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REVISION OF *PLETHIANDRA* HOOK.F.: A POLYSTAMINATE, EAST ASIAN GENUS OF *MELASTOMATACEAE*

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Plethiandra (*Melastomataceae–Melastomatoideae–Dissochaeteae*) comprises seven species in Borneo and one (*P. sessiliflora*) in the southern part of Peninsular Malaysia and central Sumatra. *Plethiandra* is easily recognized by its polystaminate androecium, having 16–40 stamens with short, straight, inappendiculate anthers. The closely related *Medinilla* has a diplostemonous androecium with 8–12 stamens and variously appendaged anthers. Ontogenetic studies in *P. hookeri* show that the increase in stamen number in *Plethiandra* results from subdivision of the stamen primordia into three or more subprimordia.

This paper provides a key, genus and species descriptions including diagnostic characters, distribution maps and ecological notes. One species, *P. tomentosa*, is newly described. During field observations on *P. hookeri* and *P. cuneata* pollination by bees and dispersal by birds and squirrels were observed.

Keywords. Androecium ontogeny, Borneo, *Dissochaeteae*, epiphytes, *Medinilla*, *Melastomataceae*, *Plethiandra*, polystaminate.

INTRODUCTION

Plethiandra Hook.f. is a small genus of *Melastomataceae* predominantly distributed in northern and western Borneo, easily recognized by its polystaminate androecium. It consists of terrestrial or epiphytic shrubs or treelets that are predominantly found in lowland and montane primary forests.

Plethiandra was established by Joseph Hooker in 1867 who described *P. motleyi* Hook.f. when working with the collections of James Motley from Sarawak (Malaysia). He erroneously noted anthers with longitudinal slits and placed *Plethiandra* in the tribe *Astronieae*. The anthers of *Plethiandra* open by pores as in the majority of *Melastomataceae* (Renner, 1993). In the treatments of Baillon (1877), Cogniaux (1891) and Krasser (1893), *Plethiandra* remained in *Astronieae*. Cogniaux (1891) described the polystaminate genus *Medinillopsis* Cogn. comprising *M. beccariana* Cogn. and *M. sessiliflora* Cogn., and placed it close to *Medinilla* Gaudich. ex DC. In 1894 and 1895 Stapf described four new species of *Plethiandra* and observed that one of them, *P. sessilis* Stapf, was almost identical to *Medinillopsis sessiliflora* (Stapf, 1895). Also recognizing these similarities, Merrill (1921) treated *Medinillopsis* as a

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synonym of *Plethiandra*. Burkill (1917) added a new *Plethiandra* species from Sarawak, *P. sahebii* Burkill, and also suggested that the polystaminate *Medinilla robusta* Cogn. should be included in *Plethiandra*. This was followed in the most recent revision of *Plethiandra* by Nayar (1974) who recognized seven species (*P. motleyi*, *P. beccariana* (Cogn.) Merr., *P. hookeri* Stapf, *P. robusta* (Cogn.) Nayar, *P. rejangensis* Stapf, *P. cuneata* Stapf and *P. sessiliflora* (Cogn.) Merr.), and one subspecies (*P. sessiliflora* Merr. var. *sessilis* (Stapf) Nayar). He placed *P. acuminata* Merr. in synonymy with *P. motleyi*, and *P. sahebii* in synonymy with *P. robusta*; *P. sessilis* was reduced to a variety of *P. sessiliflora*.

Stapf (1895) was the first to note the close relationship of *Plethiandra* and *Medinilla*, and Bakhuizen van den Brink (1943) included the genus in tribe *Dissochaeteae*. Indeed, a phylogenetic analysis of the *Dissochaeteae* based on *ndh*F sequence data showed that *Plethiandra* is nested among the representatives of *Medinilla* (Clausing & Renner, 2001a). *Medinilla* comprises c.350 species and is distributed in tropical Australia, Madagascar and throughout Southeast Asia. The phylogenetic status of *Medinilla* is still unclear. Molecular data have not yet resolved the relationships of *Medinilla* and its closest allies such as *Pachycentria* Blume and *Plethiandra* (Clausing & Renner, 2001a). Therefore, it is reasonable to maintain the morphologically well-defined *Plethiandra* instead of including it in the highly polymorphic and probably polyphyletic *Medinilla*. In habit and fruit morphology *Plethiandra* is similar to several species of *Medinilla* from Borneo (Regalado, 1990). However, *Plethiandra* can easily be distinguished by its polystaminate androecium with straight anthers lacking appendages (Fig. 1A,H). By comparison, *Medinilla* has a diplostemonous androecium of 8–12 variously bent stamens with ventral and dorsal appendages.

This paper summarizes present knowledge of *Plethiandra* and adds new observations made on herbarium material and field trips to Borneo. The ontogeny of the polystaminate androecium of *P. hookeri* is described and interpreted. A taxonomic treatment of *Plethiandra* is presented that includes a generic description, key, species descriptions, diagnostic characters, ecological notes and geographical distributions, and the description of one new species.

Materials and methods

This study is based on herbarium material obtained from AAU, BK, BKF, BM, C, E, FI, K, KEP, KLU, L, MJG, SAN, SAR, SING and UKMS and on field studies of *Plethiandra hookeri* (Mt. Kinabalu National Park, Sabah, Malaysia) and *P. cuneata* (Bako National Park, Sarawak, Malaysia). Measurements refer to dried or boiled material. For the developmental study of the androecium of *P. hookeri* young buds were collected in formalin acetic alcohol (FAA). The androecium was laid open carefully under a binocular microscope and prepared for scanning electron microscopy by dehydration in an ethanol series and acetone, critical-point drying, and sputter-coating with gold.

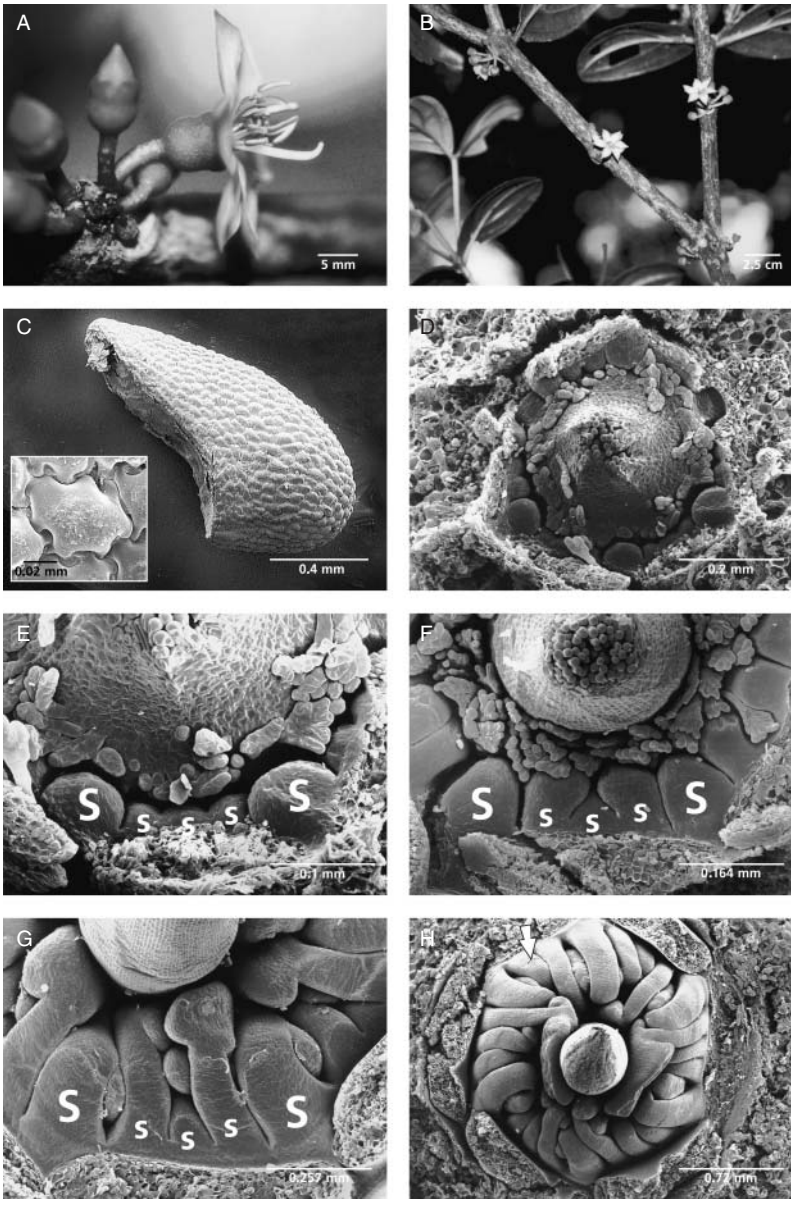

FIG. 1. Inflorescence, seed and androecium in *Plethiandra hookeri*: A, inflorescence; B, flowering branch; C, typical cuneate seed of *Plethiandra* with interdigitate testa cells (inset); D–H, development of polystaminate androecium (S = stamen primordia of outer (episepalous) whorl, s = stamen primordia of inner (epipetalous) whorl) (A–H: *G. Clausing* 138, MJG).

Results and discussion

Notes on the morphology and ecology of Plethiandra

Plethiandra species grow as terrestrial or epiphytic shrubs or treelets. In open vegetation types or at exposed sites they are usually terrestrial. In dense lowland or mountain forests, however, they are found growing epiphytically on trees, mainly at heights between 5 and 15m, occasionally up to 30m. Leaf morphology varies considerably with change of habitat. In open and exposed vegetation leaves tend to be smaller than in dense forest. Although leaf morphology within species is variable, characters such as size, shape, number of primary veins, and length of the petiole are important diagnostic characters.

Another variable character is pedicel length. Young buds are often sessile or subsessile, while older buds and flowers are distinctly pedicellate. However, the length of the pedicels after anthesis is an important diagnostic character.

The flowers of *Plethiandra* are always hexamerous. This is a rare character state in other genera of *Dissochaeteae*. In a few representatives of Regalado's *Medinilla quadrifolia*-group (Regalado, 1990) and in *Carionia* Naudin, which was included in *Medinilla* by Regalado (1995), hexamerous flowers can also be found. In contrast to Hooker (1867) who described the ovary of *Plethiandra* as four-locular, Stapf (1895) indicated that the ovary contains six locules separated by extremely thin septae.

Stamen pockets (extraovarian chambers) are always absent in *Plethiandra*. Absence of stamen pockets is also seen in several other genera of the *Dissochaeteae*, for example *Pachycentria*, *Diplectria* Kuntze and *Medinilla*, and is mostly correlated with simple, relatively short stamens with no appendages or only small ones (Clausing, 2000).

Usually only one flower in each fascicle opens per day (Fig. 1A,B), normally between 6.00 and 9.00a.m. Flowers are pollinated by bees between sunrise and 11.00a.m. The bees buzz-pollinate up to 10 flowers per plant. After pollination the flowers close, and the petals soon fall off (pers. obs. on *P. hookeri* and *P. cuneata*).

The berries of *Plethiandra* mature within 8–12 weeks. The endocarp (including the septae) disintegrates during ripening and forms the pulpa. The mesocarp contains many starch granules. The hypanthium tissue lacks starch and contains many sclereids that form a ring and are responsible for the hardness of the fruit. Birds and small mammals (e.g. squirrels) feed on the ripe fruits of *P. hookeri* (pers. obs.).

Ontogeny of the polystaminate androecium of Plethiandra hookeri *(Fig. 1D–H)*

The stamen primordia emerge in two whorls, an episepalous outer whorl and an epipetalous inner whorl. Early in their development the primordia of the inner whorl divide into three subprimordia ('s' in Fig. 1E–G), while the primordia of the outer whorl remain intact ('S' in Fig. 1E–G). The central of the three subprimordia is slightly smaller than the two outer ones. The primordia of the episepalous whorl develop into larger stamens than those of the inner whorl. The androecium of the

P. hookeri specimen studied therefore consists of six large episepalous stamens (c.1.2cm) and 18 smaller stamens (c.0.8cm) derived from the epipetalous whorl. The number of stamens in *Plethiandra* ranges from 16 to 40. In *P. hookeri* 24–40 stamens were counted. Numbers below 24 result from suppression of one or two subprimordia as shown in Fig. 1H (arrow). The ontogeny of flowers with more than 24 stamens, however, is not known. Further subdivision of the epipetalous primordia or subdivision also of the episepalous primordia are possible explanations.

Polystaminate androecia are rare in *Melastomataceae*. They have arisen independently in *Miconieae*, *Astronieae* and *Dissochaeteae* (Clausing & Renner, 2001b). Polystaminate androecia are found in several genera of the neotropical *Miconieae*, for example *Clidemia* D.Don, *Conostegia* D.Don, *Llewelynia* Pittier and *Miconia* Ruiz & Pav. (Renner, 1993). In *Conostegia*, for example, stamen number varies from 10 to 96. Even within one species the number of stamens is not uniform. For example, 20–28 stamens are found in *Conostegia dentata* Triana and 34–52 in *C. centrionoides* Markgr. var. *lancifolia* Markgr. In Old World *Melastomataceae* a polystaminate androecium is found only in *Plethiandra* and in *Astrocalyx* Merr., a monotypic genus of the *Astronieae*.

TAXONOMY OF *PLETHIANDRA*

Plethiandra Hook.f. in Benth. & Hook.f., Gen. Pl. 1: 772 (1867).
Type species: *P. motleyi* Hook.f., Borneo.
Syn.: *Medinillopsis* Cogn. in A. & C.DC., Monogr. phan. 7: 603 (1891). Type species: *M. beccariana* Cogn., Borneo (designated here).

Terrestrial or epiphytic shrubs or treelets; branchlets angular or terete, glabrous, older branches terete, striate, pustulate or smooth, glabrous, nodes thickened (Fig. 1B). *Leaves* ovate, elliptic, broadly elliptic or lanceolate, rounded, shallowly cordate or cuneate at base, acuminate, obtuse or rounded at apex, usually glabrous (except *P. tomentosa*), 3–11(–13)-plinerved with an additional pair of faint intramarginal nerves, secondary venation faint or invisible; leaves sessile, subsessile or petiolate. Flowers solitary, in pairs or up to 12 in fascicles in leaf axils or on leafless nodes, 6-merous; pedicels 1–30mm long; hypanthium cup-shaped, campanulate or urceolate, rough or smooth, sometimes with 6 prominent ribs; calyx tube c.1–2mm long, margin truncate or with 6 teeth; petals 6, white or pink; stamens 16–40, filaments thin, anthers straight, lacking appendages, 2–3mm long, opening by terminal pores (Fig. 1A); ovary 1/2 to 2/3 as long as hypanthium, 3/4 to fully adnate, usually 6-locular, crowned by a ring surrounding the base of the style, ring sparsely to densely covered with brown scurf, ovules numerous on axillary placentae, extraovarian chambers absent; style thick and 4–6mm long in bud, 10–16mm long during anthesis, filiform, stigma punctiform. *Fruit* a globose or subglobose berry, 4–10mm in diam., crowned by 1–2mm high calyx rim; seeds numerous, ovoid or cuneate, minute, smooth, with interdigitate testa cells (Fig. 1C).

Distribution. The genus is mainly distributed in primary vegetation of northwestern Borneo (Fig. 2). One species, *P. sessiliflora*, occurs at the southern tip of Peninsular Malaysia and in one location in central Sumatra (Fig. 2). The restriction to northwestern Borneo might be a collecting artefact because Kalimantan is undercollected.

Key to the species

NB For specimens that are difficult to identify see section on Anomalous specimens below.

1a. Calyx with 6 teeth, rarely very tiny (hand-lens needed) — **4. P. motleyi**
1b. Calyx truncate — 2

2a. Leaves sessile, subsessile or shortly petiolate (<10mm), leaf bases mostly rounded or shallowly cordate, rarely cuneate — 4
2b. Leaves long-petiolate (15–30mm), leaf base cuneate — 3

3a. Lamina with 3 primary veins, glabrous below — **2. P. cuneata**
3b. Lamina with 7 primary veins, with dark brown tomentum below, becoming sparser later but still visible on or near veins — **8. P. tomentosa**

4a. Pedicels 15–30mm long after anthesis — **1. P. beccariana**
4b. Pedicels less than 15mm long after anthesis — 5

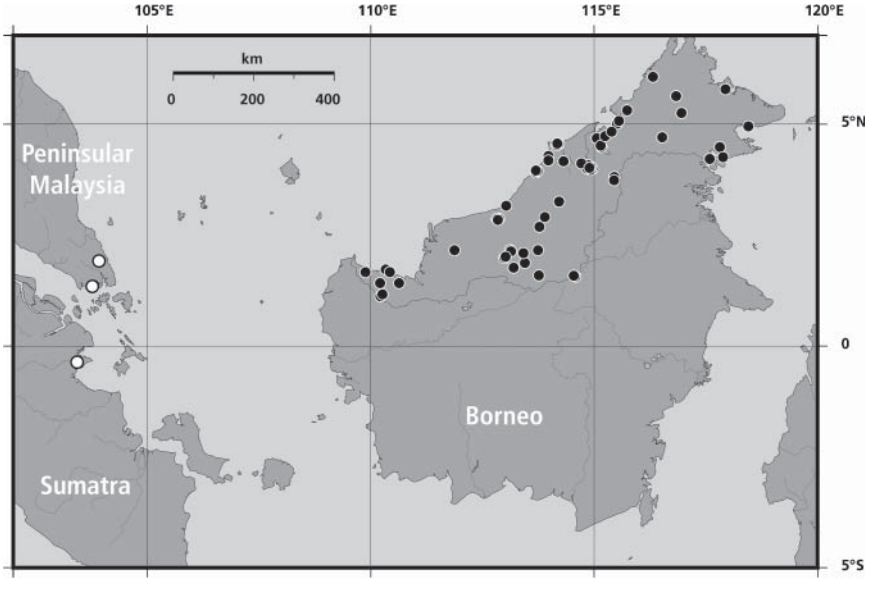

FIG. 2. Distribution of the genus *Plethiandra* (all circles) and *Plethiandra sessiliflora* (white circles).

5a. Flowering hypanthium plus calyx rim 5–8 × 4–6mm; fruiting hypanthium 8–10 × 6–7mm ____ 6
5b. Flowering hypanthium plus calyx rim 3–4 × 2–3mm; fruiting hypanthium 4–6 × 3–4mm ____ 7

6a. Pedicels 5–10mm long; leaves subsessile ____ **3. P. hookeri**
6b. Pedicels 1–2mm long; leaves sessile ____ **6. P. sessiliflora**

7a. Leaves ovate-oblong or ovate-lanceolate, tip acute, base rounded or cordate, primary veins (5–)7–13 ____ **5. P. robusta**
7b. Leaves broadly elliptic, tip and base rounded, primary veins 5 ____ **7. P. sessilis**

1. Plethiandra beccariana (Cogn.) Merr., Bibl. enum. Born. pl.: 448 (1921). **Fig. 3A,B.**
Syn.: *Medinillopsis beccariana* Cogn. in A. & C.DC., Monogr. phan. 7: 603 (1891).
Type: Malaysia, Sarawak: Bintulu, ix 1867, *Beccari* 4004 (lecto. FI!, iso. K!).

Large epiphytic shrub. *Leaves* elliptic or elliptic-oblong, 12–32 × 8–15cm, with 7–9 primary veins; petiole <5mm long (Fig. 3A). Flowers in many-flowered fascicles on older leafless branches; pedicels 15–30mm long after anthesis; hypanthia urceolate, greenish pink, 5–6 × 4–5mm (incl. calyx rim); calyx truncate; petals white, white with pinkish base, or pink; stamens c.25, equal; anthers 4–5mm, yellow. *Fruits* subglobose, 7–8 × 5–6mm, pale greenish pink becoming dark pink.

Distribution. Brunei and Sarawak (Fig. 4A).

Habitat and ecology. *Plethiandra beccariana* is found in lowland forest, most commonly in river valleys. It grows on trees at heights from 2 to 25m.

Characteristic of this species are its large, sessile, elliptic or elliptic-oblong leaves with 7–9 primary veins (Fig. 3A) and many, relatively large, long-pedicellate flowers in fascicles on older leafless parts of the branches (Fig. 3B). Because of its large leaves *P. beccariana* is easily mistaken for *P. robusta*. The main difference between the two species is the length of the pedicel which is 15–30mm in *P. beccariana* and only 2–4mm in *P. robusta*.

Additional specimens examined. BRUNEI. Temburong river valley, *W.K. Wong* 471 (AAU, SAR), *R.J. Johns* 7423 (K). SARAWAK. Sg. Iban, Linau, Belaga, *B. Lee* S.45342 (AAU, K, L, SAR); Sungei Tekalik, Menyiong, Ulu Balleh, Kapit, *O. Ismawi* S.41291 (AAU, L, SAR), *B. & K. Bremer* 1735 (SAR); Nanga Berkakap, Sungei Melatai, Batang Balleh, *Yii Puan Ching* S.48376 (AAU, SAR); Nanga Sungei Entuloh, Baleh, Kapit, *H. Othman & Rantai* S.62166 (K, KEP, SAR); Ulu Sungei Sekaloh, Niah river, Miri district, *E. Wright* S.29109 (K, L, SAN, SAR, SING); Batang Belaga, Ulu Belaga, *C. Hansen* 870 (SAR).

2. Plethiandra cuneata Stapf, Hook. Icon. pl. 25: 2418, p.2 (1895).
Type: Malaysia, Sarawak: Selabat rock, sea coast, iii 1891, *Haviland* 179 (lecto. K!; iso. BM!, SAR!, SING!).

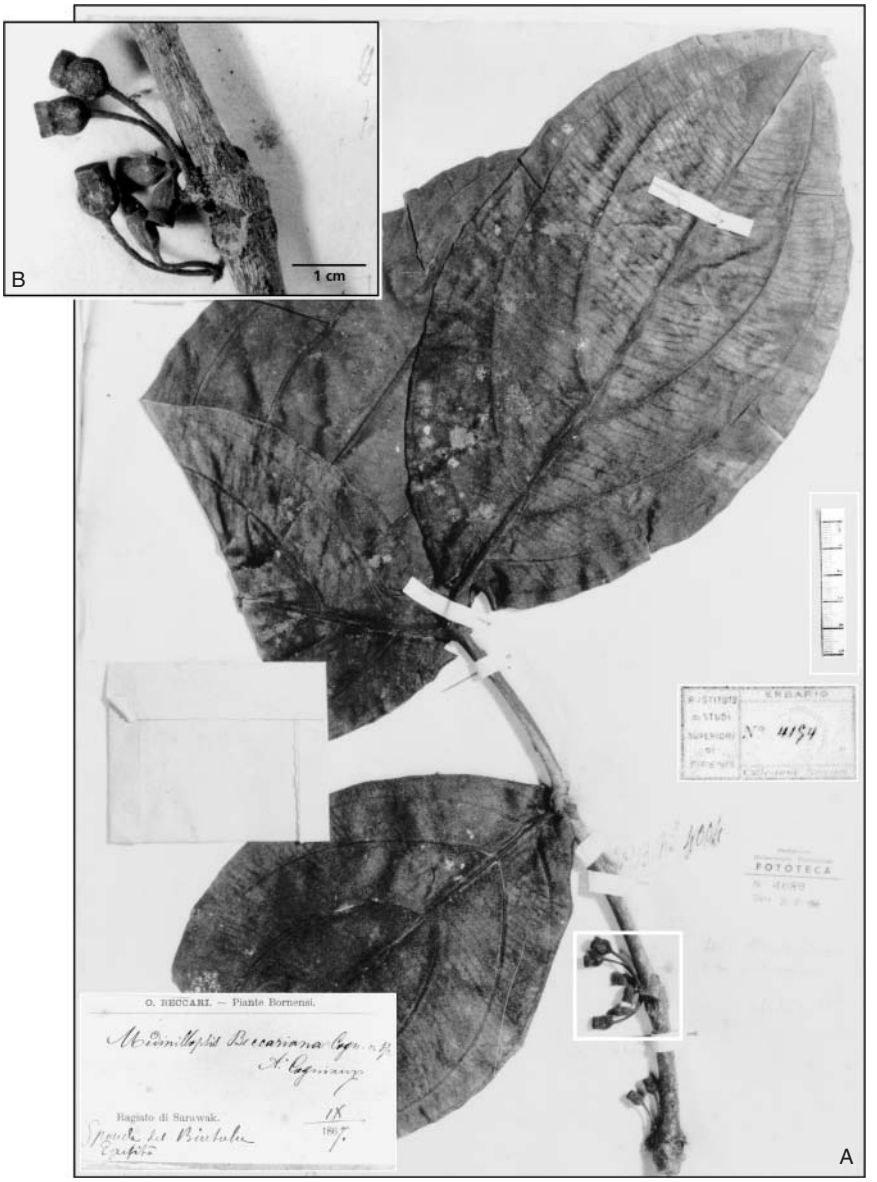

FIG. 3. Lectotype of *Plethiandra beccariana* (*Beccari* 4004, FI): A, whole specimen; B, detail of inflorescence.

Syn.: *Plethiandra rejangensis* Stapf, Hook. Icon. pl. 25: 2418, p.1 (1895). Type: Malaysia, Sarawak: Rejang, Sibu, *Haviland* 545 (lecto. K!).

Epiphytic shrub, 1–3m high. *Leaves* elliptic to obovate, base cuneate, lamina 7–17 × 3–8cm with 3 primary veins; petiole (10–)15–30mm long. Flowers solitary or in

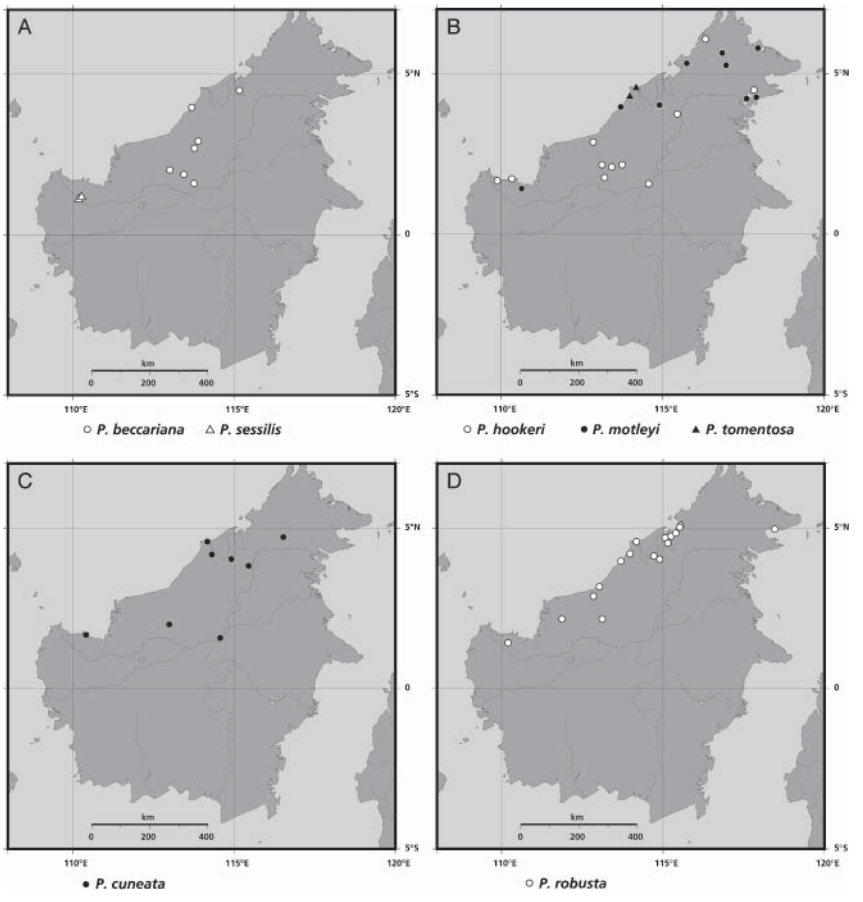

FIG. 4. Distribution maps: A, *Plethiandra beccariana* and *P. sessilis*; B, *P. hookeri*, *P. motleyi* and *P. tomentosa*; C, *P. cuneata*; D, *P. robusta*.

2–6-flowered fascicles; pedicels 8–18mm long after anthesis; hypanthia cup-shaped, pink, 3–4 × 3–4mm (incl. calyx rim); calyx truncate; petals creamy white; stamens 26–40, equal; anthers 3–4mm, yellow. *Fruits* globose, 5–6mm in diam., greenish yellow (often with purplish apex) becoming dark pink.

Distribution. Brunei, Sarawak, Sabah (Fig. 4C).

Habitat and ecology. *Plethiandra cuneata* grows as an epiphytic shrub in primary lowland forest, peat-swamp forest, and submontane mossy forest, or terrestrially in coastal vegetation (e.g. on sandstone rocks by beaches), heathland, or kerangas forests. It occurs from sea level to 1450m altitude. When epiphytic it is most common on trees at heights between 3 and 10m, but can also be found up to 25m.

Plethiandra cuneata is distinguished from other species of *Plethiandra* except *P. tomentosa* (see under that species) by its elliptic to obovate leaves with a cuneate base and long petioles. Nayar (1974) separated *P. cuneata* and *P. rejangensis* on the basis of leaf size, number of flowers per fascicle, and petal shape and size. Because of continuous variation in these characters *P. rejangensis* is treated here as a synonym of *P. cuneata*.

Vernacular names. Kayu ala (Iban) and Maraksium (Kayan).

Additional specimens examined. BRUNEI. Belait district, Ulu Sungai Mau, *N. Nangkat* 108 (AAU, SAR). SARAWAK. Bukit Bakar, *I. Paie* S.36310 (SAN); Gunung Mulu National Park, *Yii Puan Ching & Talib* S.58255 (AAU, SAR); Apad Keruma, Kalabit Highland, *Yii Puan Ching* 55934 (KEP); Marudi Forest Reserve, *Chew Wee-lek* 989 (AAU, K, L); Bako National Park, Telok Asam, *J.A.R. Anderson* S.25541 (SAR), Telok Paku, *J. Dransfield* 734 (AAU, BK), Tajong Melano, *Yii Puan Ching* S.42181 (AAU), trail to Paku beach, *G. Clausing* 150 (MJG); Bukit Tibang, Kapit district, *J.A.R. Anderson & I. Paie* S.28605 (L, SAR); R. Biak & Sut., *G.H. Pickles* 2986 (BM). SABAH. Sg. Siliawan Sepulut Forest Reserve, Keningau, *Asik Mantor* SAN113927 (SAN), Mt. Kinabalu, Poring Hot Springs, *G. Clausing* 129 (MJG).

3. Plethiandra hookeri Stapf, Trans. Linn. Soc. London, Bot. 4: 163 (1894).
Type: Malaysia, Sabah: Mt. Kinabalu, viii 1892, *Haviland* 1169 (lecto. K!, iso. SAR!).

Shrub or treelet, 1–3m high. *Leaves* elliptic to ovate, base rounded or shallowly cordate, apex obtuse or sometimes acute, lamina 8–14 × 5–9cm with 5–7 primary veins; petiole <10mm long. Flowers in 2–8-flowered fascicles; pedicels 5–10mm long after anthesis; hypanthia campanulate, 6–8 × 5–6mm (incl. calyx rim); calyx truncate; petals c.12mm long, spatulate; pedicels, hypanthia, petals and style from white to pink; stamens 24–38, subequal; anthers 3.2–5.2mm long, yellow. *Fruits* subglobose, 8–10 × 6–7mm, greenish with pink flush, becoming bright red with dark red pedicels.

Distribution. Sarawak, Sabah (Fig. 4B).

Habitat and ecology. *Plethiandra hookeri* is a shrub or treelet that grows epiphytically or terrestrially in a wide range of different vegetation types from sea level to 2500m. It grows as a terrestrial shrub or treelet in kerangas forest, low shrub vegetation on limestone, and in upper montane forests. In lowland forest, swamp forest, lower montane forest, and oak laurel forest it grows predominantly epiphytically. Leaves of specimens collected in kerangas or heath forests tend to have only faint venation; normally the primary veins are prominent.

The flowers of *Plethiandra hookeri* are the largest in the genus (Fig. 1A,B). While young buds are almost sessile, the pedicels of mature flowers are 5–10mm long.

Additional specimens examined. SARAWAK. Bukit Pantu, Melinau, Kapit, *I. Paie* S.25722 (L); Gunong Santubong, *Chew Wee-lek* 1421 (AAU, SAR), *G. Clausing* 168 (MJG); Balang/Baleh,

Ulu Balleh, *I. Paie* S.28434 (E, SAR); Tama Abu Range, Bario, *Dyg. Awa & B. Lee* S.51155 (SAR); Bukit Lumut, Ulu Amau, Mujong, Hose Mountains, *P.S. Ashton* S.21268 (KEP, SAR); Gunong Raya, *Anderson & Ding Hou* 514, Bau/Lundu, *Yii Puang Ching & Bayeng* S.45992 (AAU, KEP, L, SAN, SAR); Bukit Tibang, Kapit district, *J.A.R. Anderson* S.28510 (SAR); Ulu Anap, Tatau, *Abg. Mokhtar* S.44736 (AAU); Gunong Besi, Kpg. Rasau, Lundu, *I. Paie* S.46076 (AAU, KEP, SAR); Bukit Matang, near Kuching, *G. Clausing* 140 (MJG). SABAH. Mount Kinabalu, *G. Clausing* 138 (MJG), Syt. Benawod, Sungai Maadun, Nabawan, *Sumbing Jimpin* SAN119390 (SAN).

4. Plethiandra motleyi Hook.f. in Benth. & Hook.f., Gen. pl. 1: 772 (1867).
Type: Malaysia, Sabah: Labuan, *Motley* 380 (lecto. K!).
Syn.: *Plethiandra acuminata* Merr., Univ. Calif. Publ. Bot. 15: 226 (1929). Type: Malaysia, Sabah: Sandakan, *Elmer* 20076 (lecto. L!; iso. BM!, K n.v., L!, SING!).

Shrub, 1–2m high. *Leaves* elliptic, base cuneate, apex acute or shortly acuminate, lamina (3–)5–10(–12) × (1.5–)3–5(–6)cm with 3–5 primary veins; petiole <10mm long. Flowers solitary or in 2–4-flowered fascicles; pedicels in bud and flower 10–14mm long, after anthesis 16–25mm, red; hypanthia cup-shaped, greenish, sometimes with pink hue, 3–4 × 2–3mm (incl. calyx rim); calyx with 6 teeth c.0.5mm long; petals from white to pink; stamens 16–24, equal; anthers 1.2–1.8mm long, white, yellow or yellowish-green. *Fruits* globose, 5–6mm in diam., crowned by calyx rim of 6 teeth, green, becoming bright pink.

Distribution. Sarawak, Sabah (Fig. 4B).

Habitat and ecology. *Plethiandra motleyi* is an epiphytic shrub growing on trees in primary and secondary forests up to 25m high. It can be found in primary lowland forest, kerangas forest and secondary forest.

Plethiandra motleyi is characterized by its relatively small leaves, long pedicels and calyx rim with 6 teeth.

Additional specimens examined. SARAWAK. Gunung Mulu National Park, Sungai Mentawai, *P. Chai* S.39720 (AAU, K, KEP, L, SAN, SAR); Tg. Long Amok, Sg. Ensengai, Limbang, *R. George* S.42813 (AAU, KEP, SAR); Niah National Park, Gunong Brangin, *Yii Puan Ching* S.40183 (AAU, L). SABAH. Ranau, Ulu Sungai Bidon, *Amin* SAN110485 (SAN), Tongod, Ulu Memanam, *S. Dewol & T. Kodoh* SAN88742 (KEP, SAN); Beaufort, *Talib Bidin* SAN84667 (K, KEP, L, SAN, SAR); Tawau, Ulu Sungei Serudong, *A. Bakar* SAN26886 (K, KEP, L, SAN, SAR), *F.G. Aban* SAN31158 (K, L, SAN, SAR); Sepilok Forest Reserve, Sandakan, *J. Sinclair et al*. 9353 (E, K); Tawao, Elphinstone Province, *Elmer* 21887 (BM, K).

5. Plethiandra robusta (Cogn.) Nayar, Reinwardtia 9(1): 148 (1974). **Fig. 5A–C.**
Syn.: *Medinilla robusta* Cogn. in A. & C.DC., Monogr. phan. 7: 576 (1891). Type: Malaysia, Sarawak: Kuching, *Beccari* 542 (lecto. FI!, designated here; iso. K!); Malaysia, Sarawak: Kuching, *Beccari* 851 (syn. FI!); Malaysia, Sarawak: Bintulu, xi 1867, *Beccari* 4049 (syn. FI!).

Plethiandra sahebii Burkill, J. Straits Br. Roy. Asiat. Soc. 77: 265–269 (1917). Type: Malaysia, Sarawak: Kuching, *Burkill* s.n. (iso. K!).

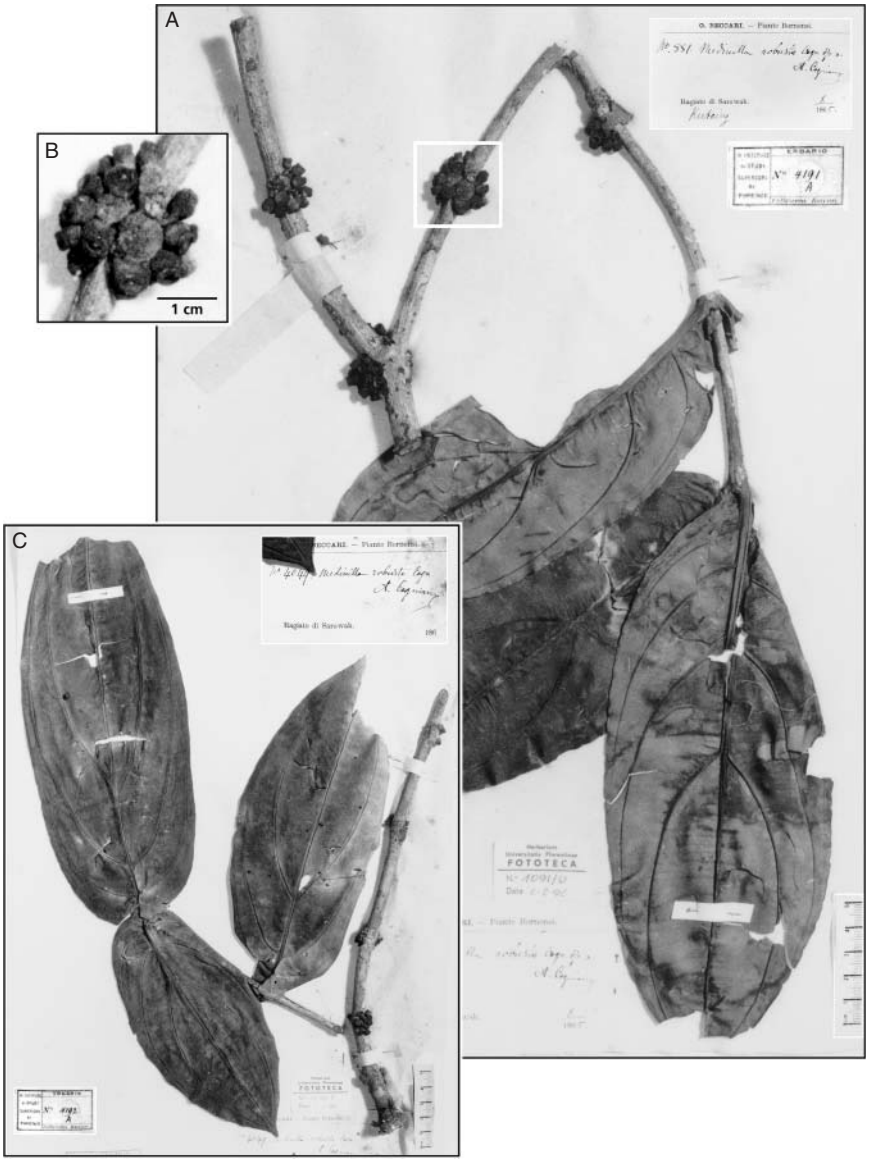

FIG. 5. Syntypes of *Plethiandra robusta*: A, whole specimen of *Beccari* 851 (FI); B, detail of inflorescence; C, whole specimen of *Beccari* 4049 (FI).

Shrub to 3m high. *Leaves* ovate-oblong or ovate-lanceolate, base rounded to cordate, apex obtuse, lamina (12–)20–30(–35) × (5–)8–14(–16)cm with (7–)9–11(–13) primary veins; petiole < 5mm long (Fig. 5A,C). Flowers in 4–16-flowered fascicles; pedicels 2–4mm long (Fig. 5B); hypanthia cup-shaped, 3–4 × 2–3mm (incl. calyx rim); calyx truncate; pedicels, hypanthia, petals, style and filaments from light

to deep pink or purple, petals rarely white tinged with pink; stamens c.28, equal; anthers c.3mm long, light yellow. *Fruits* subglobose, 4–6 × 3–4mm in diam., pedicels and ripe fruits deep pink.

Distribution. Brunei, Sarawak, Sabah (Fig. 4D).

Habitat and ecology. *Plethiandra robusta* is a large shrub that grows hemi-epiphytically in the understorey or epiphytically in trees at up to 30m high. It can be found in lowland forests (mixed dipterocarp forest, swamp forest, riverine forest), low montane forests (up to 1200m altitude), and kerangas forest. At Gunong Subis (Niah, Miri), Lambir Hills National Park, and Bukit Jebong (Bau) it grows on rocks and tree-trunks on a limestone hill.

Characteristic of *Plethiandra robusta* are the large, sessile leaves with 7–13 primary veins and short pedicels (Fig. 5). However, leaf size and number of primary veins vary considerably with habitat. The leaves are flushed red underneath and/or have reddish nerves.

Additional specimens examined. BRUNEI. Temburong, Amo, Kuala Belalong, *J. Dransfield* 7075 (SAN); Temburong, Bangar, *M.J.S. Sands* 5624 (K); Temburong, Bukit Patoi, *B.E. Smythies, G.H.S. Woods & P.S. Ashton* 5818 (KEP), *P.S. Ashton* 523 (L, K); Temburong, Temburong river, Wong Nguan rapids, *M.J.E. Coode* 6501 (KEP), *W.K. Wong* 470 (AAU, SAR); Belait, Melilas, Ulu Ingei, *M.J.S. Sands* 5959 (K); Peradayan Forest Reserve, *J. Wyatt-Smith* 8051 (KEP). SARAWAK. Sibu, Sg. Assam, Naman Forest Reserve, *J.A.R. Anderson* 12442 (SAR); Ulu Anap, Tatau, *Abg. Mokhtar* S.44739 (AAU); Kana, Bt. Naoung, *Banying ak Nyudong* S.19405 (L, SAR); Miri, Niah, Gunong Subis, *J.A.R. Anderson, S. Tan & E. Wright* S.27562 (K); Miri, Lambir Hills National Park, *I. Paie & Yeo* S.38357 (AAU, KEP, L, SAN, SAR), *R. George* S.40411 (SAR); Kapit, Bukit Raya, *P.S. Ashton* S.17761 (L, SAR); Bintulu, Tubau, Ulu Jelutong, B. Sehiwa, *Abg. Mohtar et al.* S.54206 (AAU); Gunong Mulu National Park, Sg. Mentawai, *P. Chai* S.39757 (AAU, L, SAN, SAR); Bau, Bukit Jebong, *P. Chai & I. Paie* S.25603 (L, SAR). SABAH. Sipitang, Marintaman Mengalong Forest Reserve, *S. Kokawa & M. Hotta* 2732 (SAN), *W. Meijer* SAN130249 (SAN); Sipitang, Bukit Sebuboh, *J.H. Beaman* 8723 (K, L, UKMS).

6. Plethiandra sessiliflora (Cogn.) Merr., J. Straits Br. Roy. Asiat. Soc. Spec. No.: 449 (1921). **Fig. 6A–C.**
Syn.: *Medinillopsis sessiliflora* Cogn. in A. & C.DC., Monogr. phan. 7: 603 (1891). Type: Malaya, *Beccari* s.n., 1866 (lecto. FI!, iso. K!).

Epiphytic shrub to 1.5m high. *Leaves* ovate, base rounded or shallowly cordate, apex acute, lamina 8–12 × 4–6cm with 5 primary veins; petiole < 5mm long. Flowers solitary or paired; pedicels 1–2mm long; hypanthia cup-shaped, c.4 × 5mm (incl. calyx rim); calyx truncate; stamens c.20, equal. *Fruits* subglobose, 8–9 × 7mm.

Distribution. Peninsular Malaysia (Singapore, Johore), central Sumatra (Fig. 2). The only species of *Plethiandra* recorded outside Borneo.

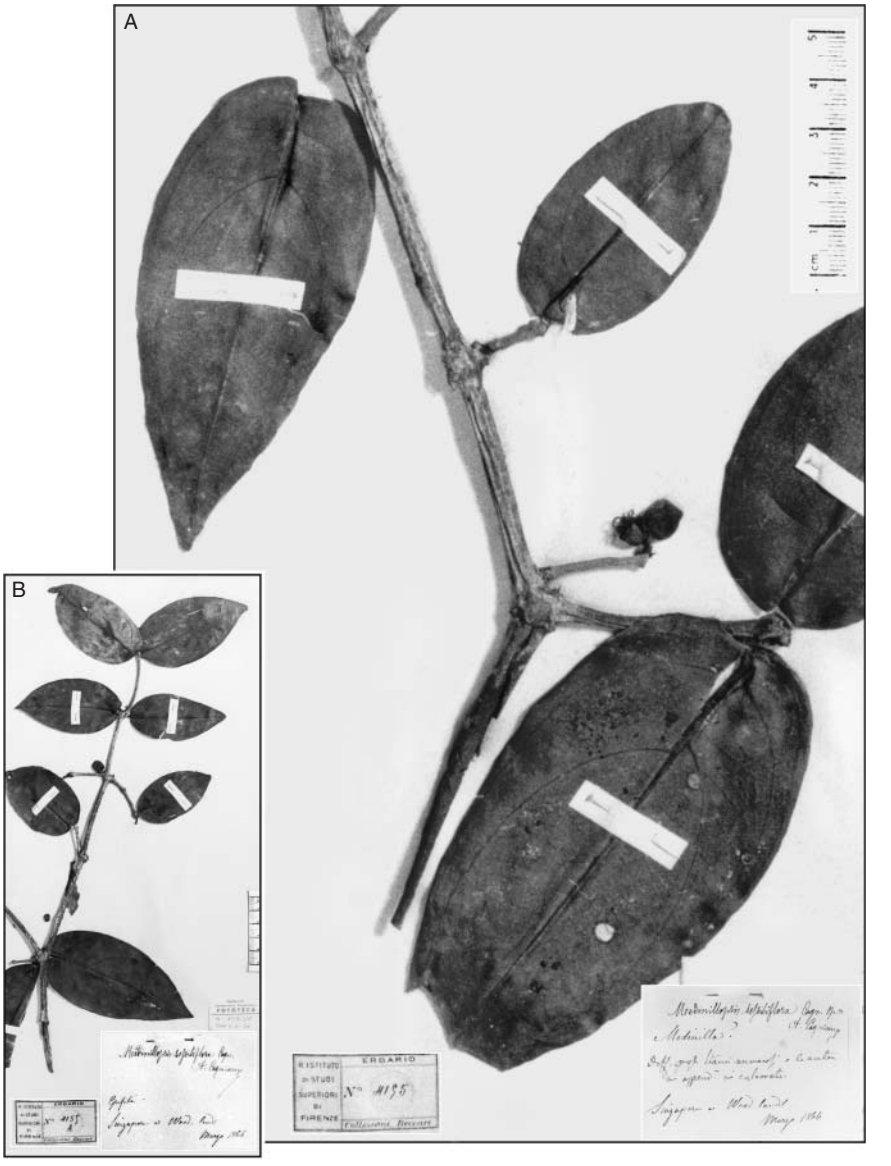

FIG. 6. Types of *Plethiandra sessiliflora*: A, *Beccari* s.n., 1866 (lecto. FI4195); B, *Beccari* s.n., 1866 (iso. FI4159).

Morphologically most similar to *P. hookeri*. Both have relatively large flowers and fruits, and ovate leaves with rounded or shallowly cordate bases. However, *P. sessiliflora* has almost sessile flowers (pedicels 1–2mm long) while the pedicels of mature flowers in *P. hookeri* are 5–10mm long. Also, the leaves of *P. hookeri* are normally subsessile while they are truly sessile in *P. sessiliflora*.

Additional specimens examined. PENINSULAR MALAYSIA. Singapore, *Beccari* s.n. (F!); Johore, Sungai Kayu, *Kiah* 32395 (not seen, fide Nayar 1974). SUMATRA. Indragiri, Muara Padjanki, *Buwalda* 6449 (not seen, fide Nayar 1974).

7. Plethiandra sessilis Stapf, Hook. Icon. pl. 25: 2418, p.1 (1895).
Syn.: *Plethiandra sessiliflora* var. *sessilis* (Stapf) Nayar, Reinwardtia 9(1): 150 (1974). Type: Malaysia, Sarawak: Penrissen, vi 1890, *Haviland* 6893 (lecto. K!).

Epiphytic shrub to 1m high. *Leaves* broadly elliptic, base rounded or shallowly cordate, apex obtuse, lamina with 5 primary veins; petiole <5mm long. Flowers in 2–6-flowered fascicles; pedicels 1–3mm long; hypanthia cup-shaped, c.4×3mm (incl. calyx rim); calyx truncate; stamens 29–31, equal (see discussion); anthers c.2.2mm long. *Fruits* subglobose, 5×4mm, dark pink when ripe.

Distribution. Sarawak (Fig. 4A).

Plethiandra sessilis is a rare epiphytic shrub known from only a few collections. It was treated as a subspecies of *P. sessiliflora* by Nayar (1974). This is not followed here. Compared with other species of *Plethiandra* these two species are not particularly similar morphologically. They differ in leaf shape (broadly elliptic with rounded base and obtuse tip in *P. sessilis*, ovate with acute tip in *P. sessiliflora*) and in fruit size (5mm long in *P. sessilis*, 8–9mm long in *P. sessiliflora*). Stapf (1895) and Nayar (1974) both recorded stamen numbers of only c.20.

Additional specimens examined. SARAWAK. Padawan, Bukit Pait, *Erwin & Paul* S.27432 (K, SAN); fide Nayar (1974) also Simanggang, Tajong Triso, *Anderson* 9793 (K, SAR), but this specimen differs from the other two in having smaller ovate leaves.

8. Plethiandra tomentosa G.Kadereit, **sp. nov. Fig. 7.**
A speciebus aliis *Plethiandrae* indumento atrobrunneo denso pilorum brevium irregulariter ramosorum peculiari in pagine inferiore et in ramis juvenibus differt.
Type: Sarawak, Lambir National Park, *B. Lee* S.46581 (holo. AAU!, iso. KEP!).

Shrub, 1–3m high; branches terete, nodes slightly swollen, young branches and leaves below (especially veins) densely covered with short, dark brown, irregularly branched scurfy indumentum. *Leaves* broadly elliptic to ovate, base cuneate, apex obtuse, lamina $17–24 \times 10–12$cm with 5–7 primary veins; petiole 15–30mm long. Flowers in 4–6-flowered fascicles, mostly on nodes of older leafless branches; pedicels 6–10mm long, pink; hypanthia cup-shaped, c.6mm long (incl. calyx rim), 6mm wide at top, pink; calyx truncate, thick, c.2mm; stamens 38, equal; anthers 3–4mm long, yellow, filaments c.3mm; style c.6mm long in bud; ovary half hypanthium length. *Fruits* globose, 7–8mm in diam. (only unripe fruits seen).

Distribution. Brunei, Sarawak (Fig. 4B), known from only two collections.

Habitat and ecology. *Plethiandra tomentosa* is recorded from lowland freshwater swamp forest.

FIG. 7. Types of *Plethiandra tomentosa* (*B. Lee* S.46581): A, whole specimen (iso. KEP); B, fruit (iso. KEP); C, detail of leaf undersurface (holo. AAU); D, inflorescence (holo. AAU); E, label.

Plethiandra tomentosa can be distinguished from all other species of *Plethiandra* by its dark brown indumentum. It shares the long-petiolate leaves only with *P. cuneata*. The latter differs however (apart from being glabrous) in having smaller leaves with only three primary veins and smaller flowers and fruits.

Additional specimen examined. BRUNEI. Kuala Ingai, Belait, *Ch. Puff, A. Igersheim & M. Martinello* 900807-1/2 (SAN).

ANOMALOUS SPECIMENS

Many specimens have hypanthia with 6 teeth, typical of *P. motleyi*, but differ from that species in leaf characters and length of the pedicels. The leaves are not elliptic as in *P. motleyi* but broadly ovate and they are cordate or rounded at the base rather than cuneate. The pedicels of buds and young flowers are 3–5mm long; after anthesis they become 5–9mm long. The pedicels of *P. motleyi* are normally 10–14mm long in buds and young flowers and 16–25mm long after anthesis. These anomalous specimens are found in wet mossy mountain forests in Sarawak at Gunong Murud [*Yii Puang Ching* S.44483 (AAU, SAR), *I. Paie* S.26407 (SAR)], Gunong Mulu [*B. Lee* S.38813 (AAU, KEP, L, SAR), *P. Chai* S.35824 (L, SAR), *Yii Puang Ching & Abu Talib* S.58264 (AAU, KEP, SAR), *G.P. Lewis* 371 (SAR), *P.J. Martin* S.38756 (AAU, KEP, L, SAN, SAR) and S.37068 (AAU, KEP, L, SAN, SAR)], and Bukit Sengkajang [*P. Chai* S.33936 (SAN, KEP)], and on the exposed limestone ridges on Gunong Api [*G. Argent & C. Jermy* 1021 (E, SAN, SAR), *R.B. Primack* S.43328 (K, L)]. They occur only at relatively high altitudes (at 2300m on Gunong Murud, between 1320 and 2200m in Gunong Mulu National Park, and on the summit ridge of Bukit Sengkajang at 1100m). Considerable variation among these specimens and lack of further material prevent me from describing them as a new species. *Plethiandra motleyi* and morphologically related specimens need to be studied in more detail.

Lee S.38263 (AAU, SAR) collected at Bukit Berar (Gunong Mulu National Park, Sarawak) and *Mokhtar & Jugah* S.41765 (AAU, K, L, SAN, SAR) collected at Ulu Sungei Kana (Tatau, Sarawak) differ from all other specimens in having large obovate leaves with 11–13 primary veins. Both plants were growing as epiphytes in lowland dipterocarp forests. The species of *Plethiandra* with leaves of comparable size are *P. robusta* and *P. beccariana*. *Plethiandra robusta* differs in having smaller flowers and fruits and ovate leaves. *Plethiandra beccariana* differs in having 15–30mm long pedicels while the pedicels in these two specimens measure 3–4mm. The material, however, is not sufficient to describe as a new species because mature flowers are missing.

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