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Wallace's line and the distribution of the liverworts of Sulawesi

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Abstract – We explore the significance of Wallace's line as a biogeographical boundary in wind-dispersed organisms based on a phytogeographical analysis of the liverworts of Sulawesi. We analysed the geographical and elevational ranges and dispersibility of 177 species of liverworts, including 44 new to Sulawesi. The majority of the species proved to be widespread in the Malesian archipelago; only two are endemic to Sulawesi. Thirteen species (7.5%) belong to the eastern Malesian element, having their westernmost border in Sulawesi. In contrast, only two are western Malesian in distribution, reaching eastwards to Sulawesi. Widespread species occur both in lowland and montane regions; those with eastern Malesian ranges are largely restricted to montane areas. Poor dispersibility (spores unisexual, asexual reproductive devices lacking) is highly characteristic of the eastern Malesian species. We conclude that the greater number of eastern than western Malesian liverwort species in Sulawesi (13 *vs* 2) is in support of Wallace's line and indicates that this border of Asiatic and Australasian biogeographic regions is also relevant to wind-dispersed organisms such as liverworts. The limited availability of suitable habitats and reproductive constraints of the eastern Malesian species may have impeded their migration westwards across Wallace's line.

Dispersal / distribution / Indonesia / liverworts / Malesian archipelago / Sulawesi / Wallace line

INTRODUCTION

Wallace's line, proposed by the British zoologist A.R. Wallace in the 19th century, is one of the best known biogeographical boundaries. The line runs through the Malesian archipelago and marks the meeting of Asian and Australian biota (Whitmore, 1981) (Fig. 1). Although first applied to the fauna of the region, Wallace's line is also accepted as a demarcation line separating the flora of the region (e.g., Van Steenis, 1950, 1979; Dransfield, 1981; Van Balgooy, 1984). The exact position of the Wallace line has been subject to much discussion. According to the original concept of Wallace (1863, 1869), the line runs through the Strait of Makassar and between Bali and Lombok, separating Sulawesi, the Lesser Sunda Islands, the Mollucas and New Guinea in the east from the Philippines, Borneo,

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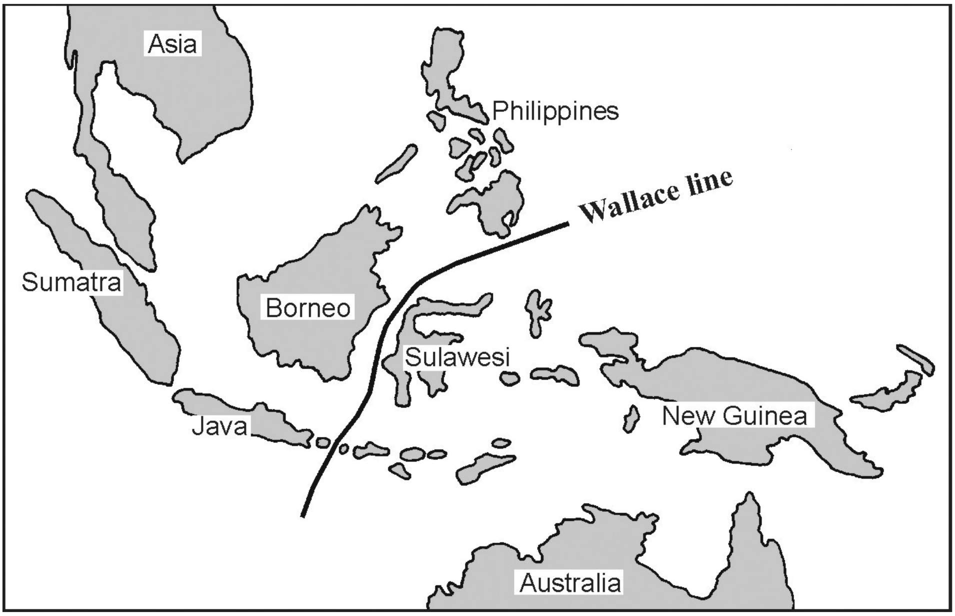

Fig. 1. Map of the Malesian archipelago showing the position of Wallace's line as originally proposed by A. R. Wallace (1863, 1869).

Java and Sumatra in the west. Some authors, including Wallace late in his life, have moved the line from west to east of Sulawesi; others failed to find evidence for the line or have proposed different ones (Simpson, 1977; Whitmore, 1981).

The effectiveness of Wallace's line as a biogeographical boundary is generally attributed to the depth of the sea channel between Borneo and Sulawesi and areas further to the south and north. The deep Makassar Strait between Borneo and Sulawesi presumably hampered the dispersal of many groups of organisms when the Sunda and Sahul shelves were exposed during glacial, sea level depressions (Moss & Wilson, 1998). In addition, the shrinking of the Asian rainforests during periods of glacial drought has been suggested as an impediment to exchanges of rain forest organisms across the Wallace line (Brandon-Jones, 1998).

While deep ocean channels may present effective dispersal barriers to various animal groups and seed plants, their effectiveness as a barrier for wind-dispersed organisms with light diaspores such as bryophytes, is less plausible. Bryophytes are a large group of plants in the Malesian archipelago with probably about 3000 species. Due to their light, wind-dispersed spores, bryophyte species may be dispersed over long distances (e.g., Van Zanten, 1977; Van Zanten & Gradstein, 1988; Muñoz *et al.*, 2004; McDaniel & Shaw, 2005; Heinrichs *et al.*, 2005) and are, therefore, generally less good indicators of past geography than seed plants (Van Zanten & Pócs, 1981). Nevertheless, bryophyte distributions within Malesia shows several distinct patterns which parallel those found in flowering plants. Tan (1984) and Tan & Engel (1986) showed that the bryophyte flora of the Philippines is predominantly western Malesian in affinity and origin, being more closely related to that of Borneo and the Malay Peninsula than that of New

Guinea. Piippo (1992) reached the same conclusion in a study of the affinities of Asiatic and Australian hepatics. Touw (1992) analyzed the moss flora of the Lesser Sunda Islands and found evidence for the recognition of South Malesia as a botanical province, earlier proposed by Van Steenis (1979) based on phanerogams. The latter authors failed to find support for Wallace's line as a phytogeographical boundary within South Malesia, however. Tan (1984, 1998) and Hyvönen (1989), moreover, found that floristic differences between western and eastern Malesia were much less conspicuous in mosses than in flowering plants.

In spite of these studies, there are still major lacunae in our knowledge of the distribution patterns of the bryophytes in the Malesian archipelago. One of the main gaps has been the bryophyte flora of Sulawesi, which has long been neglected. It is generally agreed that the biota of Sulawesi are crucial in the discussions about the Wallace line. With a total land surface of about 182,870 km^2 (Whitten *et al.,* 2002), Sulawesi is the fourth largest island of Indonesia. Phytogeographically the island is part of the Eastern Malesian Province, together with the Moluccas and New Guinea. It has a rich phanerogam flora, numbering more than 5000 species of which about 15% are endemic (Roos *et al.*, 2004). A first, recent checklist of the neglected bryophyte flora of the island lists 476 species, including 340 mosses and 134 liverworts (Gradstein *et al.,* 2005). We are not aware of any study dealing with the bryophyte geography of Sulawesi.

The purpose of the present study is to analyze the geographical and elevational distribution of the liverworts (Marchantiophyta) of Sulawesi. In particular, we explore the question whether the distributions of these wind-dispersed organisms coincide with Wallace's line as a biogeographical boundary between western and eastern Malesia.

METHODS

From the recent checklist of Sulawesi bryophytes (Gradstein *et al.*, 2005) and our unpublished bryophyte collections made in Central Sulawesi in 2005 (Aryanti *et al*., in prep.), we compiled a list of all species of liverworts (Marchantiophyta) recorded from Sulawesi and their elevational ranges. The geographical ranges and dispersibility of the species were determined based on literature analysis. Special attention was given to species reaching their western- or easternmost distributions in Sulawesi. Affinities of the liverwort flora of Sulawesi were determined by comparison with checklists of New Guinea (Grolle & Piippo, 1984), Philippines (Tan & Engel, 1986), Borneo (Menzel, 1988), Seram (Mizutani, 1986) and Indonesia (Schiffner, 1898), and the ongoing series on the liverworts of Papua New Guinea (e.g., Piippo, 1984, 1985, 1989; Grolle & Piippo, 1986; Hattori & Piippo, 1986).

RESULTS AND DISCUSSION

In total, 177 species recorded from Sulawesi were included in the analysis; 44 of these are new to the island (Table 1). Eight distribution types were recognized in the liverwort flora of Sulawesi (Table 2): 1) pantropical (throughout

Table 1. Altitudinal and geographical distribution of the liverwort species recorded from Sulawesi. Lowland: 0-1200 m. Montane: 1200-3000 m. A: Asiatic. E: Eastern Malesian. End: Endemic. M: Malesian. W: Western Malesian. Other distribution type. P: Pantropical. Pal: Paleotropical (Asia, Africa). * species new to Sulawesi.

Species	*Altitudinal distribution*		*Geographical distribution*
	lowland	*montane*	
**Acrolejeunea pycnoclada* (Taylor) Schiffn.	+	–	A
Andrewsianthus puniceus (Reinw. *et al.*) R.M.Schust.	–	+	A
**Anomocaulis flaccidus* (Steph.) Grolle	–	+	A
Aphanolejeunea grossepapillosa Horik.	–	+	A
Archilejeunea planiuscula (Mitt.) Steph.	+	+	A
Bazzania erosa (Reinw. *et al.*) Trevis.	–	+	A
Bazzania flavescens (Sande Lac. ex. Steph.) Schiffn.	–	+	E
Bazzania levieri (Steph.) N.Kitag.	–	+	A
Bazzania praerupta (Nees) Trevis.	+	+	A
Bazzania reinwardtii (Sande Lac.) Schiffn.	?	?	E
Bazzania tridens (Reinw. *et al.*) Trevis.	+	+	A
Bazzania vittata (Gottsche) Trevis.	+	+	A
Caudalejeunea recurvistipula (Gottsche) Schiffn.	+	+	A
**Chandonanthus hirtellus* (Web.) Mitt.	–	+	Pal
**Chandonanthus piliferus* Steph.	–	+	E
Cheilolejeunea celebensis (Steph.) Mizut.	–	+	End
**Cheilolejeunea ceylanica* (Gottsche) R.M.Schust. & Kachroo	+	–	A
**Cheilolejeunea imbricata* (Nees) S.Hatt.	+	–	A
**Cheilolejeunea longiloba* (Hoffm.) Kachroo & R.M.Schust.	+	–	A
Cheilolejeunea paroica Mizut.	+	–	A
Cheilolejeunea trifaria (Reinw. *et al.)* Mizut.	+	+	P
Chiastocaulon dendroides (Nees) Carl	+	+	A
Cololejeunea amphibola B.Thiers	+	+	E
Cololejeunea falcata (Horik.) Benedix	+	+	A
Cololejeunea floccosa (Lehm. & Lindenb.) Schiffn.	+	+	Pal
Cololejeunea haskarliana (Lehm. & Lindenb.) Schiffn.	+	+	A
Cololejeunea inflata Steph.	+	+	A
Cololejeunea obliqua (Nees & Mont.) Schiffn.	–	+	P
Cololejeunea peraffinis (Schiffn.) Schiffn.	+	+	Pal
Cololejeunea triapiculata (Herz.) Tixier	–	+	A
Cololejeunea verrucosa Steph.	+	–	A
Colura acroloba (Mont. ex Steph.) Ast	+	+	A
Dendrolejeunea fruticosa (Lindenb. & Gottsche) Lacout.	+	–	A
Denotarisia linguifolia (De Not.) Grolle	–	+	A
Drepanolejeunea dactylophora (Nees *et al.*) Schiffn.	+	–	A
Drepanolejeunea levicornua Steph.	+	–	A
Drepanolejeunea muricata (Gottsche) Schiffn.	+	+	A
Drepanolejeunea obliqua Steph.	–	+	A
Drepanolejeunea pentadactyla (Mont.) Steph.	+	+	A
Drepanolejeunea tenera K.I.Goebel	+	+	M
Drepanolejeunea ternatensis (Gottsche) Steph.	–	+	A
Drepanolejeunea teysmanii Gottsche ex Steph.	+	+	A
Drepanolejeunea thwaitesiana (Mitt.) Steph.	+	+	A
**Dumortiera hirsuta* (Sw.) Nees	+	–	O
Frullania apiculata (Reinw. *et al.*) Nees	+	+	P

Table 1. *(suite)* Altitudinal and geographical distribution of the liverwort species recorded from Sulawesi. Lowland: 0-1200 m. Montane: 1200-3000 m. A: Asiatic. E: Eastern Malesian. End: Endemic. M: Malesian. W: Western Malesian. Other distribution type. P: Pantropical. Pal: Paleotropical (Asia, Africa). * species new to Sulawesi.

Species	*Altitudinal distribution*		*Geographical distribution*
	lowland	*montane*	
Frullania ericoides (Nees) Mont.	+	–	P
Frullania galeata (Reinw. *et al.*) Dumort.	–	+	A
Frullania gaudichaudii (Nees & Mont.) Nees & Mont.	+	+	P
Frullania hasskarliana Lindenb.	–	+	A
Frullania integristipula (Nees) Nees	+	+	A
**Frullania neosheana* S.Hatt.	+	–	A
Frullania nepalensis (Spreng.) Lehm. & Lindenb.	–	+	A
Frullania nodulosa (Reinw. *et al.*) Nees	+	–	P
Frullania orientalis Sande Lac.	–	+	A
Frullania ornithocephala (Reinw. *et al.*) Nees	–	+	A
Frullania riojaneirensis (Raddi) Ǻngstr.	?	?	P
Frullania sarawakensis S.Hatt.	+	–	W
Frullania serrata Gottsche	+	+	P
Frullania sinuata Sande Lac.	–	+	A
Frullania ternatensis Gottsche	+	+	A
Gottschelia schizopleura (Spruce) Grolle	–	+	Pal
Harpalejeunea filicuspis (Steph.) Mizut.	–	+	A
**Herbertus pilifer* Schiffn.	–	+	E
**Heteroscyphus argutus* (Reinw. *et al.*) Schiffn.	+	+	A
**Heteroscyphus aselliformis* (Reinw. *et al.*) Schiffn.	+	+	A
Heteroscyphus coalitus (Hook.) Schiffn.	+	+	A
Heteroscyphus splendens (Lehm. & Lindenb.) Grolle	+	+	A
**Heteroscyphus wettsteinii* (Schiffn.) Schiffn.	–	+	A
**Heteroscyphus zollingeri* (Gottsche) Schiffn.	–	+	M
Jensenia decipiens (Mitt.) Grolle	+	+	A
Jubula hutchinsiae (Hook.) Dumort.	+	+	A
Jungermannia ariadne Taylor	+	+	A
Jungermannia obliquifolia (Schiffn.) Váňa	?	?	A
Jungermannia stephanii (Schiffn.) Amakawa	–	+	A
Lejeunea anisophylla Mont.	+	–	A
Lejeunea curviloba Steph.	+	–	A
**Lejeunea flava* (Sw.) Nees	+	+	P
**Lejeunea lumbricoides* (Nees) Nees	–	+	A
**Lejeunea obscura* Mitt.	+	+	A
Lejeunea patersonii (Steph.) Steph.	+	+	A
Lejeunea reinerae Ilkiu-Borges	–	+	E
**Lejeunea sordida* (Nees) Nees	+	+	A
Lepicolea rara (Steph.) Grolle	+	+	O
**Lepidolejeunea bidentula* (Steph.) R.M.Schust.	+	+	A
**Lepidozia borneensis* Steph.	–	+	M
**Lepidozia cladorrhiza* (Reinw. *et al.*) Nees	–	+	A
**Lepidozia fernandi-muelleri* Steph.	+	+	M
Lepidozia holorhiza (Reinw. *et al.*) Lindenb.	+	–	A
**Lepidozia lacerifolia* Steph.	+	–	P
**Lepidozia trichodes* (Reinw. *et al.*) Nees	+	+	A

Table 1. *(suite)* Altitudinal and geographical distribution of the liverwort species recorded from Sulawesi. Lowland: 0-1200 m. Montane: 1200-3000 m. A: Asiatic. E: Eastern Malesian. End: Endemic. M: Malesian. W: Western Malesian. Other distribution type. P: Pantropical. Pal: Paleotropical (Asia, Africa). * species new to Sulawesi.

Species	*Altitudinal distribution* *lowland*	*montane*	*Geographical distribution*
**Lepidozia wallisiana* Steph.	–	+	A
Leptolejeunea foliicola Steph.	+	–	A
Leucolejeunea xanthocarpa (Lehm. & Lindenb.) A.Evans	+	+	P
Lophocolea ciliolata (Nees) Gottsche	–	+	A
**Lophocolea costata* (Nees) Gottsche	–	+	A
**Lophocolea muricata* (Lehm.) Nees	–	+	Pal
Lopholejeunea applanata (Reinw. *et al.*) Schiffn.	–	+	A
**Lopholejeunea eulopha* (Taylor) Schiffn.	+	+	P
Lopholejeunea herzogiana Verd.	–	+	A
Lopholejeunea nigricans (Lindenb.) Schiffn.	+	+	P
Lopholejeunea subfusca (Nees) Schiffn.	+	+	P
Lopholejeunea wiltensii Steph.	–	+	A
Lopholejeunea zollingeri (Steph.) Schiffn..	–	+	A
Marchantia acaulis Steph.	+	+	A
Marchantia berteroana Lehm. & Lindenb.	+	+	O
Marchantia carrii Bischler	+	+	E
Marchantia emarginata Reinw. *et al.*	+	+	A
Marchantia geminata Reinw. *et al.*	+	+	A
Marchantia subgeminata Steph.	+	+	M
Mastigolejeunea auriculata (Wils.) Schiffn.	+	–	P
Mastigolejeunea ligulata (Lehm. & Lindenb.) Schiffn.	+	–	A
Mastigolejeunea undulata Gradst. & Grolle	–	+	E
**Mastigolejeunea virens* (Ǻngstr.) Steph.	–	+	E
Mastigophora diclados (Brid.) Nees	–	+	A
**Metalejeunea cucullata* (Reinw. *et al.*) Grolle	+	+	P
Metzgeria furcata (L.) Dumort.	–	+	O
Metzgeria leptoneura Spruce	–	+	P
Metzgeria lindbergii Schiffn.	+	+	A
Pallavicinia lyellii (Hook.) Carruth.	–	+	O
Plagiochasma appendiculatum Lehm. & Lindenb.	–	+	O
Plagiochila abietina (Nees) Lindenb.	–	+	A
Plagiochila bantamensis (Reinw. *et al.*) Mont.	+	–	A
Plagiochila celebica Schiffn. ex Inoue	–	+	End
Plagiochila frondescens (Nees) Lindenb.	+	+	A
Plagiochila fusca Sande Lac.	–	+	A
Plagiochila gymnoclada Sande Lac.	–	+	A
Plagiochila hampeana Gottsche	–	+	A
Plagiochila javanica (Sw.) Dumort.	+	+	A
Plagiochila junghuhniana Sande Lac.	–	+	A
Plagiochila manillana Mont. & Gottsche	–	+	A
**Plagiochila mastigophoroides* Inoue	–	+	E
Plagiochila renitens (Nees) Lindenb.	–	+	A
Plagiochila salacensis Gottsche	–	+	A
Plagiochila sandei Dozy ex Sande Lac.	+	+	A
Plagiochila sciophila Nees ex Lindenb.	–	+	O

Table 1. *(suite)* Altitudinal and geographical distribution of the liverwort species recorded from Sulawesi. Lowland: 0-1200 m. Montane: 1200-3000 m. A: Asiatic. E: Eastern Malesian. End: Endemic. M: Malesian. W: Western Malesian. Other distribution type. P: Pantropical. Pal: Paleotropical (Asia, Africa). * species new to Sulawesi.

Species	*Altitudinal distribution* *lowland*	*montane*	*Geographical distribution*
Plagiochila spathulifolia Mitt.	–	+	A
Plagiochila streimannii Inoue	–	+	E
Plagiochila teysmannii Sande Lac.	–	+	A
Plagiochila trapezoidea Lindenb.	–	+	A
**Plagiochilion braunianum* (Nees) S.Hatt.	–	+	A
Plagiochilion oppositum (Reinw. *et al.*) S.Hatt.	+	+	A
Pleurozia conchaefolia (Hook. & Arn.) Austin	–	+	A
Pleurozia gigantea (Web.) Lindb.	–	+	Pal
Porella acutifolia (Lehm. & Lindenb.) Trevis.	+	+	A
**Psiloclada clandestina* Mitt.	+	+	O
Ptychanthus striatus (Lehm. & Lindenb.) Nees	+	+	A
Radula campanigera Mont.	–	+	A
Radula formosa (Meissn. ex Spreng.) Nees	+	+	A
**Radula javanica* Gottsche	+	+	A
Radula nymanii Steph.	+	+	A
**Radula retroflexa* Taylor	–	+	A
Saccogynidium rigidulum (Nees) Grolle	+	–	A
Scapania javanica Gottsche	–	+	A
Schiffneria hyalina Steph.	–	+	A
Schiffneriolejeunea cumingiana (Mont.) Gradst.	+	–	A
Schiffneriolejeunea nymannii (Steph.) Gradst.	–	+	A
Schiffneriolejeunea omphalanthoides Verd.	–	+	E
Schiffneriolejeunea tumida (Nees) Gradst. var. *haskarliana* (Gottsche) Gradst. & Terken	–	+	A
Schiffneriolejeunea tumida (Nees) Gradst. var. *tumida*	+	–	A
Schistochila acuminata Steph.	+	–	A
Schistochila aligera (Nees & Blume) J.B.Jack & Steph.	+	+	A
Schistochila blumii (Nees) Trevis.	–	+	A
**Schistochila doriae* (De Not.) Trevis.	–	+	W
Schistochila sciurea (Nees) Schiffn.	–	+	A
Spruceanthus polymorphus (Sande Lac.) Verd.	–	+	A
**Stenolejeunea apiculata* (Sande Lac.) R.M.Schust.	+	–	A
Stenolejeunea thallophora (Eifrig) R.M.Schust.	–	+	M
**Syzygiella ovalifolia* Inoue	–	+	E
**Syzygiella subintegerrima* (Reinw. *et al.*) Spruce	–	+	A
**Telaranea neesii* (Lindenb.) Fulford	–	+	A
**Telaranea major* (Herz.) J.J.Engel & G.L.S.Merr.	–	+	A
Thysananthus convolutus Lindenb.	–	+	A
Thysananthus spathulistipus (Reinw. *et al.*) Lindenb.	–	+	Pal
**Trichocolea tomentella* (Ehrh.) Dum.	–	+	O
**Tylimanthus saccatus* (Hook.) Mitt.	–	+	A
**Wettsteinia inversa* (Sande Lac.) Schiffn.	–	+	A
**Zoopsis liukiuensis* Horik.	–	+	A

Table 2. Number of species per distribution type in the liverwort flora of Sulawesi.

Distribution type	*Number of species*	*Percentage*
Eastern Malesian	13	7.5%
Endemic	2	1%
Malesian	6	3.5%
Other	9	5%
Paleotropical	7	4%
Pantropical	17	9.5%
Tropical Asiatic	121	68.5%
Western Malesian	2	1%
Total	177	

the Tropics), 2) paleotropical (tropical Asia, Africa), 3) tropical Asiatic (ranging from India eastwards to the Pacific area), 4) Malesian (ranging from Sumatra eastwards to New Guinea), 5) western Malesian (ranging from Sumatra eastwards to Sulawesi and Philippines), 6) eastern Malesian (ranging from Sulawesi eastwards to New Guinea), 7) endemic (Sulawesi only), and 8) other distribution type. Of these, the tropical Asiatic species are best represented (68.5%). Species belonging to this distribution type range from India, Indochina and Japan to Malaysia, Indonesia, the Philippines and Papua New Guinea (known as the Malesian region). They are very common in the Philippines and Borneo (Tan & Engel, 1990) but less so in New Guinea and the Solomon Islands, where Australasian taxa prevail (Piippo, 1992).

Twenty four species (13.5%) have wider distributions than the tropical Asiatic ones, reaching to Africa (paleotropical) or occurring throughout the Tropics (pantropical). According to our present knowledge, only two species are endemic to Sulawesi, viz. *Plagiochila celebica* Schiffn. ex Inoue and *Cheilolejeunea celebensis* (Steph.) Mizut. (Gradstein *et al.*, 2005).

Malesian species are the third best represented (12%). Of these, the majority (13 species) are eastern Malesian species, reaching their westernmost limit of distribution in Sulawesi. Six species occur throughout the region (6) and very few (2) are western Malesian species reaching their easternmost limit of distribution in Sulawesi. The greater number of eastern than western Malesian liverwort species in Sulawesi (13 *vs* 2) is in support of Wallace's line and indicates that this widely adopted border of Asiatic and Australasian biogeographic regions may also be relevant to wind-dispersed organisms such as liverworts. These findings are of interest since earlier biogeographical studies on Malesian mosses did not reveal much evidence for Wallace's line as an effective dispersal barrier (Tan 1984, 1998, 2002; Touw, 1992).

While Wallace's line has been an effective barrier for some liverwort species, many have crossed the line successfully, from west to east or visa versa. Schuster (1972, 1983) and Piippo (1992) recorded several liverwort genera of Gondwanalandic origin which successfully crossed the Wallace line from the east and spread into tropical Asia, such as *Psiloclada* Mitt., *Zoopsis* Hook.f. ex Gottsche *et al.*, *Saccogynidium* Grolle, *Tylimanthus* Mitt. and *Jensenia* Lindb. The western Malesian *Frullania sarawakensis* S. Hatt. and *Schistochila doriae* (De Not.) Trevis. are examples of liverwort species which successfully migrated from west to east, reaching their easternmost limit in Sulawesi. Other examples of species that crossed Wallace's line from the west are given by Schuster (1983). According to Tan (1984) and Hyvönen (1989), more moss taxa migrated from the west (Philippines, Borneo) to the east (New Guinea) than vice versa. Based on phanerogams, Lam (1945) suggested that migration to Sulawesi was primarily from the north, less so from the south and the east. Only few flowering plant species seem to have reached the island directly across the Makassar Strait.

The question may be raised which factors impeded the migration of the eastern Malesian liverwort species of Sulawesi across Wallace's line. Lam (1945) suggested that eastern Malesian species of flowering plants were unable to extend their ranges to Borneo due to unfavorable environmental conditions in the latter island, such as the very poor soils and everwet climate. However, since most eastern Malesian liverworts are epiphytes of moist montane forest habitats (see below), these ecological factors are unlikely to have played a significant role in limiting their migration across Wallace's line.

A possible impact of climatological factors on the range limits of the eastern Malesian species remains unclear yet cannot be ruled out. Brandon-Jones (1998) suggested that differences in modern primate distributions on either side of the Wallace line are caused by past climatic oscillations in the region, correlating with shrinking and expansion of rain forest. However, studies on current distributions patterns of tropical liverworts failed to reveal significant correlations with past cycles of glacial drought and forest refugia (e.g., Gradstein & Costa, 2003).

Analysis of the dispersibility of the eastern Malesian liverworts is suggestive of the impact of reproductive constraints on their geographical ranges (Longton & Schuster, 1983; Van Zanten & Gradstein, 1988) All species are dioecious and sexual reproduction and spore production are impeded by unisexuality of the populations. As argued by Heinrichs *et al.* (2006) and others, the ability to reproduce asexually increases the chances of successful long range dispersal of unisexual populations. However, asexual reproductive devices are lacking or large (*Marchantia carrii*) and generally unsuitable for dispersal across sea channels. We suggest that the paucity of dispersal means and the exclusive occurrence of unisexual spores among the eastern Malesian species have functioned as a general impediment to their dispersal and serves to explain their absence west of Wallace's line.

Analysis of the altitudinal distribution of the eastern Malesian liverwort species of Sulawesi (Fig. 2), finally, on first sight suggests that elevation may also have played a role in their absence further west. Most of them are exclusively montane taxa, occurring in moist cloud forest about 1200 m. Only few are found also at lower elevation. The absence of these montane species in Borneo may be due to the lack of mountains in the eastern part of the island, hampering the establishment of these taxa. On the other hand, the linear distance between mountains >2000 m in Sulawesi and Borneo is about 6-700 km, which does not exceed the distance to high mountains further to the east of Sulawesi. Therefore, the relevance of elevation as a determining factor is at least questionable. In contrast to montane species, almost all species occurring in lowland areas of Sulawesi are widespread ones. We propose that the larger geographical ranges of the latter taxa is explained by the greater availability in the past of lowland environments on opposite sides of Wallace's line, suitable for the establishment of the lowland species.

The altitudinal distribution data (Fig. 2) also show a clear trend of reduction of the range sizes of liverwort species towards higher elevations, with endemic and eastern and western Malesian species being largely restricted to montane environments. The marked increase of species with smaller ranges

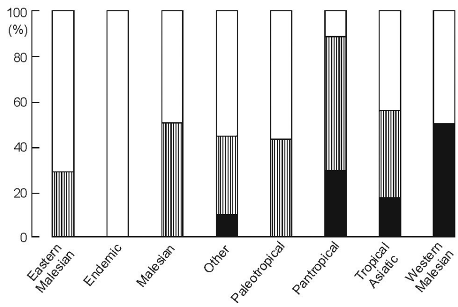

Fig. 2. Altitudinal distribution of liverwort species of Sulawesi relative to phytogeographical element. Black: lowland only (below 1200 m). White: montane only (above 1200 m). Hatched: lowland and montane.

towards higher elevations has also been observed in bryophyte species of New Guinea (Van Zanten & Pócs, 1981) and South America (Gradstein *et al.,* 1989; Churchill *et al.,* 1995; Gradstein, 1998; Nöske *et al.,* 2003), and is explained by the reduced total habitat area available in the mountains as compared with the tropical lowlands. The phenomenon has also been observed in other groups of organisms, such as birds and flowering plants (Balslev, 1988; Fjeldså *et al.,* 1999; Kessler, 2002) and shows once more that altitudinal distribution patterns of bryophytes in tropical mountains are not unlike those found in other groups of biological organisms (e.g., Frahm & Gradstein, 1991).

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