Floral morphology and relationships of *Kingdonia*

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小菅桂子・付発 鼎・田村道夫：キングドニアの花の形態と類縁

Abstract The flowers of *Kingdonia uniflora*, collected in Sechuan Province of China, were studied morphologically and anatomically. The carpel primordium develops into an obliquely cup-shaped structure and the carpel margin is unsealed at anthesis. A single carpel trace is divided into a dorsal bundle and a ventral bundle, and the latter further divided into 3 divisions. The unitegmic ovule is attached at the middle of adaxial carpel margin and seems to be hemianatropous. Flowers are protandrous and the integument covers only half of the ovule at the time of anther dehiscence. Judging from many morphological characters, *Kingdonia* seems to be not closely related to *Circaeaster* but to the Renunculaceae, especially Anemoneae.

Key words: *Circaeaster*, floral morphology, *Kingdonia*, Ranunculaceae.

*Kingdonia* was described as a genus in the Ranunculaceae by Balfour & Smith (1914). This genus is unique with a dichotomous venation and even number of leaf traces from a single gap, therefore many morphological studies have been done. Such characters are also found in *Circaeaster* and Diels (1932) emphasized the close affinity between *Circaeaster* and *Kingdonia*. Thereafter, both genera were classified into a subtribe Kingdoniinae under tribe Clematitideae (=Anemoneae) (Janchen 1949) or into subfamily Kingdonioideae (Thorne 1974). Cronquist (1968) and Thorne (1983) also agreed on the close relationship between *Kingdonia* and *Circaeaster*, and classified them not in the Ranunculaceae but in the Circaeasteraceae. While, Hutchinson (1959), Tamura (1963) and Tahktajan (1980) treated *Circaeaster* as the representative of a monotypic family Circaeasterceae and retained *Kingdonia* in the Ranunculaceae. Airy Shaw (1965) and Dahlgren (1975), however, classified *Kingdonia* under a monotypic family, Kingdoniaceae. Despite many morphological studies, the systematic position of *Kingdonia* has not been established yet.

Materials and methods

Materials were collected in May, 1986 from Gonggaling and Huanglongsi in northern
Sechuan of China at ca. 3300 m high and fixed with FAA. The voucher specimens (M. Tamura, F.-d. Pu & M.N. Tamura 1057, 1064) are preserved at the herbaria of Kobe University, of Kyoto University (KYO) and of Chengdu Institute of Biology, Academic Sinica. For microtome sectioning, materials were dehydrated through a n-butyl alcohol series, embedded in Paraplast, and sectioned at 6 μm thickness. Sections were stained with hematoxylin. Flowers were cleared in a solution of NaOH and stained with fuchsin to show the vasculature. Materials for scanning electron microscopy (SEM) were dissected and dehydrated in an ethanol-acetic amyl series, then dried in a critical point drying apparatus using CO2. They were coated with gold and observed with an Akashi Alpha-9 Mini Sem.

**Observations**

*Kingdonia uniflora* is perennial and growing on mossy ground under the subalpine conifer forests. The rhizome with several scales is elongated, creeping and well branched. At the tip of rhizome, there are 2-3 cataphylls, one foliaceous leaf and one flowering stem, or when flowering stem is not produced, 1-2 foliage leaves are present. All leafy organs are arranged in distichy. Flowering stem is scapose without cauline leaves or bracts, and produces a solitary terminal flower.

The flower is bisexual and ca. 8 mm in diameter and composed of 5 sepals, 8-13 petals, 5-8 stamens and 4-9 carpels. Floral organs are initiated centripetally in a spiral succession. There are usually five vascular bundles in the receptacle and each of them is divided into 3 divisions. The middle division enters into each sepal, then two adjacent lateral divisions join to form a new receptacle bundle and it is divided into 3 again. Thus a vascular network is formed in the receptacle. In contrast to Foster (1961), double trace vascular system of sepal was not observed (Fig. 1). Petals are smaller than sepals and consisted of a knob-like limb and a stalk (Fig. 2). Petal primordia resemble those of stamens at first but grow slower. The upper swollen part is grooved on the adaxial side (Fig. 3), where the nectariferous tissue is differentiated. The primordium of carpel develops into an obliquely cup-shaped structure and then becomes ascidiform in the lower part and folded in the upper part like *Anemone* (Fig. 4). A single ovule develops at the middle of adaxial margin and carpels are not enveloped with sepals at this time (Fig. 5, 6). The carpel is vasculated by a single trace which is divided into a ventral bundle and a dorsal bundle (Fig. 7). The ventral bundle is divided into three, and the median division enters into the ovule and two lateral ones elongate upward along both carpel margins. At the time of anthesis, the carpel margin is unsealed and the xylem in the vascular bundle, especially in the upper part, is not well developed yet. The ovule is tenuinucellate and epidermal cells are well developed near the upper part. At the time of anther dehiscence, the embryo sac is 2-nucleate stage yet and the single integument covers only half of the ovule (Fig. 6). The direction of pendulous ovule is
Figs. 1-6. *Kingdonia unijora*. Fig. 1. Cleared sepal. ×10. Fig. 2. Petals with a knob-like limb and a stalk. The limb is grooved on the adaxial side (arrows). ×50. Fig. 3. Young petals with the upper swollen part and the adaxial groove. ×50. Fig. 4. Young flower. Carpels and stamens are not enveloped by sepals (arrows). ×30. Fig. 5. Single ovule at the middle of adaxial carpel margin. ×200. Fig. 6. Longisection of a carpel with a pendulous ovule at anthesis. ×230. A, stamen; G, carpel; K, sepal.
perpendicular to the funicle, thus the ovule appears to be hemianatropous at this time. Pollen grains are tricolpate and the tectum is striate, as observed by Nowicke & Skvarla (1982) and Zang (1983).

**Discussion**

Diels (1932) insisted the relationship between Circaeaster and Kingdonia mainly by the dichotomous venation of leaves and the single pendulous orthotropous ovule. In Circaeaster two orthotropous ovules are attached to lateral walls of a carpel (Junell 1931).
While in *Kingdonia* the ovule attitude seems to be hemianatropous as far as we observed, though it was described to be orthotropous (Diel 1932, Foster 1961), anatropous (Mu 1983) or amphitropous (Hu 1985), and a single ovule is attached at the middle of adaxial carpel margin like *Anemone*. Besides these differences, *Circaeaster* differs from *Kingdonia* in the mesogomous course of the pollen tube and bisporangiate anthers (Junell 1931).

Foster (1961) emphasized that *Kingdonia* was a relict genus without obvious affinity to the Ranales. Although he emphasized the importance of the dichotomous venation, double trace of sepal and tricolporate pollen grains, the double trace is not observed and pollen grains are tricolpate like many species in the Ranunculaceae in the present study. Chang (1982) suggested that *Kingdonia* is related to *Coptis* in having short chromosomes with the basic number 9 and the double traces of petiole. But *Coptis* differs from *Kingdonia* in having follicles, bitegmic ovules and pantoporate pollen grains. In *Ranunculus*, the ovule is hemianatropous but ascending, and usually petals are well developed, the asidiform zone of carpel is not well developed and the carpel trace is divided into one dorsal bundle and two or more ventral ones. *Kingdonia* is similar to *Anemone* and its allies in having the obliquely cup-shaped structure of carpel, the carpel trace dividing into one dorsal bundle and one ventral bundle, the unitegmic pendulous ovule attaching at the middle of adaxial carpel margin, and tricolpate pollen grains. The knob-shaped petals of *Kingdonia* resemble those of *Pulsatilla*. *Kingdonia* has many aspects common to *Anemone* and its allies and may be classified in the tribe Anemoneae, though both differ from each other in cytological characters.

References


Kingdonia ではイチリソウ属などと同様に、心皮はコップ状に発達し、1個の胚珠は心皮壁の向軸側上縁の中央部につく。開花時、心皮縁は完全に閉じておらず、維管束、特に腹束上部は、まだ導管が未分化な状態である。心皮跡は1本で背腹に2分し、腹束はさらに3つに分かれ、中分束は胚珠に、両側の2本の分束は心皮縁に沿って上部に伸びて行く。このような維管束走行はイチリソウ属やセクセリソウ属などとふつうに見られる。この時期、薬はすでに裂開しているが、胚珠はまだ胚囊形成の2細胞期にあり、頸皮は1枚で胚心の半分までにしか達していない、極端な雌性先熟である。胚珠の向きについて DIELS (1932) や FOSTER (1961) は直生、MU (1983) は側生、HUら (1985) は横生と報告している。今回の観察では、胚珠は珠柄にたいす約90度に曲がって位置しており、半倒生と思われる。一方、Circaeaster では2個の直生胚珠が側軸につき、そのうち1個は退化し、中点受精を行ない、胚乳形成は造型膜 (JUNELL 1931), 薬は2室など、多くの重要な点で Kingdonia やキンボウゲ科とは異なり、類縁は認めにくい。

FOSTER (1961) は Kingdonia の二叉分歧する脈理、かくの二重管束、3孔性の花粉などはキンボウゲ科では見られないなどの理由により、この科に含めることはできないと考えた。しかし、今回の観察では、かくの二重管束は認められず、花粉はキンボウゲ科に由来される3溝性であった。Kingdonia にみられる偶数の葉跡はオオレン属に、半倒生の胚珠はキンボウゲ属に見られ、また、花弁は多くのキンボウゲ科のと同様に蜜を分泌することより、Kingdonia をこの科に分類することは妥当であろう。

JANCHEN (1949), TAMURA (1963) や BUCHHEIM (1964) は、Kingdonia をイチリソウ属に近縁と考え、キンボウゲ亜科：イチリソウ亜族：キンゴドニア亜族に分類した。また,
Chang (1985)はKingdoniaと染色体が小型で基本数が9であり、葉柄に二重管束を持つキンポウゲ科のオオレウ属との類縁を考え、カラマツソウ亜科のなかに単型属、Kingdonicaceaeをたてた。Kingdoniaとイチリンソウ属の心皮は、発生過程、維管束走行、胚珠のつく位置などにおいてよく似ており、さらに珠皮が1枚で花粉が3溝性であることも両者に共通している。また、先端がふち状に膨らんだ花弁はイチリンソウ属に近縁なオキナグサ属の花弁と似ている。一方、オオレウ属はKingdoniaとは異なり、果実は袋果、珠皮は2枚、花粉は散孔性である。Kingdoniaはイチリンソウ属などと細胞学的特徴においては異なるものの、形態的特徴には多く共通点が認められる。従って、Kingdoniaをイチリンソウ属に分類することが妥当と考える。