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Pollen morphology of extant Winteraceae: a study allowing SEM-based affiliation of its fossil representatives

FRIÐGEIR GRÍMSSON[1], ALEXANDROS XAFIS[1], FRANK H. NEUMANN[2,3], and REINHARD ZETTER[1]

[1] University of Vienna, Department of Palaeontology, Althanstraße 14 (UZA II), 1090 Vienna, Austria; e-mails: fridgeir.grimsson@univie.ac.at; alexandros.xafis@univie.ac.at; reinhard.zetter@univie.ac.at

[2] University of KwaZulu-Natal, School of Agricultural, Earth and Environmental Sciences, Carbis Road, Scottsville, Pietermaritzburg 3201, South Africa

[3] University of the Free State, Department of Plant Sciences, Nelson Mandela Drive, Bloemfontein 9301, South Africa; e-mail: fneumann1971@gmail.com

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ABSTRACT. When applying high-resolution microscopy, the pollen morphology of extant taxa can be used to classify fossil pollen, that is, to address the latter in the established systematic-phylogenetic framework. Here we investigate tetrads and pollen features of 20 different Winteraceae species, most of them belonging to the early-diverging generic lineages *Tasmannia*, *Drimys* and *Pseudowintera*. The tetrads and pollen are grouped into eleven pollen types based on diagnostic features observed by both light and scanning electron microscopy. The high-resolution scanning electron micrographs of recent material allow detailed comparison with fossil material, resulting in a more accurate affiliation of fossil tetrads/pollen to extant lineages. As a case study, early Miocene Winteraceae tetrads from South Africa are re-examined and formally described. The systematic placement of the African fossils is discussed in light of the pollen types presented here.

KEYWORDS: *Belliolum*, *Bubbia*, *Exospermum*, *Drimys*, *Pseudowinterapollis*, *Takhtajania*, *Tasmannia*, *Zygogynum*, pollen tetrads, Miocene, Africa

INTRODUCTION

The predominantly Southern Hemispheric Winteraceae (Canellales) are today the only angiosperm group known to produce tetrads of ulcerate pollen that do not disintegrate after maturation and can be found as such in the fossil record (e.g. Walker 1974, Walker & Doyle 1975, Praglowski 1979, Sampson 1981, 2000a, Coetzee & Praglowski 1988, Doyle et al. 1990a, Grímsson et al. in press). At present, Winteraceae comprise about 65 species in four to eight genera (e.g. Vink 1993), with the greatest generic and species diversity in Australasia (*Belliolum*, *Bubbia*, *Exospermum*, *Pseudowintera*, *Tasmannia*, *Zygogynum*; Vink 1970, 1977, 1983, 1985, 1988, 2003, Doust & Drinnan 2004) and America (*Drimys*; Smith 1943). A single taxon occurs in Madagascar (*Takhtajania*; Leroy 1978, 1980, Vink 1978). Phylogenetic relationships between the five main generic lineages *Drimys*, *Pseudowintera*, *Takhtajania*, *Tasmannia*, and *Zygogynum* s.l. (the latter including *Belliolum*, *Bubbia*, and *Exospermum*) can be considered resolved (Fig. 1), with all later studies (Karol et al. 2000, Doust & Drinnan 2004, Marquínez et al. 2009, Thomas et al. 2014) essentially confirming the tree of Suh et al. (1993) regardless of taxon and gene sampling. According to the molecular data, *Takhtajania* represents the first diverging branch among the extant Winteraceae, followed by *Tasmannia* and *Drimys*, the latter being sister to a clade comprising *Pseudowintera* as sister to

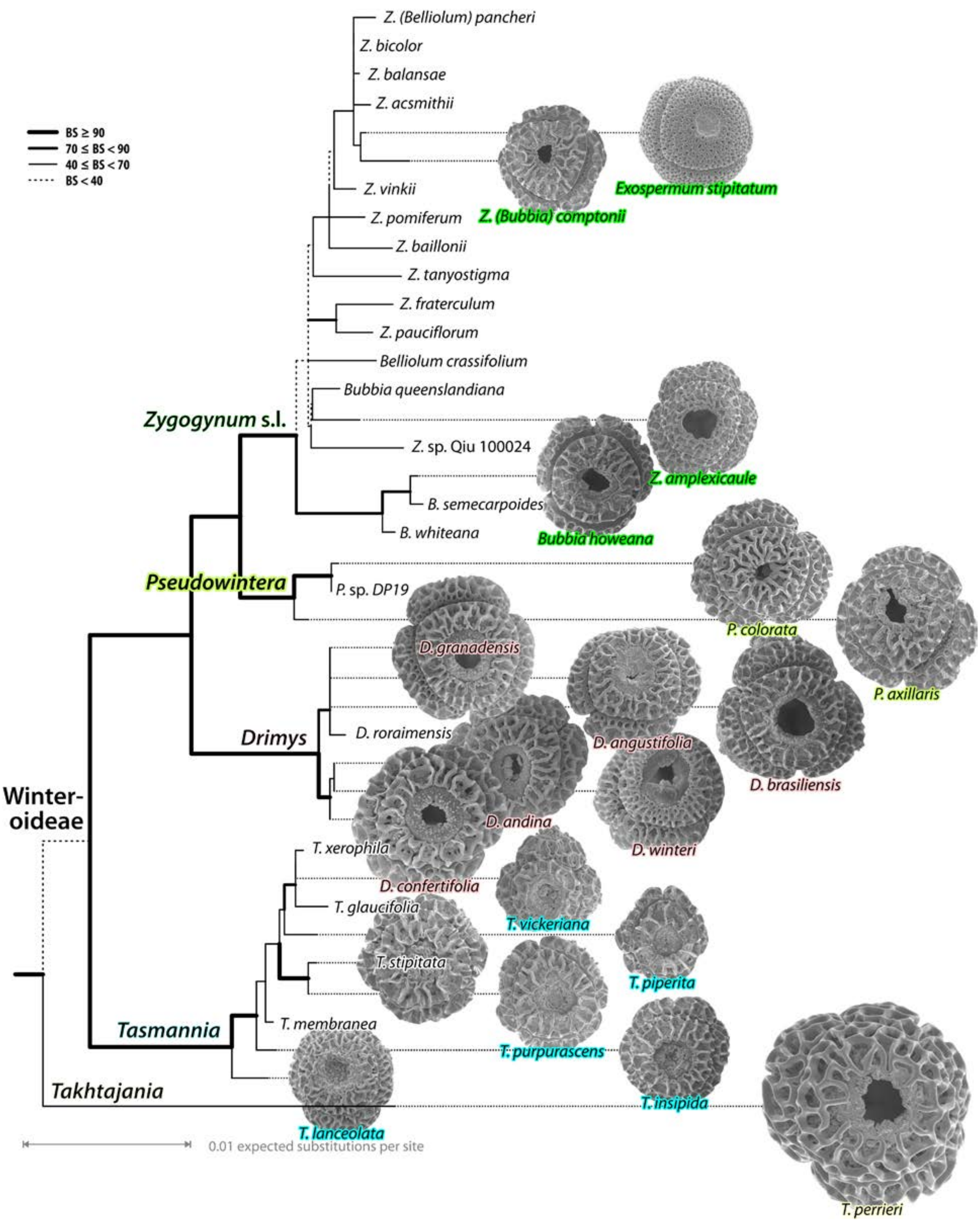

Fig. 1. Winteraceae pollen tetrads mapped on a recent phylogeny tree based on (up to) 7-gene data set (reduced taxon set; Grímsson et al. in press). The data covered (part of) the nuclear-encoded 18S rRNA gene and ITS region (ITS1, 5.8S rRNA gene, ITS2) and the plastid *trnH-psbA* intergenic spacer, the *trnK* intron/*matK* gene region, the *atpB* and *rbcL* genes, and the trnLF region (*trnL* intron, the *trnL 5' exon*, *trnL-trnF* intergenic spacer) for Winteraceae and Canellaceae (subtree not shown). Tree is rooted based on the assumption of mutual monophyly of Winteraceae and Canellaceae

Zygogynum s.l. (Fig. 1). Except for the branch informing the Winteraceae root (and defining the Winteroideae clade), the backbone branches can be unanimously supported and are relatively prominent, but inter-species/-generic relationships within *Zygogynum* s.l. seem to be complex and cannot be convincingly solved (Fig. 1) based on the currently available data (Suh et al. 1993, Karol et al. 2000, Thomas et al. 2014, Grímsson et al. in press).

Table 1. Pollen/tetrad features of extant Winteraceae species vs. African fossils

Species	*Takhtajania perrieri*	*Tasmannia insipida*	*T. lanceolata*	*T. piperita* (Phillipine)	*T. piperita* (Malaysian)	*T. purpurascens*	*T. stipitata*	*T. vickeriana*	*Drimys andina*	*D. angustifolia*	*D. brasiliensis*	*D. confertifolia*	*D. granadensis*	*D. winteri*
Plate (or not studied)	1, 2	3, 4; S1–S4	5, 6	S5, S6	7, 8	9, 10	11, 12	13, 14	15, 16	17, 18	19, 20; S7, S8	21, 22	23, 24; S9–S12	25, 26; S13–S16
Pollen Type	PT 1	PT 2	PT 2	PT 2		PT 2	PT 2	PT2	PT3	PT 3	PT 3	PT 3	PT 3	PT 3
Dispersal unit	Tetrad	Tetrad	Tetrad	Tetrad		Tetrad	Tetrad	Tetrad	Tetrad	Tetrad	Tetrad	Tetrad	Tetrad	Tetrad
Tetrad outline basal view (LM, SEM)	lobate to hexagonal	circular to hexagonal to lobate	circular to hexagonal to lobate	hexagonal to lobate	hexagonal to lobate	circular to hexagonal to lobate	hexagonal to lobate	lobate	lobate to hexagonal	lobate to hexagonal	lobate	lobate to hexagonal	lobate	lobate
Tetrad outline lateral view (LM, SEM)	lobate to octagonal	circular to octagonal	circular to octagonal	circular to octagonal	circular to octagonal	lobate to octagonal	lobate to octagonal	lobate to octagonal	circular to octagonal	circular to octagonal	lobate to octagonal	octagonal	lobate to octagonal	lobate to octagonal
Tetrad outline apical view (LM, SEM)	lobate	circular to hexagonal to lobate	circular to hexagonal to lobate	hexagonal to lobate	hexagonal to lobate	hexagonal to lobate	hexagonal to lobate	lobate	lobate to hexagonal	lobate to hexagonal	lobate	lobate to hexagonal	lobate	lobate
Tetrad (monad) diameter (LM; µm)	65–83[1]	35–39[1]	33–36[1]	32–35[1]		25–30[1]	35–38[1]	26–29	38–48[1]	33–36	45–50[1]	34–50[1]	45–55[1]	42–50[1]
Pollen interface (SEM)	Mostly closed	Closed	Closed	Open (ca 1 µm wide) or closed		Closed	Closed	Open (up to 1.5 µm wide) or closed	Closed or nearly so (<500 nm wide)	Closed or nearly so (<500 nm wide)	Closed or nearly so (<500 nm wide)	Nearly closed (<500 nm wide)	Nearly closed (<500 nm wide)	Closed or nearly so (<500 nm wide)
Apertures surrounded by an annulus-like rim (SEM; width; µm)	Yes, 2.5–6	No	No	No		No	No	No	Yes, 2.0–4.5	Yes, 2.0–3.5	Yes, 2.5–3.5	Yes, 3–4.5	Yes, 2.5–4	Yes, 2.5–4.0
Width of aperture region (SEM; µm, longest axis)*	12–17	7–10	10–11	7–10		9–12	9–11	8–11.5	13–14	9.5–12.5	11–14(–17)	13.5–17	10–15.5	10–14
(Max.) Thickness of exine (LM; µm)	4.8–5.1 (5.5)[1]	2.9–3.2 (3)[1]	2.8–2.9 (2)[1]	3–3.4 (2.5)[1]		2.8–2.9	3–3.2 (2.5)[1]	2.6–2.9	3.5–4.2	3.6–3.8	3.5–4.1 (3–3.5)[1]	3.6–4.2 (4.5)[1]	3.4–4.2 (2.5–3.5)[1]	3.5–4.0 (3.5–5)[1]
Thickness of sexine (LM; µm)	3.6–4.2 (6[2]; not used)	1.8–2.3	2.1–2.2	2.2–2.9		2.2–2.4	1.8–1.9	1.7–1.8	2.5–2.9	2.4–2.9	1.9–3.0	2.4–3.1	2.5–3.1	2.5–3.1
Thickness of nexine (LM; µm)	0.7–0.9 (1.5[2]; not used)	0.6–0.9	0.6–0.7	0.9–1.1		0.6–0.7	0.9–1.1	0.7–0.8	1.1–1.2	1.0–1.1	1–1.5	1.2–1.3	1–1.2	0.9–1.2
Sculpture of pollen (SEM)	Reticulate	Reticulate	Reticulate	Reticulate		Reticulate	Reticulate	Reticulate	Reticulate	Reticulate	Reticulate	Reticulate	Reticulate	Reticulate
Muri (SEM)	Broad and rounded	Narrow and crested	Narrow and rounded	Narrow and crested		Narrow and crested	Narrow and crested	Narrow and rounded	Narrow and crested	Narrow and crested	Narrow and crested	Narrow and crested	Narrow and crested	Narrow and crested
Diameter of (largest) lumina (SEM; µm; longest axis)	7–11	4.5–5.5	4–7	6–8		5–7	5–7	5–6	5–6	4–6	4–5.5	5–8	4–7	5–6
Number of lumina/perforations (one grain in lateral view)	ca 15/20	ca 20	ca 30	ca 15		ca 20	ca 20	ca 15	ca 25	ca 25/30	ca 20/25	ca 30	ca 25	ca 25/30
Height ratio columellae vs. Muri (SEM)	ca 1–1.5:1	ca 1:1	ca 1:1	ca 1:1		ca 1:1	ca 1:1	ca 1–2:1	ca 1:1	ca 1:1	ca 1:1	ca 1:1	ca 1:1	ca 1:1
Columellae per µm	On average 2 per 5 µm	1–2(–3)	1(–2)	1(–2)	2	1–2	1–2	1–2	1–2	1–2	1–2	1–2	1	1–2
Reticulum around aperture region (SEM)	Some free-ending muri, or adpressed	Continuous	Continuous, partly adpressed	Continuous		Continuous	Continuous	Continuous or free-ending muri	Mostly free-ending muri, or adpressed	Mostly free-ending muri, or adpressed	Mostly free-ending muri, or adpressed	Many free-ending muri, or adpressed	With free-ending muri, or adpressed	Mostly free-ending muri, or adpressed
Surface of footlayer within lumina (SEM)	Psilate	Granulate to nanoverrucate (particularly in lumina surrounding the aperture region)	Mostly granulate, to nanoverrucate in lumina surrounding the aperture region	Granulate	Psilate	Granulate to nanoverrucate (particularly in lumina surrounding the aperture region)	Granulate	Granulate	Psilate or granulate	Psilate or granulate	Psilate to granulate	Psilate or granulate	Psilate to (sparsely) granulate	Psilate or (sparsely) granulate
Free–standing columellae (SEM)	In some or nearly all lumina; always in groups of up to 10+; ≤ 1 µm (occassionally > 1 µm); gemmae, bacula, and clavae	Very rare (≤ 1 per grain); solitary; microgemmae or microclavae	Very rare (≤ 1 per grain); solitary; erect	Rare (in about every 5th lumen; usually solitary, rarely up to 3–4; usually ≤ 0.5 µm; ± circular in outline (nanoverrucae or nanogemmae)	Rare or nearly all lumina; up to 8, distributed or grouped; always < 1 µm; mostly microgemmae, some microclavae, rarely microbaculae	Rare or in most lumina; up to 6, scattered; ≤ 0.5 µm; ± circular in outline (nanoverrucae, nanogemmae)	Very rare or rare; solitary or in groups of up to six; always < 1 µm; microgemmae and microclavae	Very rare; solitary; < 1 µm; microgemmae	Rare; solitary or in groups; < 1 µm; microclavae, microgemmae)	± Rare; solitary or in groups, scattered; ≤ 0.5 µm; nanogemmae, nanoclavae	(Very) rare; usually solitary; ≤ 0.5 µm; mostly nanoclavae, or nanobacula	Rare or every 2[nd] lumen; 1–5; ≤ 0.5 µm; nanogemmae, nanoclavae, nanobaculae	Very rare; solitary; < 0.5 µm; ± circular in outline (nanoverrucae, nanogemmae?)	± Rare; solitary or in groups; ≤ 0.5 µm; nanogemmae, nanoclavae
Ulcus membrane sculpture (SEM)	Granulate to microverrucate, occassionally (fused) microrugulae (≤ 1 µm)	Granulate with usually spaced, imperfect microgemmae/clavae (≤ 1 µm, occassionally larger)	Granulate, microgemmate; few microclavae, spaced or packed, partly fused	Granulate with few wide-apart microgemmae/ clavae (≤ 1 µm), sometimes fused		Granulate, microgemmate; microgemmae spaced, rarely fused, or packed	Granulate to nanoverrucate; non-fused microgemmae/clavae ≤ 1 µm	Granulate, (nano)gemmate to (nano)clavate; larger elements spaced	Granulate to nanoverrucate, nanogemmate	Granulate to nanoverrucate, nanogemmate	Granulate to microverrucate; outer margin with occassional isolated nanobacula, nanogemmae, nanoverrucae (≤ 0.5 µm)	Granulate to microverrucate; outer margin with occassional isolated nanobacula, nanogemmae, nanoverrucae (≤ 0.5 µm)	Granulate to nanoverrucate, nanogemmate	Granulate to microverrucate; can show isolated S.E. (usually microbacula; < 1 µm)
Literature used	[1] Praglowski (1979) [2] Sampson (2000)	[1] Praglowski (1979)	[1] Praglowski (1979)	[1] Praglowski (1979)		[1] Fiser & Walker (1967)	[1] Praglowski (1979)	N/A	[1] Praglowski (1979)	N/A	[1] Praglowski (1979)	[1] Praglowski (1979)	[1] Praglowski (1979)	[1] Praglowski (1979)

Note: Table includes previously published pollen/tetrads illustrated by SEM micrographs.

* – LM indicates same type as *Z. baillonii* and *Z. bicolor*.

† – See Sampson (1983) for issues with material addressed as *Z. pomiferum*, *Z.* ~ subsp. *balansae* (= *Z. balansae*) and the newly distinguished *Z. vinkii*.
Pollen-wise, *Z. pomiferum* and *Z. vinkii* are the same, but *Z. balansae* shows a much denser reticulum approaching a perforate grain, as otherwise found only in *Exospermum*.
S.E. – Sculpture elements.

Table 1. Continued

Species	*Pseudowintera axillaris*	*P. colorata*	*P. traversii*	*Bubbia howeana*	*B.* (*Zygogynum*) *comptonii*	*Zygogynum fraterculum*	*Z. bicolor*	*Z. acsmithii*	*Z. amplexicaula*	*Z. baillonii*	*Exospermum stipitatum*	*Z. vinkii* (+ *Z. pomiferum*)†	*Zygogynum balansae*	*Pseudowinterapollis africanensis* sp. nov.
Plate (or not studied)	27, 28; S17–S20	29, 30; S21–S24	31, 32; S25–S28	33, 34	35, 36	Not studied	Not studied	Not studied	37, 38	Not studied	39, 40	Not studied	Not studied	41–43
Pollen Type	PT 4	PT 4	PT 4	PT 5	PT 6	PT7	PT 8	PT 8	PT 8	PT 8	PT 9	PT 10	PT 11	N/A
Dispersal unit	Tetrad	Tetrad	Tetrad	Tetrad	Tetrad	Tetrad	Tetrad	Tetrad	Tetrad	Tetrad	Tetrad	Monad	Monad	Tetrad
Tetrad outline basal view (LM, SEM)	lobate to hexagonal	lobate to hexagonal	lobate	lobate to hexagonal	lobate to hexagonal	circular to lobate	circular to lobate	circular to lobate	lobate	circular to lobate	circular to lobate	eq. view: circular to elliptic; p. view: circular	eq. view: circular to elliptic; p. view: circular	lobate to hexagonal
Tetrad outline lateral view (LM, SEM)	circular to octagonal to lobate	octagonal to lobate	lobate	octagonal to lobate	circular to octagonal	circular to lobate	circular to lobate	circular to lobate	lobate	circular to lobate	circular			lobate to octagonal
Tetrad outline apical view (LM, SEM)	lobate	lobate	lobate	lobate to hexagonal	lobate to hexagonal	circular to lobate	circular to lobate	circular to lobate	lobate	circular to lobate	circular to lobate			lobate to hexagonal
Tetrad (monad) diameter (LM; µm)	36–49[1] (45–62[2])	38–55[1]	45–55[1]	37–43[1]	33–39[1]	34–48	35–40[2]	35–40[1]	29–33	42–51[2]	37–43[1]	25–36[2]	26–34[1]	38–49
Pollen interface (SEM)	Closed or open (up to 1500 nm wide)	Closed or open (up to 1500 nm wide)	Closed or open (up to 1500 nm wide)	Open	Open	Closed	Closed	Closed*	Open or closed	Closed	Closed	N/A	N/A	mostly closed, sometimes narrowly open
Apertures surrounded by an annulus-like rim (SEM; width; µm)	No	No	No	Yes, 1.5–2.0	No	Yes, 2–3	No	No	No	No	No	Yes, 3–3.5[2]	Yes, c. 3.5	Yes, 0.5–2
Width of aperture region (SEM; µm, longest axis)*	6–11	5.5–9.5	6.5–11	8–10	4–6.5	3–7	5[2]	7[1]	(7–)8–9(–10)	6[2]	5–6	6–7[2]	6–10	7–9.5
(Max.) Thickness of exine (LM; µm)	3.3–3.9 (3.5–4)[1]	3.3–3.8 (2.5–3.5)[1]	3.3–4.1	2.9–3.0 (3–3.5)[1]	3.4–3.5 (2.5[1])	4.2–4.5 [SEM break] (2–4.5)[1]	2.0 [TEM] (2)[2]	(2)[1]	2.5–2.6	(4)[2]	2.3–2.7 (3)[1]	1.7 (1.5–2)[2]	2.0–2.1 [TEM] c. 2 [LM] (2–2.5)[1]	4.2–4.7
Thickness of sexine (LM; µm)	2.7–3.3	2.5–2.8	2.5–3.2	2.1	2.4	3.5–3.8 [SEM break]	1.7 [TEM]	?	1.5–1.7	?	1.4–1.7	1.0	1.6–1.8 [TEM] 1.2 [LM]	2.7–3.3
Thickness of nexine (LM; µm)	0.5–0.9	0.8–1.1	0.6–1.0	0.8–1.1	1–1.1	0.6–0.8 [SEM break]	0.3–0.4 [TEM]	?	0.8–1.1	?	0.6–0.7	0.7	0.4–0.5 [TEM] 0.8 [LM]	1.1–1.8
Sculpture of pollen (SEM)	Reticulate	Reticulate	Reticulate	Reticulate, with free-ending muri	Reticulate	Reticulate	(Micro)reticulate	(Micro)reticulate*	(Micro)reticulate	(Micro)reticulate	Perforate to nanoreticulate	Nanoreticulate to microreticulate	Perforate to nano-/microreticulate	Reticulate
Muri (SEM)	Narrow and crested	Narrow and crested	Narrow and crested	Narrow and crested	Narrow and crested	Broad and rounded	Broad and rounded	Broad and rounded*	Broad and rounded	Broad and rounded	(Broad and rounded)	Broad and rounded	(Broad and rounded)	Narrow and crested
Diameter of (largest) lumina (SEM; µm; longest axis)	5–8.5	4.5–7	4.5–6	4.5–5.5	4–6	5–11	3[2]	≤ 1[1]	≤ 3	2[2]	≤ 1	1[2]	≤ 1	6–7
Number of lumina/perforations (one grain in lateral view)	ca 20	ca 25	ca 25/30	ca 15	ca 20	ca 20	ca 40	ca 100[1]	ca 40	ca 50	ca 120	ca 100[2]	ca 150	ca 25
Height ratio columellae vs. Muri (SEM)	ca 1:1	ca 1:1	ca 1:1	ca 1:1	ca 1:1	ca 1:1	?	?	1–1.5:1	ca 1:1 (?)	?	ca 2:1	ca 2:1	ca 1:1
Columellae per µm	± 1	± 1	1–2	(2–)3	1(–2)	1	±1 [based on TEM]	?	1–2(–3)	±1 (?)	2–3 [based on TEM[1]]	±1	1–2 [TEM, SEM break]	1(–2)
Reticulum around aperture region (SEM)	With free-ending muri, or adpressed	Continuous, adpressed	With free-ending muri, or adpressed	Continuous	With free-ending muri, or adpressed	± Continuous, 1–2 gaps, sometimes adpressed	Discontinuous	?	Many free-ending muri, or adpressed	Mostly free-ending muri	Mostly free-ending muri	Many free-ending muri	Mostly free-ending muri	Free-ending muri or adpressed
Surface of footlayer within lumina (SEM)	Psilate or granulate	Psilate or granulate	Psilate or granulate	Granulate	Psilate to granulate (particularly around aperture)	Psilate	Psilate or granulate (?) [based on TEM]	?	Psilate or granulate	[Not visible]	Psilate or granulate (?) [based on TEM[1]]	[Not visible]	Psilate [according TEM]	Psilate
Free–standing columellae (SEM)	Absent or very rare; solitary; <0.5 µm; nanogemmae	Absent or very rare; solitary; <0.5 µm; nanogemmae	Absent or very rare; solitary; <0.5 µm; nanogemmae; or in every 2nd or 3rd lumen; solitary or few (up to 3–4)	In nearly all lumina; few to many (up to 11), ± scattered; ≤ 0.5 µm; nanogemmae, nanoclavae, and nanobacula	Very rare, single	In all larger lumina; up to 12, spaced, ± filling the lumen; <1 µm; gemmae, clavae	Absent	?	Absent	Absent	Absent (see also TEM in [1], fig. 8DE)	Absent (?)	Absent	Absent or rare rare; solitary or two; usually ≤ 0.5 µm; nanogemmae, nanoclavae
Ulcus membrane sculpture (SEM)	Granulate, nano- to microgemmate/verrucate/rugulate	Granulate, (nano- to) gemmate/verrucate/rugulate to imperfectly microreticulate	Granulate, nano- to microgemmate/verrucate/rugulate to imperfectly microreticulate	Granulate to microverrucate	Granulate to microverrucate or microgemmate; S.E. always densely packed	Granulate to microverrucate/-gemmate; S.E. densely packed	?	?	Granulate, nanogemmate to microverrucate; S.E. densely packed	? Microverrucate; possibly same as in *Z. amplexicaula*	Granulate to nanoverrucate	Granulate, nanoverrucate (?)	Granulate	Granulate to microverrucate and microgemmate; with densely packed distinct gemmae-verrucae, very few rugulae
Literature used	[1] Praglowski (1979) [2] Moar (1993)	[1] Praglowski (1979) [2] Moar (1993)	[3] Praglowski (1979) [2] Moar (1993)	[1] Praglowski (1979)	[1] Praglowski (1979)	[1] Van der Ham & van Heuven (2002)	[1] Lobreau-Callen (1977) [2] Praglowski (1979)	[1] Praglowski (1979)	N/A	[1] Sampson (1974) [2] Praglowski (1979) [3] Sampson (2007)	[1] Praglowski (1979)	[1] Sampson (1974) [2] Praglowski (1979) [3] Sampson (2007)	[1] Praglowski (1979) [2] „*Z. pomiferum*" in Van der Ham & van Heuven (2002)	N/A

Note: Table includes previously published pollen/tetrads illustrated by SEM micrographs.

* – LM indicates same type as *Z. baillonii* and *Z. bicolor*.
† – See Sampson (1983) for issues with material addressed as *Z. pomiferum*, *Z.* ~ subsp. *balansae* (= *Z. balansae*) and the newly distinguished *Z. vinkii*.
Pollen-wise, *Z. pomiferum* and *Z. vinkii* are the same, but *Z. balansae* shows a much denser reticulum approaching a perforate grain, as otherwise found only in *Exospermum*.
S.E. – Sculpture elements.

So far, the Winteraceae have been the focus of two dating studies using different sets of ingroup constraints and only partially overlapping gene and taxon sampling (Marquínez et al. 2009, Thomas et al. 2014). In addition, a dating study focussing on the Canellaceae (Müller et al. 2015), the sister clade of the Winteraceae, included one representative each of the most important genera of the Winteraceae. All these studies estimated (much) higher root (stem) and stem ages for the Winteraceae and Winteroideae than found in a recent study including all magnoliids (Massoni et al. 2015). Müller et al. (2015) noted that only a limited number of ingroup (Canellaceae and Winteraceae) fossils were available as dating constraints. In the best-possible (datawise) cases, fossil records and molecular dating estimates can be co-informative towards recognition of an ancient member of a clade as an actual precursor of extant taxa (e.g. Bomfleur et al. 2015). The fossil record of Winteraceae includes very few macrofossils and the palaeophytogeographic history of this archaic family must therefore rely on the palaeopalynological record. Consequently, fossil Winteraceae pollen/tetrads act as the only potential ingroup dating constraints for this family. To be able to unravel the origin, divergence and spatial history of generic lineages of Winteraceae, it is important to compare and affiliate fossil Winteraceae pollen/tetrads to those of the extant genera (generic lineages). The general morphology and ultrastructure of Winteraceae are well known and have been studied by Bailey & Nast (1943), Straka (1963), Fiser & Walker (1967), Sampson (1974, 2000a,b, 2007), Lobreau-Callen (1977), Praglowski (1979), and van der Ham & van Heuven (2002). Unfortunately, only a few of these studies provide good close-ups (SEM micrographs; Sampson 2000b, van der Ham & van Heuven 2002) showing the sculpture and aperture region (including ulcus membrane) at high enough resolution. Until now, most fossil Winteraceae pollen/tetrads have only been illustrated and described using LM (exception: SEM micrographs in Coetzee & Praglowski 1988). The only way to properly compare and/or affiliate fossil Winteraceae pollen/tetrads to extant taxa is by using combined data obtained from LM and SEM, especially from high-resolution SEM studies. Here we provide combined LM and SEM analyses of 35 samples of Winteraceae, representing seven of the eight genera and 20 of the approximately 65 species currently accepted by Vink (1970–2003). The pollen/tetrads are studied by both LM and SEM, and diagnostic features observed under high-resolution SEM are noted. All previously published literature providing micrographs has been considered in establishing our pollen types. Winteraceae pollen/tetrads can be grouped into eleven general pollen types (PTs 1–11), which are described here in detail. The two Miocene African Winteraceae pollen/tetrad types of Coetzee & Praglowski (1988) are shown to represent a single taxon formalized here. Based on the extant pollen types, the relationship of the African fossil pollen tetrads to modern taxa is re-evaluated.

MATERIAL AND METHODS

Herbarium (flowering) material from the University of Vienna (W), the Natural History Museum Vienna (WU), the Missouri Botanical Garden (MO), the Museum of New Zealand (WELT), the Allan Herbarium (CHR) and the Botanical State Collection Munich (M and MSB) was prepared according to the protocol outlined in Grímsson et al. (2017a,b). The sediments containing the here-figured fossil Winteraceae were from core sample #114755 collected at Saldanha Bay, South Africa. The sediments are believed to be of early Miocene age. For a full geological, stratigraphic, palaeontological and palaeoenvironmental background of this locality/core consult Roberts et al. (2017). The sedimentary rock sample was processed and pollen grains extracted according to the protocol outlined in Grímsson et al. (2008). The fossil Winteraceae pollen grains were investigated by both light microscopy (LM) and scanning electron microscopy (SEM) using the single-grain method as described in Zetter (1989). The description of recent and fossil Winteraceae pollen/tetrads includes diagnostic features observed in both LM and SEM. Pollen/tetrad terminology follows Punt et al. (2007) and Hesse et al. (2009). SEM stubs of extant material produced in this study are stored in the collection of the Department of Palaeontology, University of Vienna, Austria. Winteraceae fossil material (SEM stubs) from South Africa are stored in the same collection under accession numbers IPUW 7513/209 and IPUW 7513/210.

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Notes regarding the following descriptions: The annulus-like rim marks the transition zone between the footlayer and ulcus membrane. This makes it difficult to measure the actual width of the ulcus. For comparability with grains lacking an annulus-like rim we therefore did not measure the ulcus but the width of the complete aperture region marked by the absence of ectexine. Diameter (size) ranges of pollen types (PTs) in LM are based on our own measurements combined with those from the literature.

Pollen Type 1, diagnostic for ***Takhtajania***

Pl. 1, 2; Tabs 1, 2

Description. Pollen in permanent tetrahedral tetrads, tetrads radially symmetrical, heteropolar, lobate to hexagonal in basal view, lobate to octagonal in lateral view and lobate in apical view; tetrads large, 65–83 µm in diameter (LM); pollen interface mostly closed, pollen sometimes separated by narrow ≤ 1.5 µm wide groove, infratectal bridges between monads sometimes observed at interface (SEM); pollen with a distal polar aperture, pollen ulcerate, aperture outline ± circular, endexine extending beyond ectexine and thickened around ulcus, forming 2.5–6.0 µm wide annulus-like rim, aperture region 12–17 µm in diameter (SEM); pollen semitectate; exine up to 5.5 µm thick, nexine up to 1.5 µm thick, sexine up to 4.2 µm thick (LM); sculpture reticulate in LM and SEM, muri straight or curved, broad and rounded (SEM); lumina large, up to ca 11 µm in diameter, ca 15–20 lumina per pollen grain observed in equatorial view, lumina smaller along the periphery of pollen interface (SEM); columellae high and narrow, columellae equal or higher than muri (1:1 to 3:2), wide apart, on average 2 per 5 µm, broadly based (SEM); columellae and muri much shorter around apertures and pollen interface, muri often discontinuous in aperture regions (SEM); surface of footlayer within lumina psilate, with up to 10+ short (micro)gemmate, (micro) clavate and (micro)baculate free-standing columellae, free-standing columellae irregularly distributed, in groups (SEM); annulus-like rim granulate and with gradual interface to membrane (SEM); ulcus membrane granulate to microverrucate, elements occasionally fusing into microrugulae (SEM).

Species with this PT. *Takhtajania perrieri* (Capuron) Baranova & J.-F.Leroy (only species of the genus).

Remarks. PT 1 is the most distinct pollen type of extant Winteraceae, which is in line with the genetic distinctness of the species. The most prominent feature is its dimensions: the tetrads are much larger than in all other Winteraceae, the lumina are well developed and the sexine can be twice as thick or more than in other Winteraceae. Material of the species was figured in Straka (1963), Lobreau-Callen (1977), Praglowski (1979), and Sampson (2000a, b, 2007).

Pollen Type 2, diagnostic for ***Tasmannia*** (formerly ***Drimys*** sect. ***Tasmannia,*** Australasian ***Drimys***)

Pl. 3–14 and Pl. S1–S6*; Tabs 1, 2

Description. Pollen in permanent tetrahedral tetrads, tetrads radially symmetrical, heteropolar, outline circular to hexagonal to lobate in basal and apical view, circular to octagonal to lobate in lateral view; tetrads small to medium in size, 15–39 µm in diameter (LM); pollen interface mostly closed, pollen sometimes separated by a narrow ≤ 1.5 µm wide groove, infratectal bridges between monads sometimes observed at interface (SEM); pollen with a distal polar aperture, pollen ulcerate, aperture outline ± circular, without annulus-like rim, aperture region 7–12 µm in diameter (SEM); pollen semitectate; exine up to 3.4 µm thick, nexine up to 1.1 µm thick, sexine up to 2.9 µm thick (LM); sculpture reticulate in LM and SEM, muri long and of similar length, straight to curved, narrow and crested, muri fusing along periphery of pollen interface, forming perforate margin (SEM); lumina 4–8 µm in diameter, 15–30 lumina per pollen grain observed in equatorial view (SEM); columellae high and narrow, of the same height as muri (1:1), densely spaced, mostly 1–2 per µm (SEM); surface of footlayer within lumina psilate or granulate, mostly without or with up to six nano/microverrucate, nano/microgemmate and/or nano/microclavate free-standing columellae, free-standing columellae irregularly distributed, solitary or scattered (SEM); ulcus membrane granulate, nano/microgemmate, nano/microclavate and nanoverrucate (SEM).

* Plates S1–S28 available on page http://www.botany.pl/images/ibwyd/acta_paleo/Acta_Palaeobot_57_2_Grimsson_et_al_Suppl_Pl_S1-S28.pdf

Table 2. Pollen types 1 to 11 and their discriminating features; the African fossil species is included for comparison

Pollen type (taxa)	Size of dispersal unit	Annulus-like rim	Reticulum dimension[a]	Sculpture of ulcus membrane[b]	Free-standing columellae	Dispersal unit
Pseudowinterapollis africanensis	Medium	Yes	Coarse	Partly nano-/microverrucate and nano-/microgemmate	Rare or absent	Tetrad
PT 1 (*Takhtajania*)	Large	Yes	Coarse	Partly microrugulate	Common, occasionally > 1 µm	Tetrad
PT 2 (*Tasmannia*)	Small to medium	No	Coarse	Spaced S.E., some > 1 µm	Rare or absent	Tetrad
PT 3 (*Drimys*)	Medium to large	Yes	Coarse	Usually spaced S.E., up to 1 µm in some species	Rare or variable	Tetrad
PT 4 (*Pseudowintera*)	Medium	No	Coarse	Imperfectly microreticulate	Common, few per lumen	Tetrad
PT 5 (*Belliolum*, *Bubbia*, *Zygogynum*)	Medium	Yes	Coarse	Partly microverrucate	Common to rare	Tetrad
PT 6 (*Z. comptonii*)	Medium	No	Coarse	Partly microverrucate, densely packed S.E. < 1 µm	Rare	Tetrad
PT 7 (*Z. fraterculum*)	Medium	No	Coarse	Densely packed S.E. < 1 µm	Common, many per lumen	Tetrad
PT 8 (*Zygogynum*)	Medium	No	Fine	Partly microverrucate, densely packed S.E., usually < 0.5 µm[c]	Rare	Tetrad
PT 9 (*Exospermum*)	Medium	Yes	Minute (perforate)	Partly nanoverrucate	Absent	Tetrad
PT 10 (*Z. balansae*)	Medium	No	Fine	Inconspicuous	Absent	Monad
PT 11 (*Z. pomiferum*, *Z. vinkii*)	Medium	Yes	Minute (perforate)	Partly nanoverrucate	Absent	Monad

Note: Grey shading highlights features shared by the African fossils and extant pollen types.

[a] Coarse = reticulate, ≤ 30 lumina per grain in lateral view, largest lumina > 5 µm in diameter (longest axis); fine = nano- to microreticulate, > 40 lumina, lumina < 3 µm; minute = nanoreticulate to perforate, > 100 lumina/perforations, lumina/perforations ≤ 1 µm.

[b] Basic sculpture of the ulcus membrane is loosely or densely granular in all extant and fossil Winteraceae; S.E. = sculpture elements, in addition to granula mostly gemmae, sometimes erect and slightly elongated (clavae or bacula), occasionally fused and forming verrucae.

[c] Data for *Z. amplexicaula*; other species need to be re-investigated using high-resolution SEM.

Species with this PT. *Tasmannia brassii* (A.C.Sm.) A.C.Sm., *T. dictyophlebia* (Diels) A.C.Sm., *T. insipida* R.Br. ex DC., *T. lanceolata* (Poir.) A.C.Sm., *T. piperita* (Hook.f.) Miers, *T. purpurascens* (Vickery) A.C.Sm., *T. rosea* (Ridl.) A.C.Sm., *T. stipitata* (Vickery) A.C.Sm., *T. xerophila* (P.Parm.) M.Gray.

Remarks. *Tasmannia* pollen (PT 2) cannot be confused with pollen of *Takhtajania* (PT 1) or with that of *Drimys* (PT 3), the genus that traditionally included these species. The main features differentiating it from PT 1 are the dimensions of the tetrads and their exine thickness and the lack of an annulus-like rim. Despite being mostly smaller, the sculpture elements of the ulcus membrane are larger in PT 2 than in PT 3, and they usually compose clavae in PT 2 (vs. mostly verrucae in PT 3). Tetrads of this PT were figured in Fiser & Walker (1967), Lobreau-Callen (1977), Praglowski (1979) and Sampson (2007).

Pollen Type 3, diagnostic for ***Drimys*** (formerly ***Drimys*** sect. ***Drimys***, New World ***Drimys***)

Pl. 15–26 and Pl. S7–S16; Tabs 1, 2

Description. Pollen in permanent tetrahedral tetrads, tetrads radially symmetrical, heteropolar, outline lobate to hexagonal in basal and apical view, circular to lobate to octagonal in lateral view; tetrads medium to large in size, 33–55 µm in diameter (LM); pollen interface mostly clearly visible (open), pollen separated by ≤ 1.5 µm wide groove (SEM); pollen with a distal polar aperture, pollen ulcerate, aperture outline ± circular, apertures surrounded by 2.0–4.5 µm wide annulus-like rim, aperture region 9–17 µm in diameter (SEM); pollen semitectate; exine up to 5.0 µm thick, nexine up to 1.5 µm thick, sexine up to 3.1 µm thick (LM); sculpture reticulate in LM and SEM, muri long and of similar length, straight to curved, mostly narrow and crested, muri fusing along periphery of pollen interface, forming perforate margin (SEM); lumina 4–8 μm in diameter, ca 20–30 lumina per pollen grain observed in equatorial view (SEM); columellae high and narrow, of the same height as muri (1:1), densely spaced, 1–2 per 1 μm (SEM); surface of footlayer within lumina psilate or granulate, rarely with very short nano/microgemmate, nanobaculate and nano/microclavate free-standing columellae, free-standing columellae irregularly distributed, solitary or grouped (SEM); annulus-like rim granulate (SEM); ulcus membrane granulate to nano/microverrucate and/or nanogemmate and/or nano/microbaculate (SEM).

Species with this PT. *Drimys andina* (Reiche) R.A.Rodr. & Quez., *D. angustifolia* Miers, *D. brasiliensis* Miers, *D. confertifolia* Phil., *D. granadensis* L.f., *D. winteri* J.R.Forst. & G.Forst.

Remarks. The separation of *Tasmannia* (PT 2) from *Drimys* (PT 3) is well-established based on molecular data. Tetrads of PT 2 and PT 3 share several features but these are commonly found also in other members of the Winteroideae (Tab. 1). The pollen apertures and the finer sculpture of PT 3 as compared to PT 2 represent the main discriminating features. The pollen apertures are surrounded by a wide annulus-like rim in *Drimys* (PT 3), less pronounced in PT 1 (*Takhtajania*) and absent from PT 2 (*Tasmannia*) tetrads. Species showing PT 3 can be seen in Walker (1974), Walker & Doyle (1975), Lobreau-Callen (1977), Praglowski (1979), Walker et al. (1983), Doyle (2000), and Sampson (2007).

Pollen Type 4, diagnostic for ***Pseudowintera***

Pl. 27–32 and Pl. S17–S28; Tabs 1, 2

Description. Pollen in permanent tetrahedral tetrads, tetrads radially symmetrical, heteropolar, outline lobate to hexagonal in basal view, circular to octagonal to lobate in lateral view, lobate in apical view; tetrads medium to large in size, 36–55 μm in diameter (LM); pollen interface clearly visible (open), pollen separated by ≤ 1.5 μm wide groove (SEM); pollen with a distal polar aperture, pollen ulcerate, aperture outline ± circular, apertures without annulus-like rim, aperture region 6–11 μm in diameter (SEM); pollen semitectate; exine up to 4.1 μm thick, nexine up to 1.1 μm thick, sexine up to 3.3 μm thick (LM); sculpture reticulate in LM and SEM, muri varying in length, narrow and crested, curved or sinuous, muri fusing along periphery of pollen interface, forming perforate margin (SEM); lumina 4.5–8.5 μm in diameter, ca 20–30 lumina per pollen grain observed in equatorial view (SEM); columellae high and narrow, of the same height as muri (1:1), at irregular intervals, 1–2 per μm, broadly based (SEM); surface of footlayer within lumina psilate, with nanogemmate free-standing columellae, free-standing columellae rarely present (single) or occurring in nearly all lumina (few to many), free-standing columellae irregularly distributed; ulcus membrane granulate, nano/microgemmate, nano/microverrucate, nano/microrugulate to imperfectly microreticulate (SEM).

Species with this PT. *Pseudowintera axillaris* (J.R.Forst. & G.Forst.) Dandy, *P. colorata* (Raoul) Dandy, *P. traversii* (Buchanan) Dandy.

Remarks. Overall, PT 4 approaches PT 2 (*Tasmannia*) in most features but typically differs by having smaller ulci and sculpture of the ulcus membrane. The general sculpture elements of the ulcus membrane are partly accumulated in *P. axillaris*, clearly fused and enlarged in *P. colorata* (semi-imperfect microreticulum), and showing an imperfect microreticulum in *P. traversii*. This sculpture type of the ulcus membrane is unique within Winteraceae. Species showing PT 4 can be found in Lobreau-Callen (1977), Praglowski (1979), Moar (1993), and Sampson (2000b, 2007).

Pollen Type 5, characteristic for species traditionally included in ***Bubbia*** and ***Belliolum*** (members of ***Zygogynum*** s.l. group)

Pl. 33, 34; Tabs 1, 2

Description. Pollen in permanent tetrahedral tetrads, tetrads radially symmetrical, heteropolar, outline lobate to hexagonal in basal and apical view, octagonal to lobate in lateral view; tetrads medium to large in size, 33–50 μm in diameter (LM); pollen interface poorly to clearly visible (closed or open), pollen sometimes separated by narrow ≤ 1.5 μm wide groove (SEM); pollen with a distal polar aperture, pollen ulcerate, aperture outline ± circular, apertures surrounded by 1.5–3.0 μm wide annulus-like rim, aperture region 6–10 μm in diameter (SEM); pollen semitectate; exine up to 4.5 µm thick, nexine up to 1.1 µm thick, sexine up to 2.5 m thick (LM); sculpture reticulate in LM and SEM, muri short to long, straight to sinuous, mostly narrow and crested, muri fusing along periphery of pollen interface, forming perforate margin (SEM); lumina 4–11 µm in diameter, ca 10–20 lumina per pollen grain observed in equatorial view (SEM); columellae high and narrow, ± same height as muri, densely spaced, 1–3 per µm (SEM); surface of footlayer within lumina psilate or granulate, with nanogemmate, nanoclavate and nanobaculate free-standing columellae, free-standing columellae rarely (single to few) to frequently present (up to 11 per lumina), free-standing columellae irregularly distributed or occurring in groups (SEM); ulcus membrane microverrucate to microgemmate (SEM).

Species with this PT. *Belliolum burttianum* A.C.Sm., *B. crassifolium* (Baill.) Tiegh., *B. haplopus* (Burtt) A.C.Sm., *B. pancheri* (Baill.) Tiegh., *B. rivulare* (Vieill. ex P.Parm.) Tiegh.; *Bubbia archboldiana* A.C.Sm., *B. howeana* (F.Muell.) Tiegh., *B. isoneura* Tiegh., *B. megacarpa* A.C.Sm., *B. odorata* (Baker f.) Dandy, *B. semecarpoides* (F.Muell.) B.L.Burtt, *B. sororia* (Diels) A.C.Sm., *B. whiteana* A.C.Sm.

Remarks. Palynologically, tetrads of all studied species of the *Bubbia*/*Belliolum* complex (PT 5) differ from those of *Zygogynum* s.str. and its close ally, the monotypic *Exospermum*, (PTs 6–9), by showing an annulus-like rim (as in PT 3, *Drimys*). The general sculpture is the same as in *Drimys* (PT 3, aperture up to double the size) and *Pseudowintera* (PT 4, showing no annulus-like ring around the apertures), the sibling clades of the *Zygogynum* s.l. group, in contrast to the *Exospermum*-*Zygogynum* PTs 6–11. For figured material of the species showing PT 5 see Lobreau-Callen (1977), Praglowski (1979), and Sampson (2007).

Pollen Type 6, so far only in ***Zygogynum* (*Bubbia*) *comptonii*** (Baker f.) Vink

Pl. 35, 36; Tabs 1, 2

Description. Pollen in permanent tetrahedral tetrads, tetrads radially symmetrical, heteropolar, outline lobate to hexagonal in basal and apical view, circular to octagonal in lateral view; tetrads medium in size, 34–39 µm in diameter (LM); pollen interface clearly visible (open, SEM); pollen with a distal polar aperture, pollen ulcerate, aperture outline ±circular, apertures without annulus-like rim, aperture region 4–6.5 µm in diameter (SEM); pollen semitectate, exine up to 3.5 µm thick, nexine up to 1.1 µm thick, sexine up to 2.4 µm thick (LM); sculpture reticulate in LM and SEM, muri narrow and crested (SEM); lumina 4–6 µm in diameter, ca 20 lumina per pollen grain observed in equatorial view (SEM); columellae high and narrow, of the same height as muri (1:1), at regular intervals, 1–2 per µm (SEM); surface of lumina psilate to granulate, with nanogemmate and nanoclavate free-standing columellae, free-standing columellae very rare (single); ulcus membrane granulate to microverrucate or microgemmate (SEM).

Species with this PT. *Zygogynum comptonii* [= *B. comptonii* (Baker f.) Dandy]

Remarks. Tetrads of *Zygogynum* (*Bubbia*) *comptonii* (PT 6) are similar to those of the *Bubbia*/*Belliolum* complex (PT 5) but the pollen are without an annulus-like rim, have a smaller aperture, and are mostly without any free-standing columellae (vs. frequent/numerous in PT 5). Sculpture elements of the ulcus membrane are comparable to those of *Tasmannia* (PT 2) but are compact (vs. dispersed in PT 2).

Pollen Type 7, so far only in ***Zygogynum fraterculum*** Vink

Description. Pollen in permanent tetrahedral tetrads, tetrads radially symmetrical, heteropolar, outline circular to lobate in basal, lateral and apical view; tetrads medium in size, 34–48 µm in diameter (LM); pollen interface poorly visible (closed, SEM); pollen with a distal polar aperture, pollen ulcerate, aperture outline ±circular, apertures without annulus-like rim, aperture region 3–7 µm in diameter (SEM); pollen semitectate, exine up to 4.5 µm thick, nexine up to 0.8 µm thick, sexine up to 3.8 µm thick (LM); sculpture reticulate in LM and SEM, muri varying in length but long, broad and rounded, straight to curved (SEM); lumina 5–11 µm in diameter, ca 20 lumina per pollen grain observed in equatorial view (SEM); columellae high and narrow, of the same height as muri (1:1), at regular intervals, 1 per µm, broadly based (SEM); surface of lumina psilate, with microgemmate and microclavate free-standing columellae, free-standing columellae occurring in all larger lumina (up to 12 per lumina), free-standing columellae irregularly distributed; ulcus membrane microverrucate to microgemmate (SEM).

Species with this PT. *Zygogynum fraterculum.*

Remarks. Tetrads of *Zygogynum fraterculum* (PT 7) are similar to PTs 5 and 6. The pollen interface is tightly closed in PT 7 (compact circular tetrads) but clearly open in PTs 5 and 6 (open lobate to hexagonal/octagonal tetrads). The aperture region is much larger in PT 7 than in PT 6; the latter rarely has free-standing columellae but they are frequent in PT 7. Material of species showing PT 7 was figured by van der Ham & van Heuven (2002).

Pollen Type 8, characteristic of ***Zygogynum*** (s.str.) spp. with tetrads

Pl. 37, 38; Tabs 1, 2

Description. Pollen in permanent tetrahedral tetrads, tetrads radially symmetrical, heteropolar, outline circular to lobate in basal-, lateral, and apical view; tetrads medium in size, 35–51 µm in diameter (LM); pollen interface poorly visible (mostly closed; SEM); pollen in tetrads with a distal polar aperture, pollen ulcerate, aperture outline ± circular, aperture region 4–7 µm in diameter; pollen semitectate; exine up to 3.5 µm thick, nexine up to 1.1 µm thick, sexine up to 2.7 µm thick; sculpture microreticulate in LM, microreticulate to reticulate in SEM; muri varying in length but short, broad and rounded, straight (SEM); lumina small, up to ca 3 µm in diameter, 40–100 lumina per pollen grain observed in equatorial view (SEM); columellae short, equal or higher than muri (1:1 to 1.5:1), densely spaced, ± 1 per µm (SEM); surface of footlayer within lumina psilate or granulate; ulcus membrane granulate to microverrucate (SEM).

Species with this PT. *Zygogynum acsmithii* Vink, *Z. amplexicaule* (Vieill. ex P.Parm.) Vink, *Z. baillonii* Tiegh., *Z. bicolor* Tiegh., *Z. vieillardii* Baill.

Remarks. The diagnostic feature of PT 8 is its minute (microreticulate) sculpture. The resulting high number of lumina per pollen grain observed in equatorial view (ca 80; Tab. 1) is much higher than in PTs 1–7 (≤ 30), but lower than in PTs 9–11 of *Exospermum* and *Zygogynum* (≥ 150). Otherwise, the individual pollen grains forming the tetrad equal the monads of PT 10 (also *Zygogynum*), except that the apertures are not surrounded by an annulus-like rim in PT 8. For figured material of the species showing PT 8 see Sampson (1974, 2007), Lobreau-Callen (1977) and Praglowski (1979).

Pollen Type 9, characteristic for the monotypic ***Exospermum***, a close ally of ***Zygogynum*** s.str. (possibly congeneric)

Pl. 39, 40; Tabs 1, 2

Description. Pollen in permanent tetrahedral tetrads, tetrads radially symmetrical, heteropolar, outline circular to lobate in basal and apical view, circular in lateral view; tetrads medium in size, 37–43 µm in diameter (LM); pollen in tetrads with a distal polar aperture, pollen ulcerate, aperture outline ± circular, aperture region 5–6 µm in diameter (SEM); pollen semitectate; exine up to 3.0 µm thick, nexine up to 0.7 µm thick, sexine up to 1.7 µm thick (LM); sculpture microreticulate in LM, perforate to nanoreticulate in SEM; perforations (“nanolumina”) circular to elongated, up to ca 0.5 µm in diameter, ca 120 lumina per pollen grain observed in equatorial view (SEM); 2–3 columellae per µm; ulcus membrane granulate to nanoverrucate (SEM).

Species with this PT. *Exospermum stipitatum* (Baill.) Tiegh.

Remarks. The SEM sculpture of PT 9 tetrads is nearly identical to that observed in the monads of the *Zygogynum* s.str. PT 11. In analogy to the difference between PT 8 and PT 10 (both *Zygogynum*), PT 9 grains show no annulus-like rim surrounding the ulcus, in contrast to PT 11. PT 9 is the only Winteraceae with permanent tetrads having a high number of nanolumina/perforations, a feature otherwise found only in monads (PTs 10, 11). PT 9 tetrads of *Exospermum* were figured in Lobreau-Callen (1977), Sampson (1974, 2000b, 2007) and Praglowski (1979).

Pollen Type 10, ***Zygogynum*** (s.str.) monads resembling individual grains of PT 8 tetrads

Description. Monad, form spheroid, shape oblate, outline circular in polar view, circular to elliptic in equatorial view; pollen small to medium in size, polar axis 17–28 µm long, equatorial diameter 24–36 µm (LM); pollen ulcerate, distal polar aperture, aperture outlines ± circular, aperture surrounded by 3.0–3.5 µm wide annulus-like rim, aperture region, 4–7 µm in diameter (SEM); pollen semitectate, exine up to 2.5 µm thick, nexine up to 0.8 µm thick, sexine up to 1.4 µm thick (LM); sculpture microreticulate in LM, nanoreticulate to microreticulate in SEM; muri varying in length but short, broad and rounded, straight (SEM); lumina small, up to ca 1.5 µm in diameter, ca 100 lumina per pollen grain observed in equatorial view (SEM); columellae short, higher than muri (2:1), densely spaced, ± 1 per µm (SEM); ulcus membrane granulate to nanoverrucate (SEM).

Species with this PT. *Zygogynum mackeei* Vink, *Z. pomiferum* Baill. (= Z. *pomiferum* subsp. *pomiferum*), *Z. vinkii* F.B.Sampson.

Remarks. PT 10 monads are very similar to the grains of PT 8 tetrads, except that the apertures are without an annulus-like rim and the reticulum is generally coarser in PT 8 than in PT 10 (see also Remarks under PT 8). Pollen grains of PT 10 were figured by Praglowski (1979), Sampson (1974, 2000b, 2007) and van der Ham & van Heuven (2002).

Pollen Type 11, ***Zygogynum*** (s.str.) monads resembling individual grains of PT 9 (***Exospermum***) tetrads

Description. Monad, form spheroid, shape oblate, outline circular in polar view, circular to elliptic in equatorial view; pollen small to medium in size, polar axis 26–34 µm long, equatorial diameter 26–35 µm (LM); pollen ulcerate, distal polar aperture, aperture outlines ± circular, apertures surrounded by ca 3.5 µm µm wide annulus-like rim, aperture region 6–10 µm in diameter (SEM); pollen semitectate; exine up to 2.5 µm thick, nexine up to 0.4 µm thick, sexine up to 1.8 µm thick (LM); sculpture microreticulate in LM, perforate to nano/microreticulate in SEM; perforations/nanolumina circular to elongated, increasing in size from distal polar face towards proximal face, lumina up to ca 1.0 µm in diameter on proximal face (microreticulate), muri here broad and rounded, ca 150 perforations/lumina per pollen grain observed in equatorial view (SEM); ulcus membrane granulate (SEM).

Species with this PT. *Zygogynum balansae* Tiegh. (= *Z. pomiferum* subsp. *balansae* [Tiegh.] Vink)

Remarks. The SEM sculpture of PT 11 monads is virtually identical to that observed in pollen of permanent tetrads of PT 9 (*Exospermum*), and, in analogy to PT 8 tetrads versus PT 10 monads, it differs mainly by the absence/presence of an annulus-like rim around the aperture(s). This PT was figured only by Praglowski (1979, figs 9A–F).

RECENT POLLEN/TETRAD TYPES AND THEIR PHYLOGENETIC PLACEMENT

The eleven pollen types (Tabs 1, 2) share genus-diagnostic (*Takhtajania*, *Tasmannia*, *Drimys*, *Pseudowintera*, *Zygogynum* s.l. p.p.) or unique (species/species groups within *Zygogynum* s.l.) character suites that can be observed by LM and SEM. The pollen of Winteraceae in general can be diagnosed as persistent, acalymmate tetrads composed of ulcerate pollen grains with typical reticulate sculpture under LM and SEM. Dispersal via monads, found in only four Caledonian species of *Zygogynum* (s.str.; PTs 10 and 11; Tabs 1, 2), forming part of the last-diverging modern Winteraceae lineage, appears to be derived in Winteraceae (Potts & Grimm 2017, Grímsson et al. in press), as hypothesized by van der Ham & van Heuven (2002). Notably, both PTs represent grains highly similar or nearly identical to grains in the tetrads of other *Zygogynum* s.str. species and *Exospermum*, respectively (PTs 8 and 9). Another derived feature (cf. Potts & Grimm 2017) restricted to members of *Zygogynum* s.str./ *Exospermum* species complex is the finer sculpture (microreticulate to perforate) observed in these four PTs. Most tetrads are medium in size (i.e. 25–50 µm; size categories as defined by Hesse et al. 2009). Four of the five generic lineages are pollen-morphologically homogenous, each showing a single pollen type. PT 1 is restricted to the monotypic genus *Takhtajania* from Madagascar and is characterized by its dimensions: large tetrads (≥ 65 µm in diameter; ≤ 55 µm in all other Winteraceae) with ulci that can be up to 17 µm in diameter (≤ 10 µm in most other Winteraceae), and a well-developed reticulum showing the largest lumina among the Winteraceae (up to 12 µm in diameter) and the thickest sexine (6 µm; ≤ 5 µm in all other Winteraceae). Based on its character suite, PT 1 represents the most distinct pollen type of all Winteraceae and reflects the genetic distinctness of the taxon (Fig. 1). Molecular data unambiguously confirm the separation of the New World *Drimys* from the Tasmanian genus *Tasmannia* (Suh et al. 1993, Karol et al. 2000, Doust & Drinnan 2004, Marquínez et al. 2009, Thomas et al. 2014); this is reflected in their mutually exclusive pollen types (PTs 2 and 3). *Tasmannia* PT 2 tetrads are generally smaller than those of *Drimys*, and *Tasmannia* is the only genus with small tetrads (<25 µm). Nonetheless, *Tasmannia* pollen grains (PT 2) have a more prominent ulcus membrane sculpture (elements can be up to 1 µm in size). The apertures are surrounded by an annulus-like ring in *Drimys* (PT 3) but not so in *Tasmannia* (PT 2), and the nexine is conspicuously thin in *Tasmannia* (<<1 µm as compared to ≥ 1 µm in most other Winteraceae PTs including *Drimys'* PT 2). Tetrads of *Pseudowintera* (PT 4) lack unique features in LM but show a character suite not seen in any other Winteraceae under SEM (e.g. imperfectly microreticulate ulcus membrane). The high diversity of pollen types in the *Zygogynum* s.l. generic lineage (PTs 5–11) reflects the increased diversity in noncoding gene regions (Suh et al. 1993, Karol et al. 2000, Grímsson et al. in press) and correspondingly long terminal and internal branches in the respective subtree (Fig. 1). Most species traditionally included in the genera *Bubbia* and *Belliolum* share the same PT 5, which parallels PT 4 of *Pseudoewintera* in its lack of unique LM features. The only consistent, readily apparent difference between PTs 4 and 5 is the conspicuous annulus-like rim that surrounds all apertures of the latter, a feature shared with *Takhtajania* (PT 1), *Drimys* (PT 3), *Zygogynum fraterculum* (PT 7) and the New Caledonian *Zygogynum* species with monads as dispersal units (PTs 10 and 11). The highest diversity of pollen types can be found in the remaining species of the *Zygogynum* s.l. lineage, that is, species included in the genus *Zygogynum* s.str. and the closely allied monotypic *Exospermum*. Inconspicuous in size and form, the pollen interface between the grains is always closed in *Exospermum*/*Zygogynum* tetrads. Another shared feature not found in PTs 2–7 is the prominently developed, broad and convex muri. Annulus-like rims may be developed (monad PTs 10, 11) or not (tetrad PTs 7–9). Pollen types 8–11 show a (much) finer sculpture, that is, grains that are micro- to nanoreticulate (muri <1 µm) instead of reticulate and show a correspondingly higher number of lumina. The lumina decrease in size (lumina ≤ 2.5 µm in PT 8, ≤ 0.5 µm in PT 9) and are sometimes heterogenous across individual grains until the reticulum is finally replaced by a perforate surface (PTs 9, 11). Linked to this is that no free-standing columellae are found in PTs 9–11, unlike in all other PTs of extant Winteraceae (Tabs 1, 2).

DESCRIPTION OF THE AFRICAN FOSSIL WINTERACEAE TETRADS

The early Miocene South African Winteraceae pollen tetrads were previously figured and discussed by Coetzee (1981, 1983; single type, as *Pseudowinterapollis* sp. based on LM), Coetzee & Muller (1984; two types, considered to resemble recent *Drimys piperita* and *Bubbia isoneura* based on LM), Coetzee & Praglowski (1988; two types, "*Drimys piperita*-type" based on LM and SEM, and "*Zygogynum queenslandianum*-type" based on LM) and Roberts et al. (2017; single type, identified as *Pseudowinterapollis couperi* Krutzsch based on LM). None of those papers provided a detailed description of the fossils; the only measurements and descriptions given by Coetzee & Praglowski (1988) do not refer to the fossils but to recent tetrads which they considered the closest morphological analogue. Based on our study of extant material presented above and the literature record of fossil Winteraceae tetrads, it became clear that the African fossil tetrads differ from all other previously described *Pseudowinterapollis*. Here we describe them as a new morphospecies.

Family WINTERACEAE R.Br. ex Lindl.

Genus. ***Pseudowinterapollis*** Krutzsch emend. Mildenh. (Mildenhall & Crosbie 1979)

Type species. *Pseudowinterapollis couperi* Krutzsch (Krutzsch 1970) based on a specimen illustrated by Couper (1960: Pl. 5, fig. 4).

Genus diagnosis (translated from German; Krutzsch 1970, p. 408). Monoporate (ulcerate), tetrahedral pollen tetrads with partially wide reticulate sculpture, especially in subequatorial area of pollen; reticulate pattern decreasing in size towards distal polar area of pollen. Circular area surrounding an ulcerate porus at distal pole, without clear boundary. Amendment diagnosis by Mildenhall and Crosbie (1979, p. 506): "Pollen grains in obligate, tetrahedral tetrads, occasionally free; individual grains monoporate, pores distal, usually circular, size large in relation to grain, annulate to non-annulate; exine clearly stratified, sexine much thicker than nexine which thickens at apertures, sexine coarsely reticulate, clavate-baculate, sculpture reduced or absent on proximal surface."

Comment to genus diagnosis. Since the circular to elliptic aperture is positioned on the distal pole of the pollen, it is an ulcus (Erdtman 1952); some pollen appear annulate in LM because the endexine is extended beyond the ectexine and thickened surrounding the ulcus, forming an annulus-like rim; the sexine should not be addressed as clavate-baculate but columellate with columellae supporting the muri (see Punt et al. 2007, Hesse et al. 2009). Nearly all extant pollen except the monad PTs 10 and 11 would fall within the diagnosis of the fossil pollen taxon *Pseudowinterapollis*. Including most but not all members of the Winteraceae, a natural family of (inclusive) common origin (Doyle et al. 1990b, Suh et al. 1993, Karol et al. 2000, Marquínez et al. 2009, Thomas et al. 2014), the fossil pollen taxon is paraphyletic by definition (according Hennig 1950, Hennig & Schlee 1978).

Pseudowinterapollis africanensis sp.nov.

Pl. 41–43

Species diagnosis. Permanent, acalymmate, tetrahedral tetrads; pollen ulcerate, ulcus 7–9.5 µm in diameter, sculpture reticulate in LM and SEM, lumina 6–7 µm in diameter, ≤ 25 lumina per pollen grain observed in equatorial view, free-standing columellae absent or rare, ulcus membrane granulate to nano-/microverrucate and nano-/microgemmate with few rugulae.

Derivation of name. After the continent where the fossil was found.

Holotype. IPUW 7513/209.

Paratype. IPUW 7513/210.

Type locality. Saldanha Bay, South Africa

Stratigraphy. Elandsfontyn Formation

Age. Early Miocene (Roberts et al. 2017).

Description. Pollen in permanent tetrahedral tetrads, tetrads radially symmetrical, heteropolar, outline lobate to hexagonal in basal and apical view, lobate to octagonal in lateral view; tetrads medium in size, 38–49 µm in diameter (LM); pollen interface mostly closed, sometimes narrowly open; pollen with a distal polar aperture, pollen ulcerate, aperture outline ± circular, apertures surrounded by 0.5–2 µm wide annulus-like rim (costa), apertures medium-sized, ca 7–9.5 µm in diameter (SEM); pollen semitectate, exine 4.2–4.7 µm thick (sexine 2.7–3.3 µm; nexine 1.1–1.8 µm); sculpture reticulate in LM and SEM; muri narrow and crested, mostly curved (SEM); lumina 6–7 µm in diameter, ca 25 lumina per pollen grain observed in equatorial view (SEM); columellae high and narrow, same height as superimposed muri (1:1), at irregular intervals (SEM); surface of footlayer within lumina psilate, free-standing columellae rarely present (singular or in pairs), very short and globular (≤ 0.5 µm, gemmae); ulcus membrane granulate to nano-/microverrucate and nano-/microgemmate and with few rugulae (SEM).

Remarks. Prior to our study, the fossil pollen genus *Pseudowinterapollis* included three LM-diagnosed species: *P. couperi*, *P. wahooensis* (L.E. Stover) Mildenh. and *P. cranwellae* (L.E. Stover) Mildenh. All Australasian fossil Winteraceae tetrads published prior to 2011 were revised and treated by Raine et al. (2011) as synonyms of one of these three species. The *P. wahooensis* pollen tetrads (recorded from the Cretaceous to Paleocene of Australasia; see Raine et al. 2011) are much smaller than those of *P. africanensis* sp. nov. (26–31 µm vs. 38–49 µm in diameter), their pollen wall is thinner (1–3 µm vs. 4–5 µm thick) and their apertures are not surrounded by any annulus-like rim (Stover & Partridge 1973, p. 275). Both the *P. couperi* pollen tetrads (22–45 µm in diameter; recorded from the Eocene to Pleistocene of Australasia, Raine et al. 2011) and the *P. cranwellae* pollen tetrads (45–51 µm in diameter; recorded from the Eocene to Miocene of Australasia, Raine et al. 2011) overlap with *P. africanesis* sp. nov. in size. The *P. couperi* tetrads are without any annulus-like rim around the apertures (e.g. Stover & Partridge 1973, Mildenhall & Crosbie 1979), but the aperture size is similar to that of *P. africanensis* (6–10[–14] µm vs. 7–9.5 µm in diameter), and the pollen wall is of similar thickness (3.5–5 µm vs. 4–5 µm thick). The lumina of *P. couperi* are smaller than those of *P. africanensis* (3–5 µm vs. 6–7 µm in diameter). Of the three Australasian *Pseudowinterapollis* taxa, *P. cranwellae* tetrads are the most similar in LM-based morphology to the new African *P. africanensis* tetrads. The tetrads of both taxa are of similar size (43–51 vs. 38–49 µm in diameter), the apertures are of similar diameter (6–7 µm vs. 7–9.5 µm) and the apertures are surrounded by an annulus-like rim (2–3 µm vs. 0.5–2 µm wide). Since none of the Australasian *Pseudowinterapollis* species has been studied thoroughly by SEM, a further and more detailed comparison (especially sculpture, ulcus membrane, etc.) to the *P. africanensis* sp. nov. is not possible.

MORPHOLOGY OF THE AFRICAN FOSSILS COMPARED TO THAT OF RECENT TAXA

Pseudowinterapollis africanensis sp. nov. shares the primitive and commonly shared features of extant Winteraceae (Grímsson et al. in press). The pollen is dispersed as permanent tetrads and the pollen grains show reticulate sculpture and have an ulcus (Bailey & Nast 1943, Doyle et al. 1990a, Sampson 2000a, van der Ham & van Heuven 2002). This arrangement is also observed in the majority of extant Winteraceae and is documented for PTs 1–8 (Tabs 1, 2). Tetrads of *Exospermum* (PT 9) clearly differ from all other fossil and extant tetrads in their extremely compact form and perforate sculpture. Both PTs 10 (*Zygogynum balansae*) and 11 (*Z. pomiferum*, *Z. vinkii*) are dispersed as monads and are not comparable to the fossil. With respect to the character suite, tetrads of the (extant) Madagascan taxon *Takhtajania* (PT 1), the only representative of the Winteraceae in Africa, are noticeably different. *Takhtajania* (PT 1) tetrads are up to double the size of the African fossils, their annulus-like rim is usually much wider (up to 6 µm), their aperture region is much larger, and their muri are broad and rounded but narrower and crested in *Pseudowinterapollis africanensis*. Also, free-standing columellae, frequent in *Takhtajania*, are either absent or extremely rare (single or pair) in *P. africanensis*. The African fossil is similar to the basal pollen types of the Winteraceae and shares features with PTs 2–7 (Tabs 1, 2) but differs from each of them by one or more features. *Tasmannia* (PT 2) tetrads are usually smaller (15–39 µm in diameter) than those of *Pseudowinterapollis africanensis* (38–49 µm in diameter) and are without any annulus-like rim in the aperture region. The apertures and lumina in *P. africanensis* and *Tasmannia* (PT 2) are of similar size and the muri are mostly narrow and crested. In *Tasmannia* (PT 2), free-standing columellae are very rare (solitary), as in *P. africanensis*. The sculpture elements of the ulcus membrane in *P. africanensis* are comparable to those observed in some *Tasmannia* species (PT 2). Tetrads of the American *Drimys* (PT 3) overlap in size with the African fossils and display a corresponding wall with all layers overlapping in thickness. In *Drimys* (PT 3) and *Pseudowinterapollis africanensis* the size and number of lumina are in the same range, and their muri are usually narrow and crested. However, the apertures are usually much larger in *Drimys* (PT 3) than in the African fossils and the annulus-like rim is also very distinct and much broader than in *P. africanensis*. The arrangement of sculpture elements on the ulcus membrane of *Drimys* (PT 3) is also different from that observed in the African fossils. *Pseudowintera* (PT 4) tetrads are similar to the African fossils in many ways but they have no annulus-like rim. Also, the pollen wall in *Pseudowintera* is much thinner, especially the nexine (0.5–1.0 vs. 1.1–1.8 µm thick), and *P. colorata* and *P. traversi* have a (semi)imperfectly microreticulate ulcus membrane not known from any other extant or fossil taxon. Pollen types 5 to 7 share many characteristics with the African fossil tetrads and are very similar in appearance, but each species differs in at least one feature. For example, *Zygogynum comptonii* (PT 6) is like a smaller version of the fossil but without an annulus-like rim, and *Z. fraterculum* (PT 7) has smaller aperture regions, much narrower sexine, broad and rounded muri forming larger lumina, and numerous free-standing columellae. Pollen type 8 is markedly different, having (micro)reticulate sculpture and between 40–100 lumina per pollen grain in lateral view (Tabs 1, 2). Although *Pseudowinterapollis africanensis* sp. nov. shares many features with the early diverging lineages of the Winteraceae, its character suite is unique. Thus, it should not be addressed as a member of *Drimys* or the Australasian genera. Its best fit is with the ancestral pollen of all (modern) Winteraceae/ Winteroideae as reconstructed by Grímsson et al. (in press). On the other hand, pollen of the extant Madagascan and earliest diverged genus *Takhtajania* appears to be strongly derived, so we cannot exclude the possibility that the Miocene pollen was produced by the same lineage of Winteraceae (or its sister lineage). More African material from different time periods will be needed to answer this question. Older and coeval tetrads from South America and Australia need to be studied by SEM to assess whether the morphology of the Miocene South African pollen is unique to Africa and not just reflecting that of the actual primitive pollen of all Winteroideae/Winteraceae.

CONCLUSION AND OUTLOOK

The tetrad and pollen morphology of Winteraceae is unique, making this family easily recognizable in the fossil pollen record. The combination of LM and high-resolution SEM makes it possible to identify the distinguishing features and character suites of genera/species with particular geographical ranges, and their basal versus derived phylogenetic position. These tetrad/pollen features can also be studied in fossil Winteraceae and used to compare and affiliate the fossils more accurately. Only by using such combined methods (LM and SEM) and by comparing recent and fossil material can the origin, subsequent divergence and paleophytogeographic history of Winteraceae be visualized. Future work on the history of this family therefore will rely on additional combined LM and SEM investigations of extant taxa missing in this study, and on SEM-based affiliation of fossil pollen/tetrads from South America and Australasia that until now have been documented using only LM.

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PLATES

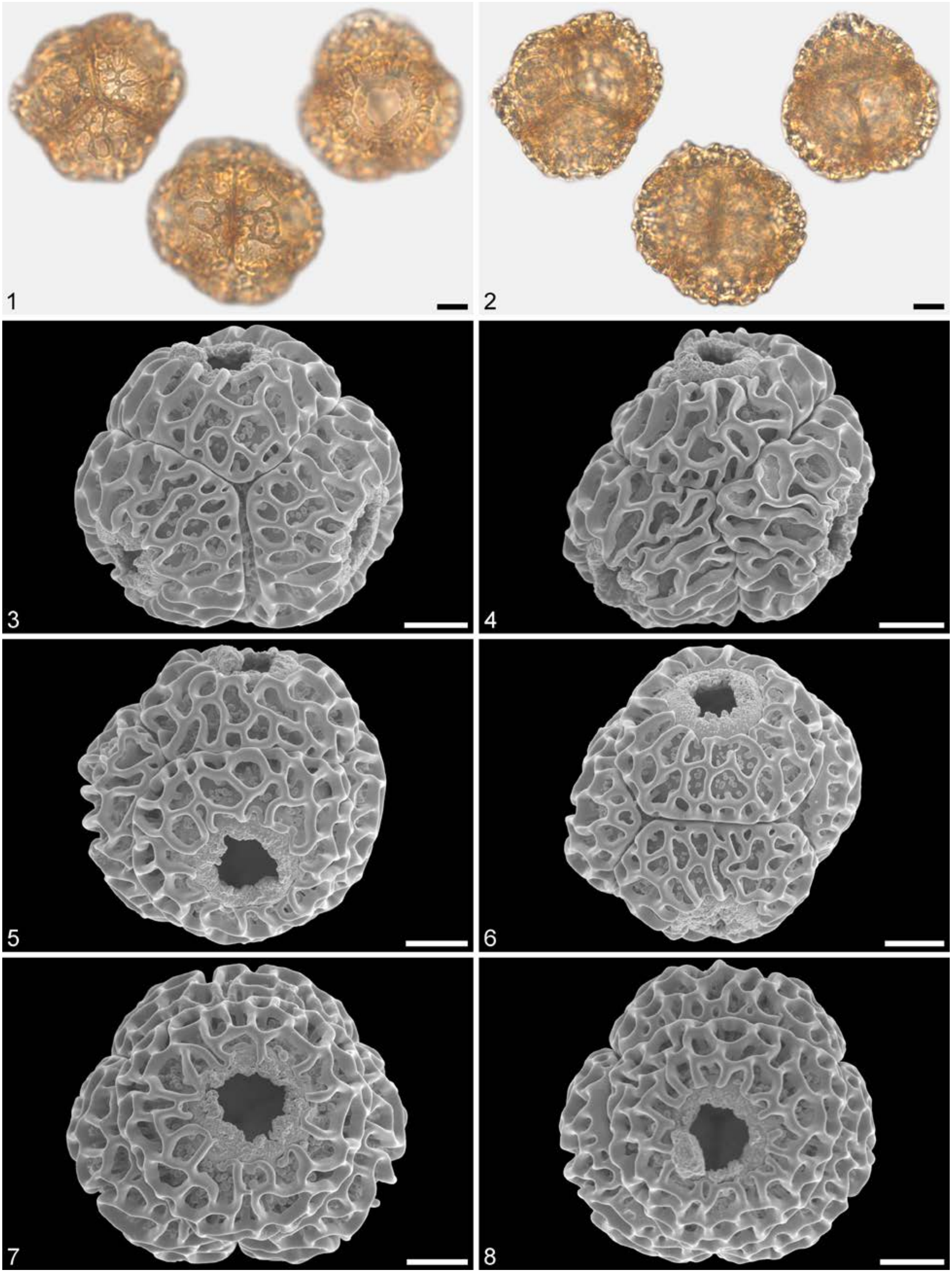

Plate 1. *Takhtajania perrieri* (Capuron) Baranova & J.-F.Leroy (MO: from Madagascar, coll. Rabenantoandro et al., s.n.); **1**. Pollen tetrads in LM, high focus, left tetrad in basal view, middle tetrad in lateral view, right tetrad in apical view; **2**. Pollen tetrads in LM, optical cross section, left tetrad in basal view, middle tetrad in lateral view, right tetrad in apical view; **3–8**. Pollen tetrads in SEM; **3**, **4**. Basal view; **5**, **6**. Lateral view; **7**, **8**. Apical view. Scale bars – 10 µm

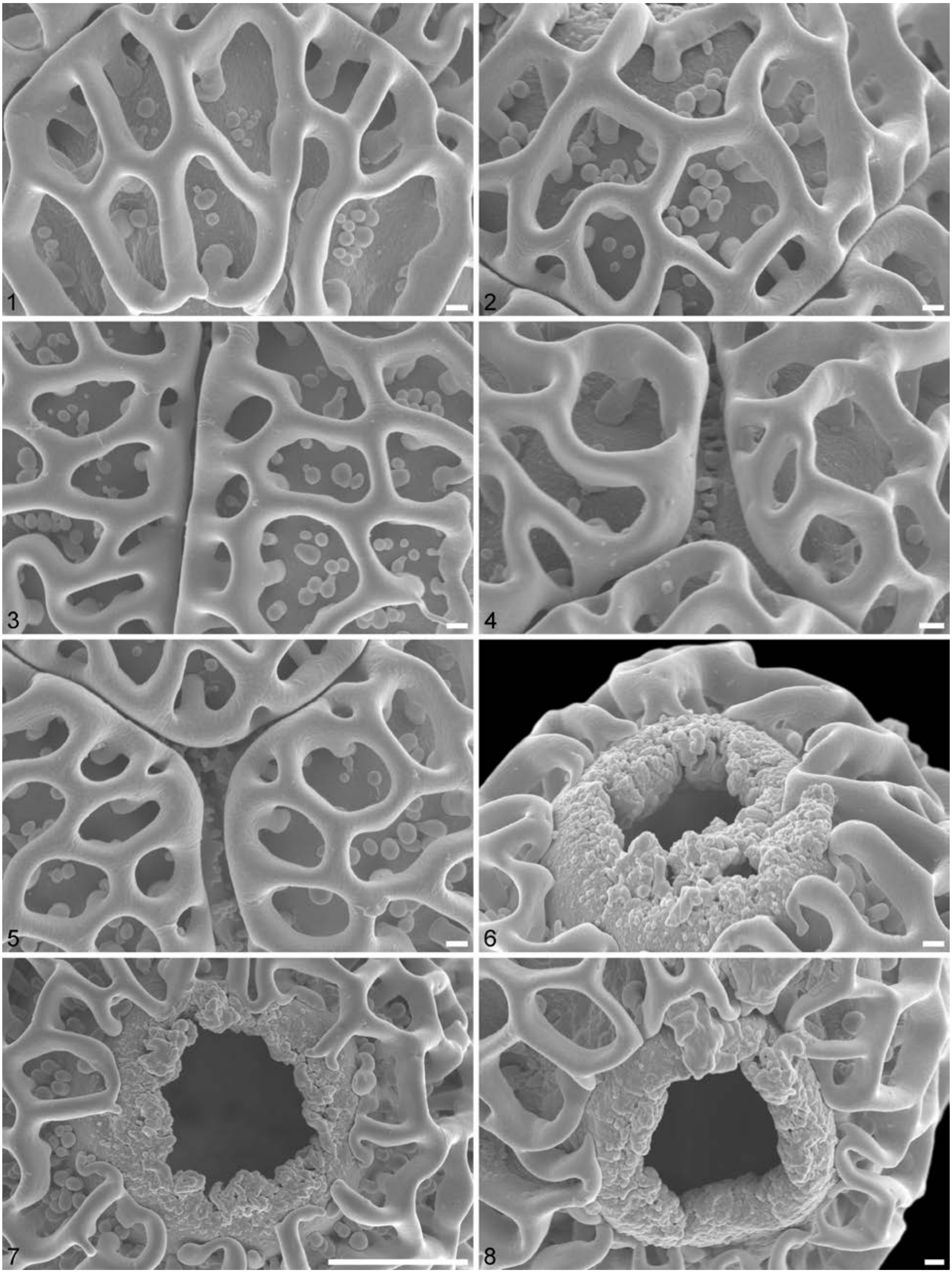

Plate 2. *Takhtajania perrieri* (Capuron) Baranova & J.-F.Leroy (MO: from Madagascar, coll. Rabenantoandro et al., s.n.); **1–8**. Close-ups of sculpture in SEM; **1**, **2**. Distal face of pollen; **3**. Pollen interface in lateral view; **4**, **5**. Pollen interface in basal view; **6–8**. Aperture. Scale bars – 10 µm (7), 1 µm (1–6, 8)

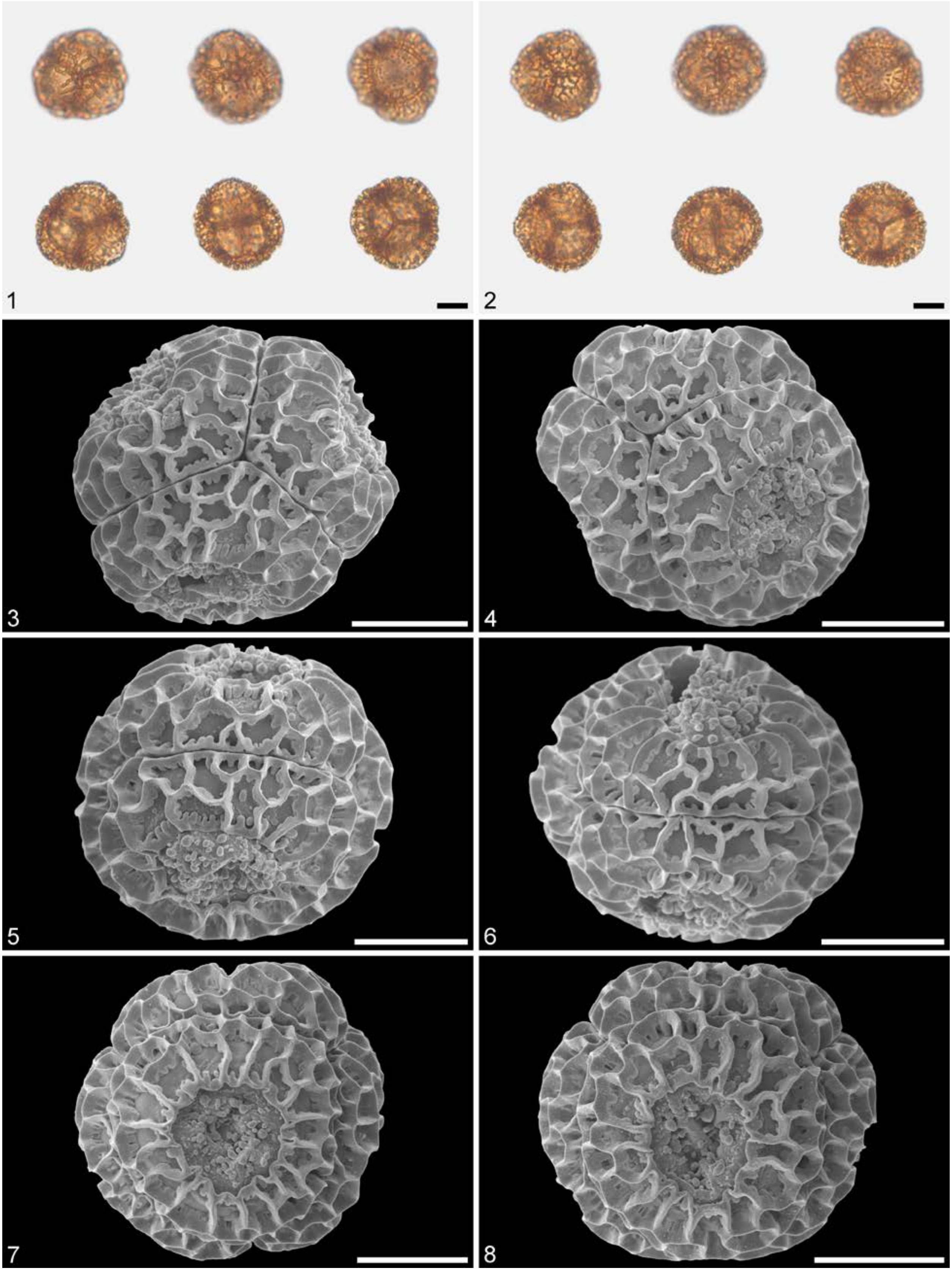

Plate 3. *Tasmannia insipida* R.Br. ex DC. (WU: from Australia, coll. unknown, s.n.); **1**, **2**. Pollen tetrads in LM, upper row at high focus, lower row in optical cross section, left tetrads in basal view, middle tetrads in lateral view, right tetrads in apical view; **3–8**. Pollen tetrads in SEM; **3**, **4**. Basal view; **5**, **6**. Lateral view; **7**, **8**. Apical view. Scale bars – 10 µm

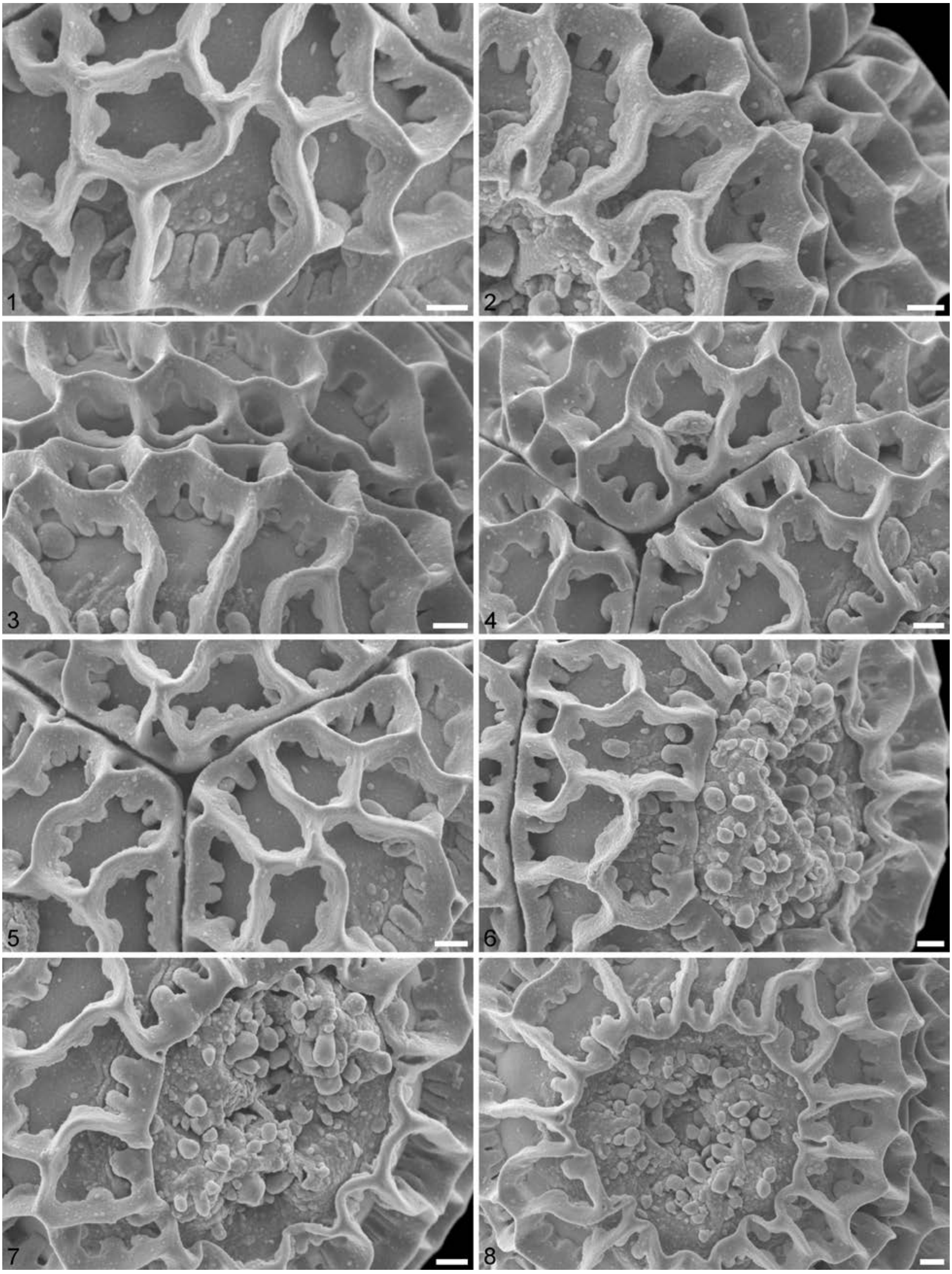

Plate 4. *Tasmannia insipida* R.Br. ex DC. (WU: from Australia, coll. unknown, s.n.); **1–8**. Close-ups of sculpture in SEM; **1**, **2**. Distal face of pollen; **3**. Pollen interface in lateral view; **4**, **5**. Pollen interface in basal view; **6–8**. Aperture. Scale bars – 1 µm

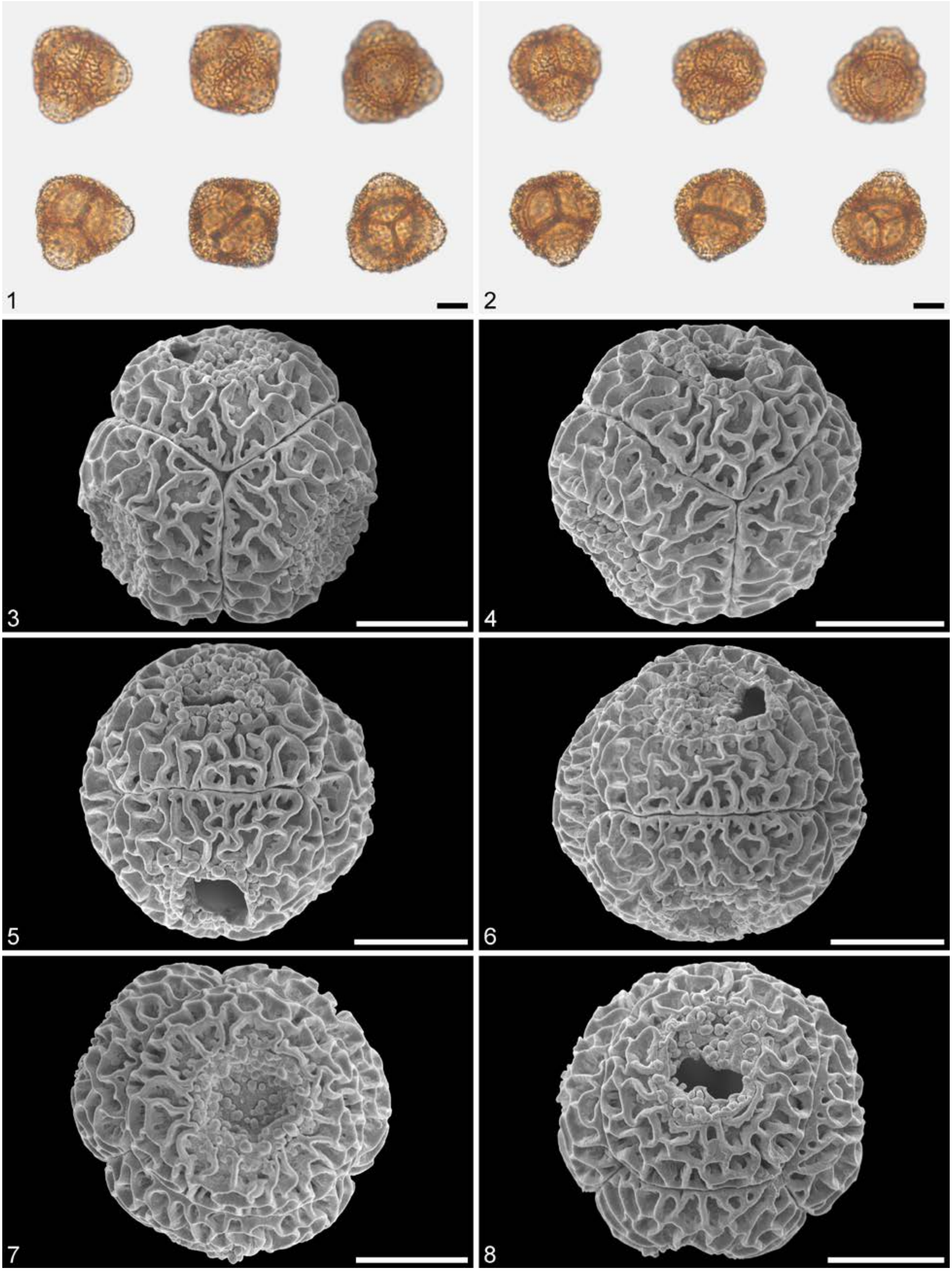

Plate 5. *Tasmannia lanceolata* (Poir.) A. C. Sm. (W 1956–0006680: from Australia); **1**, **2**. Pollen tetrads in LM, upper row at high focus, lower row in optical cross section, left tetrads in basal view, middle tetrads in lateral view, right tetrads in apical view; **3–8**. Pollen tetrads in SEM; **3**, **4**. Basal view; **5**, **6**. Lateral view; **7**, **8**. Apical view. Scale bars – 10 µm.

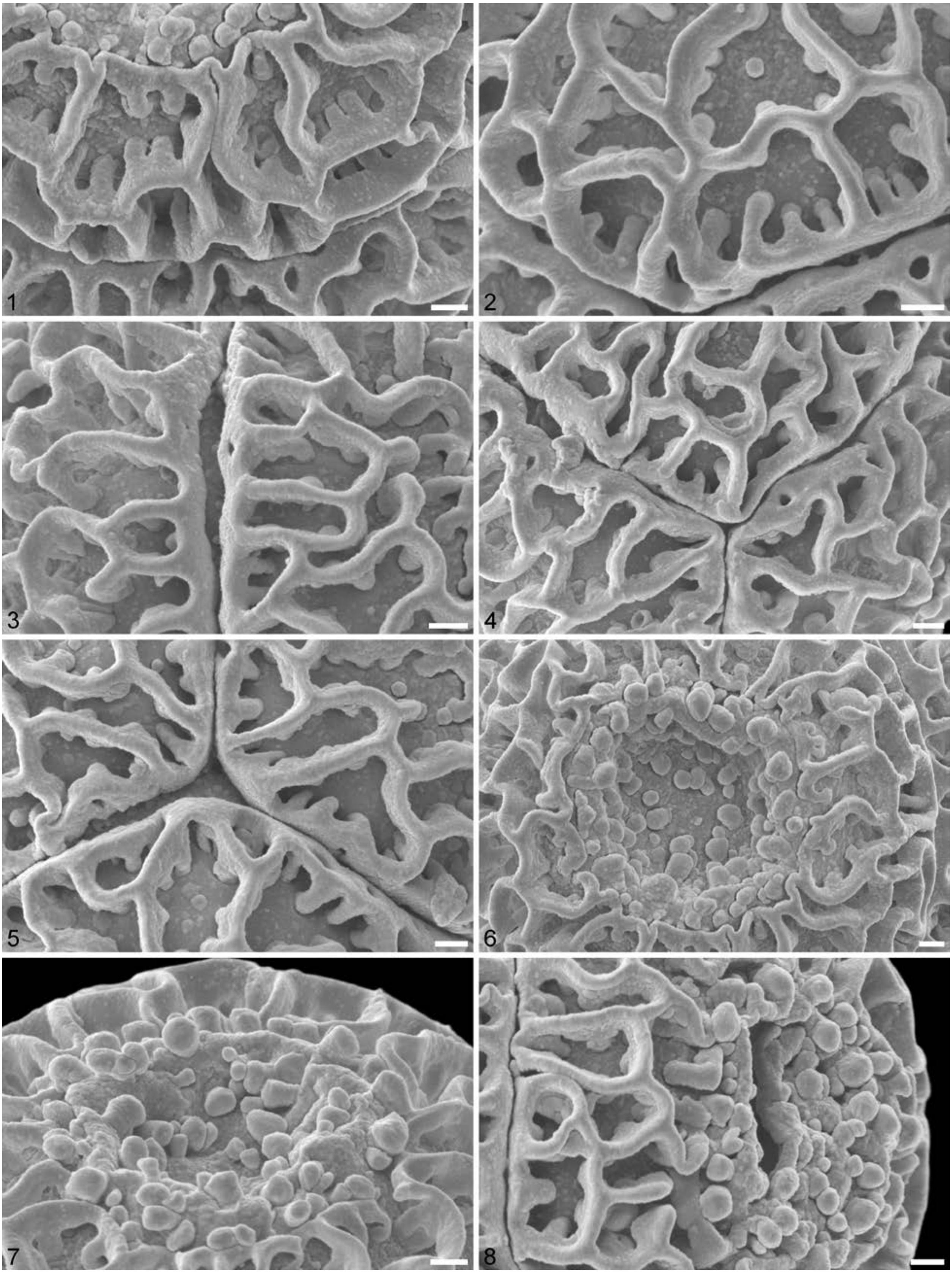

Plate 6. *Tasmannia lanceolata* (Poir.) A. C. Sm. (W 1956–0006680: from Australia); **1–8**. Close-ups of sculpture in SEM; **1**, **2**. Distal face of pollen; **3**. Pollen interface in lateral view; **4**, **5**. Pollen interface in basal view; **6–8**. Aperture. Scale bars – 1 µm

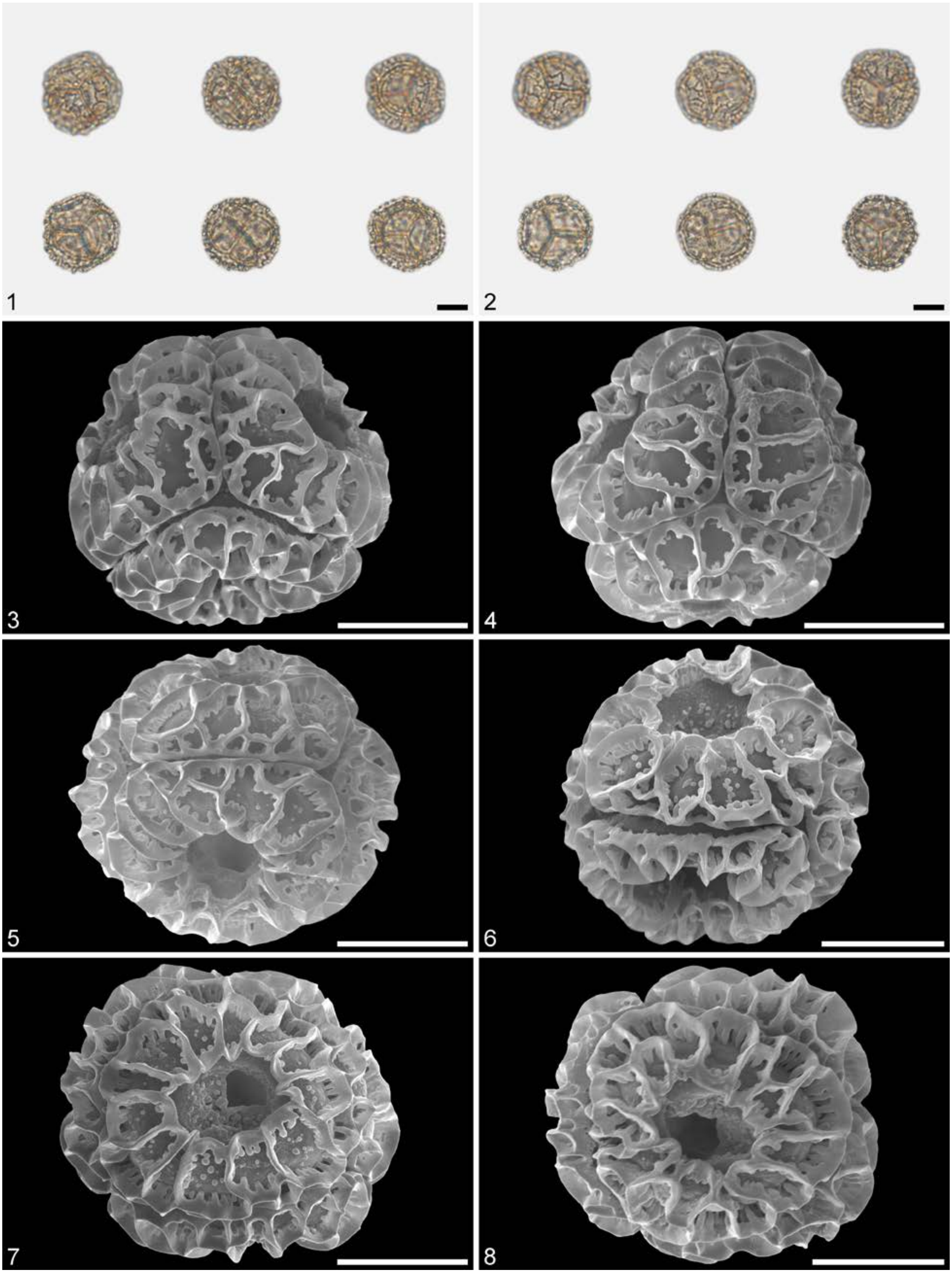

Plate 7. *Tasmannia piperita* (Hook. f.) Miers (W 0024760: from Malaysia); **1**, **2**. Pollen tetrads in LM, upper row at high focus, lower row in optical cross section, left tetrads in basal view, middle tetrads in lateral view, right tetrads in apical view; **3–8**. Pollen tetrads in SEM; **3**, **4**. Basal view; **5**, **6**. Lateral view; **7**, **8**. Apical view. Scale bars – 10 µm

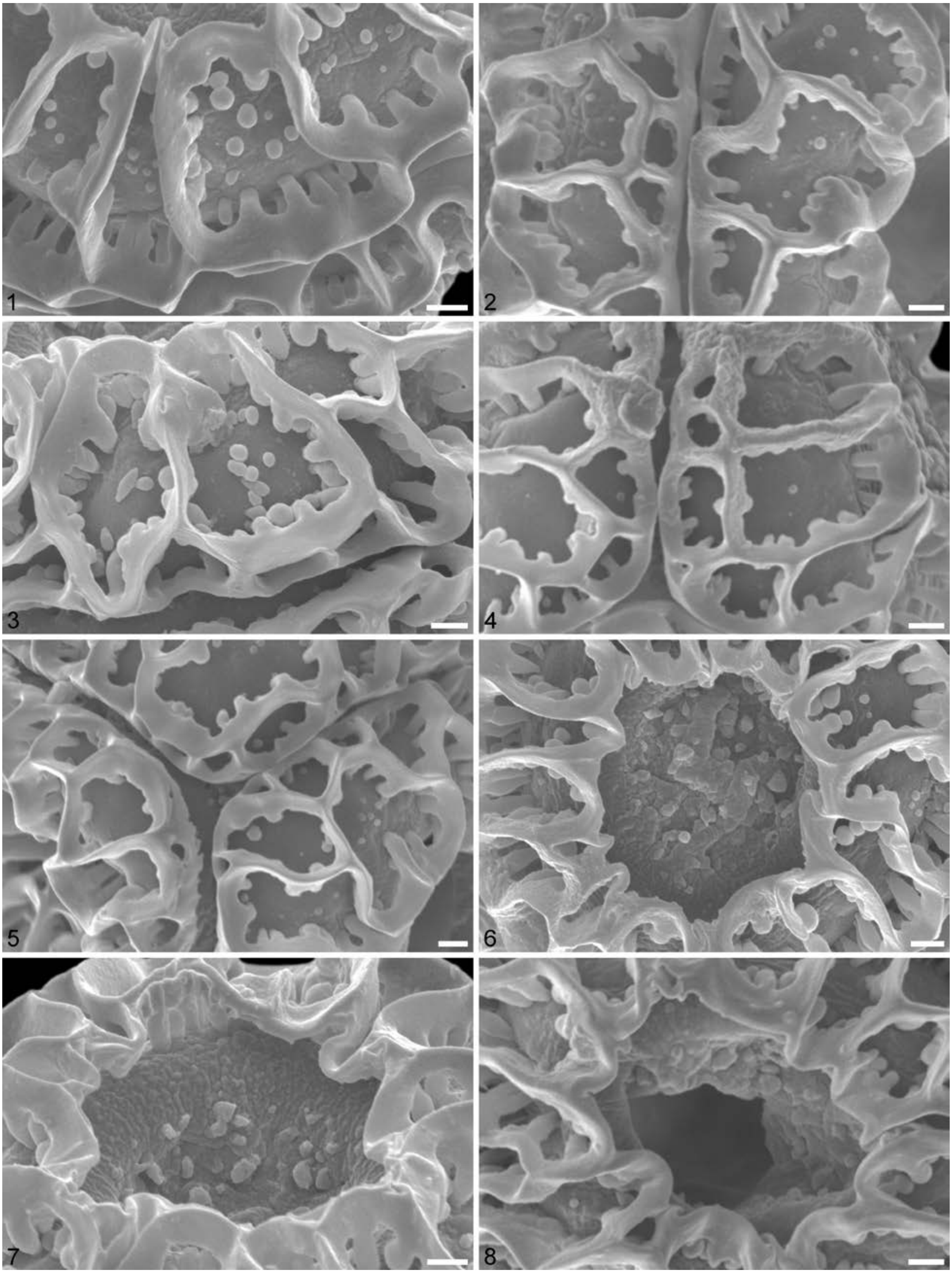

Plate 8. *Tasmannia piperita* (Hook. f.) Miers (W 0024760: from Malaysia); **1–8**. Close-ups of sculpture in SEM; **1**. Distal face of pollen; **2**. Pollen interface in lateral view; **3**. Distal face of pollen; **4**, **5**. Pollen interface in basal view; **6–8**. Aperture. Scale bars – 1 µm

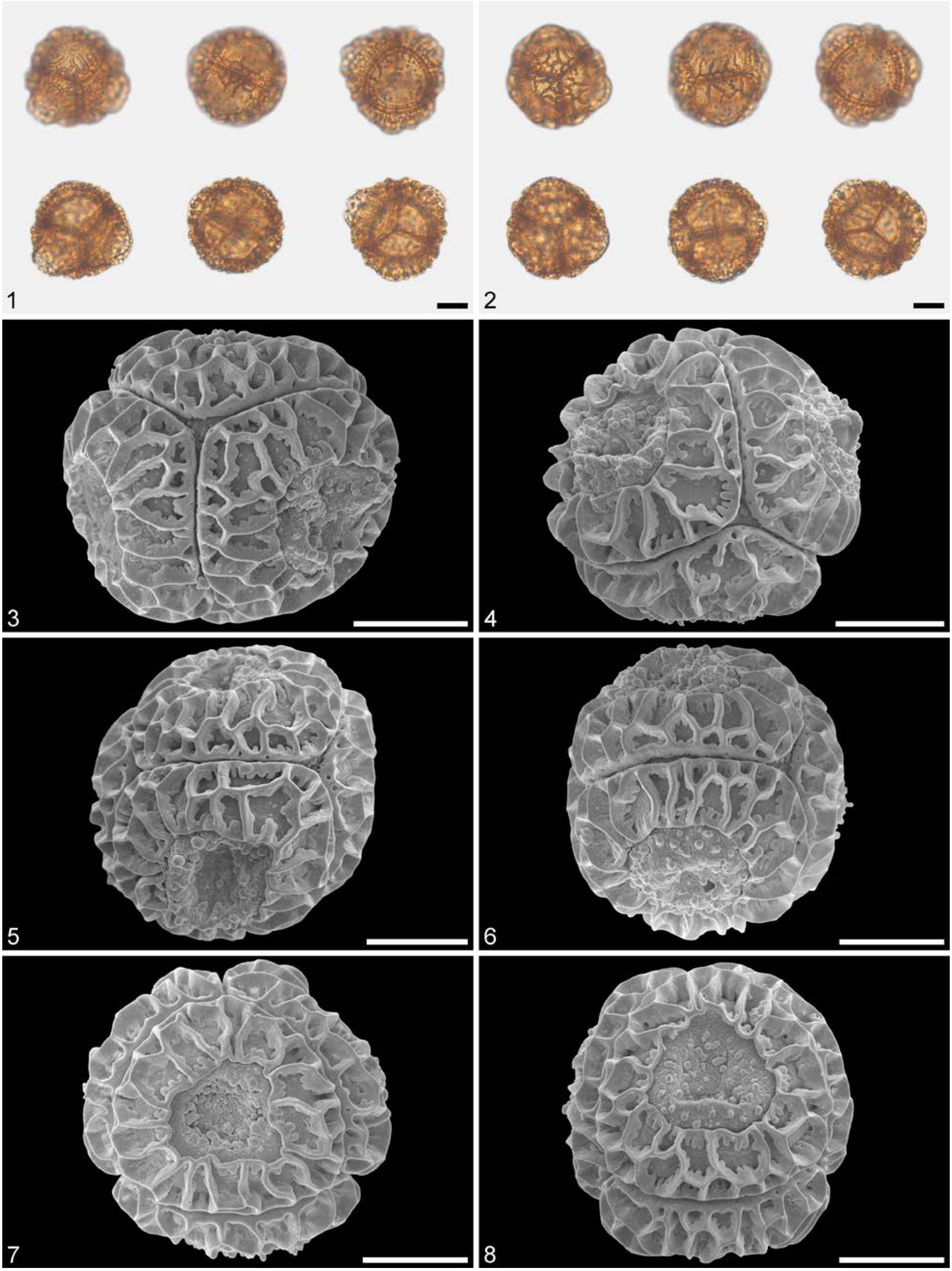

Plate 9. *Tasmannia purpurascens* (Vickery) A. C. Sm. (W 1974–0000456: from Australia); **1**, **2**. Pollen tetrads in LM, upper row at high focus, lower row in optical cross section, left tetrads in basal view, middle tetrads in lateral view, right tetrads in apical view; **3–8**. Pollen tetrads in SEM; **3**, **4**. Basal view; **5**, **6**. Lateral view; **7**, **8**. Apical view. Scale bars – 10 μm

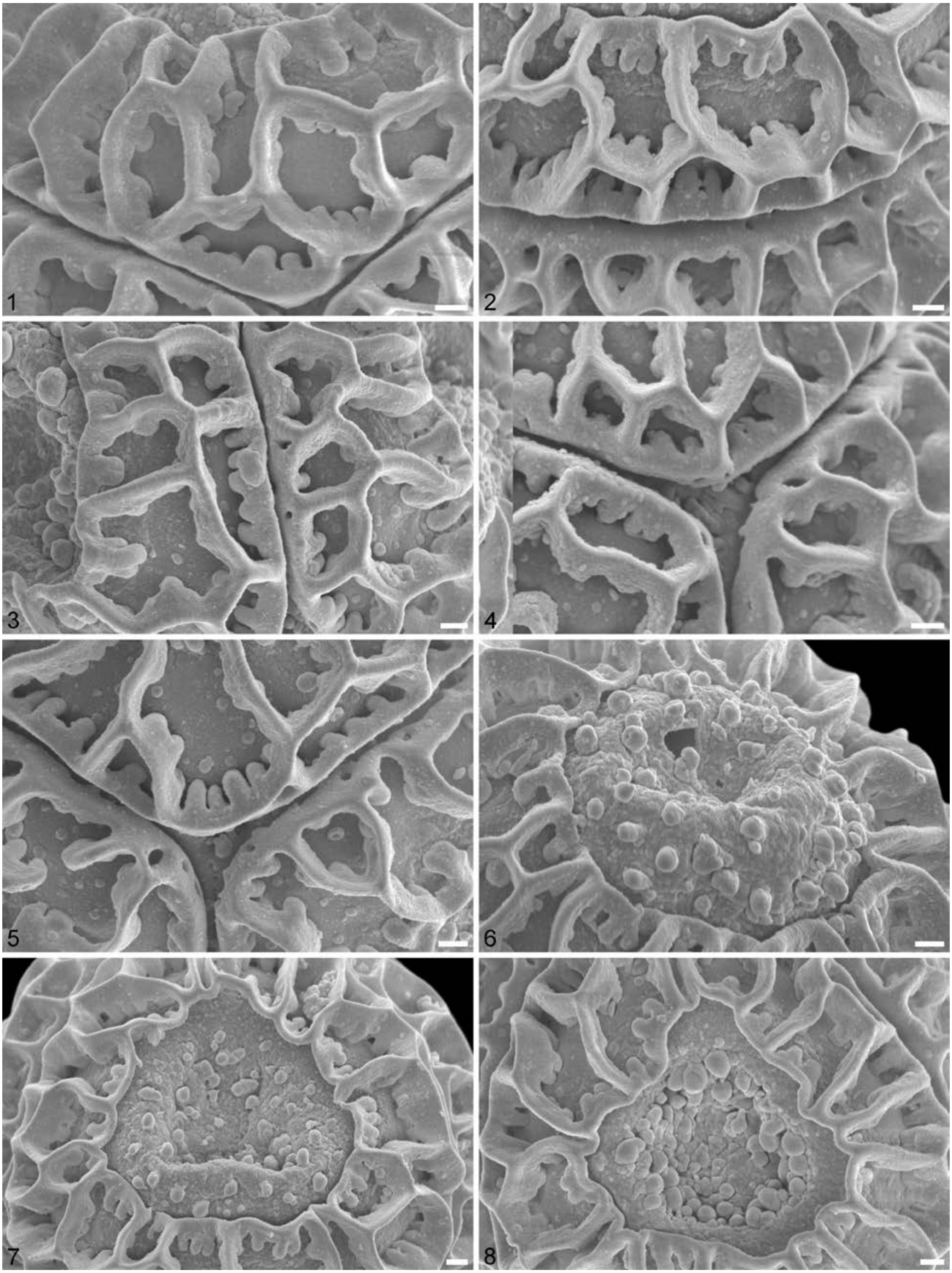

Plate 10. *Tasmannia purpurascens* (Vickery) A. C. Sm. (W 1974–0000456: from Australia); **1–8**. Close-ups of sculpture in SEM; **1**, **2**. Distal face of pollen; **3**. Pollen interface in lateral view; **4**, **5**. Pollen interface in basal view; **6–8**. Aperture. Scale bars – 1 µm

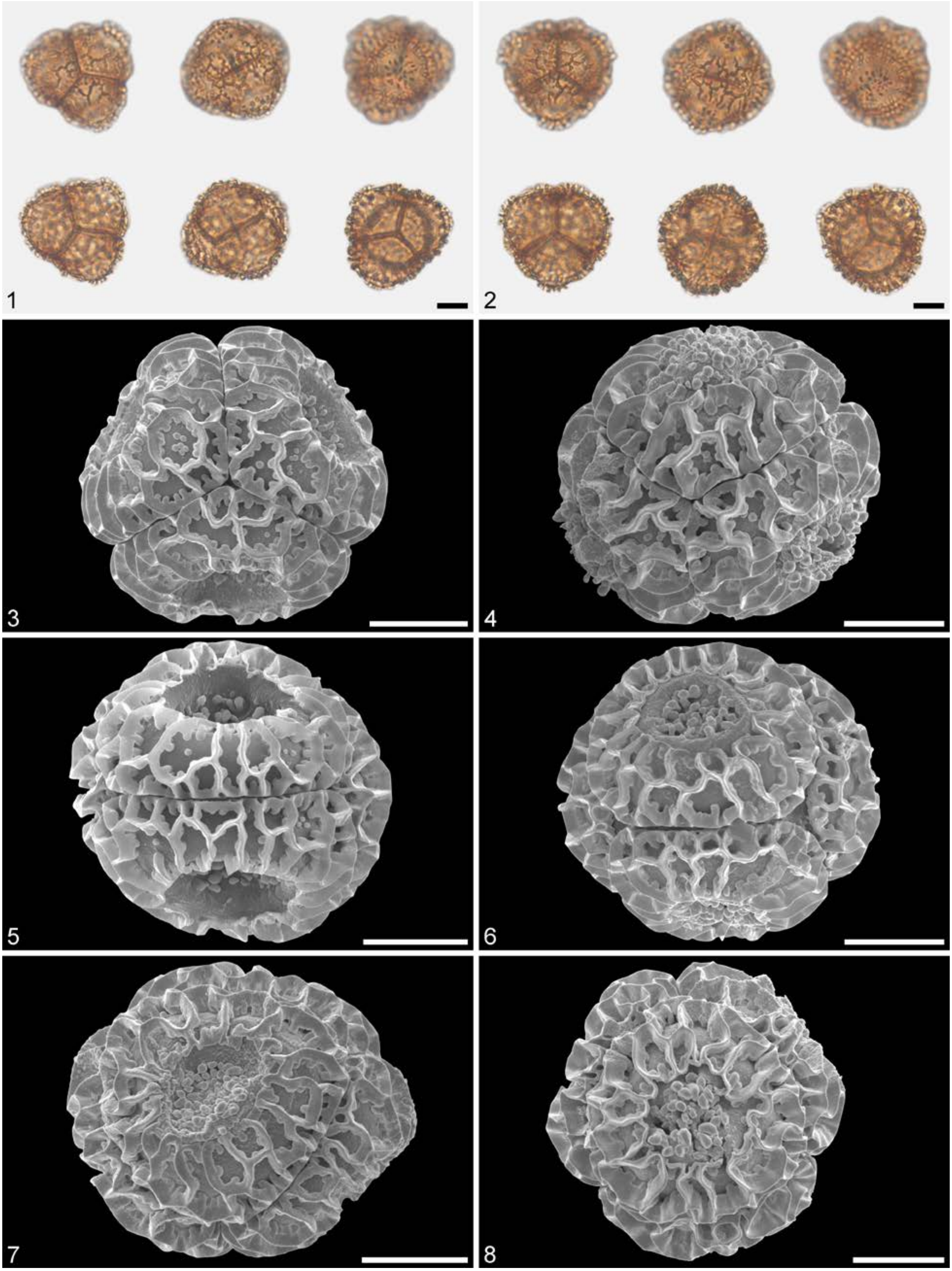

Plate 11. *Tasmannia stipitata* (Vickery) A. C. Sm. (M: from Australia, coll. H.-J. Tillich, s.n.); **1**, **2**. Pollen tetrads in LM, upper row at high focus, lower row in optical cross section, left tetrad in basal view, middle tetrad in lateral view, right tetrad in apical view; **3–8**. Pollen tetrads in SEM; **3**, **4**. Basal view; **5**, **6**. Lateral view; **7**, **8**. Apical view. Scale bars – 10 µm

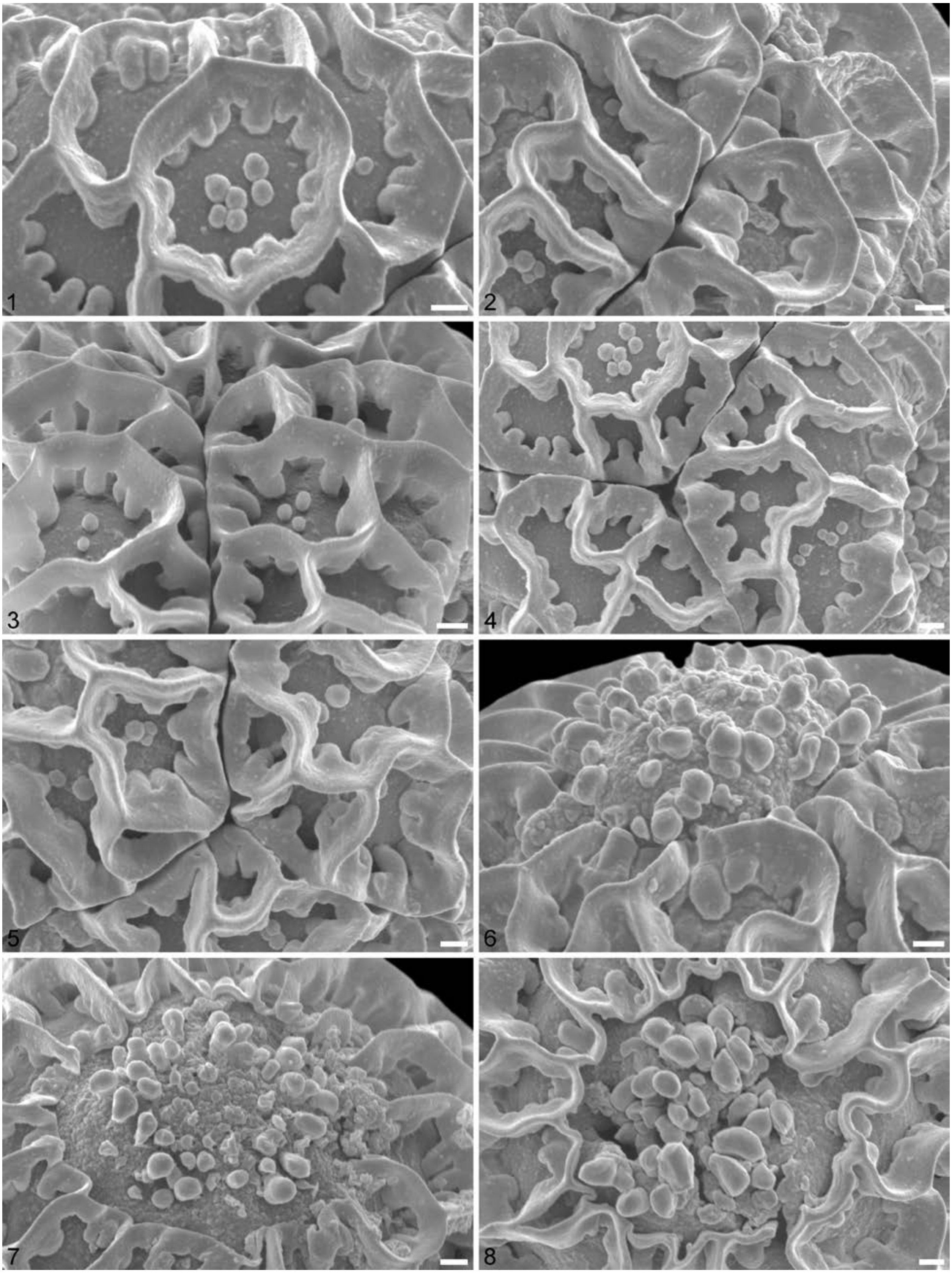

Plate 12. *Tasmannia stipitata* (Vickery) A. C. Sm. (M: from Australia, coll. H.-J. Tillich, s.n.); **1–8**. Close-ups of sculpture in SEM; **1**. Distal face of pollen; **2**. Pollen interface in lateral view; **3–5**. Pollen interface in basal view; **6–8**. Aperture. Scale bars – 1 µm

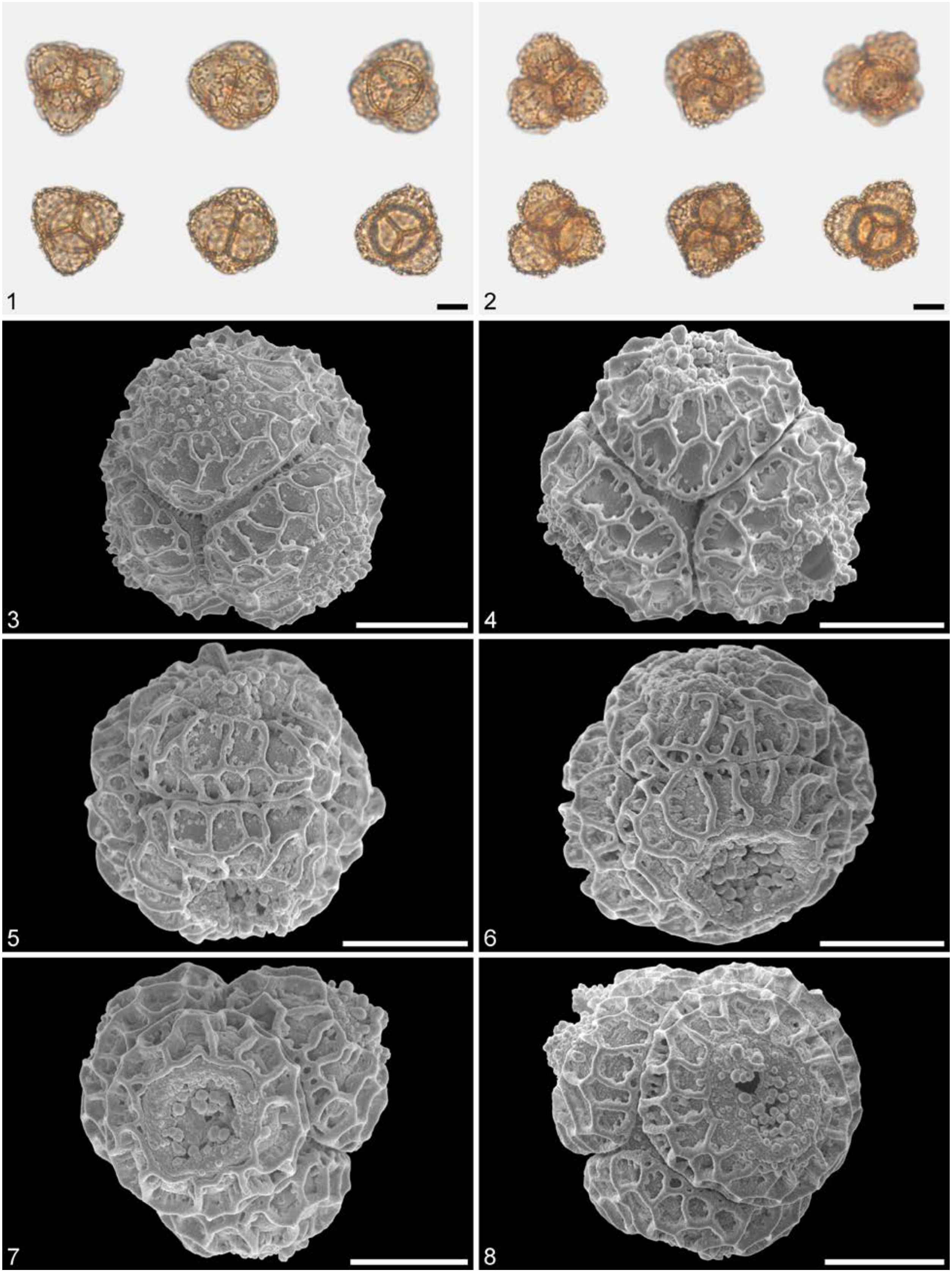

Plate 13. *Tasmannia vickeriana* (A. C. Sm.) A. C. Sm. (W 1956–0006651: from Australia); **1**, **2**. Pollen tetrads in LM, upper row at high focus, lower row in optical cross section, left tetrads in basal view, middle tetrads in lateral view, right tetrads in apical view; **3–8**. Pollen tetrads in SEM; **3**, **4**. Basal view; **5**, **6**. Lateral view; **7**, **8**. Apical view. Scale bars – 10 µm

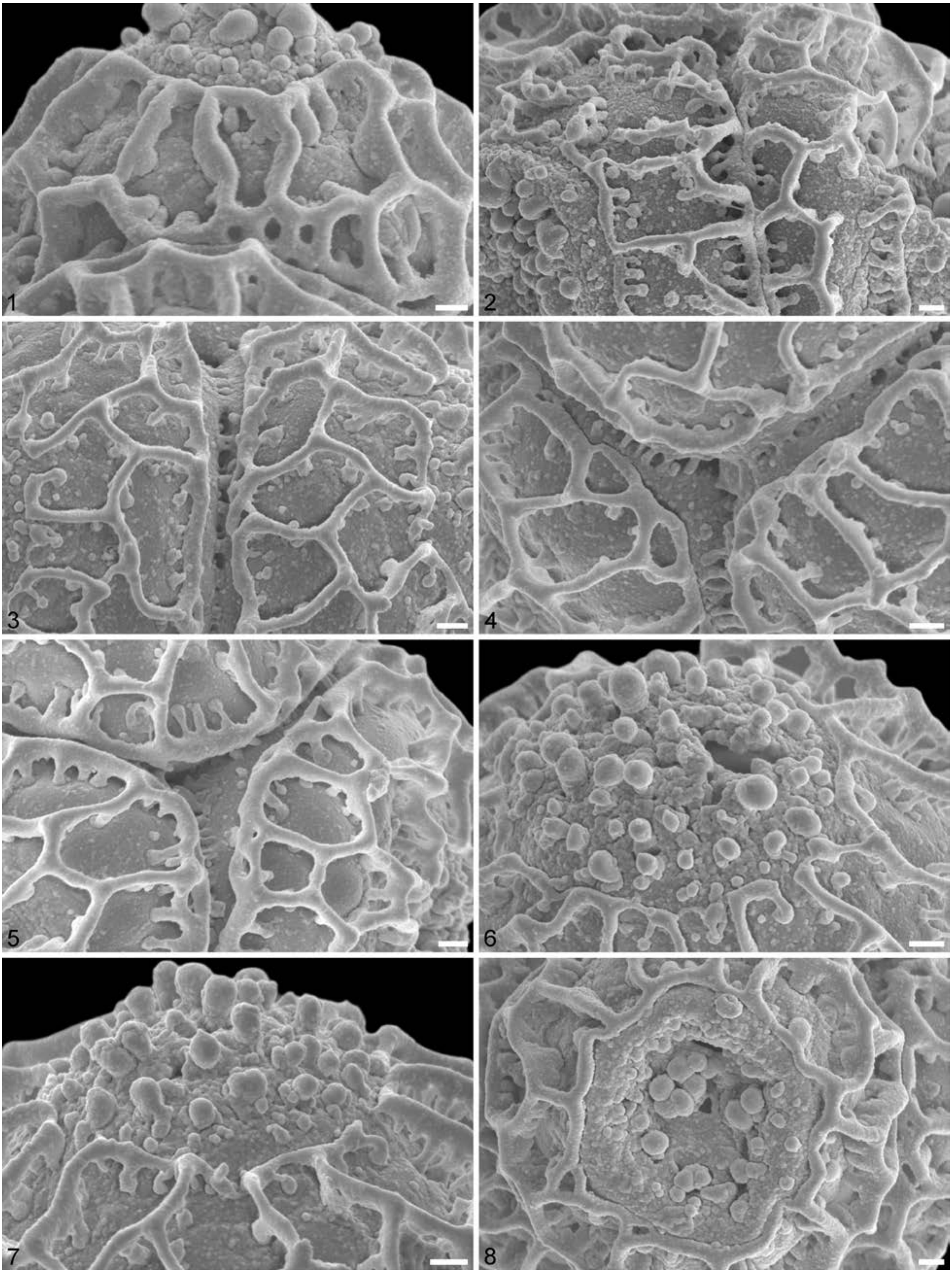

Plate 14. *Tasmannia vickeriana* (A. C. Sm.) A. C. Sm. (W 1956–0006651: from Australia); **1–8**. Close-ups of sculpture in SEM; **1**. Distal face of pollen; **2**, **3**. Pollen interface in lateral view; **4**, **5**. Pollen interface in basal view; **6–8**. Aperture. Scale bars – 1 µm

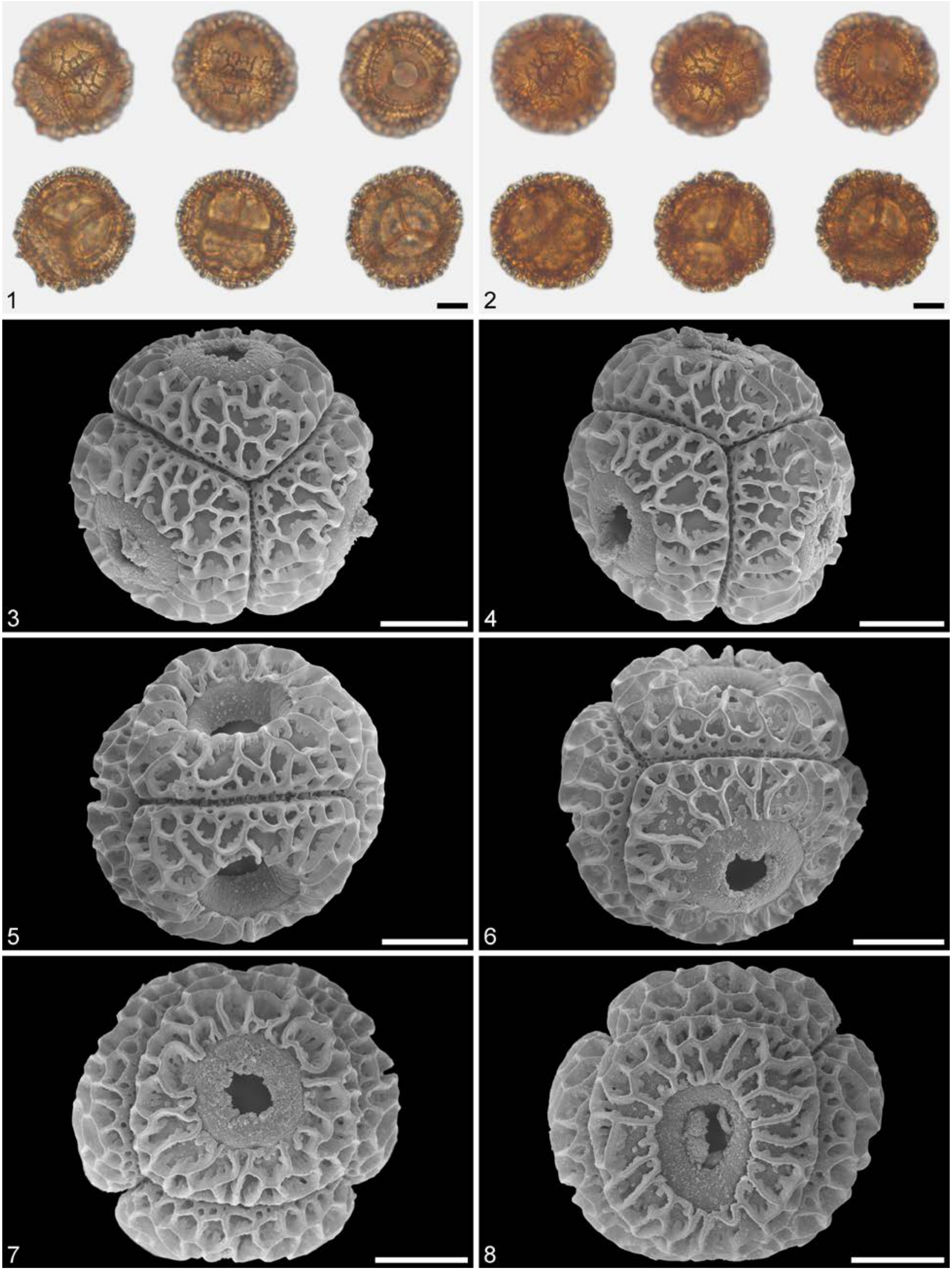

Plate 15. *Drimys andina* (Reiche) R.A.Rodr. & Quez. (WU 0072169: from Chile); **1**, **2**. Pollen tetrads in LM, upper row at high focus, lower row in optical cross section, left tetrads in basal view, middle tetrads in lateral view, right tetrads in apical view; **3–8**. Pollen tetrads in SEM; **3**, **4**. Basal view; **5**, **6**. Lateral view; **7**, **8**. Apical view. Scale bars – 10 µm

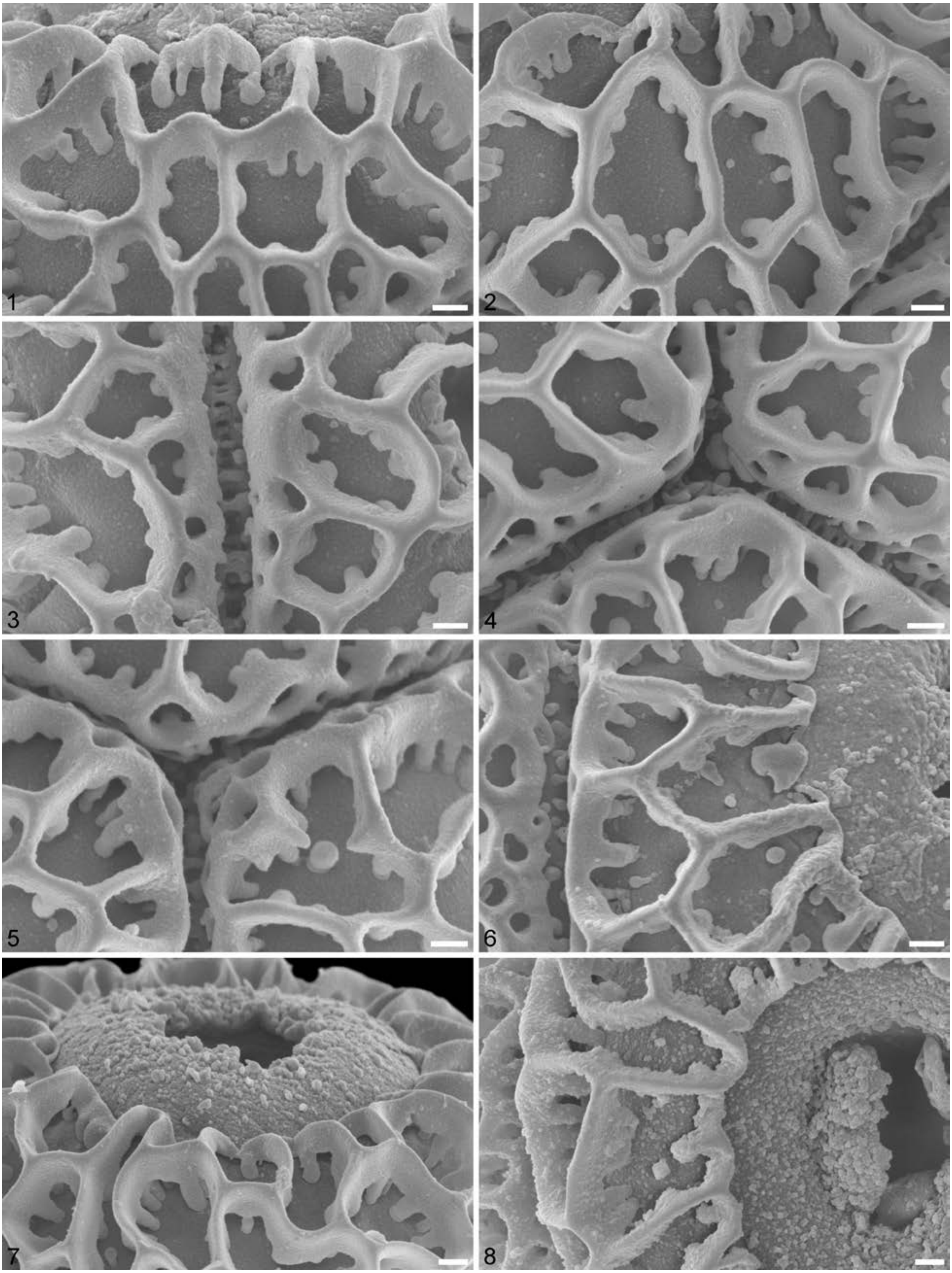

Plate 16. *Drimys andina* (Reiche) R.A.Rodr. & Quez. (WU 0072169: from Chile); **1–8**. Close-ups of sculpture in SEM; **1**, **2**. Distal face of pollen; **3**. Pollen interface in lateral view; **4**, **5**. Pollen interface in basal view; **6–8**. Aperture region. Scale bars – 1 µm

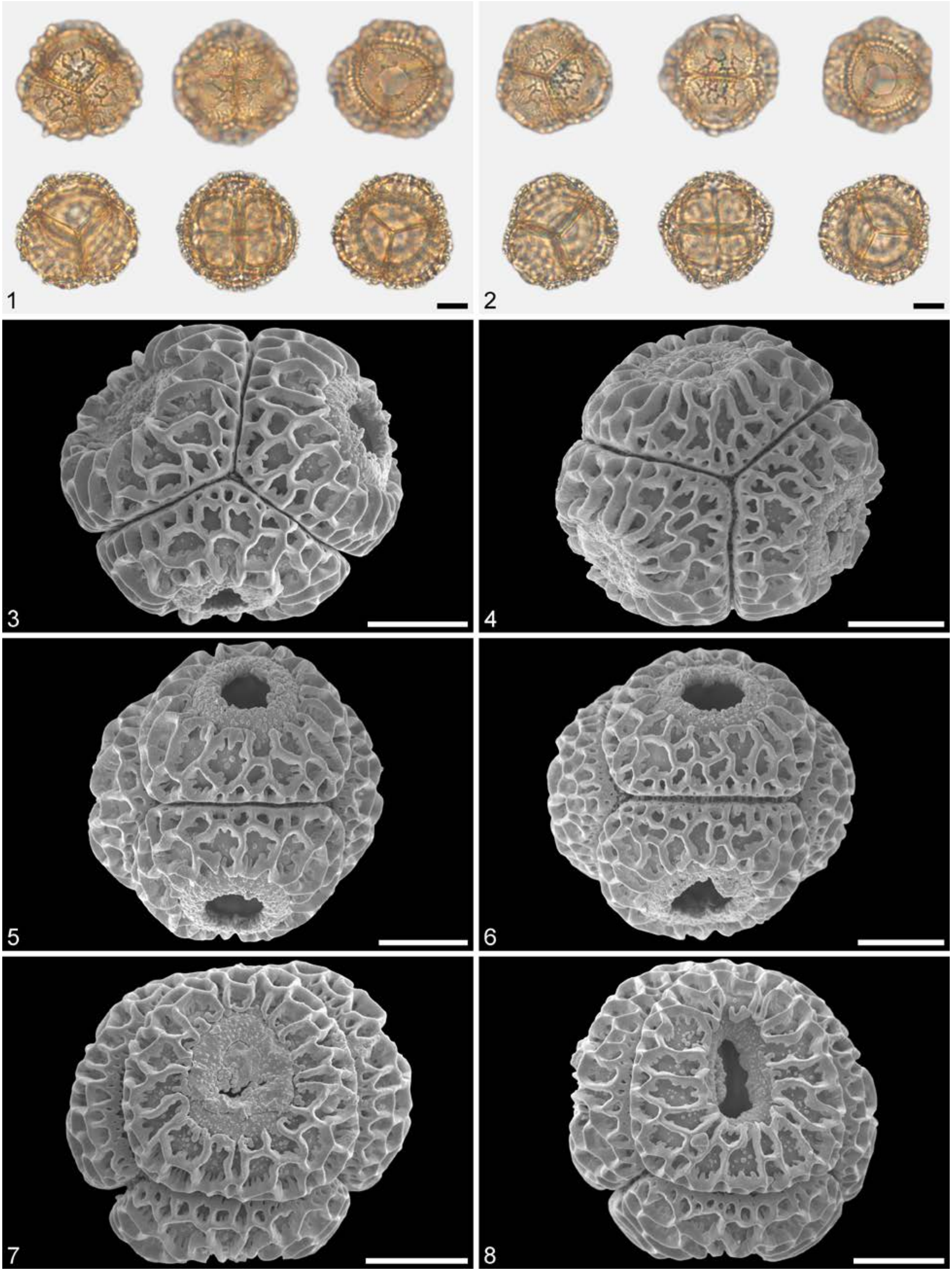

Plate 17. *Drimys angustifolia* Miers (W 1995–0004921: from Brazil); **1**, **2**. Pollen tetrads in LM, upper row at high focus, lower row in optical cross section, left tetrads in basal view, middle tetrads in lateral view, right tetrads in apical view; **3–8**. Pollen tetrads in SEM; **3**, **4**. Basal view; **5**, **6**. Lateral view; **7**, **8**. Apical view. Scale bars – 10 µm

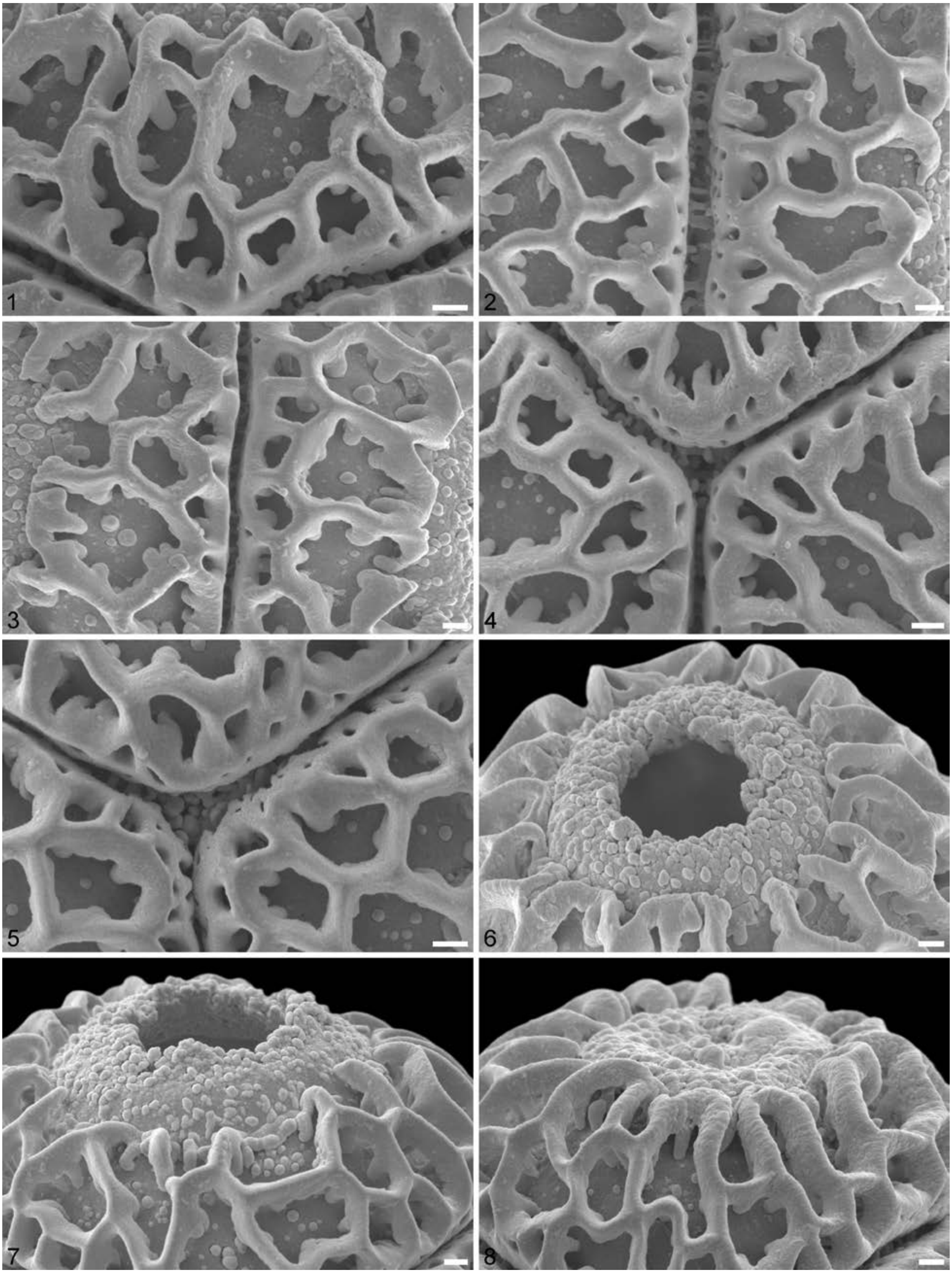

Plate 18. *Drimys angustifolia* Miers (W 1995–0004921: from Brazil); **1–8**. Close-ups of sculpture in SEM; **1**. Distal face of pollen; **2**, **3**. Pollen interface in lateral view; **4**, **5**. Pollen interface in basal view; **6–8**. Aperture. Scale bars – 1 µm

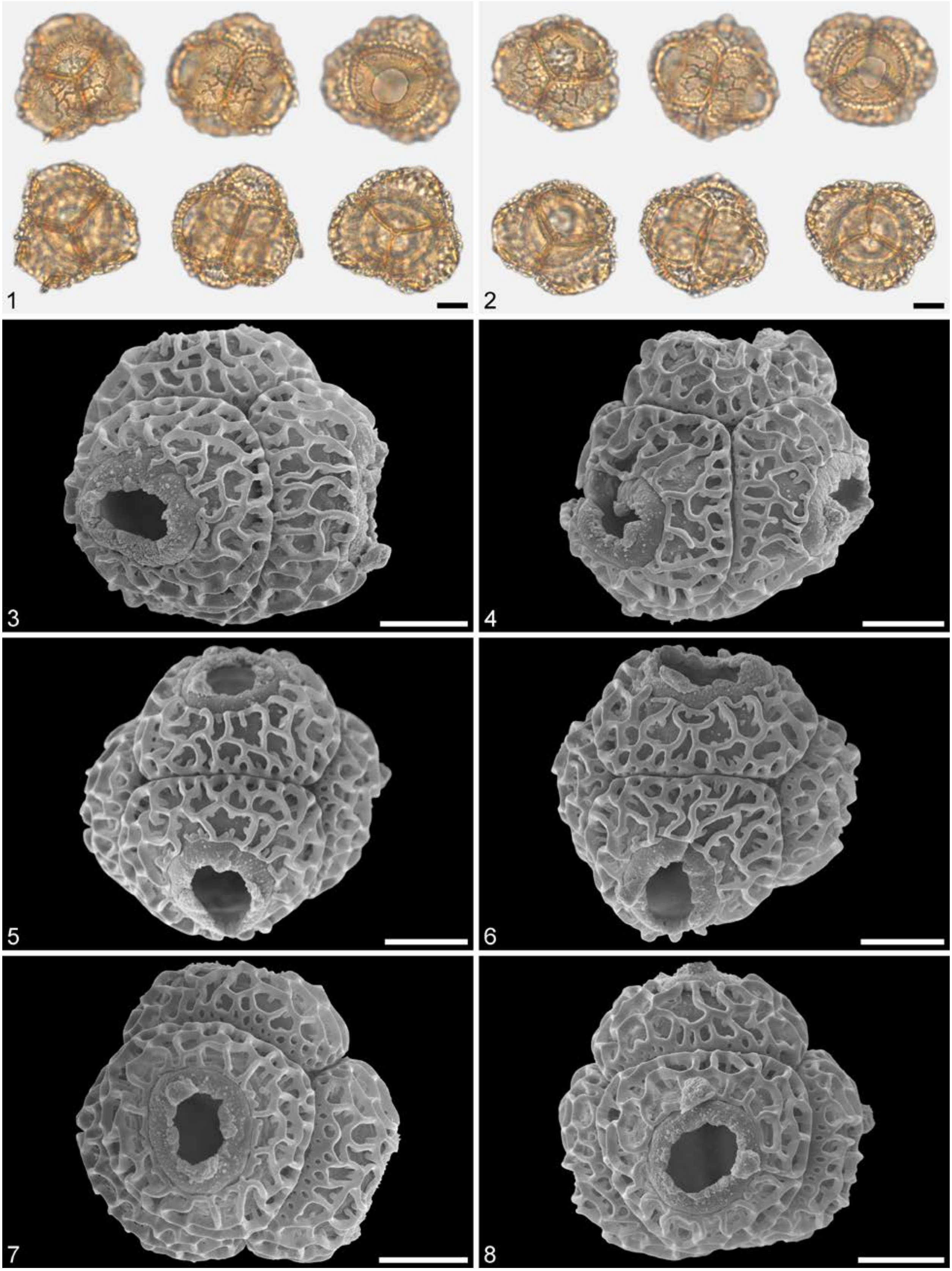

Plate 19. *Drimys brasiliensis* Miers (W 2001–0006782: from Brazil); **1**, **2**. Pollen tetrads in LM, upper row at high focus, lower row in optical cross section, left tetrads in basal view, middle tetrads in lateral view, right tetrads in apical view; **3–8**. Pollen tetrads in SEM; **3**, **4**. Basal view; **5**, **6**. Lateral view; **7**, **8**. Apical view. Scale bars – 10 µm

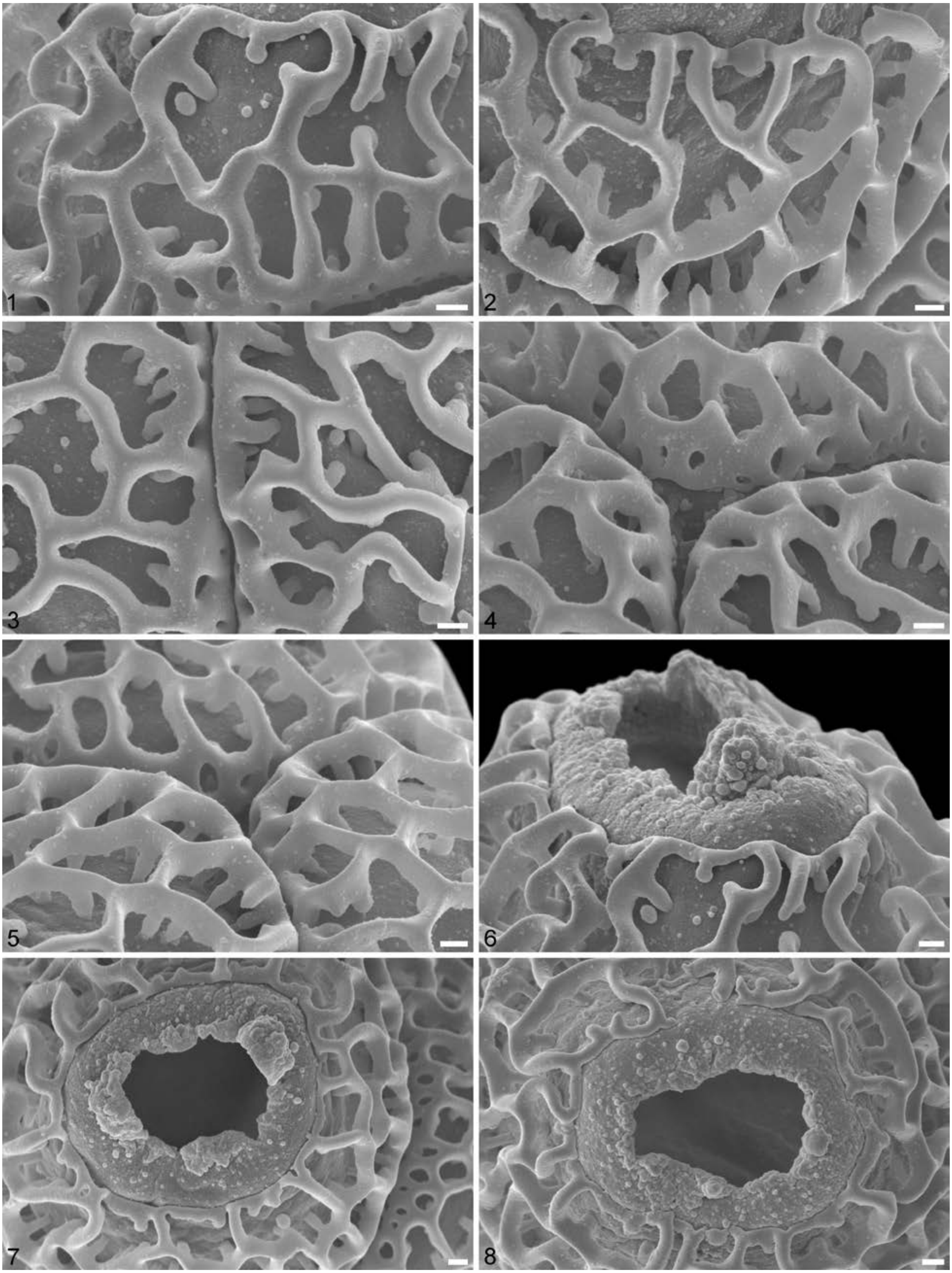

Plate 20. *Drimys brasiliensis* Miers (W 2001–0006782: from Brazil); **1–8**. Close-ups of sculpture in SEM; **1**, **2**. Distal face of pollen; **3**. Pollen interface in lateral view; **4**, **5**. Pollen interface in basal view; **6–8**. Aperture. Scale bars – 1 µm

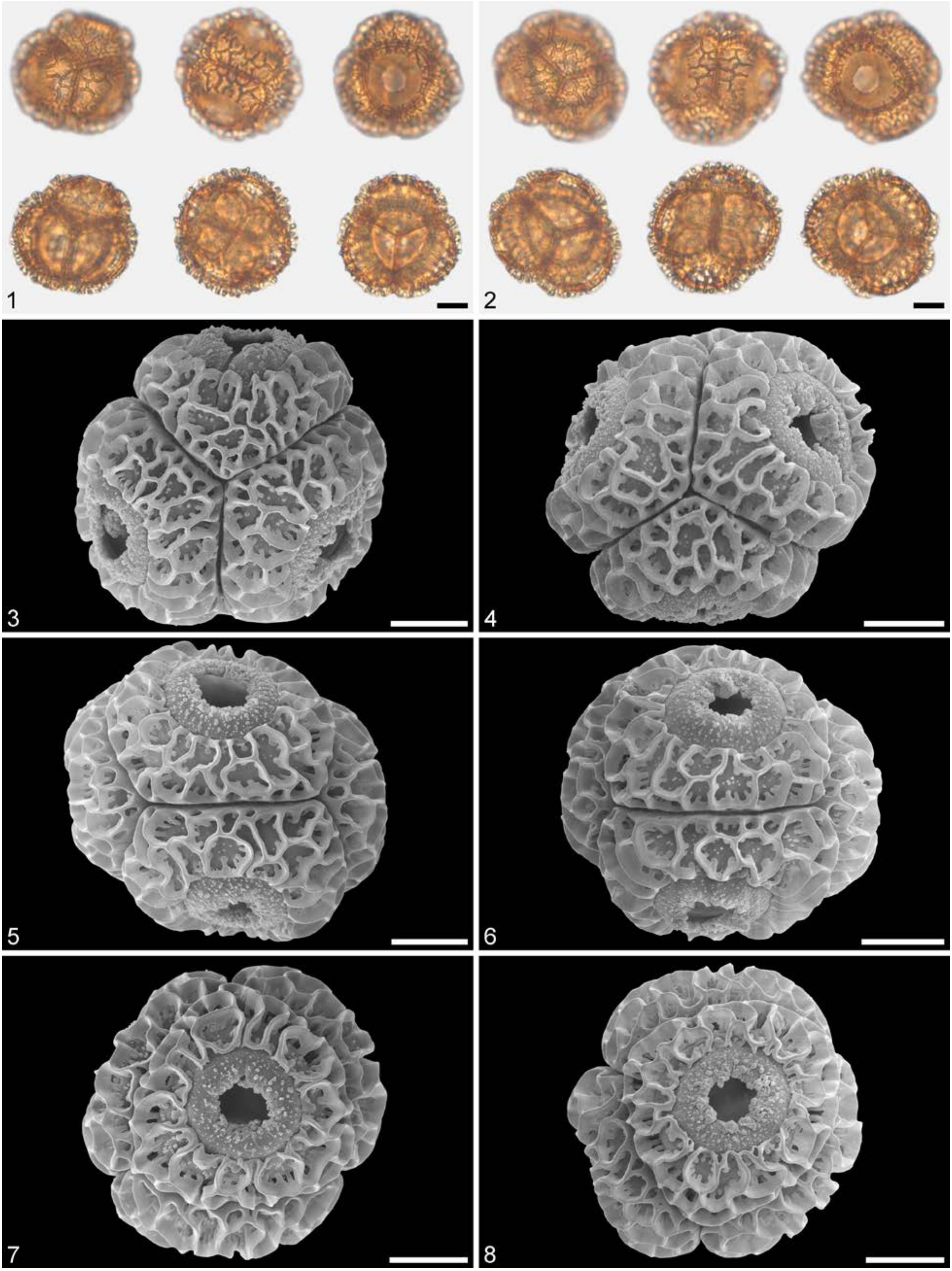

Plate 21. *Drimys confertifolia* Phil. (WU 0069300: from Chile); **1**, **2**. Pollen tetrads in LM, upper row at high focus, lower row in optical cross section, left tetrads in basal view, middle tetrads in lateral view, right tetrads in apical view; **3–8**. Pollen tetrads in SEM; **3**, **4**. Basal view; **5**, **6**. Lateral view; **7**, **8**. Apical view. Scale bars – 10 µm

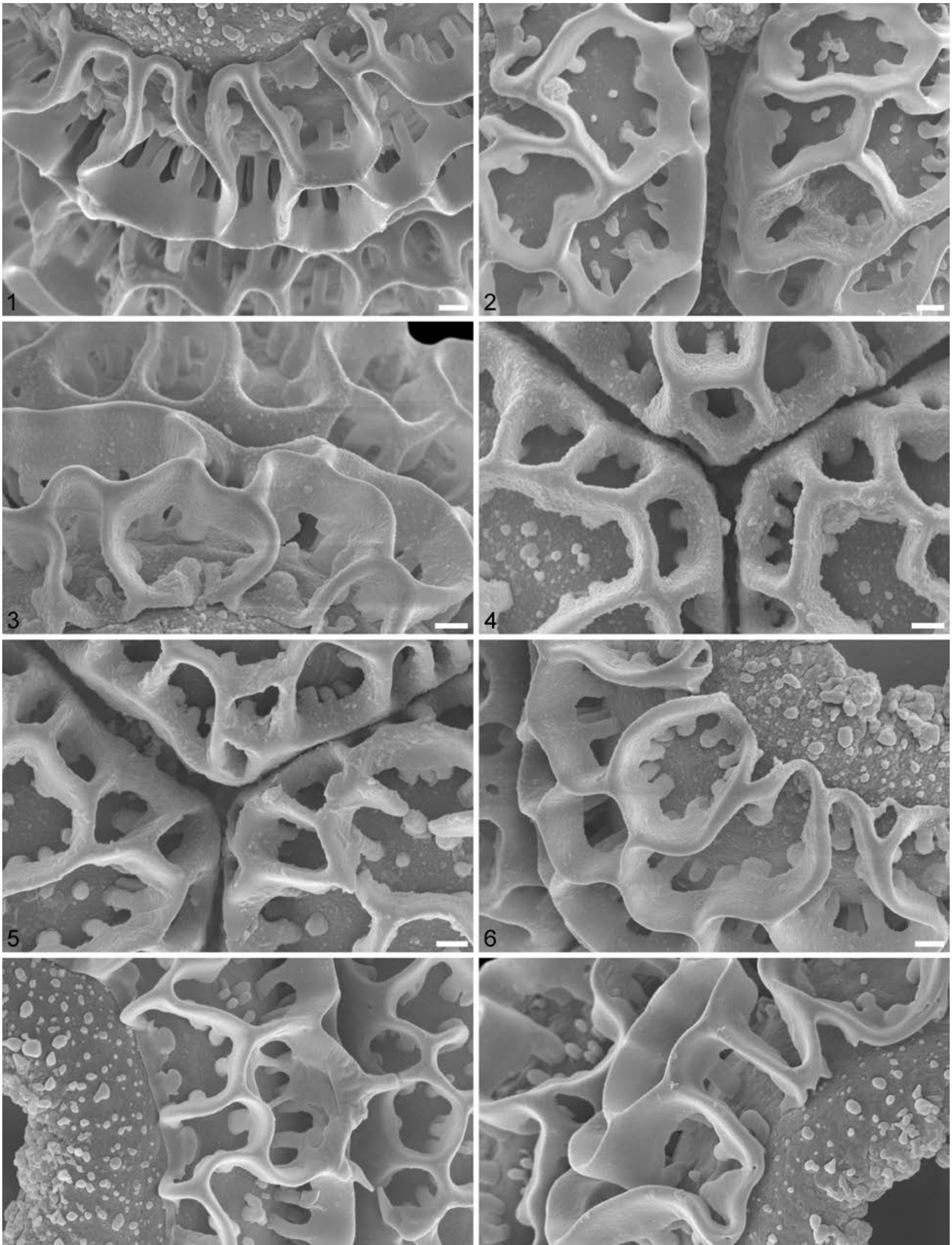

Plate 22. *Drimys confertifolia* Phil. (WU 0069300: from Chile); **1–8**. Close-ups of sculpture in SEM; **1**. Distal face of pollen; **2**, **3**. Pollen interface in lateral view; **4**, **5**. Pollen interface in basal view; **6–8**. Aperture region. Scale bars – 1 µm

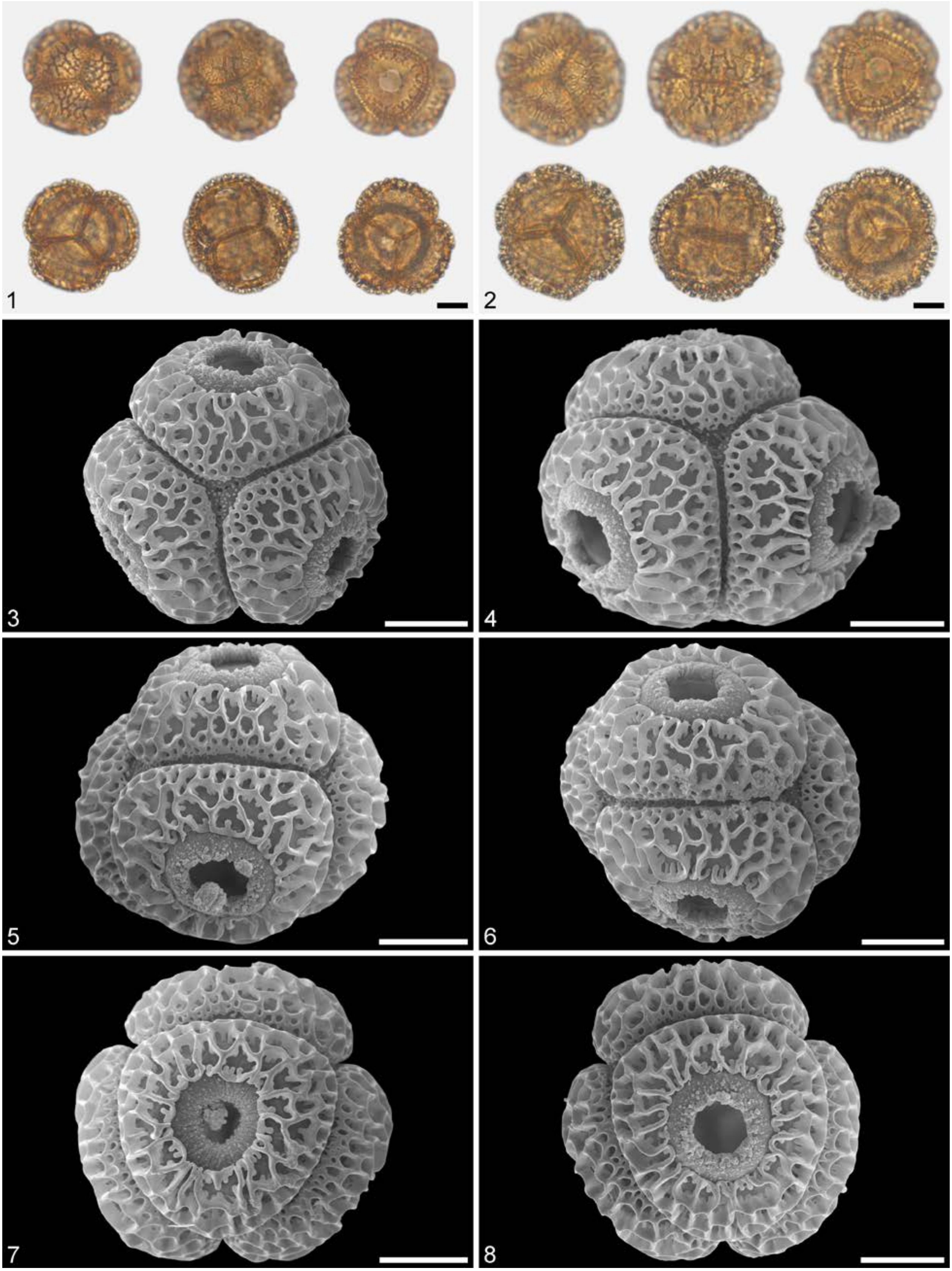

Plate 23. *Drimys granadensis* L. f. (W 1967–0009666: from Costa Rica); **1**, **2**. Pollen tetrads in LM, upper row at high focus, lower row in optical cross section, left tetrads in basal view, middle tetrads in lateral view, right tetrads in apical view; **3–8**. Pollen tetrads in SEM; **3**, **4**. Basal view; **5**, **6**. Lateral view; **7**, **8**. Apical view. Scale bars – 10 µm

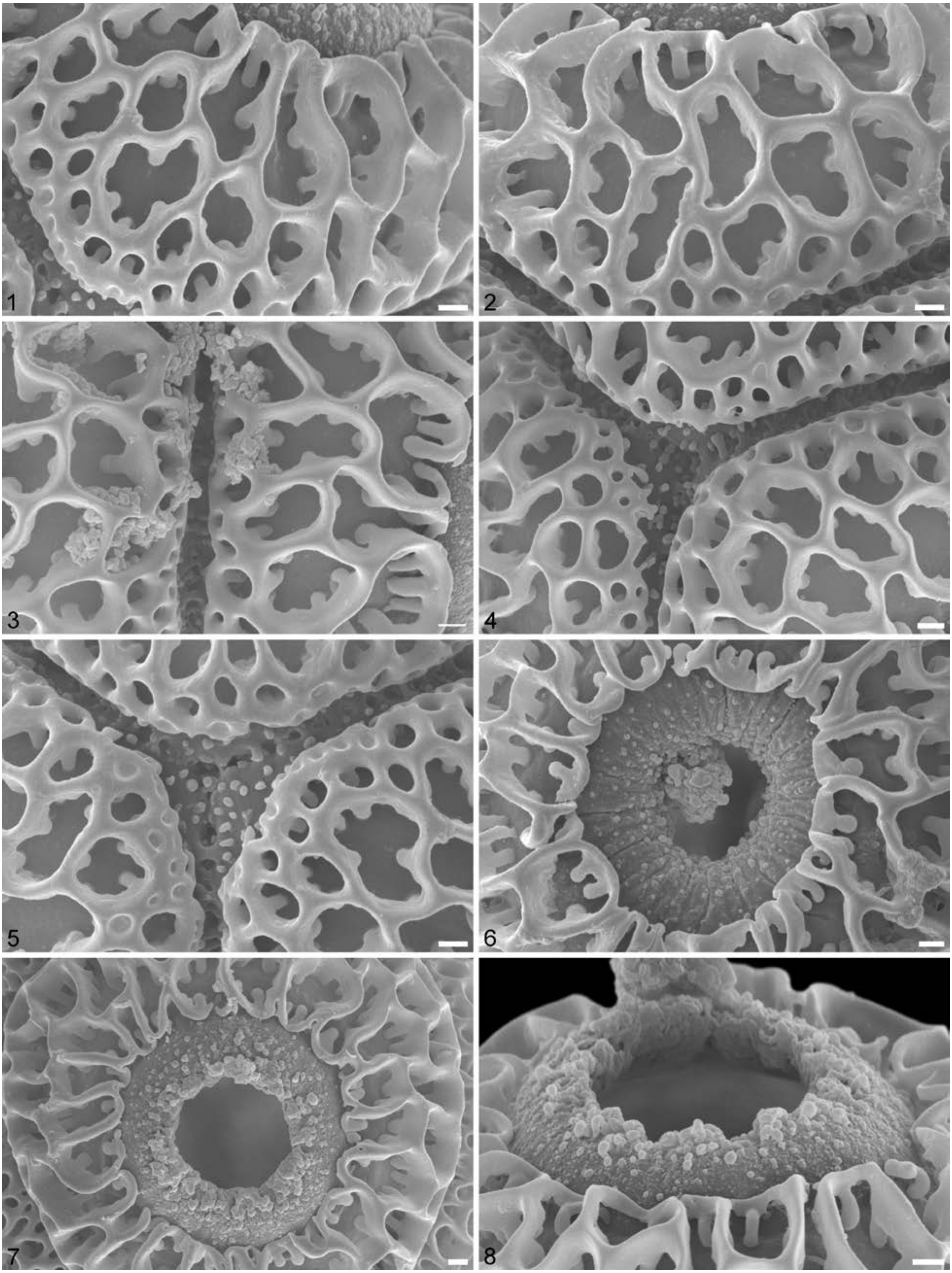

Plate 24. *Drimys granadensis* L. f. (W 1967–0009666: from Costa Rica); **1–8**. Close-ups of sculpture in SEM; **1**, **2**. Distal face of pollen; **3**. Pollen interface in lateral view; **4**, **5**. Pollen interface in basal view; **6–8**. Aperture. Scale bars – 1 µm

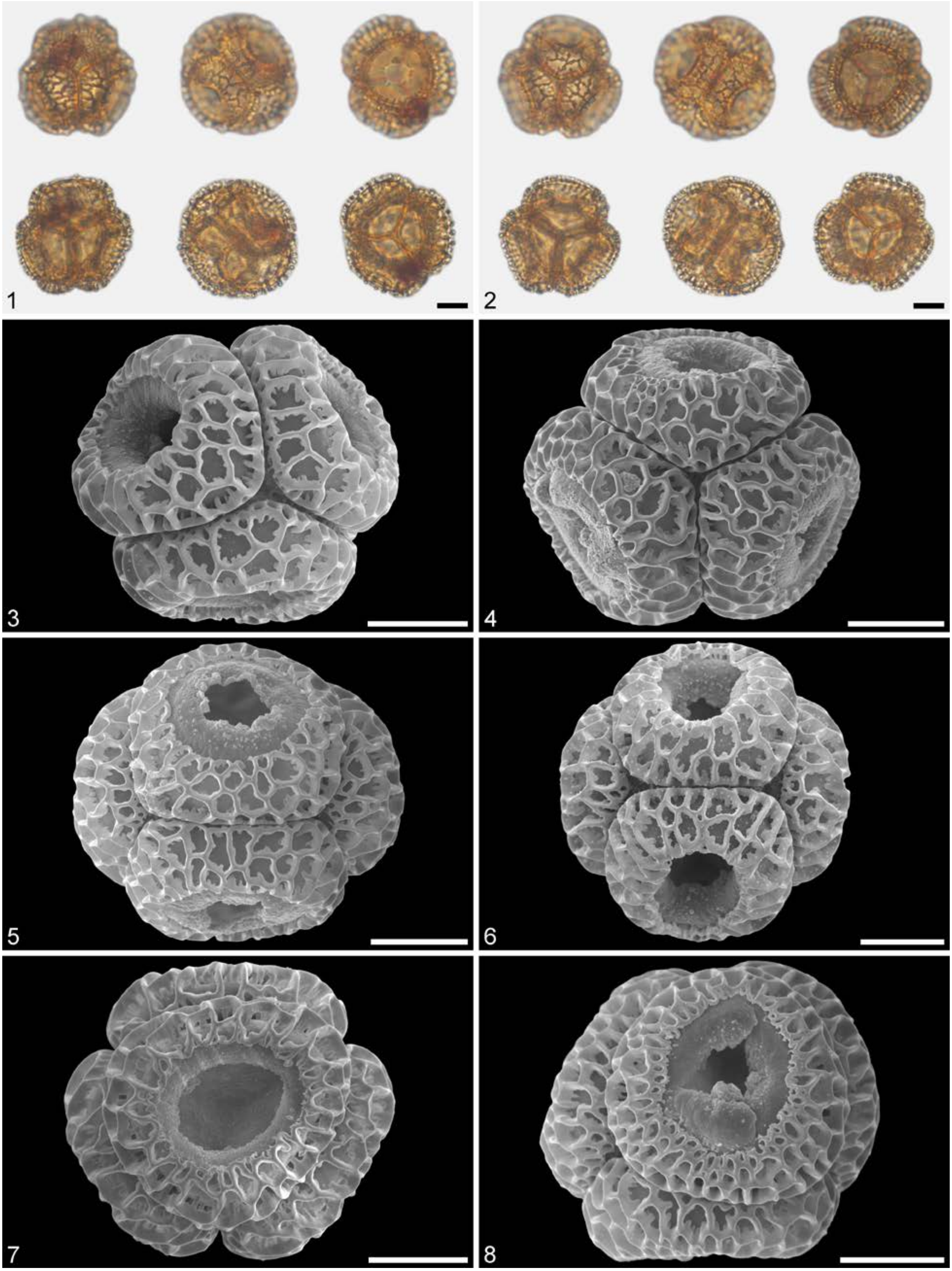

Plate 25. *Drimys winteri* J.R. Forst. & G. Forst. (W 1958–0022885: from Chile). **1**, **2**. Pollen tetrads in LM, upper row at high focus, lower row in optical cross section, left tetrads in basal view, middle tetrads in lateral view, right tetrads in apical view; **3–8**. Pollen tetrads in SEM; **3**, **4**. Basal view; **5**, **6**. Lateral view; **7**, **8**. Apical view. Scale bars – 10 μm

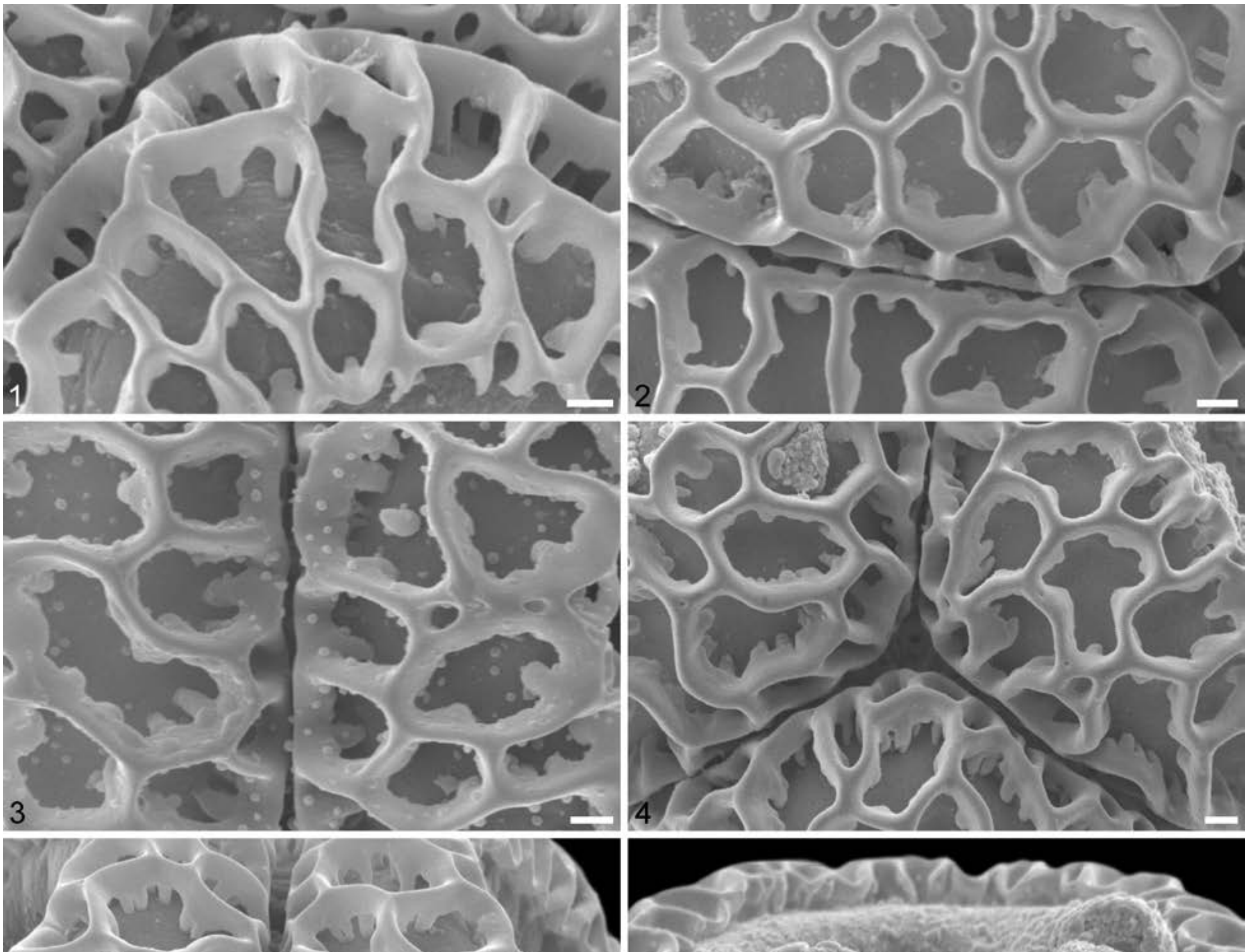

Plate 26. *Drimys winteri* J.R. Forst. & G. Forst. (W 1958–0022885: from Chile); **1–8**. Close-ups of sculpture in SEM; **1**. Distal face of pollen; **2**, **3**. Pollen interface in lateral view; **4**, **5**. Pollen interface in basal view; **6–8**. Aperture. Scale bars – 1 µm

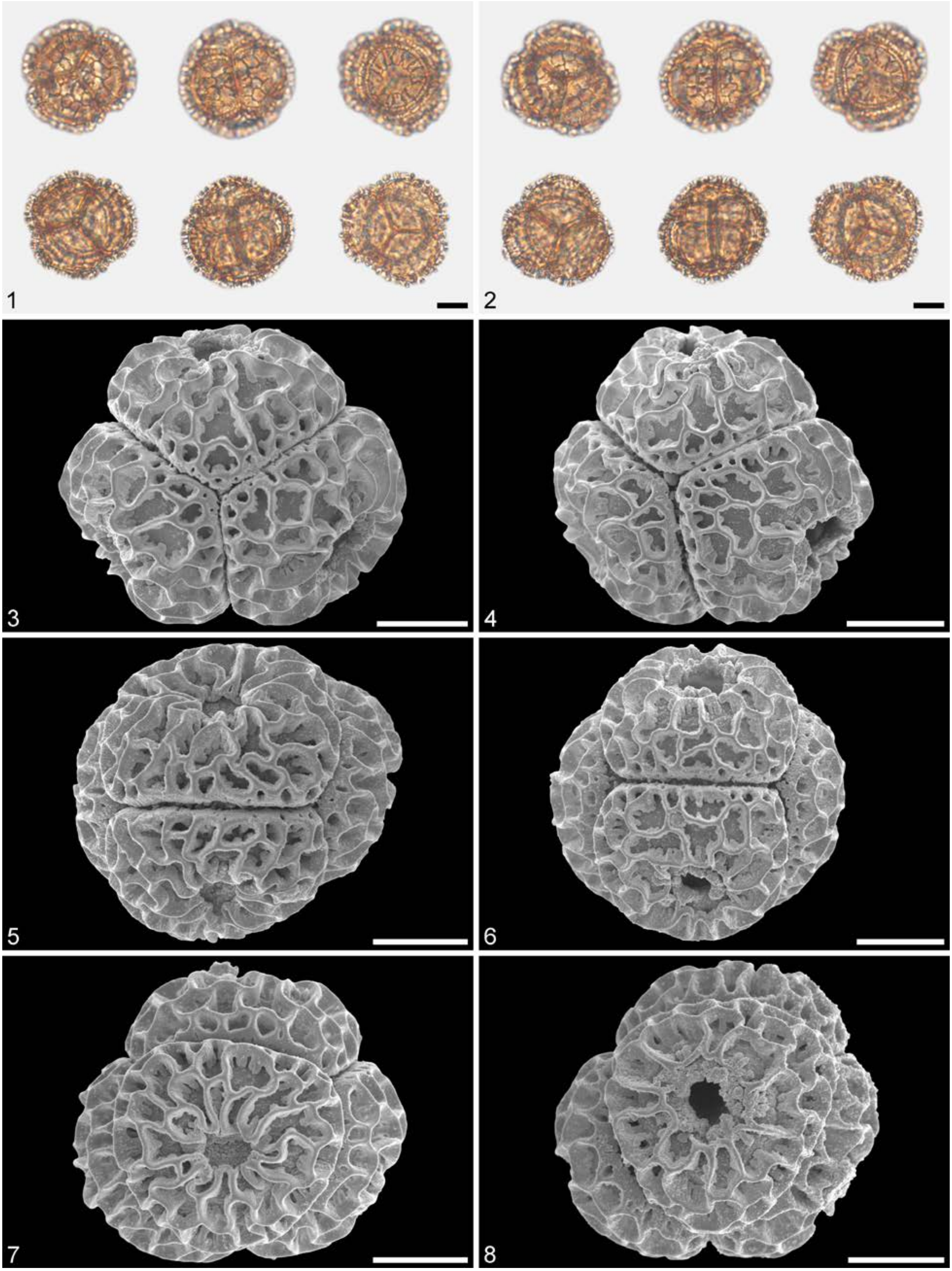

Plate 27. *Pseudowintera axillaris* (J.R. Forst. & G.Forst) Dandy (WELT SP025419: from New Zealand); **1**, **2**. Pollen tetrads in LM, upper row at high focus, lower row in optical cross section, left tetrads in basal view, middle tetrads in lateral view, right tetrads in apical view; **3–8**. Pollen tetrads in SEM; **3**, **4**. Basal view; **5**, **6**. Lateral view; **7**, **8**. Apical view. Scale bars – 10 µm

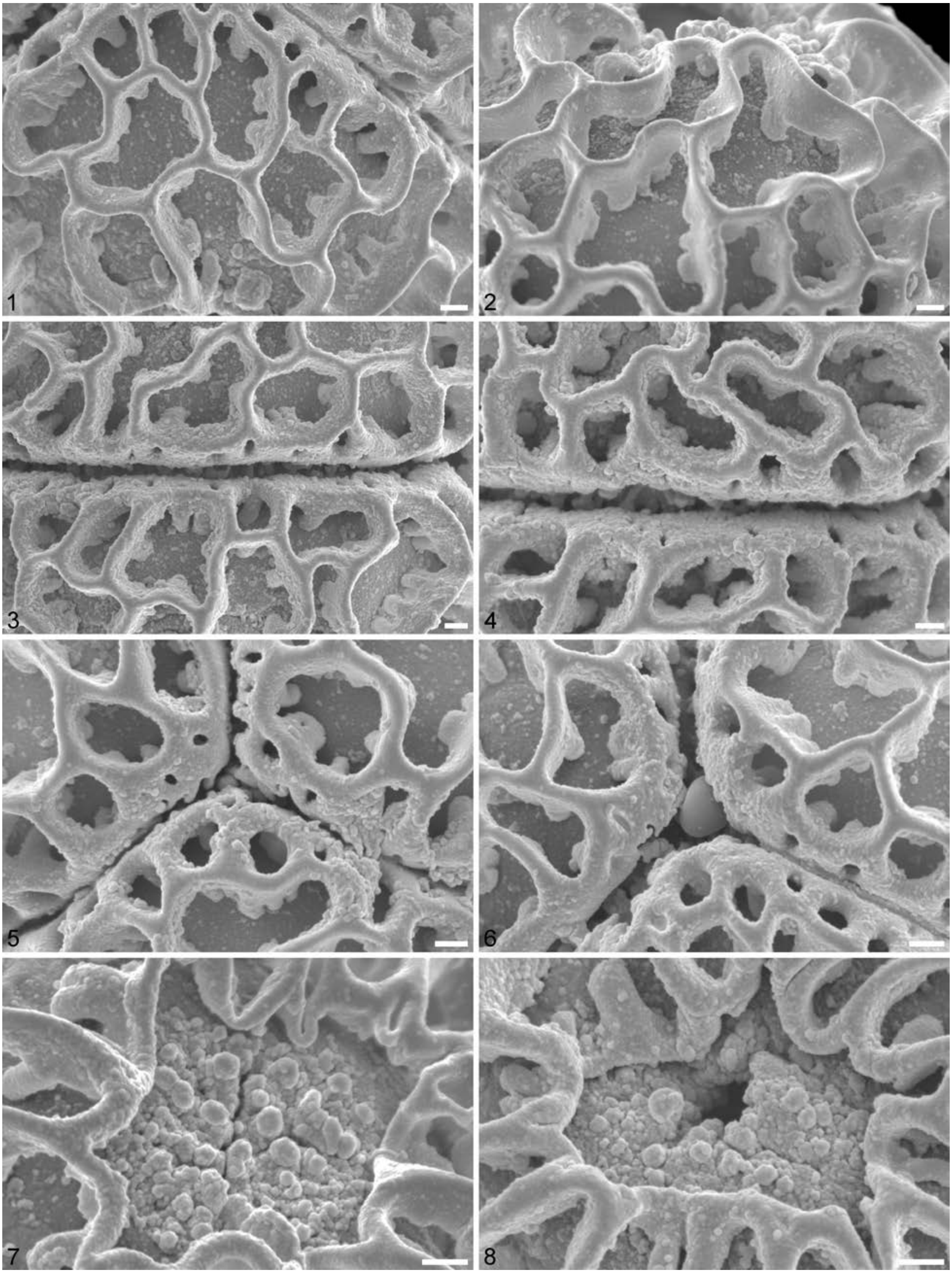

Plate 28. *Pseudowintera axillaris* (J.R. Forst. & G.Forst) Dandy (WELT SP025419: from New Zealand); **1–8**. Close-ups of sculpture in SEM; **1**, **2**. Distal face of pollen; **3**, **4**. Pollen interface in lateral view; **5**, **6**. Pollen interface in basal view; **7**, **8**. Aperture. Scale bars – 1 µm

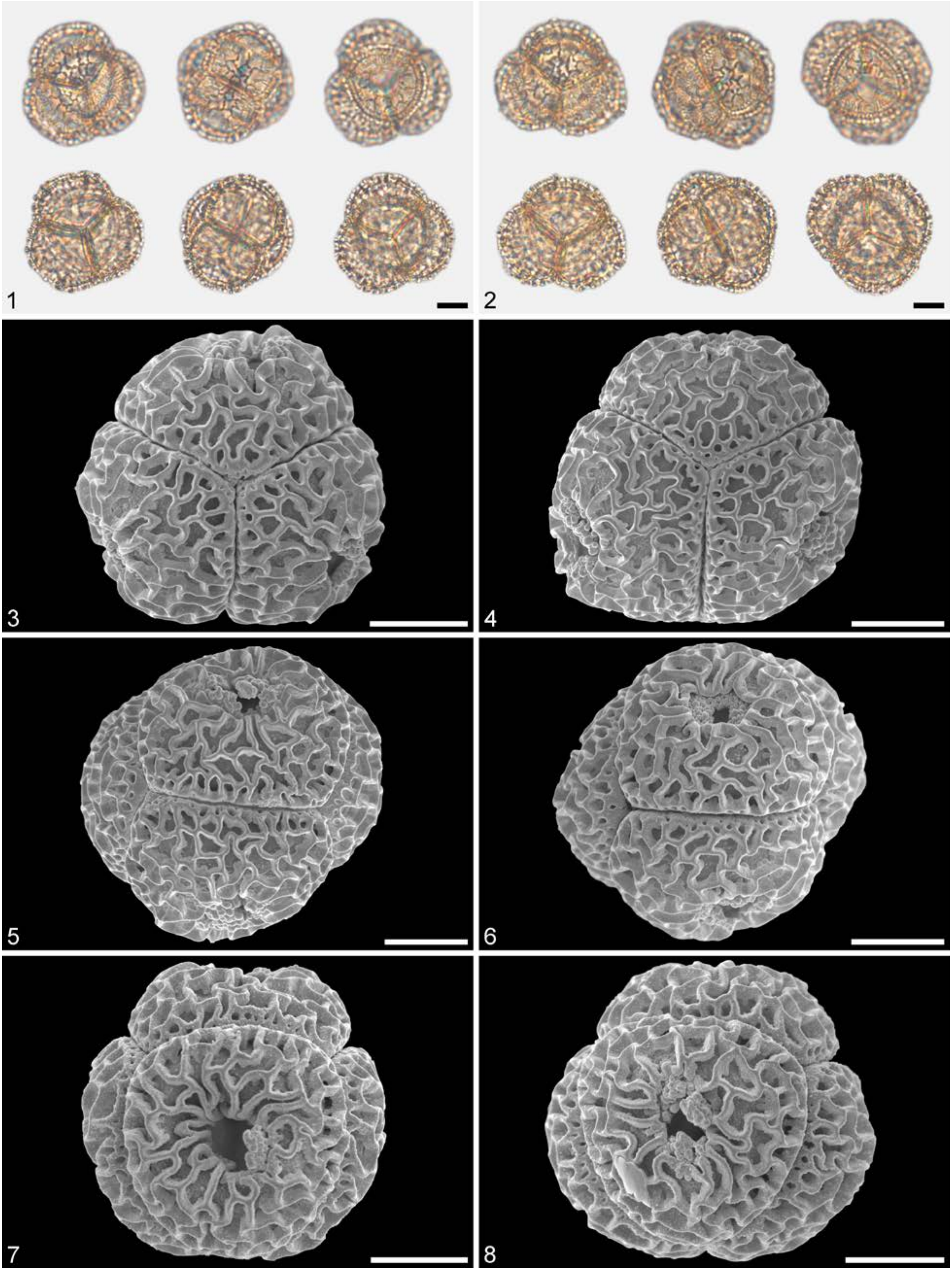

Plate 29. *Pseudowintera colorata* (Raoul) Dandy (WELT SP001218: from New Zealand); **1**, **2**. Pollen tetrads in LM, upper row at high focus, lower row in optical cross section, left tetrads in basal view, middle tetrads in lateral view, right tetrads in apical view; **3–8**. Pollen tetrads in SEM; **3**, **4**. Basal view; **5**, **6**. Lateral view; **7**, **8**. Apical view. Scale bars – 10 µm

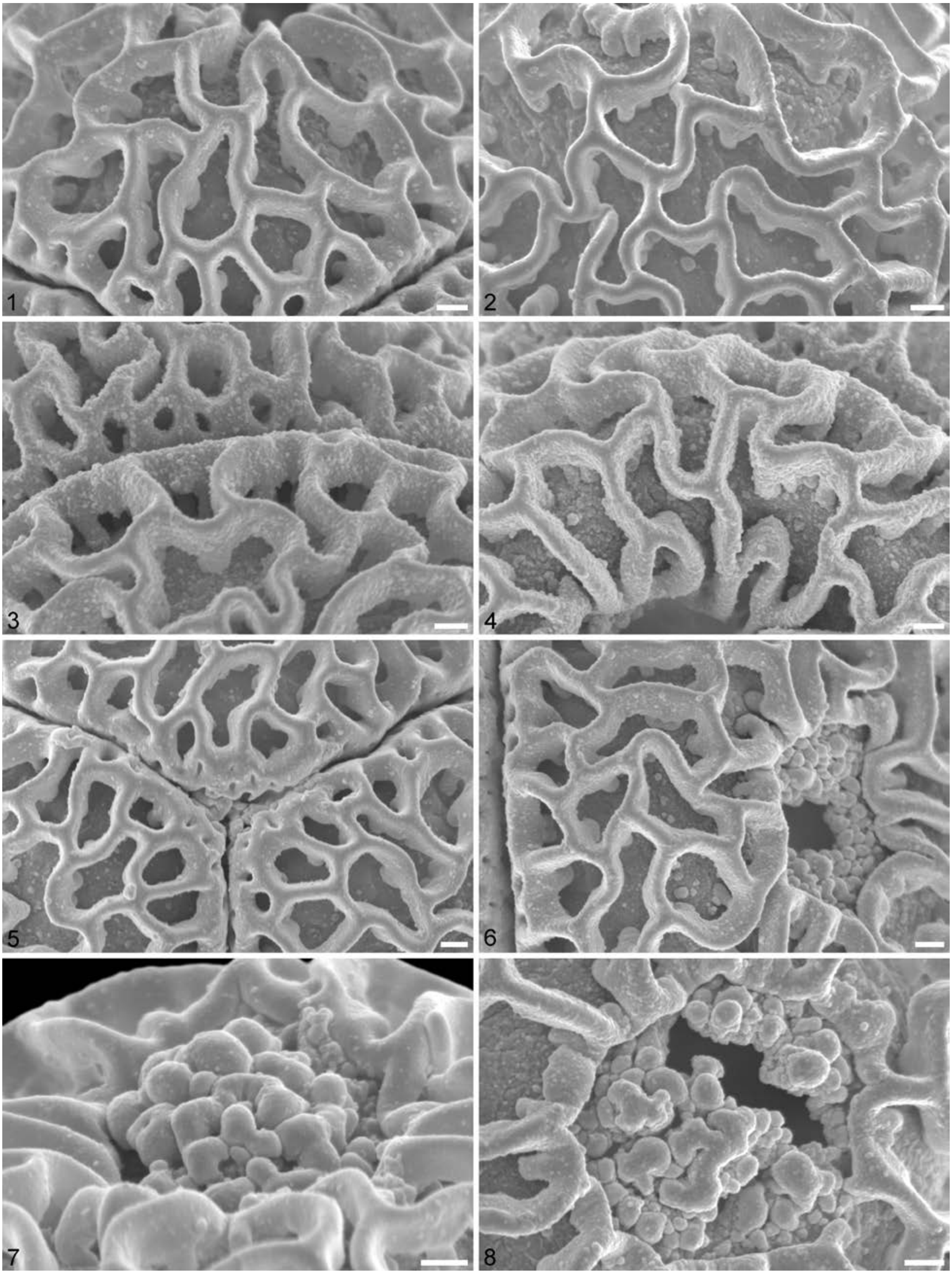

Plate 30. *Pseudowintera colorata* (Raoul) Dandy (WELT SP001218: from New Zealand); **1–8**. Close-ups of sculpture in SEM; **1**, **2**. Distal face of pollen; **3**. Pollen interface in lateral view; **4**. Distal face of pollen; **5**. Pollen interface in basal view; **6–8**. Aperture. Scale bars – 1 µm

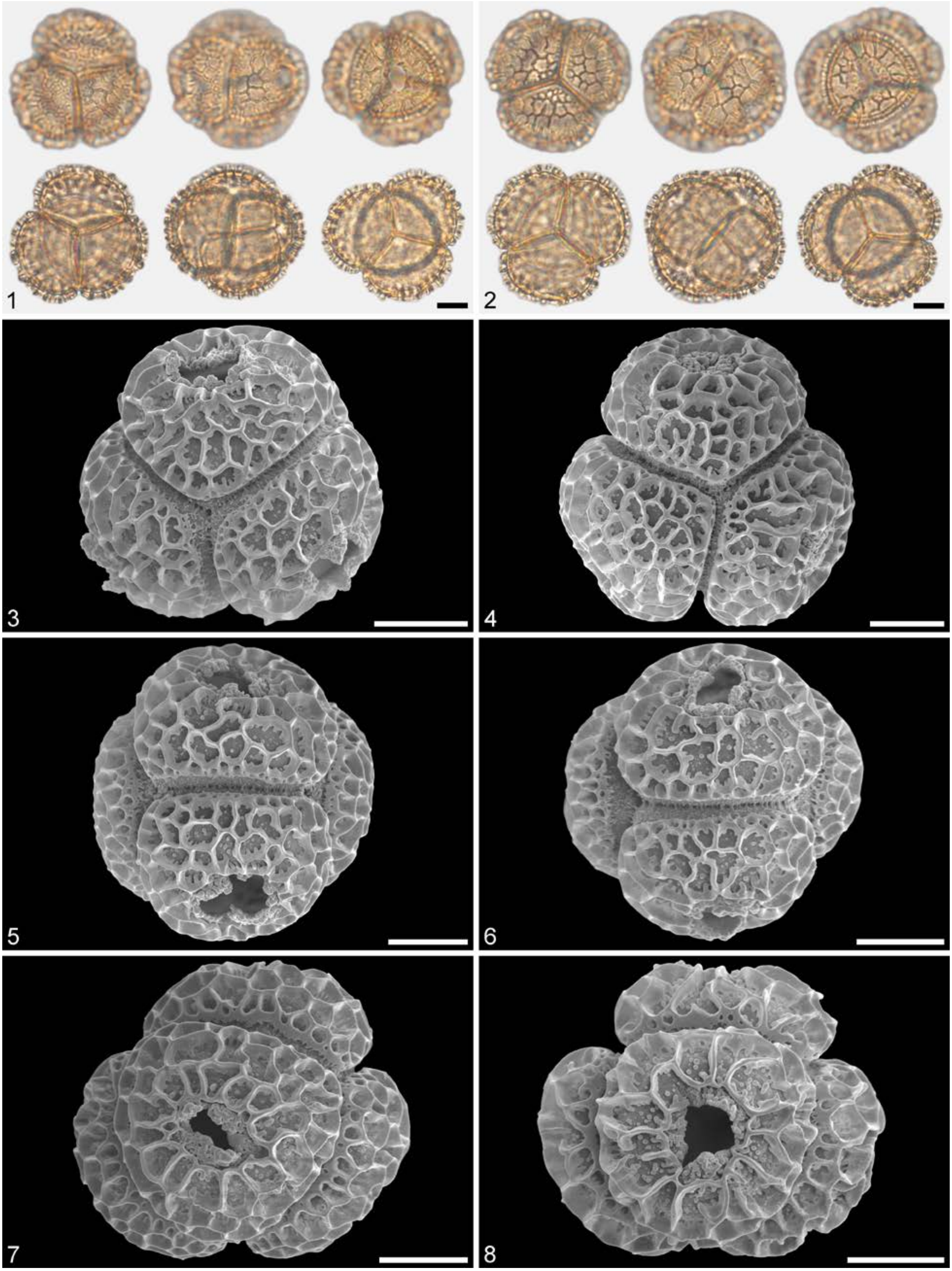

Plate 31. *Pseudowintera traversii* (Buchanan) Dandy (W: from New Zealand, coll. unknown, s.n.); **1**, **2**. Pollen tetrads in LM, upper row at high focus, lower row in optical cross section, left tetrads in basal view, middle tetrads in lateral view, right tetrads in apical view; **3–**8. Pollen tetrads in SEM; **3**, **4**. Basal view; **5**, **6**. Lateral view; **7**, **8**. Apical view. Scale bars – 10 µm

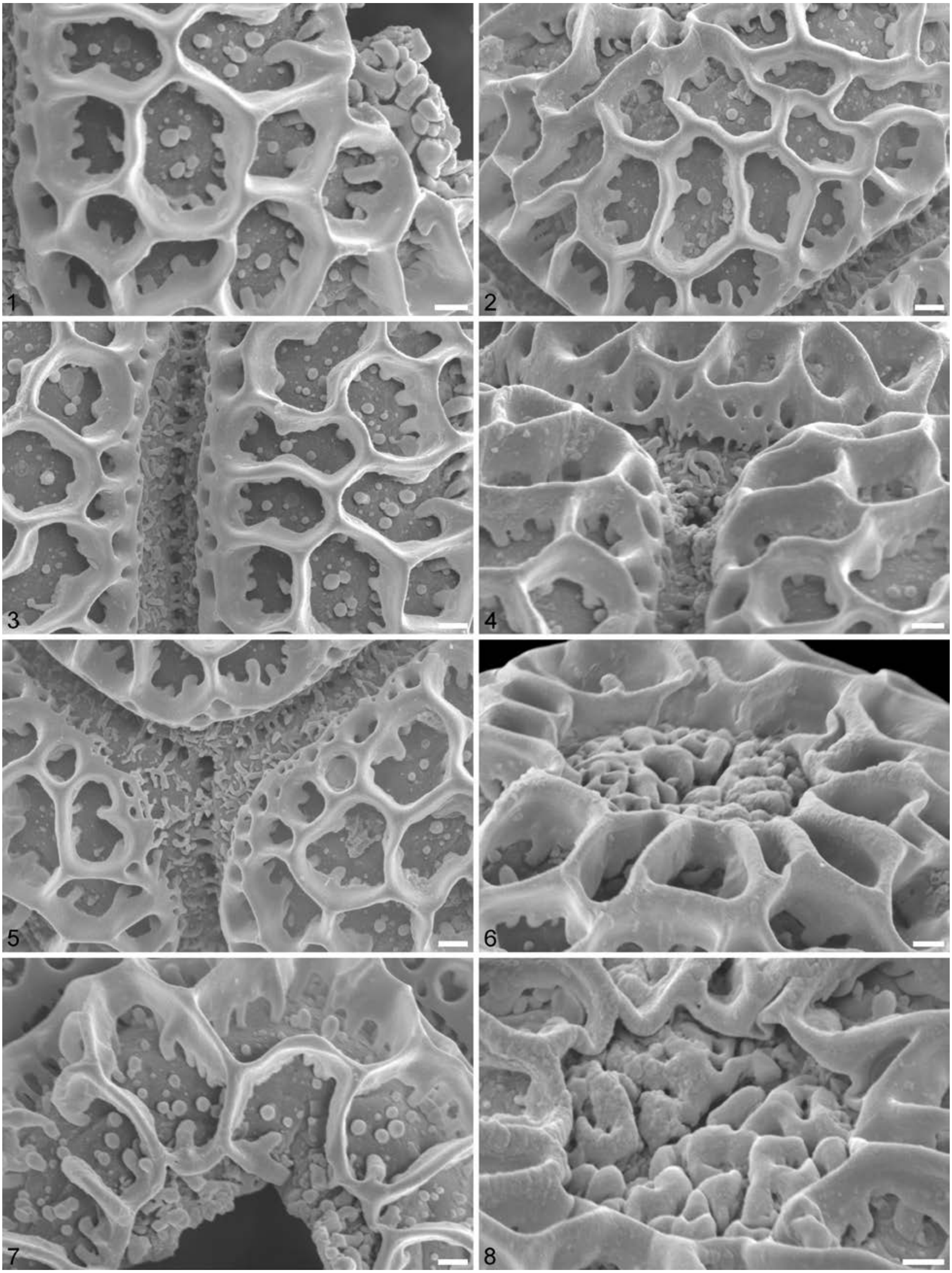

Plate 32. *Pseudowintera traversii* (Buchanan) Dandy (W: from New Zealand, coll. unknown, s.n.); **1–8**. Close-ups of sculpture in SEM; **1**, **2**. Distal face of pollen; **3**. Pollen interface in lateral view; **4**, **5**. Pollen interface in basal view; **6–8**. Aperture region. Scale bars – 1 µm

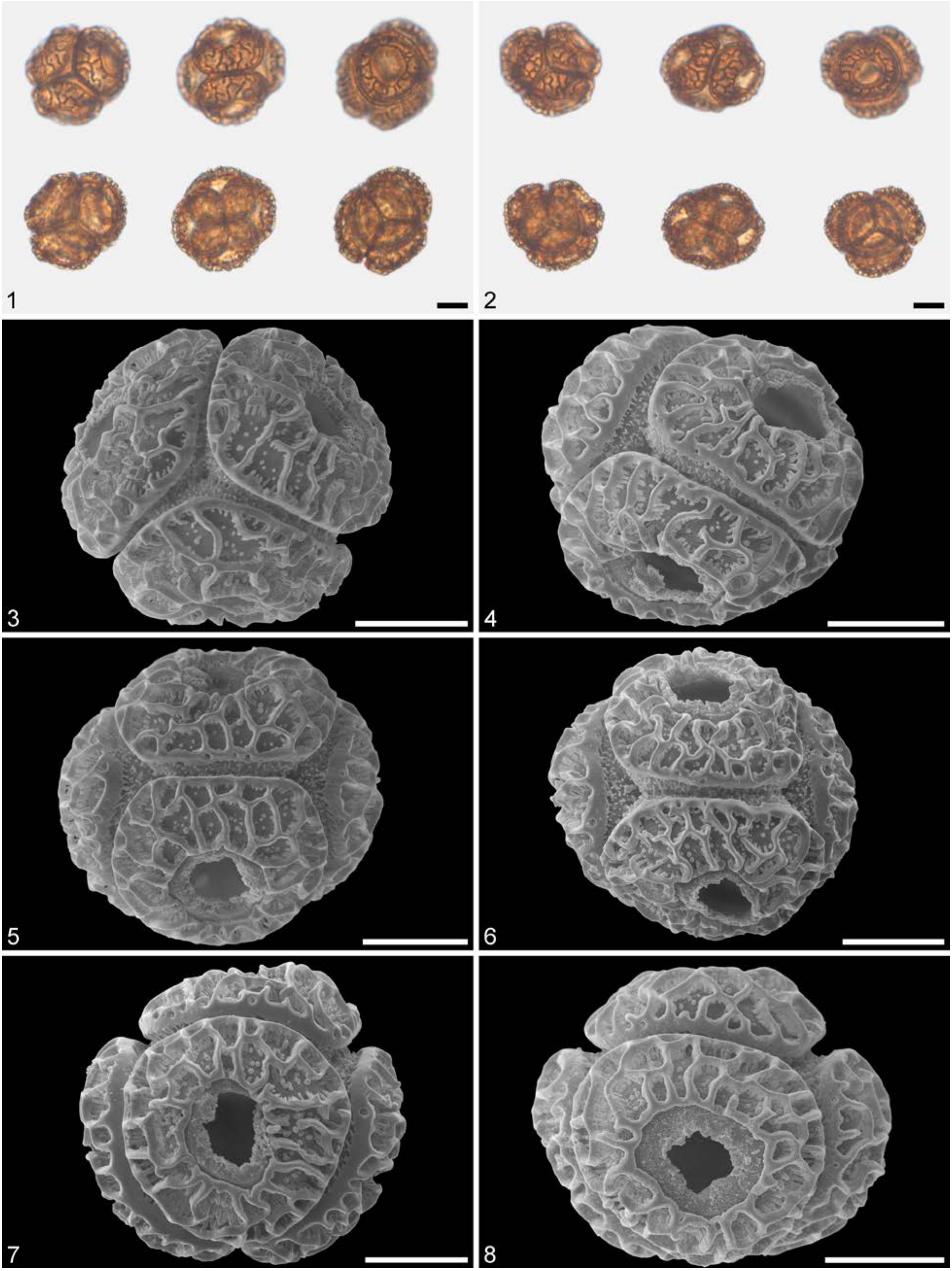

Plate 33. *Bubbia howeana* (F.Muell.) Tiegh. (WU 0029084: from Lord Howe's Island, Australia.); **1**, **2**. Pollen tetrads in LM, upper row at high focus, lower row in optical cross section, left tetrads in basal view, middle tetrads in lateral view, right tetrads in apical view; **3–8**. Pollen tetrads in SEM; **3**, **4**. Basal view; **5**, **6**. Lateral view; **7**, **8**. Apical view. Scale bars – 10 µm

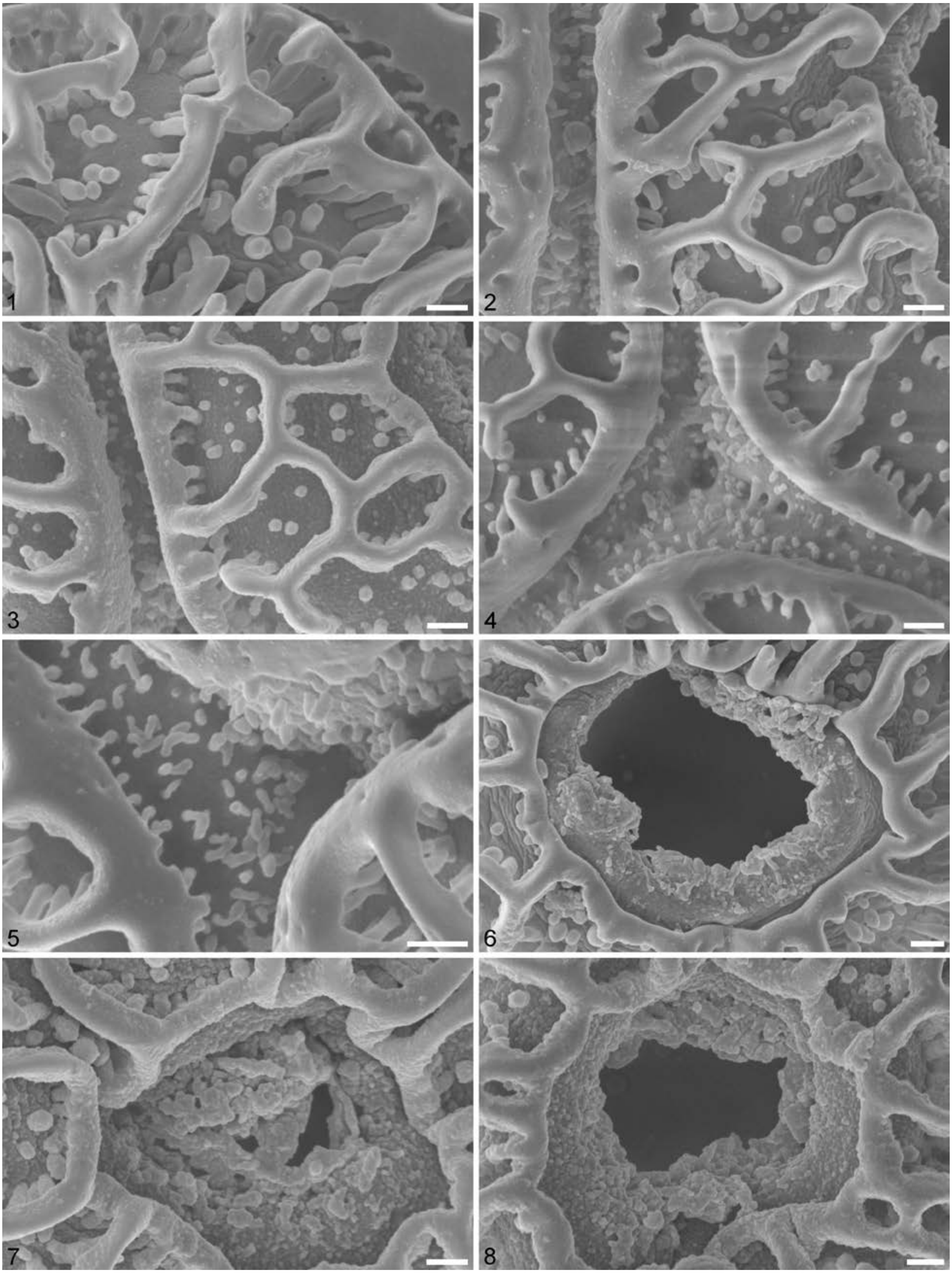

Plate 34. *Bubbia howeana* (F.Muell.) Tiegh. (WU 0029084: from Lord Howe's Island, Australia.); **1–8**. Close-ups of sculpture in SEM; **1**, **2**. Distal face of pollen; **3**. Pollen interface in lateral view; **4**, **5**. Pollen interface in basal view; **6–8**. Aperture. Scale bars – 1 µm

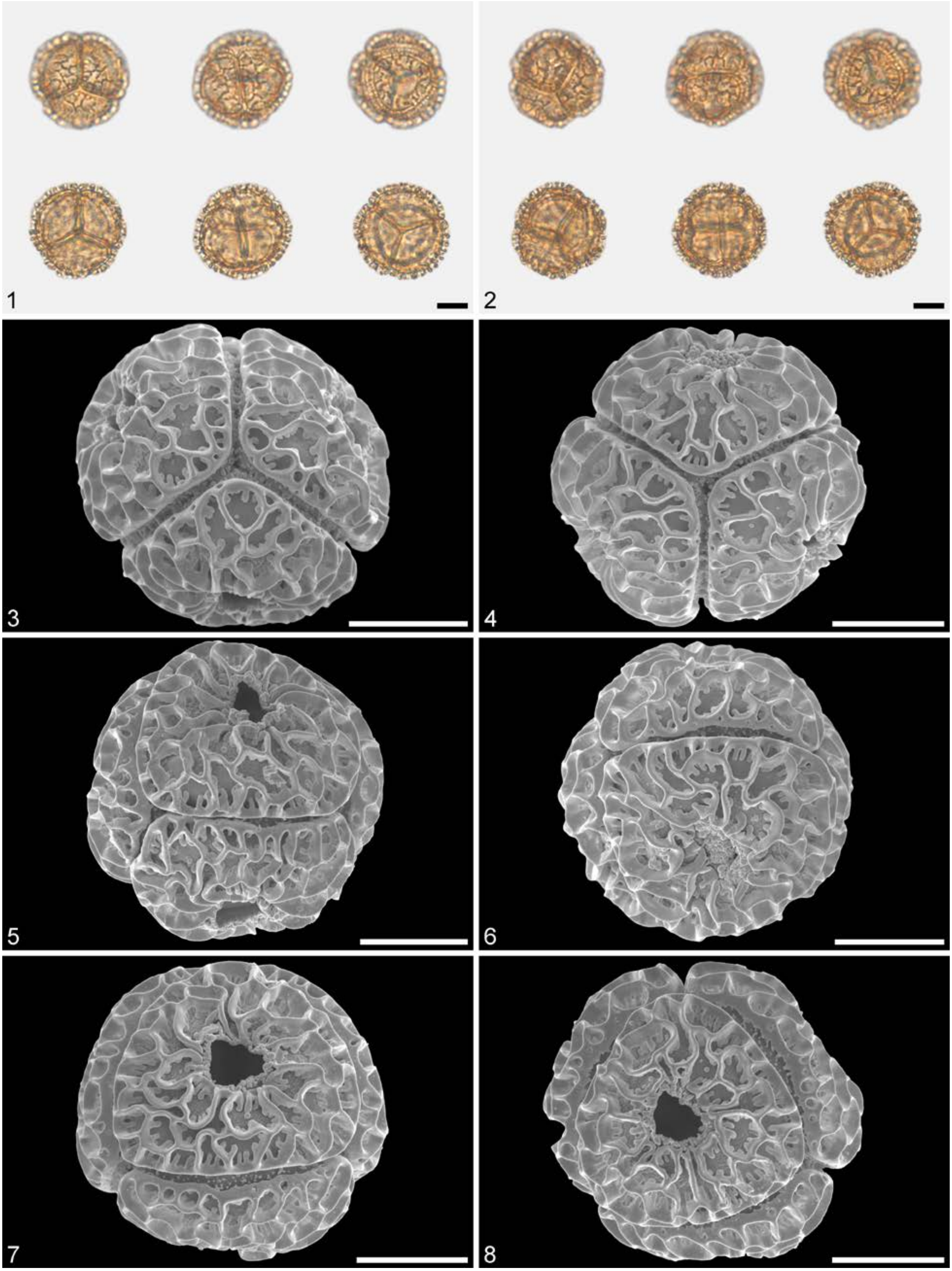

Plate 35. *Zygogynum comptonii* (Baker f.) Vink (MO: from New Caledonia, Coll. Ph. Morat, s.n.); **1**, **2**. Pollen tetrads in LM, upper row at high focus, lower row in optical cross section, left tetrads in basal view, middle tetrads in lateral view, right tetrads in apical view; **3–8**. Pollen tetrads in SEM; **3**, **4**. Basal view; **5**, **6**. Lateral view; **7**, **8**. Apical view. Scale bars – 10 µm

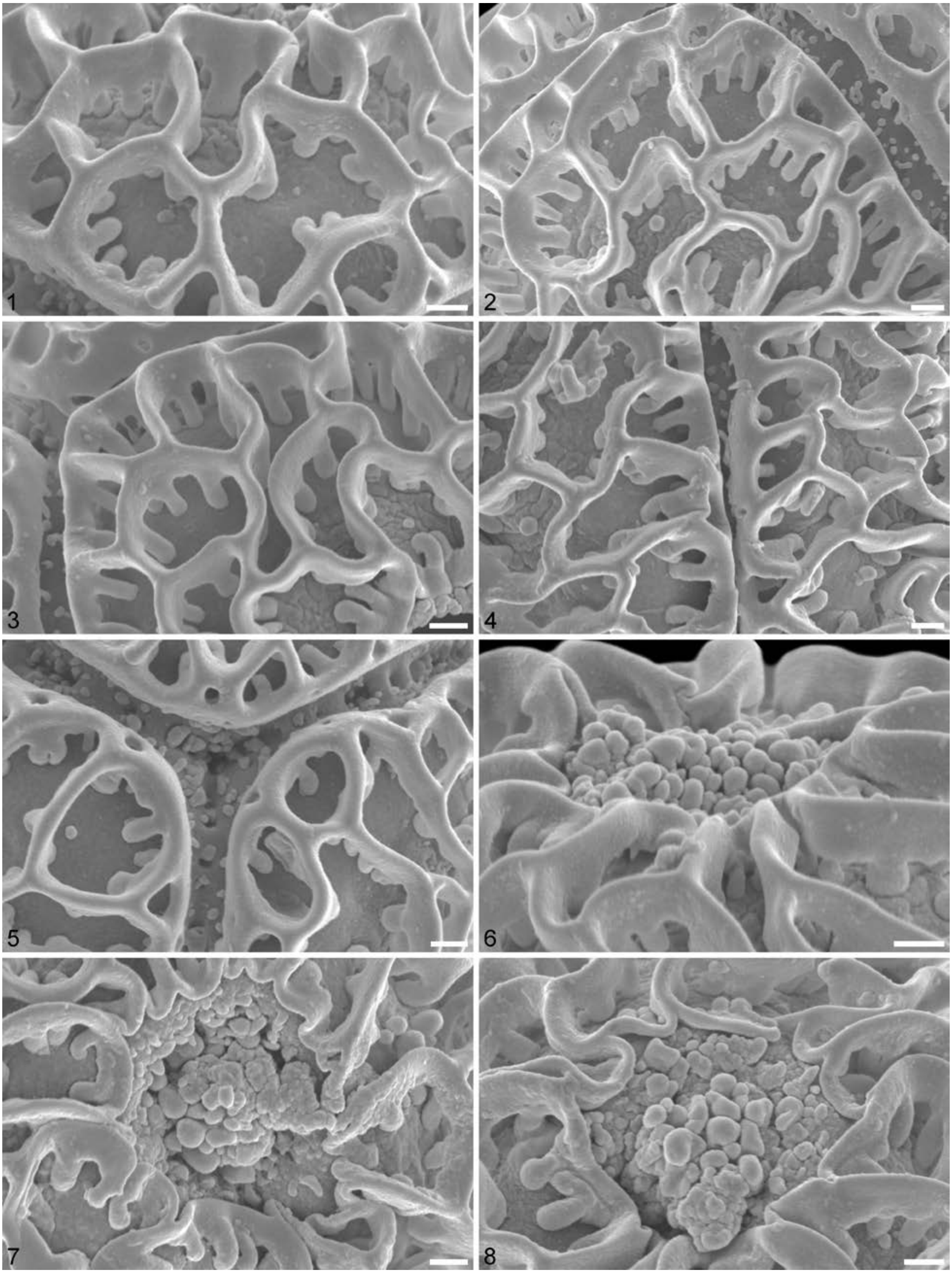

Plate 36. *Zygogynum comptonii* (Baker f.) Vink (MO: from New Caledonia, Coll. Ph. Morat, s.n.); **1–8**. Close-ups of sculpture in SEM; **1–3**. Distal face of pollen; **4**. Pollen interface in lateral view; **5**. Pollen interface in basal view; **6–8**. Aperture. Scale bars – 1 µm

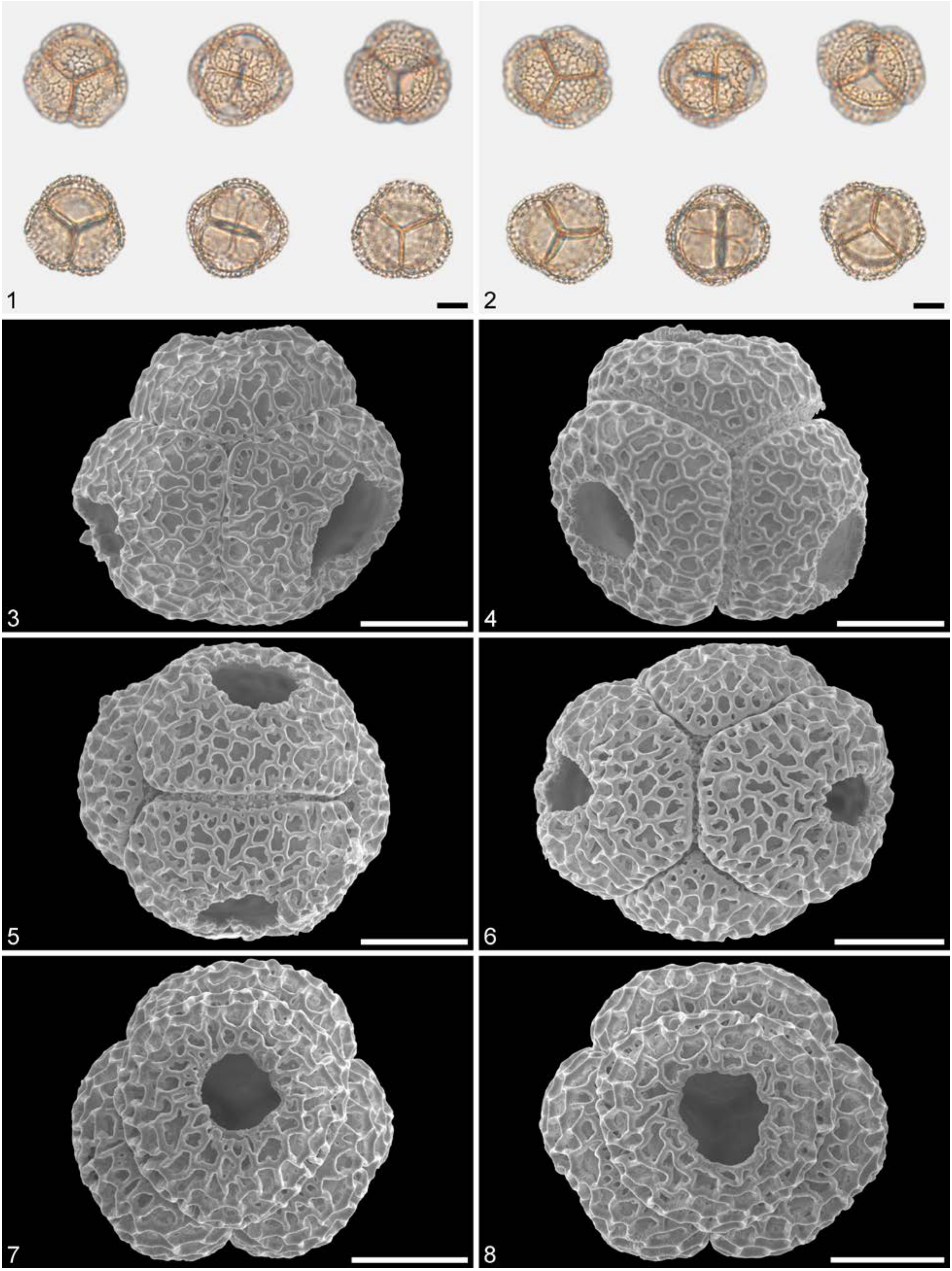

Plate 37. *Zygogynum amplexicaule* (Vieill. ex P.Parm.) Vink (MO: from New Caledonia, Coll. G. MacPerson, s.n.); **1**, **2**. Pollen tetrads in LM, upper row at high focus, lower row in optical cross section, left tetrads in basal view, middle tetrads in lateral view, right tetrads in apical view; **3–8**. Pollen tetrads in SEM; **3**, **4**. Basal view; **5**, **6**. Lateral view; **7**, **8**. Apical view. Scale bars – 10 µm

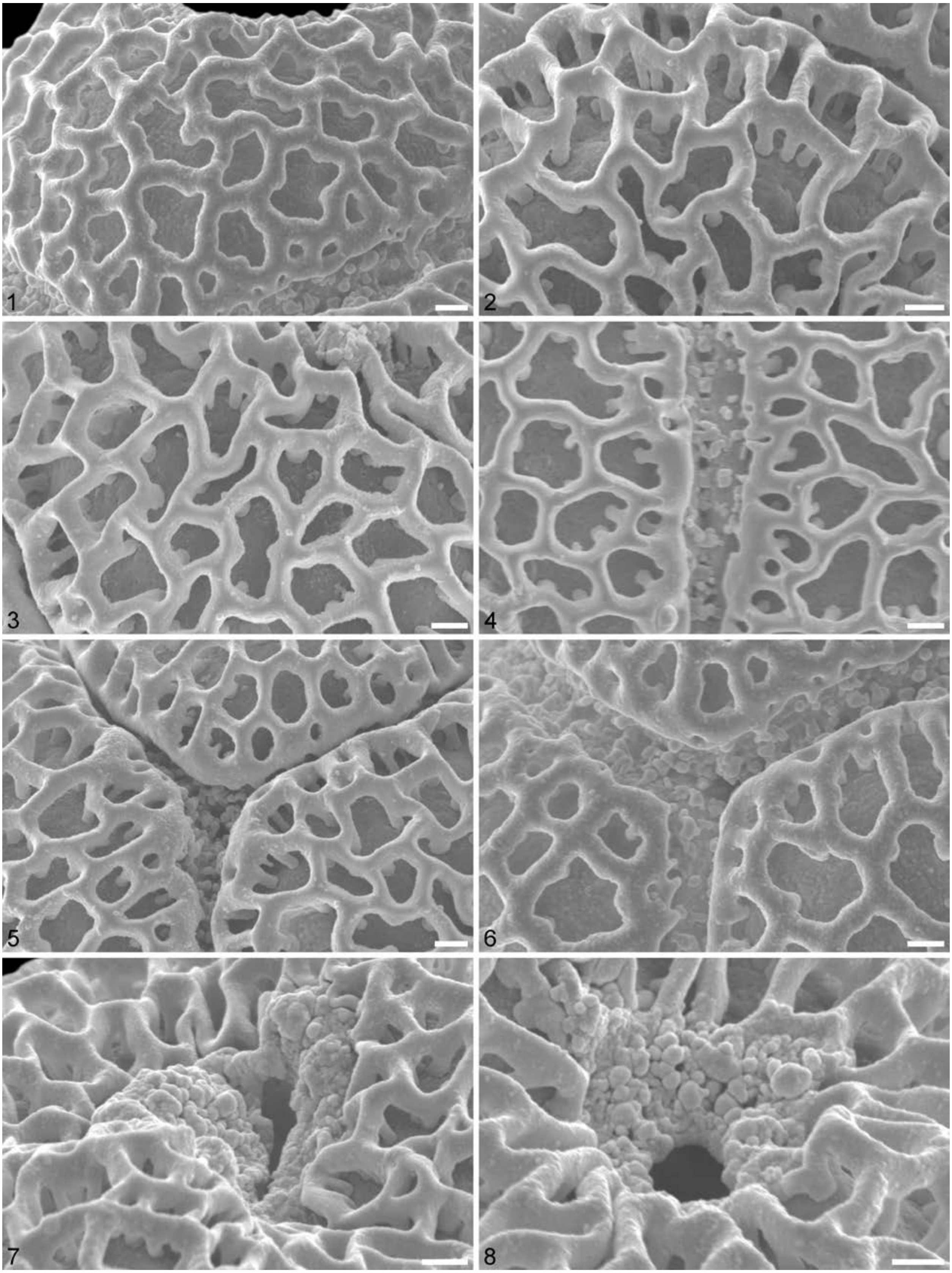

Plate 38. *Zygogynum amplexicaule* (Vieill. ex P.Parm.) Vink (MO: from New Caledonia, Coll. G. MacPerson, s.n.); **1–8**. Close-ups of sculpture in SEM; **1–3**. Distal face of pollen; **4**. Pollen interface in lateral view; **5**, **6**. Pollen interface in basal view; **7**, **8**. Aperture. Scale bars – 1 µm

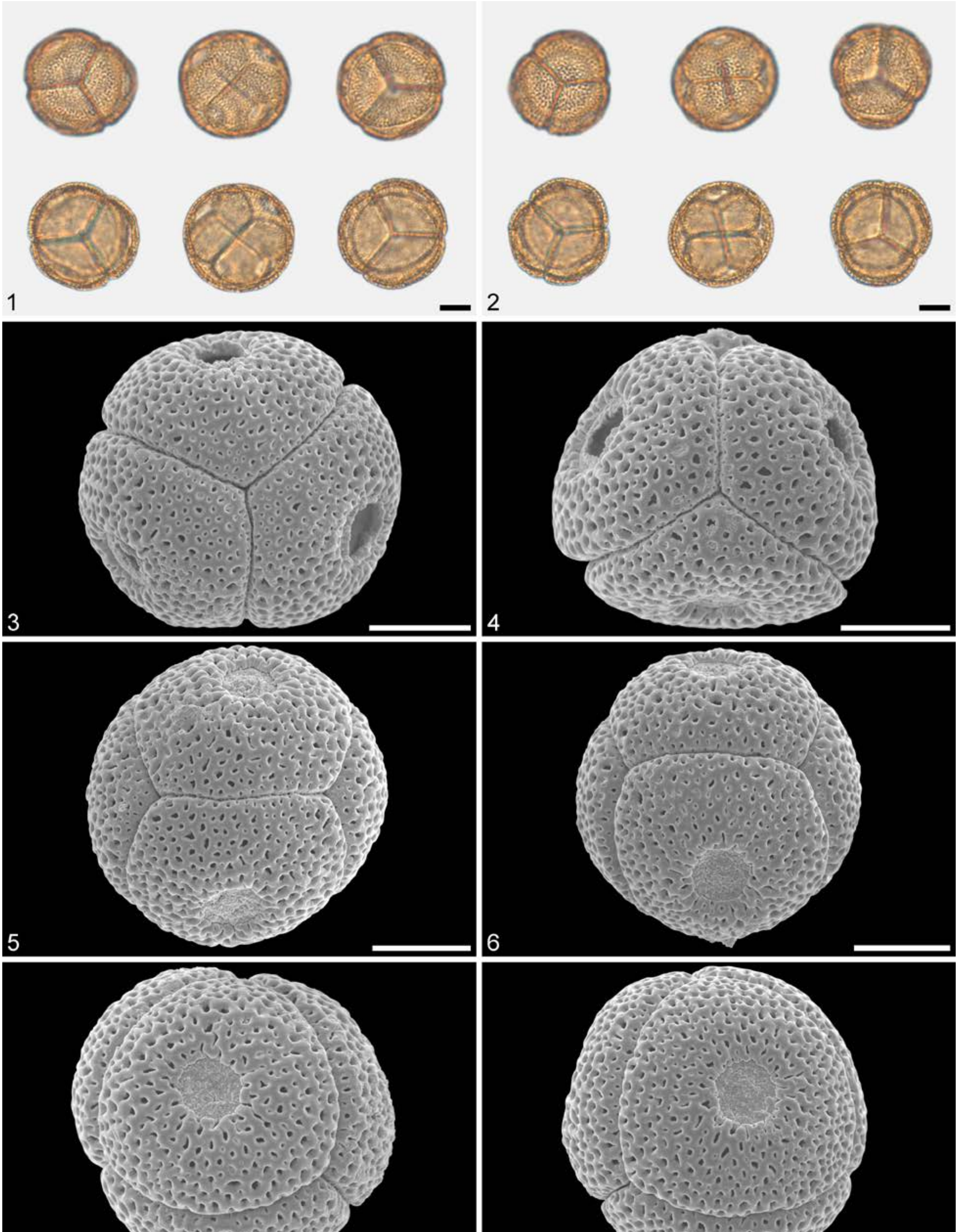

Plate 39. *Exospermum stipitatum* (Baill.) Tiegh. (MO: from New Caledonia, Coll. G. MacPerson, s.n.); **1**, **2**. Pollen tetrads in LM, upper row at high focus, lower row in optical cross section, left tetrads in basal view, middle tetrads in lateral view, right tetrads in apical view; **3–8**. Pollen tetrads in SEM; **3**, **4**. Basal view; **5**, **6**. Lateral view; **7**, **8**. Apical view. Scale bars – 10 µm

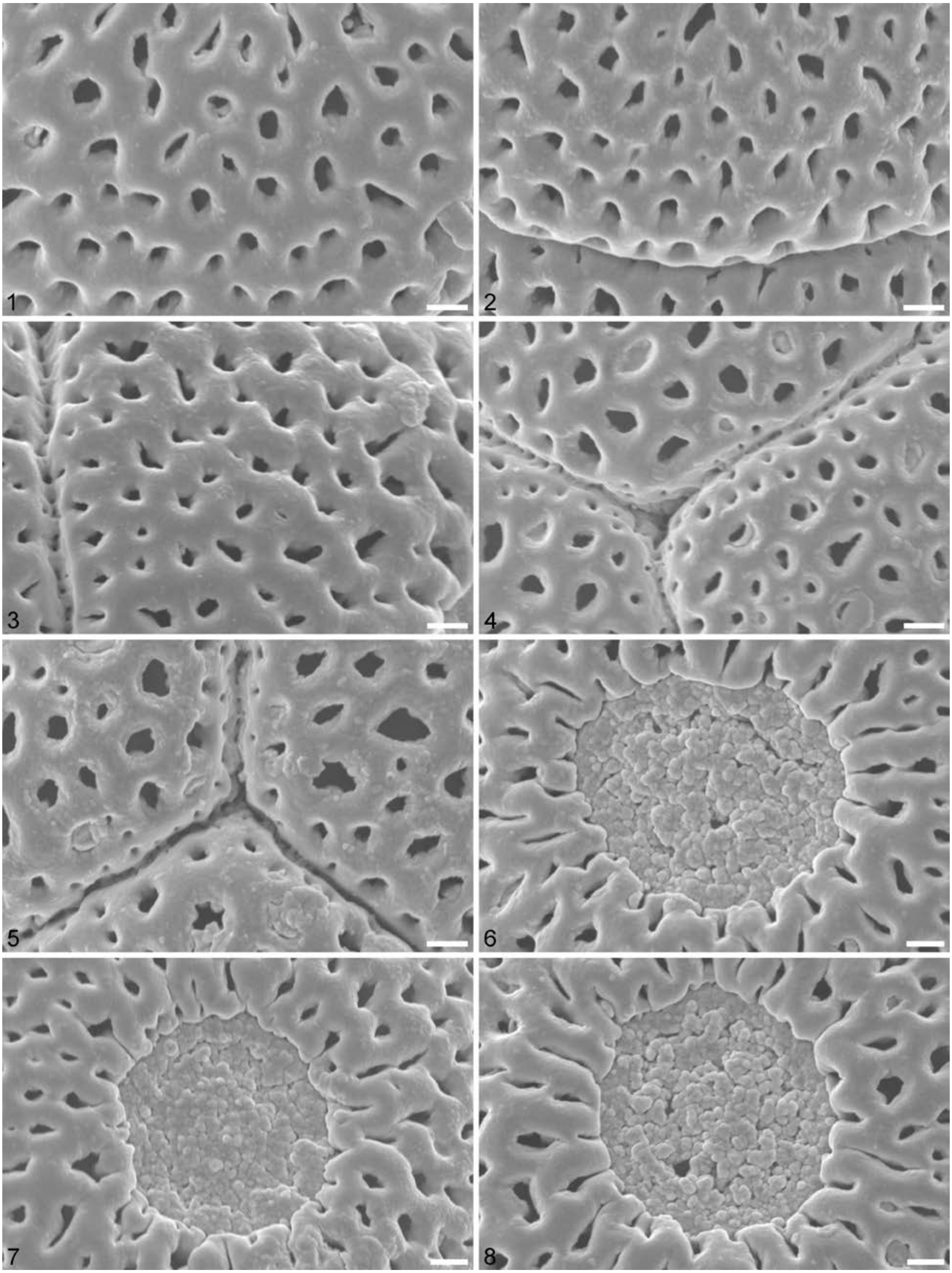

Plate 40. *Exospermum stipitatum* (Baill.) Tiegh. (MO: from New Caledonia, Coll. G. MacPerson, s.n.); **1–8**. Close-ups of sculpture in SEM; **1–3**. Distal face of pollen; **4**, **5**. Pollen interface in basal view; **6–8**. Aperture. Scale bars – 1 µm

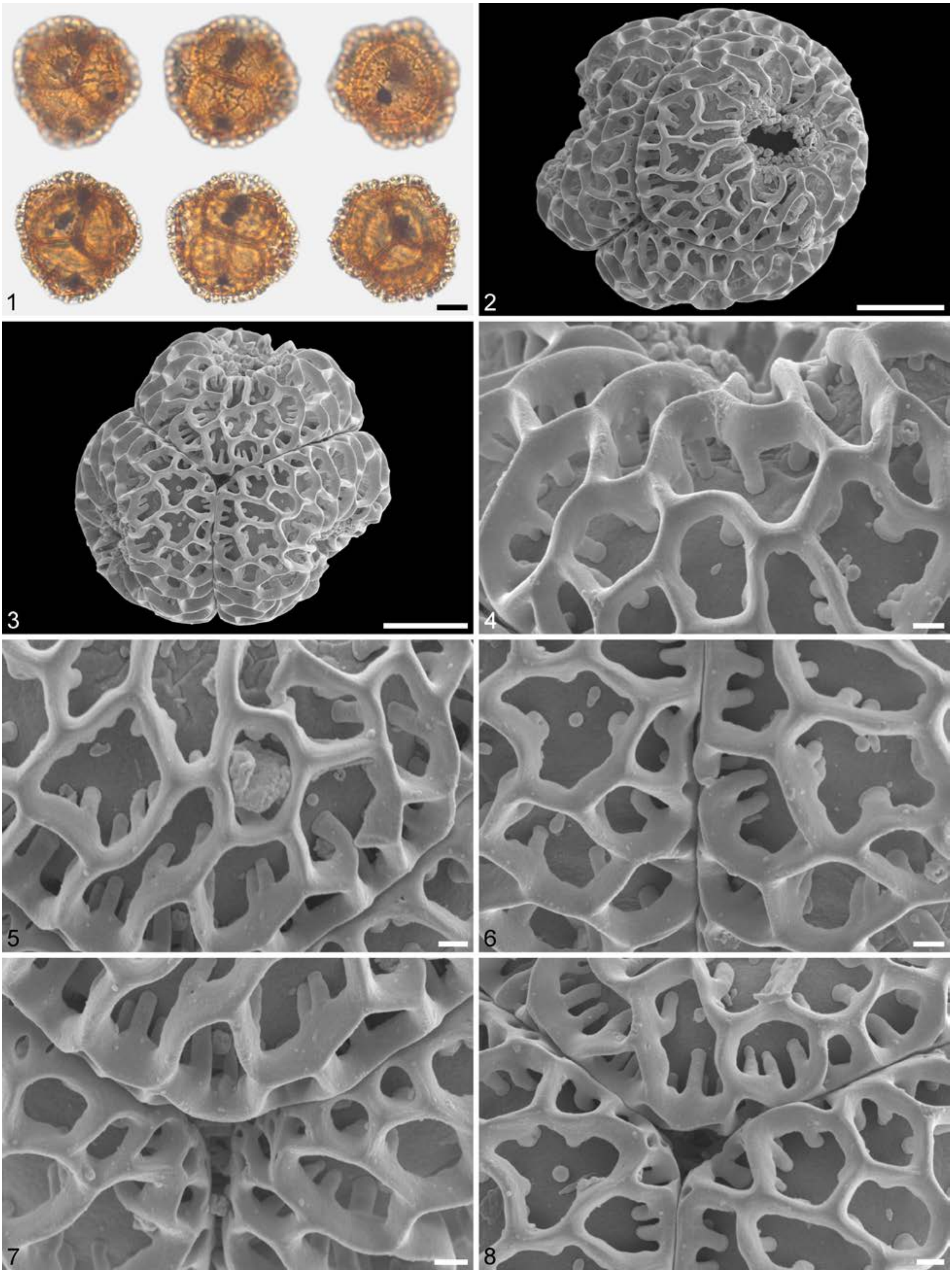

Plate 41. *Pseudowinterapollis africanensis* sp. nov. from the early Miocene of Saldanha Bay, South Africa (Holotype, IPUW 7513/209); **1**. Pollen tetrad in LM, upper row at high focus, lower row in optical cross section, left tetrads in basal view, middle tetrads in lateral view, right tetrads in apical view; **2–8**. Pollen tetrad in SEM, same grain as in Pl. 41, fig. 1; **2**. Oblique lateral view; **3**. Basal view; **4**. Distal face of pollen, close-up of Pl. 41, fig. 3; **5**. Distal face of pollen, close-up of Pl. 41, fig. 2; **6**. Pollen interface in basal view, close-up of Pl. 41, fig. 3; **7**. Pollen interface in oblique lateral view, close-up of Pl. 41, fig. 2; **8**. Pollen interface in basal view, close-up of Pl. 41, fig. 3. Scale bars – 10 µm (1–3), 1 µm (4–8)

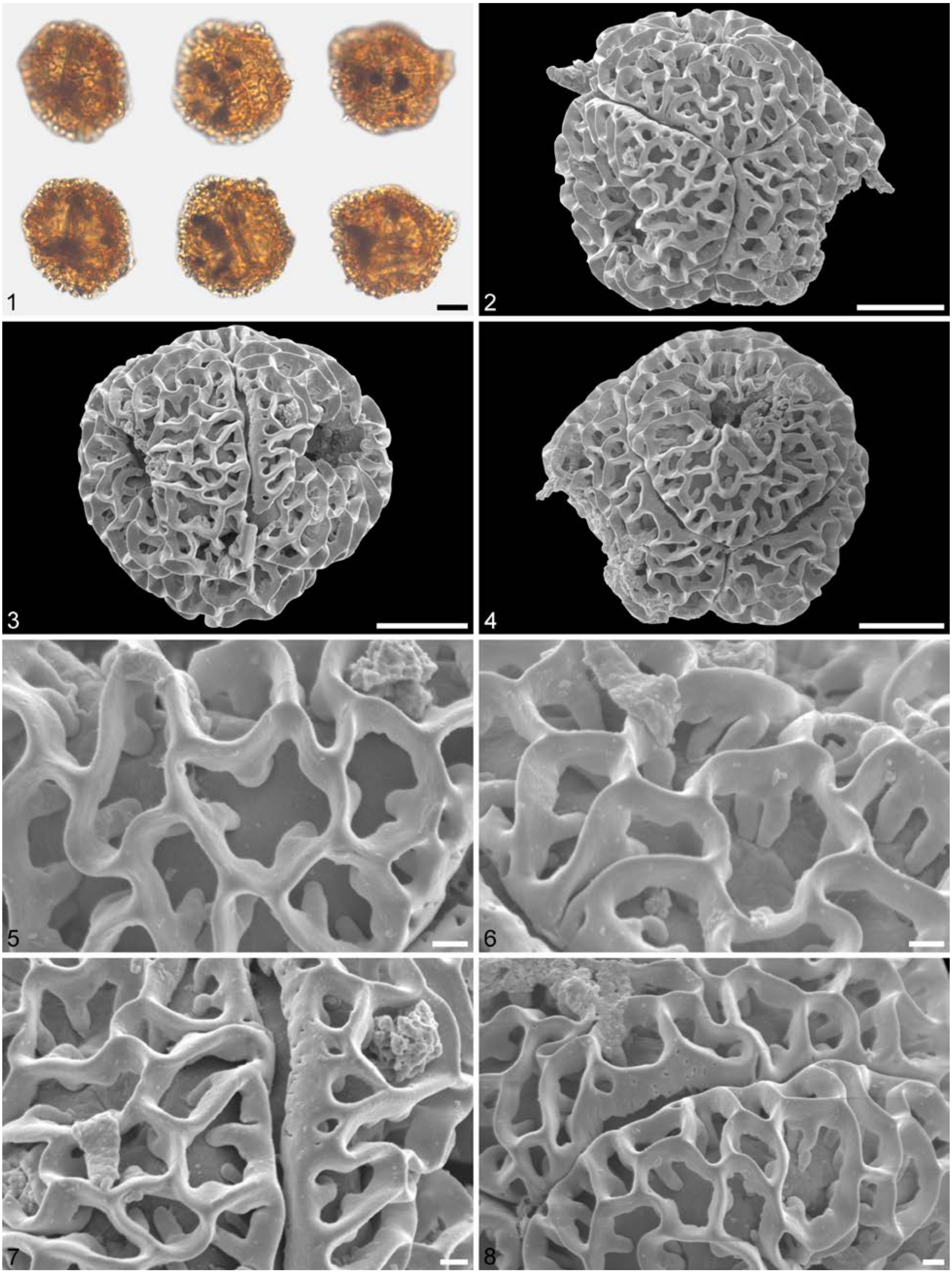

Plate 42. *Pseudowinterapollis africanensis* sp. nov. from the early Miocene of Saldanha Bay, South Africa (Paratype, IPUW 7513/210); **1**. Pollen tetrad in LM, upper row at high focus, lower row in optical cross section, left tetrads in basal view, middle tetrads in lateral view, right tetrads in apical view; **2–8**. Pollen tetrad in SEM, same grain as in Pl. 42, fig. 1; **2**. Basal view; **3**. Lateral view; **4**. Apical view; **5**. Distal face of pollen, close-up of Pl. 42, fig. 2; **6**. Distal face of pollen, close-up of Pl. 42, fig. 2; **7**. Pollen interface in lateral view, close-up of Pl. 42, fig. 3; **8**. Pollen interface in apical view, close-up of Pl. 42, fig. 4. Scale bars – 10 µm (1–4), 1 µm (5–8)

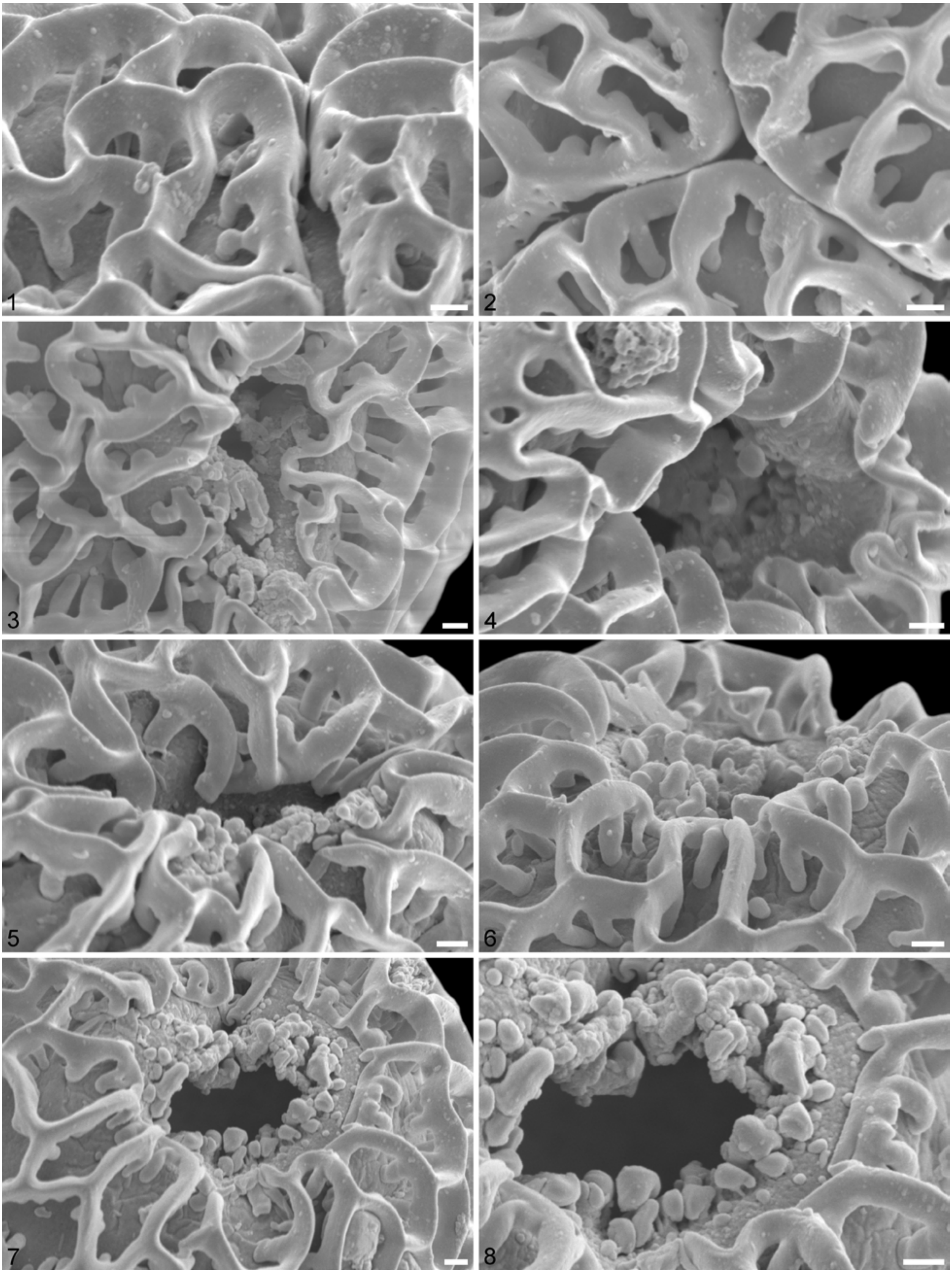

Plate 43. *Pseudowinterapollis africanensis* sp. nov. from the early Miocene of Saldanha Bay, South Africa; **1**. Pollen interface in lateral view, close-up of Pl. 42, fig. 3 (Paratype, IPUW 7513/210); **2**. Pollen interface in basal view, close-up of Pl. 42, fig. 2 (Paratype, IPUW 7513/210); **3**. Aperture, close-up of Pl. 42, fig. 4 (Paratype, IPUW 7513/210); **4**. Aperture, close-up of Pl. 42, fig. 3 (Paratype, IPUW 7513/210); **5**. Aperture, close-up of Pl. 42, fig. 3 (Paratype, IPUW 7513/210); **6**. Aperture, close-up of Pl. 41, fig. 3 (Holotype, IPUW 7513/209); **7**. Aperture, close-up of Pl. 41, fig. 2 (Holotype, IPUW 7513/209); **8**. Aperture, close-up of Pl. 41, fig. 2 (Holotype, IPUW 7513/209). Scale bars – 1 µm

Supplementary File for:

Authors: FRIĐGEIR GRÍMSSON, ALEXANDROS XAFIS, FRANK H. NEUMANN & REINHARD ZETTER

Title of paper: Pollen morphology of extant Winteraceae: a study allowing SEM based affiliation of its fossil representatives

Published in: Acta Palaeobotanica

Contents: This Supplementary File contains Supplementary Plates S1 to S28

Plate S1

Tasmannia insipida R.Br. ex DC. (M: from Australia, coll. H.-J. Tillich, s.n.).

1–2. Pollen tetrads in LM, upper row at high focus, lower row in optical cross section, left tetrads in basal view, middle tetrads in lateral view, right tetrads in apical view.

3–8. Pollen tetrads in SEM.

3–4. Basal view.

5–6. Lateral view.

7–8. Apical view.

Scale bars: 10 μm.

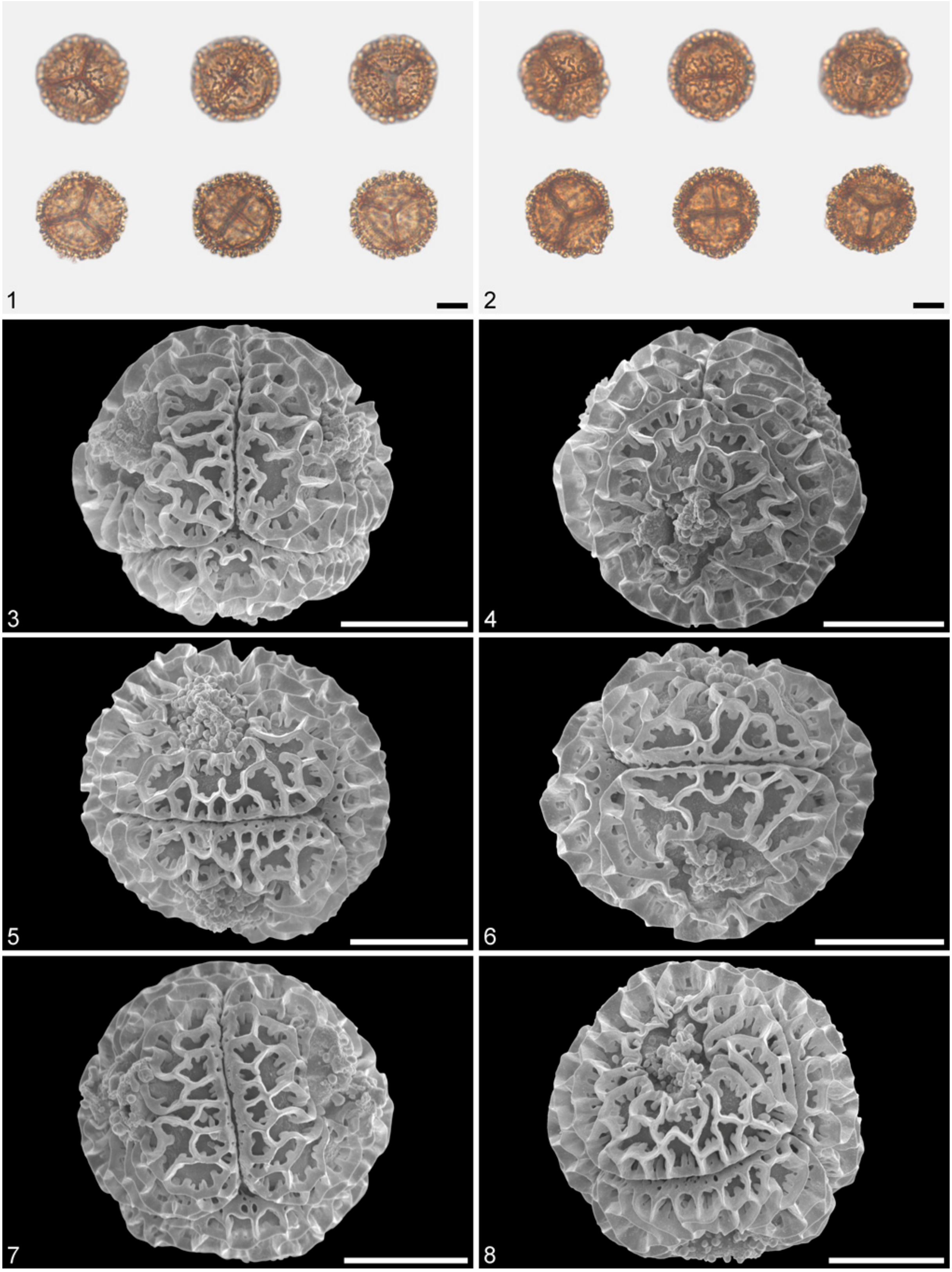

Plate S1

Plate S2

Tasmannia insipida R.Br. ex DC. (M: from Australia, coll. H.-J. Tillich, s.n.).

1–8. Close–ups of sculpture in SEM.

1–2. Distal face of pollen.

3. Pollen interface in lateral view.

4–5. Pollen interface in basal view.

6–8. Aperture.

Scale bars: 1 μm.

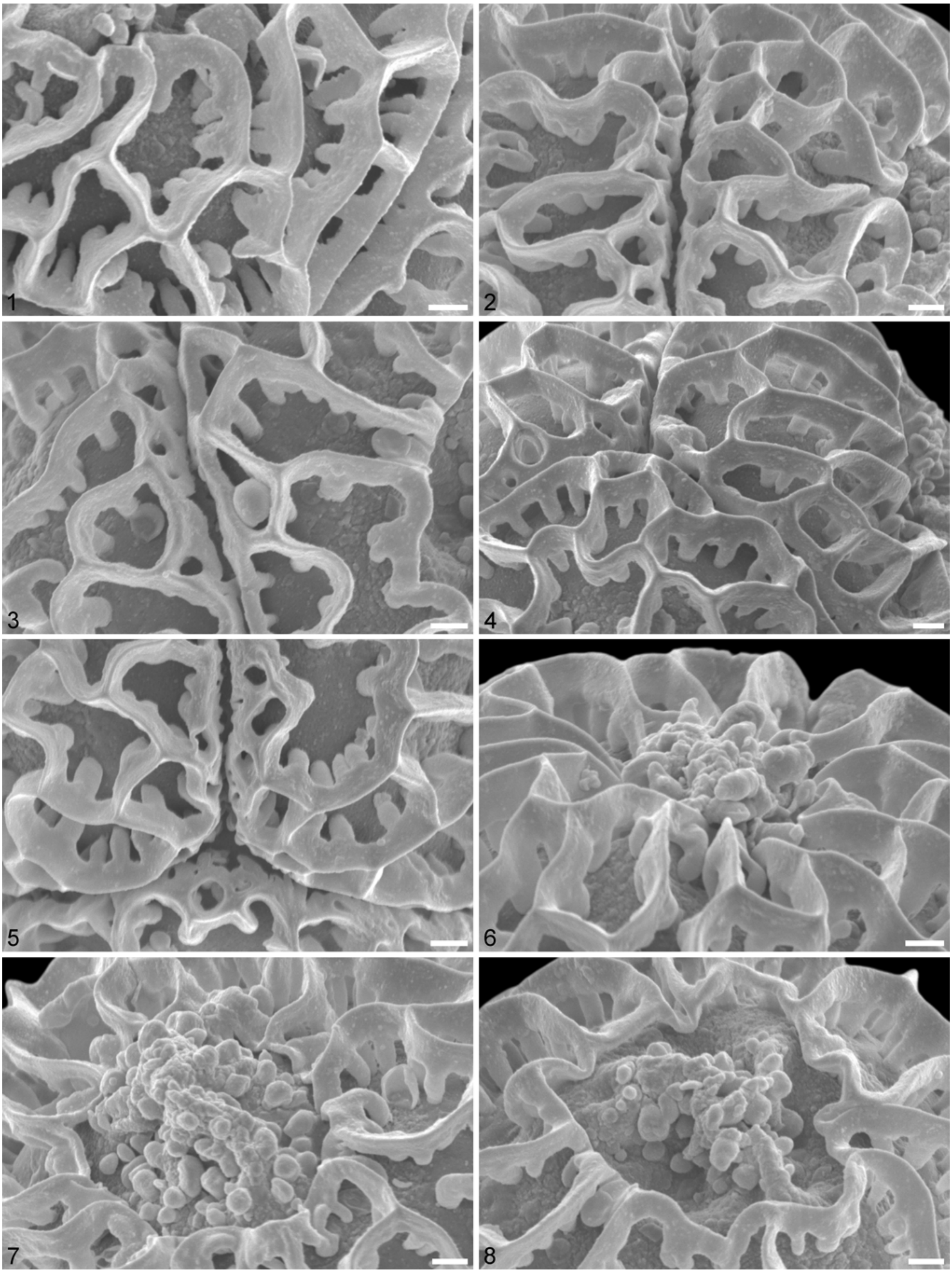

Plate S2

Plate S3

Tasmannia insipida R.Br. ex DC. (M: from Australia, coll. C.T. White, s.n.).

1–2. Pollen tetrads in LM, upper row at high focus, lower row in optical cross section, left tetrads in basal view, middle tetrads in lateral view, right tetrads in apical view.

3–8. Pollen tetrads in SEM.

3–4. Basal view.

5–6. Lateral view.

7–8. Apical view.

Scale bars: 10 µm.

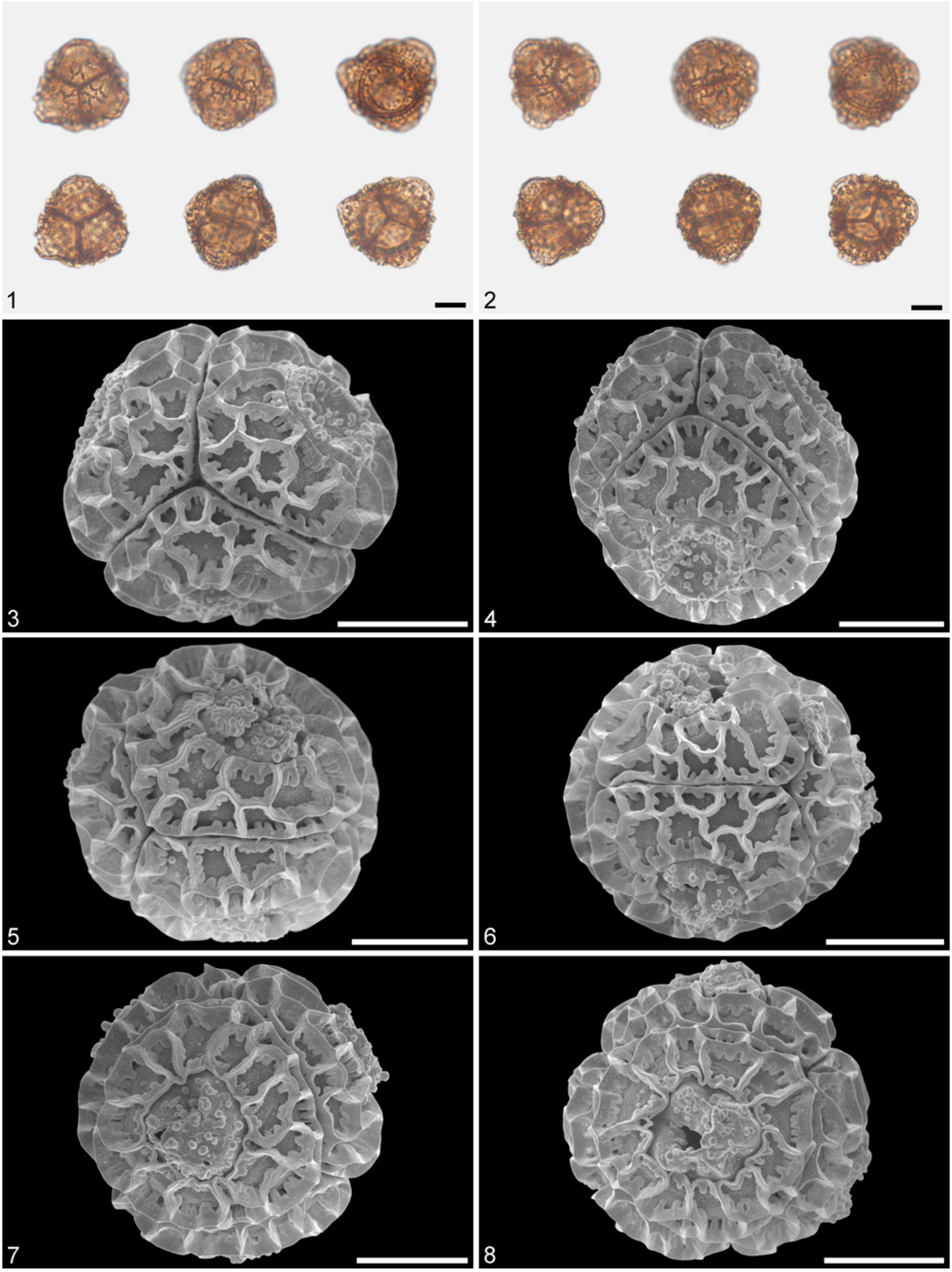

Plate S3

Plate S4

Tasmannia insipida R.Br. ex DC. (M: from Australia, coll. C.T. White, s.n.).

1–8. Close–ups of sculpture in SEM.

1–2. Distal face of pollen.

3. Pollen interface in lateral view.

4–5. Pollen interface in basal view.

6–8. Aperture.

Scale bars: 1 µm.

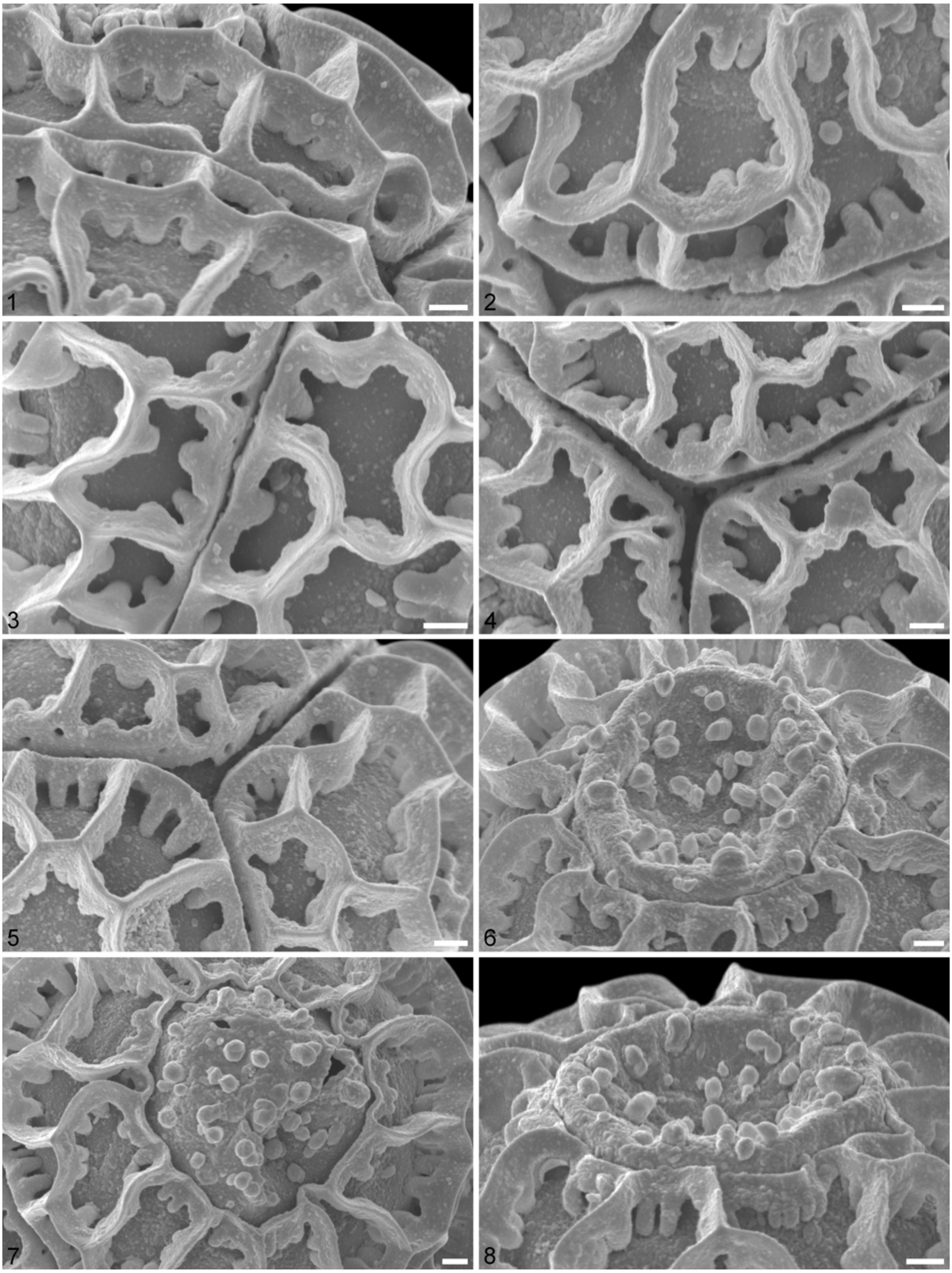

Plate S4

Plate S5

Tasmannia piperita (Hook. f.) Miers (WU: from Philippines, coll. unknown, s.n.).

1–2. Pollen tetrads in LM, upper row at high focus, lower row in optical cross section, left tetrads in basal view, middle tetrads in lateral view, right tetrads in apical view.

3–8. Pollen tetrads in SEM.

3–4. Basal view.

5–6. Lateral view.

7–8. Apical view.

Scale bars: 10 µm.

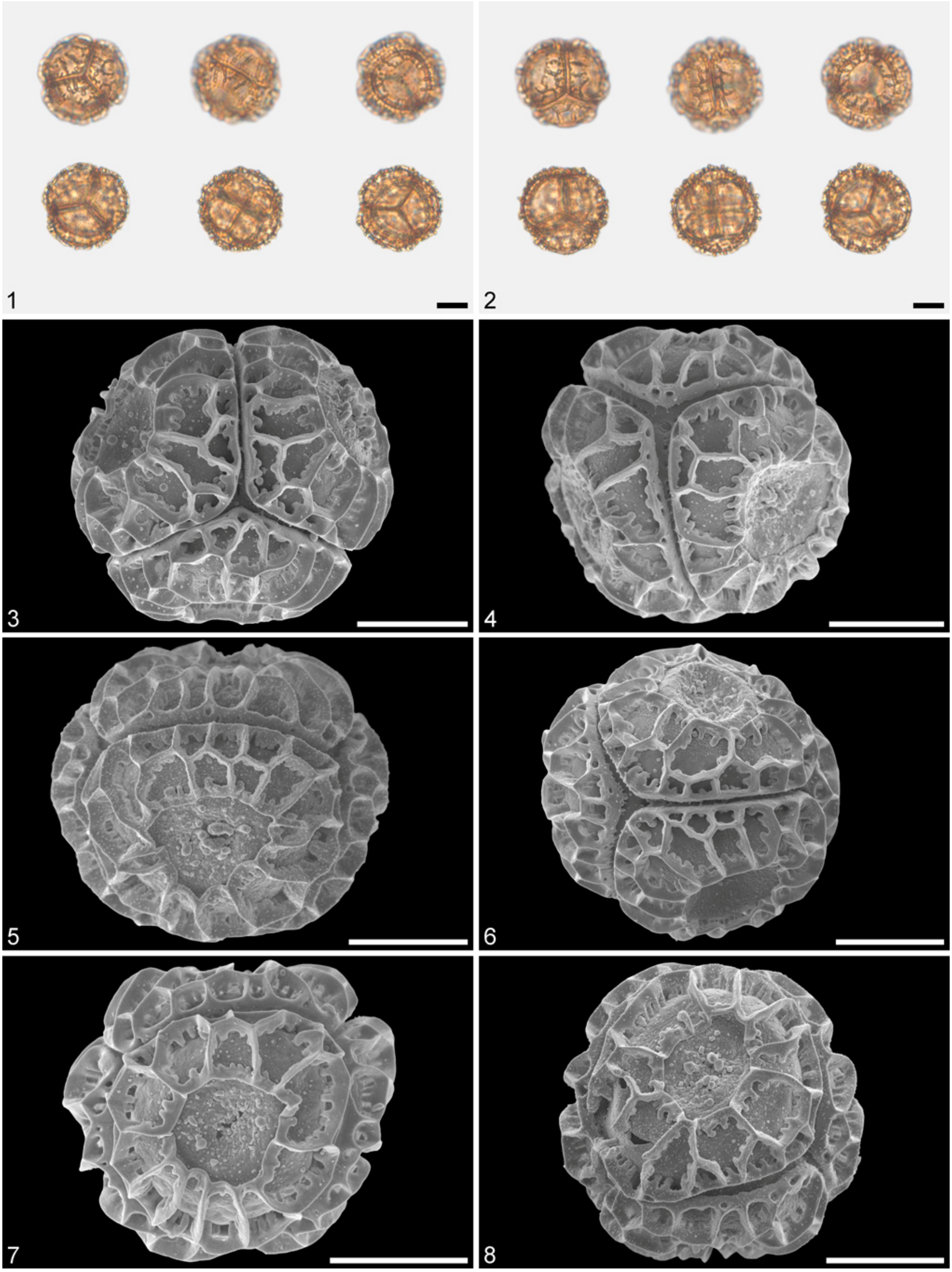

Plate S5

Plate S6

Tasmannia piperita (Hook. f.) Miers (WU: from Philippines, coll. unknown, s.n.).

1–8. Close–ups of sculpture in SEM.

1–2. Distal face of pollen.

3. Pollen interface in lateral view.

4–5. Pollen interface in basal view.

6–8. Aperture.

Scale bars: 1 μm.

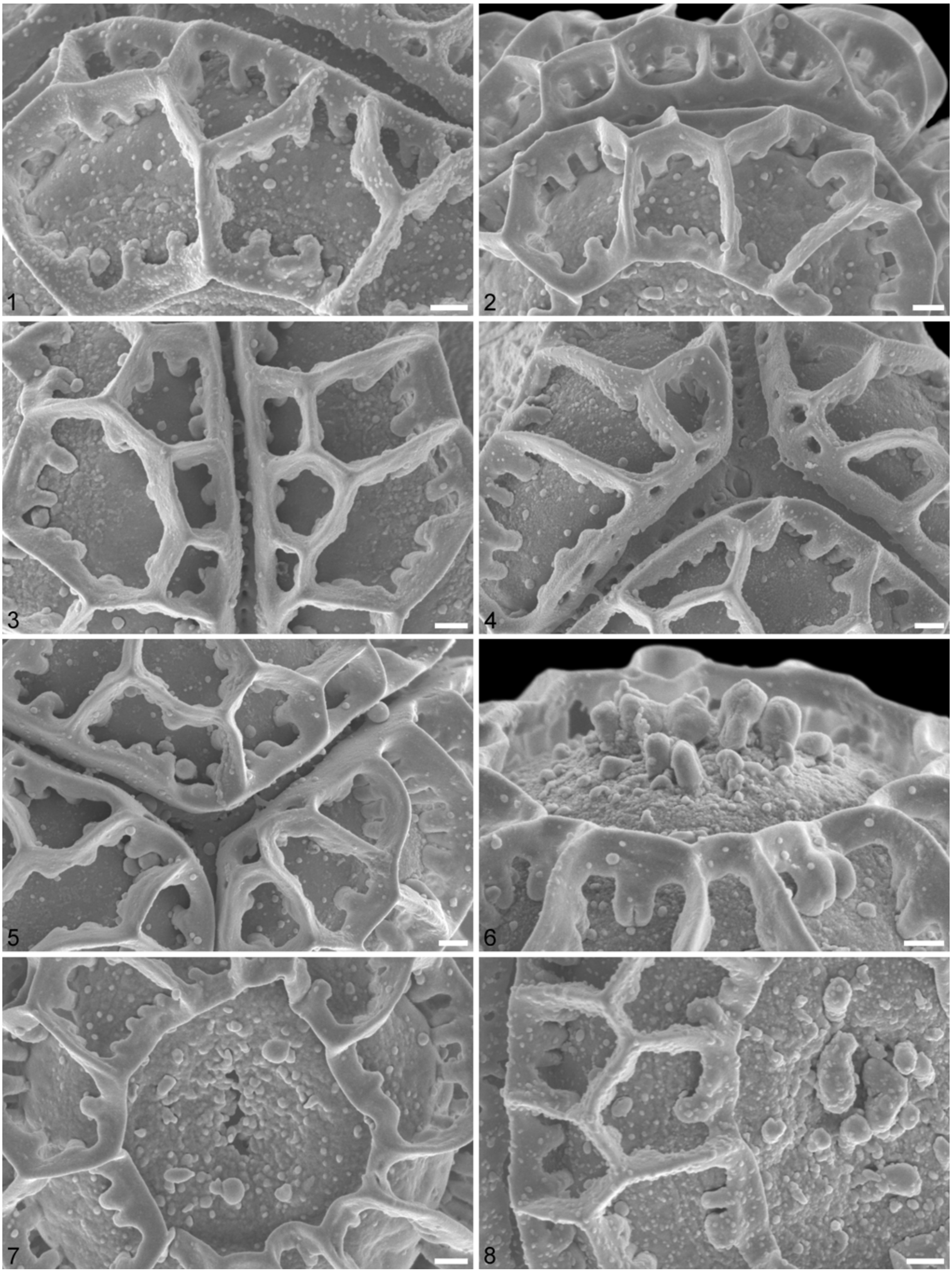

Plate S6

Plate S7

Drimys brasiliensis Miers (WU 0077153).

1–2. Pollen tetrads in LM, upper row at high focus, lower row in optical cross section, left tetrads in basal view, middle tetrads in lateral view, right tetrads in apical view.

3–8. Pollen tetrads in SEM.

3–4. Basal view.

5–6. Lateral view.

7–8. Apical view.

Scale bars: 10 µm.

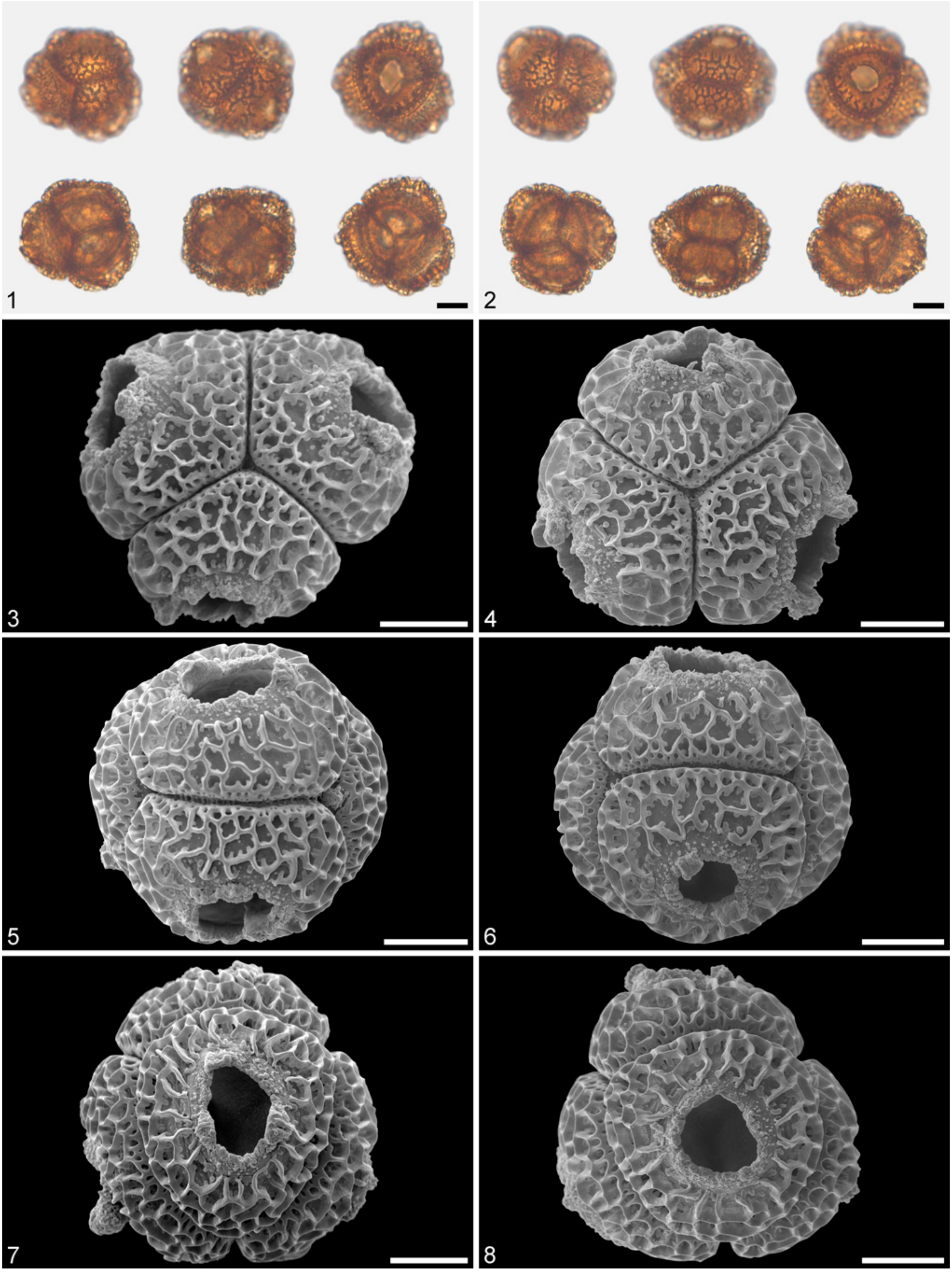

Plate S7

Plate S8

Drimys brasiliensis Miers (WU 0077153).

1–8. Close–ups of sculpture in SEM.

1. Distal face of pollen.

2. Pollen interface in lateral view.

3. Distal face of pollen.

4–5. Pollen interface in basal view.

6–8. Aperture region.

Scale bars: 1 µm.

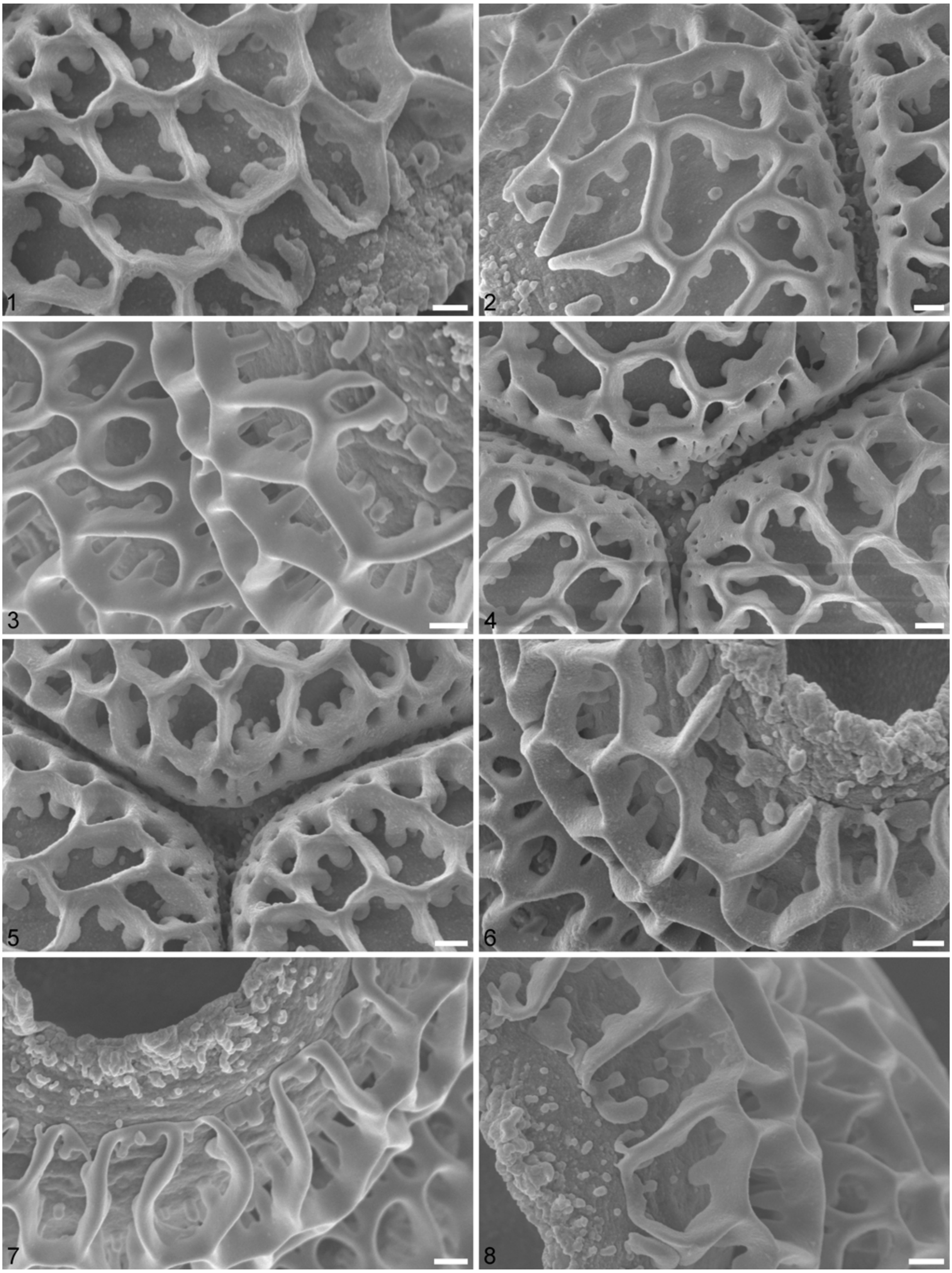

Plate S8

Plate S9

Drimys granadensis L. f. (WU: from Costa Rica, coll. Ehrendorfer, s.n.).

1–2. Pollen tetrads in LM, upper row at high focus, lower row in optical cross section, left tetrads in basal view, middle tetrads in lateral view, right tetrads in apical view.

3–8. Pollen tetrads in SEM.

3–4. Basal view.

5–6. Lateral view.

6–8. Apical view.

Scale bars: 10 µm.

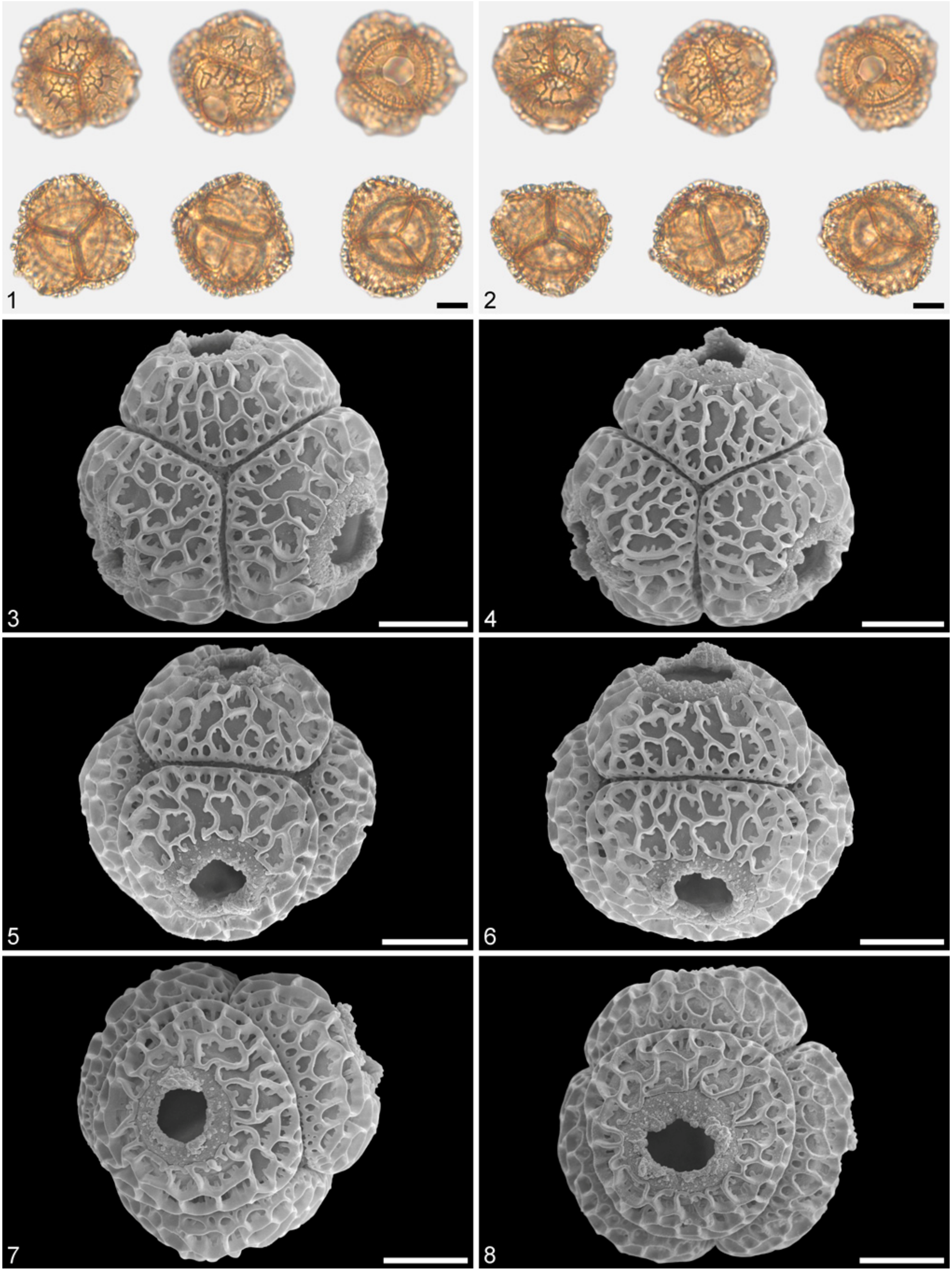

Plate S9

Plate S10

Drimys granadensis L. f. (WU: from Costa Rica, coll. Ehrendorfer, s.n.).

1–8. Close–ups of sculpture in SEM.

1. Distal face of pollen.

2. Pollen interface in lateral view.

3. Distal face of pollen.

4–5. Pollen interface in basal view.

6–8. Aperture region.

Scale bars: 1 µm.

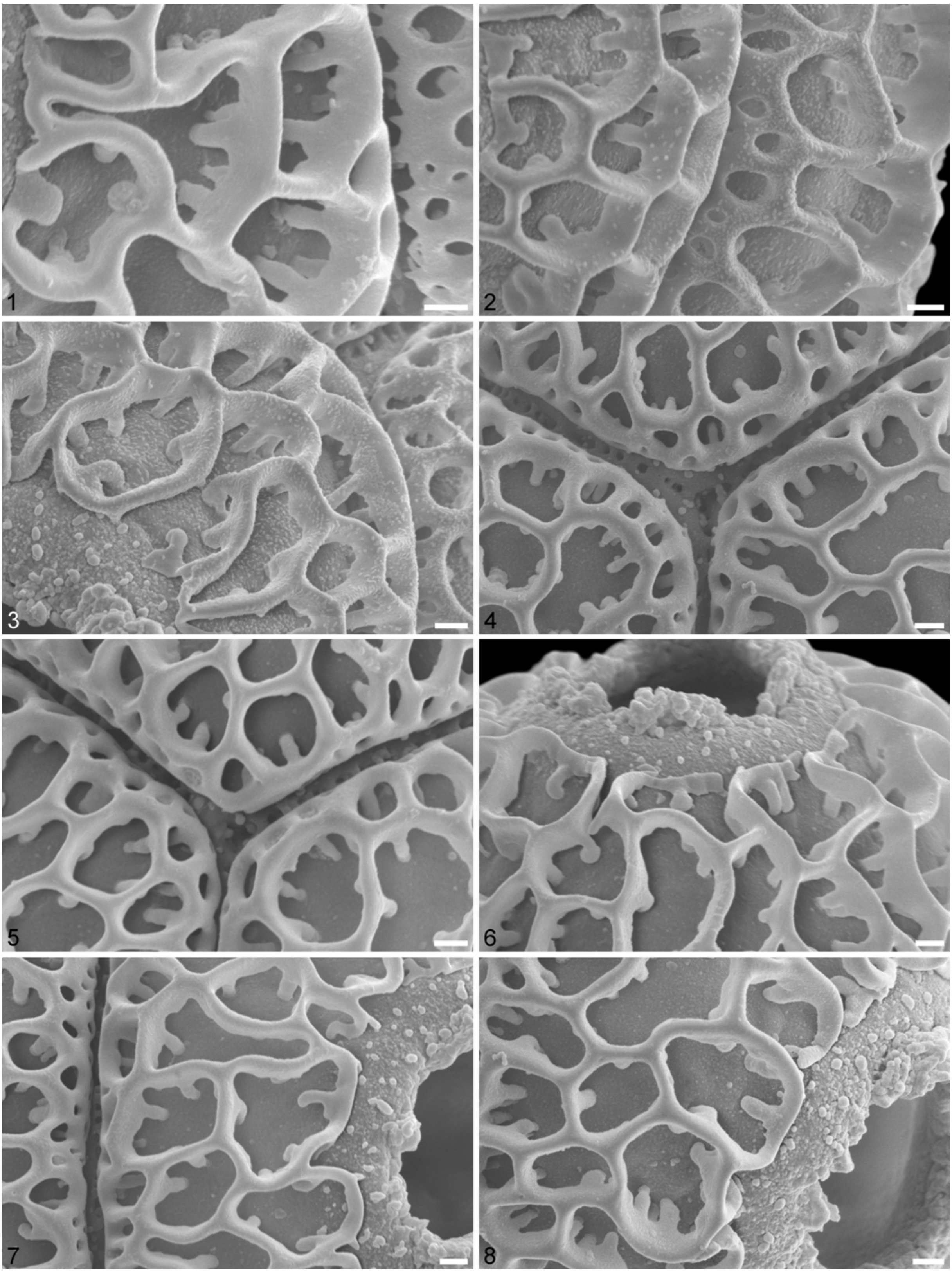

Plate S10

Plate S11

Drimys granadensis L. f. (W 1956–0020228: from Ecuador).

1–2. Pollen tetrads in LM, upper row at high focus, lower row in optical cross section, left tetrads in basal view, middle tetrads in lateral view, right tetrads in apical view.

3–8. Pollen tetrads in SEM.

3–4. Basal view.

5–6. Lateral view.

7–8. Apical view.

Scale bars: 10 µm.

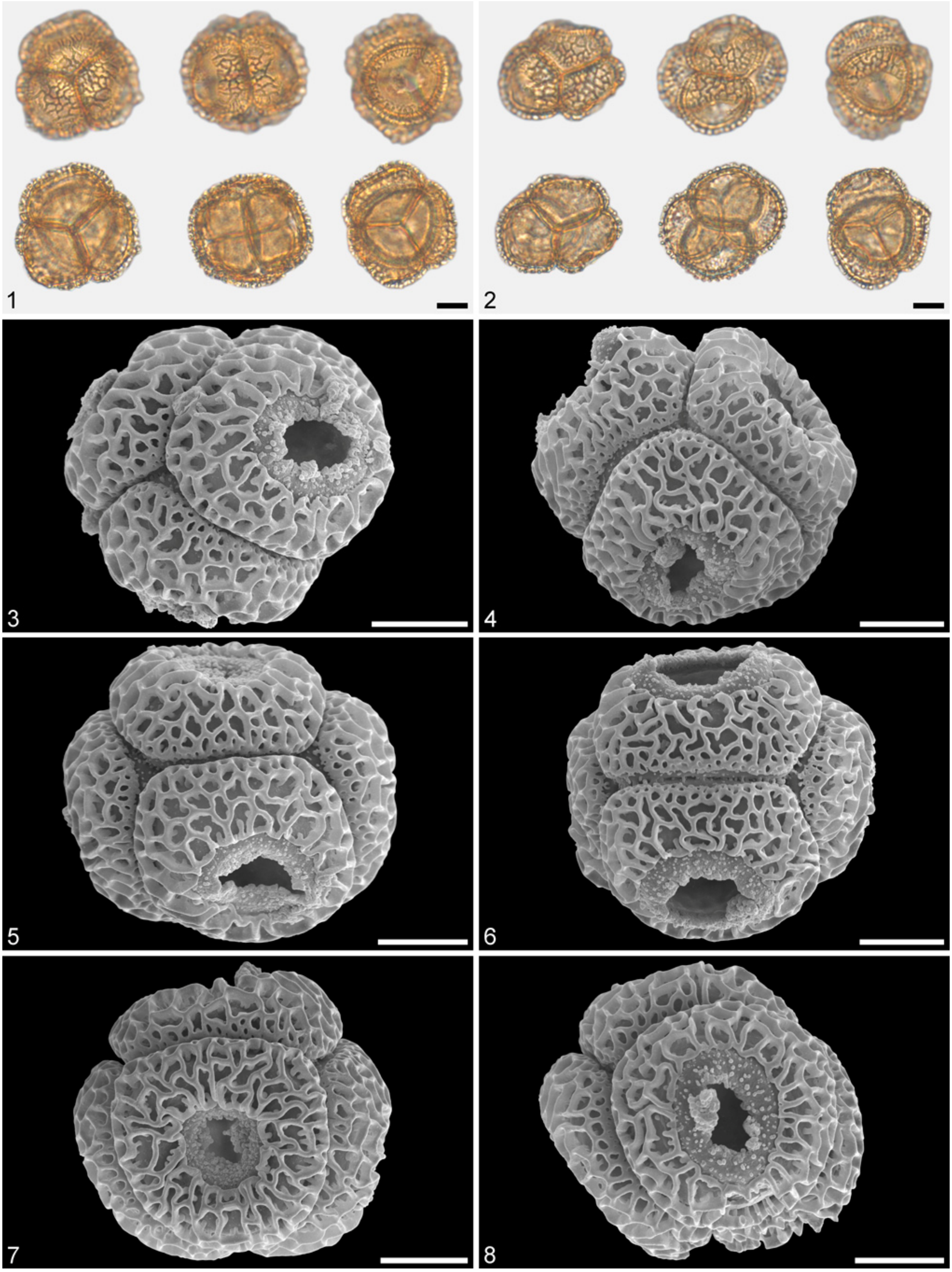

Plate S11

Plate S12

Drimys granadensis L. f. (W 1956–0020228: from Ecuador).

1–8. Close–ups of sculpture in SEM.

1–2. Distal face of pollen.

3. Pollen interface in lateral view.

4–5. Pollen interface in basal view.

6–8. Aperture.

Scale bars: 1 μm.

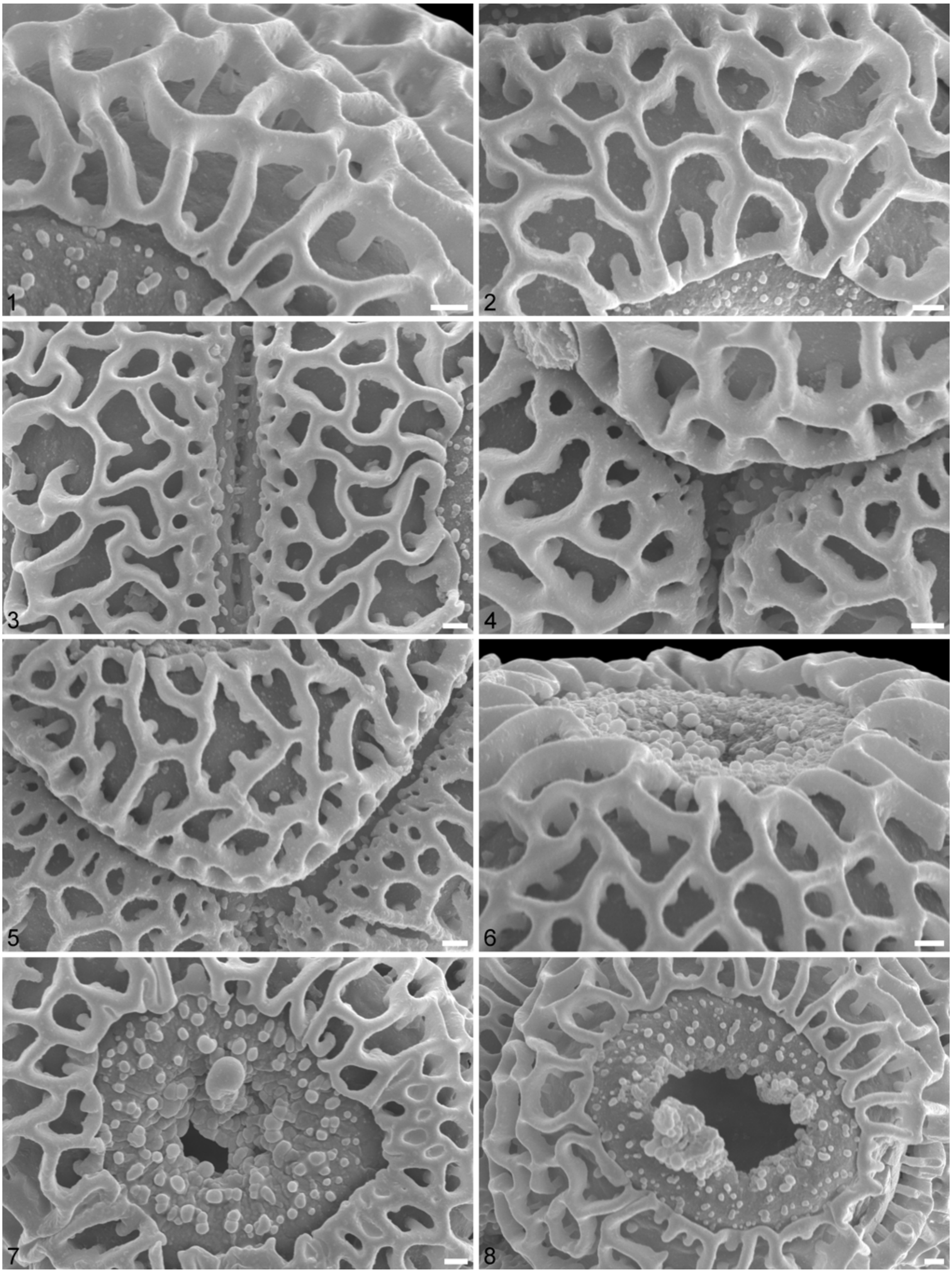

Plate S12

Plate S13

Drimys winteri J.R. Forst. & G. Forst. (W 1955–0013624: from Chile).

1–2. Pollen tetrads in LM, upper row at high focus, lower row in optical cross section, left tetrads in basal view, middle tetrads in lateral view, right tetrads in apical view.

3–8. Pollen tetrads in SEM.

3–4. Basal view.

5–6. Lateral view.

7–8. Apical view.

Scale bars: 10 µm.

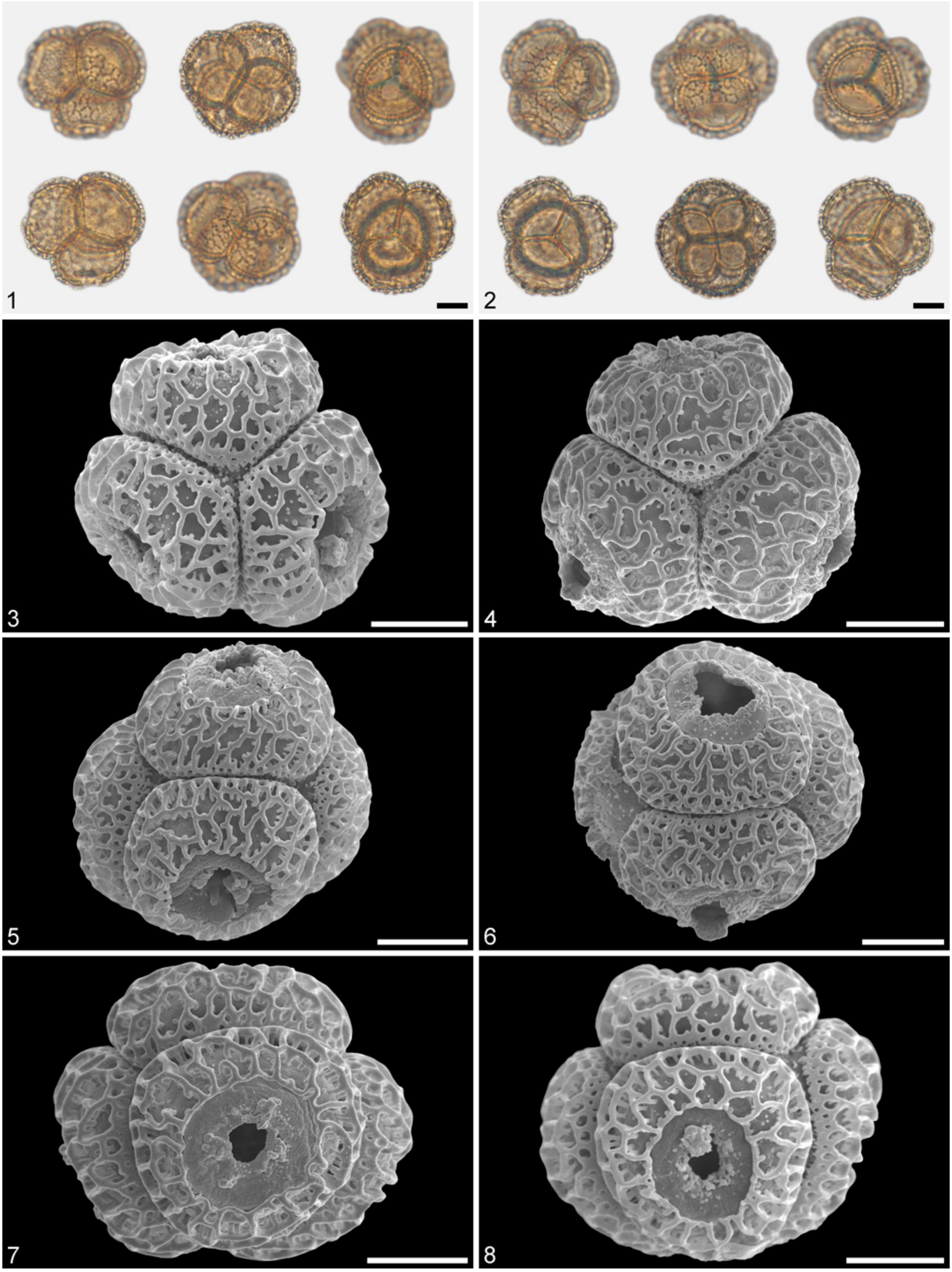

Plate S13

Plate S14

Drimys winteri J.R. Forst. & G. Forst. (W 1955–0013624: from Chile).

1–8. Close–ups of sculpture in SEM.

1–2. Distal face of pollen.

3. Pollen interface in lateral view.

4–5. Pollen interface in basal view.

6–8. Aperture.

Scale bars: 1 µm.

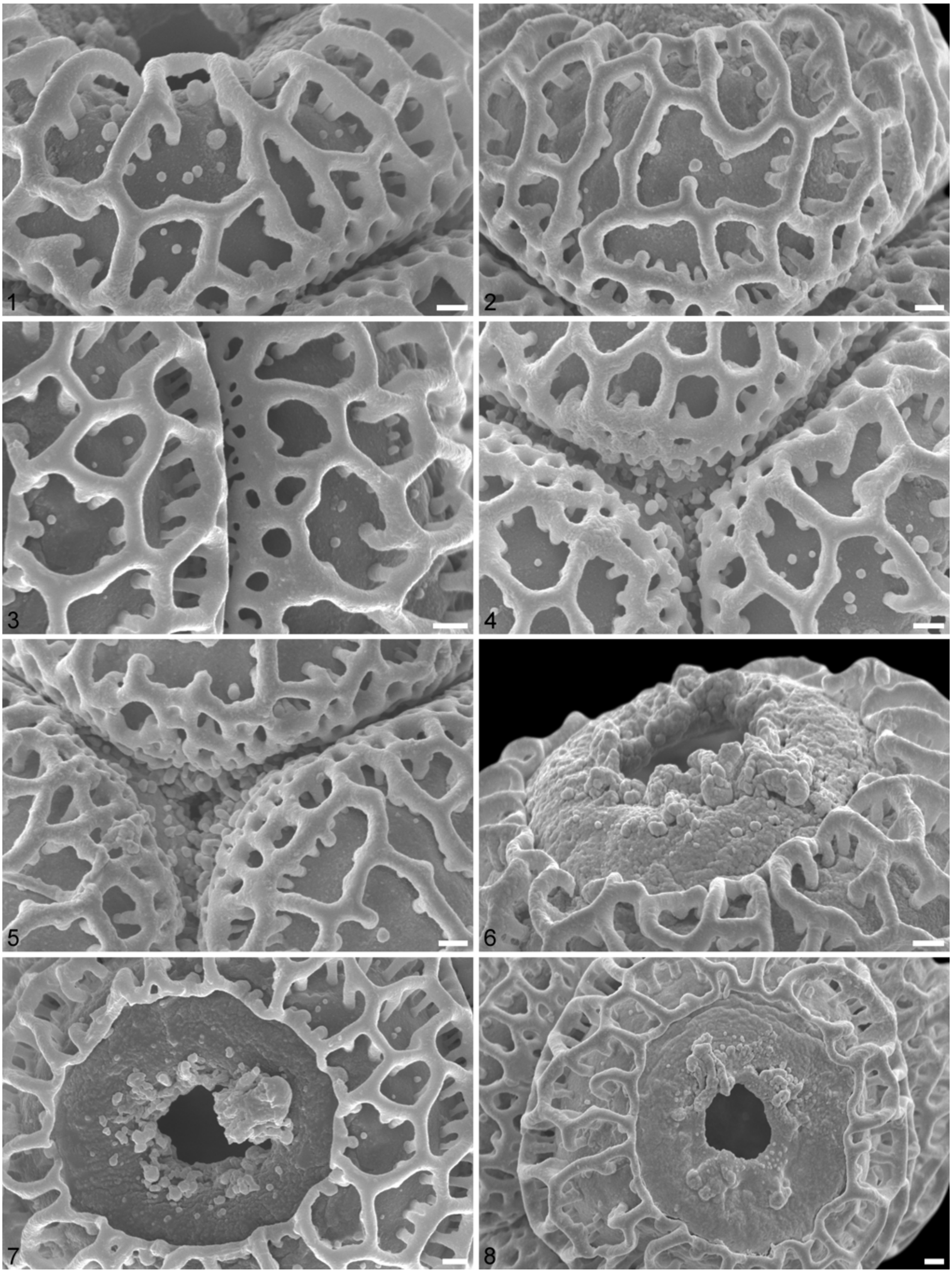

Plate S14

Plate S15

Drimys winteri J.R. Forst. & G. Forst. (WU: from Chile, coll. unknown, s.n.).

1–2. Pollen tetrads in LM, upper row at high focus, lower row in optical cross section, left tetrads in basal view, middle tetrads in lateral view, right tetrads in apical view.

3–8. Pollen tetrads in SEM.

3–4. Basal view.

5–6. Lateral view.

7–8. Apical view.

Scale bars: 10 µm.

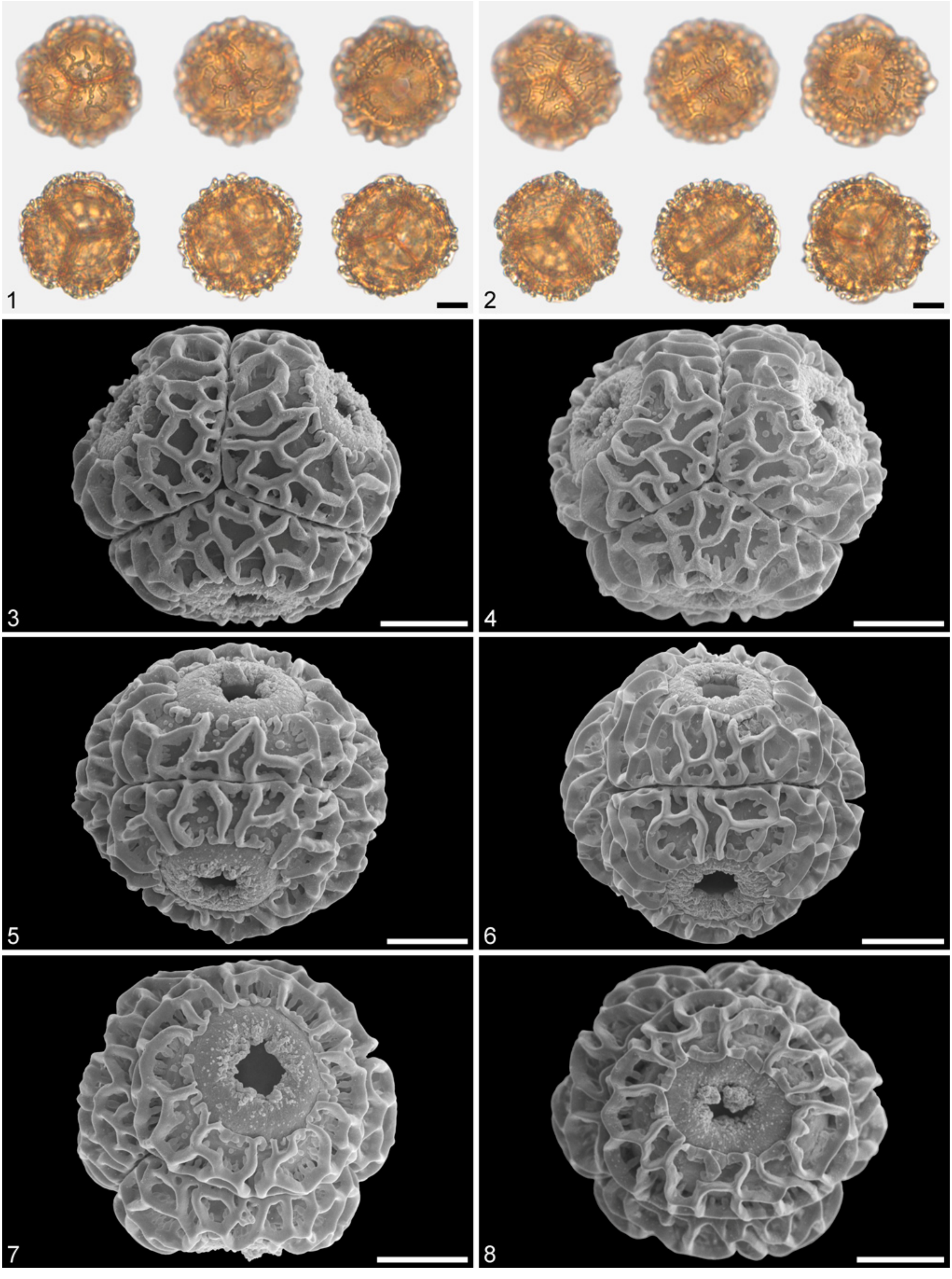

Plate S15

Plate S16

Drimys winteri J.R. Forst. & G. Forst. (WU: from Chile, coll. unknown, s.n.).

1–8. Close–ups of sculpture in SEM.

1–3. Distal face of pollen.

4–5. Pollen interface in basal view.

6–8. Aperture.

Scale bars: 1 μm.

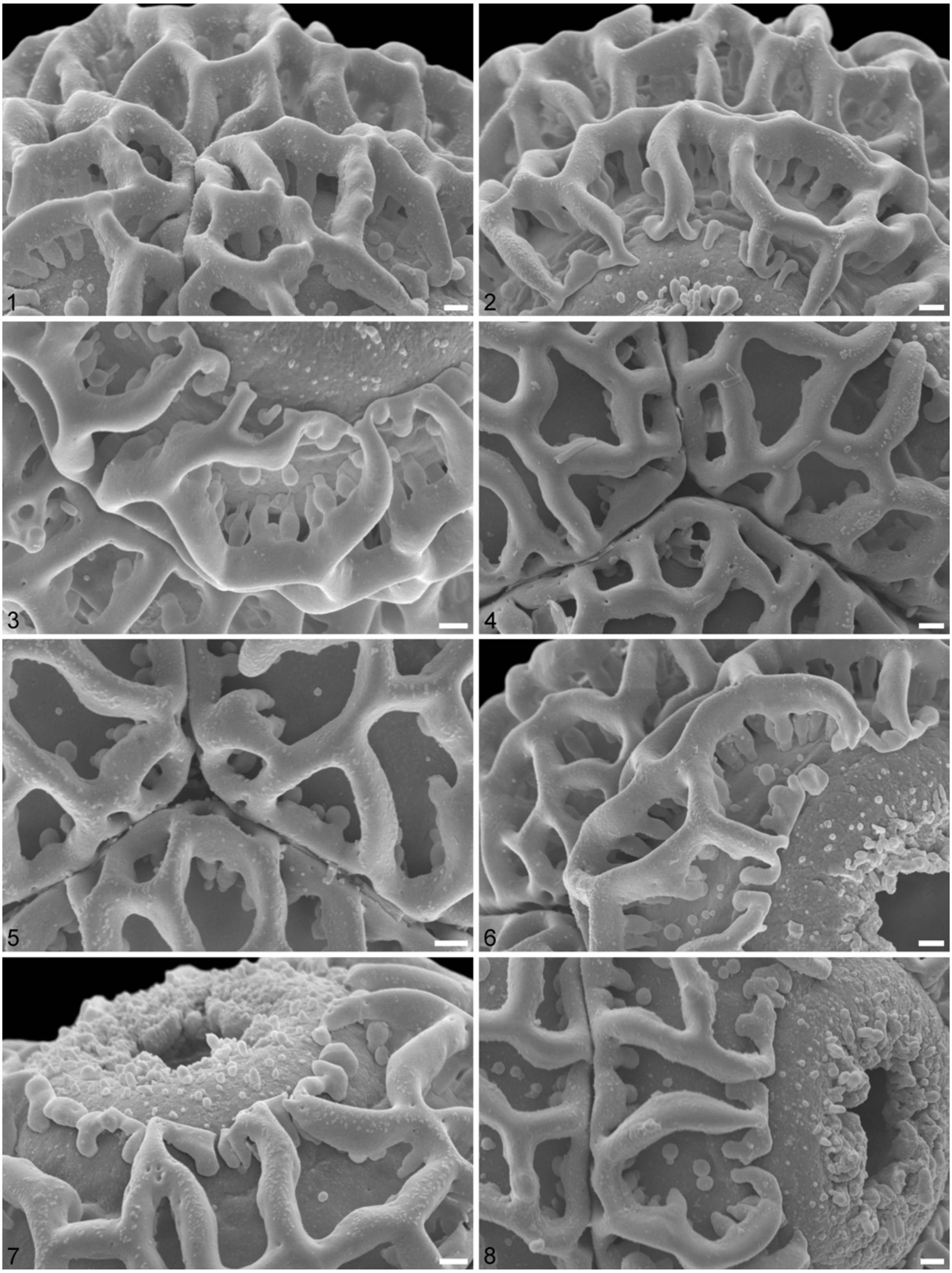

Plate S16

Plate S17

Pseudowintera axillaris (J.R. Forst. & G.Forst) Dandy (WELT SP092372: from New Zealand).

1–2. Pollen tetrads in LM, upper row at high focus, lower row in optical cross section, left tetrads in basal view, middle tetrads in lateral view, right tetrads in apical view.

3–8. Pollen tetrads in SEM.

3–4. Basal view.

5–6. Lateral view.

7–8. Apical view.

Scale bars: 10 µm.

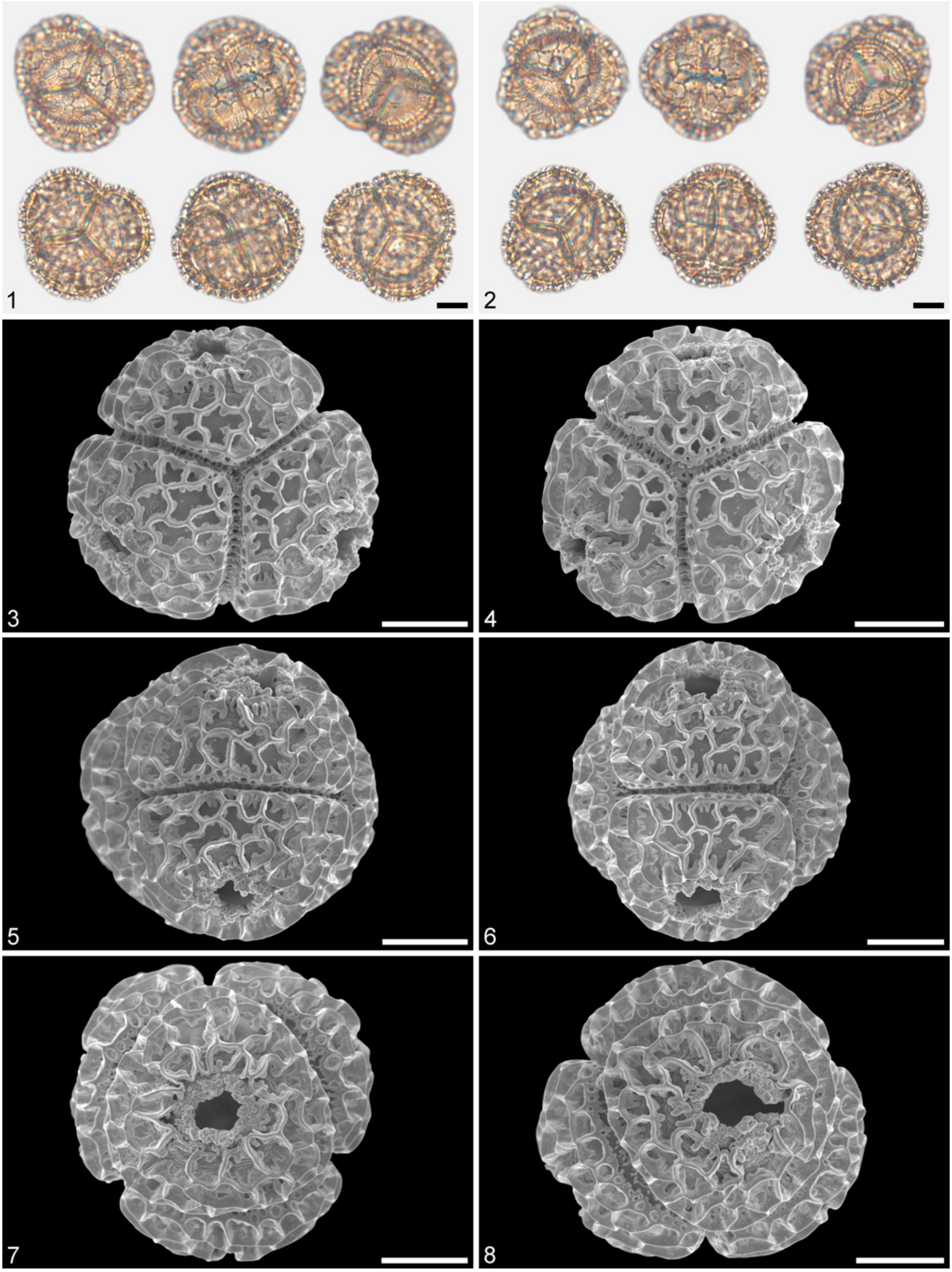

Plate S17

Plate S18

Pseudowintera axillaris (J.R. Forst. & G.Forst) Dandy (WELT SP092372: from New Zealand).

1–8. Close–ups of sculpture in SEM.

1–2. Distal face of pollen.

3–4. Pollen interface in lateral view.

5–6. Pollen interface in basal view.

7–8. Aperture.

Scale bars: 1 µm.

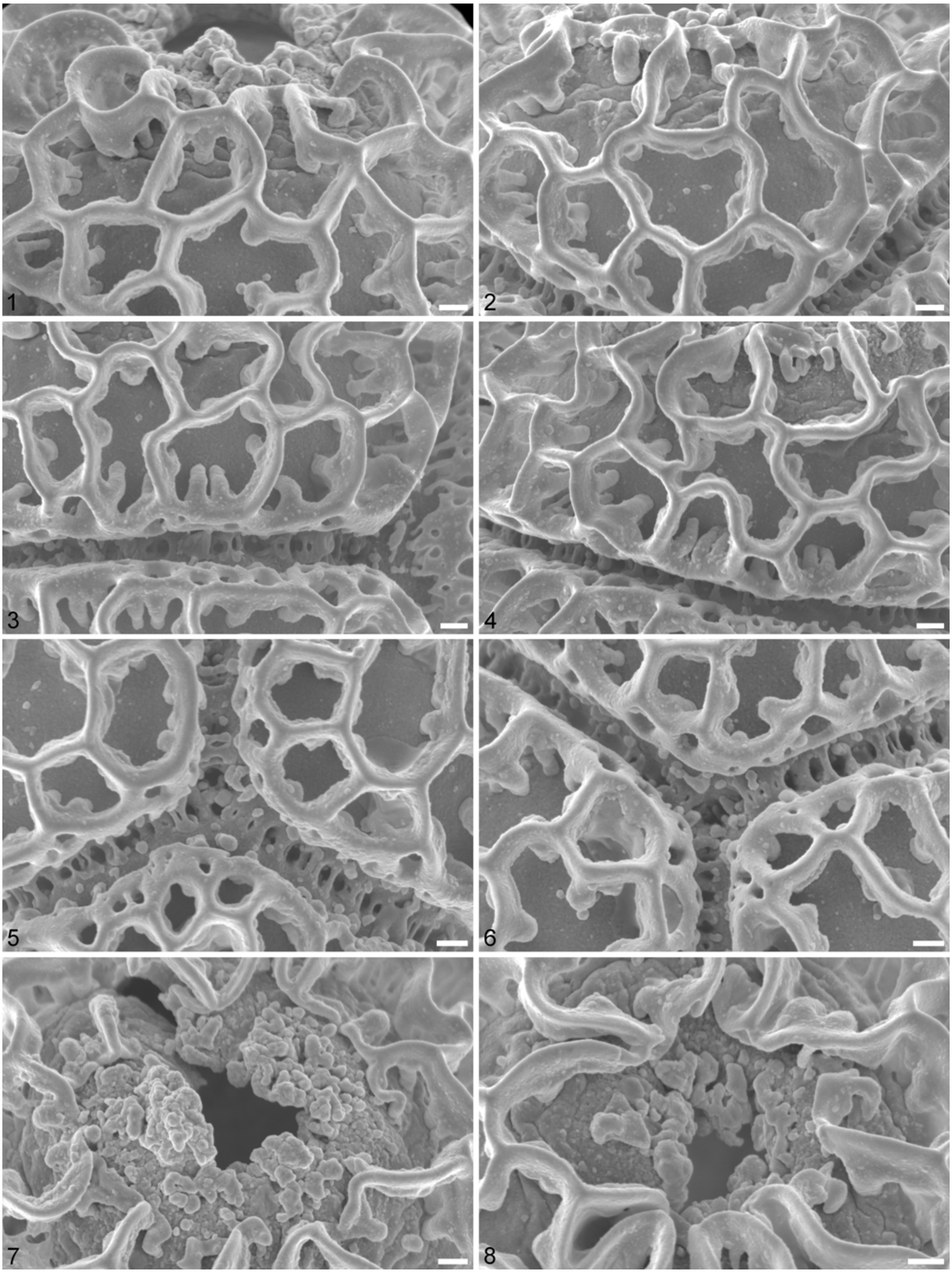

Plate S18

Plate S19

Pseudowintera axillaris (J.R. Forst. & G.Forst) Dandy (WELT SP092375: from New Zealand).

1–2. Pollen tetrads in LM, upper row at high focus, lower row in optical cross section, left tetrads in basal view, middle tetrads in lateral view, right tetrads in apical view.

3–8. Pollen tetrads in SEM.

3–4. Basal view.

5–6. Lateral view.

7–8. Apical view.

Scale bars: 10 µm.

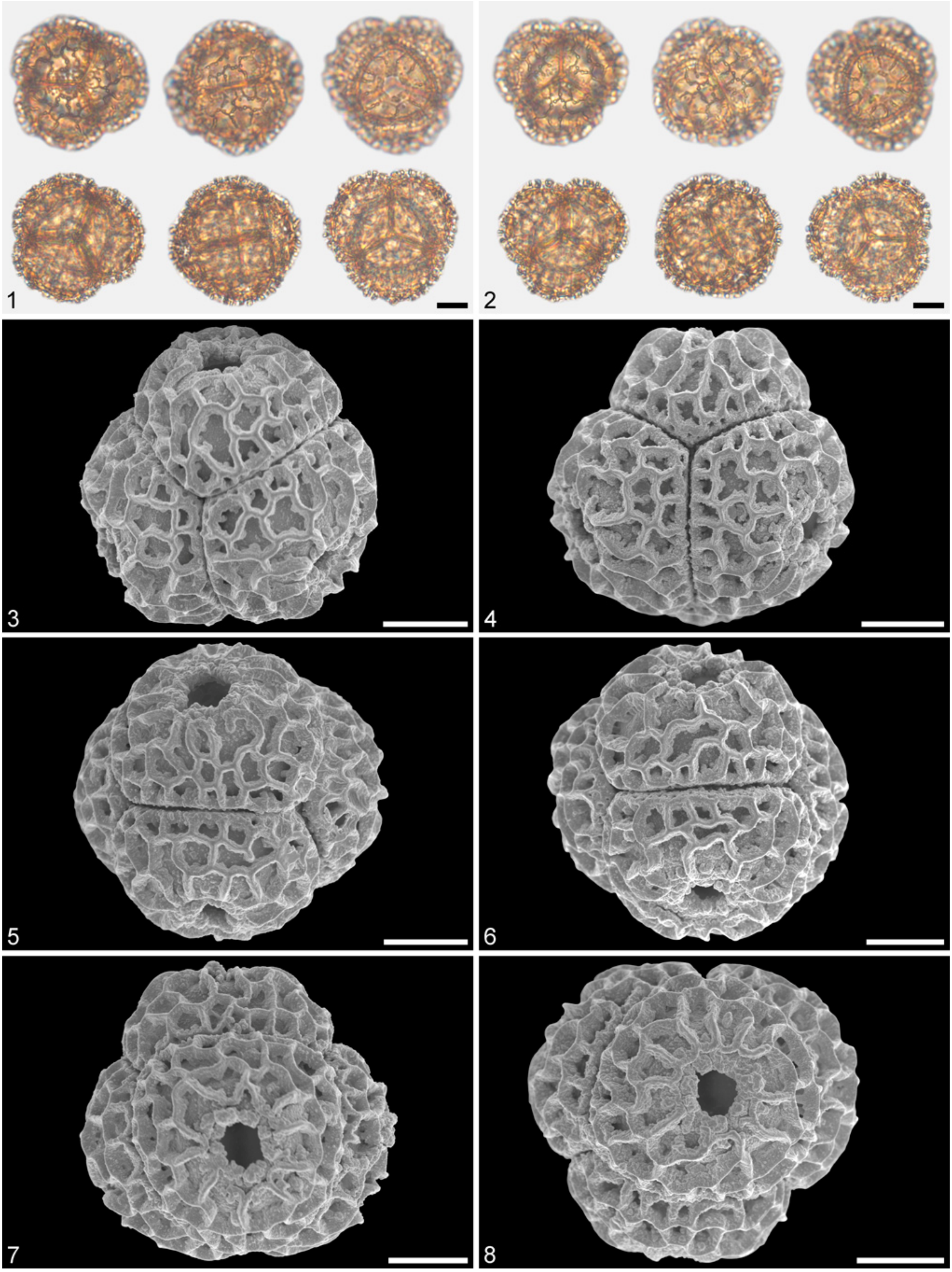

Plate S19

Plate S20

Pseudowintera axillaris (J.R. Forst. & G.Forst) Dandy (WELT SP092375: from New Zealand).

1–8. Close–ups of sculpture in SEM.

1–3. Distal face of pollen.

4. Pollen interface in lateral view.

5–6. Pollen interface in basal view.

7–8. Aperture.

Scale bars: 1 µm.

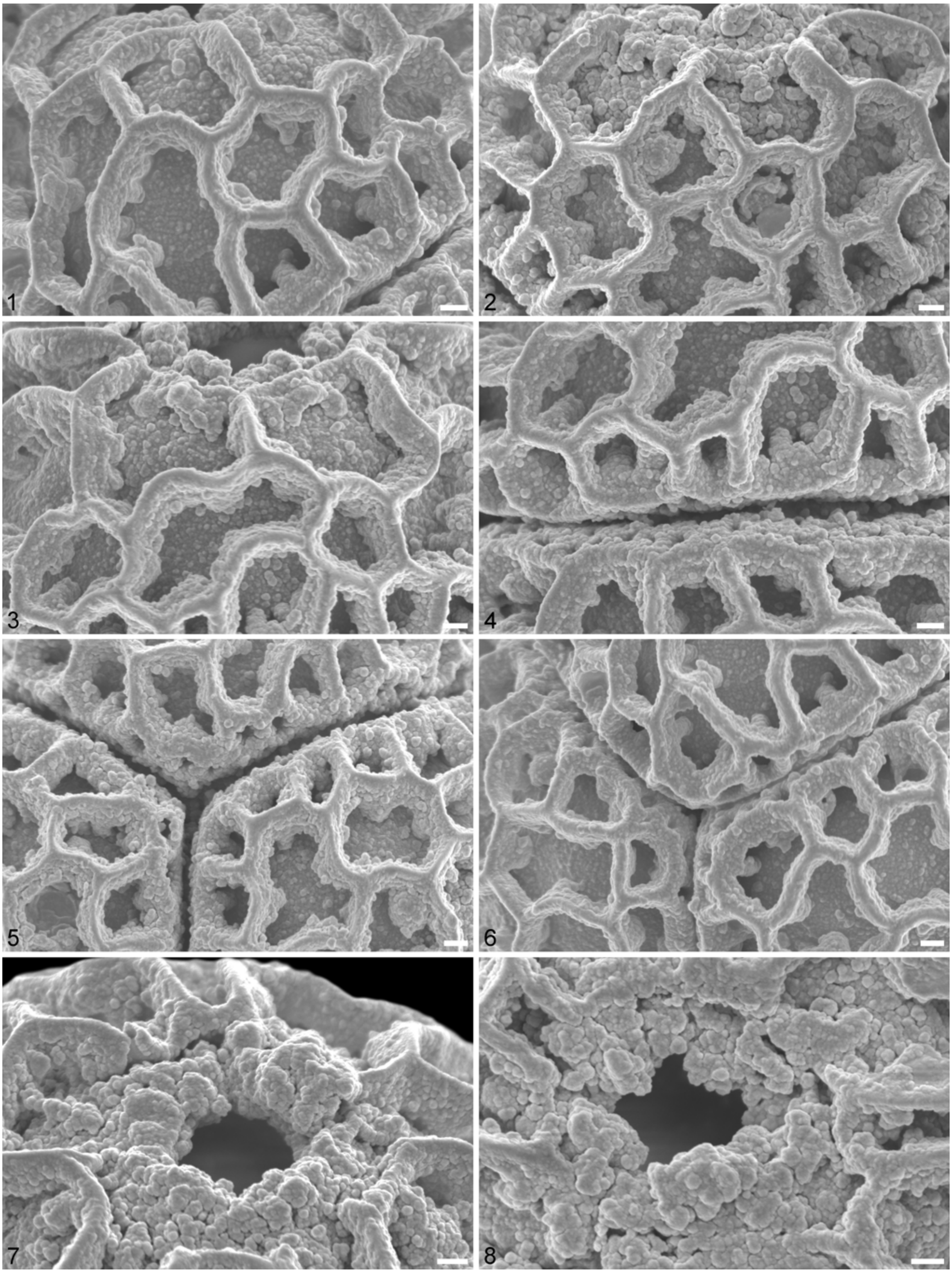

Plate S20

Plate S21

Pseudowintera colorata (Raoul) Dandy (WELT SP092383: from New Zealand).

1–2. Pollen tetrads in LM, upper row at high focus, lower row in optical cross section, left tetrads in basal view, middle tetrads in lateral view, right tetrads in apical view.

3–8. Pollen tetrads in SEM.

3–4. Basal view.

5–6. Lateral view.

7–8. Apical view.

Scale bars: 10 µm.

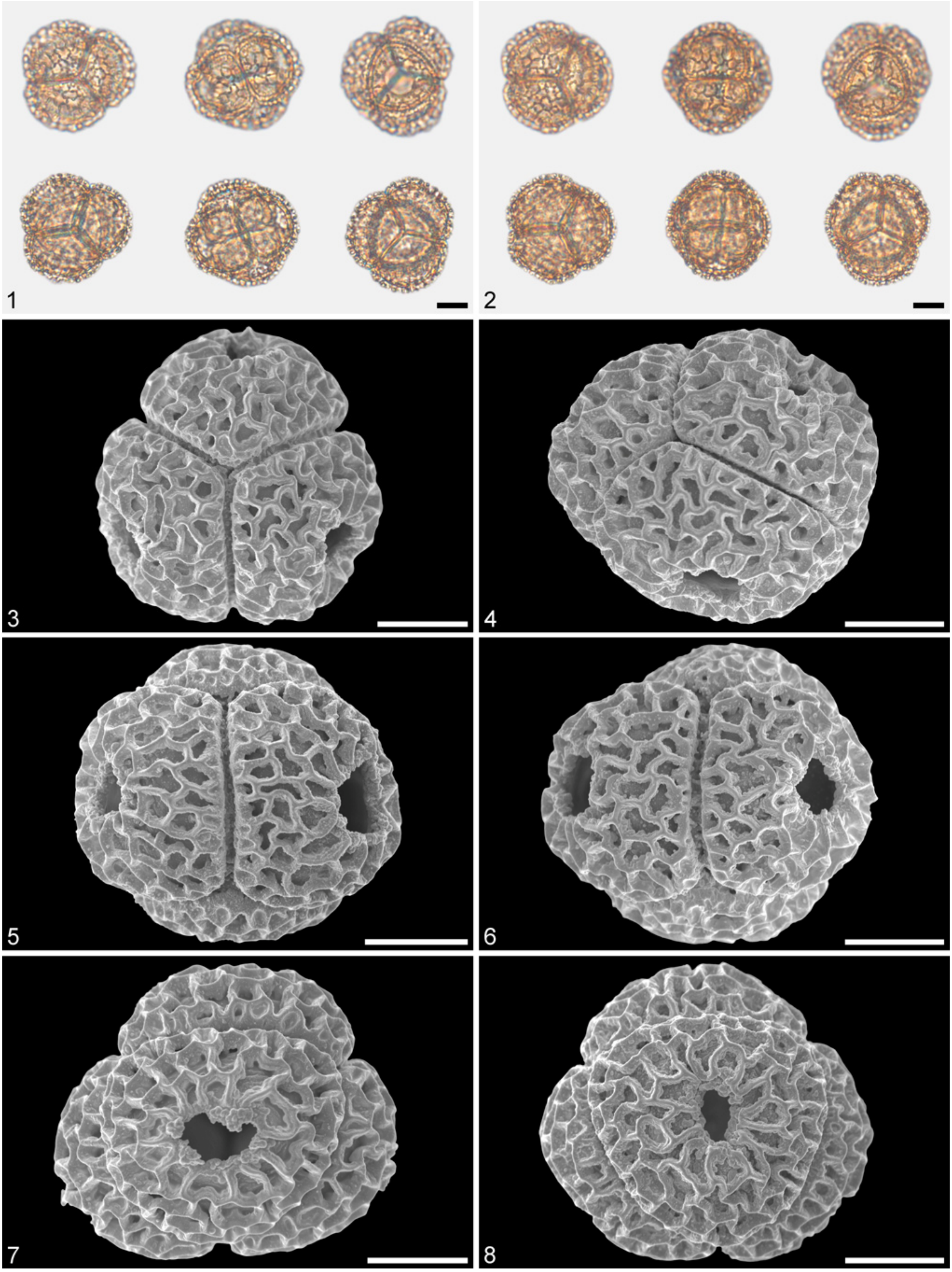

Plate S21

Plate S22

Pseudowintera colorata (Raoul) Dandy (WELT SP092383: from New Zealand).

1–6. Close–ups of sculpture in SEM.

1–2. Distal face of pollen.

3–4. Pollen interface in lateral view.

5. Pollen interface in basal view.

6. Aperture.

Scale bars: 1 µm.

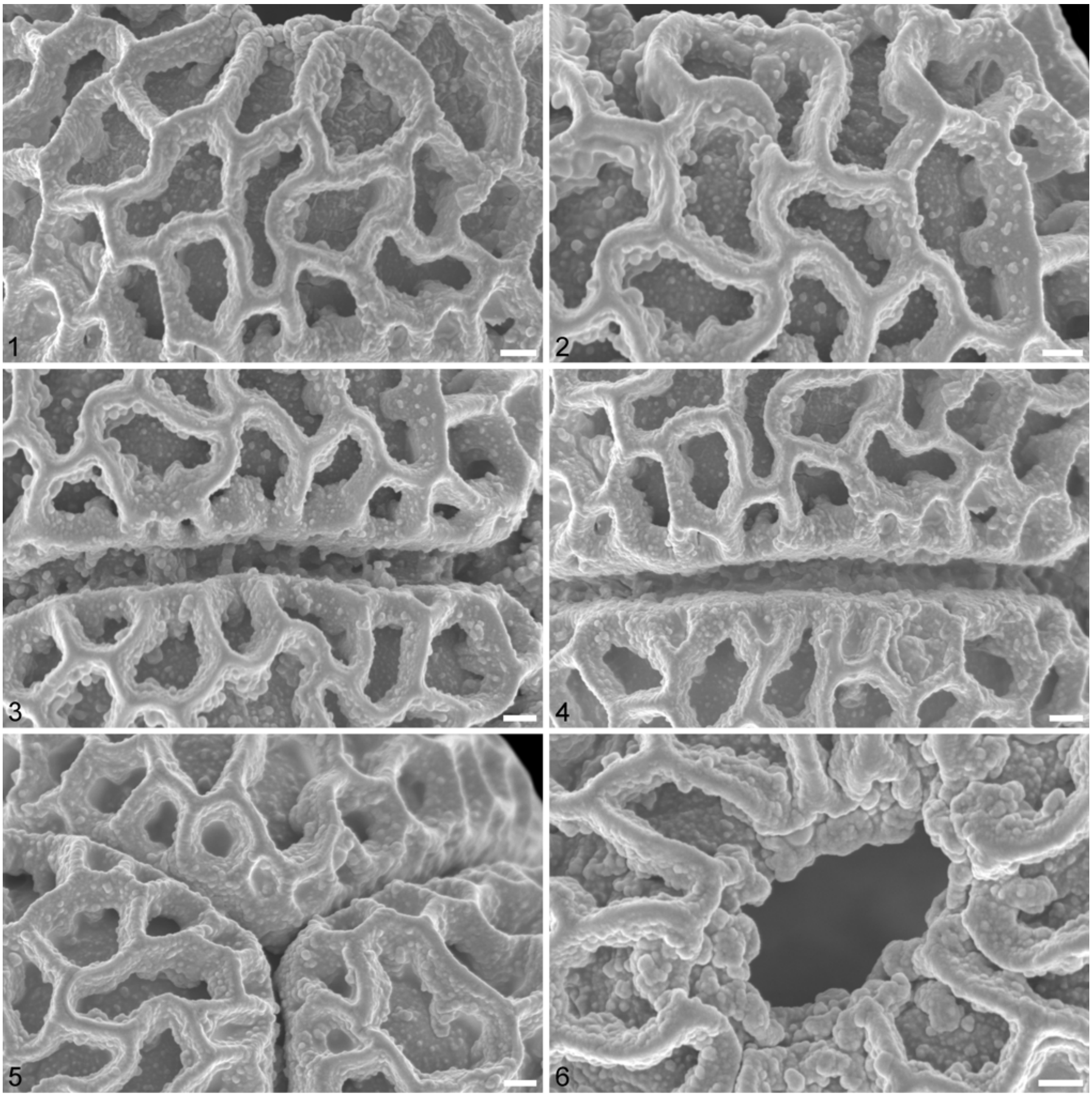

Plate S22

Plate S23

Pseudowintera colorata (Raoul) Dandy (WELT SP092400/A: from New Zealand).

1–2. Pollen tetrads in LM, upper row at high focus, lower row in optical cross section, left tetrads in basal view, middle tetrads in lateral view, right tetrads in apical view.

3–8. Pollen tetrads in SEM.

3–4. Basal view.

5–6. Lateral view.

7–8. Apical view.

Scale bars: 10 µm.

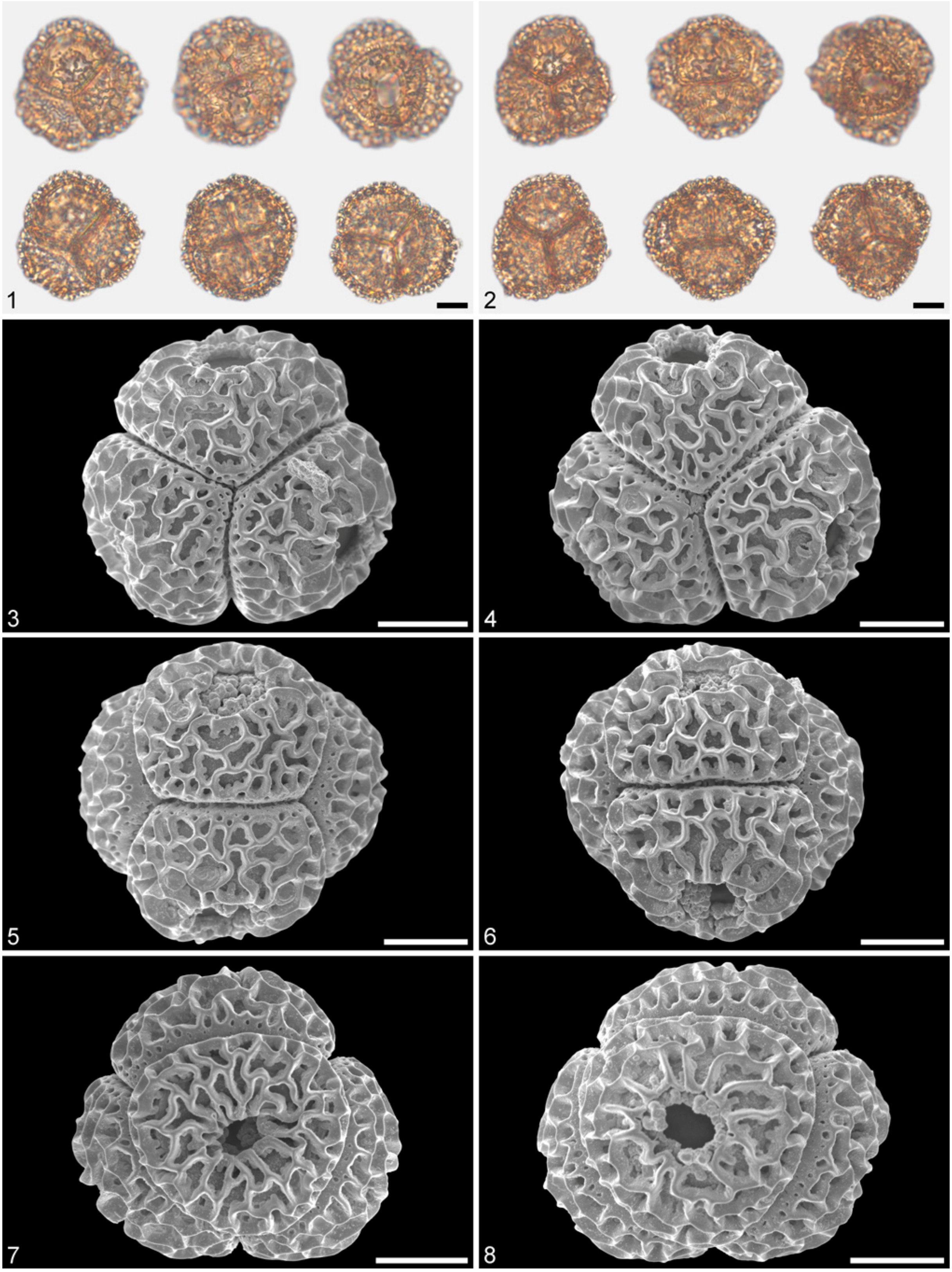

Plate S23

Plate S24

Pseudowintera colorata (Raoul) Dandy (WELT SP092400/A: from New Zealand).

1–8. Close–ups of sculpture in SEM.

1–2. Distal face of pollen.

3–4. Pollen interface in lateral view.

5. Pollen interface in basal view.

6–8. Aperture.

Scale bars: 1 μm.

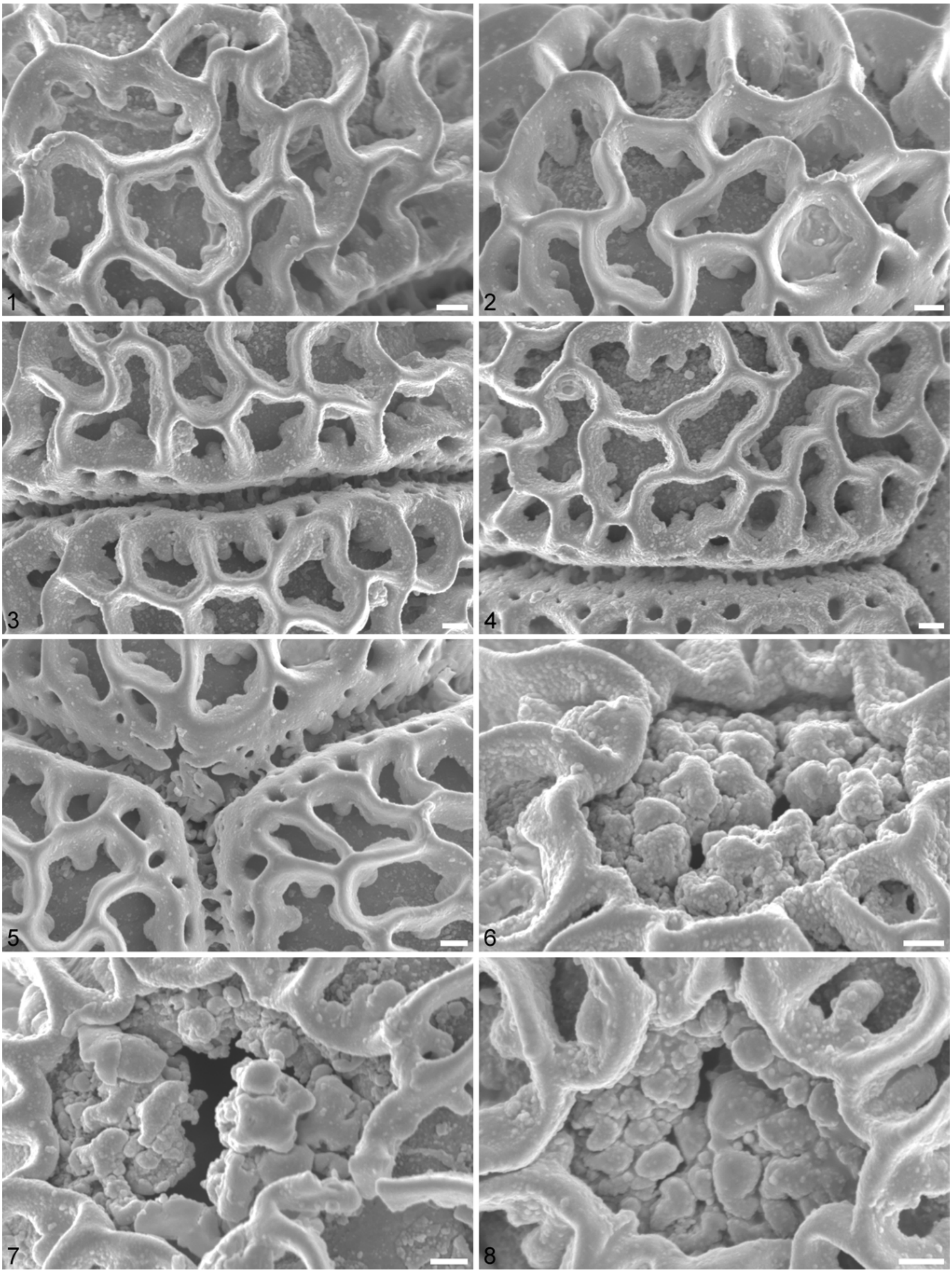

Plate S24

Plate S25

Pseudowintera traversii (Buchan.) Dandy (CHR 229918: from New Zealand).

1–2. Pollen tetrads in LM, upper row at high focus, lower row in optical cross section, left tetrads in basal view, middle tetrads in lateral view, right tetrads in apical view.

3–8. Pollen tetrads in SEM.

3–4. Basal view.

5–6. Lateral view.

7–8. Apical view.

Scale bars: 10 µm.

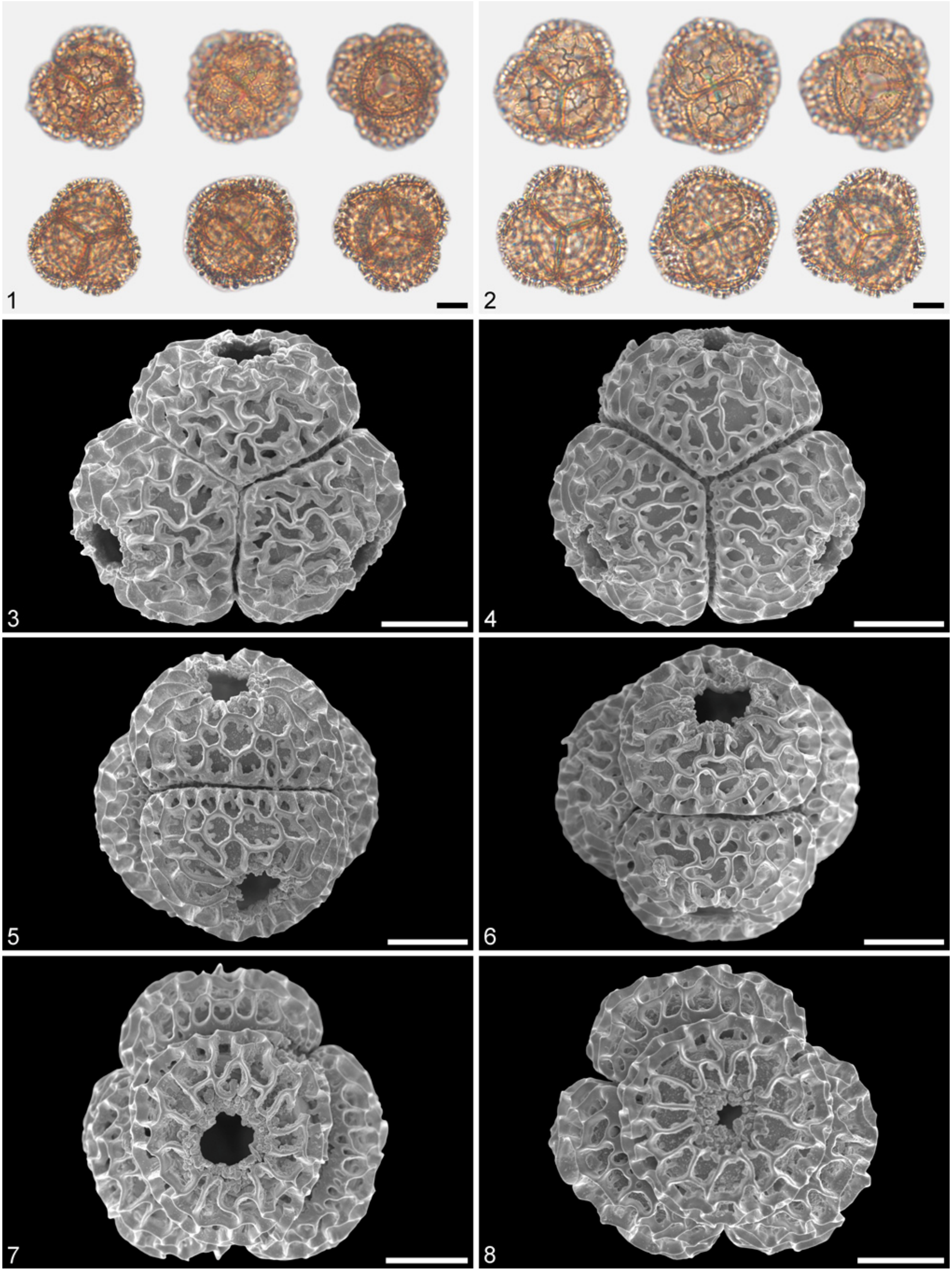

Plate S25

Plate S26

Pseudowintera traversii (Buchan.) Dandy (CHR 229918: from New Zealand).

1–8. Close–ups of sculpture in SEM.

1–2. Distal face of pollen.

3. Pollen interface in lateral view.

4–5. Pollen interface in basal view.

6–8. Aperture region.

Scale bars: 1 µm.

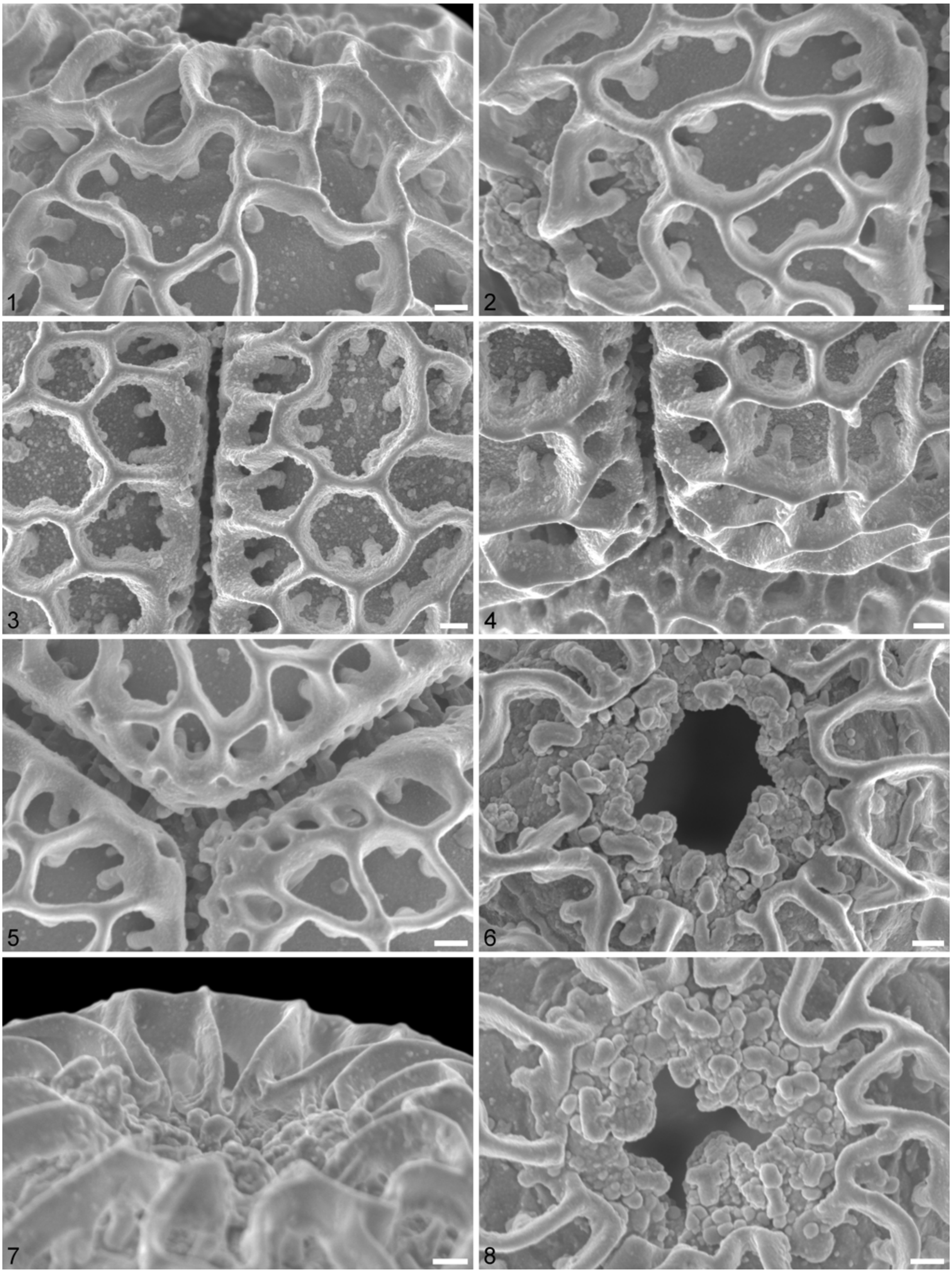

Plate S26

Plate S27

Pseudowintera traversii (Buchan.) Dandy (CHR 325595: from New Zealand).

1–2. Pollen tetrads in LM, upper row at high focus, lower row in optical cross section, left tetrads in basal view, middle tetrads in lateral view, right tetrads in apical view.

3–8. Pollen tetrads in SEM.

3–4. Basal view.

5–6. Lateral view.

7–8. Apical view.

Scale bars: 10 µm.

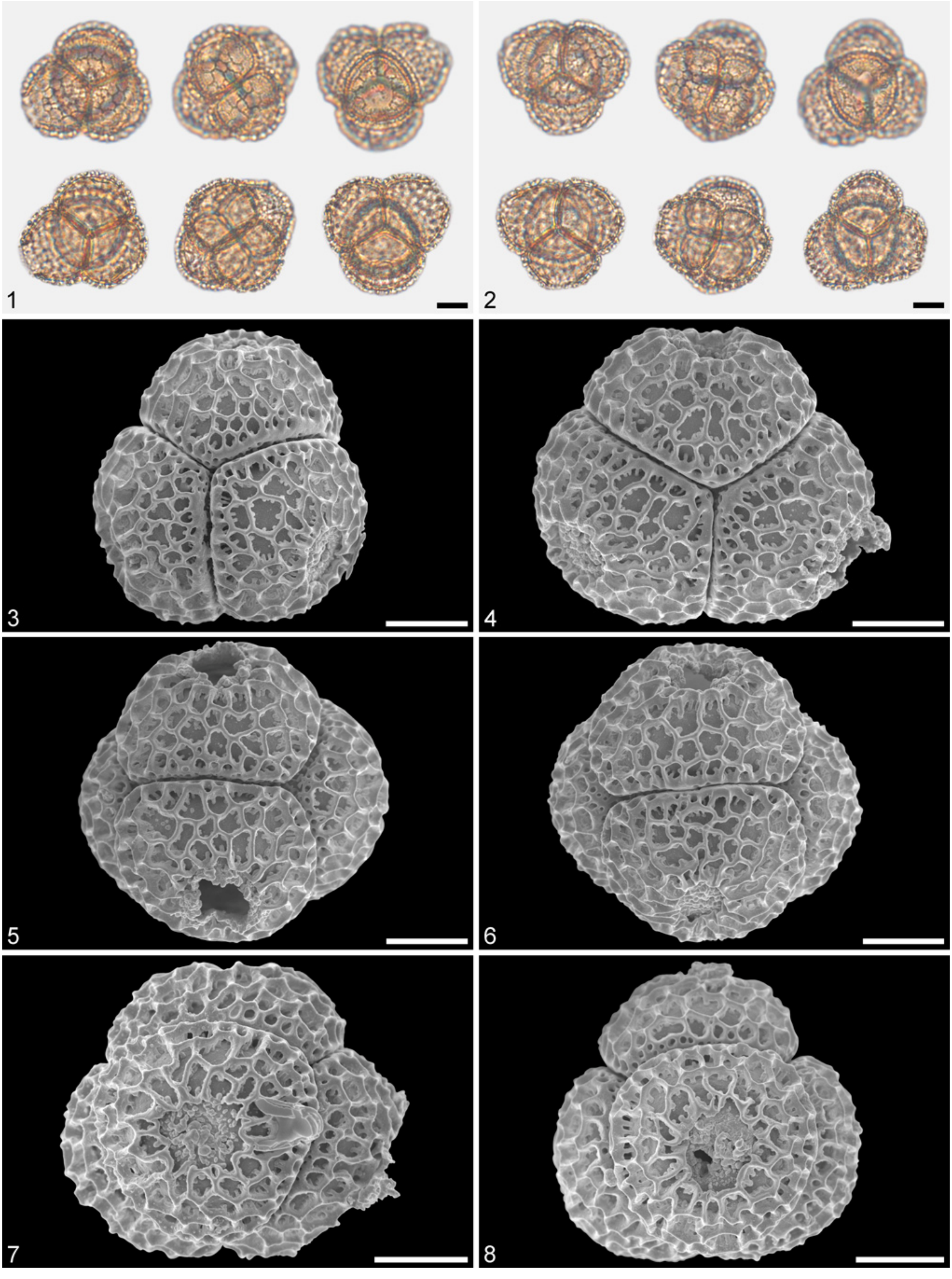

Plate S27

Plate S28

Pseudowintera traversii (Buchan.) Dandy (CHR 325595: from New Zealand).

1–8. Close–ups of sculpture in SEM.

1–2. Distal face of pollen.

3–4. Pollen interface in lateral view.

5–6. Pollen interface in basal view.

7–8. Aperture region.

Scale bars: 1 µm.

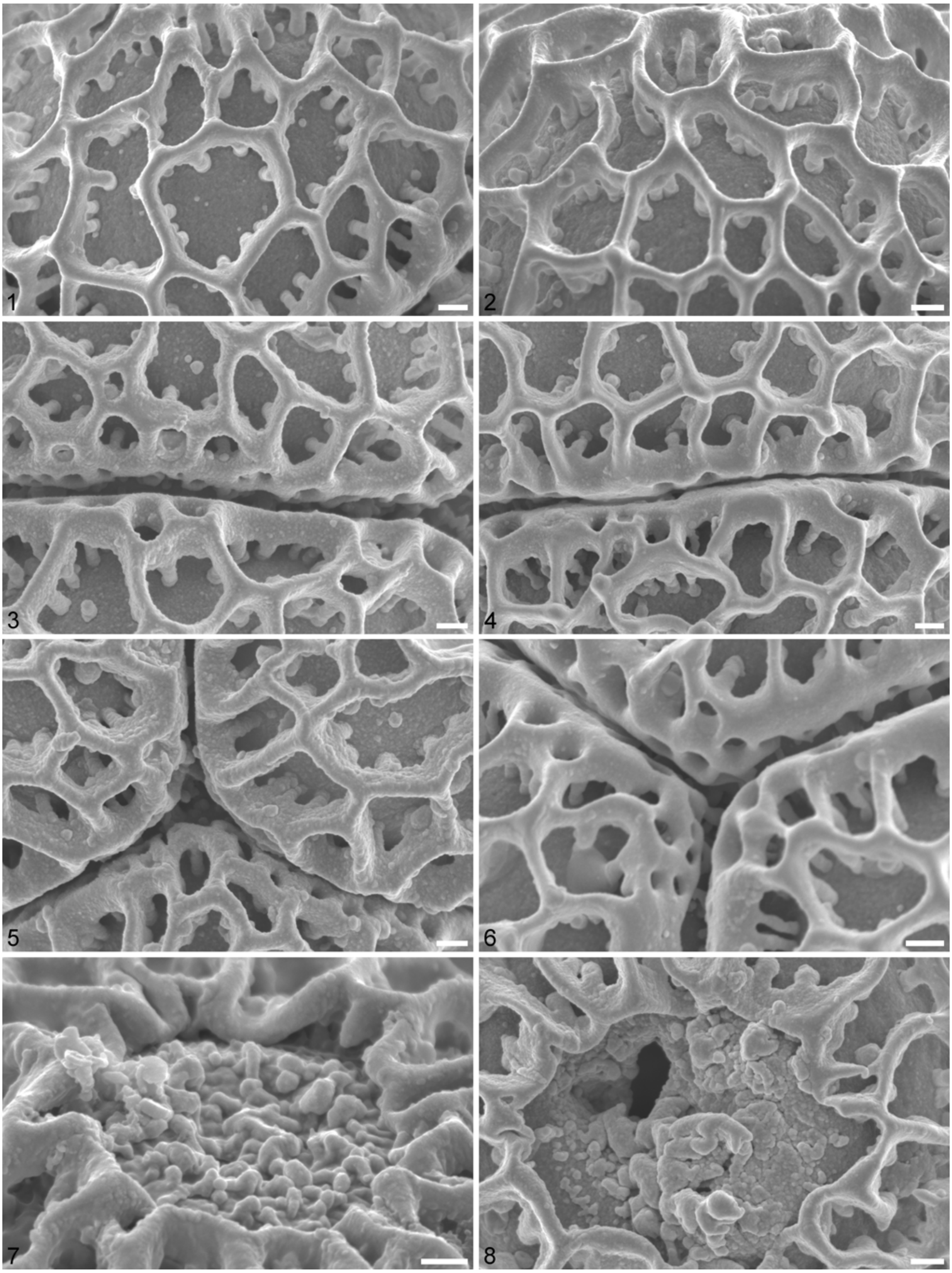

Plate S28