

# 11

## Floral ontogeny of *Acacia celastrifolia*: an enigmatic mimosoid legume with pronounced polyandry and multiple carpels

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### 11.1 Introduction

The genus *Acacia* is among the largest plant genera. It was recently treated either in a broad sense with *c.* 1450 species (Lewis, 2005) or in a strict sense (*Acacia* s.s. with *c.* 987 species). The latter follows the re-typification of *Acacia* with an Australian type (Orchard and Maslin, 2003; see also Murphy, 2008). According to Maslin (1995), the Australian species *A. celastrifolia* belongs to the '*Acacia myrtifolia* group' and is most closely related to *A. myrtifolia*. In molecular studies, only *A. myrtifolia* was sampled, which is sister to *A. pulchella* in the Pulchelloidea clade (e.g. Miller and Bayer, 2001; Miller et al., 2003; Murphy et al., 2010). Molecular sampling of the hitherto unsampled *A. celastrifolia* is highly desirable in order to verify the hypothesized close relationship with *A. myrtifolia* (e.g. Maslin, 1995).

Flowers of the genus *Acacia* s.l. are always found in globular heads or spikes. The flowers are (3-)4-5(-6)-merous, with free or united sepals and small reduced petals, which are postgenitally fused and which split open at anthesis. The androecium is

composed of many free stamens (i.e. a polyandrous androecium) and the flower is normally terminated by a single superior carpel.

*Acacia celastrifolia* deviates from this bauplan in that it has 3–7 carpels. Furthermore its exceptionally high polyandry, with more than 500 stamens, is noteworthy. Flowers of the majority of Leguminosae are terminated by a single carpel and multicarpelly in Fabales is restricted to Polygalaceae, Quillajaceae and Surianaceae. Thus, a comparative study of legume flowers with more than one carpel per flower is of special interest for a better understanding of legume flowers and their evolution.

## 11.2 Materials and methods

Floral buds and inflorescences of *Acacia celastrifolia* Benth. were collected from the Botanic Garden Graz (University of Graz, Austria) and immediately fixed in FAA (five parts formalin:five parts 100% acetic acid:90 parts 70% ethanol). Storage and further dissection was in 70% ethanol. For scanning electron microscopy (SEM), material was dehydrated through an alcohol series to absolute alcohol and critical-point dried using an Autosamdri-815B critical-point dryer. Dried material was mounted onto specimen stubs using nail polish, coated with platinum using an Emitech K550 sputter coater and examined using a Hitachi cold field emission SEM S-4700-II. More than 300 SEM micrographs were analysed and figures were processed using Adobe Photoshop CS.

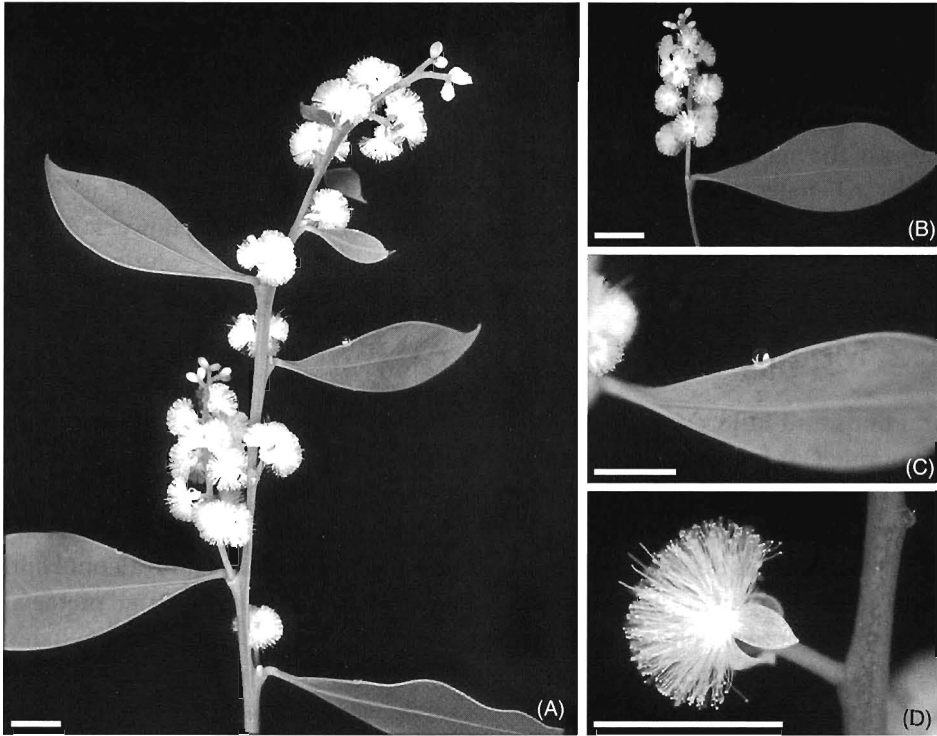
## 11.3 Results

### 11.3.1 Habitus (Fig 11.1A–D)

*Acacia celastrifolia* is a glabrous shrub of 1–3 m. Flowers are clustered in 10–20-headed racemes (Fig 11.1A). Phyllodes show a distinct midrib and a prominent gland 0.5–2 cm above the pulvinus (Fig 11.1B,C). Individual flowers form (1–) 2–3-flowered heads on 3–10 mm long peduncles. In the mature flowers the recurved petals and the highly polyandrous androecium are the most distinct characters (Fig 11.1D). Styles of the three to seven carpels are longer than the stamens and arch clearly above the level of the anthers (Fig 11.1D).

### 11.3.2 Flower formation (Fig 11.2A–D)

On the inflorescence axis (1–)2–3-flowered heads are formed in a spiral (Fig 11.1A–B, Fig 11.2A). The flowers are formed in a quick succession on a short roundish peduncle (Fig 11.2A–B) and flower subtending bracts are either formed or missing (Fig 11.2A–F). No flower preceding bracteoles are formed. Multicellular and club-shaped hairs are rarely found at the base of the floral heads (Fig 11.2E) and in groups between the individual flowers (Fig 11.2F,G).



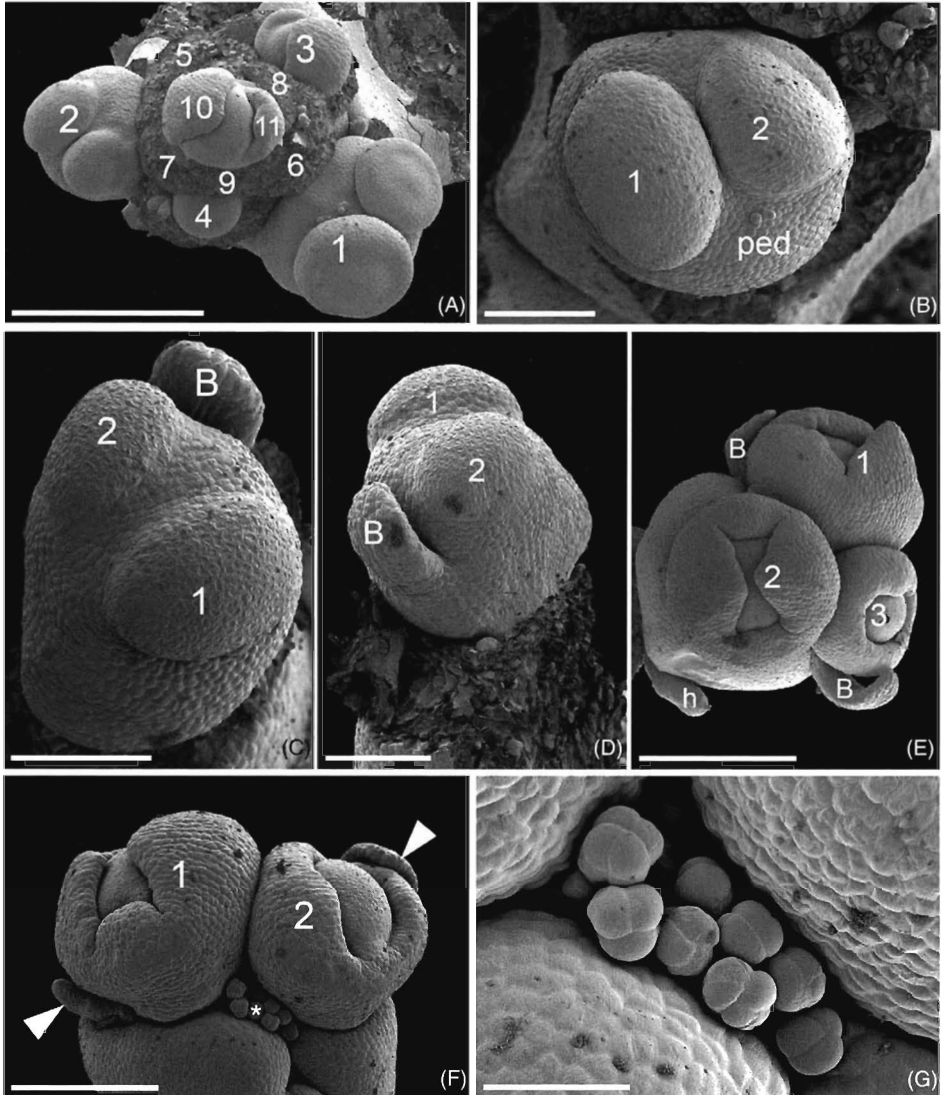
**Fig 11.1** *Acacia celastrifolia*. (A) Flowering branch. (B) Inflorescence with phyllode at its base. (C) Detail of phyllode with nectary and drop of nectar. (D) Flower with recurved petals, highly polyandrous androecium and four styles which are protruding above the level of the anthers. Scale bar = 1 cm in all. For colour illustration see plate section.

### 11.3.3 Calyx (Fig 11.3A–F)

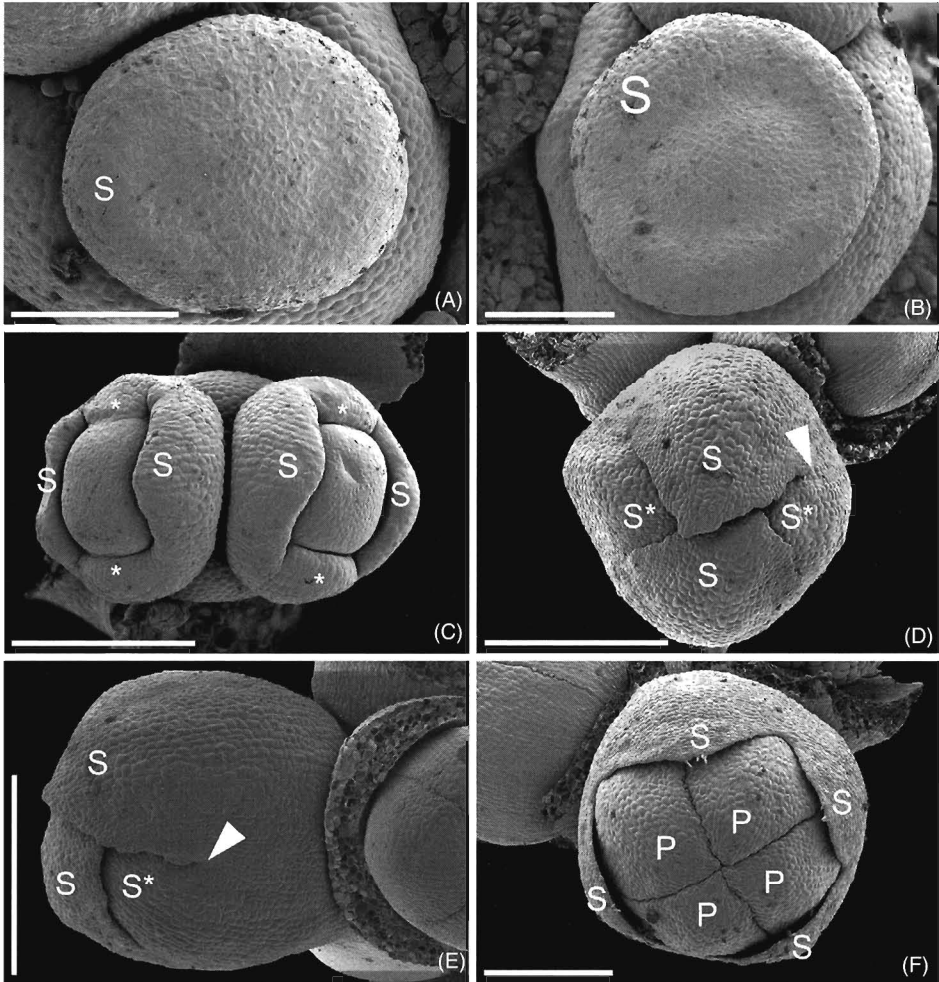
Soon after flower primordia become visible, a calyx is produced in the form of a closed ring primordium (Fig 11.3A–B). The shape of the primordium is uniform at the beginning and only later in ontogeny do four distinct lobes become discernible. The two lobes in the median position (one pointing to the main floral axis and one opposite) become larger than the two lateral ones, which become the inner sepals in later developmental stages (Fig 11.3C–D). Sepals are congenitally fused with only the upper lobes free (Fig 11.3D–E). Later in ontogeny, sepal aestivation becomes open, due to the enlarging bud and petals take over bud protection (Fig 11.3F).

### 11.3.4 Corolla (Fig 11.4A–G)

Distinctly after the sepals are formed (i.e. after a longer plastochron during which sepals are formed and enlarge), formation of four petals commences in a simultaneous pattern (Fig 11.4A). The four petals are formed apart from each other and only in some flowers are two petals formed in a very close proximity. The petals

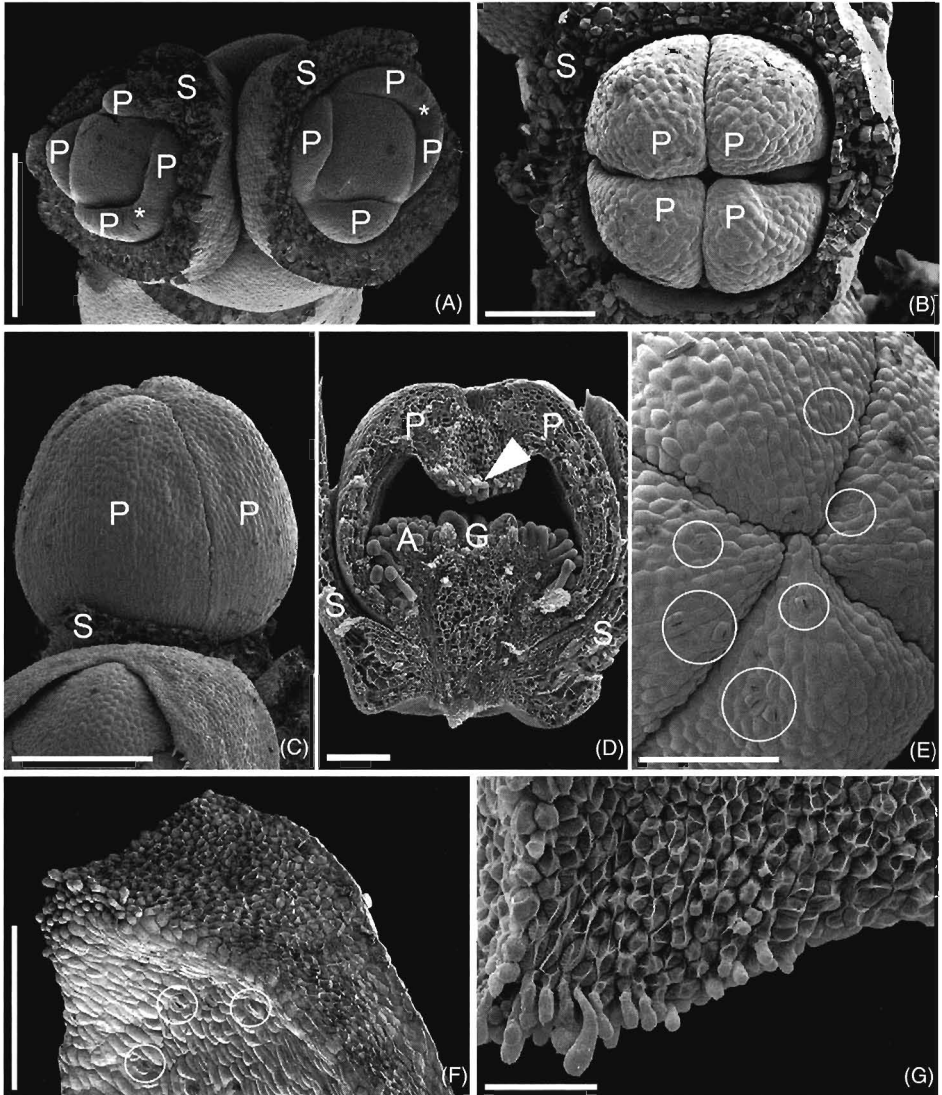


**Fig 11.2** *A. celastrifolia*, inflorescence and flower initiation. (A) Inflorescence showing spiral initiation of partial inflorescences (1-4) and their subtending bracts respectively (5-11). (B) Partial inflorescence with two flowers initiated in a short sequence on short roundish peduncle (ped). (C), (D) Two-flowered partial inflorescence showing initiation of two flowers and one flower subtending bract which can be assigned to the second flower. (E) Three-flowered partial inflorescence. Note that there is a developmental difference between the three flowers. Two flowers are subtended by bracts and at the base of the entire structure one club-shaped multicellular hair (h) is found. (F) Two-flowered partial inflorescence, each of the flowers associated to a flower subtending bract (arrowheads). Note the hairs at the base of the two flowers (asterisk). (G) Detail of (F) showing multicellular hairs. B = flower subtending bract, h = multicellular hair, ped = peduncle. Scale bars: (A) = 400  $\mu\text{m}$ ; (B)-(D) = 100  $\mu\text{m}$ ; (E) = 300  $\mu\text{m}$ ; (F) = 200  $\mu\text{m}$ ; (G) = 50  $\mu\text{m}$ .



**Fig 11.3** *A. celastrifolia*, sepal initiation and development. (A) Young flower in which the sepaloid ring primordium becomes just visible. (B) Somewhat later stage showing distinct ring primordium. (C) Two-flowered partial inflorescence. The sepals in median position are larger than the lateral sepals (asterisks). (D) Frontal view of older flower with closed calyx. The sepals in median position are covering the lateral sepals (S\*). Sepals are fused (arrowhead) and only the upper lobes remain free. (E) Lateral view of older flower showing fused calyx and free sepal lobes. (F) Frontal view of older flower in which the calyx is open and protection of the sexual organs is by the valvately closed petals. P = petal, S = sepal. Scale bars: (A), (B) = 100  $\mu$ m; (C) = 200  $\mu$ m; (D)–(F) = 500  $\mu$ m.

enlarge quickly and fuse postgenitally due to interlocking epidermal papillae, which become most prominent at the tips of the petals (Fig 11.4B–G). Petal aestivation is valvate and due to the enlarging corolla the calyx is squeezed open (Fig 11.3F). At this developmental stage petals take over the protection of the developing



**Fig 11.4** *A. celastrifolia*, petal initiation and development. (A) Two flowers in which the sepals are removed and four petals are formed simultaneously. (B) Frontal view of young flower (sepals removed). Four petals are still free from each other, petal aestivation becomes valvate. (C) Side view of older flower bud (sepals removed). Note the distinct suture between adjacent petals. (D) Median section through flower bud with short sepals in open aestivation, valvate petals with distinct papillae on the inner tips (arrowhead), androecium and gynoecium. (E) Outer petal surface of young floral bud showing many stomata (circles). (F) Stomata on the inner petal surface (circles). (G) Petal tip with distinct papillate epidermal cells and epidermal ridges in the regions of postgenital fusion. A = androecium, G = gynoecium, P = petal, S = sepal/calyc. Scale bars: (A), (F) = 300  $\mu\text{m}$ ; (B), (D), (E) = 200  $\mu\text{m}$ ; (C) = 500  $\mu\text{m}$ ; (G) = 100  $\mu\text{m}$ .

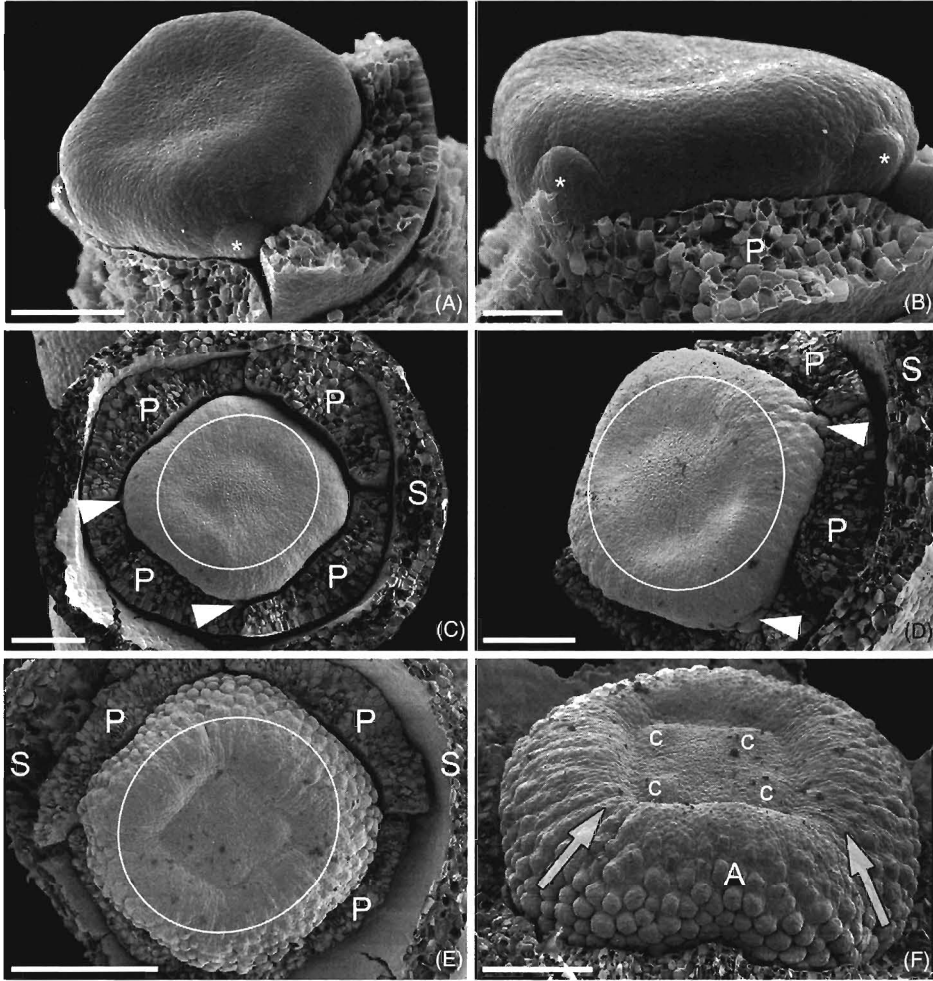
androecium and gynoecium inside the floral bud. Both on the outer and on the inner surface of the mature petals abundant stomata are found (Fig 11.4E-F).

### 11.3.5 Androecium (Figs 11.5A-F, 11.6A-E)

Androecium formation starts after a longer plastochron, during which the petals enlarge distinctly and the young floral meristem is protected by the corolla. At this developmental stage the floral meristem becomes square in shape and a distinct ring primordium becomes visible (Fig 11.5A). Formation of individual stamens starts with four larger primordia which arise at the four corners of the square alternating with the four petals (Fig 11.5A-D). Stamen formation continues in lateral and centripetal direction. Individual stamen primordia are *c.* 20  $\mu\text{m}$  in diameter (Fig 11.5D-F). In the mature flower more than 500 individual stamens are found, which arise on a distinct androecial bulge (i.e. remainder of the ring primordium) at the base of the flower (Fig 11.6A-B). The anthers of *A. celastrifolia* show two thecae separated by a broad connective (Fig 11.6C). Each theca is parted into two locules (i.e. microsporangia) and each locule is again divided by a transverse septum. The inner surface of the locules is covered with orbicules which makes their appearance granulate (Fig 11.6D). In each locule two eight-grained polyads are formed (Fig 11.6D-E). This makes a total of eight polyads and 64 pollen grains per anther. The pollen grains are heteromorphic within each polyad. Two central pollen grains can be clearly distinguished from six lateral grains (Fig 11.6E).

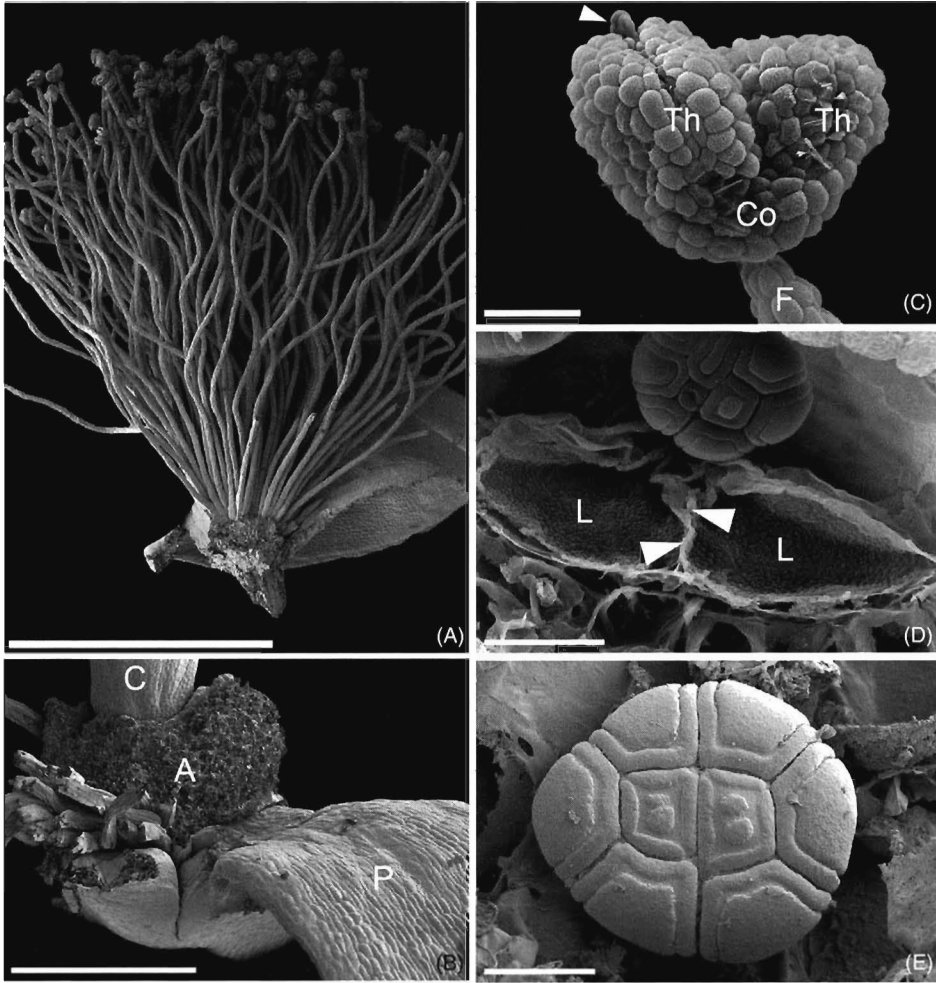
### 11.3.6 Gynoecium (Figs 11.5E-F, 11.7A-H, 11.8A-E)

Carpel formation starts before the last stamens are formed (Fig 11.5F). At this developmental stage there is a distinct separation of the androecial ring-wall and the central floral region where the carpels are formed. Following the somewhat square-shaped androecial ring-wall, the central region of the flower also becomes square shaped and in some instances at each corner of the square one carpel is formed (Fig 11.5E-F). However, in other flowers only three or up to seven carpels are formed. Carpel initiation appears, in some flowers, simultaneous (Figs 11.5F, 11.7A-B), while in others it is erratic with no distinct discernible sequence (Fig 11.7C-H). Common to all studied flowers is: (1) that the floral centre remains organ free, (2) that the carpels are formed only around this centre and (3) that the cleft of the carpels always points towards the floral centre. The mature carpel shows a long style and a small stigmatic region on top (Fig 11.8A-B). This can harbour only one single polyad (Fig 11.8B). Abundant stomata are located on the surface of the carpel and at the base a short gynophore is formed (Fig 11.8A, C-D). A maximum of eight ovules are formed within each carpel and in each ovule initially only the outer integument is visible (Fig 11.8D-E). The inner integument is formed later in ontogeny (not shown).

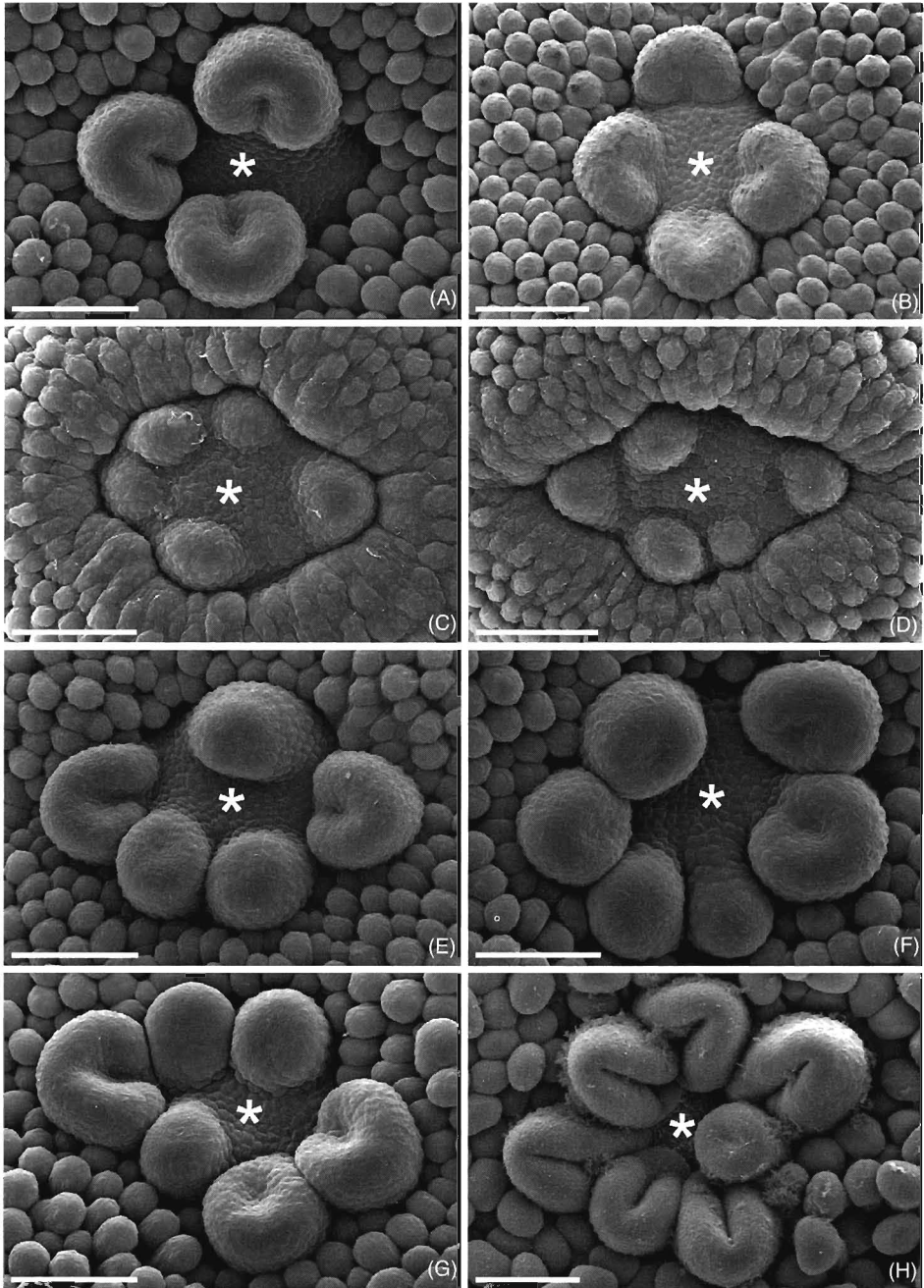


**Fig 11.5** *A. celastrifolia*, stamen initiation. Sepals and petals removed in all. (A) Frontal view of androecial ring-wall with first stamens formed (asterisks) alternating with the petals. (B) Lateral view of a bud with first formed stamens (asterisks). (C) Androecial ring-wall (circle) and first formed stamens (arrowheads) alternating with the petals. (D) Side view of somewhat older bud. Stamen primordia are formed in a centripetal pattern. (E) Older floral bud with massive androecial ring-wall (circle) distinctly separated from inner part of the flower. (F) Side view of androecial ring-wall. Arrows show the direction of stamen initiation. In the centre of the flower four carpel primordia are just formed (c). A = androecium, c = carpel primordium, P = petal, S = sepal/calyx. Scale bars: (A), (C), (D), (F) = 100  $\mu\text{m}$ ; (B) = 50  $\mu\text{m}$ ; (E) = 200  $\mu\text{m}$ .

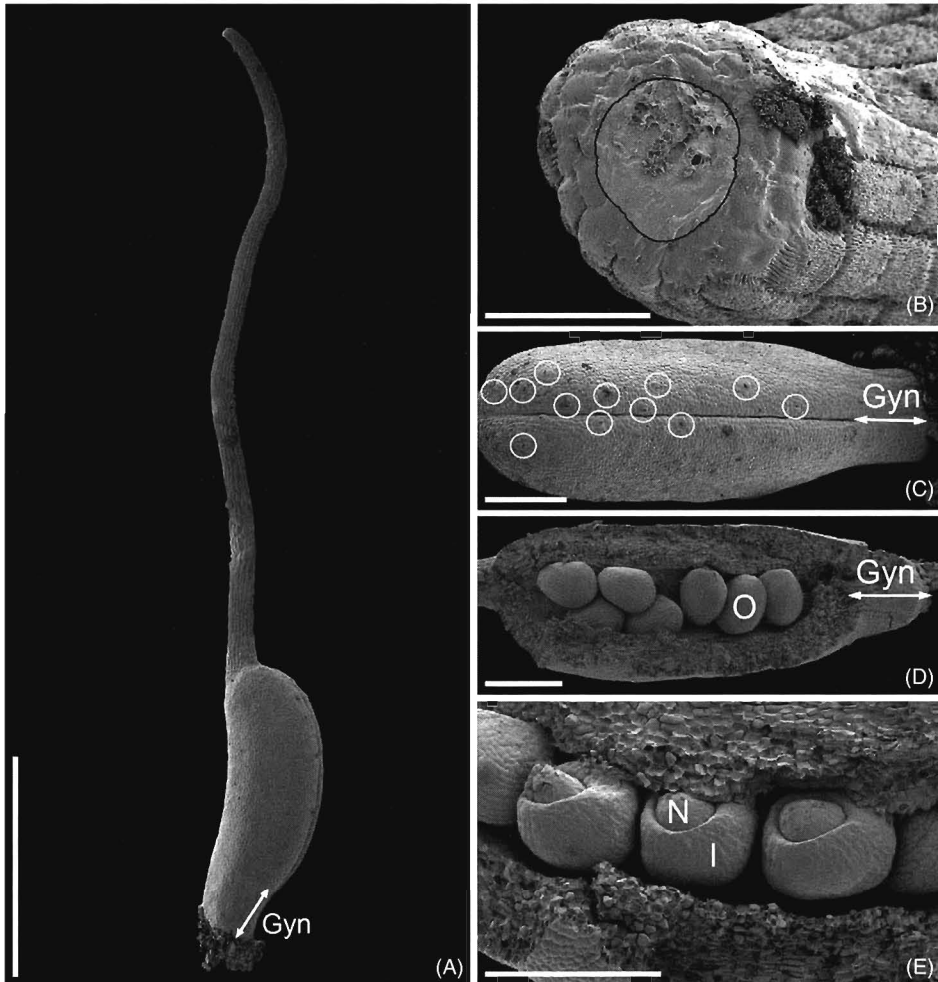




**Fig 11.6** *A. celastriifolia*, mature androecium and pollen. (A) Part of the androecium of a mature flower. Note the small anthers sitting on long filaments. (B) Base of mature flower, stamens removed leaving only a basal ring-wall of androecial tissue. (C) Versatile anther with two thecae attached to a broad connective. Note a polyad looking out of one theca (arrowhead). (D) Opened theca showing a locule which is divided by a central transverse tissue (arrowheads). Note the inner surface of the locule which is covered with orbicules (granular surface). (E) Eight-grained polyad with two central grains surrounded by six lateral grains. Note the difference of the central and the lateral grains (i.e. heteromorphic pollen). A = androecium, Co = connective, C = carpel, L = locule, P = petal, Th = theca. Scale bars: (A), (B) = 500  $\mu\text{m}$ ; (C) = 50  $\mu\text{m}$ ; (D) = 20  $\mu\text{m}$ ; (E) = 10  $\mu\text{m}$ .



**Fig 11.7** *A. celastriifolia*, carpel initiation. The organ-free floral apex is marked with an asterisk in all. Note that in all samples the carpellary cleft (if already present) is pointing towards the floral centre. (A) Three very similar carpels suggesting simultaneous initiation. (B) Four carpels initiated and very similar in size. (C)-(E). Five carpels formed in no defined sequence. (F) Six carpels formed apparently in anticlockwise sequence. (G) Six carpels formed in no discernible sequence (i.e. erratic). (H) Seven carpels formed, six are of similar developmental stage, one lags behind. Scale bars = 100  $\mu$ m in all.



**Fig 11.8** *A. celastrifolia*, mature carpel. (A) Mature carpel with a gynophore, the ovary and a long style. (B) Stigmatic area of mature carpel with the outline of a polyad projected onto its surface. Note that the polyad covers almost the entire receptive surface of the style. (C) Mature ovary with many stomata on its surface (circles) and with a distinct basal gynophore. (D) Dissected ovary with seven ovules. (E) Detail of ovules. Note that only the outer integument and the nucellus are visible. Gyn= gynophore, I = outer integument, N = nucellus, O = ovule. Scale bars: (A) = 1 mm; (B) = 30  $\mu$ m; (C)–(E) = 200  $\mu$ m.

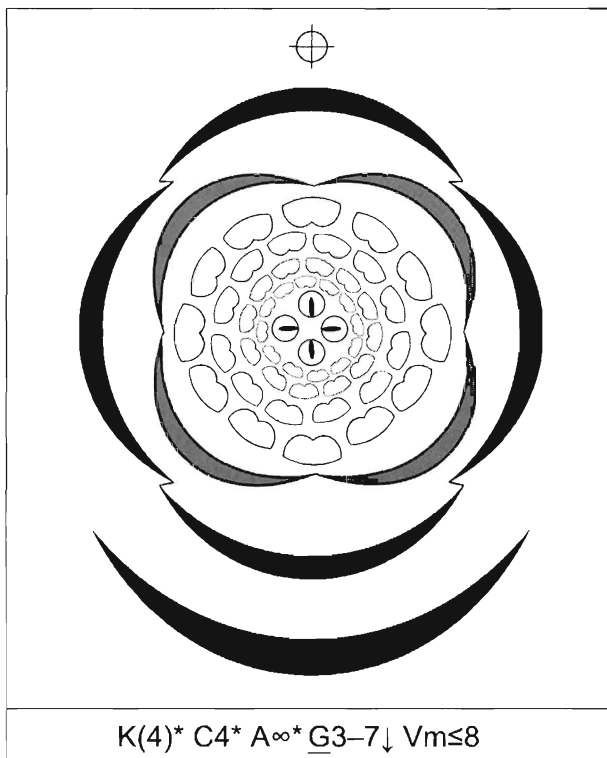
## 11.4 Discussion

### 11.4.1 Inflorescence and floral orientation

In *A. celastrifolia* the flower number per head is reduced to (1-)2-3 flowers, which contrasts with most other acacias (*Acacia* s.l.), in which the heads are many-flowered. Guinet et al. (1980) highlight that *Acacia gilbertii* is highly unusual

because of the 2–8 relatively large tetramerous flowers per head; this feature is otherwise unknown in Pulchellae but ‘identical’ with that of the phyllodinous species *A. myrtifolia* and *A. celastrifolia*. Floral orientation in Mimosoideae differs from Caesalpinioideae and Papilionoideae in that one sepal is oriented towards the main axis in mimosoids, while one petal is oriented this way in the other two subfamilies. In this respect, flowers of *A. celastrifolia* are orientated in the same way as in most Mimosoideae, with one sepal towards the main axis (Fig 11.9; see also Eichler, 1878; Tucker, 1987, 2003; Prenner, 2004a; Ronse De Craene, 2010). In other mimosoid taxa with only four sepals, a shift in orientation has occurred and a petal is pointing towards the main axis (e.g. *Mimosa pudica*, Eichler, 1878). Flower subtending bracts are found infrequently and flower preceding bracteoles are entirely missing (see Prenner, 2004c for a discussion of the occurrence of bracteoles in Leguminosae).

It is interesting to note that within a single inflorescence, organ formation starts sequentially and sepals are therefore at different developmental stages within one



**Fig 11.9** Floral diagram and floral formula. Bract and sepals in black, petals in dark grey, stamens in bright grey. Only a reduced number of stamens is shown and four carpels are shown representing the multicarpellate gynoecium which consists of 3–7 carpels. The format of the floral formula follows Prenner et al. (2010).

inflorescence (see Fig 11.2E-F). This contrasts with other Mimosoideae, where within one inflorescence organ formation commences simultaneously (i.e. the floral primordia stay organ free until the last primordium is formed and only then does organ formation start in all meristems simultaneously) (Tucker, 1992; Prenner, 2004a). In Papilionoideae and Caesalpinioideae, organ formation always starts immediately after the floral primordia are formed and therefore different ontogenetic stages can be found within a single inflorescence (c.f. Prenner, 2004d; Prenner and Klitgaard, 2008).

#### 11.4.2 Calyx

While sepal orientation follows the common mimosoid pattern (see discussion above), sepal initiation in the form of a ring meristem is a rarely documented phenomenon for the subfamily. It was only reported from the genus *Mimosa* (Gemmeke, 1982; Ramírez-Domenech and Tucker, 1989, 1990) and this is the first report for *Acacia* s.l. All other acacias studied so far show sepal initiation in a rapid sequence, in a spiral, bidirectional and reversed unidirectional sequence from the adaxial towards the abaxial side of the flower (Gemmeke, 1982; Ramírez-Domenech and Tucker, 1990; Derstine and Tucker, 1991; Gómez-Acevedo et al., 2007). Putting these data together, it is clear that sepal initiation is variable within *Acacia* s.l. However, only a small fraction of species have been studied and broader conclusions can only be made on the basis of more studied taxa. Analogous to Mimosoideae, calyx initiation in Papilionoideae is also more variable than previously thought (Prenner, 2004c).

#### 11.4.3 Corolla

The simultaneous petal formation found in *A. celastrifolia* is among the most stable characters in mimosoid floral development (Gemmeke, 1982; Ramírez-Domenech and Tucker, 1990; Prenner, 2004a; Gómez-Acevedo et al., 2007). Besides simultaneous initiation, Prenner and Klitgaard (2008) highlighted that rapid petal enlargement and early closure of the corolla is a common character in Mimosoideae. As shown here for *A. celastrifolia*, the valvate corolla takes over the protection of the sexual organs in early floral development. While in Papilionoideae petal growth is always distinctly retarded, both early and late petal enlargement can be found in Caesalpinioideae (see Prenner and Klitgaard, 2008). The petals of *A. celastrifolia* and in many other mimosoid legumes are reduced in size and therefore play a minor role in pollination biology. Nevertheless, they perform an important protective function during early floral ontogeny. In Mimosoideae, the showy function of the petals is frequently transferred to the androecium, which consists of many coloured stamens (see next section). The presence of stomata on both the inside and outside of the petals is a rare character and was found only once in *A. berlandieri*. Gómez-Acevedo et al. (2007) speculated that in *A. berlandieri* this

is nectariferous tissue which is involved in pollination biology. No such observation was made for *A. celastrifolia*.

#### 11.4.4 Androecium

*Acacia celastrifolia* is remarkable because of its extreme polyandry, with more than 500 stamens in a single flower. In an ontogenetic context the androecium of *A. celastrifolia* (and that of many other polyandrous Mimosoideae) can be seen as a stamen fascicle in which the ring meristem acts as the primary meristem, which gives rise to secondary stamen primordia (for a review of stamen fascicles see Prenner et al., 2008). This type of secondary polyandry differs from the primary polyandry of early-divergent angiosperms where stamens arise directly from primary stamen primordia (which are frequently formed in a spiral or whorled pattern). Similar to the conditions in *A. baileyana* (studied by Derstine and Tucker, 1991), stamen formation in *A. celastrifolia* starts in an antesepalous position and proliferates in a lateral direction. However *A. baileyana* shows only moderate polyandry (30–40 stamens per flower) and does not form a pronounced ring-wall, as found in *A. celastrifolia*.

Anther morphology of *A. celastrifolia* is similar to that of *Calliandra* and shows four divided locules of which each harbours a single polyad (Prenner and Teppner, 2005; Teppner and Stabentheiner, 2007). The finding of orbicules on the inner surface of the locules is another proof of this character in Mimosoideae (c.f. Huisman et al., 1998).

#### 11.4.5 Pollen and pollination

Another interesting and rather uncommon feature of *A. celastrifolia* is its eight-grained polyads. This is only half the grain number commonly found in *Acacia* s.l. (see Kenrick and Knox, 1982). Other acacias with eight grains per polyad are *A. hispidula*, *A. lineata*, *A. paradoxa* and *A. rupicola* (see Kenrick and Knox, 1982) and there is only one report of four grains per polyad in *A. baueri*. Kenrick and Knox (1982) showed that grain number per polyad is correlated with seed number per pod. Species with eight grains per polyad show two to ten ovules per pod and never more than eight seeds per mature fruit. This fits with the present observations of *A. celastrifolia*, which never showed more than eight ovules per carpel or seeds per fruit (present study; Prenner, G., pers. obs.). This balance of grain number and ovule number also makes sense considering the fact that the stigmatic surface of *A. celastrifolia* can only provide space for a single polyad.

A similar pattern of eight-grained polyads and a maximum of eight ovules per carpel were found in *Calliandra* (Prenner, 2004a; Prenner and Teppner, 2005; Teppner and Stabentheiner, 2007; Santos, 2008). However, in this genus, the correlation of the size of the stigma and the polyad is lost and the massive stigma can hold several polyads, though the number of ovules (i.e. eight) is still correlated

with the eight pollen grains per polyad. It seems possible that stigma size is here enlarged because of the special mode of pollination found in *Calliandra* (bird, bat and moth pollination are reported for the genus).

Guinet et al. (1980) discussed the rather unexpected similarities of the eight-celled polyads of *A. celastrifolia* and *A. newbeyi*, of which the latter is otherwise not closely related to the series Pulchellae. Regarding the morphology of the polyad, *A. mitchellii* also closely resembles *A. celastrifolia* (see Guinet et al., 1980 and the present study). However, this strong similarity is not reflected in recent molecular phylogenies; *A. mitchellii* is found in the Botrycephalae subclade, which is not closely related to the Pulchelloidea subclade to which *A. celastrifolia* belongs (Miller et al., 2003, Murphy et al., 2010).

Stone et al. (2003) thoroughly reviewed the pollination ecology of *Acacia* s.l. They highlighted that all members of subgenus Phyllodineae offer only pollen as a floral reward and that the most important pollinators are bees. In specific cases, other insects and nectar-feeding birds are mentioned as important pollinators. The authors also highlight the need of more taxa to be studied prior to more general assumptions and conclusions on the pollination biology in *Acacia*.

Sargent (1909, 1918) mentioned that *Acacia celastrifolia* is pollinated by 'Silver-eyes' (*Zosterops gouldi*; Passeriformes, Zosteropidae) and other honeyeaters. The birds visit the extrafloral nectaries at the base of the phyllodes and thereby come into contact with the flowers. In this case, these extrafloral nectaries can be seen as nuptial (i.e. they are involved in pollination). Knox et al. (1985) and Vanstone and Paton (1988) showed a similar condition for bird pollination of *A. terminalis* and *A. pycnantha*. Bird pollination is not exclusive and the inflorescences are also visited by insects; Bernhardt (1987) showed a broad range of bees and wasps as effective pollinators of some Australian acacias. Concerning the observation of bird-pollinated acacias, the genus appears to be a good example for a taxon where the floral morphology (nectarless, small and yellow flowers aggregated to inflorescences) does not 'fit' the actual observed syndrome of bird pollination (cf. Fenster et al., 2004).

Sargent (1909) even suggested the possibility of wind pollination in *A. celastrifolia*. However, there are no studies providing evidence for this hypothesis and the presence of pollenkitt on the surface of polyads in *Acacia* (Teppner, 2009) makes wind rather improbable as a major pollinating agent for this species.

#### 11.4.6 Gynoecium

Perhaps the most remarkable floral feature of *A. celastrifolia* is its multicarpellate gynoecium that consists of three to seven free carpels (Figs 11.5F, 11.7). Tucker (1987, p. 207) mentioned legume flowers with multiple carpels in some species of the papilionoid genus *Swartzia* (see also Cowan, 1968, 1981) and in *Archidendron* and *Affonsea* (= *Inga*) of the mimosoid tribe Ingeae (see also van Heel, 1993;

Pennington, 1997). It is intriguing that there is no report of multicarpellate species in Caesalpinioideae; this paraphyletic subfamily has the highest amount of floral diversity among Leguminosae, and Papilionoideae and Mimosoideae are nested within it (e.g. Wojciechowski et al., 2004). Within Fabales, flowers with more than one carpel are common among Polygalaceae (e.g. Prenner, 2004e; Bello et al., 2010), Quillajaceae and Surianaceae (e.g. Bello et al., 2007). Among rosids, taxa with more than five carpels in a single whorl are restricted to Myrtales, Malpighiales, Brassicales, Malvales and Sapindales (c.f. Endress and Matthews, 2006).

Van Heel (1983) studied the ontogeny of free carpels from a wide range of distantly related plants. For *Amherstia nobilis* (Caesalpinioideae) he showed abnormal gynoecia with a second smaller carpel formed in an adaxial position. One sample (his Fig 117) shows the early initiation of such an aberrant carpel situated at the proximal end of the adaxial cleft (i.e. it resembles part of the well-formed carpel rather than an entirely independent organ; see also van Heel, 1993). Besides these abnormalities, there are no well-documented instances of regularly multicarpellate flowers in Caesalpinioideae. Sattler (1973) documented one anomalous flower of the mimosoid *Albizia lophanta* with two young carpels with their sutures facing each other. While in *Albizia* this pattern must be seen as aberrant, there are other mimosoid taxa that show more than one carpel as a stable character in all flowers.

*Archidendron lucyi* is one such example of a mimosoid with five carpels that was studied in detail by van Heel (1993). In this species, carpel formation is more or less simultaneous and the five carpels are distributed more or less regularly and in most cases alternating with the petals. In contrast to *A. celastrifolia*, carpel formation in *Archidendron* starts much earlier and almost simultaneously with the formation of the first stamen primordia. The border between the androecial ring-wall and the central part of the flower on which the carpels are formed is not as sharp as in *A. celastrifolia*. It is formed only later in ontogeny when the young carpels are distinctly visible.

The discovery that in *A. celastrifolia* carpel initiation starts before the last stamens are formed, confirms Endress' (1994, p. 103) observation that early carpel initiation is a characteristic of species in which stamens are formed on a 'ring-like androecial mound'. However, early carpel formation is also frequently found in Papilionoideae with only ten stamens in two whorls (e.g. *Daviesia cordata*, Prenner, 2004d) and in Caesalpinioideae (c.f. Prenner and Klitgaard, 2008).

It is intriguing that early developmental stages in *A. celastrifolia* closely resemble the distantly related *Nelumbo* (Nelumbonaceae) (Hayes et al., 2000). In particular, the clear-cut border between androecial ring-wall and central floral meristem on which the carpels will be formed is striking. In contrast, in polyandrous and multicarpellate Ranunculaceae carpel initiation commences more or less gradually



after the stamens are formed and there is no clear-cut boundary between the zone of stamen formation and that of carpel initiation (e.g. Ren et al., 2009, 2010).

Orientation of the carpels with the cleft pointing towards the centre of the flower is similar in *Archidendron* and *A. celastrifolia*. Furthermore, in both species the central part of the flower remains organ free. Most other legumes show in this position (i.e. terminating the flower) a single carpel which is in most cases oriented with the carpellary cleft pointing towards the flower's main axis (cf. Tucker, 1987, 2003; Prenner, 2004a). However, there are exceptions, as in *A. baileyana*, where in some flowers the carpel cleft is tilted out of the median plane (Derstine and Tucker, 1991). In *A. berlandieri*, Gómez-Acevedo et al. (2007) found the position of the cleft highly variable, and in the caesalpinoid *Gleditsia* the carpel is even inverted in the flowers of some inflorescences (i.e. the cleft lies at the abaxial side of the flower) (Tucker, 1991). In papilionoid flowers there are two patterns of cleft orientation (normal and oblique) which are linked to androecial symmetry (Prenner, 2004b). In species with an asymmetric androecium (i.e. the adaxial stamen of the inner whorl is formed off the median plane) the cleft is frequently turned either to the left or to the right of the median axis. In species with a symmetric androecium (i.e. the adaxial inner stamen lies exactly in the median plane) the carpel cleft always points in exactly the adaxial direction towards the main axis.

Another interesting feature of the mature carpels in *A. celastrifolia* is the abundance of stomata on the surface. Since no secretory products were found within the flowers it seems more plausible that the stomata are important for photosynthesis. Galen et al. (1993) investigated the function of carpels in *Ranunculus adoneus* and found that due to carpellate assimilation the net carbon rates of flowers rise from negative during bud expansion to positive during early fruit growth. This variation of carbon rates in the course of anthesis is probably an understudied aspect of flowering. Recently, Earley et al. (2009) found that the inflorescences of *Arabidopsis thaliana* contribute more to lifetime carbon gain than its rosettes. This seems to suggest that flowering is not necessarily a costly investment for the plant (i.e. negative energy bill), but that reproductive structures and its surroundings can also significantly contribute to the plants carbon rate balance.

Sinha (1971) highlighted that in *A. nilotica* the integuments start to develop only when the seed formation starts. A similar instance is found in *A. celastrifolia* in which in young ovules only the outer integument is visible and the formation of the inner integument is delayed.

It would be interesting to compare the flower development of *A. celastrifolia* with that of its putative close relative *A. myrtifolia*. Similar to *A. celastrifolia*, this species also has a highly polyandrous androecium, but only one carpel per flower. To verify the close relationship of these two species, molecular sampling should be a goal for the near future.

#### 11.4.7 Is multicarpelly a 'primitive' (plesiomorphic) condition in Leguminosae?

Arber and Parkin (1907) argued that apocarpous and superior carpels represent the primitive gynoecial conditions in angiosperms. This hypothesis was supported by Endress and Doyle (2009) who reconstructed more than one carpel as ancestral and showed that a reduction to one carpel per flower has occurred several times independently.

Within Fabales, the families Polygalaceae, Quillajaceae and Surianaceae are multicarpellate. Thus, the question arises whether among legumes multicarpelly represents the 'primitive' condition from which unicarpellate flowers evolved. So far, there is no evidence for this assumption. Multicarpellate taxa are not closely related and multicarpelly apparently arose several times independently in the legume radiation. Considering the occurrence of multicarpellate taxa in related families, this character could also be interpreted as atavism (i.e. reversion to a previous evolutionary state). More obvious than a phylogenetic signal is the fact that multicarpelly seems correlated with a higher degree of polyandry. In legumes, multicarpellate flowers could therefore be a secondary phenomenon resulting from an enlarged floral meristem. The blueprint for multicarpelly can be found in the related families of Fabales. Possibly due to the extended size of the meristem there is more space available for more than one carpel (see also Endress, 1994). The study of more multicarpellate legume taxa will help to better understand this phenomenon in Leguminosae.

Another independent theory for multicarpelly in Leguminosae is that multicarpellate flowers are the result of fasciation and are in fact 'hidden inflorescences'. Extreme polyandry and moderate multicarpelly of *A. celastrifolia* can be linked with reduced flower number per head. The floral heads of most other acacias are many-flowered and the individual flowers frequently show moderate polyandry and only a single terminal carpel. In *A. retinodes*, flower heads each consist of 18–50 flowers and each flower possesses up to 50 stamens, giving a total of 1500 (30 × 50) stamens per head (in a 30-flowered head). Because of its extreme polyandry with more than 500 stamens, the (1–)2–3-flowered heads of *A. celastrifolia* show potentially the same number of 1500 (3 × 500) stamens, indicating that reduction in flower number is matched by increase in stamen number per flower. Albertsen et al. (1983) reported and analysed fasciation in soybeans (*Glycine max*). They described the fasciation of inflorescences and mentioned that flowers with multiple carpels were common. Recently Sinjushin and Gostimskii (2008) investigated the genetic control of fasciation in pea (*Pisum sativum*).

Instances of pseudanthial 'flowers' are scattered throughout angiosperms. Rozefelds and Drinnan (1998) interpreted the polyandrous flowers of *Lophozonia* (Nothofagaceae) as pseudanthia. Sokoloff et al. (2007) showed that 'flowers'

of *Tupidanthus calyptratus* (Araliaceae) are probably the result of fasciation. Strong tendencies to fasciation are also found in the reproductive units of the early branching angiosperm *Trithuria* (Hydatellaceae) (Rudall et al., 2009). These examples demonstrate that fasciation could be widespread and that there may be more 'flowers' that in fact are of a pseudanthial nature.

## 11.5 Conclusions

Together with earlier ontogenetic studies, the present study shows that even though flowers of *Acacia* s.l. are superficially uniform they show a wide range of different ontogenetic patterns. Sepal initiation is the most flexible pattern, not only in *Acacia*, but in Mimosoideae in general (e.g. Gemmeke, 1982; Ramírez-Domenech and Tucker, 1990; Prenner, 2004a; Gómez-Acevedo et al., 2007). This is similar to Papilionoideae, in which Prenner (2004c) showed a wide range of ontogenetic patterns of sepal initiation. The reason for this variability might be that sepals are not crucial for the function of these flowers during anthesis and therefore sepal initiation and sepal aestivation are of minor importance and more flexible. In contrast to the sepals, petal formation in *Acacia* and other Mimosoideae appears to be uniformly simultaneous. The reason for this could be that simultaneous organ formation is a prerequisite for the valvate petal aestivation frequently found in Mimosoideae. Regarding the androecium, secondary polyandry with primary primordia giving rise to secondary stamen primordia is a common pattern in *Acacia*. So far, a range of developmental types from 'sectorial initiation' (in *A. baileyana*, Derstine and Tucker, 1991) to ring primordia (e.g. present study; Gemmeke, 1982; Gómez-Acevedo et al., 2007) have been reported in *Acacia* s.l. The gynoecium in Leguminosae is typically very conservative and formed of a single terminal carpel, but some species of Mimosoideae–Ingeae and Papilionoideae–Swartzieae show deviations towards multicarpelly. It is possible that this character evolved secondarily and apparently linked with polyandry. However, the possibility that the correlated features of high polyandry and moderate multicarpelly are the result of fasciation should be considered in future studies.

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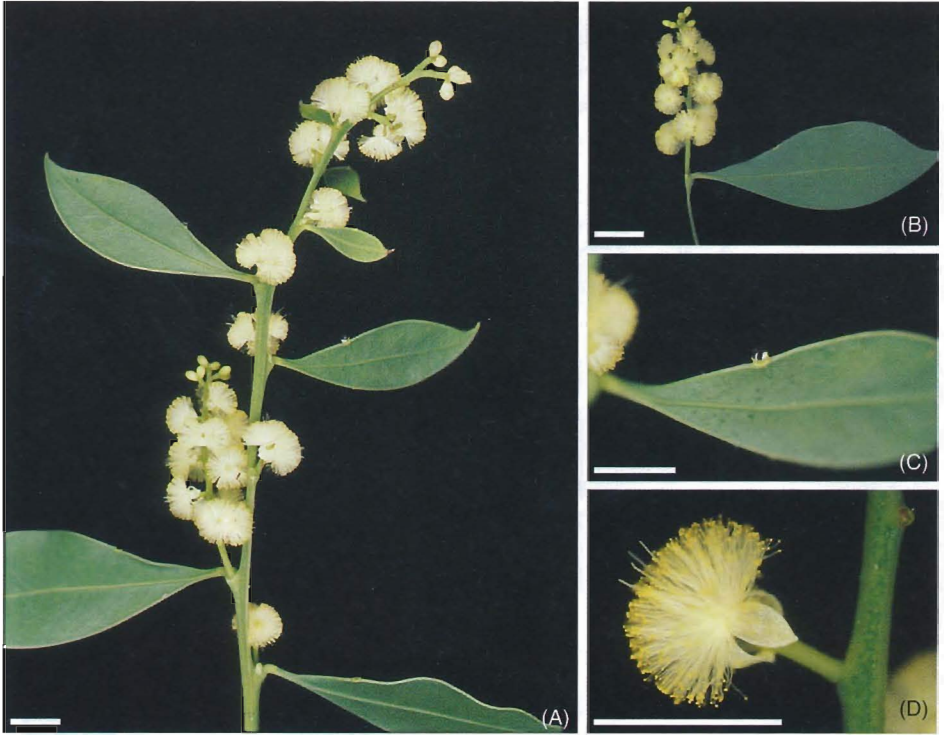
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**Fig 11.1** *Acacia celastrifolia*. (A) Flowering branch. (B) Inflorescence with phyllode at its base. (C) Detail of phyllode with nectary and drop of nectar. (D) Flower with recurved petals, highly polyandrous androecium and four styles which are protruding above the level of the anthers. Scale bar = 1 cm in all.