



Patterns of angiospermy development before carpel sealing across living angiosperms: diversity, and morphological and systematic aspects

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Almost all angiosperms are angiospermous, i.e. the ovules are enclosed in carpels at anthesis and during seed development, but angiospermy develops in different ways across angiosperms. The most common means of carpel closure is by a longitudinal ventral slit in carpels that are partly or completely free. In such carpels, the closure process commonly begins at midlength of the prospective longitudinal slit and then proceeds downward and upward. Closure by a transverse slit is rarer, but it is prominent in groups of the ANITA grade and in a few early branching monocots (some Alismatales) and some early branching eudicots (a few Ranunculaceae and Nelumbonaceae), in these eudicots combined with a more or less developed longitudinal slit. In all these cases the carpels have a single ovule in ventral median position. In ANITA lines with pluriovulate carpels, there is only a short longitudinal slit in the uniformly ascidiate carpels. In carpels with a unifacial style the closure area is narrow; this pattern is rare and scattered mainly in some wind-pollinated monocots and eudicots. In most angiosperms the carpels become closed before the ovules are visible from the outside of the still incompletely closed carpels (early carpel closure). This is notably the case in the ANITA grade and magnoliids. Delayed carpel closure, with the ovules visible before the carpels are closed, is much rarer and is concentrated in a few monocots (mainly some Alismatales and some Poales) and a few eudicots (mainly a few Ranunculales and many Caryophyllales, and scattered in some other eudicots). A kind of delayed carpel closure (with the placenta visible before closure but mostly not the ovules) also occurs in syncarpous gynoecea with a free central placenta. Most gynoecea with a free central placenta occur in the superasterids. In such gynoecea the individual carpel tips are not differentiated but the opening in young gynoecea has the shape of a circular diaphragm. In this case, when ovary septa and free carpel tips are missing, the number of carpels is sometimes unclear (Primulaceae, Lentibulariaceae, some Santalaceae). Extremely ascidiate carpels are concentrated in the ANITA grade, a few magnoliids and some early branching monocots. Aspects of potential advantages of plicate vs. ascidiate carpels with regard to flexibility of pollen tube transmitting tract differentiation are discussed. © 2015 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2015, **178**, 556–591.

ADDITIONAL KEYWORDS: carpel closure patterns – carpel development – carpel morphology – late closure of carpels – precocious development of ovules.

INTRODUCTION

Plants have an open organization, in contrast to animals. They are able to produce new organs or modules consisting of several organs from shoot apices. A consequence is that these organs themselves are open as well, more or less freely exposed, and there are no internalized organs or parts of

organs. A notable exception are the carpels in flowering plants (angiosperms), which become incurved in early development and then become closed and sealed along their rims or flanks, and by this process the ovules, the future seeds, which develop on the carpels, become completely enclosed in the carpels, a condition known as angiospermy. Earlier studies found that this sealing is not uniform in angiosperms. Most importantly, sealing is by secretion in the early diverging grade of extant angiosperms (ANITA grade), whereas in more advanced

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groups, sealing by postgenital fusion of the carpel flanks becomes more common (Doyle & Endress, 2000; Endress & Igersheim, 2000a; Endress & Doyle, 2009).

In this paper, I do not focus on carpel sealing, but on the patterns of carpel development *before* sealing occurs. Thus, the focus is on the morphological and not the histological level of angiospermy. Carpel closure, the development of angiospermy, is a morphogenetically unique process in plants. In contrast to insects and vertebrates, where closure of the neural groove into a neural tube is a well-studied process (e.g. Copp, Greene & Murdoch, 2003; Gorfinkiel, Schamberg & Blanchard, 2011; Sullivan-Brown & Goldstein, 2012), the developmental processes leading to angiospermy in angiosperms are poorly studied. Angiospermy develops from a flat or peltate young carpel or a syncarpous young gynoecium by differential growth in several directions and closure resulting in a three-dimensional shape with an intricate internal space, which retains a (closed) exit to the outer world. The inner surface of this space (as also the outer surface of the carpels) is developmentally derived from the floral apex and is thus a primary morphological surface (Endress, 2006). Also, the diversity of this process, considering the variants that occur across angiosperms, has not been comparatively studied. Here I focus in particular on four aspects. (1) What is the position of the area of closure in detail, which is reflected by the shape of the closure line or slit as seen from the surface after closure and how are different shapes of closure lines related to different forms of placentation? (2) What is the direction of closure development in carpels with longitudinal closure? (3) When does carpel closure occur during carpel development with regard to ovule development? (4) What is the systematic distribution of different patterns across angiosperms?

The sources for this paper are unpublished results of my own comparative studies of carpel development in many different groups of angiosperms. In addition, I considered a vast amount of primary literature on floral development across all larger angiosperm groups, mainly publications that use scanning electron microscopy (SEM) to demonstrate development. Although the focus of most of these papers was not primarily on the process of carpel closure and therefore in many papers the critical stages of carpel closure were not shown, there are still a large number of publications with figures that could be used for my purpose. For classification I use APG III (2009). From these broad comparative studies, previously unrecognized developmental patterns in carpel closure became apparent. It is the aim of this paper to demonstrate and discuss these patterns in a comparative ('top-down') approach across the angiosperms.

MATERIAL AND METHODS

Material used in this study is based on the following collections (abbreviations: 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. If figures from more than one collection are used, the figure number is indicated at the end of each collection.

- Achlys triphylla* DC. (Berberidaceae), *PKE 7489*, Washington State, USA.
- Amborella trichopoda* Baill. (Amborellaceae), *H. McKey 38909*, New Caledonia (Fig. 50); Botanical Garden, University of California, Santa Cruz, *s.n.*, coll. 1993 (received by H. Tobe) (Fig. 49).
- Annona cherimola* Mill. (Annonaceae), *PKE 1375*, Guatemala.
- Aquilegia vulgaris* L. (Ranunculaceae), *PKE 6749*, BGZ.
- Ascarina lucida* Hook.f. (Chloranthaceae), *PKE 6376*, New Zealand.
- Asphodeline lutea* (L.) Rchb. (Xanthorrhoeaceae; now Asphodelaceae), *PKE 7642*, BGZ.
- Austrobaileya scandens* C.T.White (Austrobaileyaceae), *B. Gray 2044*, Queensland, Australia (Fig. 67); *B. Hyland 6393*, Queensland, Australia (Fig. 68).
- Berberis vulgaris* L. (Berberidaceae), *N. Schnyder, s.n., s.d.*, BGZ.
- Brasenia schreberi* J.F.Gmel. (Cabombaceae), *R. Rutishauser s.n.*, coll. 07 2001, Ontario, Canada.
- Cabomba furcata* Schult. & Schult.f. (Cabombaceae), *PKE 00–58*, BGZ.
- Carpinus betulus* L. (Betulaceae), *PKE 923* (Fig. 45); *PKE 986* (Fig. 46), both BGZ.
- Ceratophyllum demersum* L. (Ceratophyllaceae), *PKE 9755*, BGZ.
- Cercidiphyllum japonicum* Siebold & Zucc. ex J.J.Hoffm. & J.H.Schult.bis (Cercidiphyllaceae), *PKE 6711*, BGZ.
- Chloranthus elatior* Link (Chloranthaceae), *PKE 4078*, Papua New Guinea.
- Chloranthus japonicus* Siebold (Chloranthaceae), *Y. Omori, s.n.*, coll. 20 04 79, Japan (received by S. Terabayashi).
- Cyathocalyx martabanicus* Hook.f. & Thomson (Annonaceae), *PKE 9372*, Bogor Botanical Gardens, Java, Indonesia.
- Degeneria vitiensis* L.W.Bailey & A.C.Sm. (Degeneriaceae), *E. Zogg s.n.*, coll. 1985, Fiji.
- Dillenia alata* (R.Br.ex DC.) ex Martelli (Dilleniaceae), *PKE 4304*, Queensland, Australia.
- Geranium robertianum* L. (Geraniaceae), *PKE 7224*, BGZ.
- Gunnera tinctoria* (Molina) Mirb. (Gunneraceae), *PKE 6632*, BGZ.

Gyrostemon racemigerus H.Walter (Gyrostemonaceae), *U. Hofmann 1400*, Western Australia, Australia.

Hedyosmum mexicanum C.Cordem. (Chloranthaceae), *PKE 1114*, Honduras.

Hernandia nymphaeifolia (J.Presl) Kubitzki (Hernandiaceae), *PKE 03–40*, National Tropical Botanical Garden, Kauai, Hawaii, USA.

Hunnemannia fumariifolia Sweet (Papaveraceae), *A. Karrer s.n., s.d.*, BGZ.

Hippuris vulgaris L. (Plantaginaceae), *PKE 98-5*, BGZ.

Idiospermum australiense (Diels) S.T.Blake (Calycanthaceae), *NSW 242 850*, Queensland, Australia (received by B.Hyland).

Illicium anisatum Gaertn. (Schisandraceae), *PKE 00-60*, Botanical Garden, Isole di Brissago, Switzerland.

Kitaibelia vitifolia Willd. (Malvaceae), *PKE s.n.*, coll. 1981, BGZ.

Laurus nobilis L. (Lauraceae), *PKE 2639*, cult., Switzerland.

Nelumbo nucifera Gaertn. (Nelumbonaceae), *PKE 6714*, BGZ.

Nuphar advena (Aiton) W.T. Aiton (Nymphaeaceae), *PKE 00-61*, BGZ.

Pavonia hastata Cav. (Malvaceae), *PKE s.n.*, coll. 1985, BGZ.

Pinguicula moranensis Kunth (Lentibulariaceae), *PKE 8011*, BGZ.

Polyscias racemosa (C.N.Forbes) Lowry & G.M.Plunkett (Araliaceae), *PKE 96-10*, National Tropical Botanical Garden, Kauai, Hawaii, USA.

Pseudowintera axillaris (J.R.Forst & G.Forst.) Dandy (Winteraceae), *PKE 6357*, New Zealand.

Ranunculus acris L. (Ranunculaceae), *PKE 6750*, BGZ.

Reseda phyteuma L. (Resedaceae), *PKE 98-7*, BGZ.

Rollinia mucosa (Jacq.) Baill. (Annonaceae), *PKE 9364*, Bogor Botanical Gardens, Java, Indonesia.

Sarcandra glabra (Thunb.) Nakai (Chloranthaceae), Botanical Garden Hamburg, *HBG 439-80*, Germany.

Schisandra chinensis (Turcz.) Baill. (Schisandraceae), *PKE 99-67*, BGZ.

Scrophularia nodosa L. (Scrophulariaceae), *PKE 10017*, BGZ.

Solanum lycopersicum L. (Solanaceae), *PKE 7881*, BGZ.

Tasmannia piperita (Hook.f.) Miers (Winteraceae), *PKE 4137*, Papua New Guinea.

Tetracera nordtiana F.Muell. (Dilleniaceae), *PKE 9021*, Queensland, Australia.

Trimenia papuana Ridl. (Trimeniaceae), *PKE 4087*, Papua New Guinea.

Victoria cruziana A.D.Orb. (Nymphaeaceae), *PKE 9983*, BGZ.

Zannichellia palustris L. (Potamogetonaceae), *PKE s.n.*, coll. 29 05 1971, Italy.

Zygogynum baillonii Tiegh. (Winteraceae), *PKE 6100*, New Caledonia.

The material was fixed and stored in 70% ethanol. Young carpels were studied by SEM. They were critical point dried, sputter coated with gold and studied at 20 kV with a Hitachi S-4000 microscope. Vouchers are deposited at the Institute of Systematic Botany, University of Zurich (Z).

RESULTS AND DISCUSSION

ANGIOSPERMY IN APOCARPOUS AND SYNCARPOUS GYNOCIA

In gynocia in which the carpels are free (apocarpous or unilocarpellate), each carpel becomes separately closed during development (except in rare cases discussed below under 'Intra- and intercarpellary post-genital fusion'). In gynocia in which the carpels are congenitally united (syncarpous), the situation is more complex. In cases in which only the lower part of the gynoeceum is syncarpous, but the upper part is apocarpous, at first the individual carpels become closed, also in the syncarpous zone, and then the central part of the gynoeceum, which is still open, also becomes closed (Endress, 2014). Such gynocia may have a septate or non-septate ovary in the syncarpous zone. In cases in which the gynoeceum is syncarpous along its entire length, it may also be septate or non-septate. If it is not septate (i.e. with parietal or free central placentation), the gynoeceum may become closed in its entirety, without separate closure of the individual carpels.

PATTERNS OF THE LINES OF CLOSURE IN FREE CARPELS (FIGS 1, 2)

Before focusing on the development of angiospermy, it is useful to mention briefly different patterns of the closure area after closure has occurred. After closure of a carpel the area of closure is seen as a line on the outer surface of the carpel (Fig. 1). In free carpels this line is the outer border of the ventral slit if the ventral slit is viewed as a three-dimensional structure. In most cases, the line extends longitudinally on the ventral surface of the carpel, encompassing the style (up to the stigma) and at least part of the ovary (Fig. 2A, B). The line marks the plicate zone of the carpel (terminology of Leinfellner, 1950). If one ovule is in a median position (either alone or with other, lateral ovules), a short transversally directed line is often present at the base of the ventral longitudinal

line (Fig. 2B). This additional transverse line is sometimes only conspicuous in early stages after closure and is no longer noticeable in mature carpels at anthesis. In plicate carpels with a unifacial (rounded)

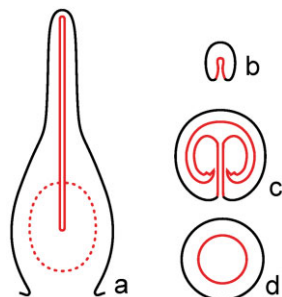


Figure 1. Schematic drawing of the most common closure pattern in free angiosperm carpels. (a) Carpel from ventral side, red: longitudinal closure area (ventral slit) and inner morphological surface, dotted: location of ovary locule. (b–d) Transverse section series of a carpel, ventral side down: (b) plicate zone of style; (c) plicate zone of ovary with ovules; (d) ascidiate zone of ovary below ovules.

style or upper part of the style, the longitudinal closure line is restricted to the ovary plus, sometimes, the lower part of the style (Fig. 2C). In largely ascidiate carpels the longitudinal slit is only short (Fig. 2D, E). An extreme case is that only a transverse line is present on top of the ovary but no longitudinal line. This occurs in some largely ascidiate carpels with a single median ovule, in which there is no style formed (Fig. 2F) or the style remains flat and is not infolded and not involved in carpel closure (Fig. 2G). The diversity of these patterns will be discussed in the systematic part of this paper.

CARPEL DEVELOPMENT BEFORE CLOSURE AND SEALING (FIGS 3–8)

The margins and the increasing flanks of a carpel curve upwards or in a ventral (adaxial) direction or combined in both directions, depending on whether the carpel is at first mainly ascidiate or mainly plicate or has an intermediate shape between ascidiate and plicate. In this early stage the developing inner carpel surface is still visible from the outside.

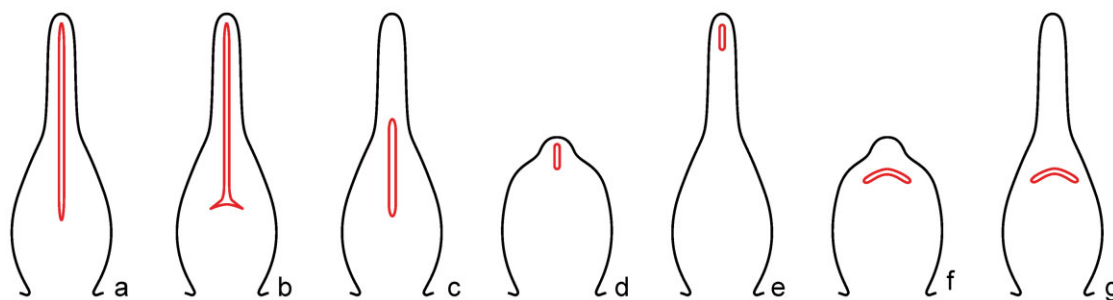
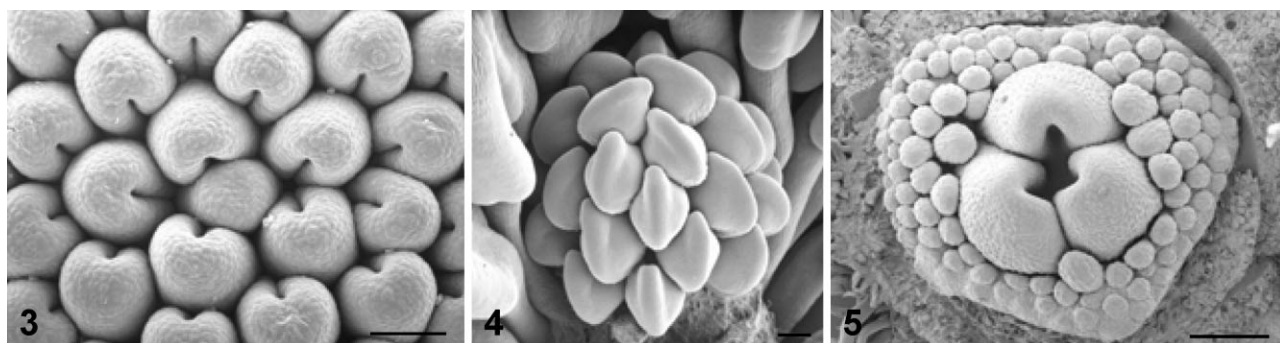
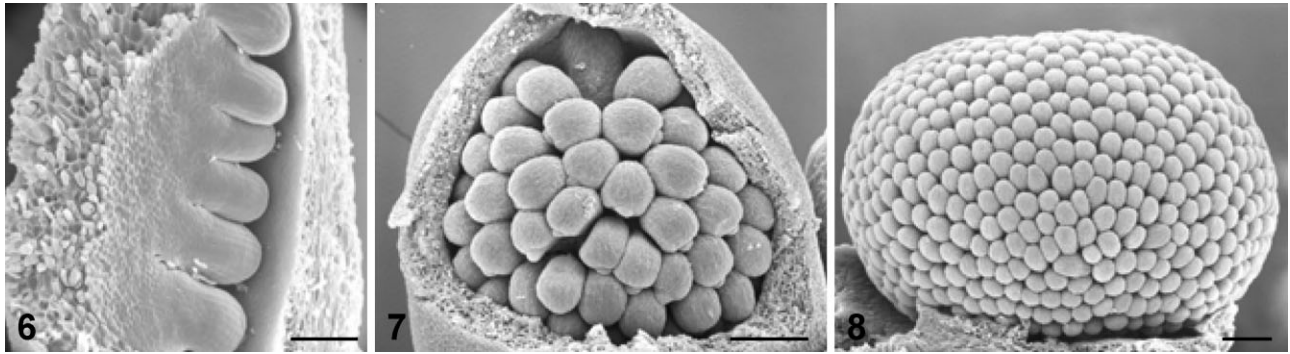


Figure 2. Schematic drawings of different closure patterns in free angiosperm carpels; red: closure area. (a) Carpel with longitudinal slit; (b) carpel with longitudinal combined with transverse slit; (c) carpel with short longitudinal slit below unifacial style; (d) carpel with short longitudinal slit and without style; (e) carpel with short longitudinal slit on top of ascidiate style; (f) carpel with transverse slit and without style; (g) carpel with transverse slit and with unifacial or flat (non-plicate) style.



Figures 3–5. Partial protection of the inner surface of still open carpels by their neighbours in pluricarpellate gynoecia. 3. *Rollinia mucosa* (Annonaceae), gynoecium, from above. 4. *Ranunculus acris* (Ranunculaceae), gynoecium, from the side. 5. *Tetracera nordtiana* (Dilleniaceae), gynoecium, from above. Scale bars: 100 µm.



Figures 6–8. Partial protection of young ovules by carpel involution and ovule curvature, in linear, protruding-diffuse and free central placenta. **6.** *Tasmannia piperita* (Winteraceae), view of longitudinally halved gynoeceum in zone of ovary: ovules curved away from ventral slit. **7.** *Solanum lycopersicum* (Solanaceae), laterally opened ovary, view of protruding-diffuse placenta, with ovules curved downwards. **8.** *Pinguicula moranensis* (Lentibulariaceae), ovary wall removed, view of free central placenta, with ovules curved downwards. Scale bars: 100 μm (Figs 6, 7); 200 μm (Fig. 8).

Often carpels, in addition, curve longitudinally in an adaxial direction so that the inner carpel surface becomes hidden early, although the carpel is not yet completely closed (Figs 3–5). These are cases of normal or ‘early’ angiospermy. If the carpels are arranged in one series they mutually protect each other with their ventral sides (*Tetracera nordtiana*; Fig. 5). If they are in several series, the dorsal sides of the inner neighbours cover the ventral sides of the outer neighbours (*Rollinia mucosa*, Fig. 3; *Ranunculus acris*, Fig. 4). This longitudinal median curvature is an early component of protecting the ovules (and the inner surface of the carpels/gynoeceum with the placenta) before complete closure. The same principle of inward curvature for protection works in anatropous ovule curvature (1) in the same direction as carpel involution (*Tasmannia piperita*; Fig. 6) and (2) sometimes in a thick, protruding placenta (*Solanum lycopersicum*; Fig. 7) or away from the floral apex in a free central placenta (*Pinguicula moranensis*; Fig. 8) (see also Endress, 2011a, for discussion). It is easiest to see into the carpel or gynoeceum in unicarpellate flowers or in such multicarpellate flowers in which the centre of the floral apex is flat and is not involved in gynoeceum formation, so that the ventral sides of the carpels are somewhat separated from each other (see Endress, 2014). In such cases the ventral side of the carpels is not obstructed from view by other carpels.

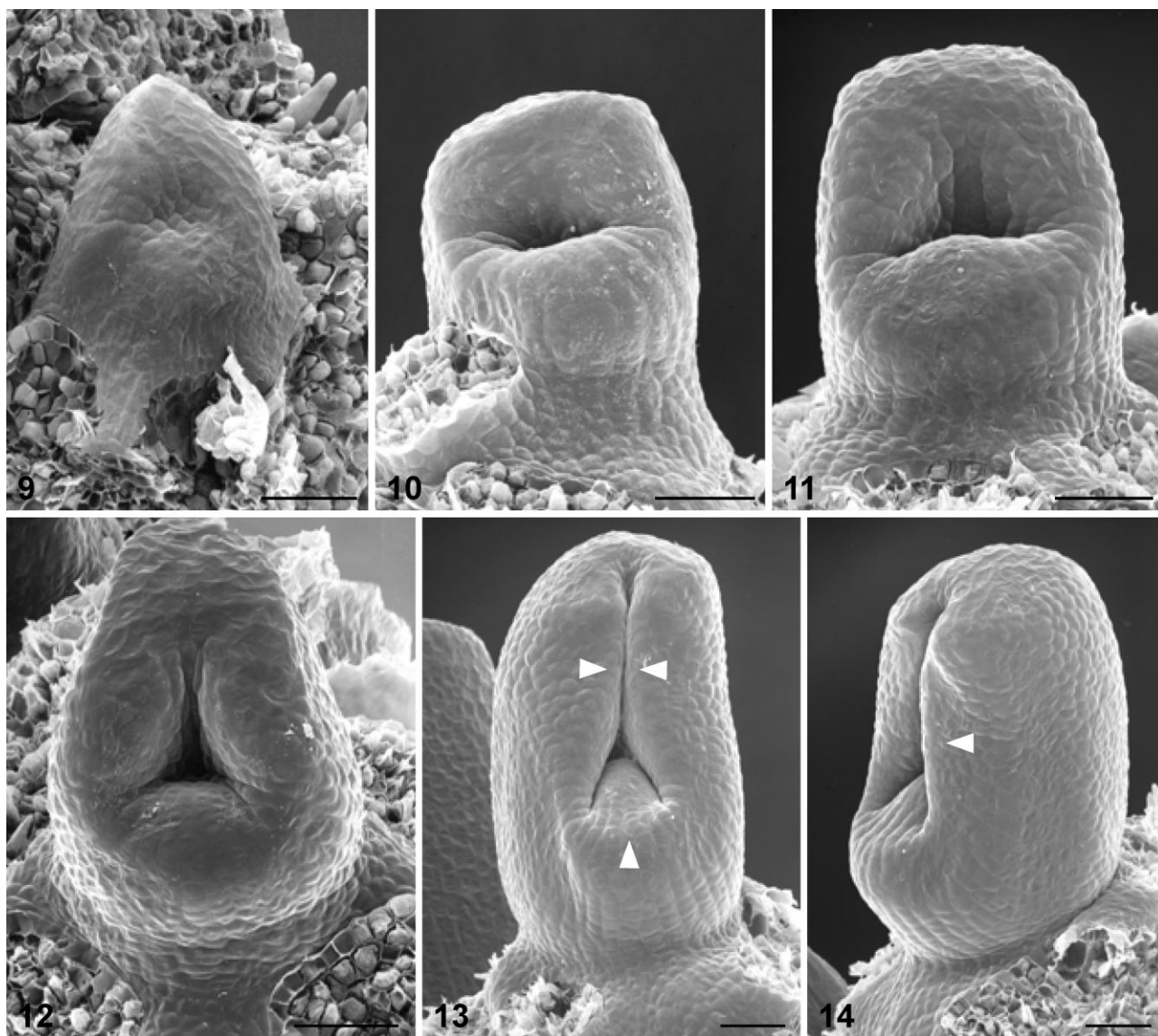
I will focus onto two aspects of diversity of the closure process. The first is the developmental direction of closure in carpels with a ventral longitudinal slit. Is it bidirectional, basipetal or acropetal, or synchronous? How is closure in highly syncarpous gynoeceia? The second is the timing of carpel closure with

regard to ovule development. Does closure take place before ovules become visible or afterwards?

DIRECTION OF CARPEL CLOSURE IN CARPELS WITH A MEDIAN LONGITUDINAL SLIT (FIGS 9–25)

Carpels that have a median longitudinal slit usually begin to become closed at mid-length and only later do the upper and lower ends become closed. This appears to be a common pattern in angiosperms that are apocarpous or have an apocarpous zone in a partially syncarpous gynoeceum. In syncarpous gynoeceia with free styles, closure and the formation of a ventral slit extends from the ovary upwards along the style. Closure at the lower and upper end of the ventral slit is somewhat delayed. This may be seen as a useful architectural pattern. If the folding or involution of the carpel begins at mid-length and continues in both directions, upwards and downwards, it may be easier and quicker to attain the final stage of angiospermy than if it begins at the upper or lower end, because of shorter distances for the closure process.

Laurus nobilis is a good example for this pattern. Carpel development was described in detail by Endress (1972b, plate 11, fig. 26A). In the present publication more micrographs are provided to focus on the closure process of the carpel (Figs 9–14). The first morphological differentiation is the formation of peltation by the appearance of a cross zone, where the margin traverses the carpel from both sides over the ventral surface (Fig. 9). By elongation of the areas below the primary margins the carpel becomes obliquely cup-shaped. It is still completely open (Fig. 10). The carpel flanks above the level of the cross zone begin to converge in their lower mid-length, which later leads to the formation of a longitudinal slit

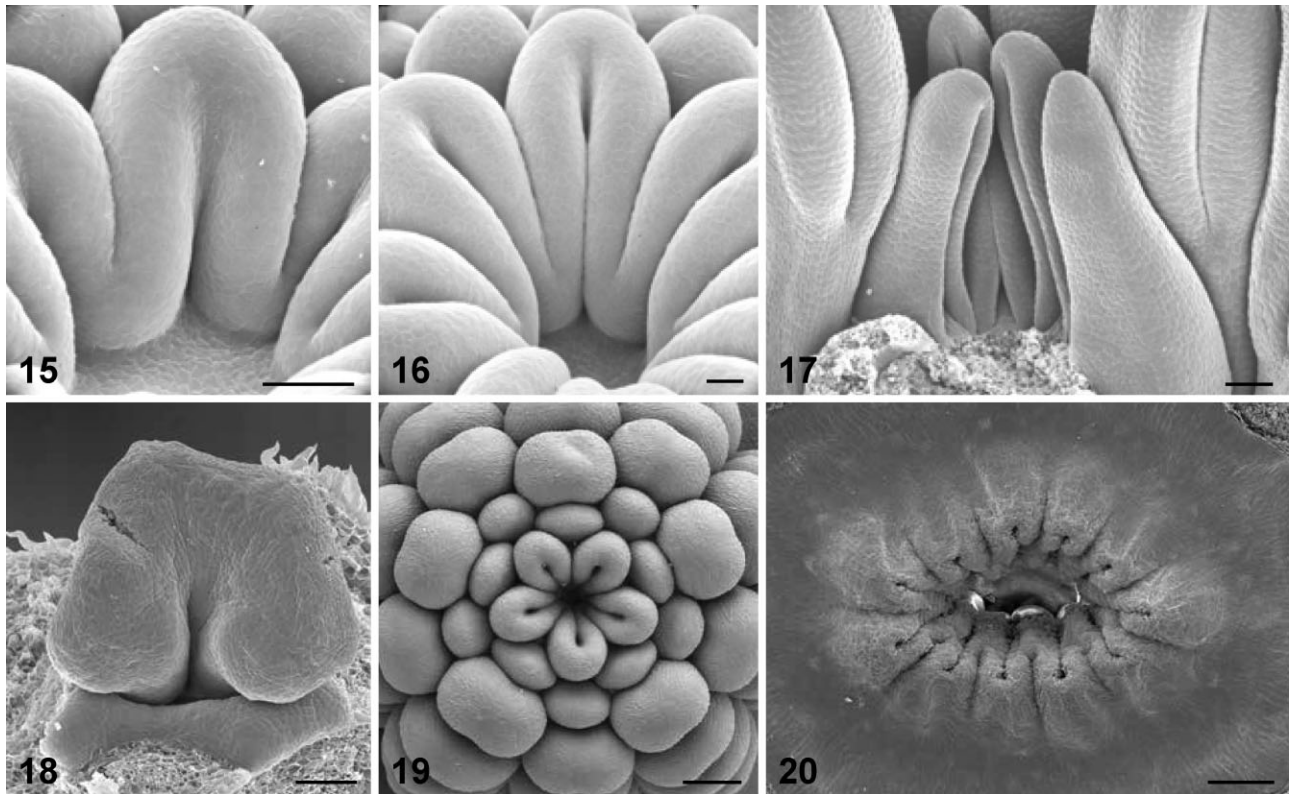


Figures 9–14. *Laurus nobilis* (Lauraceae). Development of the unilocular gynoecium, with longitudinal (and transverse) closure. The longitudinal closure begins at mid-length of the future style (marked with arrowheads in Figs 13, 14) by thickening (incurving) of the lateral flanks and proceeds further in both directions. Individual carpels have somewhat irregular outlines caused by imprints by neighbouring contiguous organs in bud. All carpels viewed from ventral side, except Figure 14 with carpel viewed from lateral side. **9.** Carpel in early peltate stage. **10.** Carpel with cross zone well developed. **11.** Carpel with flanks on both sides beginning to thicken. **12.** Carpel with flanks approaching each other. **13.** Carpel almost closed with flanks contiguous and secondary ventral rim. **14.** Same carpel, from the side. Scale bars: 50 μm .

(Fig. 11). The flanks continuously approach each other in their lower mid-length (Fig. 12) until they become contiguous in their lower mid-length (Figs 13, 14).

The same pattern of closure beginning at mid-length is illustrated here with several other examples: *Dillenia alata* (Dilleniaceae) (Figs 15, 16), *Illicium anisatum* (Schisandraceae) (Fig. 17), *Hernandia nymphaeifolia* (Hernandiaceae) (Fig. 18), *Aquilegia vulgaris* (Ranunculaceae) (Fig. 19) and *Polyscias racemosa* (Fig. 20). In *Hernandia* and *Poly-*

scias the ovary is inferior and the superior part of the carpel(s) is short, but the start of the involution is clearly at mid-length of the free part of the carpel. It appears that this pattern mainly occurs in carpels with a single median ovule or with an u-shaped placenta (placenta following the inner borders of the ventral slit and connecting both borders at the lower end of the slit; see Leinfellner, 1951b). Staedler, Weston & Endress (2009) mention that in Laurales a basal delay of closure appears to occur in the core



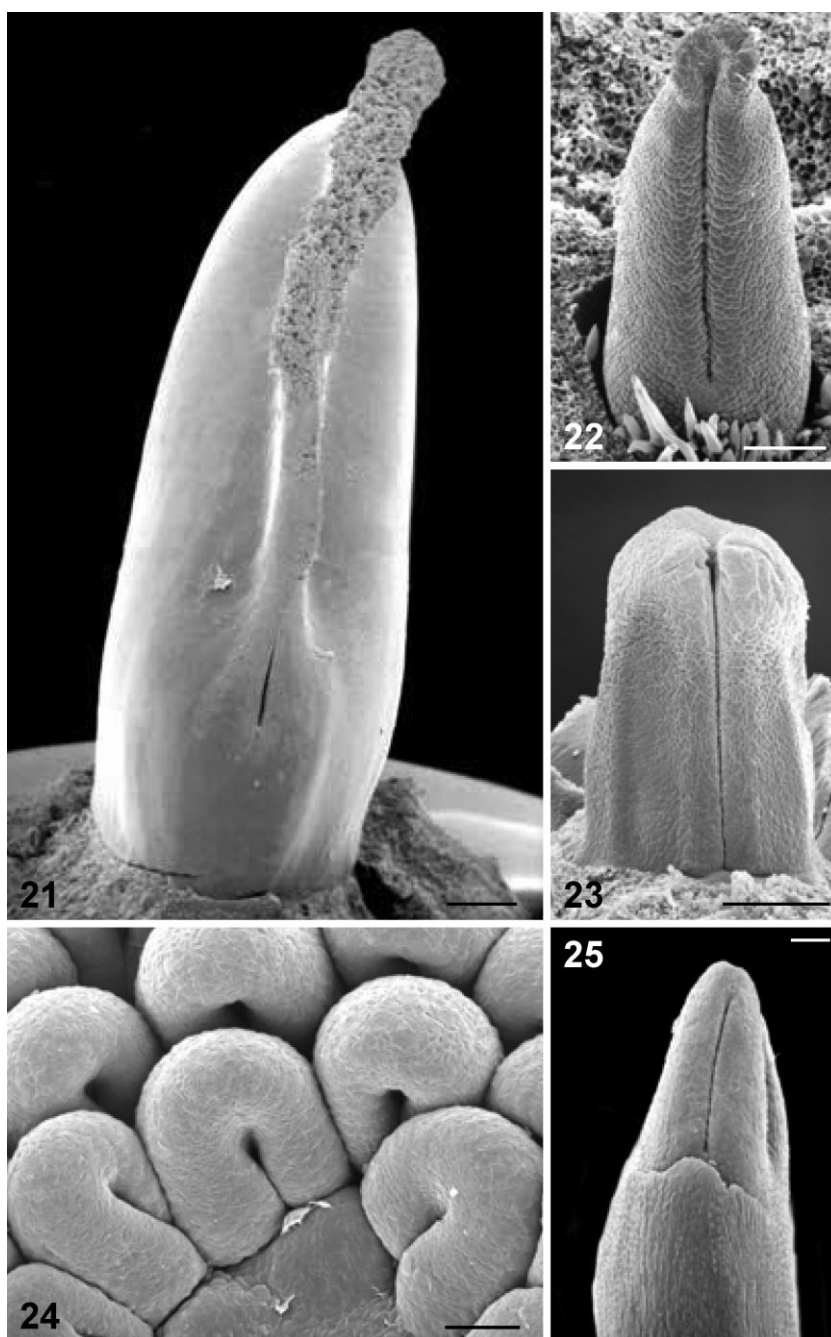
Figures 15–20. Carpels with longitudinal closure, beginning at mid-length. **15–16.** *Dillenia alata* (Dilleniaceae). **15.** Carpels still open. **16.** Carpels closed at mid-length. **17.** *Illicium anisatum* (Schisandraceae). **18.** *Hernandia nymphaeifolia* (Hernandiaceae). **19.** *Aquilegia vulgaris* (Ranunculaceae). **20.** *Polyscias racemosa* (Araliaceae). Scale bars: 50 μm (Figs 15, 16); 100 μm (Figs 17–19); 200 μm (Fig. 20).

families, which have a single median ovule, but not in Calycanthaceae, which have two lateral ovules. Other examples figured in the literature are *Knema tomentella* Warb. (Myristicaceae) (van Heel, 1983, fig. 33), *Clematis peterae* Hand.-Mazz. (Ranunculaceae) (Ren, Chang & Endress, 2010, fig. 3F), *Asteropyrum petatum* (Franch.) J.R.Drumm & Hutch. (Ranunculaceae) (Zhao *et al.*, 2012a, fig. 3G), *Sinofranchetia chinensis* (Franch.) Hemsl. (Lardizabalaceae) (Zhang, Ren & Tian, 2009, fig. 18), *Carnarvonia araliifolia* F.Muell. (Proteaceae) (Douglas, 1996, fig. 53), *Abrus precatorius* L. (Fabaceae) (Prenner, 2013, fig. 2B), *Calliandra tetragona* (Willd.) Benth. (Fabaceae) (van Heel, 1981, fig. 73), *Lupinus albus* L. (Fabaceae) (van Heel, 1981, fig. 85), *Pithecellobium dulce* (Roxb.) Benth. (Fabaceae) (van Heel, 1983, fig. 87), *Geum urbanum* Hook.f. (Rosaceae) (Smedmark & Eriksson, 2006, fig. 7D), *Sorbaria arborea* C.K.Schneid. (Rosaceae) (van Heel, 1984, fig. 27) and *Spiraea trilobata* L. (Rosaceae) (Evans & Dickinson, 1999, fig. 79).

Other patterns of non-synchronous closure of the ventral slit along its length also occur (Figs 21–25). In some plants the longitudinal slit appears to close first

in the lower part, such as in *Idiospermum australiense* (Calycanthaceae) (Staedler *et al.*, 2009, fig. 16; this study, Fig. 22), *Cyathocalyx martabanicus* (Annonaceae) (Fig. 23), *Annona cherimola* (Annonaceae) (Fig. 24), *Tasmannia piperita* (Winteraceae) (van Heel, 1983, fig. 17), *Holboellia grandiflora* Réaub. (Lardizabalaceae) (Zhang & Ren, 2011, figs 70–72), *Sargentodoxa cuneata* (Oliv.) Rehder & E.H.Wilson (Lardizabalaceae) (Zhang & Ren, 2008, fig. 7H–K), *Duparquetia orchidacea* Boiss. (Fabaceae) (Prenner & Klitgaard, 2008, fig. 6J), *Schefflera pueckleri* (K.Koch) Frodin (Araliaceae) (as *Tupidanthus calyptratus* Hook. & Thomson) (Sokoloff *et al.*, 2007, figs 65–67) and *Schefflera subintegra* (Craib) C.B.Shang (Araliaceae) (Nuraliev *et al.*, 2014, fig. 11E).

In others, the longitudinal slit appears to become closed first in the upper part, such as *Degeneria vitiensis* (Degeneriaceae) (Fig. 21) and *Penthorum sedoides* (Penthoraceae) (my pers. observ.). A basipetal pattern of closure and complete lack of closure at the base of the ventral slit was reported for *Sagittaria trifolia* (Alismataceae) (Huang, Wang & Wang, 2014, fig. 1G). In *Degeneria* I.W.Bailey & A.C.Sm. the area



Figures 21–25. Carpels with longitudinal closure, other patterns. **21.** *Degeneria vitiensis* (Degeneriaceae), carpel with peripheral opening at the base. **22.** *Idiospermum australiense* (Calycanthaceae), carpel with peripheral opening on top. **23.** *Cyathocalyx martabanicus* (Annonaceae), carpel with peripheral opening on top. **24.** *Annona cherimola* (Annonaceae), young carpels with opening on top. **25.** *Cercidiphyllum japonicum* (Cercidiphyllaceae), carpel with even closure along its length. The lobe at the base of the carpel is the subtending bract of the greatly reduced female flower. Scale bars: 50 μm (Figs 24, 25); 150 μm (Figs 21–23).

of postgenital closure is large because of broad carpel flanks; the narrow open gap at the base of the ventral slit in a preanthetic stage (Fig. 21) is present only at the carpel periphery, but is postgenitally closed

further inside. Regardless, at anthesis the carpels are not open as stated in earlier literature (e.g. Eames, 1961: 189) but completely closed by postgenital connection of the flanks (Igersheim & Endress, 1997).

Still another pattern is more or less synchronous closure along the entire length of the slit, such as in *Cercidiphyllum japonicum* (Cercidiphyllaceae) (Fig. 25) or *Bellendena montana* R.Br. (Proteaceae) (Douglas & Tucker, 1996a, figs 18, 22). The entire process of closure still needs to be studied in more detail in many of these cases to ascertain the different existing patterns.

CARPEL CLOSURE IN SYCARPOUS GYNOECIA (FIGS 26–35)

In syncarpous gynoecia closure may be different depending on the extent of congenital union of the carpels. If the upper part of the gynoecium is apocarpous for some distance, each carpel becomes separately closed before the central part of the gynoecium becomes closed. In this case, closure also results in a longitudinal slit for each carpel. An example is *Geranium robertianum* (Geraniaceae). Here the five congenitally united carpels form a star-shaped open bowl in the beginning of development (Fig. 26). This is followed by involution or folding of each individual carpel in the apocarpous zone, which continues, as seen in downward direction, by the congenitally united flanks (intercarpellary fusion) in the upper syncarpous zone in the style and upper ovary (symplicate zone; terminology of Leinfellner, 1950). This can be seen in an apical view of a young gynoecium in which the centre is not yet closed (Fig. 27). In the basal zone of the ovary, the carpels show not only intercarpellary but also intracarpellary congenital fusion (synascidiate zone; terminology of Leinfellner, 1950). The same sequence of closure formation was shown for the multicarpellate gynoecium of *Dillenia suffruticosa* (Griff.) Martelli (Dilleniaceae) (Endress, 2014, figs 1–8).

In contrast, in strongly syncarpous gynoecia, i.e. with carpel union almost to the tip of the carpels, such as in *Scrophularia nodosa* (Scrophulariaceae) (Figs 28–35), the individual carpels may not become closed before the inner surface of the different carpels becomes contiguous in the (short) apocarpous zone. At first, the two syncarpous carpels appear as a ring wall, which is slightly higher in the median plane of the gynoecium. These two sites in the median plane are at the same time the mid points of each carpel (Fig. 28). Then the two flanks of the united carpels become apparent (Fig. 29). The two flanks appear more conspicuous because the carpels have broadened. The syncarpous zone of the gynoecium has now differentiated into a synascidiate and a symplicate zone. From the outside only the symplicate zone is visible and the synascidiate zone is hidden at the base of the gynoecium. In this view the gynoecium has an elliptical contour (Fig. 30). The gynoecium

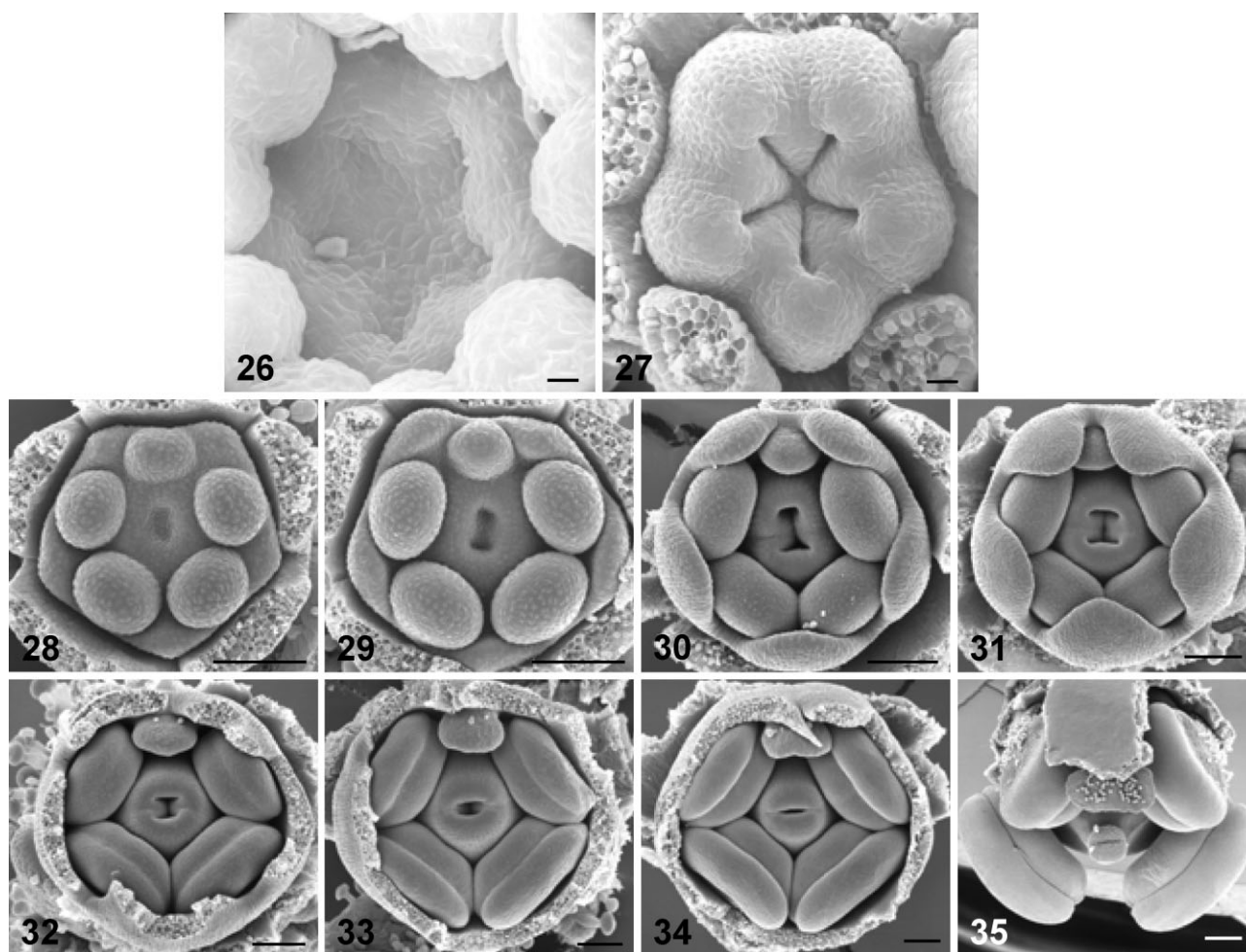
further broadens so that the outline is now more circular, and it elongates in the upper area. The flanks are still visible but have become more hidden (Fig. 31). Then the tips of the two carpels approach each other (Fig. 32). The carpels appear now to be closer together and the flanks are no longer visible from the outside (Fig. 33). The tips of the two carpels become almost contiguous and only a narrow transverse slit between the two carpels has been left at the entrance into the inside of the gynoecium (Fig. 34). Finally, the gynoecium becomes completely closed along the transverse slit, which serves both carpels (Fig. 35).

EARLY CARPEL CLOSURE (BEFORE OVULES BECOME VISIBLE FROM THE OUTSIDE)

I distinguish two patterns of carpel closure with regard to ovule development: (1) early closure in which the carpel closes at a time the ovules are not visible from the outside of the gynoecium (when the carpels or gynoecium are left intact but other floral organs are removed in case they partially or completely obstruct the view of the gynoecium); and (2) delayed closure in which ovules are visible from the outside before carpel closure. Thus, 'early' and 'late' are not absolute but relative values that can be easily observed in SEM micrographs from the outside of gynoecia without destroying them.

Early carpel closure and late appearance of ovules is most common in angiosperms. Importantly, it characterizes all early diverging angiosperms (ANITA grade plus Chloranthaceae and Ceratophyllaceae), irrespective of carpel size and ovule number. It has been reported in Amborellaceae (Endress & Igersheim, 2000b; Posluszny & Tomlinson, 2003; Buzgo, Soltis & Soltis, 2004), Hydatellaceae (Rudall *et al.*, 2007; Sokoloff *et al.*, 2010), Cabombaceae (Endress, 2001, 2005), Nymphaeaceae (Endress, 2001), Austrobaileyaceae (Endress, 1980c, 1983), Trieniaceae (Endress & Sampson, 1983), Schisandraceae (Robertson & Tucker, 1979; Erbar, 1983; Tucker & Bourland, 1994; Endress, 2001; Dong *et al.*, 2012), Chloranthaceae (Endress, 1987) and Ceratophyllaceae (Endress, 1994b).

It is also common in all four orders of magnoliids [e.g. Annonaceae (Leins & Erbar, 1996), Degeneriaceae (Swamy, 1949), Magnoliaceae (Erbar, 1983), Myristicaceae (van Heel, 1983), Calycanthaceae (Erbar, 1983; Staedler *et al.*, 2009), Hernandiaceae (Endress & Lorence, 2004), Lauraceae (Endress, 1972a,b) (this study, Figs 12–14), Monimiaceae (Endress, 1980a,b), Siparunaceae (Endress, 1972a,b), Winteraceae (Tucker, 1959; Sampson, 1964; Tucker & Gifford, 1966; Sampson & Kaplan, 1970; Vink, 1970; Sampson & Tucker, 1978; Erbar, 1983; Endress, 1986;



Figures 26–35. Syncarpous gynoecia. **26–27.** *Geranium robertianum* (Geraniaceae). Gynoecium with five carpels. **26.** Carpels still widely open (surrounded by stamens). **27.** Carpels just before they become closed, showing longitudinal prospective closure lines (ventral slits). **28–35.** *Scrophularia nodosa* (Scrophulariaceae). Gynoecium development. Gynoecium with two carpels, surrounded by four stamens and a staminode. All flowers orientated with the staminode up. **28.** The two young carpels forming a shallow depression in the centre. **29.** The two carpels forming two shallow troughs. **30.** Inner surface of the two carpels connected by a median longitudinal slit. Gynoecium with elliptical contour. **31.** Gynoecium with more circular contour by further broadening. Elongation of the upper parts. Flanks still visible but have become more hidden. **32.** Tips of the two carpels have approached each other. **33.** Carpels appear now closer together and flanks are no longer visible from the outside. **34.** Tips of the two carpels almost contiguous. Entrance into the gynoecium diminished to a narrow transverse slit. **35.** Gynoecium completely closed along the transverse slit, which serves both carpels. Scale bars: 20 μm (Figs 26, 27); 100 μm (Figs 28–34); 300 μm (Fig. 35).

Doust, 2001; Doust & Drinnan, 2004), Aristolochiaceae (Leins & Erbar, 1985, 1995; Leins, Erbar & van Heel, 1988; González & Stevenson, 2000), Piperaceae (Tucker, 1976, 1981, 1982, 1985; Liang & Tucker, 1989)]. In *Laurus nobilis* (Endress, 1972a,b, 1994a; this study, Figs 12–14) and other Laurales, the basal part of the closure of the carpel is by a short transverse secondary margin of the carpel wall, which may simulate the single ovule. However, the ovule is more inside the carpel and not visible from the outer carpel surface. *Nectandra angustifolia* (Schrad.) Nees &

Mart. (Lauraceae) is a reported borderline case, in which the placenta of the single pendant ovule is visible before closure (van Heel, 1981, fig. 59).

The phylogenetic topology of early branching monocots is still not well resolved, especially the mutual position of Acorales, core Alismatales, Araceae and Tofieldiaceae (Iles, Smith & Graham, 2013; Les & Tippery, 2013). Alismatales (in the classical circumscription, i.e. excluding Araceae and Tofieldiaceae) form two major clades, I ('Alismatales') and II ('Potamogetonales'). Alismataceae, Butomaceae and Hydro-

charitaceae constitute clade I and all other families clade II (Les & Tippery, 2013; similarly in Iles *et al.*, 2013).

In Acorales, the ovules are covered from the beginning (Buzgo & Endress, 2000). Among Alismatales, there is some diversity. In some families only late closure was found, and in others both early and late closure seem to occur. It appears that late closure is especially prominent in more advanced families with reduced flowers and mostly a single ovule per carpel, i.e. the clade called Potamogetonales in Les & Tippery (2013), whereas ovules are covered from the beginning in early diverging Alismatales, such as Tofieldiaceae and Araceae, and in Butomaceae and part of Alismataceae and Hydrocharitaceae (phylogenetic topology according to Iles *et al.*, 2013). As in other groups (some Lauraceae, core Ranunculales), there are here also problematic cases with a single median ovule per carpel. It is then often unclear whether a visible bulge represents the young ovule or a secondary bulge that serves to close the carpel at the base.

Notably the following Alismatales have been shown to have early carpel closure. Alismataceae: *Alisma plantago-aquatica* L. (van Heel, 1983, figs 156–158), *Alisma triviale* Pursh (Singh & Sattler, 1972), *Damasonium alisma* Mill. (Charlton, 2004); Limnocharitaceae: *Hydrocleys* Rich. (Sattler & Singh, 1973); Butomaceae: *Butomus umbellatus* L. (Sattler, 1973; Singh & Sattler, 1974; Charlton, 2004); Hydrocharitaceae: *Hydrocharis morsus-ranae* L. (Scribailo & Posluszny, 1985); *Vallisneria rubra* (Rendle) Les & S.W.L.Jacobs (as *Maidenia rubra* Rendle) (McConchie, 1983); Aponogetonaceae: *Aponogeton* L.f. (Singh & Sattler, 1977); Ruppiaceae: *Ruppia occidentalis* (Pentagna) Grande and *R. maritima* L. (Kaul, 1993; Lacroix & Kemp, 1997); Tofieldiaceae: *Tofieldia* Huds. (Remizowa, Sokoloff & Rudall, 2006). In early diverging Araceae the carpels (or pseudomonomerous gynoecea) appear to close early in development so that the young ovules are not visible from the surface, such as in *Orontium* L. (Buzgo, 2001). Also in other Araceae the ovules are covered from the beginning, as in *Anaphyllopsis* (Engl.) A.Hay (Barabé & Lacroix, 2008a), *Philodendron* Schott (Barabé, Lacroix & Jeune, 2002; Barabé & Lacroix, 2008b), *Schismatoglottis* Zoll. & Moritzi in H.Zollinger (Barabé *et al.*, 2004) and others.

In more advanced monocots, ovules are in general covered from the beginning (except for members of Poales and scattered taxa in other orders, as far as known to date), e.g. Dioscoreaceae: *Dioscorea* L. (Remizowa, Sokoloff & Kondo, 2010a); Nartheciaceae: *Metanarthecium* Maxim. (Remizowa & Sokoloff, 2008); Hypoxidaceae: *Curculigo* Gaertn. (Kocyan & Endress, 2001b); Doryanthaceae: *Doryanthes* Corrêa (Kocyan & Endress, 2001b); Boryaceae: *Alania* Endl.

(Kocyan & Endress, 2001b); and early diverging Orchidaceae (Kocyan & Endress, 2001a).

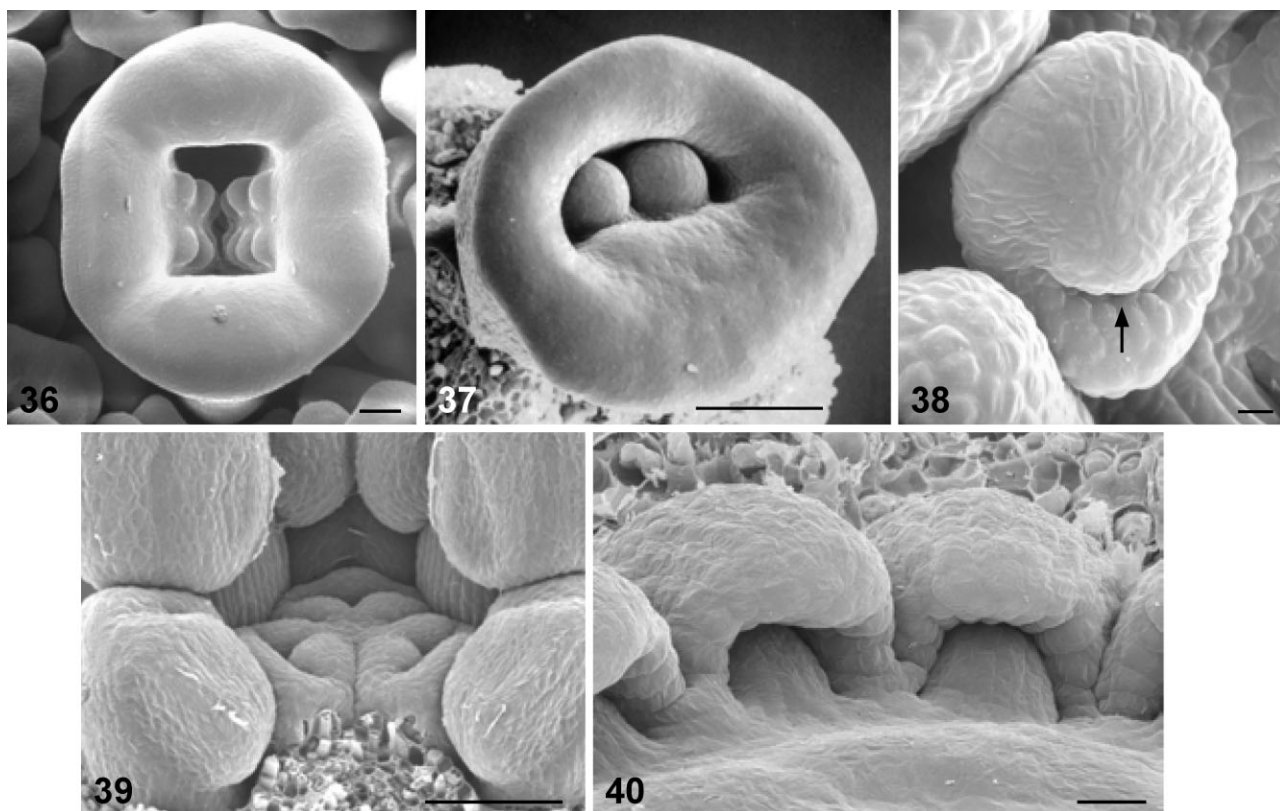
In early diverging eudicots, the behaviour is not uniform. Most clades also have the young ovules hidden in the already closed carpels. In Ranunculales, this is the case in Eupteleaceae (Endress, 1969; Ren *et al.*, 2007), most Papaveraceae (Karrer, 1991; Brückner, 1992) and, among core Ranunculales, in Lardizabalaceae (van Heel, 1983, 1984; Zhang *et al.*, 2009; Zhang & Ren, 2011), Menispermaceae (Wang *et al.*, 2006; Meng *et al.*, 2012) and Circaeasteraceae (Tian, Zhang & Ren, 2006). Most Ranunculaceae have early closure (van Heel, 1983; Erbar, 1999; Zhao *et al.*, 2011, 2012a).

In the grade of early diverging eudicots above Ranunculales, the ovules are also covered from the beginning of development, as in Sabiaceae (Wanntorp & Ronse De Craene, 2007), Proteaceae (Douglas, 1996; Douglas & Tucker, 1996a,b), Nelumbonaceae (Hayes, Schneider & Carlquist, 2000), Trochodendraceae (Chen *et al.*, 2007), Buxaceae (von Balthazar & Endress, 2002a) and Gunneraceae (Rutishauser, Wanntorp & Pfeifer, 2004). The pattern of carpel closure is unknown in Platanaceae and Myrothamnaceae.

Extreme cases of early closure (or delayed ovule development) among eudicots occur in Fagales, in which the ovules appear only late, long after carpel closure (in the extreme several months) (Betulaceae) (Endress, 1967, 1977). Considerably late ovule development also occurs in Buxaceae (von Balthazar & Endress, 2002b) and Hamamelidaceae (Endress, 1977). Such late ovule development or maturation is often associated with chalazogamy, as found in several Fagales (Sogo & Tobe, 2006b) and *Eucommia* Oliv. (Garryales) (Sogo & Tobe, 2006a).

DELAYED CARPEL CLOSURE (WITH YOUNG OVULES VISIBLE FROM THE OUTSIDE BEFORE CARPEL CLOSURE) (FIGS 36–40)

In contrast to the early closure of carpels as described in the preceding section, there are carpels that become closed only relatively late in such a way that young ovules are visible from the outside before carpel closure. This feature could be described as either delayed carpel closure or precocious ovule development. I was especially interested to see whether (1) this is correlated with other gynoeceum features, (2) this occurs predominantly in certain larger clades of angiosperms but not in others and (3) there are certain evolutionary patterns. The feature of delayed carpel closure is also of interest because it has led to confusions about the nature of carpels and ovules when some authors misinterpreted certain angiosperms as 'stachyosporous' and the gynoecea of



Figures 36–40. Delayed carpel closure, with ovules visible from the outside. **36.** *Hunnemannia fumariifolia* (Papaveraceae). Two syncarpous carpels. Several ovules visible. **37.** *Berberis vulgaris* (Berberidaceae). Single carpel with two ovules. **38.** *Achlys triphylla* (Berberidaceae). Single carpel with single ovule (arrow). **39.** *Asphodeline lutea* (Xanthorrhoeaceae). Three carpels, each with two ovules visible. **40.** *Gyrostemon racemigerus* (Gyrostemonaceae). Carpels each with a single ovule visible. Scale bars: 20 μm (Figs 38, 40); 100 μm (Figs 36, 39).

certain angiosperms as ‘acarpellate’ (e.g. Sattler, 1974). I will not deal with this interpretative aspect here but this is planned for a separate paper.

As discussed in the preceding section, a difficulty for interpretation is sometimes present in carpels with a single median ovule. There, the young ovule appears to be visible through the base of the ventral slit in young stages. However, the seeming ovule is a part of the secondary carpel margin, which covers the ovule primordium. Thus, the ovule is not visible from the outside. In some cases, it may be difficult to recognize from the outside whether the visible part is the ovule or part of the carpel margin.

Tucker & Kantz (2001) listed several angiosperms, in which ovules were visible in carpels from the outside. However, they also included there some teratological cases (*Drimys* J.R.Forst. & G.Forst., *Zygogynum* Baill.) in which normally developing carpels are closed before ovules become visible. In the present paper only normal development is considered. Tucker & Kantz (2001) also included cases illustrated with drawings in Payer (1857). These are not considered

here either because erroneous interpretations may be possible from these old drawings, although they are in general of excellent quality. *Umbellularia* (Nees) Nutt. (Lauraceae), also mentioned in Tucker & Kantz (2001) based on the description by Kasapligil (1951), does not really fit here; Kasapligil’s plate 28, fig. B, is not conclusive; the carpels appear to develop with the same pattern as in other Lauraceae (Endress, 1972b). The slightly open young carpels of Fabaceae shown in Tucker & Kantz (2001) may not represent the natural condition. Because these carpels are relatively long and slender, they may have been slightly distorted by the drying process if the flanks were not yet fused and thus did not provide stability. Other species are borderline cases, where it is not clear whether the visible part is the ovule or a secondary rim (e.g. *Trichostigma* A.Rich., *Rivina* L., Phytolaccaceae) or a placenta (*Koelreuteria* Laxm., Sapindaceae).

In extreme cases the development of the gynoecium wall is so much delayed and reduced that it remains minute and vasculature does not develop. This is known from *Dysphania glomulifera* (Nees) Paul

G. Wilson (as *D. myriocephala* Benth.) (Amaranthaceae), in which the gynoecium wall has only two cell layers (apart from some islands with three cells) and there are no vascular bundles in the gynoecial wall (Eckardt, 1967a). Also, *Dysphania plantaginella* F. Muell. has no vascular bundles in the gynoecium wall (Eckardt, 1967b,c). *Lophiocarpus* Turcz. (Lophiocarpaceae) also has an initially thin and short carpel wall (Hakki, 2013).

The most pronounced cases with delayed carpel wall development (or precocious ovule development) are (1) in gynoecia (or carpels) with a single ovule and (2) in families in which the flower bud is tightly covered by additional envelopes: in Poaceae and Cyperaceae there are sturdy glumes and in Amaranthaceae there are tight covering bracts. Hofmann (1994: 157) stated for Caryophyllales that 'It seems that the ovules in uniovulate ovaries appear earlier than the first ones in a multiovulate ovary'. The tendency seems also to be present in Alismatales. This is not surprising because in a multiovulate ovary at first a placenta of some size needs to develop before the individual ovules can be formed (see also the discussion in the section 'Free central placenta').

There is a strong correlation between delayed carpel closure and ovary position. All cases of delayed closure mentioned have superior ovaries. Problematic cases in this respect are *Adoxa moschatellina* L. and *Sambucus ebulus* L., for which Roels (1994, figs 9, 28) mentions visible ovules in still unclosed gynoecia. However, these bulges may be the placentae of the pendant ovules, and not the ovules themselves. That the figures in Erbar (1994, figs 12–14, 24) do not show ovule exposure in *A. moschatellina* supports this assumption.

The following list contains taxa with delayed carpel closure, in which ovules are visible from the outside before carpel closure.

ANITA grade

None.

Magnoliids

None (except for a few borderline cases in Lauraceae; see above).

Monocots

Alismatales-Alismataceae, *Baldellia ranunculoides* (L.) Parl. (Charlton, 2004, fig. 42); *Caldesia grandis* Sam. (one median ovule) (Liu, Lei & Hu, 2002, figs 28, 29, 31); *Caldesia parnassifolia* (L.) Parl. (Wang & Chen, 1997, fig. 15); *Luronium natans* (L.) Raf. (probably visible if it is not a secondary rim) (Charlton, 1999, fig. 28); *Ranalisma humile* (Rich. ex Kunth) Hutch. (one median ovule, exposed in the beginning) (Charlton, 1991, fig. 26); *Sagittaria trifolia* L. (Huang

et al., 2014, fig. 1C–E). **Hydrocharitaceae**, *Najas flexilis* (Willd.) Rostk. & W.L.E. Schmidt (Posluszny & Sattler, 1976a, fig. 32). **Juncaginaceae**, *Triglochin barrelieri* Loisel. (Remizowa, Sokoloff & Rudall, 2010b, fig. 6D); *Triglochin bulbosa* L. (Remizowa *et al.*, 2010b, fig. 6C); *Triglochin maritima* L. (Singh, 1973, fig. 5); *Triglochin scilloides* (Poir.) Mering & Kadereit (Posluszny, Charlton & Jain, 1986, figs 20, 22, 23); *Triglochin striata* Ruiz & Pav., Lieu, 1979, fig. 12A). **Posidoniaceae**, *Posidonia oceanica* (L.) Delile (Remizowa *et al.*, 2012, fig. 10C, D). **Potamogetonaceae**, *Lepilaena bilocularis* Kirk (one median ovule, probably visible, if it is not a secondary rim) (Posluszny & Tomlinson, 1977, fig. 6C); *Lepilaena cylindrocarpa* (Körn. ex Müll. Stuttg.) Benth. (Posluszny & Tomlinson, 1977, fig. 7F); *Potamogeton densus* L. (Posluszny & Sattler, 1973, figs 33–36); *Potamogeton illinoensis* Morong (one median ovule, probably visible, if it is not a secondary rim) (Nunes, de Lima & Moço, 2012, fig. 11); *Potamogeton lucens* L. (Charlton & Posluszny, 1991, fig. 18); *Potamogeton richardsonii* (A. Benn.) Rydb. (Posluszny & Sattler, 1974a, fig. 15); *Potamogeton zosteriformis* Fernald (one median ovule, probably visible, if it is not a secondary rim) (Posluszny, 1981, figs 25, 26); *Vleisia aschersoniana* (Graebn.) Toml. & Posl. (one median ovule, probably visible, if it is not a secondary rim) (Posluszny & Tomlinson, 1977, fig. 2E); *Zannichellia palustris* L. (Posluszny & Sattler, 1976b, figs 15, 31, 32). **Ruppiaceae**, *Ruppia maritima* L. (one median ovule, probably visible, if it is not a secondary rim) (Posluszny & Sattler, 1974b, fig. 16; Lock, Sokoloff & Remizowa, 2011, fig. 4D). **Scheuchzeriaceae**, *Scheuchzeria palustris* L. (two lateral ovules per carpel) (Posluszny, 1983, figs 20, 21). **Zosteraceae**, *Heterozostera tasmanica* (M. Martens ex Asch.) Hartog (Soros-Pottruff & Posluszny, 1995, fig. 9D); *Phyllospadix scouleri* (Soros-Pottruff & Posluszny, 1994, fig. 4A); *Phyllospadix torreyi* Hook. (Soros-Pottruff & Posluszny, 1994, fig. 6D); *Zostera japonica* Asch. & Graebn. (Soros-Pottruff & Posluszny, 1995, fig. 5D, E); *Zostera muelleri* Irmisch ex Asch. (Soros-Pottruff & Posluszny, 1995, fig. 3D).

Asparagales-Asparagaceae, *Lomandra longifolia* Labill. (Ahmad, Martin & Vella, 2008, figs 45, 47).

Asphodelaceae (Xanthorrhoeaceae), *Asphodeline lutea* (L.) Rchb. (has only two collateral ovules per carpel!) (this study: Fig. 39).

Arecales-Arecaceae, *Salacca edulis* Reinw. (perhaps, if the protrusions are not placentae) (van Heel, 1988, fig. 61).

Poales-Cyperaceae, *Ascolepis brasiliensis* (Kunth) Benth. ex C.B. Clarke (Reutemann *et al.*, 2014, fig. 4D–F); *Carex appressa* R.Br. (Barnard, 1957b, figs 19, 21); *Carex canescens* L. (Schultze-Motel, 1959, figs 11, 12); *Carex pendula* Huds. (Vrijdaghs *et al.*, 2010, fig. 16

left); *Carex plantaginea* Lam. (Schultze-Motel, 1959, fig. 7); *Cyperus capitatus* Vand. (Vrijdaghs *et al.*, 2011, fig. 3D); *Cyperus congestus* Vahl (Schultze-Motel, 1959, fig. 22); *Cyperus eragrostis* Lam. (Barnard, 1957b, fig. 10; Schultze-Motel, 1959, fig. 20); *Cyperus esculentus* L. (Sattler, 1973, fig. 49: 6–9); *Cyperus luzulae* (L.) Retz. (Vrijdaghs *et al.*, 2011, fig. 2C); *Cyperus microbulbosus* (Lye) Lye (as *Kyllingia microbulbosa* Lye) (Reynders *et al.*, 2012, fig. 8C); *Dulichium arundinaceum* (L.) Britton (Vrijdaghs *et al.*, 2005b, fig. 5F–H; Reynders *et al.*, 2012, fig. 7B, C); *Eleocharis palustris* (L.) Roem. & Schult. (Vrijdaghs *et al.*, 2009, figs 1H–K, 2A, B); *Eriophorum latifolium* Hoppe (Vrijdaghs *et al.*, 2005b, fig. 3E–H; Reynders *et al.*, 2012, fig. 14A); *Ficinia gracilis* Schrad. (Vrijdaghs *et al.*, 2005a, fig. 7I); *Ficinia minutiflora* C.B. Clarke (Vrijdaghs *et al.*, 2005a, fig. 1F–I); *Ficinia zeyheri* Boeckeler (Vrijdaghs *et al.*, 2005a, fig. 5C, E); *Fimbristylis diphylla* (Retz) Vahl (Murty & Kumar, 1972, fig. 8); *Hellmuthia membranacea* (Thunb.) R.W. Haines & Lye (Vrijdaghs *et al.*, 2006, figs 1H, I, 2A); *Isolepis antarctica* (L.) Roem. & Schult. (Vrijdaghs *et al.*, 2005a, fig. 11G, H); *Isolepis setacea* (L.) R.Br. (Vrijdaghs *et al.*, 2005a, fig. 9H, I); *Lipocarpa humboldtiana* Nees (Reutemann *et al.*, 2014, fig. 3E, F); *Pycreus bipartitus* (Torr.) C.B. Clarke (Vrijdaghs *et al.*, 2011, fig. 8D; Reynders *et al.*, 2012, fig. 8A); *Pycreus flavescens* (L.) P.Beauv. ex Rchb. (Vrijdaghs *et al.*, 2011, fig. 10D, E); *Pycreus pelophilus* (Ridl.) C.B. Clarke (Vrijdaghs *et al.*, 2011, fig. 6A); *Pycreus pumilus* (L.) Nees (Vrijdaghs *et al.*, 2011, fig. 5E); *Pycreus sanguinolentus* (Vahl) Nees (Vrijdaghs *et al.*, 2011, fig. 9F); *Rhynchospora brittonii* Gale (Lucero, Vegetti & Reinheimer, 2014, figs 4D, 6E); *Rhynchospora corymbosa* (L.) Britton (Lucero *et al.*, 2014, fig. 3E, F); *Rhynchospora terminalis* (Nees) Steud. (Lucero *et al.*, 2014, fig. 2B); *Schoenus nigricans* L. (Vrijdaghs *et al.*, 2007, fig. 1H); *Scirpoides holoschoenus* (L.) Soják (Vrijdaghs *et al.*, 2005b, fig. 7D); *Scirpus sylvaticus* L. (Schultze-Motel, 1959, figs 17, 18; Vrijdaghs *et al.*, 2005b, fig. 1B, I, J; Reynders *et al.*, 2012, figs 5B, 6D); *Scirpus validus* Vahl (Barnard, 1957b, fig. 5; Sattler, 1973, fig. 48: 7, 9); *Uncinia rubra* Colenso ex Boott (Vrijdaghs *et al.*, 2010, fig. 16 right; Vrijdaghs *et al.*, 2011, fig. 6E). **Eriocaulaceae**, *Blastocaulon scirpeum* (Mart. ex Körn.) Giul. (Coan, Stützel & Scatena, 2010, fig. 3B). **Juncaceae**, *Luzula campestris* (L.) DC. (Barnard, 1958, figs 8, 9, plate 1: 1, 6). **Poaceae**, *Bromus unioloides* Kunth (Barnard, 1957a, fig. 20); *Hordeum distichon* L. (Klaus, 1966, figs 38, 39); *Hordeum vulgare* L. (Pankow, 1962, figs 186, 187; Sattler, 1973, fig. 45: 13–16); *Moorochloa eruciformis* (Sm.) Veldkamp (Reinheimer *et al.*, 2010, fig. 2G); *Panicum maximum* Jacq. (Reinheimer, Pozner & Vegetti, 2005, fig. 21); *Urochloa mollis* (Sw.) Morrone & Zuloaga (Reinheimer *et al.*, 2010, figs 4H, I, 5B); *Zea diploperennis* Iltis,

Doebley & R.Guzmán (Sundberg & Orr, 1986, fig. 22; Sundberg, 1987, fig. 10); *Zea mays* L. (Cheng, Greyson & Walden, 1983, figs 19–22); *Zea mays* L. subsp. *mexicana* (Schrad.) Iltis (Orr *et al.*, 2002, figs 10, 25, 26); *Zea nicaraguensis* Iltis & B.F. Benz (Orr & Sundberg, 2004, figs 7, 20, 21).

Early branching eudicots

Ranunculales-Papaveraceae, *Hunnemannia fumariifolia* Sweet (Karrer, 1991, fig. 92; Endress, 1995, fig. 4H) (this study: Fig. 36); *Papaver californicum* A.Gray (Kadereit & Erbar, 2011, fig. 3D, E); *Papaver cambricum* L. [as *Meconopsis cambrica* (L.) Vig.] (Kadereit & Erbar, 2011, fig. 4H); *Papaver rhoeas* L. (Kadereit & Erbar, 2011, fig. 2F); *Romneya coulteri* Harv. (Karrer, 1991, fig. 206). **Berberidaceae**, *Achlys triphylla* DC. (Endress, 1989, fig. 10, 11) (this study: Fig. 38); *Berberis vulgaris* L. (Schnyder, 1982; Endress, 1995, fig. 4G) (this study: Fig. 37); *Caulophyllum thalictroides* (L.) Michx. (Brett & Posluszny, 1982, fig. 19). **Ranunculaceae**, *Adonis sutchuenensis* Franch. (Ren *et al.*, 2009, fig. 15); *Callianthemum taipaicum* W.T. Wang (Ren *et al.*, 2009, fig. 39); *Ceratocephala testiculata* (Crantz) Besser (as *Ceratocephala orthoceras* DC.) (Zhao *et al.*, 2012b, fig. 6N); *Halerpestes cymbalaria* (Pursh) Greene (Zhao *et al.*, 2012b, fig. 7O); *Oxygraphis glacialis* Regel (Zhao *et al.*, 2012b, fig. 8O); *Ranunculus sceleratus* L. (Zhao *et al.*, 2012b, fig. 4O, P); *Thalictrum fargesii* Franch. ex Finet & Gagnep. (not sure whether the visible part is a secondary rim or the ovule) (Ren, Gu & Chang, 2011, fig. 2F).

Core eudicots

Superrosids

Vitales-Vitaceae, *Parthenocissus inserta* (A.Kern.) Fritsch (Gerrath & Posluszny, 1989, fig. 27).

Fabales-Fabaceae, perhaps several genera, (Tucker & Kantz, 2001, several figures), but see discussion above.

Rosales-Cannabaceae, *Cannabis sativa* L. (Pankow, 1962, fig. 41). **Urticaceae**, *Laportea canadensis* (L.) Wedd. (Sattler, 1973, fig. 6: 6); *Urtica urens* L. (Pankow, 1962, figs 50–52).

Malpighiales-Euphorbiaceae, *Euphorbia cyparissias* L. (Hoppe & Uhlarz, 1981, figs 8E, 9C, 10B); *Euphorbia myrsinites* L. (Prenner & Rudall, 2007, fig. 2E–G); *Euphorbia splendens* Bojer ex Hook. (Sattler, 1973, fig. 21: 20, 21); *Euphorbia umbellata* (Pax) Bruyns (as *Synadenium grantii* Hook.f.) (Hoppe, 1985, fig. 45D). **Linaceae**, *Linum usitatissimum* L. (Schewe, Sawhney & Davis, 2011, fig. 14). **Ochnaceae**, *Ochna atropurpurea* DC. (Pauzé & Sattler, 1979, figs 5, 6). **Phyllanthaceae**, *Phyllanthus chekiangensis* Croizat & Metcalf (Zhang *et al.*,

2012, fig. 1H). **Salicaceae**, *Oncoba spinosa* Forssk. (van Heel, 1977, Photo 2); **Scyphostegiaceae**, *Scyphostegia borneensis* Stapf (van Heel, 1967, fig. 2B).

Brassicales-Gyrostemonaceae, *Gyrostemon racemigerus* H.Walter (this study, Fig. 40). **Resedaceae**, *Caylusea abyssinica* (Fresen.) Fisch. & C.A.Mey. (Sobick, 1983, figs 72, 73); *Sesamoides interrupta* (Boreau) G.López (as *Sesamoides canescens* (L.) Kuntze (Sobick, 1983, figs 92, 93).

Sapindales-Sapindaceae, *Acer saccharum* Marshall (Peck & Lersten, 1991, fig. 3). **Anacardiaceae**, *Pistacia vera* L. (Takeda, Crane & Lin, 1979, fig. 2B).

Superasterids

Caryophyllales-Amaranthaceae, *Alternanthera lanceolata* (Benth.) Schinz (as *Alternanthera microcephala* (Moq.) Schinz) (Vrijdaghs, Flores-Olvera & Smets, 2014, fig. 6D, E); *Amaranthus paniculatus* L. (Pankow, 1962, figs 83, 84, 86); *Beta trigyna* Waldst. & Kit. (Pankow, 1962, fig. 76); *Beta vulgaris* L. (Olvera, Smets & Vrijdaghs, 2008, fig. 2I); *Chenopodium album* L. (Pankow, 1962, figs 71, 72); *Chenopodium capitatum* (L.) Asch. (Hakki, 1972, figs 113, 167); *Dysphania glomulifera* (Nees) Paul G.Wilson (as *Dysphania myriocephala* Benth.) (Eckardt, 1967a, fig. 27); *Iresine calea* (Ibantz) Standl. (as *Iresine latifolia* (M.Martens & Galeotti) Benth. & Hook.f.) (Vrijdaghs *et al.*, 2014, figs 3F–H, 8D); *Pleuropetalum darwinii* Hook.f. (Ronse Decraene, Volgin & Smets, 1999, figs 19–22); *Salicornia europaea* L. (Beer, Beer & Sokoloff, 2010, fig. 9C); *Salicornia heterantha* S.S.Beer & Demina (Beer *et al.*, 2010, fig. 12F, G); *Salicornia perennans* Willd. (Beer *et al.*, 2010, fig. 8D); *Salicornia pojarkovae* N.Semenova (Beer *et al.*, 2010, figs 2A, 10D); *Tidestromia rhizomatosa* I.M.Johnst. (Vrijdaghs *et al.*, 2014, fig. 6M, N). **Caryophyllaceae**, *Cerastium arvense* L. (Roth, 1963, fig. 14B); *C. biebersteinii* DC. (Roth, 1963, fig. 16A, B); *Cerastium fontanum* Baumg. subsp. *vulgare* (Hartm.) Greuter & Burdet (as *Cerastium vulgatum* L.) (Hofmann, 1994, fig. 31); *Lepyrodiclis holosteoides* (C.A.Mey.) Fenzl ex Fisch. & C.A.Mey. (Hofmann, 1994, fig. 32); *Pseudostellaria heterophylla* (Miq.) Pax (Luo, Bian & Luo, 2012, fig. 4E, I, L); *Scleranthus annuus* L. (Pankow, 1962, fig. 133); *Silene coronaria* (Desr.) Clairv. ex Rchb. (as *Lychnis coronaria* Desr.) (Hofmann, 1994, fig. 38); *Silene vulgaris* (Moench) Garcke (Sattler, 1973, fig. 9: 11); *Stellaria aquatica* (L.) Scop. [as *Malachium aquaticum* (L.) Fr.] (Pankow, 1962, fig. 115); *Stellaria media* (L.) Vill. (Hofmann, 1994, fig. 29). **Basellaceae**, *Basella alba* L. (Pankow, 1962, fig. 110); *Basella rubra* L. (Sattler & Lacroix, 1988, figs 3–5, 13–16). **Limeaceae**, *Limeum africanum* L. (Ronse De Craene, 2013, fig. 1D). **Lophiocarpaceae**, *Corbichonia decumbens* (Forssk.) Exell (Brockington *et al.*, 2013); *Lophiocar-*

pus polystachyus Turcz. (Eckardt, 1974, fig. 27; Hakki, 2013, fig. 21). **Nyctaginaceae**, *Boerhavia diffusa* L. (Sattler & Perlin, 1982, figs 41, 45); *Bougainvillea spectabilis* Willd. (Sattler & Perlin, 1982, figs 24–27); *Mirabilis jalapa* L. (Pankow, 1962, figs 96, 97; Sattler & Perlin, 1982, fig. 54); *Neea* Ruiz & Pav. sp. (Hofmann, 1994, fig. 8); *Oxybaphus nyctagineus* (Michx.) Sweet (Hofmann, 1994, fig. 11, 12). **Plumbaginaceae**, *Acantholimon glumaceum* (Jaub. & Spach) Boiss. (De Laet *et al.*, 1995, fig. 9); *Armeria latifolia* Moris (Pankow, 1962, figs 154, 155); *Armeria maritima* (Mill.) Willd. (De Laet *et al.*, 1995, figs 22, 23); *Ceratostigma plumbaginoides* Bunge (De Laet *et al.*, 1995, fig. 51, 52); *Goniolimon tataricum* (L.) Boiss. (De Laet *et al.*, 1995, fig. 36); *Limoniastrum monopetalum* (L.) Boiss. (De Laet *et al.*, 1995, fig. 65); *Limonium platyphyllum* Lincz. (as *Limonium latifolium* (Sm.) Kuntze) (De Laet *et al.*, 1995, fig. 43); *Plumbago auriculata* Lam. (De Laet *et al.*, 1995, figs 60, 61). **Polygonaceae**, *Fagopyrum esculentum* Moench (Pankow, 1962, figs 69, 70); *Fagopyrum sagittatum* Gilib. (Sattler, 1973, fig. 8: 14); *Oxyria digyna* (L.) Hill (Galle, 1977, fig. 83); *Polygonum cuspidatum* Siebold & Zucc. (Pankow, 1962, figs 64, 65); *Polygonum divaricatum* L. (Galle, 1977, fig. 122); *Pterostegia drymarioides* Fisch. & C.A.Mey. (Galle, 1977, fig. 45); *Rheum palmatum* L. (Wang, Chen & Ding, 1992, fig. 1A, B); *Rheum pruinatum* hort. (Galle, 1977, fig. 70). **Talinaceae**, *Talinum paniculatum* (Jacq.) Gaertn. (Pankow, 1962, fig. 105).

Solanales-Convolvulaceae, *Convolvulus sepium* L. (Sattler, 1973, fig. 140: 8).

GYNOECIA WITH FREE CENTRAL PLACENTA (FIG. 8)

As an appendix to the topic of delayed carpel closure, I include here a section on gynoecia with a free central placenta because there is some structural relationship to gynoecia with delayed carpel closure. A free central placenta is present if a syncarpous gynoecium has a single locule that is completely free of septation from the beginning of development and the placenta is on a central column. In cases with numerous ovules, the free central placenta tends to remain visible before the gynoecium becomes closed, but individual ovules mostly develop only after closure. *Pleuropetalum* Hook.f. (Amaranthaceae) is an exception with ovules visible through the still open gynoecium (Ronse De Craene *et al.*, 1999). In multiovulate gynoecia with free central placenta ovule initiation is centrifugal (away from the location of the earlier floral apex) (Okamoto, 1984). In addition, the curvature of the (anatropous) ovules appears to be away from the centre of the earlier floral apex, as in Lentibulariaceae (Fig. 8) and Primulaceae (e.g. Caris & Smets, 2004). This is also the case in some multiovulate axile pro-

truding placentae, such as in several Solanaceae (e.g. Huber, 1980, figs 280, 317; this study, Fig. 7). However, this pattern is less constant across angiosperms than for free central placentae.

A seemingly free central placenta may arise from an axile placenta by two different developmental processes: (1) by histological decay of the ovary septa during flower development as in Caryophyllaceae (e.g. Rohweder, 1967); or (2) by differential development of the upper (free) part, which overgrows the short lower septate zone, which is no longer obvious at anthesis, as in *Avicennia* L. (Acanthaceae; Borg & Schönenberger, 2011). Also in *Limosella* L. (Plantaginaceae), the placenta is similar to a free central placenta (Svensson, 1928), but septa are present at the very base of the ovary (Hartl, 1956). This is also the case in some African Podostemaceae (Cook & Rutishauser, 2007).

Comparison of gynoecia with a free central placenta in unrelated families shows a striking associated morphological phenomenon. In Lentibulariaceae (Degtjareva & Sokoloff, 2012) and Primulaceae (Duchartre, 1844; Caris *et al.*, 2000; Caris & Smets, 2004), both with free central placenta, the gynoecial rim is circular, like a diaphragm, and individual carpels are not recognizable (at least in early development). The same is the case in some Santalaceae (Ram, 1957). Carpel number in Anthoboleae (Santalaceae) is often not determined with certainty (Stauffer, 1959). In *Thesium* L., stigmatic lobes are only weakly recognizable (Schaepfi, 1942). In contrast, in *Osyris* L. (Santalaceae) with basal locule formation the number of carpels is clear by more pronounced stigmatic lobes (Schaepfi & Steindl, 1937). Also in *Avicennia* there are two distinct stigmatic lobes, corresponding to the carpel tips, and early stages of ovary development are distinctly septate (Borg & Schönenberger, 2011). In such gynoecia with a diaphragm-like opening and unclear carpel number in early development, only later, when the gynoecium closes, are irregular lobes formed on its rim (see Caris *et al.*, 2000; Caris & Smets, 2004; Degtjareva & Sokoloff, 2012). These lobes are an architectural necessity for closure, a developmental byproduct, and should not be misinterpreted as carpel tips. Such architectural necessity for closure of a circular aperture in plants was discussed for the closure of micropyles in ovules by Endress (2011a). The same is probably the case in the mentioned Santalaceae, such as *Thesium*, but they have not been studied by SEM. It would be interesting to know more about the developmental relationship between these two features, the diaphragm-like circular rim of the young gynoecium (without recognizable carpel tips) and the free central placenta.

The following list shows the reported occurrence of free central placentae across angiosperms.

Rosids

Malpighiales-Podostemaceae (most African genera have a free central placenta, but 'occasionally with a rudimentary septum at the very base' (Cook & Rutishauser, 2007: 312). *Dicraeanthus* Engl. (Thiv *et al.*, 2009); *Djinga* C.Cusset (Thiv *et al.*, 2009); *Inversodicraea* Engl. ex R.E.Fr. (Thiv *et al.*, 2009); *Ledermanniella* Engl. (Ameka *et al.*, 2003, fig. 34; Thiv *et al.*, 2009); *Leiothylax* Warm. (Thiv *et al.*, 2009); *Letestuella* G.Taylor (Thiv *et al.*, 2009); *Macropodiella* Engl. (Thiv *et al.*, 2009); *Monandriella* Engl. (Thiv *et al.*, 2009); *Stonesia* G.Taylor (Thiv *et al.*, 2009).

Superasterids

Santalales-Loranthaceae (together with tendency to loss of well-developed ovules; several genera, not analysed in detail; Maheshwari, Johri & Dixit, 1957; Johri & Bhatnagar, 1960). **Olacaceae s.l.** (not with a typical free central placenta because the few ovules reach downwards into separate pockets; several genera; Fagerlind, 1947, 1948). **Misodendraceae**, *Misodendron* G.Don (Skottsberg, 1913; fig. 6). **Santalaceae** (several genera, most of them not studied in detail). *Comandra* Nutt. (Ram, 1957, fig. 10).

Caryophyllales-Amaranthaceae, *Pleuropetalum darwinii* Hook.f. (Ronse Decraene *et al.*, 1999, fig. 20).

Ericales-Primulaceae, *Ardisiandra wettsteinii* J.Wagner (Wanntorp *et al.*, 2012, fig. 3C, D); *Clavija* aff. *elliptica* Mez (Sattler, 1962, fig. 10); *Coris monspeliensis* L. (Sattler, 1962, fig. 77; Ronse Decraene, Smets & Clinckemaiellie, 1995, figs 8–10, 12); *Cyclamen persicum* Mill. (Sundberg, 1982, fig. 15); *Dehnerainia smaragdina* (Planch. ex Linden) Decne. (Sattler, 1962, fig. 26); *Lysimachia vulgaris* L. (Pankow, 1959, fig. 2D); *Maesa perlaria* (Lour.) Merr. (Caris *et al.*, 2000, figs 3F, 5E; Ma & Saunders, 2003, fig. 4J); *Primula japonica* A.Gray (Pankow, 1959, fig. 1E); *Primula tommasinii* Nyman \times *P. vulgaris* Huds. (Webster & Gilmartin, 2003, fig. 2K); *Primula* sp., (Roth, 1959, figs 4B, 5); *Samolus valerandi* L. (Pankow, 1959, fig. 3B, C; Sattler, 1962, fig. 62; Caris & Smets, 2004, fig. 9H, I).

Lamiales-Acanthaceae, *Avicennia* (but with short basal septa, which are more pronounced in early development; Borg & Schönenberger, 2011, figs 2E–H, 4A). **Lentibulariaceae**, *Pinguicula* L. (Hartl, 1956, fig. 1; Degtjareva & Sokoloff, 2012, fig. 8I; this study; Fig. 8); *Utricularia* L. (Hartl, 1956, figs 2–6). **Plantaginaceae**, *Limosella aquatica* L. (but with short basal septa; Hartl, 1956).

MODES OF SEALING AND POSTGENITAL AND CONGENITAL FUSION

Sealing means the closure of gaps. It can be by secretion or by postgenital fusion. In the context of

this paper, sealing is related to angiospermy. The term 'fusion' is tricky. For gynoecia we need to distinguish not only between congenital and postgenital fusion but also between intracarpellary and intercarpellary fusion. These distinctions are often neglected in the literature and this leads to confusion and misunderstanding. Thus, to just say that carpels are fused does not mean anything.

Postgenital fusion (epidermal fusion) is fusion of parts via their epidermis. These parts are free in early development but then fuse by their contiguous epidermis. The two counterparts connect and fusion may become so tight that the fusion area becomes difficult to see. Postgenital fusion occurs either between parts of an individual organ (e.g. flanks of a carpel), between different organs of the same kind (e.g. the carpels within a gynoecium) or between organs of different kinds (e.g. carpels and stamens). Congenital fusion (meristem fusion) is fusion of two parts by fusion of their meristems. These parts are then fused from the beginning of their development; the epidermis is not involved in the fusion process. The term is mostly used for the fusion of two or more organs (e.g. the carpels in a syncarpous gynoecium). It has sometimes also been used for parts of a single organ (e.g. for ascidiate carpels, in which the two flanks are thought to be congenitally fused in the zone where there is no ventral slit). However, this latter use is questionable as it is often uncertain whether a specific shape is the result of such fusion in evolutionary terms. Also questionable is the term 'phylogenetic fusion' (as opposed to 'ontogenetic fusion'; e.g. Cusick, 1966). A more neutral way of phrasing in such cases would be that an area is continuous (if the corresponding area consists of two separate parts in a closely related taxon), and not to use the word 'fusion', unless it is clear that in the ancestors there were separate parts, which is mostly unknown. The term 'zonal growth' is sometimes also used for congenital fusion, but taken literally zonal growth is only a consequence of meristem fusion.

Another problem is how to define postgenital fusion from merely loose postgenital connection (e.g. see Endress & Igersheim, 2000a). This remains unresolved as long as it is poorly known what happens at the biochemical, cytological and histological level of the process of fusion. What can be seen in this process is that (1) the outer walls of the epidermal cells of the separate organs make contact and (2) organ adhesion follows (Baum, 1948b; Boeke, 1971, 1973a,b; Siegel & Verbeke, 1989; Verbeke, 1992; Van der Schoot *et al.*, 1995; Lolle & Pruitt, 1999). The most detailed description of the process of postgenital fusion as yet is probably by Walker (1975a,b) on intercarpellary fusion in *Catharanthus roseus* (L.) G. Don (Apocynaceae). However, this is only one example, and does

not encompass the potential diversity. Unusual in *C. roseus* is that the process starts relatively early in development, and the fusion at maturity is tight and the location blurred.

INTRA- AND INTERCARPELLARY POSTGENITAL FUSION

In most cases of more or less apocarpous gynoecia, angiospermy develops by intracarpellary postgenital fusion. It is rather uncommon that the flanks of individual carpels remain open and fuse with those of neighbouring carpels. In this case angiospermy develops by intercarpellary fusion. This is known from two families of Gentianales, for example in *Allamanda schottii* Pohl (Apocynaceae; Fallen, 1985), *Gentiana dinarica* Beck (Gentianaceae; Leinfellner, 1950, 1951a) and *Sebaea macrophylla* Gilg (Gentianaceae; Kissling, Endress & Bernasconi, 2009) and from some Tofieldiaceae of Alismatales (Remizowa *et al.*, 2006).

More often, intercarpellary fusion occurs in combination with intracarpellary fusion. In this case, at first the individual carpels commonly become closed, and only when the carpels have reached angiospermy is there intercarpellary fusion, in addition. This has been known for a long time in cases where intercarpellary fusion is only in the apical region, such as in several Sapindales, Malvales and Gentianales (Baum, 1948a; Walker, 1975a, 1978; Endress, Jenny & Fallen, 1983; Jenny, 1988; Endress, Lorence & Endress, 1997; Bachelier & Endress, 2008, 2009; Staedler *et al.*, 2009; El Ottra, Pirani & Endress, 2013). However, it seems to occur more commonly, especially also in more cryptic cases, in which the entire length of the apocarpous zone is involved in the intercarpellary fusion. More recently, it was also found in some Crossosomatales (Matthews & Endress, 2005) and some Malpighiales (Matthews & Endress, 2008; Matthews, Amaral & Endress, 2012), and, among monocots, in some Areaceae (Stauffer & Endress, 2003; Stauffer, Barfod & Endress, 2009) and in other Tofieldiaceae than mentioned in the previous paragraph (Igersheim, Buzgo & Endress, 2001).

POLLEN TUBE TRANSMITTING TRACT (PTTT) AND CARPEL MORPHOLOGY

In carpels with a median longitudinal slit (ventral slit), pollen tubes grow inside the ventral slit along a broader or more restricted pathway, the PTTT, as seen in transverse sections. This localized PTTT allows pollen tube competition. If restricted, it is usually in the inner angle of the ventral slit. The pollen tubes grow through the cell walls of the tissue on both sides of the postgenitally connected ventral slit. In some cases, the inner angle of the ventral slit forms a hollow canal in the centre of the carpel. This

canal, which is filled or lined with secretion, may then be the PTTT, either alone or in combination with the adjacent tissue. The location of the PTTT is commonly at or close to the inner morphological surface of the carpel margin or flank. Thus, there is a diversity of possibilities for the exact location of the PTTT in detail.

In completely ascidiate carpels with a short style, the possibilities for diversity in detail of the PTTT differentiation are more restricted because a ventral slit is lacking. Here the PTTT is a hollow canal filled with secretion. This is present in *Austrobaileya* C.T.White (Endress, 1980c). Whether there are completely ascidiate carpels in which the PTTT encompasses more than the inner stylar epidermis is not known to me.

In carpels with only a transverse slit, the pathway for the pollen tubes is commonly only short. Pollen germinate either directly on or close to the slit if the slit is on top of the carpel or, if there is a short apical extension of the carpel, pollen tubes grow either at the surface of the carpel (e.g. *Berberis* L., Endress & Igersheim, 1999; in Hydatellaceae inside cell walls of long hairs, Prychid *et al.*, 2011) or inside a unifacial style. In the latter case, the PTTT is differentiated in compact tissue inside the unifacial part and thus is not connected with the morphological surface of the carpels except for the stigma (e.g. Betulaceae, Endress, 1967; Zhu *et al.*, 2014; *Passiflora* L., Bernhard, 1999). Thus, in these cases diversity of PTTT differentiation is also more restricted than in carpels with a longitudinal slit.

In syncarpous gynoecia, the PTTT of each carpel either remains separate for some distance below the level of intercarpellary fusion or they become united and form a centralized PTTT (a compitum), in which centralized pollen tube competition takes place (Endress, 1982, 2011b; Armbruster, Debevec & Willson, 2002; Wang, Armbruster & Huang, 2012). A compitum may also be formed in gynoecia with free carpels but intercarpellary postgenital fusion. The compitum is then located along this postgenital fusion area.

CLOSURE OF CARPELS WITH A TRANSVERSE SLIT

This topic is treated below in the section on 'Angiospermy patterns concentrated in the early diverging grade of extant angiosperms' because it occurs almost exclusively in early diverging angiosperms.

CLOSURE OF CARPELS WITH A UNIFACIAL STYLE (FIGS 41–46, 66)

In carpels with a unifacial style, the primary margin does not encompass the entire length of the carpel

above the ascidiate zone, but the upper part, which forms the style, is above the zone with the margins, and thus is unifacial and is round in transverse section. Accordingly, the area of closure is restricted. The feature of unifacial styles is not well studied across angiosperms. It is expected that there are many more cases than recorded in the literature. An interesting association is between wind pollination and carpels with unifacial styles as proportionally many such carpels occur in wind-pollinated plants.

The following list contains taxa with unifacial styles.

ANITA grade

Nymphaeales-Nymphaeaceae, *Victoria cruziana* A.D.Orb. (Endress, 2001, fig. 11C–F) (this study, Fig. 66).

Magnoliids

Laurales-Atherospermataceae, *Doryphora sassafras* Endl. (Endress, 1972b, plate 10: fig. 23).

Siparunaceae, *Siparuna thecaphora* (Poepp. & Endl.) A.D.C. (as *Siparuna nicaraguensis* Hemsl.) (Endress, 1972b, figs 21–24, plate 10: fig. 20).

Monocots

Poales-Poaceae, *Moorochloa eruciformis* (Sm.) Veldkamp (stigmatic branches develop late and they appear to be unifacial) (Reinheimer *et al.*, 2010, fig. 4E)

Eudicots

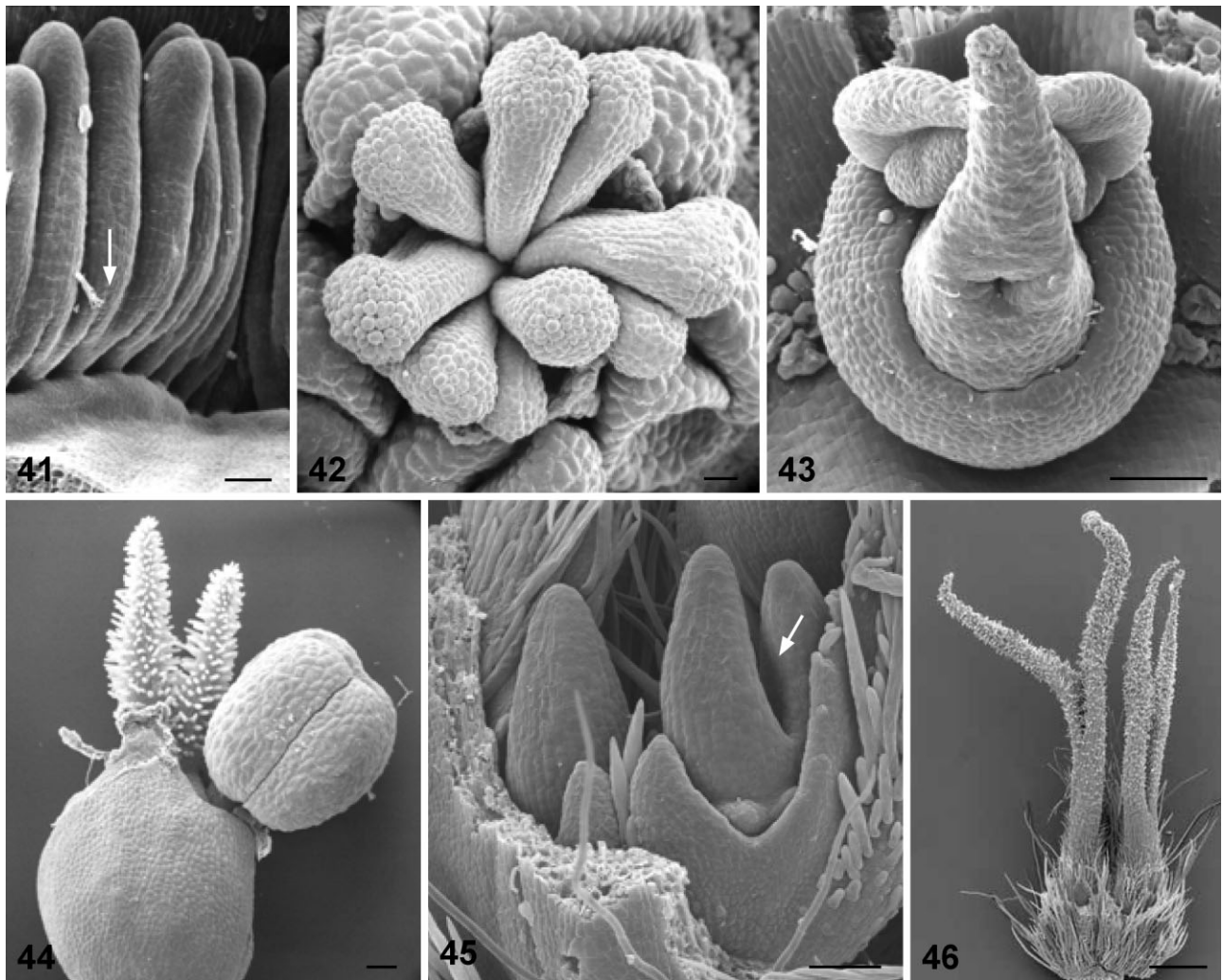
Gunnerales-Gunneraceae, *Gunnera tinctoria* (Molina) Mirb. (this study, Fig. 44).

Cucurbitales-Begoniaceae, *Begonia incana* Lindl. (Matthews & Endress, 2004, figs 56, 57); *Hillebrandia sandwicensis* Oliv. (Matthews & Endress, 2004, figs 53, 54). **Coriariaceae**, *Coriaria japonica* A.Gray (Baum-Leinfellner, 1953, fig. 1D–F); *Coriaria myrtifolia* L. (Matthews & Endress, 2004; fig. 10A–I); *Coriaria ruscifolia* L. (Guédès, 1971, fig. 31). **Corynocarpaceae**, *Corynocarpus laevigatus* J.R.Forst & G.Forst. (only stigma unifacial) (Matthews & Endress, 2004, fig. 49). **Tetramelaceae**, *Octomeles sumatrana* Miq. (Matthews & Endress, 2004, fig. 12A, 52).

Fagales-Betulaceae, *Carpinus betulus* L. (this study, Figs 45, 46); *Corylus yunnanensis* (Franch.) A.Camus (Zhu *et al.*, 2014, plate 5, figs 10, 11); *Ostrya carpinifolia* Scop. (Endress, 1967, fig. 108A, B).

Fabales-Fabaceae, *Trifolium repens* L. (Baum, 1948a, fig. 1D, E, K).

Rosales-Rosaceae, *Alchemilla arvensis* (L.) Scop. (Juel, 1918, figs 68, 69; van Heel, 1983, fig. 68); *Rhodotypos kerrioides* Siebold & Zucc. (Juel, 1918, figs 43, 44).



Figures 41–46. Carpels with unifacial style. **41.** *Kitaibelia vitifolia* (Malvaceae). Young flower. Numerous carpels, with short longitudinal slit at base of unifacial style. Upper end of longitudinal slit marked with arrow in one carpel. **42.** *Pavonia hastata* (Malvaceae). Young flower. Nine carpels visible. Styles completely unifacial. **43.** *Hippuris vulgaris* (Plantaginaceae). Young flower. One carpel, with small closure area. **44.** *Gunnera tinctoria* (Gunneraceae). Almost anthetic flower. Two carpels. Styles completely unifacial. **45–46.** *Carpinus betulus* (Betulaceae). **45.** Two young female flowers, each with two carpels (in the flower on the left only one carpel visible). Upper end of still open longitudinal slit marked with arrow in one carpel. **46.** Two anthetic female flowers, each with two carpels. Styles completely unifacial. Scale bars: 100 μm (Figs 41–43, 45); 500 μm (Figs 44, 46).

Malpighiales-Caryocaraceae, *Caryocar brasiliense* A.St.-Hil. (Matthews & Endress, 2011, fig. 30A–P).

Erythroxylaceae, *Erythroxylum coca* Lam. (Baum-Leinfellner, 1953, fig. 2K); *Erythroxylum cuneifolium* (Mart.) O.E.Schulz (Matthews & Endress, 2011, fig. 18A, C–G). **Hypericaceae,** *Hypericum* ‘Hidcote’ (Dupuy & Guédès, 1975, fig. 32). **Lacistemataceae,** *Lacistema aggregatum* (P.J.Bergius) Rusby (this study, no figure). **Linaceae,** *Linum tauricum* Willd. (as *Linum bulgaricum* Podp.) (Baum-Leinfellner, 1953,

fig. 2A–I); *Linum kingii* S.Watson (Matthews & Endress, 2011, fig. 24A–D). **Passifloraceae,** *Androsiphonia adenostegia* Stapf (Bernhard, 1999, fig. 8B); *Basananthe sandersonii* (Harv.) J.J.de Wilde (Bernhard, 1999, fig. 2C); *Passiflora racemosa* Brot. (Bernhard, 1999, fig. 4F); *Passiflora suberosa* L. (Baum-Leinfellner, 1953, fig. 2L, M); *Smeathmannia pubescens* Sol. ex R.Br. (Bernhard, 1999, fig. 2D).

Malvales-Malvaceae, *Pavonia hastata* Cav. (this study, Fig. 42); *Kitaibelia vitifolia* Willd. (this study, Fig. 41).

Caryophyllales-Caryophyllaceae, *Arenaria kotschyana* Fenzl (short) (Baum-Leinfellner, 1953, no figure); *Cerastium arvense* L. (short) (Baum-Leinfellner, 1953, no figure); *Silene dioica* (L.) Clairv. (short) (Baum-Leinfellner, 1953, no figure); *Viscaria alpina* (L.) G. Don (short) (Baum-Leinfellner, 1953, fig. 1G–I). **Phytolaccaceae**, *Phytolaca acinosa* Roxb. (short subunifacial) (Rohweder, 1965, fig. 2A).

Plumbaginaceae, *Armeria alpina* (DC.) Willd. (Leinfellner, 1950, fig. 9); *Armeria juniperifolia* (Vahl) Hoffmanns. & Link (Baum-Leinfellner, 1953, fig. 1A–C).

Lamiales-Plantaginaceae, *Hippuris vulgaris* L. (this study, Fig. 43).

GYNOECIA WITHOUT A PRIMARY MORPHOLOGICAL INNER SPACE AND THUS WITH SECONDARY LOCULE FORMATION OR WITHOUT ANY LOCULES

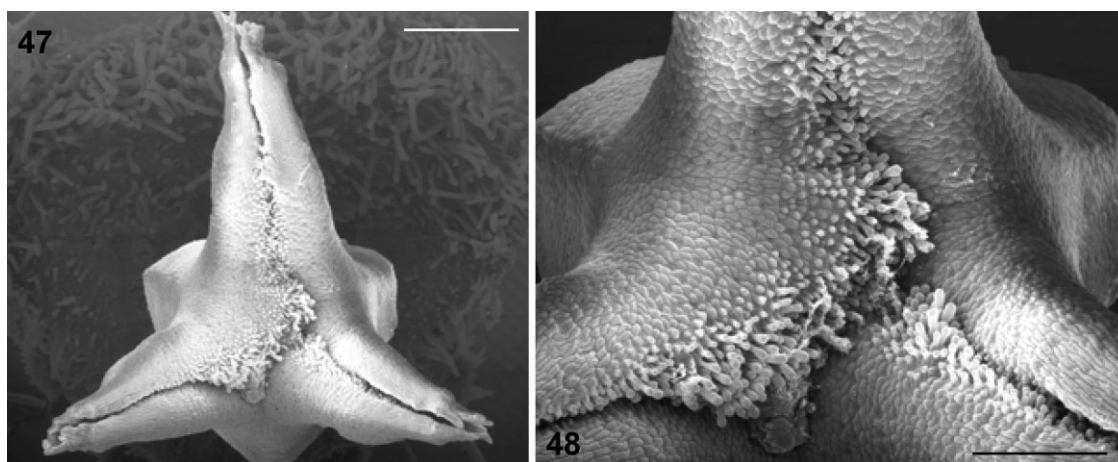
As an exception among angiosperms, in two unrelated families of parasites, the gynoecium does not have an inner morphological surface. In the gynoecium of the giant-flowered Rafflesiaceae the surface of the inner space with the ovules is not a primary morphological surface but it originates from a compact body by tissue separation (Nikolov *et al.*, 2014). Similarly, the entire plant does not develop from an embryo but from a protocorm, which is derived from a proembryo-like filament, and the shoot apex is a secondary formation from inside the protocorm, and thus also does not have a primary morphological surface (Nikolov *et al.*, 2014). As a contrasting extreme, the highly reduced and minute gynoecium of Balanophoraceae is compact and has no inner space at all; an embryo sac differentiates in this compact gynoecium without ovule formation

(Fagerlind, 1945; Eberwein, Nickrent & Weber, 2009). In *Balanophora* J.R. Forst. & G. Forst., in addition, the entire shoots are formed endogenously and thus the surface of the flowers is not derived from a primary morphological surface (Shivamurthy, Swamy & Arekal, 1981).

ARE THERE OPEN CARPELS IN ANTHETIC FLOWERS IN ANY ANGIOSPERMS? (FIGS 47, 48)

There are subtleties of when a carpel or gynoecium should be regarded as closed or still open. Broad comparative studies are lacking and most published reports are on single species. They are difficult to compare because there is no uniform basis for comparison. In addition, none of the critical cases has been studied developmentally in detail. Here I call a carpel or gynoecium open if it is not completely sealed either by secretion or by postgenital fusion at the time of pollination. Cases that are closed at anthesis but become open again after anthesis are here in the 'closed' category. With this definition there are only a few cases of plants with open carpels or gynoecia, in contrast to the number of genera or species mentioned in the literature. Cases with true or misinterpreted openness are discussed below.

Short accounts of plants with open carpels or gynoecia were given by Baum (1949) and Eames (1961). Baum (1949) mentioned *Reseda* L. In an anthetic flower the carpel margins in the stigmatic region give the impression of overlapping in an unordered fashion (this study, Figs 47, 48), similar as shown for the centre in some multicarpellate gynoecia (Endress, 2014). Thus, the gynoecium is not gaping open. However, whether it corresponds to our defini-



Figures 47–48. *Reseda phyteuma* (Resedaceae). Gynoecium syncarpous, tricarpellate. Stigma at anthesis, from above. **47.** Overview. **48.** Close-up. Scale bars: 250 μ m (Fig. 48); 500 μ m (Fig. 47).

tion of a closed gynoecium is not established without knowing whether there is sealing and not just overlapping. *Chamaerops humilis* L. was also mentioned by Baum (1949), with a reference to Juhnke & Winkler (1938), who in their figure 3 showed an ‘open carpel’. However, they did not consider that in many palms the apocarpous carpels are postgenitally united (e.g. Stauffer & Endress, 2003). If this is also the case in *Chamaerops*, the term ‘open’ would not fit our definition of open carpels. Further, *Houttuynia cordata* Thunb. and *Datisca cannabina* L. have been mentioned (Baum, 1949), which have only postfloral opening. Thus, they are not really open either.

According to Eames (1961: 189): ‘In the angiosperms, there are taxa in which the carpel is not completely closed at pollination time – *Degeneria*, *Drimys*, *Butomaceae*, *Hydrocharitaceae*, *Sparganium*, *Sassafras*, *Coptis*, *Tiarella*, *Platanus*. The “opening” is narrow, and pollen grains probably never enter the ovarian locule through it.’ . . . ‘The opening is usually quickly closed but may still be present in the mature fruit.’ At least some of these cases are also problematic. In *Degeneria*, *Tasmannia* R.Br. (as *Drimys*), *Butomaceae*, *Hydrocharitaceae* and *Platanus* L. there is clear postgenital fusion of the carpels at anthesis (Igersheim & Endress, 1997, 1998; Endress & Igersheim, 1999). Thus, they are not open. I have not seen material of *Sparganium* L., *Sassafras* J.Presl and *Coptis* Salisb. *Tiarella* L. has exceptional carpels, which are apparently neither sealed by secretion nor postgenitally fused (this study). Thus, they are ‘open’ with our definition. However, they are tightly involute with both broad flanks. In fruit the carpels are flat and act in raindrop dispersal. Seen from microtome sections, the gynoecia are also slightly involute and similarly ‘open’ in *Heuchera sanguinea* Engelm. and *Tolmiea menziesii* (Pursh) Torr. & A.Gray (Klopfer, 1969) and perhaps in *Darmera peltata* (Torr. ex Benth.) Voss (as *Peltiphyl-lum peltatum* Torr. ex Benth. (Engl.) (Saxena, 1972). Whether carpels in *Sagittaria trifolia* (Huang *et al.*, 2014) mentioned above are really open is not clear. The authors showed that in the basal ‘opening’ postgenital fusion is lacking but they do not show whether it is devoid of secretion and whether it is not appressed to the floral base.

SYSTEMATIC ASPECTS: EARLY OR LATE CARPEL CLOSURE

Early carpel closure occurs in all members of the ANITA grade and almost all magnoliids that have been studied. This is in contrast to earlier literature (Bailey & Swamy, 1951; Eames, 1961) and several textbooks, in which carpels of *Degeneria* and *Tasmannia* (as *Drimys*) have even been claimed to be

unclosed at anthesis. That the carpels are closed at anthesis in these and other early diverging angiosperms was shown by several authors (Tucker, 1959; Tucker & Gifford, 1966; Sampson & Kaplan, 1970; Igersheim & Endress, 1997; Endress & Igersheim, 2000a).

In monocots early carpel closure is present in the early diverging lineages, *Acoraceae* and part of *Alismatales* (Buzgo & Endress, 2000; Buzgo, 2001; Igersheim *et al.*, 2001), such as *Tofieldiaceae*, *Araceae* and *Butomaceae*. Late closure occurs in part of both major clades of *Alismatales* in the traditional sense (clades I and II in Les & Tippery, 2013), such as several *Alismataceae* and *Najas* L. of *Hydrocharitaceae* (clade I) and representatives of *Juncaginaceae*, *Posidoniaceae*, *Potamogetonaceae*, *Ruppiaceae*, *Scheuchzeriaceae*, *Zannichelliaceae* and *Zosteraceae* (clade II).

In early branching eudicots early carpel closure occurs in *Eupteleaceae* (Endress, 1969), most *Papaveraceae* (Karrer, 1991) and most core *Ranunculales*. However, late closure occurs in at least some *Papaveraceae* and, among core *Ranunculales*, in some *Berberidaceae* and also some *Ranunculaceae*.

In short, a trend of delayed carpel wall development (precocious ovule development) occurs in a few *Alismatales* (in both major subclades), and some *Poales* (at least part of *Poaceae* and *Cyperaceae*), in some *Ranunculales* and, especially, in many *Caryophyllales*. Among *rosids* it is not prominent and is known from only a few *fabids* and *malvids*. It is present in several *Malpighiales*. In *asterids*, it is almost absent (if *Caryophyllales* are not counted).

Although carpel closure and maturation of ovules, PTTT or stigma are not strictly correlated, there is a loose connection between them, which is to be expected for functional reasons. The genetic and phylogenetic aspects of this connection are largely unknown. In *Arabidopsis* Heynh., in the *ETTIN* mutant the stigma develops precociously (Sessions, 1997). This may give a clue to the easy and multiple evolution of such displacement in maturation of different parts of the PTTT, as the delay of maturation of the ovules has evolved many times in angiosperms.

SYSTEMATIC ASPECTS: STRUCTURAL ANGIOSPERMY PATTERNS CONCENTRATED IN LARGER CLADES

Some features are connected with certain biological properties. They are then especially present in plants with these properties. As such properties in some cases occur in larger clades, they may then be expressed as macrosystematic features. In other cases with constant occurrence or a trend of occurrence of a feature in a larger clade, such connections may not be obvious.

One of the most prominent features of macrosystematic interest is the presence of simply a transverse slit in the earliest diverging angiosperms. It occurs in those ANITA clades with completely ascidiate carpels and a single median ovule, including Chloranthaceae and Ceratophyllaceae (see list in the following section). In those ANITA lines with several ovules per carpel and likewise extremely ascidiate carpels, an (unusually) short longitudinal slit occurs, as also in a few magnoliids. That these two features are so much concentrated in the early diverging angiosperms may be due to a combination of free ascidiate carpels and the inflexible differentiation of the PTTT (see section 'Pollen tube transmitting tract'). A second, smaller group with transverse slits are some Alismatales with underwater flowers that also have completely ascidiate carpels with a single median ovule. In those, the ascidiate shape is probably an ecological advantage. For example, in *Najas* the ovary wall is only two cell layers thick (Guignard, 1901). Such a thin ovary wall would probably not be possible in a plicate carpel with a long ventral slit, because closure would be difficult. It is also possible that the gynoeceum of *Najas* is pseudomonomerous (D. Sokoloff, pers. comm.). In some early branching eudicots with uniovulate carpels a combination of transverse and short longitudinal slits is present (see list in the following section).

Unifacial styles occur in several wind-pollinated Fagales (Betulaceae) and Cucurbitales (Coriariaceae) and some other wind-pollinated groups, such as Poaceae, Gunneraceae and *Hippuris* L. in Plantaginaceae (see list above, in the section 'Closure of carpels with a unifacial style') (Matthews & Endress, 2004; Endress, 2008, 2010).

Probably they also occur in other Fagales (perhaps Casuarinaceae and Myricaceae) and other Poales but in those the carpels are not well studied developmentally. Unifaciality provides a means to increase the receptive surface. A disadvantage of unifaciality is that the efficient structure of the PTTT of plicate carpels for pollen tube selection (see above, in the section 'Pollen tube transmitting tract') is lost. However, this may be less important in a wind pollination syndrome, where pollen arrives in a more staggered fashion on the stigma than in animal-pollinated flowers.

All cases of free central placenta (except for the few Podostemaceae mentioned, at least some of which, however, have short septa at the base) are in the superasterids, such as in some families of Santalales, in Amaranthaceae, Primulaceae and Lentibulariaceae and (incomplete cases) in Acanthaceae and Plantaginaceae. In these groups the carpels tend to be more synorganized than in other core eudicots by lacking septa and forming a circular opening in early development.

SYSTEMATIC ASPECTS: ANGIOSPERMY PATTERNS CONCENTRATED IN THE EARLY DIVERGING GRADE OF EXTANT ANGIOSPERMS (FIGS 49–74)

In earlier studies it was shown that in the ANITA grade (including Chloranthaceae and Ceratophyllaceae), the carpels are almost always pronouncedly ascidiate and most representatives have carpel sealing by secretion, and not by postgenital fusion, in contrast to the majority of other angiosperms (Doyle & Endress, 2000; Endress & Igersheim, 2000a; Endress & Doyle, 2009; Williams, 2009). The present study shows, in addition, outstanding features at the morphological level.

There are two prominent angiospermy patterns. (1) In carpels with a single median ovule and lacking style the slit resulting from carpel closure is transverse, not longitudinal. Either there is no style (as commonly in the ANITA grade) or, if a style is formed, it is unifacial (*Ceratophyllum* L.) or more or less flat (*Hedyosmum* Sw.), but never plicate (and without a well-differentiated inner PTTT). Several taxa of the ANITA grade (*Amborella* Baill., *Trithuria* Hook.f. in Nymphaeales, *Trimenia* Seem. in Austrobaileyales, Chloranthaceae and Ceratophyllaceae) are characterized by such carpels (position of Chloranthaceae and Ceratophyllaceae discussed in Doyle & Endress, 2014). The only exception with plicate carpels in the ANITA grade is *Illicium* L. (Schisandraceae), in which the longitudinal slit is necessary for the unique fruit differentiation: each carpel becomes woody and opens explosively in fruit (Romanov, Bobrov & Endress, 2013). Such carpels with a transverse slit also occur in some aquatic Alismatales with reduced flowers. Otherwise this trait appears to be uncommon in angiosperms. (2) In carpels with several ovules the slit resulting from closure is longitudinal but only short. Such carpels may have an ascidiate style, such as Cabombaceae and *Austrobaileya* (Endress, 1980c, 2005). In Schisandraceae (other than *Illicium*) a style is lacking or short.

The following list contains taxa with completely ascidiate carpels with a single ventral median ovule and a transverse slit of closure (Figs 49–62, 72).

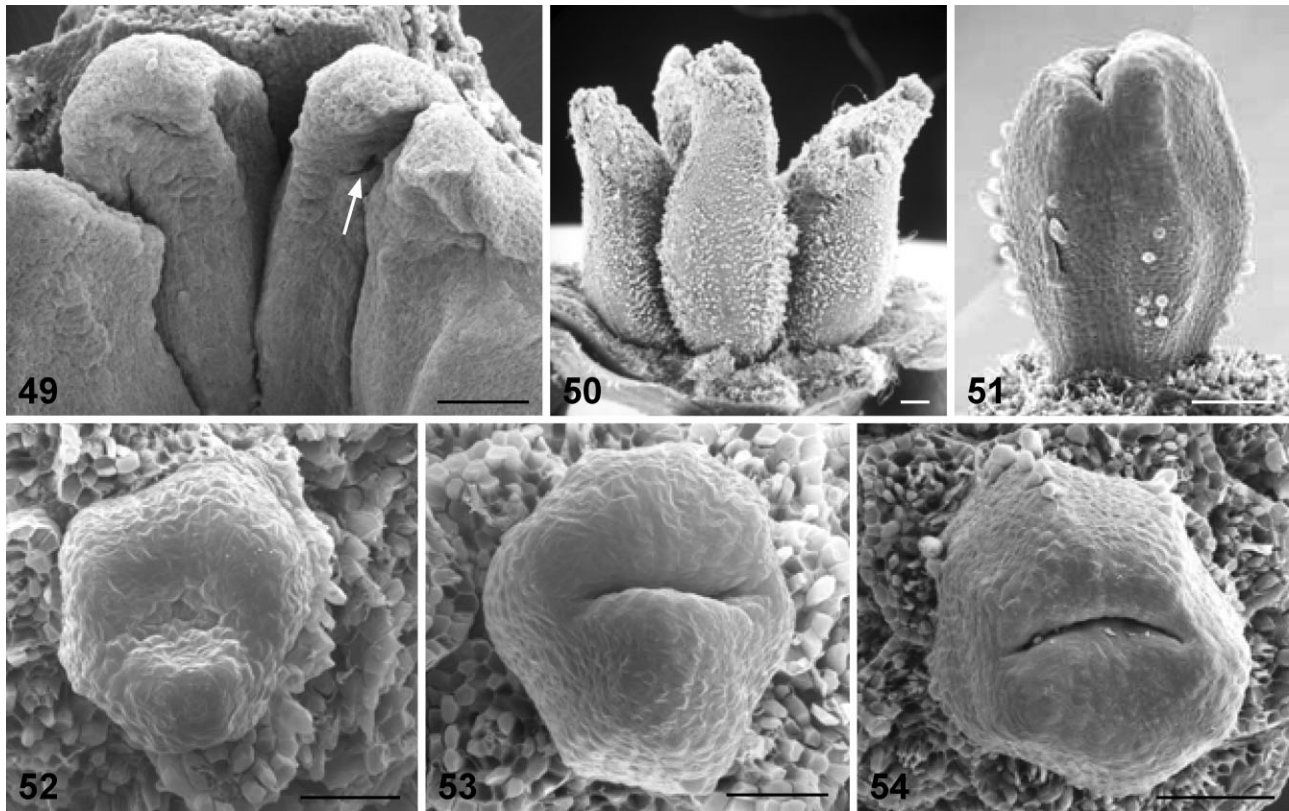
ANITA grade

Amborellales-Amborellaceae, *Amborella trichopoda* (this study, Figs 49, 50).

Nymphaeales-Hydatellaceae, *Trithuria australis* (Diels) D.D.Sokoloff, Remizowa, T.D.Macfarl. & Rudall (as *Hydatella australis* Diels) (Rudall *et al.*, 2007, figs 3C, 10E).

Austrobaileyales-Trimeniaceae, *Trimenia papuana* (Endress & Sampson, 1983, fig. 59; Endress, 2001, fig. 3G; this study, Figs 51–54).

Chloranthales-Chloranthaceae, *Ascarina rubricaulis* Solms (Endress, 1987, fig. 117, 168); *Ascarina*



Figures 49–54. Carpels with transverse slit in the ANITA grade. **49–50.** *Amborella trichopoda* (Amborellaceae). Carpels of female flowers. **49.** Young flower. Carpels with irregular shapes, imprinted by contiguous neighbouring organs by tight position in bud. Irregularly transverse slit marked by arrow. **50.** Anthetic flower. Carpels with irregularly transverse slits. **51–54.** *Trimenia papuana* (Trimeniaceae). **51.** Carpel from floral bud, from the lateral side, with transverse slit. **52–54.** Carpels from floral bud, in different developmental stages, from above, showing transverse slit. Scale bars: 50 μm (Figs 52, 53); 100 μm (Figs 49, 51, 54); 500 μm (Fig. 50).

lucida (this study, Fig. 56); *Hedyosmum mexicanum* (this study, Fig. 55); *Chloranthus elatior* Link (this study, Fig. 58, 59); *Chloranthus japonicus* (this study, Fig. 60); *Chloranthus spicatus* (Endress, 1987, fig. 92, 169); *Sarcandra chloranthoides* (Endress, 1987; fig. 167); *Sarcandra glabra* (this study, Fig. 57).

Ceratophyllales-Ceratophyllaceae, *Ceratophyllum demersum* (Endress, 1994b, fig. 4A–C; Iwamoto, Shimizu & Ohba, 2003, figs 2–6; this study, Figs 61, 62).

Monocots

Alismatales-Potamogetonaceae, *Zannichellia palustris* (this study, Fig. 72). **Ruppiales,** *Ruppia maritima* L. (Kaul, 1993, fig. 1D, E; Lacroix & Kemp, 1997, figs 1–5); *Ruppia occidentalis* S.Watson (Kaul, 1993, fig. 2B, D, F).

The following list contains taxa with completely ascidiate pluriovulate carpels with a short longitudinal slit of closure (Figs 63–71).

ANITA grade

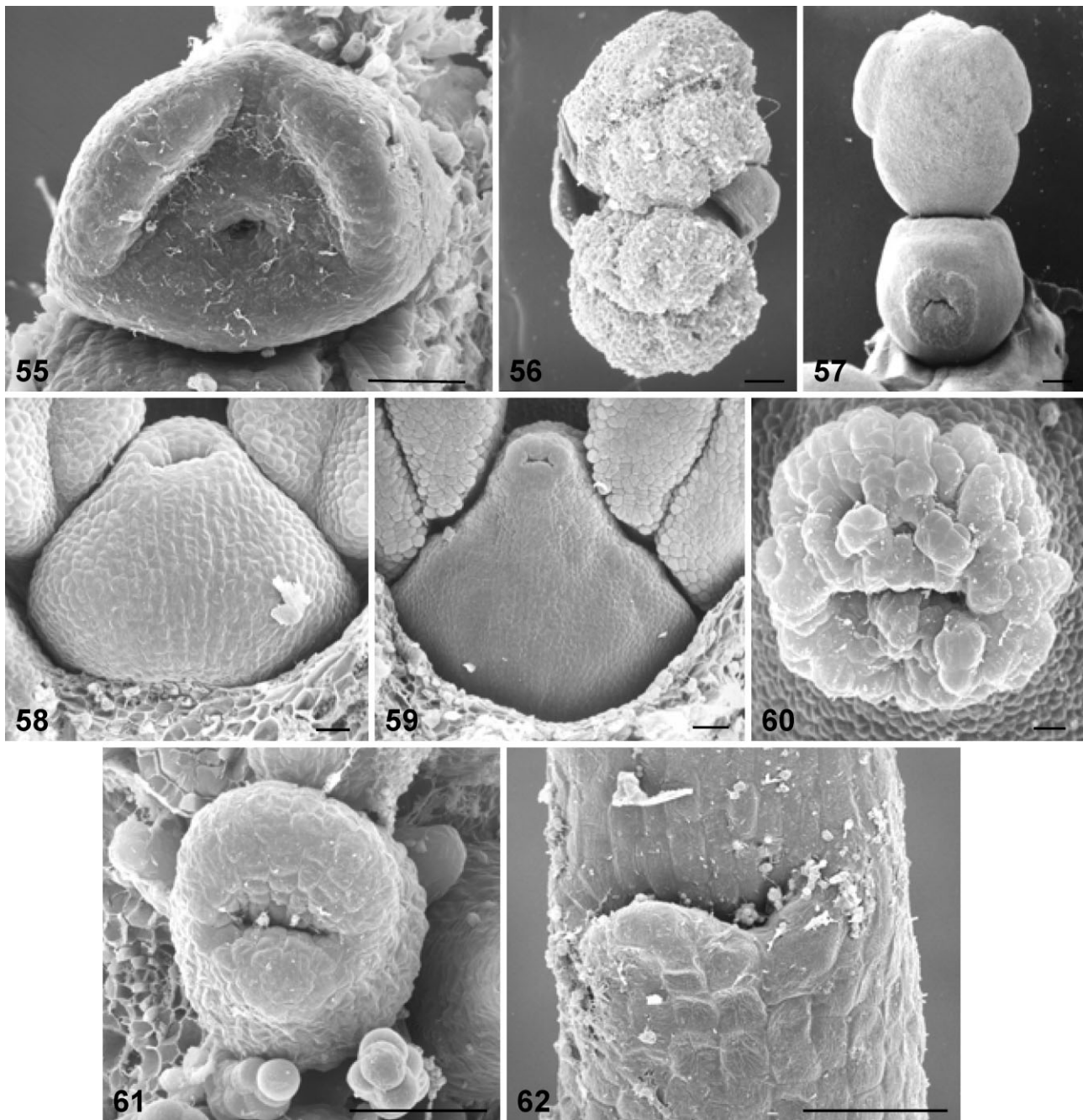
Nymphaeales-Cabombaceae, *Brasenia schreberi* (Endress, 2005, fig. 1B, E; this study, Fig. 64); *Cabomba furcata* (Endress, 2001, fig. 8F–H; this study, Fig. 63). **Nymphaeaceae,** *Nuphar advena* (Endress, 2001, fig. 9G, H; this study, Fig. 65); *Victoria cruziana* (Endress, 2001, fig. 11C–F; this study, Fig. 66).

Austrobaileyales-Austrobaileyaceae, *Austrobaileya scandens* (Endress, 1983, fig. 34; Endress, 2001, fig. 4C–E; this study, Figs 67, 68). **Schisandraceae,** *Schisandra chinensis* (see also Endress, 2001, fig. 5G; this study, Fig. 69).

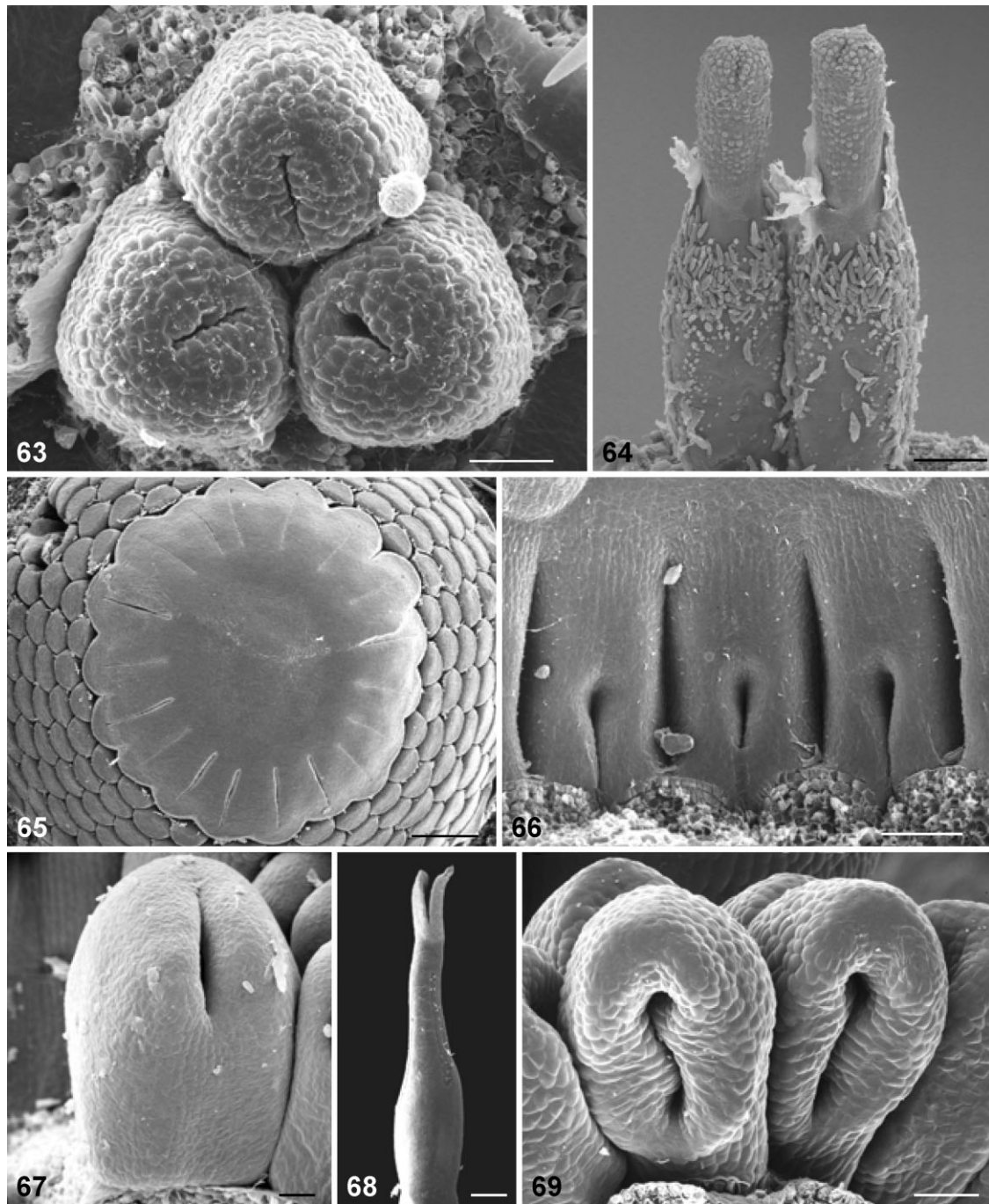
Magnoliids

Canellales-Winteraceae, *Pseudowintera axillaris* (this study, Fig. 71); *Zygogynum baillonii* (Endress, 1986, fig. 11A; this study, Fig. 70).

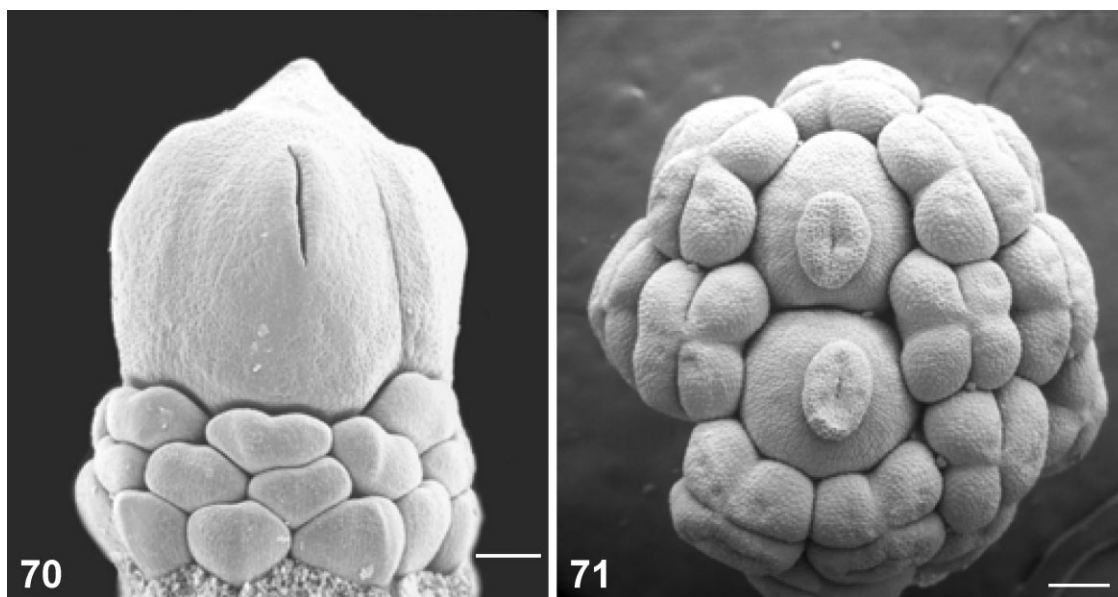
The following list contains representatives of magnoliids and early branching eudicots with uniovulate carpels in a ventral median position but, in contrast



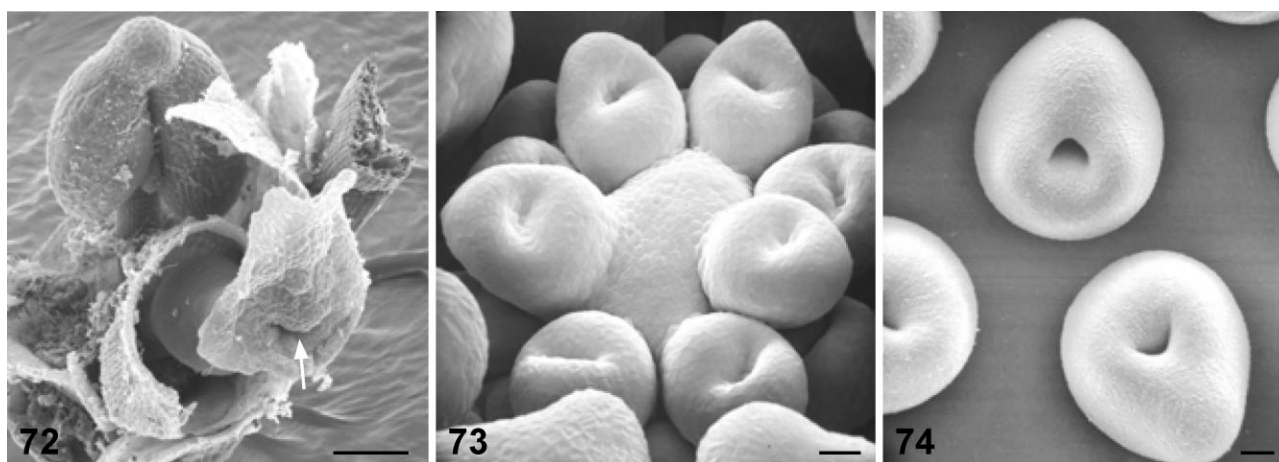
Figures 55–62. Carpels with transverse slit in Chloranthaceae and Ceratophyllaceae. **55.** *Hedyosmum mexicanum* (Chloranthaceae). Young female flower, surrounded by three tepals. The single carpel with short transverse opening. **56.** *Ascarina lucida* (Chloranthaceae). Two opposite unicarpellate female flowers. Carpels with transverse slit. **57.** *Sarcandra glabra* (Chloranthaceae). Bisexual flower with single stamen (above) and single carpel with transverse slit (below). **58–59.** *Chloranthus erectus* (Chloranthaceae). Carpels with short transverse slit. **58.** Young carpel. **59.** Somewhat older carpel. **60.** *Chloranthus japonicus* (Chloranthaceae). Anthetic carpel. **61–62.** *Ceratophyllum demersum* (Ceratophyllaceae). **61.** Young carpel. **62.** Anthetic carpel. Scale bars: 50 μm (Figs 55, 58, 60–62); 100 μm (Fig. 59); 500 μm (Figs 56, 57).



Figures 63–69. Carpels with short longitudinal slit in the ANITA grade. **63.** *Cabomba furcata* (Cabombaceae). Young gynoeceium with three carpels, from above. **64.** *Brasenia schreberi* (Cabombaceae). Two preanthetic carpels from the side. **65.** *Nuphar advena* (Nymphaeaceae). Syncarpous gynoeceium with 18 carpels, from above. **66.** *Victoria cruziana* (Nymphaeaceae). Part of gynoeceium, from ventral side. **67–68.** *Austrobaileya scandens* (Austrobaileyaceae). **67.** Young carpel, from ventral side. **68.** Anthetic carpel, from ventral side. **69.** *Schisandra chinensis* (Schisandraceae). Young carpels, from ventral side. The longitudinal slit appears relatively long, but the carpels have a relatively long compact base, which is in part not visible in the figure. Scale bars: 50 μm (Figs 63, 69); 100 μm (Figs 66, 67); 200 μm (Fig. 65); 300 μm (Fig. 64); 500 μm (Fig. 68).



Figures 70, 71. Carpels with short longitudinal slit in Winteraceae (magnoliids). **70.** *Zygogynum baillonii*. Syncarpous gynoecium, from the side. In one carpel the longitudinal slit of closure is visible, which has a seemingly dorsal position because of the specific proportions of the carpels. **71.** *Pseudowintera axillaris*. Preanthetic gynoecium with two carpels, from above. The short longitudinal closure slit is restricted to the stigmatic area of each carpel. Scale bars: 200 μm (Fig. 70); 500 μm (Fig. 71).



Figures 72–74. Transverse slit in an early diverging monocot and transverse slit combined with (at least rudimentary longitudinal slit) in early diverging eudicots. **72.** *Zannichellia palustris* (Potamogetonaceae). Reduced anthetic flower with a single carpel. Arrow points to transverse slit. **73.** *Ranunculus acris* (Ranunculaceae). Innermost free carpels of a young flower. **74.** *Nelumbo nucifera* (Nelumbonaceae). Innermost carpels of a young flower. Scale bars: 50 μm (Figs 73, 74); 200 μm (Fig. 72).

to the ANITA grade, not a simple transverse closure line but a combination of transverse and (at least rudimentary) longitudinal closure (Figs 9–14, 73, 74).

Magnoliids

Laurales-Lauraceae, *Laurus nobilis* (this study, Figs 9–14).

Early diverging eudicots

Ranunculaceae, *Ranunculus acris* (this study; Fig. 73); *Ranunculus chinensis* Bunge (Zhao *et al.*, 2012b, fig. 3M–O); *Ranunculus sceleratus* L. (Zhao *et al.*, 2012b, fig. 4O–Q); *Ceratocephala orthoceras* DC. (Zhao *et al.*, 2012b, fig. 6N, O); *Halerpestes cymbalaria* Greene (Zhao *et al.*, 2012b, fig. 7O, P); *Oxyg-*

raphis glacialis Bunge (Zhao *et al.*, 2012b, fig. 80, P). **Nelumbonaceae**, *Nelumbo nucifera* (mainly transverse), (Hayes *et al.*, 2000, fig. 2A, C; this study, Fig. 74).

CONCLUSIONS

Based on the systematic distribution there is no fundamental (morphological or phylogenetic) difference between carpels with early and delayed closure as both patterns occur in some families with otherwise similar gynoecia. Thus, a distinction between ‘carpellate’ and ‘acarpellate’ gynoecia, as proposed by, for example, Sattler (1974), is biologically unfounded and does not make sense. This aspect will be treated in a separate paper in more detail.

Delayed carpel closure is not common in angiosperms. In early diverging angiosperms late carpel closure does not occur. However, in a few larger clades that are highly nested in angiosperms it is a prominent feature. Within such clades it appears to be more common in gynoecia with a single ovule than in multiovulate gynoecia. In general it appears to occur preferentially in small, reduced flowers. Broader studies on its occurrence are needed.

Structural patterns of carpel closure lines show some systematic patterns. The pronouncedly ascidiate carpels of early branching angiosperms (ANITA grade, including Chloranthaceae and Ceratophyllaceae) have either a transverse line (if there is a single median ovule in a carpel) or a short longitudinal line (if there is more than one ovule in a carpel). A style is missing or only short and is not formed by plication (folding or curving inward) of a carpel, but by short extension of the ascidiate zone or by unifaciality or flat extension of the carpel top.

From the largely restricted occurrence of extremely ascidiate carpels in angiosperms and their concentration in the early branching grade of angiosperms we may speculate that this kind of morphology provides fewer possibilities of flexibility of differentiation of the PTTT than plicate carpels, not only for syncarpous gynoecia with compitum formation but also for apocarpous gynoecia with individual PTTTs. I posit this as a working hypothesis that needs broad study in the future.

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