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Author(s): Peter K. Endress

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EARLY FLORAL DEVELOPMENT AND NATURE OF THE CALYPTA IN EUPOMATIACEAE (MAGNOLIALES)

Peter K. Endress¹

Institute of Systematic Botany, University of Zurich, Zollikerstrasse 107, 8008 Zurich, Switzerland

Early floral development in *Eupomatiella bennettii* and *Eupomatiella laurina* was studied with scanning electron microscopy and serial microtomy to focus on initiation and development of the calyptra and initiation and phyllotaxis of the floral organs. Phyllomes preceding the calyptra are distichous or spirodistichous in arrangement. In both species, the calyptra is initiated as a smooth ring meristem encircling the floral apex. There are no traces of distinct organ primordia on this ring. After initiation, the calyptra rapidly elongates into a tubular structure, and its rim closes by irregular lobation and local formation of hairs. These lobes also behave differently than young organs in their growth pattern. The closed rim ceases to enlarge and forms a minute closed pore at anthesis. A long plastochron follows initiation of the calyptra, and the floral apex widens considerably during this time. Since a perianth is lacking, stamens and staminodes are the first floral organs initiated. They appear in a regular spiral phyllotaxis according to a Fibonacci pattern, with the contact parastichy sets of 13 and 21 for *E. bennettii* and eight and 13 for *E. laurina* (with fewer floral organs). The carpels are also spirally arranged, with the contact parastichy sets of eight and 13 for *E. bennettii* and five and eight for *E. laurina*. The calyptra in Eupomatiaceae is best interpreted as a single, amplexicaul bract. This is indicated by the floral development of Eupomatiaceae and also by comparison with the closest relatives (Annonaceae, Magnoliaceae, Himantandraceae), which have calyptra-like structures that more clearly correspond to bracts. For angiosperms in general, I suggest that bracts and tepals are not terms to be used at the same level; bracts represent a less differentiated ground state of phyllomes.

Keywords: bract, calyptra, floral development, floral phyllotaxis, *Eupomatiella*, Eupomatiaceae, Magnoliales, tepal.

Introduction

Eupomatiaceae (Magnoliales) are a monogeneric family with three species of shrubs and trees in tropical to temperate rain forests of Australia and New Guinea (Endress 1993; Jessup 2002). The flowers look like little roses that are built inside out: apparent petals are surrounded by the stamens, which are the outermost organs, and this whole flower is enclosed by a unified green envelope, which falls off like a calyptra when the flower opens (fig. 1). The apparent petals have been interpreted as inner staminodes since the discovery of the first species of the family by Brown (1814). In contrast, the interpretation of the calyptra has remained controversial.

The flowers are unique in both their morphological organization and their biology (Endress 1984a). *Eupomatiella laurina* has 1-day flowers, *Eupomatiella bennettii* has 2-day flowers (Endress 1984a), and *Eupomatiella barbata* has 1-day flowers (P. K. Endress, unpublished data). The flowers are strongly protogynous; they open in the morning when the calyptra falls off. In *E. laurina*, the flowers are in the female stage in the morning and in the male stage in the evening. In *E. bennettii*, the flowers are female on the first day and male on the second day. This extreme dichogamy prevents autogamy. In *E. laurina*, all flow-

ers that are at anthesis on a given day are strikingly synchronized. This synchrony prevents geitonogamy. In addition, there is synchrony at a higher level: *E. laurina* tends to flower in pulses; in the peak flowering time of the flowering season, there are mostly one or two flowerless days after a pulse, as observed on three individuals over the entire flowering period in a year (Endress 1984a). This, combined with dichogamy and synchrony of individual flowers, is a method to keep inbreeding at a low level. *Eupomatiella* is pollinated by small weevils of the genus *Elleschodes* (Hamilton 1897; Hotchkiss 1958; Armstrong and Irvine 1990). No other pollinators have ever been observed. Conversely, the genus *Elleschodes* has never been observed anywhere other than on *Eupomatiella* flowers (Armstrong and Irvine 1990). The valvate stamens and the histologically highly differentiated staminodes are united into a massive synandrium (Endress 1984a, 1984b; Endress and Hufford 1989). It serves as shelter and food for the pollinating beetles and, after abscission from the flower while on the forest floor, also for their larvae (Armstrong and Irvine 1990). Conversely, the gynoecium forms a smooth, flat platform, which may be difficult for the beetles to attack, thus protecting the inferior ovaries (Diels 1916; Endress 1977; Iggersheim and Endress 1997). Thus, *Eupomatiella* and *Elleschodes* form a conspicuous mutualism.

The most puzzling organ in the flowers of Eupomatiaceae is the calyptra. It has been interpreted in various ways: (1) as formed by the completely united sepals and petals (Brown

¹ E-mail pendress@systbot.unizh.ch.



Fig. 1 A–C, Flower buds with intact calypters. A, *Eupomati bennettii*. B, *E. barbata*. C, *E. laurina*. D–F, Opening flowers with detached and uplifted calypters (arrows). D, *E. bennettii*. E, *E. barbata*. F, *E. laurina*. All approximately natural size.

1814; Bailey 1899; Uphof 1959; Hutchinson 1964; Hiepko 1965); (2) as formed by the completely united sepals (von Mueller 1862); and (3) as formed by a single, amplexicaul, tubular bract (Baillon 1868a, 1868b; Diels 1916; Ozenda 1949; Eames 1961; Endress 1977). These interpretations are all based on mature flowers, partly on anatomical studies. Only Baillon (1868b) studied floral development; however, his description of early flower development (without any illustrations) is not accurate, as seen from our new results. In view of a new morphological cladistic analysis of the basal angiosperms (Doyle and Endress 2000, in preparation), it seemed useful to study floral development with new techniques in order to clarify the morphological nature of the calyptra and to gain more insight into the unusual structure of the flowers of *Eupomati*.

Since the critical early stages of floral development are short and floral buds at this stage are difficult to recognize, ample material is necessary for a detailed study. It was available from cultivated specimens, from which buds were collected over a number of years for the present study.

Material and Methods

Plants of the following collections grown in the greenhouses of the Botanical Garden of the University of Zurich were used for study: *Eupomati barbata* Jessup, collected December 27, 1990, Boonjee, Atherton Tableland, Queensland, Australia (Endress 9273a); *Eupomati bennettii* F. Muell., plants raised from seeds obtained through Queensland Naturalist Club in August 1980, collected between Brisbane and Lamington National Park, Queensland, Australia (Endress 5197); *Eupomati laurina* R. Br., plants raised from seeds collected July 23, 1977,

near Coffs Harbour, New South Wales, Australia (Endress 4019).

Flowers of different stages were collected over a period of several years, beginning in 1985. They were fixed in FAA and used for scanning electron microscopy (SEM) and for serial microtomy. Material for microtomy was embedded in Kulzer's Technovit (2-hydroxyethyl methacrylate), sectioned at 6–14 μm , and stained with ruthenium red and toluidine blue; the sections were enclosed in Histomount. For SEM studies, the specimens were critical-point dried and sputter-coated with gold.

Results

Eupomati bennettii

Eupomati bennettii is a small shrub with underground starchy tubers in subtropical Queensland. The shoots commonly die back after fruiting and are replaced by new ones from the base of the main stem, which contains numerous buds (Hotchkiss 1955; Endress 1983; Carlquist 1992). Each vegetative shoot terminates with a flower. Because flowering takes place only once a year and because each individual in the natural habitat often produces only one shoot per year, only a single flower would be produced on an individual per year and thus would not yield the material necessary for a study of early flower development. Therefore, more luxuriant greenhouse-cultivated plants that produce several shoots per year were used for this study.

Phyllotaxis of the foliage leaves is distichous. In addition, a torsion of various degrees is superimposed on this pattern, which results in a more or less strongly expressed spirodistichous phyllotaxis (fig. 2A, 2B). Distichy imposes a pendulum

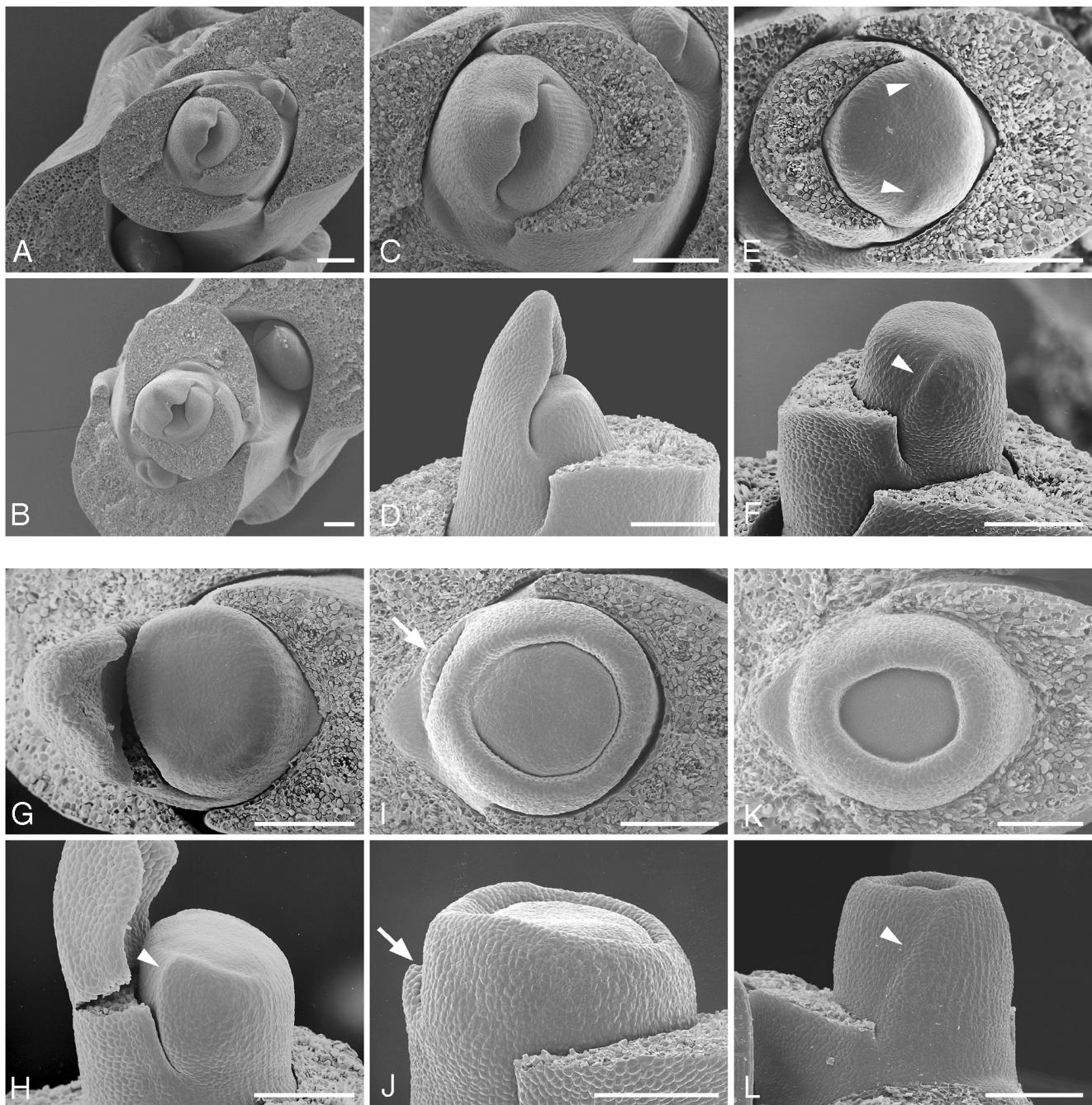


Fig. 2 SEMs of early development of calyptora and flowers of *Eupomati bennettii*. *A, B*, Two vegetative shoot apices, youngest leaves and bases of removed older leaves, before transition to floral stage, with somewhat different phyllotaxis. *A*, More or less distichous. *B*, Spirodistichous. *C, D*, Same apex as in *A*, magnified. *C*, From above. *D*, From the side. *E, F*, Apex at transition from vegetative to floral stage (arrowheads point to furrows caused by pressure of removed preceding leaf). *E*, From above. *F*, From the side. *G, H*, Apex with calyptora initiated (arrowhead points to furrow caused by pressure of partly removed preceding leaf). *G*, From above. *H*, From the side. *I, J*, Apex with ring-shaped young calyptora (preceding leaf on left side poorly developed; arrow). *I*, From above. *J*, From the side. *K–L*, Young flower, with calyptora more elongated but pore still more or less circular. *K*, From above. *L*, From the side (arrowhead points to furrow caused by removed preceding leaf). Magnification bars = 200 μ m.

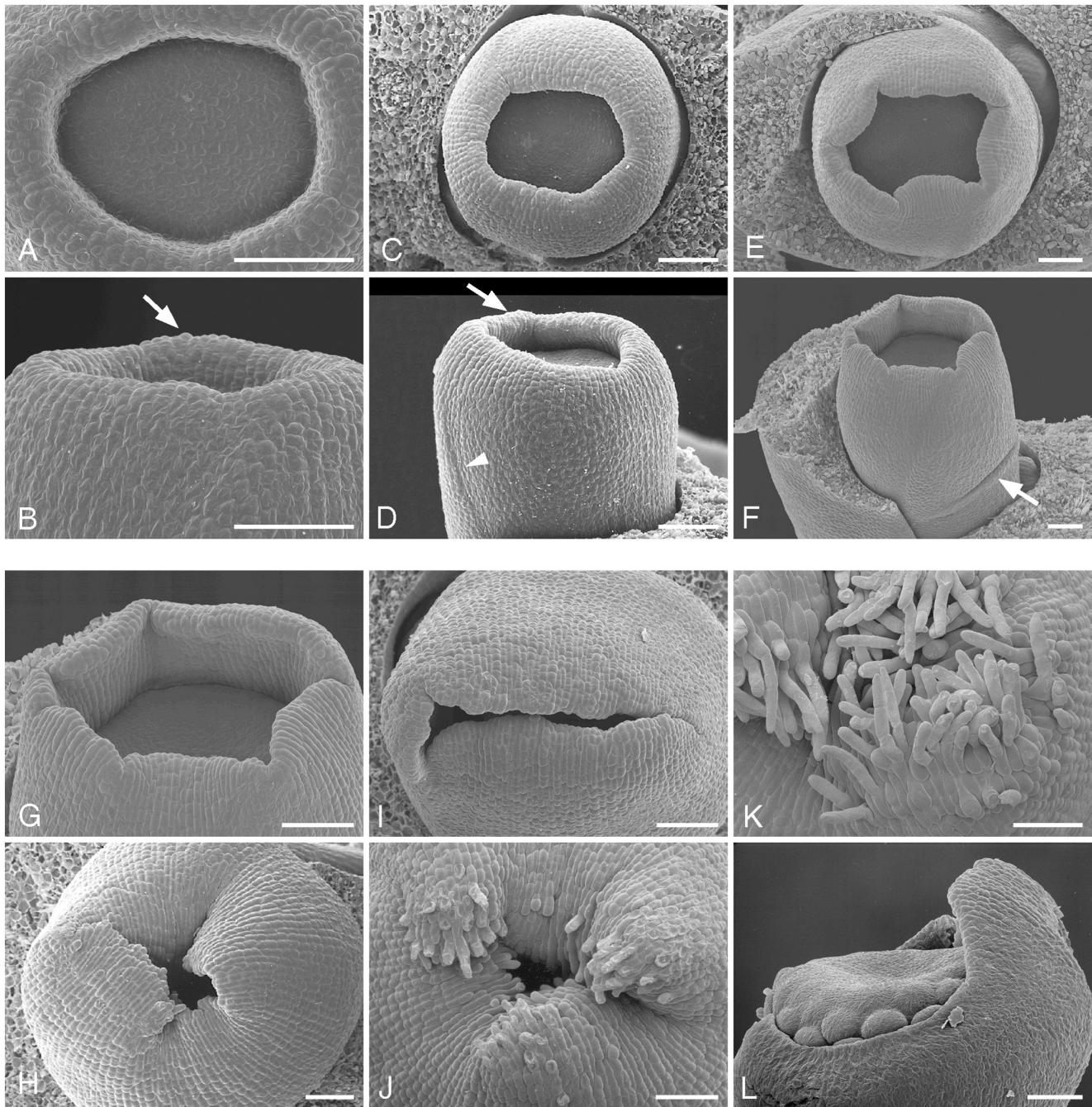


Fig. 3 SEMs of later development of calyptora and flowers of *Eupomati bennettii*. *A*, Higher magnification of fig. 2*K*. *B*, Higher magnification of fig. 2*L*, rim locally with papillate surface and locally beginning of more rapid growth (arrow). *C, D*, Rim of calyptora has become more or less five-angular. *C*, From above. *D*, From the side (arrow points to papillate area with more rapid growth beginning; arrowhead points to furrow caused by pressure of removed preceding leaf). *E, F*, Beginning of lobe formation of rim of calyptora. *E*, From above. *F*, From the side (preceding leaf on right side poorly developed; marked with arrow). *G*, Magnification of *F*; lobes with conspicuous longitudinal cell files. *H-L*, More or less closed calyptoras, showing the irregular lobe formation. *H*, With about four lobes and hair initials. *I*, With slitlike closure by two broad lobes. *J*, With five lobes and young hairs. *K*, With five lobes and partly pluricellular hairs. *L*, Abnormally formed floral bud with reduced, one-sided calyptora. Magnification bars = 100 μ m.

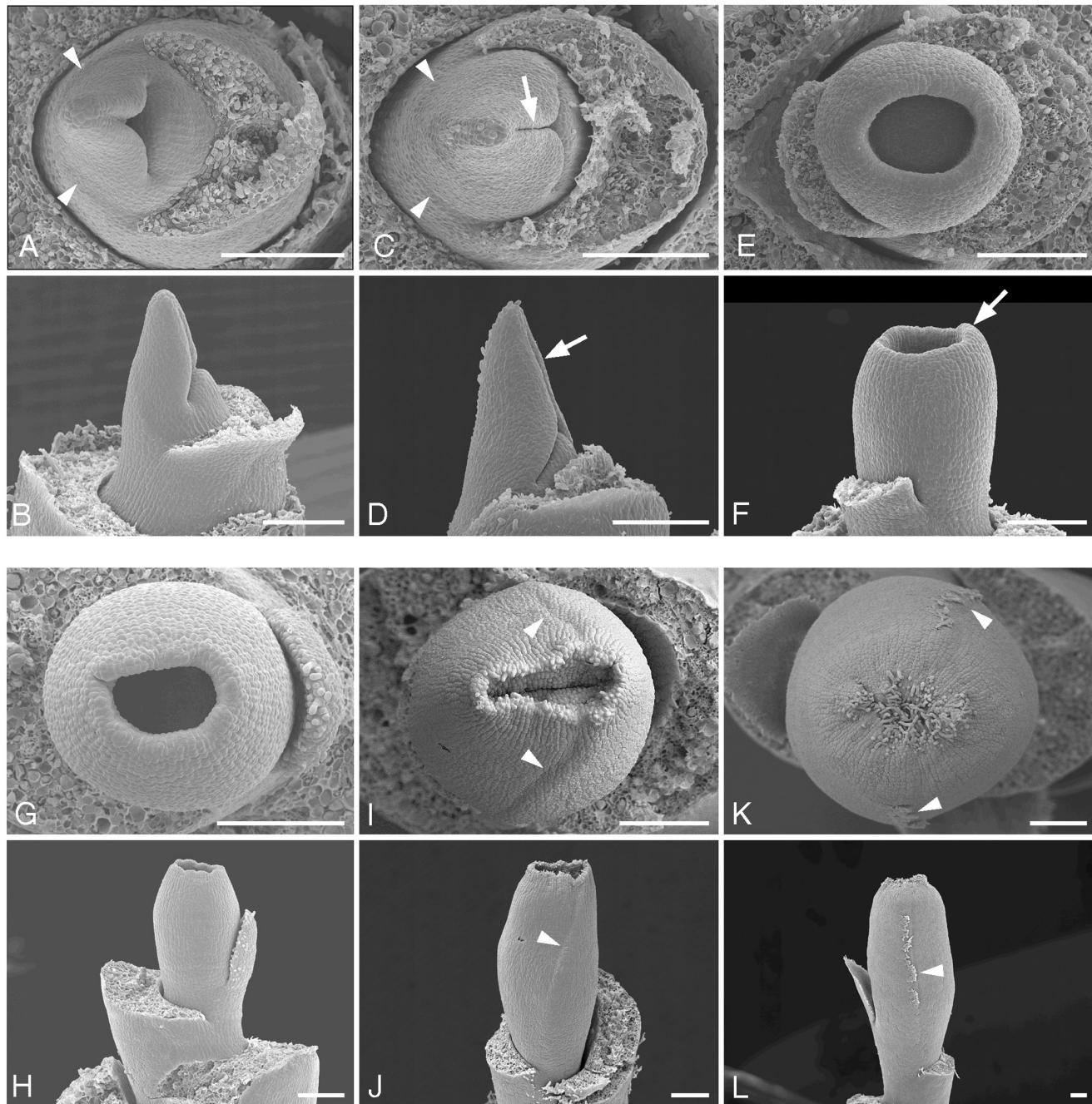


Fig. 4 SEMs of the development of calyptora and young flowers of *Eupomati laurina*. *A, B*, Vegetative shoot apex, with youngest leaf and bases of removed older leaves. *A*, From above (arrowheads point to shallow seam at base of young leaf encircling the stem). *B*, From the side. *C, D*, Vegetative shoot apex with somewhat older leaf, the margins of which are postgenitally connected (arrows). *C*, From above (arrowheads point to shallow seam at base of young leaf encircling the stem). *D*, From the side. *E, F*, Young flower with calyptora somewhat elongated but pore still more or less circular. *E*, From above. *F*, From the side (shallow tip on right side of calyptora present; arrow). *G, H*, Rim of calyptora with beginning lobe formation (preceding leaf on right side of shoot reduced). *G*, From above. *H*, From the side. *I, J*, Calyptora closed by thickening growth below the rim; beginning of hair formation at the rim (arrowheads point to furrows caused by pressure of removed preceding leaf). *I*, From above. *J*, From the side. *K, L*, Rim of calyptora closed by lobation and hair formation; preceding leaf on left side of shoot reduced (arrowheads point to furrows with hairy seams caused by pressure of removed leaf on right side). *K*, From above. *L*, From the side. Magnification bars = 200 μ m.

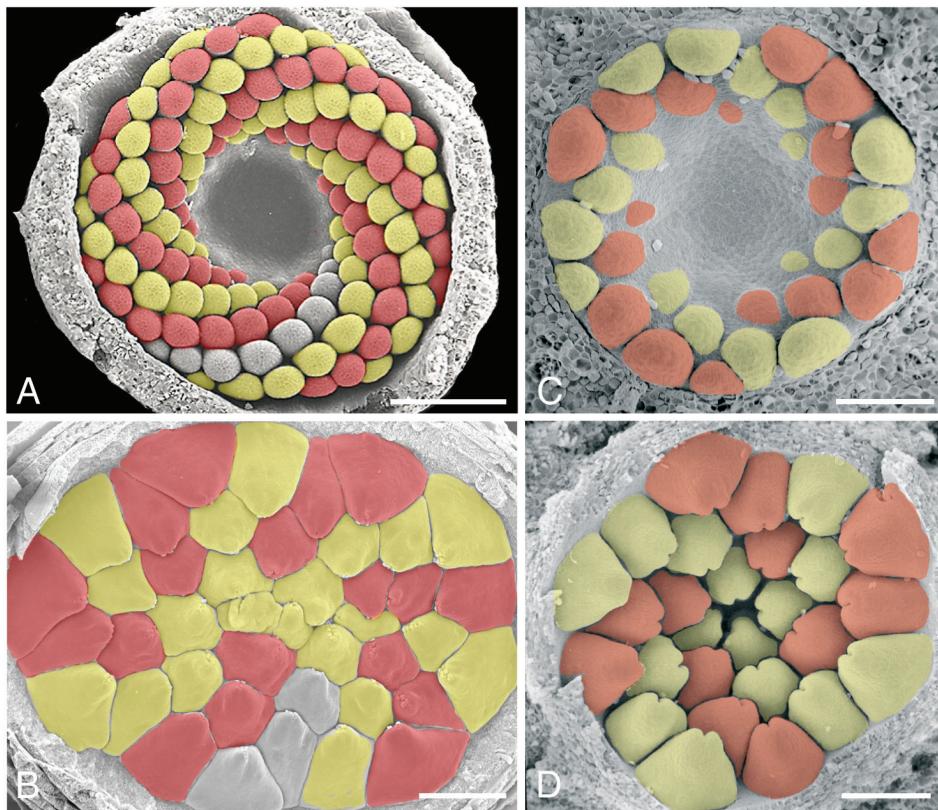


Fig. 5 SEMs of phyllotaxis of floral organs in young flowers. *A, B*, *Eupomati bennettii* (sets of 13 parastichies marked with different colors). *A*, Androecium. *B*, Gynoecium. *C, D*, *Eupomati laurina* (sets of eight parastichies marked with different colors). *C*, Androecium. *D*, Gynoecium. Magnification bars: *A* = 200 μm ; *B* = 1 mm; *C, D* = 100 mm.

symmetry on the vegetative shoot apex (fig. 2D). The vegetative shoot apex is oblique and turned away from the last initiated leaf (fig. 6A); thus, the direction of obliqueness switches back and forth each time a new leaf is produced. When the shoot apex changes from the vegetative to the floral state, it widens considerably and becomes more horizontal and radially symmetrical (fig. 2E, 2F; fig. 6B). The floral calyptra is then initiated as a smooth, homogeneous ring (fig. 2G–2J). It neither begins development on one side nor does it appear as a distinctly localized organ primordium or as several discrete primordia. Commonly, an oblique longitudinal line (furrow) runs down on two sides of the young calyptra (fig. 2H, 2L; fig. 3D). Here the surface of the calyptra is slightly deformed by pressure of the preceding leaf (phyllome) in bud. The leaves preceding the floral bud basally clasp the stem about halfway or often more (fig. 2C, 2I; fig. 8G, 8H).

A less common variant in floral bud development is that the uppermost leaf (phyllome) below the floral calyptra is highly reduced: it remains a very short scale and does not clasp more than half of the floral axis (fig. 2I, 2J; fig. 3F; fig. 6B). Thus, there is a more pronounced gap between the calyptra and this phyllome preceding the calyptra. Another structural variant, which I found in only one floral bud, was a short, one-sided calyptra, which was not closed over the floral apex and the already initiated stamens (fig. 3L).

After initiation of the calyptra, the ring meristem rapidly

elongates, grows upward like a chimney, and attains a tubular shape (fig. 2K, 2L; fig. 3A–3G). The rim of this tube prepares to close above the floral center. Before closure, the rim of the calyptra has a diameter of 250–300 μm (fig. 3A–3D). The method of closure is by irregular lobation. At first, the rim commonly becomes more or less five-angular (fig. 3C–3G). In the angles, growth of the rim is slightly delayed, and the areas of the rim between the angles develop as irregular papillate lobes by locally more active growth (fig. 3H, 3J, 3K). More rarely, I found two broad and one narrow lobe; thus, the closure appeared as a more or less straight slit (fig. 3I). These lobes make the impression of frantically growing toward each other in order to close the pore at the end of the calyptra. The lobe tips somewhat incurve over the closing center of the pore. The calyptra also thickens below the rim. At the time of apical closure, there are conspicuous oblique cell files below the inner surface of the calyptra toward the apex, which reflect the rapid thickening growth (fig. 6E, 6F). In addition to closing of the pore by these irregular lobes, unicellular and pluricellular, uniseriate hairs develop just behind the contiguous part of the mutually overlapping lobes so that the calyptra becomes crowned by a hairy tuft (fig. 3J, 3K; fig. 6H, 6I). Some hairs also border this closure zone inside the calyptra (fig. 6H). These hairs are the first parts of the calyptra to become tanniferous. The length of the calyptra is quite variable. In the basal part, the calyptra keeps widening with the enlarging flower, whereas

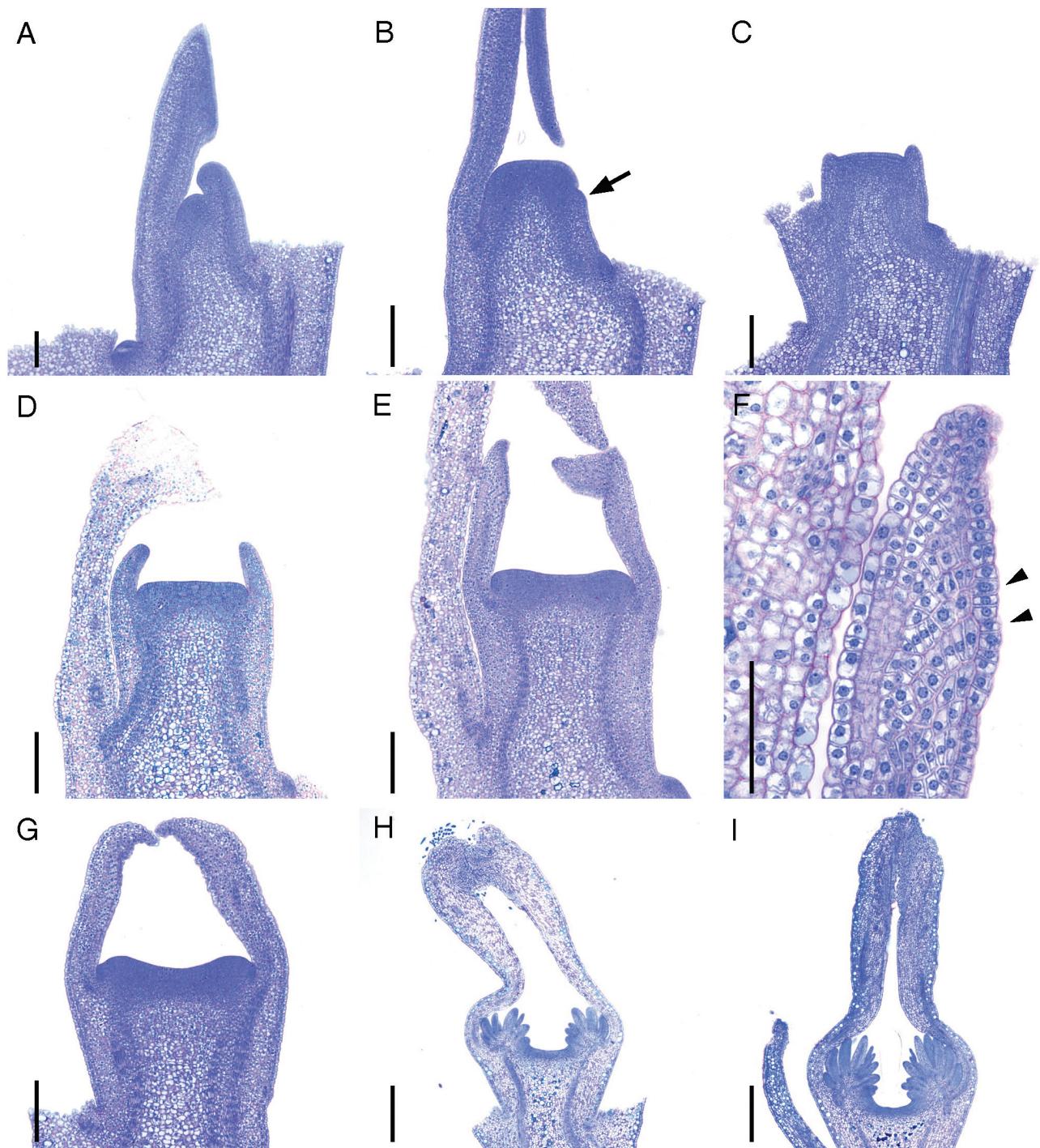


Fig. 6 Development of calyptra and young flowers, longitudinal sections, of *Eupomati bennettii*. *A*, Vegetative shoot apex before transition to floral state. *B*, Shoot apex at transition from vegetative to floral state (arrow points to poorly developed preceding leaf). *C*, Floral apex with beginning of calyptra formation. *D*, Slightly older stage. *E*, Calyptra beginning to close over the floral apex. *F*, Same but more magnified inner side of upper calyptra with oblique longitudinal cell files (arrowheads) reflecting rapid thickening process of rim of calyptra. *G*, Calyptra more or less closed. *H*, Calyptra closed and further elongated; stamen formation. *I*, Histological differentiation of calyptra far advanced; beginning of carpel formation. Magnification bars: *A–E*, $200\text{ }\mu\text{m}$; *F* = $100\text{ }\mu\text{m}$; *H*, *I* = $500\text{ }\mu\text{m}$.

in the upper part, it remains considerably more narrow, often almost terete, and the stamens do not reach into this upper part (fig. 6H, 6I). However, the walls of the calyptra are thicker toward the apex than at the base. Thickness at the base at the time of calyptra closure is about seven to eight cell layers (fig. 6G). This independence of the apical part from the basal widening process (concomitant with the widening of the floral apex) may facilitate the smooth early closure of the calyptra at its tip. The calyptra contains a large number of vascular bundles. However, as can be expected from its circular growth, there is no main vascular bundle, and the bundles do not form an obvious pattern, in contrast to the preceding leaves, which have a distinct apex and therefore a conspicuous median vascular complex (fig. 8).

After calyptra initiation, there is a long time interval (plastochron) until the primordia of the stamens become visible on the greatly widened floral apex, which is slightly concave in the center (fig. 6C–6G). The floral apex retains a two- or three-layered tunica up to carpel initiation. The stamens are initiated on the peripheral rim of the floral apex with very short plastochrons and in perfect spiral phyllotaxis. Since all organs are narrow as compared with the size of the floral apex, and even more since the outermost are smaller than the subsequent ones, it is not easy to reconstruct the ontogenetic spiral directly. However, it is easier to perceive the sets of 13 or 21 perfect contact parastichies in the androecium (fig. 5A) and the sets of eight or 13 in the gynoecium (fig. 5B), which show that there is a regular Fibonacci pattern (in 10 of 11 flowers observed). Carpel initiation begins in the progressively more concave floral center after stamen initiation is completed. At anthesis, the calyptra is relatively thin and soft; it tears somewhat irregularly around the floral base, where it is thinnest, apparently not along a preformed abscission zone, and mostly detaches completely when the floral organs spread at early anthesis (fig. 1D).

If the terminal bud at the stage of flower initiation is removed, neighboring lateral buds will be transformed into floral buds instead. Before such a lateral flower is initiated, several small distichous phyllomes are formed. The calyptra then originates in the same way as in the normal, terminal flowers.

Eupomati laurina

Eupomati laurina is a shrub or tree, which grows in rain forests from New Guinea through tropical and subtropical Eastern Australia and extends southward to temperate Victoria. In contrast to *E. bennettii*, the flowers are not initiated synchronously. Flower primordia appear over a longer time, commonly in spring or early summer, in cultivated specimens in Zurich in May or later.

In contrast to *E. bennettii*, flowers are lateral and formed in the axil of foliage leaves either singly, or more rarely, in groups of several. Each flower is commonly preceded by several small bractlike phyllomes or small foliage leaves, which are distichously arranged (and not spirodistichously as in *E. bennettii*; fig. 4A–4E). The leaf preceding the calyptra clasps the stem about halfway at its base (fig. 9E). In addition, SEM micrographs reveal that young leaves completely surround the entire stem with a shallow seam at the base (fig. 4A, 4C).

Furthermore, in contrast to *E. bennettii*, the blade completely surrounds the floral bud, and its margins are postgenitally connected (fig. 4C, 4D; fig. 9A, 9B). Therefore, buds are more difficult to dissect than those of *E. bennettii*, in which such a connection is lacking.

The development of the calyptra is similar to that in *E. bennettii*, with some slight but interesting differences in detail. In young stages, the ring tends to have a small tip on the side opposite the preceding phyllome, which may represent the reduced apex of the bract (fig. 4F). The unclosed rim of the calyptra is 150–200 μm in diameter (fig. 4E, 4F), thus slightly more narrow than in *E. bennettii*. As in *E. bennettii*, the rim begins to form irregular papillate lobes by locally more rapid growth (fig. 4G, 4H). At the time of calyptra closure, the calyptra is ca. 10 cell layers thick at the base (fig. 7A). The process of closure is somewhat different from that in *E. bennettii*. Instead of the formation of about five lobes, the pore first becomes slitlike, and both flanks of this slit close by vigorous thickening of the inner surface of the calyptra slightly below its apical rim. Hairs begin to develop at the upper rim when the inner (lower) part of the pore is completely closed. The uppermost, still unclosed part of the calyptra tip forms a shallow cup above the closed area, which becomes loosely filled with hairs (fig. 4I, 4J; fig. 7B). In contrast, such a cup is not prominent in *E. bennettii*. This cup later closes by often approximately eight small, irregular lobes. The lobes are also seamed with hairs on the outer side of the pore so that the calyptra is crowned with a tuft of hairs (fig. 4K, 4L). However, in contrast to *E. bennettii*, simple or branched hairs also sparsely develop lower down on the calyptra along lines of pressure by the margins of the preceding phyllome and also on the preceding phyllomes (fig. 4K, 4L). At the time of carpel initiation, the histological differentiation of the calyptra is far advanced, with massive groups of large stone cells toward the periphery and an inner area of tanniferous tissue (fig. 7C); scattered ethereal oil cells are being differentiated earlier (fig. 7B). The mature calyptra is shorter but more robust than in *E. bennettii* and commonly not acuminate or only with a short narrow tip (fig. 1C; fig. 7C). The difference in thickness between the lower and upper part of the calyptra is even more pronounced than in *E. bennettii*. As in *E. bennettii*, the calyptra contains a large number of vascular bundles but without an obvious pattern, in contrast to the preceding leaf, which has a distinct complex of median vascular bundles (fig. 9).

As stamens and carpels are formed, the floral center becomes even more concave than in *E. bennettii* so that the staminodes appear on a more oblique plane and then attain an almost horizontal position and therefore become densely interwoven with each other (fig. 7B, 7C). As in *E. bennettii*, they show a regular spiral Fibonacci pattern. However, since there are fewer floral organs in one series than in *E. bennettii*, the easily perceived sets of contact parastichies are those of eight and 13 in the androecium (fig. 5C) and of five and eight in the gynoecium (fig. 5D). Only in one out of 10 flowers studied for phyllotaxis was a Fibonacci pattern not present (ten contact parastichies in the androecium instead of eight). This flower had an elliptical and not circular outline, in contrast to normal flowers. At anthesis, the calyptra is relatively thick and firm; it abscises along a circular zone at the floral base and detaches completely when the stamens spread at early anthesis (fig. 1F).

Eupomati barbata

The recently described *Eupomati barbata* from tropical Queensland was observed by myself in its natural habitat in 1990 and in cultivation in the greenhouse in the Botanic Garden of the University of Zurich. Its growth form with terminal flowers and the shape of the calyptra are similar to that in *E. bennettii* (fig. 1B, 1E). The development of the calyptra was not studied.

Discussion

There are two main directions of inquiry to study the problem of the nature of the calyptra in flowers of *Eupomati*: first, by comparison with the closest relatives and the search for structures that could be similar to the calyptra in *Eupomati* (Diels 1916; Endress 1977), and second, by comparison of the development and anatomy of the organs in question in *Eupomati* with that of other organs in the same plants. A third aspect, that of the fossil record, is, at present, not rewarding for this specific problem because in *Eupomati*-like fossil flowers, the floral envelope is not well preserved (*Cronquistiflora*; Crepet and Nixon 1998).

Comparison of the Floral Envelope with That in the Closest Relatives of Eupomatiaceae

In recent phylogenetic analyses, a well-supported Eupomatiaceae-Annonaceae-clade is sister to a weakly supported clade with Magnoliaceae sister to Himantandraceae-Degeneriaceae and with Myristicaceae sister to this entire complex (combined *atp1*, *matR*, *atpB*, *rbcL*, and 18S rDNA; Qiu et al. 1999), or a Eupomatiaceae-Annonaceae-clade is sister to a clade of Degeneriaceae and Himantandraceae; Magnoliaceae are sister to these four families, and Myristicaceae are sister to these five families (combined *rbcL*, 18S rDNA, *atpB*, and morphology; Doyle and Endress 2000). In both studies, the six families together form a well-supported clade, the Magnoliales. Thus, the closest relatives of Eupomatiaceae are (1) Annonaceae, (2) Himantandraceae-Degeneriaceae-Magnoliaceae, and (3) Myristicaceae.

Among these families, Annonaceae, Magnoliaceae, and Himantandraceae have structures that are comparable to the calyptra in Eupomatiaceae. They may provide a clue to how the evolution of the calyptra in *Eupomati* can be understood because their calyptra-like structures are less modified than that in *Eupomati* (fig. 10).

In some Annonaceae, the floral bud is enclosed for some time by the preceding bract on the pedicel (fig. 11 in Endress 1977). In Magnoliaceae, the young floral bud is enclosed by a bract, which represents the lower (stipular) part of a reduced vegetative leaf. Sometimes the upper part of this leaf is still present as a rudiment, either on top of the bract or on the dorsal side of the bract (figs. 7, 9 in Endress 1977). The bract completely encircles the floral bud, and the margins are postgenitally fused. The bract is shed when the flower opens. In some flowers, two such bracts are present, one inside the other. The two bracts alternate with each other according to a distichous phyllotaxis (fig. 21b in Endress 1977).

In Himantandraceae, the flower is always enclosed by two calypratas. They are more difficult to interpret morphologically

than those of Magnoliaceae, as suggested by different interpretations in the literature. In contrast to Magnoliaceae, they are congenitally uniform sacs and not just closed by postgenital fusion. Bailey (1894) and Sprague (1915) interpreted both calypratas as single sepals. Bailey and Smith (1942) and van Royen (1962) interpreted the outer calyptara as a completely united calyx and the inner as a completely united corolla, and Bailey et al. (1943) specified, based on the floral vasculature, that the outer calyptara is composed of a pair of fused sepals and the inner composed of four fused petals. However, in one of the two species (*Galbulimima belgraveana*), it can be seen that each calyptara has two longitudinal ridges, alternating and forming a distichous pattern with the preceding smaller bracts in the same way as in Magnoliaceae with two bracts (fig. 1 in Endress 1977). Thus, it is easiest to interpret the two calypratas of *Galbulimima* as two single tubular bracts (Endress 1977), as was already proposed by Diels (1917), who compared them with the bracts in Magnoliaceae.

In Degeneriaceae, the three (to four) outermost tepals ("sepals"; Bailey and Smith 1942; Swamy 1949; Smith 1981; or are they bracts?) are only basally united (fig. 4 in Bailey and Smith 1942; P. K. Endress, personal observation), and in Myristicaceae, the only (two to) three (to five) tepals (Sauquet 2003) are strongly united. In Myristicaceae, they are clearly initiated as separate organs (Armstrong and Tucker 1986); in Degeneriaceae, their development is unknown.

For Eupomatiaceae, the interpretation of the calyptara as a single amplexicaul bract forming a saclike structure (as first suggested by Baillon 1868b) has gained even more weight after the discovery of Himantandraceae (described by von Mueller 1887; Bailey 1894), with their two completely closed calypratas, which are, thus, most similar to the calyptara in Eupomatiaceae. However, the mature calyptara in Eupomatiaceae does not have such morphological landmarks as do the calypratas in Magnoliaceae and Himantandraceae. On the contrary, it appears homogeneous in transverse section, without a rib, and without a main vascular bundle in dorsal median position (Endress 1977). But it should be noted that the leaves (phyllomes) preceding the flower clasp the axis for half of its circumference or more. Thus, even without the presence of such a large sheathing leaf base as in Magnoliaceae, only little change is needed to attain a closed calyptara, i.e., slightly more broadening and meristem fusion around the axis in the young phyllome.

Eupomatiaceae are unique in having fairly large and elaborate flowers without a perianth. The loss of a perianth may be explained evolutionarily by two preadaptations, which are also present in related families but, in those families, have not resulted in such an extreme floral construction as in Eupomatiaceae: (1) the presence of elaborate inner staminodes, which function in the attraction of pollinators (also in Degeneriaceae, Himantandraceae, and *Anaxagorea*, which is the basalmost genus of Annonaceae; cf. Endress 1984a, 1984b; Doyle et al. 2000); and (2) the presence of amplexicaul bracts, which function in the protection of floral buds (also in Himantandraceae and Magnoliaceae). Thus, both inner staminodes and bracts have taken over functions, which are otherwise exerted by tepals.

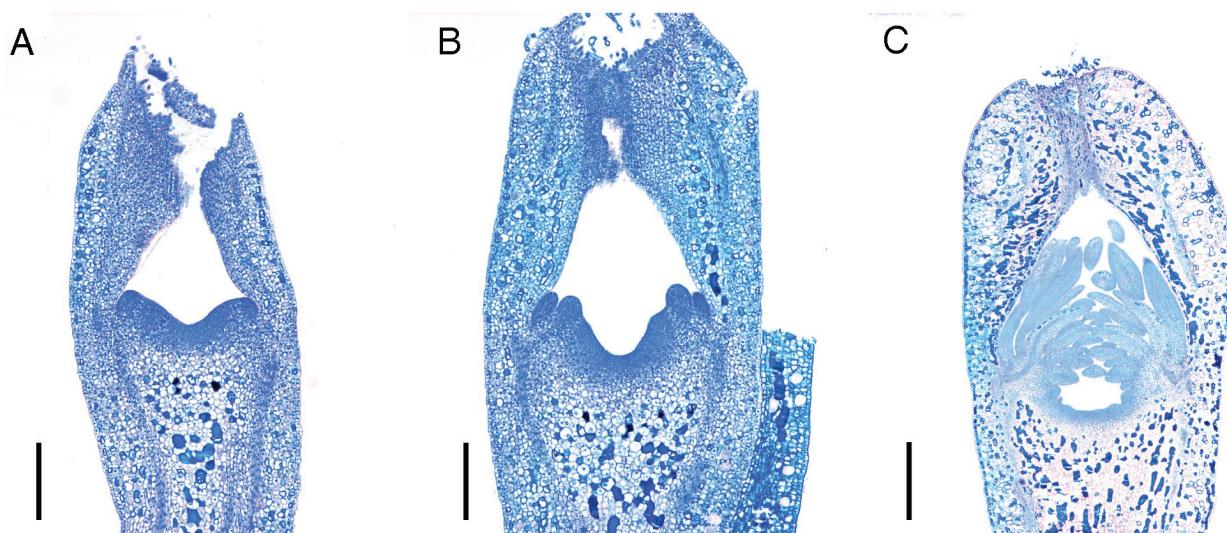


Fig. 7 Development of calyptra and young flowers, longitudinal sections, of *Eupomati laurina*. A, Flower with calyptra before closure. B, Flower with closed calyptra, stamen formation. C, Histological differentiation of calyptra far advanced; beginning of carpel formation. Magnification bars: A, B = 200 μm ; C = 400 μm .

Comparison of Calyptra Development with That of Preceding and Subsequent Organs in Eupomatiaceae

The formation of a tubular structure around a flower, starting with a smooth ring meristem around the stem, is certainly unusual and does at first sight raise the suspicion of a complex nature and not of a single organ. However, initiation and later development of the calyptra indicate the presence of only one organ. The fact that the phyllomes preceding the calyptra may clasp more than halfway around the stem and even a connection around the stem by a weak ridge at the base of these phyllomes, which probably forms some time after initiation of the organ, is visible in *Eupomati laurina*, may show the potential to form an amplexicaul organ.

The margin of the preceding leaf often produces an oblique furrow on two sides of the young calyptra by pressure. This is a secondary, superimposed form, as opposed to the primary, autonomous form (Endress 1975). If this is not taken into consideration, it may be the cause of misinterpretation of calyptra morphology in early stages because one might erroneously take the two furrows as an indication that the calyptra is composed of two parts or, because of a slight delay of development on the side where this pressure takes place, that it is initiated earlier on the other side.

A puzzling structure may be the presence of a relatively narrow and low scale preceding the calyptra in some flowers, which apparently represents a highly reduced phyllome. At first sight, this seems to make the interpretation of the calyptra as a single phyllome more difficult because, in this case, there is a larger gap between this narrow scale and the amplexicaul calyptra. However, the following developmental interpretation may explain this phenomenon. In *Eupomati bennettii*, a flower is always formed at the end of a leafy shoot. The flowers are all initiated at the same time (in early October in the cultivated specimens in Zurich). This synchrony indicates that the change of the apex from the vegetative to the floral state is

most likely induced by an external factor (probably photoperiodic). In contrast, the production of vegetative leaves is continuous before this external stimulus comes into action. It can be assumed that there is no synchrony between these two events: the initiation of a vegetative leaf and the change from the vegetative to the floral phase. If the stimulus to produce a flower comes too shortly after initiation of a leaf, this leaf primordium may no longer be able to differentiate into a foliage leaf nor be prepared to form a calyptra and thus stops differentiating, and only the next phyllome will be able to form a calyptra. In *E. laurina*, the phyllome preceding the calyptra is sometimes also reduced, but I never observed such a small scale. Only once was an abnormal flower with a one-sided calyptra seen in *E. bennettii*. Here the one-sidedness could have indicated that this calyptra was a single phyllome. An explanation for this morph could be that the stimulus to produce a flower also came early after initiation of the leaf but less so than in those flowers in which only a short scale was formed. In *E. laurina*, the rim of the calyptra tends to be highest on the side opposite of the preceding phyllome. This may also be a vague hint that the calyptra is a single organ with its tip at the highest site, or it may simply be an expression of the pendulum symmetry of the shoot. In any case, Baillon (1868b) was not correct with his statement that the bract is initiated as a croissant-shaped structure and stays open on one side for a long time, a view also expressed in his floral diagram of *E. bennettii* (Baillon 1868a, p. 251); also, the positions of the phyllomes preceding the calyptra and the phyllotaxis of the floral organs are incorrectly indicated in this diagram.

The vasculature of the calyptra is equally developed around its circumference. There is no convergence of vascular bundles to one or several major vascular traces, which would hint at a certain number of organs involved in the calyptra formation. Such equal development is to be expected for a part that grows symmetrically around a stem.

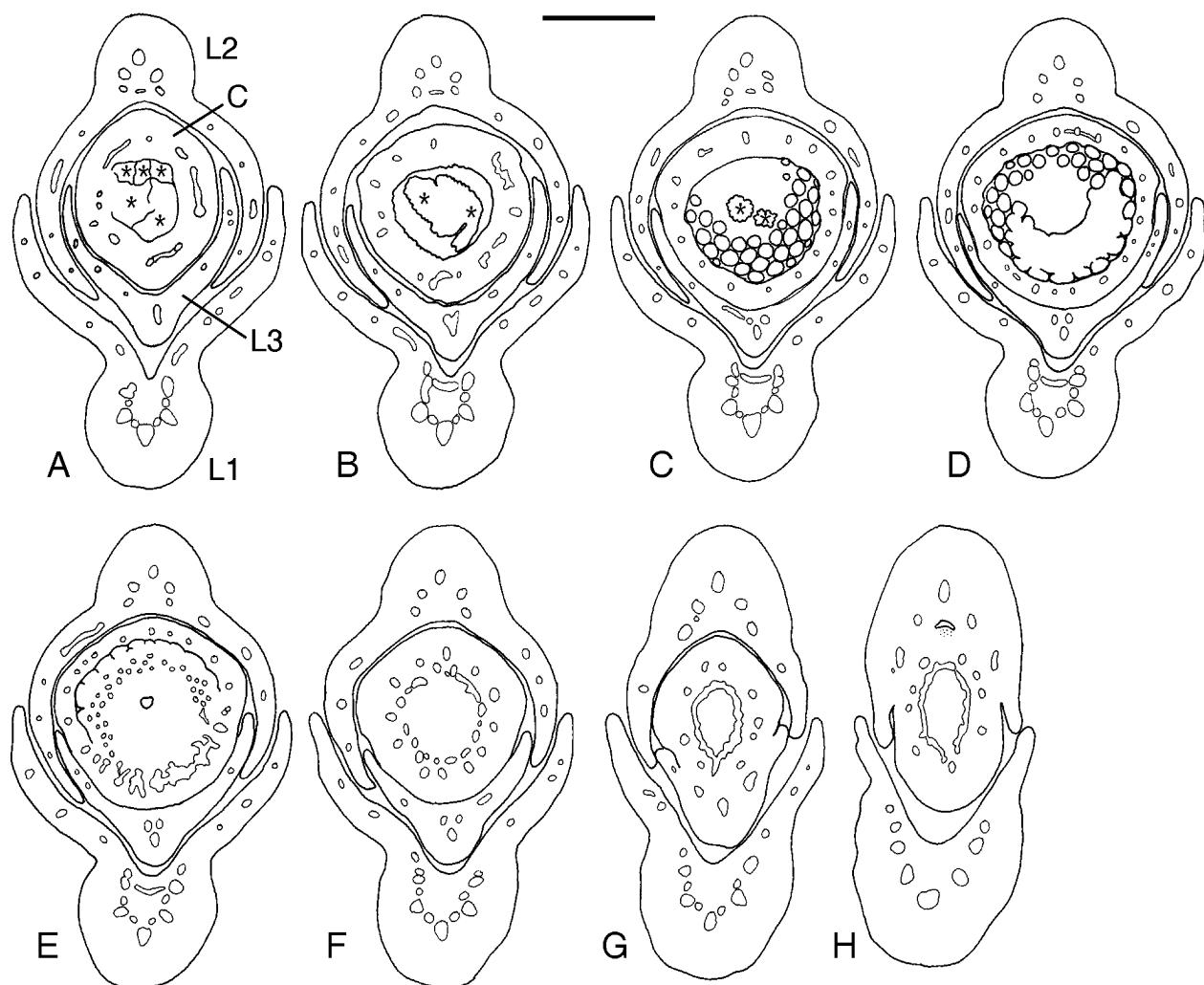


Fig. 8 Transverse section series of floral bud including calyptra (C) and three preceding leaves (L1–L3) with vascular bundles outlined of *Eupomati bennettii*. A, Upper level of calyptra closed by irregular lobes (asterisks). B, Slightly lower level. C, Upper level of androecium; in the center, the last remnants of irregular lobes (asterisks). D, Lower level of androecium. E, Lowermost level in which concavity of floral apex can be recognized by the hole in the center; attachment level of calyptra on lower side and vascular traces of calyptra joining the floral vasculature. F, Floral base below calyptra attachment. G, Attachment level of preceding leaf. H, Attachment level of second preceding leaf. Magnification bar = 0.5 mm.

In *E. bennettii* and *E. laurina*, small irregular lobes are formed, which are instrumental in closing the pore at the end of the calyptra. Are these lobes perhaps retarded organ primordia? This is unlikely because they do not originate and develop like organ primordia. These lobes behave in a strange fashion. Unlike organ primordia, which have a smooth surface, they appear as irregular bumps of locally enhanced growth with somewhat protruding epidermal cells long after calyptra initiation and when the calyptra has attained a tubular shape, and these bumps exhibit irregular, rapid marginal growth reflected by long epidermal cell files that end in the lobe margins. The irregular bumps with somewhat protruding epidermal cells are reminiscent of the bumps that fill empty spaces at the time of central closure of the gynoecium in *Dillenia* (Endress 1997). Another analogous situation in ovules is closure of the pore of an annular integument to form a tight micropyle, which

is only possible by irregular lobation or irregular thickening of the integument rim (Igersheim and Endress 1997).

As shown, the floral organs develop in a regular spiral according to the Fibonacci pattern. Thus, there is a phyllotactic gap between the vegetative region, including the calyptra, and the first floral organs. Surprisingly, there is no preformation of the floral phyllotactic pattern by other preceding organs, a situation that otherwise often leads to chaotic arrangement of floral organs (Endress 1989, 1990; Tucker 1991). Perhaps the establishment of regular spiral phyllotaxis is possible here because of the long plastochron after calyptra initiation, which allows the floral apex to attain a highly regular circular outline before stamen initiation. To have a regular spiral phyllotaxis in the androecium may be an architectural advantage to allow a smooth closure of the inner staminodes over the carpels at

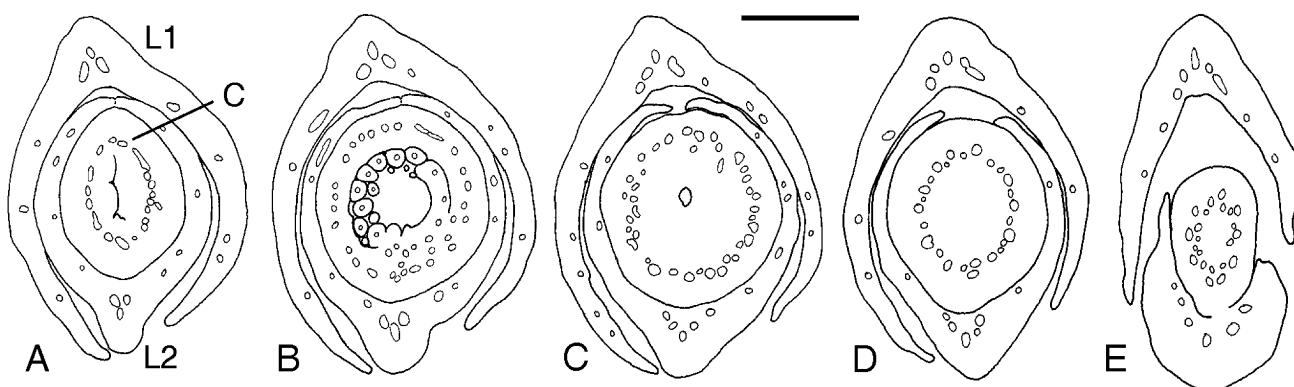


Fig. 9 Transverse section series of floral bud including calyptra (C) and two preceding leaves (L1, L2) with vascular bundles outlined of *Eupomati laurina*. A, Upper level of calyptra closed by irregular slit; margins of preceding leaf postgenitally connected. B, Level of androecium; attachment level of calyptra on lower side. C, Lowermost level at which concavity of floral apex can be recognized by the hole in the center; attachment level of calyptra. D, Floral base below calyptra attachment. E, Attachment level of preceding leaf. Magnification bar = 0.5 mm.

the transition from the female to the male phase of anthesis of a flower (Endress 1984a).

In conclusion, several observations argue against a complex interpretation of the calyptra. There is not a single positive indication that it consists of several organs. On the contrary, the easiest interpretation is as a single modified organ because already the phyllomes preceding the calyptra have clasping bases and, perhaps, because in *E. laurina*, the calyptra rim has a somewhat higher tip on the side opposed to the preceding phyllome.

Nature of Bracts and Calypteras in Angiosperms

The question of how bracts and tepals develop brings us to a more general problem. In comparative morphology, bracts and tepals are commonly viewed as two categories of phyllomes, which are distinguished at the same level: tepals are floral organs, and bracts are organs outside of the flower (Guédès 1979, p. 129; Wagenitz 1996, p. 72). But how can they be distinguished in practice in problematical cases? Or, conversely, is this distinction reasonable at all in such cases?

Can current studies shed light on this general question? Flowers have been studied over a wide range of aspects as to structure, development, ecology, and evolution. Molecular developmental genetics found key genes, which determine sepals, petals, stamens, and carpels (Coen and Meyerowitz 1991; Theissen 2001). These studies concentrated on eudicots. Unfortunately, the elusive tepals and bracts, which also play a role in flowers, have been much less studied than the other four categories mentioned.

For the moment, the term tepals may be used for the perianth parts of basal angiosperms (although the problem of petal origin is not solved, and petals may even be present in some basal angiosperms; see Endress 2001, 2003). But how to distinguish between tepals and bracts? This problem has not been treated on a broader scale. The question only came up in single families—for instance, Amborellaceae and families of Winterales and Magnoliales. The situation in each individual case may be different from what one would discuss for all clades of basal angiosperms together.

For a tentative and preliminary distinction, we may say that tepals are organs integrated in the flower organization, like sepals and petals. They occur in clades in which petals have not yet evolved: basal angiosperms and some basal eudicots. Their main functions are the protection of inner floral organs and, also, often the attraction of pollinators.

For bracts, a negative definition is easier than a positive one: bracts are simple phyllomes that are not differentiated as foliage leaves and that are not integrated in the flowers (in their mature stage). They lack some special properties. They have two major functions: (1) an ecological one: they protect vegetative shoots or flowers in their youngest stages, before the tepals or sepals take over this function; and (2) possibly an organizational one: they may pave the way for the onset of the regular floral phyllotaxis, especially in flowers of core eudicots (Endress 1994). But in anthetic flowers, they no longer play any obvious role. If A, B, and C gene activity is lacking in *Arabidopsis* mutant flowers, small green leaves are formed (Meyerowitz 1994). This is a weakly differentiated ground state, which may also be the case in bracts. It is unstudied what other kinds of activity may be present in bracts.

In a study on Buxaceae, a family of basal eudicots, the question of tepals and bracts has been discussed through an entire family, applying morphological, anatomical, and developmental aspects, and it has been shown how tough the problem is

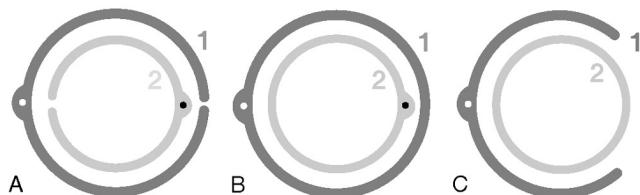


Fig. 10 Diagrams of corresponding calyptra-like floral envelopes in three families of Magnoliales. A, Magnoliaceae (1 and 2, calypteras with margins postgenitally fused and with midribs). B, Himantandraceae (1 and 2, tubular calypteras with midribs). C, Eupomatiaceae (1, preceding leaf; 2, tubular calyptera without midrib).

(von Balthazar and Endress 2002). A result is that bracts and tepals may be seen neither as categories that exclude each other nor as intergrading into each other but rather as categories at different levels of complexity. In this sense, bracts would represent a relatively simple ground state, and tepals would be more differentiated organs.

To sum up for *Eupomatiaceae*, there are two unusual developmental features in the calyptra of *Eupomatiaceae* flowers: (1) early intercalary elongation so that the upper rim of the forming calyptra is not affected by the widening of the developing flower (as a precondition for the later closure of the calyptra) and (2) closure of the calyptra by irregular lobation of the rim or the inner surface below the rim and by excessive marginal growth, incurving, and by formation of hairs on the outer side of the rim. Hair formation is remarkable because *Eupomatiaceae* plants seem otherwise entirely glabrous.

Thus, the enigma of the calyptra of *Eupomatiaceae* is not yet solved. We know now that the calyptra does not behave as if it is composed of several organs. If it is only one organ, we are not prepared to speak of a tepal but rather of a bract, although the organ is integrated in the floral architecture because, normally, tepals occur as several organs, whereas bracts may occur singly. If a bract is characterized as not included in the floral architecture, the calyptra of *Eupomatiaceae* does not completely fit this characterization because it is formed only after the shoot apex has been transformed into a floral apex, although it may be initiated already during the transition. Thus, the calyptra of *Eupomatiaceae* can be viewed as a unique evolutionary specialization derived from a bract, with no comparable counterpart outside of the Magnoliales.

Calyptras have evolved in several clades among angiosperms. In general, they are characterized by precocious early development as a tubular unit; they fall off (or split open) at the beginning of anthesis. However, they may be very different in organization. In other groups, such as some Monimiaceae (magnoliids), *Eschscholzia* (Papaveraceae, basal eudicots), or *Eucalyptus* (Myrtaceae, rosids), calyptra organization is less difficult to interpret, although their calyptras are more complicated than in *Eupomatiaceae*. In *Eschscholzia*, the calyptra is formed by two sepals (Dickson 1935; Karrer 1991). In *Eucalyptus*, the calyptra begins development with three or four distinct sepal primordia and an additional whorl of petal primordia (Drinnan and Ladiges 1989). In some Monimiaceae (Mollinedioideae), two to several whorls of tepals are involved in calyptra formation (Endress 1980). However, in all these cases, after perianth organ initiation, there is precocious intercalary elongation and basal widening. Thus, this later development is as in *Eupomatiaceae*. On architectural grounds, such a precocious intercalary development is a precondition for closed calyptra formation. In Winteraceae (Winterales, magnoliids), commonly a somewhat less early closing calyptra is formed, in *Drimys*, sometimes also from a ring primordium, but apparently two (or more) organs are involved (Hiepko 1966; Erbar and Leins 1983; Doust 2001).

Outlook

Where will we go in the future? What will molecular developmental biology contribute to the understanding of the calyptra of *Eupomatiaceae* flowers? A study by Kim et al. (2002,

in preparation), part of the “Floral Genome Project” (Baum et al. 2002; Soltis et al. 2002), is expected to widen our horizon. An integration of new developmental studies, molecular and comparative morphological in an evolutionary context, will certainly be necessary to advance in this matter. One of the difficulties at present is that we are dealing here with an unstudied organ category: bracts or tepals. To date, molecular studies have focused on the perianth in some core eudicots, in which sepals and petals are differentiated (Baum and Whitlock 1997; Albert et al. 1998, 2002; Kramer and Irish 1999, 2000). Bracts are elusive because they are commonly inconspicuous or, in *Arabidopsis*, even missing. Tepals are present in basal angiosperms but commonly not in core eudicots. Thus, a fresh look at the concept of phyllomes that are neither sporophylls nor trophophylls is necessary.

Donoghue (1994) discussed the “criterion of veracity” (after Hennig 1966) in the endeavor to elucidate phylogeny and evolution of organisms. We struggle with a giant puzzle, which cannot be solved in a few or, even, much less a single step. But at the end, every piece has to fall at its place. If the interpretation of puzzling organs for each individual case is somewhat different from what one would discuss at a higher level for all angiosperms, this could mean many different origins of similar organs. This relates to homology in a general biological sense but not historical homology. The discussion of biological homology versus historical homology (Wagner 1999, 2001; Rieppel and Kearney 2002) will certainly keep biologists of diverse brands busy in the near future.

A question at another level is, What is the special function of the calyptra in *Eupomatiaceae*? Why is there a calyptra and not simply a normal perianth? Does it provide exceptional protection against pollinating weevils? These flowers are costly: full of starch in staminodes, with many ovules, and only few fruits are produced, especially in *Eupomatiaceae barbata* and *Eupomatiaceae bennettii*. And why is the calyptra more robust in *Eupomatiaceae laurina* than in *E. barbata* and *E. bennettii*? Ecological studies at the interface of beetles and flowers and on the effect of dry periods on flower development would be important. Also, it would certainly be of interest to study the behavior of flowers and pollinators in *Himantandraceae*, which have similar calyptras but which are completely unknown in their floral biology, apparently because they form large trees with difficult access to the flowers (Endress 1984b).

The calyptra in *Eupomatiaceae* also exemplifies how difficult and time consuming some components of a morphological cladistic analysis may be, in this case of basal angiosperms (Doyle and Endress 2000, in preparation). But, conversely, these components need to be studied to understand the web of biological features—the natural history of plants—which is not possible by mere sequencing and comparison of nucleotides.

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