



The significance of meristic changes in the flowers of Sapotaceae

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Sapotaceae belongs to the heterogeneous order Ericales and exhibits extensive diversity in floral morphology. Although pentamery is widespread and probably the ancestral condition, some clades are extremely variable in merism, with fluctuations between tetramery to hexamery and octomery, affecting different floral organs to different degrees. We assessed the different states of merism in Sapotaceae to determine the evolution of this character among different clades. The floral morphology and development of nine species from eight genera were investigated using scanning electron microscopy (SEM). Furthermore, floral characters related to merism were mapped onto a phylogenetic tree to analyse the distribution and evolutionary significance of merism in the family. Developmental evidence shows that changes in merism are linked to a concerted multiplication of organs among whorls and an increase in whorls through the displacement of organs. Although pentamery is reconstructed as the ancestral condition, a reduction to tetramery or an increase to a higher merism (mainly hexamery or octomery) has evolved at least five times in the family. Fluctuations in merism between different whorls are not random but occur in a coordinated pattern, presenting strong synapomorphies for selected clades. Octomery has evolved at least twice, in Isonandreae from tetramery and in Sapoteae-Mimusopinae from pentamery. Hexamery has evolved at least three times, independently in *Northia*, the *Palaquium* clade of Isonandreae and derived from octomery in Sapoteae-Mimusopinae. Three possibilities of merism increase have been identified in Sapotaceae: (1) a concerted increase affecting all organs more or less equally (*Palaquium* clade of Isonandreae, Sapoteae); (2) a coordinated increase in petals, stamens and mostly carpels without effect on sepals (*Labourdonnaisia*, *Payena–Madhuca* clade of Isonandreae); (3) an increase in carpels independently of other organs (*Burckella*, *Letestua*, *Labramia*, etc.). A major shift affecting all Sapotaceae, except Isonandreae, is the sterilization or loss of the antepetalous stamen whorl. The presence of two fertile stamen whorls in Isonandreae indicates a possible reversal or a retained plesiomorphy. In a number of genera, stamens are secondarily increased independently of changes in merism. Descriptions of flowers listing only organ numbers are thus misleading in the inference of evolutionary relationships, as they do not differentiate between changes in merism affecting the number of perianth whorls and other changes affecting the androecium, such as sterilization, loss or occasional doubling of antepetalous stamens. © 2015 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2016, **180**, 161–192.

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INTRODUCTION

The term merism (or merosity) is derived from the Greek word *méros* (μέρος = part) and describes the

number of parts in whorls of floral organs and leaves (Ronse De Craene & Smets, 1994; Ronse De Craene, 2015). The question of how nature counts is intriguing. Numbers of elements are often invariable in a species or between related species. Examples of these are the pentadactylous system in humans and other

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vertebrates and the number of cervical vertebrae in all mammals (Running & Meyerowitz, 1996). Flowers tend to be highly conservative in their number of parts in many angiosperm clades, and families or even major clades can be recognized by constancy in their merism (Ronse De Craene, 2010, 2015). For example, monocots are basically trimerous, whereas core eudicots (Pentapetalae) are mainly pentamerous or tetramerous. Some families are highly constant in their merism, such as pentamerous Geraniaceae and Oxalidaceae, or tetramerous Brassicaceae, Onagraceae and Haloragaceae. Floral morphology and merism are not constant in all plant families: in large families, such as Myrtaceae, Rosaceae and Euphorbiaceae, for example, merism can be variable, both between and within species or even individuals.

Although merism can be constant and isomerous in all whorls (e.g. *Geranium* L., Geraniaceae, is pentamerous in all organ whorls), other taxa show a difference in merism between different whorls (anisomery). The most common changes in merism generally affect the gynoecium, in which carpel numbers are often reduced to three or two (e.g. in Caryophyllaceae and most asterids), and often the stamens in connection with the gynoecium (e.g. in Acanthaceae and Lamiaceae). Changes can be regular, by doubling the organ number within a whorl, or irregular, by addition (e.g. via irregular splitting of primordia) or loss (e.g. via fusion) of random organs. Doubling is a process generally known as *dédoublement*, which leads to the replacement of a single organ by a pair, and is frequently found in the androecium of core eudicots. *Dédoublement* can affect all organs of a whorl (e.g. in *Theobroma* L., Malvaceae), or can be random in affecting individual organs (e.g. in *Geranium*). More examples of splitting or loss of stamens have been presented by Ronse De Craene & Smets (1993, 1994, 1996). The phenomenon of meristic change is discussed further by Ronse De Craene (2015).

Sapotaceae is a medium-sized family belonging to Ericales (APG III, 2009). Ericales, as currently circumscribed, is diverse and species rich with no clearly identified morphological synapomorphies for the whole order (Schönenberger, Anderberg & Sytsma, 2005, but see Soltis *et al.*, 2005). Sapotaceae consists of shrubs and trees with an almost world-wide distribution with most diversity in the tropical and subtropical areas of South America and Asia (Swenson & Anderberg, 2005; Wilkie, 2011). There are currently *c.* 1300 recognized species in 62 genera (Swenson, Richardson & Bartish, 2008b; U. Swenson, pers. comm.). Pennington (1991, 2004), relying largely on morphology, divided Sapotaceae into five tribes: Chrysophylleae, Sideroxyleae, Omphalocarpeae, Isoandreae and Sapoteae. Using molecular data, Anderberg, Rydin & Källersjö (2002) identified *Sar-*

cosperma Hook.f. as sister to all other Sapotaceae and, subsequently, Anderberg & Swenson (2003) and Swenson & Anderberg (2005) divided Sapotaceae into three subfamilies: the small subfamily Sarcospermatoidae and the two main subfamilies Sapotoideae and Chrysophylloideae. Furthermore, it has been shown that many of the described genera are polyphyletic (Bartish *et al.*, 2005; Swenson *et al.*, 2008b). Sarcospermatoidae consists of the single genus, *Sarcosperma* (eight species), and has sometimes been considered as a separate family (e.g. Anderberg & Swenson, 2003). Sapotoideae contains more than 540 known species in 29 genera (Smedmark, Swenson & Anderberg, 2006) and relationships in that subfamily were elucidated by Smedmark *et al.* (2006), Richardson *et al.* (2014) and Armstrong *et al.* (2014). Chrysophylloideae consists of 28 genera with *c.* 600 species (Swenson *et al.*, 2008b).

The flowers of Sapotaceae are usually pentamerous (but occasionally range from tetramery to octomery and beyond) with one or more whorls of free or fused sepals and fused petals with a variable number of lobes. The androecium consists generally of a single whorl of fertile stamens opposite the petals, with an additional antesealous whorl of petaloid or scale-like staminodes and, more rarely, fertile stamens. In some species, the number of stamens is secondarily increased (Ronse De Craene, 2010). The ovary is superior with 1–30, usually uniovulate, locules (Pennington, 1991).

Changes in merism have been recognized as an important taxonomic character in Sapotaceae, especially the number and arrangement of sepals and the number of petals relative to the number of sepals (Pennington, 1991), but Anderberg & Swenson (2003) and Swenson & Anderberg (2005) have demonstrated that virtually all such ‘important’ morphological characters in Sapotaceae are homoplasious and may therefore be misleading. Floral merism can be variable in some genera and is reflected by the existence of anisomerous flowers. All floral whorls can be hexamerous or octomerous, or only part of the flower may be affected, as observed in different species of the same genus by Pennington (1991). However, the significance of this phenomenon has barely been discussed in the literature (e.g. Hartog, 1878; Baillon, 1891a; Aubréville, 1964; Swenson *et al.*, 2008a) with little or no understanding of the process affecting the changes in merism in flowers. The interpretation of flowers is hampered by the restricted amount of developmental and anatomical studies of flowers in Sapotaceae, which are limited to a few species (e.g. Hartog, 1878; Ayensu, 1972; Vink, 1995; Moncur, 1988; Caris, 1998, 2013). The only studies comparing the positional relationships of different organ whorls are by Hartog (1878) and Eichler (1875).

The aim of this investigation is twofold: (1) to comparatively study the floral development of several species to understand the process of meristic change in flowers of Sapotaceae; (2) to understand its phylogenetic significance by mapping these changes onto a cladogram. Is there a directional evolutionary process towards an increase or decrease in floral organs in certain lineages of the family, or is variation in merism spread across the family without a distinct underlying evolutionary direction?

MATERIAL AND METHODS

Obtaining suitable floral material of Sapotaceae is difficult, as few species are cultivated and flowering is mostly synchronous. The plant material used consisted of small twigs with floral buds that were collected both from the wild (in Malaysia, Belize and South Africa) and from botanic gardens (Brussels and Edinburgh) (Table 1). The floral buds of nine species of Sapotaceae were analysed. Six of these are members of Sapotoideae [*Madhuca malaccensis* (C.B. Clarke) H.J. Lam, *Manilkara zapota* (L.) Van Royen, *Palaquium amboinense* Burck., *Payena leerii* (Teijsm. & Binn.) Kurz, *Payena lucida* A. DC. and *Sideroxylon inerme* L.] and three are members of Chrysophylloideae [*Planchonella obovata* (R.Br.) Pierre, *Pouteria durlandii* (Standl.) Baehni and *Synsepalum dulcificum* (Schumach. & Thonn) Danniell]. In Sapotoideae, *M. malaccensis*, *P. amboinense*, *P. leerii* and *P. lucida* are members of tribe Isonandreae, *S. inerme* is a member of Sideroxyloideae and *M. zapota* is a member of Sapoteae.

Voucher material is preserved in 70% ethanol at the Royal Botanic Garden Edinburgh (RBGE). For floral anatomical investigations with light microscopy (LM), floral buds were dehydrated and embedded in Kulz-

er's Technovit 7100 [2-hydroxyethyl methacrylate (HEMA)]. A few buds of *M. malaccensis* were sectioned with a Leitz Minot-microtome type 1212 (at a thickness of 6–12 µm with a 170-mm Leica wedge blade) and stained with 0.05% toluidine blue. The slides were analysed and photographed under a microscope (Zeiss Axioskop with AxioCam MRc5) before assemblage on plates using Adobe Photoshop Elements 8.0.

For scanning electron microscopy (SEM), young buds were dissected under a Wild MZ8 stereomicroscope (Leica, Wetzlar, Germany), dehydrated in an absolute ethanol–acetone series and critical point dried with a K850 Critical Point Dryer using liquid CO₂ (Emitech Ltd.). Material was coated with platinum using a K575X sputter coater (Emitech Ltd.) and observed with a Supra 55VP scanning electron microscope.

To place the information obtained from the sections and SEM images into a phylogenetic context, information on the floral morphology of most genera of Sapotaceae was obtained from the literature and assembled into a character matrix (see Table 2). This was mapped onto a phylogenetic tree to trace character evolution in Sapotaceae and to illuminate evolutionary trends (Figs 9–13, see section on 'Phylogenetics of Sapotaceae').

The main sources of information were Baehni (1965) and Pennington (1990, 1991, 2004) in addition to other relevant papers (see Table 2). For exact nomenclature we used the Kew World Checklist of Selected Plant Families (<http://apps.kew.org/wcsp/home.do>). One recurrent issue regarding information in the literature is the reliability of data regarding merism, as most data were obtained from a limited number of herbarium specimens and have few field notes on the variation in floral structure in the

Table 1. Plant material used in this study

Species	Locality	Herbarium collection number	Pickled collection number
<i>Manilkara zapota</i> (L.) Van Royen	National Botanic Garden of Belgium cultivated	–	148 Lm
<i>Madhuca malaccensis</i> (C.B. Clarke) H.J. Lam.	Malaysia	PW 838	1044 Lo
<i>Palaquium amboinense</i> Burck.	Malaysia	PW 813	1020 Lo
<i>Payena leerii</i> (Teijsm. & Binn.) Kurz.	Malaysia	PW 811	1019 Lo
<i>Payena lucida</i> A. DC.	Malaysia	PW 845	1042 Lo
<i>Planchonella obovata</i> (R.Br.) Pierre	Malaysia	PW 850	1043 Lo
<i>Pouteria durlandii</i> (Standl.) Baehni	Belize	LRDC 1432	856 La
<i>Sideroxylon inerme</i> L.	Cape Peninsula, South Africa	LRDC 1374	680 Lz
<i>Synsepalum dulcificum</i> (Schumach. & Thonn.) Danniell	Royal Botanic Garden Edinburgh cultivated	–	1066 Led

LRDC, Louis Ronse De Craene; PW, Peter Wilkie.

Table 2. Merism characteristics of species used in this study

Species name	Subfamily-tribe (Pennington, 1991)	Number of species in genus	Common floral formula	Merism	Sepal number	Petal number	Stamen number	Staminode number	Carpel number	Authority
<i>Sideroxylon lycioides</i> L.	Sapotoideae- Sideroxyleae	76	K5C5A5 ⁺ +5G5	5	5(-6)	5(-6)	5(-6)	5(-6)	4-5	Baillon, 1891b; Pennington, 1990
<i>Sideroxylon persimile</i> (Hemsley) T.D.Penn.	Sapotoideae- Sideroxyleae	76	K5C5A5 ⁺ +5G5	5	5	5	5	5	(4-5)(-8)	Pennington, 1990
<i>Sideroxylon inerme</i> L.	Sapotoideae- Sideroxyleae	76	K5C5A5 ⁺ +5G5	5	5	(4-5)(-6)	(4-5)(-6)	(4-5)(-6)	(4-5)	Gerstner, 1946*; this study
<i>Sideroxylon oxyacanthum</i> Baill.	Sapotoideae- Sideroxyleae	76	K5C5A5 ⁺ +5G5	5	5	5	5	5	(3-5)	Baillon, 1891b
<i>Neohemsleya usambarensis</i> T.D.Penn.	Sapotoideae- Sideroxyleae	1	K5C5A5 ⁺ +5G5	5	5	(4) 5	(4) 5	(4) 5	5	Pennington, 1991
<i>Diploon cuspidatum</i> (Hoehe) Cronquist	Sapotoideae- Sideroxyleae	1	K5C5A0+5G1	4-5	4-5	4-5	4-5	0	1 (2)	Baehni, 1965; Pennington, 2004
<i>Mimusops elengi</i> L.	Sapotoideae- Sapoteae	41	K4+4C8A8 ⁺ +8G8	8	8	8	8	8	6-8	Hartog, 1878; Baillon, 1891a*; Lam, 1925
<i>Baillonella toxisperma</i> Pierre	Sapotoideae- Sapoteae	1	K4+4C8A8 ⁺ +8G8	8	8	8	8	8	8	Aubréville, 1961; Heine, 1963; Baehni, 1965
<i>Autranella congolensis</i> (De Wild.) A.Chev.	Sapotoideae- Sapoteae	1	K4+4C8A8 ⁺ +8G8	8	8	8	8	8	8	Aubréville, 1961; Heine, 1963
<i>Vitellaria paradoxa</i> C.F.Gaertn.	Sapotoideae- Sapoteae	1	K4+4C8A8 ⁺ +8G8	8 (10)	8 (10)	8 (10)	8 (10)	8 (10)	8 (10)	Baehni, 1965; Thompson, 1910 in Govaerts <i>et al.</i> , 2001
<i>Vitellariopsis dispar</i> (N.E.Br.) Aubr.	Sapotoideae- Sapoteae	5	K4+4C8A8 ⁺ +8G8	6-8	6-8	6-8	6-8	6-8	8-9	Aubréville, 1963a; Baehni, 1965
<i>Tieghemella heckelii</i> (A.Chev.) Pierre ex Dubard	Sapotoideae- Sapoteae	2	K4+4C8A8 ⁺ +8G8	8	8	8	8	8	8	Heine, 1963 ; Pennington, 2004
<i>Northia seychellana</i> Hook.f.	Sapotoideae- Sapoteae	1	K3+3C6A0 (6 ⁺)+6G6	6	6	6	6	0 (6 ⁺)	6	Lam; 1925; Baehni, 1965; Pennington, 1991, 2004
<i>Faucherea parvifolia</i> Le Comte	Sapotoideae- Sapoteae	11	K3+3C6A6 ⁺ +6G6	6	6	6(-8)	6(-8)	6(-8)	(5-)(6-)(8)	Aubréville, 1963a, 1963c
<i>Letestua durissima</i> (Chev.) Lecomte	Sapotoideae- Sapoteae	1	K3+3C18A0+ 18G18	12-18	(4-6)	12-18	12-18	0	(16-)(18)	Aubréville, 1961; Baehni, 1965; Pennington, 1991
<i>Labourdonnaisia calophylloides</i> Bojer	Sapotoideae- Sapoteae	7	K3+3C18A0 (18 ⁺)+18G6	12-18	6(-8)	12 (18)	12 (18)	0 (18 ⁺)	6(-8)	Baillon, 1891b; Baehni, 1965; Pennington, 1991
<i>Lecomtedoxa klaineana</i> Pierre ex Engl.	Sapotoideae- Sapoteae ^{‡‡}	5	K5C5A5 ⁺ +5G5	5	5	5	5	5	5	Aubréville, 1961 ; Baehni, 1965
<i>Neolemonniera clitandriifolia</i> (A.Chev.) Heine	Sapotoideae- Sapoteae ^{‡‡}	3	K5C5A5 ⁺ +5G5	5	5	5	5	5	5	Aubréville, 1961; Heine, 1963
<i>Inhambanella henriquezii</i> (Engl. & Warb.) Dubard	Sapotoideae- Sapoteae ^{‡‡}	2	K5C5A5 ⁺ +5G5	(4) 5 (6)	(4) 5 (6)	(4) 5 (6)	(4) 5 (6)	(4) 5 (6)	5 (6)	Baehni, 1965; Stones, 1968 in Govaerts <i>et al.</i> , 2001; Pennington, 2004
<i>Eberhardtia aurata</i> (Pierre ex Dubard) Lecomte	Sapotoideae- Sapoteae	3	K5C5A5 ⁺ +5G5	5	5	5	5	5	3-5	Pennington, 1990
<i>Payena lucida</i> (Wall. ex D.Don) A.DC	Sapotoideae- Isonandreae	21	K2+2C4+4A8+8G8	8	4	(7)-8	13-16	0	8	Lam, 1927; Wight, 1850 in Govaerts <i>et al.</i> , 2001; this study
<i>Payena leerii</i> (Teijsm. & Binn.) Kurz	Sapotoideae- Isonandreae	21	K2+2C4+4A8+8G8	8	4	8	16	0	(4-5)?8	Baehni, 1965; this study
<i>Madhuca malaccensis</i> (C.B.Clarke) H.J. Lam.	Sapotoideae- Isonandreae	107	K2+2C8A8 ⁺ +8 ⁺ G8	8	4	(8-9)10(12)	20-25	0	8(-11)	Baehni, 1965; this study
<i>Madhuca longifolia</i> (J. König ex L.) J.F.Macbr.	Sapotoideae- Isonandreae	107	K2+2C8A8+8G8	8	4(8)	8	16(-30)	0	8-11	Hartog, 1878; Baehni, 1965
<i>Madhuca neriifolia</i> (Moon) H.J.Lam	Sapotoideae- Isonandreae	107	K2+2C8A8+8G8	8	4	8	16	0	8	Baehni, 1965
<i>Madhuca hainanensis</i> Chun & Chow	Sapotoideae- Isonandreae	107	K2+2C8A30G8	8	4	8(-11)	18-30	0	6-8	Chun & How, 1958; Aubréville, 1963b
<i>Madhuca crassipes</i> (Pierre) Lam.	Sapotoideae- Isonandreae	107	K2+2C9A9+9G9	8-9	4	8-9	17-19	0	9	Lam, 1925; Baehni, 1965
<i>Madhuca utilis</i> (Ridl.) H.J.Lam	Sapotoideae- Isonandreae	107	K2+2C8A8+8G8	8	4	8	10-16	0	8	Lam, 1927; Baehni, 1965
<i>Aulandra longifolia</i> H.J.Lam	Sapotoideae- Isonandreae	3	K3+3C6A6+6 ² G6	6	6	6	18-19 [†]	0	6	Lam, 1927; van Royen, 1958b; Baehni, 1965
<i>Isonandra compta</i> Dubard	Sapotoideae- Isonandreae	10	K2+2C4A4+4G4	4	4	4	8	0	4	Dubard, 1909; Lam, 1925, 1927

Table 2. *Continued*

Species name	Subfamily-tribe (Pennington, 1991)	Number of species in genus	Common floral formula	Merism	Sepal number	Petal number	Stamen number	Staminode number	Carpel number	Authority
<i>Palaquium amboinense</i> Burck.	Sapotoideae-Isonandreae	119	K3+3C6A6+6G6	6	6	6	10–12	0	5–6	Baehni, 1965; this study
<i>Palaquium microphyllum</i> King & Gamble	Sapotoideae-Isonandreae	119	K3+3C6A6+6G6	6	6	6	12	0	6	Lam, 1925; Baehni, 1965
<i>Palaquium formosanum</i> Haiata	Sapotoideae-Isonandreae	119	K3+3C6A6+6G6	6	6	6	12	0	6	Baehni, 1965
<i>Diploknema oligomera</i> H.J.Lam	Sapotoideae-Isonandreae	7	K5C5+5A5+5G5	5	5	10	10	0	5	Lam, 1927*; van Royen, 1958a
<i>Diploknema butyracea</i> (Roxb.) H.J.Lam	Sapotoideae-Isonandreae	7	K5C10A5 ²⁻³ +5?G9	10	5 (2+3)	(8) 10	30–40‡	0	7–9	Baillon, 1891b; Lam, 1925; Baehni, 1965
<i>Burckella macropoda</i> (Krause) H.J.Lam	Sapotoideae-Isonandreae	13	K2+2C8A8+8G4	8	4	8	16	0	4 (5)	Baehni, 1965
<i>Labramia costata</i> (M.M.Hartog ex Baill.) Aubrév.	Sapotoideae-Sapoteeae	9	K3+3C6A6*+6G10-12	6	3+3	6	6	6	10–12	Aubréville, 1963a, 1963c
<i>Manilkara zapota</i> (L.) P.Royen	Sapotoideae-Sapoteeae	65	K3+3C6A6*+6G9	(5) 6	(5) 6	(5) 6	(5) 6	(5) 6	9–12	Hartog, 1878; Baehni, 1964; Caris, 2013; this study
<i>Manilkara concolor</i> (Harv. ex C.H.Wr.) Gerstn.	Sapotoideae-Sapoteeae	65	K3+3C6A6*+6G6	6 (8)	6 (8)	6 (8)	6 (8)	6 (8)	6 (8)	Gerstner, 1946* (as <i>Mimusops concolor</i>), 1948; Baehni, 1965
<i>Manilkara chicle</i> (Pitler) Gily	Sapotoideae-Sapoteeae	65	K3+3C6A6*+6G6-9	6	6	6	6	6	6–9	Gilly, 1943 (interprets petals as outer staminodes); Baehni, 1965
<i>Manilkara kauki</i> (L.) Dubard	Sapotoideae-Sapoteeae	65	K3+3C6A6*+6G6	6–7	6	6	6	6	6(–8)	Dubard, 1915; Aubréville, 1963b
<i>Pyrluma sphaerocarpum</i> (Baill.) Aubrév.	Chrysophylloideae-Chrysophylleae	2	K5C5A5*+5G5	5	5	5	5	5	5	Aubréville, 1967
<i>Planchonella obovata</i> (R.Br.) Pierre	Chrysophylloideae-Chrysophylleae	c. 110‡	K5C5A5*+5G5	5	4–5	5	5	0–5	5	Lam, 1925, 1927; Baehni, 1965; this study
<i>Planchonella kaalaensis</i> Aubrév.	Chrysophylloideae-Chrysophylleae	c. 110	K5C5A5*+5G5	5	5	5	5	5–10	5	Aubréville, 1967
<i>Planchonella baillonii</i> (Zahlbr.) Dubard	Chrysophylloideae-Chrysophylleae	110	K5C5A5*+5G5	5	5	5	5	5	(4) 5	Baehni, 1965
<i>Pouteria durlandii</i> (Standl.) Baehni	Chrysophylloideae-Chrysophylleae	c. 200	K5C5A5*+5G2	5	5	5	5	5	2	This study
<i>Pouteria vernicosa</i> T.D.Penn.	Chrysophylloideae-Chrysophylleae	c. 200	K5C5A5*+5G1	5	5	5	5	5	1	Pennington, 1990
<i>Pouteria guianensis</i> Aubl.	Chrysophylloideae-Chrysophylleae	c. 200	K4C4A4*+4G4	4	4	4	4	4	4	Baehni, 1965; Pennington, 1990
<i>Aningeria adolphi-friederici</i> (Engl.) Robyns & Gilbert	Chrysophylloideae-Chrysophylleae	6	K5C5A5*+5G5	5	5	5	5	5	5	Baehni, 1965
<i>Pouteria campechiana</i> (Kunth) Baehni	Chrysophylloideae-Chrysophylleae	c. 200	K5C5A5*+5G5	5	(4) 5 (6)	(4) 5 (6)	(4) 5 (6)	(4) 5 (6)	5–10	Baehni, 1965; Pennington, 1990
<i>Synsepalum dulcificum</i> (Schum. & Thom.) Daniell	Chrysophylloideae-Chrysophylleae	28	K5C5A5*+5G5	5	5	5	5	5	5	Baehni, 1965; Ayensu, 1972; Caris, 2013; this study
<i>Englerophytum magalimontanum</i> (Sonder) T.D.Penn.	Chrysophylloideae-Chrysophylleae	5–10?	K5C5A(5*)+5G5	5	5	5	5	0 (1–5)	(3–4) 5	Meeuse, 1960 (as <i>Pouteria</i>)
<i>Magodendron mennya</i> Vink	Chrysophylloideae-Omphalocarpeae	2	K5C5A5*+5 ²⁻ 4G5	5	5	5	10–17	5	5	Vink, 1957, 1995
<i>Omphalocarpum pachysteloides</i> Mildbr. ex Hutch. & Dalziel	Chrysophylloideae-Omphalocarpeae	27	K5C5 A5*+5 ²⁻³ G10	5	5	5	10–15	5	10	Heine, 1963; Baehni, 1965; Caris, 2013
<i>Tsebona macrantha</i> Capuron	Chrysophylloideae-Omphalocarpeae	1	K3:2C5A5*+5 ²⁻⁴ G5	5	5	5	10–20	5	5	Capuron, 1962
<i>Tridesmostemon congoense</i> (A.Chev.) Aubrév. & Pellegr.	Chrysophylloideae-Omphalocarpeae	2	K5C5A5*+5 ²⁻³ G10	5	5	5	10–15	5	10	Aubréville, 1961; Pennington, 2004
<i>Pleioluma baueri</i> (Montrouz.) Swenson & Munzinger	Chrysophylloideae-Chrysophylleae	32	K5C5A5*+5G5	5	5	5	5	5	5	Swenson <i>et al.</i> , 2007
<i>Sersalisia sessiliflora</i> (C.T.White) Aubrév.	Chrysophylloideae-Chrysophylleae	4–6	K5C5A5*+5G5	5	5	5	5	5	5	Baehni, 1938
<i>Aubreginia taiensis</i> (Aubrév. & Pellegr.) Heine	Chrysophylloideae-Chrysophylleae	1	K5C5A5*+5G8	5	5	5	5	5	7–8	Baehni, 1965; Pennington, 2004

Table 2. *Continued*

Species name	Subfamily-tribe (Pennington, 1991)	Number of species in genus	Common floral formula	Merism	Sepal number	Petal number	Stamen number	Staminode number	Carpel number	Authority
<i>Gambeya boiviniana</i> Pierre	Chrysophylloideae- Chrysophylleae	20	K5C5A0+5G5	5	5	4–5	5	0	5	Baehni, 1965
<i>Chrysophyllum</i> <i>bangweolense</i> R.E.Fr.	Chrysophylloideae- Chrysophylleae	c.80	K5C5A0+5G5	5	5	5	5	0	5	Baehni, 1965
<i>Chrysophyllum</i> <i>venezuelanense</i> (Pierre) T.D.Penn.	Chrysophylloideae- Chrysophylleae	c.80	K5C5A0+5G5	5	5	5	5	0 or 5 minute vestigis	5	Pennington, 1990
<i>Chrysophyllum cainito</i> L.	Chrysophylloideae- Chrysophylleae	c.80	K5C5A0+5G7- 10	5	5	5	5	0	7–10	Baehni, 1965
<i>Delpyodora</i> <i>macrophylla</i> Pierre	Chrysophylloideae- Chrysophylleae	2	K5C5A0+5G5	5	5	5	5	0	5	Aubréville, 1961
<i>Capurodendron</i> <i>androyense</i> Aubrév.	Chrysophylloideae- Chrysophylleae‡‡	23	K5C5A5*+5G5	5	5	5	5	5	5 (6)	Pennington, 2004
<i>Van-royena</i> <i>castanosperma</i> (White) Aubrév.¶	Chrysophylloideae- Chrysophylleae	1	K5C5A5*+5G5	5	5	5	5	5	5	Aubréville, 1963d
<i>Pycnandra comptonii</i> (Moore) Vink	Chrysophylloideae- Chrysophylleae	65	K5C5A0+5 ²⁻³ G7	?	5(–6)	6–10	15(–19)**	0	7–8	Vink, 1957; Aubréville, 1967; Swenson & Munzinger, 2010b
<i>Pycnandra francii</i> (Guillaumin & Dub.) Swenson & Munzinger‡‡	Chrysophylloideae- Chrysophylleae	65	K5C8A0+8G5	5–8	5	5–6(–10)	5–6(–10)	0	3–5	Vink, 1958; Pennington, 1991; Swenson & Munzinger, 2010b
<i>Pradosia</i> <i>surinamensis</i> (Eyma) T.D.Penn.	Chrysophylloideae- Chrysophylleae	26	K5C5A0+5G5	5	5	5	5	0	5	Pennington, 1990; Alves-Araújo & Alves, 2012
<i>Pichonia balansana</i> Pierre	Chrysophylloideae- Chrysophylleae	12	K5C5A5*+5G5	5–8	5–8	5–8	5–8	5–8	5	Pierre, 1890; Baehni, 1942; Pennington, 2004; Swenson & Munzinger, 2012, Swenson <i>et al.</i> , 2013
<i>Niemeyera antiloga</i> (F.Muell.) T.D.Penn.	Chrysophylloideae- Chrysophylleae	4	K5C5A0+5G5	5–6	5–6	5–6	5–6	0	(1)3–5	Vink, 1958; Pennington, 1991, 2004
<i>Leptostylis filipes</i> Benth.	Chrysophylloideae- Chrysophylleae	8	K2+2C8A0+8G4	8	4	5–8	5–8	0	4(–6)	Bentham & Hooker, 1876; Vink, 1957
<i>Elaeoloma</i> <i>schomburgkiana</i> (Miq.) Baill.	Chrysophylloideae- Chrysophylleae	4	K5C5A0+5G3	5	(4)–5	5(–6)	5(–6)	0	2–3	Baillon, 1891b; Baehni, 1965; Pennington, 1991
<i>Ecclinusa guianensis</i> Eyma	Chrysophylloideae- Chrysophylleae	11	K5C5A0+5G5	5	5	(4) 5	(4) 5	0	5	Eyma, 1936; Pennington, 1990
<i>Sarcaulus brasiliensis</i> (A.D.C.) Eyma	Chrysophylloideae- Chrysophylleae	5	K5C5A5*+5G5	5	5	5	5	5	5	Eyma, 1936; Pennington, 1990
<i>Chromolucuma</i> <i>rubriflora</i> Ducke	Chrysophylloideae- Chrysophylleae	5	K5C5A5*+5G3	5	5	5	5	5	(2)–3	Baehni, 1942; Pennington, 1990
<i>Microrhaphis egensis</i> (A.D.C.) Pierre	Chrysophylloideae- Chrysophylleae	38	K5C5A5*+5G5	5	5(–6)	5	5	5	5	Pennington, 1990
<i>Breivia sericea</i> Aubrév. & Pellegr.	Chrysophylloideae- Chrysophylleae	1	K5C5A5*+5G8	5	5	5	5	5	8–9	Pennington, 2004
<i>Xantolis siamensis</i> (Fletcher) van Royen	Chrysophylloideae- Chrysophylleae	14	K5C5A5*+5G5	5	5	5	5	5	(4)–5	Pennington, 2004
<i>Sarcosperma</i> <i>laurinum</i> (Benth.) Hook.f.	Sarcospermatoidae	11	K5C5A5*+5G1	5	5	5	5	5	(1)2	Bentham & Hooker, 1876; Lam, 1925; Baehni, 1965

Species used in the phylogenetic reconstructions are shown in bold; in floral formulas sterile stamens shown with °.

*These authors present a floral diagram.

†According to van Royen (1958b), stamens of *Aulandra* are in three rows. There is no clear information on their position.

‡According to Lam (1925), stamens are in three–four rows, inner antepetalous ones longest; Baillon (1891a) reported the dédoublement of the alternipetalous stamens.

§*Planchonella* was accepted by Aubréville (1964), but reduced to *Pouteria* by Pennington (1991) apart from some species. Swenson *et al.* (2013) took a broader approach and considered the highest number of species including *Iteiluma* Baill.

¶*Pouteria castanosperma* (C.T.White) Baehni, according to Pennington (1991).

**Vink (1957) gives a floral diagram for *P. fastuosum*, which is pentamerous throughout. Antepetalous stamens are in pairs or triplets. Merism of *P. comptonii* is highly variable by petal and carpel increases. Aubréville (1967) mentioned that *Pycnandra* has paired stamens opposite the petals and no staminodes. Swenson & Munzinger (2010b) mentioned six to ten petals and two stamens inserted opposite each petal lobe. Other species are pentamerous throughout (Swenson & Munzinger, 2010a,b). For mapping, we use the pentamerous flower.

††Reduced to *Niemeyera* by Pennington (1991); accepted as *Chrysophyllum francii* by Vink (1958).

‡‡Grouped in tribe Tseboneae by Gautier *et al.* (2013).

collection. The most common merism was recorded, especially in the floral formulae in Table 2. When there was variation in merism for a given species, the range of variation was recorded.

Sequences of the internal transcribed spacers (ITSs) of nuclear ribosomal DNA of representatives of most genera were used in a Bayesian analysis to construct a phylogenetic tree (voucher accessions and GenBank numbers are presented in Table 3). Multiple representatives of genera that appeared to be polyphyletic in previous analyses, including *Pouteria* Aubl. (Swenson, Bartish & Munzinger, 2007; Triono *et al.*, 2007), were included. As *Pouteria* appeared to be polyphyletic, several genera [*Sersalisia* R.Br., *Pleioluma* (Baill.) Baehni, *Van-royena* Aubrév., *Planchonella* Tiegh. and *Pyriluma* (Baill.) Aubrév.] have been resurrected from *Pouteria sensu* Pennington (1991). Bayesian analyses were conducted with MrBayes 3.1 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003). The Akaike information criterion (AIC) was used in MrModelTest (Nylander, 2004) to determine the most appropriate model for the data. Four Monte Carlo Markov chains (MCMCs) with the chain temperature set at default were run simultaneously for ten million generations, sampling trees and parameters every 10 000 generations. Tracer version 1.5 (Rambaut & Drummond, 2007) was used to determine whether each parameter had appropriate effective sample size (ESS) values. A burn-in of 10% (1000) of the trees was removed in LogCombiner. TreeAnnotator (Drummond & Rambaut, 2007) was used to select the maximum clade credibility (MCC) tree. Clade support was represented by posterior probability (PP) values, with PP values above 0.95 indicating strong support (Fig. 8, see section on 'Phylogenetics of Sapotaceae'). Different rooting options and the choice of outgroups are not considered in this article as they did not affect the outcome of the tree or the reconstruction of the character states.

A morphological matrix was created for each of the species used in the mentioned ITS analysis, in addition to other analyses (e.g. Swenson *et al.*, 2007, 2008a,b), and morphological character state changes were mapped onto the MCMC tree from the Bayesian analysis in Mesquite (Maddison & Maddison, 2010). Numbers of sepals, petals, stamens, staminodes and carpels were mapped onto the tree in different colours to indicate character evolution (Figs 9–13, see section on 'Phylogenetics of Sapotaceae'). Adobe Photoshop Elements 8.0 was used to label the trees.

RESULTS

MORPHOLOGICAL INVESTIGATION OF FLOWERS

As a result of scarcity of material, floral developmental data were only partially available for *M. malac-*

ensis, *P. amboinense*, *S. inerme* and *P. leerii*. Data for *P. obovata*, *P. durlandii*, *S. inerme* and *S. dulcificum* were based mainly on investigations of older buds. All data for the studied species are summarized in Table 2 with information on other Sapotaceae compiled from the literature.

In all species, flowers are grouped in compact cymose fascicles in the axil of a bract and preceded by two bracteoles which terminate growth before flowers are mature. As a result, bracts and bracteoles are generally overlooked in descriptions of species. Bracts and bracteoles only affect flowers in early stages and are not covered in this article.

Payena leerii, Sapotoideae (Figs 1, 2A, B, 7A)

The flowers have four sepals, eight petals, 16 stamens and mostly eight carpels in a single whorl (Fig. 7A, Table 2). Sepals are decussate and develop sequentially, and the outer median sepals are much larger than the inner lateral sepals throughout development (Figs 1A, C, 2A). The bud is somewhat compressed when the petals are formed (Fig. 1B, C). The earliest stages of petal development were not available, but petals appear to be of two sizes, reflecting an arrangement of two whorls, with the alternisepalous petals being slightly larger (Fig. 1B, C). Petals are soon connected by a common meristem ring. One side of the flower towards the last-formed sepal is occasionally delayed (Fig. 1D). At early stages, alternisepalous petals are larger than antesealous petals, but they are rapidly overtaken in size and end up as smaller outer lobes (Fig. 1B–F). The inner lobes converge to the centre of the apex and become arranged in an imbricate aestivation (Fig. 1E). The outer lobes remain shorter than the inner lobes, but also contribute to the imbricate aestivation pattern by covering the margins of the inner petals (Fig. 1E, F). Both sepals and petals develop apical trichomes and sepals, especially, are covered by a dense indumentum (Fig. 2A). The inner petals are pushed outwards by the developing style. Stamens appear at the time at which the floral bud is already covered by the rapidly developing petals. In our material, stamen numbers fluctuated between 13 (Fig. 1H) and 16 (Fig. 1G, I, J) stamens. The earliest stages of stamen development were not available, but all stamens appear to be inserted more or less in one whorl at the time of carpel development. It is not clear whether carpels arise before the stamens, as they are already well developed at a similar stage of stamen development (Fig. 1G). Stamens are compressed between perianth and gynoecium, and become more clearly arranged in two alternating whorls, as the antepetalous stamens overtake the alternipetalous stamens in size and move slightly outwards (Fig. 1H–J). No staminodes are formed, but the antepetalous stamens are slightly longer and cover the alternipetalous

Table 3. Voucher details and GenBank numbers for internal transcribed spacer (ITS) sequence data

Species	Collector and number	Provenance	GenBank number
<i>Aubregria taiensis</i> (Aubrév. & Pellegr.) Heine	<i>Enti 6871</i>	Ghana	DQ377520
<i>Aulandra longifolia</i> H.J.Lam	<i>Christensen, H. 1720</i>	Malaysia	KF597536
<i>Autranella congolensis</i> (de Wild.) A.Chev.	<i>Bokdam 4401</i>	Congo	KF686187
<i>Baillonella toxisperma</i> Pierre	<i>Dyana Ndiade B. (s.n.)</i>	Gabon	KF686188
<i>Brevia sericea</i> Aubrév. & Pellegr.	<i>Letouzey 8319</i>	Ivory Coast	DQ246666
<i>Burckella macropoda</i> (K.Krause) H.J.Lam	<i>Wilkie 818</i>	Java	KF686190
<i>Capurodendron androyense</i> Aubrév.	<i>Humbert 28855</i>	Madagascar	AM408107
<i>Chromolucuma rubriflora</i> Ducke	<i>Anderberg et al. 20</i>	Costa Rica	EF558614
<i>Chrysophyllum bangweolense</i> R.E.Fr.	<i>Malaisse 9600</i>	Tanzania to Angola/Zaire	AY552152
<i>Chrysophyllum boivinianum</i> (Pierre) Baehni	<i>McPherson 14426</i>	Madagascar	DQ246667
<i>Chrysophyllum cainito</i> L.	<i>Chantaranonthai 2304</i>	Thailand	AY552153
<i>Chrysophyllum venezuelanense</i> (Pierre) T.D.Penn.	<i>Stahl et al. 5755</i>	Mexico to Bolivia/Ecuador	DQ246673
<i>Delpyodora gracilis</i> A.Chev.	<i>Jongkind 5074</i>	Ivory Coast	DQ246674
<i>Diploknema oligomera</i> H.J.Lam	<i>Chase 1360</i>	Indonesia	KF686194
<i>Diploon cuspidatum</i> (Hoehne) Cronquist	<i>Pennington et al. 13843</i>	French Guiana	DQ246676
<i>Eberhardia aurata</i> (Pierre ex Dubard) Lecomte	<i>Hao 534</i>	China	EF558617
<i>Ecclinusa guianensis</i> Eyma	<i>Ducke Res. 05-906</i>	Brazil	DQ246677
<i>Elaeoluma schomburgkiana</i> (Miq.) Baill.	<i>Keel and Coelho 243</i>	Brazil	DQ246679
<i>Englerophyllum magalishontanum</i> (Sond.) T.D.Penn.	<i>Swenson and Karis 631</i>	South Africa	DQ246680
<i>Faucheria parvifolia</i> Lecomte	<i>Birkinshaw et al. 357</i>	Madagascar	KF686196
<i>Inhambanella henriquezii</i> (Engl. & Warb.) Dubard	<i>de Winter and Vahrmeijer 8536</i>	Natal	KF686197
<i>Isonandra compta</i> Dubard	<i>Emanuelson 3039</i>	Sri Lanka	KF686198
<i>Labourdonnaisia calophylloides</i> Bojer	<i>Capuron, 28171SF</i>	Reunion	KF686202
<i>Labramia costata</i> (Hartog ex Baill.) Aubrév.	<i>Randrianmanalinarivo 577</i>	Madagascar	KF686204
<i>Lecomtedoxa klaineana</i> (Pierre ex Engl.) Pierre ex Dubard	<i>Veldhuizen 1509</i>	Cult. Holland	AM408109
<i>Leptostylis filipes</i> Benth.	<i>Webster and Hildreth 14665</i>	New Caledonia	AY552135
<i>Letestua durissima</i> (A.Chev.) Lecomte	<i>Normand s.n.</i>	Congo	KF686206
<i>Madhuca longifolia</i> (J.König ex L.) J.F.Macbr.	<i>Hao 531</i>	Cult. South China Botanical Garden	KF686224
<i>Madhuca malaccensis</i> (C.B.Clarke) H.J.Lam	<i>Wilkie 832</i>	Peninsular Malaysia	KF686225
<i>Madhuca utilis</i> (Ridl.) H.J.Lam	<i>Pennington & Asri 10209</i>	Malaysia	KF686236
<i>Magodendron mennyae</i> Vink	<i>Takeuchi Ama and Siga 16570</i>	New Guinea	AY552114
<i>Manilkara kauki</i> (L.) Dubard	<i>Chantaranonthai 2341</i>	Thailand	KF686240
<i>Manilkara chicle</i> (Pittier) Gilly	<i>Castilo et al. 2082</i>	Guatemala	HF542839
<i>Manilkara concolor</i> (Harv.) Gerstner	<i>Swenson & Karis 635</i>	South Africa	HF542840
<i>Manilkara zapota</i> (L.) P.Royen	<i>Clayton 12</i>	Trinidad	KM370963
<i>Micropholis egensis</i> (A.DC.) Pierre	<i>Dionizia Coelho and Ernesto 73</i>	Brazil	DQ246681
<i>Mimusops elengi</i> L.	<i>Chantaranonthai 2305</i>	Thailand	KF686246
<i>Neohemsleya usambarensis</i> T.D.Penn.	<i>Borhidi et al. 84905</i>	Tanzania	DQ246684
<i>Neolemonniera clitandrifolia</i> (A.Chev.) Heine	<i>Jongkind Schmidt & Abbiu 1777</i>	Ghana	KF686249
<i>Niemeyera antiloga</i> (F.Muell.) T.D.Penn.	<i>Bartish & Jessup 4</i>	Australia	DQ154055
<i>Northia seychellana</i> Hook.f.	<i>Chong-Seng s. n.</i>	Seychelles	KF686250
<i>Ochrothallus francii</i> (Guillaumin & Dubard) Guillaumin	<i>Munzinger 965</i>	New Caledonia	AY552117
<i>Omphalocarpum pachysteloides</i> Mildbr. ex Hutch. & Dalziel	<i>Jongkind 2351</i>	Ghana	AY552151
<i>Palaquium amboinense</i> Burck	<i>Wilkie 813</i>	Java	KF686252
<i>Palaquium microphyllum</i> King & Gamble	<i>Wilkie 529</i>	Malaysia	KF686274
<i>Payena leerii</i> (Teijsm. & Binn.) Kurz	<i>Wilkie 811</i>	Java	KF686294
<i>Payena lucida</i> A.DC.	<i>Wilkie 839</i>	Peninsular Malaysia	KF686296
<i>Pichonia balansana</i> Pierre	<i>Veillon 7990</i>	New Caledonia	AY552109
<i>Planchonella obovata</i> (R.Br.) Pierre	<i>Chung and Anderberg 1166</i>	Taiwan	DQ154076
<i>Planchonella baillonii</i> (Zahlbr.) Dubard	<i>Mackee 9914</i>	New Caledonia	AY552141
<i>Pleioluma baueri</i> (Montrouz.) Aubrév.	<i>Munzinger 340</i>	New Caledonia	AY552113
<i>Pouteria adolfi-friedericii</i> (Engl.) A.Meeuse	<i>Friis Gilbert and Vollesen 3502</i>	Ethiopia	AY552115
<i>Pouteria campechiana</i> (Kunth) Baehni	<i>Wang W00798</i>	Taiwan (cultivated)	DQ246688
<i>Pouteria guianensis</i> Aubl.	<i>Poncy 1745</i>	French Guiana	DQ246690
<i>Pradosia surinamensis</i> (Eyma) T.D.Penn.	<i>Harris 1076</i>	Guyana	AY552157
<i>Pycnandra comptonii</i> (S.Moore) Vink	<i>Lowry et al. 5780A</i>	New Caledonia	AY552131
<i>Pyriluma sphaerocarpum</i> (Baill.) Aubrev.	<i>Tronchet Munzinger & Oddi 389</i>	New Caledonia	AY552139
<i>Sarcocaulus brasiliensis</i> (A.DC.) Eyma	<i>Paniagua et al. 4852</i>	Brazil	DQ246696
<i>Sarcosperma laurinum</i> (Benth.) Hook.f.	<i>Saunders 2000</i>	Hong Kong	AM408055
<i>Sersalisia sericea</i> (Aiton) R.Br.	<i>Harwood 1172</i>	Australia	AY552112
<i>Sideroxylon inerme</i> L.	<i>Nielsen s.n.</i>	Cult. Denmark	AM408078
<i>Sideroxylon oxyacanthum</i> Baill.	<i>Wood Y/75/388</i>	Yemen	AM408089
<i>Sideroxylon persimile</i> (Hemsl.) T.D.Penn.	<i>Veliz 99.7038</i>	Guatemala	AM408091
<i>Synsepalum dulcificum</i> (Schumach. & Thonn.) Daniell	<i>Welsing Merello and Schmidt 24</i>	Ghana	DQ246697
<i>Teghemella heckelii</i> (A.Chev.) Pierre ex Dubard	<i>Jongkind 3936</i>	Ghana	KF686305
<i>Van-royena castanosperma</i> (C.T.White) Aubrév.	<i>Bartish and Ford 26</i>	Australia	DQ154096
<i>Vitellaria paradoxa</i> C.F.Gaertn.	<i>Neumann 1512</i>	Benin	KF686306
<i>Vitellariopsis dispar</i> (N.E.Br.) Aubrév.	<i>Pentz 2</i>	South Africa	KM370973
<i>Xantolis siamensis</i> (Fletcher) P.Royen	<i>Smitairi (s.n.)</i>	Thailand	AY552154

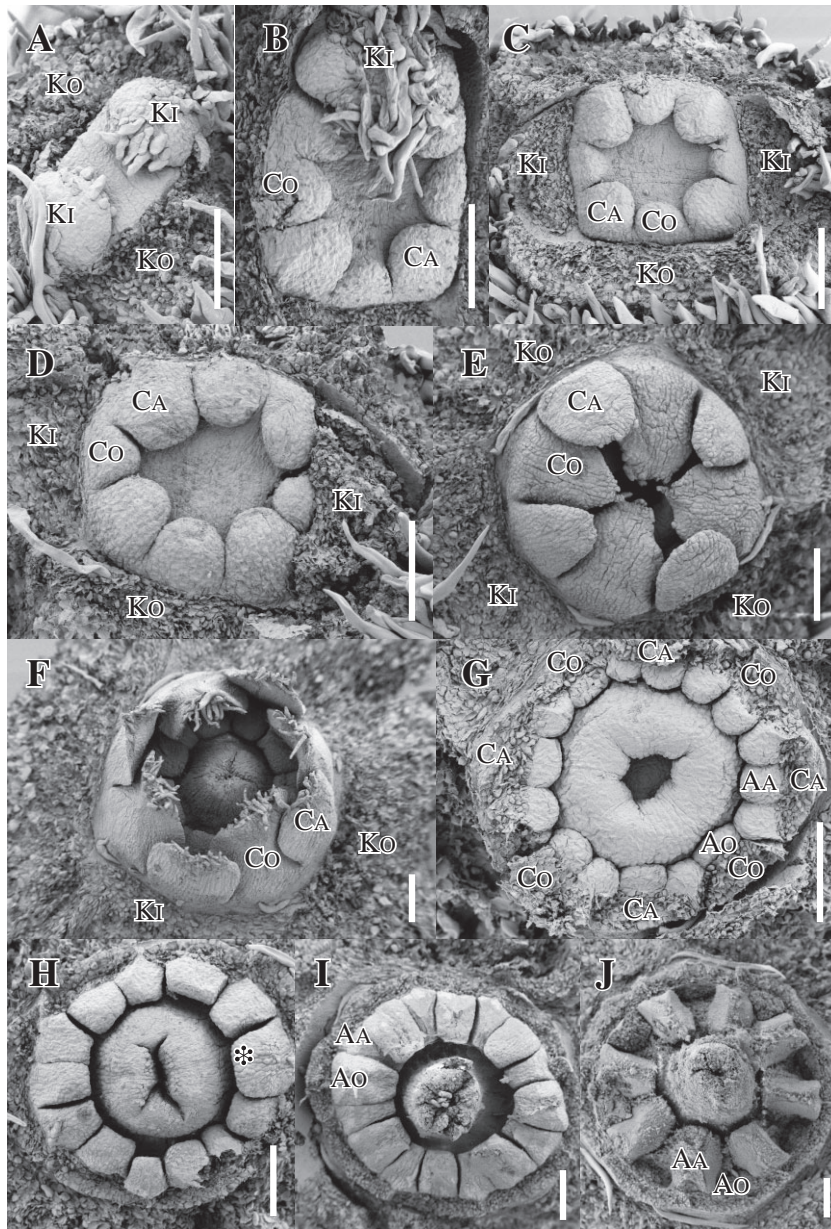


Figure 1. *Payena leerii*. Early stages in floral development. A, Sequential development of inner sepals (KI), outer sepals (KO) removed. B, Early development of the petals. Note that alternisepalous petals (CA) are larger than antesepalous (Co) petals; antesepalous petal on the left is two-lobed. C, Another view of petal development. D, Another stage of petal development. Note the unequal development of the petals. E, Later stage of petal development. Note the basal ring and alternisepalous petals overarching the flower bud. F, Older bud with gynoecium pushing through the petal tube and androecium. Note the development of apical trichomes on the petals. G, Development of alternipetalous (AA) and antepetalous (Ao) stamens and gynoecium; petals and sepals removed. H, Apical view of flower at closure of the carpels. Flower with only seven petals and a lower stamen number, one much larger and occupying the space of two stamens (asterisk). I, Apical view at early anther differentiation. Note that the antepetalous stamens are larger and more external to the alternipetalous stamens. J, Apical view, antepetalous stamens and petals removed. Note the compressed alternipetalous stamens. All bars, 100 μ m.

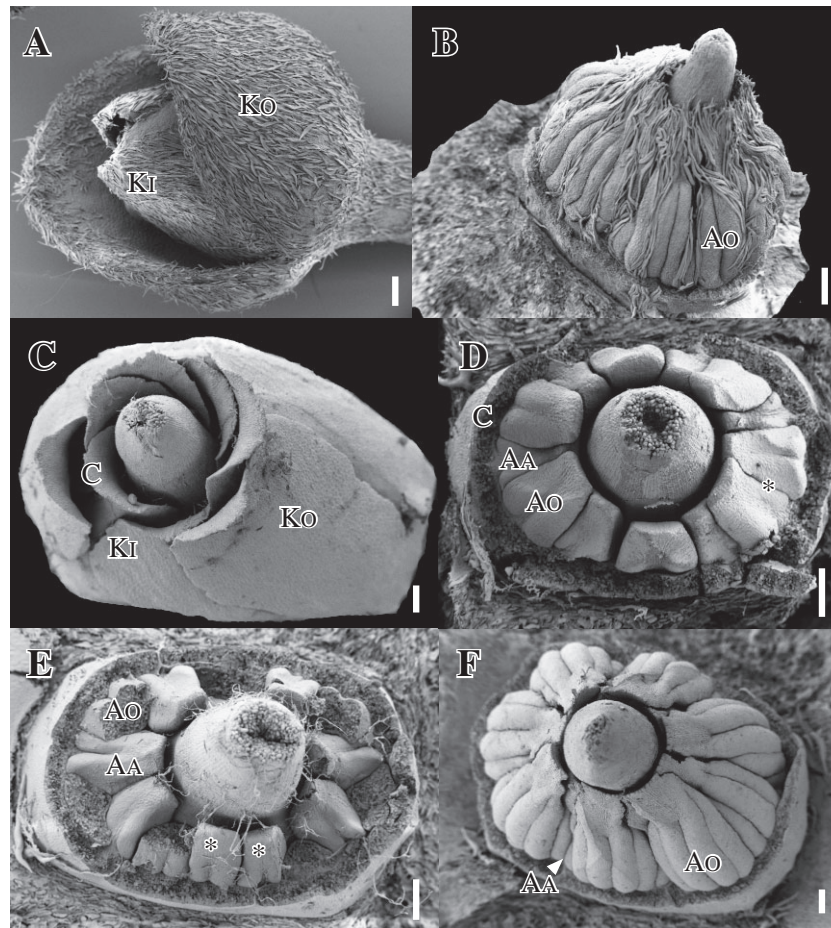


Figure 2. A, B, *Payena leerii*. C–F, *Payena lucida*. Late stages in floral development. A, Lateral view of young bud with decussately arranged sepals. B, Preanthetic bud, petals removed. Note the extrorse anthers of the antepetalous stamens completely covering the alternipetalous stamens. C, Flower at anthesis. Note the petals squeezed between the erect sepals. Only five contorted petal lobes are visible. D, Apical view of bud at stigma differentiation. Stamens arranged in two whorls with antepetalous stamens external to the alternipetalous stamens. The asterisk indicates an empty stamen position. E, Apical view at a similar stage; antepetalous stamens partly removed. Note the alternipetalous stamen pair (asterisks). F, Apical view of preanthetic bud with antepetalous stamens covering alternipetalous stamens almost completely. Bars: A, B, 200 μ m; C–F, 100 μ m. AA, alternipetalous stamen; AO, antepetalous stamen; C, petal; KI, inner sepal; KO, outer sepal.

ones (Fig. 2B). The number of carpels tends to be variable and is difficult to see; we observed mostly eight lobes of unequal size (Fig. 1G, I), although apical lobes may become postgenitally fused (Fig. 1F). The carpellary lobes become rapidly obscured by the development of stigmatic papillae and a large style emerges above the developing anthers (Figs 1I, J, 2B). Long trichomes develop on the anthers (Fig. 2B). Petal and stamen numbers may fluctuate as two smaller organs can be replaced by a larger one (Fig. 1H, asterisk).

Payena lucida, Sapotoideae (Figs 2C–F, 7A)

Only young mainly preanthetic buds were available for study. Flowers are transversally compressed with

four erect decussate sepals (Fig. 7A). Petals are compressed within the sepals and emerge beyond the sepals with the large style (Fig. 2C). The number of petals is mostly eight, although numbers can be lower (Fig. 2C). Petals and stamens are connected by a common tube. Stamens fluctuate between 14 and 16, with antepetalous stamens in older stages being external to alternipetalous stamens (Fig. 2D). Stamens are occasionally paired (Fig. 2E, asterisks) or a stamen position may be empty (Fig. 2D, asterisk). At anthesis, the outer stamens completely cover the inner stamens and develop large extrorse anthers with flap-like connective appendages (Fig. 2F).

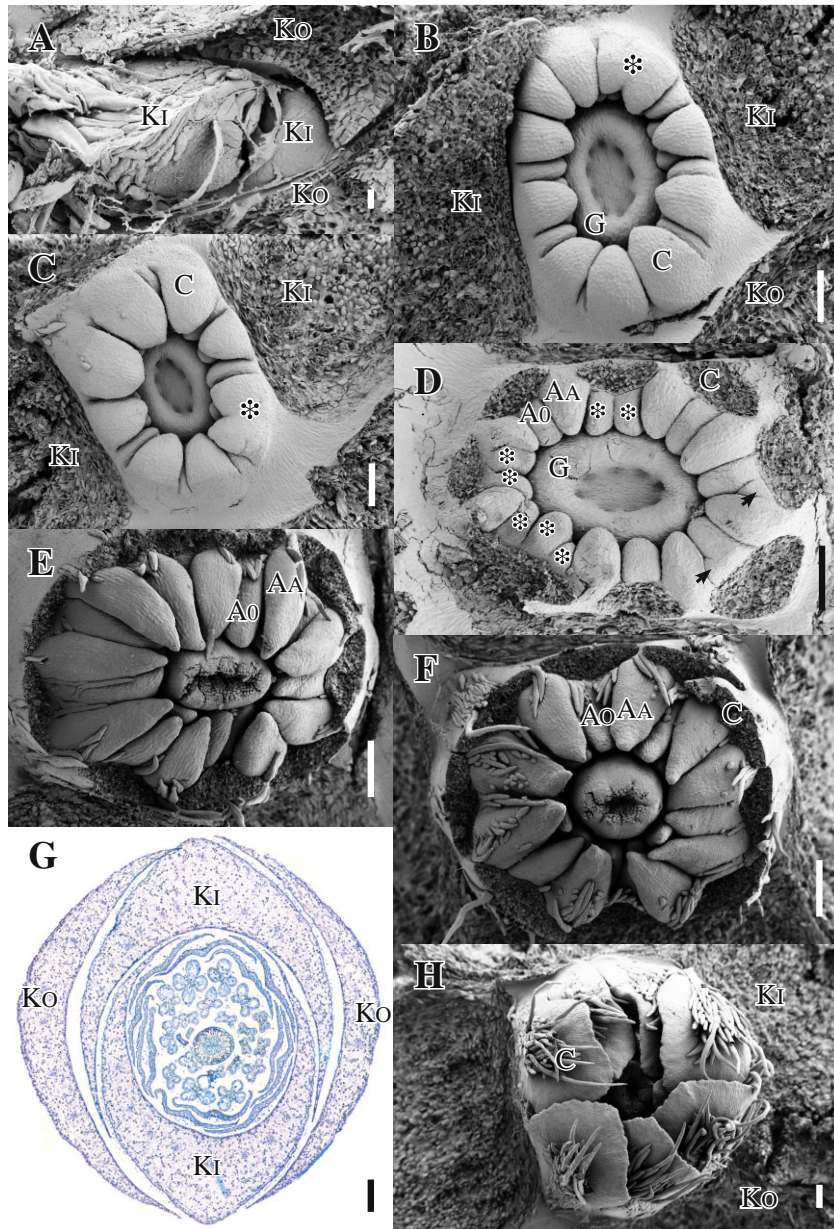


Figure 3. *Madhuca malaccensis*. Stages in floral development. A, Sequential development of sepals in two pairs, outer sepals removed. B, Apical view of development of petals, stamens and gynoecial ring primordium. Asterisk indicates joined petals. C, Another view at a similar stage to (B). Note the smaller size of petals on one side of the flower and fused petal lobes (asterisk). D, Stamen development; petal lobes removed. Note the larger alternipetalous stamens and variable number of antepetalous stamens in pairs or triplets (asterisks), occasionally forming unequal pairs (arrows). E, Older bud at stigma formation. Note the longer alternipetalous stamens covering the antepetalous stamens. F, Slightly older stage with nine petals and differentiation of anthers. Note the development of a petal–stamen tube. G, Transverse section of premature bud showing petal aestivation and organ position. H, Apical view of young petals with imbricate aestivation. Bars: A, 20 μ m; B–H, 100 μ m. AA, alternipetalous stamen; AO, antepetalous stamen; C, petal; G, gynoecial ring primordium; Ki, inner sepal; Ko, outer sepal.

Madhuca malaccensis, Sapotoideae (Figs 3, 7B)
 Sepal development is similar to that in *P. lucida*, leading to transversally strongly compressed buds in early stages of development (Fig. 3A, G). In contrast

with *P. lucida*, all petals of *M. malaccensis* appear to be inserted in a single whorl. In young flowers, the number of petals was difficult to detect as they appear simultaneously with stamens and can be confused

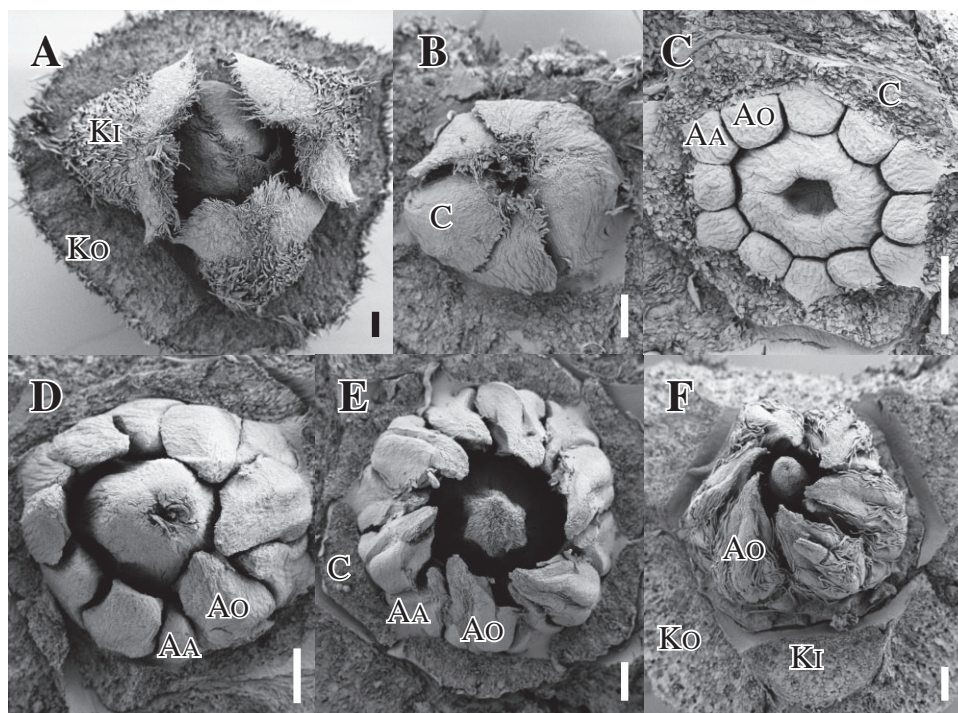


Figure 4. *Palaquium amboinense*. Stages in floral development. A, Apical view of young bud showing the arrangement of the sepals; outer whorl removed. B, Similar stage without sepals, showing petal arrangement. C, Early development of androecium and gynoecium. Note the more external position of alternipetalous stamens. D, Apical view at differentiation of stigma and anthers. Note the larger size of antepetalous stamens. E, Apical view of older bud. Note the contortion of the flower. F, Preanthetic bud showing the position of the two sepal whorls. The antepetalous stamens cover the alternipetalous stamens completely. All bars, 100 μ m; except F (200 μ m). AA, alternipetalous stamen; AO, antepetalous stamen; C, petal; Ki, inner sepal; Ko, outer sepal.

with alternipetalous stamens (Fig. 3B, C). In a few cases, petals were seen to be bilobed (Fig. 3B, C, asterisks). As in *P. lucida*, one side of the flower may grow more quickly than the other (Fig. 3B–D). The petal number fluctuates from eight to 12 (Fig. 3B–H). Petals grow rapidly and have an imbricate aestivation, with some (but not all) petals arranged in a contorted aestivation (Fig. 3G, H). One petal was frequently found to be completely outside and another completely inside (Figs 3G, H, 7B). Stamens are inserted in two whorls with the outer stamens inserted in the spaces between the petals and with the antepetalous stamens more towards the floral centre. No stages of early stamen development were available, and stamens could be confused with petals in Figure 3B, C. However, by removing the petals, the arrangement in two whorls could be seen more clearly (Fig. 3D). Stamen numbers fluctuate as much as petal numbers, with stamens in double or triple positions (Fig. 3D, asterisks, 3G). In some cases, a stamen was flanked by a smaller laterally inserted stamen (Fig. 3D, arrow). As a result, petal number does not correspond to stamen number, which fluctuates

around 21 or 22. Alternipetalous stamens grow more quickly than antepetalous ones, and become arranged as an outer whorl, with anther apices converging towards the gynoecium (Fig. 3E, F). However, in contrast with *P. lucida* or *P. amboinense*, there is no outward shift of antepetalous stamens and the alternipetalous stamens remain largest at maturity. The gynoecium arises in the shape of a ring primordium with short septa surrounding a flat centre (Fig. 3B–D). Carpel number fluctuates between eight (Fig. 3C, F), nine (Fig. 3B, D, E) and 11 (not shown). More extensive dorsal growth leads to axile placentation with stigmatic lobes corresponding to the initial carpels. As in other Sapotaceae, a large style lifts the emerging stigma lobes high above the stamens (Fig. 3E, F).

Palaquium amboinense, Sapotoideae (Figs 4, 7C)

Only a few buds were available. Flowers are hexamerous. The six sepals cover the bud in two alternating trimerous whorls; the outer whorl is larger and valvate at maturity, whereas the inner whorl has an imbricate aestivation (Fig. 4A). The arrangement of

the sepals makes the flower appear trimerous. No stages of early petal development were available, but the six petals are arranged in contorted aestivation and possess apical trichomes (Fig. 4B). The stamen number is usually 12, rarely ten or 11, in an obdiplostemonous arrangement. The earliest stages of stamen development were not available and it was not clear whether stamens precede carpels, or vice versa. The earliest stages available show the stamens arranged in two alternating whorls surrounding a well-developed ovary (Fig. 4C). The alternipetalous stamens are initially inserted slightly more towards the periphery. Antepetalous stamens overtake the alternipetalous stamens in size and shift outwards (Fig. 4D, E). Finally, the antepetalous stamens cover the alternipetalous stamens completely (Fig. 4F). During flower development, the stamens become contorted in the same way as the petals (Fig. 4D–F). Anthers are extrorse and covered with trichomes, ending in a pointed connective (Fig. 4F). The ovary arises as a five- or six-lobed rim (Fig. 4C) and a large style pushes between the stamens in preanthetic buds (Fig. 4D–F).

Sideroxylon inerme, Sapotoideae (Figs 5, 7D)

Flowers of *S. inerme* can be tetramerous (Fig. 5G), pentamerous (Fig. 5A–F) or hexamerous, but are mostly pentamerous with all organ whorls isomerous (Fig. 7D), although the number of organs may be increased or decreased in some of the whorls. All organs arise in sequential whorls. Sepals have a quincuncial arrangement, probably reflecting a 2/5 sequence of development, and rapidly cover the floral apex (Fig. 5A). The earliest stages available show petals that cover the bud in an imbricate aestivation (Fig. 5A, B). Imbrication is variable with partly contorted petals. Petals are basally united and produce a short tube (Fig. 5A, B). Associated with the common growth of the petals, five antepetalous stamen primordia and more externally inserted antesepalous staminodes arise almost simultaneously (Fig. 5A, C, D). Carpel primordia are formed on the slightly concave apex. The carpels remain clearly visible during development, whereas they are lifted by common growth and develop as a five- or four-lobed stigma emerging between stamens and staminodes (Fig. 5E–H). The fertile stamens extend in size by peripheral growth and differentiate as extrorse anthers expanding into two or a single apical lobe (Fig. 5E, F). During stamen development, the lateral flanks of the anthers encompass the staminodes that were initially inserted more externally and press them against the developing ovary (Fig. 5F, G). Staminodes are at first short and peg-like (Fig. 5F), but they extend as a flattened multi-lobed collar,

effectively sheathing the stigmas from the anthers (Fig. 5G, H).

Synsepalum dulcificum, *Pouteria durlandii*,
Planchonella obovata, Chrysophylloideae
(Figs 6, 7D)

In most Chrysophylloideae, the floral merism shows little variation, being pentamerous and sometimes tetramerous. The floral buds of *S. dulcificum* have broad petals with imbricate quincuncial aestivation (Fig. 6A). Antepetalous stamens develop broad extrorse anthers with a narrow connective appendage (Fig. 6B). The smaller staminodes are completely covered by the anthers and are compressed as narrow flaps with apical extension against the ovary (Fig. 6C). The ovary consists of five carpels (Fig. 6A) and extends into a large style between the anthers.

Flowers of *P. durlandii* are pentamerous, but there are only two fertile carpels. Sepals and petals cover buds in an imbricate aestivation (Fig. 6D). Fertile antepetalous stamens are external to small, reduced staminodes and are more or less latrorse (Fig. 6E, F). Anthers have a flattened tooth-like connective. The staminodes are short, acute and effectively compressed by the anthers (Fig. 6E, F).

The analysed flower buds of *P. obovata* were all female and had four or five sepals, five petals and ten staminodes in two whorls of five and four locules. Sepals and petals are imbricate, with sepals in a decussate arrangement (Fig. 6G, H). The fifth petal is small and opposite one outer sepal (when these are four in number); the other petals alternate with the sepals (Fig. 6G, H). The ovary is massive with an apical stigma and is surrounded at the base by a girdle of long trichomes (Fig. 6I). Staminodes are short stubs with no distinction between antepetalous and alternipetalous positions (Fig. 6I).

PHYLOGENETICS OF SAPOTACEAE

We used the MCC tree from the Bayesian analysis (Fig. 8) to map the characters (Figs 9–13). This tree is more resolved than published trees from other analyses (Swenson & Anderberg, 2005; Smedmark *et al.*, 2006; Swenson *et al.*, 2008b; Swenson, Nylander & Munzinger, 2013) and is a good representation of our current understanding of intrafamilial relationships. Bayesian support values are indicated in Figure 8. A number of genera with unclear phylogenetic relationships (*Capurodendron* Aubrév., *Tsebona* Capuron, *Inhambanella* Dubard, *Gluema* Aubrév. & Pellegr., *Neolemonniera* Heine, *Lecomtedoxa* Dubard) were better resolved as a tribe Tseboneae by Gautier *et al.* (2013). We did not include all the genera of this tribe in our analysis. The majority of clades that are

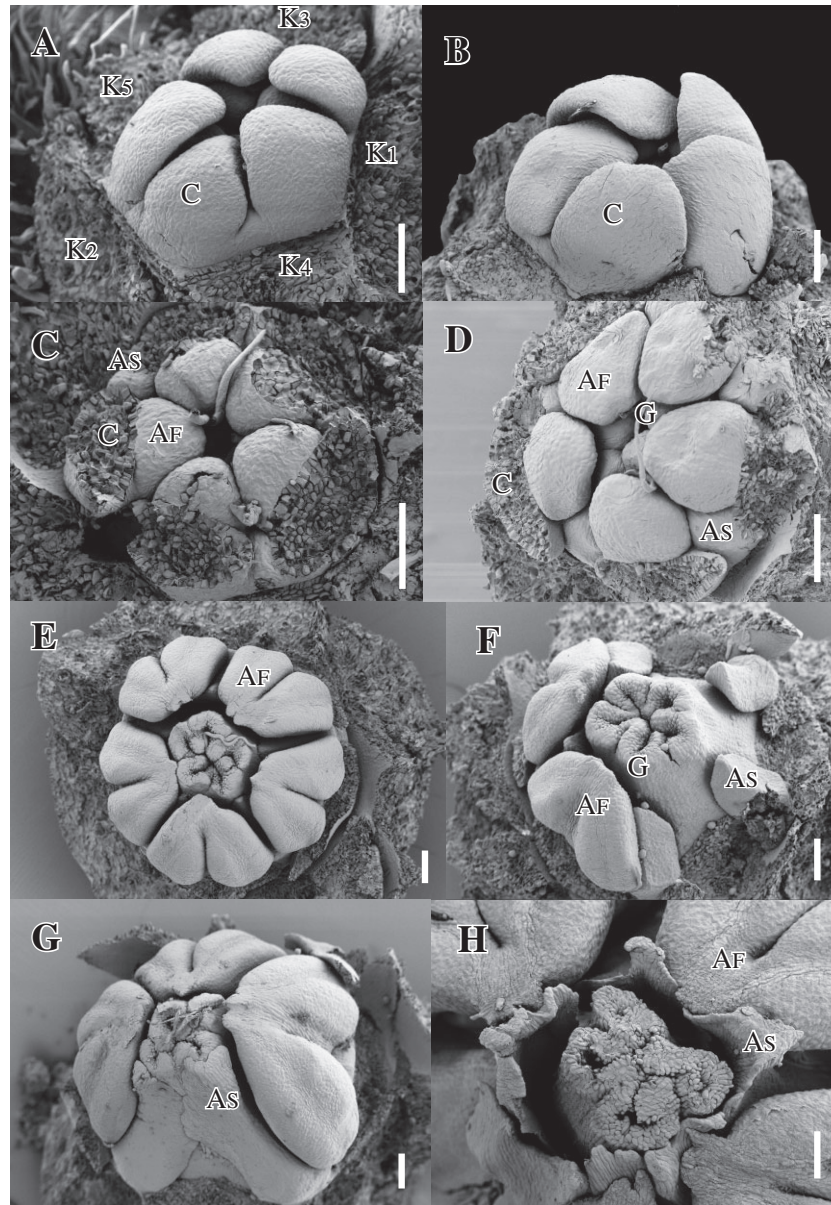


Figure 5. *Sideroxylon inerme*. Stages in floral development. A, Petals starting to cover the floral apex; sepals removed. Note the development of the common petal tube. B, Slightly older stage with partially contorted petal aestivation. C, Similar stage to (B) with petals partly dissected, showing the development of large antepetalous stamens and retarded development of antesepalous staminodes. D, Development of carpels and further development of staminodes. E, Apical view at stigma and anther differentiation. F, Lateral view of the same with partly dissected androecium. G, Partly dissected tetramerous flower showing staminodes compressed against the ovary. H, Detail of stigma, lacinate staminodes and anthers. All bars, 100 μ m. AF, fertile antepetalous stamen; AS, antesepalous staminode; C, petal; G, carpel; K1–5, sequence of carpel development.

discussed in relation to key morphological state changes are strongly supported.

PATTERNS OF MERISTIC CHANGES IN SAPOTACEAE

The diversity of floral organ arrangement and merism in the studied species of Sapotaceae is shown with

floral diagrams (Fig. 7). Other floral diagrams illustrating the positions of organs in flowers were presented by Eichler (1875), Engler (1890), Baillon (1891a), Lam (1927), Gerstner (1946) and Ronse De Craene (2010).

The following characters were mapped on the phylogenetic tree for Sapotaceae: overall merism of the

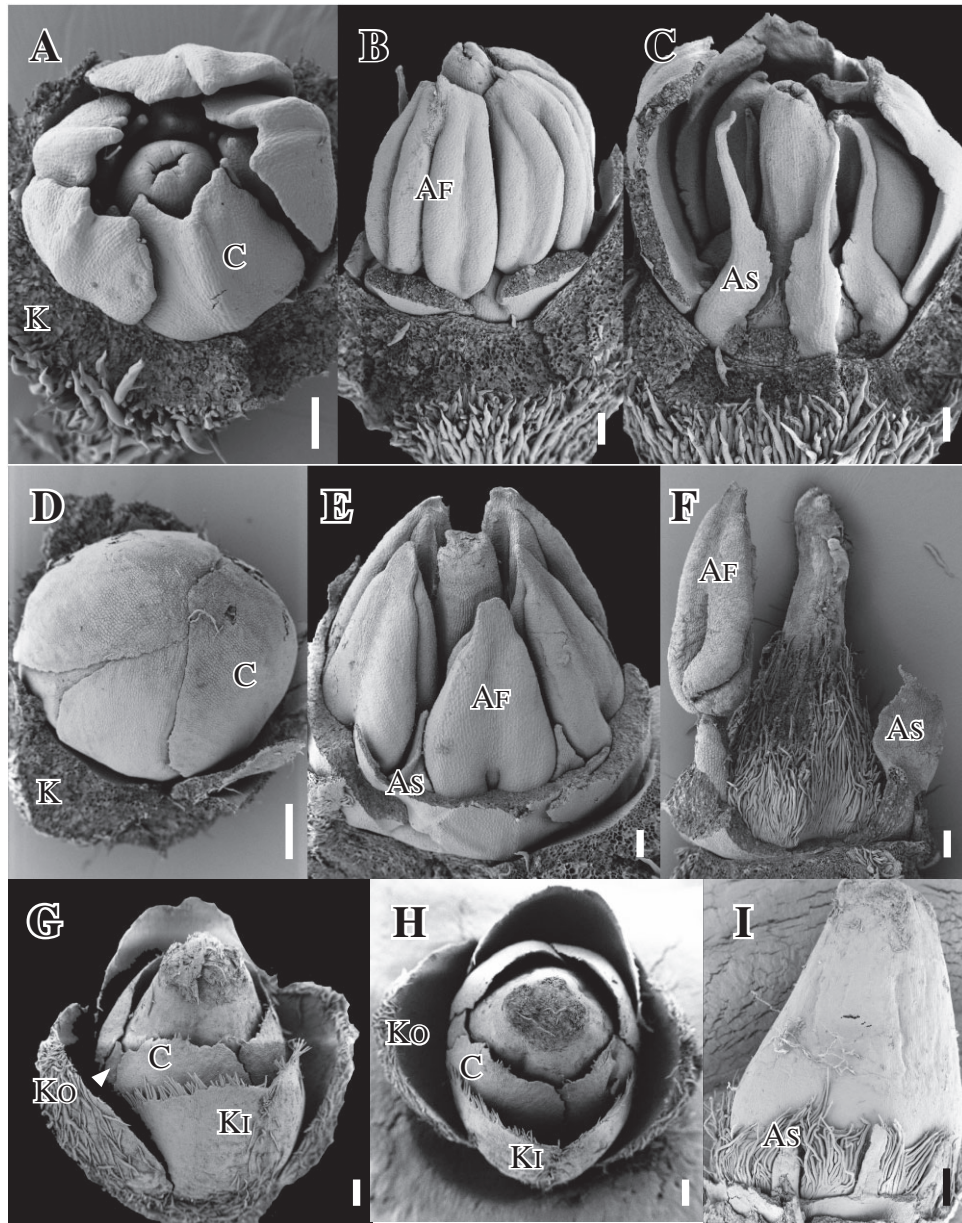


Figure 6. A–C, *Synsepalum dulcificum*. D–F, *Pouteria durlandii*. G–I, *Planchonella obovata*. Late stages in floral development. A, Apical view at stigma differentiation. Note the truncate quincuncially arranged petals. B, Lateral view of developing extrorse anthers completely covering the staminodes. C, Similar view, with anthers partially removed to expose the staminodes. D, Apical view of quincuncial petals, sepals removed. E, Lateral view of anthers, staminodes and gynoecium; petals removed. F, Lateral view of dissected preanthetic flower showing one fertile stamen and one staminode. G, H, Lateral and apical views of pistillate flower. Note fifth smaller petal opposite one outer sepal (arrowhead). I, Lateral view of pistillate flower, perianth removed. Note similar antepetalous and alternipetalous staminodes. Bars: A–D, 100 μm ; E–I, 200 μm . AF, fertile antepetalous stamen; AS, staminode; C, petal; KI, inner sepal; KO outer sepal.

flower (tetramery, pentamery, hexamery, octomery or higher merism) (Fig. 9), merism of the sepals (Fig. 10), merism of the petals (Fig. 11), merism of the androecium spread over two whorls, including stamens and staminodes (Fig. 12), and merism of the gynoecium, ranging from less than five to more than nine carpels (Fig. 13).

The overall merism of the flower (reflecting the most obvious merism shared by most organs) is shown in Figure 9. Pentamery is reconstructed as ancestral for Sapotaceae and is generally ubiquitous in Chrysophylloideae and Sarcospermatoidae. In Sapotoideae, some early-branching clades are pentamerous, but there are two transitions to octomery

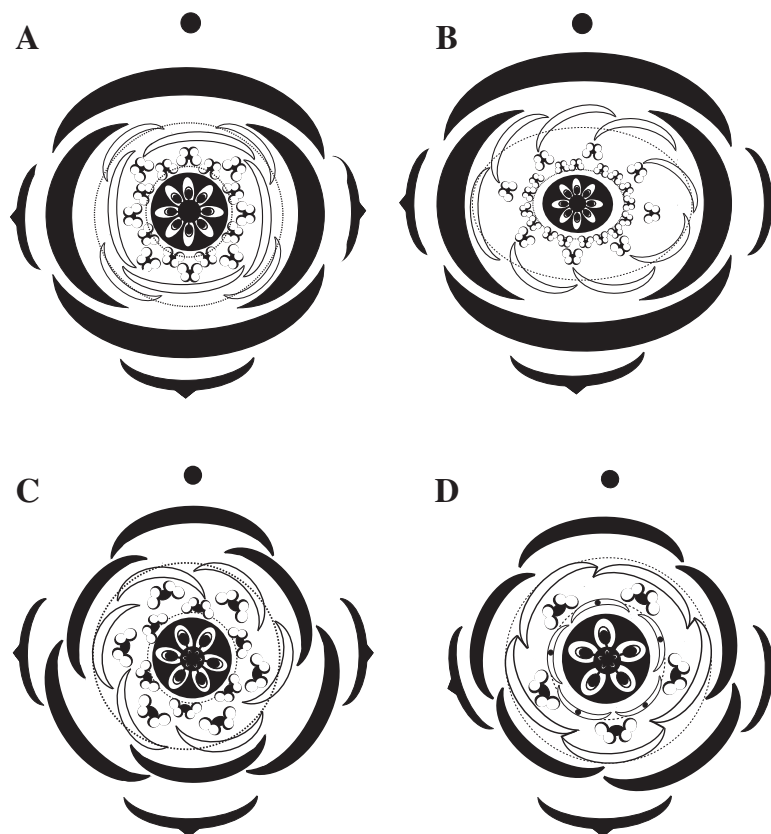


Figure 7. Floral diagrams of the studied Sapoteaceae. A, *Payena leerii*. B, *Madhuca malaccensis*. C, *Palaquium amboinense*. D, *Sideroxylon inerme*. Black dot, main shoot axis; black arcs, sepals; black arcs with triangles, bract and bracteoles and bract; white arcs, petals; white arcs with black dot, staminode; broken lines, outer and inner limits of stamen–petal tube.

and three transitions to hexamery. Octomery has arisen once in Isonandreae and once in Sapoteae. Hexamery has arisen independently three times, in two clades (*Palaquium* Blanco and *Manilkara* Adans.) and in *Northia* Hook.f. Hexamery in the *Manilkara* clade is nested in an otherwise octomerous grade, including *Mimusops* L. All organs are affected by the increase in merism (Figs 9–13), whereas the gynoecium may be further increased (e.g. in some *Manilkara* spp.: Fig. 13). *Palaquium* is sister to an octomerous *Madhuca* J.F.Gmel.–*Payena* A.DC. clade, and it is equivocal whether hexamery is derived from octomery or vice versa. All reconstructions are ambiguous regarding this question (Figs 9–13). All organs are affected by the increase to hexamery in *Palaquium*, but not the sepals in the *Madhuca*–*Payena* clade, which are reduced to four lobes (in *Burckella* Pierre, only stamens and petals are affected). *Isonandra compta* Dubard is tetramerous and nested among the octomerous taxa, but other species in this genus are hexamerous to octomerous (Baehni, 1965). In Chrysophylloideae, the *Pycnandra* Benth.–*Niemeyera* F.Muell. clade is unusual in

showing a variability in merism affecting all organs, ranging from five to eight.

The reconstruction of the merism of the sepals (Figs 10, 14) demonstrates a transition from a pentamerous calyx to either tetramery (occasionally in Chrysophylloideae, *Madhuca*–*Payena* clade), hexamery (*Palaquium*) or octomery (Sapoteae–*Mimusopinae*). In all cases (reduction or increase in sepal numbers), the change from the single-whorled quincuncial pattern of the pentamerous calyx results in an increase in the number of whorls.

The reconstruction of the merism of the petals (Fig. 11) is similar to that of the sepals with two important differences: there is an occasional increase to high numbers (up to 18: *Labourdonnaisia* Bojer, *Letestua* Lecomte) and petals are generally inserted in a single whorl because of their smaller size. *Payena* is exceptional in forming two closely connected whorls of four petals (Figs 1E, F, 7A, 14).

The distribution of androecial whorls in correlation with merism is mapped on Figure 12. Two whorls of stamens (with a sterile antesealous stamen whorl) are reconstructed as plesiomorphic in Sapoteaceae.

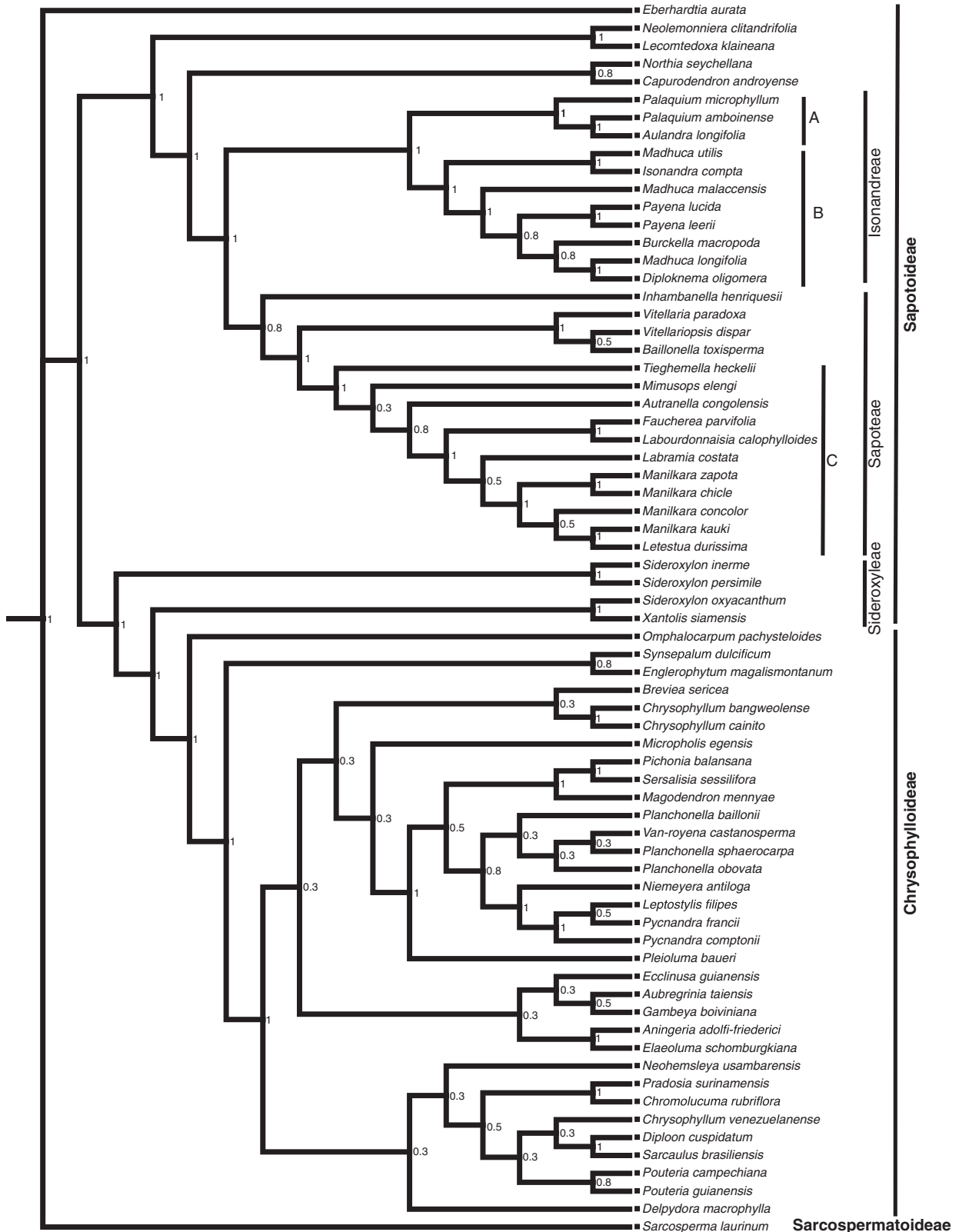


Figure 8. Maximum clade credibility (MCC) tree of Sapotaceae with Bayesian support values indicated for all branches. Main subfamilies of Swenson & Anderberg (2005) are shown. A, *Palaquium* clade; B, *Madhuca*–*Payena* clade; C, *Mimusopinae*.

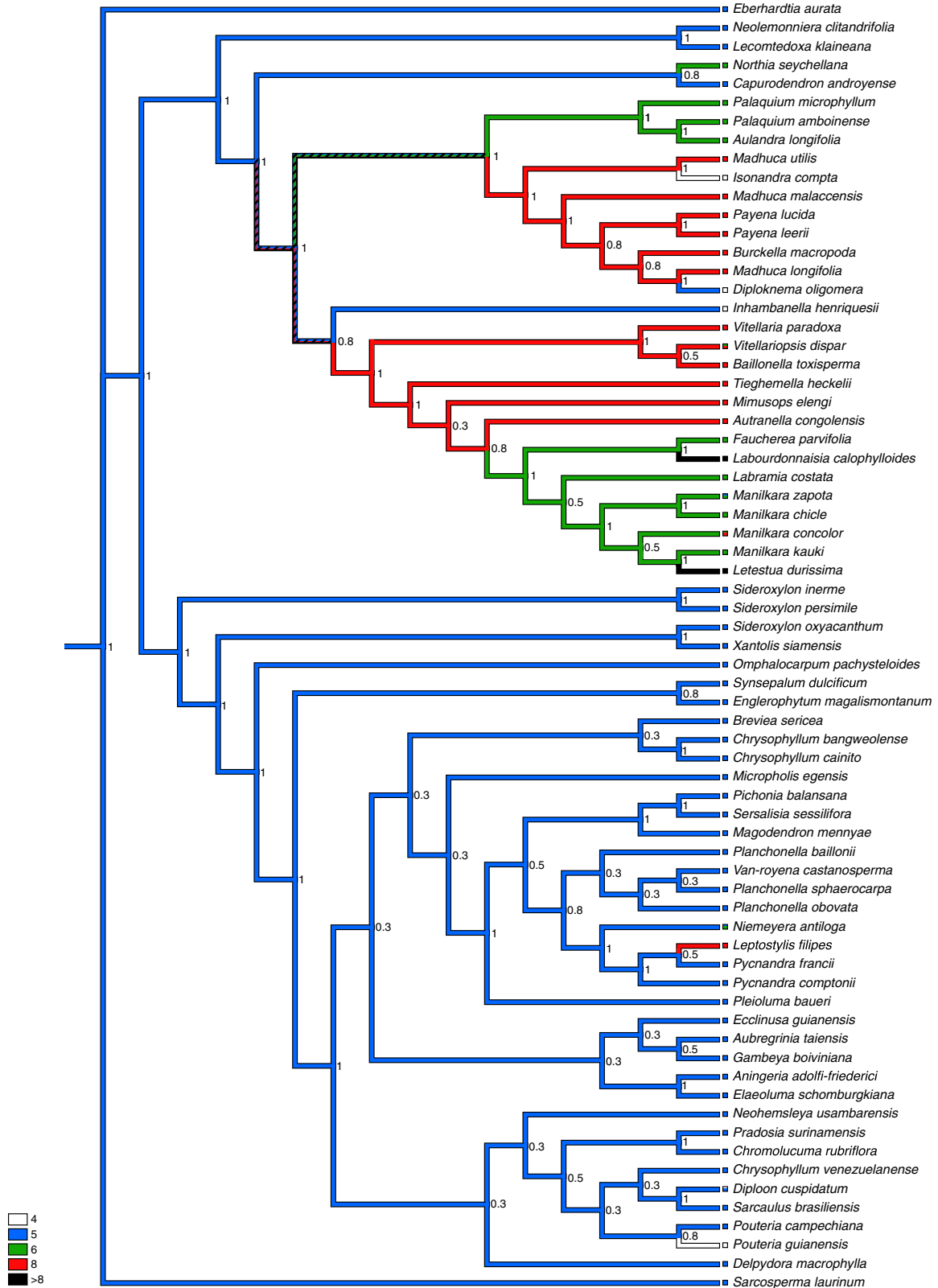


Figure 9. Reconstruction of the overall merism on the maximum clade credibility (MCC) tree of Sapotaceae.



Figure 10. Reconstruction of sepal merism in Sapotaceae.



Figure 11. Reconstruction of petal merism in Sapotaceae.

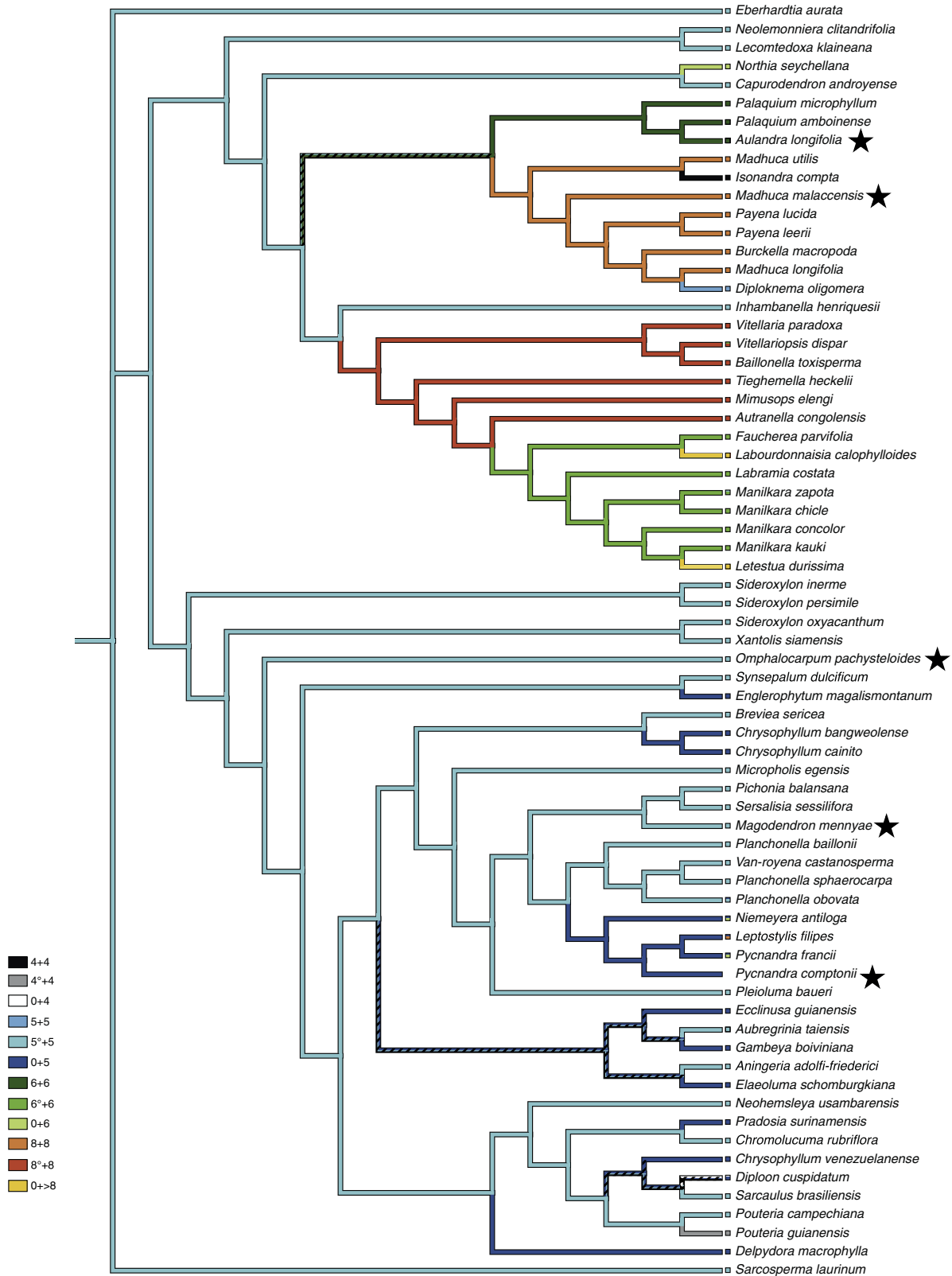


Figure 12. Reconstruction of androecium merism in Sapotaceae; numbers of whorls shown; sterile stamens shown with °; asterisks show a secondary stamen increase by subdivision of primordia independent of meristic change.

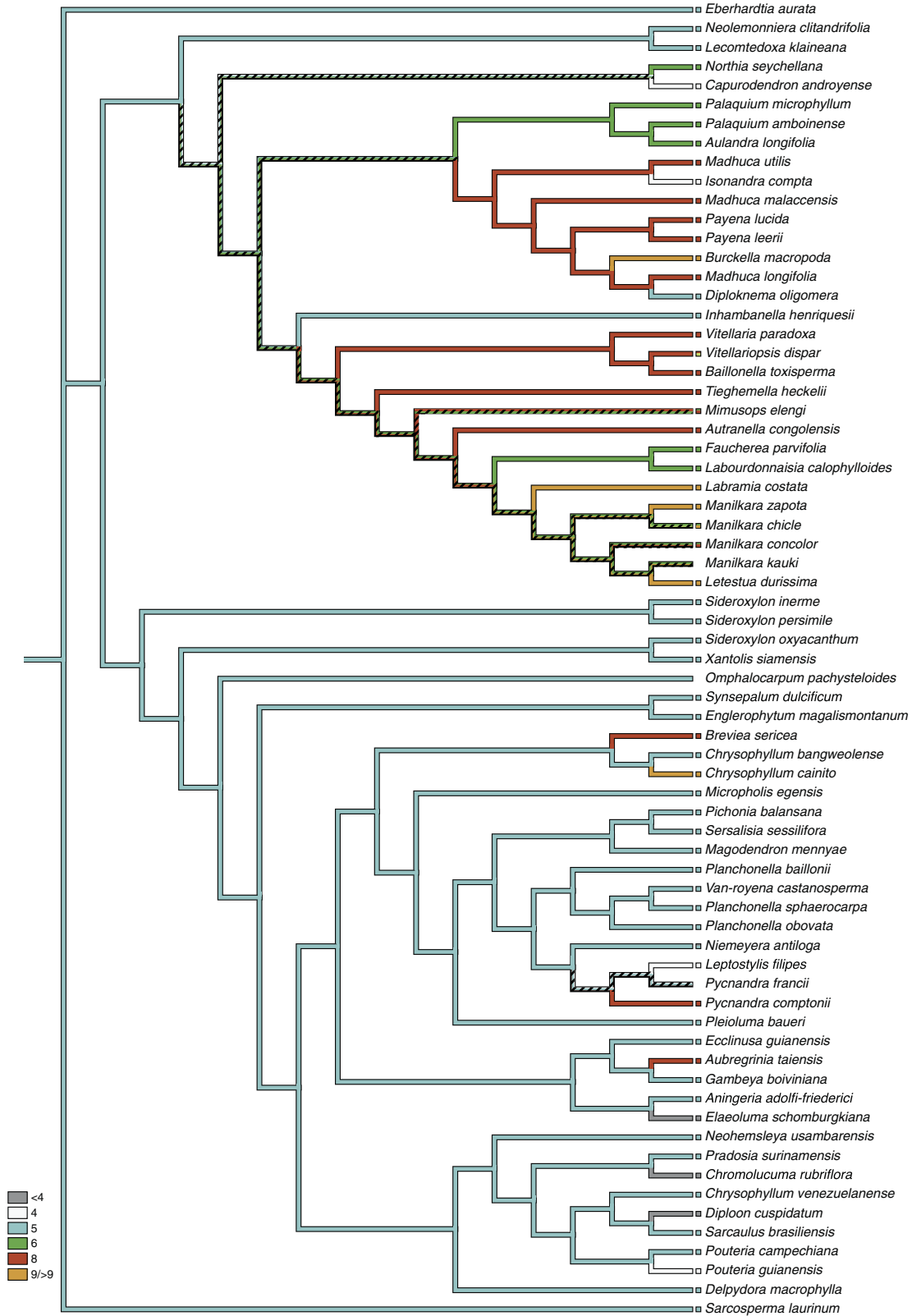


Figure 13. Reconstruction of gynoecium merism in Sapotaceae.

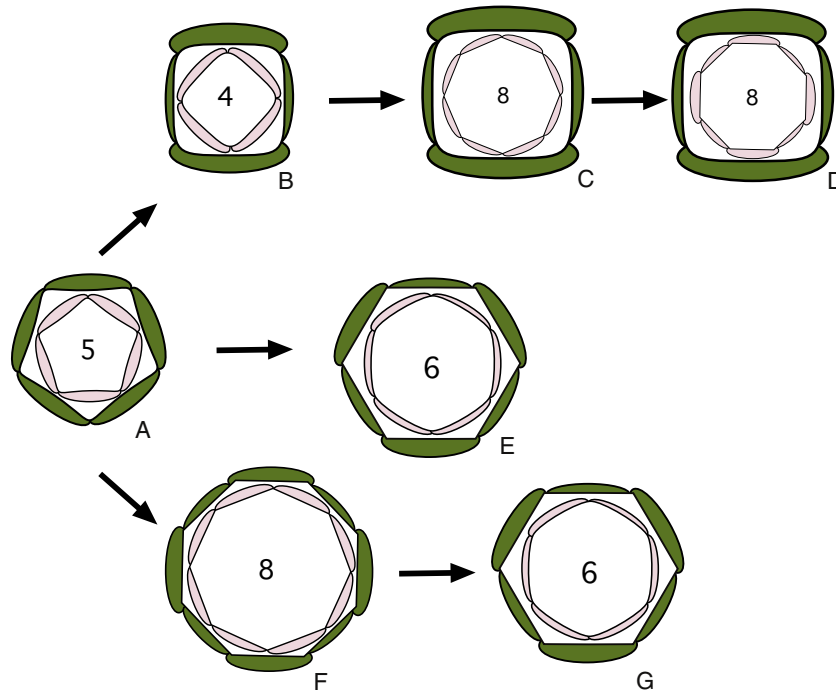


Figure 14. Diagrammatic presentation of meristic shifts in the perianth of Sapotaceae. A, Basic pentamerous merism. B, Shift to tetramery and rearrangement of the sepals in two dimerous whorls. C, D, Doubling of petal number and rearrangement in two whorls. E, Shift to hexamery and rearrangement of the sepals in two trimerous whorls. F, Isomerous increase to octomery and rearrangement of the sepals in two tetramerous whorls. G, Reduction to hexamery. Green arcs, sepals; pink arcs, petals.

The two whorls may be clearly set in two separate series or tiers, or may be inserted at the same level in a single series. In Chrysophylloideae, there is a repeated loss of the antesepalous staminodial whorl, leading to obhaplostemony. A complete loss of the antesepalous whorl is less common in Sapotoideae, but occurs in *Northia*, *Letestua* and *Labourdonnaisia*. However, the antepetalous stamen whorl is always present and fertile in Sapotaceae. Sapotoideae is most variable, with the two stamen whorls being fully fertile and androecia having antesepalous staminodes. The clade comprising *Palaquium*, *Payena* and *Madhuca* is reconstructed as two-whorled without sterilization of antesepalous stamens. This appears to be a stable synapomorphy. In all other clades, the antesepalous whorl is either staminodial or absent. The merism of the androecium is reflected in the overall merism of the flower, but appears to be most strongly correlated with the merism of the petals (Figs 9, 11). A stamen number increase by *dédoublement* of one stamen whorl has occurred independently in several genera belonging to different tribes (see Table 2, Figs 3D, 12, asterisks), but has no influence on the merism of the flower.

The merism of the gynoecium is the least stable character, ranging from one (e.g. *Diploon*, *Pouteria*

vernica, *Sarcosperma*) to 18–20 (*Letestua*, *Tsebona*) carpels (Table 2, Fig. 13). The branches leading to most Sapotoideae are equivocal because of high fluctuations in the number of carpels, although five carpels are reconstructed as the ancestral condition, and they are also found in most Chrysophylloideae. In all observed cases, the carpels are inserted opposite the sepals when isomerous. In some cases, the number of carpels exceeds that of the other whorls (e.g. *Breviea* Aubrév. & Pellegr., *Chrysophyllum cainito* L., *Manilkara* and *Pycnandra*).

DISCUSSION

BASIC FLORAL ORGANIZATION IN SAPOTACEAE

In all genera of Sapotaceae, except *Sarcosperma*, flowers are grouped in fascicles. Bracts and bracteoles are present, but are small at maturity and are easily overlooked. Eichler (1875) could not detect any bracteoles in the herbarium material he used for his floral diagrams, and other authors simply ignored them (e.g. Baillon, 1891a; Gerstner, 1946; Vink, 1995; Caris, 2013). Bracts and bracteoles obviously have no impact on changes in merism, but we include them in our diagrams (Fig. 7) for the sake of completeness.

Several authors (e.g. Bentham & Hooker, 1876; Aubréville, 1964; Baehni, 1965; Pennington, 1990, 2004) made a fundamental taxonomic distinction between taxa with a simple calyx and taxa with a double calyx. The sepals are either uniseriate (pentamerous, quincuncial with imbricate aestivation) or, more rarely, biseriate (with two alternating whorls of different size). The calyx is rarely described as polymerous with 5–12 spirally arranged sepals [*Pouteria* section *Aneulucuma* (Radlk.) T.D.Penn.: Pennington, 1991], but Aubréville (1964) suggested that this is erroneous as several bracts may become associated with the sepals and thus artificially increase their number. Although sepal morphology is an easy diagnostic character, it cannot be viewed without referring to the other organs of the flower. Here, we demonstrate that a distinction between a simple and a double calyx is misleading, as a change in the number of sepals from the pentamerous condition may lead to a rearrangement of the sepals in two whorls. A rearrangement of the sepals in two whorls occurs with a reduction (e.g. tetramery) or an increase (e.g. hexamery, octomery) in sepal number (Figs 10, 14).

Petals appear as independent primordia (Figs 1B, C, 3B–D, 4C, 5C, D, 6B). The time at which they become lifted with the stamens by the growth of an annular meristematic zone is variable and depends on the species; it is earlier in *P. leerii* (Fig. 1D–F) than in other species, where it happens at anther development (Figs 2E, F, 4F, 5A, B, 6B, E, I). In all species, we observed that the young petals are separated from the sepals by a continuous free zone (Figs 1C, D, 3B–D, 4C, 5D, E) which may be the precursor of a common tube. The growth of this common zone corresponds to Erbar's (1991) description of late sympetaly and represents a hypanthial outgrowth. Observations in other species, such as *M. zapota*, show a similar external rim at petal and stamen development (e.g. Caris, 2013). As for the sepals, the most common petal number is five, but there is more variation than for sepal numbers. The petals are pentamerous and imbricate only in Chrysophylloideae and early-branching clades of Sapotoideae. The relationship of other organ whorls is generally isomerous in Chrysophylloideae and changes are exceptions (*Pycnanandra* clade: Swenson *et al.*, 2008a; Table 2). Aubréville (1964) mentioned cases of *C. cainito* with ten petals and ten stamens, the result of a paired fusion of two flowers. There are several cases of increases or decreases in petals in Sapotoideae and the main numbers are six and eight (in a single whorl or as 4+4), more rarely 12 (6+6) or 16 (8+8). Four sepals arranged in two whorls of two are generally correlated with eight petals, especially if the inner and outer sepals are well separated in time and space

(e.g. *Madhuca–Payena* clade: Fig. 14C, D). Sepals in two whorls of three are nearly always correlated with six petals, but rarely with 12 or more petals (e.g. *Letestua*, *Labourdonnaisia*). If the sepals are arranged in two whorls of four, the petal number is generally eight and the rest of the flower is octomerous (e.g. *Mimusops*, *Vittelaria*). This pattern appears to be confined to almost all taxa of Mimusopinae (Figs 10, 11). *Madhuca malaccensis* is exceptional with an increase in merism in the petals, which does not seem to be correlated with an increase in sepals, and appears to be the result of additional doubling of some petal lobes (9–12 petals in a single whorl: Figs 3B, C, 7B).

It is important to stress that individual petals can be subdivided into several equal or unequal lobes in Sapotaceae. As a result, individual lobes of a multi-lobed corolla can be confused with a simple-lobed corolla. Some species of Sapoteae exhibit strongly segmented (usually trilobed) petals (e.g. Baillon, 1891a; Aubréville, 1964; Pennington, 1991). The presence of extra lobes on the petals can lead to incorrect interpretations of the flower structure. The lateral lobes can be smaller, equal or larger than the central lobe, which is occasionally reduced to a small ligule or thread (Aubréville, 1964; Pennington, 1990). The accessory lobes of petals may closely resemble undivided petals. Endress & Matthews (2006) mentioned 16 lacinate outer 'staminodes' and eight entire staminodes in another whorl between petals and stamens for *Mimusops commersonii* Engl. This would be highly unusual for Sapotaceae and it is more likely that these outer 'staminodes' are the lateral appendages of the petals. Gilly (1943) explicitly interpreted the petals of *Manilkara* as staminodes. The possibility for lobing of petals and also staminodes is comparable with a lateral dédoublement of stamens (see below).

The androecium is generally two-whorled and basically diplostemonous, and fertile stamens are usually restricted to an antepetalous position. The antepetalous stamens can be fertile, but are more often staminodial or occasionally absent. The stamens of the two whorls are fertile only in Isonandreae (*Isonandra* Wight, *Diploknema* Pierre, *Palaquium*, *Payena* and *Madhuca*: Table 2; Figs 2B, E, F, 3G, 4D, E, 7A–C). Antesepalous stamens are sterile in all other clades (Figs 5F–H, 6C, F, 7D), and only exceptionally not so [e.g. *Manilkara valenzuelana* (A. Rich.) T.D.Penn.: Pennington 2004]. Stamens appear independently and almost simultaneously, although it was difficult to observe the earliest stages of development because of the larger size of the petals covering the bud (Figs 1G, 3B, D, 4C, 5C). The androecium often becomes obdiplostemonous by a shift of the antesepalous stamens or staminodes to an inner position (cf.

Figs 4F, 5C–H, 7). The floral developmental data presented here demonstrate the easy inward or outward shift of stamen whorls, which happens before stamens and petals are lifted by common growth. Although the alternipetalous stamen whorl is generally formed more externally or at least at the same level as the antepetalous whorl (Figs 1G, 2G, 3D, 4C, 5D), it becomes displaced internally by the expansion of the antepetalous stamens (Figs 1I, J, 2B, D–F, 4D–F, 5E–G, 6B, E). This shift corresponds to a reinforcement of the antepetalous stamens and is observed in all genera, including those in which the antesealous stamens are fertile (Fig. 4E, F). However, contrary to most other cases of obdiplostemony, stamens opposite the petals remain fertile, whereas stamens opposite the sepals are reduced to staminodes in Sapotaceae (Ronse De Craene & Bull-Hereñu, in press).

Most species of Sapotaceae have antesealous staminodes, which are often well developed and petaloid. No examples are known in which staminodes occur in an antepetalous position (Table 2). The single case (*Gluema ivorensis* Aubrév. & Pellegr.) mentioned by Aubréville (1961) in which a staminode is superposed to a stamen is erroneous (L. Gautier, pers. comm.). The staminodes are generally well developed at maturity (Figs 5G, H, 6C, F) and may create a barrier against selfing by developing a rim around the styles (Figs 5G, H, 6C). The extent of development of the staminodes can be variable, as in *Synsepalum* (A.DC.) Daniell, where staminodes can be strongly developed, much reduced or even absent (Aubréville, 1964, described as *Pachystela* Pierre ex Radlk.). In several members of Chrysophylloideae, the staminodes are either reduced or lost, leading to flowers with a single whorl of antepetalous stamens (obhaplostemony). There is a strong analogy between processes of staminode reduction of Sapotaceae and the primuloid clade, in which antesealous staminodes are well developed or absent (Anderberg & Ståhl, 1995).

Stamen and staminode numbers are mostly five and are generally constant in Chrysophylloideae, including Sideroxyloideae. In Sapotoideae, the most common numbers are six, eight, 12, 16 or up to 36 or more (Table 2). *Letestua* and *Labourdonnaisia* show an exceptional increase in petals up to 18 lobes (Table 2) and this tends to be correlated with higher stamen numbers (Figs 11, 12). Baillon (1891b) described the flower of *Labourdonnaisia revoluta* Bojer as having six sepals in two whorls of three, 18 petal lobes forming six groups, 18 stamens and six carpels. He mentioned that the petals consist of a median interior lobe and two external accessory lobes and each lobe has one opposite stamen. This could indicate that excessive lobing of the petals (in which one petal divides into three lobes) induced a much higher increase in the original number of stamens. Other Sapoteae generally have lateral

petal lobes, which are only developed to a certain degree (Baehni, 1965; Pennington, 1991). According to Engler (1890) and Aubréville (1964), two to three whorls of stamens can be detected in some species with numerous stamens. However, the authors are uncertain about the exact position of the stamens. According to Ronse De Craene (2010), the secondary increases in stamen numbers observed in some species are probably a result of lateral stamen division, and this may lead to crowding and a displacement of stamens, as was visible in the development of *M. malaccensis* (Fig. 3D–F; cf. Engler, 1890), and is correlated with an increase in petal number. Stamen numbers can increase by *dédoublement* with up to 25–40 stamens, as found in tribes Chrysophylleae, Isonandreae and Tseboneae (e.g. *Aulandra* H.J.Lam, *Diploknema*, *Madhuca*, *Magodendron* Vink, *Omphalocarpum* P.Beauv., *Pycnandra*, *Tsebona macrantha* Capuron: Fig. 12, asterisks; Engler, 1890; Capuron, 1962; Aubréville, 1964; Vink, 1995; Pennington, 2004; Swenson *et al.*, 2008a; Caris, 2013). *Dédoublement* of stamens leads to either paired antepetalous stamens or stamen fascicles. In Omphalocarpeae, the stamen number increase is restricted to the antepetalous whorl, whereas the antesealous stamens are sterile; this appears to be a synapomorphy for the tribe (see Table 2; Caris, 2013), although *Tsebona* is now excluded (Gautier *et al.*, 2013). In all studied cases, a stamen number increase operates in a lateral position, leading to a girdle of stamens. The increase is not correlated with a carpel number increase. Swenson *et al.* (2008a) suggested that the stamen increase in *Pycnandra* is not correlated with the anisomery of flowers and that both trends are mutually exclusive. The fact that stamen number increases randomly in *Madhuca*, whereas petals and stamens are anisomeric, indicates that this is not the case in *Madhuca*. However, in other Sapotaceae, this correlation seems to be supported and indicates that these stamen number increases cannot be linked with changes in merism and must be seen as isolated evolutionary changes. Floral developmental data for species such as *Aulandra longifolia* H.J.Lam and *Diploknema butyracea* (Roxb.) H.J.Lam are currently missing (Table 2), but could be helpful in understanding patterns of stamen evolution. Increases in stamen number by *dédoublement* may or may not be correlated with the reduction or loss of antesealous stamens. Simply plotting the stamen number on phylogenetic trees will not show this correlation.

In all investigated species, the gynoecium is strongly developed without clear demarcation between ovary and style (Figs 2B–F, 3F, 4F, 5F, 6C, G–I), and, at maturity, the style is usually long, often protruding from the flower above the stamens and petals. The style is terminated by a lobed stigma,

with lobes corresponding to the individual carpels, although this is not always clearly visible (Figs 1I, J, 2E, 3E, F, 5E–H, 6A). In several species, the ovary is hairy at the base. Each locule has a single axile, descending ovule. Following the development of the stamens, the ovary arises as a lobed rim, with lobes reflecting individual carpels (Figs 1G, H, 4C, 5D), or as an indistinct rim (Fig. 3B, C). When the rim is indistinct, it is possible to discern the number of carpels by the development of septa extending to the middle of the ovary (Fig. 3B–D). The carpels are terminated by stylar lobes positioned opposite the locules (Figs 5F, 7). The ovary differentiates as a bottle-like structure with little interference on the insertion of the stamens. A comparable gynoeceal morphology has been observed in all species investigated so far (e.g. Moncur, 1988; Caris, 2013).

Carpel number is variable, but the most frequent merism is still five (with some variation to higher and lower numbers) and is more or less constant in Chrysophylloideae (Fig. 12). In Sapotoideae, carpels may increase in number in unison with an increase in merism of the whole flower (e.g. in *P. amboinense*), leading to six, eight, nine, ten or up to 18 carpels (*Letestua*) in a single whorl. In other cases, the numbers are more random, exceeding the merism of the other whorls (e.g. *Burckella*, *Manilkara*, *Labramia* A.DC., *Brevia*, *Aubregria* Heine), or the number is lower than the other whorls (*Labourdonnaisia*). Carpels can be reduced to two or even one in some genera, especially in Chrysophylloideae, such as *Pouteria*, *Elaeoluma* Baill. and *Chromolucuma* Ducke, and in *Sarcosperma* (Sarcospermatoideae) (Fig. 6F; Table 2). In contrast with the sepals and petals, all carpels remain in a single whorl.

CORRELATION BETWEEN MERISTIC CHANGE AND THE NUMBER OF WHORLS IN SAPOTACEAE

The ancestral floral merism in Sapotaceae is most likely pentamery with isomery in all whorls (floral formula: $K5C5A5+5G5$), but this *Bauplan* evolved into other floral merisms multiple times (Table 2, Figs 9, 14). *Diploknema oligomera* H.J.Lam is the only species with the ancestral floral formula. Other genera of Isonandreae have retained the two whorls of fertile stamens, but the flowers have been altered by changes in merism. In other Sapotaceae, the antesepalous stamen whorl is either staminodial or absent, and this has evolved several times independently throughout the family.

Our study indicates that changes in merism have been significant, even at lower nodes. Flowers of *Sarcosperma*, the first-branching clade of Sapotaceae, represent the common type for Sapotaceae with pentamerous flowers and antesepalous staminodes, but

the ovary is two- (rarely uni-)locular (Pennington, 2004), representing an autapomorphy. Chrysophylloideae and Sideroxyleae are mainly pentamerous throughout, with only occasional changes to tetramery or hexamery, mostly affecting all whorls together. The only major variant is the loss of the staminodial whorl affecting several species, especially in Chrysophylloideae. Members of Sapotoideae are rarely pentamerous (Sideroxyleae and Tseboneae) and generally more variable, with hexamery, tetramery and octomery affecting different whorls to different degrees (Figs 9–13).

Changes in the number of whorls linked to an increase in merism are uncommon in core eudicots. However, comparable fluctuations between tetramerous, pentamerous and hexamerous flowers have been reported in Phytolaccaceae, Polygonaceae and Loranthaceae (e.g. Ronse De Craene & Smets, 1993; Wanntorp & Ronse De Craene, 2009; Ronse De Craene, 2013, 2015). In all cases, the perianth is rearranged as two alternating whorls, as space restrictions make it impossible for all organs to be inserted at the same level. The different size of organs is probably responsible for the sudden change in merism between different whorls (Fig. 14). It is clear from our observations of octomerous and hexamerous flowers of Sapotaceae that the addition or loss of organs in a whorl will cause the original pentamerous whorl to be rearranged as two alternating whorls, thus increasing the number of whorls. An increase in the number of whorls is clearly related to the addition of organs in a limited space, and is linked to the ratio of the size of the organs to the circumference of the floral meristem (see Ronse De Craene, 2015). This leads to flowers that are apparently trimerous or dimerous, especially when the petals are missing. The reason for the breakup of initial whorls in alternating tiers is probably linked to space limitations and pressures within the flower bud. Sepals have a broad insertion area compared with the other organs of the flower. Although sepals are large and imbricately arranged, they never exceed eight parts and are generally inserted in two whorls. Petals are smaller and can be accommodated more easily as eight or more imbricately arranged organs. Compared with the petals, there is a sudden doubling of stamens, as two whorls can be spatially arranged as a single whorl. The single carpel whorl fits in the spaces between the stamens and also allows for an increase in numbers. The difference in size of the organs is linked to fluctuations in merism. Petals are exceptionally arranged as two whorls (as in *P. leerii*: Figs 1E, F, 7A, 14D) and only with excessive numbers of petals. In octomerous flowers of *Madhuca* (Fig. 3D, G, H), *P. lucida* (Fig. 2C) and hexamerous flowers of *Palaquium* (Fig. 4B), all petals tend to be inserted in

a single whorl, as there is obviously enough space for their insertion, whereas this is not the case for the sepals (Fig. 14E). Although young petals of *P. leerii* are inserted in one whorl, those alternating with sepals grow more quickly and are pushed more towards the centre of the flower than the antese-palous petals (Fig. 1E, F). This divergence is increased by unequal growth rates. The size and arrangement of organs tend to be correlated with changes in merism. As the androecium is originally made up of two whorls and because of the smaller insertion area of the stamens, no obvious increase in stamen whorls has been detected, although secondary increases in stamens may give the impression of more numerous whorls (e.g. Engler, 1890; Vink, 1957). Changes in the merism of stamens are correlated with changes in petal number and changes in the gynoecium.

Our study reveals that changes in number between different organ whorls are not random, but follow strict patterns. The concerted (mathematically regular) increase was observed and analysed by Hartog (1878) and Engler (1890), and our results support the significance of their observations.

CHARACTER OPTIMIZATION AND EVOLUTIONARY IMPLICATIONS FOR MERISTIC CHANGE

The MCC tree used to map characters is based on ITS data (Fig. 8) and is a good representation of the relationships among the genera and major clades of the family. Although the phylogenetic tree is based on only one nuclear marker, it is well supported and, in terms of relationships, does not have strongly supported conflict with published phylogenetic trees of major subgroups that are based on more or other sources of data. The majority of changes in state of the morphological characters discussed here are found at nodes that are well supported in the MCC tree.

The presence of suites of characters plotted on the phylogenetic trees seems to confirm the trends observed in the flowers of the species analysed in detail. Chrysophylloideae generally retains its ancestral condition of pentamery throughout the subfamily with few exceptions. In Sapotoideae, only the early-branching clades show a stable condition of pentamery throughout all whorls (Sideroxyleae). The larger clade contains two subclades: Sapoteae grouping the former Mimosopinae of Pennington (1991), including *Autranella* A.Chev. & Aubrév., *Baillonella* Pierre, *Mimusops*, *Tieghemella* Pierre, *Vitellaria* C.F.Gaertn. and *Vitellariopsis* Baill. ex Dubard (octomerous taxa), and members of the former Manilkarinae (mostly hexamerous taxa: *Labourdonnaisia*, *Labramia*, *Letestua*, *Faucherea* Lecompte and *Manilkara*), and Isonandreae grouping a *Madhuca*–*Payena* clade with

Palaquium (Fig. 8). A correlated increase in sepals with other floral organs affects Manilkarinae (hexamery) and Mimosopinae (octomery). In the Sapotoideae clade, where staminodes are absent (Isonandreae *sensu* Pennington, 1991), the increase in organ number mostly affects petals, stamens and carpels, but the numbers are variable and their relationship between the whorls is approximately 1 : 1. In this case, sepal number is excluded from the increase and stays relatively stable at a sequence of two plus two. Subtribe Glueminae of Sapoteae (Pennington, 1991) is poorly resolved in the molecular phylogenetic tree, although all taxa (*Inhambanella*, *Eberhardtia* Lecomte, *Neolemonniera*, *Lecomtedoxa* and *Gluema*) share pentamery with staminodes of Chrysophylloideae. Gautier *et al.* (2013) erected a new tribe, Tseboneae, containing *Capurodendron*, *Tsebona* and *Bemangidia* L.Gaut. Members of the former Glueminae were added more recently (Gautier *et al.*, 2013) as a homogeneous pentamerous clade next to Sapoteae, Isonandreae and Sideroxyleae of Sapotoideae. All former Mimosopinae group together and show octomery in all whorls (occasionally hexamery). The former Manilkarinae (including *Northia*) is generally hexamerous in all whorls, occasionally with higher carpel numbers. *Labourdonnaisia* and *Letestua* are the main exceptions, in that both can have 12–18 petals and stamens, mostly with the staminodial whorl missing (Engler, 1890; Table 2). Pennington (2004) reported that staminodes are minute or absent in Mimosopinae, indicating a tendency for loss comparable with that in Chrysophylloideae. The carpel number in this group is variable (five, six, eight or up to ten or more). *Northia* shows a similar pattern to other Manilkarinae with which it was originally grouped (Pennington, 1991): it is hexamerous throughout, but has lost the antese-palous staminodes.

As a result of sampling limitations and the relatively low support in some parts of the phylogenetic tree, the direction of evolution is not always clear, i.e. whether merism evolved from pentamery to hexamery and further to octomery, or from pentamery to octomery and then towards a reduction to hexamery (Figs 9, 14). Our observations of floral morphology and development have shown that increases in merism appear to progress in a regular sequence (except for *Madhuca*), linked with size differences of organs. There is indeed a phylogenetically significant pattern of variation in the family, with some monophyletic groups exhibiting the same or a similar meristic pattern. In the octomerous Sapoteae, all whorls are increased simultaneously, a pattern that is similar to that observed in *Sempervivum* L. of Crasulaceae (Ronse De Craene, 2010), or the increase affects only petals and stamens, or all organs except the sepals (for an overview of other families, see

Ronse De Craene, 2015). Fully tetramerous flowers are reported for some Chrysophylloideae (e.g. *Pouteria guianensis* Aubl. & Eyma) and for *I. compta* in Sapotoideae (Fig. 9), but are generally rare in the family. Hexamerous flowers appear to be more closely linked with pentamerous prototypes. In other core eudicot families, meristic increases tend to affect all whorls, or the upper three (petals, stamens, carpels) or the carpels only (e.g. *Lafoesia* Vand. in Lythraceae: Tobe, Graham & Raven, 1998; *Conostegia* D. Don in Melastomataceae: Wanntorp *et al.*, 2011; *Schefflera* J.R. Forst & G. Forst in Araliaceae: Nuraliev *et al.*, 2010; *Crossostylis* J.R. Forst. & G. Forst. in Rhizophoraceae: Setoguchi, Ohba & Tobe, 1996). In Sapotaceae, it is usually either all whorls, or petals and stamens only. Carpel number also varies greatly and is often not affected by the changes in other whorls. The pattern of the first three whorls (without the ovary) being affected simultaneously is not common in Sapotaceae.

Phylogenetic reconstructions place the presence of a staminodial whorl as ancestral for the family, as in *Sarcosperma* (Fig. 12). The absence of staminodes in Isonandreae represents a morphological synapomorphy for the clade. It is not certain whether the fully fertile antesealous stamen whorl represents a retained plesiomorphy or a reversal, which necessitates the genetic potential for staminodes to revert to fertile stamens. Sapotaceae is sister to Ebenaceae plus the primuloid clade, in which antesealous staminodes are common. A reversal to fertile stamens represents an important morphological shift within the family. Outside the *Palaquium–Madhuca–Payena* clade, the antesealous stamen whorl is generally sterile (Figs 5F, G, 6C, E, F, 7D, 12) or may be occasionally absent. Staminodes become lost in several members of Chrysophylloideae (e.g. *Chrysophyllum* L.), although their presence may vary between different species (Aubréville, 1964; Swenson *et al.*, 2008b). Swenson *et al.* (2008b) demonstrated that staminodes may be vestigial or lost in several Chrysophylloideae, and concluded that the presence of staminodes is plesiomorphic for the subfamily. This is clearly supported in our reconstruction (Fig. 12).

The phylogenetic trees make it possible to follow how numbers vary or stay constant between the whorls. Changes in merism appear to be correlated between specific whorls in some cases, but not in others. Changes in merism are generally of two kinds: isomerous and anisomerous.

Isomerous changes are increases or reductions that affect all organs to a similar degree. Examples are the transition of pentamery to tetramery (e.g. *Pouteria*, *Isonandra*) or increases to hexamery (e.g. *Palaquium*, *Northia*, *Faucherea*) and octomery (*Mimusops*, *Vittellaria*, *Vittelariopsis*, *Austranella*, *Baillonella*).

Anisomerous changes are changes in merism that are abrupt and happen generally at the limits between sepals and petals (e.g. *Payena*, *Madhuca*, *Letestua*, *Labourdonnaisia*), and more rarely between stamens and carpels (e.g. *Manilkara zapota*, *Labrarmia costata*). The petal number generally jumps to double the number of sepals or rarely triples or quadruples. Stamens generally comply with the petal increase and jump to double the petal number, if in two whorls. Carpel numbers comply with the upper stamen whorl and do not change, or they vary independently.

The reconstructions of merism on the lower branches leading to the main clades of Sapotoideae are equivocal in the main tree (Fig. 9), but also in the petal and gynoecium trees (Figs 11, 13). However, only the branch leading to Isonandreae is equivocal in the reconstructions for androecium and sepals (Figs 10, 12). This indicates that derivation of octomery from hexamery, or the opposite, is unclear in Isonandreae. Two options are possible: either octomery evolved once from pentamery at the node below the split of Sapoteae and Isonandreae, and hexamery is independently derived from octomery in Isonandreae and Sapoteae-Manilkarinae; or the node below the separation of Sapoteae and Isonandreae is pentamerous with two independent derivations of octomery. Hexamery is plesiomorphic for Isonandreae with a secondary derivation of octomery in the *Madhuca–Payena* clade. Octomery arose independently in Sapoteae and reverted further to hexamery in Sapoteae-Manilkarinae.

Evidence against the first interpretation is reflected in the different floral configurations linked with octomery. In the *Madhuca–Payena* clade of Isonandreae, the calyx is tetramerous and the other organs are generally octomerous. The fact that some species (e.g. *I. compta*, *I. gracilis* H.J. Lam) are tetramerous and isomerous for all organs indicates that octomery could have been derived from tetramery by a sudden duplication (Fig. 14C, D). This is an indication that the transition towards octomery went through a reduction in merism from five to four, followed by a doubling in the inner whorls. Lam (1927) observed that tetramerous *Isonandra* spp. showed fluctuations between four and six, especially in sepal number and arrangement. Other *Isonandra* spp. generally have a greater fluctuation in merism (six to eight: Baehni, 1965). It is also possible that the large decussately arranged sepals allowed for a duplication of the number of inner organs because of greater availability of space. Octomery found in Sapoteae subtribe Mimusopinae is radically different, as the increase in floral parts is concerted with similar numbers of organs. This supports the independent origin of octomery in these two separate clades.

Compared with octomery, there are three independent origins of hexamery. Hexamerous flowers, as in *M. zapota* and *P. amboinense*, show a concerted increase in all whorls, with a consecutive arrangement of sepals and occasionally petals in successive whorls of three, followed by 12 fertile stamens (*Palaquium*) or six stamens and six staminodes (*Manilkara*) (Figs 7C, 14E, G; Table 2). The hexamerous flowers of *Manilkara*, *Labramia* and *Faucheria* are nested in an octomerous clade (subtribe Mimuspinae), suggesting that hexamery arose by a reduction in merism from eight to six (Fig. 14F, G). This may have been caused by space restrictions or a greater stability induced by hexamery compared with octomery. However, instead of an expected six carpels, one finds up to 12 carpels, indicating two separate incidences of changes in merism. Carpel number seems to have approximately doubled in *Manilkara* after a reduction from eight to six. The hexamerous flowers of *Palaquium* are superficially similar to those of *Manilkara*, although the shape of the flower is less angular (Fig. 4, compared with Caris, 2013) and is fully isomerous in the former. A third origin of hexamery is restricted to *Northia*, although its position as sister to *Capurodendron* is not well supported.

In Isonandreae, there is no indication of a derivation of the hexamerous flower of *Palaquium* from octomerous flowers, or the opposite, and their origin may be different. As discussed previously, octomery in the *Madhuca–Payena* clade is probably derived from a tetramerous flower, such as *Isonandra*, whereas the hexamery of the *Palaquium* clade is probably derived from a pentamerous ancestor.

What are the functional advantages of an increase in merism? A higher merism is theoretically correlated with an increase in the size of the flower, although this correlation is not always certain. An increase in carpels and stamens leads to greater pollen and ovule number, and this can be ecologically advantageous (see Endress, 2014). However, increases in merism may rather be random events, linked with mechanical forces and size differences of organs in the flower (Ronse De Craene, 2015). A major question relative to differences in merism is: how do organ numbers change? When the change is constant and stable for all organs, one can assume that a single genetic change has taken place that leads to this different number. However, if organ numbers are generally more variable, it is not clear what causes the change in merism. Is it a consequence of gene duplications? Is organ number regulated by factors other than genes and, if so, why? It is difficult to speculate on the possible genetic background for variation in floral merism in Sapotaceae because there is insufficient information on the genetics underlying meristic change in general and because merism is quite vari-

able throughout the family. What is clear is that none of the actions of genes currently understood (e.g. *CLAVATA 1,3*: Clark, Running & Meyerowitz, 1993, 1995; *REVOLUTA*: Otsuga *et al.*, 2001; *PERIANTHA*: Running & Meyerowitz, 1996; *ETTIN*: Turnbull, 2005) seem to fit the patterns of floral variation observed in Sapotaceae.

CONCLUSIONS

The widespread practice to mention only the number of parts in flowers in taxonomic descriptions of species is clearly inadequate if we are to understand flower structures in a phylogenetic context. In particular, the enumeration of organ numbers and mentioning whether organs are present or absent (in the case of staminodes) are inadequate for flower descriptions without stating the exact position of organs in different whorls and what correlation exists between these whorls. An exact knowledge of the position of organs is more informative and should be performed routinely in taxonomic studies (e.g. Ronse De Craene, 2010; Ronse De Craene *et al.*, 2014).

Based on our observations, we conclude that changes in merism are linked with two patterns: a concerted multiplication of organs within whorls and an increase in whorls through displacement of organs. Moreover, fluctuations in merism between different whorls are not random, but occur in a coordinated way and can potentially present synapomorphies for selected clades.

Three possibilities of increase have been identified in flowers of Sapotaceae: a concerted increase affecting all organs more or less equally; an independent increase in carpels centrifugally affecting the androecium and petals; and a coordinated increase in petals and stamens without an effect on sepals and carpels. An increase in organs within a whorl is responsible for shifts of organs and a duplication of whorls when space becomes a limiting factor. Sepals (and, more rarely, petals) are broader organs, which will become rearranged in two whorls as the result of an increase. This is less likely for stamens and carpels, which occupy limited space on the floral receptacle.

Different factors are responsible for increases in merism and the variability in Sapotaceae. Simple genetic mutations are probably linked with the mechanical–spatial constraint for the floral organs. A functional–ecological advantage of higher merism is to have flowers with more organs (with higher stamen loads and carpels), although little to nothing is known about this in Sapotaceae. Increases in merism also lead to larger flowers, but the relevance of this has not been investigated. This study demonstrates the importance of observing the positions of organs in addition to mentioning their number in a flower, as

important synapomorphies can be recognized to describe clades of Sapotaceae. In future investigations, a detailed study of the gene regulation of floral organs may help illuminate the genetic processes driving variations in merism in Sapotaceae.

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