

THE *GESNERIACEAE* OF SULAWESI I: AN INTRODUCTION

M. MENDUM*† & H. J. ATKINS*

Sulawesi (Celebes) is the largest island in the biogeographic region of Wallacea. The *Gesneriaceae* of the island are represented by 11 genera, some of which show a very high degree of endemism. Knowledge of the origin and affinities of the flora of this island is important for an understanding of the biogeography of the area. The *Gesneriaceae* promise to be excellent models for phylogeographic analysis, but before this, basic taxonomic studies must be carried out. A list of the currently known genera and species is provided, and descriptions of new taxa will be published over the coming months.

Keywords. Biogeography, *Gesneriaceae*, Indonesia, Sulawesi, Wallacea.

The islands of SE Asia comprise one of the most geologically complex regions in the world (Audley-Charles, 1981; Hall, 1996, 1998), at the meeting point of three major tectonic plates. Its turbulent geological history and exceptionally high levels of biological endemism make this region of prime interest to biogeographers. Wallace's line, one of the most important biogeographic boundaries in the world, bisects the archipelago, and was originally thought to mark the meeting point of the Oriental and Australasian fauna and flora. Since Wallace first drew his line in 1863, many others have been drawn, reflecting different hypotheses based on the distribution patterns of different taxa (summarized in Scrivener *et al.*, 1943; Simpson, 1977). The difficulty of agreeing on a single line eventually resulted in the identification of a zone of transition in the centre of Malesia (Dickerson, 1928). Situated between areas with Asiatic and areas with Australian floras and faunas, and known as 'Wallacea', the zone exhibits a high degree of endemism (Audley-Charles, 1981; Whitten *et al.*, 1987). The limits of Wallacea itself have also been the subject of some debate (Mayr, 1944; Holloway & Jardine, 1968), but at its broadest definition it is demarcated by Wallace's original line in the west and Lydekker's line in the east (e.g. Moss & Wilson, 1998) (Fig. 1). In whichever way Wallacea has been defined, Sulawesi has always lain at its heart and is its largest island.

The biological diversity of Sulawesi shows relationships with Sundaland to the west, the Philippines to the north, and Australasia to the east (van Balgooy, 1987; Whitten *et al.*, 1987). While few plant genera are endemic to Sulawesi compared with Borneo or New Guinea for example, the level of endemism at species level is high. An understanding of the origin and affinities of the flora of this island is

* Royal Botanic Garden Edinburgh, 20A Inverleith Row, Edinburgh EH3 5LR, UK.

† Died 13 ii 2004.

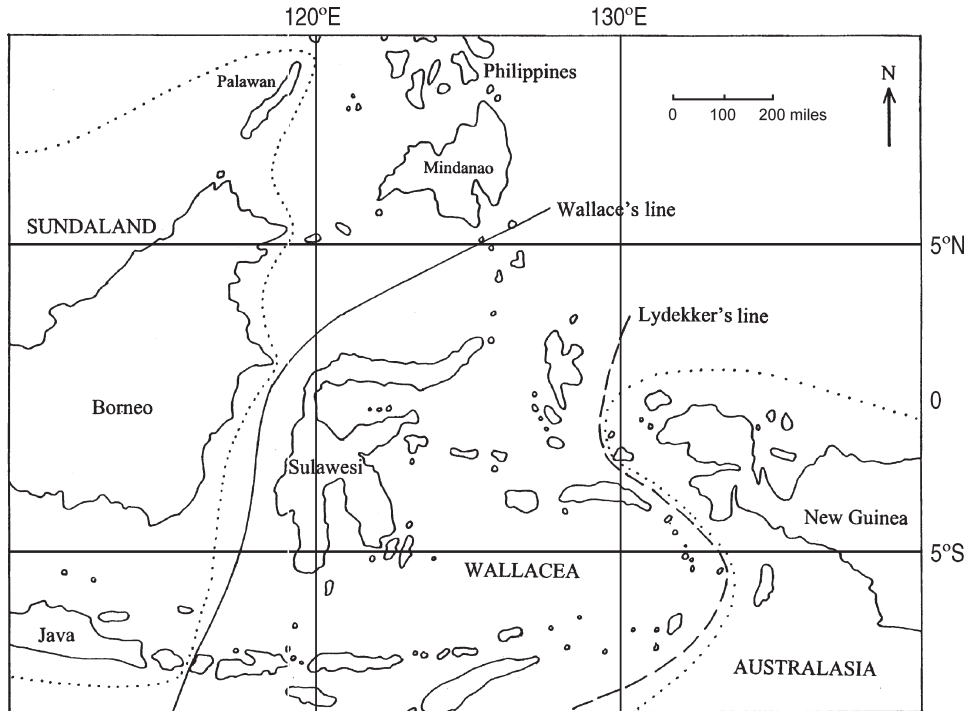


FIG. 1. Map of the SE Asian islands, showing the boundaries of Sundaland, Wallacea and Australasia.

crucial to an understanding of the biogeography of the entire region, and yet the flora of Sulawesi remains very poorly known (Frodin, 2001; Kessler, 2002) and collections are sparse. Fewer botanical specimens have been collected here than in any other major island in Indonesia (Whitten *et al.*, 1987; Kessler, 2002). In the *Gesneriaceae*, most collections are of still-undescribed taxa. There are no published accounts of the family in Sulawesi or indeed many of the Malesian islands, including Borneo. Because the degree of endemism is so high in this family, it is appropriate to treat the Malesian *Gesneriaceae* on an island-by-island basis.

The Asiatic *Gesneriaceae* (about 70 genera), except for the Chinese *Titanotrichum* (Smith *et al.*, 1997; Wang, 2002), are in subfamily *Cyrtandroideae*, but only 11 (*Aeschynanthus* Jack, *Agalmyla* Blume, *Boea* Lam., *Cyrtandra* J.R. & G. Forst., *Epithema* Blume, *Henckelia* Spreng., *Monophyllaea* R. Br., *Paraboea* (C.B. Clarke) Ridl., *Rhynchoglossum* Blume, *Rhynchotechum* Blume and *Stauranthera* Benth.) are known to occur east of Wallace's line (for details see Burt, 1998a and Hilliard & Burt, 2002) and all are recorded from Sulawesi. None of these genera is endemic east of Wallace's line, but species-level endemism is high. In *Aeschynanthus* the rates increase markedly eastwards, and current understanding indicates that in Peninsular Malaysia the rate is 23%, in Borneo about 55%, and in New Guinea over 90%. Little

is known of the taxa in Sulawesi, but levels of endemism so far are high. Four species (out of about 160 in the genus) are currently recorded from the island, but recent fieldwork has yielded at least 12 more, nine of which are still undescribed. In *Agalmyla*, all the 11 species from Sulawesi are in section *Exannularia*, and of these, seven were newly described in Hilliard & Burt's 2002 account. The section itself is confined to Wallacea. *Cyrtandra* currently contains 10 taxa from Sulawesi, and again there are at least 20 awaiting description. Three species of the limestone-loving genus *Monophyllaea* are recorded, one having been described in 2002. *Monophyllaea chinii* B.L. Burt and *M. eymae* B.L. Burt are endemic to Sulawesi, while *M. anthocrena* B.L. Burt also occurs in Ceram. A fourth entity, *M. aff. merrilliana*, is of uncertain status (Burt, 1978, 2002).

Other genera in the *Gesneriaceae* contain species with a much wider distribution. *Boea* is a genus of about 14 species; the only one so far recorded for Sulawesi is *B. philippensis* C.B. Clarke. It has an interesting distribution, occurring also in Hainan (China), Vietnam, the Philippines, Sumbawa and W Flores, somewhat similar to that seen in the insect genus *Hydropsyche* (Mey, 2003). There are three *Paraboea* species in Sulawesi, out of about 90 in the genus. Hilliard & Burt (2002) point out that, of the 11 genera occurring east of Wallace's line, *Paraboea* is the only one not yet known from New Guinea. *Epithema* has at least two Sulawesi members; although there are only about 20 species in the genus, many are widespread throughout SE Asia. The same can be said for *Rhynchoglossum* and *Rhynchotechum*, each consisting of about 12 species (Hilliard & Burt, 2002). The easternmost record for the genus *Henckelia* (c.180 spp.) was until recently from Borneo, before *H. kjellbergii* B.L. Burt was described from SE Sulawesi, with an outlying specimen from Irian Jaya (Burt, 1998b). *Stauranthera* (c.8 spp.) is distributed from India to New Guinea, but was not recorded from Sulawesi until 2002, when the widespread *S. caerulea* Merr. was collected from the northern peninsula. A list of all *Gesneriaceae* taxa so far recorded from Sulawesi is provided in the Appendix.

Molecular biogeographic analyses for Malesia, of plants or animals, are surprisingly few, especially those focusing on Sulawesi (e.g. Butlin *et al.*, 1998; Evans *et al.*, 1999; Atkins *et al.*, 2001; Brown & Guttman, 2002; Schulte *et al.*, 2002). Such analyses cannot be carried out, however, without the 'basic taxonomic spadework' being done in parallel (Holloway & Hall, 1998). As Holloway (2003) remarked, 'We have started the new century with an array of new tools but still a dearth of data'. The *Gesneriaceae* genera *Cyrtandra*, *Agalmyla* and *Aeschynanthus* are perfect tools for this type of biogeographic analysis because of their high levels of local endemism, high species numbers, and extensive coverage of the region; see Atkins *et al.* (2001) for *Cyrtandra* and Denduangboripant *et al.* (2001) for *Aeschynanthus*. Recent fieldwork has gone a small way towards providing the raw materials for such studies. New species of *Cyrtandra* and *Aeschynanthus* are described in this issue (see pp. 305–321 and 323–330) as part of continuing research into the *Gesneriaceae* of Sulawesi.

ACKNOWLEDGEMENTS

We would like to thank Dr Dedy Darnaedi, Mr Hendrian and Mr Sofyan of the Kebun Raya Bogor and Dr Irawati of the Herbarium Bogoriense for continued support and invaluable help in enabling fieldwork in Indonesia. Thanks are also due to our colleagues George Argent, Louise Galloway, Mark Newman, Steve Scott and Paul Smith, and to the people of Sulawesi who acted as our guides and porters. Recent fieldwork was funded by the Royal Botanic Garden Edinburgh, Royal Horticultural Society Blaxall Valentine Bursary, Royal Horticultural Society Queen Elizabeth QM Bursary, Merlin Trust, Royal Geographical Society, Percy Sladen Memorial Fund, University of Edinburgh Davis Expedition Fund, Systematics Association of the UK and the Stanley Smith Horticultural Trust (UK).

REFERENCES

- ATKINS, H., PRESTON, J. & CRONK, Q. C. B. (2001). A molecular test of Huxley's line: *Cyrtandra* (Gesneriaceae) in Borneo and the Philippines. *Biol. J. Linn. Soc.* 72: 143–159.
- AUDLEY-CHARLES, M. G. (1981). Geological history of the region of Wallace's line. In: WHITMORE, T. C. (ed.) *Wallace's Line and Plate Tectonics*, pp. 24–35. Oxford: Clarendon Press.
- VAN BALGOOY, M. M. J. (1987). A plant biogeographical analysis of Sulawesi. In: WHITMORE, T. C. (ed.) *Biogeographical Evolution of the Malay Archipelago*, pp. 94–102. Oxford: Clarendon Press.
- BROWN, R. M. & GUTTMAN, S. I. (2002). Phylogenetic systematics of the *Rana signata* complex of Philippine and Bornean stream frogs: reconsideration of Huxley's modification of Wallace's Line at the Oriental–Australian faunal zone interface. *Biol. J. Linn. Soc.* 76: 393–461.
- BURTT, B. L. (1978). Studies in the Gesneriaceae of the Old World. XLV: A preliminary revision of *Monophyllaea*. *Notes Roy. Bot. Gard. Edinburgh* 37: 1–59.
- BURTT, B. L. (1998a). Climatic accommodation and phytogeography of the Gesneriaceae of the Old World. In: MATHEW, P. & SIVADASAN, M. (eds) *Diversity and Taxonomy of Tropical Flowering Plants*, pp. 1–27. Calicut: Mentor Books.
- BURTT, B. L. (1998b). New species of phytogeographical interest in *Beccarinda* and *Henckelia* (Gesneriaceae). *Beitr. Biol. Pflanzen* 70: 377–382.
- BURTT, B. L. (2002). New Gesneriaceae: a *Chirita* from Vietnam and a *Monophyllaea* from Sulawesi. *Gard. Bull. Singapore* 54: 239–242.
- BUTLIN, R. K., WALTON, C., MONK, K. A. & BRIDLE, J. R. (1998). Biogeography of Sulawesi grasshoppers, genus *Chitaura*, using DNA sequence data. In: HALL, R. & HOLLOWAY, J. D. (eds) *Biogeography and Geological Evolution of SE Asia*, pp. 355–359. Leiden: Backhuys Publishers.
- DENDUANGBORIPANT, J., MENDUM, M. & CRONK, Q. C. B. (2001). Evolution in *Aeschynanthus* (Gesneriaceae) inferred from ITS sequences. *Pl. Syst. Evol.* 228: 181–197.
- DICKERSON, R. E. (1928). *Distribution of Life in the Philippines*. Manila: Bureau of Printing.
- EVANS, B. J., MORALES, J. C., SUPRIATNA, J. & MELNICK, D. J. (1999). Origin of the Sulawesi macaques (Cercopithecidae: *Macaca*) as suggested by mitochondrial DNA phylogeny. *Biol. J. Linn. Soc.* 66: 539–560.

- FRODIN, D. (2001). Floras in retrospect and for the future. *Pl. Talk* 25: 36–39.
- HALL, R. (1996). Reconstructing Cenozoic SE Asia. In: HALL, R. & BLUNDELL, D. J. (eds) *Tectonic Evolution of Southeast Asia. Geological Society Special Publication 106*, pp. 153–184. Bath: Geological Society Publishing House.
- HALL, R. (1998). The plate tectonics of Cenozoic SE Asia and the distribution of land and sea. In: HALL, R. & HOLLOWAY, J. D. (eds) *Biogeography and Geological Evolution of SE Asia*, pp. 99–131. Leiden: Backhuys Publishers.
- HILLIARD, O. M. & BURTT, B. L. (2002). The genus *Agalmyla* (*Gesneriaceae-Cyrtandroideae*). *Edinburgh J. Bot.* 59(1): 1–210.
- HOLLOWAY, J. D. (2003). An addiction to Southeast Asian biogeography. *J. Biogeogr.* 30: 161–163.
- HOLLOWAY, J. D. & HALL, R. (1998). SE Asian geology and biogeography: an introduction. In: HOLLOWAY, J. D. & HALL, R. (eds) *Biogeography and Geological Evolution of SE Asia*, pp. 1–23. Leiden: Backhuys Publishers.
- HOLLOWAY, J. D. & JARDINE, N. (1968). Two approaches to zoogeography: a study based on the distributions of butterflies, birds and bats in the Indo-Australian area. *Proc. Linn. Soc. Lond.* 179: 153–188.
- KESSLER, P. J. A. (2002). Checklist of woody plants in Sulawesi, Indonesia. *Blumea* Suppl. 14.
- MAYR, E. (1944). Wallace's line in the light of recent zoogeographic studies. *Quart. Rev. Biol.* 19: 1–14.
- MEY, W. (2003). Insular radiation of the genus *Hydropsyche* (Insecta, Trichoptera: Hydropsychidae) Pictet, 1834 in the Philippines and its implications for the biogeography of Southeast Asia. *J. Biogeogr.* 30: 227–236.
- MOSS, S. J. & WILSON, M. E. J. (1998). Biogeographic implications from the Tertiary palaeogeographic evolution of Sulawesi–Borneo. In: HALL, R. & HOLLOWAY, J. D. (eds) *Biogeography and Geological Evolution of SE Asia*, pp. 133–163. Leiden: Backhuys Publishers.
- SCHULTE, J. A., MELVILLE, J. & LARSON, A. (2002). Molecular phylogenetic evidence for ancient divergence of lizard taxa on either side of Wallace's Line. *Proc. Biol. Sci.* 270(1515): 597–603.
- SCRIVENER, J. B., BURKILL, I. H., SMITH, M. A., CORBET, A. S., AIREY SHAW, H. K., RICHARDS, P. W. & ZEUNER, F. E. (1943). A discussion of the biogeographic division of the Indo-Australian archipelago with criticism of the Wallace and Weber lines and of any other dividing lines and with an attempt to obtain uniformity in the names used for the divisions. *Proc. Linn. Soc. London* 154: 120–165.
- SIMPSON, G. G. (1977). Too many lines: the limits of the Oriental and Australian zoogeographic regions. *Proc. Amer. Phil. Soc.* 121(2): 107–120.
- SMITH, J., BROWN, K. D., CARROLL, C. L. & DENTON, D. S. (1997). Familial placement of *Cyrtandromoea*, *Titanotrichum* and *Sanango*, three problematic genera of the Lamiales. *Taxon* 46: 65–74.
- WALLACE, A. R. (1860). On the zoological geography of the Malay archipelago. *J. Linn. Soc.* 4: 172–184.
- WANG, C.-N. (2002). *Systematics, developmental biology and population genetics of Titanotrichum oldhamii (Gesneriaceae) inferred from four different gene regions*. PhD thesis, University of Edinburgh.
- WHITTEN, A. J., MUSTAFA, M. & HENDERSON, G. S. (eds) (1987). *The Ecology of Sulawesi*. Jogjakarta: Gadjah Mada University Press.

APPENDIX

Gesneriaceae taxa recorded from Sulawesi

Names in bold are thought to be endemic taxa; asterisks indicate taxa newly described in this issue.

- Aeschynanthus* (c.160 spp.; c.16 in Sulawesi)
A. albidus (Blume) Steud. (doubtful record)
A. batesii Mendum*
A. burttii Mendum*
A. celebica Koorders
A. lobaticalyx Mendum*
A. microphyllus C.B. Clarke
A. viridiflorus Teijsm. & Binn.
 plus nine undescribed species
- Agalmyla* (97 spp.; 12 in Sulawesi)
A. bicolor Hilliard & B.L. Burtt
A. brownii (Koorders) B.L. Burtt
A. exannulata Hilliard & B.L. Burtt
A. immersinerva Hilliard
A. paucipilosa Hilliard & B.L. Burtt
A. pulcherrima Hilliard & B.L. Burtt
A. remotidentata Hilliard & B.L. Burtt
A. scabriflora Hilliard & B.L. Burtt
A. sojoliana Hilliard & B.L. Burtt
A. torajiana Hilliard & B.L. Burtt
A. vogelii Hilliard & B.L. Burtt
 plus one undescribed species
- Boea* (14 spp.; one in Sulawesi)
B. philippensis C.B. Clarke
- Cyrtandra* (600 spp.; 28 in Sulawesi)
C. bruteliana Koorders
C. coccinea Blume var. *celebica* (Blume)
 C.B. Clarke
C. cuneata Blume
C. engleri Koorders
C. fasciata H.J. Atkins*
C. geocarpa Koorders
C. gorontaloensis H.J. Atkins*
C. hypogaea Koorders
C. jellesmanii Koorders
C. luteoflora H.J. Atkins*
- C. mollis* de Vriese
C. polyneura (C.B. Clarke) B.L. Burtt
C. purpurea H.J. Atkins*
C. roseiflora H.J. Atkins*
C. serratifolia H.J. Atkins*
C. spicata de Vriese
C. tenuicarpa H.J. Atkins*
 plus 11 undescribed species
- Epithema* (c.20 spp.; three in Sulawesi)
E. benthamii C.B. Clarke
E. brunonis (Wall.) Decne
E. saxatile Blume
E. sp.
- Henckelia* (c.180 spp.; one in Sulawesi)
H. kjellbergii B.L. Burtt
- Monophyllaea* (c.34 spp.; three or four in Sulawesi)
M. anthocrena B.L. Burtt
M. chinii B.L. Burtt
M. eymae B.L. Burtt
 (*M. aff. merrilliana* Kraenzl. – of uncertain status)
- Paraboea* (c.80 spp.; three in Sulawesi)
P. leporina (H.J. Lam.) B.L. Burtt
P. mataensis Z.R. Xu & B.L. Burtt
P. minahassae (Teijsm. & Binn.) B.L. Burtt
- Rhynchoglossum* (c.12 spp.; one in Sulawesi)
R. obliquum Blume
- Rhynchotechum* (c.12 spp.; one in Sulawesi)
R. parviflorum Blume
- Stauranthera* (c.8 spp.; one in Sulawesi)
S. caerulea Merr.