative macrofossil equivalents in the Miroviaceae.

Table 1. Measurements of extant and fossil Sciadopityaceae and Tsuga pollen grains, and some data from the literature. Abbreviations: verr = verrucate, rugul = rugulate, micr-verr = micro-verrucate, suprat. = supratectal, Rhaet = Rhaetian, Hett = Hettangian, Juras = Jurassic, Cretac = Cretaceous, Apt = Aptian, Alb = Albian, Camp = Campanian, Maast = Maastrichtian, Olig = Oligocene, Mioc = Miocene. Symbols: * = questionable, because the ectexine sculpture under SEM of this taxon resembles more Cupressaceae than Sciadopityaceae.

| taxon | age; place | equatorial axe in µm LM / SEM | polar axe in µm LM / SEM | leptoma size in µm LM / SEM | sculpture SEM | suprat. echinit | reference |
|-------|------------|-------------------------------|--------------------------|---------------------------|---------------|-----------------|-----------|
| Sciadopitys verticilliata extant; Japan 41.7–53.3 / 24.4–37.1 35.5–53.5 / 23.8–24.6 26.5–40 / 25.2–25.6 verr-rugul dense this paper |
| Sciadopitys verticilliata extant 38–45 / – 34–36 / – verr – Stuchlik et al. 2002 |
| Tsugapollenites macroverrucosus Jura/Cretac; Britain 45 (65) 88 / – – rugul-verr ? Couper 1958 |
| Cerebropollenites macroverrucosus Rhaet/Hett; Germany ?82 / / 342 / 16–20 / rugul-verr ? Schulz 1967 |
| Cerebropollenites thiergartii Rhaet/Hett; Germany 40 (56) 80 / – – <36 / rugul-verr ? Schulz 1967 |
| C. macroverrucosus Abl/Alb; Mongolia 35.5 / 26.6–31 31.1 / 18.3 15.5 / 10 rugul-verr loose this paper |
| C. thiergartii Abl/Alb; Austria 55.5 / 48.9 40 / 37.6 36.7 / 27.4 verr dense this paper |
| C. thiergartii Abl/Alb; Mongolia 42.4–48.7 / 33.1–37.4 / 24.4 34.4 / 20 verr dense this paper |
| Sciadopityspollenites serratus Camp/Maas; Siberia, Russia 45.5–53.3 / 26.4–35.7 36.3–37.8 / 27.2–29 37–44 / 28 verr dense this paper |
| S. serrata Oligo/Mioc; Germany 36.6–48.8/ 38.6–50.5 / – 35.5 / verr dense this paper |
| S. miniverrucatus* mid Miocene; Poland 33–46 / 33.8–36.6 / – 22.7–29.4 micr-verr – Stuchlik et al. 2002 |
| S. quintus mid Miocene; Poland 34–41 / 31.4–41.4 / – 23–29 / – dense Stuchlik et al. 2002 |
| S. tuberculatus Miocene; Poland 30–60 / 26.1–37.8 / – 26–40 / rugul-verr dense Stuchlik et al. 2002 |
| S. tulbarus* mid Miocene; Poland 36–51 / 24.3–29.1 / – 26–28 / micr-verr – Stuchlik et al. 2002 |
| S. varius mid Miocene; Poland 35–55 / – 36–38 / verr – Stuchlik et al. 2002 |
| S. verticiliatiformis* Mioc/Pho; Poland 32.8–41 / 25.3–29.7 / – – micr-verr – Stuchlik et al. 2002 |
| Sciadopityspollenites sp. mid Miocene; Poland 38–56 / – – verr – Stuchlik et al. 2002 |
| “Sciadopitys verticilliata” (fossil) Miocene; Poland 48–62 / 35.6–46 / – – verr ? Macko 1957 |
| Sciadopitys sp. Miocene; Austria 38–45 / 35–40 31–34 / – verr dense Grimsson and Zetter 2011 |
| Tsuga heterophylla extant; Brit. Columbia, Canada 73.1 / 59 / – – Ho and Sziklai 1972 |
| Tsuga mertinsiana extant; Vancouver, Canada 65.1 / 61.9 / – – Ho and Sziklai 1972 |
| Tsuga spp. extant; Japan >55 / – – – – Ueno 1957 |
| Tsuga sp. 1 Miocene; Austria 75–80 / 70–75 40–45 / 67.3–70.7 / 50–55.1 / – – Grimsson and Zetter 2011 |
| Tsuga sp. 2 Miocene; Austria 70–80 / 65–75 40–50 / 60–65 / 52 / – – Grimsson and Zetter 2011 |
| Tsuga sp. 1 Miocene; Austria 100 / 86.4 75 / 82 / – – Hofmann unpublished |
| Tsuga sp. 2 Miocene; Austria 60 / 39.2 – 33.3 / – – Hofmann unpublished |
| Tsuga heterophylla-type Oligo/Mioc; Germany 86.6 / 66.5 / – 66.6 / 57.3 / – – Sachse and Hofmann 2020 |
| Tsuga spp. Pilocene 33.6–88.2 / – – – – Kirchheimer 1934 |
family (which still has uncertain relationships to the extant Sciadopityaceae), and the fact that particularly C. thierrgartii is very similar to extant and fossil (e.g., Sciadopityspollenites serratus) pollen of Sciadopityaceae, one could speculate that the fossil Miroviaceae family is either an extinct lineage of sciadopityaceaous-like plants, or sits as a group at the base of an evolving lineage of the Sciadopityaceae that is represented today by the relict species Sciadopitys verticillata. However, no male Miroviaceae cones including pollen have been found yet to prove that this is true. On the other hand, Sciadopityspollenites taxa (S. serratus, S. quintus, S. tuberculatus, S. varius) and all Paleocene to Neogene macrofossils can undoubtedly be assigned to Sciadopityaceae.

Conclusions

The verrucate to rugulate nature of the sexine plus the supratectal micro-echinate ornamentation present on all pollen investigated here strongly indicate that they are related to Sciadopityaceae. Also, the smaller sizes of the pollen grains and the irregular shapes of the verrucae and rugulae might decrease and vary through the time of observation (Aptian through present), but we suggest that there is a clear evolutionary line leading from Cerebropollenites via Sciadopityspollenites to Sciadopitys verticillata, rather than to Tsuga, as proposed by some previous authors. However, because of the similarity of pollen of Cerebropollenites thierrgartii with fossil Sciadopityspollenites taxa and Sciadopitys verticillata, it can be only speculated whether the fossil pollen taxon Cerebropollenites is the pollen equivalent to the Miroviaceae family, and so represents an extinct lineage of “Sciadopitys”-like plants, or if this family represents a basal part of the Sciadopitys lineage, which is well documented from the Upper Cretaceous onwards in Eurasia.

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