

**REVISION OF THE GENUS PHYLLAGATHIS  
(MELASTOMATACEAE: SONERILEAE)  
II. THE SPECIES IN BORNEO AND NATUNA ISLAND**

NICOLETTA CELLINESE<sup>1</sup>

Department of Botany, Field Museum of Natural History, 1400 South Lake Shore Drive,  
Chicago, Illinois 60605-2496, USA

SUMMARY

A revision of the genus *Phyllagathis* Blume is presented under a wider generic concept than used by earlier authors. This section of the revision will focus exclusively on the species in Borneo and Natuna Island. Eighteen species are endemic to Borneo, and only *P. steenisii* is endemic to Natuna Island, a small Indonesian island off the northern coast of Sarawak. One new species is described and several new combinations are established with the inclusion of pentamerous genera into *Phyllagathis*.

**Key words:** *Phyllagathis*, Sonerileae, Borneo, Natuna Island, taxonomy.

INTRODUCTION

For a comprehensive synopsis of the genus *Phyllagathis* Blume refer to Part I: The species of Burma, Thailand, Peninsular Malaysia and Sumatra (Cellinese, 2002). As with the Malayan taxa, the species of Borneo do not form a monophyletic group (Cellinese, 1999, in prep.), and are here treated separately on the basis of convenient regional boundaries.

Nineteen species are recognized, one of which is endemic to the Indonesian Natuna Island. The majority of Bornean species occur in East Malaysia (Sarawak and Sabah) and Brunei. A few species are endemic to either Sarawak or Sabah. Although Indonesian Kalimantan comprises a large part of Borneo, it is surprising to find only *Phyllagathis gymnantha*, *P. guttata*, *P. longifolia* and *P. peltata*, none of which are endemic to Kalimantan. This situation can be attributed to paucity of collections. While Borneo as a whole is among the better collected areas of the humid tropics, collecting in Indonesian Borneo is very limited, and Kalimantan is among the least collected regions of the world (Ashton, 1989).

The genus is revised under a wider generic concept, and pentamerous genera such as *Cyanandrium* Stapf, *Enaulophyton* Steenis and *Brittenia* Cogn. are included in *Phyllagathis*, resulting in several new combinations (Cellinese, 2002).

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1) Current address: Botany Division, Peabody Museum of Natural History, Yale University, 170 Whitney Avenue, P.O. Box 208118, New Haven, CT 06520-8118, USA.

## MATERIALS AND METHODS

This work is based upon the study of herbarium specimens examined in and/or borrowed from the following herbaria: A, BM, BO, C, E, FI, GH, HBG, K, KEP, L, NY, P, SAN, SAR, SING and UKMS (Holmgren et al., 1990). Fieldwork was carried out in Sabah, Sarawak and Kalimantan during April–October 1995 and June–July 1997.

Measurements of the vegetative parts were taken from herbarium material and in the field whenever possible. Flowers and fruits were collected and stored in 70% alcohol, or, when fresh material was not available, they were taken from dried herbarium specimens, boiled and examined using a dissecting microscope. Data on the distribution and ecology were taken from specimen labels and personal observations in the field.

For the purpose of this work, I have recognized species based on the presence of unique combination of fixed morphological characters. As such, I have employed the phylogenetic species concept advanced by Nixon & Wheeler (1990).

## TAXONOMIC TREATMENT

## PHYLLAGATHIS

- Phyllagathis* Blume (1831a) 507; (1831b) 248. — Type: *Phyllagathis rotundifolia* (Jack) Blume.  
*Brittenia* Cogn. (1890) 515; (1891) 519; C. Hansen (1985) 171. — Type: *Brittenia subacaulis* Cogn.  
*Cyanandrium* Stapf (1895) pl. 2419; Gilg (1897) 7, suppl.: 263; M.P. Nayar (1965) 501. — Type: *Cyanandrium guttatum* Stapf.  
*Enaulophyton* Steenis (1932) 175, in obs., 194, 196. — Type: *Enaulophyton lanceolatum* Steenis.  
*Tylanthera* C. Hansen (1990) 632. — Type: *Tylanthera tuberosa* C. Hansen.

Herbs, subcaulescent or mostly caulescent, often prostrate and rooting, rarely stoloniferous or with tubers, variously branched to unbranched, or rarely erect single-stemmed, with a basic vestiture of minute brown glands (rarely stellate) of various density on some or all vegetative parts. *Stems* terete to subquadrangular, or rarely slightly flat, sulcate or ribbed, often prostrate and rooting, usually with an additional indumentum of rarely branched or gland-tipped hairs or bristles, internodes 0.3–6.5 cm long or in stolons to 25 cm long. *Leaves* opposite or alternate at least at the base, isomorphic, equal to subequal, rarely unequal or one leaf aborted in a pair, glabrous or with sparse long hairs, (3–)5–11(–15)-nerved, or slightly to prominently 5–7-plinerved, with 1 or 2 pairs of faint nerves in addition, at least basally, broadly ovate to elliptic, or sometimes more or less orbicular, or rarely obovate or (sub)pandurate, rarely coriaceous or bullate, base cordate to very broadly cordate or rounded, rarely narrowly rounded or cuneate or acute, apex acuminate to shortly broadly acuminate, rarely very broadly acute to rounded, margin entire, or rarely subdenticulate or subdentate to irregularly double dentate. *Petioles* present or leaves rarely sessile, usually with an additional indumentum as on stem. *Inflorescences* a terminal or rarely axillary, variously contracted thyse, with flowers arranged in opposite or slightly displaced clusters, often with lateral scorpioid branches, or a simple or rarely compound umbel, or rarely a dense head-like aggregate of scorpioid branches, or a dichasium, or rarely reduced to a solitary flower or in pair, peduncles sometimes with an additional indumentum of bristles, bracts subulate

or bristle-like, or very broadly ovate or cordate, with minute brown glands and rarely some hairs in addition. *Flowers* actinomorphic, 4- or 5-merous, usually diplostemonous, rarely haplostemonous (only in South China and Thailand species), pedicel often with a sparse indumentum usually as petiole or hypanthium. *Hypanthium* cup-shaped, campanulate or slightly urceolate, usually subquadrangular or quadrangular, very rarely ribbed or winged, usually with minute brown glands, rarely uniseriate or stellate or sometimes gland-tipped hairs or bristles, or rarely with fleshy emergences. *Sepals* broad and short, usually triangular and keeled, often connate, with a sparse indumentum as on the hypanthium, either persistent or disappearing in the mature fruit. *Petals* oblong, ovate, elliptic, or obovate, or sometimes irregularly or broadly so, glabrous or ending with a gland of the hypanthial kind, white, pink, or purple. *Stamens* 4 (only in South China and Thailand), 8 or 10, isomorphic and equal, less often dimorphic and unequal, filaments glabrous or sometimes with sparse minute gland-tipped hairs on basal half, anthers narrowly ovate in lateral view and tapering, or rarely oblong and obtuse, often slightly curved to ventral side, usually yellow, pore one, usually more or less ventrally inclined, about as wide as apex, less often minute, pollen sacs often free basally and extended below insertion of filament, connective distinct, dorsally with a tubercle or a long spur, or rarely a flat ridge (only in Thailand), occasionally inappendiculate, ventrally inappendiculate, or with filaments, ligulate appendages or auricles. *Ovary* 4- or 5-locular, usually about half as long as hypanthium, and adnate to it for one half or to its entire length, anther pockets shallow (to half-way), or deep (to the base), crown lobes usually large and surrounding base of style, rarely absent, lobes partly to fully connate, placenta axile, protruding into locules on stalks, peltate. *Style* glabrous, stigma as wide as or narrower than apex. *Fruit* a capsule usually cup-shaped, quadrangular or pentangular, rarely urceolate, and 8–10-ribbed, or ribs absent, composed of usually swollen persistent basal part of hypanthium and capsule, persistent crown lobes usually much enlarged, wedge-like, often surrounding an obpyramidal or an obconical space, placental column with or without a beak, 4- or 5-horned or horns absent, placentae stalked, disintegrating after seed dehiscence or rarely not. *Seeds* obovate or less often oblong or cuneate, rarely ellipsoid, never cochleate, sometimes angular, testa usually slightly to distinctly tuberculate, beak short blunt, strophiole usually dark brown.

## KEY TO THE TAXA

- 1a. Flowers pentamerous . . . . . 2
- b. Flowers tetramerous . . . . . 8
- 2a. Inflorescences a pleiochasium; ovary crowns absent . . . . . **19. P. subacaulis**
- b. Inflorescences umbelliform; ovary crown present . . . . . 3
- 3a. Intersepalous appendages present . . . . . 4
- b. Intersepalous appendages absent . . . . . 5
- 4a. Leaves rarely maculate; hypanthium covered with glandular hairs . . . . .
- . . . . . **9. P. jacobsoniana**
- b. Leaves always maculate; hypanthium puberulous . . . . . **7. P. guttata**
- 5a. Leaves distinctly plinerved . . . . . 6
- b. Leaves never plinerved . . . . . 7

- 6a. Leaves elliptic-ovate; stamen dorsal appendages absent . . . . . **12. P. osmantha**  
 b. Leaves lanceolate; stamen dorsal appendages present. . . . . **18. P. steenisii**  
 7a. Small herbs up to 35 cm high; stamen dorsal appendages absent . . . . . **16. P. rufa**  
 b. Large woody herbs > 35 cm high; stamen dorsal appendages present . . . . .  
 . . . . . **14. P. penrisseensis**  
 8a. Inflorescences thyrsoïd. . . . . 9  
 b. Inflorescences a pleiochasium, umbelliform, or flowers solitary. . . . . 13  
 9a. Single-stemmed shrubs; inflorescence of 1-axis thyrses; sepals conspicuously  
 thickened . . . . . **15. P. pulcherrima**  
 b. Herbs; thyrses 1- or 3-axis; sepals thin . . . . . 10  
 10a. Leaf apex obtuse to more often truncate; inflorescences much longer than  
 leaves . . . . . **11. P. longispicata**  
 b. Leaf apex acute to acuminate; inflorescences never much longer than leaves 11  
 11a. Large herbs up to 120 cm high; leaf base rounded, auriculate; inflorescence axis  
 quadrangular, winged; stamen dorsal appendages absent . . . . . **6. P. gigantifolia**  
 b. Herbs up to 40 cm high; leaf base cordate; inflorescence axis terete, not winged;  
 stamen dorsal appendages present . . . . . 12  
 12a. Leaves elliptic-lanceolate; base rounded to narrowly cordate; stamen ventral ap-  
 pendages auriculate . . . . . **10. P. longifolia**  
 b. Leaves ovate to elliptic-obovate; base widely cordate; stamen ventral appendages  
 cylindric or club-shaped. . . . . **1. P. atrovioacea**  
 13a. Inflorescences a pleiochasium . . . . . 14  
 b. Inflorescences umbelliform, or sometimes flowers solitary. . . . . 15  
 14a. Leaves peltate. . . . . **13. P. peltata**  
 b. Leaves not peltate. . . . . **8. P. gymnantha**  
 15a. Leaves peltate. . . . . **2. P. beccariana**  
 b. Leaves not peltate. . . . . 16  
 16a. Flowers always solitary; leaves strongly unequal . . . . . **4. P. dispar**  
 b. Flowers occasionally solitary, often in few-flowered umbels; leaves equal . . 17  
 17a. Leaves broadly ovate to orbicular . . . . . **3. P. brookei**  
 b. Leaves elliptic . . . . . 18  
 18a. Leaves broadly elliptic, 5–7-nerved; stamen connectives ending dorsally in a  
 spur. . . . . **5. P. elliptica**  
 b. Leaves narrowly elliptic, 3-nerved; stamen connectives ending in a U-shaped ap-  
 pendage forming an edge dorsally and two flat lobes ventrally. . . **17. P. rupicola**

**1. Phyllagathis atrovioacea** C. Hansen ex Cellin., *spec. nov.* — Fig. 1, Map 1

Folia alternata, lamina late elliptico-ovata, basi late cordata, thyrusus 1-axibus formatus.  
 — Typus: *Sibak ak Luang 22505* (A, holo K, L), Sarawak, Bukit Mersing, Anap.

Branched herbs, 20–40 cm high. *Stems* cylindric to subquadrangular, up to 14 cm long, with dense minute brown glands and sometimes also clothed with glandular hairs and dense patent up to 7.5 mm long bristles or hairs, especially at nodes. *Leaves* alternate, at least at the base, ovate to elliptic, 10–25 by 5–18.5 cm, 5–7-nerved, upper surface with sparse minute brown glands and/or glandular hairs, occasionally glabrous, lower

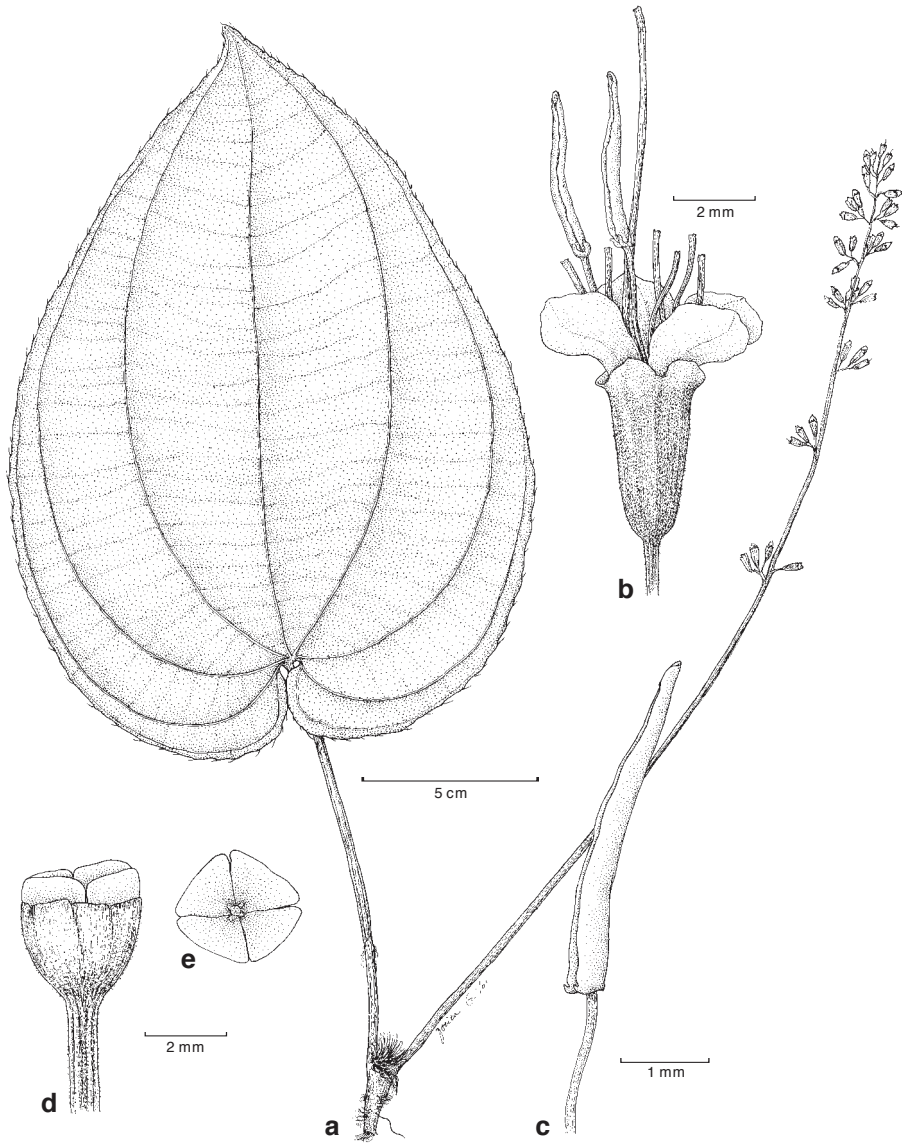


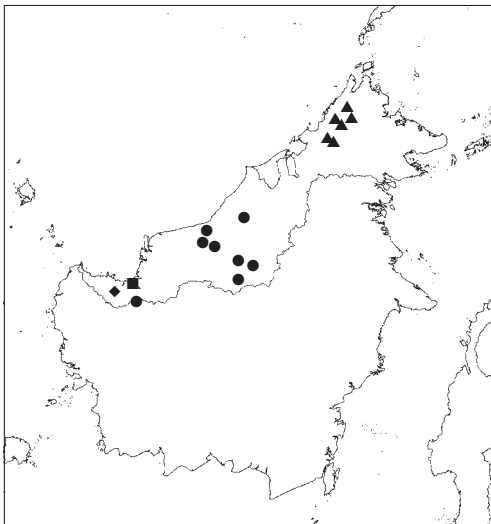
Fig. 1. *Phyllagathis atroviolacea* C. Hansen ex Cellin. a. Habit; b. flower; c. stamen, lateral view; d. capsule, lateral view; e. capsule, top view.

surface clothed with minute brown glands and/or glandular hairs mainly on nerves, sometimes also with patent bristles, base broadly cordate, less often narrowly cordate, apex slightly obtuse to acuminate, margin entire to bluntly dentate, glabrous or often ciliate. *Petioles* 2.5–18 cm long, with minute brown glands, sometimes densely clothed with hairs and 3–6 mm long thin retrorse bristles. *Inflorescences* a terminal and axillary, spike-like thyrse, 10–30 cm long, rachis with opposite or subopposite

scorpioid flowering branches and/or clusters of flowers 0.5–5 cm apart, with minute brown glands and sometimes with a few bristles at nodes, peduncle 7.5–21 cm long, usually reddish, sometimes only at the base, bracts inconspicuous to about 1–1.5 mm long and linear. *Flowers* 4-merous, pedicel to about 2–2.5 mm long in flower, 3–4.5 mm long, sometimes swollen, especially distally, in fruit. *Hypanthium* campanulate to slightly urceolate, subquadrangular, c. 3.5 by 1.7 mm, with some minute brown glands, sparsely clothed with hairs. *Sepals* low and wide, slightly emarginate, very shortly connate, 0.4–0.6 mm high, thick along middle and raised into a pointed cone close to apex, clothed as hypanthium, persistent in young fruit, perishing with upper part of hypanthium. *Petals* irregularly orbicular or obovate, 1–2.5 by 2.5–3.5 mm, thick, especially along the middle, and raised into a blunt cone close to apex dorsally, white to pink. *Stamens* 8, isomorphic, equal to subequal, filaments flat, 2.5–4 mm long, anthers narrowly ovate, attenuate, straight or slightly curved, 2.8–5 mm long including an 0.5 mm long beak, pore 1, oblique on ventral side of apex, as wide as beak, thecae somewhat undulate, bluish, purple or pink, connective distinct, ventrally at first adnate to base of anther sacs, then free and split into two club-shaped or cylindrical upwards bending appendages, dorsal appendage a c. 0.1 mm long blunt pendent spur. *Ovary* about one third to two fifths the length of hypanthium and adnate to it for all of its length, crown large, wide, with lobes fully connate, anther pockets shallow, placentae stalked. *Style* 6–11.5 mm long, glabrous, stigma small. *Capsules* cup-shaped, subquadrangular, 8-ribbed, 3–4 by 2.5–3.5 mm, with valves flushing tip of ribs, placental column with a long beak widened on apical half and with 4 longitudinal furrows, placentae entire after seed dehiscence. *Seeds* broad, triangular or cuneate, c. 0.4 mm long, testa uneven, beak large, wide, blunt.

Distribution — Sarawak (13 coll.).

Habitat — Basalt hillside in mixed dipterocarp forest, exposed silty soil on steep spurs, shaded sandstone rock of Biban formation, 220–1000 m elevation. Flowering and fruiting: April to November.



Map 1. Distribution of *Phyllagathis atroviolacea* C. Hansen ex Cellin. (●), *P. beccariana* (Cogn.) M.P. Nayar (■), *P. brookei* M.P. Nayar (◆) and *P. elliptica* Stapf (▲).

Note — This new species can be distinguished among others by the alternate and cordate leaves with wider margins. The inflorescence is a spike-like thyrse often with lateral scorpioid branches in addition to clusters of flowers. The epithet was chosen by Carlo Hansen (ined.) who referred to the occasionally coloured peduncles. Other thyrseoid species are *P. longifolia*, *P. pulcherrima*, *P. longispicata* and *P. gigantifolia*. *Phyllagathis longispicata* has distinctly truncate, glabrous leaves with a much longer inflorescence and flowers arranged in opposite fascicles. *Phyllagathis longifolia* has distinct lanceolate to elliptic leaves with flowers also arranged in clusters along the rachis. *Phyllagathis pulcherrima* is a single stemmed shrub with opposite leaves and distinctly conspicuous sepals due to their unusual thickness. *Phyllagathis gigantifolia* is a large herb with the inflorescence having a distinctly winged quadrangular axis, and additional long lateral axes, or short scorpioid lateral branches.

## 2. *Phyllagathis beccariana* (Cogn.) M.P. Nayar — Map 1

*Phyllagathis beccariana* (Cogn.) M.P. Nayar (1976) 231. — *Allomorpha beccariana* Cogn. (1891) 467. — Type: *Beccari* 495 (BR not seen, holo FI, K), Borneo, Sarawak, Banting (Batang Lupar).

Subcaulescent herbs, up to 16 cm high. *Stems* gnarled, 1–2 cm long, unbranched, with minute uniseriate hairs. *Leaves* alternate at the least at the base, otherwise decussate, obovate to elliptic, 7–20 by 4.5–9 cm, peltate or subpeltate (petiole inserted less than 0.5 cm from lower margin), 3–5-nerved with an additional pair of faint marginal nerves, upper surface glabrous, lower surface with minute brown glands and especially on nerves with sparse uniseriate hairs, base subtruncate to subcordate, apex acute to shortly acuminate, margin subdentate with 1–2 mm long thin patent bristles. *Petioles* 2.5–10 cm long, with minute uniseriate hairs, dense only along sulcus. *Inflorescences* a terminal few-flowered umbel, peduncle up to 20 cm long, with sparse minute brown glands, bracts ovate, c. 0.8 mm long. *Flowers* 4-merous, pedicel 4–7 mm long, with sparse minute brown glands. *Hypanthium* slightly urceolate, 4–5 by 1.2 mm, with sparse minute brown glands. *Sepals* broadly rounded, c. 0.5 mm long, with a keel pointed into a short bristle, with sparse minute brown glands, caducous. *Petals* 4–5 mm long, reddish. *Stamens* 8, isomorphic, equal, filaments c. 3.5 mm long, glabrous, anthers c. 3.5 mm long, pore 1, thecae undulate, straight, purplish, connective distinct, with a minute dorsal spur and two ventral lobes. *Ovary* about half the size of hypanthium, adnate to it for its full length, crown of 4 lobes fully connate, with sparse uniseriate hairs, anther pockets shallow. *Style* 8–11 mm long, with a few uniseriate hairs at least at the base, stigma small. *Capsules* and *seeds* unknown.

Distribution — Sarawak (2 coll.).

Habitat — Unknown. Flowering: October.

Note — *Phyllagathis beccariana* is known only from the type material. Its leaves are shortly peltate and the inflorescence is an umbel. *Phyllagathis peltata* is the only other species with peltate leaves; however, its inflorescence is a pleiochasium.

## 3. *Phyllagathis brookei* M.P. Nayar — Map 1

*Phyllagathis brookei* M.P. Nayar (1976) 232. — Type: *Brooke* 10416 (holo BM, L), Sarawak, Bilengki, Bakelalan.

Cauliscent, woody herb, often branched, up to 12 cm high, with raphides in many parts, and usually with dense, long, pale brown hyaline uniseriate hairs, tipped with a minute glandular cell, caducous on leaves above. *Stems* prostrate or erect and sometimes more or less rooting, with sparse long slightly curly patent bristles in addition to uniseriate hairs, internodes 1.5–6 cm long. *Leaves* opposite, decussate, isomorphic and subequal in a pair, broadly obovate to suborbicular, 2.5–3.5 by 1.6–2.8 cm, 3–5-nerved with an additional pair of faint intramarginal nerves, both surfaces with sparse minute brown glands and sometimes with up to 1 mm long curly soft hairs, base broadly rounded to subcordate, apex broadly acute to rounded, margin entire, with up to 1 mm long hairs. *Petioles* 0.6–1.3 cm long, with or without sparse, up to 6 mm long bristles, in addition to hyaline hairs. *Inflorescences* a solitary flower or up to 4 together in an umbel, terminal or axillary, sessile or subsessile, subtended by long-persistent leaf-like bracts. *Flowers* 4-merous, pedicel from 6.5 mm long in flower to 10 mm long in fruit, glabrous. *Hypanthium* campanulate, c. 4 by 3 mm, with minute brown glands and with stout, but soft to 2 mm long retrorse hairs. *Sepals* triangular, c. 1.5 mm long, shortly connate, slightly keeled, with long soft hairs on margin and basally on keel, persistent in mature fruit. *Petals* broadly obliquely obovate, 7–9 by 5–8 mm, thin, pink. *Stamens* 8, isomorphic, equal, filaments c. 3 mm long, glabrous, anthers narrowly ovate, c. 1.9 mm long, straight, yellow, pore 1, oblique on ventral side of apex, connective distinct, ventrally inappendiculate, dorsally with an 0.2 mm long pendent spur appressed to filament. *Ovary* about half the length of hypanthium, adnate to it for half its length, crowned with large, partly connate lobes, anther pockets shallow, placentae stalked. *Style* c. 6 mm, glabrous, stigma small. *Capsules* cup-shaped, slightly 8-ribbed, c. 6 by 5 mm, with valves exceeding tip of ribs by 1.5 mm and surrounding an obpyramidal space, placental column beaked, with 4 straight acicular horns, placentae disintegrating after seed dehiscence. *Seeds* unknown.

Distribution — Sarawak (4 coll.).

Habitat — Wet mossy rocks in forests at 1500–2000 m elevation. Flowering and fruiting: August and October.

Note — *Phyllagathis brookei* is a small woody herb with roundish leaves which can be also recognized by its long retrorse bristles on the hypanthium. Together with *P. dispar*, *P. rupicola* and *P. elliptica*, it forms a distinct group in having raphide crystals of calcium oxalate as well as hyaline hairs throughout vegetative and reproductive structures. This group is morphologically very different from any other Bornean species by having very few-flowered umbels, often reduced to solitary flowers with no peduncles, which is a rare condition in the genus. Moreover, these plants are distinctly caulescent and erect, although occasionally the base of the stem is prostrate and rooting. The leaves are much smaller than in any other Bornean species.

#### 4. *Phyllagathis dispar* (Cogn.) C. Hansen — Fig. 2, Map 2

*Phyllagathis dispar* (Cogn.) C. Hansen (1982) 559. — *Anerincleistus dispar* Cogn. (1891) 479. — Type: *Beccari 2400* (holo FI, K, P), Sarawak.

*Phyllagathis uniflora* Stapf (1894) pl. 2280. — Type: *Haviland 1172* (holo K, SAR, SING), Borneo, Kinabalu.

*Phyllagathis uniflora* Stapf var. *longiloba* M.P. Nayar (1976) 233. — Type: *Chew, Corner & Stainton RSNB 1262* (holo K, L, SAR, SING), North Borneo, Sungei Mamut, Ulu Langanani, Mt Kinabalu.



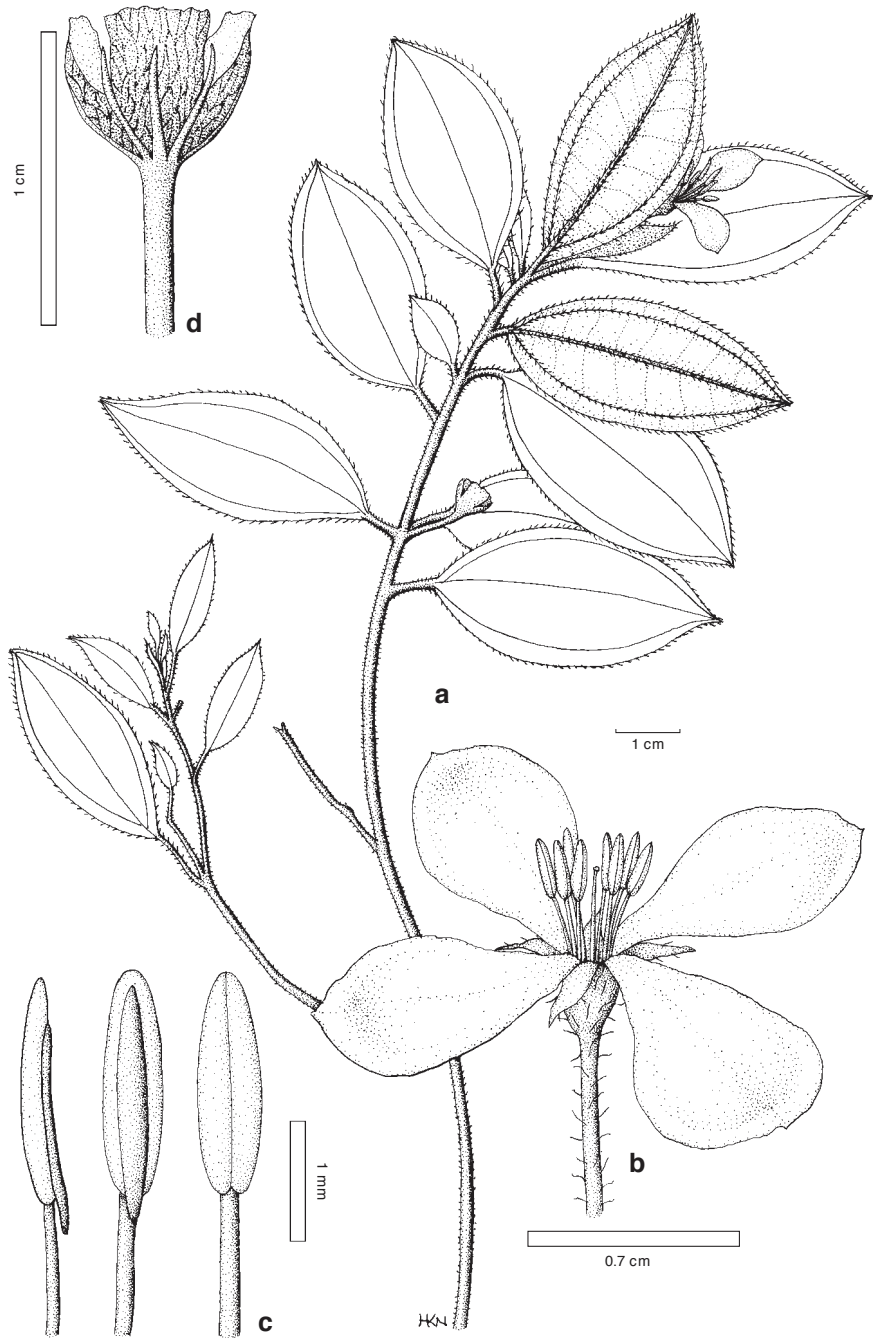
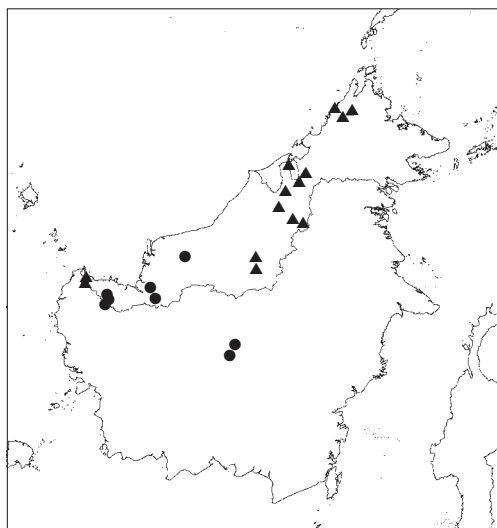


Fig. 2. *Phyllagathis dispar* (Cogn.) C. Hansen. a. Habit; b. flower; c. lateral, ventral and dorsal view of stamen; d. capsule.

Cauliscent herbs, up to 40 cm high, with raphides in many parts, and up to 2 mm uniseriate, pale brown hyaline hairs, caducous on leaves above. *Stems* prostrate and rooting basally otherwise erect, branching subquadrangular, very rarely ribbed, or terete, internodes 0.5–5 cm long. *Leaves* opposite, isomorphic and unequal in a pair, elliptic, larger leaves 4–8 by 1.3–3 cm, smaller leaves 3–11 by 1–6.5 mm, 3–5-nerved or slightly plinerved, secondary venation conspicuous, lower surface glabrescent, upper surface with a few 1–2 mm long stout soft hairs, base acute to rounded, apex acute or shortly bluntly acuminate, margin entire or subserrulate, sometimes with short bristles. *Petioles* 0.5–1.4 cm in larger leaves, 0.1–0.3 cm long in smaller leaves. *Inflorescences* a terminal or axillary solitary flower, bracts usually 2, linear, 2–5 mm long, persistent. *Flowers* 4-merous, often sessile or subsessile, otherwise pedicels 1.2–6 mm long, with hyaline hairs and minute brown glands. *Hypanthium* cup-shaped, subquadrangular, 2.5–3.5 by 1.8–2.8 mm, with sparse minute brown glands and sparse uniseriate hyaline hairs, or glabrous. *Sepals* narrowly triangular, rarely linear, 3.5–5.5 mm long, sometimes pointed into a 1 mm long bristle, shortly connate, clothed as hypanthium, persistent in mature fruit. *Petals* obovate, 7–10 by 6–6.5 mm, thin, pink. *Stamens* 8, isomorphic, equal, filaments 3.8–5 mm long, glabrous, anthers narrowly ovate, 2.1–3 mm long, straight, yellow, pore 1, oblique on ventral side of apex, connective distinct, ventrally inappendiculate, dorsally with an 0.2–0.4 mm long flat pendent spur. *Ovary* half the length of hypanthium, adnate to it for half its length, crown of 4 wide, partly connate, large lobes, placentae stalked. *Style* 7–7.8 mm long, glabrous, stigma subcapitulate. *Capsules* slightly urceolate, subquadrangular, 8-ribbed, c. 5 by 5 mm, valves emarginate, c. 1.5 mm longer than ribs and surrounding an obpyramidal space, old fruit cup-shaped, quadrangular, c. 7 by 6 mm, placental column shortly beaked, with 4 small cusp-like spreading horns, placentae disintegrating after seed dehiscence. *Seeds* obovate, tuberculate, very shortly bluntly beaked, c. 0.8 mm long, strophiole thin.

Distribution — Brunei, Sarawak and Sabah (36 coll.).



Map 2. Distribution of *Phyllagathis dispar* (Cogn.) C. Hansen (▲) and *P. guttata* (Stapf) Cellin. (●).

Habitat — Lower and upper montane rain forest, often on mossy substrate on ground, on rotting tree trunks, or on rocks, at 1000–2000 m elevation. Flowering: known from June, August, November; fruiting: from March to July.

Note — *Phyllagathis dispar* can be recognized by its strongly unequal leaves and subsessile solitary flowers. The strongly unequal leaves in a pair are known in no other species of *Phyllagathis*, but are common in *Anerinckleistus*, *Driessenia*, *Neodriessenia*, and *Sonerila*. See also the note under *P. brookei*.

### 5. *Phyllagathis elliptica* Stapf — Fig. 3, Map 1

*Phyllagathis elliptica* Stapf (1894) pl. 2279. — Lectotype: *Haviland 1286* (lecto K, designated here), Borneo, Kinabalu. Paratype: *Low s.n.* (K), Borneo, Kinabalu.

Cauliscent herbs, up to 45 cm high, with raphides in many parts, and on most parts with usually dense, long, pale brown hyaline uniseriate hairs up to 4 mm, caducous on leaves above. *Stems* erect, or often prostrate and rooting basally, subquadrangular, with sparse to dense slightly curly retrorse bristles up to 13 mm long, internodes 0.5–6 cm long. *Leaves* opposite, isomorphic, equal to subequal in a pair, elliptic or obovate, 4–11.5(–15.5) by 2.2–6.5(–7.8) cm, sometimes crowded apically on stem, 5(–7)-nerved, with an additional pair of faint outer nerves, upper surface densely covered with bristly hairs, lower surface with dense, long hyaline hairs and bristles, often tinged with red, base rounded to broadly rounded, rarely acute, apex rounded or sometimes acute to very shortly bluntly acuminate, margin entire or less often subserrulate, with about 0.5 mm long bristles. *Petioles* with a wide shallow sulcus above, (0.4–)1.2–2.2(–2.8) cm long, with retrorse bristles, dense on sides but absent in sulcus and below, sometimes a few below. *Inflorescences* an umbel, many- or few-flowered, rarely reduced to a single flower, subterminal or axillary, 3–5 cm long, almost sessile or peduncles up to 1 cm long, bracts two or three pairs, elliptic, outer ones usually leaf-like, 12–44 by 6–18 mm, inner ones less or not at all leaf-like, (0.6–)4.5–15 by (0.2–)2.2–9 mm, ciliate with up to 1.5 mm long thin bristles, otherwise clothed as leaves especially when large, persistent. *Flowers* 4-merous, pedicel 16–23(–31) mm long in flower, up to 38 mm long in fruit, glabrous or with very sparse minute brown glands. *Hypanthium* campanulate, 3–4.5 by 1.3–2.5 mm, glabrous or with sparse minute brown glands and often also some long uniseriate hairs. *Sepals* broadly attenuate to subligulate, 2–4.8 by 1–1.5 mm, shortly connate, usually 3-nerved, clothed as hypanthium and additionally with 0.5–2 mm long hairs on margin, persistent till maturity of fruit. *Petals* more or less asymmetrically obovate or ovate, 11–16 by 6.5–10 mm, pink or pale yellow. *Stamens* 8, isomorphic, equal, filaments 4.3–6.5 mm long, glabrous, anthers narrowly ovate, 2.1–3.5 mm long, slightly curved to ventral side, yellow, pore 1, small, slightly ventrally inclined, connective distinct, ventrally inappendiculate, dorsally with an 0.2–0.3 mm long spur, pendent or bent slightly backwards. *Ovary* half the length of hypanthium, adnate to it for about half of its length, anther pockets shallow, crown large, wide, lobes fully connate, placentae stalked. *Style* c. 10 mm long, glabrous, stigma small. *Capsules* cup-shaped or slightly urceolate, quadrangular, 8-ribbed, 4.5–8 by 4–7 mm, with emarginate valves exceeding the tips of the ribs by 0.8–2 mm, placental column beaked, with 0.6–1.1 mm long, acicular, slightly spaced and slightly inwards curved horns, placentae disintegrating after seed dehiscence. *Seeds* obovate, c. 0.8 mm long, testa tuberculate, beak short, blunt.

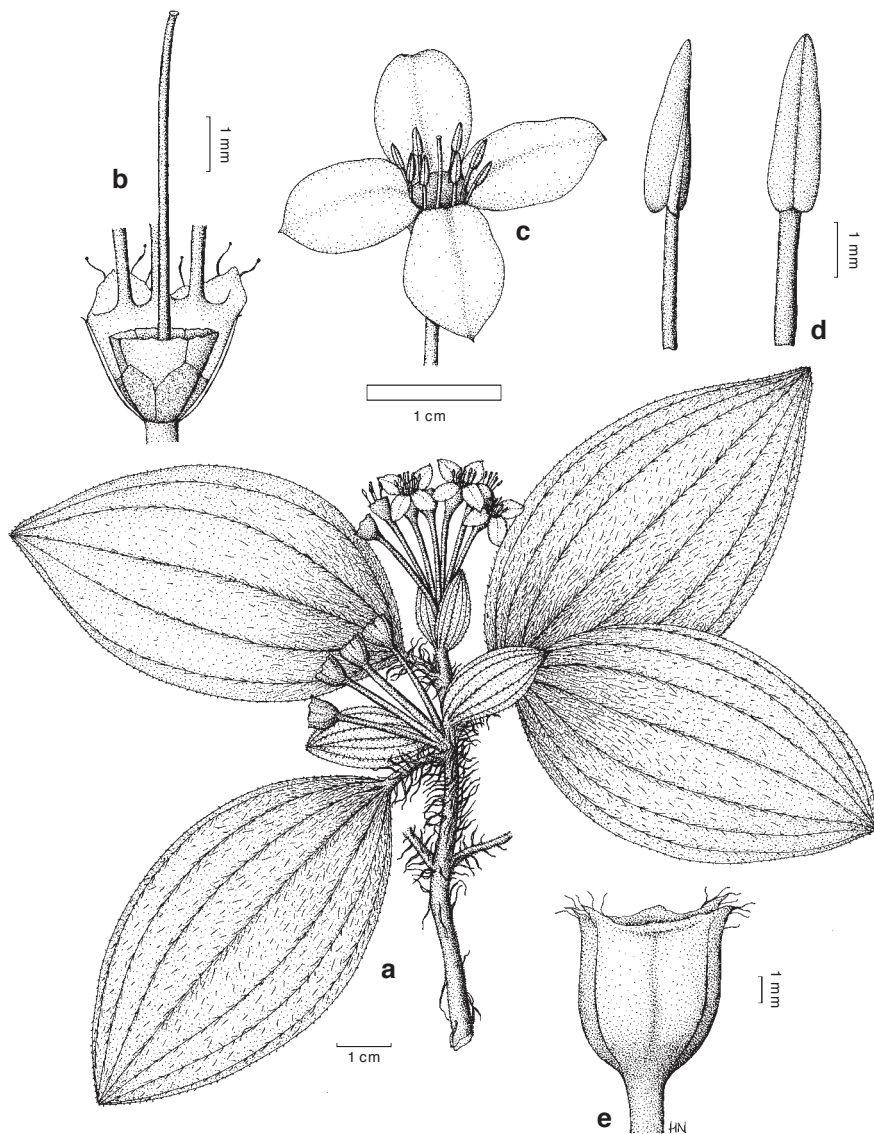


Fig. 3. *Phyllagathis elliptica* Stapf. a. Habit; b. longitudinal section of a flower showing pistil and bases of filaments; c. flower; d. lateral and ventral view of stamen; e. capsule.

Distribution — Sabah (49 coll.).

Habitat — Montane rain forest (oak-laurel, *Tristania*, *Agathis*, *Podocarpus* forests), in litter or on moss or fallen tree trunks in damp and shady places on slopes or along streams at 1250–1850 m elevation. Flowering and fruiting: all year round.

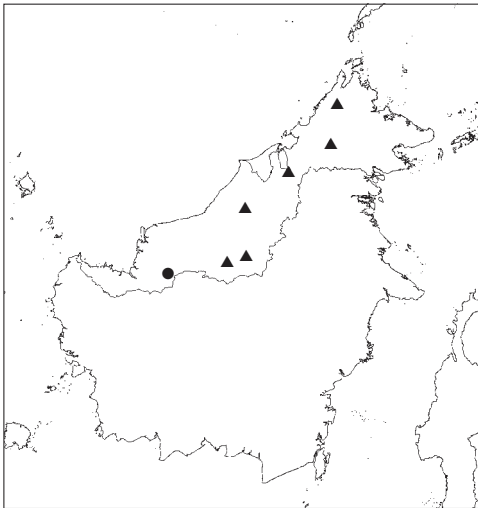
Note — This species can be recognized by its elliptic to obovate leaves and long stem and petiole bristles. See also the note under *P. brookei*.

**6. *Phyllagathis gigantifolia* M.P. Nayar — Fig. 4, Map 3**

*Phyllagathis gigantifolia* M.P. Nayar (1976) 231. — Type: *Synge 491* (holo K, L), Sarawak, Mt Dulit, Ulu Koyan.

Large herbs, 45–120 cm high, sparsely covered with minute glandular hairs. *Stems* somewhat woody, subquadrangular and 4-ribbed, internodes 1.5–3 cm long. *Leaves* decussate, opposite, isomorphic and equal, elliptic to obovate, 24–38 by 10–18 cm, 5- or 7(–9)-nerved, sometimes with an additional pair along margins at least basally, secondary venations conspicuous, both surfaces almost glabrous, base rounded and slightly auriculate, or narrowly cuneate, apex shortly acuminate, margin entire. *Petioles* winged or widely winged as if the lamina were decurrent on the petiole, (2–)4–8 cm long. *Inflorescences* a terminal thyrse, with only a quadrangular winged central axis, or with two opposite long densely scorpioid branches at the basal node, peduncle 12–35 cm long. *Flowers* 4-merous, pedicel 2–7 mm in flower up to 10 mm in fruit. *Hypanthium* cup-shaped to campanulate, subquadrangular, 2.2–3.5 by 1.5–2 mm. *Sepals* widely triangular or rounded, c. 0.6 mm high, dorsally thickened below apex, very shortly connate, persistent. *Petals* irregularly ovate to elliptic, thick along middle especially apically, 4–6 by 2.5–3.5 mm, white or pink. *Stamens* 8, isomorphic, slightly unequal, filaments flat, straight, short ones 3–3.5 mm long, long ones 4–4.5 mm long, anthers curved to ventral side, short ones c. 3 mm long, long ones c. 4 mm long, pale yellow, pore 1, oblique on ventral side, small, connective distinct, ventral appendage two small blunt tubercles, dorsally inappendiculate. *Ovary* about half the length of the hypanthium, adnate to it for its whole length, glabrous, anther pockets shallow, crown absent, placentae stalked. *Style* c. 5.5 mm long, with minute brown glands, almost straight, stigma small. *Capsules* obconical cup-shaped, c. 3 by 4.5 mm, crowned by the torus with the persistent sepals, slightly 8-ribbed, top of capsule rounded and non-acrescent, placenta c. 2 mm long, shortly stalked and not disintegrating after seed dehiscence. *Seeds* cuneate, 0.5–0.7 mm long, with a 0.2 mm pyramidal beak at chalaza, dorsally tuberculate, strophiole distinct.

Distribution — Brunei, Sarawak and Sabah (14 coll.).



Map 3. Distribution of *Phyllagathis gigantifolia* M.P. Nayar (▲) and *P. longispicata* (Cogn.) J.F. Maxwell (●).

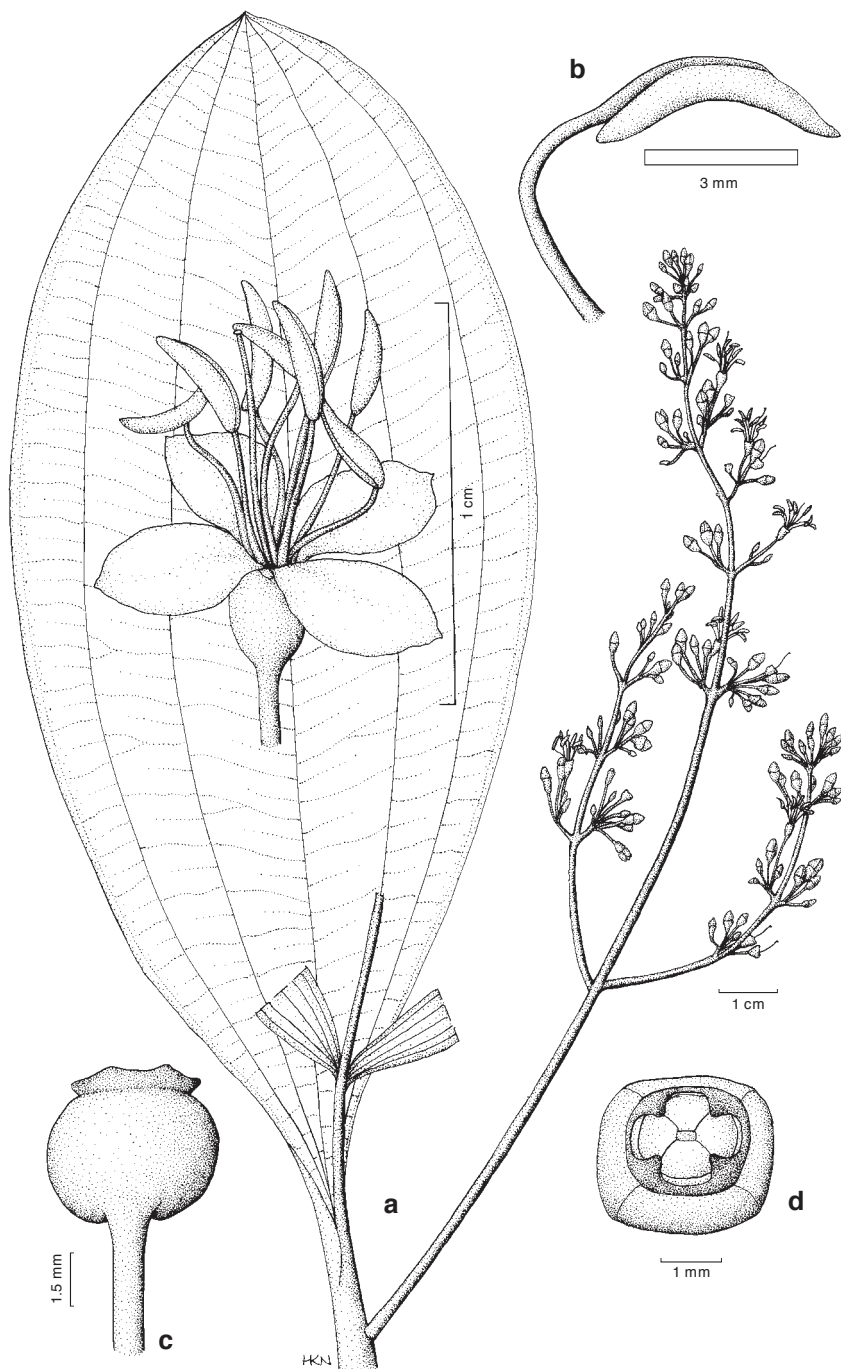


Fig. 4. *Phyllagathis gigantifolia* M.P. Nayar. a. Habit with enlarged flower superimposed on top of leaf; b. lateral view of stamen; c. capsule, lateral view; d. capsule, top view.

Habitat — Stream banks in sand, heath or moss forest, 140–1250 m elevation. Flowering and fruiting: March to September.

Note — Compared to other thyrsoid species, the inflorescence of *P. gigantifolia* is strictly terminal. The main inflorescence axis is distinctly winged and quadrangular, and may have two additional axes at the basal node, or contracted lateral scorpioid branches. See also the note under *P. atroviolacea*.

### 7. *Phyllagathis guttata* (Stapf) Cellin., *comb. nov.* — Map 2

*Cyanandrium guttatum* Stapf (1895) pl. 2419; Gilg (1897) 7, suppl.: 263 — Type: *Haviland 1549* (holo K), Sarawak, Saribas.

Rhizomatous subcaulescent, few-leaved herbs, up to 30 cm high. *Stems* very short, at most 3 cm long, thick and unbranched, with minute brown glands and long scattered bristles. *Leaves* alternate at least near the base, isomorphic, equal to subequal, ovate to somewhat orbicular, 4.5–13 by 3–11.5 cm, 7–9-nerved, with distinct secondary and tertiary nerves, upper surface maculate with white spots from the center of which a bristle arises, in addition minute brown glands, lower surface densely covered with bristles on primary, secondary and tertiary nerves, base deeply cordate, apex acute, margin minutely denticulate, hairy. *Petioles* 3.5–10 cm long, densely covered with long, patent, reddish brown hairs and minute brown glands. *Inflorescences* a terminal umbel, 15–17 cm long, peduncle 7.5–12 cm long, with scattered minute brown glands. *Flowers* 5-merous, pedicel 7–12 mm long. *Hypanthium* campanulate, 10-ribbed, 4–5 by 2.5–3 mm, with minute brown glands. *Sepals* triangular, free, c. 0.8 mm long, lobes alternating with c. 3 mm long appendages. *Petals* oblong, c. 7 mm long. *Stamens* 10, isomorphic and equal, filaments 3–4 mm, glabrous, anthers lanceolate, acuminate, 5–6 mm long, straight, usually bluish, pore 1, large, oblique on ventral side, connective distinct, dorsally inappendiculate, ventrally produced into two thick auricles. *Ovary* about two thirds the length of the hypanthium, fully adnate to it by 10 septa, anther pockets shallow, crown of 5 large lobes, denticulate and fully connate, placentae stalked. *Style* 11–12 mm long, glabrous, stigma punctiform. *Capsules* obpyramidal cup-shaped, pentangular, distinctly 10-ribbed, 5–7 by 4–5 mm, with valves surrounding an inverted frustum space, placental column with a long beak, horns absent, sometimes a few hairs present, placentae stalked and non-disintegrating after seed dehiscence. *Seeds* c. 0.7 mm long, cuneate.

Distribution — Sarawak and Kalimantan (7 coll.).

Habitat — Near river banks, growing on ground or lithophytic in slightly open or very shady places, 150–300 m elevation. Flowering and fruiting: August to March.

Note — This species is very distinct in having deeply cordate leaves with large white spots on the upper surfaces. A small bristle arises from each spot. The calyx has intersepalous appendages that are also found in *P. jacobiana*, but distinguished from it in having puberulous hypanthia.

### 8. *Phyllagathis gymnantha* Korth. — Map 4

*Phyllagathis gymnantha* Korth. (1844) 252. — Type: *Korthals s.n.* (holo L), Borneo.

*Allomorpha multinervia* Cogn. (1891) 531. — *Phyllagathis multinervis* (Cogn.) J.F. Maxwell (1982) 221. — Type: *Beccari 3441* (holo FI), Sarawak.

*Phyllagathis hirsuta* Cogn. (1894) t. 3. — Type: Cultivated (introduced from Borneo), specimen grown in Jardin Botanique de l'État, Bruxelles (holo BR).

*Phyllagathis johannis-winkleri* O. Schwartz (1931) 240. — Type: *Hans Winkler 1473a* (BO, holo HBG), West-Borneo, 'auf dem Bukit Tilung'.

*Phyllagathis johannis-winkleri* O. Schwartz var. *glaberrima* O. Schwartz (1931) 240. — Type: *Hans Winkler 1145* (holo HBG), West-Borneo, 'auf dem Bukit Mehigit'.

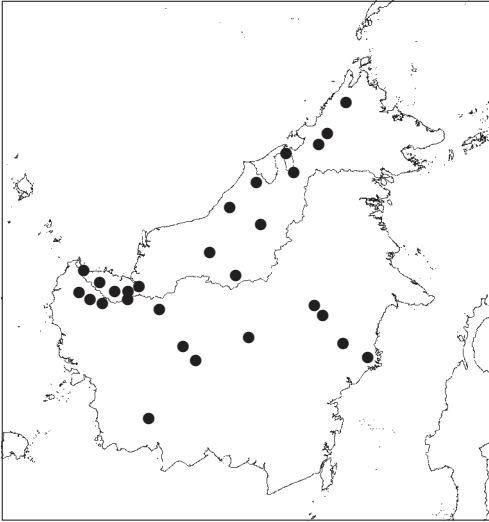
*Phyllagathis pallida* O. Schwartz (1931) 240. — Type: *Hans Winkler 275* (holo HBG), West-Borneo, 'am unteren Serawei'.

*Phyllagathis nymphaeifolia* Hallier f. ex Bakh.f. (1943) 269. — Type: *Hallier 1732* (K, holo L, NY), Borneo, G. Kenepai.

Rhizomatous subcaulescent herbs, 15–45 cm high. *Stems* short, at most 5 cm long, usually thick, gnarled, and unbranched, with dense minute brown glands and often also up to 8 mm long stout, brown bristles. *Leaves* ovate to elliptic to suborbicular, 4–26(–30) by 3–26(–30) cm, position uncertain, but if opposite certainly isomorphic and equal to subequal in a pair, 5–13-nerved, secondary and tertiary veins numerous and conspicuous, upper surface with sparse, minute, brown glands and sometimes scattered, long, ascending hairs, lower surface with minute brown glands and often with long patent hairs more dense along the veins, base cordate to very broadly cordate, apex acute to broadly acute, acuminate or rounded, rarely slightly retuse, margin entire or bluntly denticulate with often distant 0.5–3 mm long hairs. *Petioles* 2–18(–30) cm long, with sometimes dense minute glands all over, densely or sparsely covered with long patent or retrorse brown hairs, less often completely glabrous. *Inflorescences* a terminal pleiochasium (7–)14–32 cm long, sometimes two or three times as long as the leaves, peduncle 12–30(–33) cm long, forking into 4–13 mm long densely scorpioid branches, with often sparse minute brown glands, floral bracts subulate or more often bristle-like, 0.5–2 mm long. *Flowers* 4-merous, pedicel from 3 mm long in flower to 11 mm long in fruit. *Hypanthium* narrowly campanulate, quadrangular at least basally, sometimes 8-ribbed, 3–7 by 1.2–2.5 mm, with minute brown glands. *Sepals* very low and wide, rounded, c. 0.7 mm high, partially connate, with a more or less distinct keel or conical thickening often pointed into a short hair, with minute brown glands, persistent. *Petals* broadly ovate to suborbicular, sometimes wider than long, slightly thick and conically thickened dorsally, 2.8–9 by (2.8–)3.3–7 mm, whitish or purplish. *Stamens* 8, isomorphic, equal or very rarely subequal, filaments flat, (2.3–)3.2–6 mm long, glabrous or with sparse minute uniseriate gland-tipped hairs on basal half, anthers narrow, tapering, usually curving forward, 3.8–6.7 mm long, pore 1, oblique on ventral side of apex, thecae undulate, purplish, connective distinct produced into a dorsal tubercle or up to 0.5 mm long usually flat spur and into two ventral filaments adnate to base of sacs at least for two thirds their length. *Ovary* about one half the length of hypanthium, adnate to it for its full length, anther pockets shallow, crown wide, lobes fully connate, with a few minute glands or glabrous, placentae stalked. *Style* (9.5–)10–18 mm long, stigma small. *Capsules* cup-shaped, subquadrangular with 8 rounded ribs, c. 5 by 4 mm, with valves more or less flushing tips of ribs, central column with an 0.3–0.8 mm long beak ending in 0.3–1 mm short thick and blunt or longer cylindrical or tapering straight or apically inwards bent horns, placentae non-disintegrating after seed dehiscence. *Seeds* 0.5–2 mm long, obovate, with a stout blunt chalazal beak, testa almost smooth, strophiole large.

Distribution — Brunei, Sarawak, Sabah and Kalimantan (69 coll.).





Map 4. Distribution of *Phyllagathis gymnantha* Korth.

**Habitat** — Humid forests, usually close to streams, on sandstone rocks, or on clay or sandy soils on slopes or river banks, at 50–1000 m elevation. Flowering and fruiting: all year round.

**Note** — *Phyllagathis gymnantha* represents a large, variable complex of acaulescent to subacaulescent herbs. Leaf size varies from relatively small to very large and the indumentum on all parts ranges from sparse to dense. The long peduncled inflorescence is a pleiochasium made up of four densely scorpioid branches arising from a single node. The anthers are curved with distinct undulate thecae.

### 9. *Phyllagathis jacobsoniana* (M.P. Nayar) Cellin., *comb. nov.* — Map 5

*Cyanandrium jacobsonianum* M.P. Nayar (1965) 502 — Type: *Jacobs* 5433 (holo K), Sarawak, Kapit district.

Subacaulescent herbs, 20–40 cm high. *Stems* very short, at most 5 cm, unbranched, with minute glands and scattered long hairs. *Leaves* alternate at least near the base, isomorphic and equal in a pair, ovate, 9–26 by 6–16 cm, 7–9-nerved, with distinct secondary and tertiary nerves, upper surface rarely maculate, with minute glands and often sparsely setose especially along nerves, hairs 2.5–3 mm long, lower surface with small hairs along the nerves and sometimes minute glands between them, base cordate, apex acute to acuminate, margin denticulate, ciliate or glabrescent. *Petioles* 7–20 cm long, with minute glands and scattered to dense long patent hairs, occasionally glabrescent. *Inflorescences* a terminal umbel, 10–30 cm long, bracts absent, peduncle 20–25 cm long, furfuraceous in juvenile stage then becoming glabrescent. *Flowers* 5-merous, pedicel 6–12 mm long, furfuraceous. *Hypanthium* campanulate, 3–5 by 2.5–4 mm, 10-ribbed, clothed with glandular hairs 2–3 mm long. *Sepals* wide, triangular, c. 1 mm long, free, lobes alternating with long branched or unbranched appendages, clothed with minute brown glands. *Petals* oblong, 7–9 by 3–4 mm, white. *Stamens*

10, isomorphic and equal, filaments flat, 5–6 mm long, glabrous, anthers straight, acuminate, 4–5 mm long, bluish, pore 1, oblique, large, connective distinct, dorsally inapplicable, ventrally with two small auricles. *Ovary* about two thirds the length of the hypanthium, fully adnate to it by 10 septa, anther pockets shallow, crown of 5 fully connate lobes, minutely denticulate, placentae stalked. *Style* 11–12 mm long, glabrous, stigma punctiform. *Capsules* cup-shaped, pentangular, distinctly 10-ribbed, 4–5 by 5–6 mm, with valves surrounding an inverted frustum space, placental column with a long beak, horns absent, placentae stalked, non-disintegrating after seed dehiscence. *Seeds* cuneate, 0.5–0.6 mm long.

Distribution — Sarawak and Brunei (20 coll.).

Habitat — On steep slopes, or lithophytic, along stream banks, in very shady environment, 220–1350 m elevation. Flowering and fruiting: all year round.

Note — *Phyllagathis jacobsiana* is distinguished among the pentamerous flowered species in having glandular hairs covering the hypanthium and intersepalous appendages.

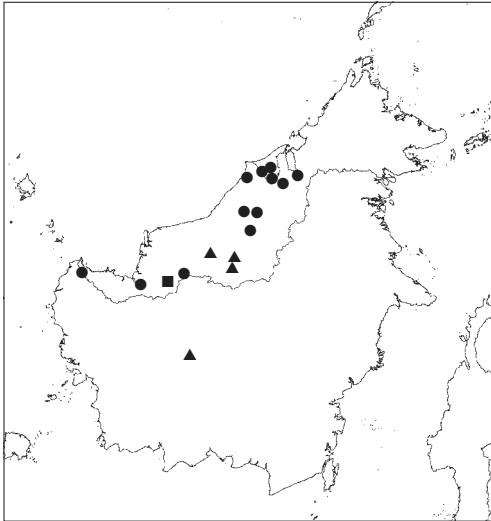
### 10. *Phyllagathis longifolia* (Cogn.) J.F. Maxwell — Map 5

*Phyllagathis longifolia* (Cogn.) J.F. Maxwell (1982) 221. — *Allomorpha longifolia* Cogn. (1891) 466. — Type: *Beccari 3837* (BR not seen, holo FI), Borneo, Sarawak.

*Phyllagathis lanceolata* O. Schwartz (1931) 239. — Type: *Winkler 1293* (holo HBG), West-Borneo, 'am Sungei Malang'.

*Phyllagathis sarawakensis* M.P. Nayar (1976) 231. — Type: *Clemens 21586* (A, holo K), Sarawak, Gat, Upper Rejang River.

Subcaulescent herbs, 15–40 cm high. *Stems* terete or subquadrangular, 2–6 cm long, little branched, with dense minute brown glands and/or glandular hairs, with some patent hairs or sometimes with long light brown stout bristles at nodes, internodes usually up to 1 cm long. *Leaves* opposite or alternate at least at the base, equal or subequal in a pair, lanceolate, elliptic to less often elliptic-ovate, 8–20 by 2.5–8 cm, 3- or 5-nerved with an additional pair of faint marginal nerves, both surfaces usually glabrous with minute brown glands, but sometimes with scattered long hairs on the lower surface, base rounded to cordate, narrow to often acute, apex acute to long acuminate, margin entire, with long appressed or rarely spreading hairs or bristles. *Petioles* 3–22 cm long, with minute brown glands and often, but mainly only on upper side, with long patent hairs to retrorse bristles. *Inflorescences* a terminal or lateral spike-like thyrse, 8–26 cm long, with minute brown glands on all parts and/or glandular hairs, peduncle 10–18 cm long, sometimes with 1 or 2 rudimentary nodes on upper half, rachis 4.5–10 cm long, with nodes 1–2.5 cm apart, with opposite, densely scorpioid few-flowered clusters, bracts subulate or narrowly ovate, 0.5–3.5 mm long. *Flowers* 4-merous, pedicel 2–6 mm long. *Hypanthium* narrowly campanulate, quadrangular and 4- or 8-ribbed at least at base, 3.5–4.5 by 1.2–1.6 mm, with sparse minute brown glands or glandular hairs, occasionally glabrous. *Sepals* rounded to triangular, 0.6–0.8 mm long, free, conspicuous due their thickness along the middle and especially apically, sometimes with a keel pointed apically into a short bristle, clothed with sparse minute brown glands or glandular hairs, persistent in mature fruit. *Petals* clawed, irregularly orbicular and widely obcordate, thick along middle, papillose, 1.8–2.5 by 1.7–2.5 mm, white to pink and sometimes bluish only on the outside. *Stamens* 8, isomorphic, equal



Map 5. Distribution of *Phyllagathis jacobsoniana* (M.P. Nayar) Cellin. (●), *P. longifolia* (Cogn.) J.F. Maxwell (▲) and *P. osmantha* (M.P. Nayar) Cellin. (■).

to subequal, filaments 2.3–4 mm long, glabrous, anthers narrowly ovate, 3–4.1 mm long, pore 1, small and oblique on ventral side, thecae undulate, purplish to deep blue, connective distinct, with a minute dorsal spur and two ventral auricles partly adnate to base of sacs. *Ovary* half the length of hypanthium, adnate to it for half its length, anther pockets shallow, crown of 4 fully connate lobes, low and wide, placentae stalked. *Style* c. 9 mm long, stigma capitulate. *Capsules* slightly urceolate, quadrangular, 8-ribbed, c. 5 by 3 mm, old fruit cup-shaped, quadrangular, 8-ribbed, 3.5–4 by 2.5–3.2 mm, with the accrescent valves surrounding an obpyramidal space and flushing tip of ribs, placental column beaked, slightly 4-fid distally, placentae disintegrating after seed dehiscence. *Seeds* unknown.

Distribution — Kalimantan and Sarawak (7 coll.).

Habitat — By streams in forests at low elevations. Flowering and fruiting: February to March and August to September.

Note — This species has lanceolate to elliptic leaves and thyrses with opposite flower clusters. See also the note under *P. atroviolacea*.

### 11. *Phyllagathis longispicata* (Cogn.) J.F. Maxwell — Map 3

*Phyllagathis longispicata* (Cogn.) J.F. Maxwell (1982) 221. — *Allomorpha longispicata* Cogn. (1890) 531; (1891) 465. — Type: *Beccari 3861* (BR not seen, holo FI), Sarawak, Scrang.

Causlescent herbs with a prostrate and rooting stem. *Stems* 11–12 cm long, with minute glands, nodes c. 1 cm apart. *Leaves* opposite, decussate, isomorphic and subequal, elliptic-ovate, 8.3–15 by 4.5–9(–10) cm, 5-nerved, both surfaces glabrous, base rounded to cordate, apex truncate or subtruncate, margin entire. *Petioles* 2–3 cm long, glabrous. *Inflorescences* a spike-like thyrses, much longer than leaves, flowers 3–5 in opposite fascicles, peduncle glabrous, 25–30 cm long. *Flowers* 4-merous, pedicel 2–4 mm long. *Hypanthium* cylindrical, 2.5–3 mm long, with scattered minute glands. *Sepals*

triangular, shortly connate, c. 0.5 mm long, clothed as hypanthium. *Petals* ovate, 1.5 mm long. *Stamens* 8, isomorphic and equal, filaments flat, c. 2 mm long, anthers 1.5–2 mm long, connective distinct, dorsally inappendiculate, ventrally with 2 short auricles, pore 1, as wide as the anther.

Distribution — Sarawak (known only from the type).

Note — The material examined was flowering only. It was not possible to dissect a flower to observe the ovary. Despite the lack of additional material, this is a distinct species because of the much longer spike-like thyrses and also the peculiar leaf shape with truncate apex, a rare feature in the genus.

### 12. *Phyllagathis osmantha* (M.P. Nayar) Cellin., *comb. nov.* — Map 5

*Cyanandrium osmanthus* M.P. Nayar (1968a) 334 — Type: *Collenette 859* (holo K), Sarawak, Ulu Lemanak.

Subcaulescent few-leaved herbs, 15–30 cm high. *Stems* very short, clothed with hairs 6–9 mm long. *Leaves* alternate at least near the base, isomorphic and equal, ovate to elliptic, 10–18 by 7–12.5 cm, 7–9-plinerved, secondary and tertiary nerves distinct, upper surface glabrous or covered with scattered small hairs, lower surface clothed with hairs along the nerves, and furfuraceous between nerves, base cordate, apex acute, margin denticulate. *Petioles* 7–10 cm long, densely clothed with hairs 3–4 mm long. *Inflorescences* a terminal umbel, few- to many-flowered, 10–14 cm long including the peduncle, glabrous or with sparse minute glands. *Flowers* 5-merous, pedicel 3–4 mm long, densely covered with hairs 3–4 mm long. *Hypanthium* widely campanulate, 5–6 by 5 mm, densely clothed with hairs. *Sepals* narrowly triangular, free, 6–7 mm long, clothed as the hypanthium. *Petals* oblong, 15–18 by 5–6 mm. *Stamens* 10, isomorphic and equal, filament flat, 7–8 mm long, anthers straight, acuminate, c. 6 mm long, pore 1, oblique, large, connective distinct, dorsal appendage absent, ventrally with 2 small auricles. *Ovary* about two thirds the length of the hypanthium, totally adnate to it by 10 septae, crowned with 5 fully connate lobes, anther pockets shallow. *Style* 12–14 mm long, glabrous, stigma punctiform.

Distribution — Sarawak (known only from the type).

Habitat — 800 m elevation. Flowering: October.

Note — *Phyllagathis osmantha* is a few-leaved pentamerous herb with large showy flowers, long calyx lobes and hairy hypanthia.

### 13. *Phyllagathis peltata* Stapf ex Ridl. — Map 6

*Phyllagathis peltata* Stapf ex Ridl. (1946) 38. — Type: *Haviland & Hose 3205* (holo K), Borneo, Baram, Mt Dulit.

Subcaulescent herbs, c. 30 cm high. *Stems* short, relatively slender, with nodes close together, with minute brown glands. *Leaves* opposite, ovate to broadly ovate, 12.5–21 by 9–17 cm, peltate (petiole inserted 1–4.5 cm from lower margin), 5-nerved, upper surface glabrous, lower surface with minute brown glands and 1–2 mm long thin bristles, base very broadly rounded, apex abruptly shortly acuminate, margin entire with 1.5–4 mm long bristles of various sizes, longer ones conspicuously thickened on basal half and tapering into a thin outer part. *Petioles* c. 14 cm long, with sparse

minute brown glands. *Inflorescences* 17–22 cm long pleiochasium, with sparse minute brown glands on all parts, peduncle 16–20 cm long, forking into four up to 6 mm long densely scorpioid branches. *Pedicels* c. 4.5 mm long in old fruit. *Capsules* 4-merous, cup-shaped, with 8 rounded ribs, c. 6.5 by 4 mm, with the accrescent valves surrounding an obpyramidal space, central column beaked, with 4 short erect blunt horns, placentae not disintegrating after seed dehiscence. *Seeds* obovate, slightly tuberculate dorsally, beak broad, blunt, inflated, strophiole large.

Distribution — Sarawak and Kalimantan (2 coll.).

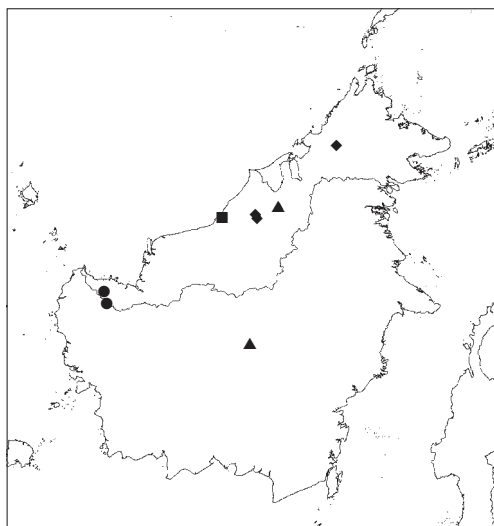
Habitat — 1000–1650 m elevation. Old fruits in March.

Note — This species is recognized by its distinctly peltate leaves and pleiochasial inflorescences. Although peltate leaves are not common in *Phyllagathis*, they are commonly found in other Sonerilean genera (e.g. *Sonerila*).

#### 14. *Phyllagathis penrissenensis* Cellin., *nom. nov.* — Map 6

*Enaulophyton sarawakense* M.P. Nayar (1965) 505, non *Phyllagathis sarawakensis* M.P. Nayar (1976) 231 (= *P. longifolia* (Cogn.) J.F. Maxwell). — Type: *Ilias* 16386 (holo K, L, SAR), Sarawak, Kuching, Gunong Penrissen.

Woody subcaulescent herbs, 35–50 cm high. *Stems* terete, 6 cm long, clothed with 9–12 mm long stout hairs, internodes up to 2.5 cm long. *Leaves* alternate at least near the base, ovate to almost orbicular, 13–31 by 13–28 cm, 5–9-nerved with two additional nerves at the base, secondary and tertiary veins distinct, upper surface glabrous or both surfaces clothed with sparse minute glandular hairs sometimes with brown up to 11 mm long patent bristles, base widely cordate, apex acute to almost rounded, margin more or less distinctly denticulate, densely to sparsely ciliate with short or long hairs. *Petioles* 11–23 cm long, clothed with minute glandular hairs and sometimes with up to 8 mm long patent bristles, at least some gland-tipped. *Inflorescences* a terminal umbel, bracts absent, peduncle subquadrangular, from 10 cm long in flower to 35 cm



Map 6. Distribution of *Phyllagathis peltata* Stapf ex Ridl. (▲), *P. penrissenensis* Cellin. (●), *P. pulcherrima* M.P. Nayar (■) and *P. rupicola* (M.P. Nayar) C. Hansen ex Cellin. (◆).

long in fruit, glabrous or sparsely covered with glands. *Flowers* 5-merous, pedicel 6–9 mm long in flower, up to 11 mm in fruit. *Hypanthium* campanulate, 4.5–8 by 2–4 mm, clothed with minute glandular hairs or glabrous. *Sepals* low and widely rounded, 1.3 mm high, thickened at middle apically and cusped, clothed with minute brown glands. *Petals* obovate, 13 by 7 mm. *Stamens* 10, isomorphic and equal, filaments 7–9 mm long, glabrous, anthers 7–9 mm long, pore 1, oblique on ventral side of apex, ventral appendage of two widening auricles 1–1.5 mm long, dorsal appendage a slightly flat spur 2–2.5 mm long. *Ovary* less than half the length of the hypanthium and adnate to it for its full length, distally interrupted by shallow anther pockets, crown of 5 large fully connate lobes, minutely denticulate, placentae stalked. *Style* 12–14 mm, glabrous, stigma small. *Capsules* obpyramidal cup-shaped, c. 4.5 by 3.5 mm, placentae non-disintegrating after seed dehiscence.

Distribution — Sarawak (3 coll.).

Habitat — Porphyritic rock face, sandstone rock, in shade, 100–1000 m elevation.

Note — This large pentamerous herb is recognized by its widely ovate and cordate leaves. The calyx lobes are very low and almost fully connate. The stamen connective is ventrally produced into two long auricles. A new name becomes necessary because the epithet is occupied by *Phyllagathis sarawakensis* M.P. Nayar (= *P. longifolia* (Cogn.) J.F. Maxwell).

### 15. *Phyllagathis pulcherrima* M.P. Nayar — Map 6

*Phyllagathis pulcherrima* M.P. Nayar (1968b) 301 — Type: *Ashton 18311* (holo K, L, SAR), Sarawak, Simalajau F.R., Ulu Sinrok.

Single-stemmed woody herbs, c. 25 cm high. *Stems* terete or at most subquadrangular and indistinctly ribbed, 11–12 cm long, clothed with minute brown glandular hairs and some patent brown hairs at nodes, internodes 0.5–1 cm long, bark brown. *Leaves* opposite, isomorphic and equal to subequal in a pair, ovate to elliptic, 11–12 by 3–3.5 cm, 3-nerved with an additional faint marginal nerve, both surfaces glabrous or clothed with sparse minute brown glands, base acute, apex attenuate, margin entire, with appressed brown hairs. *Petioles* 3–5 cm long, with minute glandular hairs and some long brown appressed hairs on upper surface. *Inflorescences* a terminal thyrse, c. 15 cm long, clothed on all parts with sparse minute glandular hairs, peduncle subangular, c. 10.5 cm long, rachis c. 4.5 cm long, branches c. 1 cm long, forked or not, scorpioid, bracts subulate, less than 1 mm long, or basal one narrowly ovate, 3.5 mm long. *Flowers* 4-merous, pedicel 6 mm long. *Hypanthium* cylindrical, quadrangular, 4-ribbed, c. 4.5 by 1.5 mm, clothed with sparse minute glandular hairs. *Sepals* rounded, c. 0.8 mm long, free, conspicuous due to their thickness, with a keel pointed apically into a short bristle, clothed with minute glandular hairs on the outside, papillose on the inside. *Petals* clawed, asymmetric, widely obcordate, thick along the middle especially apically, c. 1.8 by 1.8 mm, papillose on both surfaces, deep blue on the outside, white on the inside. *Stamens* 8, isomorphic, unequal, filaments c. 4 mm long, glabrous, anthers gradually narrowing from base to apex, straight, the shorter ones c. 3.7 mm, the longer ones 4.1 mm long, pore 1, oblique on ventral side of apex, thecae undulate, deep blue, connective distinct, ventrally split into two narrowly club-shaped lobes, dorsally produced into a short flat spur. *Ovary* about one half the length of hypanthium, totally adnate

to it for its whole length, anther pockets shallow, crown narrow, lobes fully connate, placentae narrowly stalked. *Style* 9 mm long, glabrous, stigma small.

Distribution — Sarawak, known only from the type.

Habitat — On wet shale rocks at stream head in forest. Flowering: March.

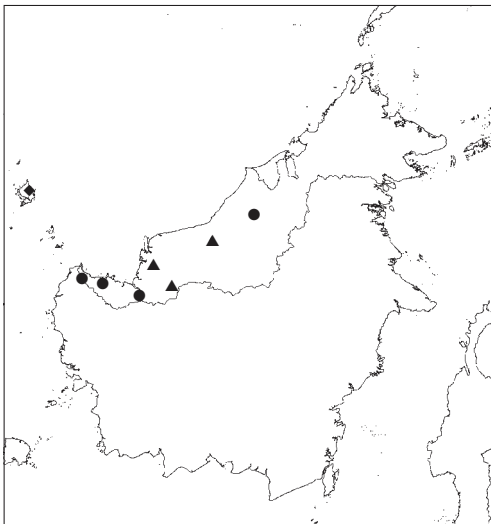
Note — *Phyllagathis pulcherrima* is distinguished by having appressed bristles on the petioles, acute leaf bases, and extraordinarily thick sepals. See also the note under *P. atroviolacea*.

### 16. *Phyllagathis rufa* (Stapf) Cellin., *comb. nov.* — Map 7

*Cyanandrium rufum* Stapf (1895) pl. 2419 — Type: *Haviland 142* (holo K), Sarawak, Matang.

*Cyanandrium glabrum* M.P. Nayar (1965) 503 — Type: *Richards 1448* (holo K), Sarawak, Mt Dulit.

Subcaulescent herbs, 20–35 cm high. *Stems* short, 5 cm long at most, quadrangular, densely to sparsely covered with long bristles. *Leaves* alternate at least at the base, isomorphic and equal to subequal, sometimes more or less coriaceous, widely ovate, 7–20 by 4.5–12 cm, 9–11-nerved, secondary and tertiary nerves distinct, upper surface glabrate to glabrous, lower surface clothed with minute hairs along the nerve or often glabrescent to glabrous, base cordate, apex acute to acuminate, margin denticulate, often ciliate. *Petioles* 6.5–18 cm long, densely covered with hairs, but often glabrescent or glabrous especially in mature plants. *Inflorescences* a terminal umbel, 12–32 cm long including the peduncle, sparsely covered with minute hairs, but often glabrescent or glabrous. *Flowers* 5-merous, pedicel 7–10 mm long, up to 13 mm in fruit. *Hypanthium* campanulate, 4–5 by 3–4 mm, usually 10-ribbed with minute short hairs or often glabrescent to glabrous. *Sepals* widely triangular, free, c. 0.8 mm long, clothed as hypanthium. *Petals* oblong, 5–7 by 3–4 mm. *Stamens* 10, isomorphic and equal, filaments flat, 3–7 mm long, anthers 4–6 mm long, acuminate, bluish, pore 1, oblique, connective distinct, ventrally with 2 small auricles, dorsally inappendiculate. *Ovary*



Map 7. Distribution of *Phyllagathis rufa* (Stapf) Cellin. (●), *P. steenisii* Cellin. (◆) and *P. subcaulis* (Cogn.) Cellin. (▲).

about two third the length of hypanthium, fully adnate to it by 10 septa, crowned by 5 fully connate lobes minutely denticulate, anther pockets shallow, placentae stalked. *Style* 6–12 mm long, puberulous to glabrous, stigma punctiform. *Capsules* obpyramidal cup-shaped, 5–6 by 4–5 mm, pentangular, distinctly 10-ribbed, with valves surrounding an obconical space, central column with a long beak, horns absent, placentae stalked, not disintegrating after seed dehiscence. *Seed* minute, cuneate, c. 0.7 mm long.

Distribution — Sarawak (10 coll.).

Habitat — Lithophytic in shaded primary forests; on gentle ridge slopes or shaded cliffs, 180–1520 m elevation. Flowering and fruiting: March to December.

Note — *Phyllagathis rufa* is a few-leaved pentamerous herb with variable indumentum, ranging from being absent to furfuraceous to dense. A similar pattern in the indumentum can be found in *P. gymnantha*. *Phyllagathis rufa* is related to *P. guttata* and *P. jacobsoniana* but differs in lacking intersepalous appendages.

### 17. *Phyllagathis rupicola* (M.P. Nayar) C. Hansen ex Cellin., *comb. nov.* — Map 6

*Perilimnastes rupicola* M.P. Nayar (1974) 173. — *Anerinacleistus rupicola* (M.P. Nayar) J.F. Maxwell (1982) 215. — Type: *Synge 503* (holo K), Sarawak, Mt Dulit, Ulu Koyan.

Somewhat woody caulescent herbs, with a forked branching, 8–60 cm high, with raphides in many parts, and on young parts with long pale brown hyaline uniseriate hairs composed of 1 (–few) much elongated inflated cells and tipped with a minute brown glandular cell. *Stem* rooting basally, subquadrangular and with 1–4 mm long, straight, stout subappressed bristles at least at nodes, internodes 0.1–4 cm long. *Leaves* opposite, isomorphic and subequal in a pair, narrowly elliptic, 3.5–7 by 0.4–1.8 cm, 3-nerved, both surfaces sparsely hairy, base narrowly cuneate, apex narrowly acute or very slightly acuminate, margin entire, glabrous. *Petioles* wide, 4–7 mm long, glabrous when old or with a few bristles as on stem on edge of sulcus. *Inflorescences* a terminal few-flowered umbel, 2–3 cm long, sessile. *Flowers* 4-merous, pedicel from 9 mm long in flower to 22 mm long in fruit, glabrous. *Hypanthium* slightly campanulate, 2.8–4 by 1.2–1.5 mm with very sparse minute brown glands, very rarely also with long intersepalous bristles. *Sepals* broad basally, shortly connate and abruptly narrowed into a subligulate lobe, 1–3 by 1 mm, glabrous. *Petals* elliptic-oblong, acute, thin, 10–13 by 4–4.5 mm, pink to magenta. *Stamens* 8, isomorphic, subequal, filaments 3–4.5 mm long, glabrous, anthers narrowly ovate, long attenuate, 4.5–6 mm long, yellow, pore 1, truncate, as wide as apex, connective distinct, very slightly prolonged below sacs, ending in a U-shaped appendage forming an edge dorsally and two flat lobes ventrally, in addition to two independent strands adnate to base of sacs. *Ovary* as long as hypanthium, crown large, with c. 0.1 mm long gland-tipped hairs on the upper margin, anther pockets shallow. *Style* 7–12 mm long, glabrous, stigma small. *Capsules* cup-shaped, quadrangular, 8-ribbed, c. 6.5 by 5.5 mm, with valves exceeding the tips of the ribs by 1.7 mm, central column with a 1 mm long beak, horns 0.7 mm long, thick basally and slender apically, straight, placentae disintegrating after fruit dehiscence, ascending from basal axils of locules.

Distribution — Sabah and Sarawak (5 coll.).

Habitat — Sandstone rocks in river bed in mossy forest at 800 m elevation. Flowering: February, September; buds and old fruits in August.



Note — *Phyllagathis rupicola* is a narrow-leaved plant distinguished by its staminal U-shaped appendage which forms an edge dorsally and two lobes ventrally. In addition, two ventral strands of connective tissue are adnate to the base of the sacs. See also the note under *P. brookei*.

### 18. *Phyllagathis steenisii* Cellin., *nom. nov.* — Map 7

*Enaulophyton lanceolatum* Steenis (1932) 175, in obs., 195, 197, non *Phyllagathis lanceolata* O. Schwartz (1931) 239 (= *P. longifolia* (Cogn.) J.F. Maxwell). — Type: *Van Steenis 1166* (holo BO, L), Natuna Island.

Erect or prostrate subcaulescent herbs clothed in many parts with appressed bristles especially at nodes where they are up to 1 cm long. *Stems* 2.5–6 cm long, with short internodes and appressed bristles. *Leaves* alternate at least near the base, isomorphic, equal, decussate, lanceolate to oblanceolate, 8–20 by 1.5–4.5 cm, 3-plinerved, upper surface glabrous, lower surface with minute brown glands and appressed bristles only on the nerves, base cuneate, apex acute, margin entire. *Petioles* 3–7 cm long, densely clothed with appressed bristles. *Inflorescences* a terminal few-flowered umbel, peduncle 11–18.5 cm long sparsely covered with minute bristles. *Flowers* 5-merous, pedicel 4–5 mm long in flowers, up to 10 mm long in fruits, glabrous. *Hypanthium* campanulate, 5–6 mm long, 5-ribbed, glabrous. *Sepals* triangular, partly connate, c. 5 mm long, conspicuous due to their thickness, glabrous. *Petals* irregularly obovate, c. 13 by 9 mm, pink. *Stamens* 10, isomorphic and equal, filaments slightly flat, 6–8 mm long, anthers attenuate, straight or almost, 6–7 mm long, pore 1, oblique on ventral side of apex, techae undulate, connective distinct, ventrally appendaged with two auricles, dorsal appendage a short spur. *Ovary* c. 2 mm high, adnate to hypanthium for its full length, crowned by 5 large lobes, fully connate, anther pockets shallow. *Style* 13–14 mm long, stigma small. *Capsules* obconical cup-shaped, 6–8 by 4–6 mm, 10-ribbed, placentae stalked, not disintegrating after fruit dehiscence, horns absent. *Seeds* minute, 0.5–0.7 mm long, oblong, shortly beaked.

Distribution — Indonesia: Natuna Island (known only from the type).

Habitat — Stream beds on gravel.

Note — A new name becomes necessary because the epithet is occupied by *Phyllagathis lanceolata* O. Schwartz (= *P. longifolia* (Cogn.) J.F. Maxwell).

### 19. *Phyllagathis subacaulis* (Cogn.) Cellin., *comb. nov.* — Map 7

*Brittenia subacaulis* Cogn. (1890) 515; (1891) 519; C. Hansen (1985) 171. — Types: *Beccari 3802* (BR not seen, lecto FI, designated by Hansen, 1985), Sarawak, ad Bellaga' et Scrang; *Beccari 3860* (FI), Sarawak, Sungei Karang Hills ('Scrang').

Subcaulescent herbs, 15–35 cm high. *Stems* terete, 0.5–6 cm long, clothed at nodes with gland-tipped bristles. *Leaves* opposite, isomorphic, equal to subequal, broadly to very broadly ovate, sometimes orbicular, 11–24.5 by 7–18 cm, 5–7-nerved, conspicuously reticulate underneath, succulent, upper surface glabrous or with minute glands and scattered short hairs, lower surface clothed with minute hairs in addition to uniseriate and multiseriate hairs, base broadly to very broadly cordate, apex very broadly acute or rounded, rarely broadly emarginate, margin entire. *Petioles* 2–11.5 cm long, clothed

with scattered to dense multiseriate soft hairs. *Inflorescences* a terminal pleiochasium made up of up to 6 scorpioid branches, peduncle 6.5–13.5 cm, glabrous, bracts broad and ligulate to ovate and spatulate, 1.5–3 mm. *Flowers* 5-merous, pedicel 1.5–2.5 mm in flowers and up to 5 mm in fruits, clothed with minute glands. *Hypanthium* campanulate, 1.5–2 mm, clothed with sparse minute glands. *Sepals* triangular, 0.8–1.4 mm long, keeled with a pointed extension exceeding the apex, clothed as the hypanthium. *Petals* irregularly obovate, c. 7 mm long, notched at the tip, pale pink. *Stamens* 10, isomorphic, equal, filaments slightly flat, 3.2–5.5 mm long, anthers oblong, curved ventrally, c. 1.8 mm long, yellow, pore 1, oblique, connective distinct, ventrally with a ligulate, apically denticulate appendage and bending upwards, dorsally with a slightly bifid spur pointing downwards. *Ovary* about two thirds the length of the hypanthium, adnate for half of its length, crown lobes absent, 5 apical glabrous humps around the style, anther pockets absent, placentae stalked. *Style* 5–6 mm long, stigma small and round. *Capsules* obconical cup-shaped, c. 3 by 3 mm, depressed apically and 10-ribbed, dehiscent loculicidally, placentae disintegrating after fruit dehiscence.

Distribution — Sarawak (9 coll.).

Habitat — Damp slopes or river banks in primary or secondary forests; on sandstone, sandy clay or basalt; 20–1000 m elevation. Flowering: July to October.

Note — This species is distinguished by having succulent, broadly to very broadly ovate, sometimes orbicular leaves, with a widely cordate base and conspicuous reticulate venation beneath. The inflorescence is a pleiochasium as in *P. gymnantha* and *P. peltata*, but the flowers are pentamerous and ovary crowns are absent.

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## INDEX TO SPECIMENS EXAMINED

The number after each collection refers to the corresponding species in the text. Only numbered or dated collections have been included.

- Aban 87662: 5 — Aban, Meijer & Dewol 94144: 5 — Abang 48257: 3 — Amin & Ismail 60307: 5 — Amin, Jarius & Francis 114138: 5 — Amin, Zaini & Francis 117276: 5 — Ampon & Saikheh 71816: 5 — Anderson 205: 4; 4517: 4; 28851: 19 — Anderson et al. 20289: 14 — Ashton 214: 4; 215: 4; 16493: 1; 16734: 1; 17795: 8; 18219: 8; 18240: 8; 18311: 15 (type); 19287: 19; 19359: 1 — Awa & Ilias 47376: 9 — Awa & Lee 47663: 9; 47977: 4; 47990: 6; 51110: 3 — Awa & Yii 46637: 9.
- Banying 16546: 6 — Beaman 6893: 4; 7122: 5; 7348: 4; 9930: 4; 10783: 4 — Beccari 495: 2 (type); 2400: 4 (type); 3441: 8 (type); 3802: 19 (type); 3837: 10 (type); 3860: 19 (type); 3861: 11 (type) — Bell 2000: 1; 2072: 4 — Boyce 268: 9 — Brooke 8559: 4; 8560: 16; 8994: 8; 8995: 10; 9248: 9; 9249: 8; 9267: 8; 9271: 10; 9450: 16; 9763: 16; 10122: 8; 10416: 3 (type) — Brooks 1044: 7 — Burley et al. 387: 8; 391: 7; 2773: 8; 2986: 8; 3133: 8; 3205: 8 — Burt 2635: 8; 8171: 14; 11270: 8; 11371: 4; 11389: 4; 11513: 9; 12706: 1; 12845: 4 — Burt & Martin 4817: 10; 4833: 1 (type); 4947: 1; 4997: 6; 5511: 4 — Burt & Woods 2521: 16; 2557: 8; 2772: 4.
- Carr 26927: 5; 27037: 5 — Cellinese 17: 6; 19: 5; 24: 5; 36: 5; 70: 7; 72: 8; 94: 4 — Chai 18967: 8; 34799: 17; 36014: 10 — Chai & Ilias 31552: 9 — Chai et al. 33112: 8 — Chew & Corner 4193: 5; 4726: 5 — Chew, Corner & Stainton 1255: 6; 1262: 4 (type); 1312: 5; 1360: 5; 1572: 4; 1716: 6; 2776: 5; 2876: 5 — Clemens 10537: 4; 20105: 16; 20362: 4; 21586: 10 (type); 27281: 8; 27570: 5; 29420: 4; 29563: 6; 32733: 8; 32959: 5; 51338: 5; 51557: 5; s.n. Penibukan: 5 — Colletette 859: 12 (type) — Coode 6485: 8; 7528: 6 — Cox 906: 5 — Croat 53132: 5 — Cultivated s.n.: 8 (type).
- Darnton 473: 5 — Daud & Tachum 35633: 8.
- Elsener 145: 8; 226: 8 — Ender 3450: 8; 4659: 8.
- Fidilis 110177: 6; 121738: 5; 125511: 5 — Forman 1080: 9 — Fuchs & Colletette 21384: 5.
- Gibbs 4422: 5.
- Hallier 1732: 8 (type) — Hansen 277: 9; 463: 4; 484: 4; 493a: 4; 616: 19; 671: 19; 772: 19; 1023: 8; 1045: 9; 1227: 8 — Haviland 142: 16 (type); 1172: 4 (type); 1286: 5 (type) 1549: 7 (type) — Haviland & Hose 3205: 13 (type) — Ding Hou 222: 5.
- Ilias 16386: 14 (type); 26518: 3; 28784: 7; 41171: 6; 42554: 1; 45192: 7 — Ilias & Azahari 35711: 8.
- Jacobs 5247: 19; 5433: 9 (type) — Jaheri 1028: 13 — James et al. 34433: 16 — Johns 7505: 8.
- Kato & Wiradinata B-6290: 8 — Keßler 382: 9 — Kiew 948: 9 — Kokawa & Hotta 4499: 5; 4516: 5; 4574: 5; 4959: 4; 5850: 4 — Korthals 30: 8 (type); s.n.: 8 (type) — Kostermans 10224: 8; 10403A: 8; 12772: 8.
- Lee 40636: 8; 44003: 16; 45528: 8; 52460: 4 — Leo et al. 71903: 8 — Low s.n.: 5 (type).
- Meijer 28711: 6; 29009: 5 — Mikil 31858: 5 — Moge & De Wilde 3688: 8; 3689: 8; 3720: 8; 4051: 8; 4239: 8 — Moulton 6697: 4; 6769: 4 — Murata et al. B-1201: 8; B-1453: 8; B-1470: 8; B-1759: 8.
- Nooteboom 935: 5; 4116: 8; 4382: 8; 4663: 8.
- Ogata 11103: 5; 11312: 5; 11313: 5 — Othman & Ashton 19994: 4 — Othman et al. 31604: 7; 49052: 9; 49062: 1; 49063: 1.
- Price 120: 5; 215: 5 — Purseglove 5377: 1 — Purseglove & Shah 4708: 16.
- Richards 1219: 8; 1394: 1; 1448: 16 (type); 2057: 6; 2467: 8; 2498: 17; 2598: 17 — Ridley 12322: 8.
- Saikheh 83203: 6 — Sands 5273: 4; 5444: 9; 5889: 9; 5945: 9 — Saw 39911: 9 — Shawan Tangki 120389: 8 — Shea 28186: 8 — Sibak ak Luang 22505: 1 — Sidek bin Kiah 21: 5 — Stevens et al. 606: 5 — Sumbing & Soludi 105323: 17 — Syngé 491: 6 (type); 503: 17 (type).
- Talip & Ejan 87010: 5 — Thomas 66: 9 — Tong 33864: 19; 34360: 8.
- Van Steenis 1166: 18 (type) — Vermeulen & Chan 394: 5.
- Winkler 275: 8 (type); 275a: 8; 1145: 8 (type); 1293: 10 (type); 1473: 8; 1473a: 8 (type) — Wong 412: 4; 536: 9; 679: 9 — Wood 911: 8.
- Yii 48307: 8; 48351: 1.

## INDEX TO SCIENTIFIC NAMES

Numbers refer to the species numbers given in the text. Synonyms are in *italics*. New species, new combinations and new names are in bold.

- Allomorpha beccariana* Cogn. 2  
*longifolia* Cogn. 10  
*longispicata* Cogn. 11  
*multinervia* Cogn. 8  
*Anerinclaestus dispar* Cogn. 4  
*rupicola* (M.P. Nayar) J.F. Maxwell 17  
*Brittenia* Cogn. [p. 70]  
*subacaulis* Cogn. 19  
*Cyanandrium* Stapf [p. 70]  
*glabrum* M.P. Nayar 16  
*guttatum* Stapf 7  
*jacobsianum* M.P. Nayar 9  
*osmanthus* M.P. Nayar 12  
*rufum* Stapf 16  
*Enaulophyton* Steenis [p. 70]  
*lanceolatum* Steenis 18  
*sarawakense* M.P. Nayar 14  
*Perilimnastes rupicola* M.P. Nayar 17  
*Phyllagathis* Blume [p. 70]  
**atroviolacea** C. Hansen ex Cellin. 1  
*beccariana* (Cogn.) M.P. Nayar 2  
*brookei* M.P. Nayar 3  
*dispar* (Cogn.) C. Hansen 4  
*elliptica* Stapf 5  
*gigantifolia* M.P. Nayar 6  
(Phyllagathis)  
**guttata** (Stapf) Cellin. 7  
*gymnantha* Korth. 8  
*hirsuta* Cogn. 8  
**jacobsiana** (M.P. Nayar) Cellin. 9  
*johannis-winkleri* O. Schwartz 8  
var. *glaberrima* O. Schwartz 8  
*lanceolata* O. Schwartz 10  
*longifolia* (Cogn.) J.F. Maxwell 10  
*longispicata* (Cogn.) J.F. Maxwell 11  
*multinervis* (Cogn.) J.F. Maxwell 8  
*nymphaeifolia* Hallier f. ex Bakh.f. 8  
**osmantha** (M.P. Nayar) Cellin. 12  
*peltata* Stapf ex Ridl. 13  
**penrissenensis** Cellin. 14  
*pallida* O. Schwartz 8  
*pulcherrima* M.P. Nayar 15  
**rufa** (Stapf) Cellin. 16  
**rupicola** (M.P. Nayar) C. Hansen ex Cellin. 17  
*sarawakensis* M.P. Nayar 10  
**steenisi** Cellin. 18  
**subacaulis** (Cogn.) Cellin. 19  
*uniflora* Stapf 4  
var. *longiloba* M.P. Nayar 4  
*Tylanthera* C. Hansen [p. 70]