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Low taxonomic resolution of papillate Cupressaceae pollen (former Taxodiaceae) impairs their applicability for palaeo-habitat reconstruction

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Abstract
The former family Taxodiaceae is currently treated as nine genera in five subfamilies of the family Cupressaceae. Pollen of the 'taxodiaceous' Cupressaceae typically has a papilla in the leptoma area and is common in Cenozoic strata because some of its genera were key elements in lignite forming swamp forests. Dispersed fossil pollen of this group are often assigned to particular genera and, based on the modern ecologies of these taxa, to particular palaeoenvironments. In this study, we investigated pollen of all nine genera of the former Taxodiaceae using light and scanning electron microscopy to evaluate whether pollen morphology can be used to discriminate modern genera of this paraphyletic group. We found few genus- or subfamily-diagnostic characters among members of taxodiaceous Cupressaceae. Features such as orbiculae and pollen and leptoma size cannot be used to discriminate subfamilies. However, three basal subfamilies share short papillae, whereas in two more derived clades (Sequoioideae and Taxodioideae) papillae are markedly longer. In the generally non-papillate core Cupressaceae, the leptoma (aperture) area may or may not possess a distinct circular thinning as also found in the basal grade of taxodiaceous Cupressaceae. Our results show that it is difficult if not impossible to distinguish genera of the ecologically distinct Taxodioideae and Sequoioideae based on pollen morphology. In view of a much wider ecological amplitude of many taxodiaceous Cupressaceae during large parts of the Cenozoic, we conclude that it is not recommendable to infer particular palaeoenvironments on the basis of dispersed taxodiaceous pollen grains alone.

Keywords: *Taxodiaceae, Cunninghamioideae, Taiwanioideae, Athrotaxidoideae, Sequoioideae, Taxodioideae, core Cupressaceae, leptoma, pollen sculpturing, phylogenetic framework, convergent evolution*

Dispersed pollen grains of papillate Cupressaceae (the former family Taxodiaceae; hereafter taxodiaceous Cupressaceae) are amongst the most abundant elements in Cenozoic pollen floras of the Northern Hemisphere (e.g. Krutzsch 1971; Stuchlik et al. 2002; Stockey et al. 2018; Hernandéz-Castillo et al. 2005; Fujiki & Ozawa 2008). The former Taxodiaceae (e.g. Page 1990) included the genera *Athrotaxis*, *Cryptomeria*, *Cunninghamia*, *Glyptostrobus*, *Metasequoia*, *Sequoia*, *Sequoiadendron*, *Taiwania*, and *Taxodium*. From a palynological point of view, this grouping appeared natural, as these genera produce non-saccate, spheroid pollen with a weak or distinct protuberance in the centre of the leptoma, the papilla (Erdtmann 1943). With the advent of molecular phylogenetic studies, it became clear that the Taxodiaceae is a paraphyletic group that forms part of a larger alliance of Cupressaceae (Brunsfeld et al. 1994; Gadek et al. 2000; Kusumi et al. 2000; Quinn et al. 2002). Currently, the nine genera of the former Taxodiaceae are accommodated in five subfamilies within Cupressaceae and form a grade that is basal to core Cupressaceae (consisting of two subfamilies Cupressoideae and Callistroideae). Both the taxodiaceous Cupressaceae and the core Cupressaceae have unambiguous fossil records from the Cretaceous (e.g. Hernandéz-Castillo et al. 2005; Sokolova et al. 2017; Stockey et al. 2018).

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Genera of the taxodiaceous Cupressaceae have frequently been identified in the dispersed fossil pollen record in Cenozoic strata. Furthermore, based on their modern distribution ranges and ecological properties they have been used to infer particular palaeoenvironments. For example, McIntyre (1991) distinguished *Metasequoia* and *Glyptostrobus* in Eocene strata of Axel Heiberg Island and referred both to warm temperate environments. From Eocene strata of Poland, Worobiec and Gedl (2018) reported the fossil-species *Inaperturopollenites concedipites* and *I. dubius* and suggested affinities with *Glyptostrobus* and *Taxodium*. In Oligocene and Miocene strata off the coast of New Jersey, Kotthoff et al. (2014) found taxodiaceous pollen, which they assigned to *Sequoia* and *Taxodium* and referred the former to well-drained and the latter to swamp conditions. Likewise, Larsson et al. (2006) distinguished between *Sequoia* (well-drained forests) and *Taxodium* (swamp forests) in Miocene strata of Denmark. Grímsson and Zetter (2011) assigned taxodiaceous pollen from Miocene strata of Austria to *Cunninghamia*, *Cryptomeria, Glyptostrobus*, and *Sequoia* and referred them to montane, swamp, and well-drained lowland environments. In another study, Biltekin et al. (2015) referred all taxodiaceous pollen (*Glyptostrobus* type) to swamp elements requiring warm climates (mega-mesothermic elements) in Miocene to Holocene strata of the Black Sea. In Neogene strata of Georgia (Transcaucasia), Shatilova et al. (2018) determined *Cunninghamia*, *Cryptomeria, Glyptostrobus*, *Metasequoia, Sequoia*, *Sequoiadendron*, and *Taxodium* and referred them as 'Arcto-Tertiary' elements. In Miocene and Pliocene strata of Italy, Bertini and Martinetto (2011) distinguished between *Sequoia*-type and *Taxodium*/*Glyptostrobus*-type referring to the former as zonal and the latter as azonal elements.

At the same time, the fossil record of these often relictual groups reveals that they were much more ecologically diverse (Schneider 1992; Dolezych & Schneider 2006, 2007) and widely distributed through large parts of the Mesozoic and Cenozoic (Farjon 2005; LePage 2007; Kunzmann et al. 2009). For example, *Sequoia* is currently part of well-drained coastal forests but was a lignite forming element during the Miocene in Europe (Jurasky 1936). Similarly, the relict genera *Cryptomeria*, *Taiwania*, and *Cunninghamia* that are confined to well-drained soils today might have been lignite-forming elements together with other conifers such as *Cathaya* and *Sciadopitys* during the Neogene (Schneider 1992; Dolezych & Schneider 2006, 2007). Today, papillate Cupressaceae occur in a wide range of habitats including swamp forests, floodplains, and well-drained lowland and upland forests under temperate climates (Farjon 2005).

Apart from uncertainties concerning the autecologies of fossil representatives of papillate Cupressaceae, it has repeatedly been noticed that based on pollen morphological grounds it is difficult to discern members of the traditional Taxodiaceae, Taxaceae, and Cupressaceae (Erdtman 1965; Kedves 1985; Bortenschlager 1990; Kohlman-Adamska 1993; Stuchlik et al. 2002; Grimm et al. 2016).

During the course of several studies of dispersed Cenozoic pollen during the past years, we experienced the same difficulties in telling apart genera of the former Taxodiaceae (e.g. Bouchal et al. 2016a, 2016b, 2017; Bouchal 2019). Given the omnipresence of such pollen grains in Cenozoic strata of the Northern Hemisphere, the aim of the present study was to document the pollen morphology of all the nine genera of the former Taxodiaceae (papillate Cupressaceae) using light microscopy (LM) and scanning electron microscopy (SEM) to assess how well they can be distinguished by means of pollen morphology. We examined whether members of the different subfamilies in the Cupressaceae share diagnostic characteristics and discussed the applicability of pollen morphology for identification of dispersed taxodiaceous pollen in the fossil record. We also briefly review various previous studies that used taxodiaceous pollen to infer distinct palaeoenvironments.

Material and methods

Forty-five samples of male pollen cones used for the present study were obtained from the herbaria Paris (P), Stockholm (S), and Vienna (W) (see Supplementary Table S1 for voucher information). Part of the material was rehydrated and critical point dried and mounted on SEM stubs; the remaining part of the material was acetolysed using standard protocols (Erdtman 1943; Halbritter et al. 2018) and mounted in glycerine jelly for LM investigation and on aluminium stubs for SEM investigation. LM photographs of non-acetolysed and acetolysed pollen were taken with an Olympus BX51 microscope equipped with an Olympus DP71 camera. Specimens were sputter coated with gold prior to SEM investigation and photographed using a Hitachi S-4300 cold field emission SEM and an ESEM FEI Quanta FEG 650 SEM. SEM stubs and pollen slides are kept at the Department of Palaeobiology, Swedish Museum of Natural History, Stockholm. The description of pollen grains follows Punt et al. (2007) and Halbritter et al. (2018). Thirty pollen grains were measured for each specimen; a minimum number of two specimens were investigated per species. In some cases, all anthers were void of pollen (see Supplementary Table S1). Among the

investigated pollen morphological characters were equatorial diameter, polar axis length, papilla length, orbiculae configuration and others (Table I, Supplementary Figure S1). Four types of papilla configuration were distinguished; (i) straight, (ii) weakly bent, (iii) sharply bent, (iv) indistinct (Figure 14, Figure S1). Cupressaceae pollen tends to rupture radially from distal (leptoma or papilla area) to proximal pole to enable gametophyte release (Southworth 1988), ruptured pollen is commonly referred to as 'hiatus' form (e.g. Kedves 1985). The term orbicules (lat. orbiculus) describes globular Ubisch bodies (Halbritter et al. 2018). In Cupressaceae, orbicules usually are nanoechinate. Orbicule diameter and the number of visible echini per orbicule were assessed for all species investigated (Figures 11–13). Of our material, only a single specimen of *Taiwania cryptomeroides* contained sparse pollen, which was not sufficient for acetolysis and mounting in glycerine jelly. The few obtained pollen grains were mounted on a SEM stub for investigation.

Systematic palynology

Family Cupressaceae Grey
Subfamily Athrotaxidoideae Quinn
Genus Athrotaxis *D.Don*
Species Athrotaxis cupressoides *D.Don*
(Figures 1A–I564, 2A–H)

Description. — Pollen, monad, shape spheroidal to oblate spheroidal, P/E 0.84–0.96, outline circular in polar view, circular to weakly elliptic in equatorial view; pollen size medium, equatorial diameter 25.3–28.9 µm (LM), polar axis including papilla 21.8–28.8 µm long (LM); leptoma indistinct, rarely detectable in LM, leptoma diameter 12.4–14.3 µm (LM), papilla indistinct (60%) to very short (< 2.7 µm), papilla shape straight (40%), papilla length 1.5–2.1 µm (LM), papilla width 2.1–3.3 µm (LM); exine 1.3–1.7 µm thick (LM), nexine as thick or slightly thinner than sexine; sculpturing in LM psilate to scabrate, sculpturing in SEM nanoverrucate, nanoverrucae of variable size, with densely spaced blunt nanoechini (Figure 2D), in acetolysed pollen nanofossulae and perforations visible (Figure 2E), sculpturing in leptoma region nanogranulate (Figure 2F); orbicules spheroid to polygonal (orbicule), with blunt echini (Figure 2G, H), orbicule diameter 0.35–0.68 µm (SEM), echini length 0.05–0.1 µm (SEM), ratio number of visible echini to orbicule diameter (µm) 24–32, orbicules irregularly distributed over entire pollen surface (LM, SEM).

Remarks. — Pollen morphology of this Southern Hemispheric genus has been studied using LM (Erdtman 1943, 1957, 1965; Van Campo-Duplan 1951) and SEM (Kvavadze 1988). In the literature, size ranges (diameter) from 14–18 µm to 27–30 µm have been reported (see Supplementary Table S2).

Subfamily Cunninghamioideae Quinn
Genus Cunninghamia *R.Br.*
Species Cunninghamia lanceolata *Hook*
(Figures 1J–Q, 2I–R, Supplementary Figures S2A–G, S3A–D)

Description. — Pollen, monad, shape oblate spheroidal to spheroidal, P/E including papilla 0.82–0.87, P/E excluding papilla 0.76–0.81, outline circular in polar view, weakly elliptic to circular in equatorial view; pollen size medium, equatorial diameter 30.4–38.5 µm (LM), polar axis including papilla 25.3–32 µm long (LM); leptoma distinct, leptoma diameter 19.2–23.4 µm (LM), papilla very short to short (< 3.9 µm), papilla shape straight (100%), papilla length 1.6–2.5 µm (LM), papilla width 2.9–4.7 µm (LM), in acetolysed specimens papilla detached leaving an ulcus; exine 1.5–2.2 µm thick (LM), nexine thinner than sexine, in some specimens sexine disconnected from nexine forming cavities (Figure 1J, N, O), disconnected sexine surrounding the leptoma forming a crown-like crest; sculpturing in LM psilate to scabrate, rugulae or folds present (Figure 2M–O), in some acetolysed specimens folds surrounding leptoma present (LM, Figure 2Q), sculpturing in SEM nanoverrucate, nanoverrucae of variable size, with densely spaced blunt to acute nanoechini (Figure 2M), in acetolysed pollen nanorugulae, nanofossulae, perforations and acute echini visible (Figure 2N), leptoma region nanogranulate to nanorugulate (Figure 2O), in acetolysed pollen nanofossulae and perforations visible (Fig-Figure 2P), papilla psilate; orbicules polygonal to star-shaped with acute echini (Figure 2Q, R), orbicule diameter 0.33–0.71 µm (SEM), echini length 0.1–0.3 µm (SEM), ratio number of visible echini to orbicule diameter (µm) 20–31, orbicules irregularly distributed over entire pollen surface (LM, SEM).

Remarks. — Several studies investigated pollen of *Cunninghamia* using LM (Jimbo 1933; Wodehouse 1935; Erdtman 1943, 1965; Ueno 1951; Van Campo-Duplan 1951), SEM (Ho & Sziklai 1973; Fujiki et al. 2005; Li et al. 2010; Lu et al.

Table I. Pollen morphological data of the investigated species of Athrotaxidoideae, Cunninghamioideae, Sequoioideae, Taiwanioideae, and Taxodioideae based on light microscopical investigation of acetolysed pollen. Measurements: (minimum) range (maximum).

Taxon	Specimen	Equatorial diameter (μm)	Polar axis (μm)	P/E including papilla (μm)	P/E excluding papilla (μm)
Athrotaxidoideae					
Athrotaxis cupressoides	P01632977 (*n* = 30)	(18.8) 25.3–28.8 (32.5)	(23.1) 24.1–26.3 (28.4)	(0.83) 0.84–0.86 (0.88)	—
	W2007-14 541 (*n* = 30)	(22.4) 25.5–28.9 (36.3)	(20.5) 21.8–28.8 (31.3)	(0.83) 0.85–0.96 (1.05)	—
Cunninghamioideae					
Cunninghamia lanceolata	P01632932 (*n* = 30)	(30) 30.4–38.5 (40,4)	(26.3) 28.6–32 (32.7)	(0.66) 0.81–0.87 (0.91)	(0.72) 0.76–0.81 (0.85)
	S-C-4119 (*n* = 30)	(27) 30.8–34.8 (37.7)	(18.8) 25.3–28.8 (32.5)	(0.77) 0.82–0.86 (0.88)	(0.71) 0.76–0.81
Sequoioideae					
Metasequoia glyptostroboides	P01656108 (*n* = 30)	(22.1) 24–26.5 (32.5)	(21.7) 23.6–26.3 (31)	(0.78) 0.94–1.04 (1.16)	(0.64) 0.8–0.91 (1.02)
	W2009-08604 (*n* = 30)	(21.8) 23.8–27.3 (30.6)	(21.4) 23.2–28.7 (32.6)	(0.8) 0.96–1.07 (1.17)	(0.6) 0.83–0.93 (0.95)
Sequoia sempervirens	W1969-13 131 (*n* = 30)	(20.3) 29–30.8 (34.7)	(26.9) 30.7–34.1 (36.8)	(0.89) 1.02–1.12 (1.64)	(0.75) 0.86–0.95 (1.35)
	W2000-13 205 (*n* = 30)	(24.4) 32.3–34.4 (40.1)	(27.4) 29.7–33.8 (39.3)	(0.87) 0.9–1.09 (1.32)	(0.74) 0.79–0.91 (1.11)
Sequoiadendron giganteum	W1952-15 491 (*n* = 30)	(22.2) 26.6–29.6 (33.1)	(22.3) 26.5–29.4 (32.9)	(0.8) 0.98–1.04 (1.25)	(0.69) 0.8–0.84 (1)
	W1993-02981 (*n* = 30)	(23.8) 26.5–29.7 (33.3)	(24.8) 29.3–31.1 (34.7)	(0.83) 1.02–1.13 (1.25)	(0.62) 0.79–0.89 (0.99)
Taxodioideae					
Cryptomeria japonica	S-C-4291 (*n* = 30)	(26.1) 27.8–30.6 (33.7)	(27.6) 31.1–34 (36.7)	(0.92) 1.08–1.15 (1.28)	(0.75) 0.84–0.89 (1)
	W2010-10 830 (*n* = 30)	(26.9) 29.8–34.7 (41.3)	(30.7) 32.2–37 (41.8)	(0.85) 1.04–1.13 (1.24)	(0.62) 0.82–0.91 (0.99)
Glyptostrobus pensilis	P01642572 (*n* = 30)	(29.1) 30.5–33.2 (36.7)	(29.6) 31.2–33.4 (37.5)	(0.9) 0.98–1.06 (1.17)	(0.79) 0.85–0.92 (1.02)
	P01642576 (*n* = 30)	(28.9) 30.1–33.2 (35)	(28.6) 31.2–33.4 (35.2)	(0.95) 0.99–1.06 (1.17)	(0.79) 0.85–0.93 (0.99)
Taxodium distichium	S-C-4370 (*n* = 30)	(23.7) 24.3–25.8 (28.9)	(21.2) 24.1–26.9 (30.7)	(0.82) 0.97–1.06 (1.18)	(0.68) 0.8–0.89 (1.04)
	W2012-12 013 (*n* = 30)	(20.5) 23.6–25.3 (29.1)	(21) 22.5–26.3 (30.3)	(0.85) 0.95–1.06 (1.13)	(0.73) 0.78–0.88 (0.93)
Taxodium mucronatum	S-C-4341 (*n* = 30)	(27.3) 29.4–32.3 (34.9)	(24.6) 28.8–31.2 (36.3)	(0.78) 0.92–1.02 (1.06)	(0.73) 0.84–0.92 (0.94)
	W2000-05875 (*n* = 30)	(25.3) 28.5–30.8 (32.6)	(26) 28.3–32 (35.8)	(0.91) 0.99–1.07 (1.13)	(0.77) 0.88–0.93 (1)

Taxon	Papilla length (μm)	Papilla width (μm)	Leptoma diameter (μm)	Papilla shape	Exine thickness (μm)	Echini/orbicule diameter
Athrotaxidoideae						
Athrotaxis cupressoides	(1.4) 1.5–2 (2.4)	(2.2) 2.7–3.1 (4)	(10.8) 12.5–14.3 (17.7)	straight or no papilla detectable	(1.2) 1.6–2.1 (1.8)	(19) 25–32 (37)
	(1) 1.6–2.1 (2.7)	(2) 2.1–3.3 (3.8)	(8.5) 12.4–13.7 (15.3)	straight or no papilla detectable	(1.1) 1.3–1.7 (1.8)	(17) 24–28 (33)
Cunninghamioideae						
Cunninghamia lanceolata	(1.4) 1.8–2.3 (3.1)	(2.7) 3.6–4.7 (5.1)	(17.9) 20.5–23.4 (26.7)	straight	(1.3) 1.6–2.2 (3.8)	(21) 26–31 (40)
	(1) 1.6–2.5 (3.9)	(2.3) 2.9–3.6 (4.5)	(13.1) 19.2–22.9 (24.9)	straight	(1.7) 1.9–2.2 (2.3)	(16) 20–26 (30)
Sequoioideae						
Metasequoia glyptostroboides	(2) 2.7–4.3 (5.7)	(2.7) 3.3–4.3 (5.8)	(11.5) 14.7–17.4 (19.4)	straight, weakly or sharply bent	(1) 1.4–1.8 (2.9)	(35) 41–49 (55)
	(2) 3–4.8 (6.5)	(2.5) 3.3–5 (7.3)	(11) 13.1–17.1 (24.5)	straight, weakly or sharply bent	(1.1) 1.3–1.8 (2.1)	(33) 44–53 (65)

(*Continued*)

Table I. (*Continued*).

Taxon	Papilla length (μm)	Papilla width (μm)	Leptoma diameter (μm)	Papilla shape	Exine thickness (μm)	Echini/orbicule diameter
Sequoia sempervirens	(3.2) 4.4–6 (7.1)	(4) 4.8–6.2 (8.9)	(12.8) 17.1–20.2 (23.2)	straight, weakly or sharply bent	(1.5) 1.6–2 (2.8)	(40) 51–62 (69)
	(2.7) 4.4–5.8 (7.7)	(2.9) 3.4–4.4 (5.1)	(16.4) 19–21 (26.1)	straight, weakly or sharply bent	(1.3) 1.7–2.3 (2.7)	(32) 25–29 (33)
Sequoiadendron giganteum	(2.9) 4.8–6.6 (8.5)	(3.5) 4.8–5.8 (7.9)	(13) 14.6–17.6 (18.7)	straight, weakly or sharply bent	(1.4) 1.6–1.8 (2.2)	(31) 34–41 (48)
	(3.5) 5.4–7.8 (9.5)	(3.6) 4.1–5.6 (6.5)	(11.8) 13.6–16.8 (20)	straight, weakly or sharply bent	(1.3) 1.6–2.3 (2.7)	(30) 33–41 (54)
Taxodioideae						
Cryptomeria japonica	(4.8) 5.9–7.8 (9.4)	(3.9) 4.8–6.2 (7.1)	(14.3) 16.3–18.3 (21.6)	straight, weakly or sharply bent	(1.3) 1.4–1.8 (2.1)	(25) 31–42 (54)
	(4) 5.9–8 (10.3)	(3.4) 4.7–5.8 (6.9)	(15.1) 18.3–20.8 (22.9)	straight, weakly or sharply bent	(1.3) 1.4–1.7 (1.9)	(34) 42–51 (76)
Glyptostrobus pensilis	(2.7) 3.8–5.2 (6.6)	(2.6) 3.6–4.7 (5.5)	(13.4) 17–19.7 (23)	straight, weakly or sharply bent	(1.1) 1.3–1.6 (1.8)	(19) 37–49 (66)
	(2.9) 4.2–5.4 (6.6)	(2.6) 3.4–4.7 (5.5)	(14.3) 16.7–18.7 (22)	straight, weakly or sharply bent	(1.1) 1.2–1.6 (1.9)	(29) 41–53 (67)
Taxodium distichium	(2.7) 3.5–5 (9.3)	(3.1) 4.5–5.3 (6.6)	(10.4) 13.4–16.2 (20.3)	straight, weakly or sharply bent	(1.3) 1.4–1.6 (1.9)	(31) 38–46 (52)
	(2.4) 3.4–5.2 (7.5)	(2.7) 3.9–5.1 (6.2)	(8.9) 13.9–16.3 (18.9)	straight, weakly or sharply bent	(1.2) 1.4–1.7 (1.9)	(33) 38–43 (60)
Taxodium mucronatum	(1.9) 2.6–4 (5.7)	(3.1) 4.2–5.4 (5.9)	(9.7) 17.5–20.3 (24.7)	straight, weakly or sharply bent	(1.3) 1.4–1.8 (2)	—
	(2.2) 3–4.4 (6)	(3.5) 4.1–5.5 (6.5)	(13.5) 18.1–19.5 (20.7)	straight, weakly or sharply bent	(1.2) 1.3–1.7 (1.9)	—

Figure 1. Light microscopy (LM) micrographs of acetolysed *Athrotaxis* and *Cunninghamia* pollen. **A–I.** *Athrotaxis cupressoides*, PV with focus on proximal pole (**A, B**), PV with focus on distal pole (**C, D**), EV (**E–G**), hiatus form (**H, I**). **J–Q.** *Cunninghamia lanceolata*. PV with focus on proximal pole (**J**), PV with focus on distal pole (**K–M, Q**), EV (**N, O**), hiatus form (**P**). Specimen P01632977 (**A, B, E, F, H, I**), W2007-14 541 (**C, D, G**), S-C-4119 (**K, L, N, P**), P01632932 (**J, M, O, Q**). Abbreviations: polar view (PV), equatorial view (EV). *Arrows* indicate papilla. Scale bars – 10 μm.

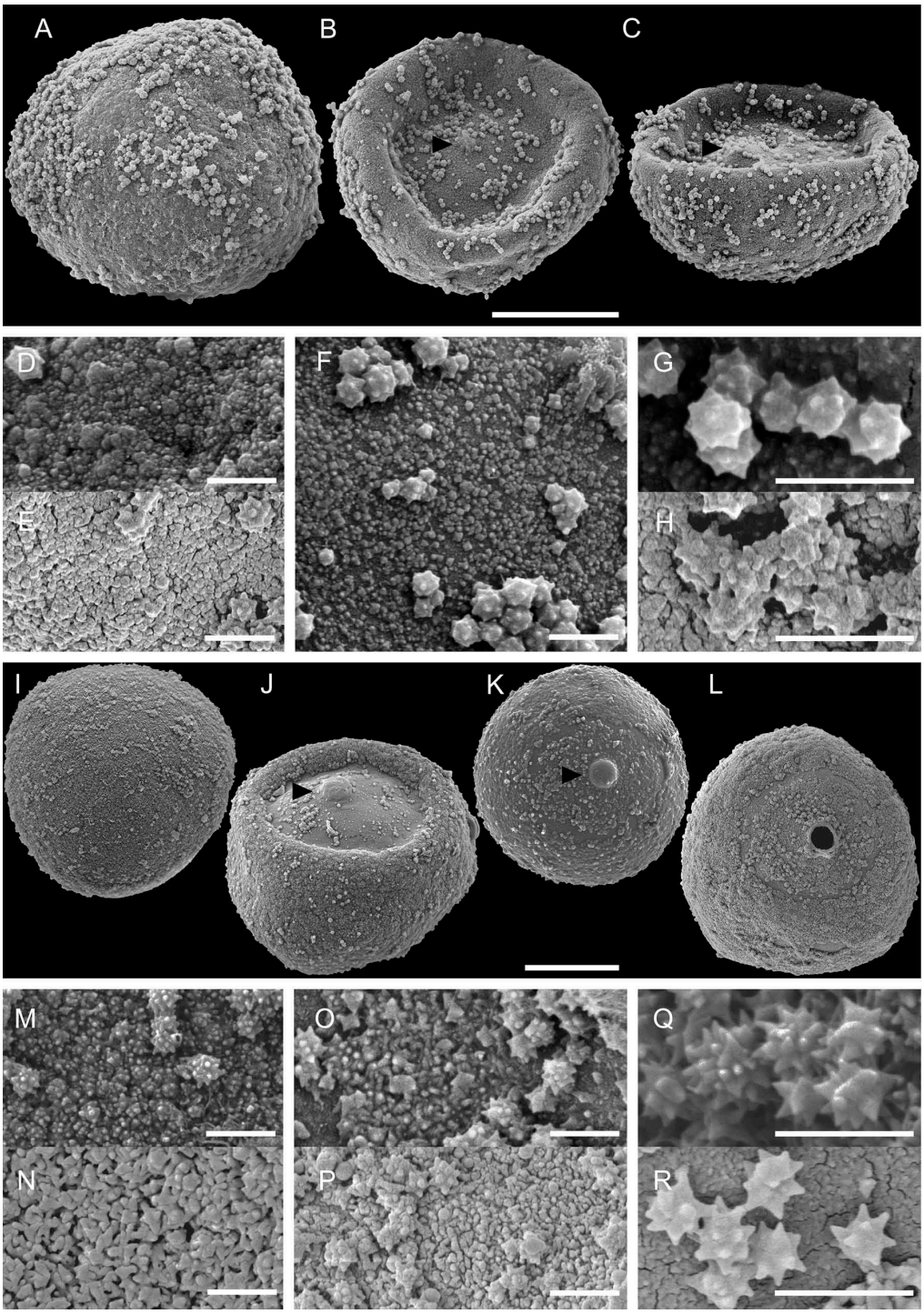

Figure 2. Scanning electron microscopy (SEM) micrographs of *Athrotaxis* and *Cunninghamia* pollen. **A–H.** *Athrotaxis cupressoides*. **A–C.** Overview, PRV (**A**), DV (**B**), EV (**C**). **D–H.** Close-ups of exine sculpturing, PRV (**D, E**), DV (**F**), orbicule detail (**G, H**). **I–R.** *Cunninghamia lanceolata*. **I–L.** Overview, PRV (**I**), EV (**J**), DV (**K**), DV with ulcus-like opening from broken off papilla (**L**). **M–R.** Close-ups of exine sculpturing, PRV (**M, N**), DV (**O, P**), orbicule detail (**Q, R**). Specimen P01632977 (**A–F**), W2007-14 541 (**G, H**), P01632932 (**I–K, Q, R**). S-C-4119 (**L–P**). Not acetolysed (**A–D, F, G, I–K, M, O, Q**), acetolysed (**E, H, L, N, P, R**). Abbreviations: proximal view (PRV), distal view (DV), equatorial view (EV). *Arrows* indicate papilla. Scale bars – 10 μm.

2011; Bykowska & Klimko 2016; Halbritter 2016a) and transmission electron microscopy (TEM) (Kvavadze 1988; Surova & Kvavadze 1988; Kurmann 1990a; Jia et al. 1998). In the literature, size ranges (diameter) from 26 to 54 μm have been given (see Table S2). In *Cunninghamia lanceolata*, the pollen wall consists of a lamellate endexine, a thin footlayer and granulate to compact sexine; nexine and sexine are of similar thickness (Kurmann 1990a; Jia et al. 1998). In some specimens, cavities occur in the infratectum (Figure 1J, N, Q, Figure S2B–D; Kurmann 1990a, figures 9, 10; Jia et al. 1998, figures 19, 20) causing a strongly sculptured (folded) pollen surface. In the leptoma area, only endexine is present, in the papilla area the pollen wall is formed by a single layer (endexine). This delicate membrane very easily breaks during fossilisation or acetolysis leaving a circular opening (not a porus). The fossil genus *Cunninghamiae pollenitis* Nagy was established for fossil pollen morphologically similar to *Cunninghamia* (Nagy 1969; Stuchlik et al. 2002); in most cases, in this fossil-taxon a circular aperture is preserved which superficially resembles a porus.

Subfamily Taiwanioideae Endl. ex K.Koch
Genus Taiwania *D.Don*
Species Taiwania cryptomerioides Hayata
(Figure 3A–F)

Description. — Orbicules spheroidal to polygonal with blunt echini (Figure 3F), orbicule diameter 0.24–0.49 μm, echini length 0.05–0.1 μm (SEM), ratio number of visible echini to orbicule diameter (μm) 33–41, orbicules irregularly distributed over entire pollen surface (SEM).

Remarks. — The investigated material did not include enough specimens for representative size measurements. In the literature, equatorial size ranges from 20 to 36 μm have been reported (Ueno 1951, 1960; Van Campo-Duplan 1951; Erdtman 1965; Kvavadze 1988; Fujiki et al. 2002; Fujiki et al. 2005; Li et al. 2010). TEM investigations indicate a tripartite pollen wall architecture in this species with a lamellate endexine, a thin footlayer, and granulate to compact sexine; nexine and sexine are of similar thickness (Chen et al. 2006). Similar to *Cunninghamia*, the leptoma pollen wall consists of endexine only and displays a thinning

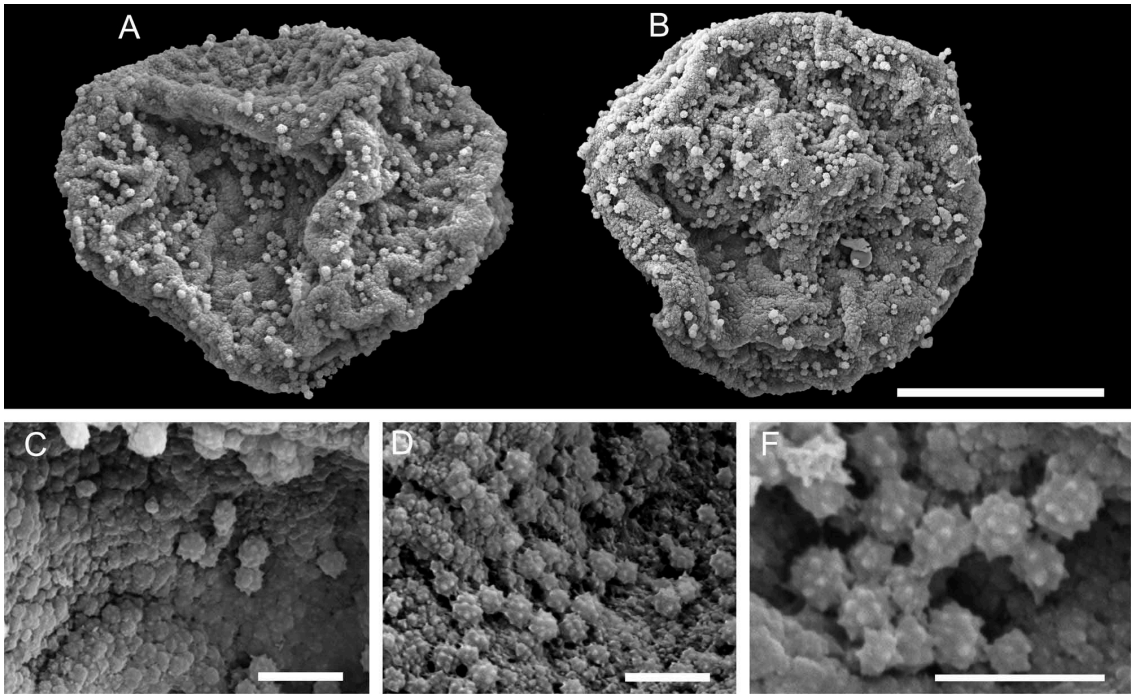

Figure 3. Scanning electron microscopy (SEM) micrographs of *Taiwania* pollen. **A–F.** *Taiwania cryptomeroides*. **A–B.** Overview, PRV. **C–F.** Close-ups of exine sculpturing, PRV (**C, D**), orbicule detail (**F**). Specimen P01654086 (**A–F**). Abbreviation: proximal view (PRV). Scale bars – 10 μm (A, B) 1 μm (C–F).

(single layer) in its centre (Chen et al. 2006, Figure 2C). The fossil genus *Taiwaniapollis* Ziembińska-Tworzydło was established to accommodate fossil pollen morphologically similar to *Taiwania* (Stuchlik et al. 2002). In most cases a circular aperture is preserved, which superficially resembles a porus.

Subfamily Sequoioideae Quinn
Genus Metasequoia *Hu & Cheng*
Species Metasequoia glyptostroboides *Hu & Cheng*
(Figures 4A–M, 5A–I, Supplementary Figures S2H–S, S3E, F)

Description. — Pollen, monad, shape spheroidal to oblate spheroidal, P/E including papilla 0.94–1.07, P/E excluding papilla 0.8–0.93, outline circular in polar view, weakly elliptic to circular in equatorial view; pollen size small to medium, equatorial diameter 23.8–27.3 µm (LM), polar axis including papilla 23.2–28.7 µm long (LM); leptoma distinct or indistinct (LM, SEM), leptoma diameter 13.1–17.4 µm (LM), papilla shape indistinct (5%), straight (52%), weakly (36%) or sharply bent (7%), papilla length 2.7–4.8 µm (LM), papilla width 3.3–5 µm (LM); exine 1.3–1.8 µm thick (LM), nexine as thick or slightly thinner than sexine; sculpturing in LM psilate to scabrate, sculpturing in SEM rugulate, verrucate, nanoverrucate, nanoverrucae of variable size, with densely spaced blunt nanoechini (Figure 5D), in acetolysed pollen fossulae visible (Figure 5E), leptoma region nanoechinate (Fig-Figure 5F, G), in acetolysed pollen perforations visible (Figure 5G), papilla nanoechinate, in some specimens papilla covered by orbicules; orbicules spheroidal to polygonal with blunt echini (Figure 5F, H, I), orbicule diameter 0.28–0.64 µm, echini length 0.05–0.1 µm (SEM), ratio number of visible echini to orbicule diameter (µm) 41–53, orbicules irregularly distributed over entire pollen surface (LM, SEM).

Remarks. — Several studies investigated pollen of *Metasequoia* using LM (Ueno 1951, 1960; Van Campo-Duplan 1951), SEM (Erdtman 1965; Li et al. 2010; Lu et al. 2011; Miyoshi et al. 2011; Halbritter 2016b) and TEM (Kvavadze 1988; Surova & Kvavadze 1988). In the literature, size ranges from 18 to 30 µm have been given (see Table S2). Aberrant pollen with enlarged papillae is occasionally present (Figure 4J). Pollen wall architecture figured by Kvavadze (1988, figures 21–24) is tripartite (lamellate endexine, thin footlayer, infratectum granulate, tectum compact), nexine thrice as thick as sexine. Leptoma and papilla consist of endexine; a circular thinning is present at the distal end of the papilla.

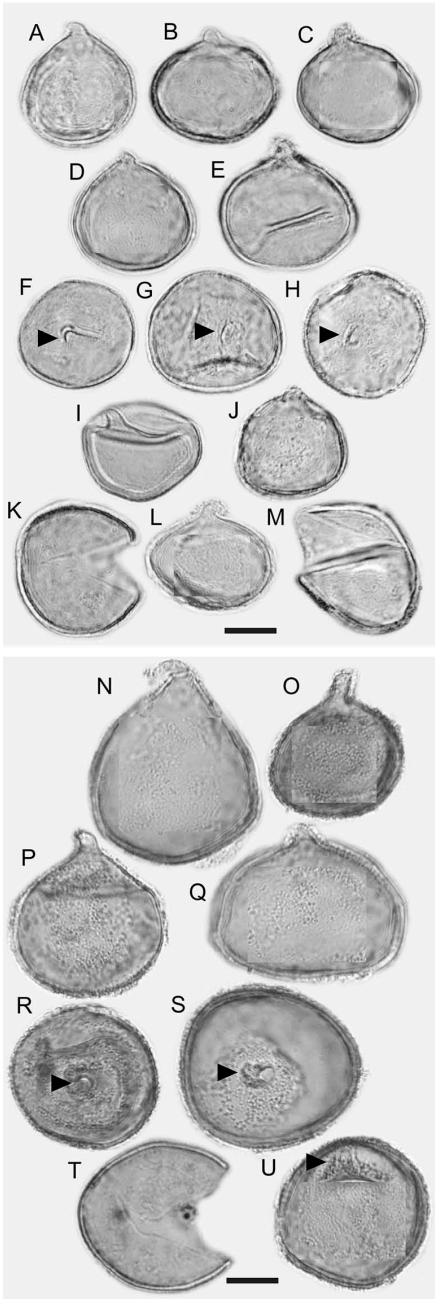

Figure 4. Light microscopy (LM) micrographs of acetolysed *Metasequoia* and *Sequoia* pollen. **A–M.** *Metasequoia glyptostroboides*, EV (**A–E, I, J, L**), PV with focus on distal pole (**F–H**), hiatus form (**K, M**). **N–U.** *Sequoia sempervirens*, EV (**N–Q**), PV with focus on distal pole (**R, S, U**), hiatus form (**T**). Specimen W2009-08604 (**A–F, I, K, L**), P01656108 (**G, H, J, M**), W2000-13 205 (**N**), W2011-01010 (**O, P, R, S, U**), W1955-4142 (**Q**), W1969-13 131 (**T**). Abbreviations: polar view (PV), equatorial view (EV). *Arrows* indicate papilla. Scale bars – 10 µm.

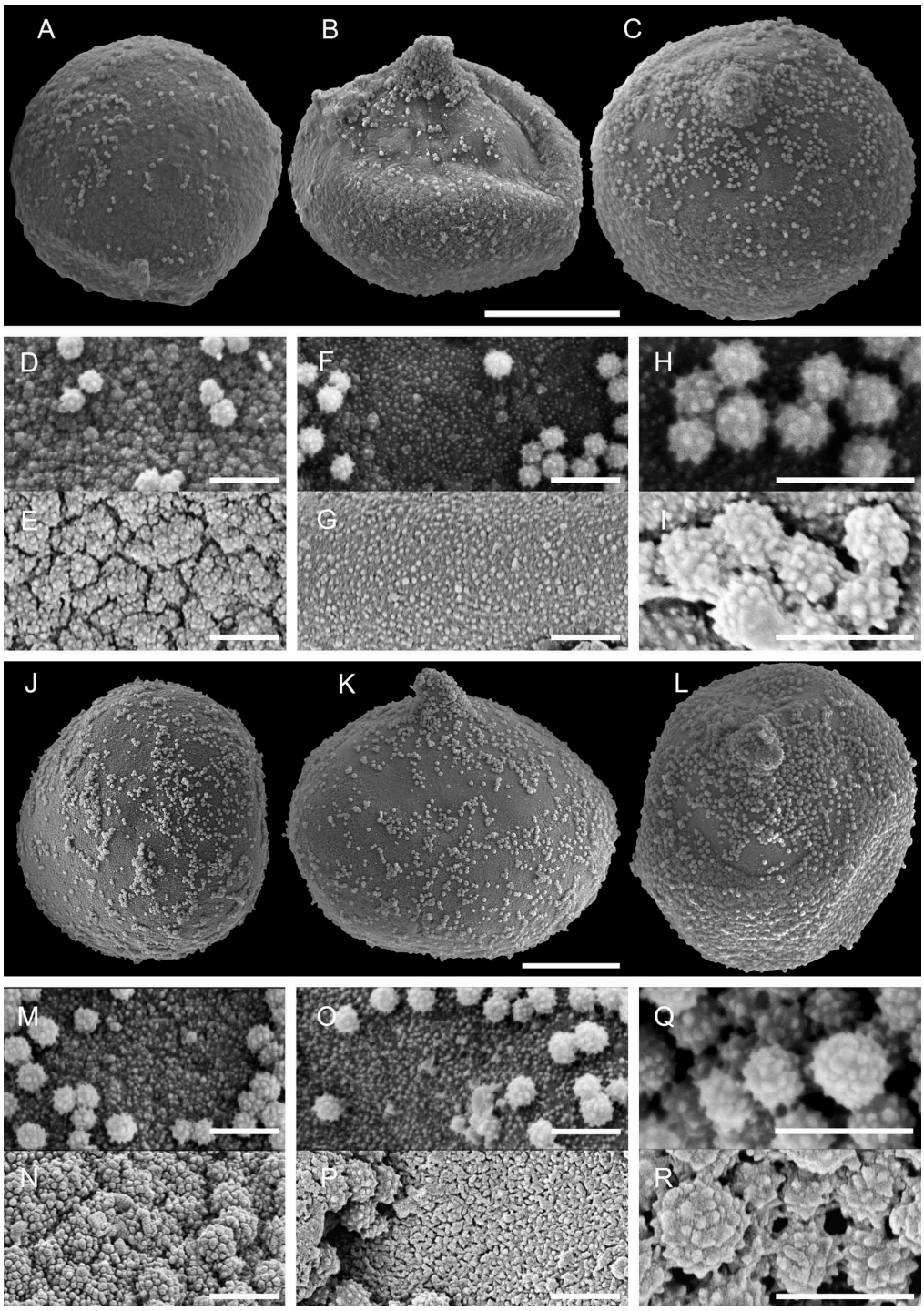

Figure 5. Scanning electron microscopy (SEM) micrographs of *Metasequoia* and *Sequoia* pollen. **A–I.** *Metasequoia glyptostroboides*. **A–C.** Overview, PRV (**A**), EV (**B**), DV (**C**). **D–I.** Close-ups of exine sculpturing, PRV (**D, E**), DV (**F, G**), orbicules (**H, I**). **J–R.** *Sequoia sempervirens*. **J–L.** Overview, PRV (**I**), DV (**J**), EV (**K**). **M–R.** Close-ups of exine sculpturing, PRV (**M, N**), DV (**O, P**), orbicules (**Q, R**). Specimen P01656108 (**A–D, F, H**), W2009-08604 (**E, G, I**), W2000-13 205 (**J, K, M, O**), W1969-13 131 (**L, N, P, Q, R**). Not acetolysed (**A–D, F, H, J–M, O, Q**), acetolysed (**E, G, I, N, P, R**). Abbreviations: proximal view (PRV), distal view (DV), equatorial view (EV). Scale bars – 10 μm.

Genus Sequoia *Endl.*
Species Sequoia sempervirens *Endl.*
(Figures 4N–U, 5J–R, Supplementary Figures S4A–F, S5A–D)

Description. — Pollen, monad, shape spheroidal to oblate spheroidal, P/E including papilla 0.9–1.12, P/E excluding papilla 0.79–0.95, outline circular in polar view, weakly elliptic to circular in equatorial view; pollen size medium, equatorial diameter 29–34.4 µm (LM), polar axis including papilla 29.7–34.1 µm long (LM); leptoma distinct (LM, SEM), leptoma diameter 17.1–21 µm (LM), papilla shape indistinct (8%), straight (49%), weakly (24%) or sharply bent (19%), papilla length 4.4–6 µm (LM), papilla width 3.4–6.2 µm (LM); exine 1.6–2.3 µm thick (LM), nexine as thick as to one-third of the thickness of the sexine; sculpturing in LM psilate to scabrate, sculpturing in SEM rugulate, verrucate, nanoverrucate, nanoverrucae of variable size, with densely spaced blunt nanoechini (Figure 5L, M), in acetolysed pollen fossulae and perforations visible (Figure 5N), leptoma region nanoechinate (Figure 5O), in acetolysed pollen perforations and nanorugulae visible (Figure 5P), papilla nanoechinate, occasionally papilla covered by orbicules; orbicules spheroidal to polygonal with blunt echini (Figure 5H, I), orbicule diameter 0.33–0.87 µm, echini length 0.05–0.1 µm (SEM), ratio number of visible echini to orbicule diameter (µm) 25–62, orbicules irregularly distributed over entire pollen surface (LM, SEM).

Remarks. — Several studies investigated pollen of *Sequoia* using LM (Wodehouse 1935; Erdtman 1943, 1965; Ueno 1951; Van Campo-Duplan 1951; Lewis et al. 1983), SEM (Ho & Sziklai 1973; Kvavadze 1988; Miyoshi et al. 2011) and TEM (Gullvåg 1966; Kedves 1985). In the literature, size ranges from 22 to 43 µm have been given (see Table S2). Investigating the ultrastructure of the pollen wall of modern *Sequoia*, Gullvåg (1966) and Kedves (1985) reported a lamellate endexine two- to three-times as thick as the ectexine, and a thin footlayer followed by a granulate infratectum with a compact tectum.

Genus Sequoiadendron *J.Buchholz*
Species Sequoiadendron giganteum *(Lindl.) J.Buchholz*
(Figures 6A–K, 7A–J, Supplementary Figures S4G–P, S5E–H)

Description. — Pollen, monad, shape spheroidal to oblate spheroidal, P/E including papilla 0.98–1.13, P/E excluding papilla 0.79–0.89, outline circular in polar view, weakly elliptic to circular in equatorial view; pollen size medium, equatorial diameter 26.5–29.7 µm wide (LM), polar axis including papilla 26.5–31.1 µm long (LM); leptoma distinct (LM, SEM), leptoma diameter 13.6–17.6 µm (LM), papilla shape indistinct (1%), straight (41%), weakly (37%) or sharply bent (21%), papilla length 4.8–7.8 µm (LM), papilla width 4.1–5.8 µm (LM); exine 1.6–2.3 µm thick (LM), nexine as thick to slightly thinner than sexine; sculpturing in LM psilate to scabrate, sculpturing in SEM (non-acetolysed and acetolysed pollen) microrugulate, microverrucate, fossulate, microverrucae and microrugulae of variable size, with densely spaced blunt nanoechini (Figure 7E–F), leptoma region nanoechinate (Figure 7G–H), papilla nanoechinate, in some specimens papilla covered by orbicules; orbicules spheroidal to polygonal with blunt echini (Figure 7I–J), orbicule diameter 0.26–0.6 µm, echini length 0.05–0.1 µm (SEM), ratio number of visible echini to orbicule diameter (µm) 33–41, orbicules irregularly distributed over entire pollen surface (LM, SEM).

Remarks. — Several studies investigated pollen of *Sequoiadendron* using LM (Ueno 1951) and SEM (Kvavadze 1988). In the literature, size ranges from 25.4 to 34 µm have been given (see Table S2). Aberrant pollen is occasionally present (Figure 5K).

Subfamily Taxodioideae Endl. ex K.Koch
Genus Cryptomeria *D.Don*
Species Cryptomeria japonica *D.Don*
(Figures 6L–R, 7K–S, Supplementary Figures S6A–H, S7A–E)

Description. — Pollen, monad, shape spheroidal to oblate spheroidal, P/E including papilla 1.04–1.15, P/E excluding papilla 0.82–0.91, outline circular in polar view, weakly elliptic to circular in equatorial view; pollen size medium, equatorial diameter 27.8–34.7 µm wide (LM), polar axis including papilla 31.1–37 µm long (LM); leptoma distinct (LM, SEM), leptoma diameter 16.3–20.8 µm (LM), papilla shape straight, weakly or sharply bent, papilla length 5.9–8 µm (LM), papilla width 4.7–6.2 µm (LM); exine 1.5–1.8 µm thick (LM), nexine as thick to slightly thinner than sexine; sculpturing in LM psilate to scabrate, some specimens rugulate (Figure 7M), sculpturing in SEM (non-acetolysed and acetolysed pollen) microverrucate, fossulate, perforate, microverrucae of variable size, with densely spaced blunt nanoechini (Figure 7N, O), leptoma region nanoechinate (Figure 7P, Q), in some

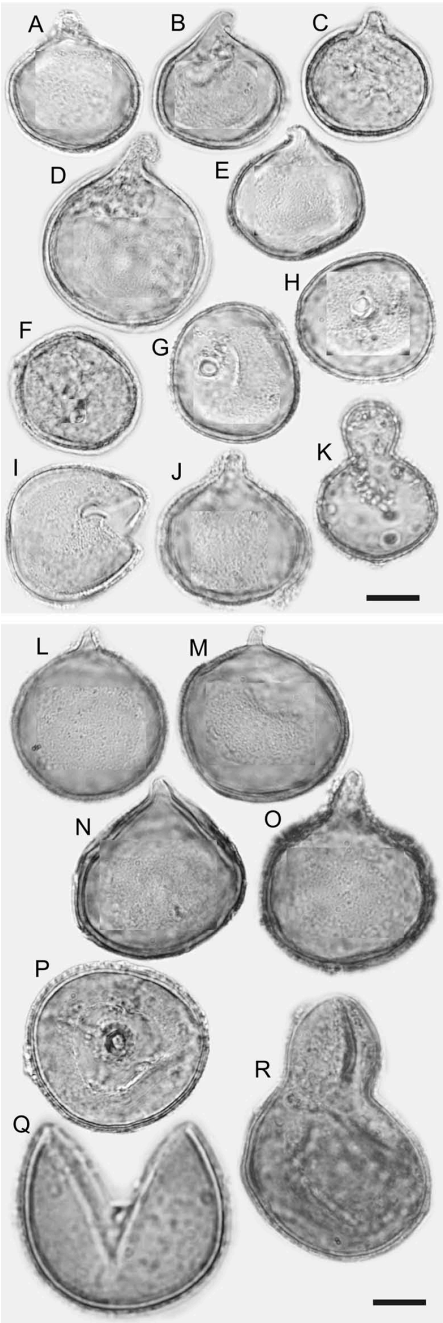

Figure 6. Light microscopy (LM) micrographs of acetolysed *Sequoiadendron* and *Cryptomeria* pollen. **A–K.** *Sequoiadendron giganteum*, EV (**A–E, I, J**), PV with focus on distal pole (**G, H**), hiatus form (**I**), aberrant pollen with enlarged papilla (**K**). **L–R.** *Cryptomeria japonica*, EV (**L–O**), PV with focus on distal pole (**P**), hiatus form (**Q**), aberrant pollen with enlarged papilla (**R**). Specimen W1952-15 491 (**A, E, G–K**), W1993-02981 (**B–D, F**), W2010-10 830 (**L, M, P**), S-C-4291 (**N, O, Q, R**). Abbreviations: polar view (PV), equatorial view (EV). Scale bars – 10 μm.

specimens folds are present in the leptoma area (Figure 7L), papilla nanoechinate, in some specimens papilla covered by orbicules; orbicules spheroidal to polygonal with blunt echini (Figure 7R, S), orbicule diameter 0.29–1.06 μm, echini length 0.05–0.1 μm (SEM), ratio number of visible echini to orbicule diameter (μm) 31–50, orbicules irregularly distributed over entire pollen surface (LM, SEM).

Remarks. — Several studies investigated pollen of *Cryptomeria* using LM (Jimbo 1933; Wodehouse 1935; Erdtman 1943, 1957; Ueno 1951; Van Campo-Duplan 1951; Beug 2004), SEM (Erdtman 1965; Ho & Sziklai 1973; Kedves 1985; Kvavadze 1988; Fujiki 2005; Fujiki & Ozawa 2007; Li et al. 2010; Lu et al. 2011; Miyoshi et al. 2011; Bykowska & Klimko 2016; Grimm et al. 2016; Halbritter 2017) and TEM (Yamada et al. 1980; Uehara & Sahashi 2000). In the literature, size ranges from 22 to 41.8 μm have been given (see Table S2). Aberrant pollen is occasionally present (Figure 5R; Kedves 1985, pl. 2, figures 11, 12). TEM investigations showed wall architecture consisting of a lamellate endexine (three-times as thick as ectexine), a thin footlayer followed by a finely granulate infratectum with an electron dense tectum (Yamada et al. 1980; Uehara & Sahashi 2000).

Genus Glyptostrobus *Endl.*
Species Glyptostrobus pensilis *(Stauton ex D.Don) K.Koch*
(Figures 8A–H, 9A–I, Supplementary Figures S6I–O, S7F–J)

Description. — Pollen, monad, shape spheroidal to oblate spheroidal, P/E including papilla 0.98–1.06, P/E excluding papilla 0.85–0.93, outline circular in polar view, weakly elliptic to circular in equatorial view; pollen size medium, equatorial diameter 30.1–33.2 μm wide (LM), polar axis including papilla 31.2–33.4 μm long (LM); leptoma distinct (LM, SEM), leptoma diameter 16.7–19.7 μm (LM), papilla shape straight, weakly or sharply bent, papilla length 3.8–5.4 μm (LM), papilla width 3.4–4.7 μm (LM); exine 1.2–1.6 μm thick (LM), nexine as thick to slightly thinner than sexine; sculpturing in LM psilate to scabrate, sculpturing in SEM (non-acetolysed and acetolysed pollen) microverrucate, fossulate, perforate, microverrucae of variable size, with densely spaced blunt nanoechini (Figure 9D, E), leptoma region nanoechinate (Figure 9F, G), papilla nanoechinate, in some specimens papilla covered by orbicules; orbicules spheroidal to polygonal with blunt echini (Figure 9H, I), orbicule diameter 0.38–0.84 μm, echini length 0.05–0.1 μm (SEM),

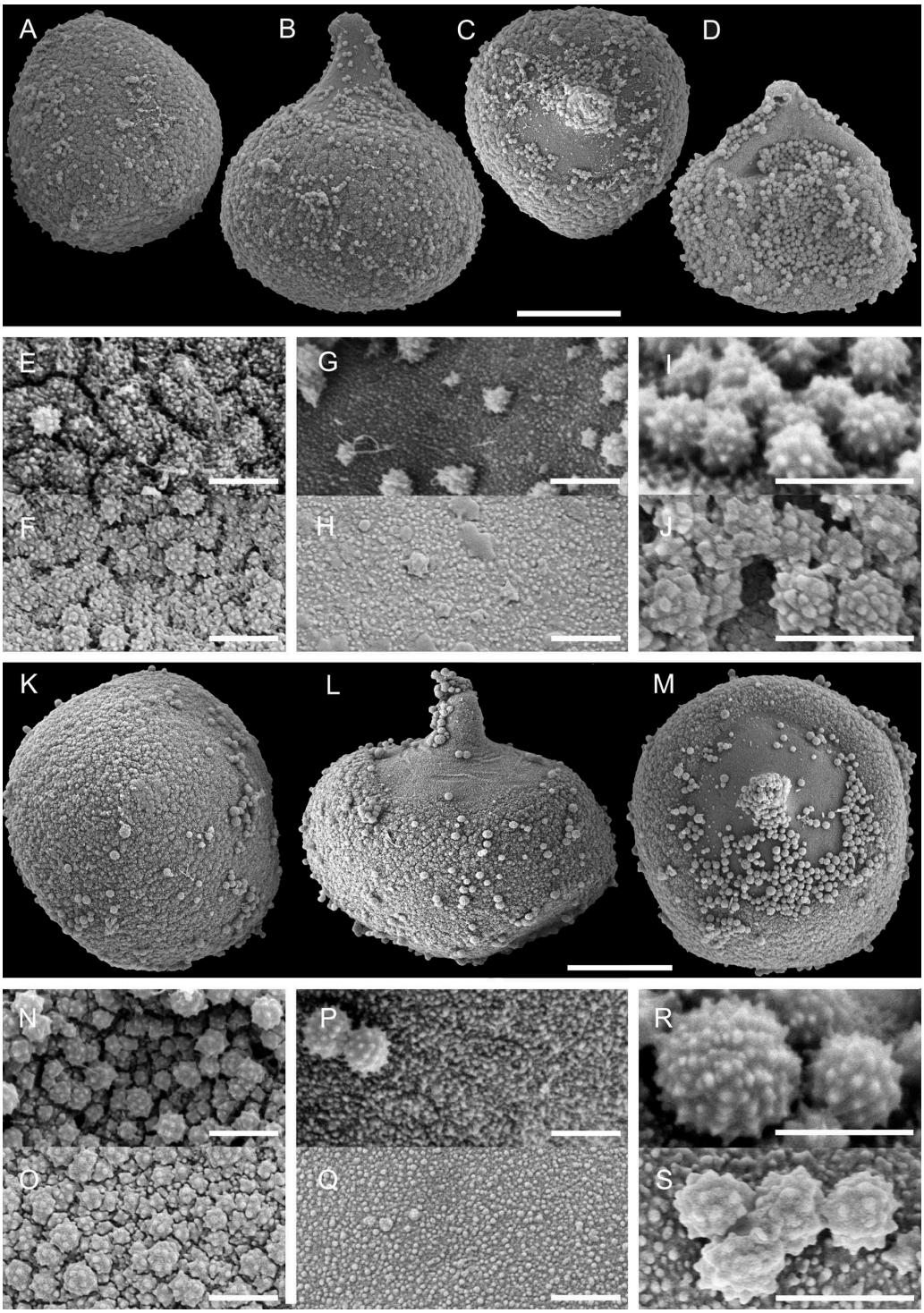

Figure 7. Scanning electron microscopy (SEM) micrographs of *Sequoiadendron* and *Cryptomeria* pollen. **A–J.** *Sequoiadendron giganteum*. **A–D.** Overview, PRV (**A**), EV (**B, D**), DV (**C**). **E–J.** Close-ups of exine sculpturing, PRV (**E, F**), DV (**G, H**), orbicules (**I, J**). **K–S.** *Cryptomeria japonica*. **K–M.** Overview, PRV (**K**), DV (**L**), EV (**M**). **N–S.** Close-ups of exine sculpturing, PRV (**N, O**), DV (**P, Q**), orbicules (**S, T**). Specimen W1952-15 491 (**A–J**), W2010-10 830 (**K, M, O**), S-C-4291 (**L, N, P, Q, R**). Not acetolysed (**A–E, G, I, K–N, P, R**), acetolysed (**F, H, J, O, Q, S**). Abbreviations: proximal view (PRV), distal view (DV), equatorial view (EV). Scale bars – 10 μm.

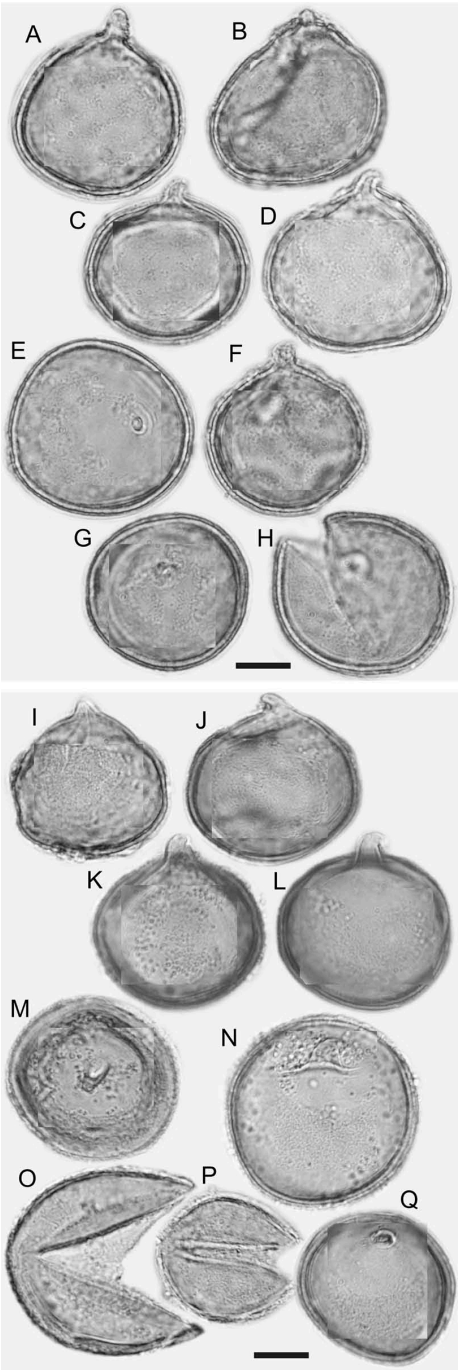

Figure 8. Light microscopy (LM) micrographs of acetolysed *Glyptostrobus* and *Taxodium* pollen. **A–H.** *Glyptostrobus pensilis*, EV (**A–D, F**), PV with focus on distal pole (**E, G**), hiatus form (**H**). **I–Q.** *Taxodium mucronatum*, EV (**I–L**), PV with focus on distal pole (**M, N, Q**), hiatus form (**O, P**). Specimen P01642576 (**A–I**), S-C-4341 (**J–O, Q**), W2000-05875 (**P**). Abbreviations: polar view (PV), equatorial view (EV). Scale bars – 10 µm.

ratio number of visible echini to orbicule diameter (µm) 37–53, orbicules irregularly distributed over entire pollen surface (LM, SEM).

Remarks. — Several studies investigated *Glyptostrobus* pollen using LM (Wodehouse 1935; Ueno 1951; Van Campo-Duplan 1951; Erdtman 1965) and SEM (Kvavadze 1988; Grimm et al. 2016). In the literature, size ranges from 25.4 to 31.8 µm have been given (see Table S2). Wodehouse (1935) reported that up to 20% of the pollen released from a pollen cone were still in tetrads. We did not encounter tetrads in our fully mature specimens.

Genus Taxodium *Rich.*
Species Taxodium distichum *(L.) Rich.*
(Supplementary Figures S8A–H, S9A–E)

Description. — Pollen, monad, shape spheroidal to oblate spheroidal, P/E including papilla 0.95–1.06, P/E excluding papilla 0.78–0.88, outline circular in polar view, weakly elliptic to circular in equatorial view; pollen size small to medium, equatorial diameter 23.6–25.8 µm wide (LM), polar axis including papilla 22.5–26.9 µm long (LM); leptoma distinct (LM, SEM), leptoma diameter 13.4–16.3 µm (LM), papilla shape straight, weakly or sharply bent, papilla length 3.4–5.2 µm (LM), papilla width 3.9–5.3 µm (LM); exine 1.4–1.7 µm thick (LM), nexine as thick to slightly thinner than sexine; sculpturing in LM psilate to scabrate, sculpturing in SEM (non-acetolysed and acetolysed pollen) microverrucate, fossulate, perforate, microverrucae of variable size, with densely spaced blunt nanoechini, leptoma region nanoechinate (Figure 8M, N), papilla nanoechinate, in some specimens papilla covered by orbicules; orbicules spheroidal to polygonal with blunt echini (Figure 8O, P), orbicule diameter 0.33–0.64 µm, echini length 0.05–0.1 µm (SEM), ratio number of visible echini to orbicule diameter (µm) 0.38–0.46, orbicules irregularly distributed over entire pollen surface (LM, SEM).

Remarks. — Several studies investigated pollen of *Taxodium distichum* using LM (Wodehouse 1935; Erdtman 1943, 1957, 1965; Ueno 1951; Willard et al. 2004) and SEM (Kedves 1985; Li et al. 2010; Tiwari et al. 2012; Grimm et al. 2016). In the literature, size ranges from 17.5 to 37 µm have been given (see Table S2).

Species Taxodium mucronatum *Ten.*
(Figures 8I–Q, 9J–R, Supplementary Figures S8I–P, S9F–J)

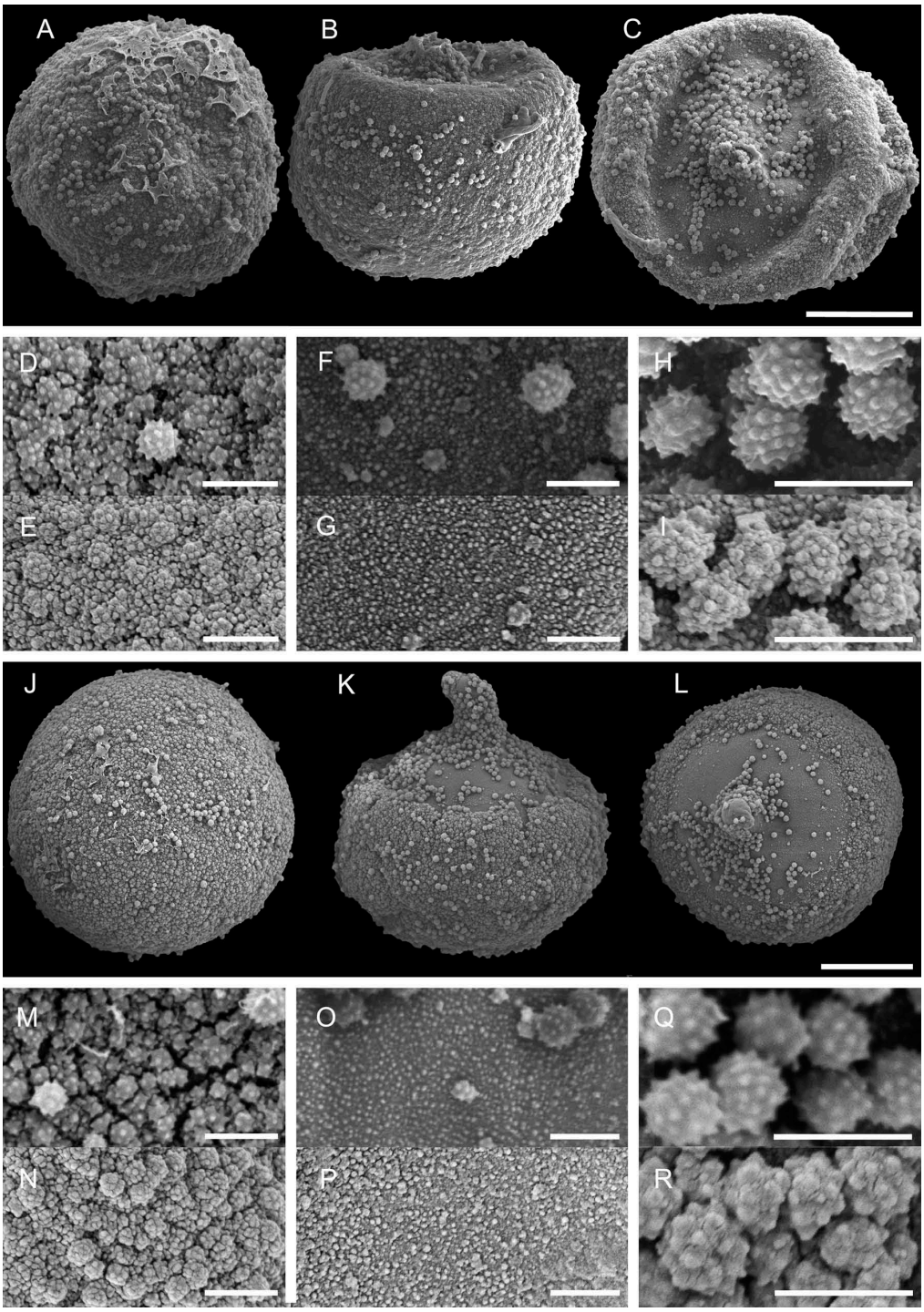

Figure 9. Scanning electron microscopy (SEM) micrographs of *Glyptostrobus* and *Taxodium* pollen. **A–I.** *Glyptostrobus pensilis*. **A–C.** Overview, PRV (**A**), EV (**B**), DV (**C**). **D–I.** Close-ups of exine sculpturing, (**D, E**) PRV, (**F, G**) DV, (**H, I**) orbicules. **J–R.** *Taxodium mucronatum*. **J–L.** Overview, PV (**J**), DV (**K**), EV (**L**). **M–R.** Close-ups of exine sculpturing, PRV (**M, N**), DV (**O, P**), orbicules (**Q, R**). Specimen P01642576 (**A–D, F, H**), S-C-4244 (**E, G, I**), W2000-05875 (**J–M, O, Q**), S-C-4341 (**N, P, R**). Not acetolysed (**A–D, F, H, J–M, O, Q**), acetolysed (**E, G, I, N, P, R**). Abbreviations: proximal view (PRV), distal view (DV), equatorial view (EV). Scale bars – 10 μm.

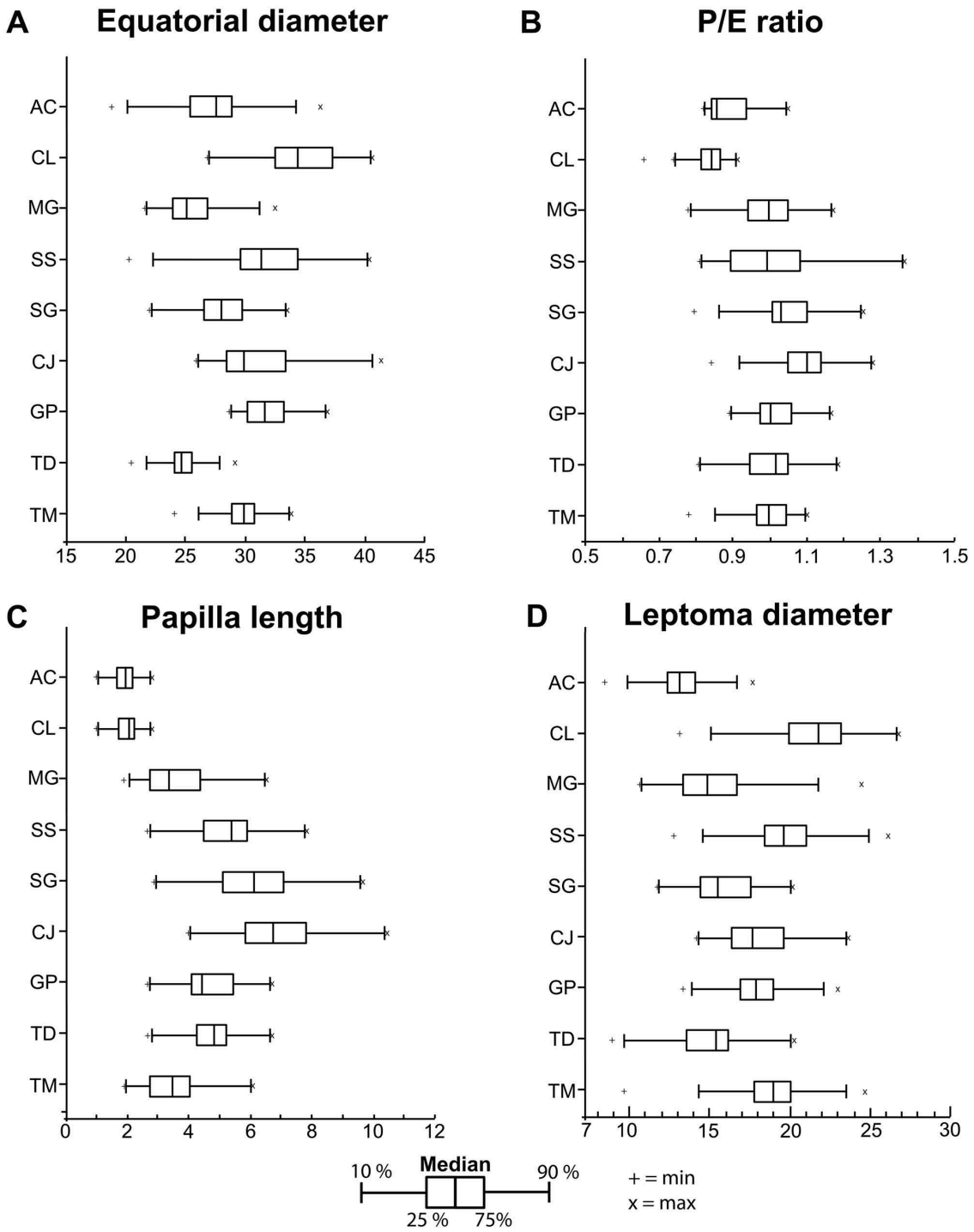

Figure 10. Morphological characters range box-plot and whisker diagrams of Athrotaxidoideae, Cunninghamioideae, Sequoioideae and Taxodioideae. *X*-Axis in μm (**A, C, D**) (n = 60). Abbreviations: *Athrotaxis cupressoides* (AC), *Cunninghamia lanceolata* (CL), *Metasequoia glyptostroboides* (MG), *Sequoia sempervierens* (SS), *Sequoia giganteum* (SG), *Cryptomeria japonica* (CJ), *Glyptostrobus pensilis* (GP), *Taxodium distichum* (TD), *Taxodium mucronatum* (TM).

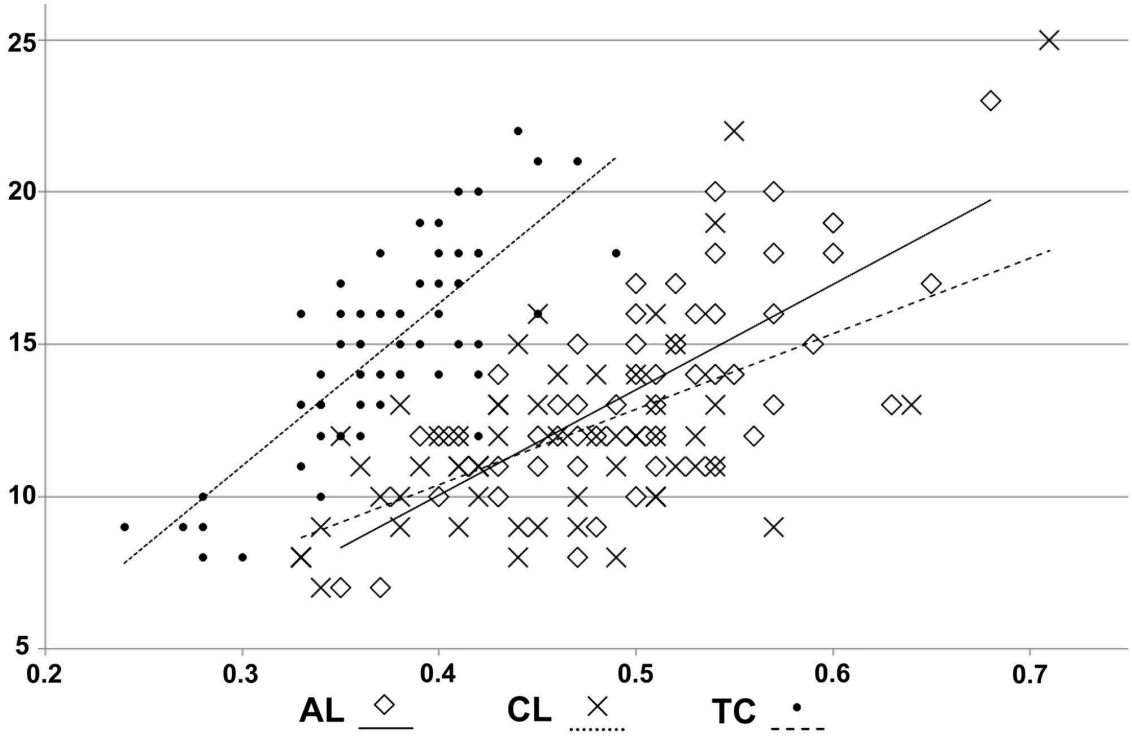

Figure 11. Echini to orbiculae diameter relation diagram of Athrotaxidoideae, Cunninghamioideae, and Taiwanioideae. *X*-Axis in µm, *Y*-axis number of visible echini (n = 60). Abbreviations: *Athrotaxis cupressoides* (AC), *Cunninghamia lanceolata* (CL), *Taiwania cryptomeroides* (TC).

Description. — Pollen, monad, shape spheroidal to oblate spheroidal, P/E including papilla 0.92–1.07, P/E excluding papilla 0.84–0.93, outline circular in polar view, weakly elliptic to circular in equatorial view; pollen size small to medium, equatorial diameter 28.5–32.3 µm wide (LM), polar axis including papilla 28.3–32 µm long (LM); leptoma distinct (LM, SEM), leptoma diameter 17.5–30.3 µm (LM), papilla shape straight, weakly or sharply bent, papilla length 2.6–4.4 µm (LM), papilla width 4.1–5.5 µm (LM); exine 1.4–1.7 µm thick (LM), nexine as thick to slightly thinner than sexine; sculpturing in LM psilate to scabrate, sculpturing in SEM (non-acetolysed and acetolysed pollen) microverrucate, fossulate, perforate, microverrucae of variable size, with densely spaced blunt nanoechini (Figure 8D, E), leptoma region nanoechinate, papilla nanoechinate, in some specimens papilla covered by orbicules; orbicules spheroidal to polygonal with blunt echini.

Remarks. — Several studies investigated pollen of *Taxodium mucronatum* using LM (Van Campo-Duplan 1951; Erdtman 1965) and SEM (Solomon et al. 1973; Kedves 1985; Li et al. 2010; Tiwari et al. 2012; Grimm et al. 2016). In the literature, size ranges from 17.5 to 32 µm have been given (see Table S1).

Discussion

Potential of pollen morphology to discern species and species groups in papillate Cupressaceae (Figures 10–14)

Among papillate Cupressaceae, two distinct groups, one with short (median length *c.* 2 µm) and one with long papilla (median > 3 to *c.* 7 µm), can be distinguished (Figures 10C, 15; Table I). Within the former group, *Athrotaxis, Cunninghamia*, and *Taiwania* form a basal grade in Cupressaceae in molecular based phylogenies (Schulz & Stützel 2007; Gadek et al. 2000; Mao et al. 2012). These taxa also tend to have the lowest P/E ratio (Figure 10B, Table I). Among this basal grade, *Cunninghamia* can be readily distinguished by cavities between endexine and ectexine (Kurmann 1990a; Jia et al. 1998). This feature is only known from *Cunninghamia* within papillate Cupressaceae. *Athrotaxis* differs

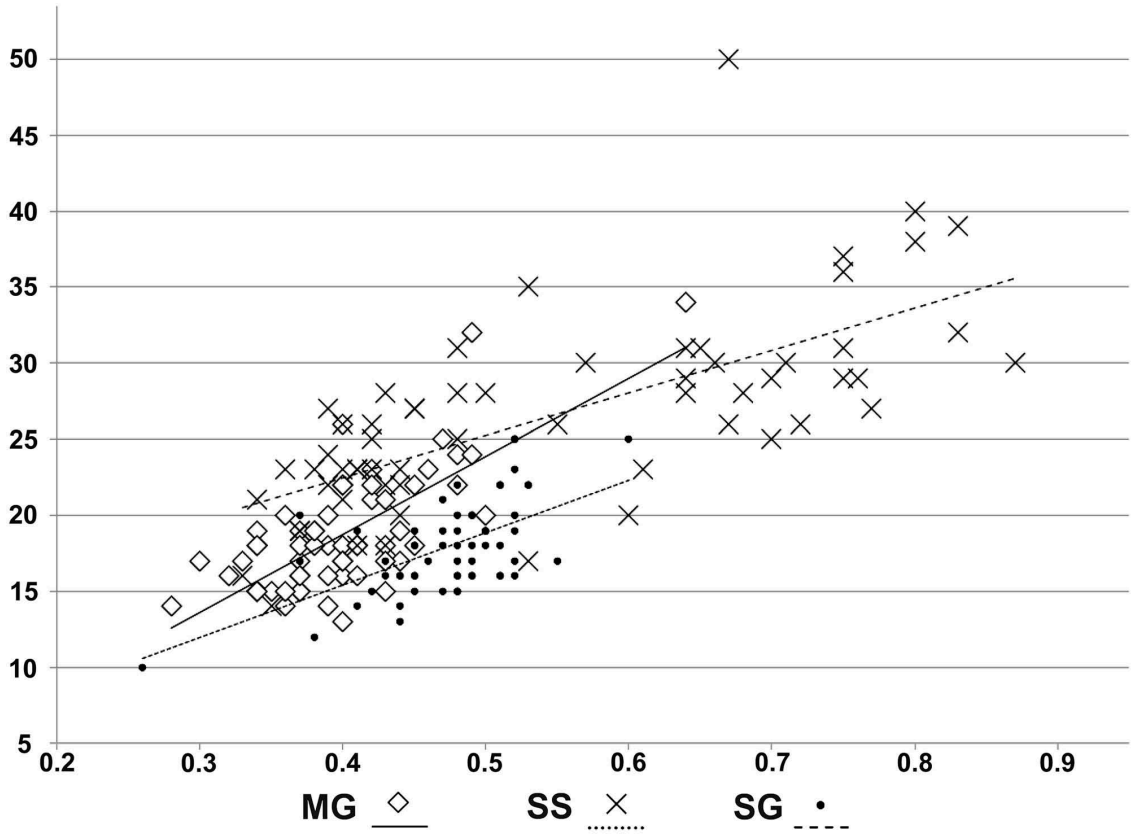

Figure 12. Echini to orbiculae diameter relation diagram of Sequoioideae. *X*-Axis in µm, *Y*-axis number of visible echini (n = 60). Abbreviations: *Metasequoia glyptostroboides* (MG), *Sequoia sempervierens* (SS), *Sequoia giganteum* (SG).

from *Taiwania* by the less densely spaced echini on the orbicules (Figure 11). Within the group comprising taxa with long papillae (Figure 10C), *Cryptomeria, Metasequoia, Sequoia, Sequiodendron, Glyptostrobus*, and *Taxodium* are remarkably similar. *Cryptomeria*, sister of *Glyptostrobus* and *Taxodium* within the Taxodioideae, tends to have slightly larger pollen than the latter two species. In the Sequoioideae, *Sequoia* has slightly larger pollen than *Metasequoia* and *Sequoiadendron* (Figure 10A, Table I). In general, size of the pollen grains of all genera investigated showed a strong overlap. Leptoma diameter did not provide further information to distinguish subfamilies (Figure 10D).

Within Taiwanioideae, Taxodioideae and Sequoioideae orbicules do not provide additional information. The number of echini per orbicule diameter does not show a significant trend (Figures 11–13) nor do the size and density of orbicules. In *Athrotaxis*, the echini density is lowest among all papillate Cupressaceae; in *Cunninghamia*, echini density is low as well, and echini are more pointed than in other taxa. In addition, configurations of LO-patterns (so-called *lux obscuritas* patterns seen in different focal planes during LM investigation; Supplementary Figure S10) have been suggested as an additional character to distinguish the former Taxodiaceae (e.g. Erdtman 1943, 1957, 1965). Since LO patterns in papillate Cupressaceae pollen are primarily the result of orbicules on the tectum, very similar patterns were observed for all species investigated (see Figure S10). Hence, we could not confirm the presence of patterns exclusively found in a single species or genus. Rather, it seems that density and distribution of orbicules depend on the timing of pollen release.

Pollen wall architecture

In Cupressaceae, the endexine is distinctly lamellate while the outer ectexine is granulate (Kurmann 1990b). For *Cryptomeria* and *Sequoia*, relatively thick, lamellate endexine (consisting of up to 16 lamellate layers) have been reported (Kedves 1985; Uehara & Sahashi 2000) while in *Cunninghamia*, endexine is made up of fewer layers (< 10; Kurmann 1990a). In addition, in

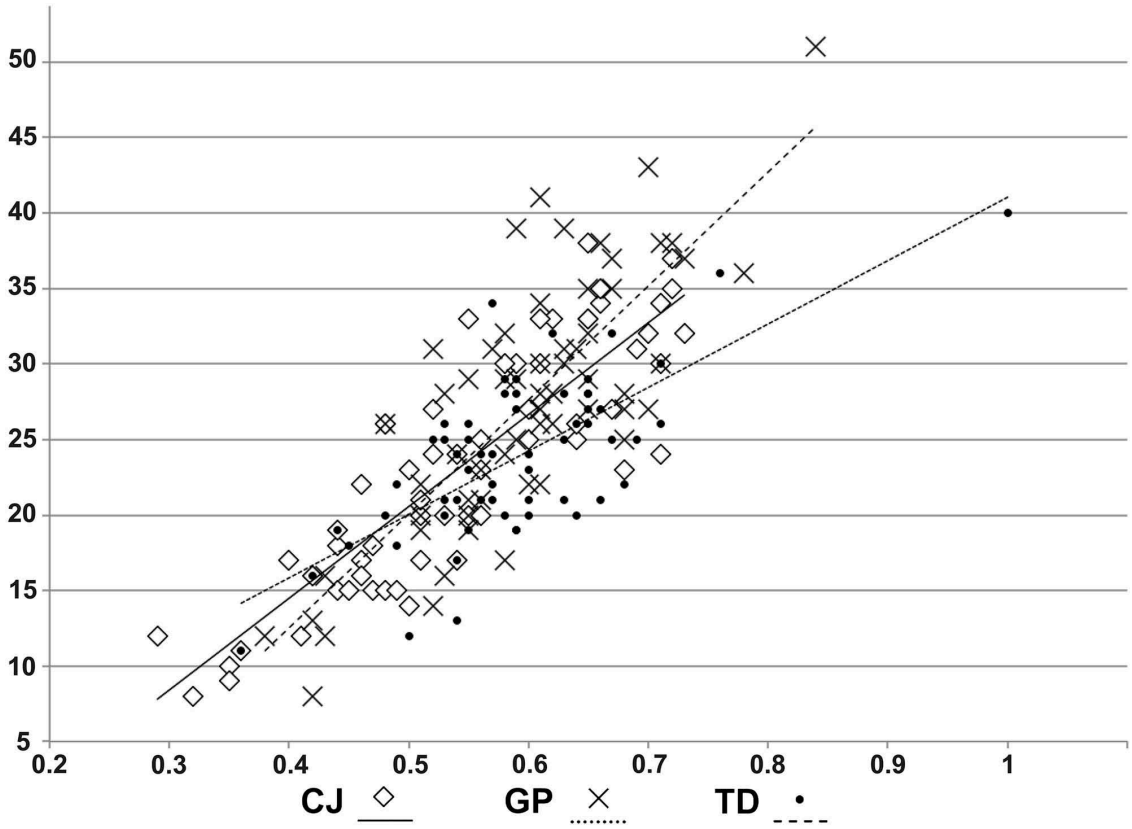

Figure 13. Echini to orbiculae diameter relation diagram of Taxodioideae. *X*-Axis in μm, *Y*-axis number of visible echini (n = 60). Abbreviations: *Cryptomeria japonica* (CJ), *Glyptostrobus pensilis* (GP), *Taxodium distichum* (TD).

Cunninghamia the granulate ectexine tends to have cavities whereby the ectexine appears only loosely attached to the endexine. This superficially resembles the sacci in pollen of Pinaceae, but see Kurmann (1990b) for general differences between alveolar and granular conifer pollen. In addition, for *Ephedra*, cavities between the lamellate endexine and the ectexine have been shown at least for wind-dispersed species (Bolinder et al. 2016).

The characteristic papillae of the former Taxodiaceae are part of the leptoma (aperture). The lamellate endexine thins out and forms a thin outer layer of the papilla. In the more primitive Sciadopityaceae and Cupressaceae, the leptoma may have a central, circular area with a markedly thin wall (consisiting of a single endexine lamella; Kurmann 1990a; 1990b; Uehara & Sahashi 2000; Uehara & Saiki 2011). Notably, the basal grade in Cupressaceae (Cunninghamioideae, Taiwanioideae, Athrotaxidoideae) has pollen with a very indistinct papilla similar to the pollen found in the core Cupressaceae (Callistroideae, Cupressoideae; Figure 15; Van Campo-Duplan 1950). In some Cupressoideae the porus-like thinning is missing, and the aperture comprises the entire leptoma. For example, in *Cupressus*, some species may possess a distinct circular thinning in the leptoma in some specimens, while others may not have this thinning (Kedves 1985). In other species, for example *Thuja plicata*, Kedves (1985) did not find circular thinnings at all. Likewise, for *Taxodium mucronatum* this author reported nearly equal amounts of papillate and non-papillate pollen grains. Hence, it might be difficult to discern members of the basal grade from Cupressoideae and Callistroideae. Among pollen of the groups with distinct papillae, Taxodioideae and Sequoioideae, we did not find any distinct features distinguishing these two groups. This has strong implications for the taxonomic assignment of dispersed fossil taxodiaceous papillate pollen grains and for inferring palaeoenvironments.

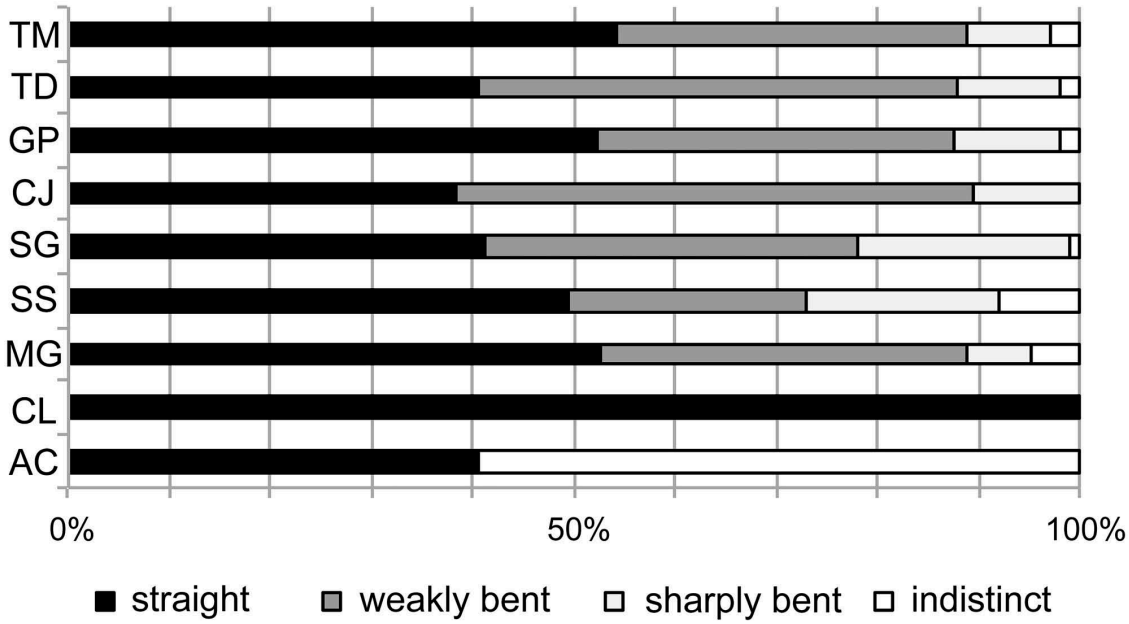

Figure 14. Papilla configuration abundance diagram of Athrotaxidoideae, Cunninghamioideae, Sequoioideae and Taxodioideae (n = 100). See Supplementary Figure S3 for schematic types of papilla configuration. Abbreviations: *Athrotaxis cupressoides* (AC), *Cunninghamia lanceolata* (CL), *Metasequoia glyptostroboides* (MG), *Sequoia sempervierens* (SS), *Sequoia giganteum* (SG), *Cryptomeria japonica* (CJ), *Glyptostrobus pensilis* (GP), *Taxodium distichum* (TD), *Taxodium mucronatum* (TM).

Taxonomic and palaeoenvironmental signal in papillate Cupressaceae pollen

Shatilova et al. (2018) published an atlas of Cenozoic dispersed pollen of Georgia (Transcaucasia) in which they recognised seven of nine genera of taxodiaceous Cupressaceae. For instance, *Cunninghamia* appears to have been restricted to Pleistocene strata in Georgia. *Cunninghamia* has a distinct pollen morphology (see above) and we agree with the determination provided by Shatilova et al. (2018, plate 49, figures 1–6). In other instances, for example the distinction between *Glyptostrobus* and *Cryptomeria* or between *Metasequoia* and *Taxodium*, evidence from pollen morphology for such distinctions is very weak. In such cases, caution is required if one does not want to introduce a biased temporal and spatial pattern of presence of particular taxodiaceous taxa. This is even more important, as modern representatives of the genera mentioned earlier show very different ecologies. In another recent article, Biltekin et al. (2015) reported a very young, Holocene, last appearance date for the genus *Glyptostrobus* in the Black Sea area. From across Europe, it appears that taxodiaceous Cupressaceae persisted until *c.* 0.5 Ma (Magri et al. 2017). Based on the results of the present study, determination of the dispersed pollen shown in Biltekin et al. (2015, plate 1, figures 5–12) appears to be difficult. *Glyptostrobus* is part of the Taxodioideae, along with *Taxodium* and *Cryptomeria*. Based on all available data, dispersed pollen of *Glyptostrobus* cannot be unambiguously distinguished from other Taxodioideae (Figures 6–9). Also, differences to Sequoioideae appear to be too subtle as to be useful for distinguishing species. In conclusion, the pollen grains from different time slices assigned to *Glyptostrobus* in Biltekin et al. (2015) appear to be difficult to assign to this particular genus in the taxodiaceous Cupressaceae. The very well-preserved Holocene sample shown by Biltekin et al. (2015) shows a pollen ornamentation virtually identical with as many genera as *Glyptostrobus, Taxodium, Cryptomeria, Sequoia, Sequoiadendron*, and *Metasequoia*. Hence, an assignment to a particular genus may potentially be misleading. In another study, Kotthoff et al. (2014) investigated Oligocene to Miocene strata off the coast of New Jersey and identified *Taxodium* and *Sequoia* based on the length of the papilla. According to the present results (Figure 10C, Table I) this may not be a reliable criterion as the papilla lengths of the two living species of *Taxodium* include that of *Sequoia*.

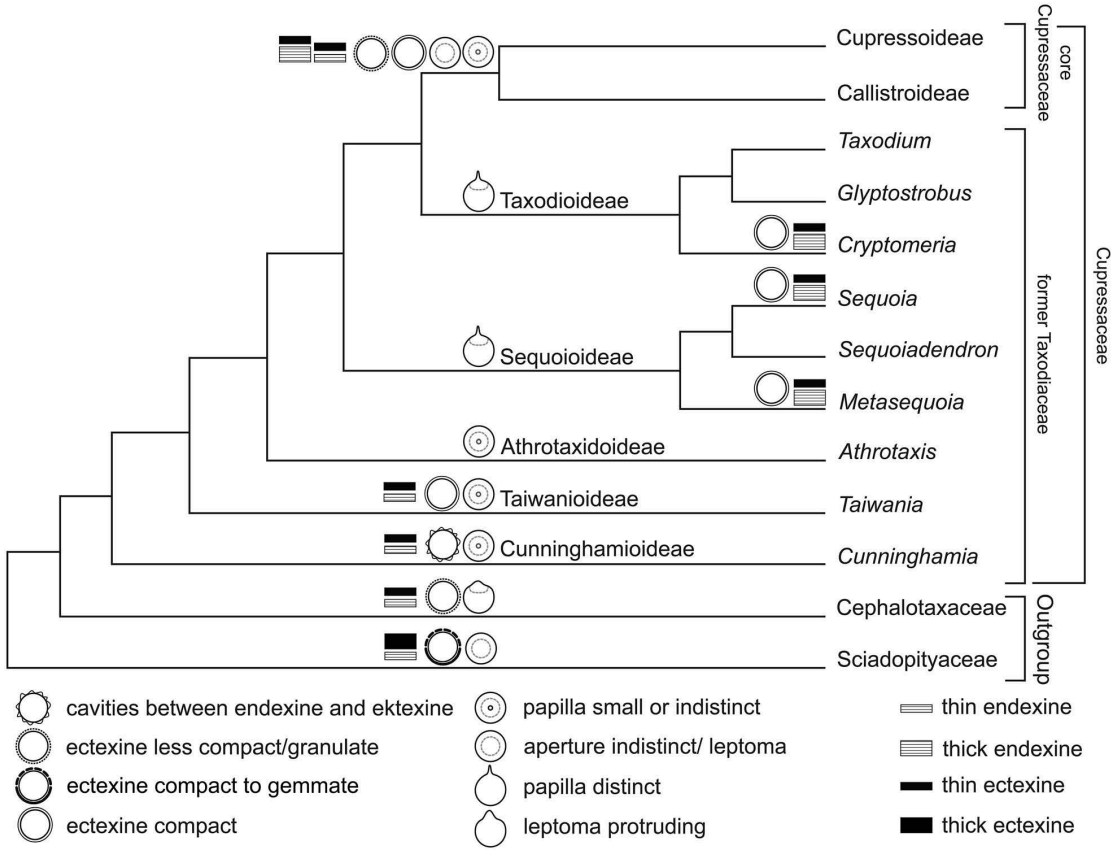

Figure 15. Phylogenetic dendrogram showing main subfamilies of Cupressaceae with their corresponding pollen morphological characters and pollen wall architecture. Additional data for pollen wall characters: Sciadopityaceae (Kvavadze 1988; Uehara & Saiki 2011), Cephalotaxaceae (Xi 1993), Cunninghamioideae (Kvavadze 1988; Kurmann 1990a; Jia et al. 1998), *Taiwania cryptomeroides* (Chen et al. 2006), *Metasequoia glyptostroboides* (Kvavadze 1988), *Sequoia sempervirens* (Kedves 1995), *Cryptomeria japonica* (Yamada et al 1980; Uehara & Sahashi 2000).

McIntyre (1991) described a pollen assemblage from Eocene strata of Axel Heiberg Island. He identified *Glyptostrobus* and *Metasequoia* using LM. Based on the mass occurrence of *Metasequoia* and the moderate abundance of *Glyptostrobus* in the macrofossil record, these identifications most likely are correct. However, if pollen morphology is taken alone, the figured pollen grains cannot unambigously be assigned to a particular genus in the Taxodioideae or Sequoioidea.

These examples illustrate the low taxonomic value of pollen morphology in discriminating Taxodioideae and Sequoioideae within the taxodiaceous Cupressaceae. At the same time, the remaining subfamilies in taxodiaceous Cupressaceae such as for example *Cunninghamia* provide sufficient informative characters to be determined to genus level.

Conclusions

The former Taxodiaceae are currently treated as five subfamilies within the Cupressaceae. Fossil dispersed taxodiaceous pollen grains have commonly been identified to genus level and based on modern ecologies of different groups this information has been used to infer distinct palaeoenvironments. In this article, we investigated pollen morphology of generally papillate Cupressaceae (*Athrotaxis, Cryptomeria, Cunninghamia, Glyptostrobus, Metasequoia, Sequoia, Sequoiadendron, Taiwania*, and *Taxodium*) in order to establish whether pollen morphology can be used to distinguish species and subfamilies. In general, we found only a few informative characters among members of papillate Cupressaceae and features such as the size of pollen, leptoma and orbicules are not useful to discriminate subfamilies/genera. We found that in a basal

grade of Cupressaceae, three subfamilies share short papillae, whereas in two more derived clades (Sequoioideae and Taxodioideae) papillae are markedly longer. In the generally non-papillate core Cupressaceae, the leptoma (aperture) area may or may not possess a distinct circular thinning as also found in the basal grade of taxodiaceous Cupressaceae (Figure 15). This shows that (i) it may be difficult to tell apart some taxodiaceous Cupressaceae from core Cupressaceae (Cupressoideae and Callistroideae) and (ii) that it is difficult if not impossible to distinguish members of the ecologically distinct Taxodioideae and Sequoioideae based on pollen morphology. Given the fact that the ecological amplitude for many taxodiaceous Cupressaceae was much wider during large parts of the Cenozoic, we conclude that it is not wise to infer particular palaeoenvironments on the basis of dispersed taxodiaceous pollen grains alone.

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Disclosure statement

No potential conflict of interest was reported by the authors.

Supplementary Material

Supplementary data for this article can be accessed here

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