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Original article

Kumiko Handa[1], Sei-ichiro Tsuji[2] and Minoru N. Tamura[3]: Pollen morphology of Japanese Asparagales and Liliales (Lilianae)

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日本産クサスギカズラ目とユリ目の花粉形態

Abstract The pollen morphology of the orders Asparagales and Liliales (Lilianae) mostly in Japan including Nartheciaceae was observed by light microscopy for 106 species of 47 genera in 14 families. Pollen grains are monad and vary from 19.2 (*Chionographis japonica*) to 196.0 μm (*Lilium longiflorum*) in the longest axis. The grain shape is usually ellipsoidal to spherical, and rarely obtuse tetrahedral (*Dianella*), tetrahedral spherical (*Chionographis*), obtuse triangular prismal (some individuals of *Tofieldia japonica*), or orange segmental (*Allium, Nothoscordum*). The pollen class is usually 1-sulcate, and rarely inaperturate (*Aspidistra, Smilax, Tupistra*), omniaperturate (*Heterosmilax, Trillium*), 2-sulcate (*Tofieldia, Uvularia*), 4-porate (*Chionographis*), 1-trichotomosulcate (*Dianella*), or 2-trichotomosulcate (some individuals of *Tofieldia japonica*). The sculpture is usually reticulate or perforate, and rarely gemmate, verrucate, clavate, granulate, or echinate. Sulci usually extend to the grains ends without marginal thickenings. The sulcus of some grains has a granulate membrane or an operculum with a sculpturing pattern similar to that of the exine. Pollen grains of the Asparagales and Liliales were classified into 20 types based on these characteristics, and recent classifications of the Asparagales and Liliales were reevaluated based on these pollen types.
Key words: Asparagales, light microscopy, Liliales, pollen morphology

要　旨　主に日本に産するクサスギカズラ目とユリ目の14科47属106種の花粉形態を光学顕微鏡で観察した。花粉粒は単粒で，長径は19.2 μm（*Chionographis japonica*）から196.0 μm (*Lilium longiflorum*)。概形はふつう楕円体から球形，まれに鈍四面体（*Dianella*），四面体型球形（*Chionographis*），鈍三角柱（*Tofieldia japonica* の一部），またはミカンの房形（*Allium, Nothoscordum*）。花粉型は，ふつうは単溝型，まれに無口型（*Aspidistra, Smilax, Tupistra*），全口型（*Heterosmilax, Trillium*），2溝型（*Tofieldia, Uvularia*），4孔型（*Chionographis*），1三叉溝型（*Dianella*），2三叉溝型（*Tofieldia japonica* の一部）。表面の彫紋はふつう網状紋から小穴紋，まれに乳頭状紋，いぼ状紋，棍棒状紋，顆粒状紋，刺状紋。発芽溝はふつう花粉の両端まで長く伸び，縁は肥厚しない。発芽溝には，花粉の彫紋に似た紋様または顆粒状紋を持つ口蓋が発達することがある。これらの形質から，クサスギカズラ目とユリ目の花粉を20タイプに分けた。このタイプ分けに基づき，クサスギカズラ目とユリ目の現在の分類を再評価した。
キーワード：花粉形態，クサスギカズラ目，光学顕微鏡，ユリ目

Introduction

Liliaceae sensu lato (s.l.) are well known for their great morphological variation. Because of the recent progress in cladistics and molecular phylogeny, the classification of the monocotyledons has been drastically revised, resulting in the renewed recognition of previously often neglected, numerous small families and orders (Dahlgren et al., 1985; Thorne, 1992; Kubitzki, 1998a, b). Liliaceae s.l. have also been divided into many small families of the newly circumscribed orders, Asparagales and Liliales.

In pollen analyses, pollen grains of the Asparagales and Liliales have seldom been identified in the genus level except for *Lilium, Hemerocallis, Hosta,* and *Allium* that have unique characteristics among seed plants

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(e.g., Schneider & Tobolski, 1985; Ooi et al., 1996; Miyaji et al., 2000). This is probably because comprehensive pollen atlases of these orders have not been published and because the pollen morphological variation in these orders has not been clarified.

In the Japanese Asparagales and Liliales, for example, only one third or one fourth of the genera have been studied pollen morphologically to clarify systematic relationships between species or genera (Ohashi, 1965; Sohma, 1978; Takahashi & Sohma, 1980, 1982, 1983; Takahashi, 1982, 1983, 1984, 1987; Takahashi & Kawano, 1989; Kurita et al., 1990). Japanese pollen atlases (Ikuse, 1956; Shimakura, 1973; Nakamura, 1980a, b) also treated several genera of the Asparagales and Liliales, but were far from comprehensive.

In the present study, the pollen morphology of the Japanese Asparagales and Liliales excluding Amaryllidaceae, Hypoxidaceae, Iridaceae, and Orchidaceae is described by light microscopy (LM) to present a pollen monograph of these orders as a basis of identification in pollen analyses. We particularly describe the sculpturing of pollen grains and the arrangement of columellae, especially LO-pattern which is indispensable for pollen analyses, but is not observable with scanning electron microsocpy (SEM). Besides Japanese specimens, we include foreign specimens important for the systematic understanding of Japanese taxa. We also aim to reevaluate the recent classifications of the Asparagales and Liliales from the observed pollen morphological diversity.

Materials and methods

We examined pollen grains of 106 species of 47 genera in 14 families covering all of the genera of Liliaceae s.l. in Japan (Table 1). Pollen grains were obtained from specimens preserved in the herbaria of the Kyoto University (KYO), the Osaka City University, the Kobe University, and the Institute of Botany, Academia Sinica, Beijing, China (PE), and from living materials which were cultivated in the botanical gardens of the Kyoto University, the Osaka Museum of Natural History, and the Osaka City University and are now transplanted in the Botanical Gardens of the Osaka City University.

For LM, flower buds were treated in 10% KOH and acetolyzed according to Erdtman (1960). The pollen grains were stained with safranin and mounted in glycerin jelly. Grain size was measured for 20 grains (whenever possible) at the longest (L), polar (P), and equatorial short axes (S). Average, minimum, and maximum values for each species are given. The morphological terminology and classification follow Punt et al. (1994) and Kubitzki (1998a, b), respectively. All the slides of the examined specimens are deposited in the Museum of Nature and Human Activities, Hyogo, Japan.

Results

Pollen grains of the Japanese Asparagales and Liliales are monad. The grain size at L varies from 19.2 μm in *Chionographis japonica* to 196.0 μm in *Lilium longiflorum*. The grain shape is usually ellipsoidal to spherical, and rarely obtuse tetrahedral (*Dianella*), tetrahedral spherical (*Chionographis*), obtuse triangular prismatic (some individuals of *Tofieldia japonica*), or orange segmental (*Allium, Nothoscordum*). The pollen class is usually 1-sulcate, and rarely inaperturate (*Aspidistra, Smilax, Tupistra*), omniaperturate (*Heterosmilax, Trillium*), 2-sulcate (*Tofieldia, Uvularia*), 4-pantoporate (*Chionographis*), 1-trichotomosulcate (*Dianella*), or 2-trichotomosulcate (some individuals of *Tofieldia japonica*). The exine structure is semitectate to tectate or rarely intectate. The exine sculpturing is usually reticulate or perforate, and rarely gemmate, verrucate, clavate, granulate, or echinate. Columellae under the reticulate sculpturing are simplicolumellate, duplicolumellate, or pluricolumellate. Sculpturings are usually large in the proximal face and become smaller gradually towards the sulcus or sulci. Fine reticulate to perforate sculpturings occur in some genera of Asparagales and Liliales. For grains with lumen diameter and muri width less than 1 μm, distinction between fine reticulate and perforate is difficult. By studying the continuity of muri and the arrangement of columellae, grains with continuous muri and reticulate columellae are designated as fine reticulate and those with any puncta and irregularly arranged columellae as perforate, if they have rugulate-like ridges on the tectum surface. Sulci usually extend to the grain ends and have no marginal thickenings. The sulcus of some grains has an operculum with a sculpturing pattern similar to the exine or is covered by a granulate membrane.

1. Nartheciaceae

a. *Petrosavia*

Pollen grains are 1-sulcate and elliptic in polar and equatorial views. Exine is semitectate. Sculpture is fine reticulate and simplicolumellate under muri. Columellae are coarse, high, and dense. Lumina become smaller towards the sulcus. Sulcus is narrow and does not extend to the grain ends.

P. sakuraii (Figs. 1-1–1-3). L : 27.6 (25.0–31.3) μm, P : 21.1 (18.8–22.5) μm, S : 23.2 (21.3–25.0) μm.

b. *Tofieldia*

Pollen grains are 2-sulcate and ellipsoid; rarely ob-

Table 1 List of studied specimens

Taxon	Locality	Voucher specimen	Pollen No.
(order not ranked)—Nartheciaceae			
Petrosavia sakuraii (Makino) Dandy	China: Yaoshan, Tseung-ynen, Kwangxi.	C. Wang 39493 KYO	KHP-97
Tofieldia coccinea Richardson	Japan: Kushiro, Hokkaido.	K. Takita 999 KYO	KHP-118
T. japonica Miq.	Japan: Mt. Akasaka, Makino, Takashima-gun, Shiga Pref.	G. Murata 18941 KYO	KHP-95
T. okuboi Makino	Japan: Mt. Gassan, Nishikawa, Nishimurayama-gun, Yamagata Pref.	T. Takahashi 41 KYO	KHP-119
T. nuda Maxim.	Japan: Makihara, Horai, Aichi Pref.	K. Torii 31/7/1960 KYO	KHP-120
Japonolirion osense Nakai	Japan: Horonobe, Teshio-gun, Hokkaido.	S. Tsugaru 4760 KYO	KHP-96
Narthecium asiaticum Maxim.	Japan: Moya, Mt. Hakkoda, Aomori Pref.	(K. Handa et al.)	KHP-50
Aletris foliata (Maxim.) Bureau et Franch.	Japan: Moya, Mt. Hakkoda, Aomori Pref.	(K. Handa et al.)	KHP-51
A. luteoviridis (Maxim.) Franch.	Japan: Tosayama, Tosa-gun, Kochi Pref.	N. Naruhashi & M. Wakabayashi 241 KYO	KHP-93
A. spicata (Thunb.) Franch.	Japan: Hanaze, Tashiro, Kagoshima Pref.	F. Konta 5015 KYO	KHP-103
Liliales—Colchicaceae			
Uvularia perfoliata L.	U.S.A.	(S. Kawano et al.) KBG*	KHP-18
Disporum sessile D. Don	Japan: Yamada, Aochi, Kusatsu, Shiga Pref.	(S. Tsuji)	KHP-16
D. smilacinum A. Gray	Japan: Mt. Yamato-katsuragi, Nara Pref.	(K. Handa et al.)	KHP-6
D. nantouense Ying	Taiwan: Mt. Tai-ping, Ilan Hsien.	M. N. Tamura et al. 10292 OCU	KHP-23
D. uniflorum Baker	Korea: Mt. Kaya, Kyongsangnam Do.	(S. Kawano et al.) KBG*	KHP-21
Liliales—Melanthiaceae			
Veratrum nigrum L.	Japan: Mt. Koryuji-dake, Kumihama, Kumano-gun, Kyoto Pref.	G. Murata 33742 KYO	KHP-116
V. stamineum Maxim.	Japan: Sannomine, Mt. Hakusan, Oono, Fukui Pref.	N. Fukuoka & Y. Inamasu 573 KYO	KHP-92
Zygadenus sibiricus (L.) Gray	Korea: Mt. Toryu.	J. Ohwi 2778 KYO	KHP-90
Heloniopsis orientalis (Thunb.) C. Tanaka	Japan: Mt. Yamato-katsuragi, Nara Pref.	(K. Handa et al.)	KHP-2
H. orientalis (Thunb.) C. Tanaka var. *flavida* (Nakai) Ohwi	Japan: Mt. Yamato-katsuragi, Nara Pref.	(K. Handa et al.)	KHP-3
Chionographis japonica Maxim.	Japan: Shoho-ji, Fujiwara, Inaba-gun, Mie Pref.	N. Fukuoka 4573 KYO	KHP-94
C. koidzumiana Ohwi	Japan: Mt. Nachi, Wakayama Pref.	G. Murata 5715 KYO	KHP-117
Liliales—Trilliaceae			
Paris tetraphylla A. Gray	Japan: Moya, Mt. Hakkoda, Aomori Pref.	(K. Handa et al.)	KHP-53
P. tetraphylla A. Gray	Japan: Mt. Iwozen, Kanazawa, Ishikawa Pref.	M. N. Tamura 2008 OCU	KHP-71
P. verticillata Bieb.	Japan: Arekinai, Shibecha, Kawakami-gun, Hokkaido.	K. Takita 176 KYO	KHP-106
Kinugasa japonica (Fr. et Sav.) Tatewaki et Suto	Japan: Mt. Karamatsu, Toyama Pref.	G. Murata & T. Shimizu 1903 KYO	KHP-72
Trillium grandiflorum (Michx.) Salisb.	U.S.A.: Rolling Run, Pennsylvania.	(S. Kawano et al.) KBG*	KHP-27
T. kamutschaticum Pallas	Japan: Hokuchodai, Nemuro, Hokkaido.	S. Tsugaru & T. Sasaki 7830 KYO	KHP-77
T. smallii Maxim.	Japan: Kanzanji, Yogo, Shiga Pref.	(S. Tsuji)	KHP-33
Liliales—Liliaceae			
Clintonia udensis Trautv. et Mey.	Japan: Kamikochi, Azumi, Minami-azumi gun, Nagano Pref.	K. Ueda et al. 17 KYO	KHP-80
Gagea japonica Pascher	Japan: Ochiishi, Nemuro, Hokkaido.	S. Tsugaru & T. Sasaki 7783 KYO	KHP-111
G. lutea (L.) Ker-Gawl.	Japan: Obirashike, Kushiro, Hokkaido.	K. Takita 112 KYO	KHP-84
Lloydia serotina (L.) Reichenb.	Japan: Mt. Senjo-dake, Nagano Pref.	K. Iwatsuki et al. 235 KYO	KHP-85
L. triflora (Ledeb.) Baker	Japan: Furenai, Shiranuka, Hokkaido.	K. Takita 981 KYO	KHP-113
Tulipa edulis (Miq.) Honda	Japan: Hitaka, Takaoka-gun, Kochi Pref.	G. Murata 17941 KYO	KHP-88
T. latifolia (Makino) Honda	Japan: Seiho-ji, Sakamoto, Fujiwara, Inabe-gun, Mie Pref.	K. Deguchi & K. Tanabe 6177 KYO	KHP-112
Erythronium japonicum Decne.	Japan: Mt. Yamato-katsuragi, Nara Pref.	(K. Handa et al.)	KHP-1
E. japonicum Decne.	Japan: Mt. Yamato-katsuragi, Nara Pref.	(K. Handa et al.)	KHP-4
Fritillaria camtschatcensis (L.) Ker-Gawl.	Japan: Nougaike, Mt. Kisokomagatake, Miyata, Kami-ina gun, Nagano Pref.	O. Pellmyr et al. 6 KYO	KHP-83
F. japonica Miq.	Japan: Seiho-ji, Sakamoto, Fujiwara, Inabe-gun, Mie Pref.	K. Deguchi & K. Tanabe 6175 KYO	KHP-110

Cardiocrinum cordatum (Thunb.) Makino	Japan: Mt. Sanpodake, Shiiba, Higashi-usuki gun, Miyazaki Pref.	G. Murata & H. Tabata 68043 KYO	KHP-87
Lilium hansonii Leichtl.	Korea: Ullung Island, Kyongsangpuk Do.	M. N. Tamura 5030 OCU	KHP-45
L. lancifolium Thunb.	Japan: Hirado Isl., Nagasaki Pref.	(Unknown)	KHP-60
L. longiflorum Thunb.	Japan: Funaura, Iriomote Isl., Okinawa Pref.	N. Fukuoka 11405 KYO	KHP-115
L. maculatum Thunb.	Japan: Ohshima Isl., Yamada, Shimohei-gun, Iwate Pref.	H. Koyama & S. Sasamua 2403 KYO	KHP-100
Liliales—Calochortaceae			
Tricyrtis macrantha Maxim. subsp. *macranthopsis* (Masam.) Kitam.	Japan: Mt. Nachi, Higashimuro-gun, Wakayama Pref.	H. Takahashi 1314 KYO	KHP-98
T. macropoda Miq.	Japan: Mt. Yamato-katsuragi, Nara Pref.	(K. Handa et al.)	KHP-65
Streptopus amplexifolius (L.) DC. var. *papillatus* Ohwi	Japan: Mt. Iwaki, Aomori Pref.	S. Kitamura 24/6/1940 KYO	KHP-81
S. streptopoides (Ledeb.) Frye et Rigg	Japan: Mt. Mashu, Teshikaga, Kawakami-gun, Hokkaido.	K. Takita 278 KYO	KHP-108
Liliales—Smilacaceae			
Heterosmilax japonica Kunth	Japan: Shimochi, Miyako Island, Okinawa Pref.	G. Koidzumi 13/6/1923 KYO	KHP-76
Smilax bracteata Presl	Japan: Mt.Katsuudake, Nago, Okinawa Pref.	T. Shimizu 85-139 KYO	KHP-104
S. china L.	Japan: Kisaichi, Katano, Osaka Pref.	(K. Handa)	KHP-29
S. nipponica Miq.	Japan: Takamatsu, Kamikawachi, Tochigi Pref.	(K. Handa)	KHP-49
Asparagales—Hemerocallidaceae			
Hemerocallis dumortieri Morren var. *esculenta* (Koidz.) Ohwi	Japan: Moya, Mt. Hakkoda, Aomori Pref.	(K. Handa et al.)	KHP-52
H. fulva L. f. *kwanso* (Regel) Kitam.	Japan: Haza, Naka, Shimane Pref.	(unknown)	KHP-59
H. thunbergii Baker	Japan: Mt. Washigamine, Shimosuwa, Nagano Pref.	(M. N. Tamura) KBG*	KHP-58
Dianella ensifolia DC.	Thailand: Phu Kradung, Loei Prov., NE.	M. N. Tamura T-60475 KYO	KHP-24
D. ensifolia DC.	Unknown.	(M. N. Tamura) KBG*	KHP-41
D. ensifolia DC.	Japan: Chijinyama, Izena Isl., Okinawa Pref.	M. Tamura et al. 26729 KOBE	KHP-89
Asparagales—Asparagaceae			
Asparagus officinalis L.	Japan: Miharadai, Sakai, Osaka Pref.	(Y. Ueda)	KHP-34
A. schoberioides Kunth	Japan: Kanmuri Isl., Wakasa bay, Kyoto Pref.	G. Murata 67755 KYO	KHP-109
Asparagales—Anthericaceae			
Chlorophytum orchidastrum Lindl.	Thailand: Phu Kradung, Loei Prov., NE.	M. N. Tamura T-60446 KYO	KHP-64
Comospermum yedoensis (Maxim.) Makino	Japan: Dainichimura, Osugidani, Miyagawa, Taki-gun, Mie Pref.	G. Murata 19763 KYO	KHP-91
Asparagales—Alliaceae			
Allium cepa L.	Japan: Koen-Minami Yata, Higashi-sumiyoshi, Osaka Pref.	(K. Handa)	KHP-14
A. macrostemon Bunge	Japan: Sugimoto, Sumiyoshi, Osaka Pref.	(K. Handa)	KHP-44
A. tuberosum Rottler	Japan: Akeshina, Nagano Pref.	(K. Handa et al.)	KHP-55
A. thunbergii G. Don	Japan: Sakeishi, Enzan, Yamanashi Pref.	N. Kurosaki 4945 KYO	KHP-114
A. victorialis L. subsp. *platyphyllum* Hulten	Korea: Ullung Island, Kyongsangpuk Do.	(M. N. Tamura et al.) KBG*	KHP-46
Nothoscordum inutile (Makino) Kitam.	Japan: Sakamoto, Tatebe, Mitsu-gun, Okayama Pref.	I. Okubo 3/10/1984 KYO	KHP-86
Asparagales—Hyacinthaceae			
Scilla chinensis Benth.	Japan: Niyodo, Takaoka-gun, Kochi Pref.	G. Murata 17382 KYO	KHP-82
Asparagales—Convallariaceae			
Polygonatum cryptanthum Lév. et Vant.	Japan: Mt. Ariake, Tsushima Isls., Nagasaki Pref.	M. N. Tamura & S. Mitsuta OCU	KHP-39
P. domonense Satake	Japan: Mt. Ibuki, Ibuki, Sakata, Shiga Pref.	M. N. Tamura 5016, 7086 OCU	KHP-70
P. domonense Satake	Japan: Irimuzu, Takine, Tamura-gun, Fukushima Pref.	M. N. Tamura & M. Tamura 710 KYO	KHP-101
P. falcatum A. Gray	Japan: Mt. Yuzuruha, Awaji Isl., Hyogo Pref.	(M. N. Tamura) KBG*	KHP-38

P. humile Fischer	Japan: Senami, Murakami, Niigata Pref.	M. N. Tamura 10294 OCU	KHP-28
P. inflatum Kom.	Japan: Taishaku-kyo, Toujyu, Hiba-gun, Hiroshima Pref.	M. N. Tamura 702 KYO	KHP-102
P. involucratum (Fr. et Sav.) Maxim	Japan: Mt. Koroi, Hayakita, Hokkaido.	(M. N. Tamura) KBG*	KHP-43
P. kingianum Collett et Hemsley	Thailand: Doi Tung, Chiang Rei Prov., N.	M. N. Tamura 7045 OCU	KHP-426
P. lasianthum Maxim.	Japan: Kanzanji, Yogo, Shiga Pref.	(S. Tsuji)	KHP-32
P. lasianthum Maxim.	Japan: Mt. Iwozen, Kanazawa, Ishikawa Pref.	M. N. Tamura 2002 OCU	KHP-69
P. macranthum (Maxim.) Koidzumi	Japan: Honsenji Temple, Futamata, Ishikawa Pref.	M. N. Tamura 2011 OCU	KHP-68
P. odoratum (Miller) Druce var. *pluriflorum* (Miq.) Ohwi	Unknown.	(M. N. Tamura) KBG*	KHP-25
P. odoratum (Miller) Druce var. *pluriflorum* (Miq.) Ohwi	Japan: Ikenokurumi, Suwa, Nagano Pref.	(M. N. Tamura) KBG*	KHP-42
P. oppositifolium (Wall.) Royle	Nepal: Dhankuta.	M. N. Tamura 5018, 5024, 7091 OCU	KHP-36
P. pubescens (Willd.) Pursh	U.S.A.: Scotto State Park.	(S. Kawano et al.) KBG*	KHP-19
P. sibiricum Delaroche et Redoute	Korea: Mt. Toraksan.	M. N. Tamura 7088 OCU	KHP-425
P. sp. nov.	China: Mt. Wawushan, Sichuan.	M. N. Tamura 8517b OCU	KHP-424
P. stenophyllum Maxim.	Korea: Mt. Samyongsan, Kangwon-do.	M. N. Tamura 5029 OCU	KHP-429
Heteropolygonatum xui W. K. Bao et M. N .Tamura	China: Mt. Wawushan, Sichuan.	M. N. Tamura 8515 OCU	KHP-431
Disporopsis arisanensis Hayata	Taiwan: Mt. Tai-ping, Ilan Hsien.	M. N. Tamura et al. 10295 OCU	KHP-37
D. longifolia Craib	Thailand: Doi Suthep, Chiang Mai Prov., N.	M. N. Tamura 10296 OCU	KHP-61
D. undulata M. N. Tamura et Ogisu	China: Mt. Omei, Sichuan.	M. N. Tamura & Ogisu 5021 PE	KHP-430
Maianthemum bifolium (L.) F. W. Schmidt	Japan: Yamanakako, Minamitsuru-gun, Yamanashi Pref.	M. Togashi 27/5/1983 KYO	KHP-107
M. dilatatum (Wood.) Nels. et Macbr.	Unknown.	(M. N. Tamura) KBG*	KHP-26
M. dilatatum (Wood.) Nels. et Macbr.	Japan: Suiren-numa, Mt. Hakkoda, Aomori Pref.	(K. Handa et al.)	KHP-54
Smilacina bicolor Nakai	Korea: Changhangli, Kyongsangpuk Do.	M. N. Tamura 7085 OCU	KHP-40
S. formosana Hayata	Taiwan: Mt. Tai-ping, Ilan Hsien.	(M. N. Tamura & M. Tamura) KBG*	KHP-20
S. hondoensis Ohwi	Japan: Mt. Iwozen, Kanazawa, Ishikawa Pref.	M. N. Tamura 2005 OCU	KHP-47
S. japonica A. Gray	Japan: Mt. Izumi-katsuragi, Osaka Pref.	(K. Handa et al.)	KHP-30
Liriope minor (Maxim.) Makino	Japan: Oharano, Saikyo, Kyoto Pref.	K. Nagai 25208 KYO	KHP-105
L. platyphylla Wang et Tang	Japan: Mt. Nonbori, Kameyama, Mie Pref.	N. Fukuoka 5101 KYO	KHP-75
Ophiopogon brevipes Craib	Thailand: Phu Kradung, Loei Prov., NE.	M. N. Tamura T-60479 KYO	KHP-63
O. jaburan (Kruth) Lodd.	Japan: Tokunoshima Isl., Wasekatsu, Isen, Oshima-gun, Kagoshima Pref.	M. Tamura et al. 26 KOBE	KHP-73
O. japonicus (L. f.) Ker-Gawler	Japan: Suzuhara, Yaotsu, Kamo-gun, Gifu Pref.	H. Takahashi 11494 KYO	KHP-74
Peliosanthes violacea Wall. ex Baker	Thailand: Doi Inthanon, Chiang-Mai Prov., N.	M. N. Tamura 10297 OCU	KHP-35
Convallaria keiskei Miq.	Japan: Watenbetsu, Shiranuka, Hokkaido.	K. Takita 318 KYO	KHP-79
Reineckia carnea (Andr.) Kunth	Japan: Iwaki-jinja, Kamigori, Ako-gun, Hyogo Pref.	N. Kurosaki 8654 KYO	KHP-78
Rohdea japonica (Thunb.) Roth	Japan: Ozo, Utsunomiya, Tochigi Pref.	(K. Handa)	KHP-48
Tupistra grandis Ridl.	Thailand: Khao Kam Paeng, Tham Tarn Lod National Park, Bo Phloi District, Kanchanaburi Prov.	(unknown)	KHP-17
Aspidistra elatior Blume	Unknown.	(M. N. Tamura) KBG*	KHP-10
Asparagales—Hostaceae			
Hosta albo-marginata (Hooker) Ohwi	Japan: Kashiwazaki, Niigata Pref.	(unknown)	KHP-56
H. capitata (Koidz.) Nakai	Japan: Aina, Yamada, kita-ku, kobe, Hyogo Pref.	N. Kurosaki 9381 KYO	KHP-121
H. longissima Honda	Japan: Motta, Takanabe, Koyu-gun, Miyazaki Pref.	T. Minamidani 27104 KYO	KHP-122
H. sieboldiana (Lodd.) Engler	Japan: Hozu, Tawaramoto, Nara Pref.	G. Murata 44552 KYO	KHP-99
H. sieboldiana (Lodd.) Engler var. *yakusimensis* Masam.	Japan: Yaku Isl., Kagoshima Pref.	(unknown)	KHP-57

KYO: Herbarium of the Kyoto University, Japan; PE: Herbarium of the Institute of Botany, Academia Sinica, Beijing, China; KOBE: Herbarium of the Kobe University, Japan; OCU: Herbarium of the Osaka City University, Japan; KBG*: living plants cultivated in the Botanical Gardens, Osaka City University; (): no voucher specimen.

tuse triangular prismatic with two trichotomosulci in *T. japonica*. Exine is semitectate or intectate. Sculpture of *T. coccinea, T. japonica,* and *T. nuda* is fine reticulate and simplicolumellate under muri. Lumina gradually become smaller towards sulci. Columellae are fine and low. *T. nuda* has the finest reticulum in these three species, and its reticulate sculpture changes successively into a perforate one. Sculpture of *T. okuboi* is verrucate, granulate, or fine reticulate. Sulci are narrow and long and are parallel to the longest axis at the opposite sides of the grain. Trichotomosulci are also narrow, occurring at the opposite sides of the grain.

T. coccinea (Figs. 1-4–1-5). L: 23.9 (21.3–26.3) μm, P: 17.2 (15.0–20.0) μm, S: 17.5 (16.3–18.8) μm.

T. japonica (Figs. 1-6–1-9). L: 37.4 (32.5–42.5) μm, P: 25.1 (21.3–30.0) μm, S: 26.6 (25.0–27.5) μm.

T. okuboi (Figs. 1-10–1-12). L: 25.4 (22.5–27.5) μm, P: 19.3 (18.8–20.0) μm, S: 20.9 (18.8–22.5) μm.

T. nuda (Figs. 1-13–1-15). L: 22.3 (20.0–23.8) μm, P: 16.0 (13.8–17.5) μm, S: 17.3 (15.0–18.8) μm.

c. *Japonolirion*

Pollen grains are 1-sulcate and circular to elliptic in polar and equatorial views. Exine is intectate with gemmate sculpture. Gemmae are ca. 1 μm in diameter and height and become smaller and denser towards the sulcus. Gemmae at the proximal face are reticulately arranged. Sulcus is narrow and does not extend to the grain ends.

J. osense (Figs. 2-1–2-3). L:24.7 (22.5–27.5) μm, P: 21.7 (18.8–25.0) μm, S: 23.5 (20.0–27.5) μm.

d. *Narthecium*

Pollen grains are 1-sulcate and elliptic in polar and equatorial views. Exine is semitectate. Sculpture is fine reticulate with simplicolumellate muri. Lumina become smaller towards the sulcus, so that the margins appear tectate. Sulcus is narrow and does not extend to the grain ends.

N. asiaticum (Figs. 2-4–2-6). L: 28.9 (25.0–35.0) μm, P: 20.4 (17.5–23.8) μm, S: 21.5 (17.5–23.8) μm.

e. *Aletris*

Pollen grains are 1-sulcate and elliptic in polar and equatorial views. Exine is semitectate to tectate. Sculpture of *A. foliata* and *A. luteoviridis* is fine reticulate with simplicolumellate muri. Lumina are ca. 2 μm wide in the proximal face and become smaller towards the sulcus. Sculpture of *A. spicata* is perforate with sparse fine columellae. Sulcus is narrow and extends near to or to the grain ends.

A. foliata (Figs. 2-7–2-9). L: 41.5 (30.0–48.8) μm, P: 25.9 (21.8–28.8) μm, S: 25.8 (22.5–32.5) μm.

A. luteoviridis (Figs. 2-10–2-12). L: 30.4 (23.8–35.0) μm, P: 19.2 (15.0–23.8) μm, S: 21.3 (17.5–23.8) μm.

A. spicata (Figs. 2-13–2-15). L: 35.7 (31.3–41.3) μm, P: 28.1 (25.0–32.5) μm, S: 28.1 (26.3–30.0) μm.

2. Liliales

1) Colchicaceae

a. *Uvularia*

Pollen grains are 2-sulcate. Grain shapes are elliptic to obtuse rectangular in polar view and elliptic to D-shaped in equatorial view: the proximal face is plane, and the distal face is convex. Exine is tectate. Sculpture is perforate with rugulate ridges on the tectum surface. Fine puncta exist between the sculptural ridges. Punctum size is uniform. Columellae are fine and dense. Sulci are narrow, not extending to the grain ends, and are almost parallel to the longest axis on the distal face. Sulcus membrane is smooth.

U. perfoliata (Figs. 3-1–3-3). L: 53.0 (48.8–57.5) μm, P: 35.6 (30.0–57.5) μm, S: 34.0 (30.0–42.5) μm.

b. *Disporum*

Pollen grains are 1-sulcate and elliptic in polar and equatorial views. Exine is tectate to semitectate, thickest at the proximal face and becoming thinner towards the sulcus. Sculpture is perforate with rugulate to reticulate ridges on the tectum surface. Puncta exist between the sculptural ridges. Puncta are large in the proximal face and become smaller towards the sulcus and grain ends. Punctum size varies among species. Columellae are fine, dense, and obscure, and are arranged next to puncta. Sulcus is narrow and does not extend to the grain ends. Sulcus membrane is smooth.

D. sessile (Figs. 3-4–3-9). L: 68.3 (62.5–75.0) μm, P: 41.7 (32.5–47.5) μm, S: 42.7 (37.5–48.8) μm.

D. smilacinum (Figs. 3-10–3-12). L: 50.6 (43.8–57.5) μm, P: 34.6 (30.0–38.8) μm, S: 36.3 (35.0–38.8) μm.

D. nantouense (Figs. 3-13–3-15). L: 49.7 (42.5–57.5) μm, P: 37.4 (35.0–41.3) μm, S: 35.4 (28.8–42.5) μm.

D. uniflorum (Figs. 3-16–3-18). L: 55.0 (47.5–62.5) μm, P: 36.3 (33.8–40.0) μm, S: 38.4 (36.3–40.0) μm.

Takahashi & Sohma (1980) described the exine sculpture of *D. sessile* and *D. smilacinum* as reticulate by LM and SEM.

2) Melanthiaceae

a. *Veratrum*

Pollen grains are 1-sulcate and elliptic in polar and equatorial views. Exine is semitectate. Sculpture is fine reticulate with simplicolumellate or duplicolumellate muri. *V. nigrum* has simplicolumellate muri with dense

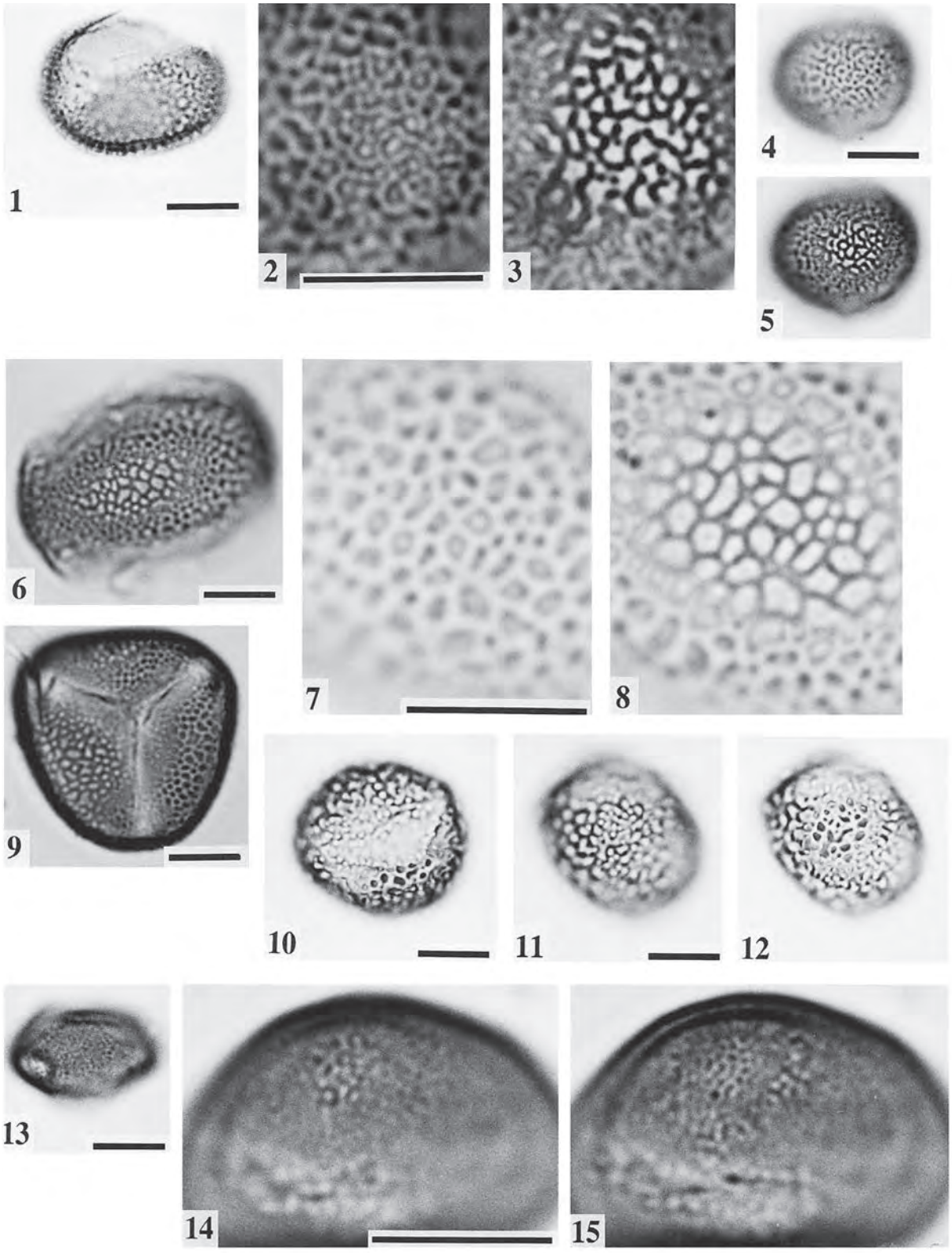

Fig. 1 Pollen grains of *Petrosavia* and *Tofieldia*. — 1–3: *Petrosavia sakuraii* (KHP-97)(1: pollen grain, 2–3: LO-pattern). — 4–5: *Tofieldia coccinea* (KHP-118)(LO-pattern). — 6–9: *Tofieldia japonica* (KHP-95)(6: grain, 7–8: LO-pattern, 9: trichotomosulcus). — 10–12: *Tofieldia okuboi* (KHP-119)(10: grain, 11–12: LO-pattern). — 13–15: *Tofieldia nuda* (KHP-120)(13: grain, 14–15: LO-pattern). Scale bars = 10 μm.

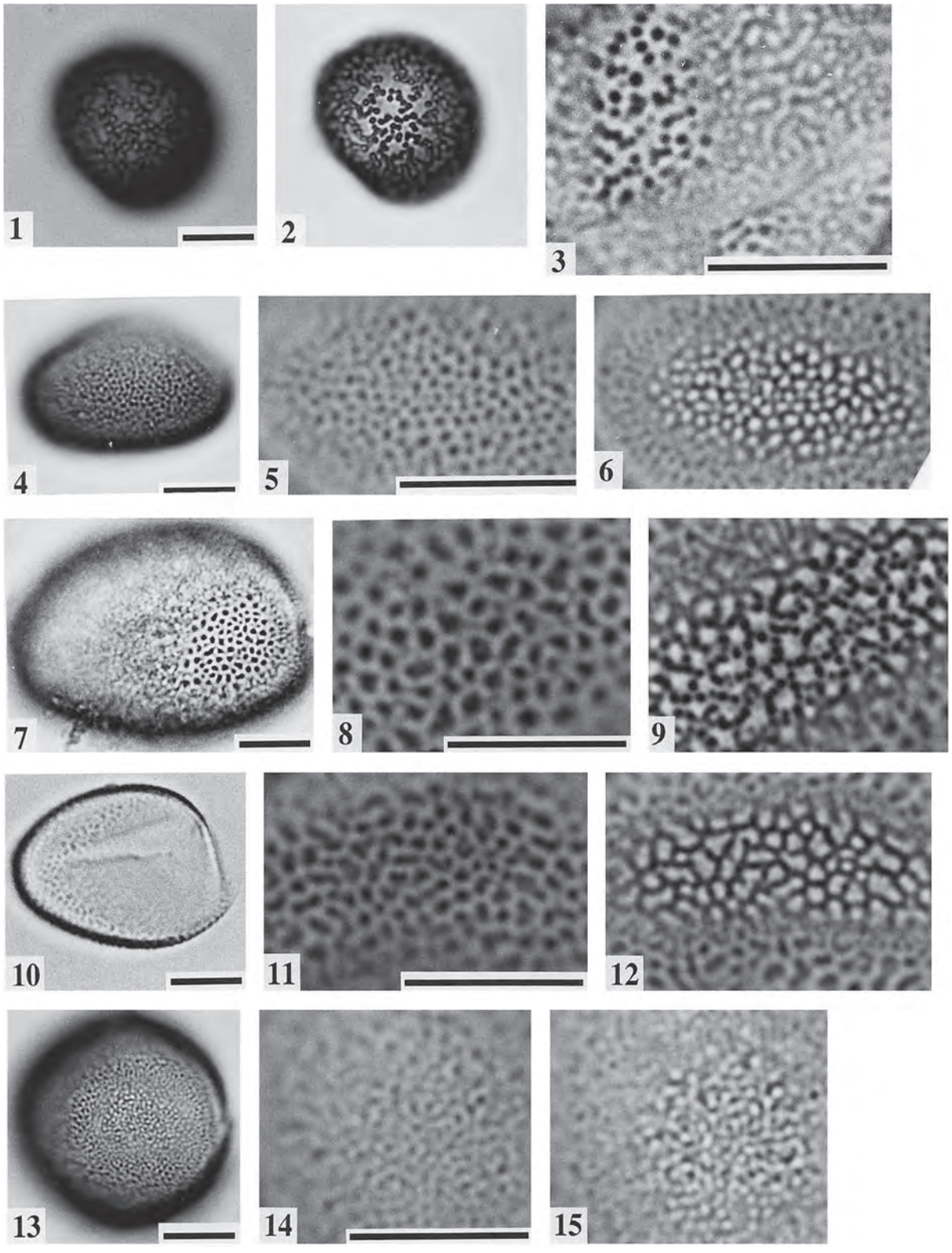

Fig. 2 Pollen grains of *Japonolirion*, *Narthecium,* and *Aletris*. — 1–3: *Japonolirion osense* (KHP-96)(1–2: LO-pattern. 3: sculptural pattern near the sulcus). — 4–6: *Narthecium asiaticum* (KHP-50)(4: grain, 5–6: LO-pattern). — 7–9: *Aletris foliata* (KHP-51)(7: grain, 8–9: LO-pattern). — 10–12: *Aletris luteoviridis* (KHP-93)(10: grain, 11–12: LO-pattern). — 13–15: *Aletris spicata* (KHP-103)(13: grain, 14–15: LO-pattern). Scale bars = 10 μm.

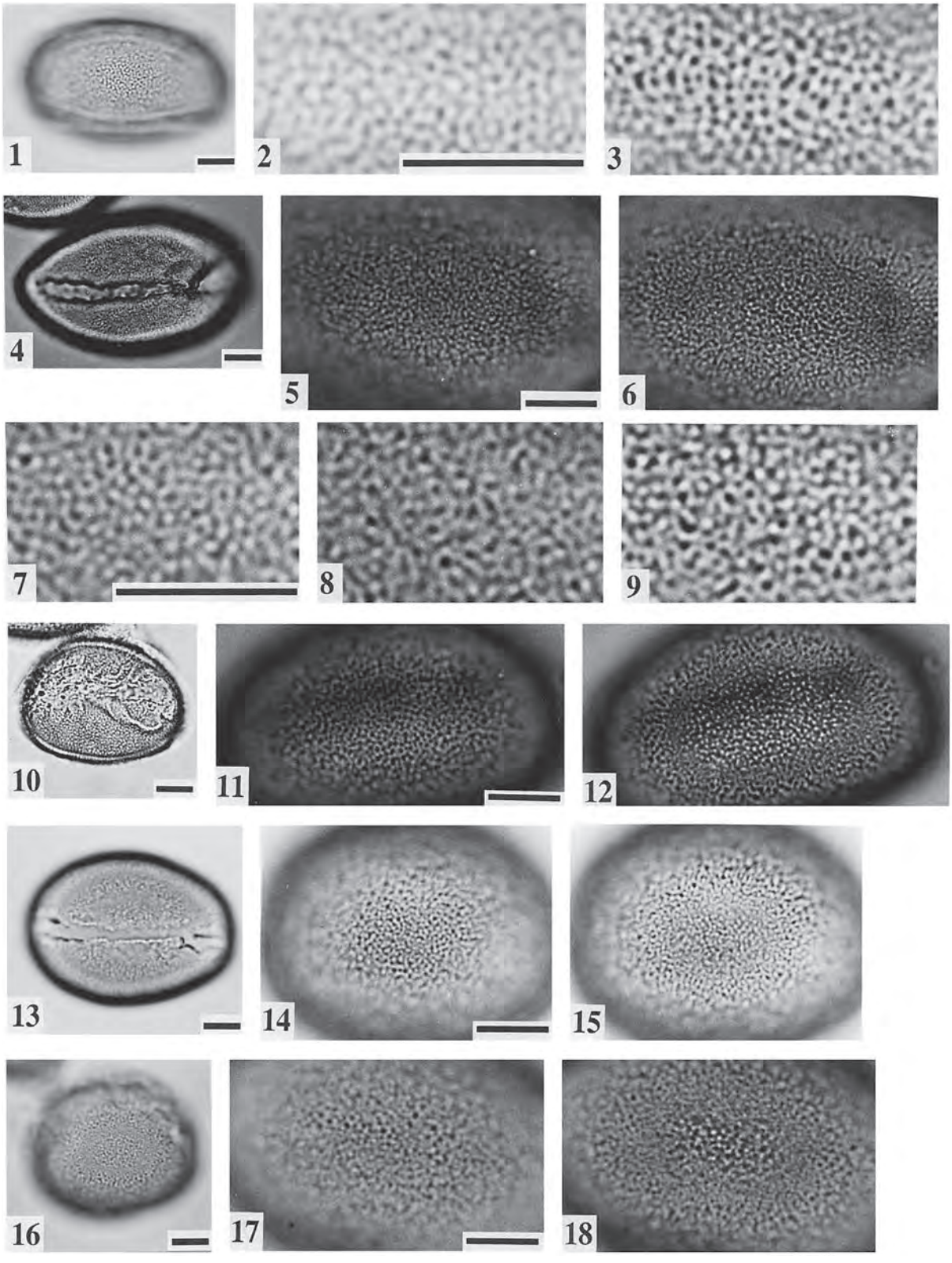

Fig. 3 Pollen grains of *Uvularia* and *Disporum*. — 1–3: *Uvularia perfoliata* (KHP-18)(1: grain, 2–3: LO-pattern). — 4–9: *Disporum sessile* (KHP-16)(4: grain, 5–9: LO-pattern). — 10–12: *Disporum smilacinum* (KHP-6)(10: grain, 11–12: LO-pattern). — 13–15: *Disporum nantouense* (KHP-23)(13: grain, 14–15: LO-pattern). — 16–18: *Disporum uniflorum* (KHP-21)(16: grain, 17–18: LO-pattern). Scale bars = 10 μm.

coarse columellae. *V. stamineum* has duplicolumel-late muri with columellae arranged alternately along the both edges of muri. Large and small lumina compose the reticulate pattern. Lumina become smaller towards the sulcus. Sulcus extends almost to the grain ends and has an operculum with a fine reticulate pattern similar to the rest of the grain surface.

V. nigrum (Figs. 4-4–4-5). L: 46.3 (38.8–52.5) μm, P: 34.2 (31.3–37.5) μm, S: 40.2 (33.8–48.8) μm.

V. stamineum (Figs. 4-1–4-3). L: 53.8 (47.5–63.8) μm, P: 37.1 (31.3–42.5) μm, S: 43.5 (35.0–50.0) μm.

b. *Zigadenus*

Pollen grains are 1-sulcate and elliptic in polar and equatorial views. Exine is semitectate. Sculpture is fine reticulate. Grains are simplicolumellate or duplicolumellate muri without intermediate patterns. Duplicolumellate grains have broad muri, and columellae are arranged along the both edges of muri. Lumina become smaller towards the sulcus. Sulcus does not extend to the grain ends and has an operculum with a fine reticulate pattern similar to the rest of the grain surface.

Z. sibiricus (Figs. 4-6–4-10). L: 57.1 (47.5–70.0) μm, P: 40.4 (32.5–47.5) μm, S: 44.0 (37.5–52.5) μm.

c. *Heloniopsis*

Pollen grains are 1-sulcate and circular to elliptic in polar and equatorial views. Exine is intectate and fine echinate. Spinule bases project inwards to produce verrucae on the inner surface of the nexine. Aperture is wide and elliptic and is not sharply defined. Sulcus is covered with a fine echinate membrane. Spinules of the sulcus membrane are smaller and denser than those at the proximal pole.

H. orientalis. L: 36.9 (35.0–38.8) μm, P: 34.4 (33.8–35.0) μm, S: 30.7 (28.8–32.5) μm.

H. orientalis var. *flavida* (Figs. 4-11–4-14). L: 45.6 (40.0–48.8) μm, P: 27.7 (25.0–30.0) μm, S: 27.5 (22.5–32.5) μm.

Takahashi (1982) described the exine ornamentation of *H. orientalis* as fine granulate with small spinules by SEM.

d. *Chionographis*

Pollen grains are 4-pantoporate and spherical to tetrahedral spherical. Exine is semitectate. Sculpture is fine reticulate and has simplicolumellate discontinuous muri. Pori are circular to elliptic, ca. 5 μm in diameter. Pori have a smooth or granular membrane and sometimes protruding margins. Pori are situated on the plane of the tetrahedron.

C. japonica (Figs. 5-1–5-3). L: 19.2 (17.5–21.3) μm.

C. koidzumiana (Figs. 5-4–5-6). L: 21.0 (18.8–23.8) μm.

Takahashi & Kawano (1989) described the exine sculptures of *C. japonica* and *C. koidzmiana* as clavate by SEM.

3) Trilliaceae

a. *Paris*

Pollen grains are 1-sulcate and elliptic in polar and equatorial views. Exine is semitectate and perforate (*P. verticillata*), or intectate and gemmate (*P. tetraphylla*). In *P. tetraphylla,* gemma size is irregular and decreases towards the sulcus. Gemma density varies in a grain. Aperture is narrow and does not extend to the grain ends. Grains of *P. verticillata* have obvious puncta and sparsely arranged columellae. Sculpturing pattern becomes smaller towards the sulcus. Sulcus is wide and does not extend to the grain ends. Sulcus membrane has small exinous islets and puncta.

P. tetraphylla (Figs. 5-7–5-9). L: 57.5 (47.5–70.0) μm.

P. verticillata (Figs. 5-10–5-12). L: 54.1 (46.3–60.0) μm, P: 40.4 (35.0–45.0) μm, S: 41.9 (38.8–46.3) μm.

Kurita et al. (1990) described the exine sculpture of *P. tetraphylla* as gemmate, fine ruglate, or scrobiculate by SEM. Takahashi (1984) described the exine sculpture of *P. tetraphylla* as gemmate or rarely rugulate and that of *P. verticillata* as foveolate by SEM.

b. *Kinugasa*

Pollen grains are 1-sulcate and elliptic in polar and equatorial views. Exine is intectate with gemmae. Gemmae become smaller and sparser towards the sulcus. Gemmae are dense and irregular in size and shape and sometimes fuse with each other. Aperture is narrow and does not extend to the grain ends.

K. japonica (Figs. 5-13–5-16). L: 78.9 (67.6–92.6) μm.

c. *Trillium*

Pollen grains are omniaperturate and hardly resistant to acetolysis. Most grains are broken, and some remain spherical. Exine is intectate to tectate. Sculpture is granulate. *T. grandiflorum* has irregularly sized, sparse verrucae.

T. grandiflorum (Figs. 6-1–6-3). L: 54.2 (43.8–67.5) μm.

T. kamutschaticum (Figs. 6-4–6-6). L: 48.9 (41.3–57.5) μm.

T. smallii (Figs. 6-7–6-9). L: 60.0 (51.3–65.0) μm.

4) Liliaceae

a. *Clintonia*

Pollen grains are 1-sulcate and elliptic in polar and equatorial views. Sculpture is perforate with supratectal gemmae. Gemmae are irregularly sized and dense. Sul-

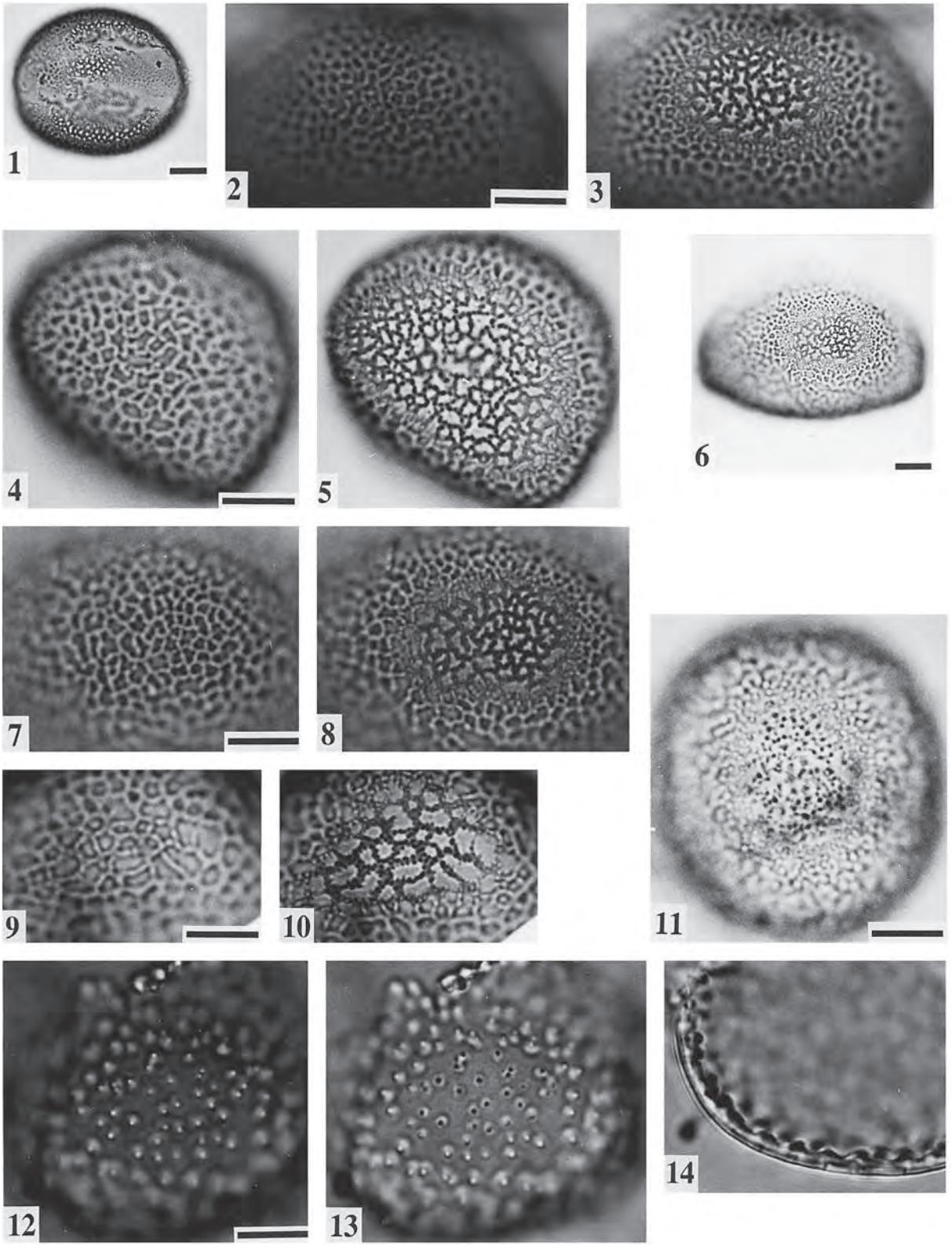

Fig. 4 Pollen grains of *Veratrum, Zygadenus,* and *Heloniopsis*. — 1–3: *Veratrum stamineum* (KHP-92)(1: grain, 2–3: LO-pattern). — 4–5: *Veratrum nigrum* (KHP-116)(LO-pattern). — 6–10: *Zygadenus sibiricus* (KHP-90)(6: grain, 7–10: LO-pattern). — 11–14: *Heloniopsis orientalis* var. *flavida* (KHP-3)(11: sculptural pattern near the aperture, 12–13: LO-pattern, 14: projections of the inner surface of the nexine under spinule bases). Scale bars = 10 μm.

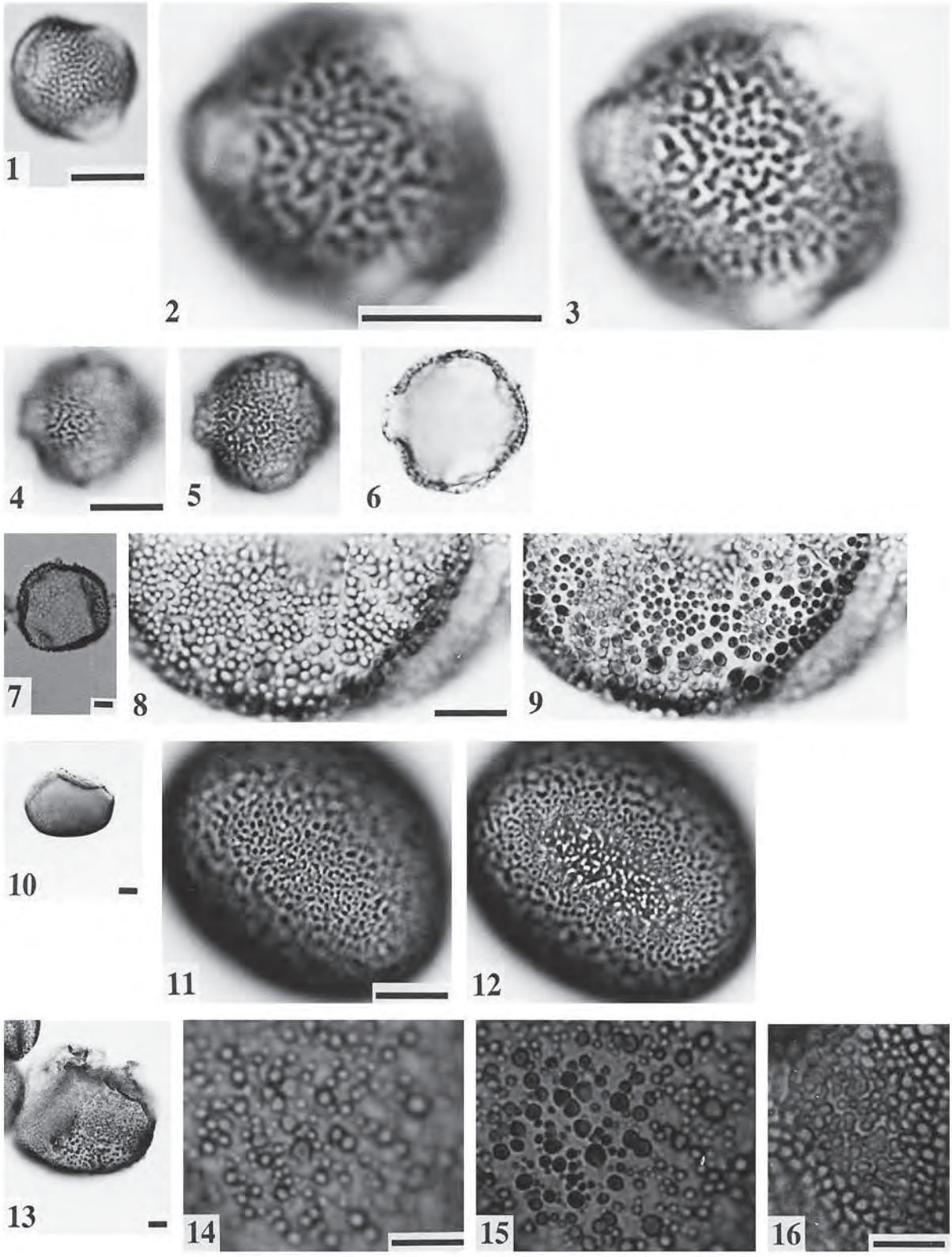

Fig. 5 Pollen grains of *Chionographi, Paris,* and *Kinugasa*. — 1–3: *Chionographis japonica* (KHP-94)(1: grain, 2–3: LO-pattern). — 4–6: *Chionographis koidzumiana* (KHP-117)(4–5: LO-pattern, 6: grain). — 7–9: *Paris tetraphylla* (KHP-53)(7: grain, 8–9: LO-pattern). — 10–12: *Paris verticillata* (KHP-106)(10: grain, 11–12: LO-pattern). — 13–16: *Kinugasa japonica* (KHP-72)(13: grain, 14–16: LO-pattern, some gemmae fuse with each other). Scale bars = 10 μm.

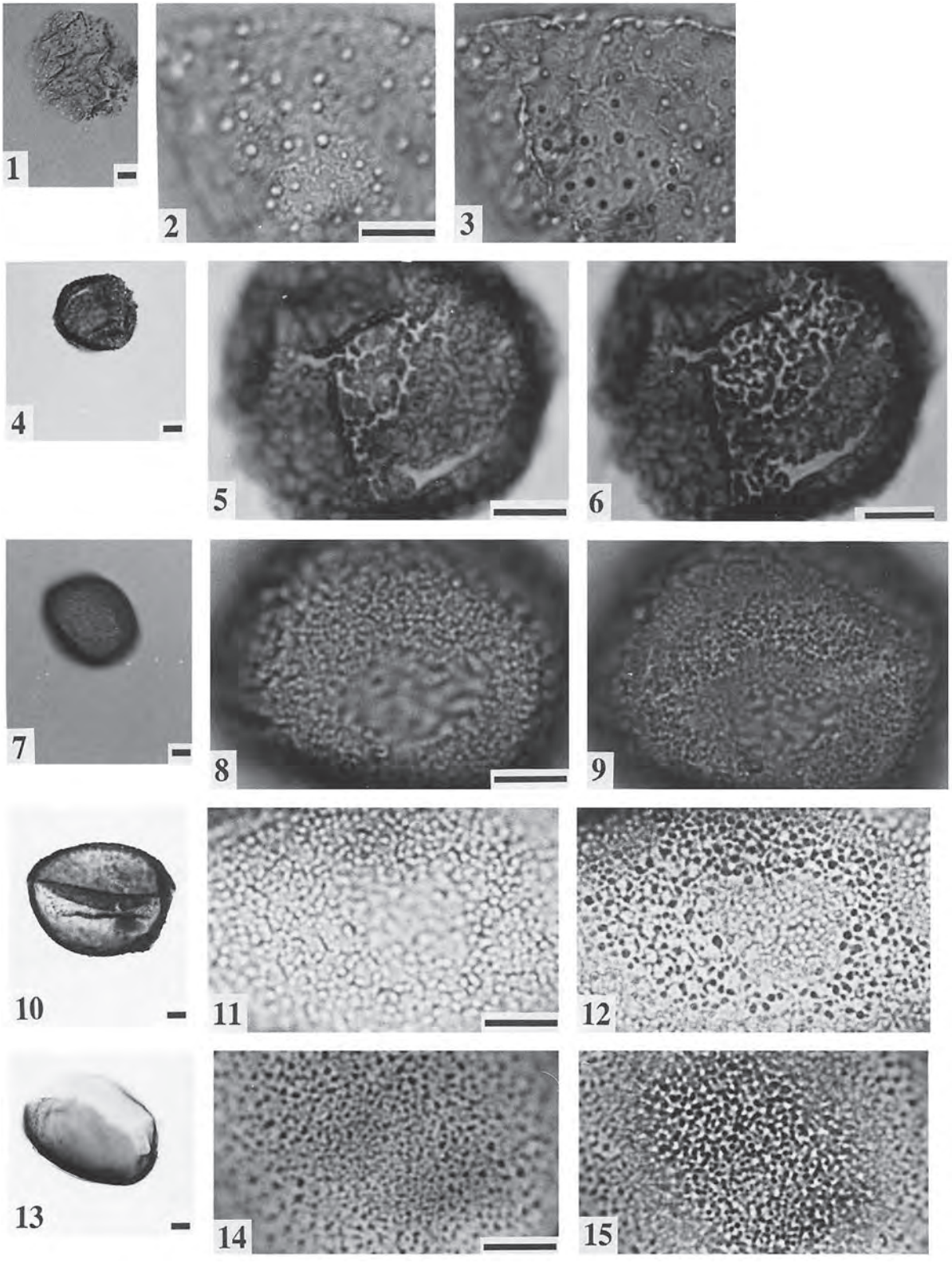

Fig. 6 Pollen grains of *Trillium*, *Clintonia,* and *Gagea*. — 1–3: *Trillium grandiflorum* (KHP-27)(1: grain, 2–3: LO-pattern). — 4–6: *Trillium kamutschaticum* (KHP-77)(4: grain, 5–6: LO-pattern). — 7–9: *Trillium smallii* (KHP-33)(7: grain, 8–9: LO-pattern). — 10–12: *Clintonia udensis* (KHP-80)(10: grain, 11–12: LO-pattern). — 13–15: *Gagea japonica* (KHP-111)(13: grain, 14–15: LO-pattern). Scale bars = 10 μm.

cus is wide with ragged margins and extends almost to the grain ends.

C. udensis (Figs. 6-10–6-12). L: 75.7 (70.0–85.0) μm, P: 55.6 (47.6–65.0) μm, S: 62.9 (60.0–65.0) μm.

b. *Gagea*

Pollen grains are 1-sulcate and elliptic in polar and equatorial views. Exine is tectate. Sculpture is perforate with rugulate ridges on the tectum surface. Grains of *G. japonica* have dense small puncta and dense coarse columellae. Grains of *G. lutea* have irregularly elongated puncta and fine columellae arranged under the edges of sculptural ridges. Sculptural pattern becomes smaller towards the sulcus. Sulcus is wide and does not extend to the grain ends. Sulcus membrane has an operculum with a sculpture similar to the exine or small exinous islets.

G. japonica (Figs. 6-13–6-15). L: 97.5 (87.6–120.0) μm, P: 66.7 (62.6–72.6) μm, S: 73.9 (65.0–90.0) μm.

G. lutea (Figs. 7-1–7-4). L: 117.9 (100.0–140.0) μm, P: 66.0 (55.0–80.0) μm, S: 75.2 (55.0–95.0) μm.

c. *Lloydia*

Pollen grains are 1-sulcate and elliptic in polar and equatorial views. Exine is semitectate with mixed sculpturing of perforate, reticulate, and gemmate. In *L. serotina,* polygonal gemmae fuse to make reticulate or perforate patterns. Columellae are fine and low and are duplicolumellately arranged under the corners of the polygonal gemmae. Grains of *L. triflora* have a fine reticulate sculpture and simplicolumellate muri. Sculpturing pattern becomes finer towards the sulcus and grain ends. Sulcus does not extend to the grain ends.

L. serotina (Figs. 7-5–7-11). L: 103.8 (82.6–125.0) μm, P: 70.2 (52.6–80.0) μm, S: 83.6 (77.6–87.6) μm.

L. triflora (Figs. 7-12–7-14). L: 102.7 (90.0–115.0) μm, P: 65.1 (57.6–77.6) μm, S: 72.9 (60.0–87.6) μm.

d. *Tulipa*

Pollen grains are 1-sulcate and elliptic in polar and equatorial views. Exine is tectate. Sculpture is perforate with rugulate ridges on the tectum surface. Columellae vary in size and density and are arranged under the ridges. Sculpture pattern becomes finer towards the sulcus. Sulcus is wide and does not extend to the grain ends. Sulcus membrane has an operculum with a sculptural pattern similar to the exine or small exinous islets.

T. edulis (Figs. 8-1–8-5). L: 99.1 (80.0–115.0) μm, P: 62.4 (52.6–70.0) μm, S: 69.1 (55.0–82.6) μm.

T. latifolia (Figs. 8-6–8-8). L: 93.5 (85.0–102.6) μm, P: 68.9 (65.0–75.0) μm, S: 84.1 (72.6–90.0) μm.

e. *Erythronium*

Pollen grains are 1-sulcate and elliptic in polar and equatorial views. Exine is semitectate. Sculpture is reticulate to perforate with mixed, large and small lumina. Sometimes discontinuous muri make gemmae. Lumina gradually become smaller towards the sulcus and grain ends. Muri are composed of gemmae polygonal in surface view. Columellae are short, slim, and obscure, and are duplicolumellate under the corners of the polygonal structure of muri. Sulcus is broad, not extend to the grain ends, and has an operculum with a sculptural pattern similar to the exine.

E. japonicum (Figs. 8-9–8-13). L: 116.8 (90.0–160.0) μm, P: 58.7 (50.0–70.0) μm, S: 62.8 (50.0–80.0) μm.

f. *Fritillaria*

Pollen grains are 1-sulcate and elliptic in polar and equatorial views. Exine is semitectate. Sculpture is reticulate to perforate. Grains of *F. camtschatcensis* are reticulate with verrucate muri varing from narrow-continuous to wide-discoutinuous. Grains with narrow muri have densely simplicolumellate muri, and grains with wide muri have obscure duplicolumellate muri. Grains of *F. japonica* are fine reticulate to perforate with discontinuous muri. Lumina gradually become smaller towards the sulcus with a margo. Sulcus is narrow and does not extend to the grain ends. Sulcus membrane is granulate.

F. camtschatcensis (Figs. 9-1–9-3). L: 86.5 (72.6–100.0) μm, P: 53.4 (42.6–62.6) μm, S: 51.3 (40.0–62.6) μm.

F. japonica (Figs. 9-4–9-6). L: 81.9 (70.0–97.6) μm, P: 50.3 (45.0–55.0) μm, S: 63.6 (60.0–70.0) μm .

g. *Cardiocrinum*

Pollen grains are 1-sulcate and elliptic in polar and equatorial views. Exine is semitectate. Sculpture is reticulate with mixed, large and small lumina and densely simplicolumellate, narrow muri. Lumina become smaller towards the sulcus. Sulcus extends near to or to the grain ends with a margo. Sulcus has an operculum with a sculptural pattern similar to the exine.

C. cordatum (Figs. 9-7–9-9). L: 88.4 (75.0–95.5) μm, P: 68.7 (57.6–75.5) μm, S: 71.2 (62.6–77.6) μm.

h. *Lilium*

Pollen grains are 1-sulcate and elliptic in polar and equatorial views. Exine is semitectate. Sculpture is reticulate with wide muri. Muri consist of coarse structures, whose surface view are quadrangular and triangular (*L. hansonii, L. lancifolium, L. maculatum*), or irregularly shaped (*L. longiflorum*). Muri become nar-

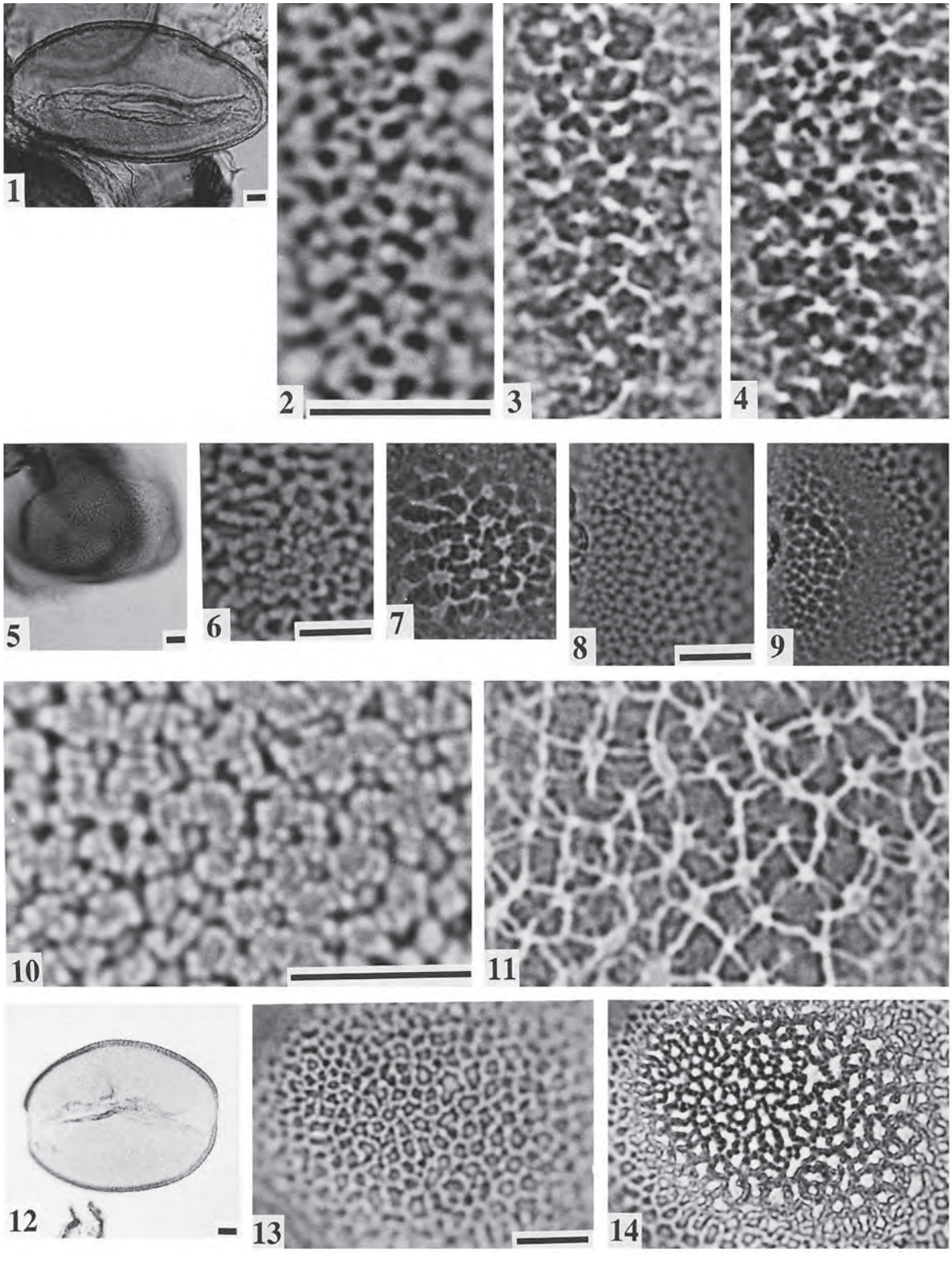

Fig. 7 Pollen grains of *Gagea* and *Lloydia*. — 1–4: *Gagea lutea* (KHP-84)(1: grain, 2–4: LO-pattern). — 5–11: *Lloydia serotina* (KHP-85)(5: grain, 6–11: LO-pattern). — 12–14: *Lloydia triflora* (KHP-113)(12: grain, 13–14: LO-pattern). Scale bars = 10 μm.

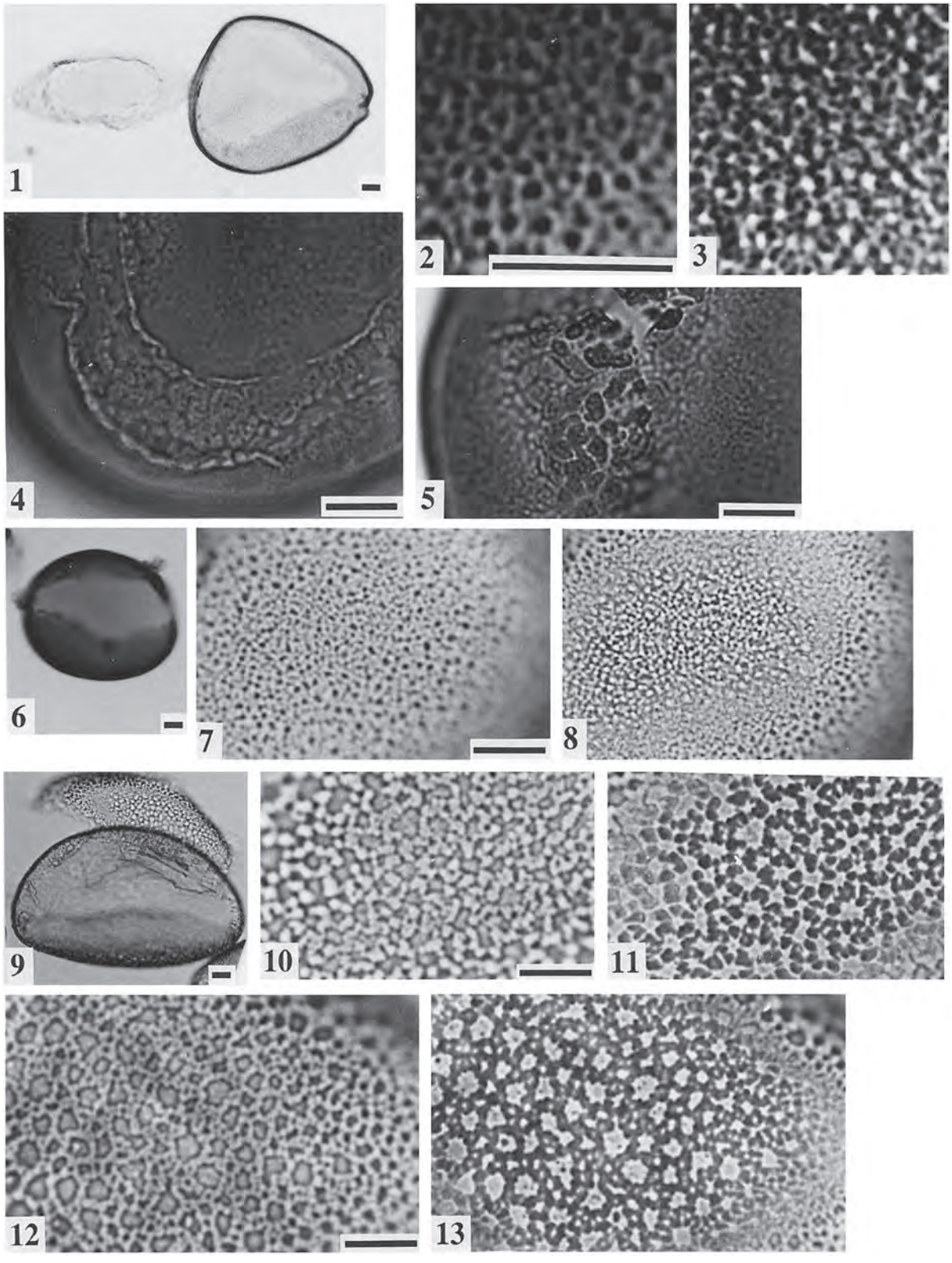

Fig. 8 Pollen grains of *Tulipa* and *Erythronium*. — 1–5: *Tulipa edulis* (KHP-88)(1: grain, 2–3: LO-pattern, 4: aperture with an operculum, 5: aperture without an operculum). — 6–8: *Tulipa latifolia* (KHP-112)(6: grain, 7–8: LO-pattern). — 9–13: *Erythronium japonicum* (9–11: KHP-1, 12–13: KHP-4)(9: grain, 10–13: LO-pattern). Scale bars = 10 μm.

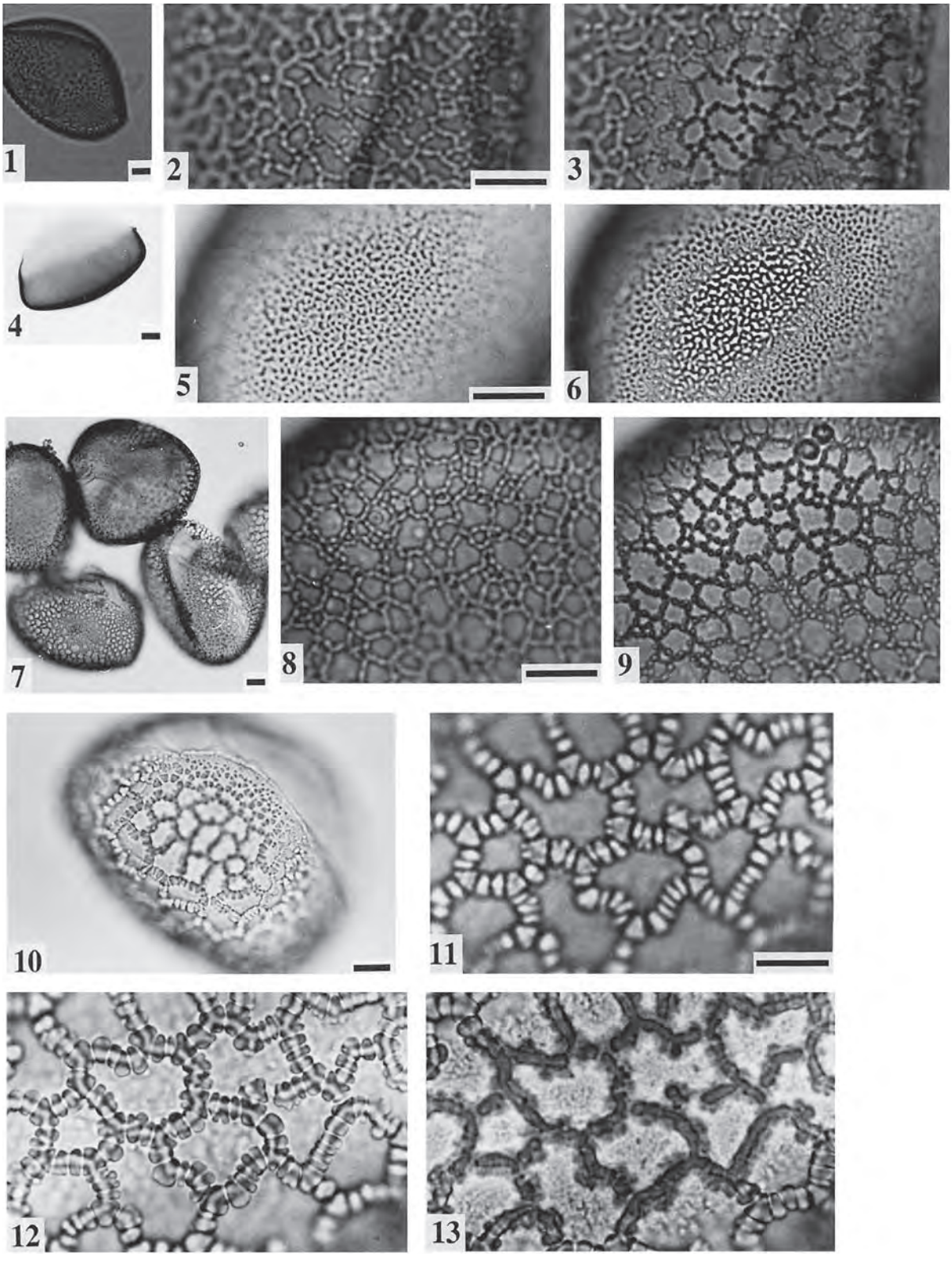

Fig. 9 Pollen grains of *Fritillaria, Cardiocrinum,* and *Lilium*. — 1–3: *Fritillaria camtschatcensis* (KHP-83)(1: grain, 2–3: LO-pattern). — 4–6: *Fritillaria japonica* (KHP-110)(4: grain, 5–6: LO-pattern). — 7–9: *Cardiocrinum cordatum* (KHP-87)(7: grains, 8–9: LO-pattern). — 10–13: *Lilium hansonii* (KHP-45)(10: grain, 11–13: LO-pattern). Scale bars = 10 μm.

row towards their bases. Columellae are low and simplicolumellate under the center of muri. The basal shape of columellae is irregularly elongated and is fine round (*L. hansonii, L. lancifolium, L. maculatum*), polygonal (*L. lancifolium*), or C-shaped (*L. longiflorum*). Lumen floors are covered with granules. Lumen size decreases sharply towards the sulcus and grain ends. Lumina on the line from the proximal pole to the grain ends are discontinuous and smaller. Sulcus does not extend to the grain ends. Sulcus membrane sometimes has an operculum with a sculptural pattern similar to the exine or granulates.

L. hansonii (Figs. 9-10–9-13). L: 85.5 (75.0–95.0) μm, P: 63.9 (60.0–70.0) μm, S: 66.4 (60.0–72.6) μm.

L. lancifolium (Figs. 10-1–10-4). L: 122.0 (118.0–140.0) μm, P: 72.5 (60.0–90.0) μm, S: 82.1 (57.6–90.0) μm.

L. longiflorum (Figs. 10-5–10-7). L: 196.0 (170.0–210.0) μm, P: 143.6 (130.0–160.0) μm, S: 135.0 (110.0–160.0) μm.

L. maculatum (Figs. 10-8–10-10). L: 153.9 (135.0–170.0) μm, P: 87.5 (85.0–90.0) μm, S: 112.5 (90.0–130.0) μm.

In the atlas of Nakamura (1980), pollen grains of *L. auratum, L. japonicum, L. speciosum, L. concolor* var. *partheneion,* and *L. medeoloides* have quadrangular and triangular shaped muri.

5) Calochortaceae

a. *Tricyrtis*

Pollen grains are 1-sulcate and elliptic in polar and equatorial views. Exine is tectate. Sculpture is perforate with rugulate ridges on the tectum surface and uniform. Puncta exist between the ridges. Columellae are coarse and dense and are arranged under the sculptural ridges. Grains of *T. macropoda* have fine puncta and columellae. Sulcus is narrow and does not extend to the grain ends. Sulcus margins of *T. macropodea* are ragged.

T. macrantha subsp. *macranthopsis* (Figs. 11-1–11-4). L: 111.9 (95.0–125.0) μm, P: 73.4 (65.0–85.0) μm, S: 79.9 (70.0–90.0) μm.

T. macropoda (Figs. 11-5–11-7). L: 57.5 (52.5–62.5) μm, P: 40.6 (32.5–45.0) μm, S: 45.4 (40.0–50.0) μm.

b. *Streptopus*

Pollen grains are 1-sulcate and elliptic in polar and equatorial views. Exine is semitectate, thickest at the proximal face and becoming thinner towards the sulcus. Sculpture is perforate or reticulate to gemmate. *S. amplexifolius* var. *papillatus* has perforate to gemmate sculpture. Puncta are elongated and irregularly shaped. Sculpture of *S. streptopoides* is reticulate to perforate with mixed, large and small lumina and is simplicolumellate under muri. Sulcus is wide and long, not extending to the grain ends, and has an operculum.

S. amplexifolius var. *papillatus* (Figs. 11-8–11-10). L: 77.0 (60.0–85.0) μm, P: 54.8 (45.0–65.0) μm, S: 58.4 (32.6–72.6) μm.

S. streptopoides (Figs. 11-11–11-13). L: 71.2 (61.5–80.0) μm, P: 55.9 (50.0–67.5) μm, S: 62.1 (55.0–67.5) μm.

6) Smilacaceae

a. *Heterosmilax*

Pollen grains are omniaperturate and have little resistance to acetolysis. Most grains are broken, and some remain spherical. Exine is intectate. Sculpture is granular with irregularly arranged granules.

H. japonica (Figs.12-1–12-3). L: 30.0 (26.3–33.8) μm.

b. *Smilax*

Pollen grains are inapertulate and spherical. Exine is intectate and echinate with sparsely arranged conical spinules. Size and density of spinules are irregular.

S. bracteata (Figs. 12-4–12-5). L: 36.5 (31.3–42.5) μm.

S. china (Figs. 12-6–12-7). L: 30.3 (26.3–35.0) μm.

S. nipponica (Figs. 12-8–12-9). L: 27.5 (25.0–31.3) μm.

3. Asparagales

1) Hemerocallidaceae

a. *Hemerocallis*

Pollen grains are 1-sulcate and elliptic in polar and equatorial views. Exine is semitectate. Sculpture is reticulate with mixed, large and small lumina, which become smaller sharply towards the grain ends. Lumina on the line from the proximal pole to the grain ends are discontinuous and smaller. Lumen floors are covered with granules. Muri are thick and apparently verrucate. Columellae are coarse, and pluricolumellate or duplicolumellate under muri. Reticulum size and columella density vary in a grain. Sulcus is narrow, not extending to the grain ends, and has a margo, but not an operculum.

H. dumortieri var. *esculenta* (Figs. 12-10–12-13). L: 134.8 (95.0–160.0) μm, P: 83.5 (70.0–92.6) μm, S: 99.8 (75.0–122.6) μm.

H. fulva f. *kwanso* (Figs. 13-1–13-4). L: 110.0 (90.0–135.0) μm, P: 64.4 (50.0–77.6) μm, S: 58.8 (45.0–67.6) μm.

H. thunbergii (Figs. 13-5–13-9). L: 114.3 (100.0–125.0) μm, P: 63.1 (60.0–70.0) μm, S: 75.8 (62.6–85.0) μm.

b. *Dianella*

Pollen grains are 1-trichotomosulcate, rarely 1-sulcate, and convex equatorial to isosceles triangular in polar view and convex triangular to elliptic in equatorial view.

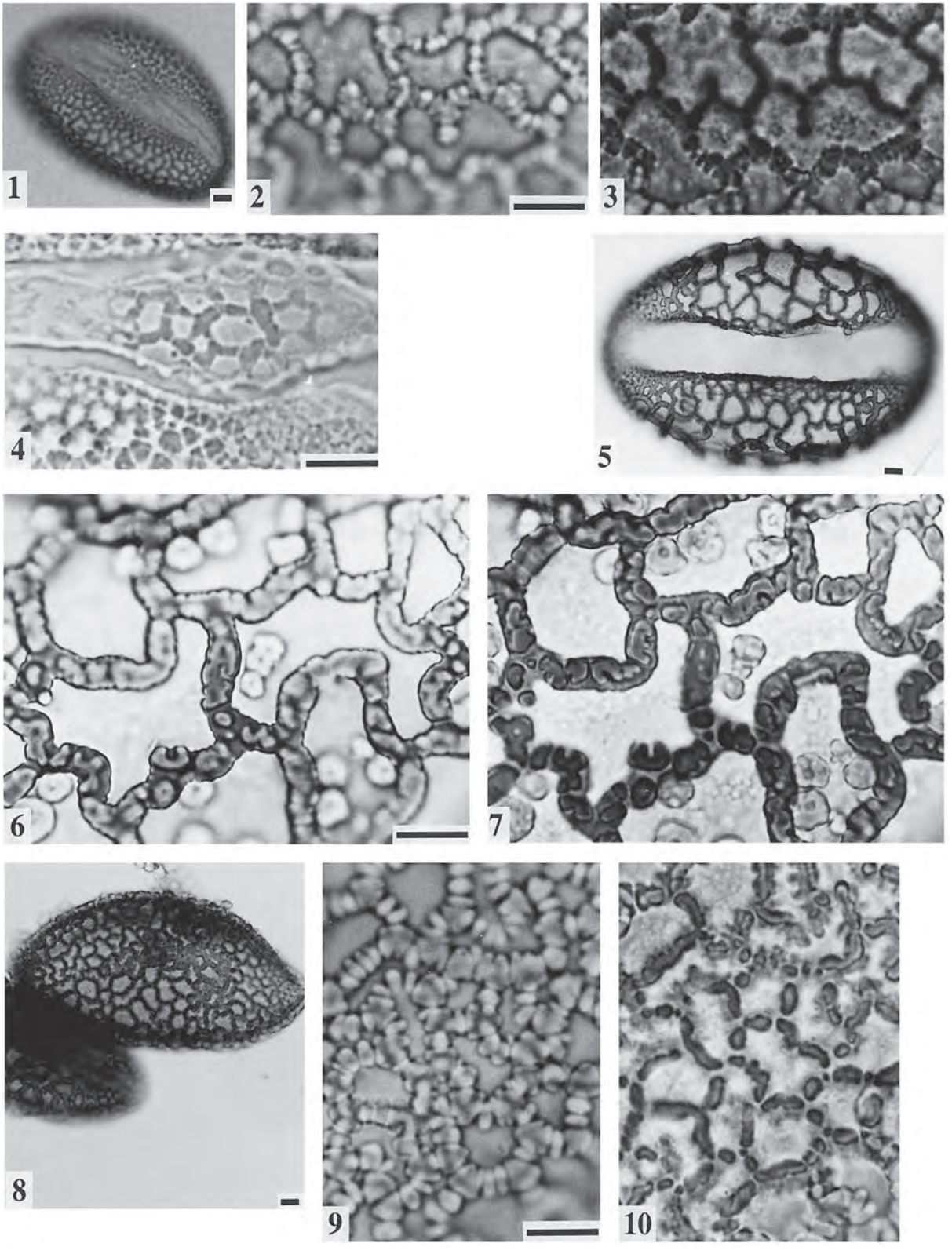

Fig. 10 Pollen grains of *Lilium*. — 1–4: *Lilium lancifolium* (KHP-60)(1: grain, 2–4: LO-pattern). — 5–7: *Lilium longiflorum* (KHP-115)(5: grain, 6–7: LO-pattern). — 8–10: *Lilium maculatum* (KHP-100)(8: grain, 9–10: LO-pattern). Scale bars = 10 μm.

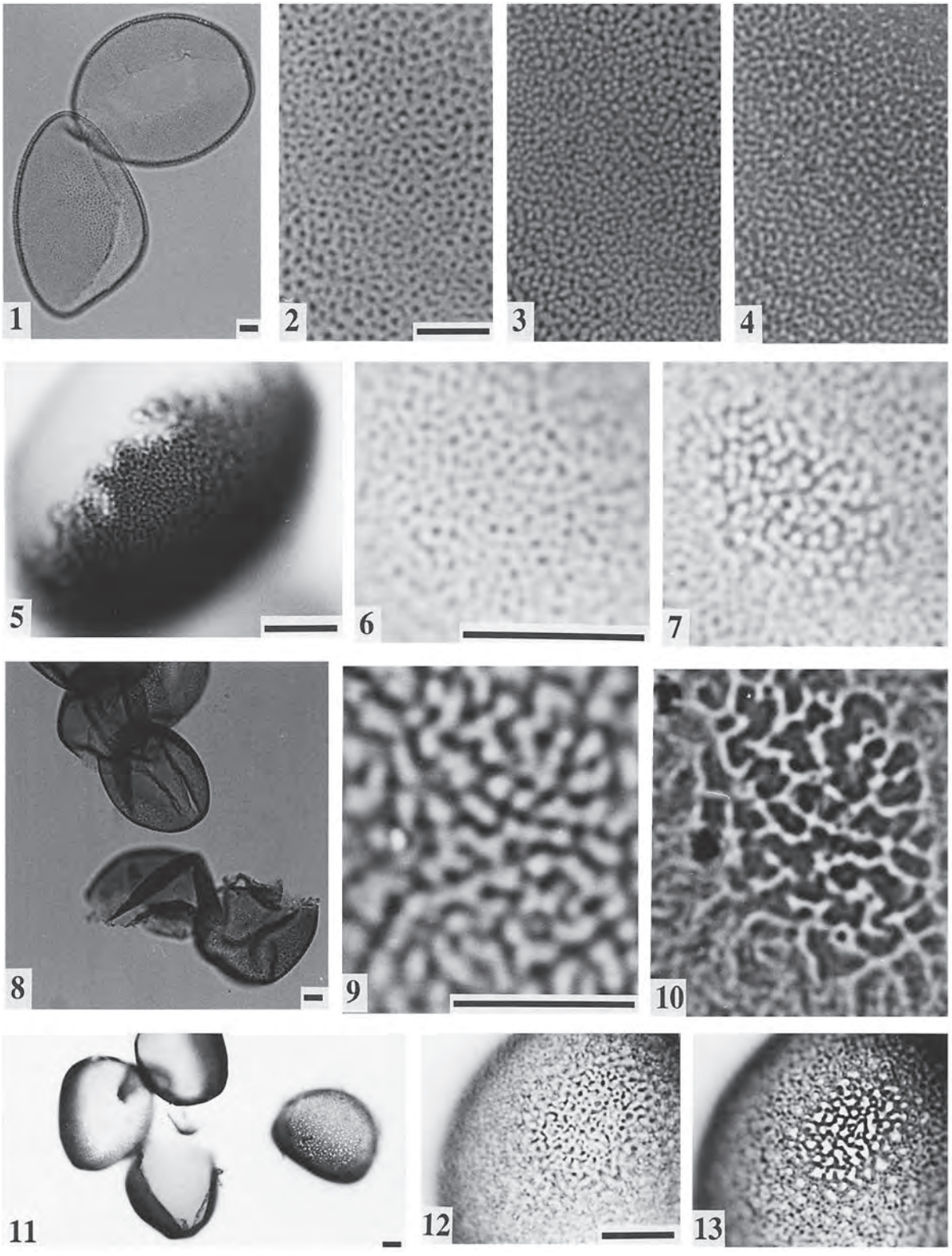

Fig. 11 Pollen grains of *Tricyrtis and Streptopus*. — 1–4: *Tricyrtis macrantha* subsp. *macranthopsis* (KHP-98)(1: grains, 2–4: LO-pattern). — 5–7: *Tricyrtis macropoda* (KHP-65)(5: grain, 6–7: LO-pattern). — 8–10: *Streptopus amplexifolius* var. *papillatus* (KHP-81)(8: grains, 9–10: LO-pattern). — 11–13: *Streptopus streptopoides* (KHP-108)(11: grains, 12–13: LO-pattern). Scale bars = 10 μm.

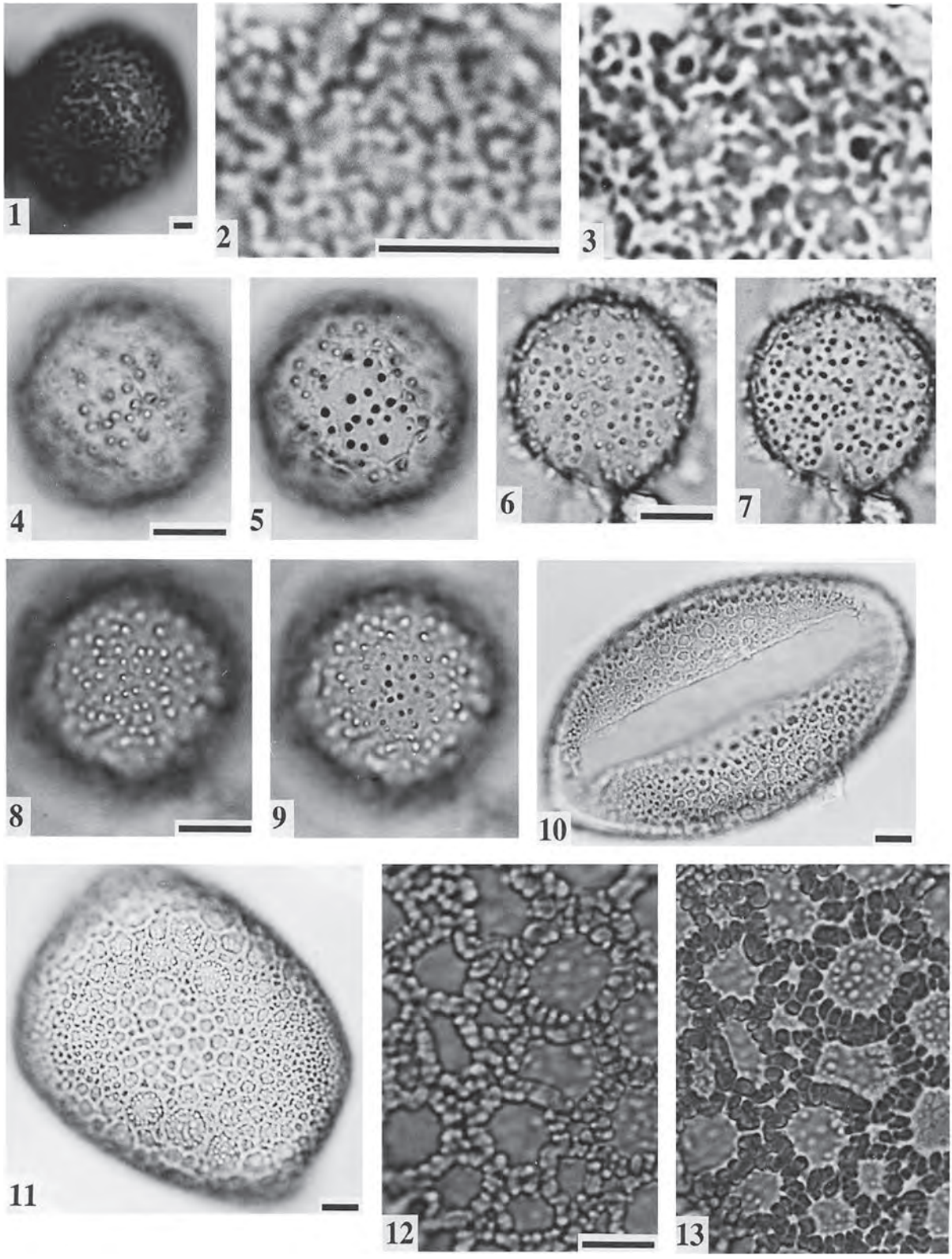

Fig. 12 Pollen grains of *Heterosmilax*, *Smilax*, and *Hemerocallis*. — 1–3: *Heterosmilax japonica* (KHP-76)(1: grain, 2–3: LO-pattern). — 4–5: *Smilax bracteata* (KHP-104)(LO-pattern). — 6–7: *Smilax china* (KHP-29)(LO-pattern). — 8–9: *Smilax nipponica* (KHP-49)(LO-pattern). — 10–13: *Hemerocallis dumortieri* var. *esculenta* (KHP-52)(10: distal face, 11: proximal face, 12–13: LO-pattern). Scale bars = 10 μm.

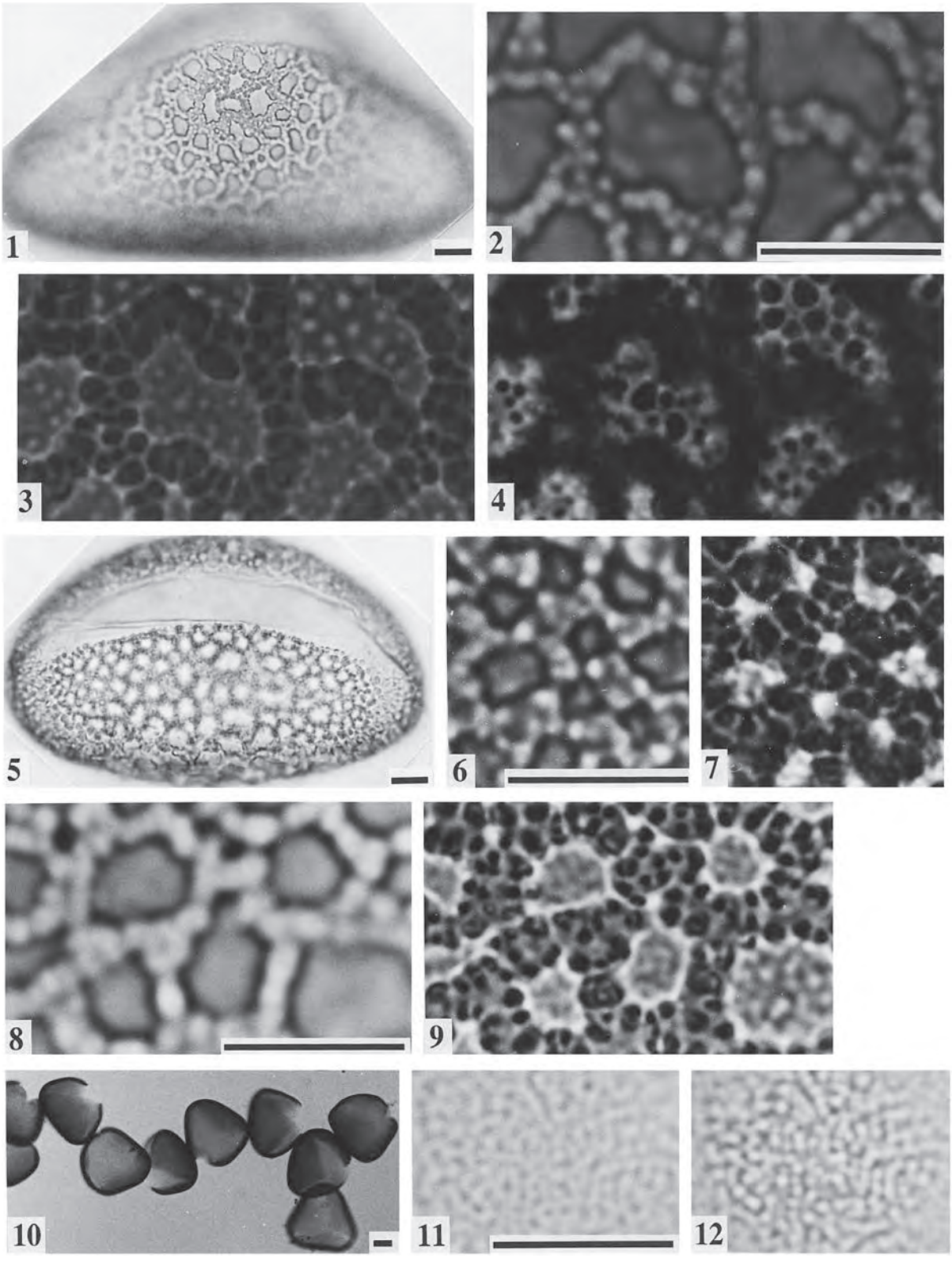

Fig. 13 Pollen grains of *Hemerocallis* and *Dianella*. — 1–4: *Hemerocallis fulva* (KHP-59)(1: grain, 2–4: LO-pattern). — 5–9: *Hemerocallis thunbergii* (KHP-58)(5: grain, 6–9: LO-pattern). — 10–12: *Dianella ensifolia* (KHP-89)(10: grains, 11–12: LO-pattern). Scale bars = 10 μm.

Exine is tectate. Sculpture is perforate with fine rugulate ridges on the tectum surface and uniform. Puncta exist between the ridges. Columellae are fine and sparse. Sulcus is narrow and extends to the grain ends.

D. ensifolia (Figs. 13-10–13-12). L: 36.7 (30.0–43.8) μm, P: 29.8 (25.0–35.0) μm, S: 30.7 (28.8–40.0) μm.

2) Asparagaceae

a. *Asparagus*

Pollen grains are 1-sulcate and elliptic in polar and equatorial views. Exine is tectate. Sculpture is perforate with dense fine columellae. Sulcus is narrow and does not extend to the grain ends.

A. officinalis (Figs. 14-1–14-2). L: 31.8 (27.5–37.5) μm, P: 27.3 (25.0–28.8) μm, S: 28.0 (25.0–31.3) μm.

A. schoberioides (Figs. 14-3–14-4). L: 44.8 (40.0–51.3) μm, P: 33.6 (28.8–37.5) μm, S: 35.4 (30.0–38.8) μm.

3) Anthericaceae

a. *Chlorophytum*

Pollen grains are 1-sulcate and elliptic in polar and equatorial views. Exine is tectate and thin. Sculpture is perforate with fine columellae. Sulcus is narrow and does not extend to the grain ends.

C. orchidastrum (Figs. 14-5–14-6). L: 54.1 (47.5–62.5) μm, P: 33.0 (30.0–37.5) μm, S: 36.9 (32.5–40.0) μm.

b. *Comospermum*

Pollen grains are 1-sulcate and elliptic in polar and equatorial views. Exine is tectate. Sculpture is perforate with rugulate ridges on the tectum surface and uniform. Puncta exist between the ridges. Columellae are coarse and dense. Sulcus is narrow and does not extend to the grain ends.

C. yedoensis (Figs. 14-7–14-10). L: 55.4 (50.0–61.3) μm, P: 39.1 (35.0–45.0) μm, S: 39.4 (30.0–47.5) μm.

4) Alliaceae

a. *Allium*

Pollen grains are 1-sulcate. Shape is acuminate elliptic in polar view and D-shaped in equatorial view: the distal face is convex, and the proximal face is plane, similar to a segment of an orange in the three-dimension. Exine is tectate, thick in the proximal face and thinner towards the sulcus. Sculpture is perforate with fine rugulate to striate ridges on the tectum surface; the ridges are most elongated in *A. macrostemon* and *A. victorialis* subsp. *platyphyllum*. Ridges become smaller towards the sulcus. Fine puncta exist between the ridges. Columellae are fine and sparse, coarsest in *A. thunbergii*. Sulcus is narrow, not extending to the grain ends and without an operculum, and occurs on the curved face of the grain.

A. cepa (Figs. 14-11–14-13). L: 42.0 (37.5–45.0) μm, P: 27.8 (21.3–27.5) μm, S: 28.4 (27.5–30.0) μm.

A. macrostemon (Figs. 14-14–14-16). L: 40.5 (37.5–43.8) μm, P: 21.8 (20.0–23.8) μm, S: 25.3 (23.8–27.5) μm.

A. tuberosum (Figs. 15-1–15-3). L: 45.8 (42.5–48.8) μm, P: 25.0 (22.5–27.5) μm, S: 27.8 (25.0–30.0) μm.

A. thunbergii (Figs. 15-4–15-6). L: 45.4 (42.5–48.8) μm, P: 24.8 (23.8–27.5) μm, S: 28.2 (26.3–30.0) μm.

A. victorialis subsp. *platyphyllum* (Figs. 15-7–15-9). L: 39.9 (36.3–43.8) μm, P: 24.2 (22.5–25.0) μm, S: 25.1 (22.5–27.5) μm.

b. *Nothoscordum*

Pollen grains are 1-sulcate. Shape is acuminate elliptic in polar view and D-shaped in equatorial view: the distal face is convex, and the proximal face is plane, similar to a segment of an orange in the three-dimension. Exine is tectate, thick in the proximal face and thinner towards the sulcus. Sculpture is perforate with rugulate or verrucate ridges on the tectum surface. Fine puncta exist between the ridges. Columellae are coarse and dense and become finer towards the sulcus. Sulcus is narrow, not extending to the grain ends and without an operculum, and occurs on the curved face of the grain.

N. inutile (Figs. 15-10–15-12). L: 51.6 (45.0–56.3) μm, P: 29.9 (25.0–33.8) μm, S: 33.4 (26.3–40.0) μm.

5) Hyacinthaceae

a. *Scilla*

Pollen grains are 1-sulcate and elliptic in polar and equatorial views. Exine is tectate to semitectate, thickest at the proximal face and thinner towards the sulcus. Sculpture is perforate with irregularly sized puncta. Puncta are large in the proximal face and become smaller towards the sulcus. Columellae are coarse and dense. Sulcus is narrow and does not extend to the grain ends. Sulcus membrane is smooth or granulate.

S. chinensis (Figs. 15-13–15-15). L: 72.2 (60.0–90.0) μm, P: 52.7 (37.5–66.3) μm, S: 54.3 (47.5–65.0) μm.

6) Convallariaceae

a. *Polygonatum*

Pollen grains are 1-sulcate and elliptic in polar and equatorial views. Exine is tectate to semitectate, thickest at the proximal face and thinner towards the sulcus. Sculpture is perforate to reticulate (*P. oppositifolium*, *P.* sp. nov.). Reticulate grains have pluricolumellate muri. Columellae are coarse and dense. In the grains with perforate sculpturing, puncta exist between the sculptural

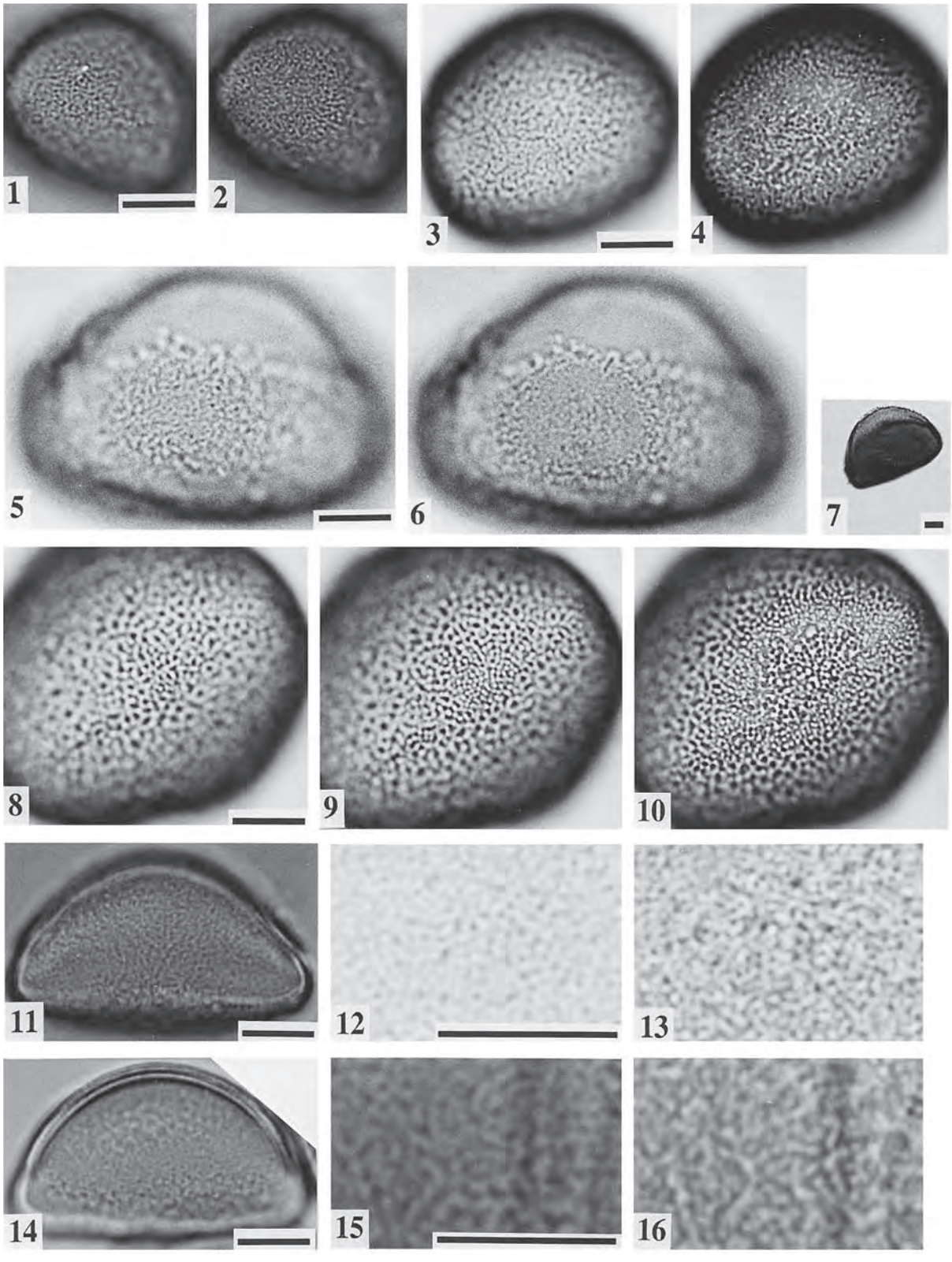

Fig. 14 Pollen grains of *Asparagus, Chlorophytum, Comospermum*, and *Allium*. — 1–2: *Asparagus officinalis* (KHP-34)(LO-pattern). — 3–4: *Asparagus schoberioides* (KHP-109)(LO-pattern). — 5–6: *Chlorophytum orchidastrum* (KHP-64)(LO-pattern). — 7–10: *Comospermum yedoensis* (KHP-91)(7: grain, 8–10: LO-pattern). — 11–13: *Allium cepa* (KHP-14)(11: grain, 12–13: LO-pattern). — 14–16: *Allium macrostemon* (KHP-44)(14: grain, 15–16: LO-pattern). Scale bars = 10 μm.

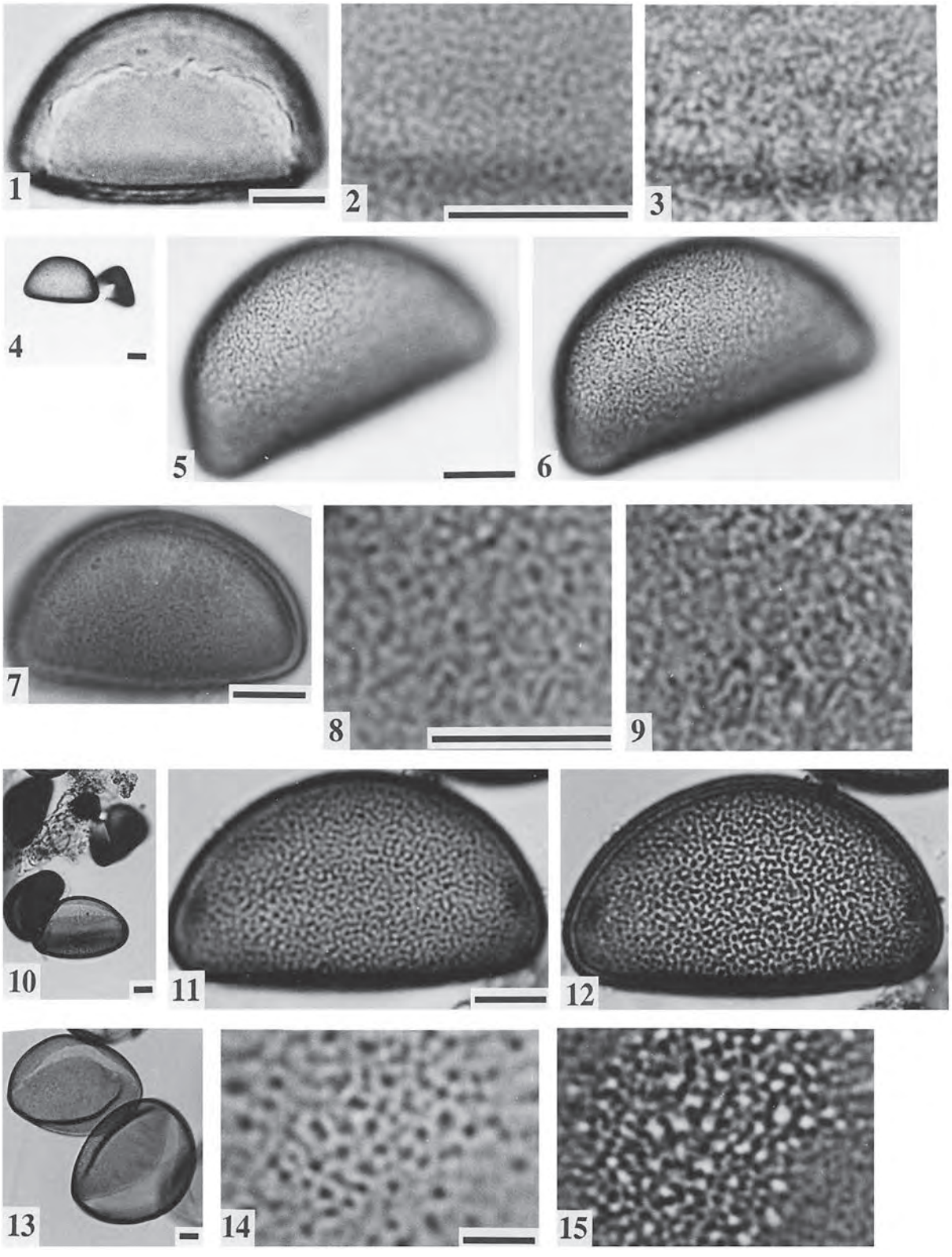

Fig. 15 Pollen grain of *Allium, Nothoscordum,* and *Scilla*. — 1–3: *Allium tuberosum* (KHP-55)(1: grain, 2–3: LO-pattern). — 4–6: *Allium thunbergii* (KHP-114)(4: grain, 5–6: LO-pattern). — 7–9: *Allium victorialis* subsp. *platyphyllum* (KHP-46)(7: grain, 8–9: LO-pattern). — 10–12: *Nothoscordum inutile* (KHP-86)(10: grains, 11–12: LO-pattern). — 13–15: *Scilla chinensis* (KHP-82)(13: grains, 14–15: LO-pattern). Scale bars = 10 μm.

ridges. Punctum size varies among species, large in *P. cryptanthum, P. stenophyllum,* and *P. pubescens,* and small in others. Puncta are large in the proximal face and become smaller towards the sulcus and grain ends. Columellae are dense, and fine or coarse (*P. macranthum, P. falcatum, P. cryptanthum, P. stenophyllum, P. inflatum*). Sulcus is narrow and does not extend to the grain ends. Sulcus membrane is smooth, granular, or with an operculum.

P. cryptanthum (Figs. 16-1–16-3). L: 50.3 (45.0–55.0) μm, P: 39.0 (35.0–42.5) μm, S: 43.1 (38.8–46.3) μm.
P. domonense (Figs. 16-4–16-6). L: 69.3 (60.0–90.0) μm, P: 45.8 (30.0–65.0) μm, S: 44.0 (37.5–65.0) μm.
P. falcatum (Figs. 16-7–16-9). L: 65.8 (55.0–70.0) μm, P: 48.0 (45.0–51.3) μm, S: 51.4 (45.0–57.5) μm.
P. humile (Figs. 16-10–16-12). L: 49.2 (42.5–52.5) μm, P: 39.8 (28.8–45.0) μm, S: 42.5 (40.0–45.0) μm.
P. inflatum (Figs. 16-13–16-15). L: 97.3 (80.0–110.0) μm, P: 72.3 (60.0–85.0) μm, S: 75.0 (65.0–85.0) μm.
P. involucratum (Figs. 17-1–17-3). L: 59.8 (55.0–65.0) μm, P: 43.5 (37.5–45.0) μm, S: 50.6 (46.3–55.0) μm.
P. kingianum (Figs. 17-4–17-6). L: 81.1 (74.0–87.5) μm, P: 52.4 (50.0–55.0) μm.
P. lasianthum (Figs. 17-7–17-11). L: 67.2 (46.3–92.6) μm, P: 49.6 (36.3–65.0) μm, S: 52.4 (40.0–70.0) μm.
P. macranthum (Figs. 17-12–17-14). L: 83.6 (70.0–100.0) μm, P: 66.7 (56.7–75.0) μm, S: 71.1 (65.0–75.0) μm.
P. odoratum var. *pluriflorum* (Figs. 18-1–18-5). L: 58.3 (47.5–67.5) μm, P: 44.7 (40.0–50.0) μm, S: 47.9 (40.0–57.5) μm.
P. oppositifolium (Figs. 18-6–18-9). L: 51.8 (42.5–57.5) μm, P: 40.3 (35.0–42.5) μm, S: 44.7 (40.0–48.8) μm.
P. pubescens (Figs. 18-10–18-12). L: 47.3 (42.5–52.5) μm, P: 38.5 (35.0–42.5) μm, S: 41.3 (38.8–45.0) μm.
P. sibiricum (Figs. 18-13–18-15). L: 64.3 (57.5–67.5) μm, P: 43.9 (33.0–50.0) μm.
P. sp. nov. (Figs. 19-1–19-4). L: 69.8 (62.5–77.5) μm, P: 47.6 (42.5–56.0) μm.
P. stenophyllum (Figs. 19-5–19-7). L: 51.6 (45.0–60.0) μm, P: 38.7 (35.0–45.0) μm.

b. *Heteropolygonatum*

Pollen grains are 1-sulcate and elliptic in polar and equatorial views. Exine is tectate, thickest at the proximal face and thinner towards the sulcus. Sculpture is perforate to reticulate with simplicolumellate muri. Columellae are coarse and dense. Lumina are large in the proximal face and become smaller towards the sulcus to make perforate sculpture. Sulcus is narrow and does not extend to the grain ends.

H. xui (Figs. 19-8–19-11). L: 52.0 (47.5–60.0) μm, P: 34.4 (27.5–47.5) μm.

c. *Disporopsis*

Pollen grains are 1-sulcate and elliptic in polar and equatorial views. Exine is semitectate to tectate. Sculpture of *D. arisaensisis* and *D. undulata* is reticulate with mixed, large and small lumina and pluricolumellate muri. Floors of some lumina are covered with granules. Sculpture of *D. longifolia* is perforate with sparse fine columellae and become finer towards the sulcus. Sulcus is narrow and does not extend to the grain ends.

D. arisanensis (Figs. 19-12–19-14). L: 60.7 (52.5–67.5) μm, P: 46.5 (42.5–50.0) μm, S: 47.4 (42.5–53.8) μm.
D. longifolia (Figs. 19-15–19-17). L: 56.9 (50.0–70.0) μm, P: 40.2 (32.0–45.0) μm, S: 40.2 (25.0–46.3) μm.
D. undulata (Figs. 19-18–19-20). L: 57.7 (51.0–65.0) μm, P: 41.8 (30.0–50.0) μm.

d. *Maianthemum*

Pollen grains are 1-sulcate and elliptic in polar and equatorial views. Exine is tectate, thickest at the proximal face and thinner towards the sulcus. Sculpture is perforate with rugulate to reticulate ridges on the tectum surface. Irregularly sized puncta exist between the ridges. Puncta are large in the proximal face and become smaller towards the sulcus and grain ends. Columellae are fine and sparse under simplicolumellate muri. Sulcus is narrow and does not extend to the grain ends. Sulcus membrane is smooth or granular.

M. bifolium (Figs. 20-3–20-4). L: 44.3 (40.0–50.0) μm, P: 34.4 (32.5–35.0) μm, S: 34.3 (30.0–36.3) μm.
M. dilatatum (Figs. 20-1–20-2). L: 39.3 (35.0–45.0) μm, P: 30.7 (23.8–37.5) μm, S: 32.2 (22.5–41.3) μm.

e. *Smilacina*

Pollen grains are 1-sulcate and elliptic in polar and equatorial views. Exine is tectate, thickest at the proximal face and thinner towards the sulcus. Sculpture is perforate with rugulate to reticulate ridges on the tectum surface. Irregularly sized puncta exist between the ridges. Lumina are large in the proximal face and become smaller towards the sulcus and grain ends. Columellae are fine and sparse under simplicolumellate muri. Sulcus is narrow and does not extend to the grain ends. Sulcus membrane is smooth or granular.

S. bicolor (Figs. 20-5–20-7). L: 50.6 (45.0–56.3) μm, P: 35.9 (27.5–42.5) μm, S: 37.1 (30.0–46.3) μm.
S. formosana (Figs. 20-8–20-10). L: 42.3 (35.0–47.5) μm, P: 33.9 (30.0–37.5) μm, S: 35.7 (32.5–40.0) μm.
S. hondoensis (Figs. 20-11–20-13). L: 46.0 (40.0–52.5) μm, P: 34.3 (30.0–37.5) μm, S: 34.7 (30.0–40.0) μm.
S. japonica (Figs. 20-14–20-19). L: 46.4 (42.5–51.3) μm,

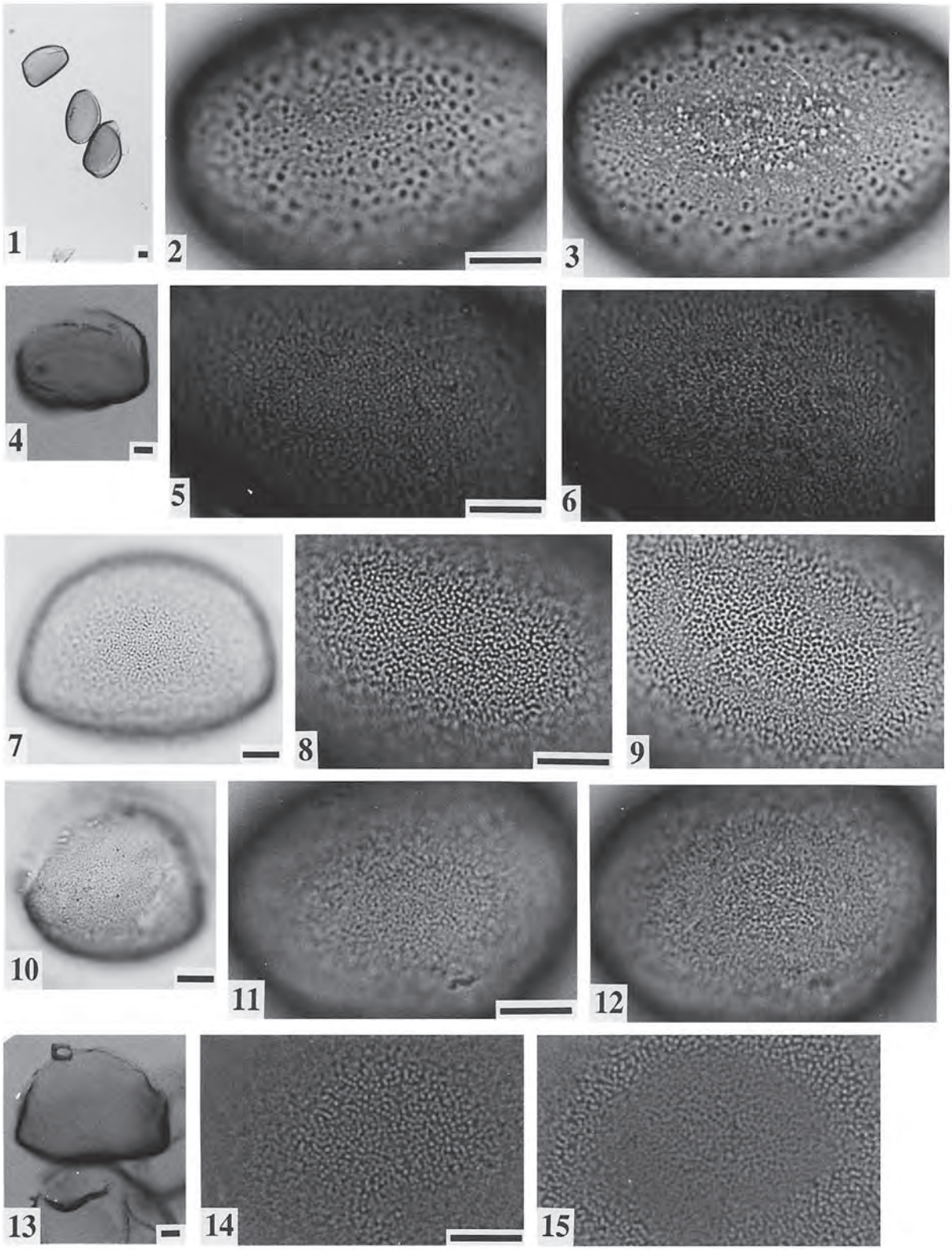

Fig. 16 Pollen grains of *Polygonatum*. — 1–3: *Polygonatum cryptanthum* (KHP-39)(1: grains, 2–3: LO-pattern). — 4–6: *Polygonatum domonense* (KHP-70)(4: grain, 5–6: LO-pattern). — 7–9: *Polygonatum falcatum* (KHP-38)(7: grain, 8–9: LO-pattern). — 10–12: *Polygonatum humile* (KHP-28)(10: grain, 11–12: LO-pattern). — 13–15: *Polygonatum inflatum* (KHP-102)(13: grain, 14–15: LO-pattern). Scale bars = 10 μm.

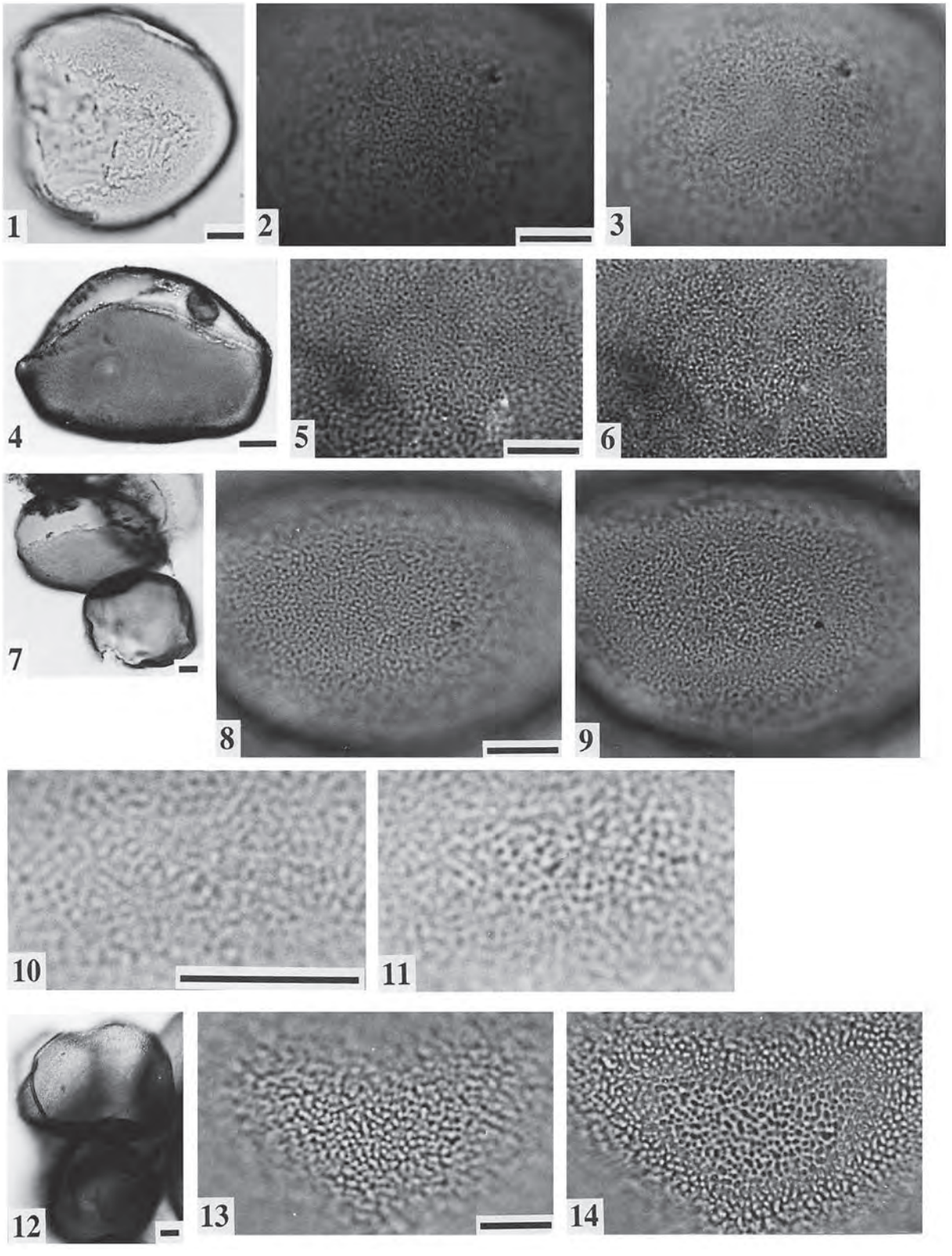

Fig. 17 Pollen grains of *Polygonatum*. — 1–3: *Polygonatum involucratum* (KHP-43)(1: grain, 2–3: LO-pattern). — 4–6: *Polygonatum kingianum* (KHP-426)(4: grain, 5–6: LO-pattern). — 7–11: *Polygonatum lasianthum* (KHP-32)(7: grains, 8–11: LO-pattern). — 12–14: *Polygonatum macranthum* (KHP-68)(12: grains, 13–14: LO-pattern). Scale bars = 10 μm.

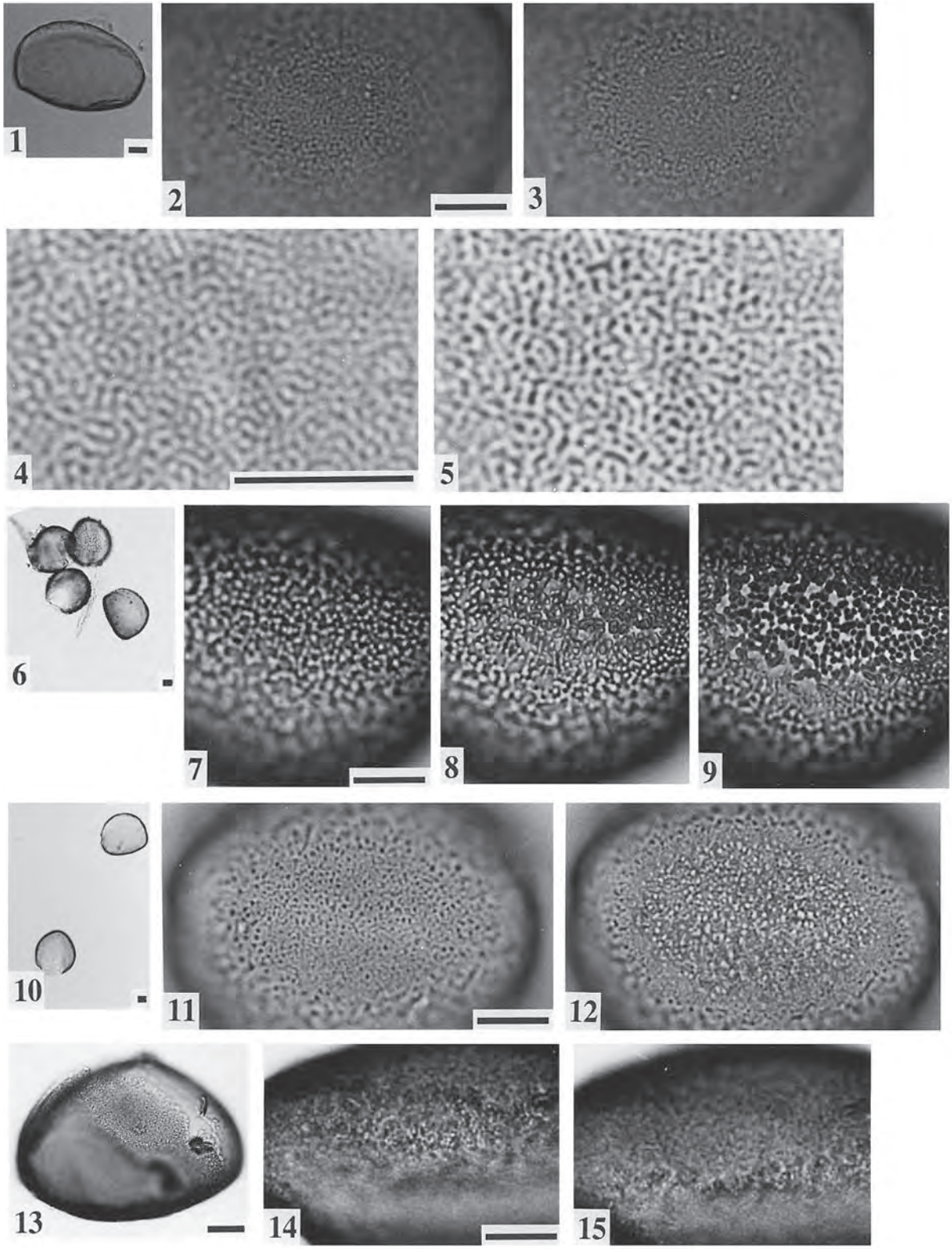

Fig. 18 Pollen grains of *Polygonatum*. — 1–5: *Polygonatum odoratum* var. *pluriflorum* (KHP-42)(1: grain, 2–5: LO-pattern). — 6–9: *Polygonatum oppositifolium* (KHP-36)(6: grains, 7–9: LO-pattern). — 10–12: *Polygonatum pubescens* (KHP-19)(10: grains, 11–12: LO-pattern). — 13–15: *Polygonatum sibiricum* (KHP-425)(13: grain, 14–15: LO-pattern). Scale bars = 10 μm.

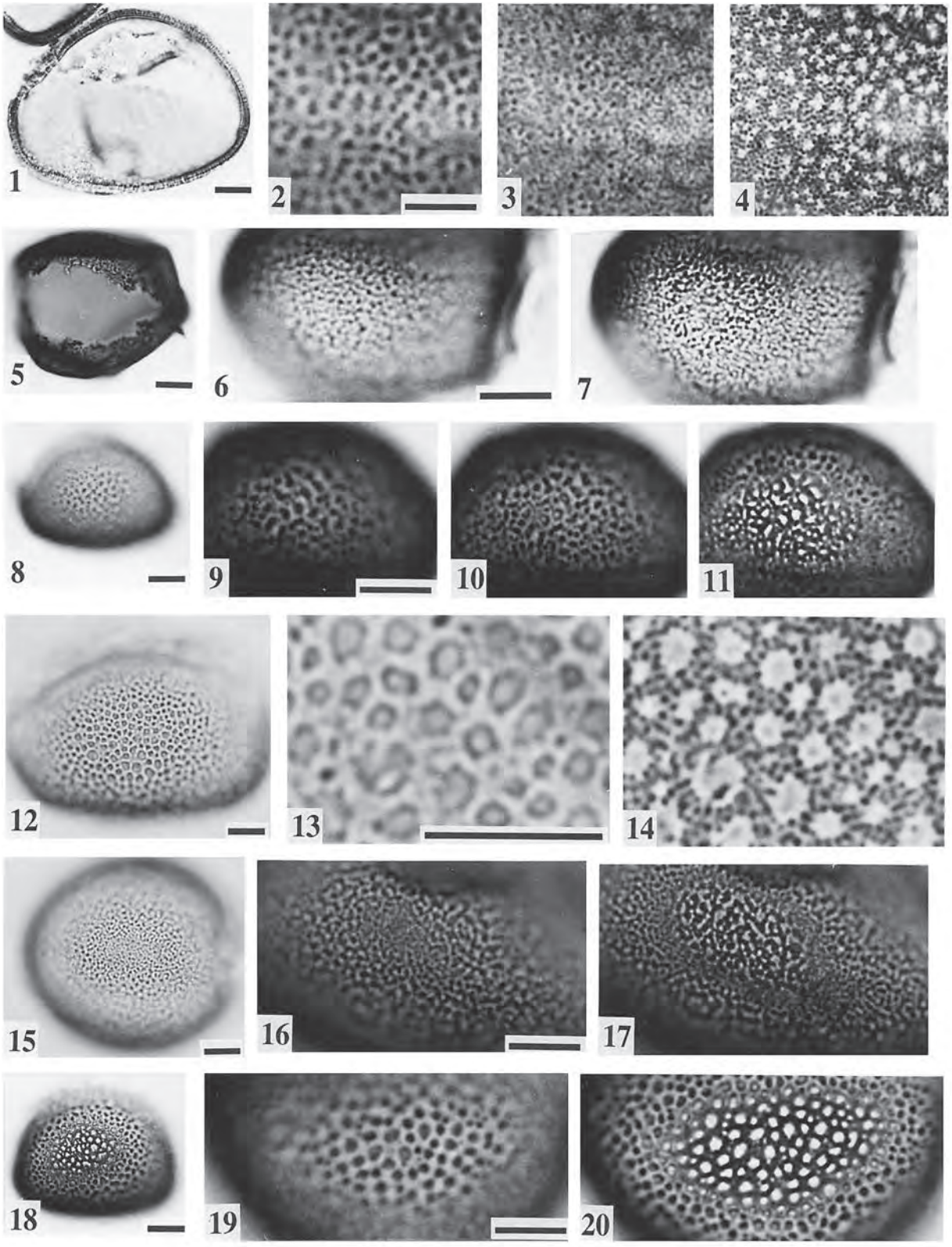

Fig. 19 Pollen grains of *Polygonatum, Heteropolygonatum,* and *Disporopsis*. — 1–4: *Polygonatum* sp. nov. (KHP-424)(1: grain, 2–4: LO-pattern). — 5–7: *Polygonatum stenophyllum* (KHP-429)(5: grain, 6–7: LO-pattern). — 8–11: *Heteropolygonatum xui* (KHP-431)(8: grain, 9–11: LO-pattern). — 12–14: *Disporopsis arisanensis* (KHP-37)(12: grain, 13–14: LO-pattern). — 15–17: *Disporopsis longifolia* (KHP-61)(15: grain, 16–17: LO-pattern). — 18–20: *Disporopsis undulata* (KHP-430)(18: grain, 19–20: LO-pattern). Scale bars = 10 μm.

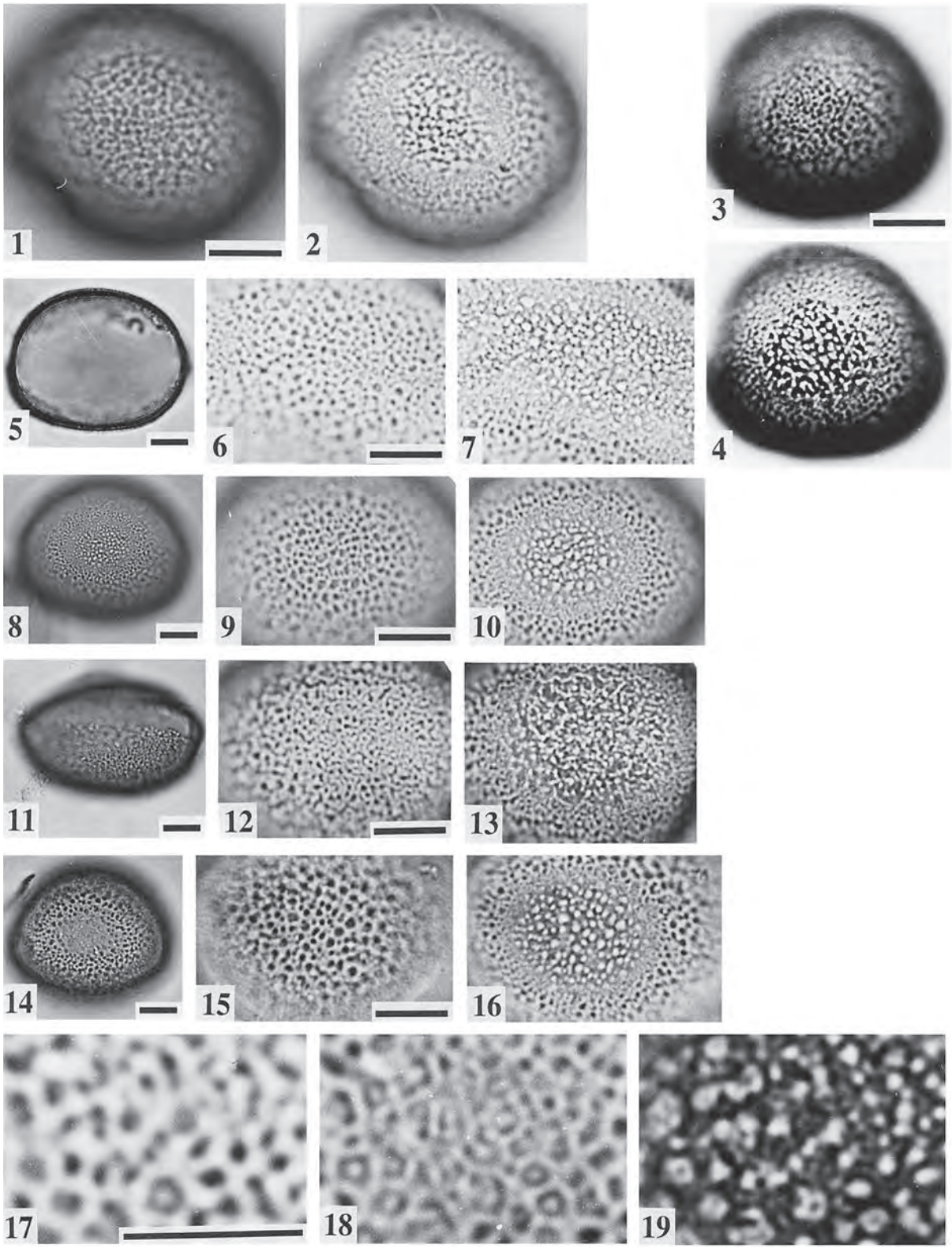

Fig. 20 Pollen grains of *Maianthemum* and *Smilacina*. — 1–2: *Maianthemum dilatatum* (KHP-26)(LO-pattern). — 3–4: *Maianthemum bifolium* (KHP-107)(LO-pattern). — 5–7: *Smilacina bicolor* (KHP-40)(5: grain, 6–7: LO-pattern). — 8–10: *Smilacina formosana* (KHP-20)(8: grain, 9–10: LO-pattern). — 11–13: *Smilacina hondoensis* (KHP-47)(11: grain, 12–13: LO-pattern). — 14–19: *Smilacina japonica* (KHP-30)(14: grain, 15–19: LO-pattern). Scale bars = 10 μm.

P: 36.9 (33.8–40.0) μm, S: 38.0 (31.3–42.5) μm.

Sohma (1978) described the exine sculpture of *S. japonica* as microreticulate and that of *S. hondoensis* as microreticulate with supratectal gemmae on the muri or without supratectal processes by SEM. Takahashi & Sohma (1983) described the exine ornamentation as reticulate with supratectal processes for *S. bicolor*, simple reticulate for *S. japonica*, simple reticulate with small compound of muri for *S. formosana,* and simply reticulate or reticulate with supratectal processes for *S. hondoensis,* by LM and SEM.

f. *Liriope*

Pollen grains are 1-sulcate and elliptic in polar and equatorial views. Exine is tectate, thickest at the proximal face and thinner towards the sulcus. Sculpture is perforate with coarse puncta, which fuse with each other to appear irregularly elongated. Puncta become smaller towards the sulcus. Columellae are fine and sparse. Sulcus is wide and extends almost to the grain ends. Sulcus membrane has ragged margins with small exinous islets, which break into segments.

L. minor (Figs. 21-1–21-3). L: 56.3 (50.0–62.5) μm, P: 44.1 (40.0–47.5) μm, S: 42.8 (35.0–50.0) μm.

L. platyphylla (Figs. 21-4–21-9). L: 46.9 (42.5–52.5) μm, P: 31.3 (27.5–35.0) μm, S: 34.0 (30.0–37.5) μm.

g. *Ophiopogon*

Pollen grains are 1-sulcate and elliptic in polar and equatorial views. Exine is tectate, thickest at the proximal face and thinner towards the sulcus. Sculpture is perforate with rugulate ridges on the tectum surface. Puncta exist between the ridges and become smaller towards the sulcus. Columellae are fine and sparse. Sulcus is wide with ragged margins and extends to the grain ends.

O. brevipes (Figs. 21-10). L: 35.8 (32.5–38.8) μm, P: 27.4 (22.5–32.5) μm, S: 27.9 (25.0–30.0) m.

O. jaburan (Figs. 21-11–21-12). L: 42.1 (38.8–47.5) μm, P: 31.5 (28.8–35.0) μm, S: 32.8 (30.0–35.0) μm.

O. japonicus (Figs. 21-13–21-14). L: 47.9 (38.8–57.5) μm, P: 34.3 (28.8–42.5) μm, S: 36.7 (30.0–41.3) μm.

h. *Peliosanthes*

Pollen grains are 1-sulcate and elliptic in polar and equatorial views. Exine is tectate, thickest at the proximal face and thinner towards the sulcus. Sculpture is perforate with rugulate ridges on the tectum surface. Puncta exist between the ridges and become smaller towards the sulcus. Columellae are fine and sparse. Sulcus is wide and extends to the grain ends. Sulcus membrane has small exinous islets, which break into segments with ragged margins.

P. violacea (Figs. 22-1–22-2). L: 34.1 (30.0–37.6) μm, P: 26.3 (22.5–30.0) μm, S: 26.7 (23.8–30.0) μm.

i. *Convallaria*

Pollen grains are 1-sulcate and elliptic in polar and equatorial views. Exine is tectate. Sculpture is perforate with fine and dense columellae. Puncta become smaller towards the sulcus. Sulcus is narrow and does not extend to the grain ends.

C. keiskei (Figs. 22-3–22-5). L: 44.0 (38.8–50.0) μm, P: 31.1 (28.8–35.0) μm, S: 33.7 (31.3–38.8) μm.

j. *Reineckia*

Pollen grains are 1-sulcate and elliptic in polar and equatorial views. Exine is tectate. Exine is thickest at the proximal face and thinner towards the sulcus. Sculpture is perforate with dense, irregularly sized puncta. Columellae are fine and sparse. Sulcus is wide and does not extend to the grain ends. Sulcus membrane has ragged margins with small exinous islets, which break into segments.

R. carnea (Figs. 22-6–22-8). L: 58.3 (47.5–70.0) μm, P: 42.0 (37.5–45.0) μm, S: 42.8 (33.8–50.0) μm.

k. *Rohdea*

Pollen grains are 1-sulcate and elliptic in polar and equatorial views. Exine is tectate, thickest at the proximal face and thinner towards the sulcus. Sculpture is perforate with irregularly sized puncta. Puncta are large in the proximal face and become smaller towards the sulcus. Columellae are coarse and dense. Sulcus is narrow and does not extend to the grain ends. Sulcus membrane is smooth or granular.

R. japonica (Figs. 22-9–22-12). L: 57.0 (50.0–67.5) μm, P: 36.8 (32.5–40.0) μm, S: 39.3 (37.5–42.5) μm.

l. *Tupistra*

Pollen grains are inaperturate and spherical to elliptic. Exine is tectate. Sculpture is perforate with supratectal verrucae. Puncta are small and sparse. Verrucae are polygonal and irregularly sized. Columellae are fine and sparse.

T. grandis (Figs. 22-13–22-15). L: 52.0 (47.5–56.3) μm.

m. *Aspidistra*

Pollen grains are inaperturate and spherical. Exine is tectate. Sculpture is perforate with supratectal verrucae. Puncta are small and sparse. Verrucae are dense, spherical, and irregular in size. Columellae are fine and sparse.

A. elatior (Figs. 22-16–22-18). L: 47.0 (40.0–55.0) μm.

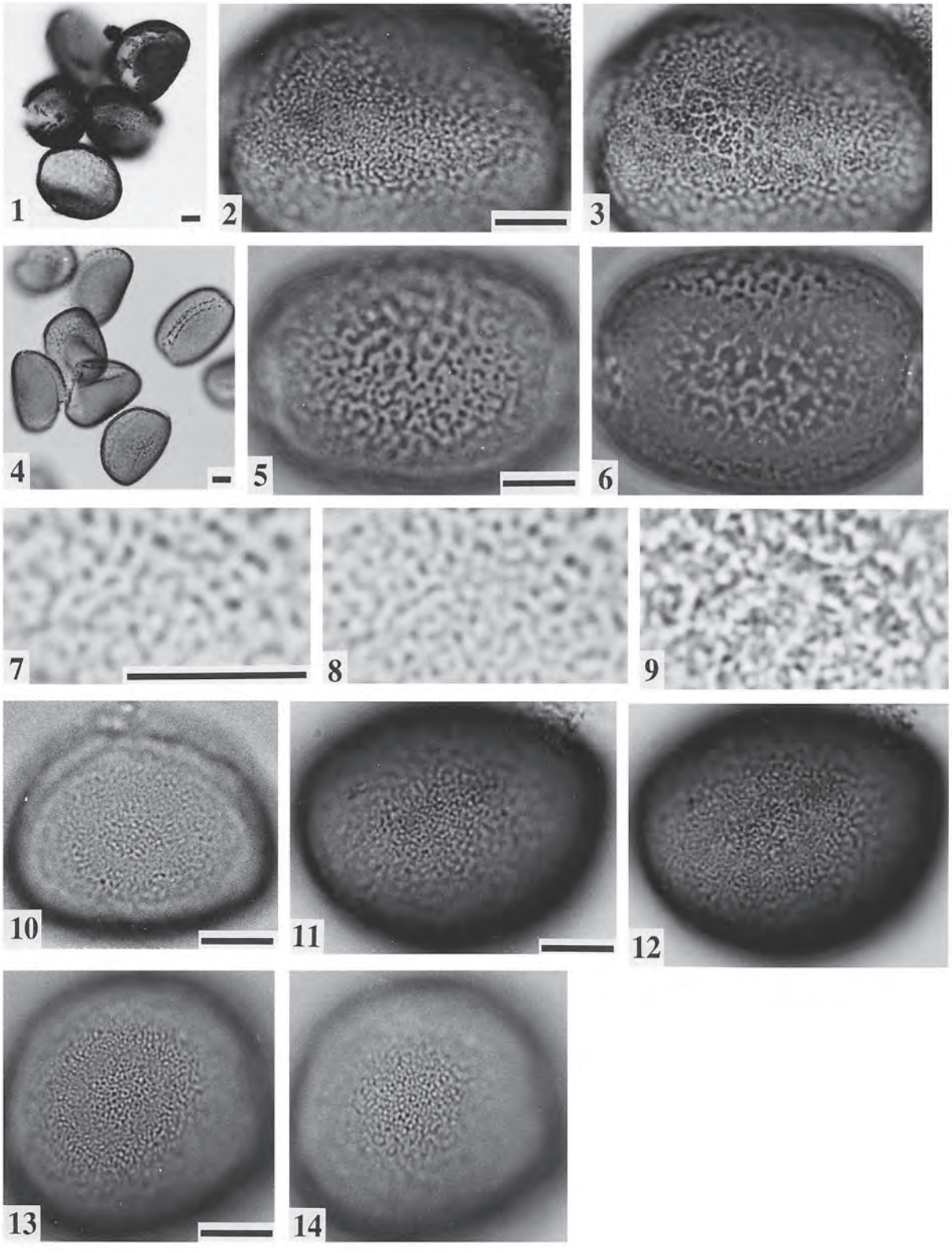

Fig. 21 Pollen grains of *Liriope* and *Ophiopogon*. — 1–3: *Liriope minor* (KHP-105)(1: grains, 2–3: LO-pattern). — 4–9: *Liriope platyphylla* (KHP-75)(4: grains, 5–9: LO-pattern). — 10: *Ophiopogon brevipes* (KHP-63)(grain). — 11–12: *Ophiopogon jaburan* (KHP-73)(LO-pattern). — 13–14: *Ophiopogon japonicus* (KHP-74)(LO-pattern). Scale bars = 10 μm.

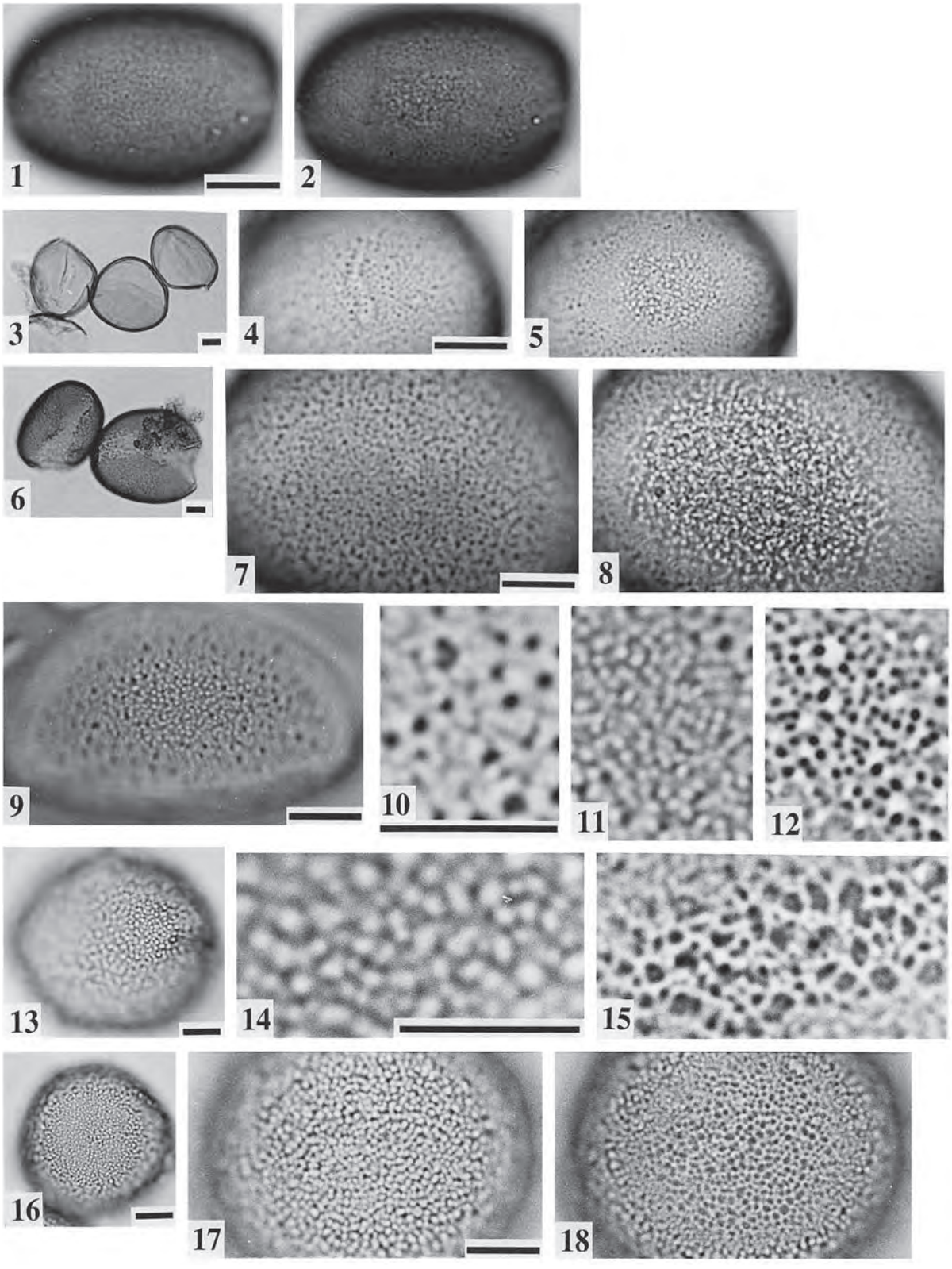

Fig. 22 Pollen grains of *Peliosanthes, Convallaria, Reineckia, Rohdea, Tupistra,* and *Aspidistra*. — 1–2: *Peliosanthes violacea* (KHP-35)(LO-pattern). — 3–5: *Convallaria keiskei* (KHP-79)(3: grains, 4–5: LO-pattern). — 6–8: *Reineckia carnea* (KHP-78)(6: grains, 7–8: LO-pattern). — 9–12: *Rohdea japonica* (KHP-48)(9: grain, 10–12: LO-pattern). — 13–15: *Tupistra grandis* (KHP-17)(13: grain, 14–15: LO-pattern). — 16–18: *Aspidistra elatior* (KHP-10)(16: grain, 17–18: LO-pattern). Scale bars = 10 μm.

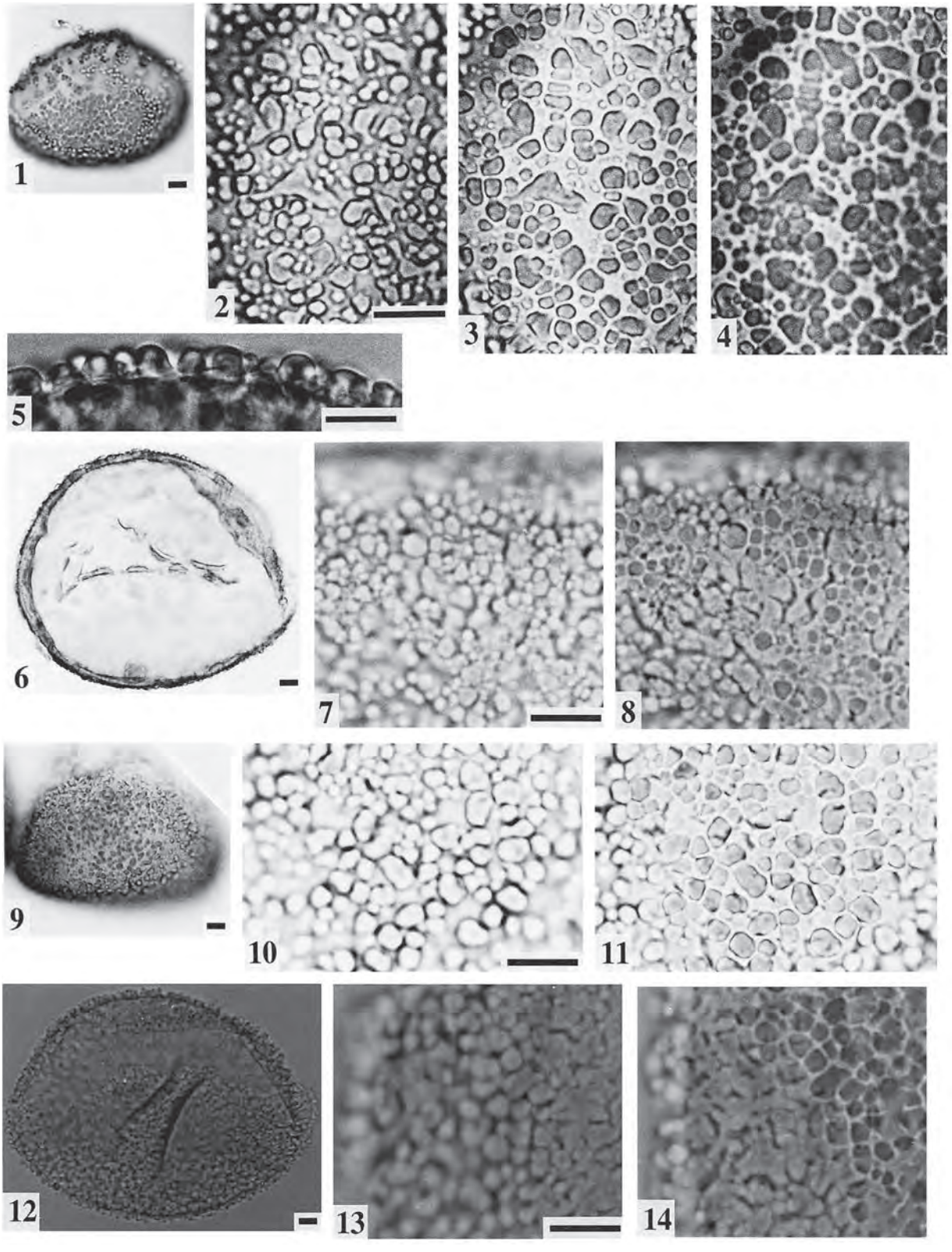

Fig. 23 Pollen grains of *Hosta*. — 1–5: *Hosta albo-marginata* (KHP-56)(1: grain, 2–4: LO-pattern, 5: shape of sculptural elements). — 6–8: *Hosta capitata* (KHP-121)(6: grain, 7–8: LO-pattern). — 9–11: *Hosta longissima* (KHP-122)(9: grain, 10–11: LO-pattern). — 12–14: *Hosta sieboldiana* (KHP-99)(12: grain, 13–14: LO-pattern). Scale bars = 10 μm.

7) Hostaceae

a. *Hosta*

Pollen grains are 1-sulcate, rarely inaperturate (*H. albo-marginata*), and elliptic in polar and equatorial views. Exine is intectate. Sculpture is gemmate or verrucate to clavate. Sculpturing elements vary in size, density, and shape; basal shape is circular, elliptic, or polygonal (*H. longissima, H. albo-marginata*), and diameter is ca. 2–5 μm in *H. albo-marginata, H. capitata,* and *H. longissima,* and ca. 2–3 μm in *H. sieboldiana*. Sometimes sculpturing elements gradually become denser and smaller toward the sulcus and connect with each other. Sulcus is wide or narrow with ragged margins and does not extend to the grain ends.

H. albo-marginata (Figs. 23-1–23-5). L: 106.7 (92.6–122.6) μm, S: 80.2 (72.6–92.6) μm.

H. capitata (Figs. 23-6–23-8). L: 170.0 μm, S: 155.0 μm.

H. longissima (Figs. 23-9–23-11). L: 135.3 (120.0–150.0) μm, P: 106.4 (95.0–120.0) μm, S: 113.8 (100.0–130.0) μm.

H. sieboldiana (Figs. 23-12–23-14). L: 141.4 (125.0–160.0) μm, P: 98.3 (90.0–110.0) μm, S: 100.0 (80.0–115.0) μm.

H. sieboldiana var. *yakusimensis*. L: 131.5 (115.0–140.0) μm, P: 66.3 (65.0–70.0) μm, S: 83.3 (80.0–90.0) μm.

Discussion

Pollen types

Based on the characteristics of pollen class, sculpturing pattern, arrangement of columellae, shape, and mean L for each genus, we classify pollen grains of the Asparagales and Liliales observed in this study into 20 types (Table 2).

***Lilium* type** (*Lilium*). Pollen class is 1-sulcate. Grains are elliptic, and L is 139.4 μm. Sculpture is reticulate with simplicolumellate muri.

***Lloydia* type** (*Cardiocrinum, Erythronium, Fritillaria, Gagea, Lloydia, Streptopus, Tricyrtis, Tulipa*). Pollen class is 1-sulcate. Grains are elliptic, and L is 74.1–114.5 μm. Sculpture is perforate, gemmate, or reticulate with duplicolumellate or simplicolumellate muri.

***Hemerocallis* type** (*Hemerocallis*). Pollen class is 1-sulcate. Grains are elliptic, and L is 119.7 μm. Sculpture is reticulate with pluricolumellate or duplicolumellate muri.

***Clintonia* type** (*Clintonia*). Pollen class is 1-sulcate. Grains are elliptic, and L is 75.7 μm. Sculpture is supratectal gemmate.

***Hosta* type** (*Hosta*). Pollen class is 1-sulcate. Grains are elliptic, and L is 137.0 μm. Sculpture is gemmate, verrucate, or clavate.

***Polygonatum* type** (*Aletris spicata, Allium, Asparagus, Aspidistra, Chlorophytum, Comospermum, Convallaria, Disporopsis longifolia, Disporum, Heteropolygonatum, Liriope, Maianthemum, Nothoscordum, Ophiopogon, Paris verticillata, Peliosanthes, Polygonatum* spp., *Reineckia, Rohdea, Scilla, Smilacina, Tupistra*). Pollen class is 1-sulcate. Grains are elliptic, and L is 34.1–72.2 μm. Sculpture is perforate.

***Allium* type.** Pollen class is 1-sulcate. Grains are orange segmental, and L is 42.7–51.6 μm. Sculpture is perforate.

***Aspidistra* type.** Pollen class is inaperturate. Grains are spherical to elliptic, and L is 47.0–52.0 μm. Sculpture is perforate.

***Dianella* type** (*Dianella*). Pollen class is trichotomosulcate. Grains are obtuse tetrahedral, and L is 36.7 μm. Sculpture is perforate.

***Uvularia* type** (*Uvularia*). Pollen class is 2-sulcate. Grains are elliptic, and L is 53.0 μm. Sculpture is perforate.

***Disporopsis arisanensis* type** (*Disporopsis arisanensis, D. undulata, Polygonatum oppositifolium, Polygonatum* sp. nov.). Pollen class is 1-sulcate. Grains are elliptic, and L is 59.2–60.8 μm. Sculpture is reticulate with pluricolumellate or simplicolumellate muri.

***Narthecium* type** (*Aletris foliata, A. luteoviridis, Narthecium, Petrosavia*). Pollen class is 1-sulcate. Grains are elliptic, and L is 27.6–35.9 μm. Sculpture is reticulate with simplicolumellate muri.

***Tofieldia* type** (*Tofieldia*). Pollen class is 2-sulcate or 2-trichotomosulcate. Grains are elliptic or obtuse triangular prismatic, and L is 27.3 μm. Sculpture is granulate, verrucate, or reticulate with simplicolumellate muri.

***Japonolirion* type** (*Japonolirion*). Pollen class is 1-sulcate. Grains are elliptic to spherical, and L is 24.7 μm. Sculpture is gemmate arranged like reticulate columellae.

***Zygadenus* type** (*Veratrum, Zygadenus*). Pollen class is 1-sulcate. Grains are elliptic, and L is 50.1–57.1 μm. Sculpture is reticulate with duplicolumellate or simplicolumellate muri.

***Chionographis* type** (*Chionographis*). Pollen class is 4-porate. Grains are spherical to tetrahedral spherical, and L is 20.2 μm. Sculpture is reticulate with simplicolumellate muri.

***Heloniopsis* type** (*Heloniopsis*). Pollen class is 1-sulcate. Grains are spherical to elliptic, and L is 41.3 μm. Sculpture is echinate.

***Paris tetraphylla* type** (*Kinugasa, Paris tetraphylla*). Pollen class is 1-sulcate. Grains are elliptic, and L is 57.5–78.9 μm. Sculpture is gemmate.

***Trillium* type** (*Heterosmilax, Trillium*). Pollen class is omniaperturate. Grains are spherical, and L is 30.0–54.4 μm. Sculpture is granulate or verrucate.

***Smilax* type** (*Smilax*). Pollen class is inapertulate. Grains are spherical, and L is 31.4 μm. Sculpture is echinate.

We present here an artificial key to these pollen types.

1. Pollen class 1-sulcate 2
1. Pollen class 2-sulcate, 1-trichotomosulcate, 2-trichotomosulcate, 4-porate, omniaperturate, inaperturate 16
2. Grains very large, L > 130 μm 3
2. Grains small to large, L < 130 μm 4
3. Sculpture reticulate with simplicolumellate muri ***Lilium* type**
3. Sculpture gemmate, verrucate or clavate ***Hosta* type**
4. Grains larger, L > 73 μm 5
4. Grains small, L < 73 μm 8
5. Sculpture gemmate on the whole grain surface 6
5. Sculpture reticulate or perforate, sometimes partly gemmate 7
6. Exine tectate ***Clintonia* type**
6. Exine intectate ***Paris tetraphylla* type** (*Kinugasa*)
7. Sculpture reticulate with pluricolumellate muri ***Hemerocallis* type**
7. Sculpture perforate, gemmate, or reticulate with duplicolumellate or simplicolumellate muri ***Lloydia* type**
8. Sculpture gemmate or echinate 9
8. Sculpture reticulate or perforate 11
9. Sculpture echinate ***Heloniopsis* type**
9. Sculpture gemmate 10
10. Grains larger, L > 40 μm ***Paris tetraphylla* type** (*Paris tetraphylla*)
10. Grains smaller, L < 30 μm ***Japonolirion* type**
11. Sculpture reticulate 12
11. Sculpture perforte 15
12. Sculpture reticulate with pluricolmellate muri ***Disporopsis arisanensis* type**
12. Sculpture reticulate with simplecolmellate or duplicolumellate muri 13
14. Grains relatively large, L > 40 μm ***Zigadenus* type**
14. Grains small, L < 40 μm ***Narthecium* type**
15. Shape of grain ellipsoidal ***Polygonatum* type**
15. Shape of grain orange segmental ***Allium* type**
16. Pollen class 2-sulcate, 1-trichotomosulcate, 2-trichotomosulcate, or 4-porate 17
16. Pollen class omniaperturate or inaperturate 20
17. Pollen class 4-porate ***Chionographis* type**
17. Pollen class 2-sulcate, 1-trichotomosulcate, or 2-trichotomosulcate 18
18. Pollen class 1-trichotomosulcate ***Dianella* type**
18. Pollen class 2-sulcate or 2-trichotomosulcate 19
19. Sculpture perforte ***Uvularia* type**
19. Sculpture reticulate, granulate, or verrucate ***Tofieldia* type**
20. Pollen class omniaperturate ***Trillium* type**
20. Pollen class inaperturate 21
21. Sculpture perforate ***Aspidistra* type**
21. Sculpture echinate ***Smilax* type**

(Note: L in this key is the mean value for each genus.)

Systematic reevaluation from pollen morphology

Nartheciaceae have small pollen grains with L ranging from 22.3 μm in *Tofieldia nuda* to 41.5 μm in *Aletris foliata*. Their pollen grains are usually ellipsoidal, but spherical in *Japonolirion* and obtuse triangular prismatic in some individuals of *Tofieldia japonica*; usually 1-sulcate and rarely 2-sulcate (*Tofieldia* spp.) or 2-trichotomosulcate (some individuals of *Tofieldia japonica*); usually reticulate with simplicolumellate muri and rarely perforate (*Aletris spicata*), granulate (some individuals of *Tofieldia okuboi)*, verrucate (some individuals of *Tofieldia okuboi),* or gemmate (*Japonolirion*). They include the *Narthecium* type, the *Tofieldia* type, the *Japonolirion* type, and the *Polygonatum* type (Table 2).

Tamura (1998b) subdivided Nartheciaceae into two subfamilies and three tribes: Tofieldioideae-Petrosavieae, Tofieldioideae-Tofieldieae, Tofieldioideae-Japonolirieae, and Narthecioideae. According to the molecular phylogenies based on DNA sequences of *rbc*L + *atp*B + 18SrDNA (Chase et al., 2000) and *mat*K genes (Fuse & Tamura, 2000), Japonolirieae were merged with Petrosavieae, and the Petrosavieae were raised to Petrosaviaceae. Tofieldieae and Narthecioideae were also raised to Tofieldiaceae and Nartheciaceae, respectively.

In pollen morphology, the two genera of the Petrosaviaceae have different types of pollen grains, *Petrosavia* the *Narthecium* type and *Japonolirion* the *Japonolirion* type. The two pollen types are similar to each other in grain size, ellipsoidal shape, and 1-sulcate aperture, but differ in sculpture. The molecular phylogenies seem to suggest that the *Japonolirion* type has derived from the *Narthecium* type, with the gemmae of the *Japonolirion* type formed from the discontinuation of the simplicolumellate muri of the *Narthecium* type.

Aletris of the Nartheciaceae includes two pollen types, the *Narthecium* type of *A. foliata* and *A. luteoviridis* and the *Polygonatum* type of *A. spicata*. The two pollen types share the common characteristics of grain size, ellipsoidal shape, and 1-sulcate aperture, but differ from each other in sculpture. Probably, in the case of *Aletris*, the *Polygonatum* type has derived from the *Narthecium* type with the puncta of the *Polygonatum* type arising

Table 2 Pollen morphology and types of the Japanese Asparagales and Liliales

Order	Family	Genus/Species	Pollen class	Shape	Sculpture	L (μm)
***Lilium* type**						
Liliales	Liliaceae	*Lilium*	1-sulcate	ellipsoid	reticulate (simplicolumellate)	139.4
***Hosta* type**						
Asparagales	Hostaceae	*Hosta*	1-sulcate	ellipsoid	gemmate, verrucate, clavate	137.0
***Clintonia* type**						
Liliales	Liliaceae	*Clintonia*	1-sulcate	ellipsoid	supratectal gemmate	75.7
***Hemerocallis* type**						
Asparagales	Hemerocallidaceae	*Hemerocallis*	1-sulcate	ellipsoid	reticulate (pluricolumellate)	119.7
***Lloydia* type**						
Liliales	Liliaceae	*Cardiocrinum*	1-sulcate	ellipsoid	reticulate (simplicolumellate)	88.4
Liliales	Liliaceae	*Erythronium*	1-sulcate	ellipsoid	perforate, reticulate (duplicolumellate), gemmate	114.5
Liliales	Liliaceae	*Fritillaria*	1-sulcate	ellipsoid	perforate, reticulate (duplicolumellate, simplicolumellate)	84.2
Liliales	Liliaceae	*Gagea*	1-sulcate	ellipsoid	perforate	107.7
Liliales	Liliaceae	*Lloydia*	1-sulcate	ellipsoid	perforate, reticulate (duplicolumellate, simplicolumellate), gemmate	103.3
Liliales	Liliaceae	*Tulipa*	1-sulcate	ellipsoid	perforate	96.3
Liliales	Calochortaceae	*Tricyrtis*	1-sulcate	ellipsoid	perforate	84.7
Liliales	Calochortaceae	*Streptopus*	1-sulcate	ellipsoid	perforate, reticulate (simplicolumellate), gemmate	74.1
***Uvularia* type**						
Liliales	Colchicaceae	*Uvularia*	2-sulcate	ellipsoid	perforate	53.0
***Dianella* type**						
Asparagales	Hemerocallidaceae	*Dianella*	trichotomosulcate	obtuse	perforate tetrahedron	36.7
***Polygonatum* type**						
(not ranked)	Nartheciaceae	*Aletris spicata*	1-sulcate	ellipsoid	perforate	35.7
Liliales	Colchicaceae	*Disporum*	1-sulcate	ellipsoid	perforate	55.9
Liliales	Trilliaceae	*Paris verticillata*	1-sulcate	ellipsoid	perforate	54.1
Asparagales	Asparagaceae	*Asparagus*	1-sulcate	ellipsoid	perforate	38.3
Asparagales	Anthericaceae	*Chlorophytum*	1-sulcate	ellipsoid	perforate	54.1
Asparagales	Anthericaceae	*Comospermum*	1-sulcate	ellipsoid	perforate	55.4
Asparagales	Hyacinthaceae	*Scilla*	1-sulcate	ellipsoid	perforate	72.2
Asparagales	Convallariaceae	*Polygonatum* spp.	1-sulcate	ellipsoid	perforate	64.9
Asparagales	Convallariaceae	*Heteropolygonatum*	1-sulcate	ellipsoid	perforate	52.0
Asparagales	Convallariaceae	*Disporopsis longifolia*	1-sulcate	ellipsoid	perforate	56.9
Asparagales	Convallariaceae	*Maianthemum*	1-sulcate	ellipsoid	perforate	41.0
Asparagales	Convallariaceae	*Smilacina*	1-sulcate	ellipsoid	perforate	46.3
Asparagales	Convallariaceae	*Liriope*	1-sulcate	ellipsoid	perforate	51.6
Asparagales	Convallariaceae	*Ophiopogon*	1-sulcate	ellipsoid	perforate	41.9
Asparagales	Convallariaceae	*Peliosanthes*	1-sulcate	ellipsoid	perforate	34.1
Asparagales	Convallariaceae	*Convallaria*	1-sulcate	ellipsoid	perforate	44.0
Asparagales	Convallariaceae	*Reineckia*	1-sulcate	ellipsoid	perforate	58.3
Asparagales	Convallariaceae	*Rohdea*	1-sulcate	ellipsoid	perforate	57.0
***Allium* type**						
Asparagales	Alliaceae	*Allium*	1-sulcate	orange segmental	perforate	42.7
Asparagales	Alliaceae	*Nothoscordum*	1-sulcate	orange segmental	perforate	51.6
***Aspidistra* type**						
Asparagales	Convallariaceae	*Tupistra*	inaperturate	sphere to ellipsoid	perforate	52.0
Asparagales	Convallariaceae	*Aspidistra*	inaperturate	sphere	perforate	47.0
***Disporopsis arisanensis* type**						
Asparagales	Convallariaceae	*Polygonatum oppositifolium*, *P.* sp. nov.	1-sulcate	ellipsoid	reticulate (pluricolumellate)	60.8

Asparagales	Convallariaceae	*Disporopsis arisanensis, D. undulata*	1-sulcate	ellipsoid	reticulate (pluricolumellate)	59.2
***Narthecium* type**						
(not ranked)	Nartheciaceae	*Petrosavia*	1-sulcate	ellipsoid	reticulate (simplicolumellate)	27.6
(not ranked)	Nartheciaceae	*Narthecium*	1-sulcate	ellipsoid	reticulate (simplicolumellate)	28.9
(not ranked)	Nartheciaceae	*Aletris foliata*, *A. luteoviridis*	1-sulcate	ellipsoid	reticulate (simplicolumellate)	35.9
***Tofieldia* type**						
(not ranked)	Nartheciaceae	*Tofieldia*	2-sulcate, 2-trichotomosulcate	ellipsoid, obtuse triangular prism	reticulate (simplicolumellate), granulate, verrucate	27.3
***Japonolirion* type**						
(not ranked)	Nartheciaceae	*Japonolirion*	1-sulcate	ellipsoid to sphere	gemmate	24.7
***Zigadenus* type**						
Liliales	Melanthiaceae	*Veratrum*	1-sulcate	ellipsoid	reticulate (duplicolumellate, simplicolumellate)	50.1
Liliales	Melanthiaceae	*Zigadenus*	1-sulcate	ellipsoid	reticulate (duplicolumellate, simplicolumellate)	57.1
***Chionographis* type**						
Liliales	Melanthiaceae	*Chionographis*	4-porate	sphere to tetrahedral sphere	reticulate (simplicolumellate)	20.2
***Heloniopsis* type**						
Liliales	Melanthiaceae	*Heloniopsis*	1-sulcate	sphere to ellipsoid	echinate	41.3
***Paris tetraphylla* type**						
Liliales	Trilliaceae	*Paris tetraphylla*	1-sulcate	ellipsoid	gemmate	57.5
Liliales	Trilliaceae	*Kinugasa*	1-sulcate	ellipsoid	gemmate	78.9
***Trillium* type**						
Liliales	Trilliaceae	*Trillium*	omniaperturate	sphere	granulate, verrucate	54.4
Liliales	Smilacaceae	*Heterosmilax*	omniaperturate	sphere	granulate	30.0
***Smilax* type**						
Liliales	Smilacaceae	*Smilax*	inaperturate	sphere	echinate	31.4

L: length of the longest axis.

from size reduction of the lumina of the *Narthecium* type.

Liliales show a wide variation of pollen morphological characters: L from 19.2 μm in *Chionographis japonica* to 196.0 μm in *Lilium longiflorum*; shape often ellipsoidal and sometimes spherical (Smilacaceae, *Chionographis, Heloniopsis, Trillium*); pollen type 1-sulcate, 2-sulcate (*Uvularia*), 4-porate (*Chionographis*), omniaperturate (*Trillium, Heterosmilax*), or inaperturate (*Smilax*); and sculpture reticulate, perforate (Colchicaceae, *Paris verticillata*, *Gagea, Lloydia serotina, Tulipa, Erythronium, Fritillaria japonica, Tricyrtis, Streptopus* spp.), gemmate (*Clintonia, Paris tetraphylla, Kinugasa, Lloydia serotina, Streptopus amplexifolius* var. *papillatus*), echinate (*Smilax, Heloniopsis*), verrucate (*Trillium grandiflorum*), or granulate (*Trillium* spp., *Heterosmilax*). Pollen grains of the Liliales include the *Lilium* type, the *Lloydia* type, the *Clintonia* type, the *Polygonatum* type, the *Uvularia* type, *Zygadenus* type, the *Chionographis* type, the *Heloniopsis* type, the *Paris tetraphylla* type, the *Trillium* type, and the *Smilax* type (Table 2).

The molecular phylogeny of Fuse & Tamura (2000) recognized three clades in Liliales: (1) Colchicaceae; (2) Liliaceae, Calochortaceae, and Smilacaceae; and (3) Melanthiaceae and Trilliaceae. In clade (2), Smilacaceae first diverged from the remaining two families. In clade (3), Melanthiaceae-Melanthieae first diverged, and Melanthiaceae-Heloniadeae were grouped with Trilliaceae. In pollen morphology, Colchicaceae of clade (1) share small perforate pollen grains. In clade (2), Smilacaceae have small and spherical pollen grains classified in the *Heterosmilax* or *Smilax* types, while Liliaceae and Calochortaceae share large ellipsoidal pollen grains. In clade (3), Melanthiaceae-Melanthieae have 1-sulcate ellipsoidal pollen grains (the *Zygadenus* type), while Melanthi-

aceae-Heloniadeae and Trilliaceae have spherical pollen grains with various apertures (the *Chionographis* type, the *Heloniopsis* type, or the *Trillium* type) except for *Paris* and *Kinugasa* which have 1-sulcate ellipsoidal pollen grains (the *Polygonatum* type or the *Paris tetraphylla* type). Thus, a relationship between Heloniadeae and Trilliaceae postulated by the molecular phylogeny has been more or less confirmed by the pollen morphological characters. Tamura (1998a) recognized Medeoloideae and Lilioideae in the Liliaceae. In pollen morphology, Medeoloideae have the *Clintonia* type, and Lilioideae do the *Lloydia* type except for *Lilium,* which was further specialized into the *Lilium* type.

Asparagales have the following pollen morphological characters: L from 31.8 μm in *Asparagus officinalis* to 170.0 μm in *Hosta capitata*); shape ellipsoidal, tetrahedral (*Dianella*), spherical (*Tupistra*, *Aspidistra*), or orange segmental (Alliaceae); pollen type 1-sulcate, 1-trichotomosulcate (*Dianella*), or inaperturate (*Tupistra*, *Aspidistra*); and sculpture perforate, reticulate (*Hemerocallis, Polygonatum oppositifolium, P.* sp. nov., *Disporopsis arisanensis,* and *D. undulata*), verrucate (*Hosta*), clavate (*Hosta*), or gemmate (*Hosta*). Pollen grains of the Asparagales include the *Hemerocallis* type, the *Hosta* type, the *Polygonatum* type, the *Allium* type, the *Dianella* type, and the *Disporopsis arisanensis* type (Table 2).

Hostaceae and *Hemerocallis* (Hemerocallidaceae) have large, ellipsoidal, 1-sulcate pollen grains with various sculptures of the *Hemerocallis* type and the *Hosta* type, while *Dianella* (Hemerocallidaceae) has small, tetrahedral, 1-trichotomosulcate pollen of the *Dianella* type. Hyacinthaceae, Anthericaceae, and Asparagaceae share the *Polygonatum* type. Convallariaceae include the *Polygonatum* type and the *Disporopsis arisanensis* type, and the *Disporopsis arisanensis* type occurrs only in Polygonateae sensu Conran & Tamura (1998). *Polygonatum* sect. *Polygonatum* always had the *Polygonatum* type, while sect. *Verticillata* sensu Tamura (1993) often has the *Disporopsis arisanensis* type. LaFrankie (1986) merged *Smilacina* with *Maianthemum*. In pollen morphology, however, the puncta of *Maianthemum* sensu stricto are smaller than those of *Smilacina*.

If we deduce the ancestral pollen type of the Liliaceae s.l. in a parsimonious manner based on the molecular phylogenies of Chase et al. (2000) and Fuse & Tamura (2000), the ancestral pollen type seems to be the *Narthecium* type or the *Polygonatum* type, which is small to medium, ellipsoidal, 1-sulcate, and perforate to fine reticulate with simplicolumellate muri.

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ジャレド・ダイアモンド（骨倉　彰訳）．2000．銃・病原菌・鉄（上・下)—1万3000年にわたる人類史の謎．上巻317 pp. ISBN4-7942-1005-1．下巻332 pp. ISBN 4-7942-1006-x．各巻本体価格1900円．草思社，東京.

本書は，翻訳書の副題にあるように，過去1万3000年間における人類の歴史を地球規模で，人類をとりまく自然環境に即して捉えなおそうとするものである。翻訳書はすでに，昨年末の朝日新聞誌上で，書評子2氏によって2000年の3冊のうちの一つとして取りあげられていたので，お読みになった方も多いであろう。

本書の中心の課題は，人類の歴史がそれぞれの大陸でなぜ個別に展開していったのかというものである。著者は，言語学と医学の素養のある進化生態学者として，様々な分野における最新の情報を駆使して，人類のおかれた自然環境に即して，地球規模のスケールで壮大な仮説を組み立てて，この課題に答えていく。身近な例としては，先に報告した縄文時代前期における沖縄と台湾あるいは中国の交流なども，国内ではあまり議論されておらず，評者も引用しそこなったが，本書で展開されているオーストロネシア人の拡散として捉えれば当然のことである。また狩猟採集から定着農耕への選択にいたる背景と条件なども，筆者のフィールドであるパプア・ニューギニアなどを例にとって考察し，定着農耕のほうが単にすぐれているという一般的な見解とは大きく異なった仮説を提示している。

翻訳書では例によって，原書で30頁ほどにおよぶ関連文献（Further Readings）が削除されている。本書の記述は一般書に即しているため，本文中には一切，引用はない。そのため関連文献に紹介されている文献が著者の思考の源であり，著者もそのように断っているのに，またまた日本語版の読者はその恩恵に預かれないのである。関連文献ではその最初に，The History and Geography of Human Genes (L. Luca Cavali-Sforza, P. Menozzi & A. Pizza. 1994. Princeton Univ. Press, Princeton, U.S.A.)という，本書の成立に密接にかかわる未翻訳の文献が紹介され，それに続いて，Arnold Toynbee の A Study of History をはじめとして，つぎつぎと包括的な文献が紹介されていく。翻訳書を手にした読者からの抗議を受けたのか，出版社は現在，ウェッブ上（http://www.soshisha.com/）で関連文献の邦訳を公開している。また関連文献が翻訳されていないことに憤った人々が，ウェッブ上（http://cruel.org /diamond/）で独自の邦訳を公開している。いずれにしても，こうした出版物は，フォンもフュメも欠いた料理をフランス料理と称して供しているようなものではないだろうか。

（能城修一）