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Diversity and Lability of Floral Phyllotaxis in the Pluricarpellate Families of Core Laurales (Gomortegaceae, Atherospermataceae, Siparunaceae, Monimiaceae)

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Abstract

Floral phyllotaxis of Laurales (Magnoliidae) is poorly and sometimes conflictingly documented, especially in the pluricarpellate families of the core Laurales (Gomortegaceae, Atherospermataceae, Siparunaceae, Monimiaceae). In this study four types of floral phyllotaxis were recovered: Fibonacci spiral, simple-whorled (decussate), complex-whorled, and irregular. Whorled and spiral phyllotaxis co-occur in all families except Gomortegaceae and even vary within a species in some Mollinedioideae (Monimiaceae). Complex-whorled floral phyllotaxis with two or more organs in a position where only one is expected and changes in merism are especially prominent in Atherospermataceae and Monimiaceae. The most elaborate complex-whorled phyllotaxis pattern (leading to 8-merous whorls) is present in flowers with a flat floral base. Presence of a hyperstigma is correlated with double positions in the perianth. Flowers with low organ number commonly have simple-whorled phyllotaxis; flowers with high organ number have complex-whorled or irregular patterns. Spiral phyllotaxis occurs in flowers with a broad range of organ numbers. Irregularities in organ sequence were found at the periphery of the gynoecium in some Atherospermataceae and Monimiaceae, involving staminodes, carpelodes, and carpels. In Laurales, floral phyllotaxis diversity appears to have evolved from spiral phyllotaxis, independently in Atherospermataceae, Siparunaceae, and Monimiaceae.

DIVERSITY AND LABILITY OF FLORAL PHYLLOTAXIS IN THE PLURICARPELLATE FAMILIES OF CORE LAURALES (GOMORTEGACEAE, ATHEROSPERMATACEAE, SIPARUNACEAE, MONIMIACEAE)

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Floral phyllotaxis of Laurales (Magnoliidae) is poorly and sometimes conflictingly documented, especially in the pluricarpellate families of the core Laurales (Gomortegaceae, Atherospermataceae, Siparunaceae, Monimiaceae). In this study four types of floral phyllotaxis were recovered: Fibonacci spiral, simple-whorled (decussate), complex-whorled, and irregular. Whorled and spiral phyllotaxis co-occur in all families except Gomortegaceae and even vary within a species in some Mollinedioideae (Monimiaceae). Complex-whorled floral phyllotaxis with two or more organs in a position where only one is expected and changes in merism are especially prominent in Atherospermataceae and Monimiaceae. The most elaborate complex-whorled phyllotaxis pattern (leading to 8-merous whorls) is present in flowers with a flat floral base. Presence of a hyperstigma is correlated with double positions in the perianth. Flowers with low organ number commonly have simple-whorled phyllotaxis; flowers with high organ number have complex-whorled or irregular patterns. Spiral phyllotaxis occurs in flowers with a broad range of organ numbers. Irregularities in organ sequence were found at the periphery of the gynoecium in some Atherospermataceae and Monimiaceae, involving staminodes, carpelodes, and carpels. In Laurales, floral phyllotaxis diversity appears to have evolved from spiral phyllotaxis, independently in Atherospermataceae, Siparunaceae, and Monimiaceae.

Keywords: floral phyllotaxis, Atherospermataceae, Gomortegaceae, Monimiaceae, Siparunaceae, Laurales.

Introduction

It has long been assumed that one of the general trends in angiosperm evolution is the evolution of whorled flowers from spiral ones (e.g., Takhtajan 1969; Kubitzki 1987; Cronquist 1988). This view was modified by Endress (1987) who, from the complex distribution of spiral and whorled flowers, hypothesized that spiral and whorled flowers coexisted in basal angiosperms and that the trend is not from spiral to whorled but from lability between spiral and whorled to stabilization of whorled patterns. Whorled phyllotaxis allows synorganization and thus has a greater evolutionary potential than spiral phyllotaxis (Endress 1987, 2006). Phylogenetic studies indicate that in basal angiosperms the evolutionary transition from a spiral to a whorled phyllotaxis or vice versa has occurred several times in the perianth and androecium (Endress and Doyle 2007, 2009; see also Ronse De Craene et al. 2003; Zanis et al. 2003 [perianth only]). Such transitions are, however, poorly understood. One of the groups in which such transitions took place is the Laurales (Ronse De Craene et al. 2003; Zanis et al. 2003; Endress and Doyle 2007, 2009).

Laurales (Magnoliidae sensu Cantino et al. 2007) comprise seven families. Calycanthaceae (nine species; Zhou et al. 2006) are sister to the rest of the order, the core Laurales (Renner 1998, 1999, 2004; Qiu et al. 1999, 2005; fig. 1). The core

Laurales consist of two subclades of three families each (Renner 2004): the clade containing Siparunaceae (53 species; Renner and Hausner 2005), Atherospermataceae (16 species; Renner et al. 2000), and Gomortegaceae (one species; Kubitzki 1993a) and the clade containing Monimiaceae (~270 species; Philipson 1993), Hernandiaceae (~60 species; Kubitzki 1969, 1993b), and Lauraceae (2500–3500 species; Rohwer 1993). Siparunaceae are sister to Atherospermataceae plus Gomortegaceae (Renner 2004). Either Monimiaceae have an unsettled position as sister to Lauraceae (Renner 1999, 2004), sister to Hernandiaceae (Qiu et al. 1999, 2006), or sister to a clade comprising Hernandiaceae and Lauraceae (Doyle and Endress 2000; Chanderbali et al. 2001; Hilu et al. 2003) or the position of Hernandiaceae, Lauraceae, and Monimiaceae is unresolved (Renner and Chanderbali 2000; Soltis et al. 2007). Monimiaceae are divided into two subfamilies, Monimioideae (*Peumus*, *Palmeria*, and *Monimia*) and Mollinedioideae (all other genera; Renner 2004), with *Hortonia* as the basalmost genus.

Flowers of Laurales commonly have a floral cup (with the exception of some Lauraceae; Rohwer 1993). Unisexual flowers are common; in the pluricarpellate core Laurales, only a few taxa have hermaphroditic flowers (Gomortegaceae, *Daphnandra*, *Doryphora*, and *Dryadodaphne* of Atherospermataceae and *Hortonia* of Monimiaceae).

In Calycanthaceae, floral phyllotaxis is uniformly spiral in the Fibonacci mode (Staedler et al. 2007). In contrast, in unicarpellate families of core Laurales, spiral floral phyllotaxis is unknown; whorled patterns are predominant (Hernandiaceae [Kubitzki 1969; Endress and Lorence 2004], Lauraceae [Mez 1889; Singh and Singh 1985; Hyland 1989; Rohwer 1993;

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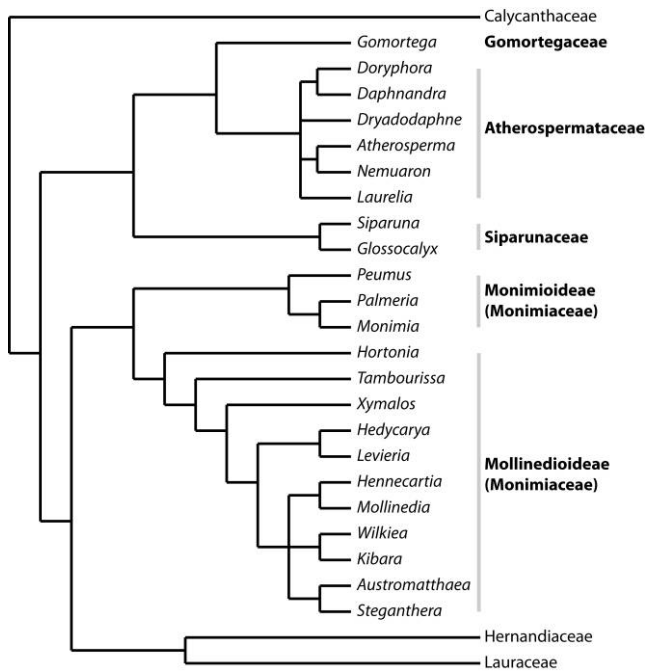


Fig. 1 Cladogram of Laurales (based on Renner 2004; Soltis et al. 2007).

Buzgo et al. 2007]). Irregular phyllotaxis has been reported in a few atepalous Lauraceae (Endress 1990).

In pluricarpellate families of core Laurales (Gomortegaceae, Atherospermataceae, Siparunaceae, and Monimiaceae), floral phyllotaxis appears to be diverse and labile. However, it is poorly documented in detail, especially for the androecium and even more so for the gynoecium. Descriptions of the floral phyllotaxis of the sole species of Gomortegaceae, *Gomortega keule*, show conflicting results (summarized in Kubitzki 1993a). Atherospermataceae appear to be diverse (Schodde 1969), but published reports also show conflicting results. Baillon (1868) mentions spiral phyllotaxis for the whole flower of *Laurelia novae-zelandiae*, but his floral diagram shows a whorled perianth and spirally arranged stamens and carpels. For the same species, Sampson (1969b) mentions perianth phyllotaxis either as opposite for the two outer tepals and spiral for the other tepals or as entirely whorled but with stamens and carpels spiral in both cases. In *Laurelia serrata*, completely tetramerous bisexual flowers were described (Stapf 1909). Schodde (1969) describes the phyllotaxis as whorled for the perianth and androecium in bisexual flowers of *Atherosperma*, *Dryadodaphne*, and *Laureliopsis* (*Laurelia philippiana*) but spiral in the androecium of male flowers of *Atherosperma*. Also described are predominantly trimerous whorls in *Doryphora sassafras* but tetramerous whorls in the perianth and a more irregular pattern in the androecium of *Doryphora aromatica*, tri- and tetramerous whorls in *Nemuaron*, decussate and spiral phyllotaxis in *Daphnandra*, and obscure whorls in *Laurelia*. Among Siparunaceae, in *Siparuna thecaphora*, phyllotaxis is decussate in most male flowers and spiral in carpels of female flowers (Endress 1972, 1980b), but it may also be irregular in other taxa of the family (Renner and Hausner 2005).

In Monimioideae, floral phyllotaxis is not known in detail (but from preliminary observations was assumed to be spiral in the perianth by Doyle and Endress [2000] and Endress and Doyle [2009]). In Mollinedioideae it is documented for whole flowers only in very few taxa. *Hortonia* has a Fibonacci spiral pattern (Endress 1980a). *Hedycarya arborea* has a whorled perianth, but stamen phyllotaxis is spiral or irregular, carpelodes are whorled, and carpels are spiral (Sampson 1969a). For most species studied, data are limited to the perianth, which is often decussate, such as in species of *Austromatthaea*, *Kairoa*, *Kibara*, *Mollinedia*, *Steganthera*, *Tambourissa*, and *Wilkiea* (Endress 1979b, 1980b; Philipson 1980, 1985). Thus, from the literature, floral phyllotaxis in Atherospermataceae and Monimiaceae appears unusually diverse and unstable.

The present work is a comparative study of floral phyllotaxis in all four pluricarpellate families of the core Laurales. A number of taxa are studied for the first time, with the aim of resolving inconsistencies in earlier descriptions. Patterns and conditions of the unusual diversity and variability of floral phyllotaxis in the core Laurales are explored, such as different organ numbers, floral structure (shape, presence of hyperstigma), and gender in unisexual flowers (figs. 2–22). Finally, the results are discussed in an evolutionary context.

Material and Methods

Collection Data

The following collections were used for this study (PKE = Peter K. Endress, S = Yannick M. Staedler, BGZ = cultivated in the Botanical Garden of the University of Zurich, cursory = cursorily studied flowers).

Gomortegaceae

Gomortega nitida Ruiz et Pav.; T. Stuessy et al. 6698, Chile (fig. 4).

Atherospermataceae

Atherosperma moschatum Labill.; PKE 2672, male flowers; Royal Botanical Gardens, Kew.

Daphnandra micrantha Benth.; PKE 4169 (fig. 5D, 5E); PKE 4327 terminal flower; PKE 4350 (fig. 5F, 5G; fig. 22B); Queensland, Australia.

Daphnandra repandula F. Muell.; PKE 4222 (fig. 5A–5C); PKE 4243 (fig. 22A); S006-32.1; Queensland, Australia.

Doryphora aromatica (F.M. Bailey) L.S. Sm.; S 006-32 (fig. 6A–6C); B.P.M. Hyland 8610; Queensland, Australia.

Doryphora sassafras Endl.; PKE 2671; Royal Botanical Gardens, Kew.

Dryadodaphne trachyphloia Schodde (ined. Schodde, 1969); B.P.M. Hyland 8261 (fig. 7A–7C); A. Ford 4791; Queensland, Australia.

Laurelia sempervirens (Ruiz et Pav.) Tul.; PKE 916 male; Royal Botanical Gardens, Kew.

Siparunaceae

Glossocalyx longicuspis Benth.; W. de Wilde 1241 (Z) male; Cameroon.

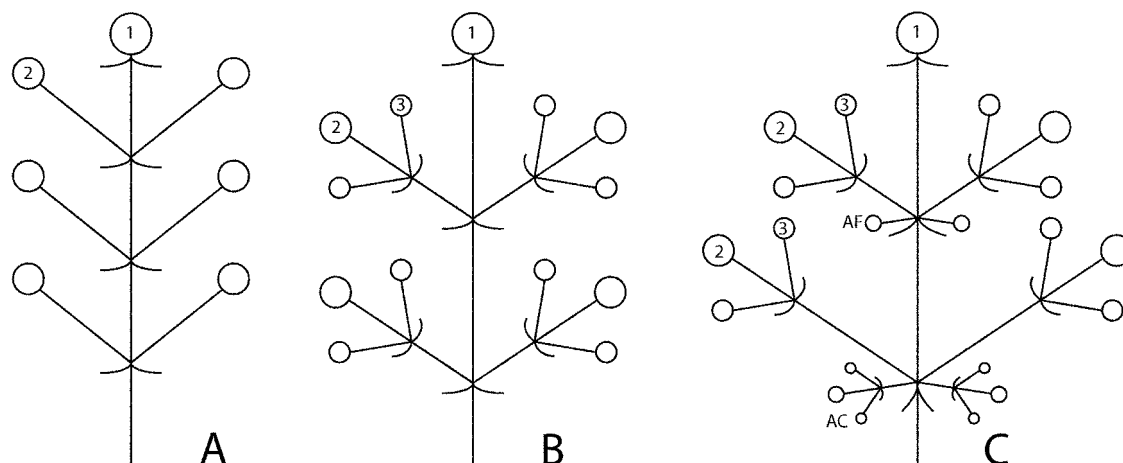


Fig. 2 Inflorescences. A, Botryoid. B, Thyrsoid. C, Thyrsoid with accessory single flowers and accessory cymes. 1–3 = branching order. AC = accessory cyme. AF = accessory flower.

Siparuna thecaphora Hemsl.; PKE 1096 male (fig. 8H–8J), Honduras; PKE 1202 male; PKE 1301 female (fig. 8K–8M); PKE 1203 female; Guatemala.

Monimiaceae, Monimioideae

Palmeria gracilis Perkins; PKE 4084 male (fig. 10A–10E); PKE 4085 female (fig. 10F, 10G); Papua New Guinea.

Peumus boldus Molina; V. Cassels s.n., male and female; Chile.

Mollinedioideae

Austromatthaea elegans L.S. Sm.; PKE 4196 male (fig. 19); PKE 9030 male and female; Queensland, Australia.

Hedycarya angustifolia A. Cunn.; L. Adams 2473 male (fig. 14A); New South Wales, Australia; R. Schodde 2462 female (fig. 14B–14E); Australian Capital Territory, Australia.

Kibara coriacea (Blume) Tul.; A.D.E. Elmer 20669 Borneo (Z) male (fig. 16A, 16B); PKE 9325 male; Botanical Garden Bogor, Java, Indonesia.

Kibara macrophylla (R. Cunn.) Benth.; PKE 9303 female; Botanical Garden Bogor, Java, Indonesia.

Levieria acuminata (F. Muell.) Perkins; S 006-75A male; S 006-75B female; Queensland, Australia.

Stegantthera ilicifolia A.C. Sm.; PKE 4070 male (fig. 20A, 20B); PKE 4051 male; PKE 4071 male; PKE 4074 male; PKE 4126 female (fig. 20C, 20D); Papua New Guinea.

Tambourissa comorensis Lorence; D.H. Lorence 2870 female; Grande Comore Island.

Tambourissa ficus (Tul.) A. DC.; D.H. Lorence 2162 female; Mauritius.

Tambourissa purpurea A.D.C.; PKE 03-3 male and female (figs. 11, 12); S08-01 male and female; Botanical Garden of the University of Zurich (original collection W. Rauh 138, Madagascar).

Wilkiea angustifolia (Bailey) Perkins; B. Gray 1913 male; Queensland, Australia.

Wilkiea cf. angustifolia (Bailey) Perkins; PKE 9216 female; Queensland, Australia.

Wilkiea huegeliana (Tul.) A. DC.; PKE 4398 male (fig. 18A–18F); PKE 4182 female (fig. 18G–18K); PKE 4313 female; PKE 4330 female (fig. 18L–18O); PKE 4331 female; Queensland, Australia.

Wilkiea longipes (Benth.) Whiffin et Foreman; B.P.M. Hyland 11669 female; Queensland, Australia.

Xymalos monospora Baill.; B.M. Browning 37 male; Zimbabwe; R. Dümmer 814 (Z) female; Uganda.

Inflorescences or flowers were fixed in FAA or 70% ethanol and stored in 70% ethanol. Plants embedded in paraplast were sectioned and stained with safranin and astra blue. Plants embedded in Kulzer's Technovit 7100 (2-hydroxyethyl methacrylate; Igersheim and Cichocki 1996) were sectioned and stained with toluidine blue and ruthenium red. Sectioned herbarium plants (all from the herbarium of the University of Zurich [Z]) were first expanded in sodium sulfosuccinate solution (Erbar 1995). The studied plants and microtome slides are stored in the Institute of Systematic Botany of the University of Zurich. Additional unsectioned flowers were cursorily studied with the stereomicroscope.

To introduce the phyllotaxis terminology we use in the descriptions (table 1), we first outline basic patterns of floral phyllotaxis that occur in the study group. We distinguish four major kinds of phyllotaxis: (1) spiral, (2) whorled with simple whorls, (3) whorled with complex whorls, and (4) irregular. Patterns 2 and 3 show a diversity of subpatterns.

1. In the Fibonacci spiral pattern (fig. 3A) the organs have an average divergence angle of 137.5° (the angles between two successively formed organs and the floral center). Often organs of the same kind occur in Fibonacci numbers (2, 3, 5, 8, 13, ...) and form series in Fibonacci numbers around the circumference of a flower. Series are analogous to whorls in whorled flowers, but they are less well circumscribed than whorls because the distances between the neighboring organs are not all the same (the divergence angle of 137.5° is not a fraction of 360°).

2. The simple-whorled pattern (fig. 3B1–3B3) has alternating whorls, each with the same number of organs. The divergence angles between the organs within a whorl are constant,

Table 1
Glossary of Terminology Used in This Article

Terminology	Definition	Illustration
Accessory cyme	Cyme borne in the axil of the same subtending bract as another lateral part of an inflorescence	Fig. 2C
Accessory flower	Flower borne in the axil of the same subtending bract as another lateral part of an inflorescence	Fig. 2C
Botryoid	Determinate raceme	Fig. 2A
Compitum	Shared pollen tube transmitting tract of all carpels of a flower	
Hyperstigma	Receptive area for pollen outside the gynoeceum; in some Mollinedioideae on the narrow floral pore formed by the floral cup and the reduced tepals	
Orthostichies	Radial straight lines connecting adjacent floral organs; characteristic for whorled phyllotaxis	
Parastichies	Spiral lines from periphery to center, connecting adjacent floral organs; characteristic for all regular phyllotaxis patterns (spiral and whorled) ^a	
Prophylls	First phyllomes (usually bracts) on a lateral branch (commonly two in transverse position in basal angiosperms and eudicots)	
Staminodes	Stamenlike sterile organs; in Laurales, staminodes are often present between the stamens and the carpels (inner staminodes)	
Thyrsoid	Determinate thyrse	Fig. 2B

^a Several sets of parastichies running to the left or to the right are always present. If the parastichy sets of opposite directions have parastichies of different steepness, the phyllotaxis is spiral; if the steepness is the same, the phyllotaxis is whorled (Endress 2006).

always a fraction of 360°. The number of organs (merism) within each whorl can be two (dimerous, decussate; fig. 3B1), three (trimerous; fig. 3B2), four (tetramerous; fig. 3B3), or rarely more. Rarely this number may change within a flower, e.g., from two to three or from three to two (by intercalation or loss of an organ from one whorl to the next).

3. In the pattern with complex whorls (fig. 3C–3F), double, triple, etc., positions occur, meaning that at the place where a single organ is expected, two (or more) organs are formed in collateral position. (a) A common case starts with two whorls of two organs each, followed by two double positions that alternate with the single organs of the preceding (dimerous) whorl—thus, four organs in two collateral pairs. The subsequent whorl consists again of four organs, but all organs now alternate with each of the four organs of the preceding whorl (fig. 3C). Thus, there is a transition from dimerous to tetramerous whorls via an intermediate whorl with two double positions. Variations of this pattern are (b) two double positions (four organs) and two simple positions (two organs), followed by six organs alternating with these and thus formation of a hexamerous whorl (fig. 3D). (c) Double positions can alternate several times in subsequent whorls without changing to simple whorls of double the number of organs (fig. 3E). (d) Instead of collateral double positions, there are collateral triple or even quadruple positions, leading to more complex-whorled patterns (fig. 3F).

4. In irregular phyllotaxis, no pattern can easily be recognized.

Differentiation between bracts and tepals is usually straightforward in eudicots and monocots but can be problematic in basal angiosperms (ANITA grade and Magnoliidae). Endress (1980b, 1980c) used four criteria to arbitrarily set such delimitations: (1) beginning of short internodes, (2) change of phyllotaxis from decussate to spiral, (3) beginning of the increase of the size of the phyllomes, and (4) beginning of branched vasculature of the phyllomes. We used the following artificial but practical working definition: phyllomes are considered to be bracts if they are directly below the floral cup. When several interpretations of the phyllotaxis of a system are possible, we favor the most simple interpretation.

Results

Gomortega (*Gomortegaceae*)

***Gomortega keule*.** A terminal flower of a botryoid sectioned (fig. 4A, 4B) is preceded by an empty bract and has nine tepals, eight stamens, four staminodes, and two carpels. Floral organs show an average divergence angle of 136.7° (±20°), in accordance with a Fibonacci spiral pattern (fig. 3A; floral diagram, fig. 22A). Only the two innermost divergence angles are more irregular (206° and 75°). The tepals form two series of five organs (with inclusion of the empty bract immediately preceding the flower), and the stamens form two series of five and three organs. Three lateral flowers sectioned (one illustrated in fig. 4C, 4D) have seven to nine tepals, eight stamens, three or four staminodes, and two carpels. As in the terminal flower, the phyllotaxis is Fibonacci spiral; only the two innermost divergence angles are more irregular in all three flowers (mean divergence angles for all organs: 137.0° ± 18°, 138.6° ± 25°, 139.6° ± 28°). Organs of the perianth and the androecium tend to be organized in series of five and three organs, respectively.

Daphnandra (*Atherospermataceae*)

***Daphnandra repandula*.** A probably terminal flower of a thyrsoid sectioned (fig. 5A–5C) has 16 tepals, eight stamens, seven staminodes, and 11 carpels. The first two tepals are opposite. The other floral organs show an average divergence angle of 137.6° (±8.5°), according to a Fibonacci spiral pattern (fig. 3A). The perianth and androecium form series of eight organs. Three flowers of a thyrsoid were cursorily studied: the terminal flower and a primary and a secondary flower of a dichasium of the thyrsoid (flowers 1–3 in fig. 2B). All flowers have Fibonacci spiral phyllotaxis. The terminal flower of the thyrsoid has 12 tepals (of which the first two are approximately opposite, continuing the phyllotaxis of the subtending bracts of the dichasia), seven stamens, eight staminodes, and 10 carpels. The primary flower of the dichasium has 11 tepals (of which the first two are transverse, approximately opposite), eight stamens, six staminodes, and 11 carpels. The sec-

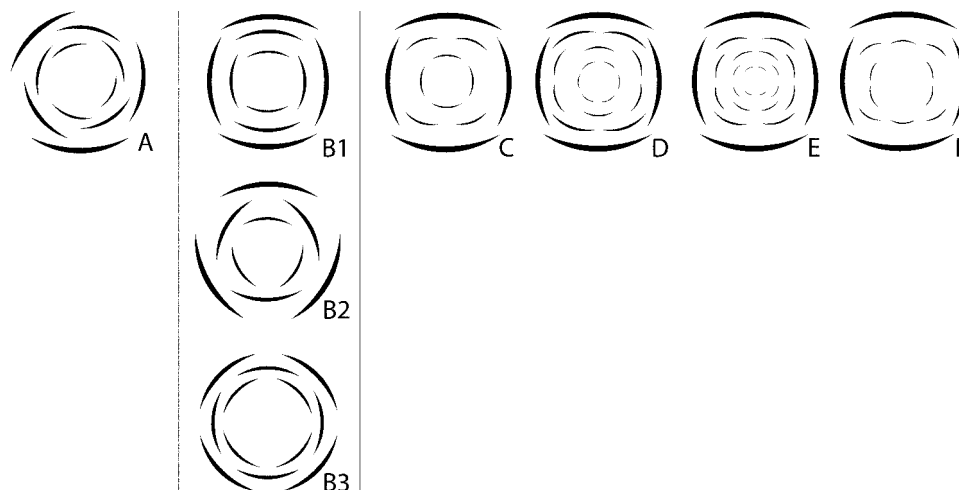


Fig. 3 Phyllotaxis patterns. *A*, Fibonacci spiral. *B1–B3*, Simple-whorled. *B1*, Decussate. *B2*, Trimerous. *B3*, Tetramerous. *C–F*, Complex-whorled. *C*, Two simple pairs, followed by a pair of double positions and a tetramerous whorl. *D*, Two simple pairs, followed by two pairs of double positions, a simple pair, and a hexamerous whorl. *E*, Two simple pairs, followed by alternating pairs of double positions. *F*, Two simple pairs, followed by a pair of triple positions and a pair of double positions.

ondary flower of the dichasium has nine tepals (of which the first two are transverse, approximately opposite), six stamens, eight staminodes, and nine carpels.

***Daphnandra micrantha*.** A probably terminal flower of a thyrsoid sectioned (fig. 5*D*, 5*E*) has 10 tepals, four stamens, eight staminodes, and four carpels. Floral phyllotaxis follows figure 3*C*. The 10 tepals (whorls 1–4) are arranged in a decussate pattern (fig. 5*D*). Whorl 4 has four tepals, arranged in two double positions (fig. 5*D*). The subsequent organs (four stamens, eight staminodes, and four carpels) form alternating tetramerous whorls (whorls 5–8). A terminal flower of collection PKE 4327 studied has a fifth simple pair of tepals. Stamines are in two whorls (of three and two organs). Two lateral flowers were studied (one illustrated in fig. 5*F*, 5*G*); the flowers have six and 10 tepals, three and four stamens, seven staminodes, and three and four carpels. In both flowers, there is a switch from tetramerous tepal whorls to trimerous staminode whorls (fig. 5*F*).

Doryphora (*Atherospermataceae*)

***Doryphora aromatica*.** A flower of a three-flowered botryoid sectioned (fig. 6*A–6C*) has four tepals, five stamens, nine staminodes (five with glands and four without), and eight carpels. The tepals form two decussate pairs. Stamens, staminodes, and carpels show an average divergence angle of $139.7^\circ (\pm 36^\circ)$, according to a Fibonacci spiral pattern (fig. 3*A*). Unexpectedly, along the ontogenetic spiral, the first two carpels are followed by the last staminode and only then by the remaining carpels (fig. 6*B*). The androecium has two series of five organs (five stamens and five staminodes with glands; see fig. 6*A*). In a sectioned gynoecium of an anthetic flower of collection Hyland 8610, the divergence angle between the innermost three staminodes and seven carpels is $139^\circ (\pm 18.24^\circ)$, in accordance with a spiral pattern in the Fibonacci mode. Two cursorily studied flowers of collection Staedler S006-32 have two decussate pairs of tepals, five stamens, 10 and eight

staminodes (five and four with glands), and nine and 12 carpels. The androecium and gynoecium appear to have Fibonacci spiral phyllotaxis.

***Doryphora sassafras*.** A terminal flower of a three-flowered botryoid sectioned (fig. 6*D*, 6*E*) has eight tepals, six stamens, 23 staminodes (six with glands and 17 without), and 10 carpels. The flower appears to have trimerous whorls, but organ aestivation suggests a more complex pattern. Floral phyllotaxis approximately follows figure 3*E* (floral diagram, fig. 22*B*). The two outermost tepals are more or less opposite (whorl 1). The subsequent 19 organs (six tepals, six stamens, seven staminodes [six with glands and one without]) form simple decussate pairs and pairs of double positions alternately (simple pairs: two, four, and six; pairs of double positions: three, five, and seven; see fig. 6*D*). One of the positions of the last pair with double positions (whorl 7) is in itself doubled and has one staminode with glands and one staminode without. The outermost staminodes without glands form an 11-merous whorl (whorl 8). The innermost staminodes (without glands, whorl 9) form a 5-merous whorl. The carpels appear to be arranged in two alternating pairs of double positions (whorls 10 and 11), plus two carpels in the center of the flower (whorl 12; see fig. 6*E*). Three further cursorily studied terminal flowers of three three-flowered botryoids have five or six tepals, six to eight stamens, 17–30 staminodes (five or six with glands and 12–24 without), and 12–17 carpels. In two of the three flowers, the arrangement of the tepals, stamens, and outermost staminodes is as in the sectioned flower. In addition, a second simple pair of stamens occurs in one flower and a pair with a stamen and a staminode with glands in the other. In the third flower, stamens and outermost staminodes are in trimerous whorls.

A lateral flower sectioned (fig. 6*F–6J*) has six tepals, six stamens, 31 staminodes (seven with glands and 24 without), and 22 carpels (the identity of the 22 innermost organs is tentative because they are in an early stage of differentiation). Floral phyllotaxis approximately follows figure 3*D* (floral diagram,

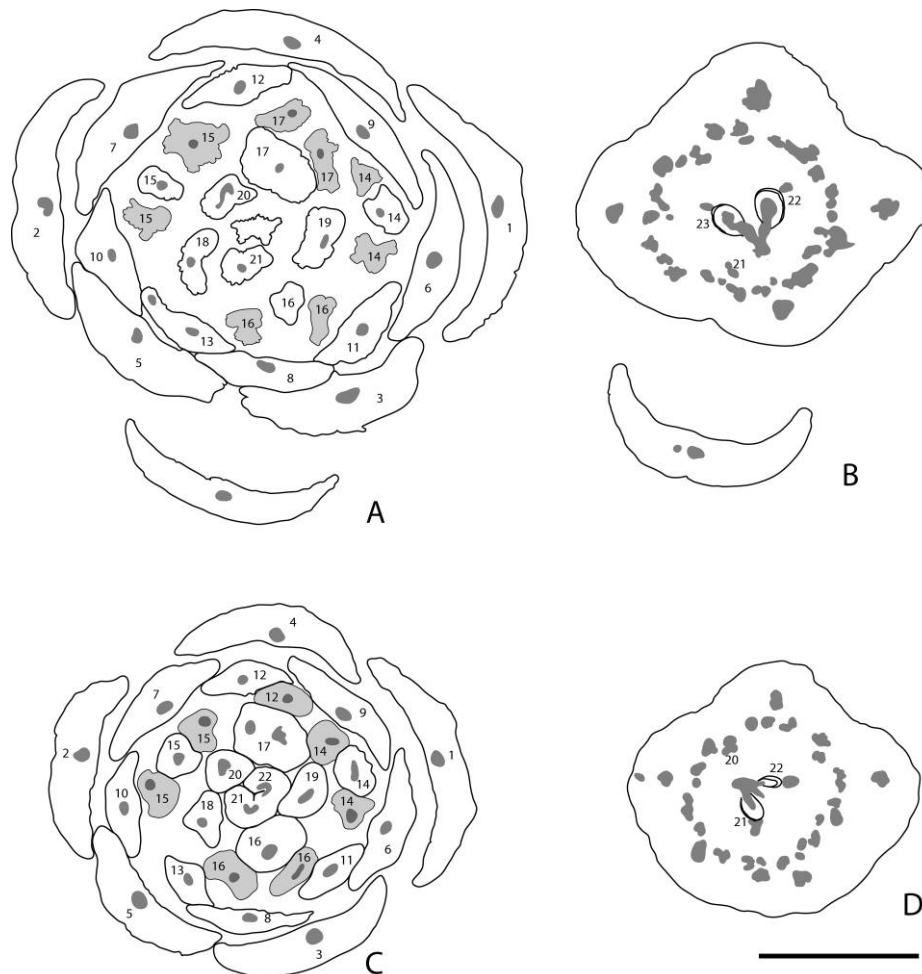


Fig. 4 Gomortegaceae, *Gomortega keule*. Transverse section series of late floral buds. *A, B*, Terminal floral bud. *A*, Level above rim of floral cup. *B*, Level of ovary. *C, D*, Lateral floral bud. *C*, Level above rim of floral cup. *D*, Level of ovary. Dark gray = vasculature; light gray = glandular appendages of stamens (and staminodes); floral organs numbered along ontogenetic spiral. Scale bar = 1 mm.

fig. 22C). Trimerous whorls are present in the outer floral organs: tepals (whorls 1 and 2), stamens (whorls 3 and 4), staminodes with glands (whorls 5 and 6), and staminodes without glands (whorl 7). In whorl 1, the unpaired tepal is abaxial. Whorls 6 and 7 each have one double position in the median plane. The staminodes of both whorls 6 and 7 are in contact with the staminodes of whorl 8. Whorls 6 and 7 together form an 8-merous system, which mediates the transition to the higher merism of the inner whorls. The inner organs form three 10-merous whorls (whorls 8–10), one 8-merous whorl (whorl 11), and four carpels in the center (whorl 12). Four cursorily studied young flowers (out of the six lateral flowers of the three inflorescences) have six tepals, six stamens, six to nine staminodes with glands, and 45–57 still undifferentiated inner organs (staminodes without glands and carpels). The perianth is as in the sectioned flower. Trimerous whorls of staminodes with glands are found in three flowers (with occasional double positions in two flowers); in the fourth flower, hexamerous whorls of staminodes with and without glands are present, and in two other flowers, hexamerous whorls of staminodes without glands are present.

Dryadodaphne (*Atherospermataceae*)

***Dryadodaphne trachyphloia*.** A lateral flower of a botryoid sectioned (fig. 7A–7C) has eight tepals (preceded by two prophylls), four stamens, 12 staminodes, and 10 carpels. Floral phyllotaxis follows figure 3C (floral diagram, fig. 22D). The prophylls (fig. 7B, 7C) and the tepals of whorls 1–3 (fig. 7A) are decussate. The four tepals of whorl 3 form two double positions (fig. 7A). Subsequent organs (four stamens, 12 staminodes, and the eight outer carpels) form tetramerous whorls (whorls 4–9), and the two inner carpels form a dimerous whorl (whorl 10). In a cursorily studied flower (A. Ford 4791), phyllotaxis and merism are the same as in the sectioned flower. Two other flowers (a terminal one and a lateral one; A. Ford 4791) have four inner carpels (instead of two), which form a tetramerous whorl.

Laurelia (*Atherospermataceae*)

***Laurelia sempervirens*.** A terminal flower of a male botryoid sectioned (fig. 7D) has eight tepals and eight stamens. Floral phyllotaxis approximately follows figure 3C. Floral phyllotaxis is decussate (whorls 1–5), except for the two innermost

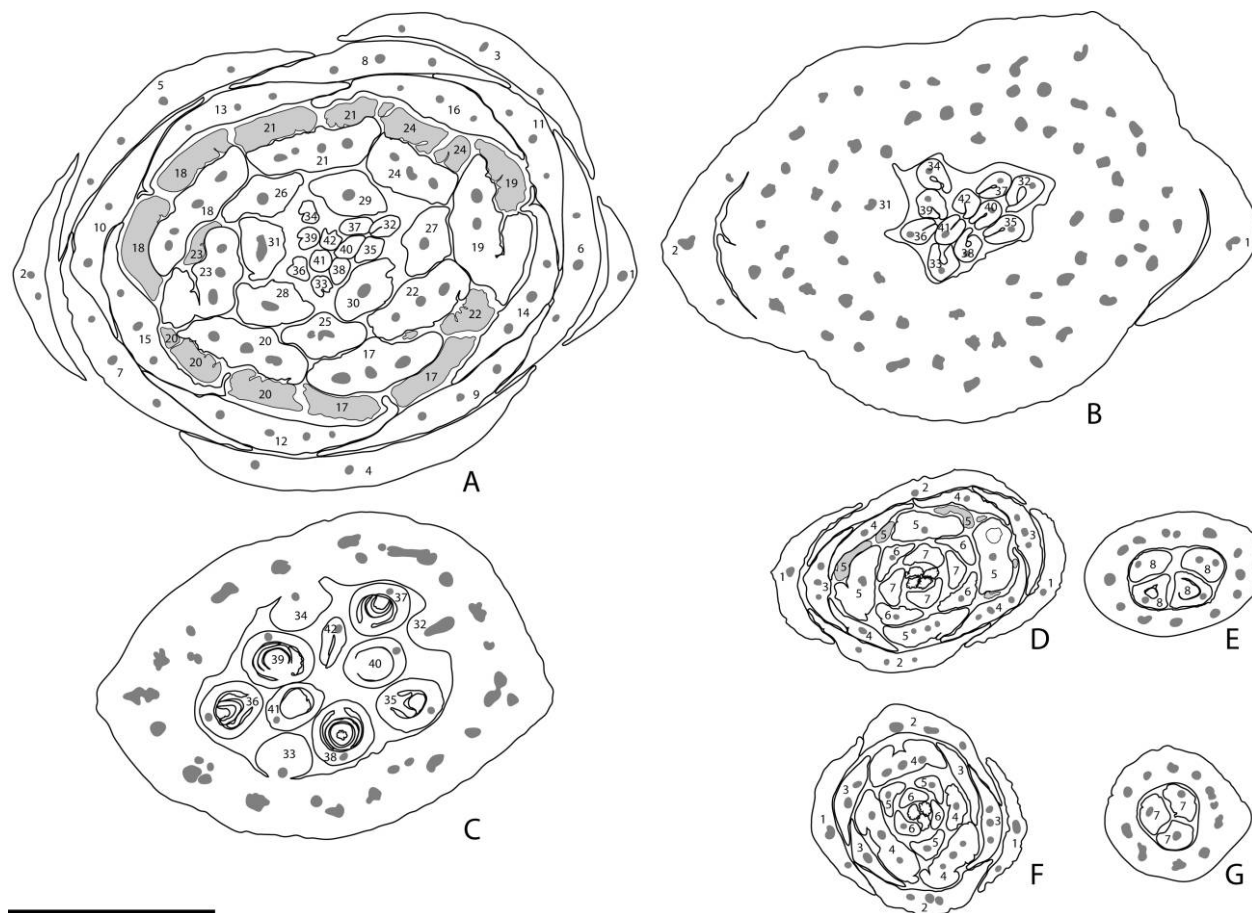


Fig. 5 Atherospermataceae. Transverse section series of late floral bud. A–C, *Daphnandra repandula*, terminal flower. A, Level of rim of floral cup. B, Level of attachment of innermost staminode. C, Level of gynoecium. D, E, *Daphnandra micrantha*, terminal flower. D, Level of rim of floral cup. E, Level of gynoecium. F, G, *Daphnandra micrantha*, lateral flower. F, Level of rim of floral cup. G, Level of gynoecium. Dark gray = vasculature; light gray = glandular appendages of stamens (and staminodes). A–C, Floral organs numbered along ontogenetic spiral. D–G, Floral organs numbered according to whorls. Scale bar = 1 mm.

stamens (whorl 6). The two outer tepal whorls are simple pairs (whorls 1 and 2); the inner four tepals and the outer four stamens are in double positions (whorls 3 and 4). The stamens of whorl 5 are a simple pair. Four cursorily studied flowers have six and eight tepals and six, 10, or 11 stamens. Two flowers have a decussate phyllotaxis with double positions in the center; tetramerous whorls of stamens are present only in the flowers with the highest number of organs (the terminal flower and one large lateral flower). The four outer tepals are always decussate. In lateral flowers with more organs (lower lateral flowers), the four inner tepals are in two double positions. The four outer stamens are in two double positions in all flowers studied. The inner stamens form a pair (upper lateral flower), two decussate pairs (lower lateral flower), or a pair followed by a tetramerous whorl (lower lateral flower) or a tetramerous whorl followed by three stamens (terminal flower).

Atherosperma (*Atherospermataceae*)

***Atherosperma moschatum*.** A male flower of a one-flowered inflorescence sectioned (fig. 7E) has eight tepals (pre-

ceded by two prophylls) and 15 stamens. Floral phyllotaxis approximately figure 3D. The organs of whorls 1–5 are decussate. However, the four tepals of whorl 3 and the four stamens of whorl 4 are in double positions. The six stamens following whorl 5 form a hexamerous whorl (whorl 6), alternating with the six organs of whorl 4 plus 5. The three inner stamens form whorl 7. In three cursorily studied flowers of three single-flowered inflorescences, each flower is preceded by two prophylls. In all three flowers, the eight tepals are decussate (whorls 1–3; whorl 3 with double positions). The number of stamens and their arrangement are variable. In one flower the 12 stamens form three tetramerous whorls. In another flower, the 14 stamens form two alternating double positions, a tetramerous whorl and a dimerous whorl. In the third flower, the 18 stamens form three decussate whorls (whorls 5 and 6 with double positions) and two tetramerous whorls.

Glossocalyx (*Siparunaceae*)

***Glossocalyx longicuspis*.** A male flower sectioned (fig. 8A–8G) has one enlarged tepal, five small tepals, and 18 stamens.

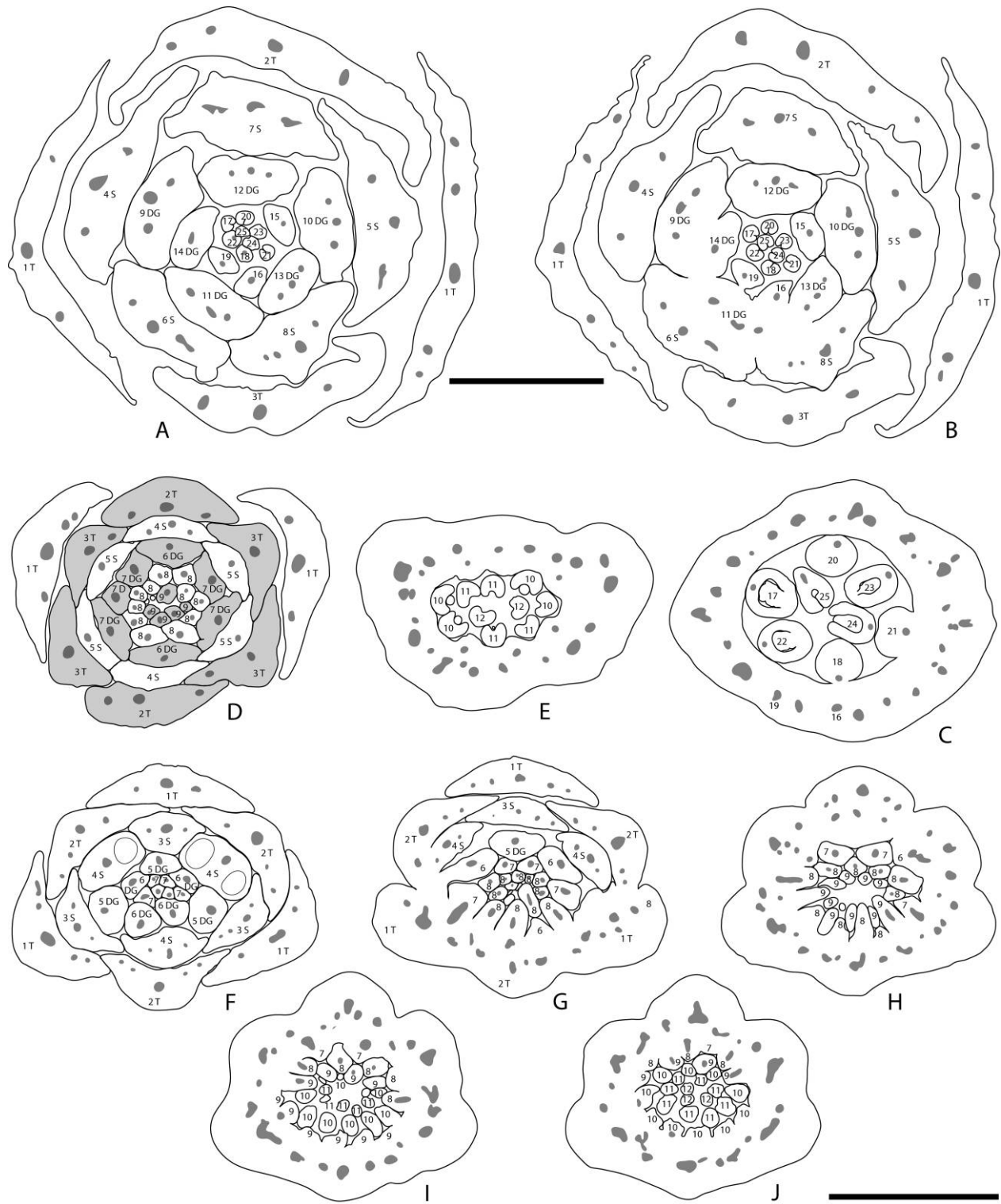


Fig. 6 Atherospermataceae. Transverse section series of floral buds. *A–C*, *Doryphora aromatica*. *A*, Level of rim of floral cup. *B*, Level of base of staminodes. *C*, Level of gynoecium. *D, E*, *Doryphora sassafras*, terminal flower. *D*, Level of rim of floral cup. *E*, Level of gynoecium. *F–J*, *Doryphora sassafras*, lateral flower. *F*, Level of rim of floral cup. *G–J*, Level of base of staminodes and carpels. Dark gray = vasculature; light gray = selected sets of organ pairs and double positions. *T* = tepal; *S* = stamen; *DG* = staminode with gland. *A–C*, Outer floral organs numbered according to whorls; inner floral organs numbered along ontogenetic spiral. *D–G*, Floral organs numbered according to whorls. Scale bars = 1 mm.

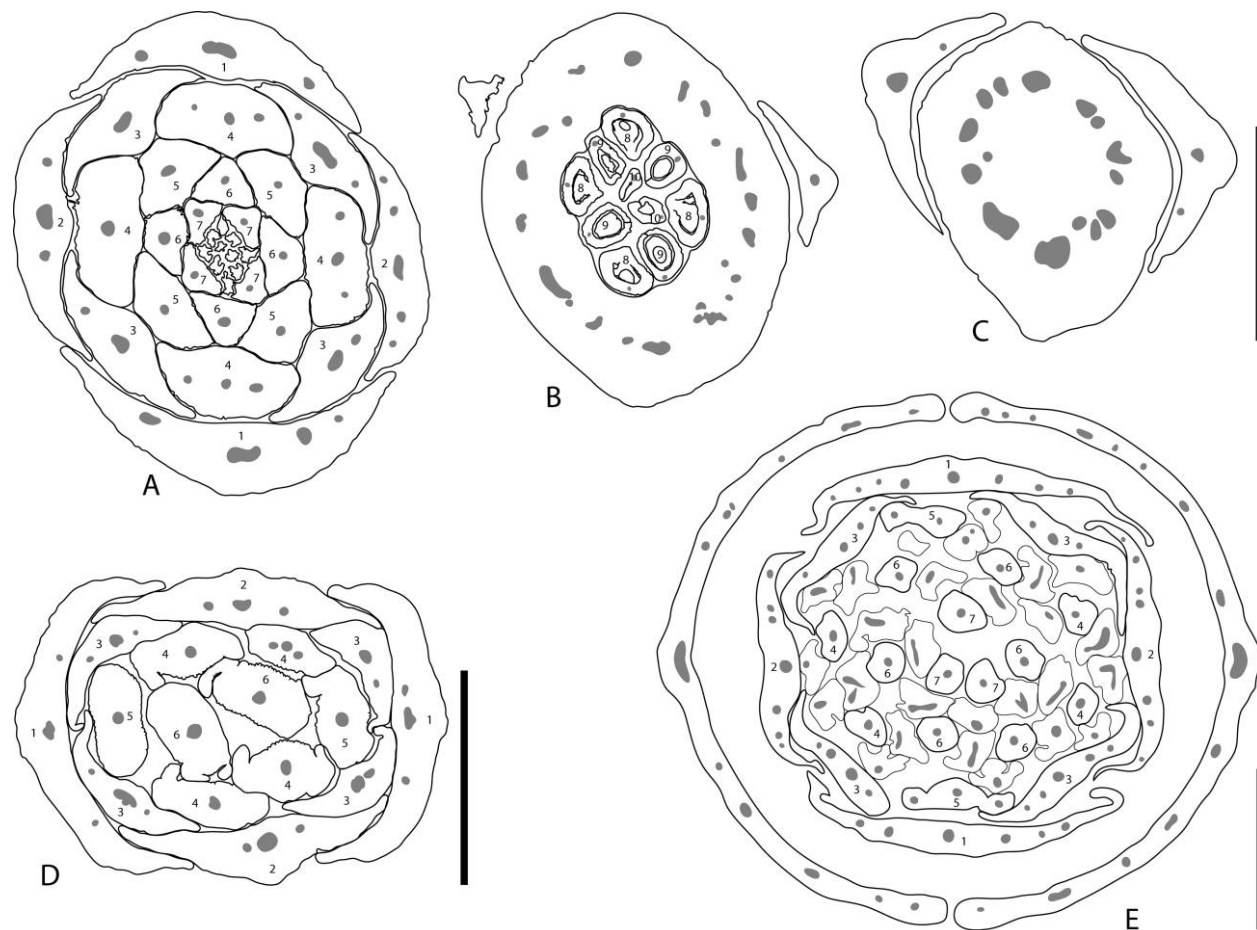


Fig. 7 Atherospermataceae. Transverse section series of late floral bud. A–C, *Dryadodaphne trachyphloia*, lateral floral bud. A, Level of rim of floral cup. B, Level of gynoecium. C, Pedicel. D, *Laurelia sempervirens*, terminal male floral bud, level of rim of floral cup. E, *Atherosperma moschatum*, male floral bud of single-flowered inflorescence, level of rim of floral cup. Gray = vasculature. Floral organs numbered according to whorls. Scale bars = 1 mm.

The tepals appear to be arranged in a whorl. The stamens show an average divergence angle of $138.4^\circ (\pm 11^\circ)$, according to a Fibonacci spiral pattern (fig. 3A; floral diagram, fig. 22E). The tepals have the shape of short knobs. They and the tip of the enlarged tepal are covered with hairs that are denser and shorter than those on the rest of the floral surface. The small tepals and the tip of the enlarged tepal stain intensely violet with ruthenium red and toluidine blue, suggesting a secretory function. The vascular trace of the enlarged tepal can be followed from its insertion on the rim of the floral cup down to the base of the peduncle, much farther down than the vascular traces of the other tepals extend before they form a stele. No floral subtending bract is found on the peduncle or at its base. A second flower from the same collection sectioned has one enlarged tepal, four small tepals, and 17 stamens. Tepal indument and histology are as in the first flower. The stamens appear to form a Fibonacci spiral pattern. Three cursorily studied flowers from the same collection have the same structure, except for one with five small tepals. It is not possible to determine the position of the studied flowers in the ramification system because of cauliflory.

Siparuna (*Siparunaceae*)

***Siparuna thecaphora*.** Two male flowers sectioned (flower 1, fig. 8H; flower 2, fig. 8I, 8J; floral diagrams, fig. 22F, 22G) have four and five tepals and six stamens. In flower 1, the tepals are decussate (whorls 1 and 2). In flower 2, they are in a pentamerous whorl (whorl 1; fig. 8I); their insertion at different levels on the floral base suggests spiral initiation. In both flowers, the stamens form three decussate pairs (whorls 3–5 in flower 1). Ten additional flowers of two inflorescences (five flowers of each; collection PKE 1202) have four or five tepals and five or six stamens. The terminal flower of a thyrsoid (with two lateral monochasia) has five tepals. For flowers of various positions in the monochasia, tepal number is not related to flower position. In the flowers of one inflorescence, the five or six stamens are decussate, but in those of the other, they form a tetramerous whorl alternating with the tepals of whorl 1 plus 2 and one or two stamens in the center.

A female flower sectioned (fig. 8K–8M) has five tepals and 13 carpels. Tepals form a pentamerous whorl (whorl 1). They are inserted at different levels on the floral cup, which suggests spiral initiation. The first nine carpels show an average divergence

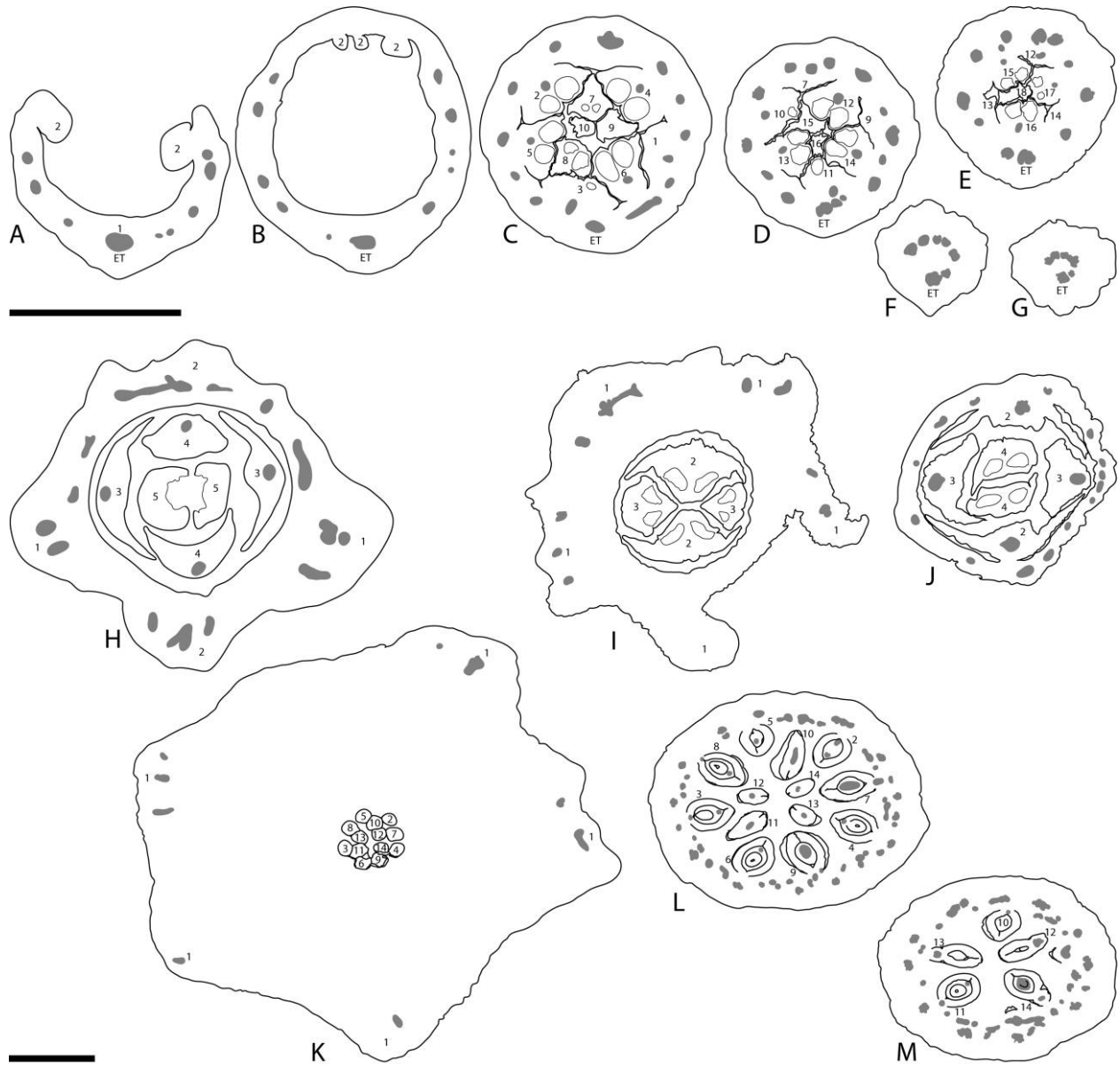


Fig. 8 Siparunaceae. Transverse section series of late floral buds. A–G, *Glossocalyx longicuspis*, male floral bud. A, Level of base of enlarged tepal and tepals. B, Level of rim of floral cup. C–E, Level of stamens. F, G, Level of pedicel. H, *Siparuna thecaophora*, first male floral bud, level of rim of floral cup. I, J, *Siparuna thecaophora*, second male floral bud. I, Level of rim of floral cup. J, Level of base of stamens. K–M, *Siparuna thecaophora*, female floral bud. K, Level of rim of floral cup. L, M, Level of gynoecium. Gray = vasculature. A–G, K–M, Outer floral organs numbered according to whorls; inner floral organs numbered along ontogenetic spiral. H–J, Floral organs numbered according to whorls. ET = dorsal bundle of enlarged tepal. Scale bars = 1 mm.

angle of $138.7^\circ (\pm 9^\circ)$, according to a Fibonacci spiral pattern (fig. 3A). The inner four carpels have more irregular positions. Carpels form series of eight and five organs. Two other sectioned flowers (collection PKE 1301) have four and six tepals and 11 carpels; the nine outermost carpels have Fibonacci spiral phyllotaxis (average divergence angles $135.1^\circ \pm 13^\circ$ and $137.9^\circ \pm 17^\circ$). Nine cursorily studied lateral flowers from three inflorescences (collection PKE 1203) have five (eight flowers) or six (one flower) tepals and nine (two flowers), 10 (six flowers), or 11 (one flower) carpels. Organ number does not

appear to depend on the position in the ramification system. Series of five carpels are common.

Peumus (*Monimioideae*, *Monimiaceae*)

***Peumus boldus*.** A lateral flower of a male botryoid sectioned (fig. 9A–9E) has 11 tepals and 36 stamens, with an average divergence angle of $137.1^\circ (\pm 11^\circ)$, according to a Fibonacci spiral pattern (fig. 3A). The floral organs form series of five organs: two series of tepals, one series including the last

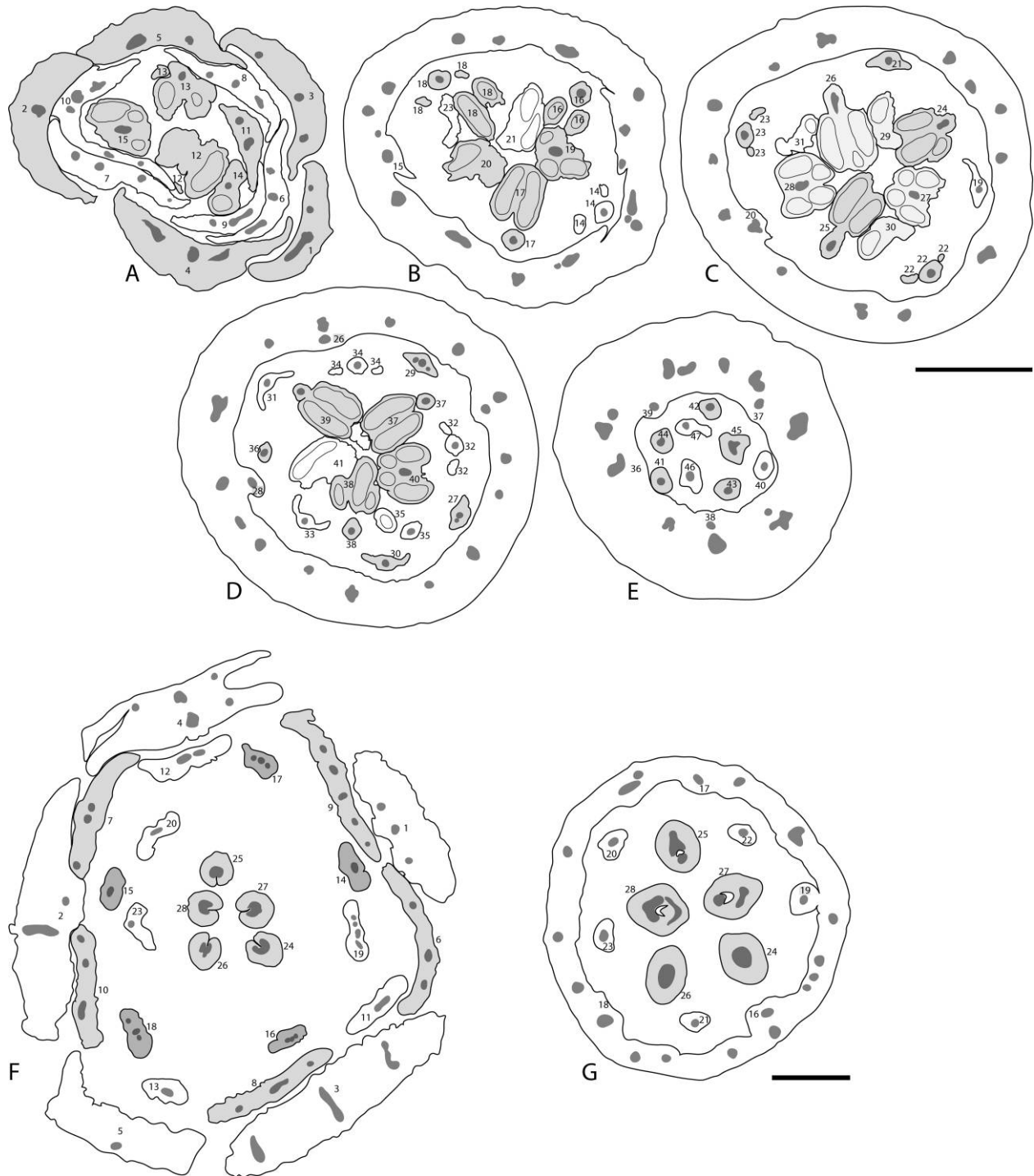


Fig. 9 Monimioideae, Monimiaceae, *Peumus boldus*. Transverse section series of late floral bud and anthetic flower. A–E, Male lateral floral bud. A, Level of rim of floral cup. B–E, Level of androecium. F, G, Female terminal anthetic flower. F, Level of rim of floral cup. G, Level of gynoecium. Dark gray = vasculature; light gray = organs forming a series. Floral organs numbered along ontogenetic spiral. Scale bars = 1 mm.

tepals and four stamens (fig. 9A), and seven series of stamens (fig. 9B–9E). Five cursorily studied flowers have 10–16 tepals and 34–43 stamens. The terminal and the lateral flower of an intact part of a botryoid do not differ from each other. Tepals form series of three, five, and eight organs (commonly five).

A terminal flower of a female botryoid sectioned (fig. 9F, 9G) has 12 tepals, 11 staminodes, and five carpels, with an average divergence angle of $137.7^\circ (\pm 12^\circ)$, according to a Fibonacci spiral pattern (fig. 3A). Tepals, staminodes, and carpels form four series of five organs (fig. 9F, 9G). Only the two

inner tepals and the outermost staminode are arranged in a series of three organs (fig. 9F). Seven cursorily studied flowers have 10–13 tepals, 10–13 staminodes, and four to six carpels. The terminal flower of a partial botryoid has more organs than two lateral flowers (13 vs. 10 and 11 tepals and six vs. four and five carpels). Staminode number does not differ between terminal and lateral flowers. Tepals form series of five and eight organs and staminodes mostly series of five organs.

Palmeria (Monimioideae, Monimiaceae)

***Palmeria gracilis*.** A probably lateral flower of a male botryoid sectioned (fig. 10A–10E) has five tepals and 27 stamens, with an average divergence angle of $136.8^\circ (\pm 19^\circ)$, according to a Fibonacci spiral pattern (fig. 3A). The tepals form a series. Three cursorily studied flowers have four, five, or six tepals and 21 or 23 stamens. The terminal flower has the smallest organ number. Floral phyllotaxis is Fibonacci spiral in all flowers. Stamens are arranged in series of eight (outer stamens) and five (inner stamens).

A probably lateral flower of a female botryoid sectioned (fig. 10F, 10G) has five tepals, one carpellode, and nine carpels. Floral organs show an average divergence angle of $135.9^\circ (\pm 13^\circ)$, according to a Fibonacci spiral pattern (fig. 3A). There is a missing position in the ontogenetic spiral (position 8, third carpel). Three cursorily studied flowers (one terminal, two lateral) have five tepals and eight, nine, or 10 carpels. The terminal flower of the three has the smallest number of carpels. Floral phyllotaxis is also Fibonacci spiral.

Tambourissa (Mollinedioideae, Monimiaceae)

***Tambourissa purpurea*.** A terminal flower of a three-flowered male botryoid sectioned (fig. 11) has 13 tepals and 34 stamens. Floral phyllotaxis approximately follows figure 3C. The tepals in whorls 1–6 are decussate, and whorls 3 and 5 have one of the two positions doubled. Phyllotaxis of the last tepals and first stamens is difficult to interpret, although it appears to follow a decussate pattern. The last tepal and the first stamen form whorl 6. Two stamens form whorl 7. Three stamens form a pair with a double position on one side (whorl 8). The four stamens of whorl 9 alternate with the stamens of whorl 8, having another double position. The next 24 stamens (whorls 10–15) form tetramerous whorls. Eight flowers cursorily studied (collection S08-01) have 23–26 stamens (five lateral flowers) or 31 and 32 stamens (three terminal flowers). Most stamens appear to be arranged in tetramerous whorls.

A female flower sectioned (fig. 12) has 29 outer sterile organs (the outer 18 of which are tepals and the inner 11 of which are secretory and vascularized and are here named carpelodes although they do not possess a locule; see “Discussion”), one carpellode with a locule, and 61 carpels. Floral phyllotaxis approximately follows figure 3E. The four outermost tepals are decussate (whorls 1 and 2). The two tepals of whorl 3 are not on the same radii as the tepals of whorls 1 and 2 but in between. The next 15 organs (whorls 4–8) are decussate. One of the positions is doubled in whorls 4, 6, and 7. Phyllotaxis of the carpelodes and first carpels is difficult to interpret, although it appears to follow a decussate pattern.

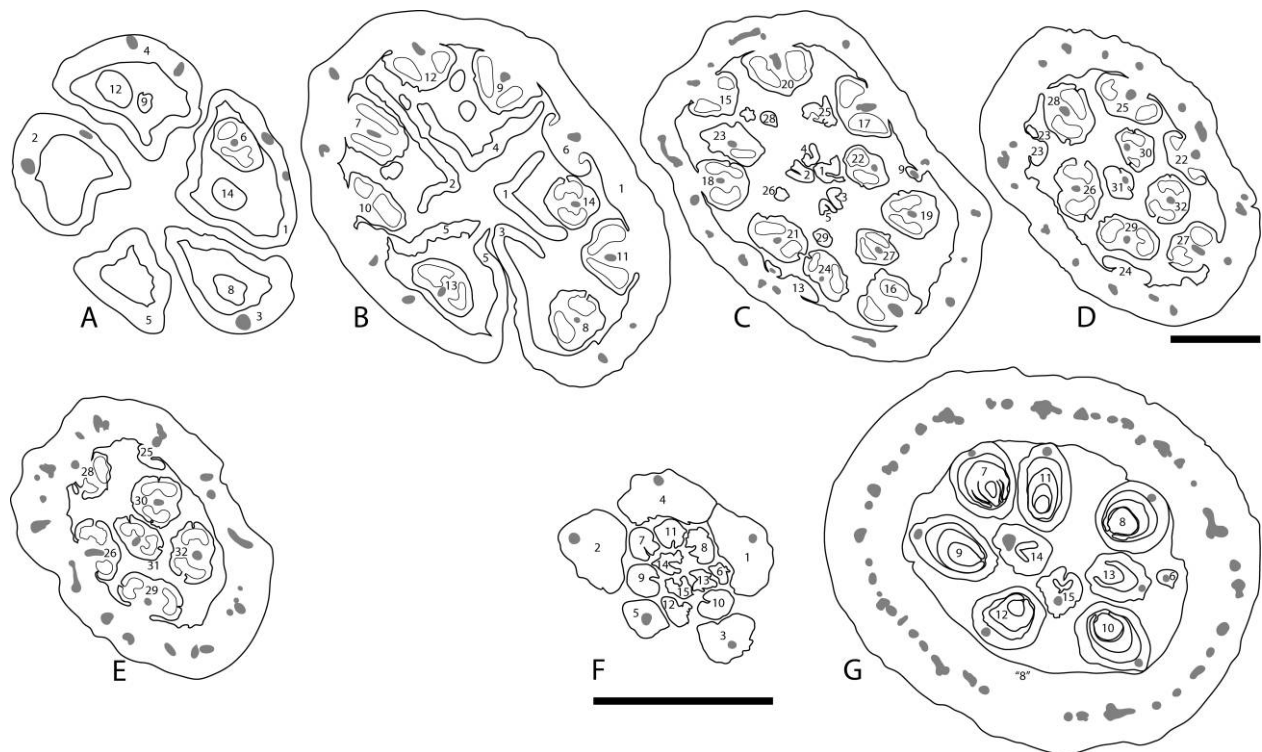


Fig. 10 Monimioideae, Monimiaceae, *Palmeria gracilis*. Transverse section series of late lateral floral buds. A–E, Male floral bud. A, B, Level of rim of floral cup. C–E, Level of androecium. F, G, Female floral bud. F, Level of rim of floral cup. G, Level of gynoecium. Gray = vasculature. Floral organs numbered along ontogenetic spiral. Scale bars = 1 mm.

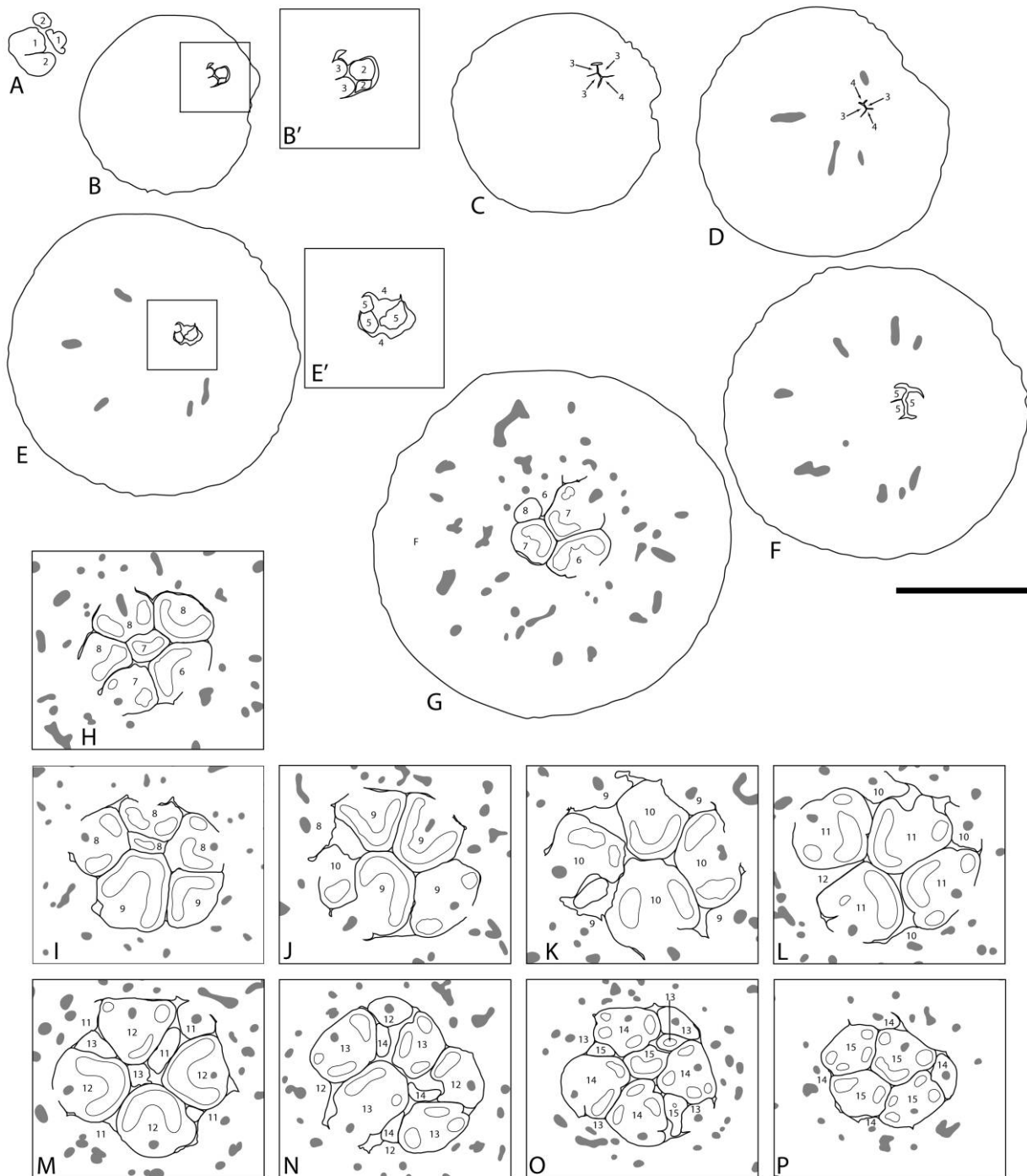


Fig. 11 Mollinedioideae, Monimiaceae, *Tambourissa purpurea*. Transverse section series of late male terminal floral bud. A–F, Level of perianth. B', Close-up of B. E', Close-up of E. G–P, Level of androecium. Gray = vasculature. Floral organs numbered according to whorls. Scale bar = 0.5 mm for B', E'; 1 mm for A–P.

Whorl 8 has five carpellobes in a double and a triple position. Whorl 9 has five organs (four carpellobes and a carpel), two carpellobes and the carpel in a triple position, and two carpellobes in a double position. Whorl 10 also has five organs (two carpellobes without locule, the carpellobes with locule, and

two carpels), three of which are in a triple position (two carpels and a carpellobes); the other two alternate with two organs of whorl 9. The six carpels of whorl 11 alternate with the organs of whorl 10 and form one double position. The next 51 carpels form nine 6-merous whorls (whorls 12–19),

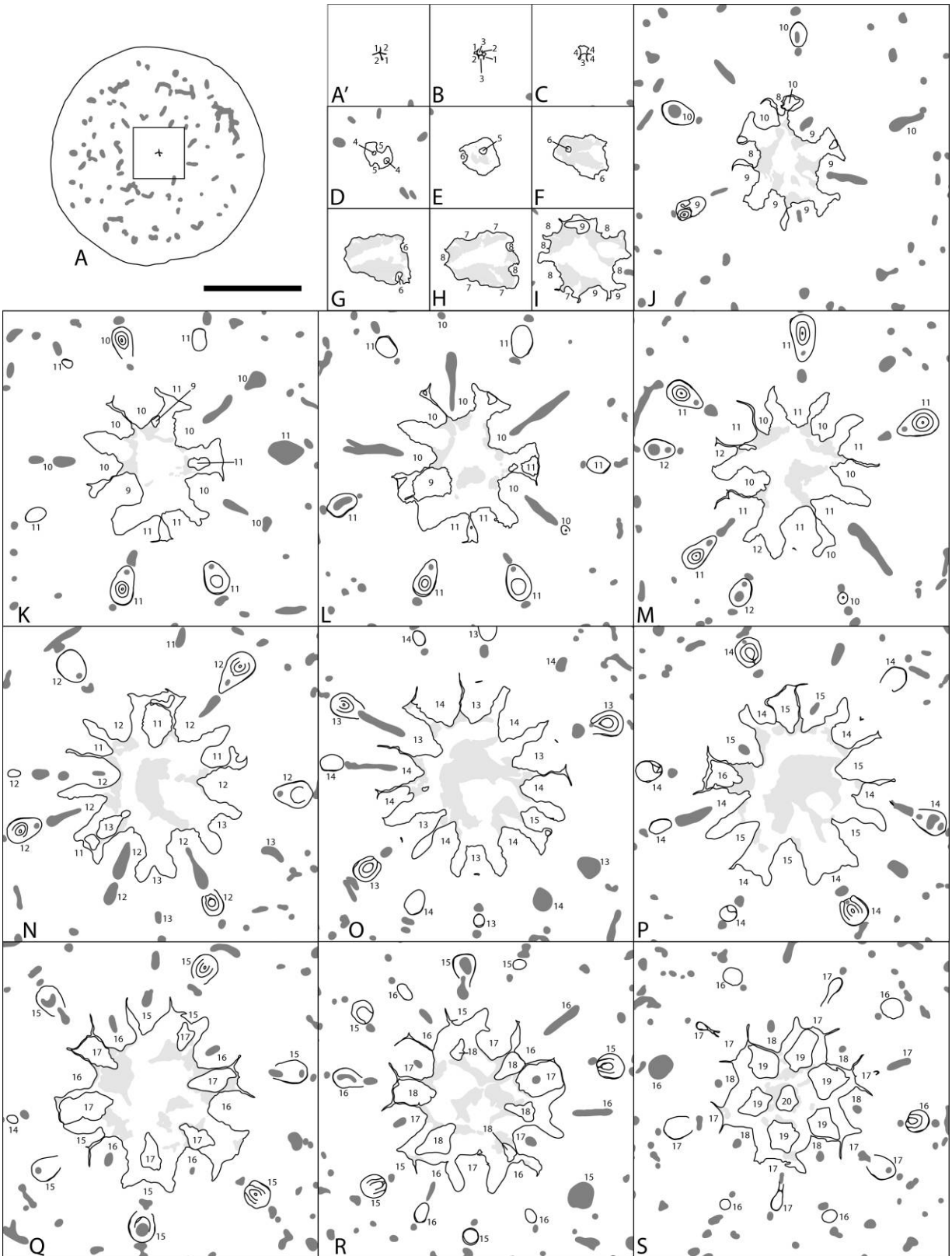


Fig. 12 Mollinedioideae, Monimiaceae, *Tambourissa purpurea*. Transverse section series of late female floral bud. A–G, Level of perianth. H, I, Level of carpelloids. J, Level of carpels and carpelloids. K–S, Level of carpels. A', Close-up of A. Dark gray = vasculature; light gray = secretion. Floral organs numbered according to whorls. Scale bar = 2 mm for A, 1 mm for A'–S.

three (whorls 12, 14, and 15) with one double position. The double positions of whorls 12 and 14 are on the same orthostichy. One carpel is in the center of the flower (whorl 20). Three flowers cursorily studied (collection S08-01) have 61, 67, and 71 carpels. Twelve to 13 orthostichies are present, which suggests arrangement in alternating hexamerous whorls. In two flowers, the number of orthostichies first increases and then decreases toward the center of the flower.

Tambourissa comorensis. A fragment of a female flower sectioned shows alternating sets of parastichies of similar steepness, although there are irregularities. This suggests whorled or irregular phyllotaxis.

Tambourissa ficus. A fragment of a female flower sectioned shows no parastichies, which suggests irregular phyllotaxis.

Xymalos (Mollinedioideae, Monimiaceae)

Xymalos monospora. A terminal flower of a male thyrsoid with accessory flowers sectioned (fig. 13A, 13B) has three tepals and seven stamens (the first stamen with only one theca). The four outermost organs form whorls 1 and 2. The seven stamens show an average divergence angle of $138.9^\circ (\pm 17^\circ)$, according to a Fibonacci spiral pattern (fig. 3A). The 17 cursorily studied flowers of the distal portion of a male inflorescence (flowers of all three ramification orders and accessory flowers of the second order) have one to five (or zero to four) tepals and three to 15 stamens. In lateral flowers there is always a tepal-like organ in median abaxial position, which may represent the subtending bract of the flower. Some flowers may be atepalous if this interpretation is correct. The highest organ number is found in the primary flowers of the dichasia; the smallest organ number is found in accessory flowers. The terminal flower has four tepals and eight stamens. Most flowers have spiral phyllotaxis, even when organ number is very low, but an irregularly whorled pattern (tetramerous) is present in the outer stamens of flowers with an even number of tepals.

Two lateral flowers of a female botryoid sectioned (flower 1, fig. 13C; flower 2, fig. 13D) have three and four tepals and

one carpel. In flower 1, the tepals form a trimerous whorl (whorl 1). In flower 2, the tepals are decussate (whorls 1 and 2). Ten cursorily studied flowers have two to six tepals (mostly four) and one carpel. Tepals are decussate. Three terminal flowers have four tepals and two preceding empty bracts.

Hedycarya (Mollinedioideae, Monimiaceae)

Hedycarya angustifolia. A probably lateral flower of a male botryoid sectioned (fig. 14A; floral diagram, fig. 22H) has eight tepals and 27 stamens. Floral phyllotaxis approximately follows figure 3C. The tepals form two simple pairs (whorls 1 and 2) and a pair of two double positions (whorl 3). The outer eight stamens form a whorl of four double positions (whorl 4). The next eight stamens alternate with the outer ones and thus form an octomerous whorl (whorl 5), followed by a heptamerous whorl (whorl 6), in which most stamens alternate with those of whorl 5. Four stamens are in the center of the flower (whorl 7). A terminal and two lateral cursorily studied flowers have eight tepals and 29–32 stamens. In all flowers the outer stamens form a whorl of four double positions (in one flower, one double position is replaced by a single position). The whorl of double positions is followed by a whorl of seven, eight, or nine organs: organ number then decreases toward the center of the flower to 7-, 6-, or 4-merous whorls. Terminal and lateral flowers do not obviously differ in organ number.

A female flower of a one-flowered inflorescence sectioned (fig. 14B, 14C) has nine tepals, nine carpelodes, and 18 carpels, with an average divergence angle of $138.5^\circ (\pm 18^\circ)$, according to a Fibonacci spiral pattern (fig. 3A). Along the ontogenetic spiral, the first two carpels are followed by the last carpelode and only then by the remaining carpels. Another female flower of a single-flowered inflorescence sectioned (fig. 14D, 14E) has eight tepals, 11 carpelodes, and 18 carpels. Floral phyllotaxis follows figure 3E. The tepals form two simple pairs (whorls 1 and 2) and a pair of double positions (whorl 3). The outer eight carpelodes form two alternating pairs of double positions (whorls 4 and 5). The next seven carpelodes form two tetramerous whorls (whorls 6 and 7); there is a carpelode missing in whorl 6. The 16 outer carpels

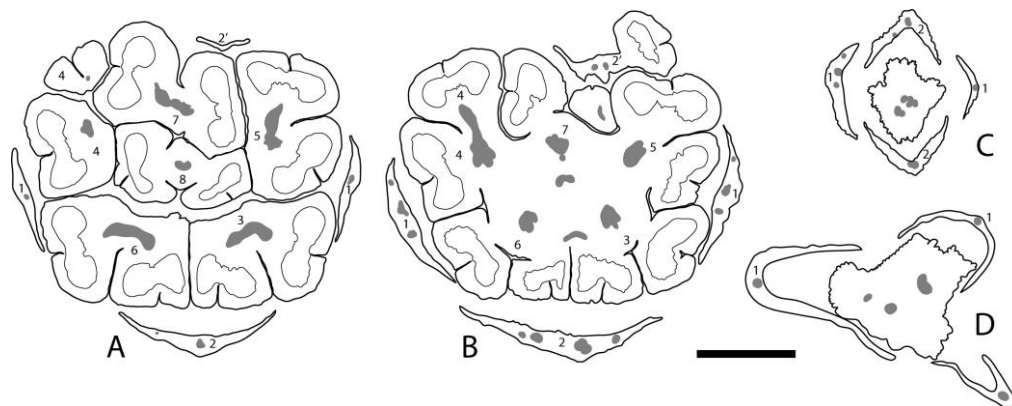


Fig. 13 Mollinedioideae, Monimiaceae, *Xymalos monospora*. Transverse section series of late floral buds. A, B, Terminal male floral bud, level of androecium. C, First female floral bud, level of rim of floral cup. D, Second female flower, level of rim of floral cup. Gray = vasculature. A, B, Outer floral organs numbered according to whorls; inner floral organs numbered along ontogenetic spiral. C, D, Floral organs numbered according to whorls. Scale bar = 1 mm.

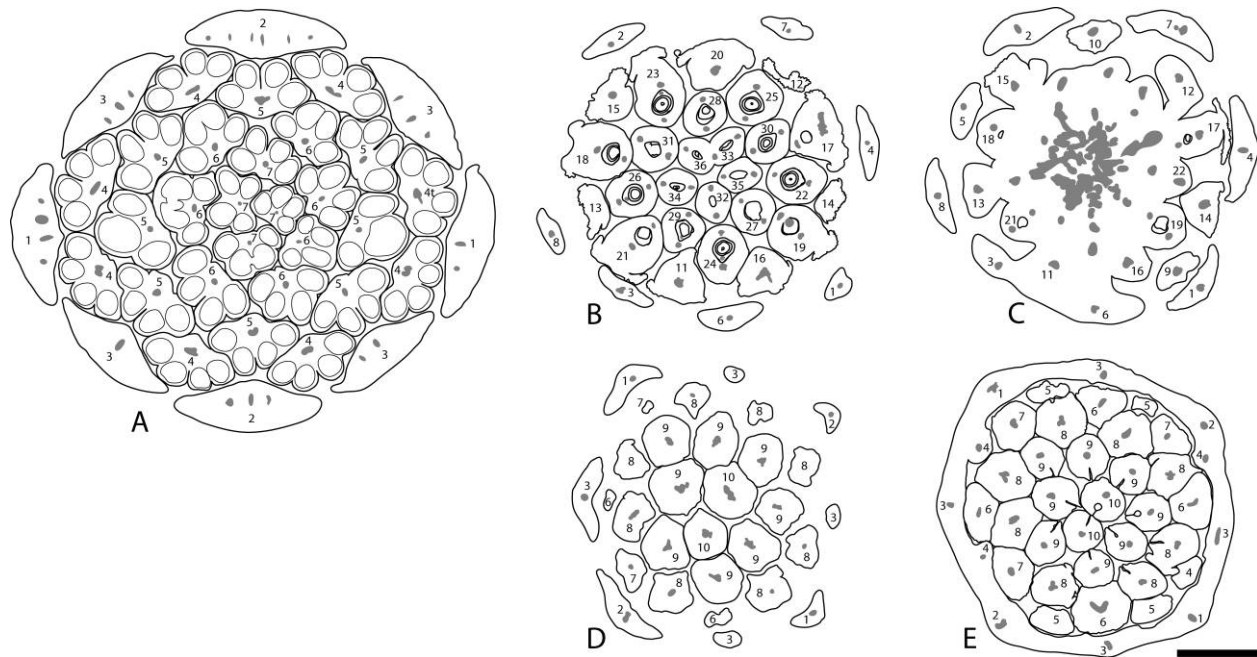


Fig. 14 Mollinedioideae, Monimiaceae, *Hedycarya angustifolia*. Transverse section series of late floral buds and anthetic flower. A, Lateral male floral bud, level of base of inner stamens. B, C, First female flower of single-flowered inflorescence. B, Level of base of inner carpels. C, Level of base of tepals. D, E, Second female flower of single-flowered inflorescence. D, Level of base of tepals. E, Level of base of outer carpels. Gray = vasculature. A, D, E, Floral organs numbered according to whorls. B, C, Floral organs numbered along ontogenetic spiral. Scale bar = 1 mm.

are arranged in two octomerous whorls (whorls 8 and 9). Two carpels are in the center of the flower (whorl 10). Five cursorily studied flowers have six (one flower) or eight (four flowers) tepals and 18–51 carpellobes and carpels. In the two flowers with the highest organ number (45 and 51 carpels and carpellobes), Fibonacci spiral phyllotaxis appears to be present, in contrast to 4- to 9-merous whorls in the other three flowers. In flowers with whorled phyllotaxis, the number of carpellobes and carpels per whorl increases (to seven to nine) and then decreases (to five or four) toward the center of the flower.

Levieria (Mollinedioideae, Monimiaceae)

***Levieria acuminata*.** A terminal flower of a male botryoid sectioned (fig. 15A) has seven tepals and 28 stamens. The outer four tepals are decussate (whorls 1 and 2). The three inner tepals and the stamens show an average divergence angle of $136.9^\circ (\pm 20^\circ)$, according to a Fibonacci spiral pattern (fig. 3A; floral diagram, fig. 22I). A lateral flower sectioned (fig. 15B, 15C) has eight tepals and 16 stamens. Floral phyllotaxis follows figure 3E (floral diagram, fig. 22J). The tepals (whorls 1–3) and the outer five stamens (whorls 4 and 5) are decussate. The two tepals of whorl 1 are in lateral position, as expected in the absence of prophylls. The positions of whorl 3 and one position of whorl 4 are doubled. The 11 inner stamens form two tetramerous whorls (whorls 6 and 7) and a group of three stamens in the center of the flower (whorl 8). Five cursorily studied flowers have five to eight tepals and 14–32 stamens. In the four lateral flowers studied, the two outermost tepals are in lateral position, as would be expected in the

absence of prophylls. Spiral phyllotaxis is present in the two flowers with the highest number of stamens (a terminal and a large lateral flower with 30 and 32 stamens). In both flowers, the outer four tepals are decussate, and the inner three tepals and the stamens are spiral. Whorled phyllotaxis occurs in the flowers with the smallest number of stamens (14, 16, and 18). The tepals and outer stamens are decussate. The inner three or four tepals and the outer four stamens are in double positions. The subsequent stamens form a 6- or 8-merous whorl and the inner stamens a 3-, 4-, or 6-merous whorl.

A terminal flower of a female botryoid sectioned (fig. 15D, 15E) has six tepals and 23 carpels. Floral phyllotaxis approximately follows figure 3E (floral diagram, fig. 22K). The six tepals (whorls 1 and 2) and the outer eight carpels (whorls 3 and 4) are decussate, and the positions of whorls 2, 3, and 4 are doubled. The next four carpels (whorl 5) form a tetramerous whorl, followed by a distorted tetramerous whorl (whorl 6) more or less alternating with whorl 5. The next six carpels form two trimerous whorls (whorls 7 and 8). A single carpel is present in whorl 9. Five cursorily studied flowers (a terminal and two lateral flowers and two detached flowers) have four to six tepals and 13–22 carpels (the terminal flower has four tepals and 21 carpels; the two lateral flowers have four and five tepals and 13 and 19 carpels). The tepals form two decussate pairs, often with one or two of the organ positions of the inner whorl doubled. In all flowers studied, the outer carpels are arranged in the same decussate pattern as the tepals, including double positions. In the inner carpel whorls organ number first increases (to four, five, seven, or nine) and then decreases (to three, occasionally five).

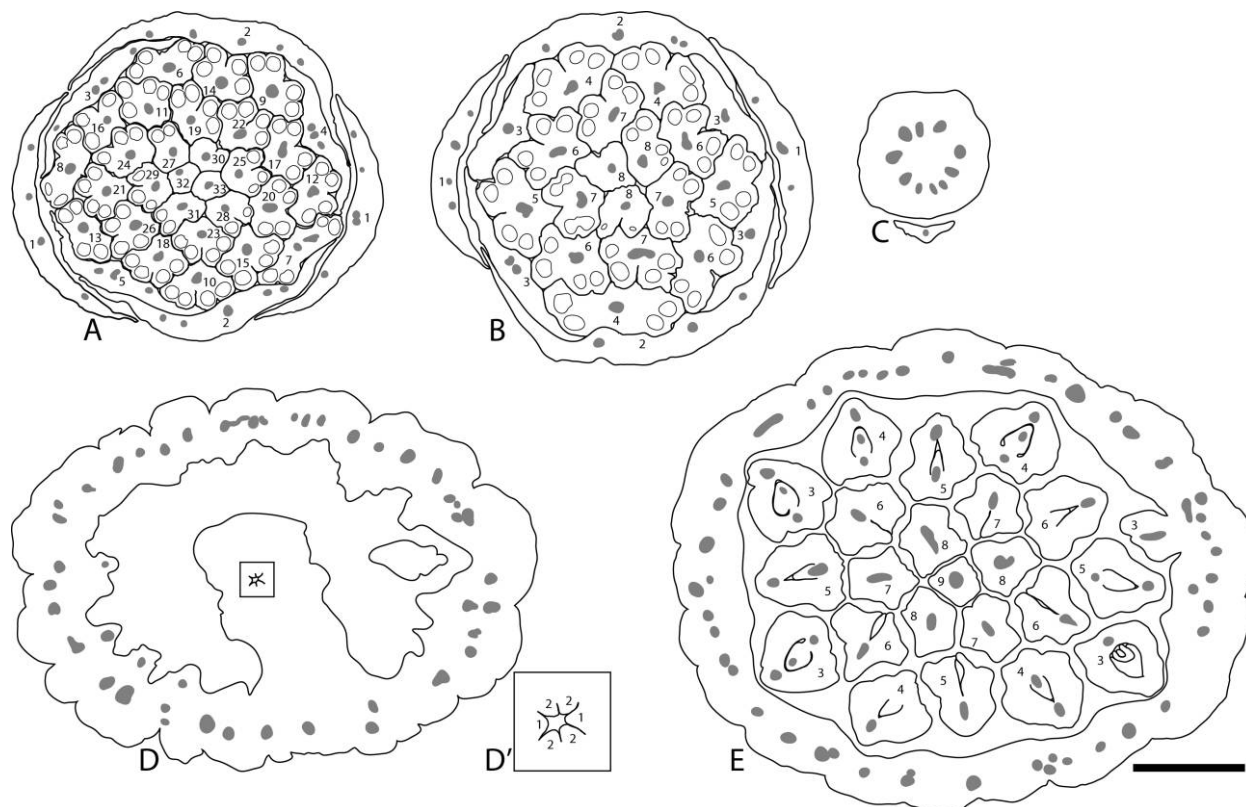


Fig. 15 Mollinedioideae, Monimiaceae, *Levieria acuminata*. Transverse section series of late floral buds. A, Terminal male floral bud, level of base of inner stamens. B, C, Lateral male floral bud. B, Level of base of inner stamens. C, Pedicel. D, E, Terminal female floral bud. D, D', Level of tepals. E, Level of gynoecium. Gray = vasculature. A, Outer floral organs numbered according to whorls; inner floral organs numbered along ontogenetic spiral. B–E, Floral organs numbered according to whorls. Scale bar = 1 mm for A–E, 0.33 mm for D'.

Kibara (Mollinedioideae, Monimiaceae)

***Kibara coriacea*.** Six sectioned lateral flowers of male thyrsoids (with accessory dichasia) studied have four or six tepals and four, six, seven, or eight stamens, all decussate (fig. 3B1; fig. 16A, 16B). The odd stamen occupies the center of the flower. All six flowers of a thyrsoid cursorily studied (collection PKE 9325) have a decussate phyllotaxis; the terminal flower has 10 tepals and 10 stamens, and the other flowers have eight tepals and six or eight stamens.

***Kibara macrophylla*.** A probably lateral flower of a female thyrsoid sectioned (fig. 16C–16E) has 10 tepals and 22 carpels. Floral phyllotaxis approximately follows figure 3E. Phyllotaxis of the tepals (whorls 1–5) and the outer 10 carpels (whorls 6–8) is decussate. The eight outer carpels (whorls 6 and 7) are in double positions. The inner 12 carpels form three tetramerous whorls (whorls 8–10). Five cursorily studied flowers of two dichasia have 10 or 12 tepals and 17 carpels (terminal flowers) and 10 or 12 tepals and 17, 19, or 20 carpels (lateral flowers). In all flowers, the tepals are decussate. Phyllotaxis of the 10 outer carpels is as in the sectioned flower. The inner carpels appear to form one or two whorls with five and two organs in the terminal flowers, with eight and two organs in one lateral flower and one whorl with seven organs in the two other lateral flowers. A female flower depicted with

the SEM shows the arrangement of the carpels in the floral cup with a hyperstigma (fig. 21D).

Wilkiea (Mollinedioideae, Monimiaceae)

***Wilkiea angustifolia*.** Inflorescences of the studied collection do not terminate in a flower but tend to revert to vegetative growth. A male flower sectioned (fig. 17A, 17B) has six tepals and four stamens. Floral phyllotaxis is decussate (fig. 3B1). Three cursorily studied male flowers do not differ from the sectioned flower.

A female flower sectioned (fig. 17C–17H) has 22 tepals and 12 carpels. Floral phyllotaxis approximately follows figure 3E. The tepals form five decussate pairs (whorls 1–5) and three pairs of double positions (whorls 6–8). The outer eight carpels also form two pairs of double positions (whorls 9 and 10). Thus, instead of a transition to a tetramerous whorl after the first whorl with double positions (whorl 6), there is a four-fold repetition of double positions. Only the innermost four carpels (whorl 11) form a tetramerous whorl. Five cursorily studied flowers have 14 (one flower), 18 (three flowers), and 19 (one flower) tepals and 12 (two flowers), 15 (two flowers), and 17 (one flower) carpels. The outer tepals form five decussate pairs and probably a pair of double positions. The inner tepals appear to be arranged in one or two pairs of double

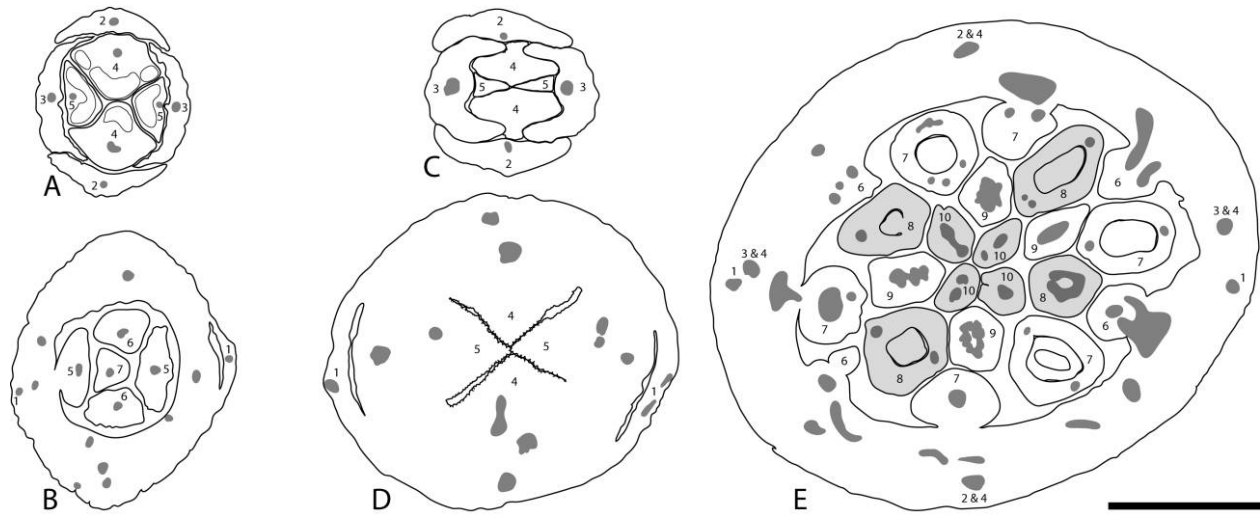


Fig. 16 Mollinedioideae, Monimiaceae. Transverse section series of late floral buds. *A, B, Kibara coriacea*, lateral male floral bud. *A*, Level of rim of floral cup. *B*, Level of androecium. *C–E, Kibara macrophylla*, lateral floral bud. *C, D*, Level of base of tepals. *E*, Level of gynoecium. Dark gray = vasculature; light gray = selected whorls of carpels. Floral organs numbered according to whorls. Scale bar = 1 mm.

(rarely triple) positions. The carpels of the two flowers with 12 carpels appear to be arranged as in the sectioned flower. The outer carpels of the flower with 17 carpels appear to form two decussate pairs of two and three or a 10-merous whorl; the inner carpels appear to form a 6-merous whorl, and there is a single carpel in the center of the flower.

***Wilkiea huegeliana*.** A lateral flower of a male botryoid sectioned (fig. 18A–18C) has six tepals and seven stamens.

Floral phyllotaxis is decussate (fig. 3B1), including the three stamens in the center of the flower (whorl 6) that form a pair in which one of the positions is doubled. Another male flower sectioned (fig. 18D–18F) has six tepals and 10 stamens. Floral phyllotaxis follows figure 3C (floral diagram, fig. 22L). The tepals (whorls 1–3) and the four outer stamens (whorl 4) are decussate, with the stamens in double positions. The inner six stamens form a tetramerous whorl (whorl 5) and a dimerous

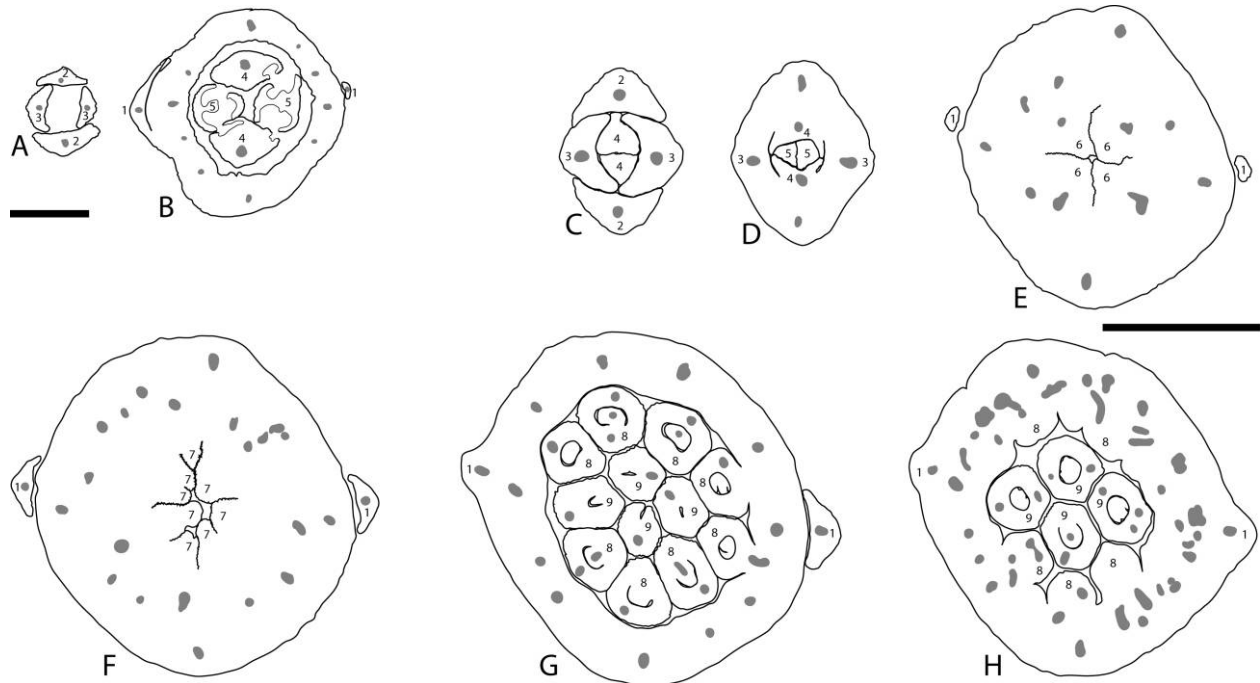


Fig. 17 Mollinedioideae, Monimiaceae, *Wilkiea angustifolia*. Transverse section series of anthetic flowers. *A, B*, Male flower. *A*, Level of rim of floral cup. *B*, Level of androecium. *C–H*, Female flower. *C–E*, Level of tepals. *G, H*, Level of gynoecium. Gray = vasculature. Floral organs numbered according to whorls. Scale bar = 1 mm.

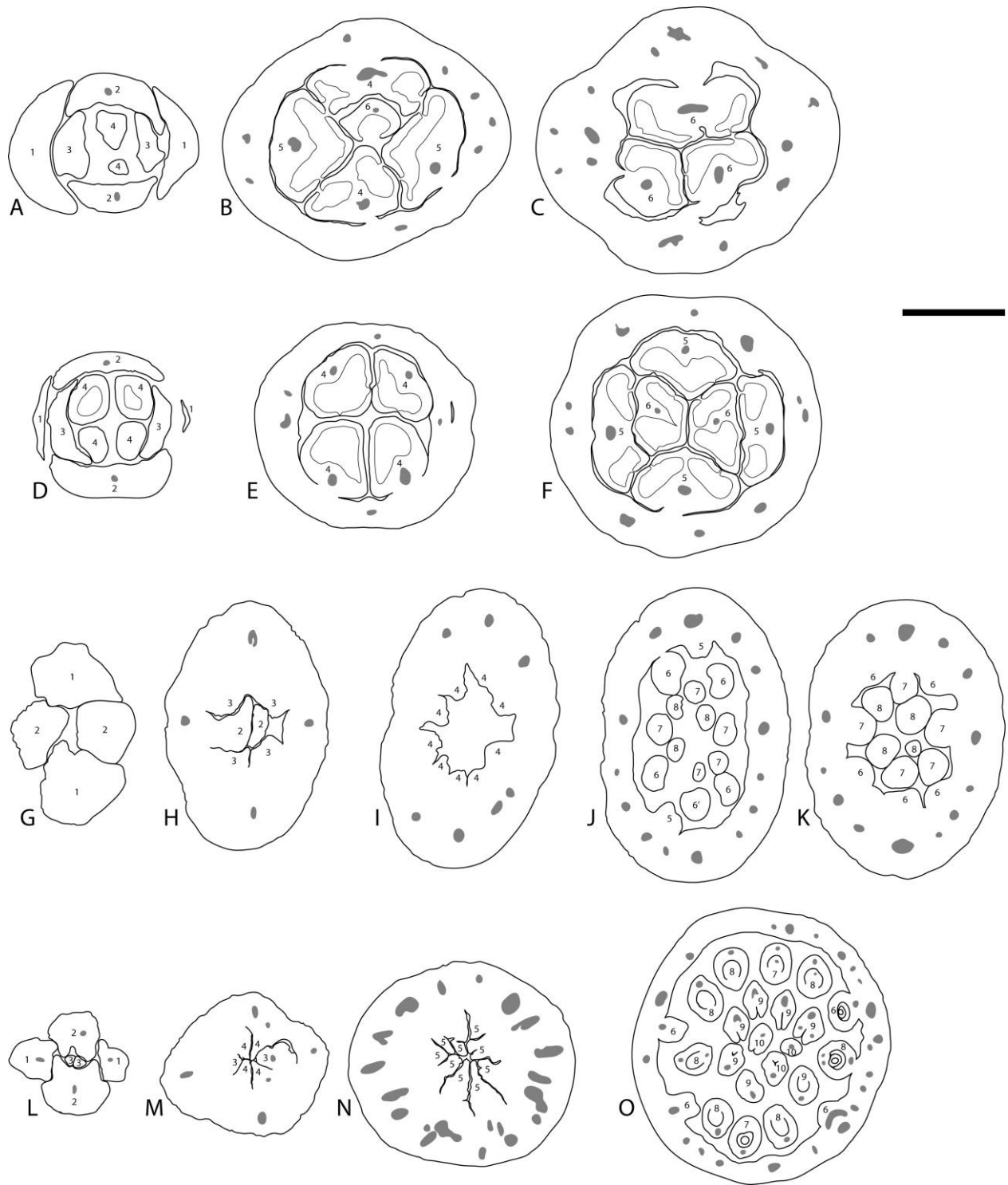


Fig. 18 Mollinedioideae, Monimiaceae, *Wilkiea huegeliana*. Transverse section series of late floral bud and anthetic flowers. A–C, Lateral male flower. A, Level of rim of floral cup. B, C, Level of androecium. D–F, Terminal male flower. D, Level of rim of floral cup. E, F, Level of androecium. G–K, Lateral female flower bud. G–I, Level of tepals. J, Level of gynoecium. L–O, Probably terminal female flower. L, M, Level of tepals. O, Level of gynoecium. Gray = vasculature. Floral organs numbered according to whorls. Scale bar = 1 mm.

whorl (whorl 6). Nine other cursorily studied flowers have four or six tepals and six, seven, eight, or 10 stamens. Organ number per flower tends to decrease in the distal portion of the inflorescence (and even the terminal flower has only four tepals and six stamens). In most flowers, floral organs are decussate, with occasionally a whorl of three stamens in the center of the flower. Only in the flower with 10 stamens are there two double positions of stamens followed by a tetramerous whorl and two stamens in the center of the flower (floral diagram, fig. 22M).

A lateral female flower of a botryoid sectioned (fig. 18G–18K) has 17 tepals and 16 carpels. The eight outer tepals are decussate (whorls 1–3; whorl 3 with double positions). The subsequent nine tepals (whorl 4) form a whorl with three double positions and one triple position. Thus, instead of forming a simple tetramerous whorl, the occurrence of multiple positions is repeated. The outer seven carpels appear to form a decussate pattern; the two outermost carpels (whorl 5) form a pair, which is followed by a double position (whorl 6; fig. 18J). The nine inner carpels form penta- and tetramerous whorls (whorls 7 and 8; see fig. 18J, 18K). Another female flower sectioned (fig. 18L–18O) has 19 tepals and 23 carpels. The 10 outer carpels form three decussate pairs (whorls 1–3) and a pair of double positions (whorl 4). The subsequent 10 tepals form a whorl with three double positions and one triple position (whorl 5). Carpel phyllotaxis appears to approximately follow figure 3D (floral diagram, fig. 22N). The outer four carpels (whorl 6) form two double positions, which are followed by two simple positions (whorl 7) and a 7-merous whorl (whorl 8). This is followed by another 7-merous whorl (whorl 9) and two carpels in the center of the flower (whorl 10). Seventeen cursorily studied flowers (six of which are from one botryoid) have 18–20 tepals and 18–36 carpels (the terminal flower has 20 tepals and 35 carpels). Tepals form two or three simple pairs, one pair of double positions, and a whorl of four double and triple positions. Carpels form two decussate pairs of double or triple positions, followed by 4-, 6-, 8-, or 12-merous whorls.

Wilkiea longipes. A female flower depicted with the SEM shows decussate phyllotaxis of the tepals (fig. 21C).

Austromatthaea (Mollinedioideae, Monimiaceae)

Austromatthaea elegans. A probably lateral flower of a male thyrsoid sectioned (fig. 19) has four tepals and 31 stamens. Floral phyllotaxis approximately follows figure 3F (floral diagram, fig. 22O). The four tepals form two decussate pairs (whorls 1 and 2). Stamens form multiple positions in a decussate pattern: four stamens in a sector (whorl 3), three stamens (whorls 4 and 5), and two stamens (whorls 6 and 7). Three stamens are in the center of the flower (whorl 8). Seven cursorily studied flowers (four loose flowers from collection PKE 4196 and three from a three-flowered thyrsoid from collection PKE 9030) have four tepals and 27 (one lateral flower), 28 (three loose flowers), 29 (one lateral flower, one loose flower), and 32 (terminal flower) stamens. Floral phyllotaxis is the same in all of them, except in whorls 7 and 8, in which the stamens form either simple or double positions.

A postanthetic female flower cursorily studied has four tepals and ~230 carpels. Parastichies are not present, which indicates irregular phyllotaxis.

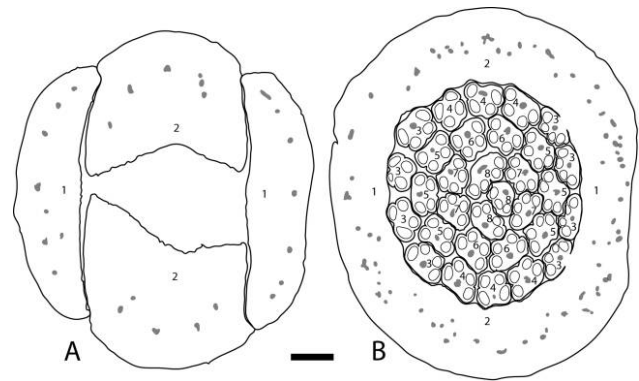


Fig. 19 Mollinedioideae, Monimiaceae, *Austromatthaea elegans*. Transverse section series of late probably lateral male floral bud. A, Level of base of tepals. B, Level of base of outer stamens. Gray = vasculature. Floral organs numbered according to whorls. Scale bar = 1 mm.

Stegantthera (Mollinedioideae, Monimiaceae)

Stegantthera ilicifolia. Three male flowers sectioned (collections PKE 4070, 4071, 4074; fig. 20A, 20B) have four tepals and two or four stamens. Floral phyllotaxis is decussate (fig. 3B1). In a fourth flower (collection PKE 4051), the stamens form a trimerous whorl with a stamen in the center. Two cursorily studied flowers (a terminal and a lateral flower of collection PKE 4074) both have four tepals and eight stamens, all decussate.

A lateral flower of a three-flowered female botryoid sectioned (fig. 20C, 20D) has four tepals and 12 carpels. Floral phyllotaxis approximately follows figure 1C. The four tepals (whorls 1 and 2) and the eight outer carpels (whorls 3 and 4) are decussate. The organ positions of whorls 3 and 4 are doubled. The four inner carpels (whorl 5) form a whorl. Three cursorily studied flowers have four tepals and 11, 15, and 16 carpels. Floral phyllotaxis is similar to that of the sectioned flower, although the number of carpels of whorls 3 and 5 differs. In the flowers with 15 and 16 carpels, the organs of whorl 4 are in triple positions, and there is a whorl of five or six carpels in the center of the flower. In the flower with 11 carpels, one of the positions of whorl 3 is single, and a whorl of four carpels is in the center. Eight cursorily studied fruits (two of which are part of an infructescence) have six to 15 carpels (fertilized or not). The terminal fruit has 15 carpels. The lateral fruit has 12 carpels.

Discussion

Diversity of Floral Phyllotaxis Patterns

Spiral floral phyllotaxis. Completely spiral floral phyllotaxis occurs (perhaps with the exception of Siparunaceae) at least partly in all families (and subfamilies) studied: Gomortegaceae, Atherospermataceae (*Daphnandra repandula*), Monimiaceae (all), Mollinedioideae (*Hortonia* [Endress 1980a], some female flowers of *Hedycarya angustifolia* [this study]). In all cases the flowers are Fibonacci spiral; Lucas spiral flowers were not found. In spiral flowers, the change from vegetative

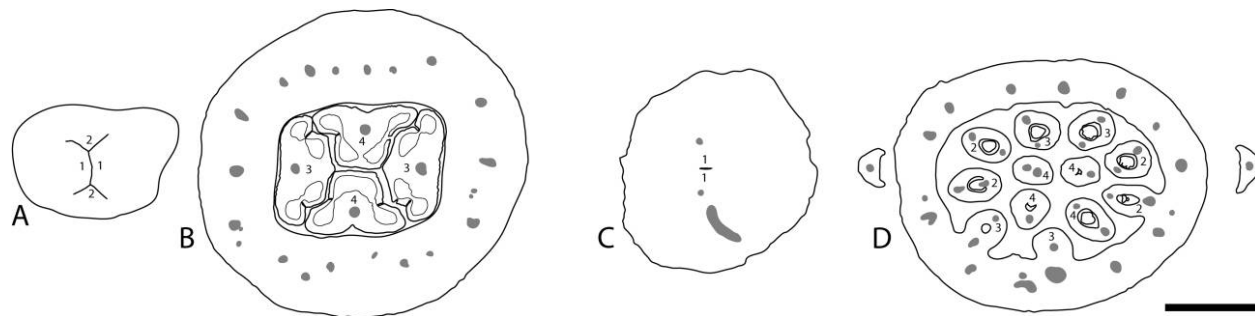


Fig. 20 Mollinedioideae, Monimiaceae, *Steganthera ilicifolia*. Transverse section series of flower and late floral bud. A, B, Male flower. A, Level of base of tepals. B, Level of androecium. C, D, Female floral bud. C, Level of tepals. D, Level of gynoecium. Gray = vasculature. Floral organs numbered according to whorls. Scale bar = 1 mm.

decussate to spiral phyllotaxis occurs in the following two ways: (1) in the terminal flower of an inflorescence, the change occurs at the transition from the uppermost bracts of the inflorescence axis to the outermost floral organs, which may still be almost opposite, and (2) in lateral flowers, the first two tepals have a transverse position, as expected from the prophylls. There are also flowers in which the transition from whorled to spiral occurs only at the transition from the perianth to the stamens or carpels, such as Atherospermataceae

(*Doryphora aromatica*), Siparunaceae (male flowers of *Glossocalyx*, female flowers of *Siparuna thecaphora*), and Mollinedioideae (male flowers of *Levieria acuminata* and *Xymalos*). In these flowers the onset of sporophyll initiation may be preceded by a long plastochron, which may shape a circular dome-shaped floral apex. This, in turn, would create Fibonacci spiral phyllotaxis (see also Eupomatiaceae; Endress 2003; or see the model in Reinhardt et al. 2003; see also Jönsson et al. 2006).

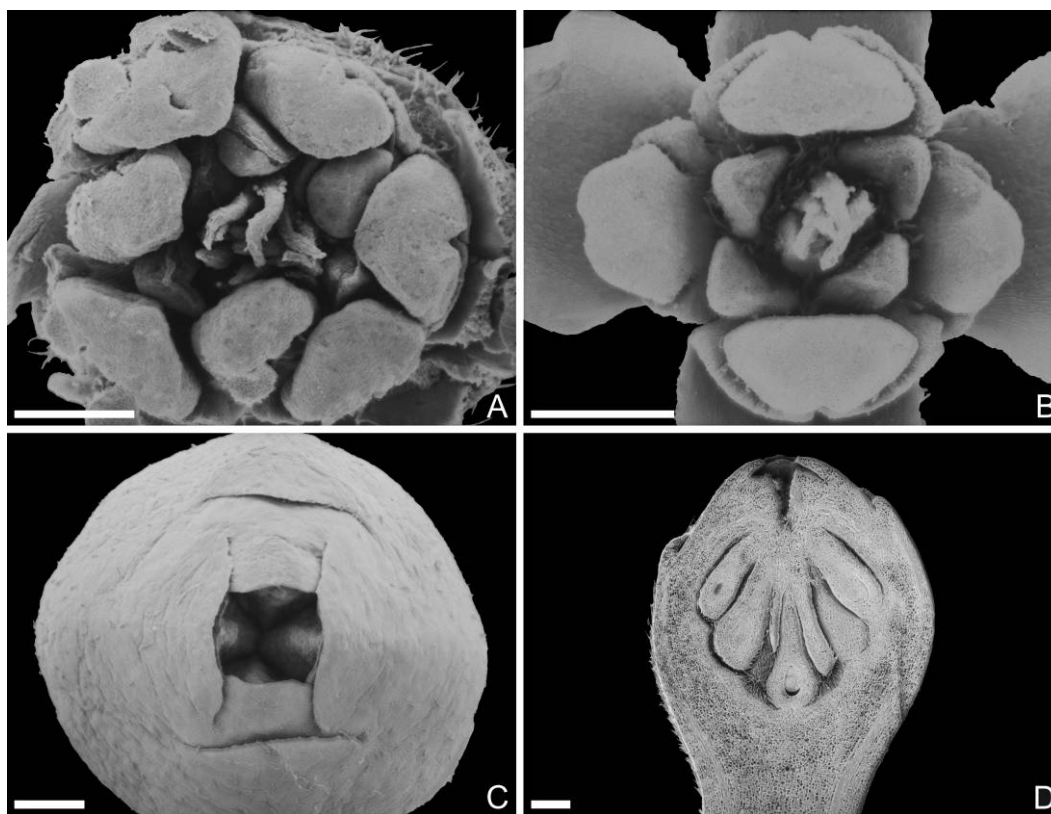


Fig. 21 SEM micrographs of flowers. A, B, Atherospermataceae. C, D, Monimiaceae. A, *Daphnandra repandula*, anthetic flower, perianth removed. B, *Daphnandra micrantha*, anthetic flower. C, *Wilkiea longipes*, anthetic female flower. D, *Kibara macrophylla*, longitudinal section of anthetic female flower. Scale bars = 0.5 mm.

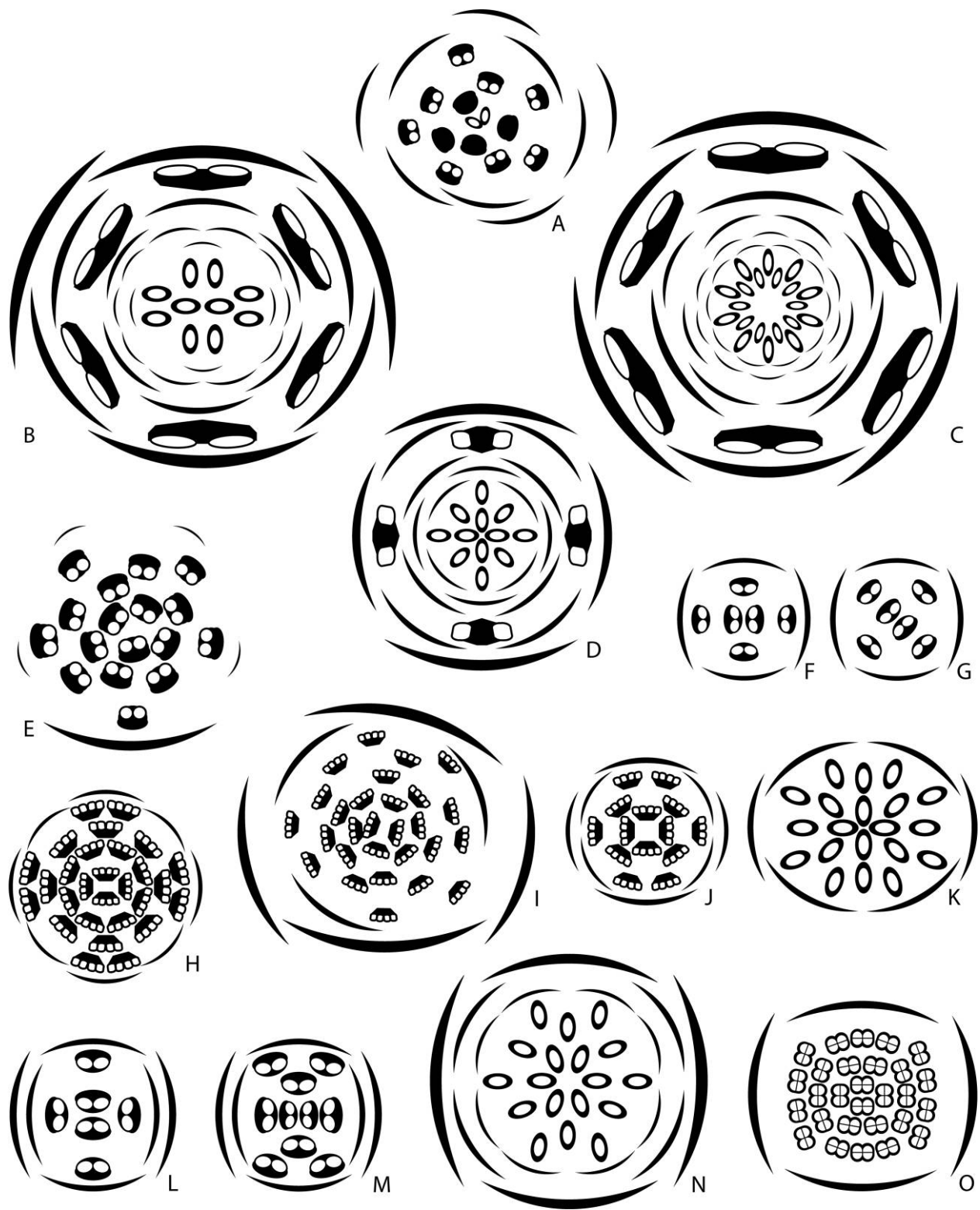


Fig. 22 Floral diagrams. A, *Gomortega keule*. B, *Doryphora sassafras*, terminal flower. C, *Doryphora sassafras*, lateral flower. D, *Dryadodaphne trachyphloia*. E, *Glossocalyx longicuspis*, male flower. F, G, *Siparuna thecaphora*, male flowers. H, *Hedycarya angustifolia*, male flower. I, *Levieria acuminata*, male flower with Fibonacci spiral phyllotaxis. J, *Levieria acuminata*, male flower with whorled phyllotaxis. K, *Levieria acuminata*, female flower. L, *Wilkiea huegeliana*, male flower with few organs. M, *Wilkiea huegeliana*, male flower with numerous organs. N, *Wilkiea huegeliana*, female flower. O, *Austromatthaea elegans*, male flower.

Simple-whorled floral phyllotaxis. Simple-whorled floral phyllotaxis, i.e., with uniformly isomerous whorls, is present in the study group only in the form of dimerous whorls. Thus, it represents a simple continuation of the decussate phyllotaxis of the leaves and the floral subtending bracts in the inflorescence. It was found in Mollinedioideae (male flowers of *Kibara coriacea*, *Stegathera ilicifolia*, and *Wilkiea angustifolia*; some male flowers of *Wilkiea huegeliana*; and some female flowers of *Xymalos*) and also in Siparunaceae (some male flowers of *S. thecaphora*). The tetramerous flowers of *Dryadodaphne trachyphloia* and *Daphnandra micrantha* (Atherospermataceae) begin with two dimerous whorls and are therefore, strictly speaking, not simple whorled from the beginning. Thus, simple-whorled floral phyllotaxis is not so common in pluricarpellate families of core Laurales. In contrast, it is pervasive in unicarpellate core Laurales, where, in addition, the floral whorls are not dimerous but largely trimerous in Lauraceae (e.g., Mez 1889; Singh and Singh 1985; Hyland 1989; Rohwer 1993; Buzgo et al. 2007) and trimerous, tetramerous, and pentamerous in Hernandiaceae (Kubitzki 1969; Endress and Lorence 2004; Kimoto and Tobe 2008). Tetramerous flowers of Lauraceae and Hernandiaceae also begin with two dimerous whorls (Endress 1987; Endress and Lorence 2004).

Complex-whorled floral phyllotaxis. The diversity in complex whorls is the most striking feature in the floral phyllotaxis in pluricarpellate families of core Laurales. These flowers do not have isomerous whorls, but merism increases or decreases once or several times between whorls. Merism increase takes place when two or more collateral organs are initiated where only one is expected (double or multiple positions). Double or multiple positions are a means of regulating organ number by flexibility of merism per whorl, in contrast to the number of whorls, as in flowers with simple-whorled phyllotaxis. Double or multiple positions also occur in other basal angiosperms (e.g., Nymphaeales [Endress 2001], Annonaceae [Endress 1987; Leins and Erbar 1996], and Aristolochiaceae [Leins and Erbar 1985]) and in basal eudicots, although double positions have not always been noticed as such in the older literature (e.g., Papaveraceae [Murbeck 1912], Ranunculaceae [Schöffel 1932]). Double or multiple positions most commonly occur at the transition from the perianth to the androecium, associated with a decrease in organ size (as in Annonaceae [Leins and Erbar 1996] or as in a number of eudicots [reviewed in Endress 1987, 1994; Ronse De Craene and Smets 1993a, 1993b]), but they may also occur earlier, within the perianth (Endress 1994, 2001; Blarer et al. 2004; this study), or later, within the androecium or at the onset of the gynoecium (this study). The term “dédoulement” was used by earlier authors (e.g., de Candolle 1813) to imply the splitting of a primordium into two. However, such a developmental splitting does not occur. What can be observed is simply a replacement of one organ by two collateral organs. This takes place because the organs are narrower than those of the preceding whorl. Therefore, we prefer the term “double position” instead of dédoulement. A special instance in which double positions are common is in tetramerous flowers of many angiosperms. There the flower commonly begins with two dimerous whorls (whorls 1 and 2). The next four organs are two pairs of double positions (whorl 3). They alternate with the four organs of the first two whorls. The four organs of

whorl 4 again alternate with those of whorl 3. Thus, the four organs of the two double positions of whorl 3 establish tetramery of the subsequent whorls. Examples among eudicots are Brassicales (Endress 1992; Ronse De Craene and Smets 1996) and Caryophyllales (Ronse De Craene and Smets 1996). In the study group this specific pattern is not common; it occurs in *Dryadodaphne* (Atherospermataceae). Among other Laurales, it is known from tetramerous Lauraceae (Endress 1987) and Hernandiaceae (Endress and Lorence 2004).

It is of special interest that double or multiple positions are very common in our study group and the site of double positions is considerably flexible. As in other plants they often occur in the outer whorls of the androecium (*D. micrantha*, *D. trachyphloia*, *Austromatthaea elegans*, and some male flowers of *W. huegeliana*). However, in Atherospermataceae and Mollinedioideae double positions also occur in the inner part of the perianth and in Mollinedioideae also in various parts of the androecium and gynoecium. An unusual and probably unrecorded pattern is the repetition (propagation) of decussate whorls with double (or multiple) positions, in which, therefore, the transition to a tetramerous whorl in the perianth and gynoecium is delayed (female flowers of *L. acuminata*, *S. ilicifolia*, and *W. huegeliana*). In more complex patterns hexa- or octomerous whorls may result. Hexamerous whorls may be formed after a dimerous whorl with two double positions, followed by a simple dimerous whorl (male flowers of *Atherosperma moschatum*, some female flowers of *W. huegeliana*). Octomerous whorls may be formed either after a tetramerous whorl of four double positions (male flowers of *H. angustifolia*, female flowers of *W. angustifolia*) or after two tetramerous whorls (some female flowers of *H. angustifolia*). Also previously unrecorded are asymmetrical transitions, in which a double position occurs only in the radius of one organ of a decussate organ pair. In the sectioned lateral flower of *Doryphora sassafras* the two last trimerous whorls of staminodes (whorls 6 and 7) each have a double position in the median plane (fig. 6F–6H). This results in an octomerous whorl, which is followed by a decamerous whorl via doubling of two positions. In female *Tambourissa purpurea* the whorls change from dimerous to hexamerous by a similar asymmetrical occurrence of double positions.

In flowers with complex whorls, the number of floral organs per whorl decreases toward the center of the flower, as discussed by Endress (1987) for other taxa. This may occur in a regular way (by whorls of similar symmetry, e.g., $8 \rightarrow 4$, in female flowers of *W. angustifolia*) or in an irregular way (e.g., $4 \rightarrow 3$, in female flowers of *L. acuminata*). Both regular and irregular decrease may even occur in the same species (e.g., *L. acuminata*).

Irregular floral phyllotaxis. Irregular phyllotaxis is found in flowers with numerous reproductive organs in Mollinedioideae (female flowers of *A. elegans* and *Tambourissa ficus*). In such female flowers there is an extensive decrease in size of the organs at the transition from the perianth to the gynoecium. For instance, in *Austromatthaea* 15–17 carpels are positioned in the sector of a single tepal. This decrease in size of the organs with regard to the size of the floral apex appears to cause a loss of order of arrangement of the carpels (see also Endress 2006). As a rule, irregular phyllotaxis appears to be linked not to an absolute number of organs above which order

would be lost but to a high number relative to a genus: *T. ficus* (2000 carpels; Lorence 1985) and *Austromatthaea* (230 carpels; this study) are irregular.

Changes in phyllotaxis patterns within flowers. Not only is there a great diversity of floral phyllotaxis patterns in core Laurales but also there may be even more than one pattern in a single flower. A transition from whorled to spiral occurs in some Atherospermataceae, Siparunaceae, and Monimiaceae. However, the reverse transition, from spiral to whorled phyllotaxis, was not observed, although such a phyllotaxis change is present in many eudicots, in which the prophylls and the sepals are initiated in a spiral sequence and the petals, stamens, and carpels in whorls (Hirmer 1931; Endress 1987).

Similarly, there are transitions from simple-whorled (decussate) phyllotaxis to complex-whorled phyllotaxis at the onset of all flowers with complex-whorled phyllotaxis. In some flowers the perianth is decussate and the complex whorls are restricted to the fertile organs (*D. trachyphloia*, some male *S. thecaphora*, male flowers of *W. huegeliana*, *A. elegans*), but in others complex whorls begin in the perianth (*D. micrantha*, *A. moschatum*, *H. angustifolia*, *L. acuminata*, female flowers of *W. angustifolia*, *W. huegeliana*, *Kibara macrphylla*, and *S. ilicifolia*). Transition from complex whorls to simple whorls is present in all flowers with complex whorls: when whorls of higher merism are initiated (almost all flowers with complex whorls) or merism decreases toward the center of the flower so that the phyllotaxis is again decussate (*Austromatthaea*).

Transition from simple-whorled phyllotaxis to irregular phyllotaxis is present in female flowers of *Austromatthaea* and appears to be due to the strong difference in size between the tepals and the carpels. Such a difference could be present in flowers of *T. ficus*, as Lorence (1985) mentions only six to eight lobes (corresponding to tepals) at the floral orifice.

Floral phyllotaxis and organ number. Flowers with few organs (fewer than 12 organs) tend to have decussate phyllotaxis, such as male flowers of *S. thecaphora* (10 or 11 organs), *K. coriacea* (eight to 12 organs), *W. angustifolia* (10 organs), *S. ilicifolia* (eight or nine organs), and some female flowers of *Xymalos monospora* (three to seven organs). However, the androecium of male flowers of *X. monospora* (three to 15 stamens) has spiral phyllotaxis. Flowers with numerous organs (more than 100 organs) tend to have irregular phyllotaxis: female flowers of *T. ficus* (~2000 carpels; Lorence 1985; this study) or *A. elegans* (~230 carpels; this study).

In flowers with an intermediate number of organs (between 15 and 100 organs), no simple correlation between organ number and floral phyllotaxis is apparent. In *Daphnandra*, more organs are present in species with spiral phyllotaxis (*D. repandula*, 32–42 organs) than in species with complex-whorled phyllotaxis (*D. micrantha*, 19–25 organs). However, in *Doryphora*, the reverse is true: fewer organs are present in species with spiral phyllotaxis (*D. aromatica*, 26–29 organs) than in species with complex-whorled phyllotaxis (*D. sassafras*, 46–77 organs).

Within the species for which different phyllotaxis occurs in flowers of the same sex (female flowers of *H. angustifolia* and male flowers of *L. acuminata*), there is a tendency for flowers with higher organ number (terminal male flowers in *L. acuminata*) to have spiral phyllotaxis and flowers with lower organ number (lateral male flowers in *L. acuminata*) to have complex-

whorled phyllotaxis. The presence of spiral and whorled flowers in the same species is also known from Winteraceae (*Drimys winteri*; Doust 2001) and Ranunculaceae (*Actaea spicata*; Schöffel 1932). In *Drimys*, as in *H. angustifolia* and *L. acuminata*, lateral flowers tend to have whorled phyllotaxis, whereas terminal flowers tend to have spiral phyllotaxis, correlated with higher organ number, and probably a more rounded floral apex shape at floral organ initiation (Doust 2001); other irregularities also occur (Erbar and Leins 1983).

In species with an intermediate number of organs and complex-whorled floral phyllotaxis, the following three cases may be distinguished. (1) Flowers with relatively low number of organs (12–18 organs, male flowers of *Laurelia sempervirens* and *W. huegeliana*): within flowers with a relatively low number of organs, flowers with below-average number of organs (lateral flowers in *L. sempervirens* but terminal flowers in *W. huegeliana*) comprise decussate pairs and only one pair of double positions, whereas in flowers with above-average number of organs (terminal flowers in *L. sempervirens* but lateral flowers in *W. huegeliana*), the pair of double positions is followed by a tetramerous whorl. (2) Flowers with relatively high number of organs (19–100 organs; most whorled Atherospermataceae and female flowers of Mollinedioideae): within flowers with relatively high number of organs, flowers with above-average number of organs (terminal flowers), two organs can be found where only one would be expected (inner whorls of the male flowers of *A. elegans*), or three or four organs may be found where only two would be expected (outer whorl of carpels in *W. huegeliana*). Similarly, in flowers with below-average number of organs (lateral flowers, accessory flowers), only one organ may be found where two would be expected (outer stamen whorl of male flowers of *H. angustifolia* and *L. acuminata*), which, in turn, tends to decrease the merism of the inner whorls. In flowers with below-average number of organs, a direct change in merism can also occur (from 4- to 3-merous whorls in staminodes and carpels in accessory flowers of *D. micrantha*). In flowers of both sexes of *T. purpurea* and female flowers of *X. monospora*, number of whorls increases in flowers with above-average number of organs (terminal flowers), but merism remains constant. (3) Flowers with more complex organ number variation: in *D. sassafras* more stamens but fewer staminodes are present in terminal flowers than in lateral flowers. Stamens are arranged in complex whorls in the terminal flowers and in simple (trimerous) whorls in the lateral flowers. Staminodes are arranged in complex whorls in both lateral and terminal flowers; however, there are three 10-merous whorls of staminodes in lateral flowers and only one in terminal flowers.

No correlation between organ number and spiral phyllotaxis was found. Organ number ranges from five (some male flowers of *Xymalos*) to 59 (some male flowers of *Peumus*). Within a species, in flowers with more organs (terminal flowers in most taxa but lateral flowers in *Palmeria gracilis*), organ number per organ series appears in higher Fibonacci numbers (8, 13) than in flowers with fewer organs (3, 5, 8).

In flowers of both sexes of *P. gracilis* and male flowers of *Hedycarya huegeliana*, terminal flowers have fewer organs than do lateral flowers. This uncommon behavior could indicate that terminal flowers may not have more organs as a rule but may simply be more plastic than lateral flowers. However,

we studied only a few inflorescences of each taxon, so this requires further studies in suitable species.

Phyllotaxis and floral shape. Flowers with a narrow, tubular floral cup (with few organs; eight to 12 inserted at the same level) have simple-whorled floral phyllotaxis (male flowers of *S. thecaphora*, *K. coriacea*, *W. angustifolia*, and *S. ilicifolia*). Flowers with a tubular floral cup (with a higher number of organs; 13–99) commonly have complex-whorled phyllotaxis, but whorl merism tends to change only once (fig. 3C; *D. micrantha*, *D. trachyphloia*, male and female flowers of *T. purpurea*, and male flowers of *W. huegeliana*). Flowers with a flat base on which organs lie but that are still enclosed in a floral cup tend to have multiple double positions and tetramerous whorls in the center of the flower (*Kibara macrophylla*, *W. angustifolia*, *W. huegeliana*, and *S. ilicifolia*). Flowers with a flat base on which organs lie and that are not enclosed in a floral cup tend to be have few double positions and hexa- and octomerous whorls (*A. moschatum*, *H. angustifolia*, and *L. acuminata*).

The more complex patterns (6- or 8-merous whorls) appear to be present in flowers in which the widening of the floral apex is not restricted by the floral cup. There is thus a trend in more open flowers toward having organs arranged in whorls or series of higher organ number than in more closed flowers. It is also among species with a flat floral base that there are flowers of the same sex with both spiral and whorled phyllotaxis (female flowers of *H. angustifolia* and male flowers of *L. acuminata*).

No specific type of floral construction appears to be correlated with spiral phyllotaxis. The floral base can be convex and the floral cup almost absent (male flowers of *X. monospora*), almost flat (male flowers of *P. gracilis* and *Peumus boldus*), concave (*Gomortega keule*), or even “closed” and urceolate (female flowers of *S. thecaphora* and *P. gracilis*).

Phyllotaxis in unisexual and bisexual flowers. In the few taxa of multicarpellate core Laurales with bisexual flowers (*Gomortega*, *Daphnandra*, *Doryphora*, *Dryadodaphne*, and *Hortonia*), spiral phyllotaxis is dominant; however, bisexual flowers with complex whorls are present in Atherospermataceae (*Daphnandra*, *Doryphora*, and *Dryadodaphne*). In most taxa studied, phyllotaxis of male and female flowers differs. This difference is correlated with different organ numbers (and perhaps shapes and sizes), floral construction, or both. In flowers in which the floral cup more or less completely encloses the reproductive organs (*S. thecaphora*, *T. purpurea*, *K. macrophylla*, *W. angustifolia*, *W. huegeliana*, and *S. ilicifolia*), male flowers tend to have fewer organs and tend to be narrower than female flowers. Female flowers are also more variable in floral merism (whorls of different merism are observed in the same part of female flowers of *K. macrophylla*, *W. angustifolia*, *W. huegeliana*, and *S. ilicifolia*). In *A. elegans*, perianth phyllotaxis is the same in male and female flowers, but there are many more carpels in female flowers than there are stamens in male flowers, so the phyllotaxis is whorled with decussate multiple positions in male flowers and irregular in female flowers.

Floral phyllotaxis and hyperstigma. A hyperstigma is present in species of *Tambourissa*, *Kibara*, *Wilkiea*, *Hennecartia* (Endress 1979a, 1980b; Endress and Igersheim 1997), and *Faika* (Philipson 1993). Such flowers have a narrow canal formed by the exit of the floral cup lined with highly reduced tepals. Flowers with a hyperstigma all have complex-whorled

phyllotaxis. Within the canal, the number of tepals at a given level is small, restricting phyllotaxis variability. All flowers with a hyperstigma have an increased number of tepals by double positions (*Tambourissa*, *Kibara*, and *Wilkiea*; Endress 1980b). In contrast, most male flowers of taxa with a hyperstigma do not have double positions of tepals (male flowers of *T. purpurea* are an exception), and their phyllotaxis is either simple-whorled (decussate; *Kibara*, *W. angustifolia*) or complex-whorled (*Tambourissa*, *W. huegeliana*). Whorled female flowers of Monimioideae without a hyperstigma, as in *Xymalos*, *Hedycarya*, *Levieria*, *Austromathaea*, and *Steghanthera*, tend to have fewer tepals than do flowers with a hyperstigma, and they tend not to have double positions in the perianth (except for *Levieria* and *Hedycarya*). *Grazielanthus* (Peixoto and Pereira-Moura 2008) is reported to have secretory tepals, but only four tepals are mentioned.

Floral monosymmetry. Floral monosymmetry is uncommon in Laurales, where it is restricted to *Glossocalyx longicuspis*, *Steghanthera stevensii* (Takeuchi 2001), and some Gyrocarpoidae of Hernandiaceae (Kubitzki 1969). In *S. stevensii*, zygomorphy of the lateral flowers appears to be due to the fusion of the floral cup with the subtending bract; terminal flowers have two large appendages, probably as the result of the fusion of the floral cup with two bracts preceding the terminal flower (terminal flowers have disymmetry). In *Glossocalyx*, the “enlarged tepal” may also be derived from a subtending bract. Arguments in favor of a subtending-bract origin are as follows: (1) no distinct subtending bract was found in our material and (2) the vasculature of the enlarged tepal is distinct from the other tepals and fuses only with that of two stamens and joins the other bundles to form a stele only in the peduncle (the vasculature of the other tepals ramify just below their base). Arguments against such an origin are as follows: (1) subtending bracts are usually minute and deciduous in Siparunaceae (Renner and Hausner 2005), which would make them easy to miss, especially on herbarium material; (2) the occurrence of flowers with two, three, or four enlarged tepals suggests that these organs have the same identity (see illustration in Fouilloy 1974), although one tepal always appears to be larger than the others; and (3) two pairs of tepals enlarge strongly during the development of the wind-dispersed fruits of *Gyrocarpus* (Kubitzki 1969), so tepal enlargement is thus present in Laurales. More observation on pickled or fresh material is needed to reach a conclusion about the origin of the enlarged “tepal” in *Glossocalyx*. Especially interesting would be a comparison of tepal differentiation in lateral and terminal flowers.

Inner staminodes: structure and function. Inner staminodes, sterile stamenlike organs between stamens and carpels in bisexual flowers, are found in several families of basal angiosperms (Endress 1984). In basal Laurales (Calycanthaceae) inner staminodes are always present (Friis et al. 1994; Crepet et al. 2005; Staedler et al. 2007). Among core Laurales, inner staminodes (often nectariferous) are present in *Gomortega* (Reiche 1896), Atherospermataceae (Schodde 1969), *Hortonia* of Mollinedioideae (Endress 1980a), and further in Lauraceae (e.g., Mez 1889; Hyland 1989; Rohwer 1993; Buzgo et al. 2007) and Hernandiaceae (Kubitzki 1969; Endress and Lorence 2004). Staminodes are also present in female flowers of *P. boldus*. In Atherospermataceae, inner staminodes are persistent and appear to play a role in the closure of the floral

cup after anthesis and recurving at fruit maturity for differential release of fruitlets (*Doryphora* and *Laurelia philippiana*; Schodde 1969). A similar function for apparently homologous organs has been described in Calycanthaceae (Staedler et al. 2007), which may be either a synapomorphy or a plesiomorphy at the order level, retained only in Calycanthaceae and Atherospermataceae. Number of (inner) staminodes is low in *Gomortega* (two to four; Brizicky 1959; Heo et al. 2004; this study), *Peumus* (10–13; this study), and *Hortonia* (two to seven; Endress 1980a), and in these genera they do not play a role in fruit development or dispersal (Doweld 2001; Heo et al. 2004; Romanov et al. 2007). The velum of Siparunaceae (Endress 1980b) and the inferior ovary of Gomortegaceae may have evolved to compensate for the loss of the protective function of the persisting staminodes during fruit development.

Carpelodes: structure and function. Carpelodes are sterile carpel-like organs. They are present in female flowers between tepals and carpels in some taxa studied (*P. gracilis*, *T. purpurea*, and *H. angustifolia*). In male flowers, carpelodes were not found.

In *T. purpurea*, the sterile organs were previously considered to be all tepals (Endress 1980b). However, it is possible to distinguish two types of organs from their shape (small knoblike organs vs. organs with a stigmalike surface), epidermis (normally staining vs. strongly staining), and vascularization (absent vs. present). The outer sterile organs are thus considered to be tepals and the inner ones carpelodes. Nevertheless, there is holocrinous secretion at the mouth of the floral pore, also involving part of the outer tepals at anthesis (Endress 1980b). Thus, the hyperstigma is made up of tepals and carpelodes. Carpelodes form whorls together with carpels but not with tepals. Carpelodes also occur in flowers without a hyperstigma, such as in *Hedycarya* (*H. angustifolia* [this study] and *Hedycarya arborea* [Sampson 1969a]). In both species, they are in two whorls at the periphery of the gynoecium. In *Hedycarya*, carpelodes may have a role in floral display, as they increase the size of a probably glistening attractive surface, and may play a role in pollinator reward. In the flowers of *Kibara* and *Wilkiea* there are also secretory organs between the outer tepals and the carpels (Endress 1980b). However, these organs are separated from the carpels by an organ-free portion of the floral cup and fall off with the tepals as a calyptra after anthesis. Both observations indicate a tepal nature for these secretory organs. In Calycanthaceae, the inner staminodes have sometimes been referred to as potential carpelodes (Hiepkko 1965), but such identity is unlikely (Staedler et al. 2008). Furthermore, organs that are unambiguously carpelodes are present in some flowers of *Idiospermum australiense* (Staedler et al. 2008). Carpelodes also appear to be present in the calycanthaceous fossil *Jerseyanthus* (Crepet et al. 2005).

Irregularities in organ sequence. Irregularities in organ sequence refer to (1) reversed organ sequence along the ontogenetic spiral in spiral phyllotaxis and whorls with two kinds of organs in whorled phyllotaxis and (2) missing organs along the ontogenetic spiral in spiral phyllotaxis or in a whorl in whorled phyllotaxis. The first case occurs in Atherospermataceae (*D. aromatica*) and in Monimiaceae (female flowers of *P. gracilis* and *T. purpurea* and some female flowers of *H. angustifolia*). The organ sequence irregularities always occur at the

transition between the sterile organs (staminodes in *D. aromatica* and carpelodes in *T. purpurea* and *H. angustifolia*) and the carpels. Such irregularities are also present at the transition between the staminodes and the carpels in Calycanthaceae (Staedler et al. 2007). As noted by Staedler et al. (2007), they were also described at the level of inflorescences in Asteraceae (between bracts, ray flowers, and disk flowers; Hirmer 1931; Bachmann 1983; Battjes and Bachmann 1996; Battjes and Prusinkiewicz 1998). These irregularities may be due to the fact that at the time of initiation, the floral apex is large in size compared to primordium size and that organ identity would depend more on the immediate sectorial neighborhood than on the position on the ontogenetic spiral in spiral flowers (*D. aromatica*, *H. angustifolia*) and on the position of the whorl in whorled flowers (*T. purpurea*).

The second case is present in a studied female flower of *P. gracilis* and *H. angustifolia*. There is a missing position in the ontogenetic spiral in the sectioned female flower of *P. gracilis*. The missing position is almost on the same radius as the last tepal initiated, which suggests that the last tepal primordium inhibited the initiation of a carpel in this vicinity, in accordance with an auxin sink model (Reinhardt et al. 2003). In *H. angustifolia*, there is a carpelode missing in whorl 6, probably because of space constraints. This appears to be the opposite phenomenon to occasional organ doubling or tripling, as in female flowers of *T. purpurea*, *W. huegeliana*, and *S. ilicifolia*.

Systematic Aspects

Gomortegaceae. Earlier reports on floral structure of *Gomortega* are conflicting regarding phyllotaxis (whorled, tetramerous [Mez 1889], spiroidal [Reiche 1896; Leinfellner 1968], spiral [Stern 1955]) or do not consider phyllotaxis at all (Buchheim 1958; Brizicky 1959). In the most recent account on floral phyllotaxis based on a review and new observations (Kubitzki 1993a, p. 318), it is described as “neither clearly spiral nor clearly trimerously whorled, but rather intermediate between both conditions.” Thus, the situation was uncertain to date. In this study we clearly show a regular spiral phyllotaxis in both terminal and lateral flowers. Only the two innermost divergence angles in the center of a flower strongly differ from the Fibonacci divergence angle, but this also is not uncommon in other families (e.g., Monimiaceae [this study] and Calycanthaceae [Staedler et al. 2007]).

Atherospermataceae. At the genus level either floral phyllotaxis is whorled (*Atherosperma*, *Dryadodaphne*, and *Nemuaron*; Schodde 1969; this study) or spiral and whorled phyllotaxis coexist (spiral in *Laurelia novae-zelandiae* [Sampson 1969b] but whorled in *L. sempervirens* [this study]; spiral in *D. repandula* but whorled in *D. micrantha* [this study]; spiral in *D. aromatica* but whorled in *D. sassafras* [this study]; to make the situation even more unstable, Schodde [1969] found whorled flowers in *D. aromatica*). Interestingly, there is no genus with exclusively spiral phyllotaxis. Among the whorled flowers, *Atherosperma*, *Dryadodaphne*, and *Laurelia* are dimorous/tetramerous (this study), whereas *Nemuaron* and *Doryphora* fluctuate between trimerous and tetramerous (Schodde 1969). Subspiral phyllotaxis, as mentioned (without definition) by Schodde (1969) for some taxa, was not found in our material. Thus, of the two major clades of the family (Renner

et al. 2000), one fluctuates between whorled and spiral, and the other is consistently whorled (except for *Laurelia*, which also fluctuates between whorled and spiral).

Siparunaceae. Flowers with completely spiral phyllotaxis so far were not found in Siparunaceae. Male flowers of *Glossocalyx* are whorled in the perianth and spiral in the androecium (this study). In *S. thecaphora* male flowers are whorled (dimerous), whereas female flowers are whorled only in the perianth but spiral in the gynoecium (this study). Male flowers of *Siparuna aspera* are also whorled (dimerous; Bello et al. 2002). The occurrence of irregular phyllotaxis was indicated for species with a high organ number (Renner and Hausner 2005). Floral organ numbers show striking intraspecific variability, with up to 72 stamens and up to 35 carpels (Renner and Hausner 2005).

Monimiaceae. Monimioideae and *Hortonia*, which is sister to all other Mollinedioideae, have spiral floral phyllotaxis. Mollinedioideae form a basal grade and a number of genera in an unresolved trichotomy (Renner 2004). Beginning in the second clade of the basal grade, floral phyllotaxis becomes highly variable. *Tambourissa* has complex whorls or phyllotaxis is irregular, the latter especially in flowers with excessively numerous organs (*T. ficus* has up to 2000 stamens and carpels; Lorence 1985), and in *Ephippiandra* simple dimerous whorls (Perkins 1925) and complex whorls (Lorence 1985) occur. *Hedycarya* and *Levieria* have both spiral and complex-whorled patterns. Of the three clades forming the mentioned trichotomy, *Steganthera* and *Austromatthaea* have simple whorls, complex whorls, and also irregular patterns (in *Austromatthaea*, with numerous organs), and in *Wilkiea* simple dimerous whorls and complex whorls occur; the Neotropical clade of *Mollinedia* and relatives has not been studied.

Evolution of floral phyllotaxis in Laurales. The basal state of floral phyllotaxis in Laurales is equivocal for the perianth (spiral or whorled) and spiral for the androecium (Endress and Doyle 2007). Calycanthaceae, which are sister to all other Laurales, have consistently spiral flowers (Staedler et al. 2007). Spiral flowers were retained in Gomortegaceae (this study) and in the basal clades of Monimiaceae (Monimioideae and *Hortonia*), whereas in the higher Mollinedioideae lability between spiral and whorled patterns and, with an excessive increase of stamens or carpels (*Austromatthaea*, species of *Tambourissa*), irregular phyllotaxis also evolved (this study). In Siparunaceae flowers are whorled in the perianth and androecium but spiral in the gynoecium (this study) but may also be irregular (Renner and Hausner 2005). In Atherospermataceae, whorled flowers are predominant, but in three genera (from both major clades) lability between whorled and spiral phyllotaxis occurs. In Hernandiaceae and Lauraceae spiral flowers are not known; in all extant species studied, phyllotaxis is whorled (Mez 1889; Kubitzki 1969; Hyland 1989; Endress and Lorence 2004; Buzgo et al. 2007; Kimoto and Tobe 2008), except for a few derived Lauraceae

(species of *Lindera* and *Litsea*) that have lost their perianth and have an irregular phyllotaxis (Endress 1990). In floral fossils ascribed to Lauraceae, phyllotaxis is also whorled (trimerous; *Mauldinia* [Drinnan et al. 1990; Viehofen et al. 2008], *Perseanthus* [Herendeen et al. 1994], *Neusenina* [Eklund 2000], *Lauranthus* [Takahashi et al. 2001], and *Potomacanthus* [von Balthazar et al. 2007]). The uniformly whorled floral phyllotaxis in both fossil and almost all extant Lauraceae suggests fixation of this pattern in the family.

Conclusions

Because floral phyllotaxis is diverse, in some genera of Atherospermataceae and Monimiaceae, even at the species level, floral phyllotaxis evolution is expected to be complex. A realistic picture of floral phyllotaxis evolution in these families would require a very broad taxon sampling, down to the species level or maybe even the population level. Nevertheless, from the distribution of this diversity, it can be concluded that lability of phyllotaxis is unusually extensive in core Laurales, and evolutionary oscillations between spiral and whorled patterns may be frequent in certain genera or species. Another approach would be to focus on species found to be especially labile in this study and to carry out developmental studies to investigate conditions leading to different patterns in more detail.

The change from simple-whorled phyllotaxis to complex-whorled phyllotaxis, and vice versa, appears to be linked to organ number and floral cup constraint. The change from complex- or simple-whorled phyllotaxis to spiral phyllotaxis within a flower, as in Mollinedioideae, is correlated only with weakly developed floral cups (flat or convex floral bases). In contrast the change from spiral to whorled phyllotaxis within a flower was not found, suggesting that this change is developmentally difficult.

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Literature Cited

- Bachmann K 1983 Evolutionary genetics and the genetic control of morphogenesis in flowering plants. *Evol Biol* 16:157–208.
 Baillon H 1868 *Histoire des plantes*. Vol 1. Hachette, Paris.
 Battjes J, K Bachmann 1996 Numerical canalization in asteracean heads. Pages 185–204 in PDS Caligari, DJN Hind, eds. *Compositae: biology and utilization*. Vol 2. Royal Botanic Gardens, Kew.

- Battjes J, P Prusinkiewicz 1998 Modeling meristic characters of asteracean flowerheads. Pages 281–312 in D Barabé, RV Jean, eds. Symmetry in plants. World Scientific, Singapore.
- Bello MA, F González, G Romero de Pérez 2002 Morfología del androceo, tapete y ultraestructura del polen de *Siparuna aspera* (Ruiz et Pavón) A. DC. (Siparunaceae). *Rev Acad Colomb Cienc Exactas Fis Nat* 26:155–167.
- Blarer A, DL Nickrent, PK Endress 2004 Comparative floral structure and systematics in Apodanthaceae (Rafflesiales). *Plant Syst Evol* 245:119–142.
- Brizicky GK 1959 Variability in floral parts of *Gomortega* (Gomortegaceae). *Willdenowia* 2:200–207.
- Buchheim G 1958 Bemerkungen zum Andrözeum der Gomortegaceae. *Willdenowia* 2:27–31.
- Buzgo M, AS Chanderbali, S Kim, Z Zheng, DG Oppenheimer, PS Soltis, DE Soltis 2007 Floral developmental morphology of *Persea americana* (avocado, Lauraceae): the oddities of male organ identity. *Int J Plant Sci* 168:261–284.
- Cantino PD, JA Doyle, SW Graham, WS Judd, RG Olmstead, DE Soltis, PS Soltis, MJ Donoghue 2007 Towards a phylogenetic nomenclature of Tracheophyta. *Taxon* 56:822–846.
- Chanderbali AS, H van der Werff, SS Renner 2001 Phylogeny and historical biogeography of Lauraceae: evidence from the chloroplast and nuclear genomes. *Ann Mo Bot Gard* 88:104–134.
- Crepet WL, KC Nixon, MA Gandolfo 2005 An extinct calycanthoid taxon, *Jerseyanthus calycanthoides*, from the Late Cretaceous of New Jersey. *Am J Bot* 92:1475–1485.
- Cronquist A 1988 The evolution and classification of flowering plants. New York Botanical Garden, Bronx.
- de Candolle A-P 1813 Théorie élémentaire de botanique. Déterville, Paris.
- Doust AN 2001 The developmental basis of floral variation in *Drimys winteri* (Winteraceae). *Int J Plant Sci* 162:697–717.
- Doweld AB 2001 Carpology and phermatology of *Gomortega* (Gomortegaceae): systematic and evolutionary implications. *Acta Bot Malacitana* 26:19–37.
- Doyle JA, PK Endress 2000 Morphological phylogenetic analysis of basal angiosperms: comparison and combination with molecular data. *Int J Plant Sci* 161(suppl):S121–S153.
- Drinnan AN, PR Crane, EM Friis, KR Pedersen 1990 Lauraceous flowers from the Potomac group (mid-Cretaceous) of eastern North America. *Bot Gaz* 151:370–384.
- Eklund H 2000 Lauraceous flowers from the Late Cretaceous of North Carolina, U.S.A. *Bot J Linn Soc* 132:397–428.
- Endress PK 1972 Zur vergleichenden Entwicklungsmorphologie, Embryologie und Systematik bei Laurales. *Bot Jahrb Syst* 92:331–428.
- 1979a Noncarpellary pollination and “hyperstigma” in an angiosperm (*Tambourissa religiosa*, Monimiaceae). *Experientia* 35: 45.
- 1979b A second species of *Steganthera* (Monimiaceae) from Australia. *Blumea* 25:315–318.
- 1980a Floral structure and relationships of *Hortonia* (Monimiaceae). *Plant Syst Evol* 133:199–221.
- 1980b Ontogeny, function and evolution of extreme floral construction in Monimiaceae. *Plant Syst Evol* 134:79–120.
- 1980c The reproductive structures and systematic position of the Austrobaileyaceae. *Bot Jahrb Syst* 101:393–433.
- 1984 The role of inner staminodes in the floral display of some relic Magnoliales. *Plant Syst Evol* 146:269–282.
- 1987 Floral phyllotaxis and floral evolution. *Bot Jahrb Syst* 108:417–438.
- 1990 Patterns of floral construction in ontogeny and phylogeny. *Biol J Linn Soc* 39:153–175.
- 1992 Evolution and floral diversity: the phylogenetic surroundings of *Arabidopsis* and *Antirrhinum*. *Int J Plant Sci* 153(suppl):S106–S122.
- 1994 Diversity and evolutionary biology of tropical flowers. Cambridge University Press, Cambridge.
- 2001 The flowers in extant basal angiosperms and inferences on ancestral flowers. *Int J Plant Sci* 162:1111–1140.
- 2003 Early floral development and the nature of the calyptra in Eupomatiaceae. *Int J Plant Sci* 164:489–503.
- 2006 Angiosperm floral evolution: morphological developmental framework. *Adv Bot Res* 44:1–61.
- Endress PK, JA Doyle 2007 Floral phyllotaxis in basal angiosperms: development and evolution. *Curr Opin Plant Biol* 10:52–57.
- 2009 Reconstructing the ancestral angiosperm flower and its initial specializations. *Am J Bot* 96:22–66.
- Endress PK, A Igersheim 1997 Gynoecium diversity and systematics of the Laurales. *Bot J Linn Soc* 125:93–168.
- Endress PK, DH Lorence 2004 Heterodichogamy of a novel type in *Hernandia* (Hernandiaceae) and its structural basis. *Int J Plant Sci* 165:753–763.
- Erbar C 1995 On the floral development of *Sphenoclea zeylanica* (Sphenocleaceae, Campanulales): SEM investigations on herbarium material. *Bot Jahrb Syst* 117:469–483.
- Erbar C, P Leins 1983 Zur Sequenz von Blütenorganen bei einigen Magnoliiden. *Bot Jahrb Syst* 103:433–449.
- Fouilloy R 1974 Monimiacées. Pages 107–116 in A Aubréville, JF Leroy, eds. Flore du Cameroun. Muséum d’Histoire Naturelle, Paris.
- Friis EM, H Eklund, KR Pedersen, PR Crane 1994 *Virginianthus calycanthoides* gen. et sp. nov.: a calycanthaceous flower from the Potomac Group (Early Cretaceous) of eastern North America. *Int J Plant Sci* 155:772–785.
- Heo K, Y Kimoto, M Riveros, H Tobe 2004 Embryology of Gomortegaceae (Laurales): characteristics and character evolution. *J Plant Res* 117:221–228.
- Herendeen PS, WL Crepet, KC Nixon 1994 Fossil flowers and pollen of Lauraceae from the Upper Cretaceous of New Jersey. *Plant Syst Evol* 189:29–40.
- Hiepkö P 1965 Vergleichend-morphologische und entwicklungsge-schichtliche Untersuchungen über das Perianth bei den Polycarpiceae. *Bot Jahrb Syst* 84:359–508.
- Hilu KW, T Borsch, K Müller, DE Soltis, PS Soltis, V Savolainen, MW Chase, et al 2003 Angiosperm phylogeny based on *matK* sequence information. *Am J Bot* 90:1758–1776.
- Hirmer M 1931 Zur Kenntnis der Schraubenstellungen im Pflanzenreich. *Planta* 14:132–206.
- Hyland BPH 1989 A revision of Lauraceae in Australia (excluding *Cassytha*). *Aust Syst Bot* 2:135–367.
- Igersheim A, O Cichocki 1996 A simple method for microtome sectioning of prehistoric charcoal specimens, embedded in 2-hydroxyethyl methacrylate (HEMA). *Rev Palaeobot Palynol* 92:389–393.
- Jönsson H, MG Heisler, BE Shapiro, EM Meyerowitz, E Mjolsness 2006 An auxin-driven polarized transport model for phyllotaxis. *Proc Natl Acad Sci USA* 103:1633–1638.
- Kimoto Y, H Tobe 2008 Embryology of *Illigera* and *Sparattanthelium* (Hernandiaceae, Laurales): family characteristics and relationships. *Int J Plant Sci* 169:391–408.
- Kubitzki K 1969 Monographie der Hernandiaceen. *Bot Jahrb Syst* 89:78–209.
- 1987 Origin and significance of trimerous flowers. *Taxon* 36: 21–28.
- 1993a Gomortegaceae. Pages 318–320 in K Kubitzki, JG Rohwer, V Bittrich, eds. The families and genera of vascular plants. Springer, Berlin.
- 1993b Hernandiaceae. Pages 334–338 in K Kubitzki, JG

- Rohwer, V Bittrich, eds. The families and genera of vascular plants. Springer, Berlin.
- Leinfellner W 1968 Über die Karpelle verschiedener Magnoliales. VI. *Gomortega keule* (Gomortegaceae). *Osterr Bot Z* 115:113–119.
- Leins P, C Erbar 1985 Ein Beitrag zur Blütenentwicklung der Aristolochiaceae, einer Vermittlergruppe zu den Monokotylen. *Bot Jahrb Syst* 107:343–368.
- 1996 Early floral developmental studies in Annonaceae. Pages 1–27 in W Morawetz, H Winkler, eds. Reproductive morphology in Annonaceae. Österreichische Akademie der Wissenschaften, Wien.
- Lorence DH 1985 A monograph of the Monimiaceae (Laurales) of the Malagasy region (southwest Indian Ocean). *Ann Mo Bot Gard* 72:1–165.
- Mez C 1889 Lauraceae Americanae. *Jahrb Bot Gart Bot Mus Berlin* 5:1–556.
- Murbeck S 1912 Untersuchungen über den Blütenbau der Papaveraceen. *K Sven Vetenskapsakad Handl* 50:1–168.
- Peixoto AL, MVL Pereira-Moura 2008 A new genus of Monimiaceae from the Atlantic Coastal Forest in south-eastern Brazil. *Kew Bull* 63:137–141.
- Perkins J 1925 Übersicht über die Gattungen der Monimiaceae sowie Zusammenstellung der Abbildungen und der Literatur über die Arten dieser Familie bis zum Jahre 1925. Engelmann, Leipzig.
- Philipson WR 1980 *Kairoa*, a new genus of Monimiaceae from Papua New Guinea. *Blumea* 26:367–372.
- 1985 Malesian species of *Kibara*. *Blumea* 30:389–415.
- 1993 Monimiaceae. Pages 426–437 in K Kubitzki, JG Rohwer, V Bittrich, eds. The families and genera of vascular plants. Springer, Berlin.
- Qiu Y-L, O Dombrowska, JH Lee, LB Li, BA Whitlock, F Bernasconi-Quadroni, JS Rest, et al 2005 Phylogenetic analyses of basal angiosperms based on nine plastid, mitochondrial, and nuclear genes. *Int J Plant Sci* 166:815–842.
- Qiu Y-L, J Lee, F Bernasconi-Quadroni, DE Soltis, PS Soltis, MJ Zanis, EA Zimmer, Z Chen, V Savolainen, MW Chase 1999 The earliest angiosperms: evidence from mitochondrial, plastid and nuclear genomes. *Nature* 402:404–407.
- Qiu Y-L, L Li, TA Hendry, R Li, DW Taylor, MJ Issa, AJ Ronen, ML Vekaria, AM White 2006 Reconstructing the basal angiosperm phylogeny: evaluating information content of mitochondrial genes. *Taxon* 55:837–856.
- Reiche K 1896 Zur Kenntnis von *Gomortega nitida* R. et Pav. *Ber Dtsch Bot Ges* 14:225–233.
- Reinhardt D, ER Pesce, P Stieger, T Mandel, K Baltensperger, M Bennett, J Traas, J Friml, C Kuhlemeier 2003 Regulation of phyllotaxis by polar auxin transport. *Nature* 426:255–260.
- Renner SS 1998 Phylogenetic affinities of Monimiaceae based on cpDNA gene and spacer sequences. *Perspect Plant Ecol Evol Syst* 1: 61–77.
- 1999 Circumscription and phylogeny of the Laurales: evidence from molecular and morphological data. *Am J Bot* 86:1301–1315.
- 2004 Variation in diversity among Laurales, Early Cretaceous to present. *Biol Skr* 55:441–458.
- Renner SS, A Chandrabali 2000 What is the relationship among Hernandiaceae, Lauraceae, and Monimiaceae, and why is this question so difficult to answer? *Int J Plant Sci* 161(suppl):S109–S119.
- Renner SS, DB Foreman, D Murray 2000 Timing transantarctic disjunctions in the Atherospermataceae (Laurales): evidence from coding and noncoding chloroplast sequences. *Syst Biol* 49:579–591.
- Renner SS, G Hausner 2005 Siparunaceae. *Flora Neotrop Monogr* 95:1–256.
- Rohwer JG 1993 Lauraceae. Pages 366–391 in K Kubitzki, JG Rohwer, V Bittrich, eds. The families and genera of vascular plants. Springer, Berlin.
- Romanov MS, PK Endress, AVFC Bobrov, AP Melikian, AP Bejerano 2007 Fruit structure and systematics of Monimiaceae s.s. (Laurales). *Bot J Linn Soc* 153:265–285.
- Ronse De Craene LP, EF Smets 1993a Dédoublement revisited: towards a renewed interpretation of the androecium of the Magnoliophytina. *Bot J Linn Soc* 113:103–124.
- 1993b The distribution and systematic relevance of the androecial character polymery. *Bot J Linn Soc* 113:285–350.
- 1996 The morphological variation and systematic value of stamen pairs in the Magnoliatae. *Feddes Repert* 107:1–17.
- Ronse De Craene LP, PS Soltis, DE Soltis 2003 Evolution of floral structures in basal angiosperms. *Int J Plant Sci* 164(suppl):S329–S363.
- Sampson FB 1969a Studies on the Monimiaceae. I. Floral morphology and gametophyte development of *Hedycarya arborea* J.R. et G. Forst. (subfamily Monimioideae). *Aust J Bot* 17:403–424.
- 1969b Studies on the Monimiaceae. II. Floral morphology of *Laurelia novae-zelandiae* A. Cunn. (subfamily Atherospermoideae). *N Z J Bot* 7:214–240.
- Schodde R 1969 A monograph of the family Atherospermataceae. PhD thesis. University of Adelaide.
- Schöffel K 1932 Untersuchungen über den Blütenbau der Ranunculaceen. *Planta* 17:315–371.
- Singh V, A Singh 1985 Floral organogenesis in *Cinnamomum camphora*. *Phytomorphology* 35:61–67.
- Soltis DE, MA Gitzendanner, PS Soltis 2007 A 567-taxon data set for angiosperms: the challenges posed by Bayesian analyses of large data sets. *Int J Plant Sci* 168:137–157.
- Staedler YM, PH Weston, PK Endress 2007 Floral phyllotaxis and floral architecture in Calycanthaceae (Laurales). *Int J Plant Sci* 168:285–306.
- 2008 Comparative gynoecium structure and development in Calycanthaceae (Laurales). *Int J Plant Sci* 170:21–41.
- Stapf O 1909 *Laurelia serrata*. *Curtis's Bot Mag*, table 8279.
- Stern WL 1955 Xylem anatomy and relationships of Gomortegaceae. *Am J Bot* 42:874–885.
- Takahashi M, PS Herendeen, PR Crane 2001 Lauraceous fossil flower from the Kamikitaba locality (Lower Coniacian; upper Cretaceous) in Northeastern Japan. *J Plant Res* 114:429–434.
- Takeuchi W 2001 An unusual new species of *Steganthera* (Monimiaceae) from Papua New Guinea. *Kew Bull* 56:995–998.
- Takhtajan AL 1969 Flowering plants, origin and dispersal. Oliver & Boyd, Edinburgh.
- Viehofen A, C Hartkopf-Fröder, EM Friis 2008 Inflorescences and flowers of *Mauldinia angustiloba* sp. nov. (Lauraceae) from middle Cretaceous karst infillings in the Rhenish Massif, Germany. *Int J Plant Sci* 169:871–889.
- von Balthazar M, KR Pedersen, PR Crane, M Stampanoni, EM Friis 2007 *Potomacanthus lobatus* gen. et sp. nov., a new flower of probable Lauraceae from the Early Cretaceous (Early to Middle Albian) of eastern North America. *Am J Bot* 94:2041–2053.
- Zanis MJ, PS Soltis, YL Qiu, EA Zimmer, DE Soltis 2003 Phylogenetic analyses and perianth evolution in basal angiosperms. *Ann Mo Bot Gard* 90:129–150.
- Zhou S, SS Renner, J Wen 2006 Molecular phylogeny and intra- and intercontinental biogeography of Calycanthaceae. *Mol Phylogenet Evol* 39:1–15.