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A COMPARATIVE STUDY OF SPORE MORPHOLOGY OF THE SUBFAMILY CRYPTOGRAMMOIDEAE GENERA

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Using the method of scanning electronic microscopy (SEM), a comparative study of twelve representatives of subfamily *Cryptogrammoideae* S.Linds. family *Pteridaceae* E.D.M.Kirchn. was carried out. A comparative study of morphological characters of investigated spores has revealed characters that allow considering the relatedness of the studied species to one subfamily – Cryptogrammoideae. These characters include: spore form is roundish-triangular, lociniate in proximal-polar and distal-polar positions; spore contour is low-crenate to smooth; distal side of the spore in an equatorial position is convex; rays of laesura are straight, raised over a sporoderm surface; exosporium is clearly defined from fine-granulate to verrucate.
Key words: *subfamily Cryptogrammoideae, family Pteridaceae, Cryptogramma, Llavea, Coniogramme, morphology of the spores, scanning electronic microscopy (SEM).*

СРАВНИТЕЛЬНОЕ ИССЛЕДОВАНИЕ МОРФОЛОГИИ СПОР РОДОВ ПОДСЕМЕЙСТВА CRYPTOGRAMMOIDEAE

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С помощью метода сканирующей электронной микроскопии (СЭМ) проведено сравнительное исследование двенадцати представителей подсемейства *Cryptogrammoideae* S. Linds. семейства Pteridaceae E.D.M. Kirchn. Исследование морфологической структуры спор позволило установить признаки, которые позволяют доказать близкое родство изученных видов к одному подсемейству – *Cryptogrammoideae*. К таковым признакам относятся: очертание спор в проксимально-полярном и дистально-полярном положениях округло-треугольное, лопастное; контур споры низко-городчатый до гладкого; в экваториальном положении дистальная сторона споры выпуклая; лучи лезуры прямые, приподнимающиеся над поверхностью спородермы; экзоспорий чётко выраженный, от мелкозернистого до бугорчатого.
Ключевые слова: *подсемейство Cryptogrammoideae, семейство Pteridaceae, Cryptogramma, Llavea, Coniogramme, морфология спор, сканирующая электронная микроскопия (СЭМ).*

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INTRODUCTION

The first ideas about closely related taxa of the genus *Cryptogramma* R. Br. ex Richards were presented by Prantl (1882). From the *Pellaea* Link group of kinship he separated the genus *Cryptogramma* with subgenera: *Cryptogramma*, *Onychium* Kaulf, *Llavea* Lag, *Anopteris* (Prantl) Diels and *Ochropteris* J. Sm.

A distinct taxonomic group – subtrib. *Cryptogrammaceae* (cryptogrammoid ferns) as part of Polypodiaceae J.Presl a. C.Presl family – was separated in 1927 (Horvat, 1927). Later Christensen (1938) raised the subtribe rank to a tribe.

By the middle of the XX century the leading pteridologists, including Pichi-Sermolli, but except Horvat and Copeland, in his works on the taxonomy of the genera *Cryptogramma*, *Onychium* and *Llavea* took them as the key genera among cryptogrammoid ferns.

In 1963, Pichi-Sermolli (1963) in his monograph combined three genera of uncertain systematic position in the separate family Cryptogrammaceae Pic. Serm. of order Pteridales. Based on the similarity of external characters of the sporophyte the family included *Cryptogramma*, *Llavea* and *Onychium*. But the current stage of the study of fern systematics has allowed reviewing the taxonomic composition of the group. The application of molecular genetic methods in relation to the cryptogrammoid ferns group has shown the strongest relationship *Onychium* with *Actiniopteris*, and *Cryptogramma* and *Llavea* with *Coniogramme* (Zhang et al., 2005; Liu et al., 2008; Schuettpelz et al., 2007, 2008; Christenhusz et al., 2011; Metzgar et al., 2013; Kuznetzov et al., 2014).

In the work about the ferns of Thailand Lindsay and Middleton (2009) specified a new combination - subfamily *Cryptogrammoideae* as a part of the family Pteridaceae, transferred the family Cryptogrammaceae in its synonyms, and chose *Cryptogramma* as type genus. Currently, in articles on the molecular phylogeny of ferns the genera *Cryptogramma*, *Llavea* and *Coniogramme* are combined into a clade «Cryptogrammoid».

The purpose of the study is to find diagnostic characters of spore morphology of *Cryptogramma*, *Llavea* and *Coniogramme* to confirm the level of their relationship and evaluate whether they belong to the subfamily *Cryptogrammoideae*.

MATERIAL AND METHODS

Spores for the study were selected from herbarium materials stored in the herbarium of the V.L. Komarov Botanical Institute of the RAS (LE), the South-Siberian Botanical Garden, Altai State University (ALTB) and the Institute of Biology and Soil Science FEB RAS (VLA).

Spores were investigated using scanning electron microscope "Philips SEM 525-M", and electron-ion scanning microscope "Quanta 200 3D" situated in Tomsk Material Testing Center for collective use of the National Research Tomsk State University and JEOL JSM-6390LA Analytical Scanning Electron Microscope of Center for collective use of the V.L. Komarov Botanical Institute of the Russian Academy of Sciences (Saint-Petersburg). Spores were fixed using a carbon adhesive tape; to reduce the influence of the charge a method of thermal spraying by chromium, carbon or gold-palladium mixture in a vacuum sputtering plant. Spore surface was scanned in high vacuum at an accelerating voltage of 2 kV and a magnification of 1000 to 7000 times, and 10,000 to 16,000 times. The measurements of spores were carried out using "SIAMS MesoPlant" and "Photometer" programs.

An analysis was performed on the following spore morphological characters: 1 – equatorial diameter, μm; 2 – polar axis; 3 – laesura length; 4 – laesura width; 5 – diameter of tubercles on the proximal side of the spore; 6 – diameter of tubercles on the distal side of the spore; 7 – excrescences diameter on the surface of exospores. Measurements were carried out in 25 replications.

RESULTS

Cryptogramma acrostichoides R.Br. 1823, in Richards., Bot. App. 7 to Franklin, Narr. Journ.: 754, 767.

SEM-description (fig. 1). Spores in a polar position are roundish-triangular, some of them with slightly concave sides (slightly lociniate), along the contour high-crenate. The equatorial diameter is (50.7)55.9–58.6(62.5) μm. The distal side in an equatorial position is convex, the proximal side slightly concave, raised only at the parts with thickened sporoderm near the ends of rays. The rays of laesura are straight, (22.4)24.2–24.3(26) μm long, (1.4)1.7–2.4(3.1) μm broad. The exosporium is verrucate; verrucate elements in outline are roundish or roundish-multiangular, small, (1.7)3.1–4.8(7.1) μm in diam. in poles (proximal and distal), considerably increasing in the equatorial part and at the corners up to (4.7)6.3–6.9(8.9) μm in diam. The surface of the exosporium has roundish excrescences on the verrucate elements. The surface of the exosporium is fine-granulate.

Investigated specimen: «U.S.A., Big Anchorage, the right bank of river Orlinaya, the mountains Chugach, Chugachsky State park, the Valley of Snow Sheep, alpine zone. 29 VII 1990. S. Kharkevich» (VLA).

Cryptogramma brunoniana Wall. ex Hook. et Grev. 1829, Icon. Fil. t. 158.

SEM-description (fig.2). Spores in a polar position are roundish triangular, with concave sides (lociniate), and high-crenate along the contour. The equatorial diameter is (47.8)48.9–50.4(52.3) μm. The distal side in an equatorial position is convex, the proximal one flat. The rays of laesura are straight (21.6)23.5–23.8(25.8) μm long, (1.6)2.0–2.9(3.8) μm broad, elevated above the surface of the sporoderm, distinctive or submerging into the sporoderm, forming a roller-like thickening 2.2–3.9 μm broad. The exosporium is verrucate. The verrucate elements are roundish-multiangular or faintly twisting, small, (2.2)3.7–3.9(5.5) μm in diam. in poles (proximal and

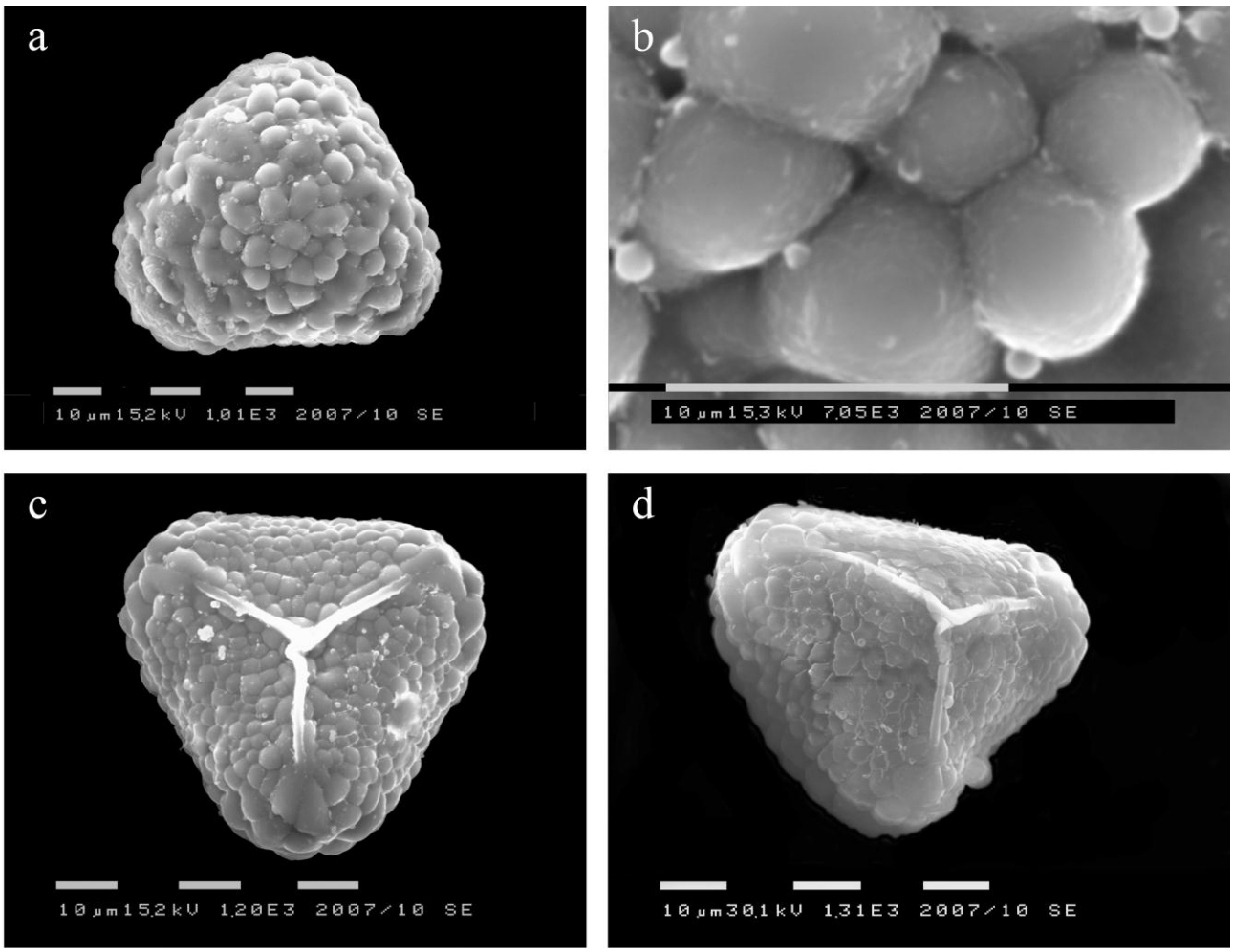

Fig. 1. SEM views of spores of *Cryptogramma acrostichoides*:
a – distal side; b– fragment of distal surface; c – proximal side; d – spore in equatorial-proximal position.

distal), and larger, up to (4.5)5.4–5.6(6.5) μm in diam. at the corners and equatorial part. The surface of exosporium is coarse-granulate.

Investigated specimen: «Sikkim, 1857, alt. 12–13000, J.J.» (LE).

Cryptogramma cascadensis E.R. Alverson, 1989, Amer. Fern Journ., 79: 95.

SEM-description (fig. 3). Spores in a polar position are roundish-triangular, with faintly concave sides (slightly lociniate), and low-crenate along the contour. The equatorial diameter is (40.4)42.8–43.9(45.8) μm. The distal side in an equatorial position is convex, the proximal one flat. The rays of the laesura are straight (17.2)18.2–18.5(19.7) μm long, (0.7)1.0–1.1(1.6) μm broad. The exosporium is verrucate. The verrucate elements in outline are roundish or roundish-multiangular, sometimes more or less fused. They are small (1.7)3.9–4.2(6.7) μm in diam. in poles (proximal and distal) and increasing up to (4)5.9–6.0(8.1) μm diam. at the corners and equatorial part.

Investigated specimen: «Plants of California, Nevada Country, №7027, Near Summit Station (Donner Pass). July 27 1903. A.A. Heller» (LE).

Cryptogramma crispa (L.) R.Br. 1823, in Rhichards. in Frankl., Narr. Journ.: 767 p. – *Osmunda crispa* L., 1753, Sp. Pl.: 1067.

SEM-description (fig. 4). Spores in a polar position are roundish-triangular, usually with concave sides (slightly lociniate), and low-crenate along the contour. The equatorial diameter is (47.0)47.4–48.2(49.0) μm. The distal side in an equatorial position is convex, the proximal slightly concave, only the rays along the laesura are elevated, especially at the parts of thickened sporoderm near the ray ends. The rays of laesura are straight and faintly twisting (20.0)21.1–21.2(22.3) μm long, (1.4)1.6–1.7(2.0) μm broad. The exosporium is verrucate. The verrucate elements in outline are roundish or roundish-multiangular, sometimes more or less fused; small

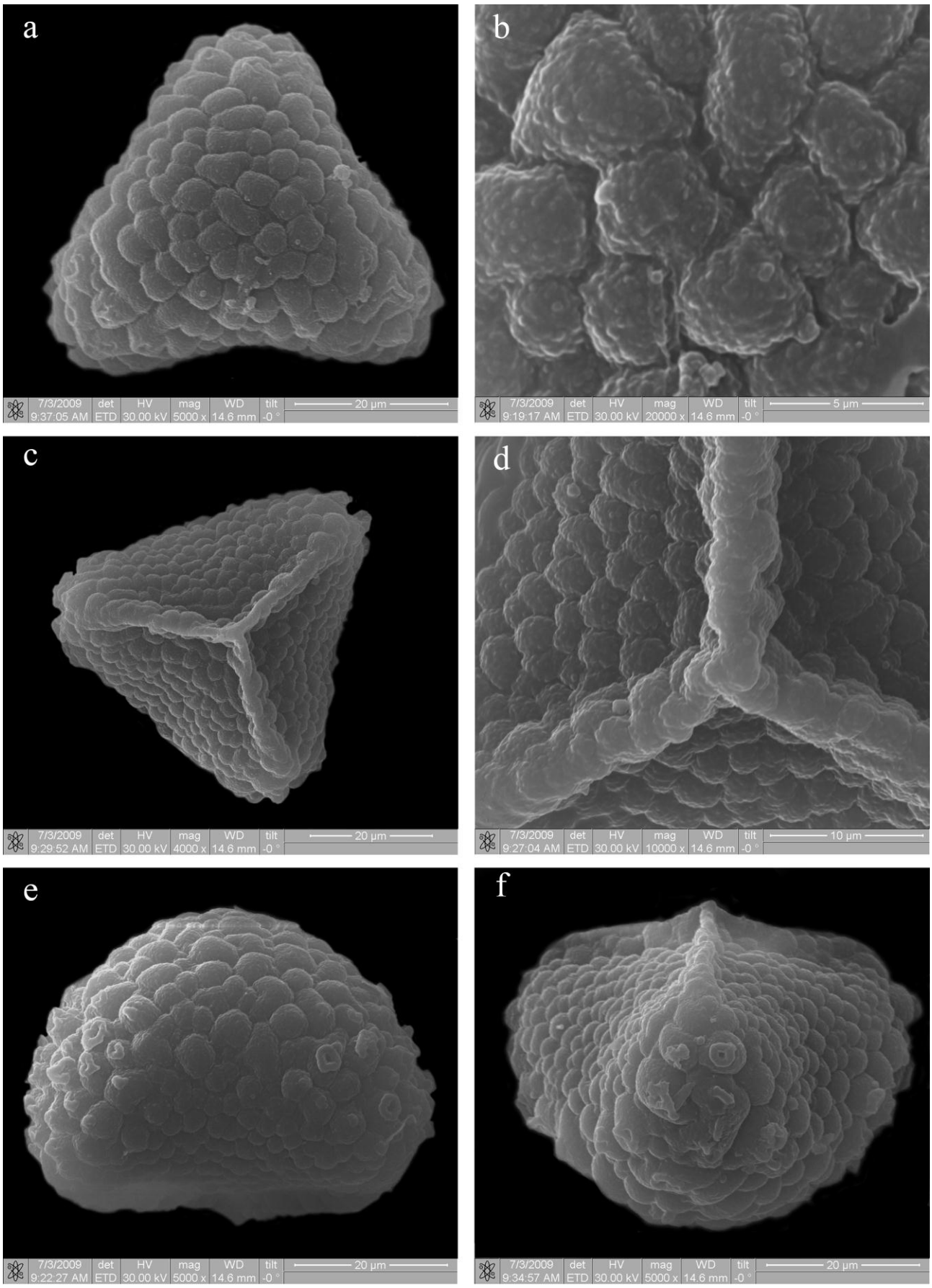

Fig. 2. SEM views of spores of *Cryptogramma brunoniana*:
a – distal side; b – fragment of distal surface; c – proximal side; d – fragment of proximal side of spore and laesura; e – spore in equatorial position; f – spore in equatorial position.

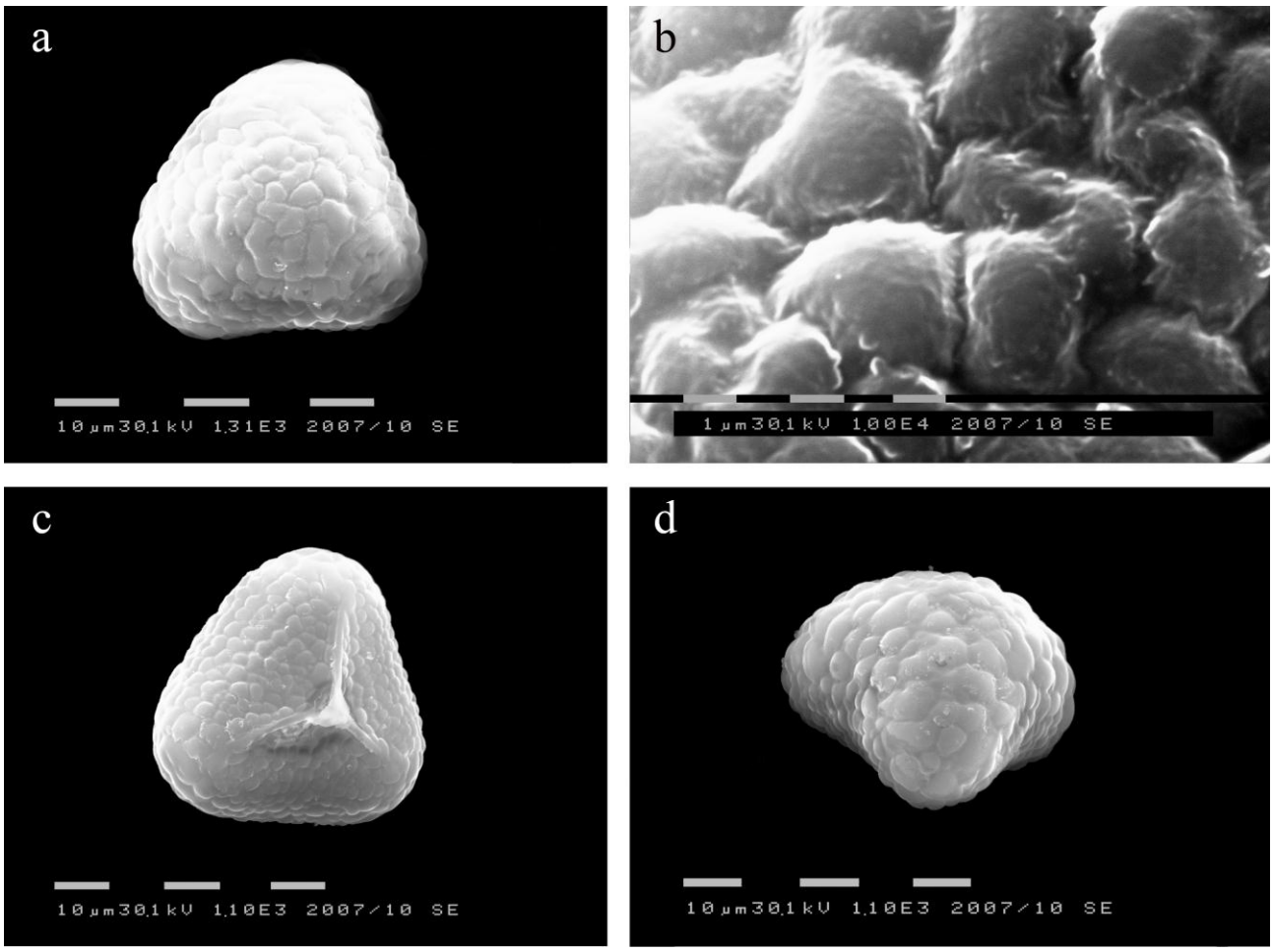

Fig. 3. SEM views of spores of *Cryptogramma cascadensis*:
a – distal side; b – fragment of distal surface; c – spore in equatorial-proximal position; d – spore in equatorial-distal position.

(1.6)2.3–2.4(3.2) μm in diam. in poles (proximal and distal) and increasing up to (2.3)2.9–3.6(4.7) μm in diam. at the corners and equatorial part The surface of the exosporium is fine-granulate.

Investigated specimen: «Murmansk district, Kirovsk. Polar-alpine botanical garden. VIII 1937. M. Kachurin» (LE).

Cryptogramma gorovoii A. Vaganov et Shmakov, 2007, Turczaninowia 1: 5.

SEM-description (fig. 5). Spores in a polar position are roundish-triangular, with faintly concave sides (slightly lociniate) or roundish, the contour high-crenate. The equatorial diameter is (48.3)52.9–54.9(58.6) μm. The distal side in an equatorial position is convex, the proximal one is flat or slightly concave with a conical top. The rays of laesura are straight, (22.4)25.8–27.6(32.0) μm long, (2.5)2.9–2.9(3.4) μm broad. The exosporium is verrucate. The verrucate elements are large, roundish or roundish-multiangular in outline, (3.8)4.9–5.6(6.4) μm in diam., equal, up to (5.8)6.2–6.4(6.9) μm in diam. at the corners and along the equator where they are fused. The surface of the exosporium is fine-granulate with the sparse roundish excrescences (0.5)0.7–0.8(1.1) μm in diam.

Investigated specimen: «Sakhalin district, the mountains Lamonon at the western sea coast, rocky places of the mountain Igara, 11903/1966. 13 VIII 1966. Pavlova, Pankov» (Holotypus, ALTB).

Cryptogramma raddeana Fomin, 1929, Vestnik Kievskogo Botanicheskogo Sada, 10: 36.

SEM-description (fig. 6). Spores in a polar position are roundish-triangular, usually with concave sides (lociniate), and high-crenate along the contour. The equatorial diameter is (40.9)42.1–43.4(45.3) μm. The distal side is convex in equatorial position, the proximal one concave, with only the rays of the laesura elevated, especially at the parts of thickened sporoderm near the ends of the rays. The rays of the laesura are straight, (15.8)17.8–17.9(19.9) μm long, (1.3)1.5–1.6(1.8) μm broad. The exosporium is verrucate. The verrucate elements in outline are roundish or roundish-multiangular, sometimes more or less fused, (3.0)4.0–4.7(6.1) μm in diam. in

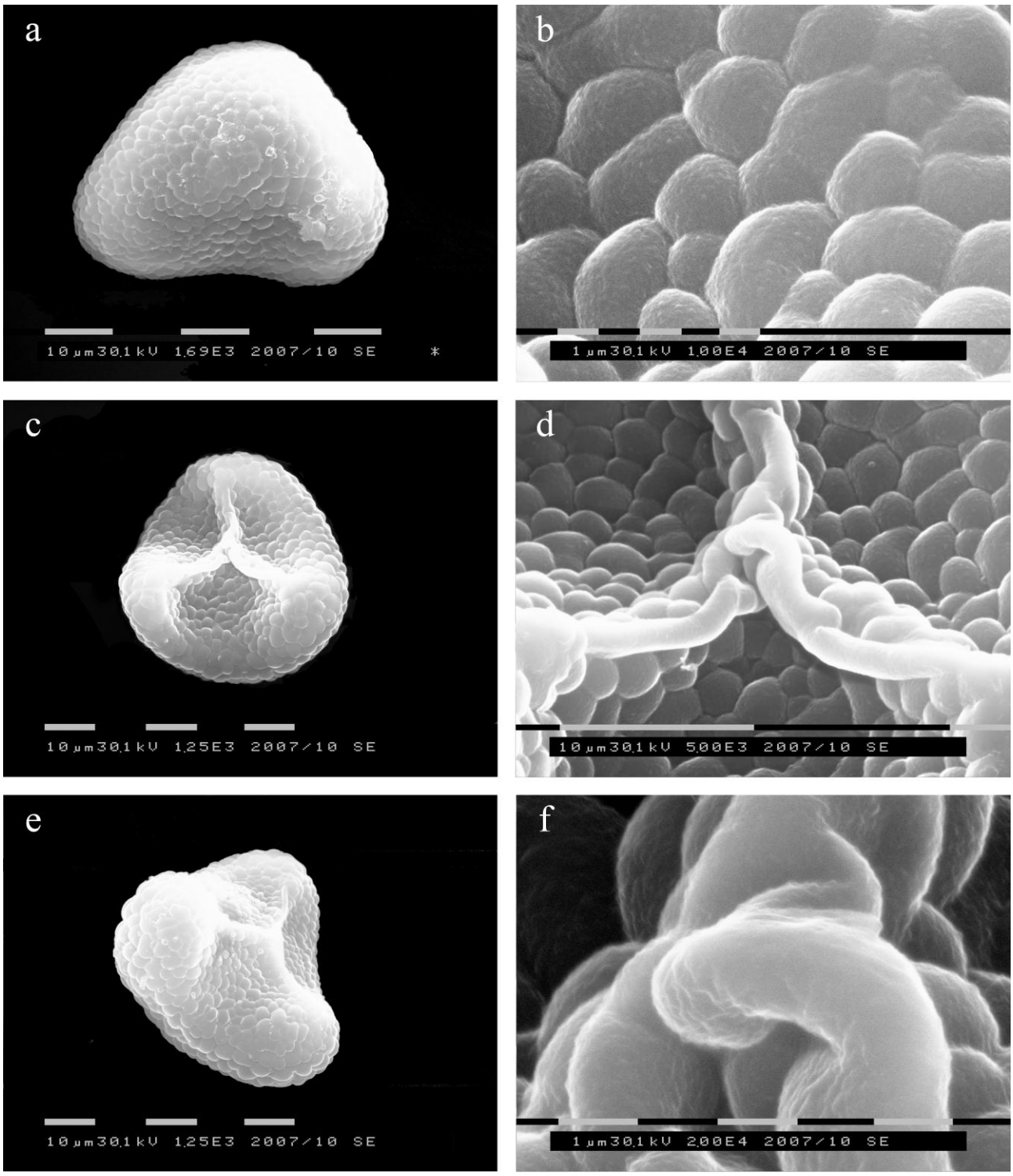

Fig. 4. SEM views of spores of *Cryptogramma crispa*:
a – distal side; b – fragment of distal surface; c – proximal side; d – fragment of proximal surface of spore and laesura; e – equatorial-proximal position; f – fragment of laesura.

poles (proximal and distal), and quite large, (5.2)5.9–6.4(7.3) µm in diam. at the corners and equatorial part. The surface of exosporium is coarse-granulate.

Investigated specimen: «Buryat Autonomous Republic, the lake Baikal. Baikalsky ridge. Head of the river Malaya Kosa. 1–3 of August 1967. T.V. Yegorova, V.N. Siplivinsky» (ALTB).

Cryptogramma sitchensis (Rupr.) T. Moore, 1857, Ind. Fil.: 67. – *Allosorus sitchensis* Rupr., 1845, Distr. Crypt. Vasc. Ross., 3: 47.

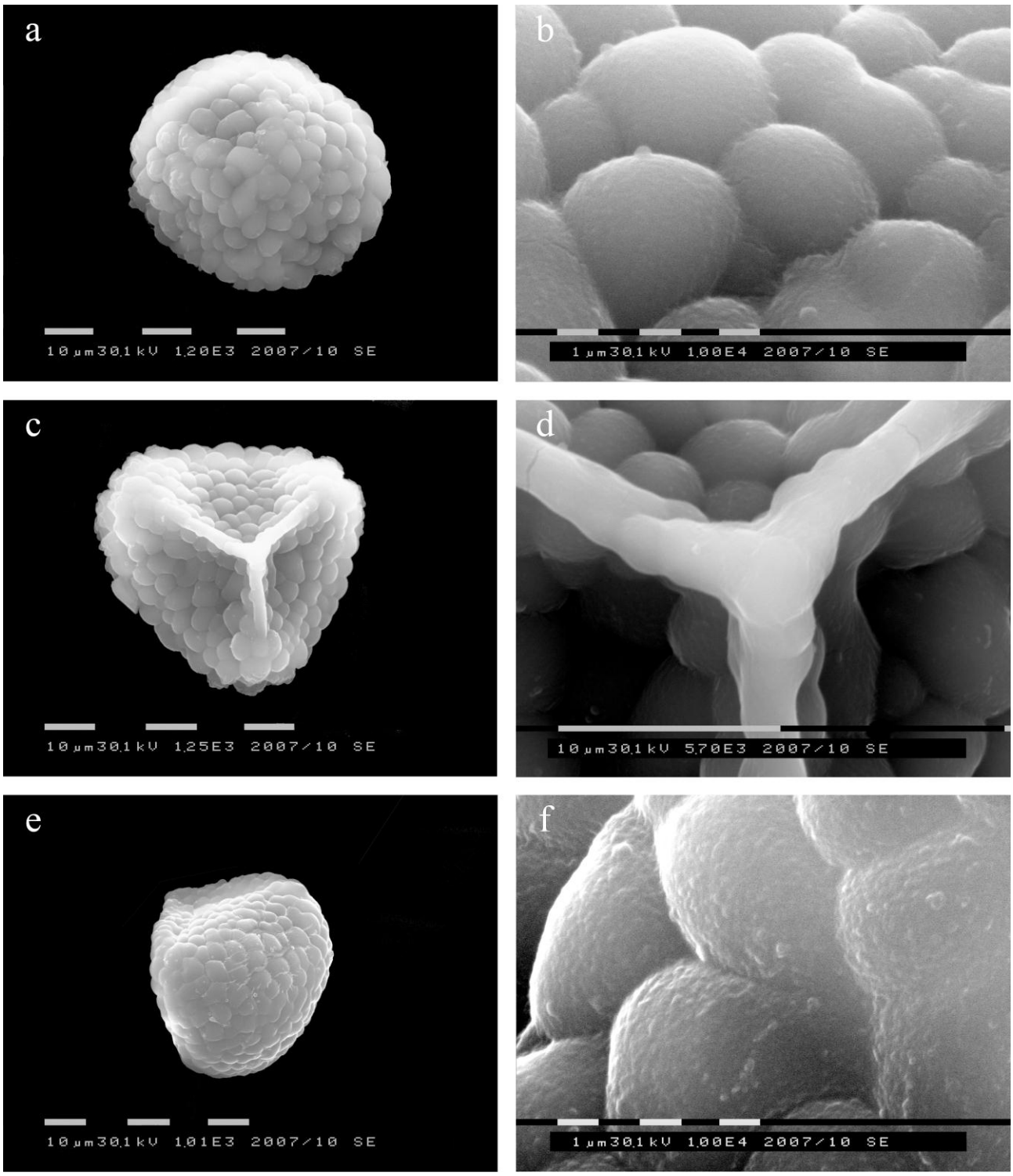

Fig. 5. SEM views of spores of *Cryptogramma gorovoii*:
a – distal side; b, f – fragment of distal surface; c – proximal side; d – fragment of spore proximal surface and laesura; e – spore in equatorial-distal position.

SEM-description (fig. 7). Spores in a polar position are roundish-triangular, with straight or slightly concave sides (slightly lociniate), and middle-crenate along the contour. The equatorial diameter is (49.8)52.1–53.0(55.9) µm. The distal side in equatorial position is convex, the proximal one is concave, raised only at the parts with thickened sporoderm near the ends of the rays. The rays of laesura are straight (22)23.4–24.2(26) µm long, (1.5)1.8–2.0(2.5) µm broad. The exosporium is verrucate. The verrucate elements in outline are roundish or roundish-multiangular, small, (2.1)2.5–2.7(3.1) µm in diam. in poles (proximal and distal), and increasing up to (4.4)5.3–6.4(8.0) µm in diam.) at the corners and equator. The surface of the exosporium is fine-granulate.

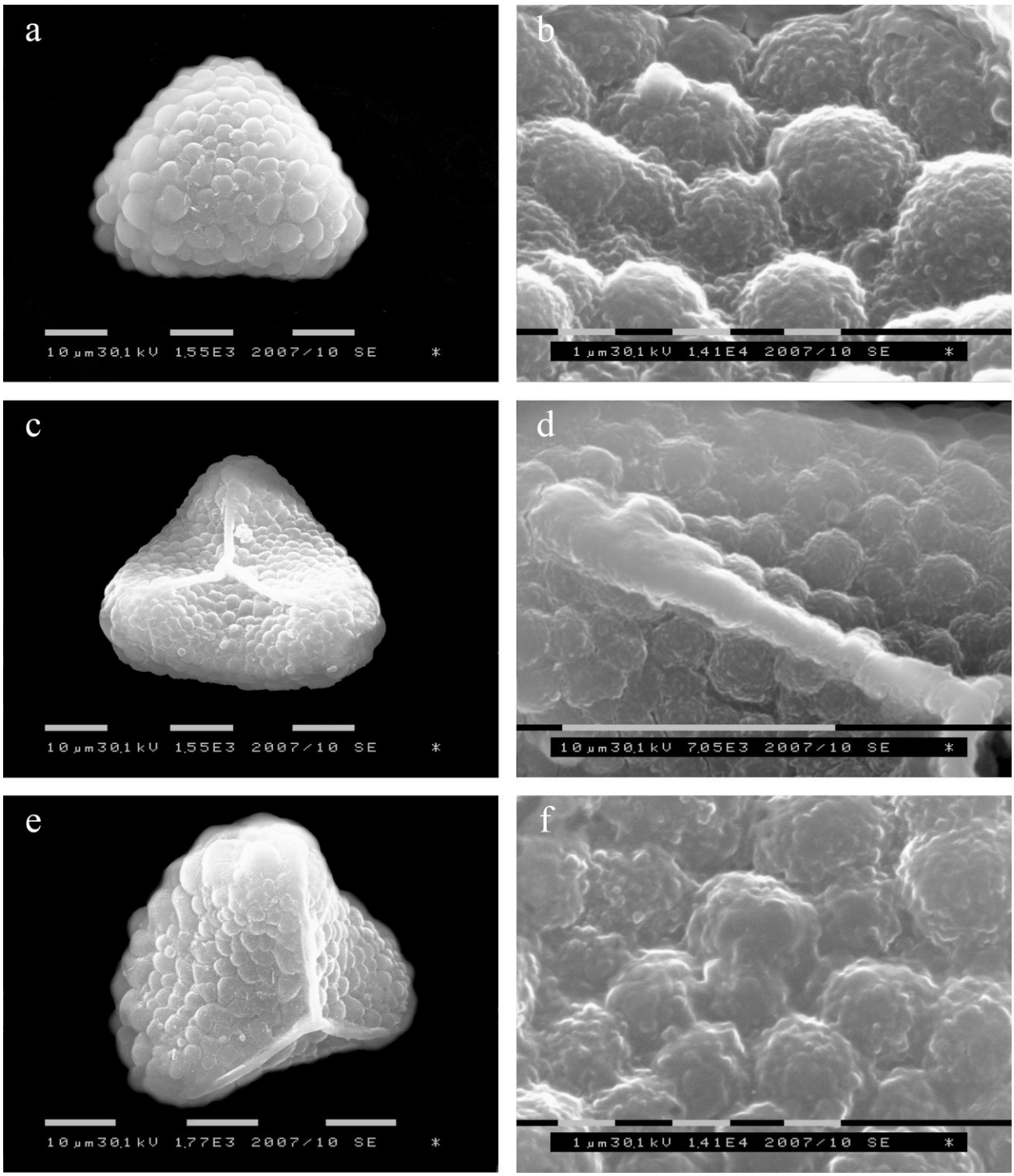

Fig. 6. SEM views of spores of *Cryptogramma raddeana*:
a – distal side; b – fragment of distal surface; c – proximal side; d – fragment of proximal spore surface and laesura; e – spore in equatorial-proximal position; f – fragment of proximal spore surface.

Investigated specimen: «U.S.A., Alaska, southeastern corner of the Big Anchorage, the mountains Chugach in the outskirts of the glacier of Byron, moraine. 22 VII 1990. S. Kharkevich» (VLA).

Cryptogramma stelleri (S.G. Gmel.) Prantl, 1882, Bot. Jahrb. 3: 413. – *Pteris stelleri* S.G. Gmel. 1768, Nov. Comm. Acad. Petr. 12: 519, tab. 12, fig. 1.

SEM-description (fig. 8). Spores in a polar position are triangular-roundish, with straight sides (non lociniate), and undulating along the contour. The equatorial diameter is (39.0)41.9–41.9(44.9) µm. The distal side

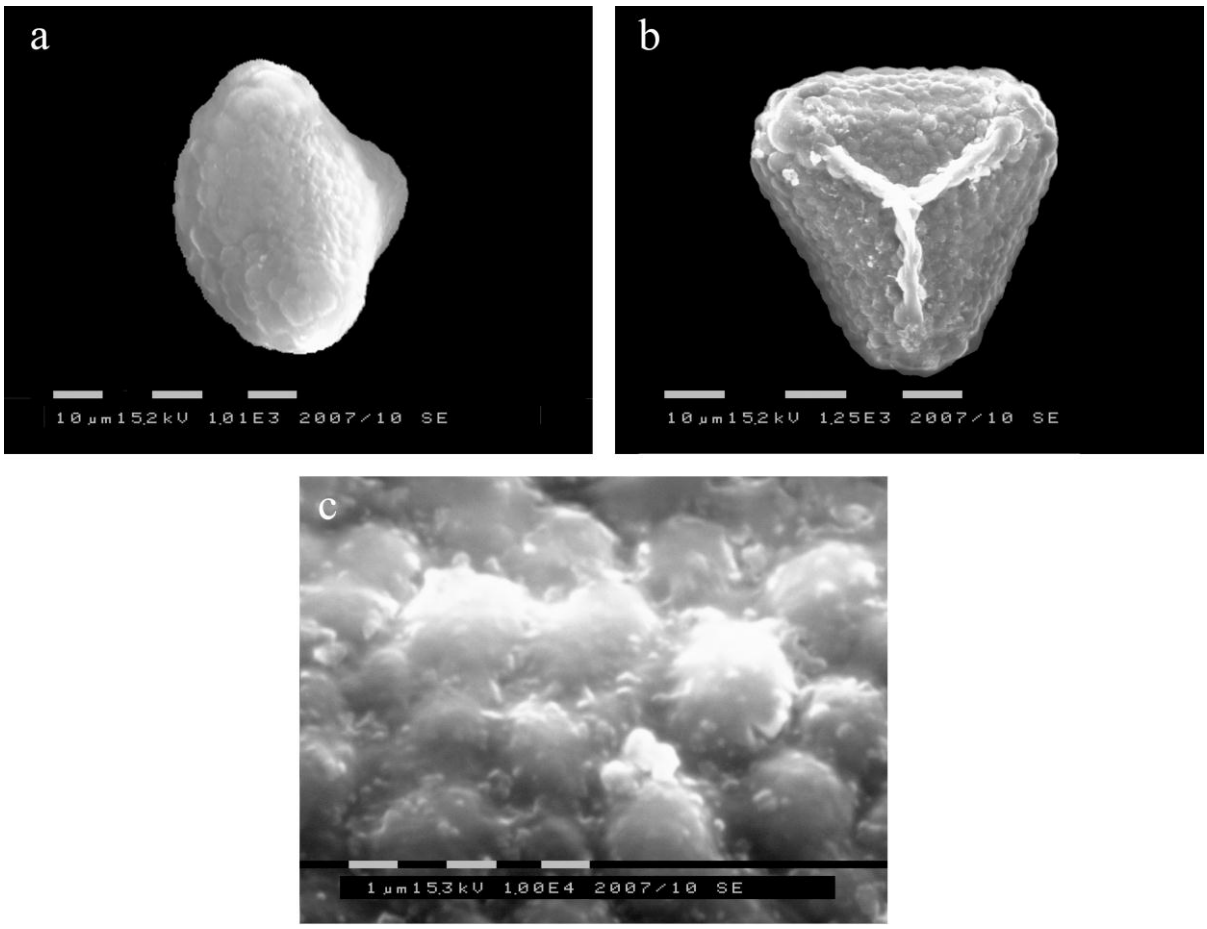

Fig. 7. SEM views of spores of *Cryptogramma sitchensis*:
a – spore in equatorial position; b – proximal side; c – fragment of distal surface

of the spore in equatorial position is hemispherical, the proximal one is convex or conical. In the sections near the ends of the laesura rays the sporoderm is non-thickened and is indistinct. The rays of laesura are straight, (18.0)21.5–22.0(25.9) µm long, (1.6)1.9–2.1(2.4) µm broad. The exosporium is coarse-verrucate. The verrucate elements are large, roundish or roundish-multiangular, different in size along the surface, from small (2.5)3.9–5.4(7.6) µm in diam. to large (3.7)4.2–4.9(5.8) µm in diam. The surface of the exosporium is fine-granulate.

Investigated specimen: «Russia, Altai Republic, the Teletskoe lake. Between the mouths of the rivers Estube and Koldor. 51°44,5' northern latitude and 87°30' eastern longitude. 12 VIII 2005. A.I. Shmakov, S.A. Diachenko, A.V. Vaganov, I.V. Naumov, R.A. Zubov» (ALTB).

Llavea cordifolia Lag. 1816, Gen. Sp. Pl.: 33.

SEM-description (fig. 9)**.** Spores in a polar position are roundish-triangular, with concave sides (lociniate), and middle-crenate along the contour. The equatorial diameter is (33.8)36.7–38.6(41.1) µm. The distal side of the spore in an equatorial position is convex, the proximal one is flat, more rarely concave, raising along the laesura rays, especially in the segments of the thickened sporoderm near the ends of laesura rays. The laesura rays are straight, (17.2)19.3–19.7(21.5) µm long, (1.9)2.6–3.2(3.5) µm broad. The exosporium is verrucate. The verrucate elements are roundish or roundish-multiangular, sometimes more or less fused, (1.3)1.6–2.2(2.9) µm in diam. at the proximal side of the spore, and (1.4)2.0–2.2(2.9) µm in diam. at the distal side. The surface of the exosporium is coarse-granulate with single large (0.8–1.2 µm) and small (0.2–0.4 µm) roundish excrescences.

Investigated specimen: «Plantae Mexicanae, State of Nuevo Leon, 13738, Under limestone cliffs, Sierra Madre, Monterey, 3000 ft. 12 III 1906. C.G. Pringle» (LE).

Coniogramme intermedia Hieron*, 1916, Hedwigia, 57(4): 301.*

SEM-description (fig. 10). Spores in a polar position are roundish-triangular, with concave sides (lociniate), and almost smooth along the contour. The equatorial diameter is (36.8)38.35–39.75(41.3) µm. The distal side of the spore in an equatorial position is convex, the proximal one is flat. The rays of laesura are straight, (17.2)17.09–18.03(19) µm long, (1.3)1.43–1.47(1.6) µm broad. The exosporium is finely-verrucate (tubercles (0.2)0.3–0.5(0.6) µm in diam). The surface of the exosporium is fine-granulate.

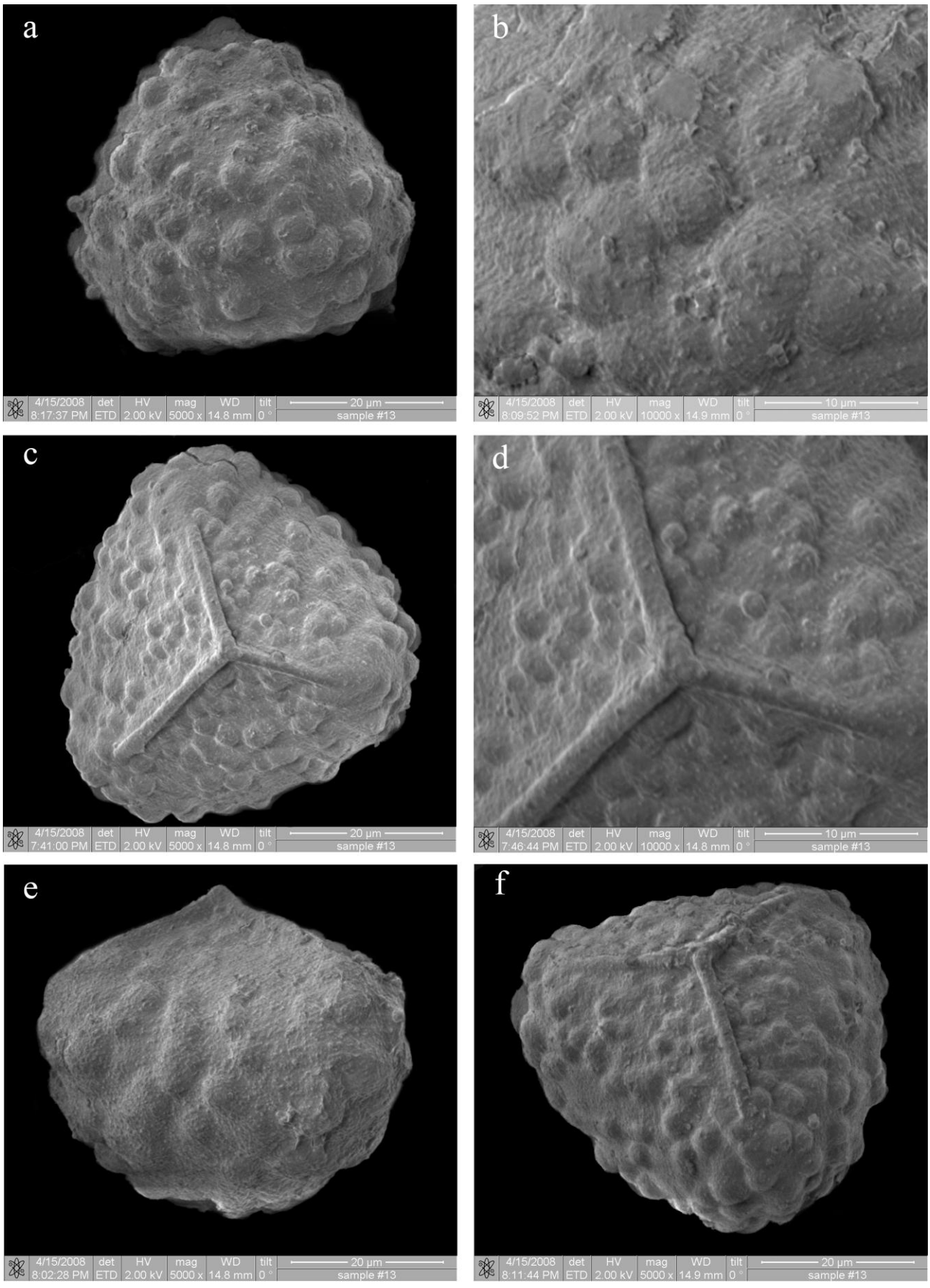

Fig. 8. SEM views of spores of *Cryptogramma stelleri*:
a – distal side; b – fragment distal surface; c – proximal side; d – fragment of spore proximal surface and laesura; e – spore in equatorial position; f – spore in equatorial-proximal position.

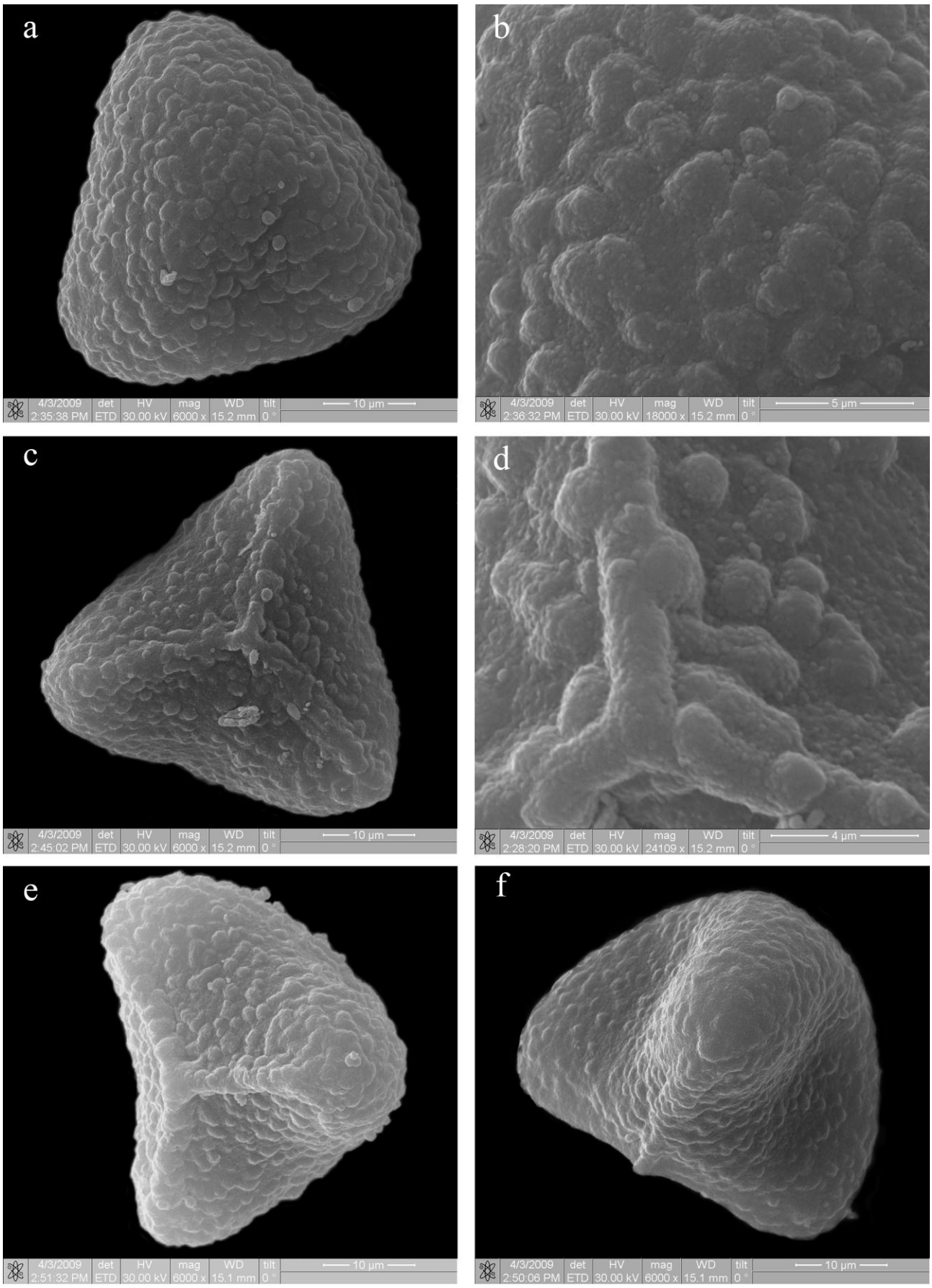

Fig. 9. SEM views of spores of *Llavea cordifolia*:
a – distal side; b – fragment of distal surface; c – proximal side; d – fragment of spore proximal surface and laesura; e, f – spores in equatorial-proximal positions.

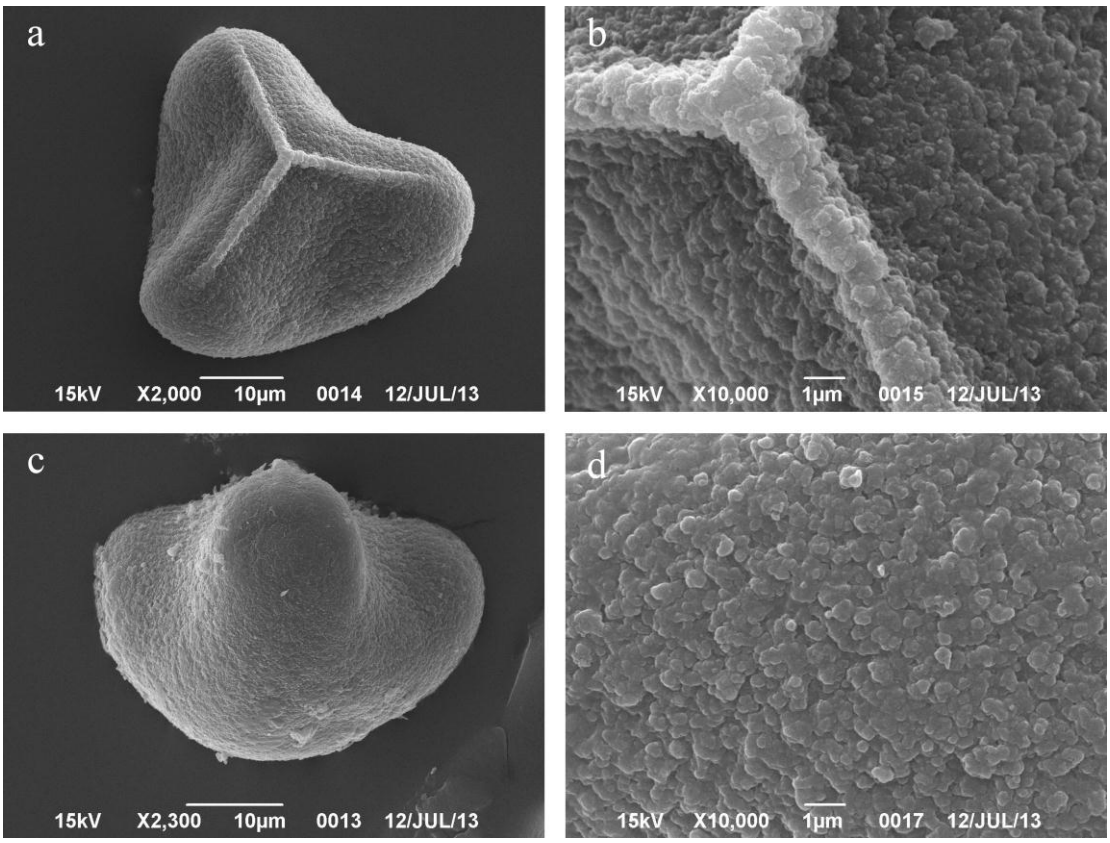

Fig. 10. SEM views of spores of *Coniogramme intermedia*:
a – proximal side; b – fragment of proximal surface and laesura; c – spore in equatorial position; d – fragment distal surface.

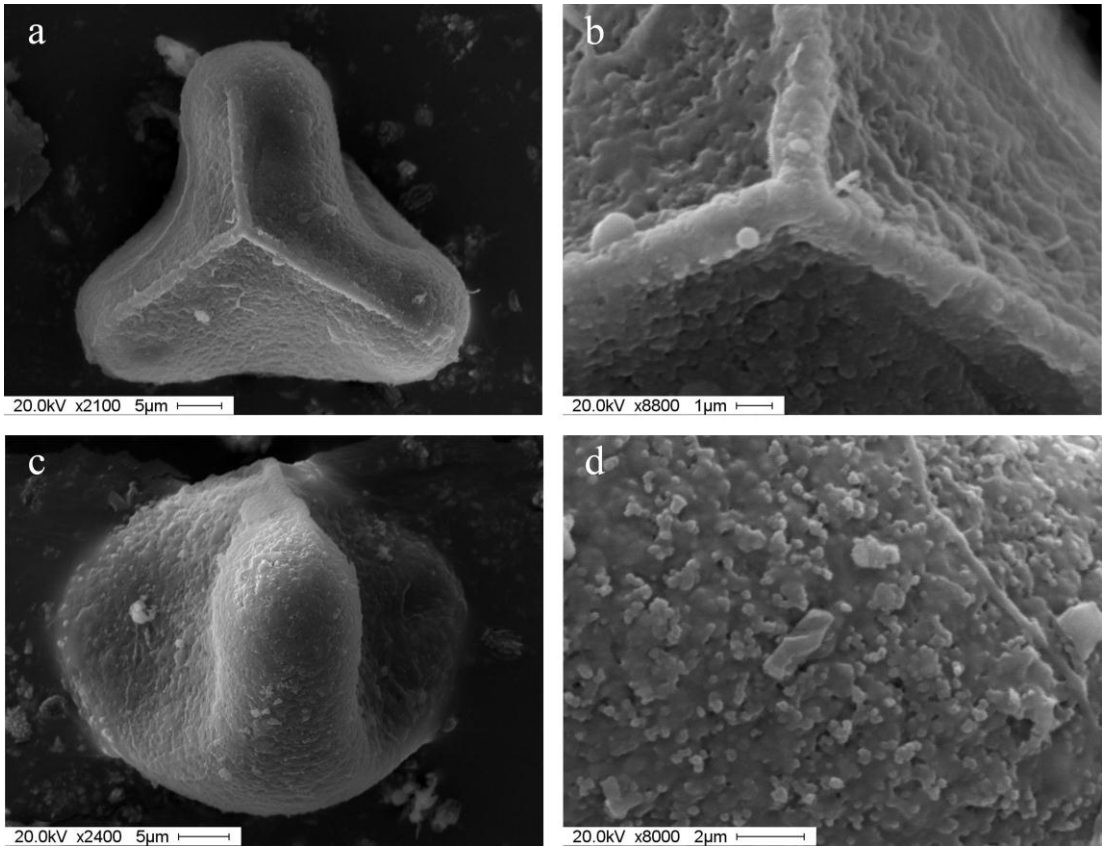

Fig. 11. SEM views of spores of *Coniogramma japonica*:
a – proximal side; b – fragment of proximal surface and laesura; c – spore in equatorial position; d – fragment distal surface.

Investigated specimen: China, Prov. Yunnan, 10 km to NW from Kunming, Chung Ju-shi. Evergreen forest. 26.IX.1958 (LE).

Coniogramme japonica (Thunb.) Diels, 1899, Nat. Pfl. 1, 4: 262. – *Hemionitis japonica* Thunb. 1784, Fl. Jap. 333.

SEM-description (fig. 11)**.** Spores in a polar position are roundish-triangular, with concave sides (lociniate), and almost smooth along the contour. The equatorial diameter is (38)39.75–40.75(42.5) μm. The distal side of the spore in an equatorial position is convex, the proximal side of the pyramid – is lifted by the laesura rays. The rays of laesura are straight, (16)17.05–18(19.1) μm long, (1.4)1.54-1.56(1.7) μm broad. The exosporium is finely-verrucate (tubercles (0,2)0,27–0,33(0,4) μm in diam). The surface of the exosporium is fine-granulate.

Investigated specimen: Yokosuka, Japan. – M. Le D` Sayatier, 1866-74. №1572 (LE).

Coniogramme fraxinea (Don) Diels, 1899, Nat. Pfl. 1, 4: 262. – *Diplazium fraxineum* D.Don, Prodr. Fl. Nepal.: 12. 1825.

SEM-description (fig. 12). Spores in a polar position are roundish-triangular, with concave sides (lociniate), and almost smooth along the contour. The equatorial diameter is (33.9) 34.7–35.7(36.5) μm. The distal side of the spore in an equatorial position is convex, the proximal side of the pyramid – is lifted by the laesura rays. The rays of laesura are straight, (15.3)15.75–16.25(16.7) μm long, (1.2)1.25–1.60(1.7) μm broad. The exosporium is finely-verrucate (tubercles (0.5)0.55–0.75(0.8) μm in diam). The surface of the exosporium is fine-granulate.

Investigated specimen: China, Plants of Kweichow Province, Alt. 1000 m. On rocky slope under shade IX.16.1931. Sori brownish. Ta Ho Yen Fan Ching Shan. Albert N. Steward, C.Y. Chiao, H.C. Cheo. №955 (LE).

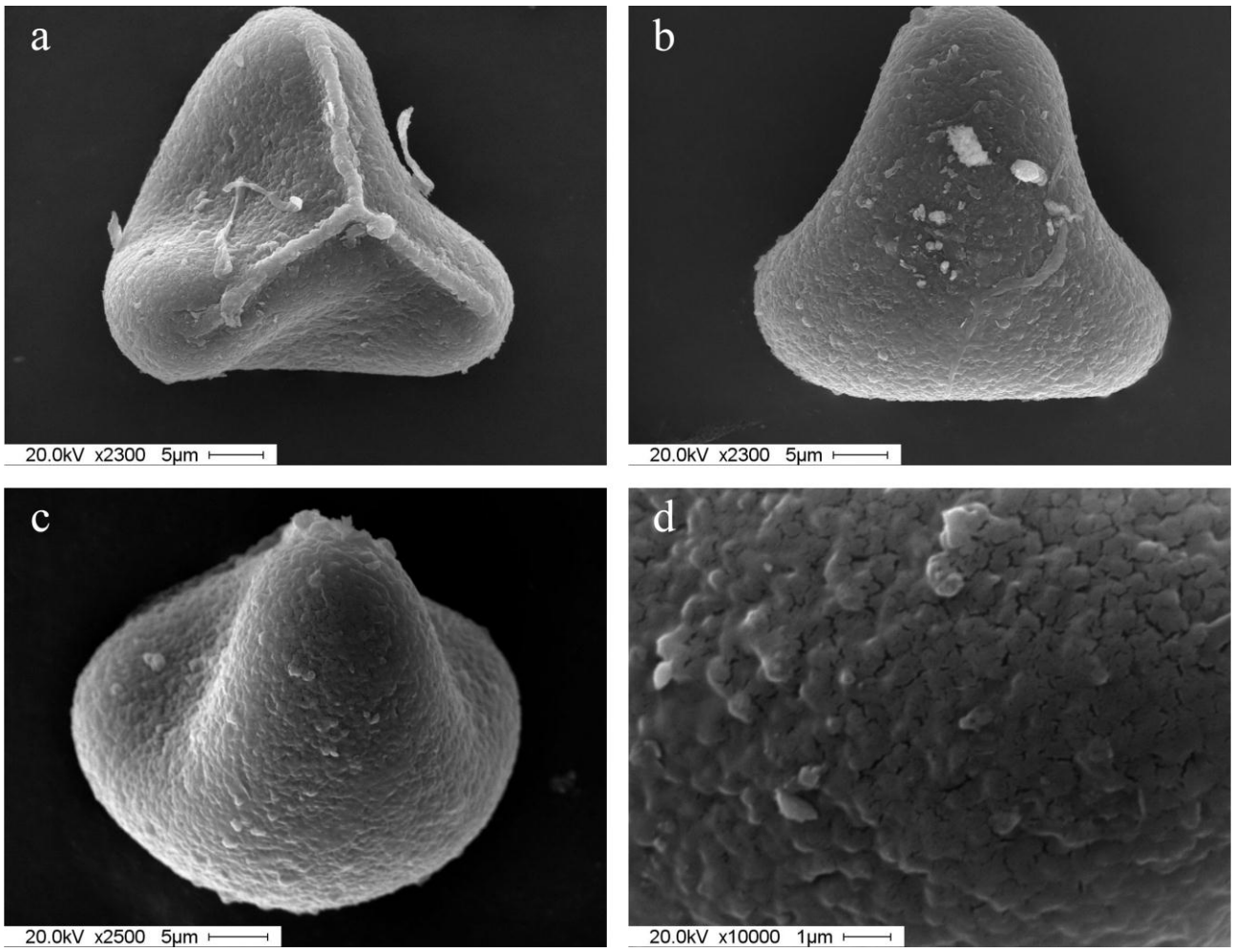

Fig. 12. SEM views of spores of *Coniogramma fraxinea*:
a – spores in equatorial-proximal positions; b – distal side; c – spore in equatorial-proximal position; d – fragment distal surface.

DISCUSSION

The analysis of the results revealed the characteristic similar features of the spore morphology of the *Coniogramme*, *Llavea* and *Cryptogramma* species, namely the form of spores in the proximal-polar and distal-polar positions roundish-triangular, lociniate; spore contour low-crenate to smooth; in the equatorial position the distal side of the spore is convex; rays of laesura are straight, ascending above the sporoderm surface; exosporium clearly defined from fine-granulate to verrucate.

The data obtained by comparing of spore morphology and morphometric parameters allowed us to conclude that the inclusion of *Coniogramme*, *Llavea* and *Cryptogramma* in the subfamily *Cryptogrammoideae* and one «cryptogrammoids» clade in the modern system of the family Pteridaceae was justified.

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