Review

Floral nectaries in Leguminosae: structure, diversity, and possible evolution

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Floral Nectaries in Leguminosae: Structure, Diversity, and Possible Evolution

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Abstract: Floral nectar is a key reward in Leguminosae despite the exceptional diversity of flowers in this family. The paper aims to summarize the available data on structure, ontogeny, regulation, and possible evolution of the leguminous floral nectaries. To date, detailed characterization of ultrastructure and mode of secretion is available only for a few representative of the family whereas the majority remains understudied from this perspective. In most cases, regardless of flower symmetry, nectaries are localized between stamens and a carpel. The nectar is usually exuded from modified stomata although the exact mode of secretion by specialized parenchyma may differ between taxa. The leguminous floral nectaries often have certain features of monosymmetry with preferentially abaxial development. Nectaries were independently lost in several lineages, and equally recurrent is the emergence of substitutive, i.e. evolutionary innovative, nectar-producing structures. Floral nectaries possess a certain degree of evolutionary inertia, i.e. they remain stable even in lineages in which flower morphology underwent significant changes compared with an ancestral plan, such as shifts in merism, symmetry, organ number and alike. Due to their evolutionary stability, floral nectaries are rarely used in taxonomy of Leguminosae.

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I. Introduction

The third largest angiosperm family, Leguminosae, displays a broad spectrum of variation of flowers differing in their symmetry, size and merism and adapted to diverse pollination strategies (LPWG, 2017; Sinjushin, 2021). However, the principal attractant of these various flowers is nectar secreted by specialized floral nectaries (FNs). Although these structures had been under morphological and anatomical investigation for more than 150 years (Caspary, 1848; Bonnier, 1879), there are still gaps in understanding their identity and possible evolution. Beyond any doubt, FNs in different angiosperm groups have a different origin which is evident from the diversity of their position within a flower and histological polymorphism (Kartashova, 1965; Bernardello, 2007). The recurrent and independent acquisition and loss of FNs in different lineages may suggest that the regulation of their development is also dissimilar in different taxa, although there are evidences that both floral and extrafloral nectaries may be controlled by the same set of genes in major clades like core eudicots (Lee et al., 2005). Summarizing data on FNs within a large diverse family, like Leguminosae, may help elucidate their evolution on a larger scale.

The existing terminology used to describe floral nectariferous structures is somewhat confused and probably excessive. Since Adanson's work of 1753, the term 'disc' (or 'disk') was introduced to define any nectar-secreting floral part (see Moore, 1936 for review). As one may see from numerous works cited in the review below, this term is often applied to designate FNs which are neither of disciform shape nor structurally discrete (Waddle & Lersten, 1973). The very term 'disc' is sometimes used to describe non-secretory floral structures which may cause confusion. For example, flowers of *Cheniella* bear a fleshy 'staminodial disc' which is hypothetically not secretory nor homologous to a 'nectariferous disc' in flowers of related cercidoid legumes (Clark et al., 2017). Alongside 'disc', a nectar-producing structure of a leguminous flower is most often referred to as 'nectary' (e.g. Davis et al., 1988). The recognizable FN parts can be called 'glands' (Sirichamorn et al., 2014).

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Different approaches were used to characterize the leguminous FNs which sometimes brought controversial results. For example, the absence of a pronounced 'disc' in flowers of *Galega* led to the conclusion that this plant is nectarless (Gulyás & Kincsek, 1982; Rodríguez-Riaño et al., 1999) whereas other papers reported its melliferous value and the diurnal dynamics of nectar secretion (Dokukin, 2009). As for detailed characteristics of FN ultrastructure and mode of secretion, these are available only for a few best studied species, mostly crops, such as broad bean (Razem & Davis, 1999) and soybean (Horner et al., 2003).

All this evidence shows that the review and analysis of the current state of knowledge on the leguminous FNs may be timely. Not only are taxonomic or evolutionary issues in focus, but also applied perspectives. Many legumes are valuable melliferous plants, often a source of monospecific honey, such as species of *Robinia*, *Melilotus*, *Trifolium* and others (e.g. Pelmenov & Kharitonova, 1986). Floral visitation by insects may be recruited to increase seed yield in some leguminous crops (Erickson, 1975) as well as to obtain heterotic hybrids (Saxena et al., 1990). The amount of nectar produced by a flower is heritable and can be a goal in breeding (Barnes & Furgala, 1978; Davis, 2001). The pollinator-friendly crop varieties are in scope of many works focused on both applied and ecological aspects (reviewed by Palmer et al., 2009).

This paper aims to bridge the existing gap in knowledge of the leguminous FNs summarizing data on their morphology, ultrastructure, and diversity. The floral structures controlling nectar storage and availability as well as cases of FN loss are also covered. The existing hypotheses on the evolutionary origin of FN in legumes are briefly revisited.

II. Morphological Diversity of the Leguminous Floral Nectaries

With rare exceptions which seem derived, the leguminous FNs are intrastaminal (or perigynous), i.e. localized between stamens and a carpel base (Caspary, 1848). If there is a more or less flat receptacle, FNs can be placed on it, as in members of the tribes Phaseoleae and Fabeae (Waddle & Lersten, 1973; Stpiczyńska, 1995; Sinjushin et al., 2022) (Figure 1h–j). In the case of a relatively deep hypanthium, especially with its wall bordering a carpel base, nectar-secreting area can cover the hypanthium wall, as in many caesalpinioid legumes including those formerly placed in the subfamily Mimosoideae (e.g. Ancibor, 1969), *Bauhinia* from the Cercidoideae (Rodrigues & Leitão, 2023) or *Erythrina*, a phaseoloid member of the Papilionoideae (de Souza et al., 2024).

Figure 1. Variation in position and morphology of floral nectaries in legumes. a–f, schemes; g–l, SEM images. In h–j and l, flowers are oriented with their abaxial sides downwards; in g (apical view) and k (longitudinal section, lateral view), the exact position of a symmetry plane is unclear. a, a more or less polysymmetric receptacular or hypanthial disc illustrated by *Calpurnia aurea* (G, herbarium material). In g, the FN is detached from the receptacle and partly ruptured. b, a monosymmetric FN with an adaxial position of secretory stomata, as in *Vicia sepium* L. (h). c, a crescent-shaped FN, as in *Anthyllis vulneraria* L. (i). d, a tubular receptacular FN of *Phaseolus vulgaris* (j) and many other legumes. e, a collar-shaped FN adnate to hypanthium, as in *Erythrina* sp. (k). f, secretory field lacking any elevation, as in *Astragalus cicer* L. (l). Red hatching = secretory parenchyma; arrowheads = nectarostomata (red in schemes, white in SEM images); arrow = damage emerging in the course of dissection; ab = abaxial domain; ad = adaxial domain; c = carpel base (or, in the case of g, the place where it was attached); fn = floral nectary; h = hypanthium; p = petals; s = sepals; st = stamens; ? = uncertain position of a secretory parenchyma. Scale bars: 300 μm.

The FNs having different localization are often referred to as substitutive nectaries. This term was introduced by Vogel (1997) who documented such structures in two leguminous lineages. In some genera of the Galegeae tribe, non-stomatal perforations on the outer surface of a staminal tube exude a sugary liquid, most likely representing phloem sap rather than nectar secreted by some special cells (Vogel, 1997). The secretory tissue on the outer surface of the monadelphous androecium in *Laburnum anagyroides* Medik. was found by Bonnier (1879). In two species of *Stylosanthes*, the genus also remarkable with its very long receptacular tubes, nectar-producing glands are produced in the adaxial part of this tube's distal portion. These glands are most likely an evolutionary innovation not homologous to conventional intrastaminal FNs of other legumes (Vogel, 1997). No such substitutive nectary is found in *Arachis* possessing similarly long floral tubes.

Certain ontogenetic plasticity of FNs within a single plant is possible. In the capitulum of *Albizia julibrissin* Durazz. and some other mimosoids, only the terminal flower has a nectariferous disc by contrast to nectarless lateral flowers (Mizusawa et al., 2023). The subterranean cleistogamous flowers of *Amphicarpaea edgeworthii* Benth. were reported to possess no FN whereas the regular above-ground flowers of the same plant are nectariferous with the annular FN (Zhang et al., 2006). Similarly, only vestigial FNs lacking nectarostomata were found in the subterranean flowers of two amphicarpic species of *Centrosema* (Jáuregui & Aponte, 2020).

As viewed from the surface, leguminous FNs usually represent some elevation surrounding a carpel base (Figure 1). The distinction of this elevation ranges significantly. In representatives of the Non-Protein Amino Acid-Accumulating (NPAAA) clade, such as members of the tribes Desmodieae, Fabeae, Milletieae, Phaseoleae, *Wisteria* and probably some others, this elevation constitutes a high collar embracing a carpel base (Figure 1d,j; Waddle & Lersten, 1973; Erickson & Garment, 1979; Nemoto & Ohashi, 1988; Teixeira et al., 2009; Sirichamorn et al., 2014; Sinjushin et al., 2022; Sinjushin, 2023). The disc may be quite low (e.g. in the Dalbergieae: Bento et al., 2021) or even lacking any elevation, as in many representatives of the Galegeae (Figure 1l; Sinjushin et al., 2022). The hypanthial field bearing secretory stomata in flowers of the Dipterigeae was referred to as the non-structural nectary by Leite et al. (2014), although this term is more frequently used for non-differentiated areas that are able to secrete nectar sporadically (reviewed by Bernardello, 2007).

The tubular FN may possess its own merism sometimes consisting of ten lobes (Galetto et al., 2000; Etcheverry & Alemán, 2005; Sirichamorn et al., 2014). In some of the Milletieae, the FN comprises ten free finger-like glands (Sirichamorn et al., 2014). These FN lobes are supplied with conductive bundles connecting them with the vasculature of stamens (Moore, 1936; Al-Nowaihi et al., 2001; Zalko et al., 2022). Interestingly, prominent lobes are found in annular FNs of some *Acacia* having a polymerous androecium (Gómez-Acevedo et al., 2007). Bernardello et al. (2004) suggested that FN lobes or protuberances increased the secretory surface. The FNs of non-collar morphology can also possess some features of association with stamens. For example, the FNs of *Styphnolobium japonicum* (L.) Schott were reported by Tucker (1997) to represent discrete pouches at each stamen's base. Beyond Leguminosae, the FNs consisting of five lobes associated with outer stamens are found in *Quillaja saponaria* Molina (Quillajaceae) belonging to the same order Fabales (Díaz-Forestier et al., 2016).

In very many leguminous flowers, FNs possess some features of monosymmetry. The glandular parenchyma may be thinner in the adaxial part of FN (Teuber et al., 1980). Collar-like FNs may be higher or lower in their abaxial part (many of the Phaseoleae: Waddle & Lersten, 1973) or interrupted in the adaxial portion (*Hardenbergia violacea* (Schneev.) Stearn: Tucker, 2006; *Lathyrus* p.p.: Sinjushin et al., 2022). The disc may acquire a semicircular or crescent shape due to preferentially abaxial development, as in some of the Fabeae, Loteae and Phaseoleae (Figure 1l; Razem & Davis, 1999; Sinjushin et al., 2022). In *Cajanus cajan* (L.) Millsp., the annular FN is monosymmetric most likely due to the external pressure from the vexillary stamen (Sinjushin, 2023).

The most frequent and easily visible feature of FN monosymmetry is the distribution of secretory stomata. Their density may be unequal between abaxial and adaxial parts of FN (Sinjushin, 2023). In many taxa (members of the Fabeae, Galegeae, Trifolieae, Loteae and others), modified stomata are only found in the abaxial part of the receptacle (Murrell et al., 1982; Stpiczyńska, 1995, Heneidak & Hassan, 2007; Sinjushin et al., 2022) (Figure 1h,i,l). In flowers of some, though not all, members of *Vicia*, the secretory stomata are placed on the ligulate outgrowth of the receptacle (Figure 1h; Stpiczyńska, 1995, Heneidak & Hassan, 2007). In *Flemingia paniculata* Benth., the stomata-bearing area of FN is bilabiate, i.e. split into separate abaxial and adaxial parts (Sinjushin, 2023).

Oppositely, the exclusively adaxial placement of nectariferous stomata is rare in legumes. Prenner (2004) reported that such stomata are on the adaxial rim of the disc in *Lespedeza thunbergii* (DC.) Nakai, although the SEM image in the paper does not exclude their development in other parts. In *L. bicolor* Turcz., the secretory stomata are distributed on all FN circumference (Sinjushin &

Ploshinskaya, in prep.). Very unusual position of nectariferous structures is found in *Deguelia* having two glands one of which is adaxial and the other is abaxial to the vexillary stamen filament (Sirichamorn et al., 2014). This morphology, in contrast to much more conventional FNs in other representatives of this group, may indicate that the FN of *Deguelia* is substitutive (see above).

Interestingly, members of Polygalaceae, another species-rich family within Fabales, also possess either annular or unilateral FNs. In the latter case, these glands are placed adaxially, i.e. in the way opposite to the FN localization in Leguminosae (Eriksen, 1993).

The monosymmetry of FN seems correlated with the zygomorphy of perianth. It is therefore of no surprise that actinomorphic or at least non-papilionate leguminous flowers, like those of caesalpinioid genera, possess polysymmetric annular FNs (Ancibor, 1969; Paiva & Machado, 2008; Rico-Alvarado & Gómez-Acevedo, 2022). However, flowers with papilionate corolla may also have more or less polysymmetric FNs or at least even distribution of secretory stomata, like in *Calpurnia aurea* (Aiton) Benth. (Figure 1g; Sinjushin, 2022).

III. Anatomy and Ultrastructure of the Leguminous Floral Nectaries

On anatomical level, the leguminous FNs have a relatively similar structure. They are covered with epidermis composed of more or less isodiametric cells. The cuticle layer is relatively thin and smooth on the FN surface (e.g. Eriksson, 1977; Konarska, 2020).

Typically, nectar is exuded from modified stomata (nectarostomata). Unlike stomata on other plant parts, these on FNs lack substomatal chambers (Picklum, 1954; Paiva & Machado, 2008) or chambers are very small (Teuber et al., 1980). Stomatal complexes on FNs and other organs may be of different types with respect to their subsidiary cells' arrangement (Sinjushin et al., 2022). Nectarostomata may be elevated above the FN surface or, oppositely, somewhat sunken (Figure 2a). They are sometimes so clustered that their guard cells contact (Figure 2b). In *Vicia faba* L., the best studied model, the pores of stomata on FNs remain open independently from light regime and seem unresponsive to factors causing the closure of foliar stomata, such as exposure to exogenous Ca^{2+} or abscisic acid (Davis & Gunning, 1993). These observations led Davis and Gunning (1993) to the conclusion that modified stomata of FNs only enabled nectar outflow and probably reabsorption rather than regulated the intensity of nectar secretion. A similar pattern of stomatal performance was recorded in pea (Razem & Davis, 1999), in which stomatal pores on FNs become closed by occlusion but not by cellular movements, and *Medicago sativa* L. (Teuber et al., 1980). No statistically reliable correlation was found between the number of stomata and nectar yield in *Medicago sativa* (Teuber et al., 1980), *Lotus corniculatus* L. (Murrell et al., 1982), and *Vicia faba* (Davis & Gunning, 1991; see also Davis, 2001).

Figure 2. Details of the leguminous floral nectaries. a, gaping and sunken nectariferous stomata of *Lathyrus latifolius* L. b, enlarged part of the FN of *Vicia sepium* from Figure 1e displaying bordering stomata (arrowheads). c, stomata (arrowheads) of the FN of *Trigonella foenum-graecum* L. occluded with large droplets of some secrete. d, a nectarostoma of *Vicia sylvatica* L. with granular deposits on its guard cells. e, hypanthium and a part of receptacle of *Tipuana tipu* covered with trichomes. f, a closer view of e with secretory stomata visible (arrowheads). Scale bars: 10 μm (d), 30 μm (a–c, F), 300 μm (e).

In *Camoensia scandens* (Welw.) J.B.Gillett, a core genistoid legume with unusual non-papilionate flowers, nectar is released from very large pores resulting from rupture of stomata together with adjacent epidermal cells (Leite et al., 2021). This mode of secretion is unusual for legumes. Both stomata and cuticle crevices were reported to exude nectar in *Sesbania cannabina* (Retz.) Poir. (Xin et al., 2000). It cannot be also excluded that in some leguminous flowers, even those previously referred to as nectarless like *Securigera varia* (L.) Lassen, nectar is exuded through outer cell walls rather than pores or stomata. Ancibor (1969) described three species of *Prosopis* as possessing hypanthial nectaries without stomata.

Areas of nectar biosynthesis (i.e. where a secretory tissue is localized) and its outflow may not fully overlap. For example, the secretory stomata are only abaxial in flowers of *Trifolium pratense* L.

but the nectariferous parenchyma is found even on the adaxial side of the receptacle, although in a smaller quantity (Picklum, 1954). The same distribution was reported by Kartashova (1965) in *Caragana frutex* (L.) K.Koch and other legumes.

The biosynthesis of nectar occurs in parenchyma, as in other angiosperms (Fahn, 1979). This consists of thin-walled isodiametric cells with dense cytoplasm, large nuclei, varying degree of vacuolization, and numerous organelles like chloroplasts and mitochondria evidencing for their functional activity (e.g. Davis et al., 1988; Konarska, 2020). The number of parenchyma layers seems correlated with flower size and ranges from four (in small-flowered vetches like *Vicia hirsuta* (L.) Gray: Stpiczyńska, 1995) to 10-14 in *Erythrina* spp. (Galetto et al., 2000), *Erythrostemon gilliesii* (Hook.) Klotzsch (Cocucci et al., 1992), and *Sophora fernandeziana* Skottsb. (Bernardello et al., 2004). The correspondence between glandular parenchyma thickness and flower sizes is especially evident in the case of congeneric species (Stpiczyńska, 1995). Parenchyma cells are packed quite densely, with little space between them, but in the distal portion of a tubular FN they may be arranged more loosely, as it was reported for *Phaseolus vulgaris* L. (Webster et al., 1982). Besides glandular cells, FNs may contain idioblasts accumulating polyphenols and tannins and probably serving to protect floral organs from herbivores and pathogens (Konarska, 2020; Kochanovski et al., 2018). Some cells of the FN and underlying non-secretory parenchyma may contain crystals of calcium oxalate or other unidentified substances (Horner et al., 2003; Konarska, 2020). The deposition of certain crystal types may be associated with FN ageing and collapse (Horner et al., 2003).

As hypothesized by Horner et al. (2003), nectar secreted by soybean FN can be supplemented by extra components produced by glandular trichomes borne on the proximal carpel surface. The supposed secretory activity of these trichomes coincides with the one of FN and the components produced can have antimicrobial activity, the phenomenon well known from other taxa (e.g. Thornburg et al., 2003). At the carpel base of *Hymenaea verrucosa* Gaertn. (Detarioideae), there is a putatively secretory 'hairy disc' which was hypothesized to contribute to nectar production (Kochanovski et al., 2018). The pericarpial nectaries were found in *Erythrina speciosa* Andrews which represent capitate trichomes secreting nectar in the course of fruit maturation (Paiva, 2009). Similarly to the extrafloral nectaries, the pericarpial nectaries most likely attract ants which protect a plant from herbivores.

Although the morphology and histology of the leguminous FNs follow the same basic plan, the mechanism of secretion may differ. In the case of pea, *Robinia viscosa* Vent., and probably *Trifolium pratense*, pre-nectar components are supposed to be actively transported through the membrane of FN cells, which is referred to as the eccrine mode (Eriksson, 1977; Razem & Davis, 1999; Konarska, 2020). In the case of granulocrine secretion, the exocytosis of vesicles containing nectar constituents takes place. This mechanism was hypothesized for *Vicia faba* (Davis et al., 1988). Finally, in *Glycine max* L. whole cells of FN disintegrate so the FN collapses in the course of maturation (the holocrine type: Horner et al., 2003).

On the periphery of glandular parenchyma, the FN is underlined with vascular bundles. There are usually ten such bundles each connected with a bundle of a stamen. This phenomenon provoked a lasting discussion on the possible androecial origin of FNs in legumes (see below). In taxa where a high tubular disc is absent, however, the vascular connection between stamens and FN may nevertheless exist. For example, Kartashova (1965) mentioned that in flowers of *Caragana frutex* vascular branches derived from vascular bundles of all stamens supply the secretory tissue of the FN while there is no discernible FN elevation in flowers of this species.

Phloem seems always present in FN venation whereas xylem is found relatively infrequently, mostly in large collar-like FNs, like those of the Phaseoleae (Gulyás & Kincsek, 1982; Webster et al., 1982; Etcheverry & Alemán, 2005) and beyond (Kochanovski et al., 2018). The robustness of phloem was found the most significant predictor of nectar yield in *Lotus corniculatus* (Murrell et al., 1982). There may be some tissue differentiation along a bundle. For example, xylem elements are found only at the base of vascular traces in *Hymenaea stigonocarpa* Mart. ex Hayne whereas distal portions of these bundles consist of phloem only and ramify producing a network within the secretory parenchyma (Paiva & Machado, 2008). Frei (1955) also highlighted a pronounced degree of differentiation of FN-supplying bundles which have xylem elements at their base and only phloem at their distal parts, either with or without companion cells. Even within a diverse genus, xylem can be present or absent in bundles of FNs; the example of *Vicia* is remarkable as xylem is found in the minute FNs of *V. tetrasperma* (L.) Schreb. (Stpiczyńska, 1995). As concluded by Frey-Wyssling (1955), xylem-innervated angiosperm FNs tend to produce more diluted nectar. This is confirmed with some examples from legumes, e.g. in *Vicia* (Stpiczyńska & Pelecki, 1999).

IV. Development of Floral Nectaries and Ontogenetic Changes in Them

All papers describing flower ontogeny in legumes agree that FNs emerge quite late, by the moment when all other floral parts are more or less differentiated (Picklum, 1954; Tucker, 1987, 1997; Horner et al., 2003; Zhang et al., 2006; Teixeira et al., 2009; Rather et al., 2021; Sinjushin, 2023). For example, in *Trifolium pratense* the FN becomes visible only when pollen tetrads are already present in thecae (Picklum, 1954). Whereas the upper rim of the FN is crenate in mature flowers of *Phaseolus vulgaris*, this FN initiates as a solitary ring without prominent apices (Sinjushin, 2023). Since the very inception, this premature FN already bears numerous stomata most of which are closed (Sinjushin, 2023).

The FNs of different taxa differ in the time of secretion outset and its duration. After examining these features in eight papilionoid species, mostly members of the Fabeae, Kartashova (1965) concluded that preanthetic buds produce very little or no nectar. Maximum secretion occurs in fully open flowers in which pollen is already germinating on the carpel's stigma. The first droplets of nectar appearing more or less synchronously with anther dehiscence were also reported in *Vicia faba* (Davis & Gunning, 1992). In *Glycine max*, secretion begins before anthesis, so in open flowers only collapsed FNs can be found (Horner et al., 2003), which seems to be also the case for *Phaseolus vulgaris* (Sinjushin, 2023) and *Amphicarpaea edgeworthii* Benth. (Zhang et al., 2006).

In pea, the number of modified secretory stomata remains more or less constant throughout all stages of flower development till senescence (Razem & Davis, 1999). However, many of the stomata become occluded on late stages with only ca. 40% of them still open in postanthetic flowers (Razem & Davis, 1999). Similar dynamics characterizes flowers of *Vicia faba* (Davis & Gunning, 1992). As nectar-exuding stomata are constantly open, their clotting on post-secretory stages may be important to prevent the entrance of pathogenic bacteria or fungi (Figure 2c,d; Razem & Davis, 1999).

The excessive amount of nectar is often resorbed by floral tissues (Bernardello et al., 2004; Kołtowski, 2004; Paiva & Machado, 2008; reviewed by Nepi & Stpiczyńska, 2008). Paiva and Machado (2008) recorded that multicellular excrescences, referred to as extrastomatic bodies, emerge from some stomatal pores of the FN on late stages of flowering in *Hymenaea stigonocarpa*. As soluble carbohydrates were detected in these bodies' cytoplasm, it was suggested that they provide the expanded surface for nectar resorption and assist stomatal plugging (Paiva & Machado, 2008).

V. Floral Structures Participating in Nectar Storage and Accessibility

None of the known legumes seems to possess true nectar spurs, like those in flowers of Orchidaceae or Balsaminaceae. In some cases, nectar can be stored in the adaxial gibbosity of the calyx, like in *Mucuna macrocarpa* Wall. (Kobayashi et al., 2018). Much more often is nectar accumulated in the nectar chamber (or nectar reservoir, nectar holder etc.), i.e. the space formed between a receptacle, staminal filaments, and a hypanthium, if present. The tubular nectar-accumulating structure can be quite long, produced of hypanthium, like in *Bauhinia* p.p. (Rodrigues & Leitão, 2023), or of fused stamens, like in *Inga* (Koptur, 1983).

In *Saraca*, the long gynophore is adnate to the inner adaxial surface of the unusually deep hypanthium, so the resulting volume can serve as a spur accumulating nectar. The disc is thought to be localized at the upper rim of the hypanthium at stamens bases (Tucker, 2000), although there was probably no special survey focused on nectar secretion in this genus. In some other leguminous flowers also having a long floral tube, nectar is usually secreted on this tube's walls in its proximal portion (Leite et al., 2015, 2021; Rodrigues & Leitão, 2023).

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There is a problem of preventing nectar from outflow, which is especially significant in pendulous or resupinate flowers. Most likely the outgrowths at staminal bases of bird-pollinated *Cadia purpurea* Forssk. (Tucker, 2002) assist in retaining nectar serving as a roof of the nectar chamber. Their contrast pigmentation is also believed to attract visitors (Cronk & Ojeda, 2008). Probably the same preventing function is fulfilled by the pocket-like ridge on the hypanthium in resupinate flowers of *Clitoria ternatea* L. (Sinjushin, 2022) and the overall shape of the FN in *Centrosema* spp. (Aponte & Jáuregui, 2019). The pubescence of the inner surface of a hypanthium (e.g. in *Tipuana tipu* (Benth.) Kuntze: Figure 2e,f; *Amburana cearensis* (Allemão) A.C. Sm.: Leite et al., 2015) could be also helpful in retaining nectar from outflow and/or evaporation. Certain types of trichomes on the soybean carpel hypothetically participate in holding the nectar and moving it upwards due to capillary effect (Horner et al., 2003). Oppositely, in explosive-opening flowers of *Mucuna macrocarpa*, nectar is accumulated in the calyx protuberance and subjected to controlled outflow. Stamens and style release only when a mammal visitor pushes the flag petal upwards simultaneously pouring nectar out due to the special hooks at the flag base (Kobayashi et al., 2018).

The access to FNs is primarily shaped by the mode of staminal fusion, especially diverse in flowers of Papilionoideae members. The fusion of stamens was reported tightly correlated with the presence of FNs in this subfamily (Rodríguez-Riaño et al., 1999). The androecium consisting of completely free stamens in a ‘flag blossom’ is hypothetically associated with a higher production of nectar (Rodríguez-Riaño et al., 1999) which, however, may be due to bird-pollination syndrome of *Anagyris foetida* L., the only species with free stamens examined by the authors of the cited paper. As Cronk and Ojeda (2008) suggested, abundant dilute nectar is a part of ornithophilous pollination syndrome.

The depth and diameter of a floral (staminal or hypanthial) tube may be also effective to select between floral visitors. In flowers of phaseoloid legumes (e.g. *Phaseolus vulgaris*), large appendages are found on the outer surface of the inner adaxial (vexillary) stamen potentially defending the nectar chamber from nectar thieves (Sinjushin, 2023).

Very common are FNs in flowers with an androecial tube interrupted in some way. In diadelphous androecium, the vexillary stamen is free whereas the other nine are fused in a tube. In this case, two clefts remain along the vexillary stamen providing the access to FNs. It is a common androecial type in *Astragalus* and some other galegoid legumes (Sinjushin et al., 2022). Sometimes bases of filaments bend outwards producing special holes (fenestrae), like in *Colutea arborescens* L. (Sinjushin et al., 2022). In many cases, the vexillary stamen reunites with adjacent ones remaining in contact with them during anthesis, i.e. imperfect postgenital fusion sensu Sokoloff et al. (2018) takes place. In this particular case, fenestrae are anyway formed either providing access to the nectar chamber or, when of small diameter, hypothetically allowing nectar outflow to the space between the staminal tube and the perianth. The latter morphology is found in *Lathyrus* p.p. (Sinjushin et al., 2022). The modes of staminal bending and mutual arrangement in di- and pseudomonadelphous androecia are very diverse even within a single genus. The adaxial side of a calyx tube may be gibbous above the fenestrae to make them easier to reach.

In flowers of some papilionoid legumes (*Pterocarpus* p.p., *Tipuana*, *Crotalaria*, *Calpurnia*), the vexillary stamen fuses with one of the adjacent ones, so only one fenestra is formed. Sometimes the staminal tube is also split from the abaxial side (*Pterocarpus* p.p., *Aeschynomene*) or the outer adaxial stamen is free (*Discolobium*). All these androecial types seem to provide access to FNs.

Di- or pseudomonadelphous androecia are usually found in nectar-producing flowers (Rodríguez-Riaño et al., 1999). The only well-known, though underexamined, exclusion is *Securigera varia* with its vexillary stamen more or less free but without conspicuous FNs (Vogel, 1997). However, the opposite associations also seem existent. Despite the frequently found view that flowers of *Galega* with their monadelphous androecia are nectarless (Rodríguez-Riaño et al., 1999; Carreck et al., 2001), they were reported to secrete nectar (Dokukin, 2009). Although the vexillary stamen is fused with others and lacks its own epidermis, its filament possesses the longest free portion. In addition, there are sparse, hypothetically nectariferous, stomata at the carpel’s base in flowers of two species of *Galega* (Sinjushin et al., 2022). Similarly, sparse and potentially secretory stomata are found at the carpel base in *Campylotropis* (Sinjushin & Ploshinskaya, in prep.) which was previously characterized as having no FNs (Nemoto & Ohashi, 1988). Both *Galega* and *Campylotropis*, although not closely related, are nested in clades with di- or psedomonadelphous androecia and probably reflect the transient stage between diadelphous nectariferous and monadelphous nectarless flowers.

Despite listed exceptions, monadelphous androecia are often associated with the absence of nectar in different lineages, such as some of the Genisteae, *Ononis* in the Trifolieae (Rodríguez-Riaño et al., 1999), *Riedeliella graciliflora* Harms in the Desmodieae (Bento et al., 2021) and probably some others. On a regulatory level, staminal fusion itself does (or may) not necessarily cause the loss of FNs. As seen in an atypical specimen of *Astragalus albispinus* Širj. & Bornm., anomalous banner morphology and monadelphy do not prevent the formation of numerous nectariferous stomata on the hypanthium (Sinjushin et al., 2022).

VI. Regulation of Flower Nectaries Development in Legumes

Although the molecular mechanisms governing FN development were studied much less than the genetic control of floral organ identity, some patterns have been dissected to date (reviewed in: Slavković et al., 2021). Two key independent regulatory pathways are known in *Arabidopsis thaliana* (L.) Heynh. (Brassicaceae). One of them is connected with a gene *CRABS CLAW* (*CRC*) which, once dysfunctional, disrupts proper carpel closure and FN development. Genes *BLADE-ON-PETIOLE1* and *2* (*BOP1*, *BOP2*) are also involved in FN ontogeny. Both *CRC* and *BOP1/2* are influenced by other genes including those determining the identity of the flower and its parts. The most important of these genes is *LEAFY* (*LFY*) (Slavković et al., 2021).

No *crc* mutants are known in legumes but the *CRC* orthologue is expressed at the abaxial part of a receptacle in *Pisum sativum* L. and *Medicago truncatula* Gaertn., i.e. exactly where FNs develop in these species (Fourquin et al., 2014). This observation suggests that *CRC* orthologues have a conserved role in the regulation of FN formation in legumes.

As for *BOP1/2*-like genes, their orthologues are known in genomes of *P. sativum*, *M. truncatula*, *Lotus japonicus* (Regel) K.Larsen, and *Lupinus angustifolius* L. (Liu et al., 2023). In pea, the mutation *cochleata1* (*coch1*) of a *BOP1/2* orthologue is known to affect floral development (Couzigou et al., 2012). In flowers of a *coch1* missense mutant with a mild expression of anomalies, nectariferous stomata were found on a receptacle whereas no such stomata were detected in flowers of a nonsense mutant with a more severe phenotype (Sinjushin, 2022). This may suggest that the *BOP1/2*-dependent control of FN development is shared between *Arabidopsis* and legumes.

There is some indirect evidence that other genes reported to control FN development in *Arabidopsis* have the same function in legumes. For example, gene *AGAMOUS* (*AG*) participates in FN development, termination of the floral meristem proliferation, and identity of stamens and carpels. The *ag* mutants of *A. thaliana* produce excessive sepals and petals instead of stamens and carpels and their FNs have altered morphology (Baum et al., 2001). A ‘double-flowering’ ornamental form of *Lotus corniculatus* with numerous petals was described as nectarless and not visited by insects (Corbet et al., 2001). However, a nectar disc with stomata is found in ‘double’ flowers of garden *Wisteria floribunda* f. *violaceoplena* (C.K.Schneid.) Rehder & E.H.Wilson, although its functionality was not tested (Sinjushin, 2022). Floral phenotypes with extra petals are known in several legume species but it has not been confirmed whether the causative mutations are in *AG*-like genes and if these ‘double’ flowers produce nectar.

As FNs are preferentially placed at the abaxial domain in many monosymmetric leguminous flowers, it is highly likely that the expression of key markers of FN development is negatively regulated by some adaxially expressed gene(s). The most important of them are the ones of the TCP family, such as orthologues of *CYCLOIDEA* (*CYC*) discovered in *Anthirrhinum majus* L. (Plantaginaceae). *CYC*-like genes are usually expressed in the adaxial part of floral meristem and play an important role in regulation of floral monosymmetry in many taxa (Preston & Hileman, 2009) including legumes (Wang et al., 2008; Xu et al., 2013). In *Pisum sativum* and *Lotus japonicus*, mutations in *CYC* orthologues affect the proper differentiation of petal types (Wang et al., 2008). One of these mutations in pea is *keeled wings* (*k*) (Wang et al., 2008). In flowers of *k* mutants, the nectar-secreting area expands to lateral parts of the receptacle whereas FN has the abaxial position in wild-type flowers (Sinjushin, 2022). This may point at the *CYC*-mediated suppression of FN development in leguminous flowers but this interaction requires a deeper examination.

If *CYC*-like genes indeed inhibit FN development in leguminous flowers, it can impose constraints on shifts in floral symmetry in the family. Acquisition of floral polysymmetry via 'dorsalisation', i.e. expansion of the adaxial developmental program to other floral domains, may cause the complete loss of FN. While in some taxa dorsalisation may result in production of extra FNs (Zhao et al., 2018), it is not the case of Leguminosae. The best, and probably only, known example of naturally occurring dorsalised leguminous 'peloria' is *Cadia* with its polysymmetric flowers clearly derived from monosymmetric ones through ectopic expression of a *CYC*-like gene (Citerne et al., 2006). However, flowers of this plant are nectariferous (Cronk & Ojeda, 2008) which agrees with probable absence of inhibition of FN development in the adaxial domain of a related genus *Calpurnia* having a papilionate corolla (Sinjushin, 2022). It means that, if FN is polysymmetric, a broader range of symmetry changes is available in a given lineage. The unusually polysymmetric flowers of *Riedeliella graciliflora* untypical for the Dalbergieae are nectarless and offer pollen as a reward (Bento et al., 2021) which may be a side effect of floral symmetry shift.

In a set of the leguminous floral mutants having anomalies in differentiation of stamens and/or perianth, such as staminal petaloidy or carpelloidy and malformed petals lacking a proper fusion, nectar-secreting stomata were found in their proper place, i.e. in the abaxial floral domain (Sinjushin, 2022). This indicates that the genetic control of FN development in legumes is considerably independent of the one of petals and stamens. Changes in androecium and perianth do not affect the ontogeny of FN which is retained in highly diverse leguminous flowers.

As flower size, a heritable trait, is correlated with nectar productivity (Davis, 2001), the latter may also be a goal in selection and breeding (e.g. Barnes & Furgala, 1978). Not only does genotype affect the nectar productivity but also a ploidy level. Tetraploid accessions of *Trifolium pratense* produce significantly more nectar than diploids which correlates with longer flower tubes in genotypes with a higher ploidy (Zaryanova, 2023).

VII. Nectarless Leguminous Flowers

Some of the legume lineages resulted in the complete loss of FNs. Nectarless flowers produce pollen as a reward, so nectarless taxa are usually characterized by some sort of functional division between anthers. As demonstrated by Paulino et al. (2016) in two nectarless members of the Genisteae tribe, *Lupinus* sp. and *Cytisus scoparius* (L.) Link, heterostameny evolved in different directions. In flowers of *Lupinus*, inner stamens have smaller anthers and push out pollen produced by the larger anthers of outer stamens. The shorter adaxial stamens of *C. scoparius* produce pollen primarily to attract insects while the abaxial stamens serve for pollination (Paulino et al., 2016). Not only do two sets of stamens differ in sizes of their anthers but also in the viability of pollen produced. The same mode of heterostameny as in *Lupinus* is also found in nectarless flowers of *Ononis* in which stamens with larger basifixed anthers alternate with those with smaller dorsifixed anthers. Heterostameny does not always mean the absence of nectar: in *Crotalaria* p.p. two distinctive staminal morphs coexist with the FN (e.g. Etcheverry et al., 2003).

Highly diversified androecia of *Senna*, as well as some other members of the Cassieae, are adapted to buzz-pollination and associate with asymmetry (including enantiostyly) and absence of nectar (Dulberger, 1981; Marazzi et al., 2007).

Some representatives of the former subfamily Mimosoideae are also known as having no floral nectaries (e.g. *Acacia* p.p.: Stone et al., 2003, *Parkia*: Pedersoli & Teixeira, 2016). Natural populations of *Prosopis glandulosa* var. *torreyana* (L.D.Benson) M.C.Johnst. include both nectarless and nectarful trees suggesting a sort of automimicry as a pollination strategy (López-Portillo et al., 1993; Golubov et al., 1999). In some cases, the loss of FNs may be counterbalanced by the development of dense many-flowered globose or spicate inflorescences attracting possible pollinators with odor (de Assis Pires & Freitas, 2008). Debatable though it may be, some of the pollinators could be attracted by the extrafloral nectaries, especially those placed near the inflorescence and visually enticing (Stone et al., 2003). The well-known anther glands of some mimosoids can serve as food bodies for insects and birds or even as mimetic ‘pseudopollen’ (reviewed by Stone et al., 2003; de Barros & Teixeira, 2016). In *Anadenanthera colubrina* (Vell.) Brenan, the absence of hypanthial or receptacular FN is compensated by substitutive nectaries in the form of secretory trichomes on petal tips (Borges et al., 2017). Not all flowers of this species possess nectaries like this. Insects are suggested to visit fragrant nectarless flowers of *Acacia retinodes* Schltdl. together with those of cohabiting nectariferous species flowering at the same time, so the pollination of *A. retinoides* itself occurs partially by deceit (Bernhardt et al., 1984).

Beyond mimosoids, scented, multistaminate and nectarless flowers of *Cyathostegia matthewsii* (Benth.) Schery (Papilionoideae) are highly likely pollinated by beetles (a very rare pollination vector in the family), although anemophily cannot be fully excluded (Lewis et al., 2003). All listed examples indicate that the absence of FNs is characteristic for highly specialized leguminous flowers having some compensatory adaptations.

VIII. Chemistry of Nectar in Legumes

Several papers are devoted to chemical composition of nectar in different leguminous species (Hokche & Ramirez, 1990; Cocucci et al., 1992; van Wyk, 1993; Koptur, 1994 and others). As in other taxa, nectar of Leguminosae contains sugars (hexoses, primarily glucose and fructose, and sucrose), amino acids, lipids, proteins as well as some other substances, such as organic acids and alkaloids. A highly influential paper by Nicolson and Thornburg (2007) can be referenced here as a thorough review of the topic.

Both the percentage of sugars in nectar and the ratio between them can be affected by environmental factors, such as temperature and soil/air moisture (Vansell, 1941). The reliable intraspecific differences in nectar parameters were reported between accessions of different origin grown in controlled conditions (Walker et al., 1974; Barnes & Furgala, 1978; Teuber et al., 1980; Cocucci et al., 1992) which evidences for heritable nature of chemical properties of the leguminous nectar. Ratio between sucrose and hexoses in each flower’s nectar can change over time due to hydrolysis (Hokche & Ramirez, 1990; Koptur, 1994).

An intriguing question to be addressed is whether chemical composition of nectar is mainly dependent on phylogeny or pollination strategy. Having examined numerous species of three tribes, van Wyk (1993) concluded that the ratio between sugars in their nectar was conserved on tribal and generic levels even in the case of related congeneric species having contrasting pollination strategies. Whereas floral morphology differed between a bird- and an insect-pollinated species of *Liparia*, their nectar composition was similar (van Wyk, 1993). The proportions of different sugars were found close between eight species of *Inga* having different pollinators (Koptur, 1994). Partially the opposite was reported for two species of *Mucuna* by Agostini et al. (2011). Some features, like flower opening mechanism, were conserved between a bird- and a bat-pollinated species. However, the nectar of the former species was fructose-dominated while the latter secreted nectar with almost equal amounts of three sugars (Agostini et al., 2011). Probably in different leguminous clades pollination syndrome and phylogeny contribute unequally to nectar composition which is of little surprise taking into account a high level of intraspecific variation of this trait and its possible complex genetic control (e.g. Mitchell, 2004).

IX. Origin, Evolution and Possible Taxonomic Implications of Floral Nectaries in Legumes

Considering the exceptional plasticity of angiosperm FNs in terms of their structure and position within a flower (Smets, 1986), the exact origin of the leguminous FNs has been a matter of debates and (re)interpretations for almost two centuries. A detailed review of existing literature on the issue was made by Moore (1936) and in a recent paper by Zalko et al. (2022). Generally, there are two opposing views on the origin and identity of the leguminous FN. The one hypothesis, first put forward by A.P. De Candolle and elaborated in details by Moore (1936), suggests that an annular FN of the Phaseoleae is derived from underdeveloped stamens, i.e. has a staminodial nature. Indeed, in many cases a disc has ten distinct lobes and is supplied by ten conductive bundles fusing with the staminal traces, as observed by Moore (1936) and earlier morphologists cited in his paper. Interestingly, the same observation led Narang (1977) to the opposite conclusion that the disc cannot be of an androecial origin: in this case, 'its vascular supply must be derived from the receptacular stele as they arise for the other stamens' (Narang, 1977: 368).

The vascular association between stamens and FN does not necessarily mean their homology. If the leguminous FN is derived from androecium, i.e. ten innermost stamens were converted into FN, this would require an ancestral state of four pentamerous androecial whorls, which was never recorded in Fabales. In all studied cases, FNs initiate much later than stamens. The own vasculature consisting of ten bundles, however, indicates that the FN initiation is patterned with respect to a pentamerous floral whorl, i.e. stamens or perianth. The alternative hypothesis is that the leguminous FN emerged as a receptacular rather than staminal outgrowth (Waddle & Lersten, 1973). It may therefore represent an organ *sui generis* unrelated to other, more conventional, floral whorls (Sinjushin, 2023).

The existence of FNs seems a symplesiomorphy of Fabales with independent losses of FNs in different lineages (Bernardello, 2007). Alongside some nectarless representatives in different lineages of Leguminosae (see above), FNs are absent from three genera of four in Surianaceae (Schneider, 2007).

In six leguminous subfamilies recognized by the LPWG (2017), FNs are described and illustrated with unequal precision. Most of the FNs characterized to date belong to the largest subfamilies, Papilionoideae and Caesalpinioideae. In the latter clade, members of the former subfamily Mimosoideae are best characterized, primarily due to an important paper by Ancibor (1969).

In Cercidoideae, members of *Bauhinia* s.l. possess long hypanthia with secretory tissue on their inner walls (Rodrigues and Leitão, 2023). Some of the members lacking hypanthia were reported to have large fleshy intrastaminal disc bearing secretory stomata (Clark et al., 2017). Frei (1955) highlighted that the FN of *Cercis siliquastrum* L. is very similar to the one of *Robinia pseudacacia* L. but no illustrations are available.

The annular FNs were reported in two species of *Hymenaea* (Paiva & Machado, 2008; Kochanovski et al., 2018) and *Copaifera langsdorffii* Desf. (Pedersoli et al., 2010) from the subfamily Detarioideae. The hypanthial FN exuding abundant nectar through nectarostomata was described in *Apuleia* from Dialioideae, whereas there are probably no FNs in flowers of *Martiodendron* from the same subfamily (Falcão et al., 2020). Flowers of *Duparquetia orchidacea* Baill., the only member of Duparquetioideae, were characterized as nectarless (Prenner & Klitgaard, 2008).

Although data on FN diversity in Leguminosae are scarce, several evolutionary tendencies can be hypothesized.

(1) Nectarless flowers (see above) obviously evolved recurrently in different leguminous lineages, so the absence of FNs cannot be interpreted as a primitive state contrary to the hypothesis of Gulyás and Kincsek (1982). Taking into account the yet understudied complexity of the regulation of FN development, it is not that easy to identify the exact sequence of causative events associated with the loss of FNs. It is unclear in each particular case whether the complete staminal fusion and the emergence of monadelphous androecium caused the obligate reduction of FN or, on the contrary, FN loss made staminal fusion possible.

(2) Sizes of FNs seem generally correlated to those of the whole flower, so the process of floral diminishing is accompanied by the reduction of FN which becomes smaller and less structurally pronounced. The results of this process can be observed in small-flowered vetches (*Vicia*) or *Astragalus* (Stpiczyńska, 1995; Sinjushin et al., 2022). Possibly the opposite process, i.e. the synchronous enlargement of a flower and FN, can also take place but there is almost no information on FN structure in legumes with exceptionally large flowers, such as *Mucuna macrocarpa* or *Sesbania grandiflora* (L.) Poir.

(3) Some lineages with zygomorphic flowers exhibit a pronounced trend towards the monosymmetric position or morphology of their FNs or at least nectar-secreting areas. The adaxial floral domain has some regulatory peculiarities which inhibit FN development. This phenomenon seems to restrict shifts in floral symmetry via homeotic dorsalization as discussed

previously. Otherwise stated, certain changes in petal differentiation may make the alteration of pollination strategy inevitable.

Floral nectaries obviously possess a certain degree of evolutionary inertia. Indeed, they remain (almost) intact when other floral parts change either abruptly, as a result of mutations, or gradually, following an evolutionary trend (e.g. flower miniaturization).

Unlike extrafloral nectaries, FN characters are rarely recruited for systematics. These may have a taxonomic value on a generic or section level. For example, FN characters were used, among others, to distinguish between several related millettioid genera by Sirichamorn et al. (2014). Stirton (1981) included morphology of a floral disc in his treatment of a group of related *Eriosema* species. Similarly, the features of FN were listed as differentiating between several related genera of the Diocleae to support molecular data (Sede et al., 2009).

A relatively low taxonomic significance of FNs can be explained by the overall stability of their morphology in large leguminous clades but, at the same time, exceptional diversity of their minor features. For example, the placement of the secretory area on the adaxial ligulate outgrowth can be interpreted as a synapomorphy of *Vicia* (Stpiczyńska, 1995). However, this characteristic morphology is absent in small-flowered species. The FN structure is difficult to examine and almost impossible to study on herbarium material which may also underlie the rare recruitment of the FN features in the systematics of legumes.

X. Conclusion

The leguminous floral nectaries associate the exceptional evolutionary stability with the overall lability of a flower. It remains enigmatic though why numerous major events in floral evolution, such as shifts in merism and symmetry, multiplication or reduction of some parts and alike, leave FNs untouched but in other cases FNs disappear from more or less 'customary' flowers.

Despite the data already accumulated, much more is needed to be discovered to judge more confidently on the evolution and functioning of the leguminous FNs. Several directions deserve further research. The first of them is a mere description of the existing diversity of FNs, especially in taxonomically unrelated taxa and the most basal representatives. Recent progress in investigation of floral secretory structures in tropical legumes (e.g. Bento et al., 2021; Leite et al., 2021) is very helpful. Very little is known about the FN functioning, such as possible modes of secretion.

Much more data is yet to be obtained in a field of genetic and physiological regulation of FN development. For long, this issue has been under examination only in model plant species, such as *Arabidopsis thaliana* (Slavković et al., 2021). However, as FNs are exceptionally diverse among angiosperms, the results of pioneer studies on FN genetics and physiology can be only cautiously approximated to other taxa, including legumes with their often monosymmetric flowers.

With the ongoing progress in studies on the leguminous FNs, it may become more clear why nectar remains the most important reward in certain angiosperm lineages and which morphological and regulatory features facilitate its broad distribution.

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