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Morphology, structure and ultrastructure of staminal nectary in *Lamprocapnos* (Fumarioideae, Papaveraceae)

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ABSTRACT

Nectaries show high a degree of variations in terms of location, morphology and structure; these characteristics are critical for systematic information. In Papaveraceae, staminal nectaries at the stamen base are only found in bisymmetric and zygomorphic flowers, but with little description on the ultra-structure of nectary available. Here we investigate structural details of flowers and nectaries of *Lamprocapnos spectabilis* using LM, SEM and TEM. The nectaries of *L. spectabilis* are initiated at the base of stamen filaments in the young bud. The oval/ball-shaped staminal nectaries are composed of four major types of tissues in general. First and outmost layers are epidermis and hypodermis with large and elliptical cells. Beneath the epidermal layers are the second type of tissue consisting of 20–30 layers of parenchyma cells which are further distinguished by two kinds of cells: smaller secretory parenchyma cells having dense cytoplasm, large nucleus and abundant cellular organelles, and larger sub-nectary parenchyma cells containing a relatively thin cytoplasm. The third type of tissue is the darkly-stained elongated cells and embedded at 8- to 12-cell-layer deep in the nectaries, and is associated with sieve tube elements and cells resembling companion cells, and they presumably belong to underdeveloped sieve tube elements or "protophloem" based on ultrastructure features such as conspicuous cell wall ingrowths and plentiful plasmodesmata. The forth type of tissue in the nectary is the simplified vascular bundle forming with only phloem. It is reasonable to suggest that secretions in the spacious intercellular spaces between secretory parenchyma cells are exuded to the exterior via micro-channel or epidermis/cuticle pathway. In conclusion, the results show that epidermis, hypodermis, secretory parenchyma, "Arber suggestive tissue (protophloem)", and phloem act coordinately in nectar production, secretion and exudation in *Lamprocapnos*. The structure of the staminal nectaries are compared within Papaveraceae and with other related groups in Ranunculales.

1. Introduction

Nectaries are specialized tissue that secretes a sugar solution involved in interactions with animals (Nepi et al., 2007). There are various types of floral nectaries, situated anywhere in the flower with different origins and types of organization (Pacini and Nicolson, 2007), and they may be located at surface level in the organ bearing them, form an outgrowth on the organ, or be concealed deep within the organ (Nepi et al., 2007). According to Fahn (2000), the nectary is made up of so-called nectariferous tissues, which consist of an epidermis usually overlying a specialized parenchymatous tissue. Three main types of nectaries are categorized: epithelial nectaries, mesophyll or mesophyllary nectaries, and trichome or trichomatic nectaries (Vogel, 1977). Another type, nectarioles were described later by Vogel (1998), which are small, few-celled nectaries, occurring singly or in clusters. In some species, so-called "vestigial nectaries" have the structure of nectaries, but no nectar is produced (Nepi et al., 2007).

Nectar-secreting structures show a high degree of variations in terms of locations and histological characters which are important for systematic information (Bernardello, 2007). In some families, the nectaries are uniform in position and morphology (e.g. Asteraceae; see Bernardello, 2007; Leins and Erbar, 2010; e.g. Lamiaceae; see Zhang et al., 2014); while in others, they differ greatly in ontogeny, morphology, and structure between species (e.g. Ranunculaceae; see Fahn, 1979; Bernardello, 2007; Nepi et al., 2007; Erbar, 2014).

Papaveraceae is a member of Ranunculales and displays three forms of floral symmetry, with two subfamilies (Fumarioideae and Papaveroideae) (Damerval and Nadot, 2007; APG III, 2009). Nectaries are only present in these bisymmetric and zygomorphic flowers of Fumarioideae (Damerval and Nadot, 2007; Sauquet et al., 2015); the ball-shaped nectaries at the stamen base are concealed by the spurs formed by petals, and nectar is secreted by the nectaries, while the spurs

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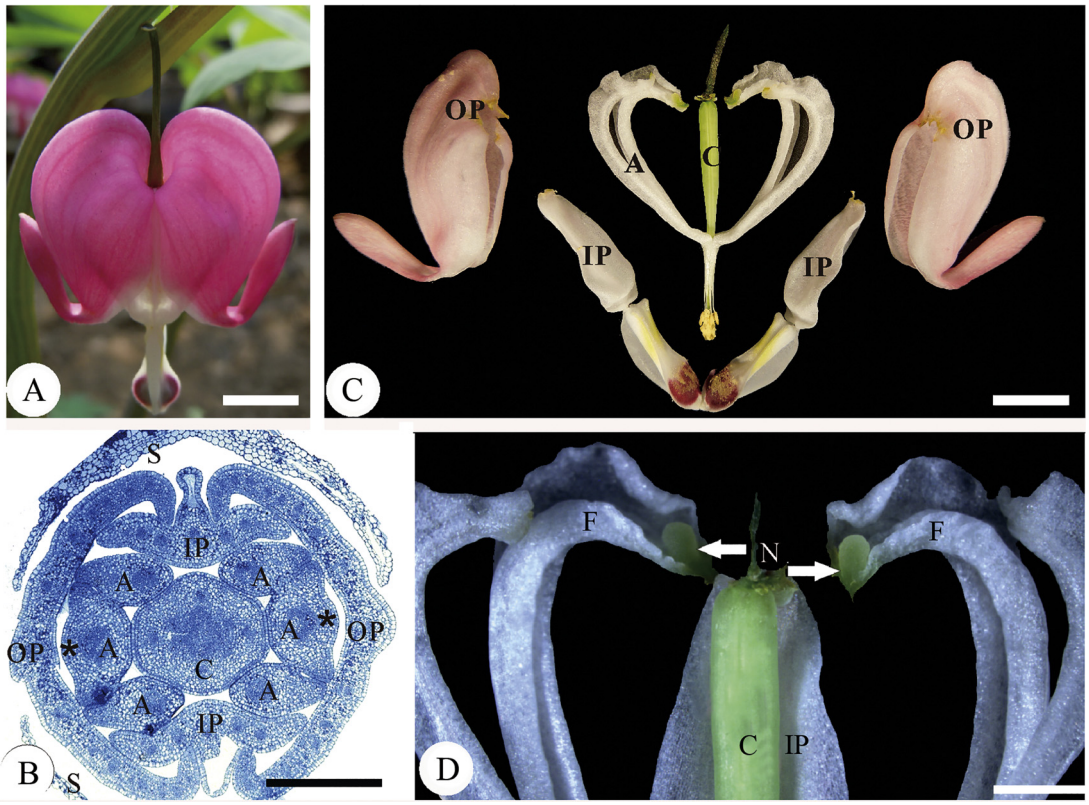

Fig. 1. Flowers of *L. spectabilis*. (A) A flower at anthesis. (B) Transverse section of a young flower; asterisks showing the staminal nectary initiations at the base of each central dithecal stamen. (C) A flower with two outer petals, two inner petals, six stamens and a carpel (two sepals fall off). (D) Magnification of upper part of C; arrows illustrating two nectaries at the abaxial bases of middle filaments. A, stamen; C, carpel; F, filament; IP, inner petal; N, nectary; OP, outer petal. Scale bars: A, C = 1.0 cm; B = 1.25 mm; D = 0.5 cm.

function as nectar holders (Lidén et al., 1993; Endress, 1995; Olesen, 1996; Leins and Erbar, 2010; Erbar, 2014). Early asymmetric development of nectary outgrowth is correlated with perianth zygomorphy in Fumarioideae (Damerval et al., 2013; Sauquet et al., 2015). Many aspects of botanical characteristics of Papaveraceae have been studied such as phylogeny, floral morphogenesis, floral symmetry, pollination, and structure (Norris, 1941; Ronse De Craene and Smets, 1990, 1992; Olesen, 1996; Lidén et al., 1997; Maloof, 2000; Becker et al., 2005; Damerval and Nadot, 2007; Damerval et al., 2013; Erbar, 2014; Sauquet et al., 2015). However, a detailed observation regarding the nectary ultra-structure in Papaveraceae (Fumarioideae) is still elusive. *Lamprocapnos* Endlicher, a genus of Fumarioideae *sensu* of Papaveraceae (APG III, 2009; formerly Fumariaceae D.C., Kubitzki et al., 1993; Wang et al., 2009), is distributed in Northeast China, North Korea and Southeast Russia (Zhang and Lidén, 2008), with the common name “bleeding heart”. *Lamprocapnos* is monotypic (*Lamprocapnos spectabilis* (Linnaeus) Fukuhara) (= *Dicentra spectabilis* (L.) Lem.) and is the sister group to the rest of subfamily Fumarioideae (core Fumarioideae) based on the morphology, as well as the data of nrDNA-ITS and rpsl6 intron sequences (Lidén et al., 1993; Sauquet et al., 2015). The flowers are bisymmetric (vs. actinomorphic in other species of Papaveraceae), 20–25 mm wide, flattened with a heart-shaped base with two 3–4 mm sepals (lanceolate and deciduous), non-fused corollas (vs. fused corollas of *Corydalis* DC.) (Zhang and Lidén, 2008). The two outer petals, 25–30 mm long, are bright pink, with a broad pouch-like base and a narrow apex; two inner petals, 22–25 mm long, are white with a prominent projection (dorsal crest) on the abaxial side, whereas the adaxial surface color is red with yellow spots. Six stamens are organized as two triplets, each consisting of two monothecal stamen and a central dithecal stamen, and the nectaries arise at the abaxial base of the central stamen filaments (Fukuhara and Lidén, 1995; Damerval et al., 2013).

The present study is the first description of the ultrastructure of the staminal nectary within Papaveraceae family, and has focused on: (1) the ultrastructure of the floral nectary in *L. spectabilis*; (2) the insight into the so-called "Arber suggestive tissue" in nectaries, a term designated by Norris (1941) to define the specialized cells (strands of elongated cells in parallel arrangement) observed in nectaries of *Dicentra* and *Hypecoum* which was originally found in Fumarioideae and Hypecoideae by Arber (1931, 1932); (3) comparison of the structure of staminal nectaries in *Lamprocapnos* with that of other groups in Papaveraceae.

2. Materials and methods

2.1. Plant materials

Flower buds of *L. spectabilis* (L.) Fukuhara were collected in Xingtai county (voucher Zhao 20140426, SANU), Hebei Province, China from August 2011 to May 2014 (alt.1000 m).

2.2. SEM (scanning electron microscopy)

For nectary development studies, about 20 flowers at different developmental stages were fixed in FAA (formalin:acetic acid:-alcohol = 5:5:90), dehydrated in alcohol series and iso-amyl acetate series, followed by critical point drying, and gold sputter coating. Observations were made using a HITACHI (S-3400N) scanning electron microscope at 15 kV.

2.3. LM (light microscopy) and TEM (transmission electron microscopy)

Flowers were fixed with 2% glutaraldehyde / 2% paraformaldehyde