

LECANANTHUS AND LEUCOCODON, TWO GENERA TO BE ADDED TO THE TRIBE SCHRADEREAE (RUBIACEAE)

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SUMMARY

The presence of a combination of various character states (epiphytic habit, adventitious rootlets in rows along the internodes; capitate, involucrate inflorescences; certain floral features such as 'hooded' corolla lobe apices; heterodistyly; fruit and seed morphology and anatomy; leaf anatomy) provides evidence that the monospecific Sri Lankan endemic *Leucocodon* and the small Malesian genus *Lecananthus* are to be added to the Schradereae, a tribe hitherto thought to be monogeneric.

INTRODUCTION

The tribe Schradereae was previously thought to be comprised of only a single genus, *Schradera* (syn. *Lucinaea*; see Puff et al., 1998b for a revision of the Asiatic taxa). When re-examining the tribe (Puff et al., 1993a), various other genera which, in one way or another, had been brought in association with the Schradereae, were discussed. Amongst these were the monospecific Sri Lankan endemic *Leucocodon* and the small Malesian genus *Lecananthus*, both of which are commonly placed in the tribe Isertieae. The two genera were believed to be "possibly \pm closely related to *Schradera*". When this earlier study was made, little material of these two genera had been seen and most data had been drawn from literature. The current paper rectifies this. It presents the results of a thorough investigation of *Leucocodon* and *Lecananthus* and provides morphological and anatomical evidence that the two are definitely to be placed in the tribe Schradereae. The present publication, moreover, includes data on some features of *Schradera* which had not been recorded previously.

MATERIAL AND METHODS

Detailed morphological, anatomical, and palynological investigations were carried out on the following collections (* = preserved material):

Leucocodon Gardner: *Leuc. reticulatum* Gardner, Sri Lanka, Sabaragamuwa Prov., Ratnapura Distr., Sinharaja forest, Puff 910805-1/1 (WU)* (Fig. 1B-H, 2, 5A-B; Fig. 1A from colour slide Puff SL-02).

Lecananthus Jack: *Lec. erubescens* Jack: Peninsular Malaysia, Johore, Shah & Noor 853 (SING) (Fig. 5F-G); -, Selangor, Nur SFN 33981 (SING) (Fig. 5H); Borneo, Sarawak, Chai S 18524 (L) (Fig. 3A-B, F, 4A-B); Sumatra, de Wilde & de Wilde-Duyffes 20535 (L) (Fig. 3C-E, G-I, 4E-F). — *Lec. peduncularis* Puff: Borneo, Sarawak, Ching S 53555 (KEP) (Fig. 4C-D, 5C-E).

Schradera Vahl: *S. montana* (Korth.) Puff, Buchner & Greimler: Borneo, Sabah, Puff 950309-1/1 (WU)* (Fig. 7); *S. nervulosa* (Stapf) Puff, Buchner & Greimler: Borneo, Sabah, Puff 950302-1/1 (WU)* (Fig. 6).

In addition, specimens of *Leucocodon* housed in the herbaria AAU, K, PDA, W, and WU (abbreviations according to Holmgren et al., 1990) were studied. For herbarium material of *Lecananthus* and *Schradera* studied, see the respective revisions of the genera (Puff et al., 1998a, 1998b).

Methods used agree with those given in Igersheim (1993). As all Kodachrome colour slides of *Leucocodon* were lost, preserved inflorescences and flowers had to be reconstituted; see Puff et al. (1996) for details on the method. Pollen terminology follows Punt et al. (1994).

RESULTS / OBSERVATIONS

The data on *Leucocodon* given below include morphological measurements (such as leaf length and width, etc.), because there is no recent revision of this monospecific genus. Information on *Lecananthus*, on the other hand, is restricted to general characteristics because a proper revision of the genus is presented in this volume (Puff et al., 1998a).

1 – LEUCOCODON

1.1 – Growth form and habit — Fig. 1A

Scandent epiphytic shrubs, climbing by means of adhesive adventitious rootlets arranged in rows along the internodes. The main stems reach, according to field observations, a length of 10 m or more.

Herbarium specimens, usually representing flowering or fruiting lateral shoots, often do not show any adventitious rootlets because the latter are normally only produced on older shoots which are in contact with the host trees.

The flowering shoots often show sympodial-monochasial branching, i.e., a new branch starts developing in the axil of one of the leaves of the leaf pair immediately below the terminal inflorescence; growth of this new axis frequently starts even before the fruits of the inflorescence are fully mature.

Stems and branches, \pm terete in section, are glabrous.

1.2 – Leaves and stipules

The decussately arranged leaves are petiolate, evergreen, and distinctly coriaceous. The leaf blades are (linear-)lanceolate to oblong-lanceolate, 70–150 \times 20–70 mm, attenuate at the base and shortly acuminate at the apex, glabrous; domatia are always absent. Petioles are 10–15 mm long.

The membranaceous, glabrous, pale to whitish-green interpetiolar stipules (Fig. 1C) are broadly oblong, large (20–30 mm), and shortly bifid at the apex. They are fused below for c. 1/3 of their length to form a basal sheath, and free above. They are deciduous and normally only present on the 3 to 4 youngest nodes of a branch. Colleters of the standard type are present on the stipule's inner surface, near their base.

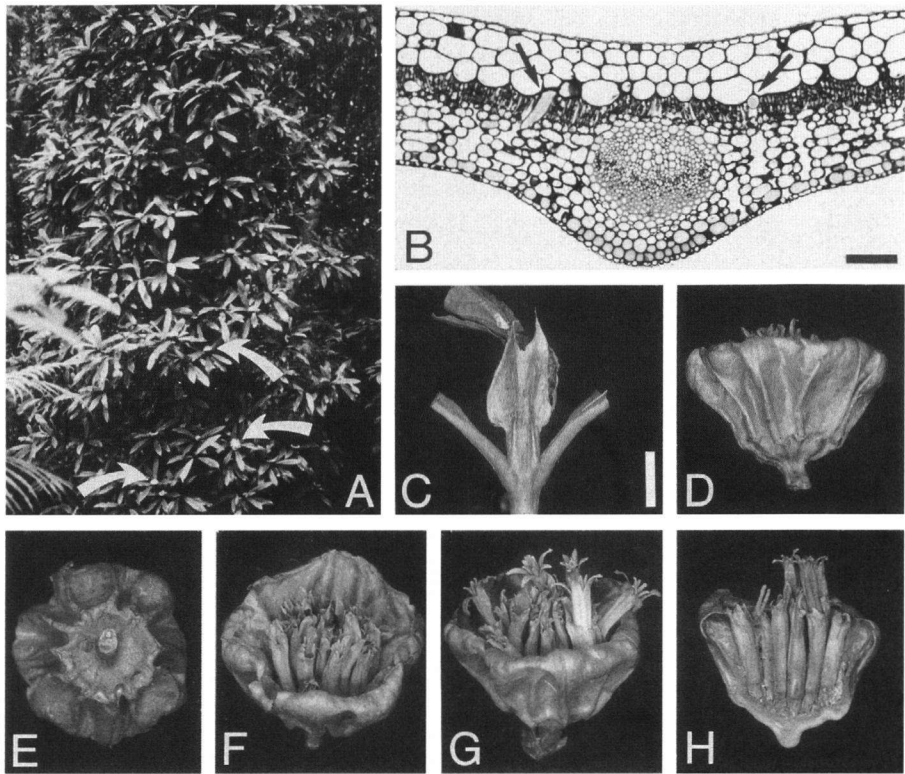


Fig. 1. Vegetative characters and involucrate inflorescences of *Leucocodon reticulatum* Gardner. — A: epiphytic plant entirely covering the trunk of a dipterocarp tree (some inflorescences visible at the ends of free shoots not attached to the host tree: arrows). — B: cross section of leaf blade in the region of a lateral vein, note several-layered hypodermis below the upper epidermis and thin palisade layer (the arrows point to raphide-containing idioblasts, the one on the right in cross section). — C: terminal portion of a vegetative shoot showing bifid stipules (leaf blades cut off; the new, developing pair of leaves protruding from the stipules). — D–H: involucre and inflorescence in different views and developmental stages; D–F, flowers still in bud and hardly protruding from the involucre; D, side view; E & F, as seen from below and obliquely from above; in F, only the long, tubular calyces of flower buds are visible (the corolla still entirely enclosed in the calyx; cf. Fig. 2C); G, with some open, short-styled flowers; H, longitudinal section. — Scale bars: 0.1 mm (B); c. 10 mm (C–H, all the same magnification).

1.2.1 – Leaf anatomy — Fig. 1B

The leaves have a several-layered thick hypodermis below the much smaller-celled upper epidermis. The mesophyll is characterized by the presence of a thick but very loose spongy mesophyll region and a dense palisade layer that occupies less than a quarter of the thickness of the entire mesophyll. There are few layers of small, narrow, elongated palisade cells; amongst them are elongated, raphide-containing idioblasts (Fig. 1B, arrows). The lower dermal tissue is comprised of very small cells. The leaves are hypostomatic; the stomatal apparatus is of the standard ‘rubiaceous type’ (cf. Wilkinson, 1979).

Leucocodon shows remarkable agreement to *Schradera*, e.g., *Schradera (Lucinaea) polysperma* (cf. Puff et al., 1993a: Fig. 2c), in virtually all of the leaf anatomical details.

1.3 – Inflorescences — Fig. 1D–H

The many-flowered, capitate inflorescences are terminal, solitary, and shortly pedunculate (i.e., almost immediately subtended by a pair of foliage leaves with bifid stipules).

They are surrounded by a conspicuous, pink to pinkish-white, cup-like or \pm campanulate, glabrous involucre, 35–50 mm in diam. and 20–40 mm high.

In younger developmental stages, the involucre is higher than the flower buds, i.e., it entirely encloses them; at anthesis, usually only the upper parts of the corollas are exerted. In fruiting stage, the margins of involucre start curving out- and backwards (see also Chapter 1.7).

The involucre shows 8–12 distinct ribs (cf. Fig. 1D–E) and an according number of \pm indistinct lobes which may or may not be toothed at the apex.

The morphological nature of the involucre is not entirely clear. Trimen (1894) noted that it is “formed of connate bracts” but we were unable to find definite proof for its origin from fused leaves/stipules. At the insertion point of the involucre, the axis broadens and then expands to become cup-like. In this region, the xylem cylinder of the peduncle splits up in a star-like fashion, giving rise to 8–12 main bundles (Fig. 1E; corresponding to the ribs seen on the outside of the involucre, cf. Fig. 1D) from which additional bundles supplying the involucre (not visible on its outside) branch off. We assume this to be an indication of an axillary origin [as in *Schradera (Lucinaea)*; cf. Puff et al., 1993a]. This, however, is still \pm speculative. Definite evidence is lacking because the available preserved material was insufficient for an ontogenetical investigation.

1.4 – Flowers

The flowers are 5-merous, except for the bicarpellate gynoecium. *Leucocodon* is heterodistylous.

The only available illustrations of flowers and floral parts (Beddome, 1874: pl. 94) are, in part, grossly inaccurate and misleading.

1.4.1 – Calyx

The calyx is differentiated into a long, basal, cylindrical tube and an asymmetrical apical part comprised of irregular teeth (Fig. 2E). The entire calyx is 15–25 mm long.

In bud, the calyx fully encloses the corolla (Fig. 2C). As the flower develops, the elongating corolla emerges from the corolla tube; in the process, the calyx often splits open lengthwise on one side.

1.4.2 – Corolla

The corollas are white, thick and \pm fleshy (cf. Fig. 2A). The aestivation of the corolla lobes is valvate (in the strict sense of Robbrecht, 1988; not valvate-induplicate as stated for *Leucocodon* by Baillon, 1880).

The corolla tube is \pm cylindrical and 25–40 mm long. Normally, the corolla of an open flower is exerted from the calyx for 10–15 mm (cf. Fig. 1G, H).

In short-styled morphs, it has a \pm swollen area, located c. 2/3 from its base; this is the region where the stigma lobes are positioned (Fig. 2C, depicting a young bud stage, does not show this). In long-styled morphs, the tube is indistinctly widened just below the throat (= location of the anthers).

The spreading to \pm recurved corolla lobes, 2.5–3.5 mm long, have hood-like apices (Fig. 2A).

The corollas are glabrous on the out- and inside except for a ring of unicellular hairs at or \pm below the insertion point of the filaments (Fig. 2C).

1.4.3 – *Androecium*

The anthers are dorsimedifixed, narrowly oblong, subsessile and entirely included in the throat in long-styled morphs. In short-styled morphs, at least 1/3 of the anthers protrude from the throat (Fig. 2A, B); the filaments are inserted immediately below the throat.

1.4.4 – *Gynoecium*

Style and stigma — The style is filiform and bears two \pm thick, conical stigma lobes (3–4 mm long). Except for the receptive stigmatic papillae, primarily on the adaxial surfaces of the stigma lobes, the style and stigmas are glabrous (Fig. 2D).

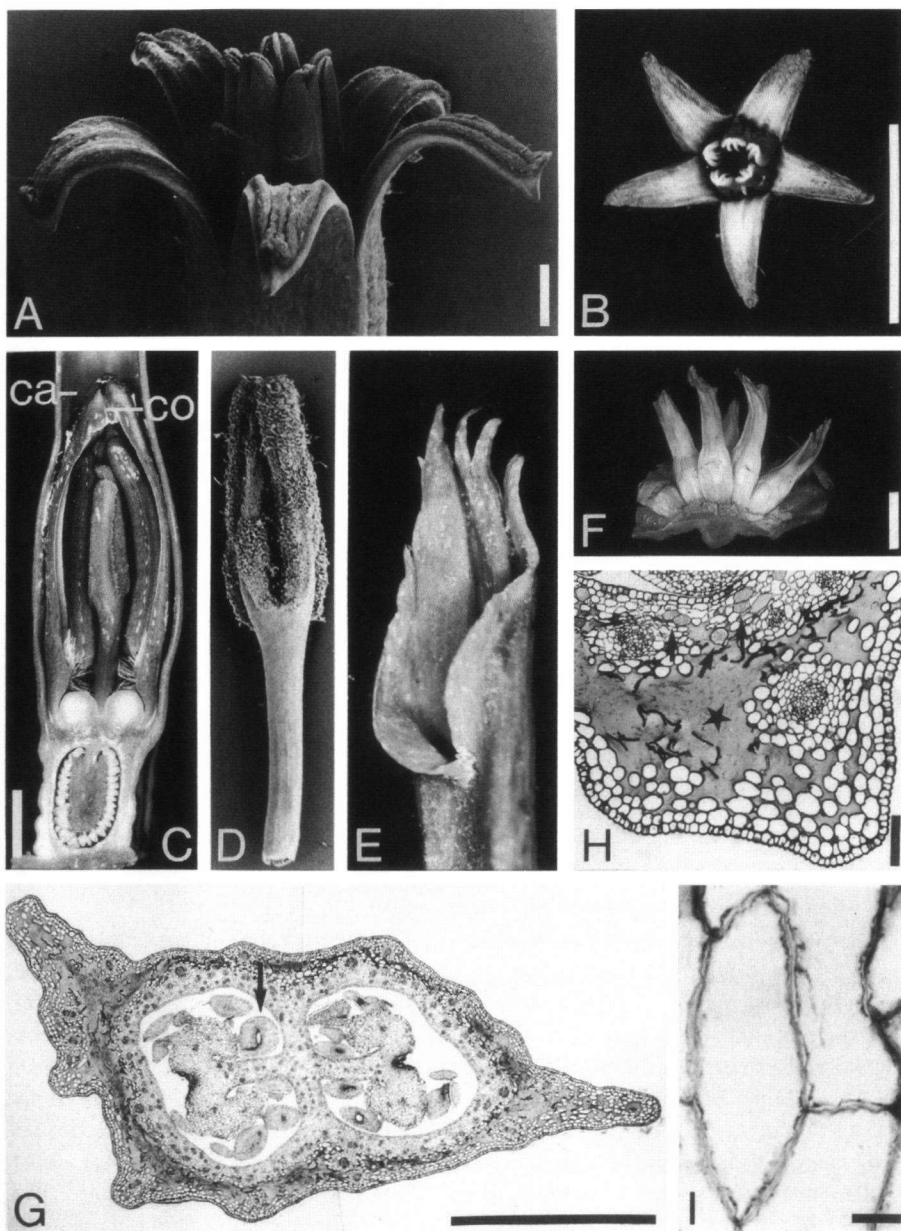
The tips of the stigma lobes are positioned below the base of the anthers in short-styled morphs (it should be noted that the spatial relationship between stigmas and anthers in the young bud stage of a short-styled flower depicted in Fig. 2C is only seemingly contradictory. During further floral development, the corolla tube will considerably elongate, thus lifting the anthers above the level of style and stigma; as opposed to the corolla, the latter will elongate only very moderately). In long-styled morphs, the uppermost part of the style and the stigma lobes are exerted [when describing the genus/species, Gardner (1846) based his description on such an individual (“style filiform, exerted ...”).]. Moreover, the stigma lobes are slightly spreading in long-styled morphs, whereas in short-styled morphs, due to spatial limitations, the stigma lobes are erect and \pm touching each other (Fig. 2D).

Ovary — Due to the large number of flowers present within an involucre and the resulting space limitations, the ovaries are very irregularly shaped, variously angled, and often laterally \pm compressed (cf. cross section, Fig. 2G).

The two locules, separated by a moderately thick septum, each contain a multiovulate peltate placenta (Fig. 2C, G). The latter is attached to the septum by means of a stipe, extending from the top of the septum to nearly down to its base. In cross section (Fig. 2G) the placenta appears \pm T-shaped (Fig. 2C shows the ovary in tangential section, cut at a right angle to the stipe). The often laterally compressed ovules, characterized by the presence of a massive integument, are always campylotropous (embryo sac \pm perpendicular to the short funicle, Fig. 2G, arrow) and strikingly similar to those of *Schradera* (*Lucinaea*; cf. Puff et al., 1993a: Fig. 6b-c).

The ovary wall shows an interesting differentiation and an unusual feature (Fig. 2G, H): Inside the small-celled ovary epidermis (corresponding to the exocarp in

fruiting stage), there are several layers of larger parenchymatic cells in which the typically 10 (or sometimes more) main vascular bundles supplying the ovary are embedded. Within this zone, there are large areas filled with mucilage (stained lilac rather than dark blue with toluidine blue; Fig. 2H, ★); these are lysigenous intercellular spaces having arisen through dissolution of entire cells. Further inward, there are again parenchymatic layers, made up of smaller cells and without mucilage. Raphide-



containing idioblasts are abundant in this region (Fig. 2H; but also in the septum and the placenta), and also minor vascular bundles. A layer of small parenchymatic cells, appearing \pm square in section, coats the locules; these also extend into the septum and the stipes of the placentas.

The roof of the ovary bears a massive, nectar-producing disk, surrounding the base of the style (already discernible in young bud-stage, Fig. 2C).

1.5 – Fruits

The fruits are white, soft, fleshy, many-seeded, and 5–7 mm high. They are ‘true’ berries (i. e., as compared to other Rubiaceae with berry-like fruits, there is not even a single sclerenchymatic cell layer coating the locules).

They are variable in shape (but never “globose berries” as in Schumann’s, 1891 description). Due to spatial reasons, they are at least basally variously angled and compressed (also compare with ‘Ovary’ in Chapter 1.4.4).

Lysigenous intercellular spaces filled with mucilage are even more prominent in mature fruits than in earlier developmental stages (compare with ‘Ovary’ in Chapter 1.4.4). The mucilage is rich in polysaccharides (tests with ruthenium stain, specific for polysaccharides, were positive).

The fruits are crowned by the persistent calyces (cf. Fig. 2F) which, at this stage, are as fleshy as the fruits themselves; calyx and fruit wall tissue are virtually indistinguishable anatomically.

1.6 – Seeds

The dark brown to blackish seeds are small (usually < 1 mm), of \pm irregular shape (often \pm polygonal) and laterally compressed.

The exotesta cells have thickened radial walls (already discernible in the immature seed depicted in Fig. 2I), but all other walls are unthickened. It could not be established with certainty whether – as in *Schradera (Lucinaea)* (Puff et al., 1993a) and in *Lecananthus* (see below; Fig. 4E) – parenchymatic endotesta layers remain intact, as the available preserved material was insufficient.

The embryo, with radicle and cotyledons of approximately the same length, is embedded in copious endosperm.

Fig. 2. Features of the fertile region of *Leucocodon reticulatum* Gardner. — A & B: short-styled flower from the side and from above, note the hooded corolla lobe apices. — C: longitudinal section of flower bud (the basal tubular portion of the calyx, ca, entirely encloses the corolla, co), note large, multiovulate placenta, ring-like disk around the base of the style, and ring of hairs immediately below the insertion point of the filaments. — D: style and bilobed stigma of short-styled flower. — E: apical part of calyx (from a bud). — F: sectioned involucrate inflorescence with fruits crowned by the persistent calyces. — G: cross section of ovary (\pm the middle of the ovary), note irregular outline, dark contents in the ovary wall, septum, the \pm T-shape of the placentas, and ovules (the arrow points to an ovule positioned such that it shows the funicle, embryo sac and micropylar canal). — H: detail of ovary wall showing idioblasts containing raphides (arrows) and dark-stained ‘mucilage’ areas (★) where the cells of the ovary walls dissolved. — I: tangential section of the exotesta of a young seed, note the beginning thickening of the radial walls. — Scale bars: c. 10 mm (F); 5 mm (B); 1 mm (A = C = D = E; G); 0.1 mm (H); 10 μ m (I).

1.7 – Pollination ecology and diaspore dispersal

Leucocodon is one of the numerous Rubiaceae with pseudanthia or “flower-like inflorescences” (cf. Claßen-Bockhoff, 1996). Within this group of Rubiaceae, she distinguishes taxa with extrafloral and floral (calyx-borne) semaphylls. *Leucocodon* belongs to the first category, for which she lists examples of 14 genera belonging to 9 different tribes.

The genus is undoubtedly ornithophilous. The pseudanthia remind of those of *Protea* species. The rather sturdy involucre most likely serves as a perching place for visiting sun-birds, attracted a) optically by the pink to pinkish-white involucre and the white flowers, and b) by the nectar, profusely produced by the disk of each flower. The pseudanthia, being terminal on lateral branches hanging away from the main body of the plant and held in an erect position (cf. Fig. 1A), moreover, are easily accessible to birds. The thick and robust corollas, not prone to easy damage by the beaks of the visiting birds, could also be seen as an adaptation to ornithophily. Flower size, too, fits for a bird-pollinated species.

The fruiting inflorescences (and involucre) are as optically attractive as in flowering stage. One change, however, is noticeable: as the fruits mature, the margin of the cup-like to \pm campanulate involucre starts to curve out- and backwards. The result is that the shiny, white, fleshy fruits (plus the persistent calyces of the same colour and texture; cf. Fig. 2F) become almost fully exposed. Although direct observations are lacking, there is no doubt that these fruits are attractive to birds (also in view of their high polysaccharide content; cf. Chapter 1.5). *Leucocodon* can, thus, safely be described as having ornithochorous diaspores.

1.8 – Pollen — Fig. 5A, B

The pollen is small, 16–23 μm , oblate spheroidal ($P:E = 0.92$) and 2-(brevi)colporate. The exine is microreticulate, heterobrochate (lumina smaller towards the aperture), and does not have any supratectal elements. Pollenkitt is present. Mature pollen grains are binucleate.

The above description is based on the investigation of acetolyzed material from a short-styled morph; information on pollen dimorphism related to heterostyly (cf. *Lecananthus* and *Schradera*, below) is, therefore, unavailable.

1.9 – Ecology, phenology, and distribution

Leucocodon occurs in primary or secondary wet forest, at altitudes ranging from 100 to 1500 m. It appears to flower and fruit virtually all year round.

The genus is endemic to southwest Sri Lanka, being centred in the Kandy, Nuwara Eliya, and Ratnapura Districts.

1.10 – Taxonomy

Leucocodon Gardner, *Calcutta J. Nat. Hist.* 7 (1846) 4; Hook. in Benth. & Hook., *Gen. Pl.* 2 (1873) 67; *Fl. Brit. India* 3 (1880) 93; Baill., *Hist. Pl.* 7 (1880) 455; K. Schum. in Engl. & Prantl, *Natürl. Pflanzenfam.* 4, 4 (1891) 64; Trimen, *Handb. Fl. Ceylon* 2 (1894) 325.

Species sola:

Leucocodon reticulatum Gardner, Calcutta J. Nat. Hist. 7 (1846) 5; Thwaites, Enum. Pl. Zeyl. (1859) 138; Bedd., Ic. Pl. Ind. Orient. 1 (1874) pl. 44; Hook., Fl. Brit. India 3 (1880) 94; Trimen, Handbook Fl. Ceylon 2 (1894) 325. — Type: *Gardner* (holo ?CAL, n.v.; CAL did not react to a loan request), Ceylon [Sri Lanka], Ambergamao Distr., c. 4000 ft.

2 – LECANANTHUS

2.1 – Growth form and habit

Woody climbing shrubs with adhesive adventitious rootlets in rows on the internodes but sometimes also in the nodal regions. They are usually epiphytic but are sometimes also reported as occurring on the ground. As in *Leucocodon*, adventitious rootlets are normally absent on the free aerial shoots that are not attached to the host plants (and are, therefore, often not seen in herbarium specimens).

Characteristic for the genus are the four distinct, often \pm wing-like, longitudinal ridges on the stems which, however, are usually only prominent on the younger shoot portions.

2.2 – Leaves and stipules

The decussately arranged petiolate leaves are always thin and \pm membranaceous. Leaf sections of reconstituted dried material revealed that a conspicuous hypodermis (as found in *Leucocodon*, cf. above) is absent. Raphides, however, are present.

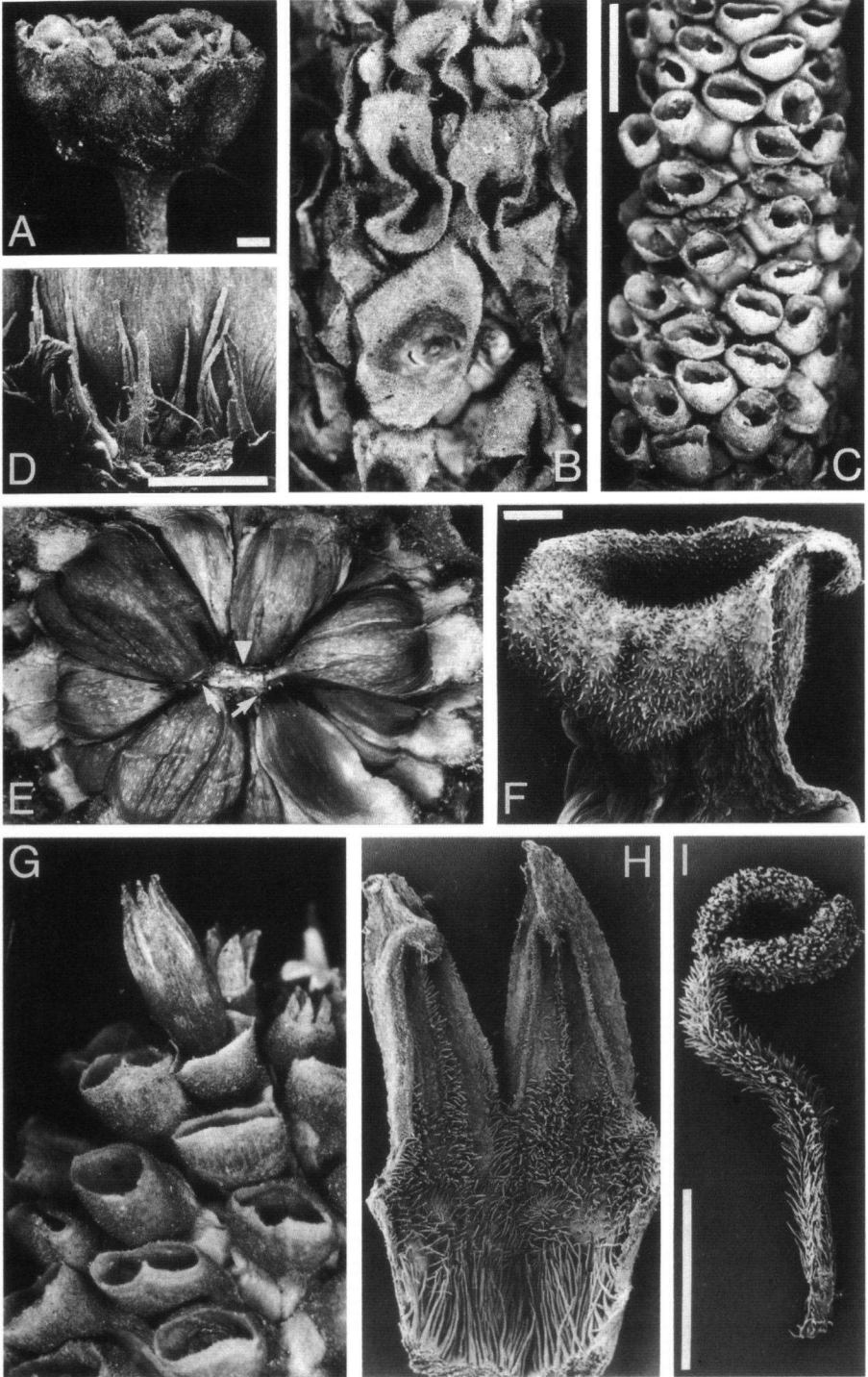
The membranaceous, small to \pm large deciduous interpetiolar stipules are (broadly) ovate to broadly triangular and entire, occasionally bifid or sometimes with up to 5 fimbriae at the tip. They are either fused below to form a basal sheath and free above or entirely free. Colleters of the standard type are present on the stipule's inner surface, near their base.

2.3 – Inflorescences

The inflorescences of *Lecananthus*, borne on short to elongated peduncles, are always many-flowered. Inflorescence shapes vary from \pm globose-capitate, ovoidal to elongated-cylindrical. The position of the inflorescences is essentially terminal, but in two species there are often also pseudo-axillary inflorescences (sylliptically growing renewal shoots, which themselves produce inflorescences, are present).

The inflorescences of *Lecananthus* are involucrate, but as opposed to *Leucocodon*, the involucre are small and inconspicuous and normally clearly seen only in young bud stage (Fig. 3A). During flower development, the enlarging ovaries push the involucre downward so that they may become almost invisible (cf. Fig. 3C).

Noteworthy is the presence of standard type colleters between the inflorescence axis and the bases of the ovaries (Fig. 3D, E), which could be interpreted as remnants of bracts; the same feature was encountered in *Schradera* (*Lucinaea*; cf. Puff et al., 1993a: Fig. 3g-h).



2.4 – Flowers

The flowers are 5- (or 6-)merous, except for the calyx and the bicarpellate gynoecium. *Lecananthus*, like *Leucocodon*, is heterodistylous.

2.4.1 – Calyx

The calyx is either glabrous or hairy and differentiated into a basal tubular part and a free upper part. The latter, never distinctly 5- (or 6-)merous, is either irregular (with 1 or, more often, 2 unequal lobes which may be small and tooth-like; Fig. 3C, G) or distinctly zygomorphic (2-lipped, with upper and lower lip being of unequal size and sometimes bearing 2, respectively 3 teeth; Fig. 3B, F).

2.4.2 – Corolla

The corollas are thick and \pm fleshy. The aestivation of the corolla lobes is valvate (in the strict sense of Robbrecht, 1988).

The funnel-shaped corolla tubes are usually somewhat longer than the spreading to recurved lobes, the latter have distinctly ‘hooded’ apices (Fig. 3G, H; as in both *Leucocodon* and *Schradera*, cf. Fig. 2A, 6D). An indumentum is only present on the inside: straight to curly hairs at or below the insertion point of the filaments and around the throat, sometimes also short, \pm curled hairs at the base of the lobes and along the lobe’s midrib (Fig. 3H).

2.4.3 – Androecium

The anthers are dorsimedifixed, \pm linear, \pm sagittate at the base, subsessile and entirely included in the corolla tube in long-styled morphs. In short-styled morphs, the anthers are mostly fully exerted and sit on filiform filaments inserted immediately below the throat.

2.4.4 – Gynoecium

Style and stigma — The filiform style is invariably densely beset with upwardly directed hairs and bears two filiform stigma lobes with longish receptive papillae (Fig. 3I).

The stigma lobes are included in the corolla tube in short-styled morphs, and \pm to distinctly exerted in long-styled morphs.

Fig. 3. Inflorescences and floral features of *Lecananthus erubescens* Jack. — A: conspicuous involucre enveloping an inflorescence in very young bud stage, some calyces are seen protruding from it (the corollas are still included inside the calyces). — B: the same as seen from above, note the \pm two-lipped calyx. — C: elongated inflorescence after anthesis, the involucre is no longer clearly discernible at the base. — D: colleters around the base of ovaries. — E: elongated inflorescence in cross section, showing the arrangement of the ovaries on the inflorescence axis (triangle), the arrows point to the location of the colleters shown in D. — F: irregularly 2-lobed calyx on young fruit. — G: detail of inflorescence shown in C, note irregular calyces. — H: open bud (long-styled morph) to show hooded corolla lobe apices and short indumentum on the lobes and longer hairs in a ring-like arrangement \pm at the insertion point of the filaments (the latter not visible; stamens removed!). — I: style with upwardly directed hairs and stigma lobes with longish papillae (from long-style flower). — Scale bars: 5 mm (B = E = G; C); 1 mm (D; F; H = I).

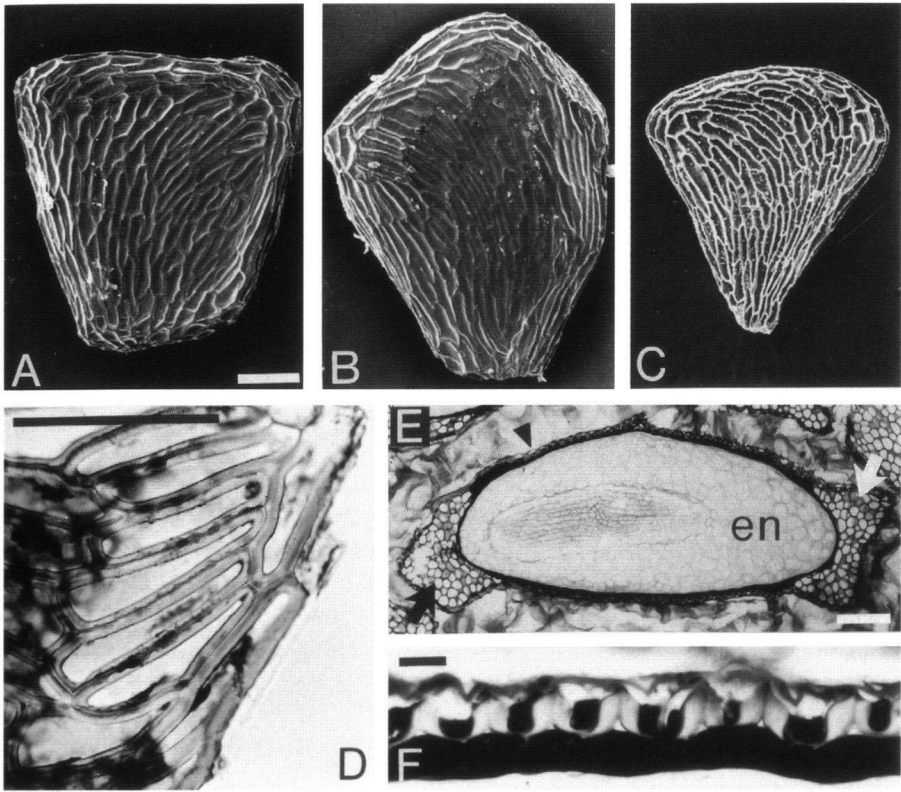


Fig. 4. Seeds of *Lecananthus* Jack (A & B, E & F, *L. erubescens* Jack; C & D, *L. peduncularis* Puff). — A & B: untreated seeds from the same fruit; C: seed with the outer tangential exotesta cell walls artificially removed; in A–C the area of attachment to the placenta is at the bottom. — D: exotesta in tangential section showing thickened radial walls. — E: cross section of laterally compressed seed, note conspicuous areas of intact endotesta layers on the side (arrows) and embryo surrounded by large-celled endosperm (en). — F: detail of exotesta and crushed endotesta layers (black), approximately from the area indicated by a triangle in D, note thickened radial walls (white-transparent) and exotesta cell lumina partially filled with black contents (tannins?). — Scale bars: 0.1 mm (A = B = C; D; E); 10 μ m (F).

Ovary — Each locule of the bilocular ovary contains a large multiovulate placenta, attached to the middle of the septum. As adequate preserved material was unavailable, detailed anatomical data cannot be provided.

The roof of the ovary bears a conspicuous nectar-producing disk, surrounding the base of the style.

2.5 – Fruits

The fruits are soft, fleshy, many-seeded ‘true’ berries (cf. *Leucocodon*, above).

Due to the lack of suitable preserved material, direct fruit anatomical comparisons with *Leucocodon* are not possible. We have ascertained, however, that raphides are

abundant in the fruit wall. Baillon's (1880: 454) statement "fructus ... intus mucilaginosus" indicates that *Lecananthus*, like *Leucocodon* has mucilage-filled intercellular spaces.

The fruits are crowned by the persistent calyx and disk.

2.6 – Seeds — Fig. 4

The blackish seeds are small (0.5–0.75 mm), ± irregularly shaped (variously angular to suborbicular) and laterally compressed.

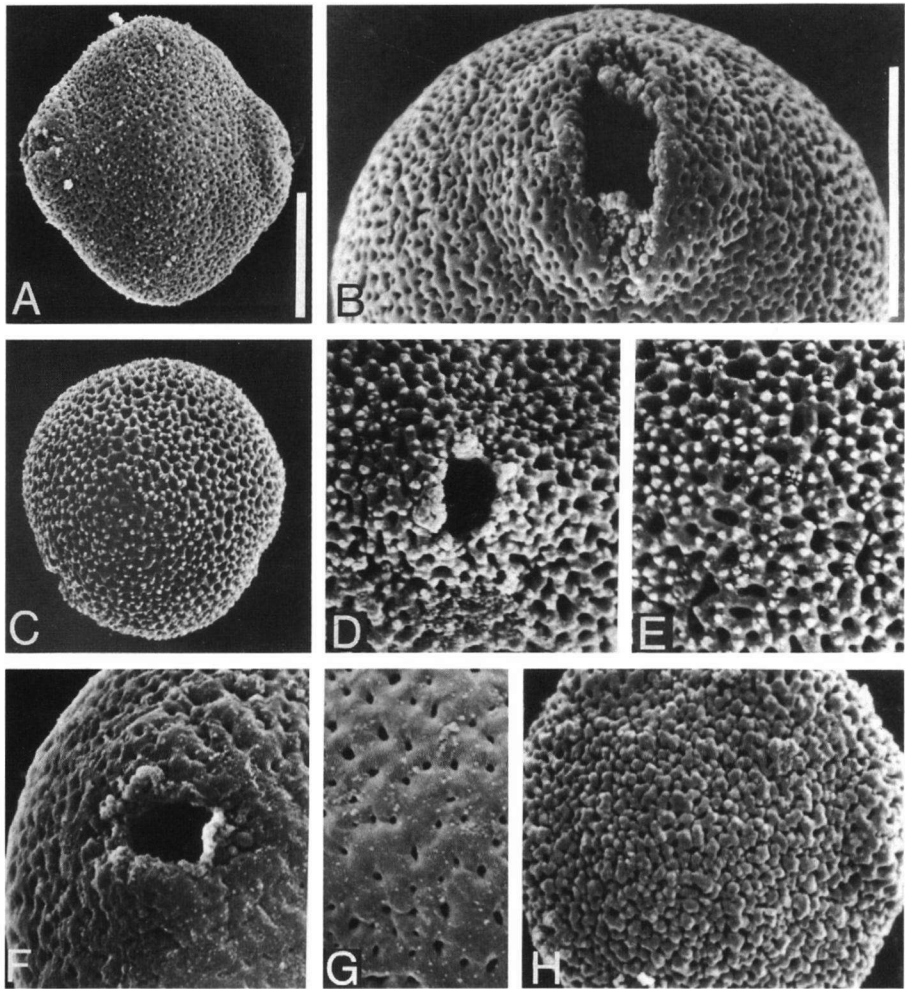
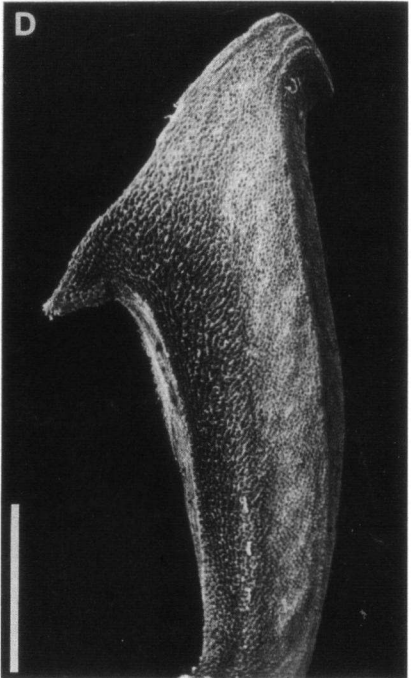
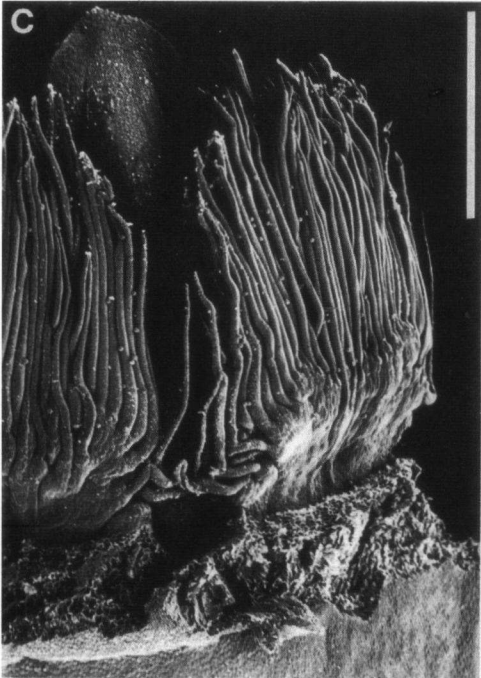


Fig. 5. Pollen of *Leucocodon* Gardner (A & B) and *Lecananthus* Jack (*L. peduncularis* Puff, C–E; *L. erubescens* Jack, F–H). A, C, polar views; B, D, F, apertures; E, G & H, apocolpium. — A–G: pollen from short-styled morphs; H: pollen from long-styled morph (of different populations). — Scale bars: 10 μ m (A = C; B = D = E = F = G = H).



The exotesta cells are rectangular to polygonal; only the radial walls have conspicuous secondary thickenings (Fig. 4D); the cells are filled with a dark-staining content, presumably tannins (Fig. 4F). Remarkably, parenchymatic endotesta layers do not become fully squashed during seed maturation but remain intact at least locally (Fig. 4E).

The endosperm, made up of rather large, \pm isodiametric cells, is copious; it can be described as fleshy. No droplets of oil were detected in the endosperm.

The embryo, with radicle and cotyledons of approximately the same length, is relatively small.

Both morphologically and anatomically, the seeds of *Lecananthus* are strikingly similar to those of *Schradera* (*Lucinaea*) (cf. Puff et al., 1993a: 467–469 & Fig. 8).

2.7 – Pollen — Fig. 5C–H

The pollen is small, 20–25 μm , spheroidal, and 3-porate to 3-brevicolporate. The exine is microreticulate to perforate, heterobrochate (lumina smaller towards the aperture), and with or without suprategal elements. Pollenkitt is present.

A pollen dimorphism related to heterostyly is noticeable: in long-styled morphs, the exine does not have any suprategal elements, and sometimes the lumina are \pm absent; in short-styled morphs, suprategal scabrae (c. 0.2 μm in diam.) are present on the exine.

The above description is based on the investigation of acetolyzed material from long- and short-styled morphs of *L. erubescens* and a short-styled morph of *L. peduncularis*; palynological data for the third species, *L. pentandrus*, are unavailable.

3 – ADDITIONS AND SUPPLEMENTS

to the character states of *Schradera* (syn. *Lucinaea*)

When revising Asiatic material of *Schradera* (see Puff et al., 1998b), we discovered that a) a few character states presented previously (Puff et al., 1993a) needed some amendments (because, when this earlier study was made, only a selection of taxa had been covered) and that b) other character states had gone unnoticed.

3.1 – Floral features

Current investigations of *Schradera* flowers revealed the presence of scale-like outgrowths in the corolla tube (Fig. 6), a feature not mentioned in Puff et al. (1993a).

They are neither universally present in the genus (discovered in 6 of the 16 Asiatic species) nor always of the same shape and position as in *S. nervulosa*, depicted here as an example (Fig. 6). They are, however, always beset with hairs.

Fig. 6. Floral features of *Schradera nervulosa* (Stapf) Puff, Buchner & Greimler (short-styled morph). — A: opened bud showing hairy scale-like outgrowths (arrows) at the throat and ring of soft, \pm curled hairs immediately below insertion point of filaments, also note hooded corolla lobe apices. — B: as A, but inside view (arrow points to scale). — C: corolla lobes removed to show scale-like outgrowths with stiff, erect hairs on the margins. — D: hood-like corolla lobe apex. — Scale bars: 1 mm (A = B; C; D).

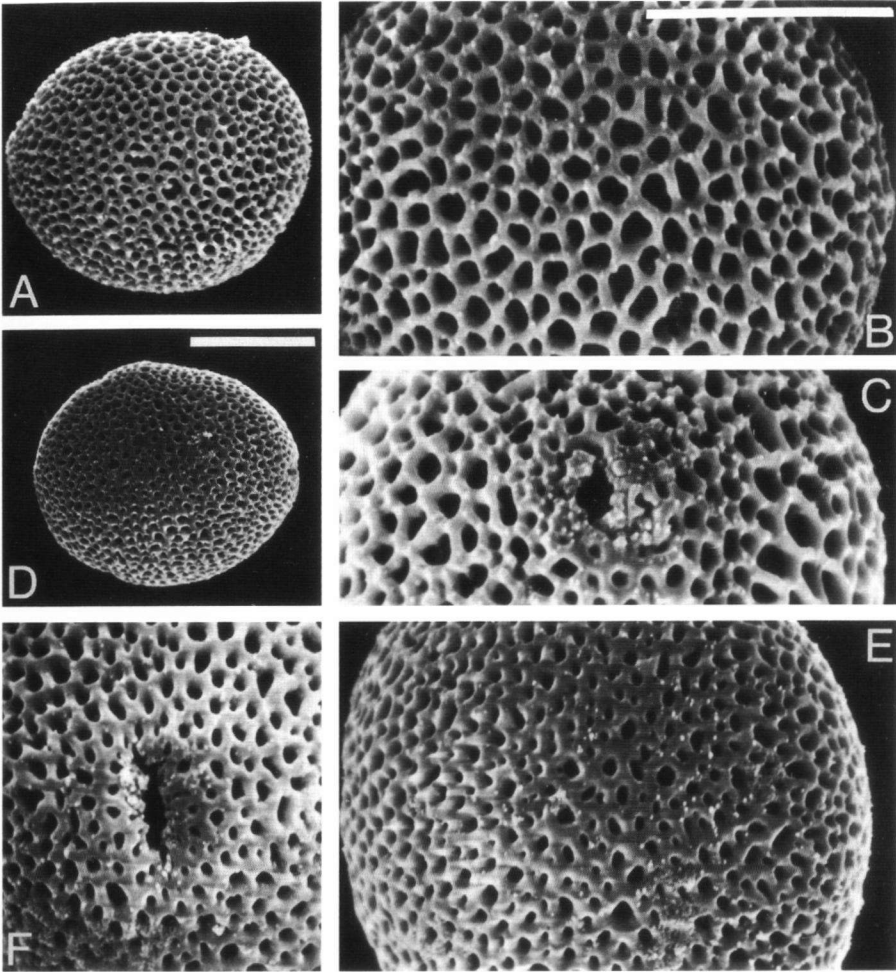


Fig. 7. Pollen of *Schradera montana* (Korth.) Puff, Buchner & Greimler (A–C from short-styled and D–F from long-styled morph of the same population). A, D, polar view; B, E, apocolpium, note difference in mesh-size; C, F, apertures, note numerous supratectal scabrae on the exine in pollen from short-styled morph. — Scale bars: 10 μm (A = D; B = C = E = F).

The occurrence of such scale-like outgrowths on the inside the corolla tube is particularly noteworthy, because they appear to be extremely rare in the Rubiaceae.

They are also documented for some taxa of the Urophyllaeae (species of *Maschalocorymbus* and *Praravinia*; Buchner, 1995).

3.2 – Fruit anatomy

As fruit anatomy was not documented for *Schradera* (*Lucinaea*) in Puff et al. (1993a), new sections were prepared in order to be able to check against *Leucocodon*. These

sections revealed that comparable lysigenous intercellular spaces, filled with lilac stained mucilage, were present. The fruits, moreover, also have raphide-containing idioblasts and (few) isolated sclerenchyma cells in the mesocarp (the latter were not found in *Leucocodon*, cf. above).

3.3 – Pollen — Fig. 7

The examination of a number of Asiatic taxa not covered previously (Puff et al., 1993a), necessitate some alterations to the original palynological characterization of *Schradera* and some comments:

The oblate spheroidal to spheroidal pollen grains are small to medium-sized, ranging from 17 to 42 μm , whereby non-acetolyzed grains are invariably larger than acetolyzed pollen from the same plant (24–42 μm vs. 17–26 μm).

The pollen grains are mostly not strictly porate (as stated in Puff et al., 1993a) but the apertures, although short, approach colpi. Pollen of *Schradera* thus is better described as being 2- or (3–)4-porate to -brevicolporate.

Both, the characterization of *Schradera* (*Lucinaea*) pollen as having no ‘supratectal structures’, and as showing no heterostyly-linked pollen dimorphism (based on the investigation of *S. polysperma*) (Puff et al., 1993a) are no longer fully accurate. The taxa investigated in detail (*S. montana*, long- and short-styled, Fig. 7; *S. nervulosa*, short-styled; *S. pseudonervulosa*, long-styled) showed that pollen from short-styled morphs have a reticulate exine with supratectal scabrae on the muri, and grains from long-styled morphs have a microreticulate exine without any supratectal elements or with just a few supratectal scabrae on the muri. There are, moreover, indications that there are heterostyly-related size differences (*S. montana*, acetolyzed pollen). In view of the ‘negative’ data for *S. (L.) polysperma* (Puff et al., 1993a) it, however, needs to be stressed that pollen dimorphism associated with heterostyly, is definitely not universally present in the genus.

DISCUSSION

The data presented here provide solid evidence that the genera *Leucocodon* and *Lecananthus* are close to *Schradera*. As summarized in Table 1, the three genera share, or are similar in, a large number of character states.

As a consequence, they should be removed from the Isertieae (syn. Mussaendeae; subfam. Cinchonoideae), a tribe in which they have been placed in both older and recent classification systems of the Rubiaceae (Hooker, 1873; Schumann, 1891; Robbrecht, 1988), and added to the Schradereae (subfam. Rubioideae), previously thought to be monogeneric (*Schradera*, syn. *Lucinaea*). A recent cladistic analysis of the Isertieae (Andersson, 1996), indirectly confirms this. He concluded that all raphidiate genera should be transferred to the Rubioideae s.l., and that “*Lecananthus* and *Leucocodon* may be close to the Schradereae”.

The conclusions reached here, moreover, are in full agreement with his cladogram (Andersson, 1996: Fig. 5), showing *Schradera*, *Leucocodon*, and *Lecananthus* in one cluster.

Table 1. Comparison of selected character states of *Schradera*, *Lecananthus* and *Leucodocon* (data for *Schradera* partly from the present publication and from Puff et al., 1993a, 1998b).

	<i>Schradera</i>	<i>Lecananthus</i>	<i>Leucodocon</i>
Habit and growth form	climbing by means of adventitious rootlets on the internodes	climbing by means of adventitious rootlets on the internodes (and sometimes also at the nodes)	climbing by means of adventitious rootlets on the internodes
Leaves: texture	thick, coriaceous, less often thin, \pm membranaceous	thin, \pm membranaceous	thick, coriaceous
leaf anatomy	+ hypodermis [or multiple epidermis?], + raphides	hypodermis absent; + raphides	+ hypodermis, + raphides
Stipules	small to large, connate at base; deciduous; entire or (seldom) bifid at tip	small to large, connate at base or not; deciduous; entire, bifid or fimbriate at tip	large, connate at base, deciduous; bifid at tip
Inflorescence: position	terminal (and pseudo-axillary)	terminal (and pseudo-axillary)	terminal
shape	capitate(-globose); many- to 1-flowered	capitate to elongated-ovoidal; always many-flowered	capitate; always many-flowered
involucre	+, small to large and \pm showy	+, small and \pm inconspicuous (except in bud stage)	+, very large and showy
Flowers	3-5-merous	5- (or 6-)merous	5-merous
Heterodistyly	+	+	+
Calyx	short, cylindrical tube, truncate above (distinct calyx lobes absent); persistent and fleshy in fruit	short basal tubular part, above with irregular, often tooth-like lobes or \pm 2-lipped; persistent and \pm fleshy in fruit	long basal tubular part, asymmetrical upper part with irregular teeth ('lobes'); persistent and fleshy in fruit
Corolla: aestivation	valvate	valvate	valvate
indumentum on inside	ring of hairs \pm at insertion point of filaments (and usually also hairs elsewhere)	ring of hairs \pm at insertion point of filaments (and usually also hairs elsewhere)	only ring of hairs \pm at insertion point of filaments
lobes	'hooded'	'hooded'	'hooded'
Ovary: ovules	campylotropous	?	campylotropous
Fruits: morphology	fleshy, 'true' berries	fleshy, 'true' berries	fleshy, 'true' berries
anatomy	fruit wall tissue with mucilage inclusions and raphides	'fructus intus mucilaginosus' (Baillon, 1880); raphides present	fruit wall tissue with mucilage inclusions and raphides
Seeds: size	small (\pm 1 mm), numerous	small (0.5-0.75 mm), numerous	small (< 1 mm), numerous
exotesta cells	only radial walls with conspicuous secondary thickenings	only radial walls with conspicuous secondary thickenings	only radial walls with conspicuous secondary thickenings
endotesta	locally remaining intact	?	locally remaining intact
embryo	radicle : cotyledon length c. 1 : 1	radicle : cotyledon length c. 1 : 1	radicle : cotyledon length c. 1 : 1
Pollen	2-3(-4)-porate to -brevicolporate, oblate spheroidal to spheroidal, 17-26 μ m (acetolyzed; larger, to 42 μ m, in non-acetolyzed material)	3-porate to -brevicolporate, spheroidal, 20-25 μ m (acetolyzed)	2-(brevi)colporate, oblate spheroidal, 16-23 μ m (acetolyzed)
Distribution	Malesia and neotropics	Sumatra, Peninsular Malaysia, Borneo	Sri Lanka

With regard to the character states of the three genera in question, two features deserve special attention:

1) The curious euryalynous situation:

First of all, the pollen differs in the number of apertures, i. e., 2-aperturate in *Leucocodon* and some *Schradera* species and 3- (or occasionally 4-)aperturate in *Lecananthus* and *Schradera* species. The former situation is rather uncommon in the Rubiaceae (possibly restricted to subfam. Rubioideae and found, e. g., in the Psychotrieae and Coussareae), whereas the latter by far dominates the family (cf. Robbrecht, 1988: 114).

Moreover, with regard to the aperture types there seems to be a gradation from porate to colporate and colpate. As the apertures are always very short in the non-porate grains, the aperture type is sometimes difficult to classify. The presently used distinction between porate and colpate has been based on external pollen morphological characters; for a full confirmation, TEM sections would be needed to reveal both exine and intine features of the apertures. The Psychotrieae is presumably the only other rubiaceous tribe in which pollen grains are either colpate, colporate or porate (or even inaperturate). All these aperture types can be found within *Psychotria*, but in that genus – unlike the Schradereae – aperture differences are mostly more distinct (cf. Johansson, 1992).

The heterostyly-linked pollen dimorphism (exine reticulate vs. microreticulate, and without vs. with supracteal scabrae in long-styled vs. short-styled morphs) found in the genera in question is, however, not unusual and known from other rubiaceous genera, e. g., *Pentanisia* or *Danais* and allies (Puff & Robbrecht, 1989; Buchner & Puff, 1993).

2) The presence of mucilage in lysigenous intercellular spaces of the ovaries and fruits:

As far as we know, a fully comparable situation is not known from any other Rubiaceae. The presence of mucilage as such – and other secretions of a similar kind – is nevertheless known to occur in the family (although rare), but it is not associated with lysigeny. In species of *Mussaenda*, for example, there are laticifers (secretory ducts with a yellowish content) in leaf, ovary and fruit tissue (Solereder, 1893; Puff et al., 1993b). In various Urophylleae, mucilage is found inside the loculi of the baccate fruits, presumably secreted by the cells coating the locules and/or placental cells (Buchner, 1995).

EMENDED TRIBAL CIRCUMSCRIPTION OF THE SCHRADEREAE

Schradereae Bremek., Rec. trav. Bot. Néerl. 31 (1934) 253, emend. Puff & Buchner.

Scandent epiphytic *shrubs* climbing by means of adhesive adventitious rootlets borne along the internodes (and sometimes also at the nodes); seldom also terrestrial. Leaves decussate, coriaceous to membranaceous, petiolate. *Stipules* interpetiolar, mostly connate below and free above, entire or bifid (seldom fimbriate) at the apex. *Inflorescences* terminal (and sometimes also pseudo-axillary), pedunculate, capitate, many- to 1-flowered; always surrounded by a large, showy to small, inconspicuous involucre of presumably axillary origin. *Flowers* 3–5(–6)-merous; heterodistylous. Calyx tubular

and truncate above, or a basal tubular part with irregular teeth or a \pm 2-lipped upper part. Corolla valvate (s. str.), thick and \pm fleshy, tube \pm as long as to longer than the lobes, the latter always 'hooded' at the apex; tube variously hairy inside (often at least a ring of hairs \pm at insertion point of filaments), sometimes with hairy scales (*Schradera*, p. p.). Stamens with linear to oblong anthers, sometimes \pm sagittate at base, without apical appendages, included and on very short filaments (long-styled morphs) or (at least partially) exerted and on longer filaments (short-styled morphs). Gynoecium bicarpellate (very rarely tricarpellate). Style simple, glabrous to hairy; stigma lobes 2 (3), filiform to short and thick; included (short-styled morphs) or somewhat to distinctly exerted (long-styled morphs). Ovary with 2 (3) locules, each with a large, multiovulate placenta (ovules campylotropous: *Schradera*, *Leucocodon*); a conspicuous nectar-producing disk, surrounding the base of the style, present on the roof of the ovary. *Fruits* truly baccate, many-seeded; fruit wall with mucilage-filled intercellular spaces. *Seeds* small, \pm irregularly shaped, only radial walls of exotesta cells with conspicuous secondary thickenings; parenchymatic endotesta layers locally remaining intact; endosperm copious; embryo small (radicle and cotyledons of \pm equal length). *Raphides* always present (especially in the leaf and ovary tissue).

Pollen — Small- to medium-sized, 2–3(–4)-aperturate, porate, colpate or colporate (colpi/colpori always very short), exine reticulate to microreticulate, with or without supracteal elements; heterostyly-linked pollen dimorphism often present (exine reticulate and with supracteal scabrae in short-styled morphs; microreticulate and without or only few scabrae in long-styled morphs).

Chromosomes — Diploid ($x = n = 11$, $2n = 22$) (*Schradera*).

Genera included — *Schradera* (syn. *Lucinaea*), *Lecananthus*, *Leucocodon*.

Distribution — Malesia (*Schradera*, *Lecananthus*); Sri Lanka (*Leucocodon*); Central to South America (*Schradera*).

KEY TO THE GENERA OF THE SCHRADEREAE

- 1a. Inflorescence capitate, 35–50 mm in diam., always many-flowered (> 20 flowers), subtended by a large, showy, pink to pinkish-white, cup-like to \pm campanulate involucre, 20–40 mm high, which largely encloses the flowers; the calyx 15–25 mm long; endemic to Sri Lanka **Leucocodon**
- b. Inflorescence capitate(–globose) and usually only 5–30 mm in diam., or ovoidal to elongated-cylindrical and to 30(–45) mm long, subtended by a flat, dish-like or \pm cup-like involucre, but the latter green to greenish-white (i. e., never as showy) and not as high (usually relatively small to inconspicuous, sometimes only clearly discernible in young bud stage); the calyx always < 10 mm high 2
- 2a. Young shoots with 4 longitudinal, often almost wing-like ridges on the internodes; inflorescences often elongated, always many-flowered (> 20 flowers); calyx above with 2 irregular and unequal lobes or 2 lips of unequal size and shape; style always densely beset with long, ascending hairs **Lecananthus**
- b. Young shoots without distinct ridges on the internodes (mostly \pm terete to about 4-angled in section); inflorescences never distinctly elongated, many- to few- and even 1-flowered; calyx truncate above (without lobes or lips); style glabrous, a little hairy or (seldom) densely hairy **Schradera**

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