Floral Development of Castanopsis cuspidata var. sieboldii*

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岡本 素治：スダジイの花葉発生

Introduction

Recently, Endress (1977) reviewed his works on Hamamelidales and Fagales and strongly suggested the similarity of these two orders based on the information on many independent characters, such as anatomical, chemical, on floral morphology and ontogeny, etc. It is evident that these two are close to each other. In some points, however, his speculation remains to be revised. One of them is the 6-merous flower of the Fagaceae. By his concept, the flowers of Fagaceae are in principle not 3-merous but 6-merous. He pointed out, “firstly, male flowers mostly have 12 stamens in a diplostemonous arrangement, secondly, the perianth is uniform, all parts behave ontogenetically like the sepals in Hamamelidaceae, thirdly, also in a 5-merous or 4-merous flower the sepals usually are not arranged in one whorl, but in a spiral or they are decussate (e.g. Disanthus, Hamamelis).” He considered that the 6-merous condition of the Fagaceous flower had derived from the 5-merous one of the Hamamelidaceae. It seems to be suggested that the perianth of the Fagaceous flower is constituted with sepals of the Hamamelidaceae, and that one whorl of the petals has disappeared.

One of the major proposals of Endress (1977) is settled on the point whether the flowers of the Fagaceae are 6-merous or 3-merous, and their apetalous conditions have resulted through reduction or not. In the Fagaceae, the taxa with 12 stamens in each flower do not hold the majority, i.e. only Fagus and four genera of Castaneoideae have constantly 12 stamens. Among them flowers of Castaneoideae always have pistil rudiments in the male and have usually 12 staminodes in the female. In this respect, the flower of Castaneoideae is primitive. In this paper, it is intended to describe the floral development of Castanopsis cuspidata var. sieboldii, and discuss the problems mentioned above.

Berridge (1914) studied the anatomy of the female flowers of Castanopsis (=Chrysolepis) chrysophylla, and showed diagrammatically the arrangement of the floral parts. It is stated that in the gamopphyllous perianth of six leaves, the three alternate lobes being

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larger and overlap the others, six outer stamens are in opposite position to the perianth lobes and six inner ones in alternate. The outer stamens develop somewhat earlier than the others. Three locules of the ovary are in the opposite position to the larger perianth lobes. In this case, it is speculated that the 12 stamens are arranged in diplostemonous condition and the petals have disappeared. According to HJELMQVIST (1948), however, BAILLON (1876) reports somewhat different conditions in the ontogenetical study of the flower of Castanea sativa. First, a stamen is laid down inside each perianth-leaf, and later, one or two younger ones may be developed at each side of the stamen. The hypothesis of ENDRESS (1977) seems to be based on such figures as in BERRIDGE (1914).

Materials and Methods

Winter buds of Castanopsis cuspidata var. sieboldii (MAKINO) NAKAI cultivated in Nagai Park, Osaka city were observed for this study. Dormant buds and unfolding ones were fixed in FAA after a preliminary examination. At the critical stage of development they were collected in every two days, and at the other stages the intervals of collecting were prolonged. It was from the end of February to the end of May that collecting and fixing were performed. The voucher specimen (M. Okamoto 2562) is in the herbarium of Osaka Museum of Natural History.

Observations

Inflorescence:

Inflorescences of Castanopsis cuspidata var. sieboldii are generally unisexual simple catkins in which single flowers are formed in the axils of bracts arranged spirally on the rachis (Fig. 1). In male inflorescences lower vigorous bracts often have more flowers, thus they resemble dichasial catkins, a more general condition of the genus. The inflorescences are formed in the axils of bud scales or leaves within winter buds. The lower catkins are male ones and larger. Until late winter floral apices stay dormant. They are oval shaped or have flattened top with slightly differentiated perianth lobes. Female spikes are formed in the axils of upper leaves, but until spring they are hardly visible as masses of the spirally arranged bracts on stipes.

Development of the male flowers:

In winter, the floral axes are in the condition of ovate-shaped primordia subtended by each bract. The first step of the development of primordium is found in a differentiation of the bracteoles: the bracteoles initiate laterally to the primordium and rim-like protuberance surrounds the abaxial base of primordium. At the same time, an axillary bud of each bracteole is formed at rather anterorial position. Usually the bud remains abortive, sometimes, it becomes secondary flower of the dichasium (Fig. 1).

After the differentiation of the bracteoles, floral axis remains slightly triangular globe. Subsequently, the floral apex becomes flat and the triangular edges become distinct espe-
cially at the two posterior corners, anterior corner is rather round. At each corner crescent shaped primordium of the outer members of perianth develops. The floral development proceeds in the posterior parts at first and then in the anterior parts.

In the alternate position to the outer tepals, primordial swellings of inner tepals appear, subsequently. Posterior one is clear and round, and anterior two are rather flat. Inception of stamen primordia which are opposite to the outer members of perianth succeed immediately to that of inner segments of perianth. The stamens opposite to the tepals are here named ‘opposite stamens’, and those alternate to the tepals ‘alternate stamens’. Subsequently, inner opposite stamens initiate in the opposite position to the inner perianth segments.

It is difficult to distinguish the order between the inceptions of inner opposite stamens and those of alternate stamens (Fig. 2). The primordia of the alternate stamens initiate as radially oblong swellings at both sides of the primordia of outer opposite stamens. Sometimes they initiate as round swellings at one side of the primordia of outer opposite stamens. They are usually six in number and look to be formed in the spaces between primordia of inner tepals and those of outer opposite stamens. Thus, twelve primordia of stamens initiate and develop. In the later stages, mature opposite stamens are facing inward. Alternate stamens which have developed from the radially oblong primordia are facing to the outer opposite stamens. In some cases, two inward facing stamens are found in the axil of outer perianth segment; they seem to correspond to an outer opposite stamen and an alternate one which developed from the round primordium.

After the inceptions of stamen primordia, gynoecial primordia begin to develop at the inside of outer opposite stamens (Fig. 2), and a hollow is formed in the center of floral apex. As the primordia have fused laterally, the hollow becomes deeper (Fig. 3). Gynoecial cavity is densely covered with the curled hairs (Fig. 5). It remains open and becomes nectariferous pistil rudiments.

Development of the female flowers:

The floral apices of the female flowers begin to differentiate just before the beginning of winter bud unfolding. Although it is difficult to distinguish the female inflorescences from the male at earlier stages, the female have some diagnostic features: they have fewer

Figs. 1–13. Early developments of the flower in Castanopsis cuspidata var. sieboldii.
1; a young male inflorescence, bracts were removed (×40). 2; young primordia of floral parts in a male flower (×80). B: axillary bud, Po: outer tepal, Pi: inner tepal, S: stamen, G: gynoecium, symbols mean the primordium of each. 3; an almost matured male flower, note the laterally facing stamens (arrowed). F: secondary flower of the dichasium, rPo: the scar of a removed outer tepal (×40). 4; pistil rudiments of a male flower, inner opposite stamens were removed (×80). 5; a mature flower, the pistil rudiments were covered with hairs (×40). 6; a young female inflorescence (×40), bracts were removed. 7; a young female inflorescence in more developed stage (×40). 8; initiations of inner perianth lobes (×80). 9; initiations of inner opposite stamens and alternate ones (×80). 10; the same as Fig. 9, more enlarged (×160). 11; outer opposite stamens, Si: inner opposite stamens. A primordium of an alternate stamen is revealed (arrowed). 11; septal region (arrowed) (×80). 12; septal protuberances meet (arrowed) and 3 slit-like ovarian cavities are developed downwardly (×160). 13; an anomalous "flower" at the top of inflorescence (×80).
flowers and each of them situated remotely; posterior and anterior parts of the flowers develop more concurrently; and the buds of bracteoles are more conspicuous (Fig. 6, 7).

In the earlier stages of development the female flowers are similar to the male ones. As the bracteoles have differentiated, almost simultaneously, the inceptions of outer perianth segments begin. In the axils of bracteoles, there formed ovate secondary apices,
which grow finally into valve meristems of the cupule (Fig. 7). The detailed descriptions and discussions will be given in a separate paper comparing with \textit{Lithocarpus}.

Until the inception of outer opposite stamens, verticillation in which there are three members in each whorl is rather regularly progressed, although the plastochrone is very short. As in the male flowers, the inceptions of inner opposite stamens and of alternate ones begin at almost the same time (Fig. 10).

As these floral parts growing, the floral apex becomes hollow. Subsequently, three gynoecial swellings appear in front of outer opposite stamens. They develop laterally and surround the hollow. As the swellings meet laterally each other, septal protuberances begin to develop downwards (Fig. 11), and join at the base of the hollow. The hollow, subsequently, is deepened, and the aperture is narrowed by the inward development of the gynoecia. At the basal part of each gynoeicum, a slit-like locule chamber is moulded through the developments of the septa, but at the upper part it grows into a column, without any sign of septal protuberances, and fuses each other laterally and ventrally. Upwardly they elongate and at the top of them stigmatic puncta are formed. On the other hand, downwardly conjunct point of septa is deepened comparatively to the floral surface (Fig. 12). They do not fuse each other, but an ascidium-like hollow is moulded at the base of each gynoeicum. Therefore, an incomplete triloculate ovary is constituted. Development of the ovules is not until next spring. At anthesis stamens (or staminodes) do not project out of the perianth.

Flower-like structures at the top of inflorescences:

Inflorescences of \textit{C. cuspidata} var. \textit{sieboldii} are primarily indeterminate and the bracts are formed and arranged spirally on the rachis from base to apex. In the axils of bracts the flowers are dichasially arranged or solitary. In the uppermost region of the rachis, bracts are arranged more densely and have small axillary buds. Consequently, there formed small flowers which have fewer floral segments. And, at the top of it a flower-like structure is frequently constituted. On the female inflorescences they are more similar to the female flower, and have staminodes and pistil-like protuberances. On the male inflorescences they are more similar to the male flower, having stamens and staminodes.

In Fig. 13, younger stage of a typical case of such a structure on a male inflorescence is shown. The scales and the primordia are, except some additional ones, arranged in a spiral which are on the continuation to that of bracts. The removed bract (0) is the last one which has small axillary bud. Outer ones (1–5) become like perianth lobes and inner ones (7–10) and additional ones become stamens or staminodes. The sixth primordium which is opposite to the first scale usually becomes intermediate form between tepal and staminode. These flower-like structures usually develop earlier than the small flowers around them. Stamens of the male one may be functionable. Pistil-like protuberances are often teratological in shape. More than half of the inflorescences have such flower-like structures, and the others have abortive residua of the inflorescence apices.
Discussions

The initiation of the floral segments seems to be essentially tri-merous verticillate, except in the case of alternate stamens. This is easily discernible in female flowers, where the retardation of anterior part is smaller. Even in the male flowers, no distinct examples have been observed where the inner whorls initiate earlier than the outer ones. Thus three outer tepals, three inner tepals, three outer opposite stamens, three inner opposite stamens and three gynoecia initiate from outside to inside in this succession. Six alternate stamens appear almost simultaneously with the inner opposite stamens in the portion between outer opposite stamens and inner tepals. This arrangement of 12 stamens differs from that of Chrysolepis chrysophylla figured by Berridge (1914), where the six alternate stamens are inside the opposite stamens. From a preliminary observation of Japanese representatives, it is suggested that the floral development of Castanea and Lithocarpus is not different from that of Castanopsis. Bailon (1876) reported the same observation in Castanea sativa (Hjelmqvist, 1948). It seems likely that the floral development of Castaneaideae is principally as that of Castanopsis described in present study. Therefore, diplostemonous arrangement which Endress (1977) supposed is not predominant in Castaneoideae.

If the flower of Castanopsis is 6-merous, it might be expected that there is clear distinction in timing between the inception of 6 perianth lobes and that of stamens. However, it is observed that 3 outer tepals, 3 inner tepals and 3 outer opposite stamens initiate successively in trimerous verticillate arrangement. This does not support the hypothesis that the flower of Castanopsis is principally 6-merous.

The inception of alternate stamens is strange and needs some discussions. Their position, being alternate to the perianth segments and nearly outer most among stamens, may suggest that they are modified petals. However, this hypothesis cannot explain the fact that their initiations are later than those of outer opposite stamens (Fig. 10).

Hjelmqvist (1948) considered that the flowers of the Fagaceae are modified inflorescences composed of a female flower in the center and the male flowers surrounding it. Bailon's investigation of Castanea is cited as a supporting evidence. This hypothesis may be convenient to interpret the nature of laterally facing alternate stamens which are subtended by outer tepals. Although they are not conclusive, some negative evidences have been shown in present study. First, the inception of tepals and opposite stamens is typical trimerous verticillation, and their relations does not seem to be that of bract and their bud. Secondly, the outer opposite stamen and the two alternate ones do not originate from common primordia. Primordium of the alternate stamen looks to appear in the space between primordium of outer opposite stamen and that of inner tepal.

In the Fagaceae, the taxa with 12 stamens in each flower do not hold the majority. Those with 6 stamens are general. Female flower of Trigonobalanus verticillata has 6 staminodes, where outer tepals, inner tepals, outer opposite staminodes, inner opposite staminodes and gynoecia are arranged in 3-merous verticillation. This arrangement is
similar to that of *Castanopsis* except the alternate stamens. It seems likely that the 3-merous verticillation is primitive condition in the flower of the Fagaceae. I guess that the alternate stamens have resulted from secondary increase of the number of the stamens which in this case might be an adaptation to entomophily (cf. Endress, 1977). In the case of Castaneoideae inward increase is limited by the presence of pistils or pistil rudiments. Therefore, they developed outward in the radially oblong space between outer opposite stamens and inner tepals. In *Fagus* the initiation of 12 stamens may be different from that of *Castanopsis*, because the male flower of *Fagus* has no well-developed pistil rudiments.

In an indeterminate inflorescence the apex is usually abortive covered with reduced bracts. However, in *C. cuspidata* var. *sieboldii* the apex of the inflorescence sometimes becomes a flower-like structure. It is likely that the “tepals” of the flower-like structure are homologous to the bracts, because their arrangement is continuous and their appearance is similar to the bracts. It is not elucidated whether the stamens and the pistils of the “flower” are bracts or their axillary buds. If they were the bracts, they are too congregated and are even situated in deviated position; if axillary buds, on the other hand, they are too remotely situated from the bracts. Although conclusive evidences are scarce, I prefer to suggest them the bracts. Although the flower-like structures are very variable, there is no stamens in the axil of outermost bract (which corresponds the scale no. 1 in Fig. 13), and no. 6 in Fig. 13 becomes an intermediate form between tepals and stamens.

I speculate the nature of this flower-like structure as follows. As the meristematic activities of the inflorescence apex being declined, the nature of shoot apex changes. As the result of the metamorphosis into definite inflorescence, the axillary bud of each bract is no longer formed. Sterile bracts are arranged spirally and congregately, and inner ones become stamen- or pistil-like structures. Thus the flower-like structure is completed. Decrease of the meristematic activities is shown by the existence of smaller flowers in uppermost regions of the inflorescences. In some indeterminate inflorescences of the flowering plants functional “terminal flowers” might be present.

**Acknowledgement**

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**Literature cited**

摘 要 スタジイの花の各花葉が発生する様子を観察した。花の初期発生では、雄花と雌花は、
ほとんど区別しがたい程、よく似ている。雌花では各花葉の発生順序は次のようなになる。外花
被(3)→内花被(3)→外花被に対生する雌ずい(3)→内花被に対生する雄ずい(3)。この内花被に対生
する雄ずいとは同時に、花被に互生する雌ずいが形成されはじめめる。その位置は外花被に対
生する雌ずいの両側である。外花被に対生する雄ずいの内側に、雌ずいの原基があらわれる。
花被に互生する雄ずいは、放射方向に細長い原基としてあらわれる。成熟した段階ではこの雌
ずいは、横向きで、一方花被に対生する雌ずいは内向きとなる。なお、雌花ではこれらの
雌ずいは生長が停止し、仮雌ずい的となり、開花時にも花被に包まれたままのことが多い。

雄花も雌花とほぼ同様の発生順序をたどる。ただし、雄花では花の向軸側の発生が、背軸側
に比べ著しく早い。雌ずいの原基も雌花に於けると同様に発生するが、子房室は最後まで閉じ
ることなく、蜜腺となる。

このような花の発生様式をどのように解釈すべきか論議した。また花序の先端に花のような
構造ができることに言及した。

抄 録
J. Ross: The radiations regime and architecture of plant stands. 391 pp., Dr.
W. Junk Publishers, 1981. $115.00

1975年に出版されたロシア語版 "Радиационный режим и Архитектоника растительного
Локрова" の英語版である。著者の Ross (Rosc) はソビエト連邦エストニア共和国の物理学
・天文学研究所大気物理部門の指導者であり、彼らのグループはこの分野における理論的、実
験的研究で大きな貢献をしてきた。本書は彼らの成果の集大成であり、また他の多くの研究者
の成果もまとめられている広範なレビューアーである。本書は 2 部に分かれており第一部は植物群
落の幾何学的構造を、第 2 部は植物群落内の放射環境を扱っている。物理学の手法を用いた理
論展開が本書の大半を占めているが、その記述はわかりやすく理論もスマートで説きやすい。
それだけに、複雑な生物界の現象と理論の間のギャップが問題になってくるわけであるが、そ
の点についてもしっかりと議論がなされている。

英語版には、ロシア語版が出版された後に発表された多くの研究成果も盛り込まれており本
書を up-to-date なものにしている。群落光合成（本書ではこのテーマは扱われていない）の
基礎的要因を統一的に扱った本書は、植物群落の物質生産、生長などを研究する植物生態学者
や農学者にとって必読の一冊である。

(原 登志彦)