



Resurrection and emended description of *Sciaphila major* (Triuridaceae)

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Abstract

This paper presents a re-evaluation of the taxonomic identity of *Sciaphila major* described from Sarawak, Borneo, Malaysia which has been considered conspecific with *S. secundiflora*. We revealed that *S. major* is clearly distinguishable from *S. secundiflora* s.s. by the arrangement of flowers on rachis (spirally and subdensely arranged vs. secundly and laxly arranged), rachis length in a fully developed inflorescence [(2–)3–6(–7) cm vs. 6–19 cm], tepal length of male flowers (2–2.3 mm vs. 3–4 mm) and the number of perianth segments (more than 6 vs. 6). By spirally-arranged and white flowers, *S. major* is most similar to *S. alba*, but is distinguishable by plant height (15–25 cm vs. 25–35 cm in *S. alba*), rachis length in a fully developed inflorescence [(2–)3–6(–7) cm vs. 8–14 cm], the number of flowers (usually less than 20 vs. usually more than 20), the arrangement of flowers on rachis (subdensely arranged vs. laxly arranged), the number of male perianth segments (usually more than 6 vs. usually 6) and the condition of floral disc (flat vs. bowl-shaped). We also provide an updated key to the species of *Sciaphila* distributed in Borneo.

Keywords: Malesia, Mycoheterotrophy, Sarawak, species revision, taxonomy

Introduction

The family Triuridaceae is a group of fully mycoheterotrophic plants that grow in deep shade understory of ever-wet forests in the tropics and subtropics worldwide, reaching their northernmost limits in temperate region of Japan (van de Meerendonk 1984). The genus *Sciaphila* Blume (1826: 514), which contains more than 40 species, is the largest group within the family (van de Meerendonk 1984, Suetsugu *et al.* 2019).

In taxonomic studies of the genus, species have been primarily discriminated on the basis of the following floral traits: bisexual or unisexual nature of flowers, number and shape of stamens and perianth segments, shape of apical perianth segments, and shape and length of styles (van de Meerendonk 1984; Hsieh *et al.* 2003; Chantanaorrapint & Thaitong 2004; Averyanov 2007; Ohashi *et al.* 2008; Xu *et al.* 2011, Suetsugu *et al.* 2016, 2019; Suetsugu & Nishioka 2017; Suetsugu 2018). However, key characters of male flowers, which are crucial for precise identification, have not been documented for some species, especially if individual specimens were too young at the time of collection (Tsukaya & Okada 2013; Tsukaya & Suetsugu 2014). Given the difficulty of precise identification, the taxonomy of *Sciaphila* remains to be revised.

The taxonomic identity of *Sciaphila secundiflora* Thwaites ex Bentham (1855: 10) has remained particularly unclear (Suetsugu *et al.* 2017, 2019, Suetsugu & Kinoshita 2020). The species was first described from Sri Lanka (Bentham

1855). Van de Meerendonk (1984) and Ohashi (2000) defined the species in a broad sense, thereby synonymising as many as 15 species with *S. secundiflora* (hereafter called *S. secundiflora s.l.*). Besides Sri Lanka, *Sciaphila secundiflora s.l.* is widely distributed in the Pacific islands, Malesia, Hongkong, Taiwan, Japan, and Korea (van de Meerendonk 1984; Ohashi 2000; Ohashi *et al.* 2008). According to van de Meerendonk (1984) and Ohashi (2000), *S. secundiflora s.l.* can be characterized by unisexual flowers (the female towards the base and the male towards the apex of the inflorescence), 4–8 equal perianth-segments of the male flower without any hair or appendage, 3 stamens, and clavate style and stigma. However, our previous investigations based on the type materials of *S. secundiflora s.l.* showed that gross morphology, floral size and shape of perianth segments often differ among the species that have been considered as synonyms of *S. secundiflora s.s.* (Suetsugu *et al.* 2019; Suetsugu & Kinoshita 2020). Therefore, it is highly likely that these treatments are based on the ambiguity of the original species description and that the species complex, in fact, comprises several distinguishable taxa. Suetsugu *et al.* (2019) revealed that both *Sciaphila tosaensis* Makino (1905: 140) and *S. megastyla* Fukuyama & Suzuki (1936: 412) are distinct species rather than synonyms of *S. secundiflora*, based on both molecular and morphological data.

The present study investigated the taxonomic identity of *Sciaphila major* Beccari (1890: 332) that was described from Sarawak, Borneo, Malaysia by examining the detailed morphology of the type specimens and specimens collected around the type locality. A thorough review of relevant literature, herbarium specimens and online digitized plant collections, including JSTOR Global Plants (<http://plants.jstor.org/>), allowed us to determine that *S. major* is clearly distinguishable from *S. secundiflora s.s.* by the arrangement of flowers on rachis (spirally and subdensely arranged vs. secundly and laxly arranged), rachis length in a fully developed inflorescence [(2–)3–6(–7) cm vs. 6–19 cm], tepal length of male flowers (2–2.3 mm vs. 3–4 mm) and the number of perianth segments (more than 6 vs. 6; Figs 1–2). In spirally arranged and white flowers, *S. major* is morphologically similar to *S. alba*, but our detailed comparison of morphological characters between these two species revealed that *S. major* can be distinguishable also from *S. alba*. Here, we provide an emended description of *S. major* based on the type specimen supplemented with newly collected specimens because some important characters were not mentioned in the protologue of the Beccari's original description (1890). We also provide an updated key to *Sciaphila* species distributed in Borneo.

Material and Methods

Plants were studied using hand lens (30–60 × magnification), stereo microscope and macro photography both in the field and in herbaria. We checked the specimens of *S. secundiflora*, *S. major* and *S. alba* kept in the following herbaria: B, BM, BRUN, FI, FR, FU, K, KYO, OL, OSA, P, SAR, SING, TI and TNS. A distribution map was drawn using QGIS 3.10 (2020).

Taxonomic Treatment

***Sciaphila major* Beccari (1890: 332) Figs. 3–5.**

Type:—MALAYSIA. Borneo, Sarawak: Kuching Division, December 1865, *O. Beccari 1210* (syntype, FI, image!), Kuching Division, Sul Monte Mattang, April 1866, *O. Beccari 1507* (syntype, FI and K, image!).

Description:—Monoecious, mycoheterotrophic, perennial herbs. Roots filiform, hairy. Stems erect, underground parts white, aerial parts white to ivory, rarely pale purple, simple or branched at the middle or base, (10–)15–25 cm tall. Scale leaves ovate to lanceolate, ca. 2.5 mm long, apex acute. Inflorescence racemose, rachis (2–)3–6(–7) cm long; flowers 8–18(–30) per inflorescence, spirally and subdensely arranged, male flowers towards the apex of the inflorescence, female flowers towards the base of the inflorescence, internodes 2–6 mm. Bracts appressed to a pedicel, triangular lanceolate, 2 mm long, apex acute. Pedicels 1.5–2 mm long in male flowers and 2–3 mm in female flowers, patent at 90° from rachis, straight. Male flowers: 6–7.2 mm in diam., perianth segments (6–)7–10, white or pale purple, equal in size, narrowly triangular, 2–2.3 mm long, 0.6 mm wide at the base, central parts thick and ridged, fused basally, opening to a flat plane at the base, apex acuminate, smooth, recurved. Floral disc surrounding the stamens, bowl-shaped. Stamens 3, sessile; anthers 2-locular, 0.6 mm long. Female flowers: 6–8 mm in diam., perianth segments (6–)7–11, white or pale purple, equal in size, narrowly triangular, 2.2–2.5 mm long, 0.7 mm wide at the base, fused

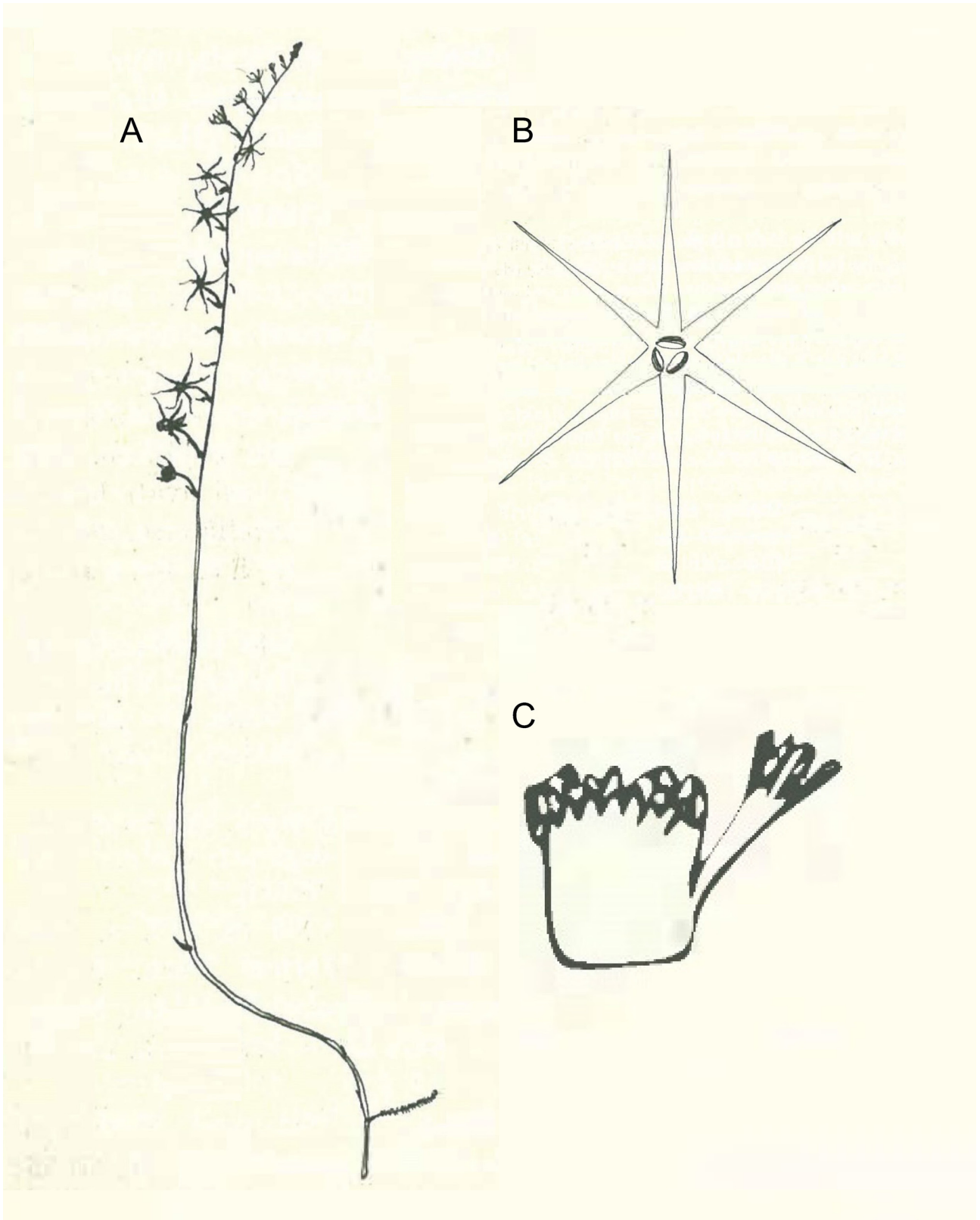


FIGURE 2. Line drawings of *Sciaphila secundiflora*. Reproduced from a monograph by Giesen (1938). A. Habit. B. Male flower. C. Immature carpel with style and stigma.

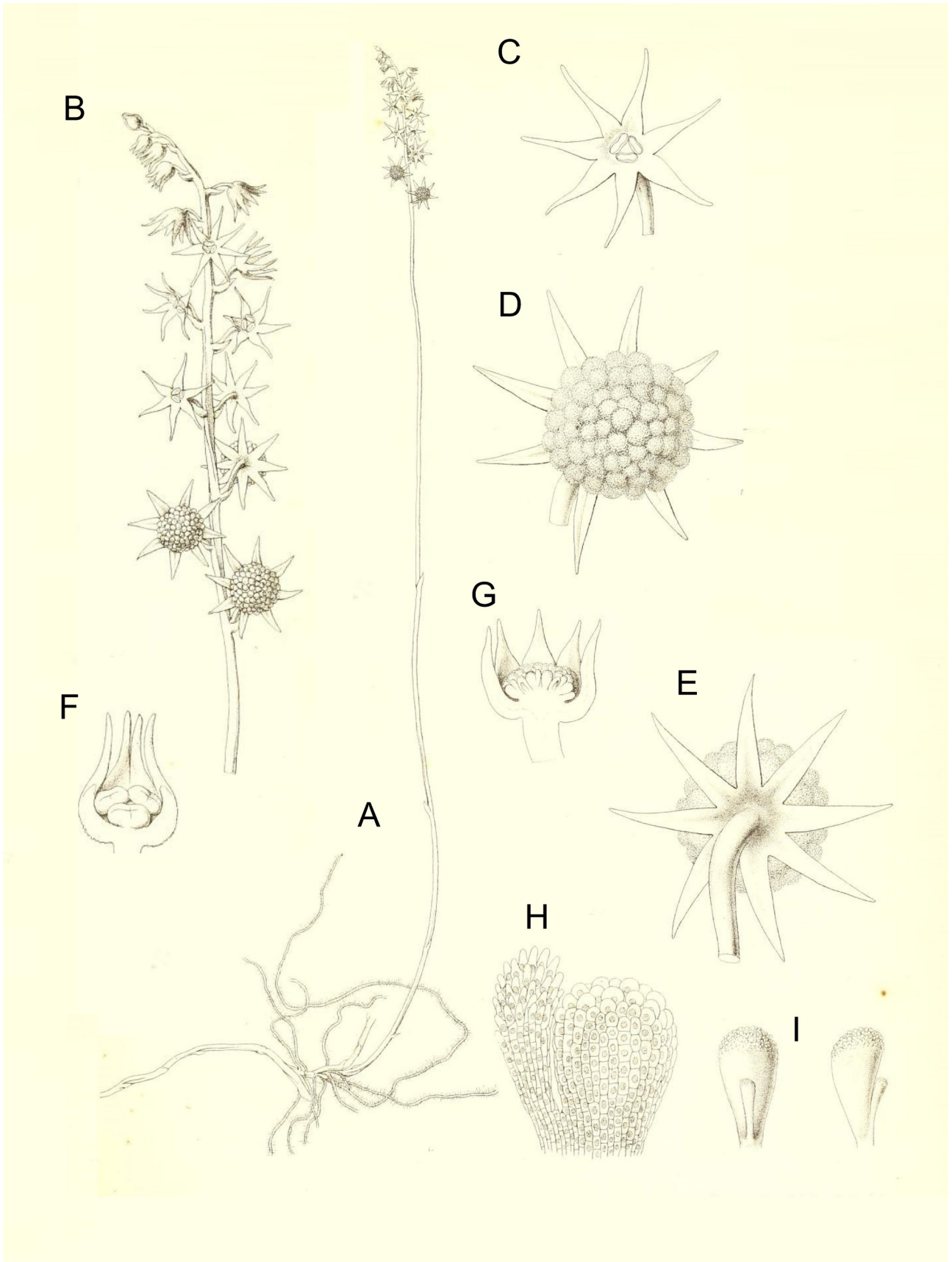


FIGURE 3. Line drawings of *Sciaphila major*. Reproduced from a paper by Beccari (1890) that is the original description. A. Habit. B. Inflorescence. C. Male flower. D–E. Female flowers. F. Immature male flower. G. Immature female flower. H. Immature carpel with style and stigma. I. Immature fruits.

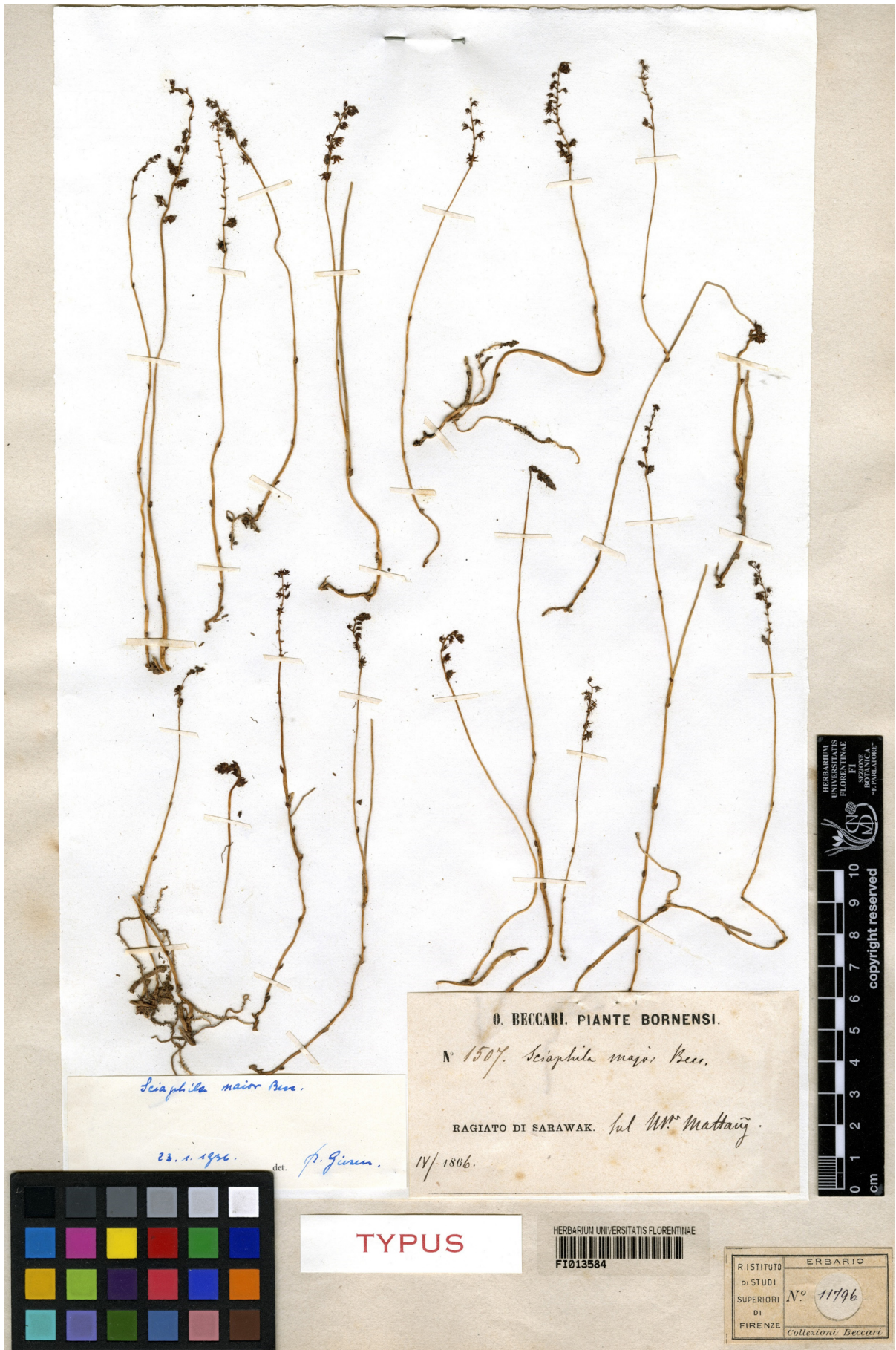


FIGURE 4. Syntype of *Sciaphila major* collected by O. Beccari at the type locality in April 1866 (FI).

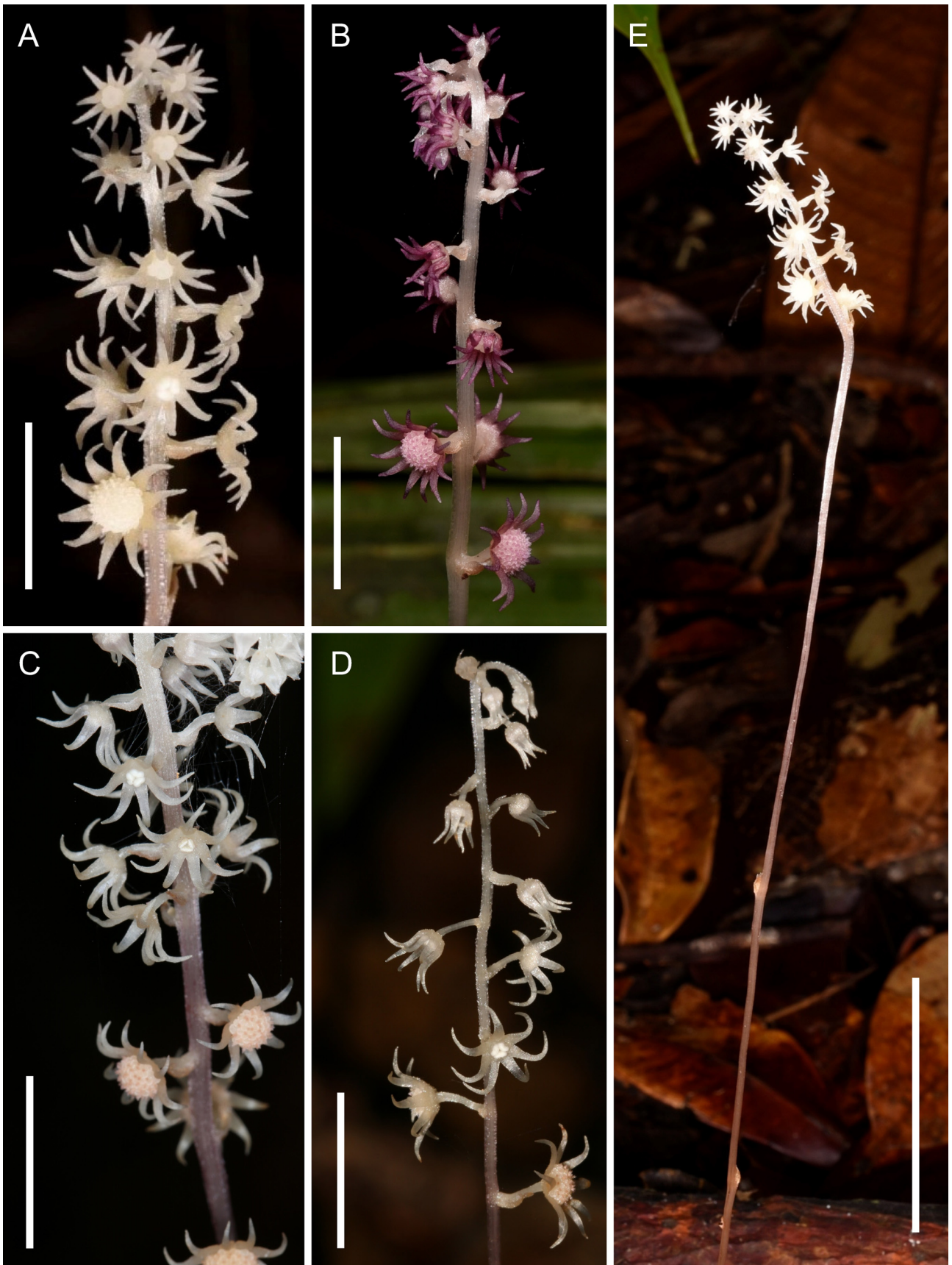


FIGURE 5. *Sciaphila major*. A–B. Inflorescence in Similajau National Park (Hroneš & Dančák 512020). C–D. Inflorescence in Kubah National Park (Sochor; Hroneš & Dančák BOR52/17). E. Flowering plant in Similajau National Park (Hroneš & Dančák 512020). (Photos: A, B, E: Michal Hroneš, C, D: Michal Sochor). Scale bars A–D = 1 cm. E = 3 c m.

Additional specimens examined:—MALAYSIA. Borneo, Sarawak, Kuching Division, Kuching district: Kuching, 6 February 1892, *Haviland s.n.* (SING); Matang, 1903, *Ridley 11707* (SING); Matang, September 1904, *Ridley s.n.* (SING); Kubah National Park, evergreen dipterocarp forest, 01°36'19.91"N, 110°11'23.15"E, alt. 317 m, 4 December 2017, *Tagane, Zhang & Komada SWK4639* (FU, SAR); Kubah National Park, along the Rapids Trail, 01°37'1"N, 110°10'0"E, 7 November 2015, *Mačát s.n.* (OL); Kubah National Park, 0.4 km NE of Matang Wildlife Centre, 01°36'41"N, 110°9'48"E, 26 January 2017, *Sochor, Hroneš & Dančák BOR52/17* (OL); Bako National Park, Telok Asam, 6 Feb 1957, *Purseglove 5584* (SING); Tanjong Dolima, Bako National Park, 7 February 1957, *Purseglove 5584* (SING); Bintulu Division: Bintulu District, Similajau National Park, trail to Batu Anchau, 03°21'44"N, 113°9'55"E, 28 January 2020, *Hroneš & Dančák 512020* (OL, SAR); Tatau District, Tubau, in mixed dipterocarp forest, preserved for water catchment for Rh. Ayaing, 03°16'14.11"N, 113°47'42.73"E, alt. 106 m, 26 January 2017, *A. Naiki, N. Okabe, A. Kawakubo, S. Tagane & Y. Takeuchi SWK4034* (FU, SAR).

Distribution:—Sarawak (Kuching and Bintulu Divisions; Fig. 6). The majority of herbarium specimens for this species was collected from Kubah National Park near Kuching which can be considered as the type locality. Beccari (1890) described the locality simply as Monte Mattang, which is an area now generally known as Matang massif where Kubah National Park is located. This species also occurs in Bako National Park, Sarawak, where field photographs were published on a website [<http://angio.bergianska.se/Bilder/monocots/Pandanales/Triuridaceae/Sciaphila/>]. Furthermore, it occurs in Bintulu district which is located more than 370 km NE of Kuching (Fig. 4). Further explorations are needed to determine the precise distribution of *S. major*, especially in western Sarawak and adjacent West Kalimantan.

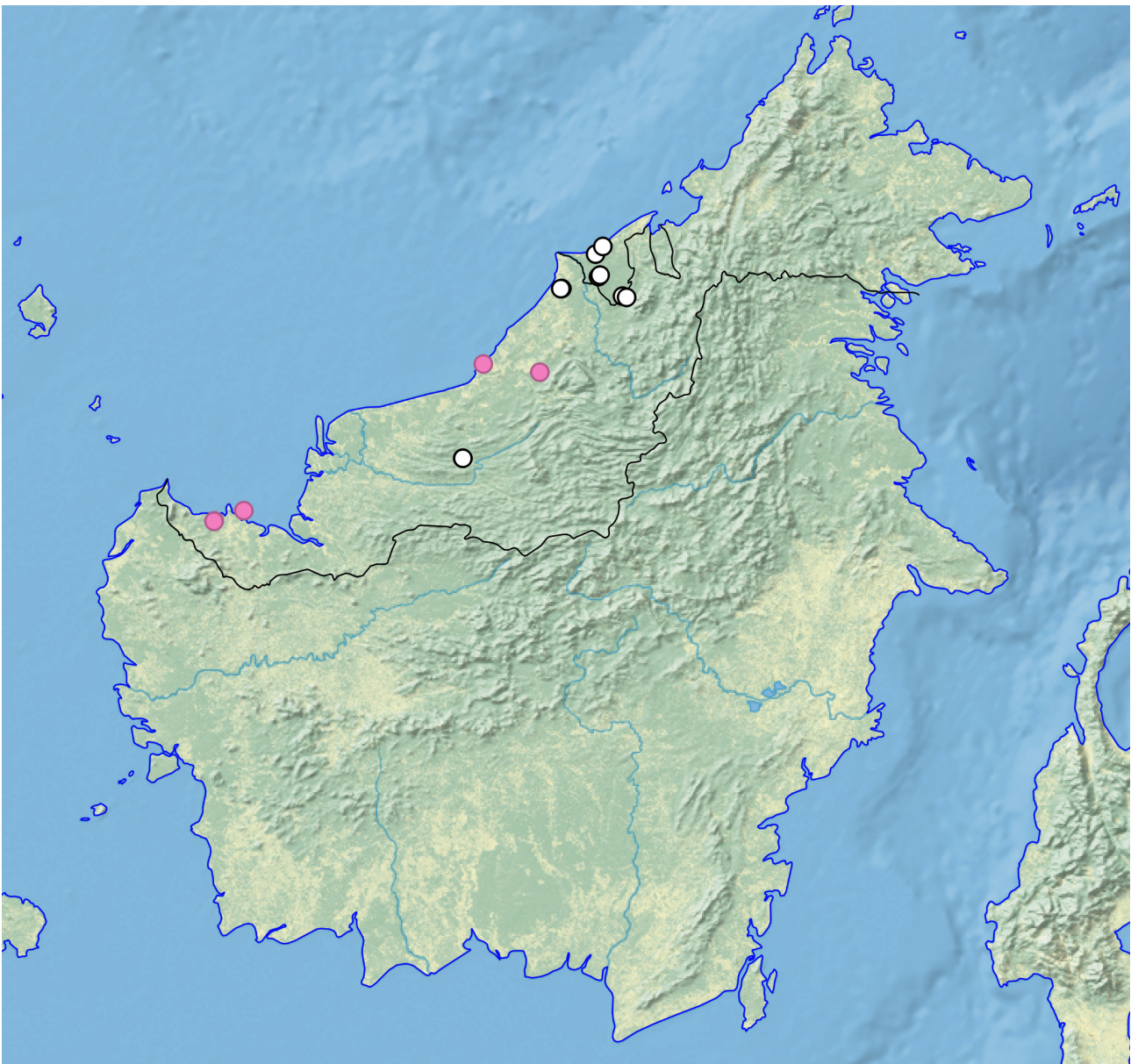


FIGURE 6. Map showing occurrence of *Sciaphila major* and *S. alba*. Pink circles: *S. major* in Borneo. White circles: *S. alba*.

Sciaphila alba Tsukaya & Suetsugu (2014: 284) Figs. 7–8.

Type:—MALAYSIA. Borneo, Sarawak: Miri Division, Miri District, Lambir Hills National Park, along the Lambir Pantu trail, under dipterocarp forest, 3 March 2013, K. Suetsugu s.n. (holotype SAR! [spirit coll.], isotype KYO! [spirit coll.]).

Description:—Monoecious, mycoheterotrophic, perennial herbs. Roots filiform, hairy. Stems erect, underground parts white, aerial parts white to pale pinkish white, unbranched, 25–35 cm tall. Scale leaves ovate to lanceolate, ca. 2.5 mm long, apex acute. Inflorescence racemose, rachis 8–14 cm long; flowers (15–)20–40 per inflorescence, spirally and laxly arranged, male flowers towards the apex of the inflorescence, female flowers towards the base of the inflorescence, internodes 3–10 mm. Bracts appressed to a pedicel, triangular lanceolate, 2 mm long, apex acute. Pedicels 2.5–3.5 mm long in male flowers and 3–4 mm in female flowers, patent at 90° from the rachis, straight. Male flowers: 7–8 mm in diam., perianth segments 6(–8), pale pinkish white or rarely reddish purple at the base, fading to pale pinkish white at apex, equal in size, narrowly triangular, 2.9–3.5 mm long, 0.5 mm wide at the base, fused basally, opening to a flat plane at the base, apex obtuse, smooth, recurved. Floral disc surrounding the stamens, flat. Stamens (2–)3, sessile; anthers 2-locular, 0.5–0.7 mm long. Female flowers: 7–8 mm in diam., perianth segments 6–7(–9), pale pinkish white, equal in size, triangular, 3.2–3.8 mm long, 0.7 mm wide at the base, fused basally, apex obtuse or acute, smooth, recurved. Carpels more than 30, ellipsoidal, 0.7–0.8 mm long, rounded at apex; style and stigma clavate, 0.8–0.9 mm long, papillate, laterally inserted a little above the base of ovary.

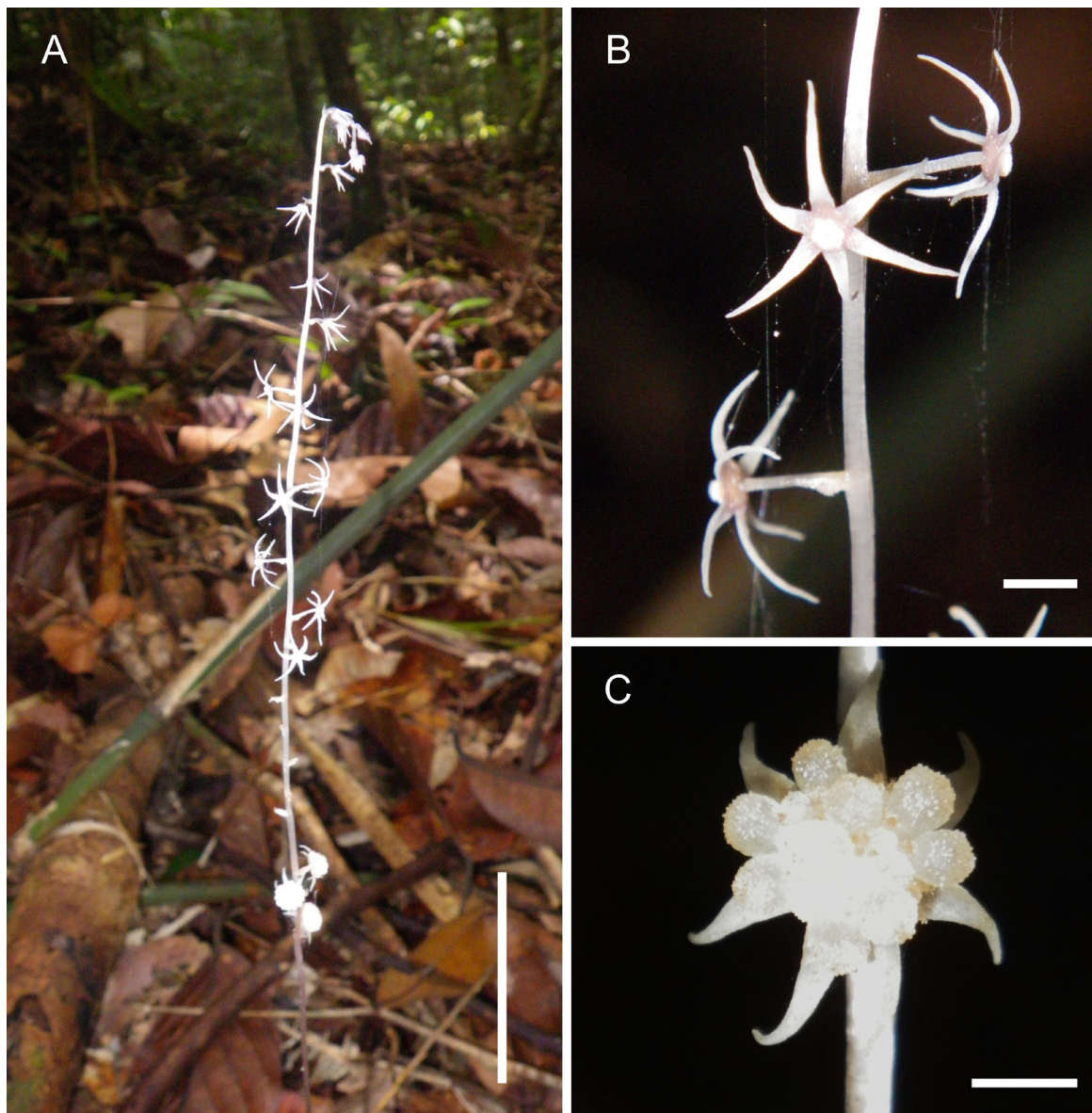


FIGURE 7. *Sciaphila alba* (from the holotype). A. Flowering plant. B. Male flowers. C. Female flower. (Photos: Kenji Suetsugu). Scale bar A = 3 cm. B, C = 2 mm.



FIGURE 8. *Sciaphila alba*. A. Inflorescence in Andulau (*Dančák 2017/56*). B. Inflorescence in Bukit Teraja (*Hroneš & Dančák 192020*). C. Inflorescence in Lambir Hills National Park (*Sochor s.n.*). (Photos: A, B: Michal Hroneš, C: Michal Sochor). Scale bar = 3 cm.

Additional specimens examined:—BRUNEI DARUSSALAM. Belait District: Teraja Forest Reserve, 18 December 1963, *M. Hotta 12710* (KYO); Bukit Teraja, between Wasai Wong Kadir and access road to the summit, 04°19'58"N, 114°26'57"E, 8 July 2019, *Dančák 2019/30* (OL); Bukit Teraja, forest SE Wasai Wong Kadir, 04°20'12"N, 114°27'5"E, 13 January 2020, *Hroneš & Dančák 192020* (BRUN); Labi, Sungai Rampayoh, c. 3.5 km above road towards Waterfall no. 2, 04°21'N, 114°28'E, alt. 40 m, 9 January 1994, *Coode 7783* (BRUN); Seria, Badas forest reserve, 04°35'N, 114°25'E, alt. 5–10 m, 24 March 1993, *Coode 7344* (BRUN); Sungai Liang Arboretum, beside the pool, 04°40'N, 114°29'E, alt. 15 m, 14 January 1994, *Dransfield 7345* (BRUN); Sungai Liang, north-western margin of Andulau forest reserve, 04°39'34"N, 114°31'19"E, 23 January 2017, *Dančák 2017/56* (OL); Melilas, Ulu Ingei, W of LP-101A, near Sungai Ingei, 04°07'N, 114°43'E, alt. 30 m, 5 March 1996, *Said BRUN 17313* (BRUN); Batu Melintang to Batu Patau, near Sarawak border, 04°06'N, 114°46'E, alt. 1–180 m, 3 January 1989, *De Vogel 8871* (BRUN). MALAYSIA. Borneo, Sarawak: Miri Division, Miri District, Lambir Hills National Park, ca. 0.4 km NW of the main entrance, in primary forest, 04°12'05"N, 114°02'27"E, alt. 130 m, 8 February 2016, *Sochor s.n.* (OL); Miri Division, Miri District, Lambir Hills National Park, en route to Gn. Pantu, 04°12'00.20"N, 114°01'43.40"E, alt. 170 m, 9 January 2017, *S. Tagane, U. Shimizu-kaya & I. Asano SWK3502* (SAR), Bintulu Division, Tatau District, Tatau,

a water catchment forest of Rh. Sayong, a kerangas forest dominated by species of Dipterocarpaceae, 02°18'52.1"N, 112°56'07.4"E, alt. 105 m, 2 February 2016, *A. Naiki et al. SWK1331* (OSA); Bintulu Division, Tatau District, Rh. Sayong, kerangas forest dominated by the species of Dipterocarpaceae, 02°18'47.00"N, 112°56'14.99"E, alt. 109 m, 29 September 2017, *Toyama, Naiki, Lawrence, Sim & Layang SWK5257* (FU).

Distribution:—Brunei Darussalam (Belait District) and Malaysia (Miri and Bintulu Divisions, Sarawak) (Fig. 6).

TABLE 1. Morphological characters of *Sciaphila secundiflora*, *S. major* and *S. alba*.

Characters	<i>S. secundiflora</i>	<i>S. major</i>	<i>S. alba</i>
Plant height	(10–)20–33 cm	(10–)15–25 cm	25–35 cm
Plant coloration	whitish purple	white to ivory, rarely pale purple	white to pale pinkish white
Rachis length	6–19 cm	(2–)3–6(–7) cm	8–14 cm
Arrangement of flowers on rachis	5–20-flowered, secundly and laxly arranged	8–18(–30)-flowered, spirally and subdensely arranged	(15–)20–40-flowered, spirally and laxly arranged
Pedicel length	2–5(–11) mm	1.5–3 mm	2.5–4 mm
Condition of floral disc	flat	bowl-shaped	flat
Number of perianth segments	constantly 6 for both male and female	7–10 for male and 7–11 for female	6(–8) for male and 6–7(–9) for female
Male flower size	7–8 mm in diam.	6–7.2 mm in diam.	7–8 mm in diam.
Shape of male perianth segments	narrowly triangular, 3–4 mm long, 0.4–0.6 mm wide at the base	narrowly triangular, 2–2.3 mm long, 0.6 mm wide at the base	narrowly triangular to acuminate, 2.9–3.5 mm long, 0.5 mm wide at the base
Female flower size	7–9 mm in diam.	6–8 mm in diam.	7–8 mm across
Position of style and stigma	laterally inserted at a little below the middle of ovary	laterally inserted at the base of ovary	laterally inserted a little above the base of ovary
Length of style and stigma	0.8 mm long, as long as ovary in the flowering stage	0.7–0.8 mm long, as long as or slightly exceeds ovary in the flowering stage	0.8–0.9 mm long, as long as or slightly exceeds ovary in the flowering stage

Data of *S. secundiflora* from Giesen (1938) and our own examination of the type specimens deposited in B, BM, FR, K and P.

Discussion

Sciaphila major is similar to *S. secundiflora* in having unisexual flowers (female ones located at the base and male ones at the apex of the inflorescence), equal perianth segments of a male flower without any hair and appendage, 3 stamens, and clavate style and stigmas. However, *S. major* is clearly distinguishable from *S. secundiflora* s.s. by the arrangement of flowers on rachis (spirally and subdensely arranged vs. secundly and laxly arranged), rachis length in a fully developed inflorescence [(2–)3–6(–7) cm vs. 6–19 cm], tepal length of male flowers (2–2.3 mm vs. 3–4 mm) and the number of perianth segments (more than 6 vs. 6; Figs 1–2). It is noteworthy that the arrangement of flowers on the rachis is secund in not only *S. secundiflora* s.s. but also most other species that have been considered as the synonyms of *S. secundiflora*. In contrast, *S. major* has spirally arranged flowers. Both types of flower arrangement are steadily recognizable by the position of flowers on the inflorescence rachis even in specimens with only a few flowers. Secund arrangement makes one sided inflorescence (Figs 1 and 2) whereas spiral inflorescences have flowers growing to several sides from the rachis. Even if the inflorescence is lax (Fig. 5B and D), the flowers point to several directions. Therefore, *S. major* is clearly distinguishable from almost all the species of the *S. secundiflora* species complex.

In having spirally arranged flowers and usually white flowers, *S. major* is most similar to *S. alba*, but can be easily distinguished by plant height (15–25 cm in *S. major* vs. 25–35 cm in *S. alba*), rachis length in a fully developed inflorescence (3–6 cm vs. 8–14 cm), the number of flowers (usually less than 20 vs. usually more than 20), the arrangement of flowers on rachis (more densely arranged vs. laxly arranged), the number of male perianth segments (usually more than 6 vs. usually 6), and the condition of floral disc (flat vs. bowl-shaped). On the other hand, Tsukaya & Suetsugu (2014) noted that *S. alba* differs from *S. secundiflora* in having much larger flowers, but further examination of the type specimens of *S. secundiflora* revealed that both *S. secundiflora* and *S. alba* have flowers 7–8 mm in diam. However, *S. alba* can be easily distinguished by the arrangement of flowers on rachis (spirally arranged vs. secundly arranged) and the number of flowers (less than 20 vs. usually more than 20). In addition, these three species can be also distinguished from each other by combination of several morphological characters other than those discussed here. For a detailed comparison of morphological characters among *S. secundiflora*, *S. major* and *S. alba*, see Table 1.

Geographically, *S. alba* and *S. major* seem to have different distribution ranges in Borneo (Fig. 4). According to available records, *S. alba* occurs mostly in Brunei and eastern Sarawak with an isolated occurrence also in central Sarawak, and *S. major* occurs mostly in western Sarawak but reaching the central Sarawak as well.

Key to the Species of *Sciaphila* in Borneo (modified after van de Meerendonk 1984)

1. Plants with bisexual and unisexual flowers	2
2. Perianth segments 4(or 5)	<i>S. betung-kerihunensis</i>
2. Perianth segments 6	3
3. Male and bisexual flowers with 3 stamens	<i>S. maculata</i>
3. Male flowers with 6 stamens; bisexual flowers with 3–6, but generally 6 stamens	<i>S. tenella</i>
1. Plants with unisexual flowers only	4
4. Perianth segments equal	5
5. Flowers secundly arranged	6
6. Male flowers 1.3–1.4 mm in diam. when flattened; perianth segments bearded at apex	<i>S. lambirensis</i>
6. Male flowers 7–8 mm in diam.; perianth segments glabrous at apex	<i>S. secundiflora</i>
5. Flowers spirally arranged	7
7. Flowers white, rarely pale purple; male flowers more than 5 mm in diam	8
8. Rachis in a fully developed inflorescence 8–14 cm long; flowers usually more than 20, male perianth segments usually 6, narrowly triangular	<i>S. alba</i>
8. Rachis in a fully developed inflorescence 3–6 cm long; flowers usually less than 20; male perianth segments usually more than 6, acuminate at apex	<i>S. major</i>
7. Flowers purple, male flowers less than 5 mm in diam	9
9. Male flowers ca. 1.2 mm in diam. when flattened; perianth segments with hairs at apex	<i>S. brevistyla</i>
9. Male flowers 3–4 mm in diam.; perianth segments without hairs at apex	<i>S. thaidanica sensu</i> Tsukaya & Okada (2013)*
4. Perianth segments unequal (3 larger alternating with 3 smaller ones)	10
10. Stamens in male flower 3	11
11. Anthers 2-lobed	12
12. Apex of perianth segments acute; perianth segments of female flowers 3 longer ones (1.0–1.2 mm long) alternating with 3 shorter ones (0.4–0.6 mm long)	<i>S. winkleri</i>
12. Apex of perianth segments obtuse; perianth segments of female flowers 3 longer ones (1.4 mm long) alternating with 3 shorter ones (1.1 mm long)	<i>S. inouei</i>
11. Anthers 3-lobed	<i>S. micranthera</i>
10. Stamens in male flower 6	<i>S. densiflora</i>

*As noted by Suetsugu (2018), *Sciaphila* sp. recently recorded as “*S. thaidanica*” by Tsukaya & Okada (2013) from Borneo will be different from *S. thaidanica* Larsen (1961: 48) described from northern Thailand in that flowers are spirally arranged on rachis (vs. secund in *S. thaidanica*; Larsen 1961). Further studies are needed to elucidate the taxonomic identity of *S. thaidanica sensu* Tsukaya & Okada (2013).

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