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The Genus *Rhaphidophora* Hassk. (Araceae-Monsteroideae-Monstereae) in Borneo

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Abstract

An alpha-taxonomic account of Bornean *Rhaphidophora* is presented as a precursor to the forthcoming Flora Malesiana *Araceae* treatment. Thirteen species are recognized, none novel. *Rhaphidophora elliptica* Ridl. 1905 (*non* 1908 = *R. elliptifolia* Merr.) and *R. megasperma* Engl., treated respectively as synonyms of *R. montana* (Blume) Schott and *R. puberula* Engl. by Boyce (1999), are resurrected as Bornean endemics. New synonyms are: *Scindapsus havilandii* Ridl., *Rhaphidophora jaculiformis* Alderw., *R. subfalcata* M. Hotta into *R. megasperma*, and *R. nigrescens* Ridl. into *R. sylvestris* (Blume) Engl. A dichotomous key to species is provided. All species are illustrated.

Contents

Introduction

Rhaphidophora Hassk. (including *Afrorhaphidophora* Engl.; c. 3 species in tropical Africa) comprises c. 100 species of small to large, occasionally enormous, root-climbing lianes (*sensu* Schimper, 1903), rarely rheophytes, distributed from tropical West Africa eastwards to the western Pacific, north to southern Japan (Ryukyu Islands) and south to Northern Australia. *Rhaphidophora* is one of the largest aroid genera represented in tropical Asia and has several nodes of diversity; the Himalaya (SE Nepal to NE Vietnam, roughly 17°—23° N), West Malesia (including southernmost peninsular Thailand), the Philippines, and East Malesia.

This is the fifth in a series of papers intended to present a complete

alpha-taxonomy of the genus *Rhaphidophora* in Asia. Accounts for Peninsular Malaysia and Singapore, the southern and western Indonesian archipelago and the Philippines have been published recently (Boyce, 1999, 2000a, 2000b) together with a partial account for New Guinea (Boyce & Bogner, 2000) and an account for Papuasia and the tropical Western Pacific appears elsewhere in this journal (Boyce, 2001). Accounts for the Himalaya, and Thailand and Indochina are being prepared and will be published separately. All morphological terms employed follow Stearn (1992).

The last complete revision of *Rhaphidophora* was that of Engler & Krause (1908). A summary of the taxonomic and nomenclatural history of *Rhaphidophora* was presented in Boyce (1999) and a partial infrageneric classification with an overview of informal morpho-taxonomic groups was proposed by Boyce (2000a). Boyce (1999) provides a detailed discussion of structure, generic limits, together with keys to the genera of monsteroid and anadendroid aroids in Malesia.

Synonymy cited is for the species, not for the review area. The reason for this is that synonymic names based on types from outside the review area are frequently applied to specimens in local herbaria.

Geography and Endemism

Borneo has a relatively poor *Rhaphidophora* flora, with comparatively few species recorded, although how much this is a reflection of inadequate collecting is not clear. However, of the 13 species recognized for the island five are endemic (compared with 2/15 in Peninsular Malaysia; 4/15 in Sumatera) and thus Borneo has, with the exception of the Philippine islands (7/11), the highest level of endemism in Sunda.

Two of the five Bornean endemics, *R. elliptica* Ridl. and *R. elliptifolia*, belong to the Indo-Malesian Hongkongensis Group (see Boyce, 2000a). Both Bornean endemics are morphologically close to west Malesian species (*R. elliptica* to *R. montana* (Blume) Schott; *R. elliptifolia* to *R. maingayi* Hook.*f.*) and are presumably endemic segregates. Another species from this group, the widespread *R. sylvestris* (Blume) Engl. (Sumatera, Peninsular Malaysia, Thailand, east to Borneo) is widespread and common in Borneo. The other Bornean endemics are *R. latevaginata* M. Hotta, *R. megasperma* Engl. and *R. cylindrosperma* Engl. & K. Krause.

Rhaphidophora latevaginata M. Hotta is a neotenic shingling species that might conceivably have arisen from a species with a pronounced heteroblastic development, e.g., *R. korthalsii* Schott (see Boyce, 2000a).

Rhaphidophora megasperma is of uncertain affinity in Sundaic Asia but has morphological similarities, e.g., clustered inflorescences subtended

by chartaceous cataphylls, to certain New Guinea species (e.g., *R. versteegii* Engl.) and is tentatively included in the Hollrungii Group (note that this group had its name changed in Boyce, 2001).

Rhaphidophora cylindrosperma is another morphologically isolated species in Sunda but with similar species (e.g., *R. schlechteri* K. Krause) east of Wallace's Line and belongs to the Neoguineensis Group. It is interesting that two of the Borneo endemic *Rhaphidophora* appear to be morphologically closer to species in Wallacean New Guinea than to any Sundaic species.

RHAPHIDOPHORA

Rhaphidophora Hassk., Flora 25 (2) Beibl. 1 (1842) 11; Schott, Gen. Aroid. (1858) 77 & Prodr. Syst. Aroid. (1860) 377—388; Miquel, Ann. Mus. Bot. Lugd.-Bat. 3 (1867) 81—82; Engl. in A. & C. DC., Monogr. Phan. 2 (1879) 238—248; Engl. in Beccari, Malesia 1 (1882) 266—272, Tab. xix 6—9, xx 1—5; Benth. & Hook. f., Gen. Pl. 3(2) (1883) 993 - 993; Engl. & Prantl, Nat. Pflanzenfam. T. 2, Ab. 3 (1889) 119—120; Engl. & Prantl, Nat. Pflanzenfam. Nachtr. 1 (1897) 58; Ridl., J. Straits Branch Roy. Asiat. Soc. 44: 185—187 (1905); Engl. & K. Krause in Engl., Pflanzenr. 37 (IV.23B) (1908) 17—53; Engl. & Prantl, Nat. Pflanzenfam. Nachtr. 3 (1908) 29; Merrill, J. Straits Branch Roy. Asiat. Soc., special number (1921) 88—90; Schott, Icones aroideae et reliquiae (IDC Microfilm) (1983) fiche nos. 28—31, 121; Mayo *et al.*, Genera *Araceae* (1997) 118—121, Pl. 14, 109 D. — *Scindapsus* Schott subgen. *Rhaphidophora* (Hassk.) Miq., Flora Ned. Indië 3 (1856) 185. — Type: *Rhaphidophora lacera* Hasskarl, *nom. illeg. pro. Pothos pertusus* Roxb. [= *Rhaphidophora pertusa* (Roxb.) Schott]

Scindapsus Schott subgen. *Pothopsis* Miq., Flora Ned. Indië 3 (1856) 187. — Type: *Scindapsus sylvestris* (Blume) Kunth [= *Rhaphidophora sylvestris* (Blume) Engl.]

[*Raphidophora* Hassk., Cat. Hort. Bogor. (1844) 58, *orth. var.*]

Medium-sized to very large, occasionally enormous, slender to robust, leptocaul or pachycaul, homeophyllous or heterophyllous, rarely neotenic [e.g., some populations of *R. beccarii* (Engl.) Engl.], root-climbing lianes, very seldom clustering and rheophytic (e.g., *R. beccarii*) and then always with a creeping juvenile stage; cut surfaces producing clear, odourless sticky juice either drying ± invisible or coagulating into yellowish, translucent jelly and eventually hardening to a brittle amber-like mass; *seedling stage*

mostly not observed but where known either leafy at germination and skototropic (see Strong & Ray, 1975) by an alternating series of congested leafy and elongated leafless shoots (e.g., *R. angustata* Schott) or germinating to give rise to a non-skototropic shingling juvenile shoot (e.g., *R. korthalsii*); *pre-adult plants* often forming modest to extensive terrestrial colonies of varying morphological and physiological form (descriptive generalisations are nearly impossible), largest terrestrial colonies generally occurring in places of less than optimum adult growth potential (e.g., depauperate tree canopy, dry, exposed sites); *adult shoot architecture* broadly divisible into three types: i. physiognomically unbranched clinging non-flowering stems rooting along their entire length giving rise to variously elaborated free lateral flowering stems (e.g., *R. lobbii* Schott, *R. puberula* Engl.), *or* ii. all stems physiognomically unbranched clinging and flowering (e.g., *R. korthalsii*), *or* iii. physiognomically unbranched leader and lateral stems clinging but only lateral stems flowering (e.g., *R. foraminifera*); *stems* with internodes of various lengths separated by variously prominent leaf scars, smooth or asperous or densely pubescent to ramentose (the last not in the review area), older stems subwoody or somewhat corky or with distinctive matt to sublustrous pale brown papery epidermis, with or without variously textured prophyll, cataphyll and petiolar sheath fibre either at the tips or along the newer sections, rarely with cataphylls and prophylls deliquescing to black mucilage later drying to leave fragmentary parchment-like remains on petioles, developing laminas and inflorescences; *flagellate foraging stems* occurring in some species, often exceedingly long, reaching the ground then rooting, variously foraging and climbing again; *clasping roots* sparsely to densely arising from the nodes and internodes, clinging to substrate; *feeding roots* rare to abundant, smooth, pubescent or prominently scaly, later often becoming woody, clinging to substrate or free; *leaves* distichous or weakly spiralled, evenly distributed or scattered or clustered distally; *cataphylls and prophylls* subcoriaceous to membranous, either soon drying and falling or degrading or deliquescing to variously textured sheaths and fibres, these where present variously clothing upper stem before eventually decaying and falling; *petiole* canaliculate to weakly carinate, smooth or pubescent, with variously prominent apical and basal genicula; *petiolar sheath* prominent, nearly reaching to overtop the geniculum, occasionally one side greatly expanded and auriculate, especially in juvenile plants, at first membranous to coriaceous, soon completely or along the margins drying chartaceous, sometimes degrading to untidy variously netted or simple fibres and later variously falling to leave a scar or disintegrating marginally or completely; *lamina* submembranous to stiffly chartaceous or coriaceous, lanceolate or oblong, ± oblique, base decurrent to unequal or cordate, apex acute to acuminate, entire to regularly pinnatifid or

perforated, if pinnate then divisions pinnatifid to pinnatisect (Stearn, 1992: 324), midrib often ± naked between segments, lamina occasionally with small to well developed perforations adjacent to the midrib and primary veins, these sometimes extending to lamina margin (fenestrations then occasionally additional to fully developed pinnae), rarely abaxially pubescent when expanding, rarely strongly concolorous at maturity; *midrib* usually prominent raised abaxially and prominently sunken, sometime flush, rarely slightly raised adaxially; *primary venation* ± pinnate; *interprimaries* mostly present, subparallel to primaries and sometimes indistinguishable from them (e.g., *R. monticola* - Philippines) but usually less prominent and often drying paler, usually glabrous, occasionally pubescent with domatia in the axils of the primary and secondary veins; *secondary venation* striate (e.g., *R. monticola*—Philippines) to reticulate (e.g., *R. korthalsii*), variously prominent, often very difficult to distinguish from primary venation (e.g., *R. angustata*); *tertiary venation* where visible reticulate to tessellate; *inflorescences* solitary to several together, first inflorescence subtended by a (usually fully developed) foliage leaf and/or a very soon disintegrating cataphyll, subsequent inflorescences usually each subtended by a prophyll and cataphyll, more rarely by a prophyll and partially to almost fully formed foliage leaf, inflorescences at male anthesis naked by disintegration of subtending cataphyll or partially to almost completely obscured by netted and sheet-like fibres; *peduncle* terete to laterally compressed; *spathe* ovate to narrowly or broadly canoe-shaped, stoutly to rather weakly beaked, barely gaping to opening almost flat at male anthesis and then usually deciduous before male anthesis is complete, occasionally persisting into the early stages of infructescence development (e.g., *R. angustata*), rarely drying and persistent (e.g., *R. megasperma*), stiff to rather softly or stoutly coriaceous, dirty-white, greenish, cream or yellow; *spadix* subglobose to clavate-cylindrical, cylindrical or fusiform, sessile or stipitate, often obliquely inserted on peduncle, tapering towards the apex; *flowers* bisexual, naked; *ovary* 1- to partially 2-locular, lower part ± bilaterally compressed, upper part ± cylindrical and variously angled, most often rhombohexagonal, those upper- and lower-most on the spadix often sterile and bereft of stigma, those uppermost frequently either scattered or partially fused to each other and forming a rudimentary appendix; *ovules* few to many, anatropous, funicle long, placentae parietal to basal, sometimes ± subaxile, partial septa variably intrusive; *stylar region* well developed, usually broader than ovary, usually truncate apically, rarely elongate-conic; *stigma* sticky at female male anthesis, punctiform, broadly elliptic or oblong, orientation circumferential or longitudinal; *stamens* 4—6; *filaments* strap-shaped; *anthers* usually prominently exserted from between ovaries at male anthesis, rarely not exserted and pollen extruded from between ovaries, thecae dehiscing

by a longitudinal slit; *infructescence* with stylar regions greatly enlarged, transversely dehiscent, the abscission developing at the base of the enlarged to massive stylar region and this falling to expose the ovary cavity with the many seeds embedded in variously coloured sticky pulp; *seeds* oblong, testa thin, smooth, embryo axile, straight, endosperm copious; *pollen* dicolpate, extended monosulcate to fully zonate, ellipsoid or hamburger-shaped, medium-sized (mean 33 μm, range 24—55 μm) (Mayo *et al,* 1997), exine foveolate, subreticulate, rugulate, fossulate, scabrate, retiscabrate, verrucate, or psilate; *chromosomes* 2n = 60, 120 (42, 54, 56) (Mayo *et al,* 1997).

Distribution: About 100 species from tropical Africa, South and South East Asia, Australia and the Pacific with extensions into the subtropical Himalaya, southern China and the southernmost islands of Japan.

Habitat: Lianescent bole-climbers, lithophytes, rarely rheophytes, usually in well drained subtropical and tropical wet, humid, or seasonally moderately dry primary and established secondary evergreen forest at low to mid-montane elevations.

Etymology: Greek *rhaphis*, *rhaphidos* (needle) and *pherô* (I bear); refers to the macroscopic (to 1 cm long), needle-like unicellular trichosclereids present in tissues.

Key to Adult Flowering Rhaphidophora in Borneo

1a. Mature leaf lamina pinnately divided 2
1b. Mature leaf lamina entire, without or without perforations, but never pinnately divided 3

2a. Flowering plants usually rheophytic, rarely low-climbing on trees beside torrential streams. Plants always associated with sandy or rocky forest streams. ..... **1. R. beccarii**
2b. Flowering plants high-climbing on forest trees. Plants not specifically associated with watercourses ..... **7. R. korthalsii**

3a. Geniculum and abaxial surface of lamina pubescent 4
3b. Geniculum and abaxial surface of lamina glabrous 5

4a. Flowering on clinging stems. Leaves of mature plants extensively perforated. Active shoot tips with black mucilage .....

..... **6. R. foraminifera**

4b. Flowering on free lateral stems. Leaves of mature plants lacking or with only with scattered, perforations. Active shoot tips lacking black mucilage ..... **12. R. puberula**

5a. Leaves always shingling, even in flowering individuals; leaf laminas stiffly coriaceous, broadly oblong-ovate-elliptic, 8—48 x 6.5—20.5 cm, bright green, slightly to markedly glaucous, base truncate-cordate to broadly cuneate. Flowering on clinging shoots .....
..... **8. R. latevaginata**

5b. Leaves spreading in adult and flowering individuals; leaf laminas variously coloured but never glaucous. Flowering on free or clinging shoots 6

6a. Stems scabrid to asperous. Spathe exterior minutely puberulent ....
..... **9. R. lobbii**

6b. Stems smooth. Spathe exterior glabrous 7

7a. Clinging stems square or rectangular in cross-section; tips of active stems with netted prophyll, cataphyll and petiolar sheath fibre .....
..... **4. R. elliptica**

7b. Clinging stems variously shaped in cross-section, including square or rectangular; tips of active stems without fibres 8

8a. Spadix stipitate; leaf lamina thickly coriaceous.... **2. R. conocephala**

8b. Spadix sessile; leaf lamina variously textured but never thickly coriaceous 9

9a. Inflorescences two, three or more together, each subtended by a prominent chartaceous prophyll and one or more chartaceous cataphyll; leaf lamina oblong-lanceolate or oblong-elliptic, entire to slightly perforated, glabrous..... **10. R. megasperma**

9b. Inflorescences almost always solitary, if two together then inflorescences not subtended by prominent chartaceous prophylls and cataphylls; leaf lamina variously shaped and almost never perforated, if perforated then apical geniculum and abaxial surface of lamina pubescent..... 10

10a. Clinging stems rectangular in cross-section 11

10b. Clinging stems more-or-less terete in cross-section 12

11a. Leaf lamina lanceolate-elliptic to falcate-lanceolate, 4.5—32 x 1.75—8.5 cm. Spadix cylindric to weakly clavate-cylindrical, 3—6 cm long ..... **13. R. sylvestris**

11b. Leaf lamina narrowly elliptic to narrowly elliptic-oblong, 20—29 x 4.5—7 cm. Spadix cylindrical, c. 5 x 1 cm ..... **5. R. elliptifolia**

12a. Leaf lamina narrowly falcate-elliptic to falcate-lanceolate or falcate-oblanceolate, 2.5—16 x 1.2—3 cm, drying uniformly pale straw-coloured. Spadix slender cylindrical, 2.5—7 cm long ... **11. R. minor**

12b. Leaf lamina subfalcate-lanceolate or oblong-elliptic, oblique, 10—19.5 x 2.5—6.5 cm, drying very dark brown. Spadix cylindrical-obtuse, 3—10 x 1 cm (fruiting specimen only) ..... **3. R. cylindrosperma**

The Species

1. Rhaphidophora beccarii (Engl.) Engl.

Rhaphidophora beccarii (Engl.) Engl. in Bot. Jahrb. Syst. 1 (1881) 181 & in Beccari, Malesia 1 (1882) 270, Tab. xix 6—9; Engl. & K. Krause in Engl., Pflanzenr. 37 (IV.23B) (1908) 46; Alderw., Bull. Jard. Bot. Buitenzorg III, 1 (1920) 382; Merrill, J. Straits Branch Roy. Asiat. Soc., special number (1921) 88; Alderw., Bull. Jard. Bot. Buitenzorg III, 4 (1922) 341. — *Epipremnum beccarii* Engl., Bull. Soc. Tosc. Ortic. 4: 268 (1879). — Type: Malaysia, Sarawak, Kuching, Oct. 1865, *Beccari PB 833* (cited as '*832*' by Engler, 1879) (FI, holo).

Rhaphidophora borneensis Engl, *Araceae exsicc. et illustr. n.* 195 & in Bot. Jahrb. Syst. 7, Beibl. 15 (1886) 1. — Type: Indonesia, Kalimantan, Mindai to Pramassan, 19 June 1882, *H. Grabowski s.n.* (B†, BM).

Rhaphidophora fluminea Ridl., J. Straits Branch Roy. Asiat. Soc. 44 (1905) 186; Engl. & K. Krause in Engl., Pflanzenr. 37 (IV.23B) (1908) 37; Merrill, J. Straits Branch Roy. Asiat. Soc., special number (1921) 89. — Type: Malaysia, Sabah, Bongaya, Dec. 1897, *Ridley s.n.* (SING, holo).

Figure 1

Small to medium-sized, heterophyllous, sometimes homeophyllous, creeping rheophyte, very rarely short liane, to 75 cm; *seedling stage* a non-skototropic shingling shoot, soon becoming spreading-leafy; *pre-adult plant* initially with ± appressed shingle-leaves, later with leaves erect or spreading and at this stage plants resembling adults in all but overall size and leaf division;

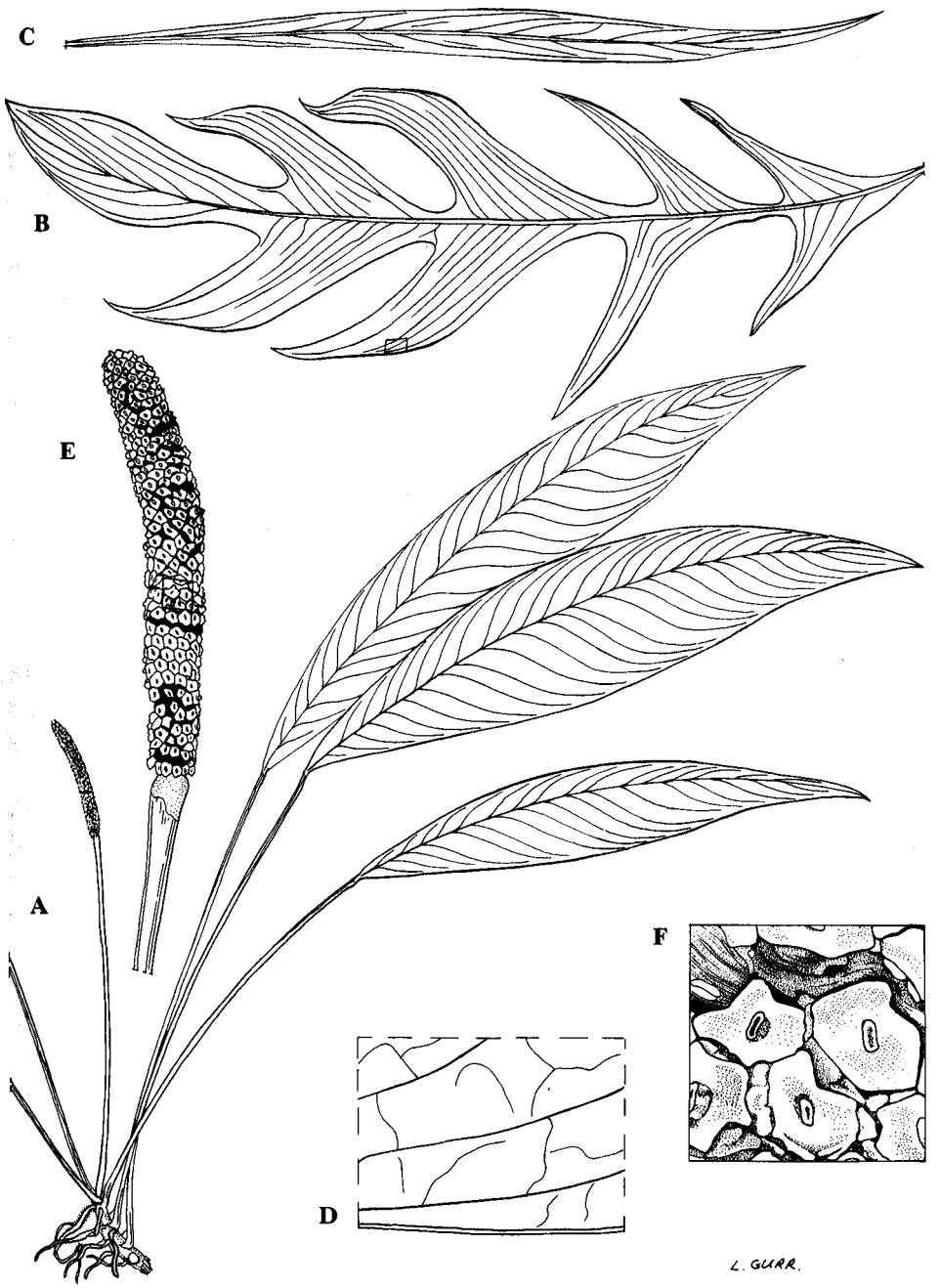

Figure 1. Rhaphidophora beccarii (Engl.) Engl.
A. habit x 1/4; B. leaf lamina x 1/4; C. leaf lamina x 1/4; D. venation detail x 4; E. inflorescence, spathe fallen x 1; F. spadix detail, post-female anthesis, pre-male anthesis x 8. A, E & F from *Stone 9637*; B & D from *Ridley s.n.*; C from *Kiew 1982*.

adult shoots clinging and flowering but main axis comprised of longer modules than axillary axes; *stems* smooth, mid- to dark green, with very sparse petiolar sheath fibre, internodes 1—7 x c. 1 cm, separated by variously prominent slightly oblique leaf scars; *flagellate foraging stems* absent; *clasping roots* very densely arising from the nodes and internodes of clinging stems, pubescent; *feeding roots* clinging, densely scaly; *leaves* distichous, appressed and shingling to erect or spreading and scattered on pre-adult shoots, tending to become distally clustered on adult shoots; *cataphylls and prophylls* membranous, soon drying and falling; *petiole* narrowly canaliculate to carinate, 8—31 x 0.3—1.5 cm, smooth, apical and basal genicula prominent; *petiolar sheath* prominent, extending to the apical geniculum, variably persistent and mostly degrading into semi-persistent weak fibres; *lamina* entire in seedling and pre-adult individuals, entire, pinnatipartite or pinnatisect in adult plants, narrowly lanceolate to oblong-elliptic, slightly oblique, 21—51 x 2—23 cm, subcoriaceous to slightly fleshy, base decurrent, apex acuminate with a moderately prominent apicule; *midrib* prominently raised abaxially, sunken adaxially; *primary venation* pinnate, raised abaxially, slightly impressed adaxially; *interprimaries* subparallel to primaries, slightly raised abaxially, ± flush adaxially, often forming a weak reticulum; *secondary venation* prominently reticulate, slightly raised; *tertiary venation* a network of broadly spaced tessellate veins arising at c. 90° from the midrib and crossing the primaries and interprimaries; *inflorescences* one to three together, subtended by a prominent cataphyll degrading to fibres before male anthesis; *peduncle* terete, 8—12 x 0.2—0.4 cm; *spathe* narrowly canoe-shaped, stoutly beaked, 6.5—7 x 1—1.5 cm, stiffly fleshy, greenish to dull white, soon falling at male anthesis; *spadix* cylindrical, sessile, inserted perpendicular to peduncle, 4.5—7 x 0.6—1 cm, dull whitish; *stylar region* rather well developed, mostly rhombohexagonal, c. 1—1.5 x 1—1.5 mm, truncate; *stigma* elliptic, longitudinally orientated, occasionally almost circular, c. 0.5 x 0.3 mm, often very prominent especially in dried material; *anthers* exserted at male anthesis; *infructescence* 7—9 x 1—2 cm, mid-green when ripe.

Distribution: Southern Thailand, Peninsular Malaysia, Sumatera (including the Lingga Archipelago) and Borneo (Sarawak, Brunei Darussalam, Sabah, West and East Kalimantan).

Habitat: Along rocky or sandy stream banks, often on rocks in stream or at waterfalls in primary to slightly disturbed or old secondary lowland forest, peatswamp forest, occasionally persisting briefly in logged over areas, occurring on a variety of substrates. Sea level to 300 m altitude.

Notes: 1. One of possibly two obligate rheophytic species (the other is *Rhaphidophora araea* P.C. Boyce - Sumatera), *R. beccarii* is immediately recognizable by its adult growth form, creeping along watercourses or attached on rocks in the water, and by the usually pinnately divided leaf laminas. Occasionally plants are seen climbing up tree trunks on the bank of torrential streams.

2. Although the pinnately divided leaf is typical of adult plants, entire leaved stenophyllous to lanceolate-leaved flowering plants are not rare. Such plants have been referred to as *R. fluminea* and occur either as pure stands or as mixed populations with the pinnate-leaved form. They are treated here as a neotenic manifestation of *R. beccarii*.

3. *Rhaphidophora borneensis*, based on a Grabowski specimen from Kalimantan, is a broad-leaved form of typical (i.e., divided-leaf) *R. beccarii*.

Other Bornean specimens seen: SARAWAK. 1st Div.: Setapok F.R., 6 miles south of Kuching, *Bogner 1507* (K, M); Sg. Entabai, *Bogner 1562* (M, US); Matang Family Park, Sg. Cina, *Boyce 719* (K); Lundu, *Brooke 8409* (L);13th Mile, Matang, *Brooke 9459* (L); Lundu, G. Gadin, *Clemens & Clemens 21934* (K); Matang F.R., 10 miles west of Kuching, *Nicolson 1282* (US); Setapok F.R., 6 miles south of Kuching, *Nicolson 1343* (L, US); Matang, *Ridley s.n.* (BM); Padawan, G. Merubong, Ulu Sg. Sluba, *Yii S51363* (K, L, SAR, US); 2nd Div.: Simanggang, *Brooke 10729* (BM, L); 3rd Div.: Kapit District, S. Bena area, *Burtt 13001, 12938* (E); 4th Div.: Lambir N.P., Mile 18, *Chai S39439* (K, KEP, L, SAR, US); 5th Div.: 8 - 9 miles from Limbang, Sg. Bakol, *Bogner 1504* (M, US); 7th Div.: En route (survey highway) from Sg. Mah to Sg. Shinonok, Ulu Sg. Minah, Bintulu District, *Hirano & Hotta 14082* (KYO); Sg. Bejangung, a branch of the Sg. Anap, Bintulu District, *Hirano & Hotta 1174* (KYO); not located: Sg. Entabai, *Bogner 1346* (K, M, US); Sg. Engkramut, *Bogner 1393* (M, US). BRUNEI DARUSSALAM. Belait: Labi, Kg. Teraja, path along Sg. Teraja, *Boyce 245* (BRUN, K, L); Temburong: Sg. Temburong at Kuala Belalong, *Boyce 396* (BRUN, K, L); Sg. Temburong near Kuala Belalong, *Jacobs s.n.* (BRUN, K, L); Sg. Temburong, just downstream from Kuala Belalong, *Wong 242* (BRUN, K, L). SABAH. Kudat: Ranau, Kg. Puas area, *Amin et al. SAN 94681* (K, KEP, L, SAN, SAR, SING); Pantai Barat: Keningau, Ulu Sg. Pingas Pingas, *Jimpin SAN 122024* (K, KEP, SAN); Keningau, Shang Lian logging area, Lanas, *Krispinus SAN 118444* (K, SAN); Keningau, Camp C area, Tiulan, *Lantoh SAN 102053* (K, KEP, L, SAN); Keningau, Ulu Sg. Matud, *Tangki SAN 119596* (K, L, SAN, SAR); Sandakan: Lamag, Ulu Sg. Lokan, *Aban & Petrus SAN 90675* (K, SAN); Sg. Lokan, *Amin et al. SAN 97483* (K, L, SAN, SAR); VJH 45 A Lungmanis, *Dewol et al. SAN 118075* (K, KEP, L, SAN); Beluran, Sg. Baba *Gibot SAN 90040* (K, L, SAN); Labuk and Sugut, western side of Bt. Doji and pass way from Telupid to Ulu Karamuak, *Kokawa & Hotta 471* (KYO, L); Telupid, Labuk and Sugut, along Sg. Meliau, foot of G. Tawai, *Kokawa & Hotta 110* (KYO, L); Mile 45 Labuk road, *Meijer SAN 44014* (K, L, SAN); KALIMANTAN. West Kalimantan: Selimban Kapuas, *Main (sub. Polak) 2092* (L); Bt. Ubili, *Nieuwenhuis 97* (BO); East Kalimantan: W. Koetai, No. 29 near L. Liah Leng, *Endert 3013* (BO, K, L); W. Koetai, No. 5 near Lahoem, *Endert 1860* (BO, K, L); Kelassar (Kelasen?), *Hallier 1555* (BO); Pulau Nibung, W. Koetai, Sg. Loewai, near Padang Loewai, *Posthumus 2173* (BO); Samarinda, mouth of Batang Mahakam, Sg.

Mukun, near Sanga Sanga, *Meijer 1136* (BO, L); No further data, *Hallier 999* (BO); Batu Lesoena, *Nieuwenhuis 219* (BO).

2. Rhaphidophora conocephala Alderw.

Rhaphidophora conocephala Alderw., Bull. Jard. Bot. Buitenzorg III, 1 (1920) 384. — Type: Indonesia, Sumatera, North Sumatera, Sibolangit, 10 May 1917, *Lörzing 5137* (BO, holo; K, L, iso).

Figure 2

Large, moderately robust, semi-pachycaul homeophyllous liane to 15 m; *seedling stage* a non-skototropic shingling shoot; *pre-adult plants* forming small terrestrial colonies of appressed shingling shoots; *adult shoot architecture* comprised of elongated, clinging, physiognomically unbranched, leafy, non-flowering stems and moderately elaborated, free, moderately leafy, flowering stems; *stems* smooth, climbing stems rectangular in cross-section, free stems more or less terete to very weakly four-angled in cross-section, larger shoot systems pendent under their own weight, without prophyll, cataphyll and petiolar sheath fibre, internodes to 7 x 1.5 cm on clinging shoots, shorter and less stout on free shoots, separated by prominent oblique leaf scars, older stems woody; *flagellate foraging stems* absent; *clasping roots* densely arising from the nodes and internodes of clinging stems, densely pubescent; *feeding roots* rare, clinging, pubescent; *leaves* weakly spiralled on clinging shoots, slightly scattered-distichous on flowering shoots; *cataphylls and prophylls* membranous, very soon drying and falling; *petiole* shallowly canaliculate adaxially, 4—7 x 0.1—0.2 cm, smooth, with a slight apical and rather prominent basal geniculum; *petiolar sheath* prominent, extending to and encircling the apical geniculum, very soon drying and falling to leave a thin continuous scar from the petiole base, around the top of the apical geniculum and back to the base, occasionally newest leaves with parchment-like sheath remain briefly adherent; *lamina* entire, falcate-lanceolate to falcate-oblong or falcate-oblanceolate, 10—29.5 x 1.5—7 cm, coriaceous, upper surfaces slightly glossy, lower surfaces less so, base minutely cordate to subovate to acute or briefly decurrent, apex subacute with a prominent apiculate apicule, margins slightly revolute in dried material; *midrib* raised abaxially, very slightly sunken adaxially; *primary venation* pinnate, raised abaxially and adaxially; *interprimaries* parallel to primaries, slightly raised abaxially and adaxially; *secondary* and *tertiary venation* slightly raised in dried specimens; *inflorescence* solitary, subtended either by a fully developed foliage leaf or by one or more subfoliar (i.e., developed petiole but atrophied lamina) cataphyll; *peduncle* slightly compressed-cylindric, 3—6 x 0.3—0.5 cm; *spathe* cigar-shaped,

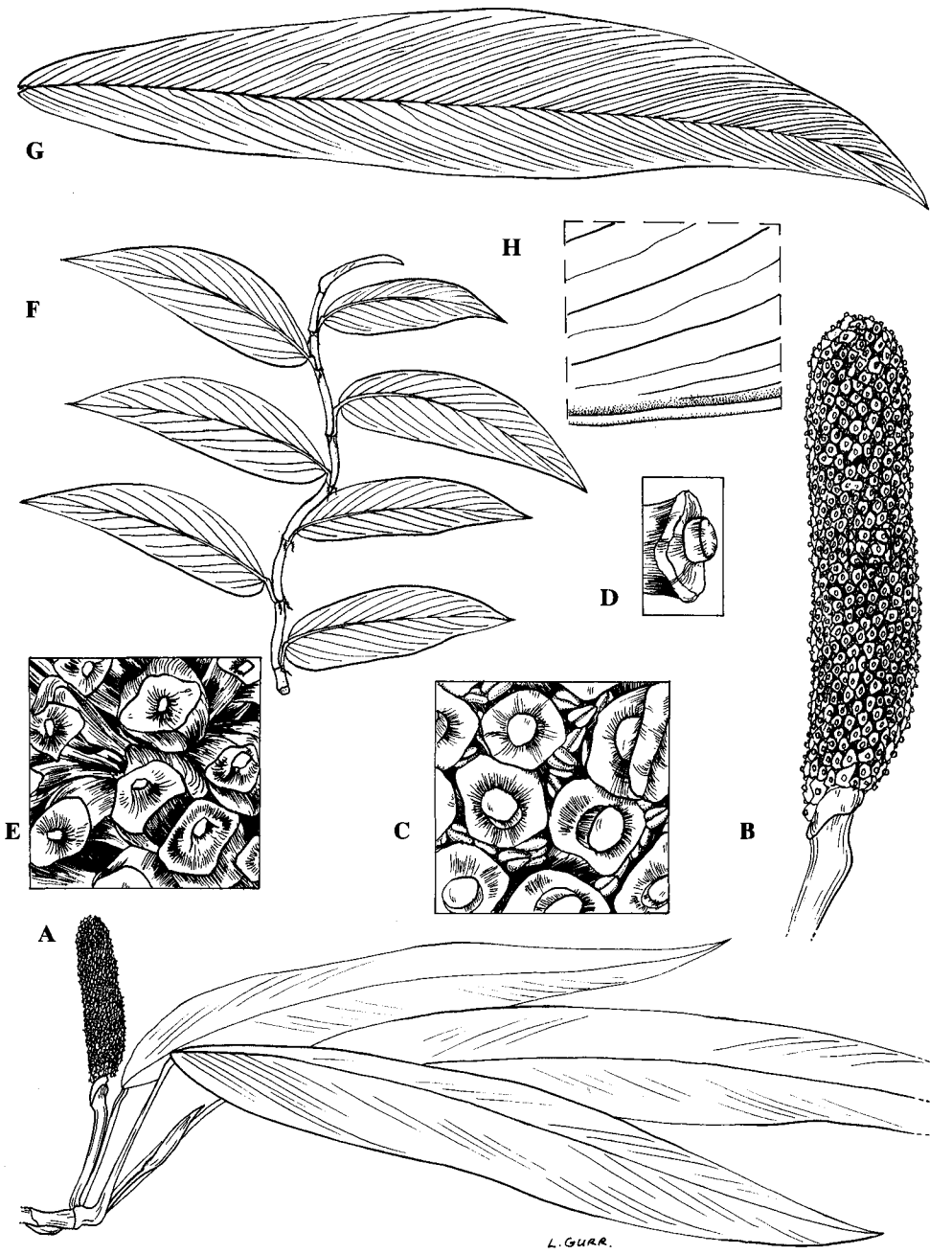

Figure 2. Rhaphidophora conocephala Alderw.
A. flowering shoot x $^1/_2$; B. inflorescence, spathe fallen x $1^1/_2$; C. spadix detail, female anthesis x 10; D. gynoecium, three quarter view x 6; E. spadix detail, post-male anthesis x 10; F. portion of pre-adult sterile shoot x $^1/_3$; G. leaf lamina x $^1/_2$; H. venation detail x 3. A – E, G. & H from *Nur SFN 7369*; F from *Lörzing 11750*.

stoutly short-beaked, 7—9.5 x 2—3.5 cm, thickly fleshy, exterior light yellow, interior darker, soon (?) falling at female anthesis; *spadix* cylindrical to slightly clavate, very shortly stipitate, light yellow, 4—5.3 x 1.2—1.5 cm; *stipe* c. 2 mm long; *stylar region* well developed, mostly rounded to rhombohexagonal, 1.2—1.3 x c. 1.2 mm, conical; *stigma* conspicuously raised-punctiform, c. 0.2 mm diam.; *anthers* slightly exserted at male anthesis; *infructescence* stoutly cylindrical, 6.5—7.5 x 1.8—2 cm.

Distribution: Sumatera, Kalimantan (East) and into the Philippines (Palawan).

Habitat: Damp primary and old secondary forest. 450—1000 m altitude.

Note: Very close to and possibly indistinguishable from *Rhaphidophora sylvestris* but consistent in the conical style topped with a prominent, raised button-like stigma and the notably more coriaceous leaves.

Other Bornean specimens seen: KALIMANTAN. East Kalimantan: Batu Penalong, Mahakam, *Wiriadinata 850* (BO, L).

3. Rhaphidophora cylindrosperma Engl. & K. Krause

Rhaphidophora cylindrosperma Engl. & K. Krause, Pflanzenr. 37 (IV.23B) (1908) 28; Merrill, J. Straits Branch Roy. Asiat. Soc., special number (1921) 88. — Type: Indonesia, northern West Kalimantan, between the greater and lesser arms of the S. Sambar, *Hallier 1164* (BO, holo).

Figure 3

Moderate leptocaul homeophyllous liane to unknown ultimate height; *seedling stage* and *pre-adult plants* not observed; *adult shoot architecture* not fully observed, flowering stems, moderately branched and leafy, apparently pendent; *stems* smooth, terete, with cataphylls and prophylls soon falling, internodes 2—3.5 x 0.8—1.2 cm, separated by prominent straight to slightly oblique leaf scars; flagellate *foraging stem* not observed; *roots* not observed; *leaves* spiro-distichous; *cataphylls and prophylls* membranous, soon falling; *petiole* canaliculate, 5—14 x 0.2—0.4 cm, basal geniculum very large and prominent, apical geniculum less so; *petiolar sheath* narrow and not prominent, extending to apical geniculum, ± short-persistent; *lamina* entire, subfalcate-lanceolate or oblong-elliptic, oblique, 10—19.5 x 2.5—6.5 cm, membranous, base acute, apex acuminate; *midrib* prominently raised abaxially, slightly impressed adaxially; *primary venation* pinnate, prominently raised abaxially, impressed adaxially; *interprimaries*

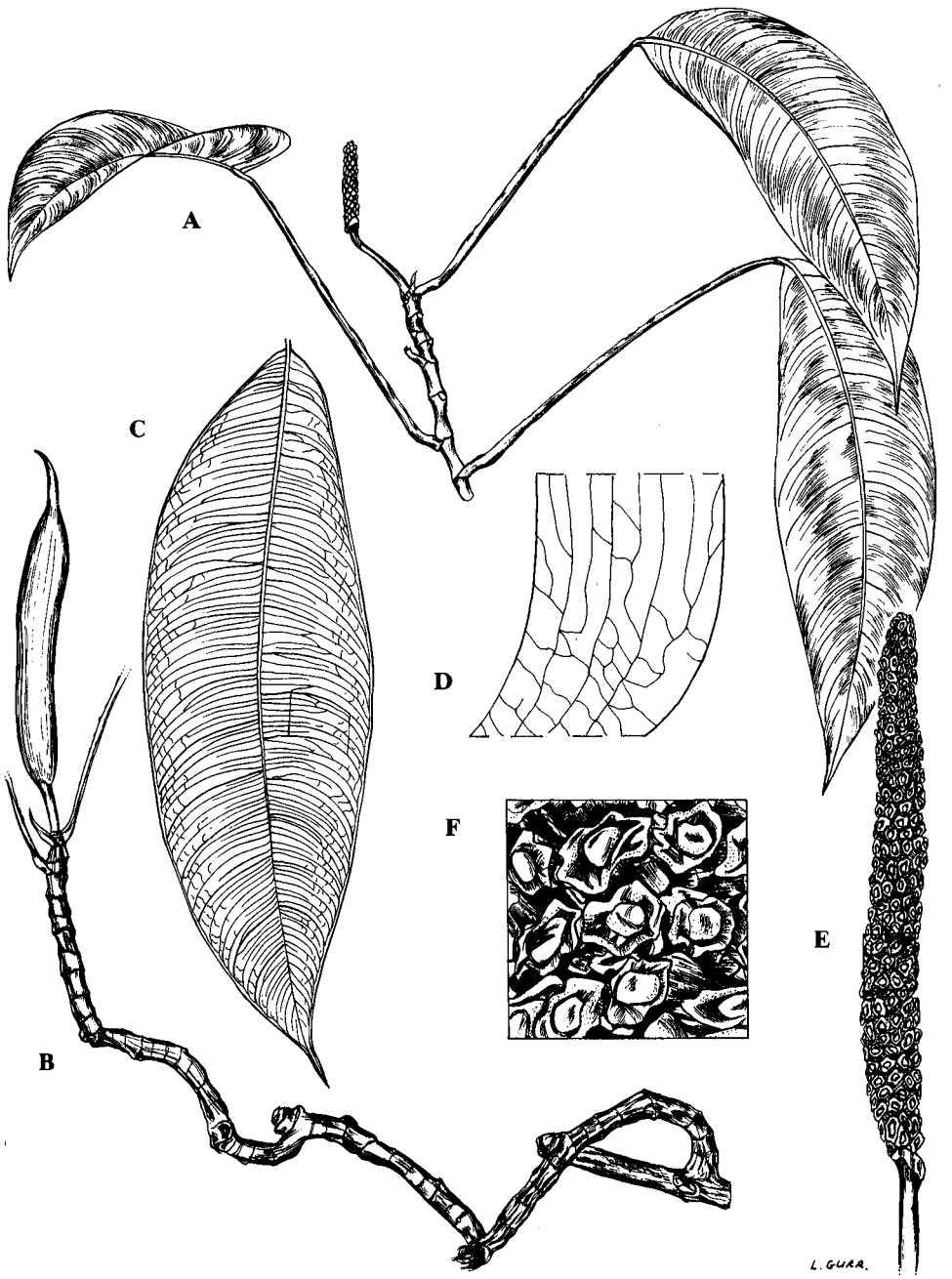

Figure 3. Rhaphidophora cylindrosperma Engl. & K. Krause
A. flowering shoot x $^1/_3$; B. flowering shoot x $^1/_2$; C. leaf lamina x $^3/_4$; D. venation detail x 2; E. inflorescence, spathe fallen x 1; F. spadix detail, post-male anthesis x 6. A, C – D from *Church et al. 1573*; B, E – F from *Sidiyasa PBU 650*.

subparallel to primaries, slightly less prominent; *secondary venation* reticulate, slightly raised abaxially; *inflorescence* solitary, subtended by a ± fully developed foliage leaf and one or more cataphylls; *peduncle* terete, 2—4 x 0.3—0.4 cm; *spathe* slender, 9—11 x 0.5 cm, apically tapering and ultimately stout beaked; *spadix* cylindrical-obtuse, sessile, inserted ± on peduncle, 3—10 x 1 cm (fruiting specimen only); *stylar region* moderately developed, slightly rhombohexagonal, c. 1.8 mm diam., ± truncate; *stigma* punctiform, raised, c. 0.3 mm diam.; *anthers* not observed; *infructescence* 3—10 x 1—1.5 cm.

Distribution: Endemic to Borneo. Sarawak (1st Division), Brunei Darussalam (Belait), Kalimantan (West, Central and East).

Habitat: Lowland primary to lightly disturbed forest. 25—200 m altitude.

Notes: 1. Superficially similar to *Rhaphidophora puberula* but differing in leaves completely glabrous and never perforated, by the smaller, more slender spadix and in flowering on long, free shoots.

2. Among the Sundaic Asian species, it is not immediately apparent to what *R. cylindrosperma* is related. The superficial similarity to species in the Hookeri Group (e.g., *R. puberula and R. foraminifera*) is not borne out by closer examination. The growth form with inflorescences often carried at the tips of short shoots arising from much longer pendent stems is reminiscent of *R. lobbii*, but *R. cylindrosperma* differs in more coriaceous leaves, different leaf venation and in having a longer, externally glabrous spathe. The long, pendent terete stems with upturned tips and small leaves recall some New Guinea species, in particular *R. schlechteri* K. Krause and I have provisionally included *R. cylindrosperma* in the Neoguineensis Group to which those species are assigned (see Boyce 2000a).

3. *Boyce 345* is provisionally included in *R. cylindrosperma* although it has much more coriaceous leaf laminas with closer venation. It may represent an undescribed species but the material is inadequate to make a decision.

Other specimens seen: SARAWAK. 1st Div: Kuching, *Hewitt s.n.* (SING). BRUNEI DARUSSALAM. Belait: Sg. Deriam, *Boyce 345* (BRUN, K, L). KALIMANTAN. West Kalimantan: Serawai, 8 km NE of Desa Jelundung, Batu Lintang, 1 km S of camp along hunting trail, *Church, Mahyer & Afriastini 1573* (BO, E, GH, K); Bt. Raya, *Nooteboom 4327* (BO, L); Central Kalimantan: Barito Ulu, P.T. Pamenang logging concession road, km 20, *Sidyasa PBU 650* (BO, K, L); East Kalimantan: Wanriset research area, road Balikpapan to Samarinda, km 15, Sg. Wain area, *Ambri & Arifin 354* (BO, L, K).

4. Rhaphidophora elliptica Ridl.

Rhaphidophora elliptica Ridl., J. Straits Branch Roy. Asiat. Soc. 44 (1905) 186; Engl. & K. Krause in Engl., Pflanzenr. 37 (IV.23B) (1908) 39—40; Merrill, J. Straits Branch Roy. Asiat. Soc., special number (1921) 88. — Type: Malaysia, Sarawak, 1st Div., Bau, July 1903, *Ridley* s.n. (SING, holo).

Figure 4

Large, occasionally very large, robust, pachycaul homeophyllous liane to 30 m; *seedling stage* a non-skototropic shingling shoot; *pre-adult plants* occasionally forming small terrestrial colonies of appressed shingling shoots; *adult shoot architecture* comprised of greatly elongated, clinging, physiognomically unbranched, leafy, non-flowering stems and long, moderately elaborated, free, leafy, flowering stems later pendent under their own weight; *stems* smooth, climbing stems broadly rectangular in cross-section, the angles often slightly winged, the surfaces between convex, free stems spreading, rectangular in cross-section, branching, growing to considerable lengths, green, later mid-brown, without fibre at the tips of active shoots, internodes to 16 x 1—2.5 cm on clinging shoots, usually shorter and less stout on free shoots, separated by large oblique leaf scars, older stems woody; *flagellate foraging stems* frequent, often of great length, ± rectangular in cross-section; *clasping roots* densely arising from the nodes and internodes of clinging stems, densely pubescent; *feeding roots* rare, clinging, pubescent; *leaves* distichous and ascending on clinging and free shoots; *cataphylls and prophylls* membranous, very soon drying and falling; *petiole* deeply grooved adaxially, 10—21.5 x 0.2—1 cm, smooth, apical and basal geniculа weakly defined; *petiolar sheath* very prominent but soon falling, extending to and encircling the apical geniculum, ligulate, very soon drying and falling to leave a continuous conspicuous scar from the petiole base, around the top of the apical geniculum and back to the base; *lamina* entire, elliptic to elliptic-lanceolate or falcate-oblong, weakly channelled along midrib, 16—25 x 2.5—8 cm, coriaceous, upper surfaces semi-glossy, lower surfaces semi-matt, base subacute to rounded or very slightly cordate, apex subacute with a somewhat prominent apiculate apicule, margins very slightly revolute in dried material; *midrib* raised abaxially, slightly sunken adaxially; *primary venation* pinnate, slightly raised abaxially and adaxially but barely visible in fresh material; *interprimaries* parallel to primaries and only slightly less prominent, very slightly raised abaxially and adaxially, ± obscure in fresh material; *secondary* and *tertiary venation* ± obscure in fresh material, visible as a very faint reticulum in dried specimens; *inflorescence* solitary, subtended by a fully developed foliage leaf and one or more membranous, soon falling cataphylls; *peduncle*

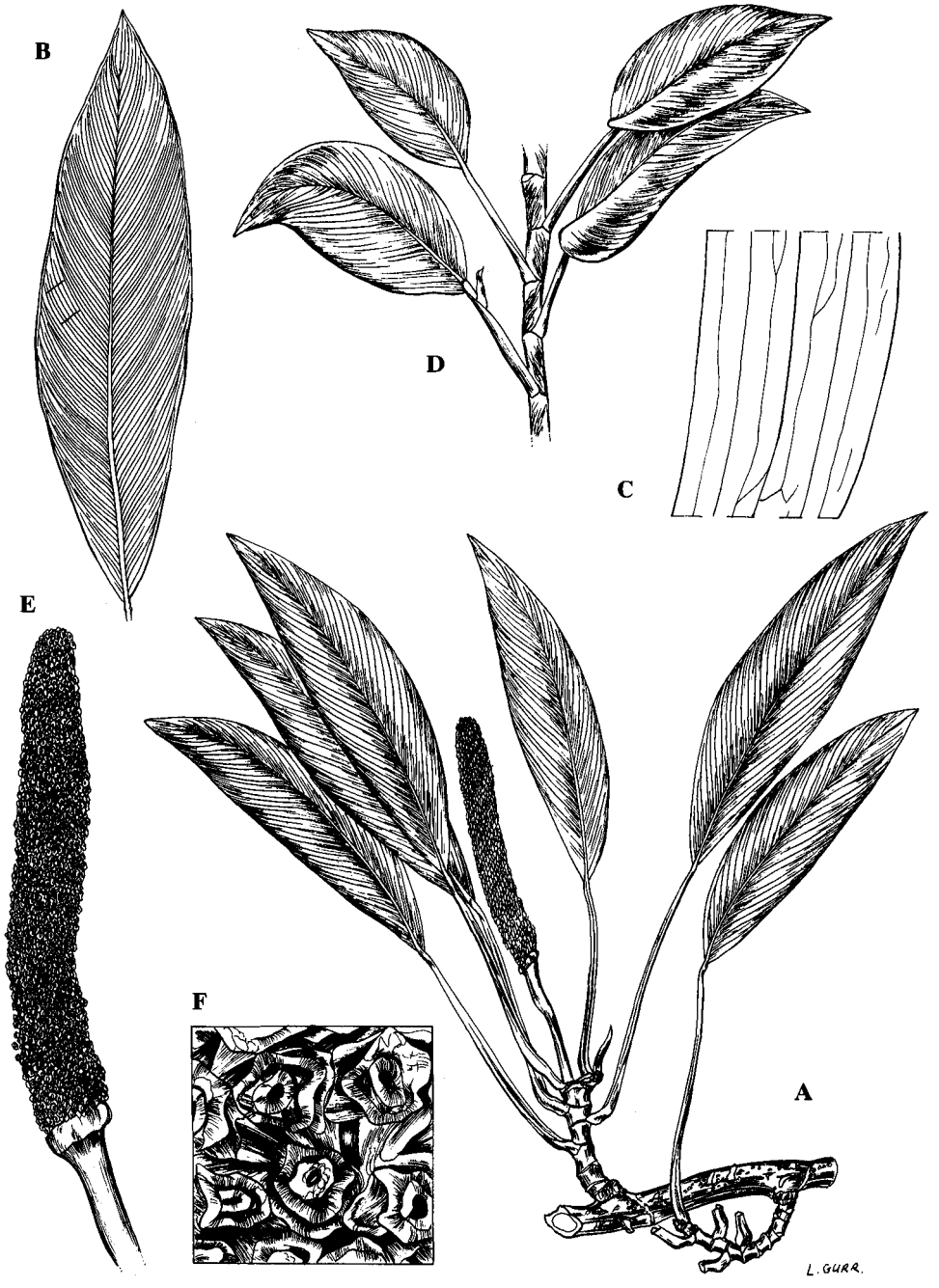

Figure 4. Rhaphidophora elliptica Ridl.
A. flowering shoot x $^{2}/_{9}$, B. leaf lamina x $^{1}/_{3}$; C. venation detail x 3; D. portion of adult sterile stem x $^{1}/_{6}$; E. inflorescence, spathe fallen x $^{1}/_{2}$; F. spadix detail, post-male anthesis x 4. A – C, E – F from *Mamit S 37665*; D. from Kew LCD acc. no. 1965-49804.

compressed-cylindric, 4—11 x 0.3—0.5 cm; *spathe* canoe-shaped, stoutly very short-beaked, 6.5—16 x 2—3.5 cm, thickly stiff-fleshy, dull yellow, paler internally, soon falling at female anthesis; *spadix* tapering-cylindrical, ± sessile, inserted level on peduncle, 8—14 x 1.5—2 cm; *stylar region* weakly rhombohexagonal, 1.8—2.2 x 1.9—2.1 mm, ± truncate; *stigma* punctiform, raised, c. 0.3 mm diam.; *anthers* barely exserted at male anthesis, pollen extruded from between ovaries; *infructescence* 10—15 x 2—2.5 cm.

Distribution: Endemic to Borneo. Sarawak (1st and 3rd Divisions), Brunei Darussalam (Muara, Temburong), Sabah (Sandakan).

Habitat: On trees and cliffs in primary to disturbed primary lowland dipterocarp and swamp forest, on a variety of substrates including limestone and shale. Sea level to 115 m altitude.

Notes: 1. Boyce (1999) treated *Rhaphidophora elliptica* as a synonym of *R. montana,* and comparison of the description above with that of *R. montana* will reveal rather few morphological differences. However, more detailed study of *R. elliptica* has demonstrated subtle but consistent differences between it and *R. montana* such that I am now recognizing the Bornean plants to be a distinct, endemic species. In particular, *R. elliptica* is distinctive in having the leaves distichous and ascending with the lamina shallowly channelled along the midrib (leaves spiro-distichous and spreading with the lamina flat in *R. montana*) and in having clinging stems considerably wider then deep (c. 4:1 v. c. 2:1 in *R. montana*). These differences, so obvious in the field, are almost completely obscured in herbarium specimens unless, as is seldom the case, they are recorded by comprehensive field data.

2. *Rhaphidophora elliptica* belongs to the taxonomically difficult the Hongkongensis Group defined by clinging, occasionally free, stems square to rectangular in cross-section, by simple, rather stiff leaves and conspicuous, membranous ligulate petiolar sheaths extending to the apical geniculum and soon falling to leave a horseshoe-shaped scar at the junction of the petiole and lamina. The use of traditional herbarium morphology has proved a woefully unsatisfactory method for delimiting species in this group and it is hoped that the establishment of an alpha-taxonomy will provide a stimulus for further study of the complex using macromolecular data, field observations and morphometric techniques.

Other specimens seen: SARAWAK. 1st Div.: Along road between Kuching and Padawan, 10 miles SW of main Kuching - Serian highway *Croat 53186* (MO); Kuching, Setapok F.R.,

Mamit S 37665 (K, KEP, L, US); One mile west of Bau, *Nicolson 1293* (US); Setapok F.R., 6 miles south of Kuching, *Nicolson 1348* (US); Bau, *Purseglove 4473* (K, L, SING); 3rd Div.: Kapit, Upper Batang Rejang, *Clemens & Clemens 21929* (GH, K, MO). BRUNEI DARUSSALAM. Muara: *Hotta 13214* (KYO, L); Temburong: Batu Apoi F.R., ridgetop west of Kuala Belalong Field Studies Centre, *Poulsen 150* (AAU, BRUN, K). SABAH. Sandakan: Sg. Lantoh, *Lantoh SAN 87848* (K, KEP, L, SAN, SAR); Kinabatangan Road, Batu Puteh, Pin-Supu F.R., Bt. Supu, *Lim et al. LSP 766* (SAN, SING).

5. Rhaphidophora elliptifolia Merr.

Rhaphidophora elliptifolia Merrill, J. Straits Branch Roy. Asiat. Soc., special number (1921) 88. — [*Rhaphidophora elliptica* Ridl., J. Straits Branch Roy. Asiat. Soc. 49 (1908) 52, *nom. illeg.*, *non* Ridl. (1905)]. — Type: Malaysia, Sarawak, 1st Div., Kuching, Oct. 3 1905, *Hewitt* 12 (SING, holo).

Figure 5

Large, robust, pachycaul homeophyllous liane to 10 m; *seedling stage* a non-skototropic shingling shoot; *pre-adult plants* occasionally forming small terrestrial colonies of appressed shingling shoots; *adult shoot architecture* comprised of greatly elongated, clinging, physiognomically unbranched, leafy, non-flowering stems and long, moderately elaborated, free, densely leafy, flowering stems; *stems* smooth, climbing stems prominently rectangular in cross-section, the surfaces slightly convex, free stems spreading, irregularly four-angled in cross-section, sometimes irregularly terete, with untidy prophyll, cataphyll and petiolar sheath fibre at the tips of active shoots, internodes to 7 x 1.5 cm on clinging shoots, shorter and less stout on free shoots, separated by large oblique to almost straight leaf scars, older stems sub-woody; *flagellate foraging stems* not observed (absent?); *clasping roots* densely arising from the nodes and internodes of clinging stems, pubescent; *feeding roots* rare, clinging, pubescent; *leaves* spiro-distichous on clinging and free shoots; *cataphylls and prophylls* membranous, soon drying and degrading into netted and tangled fibres; *petiole* deeply channelled adaxially, 10—13 x 0.3—0.4 cm, smooth, apical geniculum well defined, basal genicula rather weakly defined; *petiolar sheath* prominent, extending to and encircling the apical geniculum, briefly ligulate, soon drying and degrading into netted fibres, eventually falling to leave a continuous slight scar from the petiole base, around the top of the apical geniculum and back to the base; *lamina* entire, narrowly elliptic to narrowly elliptic-oblong, 20—29 x 4.5—7 cm, coriaceous, upper surfaces semi-glossy, lower surfaces matt, base acute to decurrent, apex attenuate with a slight apiculate apicule, margins revolute in dried material; *midrib* raised abaxially, sunken adaxially; *primary venation* densely pinnate, raised abaxially and adaxially; *interprimaries* parallel to primaries and barely less prominent,

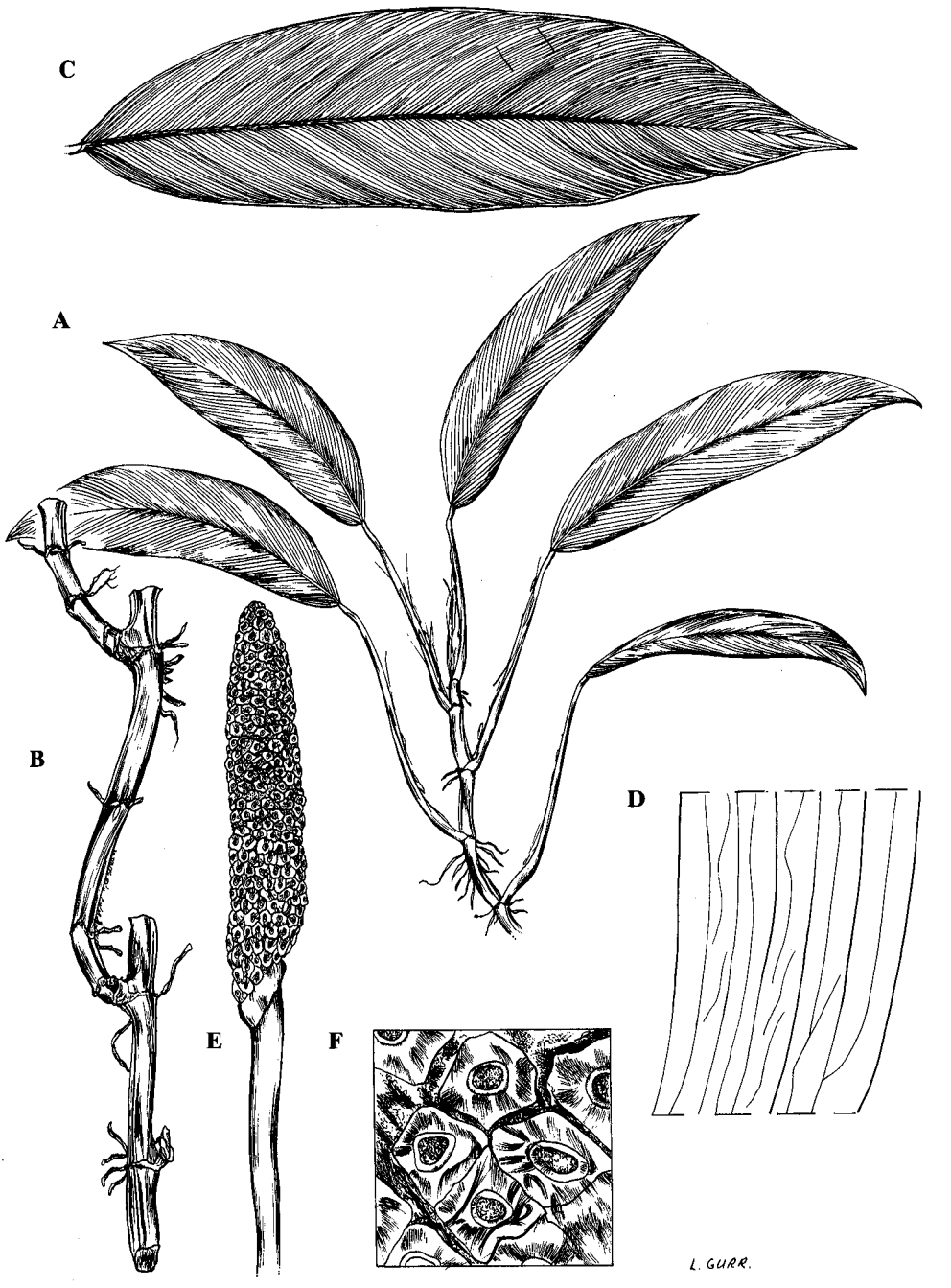

Figure 5. Rhaphidophora elliptifolia Merr.
A. portion of adult sterile stem x $^{2}/_{9}$; B. portion of older, leafless stem x $^{1}/_{3}$; C. leaf lamina x $^{1}/_{2}$; D. venation detail x 4; E. inflorescence, spathe fallen x 1; F. spadix detail, post-female anthesis, pre-male anthesis x 8. A & B from *Meijer 2101*; C – F from *Hewitt s.n.*

slightly raised abaxially and adaxially; *secondary* and *tertiary venation* ± obscure in fresh material, visible as a very faint reticulum in dried specimens; *inflorescence* solitary, subtended by a fully developed foliage leaf and netted petiolar sheath, prophyll and cataphyll fibre; *peduncle* compressed-cylindric, 5.5 x 0.3 cm; *spathe* broadly canoe-shaped, stoutly short-beaked, 6—6.5 x 2—2.5 cm, thickly stiff-fleshy, dull yellow, persistent into early fruiting; *spadix* cylindrical, ± sessile, inserted level on peduncle, c. 5 x 1 cm; *stylar region* rhombohexagonal, 1.7—2 x 1.7—2 mm, truncate; *stigma* rounded, raised, c. 0.3 mm diam.; *anthers* not exserted at male anthesis; *infructescence* c. 7 cm long (known from partial material only).

Distribution: Endemic to Borneo. Sarawak (1st Division), Kalimantan (East).

Habitat: Primary dipterocarp forest. Less than 100 m altitude.

Notes: 1. *Rhaphidophora elliptifolia* resembles Peninsular Malaysian/ Sumateran *R. maingayi* (see Boyce, 1999) in the persistent fibrous remains at the tips of active stems and the stems rectangular in cross-section, but differs in the smaller inflorescences (12—22 v. 6—6.5 cm), the spathe persistent into fruiting and the narrower, more coriaceous leaves. *Rhaphidophora elliptifolia* replaces *R. maingayi* in Borneo.

2. Confusion with *R. elliptica* is possible, although the smaller inflorescences and persistent fibre at the shoot tips readily distinguish *R. elliptifolia.*

Other specimens seen: SARAWAK. No further data, *Hewitt s.n.* (SING). KALIMANTAN. East Kalimantan, Pulau Nunukan, north of Tarakan, *Meijer 2101* (L, BO).

6. Rhaphidophora foraminifera (Engl.) Engl.

Rhaphidophora foraminifera (Engl.) Engl., Pflanzenr. 37 (IV.23B) (1908) 45; Alderw., Bull. Jard. Bot. Buitenzorg III, 4 (1922) 197. — *Epipremnum foraminiferum* Engl. in Bot. Jahrb. Syst. 25 (1898) 11. — Neotype: Malaysia, Perak, Taiping, base of Maxwell's Hill Station road, *Nicolson 1047* (US, neo; L, BH, BO isoneo; designated by Boyce, 1999).

Figures 6 & 7

Moderate to large, robust, pachycaul, homeophyllous liane to 15 m; *seedling stage* not observed; *pre-adult plants* frequently (always?) forming extensive terrestrial colonies; *adult shoot architecture* comprised of elongated, clinging, physiognomically unbranched, densely leafy, non-flowering (always?) stems and shorter clinging, densely leafy, flowering stems; *stems* smooth, mid-

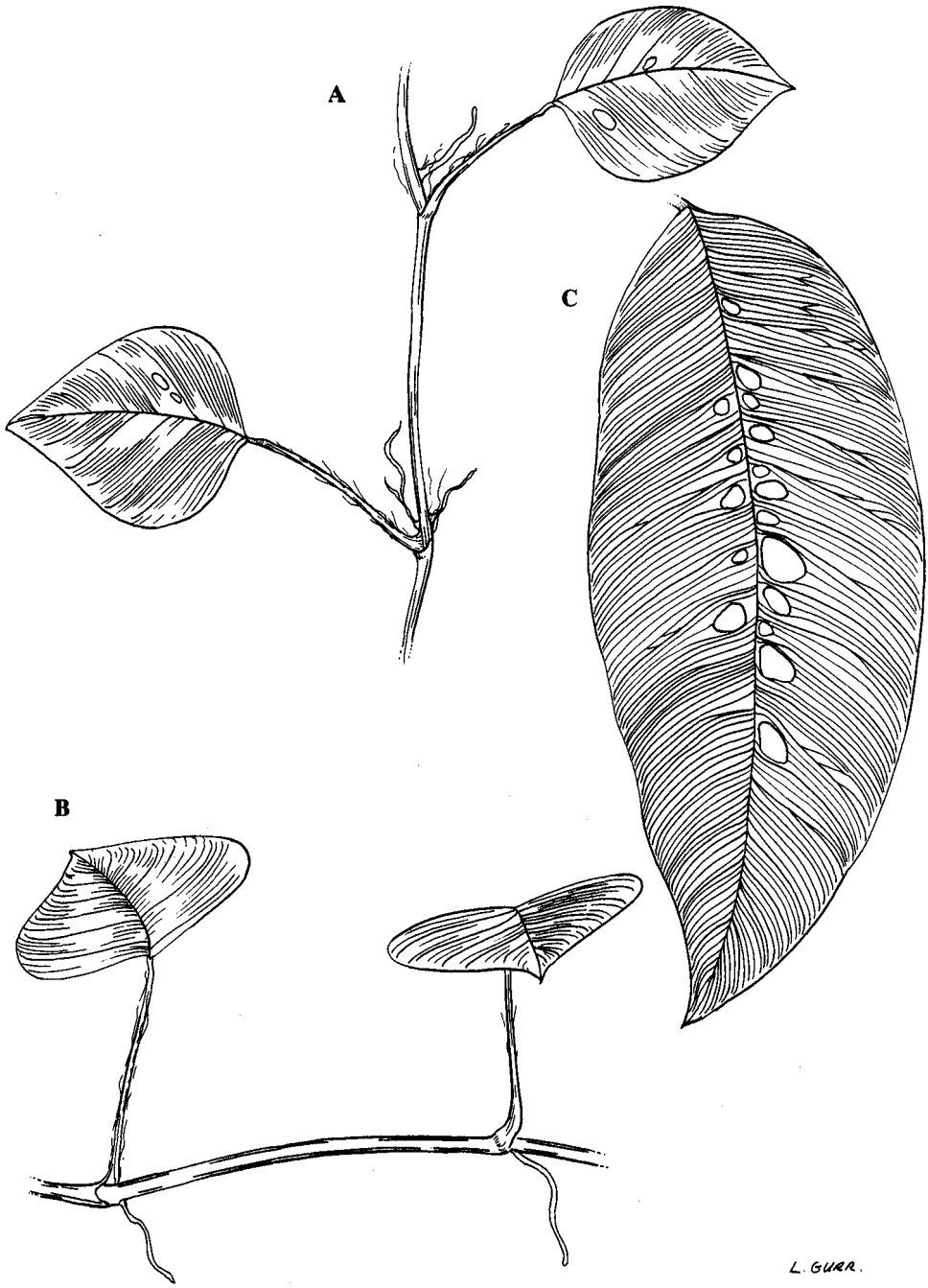

Figure 6. Rhaphidophora foraminifera (Engl.) Engl.
A. pre-adult climbing shoot x $^1/_4$; B. pre-adult terrestrial shoot x $^1/_3$; C. leaf lamina x $^1/_4$. A & B from *Nicolson 941*; C from *Boyce 722*.

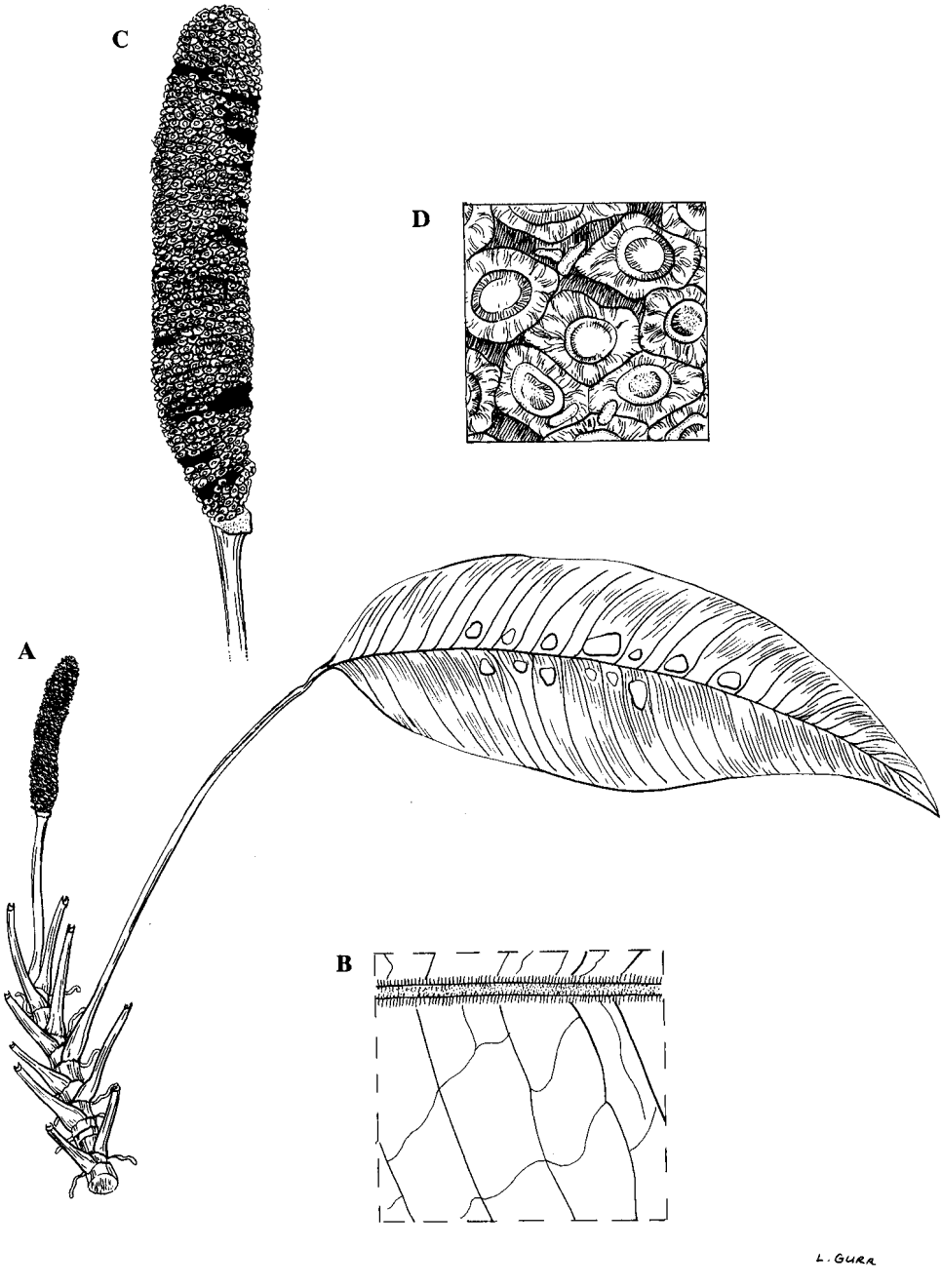

Figure 7. Rhaphidophora foraminifera (Engl.) Engl.
A. flowering shoot x $^{2}/_{15}$; B. venation detail x 6; C. inflorescence, spathe fallen x $^{2}/_{3}$; D. spadix detail, male anthesis x 6. A, C & D from *Boyce 722*; B from *Croat 53118*.

green, with cataphylls and prophylls deliquescing to black mucilage drying to leave fragmentary parchment-like remains on petioles, developing laminas, inflorescences, internodes 1—7 x 0.5—3.5 cm, separated by prominent straight to slightly oblique leaf scars; *flagellate foraging stem* absent; *clasping roots* densely arising from the nodes and internodes, pubescent; *feeding roots* clinging, exceedingly robust, densely pubescent with dense verticils of prominent corky ramenta; *leaves* distichous; *cataphylls and prophylls* membranous, soon deliquescing; *petiole* canaliculate, 22—52 x 0.4—1 cm, smooth for the most part but upper 2—4 cm and apical geniculum densely pubescent, apical geniculum prominent, basal geniculum less so; *petiolar sheath* prominent, extending to apical geniculum, ± short-persistent, degrading to weak, slightly netted fibres; *lamina* entire to slightly or extensively perforated, perforations round to rhombic, extending c. + of lamina width on each side of the midrib, ovate to oblong-lanceolate or oblong-elliptic, slightly oblique, pubescent abaxially when young, 7—53 x 6—19 cm, membranous to subcoriaceous, base rounded, acute to slightly decurrent, apex acute to acuminate; *midrib* prominently raised and densely pubescent abaxially, ± flush adaxially; *primary venation* pinnate, slightly raised abaxially and adaxially, the leaf appearing slightly quilted, pubescent in younger leaves, this indumentum mostly shed in older leaves; *interprimaries* subparallel to primaries, less prominent, slightly raised abaxially, slightly impressed adaxially; *secondary venation* reticulate, slightly raised; *tertiary venation* tessellate, slightly raised; *inflorescence* mostly subtended by one or two large cataphylls, these soon deliquescing into black mucilage, this drying and adhering patchily to developing spathe, rarely subtended by a ± fully developed foliage leaf; *peduncle* terete, 3—13 x 0.5—1.5 cm; *spathe* canoe-shaped, stoutly beaked, 10—27 x 1.5—13 cm, stiffly fleshy, dull pale to dark yellow, wide gaping at male anthesis and then briefly persistent though maturation of the stamens, eventually falling to leave a large ± scar at the base of the spadix; *spadix* cylindrical, sessile, slightly obliquely inserted on peduncle, 7—17 x 1.3—2.5 cm, dull greenish yellow; *stylar region* moderately developed, rounded to rhombohexagonal, 1—2 x 1—1.5 mm, shortly conical when fresh, drying truncate; *stigma* punctiform or elliptic and transversely orientated, raised at male anthesis but excavated in dry material, c. 0.3 mm diam.; *anthers* slightly exserted at male anthesis; *infructescence* 8—15 x 2—3 cm, dark green before ripening to greenish yellow.

Distribution: Sumatera, Peninsular Malaysia, Borneo - Sarawak (1st and 6th Divisions, but doubtless more widespread), Brunei Darussalam (Belait) and Sabah (Pantai Barat).

Habitat: On trees, rocks and cliffs in primary to disturbed secondary lowland to moist hill dipterocarp forest, on a variety of substrates including limestone and shale. 10—700 m altitude.

Notes: 1. Confusion can occur between *Rhaphidophora foraminifera* and *R. puberula*. They may be distinguished by the position of the inflorescence (on short clinging shoots in *R. foraminifera*, on short free shoots in *R. puberula*), by the presence of black mucilage produced by the deliquescing cataphylls and prophylls (present in *R. foraminifera*, absent in *R. puberula*), in leaf size of mature flowering-sized plants (to 53 x 19 cm in *R. foraminifera*, to 34 x 10.5 cm in *R. puberula*), by the more or less rounded (*R. foraminifera*) v. oblong (*R. puberula*) stylar regions, and in overall size of the plant (*R. foraminifera* is a bole climber to 15 m whereas *R. puberula* seldom climbs higher than 3 m and frequently forms large, spreading masses on rocks.)

2. Perforated leaves occur in a number of otherwise rather different-looking *Rhaphidophora* species (e.g., *R. foraminifera. R. puberula*, *R. versteegii*) suggesting that while a useful diagnostic tool, lamina perforation cannot be used to circumscribe taxonomically meaningful groups within *Rhaphidophora*.

Other Bornean specimens seen: SARAWAK. 1st Div.: Road between Kuching and Padawan, 10 m SW of main Kuching to Serian highway, *Croat 53182* (MO); 1 mile from Bau, *Nicolson 1288* (US); 6th Div: Ulu Balingian, road from Sibu to Bintulu, *Boyce 722* (K, M). BRUNEI DARUSSALAM. Belait: Labi, Kp Teraja, path along the Sg. Teraja, *Boyce 235* (BRUN, K, L, MO). SABAH. Pantai Barat: Road from Kota Kinabalu to Tambunan, Ulu Moyog, *Boyce 1391*, *1400* (K, SNP); Tambunan District, Road to Kg Tondulu, *Boyce 1414* (K, SNP); Moyog District, along road between Kota Kinabalu and Tambunan, 21 miles SE of Kota Kinabalu, W slopes of Crocker Range, *Croat 53118* (MO); Kinabatangan, Tamegang Timber Camp near Kg Pangkaian, *Hotta 1416* (KYO, L).

7. Rhaphidophora korthalsii Schott

Rhaphidophora korthalsii Schott, Ann. Mus. Bot. Lugd.-Bat. 1(1863) 129; Engl. in A. & C. DC., Monogr. Phan. 2 (1879) 246; Engl. & K. Krause in Engl., Pflanzenr. 37 (IV.23B) (1908) 49—51, Fig. 21; Alderw., Bull. Jard. Bot. Buitenzorg III, 4 (1922) 341. — Type: Indonesia, Java, *P.W. Korthals s.n.* (L, holo; L, P, iso).

Pothos celatocaulis N.E. Br., Gard. Chron. 13 (1880) 200. — *Rhaphidophora celatocaulis* (N.E. Br.) Alderw., Bull. Jard. Bot. Buitenzorg III, 1 (1920) 382 & Bull. Jard. Bot. Buitenzorg III, 4 (1922) 198. — Type: Malaysia,

Sabah, *Burbidge s.n.*, *Hort. Veitch no. 215* (K, holo; K, iso).

Rhaphidophora maxima Engl., Bull. Soc. Tosc. Ortic. 4 (1879) 269 & in Beccari, Malesia 1 (1882) 271, Tab. xx 1—5; Engl. & K. Krause in Engl., Pflanzenr. 37 (IV.23B) (1908) 48—49; Merrill, J. Straits Branch Roy. Asiat. Soc., special number (1921) 89. — Type: Sarawak, G. Gading, July 1866, *Beccari PB 2314* (FI, lecto, selected by Boyce, 1999).

Rhaphidophora tenuis Engl., Bot. Jahrb. Syst. 1 (1881) 181 & in Beccari, Malesia 1 (1882) 271—272; Engl. & K. Krause in Engl., Pflanzenr. 37 (IV.23B) (1908) 53; Merrill, J. Straits Branch Roy. Asiat. Soc., special number (1921) 90. — Types: Malaysia, Sarawak, *Beccari PB 1977* (FI lecto; B isolecto; lecto selected by Boyce, 1999).

Rhaphidophora korthalsii Schott *var. angustiloba* Ridl. *ex* Engl. & K. Krause in Engler, Pflanzenr. 37 (IV.23B) (1908) 49; Merrill, J. Straits Branch Roy. Asiat. Soc., special number (1921) 89. — Type: Malaysia, Sarawak, Matang, July 1903, *Ridley s.n.* (SING, lecto; lecto; selected by Boyce, 1999).

Rhaphidophora copelandii Engl., Bot. Jahrb. Syst. 37 (1905) 115; Engl. & K. Krause in Engl., Pflanzenr. 37 (IV.23B) (1908) 49. — Type: Philippines, Mindanao, Davao, Mt Apo, April 1904, *Copeland 1193* (PNH, holo†; B iso).

Rhaphidophora grandifolia K. Krause, Bot. Jahrb. 44, Beibl. 101 (1910) 11. — Type: Philippines, Negros, Negros Orientale, Dumaguete (Cuernos Mts), March 1908, *Elmer 9464* (PNH, holo†; B, E, K, L, LE, MO, iso).

Rhaphidophora trinervia Elmer, Leafl. Philipp. Bot. 8 (1919) 3073. — Type: Philippines, Laguna, Los Baños (Mt Maquiling), June—July 1917, *Elmer 18057* (PNH, holo†; FI, K, L, MO, P, iso).

Rhaphidophora ridleyi Merr., J. Straits Branch Roy. Asiat. Soc., special number (1921) 90. [*Rhaphidophora grandis* Ridl., J. Straits Branch Roy. Asiat. Soc. 49 (1907) 51, *nom. illeg.*, *non* Schott 1858 (India) = *R. decursiva* (Roxb.) Schott]. — Type: Malaysia, Sarawak, Tambusan, Sept. 1905, *Ridley 12414* (SING, holo).

Rhaphidophora latifolia Alderw., Bull. Jard. Bot. Buitenzorg III, 4 (1922) 341; K. Krause & Alderw., Nova Guinea 14 (1924) 213. — Type: Indonesia, Irian Jaya, Pionierbivak, 23 July 1920, *Lam 711* (BO, holo; L, iso).

Rhaphidophora palawanensis Merr., Philipp. J. Sci. 26 (1925) 451. — Type: Philippines, Palawan, Malampaya Bay, Oct. 1922, *Merrill BS 11570* (PNH, holo†; B, K, P, iso).

Rhaphidophora trukensis Hosok., J. Jap. Bot. 13 (1937) 195. — Type: Federated States of Micronesia, Chuuk (Truk) Island, near Orrip, 29 July 1939, *Hosokawa 8334* (TI , holo).

[*Epipremnum multicephalum* Elmer, Leafl. Philipp. Bot. 10 (1938) 3624, *nom. inval., descr. Angl.* — Based on: Philippines, Luzon, Sorsogon, Trosin (Mt Bulusan), May 1916, *Elmer 16061* (sheets seen at FI, K, L, MO, P, PNH†)].

Figures 8 & 9

Very large, occasionally enormous, slender to rather robust, pachycaul, heterophyllous liane to 20 m; *seedling stage* a non-skototropic shingling juvenile shoot; *pre-adult plants* never forming terrestrial colonies; *adult shoot architecture* comprised of greatly elongated, clinging, physiognomically unbranched, densely leafy, flowering stems; *stems* smooth, bright green, with sparse to copious prophyll, cataphyll and petiolar sheath fibre, especially at the stem tips, internodes to 15 x 3.5 cm, separated by prominent oblique leaf scars, older stems subwoody; *flagellate foraging stems* absent; *clasping roots* densely arising from the nodes and internodes, prominently pubescent; *feeding roots* abundant, clinging and free, very robust, densely ramentose-scaly; *leaves* distichous; *cataphylls and prophylls* membranous, soon drying and degrading to intricately reticulate persistent fibres; *petiole* shallowly grooved, upper part ± terete, (1—) 9—65 x 0.2—1.5 cm, smooth, apical and basal genicula prominent; *petiolar sheath* prominent, membranous, strongly to slightly unequal on one side, extending almost to or reaching the apical geniculum, of ± short-duration, soon degrading into persistent netted fibres, these eventually falling to leave a prominent, slightly corky scar; *lamina* of seedlings overlapping in the manner of roof shingles, entire, lanceolate, 5—11 x 3.5—6 cm, base slightly cordate, lamina of pre-adult and adult plants free, entire, pinnatipartite, pinnatisect or pinnatifid, 10—44 x 14—94 cm, broadly oblong-elliptic to oblong lanceolate, slightly oblique, membranous to chartaceous or subcoriaceous, base truncate and very briefly decurrent, apex acute to acuminate, individual pinnae 1—10 cm wide, frequently perforated basally adjacent to the midrib, thus appearing stilted; *midrib* very prominently raised abaxially, slightly sunken adaxially; *primary venation* pinnate, raised abaxially, somewhat impressed adaxially, 2—4 primary veins per pinna; *interprimaries* subparallel to primaries, slightly raised abaxially, slightly impressed adaxially; *secondary*

Figure 8. Rhaphidophora korthalsii Schott
A. pre-adult shoot x $^1/_4$; B. pre-adult shingling shoot x $^1/_4$. A from *Boyce 679*; B from *Nicolson 1712*.

venation strongly reticulate, slightly raised; *tertiary venation* invisible; *inflorescence* solitary to several together, first inflorescence subtended by a membranous prophyll and one or more cataphylls, these soon degrading to netted fibres, subsequent inflorescences subtended by one or more soon degrading cataphylls, the whole forming a mass of developing and open inflorescences and developing infructescences partially concealed by persistent netted cataphyll and prophyll remains; *peduncle* slightly laterally compressed to terete, 6—26 x 1—1.5 cm; *spathe* narrowly canoe-shaped, stoutly beaked, 10—30 x 3—5 cm, stiffly fleshy, greenish to dull yellow, gaping wide at female anthesis and then soon falling to leave a large straight scar at the base of the spadix; *spadix* cylindrical, sessile, inserted ± level on peduncle, 9—26 x 1.5—2 cm, dull green to dirty white; *stylar region* rather well developed, mostly rhombohexagonal, 1.5—2 x c. 2 mm, slightly conical; *stigma* punctiform to slightly elliptic, if the latter then mostly longitudinally orientated, c. 0.3—0.5 x 0.2—0.4 mm; *anthers* barely exserted at male anthesis; *infructescence* 14—27 x 3—3.5 cm, dark green ripening to dull orange, stylar tissue abscising to reveal orange ovary cavity pulp.

Distribution: Widespread in south tropical Asia from Sumatera and southern Thailand to Borneo and the Philippines eastwards through the tropical western Pacific. In Borneo, widespread in Sarawak, Brunei Darusslam and Sabah. In Kalimantan only recorded from East Kalimanatan.

Habitat: Primary to disturbed secondary lowland, hill and montane forest, moss forest, peatswamp forest, on trees, rocks and cliffs on a variety of substrates including limestone and ultrabasic soils. 20—1800 m altitude.

Notes: 1. *Rhaphidophora korthalsii* is a very widespread and variable species, hence the extensive synonymy. However, as with *Epipremnum pinnatum* (L.) Engl. (Boyce, 1998) there are several geographical elements that, given more intensive study, might warrant formal taxonomic recognition. Unfortunately, current herbarium material is inadequate to confirm these plants' status and more field observations are needed.

2. Sterile herbarium material lacking the pre-adult stage may prove difficult to distinguish from the *Epipremnum pinnatum* (in Borneo known wild only from east Sabah). Mature leaves of 'typical' *E. pinnatum* never have more than one primary lateral vein per pinna and the stems of *R. korthalsii* lack the prominent irregular whitish longitudinal crests and older stems the distinctive matt to sublustrous pale brown papery epidermis typical of *E. pinnatum*. The feeding roots of *R. korthalsii* are prominently scaly, while those of *E. pinnatum* are lenticellate-corky. The pre-adult stage of *R.*

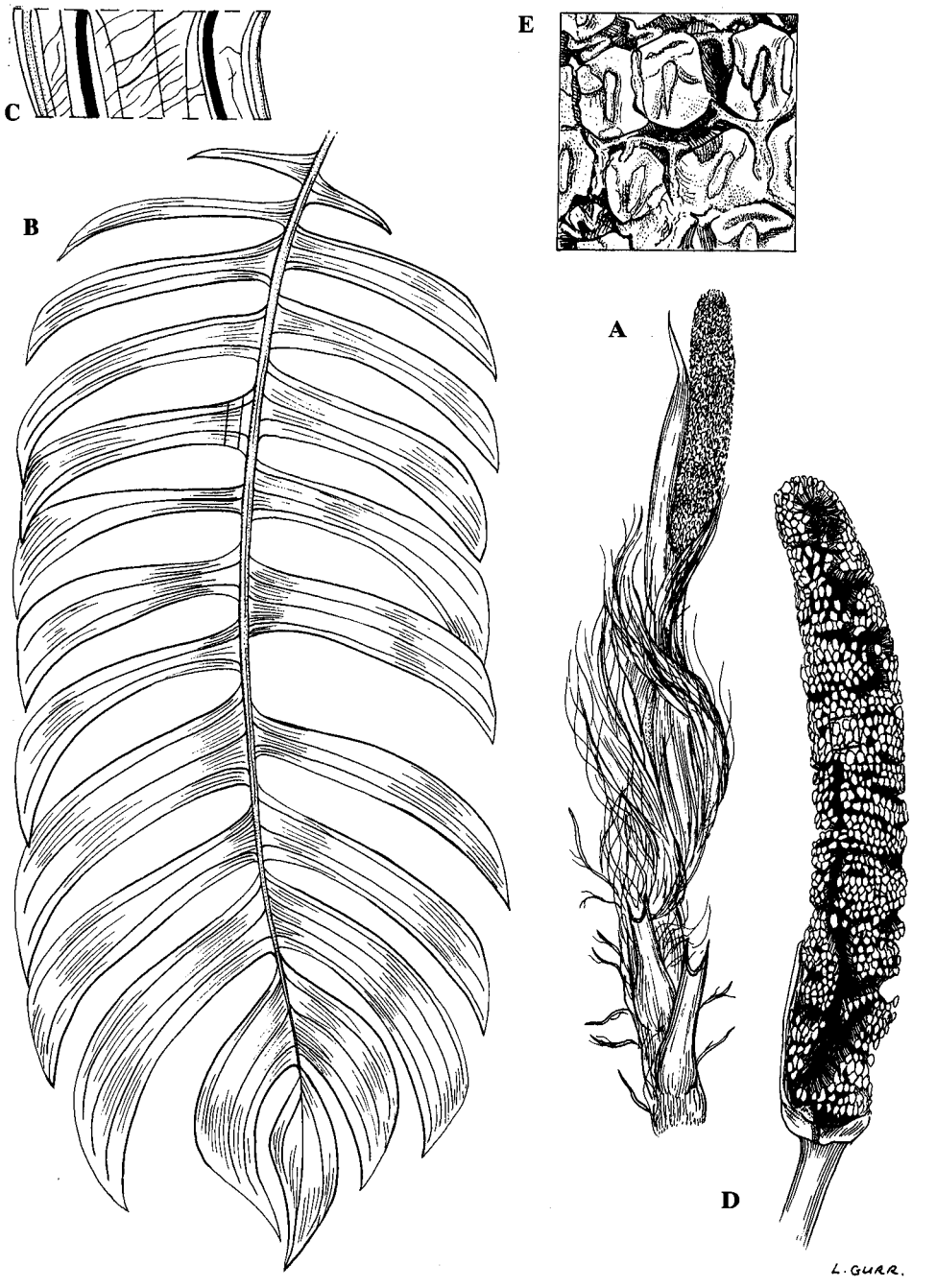

Figure 9. Rhaphidophora korthalsii Schott
A. flowering shoot, leaves removed x $^1/_2$; B. leaf lamina x $^1/_4$; C. venation detail x 2; D. inflorescence, spathe removed x 1; E. spadix detail, post-male anthesis x 8. All from *Kerr 15051*.

korthalsii is a shingle climber with oblong-elliptic to ovate, slightly falcate upwardly pointing leaves overlapping in the manner of roof tiles.

3. Fertile material of *R. korthalsii* and *Epipremnum pinnatum* is readily separated by the shape of the style apex (round v. trapezoid) and the shape and orientation of the stigma (± punctiform and circumferential v. strongly linear and longitudinal) and, if fruits are mature, by seed characters. The fruits of *R. korthalsii* each contain many small ellipsoid seeds with a brittle, smooth testa, whereas *E. pinnatum* has fruits with two large, strongly curved seeds with a bony and ornamented testa.

Other Bornean specimens seen: SARAWAK. 1st Div.: Bau, *Brooke 8998* (BM); Lundu, *Foxworthy 40* (SING); Three miles from Kuching, *Haviland & Hose 3605* (K); Kuching, *Hewitt 40* (SING); Semengoh F.R., 6 miles west of Kuching, *Nicolson 1252* (US); 1 mile west of Bau, *Nicolson 1301* (US); Bako N.P., 20 miles northeast of Kuching, Lintang Path, *Nicolson 1329* (US); Setapok F.R., 6 miles west of Kuching, *Nicolson 1341* (US); Kuching *Ridley s.n.* (SING); 3rd Div.: Hose Mountains, gorge of Sg. Simpurai, *Burtt & Martin 4926* (E); Bt. Raya, Kapit, *Soepadmo & Chai S28148* (KLU, SAR); 4th Div.: Niah, *Ahmed 64* (SAR, SING); Miri District, Niah, Sg. Sekaloh, G. Subis, *Anderson S31956* (E, K, L, SAR, SING, US); Kelabit Highlands, Apu Batu Buli, *Nooteboom & Chai 2216* (L, SAR, US); 7th Div.: Bintulu, Bt. Urang, *Brunig S 12093* (K, SAR); Eastern ridge of Bt. Kans, Bintulu district, *Hirano & Hotta 1432* (KYO); Sg. Ma'au, Dataran Tinggi Merurong, Tubau, *Othman et al. S 49050* (K, SAR); 9th Div.: Tebedu, mile 15, *Mohtar et al. S 49245* (K, SAR, US); Serian, G. Penrissen; *Paie S 16001* (K, LE, SAR). BRUNEI DARUSSALAM. Belait: Ulu Ingei, Bt. Batu Patam, lower slopes near Sg. Ingei, *Boyce 312* (BRUN, K); Temburong: Sg. Temburong above Kuala Belalong, *Argent et al. 9136* (E, K); Bt. Biang, *Ashton 154* (K, US); Sg. Temburong at Wong Nguan gorge, *Wong 1727* (BRUN, K). SABAH. Kudat: Ranau, Bt. Kulung, *Meijer SAN 122414* (SAN); Ranau, Bt. Kulung, *Meijer SAN 122429* (SAN); Ranau, Kinabalu road to Mesilau, *Mikil SAN 38691* (K, SAN); Mesilau, *Poore 131* (K); Sandakan: Paitan F.R., *Ampuria SAN 32773* (K, SAN, SING); Elopura, mile 15 Labuk Road, *Cuadra A 2237* (K, KEP, SAN, SING); Sandakan, Segalid Lokan F.R., *Gibot SAN 80977* (K, L, SAN); Lamag, Batu Puteh, *Majawat & Lasan SAN 88017* (KEP, SAN); Pantai Barat: Tambunan, road to Kg Tondulu, Kg Tondulu valley, *Boyce 1421* (K, SING, SNP); Papar, Kimanis road, *Boyce 1443* (K, SNP); Dallas, *Clemens & Clemens 26405* (BM, SING); Dallas, *Clemens & Clemens 26495* (BM, L, UC); Tenompok, *Clemens & Clemens 28813* (BM, K, SING); Upper Kinabalu, *Clemens & Clemens 29146* (BM, BO, K, L, SING, UC); Upper Kinabalu, Lilau Basin, Mesilau, Meneringtan, *Clemens & Clemens 29146a* (BM, K, L, SING); Penibukan, *Clemens & Clemens 31150* (BM, K, SING); Penataran river, *Clemens & Clemens 34298* (BM, BO, K, L, UC); Mount Kinabalu N.P., along road to summit, *Croat 53131* (MO); Lamag, Sg. Pin, *Dewol & Harum SAN 89922* (K, SAN); Ulu Segama, Danum Valley, path to Rhino Ridge, *Dransfield 6302* (K); Pedalaman: Tenom, north ridge of G. Malutut, c. 15 km north of Tenom, *Kokawa & Hotta 2455* (KYO, L); Tawau: cutting area of Luasong Camp, N.B.T. about 60 km NW of Tawau, *Kokawa & Hotta 631* (K, KYO), *Kokawa & Hotta 797* (K, KYO, P); Lahad Datu, Ulu Sg. Sanum, south of camp 111, *Stone et al. SAN 85269* (KLU, SAN); Lahad Datu, Ulu Sg. Sanum, just north of camp 111, *Stone et al. SAN 85310* (KLU, SAN). KALIMANTAN. East Kalimantan: Wanariset research area, road Samboja to Semoi, km 11, *Ambri & Arifin 331* (L); Berau, Tandung Redeb, Sg. Kelai near Long Lanuk, *Kostermans 21125* (BO, L); Berau, near Tandung Redeb,

Kostermans 21725 (BO, L, US); Danan Pentulak, Bt. Pegah, *Main (sub. Polak) 1957* (BO); Pulau Nunukan, Tarakan, *Meijer 2600* (BO); North of Tarakan, Simengkadu, *Meijer 2389* (BO).

8. Rhaphidophora latevaginata M. Hotta

Rhaphidophora latevaginata M. Hotta, Acta Phytotax. Geobot. 22 (1966) 4. — Type: Malaysia, Sarawak, 4th Division, Bintulu District, about 4 km east from Minah Camp, Sg. Kakus, 4 Oct. 1963, *Hirano & Hotta 140* (KYO, holo).

Figure 10

Moderate to very large, robust, pachycaul, homeophyllous neotenic liane to 12 m; *seedling stage* a non-skototropic shingling juvenile shoot; *pre-adult plants* forming small terrestrial colonies of shingling closely appressed leaves; *adult shoot architecture* comprised of clinging, physiognomically unbranched, shingling to very densely leafy, sterile stems and almost identical fertile stems; *stems* weakly compressed-terete to weakly rectangular in cross-section, smooth, dark green, without prophyll and cataphyll fibre but with at least upper parts with thin, black adherent petiolar sheath tissue, internodes to 12 x 2 cm, separated by prominent straight scars, but scars obscured by leaf bases on all but the oldest stems, lower parts of stem later sub-woody with slightly shiny cracking epidermis; *flagellate foraging stems* moderately well developed although often somewhat short and leafy; *clasping roots* arising densely from the nodes and internodes, prominently scaly; *feeding roots* c. 3 mm diam., brown, minutely pubescent; *leaves* distichous, appressed, ascending and shingling, becoming slightly scattered and spreading (often litter-trapping) towards fertile tips; *cataphylls and prophylls* membranous, soon drying black and persisting briefly before falling; *petiole* deeply canaliculate and winged, 3—22 x 0.5—2 cm, smooth, apical and basal genicula almost obscure in young leaves, later becoming prominent, especially the basal geniculum; *petiolar sheath* very pronounced, up to 2.5 cm wide, rather thickly membranous, prominently ligulate, outer sheath (away from climbing surface) greatly expanded and partly to completely obscuring stem, sheath turning black but persisting some considerable time, eventually rotting away to reveal two large scars extending to the top of the petiole; *lamina* broadly oblong-ovate-elliptic, 8—48 x 6.5—20.5 cm stiffly coriaceous, bright green, slightly to markedly glaucous, base truncate-cordate to broadly cuneate, very briefly decurrent, apex rounded to acute with a tiny apicule; *midrib* prominently raised abaxially, slightly sunken adaxially; *primary venation* pinnate, slightly raised

abaxially, more so adaxially; *interprimaries* sub-parallel to primaries, slightly raised on both leaf surfaces; *secondary venation* tessellate-reticulate, slightly raised abaxially, ± flush adaxially, all veins much more prominent in dried material; *inflorescence* solitary on a clinging shoot, subtended by a fully developed foliage leaf and one or more cataphylls; *peduncle* laterally compressed-cylindrical, 6.5—11 x 0.5—0.7 cm; *spathe* not observed; *spadix* stoutly cigar-shaped, sessile; *spadix* inserted ± level on stipe, 17.5 x 1.5 cm, pale green; *stylar region* rhombohexagonal, c. 2 x 1 mm, truncate; *stigma* slightly raised, elongated, longitudinally orientated, c. 0.75 x 0.2 mm; *anthers* not exserted at male anthesis; *infructescence* stoutly cigar-shaped, 15 x 2 cm, stylar region becoming convex at fruit maturity.

Distribution: Endemic to Borneo. Sarawak (1st and 7th Division), Brunei Darussalam (Temburong), Sabah (Pantai Barat and Sandakan), Kalimantan (localities not traced).

Habitat: Primary to secondary moist lowland to hill dipterocarp forest on clay and sandstone. 50—840 m altitude.

Notes: 1. Despite its remarkable appearance with densely glaucous-leafy shingling shoots ascending, often spirally, high into the canopy, and furthermore being widespread and not uncommon in Borneo, *R. latevaginata* was described only relatively recently and, remarkably, is known from only 13 herbarium specimens only two of which are more than 50 years old. Given the plant's striking appearance, it seems inconceivable that it was not noticed by early fieldworkers although quite possibly its overall similarity to the juvenile stages of the common and widespread *R. korthalsii* may have led to it being passed by as not worth collecting.

2. It is not at all clear to what *Rhaphidophora latevaginata* is related. It is the only large neotenic lianescent aroid in Borneo, although neoteny in *Rhaphidophora* occurs in three groups (Boyce, 1999; Boyce & Bogner, 2000). The similarity of the plant to the juvenile stage of *R. korthalsii* might seem compelling and the shared scaley feeding roots suggest a relationship. However, the inflorescences are quite different; the style of *R. latevaginata* is rhombohexagonal and the stigma longitudinally orientated (v. style round and stigma ± punctiform in *R. korthalsii.*)

Other specimens seen: SARAWAK. 1st Div.: Matang F.R., 10 miles west of Kuching, *Nicolson 1262* (L, US); 7th Div.: Sibu-Bintulu road, 2.3 km after bridge over the Batang Kemena, *Boyce 728* (K, M); Bintulu, about 2 - 4 km east from of Minah Camp, Sg. Kakus, *Hirano & Hotta 41* (KYO), *Hirano & Hotta 149* (KYO); Vicinity of Minah Camp (timber camp of

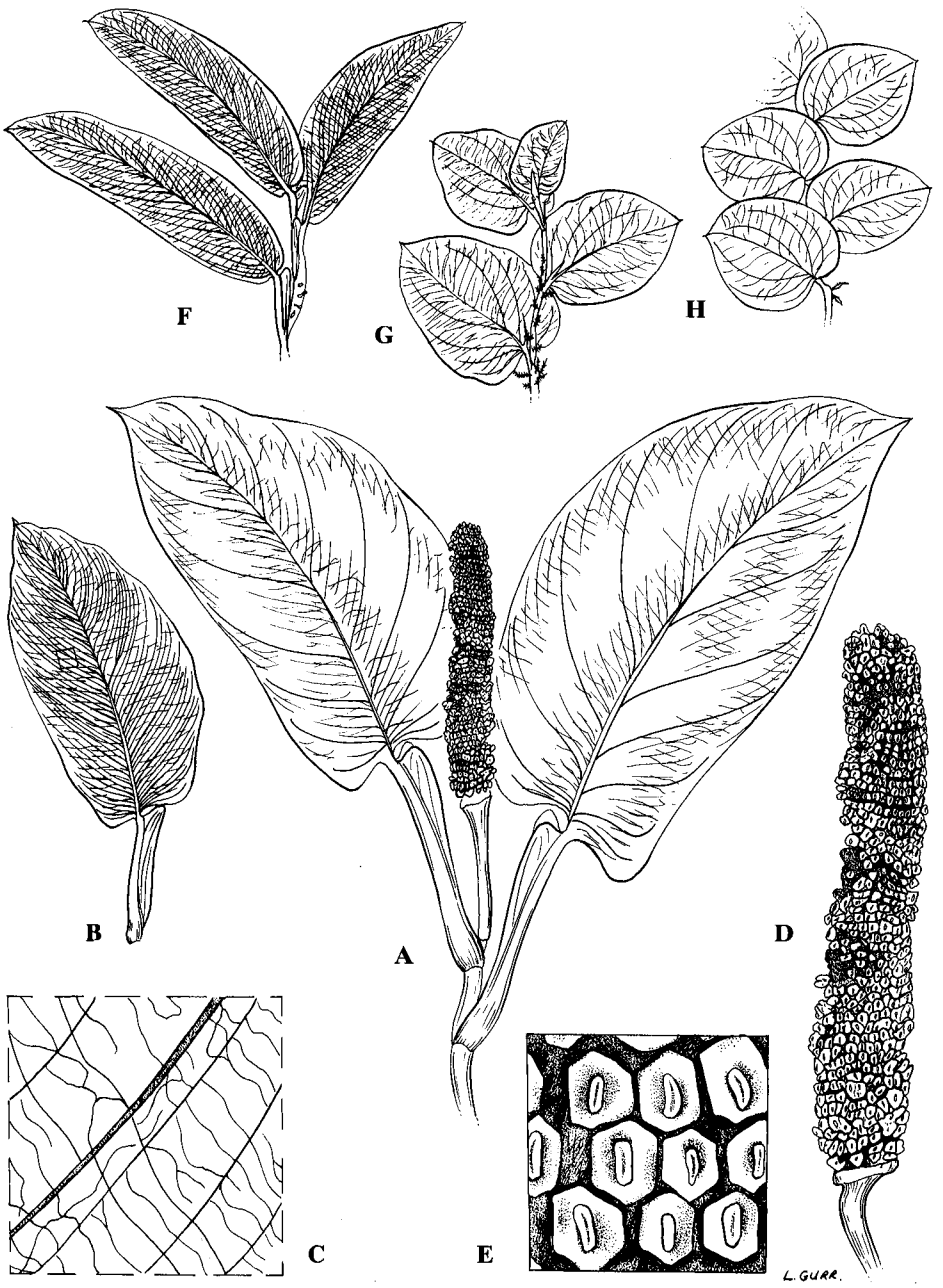

Figure 10. Rhaphidophora latevaginata M. Hotta
A. flowering shoot x $^{2}/_{9}$; B. adult leaf lamina x $^{1}/_{3}$; C. venation detail x 3; D. inflorescence, spathe fallen x $^{2}/_{3}$; E. spadix detail, early fruiting x 4; F. pre-adult terrestrial shoot x $^{1}/_{3}$; G. pre-adult terrestrial shoot x $^{1}/_{3}$; H. pre-adult terrestrial shoot x $^{1}/_{3}$. A, D & E from *Hirano & Hotta 140*; B & C from *Dewol & Meijer 131653*; F & G. from *Hirano & Hotta 149*; H from *Hirano & Hotta 41*.

L.L.B.T.C.), Sg. Kakus, *Hotta 15717* (KYO). BRUNEI DARUSSALAM. Temburong: Sg. Temburong at Kuala Belalong, *Boyce 402* (BRUN, K, L, SING, MO); Batu Apoi F.R., ridge west of Kuala Belalong Field Studies Center slope, between Danish Plot and Sg. Belalong, *Poulsen 165* (AAU, BRUN, K). SABAH. Pantai Barat: Road from Kota Kinabalu to Tambunan, Ulu Moyog, *Boyce 1389* (K, SNP); Sandakan: Phenological trail above sawmill, *Dewol & Meijer SAN 131653* (SAN); Kinabatangan District, Kg. Bilit, Bt. Bilit, *Lim et al. 1272* (SING). KALIMANTAN. Locality not traced: Batu Makele, Batu Eilander, *Raap 118* (BO); G. Dansu, Pentaclale, Pegah, *Main (sub. Polak) 1958* (BO).

9. Rhaphidophora lobbii Schott

Rhaphidophora lobbii Schott, [Bonplandia 5(2) (1857) 45, *nom. nud.*], Prodr. Syst. Aroid. (1860) 379; Engl. in A. & C. DC., Monogr. Phan. 2 (1879) 240; Engl. & K. Krause in Engl., Pflanzenr. 37 (IV.23B) (1908) 33—34; Merrill, J. Straits Branch Roy. Asiat. Soc., special number (1921) 89. — *Scindapsus lobbii* (Schott) Ender, Index Aroid. (1864) 74. — Type: Singapore, *Lobb 44* (K, holo).

Figure 11

Small to moderate, somewhat slender, leptocaul, homeophyllous liane to 5 m; *seedling* leafy at germination and skototropic by alternating series of congested leafy and elongated leafless shoots; *pre-adult plants* forming diffuse terrestrial colonies; *adult shoot architecture* comprised of greatly elongated, clinging, physiognomically unbranched, leafy, non-flowering stems and long moderately elaborated, free, densely leafy, flowering stems; *stems* puberulent-scabrid to asperous, especially on older growth, climbing stems weakly rectangular to ± terete in cross-section, free stems ± terete in cross-section, often branching extensively and growing to moderate lengths pendent under their own weight, dull brown, without prophyll, cataphyll and petiolar sheath fibre, internodes to 13 x 0.6 cm on clinging and free shoots, flowering shoots with much shorter internodes, separated by weak to rather prominent, slightly oblique leaf scars, older stems woody; *flagellate foraging stems* absent; *clasping roots* sparsely arising from the nodes and internodes of clinging stems, densely pubescent; *feeding roots* rather rare, sometimes clinging but often free, pubescent; *leaves* weakly spiralled and often sparsely arranged on clinging and proximal portions of free shoots, densely spirally-distichous distally on flowering shoots; *cataphylls and prophylls* membranous, very soon drying and falling; *petiole* grooved adaxially, 4—9.5 x 0.2—0.3 cm, smooth, with a moderate apical and prominent basal geniculum; *petiolar sheath* slightly prominent, extending beyond the apical geniculum by two ligules, very soon drying and falling in strips to leave a continuous scar from the petiole base, around the top of the apical geniculum and back to the base; *lamina* entire, narrowly elliptic

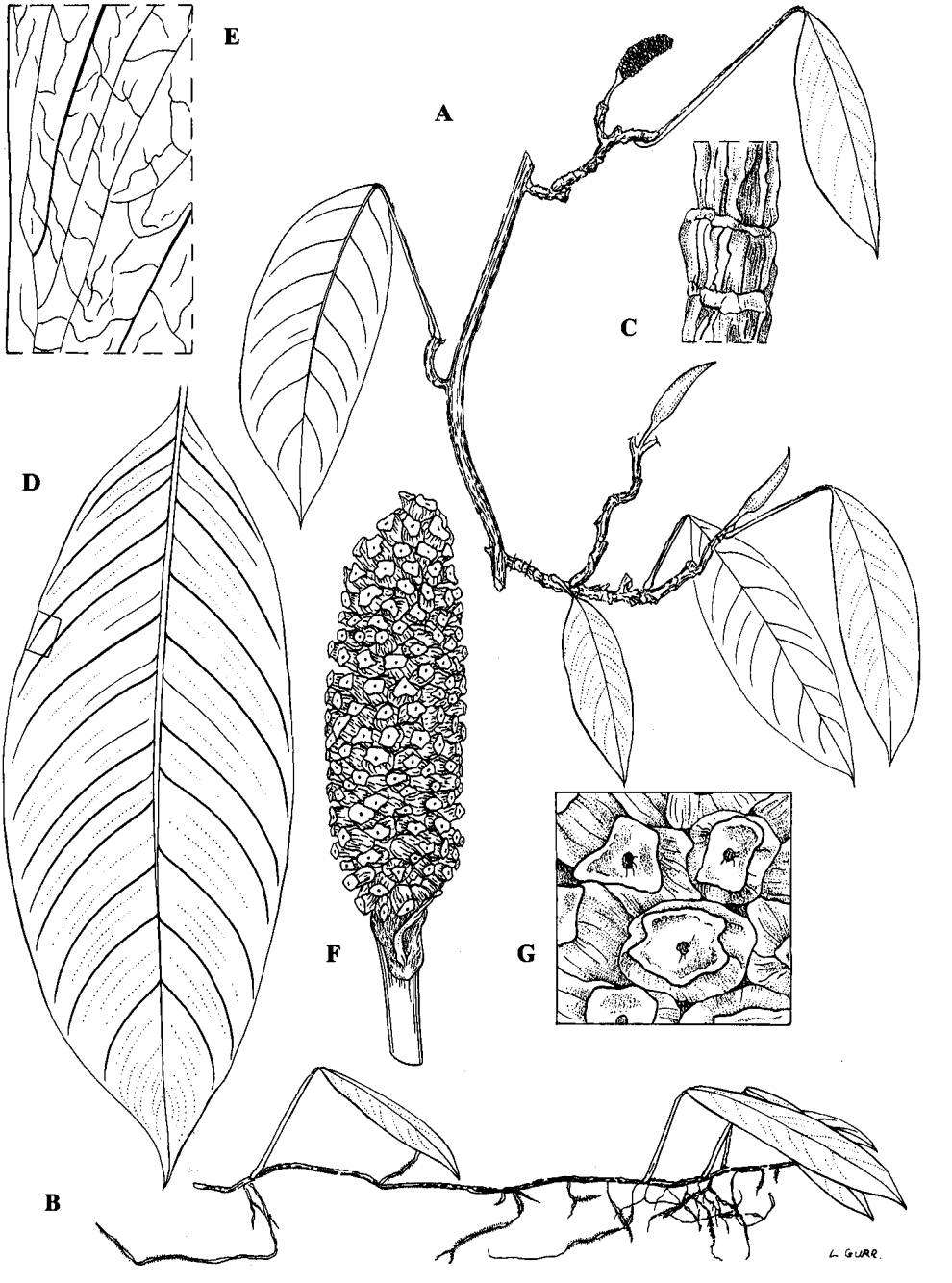

Figure 11. Rhaphidophora lobbii Schott
A. portion of stem with two flowering shoots x $^1/_3$; B. pre-adult terrestrial shoots x $^1/_3$; C. stem detail x 3; D. leaf lamina x $^3/_4$; E. venation detail x 4; F. inflorescence, spathe fallen x 2; G. spadix detail, early fruiting x 8. A & C from *Kunstler ('Dr King's Collector') 10571*; B from *Boyce 995*; D & E from *Nauen s.n.*; F & G. from *Alvins 270*.

to elliptic-lanceolate to oblong or oblanceolate, 6—24 x 2—10 cm, very softly coriaceous, upper surfaces slightly glossy, lower surfaces pale satin-matt, drying markedly discolorous, dark brown above, pale brown below, base cuneate to acute or subovate, briefly decurrent, apex acute to ovate-acuminate, with a prominent apiculate apicule; *midrib* slightly raised abaxially, slightly sunken adaxially; *primary venation* pinnate, slightly raised abaxially, prominent (dark veins against pale lamina) in dried material; *interprimaries* parallel to, but much less distinctive than, primaries, very slightly raised abaxially; *secondary and tertiary venation* ± invisible in fresh material, barely visible in dried specimens, reticulate; *inflorescence* solitary, subtended by a fully developed foliage leaf and a very soon falling cataphyll; *peduncle* compressed-cylindric, 1.5—5 x 0.15—0.4 cm; *spathe* cigar-shaped, stoutly long-beaked, 3—5 x 0.4—1 cm, thickly fleshy, exterior minutely puberulent, dull green to yellowish, soon falling at female anthesis to leave a substantial, slightly oblique, scar; *spadix* slender cylindrical, sessile, inserted level on peduncle, 3—3.5 x 0.4—0.5 cm, dull yellow-white; *stylar region* rather well developed, mostly rhombohexagonal, 1.9—2.4 x c. 2 mm, truncate; *stigma* punctiform, c. 0.3 mm diam., prominent in dried material; *anthers* barely exserted at male anthesis, pollen extruded from between ovaries; *infructescence* oblong-cylindric, 2.5—4 x 1—1.2 cm.

Distribution: Southern Thailand, Peninsular Malaysia, Singapore, Sumatera, North Borneo and into Sulawesi.

Habitat: Primary to disturbed secondary lowland dipterocarp and peatswamp forest on wet to inundated soils. Sea level to 250 m altitude.

Notes: 1. A climber distinctive by the slender, asperous stems, softly leathery leaves and minutely puberulent spathe exterior, a combination of characters unknown in any other Malesian *Rhaphidophora*. In dry material the strongly discolorous leaves, combined with the primary veins prominently darker than the abaxial leaf surface, are unmistakable.

2. In Borneo, confusion with *R. cylindrosperma* is possible although the latter differs in its more coriaceous leaves, different leaf venation and in having a longer, externally glabrous spathe.

3. *Rhaphidophora lobbii* is habitually found in wet to inundated ground, an unusual habitat for a monsteroid liane, cf. *Epipremnum amplissimum* Schott, and *E. giganteum* (Roxb.) Schott.

Other Bornean specimens seen: SARAWAK. 1st Div.: Setapok F.R., 4 miles south of Kuching,

Anderson S 23496 (SAR); Semengoh F.R., 6 miles west of Kuching, *Nicolson 1258* (US); Setapok F.R., 6 miles south of Kuching, *Nicolson 1359* (US); 2nd Div.: Simanggang, Triso P.F., *Anderson 14547* (SING); 8th Div.: Binatang, Pulau Bruit, *Anderson 8032* (SING); Sg. Kelepu, Pulau Bruit, *Anderson 8007* (L, SING); Baram, *Anderson S 3084* (SAR, SING). BRUNEI DARUSSALAM. Temburong: Selapon, village margin, *Dransfield 6917* (BRUN, K, L); Batu Apoi F.R., on ridge between Kuala Belalong and Bt. Belalong, in permanent Plot 2, *Poulsen 362* (AAU, BRUN, K); Belait: Melilas, Ulu Ingei, path from Ulu Ingei to Sg. Tupai, *Sands 5919* (BRUN, K, L); Rasau, *Van Niel 4250* (L, MO). SABAH. Sandakan: Sepilok F.R., *Gambating SAN 94588* (K, L, SAN); Sg. Dagat, *George et al. SAN 120521* (K, SAN); Kinabatangan, Tamegang Timber Camp near Kg. Pangkaian, *Kokawa & Hotta 1417* (KYO, L); Labuk Road, *Meijer SAN 38784* (K, L, SAN); Below waterfall Kebun Cina F.R., *Meijer & Dewol SAN 131749* (SAN); Bongaya F.R., *Kodoh & Aban SAN 82024* (K, L, SAN, SAR, SING). KALIMANTAN. West Kalimantan: Pontianak, *Polak 308* (BO); Sg. Banghong, *Polak 645* (BO, K); Bt. Raya, Tumbang Riang, *Veldkamp 7910* (BO, L). East Kalimantan: Wanariset, Balikpapan, *Afriastini 116* (BO); Km 79 on road from Sangui Sg. Mantaya, Kab. Kotawaringin Timur, *Argent et al. 93138* (B, E); Berau, Tandung Redeb, Sg. Kelai, near Long Lanuk, *Kostermans 21133* (BO, L); Munukan, north of Tarakan, *Meijer 2034* (BO); 'Borneo', *Korthals 149* (L) & *Korthals s.n.* (L).

10. Rhaphidophora megasperma Engl.

Rhaphidophora megasperma Engl., Bot. Jahrb. Syst. 25 (1881) 8; Engl. & K. Krause in Engl., Pflanzenr. 37 (IV.23B) (1908) 29, Fig. 9; Alderw., Bull. Jard. Bot. Buitenzorg III, 1 (1920) 383; Merrill, J. Straits Branch Roy. Asiat. Soc., special number (1921) 89. — Type: Indonesia, Kalimantan, Central Kalimantan, Tumbang Hiang, 2 Sept. 1881, *Grabowski* 48 (B, holo).

Scindapsus havilandii Ridl., J. Straits Branch Roy. Asiat. Soc. 44 (1905) 184; Engl. & K. Krause in Engl., Pflanzenr. 37 (IV.23B) (1908) 75; Merrill, J. Straits Branch Roy. Asiat. Soc., special number (1921) 91, **synon. nov.** — Type: Malaysia, Sarawak, 2nd Div., Saribas, July 1892, *Haviland 2089* (K, holo; SING, iso).

Rhaphidophora jaculiformis Alderw., Bull. Jard. Bot. Buitenzorg III, 4 (1922) 197, **synon. nov.** — Type: Indonesia, Kalimantan, no further data, 1893, *Jaheri s.n.* (BO, holo; BO, iso).

Rhaphidophora subfalcata M. Hotta, Acta Phytotax. Geobot. 22 (1966) 6, **synon. nov.** — Type: Malaysia, Sarawak, 7th Div., Bintulu, along Sg. Kakus from Sg. Tinggili to Sg. Puteh, 13 Nov. 1963, *Hirano & Hotta* 1068 (KYO, holo).

Figure 12

Moderate sized, slender to slightly robust semi-leptocaul homeophyllous creeping and climbing liane to 5 m; *seedling stage* not observed; *pre-adult*

plants forming extensive terrestrial colonies; *adult shoot architecture* comprised of greatly elongated, clinging, physiognomically unbranched, sparsely leafy, non-flowering stems and short, little-branched, free, densely leafy, flowering stems; *stems* smooth, terete in cross-section, internodes to 10 x 1.7 cm on clinging shoots, much shorter on free shoots, separated by slightly oblique leaf scars, older stems subwoody; *flagellate foraging stems* absent; *clasping roots* sparsely arising from the nodes and internodes of clinging stems, pubescent; *feeding roots* rare, clinging, pubescent; *leaves* spiro-distichous on clinging shoots, distichous on free shoots; *cataphylls and prophylls* membranous, soon drying chartaceous and persisting at the tips of flowering shoots, then falling; *petiole* grooved canaliculate, 11—29 x 0.2—0.4 cm, apical and basal geniculum moderately prominent; *petiolar sheath* wide and membranous but very soon falling and thus usually not prominent, extending almost to or reaching apical geniculum, very soon drying and degrading into very sparse, soon-falling fibres; *lamina* entire to slightly perforated, perforations round to rhombic, extending c. $^1/_4$—$^1/_2$ of lamina width on each side of the midrib, oblong-lanceolate or oblong-elliptic, oblique, 12.5—42 x 3—10.5 cm, thinly coriaceous, base unequal, rounded, weakly acute to subrounded, apex acuminate; *midrib* prominently raised abaxially, ± sunken adaxially; *primary venation* pinnate, slightly raised abaxially and adaxially; *interprimaries* subparallel to primaries, much less prominent, slightly raised abaxially and adaxially; *secondary venation* prominently reticulate, raised abaxially, less so adaxially; *inflorescence* two, three or more, together, each subtended by a prominent chartaceous prophyll and one or more chartaceous cataphylls; *peduncle* slender to somewhat stout, terete, 4—1 x 0.2—0.3 cm; *spathe* broadly canoe-shaped, stout-beaked, 4—6 x 2—3.5 cm, stiff-fleshy, dull yellow on opening, persistent into early fruiting, eventually falling to leave a prominent scar; *spadix* stoutly to somewhat slender cylindrical, sessile, inserted obliquely on peduncle, 2.5—4 x 0.5—0.7 cm, dull cream; *stylar region* mostly hexagonal, 1.1—1.2 x 1—1.1 mm; *stigma* punctiform, very prominent, 0.1—0.2 x c. 0.3 mm; *anthers* exserted at male anthesis; *infructescence* stoutly oblong-cylindrical, 3.5—5 x 1.2—1.5 cm.

Distribution: Endemic to Borneo (Sarawak (1st, 3rd, 7th and 8th Divisions) and Kalimantan (West and Central).

Habitat: Primary to disturbed secondary lowland, often riverine, forest on clay-loam. 40—130 m altitude.

Notes: 1. Distinctive in Borneo by the short leafy free side shoots bearing clusters of inflorescences subtended and interspersed by prominent

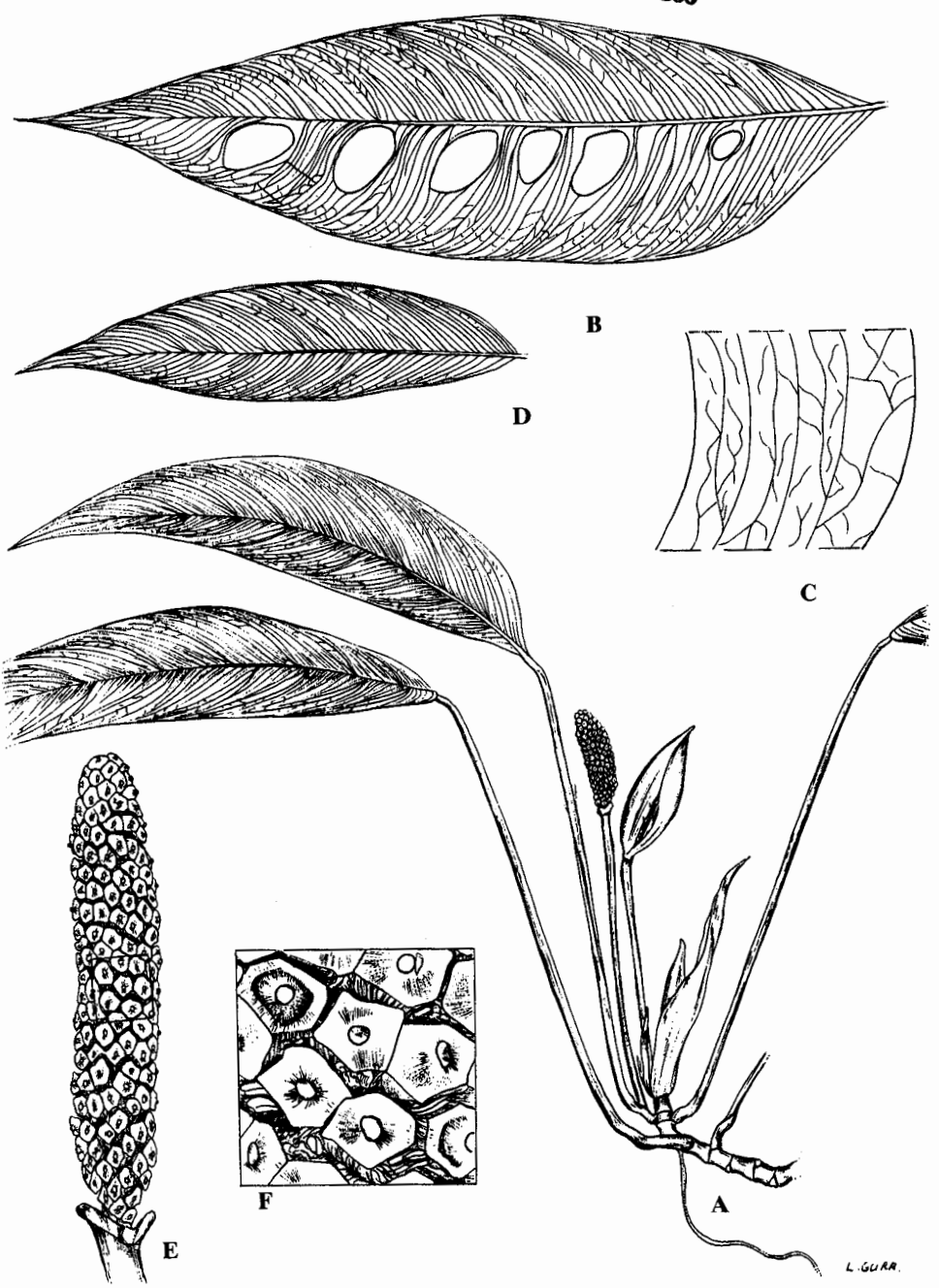

Figure 12. Rhaphidophora megasperma Engl.
A. flowering shoot x $^1/_3$; B. leaf lamina x $^1/_3$; C. venation detail x 2; D. leaf lamina x $^1/_3$; inflorescence, spathe removed x $1^1/_2$; E. spadix detail, post-male anthesis x 6; spadix detail, early fruiting x 4. A & F from *Ridley 14444*; B—E from *Burkill 6267*.

chartaceous prophylls and cataphylls and by the spathe drying and persistent into early fruiting. The clustered inflorescences subtended by chartaceous cataphylls recall some New Guinea species, notably *Rhaphidophora versteegii.*

2. Boyce (1999) merged *R. megasperma* with *R. puberula.* However, study of further Bornean specimens of both taxa clearly shows that this was in error and that *R. megasperma* is the earliest name for a Bornean endemic hitherto called *Scindapsus havilandii, Rhaphidophora jaculiformis* and *R. subfalcata.*

3. Hotta's name *R. subfalcata* has been applied to large plants of *R. megasperma* with perforated leaves. The presence of perforated and unperforated leaves in individuals of same species is not uncommon in *Rhaphidophora; R. puberula* is typical of such a phenomenon.

4. Both type sheets of Ridley's *Scindspaus havilandii* are fertile; so it is odd that Ridley should have considered it to belong to *Scindapsus* since the generic diagnostic characters, number and position of ovules (solitary and basal v. many on one or two parietal placentas), are readily observable.

5. The types of Aldrwerelt's *R. jaculiformis* match *R. megasperma* perfectly.

Other specimens seen: SARAWAK. 1st Div.: Matang, *Ridley s.n.* (K); 3rd Div.: Kapit, Sung, upper Sg. Katibas, Sg. Joh trail, *Zainudin et al. 4537* (K, UKMB); 7th Div.: Sg. Bejangung, a branch of the Sg. Anap, Bintulu District, *Hotta 15578* (KYO); 8th Div.: Bandar Sri Aman - Sibu road, 156 km before Sibu below bridge over the Sg. Undup, *Boyce 721* (K, M); Serian, Kg. Tebekang, *Othman & Munting S55097* (K, L, SAR). KALIMANTAN. West Kalimantan: Serawai, 8 km NE of Desa Jelundung, Batu Lintang, next to camp, *Church, Mahyer & Afriastini 1668* (BO, GH, K); Serawai, *Winkler 238* (E, L); Serawai, near Talok Nibung, *Winkler 1250* (E, L). Lake Tajan, *Main (sub. Polak) 1758* (BO, L); Upper Samba river, 60-80 km NNW of Tumbang Samba, Tumbang Habangoi to Tumbang Riang, *Mogea 3550* (BO, K, KEP, L); Central Kalimantan: Bt. Raya, *Nooteboom 4120* (L, BO);

11. Rhaphidophora minor Hook.f.

Rhaphidophora minor Hook.*f.*, Fl. Brit. Ind. 6 (1893) 544; Engl. & K. Krause in Engl., Pflanzenr. 37 (IV.23B) (1908) 21, Fig. 4; Merrill, J. Straits Branch Roy. Asiat. Soc., special number (1921) 89. — Type: Malaysia, Malacca, *Griffith 5988* (K, lecto; K, P, isolecto, selected by Boyce, 1999).

Rhaphidophora celebica K. Krause, Notizbl. Bot. Gart. Berlin-Dahlem. 11 (1932) 331. —Type: Indonesia, Sulawesi, northwest of the island, near

Toli-Toli, Jan. 1910, *Schlechter 20698* (B, holo).

[*Rhaphidophora palawanensis* Furtado, *nom. nud. in sched. var.*, *non.* Merr. (1925)]

Figure 13

Small to moderate, slender, leptocaul, homeophyllous liane to 6 m; *seedling* not observed; *pre-adult plants* forming diffuse terrestrial colonies; *adult shoot architecture* comprised of greatly elongated, clinging, physiognomically unbranched, leafy, non-flowering stems and long moderately elaborated, free, densely leafy, flowering stems; *stems* smooth, flexuous, climbing stems ± terete, occasionally weakly 4-angled in cross-section, free stems somewhat laterally compressed in cross-section, often branching extensively, growing to considerable lengths and pendent under their own weight with flowering tips upturned, without prophyll, cataphyll and petiolar sheath fibre, internodes to 13 x 1.2 cm on clinging and free shoots, flowering shoots with much shorter internodes, separated by weak straight leaf scars, older stems woody; *flagellate foraging stems* absent; *clasping roots* arising sparsely or singly from the clinging stems, pubescent; *feeding roots* solitary from nodes, free, stout, slightly pubescent; *leaves* weakly distichous and sparsely arranged on clinging and proximal portions of free shoots, moderately densely distichous distally on flowering shoots; *cataphylls and prophylls* membranous, very soon drying and falling; *petiole* grooved adaxially, 3—6 x 0.1—0.25 cm, smooth, with a slight apical and prominent basal geniculum; *petiolar sheath* slightly prominent, extending beyond the apical geniculum by two small ligules, very soon drying and falling in strips to leave a continuous scar from the petiole base, around the top of the apical geniculum and back to the base; *lamina* entire, narrowly falcate-elliptic to falcate-lanceolate or falcate-oblanceolate, 2.5—16 x 1.2—3 cm, thinly coriaceous, drying pale straw-coloured, base cuneate to acute or subovate, apex acute with a prominent apicule; *midrib* raised abaxially, slightly raised adaxially; *primary venation* pinnate, slightly raised on both surfaces prominent (raised) in dried material; *interprimaries* subparallel to, but much less distinctive than, primaries, sometimes degrading into weakly reticulate venation, very slightly raised abaxially; *secondary and tertiary venation* ± invisible in fresh material, barely visible in dried specimens, reticulate; *inflorescence* solitary, subtended by a fully developed foliage leaf and a very soon falling cataphyll; *peduncle* compressed-cylindric, 3—4 x 0.3—0.5 cm; *spathe* cigar-shaped, stoutly long-beaked, 3—9 x 1—1.5 cm, thin, dull green to dull yellow, soon falling at female anthesis to leave a large, straight, scar; *spadix* slender cylindrical, sessile, inserted level on peduncle, 2.5—7 x 0.5—0.6 cm, dull yellow-white; *stylar region* rather well developed, mostly

rhombohexagonal, 1.4—2 x c. 2 mm, truncate; *stigma* punctiform, c. 0.3 mm diam., slightly prominent in dried material; *anthers* well-exserted at male anthesis; *infructescence* oblong-cylindric, 4.5—7 x 1—2.5 cm.

Distribution: Southern Thailand, Peninsular Malaysia, Singapore, Sumatera, throughout Borneo (widely scattered), Sulawesi and into the Philippines (Mindanao, Palawan).

Habitat: Lowland peatswamp forest, riverine forest, rear of freshwater mangrove. Sea level to 10 m altitude.

Notes: 1. In the fresh state confusion with *Rhaphidophora sylvestris* is possible, although the thinner, more prominently veined leaf and longer spathe beak of *R. minor* Hook.*f.* are diagnostic. Dried material of *R. minor* is notable for the uniformly pale straw coloured leaves.

2. In Borneo, *R. minor* is habitually found in swampy habitats whereas elsewhere in its range it tends to be in drier places.

Other Bornean specimens seen: BRUNEI DARUSSALAM. Belait: Kuala Belait, *Van Niel 3944* (L); Seria, *Van Niel 4138* (L); Sg. Belait, *Van Niel 4634* (L). SARAWAK. 1st Div.: Kuching, *Hewitt s.n.* (K); Kuching, *Ridley s.n.* (SING); Kuching, *Ridley s.n.* (K). 7th Div.: Ulu Bawan, Balingian, *Ashton S 19585* (GH, K, L, MO, SAR, SING, US); Sg. Tengah, *Brooks 1016* (BM); Batang Lassa, near Rhuma Jumbau, *Mamit S 33623* (K, L, MO, SAR, US). SABAH. Sandakan: Beluran, Sg. Mangkayok, near Sg. Kalagan, *Meijer SAN 51617* (SAN); Ulu Dusum, *Meijer SAN 122736* (E, SAN, US). KALIMANTAN. West Kalimantan: Mempaura, *Teysmann 8105* (BO); Central Kalimantan: Sampit, *Buwalda 7917* (BO); East Kalimantan, 20 km north of Wanariset, Kg. Padang, Samboja, *Sidiyasa 1111* (K, L); Cape Genderen, Pladjoe, *Amdjah 7* (BO, K, L, SING), *Amdjah 32* (BO, L), *Amdjah 951* (BO, K, L); G. Samenggaris, *Amdjah 1084* (BO, K, L); South Kalimantan: no further data, *Winkler 3448* (L); Locality not traced: *Hallier 35, 66* (BO); Long Lansiah (?), *Teysmann 11338* (BO, L);

12. Rhaphidophora puberula Engl.

Rhaphidophora puberula Engl., Bot. Jahrb. Syst. 1 (1881) 180 & in Beccari, Malesia 1 (1882) 269—270; Engl. & K. Krause in Engl., Pflanzenr. 37 (IV.23B) (1908) 30. — Type: Indonesia, Sumatera, West Sumatera, Padang, Ajer Mantjoer, Aug. 1878, *Beccari s.n.* (FI, holo; B, iso).

Rhaphidophora scortechinii Hook.*f.*, Fl. Brit. India 6 (1893) 545; Engl. & K. Krause in Engl., Pflanzenr. 37 (IV.23B) (1908) 23. — Type: Malaysia, Perak, *Scortechini 347* (K, holo; CAL, iso).

Rhaphidophora kunstleri Hook.*f.*, Fl. Brit. Ind. 6 (1893) 546; 548; Engl. &

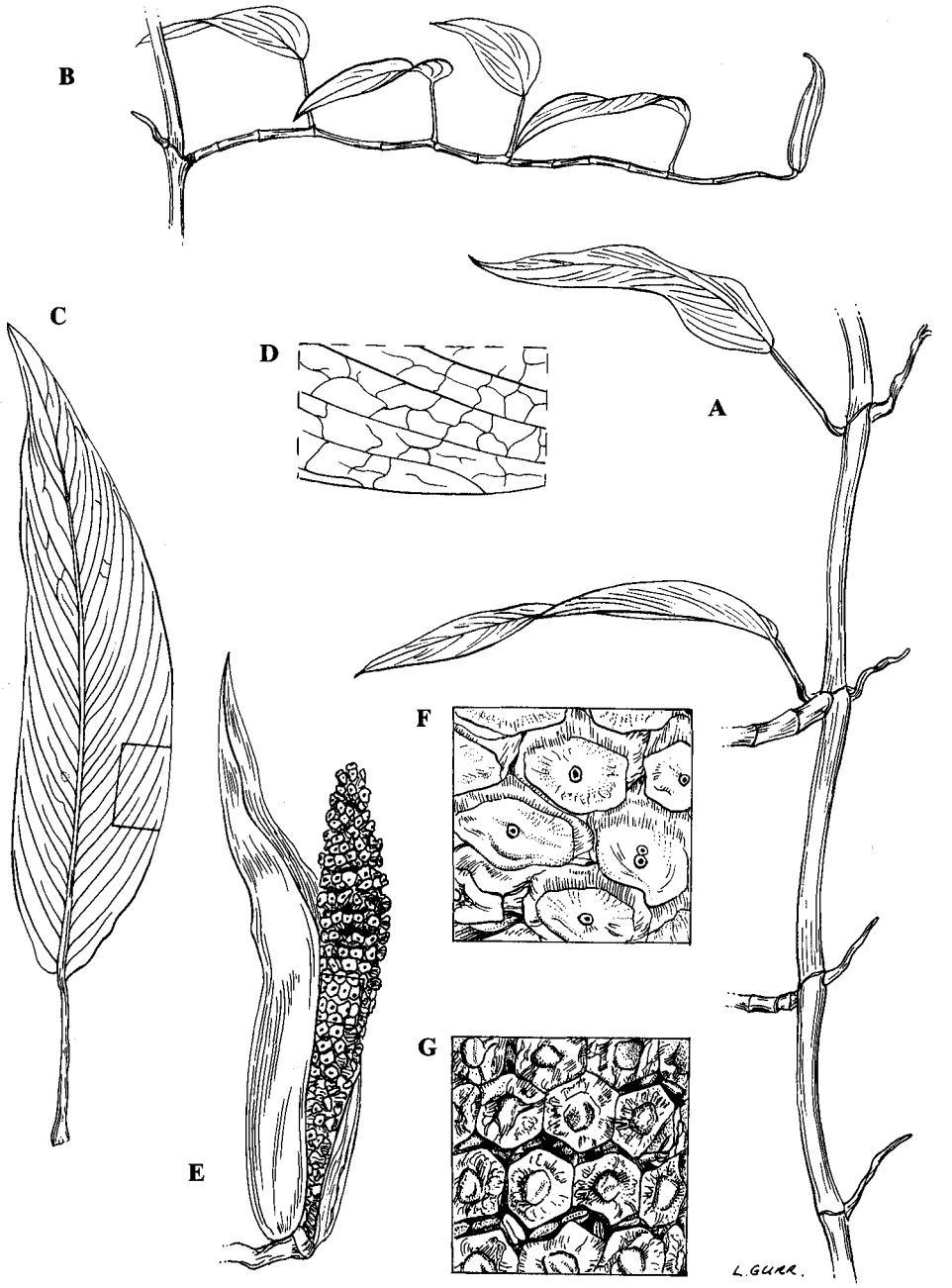

Figure 13. Rhaphidophora minor Hook.*f.*
A. portion of adult, sterile shoot x $^1/_3$; B. flowering shoot x $^1/_2$; C. leaf lamina x $^2/_3$; D. venation detail x 2; E. inflorescence, spathe just beginning to abscise x $1^1/_2$; F. spadix detail, post-female anthesis, pre-male anthesis x 8; G. spadix detail, early fruiting x 5. A & D from *Winkler 238*; B & from *Church et al. 1668*; E & F from *Hotta 1068*.

K. Krause in Engl., Pflanzenr. 37 (IV.23B) (1908) 30; Alderw., Bull. Jard. Bot. Buitenzorg III, 4 (1922) 338. — Type: Malaysia, Perak, Bt. Larut, July 1883, *Kunstler 4538* (K, lecto, selected by Boyce, 1999).

Rhaphidophora gracilipes Hook.*f.*, Fl. Brit. Ind. 6 (1893) 545; Engl. & K. Krause in Engl., Pflanzenr. 37 (IV.23B) (1908) 30, Fig. 10; Alderw., Bull. Jard. Bot. Buitenzorg III, 1 (1920) 384. — Type: Malaysia, Perak, June 1886, *Kunstler 10271* (K, lecto; BM, SING, isolecto, selected by Boyce, 1999).

Rhaphidophora batoensis Engl. & K. Krause in Engl., Pflanzenr. 37 (IV.23B) (1908) 27. — Type: Indonesia, Sumatera, North Sumatera, Kepulauan Batu, 25 Sept. 1896, *Raap 370*, (B, lecto; BO, isolecto, selected by Boyce, 1999).

Rhaphidophora hallieri Alderw., Bull. Jard. Bot. Buitenzorg III, 1 (1920) 385; Alderw., Bull. Jard. Bot. Buitenzorg III, 4 (1922) 196. — Type: Kalimantan, *Hallier 1187* (BO, holo; BO iso).

Rhaphidophora pilosula Alderw., Bull. Jard. Bot. Buitenzorg III, 1 (1920) 386; Alderw., Bull. Jard. Bot. Buitenzorg III, 4 (1922) 196. — Type: Cult. Bogor Bot. Gard, June 1919, *Alderwerelt s.n.* (BO, holo).

Figure 14

Moderate to large, rather robust, semipachycaul homeophyllous liane to 5 m; *seedling stage* not observed; *pre-adult plants* often forming small terrestrial colonies; *adult shoot architecture* comprised of elongated, clinging, physiognomically unbranched, leafy, non-flowering stems and short, usually unbranched, free, densely leafy, flowering stems; *stems* smooth, terete in cross-section, with very sparse prophyll, cataphyll and petiolar sheath fibre, this soon falling, internodes to 13 x 1.5 cm on clinging shoots, usually shorter and stouter on free shoots, separated by large, straight, corky leaf scars, older stems woody; *flagellate foraging stems* absent; *clasping roots* sparsely arising from the nodes and internodes of clinging stems, pubescent; *feeding roots* rare, clinging, pubescent; *leaves* distichous on clinging and free shoots; *cataphylls and prophylls* membranous, soon drying and degrading into very sparse fibres, these soon falling; *petiole* deeply grooved to basally canaliculate, 9—33 x 0.2—3 cm, with the distal portion and apical geniculum minutely pubescent, especially when newly expanded, apical and basal geniculum moderately prominent; *petiolar sheath* very prominent, extending to just below the apical geniculum, soon drying and degrading into sparse, soon-falling fibres; *lamina* entire to slightly perforated, perforations round to rhombic, extending c. $^1/_5$—$^1/_4$ of lamina

width on each side of the midrib, ovate to oblong-lanceolate or oblong-elliptic, oblique to falcate, minutely pubescent abaxially when young, 8—34 x 3.5—10.5 cm, thinly coriaceous to subchartaceous, base unequal, rounded, acute to slightly decurrent, apex acute to acuminate; *midrib* prominently raised and pubescent abaxially, ± sunken adaxially; *primary venation* pinnate, slightly raised abaxially and adaxially, the leaf appearing slightly quilted, pubescent in younger leaves, indumentum mostly shed in older leaves; *interprimaries* subparallel to primaries, very slightly less prominent, slightly raised abaxially, slightly impressed adaxially; *secondary venation* tessellate to weakly reticulate, slightly raised; *tertiary venation* not visible; *inflorescence* solitary, very rarely two together, fragrant of frangipani and pineapple (*fide Hay et al.* 9029) subtended by a fully developed foliage leaf and, if more than one inflorescence, then second preceded by a large cataphyll; *peduncle* strongly compressed-cylindric, 4—9 x 0.4—0.6 cm; *spathe* canoe-shaped, stoutly long-beaked, 5.5—19 x 1—6.5 cm, stiff-fleshy, dull green to dull yellow, pale yellow to apricot-orange internally, falling (after?) female anthesis to leave a large, straight scar; *spadix* very weakly clavate cylindrical, sometimes slightly curved, sessile, inserted ± level on peduncle, 3—11.5 x 1—1.6 cm, cream; *stylar region* mostly hexagonal, 1.5—2 x 2.1—2.5 mm, truncate; *stigma* punctiform, prominent, 0.5—0.75 x 0.45—0.75 mm; *anthers* exserted at male anthesis; *infructescence* stoutly oblong-cylindrical, 4.5—14 x 1.5—2 cm, glaucous.

Distribution: Sumatera, Peninsular Malaysia, Nusa Tenggara and throughout Borneo.

Habitat: On trees and rocks in primary and secondary lowland to lower/upper montane transition forest, often on steep slopes, on granite and limestone. 90—1550 m altitude.

Notes: 1. Given the overall uniformity of this species, it is quite extraordinary that *Rhaphidophora puberula* should have been redescribed no fewer than seven times based mostly on minor differences of leaf shape.

2. Superficially similar to *R. foraminifera*, especially in the perforate-leaf forms, *R. puberula* can readily be distinguished from *R. foraminifera* by the production of inflorescences on free lateral shoots and in having the active shoot tips without the characteristic black mucilage of *R. foraminifera*. Generally, flowering plants of the perforate-leaved forms of *R. puberula* have smaller leaves that are noticeably *less* perforated than those of *R. foraminifera*.

Other Bornean specimens seen: SARAWAK. 1st Div.: Matang, *Ridley s.n.* (K); 4th Div.: Baram District, G. Mulu N.P., Hidden Valley, *Argent et al. 887* (L); 7th Div.: Bintulu, Segan F.R., *Chai S31999* (K, L, SAN, SAR, SING, US). BRUNEI DARUSSALAM. Belait: Labi, track to Rampayoh waterfall, *Ahmad 15* (BRUN, K). SABAH. Sandakan: Bettohan near Sandakan, *Kloss SFN 19099* (K, L, SING); Lamag, Kinabatangan, Ulu Sg. Pin, *Madani & Saigol SAN 90180* (K, L, SAN, SAR); Pantai Barat: Keningau, Sg. Labou, *Mantor SAN 110980* (GH, K, SAN); Tuaran District, below summit of Lawa Mandau, Telekom station east of Telipok, *Meijer et al. SAN 136186* (GH, SAN); Pedalaman: Kiau, Mount Kinabalu, *Clemens 10142* (UC); Gurulau Spur, Mount Kinabalu *Clemens 10772* (UC); Dallas, *Clemens & Clemens 26453* (BM, K, L, SING); Dallas, *Clemens & Clemens 26781* (BM); Dallas, *Clemens & Clemens 26876* (BM, BO, GH, K, L, SING, UC); Tenompok, *Clemens & Clemens 26900* (BM, BO, K, L, SING, UC); Kinabalu N.P., along the road between Park H.Q. and Tenompok, *Kokawa & Hotta 3089* (KYO); Tawau: *Elmer 21593* (BO, K, L, MO, SING, UC); Sabah Foundation logging area Umas-Umas, *Krispinus SAN 87213* (K, KEP, L, SAN, SAR); Kalabakan, km 41 Imbak road, Luasong, *Krispinus SAN 95680* (K, L, SAN, SAR); Lahad Datu, Madai Caves, Madai Baturong F.R., *Kokawa & Hotta 1097* (KYO, L). Locality not traced: Pandawan, Sg. Mesopo, *Fidilis & Sumbing SAN 113389* (K, KEP, SAN); KALIMANTAN. Cult. Bogor, Y70, from Kalimantan collection, *Ashton 12626* (BM, BO) & *Nicolson 942* (BO, L, US).

13. Rhaphidophora sylvestris (Blume) Engl.

Rhaphidophora sylvestris (Blume) Engl. in A. & C., DC, Monogr. Phan. 2 (1879) 239 & in Beccari, Malesia 1 (1882) 268; Engl. & K. Krause in Engl., Pflanzenr. 37 (IV.23B) (1908) 22—25, Fig. 6 (*'silvestris'*); Alderw., Bull. Jard. Bot. Buitenzorg III, 1 (1920) 383; Merrill, J. Straits Branch Roy. Asiat. Soc., special number (1921) 90 (*'silvestris'*). — *Calla sylvestris* Blume, Catalogus (1823) 62. — *Scindapsus sylvestris* (Blume) Kunth, Enum. pl. 3 (1841) 64; Miq., Flora Ned. Indië 3 (1856) 187—188. — [*Scindapsus angustifolius* Hassk., Flora 25 (2), Beibl. 1 (1842) 12, *nom. illeg.* — *Rhaphidophora angustifolia* (Hassk.) Schott in Bonplandia 5 (1857) 45, *nom. illeg.* — based on the type of *Calla sylvestris* Blume]. — Type: Indonesia, Java, *Blume 178* (L, lecto; L, LE, isolecto, selected by Boyce, 1999).

Scindapsus lingulatus Hassk., Flora 25(2) Beibl. 1 (1842) 12; Schott, Prodr. Syst. Aroid. (1860) 378; Engl. in A. & C., DC, Monogr. Phan. 2 (1879) 248. — *Rhaphidophora lingulata* (Hassk.) Schott, Bonplandia 5 (1857) 45. — *Monstera lingulata* (Hassk.) C. Koch ex Ender, Index Aroid. (1864) 74. — Type: Indonesia, Java, *Hasskarl s.n.* (not traced, see Boyce, 1999).

Scindapsus aruensis Engl., Bull. Soc. Tosc. Ortic. 4 (1879) 270. — Type: Indonesia, Melaku, Aru Islands, Gabu-lengaw, May 1873, *Beccari s.n.* (FI, holo).

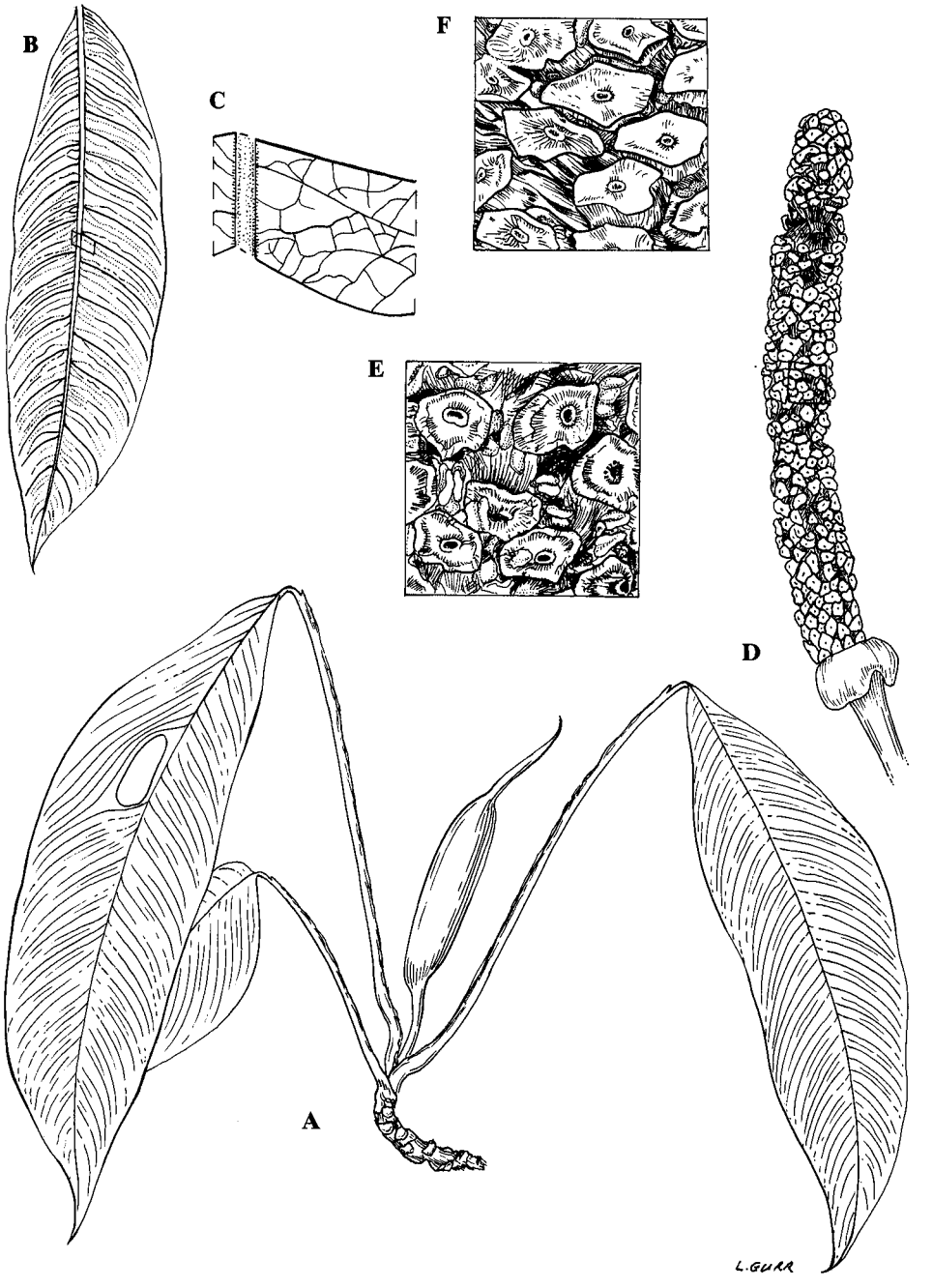

Figure 14. Rhaphidophora puberula Engl.
A. flowering shoot x $^1/_2$; B. leaf lamina x $^1/_3$; C. venation detail x 6; D. inflorescence, spathe removed x 2; E. spadix detail, post-male anthesis x 6; F. spadix detail, early fruiting x 4. A & F from *Ridley 14444*; B—E from *Burkill 6267*.

Rhaphidophora wrayi Hook.*f.*, Fl. Brit. India 6 (1893) 544; Engl. & K. Krause in Engl., Pflanzenr. 37 (IV.23B) (1908) 34. — Type: Malaysia, Perak, Larut, Besar, April 1882, *Kunstler 2939* (K, lecto, selected by Boyce, 1999).

Rhaphidophora gratissima Becc., Nelle Foreste di Borneo (1902) 604. — *Rhaphidophora sylvestris* var. *obtusata* Engl., Malesia 1 (1883) 268 — Type: Malaysia, Sarawak, 1st Div., Kuching, Nov.1865, *Beccari PB 952* (FI, holo; FI spirit 423, K, iso).

Rhaphidophora nigrescens Ridl., J. Straits Branch Roy. Asiat. Soc. 44 (1905) 185 ('*migrescens*'), **synon. nov.** — Type: Malaysia, Sarawak, 1st Div., Matang, July 1903, *Ridley* s.n. (SING, lecto, selected here). Ridley cites two conspecific syntypes, that chosen is the best specimen for identification purposes. The other syntype is: Malaysia, Sarawak, 19 June 1893, *Bartlett* s.n. (SING).

Rhaphidophora motleyana Engl. & K. Krause in Engler, Pflanzenr. 37 (IV.23B) (1908) 25; Merrill, J. Straits Branch Roy. Asiat. Soc., special number (1921) 89. — Type: Indonesia, Kalimantan, South Kalimantan, Bangarmassin, 1857—1858, *Motley 741* (K, holo).

[*Scindapsus lanceolataus* Miq. *nom. nud. in sched.* BO]

[*Pothos cucculata* Zipp. *nom. nud. in sched.* L]

Figure 15

Medium to large, occasionally very large, moderately robust, leptocaul to semi-pachycaul homeophyllous liane to 20 m; *seedling stage* a non-skototropic shingling shoot; *pre-adult plants* very seldom forming small terrestrial colonies of appressed shingling shoots; *adult shoot architecture* comprised of greatly elongated, clinging, physiognomically unbranched, leafy, non-flowering stems and long, moderately elaborated, free, densely leafy, flowering stems later pendent under their own weight; *stems* smooth, climbing stems rectangular in cross-section, the angles often slightly winged, the surfaces between slightly concave, free stems rectangular to subterete in cross-section, green, later mid-brown, without prophyll, cataphyll and petiolar sheath fibre, internodes to 2.5—5 x 0.5—1 cm on clinging shoots, usually less stout on free shoots, separated by weakly defined, slightly oblique leaf scars, older stems woody; *flagellate foraging stems* frequent, often of great length, ± rectangular in cross-section; *clasping roots* densely

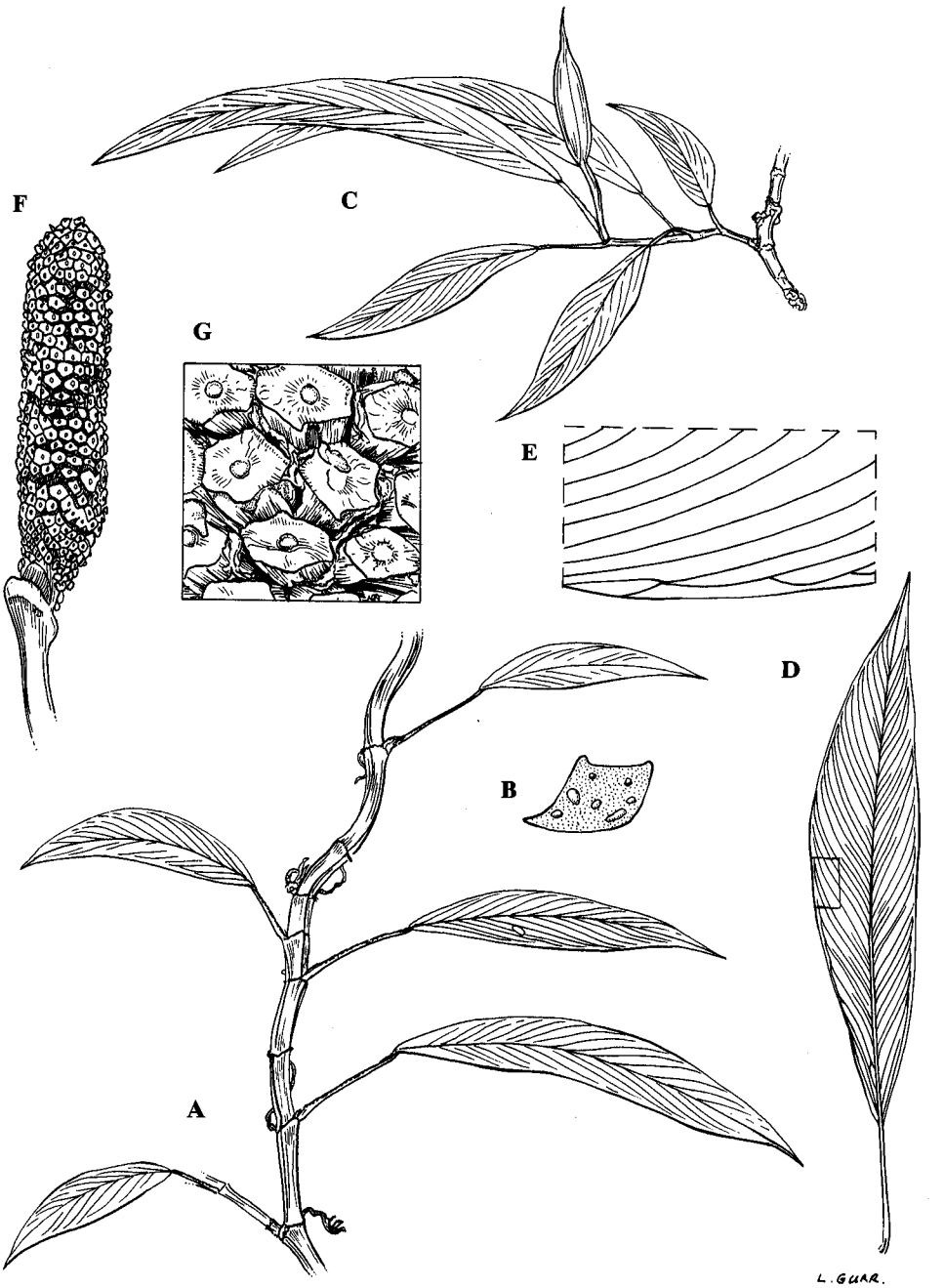

Figure 15. Rhaphidophora sylvestris (Blume) Engl.
A. portion of adult sterile stem x $^1/_3$; B. stem cross-section x 1; C. flowering shoot x $^1/_3$; D. leaf lamina x 1; E. venation detail x 4; F. inflorescence, spathe fallen x 1; G. spadix detail, post-male anthesis x 4. A & B from *Backer 11199*; C, F & G. from *de Wilde & de Wilde-Duyfjes 13830*; D & E from *Afriastini 2399*.

arising from the nodes and internodes of clinging stems, pubescent; *feeding roots* very rare, clinging, pubescent; *leaves* distichous on clinging and free shoots, those distal on flowering shoots densely so; *cataphylls and prophylls* membranous, very soon drying and falling; *petiole* deeply grooved adaxially, 1—8.5 x 0.15—0.3 cm, smooth, apical and basal genicula weakly defined; *petiolar sheath* very prominent, extending to and encircling the apical geniculum, briefly ligulate, very soon drying and falling to leave a continuous conspicuous scar from the petiole base, around the top of the apical geniculum and back to the base; *lamina* entire, lanceolate-elliptic to falcate-lanceolate, slightly to markedly oblique, 4.5—32 x 1.75—8.5 cm, thinly coriaceous, upper surfaces slightly glossy, lower surfaces semi-matt, base subacute to briefly truncate, apex acute to slightly attenuate, with a prominent apiculate apicule; *midrib* slightly raised abaxially, slightly sunken adaxially; *primary venation* pinnate, slightly raised abaxially and adaxially; *interprimaries* parallel to primaries and only slightly less prominent, very slightly raised abaxially and adaxially; *secondary* and *tertiary venation* ± obscure in fresh material, visible as a faint reticulum in dried specimens; *inflorescence* solitary, subtended by a fully developed foliage leaf; *peduncle* compressed-cylindric, 2—8.5 x 0.15—0.5 cm; *spathe* cigar-shaped, stoutly very short-beaked, 4.5—7.5 x 1—3 cm, thinly stiff-fleshy, dull yellow, paler internally, soon falling at female anthesis; *spadix* cylindric to weakly clavate-cylindrical, sessile, inserted ± level on peduncle, 3—6 x 1—2.5 cm; *stylar region* mostly rhombohexagonal, 1—2 x 1.5—2 mm, truncate; *stigma* punctiform, raised, c. 0.25—0.3 mm diam.; *anthers* exserted at male anthesis; *infructescence* 6—8 x 2—2.5 cm.

Distribution: Peninsular Malaysia, Sumatera, throughout Borneo, Java, Nusa Tenggara and Maluku.

Habitat: Primary to disturbed secondary lowland to lower montane forest on a variety of substrates including sandy loam and limestone. 120—1800 m altitude.

Note: *Rhaphidophora sylvestris* is more variable in Borneo than in other parts of its range (e.g. Peninsular Malaysia, Java) but the paucity of collections coupled with more or less continuous variation makes it impossible to be confident that more than one species is involved. Of particular note is the occurrence of plants with coriaceous leaf laminas that have variously been described as *Rhaphidophora gratissima* Becc. (syn. *R. sylvestris* var. *obtusata* Engl.) and *R. nigrescens* Ridl.. Such plants approach *R. conocephala* in appearance (and also resemble non-Bornean *R. crassifolia*), although the flat-topped styles readily distinguish them from

R. conocephala, while the juvenile shoots without conspicuously twisted stems separate them from *R. crassifolia.* Lamina thickness is not a consistent character, even between duplicates of the same collection.

Other Bornean specimens seen: SARAWAK. 1st Div.: G. Pueh (Mt Poi), base camp, *Clemens & Clemens 21935* (K); Matang, *Kochummen FRI 29145* (KEP, GH, K, L, SING); Kuching, *Ridley s.n.* (K); Puak, *Ridley 12413* (BM, K, SING); Kuching, Tiang Bekap, G. Maja, *W.L. Chew 714* (L, SING). SABAH. Pantai Barat: Ranau, Bt. Hampuan, *Amin & Jarius SAN 121155* (K, SAN); Mt Kinabalu, Bungal trail, *Clemens & Clemens s.n.* (SING); Dallas, *Clemens & Clemens 26720* (K, SING), *Clemens & Clemens 26921* (BM, BO, K, L, SING), *Clemens & Clemens 27030* (BM, BO, K, L, SING, US), *Clemens & Clemens 27312* (BM, BO, K, SING); Upper Kinabalu, Mementong, Mesilau Basin, *Clemens & Clemens 28487* (BM, K, L, SING); Tenompok, *Clemens & Clemens 29227* (BM, BO, K, L, SING, UC); Ranau, Mt Kinabalu, Mesilau valley, *Cockburn SAN 70108* (SAN); Kinabalu N.P., along Sg. Mesilau from Mesilau Camp to Mesilau Cave, *Kokawa & Hotta 3995* (KYO); Kinabalu, Penibukan, Sg. Tahubang, *Nooteboom & Aban 1582* (L). BRUNEI DARUSSALAM. Belait: Sg. Keduan, off Sg. Belait, *Forman 1174* (BRUN, K). KALIMANTAN. Central Kalimantan: Sintang, HPH km 70, west camp off main (new) logging road, *Church et al. 985* (BO, GH, K), 'Borneo', *Korthals 153, Korthals s.n.* (L).

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