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Spore morphology of *Taenitis*, *Syngramma* and *Austrogramme* species (*Pteridoideae*, *Pteridaceae*) from South-Eastern Asia

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Summary. A comparative study of spores of seven species: *Taenitis blechnoides* (Willd.) Sw., *T. hookeri* (C. Chr.) Holttum, *T. pinnata* (J. Sm.) Holttum, *Syngramma alismifolia* (Presl) J. Sm., *S. lobbiana* (Hook.) J. Sm., *S. quinata* (Hook.) Carruth., and *Austrogramme boerlageana* (Alderw.) Hennipman from South-Eastern Asia was performed using the method of scanning electronic microscopy (SEM). Spores of all examined species are trilete, tetrahedral or tetrahedral-globose. Spores of *Syngramma* and *Austrogramme* are very similar to each other in shape and ornamentation. Ornamentation of both sides of spore is similar, verrucate (microverrucate), surface covered by rodlets and granulate deposits. Spores of *Taenitis* species with conspicuous cingulum (*Taenitis blechnoides*) or without it, ornamentation of both faces of spore could be tuberculate or baculate. Spores of *Taenitis hookeri* and *Taenitis pinnata* demonstrate tendency to forming of commissural ridges. Spore size of all studied species is close: equatorial diameter of spores of *Taenitis* species varies within 24–43 µm, those for *Syngramma* species is 29.8–35.5 µm, spores of *Austrogramme boerlageana* are smallest, their equatorial diameter varies within 22.5–29.4 µm.

Морфология спор *Taenitis*, *Syngramma* и *Austrogramme* (*Pteridoideae*, *Pteridaceae*) из Юго-Восточной Азии

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

Аннотация. Методом сканирующей электронной микроскопии (СЭМ) проведено сравнительное исследование спор *Taenitis blechnoides* (Willd.) Sw., *T. hookeri* (C. Chr.) Holttum, *T. pinnata* (J. Sm.) Holttum, *Syngramma alismifolia* (Presl) J. Sm., *S. lobbiana* (Hook.) J. Sm., *S. quinata* (Hook.) Carruth. и *Austrogramme boerlageana* (Alderw.) Hennipman из Юго-Восточной Азии. Споры всех исследованных видов трехлучевые, тетраэдрические или округло-тетраэдрические. Споры *Syngramma* и *Austrogramme* сходны по форме и характеру поверхности. Скульптура обеих сторон спор бородавчатая (до мелко-бородавчатой), с гранулами на поверхности. Споры *Taenitis* с хорошо выраженной экваториальной складкой (*Taenitis blechnoides*) или без нее, скульптура обеих сторон спор бугорчатая. Споры *Taenitis hookeri* и *Taenitis pinnata* проявляют тенденцию к формированию комиссуральных складок путем слияния бугорков, расположенных вдоль лучей лезуры. Размеры спор всех исследованных видов близки: экваториальный диаметр спор видов *Taenitis* варьирует в пределах 24–43 мкм, у видов *Syngramma* – 29,8–35,5 мкм, споры *Austrogramme boerlageana* самые мелкие, их экваториальный диаметр варьирует в пределах 22,5–29,4 мкм.

Taenitis Willd. ex Schkuhr, *Syngamma* J. Sm. and *Austrogramme* E. Fourn. are paleotropical genera, which belong to taenitidoid ferns, and are classified as the members of *Taenitideae* tribe and *Taenitidoideae* R. M. Tryon subfamily of the large and diverse Pteridaceae E. D. M. Kirchn. family, or considered as distinct Taenitidaceae (C. Presl) Pic. Serm. family (Pichi Sermolli, 1977; Tryon, 1986; Tryon et al., 1990; Sánchez-Baracaldo, 2004; Smith et al., 2006). 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. E. Schuettpelz et al. (2007) considered them as the members of the pteridoid ferns within the Pteridaceae. However, R. E. Holttum, who studied the relationship between *Taenitis* and *Syngamma*, wrote “feel sure that *Syngamma* and *Taenitis* both belong to the Gymnogrammeoid ferns” (Holttum, 1975, p. 341).

R. E. Holttum (1975) recognized in *Syngamma* 17 species, including 6 species of *Craspedodictium*, that he transferred to this genus. *Austrogramme* includes five species (Hennipman, 1975). These species occur in South-Eastern Asia and Oceania on the Pacific islands and islands of Indian Ocean (Philippines, Borneo, Fiji, Malaya, New Guinea, Java, Sumatra, New Caledonia). *Taenitis* includes about 15 species occurring in Old World from India and Ceylon northward to China (Hainan Island), throughout Malesia eastward to New Guinea, southward to northern Australia (Queensland), and to Fiji in the Pacific (Holttum, 1975; Tryon, Lugardon, 1991).

Recently molecular-phylogenetic studies based on plastid DNA involving discussed genera were conducted. One of them carried out by P. Sánchez-Baracaldo (2004) based on sequences of *rps4* region of plastid DNA demonstrates the close relationship between these three Old World genera, which form clade with *Taenitis* being basal to *Syngamma* and *Austrogramme*. Two species of *Taenitis* (*T. blechnoides* (Willd.) Sw. and *T. interrupta* Hook. et Grev.) were included in the molecular analysis of *Taenitidoideae* (9 species) based on four single-gene datasets (*atpA*, *chlL*, *rbcL*, and *rps4*). The combined analysis shows the relationship between *Austrogramme*, *Syngamma*, and *Taenitis*, and places a new genus *Tryonia* sister to them (collectively) (Cochran et al., 2014). Five species of *Pteridoideae* including two species (with seven patterns) of *Taenitis*, two species of *Austrogramme*, and single species of *Syngamma* were involved in the molecular-phylogenetic study based on six plastid

regions (the *atpA* gene, the *atpB* gene, the *rbcL* gene, the *rps4* gene and *rps4-trnS* intergenic spacer, the *trnL* intron, and the *trnL-F* intergenic spacer). The monophyly of the Old World *Austrogramme* – *Syngamma* – *Taenitis* clade was confirmed; the sister genera *Austrogramme* and *Syngamma* are together sister to *Taenitis* (Zang et al., 2015, 2017). Thus, all molecular-phylogenetic study confirmed the close relationship between three paleotropic genera – *Austrogramme*, *Syngamma*, and *Taenitis*. In all published phylograms *Austrogramme* and *Syngamma* form a clade sister to *Taenitis* (Sánchez-Baracaldo, 2004; Cochran et al., 2014; Zang et al., 2015, 2017).

Spore morphology of Pteridaceae species are discussed in the numerous works (Hennipman, 1975; Tryon, Lugardon, 1991; Kuznetsov et al., 2014; Palacios-Rios et al., 2016; Vaganov, 2016). Some authors emphasize the diagnostic value of spore ornamentation in different ferns at the specific level, which can help clarify infrageneric taxonomy (Passarelli et al., 2010; Wei, Dong, 2012; Palacios-Rios et al., 2016). For different fern genera on various examples the congruence of morphological characteristics of spores with the result of molecular-phylogenetic analyzes has been shown (Gureyeva, Kuznetsov, 2015; Vaganov et al., 2017a, b, c).

Spores of some species of *Taenitis*, *Syngamma* and *Austrogramme* with using of scanning electron microscopy were examined by A. Tryon and B. Lugardon (1991): *Taenitis blechnoides*, *T. cordata* (Gaudich.) Holttum, *T. hookeri* (C. Chr.) Holttum, *T. interrupta*, *T. luzonica* (Alderw.) Holttum, *T. requiniana* (Gaud.) Copel., *Syngamma wallichii* (Hook.) Bedd., *S. cartilaginea* (Bak.) Diels, *S. alismifolia* (Presl) J. Sm., *Austrogramme decipiens* (Mett.) Hennipman, and *A. boerlageana* (Alderw.) Hennipman. E. Hennipman (1975) studied spores of four species of *Austrogramme* (*A. asplenioides* (Holttum) Hennipman, *A. boerlageana*, *A. decipiens*, and *A. francii* (Rosenst.) Hennipman), two species of *Syngamma* (*S. quinata* (Hook.) Carruth., *S. luzonica* Alderw.), and ten species of *Taenitis* (*T. blechnoides*, *T. cordata*, *T. flabelivenis*, *T. hosei* (Baker) Holttum, *T. interrupta*, *T. lanceolata* Kaulf., *T. marginata* Holttum, *T. requiniana* (Gaud.) Copel., *T. pinnata* (J. Sm.) Holttum, and *T. vittarioides* Holttum). E. Hennipman (1975) allied *Syngamma* with *Austrogramme* and distinguished them from *Taenitis* on the basis of spore morphology. A. Tryon and B. Lugardon (1991) supported this disposition. It should be noted that *Syngamma luzonica* (in Hennipman, 1975) was considered by R. Tryon and B. Lugardon as *Taenitis luzonica*.

The aim of this study is to provide details of spore ornamentation and evaluation of its diagnostic value for *Taenitis*, *Syngramma*, and *Austrogramme* species using scanning electron microscopy (SEM).

Materials and methods

Spores were obtained from herbarium specimens of seven species: *Taenitis blechnoides* (Hainan, China), *T. hookeri* (New Guinea), *T. pinnata* (J. Sm.) Holttum (Papua New Guinea), *Syngramma alismifolia*, *S. lobbiana* (Hook.) J. Sm. (both – Borneo), *S. quinata* (Hook.) Carruth. (Sulawesi), and *Austrogramme boerlageana* (Ambon) stored in PE (Herbarium of Institute of Botany, Chinese Academy of Sciences, Beijing). Only mature spores were used for SEM examination. Spores were mounted on SEM stubs using double-sided carbon adhesive tape and coated with gold in the “Quorum Q150R S” sputter-coater. Stubs were viewed and photographed with the scanning electron microscope “MiniSEM SNE-4500M” in the Laboratory of Structural and Molecular Analysis of Plants (Tomsk State University, Tomsk, Russia). Spore surface was scanned in a high vacuum at voltage of 20 kV, through 2000× and 15000× of magnification.

Equatorial diameter (distal or proximal position of spore), polar axis (equatorial position of spore),

length and width of laesura arms (proximal 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”. For terminology of sculpture elements, we primarily followed A. Tryon, B. Lugardon (1991), shape of the distal and proximal sides was described using terms by B. K. Nayar, S. Devi (1966). Spelling of the names of taxa and authors is given according to “The International Plant Name Index” (<http://www.ipni.org>).

Results and discussion

Spores of all examined species of *Taenitis*, *Syngramma* and *Austrogramme* are tetrahedral or tetrahedral-globose, trilete. In equatorial position the distal side is convex or hemispherical, proximal side is plane, 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 (equatorial flange, equatorial wing) or without it. Ornamentation of both face of spore could be tuberculate, baculate or verrucate, spore surface covered by rodlets and granulate deposits. The main morphometrical characteristics of spores are shown in the Table.

Table

Spore size of *Austrogramme*, *Syngramma* and *Taenitis* species, mean (min–max)

Вид	Equatorial diameter (µm)	Polar axis (µm)	Laesura length (µm)	Laesura width (µm)
<i>Austrogramme boerlageana</i>	26.0 (22.5–29.4)	–	13.2 (11.8–14.4)	0.8 (0.6–1.1)
<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>S. 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>S. 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>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)
<i>T. 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>T. 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)

1. *Syngramma alismifolia* (Presl) J. Sm. (Fig. 1A; Table). Spores are tetrahedral, roundish-triangular in polar position, with straight or slightly concave sides and wide-rounded corners. In equatorial position distal side is hemispherical, proximal side is convex. Proximal and distal sides are densely verrucate, with low, small, discrete or fused verrucae, 0.2–0.9 µm in width, covered by sparse rodlets. Laesura arms are straight, reaching the spore corners. Proximal side of spore is depressed between laesura arms.

Investigated specimen: Borneo E., 1953. № 01715222 (PE).

2. *S. lobbiana* (Hook.) J. Sm. (Fig. 1B, C; Table). Spores are tetrahedral-globose, roundish-triangular in polar position, with straight or slightly concave sides and wide-rounded corners. In equatorial position the distal side is hemispherical, proximal side is convex. Proximal and distal sides are irregular verrucate, surface covered by rodlets. Laesura arms are straight, reaching the spore corners. Spore may be depressed on the distal side.

Investigated specimen: № 933 Native collector. Plants of Sarawak, Borneo. Collected through the Museum for the Bureau of Science, Manila, P.I. № 01715231 (PE).

3. *S. quinata* (Hook.) Carruth. (Fig. 1D–F; Table). Spores are tetrahedral, roundish-triangular in polar position, with convex sides and wide-rounded corners. In equatorial position the distal side is hemispherical, proximal side is plane. Proximal and distal sides are verrucate, with small hemispherical verrucae 0.3–0.9 μm in diam., surface is covered by granulate deposits, especially on the distal side. Laesura arms are straight, reaching the spore corners. Spore may be depressed on the distal side.

Investigated specimens: № 6943. V. Guinen Japan, № 01715087; Selebes, G. Kjellberg, 1939, 500 alt. № 01715234 (PE).

4. *Austrogramme boerlageana* (Alderw.) Hennipman (Fig. 1D–F; Table). Spores are tetrahedral-

globose, nearly roundish in polar position. In equatorial position the distal side is hemispherical, proximal side is conical. Proximal and distal sides are verrucate with tiny hemispherical verrucae 0.2–0.4 μm in diam. (microverrucate), surface is covered by dense granulate deposits over verrucae on the both sides. Laesura arms are straight, reaching the spore corners. Proximal side of spore is slightly depressed between laesura arms.

Investigated specimen: Ambon 1939. № 01715225 (PE).

5. *Taenitis blechnoides* (Fig. 2A–C; Table). Spores are triangular with concave sides and rounded corners in polar position. In equatorial position the distal side is hemispherical, proximal side is

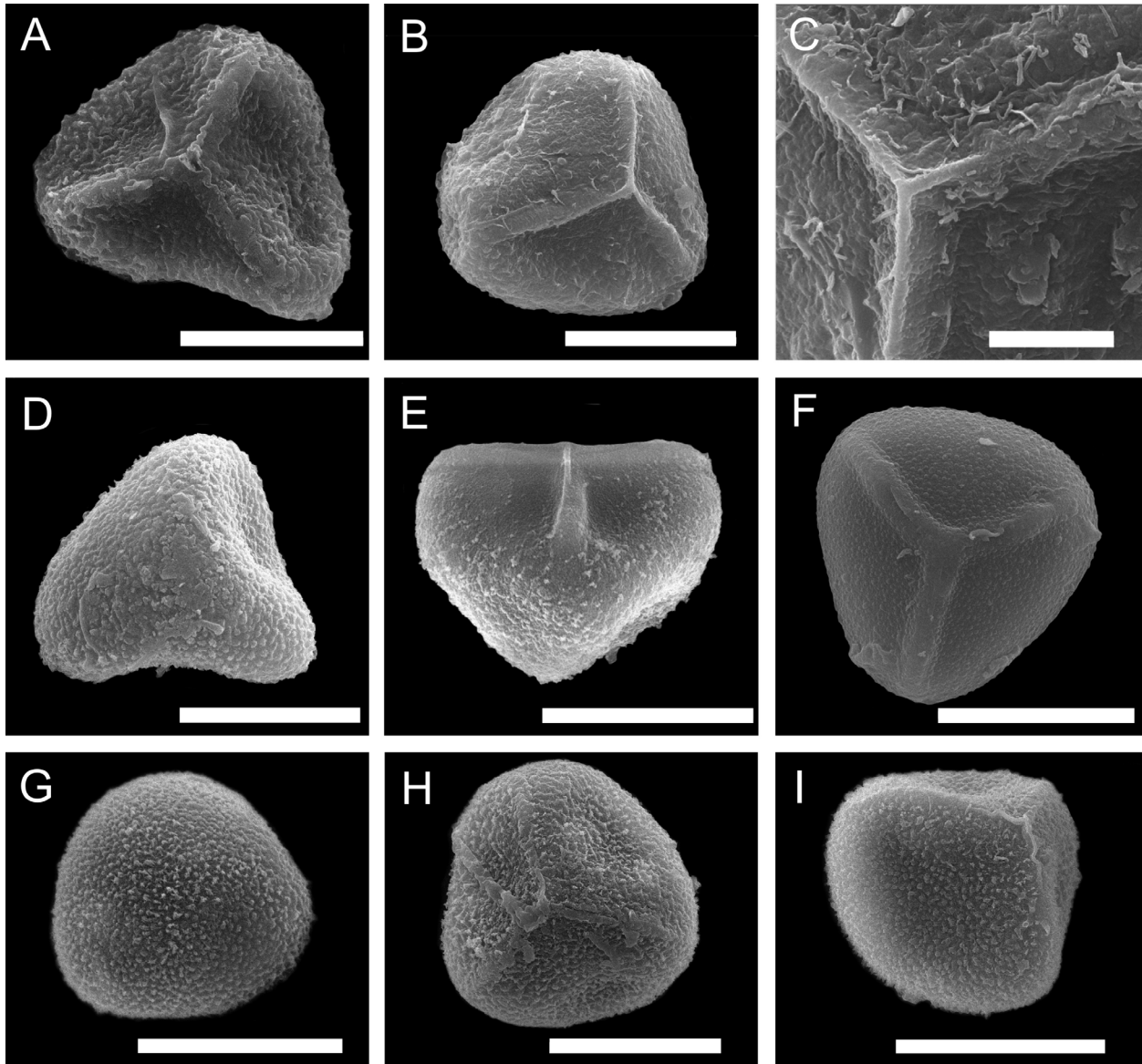


Fig. 1. SEM-micrographs of spores of *Syngramma* and *Austrogramme*: A – *Syngramma alismifolia* (Presl) J. Sm.; B–C – *S. lobbiana* (Hook.) J. Sm.; D–F – *S. quinata* (Hook.) Carruth.; G–I – *Austrogramme boerlageana* (Alderw.) Hennipman; A, F, H – proximal side; D, G – distal side; B, E, I – spore in equatorial-proximal position; C – close-up fragment of proximal side of spore and laesura arms. A–B, D–I – 20 μm ; C – 5 μm .

plane. Spores are cingulate, cingulum is conspicuous, especially in proximal view, variable in width, narrower at the corners. Laesura arms are straight, without commissural thickness. Proximal and distal sides are densely tuberculate, with low, small, discrete tubercles $0.2\text{--}0.5\ \mu\text{m}$ in diameter on proximal side and $1.8\text{--}2.5 \times 1.1\text{--}1.4\ \mu\text{m}$ on distal one. Tubercles are with fascicled rodlets on the top.

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

6. *T. hookeri* (Fig. 2D–F; Table). Spores in proximal-polar position are roundish-triangular, with concave sides and rounded corners; in distal-

polar position nearly roundish with convex sides. In equatorial view the distal side is hemispherical and proximal side is convex. Cingulum is absent. Laesura arms are straight, submerged for most of their length, with fused tubercles forming irregular ridges $1.0\text{--}2.2\ \mu\text{m}$ width situated on both sides of each laesura arm parallel to it. Spore surface between submerged part of laesura arms is with small sparse verrucae. Both proximal and distal face are densely tuberculate, with elongate discrete tubercles (bacules), $1.8\text{--}2.9 \times 0.9\text{--}1.8\ \mu\text{m}$ in size. Tubercles with rodlets on the top.

Investigated specimen: Plants of Netherlands New Guinea. 1200 m alt. Feb. 1939. № 01715229 (PE).

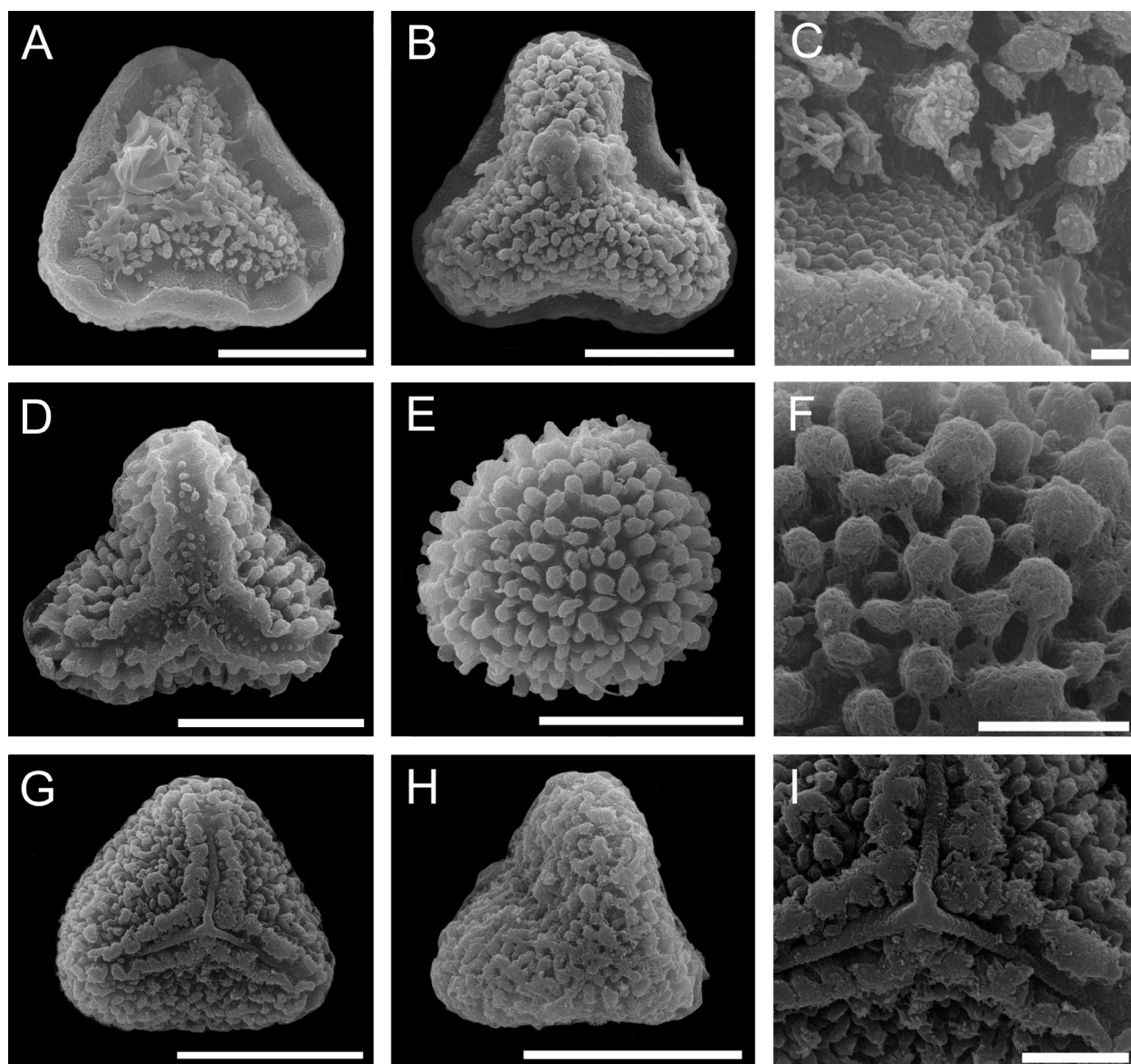


Fig. 2. SEM-micrographs of spores of *Taenitis* species: A–C – *T. blechnoides* (Willd.) Sw.; D–F – *T. hookeri* (C. Chr.) Holttum; G–I – *T. pinnata* (J. Sm.) Holttum; A, D, G – proximal side; B, E, H – distal side; C, F, I – close-up fragments of sculpture (C, F) and laesura arms (I). Scale bars: A, B, D, E, H – $20\ \mu\text{m}$, C – $1\ \mu\text{m}$; F, I – $5\ \mu\text{m}$.

7. *Taenitis pinnata* (J. Sm.) Holtt. (Fig. 1G–I; Table). Spores in proximal-polar and distal-polar position are roundish-triangular, with straight or slightly concave sides and rounded corners. In equatorial view the distal side is subconical and proximal side is conical. Cingulum is absent. Laesura arms are straight, with fused tubercles forming irregular ridges 0.6–2.2 μm width situated on both sides of each laesura arm parallel to it. Proximal face is densely tuberculate with discrete tubercles, distal face is densely rugulate-tuberculate with tubercles fused in short rugulae, 1.6–3.1 \times 0.7–1.2 μm in size. Tubercles with sparse rodlets on the top.

Investigated specimen: Plants of Papua (British New Guinea) Lake Daviumbu. Rain forest. August, 1936. № 01715232 (PE).

Spores of all examined species of *Syngamma* and *Austrogramme* are very similar to each other in shape and ornamentation and very different in these characteristics with spores of *Taenitis* species. Spores of species of the first two genera have the simple verrucate (microverrucate) ornamentation, whereas those of *Taenitis* species have a very clear tuberculate or baculate ornamentation on the distal side and tendency to forming of commissural ridges through the fusion of tubercles arranged in a row along the laesura arms. Comparison with published data on other species of *Syngamma* and *Austrogramme* shows that the spores of the different species of these genera are very similar or have insignificant differences in shape and ornamentation. Spores of *Syngamma* and *Austrogramme* species may be depressed on the distal side or between laesura arms; E. Hennipman (1975), A. Tryon and B. Lugardon (1991) indicated the same peculiarity for other species of these genera. E. Hennipman (1975) has concluded that properties of spores together with chromosome number indicate a relationship between *Austrogramme* and *Syngamma*.

Spores of three studied species of *Taenitis* are distinctive to each other. The main distinguished feature in *Taenitis blechnoides* spores is conspicuous cingulum. E. Hennipman (1975), A. Tryon and B. Lugardon (1991) also denoted presence of prominent cingulum (equatorial flange) in spores of *T. blechnoides* and its absence in *T. hookeri*. Ornamentation of spores of *T. hookeri* in compare with spores of other two species represents by elongate tubercles (bacules). Spores of two species – *T. hookeri* and *T. pinnata* demonstrate tendency to formation of commissural ridges through the fusion of tubercles arranged in a row along the laesura arms. In com-

pare with data by A. Tryon, B. Lugardon (1991), who mentioned fascicled rodlets on tubercles in *Taenitis blechnoides* and *Taenitis hookeri* spores we observed sparse (not dense) rodlets on the tubercles of the spores of all examined species. E. Hennipman (1975) and A. Tryon, B. Lugardon (1991) also indicated the significant differences in ornamentation of spores of *Taenitis* and *Syngamma* – *Austrogramme*. Judging by our study and the photos published by E. Hennipman (1975) and A. Tryon, B. Lugardon (1991), spores of the same species collected in different localities retain their characteristics.

The size (equatorial diameter) of spores of studied *Taenitis* species varies within 24–43 μm . Spores of *T. blechnoides* have the largest and *T. pinnata* – the shortest equatorial diameter. In the same time spores of *T. pinnata* are characterized by the largest polar axis, the cause of which is the shape of spore – subconical in distal and conical in proximal side. Due to submerged laesura, spores of *T. hookeri* have the shortest laesura arms: visible parts of laesura arms are 3.1 μm , whereas length of laesura arms in two other species is 10.3 and 14.7 μm in average. Spores of studied *Syngamma* species are similar to each other in size (equatorial diameter varies from 25.4 to 35.5 μm), spores of *Austrogramme boerlageana* are smaller 22.5–29.4 μm (Table). E. Hennipman (1975) indicated larger spore size for all studied genera: 45–70 μm for *Taenitis*, 40–50 μm for *Syngamma*, and 35–40 μm for *Austrogramme*. A. Tryon and B. Lugardon (1991) indicated the spore size for *Taenitis* and *Syngamma* species as 33–53 μm , for *Austrogramme* – 30–40 μm .

Similarity of spore morphology of *Syngamma* and *Austrogramme* species confirms close relationship between these genera revealed as a result of molecular-phylogenetic studies (Sánchez-Baracaldo, 2004; Cochran et al., 2014; Zhang et al., 2015, 2017). Differences of spore morphology of *Taenitis* species confirm topography of this genus as sister to *Syngamma* and *Austrogramme* (collectively) in the common clade (*Syngamma* – *Austrogramme* – *Taenitis*).

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