



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 *Cerebropollenites* taxa are the pollen equivalent of the Eurasian Miroviaceae macrofossils that have unresolved relationships with *Sciadopityaceae*, or that they might belong to a basal group in the *Sciadopityaceae*, which is quite recognizable due to the similarity of the pollen morphology of *Cerebropollenites thiergartii* and *Sciadopitys verticillata*. However, until in situ pollen within cones attributed to the Miroviaceae are found, we will not know for sure.

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. POTONIÉ, 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 mesozoicus* (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 Potonié (1967: 153), the species *Sciadopityspollenites serratus* (R. POTONIÉ et VENITZ) RAATZ ex R. POTONIÉ 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 Kvavadze 1988). The Upper Cretaceous record is 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, Herngreen et al. 1996, Larsson 2009). In later papers, *Cerebropollenites* pollen were analysed using TEM (e.g., Batten and Dutta 1997,

Shang and Zavada 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 of *Sciadopitys verticillata* to show that both the fossil genera are related.

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 Daija-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-Nyalga basin, SE of Ulaanbaatar, central Mongolia), for which the stratigraphic range has been determined by the presence of various *Pilosisporites notensis* COOKSON et M.E.DETTMANN, *Osmundacidites wellmanii* COUPER, *Aequitriradites spinulosus* (COOKSON et M.E.DETTMANN) COOKSON et M.E.DETTMANN, *Tauocusporites reduncus* (BOLKH.) STOVER, *Leptolepidites verrucatus* COUPER, *Cicatricosisporites australiensis* R.POTONIÉ, *Cyathidites australis* COUPER, *Pinuspollenites aralicus* BOLKH., *Alisporites* sp., *Cycadopites* sp., *Araucariadites australis* COOKSON, *Classopollis 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 Timerdayakh Formation come from sedimentological profiles of riverbank outcrops along the Tyung 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* SAMOJLOVITCH

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 acetolysis 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 extant *Sciadopitys verticillata* were soaked in a drop of acetolysis mixture on a glass slide and manipulated with a needle to release the pollen from the sacs. The sacs in the acetolyses 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* LUERSS., 1877

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 supracteal echini,

rugulae and verrucae 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.

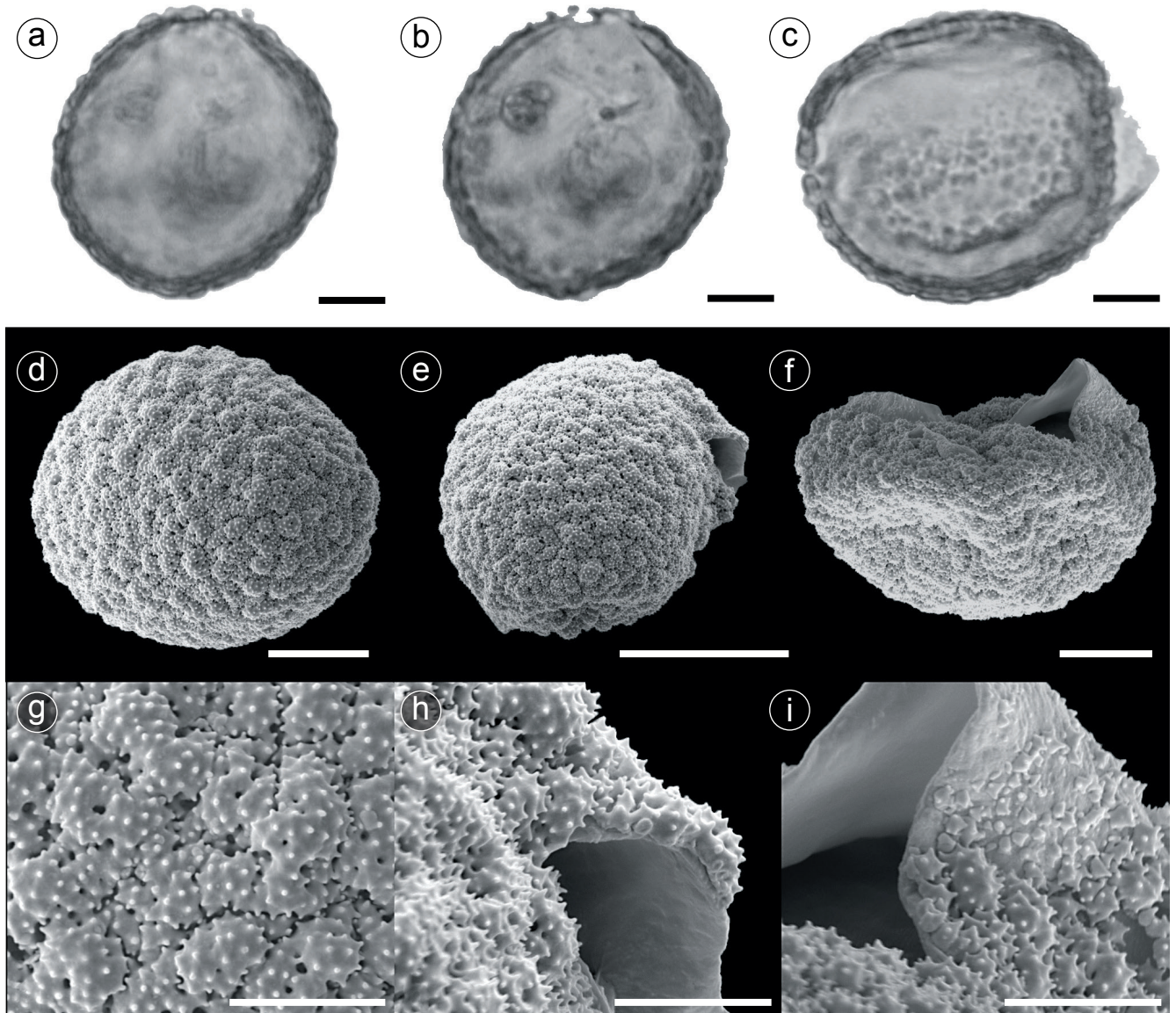
Genus *Cerebropollenites* TAGE NILSSON, 1958

Cerebropollenites thiergartii EBERH.SCHULZ, 1967

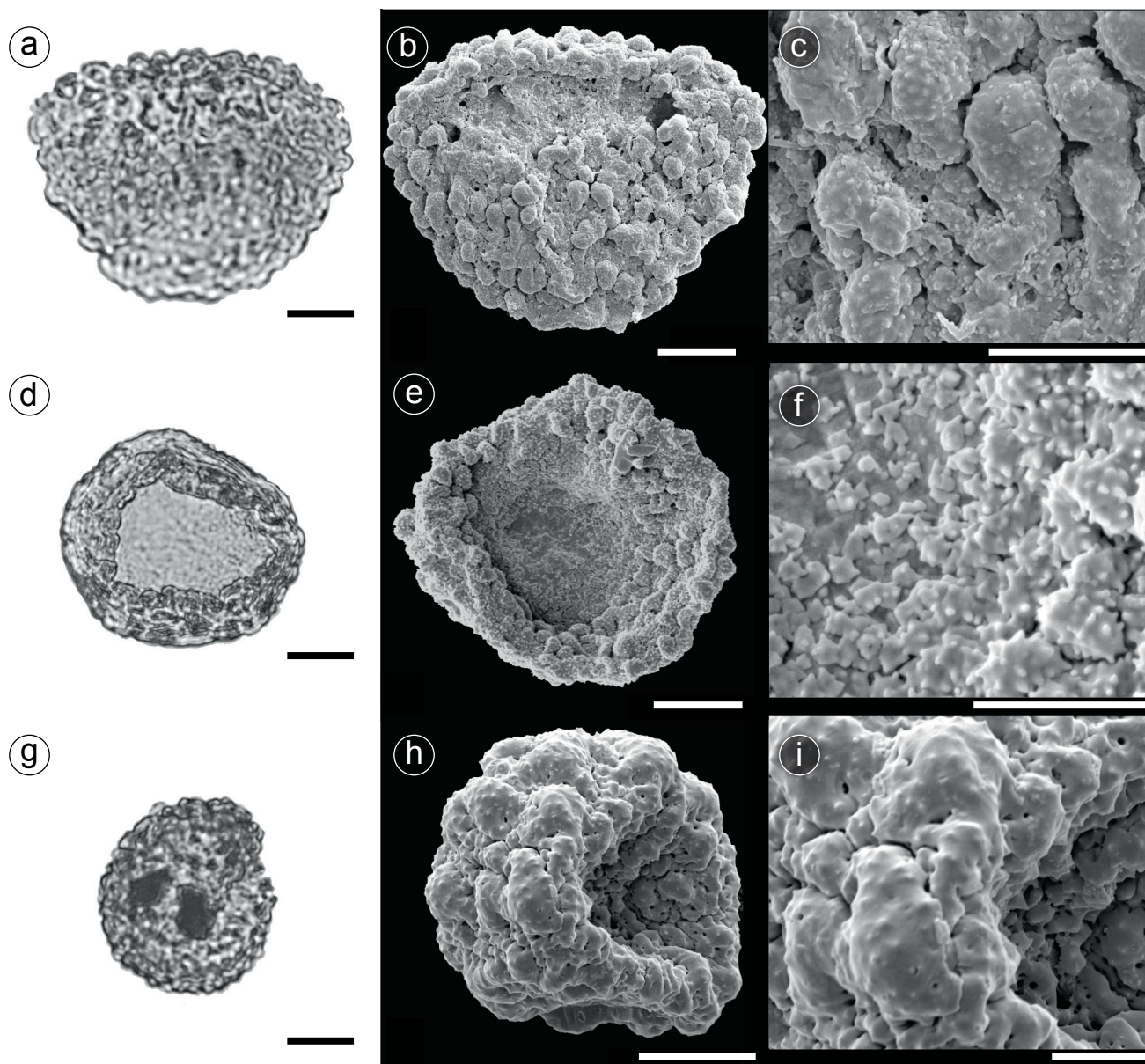
Text-fig. 2a–c

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



Text-fig. 1. Extant *Sciadopitys verticillata* pollen. a–c: LM images (scale bars 10 μm), a – polar view, b – equatorial view, c – equatorial view with well visible thinning of proximal leptoma; d–e: SEM overview images (scale bar 10 μm), d – distal polar view, e – oblique equatorial view; f – equatorial view with leptoma at top; g–i: SEM detailed images (scale bars 2 μm), g – detail of verrucate, echinate, perforate sexine of distal pol, h – wall break displaying thin nexine and verrucate, echinate sexine, i – ripped open leptoma displaying transition from verrucate sculpturing to nearly psilate state.



Text-fig. 2. Aptian to Albian *Cerebropollenites* taxa, all scale bars in LM and SEM overview images 10 µm, scale bars in SEM detailed images 2 µm. a–c: *Cerebropollenites thiergartii* from St. Pölten (Austria), a – LM image, equatorial view, b – SEM equatorial overview with visible, less sculptured leptoma, c – detail of echinate verrucae; d–f: *Cerebropollenites thiergartii* from Khovil basin (Mongolia), d – LM image polar view with well visible thin-walled leptoma, e – SEM of proximal polar view with faintly sculptured leptoma, f – SEM detailed view of transition from leptoma to normal sexine sculpturing; g–i: *Cerebropollenites macroverrucosus* from Khovil basin (Mongolia), g – LM image of oblique equatorial view, h – SEM of oblique equatorial view with concave leptoma, i – SEM detail of the rugulate to verrucate sexine and smaller sculpturing in leptoma area.

to occasionally rugulate and perforate covered with evenly spaced supracteal 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 supracteal 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.)
EBERH.SCHULZ, 1967**

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 supracteal 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)

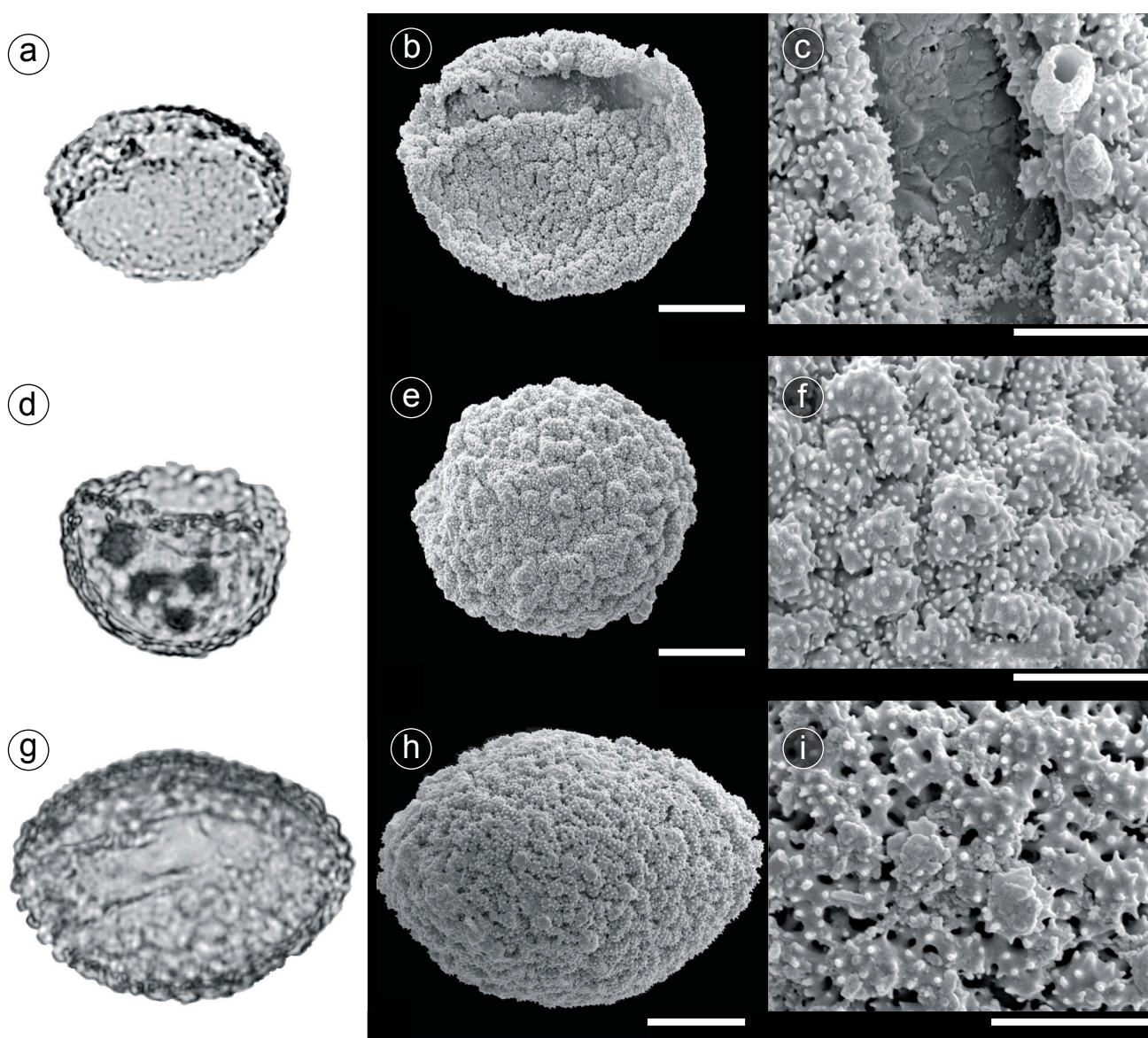
R.POTONIÉ, 1958

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 supracteal 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 subspheroidal 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 supracteal 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 considerable 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 supracteal 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 assigned to *Sciadopitys tertiaria* 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* SVESHNIK., which was then subsequently split in to *Mirovia* REYMAN. emend. by Bose and Manum (1991), *Oswaldheeria* M.N.BOSE et MANUM, *Holkopitys* M.N.BOSE et MANUM and *Sciadopityoides* SVESHNIK. emend. by Bose et Manum (1991). Species assigned to *Oswaldheeria* were then transferred back to *Mirovia* following reinvestigation of the type material (Nosova and Wcisło-Lurancic 2007). Now these genera

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. = supraterctal, 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. echini	reference
<i>Sciadopitys verticillata</i>	extant; Japan	41.7–53.3 / 24.4–37.1	35.5–43.3 / 23.8–24.6	26.6–40 / 25.2–25.6	verr-rugul	dense	this paper
<i>Sciadopitys verticillata</i>	extant	38–45 /	–	34–36 /	verr	–	Stuchlik et al. 2002
<i>Tsugaepollenites mesozoicus</i>	Juras/Cretac; Britain	45 (65) 88 /	–	–	rugul-verr	?	Couper 1958
<i>Cerebropollenites macroverrucosus</i>	Rhaet/Hett; Germany	?82 /	?42 /	16–20 /	rugul-verr	?	Schulz 1967
<i>Cerebropollenites thiergartii</i>	Rhaet/Hett; Germany	40 (56) 80 /	–	<36 /	verr	?	Schulz 1967
<i>C. macroverrucosus</i>	Abt/Alb; Mongolia	35.5 / 26.6–31	31.1 / 18.3	15.5 / 10	rugul-verr	loose	this paper
<i>C. thiergartii</i>	Abt/Alb; Austria	55.5 / 48.9	40 / 37.6	36.7 / 27.4	verr	dense	this paper
<i>C. thiergartii</i>	Abt/Alb; Mongolia	42.4–48.7 / 33.1–37.4	/ 24.4	34.4 / 20	verr	dense	this paper
<i>Sciadopityspollenites serratus</i>	Camp/Maast; Siberia, Russia	45.5–53.3 / 26.4–35.7	36.3–37.8 / 27.2–29	37–44 / 28	verr	dense	this paper
<i>S. serratus</i>	Oligo/Mioc; Germany	36.6–48.8/ 38.6–50.5	–	35.5 /	verr	dense	this paper
<i>S. miniverrucatus</i> *	mid Miocene; Poland	33–46 / 33.8–36.6	–	22.7–29.4	micr-verr	–	Stuchlik et al. 2002
<i>S. quintus</i>	mid Miocene; Poland	34–41 / 31.4–41.4	–	23–29 /	–	dense	Stuchlik et al. 2002
<i>S. tuberculatus</i>	Miocene; Poland	30–60 / 26.1–37.8	–	26–40 /	rugul-verr	dense	Stuchlik et al. 2002
<i>S. tubulus</i> *	mid Miocene; Poland	36–51 / 24.3–29.1	–	26–28 /	micr-verr	–	Stuchlik et al. 2002
<i>S. varius</i>	mid Miocene; Poland	35–55 /	–	36–38 /	verr	–	Stuchlik et al. 2002
<i>S. verticilliatiformis</i> *	Mioc/Plio; Poland	32.8–41 / 25.3–29.7	–	–	micr-verr	–	Stuchlik et al. 2002
<i>Sciadopityspollenites</i> sp.	mid Miocene; Poland	38–56 /	–	–	verr	–	Stuchlik et al. 2002
“ <i>Sciadopitys verticillata</i> ” (fossil)	Miocene; Poland	48–62 /	35.6–46 /	–	verr	?	Macko 1957
<i>Sciadopitys</i> sp.	Miocene; Austria	38–45 / 35–40	31–34 /	–	verr	dense	Grimsson and Zetter 2011
<i>Tsuga heterophylla</i>	extant; Brit. Columbia, Canada	73.1 /	59 /	–	–	–	Ho and Sziklai 1972
<i>Tsuga mertinsiana</i>	extant; Vancouver, Canada	65.1 /	61.9 /	–	–	–	Ho and Sziklai 1972
<i>Tsuga</i> spp.	extant; Japan	>55	–	–	–	–	Ueno 1957
<i>Tsuga</i> sp. 1	Miocene; Austria	75–80 / 70–75	40–45 /	67.7–70.7 / 50–55.1	–	–	Grimsson and Zetter 2011
<i>Tsuga</i> sp. 2	Miocene; Austria	70–80 / 65–75	40–50 /	60–65 / 52	–	–	Grimsson and Zetter 2011
<i>Tsuga</i> sp. 1	Miocene; Austria	100 / 86.4	75 /	82 /	–	–	Hofmann unpublished
<i>Tsuga</i> sp. 2	Miocene; Austria	60 / 39.2	–	33.3 /	–	–	Hofmann unpublished
<i>Tsuga heterophylla</i> -type	Oligo/Mioc; Germany	86.6 / 66.5	–	66.6 / 57.3	–	–	Sachse and Hofmann 2020
<i>Tsuga</i> spp.	Pliocene	33.6–88.2 /	–	–	–	–	Kirchheimer 1934

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

family (which still has uncertain relationships to the extant *Sciadopityaceae*), and the fact that particularly *C. thiergartii* 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 suprategal 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 thiergartii* 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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