Anatomy and Development of Leaves in *Chamaecrista mimosoides* and *C. nomame* (*Leguminosae-Caesalpinioideae*)

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*Chamaecrista mimosoides* (L.) Greene has a unique even-pinnate leaf with crenate-crested protuberances on the adaxial side of the rachis between leaflet pairs, which is one of the important characteristics for distinguishing it from other species with leaf rachises canaliculate. The present study clarified anatomical and developmental features of the leaves with the crenate-crested rachis in *C. mimosoides* in comparison with those with a canaliculate rachis in *C. nomame* (Makino) H. Ohashi. Transverse sections showed that the crenate-crested rachis has a protuberance constructed by continuous parenchymatous tissues composed of cells rich in chloroplasts, whereas the canaliculate one has two ridges constructed by two independent parenchymatous tissues. Developmental observations showed that the crenate-crested rachis is initiated as a single swelling of tissues, whereas the canaliculate one initiated as two parallel swellings of tissues. Both rachises have commonly two ridge bundles divided from the main vascular bundles in the petiole, but the two ridge bundles are fused into one bundle in the proximal half of the crenate-crested protuberance between leaflet pairs, and then divided into two again in the distal half. In contrast, the two ridge bundles remain separated throughout the length in the canaliculate rachis. The fused ridge bundles in the crenate-crested protuberance, moreover, branch a small bundle into the protuberance. At the distal part of the petiole there is an extrafloral nectary (EFN) in both species. The vascular bundles are supplied to the EFN from each of two ridge bundles in the petiole in *C. mimosoides*, whereas from the main vascular bundles in *C. nomame*. The repetition of fusion and separation of two ridge bundles in the crenate-crested leaf rachis seems to support the idea that the rachis is produced by fusion of two ridges of the canaliculate rachis. The chloroplast-rich cells observed in the crenate-crested protuberance as well as many stomata in the epidermis suggest that the protuberance may improve the ability of photosynthesis.

**Key words:** Anatomy, *Caesalpinioideae*, *Cassieae*, *Chamaecrista mimosoides*, *Chamaecrista nomame*, development, extra floral nectary, *Leguminosae*, leaf, leaf rachis.

The genus *Chamaecrista* Moench is a pantropical and subtropical genus of about 330 species, with greatest diversity in Central and South America and tropical Africa (Lewis 2005). Species of this genus were formerly placed as parts of the genus *Cassia* L. (Candolle 1825,

Among these Asian species, Chamaecrista mimosoides (L.) Greene is the most widely distributed species, extending into Africa (Lock 1989) and Australia (Pedley 1998). The leaf rachis of C. mimosoides was described as “of the young leaves furnished on its upper side with a crenated margin” by Wight and Walker-Arnott (1834, as Cassia angustissima Lam.). The leaf rachis, distinctly crenated or crenate-crested on the adaxial side between leaflet pairs, has been regarded as unique to C. mimosoides (or Cassia mimosoides) and adopted as a useful character distinguishing it from other species with distinct leaf rachis grooved, canaliculate or channeled along the adaxial side in floras of various regions (Ghesquière 1932, Steyaert 1950, Brenan 1967, Larsen et al. 1980, Rudd 1991, Larsen and Ding 1996, Pedley 1998, Singh 2001, Du Puy 2002). Brenan (1967) noted the leaf rachis as one of the most significant features for separating the species under the genus Cassia sensu lato in the tropical East Africa and that there is a channel running along the upper side of the leaf rachis in most species, while some species including Cassia mimosoides have a raised wing-like projection running along the upper side of the rachis. Du Puy (2002) also listed the presence or absence of a crenate crest along the upper side of the leaf rachis as one of the most useful characters in distinguishing between the species in Madagascar.

Lock (2007) considered that the solid crest of the crenate-crested rachis is produced by fusion of two ridges of the canaliculate rachis. Leaf structure including rachises has been examined in Chamaecrista (or as Cassia) by several authors such as Watari (1934, as Cassia mimosoides var. nomame), Saheed and Illoh (2010, Cassiinae including Chamaecrista mimosoides), Coutinho et al. (2013, Chamaecrista sect. Absus subsect. Baseophyllum), Francino et al. (2015, Chamaecrista sect. Absus). But Chamaecrista mimosoides (sect. Chamaecrista) itself and the unique crenate-crested leaf rachis have not been examined so far. Although the unique rachis feature has been recognized, our understandings of the structural relationships between the crenate-crested leaf rachises and canaliculate ones have been poor.

The present study aims to clarify the structural relationships between the crenate-crested rachises and the canaliculate ones in Chamaecrista. For this objective we performed anatomical and developmental analyses on the crenate-crested rachises of C. mimosoides in comparison with the canaliculate rachises of C. nomame (Makino) H. Ohashi.

**Materials and Methods**

Morphology and structure of leaf rachises were examined anatomically and organogenetically in Chamaecrista mimosoides (L.) Greene and C. nomame (Makino) H. Ohashi. Materials of C. mimosoides were collected from Hushan hill, Jianfeng, Ledong Co, Hainan, China on 21 Oct. in 1993 (Voucher: T. Nemoto et al. 1021001) and those of C. nomame collected from Narusegawa River, Junai, Nakaniida-machi, Kami-gun, Miyagi Prefecture, Japan on 18 Aug. in 1983 (Voucher: T. Nemoto 2277). Collected materials were preserved in FAA. Both voucher specimens are kept in TUS.

Leaves were examined according to the
developmental stages along some shoots from proximal to distal orders. Within a leaf the distal half was used for SEM observations and the remaining proximal half used for anatomical ones. For morphological observations using SEM, leaves were dissected and half of the leaflets were removed for enabling observation of the rachis above between leaflet pairs, then dehydrated through an ethyl alcohol series, transferred to t-butyl alcohol, freeze-dried in a Freeze Dryer VFD-21S, mounted on brass stubs, coated with gold, and observed by a JEOL JSM-6380LV scanning electron microscope. For anatomical observations, leaves were dehydrated through an ethanol series and embedded in a methacrylate resin (Technovit 7100). Sections were made using a Leica RM2165 rotary microtome at a thickness of 2 or 3 µm, stained with 0.05% Toluidine Blue O in benzoate buffer, pH 4.4 (Feder and O’Brien 1968) and then mounted with Entellan. Observations were performed with a Leica DMRX light microscope and photographs were taken with a Leica DC 200 digital camera.

**Results**

**Morphology and anatomy of the leaf rachis**

Leaves are even-pinnate both in *Chamaecrista mimosoides* and *C. nomame*. The leaf is composed of pulvinus, petiole and rachis with many regions of leaflet pair insertion. Mature leaves of *C. mimosoides* have crenate-
crested ridges between leaflet pairs on the adaxial side of their rachises and the ridges are ca. 200 μm height from the upper margin of the leaflet base (Fig. 1A). The surface of the ridges is almost glabrous. Mature leaves of *C. nomame* have rachises grooved or canaliculate on their adaxial side between leaflet pairs (Fig. 1B). Two ridges forming the groove are covered with trichomes.

Transverse sections of leaf rachises showed that the crenate-crested ridge of *Chamaecrista mimosoides* is composed of just a single swelling of tissues (Fig. 1C, E), whereas the canaliculate rachis of *C. nomame* is composed of two swellings of tissues forming the groove (Fig. 1D, F). The vascular tissues form a cylinder surrounded by sclerenchyma cells or fibers. There is one additional vascular bundle in *C. mimosoides* and two bundles in *C. nomame*. The number of these vascular bundles is in accordance with the number of ridges between leaflet pairs, and they are those called ridge bundles (Watari 1934), rib traces (Howard 1979) or accessory bundles (Coutinho et al. 2013, Francino et al. 2015). These bundles are also abaxially or externally associated with sclerenchyma cells. In *C. mimosoides*, moreover, a small seemingly vascular tissue is found in the crenate-crested swelling (Fig. 5, arrowhead). Chloroplasts contained in the parenchyma cells between the epidermis and the vascular tissues are more conspicuous in *C. mimosoides* than *C. nomame* (Fig. 1E, F).

**Development of leaf rachis between leaflet pairs**

*Chamaecrista mimosoides* — In the leaf of ca. 1.8 mm long (Fig. 2A, B), leaflet pairs are borne close to each other and club-shaped or short bottle-shaped colleters are borne on the adaxial side of the rachis. Each colleter is located just between leaflet pairs. The adaxial surface of the rachis between colleters is ca. 20 μm long and flat, on which there are no protuberances observed. The main vascular bundles of the rachis have begun differentiating. Although unicellular trichomes are already borne on the abaxial side of the rachis, they are not on the adaxial side.

In the leaf of ca. 3 mm long (Fig. 2C, D), the length of the rachis between leaflet pairs is ca. 94 μm. A protuberance is observed on the adaxial side of the rachis between leaflet pairs. The height of the protuberance from the upper margin of the leaflet base is ca. 25 μm. Unicellular trichomes have been borne between the protuberances on the adaxial side of the rachis.

In the leaf of ca. 6.5 mm long (Fig. 2E, F), the length of the rachis between leaflet pairs is ca. 135 μm. The protuberances between leaflet pairs become conspicuous, more than 50 μm in height and crenate in form. Although there are few colleters and trichomes between the crenate protuberances, the protuberance itself is still glabrous.

In the leaflet of almost mature leaf of ca. 28 mm long (Fig. 2G), the protuberance becomes more than 400 μm long in length and more than 130 μm in height. The surface is almost glabrous, but many stomata are observed differentiating on it (Fig. 2H).

*Chamaecrista nomame* — In the leaf of ca. 3.4 mm long (Fig. 3A, B), leaflet pairs are borne close to each other and short bottle-shaped colleters are borne on the adaxial side of the rachis. Each colleter is located just between leaflet pairs. The adaxial surface of the rachis between colleters is ca. 40 μm long and flat, on which there are no protuberances observed. The main vascular bundles of the rachis have begun differentiating. Although unicellular trichomes are already borne on the abaxial side of the rachis, they are not on the adaxial side.

In the leaf of ca. 4.2 mm long (Fig. 3C, D), the length of the rachis between leaflet pairs is ca. 80 μm. Two protuberances are borne in parallel on the adaxial side of the rachis between leaflet pairs or between colleters at this stage. The height of the protuberances from the upper margin of the leaflet base is less than 25μm.
Fig. 2. Leaf rachis development in *Chamaecrista mimosoides*. A. Leaf of ca. 1.8 mm long, showing the adaxial side of rachis with no protuberances initiated (arrows) between leaflet pairs. B. Transverse section of A at the rachis between leaflet pairs, showing the adaxial surface of rachis still being flat (arrow). C. Leaf of ca. 3 mm long, showing initiation of protuberances (arrows) along the adaxial side of rachis between leaflet pairs. D. Transverse section of C at the rachis between leaflet pairs, showing a protuberance (arrow). E. Leaf of ca. 6.5 mm long, showing protuberances (arrows) growing along the adaxial side of rachis between leaflet pairs. F. Transverse section of E at the rachis between leaflet pairs, showing a protuberance (arrow). G. Almost mature leaf of ca. 28 mm long, showing a protuberance (arrow) along the adaxial side of rachis between leaflet pairs. H. The protuberance of G enlarged, showing stomata (arrowheads) on the surface. c, colleter; lt, leaflet; mb, main vascular bundles of rachis; *, scar of leaflet removed. Scale bars: 20 μm (A, B); 50 μm (C–F); 100 μm (G, H).
There are no unicellular trichomes borne on the surface of the protuberances.

In the leaf of ca. 6 mm long (Fig. 3E, F), the length of the rachis between leaflet pairs is ca. 125 μm. The number of colleters between leaflet pairs increases to two and unicellular trichomes are borne on and between the protuberances. Two protuberances form a groove of ca. 40 μm in depth between them on the adaxial side of the rachis.

**Anatomical features from node to petiole**

The leaf is supplied with three foliar traces, or trilacunar type, in both species (Fig. 4A, E). After the two lateral traces divide into stipule traces, the three traces fuse with each other and
Fig. 4. Vascular system from the node of stem to petiole (A–H) and extrafloral nectary (EFN) (I–L) in *Chamaecrista mimosoides* and *C. nomame*. A–D and I. *C. mimosoides*. E–H and K and L. *C. nomame*. A, E. Node of stem, showing the departure of three foliar traces (arrows) from the vascular cylinder of stem. B, F. Middle part of pulvinus, showing the main bundles formed in arc by three leaf traces fused. C, G. Near distal end of pulvinus, showing a pair of ridge bundles (arrows) separated from the both margins of the arc of petiolar bundle. D, H. Slender part of petiole between pulvinus and extrafloral nectary, showing slight two ridges (D) vs. obvious ones (H), a pair of ridge bundles (arrows) running beneath the two ridges (D, H), main vascular bundles in arc (D) vs. those divided into three (H), and fibers externally collateral with vascular bundles (D, H). I, K. EFN borne on the distal end of petiole, showing the position of EFN closer to the first leaflet pair in I than in K and the differences in size and shape. J, L. Transverse section of petiole at EFN, showing traces (arrowhead) supplied to EFN from ridge bundle in J and from both margins of the arc of main vascular bundles in L. lt, first leaflet; mb, main vascular bundles of rachis; n, EFN; p, crenate-crested protuberance; *, scar of first leaflet removed. Scale bars: 100 μm.
form a central arc in the pulvinus (Fig. 4B, F). At the distal part of the pulvinus two vascular bundles, or ridge bundles, are separated from the central arc toward the adaxial side (Fig. 4C, G). The adaxial ridges of the petiole are slight in *Chamaecrista mimosoides* (Fig. 4D), whereas they are obvious in *C. nomame*, but a pair of ridge bundles obviously runs along the ridges in both species (Fig. 4D, H). The central arc running in the pulvinus is still as an arc in the petiole in *C. mimosoides*, whereas it divides into three bundles in *C. nomame*. These three bundles of *C. nomame* become an arc connecting to each other in the distal part of the petiole (Fig. 4L).

At the distal end of the petiole, immediately below the first leaflet pair, there is one extrafloral nectary (EFN) in both species (Fig. 4I, K). The EFN appears slightly sunken in a shallow hollow surrounded by the ridges on the adaxial side of the petiole. The EFN of *C. mimosoides* is flat and dish-shaped, while those of *C. nomame* is larger, rounded and thicker than *C. mimosoides*. The EFN tissues are composed of a layer of epidermis and parenchyma below the layer. The parenchyma appears to be composed of two areas: the distal area composed of cells with dark-stained cytoplasm, and the proximal area composed of cells without such stained cytoplasm. The vascular tissues are supplied to the EFNs from each of two ridge bundles in *C. mimosoides* (Fig. 4J), whereas they are supplied from both margins of the central vascular arc in *C. nomame* (Fig. 4L). The vascular tissues enter within the proximal area, and they appear to be composed mainly of phloem cells. The epidermis of the EFN is slightly elevated at the central area of the top in both species (Fig. 4J, L).

**Vascular system in leaf rachis through the region of leaflet pair insertion**

*Chamaecrista mimosoides* — The main vascular bundles are arranged in a circle or cylinder surrounded by a complete ring of fibers throughout the rachis (Fig. 5A–L). The ridge bundles running along the crenate-crested protuberance form a single bundle at the proximal half of the region between leaflet pairs (Fig. 5A, B, I–L). Around the middle part of the region between leaflet pairs, the height of the crenate-crested protuberance becomes the tallest and the ridge bundle is divided into two bundles (Fig. 5C). These two ridge bundles run toward the next region of leaflet pair insertion (Fig. 5D–F). Near the region of leaflet pair insertion the leaflet trace begins to depart from both sides of the main vascular cylinder of the rachis (Fig. 5F). Each of two ridge bundles branches off a bundle laterally and outward, which connects with each leaflet trace on both sides of the region of leaflet pair insertion (Fig. 5G, H), then two ridge bundles fuse to each other forming a single ridge bundle when the crenate-crested protuberance becomes increasing the height,
Fig. 6. Vascular system in leaf rachis through the region of leaflet pair insertion in *Chamaecrista nomame*. Serial transverse sections are arranged from proximal to distal parts across the region. A. Leaf rachis below the region of leaflet insertion, showing two ridge bundles (arrows) running along two ridges and leaflet bundles starting departure from the ring of main vascular bundles. B–G. Leaf rachis at the region of leaflet pair insertion, showing the division of each ridge bundle into two external and internal ones (B), the external bundles connecting with leaflet bundles on both sides (C, D), the internal bundles becoming next two ridge bundles (arrows) (D–F), and small bundle (arrowhead) apparently connecting these two ridge bundles (C–E). H, I. Leaf rachis above the region of leaflet pair insertion, showing the increasing height of ridge, the increasing depth of groove between two ridges, and two ridge bundles running under two ridges. lb, leaflet bundle; lt, leaflet; mb, main vascular bundles of rachis. Scale bar: 100 μm.
even before separating leaflets at the region (Fig. 5I). The ridge bundle continues fusing until the middle of the region between leaflet pairs (Fig. 5J–L), and then again divides into two bundles (Fig. 5A–C). Within the crenate-crested protuberance an additional small bundle is also observed departing from the fused single ridge bundle at the proximal part of the region between leaflet pairs (Fig. 5K, L). The small bundle runs until the middle part of the region between leaflet pairs and simultaneously moves toward the distal part, or the adaxial part, of the protuberance (Fig. 5A–D), and then the bundle can’t be confirmed (Fig. 5E).

Chamaecrista nomame —The main vascular bundles are arranged in a circle or cylinder surrounded by a complete ring of fibers throughout the rachis (Fig. 6A–I). The two ridge bundles run along the adaxial two ridges of the region between leaflet pairs toward the next region of leaflet pair insertion (Fig. 6A, I). Two leaflet traces begin departing from the main vascular cylinder before the region of leaflet pair insertion (Fig. 6A). At the region of leaflet pair insertion each of two ridge bundles branches off a bundle laterally and outward, which connects with each leaflet trace on both sides of the region (Fig. 6B–D). The two ridge bundles appear connected to each other by another bundle branched laterally (Fig. 6C–E, arrowheads). Although the adaxial two protuberances forming the ridges are absent throughout this region, two ridge bundles remain separating (Fig. 6B–G). After two leaflets are separated from both sides of the rachis at the region, two ridges become obvious (Fig. 6H, I).

Discussion

Comparison in external and internal morphology between two leaf rachis types

The crenate-crested leaf rachis of Chamaecrista mimosoides and the canaliculate one of C. nomame are obviously different in their external features: the former is made up of one protuberance of tissues forming two leaflet pairs, whereas the latter is made up of two protuberances of tissues forming two ridges parallel to each other between leaflet pairs. The vascular system within the rachis has the following similarities in both: (1) there are a vascular ring or cylinder, called siphonostele, at the center, and (2) there are basically a pair of ridge bundles that are detached from the adaxial margins of the vascular arc near the distal end of the pulvinus and run along the adaxial side of the petiole and the rachis of the leaf. However, a pair of ridge bundles fuses into one at the proximal half of the region between leaflet pairs in the crenate-crested rachis and they are separated into two again in the distal half of the region and in the region of leaflet pair insertion in C. mimosoides. Moreover, an additional small vascular bundle is observed in the proximal half of the crenate-crested protuberance, which is departed from the fused ridge bundle and runs upward and in the center of the protuberance. In contrast, a pair of ridge bundles is never fused into one throughout the canaliculate rachis and there are no additional bundles supplied in the two ridges in C. nomame.

Vascular system from node to petiole

Leaves of Chamaecrista mimosoides and C. nomame are both supplied with three foliar traces, the nodal structure of which is that called the trilacunar type (Sinnott 1914) and this type of nodal structure has been known as common in Leguminosae (Sinnott 1914, Sinnott and Bailey 1914, Watari 1934). The vascular bundles of the pulvinus form the central vascular arc and divide two ridge bundles from the adaxial margins of the arc at the distal part of the pulvinus in both species. A pair of ridge bundles in the petiole is commonly observed in Cassia, Senna and Chamaecrista (Watari 1934, as Cassia sensu lato).

After dividing two ridge bundles in the pulvinus, the main vascular bundles present an arc shape in the petiole in C. mimosoides, whereas they are divided into three bundles in
C. nomame. Variation of vascular bundles in the petiole was shown by Watari (1934) in *Cassia* sensu lato, and the feature of his sole material of *Chamaecrista, C. nomame* (as *Cassia mimosoides* var. *nomame*), is consistent with the present result. In *Chamaecrista* sect. *Absus*, variations in the number of ridge bundles (as accessory bundles), two or four to six, and in disposition of the vascular bundles within the petiole were reported (Coutinho et al. 2013). Phylogenetic significance of such variations has not yet confirmed critically in *Chamaecrista* sect. *Absus*. With respect to sect. *Chamaecrista*, anatomical data of leaf rachises have not yet accumulated enough for confirming its phylogenetic significance.

**Vascular system related with extrafloral nectary**

The presence of an extrafloral nectary (EFN) is one of important characteristics for distinguishing *Chamaecrista* from *Senna* and *Cassia*: the EFN is present in some of *Chamaecrista* and *Senna*, but absent in *Cassia*; the EFN of *Chamaecrista* is dish- or cup-shaped, rarely flat, while that of *Senna* is ovoid, globose, mounded, claviform or phalloid (Irwin and Barneby 1982). In *Chamaecrista* the EFNs are known from four sections (*Apoucouita, Caliciopsis, Chamaecrista* and *Xerocalyx*) and a part of sect. *Absus* (Irwin and Barneby 1982, Coutinho et al. 2012, Coutinho and Meira 2015), and the EFNs are present on the petiole/rachis, therefore also called “petiolar glands” (Irwin and Barneby 1982). The molecular phylogenetic analyses supported the presence of EFNs as synapomorphic in *Chamaecrista* (Conceição et al. 2009).

*Chamaecrista mimosoides* and *C. nomame* have similar EFNs on the petiole immediately below the first leaflet pair, but the EFNs are different in the vascular tissues supplied as well as the size and shape between both species. Coutinho et al. (2012, 2015) investigated morphology, anatomy and histochemistry of the EFNs in *Chamaecrista* sect. *Absus* and they clarified structural diversity of the EFNs as well as their features of secretion. Although no histochemical tests were applied in the present study, two parenchyma areas similar to the EFNs of sect. *Absus* were found in the EFNs of *C. mimosoides* and *C. nomame*: the distal non-vascularized area, which is composed of parenchyma with dark-stained cells, appears to correspond to the “nectary parenchyma” of sect. *Absus* (Coutinho et al. 2012, 2015), and the proximal vascularized area without dark-stained cells corresponds to the “subnectary parenchyma”. The central area of the top of the EFN, where the epidermis was more or less elevated, is assumed the site of nectar exudation also in *C. mimosoides* and *C. nomame*.

Two types of vascularization toward the EFNs were reported in the sect. *Absus* (Coutinho et al. 2012, 2015): vascularization supplied either from accessory vascular bundles, which correspond to the ridge bundles in the present study, and that from the median vascular cylinder of the rachis. The former vascularization was observed in *Chamaecrista mimosoides* and the latter in *C. nomame* in the present study. The vascular tissues of these two species are also mainly composed of phloem cells like the EFNs in the sect. *Absus*.

**Structural relationships between crenate-crested and canaliculate leaf rachises**

The crenate-crested leaf rachis of *Chamaecrista mimosoides* is initiated as a single protuberance on the adaxial surface, whereas the canaliculate one of *C. nomame* is initiated as two parallel ridgelines. Both types of leaf rachises are different from their initiation of development. The vascular system between leaflet pairs is also different in both species, there is a single ridge bundle in *C. mimosoides* and two separated ridge bundles in *C. nomame*. In *C. mimosoides*, however, the single ridge bundle partly divides into two ridge bundles in the region between leaflet pair when approaching to the region of leaflet insertion. Then, the two bundles are fused.
into a single bundle again after connecting with leaflet traces in the region of leaflet insertion. Although the developmental process does not imply the structural relationship between two types of leaf rachis, the vascular system appears to imply that the rachis with a pair of ridge bundles is original state and that the crenate-crested rachis is formed by the fusion of two ridges as considered by Lock (2007). According to Lock (2007) the top of the crest becomes flattened, sometimes with two rows of hairs in some regions of Africa, although the margins are firmly fused so that there is no groove between them. For understanding structural relationships of two rachis types further anatomical studies on these variations will provide useful evidence.

It is noteworthy that the parenchyma cells in the crenate-crested protuberance are rich in chloroplasts and there are many stomata present in the epidermis in *Chamaecrista mimosoides*. This implies that the unique crenate-crested protuberance in the genus is related with improvement of the function of photosynthesis. Because leaves and leaflets of *C. mimosoides* are obviously smaller than *C. nomame* and other related species of the genus, the crenate-crested protuberances appear to increase whole leaf area of one leaf for photosynthesis.

**Systematic implication of crenate-crested leaf rachis**

The present study clarified the anatomical and developmental features of the unique crenate-crested leaf including the parts of pulvinus, petiole, EFN and rachis in *Chamaecrista mimosoides* and revealed differences in these features from the common canaliculate leaf of *C. nomame*. Although there was the opinion that these two species are conspecific (e.g., Baker 1878, Matsumura 1902, Makino 1917, Ohashi 1966, 1982), the present evidence supports the treatment of them as two different species (e.g., Honda1938, Ohashi 1989, Huang and Ohashi 1993, Singh 2001, Ohashi et al. 2013, Ohashi 2016).

The unique crenate-crested leaf rachis was recognized as an important taxonomic characteristic for *Chamaecrista mimosoides* by Ghesquière (1932, as *Cassia*), and then Steyaert (1950, as *Cassia*) mentioned the utility of the rachis character for distinguishing species in Asian and African *Chamaecrista*. Brenan (1967) described the crenate-crested leaf rachis in four species of African *Chamaecrista* (as *Cassia exilis* Vatke, *Cassia gracilior* (Ghesq.) Steyaert, *Cassia mimosoides* L. and unknown *Cassia* sp. B). He, moreover, recognized huge variation within *Chamaecrista mimosoides* (as *Cassia mimosoides*) in Africa and distinguished seven groups, called Groups A–G without giving their names, within the species. In Madagascar Du Puy (2002) recognized 10 species, five of which have the crenate-crested leaf rachises. Although Ghesquière (1935) and Viguier (1949) attributed some of them to *Chamaecrista mimosoides* (as *Cassia mimosoides*), Du Puy (2002) distinguished them from *C. mimosoides* at species level with recognition their closer relationships with the ‘*Chamaecrista mimosoides*’ complex in Africa. The ‘*Chamaecrista mimosoides*’ complex in Africa and Madagascar appears to be important materials for understanding structural variation and systematic implication of the crenate-crested leaf rachis.

With respect to New World *Chamaecrista*, Steyaert (1950) mentioned the similar crenate-crested leaf rachis present in *Chamaecrista flexuosa* (L.) Greene (as *Cassia flexuosa* L.). Irwin and Barneby (1982) established the new ser. *Flexuosae* under *Chamaecrista* sect. *Chamaecrista* in having the leaf rachis as narrowly winged between leaflet pairs as one of the important characteristics. However, except for this characteristic there are no characteristics supporting closer relationships between *C. mimosoides* of Asia and Africa and ser. *Flexuosae* of New World. The crenate-crested rachis may be evolved independently in both regions.
Because the crenate-crested leaf rachis is rare in the genus *Chamaecrista* and the species with the canaliculate leaf rachis is located at the base in a recent molecular phylogenetic tree including Indian *Cassia*, *Senna* and *Chamaecrista* (Seethapathy et al. 2015), the crenate-crested leaf rachis is considered to be apomorph in *Chamaecrista*. For clarifying the systematic implication of these characteristics in details, morph-anatomical investigations and molecular phylogenetic analyses are needed on the whole of *Chamaecrista* sect. *Chamaecrista* as well as the *C. mimosoides* complex, especially in Old World.  

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根本智行 a, 大橋広好 b, 吳 徳邻 c: マメ科ジャケツイバラ亜科カワラケツメイ属 Chamaecrista mimosoides および C. nomame における葉の解剖および発生

カワラケツメイ属 Chamaecrista mimosoides (L.) Greene は東アジアからアフリカまで分布し、葉は比較的小型の小葉をつける偶数羽状複葉で、約 80 対にまで達する多数の小葉対からなる。さらに、葉軸の小葉対と小葉対の間の向軸側に特異な半円形の円錐型隆起をもつことで、近縁種から識別されてきた。カワラケツメイ属植物の葉軸は、一般に、小葉対と小葉対の間の向軸側に 2 列の穂状の隆起があり、中央には溝ができて、近縁種から識別されてきた。C. mimosoides にみられる円錐型隆起はたいへん希な特徴であるが、溝型葉軸との構造的な関連について詳細は知られていない。本研究では、C. mimosoides と同じ Sect. Chamaecrista に属し、一般的な溝型葉軸をもち、かつては同一種として扱わられることもあったカワラケツメイ C. mimosoides (Makino) H. Ohashi と解剖学的および発生学的に比較することで、両者の構造的な関連を明らかにすることを目的とした。

Chamaecrista mimosoides の円錐型隆起は葉緑体を多く含む单一の柔組織からできており、C. nomame の溝型葉軸の 2 列の隆起はそれぞれ独立した柔組織からできている。両者は発生過程初期から異なっており、前者では単一の隆起が、一方後者では 2 つの隆起が生じた。どちらも葉柄の中央脈から向軸側の隆起に 2 本の稜維管束 (ridge bundle) が供給される。しかし、円錐型葉軸では小葉の付着点の直後に 1 本に融合し、次の小葉付着点までの中央付近で、再度 2 本に分岐し、次の小葉付着点を過ぎると再度一本に融合する。溝型葉軸では、葉軸中央の維管束は 2 本のままである。また、円錐型葉軸では、融合した稜維管束から隆起に向かって分岐する 1 本の小さな維管束が確認された。葉柄の先端部にはどちらも花外蜜腺を 1 個もつが、C. mimosoides では稜維管束から花外蜜腺に、C. nomame では中央維管束の両端から、いずれも主に葉脈部からなる維管束が供給される。

本研究の結果は、これまで同一種とする見解もあった C. mimosoides と C. nomame を区別する新規の形質を明らかにした。また、円錐型葉軸の 2 本の稜維管束が小葉付着点間で融合を繰り返す走向パターンは、円錐型葉軸が溝型葉軸の 2 列の穂が合着してできたとする Lock (2007) の考えを支持した。さらに、円錐型隆起を構成する柔組織に多数の葉緑体が含まれ、表皮に多数の気孔が観察されることから、円錐型葉軸は葉の光合成能力の向上に係わっていることが示唆された。

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