



REVIEW ARTICLE

Multicarpellate gynoecia in angiosperms: occurrence, development, organization and architectural constraints

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Most angiosperms have gynoecia with two to five carpels. However, more than five carpels (here termed ‘multicarpellate condition’) are present in some representatives of all larger subclades of angiosperms. In such multicarpellate gynoecia, the carpels are in either one or more than one whorl (or series). I focus especially on gynoecia in which the carpels are in a single whorl (or series). In such multicarpellate syncarpous gynoecia, the closure in the centre of the gynoecium is imprecise as a result of slightly irregular development of the carpel flanks. Irregular bumps appear to stuff the remaining holes. In multicarpellate gynoecia, the centre of the remaining floral apex is not involved in carpel morphogenesis, so that this unspent part of the floral apex remains morphologically undifferentiated. It usually becomes enclosed within the gynoecium, but, in some cases, remains exposed and may or may not form simple excrescences. The area within the remaining floral apex is histologically characterized by a parenchyma of simple longitudinal cell rows. In highly multicarpellate gynoecia with the carpels in a whorl, the whorl tends to be deformed into an H-shaped or star-shaped structure by differential growth of the floral sectors, so that carpels become aligned in parallel rows, in which they face each other with the ventral sides. In this way, a fractionated compitum may still be functional. Multicarpellate gynoecia (with the carpels in one whorl or series) occur in at least one species in 37 of the 63 angiosperm orders. In contrast, non-multicarpellate gynoecia are present in at least one species of all 63 orders. The basal condition in angiosperms is more likely non-multicarpellate. Multicarpellate gynoecia are restricted to flowers that are not highly synorganized. In groups with synorganized androecium and gynoecium and in groups with elaborate monosymmetric flowers, multicarpellate gynoecia are lacking. © 2013 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2014, **174**, 1–43.

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INTRODUCTION

Carpels are the structural units of the gynoecium, the female organ complex of a flower. They are unusual among floral organs (and most other plant organs) in folding or incurving and closing during development, forming an internal space that is covered by the primary morphological surface, i.e. the surface developmentally derived from the surface of the floral apex. Thus, the primary morphological surface is continuous from the outer surface to the inner surface of the carpel (Endress, 2006). In this internal space, the ovules develop and are enclosed by the carpel walls. Thus, among floral organs, carpels are unique in two

ways: first, they have an internal morphological space and, second, in this space additional organs develop.

The carpel number in the flowers of most angiosperms is between two and five, and the carpels are mostly arranged in one whorl (Endress, 2011). In monocots, with their predominantly trimerous flowers, there are mostly three carpels in a whorl (Remizowa, Sokoloff & Rudall, 2010), and, in core eudicots, with their predominantly pentamerous flowers, there are mostly two to five carpels in a whorl (Endress, 2011). Thus, a low carpel number and carpel arrangement in one whorl are predominant in angiosperms. In addition, these carpels are mostly united, forming a compitum, i.e. a centralized pollen tube transmitting tract in which centralized selection of male gametophytes is possible (Endress, 1982;

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Armbruster, Debevec & Willson, 2002). Only in the ANITA grade, in magnoliids, early branching monocots and early branching eudicots, is the range in carpel number larger, and higher numbers are not uncommon. Then, the carpels are sometimes arranged in more than one whorl or series or in an irregular fashion (Endress, 2011). In these cases, the carpels are often not fused with each other, i.e. the gynoecium is apocarpous (choricarpous). The highest carpel number per flower given in the literature for an angiosperm is 10 000 (*Laccopetalum* Ulbr., Ranunculaceae; Tamura, 1995). Gynoecia with such exceedingly high carpel numbers have the carpels arranged in numerous whorls or series.

However, there are also clades in both core monocots and core eudicots in which carpel number is increased, although this is the case in many fewer clades than is increased stamen number. Nevertheless, in these cases of increased carpel number, the carpels are still mostly in one whorl and are still united (Ronse Decraene & Smets, 1998). In optimization studies, it appears that the range of two to five carpels in a whorl or series is ancestral in angiosperms (Doyle & Endress, 2011). Why an increase in carpel number to more than five in syncarpous gynoecia is not as common and which architectural constraints may be responsible for this limitation were briefly addressed by Endress (2006), but there is no comprehensive comparative study on such gynoecia across the angiosperms. There are two main developmental (architectural) difficulties in gynoecia in which numerous carpels are arranged in one whorl: (1) if the entire floral apex is used up and the ovary becomes closed as a unit (i.e. if angiospermy is not just in individual carpels, but involves the entire gynoecium as a unit), there are difficulties with a clean carpel closure in the centre of the gynoecium; as a consequence, the formation of a compitum that involves all carpels becomes more difficult; (2) if the centre of the remaining floral apex is not used up during gynoecium differentiation, it becomes even more difficult to form an optimal compitum, in which pollen tubes from each carpel can freely reach all other carpels.

The present comparative morphological study explores the occurrence of multicarpellate gynoecia across the angiosperms. It shows specific structural features that regularly accompany the presence of an increased number of carpels. It attempts to provide new insights into functional problems in multicarpellate gynoecia and shows how some of these problems can be overcome by special structural differentiations. It also tries to understand better some peculiar and perhaps misinterpreted structural features of multicarpellate gynoecia. The study is based on a combination of: (1) a large number of original observations

of cases that have been assembled over the years in my own research on gynoecium structure across many angiosperm clades; and (2) a broad survey of the morphological and systematic literature.

MATERIAL AND METHODS

Material used in this study is based on the following collections (PKE, Peter K. Endress; BGZ, Botanic Garden of the University of Zurich, Switzerland). The collection date is only mentioned if there is no collection number.

Aeonium tabuliforme (Haw.) Webb & Berthel. (Crassulaceae), coll. PKE 7438, BGZ.

Clusia rosea Jacq. (Clusiaceae), coll. PKE 96-04, National Tropical Botanical Garden, Kauai, Hawaii, USA.

Couroupita guianensis Aubl. (Lecythidaceae), coll. PKE 9393, Bogor Botanical Gardens, Java, Indonesia.

Crossostylis grandiflora Brongn. & Gris (Rhizophoraceae), coll. Adrian Juncosa *s.n.*, ix.1981, New Caledonia.

Duabanga grandiflora (DC.) Walp. (Lythraceae), coll. PKE 96-13, National Tropical Botanical Garden, Kauai, Hawaii, USA.

Davidia involucrata Baill. (Cornaceae), coll. PKE *s.n.*, 8.xi.1984, BGZ.

Dillenia alata (R.Br. ex DC.) ex Martelli (Dilleniaceae), coll. PKE 4304, North Queensland, Australia.

Dillenia philippinensis Rolfe (Dilleniaceae), coll. PKE 9367, Bogor Botanical Gardens, Java, Indonesia.

Dillenia suffruticosa (Griff.) Martelli (Dilleniaceae), coll. PKE 9301, Bogor Botanical Gardens, Java, Indonesia.

Flacourtia rukam Zoll. & Moritz (Salicaceae), coll. PKE 11-11, Royal Botanic Gardens Melbourne, Australia.

Gynotroches axillaris Blume (Rhizophoraceae), coll. Adrian Juncosa *s.n.*, 9.x.1981, Sarawak.

Gyrostemon brevipes Hook. ex Moq. (Gyrostemonaceae), coll. Ursula Hofmann 1274, 4.ix.1986, Australia.

Gyrostemon racemigerus H.Walter (Gyrostemonaceae), coll. Ursula Hofmann 1400, 6.ix.1986, Australia.

Illicium anisatum L. (Illiciaceae), coll. PKE 535, cult., Orselina, Canton Ticino, Switzerland.

Kitaibelia vitifolia Willd. (Malvaceae), coll. PKE 5336, BGZ.

Lagerstroemia floribunda Jack (Lythraceae), coll. PKE 03-23, National Tropical Botanical Garden, Kauai, Hawaii, USA.

Marcgravia sp. (Marcgraviaceae), coll. PKE 97-10, Monteverde, Costa Rica.

Munroidendron racemosum (C.N.Forbes) Sherff (Araliaceae), coll. PKE 96-10, National Tropical Botanical Garden, Kauai, Hawaii, USA.

Nolana paradoxa Lindl. (Solanaceae), coll. PKE 7228, Botanic Garden of the University of Marburg, Germany.

Nymphaea tetragona Georgi (Nymphaeaceae), coll. PKE *s.n.*, *s.d.*, BGZ.

Pavonia hastata Cav. (Malvaceae), coll. PKE 6793, BGZ.

Platystemon californicus Benth. (Papaveraceae), coll. PKE 4596, BGZ.

Pleiogynium solandri (Benth.) Engl. (Anacardiaceae), coll. PKE 03-04, National Tropical Botanical Garden, Kauai, Hawaii, USA.

Thottea cf. macrantha (Boerl.) Ding Hou (Aristolochiaceae), coll. PKE 9381, Bogor Botanical Gardens, Java, Indonesia.

Trochodendron aralioides Siebold. & Zucc. (Trochodendraceae), coll. PKE *s.n.*, 8.ii.1984, BGZ.

Tupidanthus calyptratus Hook.f. & Thomson (Araliaceae), coll. PKE 6113, Royal Botanic Gardens, Sydney, Australia.

The studied material was fixed and stored in 70% ethanol. Gynoecia studied with a scanning electron microscope were critical point dried, sputter coated with gold and studied at 20 kV with a Hitachi S-4000, except for one specimen (Fig. 18), which was sputter coated with platinum and studied at 10 kV with a Zeiss Supra-50 VP. The material used for microtome section series was dehydrated and embedded in paraplast. Section series, 10 µm thick, were produced with a Leitz rotary microtome, stained with safranin and Astrablue, and embedded in Eukitt. Vouchers and permanent slides of the microtome sections are deposited at the Institute of Systematic Botany, University of Zurich (Z).

RESULTS AND DISCUSSION

PATTERNS OF CARPEL ARRANGEMENT IN MULTICARPELLATE GYNOCIA

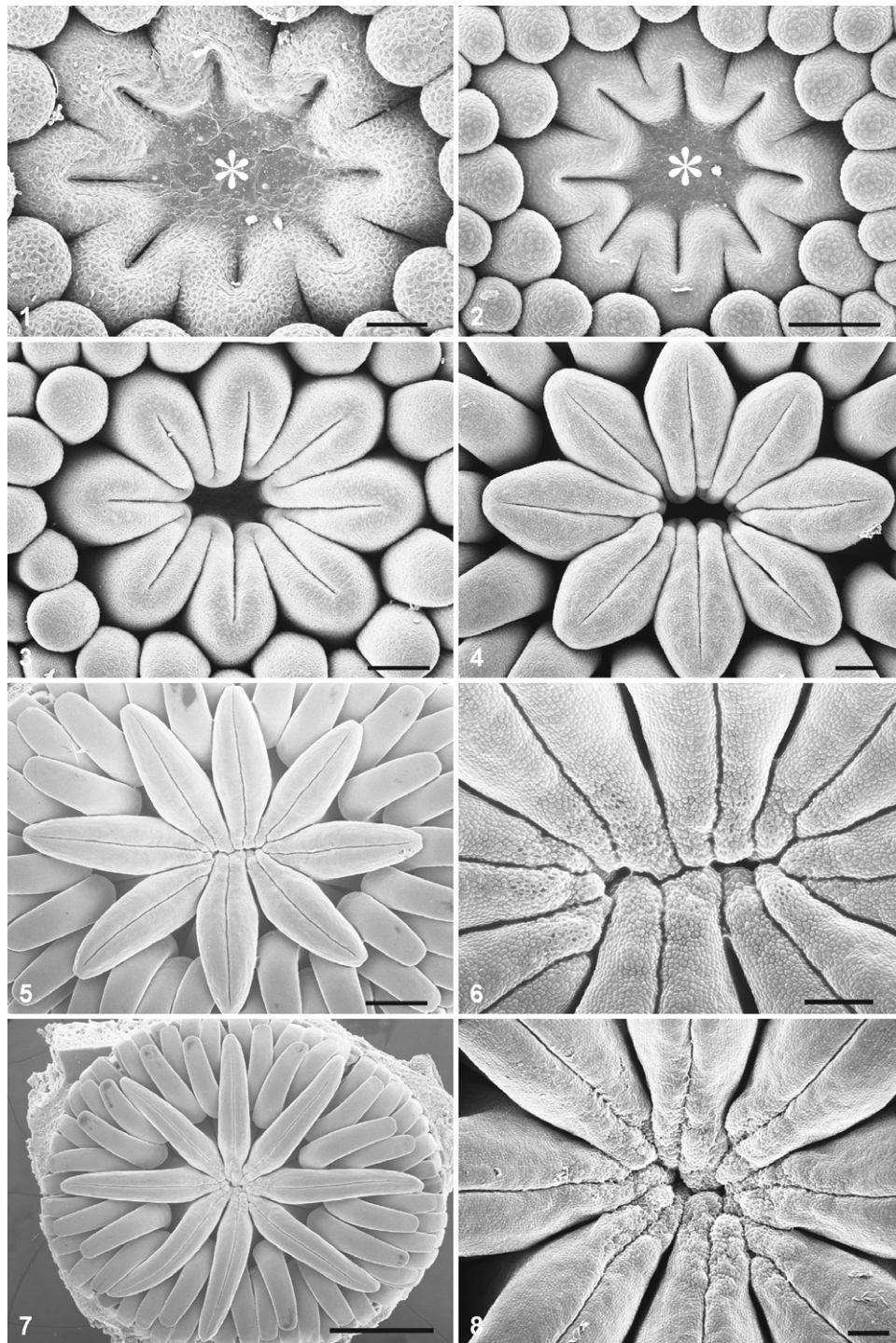
Carpels are arranged in either whorled or spiral phyllotaxis, rarely in a more or less irregular fashion (Endress, 1987, 2006; Endress & Doyle, 2007). When they are whorled, they can be in one or several whorls. In gynoecia with spiral carpel phyllotaxis, the carpels may form one (e.g. *Illicium* L.; Robertson & Tucker, 1979; Endress, 2001) or several (e.g. *Magnolia* L., Zagórska-Marek, 1994; Calycanthaceae, Staedler, Weston & Endress, 2007) series. If in a spiral gynoecium the carpels are not in just one series, one may formally count the number of carpels on a parastichy of the parastichy set with the steepest contact parastichies and use this number as the number of series

(Endress, 2006). By far the most common pattern is an arrangement of the carpels in a single whorl and more intricate forms derived from this condition. In eudicots, syncarpous gynoecia are almost always single-whorled. Exceptions with two whorls are known from the navel oranges, *Citrus sinensis* Osbeck (Lord & Eckard, 1985), the cultivated pomegranate, *Punica granatum* L., and *Gyrostemon ramulosus* Lehm. (Hufford, 1996). In *Citrus* L. and *Gyrostemon* Desf., the second whorl is irregular. In general, the presence of a single whorl is predominant in core eudicots and monocots, but also occurs partially or consistently in most families of the early branching eudicots and in a number of families among magnoliids (Endress & Doyle, 2007) and among the ANITA grade (Endress, 2001). Therefore, I mainly concentrate on multicarpellate gynoecia with all carpels in one whorl or series.

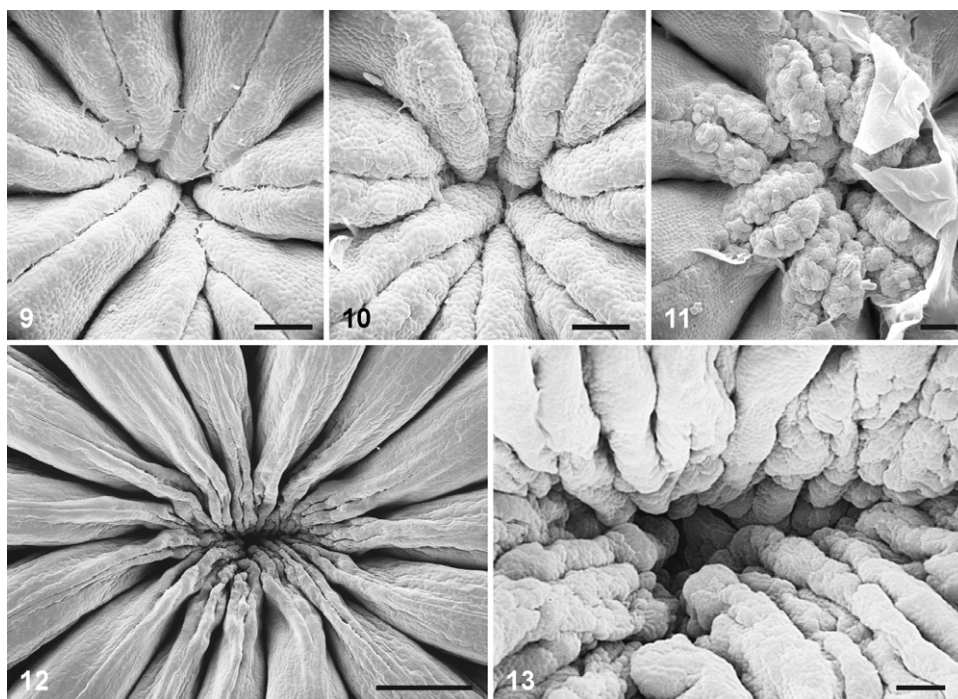
IMPRECISE CONNECTION OF THE CARPEL FLANKS IN THE CENTRE OF MULTICARPELLATE GYNOCIA DURING CLOSURE

Although it is no problem in geometry to have 15 radii meeting exactly in the midpoint of a circle, this is impossible for the ventral slits of the carpels of a 15-carpellate gynoecium for morphogenetic reasons. It is similar to the old problem of cutting a round cake regularly into 15 pieces. The meeting of the carpels in the centre of the gynoecium is more or less symmetrical if only two to five carpels are present (as is mostly the case in angiosperms). However, it becomes less symmetrical when there are a larger number of carpels. If there are too many carpels, a clean closure with a connection in the centre becomes difficult or impossible because of a lack of space. This can be seen in surface views with a scanning electron microscope or in transverse microtome sections of the gynoecium in the uppermost part of the syncarpous zone. It is especially conspicuous if the stigmatic branches radiate from the ovary outwards. Good examples are species of *Dillenia* L. (Dilleniaceae).

Dillenia spp. have a syncarpous gynoecium with long free styles. In early development, the gynoecium of *D. suffruticosa* (with mostly eight carpels) is open (Fig. 1). The carpels are basally connected at the ventral part of the flanks with their neighbours. These connected regions of the flanks grow upwards by elongation of the carpel bases, and each of these connected regions forms a shoulder in which the upper part of the carpels is oriented radially (Figs 1, 2). Closure of the gynoecium with resulting angiospermy proceeds in two steps. First, the free parts of the individual carpels close by thickening of the flanks (Figs 2, 3). Only then, as the shoulders become more prominent by their expansion towards the



Figures 1–8. *Dillenia suffruticosa* (Dilleniaceae). Floral buds. Gynoecium development, all gynoecia with eight carpels. Scanning electron micrographs. Fig. 1. Individual carpels still more or less open. Fig. 2. Individual carpels more or less closed, forming ventral slits. Fig. 3. Centre of gynoecium beginning to close. Fig. 4. Process of central closure more advanced. Carpel shoulders conspicuous. Fig. 5. Centre of gynoecium irregularly closed, carpel shoulders beginning to form irregular bumps. Fig. 6. Close-up of Fig. 5. Fig. 7. Older stage. Irregular bumps in the centre more conspicuous. Fig. 8. Close-up of Fig. 7. Remaining floral apex marked with asterisk. Scale bars: 50 μm (Fig. 1); 100 μm (Figs 2–4, 6, 8); 300 μm (Fig. 5); 1 mm (Fig. 7).



Figures 9–13. *Dillenia* (Dilleniaceae). Floral buds. Gynoecium development. Scanning electron micrographs. Figs 9–11. *Dillenia alata*. Gynoecium development, all gynoecia with seven carpels. Fig. 9. Individual carpels closed. Centre of gynoecium irregularly closed. Fig. 10. Carpel shoulders beginning to form irregular bumps. Fig. 11. Irregular bumps in the centre conspicuous, partly covered by remnants of secretion. Figs 12, 13. *Dillenia philippinensis*. Gynoecium with 15 carpels. Fig. 12. Centre of gynoecium irregularly closed. Fig. 13. Close-up of centre of gynoecium, showing the bumpy surface of the carpels. Scale bars: 100 μ m (Figs 9–11, 13); 1 mm (Fig. 12).

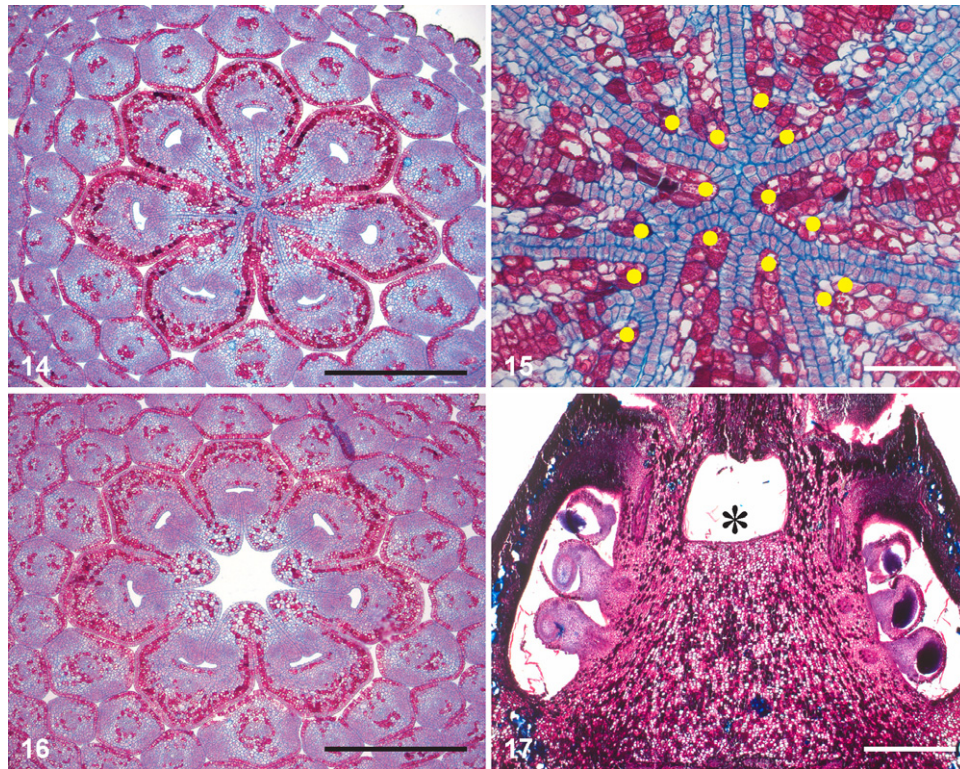
centre of the gynoecium, does the central opening of the syncarpous zone, shared by all carpels, close over the centre of the remaining floral apex (Figs 4, 5). In a view from the top it can be seen that the flanks of the carpels are slightly unequal before the central opening closes (Figs 3, 4). As a consequence, when the carpels meet in the centre, they postgenitally unite in an unorderly fashion (Figs 5–10). In this area of postgenital union, there is hypertrophic growth, resulting in an irregularly bumpy surface, which appears to be secretory (Figs 5–8). The individual carpels appear to enlarge with slightly different rates and the remaining open spaces tend to be filled with these bumps (Fig. 8). The irregular space filling and bumpy surface are especially conspicuous in *Dillenia* because the styler branches are oriented horizontally. The stigmas are located at the tip of each carpel. Whether the bumpy area in the centre of the gynoecium has an additional stigmatic function has not been critically investigated, but is unlikely (Endress, 1997).

In *D. alata*, the bumpy surface and secretion in the centre of the gynoecium where the carpel flanks meet is even more conspicuous (Figs 9–11) (see also Endress, 1997). In *D. philippinensis*, with more (c. 15) carpels, the irregularities in the centre are more

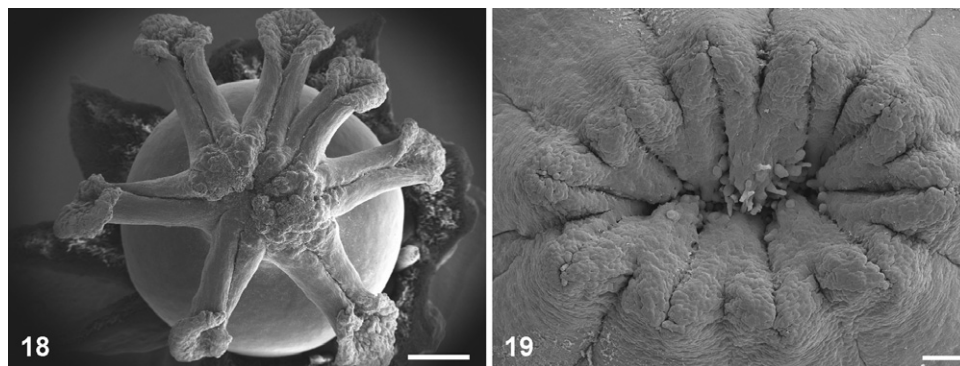
pronounced than in the other two species studied (with seven or eight carpels) (Figs 12, 13).

Because the spaces are not exactly the same size when the carpels meet in the centre, the individual carpel ventral edges attain a somewhat different size, as shown in transverse sections in *D. alata* (Figs 14, 15). The remaining floral apex is not involved in carpel formation (see section below). Transverse microtome sections of anthetic gynoecia show that the carpels are postgenitally united over the centre only in the upper part (Figs 14, 15), whereas they are not united in the centre lower down closer to the remaining apex (Fig. 16). The epidermis of the postgenitally united areas appears meristematic or secretory (Fig. 15). In longitudinal sections, the remaining apex is flat and cell rows below the apex indicate that simple longitudinal growth takes place in this region (Fig. 17). It is not clear whether there is a functional compitum. This will only be possible to determine in experimental studies.

In *Flacourtia rukam* (Salicaceae), with up to eight carpels, the mature styles are horizontally spreading, as in *Dillenia*, and the closure of the gynoecium is similarly irregular and bumpy (Fig. 18). The same is true in *Medusagyne* Baker (Ochnaceae) with c. 15–24



Figures 14–17. *Dillenia alata* (Dilleniaceae). Gynoecia. Microtome sections. Figs 14–16. Gynoecium of floral bud. Transverse sections. Fig. 14. Level of the style. Carpels connected along the flanks and in the centre. Fig. 15. Close-up of the centre of Fig. 14, showing the irregular connection of the edges of the carpel flanks (edges marked with yellow dots). Fig. 16. Level lower down, immediately above the ovary. Carpels connected only along the flanks, leaving an empty space in the centre, above the remaining floral apex, which was not involved in carpel formation. Fig. 17. Gynoecium of anthetic flower. Median longitudinal section. Remaining floral apex marked with asterisk. Empty space in the centre corresponding to that in Fig. 16. Note the vertical cell rows below the remaining floral apex (between the carpels). Scale bars: 100 μm (Fig. 15); 500 μm (Figs 14, 16); 1 mm (Fig. 17).



Figures 18, 19. Irregular gynoecium closure in the centre. Scanning electron micrographs. Fig. 18. *Flacourtia rukam* (Salicaceae). Anthetic flower. In the centre of the gynoecium, the carpels have bumpy surfaces with secretion. Fig. 19. *Munroidendron racemosum* (Araliaceae). Floral bud. The papillae in the area of gynoecium closure will later develop into hairs. Scale bars: 100 μm (Fig. 19); 1 mm (Fig. 18).

carpels (Matthews, Amaral & Endress, 2012: fig. 27). In *Munroidendron* Sherff (Araliaceae), with only short styles, the closed centre also has a bumpy surface, on which hairs grow later (Fig. 19).

UNUSUAL BEHAVIOUR OF THE FLORAL APEX IN
MULTICARPELLATE GYNOCIA: ITS CENTRE DOES NOT
TAKE PART IN GYNOCIMUM MORPHOGENESIS

Commonly, the entire floral apex becomes involved in gynoecium formation (Fig. 39A, B). However, especially in multicarpellate gynoecia, in a number of examples from many different angiosperm groups, the centre of the floral apex is not involved in gynoecium formation and remains morphologically and histologically undifferentiated ('empty') (Fig. 39A, C). This becomes more conspicuous as the carpel number of the gynoecium increases. The following list gives examples of gynoecia with the central area of the floral apex not involved in gynoecium formation:

Nymphaea L. (Nymphaeaceae, Nymphaeales) (Troll, 1933b: figs 5–7, 11, 13, 15; this paper: Fig. 37);
Illicium (Schisandraceae, Austrobaileyales) (Williams, Sage & Thien, 1993; Endress, 2001; this paper: Fig. 38);

Alisma triviale Pursh (Alismataceae, Alismatales) (Singh & Sattler, 1972: fig. 25);

Hydrocleys nymphoides (Willd.) Buchenau [Limnocharitaceae (= Alismataceae), Alismatales] (Sattler & Singh, 1973: figs 9, 10);

Limnocharis flava Buchenau [Limnocharitaceae (= Alismataceae), Alismatales] (Troll, 1932: figs 2, 4, 5; Kaul, 1976: figs 16, 18);

Enhalus Rich. (Hydrocharitaceae, Alismatales) (Troll, 1931: figs 3, 5);

Palandra O.F.Cook (Arecaceae, Arecales) (Uhl & Dransfield, 1984: figs. 37, 38);

Nigella L. (Ranunculaceae, Ranunculales) (Troll, 1933a: fig. 5; Kaussmann & Neitzel, 1972: fig. 10; Lang, 1977: figs 21, 23, 44);

Aeonium Webb & Berthel., *Adromischus* Lem., *Crassula* L., *Greenovia* Webb, *Sempervivum* L. (Crasulaceae, Saxifragales) (Wassmer, 1955: figs 44–47; this paper: Fig. 27);

Dillenia (Dilleniaceae, Dilleniales) (this paper: Figs 1, 2, 17);

Medusagyne (Ochnaceae, Malpighiales) (Dickison, 1990b: figs 3–6; Dickison, 1990c: figs 31–33; Matthews *et al.*, 2012: fig. 27g);

Gyrostemon Desf., *Tersonia* Moq. (Gyrostemonaceae, Brassicales) (Hufford, 1996: figs 5, 7–9, 11–16, 45–51; Endress, 2006: fig. 16H, I; this study: Figs 20–25);

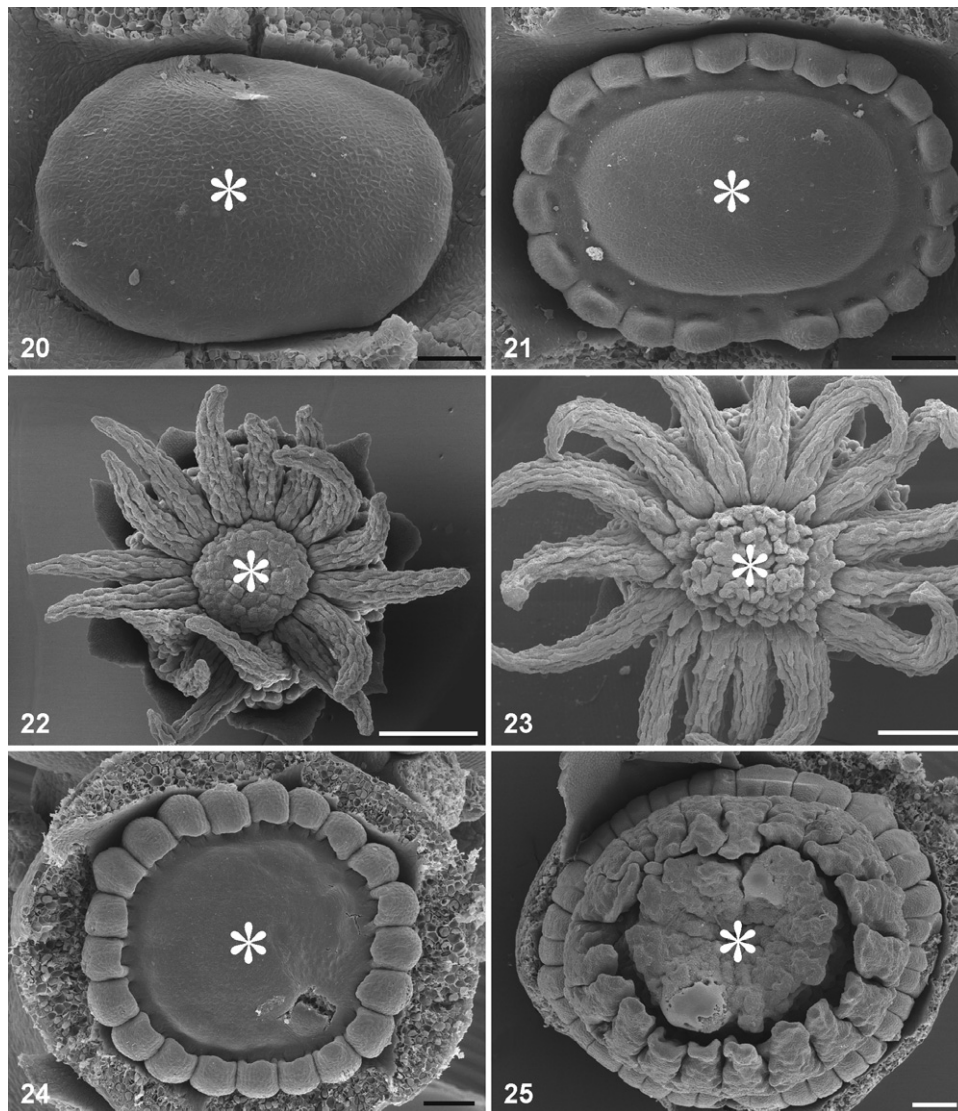
Kitaibelia Willd., *Malope* L. (*Malope* alliance, Malvaceae, Malvales) (van Heel, 1995: figs 15–18, 20–22; Endress, 2006: fig. 16E–G; this study: Figs 28–36);

Pleiogynium Engl. (Anacardiaceae, Sapindales) (Bachelier & Endress, 2009: figs 21, 41K, L, 49; this paper: Fig. 26);

Beiselia Forman (Burseraceae, Sapindales) (Bachelier & Endress, 2009: figs 4, 49).

What does this mean in terms of development? When a gynoecium is initiated, i.e. just before carpel primordia or the gynoecium primordium become(s) visible at the surface of the floral apex, the apex becomes activated and the meristematic area may deepen (Grégoire, 1938: figs 1, 2; Singh & Sattler, 1972: fig. 25; Endress, 1980b: fig. 13), whereas areas between carpels or in the centre of the apex do not become involved in this activation or are involved to a lesser degree. Commonly, this change encompasses the entire floral apex, including its central area. However, in some, mainly multicarpellate gynoecia, when the gynoecium is initiated, the centre of the floral apex is apparently not activated by the meristem of the carpel initials and is thus not involved in organ formation, but remains unused, which is seen in scanning electron micrographs by the fact that the centre of the floral apex does not change its shape but remains flat. There may be some influence on this unspent centre from the carpels in later stages of development, but, in general, this area remains parenchymatic, morphologically and histologically poorly differentiated. It may grow (elongate) passively with the growth of the carpels. In earlier literature, this undifferentiated tissue in the centre between the carpels was thought to represent the 'axis'. However, the 'axis' is not well defined because, in contrast with the floral organs, it is not a lateral or terminal organ. It is just what is left of a shoot when the leaves are subtracted. It is not well delimited. I prefer to speak of an undifferentiated remainder of the floral apex (see also the excellent discussion in Rohweder, 1963: pp. 83–87). This apex remainder grows (elongates and widens) passively with the carpels when they grow and differentiate. Histologically, the apex remainder represents a simple parenchyma, often with regular cell rows, which indicate that it has not undergone complex morphogenetic processes. In some cases, it may produce hairs or emergences (Figs 22, 23, 25).

A problem connected with the interpretation of the poorly differentiated central area between the carpels is whether such gynoecia are better regarded as syncarpous or apocarpous, especially in cases in which this central area becomes elongated during development. There has been some dispute about this (e.g. Troll, 1933a; Rohweder, 1967; Kaussmann & Neitzel, 1972; Lang, 1977). If gynoecia are described *sensu* Leinfellner (1950) (i.e. by using transverse microtome section series perpendicular to the longitudinal axis of the flower), this area would belong to the synascidiate zone. In a more differentiated approach, one may



Figures 20–25. *Gyrostemon* (Gyrostemonaceae). Remaining floral apex not involved in gynoecium differentiation and not enclosed in gynoecium during development. Scanning electron micrographs. Figs 20–23. *Gyrostemon brevipes*. Fig. 20. Gynoecium after carpel initiation (the shallow wavy line at the periphery is formed by the incipient carpels). Fig. 21. Later stage, with 21 carpels surrounding large inactive remaining floral apex. Fig. 22. Gynoecium with 16 closed carpels surrounding remaining floral apex. Fig. 23. Gynoecium with 15 closed carpels surrounding remaining floral apex; floral apex with pointed excrescences. Figs 24, 25. *Gyrostemon racemigerus*. Fig. 24. Gynoecium with 21 carpels surrounding large inactive floral apex. Fig. 25. Later stage with 21 closed carpels surrounding remaining floral apex; floral apex with irregular bumps. Remaining floral apex marked with asterisk. Scale bars: 50 μm (Fig. 20), 100 μm (Figs. 21, 24); 200 μm (Fig. 25); 1 mm (Figs 22, 23).

consider that, in some cases, the base of the carpels is not perpendicular to the longitudinal axis of the gynoecium, but that each carpel has an oblique base because it is initiated on a convex, not horizontal, floral apex.

The floral base bearing the carpels can be flat or convex. In the first case, the unspent floral apex appears to be situated ‘at the base’ of the carpels; in the second case, it can be ‘at a level of the tip or even above the tip’ of the carpels (see also Erbar, 1983;

Leins & Erbar, 2010). It is practically less feasible to describe the situation as a distortion of the floral apex. Thus, for the sake of simplicity, the inclination of the apex is usually not considered in descriptions, although, in some sense, it would be more realistic to do so (Rohweder & Endress, 1983; Leins & Erbar, 2010). The best would be to consider a combination of both in the description, but this would be even more cumbersome.



Figures 26, 27. Remaining floral apex not involved in gynoecium differentiation and not enclosed in gynoecium during development. Scanning electron micrographs. Fig. 26. *Pleio gynium solandri* (Anacardiaceae). Open flower. Fig. 27. *Aeonium tabuliforme* (Crassulaceae), anthetic gynoecium; remaining floral apex relatively small. Remaining floral apex marked with asterisk. Scale bars, 500 μm .

ENCLOSURE OR EXPOSURE OF THE UNDIFFERENTIATED REST OF THE FLORAL APEX DURING GYNOCEDIUM DEVELOPMENT

Commonly, the inactive centre of the floral apex of multicarpellate syncarpous gynoecia becomes covered and enclosed during development by the carpels and is thus not seen from the outside at anthesis, as shown, for example, for *Dillenia* (Figs 1–17) and *Kitaibelia* (Figs 32–36). In these cases, at first the individual carpels close, and then the central space that is left in the gynoecium is closed by the carpel flanks protruding towards the centre and fusing post-genitally (*Dillenia*), or by the connivent and thickening individual styles but without fusion (*Kitaibelia*).

However, in extreme cases, the undifferentiated rest of the floral apex is exposed, and is visible up to anthesis (and later) in syncarpous gynoecia, such as in *Gyrostemon* (Gyrostemonaceae) (Figs 20–25), *Pleio gynium* (Anacardiaceae) (Fig. 26) or *Aeonium* (Crassulaceae) (Fig. 27) (see also Hufford, 1996; Endress, 2006; Bachelier & Endress, 2009). In *Gyrostemon* (Figs 23, 25), the exposed apex exhibits irregular protuberances which appear to be secretory (Endress, 2006), but their function is unknown. In enclosed unspent apices, the surface remains smooth.

In apocarpous gynoecia, an unspent area in the centre of the floral apex is common (e.g. van Heel, 1983). In rare cases, it forms an exposed protrusion that functions in pollen tube transmission (*Illicium*, Austrobaileyales, Williams *et al.*, 1993; and, perhaps, *Nymphaea* and relatives, Nymphaeales, Schmucker, 1932; see also Endress, 2001; Williams *et al.*, 2010) (Figs 37, 38). The early Cretaceous fossil *Monetianthus* E.M.Friis, K.R.Pedersen, von Balthazar, G.Grimm & P.R.Crane (Nymphaeales) had a similar protrusion in the centre of the gynoecium (Friis *et al.*, 2009). In some (apocarpous) Crassulaceae, a compi-

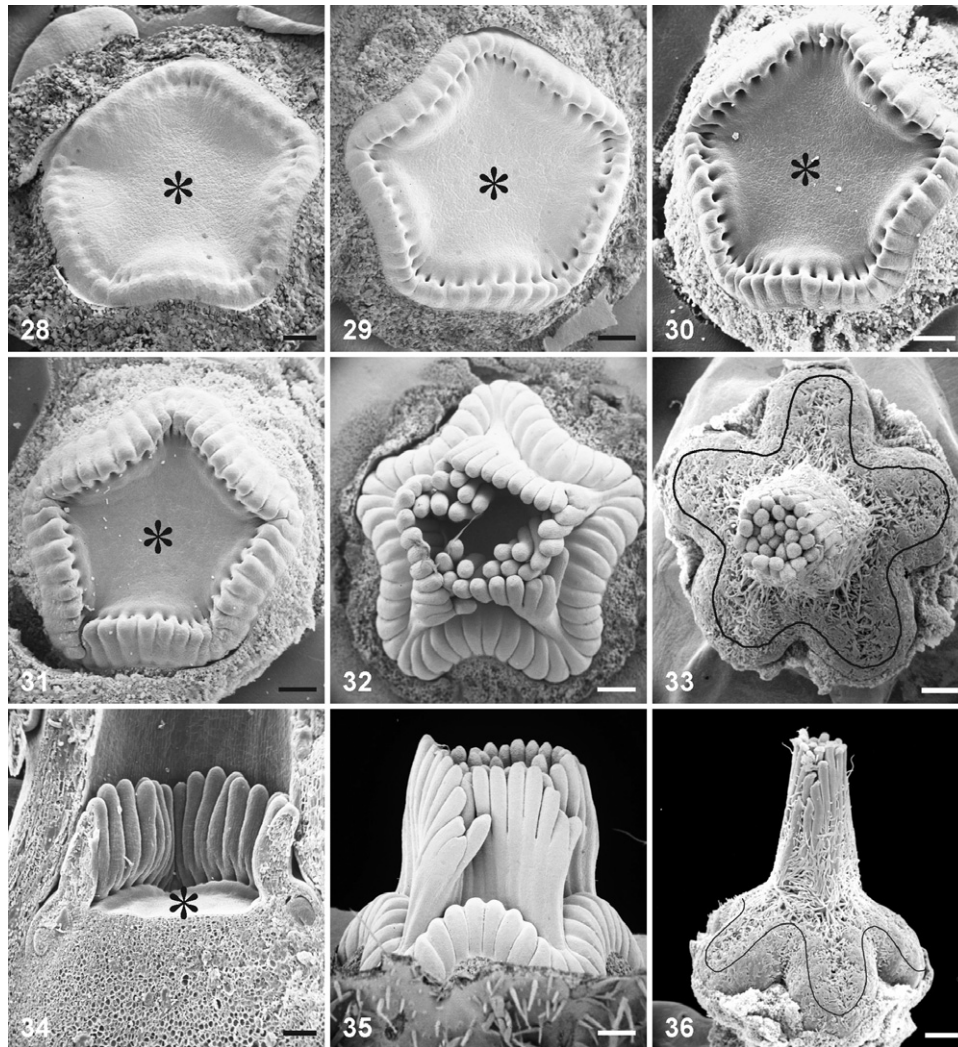
tum may be present and functional above the floral apex, directly from ventral slit to ventral slit (Wang, Armbruster & Huang, 2012).

DEFORMATION OF THE CARPEL WHORL IN MULTICARPELLATE GYNOCEDIA AND PARTIAL RETENTION OF THE COMPITUM

If, in a whorl of floral organs, the midpoints of all adjacent organs are connected by a line, this line is commonly a circle or, more exactly, a polygon. However, in a multicarpellate whorl, the line often deviates from a circle or polygon and is more complex. It is a variously deformed circle or polygon, which results by differential growth of the floral sectors: (1) an only slightly irregular circle; (2) an ellipse; (3) a convoluted line forming an H-shaped line during development (the H-shaped line forming double rows of carpels, with the carpels of the two rows directed towards each other); or (4) a sinuous, wave-like line forming a star-shaped line during development (the star-shaped line forming double rows of carpels, with the carpels of the two rows directed towards each other). In the case of a star, the number of loops may reflect the evolutionarily ancestral number of carpels or, at least, reflect the number of organs in the preceding whorl, which tends to form a mould for the following whorl during development.

I describe these four different patterns with examples.

- 1 A slightly irregular circle was shown above for *Dillenia alata* (Dilleniaceae, Fig. 14), in which the carpel flanks meet in an irregular fashion in the centre of the gynoecium. Similar cases are common. They are illustrated here, in addition, with *Gynotroches* Blume (Rhizophoraceae, Fig. 40), *Crossostylis* Forst. (Rhizophoraceae, Fig. 41), *Tro-*

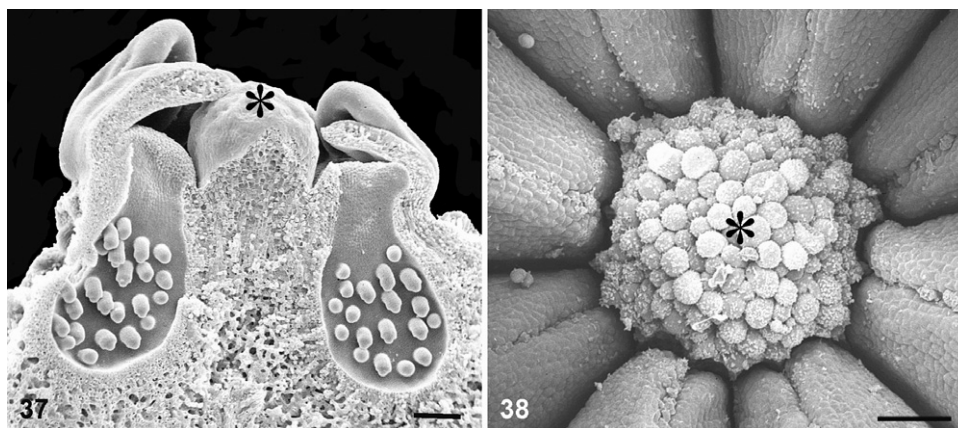


Figures 28–36. *Kitaibelia vitifolia* (Malvaceae). Gynoecium development. Remaining floral apex not involved in gynoecium differentiation, but enclosed in gynoecium during development. Carpel whorl at first pentagonal becoming star-shaped. Closure of gynoecium by carpel thickening. Ovaries uniovulate, strongly bulged. Scanning electron micrographs. Figs 28–33. From above. Figs 34–36. From the side. Fig. 28. Carpels initiated. Fig. 29. Inner surface of each carpel more prominent, especially at the five corners of the gynoecium. Fig. 30. The five corners becoming more prominent. Fig. 31. Carpel bulging on the dorsal side more conspicuous. Fig. 32. Closure of gynoecium progressing, carpels strongly bulged. Fig. 33. Gynoecium closed, carpel arrangement star-shaped, with two carpels facing each other in each ray. Fig. 34. Longitudinal section through a younger gynoecium showing the vast empty space in the centre that is not involved in carpel differentiation, dorsal bulging of carpels and elongation of the upper part of the carpels. Fig. 35. Same as Fig. 32, from the side. Fig. 36. Same as Fig. 33, from the side. Remaining floral apex marked with asterisk. Looped carpel whorl marked with line in Figs 33 and 36. Scale bars: 50 μm (Fig. 28); 100 μm (Fig. 29); 200 μm (Figs 30, 31, 34); 500 μm (Figs 32, 35); 1 mm (Figs 33, 36).

chodendron Siebold & Zucc. (Trochodendraceae, Fig. 42) and *Couroupita* Aubl. (Lecythidaceae, Fig. 43).

- 2 Often the ellipse becomes somewhat compressed or flattened, so that most carpels come to lie more or less in a double row facing each other (instead of being separated for a distance if they lay on a smooth circle). This pattern often occurs together

with pattern (1), such as in *Dillenia* spp. (Dilleniaceae) with more carpels than *D. alata* (Figs 3–8, 13, 15, 16), *Couroupita* (Lecythidaceae, Fig. 44), *Duabanga* Buch.-Ham. (Lythraceae, Fig. 45), *Davidia* Baill. (Cornaceae, Fig. 46), *Clusia* L. (Clusiaceae, Fig. 47), *Pavonia* Cav. (Malvaceae, Fig. 48) and *Platystemon* Benth. (Papaveraceae, Figs 49, 50); for *Ochna* L. (Ochnaceae), see Matthews *et al.* (2012). In



Figures 37, 38. Remaining floral apex not involved in gynoecium differentiation, but forming a protrusion functional in the pollen tube pathway (compitum). Scanning electron micrographs. Fig. 37. *Nymphaea tetragona* (Nymphaeaceae). Longitudinal section of gynoecium of floral bud. Fig. 38. *Illicium anisatum* (Illiciaceae). Floral centre of anthetic flower. Remaining floral apex (protrusion) marked with asterisk. Scale bars: 100 μm (Fig. 38); 500 μm (Fig. 37).

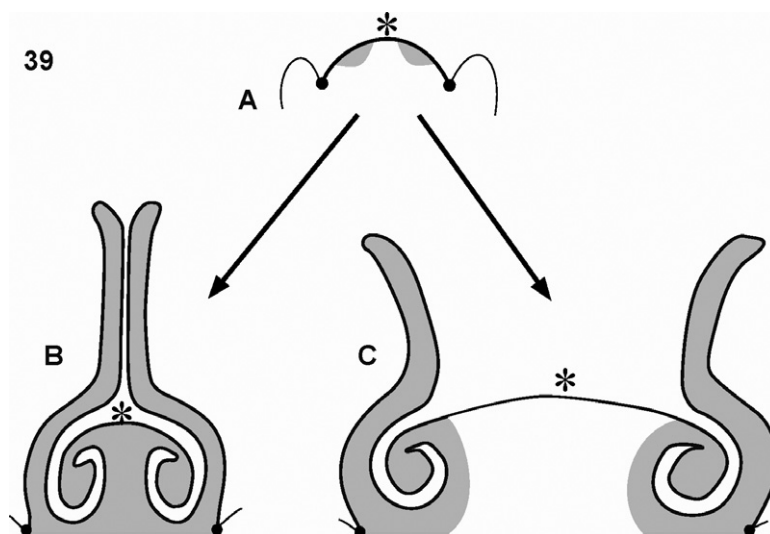
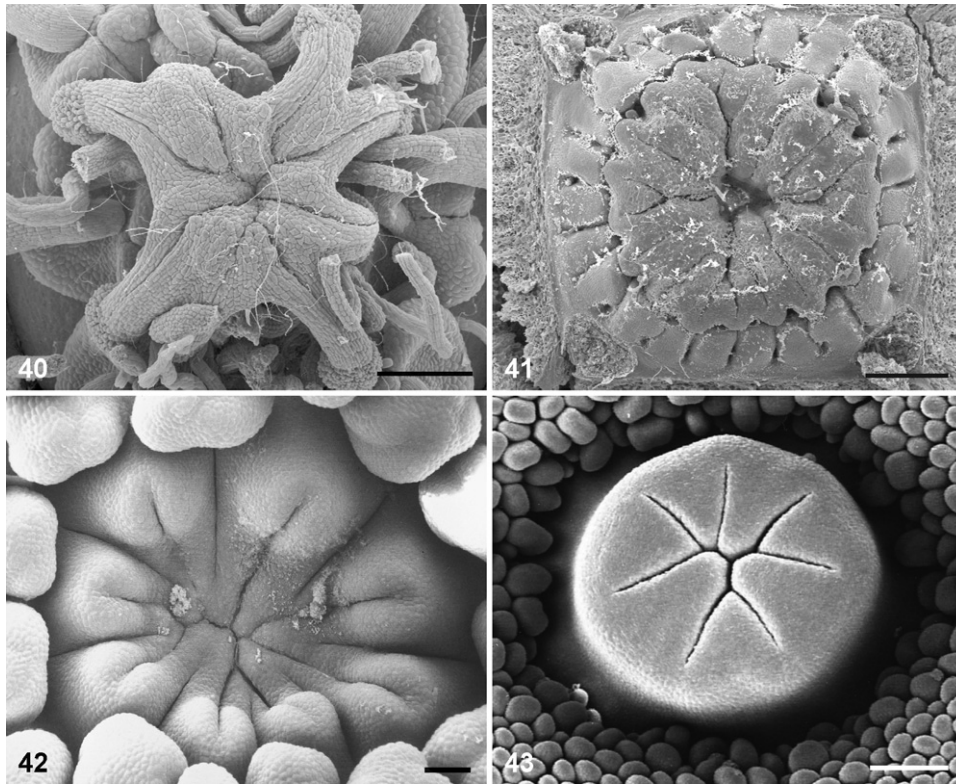


Figure 39. Schematic longitudinal sections of syncarpous gynoecia and different behaviour of the centre of the remaining floral apex. A, Remaining floral apex before gynoecium formation. B, Gynoecium with only a few carpels, with the entire remaining floral apex involved in carpel morphogenesis. C, Multicarpellate gynoecium, with the remaining floral apex (after carpel initiation) not involved in carpel morphogenesis. The thick black line marks the remaining floral apex at the time of gynoecium initiation (in A) and the resulting morphological surface of the gynoecium (in B and C). The asterisk marks the centre of the remaining floral apex. The two dots mark the periphery of the remaining floral apex (in A) and the corresponding periphery of the gynoecium (in B and C). Shaded are the carpel primordia within the floral apex (in A) and the area that is involved in carpel morphogenesis (in B and C).

the groups in which there are such parallel double rows of carpels by ‘flattening’, these rows are present at least above the ovary (in the style), where the compitum is situated. Flatness or formation of a wavy line (complex flat regions), always with double rows of carpels, is a common pattern. In addition, the carpels of one row are always directed towards the carpels of the other row, so that their ventral slits become situated close to each other.

3 Here, the double row of carpels is not only in a single line, but both ends of the line expand, each forming an additional line perpendicular to the primary line, so that the entire pattern has the shape of an ‘H’ (*Sararanga sinuosa* Hemsl., Pandanaceae, Stone, 1961; *Tupidanthus calypratus*, Araliaceae, Sokoloff *et al.*, 2007; this study: Figs 51–53). Sokoloff *et al.* (2007) called this shape for *Tupidanthus* Hook.f. & Thomson ‘butterfly-like’.



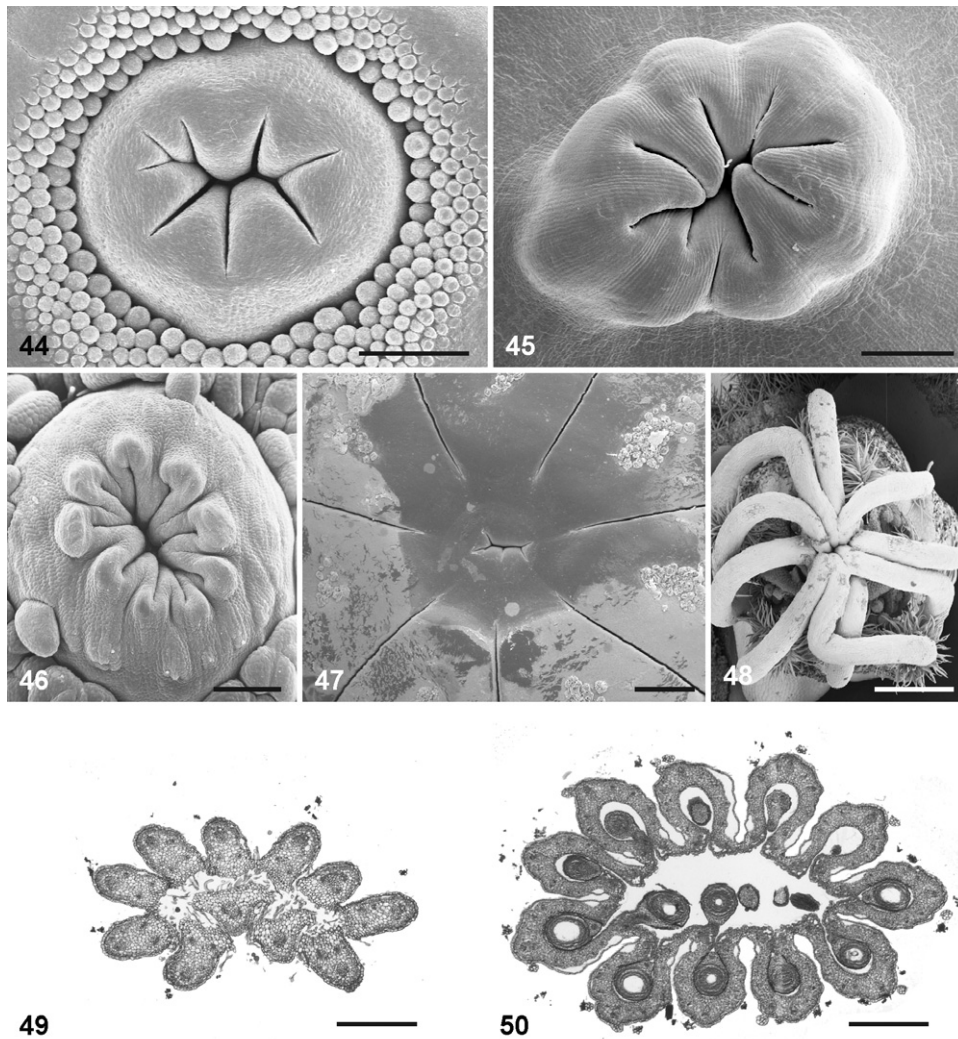
Figures 40–43. Carpel whorl with irregularly circular closure in the centre. Scanning electron micrographs. Fig. 40. *Gynotroches axillaris* (Rhizophoraceae). Anthetic gynoecium. Fig. 41. *Crossostylis grandiflora* (Rhizophoraceae). Anthetic gynoecium. Fig. 42. *Trochodendron aralioides* (Trochodendraceae). Gynoecium of floral bud. Fig. 43. *Couroupita guianensis* (Lecythidaceae). Gynoecium of floral bud. Scale bars, 200 μ m.

4 In the case of a star, the number of rays corresponds to the number of floral sectors, thus five in eudicots (*Kitaibelia*, Malvaceae; *Nolana* L.f., Solanaceae; *Timonius* DC., Rubiaceae; Figs 32, 33, 35, 36, 55) and six in monocots (Triuridaceae). van Heel (1995) used ‘wave-line’, as present in the androecium of all Malvoideae (e.g. van Heel, 1966; Rohweder, 1972; von Balthazar *et al.*, 2004, 2006; Janka *et al.*, 2008) and the gynoecium in the *Malope* alliance (as classified in Bayer & Kubitzki, 2003). Probably the same pattern with a single convoluted whorl of carpels is present in *Palaua* Ruiz & Pav. (Malvaceae) (Huertas, Schneider & Zizka, 2007); one species in the genus has a regular single whorl (Huertas *et al.*, 2007). In addition, the aberrant genus *Octolobus* Welw. (Malvaceae), in which the carpels are said to be in several whorls (Bayer & Kubitzki, 2003) or in a spiral (Cheek & Dorr, 2007), needs detailed study in this respect. In *Nolana* (Solanaceae), the increase in carpel number has been (mis)interpreted as tangential division (Cronquist, 1981; Ronse Decraene & Smets, 1998), whereas it is radial ‘division’ in a comparative

morphological sense in a convoluted whorl. Deroin (1997) did not find any pattern. Di Fulvio (1971) described the gynoecium as two-whorled. Some authors viewed the gynoecium as made up of only a few carpels that are locellate (Bondeson, 2008). However, the gynoecium was interpreted as here and discussed in more detail by Huber (1980).

The different patterns of whorl distortion with an increase in carpel number described here are schematically summarized in Figure 54: (0) regular radial in a gynoecium with only few carpels (Fig. 54A); (1) irregular radial in a moderately multicarpellate gynoecium (Fig. 54B); (2) elliptic and flattened in a more strongly multicarpellate gynoecium (Fig. 54C); (3) flattened and H-shaped in a highly multicarpellate gynoecium (Fig. 54D); and (4) flattened and star-shaped in a highly multicarpellate gynoecium (Fig. 54E).

The common pattern for (2), (3) and (4) is flattening of the whorl and contiguity of the ventral slits of at least some of the carpels. A number of such cases of flattened whorls of carpels have been figured in the

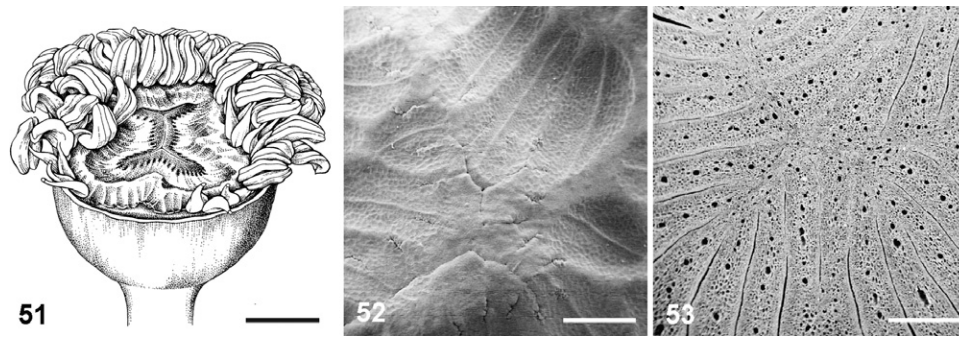


Figures 44–50. Carpel whorl with flattened (compressed) closure, carpels more or less facing each other. Figs 44–48. Scanning electron micrographs. Fig. 44. *Couroupita guianensis* (Lecythidaceae). Gynoecium of floral bud. Fig. 45. *Duabanga grandiflora* (Lythraceae). Gynoecium of floral bud. Fig. 46. *Davidia involucrata* (Cornaceae). Gynoecium of floral bud. Fig. 47. *Clusia rosea* (Clusiaceae). Gynoecium of floral bud. Fig. 48. *Pavonia hastata* (Malvaceae). Anthetic gynoecium. Figs 49, 50. *Platystemon californicus* (Papaveraceae). Anthetic gynoecium, transverse microtome section series. Fig. 49. Upper level with maximal closure of central space of gynoecium. Fig. 50. Level of ovary, showing ovules at two locations: within carpel bulges and in central space of gynoecium. Scale bars: 200 μm (Figs 44–46); 500 μm (Figs 47–50).

literature, but only rarely has their potential function as a compitum been addressed. This potential function was addressed for *Actinidia* Lindl. (Actinidiaceae, Howpage, Vithanage & Spooner-Hart, 1998) and for *Tupidanthus* (Araliaceae) and *Lacandonia* E.Martínez & Ramos (Triuridaceae, Sokoloff *et al.*, 2007). Another aspect of this deformation and compression of the inner (empty) morphological space may simply be architectural to reduce the size of the gynoecium. In Appendix 1, gynoecia with internal

flattening figured in the literature are mentioned for various groups.

If a large number of carpels are arranged in an angled whorl (polygon), the carpels in the angles tend to be further developed than those between the angles (*Alisma* L., Alismataceae, trigonal, Singh & Sattler, 1972: figs 14–16; *Kitabelia*, Malvaceae, pentagonal, this study: Figs 28, 29). In Triuridaceae, the developmental gradient may be in reverse direction (see below).



Figures 51–53. *Tupidanthus calyptratus* (Araliaceae). Fig. 51. Anthetic flower, stamens removed on one side. Carpel whorl extremely polymerous, with complex, H-shaped pattern of gynoecium closure. Figs 52, 53. Gynoecium of floral bud. Only a small part of the gynoecium (ventral slits of several carpels) visible. Fig. 52. Centre of gynoecium, viewed from above. In addition to the ventral slits of several carpels, impression marks of the stamens are visible. Scanning electron micrograph. Fig. 53. Centre of gynoecium. Transverse microtome section. Scale bars: 5 mm (Fig. 51); 1 mm (Figs 52, 53).

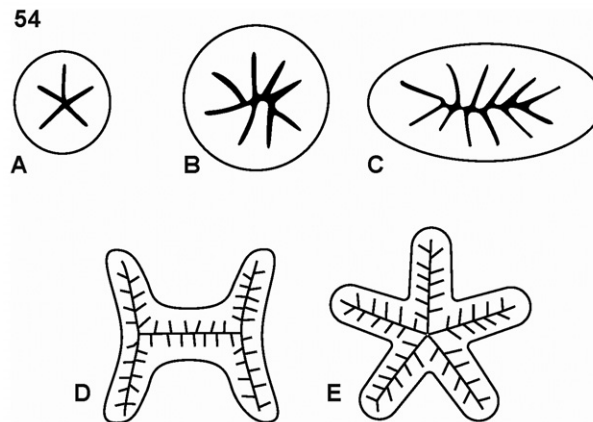


Figure 54. Schematic diagrams of different patterns of carpel whorls and closing of gynoecia. Outline of gynoecium and inner surface (ventral slits) indicated as seen from above or in transverse section. A, Gynoecium with five carpels and regular closure in the centre. B, Multicarpellate gynoecium with irregular circular closure in the centre. C, Multicarpellate gynoecium with flattened (compressed) closure. D, Highly multicarpellate gynoecium with flattened, H-shaped closure. E, Highly multicarpellate gynoecium with flattened, star-shaped closure.

THE UNUSUAL COMPITUM IN THE APOCARPOUS MULTICARPELLATE GYNOCIA OF SOME ALISMATACEAE AND TRIURIDACEAE

Although, in primitively apocarpous flowers, an extra-gynoecial compitum is often present (Endress & Igersheim, 2000a) by the contiguity of stigmas, in evolutionarily secondarily apocarpous flowers a compitum may be restored by partial postgenital union (Endress, Jenny & Fallen, 1983), or it may be lost, if it was present in the syncarpous ancestors, especially in gynoecia with highly increased carpel numbers. The position of the carpels in double rows facing each other may nevertheless allow some pollen tube growth from one carpel to its neighbours (see Triuridaceae, next section). Another unusual method is rearrangement of pollen tubes in the floral base. This

has been found in some Alismataceae in gynoecia with several whorls of free carpels (*Ranalisma* Stapf, Wang *et al.*, 2006; *Sagittaria* L., Wang, Tao & Lu, 2002; Huang, 2003; Wang *et al.*, 2006, 2012), and in Triuridaceae in gynoecia with a single sinuous whorl of free carpels (Márquez-Guzman *et al.*, 1993).

THE EXTREME AND PUZZLING FLOWERS OF TRIURIDACEAE

The numerous free carpels are arranged on ridges in radial double rows in which carpels face each other (figured for *Triuris hexophthalma* Maas by RübSamen-Weustenfeld, 1991: plate 7). This pattern was also shown for *Lacandonia schismatica* E.Martínez & Ramos (Vázquez-Santana *et al.*, 1998),

Peltophyllum luteum Gardner (Rudall & Bateman, 2006: fig. 8B; Rudall, 2008: fig. 8I) and *Triuridopsis peruviana* H.Maas & Maas (Rudall, 2008: fig. 9C). Such unusual arrangement of the carpels led Rudall (2003) and Rudall & Bateman (2006) to propose that these so-called flowers may actually be pseudanthia, which was then refuted by Ambrose *et al.* (2006). Sokoloff *et al.* (2007) and Rudall (2008) later also discussed the hypothesis of 'fasciation, or folding of an enlarged floral apex'. This comes closer to the model of a sinuous single whorl proposed here, with the loops so tightly arranged that they form radial lines (star-shaped pattern, Fig. 54E), and these radial lines may, in the extreme case, in addition, be zig-zag-shaped, so that the carpels of a primary loop may appear in two or more radial lines (e.g. fig. 65 in Ambrose *et al.*, 2006; fig. 10F in Rudall, 2008). The interpretation of the flowers of Triuridaceae as pseudanthia was also influenced by the unusual reproductive structures of the related family Pandanaceae (both families in Pandanales; phylogeny: Davis *et al.*, 2004), which were also discussed as potential pseudanthia (Rudall & Bateman, 2006). From the point of view of the present study, in both families, the reproductive structures are flowers, not pseudanthia. Both families share parallel trends towards greatly increased carpel number per flower with retention of the carpels in a single whorl. The difference is that, in Triuridaceae, this leads to a star-shaped pattern of the whorl (Fig. 54E), whereas, in Pandanaceae (*Sararanga sinuosa*, Stone, 1961: figs 1, 5), it leads to an H-shaped pattern (Fig. 54D). In another related family, Cyclanthaceae, *Cyclanthus* Poit. has inflorescences with the flowers united into several rings, and thus an unusual kind of pseudanthia (Dahlgren, Clifford & Yeo, 1985). The number of original floral units is unknown. Within a ring of united flowers the numerous carpels are positioned in two parallel rings, whereby the carpels of the upper and the lower rings face each other (Dahlgren *et al.*, 1985).

If the interpretation of the gynoecium in Triuridaceae as forming a single sinuous whorl is correct, the interpretation of a centrifugal development of carpels for *Lacandonia* (Ambrose *et al.*, 2006) and other Triuridaceae (Rudall, 2008) does not make sense, because, for a single whorl, the categories centrifugal or centripetal cannot be applied. However, there may be a gradient in carpel maturation within the loops, similar to that shown for *Kitaibelia* (Figs 28, 29).

In this light, it could even be that the so-called 'inside-out' flowers of *Lacandonia* (as first described by Martínez & Ramos, 1989) are not really 'inside-out' if the three stamens are, in fact, positioned at the tip of three upward loops of the sinuous whorl. The

flowers should be revisited to consider this possible interpretation.

DORSAL BULGING OF OVARIES

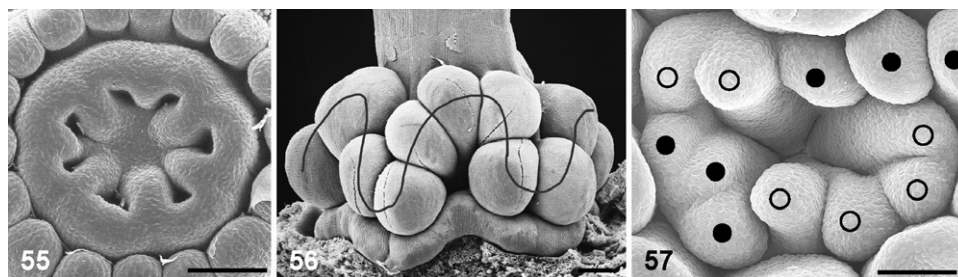
Dorsal bulging of ovaries is widespread, but not frequent, in angiosperms. It appears to be relatively more common in multicarpellate gynoecia than in gynoecia with an average number of carpels (although, where this occurs among the latter, there are some cases known in species-rich families, such as Lamiaceae and Boraginaceae). There may be two reasons why bulging is common in multicarpellate syncarpous gynoecia.

- 1 The bulging of ovaries may originate from an increased distance between the ovaries of carpels on opposite sides of the gynoecium, whereas the distal parts of the carpels are united into a single shared style. As a consequence, the ovaries attain a more horizontal than vertical direction, whereas the stylar part of the carpels is directed upwards. Examples are *Kitaibelia* and other Malvaceae (Fig 32–36), and *Gyrostemon* (Gyrostemonaceae) (Fig. 25).
- 2 Bulging of ovaries is often associated with uniovulate carpels. That there are many cases with uniovulate carpels in multicarpellate gynoecia may be seen as a compensation for increased carpel number. Examples are *Nolana* (Solanaceae) (Fig. 56) and also the genera mentioned in (1).

Bulging in carpels with several ovules is present in *Platystemon* (Papaveraceae) with six to 25 carpels (Karrer, 1991). An oddity of *Platystemon* is that, whereas most ovules are enclosed in the bulged portions, there are some that are in the central space of the ovary. It has been shown that this heteromorphism has a function in seed dispersal (Hannan, 1980; this paper; Fig. 50). The ovules in the central space are later dispersed as naked seeds, whereas the seeds from the ovules that are enclosed in the bulges remain there and are dispersed as single-seeded joints. The two different kinds of diaspores have different properties in their germination biology (Hannan, 1980).

PATHWAYS TO INCREASE CARPEL NUMBER WITHIN ONE WHORL (OR TWO WHORLS) WITH REGARD TO THE FLORAL GROUNDPLAN

Organ number in a flower is often constant from whorl to whorl. Multicarpellate gynoecia with the carpels in a whorl can evolve in three different ways: (1) an increase in organ number per whorl compared with the closest relatives is already present in the perianth; (2) the perianth whorls have remained oli-



Figures 55–57. Possible means of increase in carpel number. Gynoecia of floral buds. Scanning electron micrographs. Fig. 55. *Marcgravia* sp. (Marcgraviaceae). Additional carpels of smaller size (based on originally probably five carpels). Fig. 56. *Nolana paradoxa* (Solanaceae). Multiplication of carpels in five sectors (probably based on originally five carpels) and arrangement in five loops (marked with line). Fig. 57. *Thottea* cf. *macrantha* (Aristolochiaceae). Stigmatic lobes with irregular bifurcation and trifurcation, which appears to indicate an increase in carpel number. However, the retention of four placentae indicates the presence of four carpels. Scale bars, 100 μm .

gomerous, but organ number increases in the androecium by double or multiple positions of organs in a whorl compared with the preceding whorl (discussion in Staedler & Endress, 2009) and is carried on in the gynoecium; in some cases, the androecium at first forms a massive ring of primary meristem, from which stamens form from the secondary primordia; and (3) perianth and androecium whorls are both oligomerous and organ number increase is only in the gynoecium.

Examples of pattern (1) are *Munroidendron* (Araliaceae) with flowers with one stamen whorl (Fig. 19) and *Aeonium* (Crassulaceae) with flowers with two stamen whorls (Fig. 27). For pattern (2), some Alismatales have been studied (Sattler & Singh, 1978). They have double or multiple positions in the androecium, and the gynoecium continues with the organ numbers in each whorl of that in the androecium (*Hydrocleys nymphoides*, *Limnocharis flava*, Limnocharitaceae) or further increases the organ number per whorl (*Alisma triviale*, *Echinodorus amazonicus* Rataj, Alismataceae, Sattler & Singh, 1978). An example for pattern (3) is *Beiselia* (Burseraceae, Bachelier & Endress, 2009).

Another way of (apparent) increasing the carpel number in one whorl is by ‘compression’ of two whorls to the same level, so that they simulate a single whorl. This occurs in some Malvoideae (Malvaceae, van Heel, 1978). Other cases with two carpel whorls, but each whorl still easily distinguished (e.g. *Triglochin* L., Juncaginaceae; Endress, 1995; Remizowa *et al.*, 2010), are not mentioned in the ‘one-whorl’ list of this paper. There are borderline cases between the two possibilities. However, their distinction is not so pertinent within the framework of this paper.

An increase in carpel number may result in unequally sized carpels. An example is *Marcgravia* L. Figure 55 shows a young gynoecium with five normal septa and two smaller septa.

It has been assumed that the formation of a false septum in the median plane of a locule could be a first step for the evolutionary duplication of a carpel (Ronse Decraene & Smets, 1998). However, this seems unlikely on developmental grounds as long as it has not been shown that each ‘half’ of an (evolutionarily) original carpel has a separate primordium.

ONLY SEEMING INCREASE IN CARPEL NUMBER

In syncarpous gynoecia, the number of carpels is easiest to recognize if each carpel has a separate style and the ovary is septate. It is more difficult to recognize if the ovary is not septate or if the carpels are congenitally united up to the top of the gynoecium, and, in the extreme, if development begins without distinct carpel mounds on the floral apex. Specific differentiations may superficially simulate an increase in number.

One possibility is false septa, which develop in the median radius of each carpel, such as in Zygophyllaceae, phyllanthoids (for definition of name, see Xi *et al.*, 2012), perhaps Cistaceae and some Ericales, such as Sapotaceae and Ternstroemiaceae. *Ruizia* Cav. (Malvaceae–Dombeyoideae) has ten locules (Bayer & Kubitzki, 2003), whereas the most common carpel number in this group is five. That the formation of a ‘false’ septum and its ‘transformation’ into a complete and ‘real’ septum is an evolutionary pathway of increase in carpel number (Ronse Decraene & Smets, 1998) has not been substantiated (see above). However, such gynoecia can easily lead to morphological misinterpretations. *Siphonodon* Auct. (Celastraceae) has only five carpels (Matthews & Endress, 2005a), and not ten as reported in Ronse Decraene & Smets (1998). The ten locules belong to five carpels. The misinterpretation was caused by unusual proportions of the ovary (discussion in Matthews & Endress, 2005a). According to Murbeck (1916), *Neurada* L. (Neuradaceae) has five carpels,

but each locule has a false septum so that ten locules are formed. This is a strange statement, because Murbeck (1916) mentions ten styles. In addition, in Ronse Decraene & Smets (1995), the ten free styles are clearly shown and the gynoecium is correctly described as ten-carpellate.

Another possibility for such confusion is an increase in the number of stigmatic lobes, whereas the number of locules remains low. *Thottea* Rottb. (Aristolochiaceae) has four placentae but up to 20 stigmatic lobes (Ding Hou, 1984; Leins, Erbar & van Heel, 1988; see also fig. 39 in Ehrendorfer, 1992). This unusual situation prompted Leins *et al.* (1988) to assume that the stigmatic lobes may not belong to the gynoecium, but may be separate organs of androecial origin (*Thottea* cf. *macrantha* (Boerl.) Ding Hou; this study: Fig. 57). A simpler explanation would be that four carpels are present and that the stigmatic lobes have irregularly bifurcated several times. This has not yet been resolved.

Similar cases are present in *Pyrenacantha* Wight (Icacinaeae), which has multiply forked stigmatic lobes (Sleumer, 1942; Labat, El-Achkar & Rabevohitra, 2006), but the ovary is always unilocular with two ovules, as in other Icacinaeae *s.l.* (Sleumer, 1942). In addition, in many Euphorbiaceae (especially Acalyphoideae and Crotonoideae), the three styles or stigmatic lobes are multiply forked, but three locules are almost invariably retained. Among monocots, forking of stigmatic lobes occurs, for example, in Hydrocharitaceae; *Ottelia* Pers. has either three to ten carpels (Cook & Urmi-König, 1984) or 3–20 (Cook, Symoens & Urmi-König, 1984), depending on the interpretation of the gynoecium.

CO-VARIATION BETWEEN STAMEN AND CARPEL NUMBER WITHIN FLOWERS

Ronse Decraene & Smets (1998) discussed co-variation between stamen and carpel number within flowers using many examples. The recently revised genus *Plerandra* A.Gray (Araliaceae) with multicarpellate gynoecia, which shows this co-variation, may be mentioned here (Lowry, Plunkett & Frodin, 2013). The tendency for organ number increase in androecium and gynoecium is paralleled in the subgenera. The subgenus *Plerandra* with the highest carpel number (5–19) also has the highest stamen number (15–500) (Lowry *et al.*, 2013).

CO-VARIATION BETWEEN FLOWER SIZE AND CARPEL NUMBER

Another kind of co-variation is between flower size and carpel number. There is a trend of occurrence of gynoecia with an increased number of carpels in large

flowers. In many families or genera, the taxa with multicarpellate gynoecia (with the carpels in a whorl) have larger flowers than those with a lower number of carpels (the unusual floral size is, in some cases, even expressed in the epithet of the name).

This is shown by the following examples:

Dillenia megalantha Merr.: 14–16 carpels (vs. other species of the genus, except for *D. indica* L.; Dilleniaceae; Hoogland, 1952);

Conostegia macrantha O.Berg ex Triana: 19–22 carpels (vs. other species of the genus; Melastomataceae; Wanntorp *et al.*, 2011);

Cistus ladanifer L.: ten carpels (vs. other species of the genus; Cistaceae; Janchen, 1925);

Strasburgeria robusta (Vieill. ex Panch. & Sebert) Guillaumin: four to seven carpels (monotypic, vs. sister genus *Ixerba* A. Cunn.; Strasburgeriaceae; Dickison, 1981; Matthews & Endress, 2005b);

Duabanga grandiflora Walp.: four to nine carpels (vs. most other Lythraceae; Graham, 2007);

Roussea simplex Sm.: five to seven carpels (monotypic, vs. other genera of the family; Rouseaceae *sensu* Koontz, Lundberg & Soltis, 2007; Tank & Donoghue, 2010) [the number of five to eight carpels for *Carpodetus serratus* J.R.Forst. & G.Forst. given by Bense & Palser (1975), is possibly erroneous, as Shore (1969) and Gustafsson (2007) did not mention more than five carpels];

Brexia madagascariensis Thou. ex Ker Gawl.: five to seven carpels (monotypic, vs. other genera of the family; Celastraceae; Simmons, 2004; Matthews & Endress, 2005a);

Crossostylis grandiflora Brongn. & Gris: 20–26 carpels (vs. other species of the genus; Rhizophoraceae; Setoguchi, Ohba & Tobe, 1996);

Drypetes gossweileri S.Moore: six or seven carpels (vs. other species of the genus; Putranjivaceae; Matthews & Endress, 2013);

Lewisia rediviva Pursh: four to nine carpels (vs. other species of the genus and other genera of the family; Montiaceae; Mathew, 1989; Carolin, 1993);

Portulaca grandiflora Hook.: six or seven carpels (vs. other species of the genus; Portulacaceae; Rocén, 1927).

PATTERNS OF EVOLUTION OF MULTICARPELLATE FLOWERS

An interesting phenomenon is that, within families in which groups with very high carpel numbers occur, those with the highest carpel numbers are always phylogenetically highly nested (examples in Appendix 1). This is the case in Annonaceae (up to 400 carpels) (phylogeny: Chatrou *et al.*, 2012; Couvreur *et al.*, 2012), Monimiaceae (up to 2000 carpels) (phylogeny: Renner *et al.*, 2010), Alismataceae (up to 600 and

more carpels) (phylogeny: Chen *et al.*, 2012), Ranunculaceae (up to 10 000 and more carpels) (phylogeny: Wang *et al.*, 2009) and Rosaceae (up to 100 and more carpels) (phylogeny: Potter *et al.*, 2007).

In clades in which multicarpelly occurs, this feature may have evolved several times or evolved back to paucicarpelly. Thus, where there is a predisposition for multicarpelly to evolve, this may be an easy process. An example is *Plerandra* (Araliaceae). From the data given in the revision of the genus by Lowry *et al.* (2013), it appears that there is such flexibility. The genus contains six subgenera, in which the following ranges of carpel number occur: (two or) three, (two to) three to five, 8–12, 5–13, 5–10 (to 15), 5–19 (Lowry *et al.*, 2013). As the number five for the carpel range occurs in four of these six subgenera (and also for the stamen range), it may be the basal number for stamens and carpels in the genus.

It appears, in general, that, in groups with highly synorganized flowers, multicarpellate gynoecia are lacking. This is the case in the families with the most complex flowers, such as Apocynaceae and Orchidaceae. It is also true for other groups with synorganization of the androecium and gynoecium and secondary pollen presentation, such as Asteraceae and most Rubiaceae, and likewise in the groups with elaborate monosymmetric flowers, such as Fabaceae and all the families of Lamiales. For such elaborate floral architectures, a low and stable organ number appears to be important (see also Endress, 1990, 2011).

MACROSYSTEMATIC DISTRIBUTION OF MULTICARPELLATE GYNOECIA

In the 63 orders of angiosperms (plus Dasypogonaceae, Sabiaceae, Dilleniaceae and Boraginaceae, not assigned to orders), recognized by APG III (2009), 37 (59%) contain at least one multicarpellate species (Appendix 1). None of the 63 orders is completely multicarpellate (i.e. all contain at least one non-multicarpellate species), whereas 21 are completely non-multicarpellate and 58 contain at least one completely non-multicarpellate family (Appendix 1).

In the ANITA grade, the range of carpel numbers is large in some families. This gives the impression that there are more genera in which multicarpellate gynoecia occur than genera in which they are lacking. However, in some of these genera, non-multicarpellate gynoecia also occur. If the most common carpel numbers are considered, the picture changes. *Amborella* Baill., although some flowers are multicarpellate, most commonly has five carpels, the range being three to eight (Endress & Igersheim, 2000b; Jérémie, Lowry & Trochet, 2008). In Nymphaeales, Hydatellaceae and most Cabombaceae are

non-multicarpellate. In Austrobaileyales, Trimeniaceae are non-multicarpellate and Austrobaileyaceae are only moderately multicarpellate. In addition, highly multicarpellate flowers (with more than *c.* 20 or 30 carpels) occur only in highly nested subclades in the families in which they occur (Nymphaeaceae and Schisandraceae). Optimization studies indicate that the condition at the base of the tree of extant angiosperms was more likely non-multicarpellate than multicarpellate (Doyle & Endress, 2011).

In magnoliids, multicarpellate flowers are common in Magnoliales and Laurales, but do not occur in Piperales and are not so common in Canellales. In monocots, multicarpellate flowers occur especially in some families of Alismatales and Pandanales, but are rare in other groups (Liliales, Asparagales, Arecales, Poales), or absent, the latter specifically also in the first diverging Acorales. Early diverging eudicots exhibit the broadest range of carpel numbers (in Ranunculaceae alone 1–10 000 carpels, which also represents the range of the angiosperms as a whole). In families with diversity in carpel number, such as Papaveraceae and Ranunculaceae, the highest carpel numbers occur in nested subclades. However, two or three carpels are common and may be basal in several larger clades (Drinnan, Crane & Hoot, 1994). In rosids, there is a conspicuous imbalance between fabids and malvids. There are many instances of multicarpellate gynoecia in malvids, but few in fabids. Among fabids, the largest number of multicarpellate gynoecia is in Rosaceae, in which the carpels are free and in several whorls, an almost unique feature in core eudicots. In asterids, there is a main peak of multicarpellate gynoecia in Ericales (Ericaceae, Lecythidaceae, Sapotaceae) of the early branching asterids, and a second, weaker peak in Apiales (Araliaceae) of the campanulids. In lamiids, multicarpellate flowers are restricted to a few members of Rubiaceae and Solanaceae.

CONCLUSIONS

A general feature in multicarpellate gynoecia with the carpels in a single whorl is that the carpels tend to be arranged in parallel rows by sinuous deformation of the whorl into loops and parallel alignment of the two counterparts within a loop so that the ventral slits of the carpels within the parallel lines face each other. The simplest and most common pattern is of two loops, which form a more or less straight row of two lines of carpels. More complex patterns are H-shaped and star-shaped, commonly associated with more numerous carpels. High carpel number tends to cause disruption of compitum function. However, it may be expected that the carpel arrangement in parallel lines

may allow regional compitum function. However, compitum function has not been studied in such gynoecia.

In general, the study shows how some peculiar features of multicarpellate gynoecia, especially the carpel arrangement in loops, can be better understood by a broad comparison throughout the angiosperms. However, most of the extreme cases illustrated here have never been studied in detail in their development. It would be of interest to know in more detail how the loops develop.

There are remaining and new questions. What is the function of the bumpy secretory surface of the part that is formed in the middle of the gynoecium when the gynoecium closes in early development, if it is not a stigma? As multicarpellate gynoecia do not occur in highly synorganized flowers, it would be of interest to know in more detail how constraints work in such flowers. It could be that an increase in carpel number occurs as a mere side effect with the general increase in flower size. What kinds of fruit differentiation may favour multicarpellate gynoecia? An obvious trend is to produce one-seeded dispersal units, either as one-seeded free carpels (Alismataceae, Triuridaceae, Ranunculaceae, Rosaceae) or as one-seeded mericarps of syncarpous gynoecia (Malvaceae, *Nolana*).

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APPENDIX 1 OVERVIEW OF OCCURRENCE OF MULTICARPELLATE GYNOECIA ACROSS ANGIOSPERMS

The classification of APG III (2009) is used in this overview with almost no exceptions. A few fossil flowers were included if they were of special interest with regard to the features discussed in this paper and if their phylogenetic position was well supported. I have tried to assemble a list which is as complete as possible for the families and genera. In some genera of special interest, selected species are also mentioned.

A. CARPELS IN TWO OR MORE WHORLS OR SERIES

The carpel number indicated is the total carpel number in a flower, not the number per whorl or series.

Carpels positioned in more than one whorl or series occur in some clades of the ANITA grade, in some magnoliids, but is rare in monocots and eudicots. Among monocots, it is present in some Alismatales; among eudicots, in some early diverging eudicots (some Ranunculales, *Nelumbo*) and in some core eudicots (some Rosaceae, Malvaceae). Across all angiosperms, it is a rare feature and is restricted to apocarpous gynoecia. However, it exceptionally occurs in *Gyrostemon* and in some cultivated syncarpous plants (navel orange, pomegranate), where it gives the impression of teratologies.

ANITA grade

Austrobaileyales–Austrobaileyaceae, *Austrobaileya scandens* C.T.White (10–13), Endress, 1980c; Igersheim & Endress, 1997. **Schisandraceae**,

Kadsura Kaempf. ex Juss. (17–c. 300), Saunders, 1998; *Schisandra* Michx. (12–120), Saunders, 2000.

Nymphaeales–Cambombaceae, *Brasenia* Schreb. (4–18), Williamson & Schneider, 1993.

Magnoliids

Canellales–Winteraceae (1–50), Vink, 1993, Igersheim & Endress, 1997; *Drimys* J.R.Forst. & G.Forst. (2–24), Vink 1970; *Tasmannia* DC. (1–11(–18)), Sampson, Williams & Woodland, 1988; *Zygogynum* Baill. (1–50), Vink 1993.

Laurales–Atherospermataceae (3–50), Endress & Igersheim, 1997; *Atherosperma* Labill. (c. 24–40(–50)), Schodde, 1969; *Daphnandra* Benth. ((3)4–12(–18)), Schodde, 1969; *Doryphora* Endl. (6–12(–15)), Schodde, 1969; *Dryadodaphne* S. Moore ((5)–8–13(–16)), Schodde, 1969; *Laurelia* Juss. ((7)8–30(–45)), Schodde, 1969; *Laureliopsis* Schodde ((8)9–12(–15)), Schodde, 1969; *Nemuaron* Baill. (4–7), Philipson, 1993. **Calycanthaceae** (1–35), Igersheim & Endress, 1997; Staedler *et al.*, 2007, 2009; *Calycanthus floridus* L. (25–35), Staedler *et al.*, 2009; *Chimonanthus praecox* (L.) Link (8–10), Staedler *et al.*, 2009; *Sinocalycanthus chinensis* W.C.Cheng & S.Y.Chang (14–17), Staedler *et al.*, 2009. **Monimiaceae** (1–2000), Endress & Lorence, 1983; Lorence 1985; Endress & Igersheim, 1997; classification: Renner *et al.*, 2010. **Monimiaceae–Mollinedioideae**, *Austromatthaea* L.S.Sm. (c. 230), Staedler & Endress, 2009; *Decarydendron* Danguy (300–1000), Lorence, 1985; *Endressia* Whiffin, nom. illeg. (8–10), Whiffin & Foreman, 2007; *Ephippiandra* Decne. (15–120), Lorence, 1985; *Graziellanthus* Peixoto & Per.-Moura (10–12), Peixoto & Pereira-Moura, 2008; *Hedycarya* Forst. (5–70), Jérémie, 1982b; Staedler & Endress, 2009; *Hortonia* Wight ex Arn. (6–14), Endress, 1980a,b; *Kairoa* Philipson (8–150+), Renner & Takeuchi, 2009; *Kibara macrophylla* (A.Cunn.) Benth. (17–20), Staedler & Endress, 2009; *Kibaropsis* Vieillard ex Jérémie (40–60), Jérémie, 1982b; *Levieria acuminata* Perk. (13–23), Staedler & Endress, 2009; *Macropeplus* Perkins (many), Perkins, 1925; *Macrotorus* Perkins (7–12), Peixoto & Pereira-Moura, 2008; *Matthaea* Blume (many), Perkins, 1925; *Mollinedia* Ruiz & Pav. (6–35), Perkins 1925; *Steganthera ilicifolia* A.C.Sm. (11–16), Staedler & Endress, 2009; *Tambourissa* Sonn. (35–2000), Endress & Lorence, 1983; Lorence, 1985; *Tambourissa ficus* A.DC. (1000–2000), Endress & Lorence, 1983; Lorence, 1985; *Tambourissa purpurea* A.DC. (61–71), Staedler & Endress 2009; *Wilkiea angustifolia* (F.M.Bailey) Perkins (12–17), Staedler & Endress, 2009; *Wilkiea huegeliana* (Tul.) A.DC. (16–36), Staedler & Endress, 2009. **Monimiaceae–Monimioideae**, *Monimia* Thou. (4–14), Lorence, 1985; *Palmeria gracilis* Perkins (8–10), Staedler & Endress, 2009; *Peumus* Molina (4–6), Staedler &

Endress, 2009. **Siparunaceae**, *Siparuna* Aubl. (few to many), Philipson, 1993; *Siparuna aspera* A.DC. (10–30), Renner & Hausner, 2005; *Siparuna sessiliflora* A.DC. ((15–)20–30(–35)), Renner & Hausner, 2005; *Siparuna thecaphora* A.DC. (9–13), Staedler & Endress, 2009; *Siparuna tomentosa* Perkins (3–13(–26)), Renner & Hausner, 2005.

Magnoliales–Annonaceae (1–400), van Setten & Koek-Noorman, 1992; Igersheim & Endress, 1997; many genera are multicarpellate, but numbers are rarely provided in the literature, van Heusden, 1992; van Setten & Koek-Noorman, 1992 indicate the number of carpels at the fruiting stage, therefore the actual number of carpels may be higher; classification: Chatrou *et al.*, 2012; Couvreur *et al.*, 2012. **Annonaceae–Anaxagoreoideae**, *Anaxagorea* St.Hil. ((1)2–20), van Setten & Koek-Noorman, 1992; *Anaxagorea crassipetala* Hemsl. (18 + 1, in three whorls), Endress & Armstrong, 2011. **Annonaceae–Ambavioideae**, *Ambavia* Le Thomas (4–6), Kessler, 1993a; *Cananga* (DC.) Hook.f. & Thomson (6–25), van Setten & Koek-Noorman, 1992; *Cleistopholis* Pierre ex Engl. (2–15), van Setten & Koek-Noorman, 1992; *Cyathocalyx* Champ. ex Hook.f. & Thomson (1–15(–19)), van Setten & Koek-Noorman, 1992; *Lettowianthus* Diels (7–35), van Setten & Koek-Noorman, 1992; *Meiocarpidium* Engl. & Diels (3–6), van Setten & Koek-Noorman, 1992; *Tetrameranthus* R.E.Fr. (2–6(–7)), van Setten & Koek-Noorman, 1992. **Annonaceae–Annonoideae**; **Annonaceae–Annonoideae–Bocageae**, *Cardiopetalum* Schldtl. (3–14), van Setten & Koek-Noorman, 1992; *Cymbopetalum* Benth. (7–20), van Setten & Koek-Noorman, 1992; *Froesiodendron* R.E.Fr. (6–18), van Setten & Koek-Noorman, 1992; *Mkilua* Verdc. (8–25), van Setten & Koek-Noorman, 1992; *Porcelia* Ruiz & Pav. (8–15(–20)), van Setten & Koek-Noorman, 1992. **Annonaceae–Annonoideae–Xylopieae**, *Artabotrys* R.Br. (1–12(–15)), van Setten & Koek-Noorman, 1992; *Xylopia* L. (1–30(40)), van Setten & Koek-Noorman, 1992. **Annonaceae–Annonoideae–Duguetieae**, *Duckeanthus* R.E.Fr. (20–30), van Setten & Koek-Noorman, 1992; *Duguetia* A.St.-Hil. (5–200(–400)), van Setten & Koek-Noorman, 1992; *Fusaea* Saff. (50–100), van Setten & Koek-Noorman, 1992; *Letestudoxa* Pellegr. (100–150), van Setten & Koek-Noorman, 1992; *Pseudartabotrys* Pellegr. (75–100), van Setten & Koek-Noorman, 1992. **Annonaceae–Annonoideae–Guatterieae**, *Guatteria* Ruiz & Pav. (2–60(–70)), van Setten & Koek-Noorman, 1992. **Annonaceae–Annonoideae–Annoneae**, *Annona* L. ((3–)10–200), van Setten & Koek-Noorman, 1992; *Anonidium* Engl. & Diels (200–400), van Setten & Koek-Noorman, 1992; *Asimina* Adans. (1–7), van Setten & Koek-Noorman, 1992; *Boutiquea* Le Thomas (2–30),

van Setten & Koek-Noorman, 1992; *Disepalum* Hook.f. (4–100), van Setten & Koek-Noorman, 1992; *Goniothalamus* Hook.f. & Thomson ((1)2–40), van Setten & Koek-Noorman, 1992; *Neostenanthera* Exell (5–100), van Setten & Koek-Noorman, 1992; *Rollinia* A.St.-Hil. (10–200), van Setten & Koek-Noorman, 1992. **Annonaceae–Annonoideae–Monodoreae**, *Asteranthe* Engl. & Diels (2–7), van Setten & Koek-Noorman, 1992; *Hexalobus* A.DC. (1–6), van Setten & Koek-Noorman, 1992; *Ophrypetalum* Diels (4–7(–10)), van Setten & Koek-Noorman, 1992; *Uvariastrium* Engl. & Diels ((1)2–10), van Setten & Koek-Noorman, 1992; *Uvariadendron* (Engl. & Diels) R.E.Fr. (1–15(–60)), van Setten & Koek-Noorman, 1992; *Uvariopsis* Engl. (1–13), van Setten & Koek-Noorman, 1992. **Annonaceae–Annonoideae–Uvarieae**, *Afroguatteria* Boutique ((6–)15–70), van Setten & Koek-Noorman, 1992; *Cleistochlamys* Oliv. (1–7), van Setten & Koek-Noorman, 1992; *Dasy-maschalon* Dalla Torre & Harms (2–30), van Setten & Koek-Noorman, 1992; *Desmos* Lour. ((3–)10–40), van Setten & Koek-Noorman, 1992; *Fissistigma* Griff. (1–20(–30)), van Setten & Koek-Noorman, 1992; *Gilbertiella* Boutique (3–7), van Setten & Koek-Noorman, 1992; *Melodorum* Lour. (1–15(–20)), van Setten & Koek-Noorman, 1992; *Monanthotaxis* Baill. (1–20), van Setten & Koek-Noorman, 1992; *Pyramidanthe* Miq. ((1–)3–8), van Setten & Koek-Noorman, 1992; *Schefferomitra* Diels (3–15), van Setten & Koek-Noorman, 1992; *Sphaerocoryne* Scheff. ex Ridl. (4–30(–45)), van Setten & Koek-Noorman, 1992; *Toussaintia* Boutique (3–7), van Setten & Koek-Noorman, 1992; *Uvaria* L. (1–80), van Setten & Koek-Noorman, 1992. **Annonaceae–Malmeoideae**; **Annonaceae–Malmeoideae–Piptostigmateteae**, *Annickia* Setten & Maas (5–40(–55)), van Setten & Koek-Noorman, 1992; *Greenwayodendron* Verdc. (2–12), van Setten & Koek-Noorman, 1992; *Piptostigma* Oliv. (1–4(–10)), van Setten & Koek-Noorman, 1992; *Polyceratocarpus* Engl. & Diels (1–15), van Setten & Koek-Noorman, 1992. **Annonaceae–Malmeoideae–Malmeeae**, *Crematosperma* R.E.Fr. (4–30(–40)), van Setten & Koek-Noorman, 1992; *Ephedranthus* S.Moore (4–75), van Setten & Koek-Noorman, 1992; *Malmia* R.E.Fr. ((4–)15–100), van Setten & Koek-Noorman, 1992; *Oxandra* A.Rich. (1–15(–20)), van Setten & Koek-Noorman, 1992; *Pseudoxandra* R.E.Fr. (2–12(–15)), van Setten & Koek-Noorman, 1992; *Ruizodendron* R.E.Fr. (2–8), van Setten & Koek-Noorman, 1992; *Unonopsis* R.E.Fr. (1–25(–60)), van Setten & Koek-Noorman, 1992. **Annonaceae–Malmeoideae–Maasieae**, *Maasia* Mols, Kessler & Rogstad (numerous), Mols *et al.*, 2008. **Annonaceae–Malmeoideae–Fenerivieae**, *Fenerivia* Diels (up to 45), Saunders *et al.* 2011. **Annonaceae–Malmeoideae–Miliuseae**,

Alphonsea Hook.f. & Thomson (1–11), van Setten & Koek-Noorman, 1992; *Desmopsis* Saff. ((1)2–20), van Setten & Koek-Noorman, 1992; *Encisanthum* Becc. (3–25), van Setten & Koek-Noorman, 1992; *Fitzalania* F.Muell. (4–8), van Setten & Koek-Noorman, 1992; *Haplostichanthus* F.Muell. (1–15), van Setten & Koek-Noorman, 1992; *Marsypopetalum* Scheff. (3–30), van Setten & Koek-Noorman, 1992; *Meiogyne* Miq. ((1)2–15), van Setten & Koek-Noorman, 1992; *Miliusa* Lesch. ex A.DC. (2–30(–40)), van Setten & Koek-Noorman, 1992; *Mitrephora* Hook.f. & Thomson (1–22(–25)), van Setten & Koek-Noorman, 1992; *Neouvaria* Airy Shaw (1–4(–14)), van Setten & Koek-Noorman, 1992; *Oncodostigma* Diels (6–12), van Setten & Koek-Noorman, 1992; *Orophea* Blume (1–16), van Setten & Koek-Noorman, 1992; *Phaeanthus* Hook.f. & Thomson (4–25), van Setten & Koek-Noorman, 1992; *Polyalthia* Blume (1–50(–80)), van Setten & Koek-Noorman, 1992; *Popowia* Endl. (1–9(–14)), van Setten & Koek-Noorman, 1992; *Popowia pisocarpa* Endl. (12, in two whorls), Endress & Armstrong, 2011; *Popowia whytei* Stapf (27, in three whorls), Ronse Decraene & Smets, 1990; *Pseuduvaria* Miq. (1–20(–25)), van Setten & Koek-Noorman, 1992; *Sapranthus* Seem. (1–24), van Setten & Koek-Noorman, 1992; *Stelechocarpus* Hook.f. & Thomson ((1)2–15(–20)), van Setten & Koek-Noorman, 1992; *Stenanona* Standl. (2–7), van Setten & Koek-Noorman, 1992; *Trivalvaria* Miq. ((2)4–20(–25)), van Setten & Koek-Noorman, 1992. **Annonaceae – not classified**, *Mitrella* Miq. (1–15), van Setten & Koek-Noorman, 1992; *Tetrapetalum* Miq. (40–45), van Setten & Koek-Noorman, 1992. **Eupomatiaceae**, *Eupomatia* R.Br. (13–70), Endress, 1977, Igersheim & Endress, 1997. **Himantandraceae**, *Galbulimima* F.M. Bailey (7–28), Endress, 1977; Igersheim & Endress, 1997. **Magnoliaceae**, *Liriodendron* L. (many), Nooteboom, 1993; *Magnolia* L. (1–222), Igersheim & Endress, 1997.

Monocots

Alismatales – general, Igersheim, Buzgo & Endress, 2001. **Alismataceae**, *Baldellia* Parl. (several whorls), Charlton, 2004; *Caldesia* Parl. (2–9(–20)), Cook, 1990; (several whorls), Wang & Chen, 1997; Liu *et al.* 2002; (8–10 in a single whorl), Markgraf, 1981; *Echinodorus* Rich. & Engelm. ex A.Gray p.p. (numerous), Cook, 1990; *Echinodorus grandiflorus* (Cham. & Schltld.) Micheli (100+), Rudall, 2008; *Luronium* Raf. (several whorls), Charlton, 1999a; *Ranalisma* Stapf (in many whorls), Charlton, 1991; *Sagittaria* L. (up to 660), Salisbury, 1926; Kaul, 1967. **Butomaceae**, *Butomus* L. (6, in two whorls), Troll, 1931. **Juncaginaceae**, *Triglochin* L. (6, in two whorls), Eckardt, 1957; Endress, 1995; Remizowa *et al.*, 2010. **Potamogetonaceae**, *Pota-*

mogeton lucens L. (4–8), in two whorls if 8), Charlton & Posluszny, 1991. **Ruppiaceae**, *Ruppia* L. (4–9), Kaul, 1993; (2–19), Zhao & Wu, 2008; Lock *et al.*, 2011.

Pandanales–Triuridaceae, *Sciaphila* Blume and *Seychellaria* Hemsl. (numerous, more than one whorl), D. Sokoloff, personal communication.

Early branching eudicots

Ranunculales–Circaeasteraceae, *Kingdonia* Balf.f. & W.W.Sm. (3–9), Tamura, 1995, (5–6(–9)); Wang X-M *et al.*, 2012. **Lardizabalaceae**, *Sargentodoxa* Rehder & E.H.Wilson (48–90), Wu & Kubitzki, 1993; (up to more than 90), Zhang & Ren, 2008. **Menispermaceae**, (1–32), Diels, 1910; (mostly 1–3 to 6–12), Kessler, 1993b; *Albertisia* Becc. (4–12), Kessler, 1993b; *Anisocycla* Baill. (3–6), Kessler, 1993b; *Carroonia* F.Muell. (6), Kessler, 1993b; *Chondrodendron* Ruiz & Pav. (6), Kessler, 1993b; *Cocculus* DC. (3 or 6), Kessler, 1993b; *Dioscoreophyllum* Engl. (3–6), Kessler, 1993b; *Eleutharrhena* Forman (6), Kessler, 1993b; *Macrococculus* Becc. (5–8), Kessler, 1993b; *Pycnarrhena* Miers ex Hook.f. & Thomson (3–6), Kessler, 1993b; *Sarcopetalum* F.Muell. (3–6), Kessler, 1993b; *Sciadotenia* Miers (6–(9–15)), Kessler, 1993b; *Sphenocentrum* Pierre ((3)–9–12(–15)), Kessler, 1993b; *Spirospermum* Thou. (9), Kessler, 1993b; *Synclisia* Benth. (15–20), Kessler, 1993b; *Tiliacora* Colebr. ((3)–8–12(–30)), Kessler, 1993b; *Triclisia* Benth. (6–40), Kessler, 1993b; *Ungulipetalum* Moldenke (6–9), Kessler, 1993b. **Ranunculaceae** classification: Wang *et al.*, 2009. **Ranunculaceae–Coptidoideae**, *Coptis* Salisb. (5–15), Tamura, 1995. **Ranunculaceae–Hydrastidoideae**, *Hydrastis* J.Ellis (5–15), Tamura, 1995. **Ranunculaceae–Ranunculoideae**, *Adonis* L. (numerous), Tamura, 1995; *Adonis sutchuenensis* Franch. (17–25), Ren *et al.* 2009; *Anemone* L. (numerous), Tamura, 1995; *Anemone altaica* Fisch. ex Ledeb. (7–13), Ren, Chang & Endress, 2010; *Anemone chinensis* Bunge (240–250), Ren *et al.*, 2010; *Anemone taipaiensis* W.T.Wang (60–70), Ren *et al.*, 2010; *Anemone tomentosa* (Maxim.) C.Pei (450–470), Ren *et al.* 2010; *Aphanostemma* A.St.-Hil. (30–70 achenes), Tamura, 1995; *Archiclematis* (Tamura) Tamura (many), Tamura, 1995; *Arcteranthis* Greene (many), Tamura, 1995; *Asteropyrum* J.R.Drumm. & Hutch. (5–10), Tamura, 1995; *Barneoudia* Gay (10–55), Tamura, 1995; *Calathodes* Hook.f. & Thomson (8–30), Tamura, 1995; *Callianthemoides* Tamura (many), Tamura, 1995; *Callianthemum* C.A. Mey. (many), Tamura, 1995; *Callianthemum taipaicum* W.T.Wang (21–24), Ren *et al.*, 2009; *Caltha* L. ((2)–5–85), Tamura, 1995; *Ceratocephala* Moench (many), Tamura, 1995; *Ceratocephala orthoceras* DC. (22–54), Zhao *et al.*, 2012; *Cimicifuga* Wernisch. (1–8), Tamura, 1995; *Clematis*

Dill. ex L. (many), Tamura, 1995; *Clematis macropetala* Ledeb. (12–16), Ren *et al.*, 2010; *Clematis peterae* Hand.-Mazz. (14–18), Ren *et al.*, 2010; *Cyrtorhyncha* Nutt. (several to 15), Tamura, 1995; *Eranthis* Salisb. (2–10), Tamura, 1995; *Halerpestes* Greene (many), Tamura, 1995; *Halerpestes cymbalaria* Greene (100–145), Zhao *et al.*, 2012; *Hamadryas* Comm. ex Juss. (up to 230), Tamura, 1995; *Helleborus* Gueldenst. (2–10), Tamura, 1995; *Krapfia* DC. (60–800), Tamura, 1995; *Kumlienia* Greene (many), Tamura, 1995; *Laccopetalum* Ulbr. (up to more than 10 000), Tamura, 1995; *Megaleranthis* Ohwi (several), Tamura, 1995; *Metanemone* W.T.Wang (c. 18), Tamura, 1995; *Myosurus* L. (many, up to more than 200), Tamura, 1995; *Naravelia* Adans. (many), Tamura, 1995; *Oreithales* Schltld. (20–35), Tamura, 1995; *Oxygraphis* Bunge (many), Tamura, 1995; *Oxygraphis glacialis* Bunge (84–185), Zhao *et al.*, 2012; *Paroxygraphis* W.W.Sm. (10–40 achenes), Tamura, 1995; *Peltocalathos* Tamura (many), Tamura, 1995; *Ranunculus* L. (few to many), Tamura, 1995; *Ranunculus bungei* Steud. (72–85), Zhao *et al.*, 2012; *Ranunculus chinensis* Bunge (71–107), Zhao *et al.*, 2012; *Ranunculus sceleratus* L. (102–290), Zhao *et al.*, 2012; *Trautvetteria* Fisch. & C.A.Mey. (15–25), Tamura, 1995; *Trollius* L. ((3–)5–50), Tamura, 1995; *Trollius farreri* Stapf (5–(9)), Ren *et al.*, 2009. **Ranunculaceae–Thalictrioideae**, *Aquilegia* L. ((3–)5–(10)), Tamura, 1995; *Enemion* Raf. (3–6), Tamura, 1995; *Leptopyrum* Raf. (6–20), Tamura, 1995; *Paraquilegia* J.R.Drumm. & Hutch. (3–10), Tamura, 1995; *Thalictrum* L. (2–40), Tamura, 1995; *Thalictrum fargesii* Franch. ex Finet & Gagnep. ((3–)4–5–(9)), Ren, Gu & Chang, 2011; *Thalictrum przewalskii* Maxim. (4–9), Ren *et al.*, 2011; *Urophysa* Ulbr. (5–(8)), Tamura, 1995; *Xanthorhiza* Marshall (5, 10 (15)), Tamura, 1995.

Proteales–Nelumbonaceae, *Nelumbo* Adans. (2–38), Igersheim & Endress, 1998; Hayes *et al.*, 2000. **Platanaceae**, *Platanus* L. (6–8, in two whorls), von Balthazar & Schönenberger, 2009.

Core eudicots

Saxifragales–Paeoniaceae, *Paeonia* L. (spiral, 2–8(–15)), Tamura, 2007.

Rosids

Rosids–fabids

Rosales–Rosaceae, classification: Potter *et al.*, 2007; **Rosaceae–Dryadoideae**, *Cowania* D.Don (5–12), Kalkman, 2004; *Dryas* L. (many), Kalkman, 2004; *Dryas octopetala* L. (c. 70), Kania, 1973. **Rosaceae–Rosoideae**, *Alchemilla* L. (1–4(–12)), Kalkman, 2004; *Chamaerhodos* Bunge (5–10 or more), Kalkman,

2004; *Coluria* R.Br. ((3–)12–25), Kalkman, 2004; *Falugia* Endl. (many), Kalkman, 2004; *Filipendula* Mill. (5–15), Kalkman, 2004; *Geum* L. (several to many), Kalkman, 2004; *Oncostylus* (Schlecht.) F.Bolle (many), Kalkman, 2004; *Orthurus* Juz. (up to 15), Kalkman, 2004; *Potentilla* L. (few to many), Kalkman, 2004; *Rosa* L. (usually many), Kalkman, 2004; *Rosa multiflora* Thunb. (8–10), Kania, 1973; *Rubus* L. (many, rarely few), Kalkman, 2004; *Rubus odoratus* L. (100+), Kania, 1973; *Sieversia* Willd. (40 or more), Kalkman, 2004; *Waldsteinia* Willd. ((1)2–6(–15)), Kalkman, 2004. **Rosaceae–Spiraeoideae**, *Hesperomeles* Lindl. (4–6), Kalkman, 2004; *Eriogynia* Hook. (4–6), Kalkman, 2004; *Kerria* DC. (5–8), Kalkman, 2004; *Rhodotypos* Siebold & Zucc. ((2–)4(–6)), Kalkman, 2004.

Rosids–malvids

Myrtales–Lythraceae, *Punica granatum* L. (4–15, in one to three unequal whorls), Sinha & Joshi, 1959; (8–12, in two unequal whorls), Roth & Lindorf, 1972c.

Brassicales–Gyrostemonaceae, *Gyrostemon ramulosus* Desf. (c. 20–27, sometimes in two whorls, inner whorl often incomplete), Hufford, 1996.

Malvales–Malvaceae–Sterculioideae, *Octolobus* Welw. (30–60 or more, in three to five whorls), Bayer & Kubitzki, 2003; (8–30, said to be spirally arranged, which is most likely erroneous), Cheek & Dorr, 2007.

Malvaceae–Malvoideae, *Malvaviscus* Fabr. (10, in two whorls), van Heel 1978; *Pavonia* Cav. (10, in two whorls), van Heel, 1978; (10), this study: Figure 48; *Urena* L. (10, in two whorls), van Heel, 1978. These genera are also listed in part B, below, because they are borderline cases.

Sapindales–Rutaceae, *Citrus sinensis* Osbeck (Washington navel oranges) (c. 12 + ?, in two whorls, apparently fewer in the second whorl than in the first), Lord & Eckard, 1985.

Asterids (none)

B. CARPELS IN ONE WHORL (OR SERIES) (MOSTLY)

Carpels positioned in a single whorl (sometimes a deformed whorl) are the most common condition in angiosperms. In some cases, the carpels are in one series, but may consist of two whorls (e.g. in some multicarpellate Alismatales and Malvaceae). In cases in which it is not clear whether the locule number corresponds to the carpel number, the number of locules is given (as *n*-locular). In this list, all eudicot orders are mentioned to also emphasize in which multicarpellate gynoecia in one whorl were **not** recorded.

ANITA grade

Amborellales–Amborellaceae, *Amborella trichopoda* Baill. (5–8), Jérémie, 1982a, ((4–)5(–6)); Endress & Igersheim, 2000b; ((3–)5–8), Jérémie *et al.*, 2008.

Nymphaeales–Cabombaceae, *Cabomba* Aubl. (1–7), Williamson & Schneider, 1993; fossil *Pluricarpellatia* B.Mohr, Bernardes-de-Oliveira & D.W.Taylor (6–12, unclear whether in a single whorl), Mohr *et al.*, 2008. **Nymphaeaceae** (3–47), Igersheim & Endress, 1998; *Barclaya* Wall. (8–14), Schneider & Williamson, 1993; *Euryale* Salisb. (8–16), Schneider & Williamson, 1993; *Nuphar* Sm. (5–23(–30)), Schneider & Williamson, 1993; *Nuphar advena* R.Br. (c. 18), Endress, 2001; *Nymphaea* L. ((5–)8–35, with central protrusion of floral apex), Schneider & Williamson, 1993; *Ondinea* Hartog (3–14, with central protrusion of floral apex), Schneider & Williamson, 1993; *Victoria* Buchhoz (30–40, with central protrusion of floral apex), Schneider & Williamson, 1993; fossil *Carpesella* von Balthazar, K.R.Pedersen, P.R.Crane & E.M.Friis (13), von Balthazar *et al.*, 2008; fossil *Moneitanthus* E.M.Friis, K.R.Pedersen, von Balthazar, G.Grimm & P.R.Crane (12, with central protrusion of floral apex), Friis *et al.*, 2009.

Austrobaileyales–Schisandraceae, *Illicium* L. ((5–)7–15(–21)), spiral, in one series, with central protrusion of floral apex), Smith, 1947; Igersheim & Endress, 1997.

Magnoliids

Canellales–Canellaceae (2–6), Kubitzki, 1993a; Igersheim & Endress, 1997, *Pleodendron* Tiegh. (6), Kubitzki, 1993a; *Cinnamodendron* Endl. ((2–)4–5(–6)), Kubitzki, 1993a.

Piperales–Aristolochiaceae (4–6), Huber, 1993; Igersheim & Endress, 1998; *Saruma* Oliv. (6), Huber, 1993; *Asarum* L. (6), Huber, 1993; *Aristolochia* L. *s.l.* ((5–)6), Leins & Erbar, 1985; Huber, 1993; Igersheim & Endress, 1998.

Magnoliales–Annonaceae, *Isolona campanulata* Engl. & Diels (6), Derooin, 1997; *Monodora brevipes* Benth. (14, perhaps derived from more than one whorl), Derooin, 1997.

Monocots

Alismatales–Alismataceae, *Alisma* L. (c. 21, seemingly in one whorl), Charlton, 2004; *Alisma plantago-aquatica* L. (c. 15, centre of remaining floral apex not used for carpel formation), Kaul, 1976; (c. 20), Rudall, 2008; *Alisma triviale* Pursh (14–19, seemingly in one whorl), Singh & Sattler, 1972; *Astonia* S.W.L. Jacobs (5–15), Haynes *et al.*, 1998a; *Burnatia* Micheli (8–20), Haynes *et al.*, 1998a; *Damasonium* Mill. (6–9), Haynes *et al.*, 1998a; (6, possibly in two whorls), Charlton, 2004; *Helanthium* (Benth. & Hook.f.)

Engelm. ex J.G. Sm. (as part of *Echinodorus* Rich. & Engelm. ex A.Gray) (20 or fewer), Haynes *et al.*, 1998a; *Limnophyton* Miq. ((10–)15–20(–30)), Haynes *et al.*, 1998a; *Luronium* Raf. (6–9(–10)), Haynes *et al.*, 1998a; (up to 12, in one or two whorls), Charlton, 1999a; *Wiesneria* Micheli (3–6, possibly in two whorls if 6), Haynes *et al.*, 1998a; Charlton, 1999b.

Aponogetonaceae, *Aponogeton abyssinicus* Hochst. ex A.Rich. (3–7, whether in one whorl?), van Bruggen, 1985; *Aponogeton afroviolaceus* Lye (3–9), van Bruggen, 1985; *Aponogeton bogneri* H.Bruggen (4–6), van Bruggen, 1985; *Aponogeton desertorum* Zeyher ex A.Spreng. (3–6), van Bruggen, 1985; *Aponogeton distachyus* L.f. (3–6), van Bruggen, 1985; *Aponogeton junceus* Lehm. (3–6), van Bruggen, 1985; *Aponogeton madagascariensis* (Mirb.) H.Bruggen (3–6), van Bruggen, 1985; *Aponogeton natalensis* Oliv. (3–6(7)), van Bruggen, 1985; *Aponogeton rehmannii* Oliv. (3–6), van Bruggen, 1985. **Araceae**, *Gorgonidium* Schott ((2–)4, 5(–7)), Mayo *et al.*, 1997; *Philodendron* Schott (2–47), Mayo, 1989; *Spathantheum* Schott (6–8), Mayo *et al.*, 1997; *Taccarum* Brongn. ex Schott (3–6(7)), Mayo *et al.*, 1997. **Hydrocharitaceae**, *Boottia cordata* Wall. (9–15, flat), Kaul, 1968; (12–20), Kaul, 1969; *Enhalus* Rich. (6, remaining undifferentiated floral apex in centre of gynoecium), Troll, 1931; *Hydrocharis* L. (6), Troll, 1931; Cook & Lüönd, 1982; Scribailo & Posluszny, 1985; *Limnobium* Rich. (including *Hydromystria* Bartl.) (3–9), Cook & Urmi-König, 1983a; *Limnobium spongia* (Bosc) Steud. (6–9), Kaul, 1968; *Ottelia* Pers. (9), Troll, 1931; (3–9(–10)), Cook & Urmi-König, 1984; (3–20) Cook *et al.*, 1984; *Ottelia alismoides* Pers. (10 or more), Kaul, 1968; (6–9 or more, flat), Kaul, 1969; *Stratiotes* L. ((3–)6), Cook & Urmi-König, 1983b; *Thalassia hemprichii* (Ehrenb.) Asch. (6, flat), Kaul, 1968; *Thalassia testudinum* K.D.Koenig (9–12), Kaul, 1968; (7 or 14, flat), Tomlinson, 1969. **Limnocharitaceae**, *Buto-mopsis* Kunth (4–9), Cook, 1990; *Hydrocleys* Rich. (3 or 6), Cook, 1990; (3–8), Haynes *et al.*, 1998b; *Hydrocleys nymphoides* (Willd.) Buchenau (6), Sattler & Singh, 1978; *Limnocharis* Kunth (15–20), Haynes *et al.*, 1998b; *Limnocharis flava* Buchenau (c. 18), Kaul, 1976; (15), Sattler & Singh, 1978. **Scheuchzeriaceae**, *Scheuchzeria* L. (3(–6)), whether in one whorl?), Haynes *et al.* 1998c.

Pandanales–Cyclanthaceae, *Cyclanthus* Poit. ex A.Rich. (flowers united into rings, each with numerous carpels, carpel number per basic floral unit unknown), Dahlgren *et al.*, 1985. **Pandanaceae**, Endress, 1995, *Pandanus* Rumph. ex L.f. (3–8 up to over 13), Stone, 1967; *Sararanga* Hemsl. (10–80, 'arranged in a biseriate sinuous row'), Stone, 1961; *Sararanga sinuosa* Hemsl. (30–80, in H-shaped loops), Stone, 1961: figures 1, 5; Rudall & Bateman, 2006: figure 1H; *Sararanga philippinensis* Merr. (12–

20), Stone, 1961. **Triuridaceae** (4–80), Maas & Rübsamen, 1986; Martínez & Ramos, 1989; Rübsamen-Weustenfeld, 1991; *Kihansia lovetii* Cheek (80–100), Cheek, 2003; *Kupea jonii* Cheek (c. 25), Cheek, 2003; *Kupea martinugei* Cheek & S.A. Williams (25–60), Cheek *et al.*, 2003; *Lacandonia* E. Martínez & Ramos (60–80), Márquez-Guzman *et al.*, 1993; Vergara-Silva *et al.*, 2003; (40–80), Ambrose *et al.*, 2006; (appearing in star-shaped loops, the lines within the loops, in addition, zig-zag-shaped in figures), Rudall & Bateman, 2006; Rudall, 2008: figures 9C, 10F; *Peltophyllum luteum* Gardner (appearing in star-shaped loops), Rudall, 2008: figure 8B; *Triuris brevistylis* (in star-shaped loops), Ambrose *et al.*, 2006: figure 65.

Liliales–Melanthiaceae, *Paris* L. (up to 10), Takhtajan, 1983.

Asparagales–Asparagaceae, *Aspidistra* (likely 6 in some species), D. Sokoloff, personal communication. **Asteliaceae**, *Neoastelia* J.B. Williams (5–7), Kocyan, 2007. **Hypoxidaceae**, *Curculigo racemosa* Ridl. (3–6), Kocyan, 2007.

Arcuales–Arcaceae, *Orbignya speciosa* Barb. Rodr. (5–6), Uhl & Moore, 1971; *Palandra aequatorialis* O.F. Cook (6, in one whorl, apex not used up), Uhl & Dransfield, 1984; *Phytelephas* Ruiz & Pav. (4–10), Uhl & Dransfield, 1987; *Phytelephas aequatorialis* Spruce (5–6), Barfod & Uhl, 2001; *Phytelephas macrocarpa* Ruiz & Pav. (7–10, irregularities in the centre), Uhl & Moore, 1971: figure 104; (4–5), Barfod & Uhl, 2001; *Ammandra decasperma* O.F. Cook (6–9), Barfod & Uhl, 2001; *Aphandra natalia* (Balslev & A.J. Hend.) Barfod (6–8), Barfod & Uhl, 2001.

Poales–Centrolepidaceae, *Centrolepis* Labill. (1–30(–45)), if interpreted as euanthium, Sokoloff *et al.*, 2010; *Centrolepis exserta* (R.Br.) Roem. & Schult. (11–14, flat), Sokoloff *et al.* 2009. **Cyperaceae**, *Evandra* R.Br. (8, if the ‘flowers’ are not pseudanthial), Engler, 1892. **Poaceae**, *Melocanna* Trin. (4–6), Engler, 1892; *Ochlandra* Thwaites (4–8), Soderstrom & Londono, 1988. **Sparganiaceae**, *Sparganium* (fossil fruits with up to 7-locular gynoecium), Dorofeev, 1979.

Early diverging eudicots

Ranunculales–Eupteleaceae, *Euptelea pleiosperma* Hook.f. & Thomson (5–13), Ren *et al.*, 2007; *Euptelea polyandra* Siebold & Zucc. (8–31), Endress, 1969. **Lardizabalaceae**, *Akebia* Decne. (3 or 5–8(–15), perhaps in one series), Qin, 1997. **Papaveraceae**; *Papaver californicum* A. Gray (6–7), Kadereit & Erbar, 2011; *Papaver cambricum* L. (as *Meconopsis cambrica* Vig.) (3–11), Karrer, 1991; *Papaver rhoeas* L. (10–13), Kadereit & Erbar, 2011; *Papaver somniferum* L. (4–20), Karrer, 1991; *Platystemon califor-*

nicus Benth. (6–25, flat, carpels bulging), Karrer, 1991; *Romneya coulteri* Harv. (7–12, perhaps centre of floral apex not involved in gynoecium architecture), Karrer, 1991; *Stylomecon heterophylla* G. Taylor (4–11), Karrer, 1991. **Ranunculaceae**, *Nigella* L. (2–12), Lang, 1977.

Proteales (none).

Trochodendrales–Trochodendraceae, *Trochodendron* Siebold & Zucc. ((4–)6–17) Endress, 1986; Wu, Su & Hu, 2007; fossil *Nordenskiöldia* Heer (12–20, flat), Crane *et al.*, 1991; (14–29, flat), Manchester *et al.*, 1991; (10–16), Wang *et al.*, 2009.

Buxales (none).

Core eudicots

Gunnerales (none).

Dilleniales–Dilleniaceae, Gilg & Werdermann, 1925b; *Tetracera* L. (1–5(–8)), Horn, 2007; *Hibbertia* Andrews (1–5(–15)), Horn, 2007; *Dillenia* L. (4–20), Hoogland, 1952; ((4–)5–15(–20)), Horn 2007; *Dillenia alata* (R.Br. ex DC.) Banks ex Martelli (7–8, floral centre not incorporated into carpel differentiation), Endress, 1997; this study; *Dillenia indica* L. (14–20), Hoogland, 1952; *Dillenia megalantha* Merr. (14–16), Hoogland 1952; *Dillenia philippinensis* Rolfe (c. 15), Endress, 1997; this study; *Dillenia suffruticosa* Martelli (8, flat), Endress, 1997; this study.

Caryophyllales–Aizoaceae, *Aizoanthemum* Dinter ex Friedrich (5–10-locular), Hartmann, 1993; *Aloinopsis* Schwantes (7–12-locular), Hartmann, 1993; *Antegibbaeum* Schwantes ex C. Weber (6-locular), Hartmann, 1993; *Apatesia* N.E.Br. (8–12-locular), Hartmann, 1993; *Arenifera* A.G.J. Herre (8-locular), Hartmann, 1993; *Argyroderma* N.E.Br. (12–25-locular), Hartmann, 1993; *Astridia* Dinter (c. 6-locular), Hartmann, 1993; *Carpanthea* N.E.Br. (12–18-locular), Hartmann, 1993; *Carpobrotus* N.E.Br. (4–20-locular), Hartmann, 1993; *Cephalophyllum* Haw. (10–21-locular), Hartmann, 1993; *Cheiridopsis* N.E.Br. & N.E.Br. (10–20-locular), Hartmann, 1993; *Conicosia* N.E.Br. & N.E.Br. (10–25-locular), Hartmann, 1993; *Conophytum* N.E.Br. ((4)5(–7)-locular), Hartmann, 1993; *Corpuscularia* Schwantes (6-locular), Hartmann, 1993; *Cylindrophyllum* Schwantes (5–11-locular), Hartmann, 1993; *Dicrocaulon* N.E.Br. (4–7-locular), Hartmann, 1993; *Didymaotus* N.E.Br. (6-locular), Hartmann, 1993; *Dinteranthus* Schwantes (6–15-locular), Hartmann, 1993; *Diplosoma* Schwantes (6-locular), Hartmann, 1993; *Dracophilus* Dinter & Schwantes ((8–)10,11-locular), Hartmann, 1993; *Drosanthemopsis* Rauschert (8–10-locular), Hartmann, 1993; *Enarganthe* N.E.Br. (8-locular), Hartmann, 1993; *Erepisia* N.E.Br. (5- or c. 10-locular), Hartmann, 1993; *Fenestraria* N.E.Br. (8–16-locular), Hartmann, 1993; *Gibbaeum* Haw. (6–9-locular), Hartmann, 1993; *Glot-*

- tiphyllum* Haw. (5–14-locular), Hartmann, 1993; *Halilianthus* H.E.K.Hartmann (10-locular), Hartmann, 1993; *Hymenogyne* Haw. (8–12-locular), Hartmann, 1993; *Ihlenfeldtia* H.E.K.Hartmann (c. 10-locular), Hartmann, 1993; *Imitaria* N.E.Br. (6-locular), Hartmann, 1993; *Jordaaniella* H.E.K.Hartmann (10–25-locular), Hartmann, 1993; *Juttadinteria* Schwantes (c. 8-locular), Hartmann, 1993; *Khadia* N.E.Br. (6–10-locular), Hartmann, 1993; *Lapidaria* Dinter & Schwantes (6–8-locular), Hartmann, 1993; *Leipoldtia* L.Bolus (c. 10-locular), Hartmann, 1993; *Lithops* N.E.Br. (4–7-locular), Hartmann, 1993; *Machairophyllum* Schwantes (5–15-locular), Hartmann, 1993; *Malephora* N.E.Br. (8–12-locular), Hartmann, 1993; *Muiria* N.E.Br. (6-locular), Hartmann, 1993; *Namaquanthus* L.Bolus ((8–)12(–16)-locular), Hartmann, 1993; *Namibia* Dinter & Schwantes (c. 12-locular), Hartmann, 1993; *Nananthus* N.E. Br. (7–12-locular), Hartmann, 1993; *Octopoma* N.E.Br. (7–8-locular), Hartmann, 1993; *Odontophorus* N.E.Br. (c. 10-locular), Hartmann, 1993; *Oophytum* N.E.Br. (6-locular), Hartmann, 1993; *Ophthalmophyllum* Dinter & Schwantes ((4–)6(7)-locular), Hartmann, 1993; *Ottosonderia* L.Bolus (8-locular), Hartmann, 1993; *Pleiospilos* N.E.Br. (10–12-locular), Hartmann, 1993; *Polymita* N.E.Br. ((8–)10(–18)-locular), Hartmann, 1993; *Psammophora* Dinter & Schwantes (5–6-locular), Hartmann, 1993; *Rabiea* N.E.Br. (7–10-locular), Hartmann, 1993; *Schlechteranthus* Schwantes (c. 10-locular), Hartmann, 1993; *Schwantesia* L.Bolus (5(6)-locular), Hartmann, 1993; *Smicrostigma* N.E.Br. (7–10-locular), Hartmann, 1993; *Stayneria* L.Bolus (c. 8-locular), Hartmann, 1993; *Stomatium* Schwantes (5(6)), Hartmann, 1993; *Tanquana* H.E.K.Hartmann & Liede (10-locular), Hartmann, 1993; *Tetragonia expansa* Murray (7), Hofmann, 1973; *Titanopsis* Schwantes (6-locular), Hartmann, 1993; *Trichodiadema* Schwantes (5–8-locular), Hartmann, 1993; *Vanheerdea* L.Bolus ex H.E.K.Hartmann (8–12-locular), Hartmann, 1993; *Wooleya* L.Bolus (11–15-locular), Hartmann, 1993; *Zeuktophyllum* N.E.Br. (10-locular), Hartmann, 1993. **Cactaceae** (3 to more than 20), Barthlott & Hunt, 1993; *Epiphyllum strictum* Britton & Rose (c. 16–18), Ross, 1982; *Echinocereus reichenbachii* (Terschek ex Walp.) Britton & Rose (10+), Ross, 1982; *Opuntia engelmannii* Salm-Dyck ex Engelm. (c. 12), Ross, 1982; *Pereskia grandifolia* Haw. (c. 7), Leins & Schwitalla, 1985. **Caryophyllaceae**, *Schiedea* Cham. & Schldl. (3–10(–11)), Bittrich, 1993. **Montiaceae**, *Lewisia brachycalyx* Engelm. (5–8), Mathew, 1989; *Lewisia longipetala* (Piper) S.Clay (5–6), Mathew, 1989; *Lewisia maguirei* A.H.Holmgren (4–6), Mathew, 1989; *Lewisia nevadensis* (A.Gray) B.L.Rob. (3–6), Mathew, 1989; *Lewisia pygmaea* B.L.Rob. (3–6), Mathew, 1989; *Lewisia rediviva* Pursh (4–9), Mathew, 1989. **Phytolaccaceae**, *Anisomeria* D.Don (6), Yamazaki, 1987; fossil *Coahuilacarpon phytolaccoides* Cevallos-Ferriz, Estrada-Ruiz & Pérez-Hernández (6), Cevallos-Ferriz *et al.*, 2008; *Ercilla spicata* Moq. (6), Hofmann, 1977; *Nowickeia* J.Martínez & J.A.McDonald (7–9) is probably an abnormal *Phytolacca* L., Durán & Ayala, 2000; *Phytolacca* L. (5–15), Walter, 1906; *Phytolacca acinosa* Roxb. ((7–)8(–10)), Eckardt, 1954; (8), Rohweder, 1965; (8(–11)), Ronse Decraene *et al.*, 1997; *Phytolacca americana* L. (10), Schaeppi, 1936; Yamazaki, 1987; Ronse Decraene *et al.*, 1997; *Phytolacca chilensis* (Miers ex Moq.) H.Walter (10), Payer, 1857; *Phytolacca clavifera* W.W.Sm. (7–8), Rohweder, 1965; (8(–11)), Ronse Decraene *et al.*, 1997; *Phytolacca esculenta* Van Houtte ((7–)8(–9)), Schaeppi, 1936; (8), Yamazaki, 1987; *Phytolacca icosandra* L. (10), Payer, 1857; (7–10), Schaeppi, 1936; *Phytolacca japonica* Makino (7–9), Yamazaki, 1987; *Phytolacca polyandra* Batalin (8), Schaeppi, 1936. **Portulacaceae**, *Portulaca grandiflora* Hook. (6–7), Rocén, 1927.
- Santalales** (none).
- Saxifragales–Crassulaceae**, *Adromischus poeltzianus* Werderm. (6, floral centre not involved in carpel formation), Wassmer, 1955; *Aeonium* Webb & Berthel. ((6–)7–12(–16) or 18–32), Thiede & Eggli, 2007; *Aeonium haworthii* Webb & Berthel. (9), Wassmer, 1955; *Aeonium tabuliforme* Webb & Berthel. (7–8, floral centre not involved in carpel formation), this study: Figure 27; *Afrovivella* A.Berger (5–7), Thiede & Eggli, 2007; *Aichryson* Webb & Berthel. (6–12), Thiede & Eggli, 2007; *Crassula* L. ((2–)5(–12)), Thiede & Eggli, 2007; *Crassula argentea* Thunb. (6, floral centre not involved in carpel formation), Wassmer, 1955; *Graptopetalum* Rose ((4–)5(–10)), Thiede & Eggli, 2007; *Hypagophytum* A.Berger (10–12), Thiede & Eggli, 2007; *Monanthes* Haw. ((5–)6–8(–9)), Thiede & Eggli, 2007; *Petrosedum* Grulich (6–7(–12)), Thiede & Eggli, 2007; *Phedimus* Raf. ((4–)5–6(–7)), Thiede & Eggli, 2007; *Pseudosedum* A.Berger ((5–)6), Thiede & Eggli, 2007; *Rosularia* Stapf (5–9), Thiede & Eggli, 2007; *Sedum* L. ((3–)5(–12)), Thiede & Eggli, 2007; *Sempervivum* L. (6–18), Thiede & Eggli, 2007; *Sinocrassula yunnanensis* A.Berger (5–10, flat), Wassmer, 1955. **Penthoraceae**, *Penthorum* L. (5–(8)), Thiede, 2007.
- Rosids**
- Vitales** (none).
- Rosids–fabids*
- Zygophyllales–Zygophyllaceae**, *Augea* Thunb. (10-locular, whether 5 or 10 carpels?), Engler, 1931b; Sheahan, 2007; *Larrea* Cav. (5(–6)-locular), Sheahan,

2007; *Kallstroemia* Scop. (5 or 10–12), Engler, 1931b; (10(–12)-locular), Sheahan, 2007.

Celastrales–Celastraceae, *Brexia* Noronha ex Thouars (5–7), Simmons, 2004.

Oxalidales–Cephalotaceae, *Cephalotus* Labill. (6, with central protrusion of floral apex), Matthews & Endress, 2002. **Connaraceae**, *Agelaea* Sol. ex Planch. (5 plus sometimes additional sterile carpels), Schellenberg, 1938; *Cnestis ferruginea* DC. (5–9), Matthews & Endress, 2002. **Cunoniaceae**, *Eucryphia* Cav. (4–12(–18)), Dickison, 1978. **Elaeocarpaceae**, *Elaeocarpus* L. (2–9), Coode, 2004.

Malpighiales–Achariaceae, *Caloncoba* Gilg (c. 8), Gilg, 1925a; *Caloncoba glauca* Gilg (5–6), Bernhard & Endress, 1999; *Camptostylus mannii* Gilg (4–6), Bernhard & Endress, 1999; *Carpotroche* Endl. (4–8), Gilg, 1925a; (4–8(–10)), Fiaschi & Groppo, 2008; *Hydnocarpus* Gaertn. (3–6), Gilg, 1925a; *Hydnocarpus alcalae* C. DC. (5–7), Sleumer, 1954; *Scaphocalyx* Ridl. (5–7), van Heel, 1973; *Xylotheca* Hochst. (c. 6), Gilg, 1925a. **Calophyllaceae**, *Clusiella* Planch. & Triana (5–15), Stevens, 2007. **Caryocaraceae**, *Anthodiscus* G.Mey. (12), Prance, 1980; (8–12), Dickison, 1990a. **Clusiaceae**, *Clusia* L. (5–10), Engler, 1925a; *Clusia rosea* Jacq. (7), this study: Figure 48; *Garcinia* L. (up to 12), Engler, 1925a; (2–7(to c. 20)), Stevens, 2007; *Marila* Sw. (3–6), Stevens, 2007. **Euphorbiaceae–Acalyphoideae**, *Octospermum* Airy Shaw (8–9), Airy Shaw, 1974. **Euphorbiaceae–Euphorbioideae**, *Hura* L. (5–20), Webster, 1994; Radcliffe-Smith, 2001; *Mallotus pleiogyneus* Pax & K.Hoffm. ((7)–8–9), Kulju *et al.*, 2007. **Medusagynaceae (= Ochnaceae)**, *Medusagyne* Baker (17–24), Engler & Melchior, 1925; (c. 17–25), Cronquist, 1981; (16–19), Dickison, 1990c; (15–24, floral apex not involved in gynoeceum formation), Matthews *et al.*, 2012. **Ochnaceae**, *Brackenridgea* A.Gray ((3)5–10)), Amaral & Bittrich, in press; *Elvasia* DC. (2–5(–7)), Amaral & Bittrich, in press; *Idertia* Farron (5–6); Amaral & Bittrich, in press; *Ochna* L. (3–15), Gilg, 1925b; ((3)–5–10(–15)), Amaral & Bittrich, in press; *Ochna atropurpurea* DC. (6), Pauzé & Sattler, 1979; *Ochna integerrima* (Lour.) Merr. (13, flat), Guédès & Sastre, 1981; *Ochna kirkii* Oliv. (8–9, flat), Matthews *et al.*, 2012; *Ochna squarrosa* L. (5–15), Rao & Gupte, 1957; *Ouratea* Aubl. (5–10), Gilg, 1925b; Amaral & Bittrich, in press. **Pasifloraceae**, *Paropsiopsis* (4–6(7)), de Vos & Breteler, 2009; *Smeathmannia* ((3)4–6), de Vos & Breteler, 2009; *Viridivia* (4–6), de Vos & Breteler, 2009. **Phyllanthaceae**, *Glochidion harveyanum* Domin (8), Sutter, 1994; *Pimelodendron* Hassk. (3–21), Djarwaningsih, 2004; *Pimelodendron griffithianum* (Müll. Arg.) Benth. & Hook.f. (4–10), Djarwaningsih, 2004; *P. macrocarpum* J.J.Sm. (15–21), Djarwaningsih, 2004; *P. zanthogyne* J.J.Sm. (10–15,

flat), Djarwaningsih, 2004. **Putranjivaceae**, *Drypetes gossweileri* S.Moore (as *D. armoracia* Pax & K.Hoffm.) (5–6), Pax & Hoffmann, 1921; (6–7), Matthews & Endress, 2013. **Quinaceae (= Ochnaceae)**, *Lacunaria* Ducke (4–14), Schneider *et al.*, 2002, 2006; *Touroulia* Aubl. (6–11 styles), Engler, 1925b; (4–14), Schneider *et al.*, 2002, 2006. **Rafflesiaceae**, *Rafflesia* R.Br. ex Gray (numerous locules), Harms, 1935; Igersheim & Endress, 1998; *Rhizanthus* Dumort. (numerous locules), Harms, 1935; *Sapria* Griff. (numerous locules), Harms, 1935. **Rhizophoraceae**, *Pellacalyx cristatus* Hemsl. (c. 10, flat), Juncosa, 1988: figure 24; *Crossostylis* J.R.Forst. & G.Forst. (most species more than 5, maximum in *C. grandiflora* Brongn. & Gris, with 20–26), Setoguchi *et al.*, 1996; *Crossostylis grandiflora* Brongn. & Gris (c. 15), this study: Figure 41; *Gynotroches axillaris*, Blume ((5)–8–10), Matthews & Endress, 2011; this study: Figure 40. **Salicaceae**, *Banara* Aubl. (2–8), Gilg, 1925a; *Byrsanthus* Guillem. (4–6), Gilg, 1925a; *Calantica* Jaub. ex Tul. (3–6), Gilg, 1925a; *Dovyalis* E.Mey. ex Arn. (2–8), Gilg, 1925a; (6–7), Steyn *et al.*, 2005; ((13)–14–17), Cheek & Ngolan, 2006; *Flacourtia* Comm. ex L'Hér. (2–6), Gilg, 1925a; *Flacourtia indica* (Burm.f.) Merr. (5–6(–7)), Sleumer 1954; *Flacourtia jangomas* (Lour.) Raeusch. (4–6), Sleumer 1954; *Flacourtia rukam* Zoll. & Moritzi (4–6(–8)), Sleumer, 1954; (up to 7–8), this study: Figure 18; *Flacourtia tomentella* Miq. (4–5(–7)), Sleumer, 1954; *Homalium* Jacq. (2–6), Gilg, 1925a; (up to 8), Lescot, 1980; *Homalium barandae* Vidal ex Fern.-Vill. (7), Sleumer, 1954; *Homalium caryophyllaceum* Benth. (4–5(–7)), Sleumer, 1954; *Homalium grandiflorum* Benth. (5–8), Sleumer, 1954; *Homalium minahassae* Koord. (6–7), Sleumer, 1954; *Homalium samarense* Merr. (5–6), Sleumer, 1954; *Idesia* Scop. (3–6), Gilg, 1925a; *Itoa* Hemsl. (6), Gilg, 1925a; *Itoa stapfii* (Koord.) Sleumer ((5)–6–8), Sleumer, 1954; *Macrothumia* M.H. Alford (8–9), Alford, 2006; *Neosprucea* Sleumer (4–9), Alford, 2008; *Olmediella* Baill. (6–8), Gilg, 1925a; *Oncoba* Forssk. (c. 8), Gilg, 1925a; (c. 10), van Heel, 1977; *Patrisia* Rohr ex Steud. ((2)–3–4(–6)), Gilg 1925a; *Xylosma* G.Forst. (2–3(–4–6)), Gilg, 1925a. **Scyphostegiaceae**, *Scyphostegia* Stapf (9–13), van Heel, 1967.

Cucurbitales–Begoniaceae, *Begonia* L. (mostly 3, rarely 5)–6(–7)), de Wilde & Arends, 1979; Tebbitt, 2003; (2–3(–6)), de Wilde, 2011. **Coriariaceae**, *Coriaria* Niss. ex L. (5(–10)), Kubitzki, 2011. **Tetramelaceae**, *Octomeles* Miq. ((5)6–7(–8)), Matthews & Endress, 2004; ((5)–6–8), Swensen & Kubitzki, 2011.

Fabales–Fabaceae, *Accacia celastrifolia* Benth. (3–7), Prenner, 2011. **Polygalaceae**, *Eriandra* P.Royen & Steenis (7–8), Eriksen, 1993.

Fagales–Fagaceae, *Castanea* Mill. (6–9), Kubitzki, 1993b.

Rosales–Dirachmaceae, *Dirachma* Schweinf. ex Balf.f. (7–8), Ronse De Craene & Miller, 2004.

Rosids–malvids

Geraniales (none).

Myrtales–Myrtaceae, *Calycolpus* O.Berg (2–6), Wilson, 2011; *Campomanesia* Ruiz & Pav. ((3–)4–18), Wilson, 2011; *Decaspermum* Forst. (3–12), Wilson, 2011; *Eucalyptus* L'Hér. (2–7), Wilson, 2011; *Neofabricia* Joy Thomps. (5–12), Wilson, 2011; *Octamyrtus* Diels (4–(7)), Wilson, 2011; *Pleurocalyptus* Brongn. & Gris (4–6), Wilson, 2011; *Psidium* L. ((2–)3–5–(6)), Wilson, 2011. **Onagraceae**, *Ludwigia* L. sect. *Seminuda* P.H.Raven (4–7), Eyde, 1977; (4–6(7)), Wagner *et al.*, 2007. **Lythraceae**, fossil *Decodon* Cevallos-Ferriz & Stockey (4–6), Cevallos-Ferriz & Stockey, 1988; *Duabanga* Buch.-Ham. (4–9), Graham, 2007; *Duabanga grandiflora* Walp. (5–8), Geesink, 1970; (8, flat), this study: Figure 45; *Duabanga sonneratioides* Buch.-Ham. (up to 10), Venkateswarlu, 1937; *Ginoria* Jacq. ((2–)3–6), Graham, 2007; *Lagerstroemia* L. ((3–)6), Graham, 2007; *Lagerstroemia floribunda* Jack (6), Mayr, 1969; *Lagerstroemia flos-reginae* Retz. (6–7), Joshi & Venkateswarlu, 1935; *Punica granatum* L. (mostly 6 + 3, in two whorls), Eichler, 1878; (7), Sinha & Joshi, 1959; fossil *Shirleya grahamae* Pigg & Devore (5–7), Pigg & Devore, 2005; *Sonneratia* L.f. (4-to multilocular), Graham, 2007; *Sonneratia apetala* Buch.-Ham. (5–6), Venkateswarlu, 1937. **Melastomataceae**, *Bellucia* Neck. ex Raf. (8–15), Krasser, 1893; (12–13), Wurdack & Renner, 2002; *Clidemia octona* (Bonpl.) L.O.Williams (7–9), Wanntorp *et al.*, 2011; *Conostegia* aff. *montana* (Sw.) D.Don ex DC. (5–6), Wanntorp *et al.*, 2011; *Conostegia icosandra* (Sw. ex Wikstr.) Urb. (11), Wanntorp *et al.*, 2011; *Conostegia macrantha* O.Berg ex Triana (19–22), Wanntorp *et al.*, 2011; *Conostegia montealegreana* Cogn. (7–9), Wanntorp *et al.*, 2011; *Conostegia oerstediana* O.Berg ex Triana (13–15), Wanntorp *et al.*, 2011; *Conostegia pittieri* Cogn. (9–10), Wanntorp *et al.*, 2011; *Conostegia setosa* Triana (5–6), Wanntorp *et al.*, 2011; *Conostegia xalapensis* (Bonpl.) D.Don (4–10), Wanntorp *et al.*, 2011; *Myriasporea* DC. (8–10), Krasser, 1893; *Plethiandra* Hook.f. (6), Kadereit, 2006.

Crossosomatales–Strasburgeriaceae, *Strasburgeria* Baill. (4–7), Dickison, 1981; (4–6), Matthews & Endress, 2005b.

Picramniales (none).

Huerteales (none).

Brassicales–Capparaceae, *Capparis* L. (2–8), Ronse Decraene & Smets, 1997; *Capparis spinosa* L. (6–8, sometimes more), Leins & Metzenauer, 1979; (5–8), Karrer, 1991; (2–6), Kers, 2003; *Thylachium* DC. (6–10 placenta), Pax & Hoffmann, 1936; (6–10), Ronse Decraene & Smets, 1997; (6–10), Kers, 2003. **Gyrostemonaceae**, *Codonocarpus* Endl. (25–60),

George, 2003; *Gyrostemon* Desf. (1–30), George, 2003; *Gyrostemon brevipes* Hook. ex Moq. (c. 16–21), Endress, 2006; (c. 15–21), this study: Figures 20–23; *Gyrostemon osmus* Halford (10–12), Halford, 2005; *Gyrostemon racemigerus* H.Walter (c. 19–22), this study: Figures 24, 25; *Gyrostemon ramulosus* Desf. (15–21), Eckardt, 1971; (c. 20–32, sometimes with an additional, incomplete, whorl), Hufford, 1996; *Tersonia* Moq. (16–20), George, 2003; *Tersonia cyathiflora* (Fenzl) A.S.George (c. 16–18), Hufford, 1996. **Resedaceae**, *Caylusea* A.St.-Hil. (4–7), Kubitzki, 2003; *Sesamoides* Tourn. ex Rchb. (4–7), Kubitzki, 2003. **Tovariaceae**, *Tovaria* Baker (6–8), Fisel & Weberling, 1990.

Malvales–Cistaceae, *Cistus* L. (5–10), Janchen, 1925; (5(6–12)), Arrington & Kubitzki, 2003. **Cytinaceae**, *Cytinus* L. (6–10), Igersheim & Endress, 1998; (6–14), Burgoyne, 2006. **Malvaceae–Bombacoideae**, *Adansonia* L. (up to 8), Rao, 1954; (5–10), Bayer & Kubitzki, 2003; *Adansonia digitata* L. (up to more than 10), van Heel, 1966; Janka *et al.*, 2008; *Adansonia gibbosa* (A.Cunn.) Guymer ex D.A.Baum (7–8), Janka *et al.*, 2008. **Malvaceae–Dombeyoideae**, *Dombeya* Lam. (2–5(6)), Bayer & Kubitzki, 2003; *Eriolaena* DC. (5–10), Bayer & Kubitzki, 2003; *Eriolaena candollei* Wall. ((7–)8), Tang *et al.*, 2009; *Helmiopsiella* Arènes (5–10), Bayer & Kubitzki, 2003; *Nesogordonia* Baill. & H.Perrier (5(6)), Bayer & Kubitzki, 2003; *Ruizia* Ruiz & Pav. (10), Bayer & Kubitzki, 2003; *Trochetiopsis* Marais (5(6)), Bayer & Kubitzki, 2003. **Malvaceae–Grewioideae**, *Apeiba* Aubl. (10 to c. 20), Brunken, 2007; (scanning electron micrograph with 17), Brunken & Muellner, 2012; *Clappertonia* Meisn. (8) van Heel, 1966; (5–8), Brunken, 2007; *Desplatsia* Bocq. (6–8), Brunken, 2007; (section with 8, flat), Brunken & Muellner, 2012; *Duboscia* Bocq. (8), Brunken, 2007; *Glyphaea* Hook.f. (15), Brunken, 2007; (c. 15), Brunken & Muellner, 2012. **Malvaceae–Helicteroideae–Durioneae**, *Cullenia* Wight (5(6)), Bayer & Kubitzki, 2003; *Durio* Adans. ((3–)5(6)), Bayer & Kubitzki, 2003. **Malvaceae–Malvoideae**, *Abutilon* Mill. (5–22), Correll & Correll, 1982; (5 to many), Bayer & Kubitzki, 2003; *Acaulimalva* Krapov. (8–20), Bayer & Kubitzki, 2003; *Alcea* L. (over 15), Bayer & Kubitzki, 2003; *Allosidastrum* (Hochr.) Krapov., Fryxell & D.M.Bates (5–9), Bayer & Kubitzki, 2003; *Althaea* L. (8–25), Bayer & Kubitzki, 2003; *Anisodontea* C.Presl (5–26), Bayer & Kubitzki, 2003; *Anoda* Cav. (5–20), Bayer & Kubitzki, 2003; *Anotea* Kunth (10, in two whorls, one of them sterile), van Heel, 1978; Bayer & Kubitzki, 2003; *Bakeridesia* Hochr. (7–27), Bayer & Kubitzki, 2003; *Bastardia* Kunth (5–8), Bayer & Kubitzki, 2003; *Bastardiopsis* Hassl. (5–16), Bayer & Kubitzki, 2003; *Batesimalva* Fryxell (8–16), Bayer & Kubitzki, 2003; *Briquetia*

Hochr. (5–14), Bayer & Kubitzki, 2003; *Callianthe* Donnell (8–14(–16)), Donnell *et al.*, 2012; *Callirhoe* Nutt. (10–28), Bayer & Kubitzki, 2003; *Calyculogygas* Krapov. (13–14), Bayer & Kubitzki, 2003; *Calyptraemalva* Krapov. (45), Bayer & Kubitzki, 2003; *Cenocentrum* Gagnep. (10), Bayer & Kubitzki, 2003; *Corynoabutilon* (K.Schum.) Kearney (5–10), Bayer & Kubitzki, 2003; *Cristaria* Cav. (8–22), Bayer & Kubitzki, 2003; *Decaschistia* Wight. & Arn. ((6–)10), Bayer & Kubitzki, 2003; *Dendrosida* Fryxell (7–11), Bayer & Kubitzki, 2003; *Dirhamphis* Krapov. (12–17), Bayer & Kubitzki, 2003; *Eremalche* Greene (12–35), Bayer & Kubitzki, 2003; *Fryxellia* D.M.Bates (12), Bayer & Kubitzki, 2003; *Fuertesimalva* Fryxell (5–15), Bayer & Kubitzki, 2003; *Gaya* Gaudin (8–30), Bayer & Kubitzki, 2003; *Herissantia* Medik. (10), Correll & Correll, 1982; (10–14), Bayer & Kubitzki, 2003; *Hochreutinera* Krapov. (10–20), Bayer & Kubitzki, 2003; *Hoheria* A.Cunn. (5–8(–15)), Bayer & Kubitzki, 2003; *Horsfordia* A.Gray (6–11), Bayer & Kubitzki, 2003; *Iliamna* Greene (10–14), Bayer & Kubitzki, 2003; *Kaernemalvastrum* D.M.Bates (7–13), Bayer & Kubitzki, 2003; *Kitaibelia* Willd. (numerous), van Heel, 1995; (c. 50, in star-shaped loops), Endress, 2006; this study: Figures 28–32; *Krapovickasia* Fryxell (5–9), Bayer & Kubitzki, 2003; *Lavatera* L. (16–20), Bayer & Kubitzki, 2003; *Lawrencia* Hook. (2–11), Bayer & Kubitzki, 2003; *Lecanophora* Speg. (15–22), Bayer & Kubitzki, 2003; *Malachra* L. (10, in two whorls, one whorl sterile), van Heel, 1978; Bayer & Kubitzki, 2003; *Malacothamnus* Greene (7–14), Bayer & Kubitzki, 2003; *Malope trifida* Cav. (c. 45, in star-shaped loops), Eichler, 1878; (c. 55), van Heel, 1995; (numerous), Bayer & Kubitzki, 2003; *Malva* L. (6–12), Bayer & Kubitzki, 2003; *Malvastrum* A.Gray (8–12), Correll & Correll, 1982; ((5–)8–18), Bayer & Kubitzki, 2003; *Malvaviscus* Cav. (10, in two whorls, one of them sterile), van Heel 1978; Bayer & Kubitzki, 2003; *Malvella* Jaub. & Spach (6–10), Krapovickas, 1970; (7–10), Bayer & Kubitzki, 2003; *Meximalva* Fryxell (7–8), Bayer & Kubitzki, 2003; *Modiola* Moench (16–22), Bayer & Kubitzki, 2003; *Modiolas-trum* K.Schum. (8–15), Bayer & Kubitzki, 2003; *Monteiroa* Krapov. (10–17), Bayer & Kubitzki, 2003; *Napaea* L. (6–9), Bayer & Kubitzki, 2003; *Neobaclea* Hochr. (5–8), Bayer & Kubitzki, 2003; *Neobrittonia* Hochr. (8–12), Bayer & Kubitzki, 2003; *Nototriche* Turcz. (7–14), Bayer & Kubitzki, 2003; *Palaua* Ruiz & Pav. ((9–)20–40(–63)), carpels said to be arranged in several superimposed whorls in all species of *Palaua* except *P. sandemannii* (Sandwith) Fryxell – but no detailed study), Huertas *et al.*, 2007; (30–40), Bayer & Kubitzki, 2003; *Palaua mollendoensis* (Ulbr.) I.M.Johnst. (c. 20 in drawing, said to be arranged in several superimposed whorls), Huertas *et al.*, 2007; *Palaua sandemannii* (Sandwith) Fryxell (11 in

drawing, in only one whorl), Huertas *et al.*, 2007; *Pavonia* Cav. (10, in two whorls, one of them sterile), van Heel 1978; *Pavonia hastata* Cav. (10, in two whorls), this study: Figure 48; *Peltaea* (C.Presl) Standl. (10, in two whorls, one of them sterile), van Heel, 1978; Bayer & Kubitzki, 2003; *Periptera* DC. (7–15), Bayer & Kubitzki, 2003; *Phragmocarpidium* Krapov. (10, in two whorls, one of them sterile), van Heel, 1978; Bayer & Kubitzki, 2003; *Phymosia* Ham. (c. 20), Correll & Correll, 1982; (10–40), Bayer & Kubitzki, 2003; *Pseudabutilon* R.E.Fr. (5–10), Bayer & Kubitzki, 2003; *Rojasimalva* Fryxell (10, in two whorls, one of them sterile), van Heel, 1978; Bayer & Kubitzki, 2003; *Rhynchosida* Fryxell (8–14), Bayer & Kubitzki, 2003; *Robinsonella* Rose & Baker f. (7–30), Bayer & Kubitzki, 2003; *Sida* L. (5–12), Correll & Correll, 1982; (5–14), Bayer & Kubitzki, 2003; *Sidalcea* A.Gray (5–7), Bayer & Kubitzki, 2003; *Sidasodes* Fryxell & Fuertes (10–12), Bayer & Kubitzki, 2003; *Sidastrum* Baker f. (5–8), Correll & Correll, 1982; (5–10), Bayer & Kubitzki, 2003; *Sphaeralcea* A.St.-Hil. ((7–)10–16(–20)), Bayer & Kubitzki, 2003; *Tarasa* Phil. (6–13), Bayer & Kubitzki, 2003; *Tetrasida* Ulbr. (5–10), Bayer & Kubitzki, 2003; *Wissadula* Medik. (3–6), Bayer & Kubitzki, 2003; *Urena* L. (10, in two whorls, one of them sterile), van Heel, 1978; Bayer & Kubitzki, 2003; several genera of Malvoideae have ‘false’ septa, which imperfectly subdivide the primary locules, Bayer & Kubitzki, 2003. **Malvaceae–Sterculioideae**, *Cola* Schott & Endl. (3–10), Bayer & Kubitzki, 2003; *Pterocymbium* R.Br. (4–6), Bayer & Kubitzki, 2003; *Heritiera* J.F.Gmel. (4–5(–6)), Bayer & Kubitzki, 2003. **Muntingiaceae**, *Neotessmannia* Burret (c. 25 septa), Burret, 1924; (ovary multilocular), Bayer 2003a. **Neuradaceae**, *Neurada* L. (10, floral apex not involved in carpel formation), Ronse Decraene & Smets, 1995; Bayer, 2003b. **Thymelaeaceae**, *Octolepis* Oliv. (3–6), Herber, 2003; *Lethedon* Biehler ((8–)10(–12)), Herber, 2003; *Gonystylus* Teijsm. & Binn. (5–7), Herber, 2003.

Sapindales–uncertain position in Sapindales: fossil *Landeenia* Manchester & Hermsen (c. 18), Manchester & Hermsen, 2000. **Anacardiaceae**, *Pleiogygium* Engl. ((5–)8–12), Pell *et al.*, 2011; *Pleiogygium solandri* Engl. (7–10), Bachelier & Endress, 2009; *Trichoscypha* Hook.f. (3–4(–6)), Pell *et al.*, 2011; *Buchanania* Spreng. (4–6, only one carpel fertile), Pell *et al.*, 2011. **Burseraceae**, *Beiselia* Forman (9–12), Forman *et al.*, 1991; (9–12), Bachelier & Endress, 2009; (10(–12)), Daly *et al.*, 2011; *Boswellia* Roxb. ex Colebr. ((2–)3(–8)), Daly *et al.*, 2011. **Kirkiaceae**, *Kirkia* Oliv. (as *Pleiokirkia* Capuron) (8), Capuron, 1961; (8), Stannard, 2007; (8), Bachelier & Endress, 2008. **Meliaceae**, *Carapa* Aubl. (4–5(–6)), Mabberley, 2011; *Chisocheton* Blume (5–8), Harms, 1940; (2–8), Mabberley, 2011; *Cipadessa* Blume (5(–

6)), Mabblerley, 2011; *Clemensia* Merr. (5–8), Harms, 1940; *Dysoxylum* Blume (2–6), Mabblerley, 2011; *Ekebergia* Sparrm. (2–5(–6)), Mabblerley, 2011; *Guarea* F.Allam. (up to 12), Harms, 1940; (2–10(–14)), Mabblerley, 2011; *Humbertioturraea* J.-F.Leroy (10–14), Mabblerley, 2011; *Megaphyllaea* Hemsl. (7–9), Harms, 1940; *Melia* L. (up to 8), Harms, 1940; (4–8), Mabblerley, 2011; *Swietenia* Jacq. ((4–)5(–6)), Mabblerley, 2011; *Turraea* L. (up to 20), Harms, 1940; (10), Narayana, 1959; ((3–)4–10(–20)), Mabblerley, 2011; *Vavaea* Benth. (2–6-locular) (whether 6 carpels if 6-locular?), Mabblerley, 2011. **Nitrariaceae**, *Nitraria* L. (3(–6)), Sheahan, 2011. **Rutaceae–Rutoideae**, *Acronychia* J.R.Forst. & G.Forst. (4(–8)), Kubitzki *et al.*, 2011; *Casimiroa* La Llave ((2–)4–5(–8)), Kubitzki *et al.*, 2011; *Diplolaena* R.Br. (5(–8)), Kubitzki *et al.*, 2011; *Peltostigma* Walp. (6–10), Kubitzki *et al.*, 2011; *Toddalia* Juss. (4–7), Kubitzki *et al.*, 2011. **Rutaceae–Aurantioideae**, *Aegle* Corrêa (8–16), Engler, 1931a; (10–20), Vasil & Johri, 1964; (13), Nene & Tilak, 1977; (13–20), Ronse Decraene & Smets, 1998; (8–20), Kubitzki *et al.*, 2011; *Aeglopsis* Swingle (6), Engler, 1931a; (5–8), Kubitzki *et al.*, 2011; *Afraegle* (Swingle) Engl. (8(–10)), Kubitzki *et al.*, 2011; *Balsamocitrus* Stapf (5–8), Kubitzki *et al.*, 2011; *Citrus* L. (4 to many), Engler, 1931a; (13–20), Ronse Decraene & Smets, 1998; ((2–)5–15(–18)), Kubitzki *et al.*, 2011; *Citrus limon* (L.) Burm.f. (10–13), Roth & Lindorf, 1972b; *Citrus medica* L. (11), Nene & Tilak, 1977; *Citrus sinensis* (L.) Osbeck (c. 20, in two whorls), Lord & Eckard, 1985; *Limonia* L. (4–6), Kubitzki *et al.*, 2011; *Merrillia* (5(–6)), Kubitzki *et al.*, 2011; *Microcitrus* Swingle (4–8), Engler, 1931a; *Micromelum* Blume (2–6), Kubitzki *et al.*, 2011; *Peltostigma* Walp. (6–10), Engler, 1931a; *Poncirus* Raf. (6–8), Ying *et al.*, 1993; *Swinglea* Merr. (8–10), Engler, 1931a; (8–10), Kubitzki *et al.*, 2011. **Sapindaceae**, *Acer* L. (2 (3,5,8)), Acevedo-Rodríguez *et al.*, 2011; *Chytranthus* Hook.f. (3–8), Acevedo-Rodríguez *et al.*, 2011; *Distichostemon* F.Muell. (3(–6)), Acevedo-Rodríguez *et al.*, 2011; *Dodonaea* Miller ((2–)3–5(–6)), Acevedo-Rodríguez *et al.*, 2011; *Radlkofera* Gilg (5–7(–8)), Acevedo-Rodríguez *et al.*, 2011. **Simaroubaceae**, *Eurycoma* Jack (5(–6)), Clayton, 2011; *Holacantha* A.Gray (6–8), Clayton, 2011.

Asterids

Cornales–Hydrangeaceae, *Broussaisia* Gaudich. ((4–)5(–6)), Hufford, 2004; *Carpenteria* Torr. (5–7), Hufford, 2004; *Decumaria* L. (9), Hufford, 2001; (6–12), Hufford, 2004; *Deinathe* Maxim. (4–6), Hufford, 2004; *Dichroa* Lour. ((4–)5(–6)), Hufford, 2004. **Cornaceae**, *Davidia* Baill. (6–8), Eyde, 1963; (7, flat), Moser 1968; (7–9), this study: Figure 46.

Ericales–Actinidiaceae, *Actinidia* Lindl. (15–30), Ronse Decraene & Smets, 1998; *Actinidia arguta*

(Siebold & Zucc.) Planch. ex Miq. (c. 16–20), Gilg & Werdermann, 1925a; *Actinidia chinensis* Planch. (c. 35) (flat or wavy line, in the latter case two fruits are united), Watson & Gould, 1994; (26, flat), Guédès & Schmid, 1978; (c. 20–30), Schmid, 1978; (23), van Heel, 1987; *Actinidia deliciosa* (A.Chev.) C.F.Liang & A.R.Ferguson (30–40) (the flat compitum allows better pollen tube crossing between carpels, also those farthest away can be reached), Howpage *et al.*, 1998; *Actinidia fortunatii* Finet & Gagnep. (20), Cuong, Soejarto & Li, 2007; *Actinidia fulvicoma* Hance (14), Cuong *et al.*, 2007; *Actinidia indochinensis* Merr. (18), Cuong *et al.*, 2007; *Actinidia latifolia* (Gardner & Champ.) Merr. (c. 27, flat but carpels not contiguous in the centre), Moser 1968; (19), Cuong *et al.*, 2007; *Actinidia melanandra* Franch. (13, flat), van Heel, 1987; (c. 20), Ronse Decraene & Smets, 1998; *Saurauja* Willd. ((3–)5(–8)), Dressler & Bayer, 2004. **Ebenaceae**, *Diospyros* L. (2–8), Wallnöfer, 2004; (4–8), Venkatasamy *et al.*, 2006. **Ericaceae**, *Acrotriche* R.Br. (2–6), Paterson, 1962; (2–10-locular), Stevens *et al.*, 2004a; *Brachyloma* Sonder (4–10-locular), Stevens *et al.*, 2004a; *Cheilothea* Hook.f. (6), Stevens *et al.*, 2004a; *Comarostaphylos* Zucc. (4–6), Stevens *et al.*, 2004a; *Cyathodes* Labill. ((5–)6–10-locular), Stevens *et al.*, 2004a; *Decatoca* F.Muell. (10-locular), Stevens *et al.*, 2004a; *Empetrum* L. (6–9-locular), Stevens *et al.*, 2004a; *Erica* L. ((1–)4(–8)), Stevens *et al.*, 2004a; *Gaylussacia* Kunth (10-locular), Stevens *et al.*, 2004a; *Hemitomes* A.Gray (8), Stevens *et al.*, 2004a; *Ledothamnus* Meisn. (5(–7)), Stevens *et al.*, 2004a; *Leptocophylla* C.M.Weiller (5–7-locular), Stevens *et al.*, 2004a; *Leucopogon pedicellatus* C.T.White (9), Copeland, 1954; *Lissanthe* R.Br. (3–9-locular), Stevens *et al.*, 2004a; *Melichrus* R.Br. (4–6-locular), Stevens *et al.*, 2004a; *Newberrya* Torr. (eight parietal placentae, but four sepals, four petals and eight stamens, in terminal flowers more organs; the eight placentae alternating with the eight stamens, which suggests that the carpels alternate with the stamens), Copeland, 1934; *Pentachondra* R.Br. (5–11-locular), Stevens *et al.*, 2004a; *Pityopus oregonus* Small (7–9), Copeland, 1935a; *Planocarpa* C.M.Weiller (5–8-locular), Stevens *et al.*, 2004a; *Rhododendron* L. (5–12-locular), Stevens *et al.*, 2004a; *Trochocarpa* R.Br. (8–11-locular), Stevens *et al.* 2004a. **Lecythidaceae**, **Lecythidaceae–Lecythidoideae**, *Couroupita guianensis* Aubl. (6–7), Tsou & Mori, 2007; (6–7, more or less radial, this study: Fig. 43, or flat: Fig. 44), Endress, 1994; this study: Figures 43, 44; *Gustavia hexapetala* (Aubl.) Sm. (6), Tsou, 1994; *Gustavia macarenensis* Philipson (4–8), Tsou & Mori, 2007; *Gustavia superba* (Kunth) O.Berg (c. 7–8, flat), this study. **Lecythidaceae–Napoleonaeoideae**, *Asteranthos* Desf. (5–6), Tsou, 1994; *Napoleonaea*

P.Beauv. (5–6), Tsou, 1994. **Marcgraviaceae**, (2–8 to many), Gilg & Werdermann, 1925c; *Marcgravia* L. (3–20), Dressler, 2004; (6–10), von Balthazar & Schönenberger, 2013; *Marcgravia* sp. (6–7, irregular), this study; Figure 53; *Marcgraviastrum* (Wittm. ex Szyszyl.) de Roon & R.Dressl. (5–9), Dressler, 2004; (3–9), von Balthazar & Schönenberger, 2013. **Sapotaceae**, the following numbers are locule numbers; thus, it is possible that the actual carpel number is only half this number in cases in which there are secondary septa (see this situation for Ternstroemiaceae); however, some have an odd number of locules, such as five in *Delpyodora* and other genera; classification: Swenson & Anderberg, 2005. **Sapotaceae–Sapotoideae–Sapoteae**, *Faucherea* Lecomte ((5)6(–10)), Pennington, 2004; *Labramia* A.DC. (8–12), Pennington, 2004; *Madhuca* J.F.Gmel.((5)–8–9(–15)), Pennington, 2004; *Manilkara* Adans. (6–14), Pennington, 2004; *Manilkara* Adans. (as *Achras* L.) (10), Roth & Lindorf 1972a; (9–12), Prakash & Kiat 1982; *Mimusops* L. ((7)8), Pennington, 2004; *Mimusops commersonii* Engl. (c. 8), this study; *Northia* Hook.f. (6), Pennington, 2004; *Palaquium* Blanco ((5)6(–10)), Pennington, 2004; *Payena* A.DC. ((4)–6–8(9)), Pennington, 2004; *Tieghemella* Pierre (8), Pennington, 2004; *Vitellariopsis* Baill. ex Dubard (7–9), Pennington, 2004. **Sapotaceae–Sapotoideae–Sideroxyloae**, *Sideroxylon* L. ((1)–5(–8)), Pennington, 2004. **Sapotaceae–Chrysophylloideae**, *Aubregria* Heine (7–8), Pennington, 2004; *Brevia* Aubrév. & Pellegr. (8–9), Pennington, 2004; *Chrysophyllum* L. ((4)5(–12)), Pennington, 2004; *Ecclinusa* Mart. ((3)–5(–9)), Pennington, 2004; *Englerophytum* K.Krause ((4)5(–10)), Pennington, 2004; *Englerophytum magalismontanum* (Sond.) T.D.Penn. (as *Bequaertiodendron magalismontanum* (Sond.) Heine & J.H.Hemsl.) ((4)5(–10)), Steyn & Robbertse, 1990; *Magodendron* Vink (5–8), Vink, 1995; *Omphalocarpum* P.Beauv. (5–30), Pennington, 2004; *Pichonia* Pierre ((4)5(6)), Pennington, 2004; *Planchonella* Tiegh. (more than 5?), Swenson & Anderberg, 2005; *Pouteria* Aubl. (1–6(–15)), Pennington, 2004; *Pradosia* Liais. ((4)5(6)), Pennington, 2004; *Pycnandra* Benth. (5–8(–10)), Pennington, 2004; *Synsepalum* Baill. (5(–7)), Pennington, 2004; *Tridesmostemon* Engl. (10), Pennington, 2004. **Sapotaceae – not classified**, *Aulandra* H.J.Lam (6(7)), Pennington, 2004; *Capurodendron* Aubrév. (5(6)), Pennington, 2004; *Diplok-nema* Pierre ((5)6–15), Pennington, 2004; *Labourdonnaisia* Bojer (5–10), Pennington, 2004; *Letestua* Lecomte (16–18), Pennington 2004. **Scytopetalaceae**, *Asteranthos* Desf. (5–8), Appel, 2004; *Brazzeia* Baill. ((5)6(7)), Appel, 2004; *Scytopetalum* Pierre ex Engl. ((6)7,8), Appel, 2004. **Ternstroemiaceae**, ovary locule numbers higher than three may

be caused by secondary ‘false’ septa, Melchior, 1925; Weitzman *et al.*, 2004; this needs more study; *Archboldiodendron* Kobuski (5(–7)-locular), Weitzman *et al.*, 2004; *Freziera* Willd. ((2)3–5(6)-locular), Weitzman *et al.*, 2004; *Ternstroemia* Mutis (4–6-locular), Melchior, 1925; Weitzman *et al.*, 2004. **Theaceae**, *Pyrenaria* Blume ((3)–5–6(–10)), Stevens *et al.*, 2004b; *Gordonia* L. ((3)–5(–10)), Stevens *et al.*, 2004b; *Schima* Blume (5(–7)), Stevens *et al.*, 2004b.

Asterids–lamiids

Boraginales–Boraginaceae, *Lennoa* Lex. ((7)–8(–9)), Yatskievych & Mason, 1986; *Lennoa madreporoides* Lex. ((13)–14–15(–17)), Suessenguth, 1927; *Pholisma* Nutt. ex Hook. (6–16), Yatskievych & Mason, 1986; Endress, 2002; *Pholisma arenarium* Nutt. ex Hook. (8), Copeland, 1935b.

Icacinaceae–Pyrenacantha Wight (up to 12 or more stigmatic branches, but only one locule), Sleumer, 1942; *Pyrenacantha laetevirens* Sleumer (c. 10 stigmatic branches), Labat *et al.*, 2006; *Pyrenacantha perrieri* Labat, El-Achkar & R.Rabev. (5–7 stigmatic branches), Labat *et al.*, 2006; *Pyrenacantha rakotozafyi* Labat, El-Achkar & R.Rabev. (c. 20 stigmatic branches), Labat *et al.*, 2006.

Garryales (none).

Gentianales–Rubiaceae, an undetermined species of the *Canthium* Lam.–*Pyrostria* Roxb. *s.l.* group (8), Leroy, 1972; *Canthium confertum* Korth. group (2–6), Razafimandimbison *et al.*, 2009; *Lasianthus* Jack (2–12), Robbrecht, 1988; Robbrecht *et al.*, 1991; (c. 9), Piesschaert *et al.*, 2000; *Peponidium* (Baill.) Arènes (2–10), Razafimandimbison *et al.*, 2009; *Praravinia* Korth. ((4)5–8(–16)), Robbrecht, 1988; *Pseudopyxis* Miq. ((4)5(6)), Puff, 1989; *Pyrostria* Roxb. (incl. *Dinocanthium* Bremek., *Leroya* Cavaco and *Pseudopeponidium* Homolle ex Arènes) (2–10), Razafimandimbison *et al.* 2009; *Schizostigma* Arn. (4–7), Puff *et al.*, 1997; *Scyphochlamys* Balf.f. (4–6), Razafimandimbison *et al.*, 2009; Spermaceae (2(3–6)), Igersheim & Rohrhofer, 1993; *Timonius* DC. (more than 20); however, it is not certain whether each compartment having one ovule corresponds to an entire carpel, Robbrecht, 1988; *Timonius* DC. subgenus *Timonius* (8–10); in addition, the numerous ovules are in separate locules in vertical files, Darwin, 1993; *Timonius* subgenus *Abbottia* (F.Muell.) S.P.Darwin ((4)–6–8(–12)), plus each of these units has a vertical (radial) double file of uniovulate locules, Darwin, 1994.

Lamiales (none).

Solanales–Solanaceae, *Nolana* L. ex L.f. (5 or more than 10, depending on interpretation), Huber, 1980; *Nolana paradoxa* Lindl. (10–25, incorrectly interpreted as forming two whorls), Di Fulvio, 1971;

this study: Figure 54; *Solanum lycopersicon* L. (3–10 or more), Muller, 1940.

Asterids–campanulids

Aquifoliales–Aquifoliaceae, *Ilex* L. ((2–)4–9(–22)), Baas, 1975.

Asterales–Campanulaceae, *Canarina* L. (6), personal observation; *Michauxia* L'Hér. ((6–)8–10), Lammers, 2007; *Ostrowskia* Regel ((5–)7(–9)), Lammers, 2007. **Rousseaceae**, *Carpodetus serratus* J.R.Forst & G.Forst. (5–8), Bense & Palser, 1975 (this range of numbers possibly erroneous, not shown with illustrations; Shore, 1969 and Gustafsson, 2007 do not mention more than five carpels); *Roussea* Sm. (5–7), Takhtajan, 1997; Koontz *et al.* 2007.

Escalloniales (none).

Bruniales (none).

Paracryphiales–Paracryphiaceae, *Paracryphia* Baker f. (8–12), Swamy, 1953; (8–15), Dickison & Baas, 1977; Endress, 2002; Jérémie, 2008.

Dipsacales (none).

Apiales–Araliaceae (2–10), Wen *et al.*, 2001; *Aralia* L. (5–6), Eyde & Tseng, 1971; *Boerlagiodendron* Harms (5–14), Stone, 1962; (8–12), Eyde & Tseng, 1971; *Dendropanax* Decne. & Planch. (4–6), Eyde & Tseng, 1971; *Fatsia* Decne. & Planch. (5–10(11)), Xiang *et al.*, 2007; *Gastonia* Comm. ex Lam. (7–12), Philipson, 1970; (6–15), Eyde & Tseng, 1971; *Geopanax* Hemsl. (5–10), Eyde & Tseng, 1971; *Indokingia* Hemsl. (13), Philipson, 1970; (14–18), Eyde & Tseng, 1971; *Magalopanax* Ekman ex Harms (7–10), Eyde & Tseng, 1971; *Meryta sinclairii* (Hook.f.) Seem. (3–6), Eyde & Tseng, 1971; *Munroidendron* Sherff (12–14), Philipson, 1970; *Munroidendron racemosum* (C.N.Forbes) Sherff (c. 22, centre not involved in carpel formation), this study: Figure 19; *Octotheca* R. Vig. (15–20), Eyde & Tseng, 1971; *Oreopanax* Decne. & Planch. (5–10), Eyde & Tseng, 1971; *Osmoxylon* Miq. (8–10), Eyde & Tseng, 1971; ((4)5(6)), Xiang *et al.*, 2007; *Peckeliopanax* Harms (6–22),

Philipson, 1970; Eyde & Tseng, 1971; *Pentapanax* Seem. ((3–)5(–7)), Xiang *et al.*, 2007; *Plerandra* A.Gray (9–13), Eyde & Tseng, 1971; ((2–)3–19), Lowry *et al.*, 2013; *Plerandra* A.Gray subgenus *Costatae* G.M.Plunkett, Lowry & Frodin (8–12), Lowry *et al.*, 2013; *Plerandra* A.Gray subgenus *Dizygotheca* (N.E.Br.) Lowry, G.M. Plunkett & Frodin (5–10(–15)), Lowry *et al.*, 2013; *Plerandra* A.Gray subgenus *Gabriellarum* Lowry, G.M.Plunkett & Frodin (5–13), Lowry *et al.*, 2013; *Plerandra* A.Gray subgenus *Plerandra* (5–19), Lowry *et al.*, 2013; *Plerandra grandiflora* A.C.Sm. (8–9), Nuraliev *et al.*, 2010; *Plerandra insolita* A.C.Sm. (10), Nuraliev *et al.*, 2010; *Plerandra victoriae* Gibbs (10), Nuraliev *et al.*, 2010; *Plerandropsis* R.Vig. (10), Eyde & Tseng, 1971; *Polyscias* Forst. (4,5(–8 or more)), Xiang *et al.*, 2007; *Reynoldsia* A.Gray (6–24), Philipson, 1970; (7–22), Eyde & Tseng, 1971; *Schefflera* J.R.Forst. & G.Forst. (5–10 or more?), Eyde & Tseng, 1971; *Schefflera actinophylla* (Endl.) Harms (12, flat), Sokoloff *et al.*, 2007; Nuraliev *et al.*, 2010; (tend to be arranged in two rows, 10–11), Nuraliev *et al.*, 2011; *Schefflera hemiepiphytica* (Grushv. & Skvortsova) C.B.Shang (up to 13), Grushvitzky & Skvortsova, 1973; Sokoloff *et al.* 2007; *Schefflera heptaphylla* (L.) Frodin (6–7(–9), flat), Nuraliev *et al.*, 2011; *Schefflera octophylla* (Lour.) Harms ((6–)8(–9), flat), Nuraliev *et al.*, 2010; *Schefflera subintegra* (Craib) C.B. Shang (up to 23), Grushvitzky & Skvortsova, 1973; *Schefflera venulosa* (Wight & Arn.) Harms (6, flat), Nuraliev *et al.*, 2010; *Sciadodendron* (9–12), Eyde & Tseng, 1971; *Tetraplasandra* A.Gray (2–10), Philipson, 1970; *Tetraplasandra waialealae* Rock (5–7), Nuraliev *et al.*, 2010; *Trevesia* Vis. sp. (9), Eyde, 1967; (7–12), Eyde & Tseng, 1971; *Tupidanthus* Hook.f. & Thomson (up to 200+, carpels along H-shaped line), Eyde & Tseng, 1971; Wen *et al.*, 2001; Endress, 2002, 2006, this study: Figures 51, 52; (60–138), Sokoloff *et al.*, 2007; *Woodburnia* Prain (8–13), Eyde & Tseng, 1971.