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SANDAKANIA No. 12 **December, 1998**

CONTENTS

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A new species of *Parartocarpus* (*Moraceae*) from Sabah

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Summary. A new species, *Parartocarpus spinulosus*, is described from Sabah, so far known only from sites with ultramafic geology.

Parartocarpus was revised by Jarrett (1960). In my revision of the genus *Parartocarpus* for the Tree Flora of Sabah and Sarawak, two collections from the Telupid district in Sabah representing a peculiar taxon were noted.

Jarrett annotated a Kew duplicate of the earlier (1976) collection *Leopold* SAN 43885 as *P. venenosus* ssp. *borneensis* (Zoll. & Mor.) Jarrett. Apparently, the usually strongly emarginate apex, the strongly recurved margin and the spinulose, sandpaper-like surface of the leaf in this specimen were overlooked. *Parartocarpus venenosus* ssp. *borneensis* (Zoll. & Mor.) Jarrett sometimes has leaves with a rounded to emarginate apex, but not the sandpaper-like surface or the conspicuously recurved margin. The second collection, *Soepadmo et al.* FRI 41312, made in 1994, also has the same characters. The distinction between these two taxa is well shown by studies of leaf surface by electron microscopy which reveals differing hair types and stomata. A study of the Malesian material revealed that the unusual taxon noted here is unnamed. Moreover, there are also distinctive characters in the flowering and fruiting heads that clearly distinguish this taxon from others (see key below).

KEY TO *PARARTOCARPUS* SPECIES

1. Flowering heads bisexual; leaf lateral veins forking to form irregular, rather jagged vein-loops near the margin ..... **P. microcarpus** Corner
   Flowering heads unisexual; leaf lateral veins forming firm, smooth vein-loops near the margin 2

2. Male flowering heads and fruiting heads similar in size, small, to 1–1.5 cm across only. Leaf surface evenly covered in minutely spine-like and very sparse scattered soft hairs, sandpaper-like to the touch ..... **P. spinulosus** sp. nov.
Male flowering heads much smaller than fruiting heads, male flowering heads 2–3.5 cm across, fruiting heads 3–10 cm across. Leaf surface not spinulose, but either scantily or densely covered with soft hairs only, smooth to the touch 3

3 Peduncles densely covered in short patent hairs; bracts subtending flower heads 6–8 mm long. Syncarp processes spine-like, the spines 3–5 mm long and 2–3 mm across at their bases. Lower leaf surface densely velvety hairy all over ..... **P. bracteatus** (King) Becc.
Peduncles sparsely covered in short appressed hairs; bracts subtending flower heads 3–5 mm long. Syncarp processes truncate to flattened or spine-like, the spines mostly 4–7 mm long and 3–5 mm across at their bases. Lower leaf surface glabrous or at most with scattered hairs on the veins ..... **P. venenosus** (Zoll. & Mor.) Becc.

Parartocarpus spinulosus *R. Go* **sp. nov.** *a P. venenoso similis, sed foliorum apice valde emarginato, marginibus valde recurvatis, ambabus paginis aequaliter spinulosis differt. Typus: Soepadmo, Rena & Kalkausar, FRI 41312, Sabah, Telupid, Bukit Tawai Forest Reserved (holotypus KEP; isotypi K, L, SAN, SAR).* (Figs. 1, 2A–C)

Medium-size tree to 10 m tall, 12 cm diameter. Bark scaly to shallowly fissured, brown; inner bark yellow; sapwood pale yellow; sap milky white. Twigs with sparse appressed short hairs when young, glabrescent at maturity; stipules small, 1.5 × 1 mm, connate, caducous; terminal buds small, 1 × 1 mm, connate. Petiole 2–3 cm long, terete, sparsely stiff hairy when young to glabrescent in maturity; leaves obovate, 8–14(–16) × (4–)5–7 cm, thick-coriaceous, base cuneate with small auricular projections, apex typically strongly emarginate, rarely rounded, margin entire, conspicuously recurved when dry, with an even cover of minute spine-like hairs (giving a sandpaper-like texture to both surfaces) and soft clavate hairs; stomata on the lower surface sunken; midrib and lateral veins somewhat flat to prominent above, raised beneath; lateral veins 8–10 pairs, forming firm, smooth vein-loops near the margin. Flowering heads unisexual. Male head globose, 1–1.5 cm diameter with 4 persistent inflorescence bracts, peduncle 2–4 cm, glabrous. Female flower not seen. Flower each with 2 stamens, anthers lanceolate, basifixed, slender, 0.5–1 mm long, exserted at anthesis. Syncarp globose, up to 5 cm diameter, with blunt or truncate processes; seeds numerous, attached to a club-shaped receptacle, perianth fleshy.

DISTRIBUTION. Rare, only known from the Telupid area, Sandakan district, Sabah.

HABITAT. Mixed dipterocarp forest at about 150 m altitude, on ultramafic soil. Flowering recorded in March, fruiting in June.

TAXONOMY. The species epithet refers to the spinulose leaf surface, which gives it the sandpaper-like texture. Its closest ally is *Parartocarpus venenosus* ssp. *borneensis*, which also

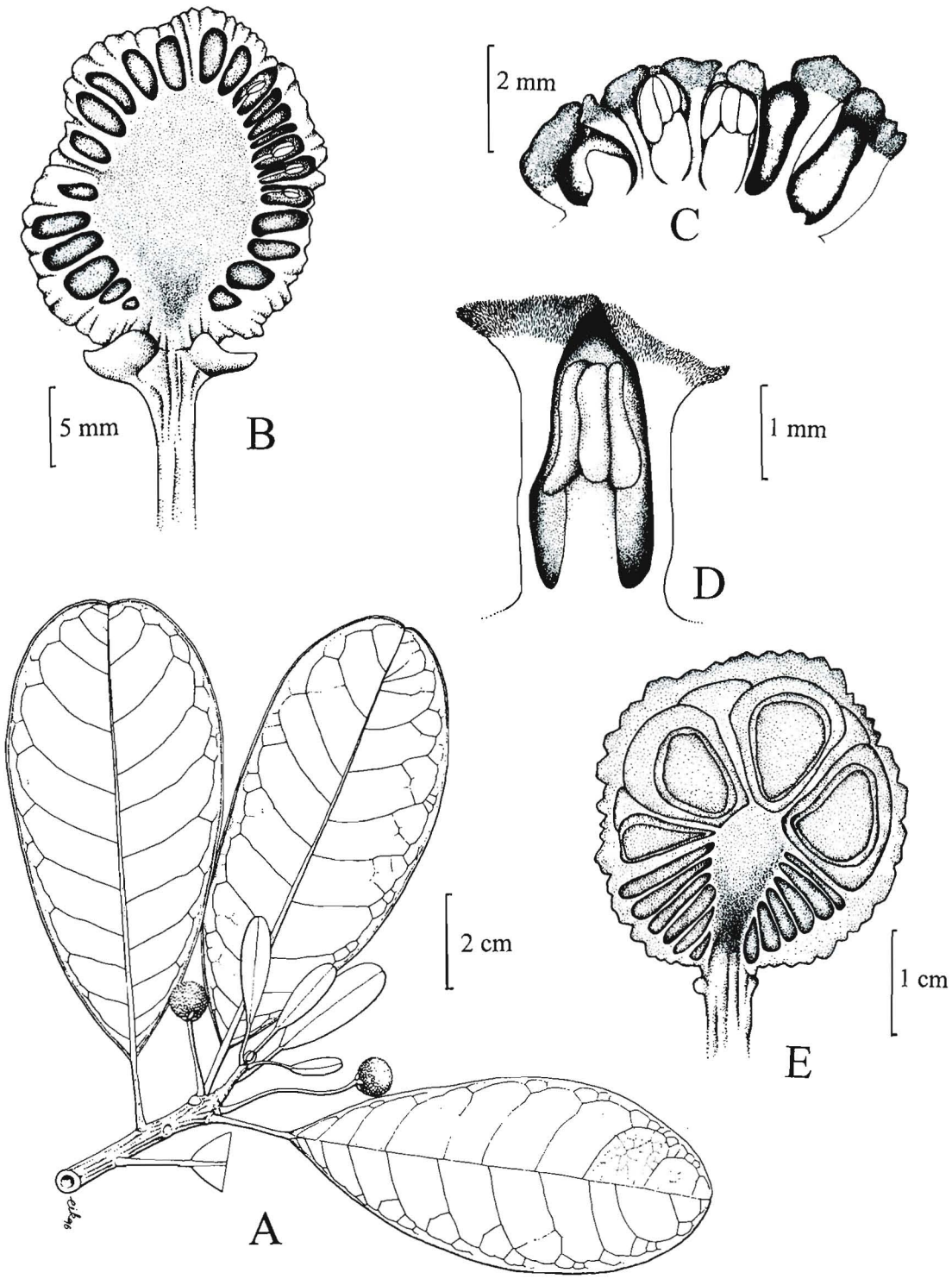

Fig. 1. *Parartocarpus spinulosus* **A**, flowering twig. **B**, cross-section of a male head. **C**, detail of cross-section through male head. **D**, male flower. **E**, cross-section of fruit-head.

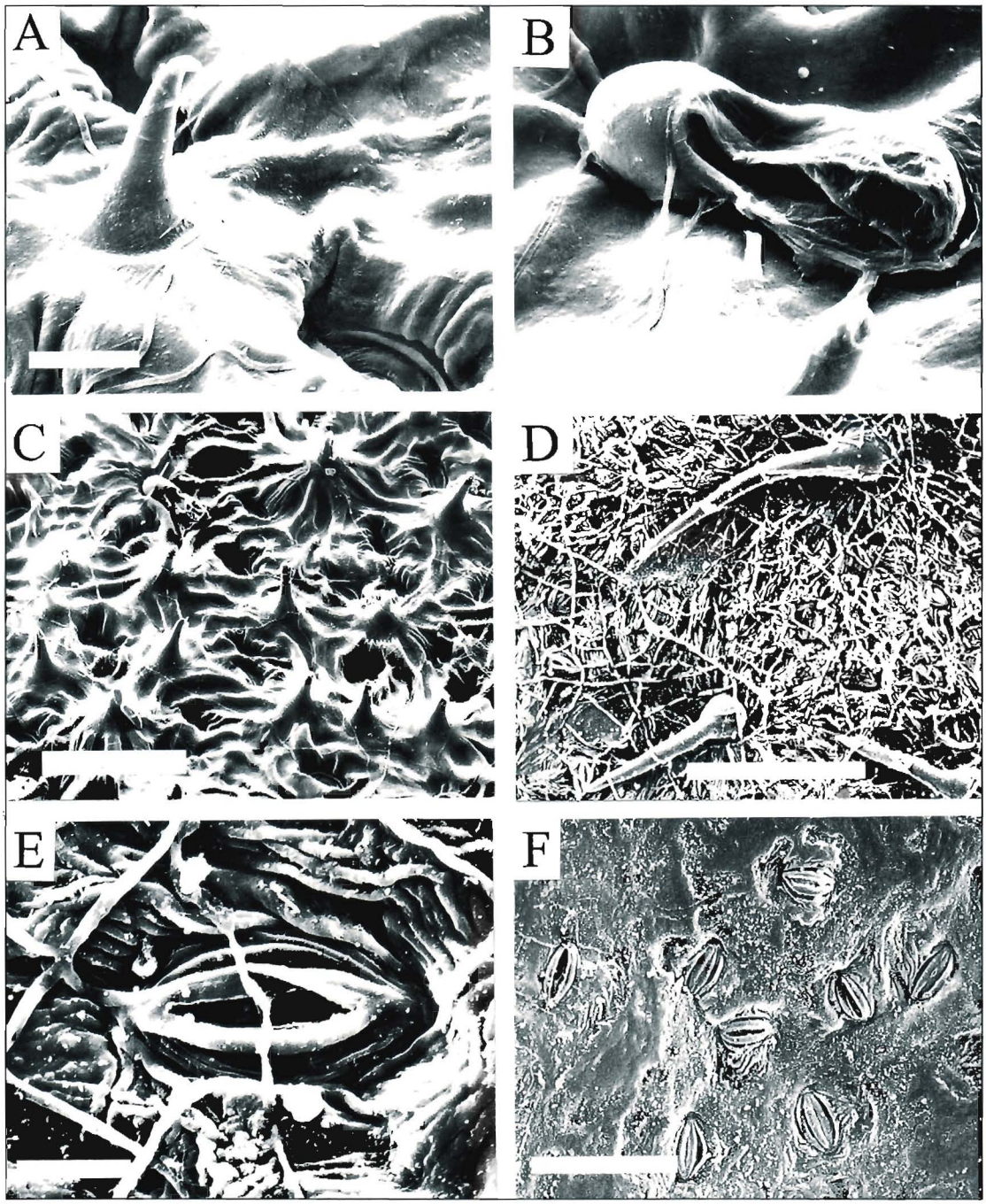

Fig. 2. Leaf surface features in *Parartocarpus spinulosus* (A–C) and *P. venenosus* ssp. *borneensis* (D & E). **A**, spine-like hairs with hooked tips on the lower surface and sunken stomata (lower right side). **B**, soft clavate hairs on the lower surface. **C**, general surface view. **D**, long soft slender unicellular hairs. **E**, stoma. **F**, the glabrous lower surface and stomata. Bar represents 20 mm (in A, B) and 100 mm (in C–F).

sometimes has a rounded to emarginate leaf apex, but not the sandpaper-like surface (Fig. 2D). Moreover, the sunken stomata on the lower leaf surface in *P. spinulosus* (Fig. 2A) distinguishes it from *P. venenosus* (Zoll. & Mor.), which has stomata at the general level of the leaf surface (Fig. 2E).

SPECIMENS EXAMINED—BORNEO. SABAH: Sandakan, Telupid, Hup Seng Logging Camp, *Leopold* SAN 43885 (K, L, SING, SAR, KEP, SAN); Upper Sg. Meliau, *Soepadmo et al.* FRI 41312 (KEP, SAN, SING, K, L, SAR).

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Jarrett, F.M. (1960) Studies in *Artocarpus* and allied genera.V. A revision of *Parartocarpus* and *Hullettia*. *J. Arn. Arb.* 41(3): 320–340.

SANDAKANIA 12 (1998): 7–24

Notes on the orchid flora of Mount Kinabalu, Borneo

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Summary. A supplement to the treatment of the Orchids of Mount Kinabalu (Wood *et al.*, 1993) is presented below. Included are references to 14 recently described taxa, 21 new records, and 5 taxa that have been reduced to synonymy or have undergone name changes. Our current estimate of the number of orchid taxa on Mount Kinabalu is 745; however, more accurate figures await taxonomic revisions of several problematic genera.

The following notice appeared in *The Orchid Review* (Vol. 3, no. 36: 356) for December 1895:—

> "Orchid Collecting in British North Borneo. The following proclamation is taken from the Official Gazette, British North Borneo, for August 1st. 1895:—Orchid Collecting.—No permit to travel for the collection of orchids in Province Keppel and the District of Kinabalu is to be issued until further orders. Any person travelling or collecting orchids without a permit is liable to a penalty of 500 dols., or to imprisonment under Proclamation VII of 1890. Sandakan, July 9th, 1895."

Although these words are as relevant today as they were 100 years ago, controlled collecting for scientific and ethnobotanical purposes continues in the environs of Mount Kinabalu. An extensive collecting programme is currently underway through *Projek Etnobotani Kinabalu* (PEK). This project, initiated in 1992, aims to link ethnobotanical research with conservation action by strengthening: 1)the link between Kinabalu Park and local communities; 2) interpretive programmes that reach most of the 200,000 visitors who come to the Park each year; 3) the scientific infrastructure available in the Natural History Museum of the Park; 4) the ability of local Dusun people to use botanical resources in a sustainable way; and 5) the assessment of the sustainability and value of plant resources in and around the Park. The PEK

collections have resulted in the addition of 13 of the 35 new orchid records for Mount Kinabalu reported here.

A team of 12 local people have been incorporated into the project as ethnobotanical collectors. Thus far they have obtained nearly 7000 herbarium specimens that have been submitted to the Royal Botanic Gardens, Kew, for identification. All of the monocotyledons, amounting to about 750 specimens, are already identified, and these include 127 orchid collections. The PEK collections have resulted in a dramatic increase in the known flora of Mount Kinabalu, including the addition of eight families, nearly 50 genera and about 150 species to the monocotyledons previously unrecorded from the mountain.

Wood *et al.* (1993) listed some 711 orchid taxa in 121 genera from Mount Kinabalu (4095 m), the highest mountain in Southeast Asia. Of these taxa, 596 were fully named, seven were questionably identified and a hundred more were incompletely identified. Since publication of the enumeration, 14 new taxa have been described, most of the types of which have been collected on Mount Kinabalu. Several additional taxa have also been recently recorded from the mountain and other information has been gathered.

For the purposes of this paper, we included all the area within Kinabalu Park and various adjacent *kampung* (villages) as parts of Mount Kinabalu. As such, Mount Tambuyukon, the third highest peak in Sabah, is included as part of this region. Mount Kinabalu and Tambuyukon are separated by less than 5 km with several mountain ridges more or less connecting them and therefore we feel justified in treating the two as a single area. We have maintained the format of the orchid checklist published by Wood *et al.* (1993) because this compilation is intended to serve as a supplement to that treatment.

RECENTLY DESCRIBED TAXA

BROMHEADIA Lindl.

1. Bromheadia cecieliae Kruizinga in *Orch. Monographs* 8: 101, fig. 39 (1997). Type: Borneo, *de Vogel* s.n., Leiden cult. no. 913892 (holotype L).

Epiphyte. Lower montane forest. Elevation: 1400 m. Flowering observed in February, July, November, to December.

Endemic to Mount Kinabalu.

Collection: Mount Kinabalu, Gurulau Spur, *Carr* SFN 27455 p.p. (SING).

2. Bromheadia lohaniensis Kruizinga & de Vogel in *Orch. Monographs* 8: 108, fig. 48 (1997). Type: Sabah, Mount Kinabalu, Lohan River, *Vermeulen* s.n., Leiden cult. no. 26690 (holotype L).

Epiphyte. Hill forest on ultramafic substrate. Elevation: 600 m. Flowering time not recorded.

Endemic to Mount Kinabalu.

Known only from the type.

3. Bromheadia longifolia Kruizinga & de Vogel in *Orch. Monographs* 8: 109, fig. 49 (1997). Type: Sabah, Keningau, Trus Madi Forest Reserve, *Leopold et al.* SAN 71909 (holotype & isotype K).

Epiphyte. Lower montane forest. Elevation: 1400 m. Flowering time not recorded.

General Distribution: Borneo.

Collection: Mount Kinabalu, Gurulau Spur, *Carr* SFN 27455 p.p. (SING).

BULBOPHYLLUM Thouars

4. Bulbophyllum anaclastum J.J. Verm. in *Blumea* 38, 1: 149, fig. 5 (1993). Type: Sabah, Mount Kinabalu, *Carr* SFN 27902 (holotype L; isotypes AMES, LAE, SING). Section *Sestochilus*.

Epiphyte. Primary forest. Elevation: 1700–1900 m. Flowering observed in June and August.

Endemic to Mount Kinabalu.

Additional collections: Mount Kinabalu, *Aban* SAN 76693 (K, SAN); *J. & M.S. Clemens* 29821 (BM). Cited under *B. uniflorum* (Blume) Hassk. by Wood *et al.* (1993).

5. Bulbophyllum cerebellum J.J. Verm. in *Blumea* 41, 2: 350, fig. 7 (1996). Type: Sabah, without precise locality, *Giles* 998 (holotype K). Section *Hirtula*.

Epiphyte. Primary forest. Elevation: 1300 m. Flowering observed in May.

Probably not endemic to Mount Kinabalu. The collector of the type, Cyril Giles, was a rubber planter based at the Sapong Estate near Tenom, who made collections in the foothills of the Crocker Range behind the estate during the 1960's.

Collection: Mount Kinabalu, *Carr* C.3470 (AMES).

6. Bulbophyllum dibothron J.J. Verm. & A. Lamb in *Blumea* 38, 2: 344, fig. 8 (1994). Type: Sabah, Crocker Range, near Tambunan, *Jongejan* cult. no. 1956 (holotype L). Section *Monilibulbus*.

Epiphyte on tree trunks and branches. Montane forest. Elevation: 1500–2000 m. Flowering observed in January.

Additional collections: Crocker Range, near Tambunan, *Lamb* AL 1294/91 (L); Mount Kinabalu, *Vermeulen, van Welzen & Lamb* 1330 (L).

7. Bulbophyllum hemiprionotum J.J. Verm & A. Lamb in *Blumea* 38, 2: 343, fig. 7 (1994). Type: Sabah, Mount Kinabalu, *Vermeulen* 467 (holotype L). Section uncertain.

Epiphyte on trunks and branches near the forest floor. Mixed high forest, and low and open forest with many rattans. Elevation: 1700–2000 m. Flowering observed in January, March, July, September and October.

Additional collections: Mount Kinabalu, *J. & M.S. Clemens* 34107 (BO, E, NY); *Lamb* AL 743/87 (L); *Vermeulen, van Welzen & Lamb* 1329 (L). Sabah, Sipitang District, Ulu Padas, near Sarawak border, *Vermeulen* 613 (L).

CALANTHE R.Br.

8. Calanthe otuhanica C.L. Chan & T.J. Barkman in *Sandakania* 9: 29, fig. 1 (1997). Type: Sabah, Mount Kinabalu, Kinabalu Lipson, 15 July 1994, *Barkman* TJB 27 (holotype SAN; isotypes K, Sabah Parks Herbarium, SING, Universiti Malaysia Sarawak Herbarium).

Terrestrial. Steep, open, well-drained areas on recent or established stabilised landslides on ultramafic substrates. Elevation: 2550–2990 m. Flowering observed in January and July.

Endemic to Mount Kinabalu.

Collection: Mount Kinabalu, Lipson area, *Barkman* TJB 60 (Sabah Parks Herbarium, Kinabalu Park, SAN).

CYMBIDIUM Sw.

9. Cymbidium kinabaluense K.M. Wong & C.L. Chan in *Sandakania* 2: 86, figs. 1 & 2 (1993). Type: Sabah, Mount Kinabalu, 20 January 1993, *Chan & Nais* s.n. (holotype SAN; isotype SNP).

Epiphyte in moss cushions near the ground. Montane forest. Elevation: 1700 m. Flowering observed in January.

Endemic to Mount Kinabalu.

DENDROBIUM Sw.

10. Dendrobium cymboglossum J.J. Wood & A. Lamb in Wood & Cribb, *Checklist Orch. Borneo*: 247, fig. 29, plate 8C (1994). Type: Sabah, Sandakan, 29 April 1895, *Governor Creagh* s.n. (holotype K).

Epiphyte. Primary forest and thickets. Elevation: *c.* 400 m. Flowering observed in May and November.

General distribution: Borneo.

Additional collections: Mount Kinabalu, Kampung Nalumad, 700 m from Mekedeu River, 5 Nov. 1996, *Daim Andau* (PEK) 937 (K). Kota Marudu District, Kampung Monggis, 3.25 miles from centre of Kampung, *c.* 400 m, 13 May 1996, *Matamin Rumutom* (PEK) 251 (K).

11. Dendrobium lamrianum C.L. Chan in *Sandakania* 5: 69, figs. 1–3 (1994). Type: Sabah, Mount Kinabalu, Silau Silau Trail, 12 December 1993, *Sumbin & Gunsalam* SNP 5134 (holotype SAN; isotypes K, SNP). Section *Distichophyllum*.

Epiphyte. Montane forest. Elevation: 1700–1800 m. Flowering observed in November and December.

Endemic to Mount Kinabalu.

Additional collections: Mount Kinabalu, Kiau View Trail, *Lamb & Phillipps* AL 161/83 (K). Sight record: Mamut Orchid Centre, *Barkman* (colour slide), February, 1998.

DENDROCHILUM Blume

12. Dendrochilum cruciforme J.J. Wood in Wood & Cribb, *Checklist Orch. Borneo*: 169, fig. 24 A & B (1994). Type: Sabah, Mount Kinabalu, Peniguppan, January 1933, *J. & M.S. Clemens* s.n. (holotype K; isotypes AMES, BO, E, HBG, L). Section *Cruciformia*.

a. var. **cruciforme**

Epiphyte. Lower montane forest; *Leptospermum/Dacrydium* forest about 8 metres high on steep east facing slopes on weathered sandstone and shale. Elevation: 900–2000 m. Flowering observed in January, March, June, August, October, November and December.

Additional collections: Mount Kinabalu: Peniguppan, *J. & M.S. Clemens* 30471 (E), *J. & M.S. Clemens* 30826 (AMES, BM, E, K), *J. & M.S. Clemens* 32220 (BM, E), *J. & M.S. Clemens* 50322 (AMES, BM, K) & *J. & M.S. Clemens* s.n. (BM, E); Penataran Basin, *J. & M.S. Clemens* 40134 (AMES, BM, E); Tinekuk Falls, *J. & M.S. Clemens* 50278 (AMES, BM,

K); Marai Parai, *Collector unknown* SFN 36563 (SING). Sabah, Kota Kinabalu to Sinsuron road, Mile 27, from roadside stall, *Bacon* 187 (E). Sabah, Crocker Range, Mount Alab, south ridge, *de Vogel* 8661 (L).

b. var. **longicuspe** J.J. Wood in Wood & Cribb, *Checklist Orch. Borneo*: 170, fig. 24 C & D (1994). Type: Sabah, Mount Kinabalu, Kadamaian River, August 1933, *Carr* C. 3675, SFN 28004 (holotype K; isotype SING).

Epiphyte. Upper montane mossy forest. Elevation: 2000–2500 m. Flowering observed in May and August.

Endemic to Mount Kinabalu.

Collection: Mount Kinabalu, Summit Trail below Layang Layang, May 1995, *Barkman* TJB 194 (Sabah Parks Herbarium, Kinabalu Park).

13. Dendrochilum pseudoscriptum T.J. Barkman & J.J. Wood in *Orchid Rev.* 104 (1209): 1, figs. 91–93 (1996). Type: Sabah, Mount Kinabalu, near Kinabalu Lipson, 20 May 1995, *Barkman* TJB 198 (holotype Sabah Parks Herbarium, Kinabalu Park, isotype K). Section *Eurybrachium*.

Epiphyte. Upper montane *Dacrydium gibbsiae* and *Leptospermum recurvum* scrub forest on ultramafic substrate. Elevation: 2700–3000 m. Flowering observed in April and May.

Endemic to Mount Kinabalu.

Additional collections: Mount Kinabalu, Summit Trail above Layang Layang, *Barkman* TJB 16 & *Barkman* TJB 18 (Sabah Parks Herbarium, Kinabalu Park); northern ridge adjacent to Low's Gully, along trail leading to Melangkap Tomis, *Barkman* TJB 183 (Sabah Parks Herbarium, Kinabalu Park).

HAPALOCHILUS (Schltr.) Senghas

14. Hapalochilus lohokii (J.J. Verm & A. Lamb) Garay, Hamer & Siegerist in *Nord. J. Bot.* 14 (6): 643 (1994). Type: Sabah, *Lamb* AL 569/86 (holotype L).

Bulbophyllum lohokii J.J. Verm. & A. Lamb in *Blumea* 38: 339, fig. 4 (1994).

Epiphyte, usually on small branches near the forest floor. Upper montane forest; moss-covered *Dacrydium* in open, sunny situations. Elevation: 1700–2000 m. Flowering observed in March and from June to October.

Additional collections: Mount Kinabalu: Kamburongoh, *Carr* SFN 27564 (L, SING); Pinosuk Plateau, cult. Kinabalu Park Mountain Garden, *Lamb* AL 820/87 (K); *Phillipps* SNP

2393 (L); *Vermeulen & Chan* 398 (L). Sabah, Crocker Range, Mount Alab, *Lamb* SAN 92317 (K, drawing only, SAN); Mount Alab, south ridge leading to summit, *Vermeulen* 651 (K, L, UKMS).

NEW RECORDS FOR EARLIER DESCRIBED TAXA

ADENONCOS Blume

15. Adenoncos major Ridl. in *J. Linn. Soc., Bot.* 32: 350 (1896). Type: Peninsular Malaysia, Johore, Batu Pahat, Ridley s.n. (syntype SING); Pahang, Kota Glanggi, *Ridley* s.n. (syntype SING); Kedah, Kedah Peak, *Ridley* s.n. (syntype SING).

Epiphyte. Primary forest. Elevation: 600 m. Flowering observed in April.

General distribution: Peninsular Malaysia and Borneo.

Collection: Mount Kinabalu, Kampung Nalumad, 13 April 1995, *Daim Andau* (PEK) 35 (K).

16. Adenoncos parviflora Ridl. in *J. Linn. Soc., Bot.* 32: 350 (1896). Type: Peninsular Malaysia, Kuala Lumpur, *Kelsall* s.n. (holotype drawing by *Ridley* K).

Epiphyte. Primary forest. Elevation: *c.* 400 m. Flowering observed in August.

General distribution: Thailand, Peninsular Malaysia, Sumatra and Borneo.

Collection: Mount Kinabalu, Kampung Melangkap Tomis, on side of Penataran River, 10 Aug. 1996, *Lorence Lugas* (PEK) 2592 (K).

AGROSTOPHYLLUM Blume

17. Agrostophyllum elongatum (Ridl.) Schuit. in *Blumea* 35(1): 165 (1990). Type: Peninsular Malaysia, Tahan River, *Ridley* s.n. (holotype SING, isotype K).

Appendicula elongata Ridl. in *Trans. Linn. Soc. London*, Bot., ser. 2, 3: 375 (1893).

Epiphyte. Lower montane forest. Elevation: 1500 m. Flowering observed in September.

Collection: Mount Kinabalu, Tenompok, 1500 m, *J. & M.S. Clemens* 26774 (K).

APPENDICULA Blume

18. Appendicula pilosa J.J. Sm. in *Icon. Bogor.* 2: 53, t. 110A (1903). Type: Kalimantan, Sungai Tjehan, *Nieuwenhuis* s.n. (holotype BO).

Epiphyte. Habitat not recorded. Elevation: not recorded. Flowering observed in May.

General distribution: Borneo.

Collection: Mount Kinabalu, 3 km from Kampung Melangkap Tomis, 12 May 1996, *Lorence Lugas* (PEK) 2127 (K).

19. Appendicula reflexa Blume, *Bijdr.*: 301 (1825). Type: Java, Tjapus, Pantjar, *Blume* s.n. (holotype BO).

Epiphyte. Primary forest. Elevation: 1200 m. Flowering observed in April.

General distribution: S.E. Asia, eastwards to New Guinea and the Pacific islands.

Collection: Mount Kinabalu, Ranau District, Kampung Himbaan, Notoki, 14 April 1993, *Doinis Soibeh* (PEK) 205 (K).

20. Appendicula undulata Blume, *Bijdr.*: 301 (1825). Type: Java, Pantjar, *Blume* s.n. (holotype BO).

var. **undulata**

Epiphyte. Primary forest. Elevation: not recorded. Flowering observed in October.

General distribution: Peninsular Malaysia, Sumatra, Java and Borneo.

Collection: Mount Kinabalu, Kampung Nalumad, 4 miles from Nalumad, Park boundary, 1 Oct. 1996, *Daim Andau* (PEK) 758 (K).

BULBOPHYLLUM Thouars

21. Bulbophyllum polygaliflorum J.J. Wood in *Kew Bull.* 39 (1): 96, fig. 15 (1984). Type: Sarawak, Mount Mulu National Park, Camp 4, along path to camp, 18 March 1978, *Hansen* 499 (holotype C; isotype K). Section *Hirtula*.

Epiphyte. Lower montane forest. Elevation: 1600 m. Flowering observed in January.

General distribution: Borneo.

Collection: Mount Kinabalu, Liwagu River, along new trail to Mesilau resort, January 1996, *Barkman* TJB 276 (Sabah Parks Herbarium, Kinabalu Park).

COELOGYNE Lindl.

22. Coelogyne asperata Lindl. in *J. Hort. Soc. London* 4: 221 (1849). Type: Borneo, ex cult. *Twisden Hodges* (holotype K).

Terrestrial or epiphytic. Growing with *Leptaspis urceolata* (Graminae). Elevation: not recorded. Flowering observed in September.

Collection: Mount Kinabalu, Ranau District, 5.5 km from Kampung Takutan, 6 Sept. 1995, *Lomudin Tadong* (PEK) 540 (K).

CORYBAS Salisb.

23. Corybas piliferus J. Dransf. in *Kew Bull.* 41 (3): 588 (1986). Type: Sabah, Nabawan, *J. Dransfield* 5129 (holotype K).

General distribution: Borneo.

Record: Mount Kinabalu, Kiau View Trail, *c.* 1500 m, Sept. 1994, sight record and photograph by *J. Dransfield.*

Corybas piliferus J. Dransf. (Photo: J. Dransfield)

DENDROBIUM Sw.

24. Dendrobium lampongense J.J. Sm. in *Bull. Dép. Agric. Indes Néerl.*, 15: 14 (1908). Type: Sumatra, Lampong, *Brautigam* s.n. (holotype BO).

Epiphyte. Primary forest. Elevation: 400 m. Flowering observed in February.

General distribution: Sumatra and Borneo.

Collection: Mount Kinabalu, Kampung Melangkap Tomis, Peramat River towards Pisoh, 2 February 1996, *Lorence Lugas* (PEK) 1716 (K).

GASTRODIA R.Br.

25. Gastrodia javanica (Blume) Lindl., *Gen. Sp. Orch. Pl.*: 384 (1840). Type: Java, Seribu, *Blume* s.n. (holotype BO).

Epiphanes javanica Blume, *Bijdr.*: 421, fig. 4 (1825).

Saprophyte. Hill forest. Elevation: 500 m. Flowering observed in April.

General distribution: China?, Japan (Ryukyu Islands), Taiwan, Peninsular Malaysia, Thailand, Java, Philippines.

Collection: Mount Kinabalu, Ranau, Nalumad, along trail to Kebun Kasim, 30 April 1995, *Barkman* TJB 187 (Sabah Parks Herbarium, Kinabalu Park).

HYLOPHILA Lindl.

26. Hylophila mollis Lindl., *Gen. Sp. Orch. Pl.*: 490 (1840). Type: Singapore, *Wallich* s.n. (holotype K).

Terrestrial. *Gymnostoma* ridge forest. Elevation: 700–1000 m. Flowering observed in April.

General distribution: Peninsular Malaysia, Singapore, Sumatra and Borneo.

Collection: Mount Kinabalu, Kota Belud, Melangkap Tomis, along Mount Doa ridge trail, 10 April 1995, *Barkman* TJB 171 (Sabah Parks Herbarium, Kinabalu Park).

OBERONIA Lindl.

27. Oberonia ciliolata Hook.f., *Fl. Brit. Ind.* 6: 181 (1890). Type: Singapore, Krangi, *Ridley* 375 (holotype K).

Epiphyte. Growing with *Miscanthus floridulus* (Graminae). Elevation: 400 m. Flowering and fruiting observed in December.

General distribution: Peninsular Malaysia, Singapore, Thailand, Sumatra, Java and Borneo.

Collection: Mount Kinabalu, Kampung Melangkap Tomis, 13 December 1995, *Lorence Lugas* (PEK) 1489 (K).

PHOLIDOTA Lindl. ex Hook.

28. Pholidota sulcata J.J. Sm. in *Icon. Bogor.* 2: 27, t. 107A (1903). Type: cult. hort. Bogor, *Hallier* s.n. (holotype BO, later dupl. BO, L). Section *Acanthoglossum.*

Epiphyte. Lower montane forest. Elevation: 600–1600 m. Flowering observed in January and August.

General distribution: Borneo.

Additional Collections: Mount Kinabalu, Kampung Lakang, 3 miles from Kampung Nalumad at boundary of Park, 16 Aug. 1996, *Daim Andau* (PEK) 479 (K). Mount Kinabalu, Pinosuk Plateau, cult. Kinabalu Park Mountain Garden, January 1996, *Barkman* TJB 272 (Sabah Parks Herbarium, Kinabalu Park).

SCHOENORCHIS Reinw.

29. Schoenorchis buddleiflora (Schltr. & J.J. Sm.) J.J.Sm. in *Nat. Tijdschr. Ned. Ind.* LXXII: 100 (1912). Type: Sumatra, Padang, *Schlechter* s.n. (holotype BO).

Saccolabium buddleiflorum Schltr. & J.J. Sm. in *Bull. Dep. Agric. Indes Neerl.* XV: 25 (1908).

Epiphyte. Open forest of small trees on ultramafic substrate. Elevation: 1500–2100 m. Flowering observed in December.

General Distribution: Sumatra, Borneo.

Additional Collections: Mount Kinabalu, Marai Parai Spur, 1985, *Argent* s.n., cult. Edinburgh Botanic Garden, flowered 1988, cult. no. C.14844 (E, K); Gurulau Spur, cult. Tenompok orchid garden, *J. & M.S. Clemens* 51057 (BM, K).

SPATHOGLOTTIS Blume

30. Spathoglottis confusa J.J. Sm. in *Bull. Jard. Bot. Buitenzorg*, ser. 3, 12: 122 (1932). Type:

Kalimantan, Sintang, Mount Kelam, *Hallier* 406a (holotype L, isotype BO).

Terrestrial. Primary forest. Elevation: not recorded. Flowering observed in May.

General distribution: Borneo.

Collection: Mount Kinabalu, Kampung Serinsim, Park boundary waterfall, 16 May 1995, *Kinsun Bakia* (PEK) 434 (K).

TAINIA Blume

31. Tainia sp. probably **T. latifolia** (Lindl.) Rchb.f. subsp. **elongata** (J.J. Sm.) H. Turner in *Orch. Monographs* 6: 80 (1992). Type: Java, Tjiawi, *Joseph* s.n. (BO).

Tainia elongata J.J.Sm. in *Bull. Dép. Agric. Indes Néerl.* 43: 18 (1910).

Terrestrial. Primary forest. Elevation: not recorded. Flowering observed in February.

General distribution: Sumatra, Java and Borneo.

Collection: Mount Kinabalu, Ranau District, Bundu Tuhan-Kampung Pahu, 17 February 1994, *Doinis Soibeh* (PEK) 725 (K).

32. Tainia speciosa Blume, *Bijdr.*: 354 (1825). Type: Java, Salak, *Blume* s.n. (holotype L).

Terrestrial. Lower montane forest on ultramafic substrate. Elevation: 1000 m. Flowering observed in May.

General distribution: Peninsular Malaysia, Thailand, Java, Borneo.

Collection: Mount Kinabalu, Kota Marudu, trail leading to summit of Mount Tambuyukon, 28 May 1995, *Barkman* TJB 195 (Sabah Parks Herbarium, Kinabalu Park).

VANILLA Mill.

33. Vanilla havilandii Rolfe in *Kew Bull.*: 236 (1918). Type: Sarawak, Kuching, *Haviland* s.n. (syntype K); Matang, *Ridley* s.n. (syntype K).

Climber. Secondary forest. Elevation: not recorded. Flowering observed in June.

General distribution: Borneo.

Collection: Mount Kinabalu, 3 miles from Kampung Nalumad, 14 June 1996, *Daim Andau* (PEK) 440 (K).

RE-DETERMINATIONS

AGROSTOPHYLLUM Blume

34. Agrostophyllum stipulatum (Griff.) Schltr. in *Bot. Jahrb.* 45, Beibl. 104: 22 (1911). Type: Peninsular Malaysia, Pinang, *Lewis* s.n. (holotype not located; neotype: *Griffith* drawing 1851 selected by Schuiteman).

subsp. **stipulatum**

Collections cited under *A. bicuspidatum* J.J. Sm. (= *A. stipulatum* (Griff) Schltr. subsp. *bicuspidatum* (J.J. Sm.) Schuit.) by Wood, Beaman & Beaman (1993) are probably referable to either subsp. *stipulatum* or *A. elongatum* (Ridl.) Schuit.

BROMHEADIA Lindl.

Four collections cited by Wood, Beaman & Beaman (1993) have been re-determined during studies towards a revision of *Bromheadia* by Kruizinga, van Scheindelen & de Vogel (1997). These are listed below:

35. Bromheadia brevifolia Ridl. in *J. Linn. Soc., Bot.* 32: 340 (1896). Types: Peninsular Malaysia, Hermitage Hill, *Ridley* s.n. (syntype not located); Sarawak, *Haviland* s.n. (lectotype SING, chosen by Kruizinga *et al.*).

Epiphyte. Lower montane forest on ultramafic substrate. Elevation: 1400 m. Flowering recorded throughout the year.

Collection: Mount Kinabalu, Mahandei River Head, *Carr* SFN 27245 (SING). Originally cited under *B. aff. aporoides* Rchb. f. *B. brevifolia* has previously been recorded from Mount Kinabalu.

36. Bromheadia ensifolia J.J. Sm. in *Bull. Jard. Bot. Buitenzorg*, ser. 3, 8: 45 (1926). Type: Sumatra, West coast, Sidjoendjoeng District, Boekit Pakano, *Theunissen* s.n., cult. *Jacobson* no. 1629 (holotype L, isotype BO

Epiphyte. Lower montane forest. Elevation: 1400–1500 m. Flowering recorded in June.

Additional Collections: Mount Kinabalu, Peniguppan, *Carr* SFN 27578 (K, SING); Tenompok, *J. & M.S. Clemens* 28818 (K). Originally cited under *B. scirpoidea* Ridl.

37. Bromheadia truncata Seidenf. in *Opera Bot.* 72: 14, fig. 5 (1983). Type: Thailand, Doi Suthep, *Seidenfaden & Smitinand* GT 2691 (holotype C).

Epiphyte. Lower montane forest. Elevation: 1400 m. Flowering observed from August until February.

Collection: Mount Kinabalu, Gurulau Spur, *Carr* 3176, SFN 27455A (SING). Originally cited under *Bromheadia* indet. *B. truncata* has been previously recorded from Mount Kinabalu.

TAXA NO LONGER KNOWN ONLY FROM MOUNT KINABALU

BULBOPHYLLUM Thouars

Bulbophyllum heldiorum J.J. Verm., *Orchids of Borneo 2*: 143, fig. 46 (1991). Mount Kinabalu, Summit Trail, *Vermeulen & Duistermaat* 547 (holotype L; isotypes K, Sabah Parks Herbarium, Kinabalu Park). Section *Globiceps*.

Collection: Sabah, Tambunan District, Mount Trus Madi, epiphytic in mossy montane forest, 1900 m, 10 March 1995, *Barkman* TJB 152 (Sabah Parks Herbarium, Kinabalu Park).

DENDROCHILUM Blume

Dendrochilum dewindtianum W.W. Sm. in *Notes Roy. Bot. Gard. Edinburgh* VIII: 321 (1915). Types: Sabah, Mount Kinabalu, *Native collector* 68 (holotype E), *Native collector* 99 (paratypes E, K). Section *Platyclinis*.

var. **dewindtianum**

Dendrochilum furfuraceum J.J.Sm. in *Bull. Jard. bot. Buitenzorg*, ser. 3, V: 55 (1922). Type: Sumatra, Sumatera Barat, Brani, 900 m, *Bünnemeijer* 3333 (holotype L).

Examination of the type of the Sumatran *D. furfuraceum* reveals no appreciable differences. The material falls within the range of variation of *D. dewindtianum* var. *dewindtianum* (Pedersen, Wood & Comber 1997).

RECENT SYNONYMY AND NAME CHANGES

ANOECTOCHILUS Blume

Anoectochilus kinabaluensis (Rolfe) J.J. Wood & Ormd. in *Orchid Rev.* 102 (1198): 216 (1994). Types: Mount Kinabalu, Gurulau Spur, 1500–1700 m, *Gibbs* 3997 (syntype BM), 1500–1700 m, *Gibbs* 4003 (syntype BM).

Goodyera kinabaluensis Rolfe in Gibbs in *J. Linn. Soc., Bot.* 42: 159 (1914).

In 1914 R.A. Rolfe described *Goodyera kinabaluensis* based on collections made on Mount Kinabalu by Lillian Gibbs. Examination of syntype material at the Natural History Museum

(BM) in London and recent collections preserved in alcohol at Kew, show this to be an *Anoectochilus* with peloric flowers. The labellum is simple and lacks the characteristic numerous thread-like calli of *Goodyera*. The column has the two ventral wings characteristic of *Anoectochilus*, which are absent in *Goodyera*.

DENDROCHILUM Blume

Dendrochilum corrugatum (Ridl.) J.J. Sm. in *Recl. Trav. bot. néerl.* 1: 65 (1904). Type: Mount Kinabalu, Marai Parai Spur, 1700 m, *Haviland* 1814 (holotype SAR). Section *Eurybrachium*.

Platyclinis corrugata Ridl. in Stapf in *Trans. Linn. Soc. Lond.* 2, IV: 233 (1894).
Acoridium corrugatum (Ridl.) Rolfe in *Orchid Rev.* XII: 220 (1904).
Dendrochilum fimbriatum Ames, *Orchidaceae VI*: 51 (1920). Type: Mount Kinabalu, Marai Parai Spur, 23 November 1915, *J. Clemens* 248 (holotype AMES).

D. corrugatum was, until now, known only from the type, *Haviland* 1814, upon which H.N. Ridley prepared one of his characteristically brief original descriptions. The extant flowers on the type have, unfortunately, suffered damage since Ridley's time. The sepals and petals and much of the labellum are missing, although the column, minus the anther-cap, is intact. Comparison at Kew of *Haviland* 1814, with the type and several other excellent collections of *D. fimbriatum* however, leaves no doubt that they are conspecific. The types of both species were collected from Marai Parai Spur, an area of ultramafic substrate on the western slopes of Mount Kinabalu. Both have unusually long roots for the size of the plant, strongly wrinkled pseudobulbs, similarly textured leaves, identical floral bracts, a similarly shaped denticulate-fimbriate labellum and an identical column with oblong, obtuse stelidia and a distinctive, prominent rostellum.

Dendrochilum dewindtianum W.W. Sm. in *Notes Roy. Bot. Gard. Edinburgh* VIII: 321 (1915). Types: Mount Kinabalu, *Native collector* 68 (holotype E), *Native collector* 99 (paratypes E, K). Section *Platyclinis*.

var. **dewindtianum**

Dendrochilum lobongense Ames, *Orchidaceae VI*: 59 (1920). Types: Mount Kinabalu, Lubang (Lobong), *J. Clemens* 116 (holotype AMES).

D. dewindtianum is a variable species abundant above 2600 m on Mount Kinabalu, particularly in forest and scrub developed on ultramafic substrate. Leaf and flower dimensions and labellum shape vary greatly throughout its range. Examination of the type of *D. lobongense* shows it to fall within this pattern of variation.

COELOGYNE Lindl.

Coelogyne genuflexa Ames & C. Schweinf., *Orchidaceae VI*: 28 (1920). Type: Mount Kinabalu, Marai Parai Spur, *J. Clemens* 251 (holotype AMES). Section *Tomentosae*.

Coelogyne reflexa J.J. Wood & C.L. Chan in *Lindleyana* 5 (2): 87, fig. 5 (1990). Type: Sabah, Mount Alab, *de Vogel* 8666 (holotype K; isotype L).

Recent comparisons made by C. L. Chan of the recently described *C. reflexa* with the type of *C. genuflexa* show the two taxa to be conspecific.

PHOLIDOTA Lindl. ex Hook.

Pholidota sigmatochilus J.J. Sm. in *Blumea* 5: 299 (1943). Type: Mount Kinabalu, below Paka-paka, *Gibbs* 4260 (holotype BM). Section *Acanthoglossum*.

Sigmatochilus kinabaluensis Rolfe in Gibbs in *J. Linn. Soc.*, Bot. 42: 155, plate 3 (1914). *Chelonistele kinabaluensis* (Rolfe) de Vogel in *Blumea* 30: 203 (1984).

Re-instatement of *Pholidota sigmatochilus* was undertaken by Barkman & Wood (1997). Study of plants in the field and herbarium revealed that *P. sigmatochilus* shares few morphological features with *Chelonistele* and is more appropriately placed within *Pholidota*. Within *Pholidota*, this taxon is closely allied to *P. clemensii* Ames and belongs in section *Acanthoglossum*.

ERRATA

BULBOPHYLLUM Thouars

Bulbophyllum ionophyllum J.J. Verm., *Orchids of Borneo* 2: 65, fig. 18 (1991). Type: Sabah, *Chan* s.n. (holotype L). Section *Aphanobulbon*.

Bulbophyllum sopoetanense sensu Wood, Beaman & Beaman, *Plants of Mount Kinabalu 2, Orchids*, plate 15B (1993), non J.J. Sm.

The plant figured by Wood *et al.* (1993) was incorrectly referred to *B. sopoetanense* J.J.Sm.

Bulbophyllum sp. Section **Sestochilus**

The plant referred to *B. microglossum* Ridl. by Wood *et al.* (plate 13B) is, according to L.A. Garay (pers. comm.), an undescribed species.

DENDROCHILUM Blume

Dendrochilum pterogyne *Carr* in *Gard. Bull. Straits Settlem.* 8: 236 (1935). Type: Mount Kinabalu, Paka-Paka, *Carr* 3541, SFN 27597 (holotype SING; isotypes AMES, K). Section *Eurybrachium*.

Dendrochilum alatum sensu Wood, Beaman & Beaman, *Plants of Mount Kinabalu 2, Orchids*, plate 40 C & D (1993), non Ames.

The plant figured by Wood *et al.* (1993) was incorrectly referred to *D. alatum* Ames.

Index to numbered Bornean collections

(type collections are indicated in **bold**; species numbers appear in brackets; AL = *Anthony Lamb*; C. = *Carr*; PEK = Projek Ethobotani Kinabalu; SAN = Sandakan; SNP = Sabah National Parks; SFN = Singapore Forest Number; TJB = *Todd J. Barkman*)

Aban: SAN 76693 (4).
Andau, Daim (PEK): 35 (15); 440 (32); 479 (28); 758 (20); 937 (10).
Argent s.n. (29).
Bacon: 187 (12a).
Bakia, Kinsun (PEK): 434 (29).
Barkman: TJB 16 (13); TJB 18 (13); **TJB 27** (19); TJB 60 (8); TJB 152 (37); TJB 171 (26); TJB 183 (13); TJB 187 (25); TJB 194 (12b); TJB 195 (31); **TJB 198** (13); TJB 272 (28); TJB 276 (21).
Carr: C. 3176, SFN 27455A (36); C.3470 (5); **C. 3675, SFN 28004** (12b); SFN 27245 (34); SFN 27455 p.p (1 & 3); SFN 27564 (11); SFN 27578 (35); **SFN 27902** (4).
Clemens, J. & M.S.: 26774 (17); 28818 (35); 29821 (4); 30471 (12a); 30826 (12a); 32220 (12a); 34107 (7); 40134 (12a); 50278 (12a); 50322 (12a); 51057 (29).
Collector unknown: SFN 36563 (12a).
Dransfield, J.: **5129** (23).
Giles: **998** (5).
Hallier: **406a** (29).
Hansen: **499** (21).
Jongejan: **1956** (6).
Lamb: **AL 569/86** (14); AL 743/87 (7); AL 820/87 (14); AL 1294/91 (6); SAN 92317 (14).
Lamb & Phillips in *Lamb*: AL 161/83 (11).
Leopold et al. **SAN 71909** (3).
Lugas, Lorence (PEK): 1489 (27); 1716 (24); 2127 (18); 2592 (16).
Phillipps: SNP 2393 (14).
Rumutom, Matamin (PEK): 251 (10).
Soibeh, Doinis (PEK): 205 (19); 725 (30).
Sumbin & Gunsalam: **SNP 5134** (11).
Tadong, Lomudin (PEK): 540 (22).

Vermeulen: **467** (7); 613 (7); 651 (14); **s.n., Leiden cult. no. 26690** (2).
Vermeulen & Chan: 398 (14).
Vermeulen & Duistermaat: **547** (37).
Vermeulen, van Welzen & Lamb: 1329 (7); 1330 (6).
de Vogel: 8661 (12a); **s.n., Leiden cult. no. 913892** (1).

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Pedersen, H. Ae., J.J. Wood & J.B. Comber (1997) A revised subdivision and bibliographical survey of *Dendrochilum* (Orchidaceae). *Opera Bot.* 130: 1–85.

Schuiteman, A. (1997). Revision of *Agrostophyllum* section *Appendiculopsis*, with notes on the systematics of *Agrostophyllum*. *Orch. Monographs* 8: 1–20, figs. 1–7, plates 1a–2a.

Wood, J.J., R.S. Beaman & J.H. Beaman (1993). *The Plants of Mount Kinabalu 2, Orchids.* Royal Botanic Gardens, Kew.

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Another new name for a ginger from Borneo

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Summary. *Amomum borealiborneense* I.M. Turner, *nom. nov.* is proposed to replace *Amomum sylvestre* Ridl., a later homonym. Smith's earlier replacement name, *Amomum ridleyi*, was invalid for the same reason as the basionym of the species. *Amomum sylvestre* Ridl. is lectotypified.

Smith (1985) pointed out that when H.N. Ridley named a ginger from Sarawak *Amomum sylvestre*, he was using a combination that had been employed before. She therefore gave the plant a new name, *Amomum ridleyi*. Unfortunately this name had also been used before, and another new name is required. I propose the new epithet *borealiborneense* as a testimony to the species' distribution in northern Borneo. A lectotype for *Amomum sylvestre* is selected in line with the suggestion of Smith (1985).

Amomum borealiborneense I.M. Turner, ***nom. nov.***
Amomum sylvestre Ridl., *J. Straits Branch Roy. Asiat. Soc.* 46 (1906) 236, *non* Lam. (1783); *Amomum ridleyi* R.M. Sm., *Notes Roy. Bot. Gard. Edinburgh* 42 (1985) 311, *non* Baker (1892). Type: *H.N. Ridley s.n.*, 1903 (lectotype, selected here, SING! acc. no. 042623), Sarawak, Kuching.

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Initial colonisation and prey capture in *Nepenthes bicalcarata* (*Nepenthaceae*) pitchers in Brunei

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Summary. Initial prey capture and colonisation of pitchers of the carnivorous plant, *Nepenthes bicalcarata* were examined in Brunei. It was found that the pitchers possess large nectaries on their external surfaces which are very active during pitcher development and are attended by numerous species of ants, which also comprise a significant proportion of the pitchers' prey once they open. The inquiline ants (*Camponotus schmitzi*) of *N. bicalcarata* do not interact with the ants which attend the external nectaries, only colonising the pitchers as they open. At this time, the other ants cease to attend the external nectaries, feeding at those around the pitcher rim and lid instead. *C. schmitzi* ants exhibit a preference for aerial pitchers, whereas the ants which attend the nectaries do not. Prey capture and colonisation of the pitchers by inquiline metazoan species occurs as soon as the pitchers open, but the majority of colonisation/capture events take place during the second week after opening. Pitcher type (aerial or terrestrial) has no effect on prey capture or colonisation by infaunal species. The presence of *C. schmitzi* affects numbers of infaunal species, perhaps because these ants prey upon members of the pitcher fauna. Prey numbers and mass are not affected by *C. schmitzi*.

Nepenthes bicalcarata (Hook. f.) is a carnivorous pitcher plant common in the peat swamp forests of north-western Borneo. Like most other *Nepenthes*, this species is a climbing vine which produces two types of pitcher, depending on the age of the plant. Young rosettes produce large, squat, urceolate pitchers that hold large quantities of fluid. These usually rest on the ground and are referred to as terrestrial or lower pitchers. Climbing stems produce smaller pitchers which are more infundibular and contain correspondingly small volumes of fluid. These are the aerial or upper pitchers. Ants comprise the bulk of prey in most *Nepenthes* and *N. bicalcarata* is no exception to this pattern (see Jebb 1991, Moran 1996, Clarke 1997a). The fluid of *N. bicalcarata* pitchers is usually acidic (pH ~ 4.5) and a large number of invertebrate species have been recorded living in the pitchers (Clarke & Kitching 1993). *N.*

bicalcarata is unique among pitcher plants in that its pitcher tendrils are hollow and are colonised by *Camponotus schmitzi* (Schuitemaker & Stärke) ants. These ants forage by swimming in the pitcher fluid and retrieving captured insects which they consume. A detailed account of this ant–plant association is provided by Clarke & Kitching (1995).

Clarke (1997a) provided a brief description of pitcher development in *N. bicalcarata*, showing that the pitchers take approximately 27 days to develop from a small bud to an open, functioning pitcher. *N. bicalcarata* pitchers have an average operational lifespan of about 230 days, but may live for over a year (Clarke 1997a). The pitchers have several large nectaries on the external surfaces. These are very active as the pitcher develops and are attended by numerous species of ants, but not by *C. schmitzi* (Clarke & Kitching 1995).

Despite recent detailed accounts of the prey and food webs in *Nepenthes* pitchers (see Jebb 1991, Kato *et al.* 1993, Moran 1996, Beaver 1979, 1983, 1985, Clarke & Kitching 1993, Mogi & Chan 1996, 1997), little is known about patterns of prey capture and pitcher colonisation during pitcher development and the period immediately after the pitchers open. This paper presents the results of experiments and observations designed to investigate the initial colonisation and prey capture patterns in *N. bicalcarata* pitchers. The effects of various factors, including pitcher type (upper or lower), the presence or absence of *C. schmitzi* ants and time upon variables such as numbers and species of infaunal organisms, and numbers and mass of prey are examined. The objective is to provide both a qualitative and a quantitative overview of these processes, forming a basis upon which further experiments can be performed.

STUDY SITE

The study site was along a 3-km stretch of an abandoned logging railway behind the township of Seria in the Belait District of Brunei Darussalam. The vegetation in this area is "alan bunga" peat swamp forest, which is dominated by the dipterocarp, *Shorea albida* Sym. This forest type is described in Whitmore (1984).

MATERIALS AND METHODS

New leaves with undeveloped pitcher buds from 41 *N. bicalcarata* plants were labeled at the site. The buds were inspected for seven weeks between October 19 and December 5, 1989. Each bud was numbered and where referred to in this text, they are denoted as such: # 2, # 16, # 37, etc.

Buds were observed to see whether nectar feeding ants were present or absent at the external nectaries. Pitcher type (upper or lower) was recorded, as was the presence or absence of the inquiline ants (*C. schmitzi*). If *C. schmitzi* colonies were established in the pitcher tendrils, the time between the start of pitcher development and colonisation was measured to the nearest day. Any evidence of herbivory on the developing pitchers was recorded.

The pitchers were observed for three weeks after opening, during which three sets of pitchers were removed and their contents analysed. Ten pitchers were examined one week after opening, nine pitchers were examined after two weeks and ten pitchers were examined after three weeks. Each of the 29 pitchers was removed intact from the plant and taken to the laboratory for examination. The number of prey items was counted, along with the number of infaunal species which had colonised each pitcher.

The dry weight of the prey was measured by removing all of the macroscopic infaunal organisms and draining the fluid from the pitcher contents through a piece of filter paper. Each piece of filter paper used was labeled and placed in a drying oven for two weeks prior to the experiment. When required, each paper was removed from the drying oven and immediately weighed to the nearest 0.0001g. After draining the pitcher contents, each paper (and contents) were returned to the drying oven for a period of ten days, after which time they were weighed again.

Descriptive statistics for each pitcher characteristic were calculated, with all means stated in the text being means ± 1 standard error (SE). Distributions of ordinal measures (e.g., presence/absence of ants, upper/lower pitchers) were compared using χ^2 homogeneity tests. One-way analysis of variance was used to test for significant differences among ratio measures (e.g., dry weight of prey, number of days to opening) for each class of pitcher (upper/lower, colonised/uncolonised by *C. schmitzi*).

One- and two-way analyses of variance were performed, using the following factors: pitcher type (upper/lower), presence/absence of *C. schmitzi* and week number (1, 2 or 3) against the following variables: numbers of infaunal species, numbers of infaunal organisms, numbers of prey organisms, and prey mass. Only results which were significant at $\alpha = 0.05$ are presented here.

OBSERVATIONS AND RESULTS

Of the 41 buds examined, two failed to develop (# 2 and # 6) and one (# 38) was either developing unusually slowly, or was failing to develop fully when the experiment was concluded (Fig. 1). Bud # 2 was damaged by herbivores during the second week of observations. Herbivory seems to be very rare in *N. bicalcarata* and this was the only evidence of it detected during the study. The external nectaries on the developing pitcher buds were attended by a variety of ants. These species were also captured by the pitchers after opening. Thirty of the buds were observed to be attended by ants during the experiment. Whether the remaining 11 buds were attended at other times, or not at all, is unknown. Of the 38 pitchers which developed fully, there were 19 upper and 19 lower pitchers. The χ^2 homogeneity test to compare the frequencies of upper and lower pitchers which were attended by ants showed that these frequency distributions are not independent ($\chi^2 = 0.0084$, 1 d.f., $p > 0.05$, $\alpha = 0.01$). Fig. 1 shows the patterns of observed attendance throughout the observation period, coupled with the time of colonisation of the pitchers by *C. schmitzi*.

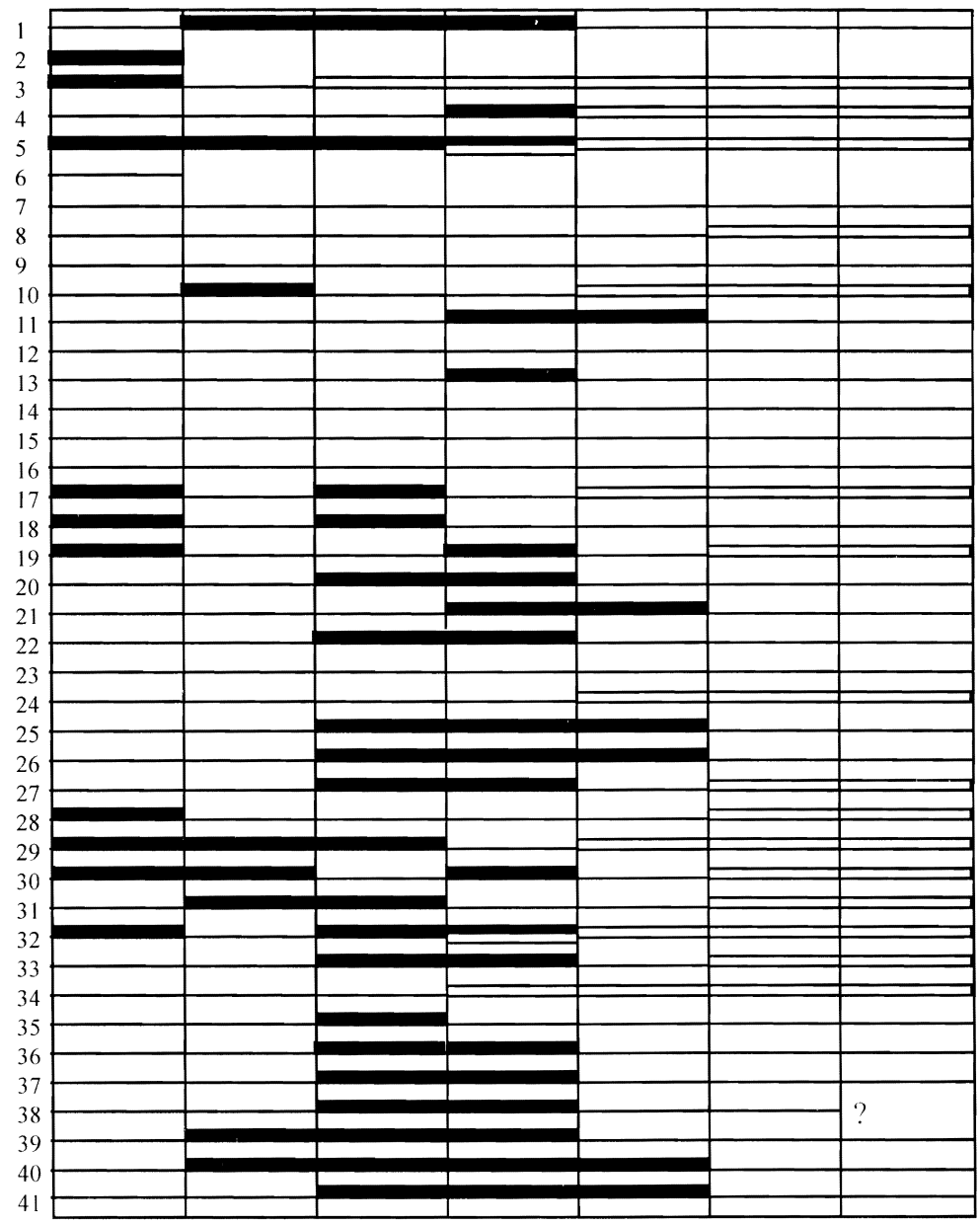

Fig. 1. Attendance of developing pitcher buds throughout the observation period.
Numbers along the left denote individual pitcher buds observed. Thin lines denote continuing development of pitcher buds. Cessation of the thin line indicates that the pitcher did not complete development. Thick, solid lines indicate observation weeks in which ants other than *C. schmitzi* were observed feeding from the nectaries on the external surfaces of the pitchers. Thick, shaded lines indicate the sampling periods when the pitchers were observed as being colonised by *C. schmitzi*. It was not possible to determine whether pitcher #38 had ceased development, or whether it was growing at an unusually slow rare.

Two patterns are apparent from Fig. 1. First, the external nectaries of the buds were regularly seen to be attended by ants other than *C. schmitzi* for the first four weeks of development. However, only six buds were attended during the fifth week and none were attended after that date. It is possible that the sampling method failed to detect the attendance of some buds by ants—no nocturnal observations were made and each pitcher could only be observed for a limited time on each visit to the field site. Nevertheless, that no ants were observed at these nectaries on any of the 41 buds after the fifth week suggests that the external nectaries become less attractive to foraging ants as the pitchers open. Whether this is because these nectaries cease or reduce their nectar output, or whether the ants are more attracted by the new sources of nectar produced by the glands inside the pitchers (which become operational as the pitchers open) is not known.

Second, there is a clear demarcation of attendance by nectar feeding ants and the arrival of *C. schmitzi* at the pitchers. This also coincides with the time at which the pitchers opened. Only two of the pitchers (# 5 and # 32) were in the process of being colonised by *C. schmitzi* at the same time other ants were seen at the external nectaries (during week 4). *C. schmitzi* ants did not exhibit any aggressive behavior towards any organisms outside the pitcher fluid so it seems unlikely that the ants attending the nectaries on the outer surfaces of the pitcher were driven away by them.

C. schmitzi colonised 16 of the 38 buds which developed into functioning pitchers during the observation period, showing a significant preference for upper pitchers over lower ones (χ^2 = 14.401, 1 d.f., $p < 0.001$, $\alpha = 0.01$). Only one pitcher (# 3) was attended by *C. schmitzi* before the fourth week of observations, with most pitchers being colonised during the sixth week. Clarke & Kitching (1995) suggested that the optimal time for colonisation by *C. schmitzi* is during the period immediately after the pitchers open: any earlier and the size of the hole bitten by the ants would become too large as the pitcher develops, perhaps leaving them vulnerable to predators. Any later and the tissues of the tendril would become so hard that the ants might have difficulty biting through them. These results support that interpretation.

Prey types and numbers, infaunal species and numbers, and pitcher types are presented in Table 1. Pitcher type (upper or lower) had no significant effects upon any of the variables examined. The only significant effect of the presence/absence of *C. schmitzi* was upon numbers of infaunal species (F = 6.935, d.f. = 1, 27, $p = 0.014$, $\alpha = 0.05$). Time (weeks 1–3) had significant effects upon numbers of infaunal organisms (F = 3.568, d.f. = 2, 26, $p = 0.043$, $\alpha = 0.05$) and prey mass (F = 5.168, d.f. = 2, 26, $p = 0.013$, $\alpha = 0.05$). There were no significant interactions between factors. All other combinations of factors and variables returned non-significant results at a = 0.05.

DISCUSSION

Attendance of external nectaries by ants

Although it is not yet possible to determine the exact role of the external nectaries on *N. bicalcarata* pitchers, it is likely that they serve to attract ants other than *C. schmitzi* for one of

Table 1. Descriptive statistics for pitcher variables.
All values are means ± 1 SE and the values for each variable were determined on a "per pitcher" basis.

Factor		Variable			
		No. of prey items	**Prey mass**	**No. of infaunal species**	**No. of infaunal organisms**
Time					
	week 1	7.500 ± 1.614	0.0320 ± 0.0030	3.200 ± 0.291	24.100 ± 4.608
	week 2	28.667 ± 3.958	0.0500 ± 0.0050	3.556 ± 0.338	74.333 ± 20.438
	week 3	42.300 ± 17.650	0.0490 ± 0.0060	4.200 ± 0.442	55.100 ± 11.930
C. schmitzi					
	present	14.000 ± 3.086	0.0429 ± 0.0042	3.077 ± 0.178	44.154 ± 10.114
	absent	35.875 ± 11.296	0.0439 ± 0.0043	4.125 ± 0.328	55.438 ± 12.945
Pitcher type					
	upper	15.667 ± 3.843	0.0433 ± 0.0038	3.467 ± 0.307	41.133 ± 9.099
	lower	37.214 ± 12.640	0.0436 ± 0.0047	3.857 ± 0.312	60.286 ± 14.267

the two reasons outlined above (i.e., to establish the pitcher as a source of nectar and/or to protect the pitchers from attack by herbivores while they develop) (see Clarke 1997a). Either theory remains plausible at this stage, and it may be that the external nectaries serve a dual purpose. The cessation of attendance of the external nectaries can be explained by both hypotheses: once the pitchers are open, nectar is most abundant within the pitcher and on the lid. Hence foraging ants will be attracted to those areas rather than the external nectaries. Similarly, if the role of the ants is to deter other animals from visiting the developing pitcher, this role would cease once the pitchers open if the plant is to catch sufficient prey. However, nectar production rates by the external nectaries have not been determined, and further experiments would provide better insights.

Selective colonisation of upper pitchers by C. schmitzi

Clarke & Kitching (1995) suggested that *C. schmitzi* colonise upper pitchers in preference to lower ones because the nest chambers of the lower pitchers may be subject to flooding after heavy rain. Although no quantitative data were provided to support this claim, these observations show that *C. schmitzi* does have a distinct preference for upper pitchers, and those lower pitchers which are held high above the ground by supporting vegetation are usually colonised by *C. schmitzi* (C. Clarke, pers. observ.), suggesting that avoidance of flooding is the reason why upper pitchers are colonised more than lower ones.

The effects of pitcher colonisation by C. schmitzi

Clarke & Kitching (1995) showed that the behaviour of *C. schmitzi* only has a detectable effect on pitcher contents when excess prey is caught. These analyses support this finding. Although *C. schmitzi* remove large prey to feed, the remains are returned to the pitcher, so their activities can not be quantified in this way: direct observation of their feeding behaviour is required. Numbers of infaunal organisms are also unaffected, but there are significantly fewer infaunal species present in pitchers colonised by *C. schmitzi*. Mogi & Chan (1997) suggested that the presence of aquatic predators in pitcher communities serves to increase overall species numbers, with the predators' feeding behaviour reducing the numbers of the most common prey species, thereby allowing less competitive species to colonise the pitchers. Although this survey lasted only three weeks, these results do not support that interpretation. It is possible that *C. schmitzi* preferentially feed on the aquatic predators, thus reducing selective pressure on their prey species, but this can not be substantiated at present. It is difficult to determine whether the results obtained in this experiment reflect the overall situation for *N. bicalcarata* pitchers without the aid of further studies.

The effects of pitcher dimorphism

Clarke (1997b) showed that pitcher dimorphism in *N. bicalcarata* has no effect on food web structure. In contrast, Moran (1996) found that pitcher dimorphism in *N. rafflesiana* (Jack) does affect the prey spectrum of that species. In *N. bicalcarata*, it appears that pitcher dimorphism is not an important determinant of either prey capture or colonisation by

metazoan species, as even the smallest fluid volumes in the upper pitchers are relatively large for *Nepenthes* (Clarke & Kitching 1993) and the pitchers are long-lived (Clarke 1997a). Although the results presented here support the findings of Clarke (1997b), it is important to emphasise that inter-specific differences in *Nepenthes* could be important in this regard and that the patterns evident in *N. bicalcarata* may not apply to other species.

The effects of time

Over the three weeks in which the open pitchers were examined, prey mass and numbers of infaunal organisms varied significantly with time. As pitchers accumulate prey and detritus after opening, it is not surprising that prey mass increases as the pitchers age. The same situation exists for numbers of infaunal organisms: colonisation of newly opened pitchers takes place over several weeks (Clarke 1992). However, for both of these variables, there is a sharp increase in mass and numbers from weeks 1–2, but very little further increase from weeks 2–3. This suggests that the pitchers catch little and are colonised by few species during the first few days after opening, but there is a burst of trapping and colonisation during the second week. Why this burst is not sustained into the third week is difficult to determine without subsequent measurements.

The prey spectrum of *N. bicalcarata* pitchers during the first three weeks is quite narrow, with all organisms falling into one of five orders (in decreasing order of abundance): Hymenoptera, Coleoptera, Hemiptera, Aranae and Orthoptera. In contrast, Moran (1996) found 11 orders of prey in *N. rafflesiana* pitchers in Brunei, but those experiments included much larger numbers of pitchers, of varying ages. Whether the corresponding burst in colonisation by infaunal species is related to increased prey capture is also unknown. Given that infaunal species numbers vary little throughout this period, it seems likely that a small subset of the *N. bicalcarata* community colonises pitchers repeatedly during the first few weeks of the pitchers' lives, with the other species arriving later.

CONCLUSIONS

The development of *N. bicalcarata* pitchers is a complex process which involves an array of invertebrates, many of which fulfill different roles for the plant. Many of these roles are not presently known or fully understood, such as that of the ants which attend the nectaries of the developing pitchers (but which are then caught by the pitchers after they open). The stark demarcation of pitcher attendance and colonisation by *C. schmitzi* is clearly linked to the opening of the pitchers, but the reasons for the demarcation are far from clear. Although *C. schmitzi* have a distinct preference for colonising aerial pitchers, there are no discernible patterns in the attendance of the nectaries by the other ants, so perhaps their behaviour is determined more by the opening of the pitchers rather than any interaction among these ants and *C. schmitzi*.

The capture of prey by the pitchers shows an increase in mass and numbers over the initial three weeks, but the observation period was clearly too short to determine whether there are

any patterns in prey capture. The infaunal species which colonised the pitchers belonged to a small group of species which colonise the pitchers repeatedly soon after they open. As with prey capture, further observations are required to determine whether this is a part of a distinct pattern or simply an artifact of the sampling procedure.

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I thank the Brunei Research Council for permitting me to carry out research on *Nepenthes* in Brunei Darussalam. I thank Dr Webber Booth and Professor Roger Kitching for their assistance and advice in relation to my research, which was supported by an Australian Postgraduate Research Award, administered by the University of New England, Armidale, Australia.

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The embryology of *Averrhoa* (*Oxalidaceae*)

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Summary. The anther of *Averrhoa* is tetrasporangiate and its wall development is of the Basic type. Cytokinesis in microspore mother cells is simultaneous and results in tetrahedral or decussate tetrads. The mature pollen grains of *A. carambola* are shed at the 2-celled stage whereas those of *A. bilimbi* are at the 3-celled stage. The mature ovule is anatropous, bitegmic, crassinucellate and the micropyle is formed by both the outer and inner integuments. The embryo sac development conforms to the monosporic *Polygonum* type. The development of endosperm follows the *ab initio* Nuclear type and the nuclear endosperm completely turns cellular only after the formation of the heart-shaped embryo. The fruit mesocarp and the combined region of the exocarp and mesocarp are deposited with tannin and calcium oxalate crystals, respectively. The seed coat is formed from the outer and inner integuments.

The Oxalidaceae comprises six genera and 875 species (Airy Shaw 1973). The woody genus *Averrhoa* L., probably of Indomalayan origin, comprises two species, *A. bilimbi* L. (commonly called "belimbing buluh" or "belimbing asam") and *A. carambola* L. (commonly called "belimbing manis", carambola, or starfruit), which are trees up to 15 m tall (Allen 1967; Veldkamp 1971). Both of them are common cultivated fruit tree species in Malaysia. Considering the large number of species in the Oxalidaceae, the number of taxa embryologically investigated is rather few—Davis (1966) and Johri *et al.* (1992) have reviewed the earlier work of Jönsson (1880), Billings (1901), Hammond (1908), Samuelsson (1913), Schürhoff (1924), Mauritzon (1934), Noll (1935), Venkateswarlu (1936), Souéges (1939), Thathachar (1942), Govindappa & Boriah (1956), Narayana (1962), Herr & Dowd (1968), Herr (1972), Kumari & Narayana (1980), Boesewinkel (1985), and Govil & Kaur (1989). Of the six genera, *Oxalis* L. and *Biophytum* DC. engaged the most attention from previous workers, concentrating more on the development of the embryo than the embryo sac.

A perusal of the literature on the embryology of *Averrhoa* reveals that the available information is too inadequate and fragmentary. Therefore, a thorough study is needed to characterise this genus from an embryological standpoint. The previous embryological work on this taxon has been reviewed by Venkateswarlu (1936), Thathachar (1942), Davis (1966), Low (1972), Kumar (1975), Dave, Patel & Rupera (1975), Tan (1977), and Ou Yang (1978). More recently a few brief reports have also appeared (Boesewinkel 1985; Govil & Kaur 1989; Johri *et al.* 1992). The present investigation, dealing with microsporogenesis, megasporogenesis, development of male and female gemetophytes, endosperm and embryo, seed coat and fruit wall in *Averrhoa*, was undertaken with the prime objective of further elucidating the embryology of *Averrhoa*.

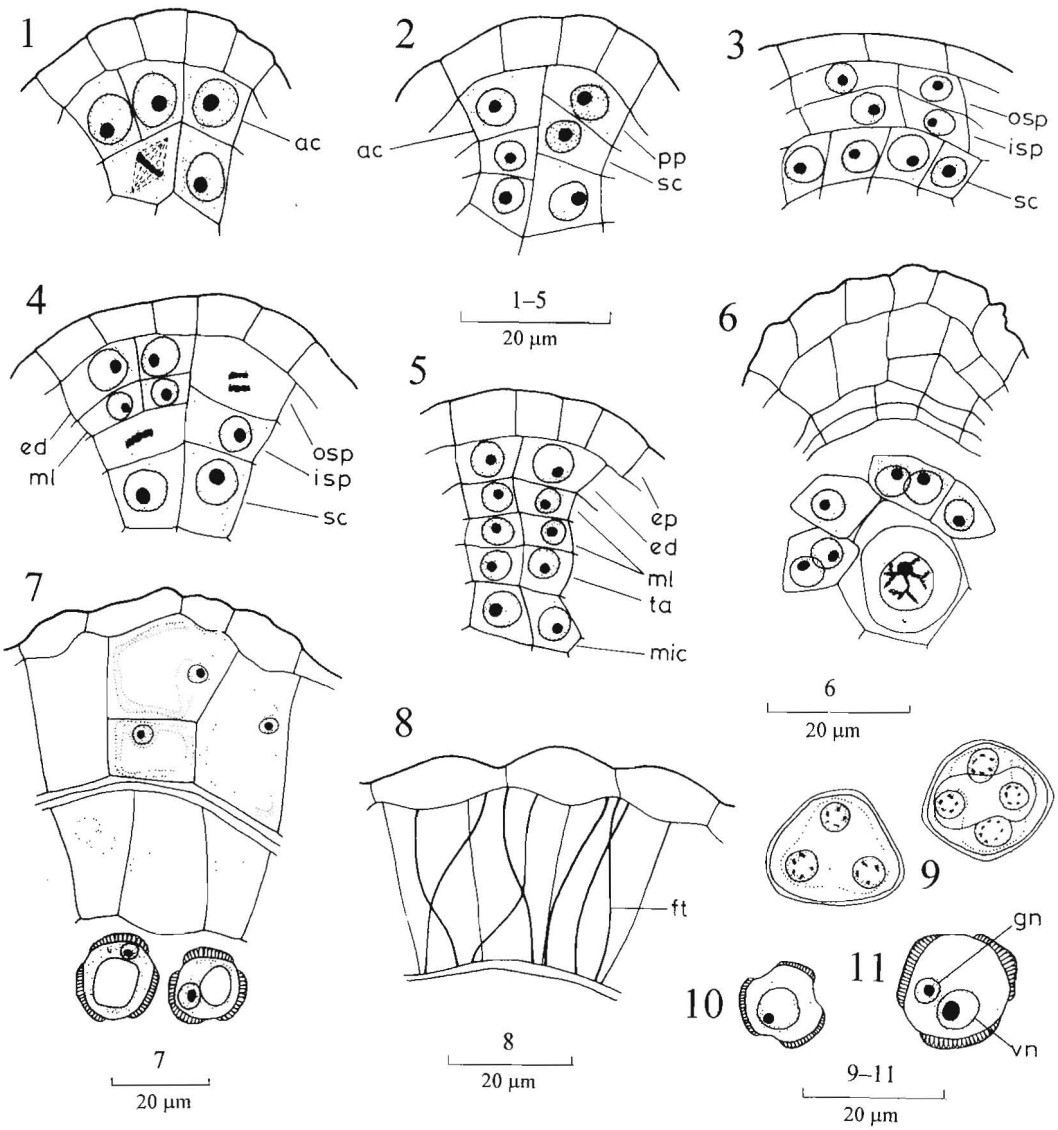
MATERIALS AND METHODS

Buds, flowers and fruits of *A. carambola* and *A. bilimbi* were collected at weekly intervals from the fruit-tree nursery, Institute for Advanced Studies, University of Malaya and the Rimba Ilmu botanical garden, University of Malaya, respectively. Two voucher specimens (KLU 40992 for *A. carambola* and KLU 40993 for *A. bilimbi*) were deposited with the Herbarium of the University of Malaya (KLU). The materials were trimmed to a suitable size and fixed on location in Craf III solution (30 ml 1% chromic acid, 20 ml 10% acetic acid, 10 ml 37% formaldehyde and 40 ml distilled water) at 10°C for at least 48 hours. Customary methods of dehydration and embedding were followed. Microtome sections were cut at 8 µm (for buds and flowers) or 10–12 µm (for fruits) and after dewaxing, were stained in 1% alcoholic (in 50% alcohol) safranin and 0.5% alcoholic (in 95% alcohol) fast green FCF. The sections were mounted in canada balsam.

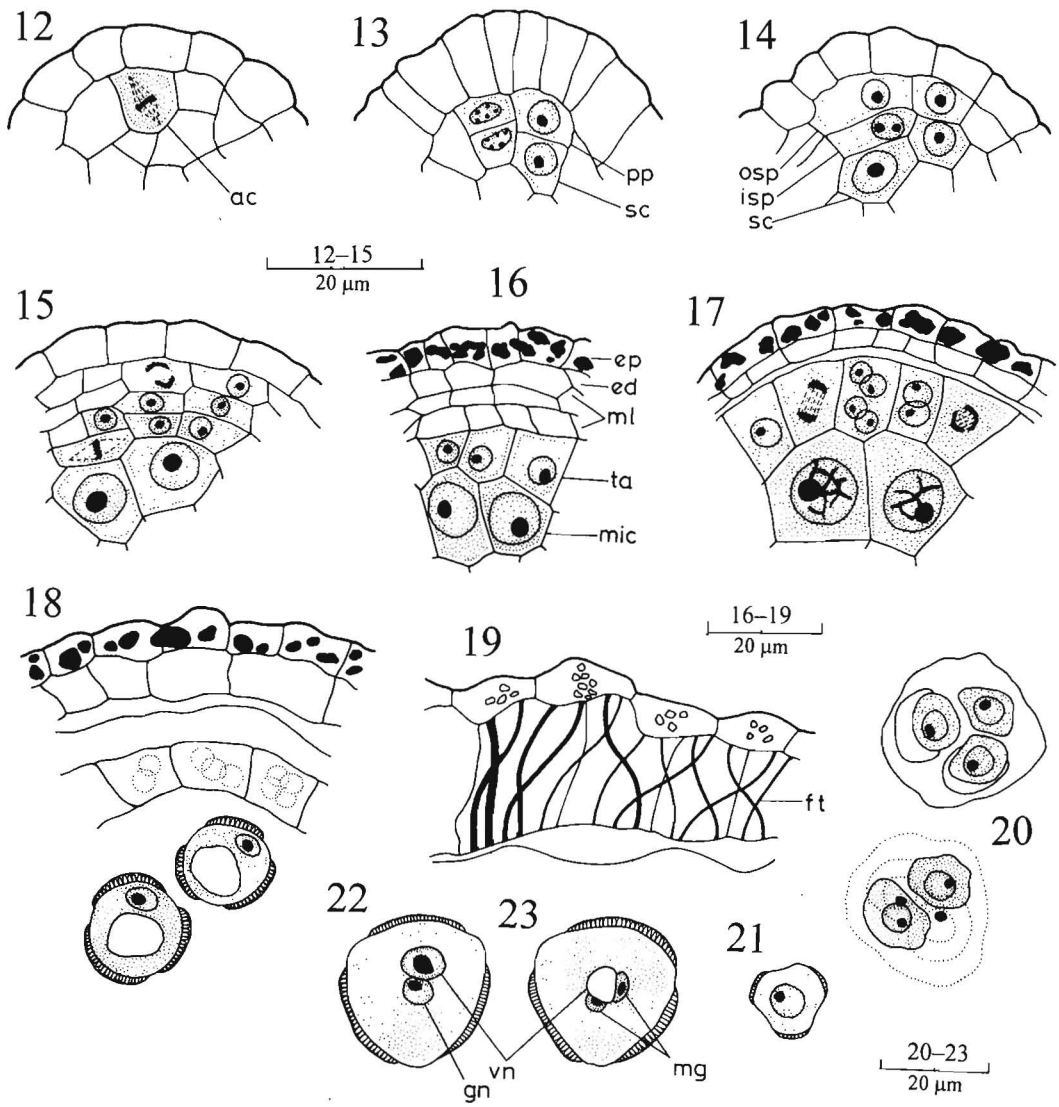
MICROSPORANGIUM, MICROSPOROGENESIS AND MALE GAMETOPHYTE

There are five stamens in a *A. carambola* flower. However, there are ten in *A. bilimbi* and these are arranged in two whorls, i.e., long-whorl and short-whorl anthers. Earlier, Davis (1966) had reported that the number of microsporangia in the anther had not been clearly determined for *Averrhoa*. However, the present study has confirmed the findings of previous work (Thathachar 1942, Low 1972, Tan 1977) that the anther is tetrasporangiate in the two species of *Averrhoa* just as in the other members of Oxalidaceae (Figs. 65, 69).

The unicellular archesporium is hypodermal (Figs. 1, 12). Occasionally, more than one archesporium can be observed in a sporangium of *Averrhoa* and their divisions are not synchronous. The archesporial cells divide periclinally to produce the primary parietal cells and sporogenous cells (Figs. 2, 13). The periclinal division of the parietal cells results in the formation of two secondary parietal layers, i.e., the outer and inner secondary parietal layers (Figs. 3, 14), and the sporogenous cells divide and subsequently differentiate into the microspore mother cells. The secondary parietal layers may divide simultaneously (in *A. carambola*) or the inner parietal divides before the outer (in both species of *Averrhoa*) producing the middle layer and the tapetum (Fig. 15). Rarely, the outer secondary parietal divides before the inner secondary parietal layer (Fig. 4). The sequence of division of



Figs. 1–11. *Averrhoa carambola,* microsporangium, microsporogenesis and male gametophyte. T.S. **Figs 1–5.** Anther wall at different development stages. **Fig. 6.** Anther wall with two to three middle layers. **Fig. 7.** Anther wall at the one-celled microspore stage with degenerating tapetal cells. **Fig. 8.** Anther wall showing fibrous endothecium. **Fig. 9.** Tetrahedral and decussate microspore tetrads. **Fig. 10.** Single microspore. **Fig. 11.** 2-celled pollen grain. ac = archesporial cell; ed = endothecium; ep = epidermis; ft = fibrous thickening; gn = generative nucleus; isp = inner secondary parietal layer; mic = microspore mother cell; ml = middle layer; osp = outer secondary parietal layer; pp = primary parietal cell; sc = sporogenous cell; ta = tapetum; vn = vegetative nucleus.



Figs. 12–23. *Averrhoa bilimbi,* microsporangium, microsporogenesis and male gametophyte. T.S. **Figs. 12–16.** Anther wall at different development stages. **Fig. 17.** Anther locule showing tapetal cells undergoing mitosis. **Fig. 18.** Anther wall at the single-celled microspore stage with degenerating tapetal cells. **Fig. 19.** Wall layers of dehisced anther showing fibrous endothecium and persistent epidermis with crystals. **Fig. 20.** Tetrahedral and decussate microspore tetrads. **Fig. 21.** Single microspores. **Fig. 22.** 2-celled pollen grain. **Fig. 23.** 3-celled pollen grain. ac = archesporial cell; ed = endothecium; ep = epidermis; ft = fibrous thickening; gn = generative nucleus; isp = inner secondary parietal layer; mic = microspore mother cell; ml = middle layer; osp = outer secondary parietal layer; pp = primary parietal cell; sc = sporogenous cell; ta = tapetum; vn = vegetative nucleus.

secondary parietal layers has not been reported in the other members of the Oxalidaceae. In addition, one of the middle layers of *A. carambola* may divide periclinally to form a third middle layer (Fig. 6). Hence, just before meiosis of the microspore mother cells, the anther wall consists of an epidermis, an endothecium, two or rarely (in *A. carambola*) three middle layers and a single-layered multinucleate tapetum (with 2–4 nucleate cells) (Figs. 5, 16). Davis (1966) stated that the anther wall of members of Averrhoaceae and Oxalidaceae (*sensu stricto*) consists of two ephemeral middle layers, as was also shown by Low (1972); Thathachar (1942) and Tan (1977) documented that *Averrhoa* species and *Biophytum sensitivum* (L.) DC. possess either one or two ephemeral middle layers.

The anther wall development of *Averrhoa* conforms to the Basic type, as in *Oxalis*, *Biophytum* (Thathachar 1942, Davis 1966), *A. carambola* (Thathachar 1942, Davis 1966, Low 1972) and *A. bilimbi* (Davis 1966, Tan 1977). At this stage the epidermal cells of *A. bilimbi* accumulate a large number of calcium oxalate crystals and a tannin-like substance (Fig. 18).

The cells of the glandular tapetum in both species of *Averrhoa* studied are initially uninucleate, then they become 2–4-nucleate just before meiosis of the microspore mother cells as reported in the present study (Fig. 17) as well as previous work (Thathachar 1942, Low 1972, Tan 1977). At this time, the tapetum layer is pushed towards the microspore mother cells and the middle layers begin to degenerate from the inner layer towards the outer layer. In *A. bilimbi* these middle layers degenerate completely at the microspore tetrad stage. The tapetum reaches maximum development during meiosis of the microspore mother cells and starts to degenerate after the formation of the microspore tetrad (in *A. carambola*) or after the release of microspore tetrads (in *A. bilimbi*) (Figs. 7, 18). There are no ubish granules (present study, Thathachar 1942, Davis 1966, Low 1972, Tan 1977) although these have been found in the tapetal cells of *Oxalis rosea* Jacq. (Davis 1966).

The microspore mother cells enlarge and show a denser cytoplasm before meiosis. The present study as well as previous work (Tan 1977, Davis 1966) has confirmed that cytokinesis in microspore mother cells is simultaneous and the tetrads formed are either tetrahedral or decussate (Figs. 9, 20), whereas *A. carambola* has earlier been reported to have tetrahedral microspore tetrads (Low 1972). Soon after tetrad formation, the microspores separate out and the wall of these microspores gradually differentiate into the exine and intine (Figs. 10, 21).

In *A. carambola*, the anthers within the same flower show synchronous development, but sometimes meiotic division in different locules of the same anther is not synchronous. An example was found of one locule with microspore mother cells at metaphase I while the others are at metaphase II or anaphase II. In *A. bilimbi*, meiotic divisions in the four locules of an anther are synchronous, but the divisions in anthers of the different whorls are not synchronous at all. For example, it was observed that the long-whorl anthers can be at the tetrad-stage while the short-whorl anthers are at the metaphase II stage. However, both whorls of anthers show the same pollen stage during anthesis (Fig. 70).

The nucleus of the one-celled pollen grain will divide mitotically to form a small generative cell and a large vegetative cell (Figs. 11, 22). Both of these cells lie either in the centre or

migrate to the periphery of the pollen grain. However, the generative cell of *A. bilimbi* on division gives rise to two spindle-shaped male gametes (Fig. 23). After gametogenesis the nucleus of the vegetative cell becomes rounded or irregular in shape and shows signs of degeneration. At maturity the pollen grains are tricolpate and shed at the 2-celled (in *A. carambola*) or 3-celled (in *A. bilimbi*) stage. The pollen grains of *Averrhoa* species and *Biophytum* were reported to be shed at the 2-celled stage (Thathachar 1942, Davis 1966, Low 1972, Tan 1977) whereas those of *Oxalis* were reported to be shed at the 3-celled stage (Davis 1966). Brewbaker (1967) points out that as many as 32% of the angiosperm families are characterised by tricellular pollen.

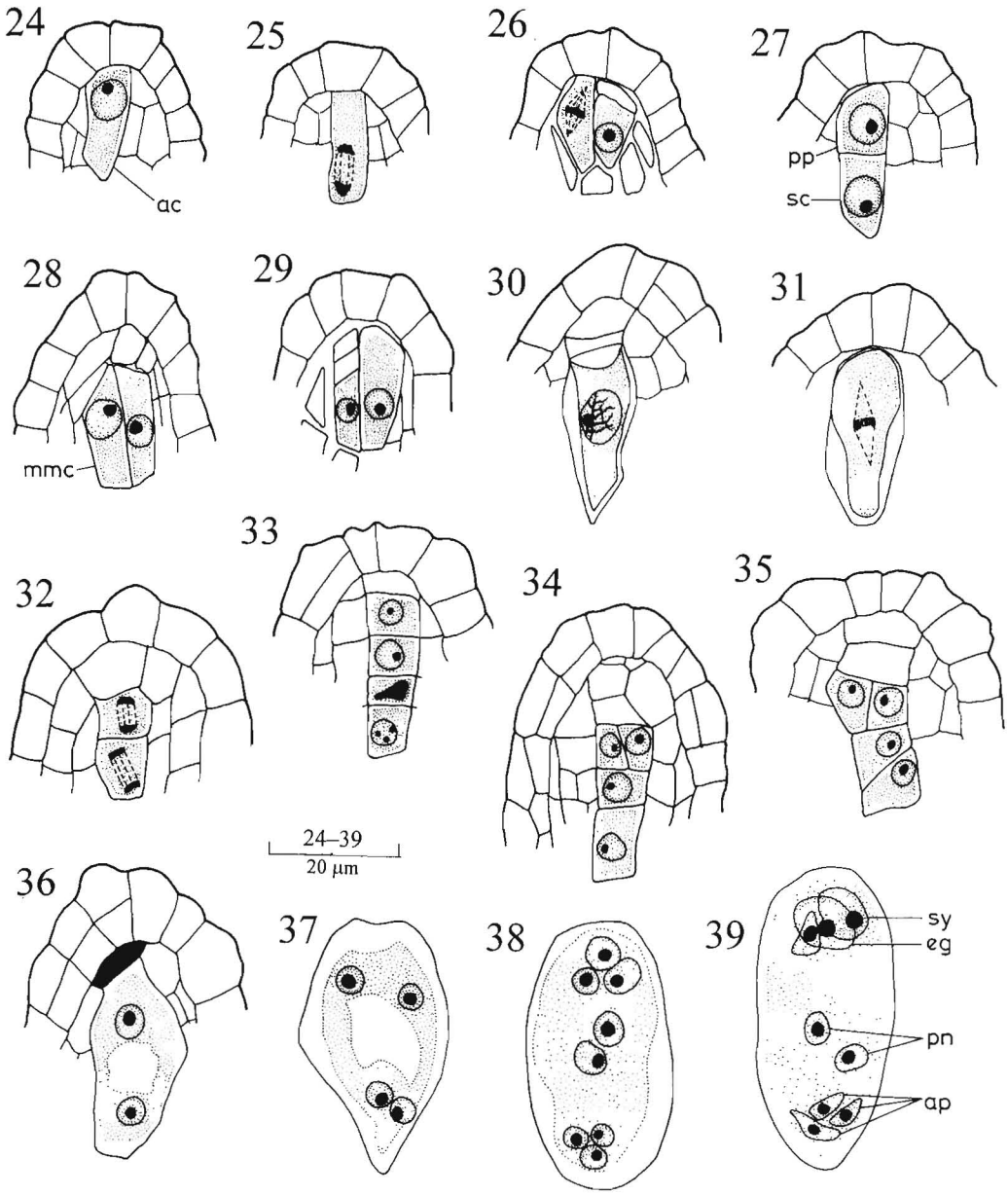
The tapetum completely degenerates and the endothecium develops fibrous thickenings when the anther is at the 1-celled (in *A. carambola*) or 2-celled (in *A. bilimbi*) pollen grain stage. At the time of dehiscence, the anther is extrorse and its wall comprises only the epidermis and the fibrous endothecium (Figs. 8, 19).

MEGASPORANGIUM, MEGASPOROGENESIS AND FEMALE GAMETOPHYTE

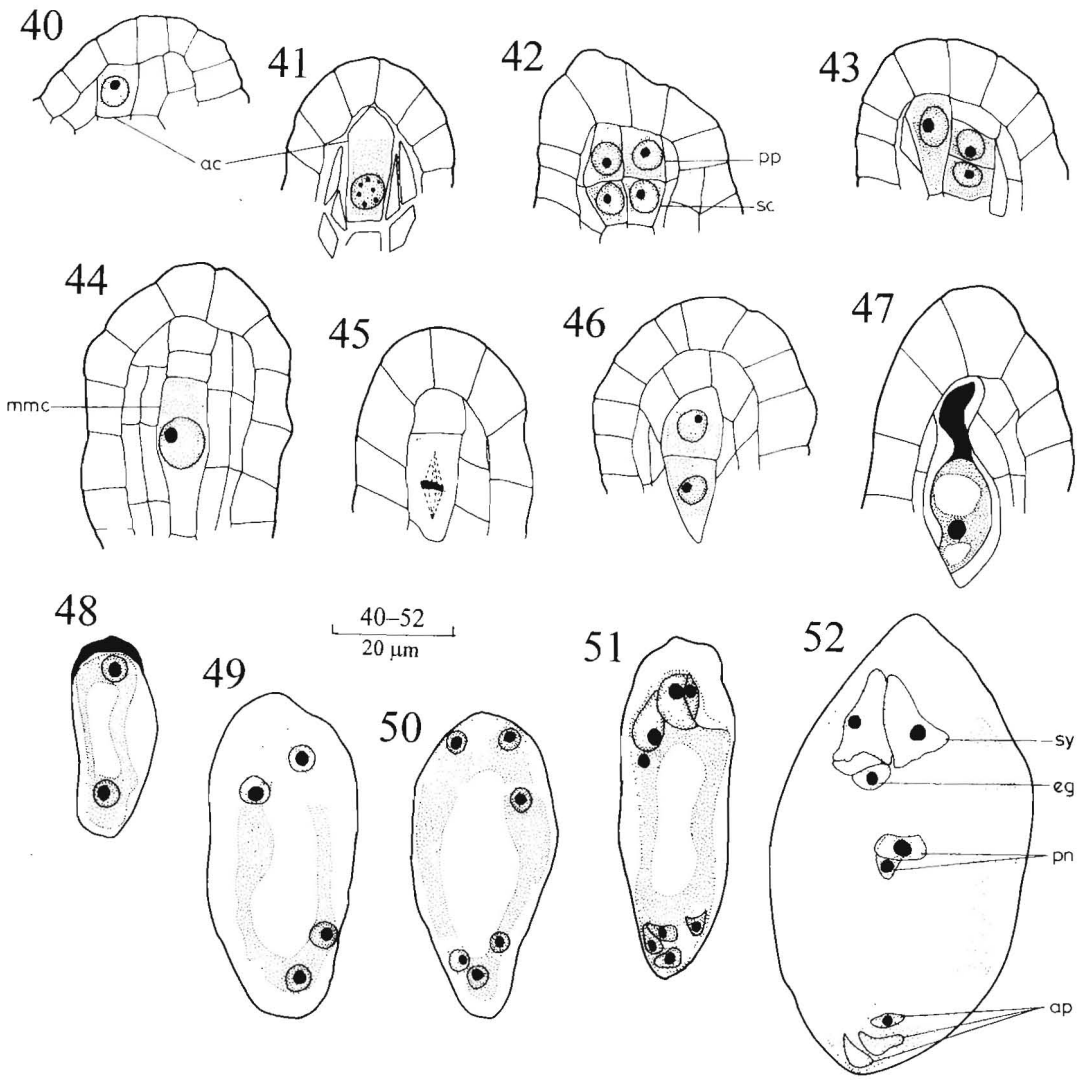
In the *Averrhoa* species studied, the mature ovule is anatropous, bitegmic and crassinucellar (Fig. 66). The micropyle is formed by both the outer and inner integuments (Fig. 67). Similar descriptions of these species have been reported (Davis 1966, Low 1972, Tan 1977). Although the ovule of various members of Oxalidaceae is anatropous and bitegmic, the nucellus is tenuinucellate as reported by Hammond (1908) for *Oxalis corniculata* L., Davis (1966) for *Oxalis* and *Biophytum*, and Bouman (1974) for *Oxalis valdiviensis* Barn. and *B. sensitivum*. Parietal cells are, however, present in both species of *Averrhoa* examined here. According to Thathachar (1942), the primary archesporial cell of *B. sensitivum* functions directly as the megaspore mother cell without cutting off any parietal tissue and therefore the ovule is tenuinucellar. Mauritzon (1934), too, did not mention the presence of parietal cells in *Biophytum* and *Radiola* Hill.

The single archesporium is an enlargement of a hypodermal cell which divides periclinally to form a primary parietal cell and a sporogenous cell that enlarges and differentiates into the megaspore mother cell (Figs. 24–27, 40–43). Both the *Averrhoa* species studied generally show only a single archesporium, though a case of twin archesporia has been observed in an ovular primodium and their divisions are not synchronous in both species (Figs. 28–29, 42–43); an occurrence of twin megaspore mother cells in *A. carambola* was observed in the same nucellus of an ovule (Fig. 28). The twin megaspore mother cells could have been derived from twin archesporia. A single archesporium has been reported in *B. sensitivum*, *Averrhoa* species (Thathachar 1942), *O. corniculata* (Hammond 1908) and other members of Oxalidaceae (Davis 1966). Nevertheless, twin archesporia were also found in *B. sensitivum* (Govindappa & Boriah 1956).

The primary parietal cell in *A. carambola* may divide to form two to three layers of nucellus at the micropylar end while in *A. bilimbi* it forms two layers of micropylar nucellar tissue (Figs. 30, 34, 44). In certain cases the primary parietal cell does not divide further and it forms



Figs. 24–39. *Averrhoa carambola,* megasporogenesis and female gametophyte. L.S. **Figs. 24–26.** Logitudinal section of hypodermal archesporial cell. **Fig. 27.** Formation of primary parietal cell and sporogenous cell. **Figs. 28–29.** Twin megaspore mother cells. **Fig. 30.** Megaspore mother cell with two layers of nucelli cells. **Fig. 31.** Megaspore mother cell at metaphase. **Figs. 32–33.** Formation of linear tetrads. **Figs. 34–35.** T-shaped tetrad. **Fig. 36.** 2-nucleate embryo sac. **Figs. 37–38.** 4- and 8-nucleate embryo sac. **Fig. 39.** Mature 8-nucleate embryo sac. ac = archesporial cell; ap = antipodal; eg = egg; mmc = megaspore mother cell; pn = polar nucleus; pp = primary parietal cell; sc = sporogenous cell; sy = synergid cells.



Figs. 40–52. *Averrhoa bilimbi,* megasporogenesis and female gametophyte. L.S. **Figs. 40–41.** Longitudinal section of hypodermal archesporial cell. **Fig. 42.** Twin primary parietal cells and sporogenous cells. **Fig. 43.** Archesporial cell, primary parietal cell and sporogenous cell. **Figs. 44–47.** Stages leading to the formation of functional megaspore. **Fig. 45.** Megaspore mother cell at metaphase. **Fig. 46.** Dyad. **Fig. 47.** Functional megaspore. **Figs. 48–52.** Stages in the development of female gametophyte. **Fig. 48.** 2-nucleate embryo sac. **Figs. 49–51.** Formation of 4-, 6- and 8-nucleate embryo sac. **Fig. 52.** Mature 8-nucleate embryo sac. ac = archesporial cell; ap = antipodal; eg = egg; mmc = megaspore mother cell; pn = polar nucleus; pp = primary parietal cell; sc = sporogenous cell; sy = synergid cells.

one layer of micropylar nucellar tissue (Figs. 45–46). However, shortly after the formation of the megaspore mother cell and dyad cells of *A. carambola*, the apical dermal nucellar cells enlarge and divide periclinally to contribute to the formation of the crassinucellar ovule. In one or two cases, the archesporium of *Averrhoa* does not divide but enlarges, elongates and functions directly as the megaspore mother cell. Therefore, the ovule has the tendency to become a tenuinucellar ovule (Figs. 31, 43).

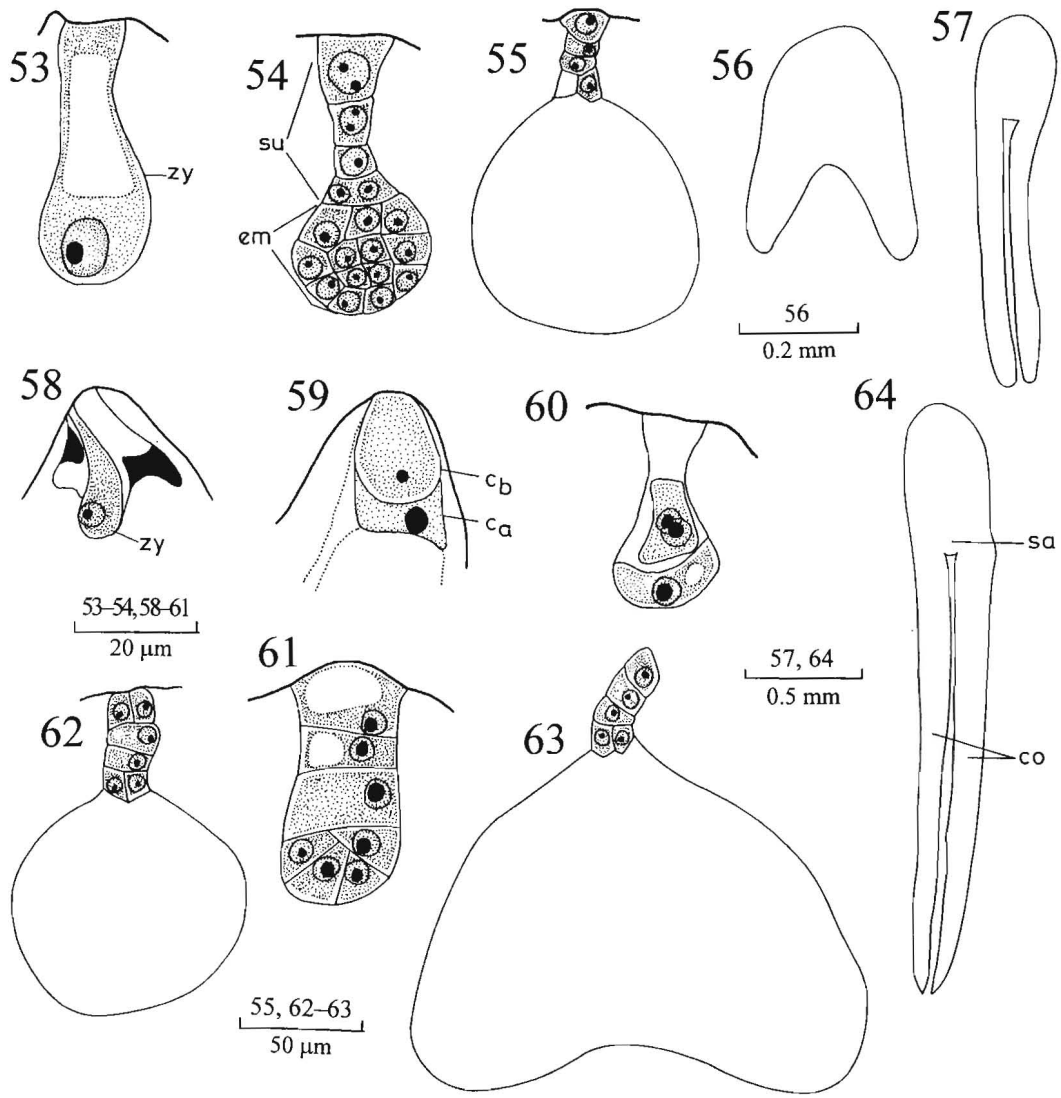
The megaspore mother cell "rests" for a long time then begins to undergo meiosis to form a dyad, followed by a tetrad through synchronous division (Fig. 32). Investigations of *Averrhoa* so far show that the megasporogenesis develops a linear tetrad of megaspores (Thathachar 1942). This is true in *A. bilimbi*, but *A. carambola* produces both linear and T-shaped tetrads (Figs. 33–35) in present study. In *B. sensitivum* (Govindappa & Boriah 1956), the dyad may divide to form a T-shaped megaspore tetrad. According to Davis (1966), linear and T-shaped megaspore tetrads have also been observed in various members of Oxalidaceae. The formation of tetrads in *A. bilimbi* is rapid and this is followed by an immediate degeneration of three micropylar megaspores (Fig. 47). At this stage the anther has produced pollen tetrads or uninucleate microspores.

The chalazal megaspore is functional and divides mitotically to form a 2-, 4- and finally 8-nucleate embryo sac (Figs. 36–39, 48–52). The mature embryo sac consists of two synergids, an egg cell, two polar nuclei and three ephemeral antipodals (Figs. 39, 52). The present study has confirmed that the embryo sac development in *Averrhoa* conforms to the monosporic *Polygonum* type (Maheshwari 1950) as reported in *A. carambola* (Thathachar 1942, Low 1972, Davis 1966), *A. bilimbi* (Thathachar 1942, Davis 1966, Tan 1977), *O. corniculata* (Hammond 1908) and *B. sensitivum* (Mauritzon 1934, Govindappa & Boriah 1956). The early work of Thathachar (1942) also revealed that the sequential formation of the embryo sac in *B. sensitivum* followed that of the 8-nucleate embryo sac of the bisporic *Allium* type.

No pyriform synergids were observed and the polar nuclei fuse close to the egg cell. The three ephemeral antipodal cells degenerate before fertilization (in *A. carambola*) or after the formation of the secondary nucleus (in *A. bilimbi*). Actual pollen tube growth and fertilization have not been observed. However, degeneration of one of the synergids followed by the fusion of the polar nuclei to form a secondary nucleus and the increase in size of the egg nucleus indicate that fertilization has taken place.

ENDOSPERM AND EMBRYO

Soon after fertilization, the primary endosperm nucleus divides to form two free nuclei that subsequently divide repeatedly to produce more nuclei to fill the enlarging embryo sac. The development of the endosperm follows the *ab initio* Nuclear type (Davis 1966). The divisions in the nuclear endosperm are not synchronous. In *A. bilimbi*, the free endosperm nuclei are uninucleolate or sometimes clearly visible as having two nucleoli, while those of *A. carambola* have only one. As the number of endosperm nuclei increases, the nuclei tend to concentrate around the micropylar and chalazal regions and also at the periphery of the



Figs. 53–64. *Averrhoa* species, embryo development. L.S. **Figs. 53–57.** *A. carambola.* **Figs. 58–64**, *A. bilimbi.* **Figs. 53, 58.** Zygote. **Figs. 54–55.** Globular embryo. **Fig. 56.** Heart-shaped embryo. **Fig. 57.** Mature straight embryo. **Figs. 59–62.** Stages leading to the formation of globular embryo. **Fig. 63.** Initiation of the cotyledons. **Fig. 64.** Mature, staight embryo. Ca = terminal cell; C_b= basal cell; em = embryo; co = cotyledon; sa = shoot apex; su = suspensor; zy = zygote.

embryo sac while the centre of the embryo sac is occupied by a large vacuole. At the globular embryo stage (with a 5-celled suspensor in *A. carambola* or a 4–6-celled suspensor in *A. bilimbi*), the nuclear endosperm turns cellular from the micropylar towards the chalazal region (in *A. carambola*) or from the chalazal and peripheral regions to the micropylar region (in *A. bilimbi*). These endosperm cells are irregular in size and shape, with large vacuoles. These cells become homogenous only after the embryo reaches the heart-shaped stage. At the late globular embryo stage, the cellular endosperm concentrates around the developing embryo, which consumes food from these cells, resulting in a region of degenerating endosperm in this area (Figs. 68, 71).

Thathachar (1942) stated that in *A. carambola* and *A. bilimbi*, the wall formation which proceeded from the periphery towards the centre of the embryo sac began only after the number of endosperm nuclei had exceeded 32. Similar observations had been made for *Averrhoa* (Davis 1966). According to Low (1972) and Ou Yang (1978), the endosperm became cellular most probably after the 64-nuclei stage and by this time the embryo had reached the 8-celled proembryo stage. Ou Yang (1978) further noted that when the endosperm reached the 32-nuclei stage, the embryo was only at the 3-celled proembryo stage.

The zygote undergoes a short resting period (Figs. 53, 58). The first division of the zygote occurs at about 7 to 10 days after fertilization. The division of the zygote is transverse, giving rise to a basal cell (C_b) and a terminal cell (C_a). The basal cell of *A. bilimbi* divides transversely first before the terminal cell, resulting in the formation of a 3-celled proembryo, while the terminal proembryo divides longitudinally to form a T-shaped 4-celled proembryo (Figs. 59–61). Subsequent divisions in this proembryo give rise to an octant proembryo followed by a globular embryo with a 2–6-celled (in *A. carambola*) or 4–6-celled (in *A. bilimbi*) suspensor (Figs. 54–55, 62). Later, it develops into a heart-shaped embryo and then a mature, straight dicotyledonous embryo with a radicle, plumule and two thin, leaf-like and equal cotyledons (Figs. 56–57, 63–64, 68, 71–73).

The development of the embryo in the family Oxalidaceae was studied by Mauritzon (1934), Noll (1935), Souéges (1939), Johansen (1950) and Narayana (1962), and classified under the *Oxalis* variation of the *Asterad* type. According to Davis (1966), the embryogeny of both the Averrhoaceae and Oxalidaceae conformed to the *Asterad* type. Thathachar (1942) reported the *Geum* variation in *A. carambola* and *A. bilimbi*, while Ou Yang (1978) observed the *Asterad* type in *A. carambola*. Hammond (1908) reported the formation of a multicellular suspensor in *O. corniculata*. He observed a multicellular haustorial-like organ formed from the basal cells of the suspensor, which forced its way through the integuments until it reached the testa.

SEED COAT

The inner integument ultimately becomes about 6–8 cell layers in thickness. The cells of the outer and middle layers are soon crushed. The inner layer of the inner integument develops into its endothelial character lining the outer side of the endosperm. These cells are

tangentially flat and thin-walled. In *A. bilimbi*, these cells contain tannins while the outer layer forms a fibrous exotegmen with reticulate wall thickenings.

The outer integument is multiplicative and may thicken up to 20 cell (in *A. bilimbi*) or 25 cell (in *A. carambola*) layers. The outer layer of the outer integument is tanniniferous. The inner layer of the outer integument of *A. carambola* develops into collenchymatous tissue, while the outer layer becomes more lignified. The middle layer is parenchymatous with tannin deposition in these cells. The cells of the inner layer of the outer integument in *A. bilimbi* contain crystals and show some slight wall thickenings (Figs. 77–78, 82–83).

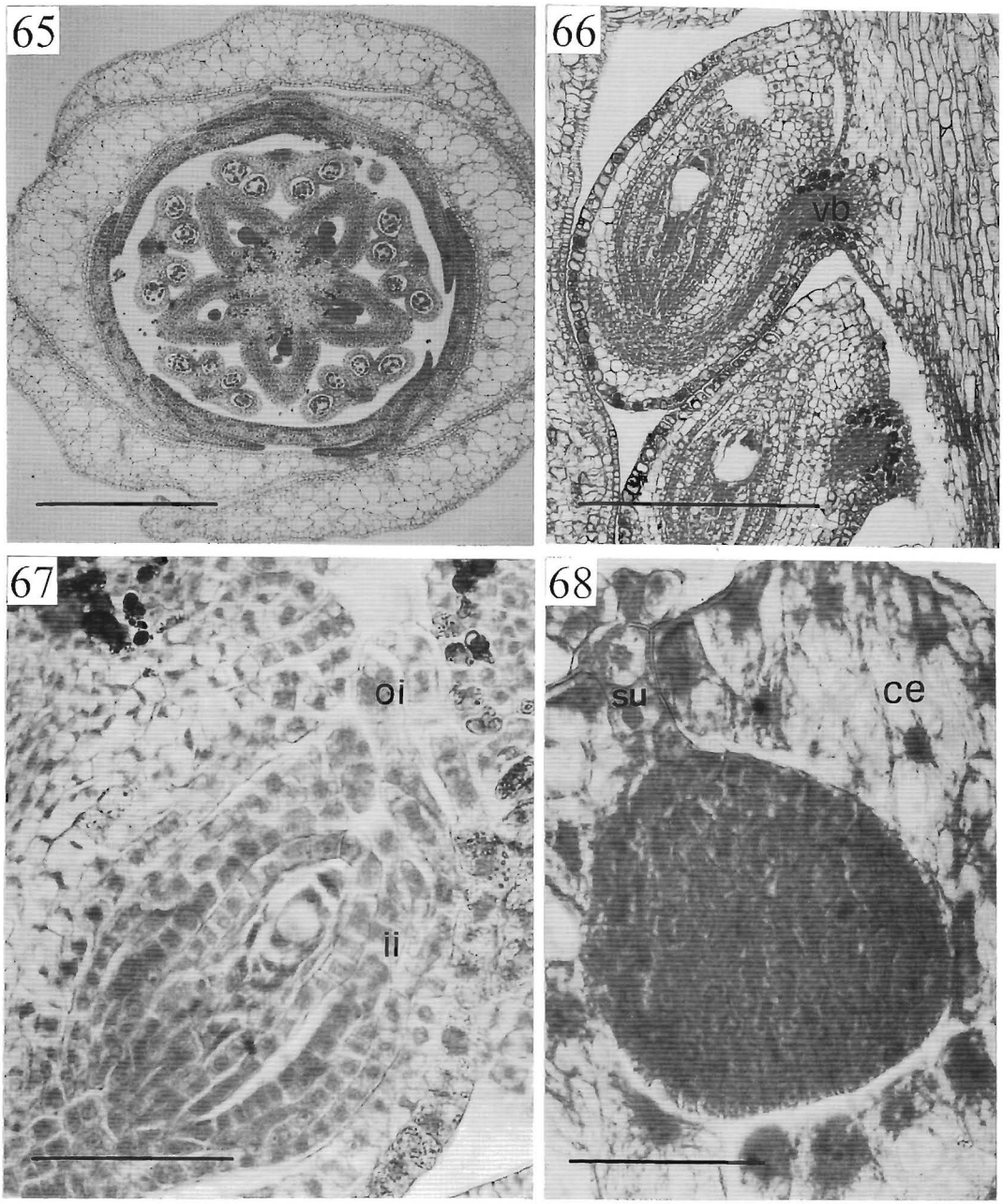
The present study confirms the observation of Boesewinkel (1985) that the inner integument of *Averrhoa* is initially 2-layered and later becomes 4–5-layered. The endothelium develops into an inner pigment layer while the middle layer is crushed and the exotegmen becomes fibrous. The outer integument becomes multiplicative by division in the inner layer, while the endotestal is deposited with crystals. This is generally similar to the seed coat of *Oxalis* and *Biophytum* (Bouman 1974), which is of simpler construction, the inner integument remaining 3-layered and the inner layer of the outer integument without so many divisions.

As the embryo develops and the endosperm becomes cellular, the inner integument becomes slightly ruminate and the outer integument becomes thinner and tanniniferous. In a mature seed, the seed coat consists of a thin layer of the outer integument densely filled with tannin substances and a thin layer of ruminate inner integuments. The rumination of the seed coat in *Biophytum* was exclusively caused by the differential, radial stretching of the cells of the middle layer of the outer integument. However, the ruminations in *Oxalis* and *Averrhoa* were caused by an increased mitotic activity of groups of cells in the middle layers of the outer integument (Boesewinkel 1985). According to Boesewinkel (1985), the mature seeds of *Averrhoa* were hardly or not ruminated in contrast to those of *Oxalis* and *Biophytum* (Bahadur, Bhaskar & Farooqui 1983).

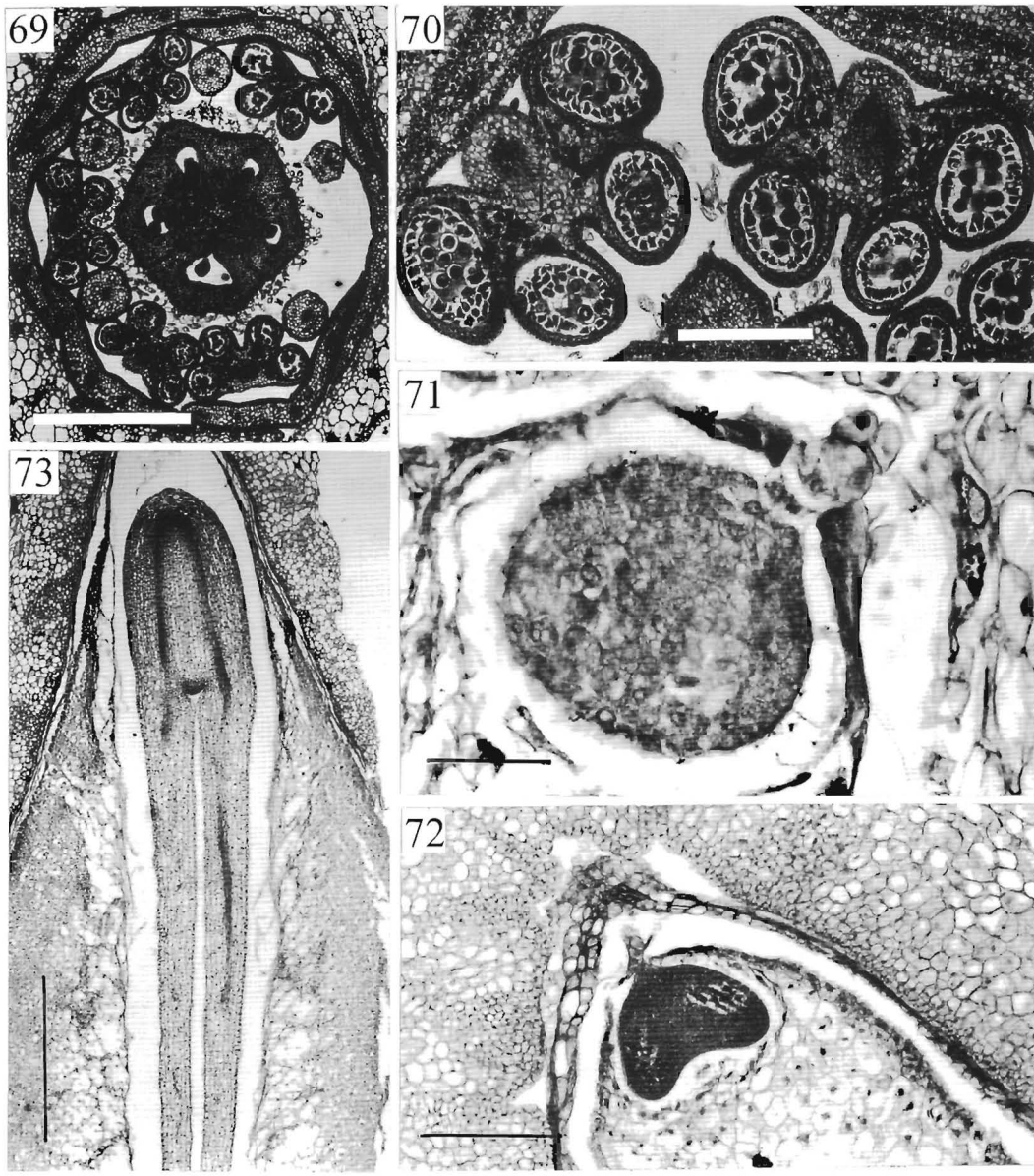
FRUIT WALL

The *Averrhoa* fruit is a fleshy berry developed from a 5-chambered, superior ovary with axile placentation. Fahn (1967) described a berry as a fruit with thick and juicy pericarp in which the following three strata can be distinguished, i.e., exocarp, mesocarp and endocarp. The pericarp of *Averrhoa* is distinguished into three layers, i.e., the outer epidermis with hypodermal layers as exocarp; the middle parenchymatous zone comprising the great bulk of the berry wall including its vasculature as mesocarp; and the inner epidermis with a few layers of parenchyma constituting a parenchymatous zone as endocarp (Kumar 1975, Lim 1975, Dave, Patel & Rupera 1975 and present study).

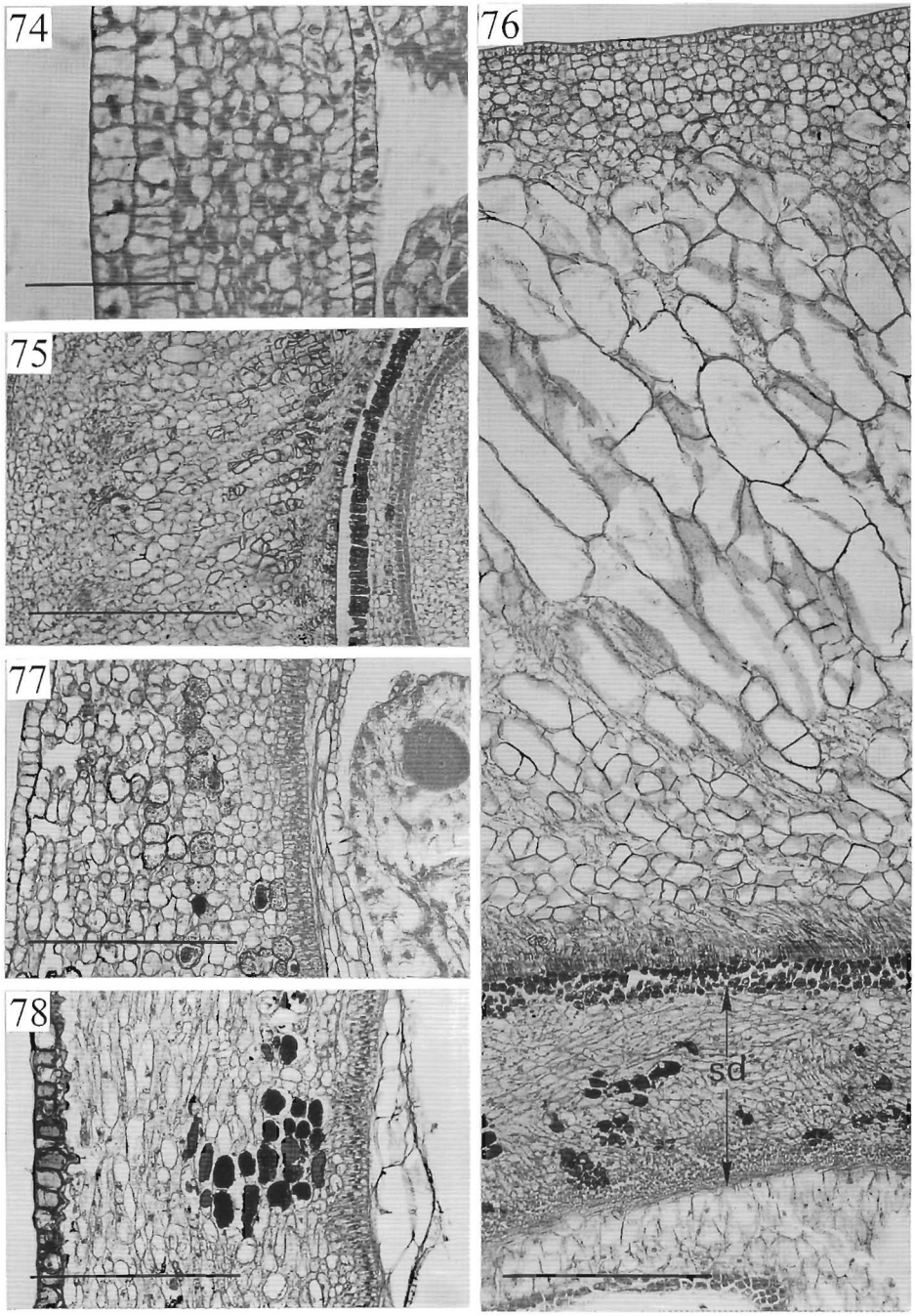
Although the anatomy of Oxalidaceae has been surveyed by Metcalfe & Chalk (1950), anatomical studies of the fleshy pericarp in *Averrhoa* are few (Kumar 1975, Dave, Patel & Rupera 1975, Tan 1977, Ou Yang 1978). The present investigation shows that at the mature embryo sac stage, the exocarp consists of two cell layers, the mesocarp has 10–12 parenchyma



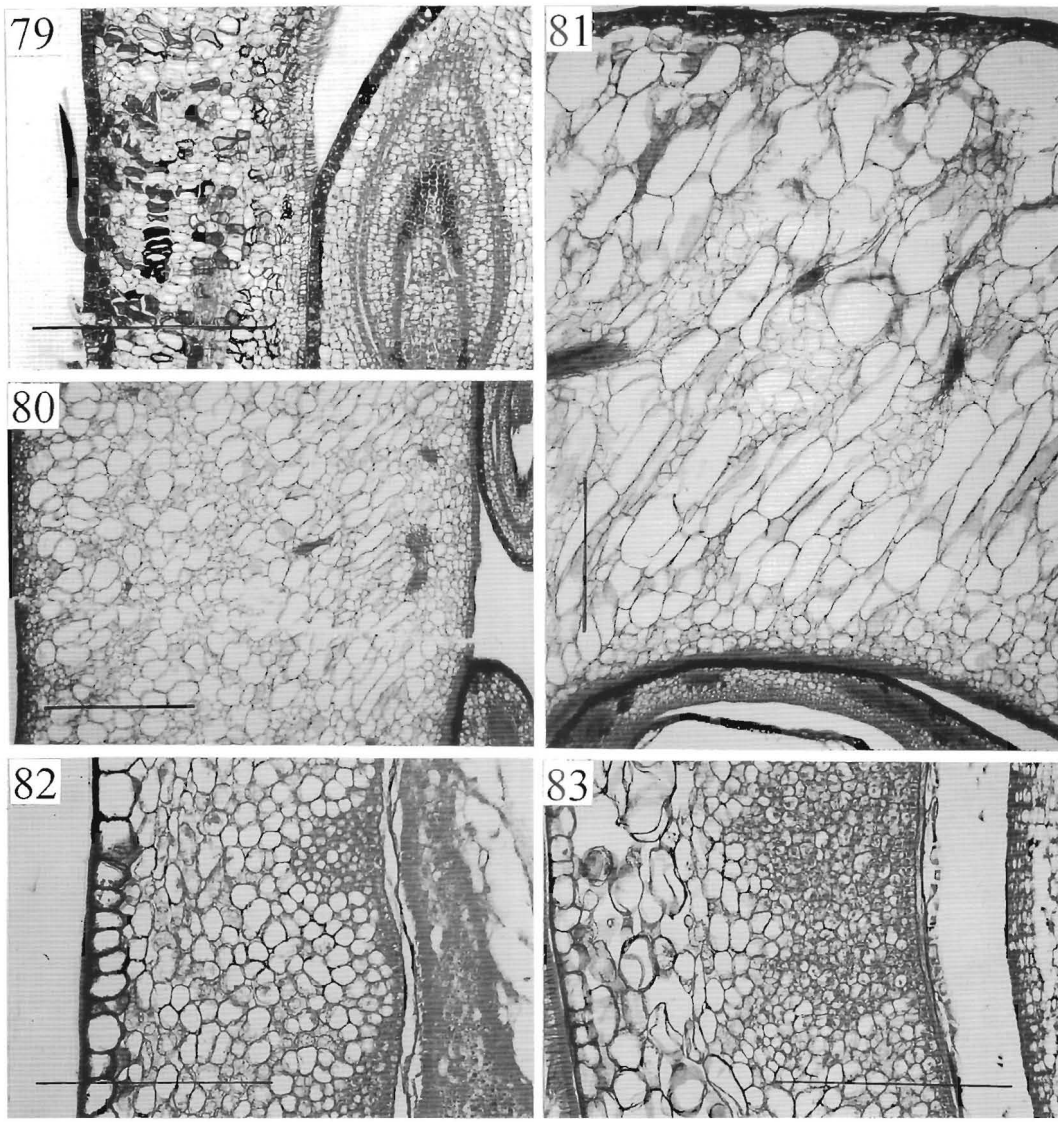
Figs. 65–68. *Averrhoa carambola.* **Fig. 65.** T.S. flower bud. Scale bar = 0.4 mm. **Fig. 66.** L.S. anatropous ovule at mature embryo sac stage showing the vascular bundle. vb = vascular bundle, scale bar = 0.25 mm. **Fig. 67.** L.S. micropyle is formed by the inner and outer integuments at the 2-nucleate embryo sac stage. ii = inner integument; oi = outer integument, scale bar = 50 mm. **Fig. 68.** L.S. globular embryo with suspensor surrounded with cellular endosperm. ce = cellular endosperm; su = suspensor, scale bar = 50 mm.



Figs. 69–73. *Averrhoa bilimbi.* **Fig. 69.** T.S. flower bud. Scale bar = 1 mm. **Fig. 70.** T.S. division of the two whorls of anthers are not synchronous, e.g. long-whorl anther at meiosis I and II while short-whorl anther at microspore mother cell stage. la = long-whorl anther; sa = short-whorl anther, scale bar = 0.4 mm. **Fig. 71.** L.S. globular embryo with suspensor surrounded with cellular endosperm. Scale bar = 75 mm. **Fig. 72.** L.S. initiation of the cotyledons. Scale bar = 0.4 mm. **Fig. 73.** L.S. mature straight embryo. Scale bar = 1 mm.



Figs. 74–78. *Averrhoa carambola.* **Fig. 74.** L.S. ovary wall at mature embryo sac stage. Scale bar = 50 mm. **Fig. 75.** L.S. fruit wall at zygote stage. Scale bar = 0.25 mm. **Fig. 76.** L.S. fruit wall at young globular embryo stage (15 cells thick). sd = seed coat, scale bar = 0.25 mm. **Fig. 77.** L.S. seed coat at globular embryo stage. Scale bar = 0.25 mm. **Fig. 78.** L.S. seed coat at heart-shaped embryo stage. Scale bar = 0.25 mm.



Figs. 79–83. *Averrhoa bilimbi.* **Fig. 79.** L.S. ovary wall at mature embryo stage. Scale bar = 0.25 mm. **Fig. 80.** L.S. fruit wall at zygote stage. Scale bar = 0.4 mm. **Fig. 81.** L.S. fruit wall at young globular embryo stage. Scale bar = 0.4 mm. **Fig. 82.** L.S. seed coat at globular embryo stage. Scale bar = 0.25 mm. **Fig. 83.** L.S. seed coat at young heart-shaped embryo stage. Scale bar = 0.25 mm.

cell layers and the endocarp is only 1–2 cells thick (Figs. 74, 79). After fertilization, the outer epidermal cells and the 2–3 layers of hypodermal cells show periclinal division and contribute to exocarp development. The mesocarp cells enlarge and their nuclei degenerate simultaneously with the nuclei of the endocarp. These cells have large vacuoles and thin walls. At this stage, the cells above the endocarp towards the centre are filled with tanniniferous material and oxalate-crystals, while the endocarp cells become thin and elongated (Figs. 75, 80). Dave, Patel & Rupera (1975) recognised the fruit wall of *Averrhoa* as the parenchymatous fleshy type with many cells containing tannin and calcium oxalate.

As the embryo sac enlarges, the cell of the exocarp and mesocarp continue to increase as well as enlarge and finally their nuclei disappear completely. However, the cells of the endocarp, in 7 to 10 cell layers, become compressed and elongated. These cells are filled with tannins and oxalate crystals. When the embryo reaches the globular stage, the cells of the outer epidermis become smaller with the outer wall cuticularized. The cuticle layer thickens at the heart-shaped embryo stage (Figs. 76, 81). Crystals of calcium oxalate are deposited in the combined region of the exocarp and mesocarp. The mesocarp cells are parenchymatous and enlarge tremendously, filled with juice. The cells with tannins are larger than the surrounding parenchyma cells. The tannin deposition in the cells are denser towards the central axis but the contents are thinner towards the exocarp of the ridges. When the fruit reaches maturity, it becomes yellow or yellowish-green while the texture of the fruit wall is softer. The exocarp cells, which are compressed by the mesocarp cells, become elongated. The mesocarp cells are filled with juice, thin-walled, irregular in shape with the intercellular binding of these cells loosened. In the *A. carambola* fruit, only a few inner epidermal cells towards the ridge are slightly thickened on their outer walls and thinly cutinised. The young immature pericarp has a firm texture but becomes softer as the fruit ripens. Such softening may be due to the chemical changes in cell content and in the structure of the cell (Esau 1953).

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Paphiopedilum kolopakingii (*Orchidaceae* : *Cypripedioideae*) —A Slipper Orchid new to Sabah

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Village collectors have recently found a population of a species of *Paphiopedilum* that has never been collected before in Sabah. The plants are large with dark green strap leaves up to 50 cm long and 5 cm broad. A few plants were flowering when collected and bore very long inflorescences over a metre and a half in length and bearing up to 10 flowers. The flowers were about the size of those of *P. stonei* (Hook.) Stein but of a greenish-buff with purple stripes on the dorsal sepal and synsepal and purple venation within the lip. The petals were linear-tapering, decurved and twisted spirally in the apical third. The staminode, an important feature in the genus, was white with buff-brown hairs on the upper margin and along the sides towards the apex.

In most features these plants agree well with the description of *P. kolopakingii* Fowlie (Fig. 1), a species previously only known from north-central Kalimantan. The Sabahan plants (Fig. 2, *L. Han & A. Lamb* KNP 08130, Kinabalu Park Herbarium) differ slightly from Kalimantan material we have examined in having more spirally twisted petals and a white staminode with a less hairy margin. The dorsal sepal is ovate and shorter than the typical from Kalimantan. Unfortunately the flowers we have examined were in poor condition and it may be that fresh flowers will more closely resemble typical Kalimantan material.

Fig. 1. *Paphiopedilum kolopakingii* Fowlie. A: habit. - B: leaf apex. - C: part of inflorescence. - D: dorsal sepal. - E: synsepal. - F: petal. - G: lip, longitudinal section. - H: column, side view. - J: column, oblique view. - K: anthers. A–C drawn from a cultivated specimen at Royal Botanic Gardens, Kew and D–K from *Fowlie s.n.* by Judi Stone. Scale: single bar divided into mm; double bar divided into cm. (Reproduced from *Orchids of Borneo Vol. 3* with kind permission of The Sabah Society and the Royal Botanic Gardens, Kew)

The exact locality of this population is unknown. The collectors claimed that it came from the eastern side of Kinabalu, but whether within the park or not is unknown. The collectors found the plants growing on a cliff and had to reach them on a rope from above. If the locality is confirmed this represents an extraordinary extension of distribution for this magnificent species which has the longest inflorescences in the genus and the most flowers per spike of any species in the section Coryopedium.

Fig. 2. Close up of flower of *Paphiopedilum kolopakingii* from Mount Kinabalu. (*L. Han & A. Lamb* KNP 08130) (Photo: A. Lamb)