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Spore morphology of the representatives of the subfamily Ceratopteridoideae (J. Sm.) R.M. Tryon from the family Pteridaceae E.D.M. Kirchn. (Pteridophyta)

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Scanning electron microscopy (SEM) was used to perform a comparative study for four representatives of the subfamily *Ceratopteridoideae* (J. Sm.) R.M. Tryon from East Asia: *Ceratopteris thalictroides* Brongn., *C. pteridoides* (Hook.) Hieron., *Acrostichum aureum* Linn., and *A. speciosum* Willd. The analysis of the external morphology of the representatives of *Ceratopteridoideae* revealed a strong difference between *Ceratopteris* and *Acrostichum*.

The external morphology of spores of *Ceratopteris* and *Acrostichum* exhibited the features characterizing the family Pteridaceae as a whole: tetrahedral spores with a three-ray laesure, from triangular-roundish to roundish, distinct exosporium with a pronounced surface ornamentation and absence of perisporium, the exosporium surface varying from smooth and rough to that covered with large tubercles and roller-like bulges.

The external morphology of spores of *Acrostichum* is quite simple, although among other representatives of the family Pteridaceae, the spores of *Ceratopteris* have distinctive features: very large equatorial diameter (106–124 μm); spores are almost roundish; distinct cylindrical folds running parallel to the corners of the spore across its extensive distal surface.

Key words: genus *Ceratopteris,* genus *Acrostichum,* subfamily *Ceratopteridoideae*, family Pteridaceae, morphology of the spores, scanning electronic microscopy (SEM).

Introduction

The representatives of *Ceratopteris* (4 species) and *Acrostichum* (2–3 species) are aquatic, semi-aquatic and helophytic ferns of pantropical distribution (Nooteboom, 2012).

Due to high polymorphism inherent in the representatives of *Ceratopteris*, the genus consists of an infinite number of forms restricted to different geographical regions. Therefore, more than 12 species were described within the genus. However, many pteridologists believe that the genus comprises only one variable species of *C. thalictroides* (L.) Brongn. (Lloyd, 1974).

The representatives of *Ceratopteris* are completely immersed in the aquatic environment and prefer such habitats as bogs, ponds, and wet ditches. On the contrary, the representatives of *Acrostichum* grow on the shores of the seas, mainly in mangrove forests, where water composition is brackish (Tryon, Lugardon, 1991; Zhang et al., 2013).

The Flora of China includes four species of the subfamily *Ceratopteridoideae* (J. Sm.) R.M. Tryon: *Ceratopteris thalictroides* Brongn., *C. pteridoides* (Hook.) Hieron., *Acrostichum aureum* Linn., and *A. speciosum* Willd. (Zhang et al., 2013). Moreover, *Ceratopteris thalictroides* and *Acrostichum aureum* show fragmented pattern of distribution along the tropical belt throughout all continents, except for Antarctica.

The species *Ceratopteris pteridoides* is prevalent mainly in Central, North and South America. In Asia, it is commonly found in China (Anhui, Hubei, Jiangsu, Jiangxi, and Shandong), Bangladesh, India, and Vietnam. The species *Acrostichum speciosum* is endemic to China (including Hainan), Malaysia, Thailand, Vietnam, and Australia (Zhang et al., 2013).

In the current fern system developed using molecular genetics methods, the representatives of the genera *Ceratopteris* and *Acrostichum* exhibit an extremely high degree of relationship (Hasebe et al., 1996; Smith et al., 2006; Schuettpelz et al., 2007; Liu et al., 2008; Schuettpelz, Pryer, 2008; Christenhusz, 2011; Schneider et al., 2013; Zhang et al., 2017).

However, the authors of early scientific works on the taxonomy of ferns emphasized the peculiarity of the external morphology of the representatives of *Ceratopteris* and defined the genus as a monotype that forms an independent family *Parkeriaceae* Hook. (Copeland, 1947; Pichi-Sermolli, 1977). Pichi-Sermolli refers the genus *Acrostichum* to the family *Pteridaceae* (Pichi-Sermolli, 1977). Later, Rolla Tryon assigns the status of the subfamily *Ceratopteridoideae* to the tribe *Ceratopterideae* J. Smith (Tryon, 1986). The data on molecular phylogeny obtained for the representatives of *Ceratopteris* and *Acrostichum*, as well as the peculiar ecology of their habitat, allow us to recognize an independent subfamily *Ceratopteridoideae* along with the four ones included in the family Petridaceae. In order to reveal the features of the external morphology of spores for the representatives of the subfamily *Ceratopteridoideae*, we examined six specimens, representatives of four species from East Asia (China, including Hong Kong and Hainan Island).

The spore morphology of the representatives of the subfamily *Ceratopteridoideae* has been poorly studied. Particularly relevant is obtaining data on the external morphology of spores of Asian *Ceratopteris* and *Acrostichum*.

The SEM method was used to analyze the spore morphology of the representatives of *Ceratopteris* on specimens from Africa (Liberia and Salvador), South America (Peru and Brazil), Cuba, India, and Australia – *C. cornuta* (P.Beauv.) Lepr., *C. pteridoides*, *C. thalictroides*, and *C. richardii* Brongn. (Tryon, Lugardon, 1991; Dettmann, Clifford, 1991). Similar to the studies of the spore morphology conducted last century (Nayar, 1968; Sahashi, 1979), micrographs of *Ceratopteris* have few exposures of microphotographs. In addition, poor quality of micrographs does not allow a detailed description of the external morphology of spores that does not provide sufficient data and complete analysis of the exosporium surface. The study of the spore morphology of *Acrostichum* was limited to specimens from tropical America (Mexico, Honduras and Guyana), Africa (Liberia,), Southeast Asia (Philippines and Cambodia), and Fiji – *A. danaeifolium* Langsd. a. Fisch., and *A. aureum* (Tryon, Lugardon, 1991).

Material and Methods

The spores for the study were selected from the herbarium material deposited in the Herbarium of the Institute of Botany of the Academy of Science of China (PE, Beijing). The spores were fixed on a slide using an electrically conductive adhesive tape, sputtered with gold using a sputter coater Quorum Q150R S, and examined under a scanning microscope Mini-SEM SNE-4500M (Korea) located in the laboratory of structural and molecular analysis of plants, TSU. The spores surface was scanned in high vacuum at voltage of 10–30 kV and magnified from 2,500 to 10,000 times. The spore dimensions and the element ornamentation were determined using photographs taken with a scanning microscope.

Results and Discussion

The description and original electron micrographs of spores of the species *Ceratopteris* and *Acrostichum* are provided below.

1. *Ceratopteris thalictroides* Brongn. (Fig. 1, a–e). Spores in the proximal-polar and distal-polar positions are triangular-roundish to roundish. The equatorial diameter is (101) 112.8 (124) μm. The polar axis is 101.7 (from 92.3 to 110) μm. In the equatorial position, the distal side of the spore is almost spherical, the proximal side is expressed only at the apex – flattened. The rays of laesura are straight (24) 28.7 (32.4) μm long, (4.45) 4.62 (4.95) μm wide, rising above the sporoderm. Roller-like folds running from the spore corners across the extensive distal surface of the spore are highly risen above the sporoderm (up to the height of laesuras) and reach the width of (3.47) 3.83 (4.29) μm. The distance between the adjacent roller-like folds is (3.0) 5.11 (7.4) μm. In the depressions between roller-like folds and laesuras, the exosporium surface is uniformly covered with elongated excrescences of (0.237) 0.312 (0.379) μm in diameter.

Investigated specimen: Deep Bay, Hong Kong. Edge of rice field. Shiu Ying Hu 5777. Oct. 6, 1968. №00587547.

2. *Ceratopteris pteridoides* (Hook.) Hieron. Christ (Fig. 2, a–e). Spores in the proximal-polar and distal-polar positions are triangular-roundish to roundish. The equatorial diameter is (106) 114.8 (121) μm. The polar axis is (92) 93.4 (96) μm. In the equatorial position, the distal side of the spore is almost spherical, the proximal side is expressed only at the apex – flattened. The rays of laesura are straight (30.5) 32.6 (34.5) μm long, (2.6) 3.2 (4.2) μm wide, rising above the sporoderm. Cylindrical folds running from the spore corners across the extensive distal surface of the spore are highly risen above the sporoderm (up to the height of laesuras) and reach the width of (3.3) 3.73 (4.5) μm. The distance between the adjacent roller-like folds is (2.8) 5.84 (10) μm. In the depressions between roller-like folds and laesuras, the exosporium surface is uniformly covered with tubercles of (0.163) 0.23 (0.317) μm in diameter.

Investigated specimen: Vicinity of Hanyang, Hupeh. Alt. 50. Habitat in water. Habit herb or water fern. S.W. Teng №302. Nov. 10, 1932. №00587529.

3. *Acrostichum aureum* Linn. (Fig. 3, a, b). Spores in the proximal-polar and distal-polar positions are triangular-roundish, non-lociniate. The equatorial diameter is (48) 50 (52) μm. The rays of laesura are straight, (14.7) 16.3 (18.2) μm long, (2.2) 2.44 (2.9) μm wide, slightly risen at the apex above the surface of the spore. The exosporium surface on the distal and proximal sides is covered with slightly protruding tubercles of (1.0) 1.28 (1.5) μm in diameter, rough.

Investigated specimen: Fairly common; moist, level land, sandy soil, seashore, semi-woody, erect. Shan Mong, Yai-hsien District. Coll. Lau S.K. №5998. Flora of Hainan, 12th Hainan Expedition.

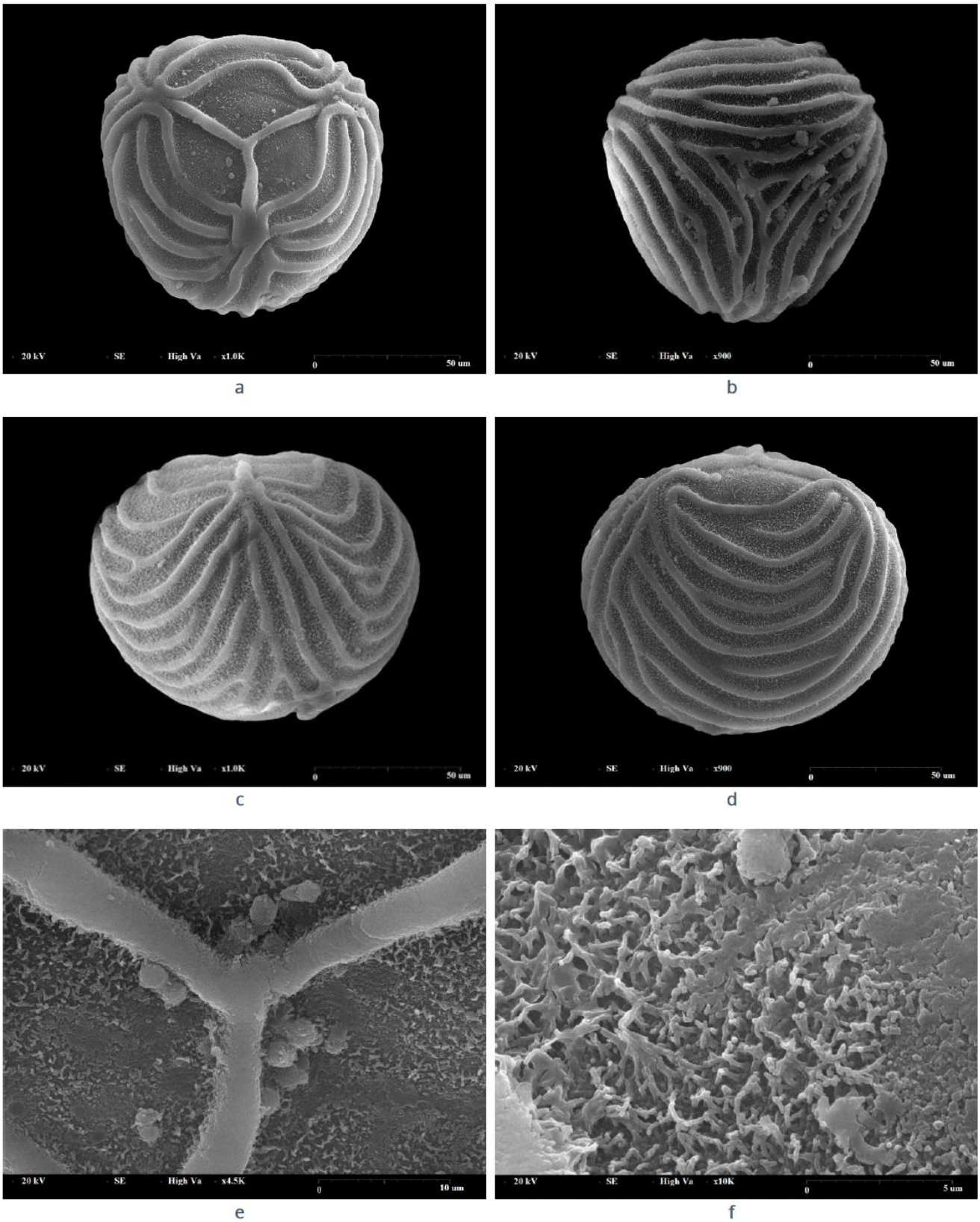

Fig. 1. SEM views of spores of *Ceratopteris thalictroides:* a – proximal side; b – distal side; c, d – spore in equatorial position; e, f – fragment of proximal surface.

4. *Acrostichum speciosum* Willd. (Fig. 4, a-c). Spores in the proximal-polar and distal-polar positions are triangular-roundish, non-lociniate. The equatorial diameter is (38) 46.6 (51.8) μm. The rays of laesura are straight (9.9) 10.7 (11.7) μm long, (0.8) 1.1 (1.3) μm wide, slightly risen at the apex above the surface of the spore. The exosporium surface on the distal and proximal sides is covered with slightly protruding tubercles of (0.3) 0.64 (0.9) μm in diameter, rough.
Investigated specimen: Hainan, Wenchang, Qinglan Reserve 19°37.30`N, 110°44.79`E. Habitat: on ground in mangrove forests. Alt.: 0 m. Coll. A. No.: S.Y. Dong a. X.C. Zhang 682. 2003-03-17. №00543730.

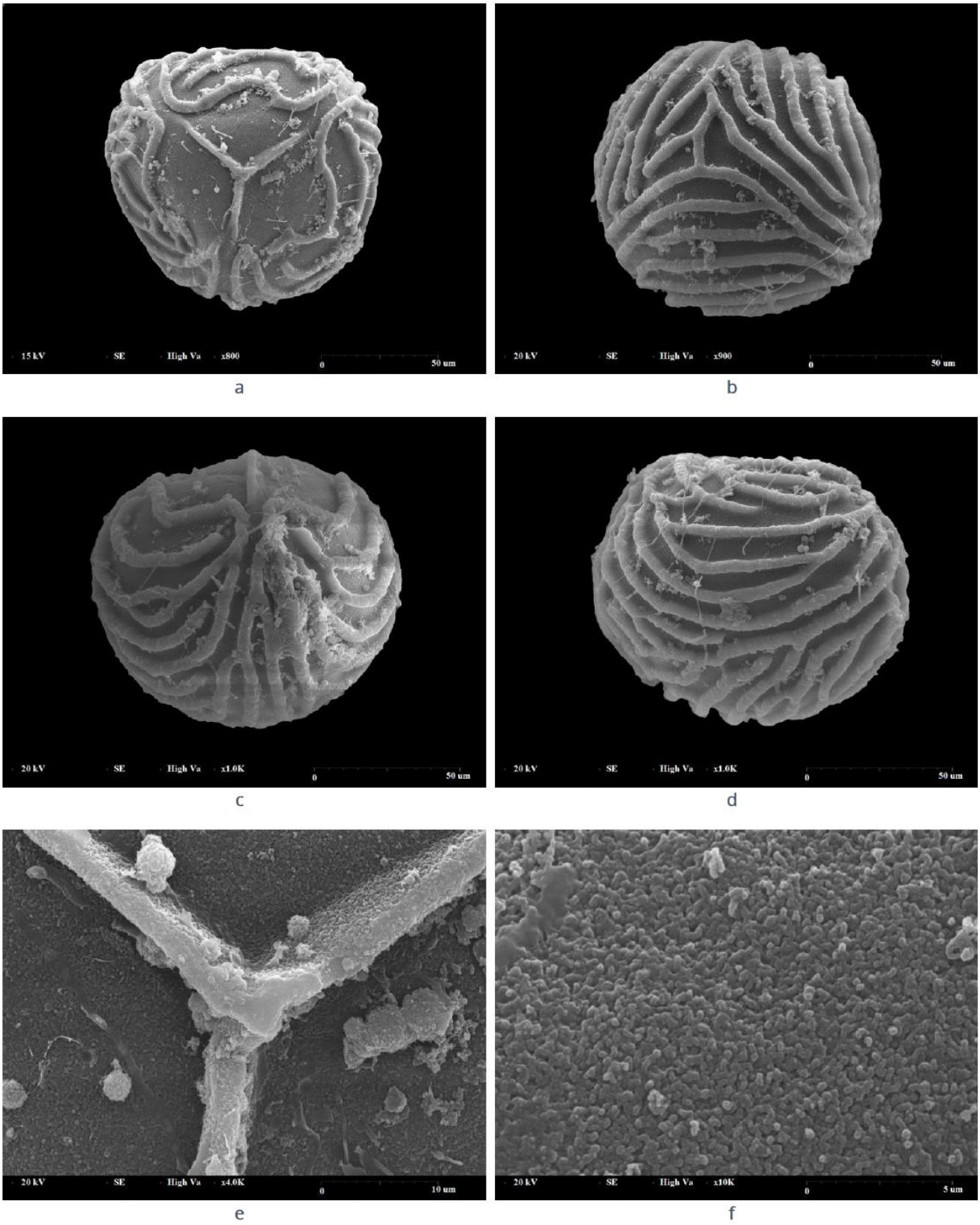

Fig. 2. SEM views of spores of *Ceratopteris pteridoides:* a – proximal side; b – distal side; c, d – spore in equatorial position; e, f – fragment of proximal surface.

The analysis of the external morphology of the spores of *Ceratopteridoideae* revealed a few features characterizing the family Pteridaceae: tetrahedral spores with a three-ray laesura, triangular-roundish to roundish, distinct exosporium with expressed ornamentation, without perisporia, the exosporium surface varying from smooth and rough to that covered with large tubercles and roller-like bulges. A strong difference in the external morphology of spores of *Ceratopteris* and *Acrostichum* has been revealed. Thus, the distinctive features of the external morphology of spores among the genera of the subfamily *Ceratopteridoideae* vary within a range that is much greater if compared to the subfamily *Cryptogrammoideae* S. Linds., which also includes a small number of genera (*Coniogramme, Cryptogramma* and *Llavea*). The other three subfamilies of the family Pteridaceae include from 12 to 20 genera, and this explains a strong variation in the morphological features of spores.

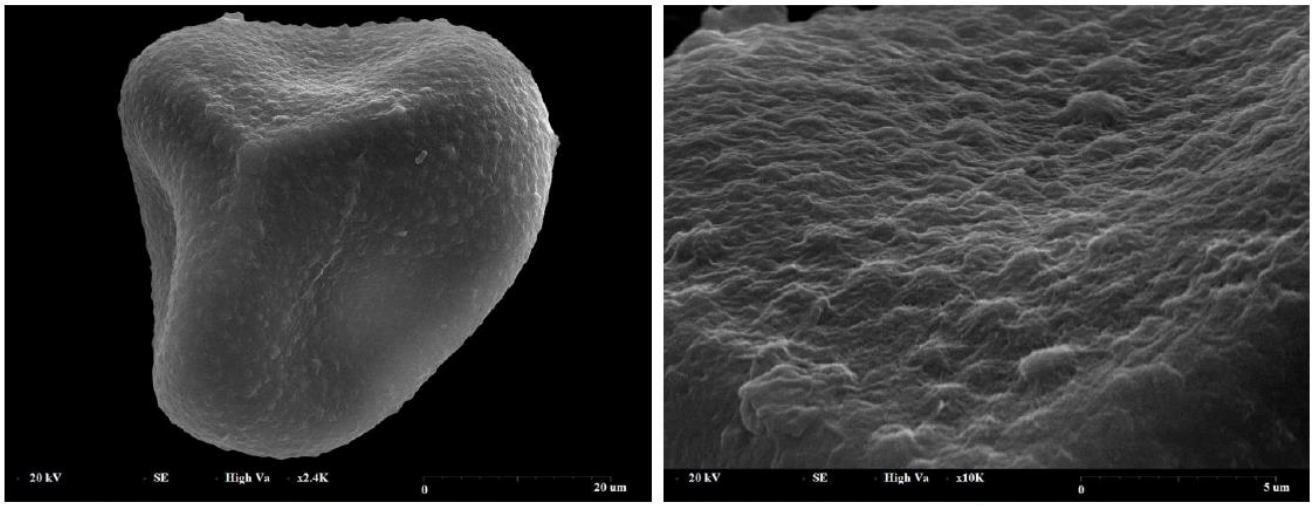

Fig. 3. SEM views of spores of *Acrostichum aureum:* a – spore in proximal-equatorial position; b – fragment of proximal surface.

The external morphology of spores of *Acrostichum* is quite simple. Its primitive structure makes the morphology similar to that of the representatives of various subfamilies of the family Pteridaceae. The morphology of spores of *Acrostichum* resembles the shape and nature of the spore surface of the representatives from the genera *Pellaea* Link, *Adiantum* L., *Coniogramme* Fée, *Llavea* Lag., and *Anopteris* (Prantl) Diels (Tryon, Lugardon, 1991; Vaganov et al., 2010; 2011; Vaganov, 2016).

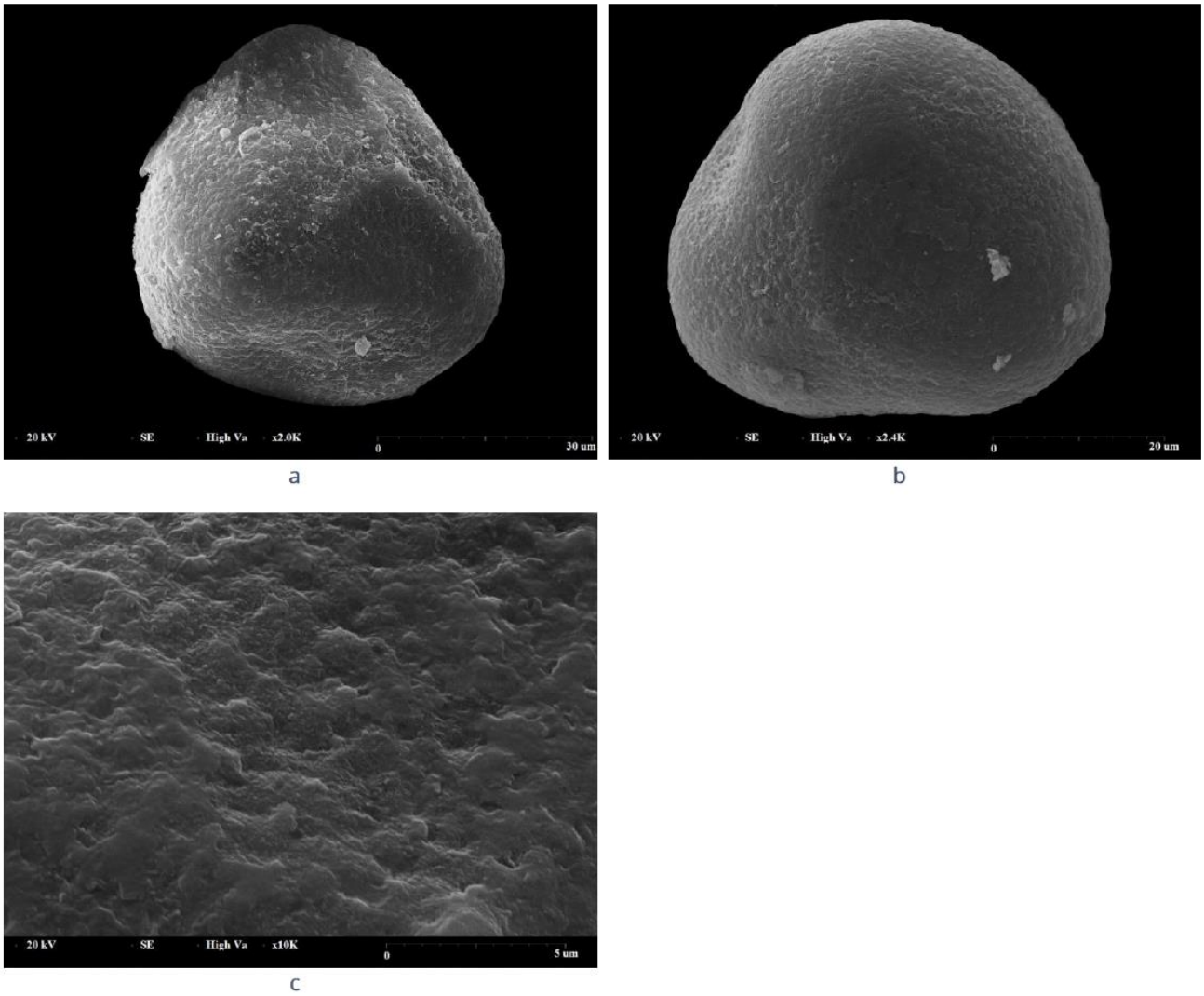

Fig. 4. SEM views of spores of *Acrostichum speciosum: a* – spore in proximal-equatorial position; b – distal side; c – fragment of distal surface.

On the contrary, the external morphology of spores of *Ceratopteris* is extremely original and not similar to that of the representatives of the family Pteridaceae. In addition, fairly large overall dimensions of the equatorial diameter of spores of the

representatives of the genus *Ceratopteris*, the distinctive features of the external morphology and very peculiar ecology of the fern habitat show its unique position in the system of the family Pteridaceae.

The study conducted using the scanning electron microscopy revealed no affinity between the ferns of the genera *Ceratopteris* and *Acrostichum* since a small number of similar features can be observed in the external morphology of spores.

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