

## A phylogenetic classification of *Phyllanthaceae* (*Malpighiales*; *Euphorbiaceae sensu lato*)

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**Summary.** A phylogenetic classification of *Phyllanthaceae* Martynov (*Malpighiales*) is presented. *Phyllanthaceae* are one of five segregates of *Euphorbiaceae sensu lato* recognised at family level by the Angiosperm Phylogeny Group. The family contains c. 2000 species in 59 presently accepted genera, 10 tribes and two subfamilies. This new classification is based on molecular studies using DNA sequence data of nuclear *PHYC* and plastid *atpB*, *matK*, *ndhF* and *rbcL* in conjunction with morphological characters. The main division into two strongly supported clades is not reflected in previous classifications, although the racemose clade (*Antidesmatoideae*) roughly corresponds to *Antidesmateae* + *Bischofiaeae* + *Hymenocardieae sensu Webster*. The fasciculate clade (*Phyllanthoideae sensu stricto*) contains all remaining tribes of *Phyllanthoideae sensu Webster*. Composition of the tribes differs considerably from previous classifications. Tribe *Jablonskieae* and subtribe *Keayodendrinae* are newly described. *Richeriella* is subsumed in *Flueggea* and the new genus *Plagiocladus* is described. *Phyllanthus sensu lato* is monophyletic excluding *Plagiocladus* and including *Breynia*, *Glochidion*, *Phyllanthodendron*, *Recherchonia* and *Sauropus*. Descriptions of the suprageneric taxa recognized are provided.

**Key words.** *Jablonskieae*, *Keayodendrinae*, *Phyllanthaceae*, *Plagiocladus*, *Richeriella*, classification, molecular phylogenetics.

### Introduction

Affinities of *Euphorbiaceae* Juss. *sensu lato* have long been unclear (reviewed by Webster 1987), and precise circumscription was complicated by the considerable diversity of vegetative, floral and fruit forms. *Euphorbiaceae sensu lato* were defined by a few shared morphological characters including unisexual flowers with superior syncarpous ovaries, apical-axile placentation and one or two epitropous ovules per locule. Characters that are usually present include alternate, stipulate leaves, actinomorphic flowers, presence of a floral disc, pistillode and obturator, as well as a tricarpetate, explosively dehiscent schizocarp leaving a central columella. The fruit type, although strongly modified in a number of genera, is a unique characteristic of this group and instantly identifies taxa which possess it as *Euphorbiaceae sensu lato*.

Molecular systematic studies in the last 15 years have illuminated family relationships and circumscriptions throughout the angiosperms. *Euphorbiaceae sensu lato* were first shown to be potentially polyphyletic by Chase

*et al.* (1993) based on *rbcL* sequence data of *Drypetes* Vahl (now in *Putranjivaceae* Meisn.) and *Euphorbia* L. (*Euphorbiaceae sensu stricto*). Since then, various publications have corroborated and refined these results with further taxon sampling (Wurdack & Chase 1996; Fay *et al.* 1997; Litt & Chase 1999; Savolainen *et al.* 2000b; Chase *et al.* 2002) and additional genetic markers (Soltis *et al.* 1997, 2000; Savolainen *et al.* 2000a; Tokuoka & Tobe 2002; Wurdack 2002; Davis & Chase 2004; Davis *et al.* 2005). The most recent classification of angiosperms (APG 2003) recognises five lineages of *Euphorbiaceae sensu lato* at family rank: *Euphorbiaceae sensu stricto*, *Pandaceae* Engl. & Gilg, *Phyllanthaceae* Martynov, *Picrodendraceae* Small and *Putranjivaceae*. All are members of *Malpighiales* Mart. in the eurosid I clade (fabids) and are currently placed unresolved or in unsupported relationships along the spine of the ordinal tree (e.g., Davis *et al.* 2005).

Composition of these five families was inferred to be coincident with taxa in Webster's (1994) and Radcliffe-Smith's (2001) infrafamilial classification

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(see summary below). The first comprehensive study of one of the segregate families, *Phyllanthaceae*, was published by Wurdack *et al.* (2004). It used *rbcl* sequence data of 52 genera including all tribes of *Euphorbiaceae-Phyllanthoideae* as well as selected outgroup taxa of the other subfamilies *sensu* Webster (1994) and Radcliffe-Smith (2001), representing all five euphorbiaceous families *sensu* APG II. Samuel *et al.* (2005) found results from *matK* and *PHYC* sequence data to be congruent with those obtained from *rbcl*. Kathriarachchi *et al.* (2005) presented the most complete phylogenetic analysis of *Phyllanthaceae* to date, combining data from five genes, plastid *atpB*, *matK*, *ndhF*, *rbcl* and nuclear *PHYC*, for 53 of 59 genera here included in the family. Wurdack *et al.* (2005) analysed the largest segregate *Euphorbiaceae sensu stricto* using *rbcl* and *trnl-F* sequence data. A

study of *Picrodendraceae* (Wurdack *et al.*, unpublished manuscript) based on four loci will include minor adjustments to the tribal classification of this group. The eight-loci phylogenetic study of all major lineages of *Malpighiales* (Wurdack & Davis, unpublished manuscript) shows a strongly supported sister-relationship of *Phyllanthaceae* and *Picrodendraceae*, which could be united as one family. A proposal to conserve *Phyllanthaceae* has been submitted (Reveal *et al.* unpublished manuscript) to allow the combination of these two groups under the earlier name *Phyllanthaceae* (*Picrodendraceae* is already conserved), whereas anyone recognising both clades at the rank of family would be able to use *Picrodendraceae*. The revised circumscriptions of segregate families (*sensu* APG 2003) from *Euphorbiaceae sensu lato* are summarised in Table 1.

Table 1.

<b>EUPHORBIACEAE SENSU STRICTO</b>	<i>Acalyphoideae</i> (excluding <i>Dicoelieae</i> and <i>Galearieae</i> ) + <i>Crotonoideae</i> + <i>Euphorbioideae sensu</i> Webster (1994) and Radcliffe-Smith (2001)
<b>PANDACEAE</b>	<i>Acalyphoideae-Galearieae sensu</i> Webster (1994) and Radcliffe-Smith (2001)
<b>PHYLLANTHACEAE</b>	<i>Phyllanthoideae sensu</i> Webster (1994) excluding <i>Drypetes</i> , <i>Phyllanoa</i> Croizat, <i>Putranjiva</i> Wall., <i>Sibangea</i> Oliv. but including <i>Croizatia</i> Steyerl., <i>Dicoelia</i> Benth., <i>Tacarcuna</i> Huft; <i>sensu</i> Radcliffe-Smith (2001) also excluding <i>Centroplacus</i> Pierre
<b>PICRODENDRACEAE</b>	<i>Oldfieldioideae sensu</i> Webster (1994) and Radcliffe-Smith (2001) excluding <i>Croizatia</i> and <i>Paradrypetes</i> Kuhlman.
<b>PUTRANJIVACEAE</b>	<i>Phyllanthoideae-Drypeteae sensu</i> Webster (1994) and Radcliffe-Smith (2001) excluding <i>Lingelsheimia</i> Pax
Excluded taxa	<i>Centroplacus</i> ( <i>Centroplacaceae</i> ), <i>Paradrypetes</i> (incertae sedis near <i>Rhizophoraceae</i> ), <i>Phyllanoa</i> ( <i>Violaceae</i> ; Hayden & Hayden 1996)

In this paper we present a phylogenetic classification of *Phyllanthaceae*, the second largest segregate of *Euphorbiaceae sensu lato*, comprising c. 2000 species in 59 genera. They are pantropical and include trees, shrubs, phyllocladous taxa, semi-succulents, annual herbs, and even a free-floating aquatic species. Vegetatively, most *Phyllanthaceae* are uniform with mainly alternate, simple, eglandular leaves with pinnate venation, entire margins, and a simple indumentum. Flowers are small and actinomorphic but display great diversity in shape, size and number of floral organs. These floral characters were used extensively in early treatments and successive classifications of *Phyllanthaceae* (as part of *Euphorbiaceae*) by Jussieu (1823, 1824), Baillon (1858), Müller (1866), Bentham (1878), Bentham & Hooker (1880) and Pax & Hoffmann (1922). From the 1950s onwards, systematics of *Euphorbiaceae sensu lato* was greatly advanced by Grady Webster who published, and later refined, a widely adopted

classification (Webster 1975, 1994). His systems incorporated evidence from palynology, karyology, phytochemistry and anatomy, and were consequently more natural than previous classifications. He took a wide view, including all five segregate families *sensu* APG (2003) in *Euphorbiaceae*. These were believed to be closely related partly on account of the characteristic euphorbiaceous schizocarp not known outside *Euphorbiaceae sensu lato*, although this is heavily modified in some taxa, and absent from *Pandaceae* and *Putranjivaceae*. *Phyllanthaceae* have particularly diverse fruit morphology, and fruits of about one third of the genera are entirely or partially indehiscent. Besides fully drupaceous or baccate fruits in genera including *Antidesma* Burm., *Bischofia* Blume, *Baccaurea* Lour., *Bridelia* Willd., *Flueggea* Willd. *pro parte*, *Jablonskia* G. L. Webster, *Margaritaria* L. f., *Phyllanthus pro parte* and *Uapaca* Baill. that are adapted to dispersal by birds or mammals, there are many taxa with semi-drupaceous or tardily dehiscent

fruits (e.g., *Pseudolachnostylis* Pax, *Spondianthus* Engl.) where dispersal mechanisms are less obvious. Extreme modification of fruit morphology for abiotic dispersal is found in *Hymenocardia* Wall. ex Lindl. and *Martretia* Beille which were treated as monogeneric families by some authors partly on these grounds (see Radcliffe-Smith 1987).

Seed coat anatomy was a major reason why several authors (Corner 1976; Meeuse 1990; Huber 1991) advocated splitting *Euphorbiaceae sensu lato* along the lines defined by numbers of ovules (two in *Phyllanthaceae*, *Picrodendraceae* and *Putranjivaceae*, one in *Euphorbiaceae sensu stricto* and *Pandaceae*). More recent studies (Stuppy 1996; Tokuoka & Tobe 1999a, 1999b, 2001) confirmed the distinctiveness of the newly recognised APG families with regards to seed coat anatomy, especially the differences between *Phyllanthaceae*, *Putranjivaceae* and *Euphorbiaceae sensu stricto*.

The primary division of *Phyllanthaceae* into two clades (fasciculate and tanniniferous, respectively) with high bootstrap support was first shown by Wurdack *et al.* (2004). The fasciculate clade is characterised by flowers being inserted on strongly contracted axes and the lack of tanniniferous epidermal cells. The tanniniferous clade possesses elongated inflorescence axes and tanniniferous epidermal cells. Exceptions to this are interpreted as secondary modifications, e.g. the contracted inflorescences in *Celianella* Jabl., *Jablonskia* and *Uapaca*, or the elongated inflorescences in *Amanoa strobilacea* Müll. Arg., *Sauropus racemosus* Beille and some Asian species of *Phyllanthus sensu stricto*. The inflorescence character has previously been used in subfamilial and tribal keys to delimit the majority of the genera in *Antidesmatoideae* as circumscribed here, including the exceptions cited above (Bentham & Hooker 1880; Pax & Hoffmann 1922; Webster 1994; Radcliffe-Smith 2001). As a consequence, these two major clades correspond remarkably well with the linear sequence of tribes in Webster (1994) and Radcliffe-Smith (2001). The fasciculate clade contains the genera of tribes 1–4, and the tanniniferous clade comprises tribes 6–8 (and 10 of Radcliffe-Smith 2001). Genera to be included in *Phyllanthoideae sensu stricto* as circumscribed here in addition to the first four tribes of Webster (1994) and Radcliffe-Smith (2001) are *Croizatia* (*Oldfieldioideae sensu Webster*), *Dicoelia* (*Acalyphoideae sensu Webster*), *Lingelsheimia* (*Phyllanthoideae-Drypeteae sensu Webster*), *Oreoporanthera* (Grüning) Hutch. and *Poranthera* Rudge (*Phyllanthoideae-Antidesmateae sensu Webster*). Necessary adjustments to the composition of *Antidesmatoideae* are the exclusion of *Phyllanoa* (*Violaceae*) and of *Oreoporanthera* and *Poranthera* (*Phyllanthoideae sensu stricto*).

Composition of the tribal clades diverges considerably from that in Webster's (1994) and Radcliffe-Smith's (2001) classifications. However, the genera with the most divergent placements based on the molecular results, including *Croizatia*, *Dicoelia*, *Lingelsheimia* and *Poranthera*, were often placed with some reservation in these earlier classifications due to lack of alternatives or insufficient knowledge of their characters. Several genera were already of doubtful distinctiveness, including *Blotia* Leandri (from *Petalodiscus* Baill. and *Wielandia* Baill.) and *Richeriella* Pax & K. Hoffm. (from *Flueggea*). Other findings were more surprising, e.g. the paraphyly of *Cleistanthus* Hook. f. ex Planch. and the polyphyly of *Leptopus* Decne. and *Savia* Willd.

This paper clarifies the nomenclature and composition of suprageneric taxa in *Phyllanthaceae* based on recent phylogenetic studies (Wurdack *et al.* 2004; Samuel *et al.* 2005; Kathriarachchi *et al.* 2005) summarised in Fig. 1. Assumed morphological synapomorphies of individual clades, including pollen, seed coat and other micromorphological characters, are discussed in detail in these three publications. The suprageneric morphological descriptions in this paper were drawn up with the help of the electronic key to the genera of *Euphorbiaceae sensu lato* (Hoffmann *et al.* 2005), and modified by original observations.

### Synopsis of taxa in Phyllanthaceae

Precise publication dates are taken from Reveal (2003). For bibliographic references to publications of genera, see Webster (1994), Govaerts *et al.* (2000) or Radcliffe-Smith (2001), unless stated otherwise below. For generic descriptions see Radcliffe-Smith (2001), but note that these descriptions apply to non-monophyletic entities in the cases of *Andrachne* L., *Cleistanthus*, *Leptopus*, *Phyllanthus* and *Savia*. Family and tribal descriptions are given in full, whereas subfamily and subtribal descriptions are differential.

**Phyllanthaceae** Martynov, nom. cons. prop.

*Phyllanthaceae* Martynov (1820: 369), as "Phyllanthoideae" validating *Phyllanthoides* Augier (1801: 44), nom. inval. (Art. 18.4; Greuter *et al.* 2000).

*Euphorbiaceae* subordo *Dispermae* Zoll. (1845: 17).

*Phyllanthaceae* J. G. Agardh (1858: 249), as "Phyllanthae".

*Phyllanthaceae* Klotzsch (1859: 246).

Type: *Phyllanthus* L.

Monoecious or dioecious trees, shrubs, herbs, rarely climbers, succulents or aquatics; four *Aporosa* species bisexual. Latex absent; resinous exudate absent or

rarely present. Indumentum present or absent, simple, rarely lepidote, stellate or dendritic. Armature absent or rarely present. Stipules present but sometimes caducous, free or rarely intrapetiolar, entire or rarely lacinate, sometimes foliaceous, rarely spinose; stipels absent or rarely present. Petioles present or rarely absent, sometimes pulvinate. Leaves usually present (very rarely absent in mature plants: phyllocladous taxa), simple (compound in *Bischofia*), alternate, spiral, subopposite, more rarely fasciculate, whorled or opposite, evenly distributed along branches or apically crowded; leaf blade symmetrical or rarely asymmetrical, not pellucid-punctate, base rarely peltate, margin entire, more rarely subentire, rarely toothed, venation pinnate or rarely reduced or slightly palmate. Foliar glands and domatia rarely present. Inflorescences axillary, more rarely cauline or terminal, with or without discernible axes (pseudanthia in *Uapaceae*). Bracts eglandular, not foliaceous or sometimes foliaceous, green or rarely white or yellow. Pedicels sometimes articulated. Flowers actinomorphic. Sepals 3–8, imbricate, rarely valvate or reduced,  $\pm$  free, rarely fused, greenish or more rarely reddish, brownish, white or yellow. Petals present or absent, (2–)4–6, green to yellow, rarely pink or maroon. Disc present or absent, staminate disc in distinct parts, extrastaminal-annular, rarely intrastaminal, or stamens inserted in cavities of the disc, pistillate disc simple or rarely double. Stamens 3–10(–19), erect in bud; filaments free or variously fused; anthers introrse, extrorse or latrorse, longitudinally dehiscent (rarely appearing oblique or horizontal) or rarely poricidal, thecae not separate and connective not enlarged or thecae separate and connective enlarged. Pistillode present or absent. Staminodes absent or rarely present. Ovary locules (1–)2–5(–15). Ovules per locule 2, often only 1 developing into seed, anatropous or rarely hemitropous, apical-axile, epitropous; obturator present. Styles present or more rarely absent, free or partially (rarely completely) fused, entire or divided (usually 2-fid, rarely 4- or multifid). Stigmas  $\pm$  terete or sometimes flattened, smooth to rarely plumose. Fruits explosively dehiscent (schizocarp), tardily dehiscent or indehiscent (drupes or berries), without sculpture, strongly veined, wrinkled, warty, keeled or rarely winged, greenish to brown or more rarely red, white or black. Seeds exarillate, not brightly coloured, or with brightly coloured sarcotesta, ecarunculate (minutely carunculate in *Celianella*); endosperm in mature seeds present or absent, cotyledons thin and flat, sometimes plicate, narrow or fleshy. Cosmopolitan except Antarctica with greatest diversity in the tropics.

There are three variants for the earliest authorship of the family name in the recent literature. Agardh

(1858) was used by Webster (1994), Klotzsch (1859) by Radcliffe-Smith (2001; as Klotzsch & Garcke), and Martynov (1820) by Reveal (2003), Stevens (2001–2004) and APG (2003). Martynov (1820) is the earliest citation of the name and adopted by the Angiosperm Phylogeny Group (APG 2003). The connection between the validation of the name by Martynov (1820) and the reference to the invalid but effectively published name of Augier (1801) is unambiguous but would only be apparent to a specialist in obscure taxonomic literature. We have nonetheless decided to use this citation for the first valid publication because the list of validly published family names of vascular plants spelling out this connection is now published (Hoogland & Reveal 2005).

**Subfamily I. Phyllanthoideae** Kostel. (Jan. – Sept. 1836: 1717), as “Phyllantheae”.

*Phyllanthoideae* Baill. ex Hassk. (7 Nov. 1859: 654), as “Phyllantheae”.

*Phyllanthoideae* Asch. (1860: 59).

Type: *Phyllanthus* L.

Monoecious or dioecious trees, shrubs, herbs, more rarely annuals, climbers, succulents or aquatics. Resinous exudate absent. Indumentum simple, very rarely dendritic or absent. Armature absent or rarely present. Stipules present, free or very rarely intrapetiolar, entire, rarely spinose; stipels rarely present. Leaves present (absent in mature plants: phyllocladous *Phyllanthus* species), simple, evenly distributed along branches; leaf base symmetrical, more rarely asymmetrical, rarely peltate, margin entire or rarely subentire (never with marginal glands). Leaf epidermis without tanniferous cells. Inflorescences usually without discernible axes. Petals present or absent. Stamens free to completely fused; anthers longitudinally dehiscent (sometimes apparently oblique or horizontally), rarely poricidal. Pistillate disc sometimes double. Ovary locules 2–6(–15). Ovules anatropous or hemitropous. Styles entire or 2-fid, sometimes 4-fid. Stigmas smooth. Fruit dehiscent, rarely indehiscent (berries or drupes), sometimes strongly veined, warty or wrinkled. Tropics to temperate zones.

This subfamily corresponds to the fasciculate clade of Wurdack *et al.* (2004), Samuel *et al.* (2005) and Kathriarachchi *et al.* (2005). It contains the first part of the linear sequence of *Phyllanthoideae sensu* Webster (1994) and Radcliffe-Smith (2001), namely the genera of their *Wielandieae*, *Amanoeae*, *Bridelieae*, *Phyllantheae*, plus *Croizatia* (formerly *Oldfieldioideae*), *Dicoelia* (formerly *Acalyphoideae*), *Lingelsheimia* (formerly *Phyllanthoideae-Drypeteae*), *Poranthera* and *Oreoporanthera* (formerly *Phyllanthoideae-Antidesmateae*).

**Tribe 1. Poranthereae** Grüning (1913: 13).

*Porantherinae* Müll. Arg. (March 1865: 55), as “Poranthereae”.

*Porantheraceae* Hurus. (15 Aug. 1954: 224).

*Porantheroideae* Pax (14 May 1890: 112).

Type: *Poranthera* Rudge. Additional taxa: *Actephila* Blume, *Andrachne* L. *sensu stricto*, *Andrachne* section *Pseudophyllanthus* Müll. Arg., *Leptopus* Decne. (excluding *Chorisandrachne* Airy Shaw), *Meineckia* Baill., *Oreoporanthera* (Grüning) Hutch., *Zimmermannia* Pax, *Zimmermanniopsis* Radcl.-Sm.

Monoecious or rarely dioecious shrubs, herbs or trees. Resinous exudate absent. Indumentum present or absent, simple. Armature absent. Stipules present, free, entire, sometimes foliaceous (*Zimmermannia*, *Zimmermanniopsis*), not spinose; stipels absent. Petioles present or absent, not pulvinate. Leaves simple, alternate or subopposite (opposite in *Oreoporanthera*), evenly distributed along branches; leaf blade symmetrical, base rarely peltate (*Meineckia peltata*), margin entire, venation pinnate or reduced (*Oreoporanthera*, *Poranthera*). Foliar glands and domatia absent. Inflorescences axillary, rarely apparently terminal (*Oreoporanthera*, *Poranthera*), without discernible axes. Bracts not foliaceous, green. Pedicels sometimes articulated. Sepals (3 — some *Poranthera*) 5–6, imbricate,  $\pm$  free, greenish, persistent. Petals present or absent, (2 — some *Actephila*, 3 — some *Actephila*, *Poranthera*) 4–6, greenish. Disc present, staminate disc in distinct parts or extrastaminal-annular, pistillate disc simple. Stamens 3–6; filaments free or variously fused; anthers introrse or extrorse, longitudinally dehiscent (poricidal in *Poranthera*, *Oreoporanthera*), thecae not separate and connective not enlarged. Pistillode present (sometimes absent in *Oreoporanthera*). Staminodes absent. Ovary locules 3. Ovules anatropous or rarely hemitropous (*Andrachne*). Styles free to completely fused, 2-fid or rarely entire (some *Actephila*, *Zimmermannia*). Stigmas  $\pm$  terete, smooth. Fruits explosively dehiscent, without sculpture, strongly veined or wrinkled, greenish to brown. Seeds exarillate, not brightly coloured; endosperm in mature seeds present or rarely absent (some *Actephila*), cotyledons thin and flat, rarely plicate (some *Actephila*) or narrow (*Oreoporanthera*, *Poranthera*). Cosmopolitan except Antarctica.

*Poranthereae* is a novel association of taxa previously thought to be unrelated, mixing three tribes and three subtribes of previous classifications. *Andrachne* and *Leptopus sensu* Webster (1994) are not monophyletic. *Andrachne* section *Pseudophyllanthus* has to be separated from *Andrachne sensu stricto* as previously suggested (Hoffmann 1994, 2000). *Chorisandrachne*, synonymised with *Leptopus* by

Webster (1994), belongs to *Wielandieae* (Katriarachchi *et al.* 2004, 2005). Final definition of generic boundaries in *Poranthereae* awaits further molecular work (Vorontsova *et al.*, unpublished data).

**Tribe 2. Bridelieae** Müll. Arg. (14 Oct. 1864: 324), as “Briedelieae”.

*Bridelioideae* Luerss. (“1882”, published Aug. 1881: 738), as “Bridelieae”.

Type: *Bridelia* Willd.

Monoecious or dioecious shrubs or trees. Resinous exudate absent. Indumentum present or absent, simple. Armature absent or rarely present (trunk of some *Bridelia* species). Stipules present, free or rarely intrapetiolar (some *Amanoa*), entire, not foliaceous, not spinose; stipels absent. Petioles present, not pulvinate. Leaves simple, alternate or subopposite, evenly distributed along branches; leaf blade symmetrical, base not peltate, margin entire or sometimes slightly crenate (some *Bridelia*), venation pinnate. Foliar glands absent. Domatia absent or present (some *Cleistanthus*). Inflorescences axillary or rarely terminal, without discernible axes or rarely apparently with elongated axes. Bracts not foliaceous or rarely foliaceous (*Amanoa*), green. Pedicels sometimes articulated. Sepals 4–6 (sometimes 7 in *Keayodendron*), imbricate (valvate in *Bridelia*, *Cleistanthus*),  $\pm$  free, greenish, persistent or caducous. Petals present or absent, (3 — *Tacarcuna tachirensis*, depending on interpretation of perianth) 4–6, greenish. Disc present, staminate disc extrastaminal-annular, rarely (*Securinega*) in distinct parts or absent, pistillate disc simple or double. Stamens 4–10 (–19 in *Tacarcuna amanoifolia*); free or variously fused; anthers introrse or latrorse, longitudinally dehiscent, thecae not separate and connective not enlarged. Pistillode present. Staminodes absent or rarely present (*Croizatia*). Ovary locules 2–4. Ovules anatropous. Styles free to completely fused (*Amanoa*), 2-fid, rarely 4-fid (*Croizatia*, *Gonatogyne*, *Pentabrachion*) or entire. Stigmas terete or flattened, smooth. Fruits explosively dehiscent, tardily dehiscent or indehiscent, without sculpture or strongly veined, warty or wrinkled, greenish to brown. Seeds exarillate, not brightly coloured; endosperm in mature seeds present or absent, cotyledons thin and flat, plicate or fleshy (*Amanoa*). Pantropical.

*Bridelieae* has the greatest number of genera of all *Phyllanthaceae* tribes, and can be subdivided in five strongly supported subtribes.

**Subtribe 2a. Amanoinae** Pax & K. Hoffm. (1922: 190).

*Amanoae* G. L. Webster (1975: 594).

Type: *Amanoa* Aubl.

Monoecious unarmed plants. Stipules free or intrapetiolar. Leaf margin entire. Domatia absent. Inflorescences with discernible axes. Pedicels not articulated. Sepals imbricate, persistent (staminate flowers) or caducous (pistillate flowers). Petals present or absent (sometimes in pistillate flowers). Staminate disc extrastaminal-annular, pistillate disc simple. Stamens 5, free; anthers introrse. Staminodes absent. Styles 2-fid. Stigmas flattened. Fruit tardily dehiscent. Endosperm in mature seeds absent or scanty, cotyledons fleshy. Tropical South America, West and West-Central Tropical Africa.

*Amanoa* is the only genus in *Brideliaceae* occurring in both the Old and the New World.

**Subtribe 2b. Saviinae** Müll. Arg. (March 1865: 63), as “Savieae”.

*Discocarpinae* Pax & K. Hoffm. (1922: 202).

*Croizatiae* G. L. Webster (1994: 55).

Type: *Savia* Willd. (section *Savia* only). Additional taxa: *Croizatia* Steyerm., *Discocarpus* Klotzsch, *Gonatogyne* Klotzsch ex Müll. Arg., *Tacarcuna* Huft.

Dioecious unarmed plants. Stipules free. Leaf margin entire. Domatia absent. Inflorescences without discernible axes. Pedicels sometimes articulated. Sepals imbricate, persistent. Petals present or absent. Staminate disc extrastaminal-annular, pistillate disc simple. Stamens 4 or 5 (– 19 in *Tacarcuna amanoifolia*), free to completely fused; anthers introrse or latrorse. Staminodes absent or rarely present (*Croizatia*). Styles 2-fid or 4-fid (*Croizatia*, *Gonatogyne*). Stigmas terete or flattened (*Discocarpus*). Fruit dehiscent. Endosperm in mature seeds present or absent, cotyledons thin and flat (*Gonatogyne*, *Savia*) or plicate. Mexico to Brazil.

*Saviinae* is entirely neotropical. Contrary to Webster (1994) and Radcliffe-Smith (2001) there are no true *Savia* species in Africa or Madagascar, they belong to *Wielandia* (*Wielandiae*). *Savia sensu lato* is not monophyletic; section *Heterosavia* belongs in *Phyllanthaceae*. The year of publication for the genus *Savia* is 1806, not 1805 as in Webster (1994) and Radcliffe-Smith (2001).

**Subtribe 2c. Keayodendrinae** Petra Hoffm., **subtrib. nov.**

Ab aliis subtribubus Brideliacearum combinatione characterum, petalis carentibus atque fructibus indehiscentibus atque abortu 1-locularibus 1-spermisque distinguenda.

Type: *Keayodendron* Leandri.

Dioecious unarmed plants. Stipules free. Leaf margin entire. Domatia absent. Inflorescences without

discernible axes. Pedicels not articulated. Sepals imbricate, persistent. Petals absent. Staminate disc extrastaminal-annular, pistillate disc double. Stamens 5 or 6, apparently free; anthers introrse. Staminodes absent. Styles deeply 2-fid. Stigmas terete. Fruit 1-locular and 1-seeded by abortion, indehiscent. Endosperm in mature seeds present, cotyledons thin, curved. West and West-Central Tropical Africa.

**Subtribe 2d. Pseudolachnostylidinae** Pax & K. Hoffm. (1922: 206).

Type: *Pseudolachnostylis* Pax. Additional taxa: *Bridelia* Willd., *Cleistanthus* Hook. f. ex Planch., *Pentabrachion* Müll. Arg.

Dioecious or monoecious plants with (some *Bridelia*) or without armature. Stipules free. Leaf margin entire or sometimes slightly crenate (some *Bridelia*). Domatia absent or present (some *Cleistanthus*). Inflorescences with (some *Bridelia*) or without discernible axes. Pedicels sometimes articulated. Sepals imbricate or valvate, caducous (pistillate flowers in *Cleistanthus*, flowers of both sexes in *Pseudolachnostylis*) or persistent. Petals present or absent. Staminate disc extrastaminal-annular, pistillate disc double (except *Pentabrachion*). Stamens 4 – 7, partially to completely fused; anthers introrse. Staminodes absent. Styles 2-fid or 4-fid (*Pentabrachion*). Stigmas terete. Fruit dehiscent or indehiscent. Endosperm in mature seeds present or scanty to absent (some *Cleistanthus*), cotyledons thin and flat, plicate or fleshy. Old World Tropics.

This subtribe includes *Brideliaceae sensu* Webster (1994) and Radcliffe-Smith (2001), plus one genus each of their *Amanoeae* and *Phyllanthaceae-Pseudolachnostylidinae*. *Cleistanthus* is not monophyletic and likely to be split into two genera, but more extensive sampling in this clade is necessary to define generic boundaries and composition. Results of the 5-gene analysis (Kathriarachchi *et al.* 2005) show *Bridelia* grouping with Asian and Australian species of *Cleistanthus*, whereas the African species of *Cleistanthus* sampled form a grade with *Pentabrachion* and *Pseudolachnostylis*. Vestured pits are only known in *Phyllanthaceae* from this subtribe (Jansen *et al.* 2001).

**Subtribe 2e. Securineginae** Müll. Arg. (late Aug. 1866: 217, 446), as “Securinegeae”.

Type: *Securinega* Comm. ex Juss. Additional taxa: *Lachnostylis* Turcz.

Dioecious unarmed plants. Stipules free. Leaf margin entire. Domatia absent. Inflorescences without discernible axes. Pedicels not articulated. Sepals imbricate, caducous (*Securinega*) or persistent

(*Lachnostylis*). Petals present (*Lachnostylis*) or absent (*Securinega*). Staminate disc extrastaminal-annular (*Lachnostylis*), or in distinct parts or absent (*Securinega*), pistillate disc simple. Stamens 5 (*Lachnostylis*) or (4 –)5(–10) in *Securinega*, free (*Securinega*) or fused halfway (*Lachnostylis*); anthers introrse. Staminodes absent. Styles 2-fid. Stigmas moderately flattened. Fruit dehiscent. Endosperm in mature seeds present (*Securinega*) or absent (*Lachnostylis*), cotyledons thin and flat (*Securinega*) or plicate (*Lachnostylis*). Southern Africa (*Lachnostylis*) and Western Indian Ocean (*Securinega*).

This Afro-Madagascan subtribe is strongly supported as sister to the remaining four subtribes.

**Tribe 3. Wielandieae** Baill. ex Hurus. (15 Aug. 1954: 339).

Wielandiidées Baill. (1858: 568), nom. inval. (Art. 18.4; Greuter *et al.* 2000).

Wielandioideae Baill. ex Hassk. (7 Nov. 1859: 653), as “Wielandieae”.

Type: *Wielandia* Baill.

Monoecious or dioecious shrubs or trees. Resinous exudate absent. Indumentum present or absent, simple. Armature absent. Stipules present, free, entire, not foliaceous, not spinose; stipels absent or rarely present (some *Astrocasia*). Petioles present, sometimes pulvinate (*Dicoelia*). Leaves simple, alternate, evenly distributed along branches; leaf blade symmetrical, base sometimes peltate, margin entire, venation pinnate. Foliar glands and domatia absent. Inflorescences axillary or cauline, without discernible axes, rarely with elongated axes (*Dicoelia*, some *Petalodiscus*). Bracts not foliaceous or foliaceous (sepaloid, *Heywoodia*), green. Pedicels not articulated. Sepals 4 – 6 (3, 6 or 8 in *Heywoodia* depending on perianth interpretation), imbricate, ± free, greenish, persistent or caducous (in pistillate flowers of *Astrocasia* and *Heywoodia*). Petals usually present, absent in *Chascotheca* (and *Heywoodia* depending on perianth interpretation), 4 – 6, greenish, maroon, or pale yellow, sometimes reduced (some *Wielandia*). Disc present or rarely absent (*Dicoelia*), staminate disc extrastaminal-annular or in distinct parts, pistillate disc simple. Stamens (3 – in some *Astrocasia*) 4 – 6(–12 in *Heywoodia*); filaments free or variously fused; anthers introrse, extrorse or latrorse, longitudinally dehiscent (appearing horizontal in *Astrocasia*), thecae not separate and connective not enlarged or rarely thecae separate and connective enlarged (*Dicoelia*). Pistillode present. Staminodes absent or rarely present (*Heywoodia*). Ovary locules 3 – 6. Ovules anatropous. Styles free or partially fused, entire or 2-fid. Stigmas ± terete, smooth. Fruits explosively

dehiscent, without sculpture, strongly veined or wrinkled, greenish to brown. Seeds exarillate, not brightly coloured; endosperm in mature seeds present or absent, cotyledons thin and flat (plicate or fleshy in *Wielandia*). Disjunct tropical distribution (except Australia).

**Subtribe 3a. Astrocasinae** G. L. Webster (1992: 315).

Type: *Astrocasia* L. B. Rob. & Millsp. Additional taxa: *Chascotheca* Urb., *Heywoodia* Sim.

Dioecious or rarely monoecious. Indumentum absent. Stipels absent or present (some *Astrocasia*). Petioles not pulvinate. Leaf base at least minutely peltate (in *Heywoodia* only in seedlings) or not peltate (some *Astrocasia*). Inflorescences axillary, without discernible axes. Perianth clearly differentiated or not (*Heywoodia*). Sepals persistent or caducous (in pistillate flowers of *Heywoodia*). Petals present or absent (*Chascotheca*), greenish. Disc present. Stamens (3 — in *Astrocasia*) 4 – 5(–12 in *Heywoodia*); filaments free to completely fused; anthers extrorse or introrse, thecae not separate and connective not enlarged. Staminodes absent or present (*Heywoodia*). Styles 2-fid. Endosperm in mature seeds present, cotyledons thin, flat. Mexico to Brazil (*Astrocasia*, *Chascotheca*), and East, South Tropical and Southern Africa (*Heywoodia*).

**Subtribe 3b. Wielandiinae** Pax & K. Hoffm. (1922: 180).

Type: *Wielandia* Baill. (including *Blotia* Leandri and *Petalodiscus* Baill.). Additional taxa: *Chorisandrachne* Airy Shaw, *Dicoelia* Benth.

Monoecious plants. Indumentum present or absent, simple. Stipels absent. Petioles not pulvinate or pulvinate (*Dicoelia*). Leaf base not peltate. Inflorescences axillary or cauline, with (*Dicoelia*) or without discernible axes. Perianth clearly differentiated. Sepals persistent. Petals present, greenish, red, white or yellow. Disc present or absent (*Dicoelia*). Stamens 5 or 6; filaments free or partly fused; anthers introrse or latrorse, thecae not separate and connective not enlarged or thecae separate and connective enlarged (*Dicoelia*). Staminodes absent. Styles 2-fid or entire (*Dicoelia*). Endosperm in mature seeds present or absent (*Wielandia*), cotyledons thin and flat (fleshy or plicate in *Wielandia*). Western Indian Ocean and East Tropical Africa (*Wielandia*), or South East Asia (*Chorisandrachne*, *Dicoelia*).

*Chorisandrachne* was synonymized with *Leptopus* by Webster (1994), but has since been shown to be sister

to *Dicoelia* (Kathriarachchi *et al.* 2004, 2005). All Western Indian Ocean taxa sometimes ascribed to *Savia* are members of *Wielandia sensu lato* (Hoffmann & McPherson, in press). *Blotia* was described in volume 8 not 88 (Leandri 1957) as erroneously given in Webster (1994). The correct reference for publication of *Petalodiscus* is Baillon (1858: Atlas, p. 40, t. 22, fig. 11 – 14), validly published as descriptio generico-specifica (Art. 42.1; Greuter *et al.* 2000). The lectotypification by Radcliffe-Smith (2001) is invalid; the correct type is *Petalodiscus platyrachis* Baill.

**Tribe 4. Phyllanthae** Dumort. (1829: 45), as “Phylanthae” [sphalm.].

Type: *Phyllanthus* L. (including *Breynia* J. R. & G. Forst., *Glochidion* J. R. & G. Forst., *Reverchonia* A. Gray, *Sauropus* Blume). Additional taxa: *Flueggea* Willd. (including *Richeriella* Pax & K. Hoffm.), *Lingelsheimia* Pax, *Margaritaria* L. f., *Plagiocladus* Brunel ex Petra Hoffm., *Savia* section *Heterosavia* Urb.

Monoecious or dioecious shrubs, trees, herbs, rarely climbers, scramblers, succulents (*Phyllanthus mirabilis* Müll. Arg.) or aquatics (*Phyllanthus fluitans* Benth. ex Müll. Arg.). Resinous exudate absent. Indumentum present or absent, simple or rarely dendritic (some *Phyllanthus*). Armature absent or rarely present (spinose branch tips in some *Flueggea*). Stipules present, free, entire, not foliaceous, sometimes spinose (some *Phyllanthus*); stipels absent. Petioles present, not pulvinate. Leaves present or rarely absent in mature plants (phyllocladous *Phyllanthus* species), simple, alternate or fasciculate, evenly distributed along branches; leaf blade symmetrical or asymmetrical, base rarely peltate (*Phyllanthus peltatus* Guillaumin), margin entire, venation pinnate. Foliar glands absent or rarely present (laminar-abaxial in some neotropical *Phyllanthus*, stipular in *Lingelsheimia*). Domatia absent. Inflorescences axillary or rarely on branches, without discernible axes, rarely with elongated axes (*Flueggea gracilis* (Merr.) Petra Hoffm., some *Phyllanthus* species). Bracts not foliaceous, green. Pedicels not articulated. Sepals 4–6 (– 7 sometimes in *Flueggea* and *Lingelsheimia*), imbricate, ± free or nearly completely fused (some *Phyllanthus*), greenish, orange, pink or white, persistent. Petals usually absent, present in *Savia* section *Heterosavia*: 5(6), well developed, greenish. Disc present or absent, staminate disc in distinct parts or extrastaminal-annular (intrastaminal in *Reverchonia*), pistillate disc simple. Stamens 2–15; filaments free or variously fused; anthers free or fused (some *Phyllanthus*) introrse or extrorse, longitudinally dehiscent (sometimes appearing oblique or horizontal in *Phyllanthus*), thecae not separate and

connective not enlarged or, rarely, thecae separate and connective enlarged (*Phyllanthus* section *Choretropsis* and subsection *Clausseniani*). Pistillode absent or present (*Flueggea*, *Savia* section *Heterosavia*, sometimes in *Lingelsheimia*). Stamnodes absent or rarely present (*Phyllanthus* section *Cicca*). Ovary locules 2–6 (– 15 in some *Phyllanthus*). Ovules hemitropous or rarely anatropous (*Savia* section *Heterosavia*). Styles free to completely fused (some *Phyllanthus*), entire or 2-fid (sometimes 3-fid in *Margaritaria*). Stigmas ± terete, smooth. Fruits explosively dehiscent or more rarely indehiscent (drupes or berries), sometimes tardily dehiscent (some *Phyllanthus*), without sculpture, strongly veined or warty, greenish to brown, red or white. Seeds exarillate and not brightly coloured or with brightly coloured sarcotesta (*Margaritaria*, some *Phyllanthus*); endosperm in mature seeds present, cotyledons thin, flat and broad or rarely narrow (*Reverchonia*). Cosmopolitan except Antarctica.

Although the most species-rich tribe (c. 1200 species), *Phyllanthae* includes no logical subtribal groupings. The other genera form a grade leading to *Phyllanthus sensu lato*. Contrary to Webster (1994) and Radcliffe-Smith (2001), *Savia* section *Heterosavia* is entirely Caribbean and absent from Africa or Madagascar, and deserves generic status (Hoffmann, unpublished manuscript). Webster’s (1984) doubt in the generic distinctiveness of *Richeriella* is confirmed by the molecular results, and this monotypic genus is here subsumed in *Flueggea*. An elongate inflorescence axis is its only substantial difference from other species of *Flueggea*.

***Flueggea gracilis*** (Merr.) Petra Hoffm., **comb. nov.**  
*Richeriella gracilis* (Merr.) Pax & K. Hoffm. (1922: 30).  
*Baccaurea gracilis* Merr., Philipp. J. Sci. 1: 203 (1906).

The other species of *Richeriella*, *R. malayana* Hend. is considered to be conspecific with *R. gracilis* by Welzen (2003). Webster (1984) recognized two sections and three subsections in *Flueggea*. It is possible that *F. gracilis* warrants the creation of another subgeneric entity, but molecular sampling in *Flueggea sensu stricto* is currently too sparse to make this decision here.

*Phyllanthus sensu* Webster (1994) and Radcliffe-Smith (2001) is both polyphyletic and paraphyletic. Brunel’s (1987) view that *Phyllanthus dianthus* Pax is to be recognised at generic rank is confirmed by the results of a more comprehensive DNA sequence analysis of this tribe (Kathriarachchi *et al.*, 2006). It is sister to *Margaritaria*, but differs from all *Margaritaria* species by having six sepals (instead of four) and two (instead of four) stamens. It also has tricarpellate schizocarps with normal explosive dehiscence, whereas *Margaritaria* has fruits composed of two to six



carpels that are irregularly fragmenting and have a brittle, papery endocarp. *Plagiocladus*, as suggested by the name, also has distinctly flattened terminal branches, whereas in *Margaritaria* this is rarely and less prominently the case. The monotypic new genus was proposed by Brunel (1987) in his doctoral thesis but was never validly published, and is here validated:

***Plagiocladus* Brunel ex Petra Hoffm., gen. nov.**

*Plagiocladus* Brunel (1987: 260), nom. inval.

Genus *Margaritariae* affinis sed sepalis 6 (nec 4), staminibus 2 (nec 4), endocarpio duro (nec chartaceo), dehiscencia fructibus regulariter loculicidali, septicidali atque septifraga (nec irregulariter in fragmenta dissolutis) differt.

Type (and only species): *Plagiocladus diandrus* (Pax) Brunel ex Petra Hoffm., **comb. nov.**

*Phyllanthus diandrus* Pax (1921: 29); Breteler (1990, published 1991: 293).

*Breynia*, *Glochidion*, *Reverchonia*, *Sauropus* (and *Phyllanthodendron* which is not universally recognised but segregated by Li 1994) are embedded in *Phyllanthus*. Distinguishing morphological characters between these five taxa are not clear-cut, and recognition of all equivalent clades at generic level would exacerbate this problem. There are, for instance, *Phyllanthus* species without pistillate discs (a character used to distinguish *Breynia*, *Glochidion* and *Sauropus* from *Phyllanthus*) including *P. elsiae*, *P. emblica* and *P. mimosoides* (Bancilhon 1971). Style morphology which is also used in generic keys is diverse in both *Glochidion* and *Phyllanthus* (e.g., Hoffmann & McPherson 2003) and may reflect specialised pollination syndromes (Kato *et al.* 2003; Kawakita *et al.* 2004; Kawakita & Kato 2004a, 2004b). *Glochidion* and the insufficiently studied *Phyllanthus* subgenus *Gomphidium* in particular appear to intergrade morphologically. Linear cotyledons (*Reverchonia*) have been shown to be an adaptation to arid habitats and homoplasious (shared with *Poranthera* and stenolobous taxa of *Picrodendraceae*). Only c. 10% of all species potentially to be assigned to this clade have been placed with molecular phylogenetic analyses, and increased taxon sampling is likely to increase the complexity of the phylogenetic tree. The great morphological diversity of *Phyllanthus sensu* Webster accommodates the five embedded taxa, which may be given sectional or subgeneric rank in future classifications. 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. We believe that instead of a paraphyletic construct, a monophyletic *Phyllanthus* in which nomenclature reflects phylogenetic relationships will be more useful for both taxonomists and researchers in other fields in the long term.

**Subfamily II. Antidesmatoideae** Hurus. (15 Aug. 1954: 322).

*Antidesmatinae* Pax (May 1890: 26); Pax & K. Hoffm. (1922: 3), as “Antidesminae”.

*Stilaginaceae* C. Agardh (13 June 1824: 199), as “ordo Stilagineae”.

*Antidesmataceae* Loud. (June – Dec. 1830: 534), as “order Antidesmeae”.

*Antidesmataceae* Sweet (1830: 460), as “ordo Antidesmeae”.

Type: *Antidesma* Burm. ex L.

Dioecious or rarely monoecious trees, shrubs or rarely perennial herbs; four *Aporosa* species bisexual. Resinous exudate sometimes present. Indumentum simple, rarely lepidote, minutely stellate or absent. Armature absent. Stipules free, rarely lacinate, not spinose, rarely absent; stipels absent. Leaves present, simple (compound in *Bischofia*), evenly distributed along branches or apically crowded, leaf base symmetrical, not peltate, margin entire, rarely subentire (sometimes with marginal glands) or toothed. Leaf epidermis usually with tanniferous cells. Inflorescences usually with discernible axes (pseudanthia in *Uapaceae*). Petals usually absent. Stamens free, rarely fused at the base; anthers longitudinally dehiscent. Pistillate disc simple. Ovary locules 1 – 5. Ovules anatropous. Styles entire or 2-fid, rarely multifid. Stigmas sometimes plumose. Fruit indehiscent (drupes) or tardily dehiscent, rarely explosively dehiscent, sometimes keeled or winged. Tropics and subtropics, absent from temperate zones.

This subfamily corresponds to the tanniferous clade of Wurdack *et al.* (2004), Samuel *et al.* (2005) and Kathriarachchi *et al.* (2005). It contains the last part of the linear sequence of *Phyllanthoideae sensu* Webster (1994) and Radcliffe-Smith (2001), namely tribes *Antidesmateae* (excluding *Phyllanthera*, *Oreoporanthera*, *Poranthera*), *Hymenocardieae*, *Bischofieae* and *Martretieae*.

Suprageneric names based on the generic name *Antidesma* are often derived as if from a Latin word (see *Antidesmeae* etc. in Hutchinson 1969; Webster 1975, 1994; Radcliffe-Smith 2001). *Antidesma* is, however, of Greek origin, the genitive singular stem (see Art. 18.1.; Greuter *et al.* 2000) is *Antidesmat-*, and suprageneric names must be based on this.

**Tribe 5. Antidesmateae** Benth. (23 Sept. 1873: 42).Type: *Antidesma* Burm. ex L.

Dioecious or rarely monoecious (*Apodiscus*, rarely in *Martretia* and *Thecacoris*) shrubs, trees or rarely perennial herbs (some *Thecacoris*). Resinous exudate absent. Indumentum present, simple or rarely lepidote (*Hieronyma*). Armature absent. Stipules present, free, entire or rarely lacinate (*Antidesma laciniatum* Müll. Arg.), sometimes foliaceous, not spinose; stipels absent. Petioles present, sometimes pulvinate. Leaves simple, alternate, rarely fasciculate (some *Thecacoris*) or opposite (some *Hymenocardia*), evenly distributed along branches; leaf blade symmetrical, base not peltate, margin entire or sometimes repand (some *Thecacoris*), venation pinnate or rarely slightly palmate (*Hymenocardia*). Foliar glands absent or present (marginal in *Antidesma vaccinioides* Airy Shaw or laminar-abaxial in *Hymenocardiaceae*). Domatia absent or present (some *Antidesma*). Inflorescences axillary, cauline or terminal, with discernible axes (short in *Leptonema*). Bracts not foliaceous, green. Pedicels not articulated. Sepals (3 — some *Antidesma*) 4–6 (–8 sometimes in *Antidesma* and *Hymenocardia*), imbricate (almost valvate in *Hymenocardia*), ± free to nearly completely fused (some *Antidesma*), greenish, persistent or rarely caducous (pistillate flowers of *Hymenocardia*). Petals usually absent, present sometimes in *Thecacoris*: 5, small, greenish. Disc present or absent, staminate disc in distinct parts, extrastaminal-annular or stamens inserted in cavities of the disc, pistillate disc simple. Stamens 2–8 (–13 in some *Antidesma*); filaments free or basally fused; anthers free, introrse or extrorse (also latrorse in *Martretia*), longitudinally dehiscent, thecae usually separate and connective enlarged (except *Hymenocardiaceae* and *Martretia*). Pistillode present or rarely absent (some *Antidesma*, *Leptonema*). Staminodes absent or rarely present (sometimes in *Thecacoris*). Ovary locules (1 – *Antidesma*) 2–4 (–5 sometimes in *Apodiscus* and *Leptonema*). Ovules anatropous. Styles present or absent, free to partially fused, entire or 2-fid. Stigmas ± terete, smooth, papillose or plumose (*Didymocistus*). Fruits indehiscent (drupes) or rarely explosively dehiscent (*Leptonema*, *Thecacoris*), without sculpture, keeled (*Martretieae*) or winged (*Hymenocardia*), greenish to brown, or black, orange, pink, purple or red. Seeds exarillate, not brightly coloured; endosperm in mature seeds present or rarely absent (*Apodiscus*), cotyledons thin and flat or rarely fleshy (*Apodiscus*). Pantropical.

**Subtribe 5a. Antidesmatinae** Müll. Arg. (March 1865: 64), as “Antidesmeae”.

Type: *Antidesma* Burm. ex L. Additional taxa: *Thecacoris* A. Juss.

Dioecious shrubs, trees or perennial herbs (some *Thecacoris*). Indumentum simple. Stipules entire (lacinate in *Antidesma laciniatum*), foliaceous (some *Antidesma*) or not foliaceous. Petioles pulvinate or not. Leaves alternate or fasciculate (some *Thecacoris*), entire or sometimes repand (some *Thecacoris*), penninerved. Foliar glands absent (marginal glands present in *Antidesma vaccinioides*). Domatia absent or rarely present (some *Antidesma*). Sepals imbricate, persistent, free to completely fused (some *Antidesma*). Petals absent (*Antidesma*) or present, greenish (*Thecacoris*). Disc present, staminate disc in distinct parts or stamens inserted in cavities of the disc, rarely extrastaminal-annular. Anthers extrorse or introrse, thecae separate and connective enlarged. Pistillode present or absent (some *Antidesma*). Staminodes absent, rarely present (sometimes in *Thecacoris*). Ovary locules 1 (*Antidesma*) or 3 (*Thecacoris*). Styles 2-fid to irregularly divided. Stigmas smooth. Fruit drupaceous (*Antidesma*) or explosively dehiscent (*Thecacoris*), without sculpture, greenish to brown (*Thecacoris*) or reddish to black (*Antidesma*). Endosperm in mature seeds present, cotyledons thin, flat. Old World Tropics.

**Subtribe 5b. Hymenocardiinae** Petra Hoffm., stat. nov. *Hymenocardiaceae* Airy Shaw (“1965”, published 8 Dec. 1964: 261).

*Hymenocardiaceae* Hutch. (1969: 747).

Type: *Hymenocardia* Wall. ex Lindl. Additional taxa: *Didymocistus* Kuhlmann.

Dioecious shrubs or trees. Indumentum simple. Stipules entire, not foliaceous. Petioles not pulvinate. Leaves alternate (rarely opposite in *Hymenocardia*), entire, penninerved (sometimes slightly palmate in *Hymenocardia*). Abaxial-laminar foliar glands present (scale-like, 40–100 µm across). Domatia absent. Sepals imbricate (to nearly valvate in *Hymenocardia*), persistent or caducous (pistillate *Hymenocardia*), ± free. Petals and disc absent. Anthers extrorse or introrse, thecae not separate and connective not enlarged. Pistillode present. Staminodes absent. Ovary locules 2. Styles 2-fid (*Didymocistus*) or entire (*Hymenocardia*). Stigmas smooth to papillose (*Hymenocardia*) or plumose (*Didymocistus*). Fruit tardily septically dehiscent, winged (*Hymenocardia*) or lobed (*Didymocistus*), greenish to brown. Endosperm in mature seeds present, cotyledons thin, flat. Tropical Africa and tropical Asia (*Hymenocardia*), or Brazil and Western South America (*Didymocistus*).

The incorrect reference to Müll. Arg. (March 1865: 64) for *Hymenocardiaceae* Hutch. in Webster (1994) and Radcliffe-Smith (2001) is most likely based on an error mistaking *Hieronymaceae* for *Hymenocardiaceae*.

**Subtribe 5c. Martretinae** *Petra Hoffm., stat. nov.*

*Martretieae* Eg. Köhler ex J. Léonard (Dec. 1989: 326).  
Type: *Martretia* Beille. Additional taxa: *Apodiscus* Hutch.

Dioecious (*Martretia*) or monoecious (*Apodiscus*) shrubs or trees. Indumentum simple. Stipules entire, not foliaceous. Petioles not pulvinate. Leaves alternate, entire, penninerved. Foliar glands and domatia absent. Sepals imbricate, persistent, ± free. Petals absent. Disc absent (pistillate flowers of *Apodiscus* and staminate flowers of *Martretia*) or present, in distinct parts. Anthers extrorse, introrse or latrorse, thecae separate and connective enlarged (*Apodiscus*), not so in *Martretia*. Pistillode present. Staminodes absent. Ovary locules 2–5. Styles entire. Stigmas smooth. Fruit tardily dehiscent, keeled, greenish to brown. Endosperm in mature seeds present but not copious (*Martretia*) or absent (*Apodiscus*), cotyledons thin and flat (*Martretia*) or fleshy (*Apodiscus*). West and West-Central Tropical Africa.

**Subtribe 5d. Hieronyminae** *Müll. Arg.* (March 1865: 64), as “Hieronymae”.

Type: *Hieronyma* Allemão, orth. cons.

Dioecious shrubs or trees. Indumentum lepidote. Stipules entire, not foliaceous. Petioles not pulvinate. Leaves alternate, entire, penninerved. Foliar glands and domatia absent. Sepals imbricate, persistent, partly fused. Petals absent. Disc present, staminate disc extrastaminal-annular. Anthers extrorse or introrse, thecae separate and connective enlarged. Pistillode present. Staminodes absent. Ovary locules 2 or 3. Styles 2-fid. Stigmas smooth. Fruit indehiscent, without sculpture, black. Endosperm in mature seeds present, cotyledons thin, flat. Mexico to Brazil.

**Subtribe 5e. Leptonematinae** *Müll. Arg.* (March 1865: 64), as “Leptonemeae”.

Type: *Leptonema* A. Juss.

Dioecious shrubs. Indumentum simple. Stipules entire, not foliaceous. Petioles not pulvinate. Leaves alternate, entire, penninerved. Foliar glands and domatia absent. Sepals imbricate, persistent, free. Petals and disc absent. Anthers extrorse or introrse, thecae separate (stipitate) and connective enlarged. Pistillode and staminodes absent. Ovary locules 4 or 5. Styles 2-fid. Stigmas slightly lacerate. Fruit dehiscent, without sculpture, greenish to brown. Endosperm in mature seeds present, cotyledons thin, flat. Madagascar.

**Tribe 6. Scepeae** *Horan.* (1847: 80).

*Scepeaceae* Lindl. (July 1836: 171), as “order”.

*Aporosaceae* Lindl. ex Planch. (1854: 265), as “ordo Aporoseae”.

*Aporoseae* Airy Shaw (1974: tab. 3701), as “Aporuseae”.

Type: *Scepa* Lindl. (= *Aporosa* Blume). Additional taxa: *Ashtonia* Airy Shaw, *Baccaurea* Lour., *Distichirrhops* Haegens, *Maesobotrya* Benth., *Nothobaccaurea* Haegens, *Protomegabaria* Hutch., *Richeria* Vahl.

Dioecious (bisexual in four *Aporosa* species) shrubs or trees. Resinous exudate absent. Indumentum present or absent; simple or stellate (some *Baccaurea*). Armature absent. Stipules present, free, entire, sometimes foliaceous, not spinose; stipels absent. Petioles present, sometimes pulvinate. Leaves simple, alternate, opposite or spiral, evenly distributed along branches or apically crowded (*Ashtonia*, *Baccaurea*, *Nothobaccaurea*); leaf blade symmetrical, base not peltate, margin entire or sometimes subentire, venation pinnate. Foliar glands absent or present (laminar-abaxial in *Baccaurea*; marginal in *Aporosa*, *Baccaurea*; basal in *Aporosa*). Domatia absent. Inflorescences axillary or cauline, with discernible inflorescence axes. Bracts not foliaceous or rarely foliaceous (some *Aporosa*, *Protomegabaria*), green. Pedicels sometimes articulated (*Baccaurea*, *Protomegabaria*). Sepals 3–6 (–7 in *Nothobaccaurea*), imbricate, ± free, brown, greenish, pink, red, white or yellow, persistent or caducous (in pistillate flowers of *Ashtonia* and *Baccaurea*). Petals absent. Disc present or absent, staminate disc in distinct parts, pistillate disc simple. Stamens 2–8 (–10 in some *Baccaurea*); filaments free; anthers introrse, extrorse or latrorse, longitudinally dehiscent, thecae not separate and connective not enlarged or rarely thecae separate and connective enlarged (some *Aporosa*). Pistillode present or rarely absent (sometimes in *Aporosa*). Staminodes absent or rarely present (*Nothobaccaurea*). Ovary locules (1—sometimes in *Maesobotrya*) 2–4 (–5 sometimes in *Ashtonia*). Ovules anatropous. Styles present or absent, free to completely fused, entire or 2-fid. Stigmas ± terete or more rarely flattened (some *Aporosa* and *Baccaurea*), smooth, papillose or plumose (some *Aporosa* and *Baccaurea*). Fruits tardily dehiscent or indehiscent (drupes), may be explosively dehiscent in *Protomegabaria*, without sculpture or keeled, greenish to brown, or orange, pink, purple, red or white. Seeds with brightly coloured sarcotesta or exarillate and not brightly coloured, endosperm in mature seeds present, cotyledons thin, flat. Pantropical except Australia.

The two recently described genera *Distichirrhops* and *Nothobaccaurea* have not been placed with molecular phylogenetic analyses. Their classification in *Scepeae* is based on their morphological characters and

placement by Haegens (2000). The placement of *Ashtonia* (not shown in Fig. 1) has been confirmed by *rbcL* sequence data (K. J. Wurdack, unpublished data).

**Tribe 7. Jablonskieae** *Petra Hoffm., trib. nov.*

Ab aliis tribubus Antidesmatoidearum combinatione characterum, axibus inflorescentiarum non distinguibilis (sed pedunculis in *Celianella* praesentibus) atque exudato resinoso carenti atque fructibus demum dehiscentibus (non indehiscentibus) distinguenda.

Type: *Jablonskia* G. L. Webster. Additional taxa: *Celianella* Jabl.

Monoecious (*Jablonskia*) or dioecious (*Celianella*) shrubs or trees. Resinous exudate absent. Indumentum and armature absent. Stipules present, free, entire, not foliaceous, not spinose; stipels absent. Petioles present (*Jablonskia*) or absent (*Celianella*), not pulvinate. Leaves simple, alternate, evenly distributed along branches; leaf blade symmetrical, base not peltate, margin entire, venation pinnate. Foliar glands absent or present (basal-marginal in *Jablonskia*). Domatia absent. Inflorescences axillary, without discernible axes (but pedunculate in *Celianella*). Bracts not foliaceous, but foliaceous bracteoles in *Celianella*, green. Pedicels not articulated. Sepals 5, imbricate,  $\pm$  free, greenish, persistent. Petals absent. Disc present, staminate disc in distinct parts (*Jablonskia*) or intrastaminal (*Celianella*), pistillate disc simple. Stamens 5; filaments free; anthers introrse, longitudinally dehiscent, thecae not separate and connective not enlarged (*Jablonskia*) or thecae separate and connective enlarged (*Celianella*). Pistillode present (*Jablonskia*) or absent (*Celianella*). Stamines absent. Ovary locules 3. Ovules anatropous. Styles free (*Jablonskia*) or partially fused (*Celianella*), 2-fid. Stigmas  $\pm$  terete, smooth. Fruits baccate, irregularly dehiscent (*Jablonskia*) or explosively dehiscent (*Celianella*), without sculpture, greenish to brown. Seeds apparently with a thin sarcotesta (*Jablonskia*) or minutely carunculate (*Celianella*); endosperm in mature seeds present, cotyledons thin, flat. Tropical South America.

**Tribe 8. Spondiantheae** G. L. Webster (1975: 594).

Subtribe *Spondianthinae* G. L. Webster (1994: 49).

Type: *Spondianthus* Engl.

Dioecious trees. Resinous exudate present. Indumentum present or absent, simple. Armature absent. Stipules present, free, entire, not foliaceous, not spinose; stipels absent. Petioles present, not pulvinate. Leaves simple, alternate or sometimes whorled, apically crowded on branches; leaf blade symmetrical, base not peltate, margin entire, venation

pinnate. Foliar glands and domatia absent. Inflorescences axillary or terminal, with discernible axes. Bracts not foliaceous, green. Pedicels not articulated. Sepals (4 or) 5, imbricate,  $\pm$  free, greenish, persistent. Petals (4 or) 5, sometimes absent in pistillate flowers, greenish. Disc present, staminate disc in distinct parts, pistillate disc simple. Stamens 5; filaments free; anthers introrse, longitudinally dehiscent, thecae not separate, connective not enlarged. Pistillode present. Stamines absent. Ovary locules 3. Ovules anatropous. Styles  $\pm$  free, 2-fid. Stigmas  $\pm$  terete, papillose. Fruits (tardily?) dehiscent, without sculpture, greenish to brown. Seeds exarillate, not brightly coloured, endosperm in mature seeds present, cotyledons thin, flat. Tropical Africa excluding western Indian Ocean Islands.

**Tribe 9. Uapaceae** *Hutch.* (1969: 747).

*Uapacinae* Müll. Arg. (March 1865: 65), as "Uapaceae".

*Uapacaceae* Airy Shaw ("1965", published 8 Dec. 1964: 270).

Type: *Uapaca* Baill.

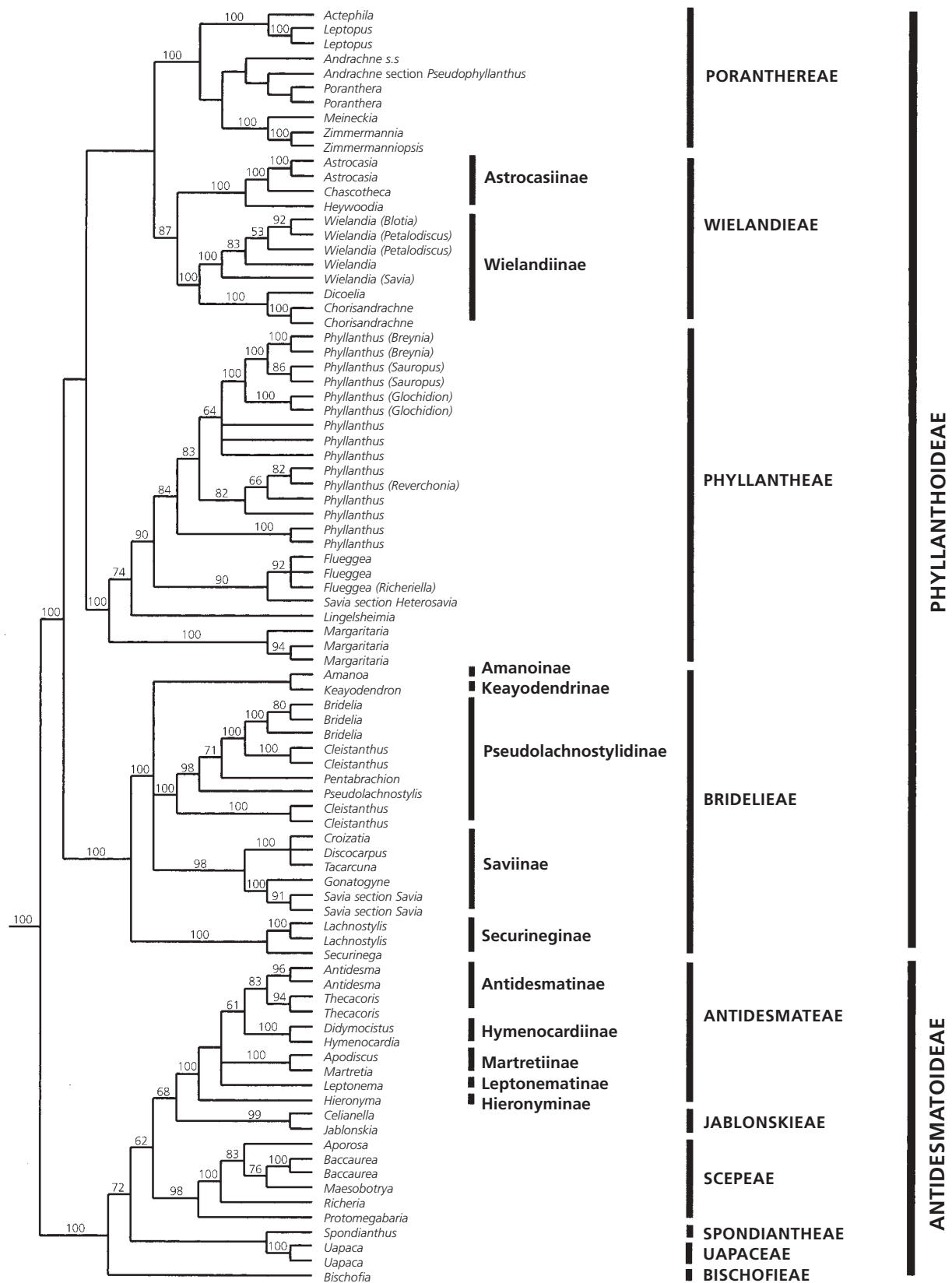
Dioecious shrubs or trees, often stilt-rooted. Resinous exudate present. Indumentum present, simple, sometimes minutely pseudo-lepidote. Armature absent. Stipules present but often caducous, free, entire, sometimes foliaceous, not spinose; stipels absent. Petioles present or nearly absent, sometimes pulvinate. Leaves simple, alternate, apically crowded on branches; leaf blade symmetrical, base not peltate, margin entire, venation pinnate. Foliar glands and domatia absent. Inflorescences axillary, without discernible axes (pseudanthia). Bracts foliaceous, white or yellow. Pedicels not articulated. Sepals 4–6, imbricate, reduced, partially (in staminate flowers) or completely (in pistillate flowers) fused, greenish, persistent. Petals absent. Disc absent. Stamens 4–6; filaments free; anthers introrse, longitudinally dehiscent, thecae not separate, connective not enlarged. Pistillode present. Stamines absent. Ovary locules (2) 3 (5). Ovules anatropous. Styles free, multifid. Stigmas flattened, smooth. Fruits indehiscent (drupes), without sculpture, greenish to brown. Seeds exarillate; endosperm in mature seeds present, cotyledons thin, flat. Africa and Madagascar (except Southern Africa).

**Tribe 10. Bischoffieae** *Hurus.* (15 Aug. 1954: 339), as "Bischoffieae".

*Bischoffiinae* Müll. Arg. (March 1865: 64), as "Bischoffieae".

*Bischoffiaceae* Airy Shaw ("1965", published 8 Dec. 1964: 252).

Type: *Bischofia* Blume.



**Fig. 1.** *Phyllanthaceae* relationships inferred from parsimony analysis of five genes (*atpB*, *matK*, *ndhF*, *PHYC*, *rbcl*), modified from Kathriarachchi *et al.* (2005). Bootstrap percentages > 50 shown above the branches. Classification in subfamilies (right column), tribes (middle column) and subtribes (left column) is mapped on the tree.

Dioecious or rarely monoecious trees. Resinous exudate absent. Indumentum present, simple. Armature absent. Stipules present, free, entire, not foliaceous, not spinose; stipels absent. Petioles present, not pulvinate; petiolules present. Leaves compound, trifoliate, alternate, evenly distributed along branches; leaflet blade symmetrical, base not peltate, margin toothed, venation pinnate. Foliar glands absent. Domatia present. Inflorescences axillary, with discernible axes. Bracts not foliaceous, green. Pedicels not articulated. Sepals 5, imbricate,  $\pm$  free, greenish, pistillate caducous. Petals absent. Disc absent. Stamens 5; filaments free; anthers introrse, longitudinally dehiscent, thecae not separate, connective not enlarged. Pistillode present. Staminodes sometimes present. Ovary locules 3 (or 4). Ovules anatropous. Styles partially fused, entire. Stigmas  $\pm$  terete, smooth. Fruits indehiscent (drupes), without sculpture, greenish to brown. Seeds exarillate; endosperm in mature seeds present, cotyledons thin, flat. Asia, Australasia and Pacific Islands.

Incertae sedis: *Chonocentrum* Pierre ex Pax & K. Hoffm.

This genus is only known from the staminate type collection made 150 years ago in Amazonia. Hayden & Hayden (1996) re-evaluated it anatomically and suggested an affiliation with *Antidesmateae* rather than *Discocarpus* as assumed by Pax & Hoffmann (1922, 1931) and accepted by (Webster (1994) and Radcliffe-Smith (2001).

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