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Cytology and Pollination Biology of Lamiaceae: A Review

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Review Article

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ABSTRACT

Extensive cytological studies had revealed the presence of diploid, tetraploid, hexaploid and octaploid species in the Family Lamiaceae. Chromosome numbers vary from 2n=2x=14 in *Salvia nemorosa* to 2n=6x=102 in *Stachys palustris* L. Diversification in the Family may be attributed to the presence of polyploidy and aneuploidy. It is an eurypalynous family with pollen grains usually radially symmetrical, isopolar, prolate-spheroidal to oblate-spheroidal or sub-oblate to sub-prolate. Xenogamy is deeply rooted, and protandry or gynodioecy, especially frequent in this family, maximizes cross-fertilization. Fruits consist of four one-seeded nutlets (mericarps) formed within a persistent calyx, with seeds dehiscing during the warmer months. Individual seeds are characterized by a prominent attachment scar that is known as a mericarp plug.

INTRODUCTION

Lamiaceae constitute a large family, ca. 220 genera and 4000 species, of cosmopolitan distribution that is particularly well represented in temperate, warm regions [1-6]. Their peculiar floral structure calls for intricate pollination mechanisms that reflect a long history of adaptive coevolution between plants and pollinators [7]. Xenogamy is deeply rooted in the Lamiaceae. Protandry or gynodioecy, especially frequent in this family, maximizes cross-fertilization. However, the evolutionary shift from xenogamy (outcrossing) to autogamy (selfing) has been mediated through decreased flower size and alterations in floral morphology which reduce the energetic cost per flower and facilitate self-pollination, respectively. Recently, a number of workers have shown that the flowers of self-incompatible and other xenogamous taxa produce more pollen grains than closely related self-compatible and/or autogamous taxa [8-10]. Flower symmetry has recently been discussed extensively, but the immediate interaction between animals and flowers and their consequences have hardly been considered. The present paper summarizes selected literature referring to floral biology, cytology, pollination biology and breeding behaviour in Lamiaceae [11-15].

LITERATURE REVIEW

Bilabiate Blossoms

Bilabiate blossoms (including lip, gullet and throat flowers) are one-way constructions that in most cases offer nectar at their base. Ventrally, they are confined by a ‘floor’, usually called the lower lip. Dorsally, they are covered by a ‘roof’, usually called the upper lip, with the reproductive surface (i.e., pollen and stigma) underneath. Floor and roof are at such a fixed distance that legitimate visitors inevitably contact the reproductive structures with their dorsal side. Bilabiate flowers thus are nototribic by definition. In most cases, the visitor path is divided into two sections of different diameters, a wider distal element, that is called the ‘pollination chamber’, and a narrow proximal part, the ‘alignment channel’. The length relationship between these two parts may vary over a wide range. Usually, the alignment channel is accessible to the mouthparts only (proboscis, beak, rostrum, snout, tongue) while the pollination chamber admits the entry of the head and even further parts of the visitor. Often the transition zone from the wide to the narrow part is of utmost importance for floral kinetics [16]. It is here that the forward movement of the visitor comes to an end, and thus it defines the fixed relationship between the pollination surfaces of the flower and the visitor. Often at this juncture a mechanical barrier is developed that may represent a nectar cover and/or part of a lever mechanism (Salvia pratensis, Lamiaceae). Usually it is the narrow alignment channel that - as a result of the depth of the nectar and the lateral constraints - defines the exact positioning of the visitor, because of the stiff fixed spatial relationship between the mouthparts in their functional position and the remainder of the visitor's body. The alignment channel has previously been termed a 'tube' when discussing flowers of Lamiaceae [17,18].

In majority of cases, the floor of the pollination chamber serves as a perch for bees. As room inside the blossom is restricted, these animals cannot reach their dorsal side with their legs (to gain pollen from there), nor can they move sideways. Exit from the flower is only possible by a rearward movement. Entrance to a blossom may be impeded in different ways, thus augmenting the efficiency of hiding the pollen. To give access to the interior of the flower, the blossom has to be opened forcefully. Thus, the interest and the actions of the visitor are deviated from the pollen. One option is to lower the end of the roof until it approaches the floor and thus nearly closes the entrance. This means that the roof has to be raised by the visitor, which requires not only an adequate settling of the feet but also a considerable physical force. In *Phlomis fruticosa* (Lamiaceae), for example, a bee contacts the lower lip while landing and first enters its proboscis into the open space between the two lips. Entry of the proboscis is not impeded and force only has to be applied when the head reaches the point of direct contact between the roof and perch; so the lifting of the upper lip only takes place when the head has already passed the region where the anthers are hidden. Thus, the bee is dusted with pollen only behind its eyes - out of its sight, insidiously from behind. In many species, the roof is in a position high above the floor and locked below enclosing the anthers. Thus, perching of a visitor is enabled, but the anthers are hidden (*Salvia*). A novel mechanism had to be evolved to cause secondary release of the pollen either by lowering the pollen presenter or by removing the cover. An example of the first device is encountered in the well-studied case of Salvia and other taxa with lever mechanisms; the second is demonstrated in *Salvia verticillata* [19].

Cytology

Comparison of chromosome characters in three species of *Thymus* (Lamiaceae) viz., *Thymus mongolicus, T. przewalskii* and *T. roseus* had revealed 2n=26 and 27 for *T. mongolicus* and 2n=26 for *T. przewalskii* and *T. roseus.* The chromosome number of 2n=26 for *T. przewalskii* and 2n=27 for *T. mongolicus* had been reported for the first time and 2n=26 for *T. roseus* and *T. mongolicus* confirmed the previous reports. Presence of one B-chromosome in the chromosome number of 2n=27 for *T. mongolicus* seemed to be responsible for its peculiar heteropycnotic body at resting stage and at high pollen stainability. Cytological observations in genus *Thymus* with 2n=24 in *T. serpyllum* have been reported for the first time [20,21]. Cytological studies of eight gamopetalous species of Lamiaceae in Western Himalaya have been conducted and compared with the previous reports **(Table 1)** [22]. Work on cytogenetic diversity of *Elsholtzia ciliata* Benth. (Lamiaceae) from Kashmir Himalaya had revealed the presence of two euploid cytomorphotypes, one diploid with n=8 and the other tetraploid with n=16, growing sympatrically but inhabiting two different habitats [23]. Chromosome number of n=8 for this species was already known while as n=16 was first time reported from India [24].

About 20 taxa of the genus *Lamium* have been studied for the chromosome numbers and in each case the base number has been reported as n=9 [25-32]. Chromosome number of 2n=18 has been reported in an endemic *Lamium moschatum* var. *rhodium* and for the first time in *L. pisidicum* [32]. The occurrence of different basic chromosome numbers in a single species have been reported in the genus *Salvia,* with *S. aegyptiaca* L. having 2n=12, 26 and 28, *S. chanroenica* ssp. *glomerifolia* Chung with 2n=14 and 16, and in *S. nemorosa* L. 2n=14 and 16 [33-38]. Thus, diversification in *Salvia* species may be attributed to the presence of polyploidy and aneuploidy in the species. Ten *Salvia* species which includes *S. spinosa*, *S. reuterana*, *S. sclarea*, *S. ceratophylla*, *S. xanthocheiala*, *S. limbata*, *S. hypoleuca*, *S. staminea*, *S. nemorosa* and *S. verticillata* had the chromosome numbers of 2n=14, 16, 20 and 22 **(Table 2)** [39]. Five species of *Salvia* (Lamiaceae) viz., *S. flava, S. digitaloides* var. *digitaloides, S. trijuga, S. castanea*

Table 1. Chromosome number, ploidy level and previous reports of investigated species.

S. No.	Name of Taxa	Chromosome Number (2n)	Ploidy level	World	Previous Chromosome Number Reports (2n) India
1.	*Calamintha clinopodium* Benth.	20	2x	20, 40	20; Mehra and Gill, 1968b; Gill, 1971a, 1984; Saggoo and Bir, 1983; 40; Vij and Kashyap, 1976.
2.	*Mentha longifolia* L.	24	2x	24, 48	18, 27; Sobti, 1962b 24; Sobti *et. al.*, 1971a, b; Gohil *et al.*, 1981; 24, 36, 48; Sobti, 1965
3.	*Nepeta govaniana* Benth.	18	2x	18	18; Gill, 1969; Gohil *et al.*, 1981.
4.	*Nepeta spicata* Benth.	18	2x		18; Gill, 1969,1984
5.	*Plectranthus rugosus* Wall ex Benth.	24	2x		24; Vij and Kashayap, 1975; 1976a; Bir and Saggoo, 1981, 1984; Saggoo, 1983; Gill, 1983
6.	*Prunella vulgaris* Linn.	28	4x	28, 28-30	28; Saggoo, 1983; Gill 1984; Bir and Saggoo, 1985; Saggoo and Bir, 1986; Bala and Gupta, 2010, 2011
7.	*Stachys sericea* Wall ex Benth.	30	2x		30; Kumar and Chauhan, 1970; Gill, 1970, 1984; Saggoo and Bir, 1983; Bir and Saggoo, 1984
8.	*Thymus serpyllum* L.	26	2x	50	24: Gill, 1984 26; Bir and Saggoo, 1980

and *S. yunnanensis* are diploid with 2n=2x=16 while as *S. przewalskii* var. *przewalskii* is a tetraploid with 2n=4x=32 **(Table 3)** [40]. Extensive cytological study of the British Labiatae (excluding *Mentha*) had revealed the presence of diploid, tetraploid, hexaploid and octaploid species **(Table 4)** [41]. *Ajuga* species growing in Japan had 2n=32 in *A. incisa, A. japonica, A. makinoi, A. yesoensis, A. tsukubana, A. decumbens, A. ciliata* var. *villosior, A. nipponensis and A. pygmaea* and 2n=64 in *A. shikotanansis* f. *hirsute* **(Table 5)**. Intraspecific polyploidy and aneuploidy have been reported in *Ajuga bracteosa* Wall. ex Benth., *A. chamaecistus* Ging., *A. genevensis* L., *A. lobata* D Don., *A. macrosperma* Wall., *A. orientalis* L., *A. reptans* and *A. spectabilis* Nakai [42-45].

Pollen Biology

Lamiaceae is an eurypalynous family [46]. Pollen grains in this family are usually radially symmetrical, isopolar, prolate-spheroidal to oblate-spheroidal or sub-oblate to sub-prolate. There are two main pollen types in Labiatae: tri- and hexacolpate, which are usually bi- and trinuleate respectively [47]. Pollen grains with four, eight, nine and ten colpi in the exine were also reported by Erdtman and Wunderlich, the tetra- and octacolpate types being regarded as modifications in polyploid forms of species with tri- and hexacolpate pollen respectively [48]. Mostly 3-8 colpate, rarely colporate, trilobed, fossaperturate, colpal membrane psilate to sub-psilate, or granulated, often perforated with sexine thicker or thinner than nexine. Tectum generally finely to coarsely reticulate, with perforated luminae, perforations variable in numbers rarely regulate-reticulate or striate-rugulate, or often sub-psilate. On the basis of aperture, tectum type and shape of pollen grains seven pollen types are recognized in the family Lamiaceae **(Tables 6,7 and 8)** [49]. Pollen grains of entomophilous taxa are characterized by compound apertures, prolate-spheroidal shape, generally large, thick walled, sticky and with reticulate tectum. Pollen characters are useful in solving complicated problems of inter-relationships between various taxa and assessment of their status in the classification, particularly with reference to the families, sub-families, tribes, genera, species and sub-species.

Pollen grains of hermaphroditic plant *Lycopus maackianus* (Lamiaceae) are small to medium (polar axis = 23.8–31.3μm, equatorial diameter = 22.5–28.8μm) in size, 6-colpate with granular membranes in aperture, mostly spheroidal and circular in polar view [50]. The exines are bi-reticulate (semi-tectate) where the muri of the primary reticulum are supported by small groups of, often thick, columellae attached directly to the foot layer [51]. Study of heterostyly in the Lamiaceae revealed the presence of two distinct floral morphs differing in style length in *Salvia brandegeei.* Pollen grains from the long- and short-styled morphs did not differ markedly in size, mean volume of pollen grains or in exine sculpturing between pollen grains of the two floral morphs. Co-occurrence of low temperature and high humidity enhances the pollen viability of *Rosmarinus officinalis* L. (Lamiaceae) [52-54]. Moreover, these conditions are able to newly raise the viability of pollen kept at higher temperatures and lower humidity. Apart from high humidity, reactivation of the pollen membrane depends on low temperature. Therefore, “vernalization” of rosemary pollen enhanced its viability, supporting that pollen behavior was adapted to winter condition and allowed flowering in winter and early spring. Pollen grains of eight *Ajuga* taxa are more or less suboblata-subprolata and tricolpatae with granulate exine sculpture in *A. chamaepitys* subsp. *chia* var. *chia*, *A. chamaepitys* ssp. *cuneatifolia*, *A. genevensis*, *A. laxmannii*, *A. orientalis* and *A. reptans*, and reticulate in *A. bombycina* and *A. chamaepitys* ssp. *chia* var. *ciliate* **(Tables 7 and 8).** Aperture features and exine structures are among the essential criteria for the determination of the phylogenetic relationships of the species of *Ajuga* [55-58].

Pollination Biology

Study of pollination biology of *Anisomeles indica* and *A. malabarica* (Lamiaceae) had revealed that the flowers of *A. indica*

Table 2. Meiotic characteristics in ten *Salvia* species.

S. No.	Species	Chromosome number (2n)	Previous counts
1	*S. nemorosa*	14	14: Mizianti *et al*., 1981 and Ghaffari and Chariat-Panahi, 1985
2	*S. hypoleuca*	22	22: Afzal-Rafii, 1980, 1981; Özdemir and Senel, 1999
3	*S. ceratophylla*	22	22: Afzal-Rafii, 1980, 1981; Özdemir and Senel, 1999
4	*S. limbata*	22	22: Afzal-Rafii, 1980, 1981; Özdemir and Senel, 1999
5	*S. verticellata*	16	16: Afzal-Rafii, 1980 and Lövkvist and Hultgård, 1999
6	*S. sclarea*	22	22: Afzal-Rafii, 1980, 1981; Özdemir and Senel, 1999
7	*S. staminea*	22	
8	*S. reuterana*	20	20: Afzal-Rafii, 1981; Ghaffari and Chariat-Panahi, 1985
9	*S. spinosa*	20	
10	*S. xanthochilla*	22	22: Afzal-Rafii, 1980, 1981; Özdemir and Senel, 1999

Table 3. Chromosome numbers of six Salvia species from China.

S.No.	Species	Ploidy level	Chromosome count (2n)
1.	*S. flava*	2x	16
2.	*S. digitaloides* var. *digitaloides*	2x	16
3.	*S. trijuga*	2x	16
4.	*S. castanea*	2x	16
5.	*S. yunnanensis*	2x	16
6.	*S. przewalskii* var. *przewalskii*	4x	32

Table 4. Chromosome Numbers in British Labiatae.

S. No.	Species	Ploidy level	Chromosome count (2n)
1	*Acinos arvensis* Lam.	2x	18
2	*Ajuga ehamaepitys* (L.) Schreb.	4x	28
3	*A. pyramidalis* L.	4x	32
4	*A. reptans* L.	4x	32
5	*Ballota nigra L. subsp. Joetida*	2x	22
6	*Betoniea officinalis* L.	2x	16
7	*Calamintha ascendens* Jord.	4x	48
8	*Calamintha nepeta* L.	4x	48
9	*C. sylvatica* Bromf.	2x	24
10	*Clinopodium vulgare* L.	2x	20
11	*Galeobdolon luteum* Huds.	4x	36
12	*Galeopsis speciosa* Mill.	2x	16
13	*G. tetrahit* L.	4x	32
14	*Glechoma hederacea* L.	4x	36
15	*Lamium album* L.	2x	18
16	*L. amplexicaule* L.	2x	18
17	*L. hybridum* Vill.	4x	36
18	*L. moluccellifolium* Fr.	4x	36
19	*L. purpureum* L.	2x	18
20	*Leonurus cardiaca* L.	2x	18
21	*Lycopus europaeus* L.	2x	22
22	*Marrubium vulgare* L.	2x	34
23	*Melittis melissophyllum* L.	2x	30
24	*Nepeta cataria* L.	2x	34
25	*Origanum vulgare* L.	2x	30
26	*Prunella laciniata*L.	4x	28
27	*P. vulgaris* L.	4x	28
28	*Salvia horminoides* Pourr.	6x	54
29	*Scutellaria galericlllata* L.	4x	32
30	*S. minor* Huds.	4x	32
31	*Stachys alpina* L.	2x	30
32	*S. arvensis* L.	2x	10
33	*S. palustris* L.	6x	102
34	*S. sylvatica* L.	8x	64
35	*Teucrium scordium* L.	4x	32
36	*T. scorodonia* L.	2x	34
37	*Thymus drucei* Ronn.	8x	50-56
38	*T. puiegioides* L.	4x	28
39	*T. serpyllum* L.	4x	24

Table 5. Chromosome numbers in ten species of Japanese Ajuga.

S. No.	Species	Chromosome number (2n)
1	*A. incisa* Maxim.	32
2	*A. japonica* Miq.	32
3	*A. makinoi* Nakai	32
4	*A. yesoensis* Maxim.	32
5	*A. tsukubana* (Nakai) Oku.	32
6	*A. decumbens* Thunb.	32
7	*A. ciliata* var. *villosior* A. Gray ex Nakai	32
8	*A. shikotanansis* f. *hirsuta* (Honda) Murata	64
9	*A. nipponensis* Makino	32
10	*A. pygmaea* A. Gray	32

and *A. malabarica* are zygomorphic, bilabiate, gullet shaped and nectariferous, and are visited by insects as well as birds for nectar and or pollen. The bees *Xylocopa latipes, X. pubescens, Amegilla* sp., *Apis florea* and *Megachile* sp., and the sunbirds of the genus *Nectarinia* are the principal pollinators of *A. indica,* while the former three and the last and the wasp *Rhynchium metallicum* are for *A. malabarica*. Pollination by *Xylocopa* and *Nectarinia* is nototribic and that by *Apis, Megachile, Amegilla* is noto- and or sternotribic. The small bodied *Trigona, Pseudapis* and *Ceratina* collected pollen sternotribically [59]. Thus, adaptation

Table 6. Pollen types in Labiatae.

Pollen type		Pollen class	P/E ratio	Ecto-aperture	Endo-aperture	Exine	Ornamentation
Type I	*Elsholtzia densa* - type	6-colpate, 6-zonacolpate	0.91	Colpus not sunken, long	Absent	Sexine thicker than nexine	Tectum psilate
Type II	*Marrubium marrubiastrum*- type	3-colpate, trizonacolpate	0.93-1.20	Colpus long, sunken	Absent	Sexine thinner/ thicker/ as thick as nexine	Rugulate-reticulate or fossulate-foveolate
Type III	*Nepata laevigata*- type	6-colpate, 6-zonacolpate	1.01-1.29	Colpus not sunken, long	Absent	Sexine thinner/ thicker/ as thick as nexine	Medium coarsely reticulate
Type IV	*Salvia aegyptiaca*- type	6-colpate, 6-zonacolpate	0.85-1.01	Colpus not sunken, long	Absent	Sexine thinner or thicker than nexine	Finely tocoarsely reticulate
Type V	*Scutellaria prostrate*- type	3-zonacolpate	0.9-1.22	Colpus long, sunken	Absent	Sexine thinner or thicker than nexine	Medium coarsely reticulate
Type VI	*Stachys parviflora*- type	3-zonacolpate	0.01-1.35	Colpus not sunken, long, narrow	Oval-circular, oval- longate	Sexine thicker than nexine or slightly thinner than nexine	Finely, medium reticulate
Type VII	*Teucrium scordum*- type	3-zonacolpate	1.26	Colpus long, sunken, narrow	Absent	Sexine thicker than nexine	Verrucate with fine scabrae

Table 7. Palynomorph of eight Ajuga taxa.

Botanical name	Pollen shape	P/E (A°)	Orname-ntation	Exine thickness (µm)	Tectum
A. bombycina	suboblata-subprolata and tricolpatae	1.27	tectatae-reticulatae	1.04	Reticule
A. chamaepitys ssp. *chia* var. *chia*	suboblata-subprolata and tricolpatae	1.32	tectatae-granulatae	1.42	Granule
A. chamaepitys ssp. *chia* var. *Ciliate*	suboblata-subprolata and tricolpatae	1.62	tectatae-reticulatae	1.02	Reticule
A. chamaepitys ssp. *cuneatifolia*	suboblata-subprolata and tricolpate	1.24	tectatae-granulatae	1.1	Granule
A. genevensis	suboblata-subprolata and tricolpatae	1.1	tectatae-granulatae	1.0	Granule
A. laxmannii	suboblata-subprolata and tricolpatae	1.11	tectatae-granulatae	1.24	Granule
A. orientalis	suboblata-subprolata and tricolpatae	0.87	tectatae-granulatae	1.64	Granule
A. reptans	suboblata-subprolata and tricolpatae	0.89	tectatae-granulatae	1.46	Granule

Table 8. General pollen characters of species found in the pollen type *Marrubium marrubiastrum*.

Name of taxa	Shape	P/E ratio	Polar length (µm)	Equatorial length (µm)	Tectum type
Ajuga bracteosa Wall. ex Benth.	Prolate	1.35	34.05 ± 0.44	25.04 ± 0.58	Finely reticulate
A. parviflora Benth.	Oblate-Spheroidal	0.914	26.6 ± 0.75	29.36 ± 1.23	Reticulate-Rugulate
Stachys flocossa Benth.	Prolate-Spheroidal	1.05	24.8 ± 0.22	23.61 ± 2.36	Medium reticulate
S. parviflora Benth.	Oblate-Spheroidal	0.94	27.5 ± 0.41	29.30 ± 0.37	Medium reticulate
S. tibetica Vatke	Prolate-Spheroidal	1.01	25.59 ± 0.19	25.39 ± 0.13	Rugulate

of both species to insect and bird pollination and to a flexible breeding system involving both selfing and crossing, safeguards their survival under changing environments. Sprengel had described the dorsal (nototribic) pollination mechanism in *Salvia*, but the morphology of the staminal lever was first recognized by Hildebrand. Claßen-Bockhoff *et al*, defined the staminal lever mechanism in *Salvia* as a functional syndrome including the modification of stamens to lever-like structures, their reversible movement, and their 'coordination' with the remaining floral structures involved in the process of pollen transfer. Despite the large number of species and great structural diversity of the flowers in *Salvia*, only melittophilous and ornithophilous flowers appear to have evolved [60]. While bee-pollinated species occur world-wide and are associated with a wide array of pollinators from small to large solitary bees, honey-bees, bumble-bees, and carpenter bees, bird-pollinated plants predominantly evolved in response to neotropical humming birds [61,62]. The only known exception in the Old World is *S. africana-lutea* L., a species from South Africa visited by sunbirds and white-eyes [63]. In *Salvia officinalis* L. pollen of the lower lever arm do not contact the stigma and thus has been reduced in most of the *Salvia* species [64]. Not only the site of pollen deposition on the pollinator's body varies between the individual flower-pollinator interactions, but so does the functionality of the lever mechanism itself. *Salvia austriaca* Jacq. is an example of plagiotribic pollination, with the widely exposed thecae striking the nectar-seeking insect from the sides. Ventral (sternotribic) pollination can be realized by resupinate flowers, or by hanging inflorescences; in either case, the insects land on the upper lip and are loaded with pollen on their ventral side. In *S. clevelandii* the thecae are exposed out of the flower and present pollen for ventral (sternotribic) pollination [64,65]. As the pollinator passes over the pollen sacs while searching for nectar, pollen is not as precisely transferred as in the species with active levers. In *S. verticillata* the bee has to push back the movable upper lip to gain access to nectar. The adaptation to pollination by insects is so strict that other ways of pollination such as wind pollination is occasional and does not contribute to seed formation. Pollination is geitonogamous while as autogamy is prevented by the length of the style much exceeding the stamens. *S. pratensis* is a gynodioecious, protandrous and perennial that is pollinated primarily by bumble bees. Flowers are arranged in whorls on flower stalks [66]. Forces ranging from 1.5mN in *S. glutinosa* to 32mN in *S. sclarea* are necessary to trigger the staminal levers and gain access to the nectar [67]. More detailed investigations in *S. pratensis*, including 55 flowers and more than 1000 individual measurements, had revealed an average value of the maximum force of 2.98±2.43mN [68]. *Ajuga* spp. are mostly visited by *Bombylius* (bee-flies) and sawflies [69]. Flowers are protandrous or homogamous in *Ajuga pyramidalis* L. which are pollinated by bees, with possible self-pollination [70]. *Rhingia campestris*, despite being the most abundant visitor for *Phyteuma spicatum* and *Ajuga reptans,* is a poor pollinator compared to bumblebees [71]. Flowers of *Salvia verbenaca* are pollinated largely by the honey bee *Apis mellifera* L. and Bombyliidae such as *Bombylius major* L. Each flower produces 0.6-1.5μl of nectar per day [72]. About 27 different insect species have been reported visiting the flowers of *Cedronella canariensis,* with the most frequent visitors being the endemic Canarian bumblebee species *Bombus terrestris* subsp. *canariensis,* the sphingid *Macroglossum stellatarum,* and various *Halictinae* spp. (*Halictidae*). These visitors are present during the entire flowering season and had accounted for 94.8% of all observed visits [73]. At the onset of flowering, *Anthophora alluaudi* has been reported as an important visitor, accounting for up to 26% of all visits per day. Three species of butterflies - *Vanessa indica, Gonepteryx cleobule* and *Pandoriana pandora* have been reported to be the irregular visitors throughout the season. *Attalus* sp. and *Thysanoptera* spp. had been present in the interior of many flowers and buds. They have been reported very frequent during the second half of the flowering season. Few nocturnal visitors include Geometrid and Noctuid moths.

Breeding Behavior

Protandry is common in the Lamiaceae, but its effectiveness as a barrier to self-fertilization differs between species as is seen that protandry effectively prevents self-fertilization in *Lavandula stoechas* L, but not in species of the genus *Nepeta,* in which pollen release and stigma receptivity are effectively separated in time but in which self-fertilization is not precluded because of within-inflorescence geitonogamy [74,75]. *S. pratensis* is dependent on an insect vector for pollination. Haque and Ghoshal in a study of reproductive systems in the genus *Salvia,* reported that the species with large, red/scarlet, nectar-producing, mainly heterostylous flowers reproduced by xenogamy, and species with small, bluish, homostylous flowers reproduced by autogamy [76]. They also reported autogamous reproduction in *Salvia verbenaca* L. Mating systems in *P. vulgaris* may be in the process of evolutionary change [77]. Hong and Moon while studying the gynodioecy in *Lycopus maackianus* Makino (Lamiaceae) revealed that the hermaphroditic individuals of *L. maackianus* are protandrous (i.e., pollen grains are shed before stigmas are receptive). After completion of anther dehiscence, the filaments bend backwards displacing the anthers laterally. At this time, the stigma elongates, the stigmatic lobes open, and eventually the stigma becomes receptive. Protandry is particularly common in Lamiaceae. Hong and Moon also reported that the stigma in *L. maackianus* is bifid, and stigmatic lobes are unequal in length, i.e., one is longer than the other. They reported the receptive stigmatic surfaces to be dry and non-papillate in both morphs. Heslop-Harrison and Shivanna categorized the stigmata of almost 1000 species of angiosperms into wet and dry types with further subdivisions on the basis of stigma morphology and specific anatomy of the receptive cells [78]. They reported the stigma to be dry and non-papillate in several taxa of Lamiaceae (e.g., *Mentha* L., *Rosmarinus* L., *Salvia* L., *Satureja* L., etc.), which is similar to the stigma of *L. maackianus*. Kulloli *et al*. investigated the nectar dynamics and pollination studies in three species of Lamiaceae, viz. *Leonotis nepetifolia* (L.) R. Br., *Leucas aspera* (Willd.) Link and *Orthosiphon thymiflorus* (Roth) Sleesen [79]. They recorded a wide array of floral foragers comprising of honey bees, butterflies, flies, ants, birds and hawk moths of these three species. They reported that honey bees (~ 66% of the total visits made by the insects) have been the major pollinators; birds and the butterflies were implicated as opportunists, rather than effective pollinators. In *L. aspera* and *O. thymiflorus*, one Dipteral member, i.e., *Pangania* sp. was reported as an occasional visitor during the daytime. Procter and Yeo have reported that ants are legitimate pollinators of Rupture wort (*Herniaria ciliolata*) [80]. Rajju and Reddi while studying the Pollination Ecology of *Hyptis sauveolens* Poit. (Lamiaceae) reported the presence of a curious mechanism of pollination operating in the species. The flowers open per day during 0700-1700 hr with a peak at 0900-1100hr. Anthers dehisced ca. 30 minutes ahead of anthesis. In the flower bud, the stigma and stamens are housed in the carina formed in the center of lower corolla lip. A slight disturbance created either by wind (above 0.8m/sec) or insect activity causes the carina to explosively unfold during which the pollen are forcibly ejected out and deposited on the inner surface of upper corolla lip/stigma. The insect visitors included bees and butterflies, but the former group consisting of *Amegilla* sp., *Apis cerana-indica, Pseudapis oxybeloides, Thyrsus histio* and *Ceratina* sp. and the hawkmoth, *Macroglossum gyrans* were most instrumental in affecting pollination. The breeding experiments showed that autogamy, geitonogamy and xenogamy are the reproductive methods, but the autogamy is more successful. Hart while investigating the Evolution of Dioecism in *Lepechinia* Willd [81]. sect. Parviflorae (Lamiaceae) reported that the species are gynodioecious and dioecious; these species had white flowers, less than 8.0mm long, and pollinated by short-tongued bees and flies. Species of *Lepechinia* sects. Salviifoliae and

Speciosae that are phylogenetically most closely related are gynodioecious and hermaphroditic; the flowers of these species are blue or violet, 11.5-40cm long, and are pollinated by long-tongued insects and birds. Hermaphroditic and gynodioecious species had larger corollas than do dioecious species. In the dioecious species of Lepechinia sect. Parviflorae the pistillate flowers have comparatively larger calyces, but smaller corollas than do the staminate flowers. Dioecism seems to be correlated with xeric habitats and weediness. *Salvia brandegeei* is a fully self- Neisess, and intramorph compatible species. This species does not possess a diallelic self-incompatibility system typical of most heterostylous plants. Pollinators visiting the species include mostly feral honey bees *(Apis mellifera),* but also bumblebees *(Bombus* sp.) and leaf-cutter bees (Megachilidae). *Cedronella canariensis* (Lamiaceae) species is not agamospermous, as was shown by the very low level of fruit set by enclosed, emasculated flowers. The species had been reported fully self-compatible and the reproduction has not been limited by pollination. *R. officinalis* plants are self-compatible but automatic self-pollination is prevented by strong protandry. Flowers of *R. officinalis* set abundant seed when cross-pollinated by hand. Insect mediated geitonogamy has been possible in the species and appears to be responsible for the lower seed set in open-pollination. Seed set by male-sterile plants indicated that gynodioecy could be considered as a strategy to increase reproductive output in *R. officinalis* [82]. *Thymus loscosii* is self-compatible as it is able to produce seeds by spontaneous selfing, but at very low rates, indicating that it is insect-dependent for pollination. Apomictic seed development is also present in the species. Seeds from females are slightly heavier and germinate earlier and at higher rates than those from hermaphrodites, even those formed by apomixis. Thus, female plants enjoy a resource allocation advantage that allows increased seed quality and contributes to the maintenance of gynodioecy [83]. In genus *Syncolostemon, Syncolostemon macranthus, S. rotundifolius* and *S. densiflorus* produce almost no seed set in the absence of pollinators, although all three species are effectively self-incompatible, as self-pollination resulted in minimal seed production compared to cross pollination [84]. Grant and Grant reported that in *Salvia apiana* Jepson (Lamiaceae) inflorescences arise from the upper nodes in spring and produce flowers from late May to July [85]. Based on the floral morphology, only some of the larger bees are capable of transferring pollen to the highly exerted stigmas. They reported that three species of *Xylocopa* and a species of *Bombus* as effective pollinators. Hummingbirds, honeybees, bombyliid flies, and small species of native bees (primarily *Anthophora*, *Diadasia* and *Osmia*) sometimes visited the flowers but are thought to be ineffective as pollinators. The protandrous flowers and presence of interspecific hybrids were consistent with an outcrossing breeding system. Inflorescences were large and many-flowered, making some self-pollination likely.

Seed Biology

Fruits in Family Lamiaceae consist of four one-seeded nutlets (mericarps) formed within a persistent calyx, with seeds dehiscing during the warmer months. Individual seeds are characterized by a prominent attachment scar that is known as a mericarp plug [86]. However, there is limited understanding about the potential role the meriplug plug structure may play in the germination process. Seeds of *Prostanthera eurybioides* F. Muell. have been found to exhibit physiological dormancy. Contrary to previous reports for other *Prostanthera* species, there has no evidence of seed coat related physical dormancy and it was concluded that the mericarp plug was acting as a mechanical barrier to ensure *in situ* germination occurs when environmental conditions are conducive to maximizing seedling survival [87]. Dormancy in *P. eurybioides* was alleviated using a range of treatments including exposing seeds to gibberellic acid, micro-excision of the mericarp plugs and subjecting seeds to a pulse dry heat treatment. In contrast, the dormancy mechanism and seed ecology for many other species within the genus remains relatively unknown. Knowledge about the germination requirements for other genera of Australian Labiatae appears similarly limited, with only one report for *Hemigenia exilis* located during an extensive literature search. Cochrane *et al*. reported that it was necessary to remove the 'seed plug' followed by a chemical treatment with gibberellic acid before seed dormancy was overcome and germination could occur [88].

DISCUSSION

Ainsley and Jones investigated overcoming the physiological seed dormancy in semi-arid *Prostanthera* (Labiatae) using three species of *Prostanthera* viz., *P. eurybioides, P. behriana* Schltdl. and *P. calycina* F. Muell. ex Benth. They used pulse dry heat treatment (80˚C for 10min); excision of the mericarp plugs, and pulse dry heat followed by mericarp plug removal for enhancing the seed germination. They obtained the highest level of germination (100%) for all three species by pre-treating seeds with a pulse dry heat treatment (80˚C, 10min) followed by removal of the mericarp plug. They concluded that non-deep physiological dormancy appears to be consistent across the genus and that the mericarp plug plays a significant role in controlling the germination process [89]. Although it has been established through seed imbibition experiments that physical dormancy is not present in *Prostanthera* the mericarp plug acts as a mechanical barrier and is involved in regulating germination. Females of *Lycopus maackianus* on average produce significantly more than 37 times as many nutlets as the hermaphrodites. In *Salvia apiana* Jepson the small nutlets fall from the dried calyx during mid to late summer but are secondarily dispersed by harvester ants and seed caching rodents. Seed traps revealed that seeds dispersed up to 3m away. Schulze *et al*. while investigating the germination and Seed Bank studies of *Macbridea alba* (Lamiaceae) reported that the dry-stored seeds declined in germinability with time and were not germinable a year after collection [90]. In *Salvia fruticosa* Miller fire and bees' effect the seed production with an average percentage of fruit-set in the unburned areas being 19.9±8.4 and in the burned areas 11.0±3.8; thus, fire has a significant effect on the fruit set [91]. In *Nepeta rtanjensis* a single plant produces approximately 2500 seeds [92]. Measured dimensions of these ellipsoid shaped grains were estimated to be 1.7±0.02mm long and 0.93±0.01mm wide. The average weight of 1000 seeds was 538mg. They reported that the germination of *N. rtanjensis* seeds did not occur in darkness and the maximum observed germination (up to 60%) was obtained after at least 8 days of exposure to continuous white light irradiation. Potassium nitrate and/or NO donors, such as sodium nitroprusside, were found completely ineffective in the germination of these seeds. *Eriope blanchetii* is partially self-compatible and both spontaneous as well as manual self-pollination produced fruits, although only 4.5% and 10%, respectively and no agamospermic fruit development with the highest fruiting success in control flowers (49%). Pollinator limitation may have played an important role, because visitors were less frequent in plants with lower number of open flowers. Considering combined pollination constraints such as dichogamy and herkogamy, it was possible that a very high percentage of the seeds in control fruits were the product of cross fertilization. It was further reported that under natural conditions, each flower produced one to three seeds, while those derived from self-pollination produced only one. A small percentage (6.2%) of the nutlets produced was reported to be directly predated by wasps of the genera *Zethus* and *Scollia*. Predation of nutlets occurred when they were still green, by means of a perforation of the base of the calyx or directly through the gullet [93]. Clavijo reported that the viability of *Ajuga iva* and *Ajuga chamaepitys* seeds did not change for at least 2 years [94]. The germination conditions for *A. iva* nutlets were much more restrictive. They reported that germination occurred only at 19-32˚C in the constant temperature tests, and only at 20/10˚C and 25/15˚C in the variable temperature tests. Absence of light significantly inhibited germination of nutlets of both species except at high temperatures.

CONCLUSION

In conclusion, every specialized nototribic construction is a bilabiate blossom. Normal cytology, floral strategies and breeding behaviour of *Lamiaceae* tend to maximize pollen economy and availability of pollinators all year round. Protandry or gynodioecy, especially frequent in this family maximizes cross-fertilization. However, the evolutionary shift from xenogamy to autogamy reduces the energetic cost per flower and facilitates self-pollination and provides the reproductive assurance. Colonization of almost all types of habitats and resilience to disturbances may be attributed to the flexible breeding system present in Lamiaceae.

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