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Evolution of floral nectary in Lamiaceae

D SANTHA KUMARI
Department of Botany, Nagarjuna University, Nagarjunanagar 522 510, India

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Abstract. The morphology and vasculature of the floral disc have been studied in 30 species of Lamiaceae to discuss its phylogeny. In Lamiaceae the disc receives vascular supply mostly from the gynoecial bundles which indicates its association with the gynoecium. Further, the evolution of both the external form and vasculature of the floral disc progressed independently. On a comparative basis the disc in prostantheroideae and scutellarioideae can be looked upon as most primitive, whilst in ocimoideae as highly evolved.

Keywords. Floral nectary; morphology; vasculature; evolution; lamiaceae.

1. Introduction

The nature of the disc in members of gamopetalae had been interpreted differently by Brown (1938), Fahn (1952, 1953), Moore (1936), Rao (1953, 1954, 1955, 1971), Rao and Ganguly (1963) and Woodson (1930) based on morphoanatomical features. In Acanthaceae, Apocynaceae, Boraginaceae and Lamiaceae a prominent disc is present close to the base of the ovary and which has been regarded to represent staminodes, carpellodes and out growth of the receptacle, basing on the organ with which it is associated. Fahn (1952, 1953) considered the disc in Lamiaceae as an out growth of the thalamus, while Kartashova (1960) regarded it as the proliferation of basal part of the ovary. Because of the highly condensed nature of the thalamus it is not possible to decide whether the disc was expansion of receptacle or ovary. But for a brief report by Hillson (1958) a comparative and comprehensive account on the morphology of floral disc based on the vascular supply among lamiacean taxa is not available. So it was felt a detailed study of the vascular supply to the disc in lamiacean taxa would likely offer enough information that might help in reorientation of our ideas in respect of this structure and its phylogeny.

2. Materials and methods

The following species have been studied:

Sub-family	Name of the plant
I Ajugoideae	*Ajuga bracteosa* Wall.
	Teucrium royleanum Wall.
II Prostantheroideae	*Westringia rigida* R. Br.
IV Scutellarioideae	*Scutellaria violacea* Heyne. ex Benth.
V Lavanduloideae	*Lavandula vera* D.C.
VII Stachydoideae	*Calamintha umbrosa* Fisch et Mey.
	Nepeta hindostana (Roth) Haines.
	Meriandra bengalensis Benth.

(*Contd.*)

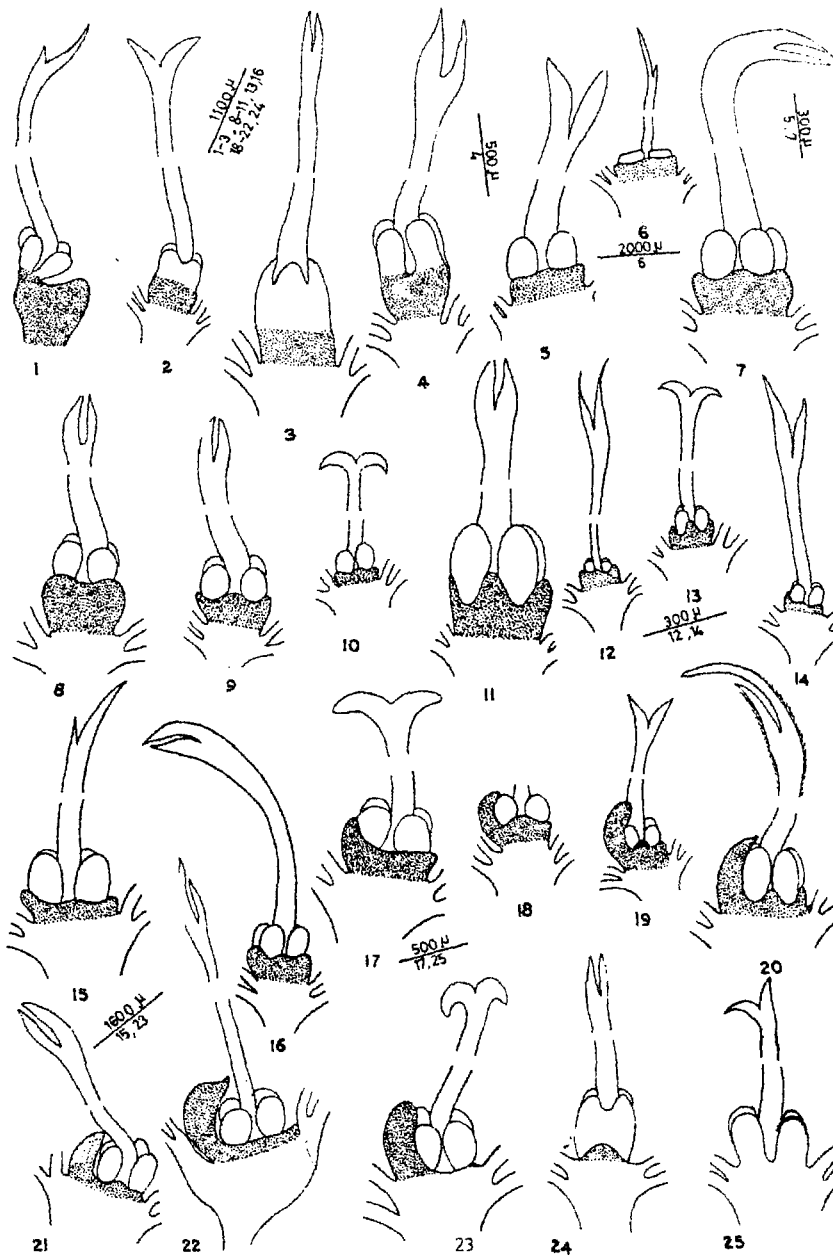
Sub-family	Name of the plant
	Salvia azeurea Lam.
	S. coccinea Juss.
	S. splendens Sello.
	S. leucantha Cav.
	Dysophylla rugosa Hook.
	D. quadrifolia Benth.
	Anisomeles malabarica R. Br. ex Sims.
	A. indica O. Kze.
	Leonotis nepetaefolia R. Br.
	Leucas diffusa Benth.
	L. mollissima Wall.
	Micromeria biflora Benth.
VII Ocimoideae	*Ocimum canum* Sims.
	O. basilicum Linn.
	O. killimandscharicum Gurke.
	Hyptis suaveolens Poit.
	Coleus scutellarioides Benth.
	Anisochilus polystachyus Benth.
	A. carnosus Wall.
	Geniosporum indicum Briq.
	G. prostratum Benth.
	Plectranthus incanus Link.

The materials were collected personally, or received from different places. Except for *Westringia rigida* R. Br. received from Kew Botanical Gardens, UK, all other species are Indian. The material was fixed in FAA. The customary methods of dehydration and clearing were followed and embedding was done in paraffin wax (60–62°C MP). Sections were cut into 10–15 μm and stained with Delafield's hematoxylin.

3. Observations

A hypogynous nectariferous disc is situated between the stamens and ovary (figures 1–24) except in *Anisomeles indica* O. Kze, where it is not discernible externally (figure 25). In rest of the taxa, it becomes differentiated from the receptacle by the time the ovary becomes lobed and shows marked variation. It is annular, entire and adnate to the basal part of ovary in *Teucrium royleanum*. Wall, *Westringia rigida* R. Br. and *Calamintha umbrosa* Fisch. et Mey. (figures 2–4), while in *Scutellaria violaceae* Heyne ex Benth., the disc gets adnated to the gynophore of the ovary (figure 1). In the remaining taxa studied presently, the disc shows adnation with the base of the ovary, and exhibits a variety of lobing higher up.

The disc is obscurely 4-lobed in *Micromeria biflora* Benth., *Leonotis nepetaefolia* R. Br., *Nepeta hindostana* (Roth) Haines, *Lavandula vera* D.C., *Geniosporum indicum* Briq., and *Ocimum canum* Sims. (figures 5–10). The disc lobes alternate with the nutlets in all except *Lavandula vera* D.C. where they are located behind the nutlets. In *Hyptis suaveolens* Poit., *Dysophylla quadrifolia* Benth., and *Ocimum basilicum* L., all the 4 lobes are equally developed (figures 11–13), while in *D. rugosa* Hook., *Leucas diffusa* Benth., *L. mollissima* Wall., *Meriandra bengalensis* Benth. and *Anisomeles*



Figures 1–25. Gynoecium in association with nectary in different members of Lamiaceae. **1.** *Scutellaria violacea.* **2.** *Teucrium royleanum.* **3.** *Westringia rigida.* **4.** *Calamintha umbrosa.* **5.** *Micromeria biflora.* **6.** *Leonotis nepetaefolia.* **7.** *Nepeta hindostana.* **8.** *Lavandula vera.* **9.** *Geniosporum indicum.* **10.** *Ocimum canum.* **11.** *Hyptis suaveolens.* **12.** *Dysophylla quadrifolia.* **13.** *O. basilicum.* **14.** *D. rugosa.* **15.** *Leucas mollissima.* **16.** *Meriandra bengalensis.* **17.** *Anisomeles malabarica.* **18.** *O. killimandscharicum.* **19.** *Anisochilus carnosus.* **20.** *Salvia splendens.* **21.** *G. prostratum;* **22.** *Coleus scutellarioides.* **23.** *Plectranthus incanus.* **24.** *Ajuga bracteosa.* **25.** *A. indica.*

malabarica. R. Br. ex Sims, the disc becomes zygomorphic consequent to the enlargement of anterior lobe (figures 14–17). In *Ocimum killimandscharicum* Gurke., *Anisochilus polystachyus* Benth., and *A. carnosus* Wall. The anterior and lateral lobes are more conspicuous than the posterior (figures 18–19), while in others, the disc exhibits unilateral development with *Salvia splendens* Sello., *S. azeurea* Lam., *S. coccinea* Juss., *S. leucantha* Cav., *Geniosporum prostratum* Benth., *Coleus scutellarioides* Benth. and *Plectranthus incanus* Link. (figures 20–23) or without (*Ajuga bracteosa* Wall.) rudimentary posterior lobe (figure 24). Anatomically, the disc is composed of small, densely cytoplasmic and prominently nucleated cells which bear plenty of reserve food materials. In *Ajuga bracteosa*, though the disc is suppressed externally on the posterior side, its presence can be marked by few layers of glandular cells (figure 53).

Associated with this difference in position and external form, the disc manifests variation even in its vascularization. The vascular bundles of the disc arise at different levels either symmetrically (figures 26–31, 50, 54, 55) or on anterior sector alone (figures 42–49, 51–53). In *Scutellaria violacea*, after the departure of second whorl of traces, the central stele gives off two dorsal carpellary traces as well as a few vascular strands in the region of gynophore (figure 28). In *Westringia rigida* after supplying the petals and stamens the remaining stele gives off 12 bundles to the ovary wall, 3 for each of the 4 sectors and also a number of strands into the disc (figures 26, 27). In *Plectranthus incanus* and *Ajuga bracteosa* the disc is unilaterally disposed with or without a rudimentary posterior lobe and derives its vascular supply only from the anterior dorsal carpellary bundle (figures 51–53). In *Coleus scutellarioides, Leucas diffusa* and *L. mollissima*, the disc obtains its vasculature from the ventrals (figures 54, 55). In *Anisomeles malabarica, Nepeta hindostana* and *Hyptis suaveolens*, the disc gets vasculature from the ventral as well as dorsal carpellary bundles (figures 30, 39–41). In *Geniosporum indicum* and *Ocimum killimandscharicum*, the disc gets vascular supply uniformly on all the sides from the plexus formed by the fusion of branches from the dorsal and ventral carpellary traces (figures 29, 37). In *Leonotis nepetaefolia* this plexus splits up into definite number of bundles to feed the wall. The disc here is fed by the bundles that are cut off towards outside from the common bundles that supply the ovary wall and disc (figures 31, 32). In *Geniosporum prostratum, Anisochilus polystachyus, A. carnosus, O. basilicum, O. canum* and species of *Salvia*, the disc receives its supply from the bundles of anterior sector alone (figures 42–46, 48). In *D. quadrifolia, Calamintha umbrosa, Teucrium royleanum* and *Nepeta hindostana*, the disc is uniformly supplied with strands derived from bundles of carpellary wall as also from the vascular strands

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Figures 26–59. Cross sections of floral receptacle showing the pattern of vascularization to the nectary in different members of Lamiaceae. **26 and 27.** *Westringia rigida* **28.** *Scutellaria violacea.* **29.** *Geniosporum indicum.* **30.** *Anisomeles malabarica.* **31 and 32.** *Leonotis nepetaefolia.* **33–35.** *Dysophylla quadrifolia.* **36.** *Calamintha umbrosa.* **37.** *Ocimum killimandscharicum.* **38.** *Teucrium royleanum.* **39 and 40.** *Nepeta hindostana.* **41.** *Hyptis suaveolens.* **42.** *G. prostratum.* **43.** *Anisochilus carnosus.* **44.** *A. polystachyus.* **45.** *O. basilicum.* **46.** *O. Canum.* **47.** *D. rugosa.* **48 and 49.** Salvia splendens. **50.** *A. indica.* **51 and 52.** *Plectranthus incanus.* **53.** *Ajuga bracteosa.* **54.** *Leucas mollissima.* **55.** *Coleus scutellarioides.* **56 and 57.** *Meriandra bengalensis.* **58.** *Lavandula vera.* **59.** *Micromeria biflora.*

(DCB, dorsal carpellary bundle; DS, disc supply; SB, sepal bundles; PB, petal bundles; SS, staminal supply; WS, wall supply; CV, common ventrals; VCB, ventral carpellary bundles).

supplied by dorsals and/or ventrals (figures 35, 36, 38, 40). In *D. rugosa* the supply is restricted to the anterior sector alone (figure 47).

In *Anisomeles indica* O. Kze., though the disc is not discernible externally, a large number of strands are given off into the region of the disc from the ventral carpellary bundles (figure 50). In *Meriandra bengalensis*, *Lavandula vera* and *Micromeria biflora*, though the disc is prominent, it does not receive vascular bundles from any of the above sources and is totally devoid of vasculature (figures 56–59).

4. Discussion

The foregoing instances suggest that even within one and the same family there can be certain important variations in the morphology and vascularization of the disc.

In a number of dicotyledonous families with superior ovaries a disc present either close to the base of the ovary or close to the bases of the stamens, or it may be present even between these two whorls. In fact, Hitchcock (1932) and Lawrence (1937) are of the opinion that a disc associated with the androecium should represent staminodes and one associated with the gynoecium should represent carpellodes and that one not closely associated with either of these two should be regarded as an outgrowth of the receptacle.

Basing on anatomical studies in Acanthaceae, Bignoniaceae and Pedaliaceae Rao (1971) considered it as a fifth whorl of floral organ receiving vascular supply from the nearest source. Woodson (1930) in Apocyanaceae, Moore (1936) in Boraginaceae have described two of the disc lobes, which are bigger and alternating with the carpels, as carpellodes and the remaining two smaller ones as part of the carpels produced as a consequence of infolding of the gynoecium. Woodson and Moore (1938) opined that the bundles of disc in some Apocynaceae are comparable to dorsal and ventral bundles of carpels but Rao and Ganguly (1963) failed to observe any such bundles reported by Woodson and Moore and therefore, gave a quite different interpretation. The interpretation sponsored by Woodson and Moore (1938) does not hold good on the grounds that one cannot interpret part of the disc as an outgrowth of carpels and the other as modified carpels.

In addition to the negative evidence given above, there is also a considerable positive evidence against this idea. In all the members of Lamiaceae, so far studied, the disc gets vasculature from the central stele far above the origin of dorsal carpellary traces or directly from the bundles of the bicarpellary pistil. In addition to this, the disc is not receiving the bundles corresponding to the dorsal, ventral and marginal bundles of abortive carpels indicating its nature as a mear enation and not a morphological entity.

Two views have been expressed regarding the morphology of disc in Lamiaceae. Fahn (1952, 1953) regards it as an out-growth of the thalamus, while Kartashova (1960) considers it as a proliferation of the base of the ovary. Both of these views are based exclusively on exomorphic features. However, it is difficult to demarcate where the thalamus ends and ovary begins externally, only the anatomical studies can decide this issue. The present study on comparative anatomy and organogeny in Lamiaceae lend support to Kartashova's (1960) interpretation of the morphology of the disc. While in other families like Acanthaceae, Bignoniaceae and pedaliaceae (Rao 1953, 1954, 1955), the disc gets vasculature from different sources like bundles of petal, stamen or from the floral stele below the level of origin of carpellary traces, in Lamiaceae the disc receives its vascular supply from the floral stele after the demarcation of dorsal carpellary traces or sometimes even from the dorsal or ventral or from the bundles of carpellary wall itself. Therefore, it can be considered as part of the gynoecium as Hitchcock (1932) and Lawrence (1937) suggested for members of Solanaceae and Boraginaceae respectively, basing on anatomical features.

Brown (1938) and Fahn (1952, 1953) believe that there is an acrocentripetal migration of the disc in its course of evolution. In view of this the disc in Lamiaceae occupies a highest position among the families of Bicarpellatae because, in all the

members studied so far, the disc shows definite association with the gynoecium and receives support from morphoanatomical grounds. Even if we accept the interpretation of Rao (1971) about the disc as an organ of sui generis and getting its supply from convenient source, the disc in Lamiaceae seems to have lost its individuality because of the great condensation of floral receptacle as well as its vasculature. Only in *Scutellaria violacea*, where the gynoecium is elevated by the presence of gynophore, the disc becomes adnated to this part of receptacle and separates from the ovarian part representing the most primitive condition among Lamiaceae. In the rest of the members, it appears as an annular or ringlike structure around the basal part of the ovary. In all the members where the disc exists, the basal part is completely annular, while the upper region may be entire or lobed to a variable degree. When annular, the disc is usually fused with the base of the ovary as noticed in *Westringia rigida*, *Teucrium royleanum* and *Micromeria biflora*.

From the present study, two lines of evolution in the disc can be visualised from entire annular one—lobed disc and reduced disc. The former can be obtained by increased proliferation of base of the ovary accompanied by cutting apart of the nutlets. Reduced disc can be derived by the reduction of the disc or lobes of the disc in the posterior sector along with the reduction of other floral organs (stamens) leading to its greater zygomorphy.

A four lobed disc, as seen in *Ocimum canum*, *O. basilicum* and *Hyptis suaveolens* represents the first line. Hand in hand with gynobasy of style, the disc also underwent lobing so that the 4 lobes alternate with the 4 nutlets. Along the second line, zygomorphy results from suppression of one (*Ocimum killimandscharicum*) or more lobes (*Ajuga bracteosa*, *Plectranthus incanus*, *Coleus* etc.) of the disc. In *Anisomeles indica* the disc is completely suppressed though its vasculature persists.

On anatomical grounds the condition seen in *Scutellaria violacea* and *Westringia rigida* should be treated as relatively primitive since the disc receives vasculature directly from the floral stele after the demarcation of carpellary dorsals. In all other members studied now, the strands for the nectary are derived at higher levels from the ovarian bundles and progressive evolution is seen in the number of sources from which the disc supply is derived. The disc receives vascular strands from 3 sources, i.e., ventrals, dorsals and wall bundles in *Nepeta hindostana*, *Calamintha umbrosa*, species of *Dysophylla* and *Teucrium royleanum*; from two sources i.e., from dorsals and ventrals in *Hyptis suaveolens*, *Dysophylla* sps. and *Anisomeles malabarica* from one source only from dorsals in *Ajuga bracteosa* and *Plectranthus incanus* or only from ventrals as in *Anisomeles indica* and *Coleus scutellarioides*. In *Micromeria biflora*, *Lavandula vera* and *Meriandra bengalensis* the disc is devoid of vasculature. Thus evolution has progressed from ancestral condition with symmetrical vascularization, towards total elimination of the internal vasculature through varied degrees of reduction in one or more sectors of the disc condition leading to zygomorphy.

The great variety seen in the vascular supply of the disc in a natural family like Lamiaceae and even in closely related species showing sometimes a wide range of variation in morphoanatomical features makes one to hesitate in deciding the phylogenetic position of subfamilies. There may or may not be a synchronization in the reduction on exomorphic and anatomical grounds. In Lamiaceae, however, the evolution in external form as well as the vasculature of the disc seems to have progressed in many directions and, that too, independent of each other.

From a comparative study of the morphoanatomical features of the disc, it appears that the conditions found in members of scutellarioideae and prostantheroideae seems to be the most primitive since the disc is externally symmetrical and receives vasculature uniformly on all the sides from the floral stele itself. In other taxa the disc shows diverse degrees of evolution and in no taxon these trends have attained such a culmination synchronously. On the whole, it can be said that the members of Ocimoideae are highly advanced since most of the members of this subfamily attained culmination of evolution in one feature or the other.

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References

Brown W H 1938 The bearing of nectaries on the phylogeny of flowering plants; *Proc. Am. Phil. Soc.* **79** 549–596

Fahn A 1952 On the structure of floral nectaries; *Bot. Gaz.* **113** 464–470

Fahn A 1953 The topography of the nectary in the flower and its phylogenetical trend; *Phytomorphology* **3** 424–426

Hillson C J 1959 Comparative studies of floral morphology of the Labiatae; *Am. J. Bot.* **46** 451–459

Hitchcock C L 1932 A monographic study of the genus *Lycium* of the Western hemispheres; *Ann. Mo. Bot. Gdn.* **19** 179–374

Kartashova N N 1960 Some data on the morphology of the flower of the Labiatae (in Russian); *Bot. Zhur. (Moskva)* **45** 109–114

Lawrence J R 1937 A correlation of the taxonomy and the floral anatomy of certain members of the Boraginaceae; *Am. J. Bot.* **24** 433–444

Moore J A 1936 Morphology of the gynobase in Martensia; *Mid. Nat.* **17** 749–752

Rao V S 1953 The floral anatomy of some bicarpellatae. I. Acanthaceae; *J. Univ. Bombay* **21** 1–34

Rao V S 1954 The floral anatomy of some bicarpellatae. II. Bignoniaceae; *J. Univ. Bombay* **22** 55–70

Rao V S 1955 The floral anatomy of some bicarpellatae. III. Pedaliceae; *J. Univ. Bombay* **23** 18–26

Rao V S 1971 The disc and its vasculature in the flowers of some dicotyledons; *Bot. Notiser.* **124** 442–450

Rao V S and Ganguly A 1963 Studies in the floral anatomy of Apocynaceae; *J. Indian Bot. Soc.* **42** 419–435

Woodson R E 1930 Studies in the Apocynaceae. I.; *Ann. Mo. Bot. Gdn.* **17** 1–212

Woodson R E and Moore J A 1938 The vascular anatomy and comparative morphology of the Apocynaceous flowers; *Bull. Torrey Bot. Club* **65** 135–165