Floral Morphogenesis in *Euptelea* (Eupteleaceae, Ranunculales)

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• *Background and Aims* Based on molecular phylogenetic studies, the unigeneric family Eupteleaceae has a prominent phylogenetic position at or near the base of Ranunculales, which, in turn, appear at the base of eudicots. The aim of the present paper is to reveal developmental features of the flowers and to put the genus in a morphological context with other basal eudicots.
• *Methods* Flowers in all developmental stages of *Euptelea pleiosperma* were collected in the wild at intervals of 7–10 d in the critical stages and studied with a scanning electron microscope.
• *Key Results* Remnants of a perianth are lacking throughout flower development. Floral symmetry changes from monosymmetric to asymmetric to disymmetric during development. Asymmetry is expressed in that the sequence of stamen initiation is from the centre to both lateral sides on the adaxial side of the flower but starting from one lateral side and proceeding to the other on the abaxial side. Despite the pronounced floral disymmetry, a dimerous pattern of floral organs was not found. The carpel primordia arise between the already large stamens and alternate with them. Stamens and carpels each form a somewhat irregular whorl. The carpels are ascidiate from the beginning. The stigma differentiates as two crests along the ventral slit of the ovary. The few lateral ovules alternate with each other.
• *Conclusions* Although the flowers have some unusual autapomorphies (wind pollination, lack of a perianth, pronounced disymmetry of the floral base, long connective protrusion, long temporal gap between androecium and gynoecium initiation, small space for carpel initiation), they show some plesiomorphies at the level of basal eudicots (free carpels, basifixed anthers, whorled phyllotaxis), and thus fit well in Ranunculales.

Key words: Basal eudicots, *Euptelea*, Eupteleaceae, floral development, floral phyllotaxis, floral symmetry, Ranunculales, systematics.

INTRODUCTION

Euptelea Sieb. et Zucc. is the only genus of Eupteleaceae, a family endemic to East Asia, with two species, *E. pleiosperma* Hook. f. & Thoms. in China and India, and *E. polyandra* Sieb. & Zucc. in Japan (Endress, 1993; Fu and Endress, 2001). Because of its structural features reminiscent of magnoliids and hamamelidids, earlier interpretations on its systematic position fluctuated between these two alliances but more recently concentrated on hamamelidids (Nast and Bailey, 1946; Takhtajan, 1980, 1997; Cronquist, 1981; Thorne, 1992). Pollen morphology and leaf architecture indicated a position in hamamelidids (Praglowski, 1975; Endress, 1986; Wolfe, 1989). Its simple, wind-pollinated flowers did not make the systematic interpretation of *Euptelea* easy (Endress, 1969, 1986).

Molecular systematic studies position Eupteleaceae in Ranunculales (APG, 1998, 2003). Initially Eupteleaceae appeared as the second clade in the grade of families (Chase *et al.*, 1993; Qiu *et al.*, 1993, 1999; Hoot and Crane, 1995; Soltis *et al.*, 1997, 2000; Hoot *et al.*, 1999; Magallón *et al.*, 1999; Zanis *et al.*, 2003). The same topology resulted from combined molecular and structural analyses (Doyle and Endress, 2000). Another topology is with Eupteleaceae as sister to all other Ranunculales, which appeared in some more recent molecular studies

(Hilu *et al.*, 2003; Soltis *et al.*, 2003; Kim *et al.*, 2004; Worberg *et al.*, 2007), but also in the combined molecular and structural study by Nandi *et al.* (1998). A third variant is that Eupteleaceae plus Papaveraceae appear as sister to the remaining Ranunculales (Qiu *et al.*, 2005). In all these recent studies Ranunculales are sister to all other eudicots. Thus the position of Eupteleaceae is invariably close to the base of eudicots.

Because of this prominent systematic position of Eupteleaceae and also the increasing focus of molecular developmental and evo-devo studies on flowers of Ranunculales (Kramer and Irish, 1999; Kramer *et al.*, 2003, 2006; Becker *et al.*, 2005; Di Stilio *et al.*, 2005; Lee *et al.*, 2005; Carlson *et al.*, 2006; Cui *et al.*, 2006; Howarth and Donoghue, 2006; Kölsch and Gleissberg, 2006; Kramer and Zimmer, 2006; Shan *et al.*, 2006; Zahn *et al.*, 2006) better knowledge of the floral development of Eupteleaceae becomes especially timely. Earlier studies in the family concentrated on *Euptelea polyandra*, in which floral structure and development, and embryology were studied with microtome section series (Endress, 1969). There is also a short study on the structure of the carpels by Leinfellner (1969), and Endress (1986) briefly described an early stage of floral development based on SEM studies. However, the present study is the first on the entire floral development of *Euptelea* investigated with the SEM, and also the first on the floral structure of

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Euptelea pleiosperma. As a number of other Ranunculales have been studied in the same way more recently, a fresh comparison within the order is now possible (Endress, 1989, 1995; Lehmann and Sattler, 1994; Feng *et al.*, 1995; Erbar *et al.*, 1998; Feng and Lu, 1998; Endress and Igersheim, 1999; Ren *et al.*, 2004; Chang *et al.*, 2005; Tucker and Hodges, 2005; Tian *et al.*, 2006; Gu and Ren, 2007; Song *et al.*, 2007; Zhang *et al.*, 2007).

MATERIALS AND METHODS

Floral buds of *Euptelea pleiosperma* Hook. f. & Thoms. were collected in different developmental stages from more than 20 individuals on Mt Taibai (voucher: Bai Gen-lu136, 137, and 144, alt. 1200–1500 m, SANU) from 2002 to 2004 at intervals of 7–10 d. The material was fixed in FAA, dehydrated in ethanol and iso-amyl acetate series, treated with critical-point drying in CO_2, vacuum evaporation, and observed with a Hitachi 800 SEM.

RESULTS

Floral morphology

Each of the 5–8 bisexual flowers is in the axil of a bract at the base of a leafy shoot (Fig. 1A, B). The pedicel is about 6–12 mm long. A perianth is absent. The 6–14 stamens are 0·8–1·9 cm long, free, and have filiform to slightly flattened filaments and red, narrowly oblong anthers. The anther is longer than the filament and has a prominent connective appendage 0·7–2 mm long. The 5–13 carpels are 1–3 mm long, free, stalked, and have an obliquely decurrent stigma along the ovary. The carpels have 1–4 ovules.

Inflorescence and shape of floral primordia

From base to apex the flowering shoot consists of 5–6 scales, followed by 5–8 bracts, each with a flower in the axil, and 4–6 foliage leaves. Flowers at the primordial stage are larger in the middle part of the inflorescence than basally and distally (Fig. 2A).
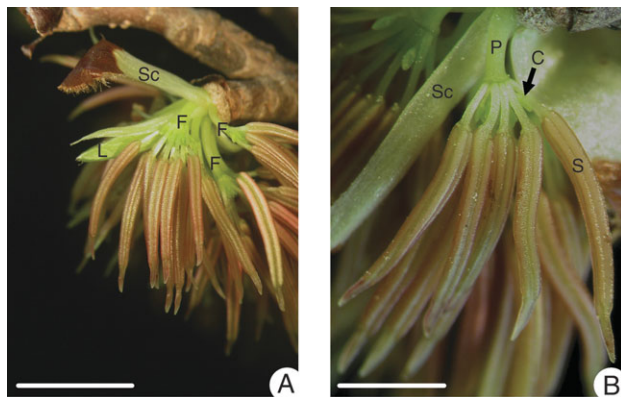

FIG. 1. Flowering of *Euptelea pleiosperma*: (A) flowering shoot; (B) flower. C, Carpel; F, flower; L, leaf; P, pedicle; S, stamen; Sc, scale). Scale bars = 0·5 mm.

The young flower is tangentially elongate and of somewhat asymmetrical shape owing to various degrees of lateral (or radial) expansion of neighbouring bracts (Fig. 2B–F).

Stamen development

Before stamen primordia become apparent, the middle part of the adaxial side of the flower becomes higher than the abaxial. Thus the floral apex becomes somewhat oblique (Fig. 2G, arrow). The first stamen primordia appear in the middle part of the adaxial side in collateral arrangement (Fig. 2H). Then additional ones arise on both sides of the first ones (Fig. 2I), and later in the middle part of the abaxial (lower) side of the flower (Fig. 2J) and finally on both sides of those. The complete set of stamens forms two rows, one on the adaxial and one on the abaxial side of the flower (Fig. 2K), joining into a flat ring (Fig. 2L). The stamens are finger-like at this stage. As they enlarge, they differentiate into a very short filament and a long anther with a connective appendage (Fig. 3A). The anther and the connective appendage become more prominent after carpel initiation (Fig. 3B, C). In later bud stage the connective appendage may attain the shape of an arrowhead (Fig. 3D, E). In the fully differentiated but undehisced anther, each theca has a longitudinal stomium that bifurcates at both ends so that the prospective dehiscence line is I-shaped (Fig. 3E–G). Thus anther dehiscence is valvate. The filament has become about as long as the anther.

No other organs were observed outside of the stamens in the young flowers (Fig. 2K, L).

The mentioned early retardation of flower development at the base of an inflorescence is also expressed at stamen initiation, as stamens in the second flower appear earlier than those in the basalmost flower (Fig. 3H). Later this basal retardation is even more pronounced, as stamens in the upper flowers of an inflorescence become longer than those of the lower (Fig. 3I).

Carpel development

There is little space left in the centre of the flower after initiation of all stamens. There are small triangular areas alternating with the stamens (Fig. 4A). Each of them enlarges and gives rise to a carpel (Fig. 4B). The carpels are slightly triangular in the beginning (Fig. 4C) but then become round (Fig. 4D, E). The carpels form the second ring (whorl) of floral organs (Fig. 4E, F) and are of different sizes, without a regular pattern; however, the transversal ones tend to be smaller than the more central ones (Figs 3B and 4E, F). The carpels elongate and differentiate into a narrower basal part and an ovoid upper part. At the base of the ovoid part, a longitudinal concavity appears (Fig. 5A), the incipient ovary locule and the first manifestation of the ascidiate zone. As the carpels enlarge, the concavity becomes deeper, resulting in a chair-like shape (Fig. 5B). In the upper part, the carpel becomes plicate as the flanks come together and form a ventral slit (Fig. 5C, D). The carpels are still of different sizes and their stalks
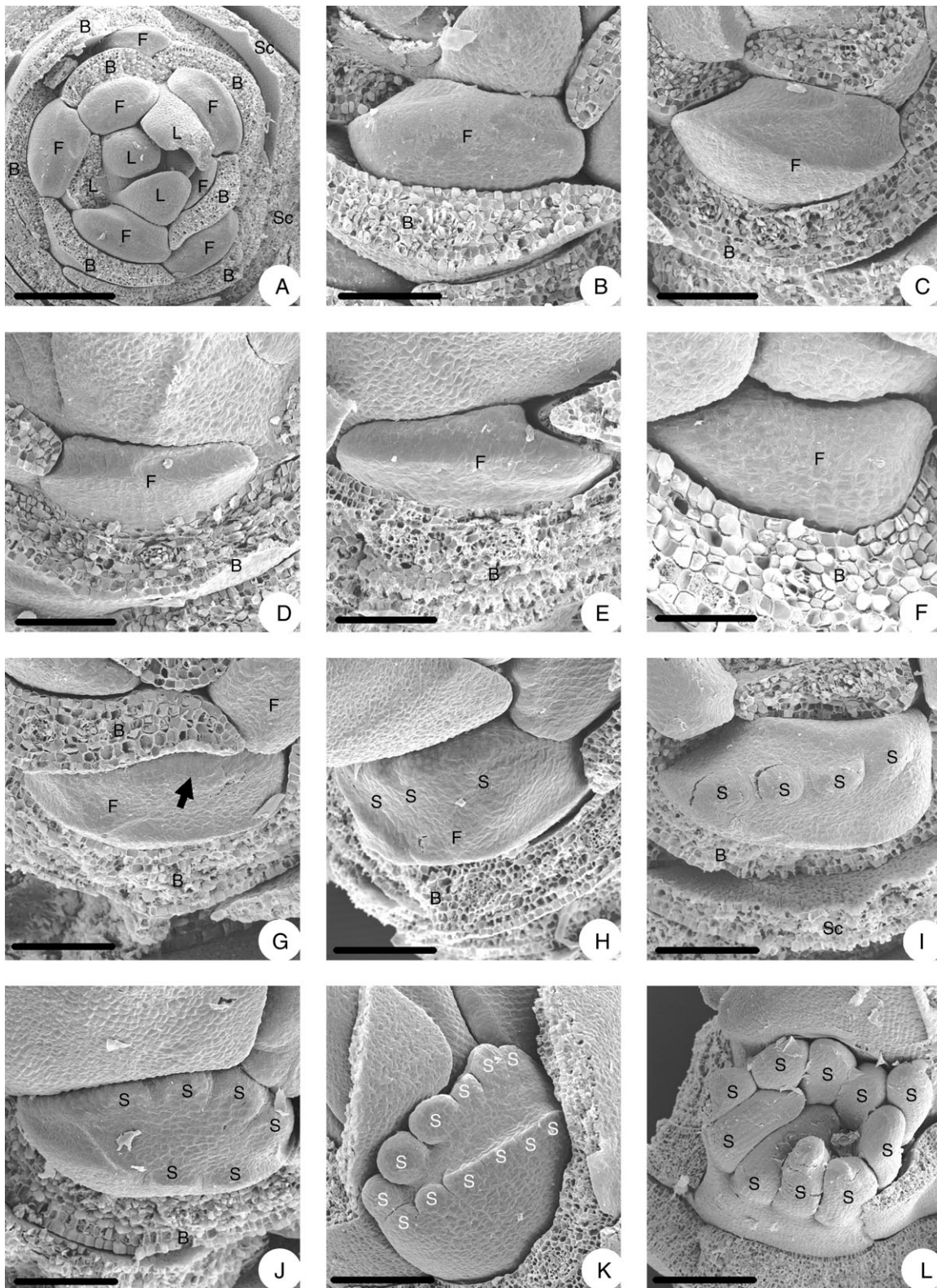
FIG. 2. Floral morphogenesis of *Euptelea pleiosperma*: (A) young inflorescence bud (scales and floral-subtending bracts removed); (B) floral primordium in the axil of a bract; (C–F) floral primordia with irregular shapes due to pressure by neighbouring bracts; (G–K) initiation of stamens (G, adaxial side of floral becoming higher, indicated by an arrow; H, first stamen primordia appear on adaxial side; I, stamen primordia more distinct; J, some stamen primordia appear on abaxial side; K, number of stamen primordia increased on both sides of flower – no other floral organ found outside the stamens); (L) stamens enlarge. B, Floral-subtending bract; F, flower; L, leaf; S, stamen; Sc, scale. Scale bars: A = 250 µm; B, C, H–J = 100 µm; D, G = 86 µm; E = 75 µm; F = 50 µm; K = 120 µm; L = 500 µm.
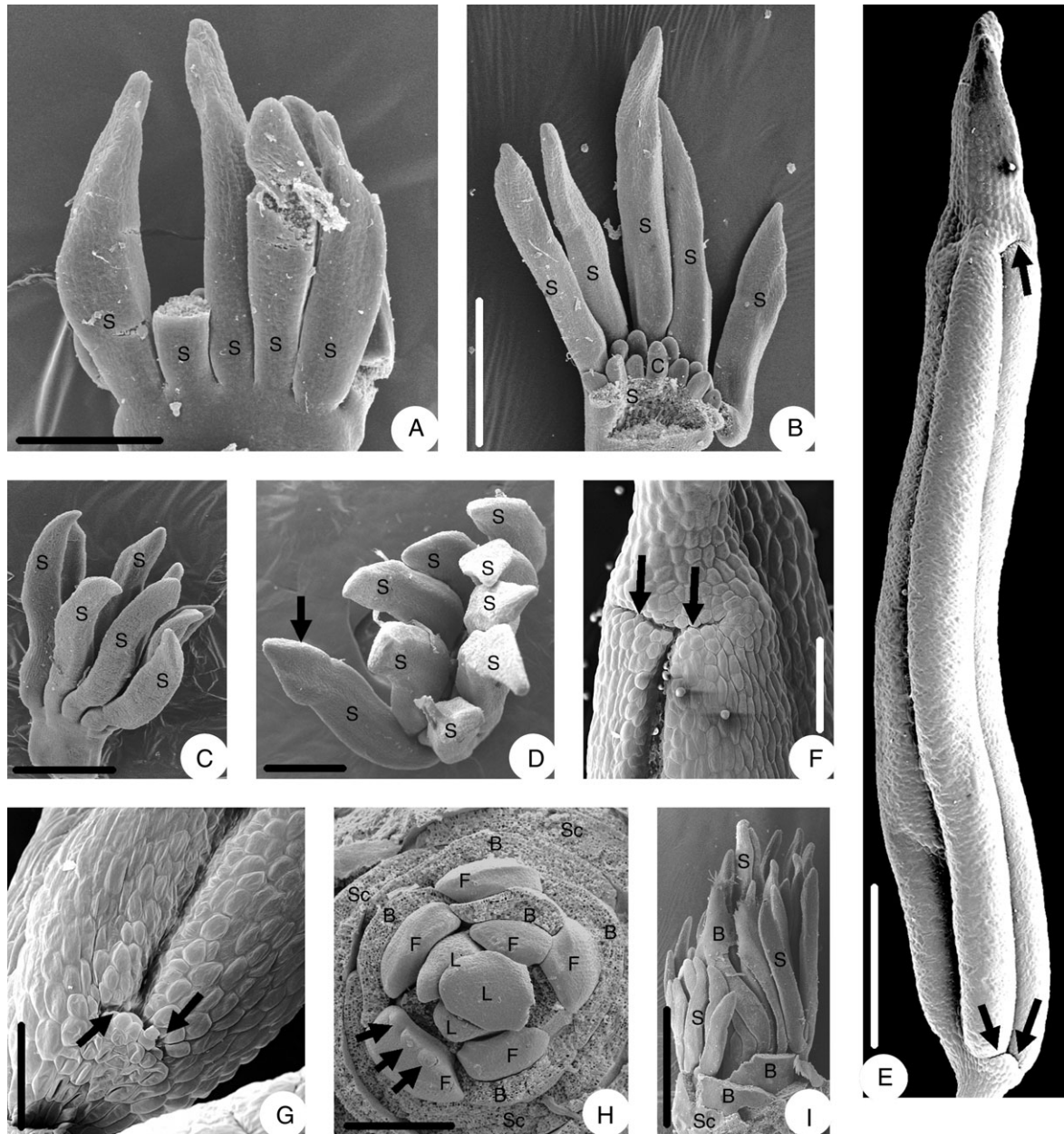
FIG. 3. Floral morphogenesis of *Euptelea pleiosperma*: (A) young stamens differentiated into anther with connective appendage, filament still very short; (B, C) stamen filaments more distinct after carpel formation; (D) young flower from above, connective appendages arrowhead-shaped; (E) mature stamen before dehiscence, showing longitudinal and horizontal extension of dehiscence lines (arrows), from side; (F) close-up of dehiscence line with horizontal extensions (arrows); (G) close-up of lower part of dehiscence line with horizontal extensions (arrows); (H) stamen primordia in the second flower from the bottom of an inflorescence appear first (arrows); (I) stamens in upper flowers are longer than those of lower flowers. B, Floral-subtending bract; C, carpel; F, flower; L, leaf; S, stamen; Sc, scale. Scale bars: A, D, H = 250 μm; B = 0·5 mm; C = 0·6 mm; E = 0·86 mm; F = 231 μm; G = 205 μm; I = 1 mm.

become obvious at this stage. With further enlargement of the carpels the ventral slit becomes more pronounced (Fig. 5E). The area flanking the ventral slit becomes more massive (Fig. 5F) and differentiates into two papillate stigmatic crests (Fig. 5G, H). In the mature carpel, the stigmatic region encompasses almost the entire length of the ovary, the carpel stalk is relatively long and slender (Fig. 5I). The two stigmatic crests have long, unicellular papillae (Fig. 5J, K). The few lateral, alternating ovules are immature at anthesis (Fig. 5L).

DISCUSSION

Floral symmetry, phyllotaxis and merism

At the time the stamens are initiated the flowers of *E. pleiosperma* appear transversely extended and somewhat irregular in shape, caused by pressure of neighbouring floral subtending bracts. This is also the case in *E. polyandra* (Endress, 1986), and an irregular floral shape occurs in general in a number of angiosperms that lack a perianth, which otherwise shapes the initial floral form (Endress, 1990).
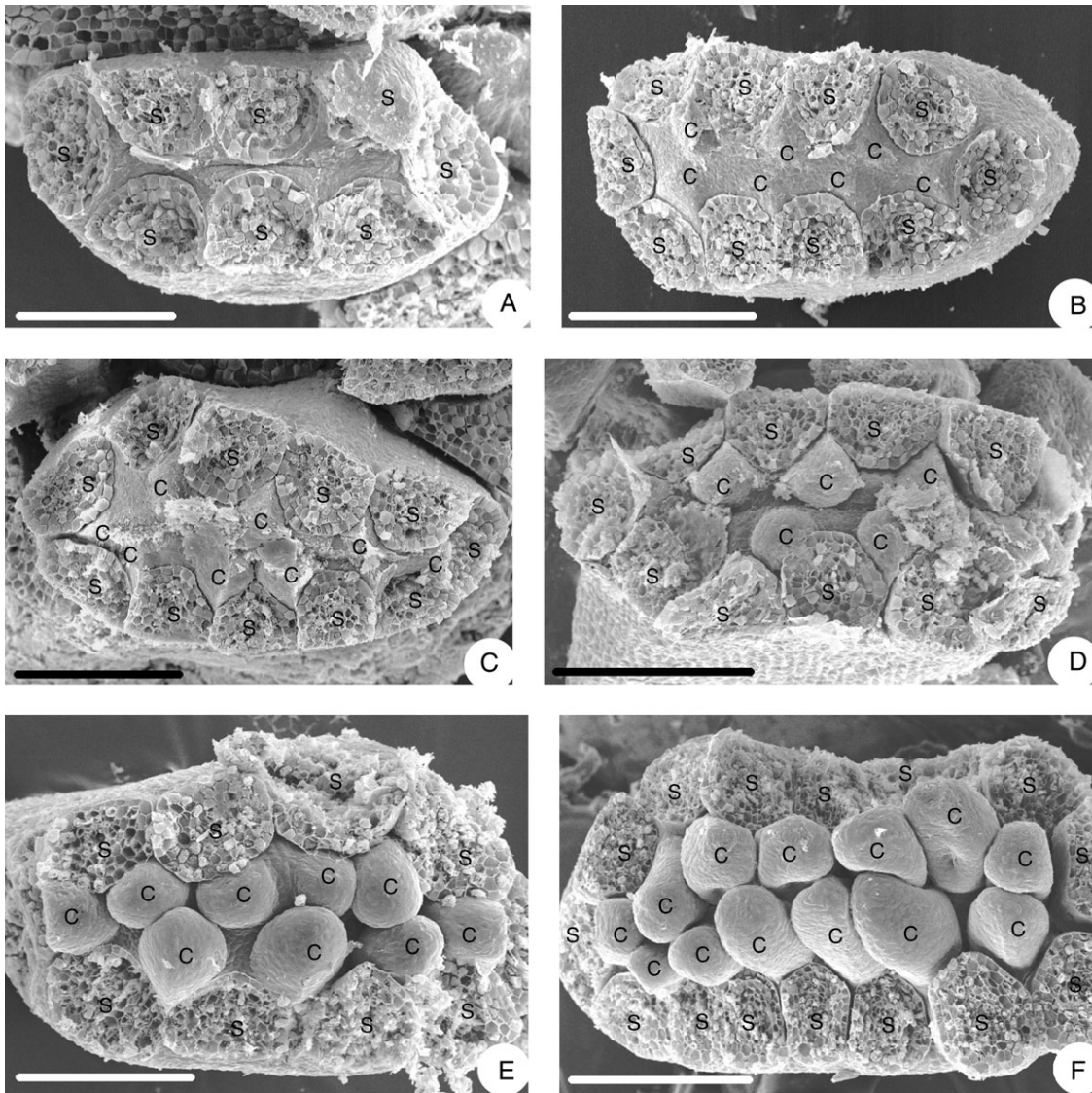
FIG. 4. Floral morphogenesis of *Euptelea pleiosperma* showing young flowers from above (stamens removed): (A) before carpel initiation; (B) carpels initiated, alternating with stamens; (C) carpel primordia enlarged, irregular in shape; (D) carpel primordia more regular in shape; (E) young carpels rounded; (F) young carpels in chair-like stage. C, Carpel; S, stamen. Scale bars: A = 100 μm; B = 136 μm; C–E = 120 μm; F = 150 μm.

The mature flowers of *E. pleiosperma* are still somewhat transversely extended, which roughly results in a disymmetric shape (for *E. polyandra*; Endress, 1986). However, in earlier stages the shape appears more monosymmetric because the adaxial side of the young flower is higher than the abaxial side (or even asymmetric because of the mentioned irregular shape). Asymmetry also occurs in the initiation sequence of the stamens, which is from the centre to both sides on the adaxial side of the flower but from one side to another on the abaxial side. The monosymmetric component of floral shape is no longer apparent in later stages. This phenomenon of transient early monosymmetry in otherwise polysymmetric flowers is not uncommon in angiosperm flowers (Endress, 2006).

The irregular size of the young carpels appears to be caused by the somewhat irregular spaces between the stamens, which tend to be larger between the central stamens than between the transverse ones (e.g. Fig. 4C).

Floral phyllotaxis appears to be irregularly whorled, with one approximate whorl of stamens and a somewhat irregularly alternating whorl of carpels. Because the flowers are transversely extended, these whorls are not circular but form narrow ellipses. There is a general trend for floral phyllotaxis to be irregular in flowers that lack a perianth. It appears that the perianth with its broad organs initiates the regular phyllotaxis of the following floral organs. In contrast, if the stamens, which are much narrower than the floral apex, are the first organs to be formed, a regular arrangement is more difficult to achieve (Endress, 1990). Another example of irregular floral phyllotaxis and lacking perianth in Ranunculales is *Achlys* (Berberidaceae) (Endress, 1989).
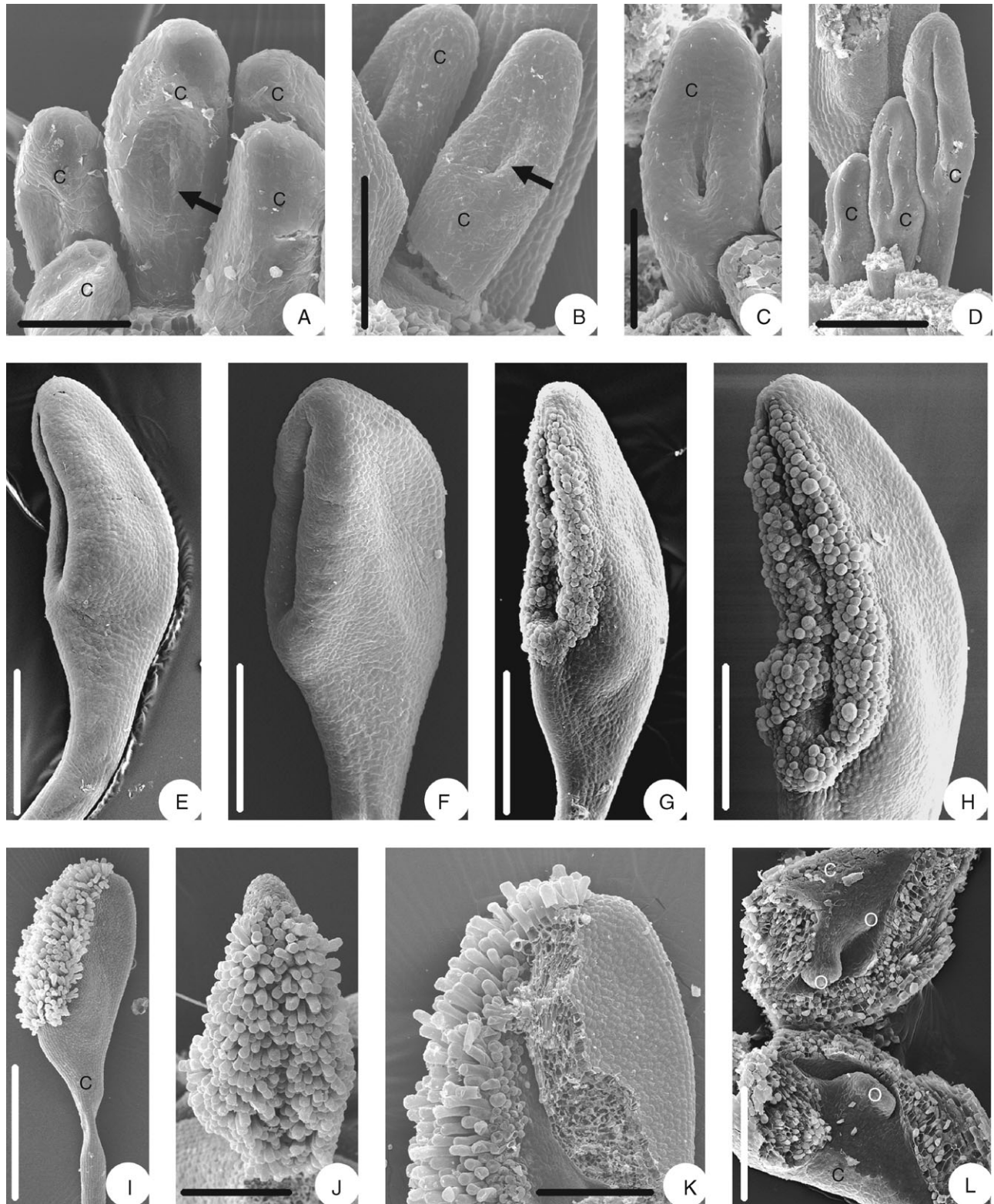
FIG. 5. Floral morphogenesis of *Euptelea pleiosperma*: (A) carpel in the centre has become concave (arrow) in the middle part; (B) carpels with concave part (arrow) deeper and extending upwards; (C) carpel flanks beginning to close; (D) carpels more or less closed and ventral slit formed, carpel stalk formed; (E) more or less closed carpel from the side; (F) carpel with stigmatic crests formed; (G) carpel with stigmatic crests becoming papillate; (H) almost mature carpel with stigmatic crests; (I) mature carpel with oblique stigma and long stalk; (J) mature stigma, from ventral; (K) upper part of carpel, with one flank removed, showing stigmatic tissue extending deep into ventral slit; (L) opened ovary, showing three young ovules. Scale bars: A, C = 60 μm; B = 100 μm; D, F, J, K = 200 μm; E, G = 270 μm; H = 231 μm; I = 0·3 mm; L = 150 μm.

The flowers are often dimerous or trimerous in basal eudicots (Drinnan *et al.*, 1994). Hoot *et al.* (1999) speculated that the floral disymmetry of *Euptelea* as described by Endress (1986) could indicate a basically dimerous groundplan. Although this is a possible scenario, floral development does not show any traits of dimery.

Comparison with other Ranunculales

In view of the systematic position of Eupteleaceae in the basal grade of Ranunculales, either as the basal branch, or the second basal branch after Papaveraceae, or in a basal branch together with Papaveraceae, as explained in the Introduction, separate comparisons of the floral structure with Papaveraceae and with the remainder of Ranunculales (Berberidaceae, Circaeasteraceae, Lardizabalaceae, Menispermaceae and Ranunculaceae) are of interest. For convenience the clade consisting of all Ranunculales families minus Eupteleaceae and Papaveraceae is here called 'core Ranunculales'.

At the outset it should be emphasized that *Euptelea* has an unusual floral biology among Ranunculales. The flowers have a wind-pollination syndrome, including lack of perianth, elongate anthers concomitant with a long connective protrusion, and carpels with a relatively large stigma with long papillae (Endress, 1969, 1986). The flowers are difficult to compare with those of other Ranunculales, because a wind-pollination syndrome is otherwise very rare in Ranunculales. Relatively similar, wind-pollinated flowers are only known from *Macleaya* and *Bocconia* (Papaveraceae) and some *Thalictrum* species (Ranunculaceae) (see fig. 6 in Endress, 2002). However, both groups, *Macleaya*/*Bocconia* and *Thalictrum* are not related to *Euptelea*, since they are both deeply nested in their respective families. Their similarity is to be interpreted as the result of convergent evolution based on a similar bauplan.

Comparison with Papaveraceae

Flowers of Papaveraceae are different from those of Eupteleaceae in having basically dimerous flowers (Karrer, 1991). Except for some derived genera the gynoecium has two carpels, and these are always completely united. A perianth is always present in Papaveraceae, although in the wind-pollinated *Bocconia* and *Macleaya* petals have been lost. Floral phyllotaxis is whorled. Only in derived groups with an increased number of stamens may stamen phyllotaxis be slightly irregular. If disymmetry in flowers of Papaveraceae is pronounced, this is caused by the formation of two spurs (Fumarioideae) or the strong dorsal development of the two carpels, such as in *Macleaya* (Papaveroideae *s.l.*), in which the fruit has two wings, whereas in *Euptelea* the pronounced disymmetry is not related to the gynoecium. Winged fruits as in *Euptelea* are only present in *Macleaya* (but not based on single carpels). Early floral monosymmetry or asymmetry is not known from Papaveraceae (monosymmetry in Fumarioideae is not median, and thus different from the early median monosymmetry in *Euptelea*). The presence of a long temporal gap between the initiation of the androecium and gynoecium in *Euptelea* is unusual and not present in Papaveraceae (Karrer, 1991). The presence of an I-shaped stomium in the thecae and a long connective appendage as in *Euptelea* is not known from Papaveraceae.

Comparison with core Ranunculales

As the floral structure in the core Ranunculales families is more diverse, a comparison with *Euptelea* is more difficult. The flowers are dimerous and trimerous (Drinnan *et al.*, 1994), with a trend to pentamery in Ranunculaceae. Phyllotaxis of dimerous and trimerous flowers is whorled (Schöffel, 1932; Hiepko, 1965; Endress, 1995), as present in part of all families, except Circaeasteraceae. Spiral floral phyllotaxis occurs in some Ranunculaceae (Schöffel, 1932; Hiepko, 1965), some Menispermaceae (Endress, 1995) and in Circaeasteraceae (Ren *et al.*, 2004; Tian *et al.*, 2006). Dimerous flowers may be disymmetric but this symmetry is never pronounced (e.g. *Thalictrum*; Schöffel, 1932; and perhaps also the basal genera *Glaucidium* and *Hydrastis*; all three genera in Ranunculaceae; or *Epimedium*, Berberidaceae). A perianth is always present in core Ranunculales, except for the derived genus *Achlys* (Berberidaceae) (Endress, 1989), which does not appear to be wind-pollinated but has brush flowers. A conspicuous temporal gap between androecium and gynoecium initiation has not been recorded in the core Ranunculales. A long connective appendage is unusual. An I-shaped stomium and thus valvate anther opening is rare but not completely absent; it is known from some Ranunculaceae (Endress and Hufford, 1989; Weber, 1993). Valvate anther opening, but of a different type, is common in Berberidaceae (Endress and Hufford, 1989). The stipitate carpels, which turn into one-seeded, winged fruitlets in *Euptelea* have a counterpart in those of *Thalictrum* (Ranunculaceae).

Such sporadic similarities with some core Ranunculales may not signify a closer relationship, but may just be an artefact due to the greater diversity of core Ranunculales than Papaveraceae, especially as the genera in question are not phylogenetically basal in the respective families. *Euptelea* shares with core Ranunculales some plesiomorphic characteristics such as basifixed anthers and free carpels. Carpel form is diverse in Ranunculales, varying between completely plicate and completely asciidate. However, pronouncedly asciidate carpels as in *Euptelea* are relatively widespread in core Ranunculales, such as in some Ranunculaceae (van Heel, 1981, 1983, 1984; Endress and Igersheim, 1999; Chang *et al.*, 2005), in Berberidaceae (Endress, 1995; Endress and Igersheim, 1999; Brückner, 2000) and Circaeasteraceae (Ren *et al.*, 2004; Tian *et al.*, 2006). In contrast, in Papaveraceae the (completely united) carpels are plicate, and asciidate carpels are only known from the derived *Romneya* (Karrer, 1991; Endress and Igersheim, 1999; Brückner, 2000). In general, in the core Ranunculales, carpels that are one- or few-seeded and are indehiscent in fruit tend to be more pronouncedly asciidate than those that

have many seeds and open longitudinally along the ventral side.

Comparison with other basal eudicots

Euptelea shares some unusual floral features with *Tetracentron*, another, though unrelated, basal eudicot [although they were sometimes classified together in the order Trochodendrales (e.g. Endress, 1986) or Trochodendranae (Takhtajan, 1997)]: (*a*) an unusually long temporal gap between the initiation of androecium and gynoecium (Chen *et al.*, 2007; this study); (*b*) only minimal increase of the floral apex after androecium formation so that the carpel primordia are squeezed in between the already large stamens (Chen *et al.*, 2007; this study); and (*c*) an I-shaped dehiscence line and valvate opening of the thecae (Endress, 1986; Hufford and Endress, 1989; Chen *et al.*, 2007; this study). In view of the phylogenetic relationships discussed above, these shared characters are either plesiomorphies or, more probably, autapomorphies.

Summarizing, the flowers of Eupteleaceae show several plesiomorphies at the level of basal eudicots (free carpels, basifixed anthers, whorled floral phyllotaxis; Ronse De Craene *et al.*, 2003; Ronse De Craene *et al.*, 2003; Endress and Doyle, 2007) and as such fit well in Ranunculales. Their unusual traits (wind pollination, lack of a perianth, pronounced disymmetry of the floral base, long connective protrusion, long temporal gap between androecium and gynoecium initiation, small space for carpel initiation) are likely autapomorphies.

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