



Recircumscription of *Polyscias* (Araliaceae) to include six related genera, with a new infrageneric classification and a synopsis of species

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With 4 tables

Abstract

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The genus *Polyscias*, described more than two centuries ago, has gone through several cycles of expansion and contraction in its circumscription, settling in the last forty years on a broad consensus that includes nearly all Paleotropical Araliaceae with pinnately compound leaves, an articulated pedicel and a gynoeceum with two to many carpels. Recent phylogenetic studies have shown that *Polyscias* is closely related to six other long-recognized genera (*Arthrophyllum*, *Cuphocarpus*, *Gastonia*, *Munroidendron*, *Reynoldsia* and *Tetraplasandra*). Because these other genera are all nested within a broad *Polyscias* sensu lato clade, substantial generic-level re-alignment is needed to avoid recognition of para- and polyphyletic groups. An earlier suggestion that each clade be recognized as a separate genus has proven impractical in light of an expanded phylogenetic analysis, which identified more than a dozen geographically coherent clades, some of which encompass significant morphological diversity but lack obvious defining synapomorphies. A more pragmatic approach is adopted here, in which all members of *Polyscias* sensu lato are treated as a single genus. Within this broadly defined genus, each clade is recognized as a subgenus, thereby retaining valuable information on evolutionary relationships while minimizing nomenclatural changes. A revised system of classification is proposed in which 159 currently recognized species are placed in *Polyscias* and assigned to 10 subgenera (seven species are left unassigned), necessitating 65 new combinations (nine at the rank of subgenus, 54 for species, and two for subspecies) and five new names.

Keywords: Araliaceae, *Polyscias*, infrageneric classification, subgenus, *Arthrophyllum*, *Cuphocarpus*, *Gastonia*, *Munroidendron*, *Reynoldsia*, *Tetraplasandra*.

Introduction

The genus *Polyscias* was described by Forster & Forster (1775) based on a single collection they made in the South Pacific while serving on board Captain James Cook's second voyage. The Forsters distinguished their new genus from other Araliaceae rec-

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ognized at the time (primarily the Linnaean genera *Aralia* L., *Hedera* L. and *Panax* L.) by several characters including the presence of 6 to 8 petals and as many stamens, 3 or 4 styles and a globose fleshy fruit containing 4 seeds. Over the next 90 years no additional species had been assigned to *Polyscias*, although during the same period over 60 taxa were described, mostly in the genus *Panax*, that are currently included in *Polyscias* by Frodin & Govaerts (2003), either as accepted species or synonyms. Between 1865 and 1894, the name *Polyscias* was applied to species just eight times, primarily by Baker (1877) for taxa occurring in the Mascarene Islands. Harms (1894-97) was the first to adopt a broader circumscription of *Polyscias*, recognizing a total of 41 species, including 33 for taxa he transferred from other genera (mostly from *Panax*). Only a few authors, however, adopted his approach in the following decades.

A subsequent shift toward a narrower definition of *Polyscias* began at the start of the 20th Century with Viguier (1905), who resurrected *Cuphocarpus* Decne. & Planch. and *Sciadopanax* Seem., and described two new genera, *Bonnierella* R. Vig. and *Tieghemopanax* R. Vig., while transferring some other taxa to *Polyscias* that had been published in the preceding decade or that Harms had overlooked. Hutchinson (1967) went even further, adopting all the same genera as Viguier along with three others that Harms had reduced into synonymy (*Botryopanax* Miq., *Eupteron* Miq., and *Sciadopanax*) plus a fourth that he described as new (*Gelibia* Hutch.). At about the same time, the trend reversed again toward defining *Polyscias* more broadly, starting with Smith & Stone (1965) and then Bernardi (1971), who placed in synonymy nearly all of the segregate genera accepted by Viguier and Hutchinson, along with *Palmervandenbroekia* Gibbs and *Kissodendron* Seem. Philipson (1977a, 1978, 1979) used a similarly broad circumscription of *Polyscias* in his treatment for *Flora Malesiana*, formally recognizing four sections within the region and transferring two Australian species previously misplaced in *Pentapanax*. This broad definition has been widely followed since (e.g., Marais 1984; Smith 1985; Lowry 1989; Lejoly & Lisowski 1999; Lowry et al. 1999; Frodin & Govaerts 2003; Callmender et al. 2009).

In a series of recent molecular phylogenetic studies (Plunkett et al. 2001, 2004a, 2004b), we identified several major clades within Araliaceae, one of which comprises *Polyscias* and a number of related genera, collectively referred to as *Polyscias* sensu lato. These studies also identified several major, well-supported clades within *Polyscias* sensu lato along with a series of smaller clades comprising one or a few species. They further revealed that *Polyscias*, as currently circumscribed, is paraphyletic with respect to six genera that have been traditionally regarded as distinct by most authors (viz. *Arthrophyllum* Blume, *Cuphocarpus*, *Gastonia* Comm. ex Lam., *Munroidendron* Sherff, *Reynoldsia* A. Gray and *Tetraplasandra* A. Gray), most of which have rarely if ever been associated directly with *Polyscias*, and three of which are themselves polyphyletic (*Cuphocarpus*, *Gastonia* and *Reynoldsia*).

These phylogenetic results clearly showed that traditional generic definitions would have to be completely overhauled in order to circumscribe monophyletic groups and provide a classification system that accurately reflects evolutionary relationships. Initially (Plunkett et al. 2001, Lowry et al. 2004) we suggested that each of the major clades of *Polyscias* sensu lato could be treated as a single genus, pointing out that such an approach would highlight phylogenetic relationships rather than obscure them.

However, in light of the conclusions reached in an expanded phylogenetic analysis of molecular data, presented in a companion paper (Plunkett & Lowry 2010), it is now evident that this approach presents serious difficulties. First, to avoid recognition of paraphyletic groups, many of the clades that would serve as potential genera are difficult to define on the basis of morphology and present few if any obvious synapomorphies, a fact that would significantly compromise the utility of the resulting classification. Moreover, such an approach would require publication of more than 100 new combinations in order to place each species in its corresponding genus. Based on these considerations, we have therefore elected instead to treat all members of the *Polyscias* sensu lato clade as a single genus (see Plunkett & Lowry 2010). Adopting a broad generic circumscription is considerably less disruptive to nomenclatural stability, requiring a total of 54 new combinations and five new names to bring all currently recognized species into *Polyscias*. Furthermore, as mentioned in our companion paper, defining *Polyscias* broadly avoids potential problems associated with the treatment of species that can not confidently be assigned to a clade (and thus to a distinct genus) based on either molecular or morphological data, including several currently recognized species (e.g., *Polyscias mollis*, *P. murrayi*, *P. purpurea*) plus many new species, mostly from Madagascar and New Caledonia, awaiting formal description.

While several of the clades identified in our phylogenetic study (Plunkett & Lowry 2010) are not well suited for recognition at the generic level, many of them contain important information on evolutionary relationships and all exhibit strong geographic structuring. In an attempt to translate the phylogeny of *Polyscias* into a workable classification system that retains this potentially useful information, we have, for several reasons, chosen to recognize each of these clades at the subgeneric level. First, by doing so we retain the option of formally recognizing sections within the subgenera, several of which appear to contain morphologically distinctive species groups that may prove to be monophyletic. Also, we avoid possible confusion with the incomplete system of four sections proposed by Philipson (1978, 1979) for the species of *Polyscias* he recognized in Malesia, several of which are of limited use in other parts of the world and do not comprise monophyletic groups (see below). Moreover, because we initially considered recognizing these groups as distinct genera (Plunkett et al. 2001, Lowry et al. 2004), treating them as subgenera would seem appropriate. Finally, recognizing subgenera within *Polyscias* is consistent with the approach we are adopting for other Araliaceae, such as some of the clades currently placed in the polyphyletic genus *Schefflera* J.R. Forst. & G. Forst.

Table 1 summarizes the correspondence between the major clades identified in our companion paper and the ten subgenera presented below. Some of these groups are well delimited and their members can be easily recognized on the basis of obvious morphological features (as indicated below in the discussion under each subgenus). Others, however, are more difficult to characterize, such as subgenus *Maralia*, which includes nearly all of the species from Madagascar and encompasses an impressive level of morphological diversity (much of which remains to be described), presumably the result of extensive local radiation and diversification. Nonetheless, each of the subgenera recognized in our classification system is geographically coherent and comprises a well supported monophyletic assemblage.

Table 1. Correspondence between the major clades within *Polyscias* sensu lato identified by Plunkett & Lowry (2010) and the subgenera of *Polyscias* recognized in the present classification system.

Clade name used by Plunkett & Lowry (2010)	Corresponding subgenus in the present classification system
Section <i>Polyscias</i> clade	A. <i>Polyscias</i> subg. <i>Polyscias</i>
Indian Ocean Basin (IOB) clade/Mascarenes subclade	B. <i>Polyscias</i> subg. <i>Grotenfendia</i>
IOB clade/Malagasy subclade	C. <i>Polyscias</i> subg. <i>Maralia</i>
Austro-Malesian clade	D. <i>Polyscias</i> subg. <i>Arthrophyllum</i>
IOB clade/ <i>Cuphocarpus</i> subclade	E. <i>Polyscias</i> subg. <i>Cuphocarpus</i>
New Guinea-Polynesia clade	F. <i>Polyscias</i> subg. <i>Tetraplasandra</i>
<i>Polyscias nodosa</i> clade	G. <i>Polyscias</i> subg. <i>Eupteron</i>
IOB clade/ <i>P. fulva</i> subclade	H. <i>Polyscias</i> subg. <i>Sciadopanax</i>
<i>Tieghemopanax</i> clade	I. <i>Polyscias</i> subg. <i>Tieghemopanax</i>
Seychelles clade	J. <i>Polyscias</i> subg. <i>Indokingia</i>

The classification system presented below is synoptic in form. Full synonymy is provided for each subgeneric name along with place of publication and an indication of the nomenclatural type (when necessary the corresponding species currently recognized in *Polyscias* is also given). At the species level, however, Frodin & Govaerts (2003) have already provided full synonymy for all species of Araliaceae recognized in their *World Checklist and Bibliography*. Thus, we have largely refrained from repeating this information except for synonyms that are currently in wide use. We formally place ten species in synonymy that were accepted as distinct by Frodin and

Table 2. Species recognized by Frodin & Govaerts (2003) but placed in synonymy in the present classification.

Name accepted by Frodin & Govaerts (2003)	Placement in synonymy in the present classification
<i>Arthrophyllum angustatum</i> (Baill.) Philipson	<i>Polyscias otopyrena</i> (Baill.) Lowry & G. M. Plunkett
<i>Arthrophyllum daenikeri</i> (Baum.-Bod.) Philipson	<i>Polyscias vieillardii</i> (Baill.) Lowry & G. M. Plunkett subsp. <i>balansae</i> (Baill.) Lowry & G. M. Plunkett
<i>Arthrophyllum glaberrimum</i> (Baum.-Bod.) Philipson	<i>Polyscias vieillardii</i> (Baill.) Lowry & G. M. Plunkett subsp. <i>balansae</i> (Baill.) Lowry & G. M. Plunkett
<i>Arthrophyllum hederoides</i> (Baum.-Bod.) Philipson	<i>Polyscias vieillardii</i> (Baill.) Lowry & G. M. Plunkett subsp. <i>balansae</i> (Baill.) Lowry & G. M. Plunkett
<i>Arthrophyllum schlechteri</i> (Harms) Philipson	<i>Polyscias otopyrena</i> (Baill.) Lowry & G. M. Plunkett
<i>Polyscias grandifolia</i> Volkens	<i>Polyscias macgillivrayi</i> (Seem.) Harms
<i>Polyscias tennantii</i> Bernardi	<i>Polyscias chapelieri</i> (Drake) Harms ex R. Vig.
<i>Reynoldsia grayana</i> Christoph.	<i>Polyscias lanutoensis</i> (Hochr.) Lowry & G. M. Plunkett
<i>Reynoldsia tahitiensis</i> Nadeaud	<i>Polyscias verrucosa</i> (Seem.) Lowry & G. M. Plunkett
<i>Reynoldsia tauensis</i> A. C. Smith & B. C. Stone	<i>Polyscias lanutoensis</i> (Hochr.) Lowry & G. M. Plunkett

Table 3. Species and infraspecific taxa recognized by Frodin & Govaerts (2003) for which a new name or a change in rank is proposed in the present classification.

Name used by Frodin & Govaerts (2003)	Name adopted in the current classification
<i>Arthropphyllum balansae</i> (Baum.-Bod.) Philipson	<i>Polyscias vieillardii</i> (Baill.) Lowry & G. M. Plunkett subsp. <i>balansae</i> (Baill.) Lowry & G. M. Plunkett
<i>Arthropphyllum crassum</i> Philipson, non <i>Polyscias crassa</i> (Hemsl.) Lowry & G. M. Plunkett	<i>Polyscias revoluta</i> (Philipson) Lowry & G. M. Plunkett
<i>Arthropphyllum ferrugineum</i> Craib, non <i>Polyscias ferruginea</i> (Hiern) Harms	<i>Polyscias thailandica</i> Lowry & G. M. Plunkett
<i>Arthropphyllum grandifolium</i> (Guillaumin) Philipson, non <i>Polyscias grandifolia</i> Volkens	<i>Polyscias mackeei</i> Lowry & G. M. Plunkett
<i>Cuphocarpus commersonii</i> Bernardi, non <i>Polyscias commersonii</i> (Drake) R. Vig.	<i>Polyscias compacta</i> Lowry & G. M. Plunkett
<i>Gastonia elegans</i> (W. Bull.) Frodin, non <i>Polyscias elegans</i> (C. Moore & F. Muell.) Harms	<i>Polyscias maraisiana</i> Lowry & G. M. Plunkett
<i>Polyscias australiana</i> (F. Muell.) Philipson var. <i>disperma</i> (F. Muell.) Philipson	<i>Polyscias disperma</i> (F. Muell.) Lowry & G. M. Plunkett
<i>Polyscias subincisa</i> (R. Vig.) Lowry	<i>Polyscias bracteata</i> (R. Vig.) Lowry subsp. <i>subincisa</i> (R. Vig.) Lowry & G. M. Plunkett

Govaerts (2003) (see Table 2) and do likewise for seven infraspecific taxa that we do not recognize. In addition to proposing five new names, we also raise one variety to the rank of species and reduce two previously recognized species to the level of subspecies (Table 3). Full information is provided on the basionym for each of the 65 new combinations made here, which include nine for infrageneric taxa, 54 for species, and two for subspecies. We have designated lectotypes for infrageneric taxa as needed in order to improve nomenclatural stability. Full citation of types for species and infraspecific taxa (and designation of lectotypes where appropriate) will, however, be provided along with listings of exsiccatae, synonymy, and other information in a forthcoming series of taxonomic revisions being prepared for each subgenus. A total of 59 names accepted by Frodin & Govaerts (2003) in the genera *Arthropphyllum*, *Cuphocarpus*, *Gastonia*, *Munroidendron*, *Reynoldsia* and *Tetraplasandra* are treated here in *Polyscias*. As an aid to those wishing to adopt our names, Table 4 indicates the correspondence between those used by Frodin & Govaerts (2003) and the ones we have adopted here.

Table 4. Index to names accepted by Frodin & Govaerts (2003) in genera other than *Polyscias* and their placement in the present classification.

Name used by Frodin & Govaerts (2003)	Current name in <i>Polyscias</i> in the present classification
<i>Arthrophyllum alternifolium</i> Maingay ex Ridl.	D2. <i>Polyscias alternifolia</i> (Maingay ex Ridl.) Lowry & G. M. Plunkett
<i>Arthrophyllum angustifolium</i> Ridl.	D2. <i>Polyscias angustifolia</i> (Ridl.) Lowry & G. M. Plunkett
<i>Arthrophyllum ashtonii</i> Philipson	D4. <i>Polyscias ashtonii</i> (Philipson) Lowry & G. M. Plunkett
<i>Arthrophyllum balansae</i> (Baill.) Philipson	D36b. <i>Polyscias vieillardii</i> (Baill.) Lowry & G. M. Plunkett subsp. <i>balansae</i> (Baill.) Lowry & G. M. Plunkett
<i>Arthrophyllum biforme</i> Philipson	D7. <i>Polyscias biforme</i> (Philipson) Lowry & G. M. Plunkett
<i>Arthrophyllum borneense</i> Baker	D1. <i>Polyscias aherniana</i> (Philipson) Lowry & G. M. Plunkett
<i>Arthrophyllum cenabrei</i> Merr.	D9. <i>Polyscias cenabrei</i> (Merr.) Lowry & G. M. Plunkett
<i>Arthrophyllum collinum</i> Philipson	D10. <i>Polyscias collina</i> (Philipson) Lowry & G. M. Plunkett
<i>Arthrophyllum crassum</i> Philipson	D.11 <i>Polyscias crassa</i> (Philipson) Lowry & G. M. Plunkett
<i>Arthrophyllum diversifolium</i> Blume	D13. <i>Polyscias diversifolia</i> (Blume) Lowry & G. M. Plunkett
<i>Arthrophyllum engganoense</i> Philipson	D15. <i>Polyscias engganoense</i> (Philipson) Lowry & G. M. Plunkett
<i>Arthrophyllum ferrugineum</i> Craib	D33. <i>Polyscias siamensis</i> Lowry & G. M. Plunkett
<i>Arthrophyllum havilandii</i> Ridl.	D16. <i>Polyscias havilandii</i> (Ridl.) Lowry & G. M. Plunkett
<i>Arthrophyllum jackianum</i> (G. Don) Frodin	D17. <i>Polyscias jackiana</i> (G. Don) Lowry & G. M. Plunkett
<i>Arthrophyllum javanicum</i> Blume	D14. <i>Polyscias elliptica</i> (Blume) Lowry & G. M. Plunkett
<i>Arthrophyllum kjellbergii</i> Philipson	D18. <i>Polyscias kjellbergii</i> (Philipson) Lowry & G. M. Plunkett
<i>Arthrophyllum lucens</i> Craib	D19. <i>Polyscias lucens</i> (Craib) Lowry & G. M. Plunkett
<i>Arthrophyllum macranthum</i> Philipson	D21. <i>Polyscias macranthum</i> (Philipson) Lowry & G. M. Plunkett
<i>Arthrophyllum macrocarpum</i> Philipson & Bui	D22. <i>Polyscias macrocarpa</i> (Philipson) Lowry & G. M. Plunkett
<i>Arthrophyllum meliifolium</i> Craib	D23. <i>Polyscias meliifolia</i> (Craib) Lowry & G. M. Plunkett
<i>Arthrophyllum montanum</i> Ridl.	D24. <i>Polyscias montana</i> (Ridl.) Lowry & G. M. Plunkett
<i>Arthrophyllum otopyrenum</i> (Baill.) Philipson	D25. <i>Polyscias otopyrena</i> (Baill.) Lowry & G. M. Plunkett
<i>Arthrophyllum pacificum</i> Philipson	D26. <i>Polyscias pacifica</i> (Philipson) Lowry & G. M. Plunkett
<i>Arthrophyllum papyraceum</i> Philipson	D27. <i>Polyscias papyracea</i> (Philipson) Lowry & G. M. Plunkett
<i>Arthrophyllum proliferum</i> Philipson	D28. <i>Polyscias prolifera</i> (Philipson) Lowry & G. M. Plunkett
<i>Arthrophyllum pulgarensense</i> Elmer	D29. <i>Polyscias pulgarensense</i> (Elmer) Lowry & G. M. Plunkett
<i>Arthrophyllum rubiginosum</i> Ridl.	D31. <i>Polyscias rubiginosa</i> (Ridl.) Lowry & G. M. Plunkett
<i>Arthrophyllum rufosepalum</i> Ridl.	D32. <i>Polyscias rufosepalum</i> (Ridl.) Lowry & G. M. Plunkett
<i>Arthrophyllum stonei</i> A. L. Lim	D35. <i>Polyscias stonei</i> (Ridl.) Lowry & G. M. Plunkett
<i>Arthrophyllum vieillardii</i> (Baill.) Philipson	D36b. <i>Polyscias vieillardii</i> (Baill.) Lowry & G. M. Plunkett subsp. <i>vieillardii</i>
<i>Cuphocarpus briquetianus</i> Bernardi	C7. <i>Polyscias briquetiana</i> (Bernardi) Lowry & G. M. Plunkett
<i>Cuphocarpus commersonii</i> Bernardi	C11. <i>Polyscias compacta</i> Lowry & G. M. Plunkett
<i>Cuphocarpus humbertianus</i> Bernardi	C19. <i>Polyscias humbertiana</i> (Bernardi) Lowry & G. M. Plunkett
<i>Cuphocarpus leandrianus</i> Bernardi	C22. <i>Polyscias leandriana</i> (Bernardi) Lowry & G. M. Plunkett
<i>Gastonia crassa</i> (Hemsl.) F. Friedmann	D11. <i>Polyscias crassa</i> (Philipson) Lowry & G. M. Plunkett
<i>Gastonia cutispongia</i> Lam.	B5. <i>Polyscias cutispongia</i> (Lam.) Baker
<i>Gastonia duplicata</i> Thouars ex Baill.	C14. <i>Polyscias duplicata</i> (Thouars ex Baill.) Lowry & G. M. Plunkett
<i>Gastonia elegans</i> (W. Bull) Frodin	B8. <i>Polyscias maraisiana</i> Lowry & G. M. Plunkett

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Gaston

Gaston

Gastor

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<i>Gastonia lionnetii</i> F. Friedmann	J12. <i>Polyscias lionnetii</i> (F. Friedmann) Lowry & G. M. Plunkett
<i>Gastonia rodriguesiana</i> Marais	B14. <i>Polyscias rodriguesiana</i> (Marais) Lowry & G. M. Plunkett
<i>Gastonia sechellarum</i> (Baker) Harms	J3. <i>Polyscias sechellarum</i> (Baker) Lowry & G. M. Plunkett
<i>Gastonia serratifolia</i> (Miq.) Philipson	F16. <i>Polyscias serratifolia</i> (Miq.) Lowry & G. M. Plunkett
<i>Gastonia spectabilis</i> (Harms) Philipson	F17. <i>Polyscias spectabilis</i> (Harms) Lowry & G. M. Plunkett
<i>Munroidendron racemosum</i> (C. N. Forbes) Sherff	F14. <i>Polyscias racemosa</i> (Forbes) Lowry & G. M. Plunkett
<i>Reynoldsia grayana</i> Christoph.	F9. <i>Polyscias lanutoensis</i> (Hochr.) Lowry & G. M. Plunkett
<i>Reynoldsia lanutoensis</i> Hochr.	F9. <i>Polyscias lanutoensis</i> (Hochr.) Lowry & G. M. Plunkett
<i>Reynoldsia marchionensis</i> F. Br.	F10. <i>Polyscias marchionensis</i> (F. Brown) Lowry & G. M. Plunkett
<i>Reynoldsia pleiosperma</i> A. Gray	F13. <i>Polyscias pleiosperma</i> (A. Gray) Lowry & G. M. Plunkett
<i>Reynoldsia sandwicensis</i> A. Gray	F15. <i>Polyscias sandwicensis</i> (A. Gray) Lowry & G. M. Plunkett
<i>Reynoldsia tahitensis</i> Nadeaud	F18. <i>Polyscias verrucosa</i> (Seem.) Lowry & G. M. Plunkett
<i>Reynoldsia tauensis</i> A. C. Sm. & B. C. Stone	F9. <i>Polyscias lanutoensis</i> (Hochr.) Lowry & G. M. Plunkett
<i>Reynoldsia verrucosa</i> Seem.	F18. <i>Polyscias verrucosa</i> (Seem.) Lowry & G. M. Plunkett
<i>Tetraplasandra flynnii</i> Lowry & K. R. Wood	F5. <i>Polyscias flynnii</i> (Lowry & K. R. Wood) Lowry & G. M. Plunkett
<i>Tetraplasandra gymnocarpa</i> (Hillebr.) Sherff	F6. <i>Polyscias gymnocarpa</i> (Hillebr.) Lowry & G. M. Plunkett
<i>Tetraplasandra hawaiiensis</i> A. Gray	F7. <i>Polyscias hawaiiensis</i> (A. Gray) Lowry & G. M. Plunkett
<i>Tetraplasandra kawaiensis</i> (H. Mann) Sherff	F8. <i>Polyscias kawaiensis</i> (H. Mann) Lowry & G. M. Plunkett
<i>Tetraplasandra oahuensis</i> (A. Gray) Harms	F11. <i>Polyscias oahuensis</i> (A. Gray) Lowry & G. M. Plunkett
<i>Tetraplasandra waialealae</i> Rock	F19. <i>Polyscias waialealae</i> (Rock) Lowry & G. M. Plunkett
<i>Tetraplasandra waimeae</i> Wawra	F20. <i>Polyscias waimeae</i> (Wawra) Lowry & G. M. Plunkett

Infrageneric classification

Polyscias J. R. Forst. & G. Forst., Char. Gen. Pl.: 32. 1775. — Type: *P. pinnata* J. R. Forst. & G. Forst. [= *Polyscias scutellaria* (N. L. Burm.) Fosberg].

A. *Polyscias* subg. *Polyscias*

= *Nothopanax* Miq. in Bonplandia 4: 139. 1865. — Type: *N. fruticosus* (L.) Miq. [= *Polyscias fruticosa* L.].

= *Bonnierella* R. Vig. in Bull. Soc. Bot. France 52: 314. 1905. — Type: *B. tahitiense* Nadeaud [= *Polyscias tahitiensis* (Nadeaud) Harms].

Members of this subgenus form a geographically and morphologically coherent group that corresponds to *Polyscias* sensu stricto or *Polyscias* sect. *Polyscias* as defined by Philipson (1978, 1979, 1995). They are characterized by having petioles with an elongated sheathing base whose margins are often scarious or membranous and sometimes alate. Dried specimens of most species in this subgenus also have a characteristic pungent odor reminiscent of aniseed or cumin (a feature that is not, however, restricted to the group). Viguier (1905) included at least one species belonging to *Polyscias* subg.

Polyscias in his new genus *Tieghemopanax* because of the presence of a bicarpellate gynoeceium (*P. macgillivrayi*) and tentatively referred three others there as well (see discussion below under subgenus *Tieghemopanax*). As circumscribed here, the native ranges of species in *Polyscias* subg. *Polyscias* collectively extend from Java across Malesia to tropical Australia, Micronesia, and Melanesia, S to Norfolk Isl. and across Polynesia to Tahiti, the eastern limit of the entire genus.

Several taxa belonging to *Polyscias* subg. *Polyscias*, especially *P. cumingiana*, *P. fruticosa*, *P. guilfoylei* and *P. scutellaria*, are widely cultivated throughout the tropics, often as living hedgerows. While these taxa are well represented in herbaria, their native ranges are unknown and few if any collections appear to represent material collected from native habitat. Moreover, although the cultivated taxa can almost always be distinguished from one another without difficulty, each exhibits significant variation, especially in leaf morphology and color (e.g., numerous variegated and dissected forms exist), which has led to the publication of many names. Taxonomic limits within these entities remain controversial and opinions have varied among recent authors regarding how best to circumscribe them. Philipson (1978, 1979) treated species broadly whereas several of the names he placed in synonymy were accepted as distinct taxa by Frodin & Govaerts (2003), including *P. balfouriana* (André) L. H. Bailey, *P. filicifolia* (C. Moore & E. Fourn.) L. H. Bailey, *P. obtusifolia* Frodin, *P. pinnata* J. R. Forst. & G. Forst. and *P. sorongensis* Gibbs. Lowry (1989) adopted Philipson's approach and we have done so here as well, preferring to defer a more detailed consideration of species limits until additional data, especially from molecular analyses, become available.

Taxa included:

- A1. *Polyscias corticata* Gibbs in J. Linn. Soc., Bot. 39: 149. 1909. — Fiji.
- A2. *Polyscias cumingiana* (K. Presl) Fern.-Vill., Nov. App.: 102. 1880. — Native range unknown, widely cultivated in the Pacific and elsewhere. — Frodin & Govaerts (2003) treat *Polyscias sorongensis* Gibbs as distinct from *P. cumingiana*, whereas Philipson (1979, 1995) and Lowry (1989) include it therein as a synonym. We prefer to follow this broad definition until a more detailed study can be conducted of this complex group.
- A3. *Polyscias fruticosa* (L.) Harms in Engl. & Prantl, Nat. Pflanzenfam. 3(8): 45. 1894. — Native range unknown, widely cultivated in the Pacific and elsewhere.
- A4. *Polyscias guilfoylei* (Bull) L. H. Bailey in Rhodora 18: 153. 1916. — Native range unknown, widely cultivated in the Pacific and elsewhere.
- A5. *Polyscias javanica* Koord. & Valeton, Bijdr. 7: 13. 1900. — Java, Lesser Sunda Isl.
- A6. *Polyscias macgillivrayi* (Seem.) Harms in Engl. & Prantl, Nat. Pflanzenfam. 3(8): 45. 1894. — Micronesia, Solomon Isl., Queensland, New Guinea.
= *Polyscias grandifolia* Volkens in Bot. Jahrb. Syst. 31: 471. 1901, syn. nov.
- A7. *Polyscias multijuga* (A. Gray) Harms in Engl. & Prantl, Nat. Pflanzenfam. 3(8): 45. 1894. — Vanuatu, Fiji, Wallis & Futuna, Norfolk Isl.
- A8. *Polyscias reineckeii* Harms in Bot. Jahrb. Syst. 25: 663. 1898. — Samoa.

- A9.** *Polyscias samoensis* (A. Gray) Harms in Engl. & Prantl, Nat. Pflanzenfam. 3(8): 45. 1894. — Samoa, Vanuatu.
- A10.** *Polyscias scutellaria* (N.L. Burm.) Fosberg in Univ. Hawaii Occ. Papers 46: 9. 1948 [= *Crassula scutellaria* Burm.f., Fl. Indica: 78. 1768.] — Native range unknown, widely cultivated in the Pacific and elsewhere. — Frodin & Govaerts (2003) regard *Polyscias pinnata* J. R. Forst. & G. Forst., the generi-type, as distinct from *P. scutellaria*, but we opt to treat the latter broadly, following Philipson (1979, 1995) and Lowry (1989), at least until more detailed studies can be conducted to elucidate relationships and improve the definition of entities within this complex assemblage.
- A11.** *Polyscias subcapitata* Kaneh. in Bot. Mag. (Tokyo) 46: 673. 1932. — Caroline Isl.
- A12.** *Polyscias tahitiensis* (Nadeaud) Harms in Engl. & K. A. E. Prantl, Nat. Pflanzenfam. 3(8): 45. 1894.
= *P. reflexa* J. W. Moore in Bernice P. Bishop Mus. Bull. 102: 35. 1933 [= *Bonnierella reflexa* (J. W. Moore) J. W. Moore in Occas. Pap. Bernice Pauahi Bishop Mus. 10: 6. 1934]. — Tahiti, Raiatea.
- A13.** *Polyscias verticillata* Stone in J. Arnold Arbor. 47: 272. 1966. — Solomon Islands, New Guinea.
- B.** *Polyscias* subg. *Grotenfendia* (Seem.) R. Vig. in Bull. Soc. Bot. France 52: 301. 1905. = *Grotenfendia* Seem. in J. Bot. 2: 247. 1864. — Lectotype (here designated): *Polyscias repanda* (DC.) Baker.
= *Gastonia* Comm. ex Lam., Encycl. 2: 610. 1788. — Type: *G. cutispongia* Lam. [= *Polyscias cutispongia* (Lam.) Baker].
= *Botryopanax* Miq. in Ann. Mus. Bot. Lugduno-Batavi 1: 5. 1863. — Type: *B. borbonica* Miq. [= *Polyscias paniculata* (DC.) Baker].

Polyscias subg. *Grotenfendia*, lectotypified here by the Réunion Island endemic *P. repanda*, corresponds to the Mascarene Islands subclade of the Indian Ocean Basin clade in the updated phylogeny of Plunkett & Lowry (2010). It comprises all 15 members of the *Polyscias* sensu lato group occurring in the Mascarenes, including taxa with articulated pedicels historically placed in *Polyscias* and others lacking an articulation that have long been referred to *Gastonia* (which is typified by another Réunion endemic, *P. cutispongia*). The oldest generic name that applies to this clade is *Gastonia*, but when it is treated as a subgenus, as we do here, Viguier's combination based on *Grotenfendia* has nomenclatural priority.

As indicated in our companion paper (Plunkett & Lowry 2010), *Gastonia* as redefined by Philipson (1970) is highly polyphyletic, comprising taxa belonging to four distinct subclades within *Polyscias* sensu lato. As circumscribed here, *Polyscias* subg. *Grotenfendia* bears little resemblance to *Gastonia* as historically treated (e.g., by Harms 1894-97) or as redefined by Philipson (1970, 1979, 1995) and adopted by many recent authors (e.g., Bernardi 1971, 1980; Friedmann 1986; Frodin & Govaerts 2003). Instead, it represents a well supported and geographically coherent group that appears to have diversified after reaching the Mascarenes via long-distance dispersal from Madagascar (Mauritius, the oldest island in the archipelago, dates from ca. 10 my;

Schlüter 2006). All members of the subgenus have radiating style arms, a feature that is not unique to species from the Mascarenes (see Philipson 1970), but which may nevertheless be of taxonomic value in combination with geography.

Taxa included:

- B1.** *Polyscias aemiliguineae* Bernardi in Candollea 29: 153. 1974. — Réunion.
B2. *Polyscias bernieri* (Baill. ex Drake) R. Vig. in Bull. Soc. Bot. France 52: 303. 1905. — Réunion.
B3. *Polyscias borbonica* Marais in Kew Bull. 39: 814. 1984. — Réunion.
B4. *Polyscias coriacea* Marais in Kew Bull. 39: 812. 1984. — Réunion.
B5. *Polyscias cutispongia* (Lam.) Baker, Fl. Mauritius Seych.: 127. 1877 [= *Gastonia cutispongia* Lam.]. — Réunion.
B6. *Polyscias dichroostachya* Baker, Fl. Mauritius Seych.: 127. 1877. — Mauritius.
B7. *Polyscias gracilis* Marais in Kew Bull. 39: 811. 1984. — Mauritius.
B8. *Polyscias maraisiana* Lowry & G. M. Plunkett, **nom. nov.** ≡ *Gastonia elegans* (W. Bull) Frodin, in D. Frodin & R. Govaerts, World Checklist Bibliog. Araliaceae: 166. 2003 [= *Terminalia elegans* W. Bull, Cat. 14: 8. 1866, non *Polyscias elegans* (C. Moore & F. Muell.) Harms. — Mauritius.
 = *Gastonia mauritiana* Marais, non *Polyscias mauritiana* Marais.
B9. *Polyscias mauritiana* Marais in Kew Bull. 39: 812. 1984. — Mauritius.
B10. *Polyscias neraudiana* (Drake) R. Vig. in Bull. Soc. Bot. France 52: 301. 1905. — Mauritius.
B11. *Polyscias paniculata* (DC.) Baker, Fl. Mauritius Seych.: 127. 1877. — Mauritius.
B12. *Polyscias repanda* (DC.) Baker, Fl. Mauritius Seych.: 128. 1877. — Réunion.
B13. *Polyscias rivalsii* Bernardi in Candollea 29: 158. 1974. — Réunion.
B14. *Polyscias rodriguesiana* (Marais) Lowry & G. M. Plunkett, **comb. nov.** ≡ *Gastonia rodriguesiana* Marais in Kew Bull. 39: 809. 1984. — Rodrigues Island.
B15. *Polyscias sessiliflora* Marais in Kew Bull. 39: 814. 1984. — La Réunion.
C. *Polyscias* subg. *Maralia* (Thouars) Lowry & G. M. Plunkett, **comb. et stat. nov.** ≡ *Maralia* Thouars, Gen. Nov. Madagasc.: 13. 1806. — Type: *M. madagascariensis* DC. [= *Polyscias maralia* (Roem. & Schult.) Bernardi, non *P. madagascariensis* (Seem.) Harms].
 = *Oligoscias* Seem. in J. Bot. 3: 179. 1865. — Type: *O. madagascariensis* Seem. [= *Polyscias madagascariensis* (Seem.) Harms].

Polyscias subg. *Maralia* is circumscribed here to include all members of the Malagasy subclade within the Indian Ocean Basin clade of *Polyscias* sensu lato (Plunkett & Lowry 2010). Of the 35 currently recognized species in this group, all except three are endemic to Madagascar: *Polyscias felicis* is restricted to the Comoro Islands, *P. stuhlmannii* is found only in northeastern Tanzania and adjacent Kenya, and *P. duplicata* is widespread in Madagascar and also occurs in the Comoros. The fact that each of these species occupies a separate, derived position within the Malagasy subclade suggests

that three independent dispersal events took place, one from Madagascar to mainland Africa giving rise to *P. stuhlmannii*, and two to the Comoros that resulted in the presence there of the other taxa.

One member of this subgenus, *Polyscias duplicata*, has always been included in the polyphyletic genus *Gastonia* primarily because its pedicels lack an articulation below the ovary. However, a second inarticulate species described by Bernardi (1971) as *P. carolorum* — which is not closely related to *P. duplicata* in the phylogeny of Plunkett & Lowry (2010) — was curiously never associated with *Gastonia* despite exhibiting its principal defining character. Moreover, Tennant (1960) described *P. stuhlmannii* var. *inarticulata* Tennant, which provides another example of the loss of an articulation within the subgenus. Plunkett & Lowry (2010) give additional information on the taxonomic value of this and other characters traditionally used to define genera in *Polyscias* sensu lato, and Plunkett et al. (2004b) examine the value of morphological features historically used to circumscribe infrafamilial taxa within Araliaceae.

Polyscias subg. *Maralia* includes four montane species described several decades ago in *Cuphocarpus*, a long-recognized segregate genus defined by having flowers with a unispellate gynoeceum. The fifth taxon traditionally placed in this genus, *C. aculeatus* (the generi-type), represents a distinct lineage (see below) in which a reduction to a single carpel has taken place, a parallelism that has likewise evolved in the taxa historically included in *Arthrophyllum*.

In his studies of *Polyscias* from Madagascar and the Comoros, Bernardi (1971, 1980) recognized a total of 28 species that we include here in subg. *Maralia*, one of which (*P. tennantii*) is placed in synonymy below. Extensive exploration in Madagascar over the last several decades has more than doubled the number of available collections, yielding numerous previously undescribed species (for example see Callmander et al. 2009). Our ongoing studies based on both historical material and these more recent gatherings indicate that at least 80 taxa remain to be described in *Polyscias* subg. *Maralia*, which will bring the total to at least 115 species, making it the largest group within the genus and also the most morphologically diverse.

Taxa included:

- C1. *Polyscias amplifolia* (Baker) Harms in Engl. & Prantl, Nat. Pflanzenfam. 3(8): 44. 1894. — Madagascar.
- C2. *Polyscias anacardium* Bernardi in Candollea 26: 50. 1971. — Madagascar.
- C3. *Polyscias andrearum* Bernardi in Candollea 26: 50. 1971. — Madagascar.
- C4. *Polyscias ariadnes* Bernardi in Candollea 26: 29. 1971. — Madagascar.
- C5. *Polyscias aubrevillei* (Bernardi) Bernardi in Candollea 26: 26. 1971. — Madagascar.
- C6. *Polyscias baretiana* Bernardi in Candollea 29: 147. 1974. — Madagascar.
- C7. *Polyscias briquetiana* (Bernardi) Lowry & G. M. Plunkett, **comb. nov.** ≡ *Cuphocarpus briquetianus* Bernardi in Bull. Soc. Bot. Suisse 76: 354. 1966. — Madagascar.
- C8. *Polyscias carolorum* Bernardi in Candollea 26: 43. 1971. — Madagascar.
- C9. *Polyscias chapelieri* (Drake) Harms ex R. Vig. in Bull. Soc. Bot. France 52: 303. 1905. — Madagascar.

- = *Polyscias tennantii* Bernardi in Candollea 26: 65. 1971, syn. nov.
- C10. *Polyscias cissiflora* (Baker) Harms in Engl. & Prantl, Nat. Pflanzenfam. 3(8): 44. 1894. — Madagascar.
- C11. *Polyscias compacta* Lowry & G. M. Plunkett, **nom. nov.** ≡ *Cuphocarpus commersonii* Bernardi in Bull. Soc. Bot. Suisse 76: 356. 1966, non *Polyscias commersonii* (Drake) R. Vig. [= *P. paniculata* (DC.) Baker]. — Madagascar.
- C12. *Polyscias confertifolia* (Baker) Harms in Engl. & Prantl, Nat. Pflanzenfam. 3(8): 44. 1894. — Madagascar.
- C13. *Polyscias cussonioides* (Drake) Bernardi in Candollea 26: 46. 1971. — Madagascar.
- C14. *Polyscias duplicata* (Thouars ex Baill.) Lowry & G. M. Plunkett, **comb. nov.** ≡ *Gastonia duplicata* Thouars ex Baill., Adansonia 12: 166. 1878. — Madagascar, Comoro Islands.
- C15. *Polyscias felicis* Bernardi in Candollea 26: 40. 1971. — Comoro Islands.
- C16. *Polyscias fraxinifolia* (Baker) R. Vig. in Bull. Soc. Bot. France 52: 303. 1905. — Madagascar.
- C17. *Polyscias gruschvitzkii* Bernardi in Candollea 26: 53. 1971. — Madagascar.
- C18. *Polyscias heineana* Bernardi in Bull. Soc. Bot. Suisse 76: 364. 1966. — Madagascar.
- C19. *Polyscias humbertiana* (Bernardi) Lowry & G. M. Plunkett, **comb. nov.** ≡ *Cuphocarpus humbertianus* Bernardi in Bull. Soc. Bot. Suisse 76: 358. 1966. — Madagascar.
- C20. *Polyscias lancifolia* (Drake) Harms ex R. Vig., Bull. Soc. Bot. France 52: 304. 1905. — Madagascar.
- C21. *Polyscias lantzii* (Drake) Harms ex R. Vig. in Bull. Soc. Bot. France 52: 304. 1905. — Madagascar.
- C22. *Polyscias leandriana* (Bernardi) Lowry & G. M. Plunkett, **comb. nov.** ≡ *Cuphocarpus leandrianus* Bernardi in Bull. Soc. Bot. Suisse 76: 359. 1966. — Madagascar.
- C23. *Polyscias madagascariensis* (Seem.) Harms in Engl. & Prantl, Nat. Pflanzenfam. 3(8): 44. 1894. — Madagascar.
- C24. *Polyscias maralia* (Roem. & Schult.) Bernardi in Candollea 26: 34. 1971. — Madagascar.
- C25. *Polyscias multibracteata* (Baker) Harms in Engl. & Prantl, Nat. Pflanzenfam. 3(8): 44. 1894. — Madagascar.
- C26. *Polyscias muraliana* Bernardi in Bull. Soc. Bot. Suisse 76: 366. 1966. — Madagascar.
- C27. *Polyscias myrsine* Bernard in Candollea 26: 54. 1971. — Madagascar.
- C28. *Polyscias nossibensis* (Drake) Harms in Bot. Jahrb. Syst. 26: 247. 1899. — Madagascar.
- C29. *Polyscias ornifolia* (Baker) Harms in Engl. & Prantl, Nat. Pflanzenfam. 3(8): 44. 1894. — Madagascar.
- C30. *Polyscias rainaliorum* Bernardi in Bull. Soc. Bot. Suisse 76: 367. 1966. — Madagascar.

- C31. *Polyscias stuhlmannii* Harms in Bot. Jahrb. Syst. 26: 244. 1899. — Kenya, Tanzania.
- C32. *Polyscias tafondroensis* (Drake) Harms ex R. Vig. in Bull. Soc. Bot. France 52: 303. 1905. — Madagascar.
- C33. *Polyscias terminalia* Bernardi in Candollea 26: 57. 1971. — Madagascar.
- C34. *Polyscias tripinnata* Harms in Engl. & Prantl, Nat. Pflanzenfam. 3(8): 44. 1894. — Madagascar.
- C35. *Polyscias zanthoxyloides* (Baker) Harms in Engl. & Prantl, Nat. Pflanzenfam. 3(8): 44. 1894. — Madagascar.
- D. *Polyscias* subg. *Arthrophyllum* (Blume) Lowry & G. M. Plunkett, **comb. et stat. nov.** ≡ *Arthrophyllum* Blume in Bijdr.: 878. 1826. — Type: *A. diversifolium* Blume [= *Polyscias diversifolia* (Blume) Lowry & G. M. Plunkett].
- = *Mormoraphis* Jack ex Wall., Numer. List [Wallich] no. 4931. 1831. — Type: *M. sumatrana* Jack ex Wall. [= *Polyscias diversifolia* (Blume) Lowry & G. M. Plunkett].
- = *Kissodendron* Seem. in J. Bot. 3: 201. 1865 ≡ *Polyscias* sect. *Kissodendron* (Seem.) Philipson in Blumea 24: 170. 1978. — Type: *K. australianum* (F. Muell.) Seem. [= *Polyscias australiana* (F. Muell.) Philipson].
- = *Eremopanax* Baill. in Adansonia 12: 158. 1878. — Type: *E. otopyrenum* Baill. [= *Polyscias otopyrena* (Baill.) Lowry & G. M. Plunkett].
- = *Nesodoxa* Calest. in Webbia 1: 100. 1905. — Type: *N. vieillardii* (Baill.) Fedde [= *Polyscias vieillardii* (Baill.) Lowry & G. M. Plunkett subsp. *vieillardii*].
- = *Irvingia* F. Muell. in Fragm. 5: 17. 1865, nom. illeg.
- = *Shirleyopanax* Domin in Biblioth. Bot. 89: 484. 1928, pro syn.

Polyscias subg. *Arthrophyllum* is currently the largest group within the genus, comprising a total of 37 species (one of which is raised here from the rank of variety) and one subspecies. The subgenus ranges from the Andaman and Nicobar Islands and southeast Asia (Peninsular Malaysia, Thailand and Laos) across Malesia (including the Philippines, New Guinea and the Bismarck Archipelago) and south through northeastern Australia to New Caledonia. *Polyscias* subg. *Arthrophyllum*, as circumscribed here, corresponds to the Austro-Malesian clade of *Polyscias* sensu lato (Plunkett & Lowry 2010) and incorporates taxa traditionally placed in *Arthrophyllum* (including the New Caledonian segregate *Eremopanax* Baill.) and *Kissodendron*, along with two species described in *Pentapanax* that were transferred to *Polyscias* by Philipson (1977a).

Many members of this group are characterized by the presence of rusty brown stellate or farinose indument, especially on vegetative shoots, young foliage and developing inflorescences. A majority of the taxa (i.e. all those previously assigned to *Arthrophyllum*) have flowers with a unicarpellate gynoeceium, a feature that clearly appears to be derived within the Austro-Malesian clade and is intimately correlated with a distinctive inflorescence structure in which two to four foliaceous, often compound bracts are borne opposite one another or in whorls, contrasting with the spiral phyllotaxy of the leaves.

While species limits are reasonably clear among the taxa historically assigned to

Eremopanax and *Kissodendron*, the same can not be said for the Malesian taxa that have unicarpellate gynoecia and have traditionally been included in *Arthrophyllum*. As mentioned in our companion paper (Plunkett & Lowry 2010), the paucity of herbarium material of many species, some of which have particularly large, complex inflorescences, prevented Philipson (1977b, 1979) from completing a revision of the Malesian taxa to his full satisfaction. A limited amount of material has become available over the last few decades (e.g., Lim 1986), but further field work will still be required before a comprehensive taxonomic treatment can be undertaken.

Taxa included:

- D1. *Polyscias aherniana* (Philipson) Lowry & G. M. Plunkett, **comb. nov.** \equiv *Arthrophyllum ahernianum* Merr. in Philipp. J. Sci., C 1 (Suppl.): 109. 1906 [= *Arthrophyllum borneense* Baker in Bull. Misc. in Inform. Kew 1896: 23. 1896, non *Polyscias borneense* Philipson]. — N. Borneo, Philippines, N. Maluku.
- D2. *Polyscias alternifolia* (Maingay ex Ridl.) Lowry & G. M. Plunkett, **comb. nov.** \equiv *Arthrophyllum alternifolium* Maingay ex Ridl. in Fl. Mal. Pen. 1: 886. 1922. — Peninsular Malaysia.
- D3. *Polyscias angustifolia* (Ridl.) Lowry & G. M. Plunkett, **comb. nov.** \equiv *Arthrophyllum angustifolium* Ridl. in J. Fed. Mal. St. Mus. 10: 136. 1920. — Peninsular Malaysia.
- D4. *Polyscias ashtonii* (Philipson) Lowry & G. M. Plunkett, **comb. nov.** \equiv *Arthrophyllum ashtonii* Philipson in Gard. Bull. Sing. 30: 303. 1977. — Borneo.
- D5. *Polyscias australiana* (F. Muell.) Philipson in Blumea 24: 171. 1978. — Australia.
- D6. *Polyscias bellendenkerensis* (F. M. Bailey) Philipson in Austrobaileya 1: 24. 1977. — Queensland.
- D7. *Polyscias biforme* (Philipson) Lowry & G. M. Plunkett, **comb. nov.** \equiv *Arthrophyllum biforme* Philipson in Bull. Mus. Natl. Hist. Nat. (Paris), sér. 4, Sect. B, Adansonia, 5: 237. 1983. \equiv *Arthrophyllum diversifolium* (Däniker) Philipson, non Blume (1826) nec *Polyscias diversifolia* (Blume) Lowry & G. M. Plunkett. — New Caledonia.
- D8. *Polyscias bipinnata* (Gibbs) Philipson in Blumea 24: 170. 1978. — New Guinea.
- D9. *Polyscias cenabrei* (Merr.) Lowry & G. M. Plunkett, **comb. nov.** \equiv *Arthrophyllum cenabrei* Merr. in Philip. J. Sci. 20: 417. 1922. — Philippines.
- D10. *Polyscias collina* (Philipson) Lowry & G. M. Plunkett, **comb. nov.** \equiv *Arthrophyllum collinum* Philipson in Gard. Bull. Sing. 30: 305. 1977. — Borneo.
- D11. *Polyscias revoluta* (Philipson) Lowry & G. M. Plunkett, **nom. nov.** \equiv *Arthrophyllum crassum* Philipson in Gard. Bull. Sing. 30: 305. 1977, non *Polyscias crassa* (Hemsl.) Lowry & G. M. Plunkett. — Borneo.
- D12. *Polyscias disperma* (F. Muell.) Lowry & G. M. Plunkett, **comb. et stat. nov.** \equiv *Kissodendron australianum* (F. Muell.) Seem. var. *dispermum* F. Muell. in Descr. Notes Papuan Pl. 5: 88. 1877. [\equiv *Polyscias australiana* (F. Muell.) Philipson var. *disperma* (F. Muell.) Philipson]. — New Guinea. — Recent examination of material of this taxon, heretofore consistently treated as a variety

- of *P. australiana*, shows that it represents a morphologically and geographically well delimited entity that warrants recognition at the species level.
- D13. *Polyscias diversifolia* (Blume) Lowry & G. M. Plunkett, **comb. nov.** \equiv *Arthrophyllum diversifolium* Blume in Bijdr., 879. 1826. — Java
- D14. *Polyscias elliptica* (Blume) Lowry & G. M. Plunkett, **comb. nov.** \equiv *Arthrophyllum ellipticum* Blume in Bijdr., 879. 1826 [= *Arthrophyllum javanicum* Blume in Bijdr., 879. 1826, non *Polyscias javanica* Koord. & Valetton]. — Java.
- D15. *Polyscias engganoense* (Philipson) Lowry & G. M. Plunkett, **comb. nov.** \equiv *Arthrophyllum engganoense* Philipson in Gard. Bull. Sing. 30: 305. 1977. — Sumatra.
- D16. *Polyscias havilandii* (Ridl.) Lowry & G. M. Plunkett, **comb. nov.** \equiv *Arthrophyllum havilandii* Ridl. in Kew Bull. 1933: 494. 1933. — Borneo.
- D17. *Polyscias jackiana* (G. Don) Lowry & G. M. Plunkett, **comb. nov.** \equiv *Hedera jackiana* G. Don in Gen. Hist. 3: 394. 1834 [= *Arthrophyllum jackianum* (G. Don) Frodin]. — Andaman & Nicobar Isl. to western and central Malesia.
- D18. *Polyscias kjellbergii* (Philipson) Lowry & G. M. Plunkett, **comb. nov.** \equiv *Arthrophyllum kjellbergii* Philipson in Gard. Bull. Sing. 30: 309. 1977. — Sulawesi.
- D19. *Polyscias lucens* (Craib) Lowry & G. M. Plunkett, **comb. nov.** \equiv *Arthrophyllum lucens* Craib in Bull. Misc. Inform. Kew 1930: 423. 1930. — Thailand.
- D20. *Polyscias mackeei* Lowry & G. M. Plunkett, **nom. nov.** \equiv *Eremopanax grandifolia* Guillaumin in Bull. Mus. Hist. Nat. (Paris) 33: 272. 1927 [= *Arthrophyllum grandifolium* (Guillaumin) Philipson], non *Polyscias grandifolia* Volkens. — New Caledonia.
- D21. *Polyscias macranthum* (Philipson) Lowry & G. M. Plunkett, **comb. nov.** \equiv *Arthrophyllum macranthum* Philipson in Bull. Br. Mus. Nat. Hist., Bot. 1: 18. 1951. — New Guinea.
- D22. *Polyscias macrocarpa* (Philipson & Bui) Lowry & G. M. Plunkett, **comb. nov.** \equiv *Arthrophyllum macrocarpum* Philipson & Bui in Adansonia, sér. 2, 17: 327. 1978. — Laos.
- D23. *Polyscias meliifolia* (Craib) Lowry & G. M. Plunkett, **comb. nov.** \equiv *Arthrophyllum meliifolium* Craib in Bull. Misc. Inform. Kew 1930: 424. 1930. — Thailand.
- D24. *Polyscias montana* (Ridl.) Lowry & G. M. Plunkett, **comb. nov.** \equiv *Arthrophyllum montanum* Ridl. in J. Fed. Mal. St. Mus. 4: 24. 1909. — Malaysia.
- D25. *Polyscias otopyreana* (Baill.) Lowry & G. M. Plunkett, **comb. nov.** \equiv *Eremopanax otopyreana* Baill. in Adansonia 12: 158. 1878. [= *Arthrophyllum otopyrenum* (Baill.) Philipson]. — New Caledonia.
- = *Eremopanax angustata* Baill. in Adansonia 12: 159. 1878, emend. Baum.-Bod., Ber. Schweiz Bot. Ges. 64: 133. 1954 [= *Arthrophyllum angustatum* (Baill.) Philipson], syn. nov.
- = *Eremopanax angustata* Baill. f. *angusticarpa* Baum.-Bod. in Ber. Schweiz Bot. Ges. 64: 134. 1954, syn. nov.
- = *Eremopanax angustata* Baill. f. *elliptica* Baum.-Bod. in Ber. Schweiz Bot. Ges. 64: 133. 1954, syn. nov.

- = *Eremopanax angustata* Baill. f. *intermedia* Baum.-Bod. in Ber. Schweiz Bot. Ges. 64: 134. 1954, syn. nov.
- = *Eremopanax angustata* Baill. f. *oblonga* Baum.-Bod. in Ber. Schweiz Bot. Ges. 64: 133. 1954, syn. nov.
- = *Eremopanax canalensis* E. G. Baker in A. B. Rendle et al. in J. Linn. Soc., Bot. 45: 323. 1921. [= *Eremopanax angustata* Baill. f. *canalensis* (E. G. Baker) Baum.-Bod.], syn. nov.
- = *Eremopanax schlechteri* Harms in Bot. Jahrb. Syst. 39: 217. 1906. [= *Arthropphyllum schlechteri* (Harms) Philipson], syn. nov.
- = *Eremopanax schlechteri* Harms f. *gracilis* Baum.-Bod. in Ber. Schweiz Bot. Ges. 64: 133. 1954, syn. nov.
- D26.** *Polyscias pacifica* (Philipson) Lowry & G. M. Plunkett, **comb. nov.** ≡ *Arthropphyllum pacificum* Philipson in Gard. Bull. Sing. 30: 306. 1977. — Maluku, Bismarck Archipelago.
- D27.** *Polyscias papyracea* (Philipson) Lowry & G. M. Plunkett, **comb. nov.** ≡ *Arthropphyllum papyraceum* Philipson in Gard. Bull. Sing. 30: 308. 1977. — Sumatra.
- D28.** *Polyscias prolifera* (Philipson) Lowry & G. M. Plunkett, **comb. nov.** ≡ *Arthropphyllum proliferum* Philipson in Gard. Bull. Sing. 30: 302. 1977. — Papua New Guinea.
- D29.** *Polyscias pulgarens* (Elmer) Lowry & G. M. Plunkett, **comb. nov.** ≡ *Arthropphyllum pulgarens* Elmer in Leaflet. Philip. Bot. 7: 2551. 1915. — Philippines.
- D30.** *Polyscias royenii* Philipson in Blumea 24: 170. 1978. — W. New Guinea.
- D31.** *Polyscias rubiginosa* (Ridl.) Lowry & G. M. Plunkett, **comb. nov.** ≡ *Arthropphyllum rubiginosum* Ridl. in Kew Bull. 1946: 40. 1946. — Borneo.
- D32.** *Polyscias rufosepala* (Ridl.) Lowry & G. M. Plunkett, **comb. nov.** ≡ *Arthropphyllum rufosepalum* Rild. in Kew Bull. 1946: 40. 1946. — Borneo.
- D33.** *Polyscias schultzei* Harms in Bot. Jahrb. Syst. 56: 410. 1921. — Makulu to New Guinea.
- D34.** *Polyscias stonei* (A. L. Lim) Lowry & G. M. Plunkett, **comb. nov.** ≡ *Arthropphyllum stonei* A. L. Lim in Malaysian Forester 43: 263. 1980. — Peninsular Malaysia.
- D35.** *Polyscias thailandica* Lowry & G. M. Plunkett, **nom. nov.** ≡ *Arthropphyllum ferrugineum* Craib in Bull. Misc. Inform. Kew 1930: 423. 1930, non *Polyscias ferruginea* (Hiern) Harms — Thailand.
- D36.** *Polyscias vieillardii* (Baill.) Lowry & G. M. Plunkett, **comb. nov.** ≡ *Eremopanax vieillardii* Baill. in Adansonia 12: 161. 1878 [= *Arthropphyllum vieillardii* (Baill.) Philipson ≡ *Nesodoxa vieillardii* (Baill.) Fedde].
- a. subsp. *vieillardii* — New Caledonia.
- b. subsp. *balansae* (Baill.) Lowry & G. M. Plunkett, **comb. et stat. nov.** ≡ *Eremopanax balansae* Baill. in Adansonia 12: 160. 1878. [= *Arthropphyllum balansae* (Baum.-Bod.) Philipson]. — New Caledonia.
- = *Eremopanax hederoides* Baum.-Bod. in Ber. Schweiz Bot. Ges. 64: 131. 1954. [= *Arthropphyllum hederoides* (Baum.-Bod.) Philipson], syn. nov.

- = *Eremopanax daenikeri* Baum.-Bod. in Ber. Schweiz Bot. Ges. 64: 132. 1954.
[= *Arthrophyllum daenikeri* (Baum.-Bod.) Philipson], syn. nov.
- = *Eremopanax glaberrima* Baum.-Bod. in Ber. Schweiz Bot. Ges. 64: 131. 1954.
[= *Arthrophyllum glaberrimum* (Baum.-Bod.) Philipson], syn. nov.
- D37. *Polyscias willmottii* (F. Muell.) Philipson in *Austrobaileya* 1: 24. 1977. — Queensland.
- D38. *Polyscias zippeliana* (Miq.) Valetton in Bull. Dép. Agric. Indes Néerl. 10: 42. 1907. — New Guinea, N Queensland.
- E. *Polyscias* subg. *Cuphocarpus* (Decne. & Planch.) Lowry & G. M. Plunkett, **comb. et stat. nov.** ≡ *Cuphocarpus* Decne. & Planch. in Rev. Hort. IV, 3: 109. 1854. — Type: *C. aculeata* Decne. & Planch. [= *Polyscias aculeata* (Decne. & Planch.) Harms].

Polyscias subg. *Cuphocarpus*, which corresponds to the *Cuphocarpus* subclade of the Indian Ocean Basin clade in our recent phylogeny (Plunkett & Lowry 2010), includes a single species, *P. aculeata*, endemic to coastal forests in eastern Madagascar. From the outset this taxon was recognized as a distinct genus because, unlike nearly all other Araliaceae known at the time, its flowers have a unilocular gynoecium, a feature also found in the species assigned to the Malesian genus *Arthrophyllum* (treated here as a subgenus within *Polyscias*). Over the last century and a half, nearly all authors have recognized *Cuphocarpus* as a distinct genus, the only major exception being Harms (1894–97), who included it in his broadly defined *Polyscias*.

Four additional species were described in *Cuphocarpus* by Bernardi (1966), all based on 20th century material collected in humid forest between 1,000 and 1,800 m elevation in northern Madagascar. Bernardi noted that they differ from the type species in having flowers borne in umbellules rather than racemes and that they have very different eco-geographic requirements, but the generic placement of these four taxa had not previously been doubted because they consistently exhibit unilocular flowers. Our phylogenetic studies show, however, that the montane species are nested within the clade recognized here as *Polyscias* subg. *Maralia* whereas the coastal taxon is sister to the largely African subgenus *Sciadopanax* (Plunkett & Lowry 2010), indicating that the evolution of a single carpel occurred on two separate occasions in Madagascar, and that *Cuphocarpus*, as defined by Bernardi (1966, 1980), is thus polyphyletic.

Taxon included:

- E1. *Polyscias aculeata* (Decne. & Planch.) Harms in Engl. & Prantl, Nat. Pflanzenfam. 3(8): 44. 1894. — Madagascar.
- = *Cuphocarpus inermis* Baker in Linn. Soc., Bot. 21: 350. 1884.
- F. *Polyscias* subg. *Tetraplasandra* (A. Gray) Lowry & G. M. Plunkett, **comb. et stat. nov.** ≡ *Tetraplasandra* A. Gray, U.S. Expl. Exped., Phan. 1: 727. 1854. — Type: *T. hawaiiensis* A. Gray [= *Polyscias hawaiiensis* (A. Gray) Lowry & G. M. Plunkett].

- = *Reynoldsia* A. Gray, U.S. Expl. Exped., Phan. 1: 723. 1854. — Lectotype: *R. sandwicensis* A. Gray [= *Polyscias sandwicensis* (A. Gray) Lowry & G. M. Plunkett], designated by Hutchinson in *Genera Fl. Pl.* 2: 58. 1968.
- = *Dipanax* Seem. in *J. Bot.* 6: 130. 1868. — Type: *D. dipyrena* (H. Mann) A. Heller [= *Polyscias kavaense* (H. Mann) Lowry & G. M. Plunkett].
- = *Triplasandra* Seem. in *J. Bot.* 6: 139. 1868. = *Tetraplasandra* sect. *Neotetraplasandra* Sherff in *Bot. Leaflet* 8: 12. 1953. — Lectotype (here designated): *T. oahuensis* (A. Gray) Seem. [= *Polyscias oahuensis* (A. Gray) Lowry & G. M. Plunkett].
- = *Heptapleurum* sect. *Pterotropia* H. Mann in *Proc. Amer. Acad. Arts* 7: 168. 1867 = *Pterotropia* (H. Mann) Hillebr. in *Fl. Hawaiian Isl.*: 149. 1888 = *Tetraplasandra* sect. *Pterotropia* (Hillebr.) Sherff in *Bot. Leaflet* 7: 10. 1952. — Lectotype (here designated): *H. kavaense* H. Mann [= *Polyscias kavaensis* (H. Mann) Lowry & G. M. Plunkett].
- = *Tetraplasandra* sect. *Eutetraplasandra* Harms in *Engl. & Prantl, Nat. Pflanzenfam.* 3(8): 29. 1894, nomen. superfl.
- = *Tetraplasandra* sect. *Nothotetraplasandra* Harms in *Engl. & Prantl, Nat. Pflanzenfam.* 3(8): 29. 1894. — Type: *T. meandra* (Hillebr.) Harms [= *Polyscias oahuensis* A. Gray] Lowry & G. M. Plunkett].
- = *Peekeliopanax* Harms in *Notizbl. Bot. Gart. Berlin-Dahlem* 9: 478. 1926. — Type: *P. spectabilis* Harms [= *Polyscias spectabilis* (Harms) Lowry & G. M. Plunkett].
- = *Munroidendron* Sherff in *Bot. Leaflet* 7: 21. 1952. — Type: *M. racemosum* (C. N. Forbes) Sherff [= *Polyscias racemosa* (C. N. Forbes) Lowry & G. M. Plunkett].

Polyscias subg. *Tetraplasandra* is circumscribed to include all of the species traditionally assigned to three central Pacific genera long regarded as closely related to one another (*Munroidendron*, *Reynoldsia* and *Tetraplasandra*), along with two Malesian species assigned by Philipson (1970, 1979, 1995) to *Gastonia* and four others he placed in *Polyscias* sect. *Eupteron* (Philipson 1978, 1979, 1995). This subgenus, which corresponds to the New Guinea-Polynesia clade in our phylogeny of *Polyscias* sensu lato (Plunkett & Lowry 2010), includes a total of 20 species that collectively range from Sumatra across Malesia to the Solomon Islands, and through southern Polynesia (Samoa, the Society Islands, and the Marquesas) to Hawaii.

Morphologically members of *Polyscias* subg. *Tetraplasandra* are rather heterogeneous, as reflected by the fact that they have historically been placed in five genera. Philipson (1970) provided a careful review of the features that he regarded as important for distinguishing *Gastonia* (which he restricted to species ranging from Malesia west to Madagascar and the Comoros) from those occurring in the central Pacific (often referred to as the *Tetraplasandra* group), although he unfortunately did not consider any of the other Malesian species we include here in the subgenus (viz. *P. belensis*, *P. borneensis*, *P. florosa* and *P. philipsonii*). Nonetheless, even without taking account of the latter taxa, Philipson (1970) acknowledged that establishing clear ge-

neric limits was problematical and could only be accomplished by using a combination of characters.

Costello & Motley (2007) examined relationships among the taxa comprising the *Tetraplasandra* group and showed that all of the species from Hawaii form a clade resulting from radiation following long-distance dispersal to the archipelago. Their findings also indicate that the taxa traditionally placed in *Reynoldsia* belong to two clades, one uniting the four species from southern Polynesia and another comprising two Hawaiian taxa, *R. sandwicensis* and the species usually placed in the segregate genus *Munroidendron*, whose long, pendant, racemose inflorescences give it a very distinctive appearance. Another curious member of this group is *P. gymnocarpa*, whose ovary appears to be fully superior, a derived condition in a family with otherwise exclusively inferior or rarely partially inferior ovaries (Costello & Motley 2004).

Several Hawaiian members of *Polyscias* subg. *Tetraplasandra* exhibit polymery. *Polyscias racemosa*, formerly treated as *Munroidendron*, has 12 to 20 petals, usually 10 or 15 stamens, and an ovary with as many as 15 carpels. Another species, *P. sandwicensis*, is typical of the taxa previously placed in *Reynoldsia* in having 8 to 12 petals and stamens, and up to 24 carpels. Similarly, several species traditionally placed in *Tetraplasandra* exhibit polymery, such as *P. hawaiiensis*, with 5-8 petals and up to 4 times as many stamens, along with a 7- to 13-carpellate ovary. Two other taxa previously included in *Tetraplasandra*, *P. waialealae* and *P. waimeae*, both endemic to Kauai, have flowers with up to 40 and 65 stamens, respectively, and produce copious nectar, suggesting possible bird pollination (Lowry 1990).

Philipson (1970, 1979, 1995) defined *Gastonia serratifolia* (Miq.) Philipson (treated here as *Polyscias serratifolia*) to encompass collections from throughout Malesia, including material from Palawan in the southwestern Philippines (described as *Tetraplasandra philipinensis* Merr.) that may represent a distinct taxon (J. Wen pers. comm.). Philipson (1970, 1979) also noted that *P. spectabilis* can reach 45 meters in height, making it the tallest Araliaceae. Lowry (1987, 1990) placed the taxa originally described as *Tetraplasandra bisattenuata* and *Triplisandra lydgatei* in synonymy under the variable Hawaiian species recognized here as *P. oahuensis*, but recent field investigations indicate that both are distinct and deserve recognition at the species level (Motley 2005; D. Lorence pers. comm.). Careful examination of collections historically treated as *Reynoldsia* shows that the two taxa from Samoa recognized by Frodin & Govaerts (2003) as *R. grayana* and *R. tauensis* represent the same entity as *R. lanutoensis* (treated here as *P. lanutoensis*), prompting us to include them in synonymy. Similarly, Frodin & Govaerts (2003) accepted both *R. tahitiensis* and *R. verrucosa* from the Society Islands, whereas we recognize only one species and therefore place the former in synonymy.

Taxa included:

- F1. *Polyscias belensis* Philipson in Bull. Brit. Mus. Nat. Hist., Bot. 1: 13. 1951. — New Guinea.
- F2. *Polyscias bisattenuata* (Sherff) Lowry & G. M. Plunkett, **comb. nov.** ≡ *Tetraplasandra bisattenuata* Sherff in Bot. Leaflet, 6: 26. 1952. — Hawaii.

- F3. *Polyscias borneensis* Philipson in J. Bot. 78: 118. 1940. — Borneo, Philippines.
- F4. *Polyscias florosa* Philipson in Blumea 24: 170. 1978. — Philippines.
- F5. *Polyscias flynnii* (Lowry & K. R. Wood) Lowry & G. M. Plunkett, **comb. nov.** ≡ *Tetraplasandra flynnii* Lowry & K. R. Wood in Novon 10: 40. 2000. — Hawaii.
- F6. *Polyscias gymnocarpa* (Hillebr.) Lowry & G. M. Plunkett, **comb. nov.** ≡ *Pterotropia gymnocarpa* Hillebr. in Fl. Haw. Isl., 150. 1888 [≡ *Tetraplasandra gymnocarpa* (Hillebr.) Sherff]. — Hawaii.
- F7. *Polyscias hawaiiensis* (A. Gray) Lowry & G. M. Plunkett, **comb. nov.** ≡ *Tetraplasandra hawaiiensis* A. Gray in U.S. Expl. Exped., Phan. 1: 728. 1854. — Hawaii.
- F8. *Polyscias kavaensis* (H. Mann) Lowry & G. M. Plunkett, **comb. nov.** ≡ *Hep-
tapleurum kavaense* H. Mann in Proc. Amer. Acad. Arts 7: 168. 1867 [≡ *Tetra-
plasandra kavaensis* (H. Mann) Sherff]. — Hawaii.
- F9. *Polyscias lanutoensis* (Hochr.) Lowry & G. M. Plunkett, **comb. nov.** ≡ *Reynoldsia lanutoensis* Hochr. in Candollea 2: 482. 1925. — Samoa.
= *Reynoldsia grayana* Christoph. in Bull. Bernice P. Bishop Mus. 128: 161. 1935, syn. nov.
= *Reynoldsia tauensis* A. C. Smith & B. C. Stone in J. Arnold Arbor. 49: 465. 1968, syn. nov.
- F10. *Polyscias lydgatei* (Hillebr.) Lowry & G. M. Plunkett, **comb. nov.** ≡ *Triplasan-
dra lydgatei* Hillebr., Fl. Hawaiian Isl.: 135. 1888. [≡ *Tetraplasandra lydgatei*
(Hillebr.) Harms] — Hawaii.
- F11. *Polyscias marchionensis* (F. Brown) Lowry & G. M. Plunkett, **comb. nov.** ≡ *Reynoldsia marchionensis* F. Brown in Bull. Bernice P. Bishop Mus. 130: 209. 1935. — Marquesas Isl.
- F12. *Polyscias oahuensis* (A. Gray) Lowry & G. M. Plunkett, **comb. nov.** ≡ *Gastonia oahuensis* A. Gray in U. S. Expl. Exped., Phan. 1: 726. 1854 [≡ *Tetraplasandra oahuensis* (A. Gray) Harms]. — Hawaii.
- F13. *Polyscias philipsonii* Bernardi in Ber. Schweiz. Bot. Ges. 76: 377. 1966. — New Guinea.
- F14. *Polyscias pleiosperma* (A. Gray) Lowry & G. M. Plunkett, **comb. nov.** ≡ *Reynoldsia pleiosperma* A. Gray in U. S. Expl. Exped., Phan. 1: 725. 1854. — Samoa.
- F15. *Polyscias racemosa* (Forbes) Lowry & G. M. Plunkett, **comb. nov.** ≡ *Tetraplasandra racemosa* Forbes in Occ. Papers Bernice P. Bishop Mus. 6: 4. 1917. [≡ *Munroidendron racemosum* (Forbes) Sherff]. — Hawaii.
- F16. *Polyscias sandwicensis* (A. Gray) Lowry & G. M. Plunkett, **comb. nov.** ≡ *Reynoldsia sandwicensis* A. Gray in U. S. Expl. Exped., Phan. 1: 724. 1854. — Hawaii.
- F17. *Polyscias serratifolia* (Miq.) Lowry & G. M. Plunkett, **comb. nov.** ≡ *Arthrophyllum serratifolium* Miq. in Fl. Ned. Ind., Eerste Bijv.: 341. 1861 [≡ *Gastonia serratifolia* (Miq.) Philipson]. — Malesia to Solomon Isl.
- F18. *Polyscias spectabilis* (Harms) Lowry & G. M. Plunkett, **comb. nov.** ≡ *Peeke-*

- liopanax spectabilis* Harms in Notizbl. Bot. Gart. Berlin-Dahlem 9: 478. 1926 [≡ *Gastonia spectabilis* (Harms) Philipson]. — New Guinea to Solomon Isl.
- F19.** *Polyscias verrucosa* (Seem.) Lowry & G. M. Plunkett, **comb. nov.** ≡ *Reynoldsia verrucosa* Seem. in J. Bot. 2: 245. 1864. — Society Isl.
= *Reynoldsia tahitiensis* Nadeaud in Enum. Pl. Tahiti: 63. 1873, syn. nov.
- F20.** *Polyscias waialealae* (Rock) Lowry & G. M. Plunkett, **comb. nov.** ≡ *Tetraplasandra waialealae* Rock in Coll. Hawaii Publ. Bull. 1: 10. 1911. — Hawaii.
- F21.** *Polyscias waimeae* (Wawra) Lowry & G. M. Plunkett, **comb. nov.** ≡ *Tetraplasandra waimeae* Wawra in Flora 56: 158. 1873. — Hawaii.
- G.** *Polyscias* subg. *Eupteron* (Miq.) Lowry & G. M. Plunkett, **comb. et stat. nov.** ≡ *Eupteron* Miq. in Bonplandia 4: 139. 1856. ≡ *Polyscias* sect. *Eupteron* (Miq.) Philipson in Blumea 24: 170. 1978. — Type: *E. nodosum* (Blume) Miq. [≡ *Polyscias nodosa* (Blume) Seem.].

As circumscribed here, *Polyscias* subg. *Eupteron* includes a single species, *P. nodosa*, which is widely distributed across Malesia and extends into the Solomon Islands, often colonizing open, disturbed habitats. It can easily be recognized by its large pinnately compound leaves up to perhaps 3 meters in length and bearing 35 to more than 50 leaflets, as well as its large paniculate inflorescences with the flowers borne in capitula.

The generic name *Eupteron*, proposed by Miquel in 1856 based on *P. nodosa* and a second species, *P. acuminata* from India and Sri Lanka, has been adopted by only a few authors during the last 150 years, most notably Hutchinson (1967). Philipson (1978, 1979, 1995) treated *Eupteron* as a section within *Polyscias*, expanding its circumscription to include several additional Malesian species with flowers arranged in umbellules or capitula, placing primary emphasis to define the group on the presence of fruits whose style arms are radiating or recurved. The results of our phylogenetic analyses show, however, that Philipson's broadened concept of the *Eupteron* group is not monophyletic; *P. nodosa* occupies an isolated position within *Polyscias* sensu lato whereas the other taxa belong to the clade we recognize here as *Polyscias* subg. *Tetraplasandra* (Plunkett & Lowry 2010). The relationships of *P. acuminata*, which we have not yet been able to include in our molecular analyses, are not clear but they most likely lie either with *P. nodosa* or with the members of subgenus *Tetraplasandra*.

Taxon included:

- G1.** *Polyscias nodosa* (Blume) Seem. in J. Bot. 3: 181. 1865. — Malesia, Philippines, Solomon Isl.
- H.** *Polyscias* subg. *Sciadopanax* (Seem.) Lowry & G. M. Plunkett, **comb. et stat. nov.** ≡ *Sciadopanax* Seem. in J. Bot. 3: 73. 1865. — Type: *S. boivinii* Seem. [≡ *Polyscias boivinii* (Seem.) Bernardi].

Polyscias subg. *Sciadopanax* comprises 13 species from Africa (including the offshore islands of São Tomé and Príncipe), Madagascar and the Comoro Islands, and corre-

sponds to the *P. fulva* subclade of the Indian Ocean clade in our phylogeny (Plunkett & Lowry 2010). Originally circumscribed by Seemann (1865) as a genus with just a single species from Madagascar, it was later expanded by Viguier (1905) to encompass five of the taxa recognized here, two from Madagascar and three from Africa (plus six others now placed in synonymy), using a circumscription identical to the one adopted below. Until recently, authors mostly treated *Sciadopanax* in its original monotypic sense, i.e., to comprise only *S. boivinii* (e.g., Harms 1894–97; Hutchinson 1967), but more recently Tennant (1968) included it in *Polyscias*, and while Bernardi (1966) initially recognized *Sciadopanax* he later placed it in synonymy as well (1971, 1980), an approach followed by Bamps (1974a, 1974b, 1989) and Beentje (1994).

Members of *Polyscias* subg. *Sciadopanax* are characterized by flowers with a bicarpellate gynoeceum and styles that are united basally to form a conical disc or stylopodium bearing two short styles or sessile stigmas. The leaves of most species have stellate, often farinose indumentum, which is also frequently found on the inflorescence. The subgenus has both evergreen species growing in humid habitats in Africa, including primary forest (such as *P. albersiana* and *P. quintasii*) and more disturbed or secondary vegetation (e.g., *P. fulva*), as well as deciduous taxa occurring in drier habitats (including *P. farinosa* and *P. kikuyuensis* in Africa, *P. mayottensis* in the Comores, and all three species in Madagascar). Some members of the group are very large, especially *P. quintasii*, a canopy tree that can reach 30 m in height, whereas others are much smaller, such as the recently discovered Central African inselberg specialist *P. aequatoguineensis*, a shrub or small tree up to only about 3 meters tall (Lejoly & Lisowski 1999).

Taxa included:

- H1.** *Polyscias aequatoguineensis* Lejoly & Lisowski in Bull. Jard. Bot. Natl. Belgique 67: 112. 1999. — Equatorial Guinea (Rio Muni), Gabon.
- H2.** *Polyscias albersiana* Harms in Bot. Jahrb. Syst. 33: 182. 1902. — Tanzania.
- H3.** *Polyscias baehniana* (Bernardi) Bernardi in Candollea 26: 21. 1971. — Madagascar.
- H4.** *Polyscias boivinii* (Seem.) Bernardi in Candollea 26: 23. 1971. — Madagascar.
- H5.** *Polyscias farinosa* (Delile) Harms in Engl. & Prantl, Nat. Pflanzenfam. 3(8): 45. 1894. — Ethiopia.
- H6.** *Polyscias floccosa* (Drake) Bernardi in Candollea 26: 22. 1971. — Madagascar.
- H7.** *Polyscias fulva* (Hiern) Harms in Engl. & Prantl, Nat. Pflanzenfam. 3(8): 45. 1894. — Tropical Africa.
- H8.** *Polyscias kikuyuensis* Summerh. in Bull. Misc. Inform. Kew 1926: 242. 1926. — Kenya.
- H9.** *Polyscias kivuensis* Bamps in Bull. Jard. Bot. Belg. 41: 249. 1971. — E Dem. Republ. Congo.
- H10.** *Polyscias letestui* C. Norman in J. Bot. 75: 167. 1937. — Gabon, Angola.
- H11.** *Polyscias mayottensis* Lowry, O. Pascal & Labat in Adansonia, sér. 3, 21: 69. 1999. — Comoro Isl. (Mayotte, Moheli).

- H12. *Polyscias quintasii* Exell in Cat. Vasc. Pl. S. Tome: 195. 1944. — São Tomé, Príncipe.
- H13. *Polyscias richardsiae* Bamps in Bull. Jard. Bot. Belg. 47: 260. 1977. — Tanzania.

- I. *Polyscias* subg. *Tieghemopanax* (R. Vig.) Lowry & G. M. Plunkett, **comb. et stat. nov.** \equiv *Tieghemopanax* R. Vig. in Bull. Soc. Bot. France 52: 305. 1905. — Lectotype: *T. balansae* (Baill.) R. Vig. [\equiv *Polyscias balansae* (Baill.) Harms], designated by Hutchinson in Genera Fl. Pl. 2: 75. 1967.
- = *Gelibia* Hutch., Genera Fl. Pl. 2: 57. 1967 \equiv *Polyscias* sect. *Gelibia* (Hutch.) Philipson in Blumea 24: 169. 1978. — Type: *G. branderhorstii* (Harms) Hutch. [= *P. elegans* (C. Moore & F. Muell.) Harms].
- = *Montagueia* E. G. Baker in Rendle et al. in J. Linn. Soc., Bot. 45: 291. 1921. — Type: *M. haplostemon* E. G. Baker [= *P. cissodendron* (C. Moore & F. Muell.) Harms].

Polyscias subg. *Tieghemopanax* corresponds to the *Tieghemopanax* clade identified in several recent studies (Eibl et al. 2001; Lowry et al. 2004; Plunkett et al. 2001, 2004b) and confirmed in our companion paper (Plunkett & Lowry 2010). This group was first recognized by Viguier (1905) as a new genus, which he circumscribed to include species whose flowers have a bicarpellate gynoecium and styles that are free or united only at the base. He recognized 26 species, including 20 from New Caledonia (eight of which are accepted below, either as species or subspecies, with the remainder placed in synonymy), along with five occurring in Australia (three of which we do not include in subgenus *Tieghemopanax*, i.e., *P. macgillivrayi*, *P. mollis* and *P. murrayi*) and one from Madagascar (*P. cussonioides*, which we place here in subgenus *Maralia*). Viguier (1905) also doubtfully assigned three other species to his new genus, all of which we place in *Polyscias* subg. *Polyscias* (viz., *P. multijuga*, *P. reineckeii* and *P. samoensis*). Over the last century, *Tieghemopanax* was accepted by only a few authors (e.g., Guillaumin 1938; Hutchinson 1967) while most others (e.g., Smith & Stone 1965; Stone 1965; Bernardi 1971; Smith 1985; Lowry 1989; Frodin & Govaerts 2003) included it within *Polyscias*.

Members of *Polyscias* subg. *Tieghemopanax* form a morphologically and geographically coherent group. In addition to sharing the diagnostic features used by Viguier (1905), all of the taxa included here have leaves that lack a sheathing petiole base (except in *P. elegans*, whose petiole is weakly clasping). There is also a tendency toward having leaflets that are thick and often coriaceous (notable exceptions being *P. bracteata* subsp. *bracteata*, *P. cissodendron*, *P. crenata* and *P. schmidii*). The group is centered in New Caledonia, where ten of the 15 currently recognized species occur (all except one endemic), with two species occurring in Fiji, one in NE Australia and New Guinea, one endemic to Australia, and one restricted to Vanuatu. Recent field work and herbarium studies have revealed 12 additional species, all endemic to New Caledonia, which are being described in a forthcoming revision (Lowry & Plunkett in prep.).

Taxa included:

11. *Polyscias balansae* (Baill.) Harms in Engl. & Prantl, Nat. Pflanzenfam. 3(8): 44. 1894. — New Caledonia.
 12. *Polyscias bracteata* (R. Vig.) Lowry in D. Frodin & R. Govaerts, World Checklist Bibliogr. Araliaceae: 284. 2004. — New Caledonia.
 - a. subsp. *bracteata*. — New Caledonia.
 - b. subsp. *subincisa* (R. Vig.) Lowry & G. M. Plunkett, **comb. et stat. nov.** \equiv *Tieghemopanax subincisus* R. Vig. in Bull. Soc. Bot. France 52: 307. 1905. [\equiv *Polyscias subincisa* (R. Vig.) Lowry]. — New Caledonia.

= *Tieghemopanax sessiliflorus* R. Vig. in Bull. Soc. Bot. France 52: 308. 1905, syn. nov.
 13. *Polyscias cissodendron* (C. Moore & F. Muell.) Harms in Engl. & Prantl, Nat. Pflanzenfam. 3(8): 45. 1894. — New Caledonia, Lord Howe Island, Vanuatu, Santa Cruz Isl.
 14. *Polyscias crenata* (Pancher & Sebert) Frodin in D. Frodin & R. Govaerts, World Checklist Bibliogr. Araliaceae: 285. 2004. — New Caledonia.
 15. *Polyscias culminicola* A. C. Smith in Contrib. U.S. Natl. Herb. 37: 85. 1967. — Fiji.
 16. *Polyscias dioica* (Vieill. ex Pancher) Harms in Engl. & Prantl, Nat. Pflanzenfam. 3(8): 45. 1894. — New Caledonia.
 17. *Polyscias elegans* (C. Moore & F. Muell.) Harms in Engl. & Prantl, Nat. Pflanzenfam. 3(8): 45. 1894. — New Guinea, NE Australia.
 18. *Polyscias joskei* Gibbs in J. Linn. Soc., Bot. 39: 148. 1909. — Fiji.
 19. *Polyscias lecardii* (R. Vig.) Lowry in D. Frodin & R. Govaerts, World Checklist Bibliogr. Araliaceae: 291. 2004. — New Caledonia.
 110. *Polyscias microbotrys* (Baill.) Harms in Engl. & Prantl, Nat. Pflanzenfam. 3(8): 45. 1894. — New Caledonia.
 111. *Polyscias pancheri* (Baill.) Harms in Engl. & Prantl, Nat. Pflanzenfam. 3(8): 45. 1894. — New Caledonia.
 112. *Polyscias sambucifolia* (Sieb. ex DC.) Harms in Engl. & Prantl, Nat. Pflanzenfam. 3(8): 45. 1894. — E & SE Australia.
 113. *Polyscias schmidii* Lowry in Bull. Mus. Natl. Hist. Nat., Paris, sér. 4, sect. B, Adansonia 11: 140. 1989. — Vanuatu.
 114. *Polyscias scopoliae* (Baill.) Lowry in D. Frodin & R. Govaerts, World Checklist Bibliogr. Araliaceae: 298. 2004. — New Caledonia.
 115. *Polyscias weinmanniae* (Baill.) Harms in Engl. & Prantl, Nat. Pflanzenfam. 3(8): 45. 1894. — New Caledonia.
- J. *Polyscias* subg. *Indokingia* (Hemsl.) Lowry & G. M. Plunkett, **comb. et stat. nov.** \equiv *Indokingia* Hemsl. in Hooker's Icon. Pl. 29: t. 2805. 1909. — Type: *I. crassa* Hemsl. [\equiv *Polyscias crassa* (Hemsl.) Lowry & G. M. Plunkett].

Polyscias subg. *Indokingia* corresponds to a small group referred to in our companion paper as the Seychelles clade (Plunkett & Lowry 2010), which comprises just three species, all endemic to the Seychelles Islands. Hemsley (1909) described *Indokingia* to

accommodate the species referred to here as *P. crassa*, which he curiously distinguished from the unrelated (albeit also polymerous) palmate-leaved genus *Tupidanthus*, mentioning only that the new plant from the Seychelles had foliage that resembled *Gastonia cutispongia* from Réunion. Friedmann (1986) transferred this taxon to *Gastonia* and described a new species in that genus, both of which possess inarticulate pedicels, a feature shared with the third Seychelles species that had been included in *Gastonia* by Harms nearly a century earlier (1894-97).

Many groups of plants show strong phytogeographic ties between the Seychelles and Madagascar (Schatz 1996), at least in part reflecting their geological history (the two landmasses were connected until the Seychelles separated and began to move northward with the Indian plate ca. 88 ma; Storey et al. 1995). The results of our phylogenetic studies (Plunkett & Lowry 2010) suggest, however, that the taxa in *Polyscias* subg. *Indokingia* are not closely related to species in either subgenus *Maralia* or *Sciadopanax*, the two groups present on Madagascar, but rather have evolved from a common ancestor that colonized the archipelago from the east, most likely somewhere in Australasia.

Taxa included:

- J1. *Polyscias crassa* (Hemsl.) Lowry & G. M. Plunkett, **comb. nov.** \equiv *Indokingia crassa* Hemsl. in Hooker's Icon. Pl. 29: t. 2805. 1906. [\equiv *Gastonia crassa* (Hemsl.) F. Friedmann]. — Seychelles.
- J2. *Polyscias lionnetii* (F. Friedmann) Lowry & G. M. Plunkett, **comb. nov.** \equiv *Gastonia lionnetii* F. Friedmann in Bull. Mus. Natl. Hist. Nat., Paris, sér. 4, sect. B, Adansonia 4: 253. 1986. — Seychelles.
- J3. *Polyscias sechellarum* Baker in Fl. Mauritius Seych.: 128. 1877. [\equiv *Gastonia sechellarum* (Baker) Harms]. — Seychelles.
- K. *Polyscias* subg. *Palmervandenbroekia* (Gibbs) Lowry & G. M. Plunkett, **comb. et stat. nov.** \equiv *Palmervandenbroekia* Gibbs in Fl. Arfak Mts.: 162. 1917. \equiv *Polyscias* sect. *Palmervandenbroekia* (Gibbs) Philipson in Blumea 24: 171. 1978. — Type: *Palmervandenbroekia papuana* Gibbs \equiv *Polyscias palmervandenbroekii* Bernardi, non *Polyscias papuana* (Miq.) Seem. (1965).

Polyscias subg. *Palmervandenbroekia* is a small, geographically restricted group of five species occurring in mid- to high-elevation primary forest on New Guinea (the Vogelkop Peninsula, Cyclops Mountains and the central range in West Papua and Papua, Indonesia, as well as the Western District of Papua New Guinea). Gibbs (1917) described the monotypic genus *Palmervandenbroekia* to accommodate a distinctive new species (*P. papuana*) characterized by flowers with a bicarpellate gynoeceum and united styles forming a short, beak-like projection in fruit. Bernardi (1971) placed *Palmervandenbroekia* in synonymy under *Polyscias* and published a new name for the type species as the combination in the latter genus was already occupied. Philipson (1978) formally recognized the group as a section within *Polyscias* and described three new species based on material examined in preparation for his revision of Araliaceae for *Flora Malesiana* (Philipson 1978).

Philipson (1995) suggested that a fifth species from the mountainous interior of New Guinea, described as *Polyscias roemeriana* Harms, might also belong to the *Palmervandenbroekia* group, based on the description provided by Harms (1921), and in particular on the presence of a compact inflorescence, flowers with a bicarpellate gynoeccium, and long, united styles. Phillipson pointed out that if this placement were correct, *P. roemeriana* would surely represent a distinct member of the *Palmervandenbroekia* group by virtue of its bipinnate (vs. once-pinnate) leaves. He refrained, however, from placing *P. roemeriana* among the species he recognized, treating it instead as an insufficiently known taxon because the holotype at Berlin had been destroyed and he had not found any additional material. While examining the unidentified material of *Polyscias* at the herbarium in Leiden, a collection with bipinnate leaves made in 1988 in central New Guinea was found that appeared to belong to *Polyscias* subg. *Palmervandenbroekia*. Careful comparison of this gathering with the protologue of *P. roemeriana* clearly shows that it belongs to this taxon. We have therefore listed *P. roemeriana* below as the fifth member of the subgenus, and have designated this recently identified collection as its neotype.

We have not yet been able to include any members of *Polyscias* subg. *Palmervandenbroekia* in our molecular phylogenetic studies, but there seems little doubt that the group belongs to *Polyscias* sensu lato. Moreover, the distinctive morphology of these species, combined with their restricted geographic range and similar ecological preferences, strongly suggest that they form a clade. Until phylogenetic data become available and we are able to determine the position of the *Palmervandenbroekia* group within *Polyscias*, we have opted to follow the approach used for the main clades elucidated by our molecular studies (Plunkett & Lowry 2010) and recognize this distinctive entity at the subgeneric rank.

Taxa included:

- K1.** *Polyscias palmervandenbroekii* Bernardi in Candollea 26: 16. 1971. \equiv *Palmervandenbroekia papuana* Gibbs (1917), non *Polyscias papuana* (Miq.) Seem. (1865). — W Papua.
- K2.** *Polyscias jacobsii* Philipson in Blumea 24: 171. 1978. — W Papua.
- K3.** *Polyscias roemeriana* Harms in Bot. Jahrb. Syst. 56: 411. 1921. — Type: Indonesia, Papua: Valentijn Mts., trail between Koruppun and Angguruk, 'Menagmok' forest camp, 4°24'S, 139°37'E, 2600 m, 19.VII.1988, *J.-M. Mangen 2131*, neotype L (0794866)!, isoneotype: A (image seen). — New Guinea. — As the holotype at Berlin [Southwest New Guinea, *von Roemer* (Exped. Lorentz) 1239, B†] was destroyed and no isotypes have been located, we have designated the only other known collection, gathered some 100 km to the east of the original locality, as the neotype.
- K4.** *Polyscias sleumeri* Philipson in Blumea 24: 171. 1978. — W Papua.
- K5.** *Polyscias vogelkopensis* Philipson in Blumea 24: 171. 1978. — W Papua.

Taxa incertae sedis:

- Polyscias acuminata* (Wight) Seem. in J. Bot. 3: 181. 1865. — S. India, Sri Lanka.
— This species was originally included in the genus *Eupteron* along with

P. nodosa, but its relationships can not easily be deduced from morphology and may alternatively lie with the members of *Polyscias* subgenus *Tetraplasandra*. The placement of *P. acuminata* within our classification of *Polyscias* will therefore have to wait until we are able to obtain molecular sequence data.

Polyscias macdowallii (F. Muell.) Domin in *Biblioth. Bot.* 89: 483. 1928. — Queensland. — This species, which was accepted by Frodin & Govaerts (2003), appears to be similar (if not identical) to *P. mollis* based on published descriptions. However, because we have not yet been able to examine any authentic material, we prefer to refrain from assigning *P. macdowallii* to a subgenus until morphological and/or molecular data are available that provide an indication of its relationships.

Polyscias mollis (Benth.) Harms in *Engl. & Prantl, Nat. Pflanzenfam.* 3(8): 45. 1894. — Queensland. — The placement of this species remains poorly resolved and/or weakly supported in the phylogenetic trees based on molecular data. In some trees, *P. mollis* is part of a basal polytomy. In other trees, it is sister to a clade comprising *P. purpurea* (see below) and the taxa forming *Polyscias* subg. *Arthrophyllum*, or allied to a much larger clade uniting subgenera *Maralia*, *Grotenfendia*, *Sciadopanax*, *Cuphocarpus*, *Tetraplasandra*, *Indokingia* and *Tieghemopanax*. Given these disparities, it would be premature to assign *P. mollis* to any of the subgenera recognized here.

Polyscias murrayi (F. Muell.) Harms in *Engl. & Prantl, Nat. Pflanzenfam.* 3(8): 45. 1894. — Queensland. — Frodin & Govaerts (2003) recognized this taxon, indicating that it occurs in New South Wales, Queensland and Victoria. Philipson (1979, 1995) noted that *P. murrayi* is similar to *P. ledermannii* from New Guinea, which he included in his expanded (and polyphyletic) *Polyscias* sect. *Eupteron*. Examination of specimens in several herbaria confirms that the leaves, inflorescences and fruits of these two species indeed share a strong resemblance, supporting Philipson's idea that they are closely related. Unfortunately, our phylogenetic trees provide little clue as to the placement of *P. murrayi* (which falls in a polytomy at or near the base of *Polyscias* sensu lato), and we have not been able to obtain samples of *P. ledermannii* for use in molecular studies. Both species are thus left incertae sedis.

Polyscias ledermannii Harms in *Bot. Jahrb. Syst.* 56: 409. 1921. — New Guinea. — As noted above, this species is morphologically very similar to *P. murrayi* and will probably prove to be its closest relative.

Polyscias pentamera (Baker) Harms in *Engl. & Prantl, Nat. Pflanzenfam.* 3(8): 44. 1894. — Madagascar. — This species appears to fall within the range of morphological variation exhibited by members of *Polyscias* subg. *Maralia*, and we would have no difficulty including it there were it not for the fact that it is placed outside the corresponding clade in our molecular phylogeny (Plunkett & Lowry 2010). Instead, *P. pentamera* occupies an unresolved position at the base of the large Indian Ocean Basin clade, which also includes four other clades represented by subgenera *Grotenfendia*, *Cuphocarpus*, *Sciadopanax* and *Maralia*, a finding that is rather difficult to reconcile with both morphology and geography. We anticipate that additional data might confirm the inclusion of

P. pentamera in subgenus *Maralia*, but until that time we prefer to refrain from assigning it there.

Polyscias purpurea C. T. White in Proc. Roy. Soc. Queensland 47: 64. 1935 (publ. 1936). — Queensland. — The placement of this species tracks closely that of *P. mollis* in the phylogenetic trees based on molecular data (see above). Neither taxon falls consistently in any single clade, and no clear indication of their relationships can be deduced from morphology or geography. We therefore prefer to take a conservative approach, leaving both species unplaced, pending future research.

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