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Autor: Crandall-Stotler, Barbara / Geissler, Patricia

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Sporophyte development and structure in Spruceanthus marianus (Gott.) Mizut., with special reference to capsule wall differentiation

BARBARA CRANDALL-STOTLER

&

PATRICIA GEISSLER

ABSTRACT

CRANDALL-STOTLER B. & P. GEISSLER (1983). Sporophyte development and structure in Spruceanthus marianus (Gott.) Mizut., with special reference to capsule wall differentiation. *Candollea* 38: 105-124. In English, German abstract.

A combination of serial paraffin sectioning and SEM techniques were used to trace the morphogenetic events responible for a plurifenestrate capsule wall thickening pattern from the state of embryo to the state of mature capsules in the Lejeuneaceous taxon *Spruceanthus marianus*. Exospore sculpturing is completed before tetrad separation and is accompanied by the deposition of elater thickenings and initial phases of capsule wall modification: nodular thickenings along the radial walls of the outer cells and a sheet of safranin-staining material laid down on the inner wall surfaces of the inner cells, except in scattered pit field zones where perforations develop after completion of sporogenesis.

ZUSAMMENFASSUNG

CRANDALL-STOTLER B. & P. GEISSLER (1983). Entwicklung und Aufbau des Sporophyten von Spruceanthus marianus (Gott.) Mizut. unter besonderer Berücksichtigung der Kapselwanddifferenzierung. *Candollea* 38: 105-124. Englisch, deutsche Zusammenfassung.

Die Entwicklung der plurifenestraten, netzartigen Kapselwandverdickungen von *Spruceanthus marianus (Lejeuneaceae)* wurde vom Embryonalstadium an bis zur reifen Kapsel anhand von Paraffinschnittserien und REM-Aufnahmen untersucht. Die Exosporornamentierung wird vor der Trennung der Tetraden abgelagert, gleichzeitig mit den Elaterenverdickungen und den Anfängen der Differenzierung der Kapselwandzellen: Knotige Verdickungen an den Radialwänden der Aussenzellen und durch Safranin gefärbte Platten auf der Innenschicht, die nur zerstreut Tüpfelzonen freilassen, wo nach vollendeter Sporogenese die Perforationen entstehen.

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Evaluation of meaning, or usefulness, either functionally or phylogenetically, of any anatomical character necessitates having comprehensive information about that character. When assessing the significance of character variation within a taxonomic unit, for example, it is extremely relevant to know how that same character varies during the ontogeny of a single organism. This type of input is particularly significant in taxa where adaptive trends have involved abbreviated reproductive cycles and concomitant phenotypic expressions of developmental arrest. Such life cycle compression, which must assuredly be accompanied by abridged character development, characterizes a majority of Lejeuneaceous genera (SCHUSTER, 1980).

In recent systematic treatments of the *Lejeuneaceae* Cas.-Gil (MIZUTANI, 1961; GRADSTEIN, 1975) the sporophytic traits of seta anatomy, capsule wall thickening pattern and elater morphology have provided a base for subfamily arrangements. Within this family, however, few data have been accumulated on the sequence of ontogenetic changes which occur in seta, capsule walls and elaters within a single taxon. This informational gap exists because of general inaccessibility of sporophytic stages from tropical taxa, synchrony of sporophyte development in many taxa and the rapid development and subsequent deterioration of sporophytes in collected materials. Fortunately, during a collecting trip to Morobe Province, Papua New Guinea, the second author collected two sporophyte-containing populations of *Spruceanthus marianus* (Gott.) Mizut. [= *Archilejeunea marianus* Gott.] (see the *addendum* for discussion concerning this synonymy). Within the populations sporophytes at several different developmental stages were evident. These collections then provided the impetus for gathering more detailed data on sporophyte development in the *Lejeuneaceae*, with particular reference to sequential changes in capsule wall morphology.

Material and Methods

Portions of two populations of *Spruceanthus marianus,* from a mesophytic, mixed *Castanopsis* forest at Wau, Mt. Missim, Morobe Province, Papua New Guinea, were field-fixed in formyl-acetic acid-alcohol (FAA) on August 6, 1981. Additional samples of each were transferred to culture dishes of vermiculite moistened with HATCHER'S (1965) growth medium, and placed in an environmental chamber, with a 16 hr/8 hr day/night cycle, at 18°C day/14°C night temperatures. A light intensity of 325 lux providing for four microwatts/(cm^2/nanometer) red, three microwatts/(cm^2/nanometer) blue, and 0.5 microwatts/(cm^2/nanometer) far red wavelengths was maintained. Voucher specimens of each *(Geissler, 7911; 7918)* were deposited in the Conservatoire et Jardin botaniques, Genève (G) and in the private herbarium of R. Stotler (hb Stotl.). Morphological comparisons of mature forms were made with the following specimens, loaned by the New York Botanical Gardens (NY):

– *Spruceanthus mamillilobulus* (Herz.) Verd. – **China:** Kweitschou, nr Kutschou, 300 m, *Handel-Mazzetti 10 867.*

– *Spruceanthus marianus* (Gott.) Mizut. – **Papua New Guinea:** Koitaki, Owen Stanley Range above Port Moresby, 1500′, *Carr 11945.*

– *Spruceanthus polymorphus* (Sande Lac.) Verd. – **Japan:** Hyuga Prov., Obi-Machi, *Hattori 11/19/1947;* Kagoshima Pref., nr Hekka, Osumi Pen., 600 m, *Mizutani 5/13/1959*; Mie Pref., Ise Shrine, Ise, *Magofuku 1524.* **Java occ.:** Res. Batavia; G. Gede, 1100 m, *Schiffner IV 1894;* G. Salak, 900-1200 m, *Schiffner I 1893;* G. Boeroeng, 300 m, *Schiffner XII 1893.* **Peninsula Malaccensis:** Pahang, S. Sat, *M. R. Henderson VII 1929.* **Hawaii:** Oahu; Mt. Konahuanui, above Manoa, *Heller* s.n.

– *Spruceanthus semirepandus* (Nees) Verd. – **Japan:** Miyazaki Pref., Inohaye Valley in Kitago, *Hattori 2/16/1956.*

Sporophytes at various developmental stages in both field-fixed and cultured samples were prepared for serial microtome sectioning using standard paraffin embedding methods (JOHANSEN, 1935). Similar fertile shoots were hand-dissected, dehydrated to 100% ethanol, infiltrated with amyl acetate and dried with critical point techniques, using CO_2 as the transitional fluid. A gold-palladium target was used for specimen coating, and SEM viewing employed an ISI Alpha 9 counter top, scanning electron microscope in Carbondale and a Camscan III in Geneva.

Fig. 1-5. – *Spruceanthus marianus* (Gott.) Mizut. – 1. Median leaf cells showing oil bodies, surface view, × 1200. – 2. Male inflorescence, ventral view, × 70. – 3. Female inflorescence in early stages of embryology, showing three ventral perianth keel and a single *Radula* type subfloral innovation, ventral view, × 112. – 4. Female inflorescence at an intermediate stage of sporophyte development, with three ventral perianth keels still apparent and *Radula* type subfloral innovation further developed, ventral view, × 40. – 5. Three "pseudolateral" female inflorescences, borne on subsequent subfloral innovations, at mature sporophyte stages with bracteoles removed, ventral view, × 23. [Be, basal portion of detached female bracteole; R, first leaf of *Radula* innovation, basiscopic in position.].

Fig. 6-10. – *Spruceanthus marianus* (Gott.) Mizut. – 6. Horizontal longitudinal section of a two-celled embryo enclosed in an archegonial venter; note the large nucleus and chromatin in the hypobasal cell; perianth stage comparable to that illustrated in figure 3, × 300. – 7. Transverse section through the capsule/seta zone of an embryo at the quadrant stage of development; the embryo at this stage consists of a single foot cell, four seta cells and four capsule cells; × 835. – 8. Horizontal longitudinal section of an older embryo in which initial endothecium/amphithecium differentiation is evident; the foot still consists of a single large cell and the seta is comprised of a single tier of four cells; × 300. – 9. Horizontal longitudinal section of a sporophyte at the archesporial stage of development, showing a two-cell-layered capsule wall with the inner and outer cell dimensions fairly equal, × 220. – 10. Higher magnification of the capsule seen in figure 9, × 1330. [B, bract; Ca, calyptra; IW, inner capsule wall cell; OW, outer capsule wall cell; am, amphithecium; ar, archesporium; b, basal cell of capsule; cw, two-layered capsule wall; e, epibasal cell; en, endothecium; f, foot; h, hypobasal cell; i, calyptra-capsule interface; n, nucleus of sporophyte quadrant cells; p, perianth; s, seta.].

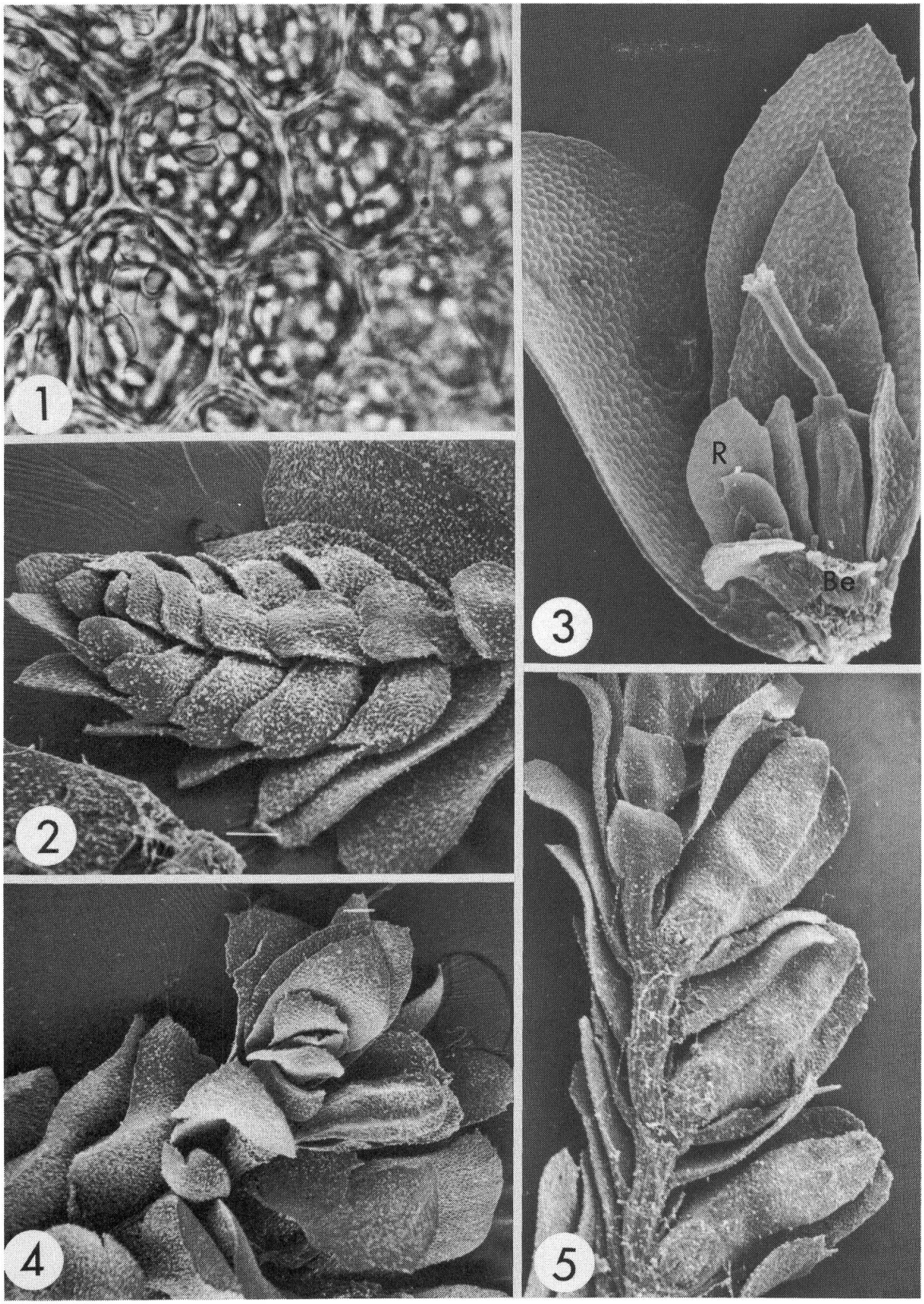
Fig. 11-15. – *Spruceanthus marianus* (Gott.) Mizut. – 11. Oblique longitudinal section of a capsule in which spore mother cell initials and elater initials are differentiated; radial expansion of outer wall cells is also evident; × 1000. – 12. Horizontal longitudinal section of a sporophyte at the lobed, spore mother cell stage, showing pronounced dimensional differences between inner and outer capsule wall cells, × 140. – 13. Horizontal longitudinal section of a capsule containing spore tetrads at initial wall sculpturing phases; safranin bonding materials appear as punctae on the tetrads and as scattered, thin bands on the inner wall cell surfaces; × 500. – 14. Horizontal longitudinal section of a capsule at mature spore stage, showing nodular and plurifenestrate thickening pattern of outer and inner capsule walls, respectively, × 600. – 15. Scanning electron micrograph of a spore tetrad with well developed punctae and rosettes, × 1750. [IW, inner capsule wall cell; OW, outer capsule wall cell; el, elater initial; sp, spore mother cell initial; t, safranin-bonding thickening material.].

Fig. 16-20. – *Spruceanthus marianus* (Gott.) Mizut. – 16, 17. Interior of capsule in spore tetrad stage, showing alternating rows of tetrads and elaters; scattered, unthickened depressions are visible throughout the inner wall surfaces, and protoplasmic remnants are evident in sectioned inner and outer wall cells, × 600. – 18. Newly dehisced capsule, showing apically attached elaters, × 115. – 19. Median region of an elater from an opened capsule, with a unispiral thickening band and scattered external sculpturing, × 1650. – 20. Inner capsule wall cells at the spore tetrad stage, showing pit-like depressions in the thickened inner wall, × 1100. [IW, inner capsule wall cell; OW, outer capsule wall cell; el, attached elater.].

Fig. 2l-25. – *Spruceanthus marianus* (Gott.) Mizut. – 2l. Higher magnification of inner wall cell illustrated in figure 20, × 2850. – 22. A single pit depression in the inner wall surface of an inner capsule wall cell, × 6000. – 23. Longitudinal section of the capsule wall in the spore tetrad stage, as viewed with a scanning electron microscope, × 1810. – 24. Inner capsule wall cells after spore tetrad separation, but before germination, showing the initial stages of perforation at the pit areas, × 1700. – 25. Spores in a mature capsule, × 2000. [IW, inner capsule wall cell; OW, outer capsule wall cell.].

Fig. 26-30. – *Spruceanthus marianus* (Gott.) Mizut. – 26. A single rosette pattern on a mature spore, similar to those of figure 25, × 6000. – 27. Mature sporophyte, soon after capsule dehiscence, × 36. --28. Horizontal longitudinal section of the foot of a mature sporophyte, × 210. – 29. Seta and basal cells of the outer capsule wall, after dehiscence, × 250. – 30. Valve apex, outer capsule wall of dehisced capsule, surface view, × 250. [Ca, basal portion of calyptra; V, valve margin; p, basal portion of perianth; t, nodular, trigonal thickening material of the outer capsule wall.].

Fig. 31-35. – *Spruceanthus marianus* (Gott.) Mizut. – 31. Valve middle, inner capsule wall of dehisced capsule, surface view, × 250. – 32. Scanning electron micrograph of lower half of inner capsule wall surface, after dehiscence, × 50. – 33. Valve apex, inner wall surface after dehiscence, showing the perforated nature of the fenestrae, × 375. – 34. Higher magnification of inner capsule wall cell in a dehisced capsule, showing the perforated nature of the fenestrae, × 1900. – 35. A single perforation, or fenestra, of the inner capsule wall surface, × 6000. [p, perforation as seen with light microscopy.].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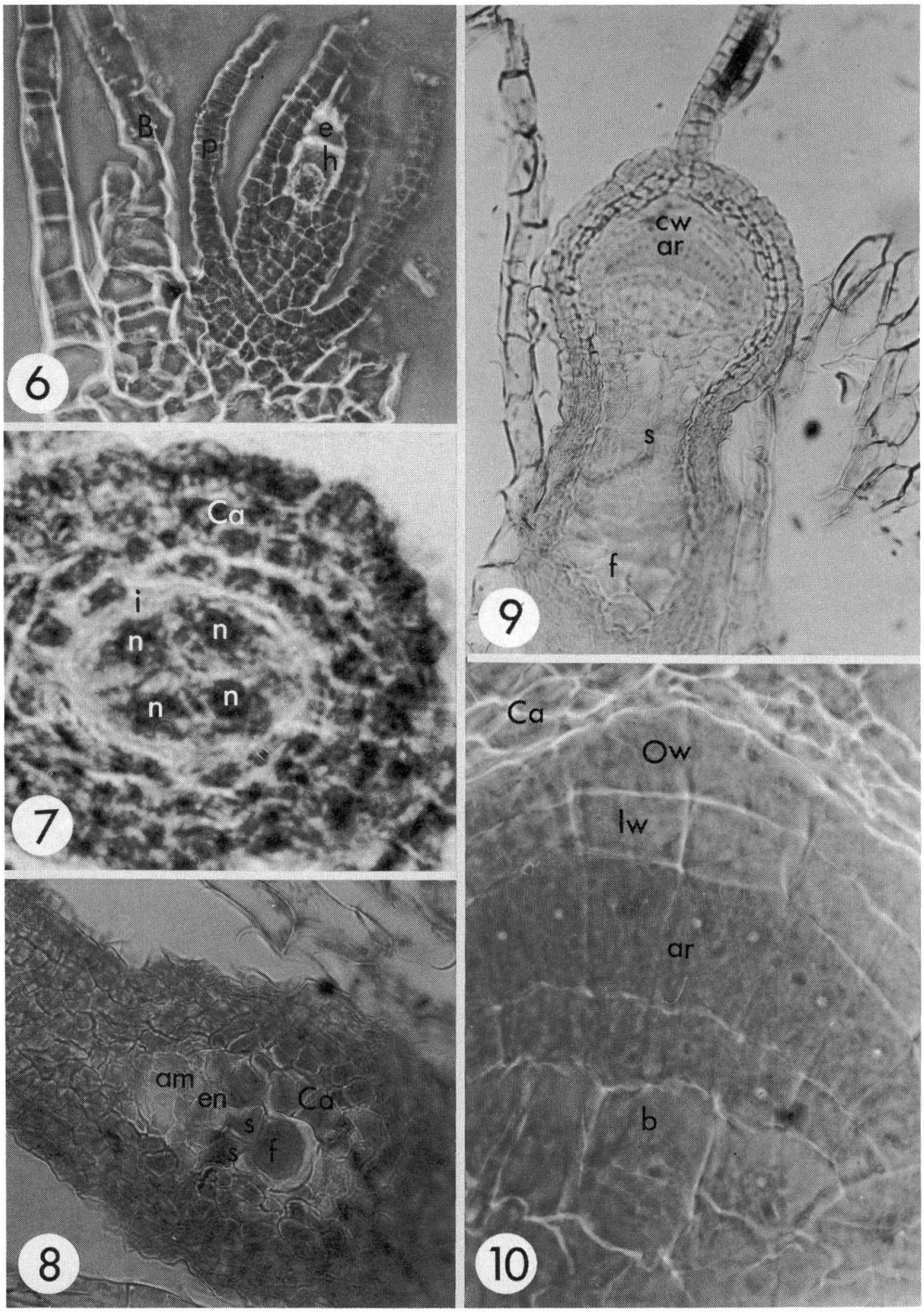
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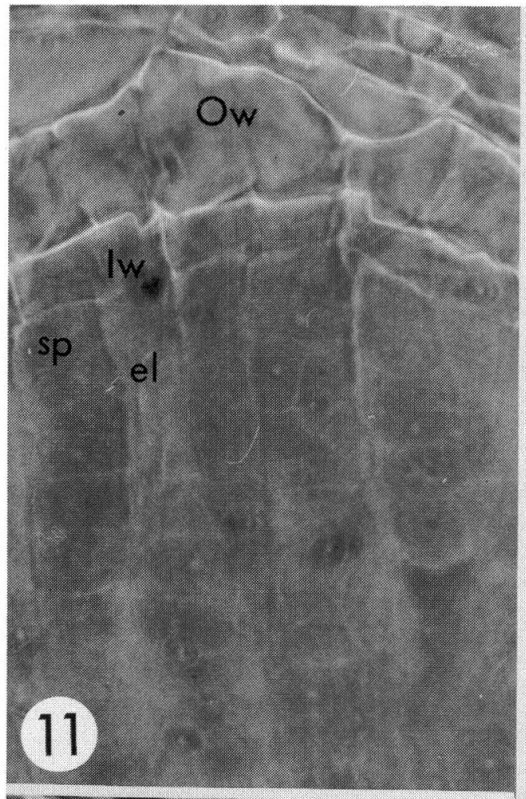
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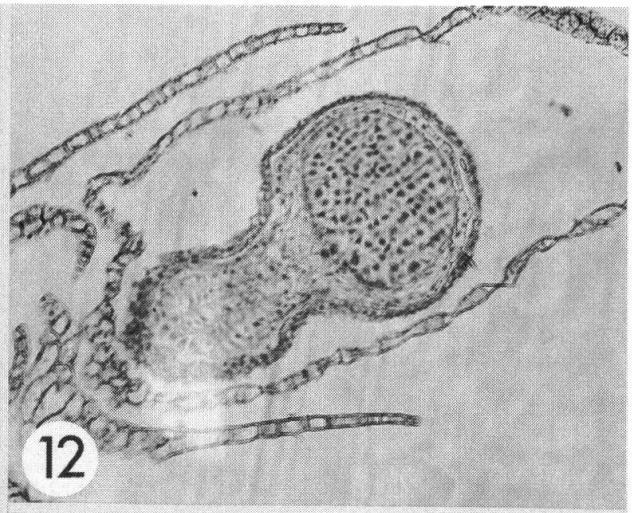
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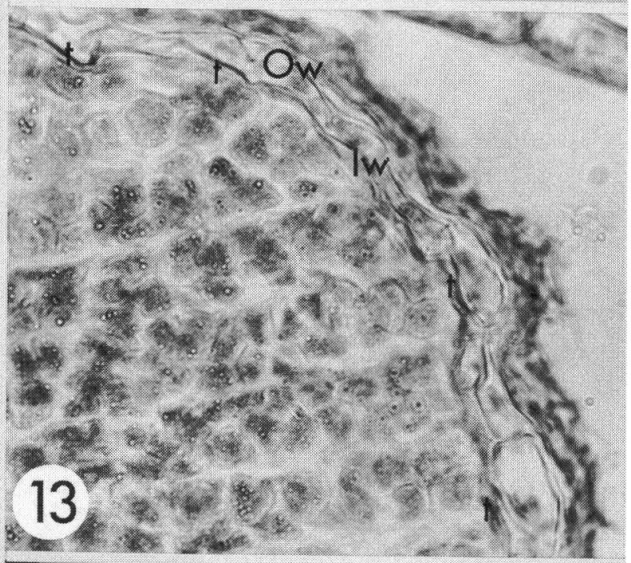
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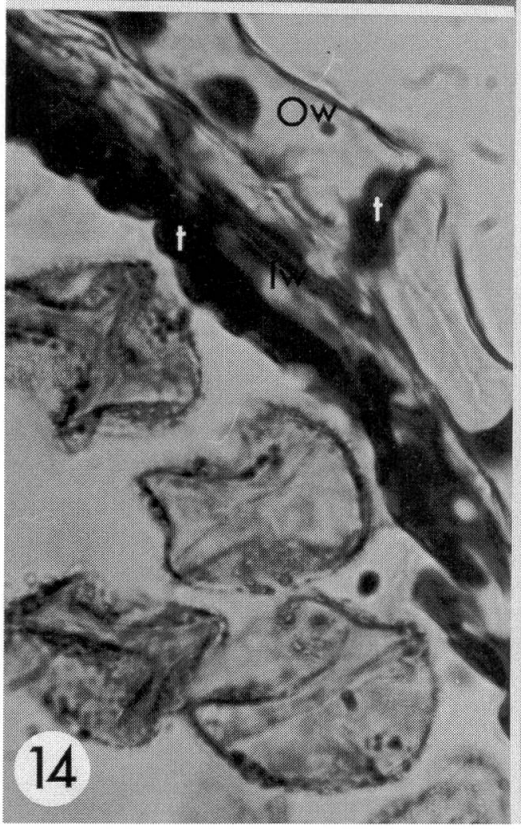
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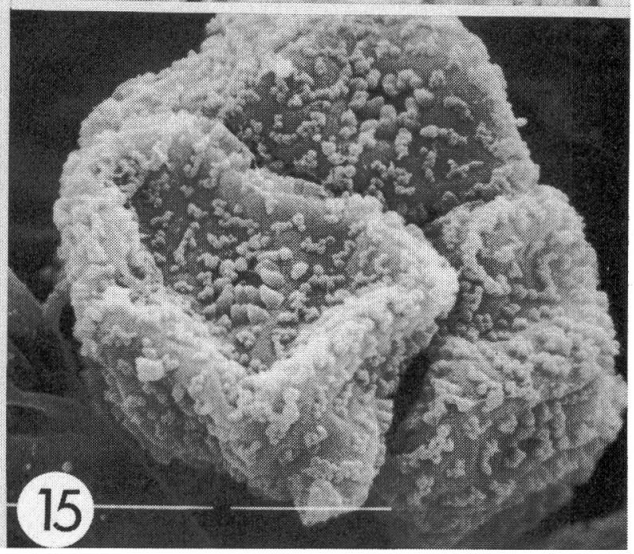
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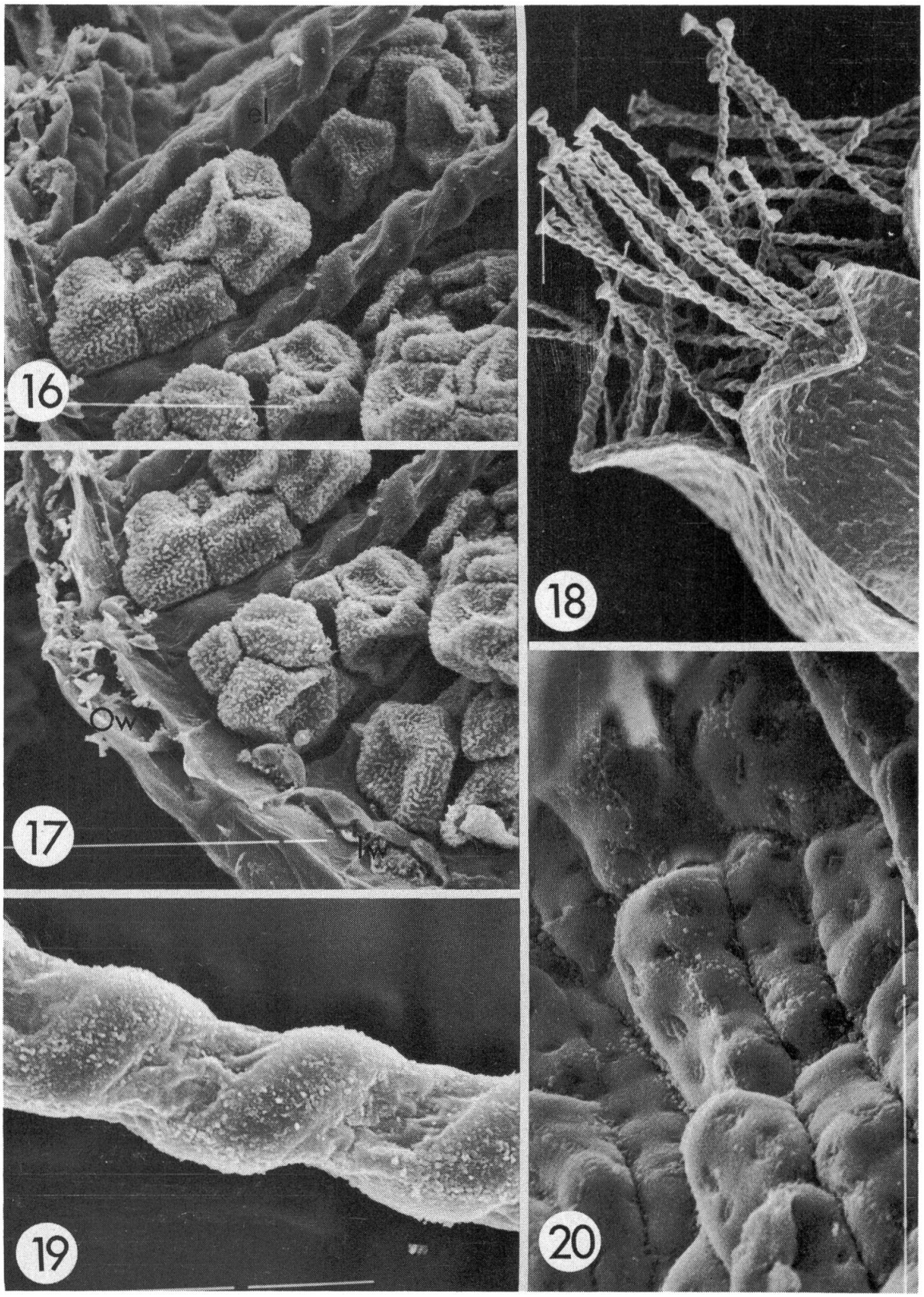
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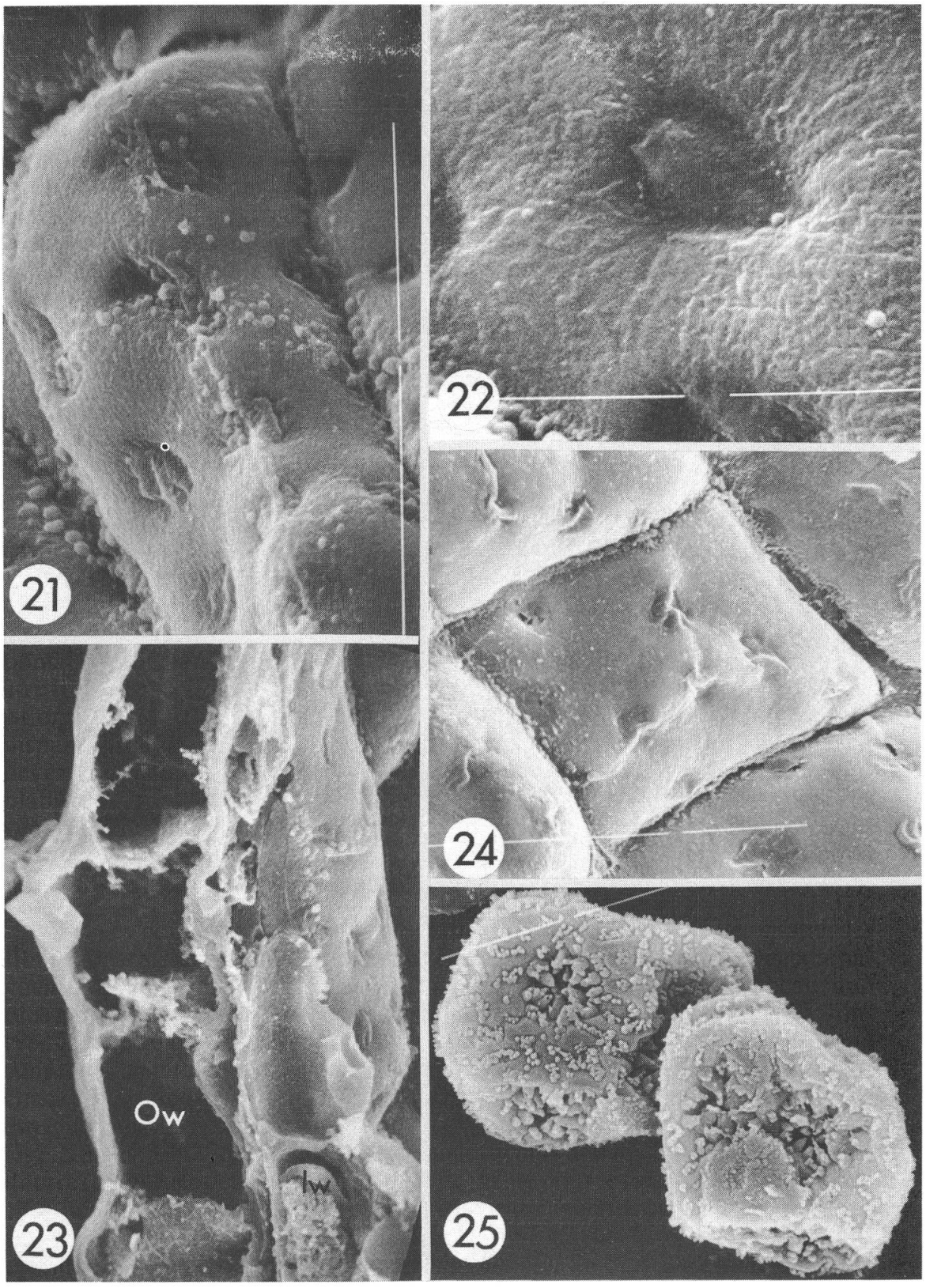
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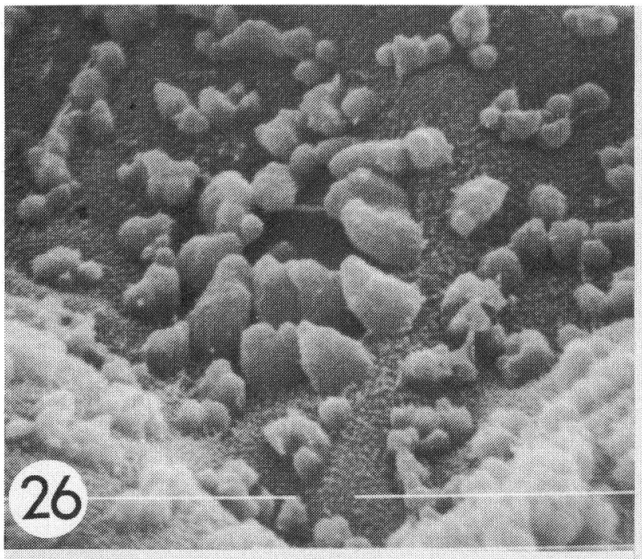
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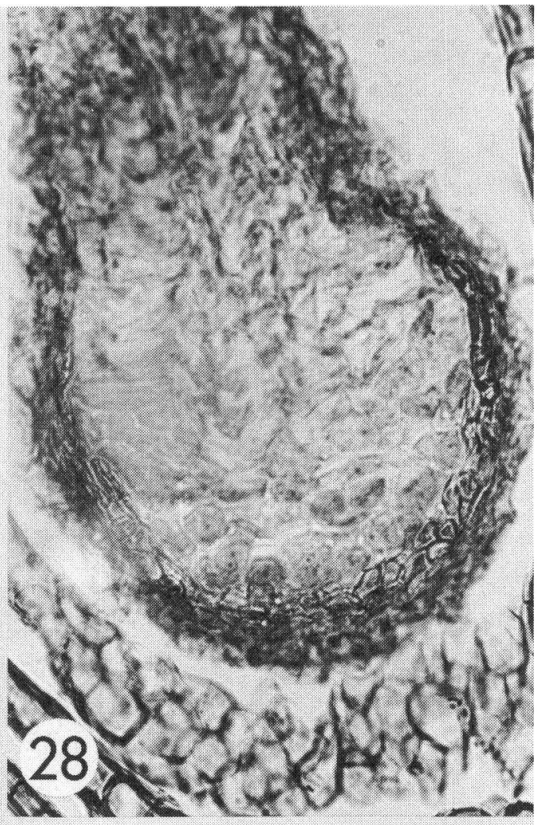
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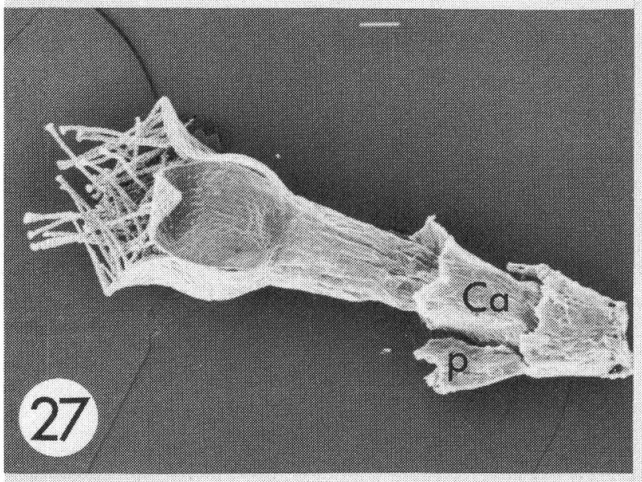
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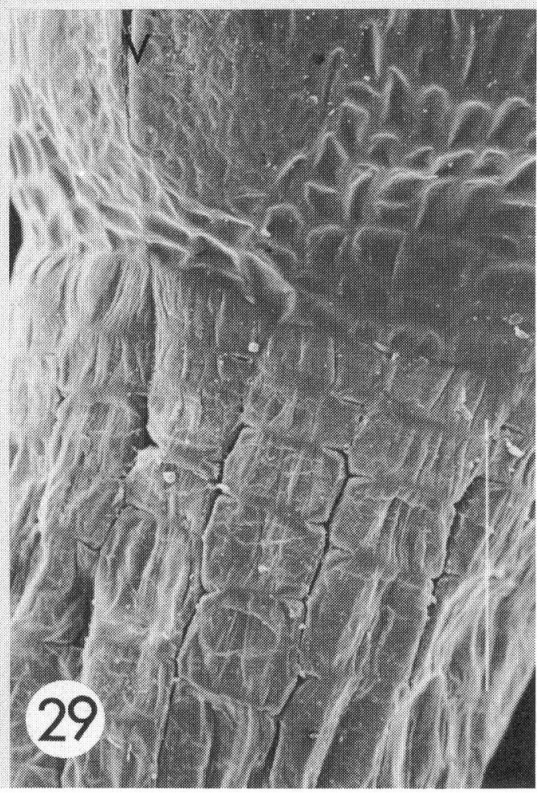
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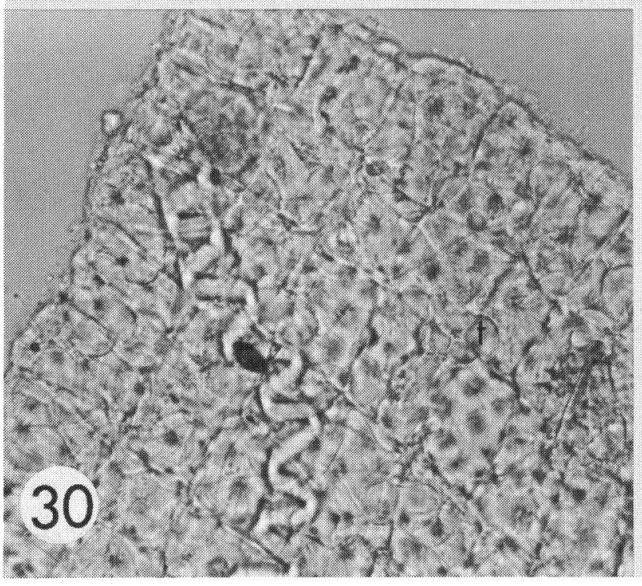
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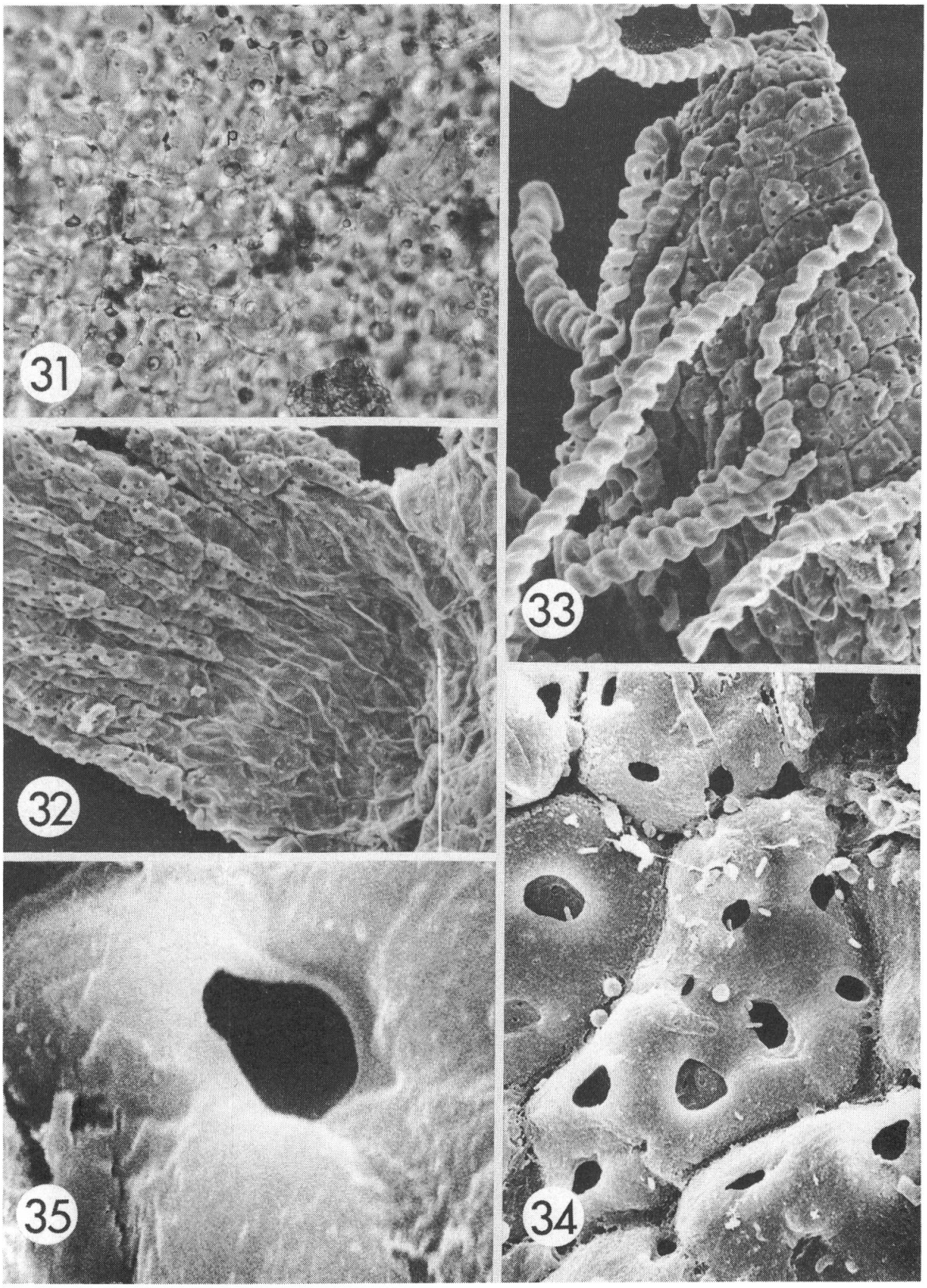
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Results and Discussion

Like many genera in the *Lejeuneaceae* Cas.-Gil, *Spruceanthus marianus* is monoecious, with the male inflorescences terminating some branches (Fig. 2) and the females, others (Fig. 3-5). The 5-20 series of male bracts are hypostatic and male bracteoles, which are only slightly smaller than the underleaves, persist throughout the inflorescence. The female inflorescence consists of a single series of perichaetia and a beaked perianth, enclosing a solitary archegonium (Fig. 3, 6).

Differentiation of the female inflorescence is always initiated with the formation of a bract from one of the lateral merophytes. The other bract is formed next so that the bracteole is always the last formed element of the perichaetium. The perianth initially encloses only the base of the archegonium (Fig. 3, 6), the long neck of which protrudes into the perichaetial enclosure. The archegonium is structurally typical of the *Jubuloideae;* i.e., it comprises a short broad stalk, a bistratose venter and a long, slightly twisted neck with irregular slime-secreting cover cells in the opened stage (Fig. 3). The bracts, at maturity, are slightly smaller than the vegetative leaves, and are unequally divided into large lobes that are narrowly oblong to narrowly ovate in outline, with small, scattered marginal teeth, and much smaller, plane lobules with broadly acute to obtuse apices. The bracteoles are 2-3 times as large as the underleaves, and obovate in outline with the apices truncate to retuse and the margins entire to occasionally toothed. The perianth is initially six-keeled, with one dorsal, two lateral and three ventral folds all well defined (Fig. 3, 4). These keels, or folds, which are produced by the continued activity of meristematic cells located along the keel ridges, continue to enlarge during early stages of perianth expansion and concomitant sporophyte growth (Fig. 4). Development of the median ventral keel, however, ceases before capsule enlargement occurs. Consequently, in perianths enclosing fully differentiated sporophytes this keel is lacking, having been distended by the expansive forces of the growing sporophyte (Fig. 5). The apparent difference between mature *S. polymorphus* perianths and those of *S. marianus* is, thus, due to a foreshortened developmental event in the latter and does not represent significant structural divergence.

As in other species of *Spruceanthus, Radula* type subfloral innovations develop in association with one or rarely both of the bracts (Fig. 3-5). The innovation leaf spiral is of the *Radula-Lejeunea* type, i.e., basiscopic leaf to underleaf to acroscopic leaf. According to MIZUTANI (1970) this pattern characterizes other species of *Spruceanthus,* while the *Radula-Jubula* pattern, i.e., underleaf to basiscopic leaf to acroscopic leaf, occurs in *Archilejeunea* (Spruce) Schiffn. Hence, in this feature, too, *S. marianus* is akin to *S. polymorphus*. The innovations themselves frequently produce inflorescences with additional innovations after only a few cycles of vegetative segmentation so that it is not uncommon to see several closely aligned pseudolateral inflorescences along a shoot (Fig. 5).

Embryogenesis begins with an unequal division of the fertilized egg into a small epibasal and large hypobasal cell (Fig. 6). A subsequent horizontal division in one of these cells then forms a three-celled, filamentous embryo. Unfortunately, it could not be determined with certainty which of the two divides, although the appearance of condensed chromatin in the hypobasal cell (Fig. 6), and subsequent cell dimensions suggest that it is the hypobasal cell which gives rise to foot and seta precursors. Formation of both foot and seta from hypobasal cell derivatives is common in the Marchantiopsida (ANDERSEN, 1929; McNAUGHT, 1929; SCHUSTER, 1966), but has not yet been reported in *Jungermanniopsida* (KIENITZ-GERLOFF, 1874; LEITGEB, 1875; SCHERTLER, 1979). However, the degree of variability possible is unknown since initial embryological stages have been studied in only a very few taxa.

Regardless of how derived, the upper, middle and basal cells of the embryo ultimately form the capsule, seta and foot of the sporophyte, respectively. The foot initial remains undivided as both seta and capsule initials undergo two series of vertical divisions to form in each, a quadrant of cells (Fig. 7). The upper quadrant continues to divide as the seta quadrant enters a brief dormant stage (Fig. 8). Following formation of two to four tiers of capsular quadrants, a single cell-layered amphithecium is separated from the internal endothecial zone by periclinal divisions in each cell. A similar, but somewhat slower cycle of division occurs in the single-tiered seta quadrant to form four external and four internal seta initials. Each external cell undergoes two complete division sequences so that ultimately 16 outer cells surround the four inner ones. Non-synchronous transverse divisions within inner and outer seta cell zones, accompanied by slower nondirectional divisions in the foot initial coincide with further stages of capsule differentiation (Fig. 9).

As differentiation proceeds, each amphithecial cell divides periclinally, and the two-layered capsule wall is established (Fig. 10). Basal cells of the endothecium, which are more or less quadrate in outline, become vacuolate and are easily distinguished from the elongate cells of the archesporial zone above (Fig. 9). Each archesporial cell, in turn, segments into a quadrate basal and rectangular anterior cell, the former, differentiating into the central zone of the inner capsule wall and the latter producing the spores and elaters (Fig. 10). Spore and elater initials alternate with each other in both planes and as a result any spore rank is associated with four elater initials (Fig. 11, 12, 16, 17). Each elater initial loses division potential at this stage, while spore initials divide many times transversely to form 20 or more spore mother cell initials (Fig. 11).

Distinctions between inner and outer capsule wall cells, likewise, begin to appear at this stage. The outer cells expand considerably in radial diameter and appear rather vacuolate, while the inner cells remain densely cytoplasmic with a 2.5-3.5 μm radial diameter. By the time the quadrilobed spore mother cells appear within the archesporium, the outer wall cells are quadrate in outline and measure 15-16 μm in diameter and the inner are rectangular in outline and measure 15-16 μm × 2.5-3.5 μm (Fig. 12). Throughout sporogenesis, further

differential expansion occurs so that in the mature capsule outer cells measure 27-30 μm in both width and length, while inner cells are 27-30 μm long and 16-20 μm wide (Fig. 13, 14). Inner wall cell enlargement, in fact, occurs only in very late stages of growth and appears to be accompanied by the decomposition of inner and outer wall thickenings.

Spore wall, elater and capsule wall thickening materials are first evident after the formation of spore tetrads from the spore mother cells, i.e., after meiotic divisions are complete (Fig. 13). This material, which is pale yellow in living specimens, bonds safranin in sectioned and stained preparations and can be first discerned as small globules on the tetrad walls and irregular thin sheets on the innermost walls of the inner capsule wall cells (Fig. 13). Light microscope sections suggest that spore wall ornamentation is completely exinous (Fig. 13, 14), although, of course, TEM preparations are necessary for absolute confirmation of this fact. At least when the safranin-staining globules, or punctae, first appear on the wall surfaces, the tetrads seem to be enclosed by a thin common outer wall, i.e., the special spore mother cell wall. All exospore ornamentations, including the radiating spines which form typical Lejeuneaceous rosettes, develop prior to tetrad separation (Fig. 15-A) in contrast to *Frullania dilatata* (L.) Dum. where rosettes appear as the spore expands after disjoining from the tetrad (NEIDHART, 1979).

Capsules in which sculptured tetrads occur also possess vertically oriented elaters with complete, unispiral, pale yellow thickening bands. The thickening bands encircle the free, flattened, orbicular bases of the elaters and extend in an even spiral to just below the apical attachments to the valve wall. They do not appear to be confluent with the inner wall thickenings themselves. The tapered elater typically remains attached to the upper portions of the inner capsule wall, even after the valves open (Fig. 16-18). The unispiral bands are, in turn, ornamented with very small, randomly scattered punctae (Fig. 19). Each elater measures 12-14 μm in diameter, about one-third the diameter of the developing tetrads.

Likewise, at the sculptured tetrad stage pronounced modification of inner wall surfaces are evident (Fig. 14, 16, 20-23). Safranin-binding, thickening material covers, more or less evenly, the inner tangential wall of each inner cell except for 4-12 large, pitted regions which appear as depressed areas in scanning electron micrographs (Fig. 20-22). In sectioned, light microscope preparations these pits do not bond safranin and hence appear as clear holes in the wall surface (Fig. 14). The pit regions are randomly distributed, circular to oblong in outline and range from 3.0-3.5 μm in diameter. Outer wall cells concomitantly develop pale yellow, I-shaped thickening bands along some of the radial walls (Fig. 14, 23). Both inner and outer wall cells remain protoplasmic until wall deposition is completed, as evidenced by the presence of internal cellular debris in hand-sectioned SEM viewed specimens (Fig. 23). This could, at least, suggest that the wall cells themselves are the source of the deposition materials.

In capsules in which separated, green, swollen spores are found, the protoplasmic contents of elaters, and wall cells are fully deteriorated, and small perforations begin to form in the unthickened, inner wall depressions (Fig. 24). The spores are irregular in shape and display a curved distal face and five or more polyhedral, lateral faces converging on a proximal ridge (Fig. 25). Each spore possesses numerous, locally clustered papillae, averaging 0.5 μm in height, and at least four sunken rosette formations. Each rosette consists of two circular ranks of large (1.0-1.5 μm high), tooth-shaped projections which incurve to overtop a thin area in the exospore wall (Fig. 25, 26). The orientation of the rosette projections around these exine depressions suggests that the rosette structures could possibly function in water absorption, following spore dispersal. A potential for water uptake through the spore wall would be particularly critical since spore germination is endosporic and precocious. The spore, when released from the capsule, is metabolically active, growing through mitotic divisions. Until it emerges from the spore wall, continued growth requires efficient water uptake through the exine, with maximum conservation of internal water. The pore-like semblance of the rosette would likely provide for both.

When the endosporic sporelings have reached the three- to four-celled stage, the seta elongates through vertical expansion of its cells. This action pushes the capsule beyond the investing calyptra, perianth and bracts. Tensions created by evaporation from the outer capsule wall cells cause the valves to roll back along four lines of dehiscence (Fig. 27). The elaters, which are also drying, spring outward, flinging the multicellular spores out of the capsule. Rewetting at this stage will induce the valves and attached elaters to fold back inwards toward the spore mass in much the same manner as peristome teeth move. Once the valves are completely reflexed so that the inner capsule wall is fully exposed, the ability to re-close is lost.

The foot of the mature sporophyte is bulbous to rapiform and comprised of numerous, isodiametric cells, ranging from 22-28 μm in diameter (Fig. 28). It is seven to ten cells broad at its widest point and seven to eight cells high. Seta cell arrangement is nonarticulate (Fig. 29). Elongation doubles the dimensions of the vertical walls so the cells, after elongation, are quadrate in outline. Except near the valve borders, the outer capsule wall cells in dehisced capsules are collapsed toward the inside (Fig. 29) and translucent (Fig. 30). In surface view they are quadrate to rectangular, from 32-46 μm × 32-35 μm in dimensions, with nodular, pale yellow trigones that can measure to 14.5 μm across.

The plurifenestrate pattern of the upper two-thirds of the inner capsule wall is now also evident (Fig. 31). Viewed with a light microscope, the fenestrae appear simply as rounded areas that are devoid of the pale yellow inner wall materials. Scanning electron micrographs, however, demonstrate conclusively that they are, in fact, perforations in the wall surface (Fig. 32-35). The distribution of the perforations correlates with the pattern of depressions seen at the spore tetrad stage (Compare Fig. 20-22 with Fig. 32-35). Slight cell enlargement

accompanies these last stages of inner wall modification; i. e., average inner wall cell lengths expand from 25-28 μm in the tetrad containing capsule to 30-34 μm in the dehisced capsule. Likewise, the fenestral perforations measure 4.4-6.6 μm in diameter as compared to the 3.0-3.5 μm dimensions of the original depressions. Such dimensional changes might suggest that formation of the perforations is due merely to tearing at points of weakness as the wall expands. On the other hand, the smooth, even outlines and rather constant shapes of the perforations (Fig. 34, 35) are indicative of exactive degeneration similar to that responsible for the formation of pits in liverwort hydroids (BURR & al., 1974; SMITH, 1966; HÉBANT, 1977). That the fenestrae pattern represents previous plasmadesmatal arrangements, as is the case with hydroid perforations, is however, not probable since these cell surfaces are free from contact with other cells throughout most of their development. A definitive explanation of fenestrae formation will require TEM studies of comparable morphogenetic stages. Likewise, hypotheses concerning the adaptive and subsequent evolutionary significance of this type of capsule wall anatomy must await detailed comparative studies of annular, reticulate and monofenestrate patterns.

Conclusions

Observations of sporophyte ontogeny in *Spruceanthus marianus*, made with the combinations of light and scanning electron microscopy techniques, have resulted in several findings that are pertinent to understanding the biology of the *Lejeuneaceae*. Although a three-celled, filamentous embryo is characteristic of the Jungermanniopsida, as defined by STOTLER & CRANDALL-STOTLER (1977), the development of both foot and seta from hypobasal derivatives has not been previously reported in this class. Differential rates of capsule division and early growth of the foot and seta allow for rapid formation of the archesporium with minimal energy output for vegetative growth, and appear to be responsible for reduction in overall sporophyte size. Comparable mitotic delay mechanisms have not been evidenced in other groups in which sporophyte reduction occurs, including the *Jubulaceae* Klinggr. (HY, 1884; CRANDALL-STOTLER & GUERKE, 1980) and the *Corsiniaceae* Engl. (LEITGEB, 1879). In sharp contrast to the more generalized, spindle-shaped embryo that results from synchronous division rates (SCHERTLER, 1979; fig.24), *Spruceanthus* embryos display an enlarged, spherical capsule and narrowed seta and foot after only a few division sequences. The extent of other embryological variation within the *Lejeuneaceae* would surely be useful in evaluating adaptive trends.

The events of inner and outer capsule wall cell specialization are of particular interest. The discovery that the multiple fenestrae are wall perforations produced from zones free of secondary deposition raises perplexing questions as to function and cellular significance of inner capsule wall thickening patterns.

Likewise, the synchronous deposition of capsule wall, elater and sporoderm thickenings raises questions as to the sources and chemical features of these materials. Similar safranin-bonding qualities in each structure suggest chemical relationship, which only future studies can elucidate. The distinct structural differences of inner and outer capsule wall layers are, of course, correlated with dehiscence mechanisms, but one must also wonder if the perforate mature of the inner wall is also correlated with the environmental necessities of precociously germinating spores.

The process of exine sculpturing, reported for the first time in a Lejeuneaceous taxon, is distinct from that reported in the *Jubulaceae* (NEIDHART, 1979). All ornamentation is deposited prior to tetrad separation and appears to be exinous as compared to the possible perinous deposits of *Frullania dilatata*. Rosettes, while present, are few in number and also appear in tetrad stages in contrast to the numerous rosettes which appear only during spore enlargement in *Frullania*. Overall, this first modern study of embryology and subsequent sporophyte morphogenesis in a Lejeuneaceous taxon demonstrates the importance of such investigations in filling informational gaps and broadening the data base that is essential to phylogenetic judgments.

Addendum

In an earlier publication (CRANDALL-STOTLER & GEISSLER, 1983) these populations were referred to *Spruceanthus polymorphus* (Sande Lac.) Verd. The subsequent opportunity to study Japanese populations of *S. semirepandus* (Nees) Verd., Japanese, Javan and Hawaiian populations of *S. polymorphus,* a Chinese population of *S. mamillilobulus* (Herz.) Verd., and an additional population of similar organisms from Koitaki, New Guinea has convinced us that the New Guinean plants should be referred to *S. marianus* rather than *S. polymorphus*. Although these taxa are of somewhat similar facies (VERDOORN, 1934), *S. marianus* is distinct in the following traits: the leaves are generally entire with a subacute to acute rather than obtuse apex, and with the postical margin being straight to weakly arched and smooth rather than being conspicuously arcuate and undulate to crispate; the underleaves are broadly ovate to suborbicular, entire and no more than twice the width of the stem unlike the broader, occasionally toothed and usually crispate forms of *S. polymorphus;* female bracts and bracteoles likewise are more or less entire and non-crispate and the mature perianth is 5-keeled, with 1 dorsal, 2 lateral and 2 broad ventral keels, as compared with the 6-keeled perianths of *S. polymorphus*, where 3 sharp ventral keels occur.

The *marianus* character assemblage has traditionally been ascribed to the genus *Archilejeunea* (Spruce) Schiffn. MIZUTANI (1966) transferred this taxon to *Spruceanthus*, indicating that there are many similarities, particularly between *S. marianus* and *S. polymorphus*. GROLLE (1978) and GRADSTEIN &

INOUE (1980) have recognized this alignment and in fact, GRADSTEIN (1975) has suggested that perhaps many more species presently assigned to *Archilejeunea* should be ascribed to *Spruceanthus*. According to GRADSTEIN (1975), oil body morphology may be a useful character in separating these two closely related units. *Spruceanthus* is reported to have numerous, small homogenous oil bodies (SCHUSTER & HATTORI, 1954; MIZUTANI, 1961; GRADSTEIN, 1975), while *Archilejeunea,* with the known exception of *A. kiushiana* (Horik.) Verd., possesses larger, segmented oil bodies (GRADSTEIN, 1975). Recently, UDAR & AWASTHI (1982) proposed that *Spruceanthus marianus* is, indeed, an *Archilejeunea* as previously aligned, based on the discovery of elongate, segmented oil bodies in the leaf cells of plants from India. Our observations of populations from New Guinea, likewise, show in growing, green shoots segmented oil bodies (Fig. 1). Cells of the middle, which measure 20-26 µm, possess 10-15 colorless, elongate oil bodies, measuring 2.5-3.0 × 7.4-8.0 µm in complete concurrence with Udar and Awasthi's observations.

That this character necessarily denotes "a genuine species of *Archilejeunea*" (UDAR & AWASTHI, 1982), however, is debatable. Oil body morphology does vary with the amount of drying and level of deterioration of a specimen. Homogenous forms may become segmented with specimens drying and segmented forms can also become homogenous (GRADSTEIN, 1975). Indeed, delimitation of generic categories should await detailed analysis of *all* characters in both taxa, including a survey of oil body variability and its significance. For the present, we shall follow MIZUTANI's (1966) placement of these organisms in *Spruceanthus marianus* (Gott.) Mizut. because of the long recognized morphological similarities with other *Spruceanthus* species.

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REFERENCES

ANDERSEN, E. N. (1929). Morpholgy of sporophyte of Marchantia domingensis. *Bot. Gaz.* 88: 150-166.

BURR, R. J., B. G. BUTTERFIELD & C. HÉBANT (1974). A correlated scanning and transmission electron microscope study of the water-conducting elements in the gametophytes of Haplomitrium gibbsiae and Hymenophyton flabellatum. *Bryologist* 77: 612-617.

CRANDALL-STOTLER, B. & P. GEISSLER (1983). Embryogenesis and capsule wall differentiation in Spruceanthus polymorphus. *ASB Bull.* 30 (in press).

– & W. R. GUERKE (1980). Developmental anatomy of Jubula Dum. (Hepaticae). *Bryologist* 83: 179-201.

GRADSTEIN, S. R. (1975). A taxonomic monograph of the genus Acrolejeunea (Hepaticae). *Bryoph. Biblioth.* 4: 1-162.

– & H. INOUE (1980). Studies on Lejeuneaceae subfam. Ptychanthoideae, V. A review of the species from Ceylon. *Bull. Natl. Sci. Mus., ser. B. (Bot.)* 6: 23-32.

GROLLE, R. (1978). Die Lebermoose der Seychellen. *Wiss. Z. Friedrich-Schiller-Univ. Jena, Math.-Naturwiss. Reihe* 27: 7-17.

HATCHER, R. E. (1965). Towards the establishment of a pure culture collection of Hepaticae. *Bryologist* 68: 227-231.

HÉBANT, C. (1977). The conducting tissues of bryophytes. *Bryoph. Biblioth.* 10: i-xi, 1-157, Pl. 1-80.

HY, F. (1884). Recherches sur l'archégone et le développement du fruit des Muscinées. *Ann. Sci. Nat., sér.* 6, 18: 105-206, pl. 9-14.

JOHANSEN, D. A. (1935). Dehydration and infiltration. *Science* 82: 253-254.

KIENITZ-GERLOFF, F. (1874). Vergleichende Untersuchungen über die Entwickelungsgeschichte des Lebermoos-Sporogoniums. *Bot. Zeitung (Berlin)* 32: 161-172, 193-204, 209-217, 224-235.

LEITGEB, H. (1875). *Untersuchungen über die Lebermoose. II. Die foliosen Jungermannieen.* Jena.

– (1879). *Untersuchungen über die Lebermoose. IV. Die Riccieen.* Graz.

McNAUGHT, H. L. (1929). Development of sporophyte of Marchantia chenopoda. *Bot. Gaz.* 88: 400-416.

MIZUTANI, M. (1961). A revision of Japanese Lejeuneaceae. *J. Hattori Bot. Lab.* 24: 115-302.

– (1966). Supplement to "Revision of Japanese Lejeuneaceae". II. *J. Hattori Bot. Lab.* 29: 290-293.

– (1970). Branching types of Lejeuneaceae. *Misc. Bryol. Lichenol.* 5: 81-96.

NEIDHART, H. V. (1979[1980]). Comparative studies of sporogenesis in bryophytes. *In:* CLARKE, G. C. S. & J. G. DUCKETT (eds.), *Bryophyte Systematics,* pp. 251-280. Academic Press, New York, London. [= *Syst. Ass. Special Vol.14*].

SCHERTLER, M. M. (1979). Development of the archegonium and embryo in Lophocolea heterophylla. *Bryologist* 82: 576-582.

SCHUSTER, R. M. (1966). *The Hepaticae and Anthocerotae of North America, vol. I.* New York, London.

– (1980). *The Hepaticae and Anthocerotae of North America, vol. IV.* New York.

– & S. HATTORI (1954). The oil-bodies of the Hepaticae. II. The Lejeuneaceae. *J. Hattori Bot. Lab.* 11: 11-86.

SMITH, J. L. (1966). The liverworts Pallavicinia and Symphyogyna and their conducting system. *Univ. Calif. Publ. Bot.* 39: 1-83, Pl. 1-18.

STOTLER, R. E. & B. CRANDALL-STOTLER (1977). A checklist of the liverworts and hornworts of North America. *Bryologist* 80: 405-428.

UDAR, R. & U. S. AWASTHI (1982). The status of Spruceanthus marianus (Gott.) Mizut. in India. *J. Bryol.* 12: 33-36.

VERDOORN, F. (1934). Studien über asiatische Jubuleae. De Frullaniaceis XV. Die Lejeuneaceae Holostipae der Indomalaya unter Berücksichtigung sämtlicher aus Asien, Australien, Neu-Seeland und Ozeanien angeführten Arten. *Ann. Bryol. Suppl.* 4: 40-192.

Addresses of the authors: B. C.-S.: Department of Botany, Southern Illinois University, Carbondale IL 62901. U.S.A.

P. G.: Conservatoire et Jardin botaniques de la Ville de Genève, Case postale 60, CH-1292 Chambésy/GE.