



Pollen morphology of *Youngia* and six related genera (Asteraceae: Cichorieae) and its systematic significance

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Abstract

The pollen morphology of 15 species representing four sections of *Youngia* and 11 species from six other genera of the tribe Cichorieae was investigated. Measurements and observations were conducted through scanning electron microscopy. This study aims to provide new and useful information regarding the extent of pollen morphological diversity within the genus *Youngia* and related genera in the tribe Cichorieae and thus to contribute to a better understanding of the taxonomy and evolution of these groups. Six pollen types, distinguished primarily by the number of apertures and spines in the polar region, are described. Palynological characters are not useful for the delimitation of *Youngia* and its closely related genera *Crepidiastrum*, *Ixeridium*, and *Crepis* at the generic level, and did not fully resolve the relationships between the groups. The distinction of *Faberia* from the other members of the subtribe Crepidinae is supported by the pollen characters. Pollen morphology also did not support that *Youngia* sect. *Desiphylum* sensu Babcock and Stebbins may be separated at the generic level either as *Tibetoseris* or *Pseudoyoungia*. Four pollen types were found in *Youngia* s.l., i.e. *Y. racemifera* type, *Y. japonica* type, *Y. prattii* type and *Y. sericea* type, which partly reflect the sectional classification of *Youngia* sensu Babcock and Stebbins. The systematic position of *Y. racemifera* should be reconsidered according to pollen characters. The pollen data suggest that *Y.* sect. *Mesomeris* is not monophyletic, and the relationships of its species require further examination.

Introduction

The circumscription of the genus *Youngia* Cassini (1831: 88) (Asteraceae: Cichorieae) remains controversial, and the genus has traditionally been difficult to delimit from the other genera of the tribe Cichorieae, such as *Crepis* Linnaeus (1753: 805), *Paraixeris* Nakai (1920: 155), *Faberia* Hemsley (1888: 479), and *Prenanthes* Linnaeus (1753: 797) s.l. (incl. *Nabalus* Cassini (1825: 94)) (Babcock & Stebbins 1937, Kitamura 1942, Shih 1993, 1997, Shih & Kilian 2011). *Youngia* as a genus was first described by Cassini (1831: 84) and later was treated as a section under *Crepis* (Bentham 1873: 163). Babcock & Stebbins (1937) restored the generic status of *Youngia* and subdivided this genus into six sections.

The genus *Youngia* has not been completely revised yet. However, several papers included partial revisions and descriptions of new species. Sennikov & Illarionova (2008) changed the circumscription of *Youngia* on the basis of carpological analysis. They separated three genera from *Youngia*, namely *Tibetoseris* Sennikov in Sennikov & Illarionova (2008: 96) (syn. *Youngia* sect. *Desiphylum* Babcock & Stebbins (1937: 25)), *Sonchella* Sennikov in Sennikov & Illarionova (2008: 96) (syn. *Youngia* sect. *Stenophytum* Babcock & Stebbins (1937: 25)), and *Crepidifolium* Sennikov in Sennikov & Illarionova (2008: 96) (syn. *Youngia* sect.

Crepidopsis Babcock & Stebbins (1937: 25)). Sennikov and Illarionova also suggested that *Y. silhetensis* (Candolle 1838: 218) Babcock & Stebbins (1937: 104) and *Y. racemifera* (Hooker 1881: 397) Babcock & Stebbins (1943: 229) should be transferred to *Faberia*. *Tibetoseris* originally included the five species of Babcock and Stebbins's *Youngia* sect. *Desiphylum* and also the two species described later, *Y. sericea* Shih (1995: 185) and *Y. cristata* Shih & Cai in Shih (1995: 186). Maity & Maiti (2010) redefined *Tibetoseris* to include only its type species *T. depressa* (Hooker & Thomson in Hooker 1881: 397) Sennikov in Sennikov & Illarionova (2007: 1750) and segregated its other species into a new genus, *Pseudoyoungia* Maity & Maiti (2010: 32). The only species of *Parasyncalathium* Zhang *et al.* (2011: 1680), *P. souliei* (Franchet 1895: 257) J.W. Zhang *et al.* (2011: 1680) (incl. *Syncalathium orbiculariforme* Shih (1993: 31)), is very similar to *T. depressa* in its dwarf habit and is included for comparison in our study. Recently Liu & Ho described two new species: *Youngia cyanea* Liu & Ho (2001: 554) and *Y. zhenduoi* Liu & Ho (2001: 554). Tzvelev (2007) removed these two species from *Youngia* to *Chaetoseris* Shih (1991: 398) (*Lactuca* s.l.), and Shih & Kilian treated them as a single species of Lactucinae: *Cicerbita zhenduoi* (S.W. Liu & T.N. Ho) Kilian in Shih & Kilian (2011: 216). Besides, Kitamura (1942) considered *Paraixeris* as a section of the broadly defined *Youngia*. Carpological and cytological investigations by Pak & Kawano (1990, 1992) provided no support for the inclusion of *Paraixeris* into *Youngia* and demonstrated that it cannot be separated from the genus *Crepidiastrum* Nakai (1920: 147). Molecular data also indicated that *Paraixeris* is nested within *Crepidiastrum* (Kilian *et al.* 2009, Peng *et al.* in press). *Faberia nanchuanensis* Shih (1995: 195) was subsequently separated into the monotypic genus *Faberiopsis* Shih & Chen (1996: 439) because of its 3-lobed corolla, presumably different from the 5-toothed corolla of *Faberia*. More comprehensive observations on the variability of corolla in this species convincingly demonstrated that the 3-lobed corolla is a rare morphotype that occurs with the 5-toothed corolla in the same populations; consequently *Faberiopsis* was merged with *Faberia* (Liu *et al.* 2012).

Molecular phylogenetic analysis of Crepidinae by Kilian *et al.* (2009) confirmed that *Crepidifolium* is not part of *Youngia*. The generic limits and relations in Cichorieae have always been difficult to define. Kilian *et al.* (2009) analyzed the phylogeny of Cichorieae and discussed the relationships among the subtribes and genera of the group. This analysis provided a framework for our investigation of the palynological characters in *Youngia* and related genera.

Besides of the problematic delimitation of the genus itself, the species-level taxonomy of *Youngia* is partly unresolved. This is particularly important for our study, as Shih & Kilian (2011) found that approximately 22 of the 30 species of *Youngia* are endemic to China. Palynology often provides new sets of characters, which can be compared to the robust hypothesis of relationships shown in a DNA-based phylogenetic tree (Wortley *et al.* 2007). Pollen characters can facilitate the investigation of problematic taxa and explain the systematic relationships among species in infra-generic and inter-generic relationships. However, the pollen data of *Youngia* are incomplete (Gao 2007, Wang *et al.* 2009). The most comprehensive pollen studies in Crepidinae and Lactucinae are those by Blackmore (1976), Askerova (1982), He (1990), Blackmore & Persson (1996), Lack (2007), Gao (2007), and Wang *et al.* (2009). Gao (2007) studied the morphology of eight genera in Lactucinae and found that pollen morphology is useful for classification of species within Lactucinae but not for the generic classification. Wang *et al.* (2009) demonstrated that in China the pollen morphology of Crepidinae and Lactucinae is difficult to compare with taxonomic and phylogenetic results because of several factors, including missing data on many taxa.

The systematic developments outlined above indicate that the circumscription of *Youngia* is ambiguous. Thus, this study aims to explore the palynological properties of *Youngia* and putatively related genera, including *Crepidiastrum*, *Crepis*, *Ixeridium*, *Faberia*, *Parasyncalathium*, and *Nabalus*, and elucidate their taxonomical value. To achieve these objectives, we provided the first pollen data on 24 species of these genera.

Materials and methods

Pollen samples were obtained from 15 species of *Youngia* sensu Babcock & Stebbins (1937, 1943), representing different sections. Eleven species of six genera of Cichorieae (most species were from subtribe Crepidinae), which were considered to have close systematic relationships with or similarity to *Youngia*, were also sampled. The material was collected mostly in the field, except for the use of a few herbarium specimens kept at the Chengdu Institute of Biology, Chinese Academy of Sciences (CDBI) (Appendix). Details on the herbarium vouchers are included in the list of examined specimens. All pollen samples were prepared for viewing with a scanning electron microscope (SEM). Grains were measured based on SEM images. Only correctly formed pollen grains (20 per specimen) were measured; 740 pollen grains were examined in total. The pollen grains were air-dried, directly mounted on stubs, and sputter-coated with gold palladium. SEM examination was performed using a JSE-5900 microscope at 20kV. The images were digitally processed, and the final plates were prepared using Adobe PhotoShop 7. Descriptive terminology was based on Punt *et al.* (2007).

Results

Pollen grains of *Youngia* and related genera are 19–47 μm in diameter, suboblate, oblate-spheroidal, spheroidal, or prolate-spheroidal in shape; round or angular (subtriangular to subhexagonal) in polar view; and circular or elliptic in equatorial view. The grains are tricolporate or tetracolporate, and echinolophate. The spines are roughly conical or distinctly broader at their bases and range from 1.5 μm to 4.5 μm in height (Table 1). The most variable character within these species is the extent of the polar regions, which vary from a single lophate with one row of spines to an extensive area with many spines. All genera have six abpolar lacunae that are rounded or angular (broader toward the poles). Six parapolar lacunae are also observed, although these are rudimentary or absent in several sub-lophate grains. The parapolar lacunae are pentagonal, but they appear to be triangular in several species. Three polar lacunae are observed, which are rounded (circular or elliptic) or hexagonal (broader toward the poles) and connected to the abpolar lacunae by narrow or broad openings.

Pollen descriptions for the taxa studied

1. *Youngia* sensu Babcock & Stebbins (1937, 1943)

The pollen grains of *Youngia* are 21–47 μm in diameter, oblate-spheroidal, elliptic in equatorial view, hexagonal with convex sides in polar view, tricolporate, and echinolophate. The parapolar lacunae are large and pentagonal. Each ectocolpus is divided into three lacunae connected by narrow interlacunar gaps. The abpolar lacunae are large, angular, and broader toward the poles. The polar areas vary from small to moderately extensive or to very extensive, with 0–19 spines (Table 1).

1a. *Youngia* sect. *Youngia* (Babcock & Stebbins 1937: 26)

The pollen grains are 21 μm to 33 μm in diameter; oblate-spheroidal, elliptic in equatorial view, hexagonal with convex sides in polar view, tricolporate, and echinolophate. The parapolar lacunae are large and pentagonal. Each ectocolpus is divided into three lacunae connected by narrow interlacunar gaps. The abpolar lacunae are large, angular, and broader toward the poles. The spines are short (1.4 μm to 3.0 μm) and tapered. The polar areas are small, each with 0–4 spines (Table 1).

Species examined: *Youngia japonica* (Linnaeus 1767: 107) Candolle (1838: 194) (Figures 1A and 1B), *Y. erythrocarpa* (Vaniot 1903: 319) Babcock & Stebbins (1937: 102) (Figure 6B), *Y. heterophylla* (Hemsley 1888: 475) Babcock & Stebbins (1937: 87) (Figure 5E and 5F), *Y. rosthornii* (Diels 1901: 632) Babcock & Stebbins (1937: 92) (Figures 1C and 1D), and *Y. rubida* Babcock & Stebbins (1937: 100) (Figures 1E and 1F).

TABLE 1. Pollen characters for the species examined in this study; only variable characters are shown (see text for further explanations).

Species	Lacunar shape	Interlacunar gap	Equatorial shape	Polar region spine number	Equatorial diameter	Spine length	Polar regions
<i>Crepis bodinieri</i>	P	narrow	S	4–8	30–39	1.0–2.2	S–M
<i>Crepis napifera</i>	P	broad	OS,S	5–8	24–30	2.2–2.8	M
<i>Crepis rigescens</i>	P	broad	OS	3–8	34–40	1.1–1.9	M
<i>Crepidiastrum sonchifolium</i>	P	narrow	OS	4–6	19–22	1.3–1.6	M
<i>Fabera nanchuanensis</i>	T	broad	OS	0	36–45	2.2–3.6	M
<i>Faberia sinensis</i>	T	narrow	OS	0–3	29–35	2.8–4.7	M
<i>Ixeridium beauverdianum</i>	p	narrow	OS	0	27–29	1.4–2.1	S
<i>Ixeridium dentatum</i>	P	narrow	OS	4–9	27–33	1.1–1.6	M
<i>Syncalathium orbiculariforme</i>	P	narrow	OS	5–6	29–36	2.7–3.4	E
<i>Parasyncalathium souliei</i>	P	narrow	OS	5–6	36–43	3.7–4.3	E
<i>Youngia cineripappa</i>	P	broad	OS	0–2	30–33	1.5–2.9	S
<i>Youngia erythrocarpa</i>	P	broad	OS	0–2	24–31	1.0–2.1	S
<i>Youngia henryi</i>	P	narrow	OS	4–6	29–34	2.0–2.6	M
<i>Youngia heterophylla</i>	P	narrow	OS	0	31–33	1.4–2.9	S
<i>Youngia japonica</i>	P	narrow	OS	0–2	25–31	1.4–2.3	S
<i>Youngia hastiformis</i>	P	narrow	OS	10–14	25–30	2.2–3.3	E
<i>Youngia paleacea</i>	P	broad	OS	10–14	35–38	2.2–3.6	V
<i>Youngia pilifera</i>	P	narrow	OS	13–15	27–33	1.1–2.0	V
<i>Youngia prattii</i>	P	broad	OS	4–5	29–34	1.3–1.7	M
<i>Youngia racemifera</i>	Irregular	broad	OS	13–17	44–47	3.6–4.4	V
<i>Youngia rosthornii</i>	P	narrow	OS	3	26–33	1.3–2.6	S
<i>Youngia rubida</i>	P	narrow	OS	0–4	21–29	1.2–1.8	S
<i>Youngia simulatrix</i>	P	narrow	OS	11–19	22–29	2–2.8	V
<i>Youngia wilsonii</i>	P	broad	OS	7–9	25–33	2.0–2.6	E
<i>Youngia sericea</i>	P	narrow	OS	13–16	28–34	2.1–2.8	V
<i>Nabalus tatarinowii</i> subsp. <i>macrantha</i>	P	narrow	OS	8–10	27–33	2.7–3.1	M

Shape: O—oblate; OS—oblate-spheroidal; P—nearly pentagon; T—nearly trapezium; S—spheroidal. Ornamentation: EL—echinolophate; SE—sub-echinolophate. Polar regions: E—extensive; M—moderately extensive; S—small; V—very extensive.

1b. *Youngia* sect. *Mesomeris* (Babcock & Stebbins 1937: 26)

The pollen grains are 25 µm to 38 µm in diameter, oblate-spheroidal, elliptic in equatorial view, hexagonal with convex sides in polar view, tricolporate, and echinolophate. The paraporal lacunae are large and pentagonal. Each ectocolpus is divided into three lacunae, connected by narrow interlacunar gaps. The abporal lacunae are large, angular, and broader toward the poles. The spines are 1.4 µm to 3.6 µm long and tapered. The polar areas vary from small to moderately extensive, each with 0–15 spines (Table 1).

Species examined: *Youngia cineripappa* (Babcock 1928: 325) Babcock & Stebbins (1937: 60) (Figures 2A and 2B), *Y. pilifera* Shih (1995: 183) (Figures 2C and 2D), *Y. paleacea* (Diels 1912: 202) Babcock & Stebbins (1937: 67) (Figures 2E and 2F), *Y. wilsonii* (Babcock 1928: 331) Babcock & Stebbins (1937: 79) (Figures 3E and 3F), *Y. prattii* (Babcock 1928: 331) Babcock & Stebbins (1937: 81) (Figures 3A and 3B), *Y. henryi* (Diels 1901: 633) Babcock & Stebbins (1937: 83) (Figures 3C and 3D), and *Y. hastiformis* Shih (1995: 185) (Figures 8C and 8D).

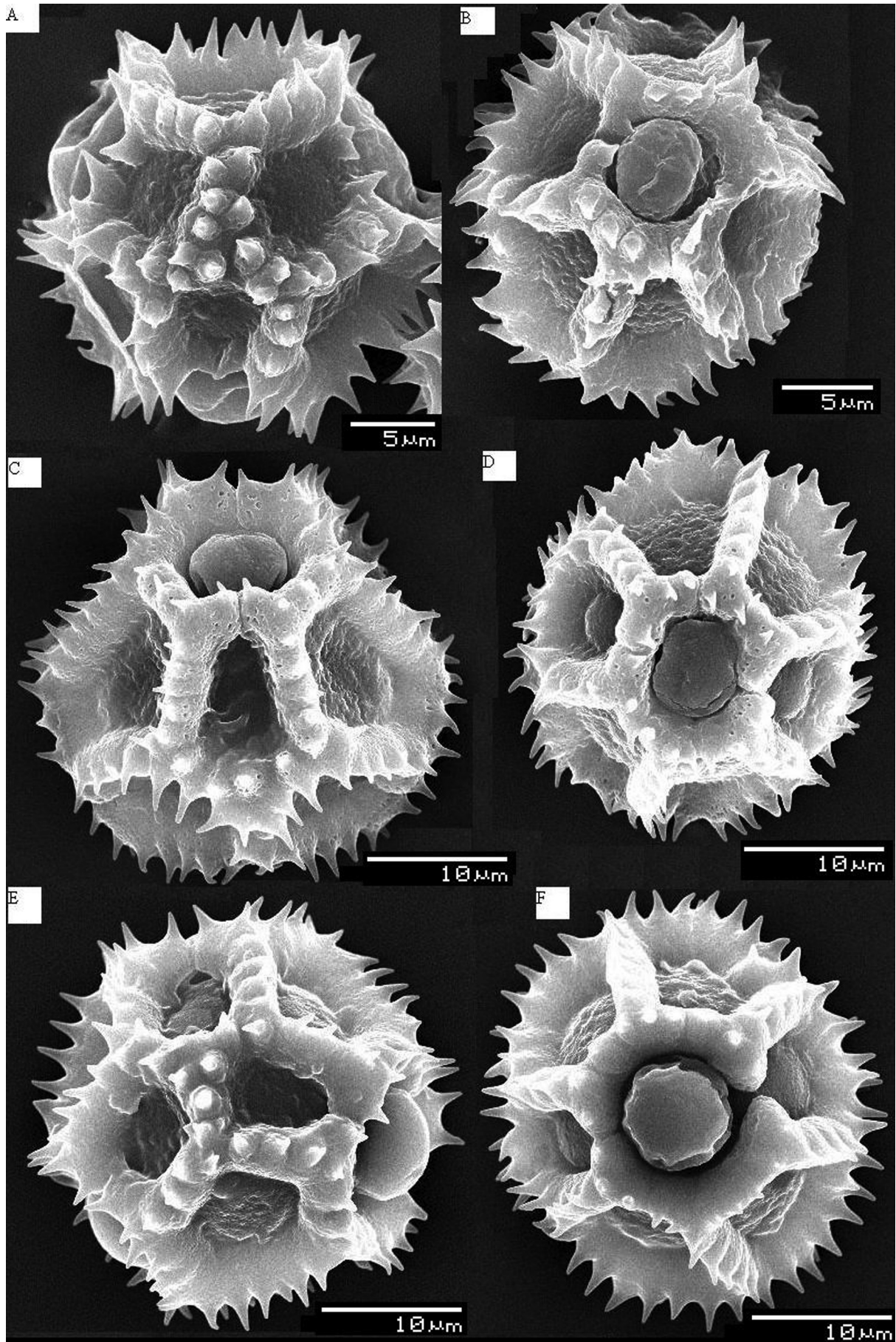


FIGURE 1. SEM micrographs of pollen grains of *Youngia*. **A, B.** *Y. japonica*: **A.** polar view; **B.** equatorial view. **C, D.** *Y. rosthornii*: **C.** equatorial view; **D.** polar view. **E, F.** *Y. rubida*: **E.** polar view; **F.** equatorial view.

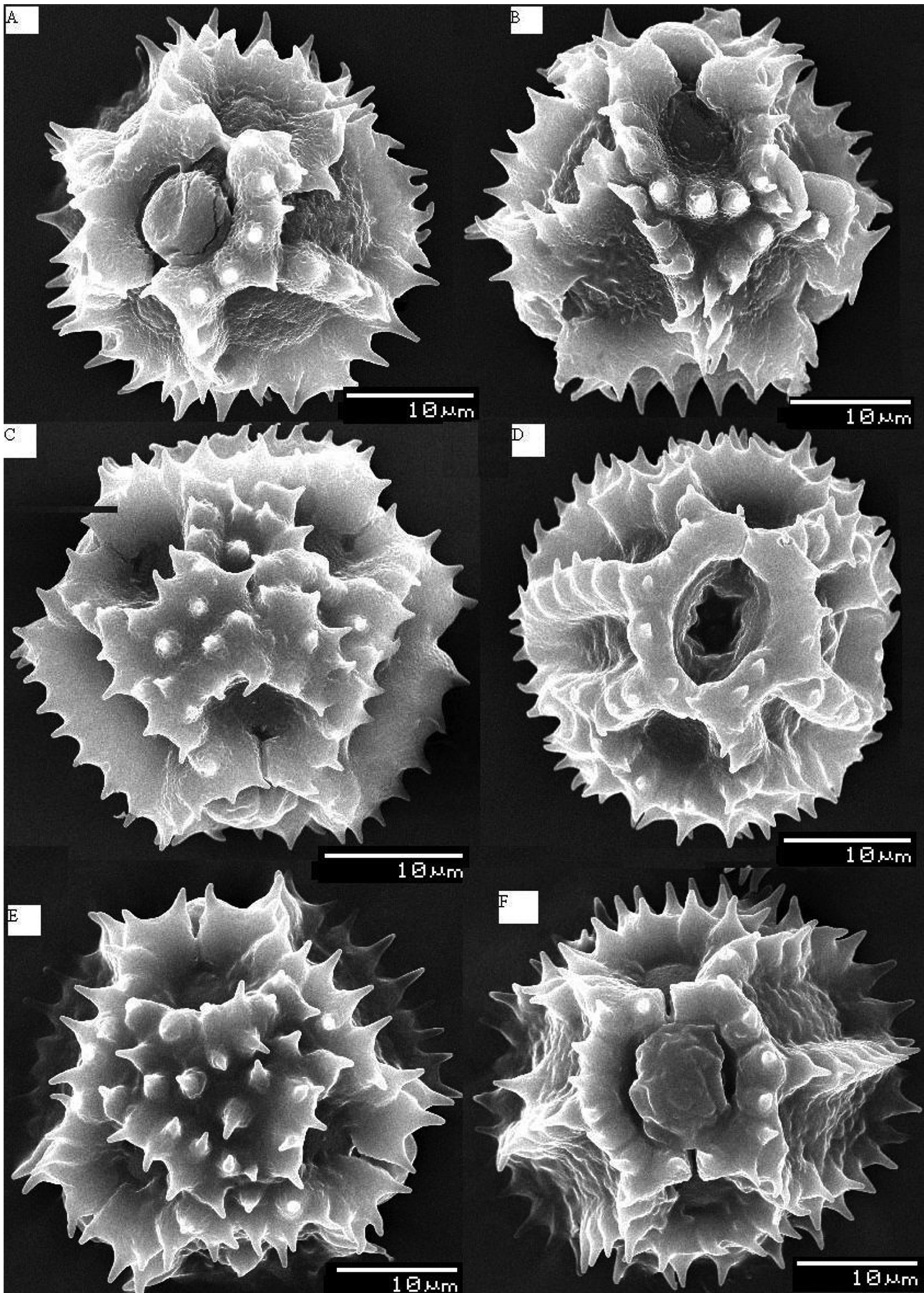


FIGURE 2. SEM micrographs of pollen grains of *Youngia*. A, B. *Y. cineripappa*: A. equatorial view; B. polar view. C, D. *Y. pilifera*: C. polar view; D. equatorial view. E, F. *Y. paleacea*: E. polar view; F. equatorial view.

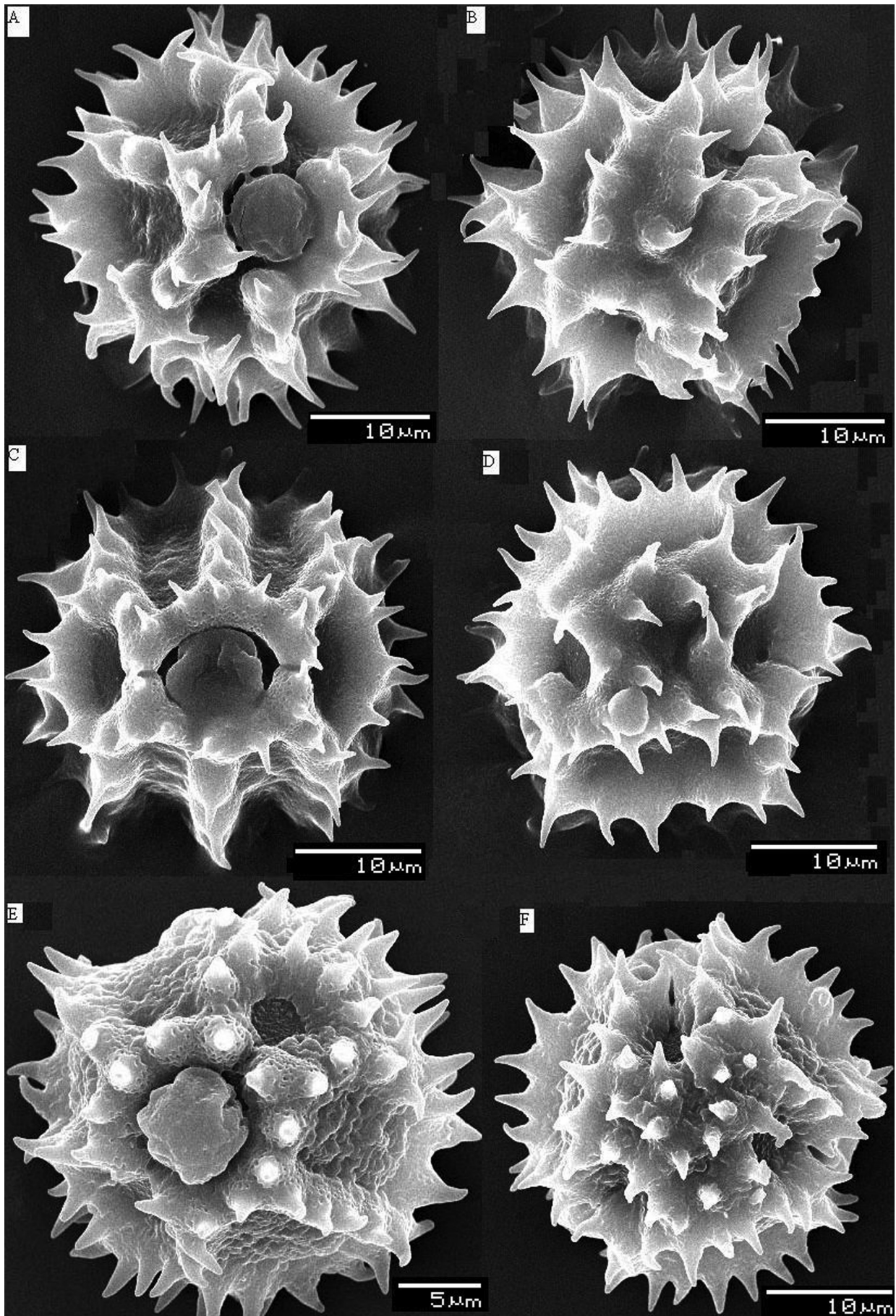


FIGURE 3. SEM micrographs of pollen grains of *Youngia*. **A, B.** *Y. prattii*: **A.** equatorial view; **B.** polar view. **C, D.** *Y. henryi*: **C.** equatorial view; **D.** polar view. **E, F.** *Y. wilsonii*: **E.** equatorial view; **F.** polar view.

1c. *Youngia* sect. *Stenophytum*

The pollen grains are 44 μm to 47 μm in diameter, oblate-spheroidal, elliptic in equatorial view, hexagonal with convex sides in polar view, tricolporate, and echinolophate. The paraporal lacunae are large and pentagonal. Each ectocolpus is divided into three lacunae connected by narrow interlacunar gaps. The abporal lacunae are relatively large, angular, and broader toward the poles. The spines are long (3.6 μm to 4.4 μm) and tapered. The polar areas are very extensive, each with 13–17 isolated central spines (Table 1).

Species examined: *Youngia racemifera* (Figures 4A and 4B).

1d. *Youngia* sect. *Desiphylum*

The pollen grains are 22 μm to 34 μm in diameter, oblate-spheroidal, elliptic in equatorial view, hexagonal with convex sides in polar view, tricolporate, and echinolophate. The paraporal lacunae are large and pentagonal. Each ectocolpus is divided into three lacunae connected by narrow interlacunar gaps. The abporal lacunae are relatively large, angular, and broader toward the poles. The spines are long (2.4 μm to 2.8 μm) and tapered. The polar areas are very extensive, each with 11–19 spines (Table 1).

Species examined: *Youngia simulatrix* (Babcock 1928: 329) Babcock & Stebbins (1937: 39) (Figures 4E and 4F) and *Y. sericea* (Figures 4C and 4D).

2. *Faberia*

The pollen grains are 29 μm to 45 μm in diameter, oblate-spheroidal, circular in equatorial view, circular or elliptic in polar view, tetracolporate, and echinolophate. The paraporal lacunae are small. The spines are long (2.2 μm to 3.6 μm). The polar areas are moderately extensive, with 0–3 isolated central spines (Table 1).

Species examined: *Faberia nanchuanensis* (Figures 5A and 5B) and *F. sinensis* Hemsley (1888: 479) (Figures 5C and 5D).

3. *Ixeridium*

The pollen grains are 27 μm to 33 μm in diameter, oblate-spheroidal, elliptic or hexagonal in equatorial view, subtriangular in polar view, tricolporate, and echinolophate. The paraporal lacunae are large and pentagonal. Each ectocolpus is divided into three lacunae connected by narrow interlacunar gaps. The abporal lacunae are large, angular, and broader toward the poles. The spines are short (1.3 μm to 2.1 μm) and tapered. The polar areas are small to moderately extensive, with 0–9 isolated central spines (Table 1).

Species examined: *Ixeridium dentatum* (Thunberg in Murray 1784: 715) Tzvelev (1964: 392) (Figures 7A and 7B) and *I. beauverdianum* (Léveillé 1910: 450) Springate in Grierson & Springate (2000: 402) (Figures 7C and 7D).

4. *Crepidiastrum*

The pollen grains are 19 μm to 22 μm in diameter, oblate-spheroidal, elliptic or hexagonal in equatorial view, subtriangular in polar view, tetracolporate, and echinolophate. The paraporal lacunae are large and pentagonal. Each ectocolpus is divided into three lacunae connected by narrow interlacunar gaps. The abporal lacunae are large, angular, and broader toward the poles. The spines are short (1.3 μm to 1.6 μm) and tapered. The polar areas are small to moderately extensive, with 4–6 isolated central spines (Table 1).

Species examined: *Crepidiastrum sonchifolium* (Maximowicz 1859: 180) Pak & Kawano (1992: 58) (Figures 7E and 7F).

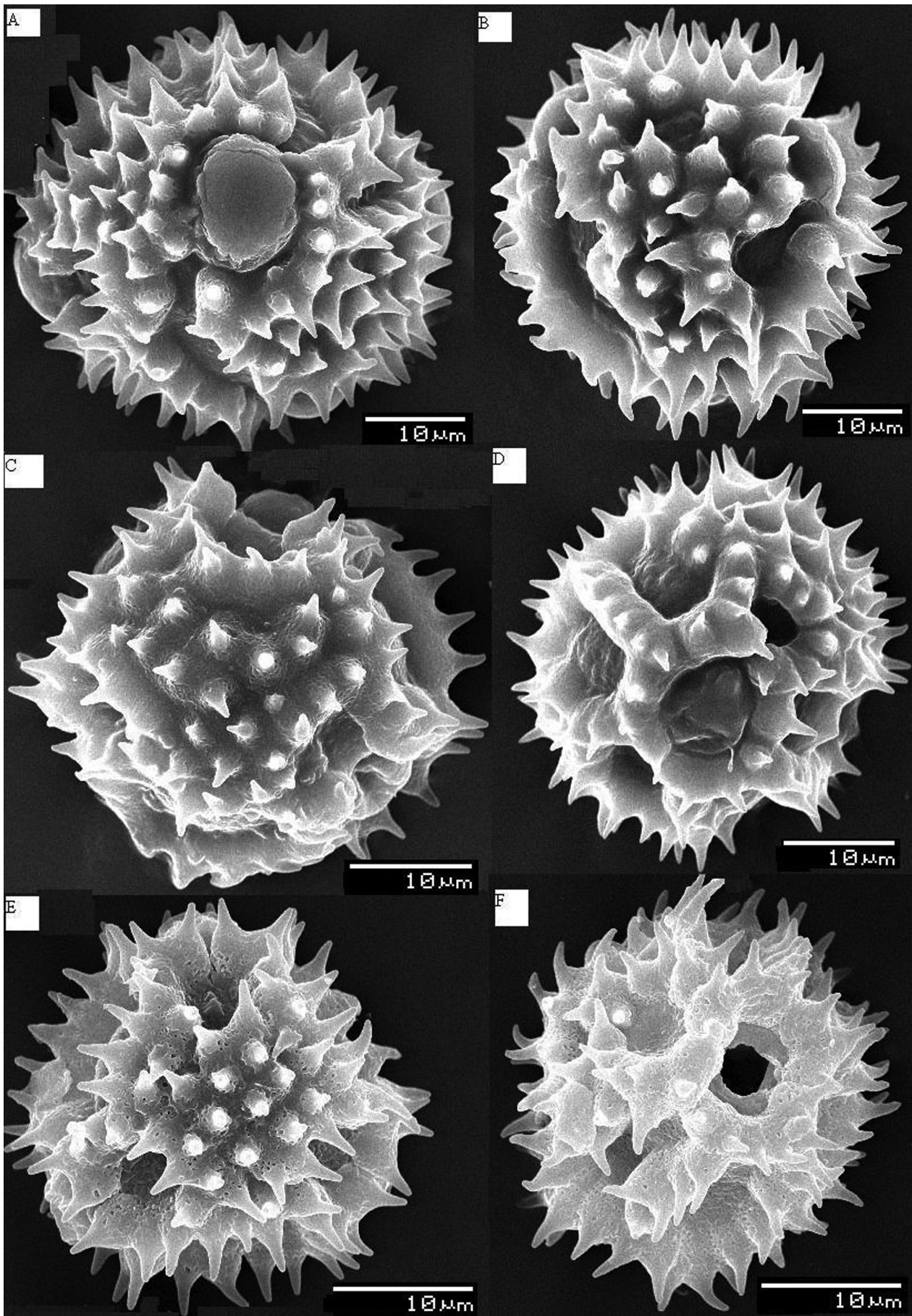


FIGURE 4. SEM micrographs of pollen grains of *Youngia*. A, B. *Y. racemifera*: A. equatorial view; B. polar view. C, D. *Y. sericea*: C. polar view; D. equatorial view. E, F. *Y. simulatrix*: E. polar view; F. equatorial view.

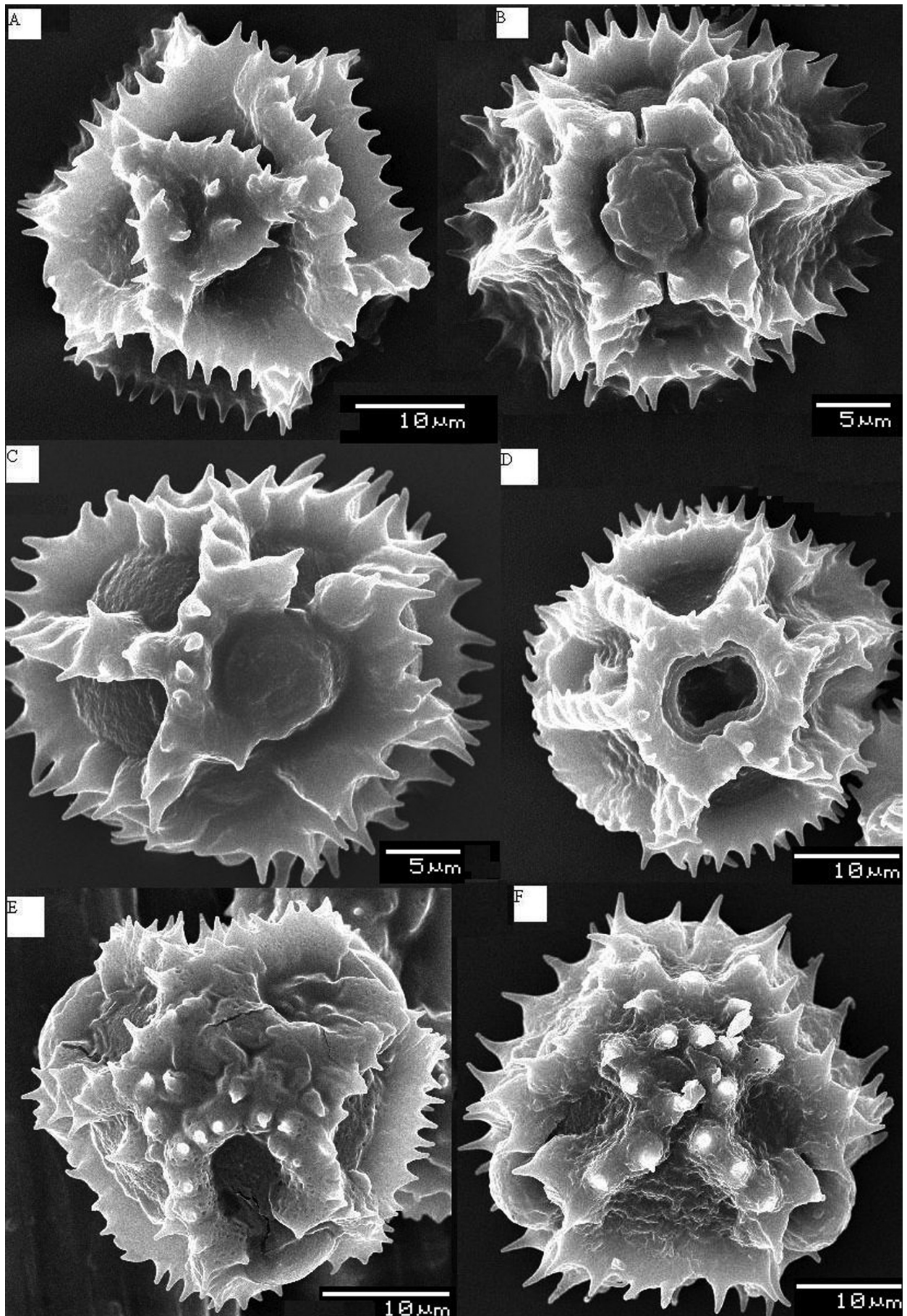


FIGURE 5. SEM micrographs of pollen grains of *Faberia* and *Youngia*. **A, B.** *F. nanchuanensis*: **A.** equatorial view; **B.** polar view. **C, D.** *F. sinensis*: **C.** equatorial view; **D.** polar view. **E, F.** *Y. heterophylla*: **E.** equatorial view; **F.** polar view.

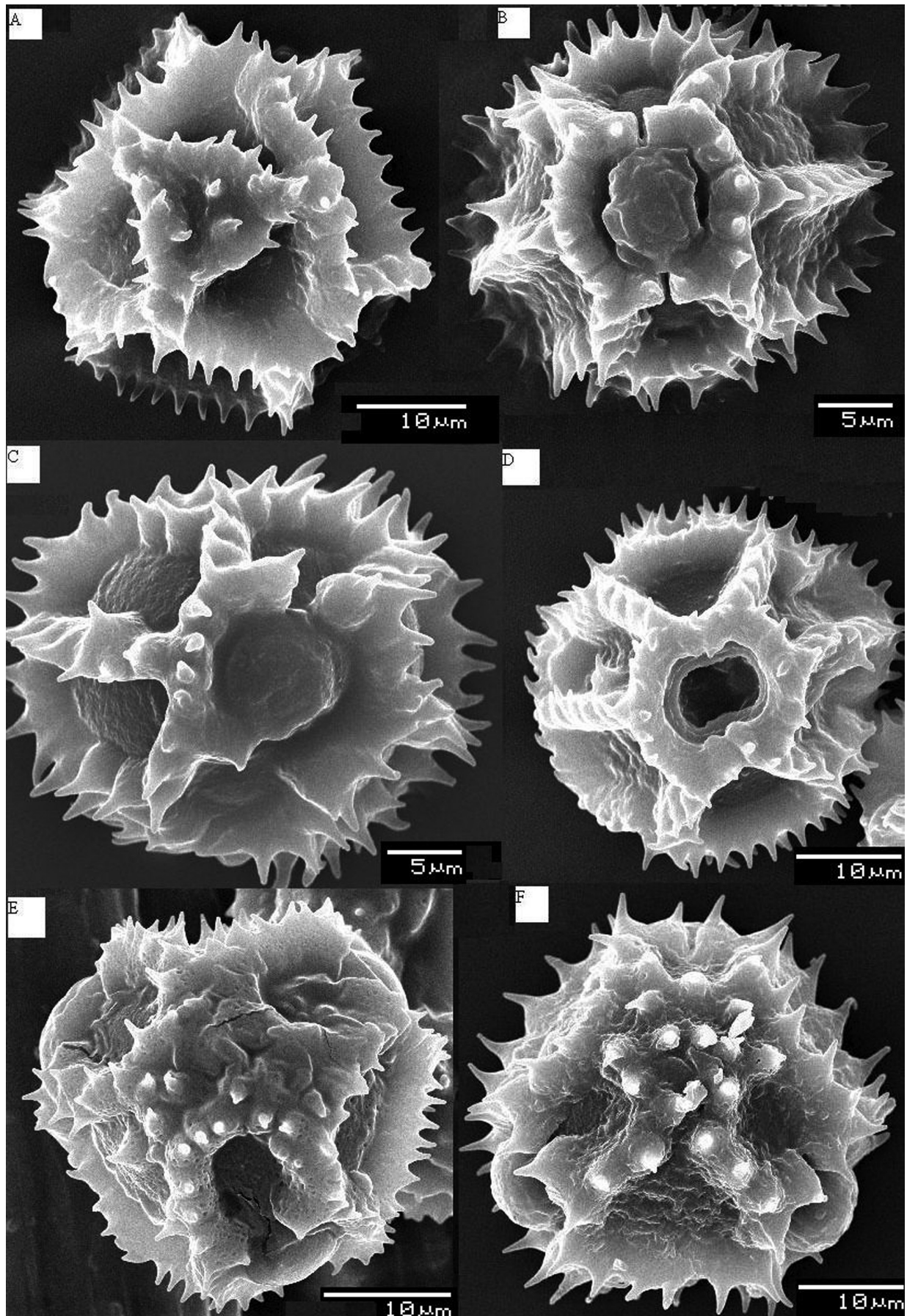


FIGURE 6. SEM micrographs of pollen grains of *Crepis*, *Youngia*, and *Syncalathium*. **A.** *C. bodinieri* (polar view). **B.** *Y. erythrocarpa* (equatorial view). **C.** *C. hapifera* (equatorial view). **D.** *C. bodinieri* (equatorial view). **E.** *C. rigescens* (polar view). **F.** *S. orbiculariforme* (polar view).

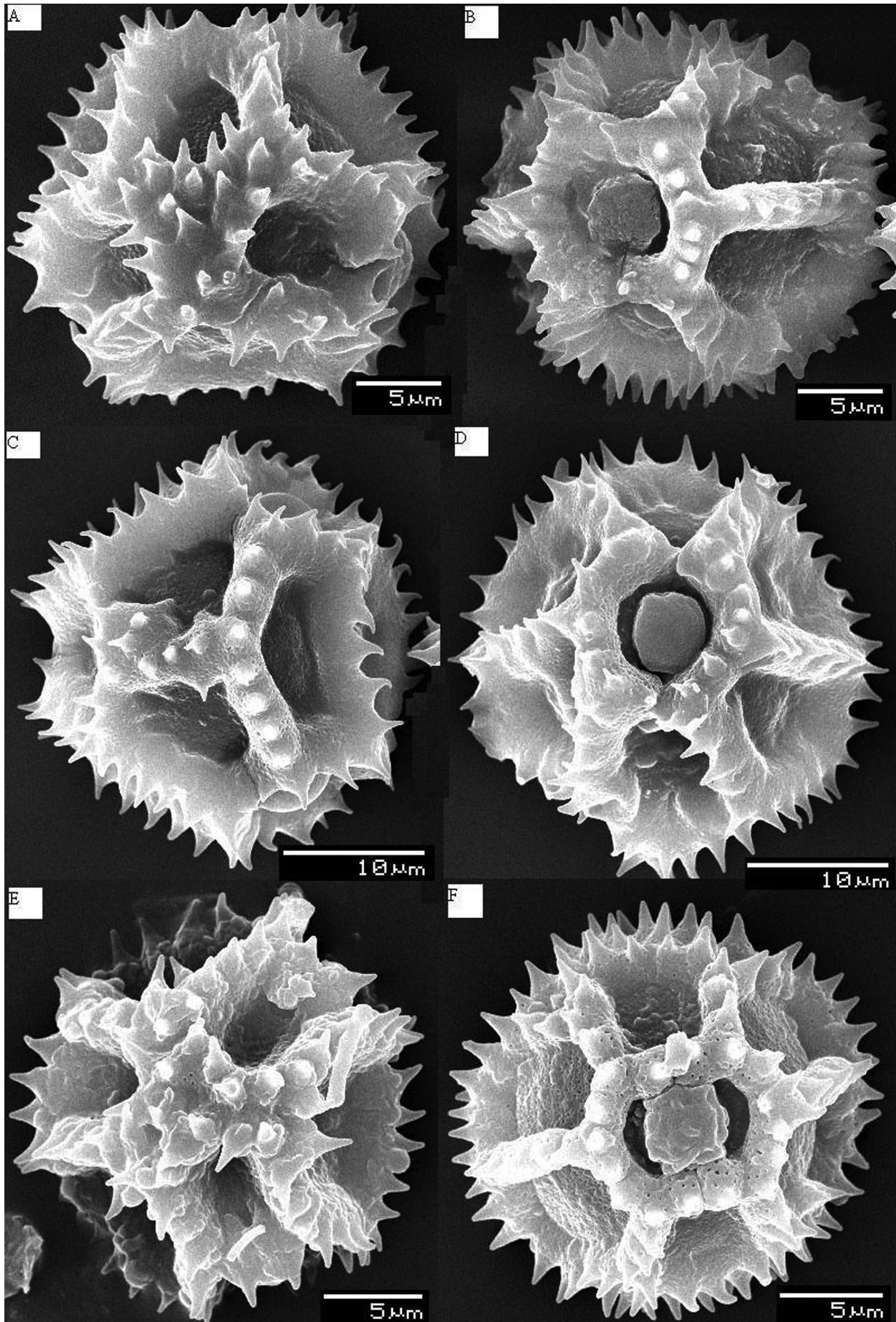


FIGURE 7. SEM micrographs of pollen grains of *Ixeridium* and *Crepidiastrum*. A, B. *I. dentatum*: A. polar view; B. equatorial view. C, D. *I. beauverdianum*: C. polar view; D. equatorial view. E, F. *C. sonchifolium*: E. polar view; F. equatorial view.

5. *Crepis*

The pollen grains are 24 µm to 40 µm in diameter, oblate-spheroidal, elliptic in equatorial view, circular or subtriangular in polar view, tricolporate, and echinolophate. Each ectocolpus is divided into three lacunae connected by narrow interlacunar gaps. The abporal lacunae are large, angular, and broader toward the poles. The spines are short (1.0 µm to 2.8 µm). The polar areas are moderately extensive, with 4–8 isolated central spines (Table 1).

Species examined: *Crepis bodinieri* Lévillé (1915: 15) (Figures 6A and 6D), *C. napifera* (Franchet 1895: 292) Babcock (1947: 629) (Figure 6C), and *C. rigescens* Diels (1912: 202) (Figure 6E).

6. *Parasyncalathium*

The pollen grains are 29 µm to 43 µm in diameter, oblate-spheroidal, elliptic in equatorial and polar views, tricolporate, and echinolophate. Each ectocolpus is divided into three lacunae connected by narrow interlacunar gaps. The abporal lacunae are large, angular, and broader toward the poles, and the paraporal lacunae are also large. The spines are 2.7 µm to 4.3 µm long, with broad conical bases. The polar areas are moderately extensive, each with 5–6 isolated central spines (Table 1).

Species examined: *Parasyncalathium souliei* (Figures 8A and 8B) and *Syncalathium orbiculariforme* (Figure 6F).

7. *Nabalus*

The pollen grains are 27 µm to 33 µm in diameter, spheroidal or oblate-spheroidal, circular or elliptic in equatorial view, hexagonal in polar view, tricolporate, and echinolophate. Each ectocolpus is divided into three lacunae, connected by narrow interlacunar gaps. The abporal lacunae are large, angular, and broader toward the poles. The spines are 2.7 µm to 4.3 µm long, with broad conical bases. The polar region is with irregular fissures. The polar areas are moderately extensive, each with 8–10 isolated central spines (Table 1).

Species examined: *Nabalus tatarinowii* subsp. *macrantha* (Stebbins in Walker 1941: 672) Kilian in Shih & Kilian (2011: 342) (Figures 8E and 8F).

Discussion

Pollen morphology in *Youngia*

Pollen grains in *Youngia* have highly divergent macro-morphological characters. Four pollen types can be found in *Youngia* (see Key to Pollen Types below). The pollen morphology in *Y. sect. Desiphylum* is very homogeneous. The polar regions are very extensive. Although *Y. sericea* and *Y. simulatrix* were separated into *Tibetoseris* by Sennikov & Illarionova (2008), and later into *Pseudoyoungia* by Maity & Maiti (2010), the pollen morphology of *Y. sericea*, *Y. simulatrix* and *Y. paleacea* (the latter belongs to *Y. sect. Mesomeris* sensu Babcock & Stebbins) shows no significant difference. Thus the pollen of these species belongs to the same *Y. sericea* type. The pollen data do not support the generic status of *Tibetoseris* or *Pseudoyoungia* and confirm the inclusion of *Pseudoyoungia* into *Youngia* (Shih & Kilian 2011).

The pollen grain characters of *Youngia racemifera*, including (sub-)lophate grain size, spine number, and spine height, significantly deviate from the other species of *Youngia* but somewhat resemble those of the *Dubyaea atropurpurea* (Franchet 1895: 294) Stebbins (1940: 56) clade (Wang *et al.* 2009) in terms of its sub-lophate grain shape. These findings show that the systematic classification of *Y. racemifera* warrants reconsideration. However, these results do not support the transfer of *Y. racemifera* to *Faberia*, as proposed by Sennikov & Illarionova (2007).

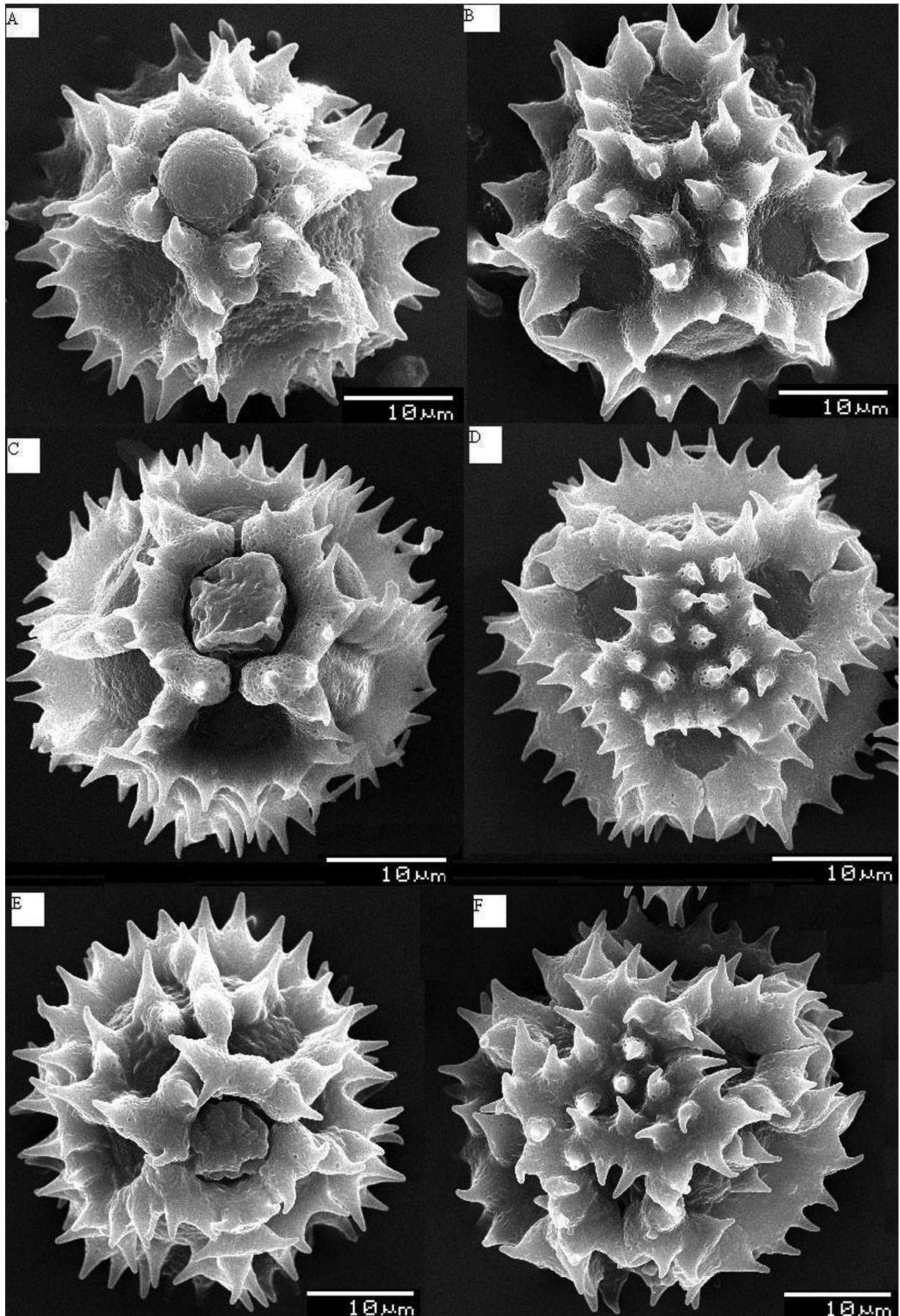


FIGURE 8. SEM micrographs of pollen grains of *Parasyncalathium*, *Youngia*, *Nabalus*, and *Syncalathium*. A. *P. souliei* (equatorial view). B. *S. orbiculariforme* (polar view). C, D. *Y. hastiformis*: C. equatorial view; D. polar view. E, F. *N. tatarinowii* subsp. *macrantha*: E. equatorial view; F. polar view.

The results are partly consistent with the sectional classification by Babcock and Stebbins. The palynological characters of *Youngia* sect. *Youngia* are very homogeneous (*Y. japonica* type), with small polar regions, and only a slight difference in the spine number is observed among the species. Both the polar regions and spine number of the pollen grains in *Y.* sect. *Mesomeris* are variable. Three pollen types can be found in this section. *Youngia henryi* and *Y. prattii* are distinct from the other species in their section (*Y. prattii* type), with the moderately extensive polar region size and spine number. The pollen characters of *Y. cineripappa* resemble those of *Y. japonica*, with small polar regions and 0–2 spines, in contrast to those of other species in *Y.* sect. *Mesomeris*. *Youngia paleacea*, *Y. pilifera* and *Y. hastiformis* (*Y. sericea* type) have more spines than the other species in this section and thus show a closer relationship with *Y. sericea*, which also resembles *Y. atripappa* (Babcock 1928: 324) Kilian in Shih & Kilian (2011: 254) (Wang *et al.* 2009). The morphological convergence in pollen of these species may be related to the habitat similarity. *Youngia* sect. *Mesomeris* is not homogeneous and has been recently reclassified on morphological grounds by Sennikov & Illarionova (2007). Its relationships with other species need to be determined further.

In most cases, pollen morphology in a single particular species is invariable. In *Youngia paleacea*, however, both spherical (Figure 13A) and triangular pollen grains (Figure 13B) can be found. A considerable morphological variation was detected in *Y. paleacea* by Babcock & Stebbins (1937), who recognized three subspecies of this species. The observed differences in pollen morphology of *Y. paleacea* may correspond to the morphological differences, and further studies are needed to reveal the taxonomic significance of this variability.

Pollen morphology in the other genera

The most variable pollen characters in this study are the size of the polar area and the spine number in different species. All the scanned pollen can be divided into five types (see Key to Pollen Types below). *Faberia nanchuanensis* and *F. sinensis* are very distinct from the other species of the subtribe Crepidinae, in which they were previously included (Kilian *et al.* 2009), because of their tetracolporate pollen (*F. nanchuanensis* type). Up to now, only few species were reported with tetracolporate pollen in the tribe Cichorieae. No species in the subtribe Crepidinae has the tetracolporate pollen, but this pollen type was recorded in *Sonchus* (Qureshi *et al.* 2002, He 1990), which phylogenetic placement is the subtribe Hyoseridinae (Kilian *et al.* 2009). It is tempting to suggest that *Faberia* may have a closer relationship with Hyoseridinae instead of its former placement to Crepidinae. But the ITS phylogeny of Cichorieae shows that *Faberia* is one of the basal branches of Lactucinae (Shih & Kilian 2011). The pollen morphology of *F. nanchuanensis* and *F. sinensis* is very similar. Our results support that *Faberiopsis nanchuanensis* should be included in *Faberia* (Liu *et al.* 2011). These results are consistent with the current classifications (Shih & Kilian 2011), and with the karyological analysis of *Faberia* (Liu *et al.* 2012).

According to Zhang *et al.* (2011), *Syncalathium souliei* (Franchet 1895: 257) Ling (1965: 286) (Figure 8A) and *S. orbiculariforme* is the same species of Lactucinae, which is not part of *Syncalathium* s.str. (Crepidinae) and is now treated as *Parasyncalathium souliei*. Our results confirm that the two species can be treated as one in terms of the pollen morphology. We originally assumed that *Parasyncalathium* and *Youngia* sect. *Desiphylum*, both growing in sub-alpine habitats, may have similar pollen characters. The actual observations contradicted to our hypothesis, because pollen grains of *P. souliei* have smaller polar regions and fewer spines in polar regions.

Nabalus tatarinowii subsp. *macrantha* is distinct from other species because of irregular fissures in the polar region. The pollen data do not support an assumption that *N. tatarinowii* subsp. *macrantha* has a close relationship with the other species examined.

The pollen morphology of *Crepis* is homogeneous. The pollen of *Crepis bodinieri*, *C. napifera* and *C. rigescens* is similar with moderately extensive polar areas and 4–8 isolated central spines. The pollen grains are of the *Youngia prattii* type.

The pollen morphology of the two species of *Ixeridium* is different. The pollen of *I. beauverdianum* is of the *Youngia japonica* type, whereas the pollen of *I. dentatum* is of the *Y. prattii* type. The pollen of

Crepidiastrum sonchifolium is of the *Y. prattii* type. In these cases the pollen morphology does not show a clear difference at the generic level.

The pollen characters are not useful to determine the relationships of *Youngia* sect. *Youngia*, *Y. sect. Mesomeris*, *Ixeridium*, *Crepidiastrum*, and *Crepis*. Thus, pollen characters are of questionable value in the classification of closely related genera, although achene characters and other morphology are distinct in different genera of Cichorieae (Shih 1993, Sennikov 1997, Sennikov & Illarionova 2007). Gao (2007) and Wang *et al.* (2009) found that the pollen characters of *Youngia* and closely related genera are difficult to match the recent systematic and phylogenetic results. Pollen characters are highly homoplastic and subject to convergence through repeated parallel evolutionary events, and may have converged under habitat pressure. Base ornamentation varies with the species. In this study, the base ornamentation in most species is smooth or slightly concave (Figures 9–12). By contrast, the ornamentation in *Youngia paleacea* and *Y. simulatrix* (Figure 11) is deeply concave, similar to perforation. This character cannot be used to distinguish between different genera and may be associated with alpine habitats.

Key to the pollen types delimited in this study

1. Pollen tetracolporate, lacunae 14..... *Faberia nanchuanensis* type
- Pollen tricolporate, lacunae 15..... 2
2. Pollen sub-lophate, pollen size 44 μm to 47 μm , spine height 3.6 μm to 4.4 μm , lacuna irregular
..... *Youngia racemifera* type
- Pollen lophate, pollen size 19 μm to 40 μm , spine height 1.4 μm to 2.9 μm , lacuna pentagonal 3
3. Polar region with irregular fissures..... *Nabalus tatarinowii* subsp. *macrantha* type
- Polar region without fissures 4
4. Spine number 0–4 in polar region, polar region small *Youngia japonica* type
- Spine number 4–19 in polar region..... 5
5. Spine number 4–9 in polar region, polar region moderate *Youngia prattii* type
- Spine number 10–19 in polar region, polar region extensive..... *Youngia sericea* type

Conclusions

The pollen morphology does not support an assumption that *Youngia* sect. *Desiphylum* sensu Babcock & Stebbins may be treated as a separate genus (*Tibetoseris* or *Pseudoyoungia*). The pollen data are not useful to determine the relationships of *Y. sect. Youngia*, *Y. sect. Mesomeris*, *Ixeridium*, *Crepidiastrum*, and *Crepis* at the generic level. The pollen characters suggest that *Y. racemifera* is not a member of *Faberia*, and its systematic position should be reconsidered. *Youngia* sect. *Mesomeris* is not monophyletic, and its relationships with other species warrant reconsideration based on the pollen data. The distinction of *Faberia* from the other species of the subtribe Crepidinae is supported by the tetracolporate pollen.

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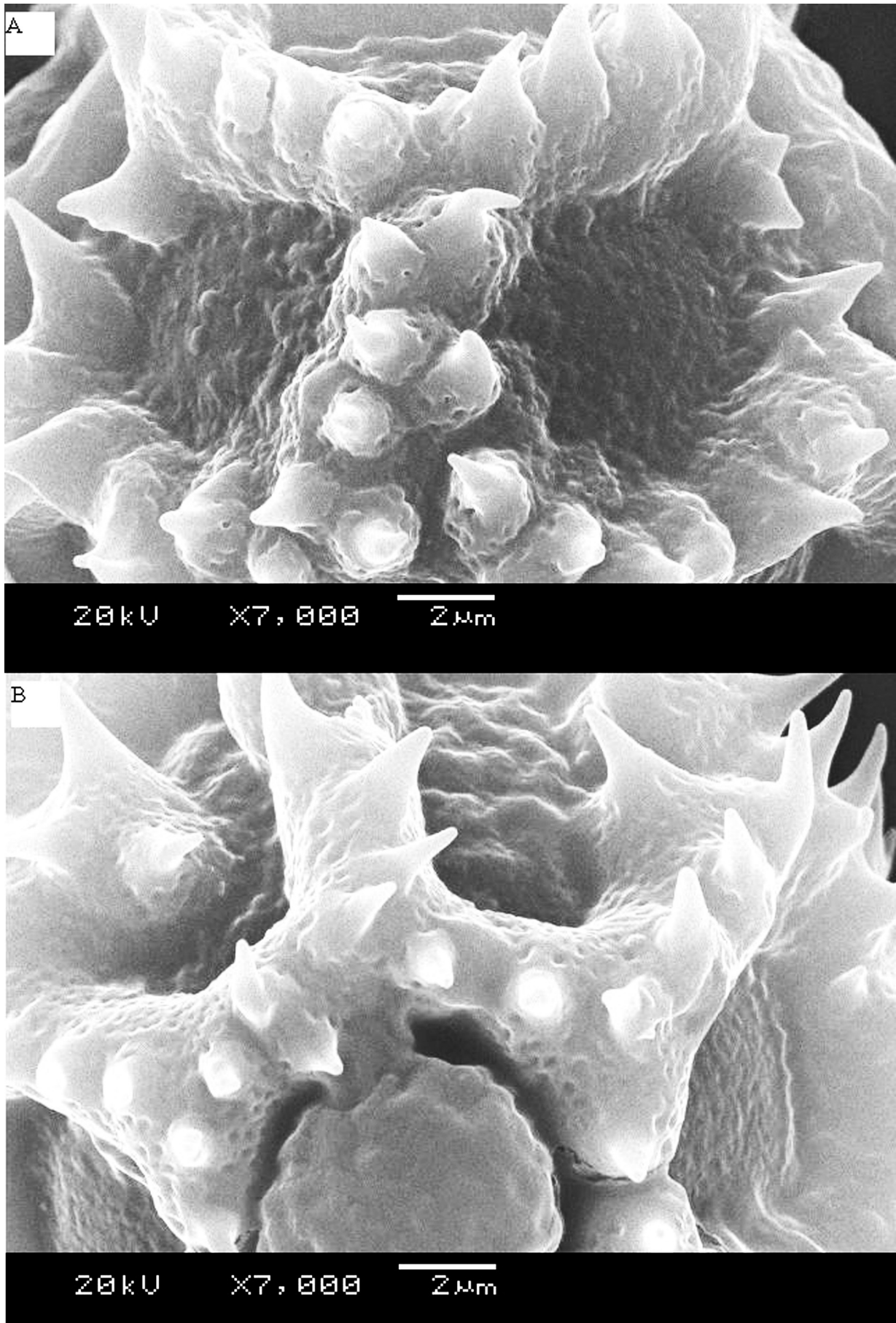


FIGURE 9. Partial enlarged SEM micrographs of pollen grains of *Youngia*. A. *Y. japonica*. B. *Y. rubida*.

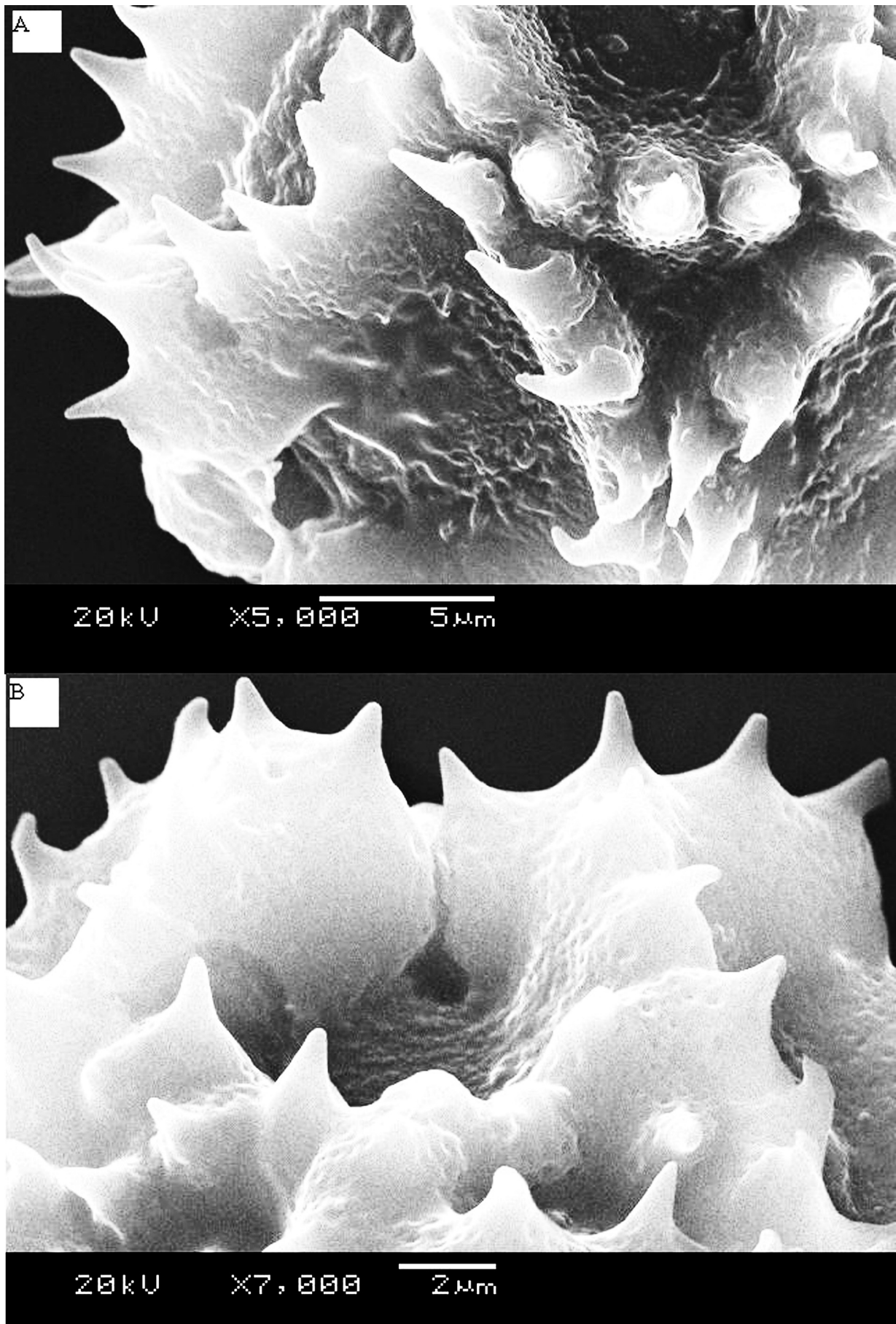


FIGURE 10. Partial enlarged SEM micrographs of pollen grains of *Youngia*. A. *Y. cineripappa*. B. *Y. pilifera*.

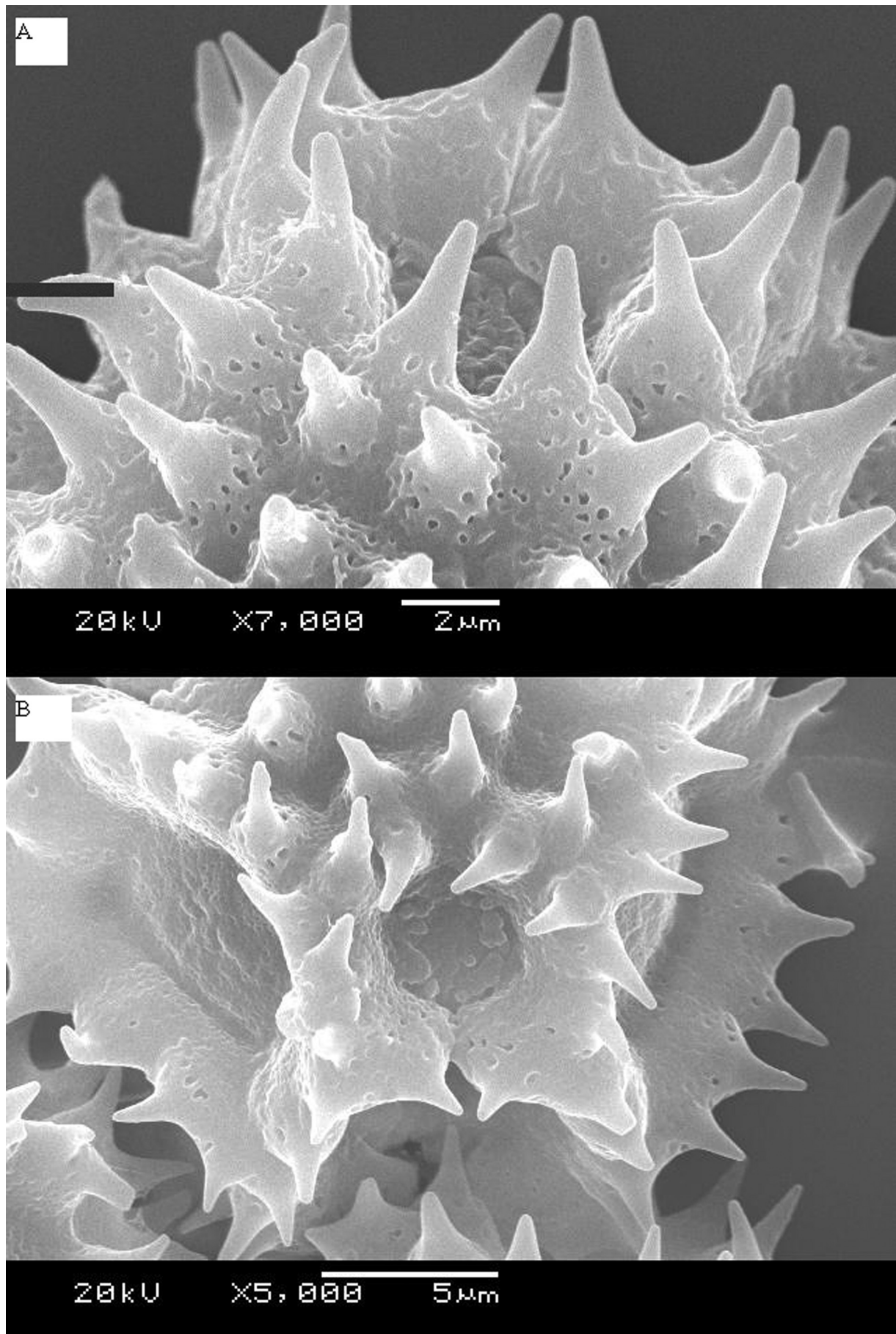


FIGURE 11. Partial enlarged SEM micrographs of pollen grains of *Youngia*. A. *Y. simulatrix*. B. *Y. paleacea*.

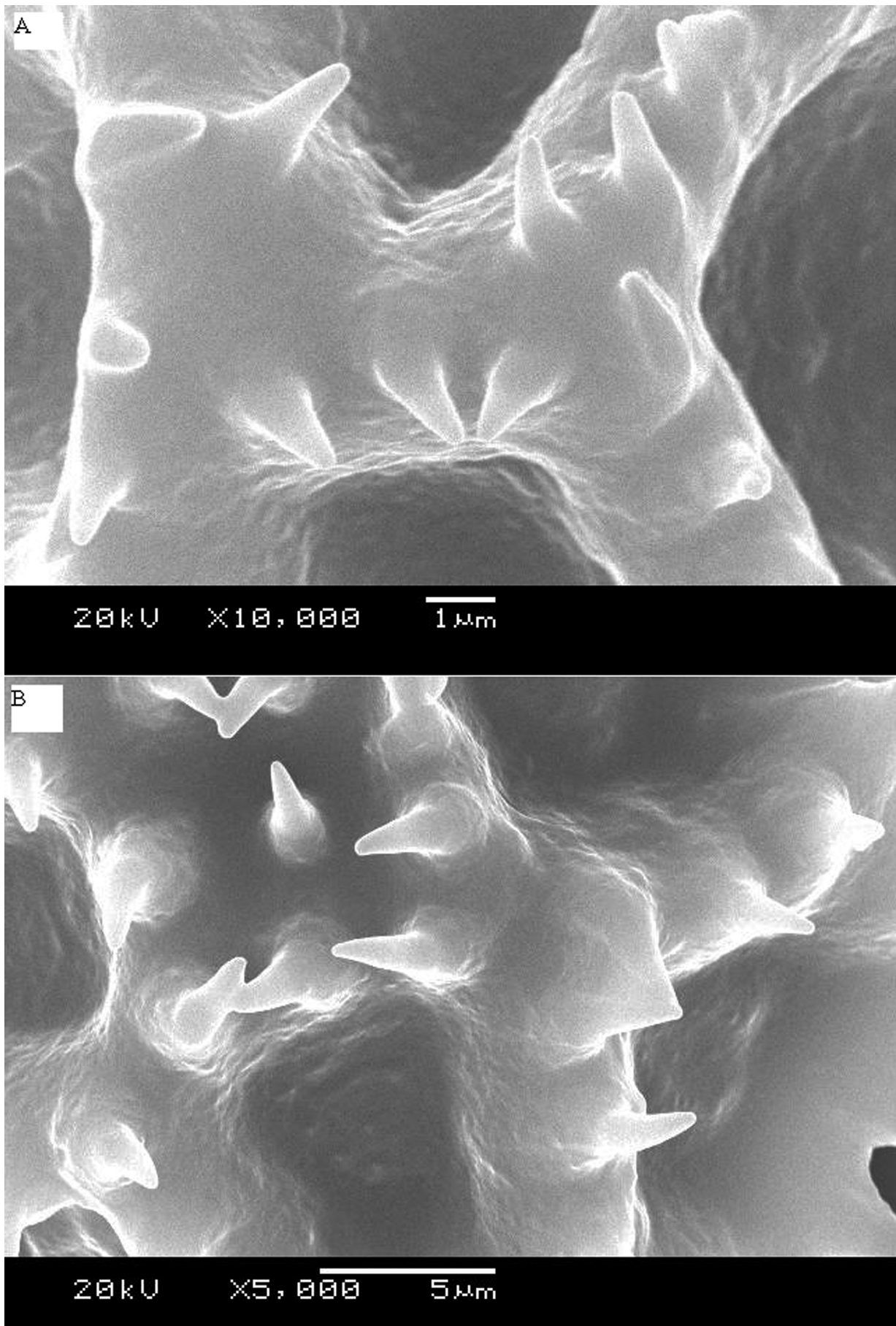


FIGURE 12. Partial enlarged SEM micrographs of pollen grains of *Youngia* and *Faberia*. A. *Y. heterophylla*. B. *F. sinensis*.

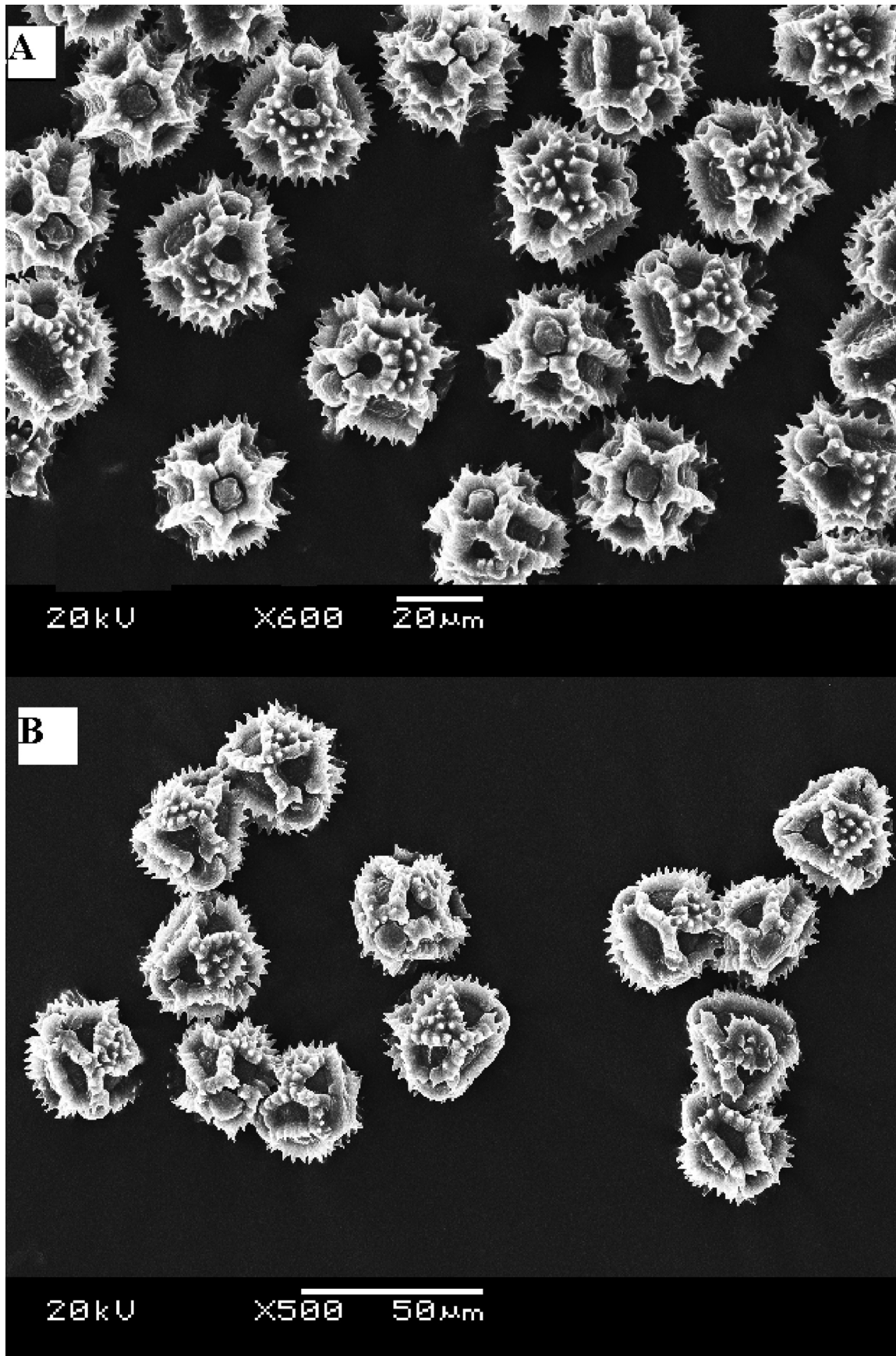


FIGURE 13. SEM micrographs of pollen grains of *Youngia paleacea*. A. Spherical pollen grains. B. Triangular pollen grains.

Appendix

Specimens investigated

- Crepis bodinieri*—CHINA. Sichuan, Yanbian, 21 Apr 2003, X.F. Gao, Y.L. Peng & Z.H. Li 4327 (CDBI)
Crepis napifera—CHINA. Sichuan, Luding, X.F. Gao, 23 Sep 2002, Y.L. Peng & G. Sun 3801 (CDBI)
Crepis rigescens—CHINA. Sichuan, 15 Jun 2010, X.F. Gao, Y.L. Peng, B. Xu & X. Zheng 11921 (CDBI)
Fabera nanchuanensis—CHINA. Chongqing, Nanchuan, 19 Jul 2010, Y.L. Peng 252 (CDBI)
Faberia sinensis—CHINA. Sichuan, E'mei, 4 Jul 2010, Y.L. Peng 176 (CDBI)
Ixeridium beauverdianum—CHINA. Sichuan, Baoxing, 17 Jun 2010, X.F. Gao, Y.L. Peng, B. Xu & X. Zheng 11693 (CDBI)
Crepidiastrum sonchifolium—CHINA. Sichuan, Nanping, 6 Jul 1983, Plant Expedition Group 30449 (CDBI)
Ixeridium dentatum—CHINA. Sichuan, Yanbian, 20 Apr 2003, X.F. Gao 4159 (CDBI)
Nabalus tatarinowii subsp. *macrantha*—CHINA. Sichuan, Pengzhou, 21 Jun 2006, S.H. Liu 255 (CDBI)
Parasyncalathium souliei—CHINA. Xizang, Chayu, 31 Aug 2003, X.F. Gao & W.G. Tu 6733 (CDBI)
Syncalathium orbiculariforme—CHINA. Sichuan, Yajiang, 12 Sep 1974, Q.Q. Wang 4985 (CDBI)
Youngia cineripappa—CHINA. Sichuan, Baoxing, 17 Jun 2010, X.F. Gao, Y.L. Peng, B. Xu & X. Zheng 11974 (CDBI)
Youngia erythrocarpa—CHINA. Hubei, Shenglongjia, 10 Sep 2010, L. Zhang & Z.Z. Zhu 88 (CDBI)
Youngia hastiformis—CHINA. Sichuan, Qianling, 7 Aug 1974, Anonymous 5641 (SZ)
Youngia henryi—CHINA. Sichuan, Baoxing, 24 Jul 2010, Y.L. Peng 382-1 (CDBI)
Youngia heterophylla—CHINA. Chongqing, Nanchuan, 19 Jul 2010, Y.L. Peng 308-1 (CDBI)
Youngia japonica—CHINA. Sichuan, Baoxing, 17 Jun 2010, X.F. Gao, Y.L. Peng, B. Xu & X. Zheng 11985 (CDBI)
Youngia paleacea—CHINA. Sichuan, Kangding, 27 Jul 2010, Y.L. Peng 457-1 (CDBI)
Youngia paleacea—CHINA. Sichuan, Kangding, 27 Jul 2010, Y.L. Peng 439-2 (CDBI)
Youngia pilifera—CHINA. Sichuan, Jiulong, 12 Jun 2010, X.F. Gao, Y.L. Peng, B. Xu & X. Zheng 11779-1 (CDBI)
Youngia prattii—CHINA. Sichuan, Pingwu, 4 May 2010, Y.L. Peng 325-1 (CDBI)
Youngia racemifera—CHINA. Sichuan, Kangding, 28 Aug 2008, Y.L. Peng & W.G. Tu Gaoxf-0841 (CDBI)
Youngia rosthornii—CHINA. Sichuan, Luding, 15 Jun 2010, X.F. Gao, Y.L. Peng, B. Xu & X. Zheng 11926 (CDBI)
Youngia rubida—CHINA. Sichuan, Chongzhou, 20 Apr 2010, Y.L. Peng 123-1 (CDBI)
Youngia simulatrix—CHINA. Sichuan, 14 Aug 1980, Anonymous 28412 (CDBI)
Youngia sericea—CHINA. Xizang, Chayu, 31 Aug 2003, X.F. Gao & W. G. Tu 6747 (CDBI)
Youngia wilsonii—CHINA. Sichuan, Baoxing, 24 Jul 2010, Y.L. Peng 351-1 (CDBI)

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