

THE TAXONOMY, DISTRIBUTION AND ECOLOGY OF THE EPIPHYTIC MALESIAN ANT-FERN *LECANOPTERIS* REINW. (POLYPODIACEAE)

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Abstract

Lecanopteris comprises 13 epiphytic species with expanded rhizomes which shelter ants in a mutualistic association. Taxonomic descriptions and a key are given. In subgenus *Myrmecopteris*, *L. sinuosa* occurs throughout Malesia, in most habitats below 800 m a.s.l., especially in the ant-epiphyte communities of dry forest. *Lecanopteris crustacea* is confined to Bornean, Sumatran and Malaysian lowland dipterocarp canopies. Its sister species, *L. sarcopus* occurs in intact and disturbed forest from 400-1200m in the Philippines and Sulawesi. *Lecanopteris mirabilis* is found in New Guinea, Ambon and Seram, and is locally abundant in undisturbed mid-montane forest. Subgenus *Lecanopteris* consists of three groups, typified by *L. curtisii*, *L. pumila* and *L. darnaedii*. *Lecanopteris curtisii* forms distinct races in New Guinea, the Philippines, Sumatra, Java and Borneo. It is a rare member of intact or old disturbed hill forest between 400 m and 1200 m. The *L. pumila* group contains three endemics of lower montane forest in Sulawesi: *L. celebica*, *L. carmosa* and *L. balgooyi*, and a Philippine endemic, *L. luzonensis*. *Lecanopteris pumila* is found in mid-montane forest and ridgetops in Malaysia, Sumatra and Borneo, where it forms distinct races. The *L. darnaedii* group is endemic to Sulawesi; the three species are allopatric and found in undisturbed mid-montane forest. Myrmeco-epiphytic communities, inhabited by *Iridomyrmex cordatus*, are found in Bornean heath forest and New Guinean savannah. The ants contribute to the spread of ant-epiphytes by planting their propagules in the ant carton surrounding *L. sinuosa*. The only ecological characteristic common to *Lecanopteris* apart from myrmecophytism is heliophily, confining individuals to habitats with open canopies or tree crowns. No preference is manifested for host species, but *Lecanopteris* tends to grow on rough-barked trees.

Introduction

The ant-associated fern genus *Lecanopteris* Reinw. comprises 13 species which are largely confined to Malesia, and is characterised by a highly modified rhizome which shelters ants. Despite its remarkable biology and morphology, the genus remained in relative obscurity for 150 years after its first description by Reinwardt in 1828. Recently it has been the simultaneous subject of a D. Phil. thesis and a taxonomic monograph (Gay 1990; E. Hennipman *unpub.*). This article provides taxonomic descriptions based on field and herbarium material and a detailed account of the ecology and distribution of *Lecanopteris*.

The ant association, rhizome structure and evolution of *Lecanopteris* have been described by Gay (1990, 1991, 1993, *in press*) and Gay & Hensen (1992). Every member of the genus possesses a hollow or expanded rhizome which is used as a domatium by ants. Rhizome form varies from a solid, arched domatium (*L. mirabilis* (C. Chr.) Copel.) to dimorphism of solid and hollow rhizomes (*L. sarcopus*

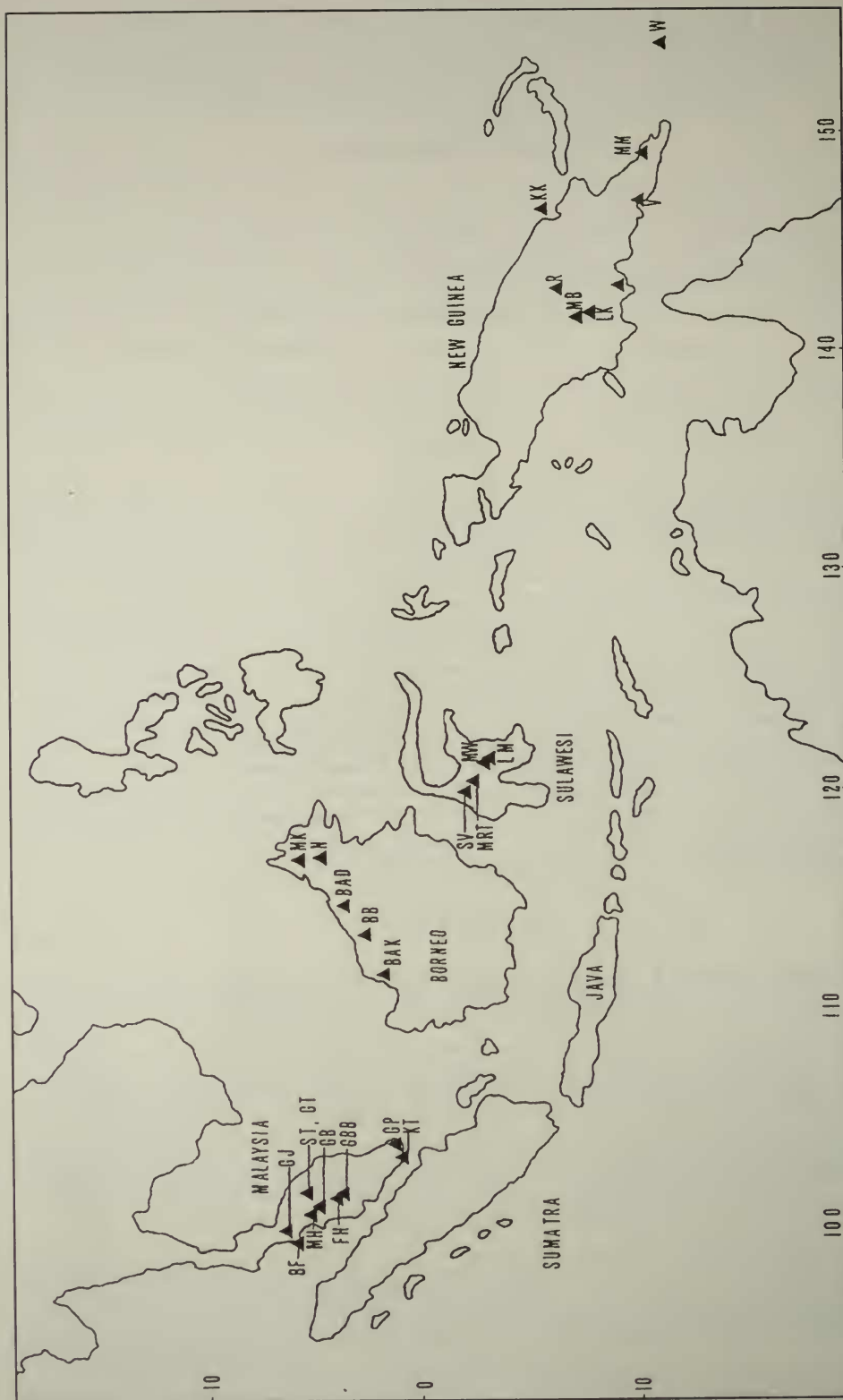


Fig. 1. The field sites

Teysm. & Binnend.), a single gallery (*L. sinuosa* Wall. ex Hook., *L. pumila* Bl.) or a double gallery (*L. darnaedii* Hennipman) (Gay 1993). In a given habitat, a constant ant species from the genera *Crematogaster* or *Iridomyrmex* nests, rears larvae and deposits debris in the rhizome, and may build carton runways and keep coccids in the vicinity. When the fern's geographical or altitudinal range is wider than that of the ant, another ant species replaces the major inhabitant beyond the limits of the former's range, showing that in this mutualism host/ant specificity is a function of ecology rather than evolution. Ant faeces and debris dumps within the rhizome provide a source of nutrients for *Lecanopteris* (Gay *in press*). The mutualism is based on acquisition of a nest by the ants, and nutrient uptake for the ferns.

Materials, Methods and Sources

Ecological data were obtained from field observations in Papua New Guinea, Peninsular Malaysia, Borneo and Sulawesi for eight species of *Lecanopteris* (*L. mirabilis*, *L. crustacea*, *L. pumila*, *L. curtisii* s.l., *L. sarcopus*, *L. sinuosa*, *L. celebica* and *L. darnaedii*). Field sites are listed in Appendix 1 and shown in Fig. 1. Data were recorded using two proformas: the first described each individual *Lecanopteris* recorded at a site, and the second recorded the habitat, following the technique developed by Webb, Tracey and Williams (1976) for comparative physiognomic analysis of Australian and New Guinean forest types. Herbarium specimen labels yielded limited information on habitats; relevant collections are appropriately cited.

Herbarium specimens of all species, and wild and cultivated plants where possible, were examined for the taxonomic descriptions. Spore, sporangium and venation characters are from Hettterscheid and Hennipman (1984), Hennipman (1986) and Hennipman and Verduyn (1987). Other authors are cited where appropriate. Specimens from the following herbaria were used: Kew (K); the Natural History Museum (BM); Lae (LAE); Port Moresby (UPNG); Singapore (SING); Kepong (KEP); Leiden (L); Berlin (B); Utrecht (U); Bogor (BO); New York (NY); Munich (M) and Michigan (MICH). The distribution maps are based on herbarium material and are after Hennipman (1986, and *unpub.*). The following abbreviations are used in the text: G. = Gunung (mountain); S. = Sungei (river); s. n. = un-numbered herbarium specimen; s. d. = specimen without date.

Taxonomic Account

LECANOPTERIS Reinwardt

Flora 3: 48 (1825); *Onychium carnosum* Reinwardt, in Syllog. Plantarum 2: 2 (1824), nom illeg. non Kaulfuss (1820); Copeland, Gen. Fil.: 205 (1947); Holttum, Revised Flora of Malaya Volume 2, Ferns of Malaya: 208 (1955); Hennipman, in Kew Bull. 41: 783 (1986); Hennipman and Verduyn, Blumea 32 : 313 (1987).

Type : *Lecanopteris carnosa* (Reinw.) Blume.

Myrmecophila (Christ) Nakai, in Bot Mag, Tokyo 43: 6 (1929) nom illeg, non Rolfe (1917). *Polypodium* sect. *Myrmecophila* Christ, Farnkr.: 12(1987). *Myrmecopteris* Pic. Ser., in Webbia 31:239 (1977).

Lectotype : *Lecanopteris sinuosa* (Wall. ex Hook.) Copel., selected by Pichi Sermolli.

Epiphytic or very rarely epilithic ferns of moderate size. *Rhizome* forming a domatium, creeping, much to little-branched; monomorphic, rarely dimorphic or subdimorphic; hollow with one or two gallery systems, or solid and arched, pale green, opalescent or glaucous when living, black when dead; glabrous, spiny, or bearing filamentous hairs or coralloid excrescences (subg. *Lecanopteris*) or translucent, dark-centred, circular, dense or sparsely set peltate scales (subg. *Myrmecopteris*). Always ant-inhabited. *Phyllopodia* usually distinct, hollow and prominent or solid and unprotruding. *Stipes* absent to elongate, glabrous, often dark brown. *Fronde*s pale to dark green, simple to deeply pinnatifid, chartaceous to coriaceous, articulate to phyllopodia, distichous along rhizome, erect to ascending. Aborted fronds sometimes present as spines or excrescences in subg. *Lecanopteris*. Venation a complex network of areoles with included free veins. *Sori* rounded, immersed in the lamina, either in a single row on either side of the midrib and costae (subg. *Myrmecopteris*) or on round, oval or boat-shaped extra-marginal projections (subg. *Lecanopteris*). *Sporangia* on triseriate stalk; annulus longitudinal, interrupted and consisting of c. 13 thickened cells. Usually 64, rarely 16, spores per sporangium. *Spores* monolete, orange, smooth and translucent, filamentous in *L. mirabilis*.

Subgenus *Myrmecopteris*: Rhizome hollow or solid, densely covered with orbicular, dark-centred peltate scales with translucent margins which hide the rhizome colour. Rhizome does not blacken with age. *Sori* always immersed on the lamina. Rhizome usually, but not always, much-branched.

Species: *L. mirabilis*, *L. sarcopus*, *L. crustacea*, *L. sinuosa*.

Subgenus *Lecanopteris*: Rhizome always hollow, glabrous, except for an indumentum of scattered branched hairs and dark brown scales at the apices. Rhizome bright pale green, opalescent or glaucous when young, blackening with age. *Sori* immersed in re-curved extra-marginal lobes, except in *L. spinosa* and *L. balgooyi*, where they are immersed on the lamina. Rhizome always much-branched.

Species: *L. curtisii*, *L. pumila*, *L. celebica*, *L. carnosa*, *L. luzonensis*, *L. balgooyi*, *L. spinosa*, *L. holttumii*, *L. darnaedii*.

KEY TO THE SPECIES

- 1a. Rhizome with a dense or scattered covering of peltate scales which hide the rhizome colour (subg. *Myrmecopteris*) 2
- 1b. Rhizome macroscopically glabrous, bright green when young, blackening with age (subg. *Lecanopteris*)..5
- 2a. Rhizome solid, arched and plate-like; scales thinly scattered over its surface; fronds pinnatifid 1. *L. mirabilis*
- 2b. Rhizome completely or partly hollow, not arched and plate-like; densely covered with scales; fronds pinnatifid or entire 3
- 3a. Rhizome dimorphic, consisting of solid cylindrical frond-bearing main branches and hollow, ovate, frondless side branches; peltate scales black-centred. Fronds pinnatifid 2. *L. sarcopus*
- 3b. Rhizome monomorphic, hollow except for the apical 2- 3 cm; peltate scales black or brown centred. Fronds pinnatifid or entire 4
- 4a. Peltate scales brown-centred. Fronds pinnate; rhizome much-branched.....3. *L. crustacea*
- 4b. Peltate scales black-centred. Fronds entire; rhizome much or little-branched.....4. *L. sinuosa*
- 5a. Rhizome with a waxy sheen, glaucous, never spiny; extra-marginal sori boat-shaped 5. *L. curtisii*
- 5b. Rhizome green, with scattered or dense spines derived from aborted fronds or epidermal outgrowths, hollow or solid, or with coralloid excrescences derived from aborted phyllopodia, or spineless but bearing an indumentum of glandular hairs 6
- 6a. Spines or excrescences derived from modified undeveloped fronds and replacing some fronds, in two rows along the rhizome. A single gallery system within rhizome. Phyllopodia hollow, protruding 7
- 6b. Spines derived from epidermal outgrowths and densely covering rhizome. Two gallery systems in rhizome. Phyllopodia solid, not protruding 11
- 7a. Spines hollow. Fronds entire to pinnatifid 6. *L. balgooyi*
- 7b. Spines solid, or replaced by coralloid excrescences. Fronds pinnatifid 8
- 8a. Rhizome covered with short coralloid excrescences 1-3 cm long, derived from modified undeveloped fronds 7. *L. carnosa*
- 8b. Rhizome with a more or less dense covering of solid spines, no excrescences 9
- 9a. Large stout plants, rhizome diameter 2.5-3.5 cm. Fronds up to 1 m long. Spines abundant on rhizome 8. *L. celebica*
- 9b. Small to moderate sized plants rhizome diameter 1.5-2.5 cm. Fronds not more than 45 cm long. Spines very sparse, never abundant 10
- 10a. Rhizome bearing a dense indumentum of branched hyaline to brown glandular hairs. Luzon 9. *L. luzonensis*

- 10b. Rhizome apices with an indumentum of scattered brown glandular hairs and scale. West Malesia 10. *L. pumila*
- 11a. Fronds entire with sori inserted on lamina in two rows on either side of rachis 11. *L. spinosa*
- 11b. Fronds pinnatifid with sori immersed on extra-marginal lobes or sessile on lamina 12
- 12a. Veins strongly sclerified, appearing black.
..... 12. *L. darnaedii*
- 12b. Veins slightly sclerified, appearing green.
..... 13. *L. holttumii*

Subgenus *Myrmecopteris*

1. *Lecanopteris mirabilis* (C. Chr.) Copel.

Fig. 2.

Univ. Calif. Pub. Bot. 16: 123 (1929) ('mirabile'), Gen. Fil.: 205 (1947). *Myrmecopteris mirabilis* (C. Chr.) Pic. Ser., in Webbia 31: 237 (1977). *Polypodium imbricatum* Karsten, in Ann. Bot. Jard. Buit. 12: 168 (1895), nom. illeg. non Liebm. (1849). *Polypodium mirabile* C. Chr., Ind. Fil.: 545 (1906), nom. nov. pro *Polypodium imbricatum* Karsten (1895) non Liebm. (1849). *Pleopeltis imbricata* Alderw., in Bull. Dept. Agric. Ind. Neerl. 27: 3 (1909), nom. nov. pro *Polypodium imbricatum* Karsten (1895) non Liebm. (1849). *Polypodium ulotheca* Brause, in Bot. Jahrb Syst. 56: 204 (1920). *Myrmecophila ulotheca* (Brause) Ching, in Sunyatsenia 5(4): 260 (1940). *Myrmecopteris ulotheca* (Brause) Pic. Ser., in Webbia 31: 237 (1977). Type: *Ledermann 12641*, New Guinea (B).

Rhizome solid, arched and plate-like, 10-20 cm wide, forming a domatium between the dark-coloured rhizome underside and the host tree surface, ant-inhabited, branching sympodial and occasionally lateral, with scattered dark-centred, orbicular, peltate scales 1-1.5 mm diam., denser on the rhizome edges and underside. *Phyllopodia* solid, not prominent. *Stipes* dark brown, 10-30 cm long, basal diameter 2-5 mm. *Fronds* dark green, deeply pinnatifid, winged at their bases, 10-15 x 30-90 cm, glabrous, coriaceous, monomorphic; apex and lobes rounded, lobes perpendicular to the rachis, basal lobes narrower than median ones; veins forming a series of areoles with a freely branching recurrent vein. *Sori* deeply immersed on lamina, 2 mm diameter, circular, in a single row on either side of the the main veins of the lamina lobes, forming projections 1 mm high on the upper frond surface. *Spores* filamentous, 75 x 60 µm; filaments 1300-1900 µm, 16 spores per sporangium.

Representative specimens: **New Guinea**: *Croft 539*, Bululo-Aseki road, 20 km east of Aseki, Morobe Province, montane rain forest, 2300 m asl. (LAE); *Womersley NGF 24942*, Awande, nr. Okapa, Eastern Highlands Province, *Castanopsis* rain forest, 5800 ft asl. (LAE); *Gay 960*, Mt Mon, Milne Bay Province, mid-montane rain forest (K).

2. *Lecanopteris sarcopus* (Teysm. & Binnend.) Copel.

Univ. Calif. Publ. Bot. 16: 123 (1929). *Drynaria lomarioides* J. Sm., in Hook. J. Bot. 3: 397 (1841), nom. nud.. *Polypodium lomarioides* Kunze ex Mett., in Abh. Senckenb. Naturf. Ges. 2: 102 pl. 2 (1856). *Pleopeltis*

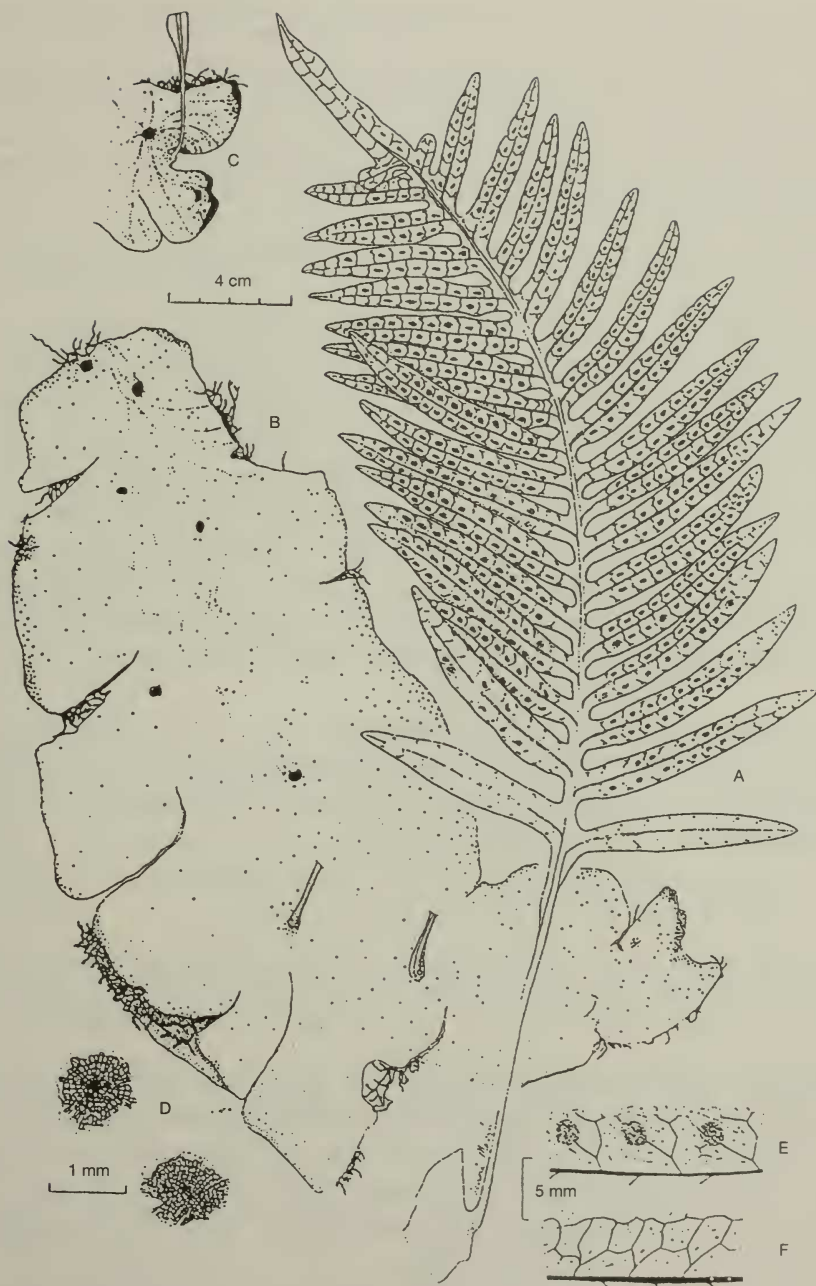


Fig. 2. *Lecanopteris mirabilis*

- | | |
|-------------------------|------------------------------|
| A: mature fertile frond | D: peltate scales |
| B: rhizome | E: venation of fertile frond |
| C: rhizome apex | F: venation of sterile frond |

Drawing by Jenni Marsh

lomarioides (Kunze ex Mett.) Copel., in Univ. Calif. Publ. Bot. 16: 123 (1929). *Myrmecopteris lomarioides* (Kunze ex Mett.) Pic. Ser., in Webbia 31: 240 (1977). Type: *Cuming 243*, Nueva Vizcaya, Luzon, Philippines (iso in BM, L, P, US). *Polypodium sarcopus* Teysm. & Binnend., in Natuurk. Ned. Ind. 29: 241 (1867). *Pleopeltis sarcopus* (Teyism. & Binnend.) Alderw., in Bull. Dept. Agric. Ind. Neerl. 27: 3 (1909). *Myrmecophila sarcopus* (Teyism. & Binnend.) Ching, in Sunyatsenia 5 (4): 259 (1940). *Myrmecopteris sarcopus* (Teyism. & Binnend.) Pic. Ser., in Webbia 31: 240 (1977). Type: *Teysmann and de Vries 75*, Manado, Minahassa, Sulawesi (iso in BM, K, L). *Polypodium sauvinierei* Baker, Ann. Bot. (1891), 480. Type: *De la Sauvinière 382*, "route de Sukur à Sawan", Minahassa, Sulawesi (K).

Rhizome creeping, dimorphic, consisting of solid, cylindrical, frond-bearing rhizomes 1-2 cm diameter which produce hollow, frondless lateral branches tapering at their apices, 2-3 cm diameter and forming an ant-inhabited domatium with a dark inner wall, much-branched; densely covered in translucent, orbicular, dark-centred, peltate scales, 1-2 mm diam. *Phyllopodia* solid, prominent, 1-1.5 cm high. *Stipes* 10-30 cm long, dark brown. *Fronde*s mid-green, deeply pinnatifid, winged at their bases, 20-140 cm long, glabrous, coriaceous, monomorphic; apex and apices of lobes ovate; veins forming a series of areoles with a freely branching recurrent vein. *Sori* deeply immersed in lamina, 1-2 mm diameter, circular, in a single row on either side of the rachis and main veins, forming projections on the upper frond surface. *Sporangia* c. 500 µm long. *Spores* biconvex.

Representative specimens: **Sulawesi**: *Koorders 17115b*, Minahassa (L); *Hennipman 6079*, along Malili-Soroako road, nr Wasuponda, S Sulawesi, 440 m asl. (L); *Gay 1262*, Lake Matano, nr Soroako. **Philippines**: *Cuming 241*, 242, Luzon (K).

3. *Lecanopteris crustacea* Copel.

Univ. Calif. Pub. Bot. 12: 406 (1931). *Polypodium lomarioides* Kunze ex Mett., Farng. 1, Polypod. Tab. 2, Figs 18-19 (1856). *Pleopeltis lomarioides* (Kunze ex Mett.) Moore, in Ind. Fil.: 78 (1857). *Phymatodes crustacea* (Copel.) Holttum, Ferns of Malaya: 190 (1955). Type: *Burchard 158*, UC. 391610(UC.).

Rhizome creeping, hollow, forming an ant-inhabited domatium with a dark inner wall, much-branched, sub-dimorphic, 3-5 cm diameter; thickly covered in orbicular peltate scales 1-2 mm diameter with ferruginous centres and translucent edges. *Phyllopodia* solid, not prominent. *Stipes* 10-15 cm long, dark brown. *Fronde*s mid-green, deeply pinnatifid, winged at their bases, 30-60 cm long, lobe and frond apices rounded, fertile fronds more deeply lobed than sterile fronds; veins forming a series of areoles with a freely branching recurrent vein. *Sori* circular, deeply immersed on lamina in a single row on either side of the rachis and main veins, forming projections 1 mm high on the upper lamina surface. *Spores* biconvex.

Representative specimens: **Sarawak**: *Richards 2259*, Mt Dulit, rain forest, 300 m asl. (K). **Sumatra**: *de Wilde & de Wilde Duyffjes 19464*, G. Leuser Forest Reserve, Aceh, recently logged forest (L). **Kalimantan**: *Kostermans 9793*, Mentawi

River, Balikpapan Dist., low wetland (BO).

4. *Lecanopteris sinuosa* (Wall. ex Hook.) Copel.

Fig. 3.

Univ. Calif. Pub. Bot. 12: 123 (1929). *Polypodium sinuosum* Wall. ex Hook., Spec. Fil. 5: 61, pl. 284 (1864) *Pleopeltis sinuosa* (Wall. ex Hook.) Beddome, Ferns of British India pl. 8 (1865); Alderw., in Bull. Dept. Agric. Ind. Neerl. 27: 3 (1909). *Phymatodes sinuosa* (Wall. ex Hook.) J. Sm., Ferns British and Foreign, 2nd ed.: 296 (1877). *Myrmecophila sinuosa* (Wall. ex Hook.) Nakai ex Ito, in J. Jap. Bot. 11: 98 (1935). *Myrmecopteris sinuosa* (Wall. ex Hook.) Pic. Ser., in Webbia 31: 240 (1977). Type: Wallich 2231, (K).

Rhizome hollow, forming an ant-inhabited domatium with a dark inner wall, stout, creeping, 1-2 cm diameter, little or much-branched, densely covered with orbicular, dark-centred peltate scales with translucent margins 1-2 mm diam. *Phyllopodia* hollow, prominent, 1-1.5 cm high. *Stipes* brown to green, 3-8 cm long. *Fronde*s mid to pale bright green, entire, occasionally slightly crenate (especially fertile fronds), winged at their bases, glabrous, 2-3 x 15-30 cm, coriaceous, monomorphic, apex rounded; veins forming a series of large areoles with a branching recurrent vein. *Sori* immersed, circular to rarely elliptical, in a single row on the lamina on either side of the rachis, 3-5 mm diameter, forming projections on the upper lamina surface. *Sporangia* c. 300 µm long. *Spores* biconvex.

Representative specimens: **New Guinea**: Croft 496, nr Agamoia, Fergusson Is., Milne Bay Province, disturbed lowland forest, 50 m asl. (LAE); Howcroft, Lae 64023, Wutung, Vanimo Subdistrict, on hoop pine, 800 m asl. (LAE). **Peninsular Malaysia**: Gay 1208, banks on S. Tahan, Taman Negara, 30 m asl. (K). **Sulawesi**: Darnaedi 1851, Lake Matano area, Soroako, S. Sulawesi (BO,L)

Subg. Lecanopteris.

5. *Lecanopteris curtisii* Baker

Fig. 4.

J. Bot. 19 (n. s.) 10: 366 (1881). *Lecanopteris saccata* Alderw., in Bull. Jard. Buit. 2 (23): 14 (1916). Type: Curtis, Sumatra, s. n., s. d. (K). *Lecanopteris philippinensis* Alderw., in Bull. Jard. Bot. Buit. 2 (1): 8 (1911). Type: Elmer 10491, Todaya District of Davao, Mt Apo (L, K, P iso). *Lecanopteris deparioides* (Ces.) Baker, in J. Bot. 19 n. s. 10: 366 (1881). *Polypodium deparioides* Christ, Farnkraute der Erde: 116 (1897), nom. illeg. non Baker (1879). *Davallia deparioides* Ces., Fel. di Bor.: 13 (1876). *Lecanopteris incurvata* Baker, in Ann. Bot. 8 (30): 123 (1894). Type: Hancock 88, Between Kroe and Liwa, Barisan Mts, Sumatra (K). *Lecanopteris macleayi* Baker, Malesia 2: 244 (1886). *Pleopeltis macleayi* (Baker) Alderw., in Bull. Dept. Agric. Ind. Neerl. 27: 2 (1909). *Polypodium barisanicum* Alderw., Malayan Ferns.: 627 (1908), nom. nov. pro *Lecanopteris incurvatum* Baker (1894) non *Polypodium incurvatum* Blume (1828). *Polypodium naviculare* Alderw., Malayan Ferns.: 627 (1908), nom. nov. pro *Lecanopteris curtisii* Baker (1881) non *Polypodium curtisii* Baker (1881). *Polypodium patelliferum* Burck., in Ann. Jard. Bot. Buit. 4: 96. Tab. 7 (1884).

Rhizome creeping, hollow, forming an ant-inhabited domatium with a dark inner wall, much branched, 2-3 cm diameter, glaucous with a waxy sheen, glabrous except for a scattering of scales at the apex. *Phyllopodia* prominent, 1-1.5 cm high, hollow. *Stipes* 10-25 cm long, dark brown. *Fronde*s mid-green, 10-20 x 30-70 cm,

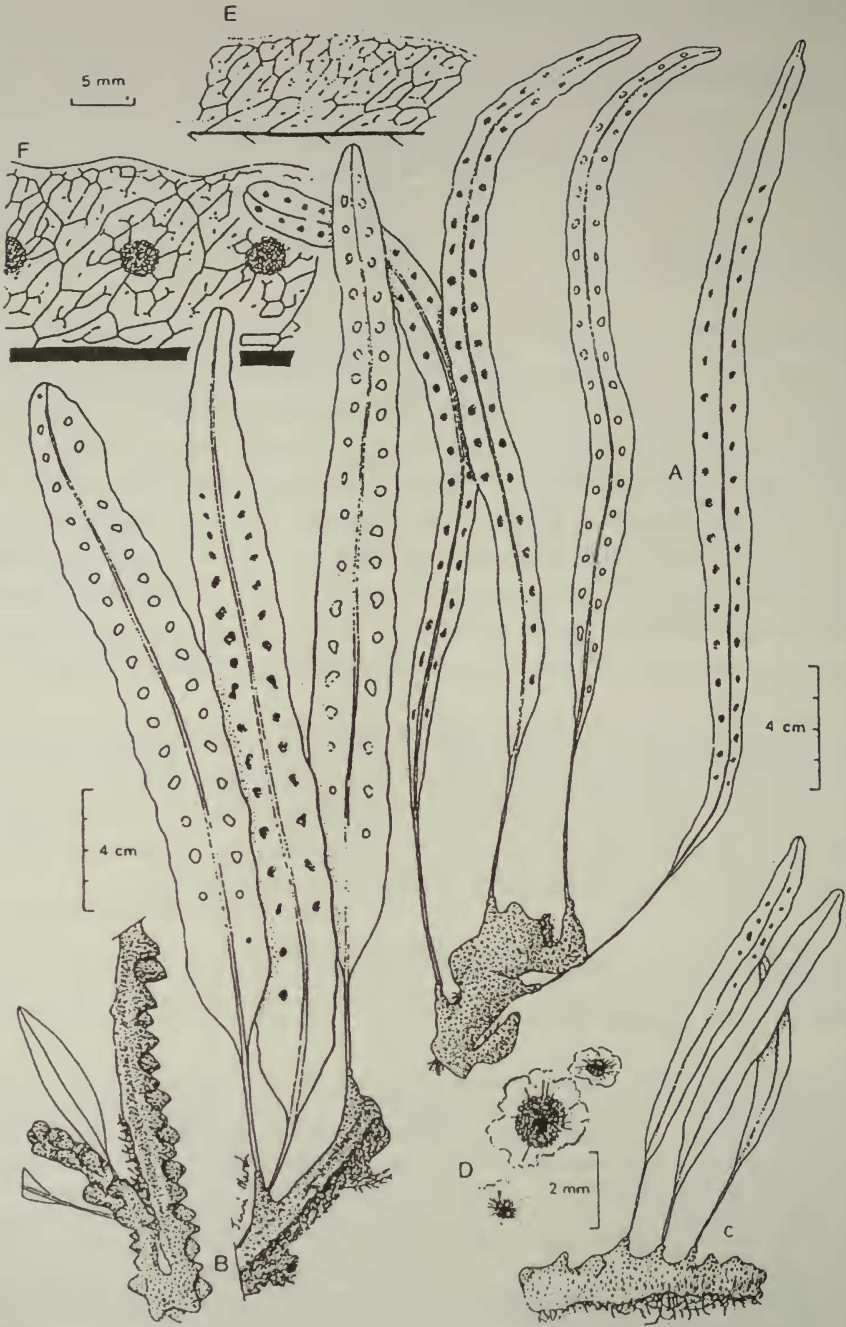


Fig. 3. *Lecanopteris sinuosa*

- | | |
|------------------|------------------------------|
| A: fertile frond | D: peltate scales |
| B: rhizome | E: venation of sterile frond |
| C: rhizome apex | F: venation of fertile frond |

· Drawing by Jenni Marsh

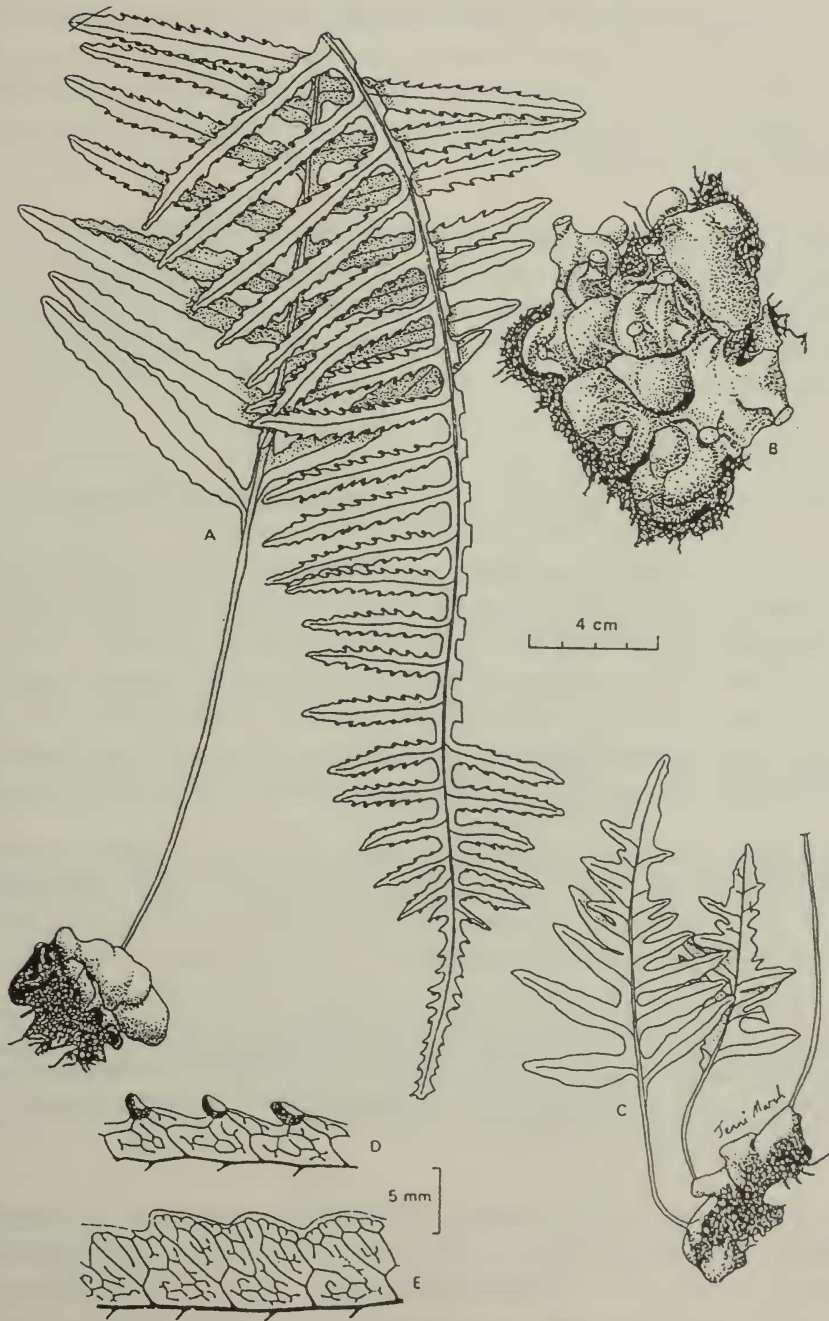


Fig. 4. *Lecanopteris curtisii*

- | | |
|------------------------------|---|
| A: fertile frond | D: venation of fertile frond,
showing boat-shaped sori |
| B: rhizome | |
| C: apical rhizome and fronds | E: venation of sterile frond |

Drawing by Jenni Marsh

deeply pinnatifid; winged at bases, apices of lobes rounded, lobed perpendicular to rachis, basal lobes not reduced, glabrous, chartaceous, glaucous on undersides; veins forming a series of areoles with freely branching recurrent veins. *Sori* on extramarginal teeth, immersed in boat-shaped involucre, each tooth supplied by a main vein. *Spores* biconvex.

Representative specimens: **New Guinea**: *Jacobs 9148*, 20 km SSW of Lake Kutubu, Southern Highlands Province, primary forest on limestone (LAE); *Womersley, NGF 13856*, Wagau, Hersog Mts, Morobe Province, 3800 ft asl. (LAE). **Java**: *Docters van Leeuwen 11571*, "by Buitenzorg" (L). **Sumatra**: *Yates 2334*, Toetepan, Tapanoeli (L).

6. *Lecanopteris balgooyi* Hennipman

Kew Bull. 41: 783 (1986). Type: *Hennipman 5650*, Sopu Valley, C. Sulawesi (L, holo; BO, K, U iso).

Rhizome creeping, hollow, forming an ant-inhabited domatium with a dark inner wall, much-branched, 2-3 cm diameter, glabrous, with hollow spines homologous with undeveloped fronds on the phyllopodia. *Phyllopodia* hollow, prominent. *Stipes* dark brown. *Fronde*s bright green, entire to pinnatifid, winged at their bases, apices of lobes rounded, 25-45 cm long, glabrous, chartaceous. *Sori* deeply immersed on lamina in a single row on either side of rachis or the main vein in pinnatifid fronds. *Sporangia* c. 900 µm long. *Spores* bi- to planoconvex.

Representative specimens: **Sulawesi**: *Hennipman 5650*, Sopu Valley (Type), *Hennipman 6059*, Mt Wawonseru, S.W. of Soroako, 1000 m asl (L, BO, K, U).

7. *Lecanopteris carnosa* (Reinw.) Blume

Enum. Fl. Javae Fil. (1829) pl. 94a; *Becc.*, *Malesia* 2: 224 (1886); *C. Chr.*, *Ind. Fil. Suppl.* 1: 117 (1913). *Onychium carnosum* Reinw., in *Sylog. Plant.* 2: 3 (1824). *Polypodium lecanopteris* Mett., in *Ann. Mus. Lugd. Bat.* 2: 224 (1886), nom. nov. pro *Onychium carnosum* non *Polypodium carnosum* Mett. (1857). *Pleopeltis carnosa* (Reinw.) Alderw., in *Bull. Dept. Agric. Ind. Neerl.* 27: 3 (1909). *Polypodium carnosum* H. Christ, in *Verh. Nat. Ges. Basel* 11: 26, nom. illeg. (1895) non Mett. (1857). Type: *Reinwardt s. n., s. d.*, Minahassa, Sulawesi (L, holo; BM, iso)

Rhizome creeping, hollow, forming an ant-inhabited domatium with a dark inner wall, much-branched, 1.5-2.5 cm diameter, covered with an indumentum of branched glandular hairs. *Phyllopodia* prominent, hollow, some bearing coralloid excrescences homologous with undeveloped fronds. *Stipes* dark brown, 10-20 cm long. *Fronde*s mid-green, chartaceous, glabrous, deeply pinnatifid, winged at their bases, apices of lobes rounded, 30-90 cm long. *Sori* circular, deeply immersed on orbicular extra-marginal lobes, 2-3 mm long. *Sporangia* c. 1250 µm long. *Spores* planoconvex.

Representative specimens: **Sulawesi**: *Alston 15637*, G. Mahawu, 900 m asl. (BM);

de Vogel & Vermeulen 7141, Bolaang Mongondow, N. Sulawesi (L).

8. *Lecanopteris celebica* Hennipman

Blumea 32 (2): 313 (1987). Type: *Hennipman 5665*, nr Biromaru, Central Sulawesi, 1000-1250 m asl. (L, holo; BM, BO, U, iso).

Rhizome creeping, 2.5-3.5 cm diameter, hollow, forming an ant-inhabited domatium with a dark inner wall, much-branched, covered with an indumentum of branched glandular hairs to 1 mm long at the apices, and scattered solid spines 2-3 mm long homologous with undeveloped fronds. *Phyllopodia* hollow, 1-1.5 cm high. *Stipes* dark brown, 10-20 cm long. *Fronde*s mid-green, chartaceous, glabrous, deeply pinnatifid, winged at their bases, apices of lobes rounded, 40-90 cm long; veins anastomosing, areoles with recurrent free veins. *Sori* circular, deeply immersed on orbicular extra-marginal lobes, each lobe supplied by a main vein, 2-3 mm diameter. *Sporangia* c. 1000 µm long. *Spores* planoconvex.

Representative specimens: **Sulawesi**: *Hennipman 5993*, Mt. Wawonseru, nr Soroako (BO, L, U); *Gay 1250*, Sopa Valley, 80 km south-east of Palu, 1000 m asl.

9. *Lecanopteris luzonensis* Hennipman

Blumea 32: 311 (1987). *Lecanopteris carnosa* auct. non. (Reinw.) Blume; Copeland, *Fern Flora of the Philippines* 3: 499 (1960). Type: *Hennipman 7820*, Quezon Province, nr Real, Luzon (L).

Rhizome creeping, 1.5-2.5 cm diameter, hollow, forming an ant-inhabited domatium with a dark inner wall, much-branched, apices covered with an indumentum of branched glandular hairs, and scattered solid spines homologous with undeveloped fronds. *Phyllopodia* hollow, prominent, 1-1.5 cm high. *Stipes* dark brown, 5-10 cm long. *Fronde*s bright green, chartaceous, glabrous, deeply pinnatifid, winged at their bases, apices of lobes acute to rounded, 12-45 cm long; veins anastomosing, areoles with recurrent free veins. *Sori* oval, deeply immersed on reflexed extra-marginal lobes, each lobe supplied by a main vein, 1.5-2 mm diam.. *Sporangia* c. 1000 µm long. *Spores* biconvex.

Representative specimens: **Philippines**: *Whitford 334*, Mt Mariveles, Batan Province (K, Mich, NY, P); *Elmer 22092*, Camp Stotsenberg, Mt Pinatubo, Pampanga (BM, K, L, NY); *Loher 13430*, Paningtingan, Rizal Province (M).

10. *Lecanopteris pumila* Blume.

Flora Javæ Fil., pl. 94b (1829) (sin. desc.). *Lecanopteris nieuwenhuisenii* Christ., in *Ann. Jard. Bot. Buit.* 20: 127 (1899). Type: *Nieuwenhuisen 496*, Batoe Lesong, Borneo (K).

Rhizome creeping, hollow, forming an ant-inhabited domatium with a dark inner wall, much-branched, 1.5-2.5 cm diameter, with scattered scales and branched hairs

to 1 mm long at apices but otherwise glabrous. *Phyllopodia* hollow, prominent, 1-1.5 cm high. *Stipes* dark brown, 7-10 cm long. *Fronde*s bright green, chartaceous, glabrous, deeply pinnatifid, winged at their bases, apices of lobes rounded, 4-6 x 20-40 cm; veins anastomosing, areoles with recurrent free veins. *Sori* circular, deeply immersed on orbicular extra-marginal lobes, each lobe supplied by a main vein, 2-3 mm diameter. *Spores* biconvex.

Representative specimens: Peninsular Malaysia: Henderson 11072, Rhododendron Hill, Cameron Highlands, Pahang, 5200 ft asl. (SING); *Gay 1078*, G. Beremban, Cameron Highlands, Pahang, 1600 m asl. (K,); *Henderson 11817*, G. Hijau, Perak, 4750 ft asl. (SING). **Borneo: Jermy 13247**, G. Mulu, Sarawak, 1790 m asl. (BM).

11. *Lecanopteris spinosa* Jermy & Walker

Fern Gaz. 11: 167 (1975). Type: *Jermy 7609*, Latimojong Mts, South Sulawesi, 1950 m asl. (BM holo; BO, GH, L iso).

Rhizome creeping, hollow, forming an anti-inhabited domatium with a dark inner wall, much-branched, 2.5-3.5 cm diamter, densely covered with sharply pointed spines up to 6 mm long which are epidermal outgrowths. *Phyllopodia* solid, not prominent. *Stipes* short to absent, winged if present. *Fronde*s bright green, coriaceous, glabrous, lobed to entire and crenate, apices rounded, 20-30 cm long; veins anastomosing, areoles with included free veinlets. *Sori* circular, deeply immersed on lamina, forming projections on its upper surface, 2-3 mm diameter. *Spores* monolete.

Representative specimens: Sulawesi: Jermy 7609 (type); *Walker T. 12179* (BM), Latimojong Mts, locality as type.

12. *Lecanopteris darnaedii* Hennipman

Kew Bull. 41: 785 (1986). Type: *Hennipman 5322*, Mt Roroka Timbu, Central Sulawesi, 2425 m asl. (L, holo; BO, K, U, iso).

Rhizome creeping, hollow with two gallery systems, forming an anti-inhabited domatium with a dark inner wall, much-branched, of massive construction, 3.5-4.5 cm diam., densely covered with sharply pointed spines 2-3 mm long which are epidermal outgrowths. *Phyllopodia* solid, not prominent. *Stipes* dark brown, 15-25 cm long. *Fronde*s dark green, coriaceous, glabrous, deeply pinnatifid, winged at their bases, apices of lobes rounded, 20-80 cm long; veins strongly sclerified, appearing black. *Sori* circular, immersed on unstalked reflexed extra-marginal lobes, 3 mm diam. *Sporangia* c. 900 μ m long. *Spores* monolete, 55-65 by 35-45 μ m.

Representative specimens: Sulawesi: Darnaedi 1564 (BO, K, L); *Hennipman 5322*

(type); *Gay 1260*, all Mt Roroka Timbu, Central Sulawesi, 2300-2500 m asl. (K).

13. *Lecanopteris holttumii* Hennipman

Blumea 32: 313 (1987). Type: *Lack & Grimes 1743*, Mt Tambusisi, Morowali Province, East Central Sulawesi (K).

Rhizome creeping, hollow with two gallery systems, forming an ant-inhabited domatium with a dark inner wall, much-branched, of massive construction, 3.5-4.5 cm diam., densely covered with sharply pointed spines 2-3 mm long which are epidermal outgrowths. *Phyllopodia* solid, not prominent. *Stipes* dark brown, 15-25 cm long. *Fronde*s dark green, coriaceous, glabrous, deeply pinnatifid, winged at their bases, apices of lobes rounded, 20-80 cm long; veins hardly sclerified, appearing green. *Sori* circular, immersed on unreflexed, stalked extra-marginal lobes, 3 mm diam. *Sporangia* c. 900 µm long. *Spores* monoletic.

Representative specimen: Type specimen.

Distribution

Lecanopteris is largely confined to Malesia; only *L. sinuosa* has a range extending marginally beyond the borders of this floristic region (Figs 5-8). Wallace's Line is a convenient means of demarcation for subg. *Myrmecopteris* apart from *L. sinuosa*; *L. mirabilis*, *L. sarcopus* and *L. crustacea* are allopatric species. *Lecanopteris mirabilis* is found east of Wallace's Line in New Guinea, Ambon and Seram, *L. crustacea* to its west, in Borneo, Sumatra and Peninsular Malaysia, and *L. sarcopus* on either side of this floristic divide. *Lecanopteris sarcopus* occurs in Sulawesi, whose biota has Australian affinities, and in the Philippines, where Asian elements predominate in the flora. *Lecanopteris sinuosa* is found throughout Malesia, and extends into southern Taiwan, Queensland (Australia), Vanuatu and the Solomon Islands (Fig. 5).

Subgenus *Lecanopteris* consists of three species groups. The *L. curtisii* group contains a wide-ranging species, *L. curtisii*, found in New Guinea, Borneo, Java and Sumatra, and the Philippines. The New Guinean form of *L. curtisii* may be given specific rank, *Lecanopteris philippinensis* is sunk into *L. curtisii* (E. Hennipman unpub.). Here the group is treated as one wide-ranging, disjunct species, *L. curtisii* s.l. (Fig. 6).

The *L. pumila* group outside Sulawesi consists of *L. luzonensis*, endemic to the Philippines, and the wide-ranging *L. pumila*, which occurs in Peninsular Malaysia, Borneo and Sumatra. This group is most speciose in Sulawesi, where the endemics *L. balgooyi*, *L. celebica* and *L. carnosa* are found. *Lecanopteris carnosa* occurs in northern Sulawesi. *Lecanopteris celebica* and *L. balgooyi* are sympatric at their only two known localities in central Sulawesi, but seem to be ecologically

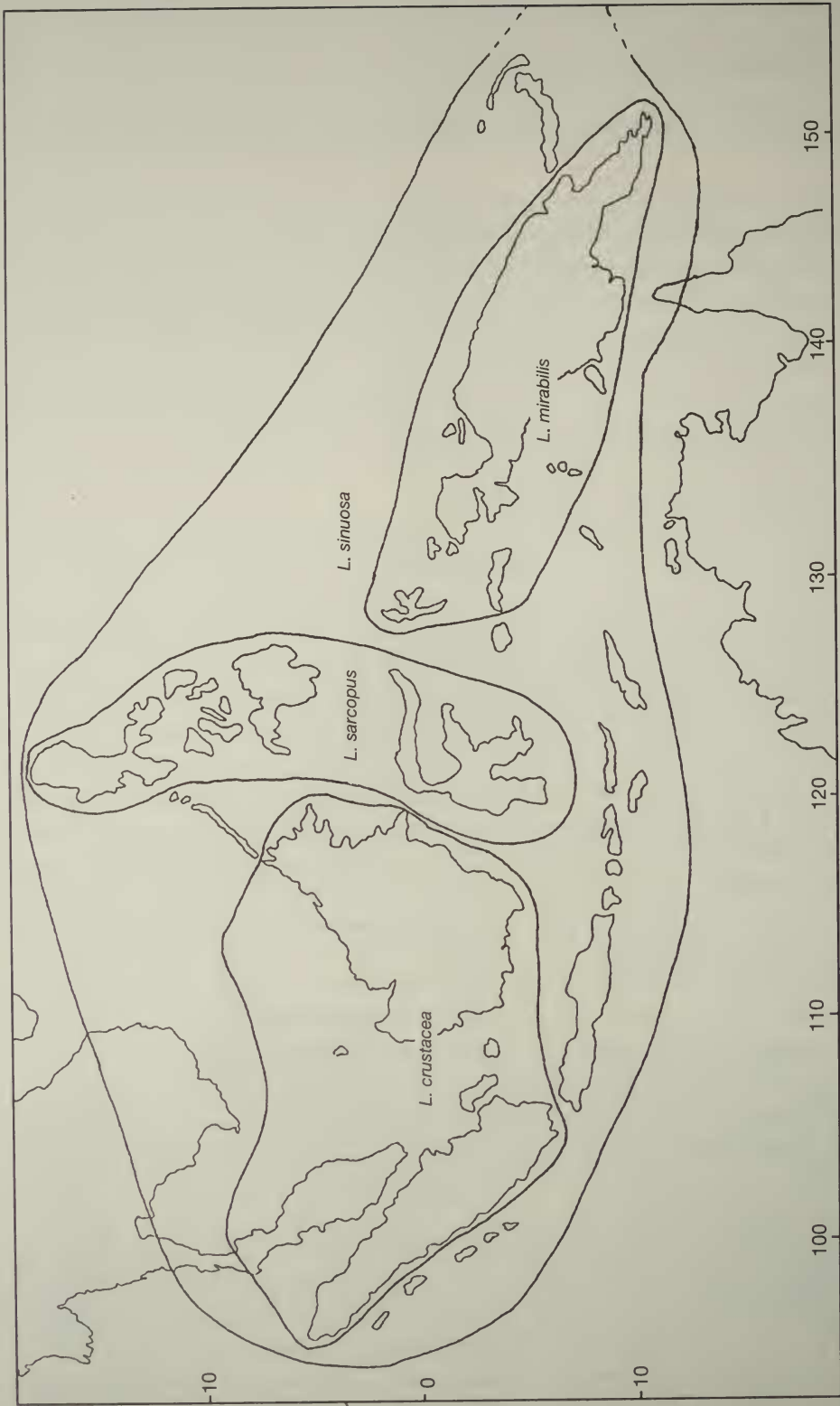


Fig. 5. The distribution of subgenus *Myrmecopteris*

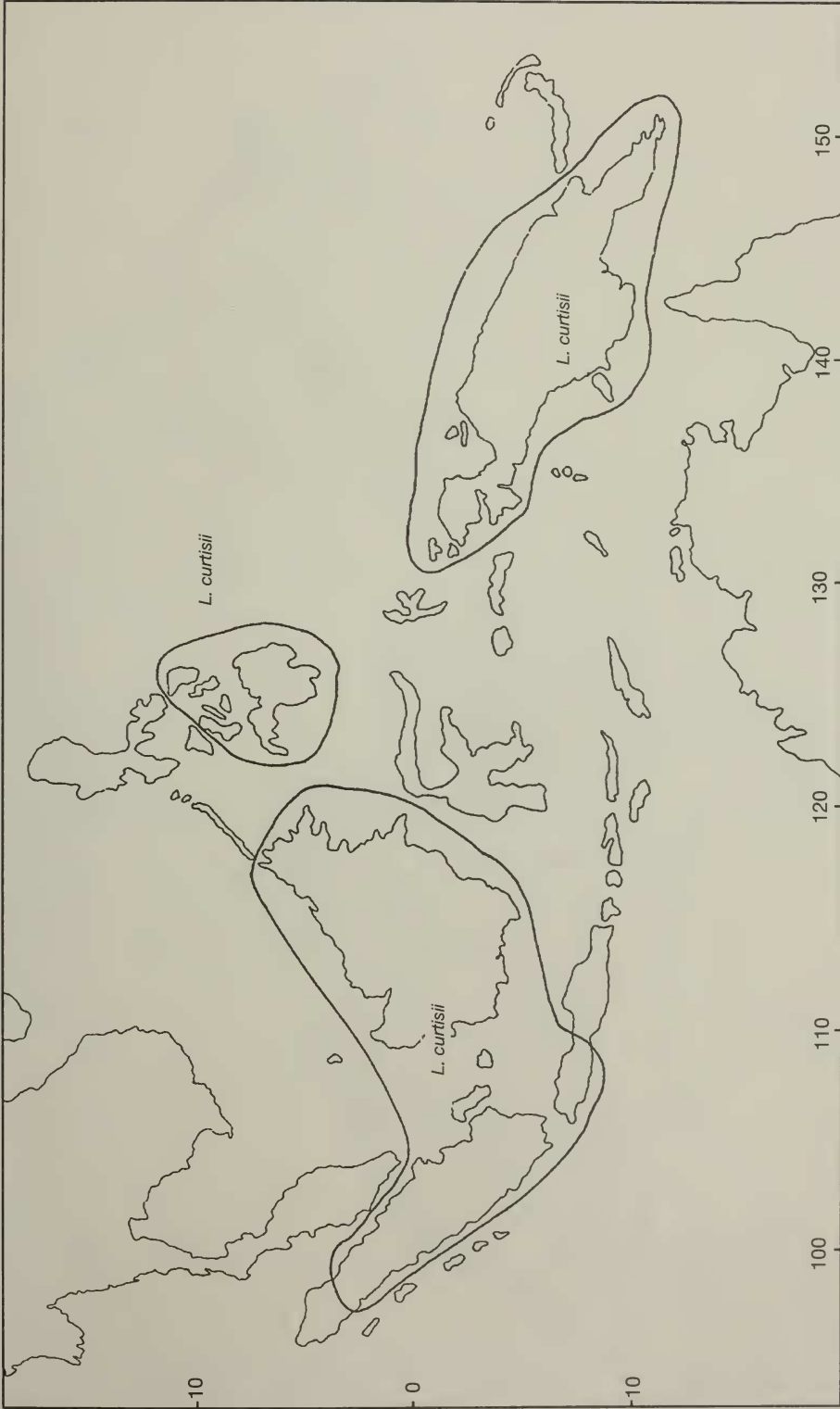


Fig. 6. The distribution of the *Lecanopteris curtisii* group

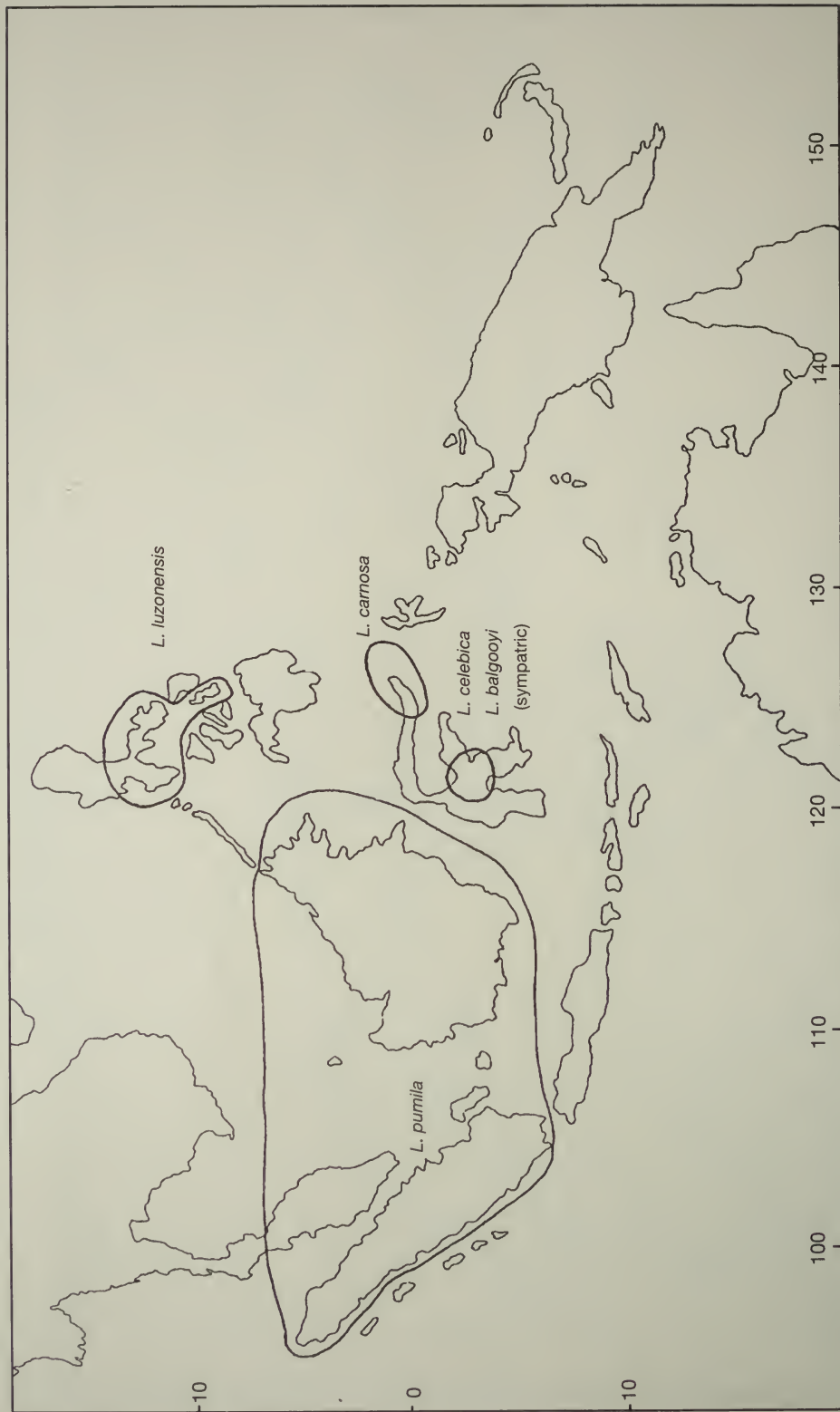


Fig. 7. The distribution of the *Lecanopteris pumila* group

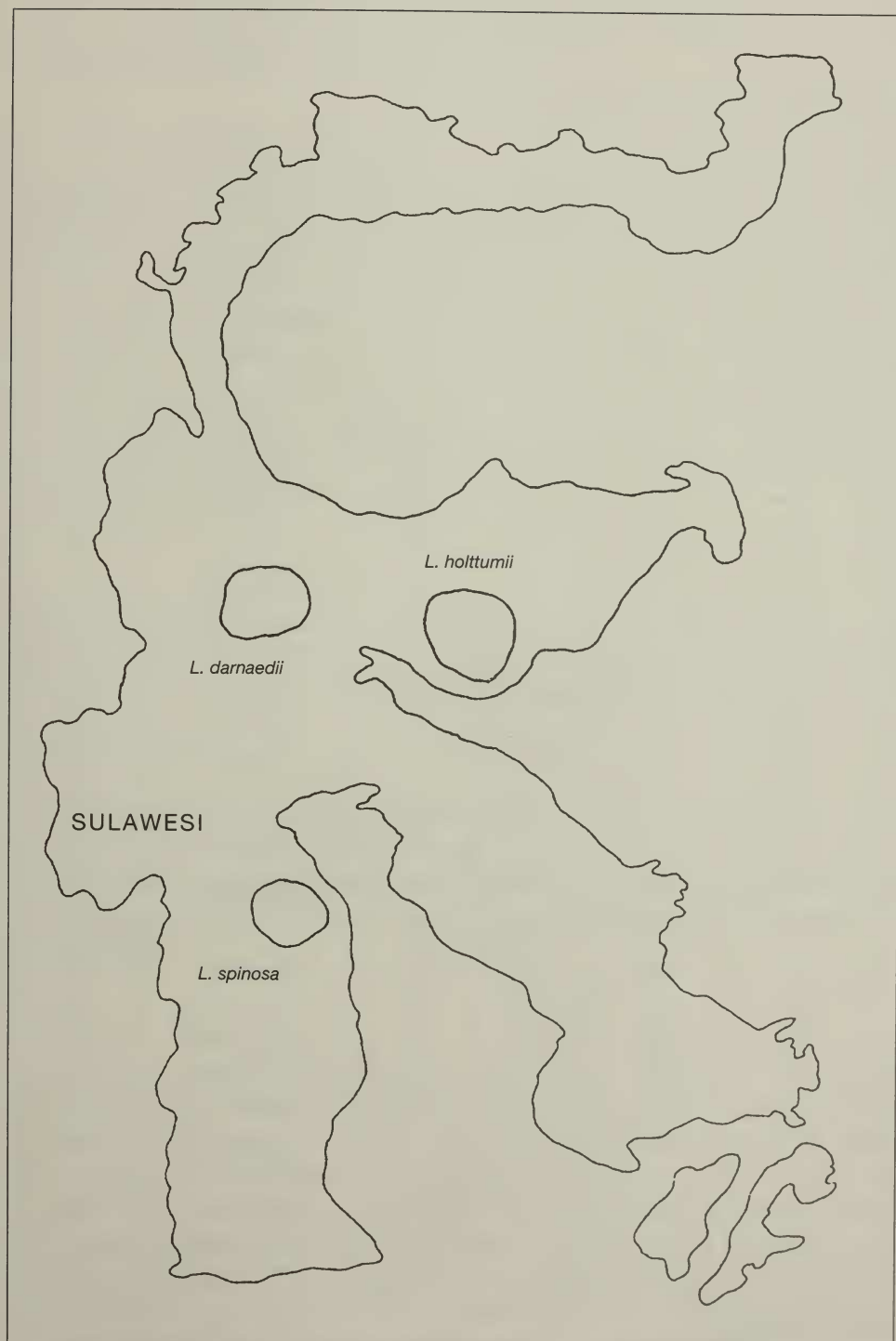


Fig. 8. The distribution of the *Lecanopteris darnaedii* group

Table 1: The physical nature of the field sites.

Climatic data was obtained from "Maps of New Guinea", an Office of Forests publication for Papua New Guinea, and from Walter and Leith (1967) for the other sites.

Site abbreviations are given in Appendix 2.

Species	Site	Alt. (m)	Rainf. (mm)	Temp. (°C)	Soil type	No. of plants
<i>L. sin</i>	LK	700	****	**	limestone-derived, thin	108
<i>L. sin</i>	BR	0-50	2097	27	alluvial, coarse	121
<i>L. sin</i>	KK	0-30	2482	28	volcanic	36
<i>L. sin</i>	B	150	3968	27	siliceous, acid, thin	63
<i>L. sin</i>	N	470	3406	28	siliceous	9
<i>L. sin</i>	BAD	50	3187	27	siliceous	20
<i>L. sin</i>	BF	50	3159	27	alluvial	7
<i>L. sin</i>	KT	40	2989	27	alluvial	6
<i>L. sin</i>	GP	600	2784	27	waterlogged, over sandstone	4
<i>L. sin</i>	GJ	800	357	**	quartzite and granite derived	3
<i>L. mir</i>	R	2200	2622	21	brown loam	47
<i>L. mir</i>	MM	2000	****	**	brown loam	51
<i>L. cur</i>	MB	700	****	**	volcanic	13
<i>L. cru</i>	BB	20	3406	28	peaty, waterlogged	1
<i>L. cru</i>	KTH	30	****	**	alluvial	6
<i>L. pum</i>	GBB	1500	****	**	quartzite derived, thin	14
<i>L. pum</i>	CH	1400-1850	2644	18	brown loam	54
<i>L. pum</i>	BH	1600	3088	21	brown loam	63
<i>L. pum</i>	FH	1400	2616	20	brown loam	33
<i>L. pum</i>	GT	1800	2819	18	thin, impoverished	22
<i>L. pum</i>	K	1900	3239	19	brown loam	19
<i>L. cel</i>	SV	700	****	**	alluvial	30
<i>L. cel</i>	MW	600	****	**	limestone-derived, thin	19
<i>L. dar</i>	MRT	2300	****	**	brown loam	10
<i>L. sar</i>	LM	400	****	**	sandy, alluvial	12

* = data not available

separated. All other species in the *L. pumila* group are allopatric (Fig. 7). All three species comprising the *L. darnaedii* group are endemic to Sulawesi, known only from their type localities, and are allopatric (Fig. 8).

The centre of diversity of *Lecanopteris* is undoubtedly Sulawesi, where eight of the 13 species, including six endemics, are found. This is paradoxical in terms of the pteridophyte biogeography of Malesia. New Guinea has the greatest diversity of pteridophytes, containing 2000 species compared with 1000 in Borneo (Parris 1985). Three species of *Lecanopteris* occur in New Guinea: *L. mirabilis*, *L. sinuosa* and *L. curtisii*; Borneo contains the latter two species, and also *L. pumila* and *L. crustacea*. All these species are found in Peninsular Malaysia except for *L. mirabilis* and *L. curtisii*. The Philippines have an endemic, *L. luzonensis*, which has strong affinities with *L. pumila*; *L. sarcopus*; the wide-ranging *L. sinuosa*; and *L. curtisii* s. l. (syn.: *L. philippinensis*). *Lecanopteris* is poorly represented on Java, where only the widespread *L. sinuosa* and *L. curtisii* occur. The distribution of *Lecanopteris* in relation to its speciation is considered below.

Ecology

The most apparent feature of the ecology of *Lecanopteris* is its interaction with ants. This however is only one component of the constraints and requirements which determine its geographical and environmental distribution.

The abiotic environment

The abiotic environment of epiphytes is partly mediated by their host trees and may bear little relation to conditions on the forest floor or in the canopy. Table 1 shows physical features of habitats where *Lecanopteris* was recorded. The ecology of *L. sinuosa* (402 plants) and *L. pumila* (206 plants) has been documented in greatest detail.

Climate

The only member of *Lecanopteris* with a range extending into seasonal habitats is *L. sinuosa*. It occurs in Southeast Thailand, north of the Kra Isthmus, which is a major climatic and floristic divide, separating the moist tropics from seasonal regions. Within the tropics, this species is known from the seasonal savannahs of Central and Western Provinces, Papua New Guinea, and Bako heath forest, Sarawak, which have pronounced dry seasons of three to five months (Paaijmans 1976). Moisture stress in plants is related to the soil's capacity to absorb and retain water as well as the amount of precipitation; although the ridgetop vegetation inhabited by *L. pumila* in Malaysia has high and even rainfall (Table 1), the thin siliceous soil and steep topography causes periodic water shortage (Whitmore 1984).

Lecanopteris mirabilis is confined to moist, cloudy mid-montane forest, and *L. crustacea* to lowland evergreen and swamp forests. All the Sulawesi species are found in montane environments with a seasonal rainfall, except *L. sarcopus*, which inhabits ever-wet lowland and hill areas, as does *L. curtisii* in Papua New Guinea.

Daytime temperatures are high and equable in the habitats of all species (18–28° C). Altitude rather than latitude causes a decrease in temperature in the upper elevations of the range for *L. mirabilis*, *L. darnaedii* and *L. pumila* (Table 1). Within the tropics, precipitation is a greater limiting factor than temperature in determining colonisable habitats.

Soil nutrient status

In certain environments such as savannah, ridge forest and heath forest the nutrient-poor conditions are a contributory factor allowing wide-ranging *Lecanopteris* species to become locally dominant on the stunted vegetation; otherwise no *Lecanopteris* species has its geographical or ecological distribution curtailed by dependence on presence of an impoverished soil.

Lecanopteris sinuosa is found in a wide range of vegetation types, and its dominance varies greatly. It is most abundant in fire maintained or oligotrophic environments such as the savannahs of Western Province, Papua New Guinea and Bornean heath forest. The preponderance of nutritive myrmecophytism in nutrient-poor habitats has been described by Janzen (1974) and Thompson (1981), and is considered in more detail below. However *L. sinuosa* was not universally common in nutrient-constrained habitats: it was never abundant in peat-swamp forest, which does not harbour the myrmeco-epiphytic communities of heath forest, and was rare in the siliceous-soiled heath forests at Nabawan (Brunei) and G. Panti (Peninsular Malaysia).

Few other *Lecanopteris* species occur in nutrient-poor habitats. *Lecanopteris crustacea* was collected at Badas swamp forest, Brunei (Gay s. n.), and regularly inhabits waterlogged forest (Fr. E. Schmutz 4930; Anderson 8544, Borneo). *Lecanopteris pumila* is a dominant epiphyte in the stunted vegetation of impoverished quartzite ridgetop soils in Peninsular Malaysia, but is also abundant in mid-montane environments. *Lecanopteris curtisii* has been collected from limestone ridges around Lake Kutubu, Papua New Guinea (Jacobs 9184), but again is not restricted to such sites. *Lecanopteris sinuosa* and *L. pumila* are abundant at some oligotrophic sites, but *L. crustacea* and *L. curtisii* are scarce.

Table 2: The range of vegetation types inhabited by *Lecanopteris*

Species	1	2	3	4	5	6	7	8	9	10
<i>L. mirabilis</i>	-	-	+	+	-	-	-	+	-	-
<i>L. sarcopus</i>	-	-	+	+	-	-	-	-	+	+
<i>L. crustacea</i>	+	+	-	-	-	-	-	-	-	-
<i>L. sinuosa</i>	+	+	-	-	-	+	+	+	+	+
<i>L. curtisii</i>	-	-	+	+	-	-	-	-	-	+
<i>L. pumila</i>	-	-	-	+	+	-	-	-	+	+
<i>L. luzonensis</i>	-	-	-	+	+	-	-	-	?	?
<i>L. balgooyi</i>	-	-	+	-	-	-	-	-	-	-
<i>L. celebica</i>	-	-	+	-	-	-	-	-	+	+
<i>L. carnosa</i>	-	-	+	+	-	-	-	-	?	?
<i>L. spinosa</i>	-	-	-	+	-	-	-	-	-	-
<i>L. darnaedii</i>	-	-	-	+	-	-	-	-	-	-
<i>L. holtumii</i>	-	-	-	+	-	-	-	-	-	-

Key

1 = lowland rain forest

2 = swamp forest

3 = lower montane or hill forest

4 = mid-montane forest

5 = summit or ridgetop vegetation

6 = heath forest

7 = savannah

8 = mangrove swamps

9 = man-disturbed vegetation

10 = secondary re-growth

+ = recorded from vegetation

- = not recorded

? = likely to be present but not recorded

The biotic environment**Vegetation types inhabited by *Lecanopteris***

Table 2 shows that the habitats of the entire genus span a wide range of forest types described by Whitmore (1984). Some species, such as *L. darnaedii*, are restricted to a single forest type, and others such as *L. sinuosa* and *L. sarcopus* have a wide ecological tolerance. Formations in which *Lecanopteris* is rare are described briefly; for more detailed descriptions, see Whitmore (1984).

Wet lowland forests

Lowland rain forest is not considered an abundant or diverse habitat for ant-

epiphytes, although understorey trees such as *Aphanamixis myrmecophila* (Meliaceae), *Leonardoxa africana* (Leguminosae) and *Barteria fistulosa* (Passifloraceae) are common. Few ant-epiphytes have been recorded from Malesian lowland rain forest; only one infrequently collected species of *Lecanopteris* is regularly found, *L. crustacea*, and *L. sinuosa* have rarely been collected there. The infrequency of *L. crustacea* may partly be a function of its inaccessibility in tree crowns 50 m high. Seventeen fallen rhizomes were found on the forest floor around Kuala Tahan, Taman Negara, Peninsular Malaysia, indicating that *L. crustacea* may be locally common. This forest was dipterocarp-dominated and 35 - 40 m in height. Canopy epiphytes were abundant, but there were few on trunks and lower branches. It has also been recorded as a canopy epiphyte from lowland mixed dipterocarp forest in the Danum Valley, Sabah (Parris 10777).

Freshwater swamp forest is a frequent habitat of *L. crustacea* (Kostermans 9793). This formation is similar to lowland rain forest, but with some marked differences: the canopy is lower, and species composition tends towards dominance by few or a single species (*Shorea albida* (Dipterocarpaceae) in Borneo; *Camposperma brevipetiolatum* (Lauraceae) in Papua New Guinea). Inundation in these forests is periodic and usually due to flooding of rivers. The fern *Platynerium ridleyi* (Polypodiaceae) has been collected twice in association with *L. crustacea* and its ants (*Camus* 660, Borneo, Franken & Roos 341, Sumatra), and may participate in a 'loose' antplant mutualism, as suggested by the observations of Paterson (1982). *Platynerium ridleyi* has no domatium, but produces nectar from nectaries on its fronds. *Lecanopteris sinuosa* was infrequently found in freshwater swamp forest in Western Province, Papua New Guinea (Gay s. n.). These are the only *Lecanopteris* species recorded from freshwater swamp forest, and are also known from riverine forest (*L. crustacea*, Hirano and Hotta 177). *Lecanopteris sinuosa* was found on the banks of the Binaturi River, Western Province, Papua New Guinea, and *L. crustacea* on the S. Tahan, Peninsular Malaysia (both Gay s. n.). Such forest is similar to rain forest, but less dense and of lower stature (25 - 35 m). Epiphytes are abundant on trunks and branches as well as in the crowns.

Moist lowland forest does not contain great abundance or diversity of *Lecanopteris* species. Only *L. crustacea*, which is confined to these formations, and *L. sinuosa*, which is infrequently found there as a function of its generalist ecology, are represented.

Montane forest

The greatest diversity of *Lecanopteris* is found at altitudes of 1000 - 2000 m: *L. pumila* in Peninsular Malaysia and Borneo; *L. curtisii* in New Guinea, Sumatra and the Philippines; *L. mirabilis* in New Guinea; *L. spinosa*, *L. darnaedii*, *L. carnosa*, *L. holttumii*, *L. celebica* and *L. balgooyi* in Sulawesi. The habitats in which they occur span lower montane forest for *L. curtisii*, *L. celebica* and *L. balgooyi*; mid-

montane forest for *L. darnaedii*, *L. holtumii*, *L. spinosa*, *L. carnosa* and *L. mirabilis*, and stunted ridgetop forest for *L. pumila*.

Lower montane forest is shorter than lowland forest (15 - 35 m), and begins at 800 - 1000 m in mountain ranges. Epiphytes are abundant and there are few big woody climbers. *Lecanopteris curtisii* inhabits this formation locally in New Guinea (e.g. on Mt. Bosavi), as does *L. celebica* in South Sulawesi (Mt. Wawonseru) and *L. mirabilis* in Seram. Individuals seen were usually in tree crowns.

Lecanopteris darnaedii in Sulawesi and *L. mirabilis* in Papua New Guinea were found in mid-montane forest (c. 2000 m asl.), with a canopy height of 20 - 25 m. This forest type was similar to lower montane forest apart from dominance of a few tree species (*Castanopsis acuminatissima* in the highlands of New Guinea, *Agathis damar* on Mt. Roroka Timbu, Sulawesi), and more abundant epiphytes.

Stunted ridgetop forest inhabited by *L. pumila* was found at 1500 - 1800 m in the Genting Highlands (G. Bunga Buah), the Cameron Highlands (G. Beremban), and G. Tahan (all in Peninsular Malaysia). Exposure and moisture stress, rather than the sole effect of altitude, contribute to nutrient impoverishment and cause stunting of vegetation. The summit/ridgetop nature of the vegetation was similar at all sites: the canopy was 5 - 8 m high, tree cover was not continuous, and *L. pumila* was an abundant or dominant epiphyte. Ericaceae dominated the tree flora (*Vaccinium* and *Rhododendron* spp.); *Dacrydium deccarii* (Podocarpaceae) was also common. The vegetation was microphyllous and sclerophyllous. Ground cover was a dense thicket of rhizomatous ferns such as *Matonia pectinata* (Matoniaceae) and *Dipteris conjugata* (Polypodiaceae).

Lecanopteris has never been found above the tree line. This may seem self-evident for an epiphyte, but *Myrmecodia lamii* grows on the ground at 3600 m on Doormantop, Irian Jaya (Jebb 1985).

Impoverished or disturbed habitats

Mangrove swamps, forest on limestone, savannah, heath forest and secondary forest are all either nutrient-poor or have had their structure and species composition affected by human activity.

Lecanopteris sinuosa and *L. mirabilis* are the only members of the genus known from mangrove swamps: *L. sinuosa* was recorded from Bako, Sarawak, and near Lae, Papua New Guinea (both Gay *s. n.*), and *L. mirabilis* from Air Besar, Seram (B.S. Parris *pers. comm.*). *Lecanopteris sinuosa* was not abundant at either locality, and absent from mangrove swamps in Madang, where *Hydnophytum* is found, in Western Province, Papua New Guinea, and Sungei Buloh, Peninsular Malaysia.

Lacustrine limestone forest around Lake Kutubu, Papua New Guinea, had abundant in *L. sinuosa*, especially at the lake edge. The canopy was 5 - 11 m, and tree cover was not dense. Epiphytes were abundant, and *L. sinuosa* frequently covered branches or entire trees. Limestone forest at Mulu, Sarawak, yielded no *L. sinuosa*, which has not been recorded there. *Lecanopteris curtisii* has been collected from *Nothofagus*-dominated limestone ridges at 100 m asl around Lake Kutubu (Jacobs 9148).

The savannah in Western Province, Papua New Guinea, is referred to by Whitmore (1984) as monsoon forest, but the locality studied around the Binaturi River was grassland with trees rather than continuous tree cover. The accepted origin for the southern savannahs and seasonal forests of New Guinea is that they result from gradual degradation by burning of pre-existing alluvial forest. Whether the present cover is treeless grassland, scattered trees or open forest depends on the frequency and intensity of the burning (Paaijmans 1976). The most striking feature of these savannahs is the great abundance of myrmeco-epiphytes: *Myrmecodia tuberosa*, *Hydnophytum mosleyanum*, *Lecanopteris sinuosa*, *Dischidia rafflesiana* and *D. nummularia*. The myrmecophytic aspect of this vegetation is considered below. *Lecanopteris sinuosa* is a common and locally dominant epiphyte. In the locality studied, tree crowns did not touch one another and trunks were 3-10 m apart. The dominant tree species were *Eucalyptus* spp., *Melaleuca* sp., *Banksia dentata*, *Tristania* spp., *Timonius timon* and *Planchonella* sp. Bark was pale and often flaky; leaves were sclerophyllous, and except for *Banksia*, microphyllous. There was a dense, often impeding cover of Kunai grass (*Imperata cylindrica*). Epiphytes, other than the abundant myrmecophytes, were rare.

Bornean heath forest rivals New Guinea savannahs in abundance of myrmeco-epiphytes of related species, except for the replacement of *Hydnophytum mosleyanum* by *H. formicarum* and *Dischidia rafflesiana* by *D. astephana*. This forest type is found on impoverished, siliceous, acidic, often podsolised soils derived from Quaternary marine deposits (Bruning 1974). The greatest density of ant-epiphytes occurs in the padang (lit., open space, field), at Bako National Park, Sarawak, which is a more open formation than true heath forest or kerangas (lit., where rice will not grow) (Browne 1952). Tree height in padang was 4 - 10 m, and tree crowns barely touched one another. Soil was thin and patches of bare rock were visible. Myrtaceae dominated the tree flora: *Tristania* sp., *Baeckia frutescens* and *Eugenia multibracteosa* were common species. Other abundant species were *Ploiaria alternifolium*, *Pternandra coerulescens* and *Dacrydium beccarii*. Although Janzen (1974) found few individuals of *L. sinuosa* in his study of myrmeco-epiphytes at Bako, it was an abundant and apparent member of the ant-epiphyte community.

The kerangas, or pole forest, had a canopy height of 15 - 20 m at Nabawan and Badas in Borneo. *Tristania obovata* and *Timonius flavescens* were common tree species. *Lecanopteris sinuosa* was not abundant in either of these kerangas forests; nine and 20 plants respectively were recorded.

Peninsular Malaysian heath forests are not as widespread as those in Borneo, but occur along the east coast on the plateaux of G. Pantii, G. Lesong, and G. Janing in the south of the peninsula, and on the quartzite upper slopes of the anomalous, isolated mountain G. Jerai in the north. *Lecanopteris sinuosa* was never common in Malaysia, only rare scattered individuals being found, in contrast to its abundance in Borneo and New Guinea. Four individuals were recorded on G. Jerai and three on G. Pantii. It is also reported from the Endau-Rompin heath forests in small numbers (Wong, Saw & Kochummen 1987; Saw L. G. *pers. comm.*). Gunung Pantii supported a tree cover similar in density to Bornean kerangas. Canopy height was 20 m. Gunung Jerai differed in floristic composition from the mountains in the Main Range in its possession of a 'montane myrtaceous flora' (K. M. Wong *unpub.*) between 800m and 1000 m, where *L. sinuosa* is infrequently found. Canopy cover was continuous but not closed. Common tree species were *Eugenia spicata* (Myrtaceae), *Tristania merguensis* and *Adinandra acuminata*. Epiphytes other than myrmecophytes were uncommon.

Heath forest is interspersed with peat swamp forest in Borneo. This swamp forest is periodically waterlogged and occurs as lenses around the surrounding kerangas. *Lecanopteris sinuosa* (two plants) and *L. crustacea* (one plant) were found in a *Shorea albida*-dominated peat swamp forest at Badas, Brunei, but not in a similar habitat at Nabawan. Thus these species occur in peat swamp forest but are not common.

Lecanopteris sinuosa, *L. curtisii*, *L. pumila*, *L. sarcopus* and *L. celebica* are all found in disturbed areas or secondary forest, but none are confined to these habitats. *Lecanopteris sinuosa* was common on coconut plantations in Madang Province and locally in abandoned gardens at Lake Kutubu, Karkar Island and Woodlark Island, all in Papua New Guinea. *Lecanopteris sarcopus*, *L. celebica* and *L. pumila* were locally common on roadside trees, and also established on young regeneration in logged areas, as did *L. mirabilis*. *Lecanopteris curtisii* was found in old secondary forest on Mt. Bosavi, Papua New Guinea.

Lecanopteris as a member of the far-eastern ant-epiphyte communities

The assemblies of ant-epiphytes found in seasonal or disturbed habitats mentioned above have no parallel with any other plant communities. The abundance of *Myrmecodia*, *Hydnophytum*, *Dischidia* and *Lecanopteris*, the low species diversity of inhabitant ants (*Iridomyrmex cordatus*) and host plants, and the paucity of other epiphyte species are features unique to these habitats.

Only widespread species of each ant-epiphyte genus are found in these communities (*L. sinuosa*; *M. tuberosa*; *H. formicarum*; *H. mosleyanum*), all of which appear to be used equally by *I. cordatus*; single colonies are not species-specific but nest in all four genera. The range of nests available to the ants derives from a variety of plant organs: leaves in *Dischidia*, swollen hypocotyls in *Myrmecodia* and *Hydnophytum*, and *Lecanopteris* rhizomes.

The benefit gained by the ants is similar in all plant species: a nest site, with sporadic food from the nectaries of *Myrmecodia*. Since the same colonies live in any hollow epiphyte, all the plants receive nutrients from their inhabitants, and *Dischidia* may also use ant-derived CO₂ in photosynthesis. The rubiaceaceous ant-epiphytes predominate numerically, taxonomically and possess the most complex modifications: a network of chambers, either smooth or rough-walled, in which brood and debris are kept respectively (Huxley 1978).

The high abundance and low diversity of these communities corresponds with a stress-tolerant strategy (Grime 1979). The ant-epiphytes may originally have become part of these communities by virtue of their ability to withstand the high insolation, moisture shortage and limited nutrient availability, but their present predominance is likely to have been achieved and maintained by the ant association. *Iridomyrmex cordatus* plants seeds of *Myrmecodia* and *Hydnophytum* in ant carton and tends juvenile ant-epiphytes surrounding adult plants (Gay *in press*), thus contributing to the great abundance of living nests on trees and also to their clumped distribution. Noticeable features of ant-epiphyte communities are the great numbers of *Myrmecodia* and *Hydnophytum* seedlings in ant carton (which are most abundant around *L. sinuosa* because of its linear form) and the disparity between trees bearing as many as 50 mature *Myrmecodia* and *Hydnophytum*, festooned with *Lecanopteris* and *Dischidia*, and those with no epiphytes at all.

Ant-epiphyte distribution over area has an 'all or nothing' nature; overwhelming abundance contrasts with complete absence in seemingly similar and neighbouring areas of savannah in Western Province, Papua New Guinea. The ant-epiphyte community is self-perpetuating, and is more likely to increase in density than to spread beyond the range of established or daughter colonies. As an ant colony grows, it expands into greater numbers of plants on the same or a neighbouring tree. It reproduces to give daughter colonies which will inhabit more distant ant-epiphytes. Inter and intraspecific competition amongst the epiphytes for nesting ants is not likely to be intense; increased numbers of plants of any species will result in ant colony expansion and a need for more nest sites concomitantly increasing the abundance of all ant-epiphyte species. In every lowland ant-epiphyte community where all four genera are found, *Myrmecodia* and *Hydnophytum* are more abundant than *Lecanopteris* and *Dischidia*, but the latter two genera are present in the shared habitats in greater numbers than where they are the sole ant-epiphytes. This suggests that they benefit from the abundance of *Iridomyrmex cordatus*, and thus

indirectly from the presence of the other genera.

Lecanopteris pumila and *Dischidia astephana* comprise a less striking ant-epiphyte community which is found in mid-montane forests and stunted ridgetop forests of Peninsular Malaysia. This community is less abundant, diverse and exclusive in terms of ant-epiphytes than that of the savannahs and heath forests, but these two species, inhabited by the ant *Crematogaster treubi*, predominate in the canopy. The mid-montane forest which they inhabit is closed, and *L. pumila* is largely confined to the crowns of trees. In the more open ridgetop environment, it is found equally on trunks and lower branches. Non-ant-epiphytes are as infrequent in ridgetop forest as they are in savannah or heath forest. *Lecanopteris pumila* is more abundant and apparent than *D. astephana*; single rhizome clumps achieve lengths of over 80 cm (Gay 1990).

The bulk of an *L. pumila* rhizome, and its habit of growing on slender branches on tree crowns, may be an agent of gap formation on a small scale in montane forests. Large, mature plants on slim branches are common on the forest floor; the weight of an *L. pumila* may contribute to branch death or fall. Having fallen, a small gap results via which light penetrates the canopy and changes the nature of plant growth (Grubb 1977).

It is uncommon for a guild of mutualists to determine community structure of their synusium to such an extent as the ant-epiphytes. Lowland ant-epiphyte communities undoubtedly dominate as a partial result of their association; plants gaining nutrient source and improved chances of establishment, and ants a nest.

Lecanopteris on the host tree

Host tree species

Host trees of all *Lecanopteris* individuals recorded were collected and identified to discover any host preference in a habitat. Results are tabulated by species of *Lecanopteris* in Appendix 2.

No species of *Lecanopteris* is epilithic as well as epiphytic, unlike members of the closely related polypodiaceous genera *Microsorium* and *Phymatodes*, where the same species may be terrestrial, epilithic and epiphytic. The label on the unique existing specimen of *L. holttumii* describes the plant as epiphytic or epilithic, but this is more likely to refer to fallen individuals (Lack & Grimes 1743).

Cultivated *Artocarpus* spp., *Theobroma cacao* and *Cocos nucifera* were common hosts for *L. sinuosa* in artificial habitats at Lake Kutubu and Karkar Island, Papua New Guinea. In Western Province, Papua New Guinea, around the Binaturi River, *L. sinuosa* occurred 40 out of 121 times on *Planchonella* sp., and was

conspicuously absent from the dominant *Eucalyptus* and *Melaleuca*, perhaps because their peeling bark prevented establishment.

Lecanopteris mirabilis at Roguts, Western Highlands, Papua New Guinea, was largely found growing on *Castanopsis acuminatissima* (24 out of 47 individuals). This tree forms almost pure stands in lower montane forest in New Guinea (Paaijmans 1976). On Mt. Mon in the Owen Stanley Range, Papua New Guinea, *L. mirabilis* was more catholic in host specificity, occurring on *C. acuminatissima* only 11 out of 51 times. The other two species found in large numbers, *L. pumila* and *L. celebica* showed no host preference; the high numbers of *L. pumila* recorded from *Ficus sp.* come from a single tree on Fraser's Hill, Malaysia.

No correlation was found between coccid cultivation by inhabitants of *Lecanopteris* and host tree. This was contrary to Janzen's observations for all myrmeco-epiphytes in Sarawak (1974) and the work of Weir & Kiew (1986) on *Dischidia* and *Leptospermum*. The lack of selectivity of host tree species by both *Lecanopteris* for a substrate and the ants for a nest environment, suggests that both parties have a wide tolerance of their immediate surroundings.

Host bark type

The nature of the host tree bark was classified into ten categories, following those of Webb, Tracey and Williams (1976). The bark types and the relative numbers of individuals of each *Lecanopteris* species are shown in Table 3.

All species show a marked preference for rough-barked trees (types 3, 4 & 5); 517 out of 798 plants were found on hosts with such bark. Trees with rough, fissured bark accounted for 190 individuals, and rough bark with dimples, scrolls, craters or coarse pustules, for a further 327 plants. 156 plants were found on trees with smooth, finely cracked bark. Poorly represented categories were: upper stem smooth, lower not; "papery" and "fibrous". These categories were not abundant in most vegetation types, rather than being avoided by *Lecanopteris*, except in the savannahs of Western Province, Papua New Guinea, where they were common but did not bear *L. sinuosa*. The surfaces of many hosts, especially in montane forest, were covered in moss, but this was not systematically recorded.

The predominance of rough-barked hosts is not surprising; this surface affords better purchase for epiphytic roots and traps more debris in its ridged surface. Effects of host bark type can be substantially mediated by the presence of other epiphytes or mosses on which *Lecanopteris* may grow, rather than being in direct contact with the bark.

Table 3. Bark types of host trees

Bark type	<i>L. sin</i>	<i>L. pum</i>	<i>L. mir</i>	<i>L. cel</i>	<i>L. cru</i>	<i>L. cur</i>	<i>L. sar</i>	<i>L. dar</i>
1	10	16	0	0	0	0	1	0
2	58	36	33	23	1	2	3	0
3	68	29	2	0	0	1	0	0
4	50	21	11	0	0	4	0	0
5	135	103	47	15	5	9	8	10
6	11	0	0	9	0	0	0	0
7	19	0	0	0	0	0	0	0
8	7	0	0	0	0	0	0	0
9	4	0	0	0	0	0	0	0
10	0	0	0	0	0	0	0	0

- | | |
|---|--|
| 1) Smooth and glassy. | 6) Flaky and scaly. |
| 2) Smooth with fine cracks/pustules. | 7) Transverse hoops or ridges. |
| 3) Rough with fissures > 1 cm deep. | 8) Papery. |
| 4) Rough with shallow fissures. | 9) Fibrous. |
| 5) Rough with crater/scrolls/dimples/coarse pustules. | 10) Upper stem glassy smooth, lower not. |

Ecological and biogeographical aspects of speciation in *Lecanopteris*

The two subgenera of *Lecanopteris* have different distribution patterns (Figs 2 to 5). Subg. *Myrmecopteris* consists of three allopatric species whose main distinction lies in their rhizome differentiation, *L. mirabilis*, *L. sarcopus* and *L. crustacea*. It also contains the wide-ranging *L. sinuosa*. Their speciation, apart from *L. sinuosa*, can be envisaged as allopatric, with existing variation in the gene pools of ecotypes intensifying into specific barriers upon geographical and ecological isolation. The three species all have distinct habitat requirements: *L. mirabilis* inhabits montane forests; *L. crustacea* is confined to lowland forests, and *L. sarcopus* is found in disturbed hill forest. *Lecanopteris sarcopus* and *L. crustacea* are most similar to one another, differing in scale colour, frond texture and in the dimorphism of the *L. sarcopus* rhizome.

The total range of the genus is encompassed within that of *L. sinuosa*. Its opportunistic ecology and wide geographical range are characteristic of weedy pioneer species. These are typically variable in form, have high phenotypic plasticity, but tend not to speciate in the varied environments which they inhabit; their genotypic or phenotypic flexibility can accommodate a range of conditions. The wide distribution of *L. sinuosa* supports its position as a possible ancestral species in *Lecanopteris*, but this is countered by its opportunistic ecology. It may have been able to colonise new habitats as its range expanded, whereas species with

more specialised requirements failed to establish.

Distribution patterns in subg. *Lecanopteris* are distinct from one another, and from *Myrmecopteris*. *Lecanopteris curtisii* s.l. is a wide-ranging species, second only to *L. sinuosa* (Figs 5 & 6). On each of the major land masses in the Malesian Archipelago, it forms more or less distinct races, one of which is currently recognised as a species (*L. philippinensis*). It is interesting to note that both *L. sinuosa* and *L. curtisii*, the most wide-ranging species, possess fewest apomorphies in their subgenera: *L. curtisii* bears none of the rhizome excrescences which characterise the *L. pumila* and *L. darnaedii* groups; and the external morphology of *L. sinuosa* is most similar to a polypodiaceous non-ant-fern. Thus variability in form, probably resulting from a wide geographical range, is found with a low number of apomorphies.

The *L. pumila* group comprises one wide-ranging and morphologically variable species, *L. pumila*; one endemic in the Philippines, and three in Sulawesi. Two of these endemics, *L. carnosa* and *L. celebica*, are abundant in Sulawesi and have a generalist ecology. They are sister species, differing only in the nature of their aborted phyllopodia: *L. carnosa* bears excrescences, and *L. celebica*, spines. Neither their distribution nor their generalist ecology indicates speciation resulting from interrupted gene flow caused by the appearance of physical barriers in a pre-existing population. A mutation isolating the populations and preventing interbreeding is possible, but there is no evidence for it. The third Sulawesi species from the *L. pumila* group, *L. balgooyi*, is geographically sympatric with *L. celebica*, but little is known of its distribution and ecology.

The *L. darnaedii* group is endemic to Sulawesi and consists of three similar species, each only known from its type locality (Fig. 8). Speciation in the *L. darnaedii* group is more plausibly envisaged as a series of range expansions than as isolation of existing populations. Founder effects in the colonising populations, causing genetic revolutions and speciation, are consistent with the small numbers and narrow distribution of these species.

Discussion

Lecanopteris exhibits a wide variety of geographical range and ecological tolerance. *Lecanopteris sinuosa* is found in every habitat within its altitudinal range save lowland evergreen rain forest, either as a dominant, abundant, common or (frequently) rare component. This correlates with a geographical range exceeding that of all other members of the genus; it is the sole representative beyond the Kra Isthmus, in the Solomon Islands, Vanuatu, the Thursday Islands, N. Queensland and Taiwan. *Lecanopteris sarcopus* is less wide-ranging and ecologically tolerant than *L. sinuosa*, but inhabits a variety of vegetation types in Sulawesi and the Philippines.

In contrast, a highly restricted range and tolerance is exhibited by the Sulawesi endemics *L. darnaedii*, *L. spinosa* and *L. holtumii*, which are only known from their type localities in montane forest (Fig. 8). Also restricted to Sulawesi but with a wider ecological tolerance are *L. carnosa*, *L. celebica* and *L. balgooyi*. *Lecanopteris mirabilis* and *L. sarcopus* both have wide distributions but are ecologically confined to mid-montane and lowland evergreen forest respectively. The former is locally abundant, the latter only known from scattered individuals. It should be emphasised for both these species that their ecological tolerance may be broader than the scope of fieldwork for this study, indicated by the discovery of *L. mirabilis* in a mangrove swamp in Seram (B.S. Parris, *pers. comm.*).

The *L. curtisii* complex has a wide and a disjunct distribution, but is local in occurrence and never abundant. The distribution of *L. pumila* is similar to that of *L. crustacea* but it is far more abundant and inhabits montane forest (Figs 5 & 7).

Thus opportunistic ecology and wide range are positively correlated in *L. sinuosa* and to a lesser extent in *L. sarcopus*, and the reverse is true for the Sulawesi montane endemics. *Lecanopteris pumila*, *L. celebica*, *L. mirabilis* and *L. curtisii* either have wide ranges and limited tolerance, or vice versa.

The distribution of *Lecanopteris* species contrasts strongly with that of the rubiaceous ant-epiphytes, but similarities exist at the level of generic distribution. Both *Hydnophytum* and *Myrmecodia* extend beyond Malesia, into Cape York Peninsula, Australia, and the Solomon Islands. *Hydnophytum* is also found in the Andaman Islands, southern Indochina and Fiji (Huxley & Jebb 1991). The wider range of *Hydnophytum* compared to *Myrmecodia* parallels that of subg. *Myrmecopteris* relative to subg. *Lecanopteris*, as do the relative levels of specialisation for the ant association. The centre of species diversity of *Myrmecodia* and *Hydnophytum* is New Guinea; only four species of *Hydnophytum* are found in the rest of Malesia and a few species of *Myrmecodia*, including three in Cape York Peninsula (Huxley & Jebb 1991). *Dischidia* is most diverse in the Philippines, with double chambered domatia occurring in the species there (Rintz 1980).

The different centres of diversity in the far-eastern genera of ant-epiphytes: Sulawesi for *Lecanopteris*; New Guinea for the Rubiaceae, and the Philippines for *Dischidia*, suggest that the combination of unique environmental conditions in these regions was not the only selective pressure operating during speciation in these groups. The potential for speciation can be attributed more to intrinsic factors such as the release of variability, and to stochastic processes, than on external events dependent on a particular area.

Sympatry is rare in *Lecanopteris*; where geographical ranges overlap, ecological isolation occurs. On the two occasions that sympatry has been observed in the field, *L. sinuosa* has been found with *L. curtisii* and *L. crustacea* (Gay, *pers. obs.*).

No host preferences beyond common tree species were exhibited by any *Lecanopteris* species in any habitat, nor was the nature of the host bark an obvious constraint on colonisation.

No constant patterns between the species and their environment emerge from the ecological data, but the genus shares one unifying characteristic in addition to myrmecophytism. All species are predominantly found either in disturbed or stunted vegetation which allow a high level of illumination such as heath forest, ridgetops or roadsides (*L. sinuosa*, *L. sarcopus*), or in taller, closed montane or lowland forest in the crowns of canopy trees (*L. mirabilis*, *L. crustacea*, *L. darnaedii*, *L. curtisii* s.l.). The genus comprises only heliophiles; individuals are rarely found in deep shade, where they are small and stunted. *Lecanopteris pumila* adopts both habits; on ridgetops it grows in any position on scattered trees, and in closed montane forest it is inaccessible in the crowns of canopy trees.

The stunted forests, in which *Lecanopteris* species reach their greatest abundance, lack height and density as a result of nutrient impoverishment and periodic water stress. Whitmore (1984) emphasised the ecophysiological similarity between heath forest and upper montane forest; both formations have xerophytic and oligotrophic characteristics, acidic soils, and share certain disjunct species such as *Baeckia frutescens* (Myrtaceae). The vegetation types in which *L. sinuosa* and *L. pumila* are dominant are extreme forms of heath and upper montane forest: padang and ridgetop habitats. Neither habitat has a continuous tree cover, and both are oligotrophic.

In heath forest, ridgetops and the fire-maintained savannahs of Western Province, Papua New Guinea, myrmecophytes are the dominant and practically the sole epiphytes. No ant-epiphytes are restricted to these habitats, but occur elsewhere at a lower density. An adaptive explanation for the dominance of myrmecophytes has been suggested by Janzen (1974); that myrmecophytes, by virtue of their ant association, utilise nutrients unavailable to other epiphytes. Ant feeding of host plants has been demonstrated in *Myrmecodia* sp. (Huxley 1978), *Hydnophytum* (Rickson 1976) and *Lecanopteris* (Gay, *in press*). However, the unique exploitation of a resource may be simplistic as a sole explanation for the dominance of ant-epiphytes in such habitats. The savannahs of New Guinea are fire-maintained rather than nutritionally impoverished, and the myrmeco-epiphytic community is as dominant there as in Bornean heath forests. Ant-epiphytes are not common in peat swamp forest, which is also an oligotrophic environment. Non-ant epiphytes can flourish in these habitats by colonising the abundant ant carton, as do *Dischidia nummularia* (Asclepiadaceae) and *Bulbophyllum* sp. (Orchidaceae).

Whitmore (1984) noted that it is presently uncertain whether heath forest is stunted by a deficit of water or of nutrients. All myrmeco-epiphytes are capable of withstanding desiccation; most have sclerophyllous leaves or

fronds, and their domatia are fleshy with coriaceous epidermes. Indeed, Yapp (1902) speculated at length whether the *Lecanopteris* rhizome arose as a water storage organ, later exploited by ants. In terms of water conservation, sclerophylly is an adaptation, but rhizome or tuber form may be an exaptation (Gould & Vrba 1982), a by-product of domatium elaboration. The ability to withstand periodic water shortage, especially as epiphytes, must be contributory to the abundance of myrmeco-epiphytes in these xeric habitats.

Another feature common to all habitats where ant-epiphytes dominate the epiphyte flora is the open canopy allowing light to reach epiphytes growing anywhere on the trees, not only in the crowns. A requirement for light as the sole unifying factor in *Lecanopteris* ecology has been discussed above, and the highly insolated environment is another partial explanation for the density of ant-epiphytes, although not for the absence of other sun epiphytes.

Thus the great abundance of ant-epiphytes in padang, ridgetop and savannah vegetation is due to an interaction of factors: nutrient shortage, which is only applicable in the first two habitats; periodic moisture stress, and high insolation, which are found in all three habitats. The ant association is partially but not solely responsible for their dominance in these habitats. *Lecanopteris* is represented in most other Malesian forest types (Table 2), but is rare or common, rather than dominant.

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Appendix 1: Field Sites

Lake Kutubu, 6°30'S, 143°10'E. Southern Highlands Province, Papua New Guinea (LK).

Binaturi River, between Kunini and Giringarede villages, 9°40'S, 143°E. Western Province, Papua New Guinea (BR).

Kar Kar Island, 4°40'S, 146°E. Madang Province. Papua New Guinea (KK).

Roguts village, 5°50'S, 144°20'E. Angelimp subdistrict. Western Highlands Province, Papua New Guinea (R).

Mt. Mon, 9°40'S, 149°40'E. near Bonenau village, Agaun Mission and Mt. Dayman, Milne Bay Province, Papua New Guinea (MM).

Mt. Bosavi, 6°30'S, 142°55'E. Milne Bay Province, Papua New Guinea (MB).

Woodlark Island, 9°10'S, 152°30'E. Milne Bay Province, Papua New Guinea (W).

Varirata National Park, 9°10'S, 152°30'E. Milne Bay Province, Papua New Guinea (V).

Gunong Bunga Buah, 3°35'N, 101°40'E. Genting Highlands, Selangor State, Peninsular Malaysia (GBB), literally "the mountain of flowers and fruits".

Gunong Beremban, 4°20'N, 101°40'E. Cameron Highlands, Pahang State, Peninsular Malaysia (GB).

Gunong Jasar, 4°20'N, 101°35'E. Cameron Highlands, Pahang State, Peninsular Malaysia (GJ).

Maxwell's Hill, 4°55'N, 100°55'E. Perak State, Peninsular Malaysia (MH).

Fraser's Hill, 3°45'N, 101°35'E. Selangor State, Peninsular Malaysia (FH).

Cameron Highlands (CH). Pahang State, Peninsular Malaysia.

Gunong Tahan, 4°40'N, 102°20'E. Taman Negara, Peninsular Malaysia (GT).

Sungai Tahan, 4°40'N, 102°30'E. Taman Negara, Peninsular Malaysia (ST).

Batu Ferringhi water catchment area, 5°20'N, 100°20'E. Penang Island, Peninsular Malaysia (BF).

Gunong Jerai, 5°35'N, 100°30'E. Kedah State, Peninsular Malaysia (GJ).

Kota Tinggi, 1°55'N, 103°55'E. Johore State, Peninsular Malaysia (KT).

Gunong Pantii, 1°55'N, 103°52'E. Johore State, Peninsular Malaysia (GP).

Bako National Park, 1°40'N, 110°E. Sarawak, East Malaysia (BAK).

Nabawan, 4°30'N, 116°20'E. near Keningau, Sabah, East Malaysia, Borneo (N).

Mt. Kinabalu, 6°10'N, 116°40'E. Sabah, East Malaysia, Borneo (MK).

Badas, 4°40'N, 114°40'E. Brunei, Borneo (BAD).

Bukit Basang, 4°40'N, 114°43'E. Brunei, Borneo (BAS).

Sopu Valley, 2°40'S, 121°10'E. Near Dongi Dongi logging camp, 80 km South-East of Palu, Central Sulawesi, Indonesia (SV).

Mt. Roroka Timbu, 1°10'S, 120°20'E. Central Sulawesi, Indonesia (MRT).

Lake Matano, 1°30'S, 102°20'E. Near Soroako, South Sulawesi, Indonesia (LM).

Mt. Wawonseru, 1°30'S, 102°10'E. Near Soroako, South Sulawesi, Indonesia (MW).

Appendix 2 : Hosts of *Lecanopteris*

L. sinuosa

<u>Site</u>	<u>Host species</u>	<u>Frequency</u>
LK	<i>Artocarpus</i> sp. (Mor.)	18
LK	<i>Pandanus</i> sp. (Pand.)	16
LK	<i>Sterculia</i> sp. (Sterc.)	1
LK	<i>Dracaena</i> sp. (Agav.)	1
LK	<i>Cyathea</i> sp. (Cyath.)	4
LK	<i>Schefflera</i> sp. (Hed.)	4
LK	<i>Ficus</i> sp. (Mor.)	3
LK	<i>Dysoxylon</i> sp. (Mel)	5
BR	<i>Nauclea orientalis</i> (Rub)	1
BR	<i>Timonius timon</i> (Rub.)	11
BR	<i>Planchonella</i> sp. (Sapot.)	40
BR	<i>Glochidion</i> sp. (Euphorb.)	2
BR	<i>Eucalyptopsis</i> sp. (Myrt.)	1
BR	<i>Dillenia</i> sp. (Dillen.)	8
BR	<i>Xylocarpus</i> sp. (Mel.)	2
BR	<i>Banksia dentata</i> (Prot.)	1
BR	<i>Planchonia</i> sp. (Lecythid.)	1
BR	<i>Antidesma</i> sp. (Euphorb.)	3
KK	<i>Theobroma cacao</i> (Sterc.)	28
KK	<i>Plumeria</i> sp. (Apocyn.)	2
KK	<i>Cocos nucifera</i> (Palm.)	4
KK	<i>Toona</i> sp. (Mel)	1
V	<i>Casuarina</i> sp. (Cas.)	6
V	<i>Hevea brasiliensis</i> (Euphorb.)	2
GJ	<i>Dracaena</i> sp. (Agav.)	1
GJ	<i>Leptospermum flavescens</i> (Myrt.)	2
KT	<i>Hopea polyalthioides</i> (Dipt.)	4
KT	Theaceae indet.	1
KT	<i>Artocarpus</i> sp. (Mor.)	1
GP	<i>Eugenia syzygioides</i> (Myrt.)	4
BF	<i>Parinari</i> sp. (Chrysobal.)	5

<u>Site</u>	<u>Host species</u>	<u>Frequency</u>
BAD	<i>Agathis borneensis</i> (Arauc.)	1
BAS	<i>Casuarina nobilis</i> (Cas.)	3
BAS	<i>Gertnera</i> sp. (Rub.)	3
BAS	<i>Timonius flavescens</i> (Rub.)	8
BAS	<i>Tristania obovata</i> (Myrt.)	3
NAB	<i>Vaccinium</i> sp. (Eric.)	1
BAK	<i>Ixonanthes becarrii</i> (Ixon.)	9
BAK	<i>Casuarina</i> sp. (Cas.)	8
BAK	<i>Parastemon spicatum</i> (Chrysobal.)	9
BAK	<i>Dacrydium becarrii</i> (Podoc.)	5
BAK	<i>Cratoxylum</i> sp. (Guttif.)	1
BAK	<i>Baekia frutescens</i> (Myrt.)	12
BAK	<i>Calophyllum austrocoriaceum</i> (Guttif.)	3
BAK	<i>Eugenia multibracteosa</i> (Myrt.)	7
BAK	<i>Ploiarium alternifolium</i> (Theac.)	6
BAK	Mangrove indet.	8

L. pumila

GB	<i>Symingtonia populnea</i> (Ham.)	3
GB	<i>Garcinia rostrata</i> (Guttif.)	5
U	<i>Lithocarpus rassa</i> (Fag.)	26
GB	<i>Knema</i> sp. (Myrist.)	2
GB	<i>Ardisia</i> sp. (Myrsin.)	6
GB	<i>Eugenia attenuata</i> (Myrt.)	4
GB	<i>Quercus lineata</i> (Fag.)	2
GB	<i>Lithocarpus</i> sp. (Fag.)	1
GB	<i>Prunus</i> sp. (Ros.)	1
GB	<i>Cinnamomum scortechinii</i> (Laur.)	2
GB	<i>Rhodoleia championii</i> (Ham.)	4
MH	<i>Adinandra</i> sp. (Theac.)	1
MH	<i>Weinmannia blumei</i> (Cunon.)	36
MH	<i>Vaccinium</i> sp. (Eric.)	1
MH	<i>Ficus chartacea</i> (Mor.)	2
GBB	<i>Vaccinium bancanum</i> (Eric.)	14

<u>Site</u>	<u>Host species</u>	<u>Frequency</u>
FH	<i>Ficus</i> sp. (Mor.)	33
GT	<i>Rhododendron wrayii</i> (Eric.)	3
GT	<i>Vaccinium</i> sp. (Eric.)	19
K	<i>Lithocarpus</i> sp. (Fag.)	11
U	Dead	36

L. mirabilis

MM	<i>Engelhardia rigida</i> (Jug.)	1
MM	Rubiaceae indet.	1
MM	Moraceae indet.	1
MM	<i>Galbulimina belgaveana</i> (Himant.)	1
MM	<i>Planchonella</i> sp. (Sapot.)	8
MM	<i>Nothofagus grandis</i> (Fag.)	2
U	<i>Elaeocarpus culminicola</i> (Elaeoc.)	2
MM	<i>Linociera</i> sp. (Oleac.)	9
MM	<i>Syzygium</i> sp. (Myrt)	5
U	<i>Castanopsis acuminatissima</i> (Fag.)	35
MM	<i>Weinmannia ledermanni</i> (Cunon.)	2
R	<i>Saurauia</i> sp. (Actinid.)	3
R	Leguminosae indet.	1
R	<i>Adenanthera</i> sp. (Leg.)	2
R	<i>Schefflera</i> sp. (Hed.)	1
R	<i>Ardisia</i> sp. (Myrsin.)	2
R	<i>Garcinia</i> sp. (Guttif.)	6
U	Dead	6
U	Indet.	2

L. crustacea

BAD	<i>Shorea albida</i> (Dipt.)	1
KT	Dipterocarpaceae indet.	5