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A Study on the Pollen Morphology of Six Sections in Subgenus *Salix* L. (Salicaceae)[1]

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버드나무 亞屬 6節 花粉의 形態에 關한 硏究[1]

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ABSTRACT

The pollen morphology of 15 species, 2 varieties and 1 forma belonging to 6 sections of the subgenus *Salix* was investigated by means of light and scanning electron microscopy. From a pollen-morphological point of view, subgenus *Salix* is stenopalynous. Species from six sections have been distinguished on the basis of pollen morphology, and a key for their identification using pollen is presented. Based on pollen morphology, *S. jessoensis* (section *Subalbae*) is the most distinct of the species studied. Species of section *Humboldtianae* appear to be the most evolved in this subgenus with a closer relationship to section *Amygdalinae* than any other section of this subgenus.

Key words : Salix ; *Salicaceae* ; *pollen morphology*

要 約

버드나무亞屬 6節, 15種, 2變種, 1品種에 對한 花粉形態를 光學顯微鏡(LM)과 走査型 電子顯微鏡(SEM)으로 觀察 하였든바 버드나무 亞屬의 花粉은 同型 花盆群이였으며 花粉의 形態學的 特徵에 依하여 6節에 對한 花粉 檢索表를 만들 수 있었다. 또한 *Amygdalinae* 節과 近緣關係에 있을 것으로 생각되는 *Humboldtianae* 節은 本亞屬中에서 가장 進化된 것으로 보인다.

INTRODUCTION

Salix L. (willows) is a genus of about 400 to 500 species distributed mainly in the northern parts of North America and Europe, and in the mountains of China (Argus, 1986). In many countries, including Korea and Canada, willows are planted widely as they provide for many human needs and are good ornamental and shade trees and shrubs.

Salix is classified in two subgenera : *Salix* L. and *Vetrix* Dumortier. Subgenus *Salix* is the more primitive of the two subgenera. It is sharply isolated morphologically from the more advanced willows of the other subgenus (Dorn, 1976).

Recently, the taxonomy of North American *Salix* has been studied in detail (Argus, 1973, 1986). Also, willow genetics and breeding have received attention for biomass production (Anderson *et al.*, 1983). Pollen morphology has also

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been studied as a criterion for taxonomy of *Salix* (Straka, 1950; Beug, 1963; Fœgri, 1964; McAndrew, 1973; Križo, 1973, 1977; Ueno, 1975; Petrovič, 1976; Kim, 1984). However, pollen morphology has not been used for the identification and classification species of subgenus *Salix*.

The objective of this study is to contribute to the understanding of the taxonomy of *Salix* via pollen morphology and to evaluate the usefulness of pollen morphology in studying phylogenetic relationships within subgenus *Salix*. The present contribution describes the pollen morphology of 15 species, two varieties and one froma belonging to 6 sections of subgenus *Salix* and discusses the diagnostic value of certain morphological characteristics of pollen grains.

MATERIALS AND METHODS

Materials were obtained from herbarium specimens at the Royal Ontario Museum(ROM) and the National Museum of Natural Sciences of Canada(CAN) and also from fresh specimens (Appendix 1). A total of 15 species, 2 varieties and 1 forma belonging to 6 sections of subgenus *Salix* have been investigated. The materials were prepared using Erdtman's(1960) standard acetolysis method for optical studies and pollen measurement.

The pollen descriptions are based on both light microscope(LM) and scanning electron microscope (SEM) observations. The LM studies were made using oil immersion and are based on observations of 20 or more pollen grains per sample. Exine thickness has been measured in the centre of mesocolpia of pollen grains in equatorial view. The taxonomy follows Dorn(1976), and species within sections are arranged in alphabetic order. The SEM studies used acetolysed pollen grains suspended in a drop of absolute ethanol and transferred to brass stubs. The specimens were gold-palladium coated, using a polaron E 5000 sputter coater. Scanning micrographs were taken with I.S.I. Super Mini-SEM using Kodak panatomic X film.

The terminology of pollen morphology mainly follows that of Erdtman(1969) and Praglowski and Raj(1979).

RESULTS

Pollen morphological data are presented in Table 1.

General pollen description

Pollen grains of all studied specimens were monads, prolate to subprolate, isopolar, radially symmetrical, and three-colpate to three-colporoidate. The polar axes(P) were 14-31 μm, the equatorial diameters(E) 12-24 μm, and the P/E ratio 116-145. The shape of the pollen grains in the polar view were rounded to rounded triangular, and in the lateral view were rounded to elliptic. The exines were 0.9-2.0 μm thick. The exines were distinctly reticulate; the brochi were regular or irregular, the brochal sizes decreased towards the colpi area and poles. The diameter of muri varied considerably and could be larger or smaller than those lumina, the edge of muri were acute or blunt and the surfaces of muri were scrabrate or psilate. The lumina were oval, round, elliptic, diamond or polygonal in shape.

The colpi were 10-25 μm long, 1-7 μm wide, with tapered or blunt ends; the membrane of colpi were studded with densely spaced pointed spinules or polygonal processes. The lengths of spinules and the diameters of the colpi membranes were 0.1-0.5 μm.

A key to the classification of sections of subgenus *Salix* on the basis of pollen morphology is given in Table 2.

Sectional Descriptions

The pollen morphology measurements are indicated in Table 1 for each species studied. In the following, these measurements are averaged for the species in the six sections described, with special references made to species within each section, when necessary.

Table 1. Pollen Morphological Data of Subgenus *Salix*

Taxa	Pollen grain size (μm) P	E	Shape P/E	Aperture (μm) Colpi length	Colpi width	Exine Thickness (μm)	Sculpture	Remarks
Sect. *Humboldtianae* Pax								
S. amygdaloides Anderss.	21.8±1.2	15.1±0.7	144 pro	17.3±1.1	2.1±0.21	1.2±0.09	retic.	Brochi regular
S. caroliniana Michx.	27.4±1.2	19.6±1.1	140 pro	22.6±1.4	1.9±0.08	1.9±0.08	〃	〃
S. gooddingii Ball	24.6±1.3	17.4±1.5	131 pro	19.6±1.2	1.9±0.11	2.1±0.09	〃	〃
S. nigra Marsh.	24.7±1.4	18.0±0.8	137 pro	20.1±1.4	1.7±0.09	1.2±0.08	〃	
Sec. *Salicaster* Dumortier								
S. lasiandra Benth.	24.7±1.4	17.4±1.4	142 pro	19.7±1.4	5.2±0.61	1.1±0.09	〃	
S lasiandra var. *lasiandra* Benth.	27.2±2.1	18.7±1.1	145 pro	22.9±1.9	5.3±0.41	1.5±0.09	〃	
S. lucida Muhl.	21.8±1.1	16.3±1.1	134 pro	16.8±1.1	5.7±0.52	1.7±0.12	〃	
S. pentandra L.	21.4±1.4	18.3±1.3	167 subb	17.8±0.9	6.8±0.85	1.6±0.05	〃	
S. serissima (Bailey) Fern.	25.2±1.4	20.6±1.0	122 subp	22.2±1.5	5.9±0.21	1.8±0.21	〃	
Sect. *Longifoliae* Pax								
S. exigua Nutt.	14.9±1.1	12.7±1.1	118 subp	11.5±0.8	2.4±0.12	1.2±0.08	〃	
S. melanopsis Nutt.	15.7±0.8	13.9±0.7	114 subp	11.6±0.8	1.3±0.09	1.7±0.09	〃	
S. sessilifolia Nutt.	17.3±1.0	12.8±1.0	134 pro	13.3±1.3	1.6±0.08	1.1±0.09	〃	
Sect. *Salix* L.								
S. alba var. *calva* Meg.	18.3±0.9	15.8±1.1	116 subp	15.3±1.2	2.6±0.15	1.0±0.08	〃	
S. fragilis L.	17.1±1.2	14.2±0.7	121 subp	14.3±0.8	2.4±0.13	1.4±0.08	〃	
Sect. *Subalbae* Koidzumi								
S. babylonica L.	29.5±1.4	22.7±1.6	129 subp	23.7±1.1	5.5±0.32	1.7±0.12	〃	
S. jessoensis seem.	21.4±1.0	17.7±0.8	121 subp	17.7±0.8	2.4±0.11	1.7±0.11	〃	Muri diameter larger than lumen
S. matsudana for. *tortuosa* Koidz	23.8±2.4	15.7±1.3	130 subp	21.8±2.5	5.8±0.52	1.0±0.12	〃	
Sect *Amygdaline* Koch								
S. triandra L.	16.8±0.9	13.9±0.9	121 subp	13.9±1.1	0.9±0.08	1.1±0.09	〃	Brochi regular

Abbreviations : P=Polar axis ; E=Equatorial diameter ; P/E=P/E ratio(%) ; pro=prolate ; subp=subprolate.

Table 2. Pollen key to the sections of subgenus *Salix*

1. Brochi more or less regular
   2. Equatorial view prolate, P/E over 137.
      ...Sect. *Humboldtianae*
   2. Equatorial view subprolate, P/E under 121.
      ...Sect. *Amygdalinae*

1. Brochi more or less irregular
   3. Colpus width wide, over 5 μm.
      4 . Muri edge blunt, surface scabra.
      ...Sect. *Subalbae*
      except *S. jessoensis*
      4. Muri edge acute, surface psilate.
      ...Sect. *Salicaster*

   3. Colpus width narrow, under 3 μm.
      5 . Lumen inside sparcely piloid.
      ...Sect. *Longifoliae*
      5. Lumen inside densely piloid.
      ...Sect. *Salix*

Sect. *Humboldtianae* Pax (Figs. 1-4, 24)

Pollen grains were prolate, polar axes(P) 21-29 μm, equatorial diameters(E) 14-21 μm, P/E 137-144. Exines were 1.1-2.2 μm thick; brochi had regular arrangement when compared to brochi of most other sections (except *Amygdalinae*), the brochi shape displayed diversity. The lumina shapes were oval or elliptic (*S. amygdaloides*) and diamond or polygonal (*S. gooddingii*). Inside of the lumina were piloids; the diameters of muri were usually 0.2-0.3 μm, the surfaces of the muri were psilate. The colpi were three-colporoidate, 16-24 μm long, 1.6-2.0 μm wide, the colpi margins were tapered, and ora were lolongate(Fig. 4).

Sect. *Salicaster* Dumortier (Figs. 5-7).

Pollen grains were subprolate to prolate, polar axes 20-29 μm, equatorial diameters 15-22 μm, P/E 117-145. Exines were 1-2 μm thick; the brochi were in irregular arrangement when compared to sections *Humboldtianae* and *Amygdalinae*; the lumina shapes were elliptic or polygonal, the diameters of muri were 0.2-0.4 μm, the muri edges were acute, the muri surfaces were psilate; the lumina lengths and diameters were usually 0.4-0.8 μm, occasionally 3 μm, the inside of lumina were densely piloid (*S. lucida*) or sparsely piloid (*S. lasiandra*). The colpi were three-colpate, 16-25 μm long, 5-8 μm wide, the membranes of colpi were studded with densely spaced spinules, occasionally irregular rupturing with a few process.

Sect. *Longifolia* Pax (Figs. 9-12, 20).

Pollen grains were subprolate to prolate, polar axes were 14-18 μm, equatorial diameters 12-15 μm, P/E 114-134. The exines were 1.1-1.8 μm thick; brochi were in irregular arrangement, the edges of muri were acute, the diameters of muri were 0.2-0.4 μm, the lumina shapes were elliptic or polygonal and the inside of lumina sparcely piloid, lumina length and diameters 0.3-1.4 μm. The colpi were three-colpate, 8-15μm long, 1.2-2.5 μm wide; the membranes of colpi were studded with pointed spinules and triangle, rectangle or polygonal process; the area next to colpi were thickened.

Sect. *Salix* L. (Figs. 17-19).

Pollen grains were subprolate, polar axes 16-19 μm, equatorial diameters 14-17 μm, P/E 116-121. Exines were 0.9-1.5 μm thick: the brochi were irregular, the lumina shape were elliptic or polygonal, the lumina diameters were 0.2-2.1 μm, and the inside of lumina densely piloid; the edges of muri were acute (*S. fragilis*) or flat-topped (*S. alba* var. *calva*). The colpi were three-colpate, 13-17 μm long, 2.3-2.9 μm wide, the membranes of colpi were densely studded with spinules.

Sect. *Subalbae* Koidzumi (Figs. 8, 13-16).

Pollen grains were subprolate, polar axes 20-31 μm, equatorial diameters 14-24 μm, P/E 121-130. Exines were 0.9-1.8 μm thick; brochi were irregular, the shapes of brochi were polygonal (*S. babylonica* and *S. matsudana* for. *tortuosa*) or irregular (*S. jessoensis*); the lumina shapes were oval, elliptic or polygonal, inside of lumina were piloid, the lumina diameters were similar to muri diameters (0.2-0.5 μm), exceptionally the muri diameters of *S. jessoensis* larger than that of lumina; the muri surfaces had scabra(*S. matsudana* for. *tortuosa* and *S. babylonica*) except for *S. jessoesis*. The colpi were three-colpate, 17-25μm long, 2.3-6.3 μm wide; the colpus membranes were studded with spinules or irregular process.

Sect. *Amygdalinae* Koch (Figs. 21-23).

Pollen grains were subprolate, polar axes 16-18 μm, equatorial diameters 13-15 μm, P/E 121. Exines were 1.0-1.3 μm long; brochi were in regular arrangement, lumina shapes were oval or elliptic, lumina lengths and diameters were 0.1-1.0 μm, inside of the lumina were piloid; the surfaces of muri were psilate. The colpi were three-colpate, 13-15 μm long, 0.9-1.0 μm wide; the margin of colpi were comparatively blunt, the membranes of colpi were studded with sparcely spaced spinules.

DISCUSSION

The pollen of subgenus *Salix* is stenopalynolous. The sectional and specific delineation of pollen using LM is less certain than in SEM which can distinguish the colpus, brochi, muri and lumen.

Pollen grains of this subgenus are small to medium size, 14-31 μm. The following pollen grain sizes are indicated in the literature for genus *Salix* : 15-35 μm (Lüdi, 1950) ; 20-36 μm (Erdtman, 1952) ; 20-38 μm (Straka, 1952) ; 18-35 μm (Risch, 1960) ; 15-36 μm (Kuprijanova, 1965). These results, as well as ours, indicate variability in the size of pollen grains. Several literature references state that similar problems can be expected also in other taxa (Medvecká 1975 ; Krìžõ, 1980). Thus the size of pollen grains does not appear useful as a taxonomic criterion in separating species.

The longest colpi length was 23.7±1.1 μm in *S. babylonica*, and the shortest colpi length was 11.5±0.8 μm in *S. exigua*. The colpi length seemed to be directly related to polar axis.

Colpi of *Salicaster* and *Subalbae* sections are very wide (over 5 μm) and distinguishable these in from other sections.

Lüdi(1950) was the first to publish on *Salix* pollen morphology. He distinguished five subgroups based on pollen sculpture : 1. faintly verrucose, 2. densely and finely verrucose, 3. coarsely verrucose, 4. sharply verrucose, almost finely spinulous, 5. reticulate verrucose. Čzeň (1964) reported that the colpi of *Salix* pollen were long and narrow, with straight margins, the end of the colpi were pointed, their membrane was smooth. Kuprijanova(1965) reported that colpi were long and deep with pointed ends which almost reach the poles. Both Čzeň(1964) and Kuprijanova(1965) agreed that the ends of the colpi were pointed. However, as established in this study, the ends of colpi were pointed in some sections and blunt in others.

Straka(1952) reported that the brochal size decreased toward the poles. However, we found in this study a greater decrease in the brochal size in the direction of the colpus. Also, Čzeň (1964) reported that the brochi were from 0.92-3.20 μm in size, however, we found that in some cases brochi were less than 0.5 μm. Križo(1980) reported that muri were straight, or variously, irregularly curved, and that sometimes they were branched with extensions of different lengths which led into brochi. Our data support this finding of Križo(1980), however, we observed that the diameter of the muri was larger than that of lumina.

Bases on pollen morphology, *S. jessoensis* appears to be the most distinctive species in *Subalbae* section. The muri diameter of *S. jessoensis* is larger than the lumen diameter, while the muri diameter of other species of *Subalbae* section are smaller than the lumen diameter. Also, the colpus of *S. jessoensis* is wider than that of other species of *Subalbae* section.

Based on our observations it may be appropriate to reconsider the taxonomic relationships within this section. Pollen morphology suggest that species of *Humboldtianae* section are the most evolved in this subgenus, since they have only pores on the colpus.

Species of *Humboldtianae* section have a closer relationship to *Amygdalinae* section than to other sections since they have similar brachal arrangements.

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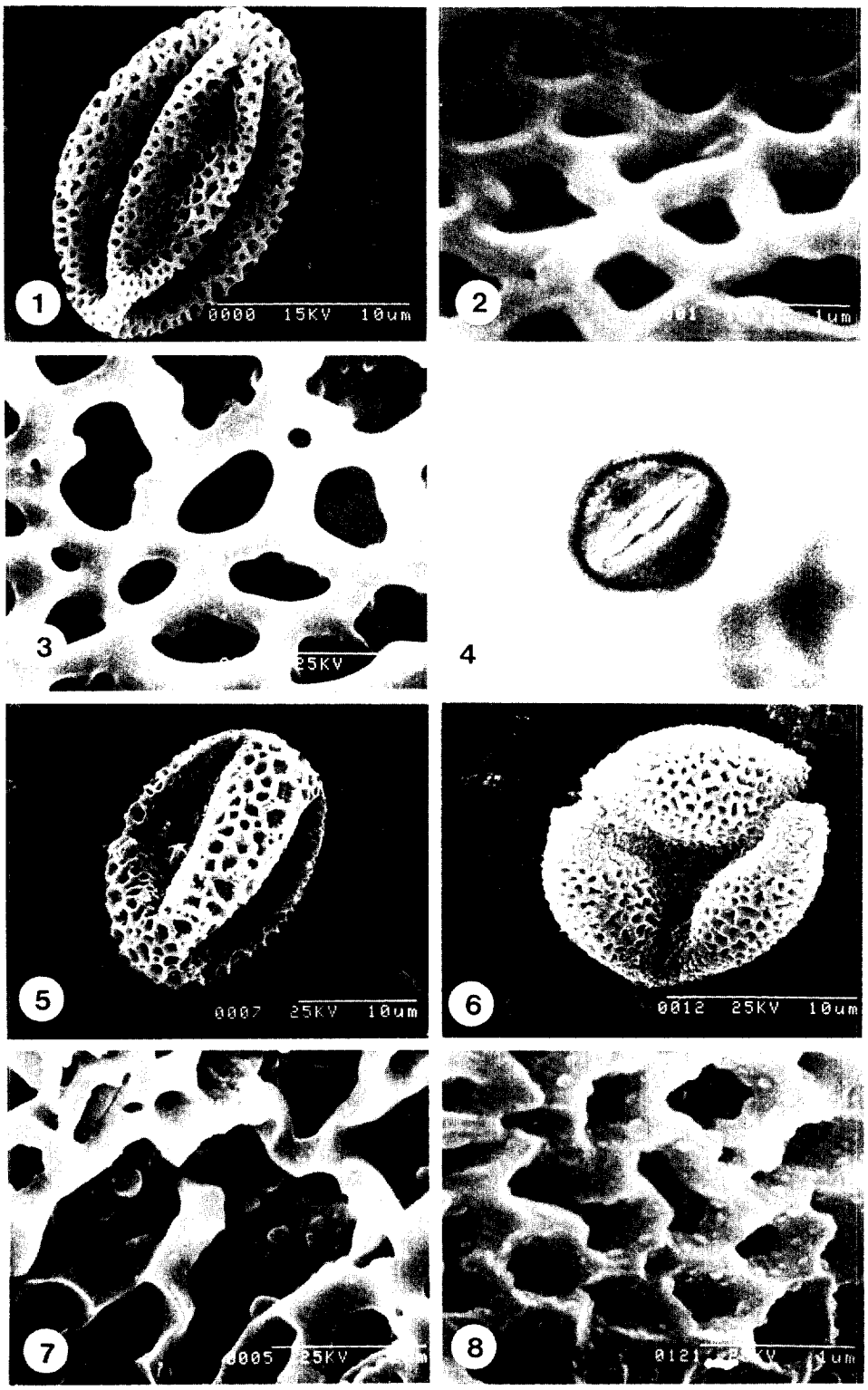
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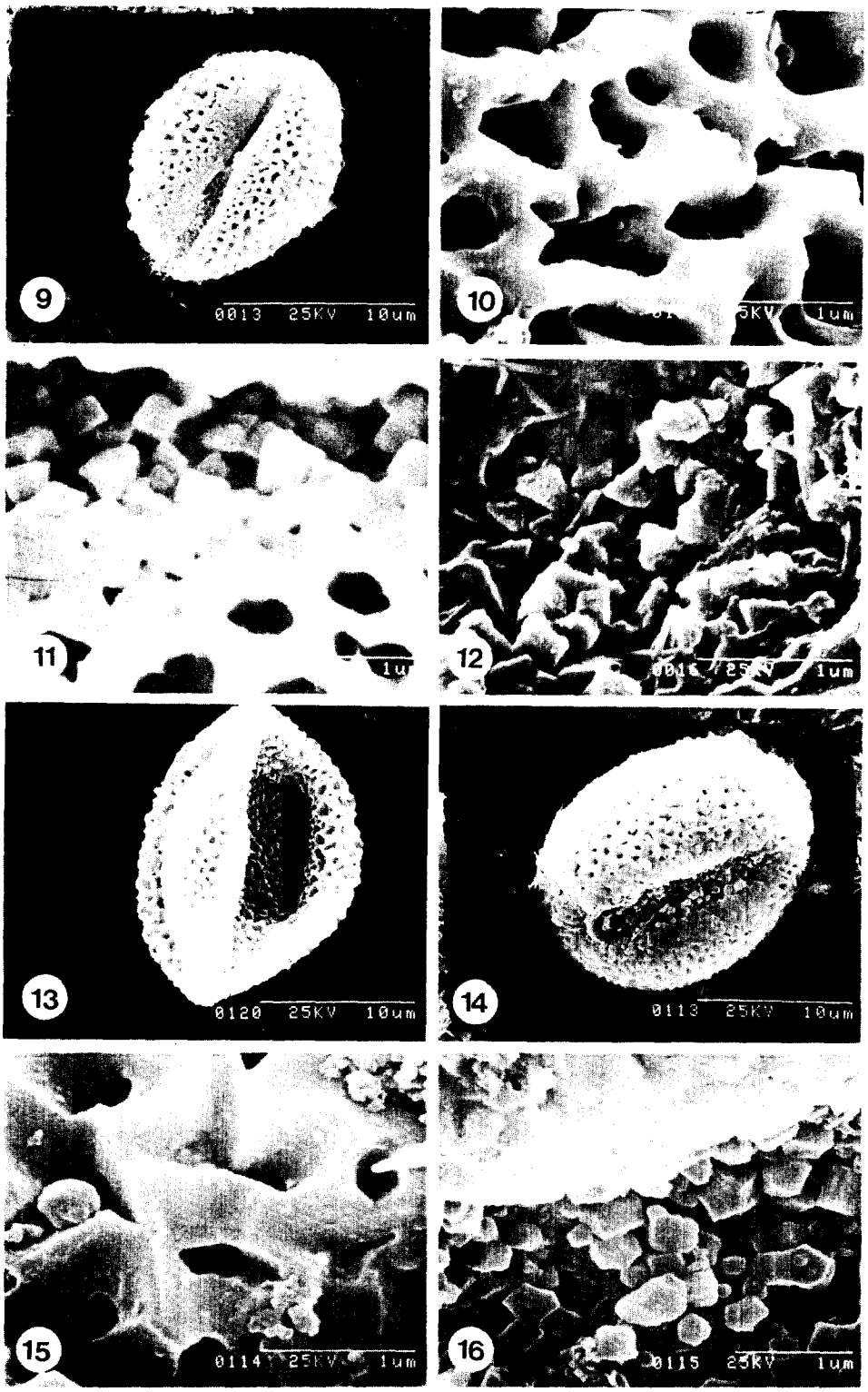
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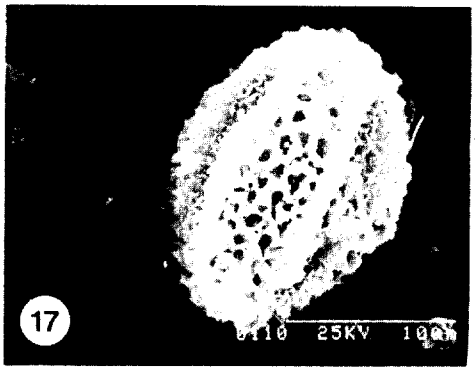

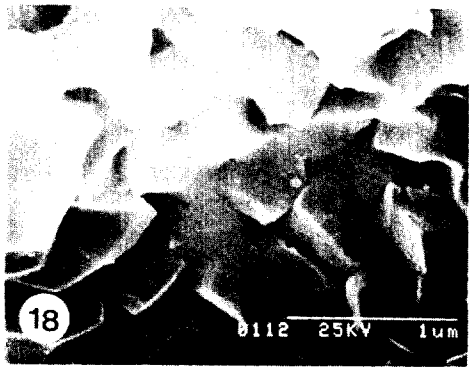

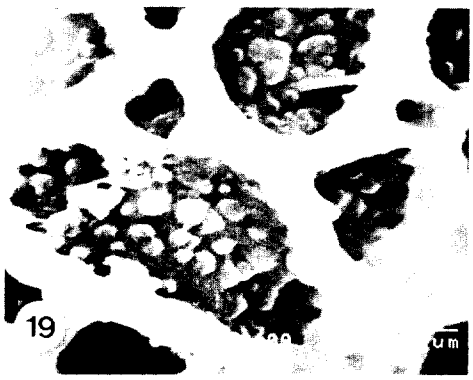

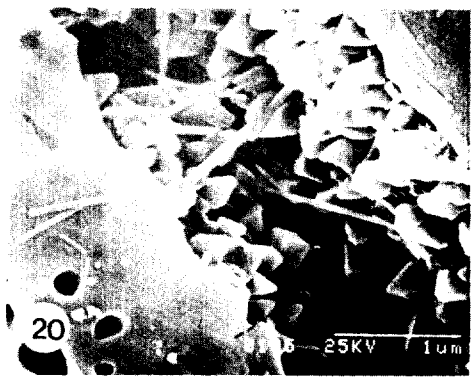

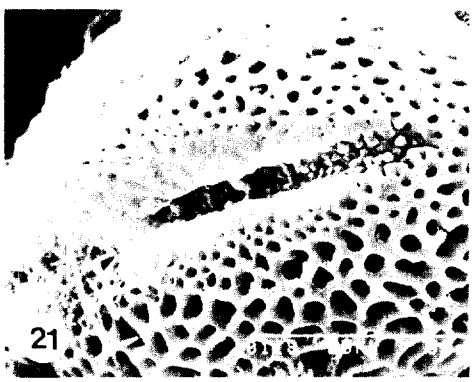

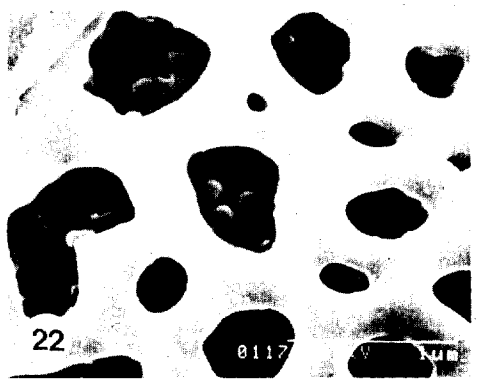

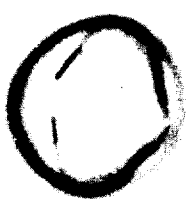

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APPENDIX I. SPECIMENS INVESTIGATED

Sect. *Humboldtianae* Pax

S. amygdaloides Anderss. Canada, Monarch Southern Alberta, June 5, 1941, W. C. McCalla 6600 (ROM)[1].

S. caroliniana Michx. Canada, Greenville, April 27, 1968, M.C. Helm & C. Wilton 1183 (ROM).

S. gooddingii Ball. U.S.A., Maricopa, Arizona, March 6, 1984, G.W. Argus 11365 (CAN)[2].

S. nigra March. Canada, Yorkshire Island, June 11, 1964, R. Hainsult s.n. (ROM).

Sect. *Salicaster* Dumortier

S. lasiandra Benth. Canada, Campsite, May 31, 1970, M.G. Dumais 4950 (ROM).

S. lasiandra var. *lasiandra* Benth. Canada, Banff Nat. Park, June 11, 1946, W.C. McCalla 9120 (ROM).

S. lucida Muhl. Canada, Fisherman's Island, June 8, 1924, S.L. Thompson 466 (ROM).

S. pentandra L. Canada, Thomas, Elgin Co., Ontario, May 30, 1954, L.E. James 2442 (ROM).

S. serissima (Bailey) Fernald. Canada, Winzsk, Hudson Bay, June 20, 1958. W.K.W. Baldwin, s.n. (ROM).

Sect. *Longifoliae* Pax

S. exigua Nutt. Canada, Green River, Ontario. September 19, 1987. A. Mosseler, s.n. (Fresh specimen).

S. melanopsis Nutt. Canada, Banff Nat. Park, June 16, 1942, C.R. Ball 1960 (ROM).

S. sessilifolia Nutt. U.S.A., Bingen, June 16, 1920, W.N. Suksdorf s.n. (CAN).

Sect. *Salix* L.

S. alba var. *calva* Meg. Canada, Kentville, King, May 30, 1941, A.E. Roland s.n. (ROM).

S. fragilis L. Canada, Lisle, Tosorontio TP, June 5, 1956, J.N. Soper 6293 (ROM).

Sect. *Subalbae* Koidzumi

S. babylonica L. Korea (S), Jeonbug Nat. Univ., April 6, 1986, K.H. Kim, s.n. (Fresh specimen).

S. jessoensis Seem. U.S.A., Arnold Arboretum of Harvard Univ., September 5, 1984, G.W. Argus s.n. (CAN).

S. matsudana for. *tortuosa* Korea (S), Jeonbug Nat. Univ., April 9, 1985, K.H. Kim s.n. (Fresh specimen).

Sect. *Amygdalinae* Koch

S. triandra L. USSR, Troitsk, June 20, 1946, L. A. Utkin s.n. (CAN).

Figs. 1, 2. *Salix gooddingii*. 1. Pollen grain in equatorial view, showing regular arrangement of brochi (SEM x 3,400). 2. Part of exine structure, showing polygonal and diamond lumen shape (SEM x 34,000).

Figs. 3, 4. *S. amygdaloides*. 3. Part of exine structure, showing oval or elliptic lumen shape (SEM x 26,000). 4. Pollen grain in equatorial view, showing colporoidate (LM x 1,400).

Fig. 5. *S. lucida*. Pollen grain in equatorial view, showing irregular arrangement of brochi (SEM x 2,300).

Fig. 6. *S. lasiandra* var. *lasiandra*. Three-colpate pollen grain in polar view (SEM x 3,400).

Fig. 7. *S. serissima*. Part of exine structure, showing muri with acute edge, surface of muri psilate (SEM x 13,000).

Fig. 8. *S. matsudana* for. *tortuosa*. Part of exine structure, showing muri with blunt edge, surface of muri scabrate (SEM x 26,000).

Figs. 9, 10. *S. exigua*. 9. Pollen grain in equatorial view, showing narrow colpus (SEM x 4,000). 10. Part of exine structure, showing muri with pointed edge (SEM x 26,000).

Fig. 11. *S. sessilifolia*. Part of colpus area, showing small lumina near colpus (SEM x 26,000).

Fig. 12. *S. exigua*. Colpus membrane studded with pointed spinules and triangle,

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[1] ROM = Royal Ontario Museum, Toronto, Canada, herbarium specimen.

[2] CAN = National Museum of Natural Sciences, Ottawa, Canada, herbarium specimen.

rectangle or polygonal process(SEM x 26,000).

Fig. 13. *S. matsudana* for. *tortuosa*. Pollen grain in equatorial view, showing wide colpus (SEM x 2,600).

Figs. 14, 16. *S. jessoensis*. 14. Pollen grain in equatorial view, showing thick colpus area, and the colpus membrane(SEM x 2,600). 15. Part of exine structure, showing that the diameter of muri is larger than lumen(SEM x 26,000). 16. Part of colpus membrane, showing irregular process(SEM x 20,000).

Figs. 17, 18. *S. fragilis*. 17. Pollen grain in equatorial view, showing irregular and uneven brochi(SEM x 2,600). 18. Part of colpus membrane, showing even spinules (SEM x 26,000).

Fig. 19. *S. alba* var. *calva*. Part of exine structure, showing piloids in lumen (SEM x 20,000).

Fig. 20. *S. exigua*. Part of colpus membrane, showing uneven spinules and irregular process(SEM x 20,000).

Figs. 21, 23. *S. triandra*. 21. Pollen grain in equatorial view, showing that brochal size decreases in the direction of colpus area (SEM x 6,500). 22. Part of exine structure, showing piloids in lumen(SEM x 26,000). 23. Pollen grain in equatorial view(LM x 1,800).

Fig. 24. *S. gooddingii*. Pollen grain in equatorial view(LM x 1,800).

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