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Spore morphology of *Taenitis*, *Syngamma*, and *Austrogramme* species (*Pteridoideae*, *Pteridaceae*) from South-Eastern Asia and Oceania. II

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Summary. This paper continues consideration of the spores of three paleotropical fern genera – *Taenitis*, *Syngamma*, and *Austrogramme* (*Pteridoideae*, *Pteridaceae*) from South-Eastern Asia and Oceania. At the second stage, we carried out a comparative scanning electron microscopy study of spores of three species of *Austrogramme*, four species of *Syngamma*, and six species of *Taenitis* and added information about previously studied spores of seven species of these genera. Spores of all examined species are trilete, tetrahedral or tetrahedral-globose with convex to hemispherical distal side and plane, convex or conical proximal side. The spores of *Austrogramme* species are the smallest, simplest in ornamentation and similar to each other. Sculpture of the proximal and distal sides are microverrucate, the surface of the spores is covered by granular deposits. Spores of most *Syngamma* species are very similar to spores of *Austrogramme* species in shape and surface sculpture: their distal and proximal surfaces are microverrucate, whereas the spores of *S. borneensis* and *S. cartilagidens* have the low-tuberculate sculpture. Spores of *Taenitis* species are very different from the spores of *Austrogramme* and *Syngamma*. Seven of nine studied species have spores with well-expressed cingulum (*T. blechnoides*, *T. cordata*, *T. diversifolia*, *T. interrupta*, *T. luzonica*, *T. obtusa*, and *T. requiniana*), three species (*T. cordata*, *T. hookeri*, and *T. pinnata*) have spores with prominent laesural ridges. The spores have well-expressed ornamentation – tuberculate, baculate, rugate, tuberculate-rugate. The most conspicuous character of the ornamentation of spore surfaces is the presence of rodlets associated with sculpture elements. The densest rodlets are characteristic of *Taenitis diversifolia*, *T. luzonica*, *T. obtusa*, and *T. requiniana*. Spore size (equatorial diameter) ranges on average between 22 µm and 37 µm in *Austrogramme*, between 27 µm and 41 µm in *Syngamma*, and between 26 and 51 µm in *Taenitis* species.

Морфология спор *Taenitis*, *Syngamma* и *Austrogramme* (*Pteridoideae*, *Pteridaceae*) из Юго-Восточной Азии и Океании. II

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Ключевые слова: морфология спор, сканирующая электронная микроскопия (СЭМ), *Austrogramme*, Pteridaceae, Pteridoideae, *Syngramma*, *Taenitis*.

Аннотация. Статья продолжает публикацию данных о морфологии спор трех палеотропических родов папоротников – *Taenitis*, *Syngramma* и *Austrogramme* (Pteridoideae, Pteridaceae) из Юго-Восточной Азии и Океании. На втором этапе методом сканирующей электронной микроскопии (СЭМ) проведено сравнительное исследование спор 3 видов *Austrogramme*, 4 видов *Syngramma* и 6 видов *Taenitis*, добавлены сведения о спорах 7 видов этих родов, изученных ранее. Споры всех изученных видов трехлучевые, тетраэдрические до почти шаровидных с выпуклой или полусферической дистальной и уплощенной, выпуклой или конической проксимальной сторонами. Споры видов *Austrogramme* самые мелкие, с наиболее простой скульптурой, сходны по морфологии. Скульптура спор микробородавчатая, на поверхности имеются гранулярные отложения. Споры большинства видов *Syngramma* имеют микробородавчатую скульптуру, по форме и скульптуре поверхности они сходны со спорами видов *Austrogramme*; у *S. borneensis* и *S. cartilaginea* споры бугорчатые, бугры низкие. Споры видов *Taenitis* значительно отличаются от спор видов *Austrogramme* и *Syngramma*. Семь из девяти исследованных видов (*Taenitis blechnoides*, *T. cordata*, *T. diversifolia*, *T. interrupta*, *T. luzonica*, *T. obtusa* и *T. requiniana*) имеют споры с отчетливо выраженным цингулюмом (экваториальная складка), для спор трех видов – *T. cordata*, *T. hookeri* и *T. pinnata* – характерны выраженные комиссуральные складки. Споры имеют хорошо выраженную скульптуру – бугорчатую, удлинненно-бугорчатую, складчатую или бугорчато-складчатую. Наиболее заметным признаком орнаментации спор видов *Taenitis* являются стерженьки, густо покрывающие скульптурные элементы спор. Наиболее густо покрыта стерженьками поверхность спор у *Taenitis diversifolia*, *T. luzonica*, *T. obtusa* и *T. requiniana*. Размеры спор (экваториальный диаметр) варьируют в среднем в пределах 22–37 мкм у *Austrogramme*, 27–41 мкм у *Syngramma* и 26–51 мкм у *Taenitis*.

This paper continues consideration of spore morphology of three paleotropical fern genera – *Taenitis* Willd. ex Schkuhr, *Syngramma* J. Sm., and *Austrogramme* E. Fourn. R. E. Holttum (1975) was the first, who studied the relationship between *Taenitis* and *Syngramma* and considered them to the Gymnogrammeoid ferns. Different authors considered these three fern genera as belonging to the separate family Taenitidaceae (C. Presl) Pic. Serm. or classified them as members of *Taenitidoideae* R. M. Tryon subfamily of the large and diverse family Pteridaceae E. D. M. Kirchn (Pichi Sermolli, 1977; Tryon, 1986; Tryon et al., 1990; Sánchez-Baracaldo, 2004; Smith et al., 2006). E. Schuettpelz et al. (2007) considered them as the members of the pteridoid ferns within the Pteridaceae. M. J. M. Christenhusz et al. (2011) and L. Zhang et al. (2015, 2017) classify these three genera to subfamily *Pteridoideae* C. Chr. ex Crabbe, Jermy et Mickel. The last to date PPG-system (PPG1, 2016) classifies these genera to suborder Pteridineae J. Prado et. Schuettp., family Pteridaceae and subfamily *Pteridoideae* Link sensu Zhang et al. (2015). This system recognizes all three genera sensu Tryon et al. (1990); each genus is considered as monophyletic (*Taenitis* and *Austrogramme*) (Cochran et al., 2014) or assumed to be monophyletic (*Syngramma*). Within *Austrogramme*, this system recognizes about six species, within *Taenitis* and *Syngramma* – about

15 species in each. M. Kato (1988) found the genus *Taenitis* consists of 17 species.

The representatives of *Austrogramme* occur in New Caledonia, New Guinea, the Moluccas, and the New Hebrides. Species of *Syngramma* inhabit Malaya to the Philippine Islands, New Guinea, and east to Fiji and the Caroline Islands (Palau), seven species occur in Borneo. The *Taenitis* species are distributed from southern India and Ceylon to Hainan, through Malesia to northern Queensland and Fiji, nine of them occur in Borneo (POWO. URL: <http://powo.science.kew.org/>).

The molecular-phylogenetic studies of the last decade based on six plastid regions (*atpA*, *atpB*, *rbcl*, *rps4* genes, *rps4-trnS* and *trnL-F* intergenic spacers, and *trnL* intron) confirmed the close relationship among three paleotropic genera – *Austrogramme*, *Syngramma*, and *Taenitis*. In all published phylograms, these three genera form monophyletic clade, where *Taenitis* is sister to *Austrogramme* and *Syngramma* (Cochran et al., 2014; Zang et al., 2015, 2017).

Spore morphology of species of the large fern family Pteridaceae has been discussed in the numerous works (Hennipman, 1975; Tryon, Lugardon, 1991; Palacios-Rios et al., 2016; Chao, Huang, 2018; Irfan et al., 2021) including ours (Kuznetsov et al., 2014; Vaganov, 2016; Vaganov et al., 2017a–d, 2018a). Most authors emphasize

the diagnostic value of spore ornamentation at the specific or section levels. The congruence of morphological characteristics of spores with the result of molecular-phylogenetic analyzes has been shown for different fern genera on various examples (Gureyeva, Kuznetsov, 2015; Vaganov et al., 2017a–c). Data of spore morphology of some species of *Austrogramme*, *Syngramma*, and *Taenitis* obtained using scanning electron microscopy were published in 1991 by A. Tryon and B. Lugardon (11 species in sum). Based on the spore structure of 16 species of these three genera, E. Hennipman (1975) considered the study of the spores to be promising for comprehension of the relationships within Pteridaceae. We also have earlier given the spore characteristics of seven species of these genera (Vaganov et al., 2018b).

The aim of this work is a comparative morphological study of the spores of *Taenitis*, *Syngramma*, and *Austrogramme* using scanning electron microscopy (SEM) and evaluation, whether the spore characteristics have the value for phylogeny of these genera.

Materials and methods

Mature spores for SEM examination were obtained from herbarium specimens of 11 species stored in P (Paris vascular plant Herbarium Muséum national d'Histoire naturelle, MNHN, Paris, France): *Taenitis cordata* (Gaudich.) Holttum, *T. diversifolia* Holttum, *T. luzonica* (Alderw.) Holttum., *T. obtusa* Hook., *T. requiniana* (Gaudich.) Copel., *Syngramma grandis* (Copel.) C. Chr., *S. spathulata* (C. Chr.) Holttum, *S. wallichii* (Hook.) Bedd., *Austrogramme decipiens* (Mett.) Hennipman, *A. francii* (Rosenst.) Hennipman, and *A. marginata* (Mett.) E. Fourn, and two species stored in PE (Herbarium of Institute of Botany, Chinese Academy of Sciences, Beijing, China): *Taenitis interrupta* Hook. et Grev. and *Syngramma cartiligidens* (Bak.) Diels. Furthermore, we used the data on spore morphology obtained by us earlier (Vaganov et al., 2018) for *Austrogramme boerlageana* (Alderw.) Hennipman, *Syngramma alismifolia* (Presl) J. Sm., *S. lobbiana* (Hook.) J. Sm., *S. quinata* (Hook.) Carruth., *Taenitis blechnoides* (Willd.) Sw., *T. hookeri* (C. Chr.) Holttum, *T. pinnata* (J. Sm.) Holttum. As a result, the spore morphology of four species of *Austrogramme*, eight species of *Syngramma*, and nine species of *Taenitis* were studied.

The spelling of the names of taxa and authors is given according to “The International Plant Name Index” (IPNI, <http://www.ipni.org>).

The SEM studies were conducted in the Institute for Water and Environmental Problems (Barnaul, Russia) using a “Hitachi S 3400 N” electronic scanning microscope and in Tomsk State University (Tomsk, Russia) with the scanning electronic microscope “Mini-SEM SNE-4500M”. Spores were applied on double-sided carbon adhesive tape, fastened on the object table with a diameter of 10 mm. The spore surface was coated in the sputter-coaters “Emitech SC 7620/QT S” (with the gold-palladium mixture) and “Quorum Q150R S” (with gold). The spore surface was scanned in a high vacuum at a voltage of 20 kV through 2000× and 15000× of magnification.

Equatorial diameter (as seen in the polar position of spore), polar axis (as seen in the equatorial position of spore), length and width of laesura arms (on the proximal position of spore), the width of cingulum (as seen in the polar position of spore) were measured for 10–20 spores of each species. All measurements were made on SEM-micrographs of spores using the computer program “Image J”.

The shape of the distal and proximal sides was described using terms of B. K. Nayar, S. Devi (1966). The following terms were used to denote structural elements of the spores (combination of terms used by Nayar, Devi, 1966; Tryon, Lugardon, 1991; Lellinger, 2002; Palacios-Rios et al., 2016; Chao, Huang, 2018):

– cingulum (equatorial flange, equatorial ridge) – a solid continuous, thickened portion of the exospore at the equator of the spore separating the proximal and distal sides of spore;

– laesura arms – three thickened or unthickened scars on the surface of spore;

– laesural ridge (commissural ridge, commissural flange, ridge-like torus) – conspicuous ridges flanked the laesura arms and parallel of them;

sculptural elements:

– verrucae – small elements, irregular in form, obtuse to round on apex; surface verrucate (covered with verrucae) or microverrucate (covered with very small verrucae);

– tubercle – knob-like elements regular in form; surface tuberculate (covered with tubercles);

– baculae – elements 1.5× longer than wide, cylindrical, with obtuse to round apex; surface baculate (covered with baculae);

– rugae – wide rounded folds; surface rugate (covered with rugae);

– rugulae – small rugae (wrinkles); surface rugulate (covered with rugulae) or microrugulate (covered with very small rugulae);

ultrastructures on the outer spore layer:

- rodlets – thin, short, filiform structure, situated on the outer spore layer;
- granulate deposits – small excretion on the outer spore layer.

Results and discussion

Spores of all examined species of *Austrogramme*, *Syngramma*, and *Taenitis* are trilete, tetrahedral or tetrahedral-globose. In equatorial position, the distal side is convex to hemispherical, proximal side is flat, convex or conical. In polar position, spores are triangular, roundish-triangular or nearly roundish with straight or concave sides and rounded corners. Spores with cingulum or without it. Ornamentation of both sides of the spore may be verrucate, tuberculate, baculate, or rugate, spore surface covered by rodlets and granulate deposits. In spores of some species, the laesura arms are flanked by laesural ridges that can be well-defined entire or interrupted. The main morphological and biometrical characteristics of spores are shown in tables 1 and 2.

The spores of the *Austrogramme* species are the smallest, simplest in ornamentation and similar to each other. Spores are tetrahedral-globose in equatorial view, often with depressions on the proximal side between laesura arms. In polar position, spores are triangular-roundish or nearly

roundish with straight, concave or convex sides. The proximal and distal sides are microverrucate, with verrucae 0.2–0.4 μm in diam. in *A. boerlageana*, or verrucate, with verrucae 0.4–1.2 μm in diam. in *A. decipiens*, *A. francii*, and *A. marginata*. The surface of the spores of three species is covered by granular deposits, dense in *A. boerlageana*, scattered in *A. francii* and rare in *A. marginata*. The spore surface of *A. decipiens* is covered by rodlets rather than granular deposits. Laesura arms are straight, 0.6–1.1 μm in length. In spores of *A. marginata*, laesura arms immersed in the narrow laesural ridges that are reached to the spore corners and covered by scattered verrucae (Fig. 1, Table 1). The equatorial diameter ranges between 22.5 μm and 36.7 μm and the polar axis – between 14.8 μm and 20 μm . The smallest spores are characteristic of *A. francii* and *A. marginata* (Table 2).

The spores of most *Syngramma* species are very similar to spores of the *Austrogramme* species in shape and surface sculpture. In equatorial view, spores of *Syngramma alismifolia*, *S. borneensis*, *S. cartiligidens*, and *S. wallichii* are tetrahedral-globose with depressions between laesura arms on the proximal side. In polar position, spores are triangular, roundish-triangular or nearly roundish with straight, slightly concave or convex sides and wide-rounded corners. Distal and proximal surfaces are microverrucate in *S. quinata*, *S. lobbiana*,

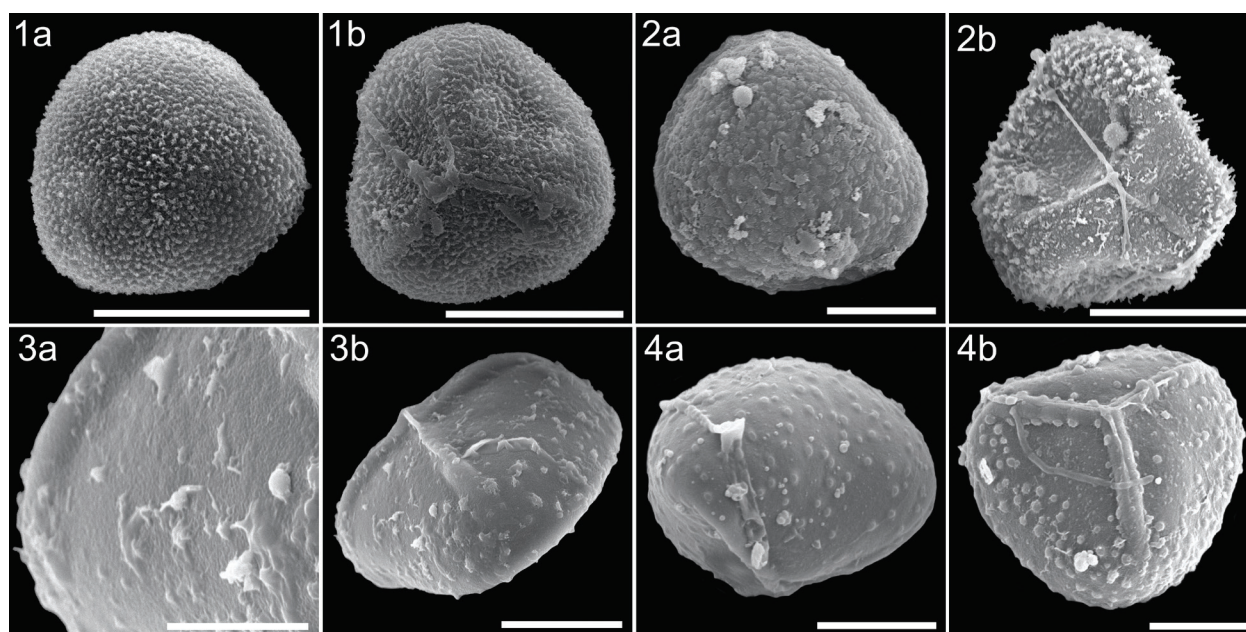


Fig. 1. SEM-micrographs of the spores of *Austrogramme* E. Fourn.: 1 – *Austrogramme boerlageana* (Alderw.) Hennipman: a – distal side; b – proximal side; 2 – *Austrogramme decipiens* (Mett.) Hennipman: a – distal side; b – proximal side; 3 – *Austrogramme francii* (Rosenst.) Hennipman: a – fragment of equatorial-proximal side of spore and laesura arms, b – spore in equatorial-proximal position; 4 – *Austrogramme marginata* (Mett.) E. Fourn.: a – spore in equatorial-distal position, b – proximal side. 1a, 1b, 2b – 20 μm ; 2a, 3b, 4a, 4b – 10 μm ; 3a – 5 μm .

Table 1

The main spore features in *Austrogramme*, *Syngamma*, and *Taenitis* species

Species / Status / Distribution	Form of spore in polar position	Cingulum	Laesural ridge	Distal face ornamentation	Proximal face ornamentation	Rodlets	Granular deposits
<i>Austrogramme boerlageana</i> * / Accepted / Maluku	nearly roundish	–	–	microverrucate, with dense regular verrucae	microverrucate, with dense regular microverrucae	–	dense on both sides
<i>Austrogramme decipiens</i> / Accepted / New Caledonia, Vanuatu	triangular-roundish	–	–	microverrucate, with dense regular microverrucae	microverrucate, with dense regular microverrucae	scattered in proximal side	
<i>Austrogramme francii</i> / Accepted / New Caledonia	roundish-triangular	–	–	verrucate, with irregular scattered verrucae	verrucate, with irregular scattered verrucae	–	scattered on both sides
<i>Austrogramme marginata</i> / Accepted / New Caledonia	triangular-roundish	–	entire, with small tubercles	verrucate, with scattered verrucae	verrucate, with scattered verrucae	–	rare on both sides
<i>Syngamma alismifolia</i> * / Accepted / Borneo, Cambodia, Jawa, Malaya, Maluku, Nicobar Is., Philippines, Sulawesi, Sumatera, Thailand, Vietnam	roundish-triangular	–	–	microverrucate	microverrucate	scattered	–
<i>Syngamma borneensis</i> / Accepted / Bismarck Archipelago, Borneo, Caroline Is., Fiji, Malaya, Solomon Is., Sulawesi	triangular	–	–	tuberculate	smooth	–	–
<i>Syngamma cartilagidens</i> / Accepted / Borneo, Malaya	triangular	–	–	tuberculate, with tubercles fused in ridges parallel spore sides	tuberculate	–	–
<i>Syngamma grandis</i> / Accepted / New Guinea	nearly roundish	–	–	microverrucate	microverrucate	–	–
<i>Syngamma quinata</i> * / Accepted / Borneo, Maluku, New Guinea, Santa Cruz Is., Solomon Is., Sulawesi, Sumatera, Vanuatu	roundish-triangular	–	narrow, entire	microverrucate, with dense microverrucae	microverrucate, with scattered microverrucae	–	–
<i>Syngamma lobbiana</i> * / Accepted / Borneo	roundish-triangular	–	–	microverrucate	microverrucate	scattered	–

Table 1 (continuation)

Species / Status / Distribution	Form of spore in polar position	Cingulum	Laesural ridge	Distal face ornamentation	Proximal face ornamentation	Rodlets	Granular deposits
<i>Syngamma spathulata</i> / Accepted / Fiji, Solomon Is.	roundish-triangular	–	–	microverrucate	microverrucate	scattered	–
<i>Syngamma wallichii</i> / Accepted / Borneo, Malaya, Maluku, Philippines, Sulawesi, Sumatera	roundish-triangular	–	–	microverrucate	microverrucate	scattered, appressed to the surface	–
<i>Taenitis blechnoides</i> * / Accepted / Bismarck Archipelago, Borneo, Cambodia, Caroline Is., Hainan, Laos, Lesser Sunda Is., Malaya, Maluku, Myanmar, New Guinea, Nicobar Is., Northern Territory, Philippines, Australia (Queensland), Solomon Is., Sri Lanka, Sulawesi, Sumatera, Thailand, Vietnam	triangular, with concave sides and rounded corners	continuous, slightly undulate	–	densely tuberculate, with low, small, discrete tubercles	densely tuberculate, with low, small, discrete tubercles	fascicled rodlets above tubercles	–
<i>Taenitis cordata</i> / Accepted / Philippines, Sulawesi	triangular-roundish	continuous, entire	broad, entire	rugate, with low sinuous rugae	rugate, with low sinuous rugae	–	scattered
<i>Taenitis diversifolia</i> / Accepted / Australia (Queensland), Solomon Is., Vanuatu	triangular	continuous, entire	–	densely tuberculate	densely tuberculate	dense fascicled rodlets associated with tubercles and dense rodlets on the cingulum margin	–
<i>Taenitis hookeri</i> * / Accepted / Bismarck Archipelago, Borneo, Fiji, New Guinea, Solomon Is.	roundish-triangular, with concave sides and rounded corners	–	formed by fused or coalescent tubercles with verrucae between laesural ridge and laesura arms	densely baculate	densely baculate	rodlets associated with tubercles	–

Table 1 (end)

Species / Status / Distribution	Form of spore in polar position	Cingulum	Laesural ridge	Distal face ornamentation	Proximal face ornamentation	Rodlets	Granular deposits
<i>Taenitis interrupta</i> / Accepted / Assam, Bangladesh, Borneo, Malaya, Sulawesi, Thailand	triangular	continuous, entire	–	densely tuberculate-rugate	densely tuberculate-rugate	rodlets on tubercles	–
<i>Taenitis luzonica</i> / Not accepted, Synonym of <i>Austrogramme luzonica</i> (Alderw.) M. Kato. / Philippines	triangular	continuous, entire	–	tuberculate with low tubercles	tuberculate with low tubercles	dense rodlets covered the spore surface and cingulum	–
<i>Taenitis obtuse</i> / Accepted / Borneo	triangular-roundish	undulate, interrupted in the corners	–	densely tuberculate	densely tuberculate	dense fascicled rodlets associated with tubercles	–
<i>Taenitis pinnata</i> * / Accepted / Fiji, Northern Territory, Western Australia	roundish-triangular	–	formed by fused or coalescent tubercles	densely tuberculate	densely rugulate-tuberculate	sparse rodlets associated with tubercles	–
<i>Taenitis requiniana</i> / Accepted / Malaya, Maluku, New Guinea, Sulawesi, Vanuatu	triangular-roundish	continuous, entire	–	densely tuberculate	densely tuberculate	dense fascicled rodlets associated with tubercles and sparse rodlets on the cingulum margin	–

Table 2

Size of spores and their elements in *Austrogramme*, *Syngramma*, and *Taenitis* species, mean (min–max)

Species	Equatorial diameter, μm	Polar axis, μm	Laesura length, μm	Laesura width, μm	Cingulum width, μm
<i>Austrogramme boerlageana</i> *	26.0 (22.5–29.4)	ND	13.2 (11.8–14.4)	0.8 (0.6–1.1)	–
<i>Austrogramme decipiens</i>	27.7 (22.8–31.2)	ND	12.8 (12.1–13.6)	0.7 (0.6–0.9)	–
<i>Austrogramme francii</i>	24.8 (23.0–36.7)	15.8 (14.8–16.8)	9.6 (8.9–10.5)	0.7 (0.6–0.9)	–
<i>Austrogramme marginata</i>	24.8 (23.4–25.9)	19.2 (18.5–20.0)	11.5 (10.7–12.4)	0.4 (0.3–0.6)	–
<i>Syngramma alismifolia</i> *	31.9 (29.8–33.4)	24.8 (24.2–25.3)	7.6 (6.9–8.3)	0.7 (0.4–0.9)	–
<i>Syngramma borneensis</i>	30.8 (28.0–33.0)	28.0 (27.6–28.3)	11.7 (10.8–11.4)	1.13 (1.0–1.3)	–
<i>Syngramma cartilagidens</i>	30.9 (30.3–32.3)	28.4 (26.5–30.1)	15.6 (14.6–16.7)	0.8 (0.3–1.1)	–
<i>Syngramma grandis</i>	27.3 (26.0–30.5)	24.9 (23.6–26.2)	10.8 (9.3–12.5)	0.7 (0.6–0.8)	–
<i>Syngramma quinata</i> *	28.2 (25.4–29.8)	23.4 (21.2–25.5)	8.7 (7.5–10.2)	0.4 (0.2–0.7)	–
<i>Syngramma lobbiana</i> *	33.9 (31.2–35.5)	24.3 (23.3–25.0)	10.5 (8.6–12.6)	0.7 (0.4–1.0)	–
<i>Syngramma spathulata</i>	37.3 (34.2–40.8)	27.1 (26.4–27.8)	18.2 (16.6–21.7)	2.3 (1.9–2.6)	–
<i>Syngramma wallichii</i>	31.5 (30.3–33.8)	28.3 (27.6–29.0)	17.7 (16.5–19.2)	1.0 (0.5–1.4)	–
<i>Taenitis blechnoides</i> *	40.4 (39.0–42.7)	26.2 (25.5–27.7)	14.7 (13.8–16.0)	1.0 (0.8–1.1)	ND
<i>Taenitis cordata</i>	51.3 (49.5–54.8)	40.3 (38.5–42.2)	17.6 (16.4–18.5)	1.2 (1.0–1.4)	7.8 (6.5–9.2)
<i>Taenitis diversifolia</i>	41.5 (38.5–44.9)	33.2 (31.9–34.6)	15.8 (14.6–17.0)	1.0 (0.7–1.2)	2.9 (1.8–3.7)
<i>Taenitis hookeri</i> *	31.0 (30.2–32.4)	24.4 (23.5–25.6)	3.1 (2.1–4.6)	0.6 (0.5–0.7)	–
<i>Taenitis interrupta</i>	44.6 (41.8–47.9)	33.4 (32.5–34.2)	16.7 (14.4–21.4)	0.8 (0.6–1.0)	2.9 (2.0–3.7)
<i>Taenitis luzonica</i>	40.9 (37.1–45.4)	24.4 (22.2–26.5)	19.9 (16.4–21.8)	1.6 (1.5–1.9)	8.8 (8.0–9.4)
<i>Taenitis obtusa</i>	41.9 (37.0–46.3)	31.7 (29.4–33.6)	13.9 (12.2–15.1)	0.9 (0.5–1.2)	3.1 (2.3–4.0)
<i>Taenitis pinnata</i> *	26.5 (24.0–29.0)	28.4 (27.5–29.2)	10.3 (10.1–10.5)	0.9 (0.8–1.0)	–
<i>Taenitis requiniana</i>	41.8 (40.1–43.8)	32.6 (31.7–33.9)	16.2 (15.4–17.5)	1.0 (0.8–1.2)	2.8 (2.3–3.2)

Note: ‘–’ means lack of the feature; ND – no data; an asterisk indicates the species with published data for spore size (Vaganov et al., 2018).

S. spatulata, and *S. wallichii*, microrugulate in *S. lobbiana*. Spores of *S. grandis* have microrugulate distal face and microverrucate proximal one. The spores of *S. borneensis* and *S. cartilagidens* have the most distinctive sculpture. The distal surface of spores of both species is low-tuberculate with regular tubercles 1.4–3.9 μm in diam.; in spores of *S. cartilagidens*, tubercles fused in three ridges situated parallel spore sides. The proximal surface of spores of *S. cartilagidens* is tuberculate with irregular tubercles 1.4–2.3 μm in diam.; proximal side of *S. borneensis* is smooth. Spores of only one species – *S. quinata* – have laesura arms immersed

in the narrow laesural ridges that are reached to the spore corners. Surface of spores of *S. lobbiana*, *S. spatulata*, and *S. wallichii* are covered by scattered rodlets. Laesura arms are straight, reaching the spore corners, longest in *S. spathulata* and *S. wallichii* and shortest in *S. alismifolia* and *S. quinata* (Fig. 2–3; Table 1). The equatorial diameter of *Syngramma* spores ranges between 27 μm to 40.8 μm , polar axis – between 21 μm to 30 μm . The smallest spores are characteristic to *S. grandis* and *S. quinata*, the largest – to *S. lobbiana* and *S. spathulata* (Table 2).

Spores of *Taenitis* species in equatorial view have more or less flattened or depressed (in

T. cordata) proximal part and mostly hemispherical distal part; spores of *T. hookeri* and *T. pinnata* are nearly globose. Three of the most noticeable features are characteristic for the *Taenitis* spores: cingulum, laesural ridges and tuberculate surface (Fig. 4–5). Seven of nine studied species have spores with cingulum: *T. blechnoides*, *T. cordata*, *T. diversifolia*, *T. interrupta*, *T. luzonica*, *T. obtusa*, and *T. requiniana*. Cingulum in spores of most

species is continuous, variable in width, sometimes narrower at the corners, undulate (*T. obtusa*), or entire (remaining species). The widest cingulum is characteristic for *T. luzonica* (8.0–9.4 μm), cingulum in *T. cordata* spores is wide (6.5–9.2 μm) and thick (in equatorial view) (Fig. 4–5, Table 2). Spores of *T. hookeri* and *T. pinnata* are non-cingulate. Spores of three species have the prominent laesural ridges, entire in *T. cordata* and interrupted, formed by

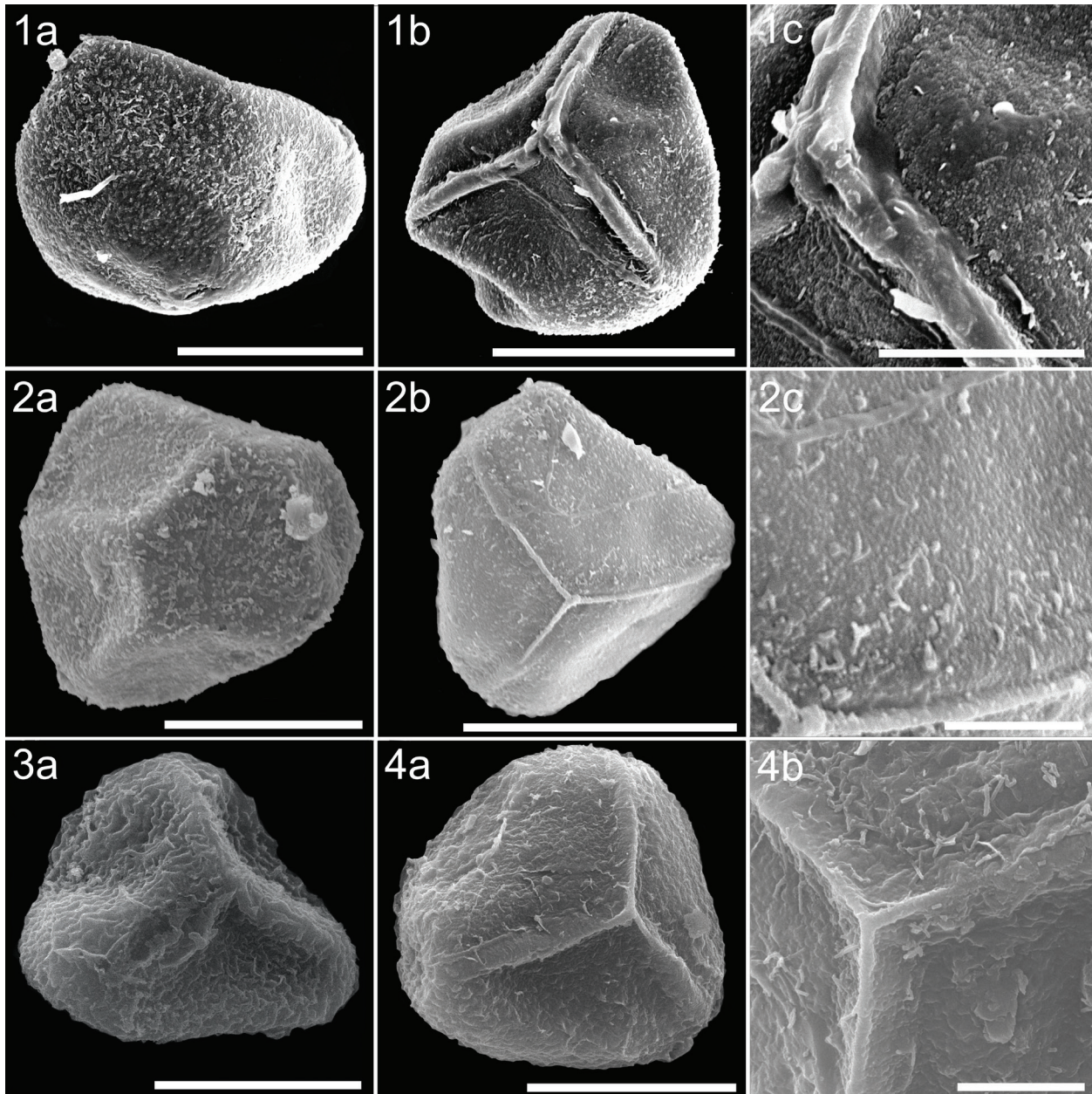


Fig. 2. SEM-micrographs of the spores of *Syngamma* J. Sm.: 1 – *Syngamma borneensis* (Hook.) J. Sm.: a – distal side; b – proximal side; c – fragment of proximal side of spore and laesura arms; 2 – *Syngamma cartiligidens* (Baker) Diels: a – distal side; b – spore in proximal-equatorial position; c – fragment of proximal side of spore and laesura arms; 3 – *Syngamma grandis* (Copel.) C. Chr.: a – distal side; b – proximal side; c – fragment of proximal side of spore and laesura arms; 4 – *Syngamma quinata* (Hook.) Carruth.: a – distal side; b – proximal side; c – fragment of proximal side of the spore and laesura arms. 1a, 1b, 2a, 2b, 3a, 3b, 4a, 4b – 20 μm ; 1c, 2c, 3c, 4c – 5 μm .

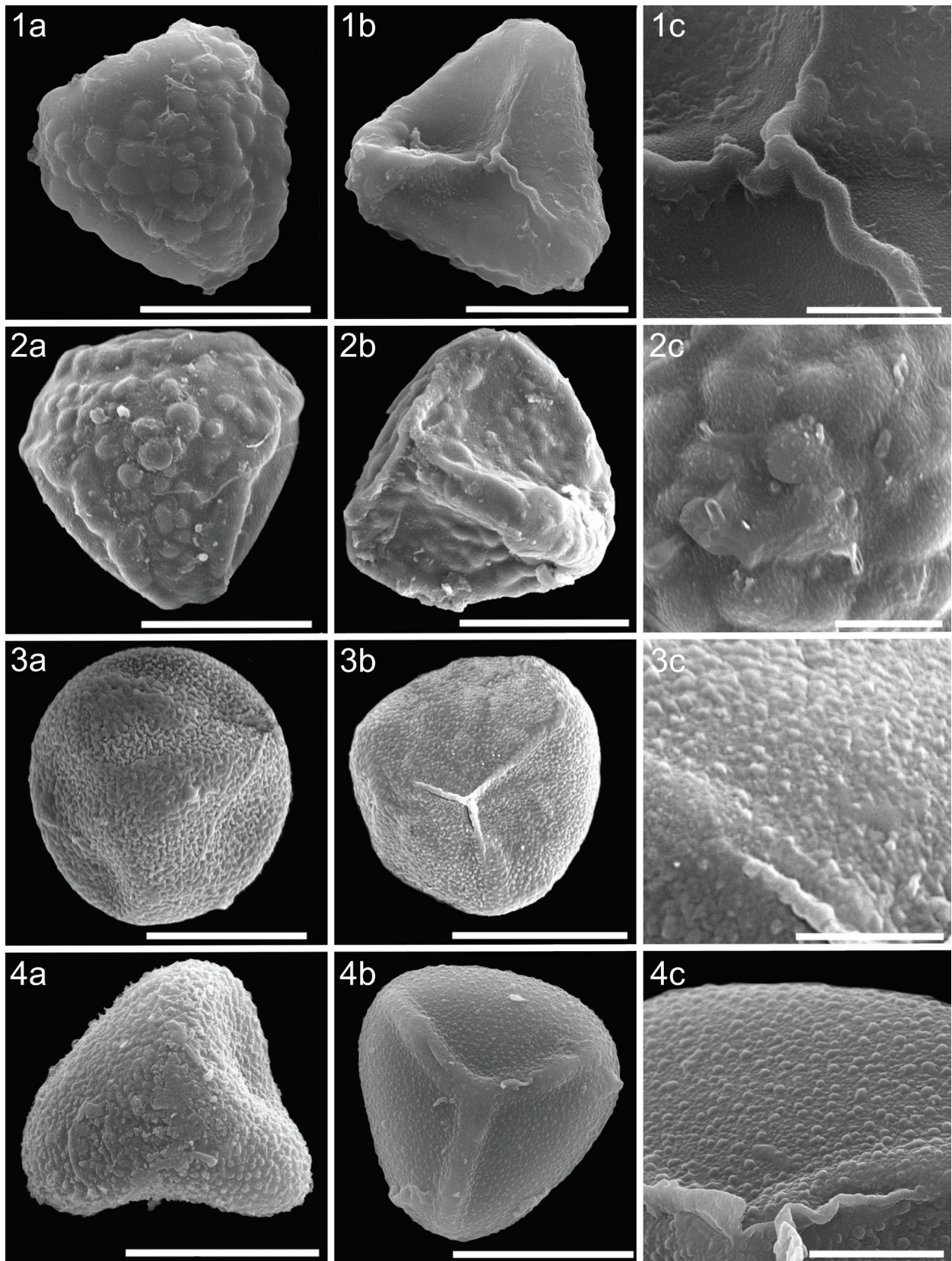


Fig. 3. SEM-micrographs of the spores of *Syngamma* J. Sm.: 1 – *Syngamma spatulata* (C. Chr.) Holttum: a – spore in equatorial position; b – spore in proximal-equatorial position; c – fragment of proximal side of spore and laesura arms; 2 – *Syngamma wallichii* (Hook.) Bedd: a – distal side; b – proximal side; c – fragment of proximal side of spore and laesura arms; 3 – *Syngamma alismifolia* (C. Presl) J. Sm.: a – spore in proximal-equatorial position; 4 – *Syngamma lobbiana* (Hook.) J. Sm.: a – spore in proximal-equatorial position; b – fragment of proximal side of spore and laesura arms. 1b, 2b – 30 μm ; 1a, 2a, 3a, 4a – 20 μm ; 1c – 10 μm ; 2c, 4b – 5 μm .

arranged in the rows fused tubercles in spores of *T. hookeri* and *T. pinnata*. Ornamentation of distal and proximal surfaces in spores of most species is densely tuberculate, in spores of *T. hookeri* – baculate, in spores of *T. interrupta* and *T. pinnata* – tuberculate-rugate, and in *T. cordata* – rugate (Fig. 4–5). The most conspicuous character of the ornamentation of spore surfaces is the presence of rodlets associated with tubercles: rodlets are mostly fused in tufts and situated on the top of tubercles.

The most visible and dense rodlets are characteristic for spores of *Taenitis diversifolia*, *T. luzonica*, *T. obtusa*, *T. requiniana*; in *T. diversifolia*, rodlets fused in tufts and associated with the top of tubercles form especially expressed regular net (Fig. 5). The low-tuberculate surface in *T. luzonica* spores is densely covered mostly by adpressed rodlets. Cingulum may be smooth (*T. blechnoides*, *T. cordata*, *T. interrupta*) or covered by dense rodlets (*T. luzonica*); in *T. diversifolia* and

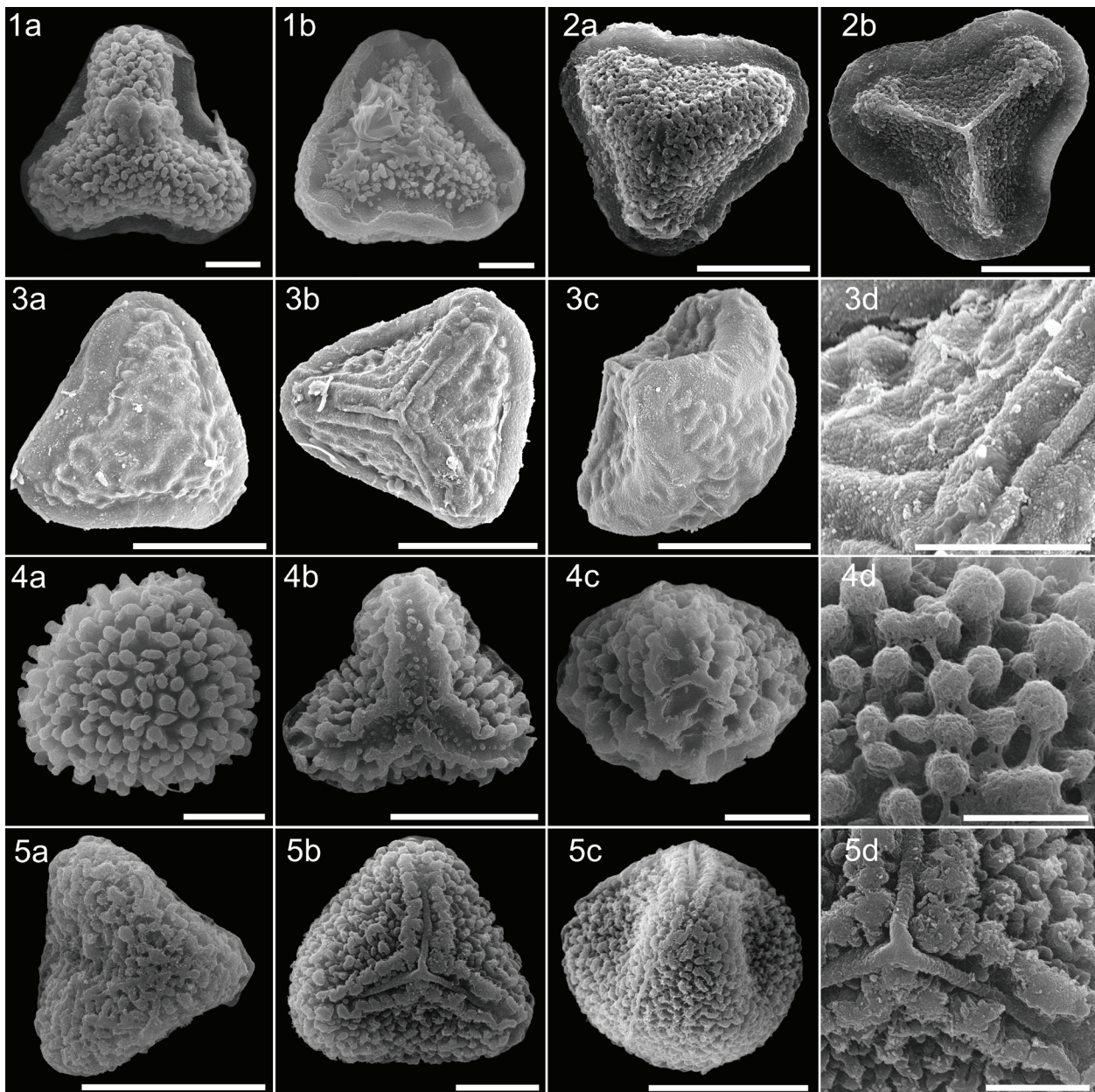


Fig. 4. SEM-micrographs of the spores of *Taenitis* Willd. ex Schkuhr: 1 – *Taenitis blechnoides* (Willd.) Sw.: a – distal side; b – proximal side; 2 – *Taenitis interrupta* Hook. et Grev.: a – distal side; b – proximal side; 3 – *Taenitis cordata* (Gaudich.) Holttum: a – distal side; b – proximal side; c – spore in equatorial-proximal position; d – fragment of equatorial-proximal side of spore and laesura arms; 4 – *Taenitis hookeri* (C. Chr.) Holttum: a – distal side; b – proximal side; c – spore in equatorial position; d – fragment of distal side of spore and laesura arms; 5 – *Taenitis pinnata* (J. Sm.) Holttum: a – distal side; b – proximal side; c – spore in equatorial position; d – fragment of proximal side of spore and laesura arms. 1a, 1b, 3d, 4a, 4c, 5b – 10 μm ; 2a, 2b, 4b, 5a, 5c – 20 μm ; 3a, 3b, 3c – 30 μm ; 4d, 5d – 5 μm .

T. requiniana, rodlets situated also on the cingulum margin. Laesura arms are prominent in spores of *T. interrupta* and *T. luzonica* and are depressed and obscured by dense rodlets in spores of *T. blechnoides*, *T. diversifolia*, *T. obtusa*, and *T. requiniana* (Fig. 4–5). Spores of *Taenitis* species are larger than spores of *Austrogramme* and *Syngramma*, equatorial diameter ranges in most species between 40 and 51 μm on average, polar axis – from 24 to 40 μm . Two species – *Taenitis hookeri* and *T. pinnata* – have small spores, 26–31 \times 26–28 μm on average (Table 2).

On the whole, our examination of four species of *Austrogramme*, seven species of *Syngramma*, and nine species of *Taenitis* showed that *Syngramma* and *Austrogramme* are very similar to each other in the spore shape and ornamentation and very different in these spore characteristics of *Taenitis* species. *Syngramma* and *Austrogramme* have simple spores with a weakly expressed ornamentation (microverrucate or microrugulate sculpture). Only two species of *Syngramma* have spores with low-tuberculate ornamentation. In comparison with spores of *Syngramma* and *Austrogramme*, spores of *Taenitis* species have a more complex structure and noticeable ornamentation: the presence of cingulum, laesural ridges and a very clear tuberculate (as an option – baculate) or rugate sculpture.

Other authors who studied the spores of *Austrogramme*, *Syngramma*, and *Taenitis* indicated the same characters for the same and other species of these genera. E. Hennipman (1975) emphasized that spores of *Taenitis* are very different from those in *Austrogramme* and *Syngramma*, and are of two kinds either with or without a cingulum. A. Tryon and B. Lugardon (1991) described the similar features for spores of these genera. Furthermore, E. Hennipman (1975) considered that differences in chromosome number in *Taenitis* are associated with the presence or absence of a cingulum. On the basis of the spore morphology and chromosome number, E. Hennipman (1975) considered that *Syngramma* is distinguished from *Taenitis* and related with *Austrogramme*; A. Tryon et. B. Lugardon (1991) supported this disposition. Published data indicate a comparatively larger spore size than the ones we found. E. Hennipman (1975) indicated larger spore size for all studied genera: 45–70 μm for *Taenitis*, 40–50 μm for *Syngramma*, and 35–40 μm for *Austrogramme*. A. Tryon and B. Lugardon (1991) reported the spore size for the *Taenitis* and *Syngramma* species as 33–53 μm , for *Austrogramme* – 30–40 μm . Spores of species not involved in

our studies have features specific for the species of the corresponding genera. Judging by the published photos, *Austrogramme asplenioides* (Holttum) Hennipman has simple spores with microverrucate surface and granular deposits on it (Hennipman, 1975), spores of *T. hosei* (Baker) Holttum lack a cingulum. Based on the properties of the spores and chromosome numbers, E. Hennipman (1975) indicated the relationship between *Austrogramme* and *Syngramma*; the relationship between *Austrogramme* and *Taenitis* seems less obvious, also in view of the variation of the paraphyses in the three genera studied. Based on leaf morphology, M. Kato (1993) considered *Taenitis pinnata* as the most primitive; the other species represent different lines of reduction and specialization.

According to database “POWO: Plants of the world online” (POWO. URL: <http://powo.science.kew.org/>), all studied species except *Taenitis luzonica* are now accepted, disagreements exist only in relation to *Taenitis luzonica*: the name *T. luzonica* is considered as a synonym of the name *Austrogramme luzonica* (Alderw.) M. Kato. This species was described as *Syngramma luzonica* Alderw. (1920). R. E. Holttum (1975) transferred it from *Syngramma* to *Taenitis* (*T. luzonica*), and M. Kato (1988) considered it as belonging to *Austrogramme* (*A. luzonica*). On the whole, spore morphology of three studied genera is congruent with the result of molecular-phylogenetic studies (Sánchez-Baracaldo, 2004; Cochran et al., 2014; Zhang et al., 2015, 2017), which shows the close relationship between *Syngramma* and *Austrogramme* and the position of *Taenitis* as a sister to *Syngramma* and *Austrogramme* (together) in the collective clade (*Syngramma* – *Austrogramme* – *Taenitis*). *Taenitis luzonica* was not involved in molecular-phylogenetic studies, but by the morphology of spores, it is closer to other *Taenitis* species than to species of *Syngramma* or *Austrogramme*. So we support the opinion of R. E. Holttum (1975) that this taxon belongs to *Taenitis* (*T. luzonica*).

The spore morphology of all investigated genera is consistent with the division into sections suggested by R. E. Holttum (1975) for *Syngramma* and *Taenitis* and by E. Hennipman (1975) for *Austrogramme*. The *Syngramma* species of the section *Syngramma* (*S. alismifolia*, *S. lobbiana*, *S. spathulata*, *S. wallichii*, *S. guinata*) have spores with poorly expressed sculpture, whereas *S. borneensis* and *S. cartiligidens* belonging to the section *Toxopteris* (Trev.) C. Chr. have the distinct low-tuberculate sculpture. The *Taenitis* species belonging to the

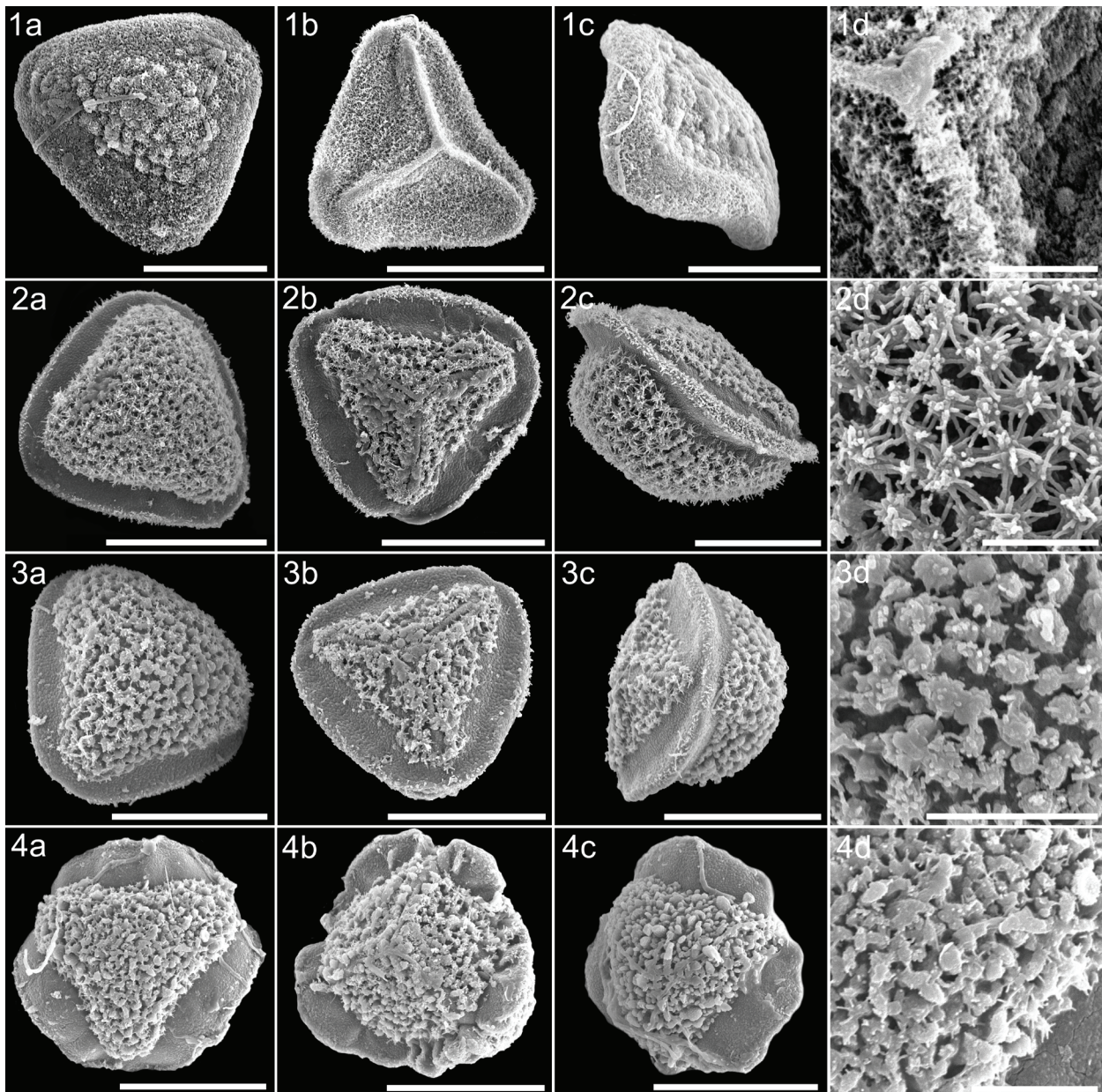


Fig. 5. SEM-micrographs of the spores of *Taenitis* Willd. ex Schkuhr: 1 – *Taenitis luzonica* (Alderw.) Holttum: a – distal side; b – spore in proximal-equatorial position; c – spore in equatorial-distal position; d – fragment of proximal side of spore and laesura arms; 2 – *Taenitis diversifolia* Holttum: a – distal side; b – proximal side; c – spore in equatorial position; d – fragment of distal side of spore and laesura arms; 3 – *Taenitis requiniana* (Gaudich.) Copel.: a – distal side; b – proximal side; c – spore in equatorial position; d – fragment of distal side of spore and laesura arms; 4 – *Taenitis obtusa* Hook.: a – distal side; b – proximal side; c – spore in distal-equatorial position; d – fragment of distal side of spore and laesura arms. 1a, 1c, 2c – 20 μm ; 1b, 2a, 2b, 3a, 3b, 3c, 4a, 4b, 4c – 30 μm ; 3d, 4d – 10 μm ; 1d, 2d – 5 μm .

section *Taenitis* (*T. blechnoides*, *T. interrupta*, *T. obtusa*) have spores with cingulum close in width, without laesural ridges. Spores of *T. hookeri* and *T. pinnata* belonging to the section *Loxodictyum* Holttum lack cingulum but have interrupted laesural ridges formed by arranged in rows fused tubercles. The only one species – *Taenitis luzonica* – attributed by R. E. Holttum (1975) to the section *Loxodictyum* did not correspond in the spore morphology to other

species of this section: its spores have relatively wide cingulum, but lack laesural ridges, the entire surface of the spore including cingulum is densely covered with rodlets. The members of the section *Platytaenia* (Kuhn) Holttum – *T. requiniana* and *T. diversifolia* – have very similar spores with cingulum, densely tuberculate sculpture, and dense fascicled rodlets associated with tubercles and situated on the cingulum margin as well. *Taenitis*

cordata (section *Schizolepton* (Fée) Holttum) have spores with cingulum, entire laesural ridges, rugate sculpture, and scattered granular deposits rather than rodlets. Species of *Austrogramme* belonging to different sections have not so well-expressed differences in the spore morphology. Species from type section (*A. fancii* and *A. marginata*) have the smallest spores with scattered verrucae whereas species from the section *Asplenopsis* (Kuhn) Hennisman (*A. boerlageana* and *A. decipiens*) have spores with dense regular disposed microverrucae. As shown by E. Hennisman (1975), spores of *A. asplenioides* have the same sculpture.

Conclusion

The results of this study confirm the diagnostic value of the spore morphology for the phylogeny and taxonomy of three fern genera – *Austrogramme*, *Syngramma*, and *Taenitis*. Spores of *Austrogramme* and *Syngramma* are the simplest in ornamentation and similar to each other, whereas spores of the *Taenitis* species are very different from spores of *Austrogramme* and *Syngramma*. This corresponds to molecular-phylogenetic studies according to

which *Austrogramme* and *Syngramma* have a closer relationship to each other, and *Taenitis* takes a sister position to both of them. Differences in the spore morphology correlate with the division of genera into sections.

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Specimens investigated

- Austrogramme boerlageana*** (Alderw.) Hennisman: Ambon 1939 (PE, № 01715225).
- Austrogramme decipiens*** (Mett.) Hennisman: Sector OCE (Oceania). № 1608. Mont Humboldt (Nouvelle Calédonie). 12 octobre 1869 (P, P01577226).
- Austrogramme francii*** (Rosenst.) Hennisman: Sector OCE (Oceania). New Caledonia. Forêt de Tao. Coll.: Franc. № 1427. 1910-1. Alt. 500 (P, TYPE, P00607896).
- Austrogramme marginata*** E. Fourn.: Sector OCE (Oceania). New Caledonia. Bords des ruisseaux à Balade. Coll.: E. Vieillard. № 1642. 1855/1860 (P, ISOTYPE, P00607898).
- Syngamma alismifolia*** (C. Presl) J. Sm.: Borneo E., 1953 (PE, № 01715222).
- Syngamma borneensis*** (Hook.) J. Sm. Malaysia, Sarawak. № 56 (PE, № 01715227).
- Syngamma cartilagineus*** (Baker) Diels: Sector OCE (Oceania). Borneo. Indonesia. Banting, Sarawak, Borneo. Coll.: Christ. 1919-2-9 (P, P01319602); dt.: 1936/05/31. Tokone. Kota Tinggi. Malay Peninsula. Kota Tinggi. 31.05.36 (PE, № 01715228).
- Syngamma grandis*** (Copel.) C. Chr.: Sector OCE (Oceania). Solomon. Bougainville Island: Kugumaru, Buin. Coll.: S. F. Kajewski. № 1869. 1930-6-28. Alt. 150 (P, P01313719).
- Syngamma quinata*** (Hook.) Carruth.: № 6943. V. Guinen Japen, № 01715087; Selebes, G. Kjellberg, 1939, 500

alt. (PE, № 01715234).

Syngramma lobbiana (Hook.) J. Sm.: № 933 Native collector. Plants of Sarawak, Borneo. Collected through the Museum for the Bureau of Science, Manila, P. I. (PE, № 01715231).

Syngramma spathulata (C. Chr.) Holttum: Sacteur ASI (Asie). Jamindan Capiz Province Panay. № 31307. Coll.: M. Ramos, G. Edano. April-May 1918 (P, P01398822).

Syngramma wallichii (Hook.) Bedd. Sacteur ASI (Asie). Cagayan Prov., Luzon. Coll.: Maximo Ramos. Mar. 1909 (P, P01398821).

Taenitis cordata (Gaudich.) Holttum: Sector ASI (Asia). Indonesia, Rawak. 1823. Coll.: C. Gaudichaud. (P, P00607823).

Taenitis blechnoides (Willd.) Sw.: Hainan. Shan Mong, Fairly common: dry, gentle slope, clay, thicket, erect. Coll. Lau S. K., Det. E. D. Merrill, Dec. 23, 1933. № 2935 (LE).

Taenitis diversifolia Holttum: Sector OCE (Oceania). №4881. Alt. 100 ft. Maramasike. A. F. Braithwaite 26.11.1965 (P, P01482652).

Taenitis hookeri (C. Chr.) Holttum: Plants of Netherlands New Guinea. 1200 m alt. Feb. 1939 (PE, № 01715229).

Taenitis interrupta Hook. et Grev.: Indonesia. Coll.: A. H. G. Alston. № 13127. dt.: 1954/01/20 (PE, № 01595231).

Taenitis luzonica (Alderw.) Holttum: Sector ASI (Asia). Philippines. Guinayangan, province of Tayabas, Luzon. L. Escritor. 1913-3 (P, P01308663).

Taenitis obtusa Hook.: Sector ASI (Asia) (P, P01467801).

Taenitis pinnata (J. Sm.) Holtt.: Plants of Papua (British New Guinea) Lake Daviumbu. Rain forest. August, 1936 (PE, № 01715232).

Taenitis requiniana (Gaudich.) Copel.: Sector ASI (Asia). Indonesia, Rawak. Coll.: C. Gaudichaud. (P, P00607819).