

Chapter 1: General Introduction and Aims

Systematic position of *Synostemon*

The genus *Synostemon* F.Muell. (Phyllanthaceae, Phyllantheae, Flueggeinae), when described by Ferdinand von Mueller (1858), was included in Euphorbiaceae, in subfamily Phyllanthoideae (e.g. Müller Argoviensis 1864; Pax and Hoffmann 1922, 1931; Airy Shaw 1969; Webster 1975; Webster 1994), in tribe Phyllantheae subtribe Flueggeinae. Analyses using molecular data (Wurdack and Chase 1996; Wurdack and Chase 1999) indicated the *Euphorbiaceae sensu lato* should be split, the subfamilies raised to the rank of family. The *Phyllanthoideae* also had included *Drypetes* Vahl and relatives, and these were removed to *Putranjivaceae* (Angiosperm Phylogeny Group III, 2009–, accessed January 2012).

Generic delimitation in Phyllanthaceae tribe Phyllantheae is contentious, particularly in the circumscription of the type genus, *Phyllanthus* L. (e.g. Müller Argoviensis 1864; Pax 1893; Webster 1994; Hoffmann *et al.* 2006; Kathriarachchi *et al.* 2006. see Table 1). These will be further discussed at some length below.

Synostemon at generic rank

The genus *Synostemon* F.Muell., was described by Mueller (1858) to accommodate his new species, *S. ramosissimus* F.Muell. and *S. glaucus* F.Muell., both collected on the epic traverse of tropical Australia by the Northern Australian Exploring Expedition under the command of Augustus Gregory (1858). The genus was promptly subsumed into a broad *Phyllanthus* by Müller Argoviensis (1864) at sectional rank. This sinking of *Synostemon* was followed in *Flora Australiense* by Bentham (1873) and most subsequent state and regional Flora treatments (Bailey 1900; Black 1948; Willis 1972; Stanley and Ross 1983). Eichler (1965), for his *Supplement to Black's 'Flora of South Australia'* placed *Synostemon* as a synonym of *Glochidion* J.Forst & G.R.Forst., there making two new combinations and validating a name for three species then thought to occur in South Australia, *G. ramosissimus* (F.Muell.) H.Eichler, *G. trachyspermum* (F.Muell.) H.Eichler and *G. thesioides* H.Eichler, a nomen novum for *Phyllanthus thesioides* Benth. *nom. illeg.* (1876).

Synostemon bacciformis (L.) G.L. Webster has a more complicated nomenclatural history, as presented by Webster (1960). The species had been named *Phyllanthus bacciformis* L. (Linnaeus 1774), but another Linnaean name *Agyneia impubes* L. had been misapplied by Ventanat (1800) to a collection of the species from Mauritius. Müller Argoviensis (1866) had realised *Agyneia* L. was congeneric with *Glochidion* J.R. Forst & G. Forst. but maintained the genus in Ventanat's (1801) sense. Bentham in Bentham and Hooker (1880) pointed out that *Agyneia* sensu Ventanat (1801) non L. (1774) scarcely differed from *Phyllanthus* sect. *Synostemon* (F. Muell.) Müll. Arg., where he had previously placed Australian species (Bentham 1873). Webster (1960) provided a combination for *Phyllanthus bacciformis* L. under *Synostemon*, regarding the genus as distinct.

Synostemon was resurrected to generic rank by Airy Shaw (1978), and in that paper a new species was named from New Guinea, *S. sphenophyllus* Airy Shaw, and a combination for one Australian species, *S. albiflorus* (Müll. Arg.) Airy Shaw, was published. Earlier, *S. ramosissimus* had been nominated as lectotype of the genus (Wheeler 1975).

Two years after reinstating *Synostemon* to generic rank, Airy Shaw (1980b: 205) expressed doubts on the standing of the genus:

“... *Sauropus*, from which *Synostemon* is not distinct and with which it will eventually have to be merged. I refrain from taking this step until a complete revision of the Australian species has been undertaken, with reference to the remainder of the genus in continental Asia and Malesia.”

That same year, Airy Shaw (1980c) appears to have lost his restraint and subsumed *Synostemon* into *Sauropus*. In that publication he named two new species, four new varieties and provided 18 new combinations. He must have thought this constituted enough revisionary work on *Synostemon* to allow the two genera to be regarded as congeneric. However, the following year Airy Shaw (1981) provided new combinations for *Synostemon* species occurring within the area covered by the *Flora of Central Australia*; unfortunately these were invalid as the basionyms cited lacked place of publication. Although this appears on chronology to be a reversal of Airy Shaw's generic concepts, I suspect the delay in publication of *Flora of Central Australia* probably provides a better explanation.

This taxonomic history is summarised in Table 1.1. *Synostemon bacciformis* (L.) Airy Shaw, widespread around the Indian Ocean and until this project not recorded for Australia, is not included because that species had generally been included in *Agyneia* L. nom. rej., an heterotypic synonym of *Glochidion* nom. cons. (Govaerts *et al.* 2000) as *Agyneia bacciformis* (L.) A.Juss. (1824).

Table 1.1. Taxonomic history (selection) of *Synostemon* and related genera. Note that *Sauropus* was unknown from Australia at the time of Bentham's writing 'Flora Australiensis'.

Author/ genus	J. Müller Argoviensis (1866)	Bentham (1873)	Pax & Hoffmann (1922)	Airy Shaw (1978)	Airy Shaw (1980c)	Webster (1994)	Hoffmann <i>et al.</i> (2006)
<i>Breynia</i>	<i>Breynia</i>	<i>Breynia</i>	<i>Breynia</i>	<i>Breynia</i>	<i>Breynia</i>	<i>Breynia</i>	<i>Phyllanthus</i>
<i>Glochidion</i>	<i>Phyllanthus</i>	<i>Phyllanthus</i>	<i>Glochidion</i>	<i>Glochidion</i>	<i>Glochidion</i>	<i>Glochidion</i>	<i>Phyllanthus</i>
<i>Sauropus</i>	<i>Sauropus</i>	-	<i>Sauropus</i>	<i>Sauropus</i>	<i>Sauropus</i>	<i>Sauropus</i>	<i>Phyllanthus</i>
<i>Synostemon</i>	<i>Phyllanthus</i>	<i>Phyllanthus</i>	<i>Sauropus</i>	<i>Synostemon</i>	<i>Sauropus</i>	<i>Sauropus</i>	<i>Phyllanthus</i>

Recent revisionary studies in *Sauropus/Synostemon*

Revisionary studies into Australian *Sauropus* were carried out by Hunter and Bruhl (1997a, 1997b, 1997c) towards a preliminary treatment of the genus for the *Flora of Australia* project. Eleven species and one subspecies were named as new, together with one new combination. Their approach was intuitive based on morphological species concepts; no phenetic analyses were run. Generally a broad species concept was adopted; this is discussed further below in species concepts.

In his studies of Asian *Sauropus*, van Welzen (2003) presented a cladistic analysis based on morphological and palynological datasets. *Synostemon* was maintained within *Sauropus* but van Welzen suggested there were grounds for again segregating *Synostemon* from *Sauropus*.

Sauropus/Synostemon subsumed?

A series of phylogenetic analyses of *Phyllanthaceae* and tribe *Phyllantheae* (Wurdack *et al.* 2004; Kathriarachchi *et al.* 2005; Kathriarachchi *et al.* 2006) culminated in a revised

classification of the family (Hoffmann *et al.* 2006). This presented a broadened *Phyllanthus* as the preferred generic option subsuming *Breynia*, *Glochidion*, *Sauropus* and *Synostemon* into a “giant” genus of some 1300 species. The genera now recognised, and certain clades they indicated, would be treated at the rank of subgenera. The authors stated (Kathriarachchi *et al.* 2006, p. 645):

“As circumscribed here, *Phyllanthus* includes the members of *Phyllanthus* sens. Webster (1994) and Radcliffe-Smith (2001), plus *Breynia*, *Glochidion*, *Sauropus* and *Reverchonia*... These changes increase the number of *Phyllanthus* species from 833 to 1269 according to the species counts in Govaerts *et al.* (2000). Broad nomenclatural adjustments will be necessary to obtain a phylogenetic classification for this large group, but we feel that this solution is preferable to maintaining a paraphyletic construct or recognizing more than 20 clades of *Phyllanthus s.l.* at the generic rank.”

This proposal for a giant *Phyllanthus* was iterated by Hoffmann *et al.* (2006, p. 45):

“Rather than recognising over 20 (Kathriarachchi *et al.* 2006) *Phyllanthus* clades that could be distinguished only by specialists at generic rank, we favour enlargement of *Phyllanthus* to include *Breynia*, *Glochidion*, *Reverchonia* and *Sauropus*. We acknowledge that a number of new combinations are necessary to translate these findings into practice at the species level and that some upset of botanical nomenclature especially in South East Asian botany is unavoidable.”

A new classification of Phyllanthaceae was more-or-less formalised (Hoffmann *et al.* 2006) but new combinations for *Sauropus*, *Breynia* and *Glochidion* under *Phyllanthus* were not provided. Sampling intensity was very low in the analysis on which this classification was based; only a single Australian endemic of *Sauropus/Synostemon*, *Sauropus elachophyllus* (F.Muell. ex Benth.) Airy Shaw, was sampled.

Studies on the status of *Sauropus*

Research by Kanchana Pruesapan and Professor van Welzen at Leiden University was primarily directed towards the problem genus *Sauropus*, with a large South East Asian component and also including Australian *Synostemon*. Professor Bruhl and I were invited to collaborate, providing data and leaf samples for the study. Van Welzen’s (2003) suggestion that *Synostemon* should probably be segregated again from *Sauropus* was corroborated by phylogenetic analysis using nuclear ITS and plastid *matK* sequence data

(Pruesapan *et al.* 2008). *Synostemon* was retrieved as monophyletic, sister to *Breynia* J.R.Forst. & G.Forst., in which *Sauropus sensu stricto* was embedded (Appendix 1). *Sauropus elachophyllus*, the only Australian species in the genus sampled in the analysis of Kathriarchichi *et al.* (2006) was included in the *Synostemon* clade with both of Mueller's species of *Synostemon* including the lectotype of the genus, *S. ramosissimus* (Wheeler 1975), corroborating van Welzen's (2003) suggestion that the genus should be reinstated.

Webster and Carpenter (2008, p. 606) presented the alternatives:

“There are two almost equally distasteful solutions to these problems in classification (1) a circumscription more conservative than that of Müller Argoviensis (1866), in which *Glochidion*, *Breynia* and *Sauropus* are incorporated into *Phyllanthus* as subgenera; or (2) the splitter's solution of maintaining these three genera but breaking up *Phyllanthus* into a number of smaller genera.”

Our alternative hypothesis is that with denser sampling, paraphyletic *Phyllanthus* can be resolved into monophyletic diagnosable groups that can be recognised as genera, many with current names at generic rank such as *Synostemon*, *Breynia* and *Glochidion*. To that end, option 2, with *Phyllanthus* dismembered into some 20 genera, is that pursued in these and our on-going studies.

Species concepts in *Synostemon/Sauropus*

The most recent taxonomic treatments of *Synostemon* by Airy Shaw (1980a, 1980b, 1980c under *Sauropus*) and Hunter and Bruhl (1977a; 1997b under *Sauropus*) have implicitly employed a morphological or phenetic species concept, i.e. species defined by suites of co-varying attributes (Stuessy 1990). No independent analyses were undertaken to test species' boundaries.

Within his circumscription of *Sauropus trachyspermus* (F.Muell.) Airy Shaw, Airy Shaw (1980c) included *Phyllanthus rhytidospermus* Müll.Arg. Hunter and Bruhl (1997a) went further with their “lumping”, also subsuming *Sauropus hubbardii* Airy Shaw, *S. sp. A sensu* Flora of the Kimberley Region (Wheeler 1992) as well as *Phyllanthus rhytidospermus* into *S. trachyspermus*. Preliminary morphological examination suggests a

Sauropus trachyspermus sensu Hunter and Bruhl (1997a) is a heterogeneous species aggregate.

The approach in this study is initially a morphological species concept (Stuessy 1990) in the intuitive recognition of putative new taxa. In line with de Queiroz (2007) additional lines of evidence will be sought to assess species' limits and status within a phylogenetic context. Species limits will be tested using graphical and statistical analysis of morphological data sets (Sneath and Sokal 1973).

Intraspecific ranks in *Synostemon/Sauropus*

In Australian *Sauropus*, Airy Shaw (1980c) had named two varieties of *Sauropus elachophyllus* (F.Muell. ex Benth.) Airy Shaw, *S. elachophyllus* var. *glaber* Airy Shaw and *S. elachophyllus* var. *latior* Airy Shaw. Hunter and Bruhl (1997a) named a new subspecies, *Sauropus stenocladus* subsp. *pinifolius* J.T.Hunter & J.J.Bruhl. Within a genus, the criteria for the grouping of populations into a named variety or subspecies should be equivalent but formalisation of infraspecific variation by the application of varietal or subspecific rank remains problematic in *Synostemon/Sauropus*. The international code of nomenclature for algae, fungi and plants (McNeill *et al.* 2012) allows both ranks but provides no guide to their application. Stuessy *et al.* (2009) recommended that for nomenclatural stability that ranks remain unchanged unless there is compelling evidence. In this regard, standardisation of the application of rank across a genus must present a strong case.

In this study, we apply the rank of subspecies, following the practice commonly applied in Australia (Walsh 2015) requiring groupings of populations with distinct regional facies (Stace 1989) and the presence of intergrading forms (Stebbins 1950) which we interpret as the 'grey zone' of speciation of de Queiroz (2007). Varietal rank could have been used if distributions were sympatric and morphological differences were more trivial. If a cline is demonstrated, morphologically similar populations showing a geographical grouping may be formally recognised. In Australia, examples where the extremes of a cline are named at the rank of subspecies are *Daviesia mimosoides* (Crisp 1991) and *Banksia integrifolia* (Thiele and Ladiges 1994).

Aims of project

Overall goals of the project were to test more soundly the generic boundaries of *Sauropus*, *Synostemon* and *Breynia*, and to test delimitation of species in the *Synostemon* clade.

The specific aims (addressed in each of the subsequent data chapters) are:

1. to test more soundly, using molecular data, the generic boundaries of *Sauropus*, *Synostemon* and *Breynia* (Chapter 2)
2. to clarify relationships using combined molecular and morphological data and to provide a revised generic circumscription and infrageneric classification in *Breynia* and to provide the required nomenclatural changes (Chapter 3)
3. to validate the name of a recently discovered, narrowly endemic and potentially threatened new species of *Synostemon* (Chapter 4)
4. to test relationships of the ‘Queensland clade’ using an expanded molecular dataset including all described and putative new species in *Synostemon* (Chapter 5)
5. to test, in both *Synostemon ramosissimus* and *S. rigens*, if morphological differences constitute a longitudinal cline and if formal recognition of new taxa is warranted (Chapter 6)
6. to clarify species limits of *Synostemon trachyspermus* and putative related species using denser sampling and molecular data (Chapter 7)
7. to clarify relationships and species limits in the ‘Top End clade’ and to test the status of *Sauropus decrescentifolius* and infraspecific taxa of *S. elachophyllus*. (Chapter 8)
8. to present a synopsis of the genus including data on publication of protologues, typification and distribution of all species, and identification keys (Chapter 9).

Relevance of project

Biodiversity

The project aimed to increase our knowledge of biodiversity, particularly of the Australian members of *Synostemon/Sauropus* that preliminary morphological assessment suggests include putative new species, as well as species submerged in species complexes or heterogeneous species aggregates.

Conservation

Several species of Australian *Sauropus/Synostemon* are narrowly endemic, particularly the species of the Arnhem Land escarpment (Hunter and Bruhl 1997a). Assessment of the distributional extent of species and population size estimates for conservation purposes has been carried out to a limited extent (e.g. Western Australian Herbarium 1998–; Cowie 2005). Confusion over the application of some names has considerably hampered conservation and management. Conservation coding will follow the guidelines of IUCN (2014).

Plant products

Phyllanthaceae are well known as a source of pharmaceuticals (Unander *et al.* 1995; Calixto *et al.* 1998). The single record of ethnobotanical use of *Synostemon* in Australia is of *S. glaucus*, used by the Kunwinjki people of Arnhem Land as an antiseptic (Smith 1991). Although unrecorded for ethnomedicinal use in Australia, the widespread *S. bacciformis* yields the triterpenoid saponin glochidone (Rao *et al.* 2004 as *Agyneia bacciformis*), an anti-inflammatory. This species is used in southern India against indigestion (Muralidharan and Narasimhan 2012). Species delimitation and distributional data will facilitate future bioprospecting in Australian Phyllanthaceae.

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**Chapter 2: Phylogeny and proposed circumscription of *Breynia*,
Sauropus and *Synostemon* (Phyllanthaceae),
based on chloroplast and nuclear DNA sequences**

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[PDF of published paper follows]

**Chapter 3: Phylogenetic reconstruction prompts taxonomic changes in
Sauropus, *Synostemon* and *Breynia* (Phyllanthaceae, Phyllanthaceae)**

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and Jeremy J. Bruhl

[PDF of published paper follows]

**Chapter 4: *Synostemon hamersleyensis* (Phyllanthaceae,
Phyllanthaceae), a new species endemic to the Pilbara, Western
Australia**

Ian R.H. Telford and Jeremy Naaykens

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**Chapter 5: Molecular data consistently retrieve a ‘Queensland clade’ of
Synostemon (Phyllanthaceae, Phyllanthaeae)
with distinctive floral morphology**

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Chapter 6: Clinal variation across Australia in two eremaeen species of *Synostemon* (Phyllanthaceae, Phyllanthaceae) demonstrated using morphological and molecular data

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Chapter 7: Morphological and molecular data show *Synostemon trachyspermus* (Phyllanthaceae, Phyllanthaeae) to be a heterogeneous species assemblage

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Chapter 8: Morphological and molecular data corroborate an enlarged crown radiation in *Synostemon* (Phyllanthaceae, Phyllanthaceae) in tropical Australia concealed by heteromorphic species concepts

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**Chapter 9: Synopsis of *Synostemon* (*Phyllanthaceae*, *Phyllantheae*)
including the description of two new species, four new combinations and
emended descriptions**

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Chapter 10: General Conclusions

Introduction

The focus of this study was the elucidation of the biodiversity of the *Synostemon* clade. The clade was first retrieved in our initial analysis using molecular data of *Sauropus* and related genera (Pruesapan et al. 2008, Appendix 1). Firstly, generic boundaries in *Sauropus* Blume, *Synostemon* F.Muell. and *Breynia* J.R.Forst. & G.Forst. had to be defined. Analysis with denser sampling corroborated that *Sauropus* should be dismantled with the mainly Asian and Malesian species transferred to *Breynia* and the mainly Australian species to *Synostemon*. From there, subclades consistently retrieved in the *Synostemon* clade were investigated. In general, these studies have yielded a broader knowledge of the systematics of Phyllanthaceae tribe Phyllanthaeae, particularly in the biodiversity of *Synostemon* and its distributional patterns and drawn attention to the conservation status of taxa.

Summary of findings against aims of the project

Circumscription of genera

All molecular analyses retrieved *Synostemon* as monophyletic, sister to a *Breynia/Sauropus* clade, with synapomorphies allowing recognition (Pruesapan *et al.* 2012; Chapter 2). For this sister clade, the name *Breynia* has priority. Within the *Breynia* clade are two subclades where subgeneric rank is applicable; that including the type (*Breynia disticha* J.R.Forst. & G.Forst.) assumes the autonym, *Breynia* subgen. *Breynia*, while the other with the type of *Sauropus* (*S. albicans* Blume = *S. androgynus* (L.) Merr.) becomes *Breynia* subgen. *Sauropus* (Van Welzen *et al.* 2014; Chapter 3).

Our working alternative approach is that with denser sampling, paraphyletic *Phyllanthus* can be resolved into monophyletic, diagnosable groups, the major clades recognised at generic rank. Many of these diagnosable groups have current names at that rank (*Synostemon*, *Breynia* and *Glochidion*) or names available at generic rank (*Cicca* L., *Embllica* Gaertn., *Eriococcus* Hassk., *Kirganelia* Juss., *Nymanina* K.Schum., *Phyllanthodendron* Hemsley and *Urinaria* Medic.). This approach is as justifiable as the alternative and our explanations and future directions are presented below.

Delimitation of species

In the series of papers presented—following intuitive morphological recognition of new taxa—species boundaries were tested, including those of species that had been submerged within complexes or heterogeneous aggregates. Morphometric analyses were used for the *Synostemon ramosissimus* and *S. rigens* groups (Chapter 6). Cladistic analyses using nrITS sequence data were used to investigate relationships in the major subclades of *Synostemon*: the ‘Queensland clade’ (Chapter 5); the ‘Trachyspermus clade’ (Chapter 7) and the ‘Top End clade’ (Chapter 8).

Together this has made a considerable advance in our knowledge of the biodiversity of *Synostemon* with 40 species recognised here, compared with 27 following the last revisionary study (Hunter and Bruhl 1997a, 1997b, 1997c as *Sauropus*). Ten new species have been named: *Synostemon angustus* I.Telford & J.J.Bruhl, *S. cowiei* I.Telford & J.J.Bruhl, *S. decumbens* I.Telford & J.J.Bruhl, *S. hamersleyensis* I.Telford & Naaykens, *S. inaequisepalus* I.Telford & J.J.Bruhl, *S. judithae* I.Telford & J.J.Bruhl, *S. kakadu* I.Telford & J.J.Bruhl, *S. nitmiluk* I.Telford & J.J.Bruhl, *S. spinosus* I.Telford & J.J.Bruhl and *S. umbrosus* I.Telford & J.J.Bruhl; three species have been reinstated from synonymy: *S. hubbardii* (Airy Shaw) I.Telford & Pruesapan, *S. lissocarpus* (S.Moore) I.Telford & Pruesapan and *S. rhytidospemus* (Müll.Arg.) I.Telford & Pruesapan and infraspecific variation formalised in *S. elachophyllus* (F.Muell. ex Benth.) I.Telford & Pruesapan, *S. ramosissimus* F.Muell. and *S. rigens* F.Muell. This updated nomenclature, together with distributional data and a key to species, summed up in the conspectus of the genus (Chapter 9), will facilitate its application, particularly in conservation planning.

Relevance of project*Conservation*

With many species of *Synostemon* of restricted distribution and several known from few populations, these studies will draw attention to those species warranting conservation initiatives. Currently no species are listed under the Australian Federal Environmental Protection and Conservation Act. The single, previously listed species, *S. filicinus* (J.T.Hunter & J.J.Bruhl) I.Telford & Pruesapan (Vulnerable, as *Sauropus filicinus* J.T.Hunter & J.J.Bruhl), was removed from the list of Threatened Flora in 2011 following population surveys (Woinarski *et al.* 2007).

New and revised species of conservation concern are *Synostemon anemoniflorus* (J.T.Hunter & J.J.Bruhl) I.Telford & Pruesapan, *S. angustus* I.Telford & J.J.Bruhl, *S. gracilis* (J.T.Hunter & J.J.Bruhl) I.Telford & Pruesapan, *S. spinosus* I.Telford & J.J.Bruhl and *S. umbrosus* I.Telford & J.J.Bruhl. *Synostemon spinosus* is of particular concern, being known from two populations near Blackwater in central Queensland, one adjacent to open-cut coal mining.

Pharmaceutical products

Phyllanthaceae are well known as a source of pharmaceuticals (Unander *et al.* 1995 and references therein; Calixto *et al.* 1998). *Synostemon glaucus* is the only species recorded as having ethnomedicinal use (Smith 1991). In Arnhem Land, the rootstocks are pounded in water to produce an antiseptic wash. *Synostemon bacciformis* yields the triterpenoid saponin glochidone (Rao *et al.* 2004 as *Agyneia bacciformis*), an anti-inflammatory. Although ethnomedicinal use of this species is not known in Australia, in southern India this species is used against indigestion (Muralidharan and Narasimhan 2012).

Known species limits and distributional patterns are an advantage in bioprospecting in a species rich genus such as *Synostemon* of unknown potential.

Future directions

Infrageneric classification in Synostemon

Additional genetic markers will be incorporated into the phylogenetic analysis of *Synostemon* in an attempt to resolve the basal polytomy presently retrieved when nrITS sequence data alone are used. Sequences from an additional nuclear region, PHYC, and two cpDNA regions, *accD-psaI* and *trnS-trnG* for all species will be incorporated into the dataset.

A fully resolved phylogeny will provide a sound basis for a stable infrageneric classification. Already, strongly supported clades with morphological synapomorphies such as the ‘Top End clade’ and the ‘Trachyspermus clade’ indicate usefulness of a division at sectional rank.

Revised biogeography of Synostemon

Another spin-off of a better resolved phylogeny would be biogeographical analyses such as divergence time analysis using BEAST and dispersal-vicariance analysis using DIVA and the complimentary S-DIVA.

Hypotheses on the historical biogeography of Australian *Synostemon* (as *Sauropus*) were put forward in Hunter (2005) but these were based on an outdated classification and apparent surmises of relationships not implied from phylogenetic analysis. Our phylogenetic analyses using molecular data indicate that *Synostemon* and *Breynia* share a common ancestor (Pruesapan *et al.* 2008, 2012; Van Welzen *et al.* 2015) and the dated phylogeny presented in Van Welzen *et al.* (2015) estimates the age of their ancestral crown node at 24.5 (34.3–15.2) Ma. The ancestral area was optimised in northern and western Thailand. This suggests that the ancestor of the widespread Indian and western Pacific coastal *Synostemon bacciformis* was important in dispersal to Australia. With the considerable radiation of *Synostemon* in Australia, the cause of speciation, for example aridification as a vicariant event, could be questioned.

Maintenance of Synostemon at generic rank

Our collaboration in continuing research in Phyllanthaceae is towards our alternative hypothesis with the maintenance of *Synostemon*, *Breynia* and *Glochidion* at generic rank. Revised classifications recently published (Nickrent *et al.* 2010; Linder and Hardy 2010) put forward criteria that should be followed in the application of changes in classification: (1) monophyly, (2) nomenclatural stability, (3) informativeness and (4) recognisability. Backlund and Bremer (1998) considered that preservation of groups that are well established in the literature and optimal genus size should also be considered.

We propose to circumscribe smaller monophyletic groups (criterion 1) at generic rank, largely the subgenera proposed by Kathriarachchi *et al.* (2006) and Hoffmann *et al.* (2006). Hoffmann's (2006: 46) claim that "... some upset of botanical nomenclature especially in South East Asian botany is unavoidable ..." is an understatement. Retaining *Glochidion*, *Breynia* and *Synostemon* would cause less disruption to botanical nomenclature (criterion 2) in southern Asia, Malesia, Australia and the Pacific islands. *Cicca*, *Emblica*, *Phyllanthodendron*, *Glochidion* and *Breynia* are still widely in use as generic names. The proposed subgenera at generic rank would be more informative (criterion 3) in their

predictability and because of their biogeographic and ecological associations. Many of these clades proposed as subgenera have readily recognisable macro-morphological synapomorphies (criterion 4). Of these proposed segregate (or reinstated) genera, the largest number occur in the region encompassed by southern Asia, Malesia, Australia and the Pacific islands, e.g. *Breynia*, *Cicca*, *Emblica*, *Glochidion*, *Gomphidium*, *Macraea*, *Nymanina*, *Phyllanthodendron*, *Synostemon*, and these are certainly not taxa that “could be distinguished only by specialists at generic rank” (Hoffmann 2006: 46).

Wagner and Lorence (2011) transferred Pacific oceanic island species of *Glochidion* to *Phyllanthus* on advice from Wurdack (W.L. Wagner, pers. comm., 2011) that the subsuming of those genera nested in *Phyllanthus* in the Katriarchchi *et al.* (2006) analysis, such as *Glochidion*, into an enlarged *Phyllanthus* was a “fait accompli”. However, the recommendation of a giant *Phyllanthus* is not finding overall acceptance. In ‘Flora of China’ (Li and Gilbert 2008: 190) retain “easily recognizable [segregate genera]...for convenience”, such as *Phyllanthodendron* and *Glochidion*. Chakrabarty and Balakrishnan (2009) published new combinations for *Breynia*, *Glochidion* and *Sauropus* under *Phyllanthus*; in less than three years, probably in response to Pruesapan *et al.* (2012), they reverted to *Breynia* at generic rank (Chakrabarty and Balakrishnan 2012).

We agree that a paraphyletic construct for *Phyllanthus* s. lat. for an assemblage of clades with nested clades maintained as other genera is untenable, but an unrecognisable and unmanageable “giant” *Phyllanthus*, with recognition of species groups transferred to subgeneric rank, is unworkable. Our studies, in addition to morphological and palynological data (Webster and Carpenter 2002; Sagun and van der Ham 2003; Webster and Carpenter 2008), have persuaded us the recognition of a giant *Phyllanthus* is premature. We are working towards a strongly supported, densely sampled phylogeny of Phyllantheae, and this is essential before a revised classification of the tribe is presented.

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Appendix 1: Delimitation of *Sauropus* (Phyllanthaceae) based on plastid *matK* and nuclear ribosomal ITS DNA sequence data. *Annals of Botany* 102, 1007–1018

Kanchana Pruesapan, Ian R. H. Telford, Jeremy J. Bruhl, Stephan G. A. Draisma,
Peter C. van Welzen (2008).

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Appendix 2: Historical Biogeography of *Breynia* (Phyllanthaceae): What caused speciation? (accepted by *Journal of Biogeography*, Mar. 2015)

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