EARLY FLORAL DEVELOPMENT OF CAMELLIOIDEAE (THEACEAE)

CHIH-HUA TSOU

Institute of Botany, Academia Sinica, Nankang, Taipei, Taiwan 115, Republic of China

The early floral development of Camellioidae was studied. Two major evolutionary lineages were recognized for this subfamily. The earlier evolved lineage (Camellia, Polyspora, and Pyrenaria) has normally 11–14 perianth members, which are initiated in a continuous spiral and are differentiated into sepal and petals at late floral development, and numerous stamens initiated individually and centrifugally on the whole androecial region. The later derived lineage (Franklinia, Hartia, Schima, and Stewartia) has five sepals and five petals arranged in two whorls, and numerous individual stamens originating centrifugally from the five petal-opposed zones. Hartia-Stewartia and Franklinia-Schima further diverged as two branches — the former is characterized by having androecial fascicles and axile-basal placentation. The androecial fascicle is considered to be derived within this subfamily. The latter exhibits a higher degree of carpellar congenital fusion and axile-central placentation, and as a whole, is concluded to be the most advanced group in the Camellioidae. A taxonomic treatment of the Camellioidae at the tribal level is also proposed.

Key words: Camellia; Camellioidae; floral ontogeny; Gordoniaceae; phylogeny; Stewartiaceae; Theaceae.

This is a part of a series of studies on the Theaceae, which hopes to improve our understanding of the features and the phylogeny of this family (Tsou, 1995, 1997). The flowers of Camellioidae are rather uniform in gross morphology. In general, they are solitary, medium to large, showy, actinomorphic, and with 10–14 sepals and petals, numerous exerted stamens, and a superior ovary. Such a character combination is crucial in defining the Camellioidae. Nonetheless, the high degree of uniformity of the camellioid flowers makes the floral characters much less useful in the taxonomy at tribal and generic levels. Earlier authors, such as Melchior (1925, 1964) and Airy-Shaw (1936), used a single floral character in their tribal assignments, i.e., whether the sepals and petals gra-
date abruptly or not, whereas later authors, such as Sealy (1958) and Keng (1962), considered this criterion unten-
table and used only fruit and seed characters in their keys to the tribes, subtribes, or genera of the Camellioidae.

In the last decade, floral development has come to be indispensable for an integrated study of any higher rank taxon (Leins, Tucker, and Endress, 1988; Endress, 1994; Tucker, 1996). In the Camellioidae, Erbar (1986) studied Stewartia pseudocamellia, and Sugiyama (1991) examined Camellia japonica. In S. pseudocamellia (Erbar, 1986), the five sepals appear in a whorl as do the five petals. The androecium and gynoecium both originate from a deeply sunken floral apex; the androecium first develops as a five-fascicle cluster of primordia, then individual stamen primordia appear on its surface. The gynoecium is five-carpellate, and the placentation is axial-basal. In C. japonica (Sugiyama, 1991), the 13–18 perianth primordia are initiated in a single spiral, with sepal and petals indistinguishable at early developmental stages. The floral apex is slightly concave. No androecial fascicles are initiated, and the individual stamens appear directly on the surface of the androecial region in a spiral-centrifugal order. The gynoecium consists of three carpels, and the placentation is axile-central. In short, for the early floral development of all four floral categories, S. pseudocamellia and C. japonica differ greatly in their aestivation, structure of androecium, number of perianth members, and their placentation.

No one has seriously addressed the evolutionary nature of the uniformity of mature camellioid flowers. Did the flowers of this subfamily evolve so slowly that high homogeneity has been maintained? Or, is this similarity merely superficial and thus represents a convergence? Erbar’s (1986) and Sugiyama’s (1991) ontogenetic works, when considered together, have already indicated that the great similarity between the flowers of Camellia and Ste-
wartia is indeed superficial and that very different patterns of early floral development have evolved in the Camellioidae.

Because the floral ontogeny of only two genera in the Camellioidae have been investigated and because early floral development seems to contain valuable information about the evolution of the Camellioidae, a subject poorly understood and a topic rarely discussed, I undertook the present study to bridge the wide gaps in our knowledge of floral development in the Camellioidae and to discover more useful characters for the phylogenetic reconstruction of this subfamily. Among the ten camellioid genera currently recognized by me (Apterosperma, Camellia s.l., Franklinia, Gordonia s.s., Hartia, Polyspora, Pyrenaria s.l., Schima, Sinopyrenaria, and Stewartia), the floral ontogeny of seven genera was examined using scanning electron microscopy. Apterosperma, Gordonia...
s., and Sinoppyrena are not documented due to the lack of very young material; nevertheless, their small/medium buds and flowers were available and examined under a dissecting microscope for a more comprehensive analysis.

MATERIALS AND METHODS

Floral buds of different sizes and open flowers of 12 species from ten camelliod genera were collected from various countries (Table 1). They were fixed in FAA (5 parts formalin:5 parts acetic acid:90 parts 70% ethyl alcohol) immediately after detachment. After being fixed for at least 48 h, plant materials were transferred to 50% ethyl alcohol. Very young floral buds of nine species from seven genera (Table 1) were carefully dissected under a dissecting microscope and ultrasonically cleaned in 50% ethyl alcohol, dehydrated through an ethyl alcohol:acetone series, and then dried with a Hitachi HCP-2 critical point dryer. Pieces of material were mounted on aluminum stubs with Scotch double adhesive tape, coated with gold in a Hitachi IB-2 ion coater, and then observed with a Zeiss-950 scanning electron microscope. The remaining three samples with small and medium but no very young floral buds were dissected and observed under a dissecting microscope.

RESULTS

As a whole, the seven genera examined exhibit a broad range of variation in the early development of four catagories of floral organs. Hartia (villosa) and Stewartia (pseudocamellia) are hardly distinguishable, and they can hence be grouped as Hartia + Stewartia for comparison purposes. Camellia, Franklinia, Hartia + Stewartia, Polyspora, Pyrenaria, and Schima differ from one another by one or a few characteristics.

Two major genus groups can be recognized on the basis of perianth phyllotaxy and the timing of differentiation of sepal and petals. In Group I (Camellia, Polyspora, and Pyrenaria), the 11–16 perianth members are initiated quincuncially and differenate into sepal or petal only at late floral development. Distinctions among these three genera are rather limited, and subgrouping appears unnecessary. In Group II (Hartia, Stewartia, Franklinia, and Schima), the calyx and corolla are distinct at inception, and the five sepal and five petals are each arranged in one whorl though the members of each whorl are of spiral initiation. Within Group II, two subgroups are recognizable on the basis of the very different patterns of androecial and gynoecial development. In Group IIA (Hartia and Stewartia), individual stamens are initiated from five androecial fascicles and the placenta is axile-basal, whereas in Group IIB (Franklinia and Schima), no androecial fascicles are formed and the placenta is axile-central.

Because of the high similarity in floral development between or among the members of the same (sub-)group, I take the (sub-)groups as the units of description so as to avoid unnecessary repetition.

Group I: Camellia, Polyspora, and Pyrenaria

Perianth initiation—The 11–16 perianth primordia are initiated in a spiral sequence (Figs. 1, 4, 22, 23, 34), with a parastichy number of most likely two or three. The young perianth members are homogeneous in appearance and their bases are basically triangular (Figs. 14, 23, 34). In Polyspora axillaris and Pyrenaria shinkoensis, the young perianth members remain basally triangular for a period of time, and the circumference of floral buds is thus multangular (Figs. 23, 25, 34, 37), whereas the bases of young perianth members of Camellia soon become crescent shaped and the floral buds appear rounded in outline (Figs. 1, 14). During late floral development, the outer perianth members remain small, stout, and brownish, but the inner five to seven members become large, flattened, and light-colored. However, this morphological transition is gradual, and there is no clear-cut demarcation between sepal and petals in fully developed flowers.

Androecium initiation—When the androecium is about to originate, the floral apex is saucer-like, the gynoecial part is flattened, and the androecial part is a ring primordium (Figs. 13, 35). On the slope of the ring primordium, ~10–13 stamen primordia appear along the footline to form the first whorl (Figs. 2, 13, 24, 35). They are not initiated synchronously. The stamens of the second and the following whorls are then initiated in a centrifugal sequence. In general, the primordia of the outer whorl emerge alternately with those of the immediate inner whorl (Figs. 4, 9, 16, 17, 27, 32, 38, 41). However, opposite positions were also observed (Fig. 5). The stamen initiation is not of typical spiral phyllotaxy and should be assigned as irregular. It has no correlation with the two-fifths spiral of the perianth members, either.

There are a total of 35–40 stamen primordia arranged in two whorls in Camellia hengchunensis and C. tenuifolia (Figs. 6, 10), ~100 in three whorls in C. sinensis (Fig. 17), ~300 in four (–five) whorls in Polyspora axillaris (Fig. 32), and 150–190 stamens in three (–four) whorls in Pyrenaria shinkoensis (Fig. 41). The just-emerged stamen primordium ranges from 40 to 45 μm in...
The number of stamen primordia a floral bud would finally contain is correlated with the outward expansion of the ring primordium by the time stamen initiation is complete.

Gynoecium initiation—The gynoecium is initiated within the above-described central flattened base of the floral apex. The gynoecium of the three Camellia species and Pyrenaria shinkoensis comprises three carpels, and that of Polyspora axillaris comprises five. But occasionally, four-carpellate gynoecia are present in C. hengchunensis (Fig. 7) and two-carpellate ones in P. shinkoensis (Fig. 37). The gynoecial development in all of the five samples examined is similar. Carpel primordia emerge separately (Figs. 2, 13, 26, 35, 36), first appearing as more or less hemispherical bulges (Figs. 3, 15, 26, 37, 38). These bulges then expand more in lateral directions than in other directions (Figs. 4, 16, 28, 39). Later, the two lateral sides of such a primordium involute so that the carpellary chamber becomes more and more evident on the ventral side—thus, an ascidiate carpel takes shape (Figs. 5, 17, 29, 40). Postgenital fusion between the carpels takes place sooner or later after this stage, resulting in a syncarpous gynoecium (Figs. 5, 9, 18, 19, 29, 30, 40, 41). With the ongoing postgenital carpellary fusion process, the gynoecium finally becomes a transversely rounded multicarpellate ovary with a tri-arched or five-arched, opened, apical extension (Figs. 6, 7, 10, 20, 31, 32, 33, 34, 35, 36). The ventral sides of the constituent carpels fuse as well, and a central column is formed, with the cross zones only up to the middle part of the locules. Later, the style and stigma are differentiated, and the free apical part of each carpel develops into a stigmatic branchlet. Many rows of the epidermal cells of the ovarian outer surface develop as ascending, unicellular trichomes (Figs. 8, 11, 12, 20, 42). All floral buds examined develop axile-central placenta. The ovary is evidently superior, with the attachments of both androecium and gynoecium on the flat surface of receptacle (Figs. 20, 33, 42).

In samples of Camellia and Pyrenaria, the three carpel primordia in a gynoecium usually originate sequentially but unrelated to the phyllotaxis of stamens and perianth members; nevertheless, in a few buds of Pyrenaria shinkoensis, the initiation sequence of the carpels resumed the two-fifths spiral sequence finished by the perianth members (Fig. 39). In samples of Polyspora, the initiation sequence of the five carpels in a gynoecium cannot be ascertained due to the very weak size difference among the carpel primordia (Figs. 25–27).

Though the early gynoecial development of the five samples examined is similar, as summarized above, differences do exist among the three genera. First, Polyspora axillaris and Pyrenaria shinkoensis have a moderately long style ending with a capitate stigma, whereas the three Camellia species examined have a short to very short style ending with a long and branching stigma.
(Figs. 8, 12, 21). In *Camellia*, each stigmatic branch has its own pollen-transmitting duct, and all of the pollen-transmitting ducts are confluent in the stylar region. The three stigmatic branches of *C. hengchunensis* differ in length and are of bilateral symmetry (Fig. 8). Second, the five carpels of a *P. axillaris* flower typically do not initiate until the stamens of the second whorl start to emerge (Figs. 24–26), whereas in the four samples from the other two genera carpel primordia initiate synchronously with the stamen primordia of the first whorl (Figs. 2, 13, 35).
Group IIa: Hartia and Stewartia—Erbar (1986) has published an intensive account of the floral development of Stewartia pseudocamellia. Though my SEM photographs of the same species do not show additional information to that of Erbar (1986) and though the early floral development of Hartia villosa is highly similar to that of *S. pseudocamellia*, I will describe early floral development of Hartia and Stewartia in detail to illustrate my different interpretation.

Perianth initiation—The five sepal primordia (Fig. 43) and the five petal primordia (Fig. 44) are situated in a whorl though initiated in a two-fifths spiral sequence, whereas the spiral of calyx is not continued by the corolla. Thus the petals are not in episepalous positions. This whorled arrangement may result from a comparatively rather rapid emergence of the five sepal/petal primordia relative to the elongation of the floral apex. Within the calyx whorl, the bases of the later four (the second to the fifth) young sepals are much compressed laterally in the calyx whorl, the bases of the later four (the second mordia before the inception of individual stamen primordia (C) appear as round mounds. Scale bar = 200 μm. 28. Young carpels not yet fused but already appearing ascidiate. Scale bar = 40 μm. 29. Young carpels just slightly fused at the base. The carpelar chamber is distinct (arrow). Scale bar = 40 μm. 30. High magnification of three fused carpels showing their carpellary chambers (arrows). Scale bar = 40 μm. 31. Young gynoecium showing the closing of carpellary chambers (arrows). Scale bar = 100 μm. 32. Older floral bud. Its outermost stamens have just originated whereas inner stamens have already differentiated into anthers and filaments, and the gynoecium is well developed. Scale bar = 200 μm. 33. Longitudinal view of a dissected floral bud showing the superior position of the ovary (O) and young stamens (S). Scale bar = 200 μm.

due to that of *H. villosa*, the number of stamen primordia appearing on each fascicle varies greatly during the early initiation process (Figs. 46, 47). For example, when the first two fascicles have already developed 12–15 primordia respectively, the smallest fascicle has <5 (Fig. 46). After the stamens are all initiated, the five fascicles become less distinct. Later, when the stamens grow much bigger and are much pressed against each other (Fig. 49), the arrangement of stamens in *Hartia* and *Stewartia* appears highly similar to that of the Group I.

Gynoecium initiation—During the initiation of the lowermost/innermost one or two rows of stamens, carpel primordia appear one by one right opposite to the five androecial fascicles (Fig. 48); consequently, the five petals, five stamen groups, and five carpels are arranged in five radiate lines (Fig. 53). The carpel primordia are tangentially elongated, rather than hemispherical, bulges at inception (Fig. 48). In *S. pseudocamellia*, the inception of the five carpels is neither synchronous nor of a typical spiral. The two carpel primordia spatially associated with the first two androecial fascicles indeed develop first, but the other three carpels are usually of similar size, so their initiation sequence cannot be determined. In *H. villosa*, the carpels are so sunken that the carpel initiation sequence cannot be detected. In both taxa, the five carpels soon reach similar size, and grow faster in the longitudinal rather than other directions before starting to roll in at their individual bases (Fig. 53). Subsequently, each carpellary chamber becomes evident. Then the five carpels begin to fuse laterally at their bases to form a ringlike syncarpous gynoecium. The syncarpous gynoecium elongates fast and soon differentiates into an ovary, a short style, and a big five-lobed stigma (Fig. 49). The pollen-transmitting canal is five-armed (Fig. 49). The five carpels are very poorly fused along their ventral sides even at floral maturity. The five carpels are plicate. Within each ovarian locule, ovules are originated from the slope connecting the ventral sides and the locule base. Thus the placenta may be designated as axial-basal (Figs. 50, 54).

Group IIIb: Franklinia and Schima—Perianth initiation of Schima superba var. kankoensis—The pattern of perianth initiation of *S. superba* var. *kankoensis*
Figs. 34–42. Floral development of *Pyrenaria shinkoensis*. 34. Floral axis after the perianth initiation is just completed, showing the concave floral apex, triangular bases of most perianth members, and the counterclockwise spiral of perianth phyllotaxy. Scale bar = 200 μm. 35. Floral apex showing the initiation of earlier stamens (S) on the ring-like androecial primordium and a carpel primordium (*). Scale bar = 40 μm. 36. Initiation of stamens (S) of the second whorl and early development of carpels (C). Scale bar = 100 μm. 37. Floral axis showing the clockwise spiral of perianth phyllotaxy, triangular bases of perianth members, and only two carpel primordia. Scale bar = 200 μm. 38. Floral apex showing the initiation of stamens (S) of the second and third whorls and three separated carpel primordia (C). Scale bar = 100 μm. 39. Three young carpels (C) of different sizes, showing the continuation of phyllotaxy from perianth members to carpels. Scale bar = 200 μm. 40. Three young carpels well fused and assuming an ascidiate form. Scale bar = 100 μm. 41. Nearly all stamens initiated. The androecium and gynoecium are slightly deformed due to the pressure of the innermost perianth members. Scale bar = 200 μm. 42. Floral bud with partial stamens removed, showing the horizontal surface of the receptacle. Scale bar = 200 μm.
Table 2. Measurements of the diameter of stamen primordia and the basal width of the androecial ring primordium, as well as the calculated number of the stamen primordia present in the androecium when stamen initiation was completed, of five species of *Camellia*, *Polyspora*, and *Pyrenaria*.

<table>
<thead>
<tr>
<th>Species</th>
<th>Diameter of the just-initiated stamen primordium (μm)</th>
<th>Basal width of the androecial ring primordium (stage 1)* (μm)</th>
<th>Basal width of the androecial ring primordium (stage 2) (μm)</th>
<th>Number of whorls</th>
<th>No. of stamen primordia present</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>C. hengchunensis</em></td>
<td>45</td>
<td>80–90</td>
<td>110–150</td>
<td>2</td>
<td>35–42</td>
</tr>
<tr>
<td><em>C. sinensis</em></td>
<td>45</td>
<td>60–90</td>
<td>150–200</td>
<td>3</td>
<td>100–120</td>
</tr>
<tr>
<td><em>C. teniuifolia</em></td>
<td></td>
<td>100–120</td>
<td>200 ?</td>
<td>3 (4)</td>
<td>37–40</td>
</tr>
<tr>
<td><em>Pol. axillaris</em></td>
<td>40</td>
<td>60–100</td>
<td>250–300</td>
<td>4 (5)</td>
<td>ca. 300</td>
</tr>
<tr>
<td><em>Pyr. shinkoensis</em></td>
<td>40–45</td>
<td>90–100</td>
<td>37±40</td>
<td></td>
<td>150–190</td>
</tr>
</tbody>
</table>

* Basal width of the androecial ring primordium refers to the distance from the margin of gynoecium to the outer rim of androecium.

**Androecium initiation of *S. superba* var. kankoensis**

Both the androecium and gynoecium begin to develop just after the perianth initiation is completed (Figs. 56, 58). The androecial part is composed of five peripheral slopes as mentioned above (Fig. 56), which are actually five petal-opposed androecial zones separated by five grooves (Figs. 58, 59). Within each zone, stamen primordia first appear on the lowermost margin, but the very first ones emerge on the two sides of this marginal area where free space available for primordia is evidently larger than in the middle part (Figs. 57, 58). The initiation zones in front of the first two or even three petals are generally broader than the others, and they normally produce stamen primordia earlier (Figs. 58, 59). For example, while four to five stamen primordia have already developed in the first two initiation zones, only one or two appear on others (Fig. 58). There are some five stamen primordia on the lowermost margin of each zone, and on average 23–26 primordia constitute the lowermost/innermost whorl (Fig. 60). Each initiation zone expands upward and outward continuously, followed immediately by the inception of the stamens of higher orders — thus the stamen phyllotaxy in each androecial zone is centrifugal. The five grooves demarcating the initiation zones, though rather distinct in the beginning (Figs. 58–62), become more and more obscure when stamens get crowded and eventually invisible after the stamens of the third rows are initiated (Figs. 63, 64). During early development, the receptacle region supporting the androecium and gynoecium bends in a way that the floral apex becomes dish-like, rendering the axis of the stamens of the outermost whorl horizontally oriented (Figs. 63–66).

**Gynoecium initiation of *S. superba* var. kankoensis**

As stated before, the gynoecium and androecium begin to develop at about the same time (Figs. 56, 58). The common primordium of the gynoecium rises up slowly until nearly half of the stamens of the innermost whorl have originated, when the bulges of individual carpels emerge quincuncially, each opposing a stamen-initiation zone and a petal (Figs. 58, 59, 60). The individual carpel primordium was observable by its apical part only, indicating a high degree of congenital fusion between the five carpel primordia at their bases (Figs. 58, 59, 60). Before the stamens of the innermost whorl are all initiated the first carpel primordium has already assumed the ascidiate form (Fig. 60). The five young carpels then grow to a comparable size. Their ventral syncarps are prominent and just slightly lower than the tips of individual primordia (Figs. 61–63). After this stage, the syncarpous gynoecium gradually becomes urn-shaped (Figs. 63–66). During subsequent development, a slender style and a capitate stigma are differentiated. The placenta is axile-central. The base of the ovarian cavities is slightly embedded within the receptacle, but the ovary position has not yet reached the condition of typical semi-inferior.

**Franklinia alatamaha** — Limited by the material available, the earliest floral development of *F. alatamaha* was not followed. Nevertheless, the floral developmental characteristics of *Franklinia*, as revealed from the available material (Figs. 67–69), are quite similar to those of *S. superba* var. *kankoensis* (Figs. 63, 64, 66). The youngest stage observed is represented by the co-existence of three-to-four stamen whorls and a gynoecium of five similar-sized and highly fused ascidiate young carpels (Fig. 67). In Fig. 67, a short groove on the androecial slope is visible, implying that this androecium is likely to be composed initially of five stamen-initiation zones as in *Schima*. In short, in terms of floral development, the overall middle stages of *F. alatamaha* shown by Figs. 67–69 are very similar to the comparable stages of *S. superba* var. *kankoensis*, particularly when one takes into consideration the very early carpellar fusion (compare Fig. 67 with Fig. 63) and the developmental manner of the receptacle (compare Figs. 68, 69 with Figs. 64, 66). Among other crucial similarities between *Franklinia* and *S. superba* (data not shown for *Franklinia*) are the whorled...
arrangement of sepals and petals, the petal-opposed carpels, and the axile-central placenta.

**DISCUSSION**

The adequacy of the grouping system—Camellioideae is strongly supported as a monophyletic subfamily (Tsou, 1996, 1997). Among the ten camelliod genera I currently recognize, the early floral development of seven is here reported, and the generic-level sampling of this study is sufficiently high. Although the floral ontogeny of the other three monotypic genera, Apterospperma, Gordonia s.s., and Sinopyrenaria, was not studied by scanning electron microscopy, some of their important floral features were clarified by examining the available small buds under the dissecting microscope and through a literature search (Apterospperma: Chang, 1976; Gordonia: Kobuski, 1951; Wood, 1959; Sinopyrenaria: Hu, 1956). The three genera are not especially different in gross morphology within the Camellioideae. They have been merged into or combined with Schima, Polyspora, and Pyrenaria, respectively, in different taxonomic treatments. Careful examination of their floral features shows that small floral buds of Sinopyrenaria yunnanensis have two bracteoles, followed by 11–12 spirally arranged perianth members, without distinct demarcation between calyx and corolla and with a superior ovary and central axis placental.

This strongly suggests the monotypic Sinopyrenaria is a member of Group I. As for Apterospperma oblata and Gordonia lasianthus, their five sepals and five petals are arranged in two respective whorls. These two floral parts can be distinctly recognized by position, size, and texture. In addition, they have axile-central placentas. The monotypic Apterospperma and Gordonia can thus be assigned to Group IIb. As a conclusion, the floral ontogeny of the three genera, though not yet investigated, seems not exceedingly peculiar within the subfamily and fits well into the present grouping system without any problem. Therefore, this grouping system seems to accommodate well all major floral developmental patterns present in the extant Camellioideae and is consequently adequate for the evolutionary and phylogenetic discussions presented below.

Major floral developmental characters—Compared with the gross morphology of mature flowers, the early floral development of Camellioideae is far more diverse: genera may express differently in all or some of the four categories of floral organs, and many ontogenetic characters exhibit interesting intergeneric variations. The most important is that some two-state characters covery in presumably related genera within the subfamily. These major characters are as follows: (1) the degree of congenital carpellary fusion (CCF) – low vs. high; (2) the arrangement of perianth-members – spiral vs. whorled; (3) the timing of differentiation between sepals and petals – occurring at late floral development vs. in the very beginning of their inception; (4) the androecial zonation for stamen initiation – zonated vs. unzonated; (5) androecial fascicles – presence vs. absence; (6) placental – axile-central vs. axile-basal; (7) ovary position – superior vs. intermediate between superior and semi-inferior.

The polarity of character 1 can be determined by consensus. The trend of syncarpy from apocarpy has long been supposed to be one major evolutionary trend in the angiosperms (Eames, 1961; Stebbins, 1974; Endress, 1994); though cases of secondary apocarpy have been reported (Endress, Jenny, and Fallen, 1983; Fallen, 1986; Jenny, 1988; Ramp, 1988) from the following few unrelated orders: Malvales (Sterculiaceae), Sapindales (Rutaceae, Simaroubaceae), and Gentianales (Apocynaceae, Asclepiadaceae). In highly advanced plant groups, the syncarpous ovary is normally inferior and developed from a highly congenitally fused common primordium (Sattler, 1973). It is believed that during the modification process from apocarpy to syncarpy, a gradual strengthening of CCF must take place. Accordingly, within Camellioideae, an on-average rather primitive group among those syncarpous ones, the CCF may be reasonably assumed to have evolved from a low to high level.

The whorled state of character 2 is generally considered to be a prerequisite for the evolution from aposepaly to synsepaly and from apopetally to sympetalaly (Endress, 1987). It is also more prevalent than the spiral state in those dicots of middle and higher evolutionary levels (Endress, 1987, 1994). Nevertheless, because reversal from whorled back to spiral pattern is possible (Endress, 1987), the polarity determination of character 2 is thus in need of a more intensive analysis.

As for character 3, I find no reliable criteria to judge the relative primitiveness between early and late differentiation of sepals and petals in the camellioid flowers.

Characters 4 and 5 are interrelated. Generally speaking,
for a multistaminate androecium in the dicots, individual stamens may arise as primary primordia on the receptacle, as secondary primordia from a ring-like primary primordium, or as secondary ones within the fixed-numbered, separated primary primordia (Ronse Decraene and Smets, 1992; Endress, 1994, fig. 2.37). In the Camellioidae, the latter two patterns occur in Group I and Group II, respectively. In many unrelated nonmagnoliid dicot orders the co-occurrence of these two patterns of multistaminate androecia in a family is fairly common (Ronse Decraene and Smets, 1992, Table 1), and the transition between these two patterns is poorly understood. In addition, the debate on the origin of androecial fascicles in angiosperms remains unsettled (Leins and Erbar, 1991; Ronse Decraene and Smets, 1992); therefore, for Camellioidae, the polarity of characters 4 and 5 cannot be determined at this moment.

Erbar (1988) claimed that “Several similarities in flower development between Stewartia and the primitive cactus Pereskia indicate a relationship between Dilleniidae and Caryophyllidae.” She then considered the complex androecia (i.e., androecial fascicles) to be archaic within the Dilleniidae (Erbar, 1986, 1988). This viewpoint is, in my opinion, questionable. Androecial fascicles occur in numerous phylogenetically unrelated families of Dilleniidae, Rosidae, and Centrospermae. A comparison between the androecial fascicle development of Hartia + Stewartia (my work) and that of the Metrosideros group of Myrtaceae (Orlovich et al., 1996) reveals a much greater similarity than that between Stewartia and Pereskia. In Hartia + Stewartia and the Metrosideros group the androecial fascicles are initiated from the petal-opposed regions of a deeply concave floral apex, whereas in Pereskia the fascicles are alternate with petals and emerge from a convex floral apex (Leins and Schiwitalla, 1986). Furthermore, the myrtaceous androecial fascicles are within-family secondary structures (Johnson and Briggs, 1984) and might not be homologous among different taxa (Drinnan and Ladiges, 1991). Therefore, because the very strong resemblance between Hartia + Stewartia and the Metrosideros group in the developmental features of androecial fascicles is undoubtedly superficial, Erbar’s (1988) evolutionary conclusion based on connecting Stewartia with Pereskia is simply not convincing. Since the androecial structure may be highly variable within a family, whether the androecial fascicle is a prim-

---

Figs. 57–69. Floral development of Franklinia alatamaha. 67. Young floral bud with highly fused carpels while stamen initiation has not yet been completed. Note a remaining groove (arrow) between two groups of stamens and the receptacle beneath the androecium much elevated. Scale bar = 200 μm. 68. Floral apex with around four whorls of stamens and a syncarpous gynoecium. Scale bar = 100 μm. 69. Older floral bud with stamen initiation completed. The gynoecium is now closed at the apex. Stamens of outer whorls are mostly in horizontal orientation. Scale bars = 200 μm.
Table 3. Ten important characters were applied to the cladistic analysis in this study. Their expressions in the three genus groups and the assumed ancestor are here indicated. Polarity of character state has been assessed for characters 1, 7, 8, and 9. Asterisks refer to the derived state; the more asterisks a state has, the more derived it is.

<table>
<thead>
<tr>
<th>Character</th>
<th>Group I (Camellia, Polyspora, Pyrenaria)</th>
<th>Group Ia (Hartia, Stewartia)</th>
<th>Group Ib (Franklinia, Schima)</th>
<th>Assumed ancestor</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Degree of congenital carpel-fusion</td>
<td>low</td>
<td>low</td>
<td>high*</td>
<td>low</td>
</tr>
<tr>
<td>2. Arrangement of perianth-members</td>
<td>spiral</td>
<td>whorled</td>
<td>whorled</td>
<td>?</td>
</tr>
<tr>
<td>3. Timing of differentiation between sepals and petals</td>
<td>in late floral development</td>
<td>at inception</td>
<td>at inception</td>
<td>?</td>
</tr>
<tr>
<td>4. Stamen initiation</td>
<td>spiral</td>
<td>in five petal-opposed regions</td>
<td>in five petal-opposed regions</td>
<td>?</td>
</tr>
<tr>
<td>5. Androecial fascicles</td>
<td>absent</td>
<td>present</td>
<td>absent</td>
<td>?</td>
</tr>
<tr>
<td>6. Placentation</td>
<td>axile-central</td>
<td>axile-basal</td>
<td>intermediate between superior and semi-inferior or*</td>
<td>superior</td>
</tr>
<tr>
<td>7. Ovary position</td>
<td>superior</td>
<td>superior</td>
<td>type I (intermediate)*</td>
<td>type II**</td>
</tr>
<tr>
<td>8. Form of pseudopollen</td>
<td>type I</td>
<td>type II (intermediate)*</td>
<td>type III**</td>
<td>type I</td>
</tr>
<tr>
<td>9. Ovular vasculature</td>
<td>into outer integument</td>
<td>intermediate*</td>
<td>into inner integument**</td>
<td>into outer integument</td>
</tr>
<tr>
<td>10. Chromosome number</td>
<td>( N = 15 ) (30, 45)</td>
<td>( N = 15, 18 )</td>
<td>( N = 15 ) (30, 45)</td>
<td>( N = 15, 18 )</td>
</tr>
</tbody>
</table>

Note: References for character 8 are in Tsou [1996, 1997]; references for character 9 are in Tsou [1997]; and references for character 10 are as follows: Camellia—Ackerman, 1971; Kondo, 1977; Zhang and Ming, 1995; Franklinia—Santamour, 1963; Hartia—Oginuma et al., 1994; Li, 1996; Polyspora—Mehra, 1976; Pyrenaria (including Tutchera)—Santamour, 1963; Ackerman, 1971; Oginuma et al., 1994; Schima—Mehra, 1976; Ono, 1977; Gill et al., 1984; Huang et al., 1985; Stewartia—Santamour, 1963.

Cladistic analysis of ten characters—Among the above seven floral-developmental characters, only two (1 and 7) can be definitely determined for their polarity. A more intensive polarity analysis is consequently required for a sufficient understanding of the floral evolution in the Camellioidae. For this purpose, three additional characters from other aspects were lumped together with the foregoing seven (in a continuing sequence, see Table 3) for a cladistic analysis employing PAUP 3.1.1 (Swofford, 1993). Characters 8 and 9 are embryological (Tsou, 1996, 1997), and character 10 is cytological. In each of the seven genera of the three (sub-)groups, the baseline data accumulation of all of these ten characters is satisfactory. Particularly significant is that within each (sub-)group all, except character 10 (in Subgroup IIa), of these ten characters are expressed consistently. [Character 10 in Subgroup IIa, \( N = 18 \) in Hartia, whereas \( N = 15 \) in Stewartia, apparently represents a transition between Group I (\( N = 15 \)) and Subgroup IIb (\( N = 18 \).)] To my knowledge, no other salient characters of the Camellioidae have been studied for all these seven genera and have the character state uniformly expressed in each (sub-)group.

The polarities of characters 8 and 9 have been determined in my earlier papers (Tsou, 1996, 1997). Character 8 is of utmost importance because in angiosperms the sort of pseudopollen transformed from connective cells is so far unknown outside the Camellioidae. The three types of camellioid pseudopollen are differently constructed in their secondary cell walls. Interestingly and significantly, the taxonomic distribution of these three pseudopollen types corresponds exactly to the three (sub-)groups classified in the beginning of the present paper.

Neither Ternstroemioidae nor any other extant taxon was chosen as the outgroup for the current analysis because Ternstroemioidae as well as those thealean and ebeanalean families is rather dissimilar to the Camellioidae in the overall expression of these ten characters. Instead, an assumed ancestor was taken as the outgroup for convenience. It was simply defined as a taxon expressing the primitive states of the four characters (char-
acters 1, 7, 8, and 9) whose polarity has been assessed (Tables 3, 4).

A single most parsimonious tree (Fig. 70) was generated through either heuristic, exhaustive, or branch-and-bound search, with the tree length = 12, CI (consistency index) = 1.0, RI (retention index) = 1.0. With this cladogram, the polarities of the six characters (characters 2–6, 10) previously undeterminable can now be assessed with a reasonable reliability. The following states are most probably pleisiomorphic within Camellioideae for their respective characters: spiral arrangement of perianth members (character 2), which conforms to the general trend of angiosperms; late differentiation between sepals and petals (character 3); absence of androecial zonation and stamens originating from the whole ring primordium (character 4); absence of androecial fascicles (character 5); axile-central placation (character 6); matching the consensus opinion about angiosperms; and 15 haploid chromosomes (character 10).

My results suggest a homologous nature for sepals and petals in the Camellioideae. In addition, Erbar’s (1988) claim that the androecial fascicles are primitive within Theaceae is opposed. The evolution of androecial fascicles within the Camellioideae is unrelated to other plant groups. I assume that it is basically coupled with the evolution of the integrated floral organization within the Camellioideae, which evolved from a somewhat chaotic and less precise pattern — with unfixed numbers of sepals, petals, and stamens and with less definite correlations among the positions of perianth members, stamens, and carpels — toward a much more definite and ordered pattern with fixed number (5) in sepals, petals, androecial primordial zones, and carpels; and fixed spatial arrangement among these four floral categories.

In addition, Keng’s (1962) suggestion that the axile-central placation is derived within Camellioideae is also rejected. I consider axile-central placation to be ancestral in this subfamily. In the lineage of Hartia-Stewartia the central axis of the ovary has been reduced to the ovarian base, and the axile-basal placation was consequently derived.

**Tribal taxonomy and phylogeny of Camellioideae**

Though produced chiefly for the understanding of the floral evolution in Camellioideae, the cladogram (Fig. 70) simultaneously, in my opinion, presents the major taxonomic differentiation within the subfamily. Thus, the (sub-)groups I, IIa, and IIb — originally distinguished by their distinct perianth phylloxy, timing of the differentiation between sepals and petals, and patterns of androecial and gynoecial development, and further supported by the chromosome numbers and embryological data — can be directly converted to formal taxonomic categories as follows:

**Tribe Camellieae** (= Group I) — *Camellia* s.l., *Polyspora*, *Pyrenaria* s.l., *Sinopyrenaria* (Laplacea and Parapyrenaria with generic status uncertain, may be merely an element of *Polyspora* and *Pyrenaria*, respectively.)

**Tribe Gordonieae** (= Group II) —

Subtribe Stewartiinae (= Subgroup IIa): *Hartia, Stewartia*

Subtribe Gordiniinae (= Subgroup IIb): *Apertosperma, Franklinia, Gordonia* s.s., *Schima*

The classification proposed here matches well with Airy-Shaw’s (1936) and Melchior’s (1964) tribal/subtribal treatments, but differs from the others to a greater extent (Melchior, 1925; Sealy, 1958; Keng, 1962; Deng and Baas, 1991). This is mainly because the floral character employed by Airy-Shaw and Melchior, whether sepals and petals are sharply dissimilar, is very significant because this character is associated with two fundamental transitions in the early floral development of Camellioideae, i.e., the arrangement of perianth members and the timing of the differentiation between sepals and petals. On the other hand, most of the other treatments usually overlooked floral characters and put too much weight on fruit characters, which lead to mistakes like lumping *Polyspora* (including *Laplacea*) with *Gordonia* s.s. and *Schima* because they had capsules and winged seeds in common. In fact, such a grouping is not reliable because the wing of *Polyspora* seeds is developed from the mesophyll of the raphe whereas that of *Schima* seeds is derived from the epidermis of outer integument on the antiraphe side (Tsou, 1997).
1997). On the other hand, *Gordonia* s.s. and *Schima* having an intimate relationship with *Franklinia*, a genus without winged seeds, is strongly supported by cytology (Table 3), embryology (Table 3 and unpublished data), floral development (the present study), and molecular data (Prince and Parks, 1997). *Apterosperma*, another genus without winged seeds, seems phylogenetically close to these three genera based on the limited information on floral features (the present study) and pseudopollen (Tsou, 1996). In the Camellioideae the evolution of fruit and seed seems less conservative and much more diversified than the evolution of early floral development. Implications of fruit and seed characters in phylogenetic considerations among the camellioïd genera need to be confirmed with developmental data.

The phylogenetic relationships among the camellioïd tribes/subtribes have been proposed only by Keng (1962). According to his Fig. 30, he considered Camellioideae (including *Camellia* s.l. and *Pyrenaria* s.l.) to be the latest evolved and Gordoniæae (including *Franklinia*, *Gordonia* s.s., *Polyspora*, and *Schima*) the earliest branch. My results in Fig. 70 suggest that, on average, Camellioideae (*Camellia* s.l., *Polyspora*, and *Pyrenaria*) appears to be the most primitive branch and subtribe Gordoniæae (*Apterosperma, Franklinia, Gordonia* s.s., and *Schima*) of the Gordoniæae the most advanced. Among the latter four genera, *Schima* is proposed as the most advanced genus within the Camellioideae. Such a phylogenetic hypothesis is congruent with my earlier conclusion on *Camellia, Franklinia, and Schima* based on eight embryological characters (Tsou, 1997).

**LITERATURE CITED**


SUGIYAMA, M. 1991. Scanning electron microscopy observation on ear-


