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Revision of the Genus *Christensenia*

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The present revision of *Christensenia* is the first for this genus. Observations of external and internal foliar morphology, with particular emphasis on valid taxonomic characters of pinna indument and epidermis and soral paraphyses have shown that the taxa of the genus are *C. aesculifolia* Blume subsp. *aesculifolia* and subsp. *korthalsii* (de Vriese) Rolleri and *C. lobbiana* (de Vriese) Rolleri. Synangium outline, number of sporangia per synangium, and spore morphology are not systematically important. The morphology and physiology of adult porocyclocytic stomates and the presence, chemical composition, and density of microprojections of the mesophyll cell walls are adaptive and vary according to ambient humidity.

The generic name *Christensenia* was proposed by Maxon (1905) to replace the later homonym *Kaulfussia* Blume. De Vriese and Harting (1853) recognized four species of *Kaulfussia*, *K. aesculifolia* Blume (Java and the Philippines), *K. assamica* Griff. (Assam), *K. korthalsii* de Vriese (Sumatra and the Philippines), and *K. lobbiana* de Vriese (Java). Baker (1874, p. 444) synonymized the three later species in *K. aesculifolia*, and most later scholars agreed, including Maxon (1905), although he did acknowledge variation within the inclusive species *C. aesculifolia* (Blume) Maxon. Christ (1907) described *C. cumingiana* from the Philippines. Christensen (1938, p. 528) mentioned "2 Malayan species" without naming them. Copeland (1909) recognized *C. aesculifolia*, distributed from Malaysia to northern India, and *C. cumingiana*, from the Philippines. Later, Copeland (1958, pp. 27–28) reduced the latter species to *C. aesculifolia* and stated for it a general distribution from India to the Philippines, including Sumatra and Java. A similar concept was adopted by Holttum (1955, pp. 45–46). Ching (1940) separated *Christensenia* from the Marattiaceae into a new family Christenseniaceae and recognized two species, *C. aesculifolia* and *C. cumingiana*, to which he later (Ching, 1959, p. 65) added *C. assamica* (Griff.) Ching. Pichi Sermolli (1970, p. 234) adopted Ching's segregation of the Christenseniaceae. Braithwaite (1977), Walker (1979), Hill and Camus (1986), and Camus (1990, p. 177–178) analyzed different aspects of the genus, but considered it to be monospecific.

MATERIALS AND METHODS

Specimens were examined from the Muséum National d'Histoire Naturelle, Paris (P), the Instituto Darwinion, San Isidro (SI), and the United States National Herbarium, Washington (US). Some 50–80 microscope slides were made of fragments from each taxon and are deposited at the Museo de La Plata.

Adult pinnae were cleared for 24 hr. with aqueous 2.5% NaOH and saturated aqueous chloral hydrate. To minimize fragility of the samples after they were cleared, they were treated with a mixture of 540 ml 95% ethanol, 210 ml distilled water, 240 ml glycerine, and a few drops of formalin, which gave them elasticity and new strength. Staining material after this treatment gave better results.

General stains used were ferric chloride-tannic acid (Foster, 1934), Chlorazol Black E (Gurr, 1966, p. 275), Safranin-Aniline Blue (Gurr, 1966, p. 306), and 1% aqueous Ruthenium Red. Several authors (Johansen, 1940, p. 200; Venning, 1934, p. 20, and

D'Ambrogio de Argüeso, 1986, p. 76) used different concentrations of Ruthenium Red; I found that 1% is adequate and fast-acting (20–30 sec.).

Specific stains used to reveal the nature of epidermal cell walls, papillae and trichome walls, and microprojections of mesophyll cell walls were Toluidine Blue and zinc chloride-iodine (D'Ambrogio de Argüeso, 1986, pp. 70, 72), Indophenol Blue (Peacock, 1966), Methylene Blue (Johansen, 1940, pp. 200), and Ruthenium Red, as explained above.

Specific stains and methods used to reveal the nature and contents of trichome cells were the preceding (except for zinc chloride-iodine) plus Lugol's Solution, iodine (both according to Johansen, 1940, pp. 183, 189 and D'Ambrogio de Argüeso, 1986, p. 75), Sudan IV in ethylene glycol (Gurr, 1966, p. 313–314), the Per-iodic-Schiff (PAS) method (Gurr, 1966, p. 296–298), and Sudan IV in saturated isopropanol, a technique I developed.

EPIDERMAL PATTERNS AND CELL WALLS

Cell sizes and wall patterns differ in the epiphyll and hypophyll. Wall patterns seen in cleared preparations are straight, angular, or sinuous (Figs. 1L, H, E), and the latter two kinds may be either frequent or subfrequent (e.g., sinuous-frequent, angular-subfrequent). Walls themselves seen in cross-section show different degrees of thickening across the walls and differences in regularity of thickening along the walls.

The epiphyll cells of *C. aesculifolia* subsp. *aesculifolia* (Fig. 1A) are larger and have slightly thinner walls (Fig. 1B) than those of the other taxa (Figs. 1E, F, I, J). The cells are elongate (1:w = 2–3:1) in *C. aesculifolia*, but are nearly isodiametric in *C. lobbiana*. All epiphylls have a sinuous-frequent pattern (Figs. 1A, E, I). The sinuosities are slightly more marked in *C. lobbiana* (Figs. 1I, J) than in the other taxa. The wall thickenings are generally more marked in *C. aesculifolia* subsp. *aesculifolia* and in *C. lobbiana* (Figs. 1B, J) than in some material of *C. aesculifolia* subsp. *korthalsii* (Fig. 1F), and the latter subspecies has more irregular thickenings.

The epiphyll patterns of *Christensenia* are noticeably like those of some *Danaea* species, especially *D. nodosa* (L.) J. E. Smith, whereas *Marattia* and other *Danaea* species have angular epiphylls (Rolleri et al., 1987).

The hypophylls are more variable than the epiphylls. In *C. aesculifolia* subsp. *aesculifolia*, the pattern is sinuous-subfrequent with shallower sinuosities, the cells are somewhat elongate (1:w = 2–3:1), and the cells are more irregularly thickened than in the epiphyll (Figs. 1C, D). In *C. aesculifolia* subsp. *korthalsii*, the pattern is angular-subfrequent, the cells are more elongate (1:w = 2–4:1), and the thickened areas of the cells are irregular (Figs. 1G, H). In *C. lobbiana*, the pattern is polygonal, some of the cells are subsodiametric (1:w = 1–2:1), and the walls are irregularly thickened (Fig. 1K, L).

STOMATA

The stomata are basically cyclocytic. The guard cells are strongly arcuate and circumscribe the stomatal pore, which may be up to 200–240 μm in diam. and which may be found in every degree of openness, presumably depending upon ambient climate. The subsidiary cells are arranged in 2–3(5) cycles of narrow, arcuate cells that are distinct from the adjacent epidermal cells. Unlike most stomata, all the cells in *Christensenia*, including even the fourth and fifth cycles of subsidiary cells, protrude above the plane of the epidermis.

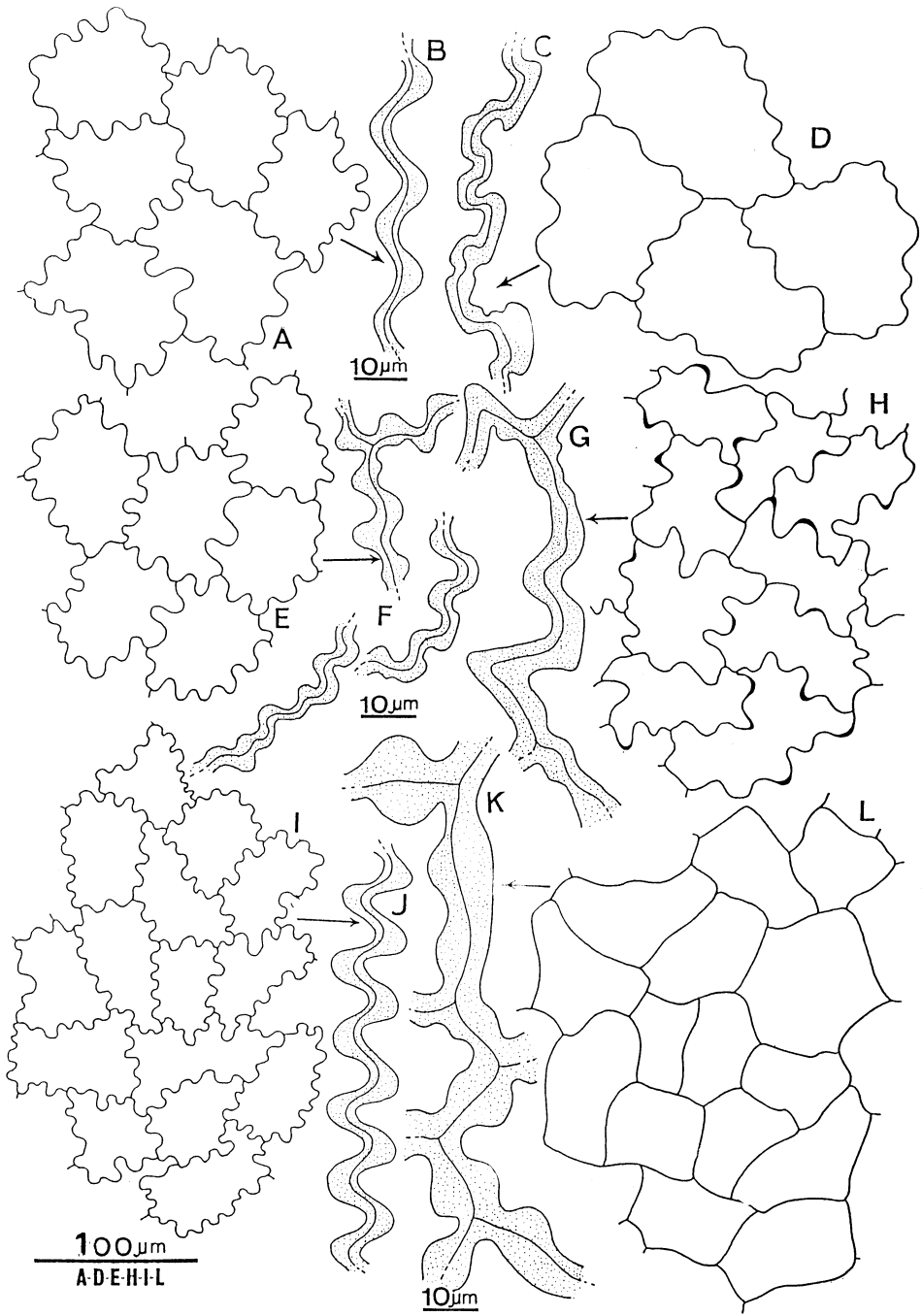


Fig. 1. Epidermal patterns and details of cell walls in *Christensenia*. A–D. *C. aesculifolia* subsp. *aesculifolia*. A, B. Epiphyll. C, D. Hypophyll. E–H. *C. aesculifolia* subsp. *korthalsii*. E, F. Epiphyll. G, H. Hypophyll. I–L. *C. lobbiana*. I, J. Epiphyll. K, L. Hypophyll.

Rolleri et al. (1991a) studied the ontogeny, development, and physiology of these stomata in *C. lobbiana* (as *cumingiana*), which they named porocyclocytic. In this species the ontogeny is perigenous. The typical cyclocytic stomata of other genera of the Marattiales, which also can be seen in apical and marginal areas of *Christensenia* pinnae, represent a phase toward the fully developed porocyclocytic stomata of *Christensenia*.

In *C. aesculifolia* subsp. *aesculifolia*, the paired guard cells are very large and strongly arcuate; in subsp. *korthalsii* a third guard cell has rarely been seen; in *C. lobbiana*, the guard cells occasionally divide anticlinally after the pore is formed, and up to 5 of them can be found in a single stoma in the pinna apices, intermingled with more typical stomata having a single pair of guard cells.

Rolleri et al. (1991a) interpreted the porocyclocytic stomata as an adaptation to the functions primarily of gas exchange and secondarily of liquid water secretion, as if the stomata were hydathodes. Given the highly humid ambient conditions of *Christensenia*, the stomata probably act in these ways alternately.

TRICHOMES

The epiphylls of *Christensenia* are always glabrous. The hypophyll of *C. aesculifolia* subsp. *aesculifolia* is subglabrous (Figs. 2A–E) to glabrous, with a scattering of branched hairs and a few uniseriate hairs. The costae and veins bear a few scales and occasionally smooth papillae. The hypophylls of the other taxa have a random mixture of indument types in the veins and lamina surface, giving them a characteristic trichomatose appearance that is easily seen at low magnifications. The hypophylls of *Danaea* bear a similar indument (Rolleri et al., 1991b).

The trichomes of *Christensenia* are all glandular in nature. Tests for fats were strongly positive for capitate cells and papillae, whereas tests for starch, saponine, essential oils, inuline, and proteins were negative. In contrast, the trichomes of *Danaea* are tanniferous. Trichome walls are cellulosic with weak traces of a cutin layer. Although four kinds of trichomes can be distinguished, intermediate stages between papillae and unbranched hairs, between unbranched and branched hairs, and between branched hairs and scales are known, and all probably share a common ontogenetic ancestor. This is confirmed by microchemical assays, which tend to show that all trichomes of the hypophyll are of the same origin.

Globose papillae. — Protruding, dome-shaped, reddish-brown papillae with a smooth or irregular surface (Figs. 3A, Y, A', F', 4A–B).

Uniseriate hairs. — Straight or curved, with a cylindrical or subconical basal cell, 1 to 7 cylindrical body cells that can be shorter than the basal cell, and a capitate apical cell (Figs. 2F–J, A'–C', 3B–E, I–N, B'–F').

Branched hairs. — Straight or rarely curved, with a cylindrical or subconical basal cell, a paucicellular body prolonged into short, paucicellular or uniseriate processes, and a capitate cell at the apex of each process. These trichomes are very diverse (Figs. 2A–E, S–Y, D', 3F–G, P–U). Some appear to be transitional between uniseriate hairs and branched hairs (Figs. 2K, 3O).

Scales. — Pluricellular, with a cylindrical basal cell, a partially to totally flattened body, with very short, paucicellular or unicellular processes, and a capitate cell at the apex of each process (Figs. 2Z, E', 3H, V–X, G'). Some appear to be transitional between branched hairs and scales (Figs. 2L–R, 3P–T). Despite their flattened bodies, these scales are not coordinate with the scales that are typical of the higher ferns, which appear to dif-

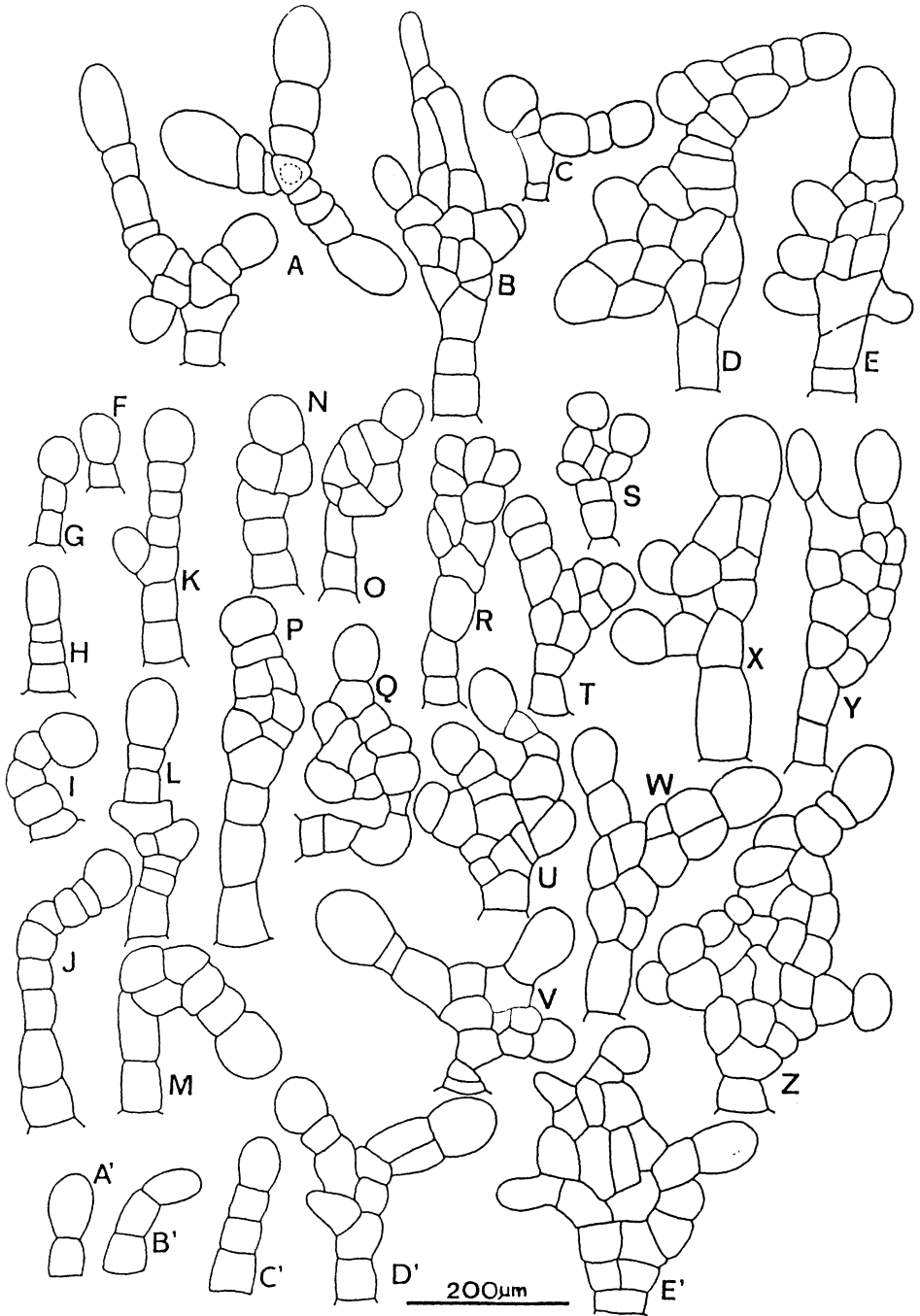


Fig. 2. Trichomes of the lamina surface in *Christensenia*. A-E. *C. aesculifolia* subsp. *aesculifolia*. F-Z. *C. aesculifolia* subsp. *korthalsii* and *C. lobbiana* types in common. A'-E'. Additional types in *C. lobbiana* (superficial papillae not shown).

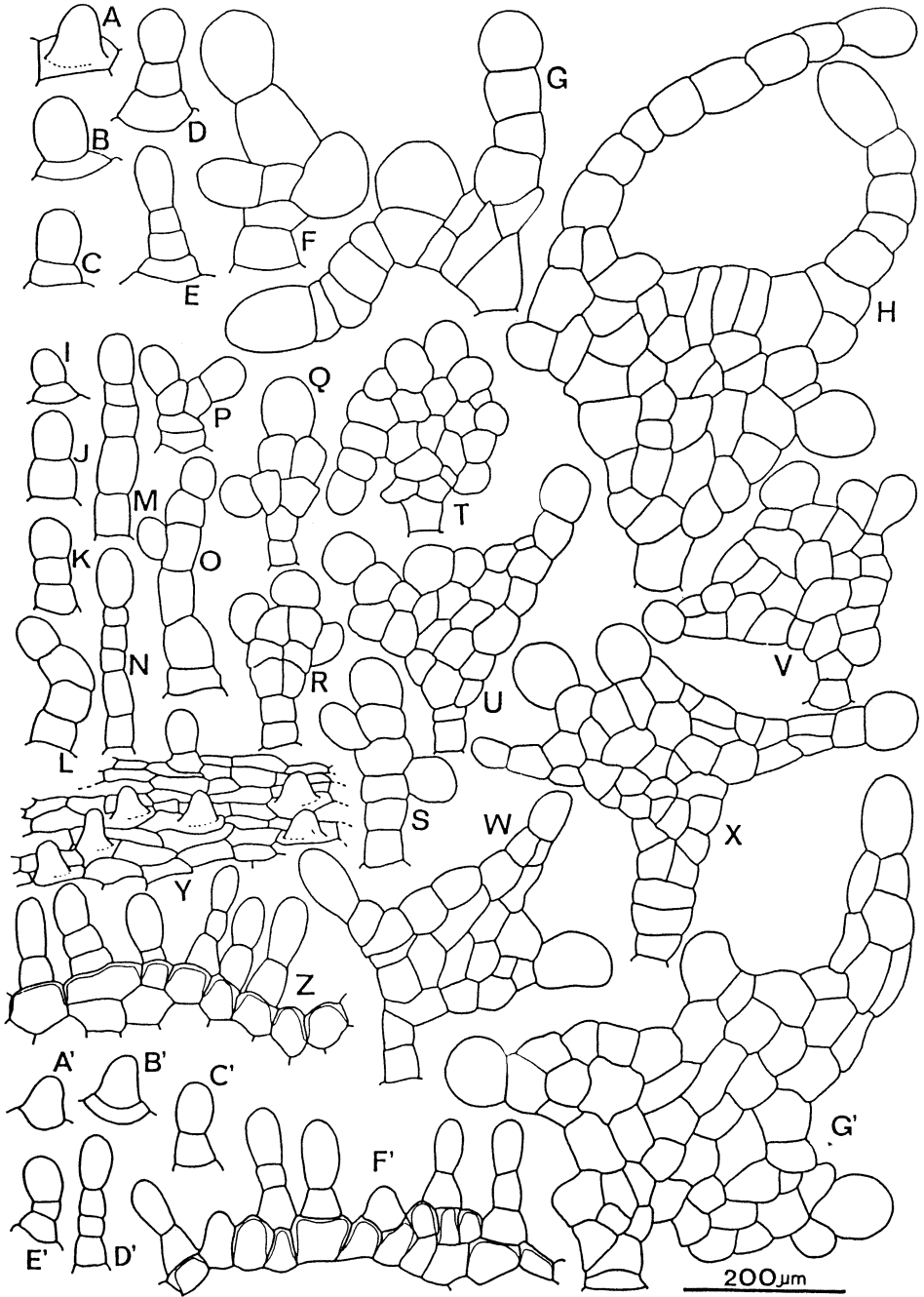


Fig. 3. Trichomes of the veins in *Christensenia*. A–H. *C. aesculifolia* subsp. *aesculifolia*. I–Z. *C. aesculifolia* subsp. *korthalsii*. A'–G'. *C. lobbiana*. Y. Secondary vein as seen in surface in *C. aesculifolia* subsp. *korthalsii*. Z. Same in cross-section. F'. Cross-section of vein. H, X, and G. Scales.

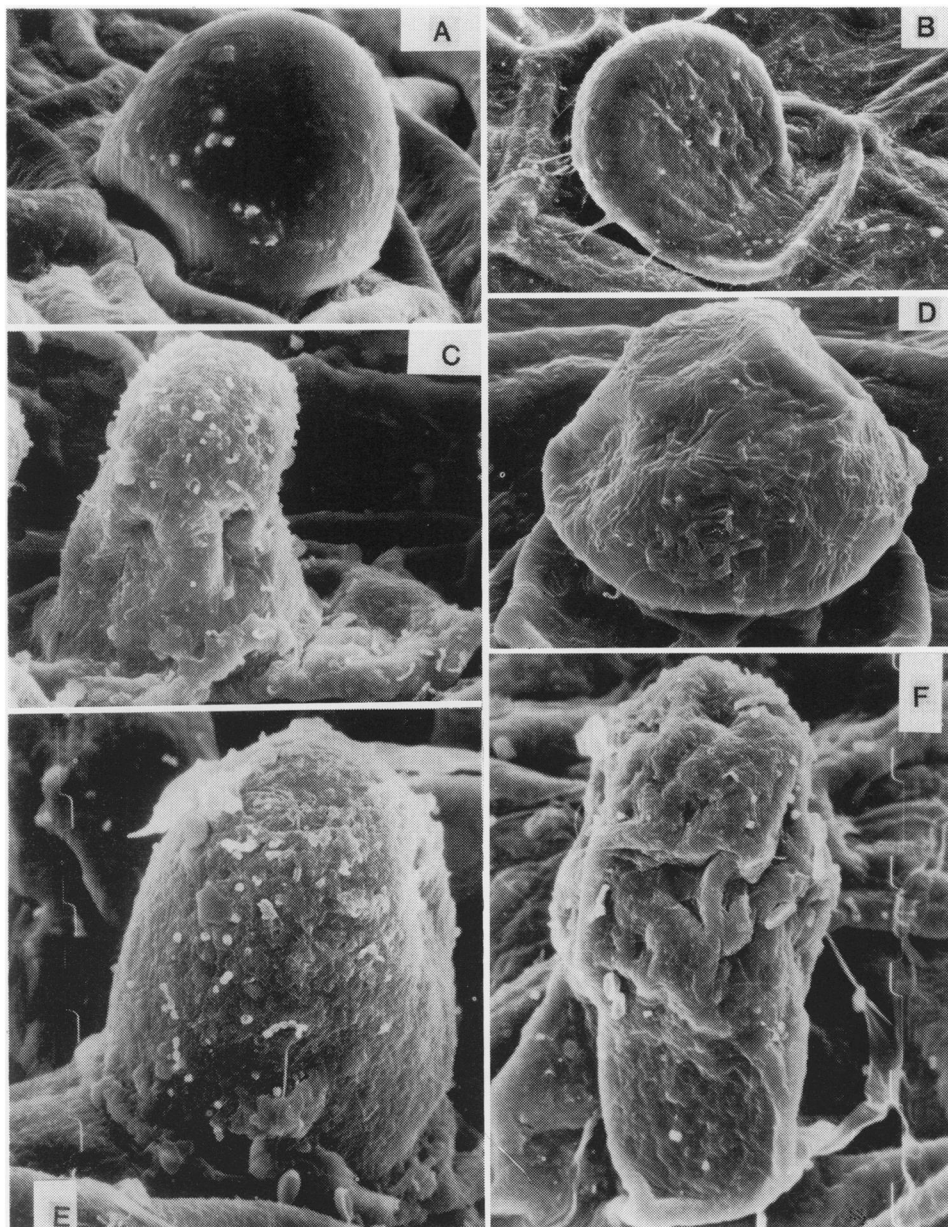


Fig. 4. SEM photographs of trichomes in *Christensenia*. A. Smooth papilla on secondary veins of *C. aesculifolia* subsp. *korthalsii* (abundant and dense). B. Small, superficial papilla in *C. lobbiana*. C-D. Bicellular trichomes in *C. aesculifolia* subsp. *korthalsii*. E. Large, rugose papilla on lamina and near veins in *C. lobbiana*. F. Bicellular trichome in *C. lobbiana*. Magnifications: A-B, x1500; C-F, x2000.

fer more markedly from hairs. Although they are the final developmental phase of trichomes in *Christensenia*, they appear to be an expansion of branched hairs.

MICROPROJECTIONS OF MESOPHYLL CELL WALLS

The laminae of *Christensenia* lack a typical photosynthetic palisade layer. The mesophyll cells are uniform, Y-branched, and connected by their ends, leaving wide intercellular spaces. They can be seen clearly through the ample stomatal pores and their most outstanding characteristics, the rod- or club-shaped microprojections of their outer walls (Figs. 5, 6). Luerksen (1873) illustrated them for *C. aesculifolia* sensu lato (as *Kaulfussia*) and also noted their appearance in roots, rhizomes, and stipes of *Angiopteris* (Luerksen, 1875). He thought the microprojections were composed of cellulose and cutin. Bary (1884) described them as projections of the cellular walls. Gardiner (1885) described them as composed of mucilage in *Aspidium filix-mas*, *Blechnum brasiliense*, and other ferns. Schenk (1886) stated that their composition does not include cellulose or waxes and that their biological meaning was enigmatic. Campbell (1911, p. 204) described them as "mainly composed of calcium pectate." Pettit (in Hill and Camus, 1986) suggested that they do not contain either proteins or lipids and that tests point to the presence of polysaccharides.

The microchemical tests I carried out indicated a general presence of hydroxylate polysaccharides (predominately cellulose) and traces of pectinate mucilages in the rounded ends of the microprojections and also in their lateral walls (mixed with cellulose).

The microprojections vary in density and relative size. The longest and narrowest microprojections are found in *C. aesculifolia* subsp. *aesculifolia*, especially from the Solomon Islands (Figs. 5D–E); the shortest, sometimes verrucose and with rounded ends, are found in *C. aesculifolia* subsp. *korthalsii* (Figs. 6D). The microprojections of *C. lobbiana* are similar to those of *C. aesculifolia*, but are more densely distributed (Figs. 6E–I). Variability may be related to habitat, rather than being taxonomically diagnostic. One could hypothesize that the presence of microprojections is related to the efficiency of water movement and retention within the pinnae. The mesophyll is poorly developed, only a few layers thick, and so the movement of water and water vapor within it would be strongly facilitated by the large stomatal pores. The microprojections on the outer walls of mesophyll cells would enlarge their hygroscopic surface, insuring a constant and dynamic water balance. The mucilaginous tips of the microprojections suggests this hygroscopic function.

SYNGANGIAL RECEPTACLES AND PARAPHYSES

The syngangia of *Christensenia* are elevated above the lamina surface by parenchymatous receptacles that appear dome-shaped in cross-section. The parenchyma on which the syngangium lies is sclerosed, and the cells are lignified (microchemical tests indicate a high concentration of polyphenols in the cell walls). When the syngangium is shed, the circular or elliptical scar formed by the dark brown, sclerosed cells is easily visible. Hill and Camus (1986) did not study the receptacles in detail and used the term placenta for them. However, that term has angiospermic connotations and need not be used in preference to the term receptacle.

Paraphyses are borne on the perimeter of the receptacles. Although paraphyses stain intensely with Ruthenium Red, they are eglandular and their cell walls are very thin and

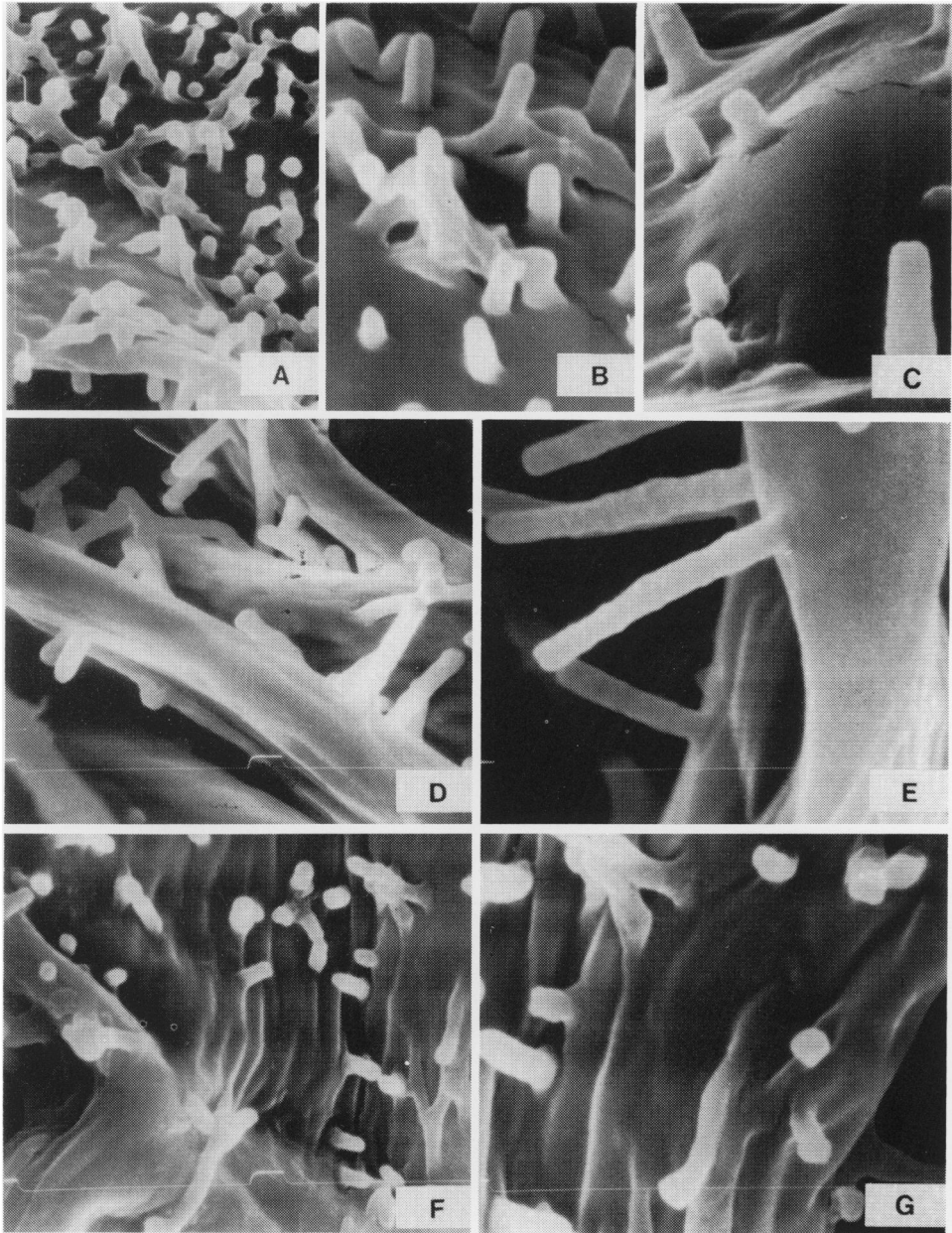


Fig. 5. Microprojections of mesophyll cell walls in *Christensenia aesculifolia* subsp. *aesculifolia*. A–C. From Java (Zollinger 1902, P). D–E. From the Solomon Islands (Braithwaite 4220, P). F–G. From Java (Buysman 2607, P). Magnifications: A, D, F, X5000; B, C, E, G, X10000.

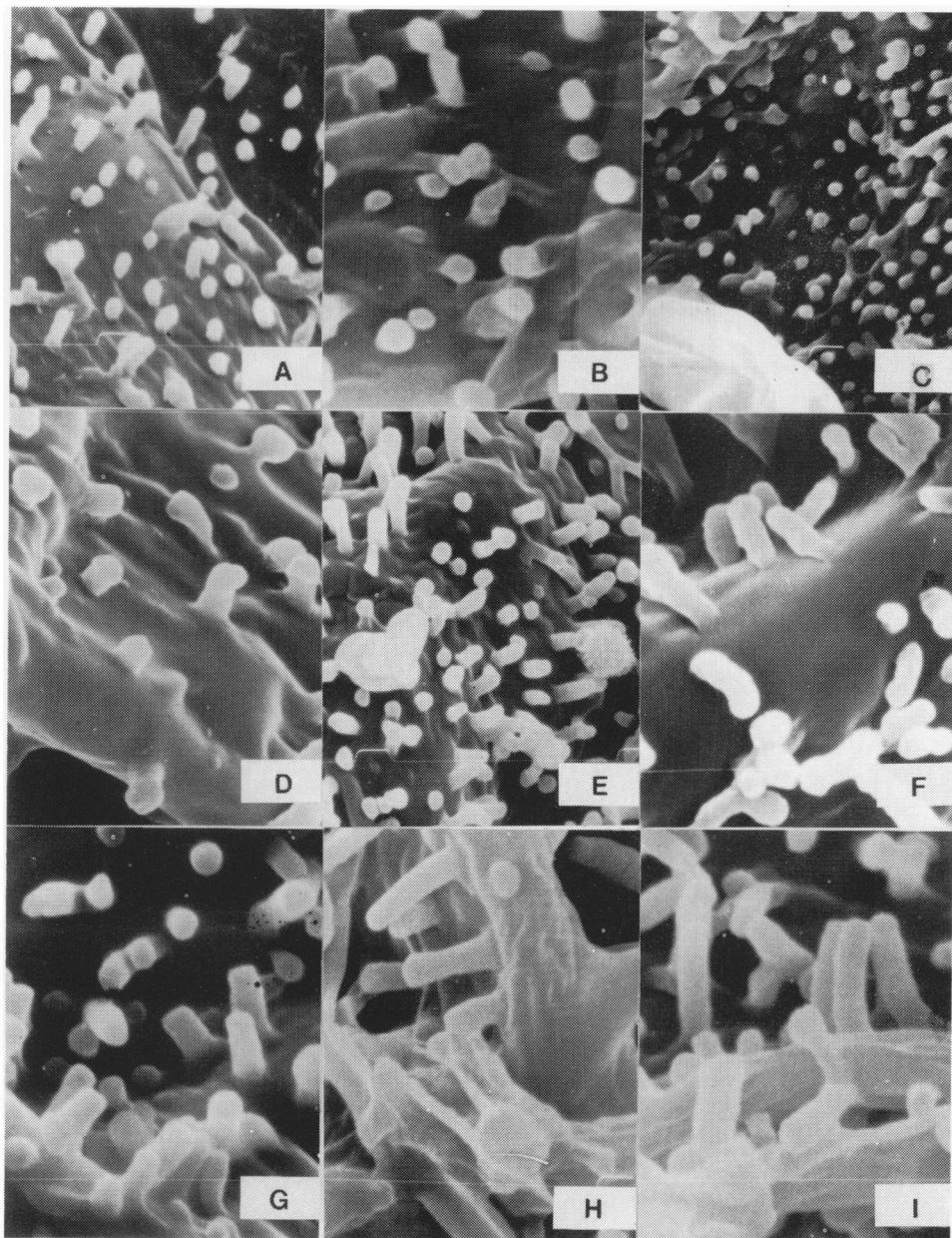


Fig. 6. Microprojections of mesophyll cell walls in *Christensenia*. A–B. *C. aesculifolia* subsp. *korthalsii* from Sumatra (Brooks 70.S, P). C–D. Same, from the Philippines (Copeland 2063, P). E–I. *C. lobbiana* from the Philippines. E–F. *Copeland s.n.* (P). G–H. *Edaño 36839* (P). I. *Robinson 17914* (P). Magnifications: A, C, E, X5000. B, D, F–I, X10000.

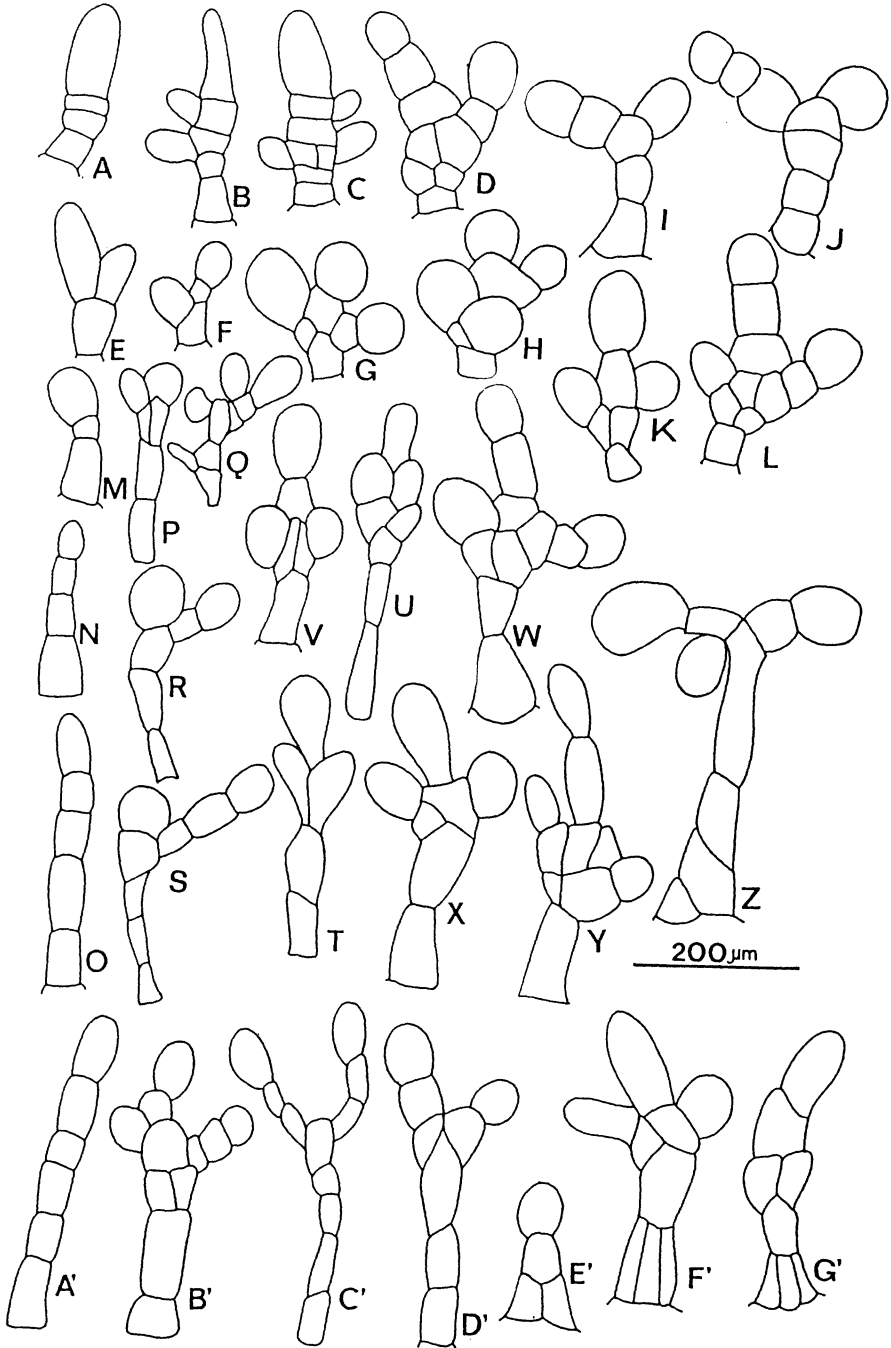


Fig. 7. Paraphyses in *Christensenia*. A–J. *C. aesculifolia* subsp. *aesculifolia*. K–Z. *C. aesculifolia* subsp. *korthalsii*. A'–G'. *C. lobbiana*.

cellulosic. Some of the hair-like paraphyses differ in shape and density in the taxa. Most paraphyses are uniseriate (Figs. 7A, M–O, A'), but a few are Y-shaped (Figs. 7I–J, Z, C'–D'). In *C. lobbiana*, paraphyses with a 3-celled base were seen (Figs. 7F'–G'). A few paraphyses resemble variously branched hairs (Figs. 7W–Y). Paraphyses having the form of small triangular, caducous scales have been observed occasionally at the edge of receptacles of young synangia of all taxa. These are of no taxonomic significance. Hill and Camus' (1986) term placental hair need not supplant the more usual term paraphysis.

TAXONOMIC TREATMENT

Christensenia Maxon, Proc. Biol. Soc. Wash. 18:239. 1905. — TYPE: A renaming of *Kaulfussia* Blume, and so based on the type of that name.

Kaulfussia Blume, Enum. Pl. Javae 2:260. 1828, nec Dennst. Schlüssel Hortus Malab. 30. 1818, nec Nees Horae Phys. Berol. 53, f. 11. 1820. — TYPE: *Aspidium aesculifolium* Blume [= *Kaulfussia aesculifolia* (Blume) Blume].

Macrostoma Griff. Asiat. Res. 19:108. 1836, non Hedwig, Gen. Pl. 102. 1806, which is *Macrostema* Pers. Syn. Pl. 1:185. 1805.

Plants terrestrial, at 1–1000 m elevation, usually in very dark shade in undisturbed forests on banks of small streams or rivers or on humid slopes. Rhizomes short-creeping, subascending, or erect, carnose to subcarnose, scaly, the scales basifixed, wide and rounded with undulate margins, castaneous with reddish spots. Stipes 1 or more, 8–35(45) cm long, stiff, carnose, slightly to deeply canaliculate, papillose and with scattered trichomes, the papillae very dense, bright reddish-brown, the trichomes similar to those of the costae. Fronds simple, ternate, or palmate with five pinnae. Laminae lanceolate or broadly so in simple fronds, nearly symmetrical to irregular, usually with a shallowly cordate or irregularly rounded base, this sometimes widened and undulate, with an acute, acuminate, or rarely obtuse-cuspidate apex. Pinnae of compound fronds sessile or nearly so, in ternate laminae the terminal one generally symmetrical, with a cuneate base and an acute or acuminate apex, the lateral pair pedate, sometimes quite reduced, in palmate laminae the terminal pinna similar, the basal pair strongly pedate or reduced or even curved. Laminae herbaceous, spongy, subcoriaceous, coriaceous, or carnose, the epiphyll smooth, bright dark green, the hypophyll opaque, light green to pale yellow. Costae and primary veins abaxially rigid and prominulous, roughly striate, indurated, and subglabrous, or slightly prominulous, not indurated, and distinctively papillose-trichomatose. Secondary veins anastomosing to form a reticulum of polygonal areolae with free included veinlets. Trichomes, if present, all glandular, a mixture of papillae, uniseriate hairs, branched hairs with a paucicellular body, and more elaborated scales with a pluricellular body and uniseriate processes, all with thin, cellulosic, slightly cutinized walls. Synangia circular to elliptic, the fused sporangia 8–12. Receptacles prominulous, mostly parenchymatous, but with the surface cells sclerosed. Paraphyses bordering the receptacles uniseriate and pluricellular or more commonly similar to the branched hairs of the lamina, but with more delicate, thinner walls and lacking glandular apical cells. Spores monoletic, elliptic in polar view, with a conical/spinulose ornamentation of close, short, sharp, but soft, spine-like processes throughout.

Distribution: India, Burma, Malaya, Sumatra, Java, Borneo, the Philippines, and the Bismark and Solomon Islands (Fig. 8).

KEY TO *CHRISTENSENIA*

1. Plants small to medium (up to 35 cm long); stipes densely papillose, often carnose, (9)10–23(25) cm long; fronds simple, occasionally ternate, rarely palmate, the lamina (or terminal pinna in compound fronds) lanceolate to broadly so, 9–10(15) cm long, 3–4(9) cm wide; lateral basal pinnae, if any, reduced in ternate fronds, pedate in palmate ones; laminae herbaceous to spongy, often subcarose; veins and lamina surface papillose-trichomatose, the trichomes diverse, bright, reddish-brown throughout. Laminae green adaxially, yellowish-green abaxially 3. ***C. lobbiana***

1. Plants medium to large (30–80 cm long); stipes (6)18–36(50) cm long, not densely papillose, stiff, deeply canaliculate in large fronds; fronds palmate, occasionally ternate, rarely simple, the terminal pinna (or lamina in simple fronds) lanceolate to rhomboidal, 15–18(25) cm long, 7–9(15) cm wide; lateral suprabasal pinnae, if any, asymmetric to pedate; lateral basal pinnae, if any, pedate; laminae herbaceous, papyraceous, subcoriaceous, or coriaceous; veins and lamina surface papillose-trichomatose, subglabrous, or glabrous, the trichomes, if any, diverse or reduced, yellowish except for the reddish-brown glandular cells..... 2

2. Indument diverse, the costae, veins, and lamina surface mostly papillose-trichomatose, the last abundantly so, the trichomes reddish-brown to reddish, mixed with dense papillae; laminae herbaceous to papyraceous, dark green adaxially, pale green abaxially.....

2. ***C. aesculifolia* subsp. *korthalsii***

2. Indument reduced to absent, the veins with scattered scales and occasional papillae not visible to the naked eye, the lamina surface with a few trichomes but no papillae; laminae subcoriaceous to coriaceous, green adaxially, pale green abaxially (or slightly yellowish in specimens from the Bismarck Archipelago and the Solomon Islands.....

1. ***C. aesculifolia* subsp. *aesculifolia***

1. ***Christensenia aesculifolia*** (Blume) Maxon, Proc. Biol. Soc. Wash. 18:240. 1905, subsp. ***aesculifolia***. — *Aspidium aesculifolium* Blume, Enum. P1. Javae 2:143. 1828. — *Kaulfussia aesculifolia* (Blume) Blume, Enum. P1. Javae 2:260. 1828. — TYPE: Java, “crescit in Javae Provinciae Bantam,” *Blume* (holotype L not seen Morton photo 766 US; isotype P? not seen).

Plants terrestrial, robust, up to 70(80) cm long; rhizomes erect to suberect, short, carnose, scaly, the scales large, rounded, undulate to subentire, bicolorous, castaneous with reddish spots; stipes fleshy when young, stiff and canaliculate at maturity, subpapillose and with scattered, small, castaneous-reddish scales; fronds palmate or occasionally ternate, the terminal pinna rhomboidal to broadly lanceolate, up to 22–25 cm long, 11–15 cm wide, cuneate at the base, acute to acuminate at the apex, the distal pinnae, if any, asymmetrical, the proximal pinnae pedate to almost crescent-shaped; laminae papyraceous to coriaceous, their margins entire or slightly undulate, revolute, subpapillose; costae prominent, rigid, indurated, glabrous to subglabrous, with scattered, variously branched hairs and scales; primary veins prominulous and rigid; lamina surface glabrous to subglabrous, sometimes with scattered, variously branched hairs, papillae absent; synangia usually circular, the fused sporangia 8–10; receptacles circular to elliptical;

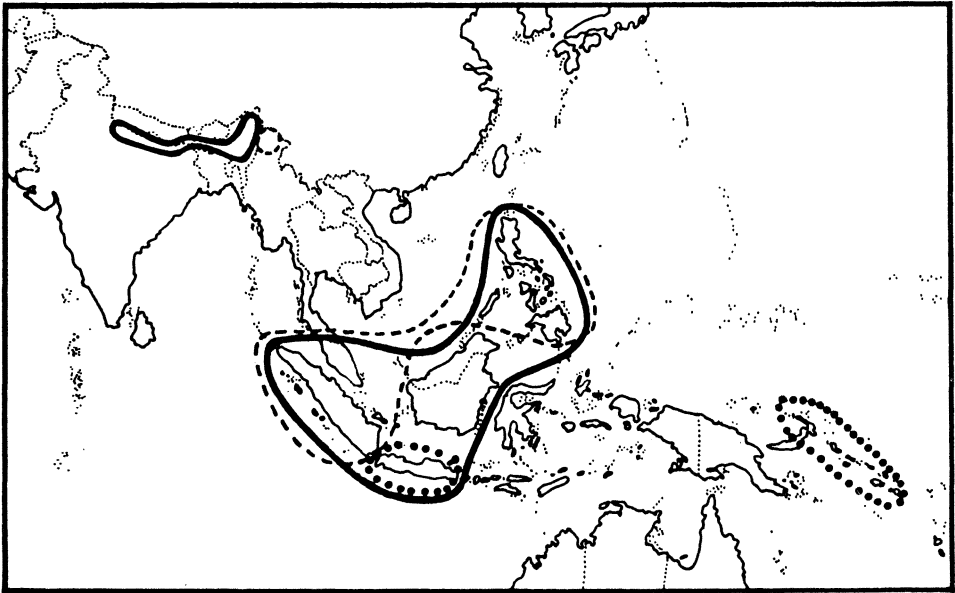


Fig. 8. Geographical distribution of the taxa of *Christensenia*. Solid line = *C. aesculifolia* subsp. *aesculifolia*. Dotted line = *C. aesculifolia* subsp. *korthalsii*. Dashed line = *C. lobbiana*.

paraphyses commonly short, paucicellular, simple, forked, or branched; scales small, caducous.

Cytology. — Previous cytological studies recorded $2n = 80$ for plants from Borneo (Walker, 1979) and $2n = 160$ for plants from the Solomon Islands (Braithwaite, 1977). Both numbers are based on $x = 40$, also known for other genera of Marattiales. Although the Solomon Island plants are tetraploid, they show no essential morphological differences from other, presumably diploid, specimens of this subspecies. At present, it seems best to include the tetraploids in subsp. *aesculifolia* pending further study, especially of the nature and origin of their tetraploid condition.

Specimens examined: JAVA: Salak, *Raciborski s.n.* (US); Batavi, Perbati, W slope of Mt. Salak, *Palmer & Bryant 670* (US); Basamala, *Raciborski s.n.* (P); Indat [?] Mountain, *Forbes 550* (US); near Bogor, *Buysman 2607* (P); without specific locality, *Zollinger 1902* (P). BISMARCK ARCHIPELAGO: New Ireland: Namatanai, Mandiu Lake 6 km WNW of Taron, *Croft (LAE) 68399* (US). SOLOMON ISLANDS: E. San Cristóbal, lower reaches of Sumaro River, *Braithwaite 4215* (BM, P); E. San Cristóbal, just below confluence of Warahito and Pagato rivers, *Braithwaite 4220* (BM, P).

2. *Christensenia aesculifolia* subsp. *korthalsii* (deVriese) Rolleri, comb. nov. — *Kaulfussia korthalsii* de Vriese, Ned. Kruidk. Arch. 1(3):186. 1852. — TYPE: Sumatra, *Korthals s.n.* (holotype L not seen Morton photo 767 US).

Kaulfussia assamica Griff. Asiat. Res. 19:108. 1856. — *Christensenia assamica* (Griff.) Ching, Fl. Reipub. Pop. Sinica 2:65. 1959. — TYPE: "Assam," *Griffith 1696* (holotype BM not seen photocopy BM; isotype P).

Plants terrestrial, flexible, delicate, up to 40–45 cm long; rhizomes short, *carinose*, scaly, the scales adherent, large, castaneous with reddish spots, the margins entire to undulate; stipes sub*carinose* in smaller plants (juveniles?) to somewhat rigid, stiff and striate in the largest plants, scaly, the scales scattered, small, peltate, castaneous to reddish brown; fronds ternate, occasionally palmate, rarely simple, the terminal pinna (or lamina in simple fronds) lanceolate to narrowly so, 15–18 cm long, 7–9 cm wide, slightly ascending and curved; laminae herbaceous, rarely papyraceous, with plane or slightly revolute margins, these sub*papillose*, usually undulate, serrate, or serrate-denticulate, rarely entire; costae and veins *papillose-trichomatose*, densely covered with papillae, the hairs and scales diverse; *synangia* commonly circular, the *sporangia* 8–12; *receptacles* circular; *paraphyses* similar to branched trichomes, but *eglandular* and more delicate.

Specimens examined: INDIA: Assam, Margherita, Lakhimpur District, *Mann s.n.* (US); “Assam, Ind. angl.,” *Griffith s.n.* (P, possible isotype of *K. assamica*); Assam, Makumi Forest, Lakhimpur, *Mann s.n.* (P). MALAYA: Selangor, *Molesworth-Allen 2439* (US); Perak, Larut, *King 4784* (P); Perak, *Scortechini s.n.* (P); Perak, Batang Padang, *Ridley 13927, 13928* (P); without locality, *Ridley 14244* (P). SUMATRA: Lebong Tandai, Benkoelen, *Brooks 70.S* (P, US), *113.S* (P); without locality, *Hancock 29* (US); Sarawak, near Kuching, above ‘Rajah’ bungalow 3/4 of the way to Mt. Matang, *Molesworth-Allen 8146* (US); Central Kalimantan, Bukit Raya and upper Samba River 60–80 km NNW of Tumbang Samba, base camp Tumbang Riang, *Mogea 3637* (US). PHILIPPINES: Mindanao, Davao, Todaya, Mt. Apo, *Elmer 11275* (P, US); Negros, Luzon, *Copeland 2063* (P, US); Camarines, Mt. Isarong, *Ramos 7513* (P, US); Mt. Maquiling, *Copeland s.n.* (P); Luzon, Rizal, Panintingan, *Loher 13568* (P).

3. *Christensenia lobbiana* (de Vriese) Rolleri, comb. nov. — *Kaulfussia lobbiana* de Vriese in de Vriese and Harting, Monogr. Marattiac. 14. 1853. — TYPE: “Habitat in insulam Javam,” *Lobb* (K-Hb. Hook. not seen). [Note the polygonal epidermal pattern of the hypophyll illustrated in figs. 5A–D.]

Christensenia cumingiana Christ, Philippine J. Sci., Bot. 2:186. 1907 — TYPE: Philippines, Mindanao, Prov. Zamboanga, *Copeland s.n.* (MICH not seen; possible isotype US).

Plants terrestrial, generally small, (18)20–30(32) cm long; rhizomes suberect to short-creeping, short, bearing several stipes, scaly, the scales large, round, adherent, castaneous with reddish spots, with undulate or entire margins; stipes *carinose*, often slightly striate, not rigid or canaliculate, pale yellow with red spots, *papillose*; fronds simple or rarely ternate; simple laminae and terminal pinnae of ternate laminae lanceolate; lateral pinnae asymmetrical, pedate, sometimes reduced, sessile, lanceolate to triangular, rounded-lobate, rounded-undulate, and very irregular (small pinnae occasionally asymmetrically cuneate) at the base, the margins undulate, serrate, or lobate, the laminae usually spongiöse; reddish to castaneous-reddish, glandular papillae, hairs, and scales of all types present on the costae, veins, and lamina surface, contrasting with the pale yellow hypophyll; *synangia* frequently elliptic, with 9–12 fused *sporangia*; *receptacles* elliptic or circular; *paraphyses* abundant, similar to branched trichomes, but delicate and *eglandular*.

Specimens examined: BURMA: Warzup [Warazup], *Sidney 2* (US). MALAYA: Kepong, Sungei Kerod, near Kuala Lumpur, Selangor, *Molesworth-Allen 24344* (US).

SUMATRA: Indragiri, "in silvis prope pl. Lalh.," *Burchard 46* (P). PHILIPPINES: Mindanao, Prov. Zamboanga, San Ramón, *Copeland 152* (US, possible isotype of *C. cumingiana*), *Copeland s.n.* (P, possible isotype of *C. cumingiana*); Mindanao, Zamboanga, *Edaño 36838, 36839* (both P, US); Capiz, Panay, *Ramos & Edaño 31199* (US); Luzon, Mt. Maquiling, *Robinson 17914* (P, US), *Robinson 17199* (US); Sorsogon, Mt. Bulusan, *Elmer 15915* (P, US).

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