The rise and fall of Sauropus (Phyllanthaceae) : a molecular phylogenetic analysis of Sauropus and allies

Pruesapan, K.

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Historical biogeography of *Sauropus/Breynia* (Phyllanthaceae)[*]

Kanchana Pruesapan and Peter C. van Welzen

Abstract

It has been proposed to synonymise *Sauropus* with *Breynia* based on molecular and morphological phylogenetic analyses. The *Sauropus* part of an extended *Breynia* is divided over two groups, section "*Cryptogynium*" and subgenus "*Sauropus*". Our results suggest that the ancestral origin of *Breynia* sensu lato might be on the former Sibumasu block (the union of the western half of Thailand and the Malay Peninsula). Section "*Cryptogynium*" clearly has its ancestral origin in North and West Thailand corresponding with a climate with a prolonged dry period. Subgenus "*Sauropus*" most likely originated in Peninsular Thailand and the Malay Peninsula, the species prefer a more continuously wet climate.

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Introduction

The circumscription of *Sauropus* Blume (Phyllanthaceae) is as described in Pruesapan et al. (2008, see also Chapter 2) in anticipation of the acceptance of the formal change of all species names to *Breynia* (Chapter 4; Telford et al., in prep.). A brief overview of the taxonomic history of the genus is necessary to understand the exact scope of this study. Airy Shaw (1980a) united *Sauropus* with *Synostemon* F.Muell., a genus almost completely endemic to Australia (Van Welzen, 2003; Hunter, 2005; Table 5.1). Recent molecular work by Pruesapan et al. (2008) showed that *Synostemon* is a monophyletic clade, sister to a clade consisting of *Sauropus* and *Breynia* J.R.Forst. & G.Forst. The formalisation of the decision to separate *Synostemon* from *Sauropus* has to await the revision by Telford and co-authors. Then all name combinations for species once newly described under *Sauropus* will be made within *Synostemon*.

The phylogenetic analysis by Pruesapan et al. (2008) also showed that *Sauropus* and *Breynia* form a monophyletic group with *Breynia* embedded in a paraphyletic *Sauropus*. The two genera will be united under the older name *Breynia*, for which a proposal has been submitted toTaxon (Pruesapan et al., in review; Chapter 4). We will refer to the combination of both genera as *Breynia* sensu lato (s.l.); *Breynia* in the strict sense (s.s.) is the old circumscription of *Breynia*. *Breynia* s.l. will be subdivided into two monophyletic subgenera, subgen. "*Sauropus*" (new rank not yet formalised, comprises the former *Sauropus* sections *Glochidoidei*, *Schizanthi* and *Sauropus*), and subgen. *Breynia*. The latter is subdivided into section *Breynia* (equals *Breynia* s.s.) and section "*Cryptogynium*" (name also not yet formalised, comprises former *Sauropus* sections *Cryptogynium* and *Hemisauropus*, see Chapter 4). Section *Breynia* contains c. 30 species, which range from India to Australia and New Caledonia. The genus is recently revised for Thailand (Van Welzen & Esser, 2005) and is presently being revised for Malesia (Esser & Stuppy., in prep.). The main centre of diversification for *Sauropus* is Southeast Asia main land (Thailand up to Vietnam), where most endemic species are found (Table 5.1). Airy Shaw (1972) already reported 22 species for Thailand, Van Welzen (2003) 26 and recently three more species were newly described (Van Welzen & Pruesapan, in press).

Table 5.1. List of endemic and widespread species of *Sauropus* Blume and *Synostemon* F.Muell by Van Welzen (2003) and Hunter (2005) (Australian *Sauropus* indicated here as *Synostemon* species).

Malesian endemic species	Australian endemic species
Sauropus asymmetricus Welzen	Most *Synostemon* species
S. calcareous M.R.Hend.	
S. micrasterias Airy Shaw	
S. shawii Welzen	
Thai endemic species	
S. amabilis Airy Shaw	
S. amoebiflorus Airy Shaw	
S. asteranthos Airy Shaw	
S. granulosus Airy Shaw	
S. kerrii Airy Shaw	
S. poomae Welzen & Chayamarit	
S. pulchellus Airy Shaw	
Widespread species	**Widespread species**
S. androgynus (L.) Merr.	*Synostemon bacciformis* (L.) G.L.Webster
S. macranthus Hassk.	
S. rhamnoides Blume	

The study presented here will concentrate on *Sauropus* in the strict sense, without *Breynia* and without *Synostemon* (thus will deal with subgenus "*Sauropus*" and section "*Cryptogynium*"). We will still refer to the name *Sauropus* (in consistence see Chapter 4), because all new combinations for the *Sauropus* species within *Breynia* have not been published yet. Name combinations not yet published are not formally described here and will be between inverted commas.

The aim of this study is to show the historical biogeography of *Sauropus* s.s. whereby speciation and geographic diversification will be discussed.

Material and methods

Sampling

The phylogeny of *Sauropus* s.s. and allies based on molecular and qualitative morphological data in Chapter 4 (see Figs. 4.1--2) provides the historical information for the biogeographical analysis. The phylogeny does not contain all species, only 23 species of *Sauropus* are included. Added are seven species of *Breynia* s.s., six species of *Synostemon* and the outgroup *Notoleptopus decaisnei* (Benth.) Voronts. & Petra Hoffm. The species used and their distributions are shown in Table 5.2.

Table 5.2. Species used in the analysis and their distribution areas. Species names between inverted commas are new or the combinations are new, they are without author names, the latter are also absent with the species mentioned in Table 5.1. The area abbreviations refer to Fig. 5.1: A = N.E. Australia, B = New Guinea and Solomon Islands; C = Wallacea (Philippines, Sulawesi, Moluccas, Java, Lesser Sunda Islands), D = Borneo; E = Sumatra; F. = Malay Peninsula and Peninsular Thailand; G = South-eastern Thailand; H = East Thailand (Korat Plateau); I = Central Thai lowlands; J. Northern and Western Thailand, K = India to Myanmar; L = Indochina and S.E. China.

Species	Distributions	Species	Distributions
Breynia discigera Müll.Arg.	EFGIJL	*S. macranthus* Hassk.	ABCDEFJKL
B. glauca Craib	GHIJL	*S. micrasterias* Airy Shaw	D
B. mollis J.J.Sm.	B	*S. orbicularis* Craib	IJ
B. "novoguineensis"	B	*S. poomae* Welzen & Chayam.	J
B. oblongifolia (Müll.Arg.) Müll.Arg.	AB	*S. quadrangularis* (Willd.) Müll.Arg.	FGHIJKL
B. retusa (Dennst.) Alston	FGIJKL	*S.* "*repens*"	J
B. vestita Warb.	B	*S. rhamnoides* Blume	CDEFG
Sauropus amoebiflorus Airy Shaw	J	*S. similis* Craib	IJL
S. androgynus (L.) Merr.	ABCDEFGHIJKL	*S. suberosus* Airy Shaw	F
S. asteranthos Airy Shaw	HJ	*S. thyrsiflorus* Welzen	J
S. bicolor Craib	IJL	*S. villosus* (Blanco) Merr.	CEF
S. brevipes Müll.Arg.	FIJL	*Synostemon bacciformis* (L.) G.L.Webster	ABCDFGHJKL
S. "*carnosa*"	F	*S. hirtellus* F.Muell.	A
S. discocalyx Welzen	F	*S.* "*kakadu*"	A
S. garrettii Craib	IJL	*S. sphenophyllus*	B
S. granulosus Airy Shaw	I	*S.* "*spinescens*"	A
S. hirsutus Beille	HIJL	*S. trachyspermus* (F.Muell.) Airy Shaw	A
S. kerrii Airy Shaw	HJ	**outgroup**	
S. "*lithophila*"	G	*Notoleptopus decaisnei* (Benth.) Voronts. & Petra Hoffm.	ABC

Areas

The complete distribution area is subdivided into twelve areas (Fig. 5.1). The areas fall into two categories. a. Areas 'of endemism' that contain at least one endemic species (shaded areas showing in Fig. 5.1: A, B, D, F, G, I, J). b. Areas in which none of the species analysed is endemic, these are combined into continuous areas that are as large as possible based on the species distributions (white circled areas in Fig. 5.1: C, E, H, K, L).

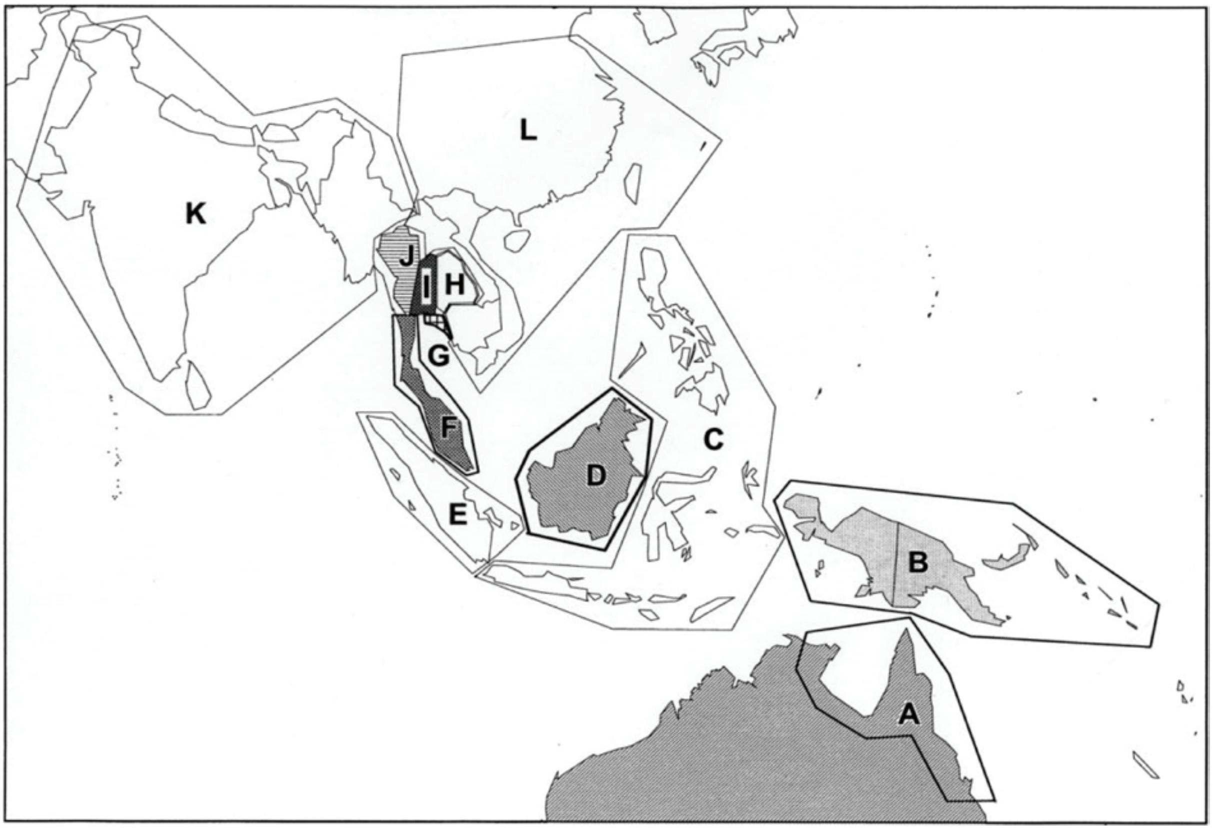

Fig. 5.1. Distribution map of *Sauropus* species: A = Australia, B = New Guinea (plus Solomon Island), C = Central Malesia, D = Borneo, E = Sumatra, F = Peninsular Thailand and Malay Peninsula, G = Southeastern Thailand, H = East Thailand, I = Central Thailand, J = North and West Thailand, K = India up to Myanmar, and L = Cambodia, China, Laos and Vietnam.

Analyses

The Statistical Dispersal-Vicariance Analysis (S-DIVA; Yu et al., 2010a, b, c) was used for the historical biogeographic analysis. This program uses DIVA (Ronquist, 1997, 2001) and provides a user-friendly interface next to the implementation of likelihood methods (Nylander et al., 2008; Harris & Xiang, 2009), which handle the uncertainty in nodal optimization. The tree data set was obtained via PAUP* v4.0b10 (Swofford, 2003); for settings and matrices see Chapter 4 (Appendix 4.1—3). S-DIVA can only analyse fully bifurcated trees, thus trees were optimized with the option zero-length branches not collapsed. The two resulting cladograms were used as Trees input and trees were condensed for the final tree. The distribution data were analysed in two ways, all twelve areas included (both categories of areas) and only the seven areas with endemic species (first category). In total four S-DIVA analyses were performed, two for each set of distribution data, one without limits on the maximum number of areas reconstructed per ancestral nodes (12 and 7 areas, respectively), and another in which the limit was set to the minimum (2 areas) to reduce ambiguities at the more basal nodes of the tree.

Results

The 2 most-parsimonious trees of 37 taxa were analysed with S-DIVA. The analysis of the first data set with 12 areas and the maximum number of areas on the internal nodes produced an area optimization that required 78 dispersal events. Constraining the program via maxareas = 2 yielded a more realistic scenario (Fig. 5.2), but the cost rose to 85 dispersal/extinction steps. The analyses of the seven areas of 'endemism' with all possible area combinations per node resulted in a cost of 47, with only two areas per node the costs was 50. The optimisations for the ancestral nodes were mostly congruent for the main clades (1—4, Fig. 5. 2), therefore only one figure will be discussed.

Basally the ingroup splits into *Synostemon* (Clade 1, Fig. 5.2) and *Breynia* s.l. (other clades). *Synostemon* is a mainly Australian group, thus optimisations on the internal nodes are all Australian (Fig. 5.1: area A) except for *S. sphenophyllus* Airy Shaw and *S. bacciformis*. On the node beneath *S. sphenophyllus* and *S. "spinescens*" the optimisation indicates dispersal to New Guinea followed by vicariance between *S. sphenophyllus* (New Guinea) and *S. "spinescens*" (Australia). Basally, *S. bacciformis* shows much dispersal (but see discussion also).

The radiation of *Breynia* s.l. showed a separation into 2 clades (Fig. 5.2: Clades 2 and 3+4). S-DIVA favors three optimal ancestral areas for *Breynia* s.l.: Peninsular Thailand and Malay Peninsula to West and North Thailand (Fig. 5.1: FJ), Peninsular Thailand and Malay Peninsula (Fig. 5.1: F) or West and North Thailand (Fig. 5.1: J). Thus, seemingly the ancestral area of *Breynia* s.l. is at least in a part of Thailand.

S-DIVA shows almost the same optimisation for the root of Clade 2 (Fig. 5.2), subgenus "*Sauropus*", but here two partly competing areas may be ancestral: either Peninsular Thailand and Malay Peninsula (Fig. 5.1: F) or Peninsular Thailand and Malay Peninsula to North and West Thailand (Fig. 5.1: FJ). In this clade there is a high degree of dispersal shown by *S. androgynus*, *S. macranthus*, and *S. rhamnoides*, and less so by *S. villosus* and *S. garrettii*.

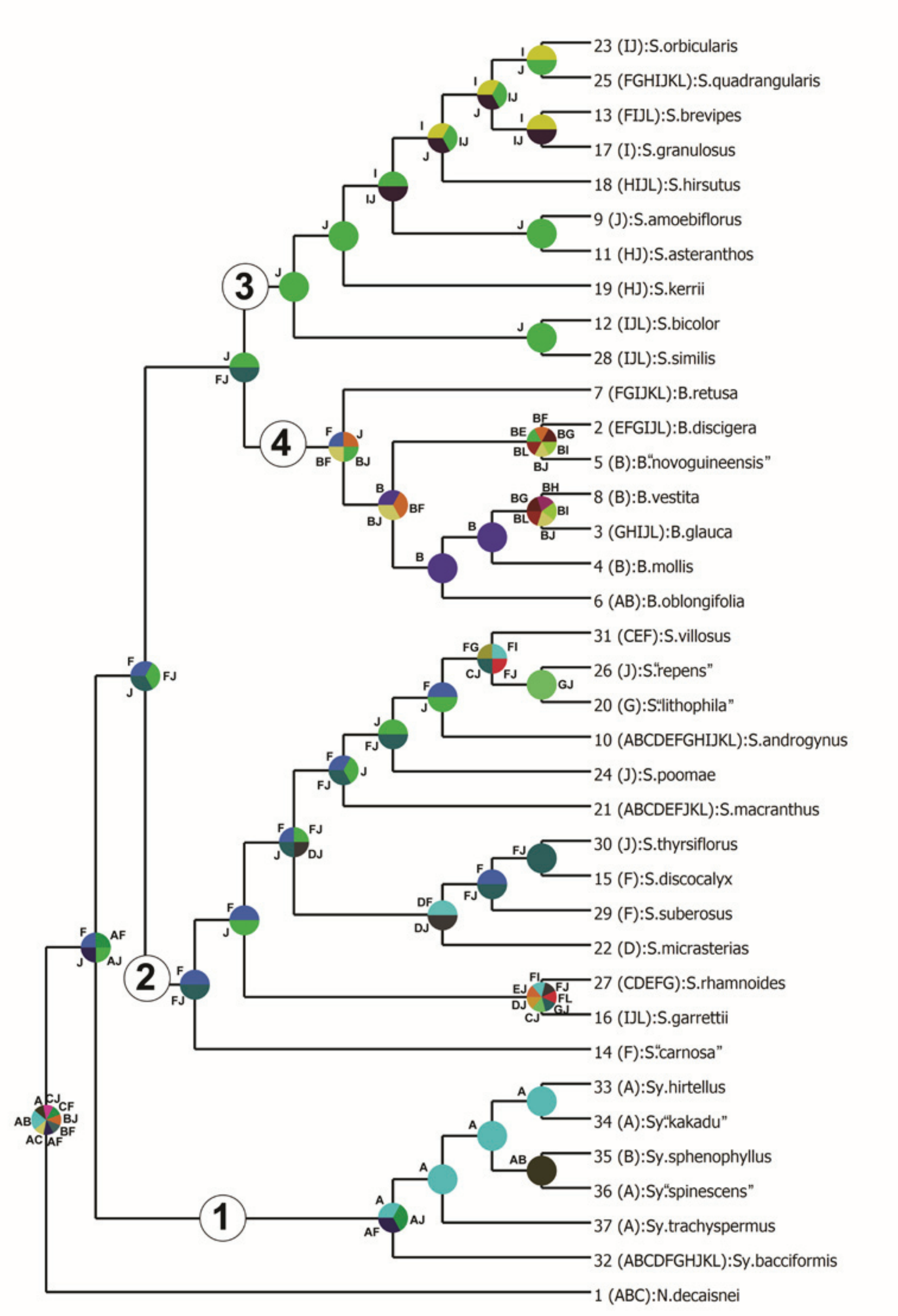

Fig. 5.2. The ancestral areas resulted from S-DIVA. Clade 1 = *Synostemon* species, Clade 2 = *Breynia* section "*Sauropus*", Clade 3 = *Breynia* section "*Cryptogynium*", and Clade 4 = *Breynia* section *Breynia*. Clades 2—4 represent *Breynia* s.l. (indicated in the tree as original names).

Clades 3 and 4 (Fig. 5.2), subgenus *Breynia*, have areas West and North Thailand (Fig. 5.1: J) or Peninsular Thailand and Malay Peninsula to North and West Thailand (Fig. 5.1: FJ) as competing areas of origin. In Clade 3 (Fig. 5.2), section "*Cryptogynium*", West and North Thailand (Fig. 5.1: J) is the area of origin. In this clade especially *S. quadrangularis* shows dispersal. Clade 4, section *Breynia*, has various, sometimes disperate options as ancestral area (e.g., New Guinea, area B, either together with Peninsular Thailand and Malay Peninsula, area F, or with West and North Thailand, area J; Fig. 5.1).

Discussion

Recently, Kodandaramaiah (2010) critisised DIVA. For DIVA he recommended to add the outgroups and to make at least two analyses, one with the maximum number of areas per node and the other with only two areas per node. In this way spurious optimisations would be prevented. We used both optimisations (see above) and we added *Notoleptopus decaisnei* as the outgroup. However, in our analysis it is not helpful for two reasons. *Notoleptopus decaisnei* is not the sister group of *Breynia* s.l. and *Synostemon*, thus its distribution may not relate or only very indirectly to that of the ancestral species of the ingroup. Furthermore, the optimisations for the basal node show combinations of areas from the western and eastern part of the Malay Archipelago, which are geologically impossible (e.g. an ancestral area consisting of Australia and a part of Thailand and Malaysia). More important is the inclusion of a part of *Synostemon* in the analysis. This is the sister group of *Breynia* s.l. and as such it can act as local outgroup for *Breynia* s.l.

Synostemon is an Australian genus with the exception of two species (*S. sphenophyllus* is endemic to New Guinea and *S. bacciformis* is widespread from the Indian Ocean, India and Southeast Asia to Australia). None of the *Sauropus* s.s. species is endemic in Australia, but two widespread species are found in Australia (*S. androgynus* and *S. macranthus*). Therefore, we only refer to Australia as one area, but Australia can easily be subdivided into various areas of endemism, which along the east coast reflect the breakup of the rainforest during the northward tectonic movement of the Australian-New Guinean plate (e.g., Van Welzen et al., 2003 and references therein). The sample of *Synostemon* is too incomplete to make an indepth historical biogeographic analysis, which will have to await the completion of the revision (Telford et al., ms.). Fig. 5.2 just shows that most species and ancestral species are Australian.

Pivotal is perhaps the basal split off of *S. bacciformis*, the only widespread taxon, which overlaps in distribution with *Sauropus* s.s. It is a mainly littoral species and quite likely the seeds can withstand sea water. This species (or its ancestor) may have rifted from Africa (where species of *Flueggea*, one of the outgroups in the cladistic analyses, also occur) to India and the Malay Archipelago via the Southwest Monsoon current. *Synostemon bacciformis* or its ancestor may have been the ancestor of *Breynia* s.l., which makes F (Peninsular Thailand and the Malay Peninsula: sea coast) and somewhat less J (West and North Thailand) a likely candidate as ancestral area, certainly not the combinations between Australia (area A) and areas F and J.

The *Breynia* s.s. clade (Clade 4 in Fig. 5.2) is also poorly represented. It is likely that this part of the cladogram will change when more taxa are included. The present data suggest dispersal from Southeast Asia to New Guinea, at least once and perhaps even twice (*B. "novoguineensis"* and the clade *B. oblongifolia-B. vestita* with a reverse movement for *B. glauca*). The species with an Asian distribution are all widespread, which indicates that they are well capable of dispersal. This can be explained by the fruit type. *Sauropus* s.s. mainly has a typical 'Euphorbiaceae' fruit, which explodes when dry, falling apart in six fruit segments and the seeds, thereby shattering the seeds around for perhaps up to ten meter. *Breynia* s.s. has a fruit coat that is more fleshy and dehisces tardily, it is attractive to birds (red) or other animals and these are likely to be the dispersers (Webster, 1956, Esser, 2003). The pollination of *Breynia* s.s. also differs from *Sauropus* s.s. *Sauropus* flowers are reported to be visited (pollination still questionable) by flower flies (*Paragus*, Syrphidae) and bees (*Halictus*, Halictidae). However, in comparison with *Sauropus* s.s., the species of *Breynia* s.s. have reduced stigmas except for *B. retusa*, which still has a style and functional stigmas and is probably the only one not pollinated by moths of the genus *Epicephala* (Gracillariidae; Kato et al., 2003; Kawakita & Kato, 2004a, b, 2009). Females of these moths actively collect pollen and pollinate the pistillate flowers (besides oviposition). The various species of *Breynia* s.s. may be limited in their distribution by their pollinator, though it is still unknown whether co-evolution resulted in a one to one relationship between pollinator and pollinated species.

In Clades 2 and 3 (Fig. 5.2), *Sauropus* s.s., the areas J and F (or combined; Fig. 5.1) generally form the optimized distributions of the ancestral species. These two areas together constitute the Sibumasu block. This block, together with the Indochina block, is made up of the two tectonic microplates that constitute Thailand. These microplates with others like South China, North China, broke off from the northern margin of Gondwanaland (probably India-N/NW Australian margin: Metcalfe, 1998). The South China, North China and Indochina block probably rifted away from Gondwanaland in Devonian times (410-360 Ma), Sibumasu in the Early Permian (300-270 Ma); the areas amalgamated with Laurasia during the Late Triassic (c. 200 Ma; Metcalfe, 1998). Later, the Southeast Asia mainland rotated 90° clockwise to its present position when India collided with Asia. It seems that the area was already formed well before most modern planes evolved and it is strange that taxa are still confined to the Sibumasu block. An alternative explanation is that the Korat plateau (part of Thailand that forms the western edge of the Indochina Block) is a sandstone plateau, which does not only have a different type of soil, but also a much drier climate and more open vegetation. Many species of *Sauropus* s.s. are restricted to wet evergreen forest (e.g., the ones with long inflorescences like *S. discocalyx*, *S. thyrsiflorus*, but also *S.* "*repens*" with axillary flowers) and they are absent in drier climates.

Halfway area F (Peninsular Thailand – Malay Peninsula) the boundary of the Malesian phytogeographic area is found (Van Steenis, 1950; Raes & Van Welzen, 2009), the Kangar (Malaysia)-Pattani (Thailand) line. Seemingly, this climatological border between wet evergreen forest in Thailand (short dry season) and everwet rain forest in Malaysia (no dry season) does not influence the distributions of *Sauropus* s.s. species. The northern boundary of F coincides with the Thai Peninsular phytogeographic region (e.g., see Smitinand, 1958, for a traditional circumscription based on collecting localities, and the Thai Biogeography Group, TBG, in prep., for a circumscription based on species distribution models). Area G (south-eastern Thailand) is interesting. It has an endemic species (Table 5.2) and as such it is considered as a separate region here. Smitinand (1958) considers this area to constitute a distinct floristic region. However, the TBG (in prep.) shows that it is part of the Peninsular floristic region (area J). In our cladogram *S.* "*repens*" (area J) and *S.* "*lithophila*" (area G) are sister species, thus confirming the relation between the floras in both areas.

Area J (West and North Thailand, Fig. 5.1) corresponds with the Northern floristic region in Thailand as defined by TBG (in prep.), which has extensions into the southwestern province of Kanchanaburi. Area I (Fig. 5.1) conforms with the Central region of Smitinand

(1958) and TBG (in prep.). This area harbours very few endemic species as it is highly cultivated and covered with rice fields.

In Clade 3 (Fig. 5.2) there seems to be a general dispersal from area J or areas IJ (Fig. 5.1) to eastern Thailand (Area H, Fig. 5.1, e.g., *S. asteranthos*, *S. kerrii*) and/or Indochina and China (Area L, Fig. 5.1, e.g., *S. bicolor*, *S. brevipes*, *S. similis*). Clade 2 hardly shows this dispersal route, only *S. garrettii* and widespread species as *S. androgynus*, *S. macranthus* and *S. rhamnoides*. The latter three species and *S. quadrangularis* in Clade 3 are the only species that also extended towards the west, to India and Sri Lanka. Probably a secondary centre of speciation originated in this area. Unfortunately, the Indian endemic species could not be included in our phylogeny, but they have representatives in Clade 2 and 3 (Pruesapan et al., in review, Chapter 3). Another secondary centre of speciation is in Vietnam/South China. These species were poorly represented in the phylogenetic analysis. Analysed were *S. spatulifolius* Beille and *S. thorelii* Beille, which both occurred higher up in Clade 2 (Pruesapan et al., 2008; Chapters 2 and 3). Unfortunately, we only had collecting localities of cultivated material of these two species.

Clade 3 (Fig. 5.2) is restricted to Southeast and South Asia main land and does not extend into Malesia (areas C—E, Fig. 5.1). Seemingly, these species all prefer a dry period during a part of the year. The three widespread species in Clade 2 (*S. androgynus*, *S. macranthus* and *S. rhamnoides*) and *S. villosus* show dispersal into Malesia. The geological history of Malesia is also complex. The western half (roughly west of the famous Wallace line, including Borneo, Sumatra, Java and part of Sulawesi) broke off as microplates from the Australian part of Gondwanaland and rifted north (Audley-Charles, 1987), a process that probably started during Jurassic times (c. 160 Ma), after which amalgamation followed in the Late Cretaceous (c. 90 Ma). The eastern part of Malesia is also formed by microplates, which again broke off from the Australian continent, this process started c. 50 Ma and amalgamation is still continuing (Audley-Charles, 1987; Hall, 2009). During the Pleistocene glacial periods the Sunda Shelf became dry land (Voris, 2000; Woodruff, 2003; Sathiamurthy & Voris, 2006) whereby a broad land connection originated between Southeast Asia mainland and the Larger Sunda Islands (Borneo, Sumatra, Java plus Bali). The central Malesian region (Area C in Fig. 5.1) always contained sea passages, but these became quite narrow, e.g., between Bali and the Lesser Sunda Islands and between Borneo and Sulawesi. At the eastern side of Malesia the

Sahul Shelf between New Guinea and Australia also became dry land, while many islands in the Moluccas and Philippines were also united. The four widespread species can thrive under very secondary conditions and species like *S. androgynus* and *S. rhamnoides* have rather fleshy fruits, which are probably dispersed by animals. The fruit flesh of *Sauropus macranthus* is reported to be edible. Its seeds/fruits may also be dispersed by birds or be eaten by other larger animals; these fruits have a very long pedicel (up to 7.5 cm; Van Welzen, 2003), stick out of the foliage and present a ready bite for dispersers. Esser's (2003) study supported the dispersal hypothesis of these species. He reported that many Malesian genera of Euphorbiacese s.l. show species with zoochory. However, he discussed that fleshy fruits have a limited distribution, the very widespread genera usually have dry explosive fruits, but he could not explain why. These three species may have dispersed independently or the ancestor of the clade may have been widespread, because an endemic species, *S. micrasterias*, is found near Kuching on Borneo. The latter is probably the only species that adapted to everwet rain forest.

Sauropus s.s. comprises quite a few habitat specialists. *Sauropus heteroblastus* Airy Shaw (probably part of Clade 3, not included in the analyses) is a rheophyte on river banks in Thailand, Cambodia and Vietnam, with only 1—3 small leaves on very short branches. A number of species are local endemics in limestone areas (*S. poomae* in Area J, *S.* "*lithophila*" in Area G, and *S. calcareous* (not included in the analyses), *S.* "*carnosa*", and *S.* "*obscurus*" (not included in the analyses) in area F) or are restricted to the dark forest floor in everwet forest (*S.* "*repens*" and *S. thyrsiflorus* in area J and *S. discocalyx* in area F).

Conclusions

The ancestral area of *Breynia* s.l. is probably the Sibumasu block, either because of an old origin or a limited ecological niche (preferring richer soils and a not too long dry climate as in eastern Thailand). Dispersal into Vietnam and South China and independently to India and Sri Lanka resulted in secondary centres of speciation in these two areas. Several species also dispersed into the Malesian area, even up to Australia, but this did not result in another secondary centre of origin (only one local endemic near Kuching on Borneo). The latter may be due to the fact that the dispersal was relatively recent during glacial periods.

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