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

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Citation
Pruesapan, K. (2010, November 23). *The rise and fall of Sauropus (Phyllanthaceae) : a molecular phylogenetic analysis of Sauropus and allies*. Retrieved from https://hdl.handle.net/1887/16170

Version:	Corrected Publisher's Version
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Downloaded from:	https://hdl.handle.net/1887/16170

Note: To cite this publication please use the final published version (if applicable).

Summary and Conclusions

Sauropus Blume (Phyllanthaceae/Euphorbiaceae sensu lato) has a variable habit, species are woody herbs, shrubs or sometimes small trees. The species are distributed from Mauritius and India to Southeast Asia, Malesia and Australia. *Sauropus* in the broad sense comprises two regional centres of speciation; the one in Southeast Asia mainland is occupied by *Sauropus* in the strict sense, while the other one is found on Australia and consists of the former genus *Synostemon* F.Muell. The morphological characters of both groups are similar to a high degree. *Sauropus* also shows a strong resemblance with *Breynia* J.R.Forst. & G.Forst., but both were never combined in previous studies, because they look quite distinct in their flowers; which are indeed always used to separate both genera. Besides problems on the generic level, there are also challenges at the infrageneric level, because the species lately described do not fit the infrageneric classification of *Sauropus*. The aim of this research project is to clarify the relationships between all species of *Sauropus* and its allies and to present a new classification.

Are Southeast Asian Sauropus and Australian Synostemon monophyletic?

Molecular phylogenetic studies so far focused on the genus *Phyllanthus* L. They showed that *Sauropus* (including *Synostemon*) and its related genera *Breynia* and *Glochidion* J.R.Forst. & G.Forst. should be united with *Phyllanthus* to create a monophyletic genus. The molecular phylogenetic studies presented here investigate the relationships among the genera *Sauropus*, *Breynia*, and *Glochidion* in relation to *Phyllanthus* and are based on sequence data of chloroplast (*accD-psaI*, *matK*, *trnG-trnS*) and nuclear (ITS and *PHYC*) DNA markers, which are analysed under maximum parsimony and Bayesian inference. The analyses show that *Sauropus* in the broad sense is composed of two distinct groups, the former Australian *Synostemon* and the Southeast Asian *Sauropus* in the strict sense. *Synostemon* is monophyletic and it is clearly proven that *Synostemon bacciformis* (L.) G.L.Webster was misplaced under *Sauropus* in the morphological phylogeny by Van Welzen (2003).

Synostemon has to be recognised again on generic level. It forms a sister clade of a clade that combines *Sauropus* in the strict sense with the monophyletic *Breynia* embedded in it. *Sauropus*/*Breynia* and *Synostemon* are sister to *Glochidion* and all are embedded within the paraphyletic *Phyllanthus*. The phylogeny of the species rich *Phyllanthus* is still far from completed and the results strongly support the distinction of monophyletic groups such as *Glochidion*, *Synostemon*, and *Sauropus/Breynia*. These genera are recognisable, while union with *Phyllanthus* (suggested by Hoffmann and co-authors in 2006) will turn the latter into an unrecognisable monolithic giant of a genus. It is a much better strategy to use the complete phylogeny of *Phyllanthus* to render it into smaller, monophyletic genera that can be characterized.

Does the molecular phylogeny corroborate the infrageneric groups within Sauropus in the strict sense?

Airy Shaw (1969) created the latest infrageneric classification. His sections were widely accepted. However, there are sections that show overlap in morphological characters and several researchers found it impossible to classify their new species in any of the sections. Airy Shaw himself also encountered problems when he unified *Synostemon* with *Sauropus*. In order to determine the evolutionairy quality of the sections, a phylogenetic analysis based on molecular markers was executed in which the taxon selection represented all sections, together with as many unplaced species as possible. The sequence data and techniques used for this study are stated in the above section. The results show, that only two infrageneric groups can be recognized within *Breynia/Sauropus* in the strict sense. The first group is the combination of the former sections *Glochidioidei* Airy Shaw, *Sauropus*, and *Schizanthi* Pax & K.Hoffm. The second group combines the former sections *Cryptogynium* Müll.Arg. and *Hemisauropus* Müll.Arg. together with the genus *Breynia*. This second clade falls apart into two groups, *Breynia* in its original circumscription and the two former *Sauropus* sections. The results also show that *Sauropus spatulifolius* Beille, originally placed in section *Cryptogynium*, has to be transferred to the first group. The unplaced species included in the analysis could easily be classified; they are *Sauropus discocalyx* Welzen, *Sauropus poomae* Welzen & Chayam., *Sauropus thyrsiflorus* Welzen, and three recently discovered and still unpulished new species *Sauropus* "*carnosa*", *Sauropus* "*lithophila*", and *Sauropus* "*repens*".

What is the phylogenetic position of Breynia and Sauropus?

The molecular phylogenetic results in this thesis necessitate nomenclatural changes, because *Breynia* is embedded within *Sauropus* in the strict sense. If a monophyletic and recognisable group is a prerequisite for a good classification, then combining both genera under *Breynia* is the best option. *Breynia* is the oldest name on the genus level, because it was already described by Forster & Forster in 1775, whereas Blume much later described *Sauropus* in 1825. The combination of both genera is *Breynia* in the broad sense. The combined genus has two clades. It is also possible to recognize these at generic level, which will then be a differently circumscribed *Sauropus* and a larger *Breynia*. However, then within both groups many species will show the same morphological characters and then the genera cannot easily be identified. Three groups can be recognized within *Breynia* in the broad sense. The basal split in the phylogeny can be used to distinguish subgenera, group one is Subgenus "*Sauropus*" (a name already proposed by Pax and Hoffmann in 1922), which combines the former *Sauropus* sections *Glochidioidei*, *Sauropus*, and *Schizanthi*. Group two is Subgenus *Breynia*, which can be divided into two sections. Section "*Cryptogynium*" will combine the former *Sauropus* sections *Cryptogynium* and *Hemisauropus* (the name *Cryptogynium* was published first); the second section is called *Breynia* and contains all *Breynia* species.

Can the clades be classified as genera and infrageneric taxa and are they recognisable morphologically?

The current genera *Breynia*, *Glochidion*, *Phyllanthus*, *Sauropus* and *Synostemon* have flowers without petals. Typical for *Phyllanthus* is the presence of discs or disc glands, which are absent in the others. *Glochidion* is recognized by its united, unsplit stigmas, *Breynia*, *Sauropus* and *Synostemon* have branched stigmas. *Breynia* and *Sauropus* were always distinguished by the differences in calyx shape, typical for *Breynia* are tubulate to campanulate calyces and disc-like ones in *Sauropus*. The results in this thesis show that *Synostemon* should be reinstated as a distinct genus. Unfortunately, *Synostemon* blurs the generic distinction between *Breynia* and *Sauropus*, because it has species with both disc shapes, tubulate ones like *Breynia* and disc-like ones as in *Sauropus*. However, the fruit and seed are useful to recognize the genera. *Synostemon* has an ovate ovary with an obtuse or lobed apex; the lobes surround a depressed area where the stigmas are inserted; the stigmas

are generally erect, not split or slightly bifid to mostly split less than halfway, the stigma branches are not coiled; the fruits are more or less ovoid, and higher than wide, the apex is usually obtuse, but in some species lobed and the seeds are usually strongly ornamented and three to four times as long as wide, the hilum is hollow and covers about half the length of the seed. *Breynia* and *Sauropus* species share a subglobose ovary, often flattened apically, and the stigmas are split halfway to completely split, the stigma branches are often horizontal and coiled or (relatively) short and non-functional; the fruits are subglobose or depressed globose, wider than long and the seeds are more or less smooth and about twice as long as wide, with the adaxial cavity of the hilum much larger than that of *Synostemon*.

The phylogenetic trees show that infrageneric groups can be distinguished in *Synostemon*. However, the genus is still under revision, thus a formal classification has to wait till the revision by Telford and co-authors is finished.

The three infrageneric groups in *Breynia* in the broad sense can be characterized with the aid of leaf and flower characters. Subgenus "*Sauropus*" has large leaves and an ovary without a marginal rim. Subgenus *Breynia* has small leaves and ovaries with or without a marginal rim. Within Subgenus *Breynia* section "*Cryptogynium*" can be recognized by the presence of a marginal rim on top of the ovary, horizontal coiled stigmas and the anthers underneath the horizontal or diagonal arms of the androphore, whereas section *Breynia* usually lacks the rim, has reduced, upright straight stigmas and the anthers are vertical along the androphore.

How did Breynia and allied genera evolve geographically?

The historical biogeography of *Breynia* and *Synostemon* was analysed with the computer program S-DIVA. The basal species in the phylogeny of *Synostemon* is the very widespread *Synostemon bacciformis* (Mauritius, throughout Asia and Malesia to Australia). This species or its ancestor may be the origin of the Asian *Breynia* in the broad sense and the further Australian (sometimes New Guinean) *Synostemon*. *Breynia* in its broad sense has its origin in the western half of Thailand and the Malay Peninsula. This area coincides with what is known geologically as the Sibumasu block, a microplate that ever broke of from the Australian continent when it was still part of Gondwana. Both former *Sauropus* groups (subgenus "*Sauropus*" and section "*Cryptogynium*") showed independent dispersal to India and Vietnam, where secondary centres of speciation are found. Subgenus "*Sauropus*" probably

has its origin in Peninsular Thailand and the Malay Peninsula, while section "*Cryptogynium*" has an ancestral origin in North and West Thailand. Section *Breynia* is still under revision and as only few of the species were included, it is impossible to make a clear statement regarding its historical biogeography. It probably also has its origin in Southeast Asia mainland, but shows one or two times dispersal towards Australia with a secondary centre of speciation in New Guinea.

Future studies

The studies presented in this thesis show a better understanding of the evolution *Breynia* in the broad sense, *Synostemon* and their related genera. This information already helped the ongoing revision of *Synostemon*. It also helped to distinguish new species in subgenus "*Sauropus*". Unfortunately, a large part of *Breynia* in the broad sense is in need of revision. The Malesian species of Section *Breynia* are almost revised, but all Indochinese, Chinese and Indian species should also be included in the revisions. Once done, then all data can be analysed and the resulting phylogeny will form the basis for a much better biogeographic understanding.