Floral anatomy of the mangrove genus
_Lumnizera_ (Combretaceae)*

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福岡誠行・伊藤元己・岩槻邦男：ヒルギモドキ属
（シクシ科）の花の内部形態

The mangrove is one of the representative forests in the tropical vegetation and is developed to the greatest extent in the wet tropics where typical rain forests are developed (RICHARDS, 1952). The mangrove plants have in common such characters as viviparous seed and peculiar root system, and are often cited as a remarkable example of convergent evolution with adaptation to particular habitat of the tidal zone at the river mouth and nearby seashore.

The mangrove consists of such species as 1) confined to this type of vegetation, 2) facultatively growing in the mangroves, and 3) spontaneously found in this type of particular habitat. The number of the obligate mangrove species is not many and belong to various unrelated families. It is not known precisely whether the adaptation to the tidal water habitat has been performed in parallel line in various families.

The origin and diversification of the mangrove species have been discussed from various aspects (STEENIS, 1958) but analytical works are still few. Comparative anatomical features are often taken up in tracing the phylogenetical relationships among the higher plants. However, the floral anatomy of the mangrove species has been observed only on a few representatives. _Bruguiera_ and _Rhizophora_ (Rhizophoraceae) was observed by ORCHARD (1975), _Lumnitzera_ (Combretaceae) by VENKATESWARLU and RAO (1970), _Avicenia_ (Verbenaceae) by RAO (1952). Thus, the observation of the floral anatomical characters is necessary to give a basic information to elucidate the natural history of the mangrove.

The family Combretaceae includes mangrove genera. EXCELL and STACE (1966) enumerated 20 genera in Combretaceae with two subfamilies. Subfamily Combretoidae was subdivided into two tribes. Tribe Lagunculariae consists of three genera,
Macropteranthes, Laguncularia, and Lumnitzera. Among them, Macropteranthes grows in inland. Two others of this tribe are the obligate mangrove genera. Laguncularia occurs in tropical America and West Africa, and Lumnitzera occurs in Asia, the Pacific, North Australia, and East Africa. The other tribe, Combretaceae, consists of 16 genera, including Combretum and Terminalia. Flowers of the Combretaceae characteristically have a uniloculate inferior ovary, anatropous ovules pending from the apex of locule, a long funicle, an unbranched stigma, and usually a long floral tube.

Floral anatomy of the Combretaceae was observed by Tlagi (1969) on four genera and seven species: Anogeisus (1 sp.), Combretum (2 spp.), Quisqualis (1 sp.), and Terminalia (3 spp.). Venkateswarlu and Rao (1970) published results of their more extensive observations on 10 genera and 20 species, including the mangrove genus Lumnitzera (L. racemosa and L. littorea), and concluded that the genus Lumnitzera had the most primitive features in this family. It seems rather peculiar that the genus confined to such a particular vegetation as the mangrove forms a basal stock of a phyletic group. In order to elucidate phylogenetically distinct aspect of the mangrove plants it is necessary to reexamine whether the genus preserves such primitive features, growing in such a distinct and evolutionary derived habitat. In this study, floral anatomical characters of four Combretaceous species are observed in detail and discussed from a systematic viewpoint.

Materials and Methods

The following three genera and four species of Combretaceae were investigated on the floral anatomical characters. They were selected to represent both the mangrove and non-mangrove members of this family. All voucher specimens are preserved in the Herbarium of Kyoto University (kyo).

Combretum pilosum Roxb. Klung, Chanthaburi, Thailand, N. Fukuoka & M. Ito T-35087.


Lumnitzera racemosa Willd. Irionote Island, Ryukyu, Japan, N. Fukuoka & M. Ito 148.

Terminalia catappa L. Ishigaki Island, Ryukyu, Japan, N. Fukuoka & M. Ito 339.

Flowers were fixed in the field and stored in 75% ethyl alcohol. For anatomical observation all materials were softened with 5% KOH at 60°C for two to three hours and kept for several hours at room temperature to make sectioning easier. Flowers thus treated were dehydrated through an n-butyl-alcohol series, embedded in paraffin-wax, and serially sectioned. Sections were cut at thickness of 10 μm to 20 μm, and stained with safranin. Several flowers were cleared by commercial bleach.
Fig. 1. Cross sections of flower in *Lumnitzera racemosa*. (A & B: ×29; C~F: ×18) A. At receptacle; B. At bottom of locule; C. Above middle level of locule; D. Near upper one-third of locule; E. At upper level than D; F. At level of base of sunken disc; G. At base of floral tube; and H. At upper level than G. b: bracteole bundle; cm: median sepal one; cms: stamen-median sepal one; o: bundle around locule supplying ovule and style; s: stamen bundle; head of arrow: disc one.
Fig. 2. Flowers of *Lumnitzera racemosa* (A) and *L. littorea* (B-D). (A: ×19, B: ×38, C & D: ×96)

A. Longitudinal section in upper half of ovary (d: sunken disc; head of arrow: bundle supplying ovule and style;  B. Cross section in upper half of ovary;  C. Near apex of locule (head of arrow: connections between placentas and ovary wall; and  D. At still upper level than C showing another connection between them (head of arrow: bundles supplying placenta).
Observations

1. Floral anatomy of *Lumnitzera*.

The floral anatomy of *Lumnitzera* was observed by Venkateswarlu and Rao (1970), although the results of their observations differ from those of ours in many respects and their descriptions are too fragmentary to realize all features. The floral anatomy of *Lumnitzera* is, therefore, described here in detail.

The flower is bisexual and more or less bisymmetric (Fig. 4–B). Calyx-lobes are valvate in bud, and petals are contorted. Stamens are nine or ten in number in *L. racemosa* and six to eight in *L. littorea* (or ten, Venkateswarlu and Rao, 1970). In both species, antisepalous stamens are always five. In *L. littorea* antipetalous stamens are one to three, and one of them is usually filiform and sterile. There is no stamen observed at the ventral side, where a style is adnate to the base of the short floral tube (Fig. 4–B). The inferior ovary is compressed dorsal-ventrally in *L. racemosa* (Figs. 1–C, D) but in *L. littorea* not compressed (Fig. 2–B), and is fused by two bracteoles in different levels at higher position. A locule usually contains three or four pendulous ovules in both the species (Figs. 2–A, C), but some flowers of *L. racemosa* bear two or five ovules. A round placenta is attached to the ovary wall at the uppermost level of locule (Fig. 2–A). The ovules are not positioned at the same level (Figs. 2–C, D). In some flowers of *L. littorea*, ovules are borne at three or four points on the ovary wall in relation to the number of ovules (Figs. 2–C, D). A placenta is divided into the same number as that of ovules except for uppermost portion of locule. An annular disc is sunken in inferior ovary in *L. racemosa* (Figs. 1–F, G; 2–A). In *L. littorea* the sunken disc is not annular, and is lacking at the part where a style is adnate to.

The description of floral vasculature will be started with that of *L. racemosa*. In a short pedicel, there are one rhomboidal, two round, or two U-shaped bundle(s). At the lowest level of the ovary, two bundles are thickened and assume V-shape in cross section. These two V-shaped bundles fuse with each other at the opposite ends of their respective arms to form a continuous bundle. This continuous bundle divides upwardly and radially into six to nine separate bundles just below the bottom of locule (Figs. 1–A, B). Of these bundles, the two opposite bundles closest to two opposite bracteoles give off bracteole bundles which are usually distinct even at the base of receptacle (Figs. 1–A, B). The bracteole bundle forks upwardly into three in the bracteole lamina.

The six to nine bundles in the ovary wall successively divide upwardly and radially (Figs. 1–B~F). At the middle level of locule 10 to 15 bundles are observed. Near this level the bundles successively give off inwardly vascular branches and smaller ones. The smaller bundles running between the inner bundles and the outer bundles become more distinct from the outer bundles (Fig. 1–D), as the outer bundles move upwardly toward the periphery of ovary wall. The inner bundles are about 13 to 14 in number and remain around the locule (Fig. 1–D), and become concentric at the upper one-
third of the locule. These concentric bundles divide upwardly toward tangential and radial directions, so that about 25–30 small bundles are observed around the locule (Fig. 1–F). About eight of these innermost bundles become bicolateral, and enter into the placenta above the locule and then come down into funicles (Fig. 2–A). There are some cases in which each of three or four ovules is supplied by one, two, or three distinct bundles. In these cases the fusion of placentas (represented by funicles) is so imperfect that the three or four placentas are distinguishable from one another.

Above the level where ovule bundles depart, all the bundles remaining in the center of the ovary run up into a style (Figs. 1–G, H). The number of these bundles is about 20–25. Among them about ten outer bundles are relatively large, and the other inner ones smaller. The former extends to the top of the style, while the latter ends blindly in a lower half of the style.

Just above the level where the bundles supplying the periphery of the ovary wall separate from those around the locule, they give off inwardly nine to eleven small bundles (Fig. 1–D, arrows). In addition, one to four of the bundles around the locule give off vascular branches outwardly. Thus, 11–15 bundles in total arrange in a circle in cross section between the circles formed by the bundles in the periphery and by those around the locule (Figs. 1–D, F). Some of the 11–15 bundles divide radially in the lower level than this. Just below the level of the disc, every bundle in this circle forks into several bundles and enters the disc.

At the level where the disc bundles (i.e. the bundles supplying the disc) are arranged in a circle, there are 21–29 bundles in the epiphery of the ovary (Fig. 1–F). These bundles vary in size, with ten larger bundles of them being upwardly distinguishable from the other bundles (Figs. 1–F, H). The bundles in the periphery may divide radially and give rise to 27–33 bundles at the maximum at the level of disc (Fig. 1–F). Of the 10 larger bundles, five bundles diverge upwardly tangentially (Fig. 1–G), and successively supply five antisepalal stamens and five calyx-lobes (Figs. 1–G, H). At the level where the antisepalal stamens are free, the antipetalal stamen bundles are branched off inwardly from the remaining five of the ten larger bundles (Fig. 1–G), stamen-petal-compound lateral sepal bundles. After separating stamen bundle petal-compound lateral sepal bundle divides into a petal bundle inwardly and two lateral sepal bundles outwardly above the level where antipetalal stamen is free. A petal bundle forks into three at the very base of petal. Such separation of the stamen-petal-compound lateral sepal bundles occurs at first at the dorsal side of the flower and then at the ventral side, according to the separation of filaments and petals from a floral tube (Figs. 1–G, H). On the other hand, the remaining smaller bundles of the peripheral wall end blindly near the level where the antisepalal stamens are free. Each calyx-lobe receives three bundles, of which the larger median upwardly trifurcates.

The floral vasculature of L. littorea is fundamentally the same as that of L. racemosa, but differs in minor points, especially with respect to the course of bracteole bundles as
Fig. 3. Cross section of ovary above locule in *Lumnitzera littorea*. (A: ×48; B: ×30) cm: median sepal bundle; lc: lateral sepal one; p: petal one; s: stamen one.

Fig. 4. Floral vasculature of *Lumnitzera*. A. Diagram showing vasculature of flower in *L. racemosa*; B. longitudinal section of flower in *L. littorea* (×5). b: bracteole; c: calyx-lobe; p: petal; s: stamen.
well as that of the bundles in the periphery of the ovary wall. In L. littorea an elliptic bundle gives off outwardly the medina bundle to each of two bracteoles at the base of receptacle, and the other bracteole bundles (0-2 in number) are branched at still the upper level. One, two, or rarely three bundles run into the lower bracteole. In the case when only one bundle runs into it, this bundle enters, without branching, the short free part of bracteole, or divides into three in the fused part. When two bundles are branched off, one of them divides into two, and then three bundles enter the free part. The upper bracteole is usually supplied by three distinct bundles, or rarely by two, each of which divides into two.

After the departure of two median bracteole bundles, an elliptic bundle divides into two. These two divide radially in a lower half of a part below the locule and subsequently the bundles divide radially and tangentially between the bottom and the top of ovary. At the bottom of locule there are about 20 bundles that scatter in the middle portion of ovary wall. At the upper two-thirds of the locule the inner and small bundles in the ovary wall move inwardly. These bundles are arranged in a circle and then scattered around the locule as the result of radial and tangential divisions as in L. racemosa. After these bundles move inwardly, there are about 60 bundles observed in the periphery of ovary wall (Fig. 2-B). Among them the inner and small bundles move inwardly and are scattered in the disc.

All of these about 60 bundles run up in the floral tube. Among them several smaller bundles end blindly. Most of the bundles are gathering into ten groups in still upper level (Fig. 3-A). Each of the five groups consists of an antipetalous stamen bundle (sometimes lacking), three petal bundles, and two lateral sepal bundles (Fig. 3). Each of the other five groups consists of an antisepalous stamen bundle and a median sepal bundle arranged in a pair (Fig. 3). The other bundles do not form any groups

Fig. 5. Cross section of flower in Terminalia catappa (A & B) and Combretum pilosum (C). A. In upper half of ovary (×29); B. At base of style (×72); and C. At uppermost level of locule (×45).
and enter into the base of calyx-lobes.

2. Floral anatomy of *Combretum* and *Terminalia.*

These two genera were described on their floral anatomical features by Tiagi (1969) and Venkateswarlu and Rao (1970). Tiagi (1969) described them in detail, and his results well match those of our observation. Therefore, only additional descriptions will be given below.

In *Combretum pilosum* the locule contains two ovules (Fig. 5–C) and the disc is not observed. Five bundles run up in the ovary wall and are position opposite the calyx-lobes or sepals (Fig. 5–C). These bundles are flat in a tangential direction as observed by Tiagi. Figure 6 shows the vasculature of these five bundles in the floral tube of *Combretum pilosum.* An antisepalous stamen bundle is branched off inwardly from each of these five. Above this level each of the five bundles gives off laterally a few branches each on both sides ending blindly in floral tube. The antipetalous stamen is supplied by two or three bundles branched off laterally from adjacent bundles below the stamen. These lateral branches fuse to an alternate bundle forming a conjugated bundle which then enters the stamen. According to Tiagi (1969), this bundle divides tangentially into an antipetalous stamen and a petal bundle in the petalous genera, *Combretum* and *Quisqualis.* Venkateswarlu & Rao (1970) described, however, that the bundles originating from two adjacent bundles give off the supply for the antipetalous stamen and the petal midrib as well as for the conjoint sepal margins successively in *Combretum, Guiera* and *Quisqualis.* We traced the vascular course carefully by serial cross sections as well as cleared materials of *Combretum pilosum,* and found that the antipetalous stamen bundle enters the stamen alone. The petal bundles are formed by lateral branches given off newly from two adjacent bundles. A petal bundle forks into three at the base of the petal. Five bundles run up to the apex of five calyx-lobes giving off several lateral branches on the way.

According to Tiagi (1969), an alternisepalous (antipetalous) stamen bundle is formed in the apetalous genera, *Anogeisus* and *Terminalia,* in the same way as in the petalous genera mentioned above. Tiagi noted that this bundle may further give off a few marginal bundles of sepals on either side. In our observation, however, all of the alternisepalous stamen bundles of *Terminalia catappa* enter the stamen as in the case of *Combretum pilosum.* Then, each of the five bundles which are opposite the calyx-lobes gives off horizontally one lateral branch on each side and that branch runs up along the margin of calyx-lobe.

Tiagi (1969) also described five bundles running in the ovary wall of *Terminalia arjuna* and *T. beleria,* and Venkateswarlu and Rao (1970) also observed those five bundles in *T. arjuna, T. catappa, T. chebula,* and *T. myriocarpa.* In *T. catappa,* however, we observed that the ovary wall has more numerous bundles, as observed by Tiagi. Many bundles, varying in number from eight to 12, repeat fusion and division (Fig. 6).
These bundles give off many branches ending blindly in all the directions (Fig. 5-A) at levels between the bottom and the top of locule. Near the top of inferior ovary these bundles reduce in number into five. Above this level the vasculature in the floral tube is fundamentally the same as in Combretum and the others.

According to Tiagi (1970) the style of Terminalia catappa is supplied by two dorsal and four marginal bundles; however, according to Venkateswarlu and Rao (1970), it receives two dorsal and two ventral bundles. Based on our observation, there are two flattened bundles facing placentas in the center of ovary just below the level where ovular bundles depart. The ovular bundles are branched off from the center of these flattened bundles. After then each of the two flattened bundles divides radially and upwardly into two bundles. Among the four bundles the two bundles originating from the different flattened bundles unite into a new flattened bundle at dorsal side of locule, alternate position to placenta. These bundles become circular in slender sterile beak and run up in a style (Fig. 5-B).

Discussion

In Terminalia catappa, the bundles in ovary wall give off short branches (Tiagi,
1969). Tiagi regarded these branches as the vascular stubs of lost ovules. Based on this observation Tiagi explained that an unique placentation of Combretaceae has derived from the parietal placentation bearing numerous ovules on each placenta. In our observation, such branches are given off in all directions (Fig. 5-A) even below and above the locule, without any anatomical relation to ovules. Thus, the vascular branches are hardly considerable to be the vascular stub of the lost ovules. In T. catappa, although many bundles are present in ovary wall, they reduce into five at the base of floral tube as in the other species of Terminalia (Tiagi, 1969), and the vasculature in the floral tube is fundamentally the same as that of the other species. Considering this fact, the peculiar vasculature of T. catappa, which grows in sea coast, may be regarded as not representative of a primitive state but the derivative from the ovary wall vasculature involving only five bundles. The placentation of Combretaceae is apparently parietal at the top of the locule (Figs. 2-C, D; 5-C). We agree with Tiagi on his consideration that the apical placentation of Combretaceae was derived from the parietal one, although we cannot agree on the point that the common ancestors of the Combretaceae have many ovules on the placenta. However, there is no evidence indicating that an ancestral Combretaceae had a multiovulate locule. Further studies on the placentation of this family are necessary.

In Combretaceae the uniloculate ovary has an apical placentation and the style is simple, so the number of carpels constituting a pistil had been unknown. Tiagi (1969) reported that the number of ovules agrees usually with that of dorsal bundles. According to Venkateswarlu and Rao (1970), the number of dorsal bundles is the same as or twice as many as that of placenta. In Combretum pilosum, the number of dorsal bundles observed here agrees with that of ovules (Fig. 5-C). In Terminalia catappa, on the other hand, a style is supplied by a vascular ring (Fig. 5-B), so the dorsal and ventral bundles can not actually be distinguished. Venkateswarlu and Rao concluded that the pistil of Lumnitzera consisted of eight carpels on the basis of the fact that the style received eight dorsal bundles. In our observation, however, the style is supplied by more than twenty bundles that are not arranged in a circle in cross section (Fig. 1-G; 2-C, D). In Terminalia catappa and two species of Lumnitzera, it is rather difficult to trace the dorsal bundles among those entering the style. In the former species, there are two placentas each of which is supplied by a single bundle. In the latter two species the placenta and its vascular supply are not so distinct, and only in some cases of L. littorea the presence of three or four connections (placentas) between ovules and ovary wall is confirmed (Figs. 2-C, D). The apical placentation of Combretaceae may be what has been derived from the parietal placentation, as mentioned above. The number of ovules accords exactly with that of placentas. Therefore, the number of carpels constituting a pistil can be estimated by counting that of ovules. In Lumnitzera, thus, a pistil consists of three, four, or rarely two or five carpels.
Venkateswarlu & Rao (1970) regarded Lumnitzera as the most primitive genus of Combretaceae, because the genus possesses such features as racemose inflorescence, three-traced sepal, the presence of petal, richly vascularized annular disc, and the pistil composing of probably eight carpels. The inflorescence of Lumnitzera is fundamentally the same as that of Combretum and Quisqualis (Excell, 1954). The sepal is three-traced in Lumnitzera and one-traced in the other genera observed, although the former feature may be related to the broader form of sepal. The petal is present in Lumnitzera as well as in Combretum and Quisqualis, and petalous genera are usually regarded as primitive; and most of the other genera are apetalous. A petal bundle forks into three at the base in all petalous genera observed, except in L. littorea in which the three petal bundles are distinct even in the part of inferior ovary. This feature in the last species may be referred to as a rather specialized character. Venkateswarlu & Rao noted that the non-vascularized disc seemed to be resulted from the reduction of bundles from the vascularized disc. This speculation is not acceptable, because the morphology of disc is different between Lumnitzera and the others. They also regarded the disc of Lumnitzera as primitive based on Fahn's idea (1953) that the phylogenetic migration of the nectariferous tissue is acrocentripetal. Following Fahn, Lumnitzera may even be referred to as more advanced in the position of the disc than the others, because the disc is on the top of inferior ovary in Lumnitzera but on the floral tube in other genera. The disc of Lumnitzera may be specialized than a swollen disc common to other genera. A pistil consists of three, four, or rarely two or five carpels in Lumnitzera, contrary to Venkateswarlu and Rao's observation to be eight. Two bracteoles are completely fused to ovary and this feature is also referable to as advanced. Thus, the mangrove genus, Lumnitzera, is characterized by a combination of the primitive and advanced features.

On the basis of floral anatomical characters, Lumnitzera stands out from all other genera of Combretaceae. In Lumnitzera the bundles in the periphery of the ovary wall increase in number in the upper part of ovary. Of these bundles, the five distinct bundles are five antisepalous stamen-median sepal bundles and the other five distinct bundles are five antipetalous stamen-petal-compound lateral sepal bundles. The remaining bundles divide into smaller ones and end blindly near the level at the base of floral tube. These small bundles may be subsidiary ones of calyx vasculature. The increase of the number of bundles in the periphery of ovary wall is resulted from the division of subsidiary bundles in Lumnitzera racemosa and it is from that of the bundles supplying stamens, petals, sepals and subsidiary bundles in L. littorea. In the other genera, except in Terminalia catappa, there are five bundles in the ovary wall. These five bundles are flattened tangentially in the ovary wall in Anogeisus (Tiagi, 1969) and Combretum, and not in Quisqualis (Tiagi, 1969) and Terminalia. Near the top of ovary the bundles become round in Anogeisus and Combretum and run up in the floral tube. From the floral anatomical point of view, as mentioned above, Lumnitzera and the others
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seem to have evolved independently in different lines of specialization: the increase in
number of bundles by division occurs in the former, and the decrease by fusion occurs
in the latter.

Summarizing the observations of the floral anatomical features, it is suggested to
separate *Lumnitzera* distantly from the inland genera of this family. As *Laguncularia*
has not been observed for the floral anatomical features, it is difficult to conclude the
systematic position, although our suggestion based on the comparison of external mor-
phology is that it is related to *Lumnitzera*.

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摘要 シクシ科 Combretaceae は主に熱帯・亜熱帯に分布し、20属450種からなる。この
内ヒルギモドキ属 Lumnitzera と Laguncularia 属がマングロープに生育する。

*TIAGI*はシクシ科の4属7種について花の内部形態を観察し、この科の頂生胎座型は多数
の胚珠をもつ側膜胎座型から由来したと考えた。胎座が側膜状となるのでこの考えに賛成で
ある。しかし彼はコパティシ Terminalia catappa の子房壁における水平に分枝される短い管
束の枝を消失した胚珠へ入る管束の痕跡とみなしているが、この解釈には無理がある。

*VENKATESWARLU & RAO* はヒルギモドキ属 2種を含む10属20種の花の内部形態を報告し
た。彼らはヒルギモドキ属が、総状花序で、花は花冠があり、花弁が3管束性で、花盤が多
数の管束を受け、雌しつが8心皮性であることから、シクシ科の中で最も原始的であるとし
た。しかし小苞は子房に強く合着し、花弁は下位子房に埋没した特殊な型であり、雌しつの退
化もみられる。

シクシ科は花の管束走行からヒルギモドキ属にみられるような、子房壁の管束が27～60本
と数が多い群と、子房壁に5本の管束がある群に分けられる。一方は分裂により増数し、他方
は合着により減数したと考えられる。

マングロープといった特殊な環境に生えるヒルギモドキ属が原始的であるとは考えにくい。
むしろ花の管束走行から推測できるように、ヒルギモドキ属とその他の群はそれぞれ特殊化し、
これら2群は分類学的に謎道な関係にあると考えられる。