ANATOMY, PALYNOLOGY AND FLORAL DIVERSITY OF THE GENUS *LAMIUM* L. (LAMIACEAE) IN TURKEY

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ANATOMY, PALYNOLOGY AND FLORAL DIVERSITY OF THE GENUS *LAMIUM* L. (LAMIACEAE) IN TURKEY

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ABSTRACT

ANATOMY, PALYNOLOGY AND FLORAL DIVERSITY OF THE GENUS *LAMIUM* L. (LAMIACEAE) IN TURKEY

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Lamium L. is the type genus of subfamily Lamioideae and the family Lamiaceae. Due to the absence of recognizable morphological characters, circumscription of the genus has undergone many changes through time. Turkey is the main biodiversity center of the genus with 36 taxa, 18 of which are endemic.

Even though many genera in the subfamiliy Lamioideae have been subjected to various anatomical and micromorphological studies, a comprehensive investigation of the genus *Lamium* is still lacking. In the first part of this study, the anatomical (root, stem, leaf and petiole) and micromorphological (trichome and pollen morphology) characteristics of the *Lamium* species in Turkey are presented and their taxonomic implications are discussed. Together with gross morphology, such anatomical and micromorphological characters are proved to be taxonomically informative in the delimitation of certain infrageneric taxa.

In the second part of this study, pollination biology and floral diversity of bee pollinated *Lamium* species; including *Lamium villosifolium* and *L. album* subsp. *crinitum*, which grow sympatrically in Isik Mountain, Kizilcahamam, were investigated. Two *Lamium* species are clearly adapted to pollination by Apiodea.

Field and laboratory investigations revealed that co-occuring *Lamium* species are isolated from each other on the basis of morphological, mechanical and altitudinal aspects. The diversity of floral constructions increases the mechanical isolation by attracting different pollinators and by loading pollen on different parts of pollinator`s bodies. Change in the plant population density along the altitudinal gradient clearly triggered the pollinator assemblage variation.

Keywords: Anatomy, Palynology, Micromorphology, *Lamium*, Pollination, Systematics

ÖZ

TÜRKİYE'DE BULUNAN *LAMIUM* L. (LAMIACEAE) CİNSİNİN ANATOMİ, POLEN VE ÇİÇEK ÇEŞİTLİLİGİ ÜZERİNE ÇALIŞMALAR

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Lamium L. cinsi Lamiaceae familyasının ve Lamioideae alt familyasının tip cinsidir. Ayırt edici karakterlerin azlığı sebebi ile, cinsin sınırları zaman içinde pek çok kez değişikliğe uğramıştır. Türkiye`de, 16 tanesi endemik olmak üzere, 36 takson yayılış göstermektedir ve ülkemiz cinsin biyoçeşitlilik merkezidir.

Altfamilya Lamioideae içindeki pek çok cins üzerinde anatomik ve mikromorfolojik çalışmalar yapılmış olsa da, *Lamium* cinsi üzerinde bu tip çalışmalar oldukça azdır. Bu çalışmanın ilk kısmında, Türkiye`deki *Lamium* türlerinin anatomik (kök, gövde, yaprak ve petiol anatomisi) ve mikromorfolojik (tüy ve polen morfolojisi) özellikleri verilmiş, bu karakterlerin taksonomik önemi tartışılmıştır. Bütüncül morfolojik özellikler ile beraber, anatomik ve mikromorfolojik karakterlerin bazı tür ve tür altı kategorilerde taksonomik öneminin olduğu belirlenmiştir.

Bu çalışmanın ikinci kısmında, Kızılcahamam Işık Dağı alanında yayılış gösteren iki *Lamium*;

L. villosifolium ve *L. album* subsp. *crinitum* türlerinin tozlaşma biyolojisi ve çiçek çeşitliliği üzerinde çalışmalar yapılmıştır. Bu iki *Lamium* türü, belirgin bir şekilde arılarla tozlaşmaya adapte olmuştur.

Arazi ve laboratuvar calışmaları ışığında iki *Lamium* türü birbirlerinden morfolojik, mekanik ve yükseklik özellikleri açısından ayrılmaktadır. Çiçek morfolojilerindeki farklılık, mekanik izolasyonu arttırmakta, polenlerin tozlaştırıcı vücütlarının farklı bölgelerinde taşınmasını sağlamaktadır. Yüksekliğe bağlı olarak değişim gösteren bitki popülasyon yoğunluğu, tozlaştırıcı birliğinde farklılıklara sebep olmaktadır.

Anahtar kelimeler: Anatomi, Palinoloji, Mikromorfoloji, *Lamium*, Polinasyon, Sistematik

To my parents

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TABLE OF CONTENTS

CHAPTERS

LIST OF TABLES

TABLES

LIST OF FIGURES

FIGURES

ABBREVIATIONS

ANK	Ankara University Herbarium
BM	The Natural History Museum, London
cm	centimeter
E	Royal Botanic Garden *Edinburgh*
Eur-Sib	Euro-Siberian
GAZI	Gazi University Herbarium
Ir-Tur	Irano-Turanian
K	Royal Botanic Gardens, Kew
km	kilometer
m	meter
mm	milimeter
Med	Mediterranean
Mt.	Mountain
s.l.	sensu lato
sect.	section
subg.	Subgenus
subsp.	subspecies
var.	variety

CHAPTER 1

INTRODUCTION

1.1 Brief History of the Lamiaceae

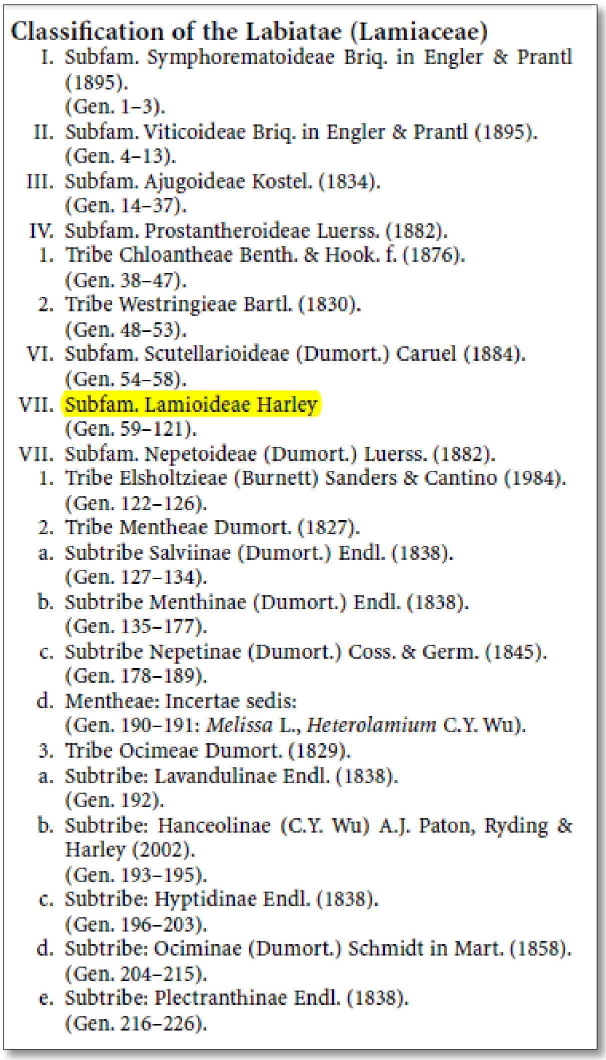
The family Lamiaceae Martinov, one of the most distinctive angiosperm families, has long been a target group for study for many botanists (Stevens; 1984). Labiatae includes annual, biennial and perennial herbs, shrubs or trees that have near-cosmopolitan distribution, but are absent from the coldest regions of high latitude or altitude (Harley; 2004, Thorne; 1992). The family contains 236 genera and about 7000 species (Harley; 2004). The family is known for many aromatic plants that are economically very important, especially in the Mediterranean region and in many parts of Asia. The species of *Salvia* (sage), *Mentha* (perppermint), *Thymus* (tyme), *Origanum* (oregano), *Rosmarinus* (rosemary), which are noted for their essential oils, are used for culinary purposes (Harley et al. 2004). Many members of the Lamiaceae are rich in nectar, which is important for the production of honey that is produced from the natural vegetation of especially the Mediterranean area (Harley et al. 2004). 236 genera that comprise the Labiateae, nearly half of the known species are restricted to the 10 largest genera, such as; *Salvia* (900 spp.), *Clerodendrum* (500 spp.), *Scutellaria* (360 spp.), *Stachys* (300 spp.), *Teucrium* (250 spp.), *Thymus* (220 spp.) (Harley et al. 2004).

Most species in the family have square stems, opposite leaves, two-lipped flowers, a deeply four-lobed ovary and four stamens. The Lamiaceae have long been considered closely related to Verbenaceae with many characters in common. The Lamiaceae is generally separated from Verbenaceae on the basis of its gynoecium and fruit structure. Genera with an almost entire ovary were included in Verbenaceae however they were then transferred to Lamiaceae and most recently, they are accepted in the Lamiaceae (Junell; 1934, Cantino et al. 1992, Harley et al. 2004, Govaerts et al., 2010).

The classification of the Lamiaceae by Briquet (1895-1897) was influenced by and was largely based on a series of comprehensive treatments of Bentham (1832-1836; 1848; 1876). The most significant alteration of Briquet to Bentham`s classification was the merging of four tribes into a large subfamily Lamioidae (Stachyoideae), which was considered as para- or polyphyletic by Cantino & Sanders (1986). On the basis of palynological features, Erdtman (1945) proposed an alternative classification of the Lamiaceae, dividing the family into two subfamilies; Lamioideae, with tricolpate and binucleate pollen, and Nepetoideae with hexacolpate and tri-nucleate pollen.

In addition of a variety of embryological and phytochemical characters, Erdtman`s division was highly supported (Wunderlich, 1967; Cantino & Sanders, 1986). Bentham being unaware of the characters that delimit Erdtman`s subfamilies, his tribal classification showed high congruence with Erdtman`s subfamilial classification; thus he was recognized as a genius herbarium taxonomist (Cantino & Sanders, 1986). Erdtman`s division was further analysed by Cantino & Sanders (1986) using a broader range of characters, in which they concluded that; Nepetoideae appeared to be monophyletic whereas Lamioideae was not. The monophyly of Nepetoideae was also indicated in various molecular analyses (e.g. Wagstaff et al., 1995; Wagstaff & Olmstead, 1997). Nepetoideae may have been derived early in the history of the family and the gynobasic stye may have evolved independently in Lamioideae (Wagstaff et al. 1998). Since Wagstaff et al. (1998), no phylogenetic analyses including the seven subfamilies of the Lamiaceae has been published.

Subsequently, in the clearer picture of the subfamilial classification of the Lamiaceae, Harley et al. (2004) divided the family into seven subfamilies however the relationships among the subfamilies will remain a mystery until a more comprehensive phylogenetic study is done. The recent infrafamilial classification of the Lamiaceae is given in Figure 1.



Classification of the Labiatae (Lamiaceae)

I. Subfam. Symphorematoideae Briq. in Engler & Prantl (1895).
(Gen. 1–3).
II. Subfam. Viticoideae Briq. in Engler & Prantl (1895).
(Gen. 4–13).
III. Subfam. Ajugoideae Kostel. (1834).
(Gen. 14–37).
IV. Subfam. Prostantheroideae Luerss. (1882).
1. Tribe Chloantheae Benth. & Hook. f. (1876).
(Gen. 38–47).
2. Tribe Westringieae Bartl. (1830).
(Gen. 48–53).
VI. Subfam. Scutellarioideae (Dumort.) Caruel (1884).
(Gen. 54–58).
VII. Subfam. Lamioideae Harley
(Gen. 59–121).
VII. Subfam. Nepetoideae (Dumort.) Luerss. (1882).
1. Tribe Elsholtzieae (Burnett) Sanders & Cantino (1984).
(Gen. 122–126).
2. Tribe Mentheae Dumort. (1827).
a. Subtribe Salviinae (Dumort.) Endl. (1838).
(Gen. 127–134).
b. Subtribe Menthinae (Dumort.) Endl. (1838).
(Gen. 135–177).
c. Subtribe Nepetinae (Dumort.) Coss. & Germ. (1845).
(Gen. 178–189).
d. Mentheae: Incertae sedis:
(Gen. 190–191: *Melissa* L., *Heterolamium* C.Y. Wu).
3. Tribe Ocimeae Dumort. (1829).
a. Subtribe: Lavandulinae Endl. (1838).
(Gen. 192).
b. Subtribe: Hanceolinae (C.Y. Wu) A.J. Paton, Ryding & Harley (2002).
(Gen. 193–195).
c. Subtribe: Hyptidinae Endl. (1838).
(Gen. 196–203).
d. Subtribe: Ociminae (Dumort.) Schmidt in Mart. (1858).
(Gen. 204–215).
e. Subtribe: Plectranthinae Endl. (1838).
(Gen. 216–226).

Figure 1. Classification of the family Lamiaceae (Harley et al., 2004)

At its current circumsciption, the family consists of seven subfamilies, of which Lamioideae is the second largest with about 1250 species in 63 genera (Harley et al., 2004). The members of the subfamily are characterized by a gynobasic style, tricolpate pollen grains, albuminous seeds and pathulate embryos (Harley et al., 2004). In the subfamily, about half of the total number of species belongs to only four genera (*Leucas*, *Phlomis*, *Sideritis* and *Stachy*s) and there are a large number of monotypic genera which clearly reflects the taxonomic challenges of the Lamioids. Since Harley et al. (2004), a phylogenetic framework for the subfamily Lamioidae was produced by Scheen et al. (2010) and they divided the subfamily to 9 tribes. Later on, Bendiksby et al. (2011a) produced an updated phylogeny of the lamioid genera that were omitted in the study of Scheen et al. (2010); in which genus *Lamium* were placed in tribe Lamieae, together with *Eriophyton* s.l. and *Stachyopsis*.

1.2 General Characteristics of *Lamium* species

The common name of the genus `deadnettle` refers to the resemblance of the vegetative parts of *Lamium album* to distantly related stinging nettles (*Urtica dioica*; Urticaceae), however the members of the genus *Lamium* do not have such stinging hairs and this may suggest a harmless mimicry (Brown et al. 1991).

The deadnettle flower has five spiky sepals, which are joined at the base to make a cup-like shape. Five joined petals form the corolla, of which the uppermost is well-developed and forms the two-lipped flower structure. There are four stamens under the upper lip of the flower and their filaments are joined to the corolla tube. The forked (bifid) stigma and the long style end with a four-lobed ovary (Figure 2).

Lamium species possess antioxidant, anti-inflammatory, astringent, antispasmodic, antiseptic, uterotonic properties and are used as official and folk medicines in Anatolia, China and Europe, which are useful for problems as menorrhagia, paralysis, hypertension, chronic bronchitis, prostrate and scrofula

Bremness, 1995; Baytop, 1999). Also some *Lamium* species are grown as ornamental plants in gardens and parks (Rudy, 2004).

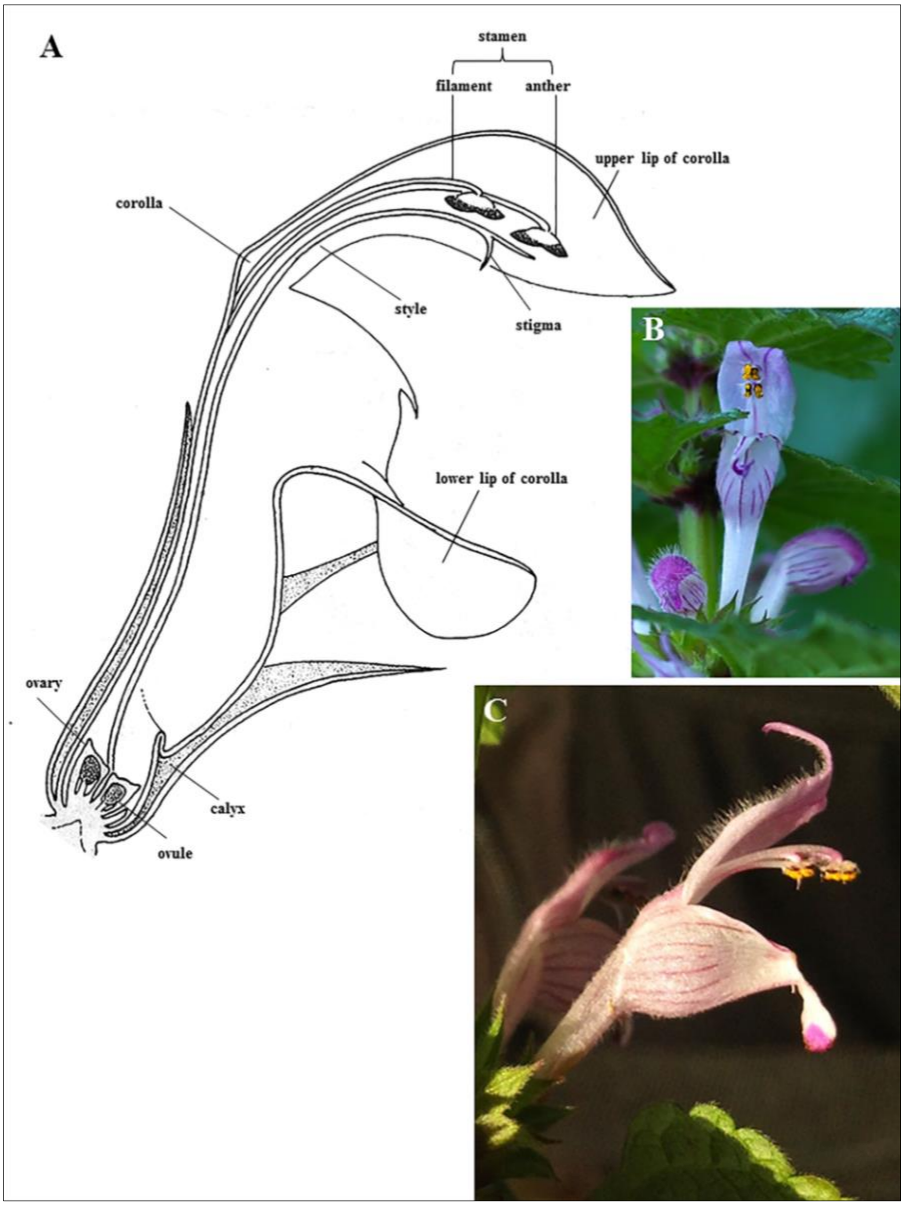


Figure 2. Flower structure of A; *Lamium album* L., B & C *Lamium cariense* R.R.Mill.

1.3 Taxonomic History of the genus *Lamium*

Lamium L., the type genus of subfamily Lamioideae and the Lamiaceae, comprises 16-38 species, depending on the circumscription of the genus (Briquet 1895-1897; Mennema 1989; Harley et al. 2004; Bendiksby et al. 2011a). *Lamium* includes both annual and separate herbaceous plants that are widely distributed throughout temperate Eurasia, where its center of diversity lies in the Irano-Turanian and Mediterranean regions (Mennema 1989).

Delimitation of *Lamium* from its related genera has been an important challenge in the taxonomic history of the genus. Due to the absence of recognizable morphological characters, circumscription of the genus has undergone many changes through time. Several East Asian labiates with uncertain generic position have been placed in *Lamium* which served as a repository genus (Mennema 1989).

In Species Plantarum (1753), Linneaeus recognized 5 species and 1 variety of *Lamium*. Then in 1763, he increased the species number to 8. In 1800, Willdenow recognized 13 *Lamium* species. Bentham (1848) and Briquet (1897) recognized 35 and 38 species, respectively. Since then, over 160 names have been described at species and infraspecific rank. In his monograph, Mennema (1989) treated many of the earlier species, distributed both in Turkey and in the World, as subspecies, varieties or synonyms and reduced the species number to 16 in the world. In his monograph, Mennema (1989) recognized 3 subgenera; *Orvala* (L.) Briq., *Galeobdolon* (Adans.) Asch and *Lamium* L.; with 3 sections: sect. *Amplexicaule* Mennema, sect. *Lamium* and sect. *Lamiotypus* Dumort. In subgenus *Lamium* (Table 1). However, the infrageneric classification proposed by Mennema (1989) contrasts with his intuitive phylogenetic tree, morphological and molecular investigations (Ryding, 2003; Bendiksby et al. 2011b).

Table 1. Infrageneric classification of the genus *Lamium* by Mill (1982) and Mennema (1989).

Taxon and Number of Species			**Mill (1982), Flora of Turkey**	**Mennema`s Monograpgh (1989)**
1	1	*Sect. Lamium*	*Lamium lycium*	*L. garganicum* subsp. *striatum* var. *striatum*
2	2		*L. cariense*	
3	3		*L. pisidicum*	
4	4		*L. tenuiflorum*	
5	5		*L. veronicifolium*	
6	6		*L. garganicum* subsp. *striatum*	
7			*L. garganicum* subsp. *reniforme*	
8			*L. garganicum* subsp. *nepetifolium*	
10			*L. garganicum* subsp. *rectum*	
11			*L. garganicum* subsp. *lasioclades*	
12			*L. garganicum* subsp. *pulchrum*	
13			*L. garganicum* subsp. *laevigatum*	*L. garganicum* subsp. *garganicum*

Table 1 (cont`d)

Taxon and Number of Species			**Mill (1982), Flora of Turkey**	**Mennema`s Monograpgh (1989)**
14	7	*Sect. Lamium*	*L. microphyllum*	*L. garganicum* subsp. *striatum* var. *microphyllum*
15	8		*L. cymbalarifolium*	
16	9		*L. sandrasicum*	
17	10		*L. armenum* subsp. *armenum*	*L. garganicum* subsp. *striatum* var. *armenum*
18			*L. armenum* subsp. *sintenisii*	
19	11		*L. ehrenbergii*	*L. purpureum* var. *ehrenbergii* *L. purpureum* var. *purpureum*
20	12		*L. purpureum* var. *purpureum*	
21			*L. purpureum* var. *aznavourii*	
22	13	*Sect. Amplexicaule*	*L. eriocephalum* subsp. *eriocephalum*	*L. eriocephalum*
23			*L. eriocephalum* subsp. *glandulosidens*	
24	14		*L. amplexicaule*	*L. amplexicaule*
25	15		*L. aleppicum*	
26	16		*L. macrodon*	*L. macrodon*

Table 1 (cont`d)

Taxon and Number of Species			Mill (1982), Flora of Turkey	Mennema`s Monograpgh (1989)
27	17	Sect. *Lamiotypus*	*L. maculatum* var. *maculatum*	*L. maculatum*
28			*L. maculatum* var. *villosifolium*	
29	18		*L. gundelsheimeri*	
30	19		*L. truncatum*	
31	20		*L. album*	subsp. *album*
32	21		*L. crinitum*	subsp. *crinitum*
33	22		*L. leucolophum*	
34	23		*L. tomentosum* var. *hakkariense*	*L. tomentosum*
35			*L. tomentosum* var. *tomentosum*	
36			*L. tomentosum* var. *filicaule*	
37			*L. tomentosum* var. *alpestre*	
38	24		*L. sulfureum*	
39	25		*L. moschatum* var. *moschatum*	*L. moschatum* subsp. *moschatum*
40			*L. moschatum* var. *rhodium*	

Table 1 (cont`d)

Taxon and Number of Species			**Mill (1982), Flora of Turkey**	**Mennema`s Monograpgh (1989)**
41		*Sect. Lamiotypus*	*L. moschatum* var. *micranthum*	*L. moschatum* subsp. *micranthum*
42	26		*L. ponticum*	
43	27		*L. galactophyllum*	
44	28	*NI*	*L. tschorochense*	*NI*
45	29	*NI*	*L. vreemanii*	*NI*
47	31	*NI*	*L. artvinense* *(Galeopsis bifida)*	*NI*
48	32	*NI*	*Lamium orientale (Wiedemannii orientalis)*	*NI*
49	33	*NI*	*Lamium multifidum (Wiedemannii 10eparate10)*	*NI*
50	34	Subg. *Galeobdolon*	*Lamium galeobdolon (Galeobdolon luteum)*	*Lamium galeobdolon* subsp. *montanum*
51	35	Subg. *Orvala*	*NI*	*Lamium orvala*

NI: not indicated

Lamium galeobdolon (L.) L., which is morphologically very distinct, has been included in separate genera as *Lamiastrum* Heist. Ex Fabr. Or *Galeobdolon* Adans. On the other hand, Harley et al. (2004) and Govaerts et al. (2010) included the species in *Lamium*. According to the latest molecular phylogenetic studies by Bendiksby (2011b) and Krawczyk (2013a, b), including the species in a separate genus is not suggested.

The generic classification of *Wiedemannia* Fisch. & C.A. Mey. Has varied in literatures. *Lamium multifidum* L., previously described as a *Lamium* species, later assigned to *Wiedemannia* by Bentham (1848). Similarly, *L. orientale* (Fisch. & C.A. Mey.) E.H.L. Krause was previously included in *Wiedemannia* by Fischer & Meyer (1838). However, the two species of *Wiedemannia* have been included in *Lamium* (Krause 1903; Ryding 2003) and their classification was adopted by Harley et al. (2004) and Govaerts et al. (2010). According to Bendiksby et al. (2011b), *Wiedemannia* is phylogenetically nested within *Lamium*.

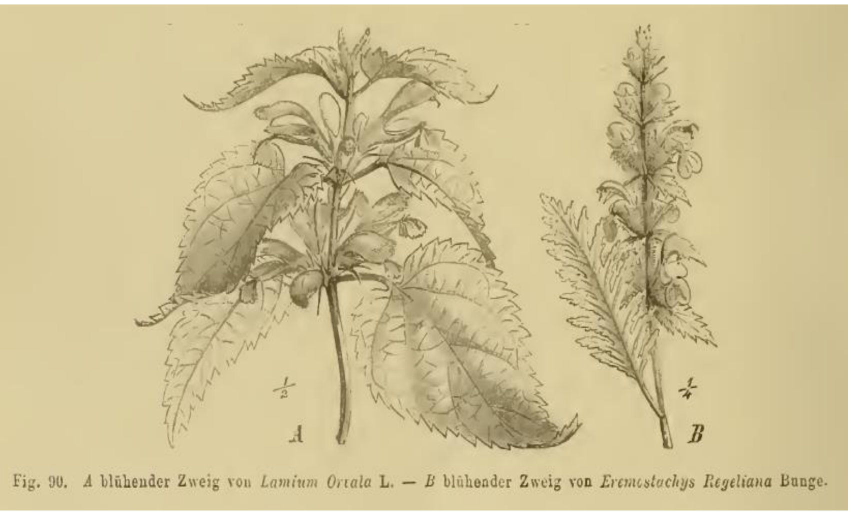


Figure 3. An illustration of *Lamium orvala*, from Briquet (1897)

In a recent molecular study on the subfamily Lamioideae, Scheen et al. (2010) proposed tribe Lamieae to encompass *Lamium* s.str. and taxa that have been assigned to the separate genera *Lamiastrum* Heist. Ex Fabr. And *Wiedemannia* Fish. & C.A. Mey. Subsequently, the problematic East Asian *Lamium* species are transferred to *Matsumurella* Makino and *Eriophyton* Benth. (Bendiksby et al., 2011a). Another recent molecular phylogenetic study on various *Lamium* taxa (Krawczk et al., 2014) and the problematic *L. galeobdolon* (Krawczyk et al., 2013) still has not enlightened the problems in this particular genus. Many of the Turkish endemic species were not included in the previous phylogenetic studies. Thus, a monographic work on the genus, comprising the Turkish endemics is urgently needed.

In Flora of Turkey, Mill (1982) recognized 27 species, reaching a total of 43 taxa with subspecies and varieties. In the following years, 4 more species of *Lamium* were described or recorded from Turkey (Duman, 2000). Turkey is the main biodiversity center of the genus with 47 taxa, ca. 52% of which are endemic (Mill 1982; Duman, 2000). Since most of the infrageneric treatments were conducted on herbarium specimens, it is an urge to conduct a revisional work on the genus in Turkey to solve its taxonomic problems.

1.4 Anatomical and Micromorphological Studies on the Lamiaceae

1.4.1 Anatomy

The concept of character is fundamental to the discipline of taxonomy, where they provide the basic information for identification and classification processes. The description and characterization of plants is the primary process in clarifying patterns of evolution (Dickison, 2000). Thus every available character and its states are valuable in systematics. Anatomical properties or the internal structures of plant organs are a significant source of data for the classification of plants. Anatomy and physiology of plants are closely correlated where those features of plants has changed with novel mechanisms. These features are of significant adaptive value and provide valuable characters in elucidating phylogenetic relationships and in assessing homology. Therefore, anatomical data can be taxonomically informative in studying plant systematics (Dickison, 2000; Simpson, 2006).

Many studies on the morphological and anatomical structures in some genera of Lamiaceae have been shown that these data are useful at different taxonomic levels (Wojciechowska, 1966; Hedge, 1970; Husain et al., 1990; Demissew and Harley 1992; Ryding, 1992, 1994, 1995; Marin et al., 1994, 1996; Turner and Delprete, 1996; Guerin, 2005; Salmaki et al., 2008; Kahraman et al., 2011). The usefulness of anatomy and its implication in the systematics of Lamiaceae are well known from various comprehensive works (Laber, 1954; Bech, 1963; Bokhari and Hedge, 1971; Metcalfe and Chalk, 1979; Ryding, 1993, 1994, 2007; Bosabalidis and Kokkini, 1997). Such that; the structure of vascular bundles in petioles has been demonstrated to have taxonomic significance in the family Lamiaceae (Metcalfe and Chalk, 1972). Moreover, comparative leaf anatomy including characteristics of leaf transverse sections in higher plants has indicated to be of great significance in species delimitation (Radford et al., 1974; Stace, 1984; Simpson, 2006). For example, comparative leaf anatomy has also been shown to be useful in delimitation of taxa in various genera of Lamiaceae (Bokhari and Hedge, 1971: *Salvia*; Azizian and Culter, 1982: *Phlomis* and *Eremostachys*).

There are several studies on taxonomy, morphology, anatomy, trichome micromorphology, palynology and cytology of *Lamium* species (Mill, 1982; Gill, 1983; Mennema, 1989; Abu-Asab and Cantino, 1994; Baran and Özdemir, 2009, 2011; Celep et al., 2011). However, anatomical features of most *Lamium* species have not been investigated yet.

1.4.2 Palynology

Palynology, the study of pollen grains, has provided valuable characters that have been used in elucidating phylogenetic relationships among plants. Pollen grains have variable parameters, such as, size, shape and the number and position of apertures. Especially, the pollen wall bears extremely diverse structure and sculpture. In plant systematics, the characteristics of these features are as important as any other morphological data. For this reason, palynological studies are used extensively in plant systematics (Simpson, 2006; Hesse, 2009).

Pollen morphological studies in various genera of the family Lamiaceae have been carried out by many authors (Erdtman, 1945; Wunderlich, 1967; Cantino and Sanders, 1986; Abu-Asab and Cantino, 1989, 1992, 1993a, b, 1994; Harley et al., 1992; Harley, 1992; Wagstaff, 1992; Celenk et al., 2008a, b; Moon et al., 2003, 2008a; Salmaki et al., 2008; Hassan et al., 2009; Özler et al., 2011). Most of the palynological studies including the members of the Lamioideae have focused on certain genera (Huyn, 1972; Bassett and Munro, 1986) whereas the most comprehensive palynological work on the subfamily was conducted by Abu-Asab and Cantino (1992, 1994), supporting the segregetaion of certain genera on the basis of pollen morphology however their work comprises only a few *Lamium* species. Even though many genera in the subfamiliy Lamioideae have been subjected to various palynological works, a comprehensive palynological investigation of the genus *Lamium* is still lacking. Such micromorphological characters may show to be informative in the delimitation of infrageneric taxa. It may be a good case study giving evidence for the usefulness of pollen morphological characters of the genus for its phylogeny and classification.

1.4.3 Trichome Morphology

Many plants have smooth or non-sculptured epidermal surfaces whereas a large number of them have an indumentum bearing hairs or trichomes. There are various types of trichomes that arise from the surface of plants, such as, unicellular or multicellular trichomes without any secretions and glandular trichomes that produce essential oils with secretions (Dickison, 2000).

The taxonomic value of indumentum and its sytematic importance is well known in Lamiaceae and in related families Verbenaceae and Scrophulariaceae and is suggested to be useful in phylogenetic reconstruction of the mentioned families (Abu-Asab & Cantino, 1987; Cantino, 1990). Cantino (1990) conducted a comprehensive study of Lamiaceae and Verbenaceae with emphasis on the systematic importance of micromorphological data and this study focused mainly on the subfamily Lamioideae *sensu* Erdtman (1945). Through time, trichome micromorphology has been shown to be useful in many genera of the Lamiaceae (Ascensao et al., 1995; Baran & Ozdemir, 2009; Bosabalidis, 1990; Celep et al., 2011, 2014; Corsi & Bottega, 1999; Giuliani et al., 2008; Demissew & Harley, 1992; Marin et al., 1994; Moon et al., 2009; Navarro, 1995; Navarro & Oualidi, 2000; Puech, 1984; Zarre et al., 2008). There are a few studies comprising the trichome micromorphology of *Lamium* species (Baran & Ozdemir, 2009, 2011; Celep et al. 2011).

1.5 Phytogeographic Distribution and Endemism ratio of *Lamium* species in Turkey

Turkey is divided into three phytogeographical regions, which are Euro-Siberian (Euxine provinence), Mediterranean (Mediterranean provinces of West Anatolia, Taurus and Amanos mountains) and Irano-Turanian (Central and Eastern Anatolia) phytogeographical regions (Figure 4). Each phytogeographical region covers different floristic composition (Davis, 1965).

Turkey is the main biodiversity center of the genus with 47 taxa, ca. 52% of which are endemic (Duman, 2000; Mill, 1982). The distribution of the genus *Lamium* can be indicated as temprate Eurasiatic (Mennema, 1989). They are distributed in Western Europe to Eastern Asia, including Northern Africa, North of the Atlas Mountains and Macaronesia. Its center of diversity is found in the Irano-Turanian and the Mediterranean phytogeographical regions. Basically, taxa of the genus *Lamium* possess habitats which are forests, rocky mountain slopes and cultivated fields (Mennema, 1989). The altitudinal range in the genus *Lamium* is quite large, from sea-level to 4800 meters (Mennema, 1989).

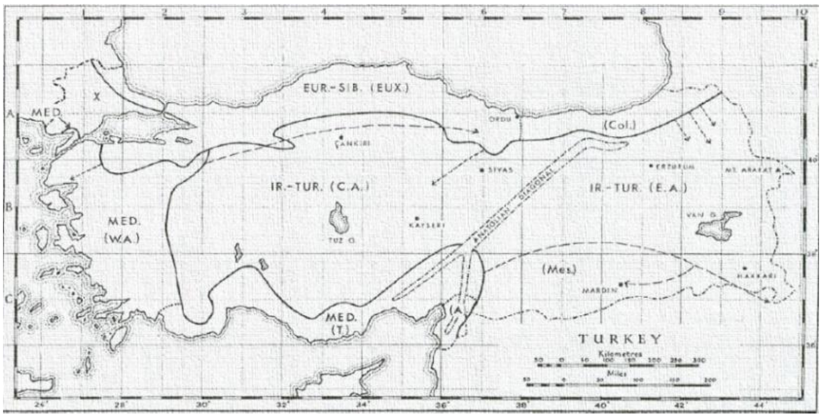
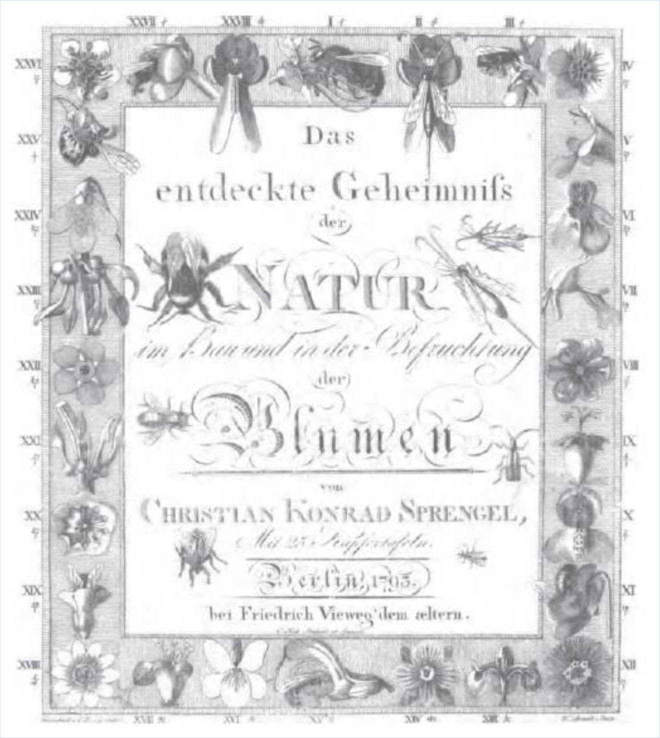


Figure 4. Davis` grid map of Turkey.

1.6 Historical Background of Pollination Biology

"*When I carefully examined the flower of the wood cranesbill (Geranium sylvaticum) in the summer of 1787, I discovered that the lower part of its corolla was furnished with fine, soft hairs on the inside and on both margins. Convinced that the wise creator of nature had not created even a single tiny hair without definite purpose, I wondered what purpose these hairs might serve. And it soon came to my mind that if one assumes that the five nectar droplets which are secreted by the same number of glands are intended as food for certain insects, one would at the same time not think it unlikely that provision had been made for this nectar not to be spoiled by rain and that these hairs had* *been fitted to achieve this purpose*." (from `Discovery of the Secret of Nature in the Structure and Fertilization of Flowers` by Christian Konrad Sprengel 1793, Translated by Peter Haase, University of Canterbury, Christchurch, New Zealand).

By the time Sprengel announced his book (1790), he defined himself a "philosophical botanist". He aimed to explain the structure and purpose of the floral organs. In his book, he described how he arrived at his discoveries, giving case histories. In every observation, he discussed how the floral organs function and what kind of insects transmits the pollen. He examined the flowers in their natural habitats without any special equipment but with a simple pocket lens; "….. *One must try to catch nature in action*" he said. Sprengel lived for another 23 years after the publication of his book. He never wrote a second volume since his book received no positive response and his discoveries remained forgotten for almost seven decades (Vogel, 1996).



Das
entdeckte Geheimniſs
der
NATUR
im Bau und in der Befruchtung
der
Blumen
von
CHRISTIAN KONRAD SPRENGEL,
Mit 25 Kupfertafeln.
Berlin, 1793.
bei Friedrich Vieweg dem ælteren.

Figure 5. The title page to C.K. Sprengel's book "Discovery of the secret of nature in the structure and fertilization of flowers" published in 1793

Another man of genius, Charles Darwin, noticed Sprengel`s work and rescued it from oblivion. The apparent tendency of flowering plants to avoid self-fertilization and how important a part insects play in the pollination of many plants was observed from innumerable observations by Sprengel, which did not escape Darwin`s notice. (Vogel, 1996) To make empirical observations of British orchids (1862), Darwin adopted the methods of Sprengel and the results provided strong support for his own theory. Finally, Sprengel`s work received publicity among botanists in late 19th century.

Figure 6. The 16th copperplate from Sprengel's book. Figures 8 and 9 illustrate the horizontal flowers of *Lamium album* (Lamiaceae)

"In the following summer I investigated the forget-me-not (Myosotis palustris). Not only did I find that this flower possesses nectar but also that this nectar is completely protected from rain. At the same time I noticed the yellow ring which surrounds the opening of the corolla tube and contrasts well against the sky-blue color of the corolla lobes. I thought this feature might be related to insects too. Should nature have particularly colored this ring for the purpose of showing the insects the way to the nectar container? With this hypothesis in mind, I examined other flowers and found it confirmed by most of them. I saw that those flowers whose corolla is differently colored in one place than it is elsewhere always have these ***spots, figures, lines, or dots of particular color*** *where the entrance to the nectary is located. Now I deduced from the particular to the general. If, I thought, the corolla is specifically colored in a particular place for the sake of insects, then it is colored altogether for the insects."* (From `Discovery of the Secret of Nature in the Structure and Fertilization of Flowers` by Christian Konrad Sprengel 1793, see Figure 7).

Figure 7. The yellow ring surrounding the opening of the corolla tube of *Myosotis palustris* (L.) Nathh., which was noticed by Sprengel in 1793.

1.7 Why Study Pollination Biology?

The flowering plants comprise about one-sixth of all identified species on earth while the insects nearly two-thirds (Wilson, 1992). The interactions among these plants and animals constitute the important elements of terrestrial ecosystems.

In angiosperms, it is the flowers that take the crucial role for reproduction. The sexual reproduction in angiosperms has three sequential stages: pollination, fertilization, and seed maturation (Lyons et al., 1989). The first of these stages is basically the concern of field biologists while the other two stages are more suitably studied in the laboratory.

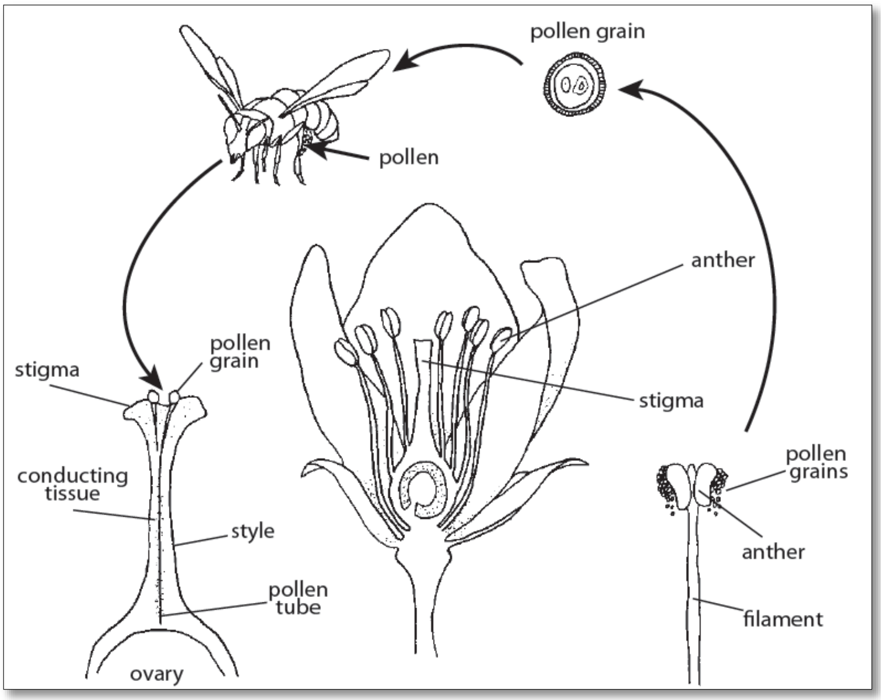


Figure 8. The processes of pollination in a typical angiosperm flower, showing the route taken by pollen from anther to stigma (followed by pollen tube growth into the style) (Modified from Barth, 1985)

Pollination biology studies draws from many biological, chemical and physical disciplines such that,

- *taxonomy* is represented in the identification of both plants and their pollinators;
- *morphology* in the description of flowers or pollinatos;
- *population* and *quantitative genetics* in the study of floral traits, plant population structure, and breeding systems;
- *Animal behavior* in the study of pollinator movements, and so on.

Pollination biology is studied for a variety of reasons. First of all, plant-pollinator interactions can provide the most important examples of coevolution. Plant-pollinator interactions provide significant examples of adaptive radiation (Willmer, 2011). Both plants and their visitors are good examples for community ecology studies (Inouye, 1978). Flowers and their pollinators provide basis for the studies of reproductive success (Campbel, 1989; 1991). In addition, pollinators are essential for many vegetable and fruit crops, which imply the economic reasons for studying pollination biology (Free, 1970a, b). Thus, flower-animal mutualism has been a center of focus for ecologists, which provides many insights into the fundamental aspects of biology, from behavior and reproduction to evolution and ecology (Willmer, 2011). Below, Figure 6 illustrates the key interactions of major biological themes in the study of pollination ecology. It is obvious that, pollination ecology have had major impacts on general ecology and evolutionary theory.

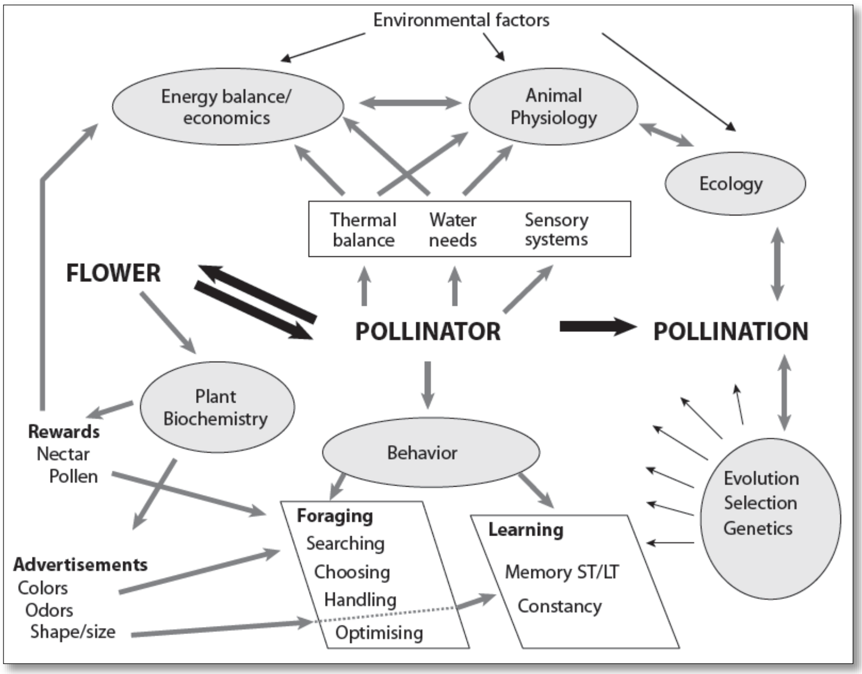


Figure 9. Key interactions of major biological topics promoting interest in the study of pollination (Willmer, 2011)

Although there are many techniques and equipments available, the primary technique of pollination ecology is the same today as in Sprengel's or Darwin's days: *"consistent observation of what really happens in nature, in the original, natural habitat of the plant under investigation*" (Faegri and van der Pijl 1979). Careful observations, combined with manipulative experiments, will provide answers to almost any question in anthecology.

1.8 Pollination Syndromes

Convergent evolution is indicated by correlated features in species of distantly related taxa (Ollerton et al., 2009). The structural modifications in many species of angiosperms are correlated with their specific pollination vector transferring the pollen, where specialized pollination mechanisms are evolved (Simpson, 2006). In pollination ecology, `pollination syndromes` can be defined as suites of flower traits that reflect convergent adaptations of flowers, in response to natural selection imposed by different animal species (Faegri & van der Pijl, 1979; Proctor et al., 1996). Similar pollinators, shared by many different plant species, may drive convergent evolution on plants to reflect simiral floral traits (Fenster et al. 2004). The concept claims that plant species specialize on specific groups of animals that exert similar selective pressure on floral traits (Fenster et al. 2004). These sets of floral traits include flower shape, size, colour, odour, reward type and amount, nectar composition and phenology.

The pollination syndromes concept was developed by Federico Delpino (1873-1874). The concept has been useful for understanding the plant-pollinator interactions and has played a central role in many reviews of others (Faegri and van der Pijl, 1979; Fenster et al. 2004; Proctor et al. 1996). Nearly all earlier studies on pollination biology were organized around this concept of syndromes for almost two centruies (Willmer, 2011).

However, the concept as providing a framework for plant-pollinator interactions is rather out of date (Ollerton et al. 2009). Various studies focused on generalization in pollination systems thus the correalation of floral traits with pollinators has been questioned (Waser et al., 1996).

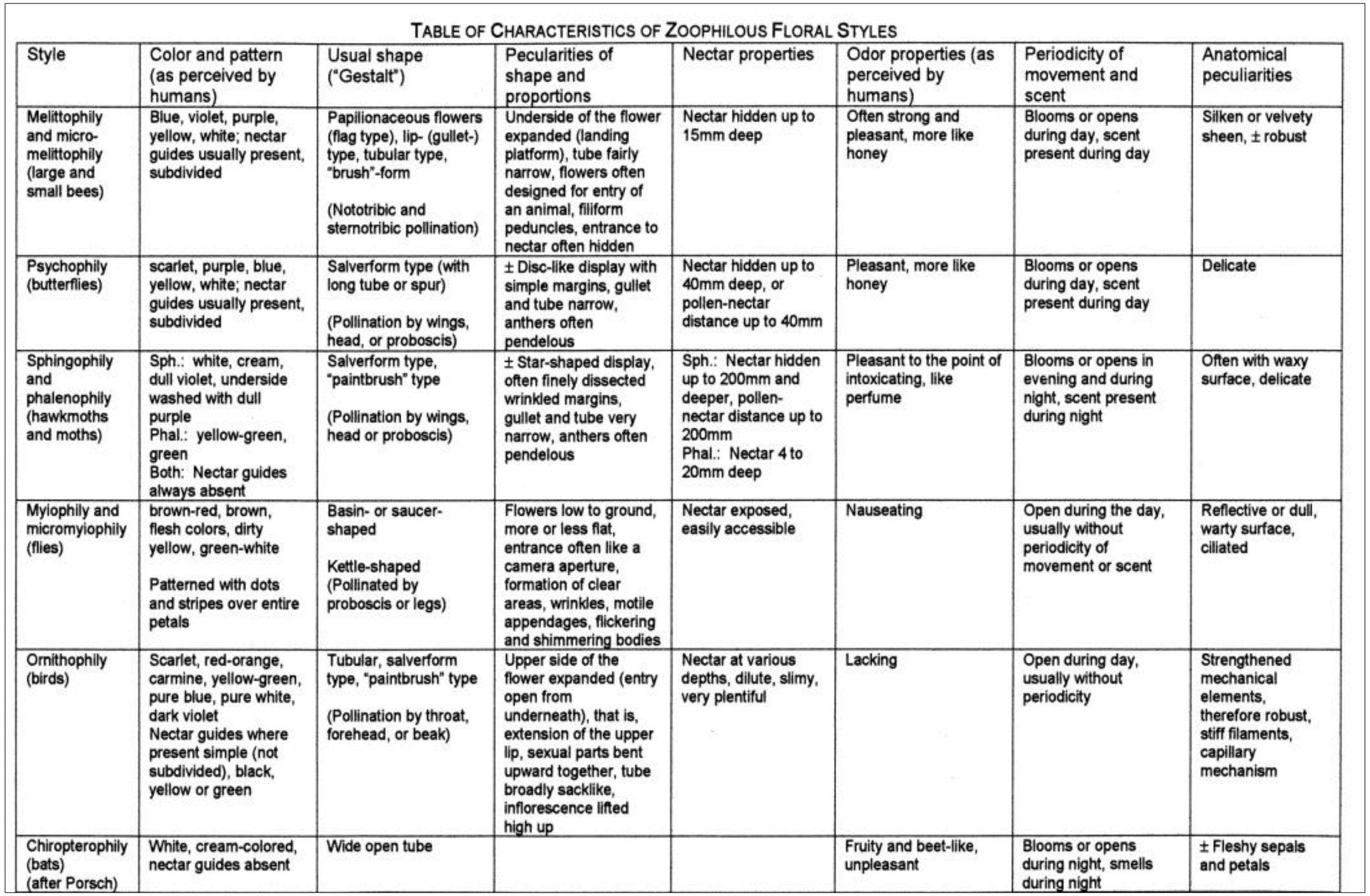


TABLE OF CHARACTERISTICS OF ZOOPHILOUS FLORAL STYLES

Style	Color and pattern (as perceived by humans)	Usual shape ("Gestalt")	Pecularities of shape and proportions	Nectar properties	Odor properties (as perceived by humans)	Periodicity of movement and scent	Anatomical peculiarities
Melittophily and micro-melittophily (large and small bees)	Blue, violet, purple, yellow, white; nectar guides usually present, subdivided	Papilionaceous flowers (flag type), lip- (gullet-) type, tubular type, "brush"-form (Nototribic and sternotribic pollination)	Underside of the flower expanded (landing platform), tube fairly narrow, flowers often designed for entry of an animal, filiform peduncles, entrance to nectar often hidden	Nectar hidden up to 15mm deep	Often strong and pleasant, more like honey	Blooms or opens during day, scent present during day	Silken or velvety sheen, ± robust
Psychophily (butterflies)	scarlet, purple, blue, yellow, white; nectar guides usually present, subdivided	Salverform type (with long tube or spur) (Pollination by wings, head, or proboscis)	± Disc-like display with simple margins, gullet and tube narrow, anthers often pendelous	Nectar hidden up to 40mm deep, or pollen-nectar distance up to 40mm	Pleasant, more like honey	Blooms or opens during day, scent present during day	Delicate
Sphingophily and phalenophily (hawkmoths and moths)	Sph.: white, cream, dull violet, underside washed with dull purple Phal.: yellow-green, green Both: Nectar guides always absent	Salverform type, "paintbrush" type (Pollination by wings, head or proboscis)	± Star-shaped display, often finely dissected wrinkled margins, gullet and tube very narrow, anthers often pendelous	Sph.: Nectar hidden up to 200mm and deeper, pollen-nectar distance up to 200mm Phal.: Nectar 4 to 20mm deep	Pleasant to the point of intoxicating, like perfume	Blooms or opens in evening and during night, scent present during night	Often with waxy surface, delicate
Myiophily and micromyiophily (flies)	brown-red, brown, flesh colors, dirty yellow, green-white Patterned with dots and stripes over entire petals	Basin- or saucer-shaped Kettle-shaped (Pollinated by proboscis or legs)	Flowers low to ground, more or less flat, entrance often like a camera aperture, formation of clear areas, wrinkles, motile appendages, flickering and shimmering bodies	Nectar exposed, easily accessible	Nauseating	Open during the day, usually without periodicity of movement or scent	Reflective or dull, warty surface, ciliated
Ornithophily (birds)	Scarlet, red-orange, carmine, yellow-green, pure blue, pure white, dark violet Nectar guides where present simple (not subdivided), black, yellow or green	Tubular, salverform type, "paintbrush" type (Pollination by throat, forehead, or beak)	Upper side of the flower expanded (entry open from underneath), that is, extension of the upper lip, sexual parts bent upward together, tube broadly sacklike, inflorescence lifted high up	Nectar at various depths, dilute, slimy, very plentiful	Lacking	Open during day, usually without periodicity	Strengthened mechanical elements, therefore robust, stiff filaments, capillary mechanism
Chiropterophily (bats) (after Porsch)	White, cream-colored, nectar guides absent	Wide open tube			Fruity and beet-like, unpleasant	Blooms or opens during night, smells during night	± Fleshy sepals and petals

Figure 10. A facsimile of the table from Vogel 1954, representing the precursor of the recent pollination syndomes (Waser, 2006)

1.9 Evolutionary Patterns in the Lamiaceae

The family Lamiaceae has long been associated with insects that facilitate the process of cross-pollination. Cross-pollination is supported by the floral and inflorescence architectures and breeding systems. Protandry and protogyny are typical in flowers of the Lamiaceae and separation of maturation of anthers and stigma requires a vector that is associated with the process of pollen transfer. Such mechanisms that have evolved in the Lamiaceae is called `indispensable link of pollen transport` (Macior, 1974).

Lamiaceaea and Scrophulariaceae both have two carpellate superior ovaries and bilabiate flowers; however, the latter produces many seeds. Lamiaceaea produce only four seeds per flower. Presumably, this reduction in seed number is offset by reinforcement of genetic variability due to outcrossing In addition, Lamiaceae flowers mature from the base and the flowering period is for several weeks, which increases outcrossing (Cruden, 1977).

Bilabiate flowers occur in many linages of the angiosperms. Bilabiate flower constructions protect the pollen againt pollen collecting bees; in addition render the pollination process more precisely (Westekamp and Classenbockhoff, 2007). The zygomorphic five-lobed sympetalous flowers of Lamiaceae are basically bisexual with four or two stamens. A nectary disc is at the base of the ovary. The structure of the zygomorphic flowers demands precision on the transfer of pollen from anthers to stigma, especially an intelligent pollinator (Heinrich, 1979). Most species from various genera in the family Lamiaceae (e.g. *Lamium, Stachys, Salvia*) have 2-lipped (bilabiate) flowers where nototribic pollination may occur (Harley, 2007).

Members of the family Lamiaceae, in which both nectar and pollen being the principal rewards, are pollinated by bees, birds, flies, wasps, butterflies and hawkmoths (Huck, 1992). Bees are by far the most frequent pollinators in the family (Vogel, 1954; Hedstrom, 1985; Dafni et al., 1988; Proctor and Yeo, 1972; Huck, 1987). The species with bilabiate flowers, in which the nectar is less accessible, tend to rely on fewer pollinator species (Harley et al., 2004). Many species in the family have corollas with coloured nectar-guides particularly on the lower lip, which suggest the close associations between bees and labiates (Harley et al. 2004, Figure 10, 11 and 12).

Sprengel (1793) was the first to discuss the interactions among insects and flowers in the Lamiaceae. His way of reasoning and methodology further influenced many others (Muller, 1883; Darwin, 1876; Correns, 1891; Knuth, 1895-1905) and pollination ecology in the Lamiaceae gained attention. In 20th century, Vogel (1954), Proctor & Yeo (1973), van der Pijl (1972), Faegri and van der Pijl (1979) presented work on pollination biology and syndromes in many genera of the family.

Many pollination biologists have documented observations on various genera of the Lamiaceae (Harley et al., 1971; Hedge, 1972; Hedstrom, 1985; Nilsson et al., 1985; Keller and Armbruster, 1989; Classen-Bockhoff et al., 2004; Wester and Classen-Bockhoff, 2006a, 2006; Wester and Classen-Bockhoff, 2007; Zhang et al., 2011; Celep et al., 2014).

Figure 11. Spots and lines on the lower lip of *Salvia blepharochlaena* Hedge & Hub.-Mor. and *Salvia recognita* Fisch. & C.A.Mey., an example of landing place and nectar guide for bees.

The studies on the self and cross pollination properties of genus *Lamium* showed that *Apis mellifera* (honeybee) and some *Bombus* (bumblebee) species are involved in the process of pollination of the genus and *Lamium* species are self-compatible plants serving as hosts for many insect species (Savchenko et al. 2001; Macior, 1978; Sönmez and Altan, 1992; Sıralı and Deveci, 2002; Sabuncu et al., 2002; Eltz, 2006). The development of cleistogamous flowers in some species of *Lamium* has been studied by various authors (Allard, 1944; Lord, 1979, 1982).

Recently, there are a few studies which particularly focused on the nectar production (Marina et al., 2004), nectar content and abundance (Sulborska et al., 2014) and altitudinal variations on floral traits (Hattori et al., 2015; Kuriya et al., 2015) of some members of the genus *Lamium*. Thus the pollination mechanism of the genus is worth studying.

Figure 12. Spots and lines on the lower lip and flower entrance of *Lamium purpureum* L., an example of landing place and nectar guide for insects.

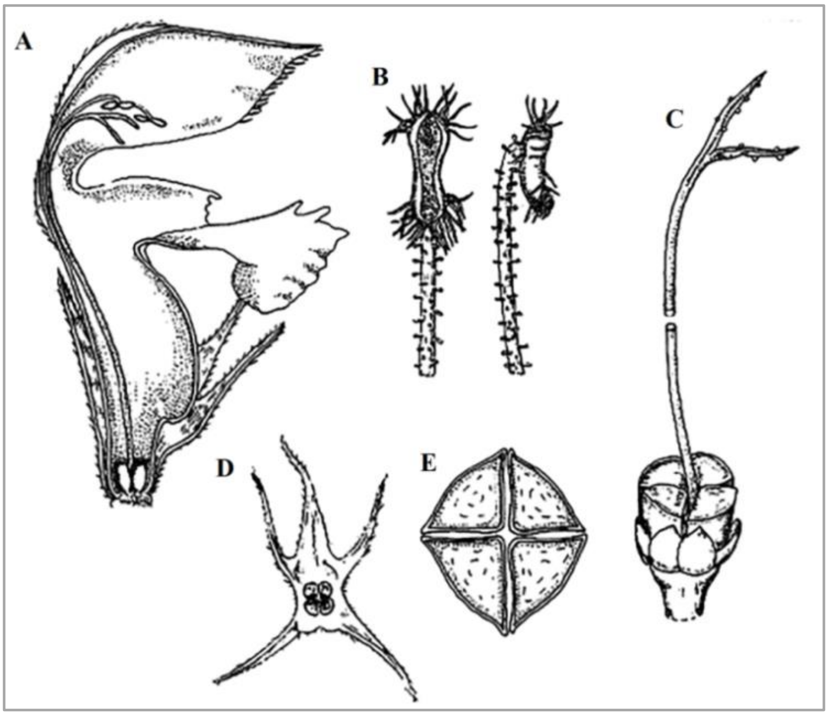


Figure 13. *Lamium album* (white dead-nettle) flower. (A) longitudinal section of the bisexual flower with its 2-lipped corolla surrounded at the base by the tubular 5-lobed calyx. (B) Anthers, (C) Style, (D) Calyx, (E) Four-lobed ovary.

1.10 Objectives of the Study

The taxonomic problems are defined for the genus *Lamium*. It is important to gather as many characters as possible to solve the taxonomic problems in the genus. Therefore, main objectives of this study are;

- To describe *anatomical* features of vegetative organs (i.e. roots, stems, leaf blades and petioles) of the genus *Lamium* and their taxonomic significance.

- To present a detailed analysis of the micromorphological characters of vegetative and reproductive organs of the genus *Lamium* and their diagnostic values.

- To present a detailed analysis of palynological characteristics of the genus *Lamium* and their taxonomic significance.

- To present a detailed analysis of trichome micromorphological characteristics of the genus *Lamium* and their taxonomic significance.

- To explain the phytochoria of the genus *Lamium* in Turkey (i.e. distribution, phytogeography, phenology and altitudinal range of each taxon).

- To explain the pollination mechanisms of two sympatric species (*Lamium villosifolium* and *L. album* subsp. *crinitum*), particularly to determine the plant-pollinator interactions, flower-pollinator fitness and pollinator preferences.

CHAPTER 2

MATERIAL AND METHODS

2.1 Plant Material

All of the plant material examined in this study were collected in the project called “The Taxonomic Revision of Genus *Lamium* in Turkey” (Project No: 112-T-13) which was funded by The Scientific and Research Council of Turkey (TUBITAK) between September 2012-September 2015. During the project, many samples were collected from all over Turkey and these samples are stored as herbarium material in Gazi University. In addition, ANK, BM, E and K herbaria were visited to investigate various specimens. Plant materials from particular taxa were gathered for palynological work from BM, E and K herbaria. The specimens were cross-checked with the keys provided by Mill (1982), Mennema (1989) and the *Lamium* accounts given in *Flora Orientalis* (Bentham, 1848) and other various floras (Boissier, 1879; Briquet, 1897).

2.2 Anatomical Methods

Anatomical investigations were carried out with fresh specimens kept in 70% ethanol. The paraffin wax method was applied for obtaining the cross-sections of the various parts of the plant specimens, such as; roots, stems, leaves and petioles. the specimens were embedded in paraffin and were sectioned at 10-12-15 micrometer thickness, with a Leica RM212RT microtome. The sections were stained with safranin-fast green, with some modifications due to the different staining times plant specimens. The sections were then mounted on slides with Entellan. All slides were investigated and photographed with a Leica DM1000 light microscope. All of the measurements were performed using Carnoy 2.0 (Johansen, 1944; Metcalfe & Chalk; Schols et al. 2002).

2.3 Palynological Methods

Pollen grains of *Lamium* were studied by light microscopy (LM) and scanning electron microscopy (SEM). Standard acetolysis method (Erdtman, 1960) destroys the colpus membranes, effecting the natural pollen shape and size (Demissew and Harley, 1992; Moon et al. 2008a, b). In order to retain the natural form of the pollen grains, the Wodehouse (1935) method was used. Pollen grains were treated with 70% ethanol for the removal of oily substances for light microscopy. Then they were embedded in glycerine jelly stained with basic fuchsin. The investigations and measurements of pollen graines were conducted with a Leica light microscope. Pollen grains were observed and micrographs were obtained at maginifications ranging from x20 to x100.

For SEM, pollen grains were placed directly to stubs with double-sided adhesive tape and they were coated with gold using a Hummer VII gold coating apparatus. Pollen grains were observed and micrographs were obtained at maginifications ranging from x1000 to x18,000 with a JEOL-6060 scanning electron microscope at TPAO (Turkish Petroleum Anonymn Coorporation, Ankara) to determine the exine ornamentation.

Polar axis (P), equatorial axis (E), colpus length (Clg), colpus width (Clt), mesocolpium thickness, apocolpium diameter, exine thickness (Ex) and intine thickness (In) of 30 fully developed grains were measured. The P/E ratios were calculated. All of the measurements were performed using Carnoy 2.0 (Schols et al. 2002). The pollen terminology follows Faegri and Iversen (1975), Walker and Doyle (1975), Abu-Asab and Cantino (1994), Halbritter et al. (2007) and Punt et al. (2007).

2.4 Trichome Micromorphology Methods

Trichomes were obtained from stems, leaves and calyces and studied with a stereo microscope. For the scanning electron microscopy (SEM), small pieces of stems, leaves and calyces were fixed on aluminum stubs using double-sided adhesive, and then were coated with gold using a Hummer VII gold coating apparatus. The SEM micrographs were taken with a JEOL-6060 scanning electron microscope at TPAO (Turkish Petroleum Anonymn Coorporation, Ankara) The type of indumentum was described and classified. The general classification scheme and the terminology follow Roe (1971), Cantino (1990), as well as Navarro and El Oualidi (2000).

2.5 Distribution and Ecological Data of the *Lamium* species

3 years of field investigations were conducted to gather the locality, distributional, phenological and altitudinal information on the members of the genus *Lamium*. Global Positioning System (GPS) is used for collecting the locality and geographical coordinates of the studied taxa. The grid system 2^ox2^o of Davis (1965-1985) is used to produce distribution maps of all taxa.

2.6 Pollination Biology Methods

Two sympatric *Lamium* species (*Lamium villosifolium* and *Lamium album* subsp. *crinitum*) growing in Isik Mountain, Kizilcahamam area were chosen for pollination biology observations. Two *Lamium* species differ in their floral morphology. Detailed information about the floral morphology and phenology of the *Lamium* species, as well as the techniques needed for pollinator observations are given in the following subcaptions. Herbarium vouchers and flower samples fixed in 70% ethanol are deposited at Middle East Technical University, Plant Systematics Lab.

2.6.1 *Lamium* species

- *Lamium villosifolium*

It is an endemic, stoloniferous perennial species. The species is a Euro-Siberian element. The bilabiate (2 lipped) flowers (corolla) are magenta to purplish. The verticillasters are (1-)2-4(-5), (4-)6-8- flowered. Upper lip of the corolla is entire and there is a hairy annulus at the base of the corolla tube. The flowering period is between April and July. The species is distributed at elevations between 1500-1800 meters.

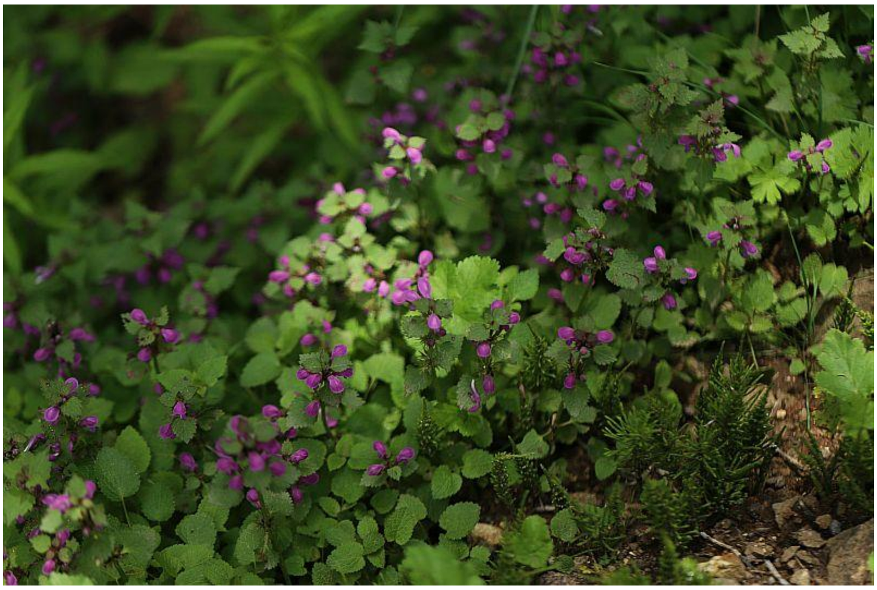


Figure 14. *Lamium villosifolium* in Isik Mountain

- *Lamium album* subsp. *crinitum*

It is a stoloniferous perennial species. The species is an Irano-Turanian element. The bilabiate flowers are white. The verticillasters are 2-8, 8-10- flowered. Upper lip of the corolla is entire and there is a hairy annulus at the base of the corolla tube. The flowering period is between April and September. The species is distributed at elevations between 1500-2400 meters.

2.6.2 Study Sites

Field observations and investigations were conducted in Isik Mountain, Kizilcahamam from 01/06 to 01/07 in 2014 and 15/06 to 15/07 in 2015. The observations in 2015 started more or less two weeks later than the previous year, due to the heavy rainfall in Ankara. The *Lamium* species were investigated at three natural populations in Isik mountain region, starting from an elevation of 1580 m to the mountain summit ca. 2062 m (Table 2). The distance between the first plot and the summit area was ca. 4 km.

Figure 15. Study site; *L. villosifolium* and *L. album* subsp. *crinitum* in Isik Mountain

3.6.3 Morphometric Measurements

After succesfull observations on plant populations, plant materials were collected and the internal structure and morphology of their flowers were investigated. From a number of longitudinal sections of flowers, morphological measurements were made using Leica DM 1000 binoculer light microscope with a Leica DFC 280 camera. For further analysis, fresh flowers and buds were fixed in 70% ethanol.

Floral structures were measured morphometrically from various characters such as; (b) flower length, (c) length of corolla tube, (d) flower entrance – dH, horizontal; dV, vertical-, (e) distance flower entrance to nectar cover, (f) distance thecae to nectar cover, (g) length of long anther, (h) length of short anther, (i) theca length, (j) style in natural position. At least, 30 fresh flowers were measured from each *Lamium* species. Their minimum, maximum range, mean and standard deviations were calculated. The pollinators were captured and then;

- They were investigated for the pollen deposition sites with Leica DM 1000 binoculer light microscope with a Leica DFC 280 camera.
- They were measured morphometrically on various characters; such as, (a) head height, (b) length of maxillae, (c) glossa length, (d) maximum head width, (e) head width below eyes, (f) head length (f1: anterior head part, f2: posterior head part), (g) thorax (g1: anterior thorax, g2: posterior thorax), (h) abdomen (Figure 16).

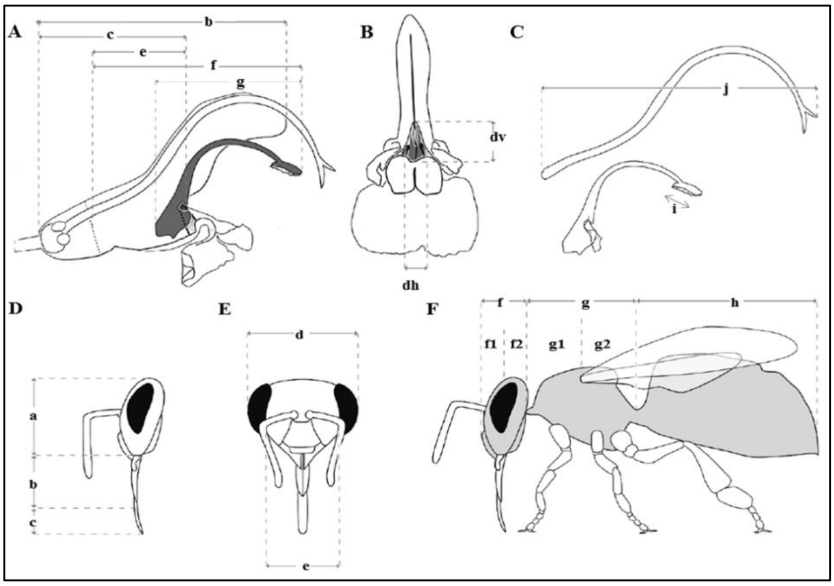


Figure 16. Flower and insect morphometry. **(**A–C) Measurements on *Lamium* flowers. (A) Longitudinal section of a flower. (B) Front view. (C) Shape of stamen and style in natural position. (D–F) Measurements on insects. (D, E) Side and front view head, (F) side view of insect, (Figure from Celep et al., 2014).

2.6.4 Pollinator Observations

In 2014, flower visitors were observed two times in a week, starting at 8.30 am to 17.00 pm. In 2015, the weather conditions were different from the previous year however; the observations were made whenever weather was suitable. It was evident that pollinator activity was affected with the heavy rainfall in the area.

Insect species were identified by Dr. Fatih Dikmen, Istanbul University. Since this study focuses on the legitimate flower visits, the insects were defined as pollinators if they got into contact with pollen and stigma. It is important to document pollinator`s behavior, photographs and video camera recordings were produced with a Canon 6 D full frame camera + 100 mm macro lens, (Canon, Tokyo, Japan). In this study, single visit experiments allowing quantification of pollinator effectiveness (Ne'eman et al., 2010) were not conducted. Instead, pollen transfer and behavior of the pollinators are quantified and compared as their relative pollinator efficiency on the *Lamium* species.

For the pollination observations, video recordings and photographs were analyzed for each of the visitor/pollinator species. In a defined area of *Lamium* populations;

- We recorded the frequency of each pollinator species while observing the visitation of other insect visitors.
- We recorded the handling time of each pollinator per flower visit, i.e. the duration from landing on the lower lip to leaving the flower after absorbing nectar.
- For analyzing the success of each pollinator, the percentage of visits with contact of pollen and/or stigma was recorded.
- Macro lens, close-up photographs and video recordings provided precise information about the insect visits whether they are legitimate or not.

- Based on 44 videos covering 84 minutes 33 seconds, handling time, duration of stay at an infloresscense and number of flowers visited/inflorescence of the pollinators were calculated. Captured bees were examined with a dissecting microscope to verify the pollen deposition site and to quantify the pollen load on insect`s body.

2.6.5 Statistics

Statistical analyses — One-way ANOVA, followed by Tukey's studentized range test (P < 0.05), was used to test for differences in handling time, number of visited flowers per inflorescence, duration of stay at an inflorescence and pollen load among the main pollinator species (five bee species: *Apis mellifera*, *Bombus argillaceus*, *Bombus lucorum*, *Bombus pascuorum*, *Bombus lapidarius*). Minitab (version 17, Minitab, State College, Pennsylvania, USA) was used for analyzing the data.

CHAPTER 3

3. RESULTS AND DISCUSSION

3.1 Final Taxonomic Treatment Results;

The taxonomic result of 3 years-field work is represented below (Table 2). The infrageneric classification of Mill (1982) and Mennema (1989) is compared to the taxonomic revision results of ours (Table 2). The characteristics and usefulness of anatomical and micromorphological characters are represented in the following subchapters.

Table 2. Final taxonomic treatment of the genus *Lamium* and previous infrageneric classifications of Mill (1982) and Mennema (1989)

Taxon and species number			**Mill (1982), Flora of Turkey**	**Mennema (1988), Monograph**	**Final Taxonomic treatment results**
1	1	_Sect. Lamium_	*_Lamium lycium_	_L. garganicum_ subsp. _striatum_ var. _striatum_	*_Lamium lycium_
2	2		*_L. cariense_		*_L. cariense_
3	3		*_L. pisidicum_		_L. garganicum_ subsp. _striatum_
4	4		*_L. tenuiflorum_		
6	6		_L. garganicum_ subsp. _striatum_		
7			_L. garganicum_ subsp. _reniforme_		
8			*_L. garganicum_ subsp. _nepetifolium_		
10			_L. garganicum_ subsp. _lasioclades_		_L. garganicum_ subsp. _lasioclades_
11			_L. garganicum_ subsp. _rectum_		_L. garganicum_ subsp. _rectum_
12			*_L. garganicum_ subsp. _pulchrum_		
13			_L. garganicum_ subsp. _laevigatum_	_L. garganicum_ subsp. _garganicum_	_L. garganicum_ subsp. _laevigatum_
			*_L. veronicifolium_		
14	7		*_L. microphyllum_	_L. garganicum_ subsp. _striatum_ var. _microphyllum_	*_L. microphyllum_
15	8		*_L. cymbalarifolium_		*_L. cymbalarifolium_
16	9		*_L. sandrasicum_		*_L. sandrasicum_
17	10		_L. armenum_ subsp. _armenum_	_L. garganicum_ subsp. _striatum_ var. _armenum_	*_L. armenum_ subsp. _armenum_

Table 2 (cont`d)

Taxon and species number			**Mill (1982), Flora of Turkey**	**Mennema (1988), Monograf**	**Final Taxonomic treatment results**
18		*Sect. Lamium*	**L. armenum* subsp. *sintenisii*		**L. armenum* subsp. *sintenisii*
19	11		*L. ehrenbergii*	*L. purpureum* var. *ehrenbergii* *L. purpureum* var. *purpureum*	*L. ehrenbergii*
20	12		*L. purpureum* var. *purpureum*		*L. purpureum*
21			**L. purpureum* var. *aznavourii*		
22	13	*Sect.Amplexicaule*	**L. eriocephalum* subsp. *eriocephalum*	*L. eriocephalum*	**L. eriocephalum* subsp. *eriocephalum*
23			**L. eriocephalum* subsp. *glandulosidens*		**L. eriocephalum* subsp. *glandulosidens*
24	14		*L. amplexicaule*	*L. amplexicaule var. amplexicaule*	*L. amplexicaule* subsp. *amplexicaule* var. *amplexicaule*
25	15		*L. aleppicum*	*L. amplexicaule var. aleppicum*	*L. amplexicaule* subsp. *amplexicaule* var. *aleppicum*
					***L. amplexicaule** **subsp. *vanense* Fırat & Celep**
26	16		*L. macrodon*	*L. macrodon*	*L. macrodon*
27	17	*Sect. Lamiotypus*	*L. maculatum* var. *maculatum*	*L. maculatum*	*L. maculatum*
28			**L. gundelsheimeri*		
29	18		*L. truncatum*		
30	19		**L. maculatum* var. *villosifolium*		**L. villosifolium*

Table 2 (cont`d)

Taxon and species number			Mill (1982), Flora of Turkey	Mennema (1988), Monograf	Final Taxonomic treatment results
31	20	_Sect. Lamiotypus_	_L. album_	subsp. _album_	_L. album_ subsp. _album_
32	21		_L. crinitum_	subsp. _crinitum_	_L. album_ subsp. _crinitum_
33	22		*_L. leucolophum_		
34	23		_L. tomentosum_ var. _hakkariense_	_L. tomentosum_ var. _tomentosum_	_L. tomentosum_ var. _tomentosum_
35			_L. tomentosum_ var. _tomentosum_		
36			_L. tomentosum_ var. _filicaule_		_L. tomentosum_ var. _filicaule_
37			_L. tomentosum_ var. _alpestre_		_L. tomentosum_ var. _alpestre_
38	24		*_L. sulfureum_		
39	25		_L. moschatum_ var. _moschatum_	_L. moschatum_ subsp. _moschatum_	_L. moschatum_
40			_L. moschatum_ var. _rhodium_		
41			_L. moschatum_ var. _micranthum_	_L. moschatum_ subsp. _micranthum_	**_L. micranthum_ (Boiss.) Celep**
42	26		*_L. ponticum_		*_L. ponticum_ subsp. _ponticum_
					*L. ponticum subsp. anatolicum Celep
43	27		*_L. galactophyllum_	_L. galactophyllum_	*_L. galactophyllum_
44	28	_NI_	*_L. tschorochense_	_Published later_	*_L. tschorochense_
45	29	_NI_	*_L. vreemanii_	_Published later_	_L. album_ subsp. _crinitium_
46	30	_NI_	_Lamium orientale_	_NI_	*_Lamium orientale_

Table 2 (cont`d)

Taxon and species number			**Mill (1982), Flora of Turkey**	**Mennema (1988), Monograf**	**Final Taxonomic treatment results**
47	31	*NI*	*Lamium multifidum*	*NI*	*Lamium multifidum*
				NI	***_Lamium bilgilii_ Celep & Duran**
				NI	***_Lamium cappadocicum_ Celep & Karaer**
48	32	Subg. *Galeobdolon*	*Galeobdolon luteum*	*Lamium galeobdolon*	Genus *Galeobdolon*

NI; not indicated, new taxa presented in the taxonomic revision of the genus *Lamium* (Celep et al. 2015, unpublished data) are written in bold. * indicates the endemic taxa.

3.2. Ecology, Endemism and Phytogeography of the Species

In this subchapter, the distribution, phenology, altitudinal range and phytogeographical information of the *Lamium* species are given. Pictures showing the general floral characteristics of the *Lamium* species are given (Figs. 17-25). The phytogeographical regions (Table 3), flowering period (Table 4) and altitudinal gradient (Table 5) of the *Lamium* species are represented.

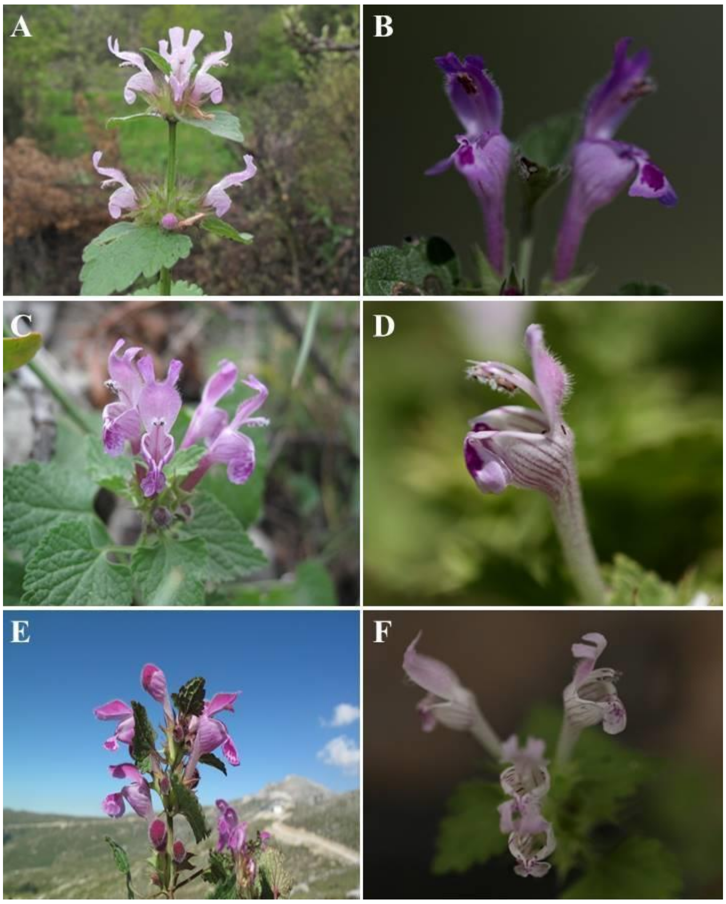


Figure 17. Photographs of; A: *L. lycium* B: *L. cariense* C: *L. garganicum* subsp. *striatum* (*L. pisidicum*) D: *L. garganicum* subsp. *striatum* (*L. tenuiflorum*) E: *L. garganicum* subsp. *laevigatum* (*L. veronicifolium*) F: *L. garganicum* subsp. *striatum* (*L. garganicum* subsp. *reniforme)*

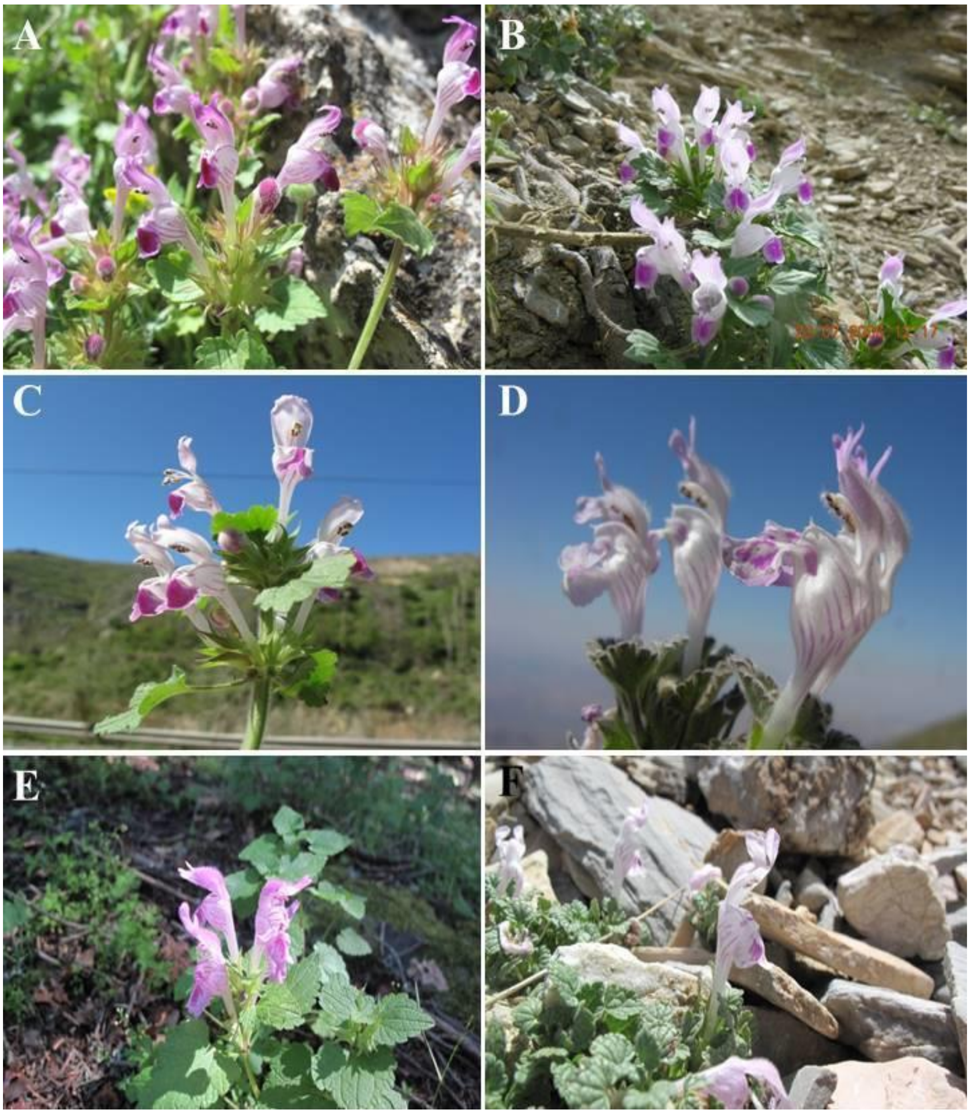


Figure 18. Photographs of A: *L. garganicum* subsp. *striatum* (*L. garganicum* subsp. *nepetifolium*) B: *L. garganicum* subsp. *rectum* C: *L. garganicum* subsp. *lasioclades* D: *L. garganicum* subsp. *rectum* (*L. garganicum* subsp. *pulchrum*) E: *L. garganicum* subsp. *laevigatum* F: *L. microphyllum*

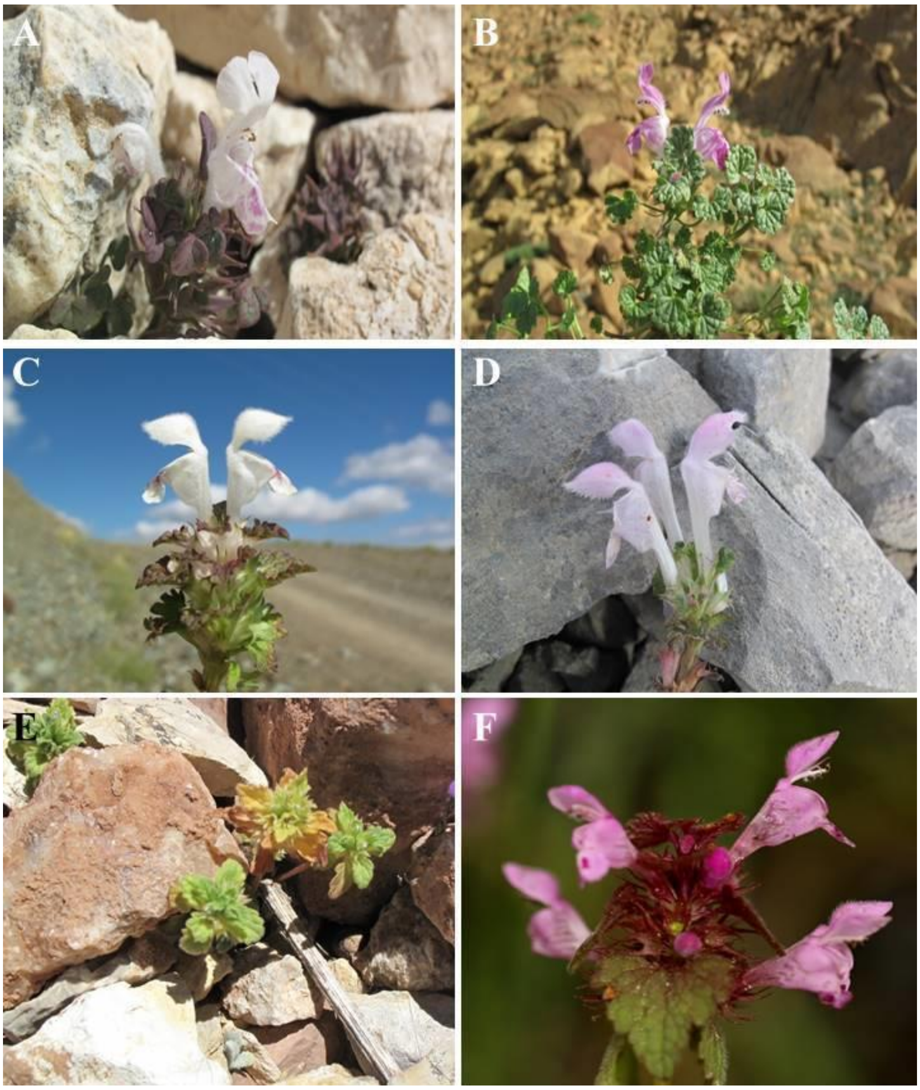


Figure 19. Photographs of; A: *L. cymbalarifolium* B: *L. sandrasicum* C: *L. armenum* subsp. *armenum* D: *L. armenum* subsp. *sintenisii* E: *L. ehrenbergii* F: *L. purpureum* (*L. purpureum* var. *purpureum*)

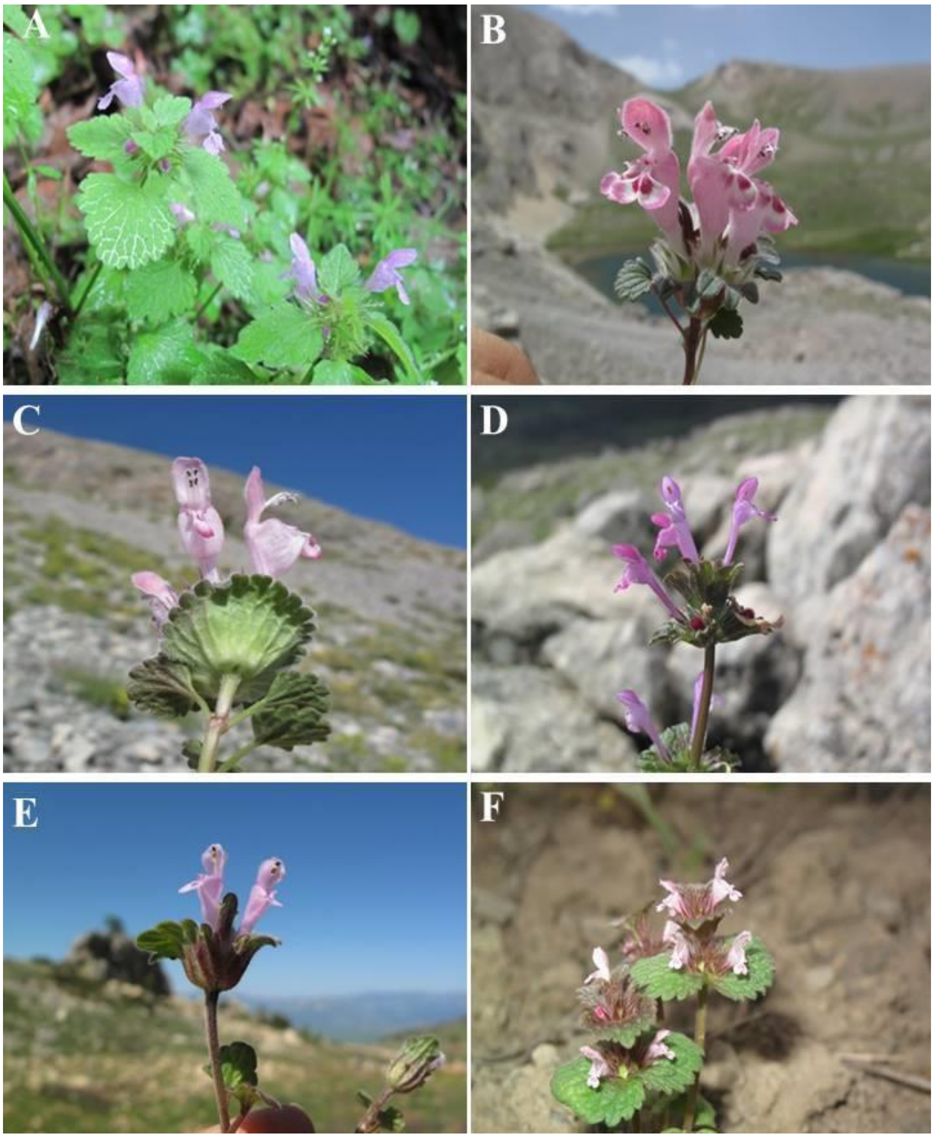


Figure 20. Photographs of; A: *L. purpureum* (*L. purpureum* var. *aznavouri*) B: *L. eriocephalum* subsp. *eriocephalum* C: *L. eriocephalum* subsp. *glandulosidens* D: *L. amplexicaule* subsp. *amplexicaule* var. *amplexicaule* (*L. amplexicaule*) E: *L. amplexicaule* subsp. *amplexicaule* var. *aleppicum* (*L. aleppicum*) F: *L. macrodon*

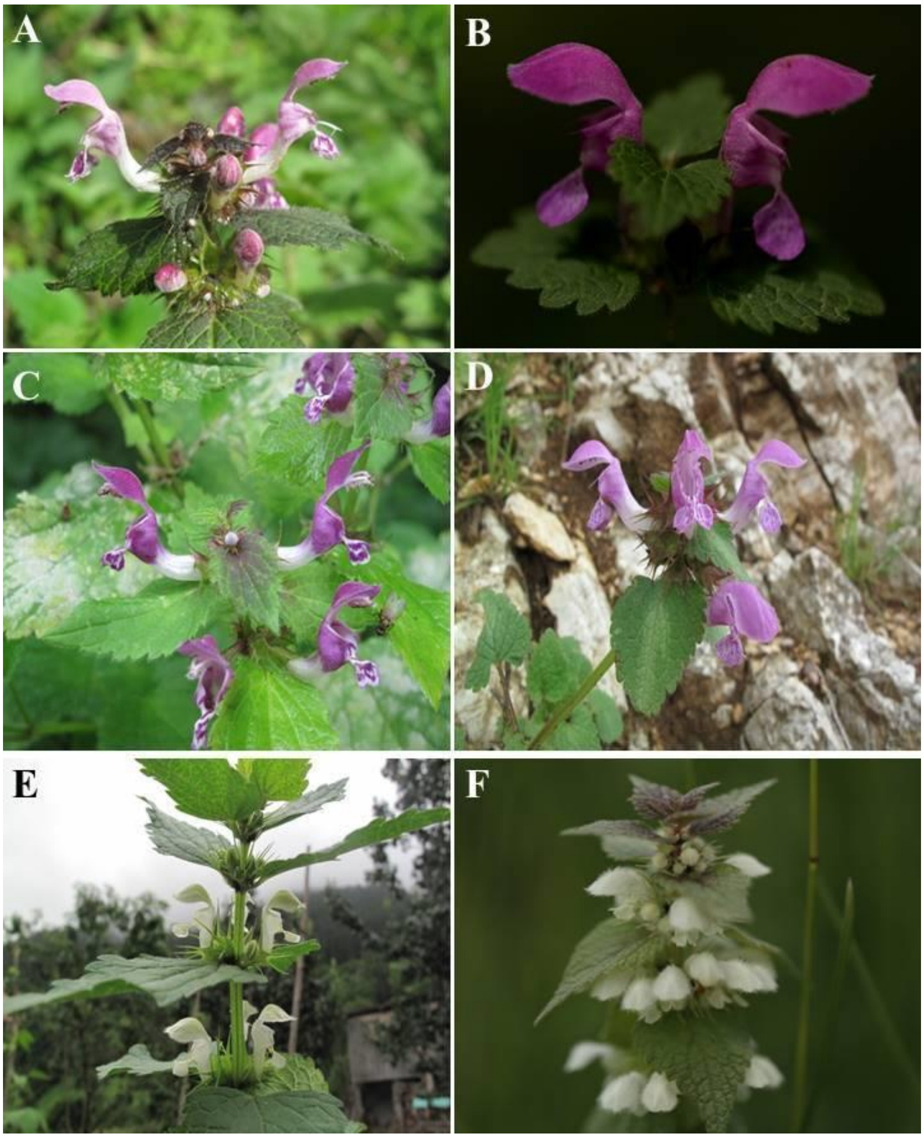


Figure 21. Photographs of; A: *L. maculatum* (*L. maculatum* subsp. *maculatum*) B: *L. villosifolium* (*L. maculatum* subsp. *villosifolium*) C: *L. maculatum* (*L. gundelsheimeri*) D: *L. maculatum* (*L. truncatum*) E: *L. album* subsp. *album* F: *L. album* subsp. *crinitum* (*L. crinitum*)

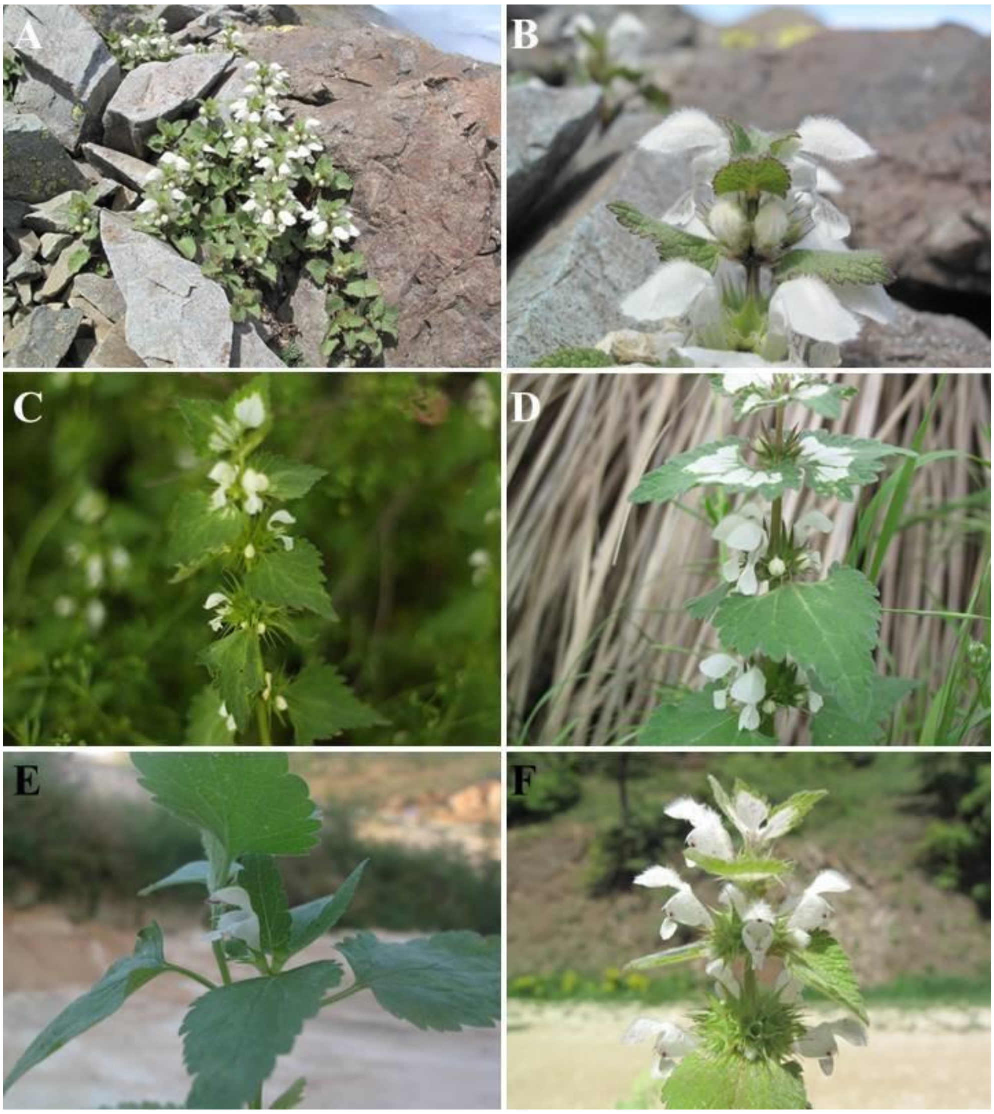


Figure 22. Photographs of; A: *L. tomentosum* var. *tomentosum* B: *L. tomentosum* var. *alpestre* (*L. sulfureum*) C: *L. moschatum* (*L. moshatum* var. *moshatum*) D: *L. moschatum* (*L. moshatum* var. *rhodium*) E: *L. micranthum* F: *L. ponticum* subsp. *ponticum* (*L. ponticum*)

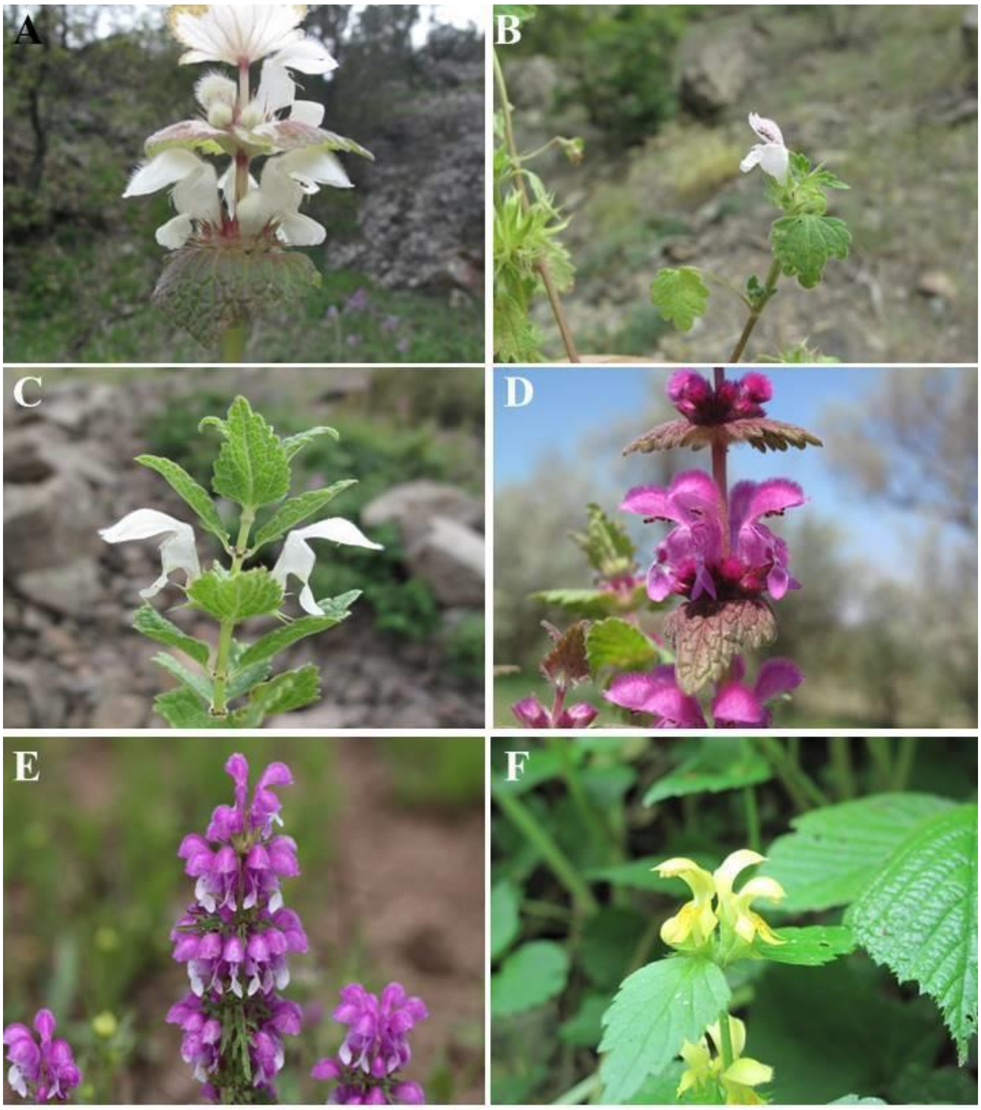


Figure 23. Photographs of; A: *L. galactophyllum* B: *L. tschoroense* C: *L. album* subsp. *crinitum* (*L. vremanii*) D: *L. orientale* E: *L. multifidum* F: Genus *Galeobdolon* (*L. galeobdolon* subsp. *montanum*)

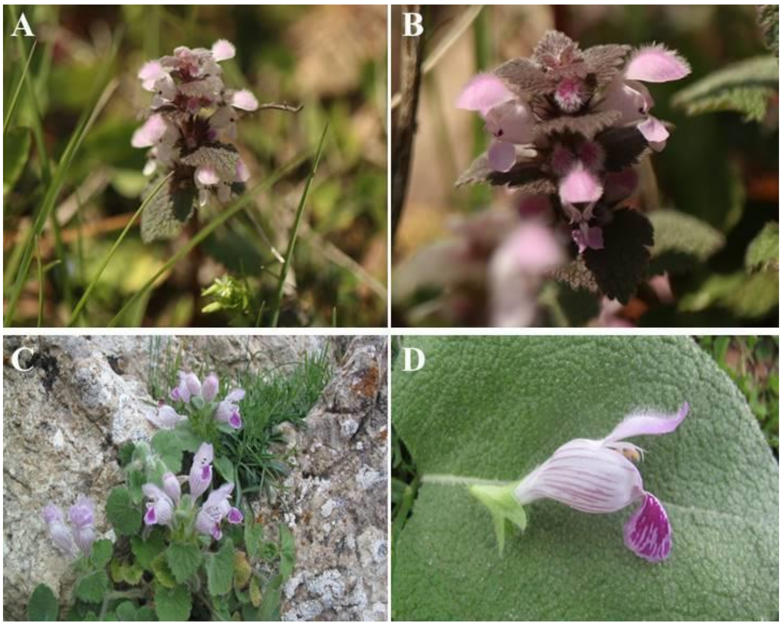


Figure 24. Photographs of; A, B: *L. ponticum* subsp. *anatolicum* Celep C, D: *Lamium bilgilii* Celep & Duran

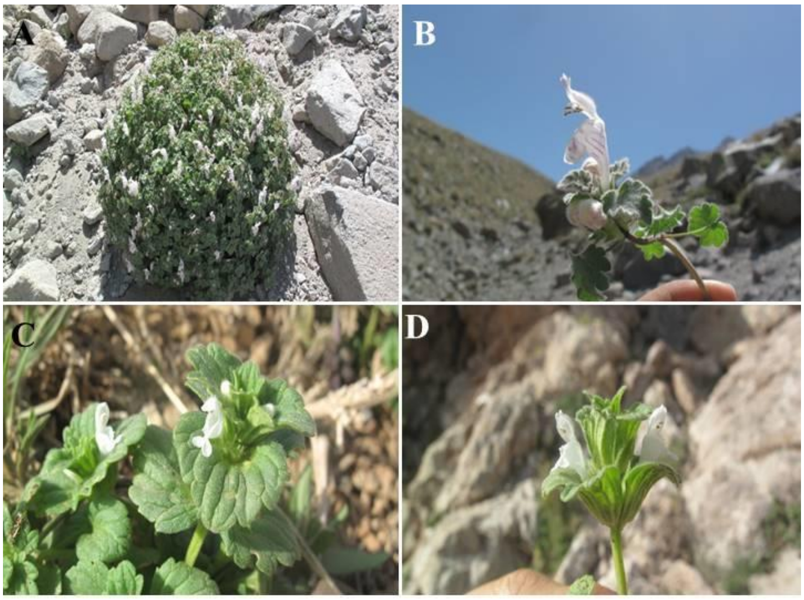


Figure 25. Photographs of; A, B: *Lamium capadocicum* Celep & Karaer C, D: *L. amplexicaule* subsp. *vanense* Fırat & Celep

3.2.1 Endemism and Phytogeography

The results indicated that, there are 36 taxa (25 species) in Turkey and 18 taxa are endemic. Thus the endemism ratio is indicated as 50%. The distribution of phytogeographical regions of 36 taxa is as follows; 16 taxa are distributed in the Irano-Turanian (Ir-Tur.), 10 taxa are distributed in the Mediterranean (Medit.) and 10 taxa are distributed in Euro-Siberian (Eu-Sib.) phytogeographical region (Table 3).

8 endemic taxa (*L. lycium*, *L. cariense*, *L. microphyllum*, *L. cymbalariifolium*, *L. sandrasicum*, *L. eriocephalum* subsp. *eriocephalum*, *L. eriocephalum* subsp. *glandulosidens* and *L. bilgilii*) are Mediterranean, 5 endemic taxa (*L. armenum* subsp. *armenum*, *L. amplexicaule* subsp. *vanense*, *L. galactophyllum*, *L. orientale* and *L. capadocicum*) are Irano-Turanian and 5 endemic taxa (*L. armenum* subsp. *sintenisii*, *L. villosifolium*, *L. ponticum* subsp. *ponticum*, *L. ponticum* subsp. *anatolicum* and *L. tschorochense*) are Euro-Siberian element. Most of the endemic species are distributed in alpine mountain regions and are in bloom in between May and July.

Table 3. Phytogeographical Regions of the *Lamium* species (Endemic taxa in bold).

	Medit	**Ir-Tur**	**Eu-Sib**
L. lycium	🟨		
L. cariense	🟨		
L. garganicum subsp. *striatum*		🟩	
L .garganicum subsp. *lasioclades*		🟩	
L .garganicum subsp. *rectum*		🟩	
L. garganicum subsp. *laevigatum*			🟦
L. microphyllum	🟨		
L. cymbalariifolium	🟨		
L. sandrasicum	🟨		
L. armenum **subsp.** ***armenum***		🟩	
L. armenum **subsp.** ***sintenisii***			🟦
L. ehrenbergii		🟩	
L. purpureum			🟦
L. eriocephalum **subsp.** ***eriocephalum***	🟨		
L. eriocephalum **subsp.** ***glandulosidens***	🟨		
L. amplexicaule subsp. *amplexicaule var. amplexicaule*			🟦
L. amplexicaule subsp. *amplexicaule* var. *aleppicum*		🟩	
L. amplexicaule **subsp.** ***vanense***		🟩	
L. macrodon		🟩	
L. maculatum			🟦
L. villosifolium			🟦
L. album subsp. *album*			🟦
L. album subsp. *crinitum*		🟩	
L. tomentosum var. *tomentosum*		🟩	
L. tomentosum var. *alpestre*		🟩	
L. moschatum	🟨		
L. micranthum	🟨		
L. ponticum **subsp.** ***ponticum***			🟦
L. ponticum **subsp.** ***anatolicum***			🟦
L. galactophyllum		🟩	
L. tschorochense			🟦
L. orientale		🟩	
L. multifidum		🟩	
L. bilgilii	🟨		
L. capadocicum		🟩	

Endemic taxa in bold

3.2.2 Phenology and Altitudinal Range of the *Lamium* Species

The species stars to blossom in January-February in coastal regions of Turkey. *Lamium purpureum* and *L. amplexicaule* can be examples of earliest blooming species. Especially the species in Mediterranean phytogeographical region (e.g. *Lamium lycium* and *L. cariense*), start to bloom in February. The period between April and July is the highest blooming period for the Lamium species. The species adapted to higher altitudes (e.g. *Lamium eriocephalum*, *L. cymbalarifolium*, *L. microphyllum*, *L. cariense*, *L. armenum* ve *L. tomentosum*) are in full bloom especially between June-August (Table 4 and 5).

The distribution of the *Lamium* species in terms of altitude is quite remarkable, starting from elevations close to sea level to ca. 3700 meters. Generally, endemic species are distributed at mid (600-1800 meters) and high (1800-3700 meters) elevations. Especially, *L. microphyllum*, *L. cymbalarifolium* and *L. sandrasicum*, which are morphologically very similar, are distributed and localized in the Southwest Mediterranean mountain tops (Table 5). *Lamium eriocephalum* subsp. *eriocephalum* and *L. eriocephalum* subsp. *glandulosidens* are distributed across the Aladag-Bolkar Mountain to Dedegöl Mountain, Isparta, and Geyik Mountain, Antalya at high elevations. In central Anatolia, the new endemic species *L. cappadocicum* is quite remarkable and is distributed in Hasan Mountain, Aksaray at high elevations. In Blacksea region, *L. armenum* subsp. *armenum* ve *L. armenum* subsp. *sintenisii* are the endemic species adapted to high elevations (Table 5).

Lamium amplexicaule and *L. purpureum* are distributed at elevations starting from sea level up to 1600 meters. The new taxon *L. amplexicaule* subsp. *vanense* is a remarkable subspecies, distributed at elevations higher than 2700 meters (Table 5).

Table 4. Phenology of the *Lamium* species (Endemic taxa in bold, months are indicated in numbers from 1 to 10- January to October).

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
L. lycium		■	■	■	■	■				
L. cariense		■	■	■	■	■	■			
L. garganicum subsp. *striatum*		■	■	■	■	■	■	■	■	
L .garganicum subsp. *lasioclades*				■	■	■	■			
L .garganicum subsp. *rectum*					■	■	■			
L. garganicum subsp. *laevigatum*				■	■	■	■			
L. microphyllum						■	■	■		
L. cymbalariifolium						■	■	■		
L. sandrasicum						■	■	■		
L. armenum subsp. _armenum_						■	■	■		
L. armenum subsp. _sintenisii_						■	■	■		
L. ehrenbergii			■	■	■					
L. purpureum	■	■	■	■	■	■	■			
L. eriocephalum subsp. _eriocephalum_						■	■	■		
L .eriocephalum subsp. _glandulosidens_						■	■	■		
L. amplexicaule subsp. *amplexicaule* var. *amplexicaule*	■	■	■	■	■	■	■	■		
L. amplexicaule subsp. *amplexicaule* var. *aleppicum*				■	■	■				
L. amplexicaule subsp. _vanense_				■	■					
L. macrodon			■	■	■	■	■			
L. maculatum			■	■	■	■	■			
L. villosifolium				■	■	■	■			
L. album subsp. *album*				■	■	■	■	■	■	
L. album subsp. *crinitum*				■	■	■	■	■	■	

Table 4 (cont`d)

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
L. tomentosum var. *tomentosum*						🟨	🟨	🟨		
L. tomentosum var. *alpestre*						🟨	🟨	🟨		
L. moschatum		🟨	🟨	🟨	🟨					
L. micranthum			🟨	🟨	🟨	🟨				
L. ponticum* subsp. *ponticum				🟨	🟨					
L. ponticum* subsp. *anatolicum				🟨	🟨					
L. galactophyllum					🟨	🟨				
L. tschorochense				🟨	🟨					
L. orientale					🟨	🟨	🟨			
L. multifidum						🟨	🟨			
L. bilgilii						🟨	🟨			
L. capadocicum						🟨	🟨	🟨		

Endemic taxa in bold

Table 5. Altitudinal gradient of the *Lamium* species.

	0-300	300-600	601-900	901-1200	1201-1500	1501-1800	1801-2100	2101-2400	2401-
L. lycium			🟨	🟨	🟨	🟨	🟨		
L. cariense			🟨	🟨	🟨	🟨	🟨		
L. garganicum subsp. *striatum*			🟨	🟨	🟨	🟨	🟨	🟨	🟨
L .garganicum subsp. *lasioclades*				🟨	🟨				
L .garganicum subsp. *rectum*						🟨	🟨	🟨	🟨
L. garganicum subsp. *laevigatum*			🟨	🟨	🟨	🟨	🟨	🟨	
L. microphyllum								🟨	
L. cymbalariifolium								🟨	
L. sandrasicum							🟨	🟨	
L. armenum* subsp. *armenum							🟨	🟨	🟨
L. armenum* subsp. *sintenisii							🟨	🟨	🟨
L. ehrenbergii		🟨	🟨	🟨	🟨	🟨	🟨		
L. purpureum	🟨	🟨	🟨	🟨	🟨	🟨			
L. eriocephalum* subsp. *eriocephalum						🟨	🟨	🟨	🟨
L .eriocephalum* subsp. *glandulosidens							🟨	🟨	🟨
L. amplexicaule subsp. *amplexicaule* var. *amplexicaule*	🟨	🟨	🟨	🟨	🟨	🟨	🟨	🟨	
L. amplexicaule subsp. *amplexicaule* var. *aleppicum*		🟨	🟨	🟨	🟨				
L. amplexicaule* subsp. *vanense									🟨
L. macrodon		🟨	🟨	🟨	🟨	🟨	🟨	🟨	🟨
L. maculatum		🟨	🟨	🟨	🟨	🟨			
L. villosifolium					🟨	🟨			
L. album subsp. *album*		🟨	🟨	🟨	🟨	🟨	🟨	🟨	🟨
L. album subsp. *crinitum*					🟨	🟨	🟨	🟨	🟨
L. tomentosum var. *tomentosum*								🟨	🟨
L. tomentosum var. *alpestre*								🟨	🟨
L. moschatum	🟨	🟨	🟨	🟨					
L. micranthum	🟨								

Table 5 (cont`d)

	0-300	300-600	601-900	901-1200	1201-1500	1501-1800	1801-2100	2101-2400	2401-
L. ponticum **subsp.** ***ponticum***		🟨	🟨	🟨	🟨				
L. ponticum **subsp.** ***anatolicum***				🟨					
L. galactophyllum					🟨	🟨	🟨		
L. tschorochense		🟨							
L. orientale			🟨	🟨	🟨	🟨			
L. multifidum				🟨	🟨	🟨	🟨	🟨	
L. bilgilii							🟨		
L. capadocicum							🟨	🟨	🟨

Endemic taxa in bold

3.2.3. Geographical Distribution of the *Lamium* species

The geographical distribution of 36 taxa is represented. Figure 26 shows the latitudinal zones (ABC, AB, BC, AC, A, B and C) and the frequency (localities) of each taxa in the latitudinal zones. For example, *L. amplexicaule* subsp. *amplexicaule* var. *amplexicaule* is recorded in 46 localities and is distributed at 3 latitudinal zones (ABC). Thus, the taxon is indicated as a widespread subspecies in Turkey (Figure 27). On the other hand, *L. bilgilii, L. micranthum, L. microphyllum, L. sandrasicum* are found only at one locality and one latitudinal zone (C). Thus, these taxa are indicated as rare species (Figure 29). According to our results, there are 7 taxa that are found in 3 latitudinal zones, such as; *L. amplexicaule* subsp. *amplexicaule* var. *amplexicaule, L. garganicum* subsp. *striatum, L. macrodon, L. orientale, L. album* subsp. *crinitum, L. album* subsp. *album* and *L. moschatum* (arranged from high frequency to low frequency, Figure 26). There are 3 taxa that are found in 2 latitudinal zones (Figure 28), such as; *L. villosifolium, L. multifidum* ve *L. armenum* subsp. *armenum* (arranged from high frequency to low frequency, Figure 26). Particularly, in AC latitudinal zone, there is only one species, such as; *L. maculatum*. In BC latitudinal zone, there are 4 taxa, such as; *L. cariense, L. ehrenbergii, L. tomentosum* var. *tomentosum, L. garganicum* subsp. *lasioclades* (Figure 26).

There are 9 taxa that are distributed in latitudinal zone A, such as *L. purpureum, L. galactophyllum, L. garganicum* subsp. *laevigatum, L. tomentosum* var. *alpestre, Galeobdolon luteum, L. ponticum* subsp. *ponticum, L. armenum* subsp. *sintenisii, L. ponticum* subsp. *anatolicum, L. tschorochense* (Figure 29). There are 2 taxa that are distributed in latitudinal zone B, such as *L. amplexicaule* subsp. *vanense* and *L. cappadocicum* (Figure 29). There are 10 taxa that are distributed in latitudinal zone C, such as; *L. lycium, L. garganicum* subsp. *rectum, L. amplexicaule* subsp. *amplexicaule* var. *aleppicum, L. cymbalariifolium, L. eriocephalum* subsp. *eriocephalum, L. erocephalum* subsp. *glandulosidens, L. bilgilii, L. micranthum, L. microphyllum ve L. sandrasicum* (Figure 29).

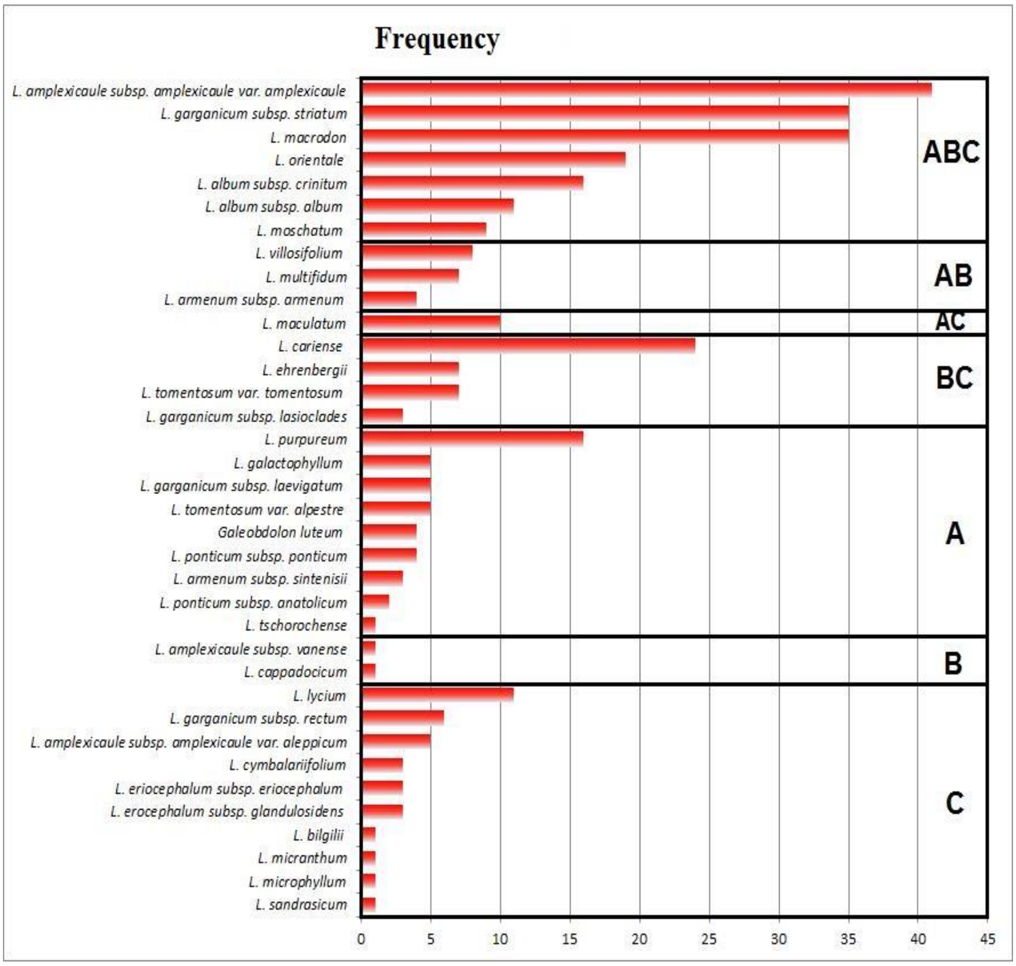


Figure 26. The frequency of *Lamium* taxa in the latitudinal zones (ABC, AB, BC, AC, A, B and C)

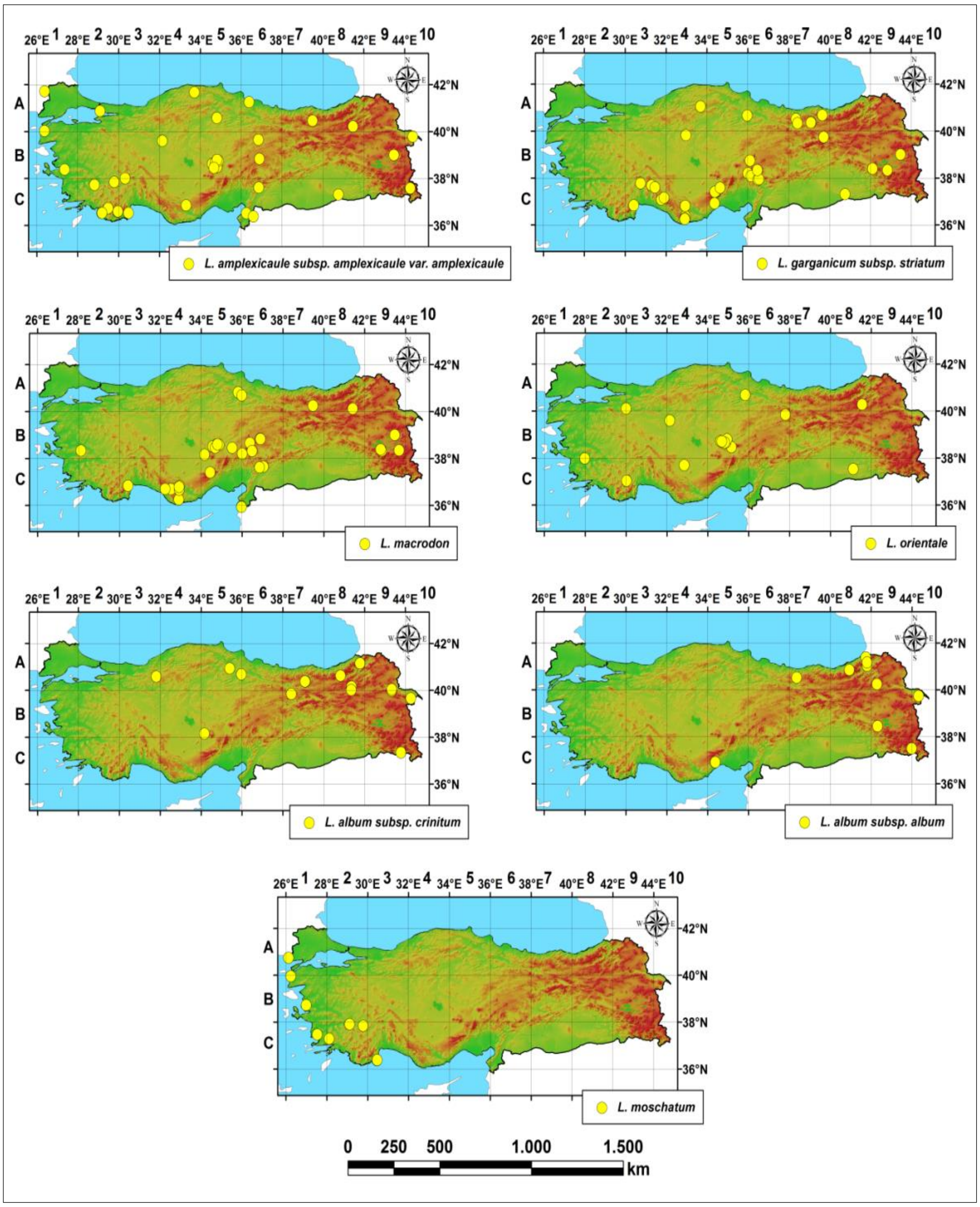


Figure 27. Taxa distributed in 3 latitudinal zones (ABC)

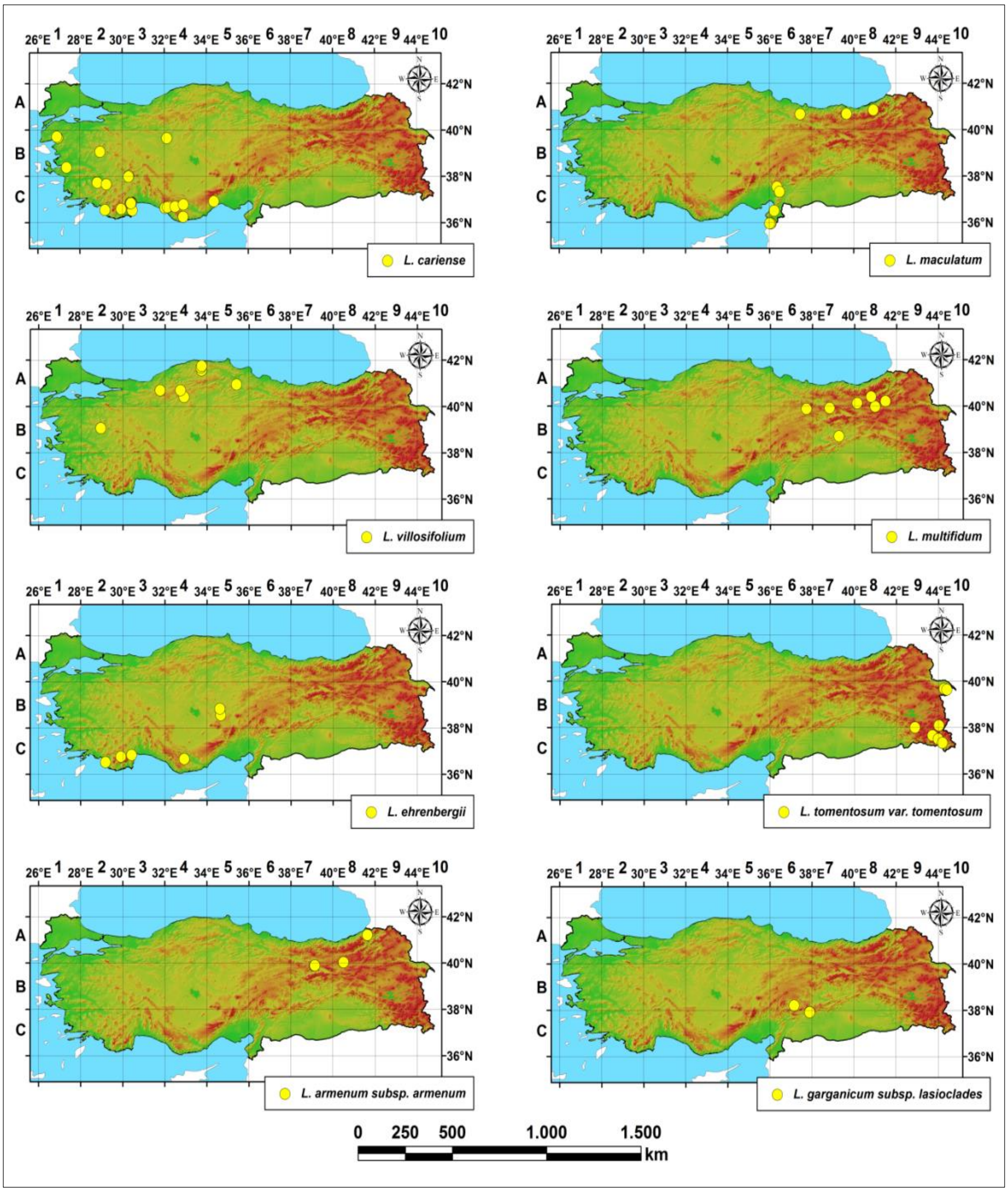


Figure 28. Taxa distributed in 2 latitudinal zones (AB, AC and BC)

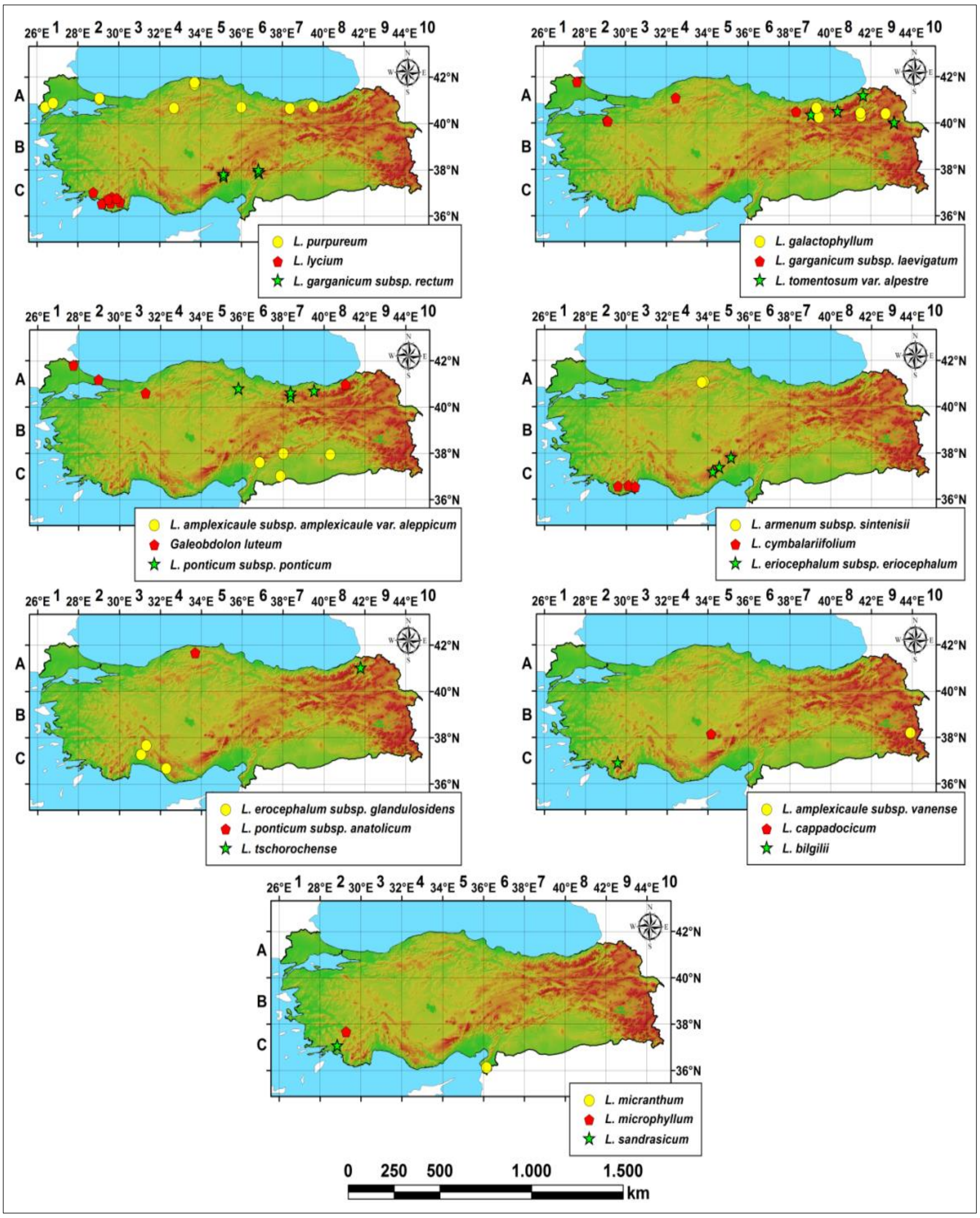


Figure 29. Taxa distributed in one latitudinal zone (A, B and C)

3.3 Anatomical Features of the Genus *Lamium*

Here, the anatomical properties of *Lamium* species are presented. The anatomical characters assessed for root, stem, leaf and petioles among the species are summarized in Tables 6-9. Selected LM photos of cross-sections are presented in Figs. 30-33. Voucher information of the *Lamium* species studied for their anatomical properties is given in Table 10.

3.3.1 Root Anatomy

The outermost surface of the roots is coated by a thin or thick layer of periderm which is crushed or broken up. Below the periderm, the multi-layered cortex is composed of large parenchymatous cells, whick are heterogeneous in size and shape. Below the cortex tissue, a single layer of endodermis is observed in a small number of species. In the vascular tissue, phloem and xylem elements are observed. The vascular cambium between xylem and phloem is sometimes inconspicuous. The xylem is composed of vessel members and tracheids. The vessel members are oval, round or polygonal. Xylem rays are observed in xylem tissue, which are composed of 1 to 8 radial rows of rectangular parenchymatous cells. For example in *L. cymbalariifolium* and *L. sandrasicum*, the maximum number of rays is 8, while it is only 1-2 layered in *L. tomentosum* var. *tomentosum*, *L. garganicum* subsp. *striatum*, *L. garganicum* subsp. *rectum*, *L. purpureum*. In most of the roots of the species, there is no central pith as the xylem covers all the central portion of the root (Figure 30).

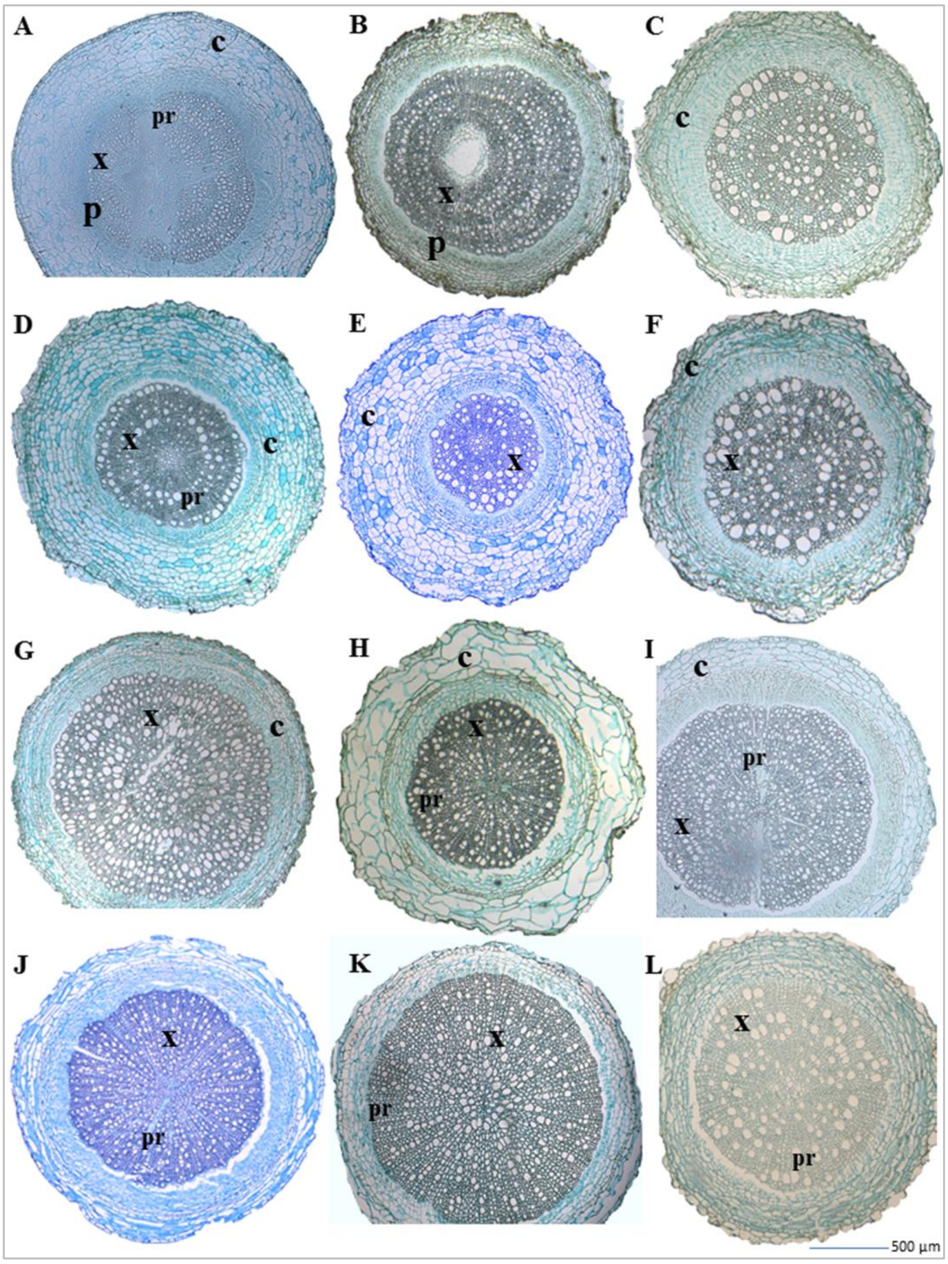


Figure 30. Transverse section of root parts of selected *Lamium* taxa. A: *L. cymbalarifolium*, B: *L. sandrasicum*, C: *L. garganicum* subsp. *striatum*, D: *L. lycium*, E: *L. microphyllum*, F: *L. garganicum* subsp. *lasioclades*, G: *L. armenum* subsp. *sintenisii*, H: *L. purpureum*, I: *L. eriocephalum* subsp. *glandulosidens*, J: *L. amplexicaule* subsp. *amplexicaule* var. *aleppicum*, K: *L. orientale* L: *Galeobdolon*

(*L. galeobdolon* subsp. *montanum*). pe; peridermis, c; cortex, p; phloem, pr; pith rays, x; xylem.

3.3.2 Stem Anatomy

In cross sections, the stems are mostly quadrangular (squarish to rectangular) to more or less circular. The epidermis is composed of a single-layer of square, rectangular or oval shaped cells and is covered by a thin or thick cuticle. In most of the species, multi-layered (1 to 7 layers) plaque collenchyma cells are located at the corners of the stem. The collenchyma tissue at the corners is significantly wider in *L. lycium*, *L. cariense*, *L. garganicum* subsp. *striatum*, *L. garganicum* subsp. *lasioclades*, *L. album* subsp. *album*, *L. moschatum*, *L. album* subsp. *crinitum*.

However, the collenchyma tissue is thinner in *L. garganicum* subsp. *laevigatum*, *L. microphyllum*, *L. ehrenbergii* and *L. tschorochense,* while it is absent in *L. cymbalariifolium* and *L. sandrasicum*.

The cortex is formed by parenchymatous cells of oval, round and rectangular shape with or without intercellular spaces. There are 4 main vascular bundles at the corners. Moreover, one or two small vascular bundles between corners can be observed. A large pith region with hexagonal and mostly orbicular parenchymatic cells is present in the center however, in some taxa the pith region is absent in the center of the stem. The vascular bundles at the corners are larger than those between the corners.

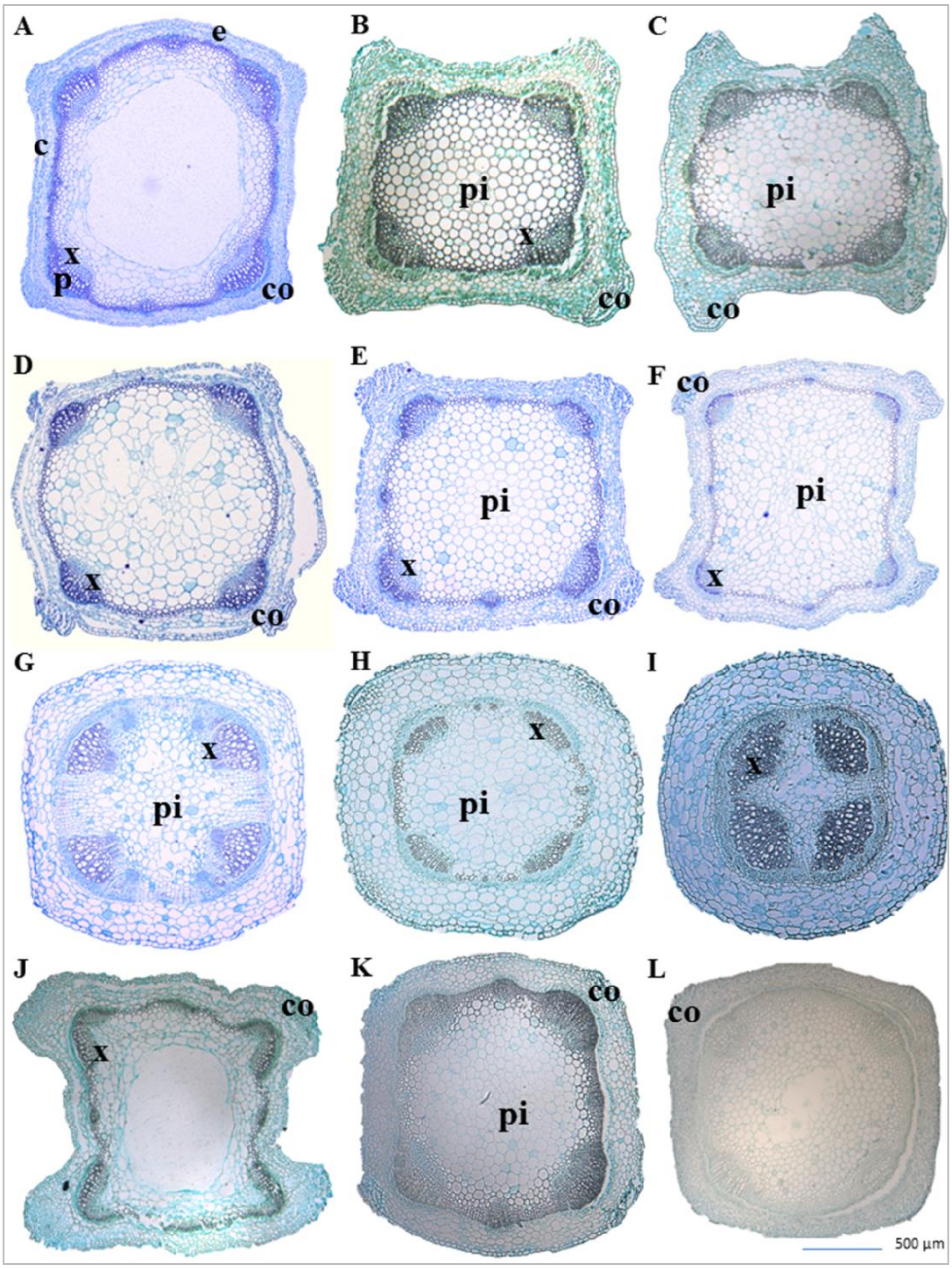


Figure 31. Transverse section of stem parts of selected *Lamium* taxa. A: *L. cariense*, B: *L. garganicum* subsp. *striatum*, C: *L. tomentosum* var. *tomentosum*, D: *L. amplexicaule* subsp. *amplexicaule* var. *amplexicaule*, E: *L. amplexicaule* subsp. *amplexicaule* var. *aleppicum*, F: *L. macrodon*, G: *L. eriocephalum* subsp. *eriocephalum*, H: *L. eriocephalum* subsp. *glandulosidens*, I: *L. cymbalarifolium*, J: *L. garganicum* subsp. *lasioclades*, K: *L. orientale*, L: *Galeobdolon* (*L. galeobdolon*

subsp. *montanum*). e; epidermis, c; cortex, co; collenchyma, p; phoem, x; xylem, pi; pith region.

3.3.3 Leaf Anatomy

The upper and lower epidermides of the lamina and midrip are covered with a thin cuticle layer. The epidermis is formed by oval and rectangular cells and is single layered on adaxial and abaxial surfaces. Upper epidermal cells are larger in size than lower epidermal cells. The leaf is of the bifacial type. In dorsiventral leaves, the mesophyll is differentiated into palisade and spongy tissues. Elongated rectangular palisade parenchyma and isodiametric spongy parenchyma cells form the mesophyll. The palisade parenchyma is 1 to 4 layered, followed by the spongy parenchyma cells which are 1 to 4 layerd with intercellular spaces in the investigated species. Among them, the palisade parenchyma is 3-4 layered in *L. eriocephalum* subsp. *eriocephalum* (whereas it is 1–2 layered in *L. album subsp. album* (sect. *Lamiotypus*). The spongy parenchyma is 2-4 layered in *L. macrodon* (sect. *Amplexicaule*) whereas it is 1-2 layered in *L. garganicum* subsp. *striatum* (sect. *Lamium*).

The midrib forms a projecting part. Transverse section of the midrip shows that the adaxial surface is flat to concave and the abaxial surface is convex. There is a single vascular bundle in the center. Vascular bundle is surrounded by a parenchymatic bundle sheat. The central vascular bundle is/are open U-shaped in *L. cariense*, *L. garganicum* subsp. *striatum*, *L. microphyllum*, *L. garganicum* subsp. *laevigatum*, *L. purpureum* (sect. *Lamium*); round U-shaped in *L. lycium* (sect. *Lamium*); continuous arc with incurved ends in *L. maculatum* and *L. villosifolium*, (sect. *Lamiotypus*) and rounded in *L. galactophyllum* (sect. *Lamiotypus*). There are no small accesory vascular bundles in the midrib in the investigated taxa.

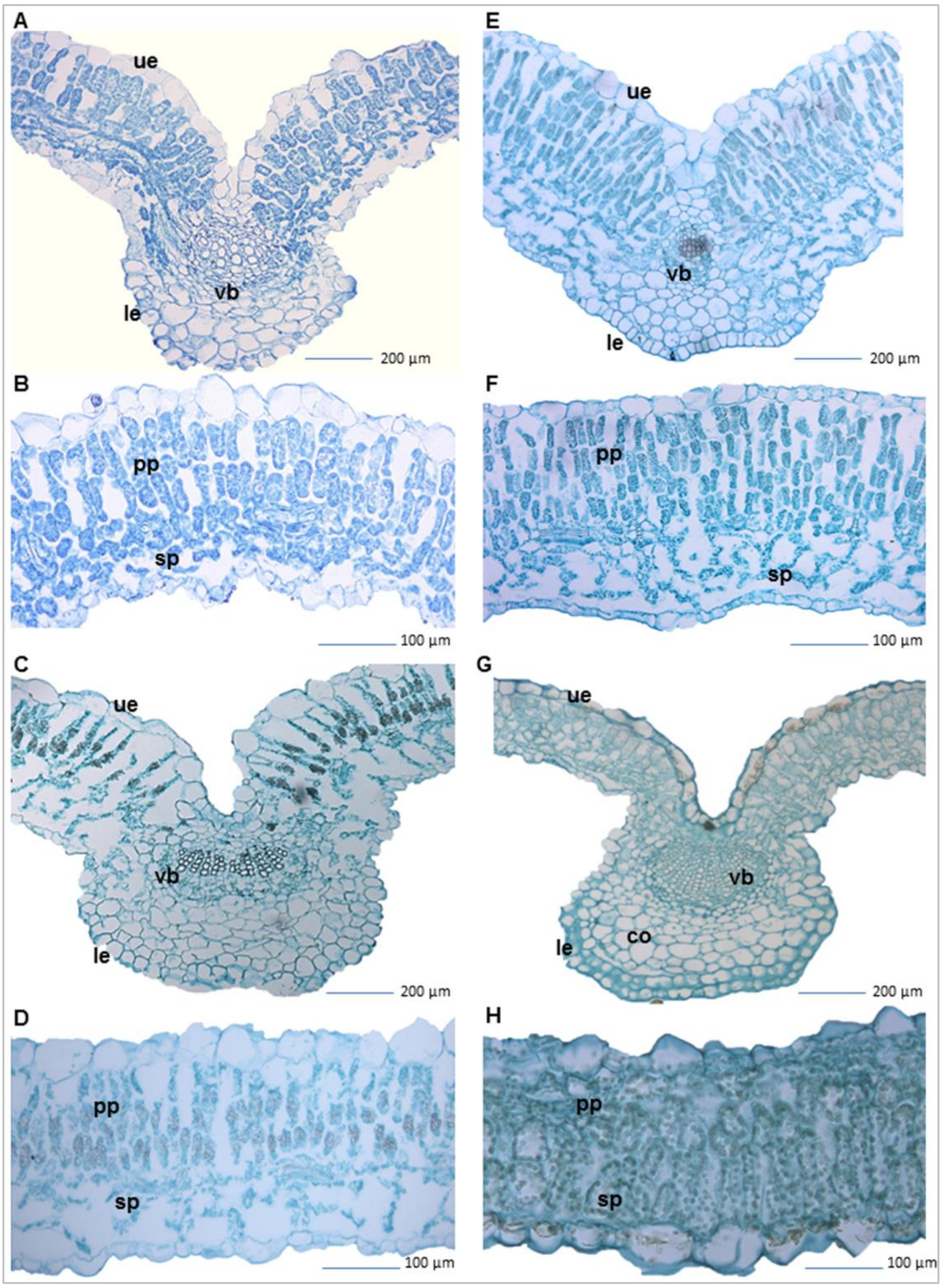


Figure 32. Transverse section of leaf blades and midrip of selected *Lamium* taxa. A & B: *L. microphyllum*, C & D: *L. orientale,* E & F: *L. tomentosum* var. *alpestre*, G & H: *L. album* subsp. *album*. le; lower epidermis, ue; upper epidermis, pp; palisade parenchyma; ss; spongy parenchyma.

3.3.4 Petiole Anatomy

Cross-sections of petioles can be categorized into three basic types: open U-shaped (e.g., *L. lycium*, *L. cariense*, *L. garganicum* subsp. *laevigatum*, *L. garganicum* subsp. *rectum*, *L. armenum* subsp. *armenum*, *L. maculatum*), open V-shaped (e.g., *L. garganicum* subsp. *striatum*) and open sickle shaped (e.g. *L. album* subsp. *crinitum*, *L. tschorochense*). The epidermal cells of both surfaces are more or less rectangular to oval. The upper and lower cell walls of the epidermis are thicker than the lateral walls. The upper surface of the epidermis is covered with a thin or thick cuticle. Angular collenchymatous cells can be observed at the corners of the petioles, below the epidermis, with 1 to 5 layers. Ground tissue is composed of parenchymatous cells with various size and shape (Figure 33).

The shape of the central vascular bundle can be categorized as; Open U-shaped with incurved ends (e.g. *L. lycium*, *L. cariense*, *L. garganicum* subsp. *laevigatum*, *L. villosifolium*, *L. ponticum* subsp. *ponticum*), Open U-shaped (e.g. *L. garganicum* subsp. *striatum*, *L. garganicum* subsp. *laevigatum*, *L. purpureum*, *L. album* subsp. *crinitum*, *L. orientale*), Round U-shaped (e.g. *L. garganicum* subsp. *rectum*, *L. cymbalariifolium*, *L. sandrasicum*, *L. tschorochense*), Rounded (e.g. *L. purpureum*, *L. ehrenbergii*, *L. galactophyllum*). A single median vascular bundle accompanied by one small subsidary bundles at each wing is observed in the transverse section of studied taxa. Transverse sections of the petioles show that the adaxial surface is convex while the abaxial surface is concave. The petiolar wings can be recognized with ease as in *L. garganicum* subsp. *lasioclades*. The wings can be obscure as in *L. tomentosum* var. *alpestre* (Figure 33).

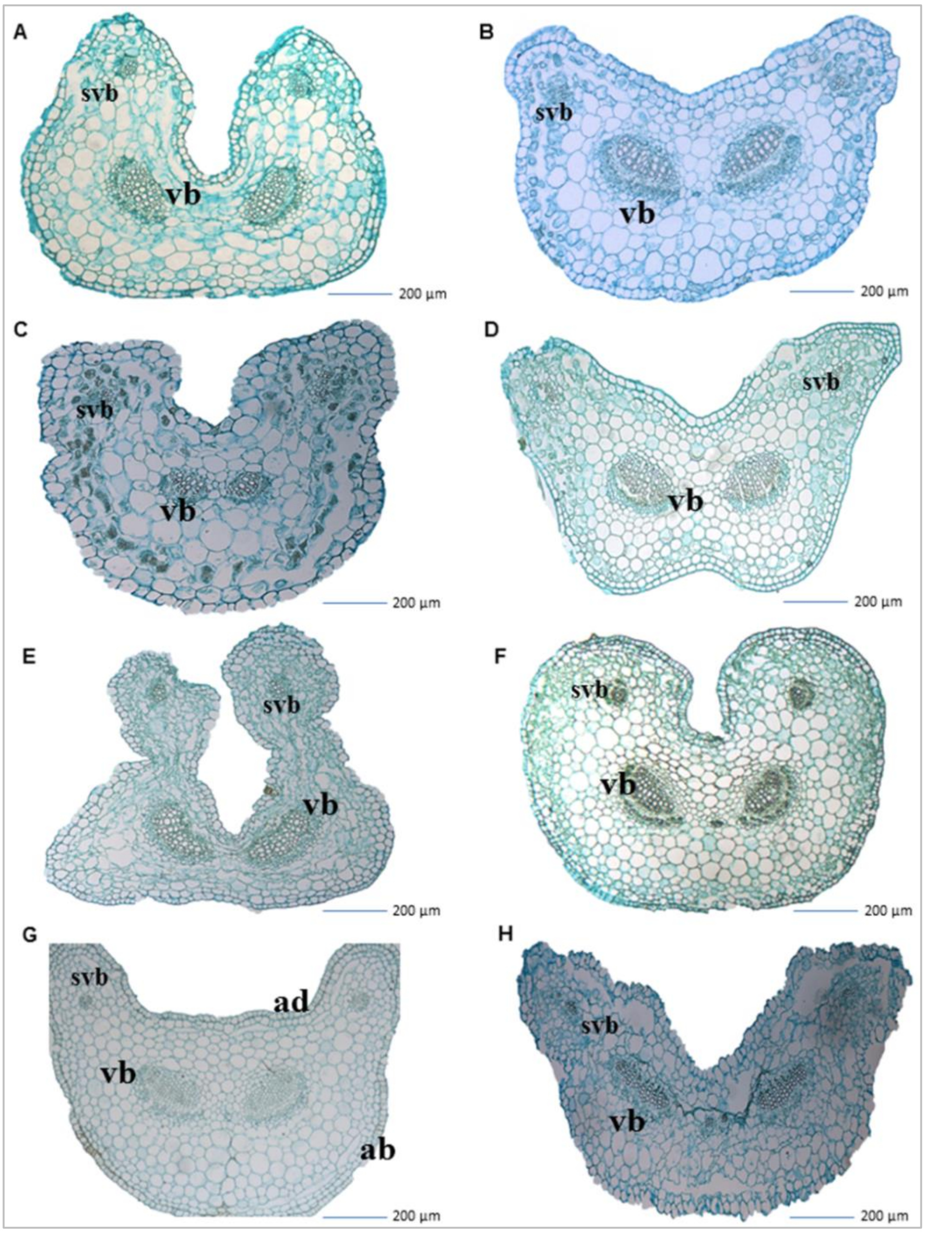


Figure 33. Transverse section of petioles of selected *Lamium* taxa. A: *L. lycium*, B: *L. tomentosum* var. *alpestre*, C: *L. cymbalarifolium* D: *L. garganicum* subsp. *striatum* E: *L. garganicum* subsp. *lasioclades* F: *L. garganicum* subsp. *laevigatum* G: *Galeobdolon* (*L. galeobdolon* subsp. *montanum*) H: *L. orientale*. ab; abaxial epidermis, ad; adaxial epidermis, vb; vascular bundle, svb; subsidary vascular bundle.

3.3.5 Systematic Implications of Vegetative Anatomy in the genus *Lamium*

Metcalfe and Chalk (1972) pointed out some useful information about root anatomy of the family Lamiaceae. Such that, the pith rays in the roots of the family are composed of 2-12- or more-rowed cells. Our findings are consistent with those of Metcalfe and Chalk (1972) and some other investigated members of the Lamiaceae (Dinç and Öztürk, 2008; Baran and Özdemir, 2009; Baran and Özdemir, 2011; Celep, et al. 2011; Baran and Özdemir, 2012, 2013; Kahraman et al., 2010a, 2010b). It is reported that the root centre is filled with primary xylem in some Lamiaceae members (Özdemir and Senel 1999; Uysal 2002; Baran and Özdemir 2006; Özdemir et al. 2008, 2009). According to the transverse section of root and stem parts, some characters are found to be taxonomically informative. Pith ray rows in the roots are partly significant for some species. Such that, there are 1-8 rows of pith ray in *L. cymbalariifolium* and *L. sandrasicum*. However, in the numerical taxonomic tree, the species are grouped together with *L. lycium*, *L. cariense*, *L. garganicum* subsp. *striatum*, *L. garganicum* subsp. *rectum*, *L. garganicum* subsp. *lasioclades*, *L. garganicum* subsp. *laevigatum*, *L. microphyllum*, *L. capadocicum* and *L. bilgilii*, which have 1-3 rows of pith ray. It is evident from the gross morphology that, *L. cymbalariifolium* and *L. sandrasicum* are only similar to the `*garganicum* complex` on the basis of their corolla morphology. In addition to the morphological characters, root anatomical data is a taxonomically significant character for these two endemic species. Similarly, *L. maculatum* and *L. villosifolium* have 1-6 rows of pith rays in their roots. Therefore, in addition to the morphological characters, root anatomical data is a taxonomically significant character for these two species.

The characteristic feature of the Lamiaceae family is a quadrangular stem and a well-developed collenchyma, supporting the tissues at the corners of the stem and a developed sclerenchymatic tissue surrounding the vascular tissue (Metcalfe and Chalk 1972). A well-developed plaque collenchyma was clearly distingushable at the corners of the cross-sections of the quadrangular stems of some species.

However, sclerenchyma was hardly present in the cross-section of neither the stem nor the root, in contrast to those described by Metcalfe and Chalk (1972). Our findings are consistent with some other investigated members of *Lamium* (Baran and Özdemir, 2009; Baran and Özdemir, 2011; Celep, et al. 2011; Baran and Özdemir, 2012, 2013).

The presence of collenchymatous tissue at the corner of stems and their number of layers are found to be taxonomically informative characters. Such that, *L. eriocephalum* subsp. *eriocephalum* and *L eriocephalum* subsp. *glandulosidens* do not have collenchymatous tissue at the corner of their stems. These two species were included in sect. *Amplexicaule* (Mennema, 1989). However, other members of sect. Amplexicaule (*L. amplexicaule subsp. amplexicaule var. amplexicaule*, *L. amplexicaule subsp. amplexicaule var. aleppicum*, and *L. macrodon*) have 3-5 layered collenchymatous tissue at the corner of their stems. Moreover, the gross morphology of *L. eriocephalum* subsp. *eriocephalum,* reveales some differences from the other members of sect. *Amplexicaule*. Thus, the presence of collenchymatous tissue at the corners of the stem is a valuable character for this particular section. Similarly, *L. cymbalariifolium* and *L. sandrasicum* do not have collenchymatous tissue at the corners of their stem. However, *L. lycium L. cariense*, *L. garganicum* subsp. *striatum*, *L. garganicum* subsp. *rectum*, *L. garganicum* subsp. *lasioclades*, *L. garganicum* subsp. *laevigatum L. microphyllum*, *L. capadocicum* and *L. bilgilii* have 3-6 layered collenchymatous tissue at the corner of their stems. Thus, the presence of collenchymatous tissue at the corners of the stem is a valuable character for these two endemic species.

Lamium armenum subsp. *armenum* and *L. armenum* subsp. *sintenisii* which were included in sect. *Lamium* by Mennema (1989), have 2-3 layered collenchymatous tissue at the corners of their stem. However, these two species are morphologically very different from the members of sect. *Lamium*, in which there are 3-6 layers of collenchymatous tissue at the corners. In addition to the morphological characters, stem anatomical data is a taxonomically significant character for these two species.

The structure of vascular bundles in the crosssection of the petiole in Lamiaceae species may be important for taxonomy (Metcalfe & Chalk 1972). The analysis of the petiole cross-section showed that 2 collateral vascular bundles were present in the centre and 1 bundle was present at each end of the cross-section of all investigated *Lamium* species. Our findings are consistent with some other investigated members of *Lamium* (Baran and Özdemir, 2009; Baran and Özdemir, 2011; Baran and Özdemir, 2012, 2013).

According to the transverse section of leaf and petiole parts, some characters are found to be taxonomically informative. Regarding the shape of leaf midrip tranverse section, *L. cymbalariifolium* and *L. sandrasicum* have rounded vascular bundles in the midrip of their leaves. They are distinguished from other members of the species group on the basis of this particular character. The number of palisade and spongy paranchyma layers in the leaf mesophyll tissue is not a taxonomically informative character among the investigated species. Regarding the transverse section of the petiole anatomy, *L. microphyllum*, *L. cymbalariifolium* and *L. sandrasicum* have round shaped petioles. In addition, *L. microphyllum*, *L. cymbalariifolium* and *L. sandrasicum* do not have collenchymatous tissue at the corner of their petioles. Compared to the `*garganicum* complex`, these three species have a rather distinct position with respect to this character. The petioles of *Lamium eriocephalum* subsp. *eriocephalum*, *L. eriocephalum* subsp. *glandulosidens, L. amplexicaule subsp. amplexicaule var. amplexicaule, L. amplexicaule subsp. amplexicaule var. aleppicum* and *L. macrodon* do not have collenchyma at the petiole corners, thus, this character is of taxonomic importance for sect. *Amplexicaule*.

The anatomical properties of *L. orientale* and *L. multifidum* support their inclusion in the genus *Lamium*, where they were previously assigned to genus

Wiedemannia (Fischer and Meyer, 1838). Later on, both were included in Lamium (Krause, 1903; Ryding, 2003; Harley, 2004; Govaerts et al., 2010). The anatomical findings of the present study and a recent comparative study (Atasagun et al., 2015) on the taxa are consistent however both species are included in *Wiedemannia* in that study.

Gross morphology of *Lamium galeobdolon* subsp *montanum* reveals that, the transfer of the species to a separate genus seems to be legitimate. The anatomical results may support the inclusion of *L. galeobdolon* subsp. *montanum* in the genus *Lamium*. Moreover, the integration of *Galeobdolon* and *Lamium* seems to be legitimate by Bendiksby et al. (2011b) and Krawczyk et al. (2013, 2014) however its taxonomic placement is not settled.

***In Tables 6-9, taxa in parenthesis are the synonyms of the taxa written in red.**

Table 6. Characterization of the root and stem components in *Lamium*.

Taxon	**Root**			**Stem**			
	Peridermis Cell	**Cortex Cell**	**Nb of pith ray rows**	**Epidermis Cell**	**Cortex Cell**	**COL Layer**	**Nb of VB (+; SVB)**
L. lycium	36.32 ± 6.53 (25.13–50.89)	48.81 ± 9.50 (33.86–62.53)	1–3	20.74 ± 3.85 (15.51–24.64)	37.76 ± 6.60 (25.42–48.62)	5–6	4 (+4)
L. cariense	29.76 ± 5.67 (22.49-44.74)	24.49 ± 4.81 (18.93–34.42)	1–3	19.92 ± 2.78 (12.99–24.45)	29.72 ± 4.50 (22.63–35.46)	4–5	4 (+4)
L. garganicum subsp. *striatum* (*L. pisidicum*)	25.85 ± 2.62 (20.95–30.91)	42.13 ± 7.98 (26.06–52.50)	1–2	16.03 ± 3.45 (8.39–21.41)	26.96 ± 5.17 (19.75–38.42)	4–5	4
L. garganicum subsp. *striatum* (*L. tenuiflorum)*	30.12 ± 5.78 (19.18–47.78)	37.11 ± 6.67 (28.05–51.72)	1–2	23.08 ± 3.79 (16.67–29.28)	35.38 ± 7.21 (18.38–49.39)	3–4	4
L. garganicum subsp. *striatum* (*L. garganicum* subsp. *reniforme*)	30.57 ±3.88 (24.59–34.19)	30.12 ±17.27 (12.33–7.20)	1–2	46.90 ± 21.10 (17.33–86.68)	55.23 ±15.99 (32.12–73.82)	1–2	4
L. garganicum subsp. *striatum* (*L. garganicum* subsp. *nepetifolium)*	20.18 ± 5.05 (13.90–31.12)	23.49 ± 5.55 (14.70–35.71)	1–2	13.71± 3.58 (7.77–21.33)	25.28 ± 5.05 (15.55–35.07)	3–4	4
L. garganicum subsp. *rectum*	34.53 ± 8.87 (27.11–57.35)	29.16 ±7.14 (22.19–50. 11)	1–2	17.04 ± 3.28 (12.40 – 22.09)	34.49 ± 4.52 (23.92 – 42.99)	4–5	4 (+4)
L. garganicum subsp. *lasioclades*	34.53 ± 8.87 (27.11–57.35)	29.16 ±7.14 (22.19–50. 11)	1–2	17.04 ± 3.28 (12.40–22.09)	34.49 ± 4.52 (23.92–42.99)	5–6	4 (+4)
L. garganicum subsp. *rectum* (*L. garganicum* subsp. *pulchrum)*	39.92 ± 11.11 (25.19–62.63)	55.35±18.07 (32.26–87.34)	1–2	24.46 ±6.06 (15.62–34.94)	52.70± 11.09 (31.41–72.69)	1–2	4
L. garganicum subsp. *laevigatum*	39.39 ± 9.34 (26.46–52.50)	40.05 ±8.27 (25.26–46.58)	1–3	29.86 ±7.05 (17.37–43.04)	61.47 ±13.57 (41.06–89.63)	2–3	4
L. garganicum subsp. *laevigatum* (*L. veronicifolium)*	27.72 ± 6.99 (21.41–44.32)	21.78± 2.90 (17.97–26.50)	1–2	30.21± 9.35 (18.38–41.98)	66.74± 8.61 (52.56–87.03)	1–2	4
L. microphyllum	31.65 ± 5.10 (22.21–43.89)	29.43±4.18 (21.18–41.44)	1–3	29.94±3.45 (24.78–34.18)	57.36±14.34 (38.52–76.54)	1–2	4
L. cymbalariifolium	41.04 ±5.11 (34.96–48.19)	61.36±13.08 (42.41–79.18)	1–8	37.77±6.90 (28.91–49.53)	56.75±5.16 (46.18–65.77)	Absent	4
L. sandrasicum	29.56 ± 5.34 (18.36–38.12)	36.31± 9.45 (16.72–53.91)	1–8	37.18 ±6.25 (31.61–46.07)	38.53 ±7.41 (28.34–59.37)	Absent	4

Table 6 (cont`d)

Taxon	**Root**			**Stem**			
	Peridermis Cell	**Cortex Cell**	**Nb of pith ray rows**	**Peridermis Cell**	**Cortex Cell**	**COL Layer**	**Nb of VB (+; SVB)**
L. armenum subsp. *armenum*	27.47 ± 8.78 (17.37–43.88)	21.25± 5.48 (13.30–30.43)	1–4	40.65 ±11.71 (22.53–69.03)	74.92 ±18.71 (46.14–106.25)	2–3	4
L. armenum subsp. *sintenisii*	34.51 ± 4.95 (25.19–42.04)	41.35± 11.95 (26.57–75.14)	1–3	31.73± 5.90 (21.09–43.42)	53.06± 12.34 (30.29–80.27)	2–3	4
L. purpureum *(L. purpureum* var. *purpureum)*	55.29 ± 10.44 (41.07–69.86)	69.04±15.88 (47.59–101.07)	1–2	22.50 ± 4.94 (15.13–30.26)	50.06 ± 9.49 (31.86–57.24)	3–4	4 (+4)
L. purpureum *(L. purpureum* var. *aznavourii)*	37.77 ± 3.57 (32.75–44.67)	72.25±19.50 (51.11–115.55)	1–2	28.59±6.02 (17.09–45.23)	43.85±9.71 (24.15–57.95)	3–4	4 (+4)
L. eriocephalum subsp. *eriocephalum*	35.43 ± 7.28 (25.04-48.46)	22.29 ± 4.42 (17.54-31.19)	1–2	42.94±8.86 (28.83-62.08)	85.76±11.85 (61.19-117.34)	Absent	4
L .eriocephalum subsp. *glandulosidens*	70.20 ± 17.68 (42.25–93.00)	79.39± 15.96 (55.26–115.36)	1–4	35.51 ± 9.17 (19.97–46.26)	58.88 ± 10.91 (44.93–71.54)	Absent	4
L. amplexicaule subsp. amplexicaule var. amplexicaule (L. amplexicaule)	38.16±7.24 (25.31-53.47)	85.19±13.54 (60.86-124.72)	1–2	17.75±4.39 (12.61-29.64)	44.09±9.39 (26.72-66.41)	3–4	4
L. amplexicaule subsp. amplexicaule var. aleppicum (L. aleppicum)	37.56±7.31 (28.09-53.08)	34.9±6.48 (23.62-48.68)	1–3	23.85±3.38 (17.35-31.54)	30.42±5.04 (21.79-51.23)	4–5	4 (+4)
L. macrodon	25.14±4.50 (14.16-28.70)	20.24±4.58 (11.87-26.14)	1–2	19.67±2.77 (16.06-25.24)	44.28±9.52 (31.34-63.88)	4–5	4 (+4)
L. ehrenbergii	24.13±5.74 (16.06–39.37)	39.94±9.55 (23.45–55.78)	1–2	24.71±5.53 (17.03–33.83)	29.69±4.30 (21.41–36.69)	1–2	4
L. maculatum *(L. maculatum* var. *maculatum)*	25.53 ± 2.41 (23.84–29.08)	26.98 ± 6.50 (19.75–42.71)	1–6	16.30 ± 1.75 (13.25–18.72)	25.70 ± 4.81 (17.94–34.40)	4–5	4
L. villosifolium *(L. maculatum* var. *villosifolium)*	23.10 ± 2.99 (18.71–26.70)	36.70 ± 7.16 (22.71–50.95)	1–5	20.69 ± 3.30 (13.74–25.03)	50.89 ± 7.70 (39.67–70.86)	4–5	4
L. maculatum *(L. gundelsheimeri)*	38.14 ± 6.14 (21.15–48.16)	43.43 ± 8.41 (23.25–56.06)	1–6	16.44 ± 3.12 (11.30–20.95)	39.08 ± 7.07 (30.42–55.07)	3–4	4
L. maculatum *(L. truncatum)*	42.78±12.15 (24.99-74.66)	26.21±7.20 (15.25-39.35)	1–4	23.26±4.91 (14.80-32.49)	41.12±11.18 (24.78-65.82)	6–7	4 (+4)

Table 6 (cont`d)

Taxon	Root			Stem			
	Peridermis Cell	**Cortex Cell**	**Nb of pith ray rows**	**Peridermis Cell**	**Cortex Cell**	**COL Layer**	**Nb of VB (+; SVB)**
L. album subsp. *album* *(L. album)*	18.14 ± 3.54 (13.68–26.23)	21.26 ± 3.15 (14.20–26.54)	1–3	14.49 ± 1.93 (10.61–17.25)	22.85 ± 4.00 (15.73–29.87)	6–7	4
L. album subsp. *crinitum* *(L. crinitum)*	20.84 ± 2.91 (16.77–26.77)	39.49 ± 9.60 (21.88–56.19)	1–2	22.90 ± 2.40 (18.15–24.83)	58.67 ± 14.02 (38.34–70.13)	5–6	4 (+4)
L. tomentosum var. *tomentosum*	45.68 ±10.43 (31.28–65.94)	30.87± 6.01 (24.16–43.25)	1–2	21.27± 4.23 (12.13–26.68)	35.03± 7.40 (24.15–48.52)	3–4	4
L. tomentosum var. *alpestre* *(L. sulfureum)*	20.99 ± 4.83 (15.11–34.45)	31.59 ± 4.41 (26.24–39.40)	1–2	21.34 ± 2.57 (18.92–25.68)	47.27 ± 9.15 (33.86–68.33)	3–4	4
L. moschatum *(L. moschatum* var. *moschatum)*	31.41 ± 4.02 (24.16–36.41)	20.44 ± 4.77 (15.12–30.16)	1–3	26.48 ± 4.22 (20.44–43.78)	45.78 ± 7.15 (30.74–60.16)	4–5	4 (+4)
L. moschatum *(L. moschatum* var. *rhodium)*	32.33 ± 3.98 (25.22–37.89)	21.27 ± 5.09 (14.83–31.22)	1–2	28.11± 5.85 (21.22–44.38)	49.85 ± 8,81 (31.82–61.47)	4–5	4 (+4)
L. micranthum *(L. moschatum var. micranthum)*	31.22 ± 3.41 (24.11 – 36.41)	21.27 ± 5.09 (14.83 – 31.22)	1–2	27.17± 5.56 (22.21 – 43.33)	48.33 ± 7.43 (32.11 – 60.43)	4–5	4
L. ponticum subsp. *ponticum* *(L. ponticum)*	37.26 ± 10.05 (26.42–57.40)	38.71 ± 6.80 (25.89–50.51)	1–3	21.44 ± 2.26 (18.28–24.66)	54.13 ± 9.94 (29.06–73.23)	4–5	4 (+4)
L. galactophyllum	26.85 ± 2.54 (23.07–31.30)	40.29 ± 12.46 (26.41–50.26)	1–6	17.68 ± 1.83 (14.87–21.30)	29.13 ± 6.12 (20.49–43.63)	3–4	4 (+4)
L. tschorochense	25.15 ± 5.31 (14.56–37.41)	32.61 ± 4.89 (14.57–41.57)	1–4	14.54 ± 4.18 (8.73–23.19)	41.47 ± 7.54 (16.58–63.62)	1–2	4
L. album subsp. *crinitum* *(L. vreemanii)*	27.05 ± 6.37 (16.66–39.80)	35.66 ± 6.57 (18.07–45.77)	1–2	15.67 ± 3.88 (9.62–25.09)	44.97± 24.90 (18.38–130.62)	5–6	4 (+4)
L. orientale	32.34± 9.51 (19.17–48.34)	29.22±5.96 (19.27–39.02)	1–4	32.09±4.50 (24.71–40.65)	54.29±5.32 (46.98–62.25)	2–3	4 (+4)
L. multifidum	33.24 ± 9.12 (20.26 – 49.21)	31.65 ±4.22 (19.09 – 41.12)	1–3	33.11±4.03 (25.56 – 41.34)	55.31±4.12 (48.32 – 65.32)	4–5	4 (+4)

Table 6 (cont`d)

Taxon	**Root**			**Stem**			
	Peridermis Cell	**Cortex Cell**	**Nb of pith ray rows**	**Peridermis Cell**	**Cortex Cell**	**COL Layer**	**Nb of VB (+; SVB)**
Galeobdolon *(L. galeobdolon* subsp. *montanum)*	21.45 ± 3.64 (15.39–28.71)	24.85 ± 5.05 (17.90–40.41)	1–4	12.87 ± 1.94 (9.78–16.36)	22.62 ± 4.88 (15.80–31.26)	3–4	4
L. bilgilii	39.14 ±6.02 (32.96–45.78)	59.36±11.08 (40.12–76.12)	/	23.16±4.81 (14.78-32.44)	39.18 ± 7.17 (29.42–53.07)	3–4	4 (+4)
L. ponticum subsp. *anatolicum*	43.68 ±9.43 (30.28–61.94)	29.80± 6.41 (24.16–42.78)	1–3	24.26±4.91 (15.80-31.49)	40.85 ± 8.71 (22.15–55.95)	4–5	4 (+4)
L. cappadocicum	30.22 ± 3.49 (25.11 – 35.74)	20.27 ± 5.19 (14.78 – 30.22)	1–2	26.17± 5.51 (22.21 – 41.78)	46.33 ± 6.43 (32.11–58.32)	2–3	4
L. amplexicaule subsp. *vanense*	40.14 ±5.44 (33.96–49.24)	55.36±10.08 (39.41–80.18)	1–2	21.55 ± 4.11 (15.04–30.26)	48.67 ± 10.12 (33.34–68.13)	1–2	4

COL: Collenchyma, VB: Vascular Bundle, SVB: Subsidary Vascular Bundle.

Table 7. Characterization of the leaf components in *Lamium*. Column headings MB number, MB shapes correspond to the midrib of leaf and PPL, SPL to its lamina, /; no data.

Taxon	**Midrib parenchyma**	**Midrib Trachea**	**VB number**	**VB shape**	**PPL**	**SPL**
L. lycium	21.05 ± 4.98 (16.13–24.47)	7.82 ± 0.83 (6.33–9.21)	1	Rounded U	2	1–2
L. cariense	19.35 ± 3.96 (12.97–29.43)	8.77 ± 0.90 (7.21–10.34)	1	Open U	2–3	1–2
L. garganicum subsp. *striatum* *(L. pisidicum)*	25.02 ± 4.59 (16.95–33.01)	9.10 ± 1.12 (7.12–10.55)	1	Open U	2–3	2–4
L. garganicum subsp. *striatum* *(L. tenuiflorum)*	29.72 ± 6.22 (22.77–40.47)	9.65 ± 1.60 (7.67–13.50)	1	Rounded	2–3	1–2
L. garganicum subsp. *striatum* *(L. garganicum* subsp. *reniforme)*	21.64 ± 6.3310.38–25.98)	7.17 ±1.77 (4.48–10.02)	1	Open U	2–3	2–3
L. garganicum subsp. *striatum* *(L. garganicum* subsp. *nepetifolium)*	/	/	/	/	/	/
L. garganicum subsp. *rectum*	/	/	/	/	/	/
L. garganicum subsp. *lasioclades*	22.47 ± 4.68 (16.64–29.95)	11.13 ± 1.41 (8.28–13.50)	1	Open U	2	1–2
L. garganicum subsp. *rectum* *(L. garganicum* subsp. *pulchrum)*	22.47 ± 4.68 (16.64–29.95)	11.13 ± 1.41 (8.28–13.50)	1	Open U	2	2
L. garganicum subsp. *laevigatum*	21.15 ± 7.98 (7.90–32.55)	6.79 ± 1.54 (5.19–10.05)	1	Open U	2–3	3–4
L. garganicum subsp. *laevigatum* *(L. veronicifolium)*	26.02 ± 8.80 (15.59–43.34)	10.34 ± 2.46 (5.35–13.67)	1	Open U	2	3–4
L. microphyllum	29.43 ± 5.13 (23.46–42.57)	8.81 ± 1.36 (6.99–11.19)	1	Open U	2–3	2–3
L. cymbalariifolium	26.42 ± 3.83 (21.26–35.36)	9.07 ± 2.09 (6.29–11.20)	1	Rounded	3–4	2–3
L. sandrasicum	21.48 ± 7.33 (11.71–30.84)	6.73 ± 1.26 (9.29–4.82)	1	Rounded	2–3	2–3

Table 7 (cont`d)

Taxon	**Midrib parenchyma**	**Midrib Trachea**	**VB number**	**VB shape**	**PPL**	**SPL**
L. armenum subsp. *armenum*	28.48 ± 8.75 (16.55–43.04)	8.75 ± 2.17 (5.88–13.74)	1	Open U	2–3	2
L. armenum subsp. *sintenisii*	47.17 ± 6.69 (39.90–59.48)	9.10 ± 1.53 (6.08–10.97)	1	Rounded	3–4	3–4
L. purpureum *(L. purpureum* var. *purpureum)*	21.37 ± 2.75 (17.56–24.61)	9.69 ± 1.33 (7.29–12.22)	1	Open U	2	1–2
L. purpureum *(L. purpureum* var. *aznavourii)*	28.74 ± 5.06 (22.31–41.59)	9.68 ±1.76 (7.90–12.82)	1	Open U	1–2	1–2
L. eriocephalum subsp. *eriocephalum*	22.12±2.81 (15.95–26.58)	8.81±0.89 (6.17–10.25)	1	Open U	3-4	2-4
L .eriocephalum subsp. *glandulosidens*	23.62 ± 3.45 (18.95–29.96)	10.15 ± 1.43 (7.97–13.40)	1	Open U	3-4	2-3
L. amplexicaule subsp. amplexicaule var. amplexicaule *(L. amplexicaule)*	24.33±4.06 (18.88-35.78)	8.91±1.51 (6.65-11.47)	1	Open U	2-3	2-3
L. amplexicaule subsp. amplexicaule var. aleppicum *(L. aleppicum)*	26.12±5.78 (16.62-44.83)	11.52±1.35 (14.25-9.45)	1	Open U	2-3	2-3
L. macrodon	35.66 ± 8.43 (22.68-51.2)	12.88±1.55 (10.19-16.07)	1	Rounded	1-3	2-4
L. ehrenbergii	21.33 ± 4.53 (16.17–31.10)	6.93 ± 1.08 (5.27–8.16)	1	Rounded	2–3	2–3
L. maculatum *(L. maculatum* var. *maculatum)*	26.65 ± 4.53 (19.34–36.34)	9.87 ± 0.88 (8.08–11.44)	1	Continuous arc with incurved ends	1	1–2
L. villosifolium *(L. maculatum* var. *villosifolium)*	21.14 ± 2.34 (18.14–26.23)	7.95 ± 1.24 (6.52–9.30)	1	Continuous arc with incurved ends	1–2	1–2

Table 7 (cont`d)

Taxon	**Midrib parenchyma**	**Midrib Trachea**	**VB number**	**VB shape**	**PPL**	**SPL**
L. maculatum *(L. gundelsheimeri)*	40.08 ± 7.93 (30.52–57.55)	13.79 ± 1.92 (11.77–17.90)	1	Continuous arc with incurved ends	1	1–2
L. maculatum *(L. truncatum)*	36.42±10.47 (20.02-59.66)	13.69±3.07 (9.20-19.27)	1	Continuous arc with incurved ends	1–2	2–3
L. album subsp. *album* *(L. album)*	23.98 ± 5.42 (14.83–37.66)	7.25 ± 0.83 (5.65–9.07)	1	Continuous arc with incurved ends	1–2	2–3
L. album subsp. *crinitum* *(L. crinitum)*	27.32 ± 5.30 (20.81–37.02)	11.26 ± 1.64 (9.29–13.21)	1	Open U	2	2
L. tomentosum var. *tomentosum*	18.87 ± 4.70 (12.02–25.20)	8.18 ± 1.54 (5.91–11.39)	1	Open U	2–3	2–3
L. tomentosum var. *alpestre* *(L. sulfureum)*	32.75 ± 5.38 (26.10–44.27)	10.85 ± 1.63 (7.39–13.42)	1	Open U	3–4	2–3
L. moschatum *(L. moschatum* var. *moschatum)*	32.16 ± 5.15 (19.45–47.05)	9.14 ± 0.79 (7.88–11.12)	1	Open U	1–2	2–3
L. moschatum *(L. moschatum* var. *rhodium)*	33.06 ± 6.12 (20.26–48.22)	8.64 ± 0.86 (7.27–10.50)	1	Open U	1–2	1–2
L. micranthum *(L. moschatum var. micranthum)*	34.06 ± 6.32 (21.32–48.22)	8.65 ± 0.71 (7.76–10.34)	1	Continuous arc with incurved ends	1	1–2
L. ponticum subsp. *ponticum* *(L. ponticum)*	25.63 ± 4.27 (19.81–35.54)	11.31 ± 1.33 (8.12–12.90)	1	Open U	2–3	2
L. galactophyllum	24.54 ± 3.72 (17.85–29.59)	6.99 ± 0.84 (5.75–7.36)	1	Rounded	1–2	1–2
L. tschorochense	/	/	/	/	/	/
L. album subsp. *crinitum* *(L. vreemanii)*	26.58 ± 6.75 (15.45–40.12)	9.25 ± 3.20 (4.16–14.89)	1	Continuous arc with incurved ends	1	1–2

Table 7 (cont`d)

Taxon	Midrib parenchyma	Midrib Trachea	VB number	VB shape	PPL	SPL
L. orientale	27.67 ± 3.89 (21.01–33.11)	9.89 ± 1.14 (8.60–11.38)	1	Open U	1–2	2
L. multifidum	28.66±3.67 (22.21–34.34)	10.02±1.09 (8.33–12.31)	1	Open U	1–2	1–2
Galeobdolon *(L. galeobdolon* subsp. *montanum)*	24.57 ± 5.37 (13.82–33.28)	7.83 ± 1.32 (5.88–9.71)	1	Open U	1–2	2–3
L. bilgilii	32.06 ± 6.12 (22.26–50.11)	8.72 ± 0.68 (7.25–10.78)	1	Open U	2	2–3
L. ponticum subsp. *anatolicum*	25.41 ± 4.18 (18.67–34.87)	11.78 ± 1.21 (8.42–13.11)	1	Continuous arc with incurved ends	2–3	2
L. cappadocicum	23.54 ± 3.82 (16.68–28.71)	7.12 ± 0.77 (5.74–8.98)	1	Open U	2–3	2–3
L. amplexicaule subsp. *vanense*	20.33±4.44 (16.81-31.74)	7.96±1.65 (6.42-11.04)	1	Open U	1–2	1–2

VB: Vascular Bundle, PPL: Palisade Parenchyma Layer, SPL: Spongy Parenchyma Layer

Table 8. Characterization of the petiole components in *Lamium*. /; no data. TS shape: Transverse Section shape of the petioles

Taxon	**TS shape**	**Adaxial epidermis**	**Abaxial epidermis**	**Cortex cell**	**Trachea cell**
L. lycium	U-shaped	19.92 ± 5.24 (12.35–32.88)	21.01 ± 3.72 (14.93–27.56)	44.53 ± 8.20 (30.26–55.93)	9.61 ± 1.40 (7.33–12.29)
L. cariense	U-shaped	13.86 ± 2.00 (11.66–16.79)	16.78 ± 2.24 (13.36–20.31)	26.01 ± 5.14 (18.42–35.62)	13.31±1.57 (10.4715.95)
L. garganicum subsp. *striatum* *(L. pisidicum)*	V-shaped	21.49 ± 4.32 (14.88–27.14)	18.52 ± 3.18 (12.65–22.65)	34.56 ± 6.10 (23.63–46.17)	11.40 ± 1.80 (9.44–13.80)
L. garganicum subsp. *striatum* *(L. tenuiflorum)*	U-shaped	15.68 ± 3.45 (9.56–22.05)	16.64 ± 3.35 (11.27–22.18)	25.40 ± 6.58 (16.68–34.87)	10.73 ± 1.35 (8.76–12.95)
L. garganicum subsp. *striatum* *(L. garganicum* subsp. *reniforme)*	U-shaped	/	/	/	/
L. garganicum subsp. *striatum* *(L. garganicum* subsp. *nepetifolium)*	U-shaped	/	/	/	/
L. garganicum subsp. *rectum*	U-shaped	18.71 ± 3.66 (13.69 –25.91)	14.15 ± 4.19 (11.77– 22.14)	30.98 ± 4.66 (21.99–40.22)	11.04±1.11 (8.81 – 13.13)
L .garganicum subsp. *lasioclades*	U-shaped	18.71 ± 3.66 (13.69–25.91)	14.15 ± 4.19 (11.77–22.14)	30.98 ± 4.66 (21.99–40.22)	11.04 ± 1.11 (8.81–13.13)
L. garganicum subsp. *rectum* *(L. garganicum* subsp. *pulchrum)*	U-shaped	27.88 ± 7.04 (18.94–45.63)	25.90 ± 4.40 (20.61–33.32)	61.24 ±15.98 (34.71–97.25)	8.96 ± 1.95 (5.82–13.49)
L. garganicum subsp. *laevigatum*	U-shaped	27.08 ± 8.67 (10.82–42.66)	23.10 ± 3.31 (17.45–30.87)	51.28 ± 9.19 (36.02–71.15)	14.11 ± 3.00 (8.49–20.13)
L. garganicum subsp. *laevigatum* *(L. veronicifolium)*	U-shaped	20.27 ± 5.42 (11.03–28.58)	22.10 ± 2.09 (18.88–26.69)	44.33± 10.45 (29.74–56.28)	8.45 ± 2.18 (4.59–11.94)
L. microphyllum	U-shaped	18.59 ± 3.80 (11.53–24.36)	16.05 ± 3.03 (11.91–22.80)	31.84 ± 5.79 (22.38–44.17)	8.23 ± 1.03 (6.53–9.54)
L. cymbalariifolium	U-shaped	26.79 ± 4.14 (21.16–33.48)	27.45 ± 3.17 (22.66–35.12)	50.86 ±10.33 (27.52–60.16)	11.69 ± 2.26 (8.48–16.16)
L. sandrasicum	U-shaped	22.21 ± 8.96 (10.47–42.14)	20.96 ± 4.68 (13.37–30.21)	39.46 ± 7.53 (30.32–54.56)	9.74 ± 2.27 (6.49–12.86)
L. armenum subsp. *armenum*	U-shaped	28.21 ±7.47 (16.16–44.14)	32.90 ± 6.30 (19.60–42.00)	61.42 ± 7.06 (46.52–72.96)	9.68 ± 1.71 (6.08–12.73)
L. armenum subsp. *sintenisii*	U-shaped	21.54 ± 5.57 (11.62–37.01)	28.95 ± 8.20 (49.69–17.83)	31.83 ± 8.62 (22.93–53.42)	7.73 ± 1.88 (5.01–11.53)
L. purpureum *(L. purpureum* var. *purpureum)*	U-shaped	17.47 ± 1.90 (15.48–20.77)	15.11 ± 1.56 (14.22–19.18)	34.66 ±5.46 (27.49–42.87)	10.70 ± 1.30 (7.65–13.11)
L. purpureum *(L. purpureum* var. *aznavourii)*	U-shaped	28.67 ± 5.30 (25.30–40.22)	25.77 ± 4.12 (21.15–38.16)	57.98 ±15.37 (43.40–95.04)	14.66±2.85 (11.62–21.16)
L. eriocephalum subsp. *eriocephalum*	U-shaped	22.76±4.09 (13.41-28.67)	25.92±4.45 (18.51-36.29)	35.96±5.37 (24.81-46.34)	11.71±2.16 (8.93-16.43)
L .eriocephalum subsp. *glandulosidens*	U-shaped	24.67 ± 4.25 (18.09 –29.38)	29.78 ± 3.35 (25.13–37.25)	50.25 ±12.27 (33.64–86.02)	13.49 ± 2.58 (8.13–17.31)

Table 8 (cont`d) TS shape: Transverse Section shape of the petioles

Taxon	TS shape	Adaxial epidermis	Abaxial epidermis	Cortex cell	Trachea cell
L. amplexicaule subsp. amplexicaule var. amplexicaule (L. amplexicaule)	U-shaped	21.51±4.03 (13.35-32.56)	19.62±4.56 (13.78-23.55)	18.03±3.65 (13.58-23.82)	10.12±1.07 (8.46-12.73)
L. amplexicaule subsp. amplexicaule var. aleppicum (L. aleppicum)	U-shaped	23.51±5.03 (15.35-35.84)	21.62±3.76 (15.53-26.39)	34.54±5.97 (25.88-52.94)	10.62±1.56 (7.56-13.64)
L. macrodon	U-shaped	24.40 ± 3.94 18.00–32.71	26.58 ± 3.55 21.75–32.65	52.57 ± 15.66 31.65–97.89	11.82 ± 1.79 8.48–15.45
L. ehrenbergii	U-shaped	21.71 ± 3.85 (17.37–28.63)	20.48 ± 2.98 (16.44–27.13)	32.56 ± 6.12 (21.86–42.96)	6.74 ± 1.03 (5.48–7.94)
L. maculatum *(L. maculatum* var. *maculatum)*	U-shaped	14.17 ± 2.09 (10.40–17.44)	11.59 ± 1.90 (8.69–14.57)	34.87 ± 5.22 (27.48–43.86)	9.87 ± 1.40 (7.69–12.94)
L. villosifolium *(L. maculatum* var. *villosifolium)*	U-shaped	18.50 ± 4.17 (12.92–26.29)	19.43 ± 2.30 (15.47–24.93)	42.39 ± 8.48 (29.71–62.30)	9.08 ± 1.44 (6.20–12.01)
L. maculatum *(L. gundelsheimeri)*	U-shaped	17.74 ± 3.08 (13.22–23.83)	21.12 ± 2.55 (16.64–25.14)	42.59 ±10.23 (32.04–67.43)	16.74±1.75 (13.99–21.42)
L. maculatum *(L. truncatum)*	U-shaped	20.31±3.77 (14.15-26.72)	19.58±2.96 (13.46-23.80)	32.92±12.35 (26.46-62.52)	17.19±2.96 (11.80-23.18)
L. album subsp. *album* *(L. album)*	U-shaped	14.90 ± 2.25 (10.97–21.75)	14.07 ± 1.10 (12.27–15.25)	24.58 ± 3.51 (16.00–30.09)	8.75 ± 1.35 (6.35–10.45)
L. album subsp. *crinitum* *(L. crinitum)*	Open sickle shaped	18.98 ± 3.69 (14.37–26.10)	19.68 ± 2.71 (16.27–25.82)	28.75 ± 3.58 (20.45–34.19)	12.60 ± 1.53 (9.07–14.86)
L. tomentosum var. *tomentosum*	U-shaped	19.73 ± 4.54 (10.92–25.37)	29.28 ± 5.73 (18.60–39.20)	55.08 ±12.38 (40.70–79.16)	10.06 ± 1.54 (7.78–12.68)
L. tomentosum var. *alpestre* *(L. sulfureum)*	U-shaped	18.68 ± 2.61 (15.57–24.26)	20.47 ± 3.54 (12.93–25.08)	46.05 ±11.18 (29.17–65.75)	13.37±1.90 (10.97–18.29)
L. moschatum *(L. moschatum* var. *moschatum)*	U-shaped	18.92 ± 2.12 (14.74–22.16)	19.21 ± 2.06 (15.41–24.18)	45.78 ±8.78 (30.12–64.11)	14.78±1.55 (12.44–20.14)
L. moschatum *(L. moschatum* var. *rhodium)*	U-shaped	19.92 ± 2.37 (15.30–23.09)	19.12 ± 2.07 (16.60–23.09)	47.30 ± 9.63 (32.02–65.44)	15.40±1.84 (13.42–20.13)

Table 8 (cont`d) TS shape: Transverse Section shape of the petioles

Taxon	TS shape	Adaxial epidermis	Abaxial epidermis	Cortex cell	Trachea cell
L. micranthum *L. moschatum var. micranthum*	U-shaped	20.54 ± 2.43 (15.45 – 23.12)	19.42 ± 2.34 (16.54–23.39)	46.43 ±8.65 (33.12 – 64.40)	15.20±1.54 (14.12–21.33)
L. ponticum subsp. *ponticum* *L. ponticum*	U-shaped	19.13 ± 2.15 (15.40–22.41)	20.59 ± 2.44 (16.01–23.72)	43.08 ± 7.31 (28.98–58.43)	13.60±1.47 (11.32–15.84)
L. galactophyllum	U-shaped	19.07 ± 5.01 (12.99–28.18)	17.69 ± 2.55 (13.41–21.21)	33.86 ± 7.57 (24.28–57.40)	8.70 ± 0.82 (7.60–9.94)
L. tschorochense	Open sickle shaped	18.17 ± 4.61 (11.69–27.45)	16.29 ± 3.11 (12.45–20.02)	30.33 ± 6.58 (21.78–54.11)	8.66 ± 1.45 (7.76–10.11)
L. album subsp. *crinitum* *L. vreemanii*	Open sickle shaped	24.81 ± 6.53 (13.22–32.33)	19.25 ± 4.53 (11.55–27.15)	42.11 ±18.99 (17.65–87.74)	13.36± 3.37 (9.68–23.46)
L. orientale	U-shaped	22.25 ± 3.48 (17.44–27.40)	20.27 ± 2.77 (15.74–24.32)	44.27 ±11.67 (34.79–60.82)	13.66 ± 3.87 (8.48–19.94)
L. multifidum	U-shaped	23.55±2.33 (18.31–28.44)	21.47±2.34 (16.81–25.34)	46.77±10.33 (35.89–62.65)	14.64±3.65 (9.49–20.34)
Galeobdolon *L. galeobdolon* subsp. *montanum*	U-shaped	12.65 ± 1.55 (10.22–15.89)	13.41 ± 2.19 (9.51–17.19)	30.70 ± 6.40 (23.79–47.07)	7.13±1.04 (6.18–9.04)
L. bilgilii	U-shaped	23.51±2.37 (19.31–27.74)	22.47±2.19 (18.81–24.89)	62.72 ± 6.07 (48.52–75.16)	9.62 ± 1.41 (6.12–12.71)
L. ponticum subsp. *anatolicum*	U-shaped	21.14 ± 2.33 (16.78–23.41)	21.36 ± 2.78 (17.01–24.21)	31.72 ± 5.42 (23.45–48.07)	8.78 ± 1.10 (7.87–10.06)
L. cappadocicum	U-shaped	25.51±5.03 (16.35-36.94)	24.65±3.71 (15.53-31.39)	34.77±5.97 (25.17-52.44)	10.17±1.87 (7.78-13.71)
L. amplexicaule subsp. *vanense*	U-shaped	22.18±5.17 (14.35-33.45)	22.77±3.88 (15.47-27.24)	32.55±5.97 (24.81-51.94)	11.62±1.17 (7.78-14.14)

Table 9. Characterization of the petiole components in *Lamium*. MB: Median bundle, LB: Lateral bundle, COL: Collenchyma, /; no data.

Taxon	**MB number**	**MB shape**	**LB number**	**COL (corners)**	**COL Layer**
L. lycium	2	Open U-shaped with incurved ends	2	+	1-2
L. cariense	2	Open U-shaped with incurved ends	2	+	1-2
L. garganicum subsp. *striatum* *(L. pisidicum)*	2	Open U-shaped	2	+	1-2
L. garganicum subsp. *striatum* *(L. tenuiflorum)*	2	Open U-shaped	2	Absent	Absent
L. garganicum subsp. *striatum* *(L. garganicum* subsp. *reniforme)*	/	/	/	/	/
L. garganicum subsp. *striatum* *L. garganicum* subsp. *nepetifolium*	/	/	/	/	/
L. garganicum subsp. *rectum*	2	Open U-shaped with incurved ends	2	+	1
L. garganicum subsp. *lasioclades*	2	Open U-shaped with incurved ends	2	+	1-2
L. garganicum subsp. *rectum* *(L. garganicum* subsp. *pulchrum)*	2	Round U-shaped	2	+	1-2
L. garganicum subsp. *laevigatum*	2	Open U-shaped with incurved ends	2	+	1-2
L. garganicum subsp. *laevigatum* *(L. veronicifolium)*	2	Open U-shaped	2	Absent	Absent
L. microphyllum	2	Open U-shaped + rounded	2	Absent	Absent
L. cymbalariifolium	2	Round U-shaped	2	Absent	Absent
L. sandrasicum	2	Round U-shaped	/	Absent	Absent
L. armenum subsp. *armenum*	2	Open U-shaped	2	+	1-2
L. armenum subsp. *sintenisii*	2	Open U-shaped	2	+	1-2
L. purpureum *(L. purpureum* var. *purpureum)*	2	Open U-shaped	2	+	1

Table 9 (cont`d) MB: Median bundle, LB: Lateral bundle, COL: Collenchyma, /; no data.

Taxon	MB number	MB shape	LB number	COL (corners)	COL Layer
L. purpureum *(L. purpureum* var. *aznavourii)*	2	Rounded	2	+	1-2
L. eriocephalum subsp. *eriocephalum*	2	Open U-shaped	2	Absent	Absent
L .eriocephalum subsp. *glandulosidens*	2	Open U-shaped	2	Absent	Absent
L. amplexicaule subsp. amplexicaule var. amplexicaule *(L. amplexicaule)*	2	Open U-shaped	2	Absent	Absent
L. amplexicaule subsp. amplexicaule var. aleppicum *(L. aleppicum)*	2	Open U-shaped	2	Absent	Absent
L. macrodon	2	Open U-shaped	2	Absent	Absent
L. ehrenbergii	2	Rounded	2	+	1-2
L. maculatum *(L. maculatum* var. *maculatum)*	2	Open U-shaped with incurved ends	2	+	1-5
L. villosifolium *(L. maculatum* var. *villosifolium)*	2	Open U-shaped with incurved ends	2	+	1-2
L. maculatum *(L. gundelsheimeri)*	2	Open U-shaped with incurved ends	2	+	1-2
L. maculatum *(L. truncatum)*	2	Open U-shaped with incurved ends	2	+	1-2
L. album subsp. *album* *(L. album)*	2	Open U-shaped with incurved ends	2	+	1-3
L. album subsp. *crinitum* *(L. crinitum)*	2	Open U-shaped	2	+	1-4

Table 9 (cont`d) MB: Median bundle, LB: Lateral bundle, COL: Collenchyma, /; no data.

Taxon	MB number	MB shape	LB number	COL (corners)	COL Layer
L. tomentosum subsp. *tomentosum*	2	Open U-shaped with incurved ends	2	+	1-3
L. tomentosum var. *alpestre* *(L. sulfureum)*	2	Open U-shaped	2	+	1-2
L. moschatum *(L. moschatum* var. *moschatum)*	2	Open U-shaped	2	+	1-2
L. moschatum *(L. moschatum* var. *rhodium)*	2	Open U-shaped	2	+	1-3
L. micranthum *(L. moschatum var. micranthum)*	2	Open U-shaped with incurved ends	2	+	1-2
L. ponticum subsp. *ponticum* *(L. ponticum)*	2	Open U-shaped with incurved ends	2	+	1-3
L. galactophyllum	2	Rounded	2	+	1-2
L. tschorochense	2	Round U-shaped	2	+	1-2
L. album subsp. *crinitum* *(L. vreemanii)*	2	Open U-shaped	/	+	1-3
L. orientale	2	Open U-shaped	2	+	1-2
L. multifidum	2	Open U-shaped	2	+	2-3
Galeobdolon *(L. galeobdolon* subsp. *montanum)*	2	Open U-shaped with incurved ends	2	+	1-2
L. bilgilii	2	Open U-shaped	2	-	-
L. ponticum subsp. *anatolicum*	2	Open U-shaped	2	+	1-2
L. cappadocicum	2	Open U-shaped	2	Absent	Absent
L. amplexicaule subsp. *vanense*	2	Open U-shaped	2	Absent	Absent

Table 10. Voucher specimens of the genus *Lamium* examined for their anatomical properties.

Taxon	**Locality**
L. lycium	Turkey, Muğla, Fethiye, Babadağ, F.Celep 1789 18.04.2013
L. cariense	Turkey, Antalya, Elmalı, F.Celep 1797 18.04.2013
L. pisidicum	Turkey, Isparta, Davraz mountain, F.Celep 1914 01.06.2013
L. tenuiflorum	Turkey, Karaman, Ermenek, F.Celep 1819 21.04.2013
L. garganicum subsp. *reniforme*	Turkey, Kahramanmaraş, Binboğa Mt, F.Celep 1845 25.4.2013
L. garganicum subsp. *nepetifolium*	Turkey, Adana, Saimbeyli, F.Celep 1847 25.04.2013
L. garganicum subsp. *rectum*	Turkey, Kahramanmaraş, Süleymanlı, F.Celep 3816 20.05.2015
L .garganicum subsp. *lasioclades*	Turkey, Kahramanmaraş, Elbistan, F.Celep 1842 24.04.2013
L. garganicum subsp. *pulchrum*	Turkey, Niğde, Aladağlar, F.Celep 2005 25.10.2013
L. garganicum subsp. *laevigatum*	Turkey, Bursa, Uludag, F.Celep 3756, 24.4.2014
L. veronicifolium	Turkey, Bursa, Uludağ, BB 3916, 10.07.2013
L. microphyllum	Turkey, Muğla, Fethiye Babadağ, F.Celep 1790 18.04.2013
L. microphyllum	Turkey, Denizli, Honaz Mountain, F.Celep, 2014
L. cymbalariifolium	Turkey, Antalya, Elmalı, F.Celep 3780 27.06.2014
L. sandrasicum	Turkey, Muğla, Sandras mountain, BB 3921, 12.07.2013
L. armenum subsp. *armenum*	Turkey, Erzurum, Aşkale, F.Celep 1994 28.07.2013
L. armenum subsp. *sintenisii*	Turkey, Kastamonu, Ilgaz Mt, F.Celep 2002 30.07.2013
L. purpureum var. *purpureum*	Turkey, Kızılcahamam, Işık Mt, F.Celep 1854 12.05.2013
L. purpureum var. *aznavourii*	Turkey, Istanbul, Beykoz, Göksu, F.Celep 2340 09.05.2014
L. eriocephalum subsp. *eriocephalum*	Turkey, Niğde, Aladağlar , BB 3913, 08.07.2013
L .eriocephalum subsp. *glandulosidens*	Turkey, Antalya, Alanya, Gökbel F.Celep 3558, 13.07.2014
L. amplexicaule	Turkey, Muğla, Fethiye, Babadağ, F.Celep 1794 18.04.2013
L. aleppicum	Turkey, Kahramanmaraş Ahırdağı, F.Celep 1836 24.04.2013
L. macrodon	Turkey, Antalya, Alanya, Gökbel, F.Celep 1811 20.04.2013
L. ehrenbergii	Turkey, Antalya, Elmalı, F.Celep 1917 02.06.2013
L. maculatum var. *maculatum*	Turkey, Trabzon, Maçka, F.Celep 1878 15.05.2013
L. maculatum var. *villosifolium*	Turkey, Amasya, Tavşan Mt, F.Celep 1856 13.05.2013
L. gundelsheimeri	Turkey, Rize, Çamlıhemşin, F.Celep 1980 24.07.2013
L. truncatum	Turkey, Hatay, İskenderun, F.Celep 1825 22.04.2013
L. album subsp. *album*	Turkey, Mersin, Fındıkpınarı, F.Celep 1823 22.04.2013
L. crinitum	Turkey, Amasya, Tavşan Mt, F.Celep 1855 13.05.2013
L. tomentosum var. *tomentosum*	Turkey, Van, OT 8581, 2013
L. sulfureum	Turkey, Bayburt, Çaykara, F.Celep 1977 24.07.2013
L. moschatum var. *moschatum*	Turkey, Antalya, Olimpos, F.Celep 1798 17.04.2013
L. moschatum var. *rhodium*	Turkey, Denizli, F.Celep 1780, 16.04.2013
L. moschatum var. *micranthum*	Turkey, Hatay, F.Celep 3829, 21.05.2015
L. ponticum	Turkey, Giresun, Tamdere, F.Celep 187114.05.2013
L. galactophyllum	Turkey, Erzurum, Tortum, F.Celep 1896 17.05.2013
L. tschorochense	Turkey, Artvin, Yusufeli, F.Celep 1886 17.05.2013
L. vreemanii	Turkey, Erzurum, Tortum, F.Celep 1989 28.07.2013
L. orientale	Turkey, Nevşehir, Göreme, F.Celep 2457 12.05.2014
L. multifidum	Turkey: Erzurum, Pazaryolu, F.Celep, 2015
L. galeobdolon subsp. *montanum*	Turkey, Rize, Çamlıhemşin, F.Celep 1882 16.05.2013
L. ponticum subsp. *anatolicum*	Turkey, Kastamonu, Kure, F.Celep 3840, 01.05.2015
L. bilgili	Turkey, Burdur, Altinyayla, F.Celep 3860, 05.06.2015
L. cappadocicum	Turkey, Hasan mountain, F.Celep 3629, 11.07.2014
L. amplexicaule subsp. *vanense*	Turkey, Van, Güzeldere Geçidi, F.Celep, 2015

3.4 Trichome Micromorphology

Different types of observed trichomes and their distribution in *Lamium* species are provided in Table 11. Selected SEM micrographs of various trichome types are illustrated in Figures 34-40. In general, two types of trichomes are observed on leaf blades, calyces and stems; non-glandular and glandular trichomes. These two types can further be divided into subtypes.

Non-glandular trichomes (NG) can be categorized as; short (NG1) and long (NG2). Glandular trichomes (G) can be categorized as; capitate (G1-G2-G3) and peltate (G4) trichomes. Subsessile or sessile (G1), short stalked (G2) and long stalked (G3) are three subtypes of capitate glandular trichomes. The most common type of trichomes in studied species is short (NG1) and long (NG2) nonglandular trichomes and short stalked (G2) capitate glandular trichomes.

3.4.1 Nonglandular Trichomes

Among nonglandular trichomes, size, cell number and presence of papillae on trichome surface are considered as valuable characters (Fig. 34). In terms of size, simple non-glandular trichomes are either short (NG1; from 50 µm in *L. microphyllum*; Fig. 34 A to 1000 µm in *L. tomentosum* var. *alpestre*), long (NG2 from 1500 µm in *L. tomentosum* var. tomentosum; Fig. 36 C&D, *L. eriocephalum* subsp. *glandulosidens*; Fig. 37 C&D and *L. orientale*; Fig. 38 C&D to 2000 µm in *L. bilgilii*; Fig. 39).

Simple nonglandular trichomes have some characteristic features on their surface such as they have papillate surfaces (e.g. *L. garganicum* subsp. *lasioclades* and *L. ponticum* subsp. *anatolicum*, Figs. 34 F and 40, respectively). Detailed SEM analysis revealed that, in all examined specimens, NG trichomes have papillate surfaces.

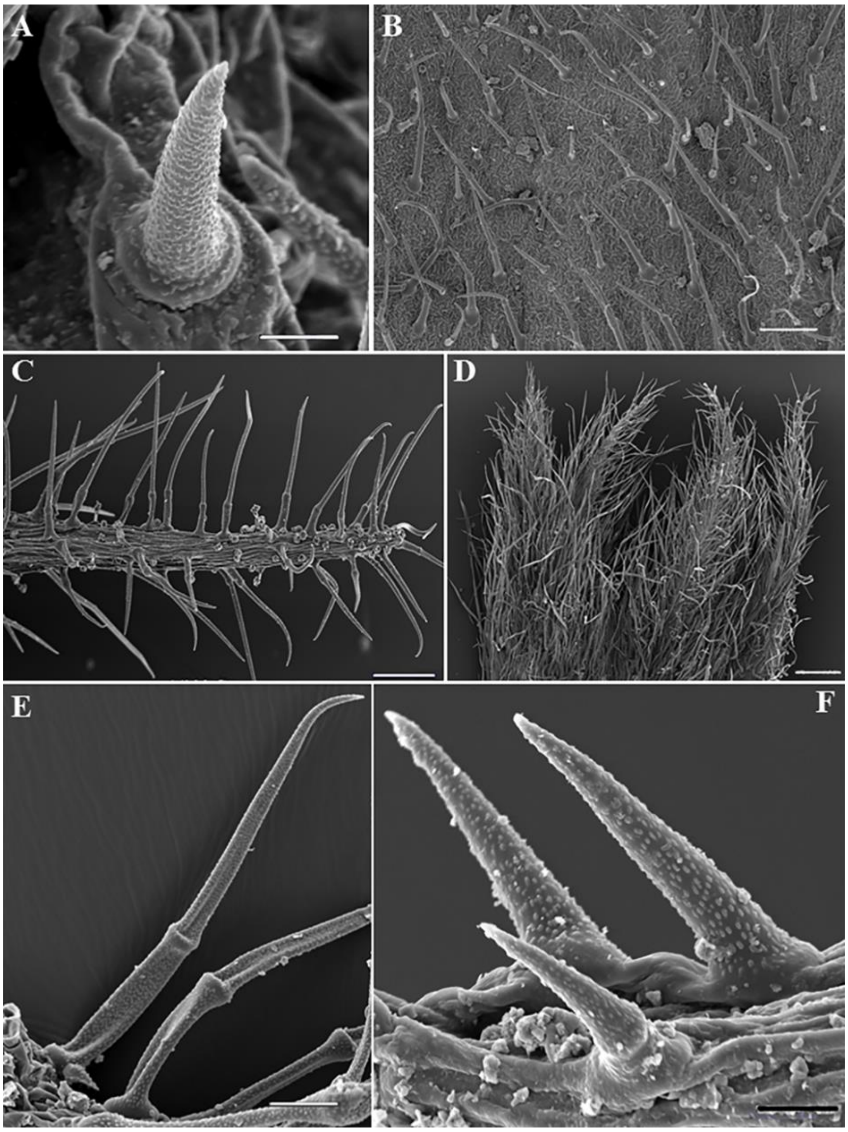


Figure 34. Scanning electron micrographs of nonglandular trichomes of selected *Lamium* taxa. A, *L*. *microphyllum*. Simple short nonglandular trichomes on calyx (scale 20 µm). B, *L*. *album* subsp. *album*. Long and short uniseriate nonglandular trichomes at adaxial leaf surface (scale 200 µm). C, *L*. *lycium*. Long nonglandular trichomes on the apex of calyx (scale 200 µm). D, *L*. *amplexicaule* subsp. *amplexicaule* var. *aleppicum*. Simple long nonglandular trichomes on calyx (scale 500 µm). E, *L*. *cappadocicum*. Long uniseriate nonglandular trichome at adaxial leaf surface (scale 50 µm). F, *L*. *garganicum* subsp. *lasioclades*. Simple short nonglandular trichomes on the apex of calyx (scale 20 µm).

3.4.2 Glandular Trichomes

Analysis of LM and SEM studies revealed three types of capitate glandular trichomes in *Lamium* species (Fig. 35). The first type (G1) represents the subsessile and sessile capitate glandular trichomes, with a basal cell, a stalk cell and a unicellular head (e.g. *L. armenum* subsp. *armenum*; Fig. 35 A) The second form (G2) respresents the short stalked capitate glandular trichomes (length of the stalk up to 20 µm; e.g. *L. cymbalarifolium*; Fig. 35 D and *L. garganicum* subsp. *rectum*; Fig. 35 G). The third form (G3) is of long stalked glandular trichomes which are found only in the new taxon (length of the stalk up to 200 µm; e.g. in *L. bilgilii*, Figure 39). Peltate glandular trichomes (G4) consist of a basal cell, a short stalk cell and a multicellular head (e.g. *L. maculatum*; Fig. 35 B).

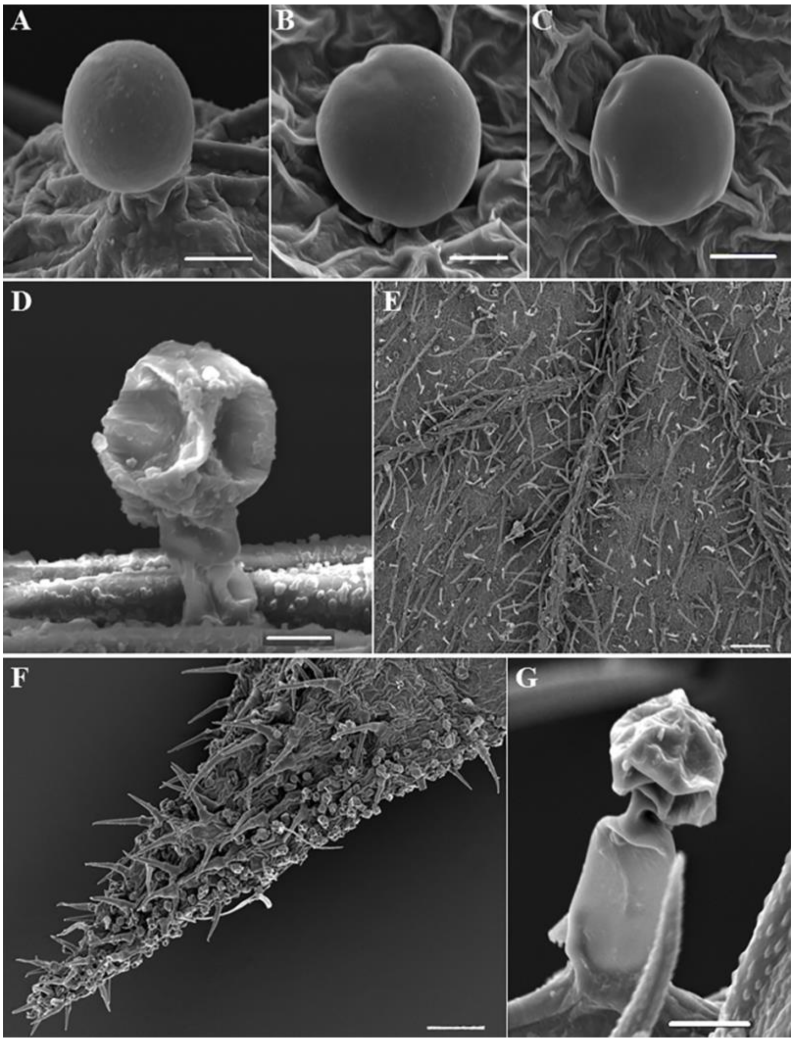


Figure 35. Scanning electron micrographs of glandular trichomes of genus *Lamium*. A, *L. armenum* subsp. *armenum*. Short stalked capitate glandular trichomes on the calyx (scale 20 μm). B, *L. maculatum*. Short stalked capitate glandular trichomes on the abaxial leaf surface (scale 20 μm). C, *L. maculatum*. Short stalked capitate glandular trichomes on the abaxial leaf surface (scale 20 μm). D, *L. cymbalarifolium*. Short stalked capitate glandular trichomes at abaxial leaf surface (scale 20 μm). E, *L. album* subsp. *album*. short stalked capitate glandular and nonglandular trichomes on the abaxial leaf surface (scale 200 μm). F, *L.microphyllum*. Simple short nonglandular and short stalked capitate glandular trichomes on the apex of calyx (scale 200 μm). G, *L. garganicum* subsp. *rectum*. Short stalked capitate glandular trichomes on the apex of calyx (scale 20 μm).

3.4.3 Systematic Implications of Trichome Morphology

Trichomes can be of great systematic significance and various trichome types are used for diagnostic purposes in association with other characters (Khokhar et al., 2012). Mennema (1989) have reported that glandular hairs are not observed on the leaves of the genus *Lamium*. According to the morphological description of various species of *Lamium* by Mill (1982), the calyx is reported to be glandular. According to the detailed investigation of the indumentum, various types of trichomes are found to be taxonomically informative in the genus *Lamium*. Basically, there are two types of trichomes, as nonglandular and glandular trichomes. These two types can be further divided in subtypes however; nonglandular and glandular hairs are found on stems, upper and lower side of the leaves and calyces. Such that, both nonglandular and glandular hairs are found particularly at the tip of calyces.

The anatomical observations on various *Lamium* species showed that glandular hairs are present on the stem, petiole, leaf, bract, bracteole, calyx, corolla and even generative organs of the investigated taxa, which were also indicated previously, (*L. lycium*, Baran and Ozdemir, 2009 and *L. moschatum* var. *rhodium*, Baran and Ozdemir, 2011). Two main types of glandular hairs, peltate and capitate, can be distinguished by head size and stalk length (Abu-Asab & Cantino, 1987). Also, *L. pisidicum* bears capitate and peltate hairs as lately reported in some *Salvia* species in the literature (Baran et al., 2010a, b; Baran and Ozdemir, 2013; Kahraman et al., 2010). Peltate glandular hairs with a four-celled head were reported for *Lamium galeobdolon* (Uphof and Hummel, 1962). In addition, peltate glandular hairs which are more than 4-celled and long stalked were reported in *L. pisidicum* (Baran and Ozdemir, 2013).

Lamium lycium bears both capitate hairs and peltate hairs (Baran & Ozdemir, 2009) while *L. moschatum* var. *rhodium* bears capitate glandular hairs which have cup-shaped head and both the peltate hairs (Baran & Ozdemir, 2011). The most common structure of peltate hairs of Lamiaceae is a secretory head of four central cells and 6-14 peripheral cells (Werker 1993).

Scanning electron microscopy investigations revealed that, the new taxa; *L. bilgilii* bears the long non-glandular trichomes, which is observed only in this particular species. The non-glandular trichomes on the stem are taxonomically informative particularly at the species level; such as, L. garganicum subsp. laevigatum do not bear nonglandular trichomes on the stem. However, other members of the `*garganicum* complex` have nonglandular trichomes on their stem.

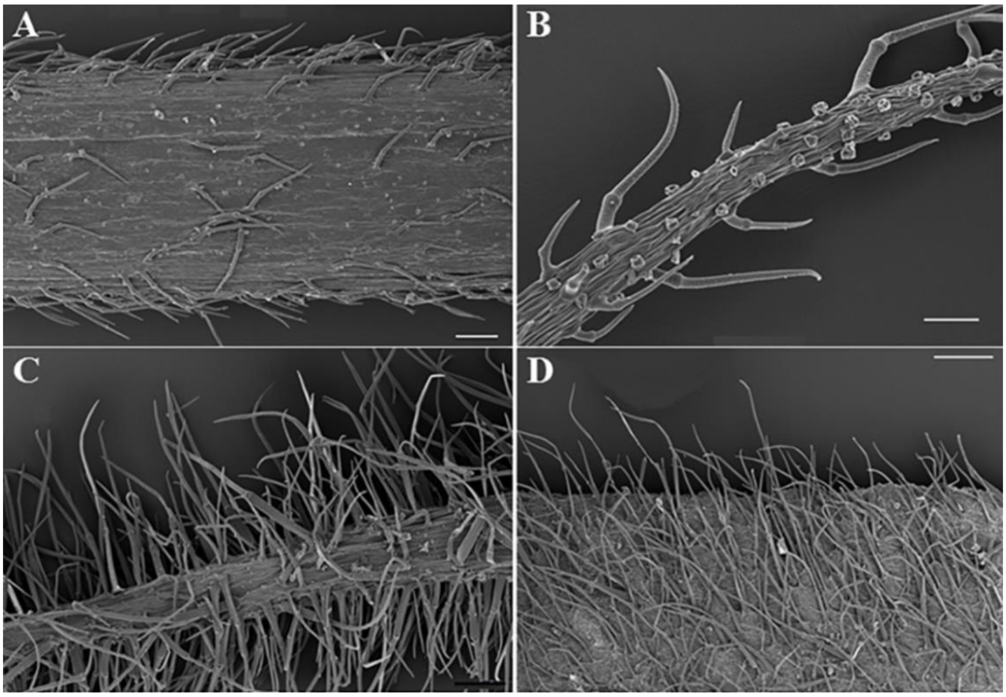


Figure 36. SEM micrographs of trichomes of; A&B, *L. villosifolium*, nonglandular trichomes on the stem (A) and nonglandular and capitate glandular trichomes the calyx (B) (scale 500 µm, 100 µm respectively) C&D, *L. tomentosum* var. *tomentosum*, long nonglandular trichomes on the calyx (C) and the adaxial leaf surface (D) (scale 200 µm, 500 µm respectively)

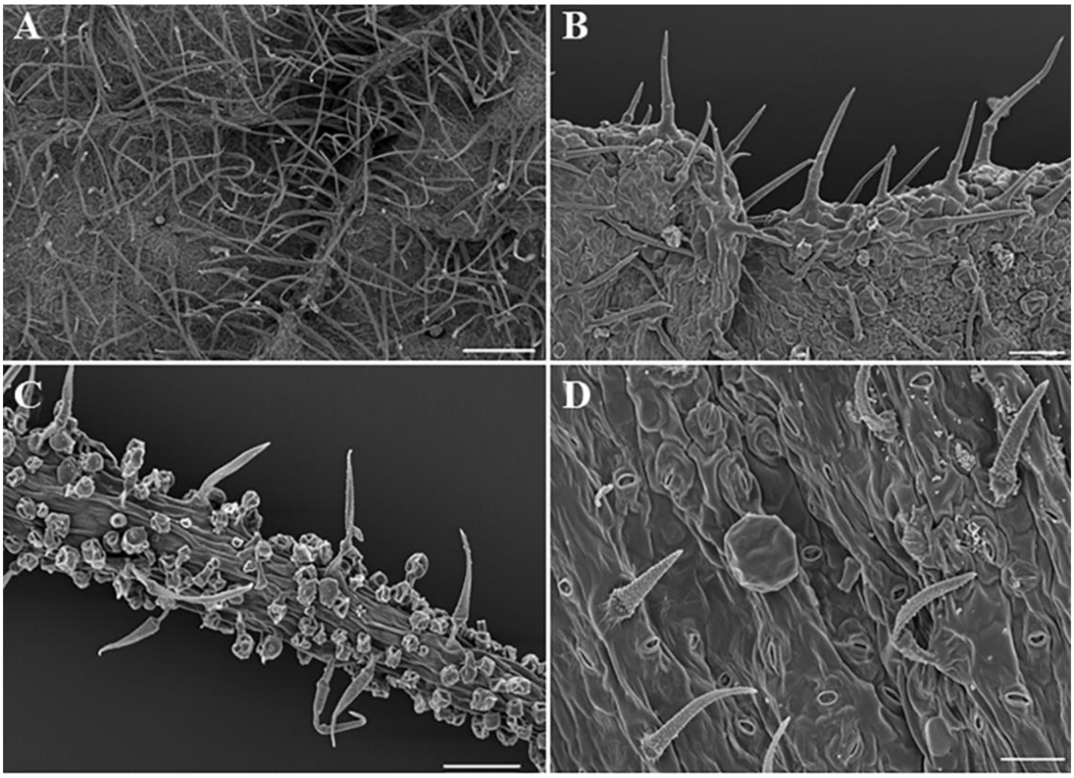


Figure 37. SEM micrographs of trichomes of; A, *L. lycium*, nonglandular trichomes on the abaxial leaf surface (scale 200 µm) B, *L. armenum* subsp. *armenum* nonglandular and capitate glandular trichomes on the abaxial leaf surface (scale 100 µm) C&D, *L. eriocephalum* subsp. *glandulosidens.* Nonglandular and capitate glandular trichomes on the calyx (C) and the abaxial leaf surface (D) (scale 100 µm, 50 µm respectively)

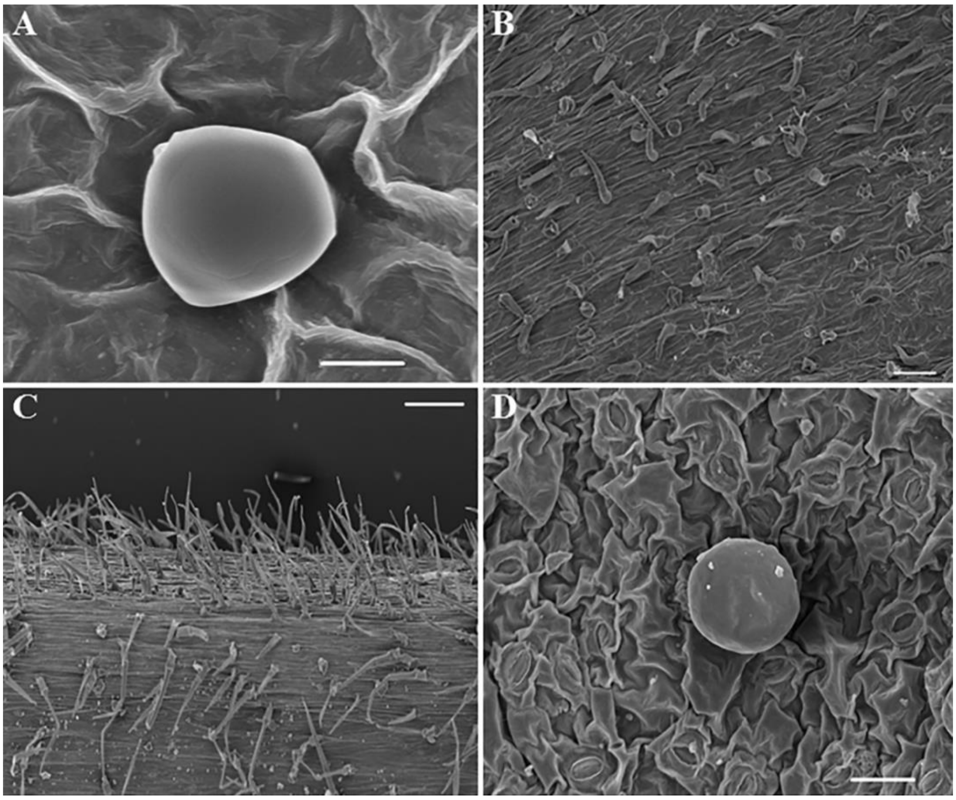


Figure 38. SEM micrographs of trichomes of; A, *L. micrantum*, peltate trichomes on the abaxial leaf surface (scale 10 µm) B, (Genus *Galeobdolon*) *L. galeobdolon* subsp. *montanum*, nonglandular and peltate trichomes on the calyx (scale 100 µm) C&D, *L. orientale*, Nonglandular trichomes on the stem (C) peltate trichomes on the abaxial leaf surface (D) (scale 200 µm, 20 µm respectively)

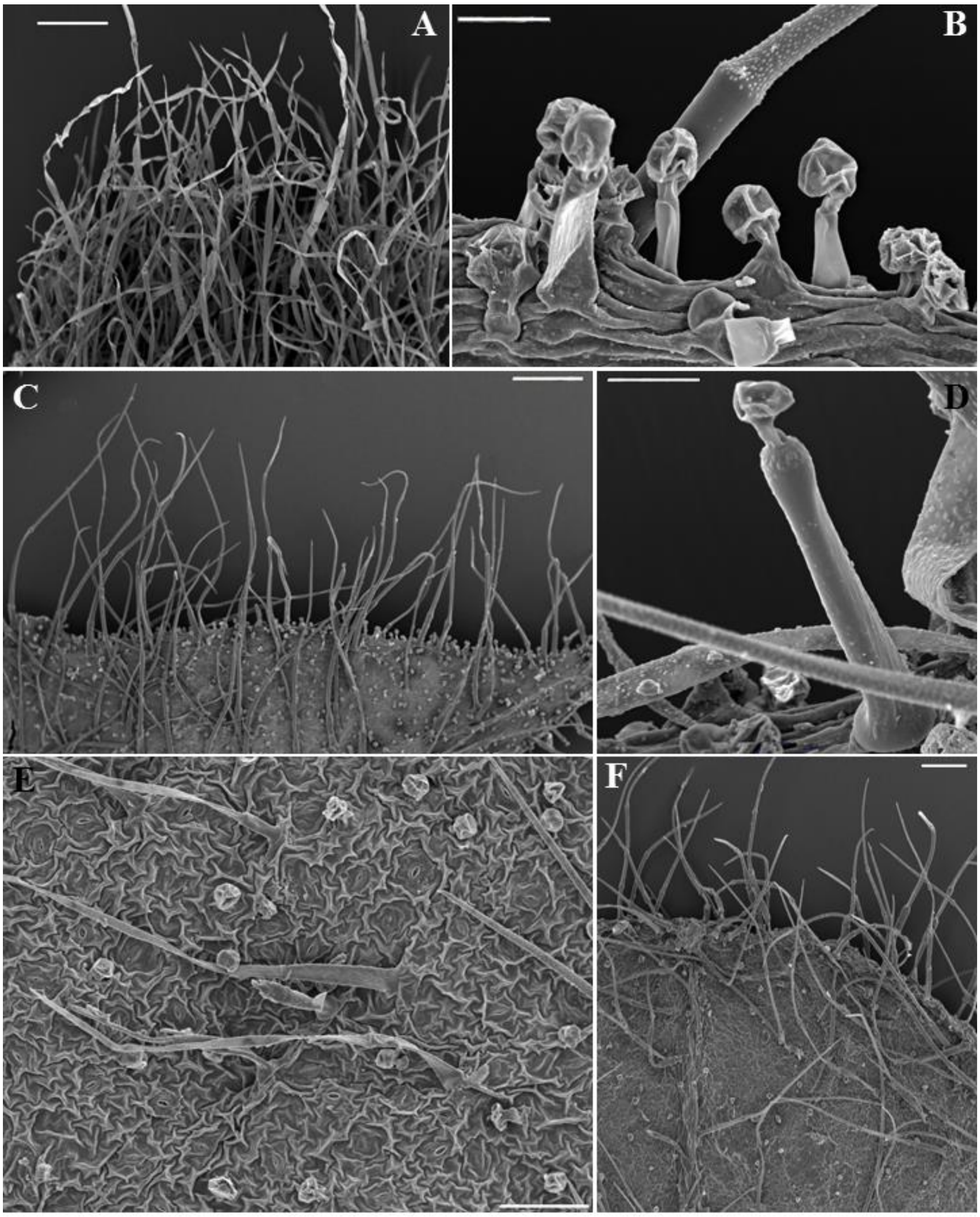


Figure 39. SEM micrographs of trichomes of; *L. bilgilii*. A; long nonglandular trichomes on the stem, B; short stalked capitate glandular trichomes on the calyx, C; long nonglandular trichomes on the calyx, D; long stalked capitate glandular trichomes on the calyx, E; long nonglandular and short stalked capitate glandular trichomes on the adaxial leaf surface, F; long nonglandular and peltate glandular trichomes on the abaxial leaf surface (scale bars: A; 200 μm, B; 50 μm, C; 500 μm, D; 50 μm, E; 100 μm, F; 200 μm)

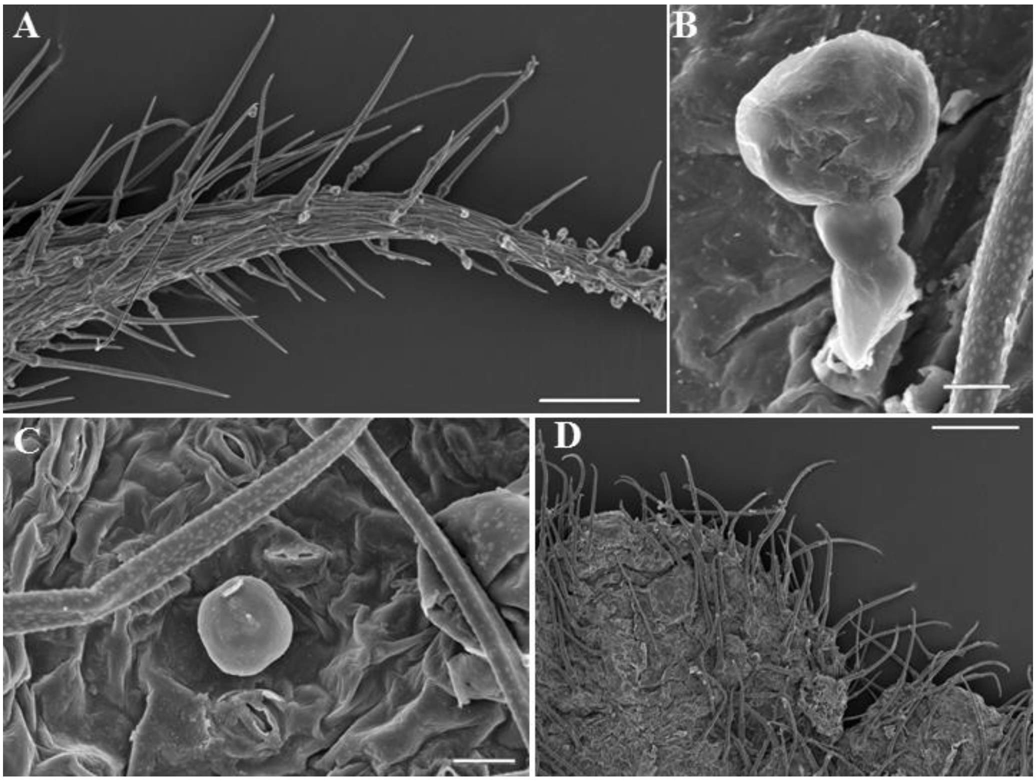


Figure 40. SEM micrographs of trichomes of; *L. ponticum* subsp. *anatolicum*. A; long nonglandular and short stalked capitate glandular trichomes on the calyx teeth, B; short stalked capitate glandular trichomes on the calyx, C; peltate glandular trichomes on the abaxial leaf surface, D; long nonglandular trichomes on the adaxial leaf surface (scale bars: A; 200 µm, B; 10 µm, C; 20 µm, D; 500 µm)

***In Table 11, taxa in parenthesis are the synonyms of the taxa written in red.**

Table 11. Charazterization of the trichome components in *Lamium* species.

	Leaf						**Stem**			**Calyx**		
	Abaxial surface			**Adaxial surface**								
	NG (NG1 + NG2)	**G (G1+ G2+G3)**	**PELTAT (G4)**	**NG (NG1 + NG2)**	**G (G1+G2 +G3)**	**PELTAT (G4)**	**NG (NG1 + NG2)**	**G (G1+G2+G3)**	**PELTAT (G4)**	**NG (NG1 + NG2)**	**G (G1+ G2+G3)**	**PELTAT (G4)**
L. lycium	+++	-	-	+++	-	-	+++	+		+++	+	-
L. cariense	+++	++	+	+++	-	-	+	-	-	++	+	-
L. garganicum subsp. *striatum* (*L. pisidicum)*	+	-	+	+	-	-	-	-	-	++	+	+
L. garganicum subsp. *striatum* (*L. tenuiflorum)*	+++	-	-	+++	-	+	+++	-	-	+++	+	+
L. garganicum subsp. *striatum* (*L. garganicum* subsp. *reniforme)*	+	-	-	+	-	-	+	-	-	+	+	+
L. garganicum subsp. *striatum* (*L. garganicum* subsp. *nepetifolium)*	+	-	+	+	-	-	+	-	-	++	+	++
L. garganicum subsp. *rectum*	+++	-	+	+++	-	-	+	-	-	++	+	+
L. garganicum subsp. *lasioclades*	+++	-	++	+++	-	-	++++	-	-	+++	+	+
L. garganicum subsp. *laevigatum*	-	-	++	-	-	+	-	-	+	++	-	++
L. garganicum subsp. *laevigatum* (*L. veronicifolium)*	++	-	-	+++	-	-	-	-	-	+++	+	+

Table 11 (cont`d) NG: Nonglandular, G: Glandular, +++, dominant; ++, present; + rarely present; -, absent

	Leaf						Stem			Calyx		
	Abaxial surface			Adaxial surface								
	NG (NG1 + NG2)	**G (G1+ G2+G3)**	**PELTAT (G4)**	**NG (NG1 + NG2)**	**G (G1+ G2+G3)**	**PELTAT (G4)**	**NG (NG1 + NG2)**	**G (G1+ G2+G3)**	**PELTAT (G4)**	**NG (NG1 + NG2)**	**G (G1+ G2+G3)**	**PELTAT (G4)**
L. microphyllum	+	-	+	++	-	+	-	-	-	+	+	+
L. cymbalarifolium	-	-	-	-	+	+	-	-	-	+++	++	+
L. sandrasicum	+	-	++	+	-	+	+	-	+	+++	+++	++
L. armenum subsp. *armenum*	++	-	++	++	-	-	-	-	+	+++	+++	-
L. armenum subsp. *sintenisii*	++	-	+	++	-	++	-	-	-	+	++	-
L. ehrenbergii	++	-	+	++	-	-	+	-	-	+++	+	+
L. purpureum *(L. purpureum* var. *purpureum)*	++	-	-	++	-	-	+	-	-	++	+	+
L. purpureum *(L. purpureum* var. *aznavourii)*	+	-	-	++	-	-	+	-	-	+++	+	+
L. eriocephalum subsp. *eriocephalum*	+++	-	++	+++	-	-	+	-	-	++++	+++	+
L. eriocephalum subsp. *glandulosidens*	+++	-	+	+++	-	+	+	-	-	++++	+++	+

Table 11 (cont`d) NG: Nonglandular, G: Glandular, +++, dominant; ++, present; + rarely present; -, absent

	Leaf						**Stem**			**Calyx**		
	Abaxial surface			**Adaxial surface**								
	NG (NG1 + NG2)	**G (G1+ G2+G3)**	**PELTAT (G4)**	**NG (NG1 + NG2)**	**G (G1+ G2+G3)**	**PELTAT (G4)**	**NG (NG1 + NG2)**	**G (G1+ G2+G3)**	**PELTAT (G4)**	**NG (NG1 + NG2)**	**G (G1+ G2+G3)**	**PELTAT (G4)**
L. eriocephalum subsp. *glandulosidens*	+++	-	+	+++	-	+	+	-	-	++++	+++	+
L. amplexicaule subsp. amplexicaule var. amplexicaule *(L. amplexicaule)*	+	-	-	++	-	-	+	-	-	+++	+	+
L. amplexicaule subsp. amplexicaule var. aleppicum *(L. aleppicum)*	++	-	+	++	-	+	+++	-	-	++++	+	+
L. maculatum *(L. maculatum* var. *maculatum)*	+	-	-	++	-	-	++	-	-	+++	+	+
L. villosifolium *(L. maculatum* var. *villosifolium)*	+	-	+	+	-	-	+	+	-	++	+	+
L. maculatum *(L. gundelsheimeri)*	+++	-	++	+++	-	+	++	-	+	++	+	+
L. maculatum *(L. truncatum)*	+++	-	+	+++	-	++	++	-	+	++	++	+
L. album subsp. *album* *(L. album)*	++	-	+	++	-	+	++	-	+	++	+	++
L. tomentosum var. *tomentosum*	+++	-	++	+++	-	+	+	-	+	++++	+	+
L. tomentosum var. *alpestre* *(L. sulfureum)*	++		++	+++	-	-	-	-	-	+++	+	+

Table 11 (cont`d) NG: Nonglandular, G: Glandular, +++, dominant; ++, present; + rarely present; -, absent

	Leaf						Stem			Calyx		
	Abaxial surface			Adaxial surface								
	NG (NG1 + NG2)	**G (G1+ G2+G3)**	**PELTAT (G4)**	**NG (NG1 + NG2)**	**G (G1+ G2+G3)**	**PELTAT (G4)**	**NG (NG1 + NG2)**	**G (G1+ G2+G3)**	**PELTAT (G4)**	**NG (NG1 + NG2)**	**G (G1+ G2+G3)**	**PELTAT (G4)**
L. moschatum *(L. moschatum* var. *moschatum)*	+++	++	+	+++	-	-	+	-	-	+++	+	+
L. moschatum *(L. moschatum* var. *rhodium)*	++	-	-	++	-	+	+	-	-	++	-	+
L. micranthum (*L. moschatum* var. *micranthum*)	++	-	++	++	-	-	+	-	-	+++	++	+
L. galactophyllum	++	-	-	+	-	-	+	-	-	+++	+	-
L. tschorochense	++	-	-	++	-	-	+	-	-	++	++	+
L. album subsp. *crinitum* *(L. vreemanii)*	+	-	-	++	-	-	+++	+	+	++	+	+
L. orientale	+	-	+	++	-	-	+++	-	+	+++	++	+
L. multifidum	+	-	-	+	-	+	+++	-	-	++++	+	+
Genus *Galeobdolon* *(L. galeobdolon* subsp. *montanum)*	++	-	+	++	-	+	+++	-	+	+	-	+
L. bilgilii	++	-	++	++	-	++	++++	+	++	++++	+++	+
L. ponticum subsp. *anatolicum*	++	-	-	+++	-	-	+++	-	-	+++	+	+
L. cappadocicum	++++	-	+	++++	-	-	+	-	-	++++	++	+

Table 12. Voucher specimens of the genus *Lamium* examined for their trichome properties

Taxon	**Locality**
Lamium lycium	Turkey, Muğla, Fethiye, Babadağ, F.Celep 1789 18.04.2013
L. cariense	Turkey, Karaman, Ermenek, F.Celep 1820, 21.4.2013
L. pisidicum	Turkey, Isparta, Davraz mountain, F.Celep 1914, 1.6.2013
L. tenuiflorum	Turkey, Karaman, Ermenek, F.Celep 1819, 21.4.2013
L. garganicum subsp. *reniforme*	Turkey, Trabzon, Macka, F.Celep 1880, 15.5.2013
L. garganicum subsp. *nepetifolium*	Turkey, Adana, Tufanbeyli, F.Celep 1849, 25.4.2013
L. garganicum subsp. *rectum*	Turkey, Kahramanmaras, Berit mountain, F.Celep 3556, 5.7.2007
L. garganicum subsp. *lasioclades*	Turkey, Adiyaman, Golbasi, F.Celep 2271, 26.4.2014
L. garganicum subsp. *pulchrum*	Turkey, Nigde, Aladaglar, F.Celep 3746, 22.06.2014
L. garganicum subsp. *laevigatum*	Turkey, Bursa, Uludag, F.Celep 3756, 24.4.2014
L. veronicifolium	Turkey, Bursa, Uludag, F.Celep 3756, 24.6.2014
L. microphyllum	Turkey, Denizli, Honaz mountain, F.Celep 3769, 26.6.2014
L. cymbalarifolium	Turkey, Antalya, Elmali, F.Celep 3780, 27.6.2014
L. sandrasicum	Turkey, Denizli, Sandras mountain, F.Celep 3773, 26.6.2014
L. armenum subsp. *armenum*	Turkey, Erzincan, Sakaltutan, F.Celep 2001 29.07.2013
L. armenum subsp. *sintenisii*	Turkey, Kastamonu, Ilgaz mountain, F.Celep 2002 30.07.2013
L. ehrenbergii	Turkey, Antalya, Elmali, F.Celep 1926, 2.6.2013
L. purpureum var. *purpureum*	Turkey, Ankara, Kızılcahamam, Işık mt., F.Celep 1854 12.05.2013
L. purpureum var. *aznavourii*	Turkey, Istanbul, Beykoz, Göksu, F.Celep 2340 09.05.2014
L. eriocephalum subsp. *eriocephalum*	Turkey, Adana, Pozanti, F.Celep 3635, 12.7.2014
L. eriocephalum subsp. *glandulosidens*	Turkey, Antalya, Sariveliler, F.Celep 3644, 13.7.2014
L. amplexicaule	Turkey, Ankara, METU campus, Z.Atalay 1001, 16.4.2014
L. aleppicum	Turkey, Kahramanmaras, Ahir mountain, F.Celep 1836, 24.4.2013
L. macrodon	Turkey, Erzurum, F.Celep 1900, 17.5.2013
L. maculatum var. *maculatum*	Turkey, Trabzon, Sumela, F.Celep 1881, 15.5.2013
L. maculatum var. *villosifolium*	Turkey, Ankara, Kizilcahamam, Isik mt.,, F.Celep 1853, 12.5.2013
L. gundelsheimeri	Turkey, Rize, Çamlıhemşin, F.Celep 1980 24.07.2013
L. truncatum	Turkey, Keldagi, F.Celep 1834, 23.4.2013
L. album	Turkey, Rize, Camlihemsin, F.Celep 1979, 24.7.2013
L. crinitum	Turkey, Sivas, Kosedag, F.Celep 1903, 18.5.2013
L. tomentosum var. *tomentosum*	Turkey, Van, OT 7993, 2013
L. sulfureum	Turkey, Bayburt, Çaykara, F.Celep 1977, 24.07.2013
L. moschatum var. *moschatum*	Turkey, Antalya, Olimpos, F.Celep 1798 17.04.2013
L. moschatum var. *rhodium*	Turkey, Denizli, F.Celep 1780, 16.04.2013
L. moschatum var. *micranthum*	Turkey, Hatay, F.Celep 3829, 21.05.2015
L. ponticum	Turkey, Giresun, Tamdere, F.Celep 1871, 14.5.2013
L. galactophyllum	Turkey, Erzurum, Tortum, F.Celep 1896, 17.05.2013
L. tschorochense	Turkey, Artvin, Yusufeli, F.Celep 1886, 17.5.2013
L. vreemanii	Turkey, Erzurum, Tortum, F.Celep 1989, 28.7.2013
L. orientale	Turkey, Sivas, Imrali, F.Celep 1904, 18.5.2013
L. multifidum	Turkey, Erzurum, Pazaryolu, F.Celep 3611, 2015
L. galeobdolon subsp. *montanum*	Turkey, Rize, Camlihemsin, F.Celep 1882, 16.5.2013
L. ponticum subsp. *anatolicum*	Turkey, Kastamonu, Kure, F.Celep 3840, 01.05.2015
L. bilgili	Turkey, Burdur, Altinyayla, F.Celep 3860, 05.06.2015
L. capadocicum	Turkey, Hasan mountain, F.Celep 3629, 11.07.2014

3.5 Palynology (Pollen Micromorphology)

The investigated pollen morphological characters are given in Tables 13-14. LM photos and SEM micrographs are given in Figures 41-42 and Figures 43-71, respectively. The palynological characters are explained in separate subtitles below. Voucher information for the present palynological study is given in Table 16.

3.5.1 Size and Shape

The pollen grains are monads. In equatorial view, the shape of the pollen grains ranges from suboblate to subprolate (P/E = 0.91–1.18). The polar axis ranges from 21.65 µm in *L. tomentosum* var. *tomentosum* to 39.96 µm in *L. orvala*, subgenus *Orvala* and the equatorial diameter ranges from 22.54 µm in *L. album* subsp. *crinitum* to 40.18 µm in *L. eriocephalum* subsp. *eriocephalum*, (Table 13). Most taxa studied are prolate spheroidal (Table 13). However, shape classes can vary within taxa. The amb shape is triangular and circular in the studied taxa (Figs. 43–71).

3.5.2 Apertures

Pollen grains are radially symmetrical, isopolar and tricolpate in all taxa. Simple colpi are elongated and narrowing at the poles. Colpus length varies from 14.42 µm, in *L. lycium*, to 32.90 µm, in *L. multifidum*. Colpus width ranges from 2.96 µm, in *L. macrodon* to 12.43 µm, in *L. garganicum* subsp. *striatum*. They have granulate, granulate–scabrate, scabrate and baculate membranes (Figs. 43-71). Mesocolpial area varies from 7.53 µm, in *L. moshatum* to 18.72 µm, in *L. cymbalariifolium*. Apocolpium diameter ranges from 2.10 µm, in *L. eriocephalum* subsp. *glandulosidens* to 7.22 µm, in *L. tomentosum* var. *tomentosum* (Table 14).

3.5.3 Exine Ornamentation

The exine sculpturing pattern investigated with SEM reveals three distinct types of surface ornamentations as reticulate, granulate and microreticulate, respectively (all SEM micrographs of pollen grains, see Figs. 41–71). Based on the detailed configuration of the exine ornamentation pattern, reticulate and granulate sculpturing patterns can be subdivided into subtypes. The ranges of exine and intine thickness are 0.64–1.91 μm and 0.39–1.06 μm, respectively (Table 14). The previous taxonomic treatments (Mill, 1982; Mennema, 1989) and pollen sculpturing pattern variations are given in Table 15.

Reticulate Exine Sculpturing Pattern

The reticulate sculpturing pattern is observed in 26 taxa (see Table 13) and can be divided into subtypes based on various features, i.e. in the shape and perforations of the lumina and the characteristics of the muri. Type 1a and Type 1b are charactarized with angular primary lumina and non-undulate muri, which only differentiate by the number of perforations they possess. The number of perforations is observed and indicated as; the number of perforations per 25 μm^2. The number of perforations is <5 in reticulate Type 1a in 17 taxa (Figs. **43** d, e, f; **44** d, e, f; **45** d, e, f; **46** a, b, c; **46** d, e, f; **47** a, b, c; **47** d, e, f; **48** a, b, c; **48** d, e, f; **49** a, b, c; **49** d, e, f; **50** a, b, c; **50** d, e, f; **51** d, e, f; **54** a, b, c; **54** d, e, f; **59** a, b, c, Table 13). The number of perforations is >5 in reticulate Type 1b in 5 taxa (Figs. **43** a, b, c; **44** a, b, c; **45** a, b, c; **51** a, b, c; **71** a, b, Table 13). Reticulate Type 1c is charactarized with prolonged primary lumina without perforations, and long and undulate muri, which is observed in 5 taxa (Figs. **52** a, b, c; **52** d, e, f; **53** a, b, c; **53** d, e; **53** f; Table 13).

Granulate Exine Sculpturing Pattern

The granulate sculpturing pattern is observed in 19 taxa (Table 13) and is charactarized by small, more or less spherical supratectal processes. This sculpturing pattern can be further divided into subtypes based on the presence or absence of perforations. Granulate sculpturing pattern with perforations (Type 2a) is observed in 15 taxa (Figs. **55** a, b, c; **55** d, e, f; **56** a, b, c; **56** d, e, f; **57** a, b, c; **57** d, e, f; **58** a, b, c; **60** a, b, c; **61** a, b, c; **61** d, e, f; **61** g, h, i; **62** a, b, c; **65** a, b, c; **66** a, b, c; **67** a, b, c, Table 13). Psilate-like, smooth granulate surfaces without perforations (Type 2b) is observed in 4 taxa (Figs. **63** a, b, c; **63** d, e, f; **64** a, b, c; **71** c, d, Table 13).

Microreticulate Exine Sculpturing Pattern

The microreticulate sculpturing pattern, which is charactarized with more or less rounded and diameter smaller than 1 μm of lumina, is observed in 4 taxa; *L. galeobdolon* subsp. *montanum, L. galeobdolon* subsp. *flavidum, L. flexuosum* and *L. orvala* (Type 3, Figs. **68** a, b, c; **68** d, e, f; **69** a, b, c; **70** a, b, c, Table 13).

3.5.4 Systematic Impliactions of Pollen Morphology in the genus *Lamium*

The observed exine sculpturing patterns in *Lamium* are defined as reticulate, granulate and microreticulate. Reticulate and microreticulate exins are present in the majority of the species belonging to subfamily Lamioideae and in other Lamiaceae genera (Wagstaff, 1992; Abu-Asab and Cantino, 1992, 1994; Celenk et al., 2008a, b; Moon et al., 2008a, b, c; Özler et al., 2011, 2013) whereas granulate sculpturing pattern is observed in a few genera including *Lamium*. Suprareticulate (referred to as bireticulate by some authors; Demissew and Harley, 1992; Harley et al., 1992) exins are apomorphic in Lamiaceae as a whole but it is rather a plesiomorphic condition in subfamily Lamioidae (Cantino, 1992a). Derived states as psilate, granulate, rugulate and suprareticulate-rugulate forms of sculpturing pattern and branched columellae occur in some members of Lamioids. Similar pollen features suggest relationships within and between certain genera in Lamioidae (Abu-Asab and Cantino, 1994). The palynological data of species examined are comparable to previously conducted study. Palynological work including various species of *Lamium*, Abu-Asab and Cantino (1994) placed *Lamium* within subfamily Lamioideae, with tricolpate pollen.

The present study indicates that all examined taxa possess tricolpate pollen grains, which is a plesiomorphic state in subfamily Lamioidae. On the other hand, derived states as tetracolpate and 6-pantocolpate pollen grains also occur in some members of the subfamily. Among the investigated taxa, palynological properties of *L. album, L. flexuosum, L. galeobdolon, L. garganicum, L. moschatum, L. purpureum* and *L. orientale* (as *Wiedemannia orientalis*) are provided by Abu-Asab and Cantino (1994). Most of the taxa they investigated correlate with our current results, except for the P/E ratios. The slight variations in measurements are likely due to differences in preparation. Recent palynological study (Firdous et al., 2015) on some species of *Lamium* revealed fossualte (*L. album*) and microreticulate (*L. amplexicaule*) ornamentation.

Infrageneric delimitation, systematic and phylogenetic implications of exine sculpturing pattern

Abu-Asab and Cantino (1994) supported Mennema's inclusion of the subg. Galeobdolon in the genus *Lamium* since *Lamium galeobdolon* and *L. flexuosum* have similar sculpturing pattern (microreticulate). According to their nuclear data (Bendiksby et al., 2011b), morphologically very distinct *L. galeobdolon* (= *Galeobdolon*), forms a sister group to the remaining *Lamium* species. However, *Lamium* taxa did not form a monophyletic clade and no such distinction was found between the genera in Krawczyk's nuclear region analysis (2013). However, the cpDNA tree of Bendiksby et al. (2011b) is not congurent with the nuclear trees, thus L. galeobdolon is not evaluated in a seperate genus. The similar results found by Krawczyk et al. (2013, 2014) in their cpDNA tree. Thus, the integration of *Galeobdolon* and *Lamium* seems to be legitimate by Bendiksby et al. (2011b) and Krawczyk et al. (2013, 2014). Our pollen morphological results may support the inclusion of L. galeobdolon subsp. montanum and *L. galeobdolon* subsp. *flavidum* in the genus *Lamium*. However, the taxonomic placement is not settled. *Lamium orientale* and *L. multifidum* with reticulate sculpturing pattern support their inclusion in the genus *Lamium* however the phylogenetic placement of the species remains uncertain (Bendiksby et al., 2011b).

The variation in the shape of primary lumina and muri and number of perforations within the general class of reticulate sculpturing, further lead to the division of this type of exine sculpturing pattern to subtypes. Exine having angular primary lumina and non undulate muri, with or without perforations, exist in the majority of investigated *Lamium* species, especially in the sect. *Lamium* (Table 2), specifically in *Lamium garganicum* complex which includes many endemic species and subspecies distributed in Turkey that were previously regarded as synonyms or infraspecific taxa by Mennema (1989). For example, *Lamium lycium, L. cariense, L.*

garganicum subsp. *striatum, L. garganicum* subsp. *reniforme, L. garganicum* subsp. *rectum, L. garganicum* subsp. *lasioclades,* were regarded as a synonym of *L. garganicum* subsp. *striatum* var. *striatum* by Mennema (1989). The morphological characters of the taxa are mostly overlapping and are delimiting the taxa to some degree. Moreover, pollen morphological characters are not strongly delimiting taxa from each other in this particular complex.

L. microphyllum, L. cymbalarifolium and *L. sandrasicum* with reticulate sculpturing pattern, are all endemic to Turkey and they were regarded as a synonym of *L. garganicum* subsp. *striatum* var. *microphyllum* by Mennema (1989). Based on our field and morphological observations, these taxa should be treated as valid species however, pollen morphology does not provide support for delimiting the taxa in this particular complex.

Turkish endemic taxa (Mill, 1982) *L. armenum* subsp. *armenum* and *L. armenum* subsp. *sintenisii* that have granulate sculpturing pattern were regarded as a synonym of *L. garganicum* subsp. *striatum* (Sibth. & Smith) Hayek var. *armen*um (Boiss.) Mennema, and were included in sect. *Lamium* by Mennema (1989). However, Krawczyk et al. (2013, 2014) found a strongly supported relation between *L. moshatum* (sect. *Lamiotypus*) and *L. armenum* subsp. *armenum* (seen as *L. garganicum* var. *armenum* in their tree) (sect. *Lamium*, according to Mennema, 1989) in their molecular phylogenetic trees. In addition, based on our palynological results, *L. armenum* should be excluded from *L. garganicum* complex and should be treated as a valid species as Krawczyk et al. (2013b) stated.

Crossings between *L. amplexicaule* and *L. purpureum* resulted in hybrid plants that were morphologically highly similar to *L. confertum* (Bernstrom, 1955). It is also confirmed by Bendiksby et al. (2011b) that *L. confertum* is an allotetraploid hybrid between *L. amplexicaule* and *L. purpureum*. The species have reticulate sculpturing pattern that falls within sect. *Lamium* and its sculpturing is much more similar to that of *L. purpureum* rather than *L. amplexicaule*.

Reticulate sculpturing pattern is observed in the majority of sect. *Lamium* members, with the exception of *L. eriocephalum* subsp. *eriocephalum* (belonging to sect. *Amplexicaule*) shows a rather distinct ornamentation from the other members of sect. *Amplexicaule* (Table 3). Gross morphological features of the species and palynological data may support its segregation from sect. *Amplexicaule* however, together with *L. aleppicum*, *L. macrodon*, they represented a strongly supported group in nuclear phylogenies (Bendiksby et al., 2011b). *Lamium bifidum*, assigned to sect. *Lamium* by Mennema (1989), has similar sculpturing pattern with the members of sect. *Amplexicaule* rather than the members of the sect. *Lamium*, moreover a close relationship between *L. amplexicaule* var. *amplexicaule* and *L. bifidum* were identified in the latest phylogenetic studies (Bendiksby et al., 2011b; Krawczyk et al., 2014). Thus, pollen morphology of *L. bifidum* provides support for its transfer to sect. *Amplexicaule*.

Species with granulate sculpturing pattern fall only within sect. *Lamiotypus* (Table 4). *Lamium gundelsheimeri and L. truncatum* have granulate sculpturing pattern, were regarded as synonyms of *L. maculatum* (Mennema, 1989). Morphological characters are not strongly delimiting the taxa. Moreover, pollen morphology does not provide evidence for their separation from each other. The *album* - *tomentosum* and *L. moshatum* group that have granulate sculpturing pattern, fall within sect. *Lamiotypus*, which was also reported by Abu-Asab and Cantino (1994). Moreover, the *album* - *tomentosum* group were placed in the same clade with a high resolution in all phylogenetic studies (Bendiksby et al., 2011b; Krawczyk, 2014). But pollen morphology does not strongly separate the infraspecific taxa both in the *album* - *tomentosum* and *L. moshatum* group (Table 4). One distinction of, *L. album* subsp. *barbatum* has reticulate sculpturing pattern, which is not observed in any members of section *Lamiotypus* (Table 4).

Monophyly of the subg. *Lamium* (including sect. *Lamium*, sect. *Amplexicaule* and sect. *Lamiotypus*) is cladistically supported by morphology (Ryding, 2003). However, monophyly of the subg. *Lamium* is neither contradicted nor supported by Bendiksby et al. (2011b). According to Bendiksby et al. (2011b), Mennema’s (1989) three sections within the subg. *Lamium* are para- or polyphyletic in the molecular trees and his infrageneric classification better to be abandoned. In our results, three different sculpturing pattern observed in the subgenus *Lamium* partly supported Mennema`s infrageneric classification.

Lamium orvala (subgenus *Orvala*) possess microreticulate sculpturing pattern which is similar to the members of the subgenus *Galeobdolon*. Moreover, the close relation of *L. orvala* belonging to Mennema's (1989) monotypic subg. *Orvala* with subg. *Galeobdolon* members, is supported by molecular tree topologies (Bendiksby et al., 2011b; Krawczyk et al., 2013).

A recent work on *L. orientale* and *L. multifidum* indicated that, two species have reticulate exine sculpturing patter (Atasagun et al., 2015). Their finding is supported by the present study and the inclusion of *Lamium orientale* and *L. multifidum* in the genus *Lamium* is supported however; the phylogenetic placement of the species remains uncertain (Bendiksby et al., 2011b).

Morphologically distinct *Lamium galeobdolon* subsp *montanum*, has microreticulate exine ornamentation, which shows rather a distinct sculpturing pattern compared to the remaining *Lamium* species. The palynological results neither support nor decline the inclusion of *L. galeobdolon* in the genus *Lamium*. Regarding the gross morphology of the spcecies, it would seem legitimate to include the species in the genus *Galeobdolon* in the final taxonomic treatment, however; the integration of *Galeobdolon* and *Lamium* seems legitimate by Bendiksby et al. (2011b) and Krawczyk et al. (2013, 2014).

***In Tables 13 and 14, taxa in parenthesis are the synonyms of the taxa written in red.**

Table 13. Pollen morphological data of the *Lamium* species.

Taxon	**P (µm)**	**E (µm)**	**Shape**					**Sculpturing type**	**SEM Fig.**
			SO	**OS**	**S**	**PS**	**SP**		
L. lycium	28.23 ± 0.77 (26.91 – 30.01)	27.23 ± 1.22 (24.60 – 29.02)	-	++	++	+++	+	Ret 1b	84 a, b, c
L. cariense	30.15 ± 1.19 (27.54 – 32.08)	27.46 ± 1.12 (25.91 – 29.44)	-	-	-	+++	+	Ret 1a	84 d, e, f
L. garganicum subsp. *striatum* *(L. pisidicum)*	28.64 ± 1.32 (26.34 – 31.41)	28.32 ± 1.38 (26.37 – 31.43)	-	++	+++	+++	-	Ret 1b	85 a, b, c
L. garganicum subsp. *striatum* *(L. tenuiflorum)*	32.25 ± 0.82 (30.73 – 33.81)	32.03 ± 0.89 (30.50 – 33.64)	-	++	+	+++	-	Ret 1a	85 d, e, f
L. garganicum subsp. *striatum* *(L. garganicum* subsp. *reniforme)*	27.97 ± 0.70 (26.78 – 29.16)	29.80 ± 1.22 (27.40 – 31.41)	+	+++	+	-	-	Ret 1a	86 d, e, f
L. garganicum subsp. *striatum* *(L. garganicum* subsp. *nepetifolium)*	27.20 ± 0.77 (26.12 – 28.69)	29.07 ± 1.13 (27.31 – 31.53)	+	+++	+	+	-	Ret 1a	87 a, b, c
L .garganicum subsp. *rectum*	31.84 ± 2.02 (27.67 – 34.90)	31.18 ± 1.47 (28.68 – 33.45)	-	++	+	+++	-	Ret 1a	87 d, e, f
L .garganicum subsp. *lasioclades*	29.20 ± 0.83 (27.24 – 30.63)	30.52 ± 0.74 (29.31 – 32.16)	-	+++	+	+	-	Ret 1a	88 a, b, c
L. garganicum subsp. *laevigatum*	26,89 ± 0.84 (25.42 – 28.42)	28.28 ± 0.74 (26.76 – 29.43)	-	+++	+	-	-	Ret 1a	89 a, b, c
L. garganicum subsp. *laevigatum* *(L. veronicifolium)*	28.73 ± 0.97 (27.11 – 30.44)	28.81 ± 0.86 (27.74 – 30.26)	-	+++	+	++	-	Ret 1b	86 a, b, c
L. microphyllum	28.32 ± 0.72 (27.12 – 29.75)	29.66 ± 0.97 (28.11 – 31.40)	-	+++	+	+	-	Ret 1a	89 d, e, f
L. cymbalariifolium	33.36 ± 1.43 (29.32 – 35.02)	32.60 ± 1.07 (31.02 – 34.86)	-	+	++	+++	-	Ret 1a	90 a, b, c
L. sandrasicum	28.91 ± 0.78 (27.89 – 30.73)	31.48 ± 1.43 (29.45 – 34.42)	++	+++	+	-	-	Ret 1a	90 d, e, f
L. armenum subsp. *armenum*	31.51 ± 0.56 (30.31 – 32.51)	32.07 ± 0.70 (30.45 – 33.20)	++	+++	+	+	-	Gr 2a	96 a, b, c
L. armenum subsp. *sintenisii*	32.72 ± 1.01 (30.89 – 34.70)	32.63 ± 1.01 (30.56 – 34.86)	-	++	+++	++	-	Gr 2a	96 d, e, f
L. purpureum *(L. purpureum* var. *purpureum)*	28.23 ±1.32 (26.18 – 31.72)	30.23 ± 1.03 (28.40 – 32.21)	++	+++	+	+	-	Ret 1a	91 a, b, c
L. purpureum *(L. purpureum* var. *aznavourii)*	27.96 ± 0.76 (26.53 – 29.53)	30.85 ± 0.87 (29.80 – 32.95)	-	+	-	+++	-	Ret 1a	91 d, e, f
L. eriocephalum subsp. *eriocephalum*	35.21 ± 1.62 (32.16 – 38.91)	33.22 ± 2.22 (30.14 – 40.18)	-	+	-	+++	-	Ret 1b	92 a, b, c
L .eriocephalum subsp. *glandulosidens*	32.07 ± 1.78 (30.03 – 35.57)	32.53 ± 1.54 (30.55 – 35.97)	-	+++	+	++	-	Ret 1a	92 d, e, f

Table 13 (cont`d)

Taxon	P (µm)	E (µm)	Shape					Sculpturing type	SEM Fig.
			SO	OS	S	PS	SP		
L. amplexicaule subsp. amplexicaule var. amplexicaule (L. amplexicaule)	26.96 ± 1.29 (24.18 – 29.12)	25.98 ± 1.20 (24.27 – 28.82)	-	+	+	+++	-	Ret 1c	93 a, b, c
L. amplexicaule subsp. amplexicaule var. aleppicum (L. aleppicum)	30.11 ± 1.99 (27.44–35.48)	28.62 ± 2.22 (26.22 – 33.29)	+	+	+	+++	+	Ret 1c	93 d, e, f
L. macrodon	32.23 ± 1.28 (30.6 – 35.41)	28.10 ± 2.61 (25.72 – 33.82)	-	+	-	+	+++	Ret 1c	94 a, b, c
L. bifidum	/	/	/					Ret 1c	94 d, e
L. confertum	/	/	/					Ret 1b	94 f
L. maculatum *(L. maculatum* var. *maculatum)*	30.72 ± 1.47 (27.67 – 32.88)	29.85 ± 0.83 (28.11 – 31.28)	-	++	+	+++	-	Gr 2a	97 a, b, c
L. villosifolium *(L. maculatum* var. *villosifolium)*	28.34 ± 0.74 (26.93 – 29.55)	27.70 ± 0.67 (26.12 – 28.77)	-	+	++	+++	-	Gr 2a	97 d, e, f
L. maculatum *(L. gundelsheimeri)*	26.11 ± 0.47 (25.39 – 27.04)	28.44 ± 1.17 (26.63 – 30.25)	++	+++	-	+	-	Gr 2a	98 a, b, c
L. maculatum *(L. truncatum)*	30.36 ± 0.57 (29.32 – 31.63)	29.41 ± 0.87 (27.54 – 30.84)	-	+	+	+++	-	Gr 2a	98 d, e, f
L. album subsp. *album* *(L. album)*	27.87 ± 0.71 (26.13 – 28.87)	27.65 ± 0.70 (25.53 – 28.92)	-	++	+	+++	-	Gr 2a	99 a, b, c
L. album subsp. *barbatum*	23.52 ± 0.61 (22.53– 25.12)	24.32 ± 0.56 (23.16 – 25.36)	-	+++	+	+	-	Ret 1a	100 a, b, c
L. album subsp. *crinitum* *(L. crinitum)*	27.30 ± 0.81 (25.65–28.77)	27.46 ± 1.17 (25.90 – 30.42)	-	+++	+	++	-	Gr 2a	101 a, b, c
L. tomentosum subsp. *tomentosum*	23.96 ± 1.36 (21.65–26.93)	25.23 ± 0.75 (24.09 – 27.02)	+	+++	+	++	-	Gr 2a	102 a, b, c
L. tomentosum var. *filicaule*	23.81 ± 0.92 (22.45–25.72)	24.41 ± 0.93 (23.15 – 26.28)	-	+++	+	+	-	Gr 2a	102 d, e, f
L. tomentosum var. *tomentosum* *(L. tomentosum* var. *hakkariense)*	26.07 ± 1.69 (26.14–29.67)	26.65 ± 0.76 (24.93 – 27.74)	+	+++	+	+	-	Gr 2a	102 g, h, i
L. tomentosum var. *alpestre* *(L. sulfureum)*	26.20 ± 1.05 (24.15 – 27.70)	25.64 ± 0.65 (24.40 – 26.94)	-	++	+	+++	-	Gr 2a	103 a, b, c
L. moschatum *(L. moschatum* var. *moschatum)*	24.83± 0.52 (24.12 – 25.77)	26.43 ± 0.68 (24.82 – 27.66)	-	+++	-	+	-	Gr 2b	104 a, b, c

Table 13 (cont`d)

Taxon	P (µm)	E (µm)	Shape					Sculpturing type	SEM Fig.
			SO	OS	S	PS	SP		
L. tomentosum var. *alpestre* *(L. sulfureum)*	26.20 ± 1.05 (24.15 – 27.70)	25.64 ± 0.65 (24.40 – 26.94)	-	++	+	+++	-	Gr 2a	103 a, b, c
L. moschatum *(L. moschatum* var. *moschatum)*	24.83± 0.52 (24.12 – 25.77)	26.43 ± 0.68 (24.82 – 27.66)	-	+++	-	+	-	Gr 2b	104 a, b, c
L. moschatum *(L. moschatum* var. *rhodium)*	25.09 ± 0. 89 (23.00 –26.40)	24.87 ± 0.91 (23.40 – 26.50)	-	+	+	+++	-	Gr 2b	104 d, e, f
L. ponticum subsp. *ponticum* *(L. ponticum)*	31.95 ± 0.83 (29.98 – 33.60)	32.03 ± 1.26 (30.13 – 34.10)	-	+++	+	++	-	Gr 2b	105 a, b, c
L. galactophyllum	27.98 ± 0.78(26.78 – 29.72)	27.50 ± 0.61 (26.77 – 29.36)	-	+	++	+++	-	Gr 2a	106 a, b, c
L. tschorochense	26.17 ± 1.46 (23.66 – 28.71)	26.07 ± 1.41 (23.18 – 28.45)	-	+	++	+	-	Gr 2a	107 a, b, c
L. album subsp. *crinitum* *(L. vreemanii)*	24.21 ± 0.53 (23.47 – 25.44)	24.84 ± 1.45 (22.54 – 26.89)	+	+++	-	+	-	Gr 2a	108 a, b, c
L. orientale	26.99 ± 0.79 (25.49 – 28.24)	26.24 ± 0.80 (24.81 – 27.79)	-	++	-	+++	-	Ret 1a	95 a, b, c
L. multifidum	35.20 ± 1.33 (33.49 – 38.72)	29.82 ± 0.90 (27.15 – 30.98)	-	-	-	++	+++	Ret 1a	95 d, e, f
Galeobdolon *(L. galeobdolon* subsp. *montanum)*	27.93 ± 1.46 (24.70 – 29.66)	27.03 ± 1.39 (23.15 – 29.88)	-	+	+	+++	+	Micret 3	109 a, b, c
Galeobdolon *(L. galeobdolon* subsp. *flavidum)*	28.62 ± 1.16 (26.45 – 30.46)	29.19 ± 1.21 (26.21 – 31.35)	-	+++	+	++	-	Micret 3	109 d, e, f
L. flexuosum	24.81 ± 0.92 (23.72 – 27.18)	24.59 ± 1.06 (23.21 – 26.82)	-	++	++	+	-	Micret 3	110 a, b, c
L. orvala	36.40 ± 1.47 (34.29 – 39.96)	33.19 ± 1.29 (31.10 – 35.92)	-	-	+	++	++	Micret 3	111 a, b, c
L. bilgilii	29.13 ± 1.25 (28.41 – 33.10)	32.05 ± 0.83 (29.10 – 33.75)	-	+++	+	+	-	Ret 1b	112 a, b
L. ponticum subsp. *anatolicum*	30.44 ± 0.80 (27.78 – 32.49)	31.13 ± 1.15 (30.14 – 34.44)	-	+++	+	+	-	Gr 2b	112 c, d
L. capadocicum	29.21 ± 1.28 (27.45 – 32.06)	31.07 ± 0.77 (30.05 – 33.01)	+	+++	+	+	-	Ret 1a	88 d, e, f

P polar axis, *E* equatorial diameter, *SO* suboblate, *OS* oblate spheroidal, *S* spherical, *PS* prolate spheroidal, *SP* subprolate. +++, dominant; ++, present; + rarely present; -, absent; /, no data, Ret: reticulate, Gr: granulate, Micret: microreticulate, All measurements in µm.

Table 14. Pollen morphological data (with mean values and standard deviations) of *Lamium* L. species

Taxon	**Clg**	**Mesocolpium**	**Apocolpium**	**Exine thickness**	**Intine thickness**
L. lycium	18.47 ±1.41 (14.42 – 23.81)	12.09±1.93 (8.83 – 14.86)	3.06 ± 0.72 (2.40 – 4.02)	0.80±0.20	0.53±0.13
L. cariense	24.97±2.28 (21.59 – 27.66)	14.05±1.89 (12.71 – 16.01)	3.37 ± 0.98 (2.21 – 4.57)	0.89±0.18	0.61±0.18
L. garganicum subsp. *striatum* *(L. pisidicum)*	26.79±2.01 (22.24 – 29.66)	12.70±1.36 (11.14 – 14.62)	3.72 ± 0.85 (2.86 – 4.56)	0.82±0.14	0.39±0.08
L. garganicum subsp. *striatum* *(L. tenuiflorum)*	24.36±2.30 (20.15 – 26.56)	15.72±1.07 (13.54 – 17.56)	4.40 ± 0.91 (2.59 – 5.86)	0.95±0.18	0.64±0.12
L. garganicum subsp. *striatum* *(L. garganicum* subsp. *reniforme)*	22.59±1.18 (21.34 – 24.19)	15.77±0.76 (15.28 – 17.10)	4.65 ± 1.13 (3.00 – 6.34)	1.08±0.23	0.53±0.11
L. garganicum subsp. *striatum* *(L. garganicum* subsp. *nepetifolium)*	22.61±1.26 (21.75 – 24.77)	16.13±1.43 (14.14 – 17.98)	3.82 ± 0.71 (3.12 – 5.30)	1.91±0.18	1.06±0.32
L .garganicum subsp. *rectum*	21.77±1.44 (20.16 – 23.71)	16.45±1.16 (13.52 – 17.88)	3.58 ± 0.66 (3.10 – 5.11)	1.10±0.12	0.89±0.16
L .garganicum subsp. *lasioclades*	23.71±1.14 (21.89 – 24.97)	17.36±1.08 (16.11 – 18.05)	3.15 ± 0.83 (2.56 – 4.66)	0.92±0.16	0.59±0.16
L. garganicum subsp. *laevigatum*	22.52±1.42 (20.30 – 24.26)	17.10±0.87 (16.96 – 18.29)	3.69 ± 0.90 (2.83 – 4.75)	1.67±0.40	0.77±0.15
L. garganicum subsp. *laevigatum* *(L. veronicifolium)*	21.98±1.77 (19.93 – 25.11)	15.90±1.41 (14.36 – 17.95)	4.89 ± 1.03 (3.40 – 6.06)	1.64±0.18	0.73±0.22
L. microphyllum	22.94±1.28 (21.07 – 23.96)	14.43±1.40 (12.76 – 16.33)	4.12 ± 0.89 (2.93 – 5.73)	0.81±0.10	0.57±0.12
L. cymbalariifolium	28.68±1.21 (26.64 – 30.51)	15.76±2.29 (13.69 – 18.72)	3.84 ± 0.56 (3.11 – 4.48)	0.97±0.31	0.60±0.10
L. sandrasicum	22.48±1.25 (20.61 – 24.96)	16.82±1.14 (15.34 – 18.70)	5.12 ± 1.06 (4.12 – 6.30)	1.54±0.28	0.68±0.12
L. armenum subsp. *armenum*	25.26±1.58 (23.91 – 27.54)	14.91±1.72 (12.25 – 18.42)	4.11 ± 0.65 (2.83 – 4.96)	1.54±0.32	0.76±0.12
L. armenum subsp. *sintenisii*	26.47±2.11 (23.14 – 30.67)	11.16±1.31 (10.01 – 12.58)	3.12 ± 0.16 (2.12 – 5.16)	1.66±0.34	0.90±0.22
L. purpureum *(L. purpureum* var. *purpureum)*	24.29±2.00 (22.19 – 25.35)	15.92±0.50 (15.50 – 16.82)	3.75 ± 0.79 (2.80 – 5.18)	0.95±0.32	0.67±0.21
L. purpureum *(L. purpureum* var. *aznavourii)*	23.16±1.28 (21.15 – 25.16)	14.92±0.70 (14.01 – 15.83)	3.47 ± 0.85 (2.58 – 4.66)	0.88±0.21	0.68±0.21
L. eriocephalum subsp. *eriocephalum*	24.08±2.36 (22.14 – 26.18)	16.63±1.02 (15.86 – 18.55)	4.34 ± 0.40 (3.93 – 4.73)	1.06±0.22	0.41±0.10
L .eriocephalum subsp. *glandulosidens*	26.20±1.40 (24.48 – 28.55)	16.18±1.57 (14.18 – 18.06)	3.37 ± 0.86 (2.10 – 3.50)	0.99±0.24	0.61±0.20
L. amplexicaule subsp. amplexicaule var. amplexicaule (L. amplexicaule)	20.56±0.83 (19.16 – 22.85)	14.03±2.40 (12.53 – 16.80)	4.87 ± 1.49 (3.66 – 6.48)	1.05±0.02	0.42±0.10

Table 14 (cont`d)

Taxon	**Clg**	**Mesocolpium**	**Apocolpium**	**Exine thickness**	**Intine thickness**
L. amplexicaule subsp. amplexicaule var. aleppicum (L. aleppicum)	22.76±2.00 (20.14 – 25.78)	14.59±1.52 (13.32 – 16.53)	4.48 ± 1.08 (3.33 – 5.56)	1.30±0.20	0.39±0.11
L. macrodon	23.83±1.22 (20.15 – 25.18)	16.58±0.64 (15.88 – 17.14)	5.13 ± 0.41 (4.69 – 5.88)	1.04±0.10	0.57±0.11
L. bifidum	/	/	/	/	/
L. confertum	/	/	/	/	/
L. maculatum *(L. maculatum* var. *maculatum)*	22.47±1.85 (22.47 – 27.49)	13.27±1.36 (11.95 – 13.20)	4.09 ± 1.24 (3.28 – 5.52)	1.53±0.20	0.82±0.18
L. villosifolium *(L. maculatum* var. *villosifolium)*	22.05±1.29 (20.24 – 24.50)	12.61±0.67 (11.82 – 13.11)	3.14 ± 0.24 (2.88 – 3.24)	1.54±0.28	0.75±0.19
L. maculatum *(L. gundelsheimeri)*	21.15±1.62 (19.08 – 23.97)	14.94±1.20 (13.21 – 16.06)	3.64 ± 1.03 (2.40 – 5.21)	1.64±0.47	0.83±0.17
L. maculatum *(L. truncatum)*	23.82±1.39 (21.76 – 25.14)	15.34±1.20 (13.05 – 16.32)	3.54 ± 0.80 (2.90 – 4.43)	0.96±0.24	0.56±0.30
L. album subsp. *album* *(L. album)*	22.25±1.67 (19.75 – 24.78)	11.75±1.27 (10.21 – 13.40)	4.04 ± 0.64 (3.32 – 4.53)	1.08±0.31	0.61±0.22
L. album subsp. *barbatum*	15.98± 0.88 (14.52 – 16.71)	9.23±0.65 (8.56 – 10.02)	4.70±0.45 (4.01 – 5.12)	0.64±0.11	0.71±0.13
L. album subsp. *crinitum* *(L. crinitum)*	22.87±2.51 (20.46 – 28.05)	11.24±1.33 (10.18 - 13.43)	3.15 ± 0.29 (2.86 – 3.44)	1.83±0.60	0.74±0.22
L. tomentosum subsp. *tomentosum*	18.89±1.59 (17.00 – 22.29)	13.67±1.10 (12.07 – 15.32)	3.31 ± 0.55 (2.71 – 4.00)	1.49±0.17	0.65±0.13
L. tomentosum var. *filicaule*	17.85±1.90 (15.68 – 21.16)	11.87±0.78 (11.16 – 13.15)	6.20±0.50 (5.65 – 6.85)	0.72±0.08	0.63±0.04
L. tomentosum var. *tomentosum* *(L. tomentosum* var. *hakkariense)*	19.18±1.46 (17.60 – 22.70)	13.43±1.06 (11.87 – 14.94)	6.16±0.67 (5.54 – 7.22)	0.71±0.03	0.59±0.03
L. tomentosum var. *alpestre* *(L. sulfureum)*	19.71±2.34 (16.87 – 21.77)	14.19±0.78 (13.51 – 15.04)	3.52 ± 0.60 (2.82 – 3.89)	1.68±0.33	0.55±0.12
L. moschatum *(L. moschatum* var. *moschatum)*	19.09±0.81 (17.96 – 20.64)	15.46±0.65 (14.71 – 15.84)	3.23 ± 0.27 (2.94 – 3.48)	1.52±0.33	0.66±0.16
L. moschatum *(L. moschatum* var. *rhodium)*	19.53±0.80 (18.14 – 20.43)	8.57±0.68 (7.53 – 9.62)	3.63±0.26 (3.21 – 4.05)	0.81±0.21	0.62±0.13
L. ponticum subsp. *ponticum* *(L. ponticum)*	25.05±2.68 (19.00 – 27.34)	15.01±0.94 (13.38 – 16.13)	3.89 ± 1.04 (2.79 – 5.49)	1.44±0.24	0.66±0.13

Table 14 (cont`d)

Taxon	**Clg**	**Mesocolpium**	**Apocolpium**	**Exine thickness**	**Intine thickness**
L. galactophyllum	21.63±1.11 (20.44 – 23.09)	14.74±1.19 (13.67 – 16.03)	3.05 ± 0.44 (2.45 – 3.53)	1.10±0.31	0.65±0.10
L. tschorochense	20.15±1.15 (19.14 – 22.45)	13.15±1.12 (12.18 – 15.17)	2.89 ± 0.23 (2.11 – 3.05)	0.95±0.26	0.62±0.12
L. album subsp. *crinitum* *(L. vreemanii)*	19.32±0.52 (17.22 – 19.89)	11.52±0.43 (11.06 – 11.90)	2.89 ± 0.70 (2.25 – 3.62)	0.94±0.14	0.65±0.10
L. orientale	21.77±1.97 (16.61 – 23.53)	11.57±1.62 (9.59 – 13.99)	2.51 ± 0.21 (2.32 – 2.75)	0.76±0.18	0.81±0.18
L. multifidum	28.81±1.81 (27.02 – 32.90)	13.53±0.77(12.75 – 15.20)	4.10±0.48(3.46 – 4.60)	0.96±0.12	0.73±0.10
Galeobdolon *(L. galeobdolon* subsp. *montanum)*	20.88±2.03 (18.15 – 22.95)	14.64±1.82 (13.02 – 17.88)	4.21 ± 1.04 (3.69 – 5.41)	1.43±0.23	0.71±0.32
Galeobdolon *(L. galeobdolon* subsp. *flavidum)*	24.55±0.69 (23.66 – 25.80)	14.02 ± 1.41 (11.79 – 16.04)	3.31 ± 0.49 (2.36 – 4.26)	0.92 ± 0.13	0.71±0.13
L. flexuosum	18.18±1.44 (16.21 – 21.12)	12.54±1.87 (10.01 – 14.63)	4.52±0.51 (4.06 – 5.32)	0.70±0.12	0.61±0.12
L. orvala	29.94±1.42 (28.25 – 32.02)	15.98±0.92 (14.76 – 17.95)	5.83±0.36 (5.45 – 6.52)	0.81±0.04	0.57±0.05
L. bilgilii	25.45 ± 2.16 (22.16 – 28.11)	17.21±0.88 (14.78 – 17.02)	4.78 ± 1.04 (3.75 – 6.17)	1.10±0.41	0.68±0.24
L. ponticum subsp. *anatolicum*	26.15 ± 2.41 (20.05 – 27.49)	16.41±0.96 (14.14 – 16.93)	4.14 ± 1.17 (3.71 – 5.97)	1.12±0.26	0.71±0.12
L. capadocicum	24.25±1.45 (21.80 – 26.99)	14.63±1.41 (12.44 – 16.11)	2.79 ± 0.68 (2.19 – 3.93)	0.97±0.21	0.46±0.11

Clg: colpus length, Clt: colpus width, /: no data. All measurements in µm.

Table 15. Previous taxonomic treatments on the studied taxa made by Mill (1982) and Mennema (1989), and pollen sculpturing pattern observed in the present study.

		Mill (1982)	**Mennema (1989)**	**Pollen sculpturing type**
1	Sect. *Lamium*	*Lamium lycium*	*L. garganicum* subsp. *striatum* var. *striatum*	Reticulate 1b
2		*L. cariense*		Reticulate 1a
3		*L. pisidicum*		Reticulate 1b
4		*L. tenuiflorum*		Reticulate 1a
5		*L. veronicifolium*		Reticulate 1b
6		*L. garganicum* subsp. *reniforme*		Reticulate 1a
7		*L. garganicum* subsp. *nepetifolium*		Reticulate 1a
8		*L. garganicum* subsp. *rectum*		Reticulate 1a
9		*L. garganicum* subsp. *lasioclades*		Reticulate 1a
10		*L. garganicum* subsp. *pulchrum*		Reticulate 1a
11		*L. garganicum* subsp. *laevigatum*	*L. garganicum* subsp. *garganicum*	Reticulate 1a
12		*L. microphyllum*	*L. garganicum* subsp. *striatum* var. *microphyllum*	Reticulate 1a
13		*L. cymbalarifolium*		Reticulate 1a
14		*L. sandrasicum*		Reticulate 1a
15		*L. armenum* subsp. *armenum*	*L. garganicum* subsp. *striatum* var. *armenum*	Granulate 2a
16		*L. armenum* subsp. *sintenisii*		Granulate 2a
17		*L. purpureum* var. *purpureum*	*L. purpureum* var. *purpureum*	Reticulate 1a
18		*L. purpureum* var. *aznavourii*		Reticulate 1a
19		*NI*	*L. bifidum*	Reticulate 1b

Table 15 (cont`d)

		Mill (1982)	**Mennema (1989)**	**Pollen sculpturing type**
20		*NI*	*L. confertum*	Reticulate 1a
21	Sect. *Amplexicaule*	*L. eriocephalum* subsp. *eriocephalum*	*L. eriocephalum*	Reticulate 1b
22		*L. eriocephalum* subsp. *glandulosidens*		Reticulate 1a
23		*L. amplexicaule*	*L. amplexicaule*	Reticulate 1c
24		*L. aleppicum*		Reticulate 1c
25		*L. macrodon*	*L. macrodon*	Reticulate 1b
26	Sect. *Lamiotypus*	*L. maculatum* var. *maculatum*	*L. maculatum*	Granulate 2a
27		*L. maculatum* var. *villosifolium*		Granulate 2a
28		*L. gundelsheimeri*		Granulate 2a
29		*L. truncatum*		Granulate 2a
30		*L. album*	L. *album* subsp. *album*	Granulate 2a
31		*NI*	*L. album* subsp. *barbatum*	Reticulate 1a
32		*L. crinitum*	*L. album* subsp. *crinitum*	Granulate 2a
33		*L. tomentosum* var. *hakkariense*	*L. tomentosum*	Granulate 2a
34		*L. tomentosum* var. *tomentosum*		Granulate 2a
35		*L. tomentosum* var. *filicaule*		Granulate 2a
36		*L. sulfureum*		Granulate 2a
37		*L. moschatum* var. *moschatum*	*L. moschatum* subsp. *moschatum*	Granulate 2b
38		*L. moschatum* var. *rhodium*		Granulate 2b
39		*L. ponticum*		Granulate 2b
40		*L. galactophyllum*	*L. galactophyllum*	Granulate 2a

Table 15 (cont`d)

		Mill (1982)	Mennema (1989)	Pollen sculpturing type
41	*NI*	*L. tschorochense*	*NI*	Granulate 2a
42	*NI*	*L. vreemanii*	*NI*	Granulate 2a
43	*NI*	*L. orientale (Wiedemannii orientalis)*	*NI*	Reticulate 1a
44	*NI*	*L. multifidum (Wiedemannii multifida)*	*NI*	Reticulate 1a
45	Subg. *Galeobdolon*	*L. galeobdolon (Galeobdolon luteum)*	*L. galeobdolon* subsp. *montanum*	Microreticulate 3
46		*NI*	*L. galeobdolon* subsp. *flavidum*	Microreticulate 3
47		*NI*	*L. flexuosum*	Microreticulate 3
48	Subg. *Orvala*	*NI*	*L. orvala*	Microreticulate 3

NI; not included

Table 16. Voucher specimens of genus *Lamium* examined for their palynological properties

Taxon	**Locality**
L. lycium	Turkey, Muğla, Fethiye, Babadağ, F.Celep 1789 18.04.2013
L. cariense	Turkey, Aydın, Karacasu, Babadağ, F.Celep 1782 16.04.2013
L. pisidicum	Turkey, Isparta, Davraz mountain, F.Celep 1914 01.06.2013
L. tenuiflorum	Turkey, Karaman, Ermenek, F.Celep 1819 21.04.2013
L. garganicum subsp. *reniforme*	Turkey, Kahramanmaraş, Binboğa mt., F.Celep 1845 25.04.2013
L. garganicum subsp. *nepetifolium*	Turkey, Adana, Saimbeyli, F.Celep 1847 25.04.2013
L .garganicum subsp. *rectum*	Turkey, Kahramanmaraş, Berit mountain, F.Celep 3556, 05.07.2007
L .garganicum subsp. *lasioclades*	Turkey, Adıyaman, Gölbaşı to Doğanşehir, F.Celep 1839 24.04.2013
L. garganicum subsp. *laevigatum*	Turkey, Bursa, Uludağ, F.Celep 3559, 24.06.2014
L. veronicifolium	Turkey, Bursa, Uludağ, BB 3916, 10.07.2013
L. microphyllum	Turkey, Muğla, Fethiye Babadağ, F.Celep 1790 18.04.2013
L. cymbalariifolium	Turkey, Antalya, Elmalı, Kızlarsivrisi, F.Celep 3560, 27.06.2014
L. sandrasicum	Turkey, Muğla, Sandras mountain, BB 3921, 12.07.2013
L. armenum subsp. *armenum*	Turkey, Erzincan, Sakaltutan, F.Celep 2001 29.07.2013
L. armenum subsp. *sintenisii*	Turkey, Kastamonu, Ilgaz mountain, F.Celep 2002 30.07.2013
L. purpureum var. *purpureum*	Turkey, Ankara, Kızılcahamam, Işık mt.,, F.Celep 1854 12.05.2013
L. purpureum var. *aznavourii*	Turkey, Istanbul, Beykoz, Göksu, F.Celep 2340 09.05.2014
L. eriocephalum subsp. *eriocephalum*	Turkey, Niğde, Aladağlar , BB 3913, 08.07.2013
L .eriocephalum. subsp. *glandulosidens*	Turkey, Antalya, Alanya, Gökbel F.Celep 3558, 13.07.2014
L. amplexicaule	Turkey, Muğla, Fethiye, Babadağ, F.Celep 1794 18.04.2013
L. aleppicum	Turkey, Kahramanmaraş Ahırdağı, F.Celep 1836 24.04.2013
L. macrodon	Turkey, Antalya, Alanya, Gökbel, F.Celep 1811 20.04.2013
L. bifidum	Macedonia, Pisoderion, AHC Alston & NY Sandwith 513, 1932 (K)
L. confertum	Finland, Coll-Harold Wundberg 893 22.07.1933 (K)
L. maculatum var. *maculatum*	Turkey, Trabzon, Maçka, F.Celep 1878 15.05.2013
L. maculatum var. *villosifolium*	Turkey, Ankara, Kızılcahamam, Işık mt., F.Celep 1853 12.05.2013
L. gundelsheimeri	Turkey, Rize, Çamlıhemşin, F.Celep 1980 24.07.2013
L. truncatum	Turkey, Hatay, İskenderun, F.Celep 1825 22.04.2013
L. album subsp. *album*	Turkey, Mersin, Fındıkpınarı, F.Celep 1823 22.04.2013
L. album subsp. *barbatum*	Japan, Honshu, Murata & Iwatsuki 642 12.05.1968 (K)
L. crinitum	Turkey, Amasya, Tavşan mountain, F.Celep 1855 13.05.2013
L. tomentosum var. *tomentosum*	Turkey, Van, OT 7993, 2013
L. tomentosum var.*filicaule*	Turkey, Van, Artos mountain, Coll. E. M. Rix et al 744 1968 (E)
L. tomentosum var.*hakkariense*	Turkey, Hakkari, Cilo mountain, Davis 24060 08.08.1954 (E)
L. sulfureum	Turkey, Bayburt, Çaykara, F.Celep 1977 24.07.2013
L. moschatum var. *moschatum*	Turkey, Antalya, Olimpos, F.Celep 1798 17.04.2013
L. moschatum. var. *rhodium*	Turkey, Denizli, F.Celep 1780, 16.04.2013
L. ponticum	Turkey, Amasya, Akdağ, F.Celep 1866 14.05.2013
L. galactophyllum	Turkey, Erzurum, Tortum, F.Celep 1896 17.05.2013
L. tschorochense	Turkey, Artvin, Yusufeli, F.Celep 1886 17.05.2013
L. vreemanii	Turkey, Erzurum, Tortum, F.Celep 1989 28.07.2013
L. orientale	Turkey, Nevşehir, Ürgüp, F.Celep 1850 25.04.2013
L. multifidum	Turkey, Erzurum, Coll. Stainton & Henderson 6137 09.07.1960 (E)
L. galeobdolon subsp. montanum	Turkey, Rize, Çamlıhemşin, F.Celep 1882 16.05.2013
L. galeobdolon subsp. *flavidum*	Österreich, Oberösterreich, E. Vitek 96-248 28.05.1996 (E)
L. flexuosum	Algeria, Djurdjura, Davis 59242 19.06.1975 (E)
L. orvala	Italy, Treviso, Asolo, Davis 34007 07.04.1960 (E)
L. ponticum subsp. *anatolicum*	Turkey, Kastamonu, Kure, F.Celep 3840, 01.05.2015
L. bilgilii	Turkey, Burdur, Altinyayla, F.Celep 3860, 05.06.2015
L. cappadocicum	Turkey, Aksaray, Hasan Montain, F.Celep 3557 11.07.2014
E, Royal Botanic Garden Edinburgh; K, Royal Botanic Gardens, Kew.	

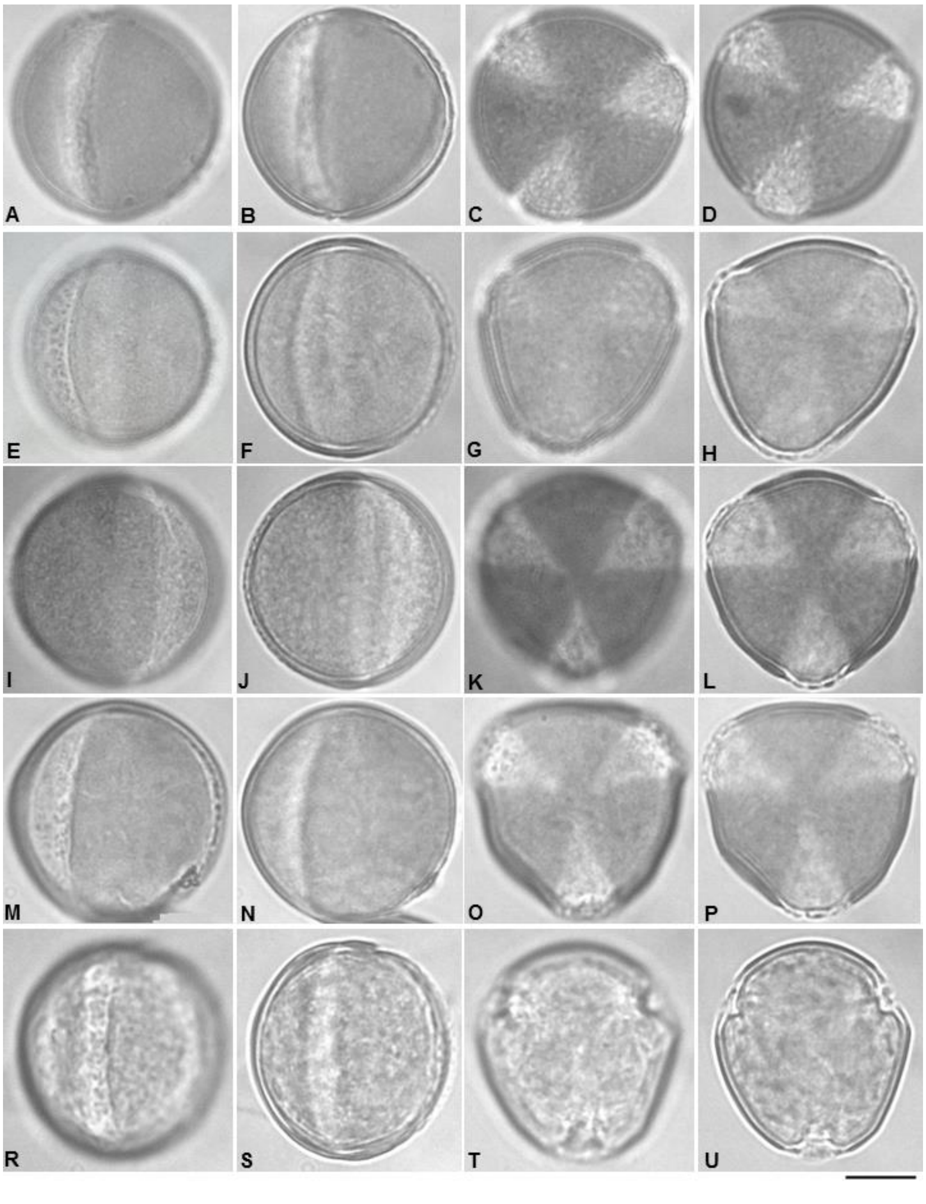


Figure 41. Light microscope photos of pollen grains of A, B, C, D *L. cariense*; E, F, G, H *L. lycium*; I, J, K, L *L. garganicum* subsp. *striatum*; M, N, O, P *L. garganicum* subsp. *laevigatum*; R, S, T, U *Galeobdolon* Scale bar 20 μm

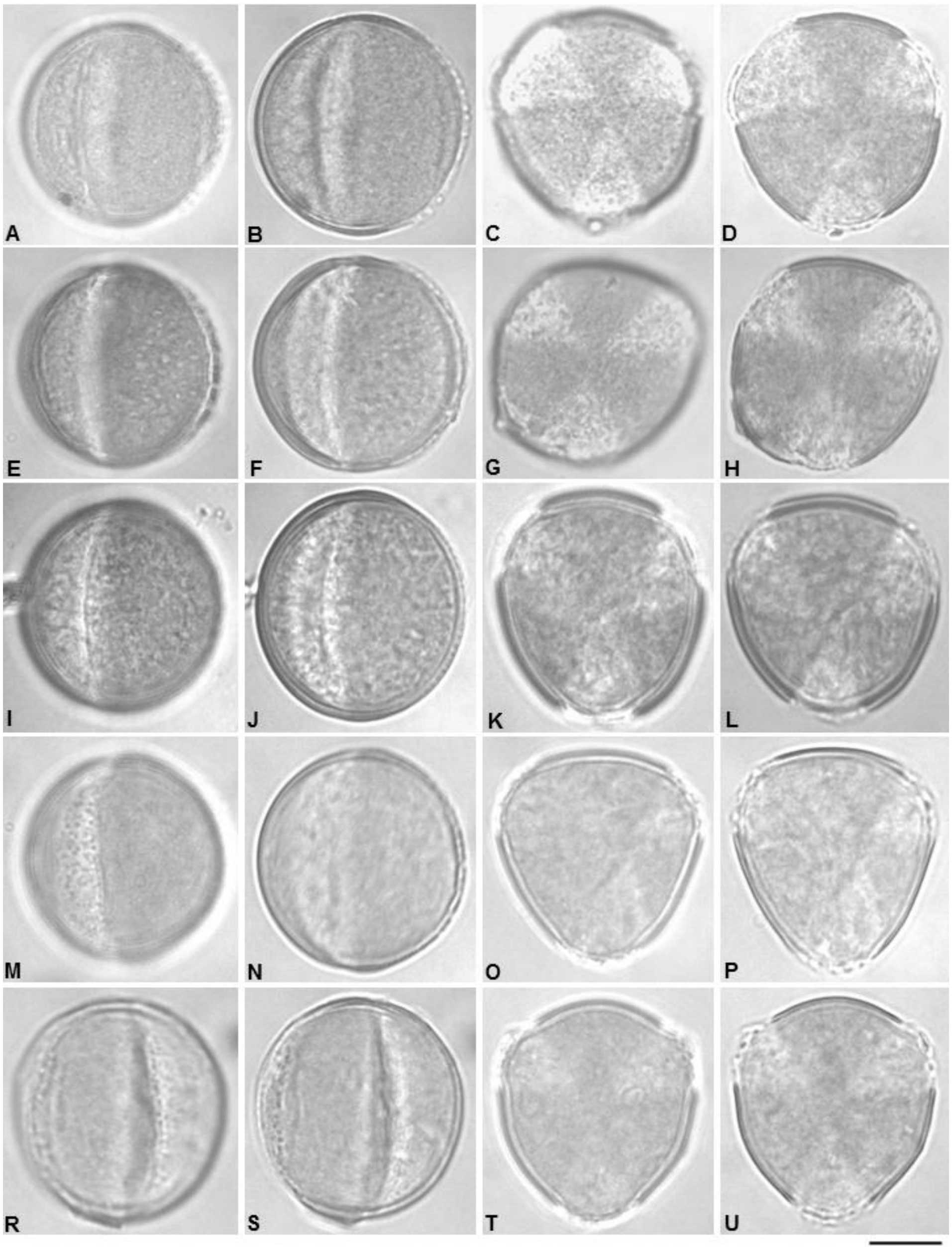


Figure 42. Light microscope photos of pollen grains of; A, B, C, D *L. amplexicaule* subsp. *amplexicaule* var. *amplexicaule*; E, F, G, H *L. amplexicaule* subsp. *amplexicaule* var. *aleppicum*; I, J, K, L *L. album* subsp. *album*; M, N, O, P *L. tomentosum* var. *tomentosum*; R, S, T, U *L. moshatum* Scale bar 20 µm

Reticulate Exine Sculpturing Pattern

The reticulate sculpturing pattern is observed in 26 taxa (Table 15). Type 1a, Type 1b and Type 1c: Figs. 43-54. For each SEM figure (Figs. 43-71); Scale bars, 5 µm for polar and equatorial views, 1 µm for surface details.

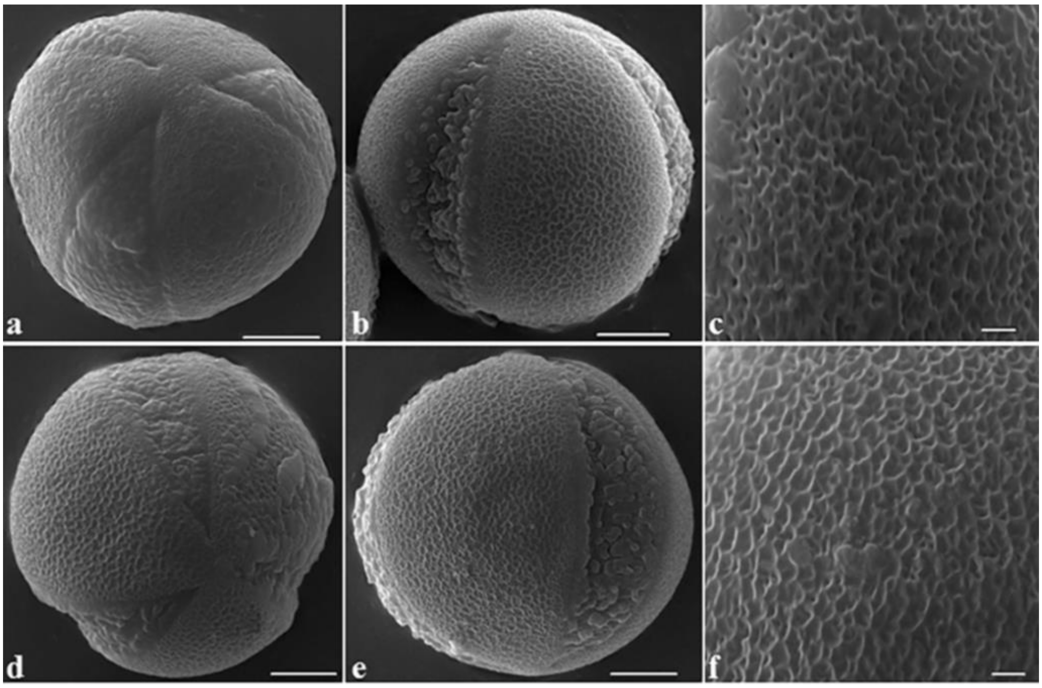


Figure 43. SEM micrographs of pollen grains of; a, b, c *L. lycium*; d, e, f *L. cariense*

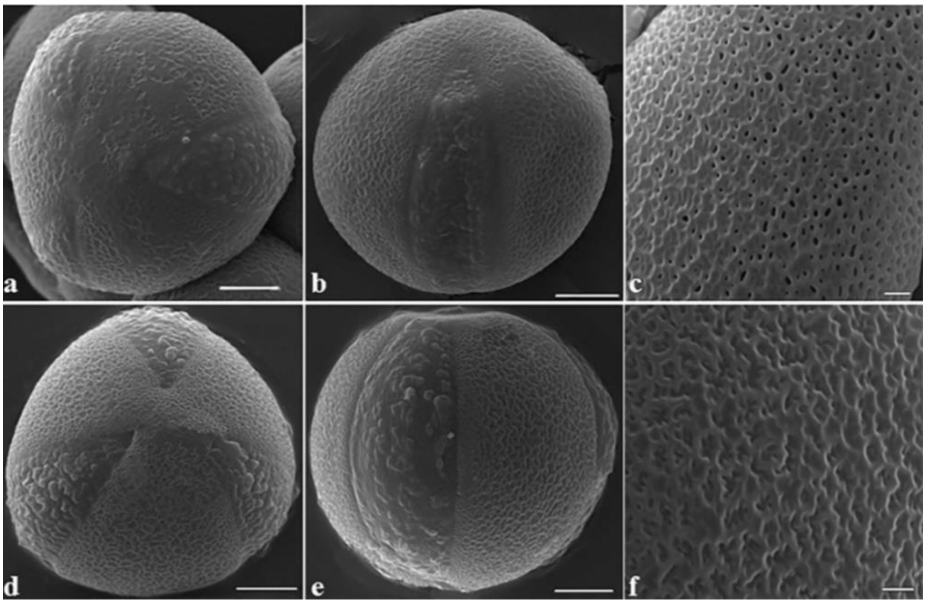


Figure 44. SEM micrographs of pollen grains of; a, b, c *L. garganicum* subsp. *striatum* (*L. pisidicum*); d, e, f *L. garganicum* subsp. *striatum* (*L. tenuiflorum*)

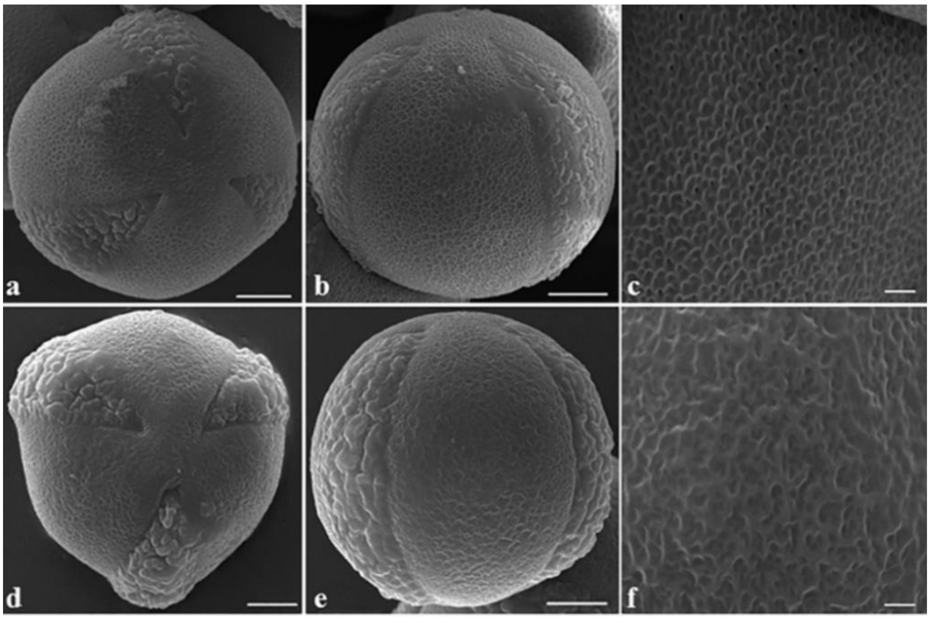


Figure 45. SEM micrographs of pollen grains of; a, b, c *L. garganicum* subsp. *laevigatum* (*L. veronicifolium*); d, e, f *L. garganicum* subsp. *striatum* (*L. garganicum* subsp. *reniforme*)

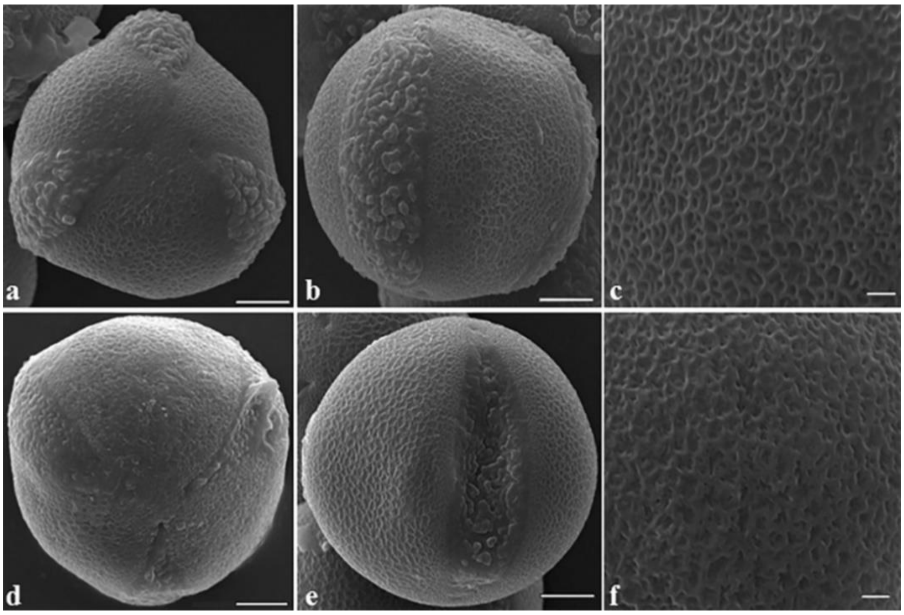


Figure 46. SEM micrographs of pollen grains of; a, b, c *L. garganicum* subsp. *striatum* (*L. garganicum* subsp. *nepetifolium*); d, e, f *L. garganicum* subsp. *rectum*

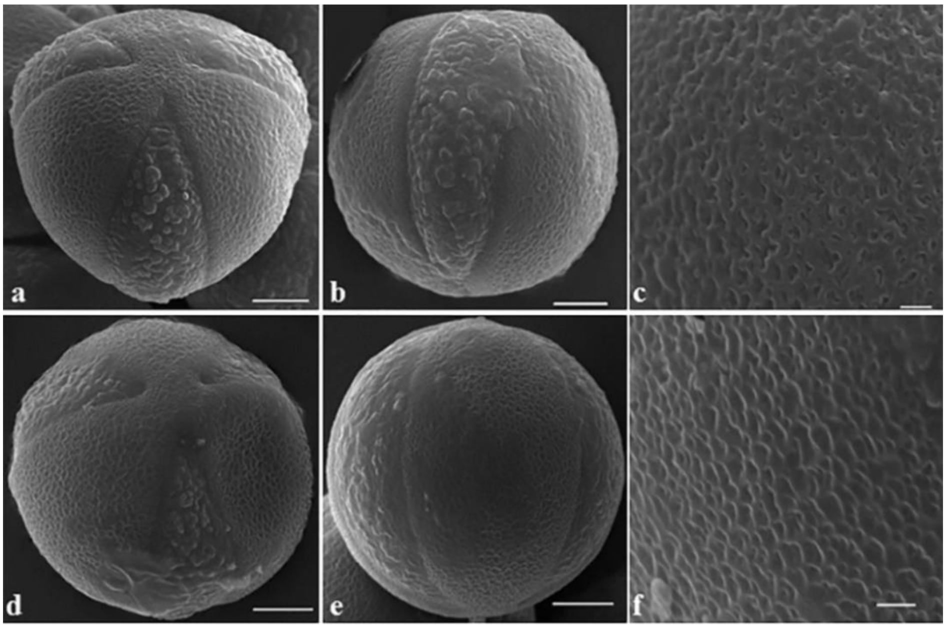


Figure 47. SEM micrographs of pollen grains of; a,b, c *L. garganicum* subsp. *lasioclades*; d, e, f *L. capadocicum* (*L. garganicum* subsp. *pulchrum*)

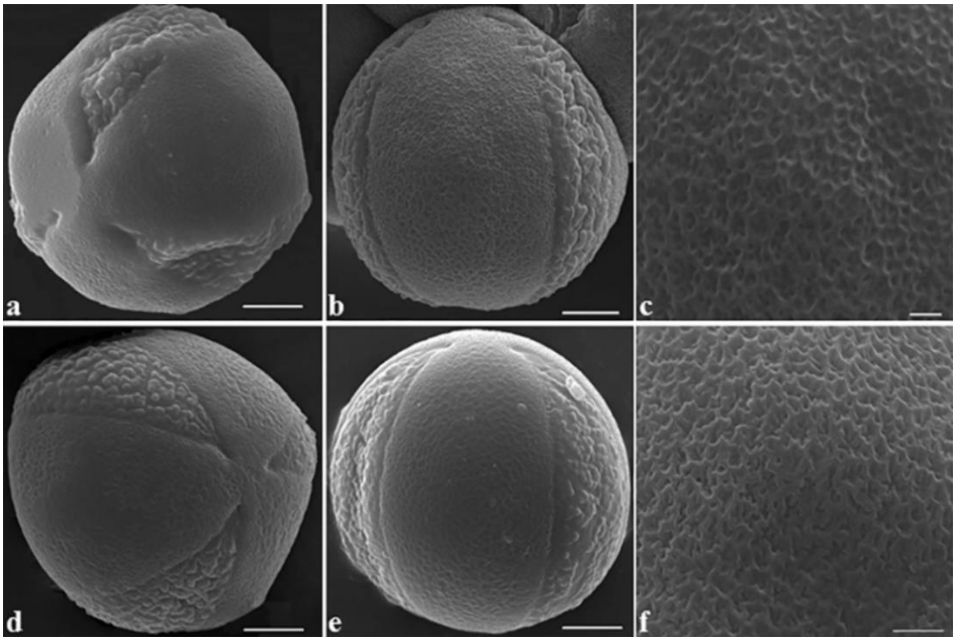


Figure 48. SEM micrographs of pollen grains of; a, b, c *L*. *garganicum* subsp. *laevigatum*; d, e, f *L*. *microphyllum*

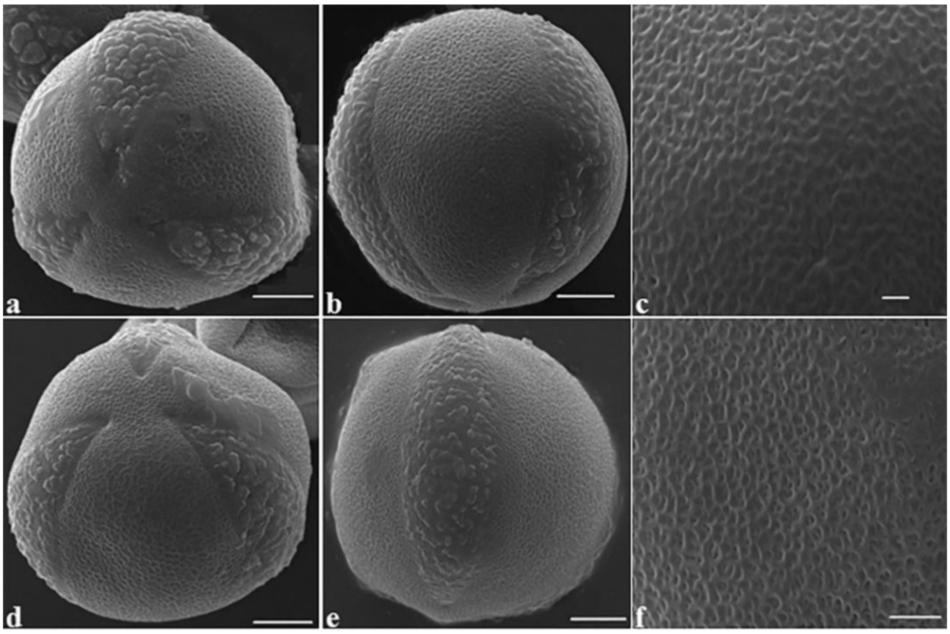


Figure 49. SEM micrographs of pollen grains of; a, b, c *L*. *cymbalariifolium*; d, e,f *L*. *sandrasicum*

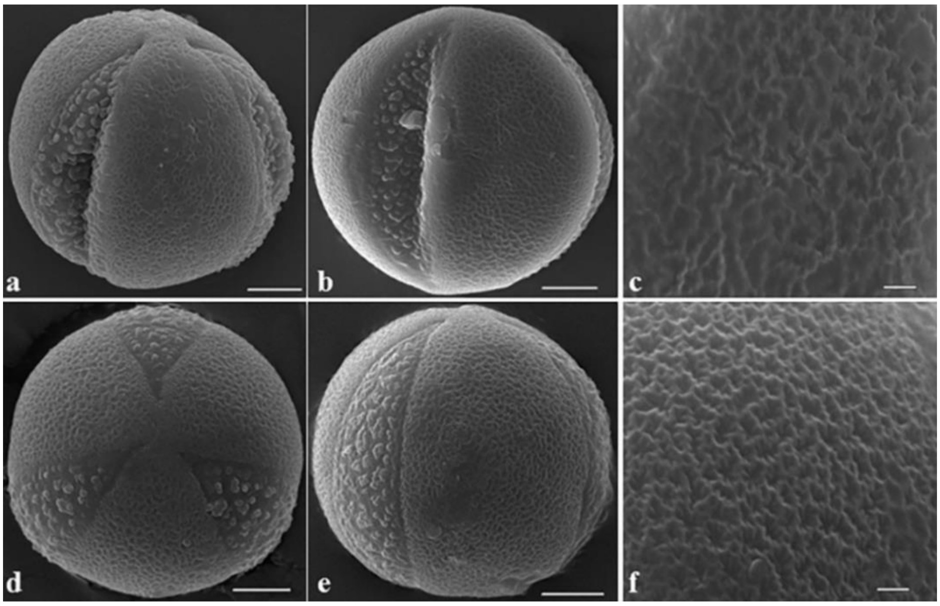


Figure 50. SEM micrographs of pollen grains of; a, b, c *L. purpureum* (*L. purpureum* var. *purpureum*); d, e,f *L. purpureum* (*L. purpureum* var. *aznavourii*)

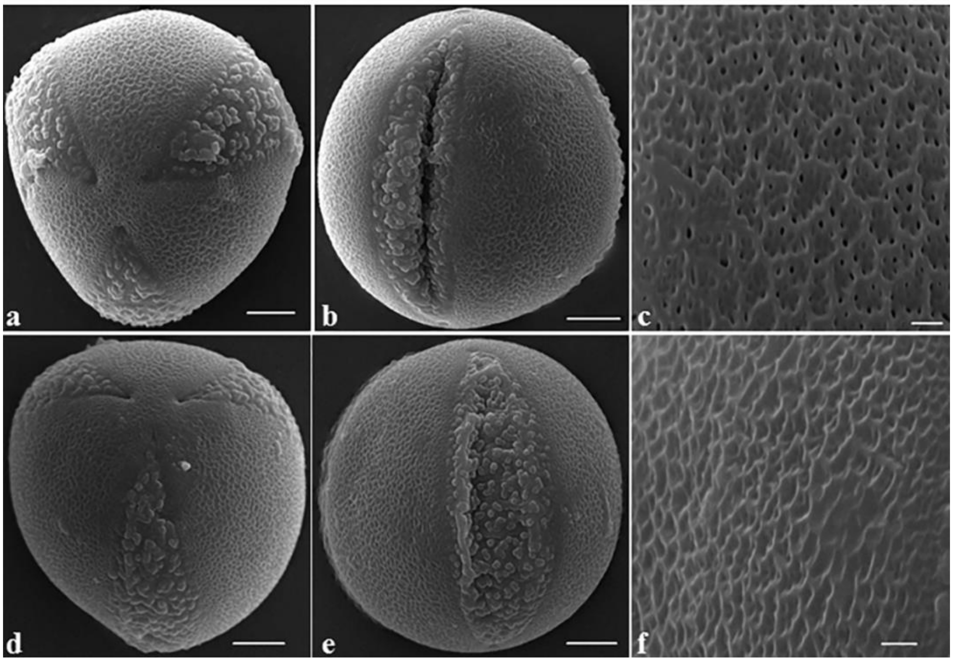


Figure 51. SEM micrographs of pollen grains of; a, b, c; *L. eriocephalum* subsp. *eriocephalum* d, e, f; *L. eriocephalum* subsp. *glandulosidens*

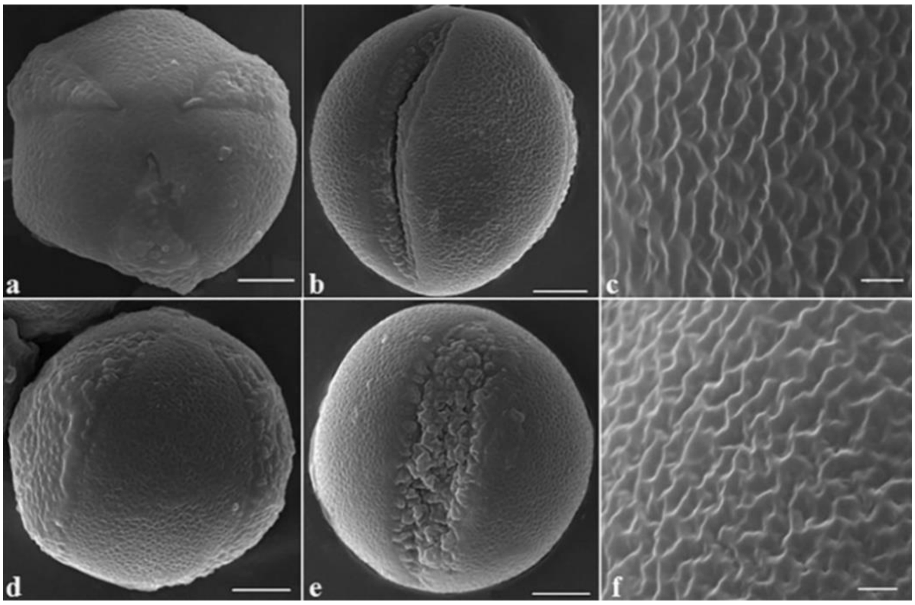


Figure 52. SEM micrographs of pollen grains of; a, b, c; *L. amplexicaule* subsp. *amplexicaule* var. *amplexicaule* (*L. amplexicaule*) d, e,f; *L. amplexicaule* subsp. *amplexicaule* var. *aleppicum* (*L. aleppicum*)

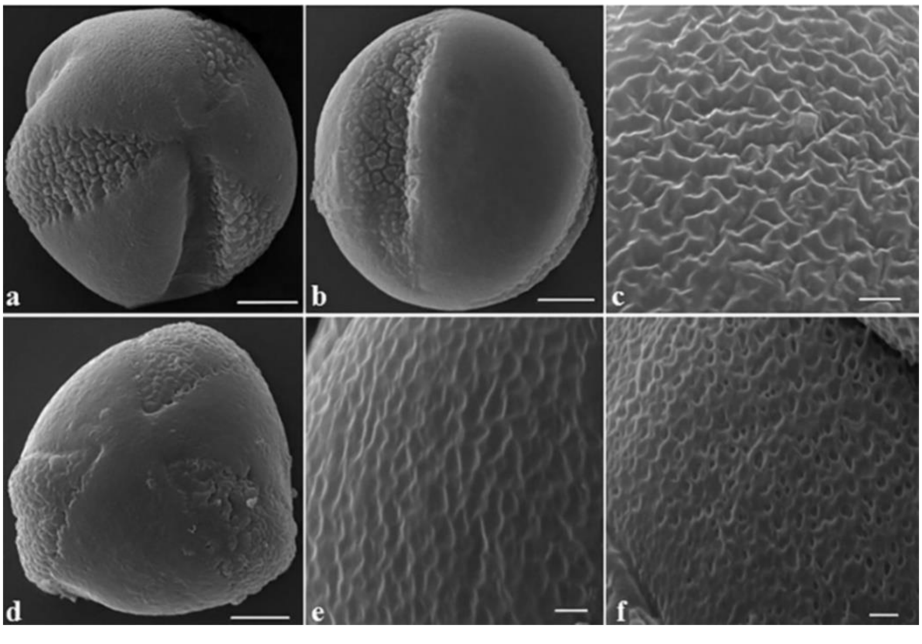


Figure 53. SEM micrographs of pollen grains of; a, b, c; *L. macrodon* d, e; *L. bifidum* f; *L. confertum*

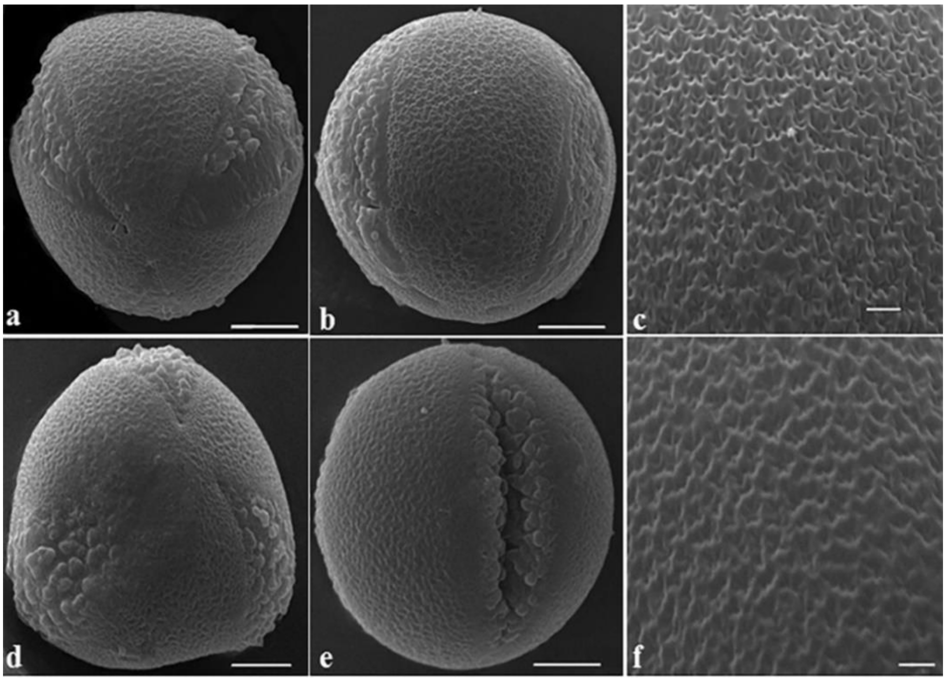


Figure 54. SEM micrographs of pollen grains of; a, b, c; *L. orientale* d, e,f; *L. multifidum*

Granulate Exine Sculpturing Pattern

The granulate sculpturing pattern is observed in 19 taxa (Table 15). Granulate sculpturing pattern with perforations: Type 2a, Figs. 55, 56, 57, 58, 59, 60, 61, 62, 65, 66, 67. Psilate-like, smooth granulate surfaces without perforations: Type 2b, Figs. 63, 64. For each SEM figure (Figs. 43-71); Scale bars, 5 µm for polar and equatorial views, 1 µm for surface details.

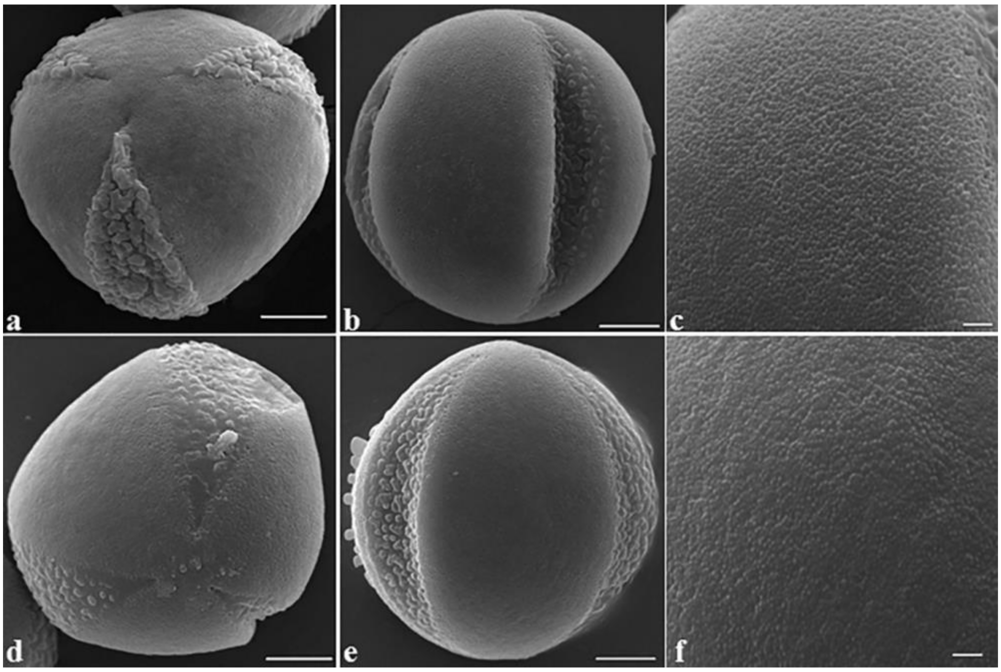


Figure 55. SEM micrographs of pollen grains of; a, b, c; *L. armenum* subsp. *armenum* d, e, f; *L. armenum* subsp. *sintenisii*

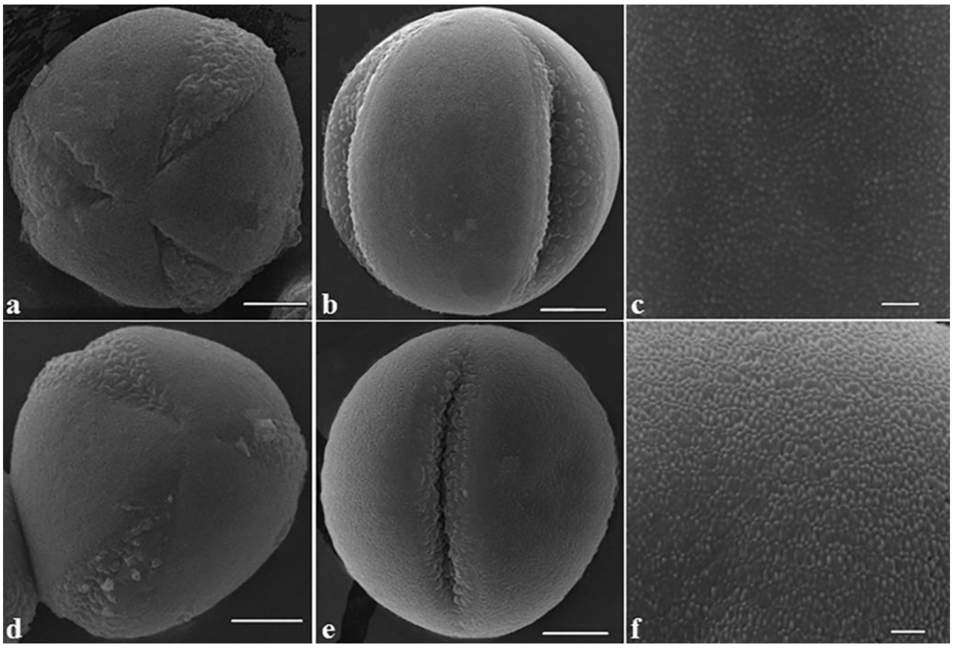


Figure 56. SEM micrographs of pollen grains of; a, b, c; *L. maculatum* (L. *maculatum* var. *maculatum*) d, e, f; *L. villosifolium* (*L. maculatum* var. *villosifolium*)

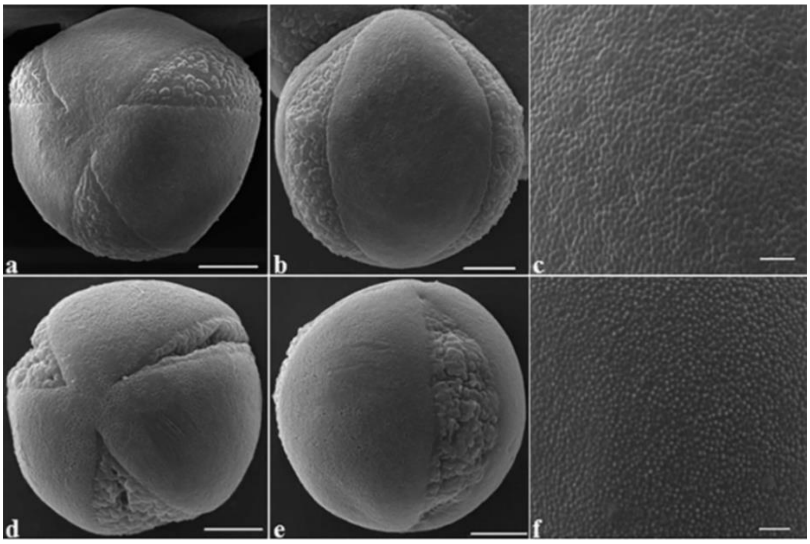


Figure 57. SEM micrographs of pollen grains of; a, b, c; *L. maculatum* (*L. gundelsheimerii*) d, e, f; *L. maculatum* (*L. truncatum*)

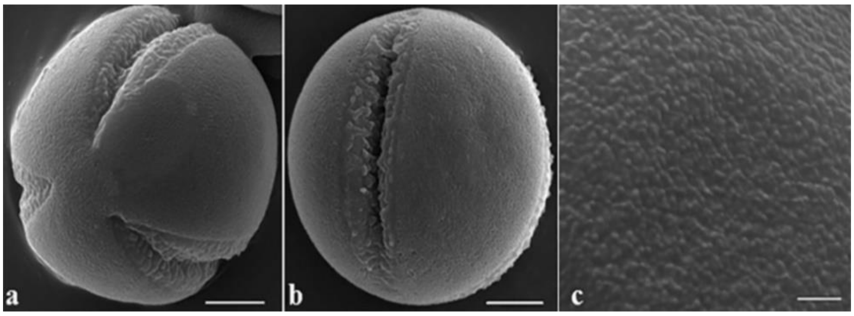


Figure 58. SEM micrographs of pollen grains of; a, b, c; *L. album* subsp. *album*

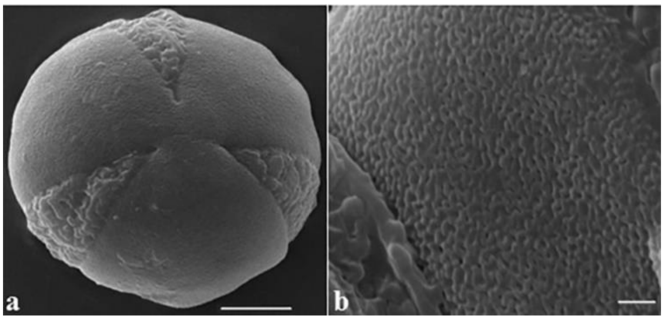


Figure 59. SEM micrographs of pollen grains of; a, b; *L. album* subsp. *barbatum*

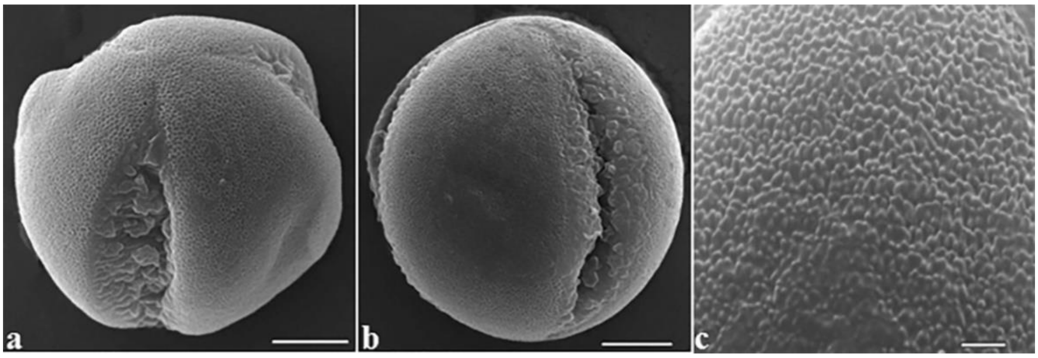


Figure 60. SEM micrographs of pollen grains of; a, b, c; *L. album* subsp. *crinitum* (*L. crinitum*)

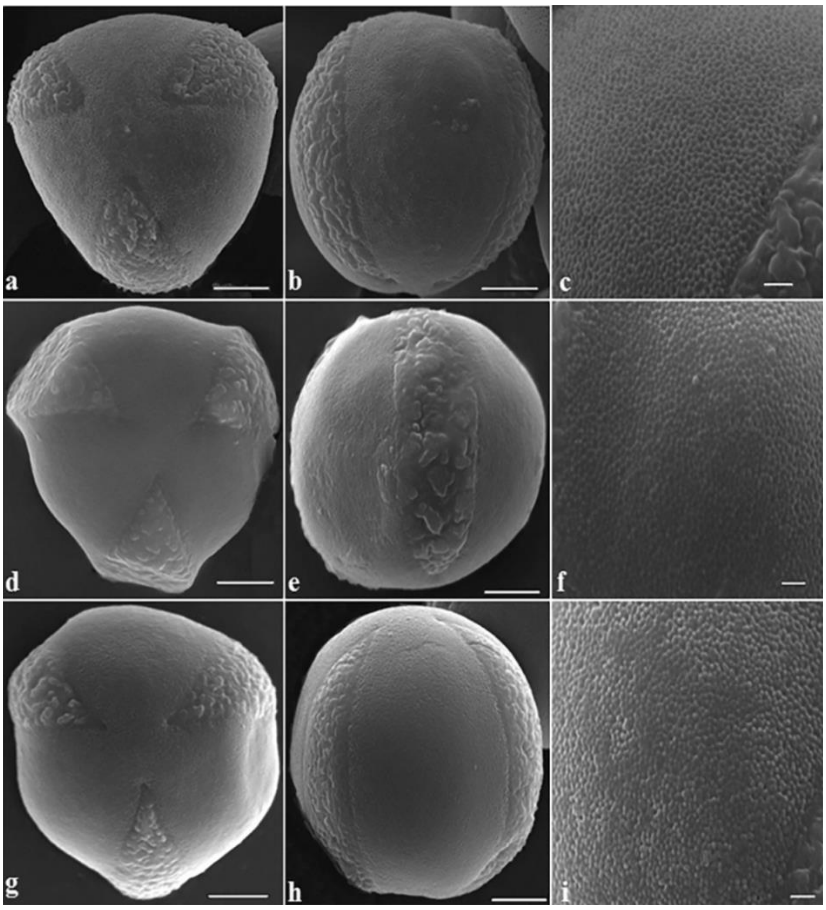


Figure 61. SEM micrographs of pollen grains of; a, b, c; *L. tomentosum* var. *tomentosum* d, e, f; *L. tomentosum* var. *filicaule* g, h, i; *L. tomentosum* var. *tomentosum* (*L. tomentosum* var. *hakkariense*)

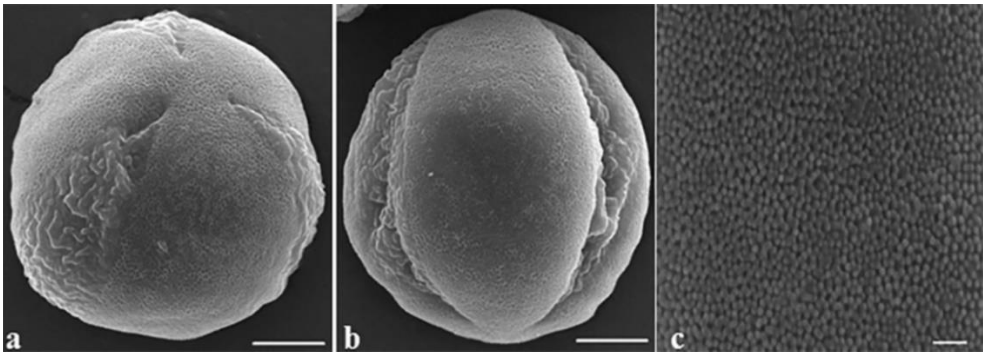


Figure 62. SEM micrographs of pollen grains of; a, b, c; *L. tomentosum* var. *alpestre* (*L. sulfureum*)

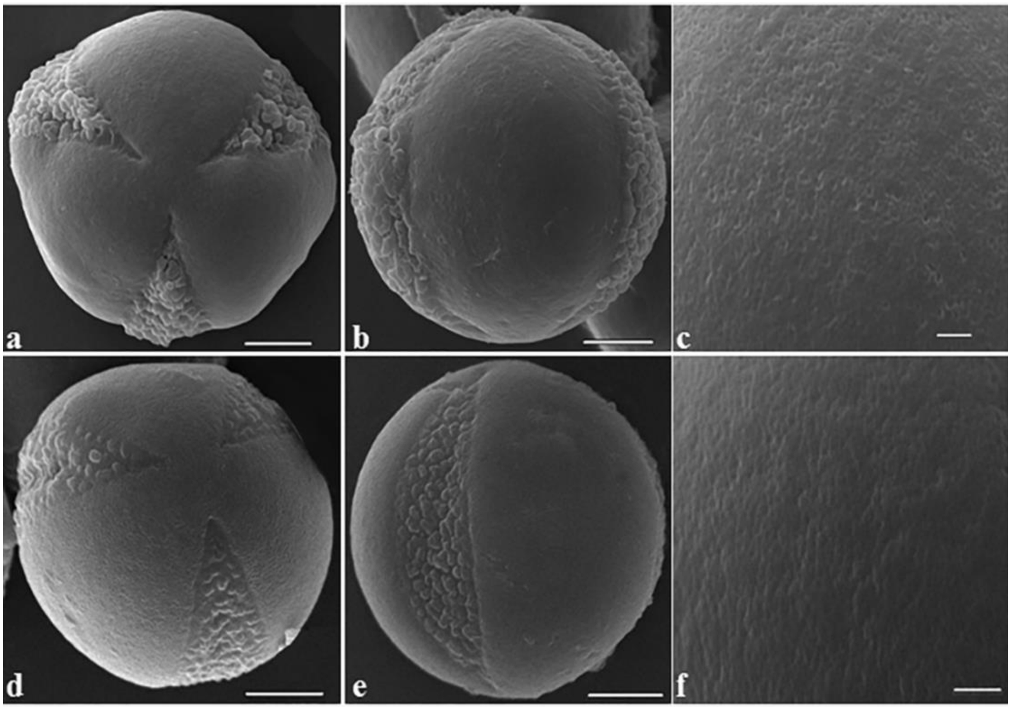


Figure 63. SEM micrographs of pollen grains of; a, b, c; *L. moshatum* (*L. moshatum* var. *moshatum*) d, e, f; *L. moshatum* (*L. moshatum* var. *rhodium*)

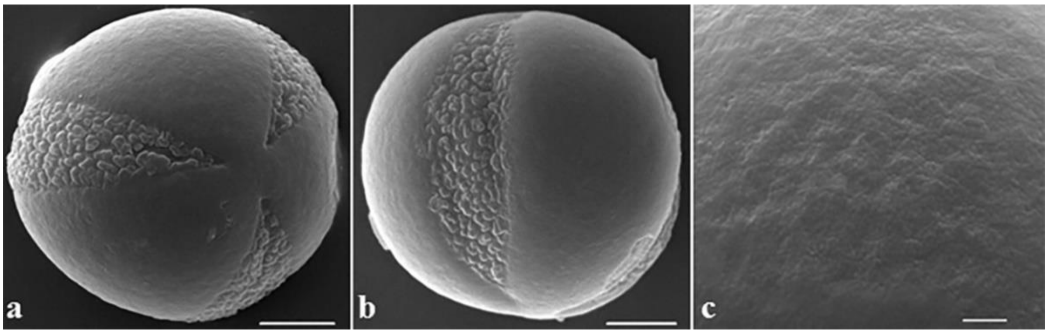


Figure 64. SEM micrographs of pollen grains of; a, b, c; *L. ponticum* subsp. *ponticum* (*L. ponticum*)

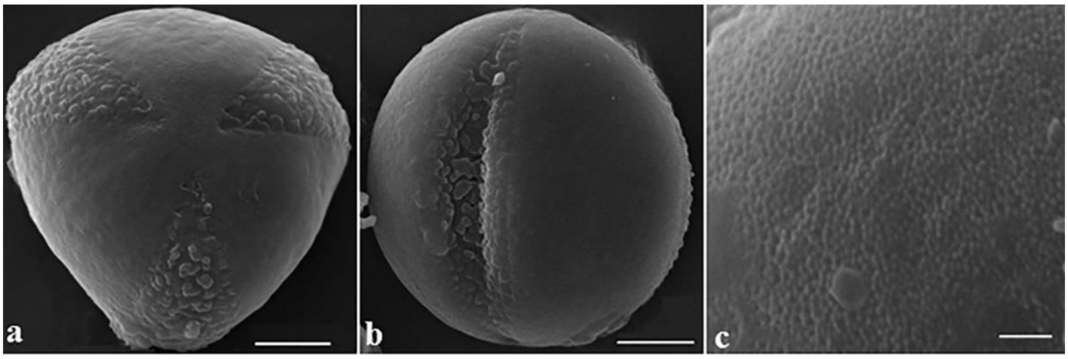


Figure 65. SEM micrographs of pollen grains of; a, b, c; *L. galactophyllum*

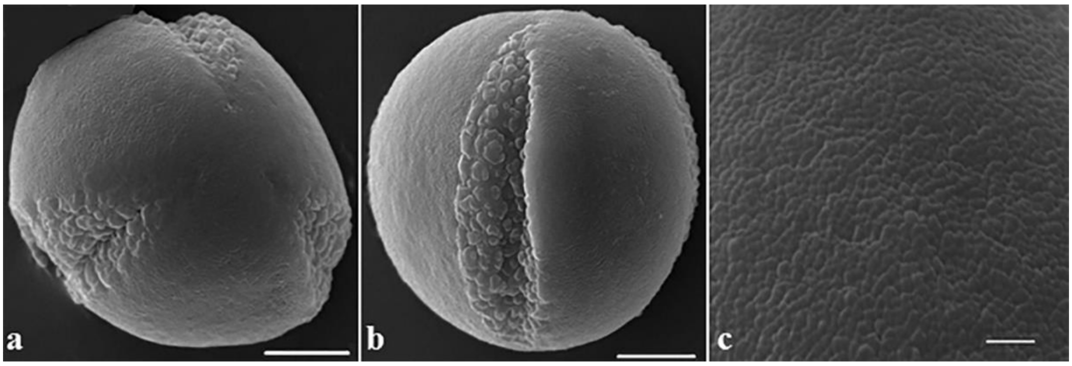


Figure 66. SEM micrographs of pollen grains of; a, b, c; *L. tschorochense*

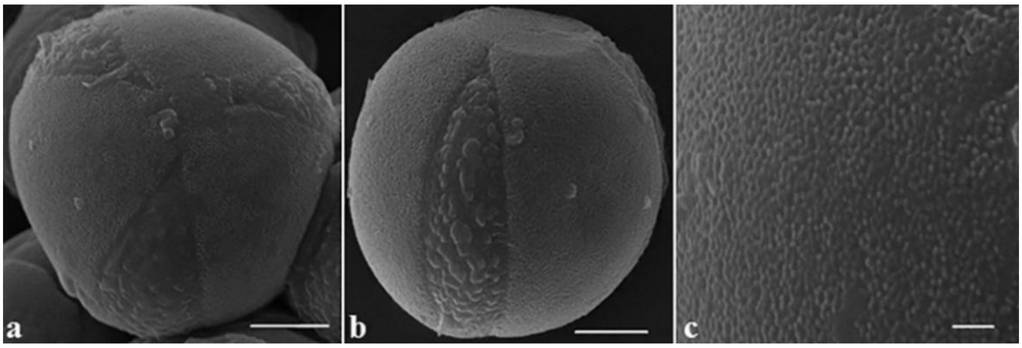


Figure 67. SEM micrographs of pollen grains of; a, b, c; *L. album* subsp. *crinitum* (*L. vremanii*)

Microreticulate Exine Sculpturing Pattern

The microreticulate exines are observed in 4 taxa. (Type 3, Figs. 68, 69, 70). For each SEM figure (Figs. 43-71); Scale bars, 5 µm for polar and equatorial views, 1 µm for surface details.

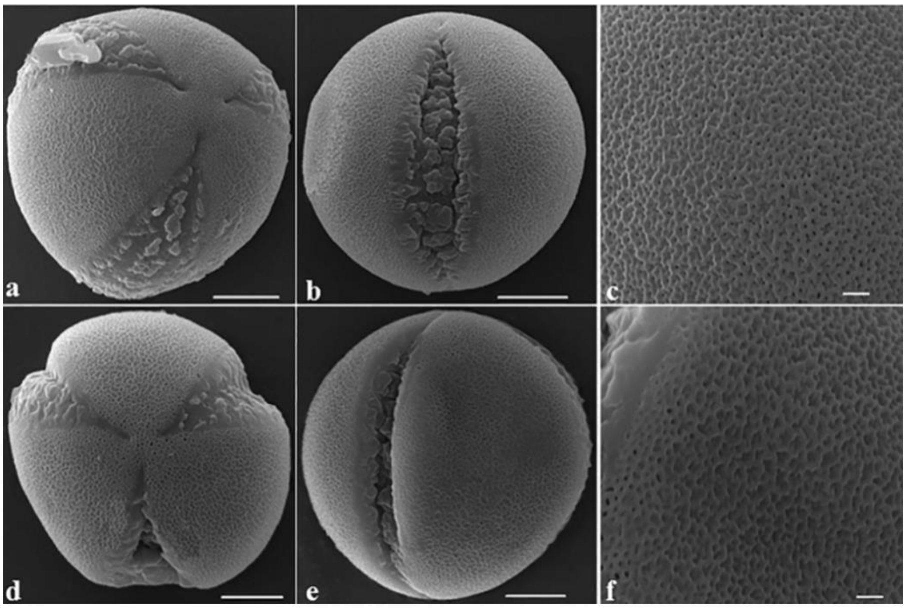


Figure 68. SEM micrographs of pollen grains of; Genus *Galeobdolon* a, b, c; *L. galeobdolon* subsp. *montanum* d, e, f; *L. galeobdolon* subsp. *flavidum*

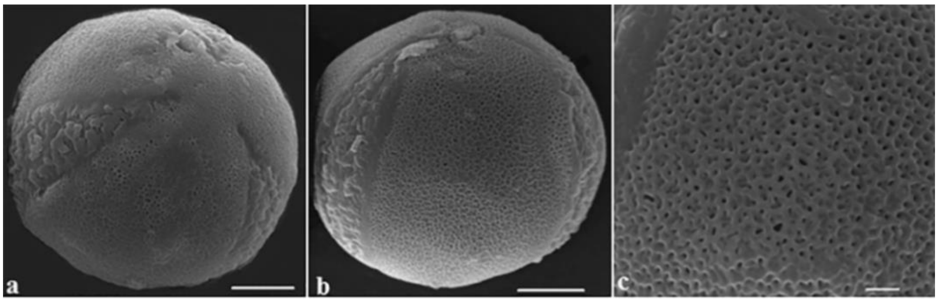


Figure 69. SEM micrographs of pollen grains of; a, b, c; *L. flexiosum*

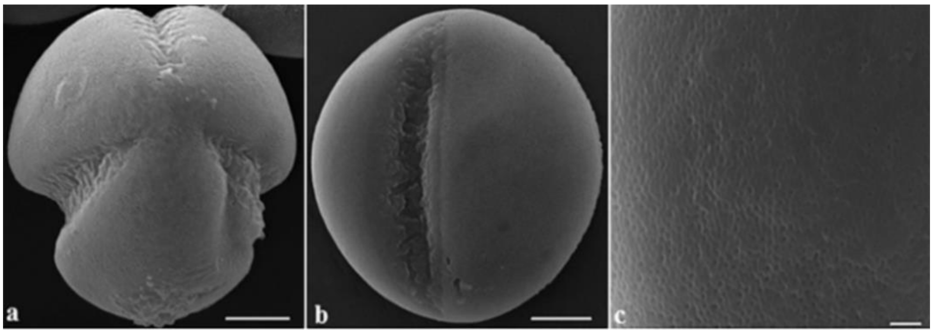


Figure 70. SEM micrographs of pollen grains of; a, b, c; *L. orvala*

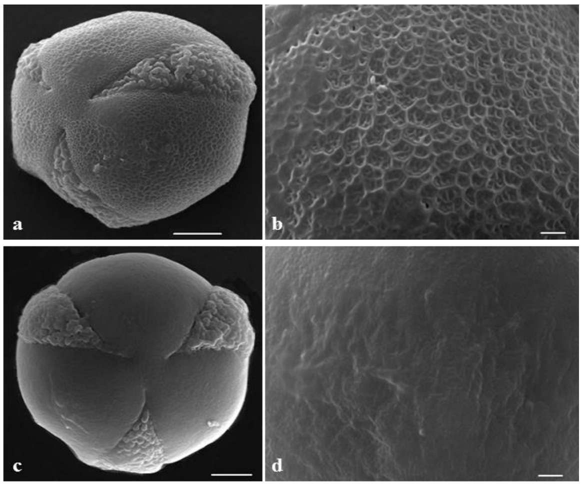


Figure 71. SEM micrographs of pollen grains of; a, b; *L. bilgilii* c, d; *L. ponticum* subsp. *anatolicum*

3.6 Pollination Biology of two *Lamium* species

In order to understand and illuminate the pollination mechanisms in the genus *Lamium*, two sympatric *Lamium* species; *L. villosifolium* and *L. album* subsp. *crinitum* were chosen and were observed in their natural habitat.

3.6.1 Population Size and Environment

The vegetation in Isik Mountain area was dominated by *Pinus sylvestris* L. and *Abies nordmanniana* subsp. *bornmulleriana* (Mattf.) Silba (Table 16). *Lamium villosifolium* and *L. album* subsp. *crinitum* were growing side by side (Figure 72). In 3 stations, the populations of each *Lamium* species differed in terms of density. It was evident from the observations that, the population size of *L. villosifolium* declined along the altitudinal gradient, where at the 3rd station; it reached its minimum abundance. In contrast, the population size of *L. album* subsp. *crinitum* gradually increased along the altitudinal gradient (Table 16).

Figure 72. Habit of *L. villosifolium* and *L. album* subsp. *crinitum*

Table 17. Selected study sites for pollination observations

Locality Isik Mountain, Kizilcahamam	GPS coordinates and elevation	*Lamium* species (population size)		Vegetation
		v	*c*	
1st station	N 40° 41' 00.00" E 32° 43' 46.99" 1580 m 400m2	++++ 50 individuals	+ 10 individuals	Underforest (*Pinus sylvestris*. - dominating species, *Abies nordmanniana* subsp. *bornmulleriana*)
2nd station	N 40° 40' 42.21" E 32° 45' 19.75" 1840 m 400m2	+++ 40 individuals	++ 20 individuals	Underforest (*Pinus sylvestris*, *Abies nordmanniana* subsp. *bornmulleriana* – dominating species)
3rd station	N 40° 39' 57.65" E 32° 46' 04.82" 2062 m 10x35m=350m^2	+ 10 individuals	++++ 60 individuals	Subalpine (*Juniperus* sp., *Festuca* sp., *Poa* sp., *Myosotis* sp.)

v; *L. villosifolium*, c; *L. album* subsp. *crinitum*

Figure 73. GoogleEarth image of Isik Mountain; located in northwest of Turkey, close to Kizilcahamam district of Ankara.

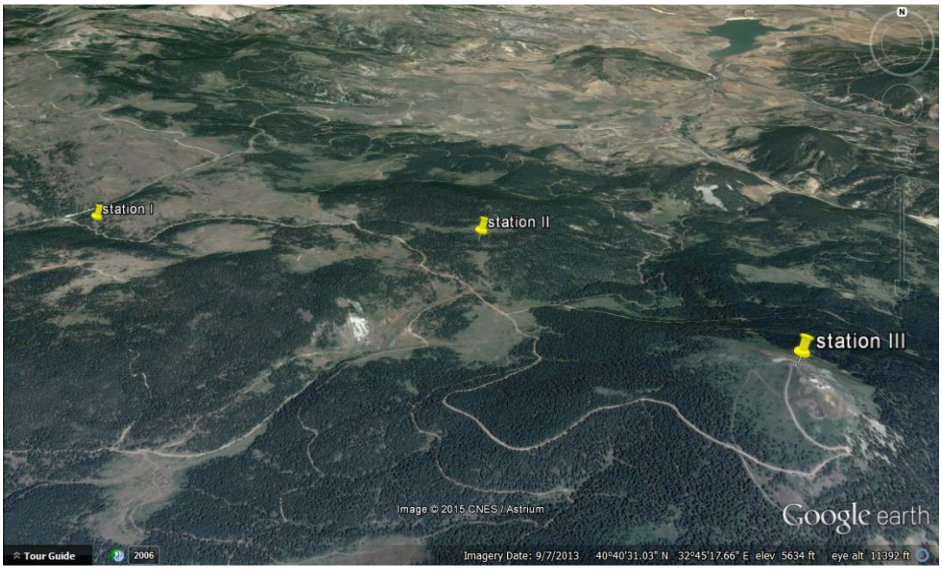


Figure 74. Google Earth image representing the selected study sites in Isik Mountain. (1st and 2nd station are 2.2 km apart, 2nd and 3rd station are 1.6 km apart- from bird`s eye view).

Figure 75. Station 1 at Isik Mountain.

Figure 76. Station 2 at Isik Mountain.

Figure 77. Station 3 at Isik Mountain (mountain summit).

3.6.2 Flower Morphology

Lamium villosifolium has zygomorphic, two lipped flowers. The upper lip is falcate and the white lower lips are wide and have purple spots (Figure 78). The four stamens adhere to the lateral corolla wall. The verticillasters are (1-)2-4(-5), (4-)6-8-flowered. Both the stamens and style are hidden below the upper lip (Figure 80). The corolla tube is longer compared to *Lamium album* subsp. *crinitum*. *Lamium album* subsp. *crinitum* has zygomorphic, two lipped flowers. The upper lip is nearly falcate and the lower lips are narrow. The four stamens adhere to the lateral corolla wall. Both the stamens and style are hidden below the upper lip (Figure 79). The verticillasters are 2-8, 8-10- flowered.

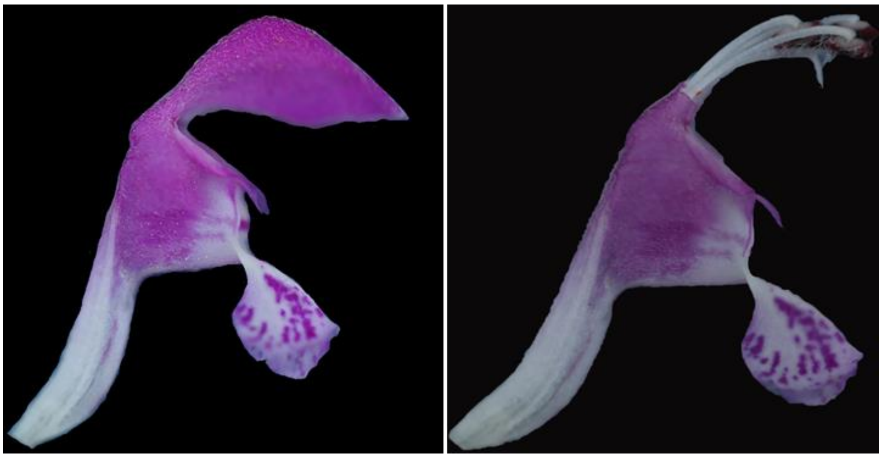


Figure 78. Corolla morphology of *Lamium villosifolium*; both stamens and style are hidden below the upper lip of corolla.

Figure 79. Corolla morphology of *Lamium album* subsp. *crinitum*, both stamens and style are hidden below the upper lip of corolla.

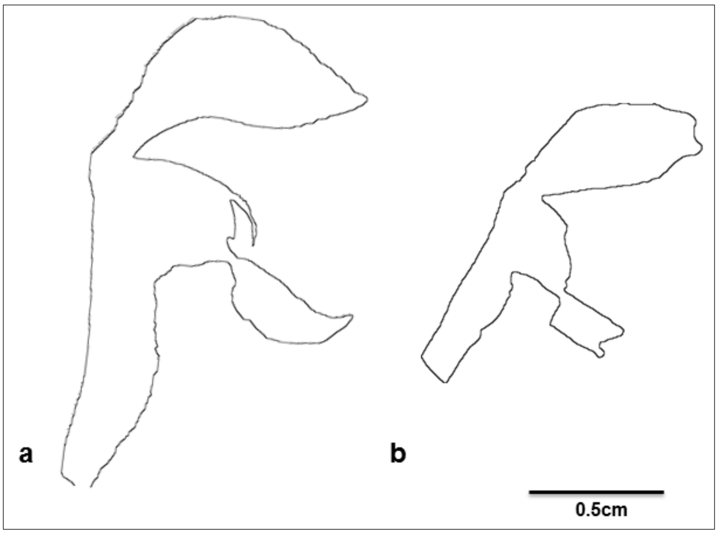


Figure 80. Vector drawings of (a) *L*. *villosifolium* and (b) *L*. *album* subsp. *crinitum*; scale, 0.5 cm.

Figure 81. Various patterns on the flower entrance of *L*. *villosifolium* (left) and *L*. *album* subsp. *crinitum* (right) as visual clues for the pollinators, indicating the flower entrance.

3.6.3 Flower Visitors

Inflorescences of *L. villosifolium* and *L. album* subsp. *crinitum* were visited by a variety of bee species at all stations. 5 bee species (*Bombus argillaceus* Scopoli, *B. lapidarius* L., *B. pascuorum* Scopoli, *B. lucorum* L. and *Apis mellifera* L.) from 2 different genera (*Bombus* and *Apis*) are observed as pollinators. *Bombus argillaceus*, *B. lapidarius* and *B. pascuorum* were observed at all sites. However, *Bombus lucorum* and *Apis mellifera* were observed only at 3rd station and 2nd+3rd station, respectively. In addition, *Bombylius fulvescens* Wiedemann (Bombyliidae) was observed only a few times, sucking nectar from flowers of *L. villosifolium*, by hovering in front of the flower entrance, but pollination was not confirmed (Figure 138).

All of the observed bee species were identified as pollinators. It was evident from the flower morphology that, four anthers were hidden below the upper lip of corollas thus, pollen deposition on the bee`s body were observed only when the bee finished sucking the nectar from the flower tube, while moving from one flower to the other/or to another inflorescence. Although the stigmas were hidden below the upper lip like the anthers, stigma contact of bees were highly probable due to the closeness of anther and stigma.

The site of pollen deposition on the pollinator`s body was easily identified by the bright orange (*L. villosifolium*) and lemony yellow (*L. album* subsp. *crinitum*) color of the pollen grains. At 1st and 2nd station, *B. argillaceus*, *B. lapidarius* and *B. pascuorum* were observed as pollinators. *L. villosifolium* and *L. album* subsp. *crinitum* shared *B. lapidarius* and *B. pascuorum* and the relative frequencies of the bee species were different at 1st and 2nd station (Table 18). Highest pollinator frequency and species diversity was observed in the 3rd station however; the dominating bee species was recorded as *B. lapidarius* (see frequency -percentage-values, Table 21).

Table 18. Pollinator visiting frequency at 3 stations

	B. argillaceus	*B. lapidarius*	*B. lucorum*	*B. pascuorum*	*A. mellifera*
1st station					
L. villosifolium	+++	+	-	+++	-
L. album subsp. *crinitum*	-	++	-	+	-
2nd station					
L. villosifolium	+++	+	-	++++	-
L. album subsp. *crinitum*	-	+++	-	+	-
3rd station					
L. villosifolium	+	+	-	+	-
L. album subsp. *crinitum*	-	++++	+	+	+

Pluses indicate pollinator visiting frequency from very high (++++: observed continuously on plant), high (+++: 8-10 times/observation period), medium (++: 5-8 times/observation period), low (+, <5 times/observation period)

Bombus argillaceus (Scopoli, 1805)

Bombus argillaceus is an abundant bumblebee in the Western part of Anatolia and belongs to the subgenus *Megabombus* (Rasmont & Flagothier, 1996). *Bombus argillaceus* is a large bumblebee and the males and workers are considerably smaller than the queen. In Turkey, the species lives at an altitudinal range of 400-2855 meters where 80% of the observations indicate 900-1870 meters range (Rasmont & Flagothier, 1996). *Bombus argillaceus* often coexists with *B. pascuorum*, *B. terrestris*, *B. zonatus* and *B. sylvarum* (Rasmont & Flagothier, 1996). *Bombus argillaceus* was the largest bee species among the pollinators (total body length 25.7 mm, n=5). The species was observed only on *L. villosifolium* at all sites. The species easily handled the corolla and had the shortest handling time (1.78 sec, n=22, Table 21) among the pollinators of *L. villosifolium*. The species was loaded with pollen on the anterior head during the feeding process (Figures 123-127).

Figure 82. *Bombus argillaceus* on *L. villosifolium*.

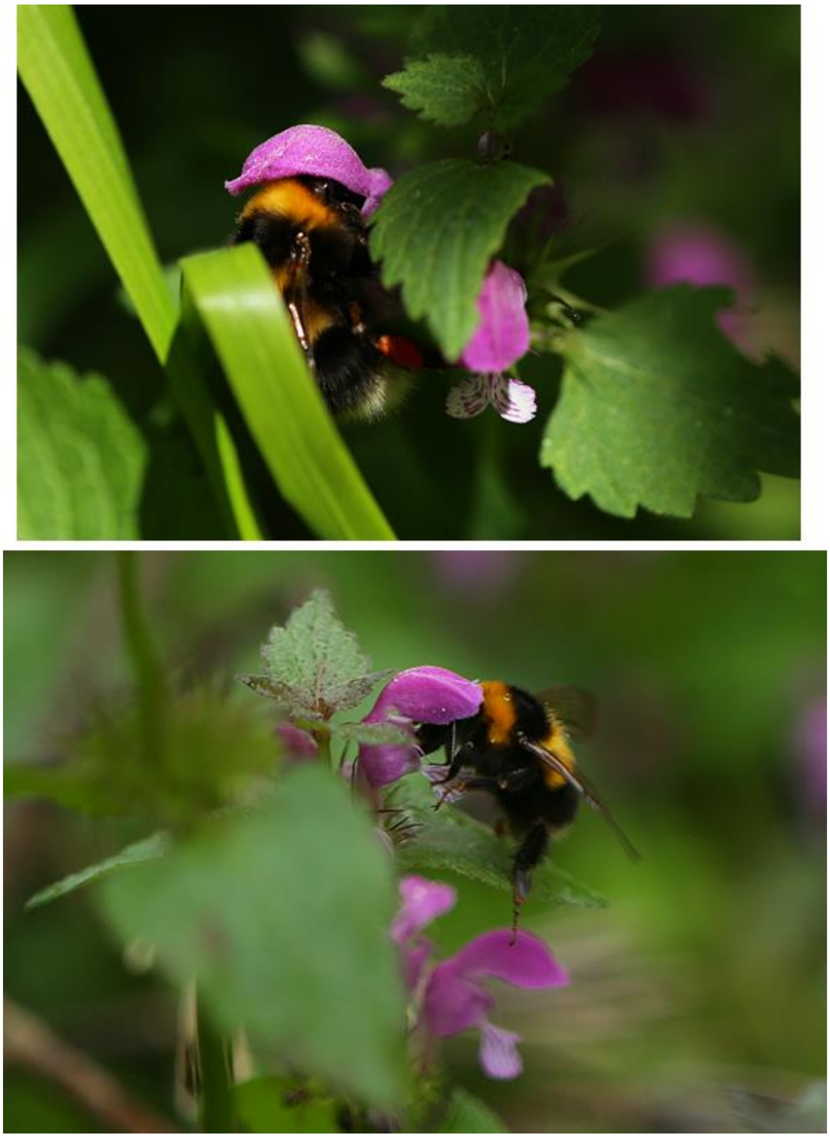


Figure 83. *Bombus argillaceus* on *L. villosifolium*

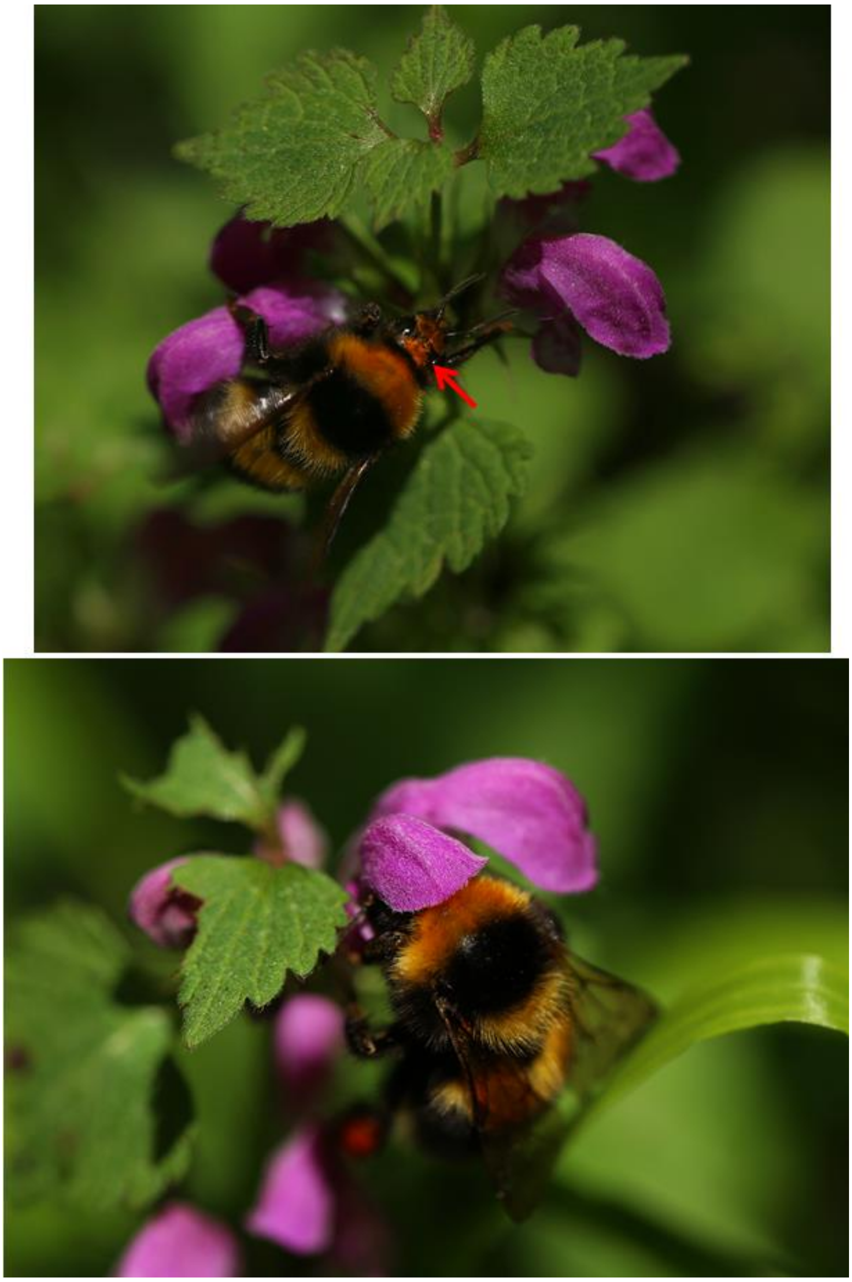


Figure 84. *Bombus argillaceus* on *L. villosifolium*

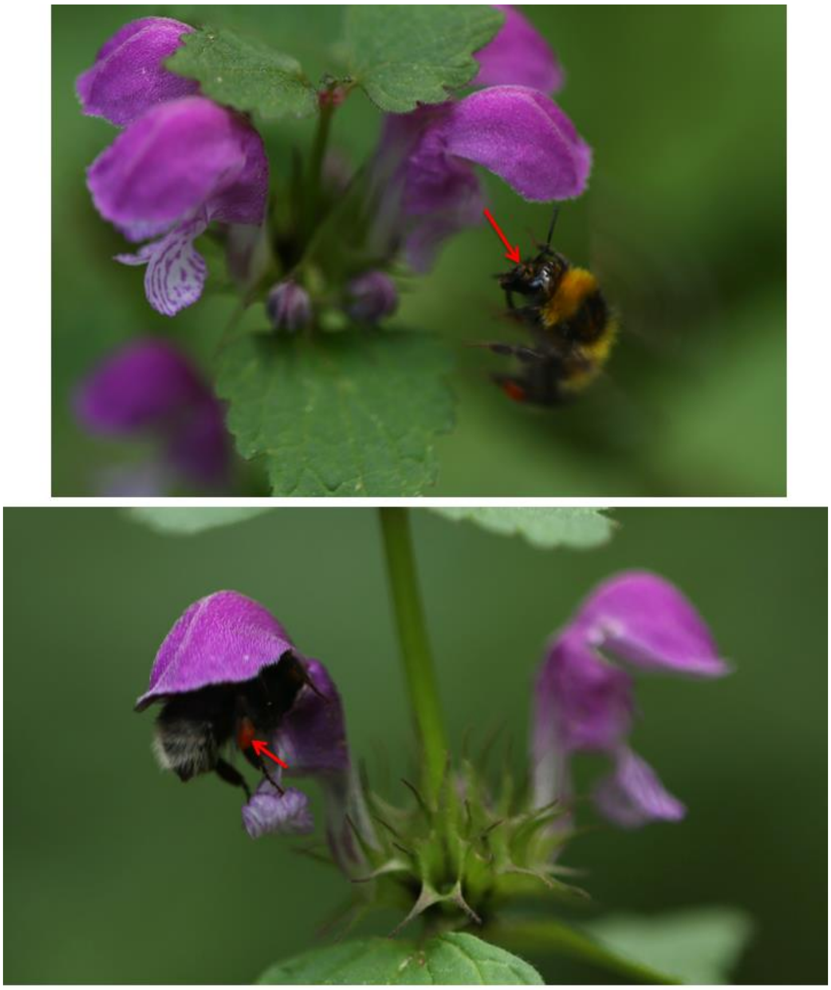


Figure 85. *Bombus argillaceus* worker on *L. villosifolium*

Bombus lapidarius (L., 1758)

Bombus lapidarius (red-tailed bumblebee) belongs to the subgenus *Melanobombus*. This species is typically recognized by their black body with red markings around the abdomen. Its nominal subspecies can be observed in the mountains of the western Turkey. *Bombus lapidarius* subsp. *lapidarius*, which is regarded as a wood-edge species, lives at an altitudinal range of 775-2390 meters (Rasmont & Flagothier, 1996). Compared to the other *Bombus* pollinators, the species is the second largest pollinator species (total body length 22.7 mm, n=16). *Bombus lapidarius* was by far the most common and frequent pollinator species, particularly for *L. album* subsp. *crinitum*. However, it was observed less frequently on *L. villosifolium* together with *B. pascuorum*. The species was frequently observed in 3rd station, where *L. album* subsp. *crinitum* is much more abundant than *L. villosifolium* (Table 21). The handling time of the species differed on each *Lamium* species (2.58 sec, n=15, on *L. villosifolium* and 1.79 sec, n=32, on *L. album* subsp. *crinitum*, Table 21). The average handling time per flower (1.79 sec) was shorter than any other pollinator of *L. album* subsp. *crinitum*. The species was loaded with pollen on the anterior and posterior head part during the feeding process (Figures 128-131).

Figure 86. *Bombus lapidarius* on *L. villosifolium*

Figure 87. *Bombus lapidarius* on *L. album* subsp. *crinitum*

Figure 88. *Bombus lapidarius* on *L. album* subsp. *crinitum*

Figure 89. *Bombus lapidarius* on *L. album* subsp. *crinitum*

Bombus lucorum (L., 1761)

Bombus lucorum (white-tailed bumblebee, subgenus *Bombus*) is a widespread and common bumblebee species all over Europe. Subgenus *Bombus sensu stricto* contains five species in Europe (*B. terrestris*, *B. sporadicus*, *B. magnus*, *B. lucorum* and *B. cryptarum*) (Waters et al., 2011). *Bombus lucorum* complex (term first used by Scholl and Obrecht, 1986) represented the three taxa (*B. lucorum*, *B. magnus*, *B. cryptarum*) that can not be easily distinguished by their appearances (Waters et al., 2011). The species has been distinguished from *B. terrestris* by most of authors however the distinction between *B. lucorum* and *B. cryptarum* is recent (Rasmont & Flagothier, 1996). The yellow thorax hairs of *B. terrestris* are more dull orangey while those of *B. lucorum* are more lemony. The species is regarded as true forest species (Rasmont, 1988). *Bombus lucorum* was observed only on *L. album* subsp. *crinitum* at the 3rd station, with very low frequencies. The species was small in size compared to other *Bombus* pollinators (total body length 19.1 mm, n=2). The species was more or less fast in handling the flowers (2.80 sec) (Table 21). Photographs and videos revealed that, the species was loaded with pollen on its anterior head part (Figure 132).

Figure 90. *Bombus lucorum* on *L. album* subsp. *crinitum*

Bombus pascuorum (Scopoli, 1763)

Bombus pascuorum (common carder-bee, subgenus; *Thoracobombus*) is a very widespread species all over Europe and lives in a variety of habitats. *Bombus pascuorum* is also a variable species with many subspecies and there are 3 subspecies in Turkey (Rasmont & Flagothier, 1996). *Bombus pascuorum*, which is regarded as a wood-edge species, lives at an altitudinal range of 3-2300 meters, with 80% of the observations between 800-1740 meters (Rasmont, 1988; Rasmont & Flagothier, 1996). Generally, *B. pascuorum* is found together with *B. lapidarius* and *B. hortorum*. In the West-Palaearctic, *B. pascuorum* is well known as the most polytrophic bumblebee species where it forages on hundreds of flowers species (Rasmont & Flagothier, 1996). *Bombus pascuorum* were smaller in size compared to other pollinators (total body length 21.6 mm, n=8). The handling time of the species differed on each *Lamium* species (2.58 sec, n=32, on *L. villosifolium* and 2.81 sec, n=22, on *L. album* subsp. *crinitum*, Table). The subspecies, *B. pascuorum* subsp. *olympicus* was observed in this study, especially the species visited *L. villosifolium* frequently in the 1st and 2nd station (Figures 133-134). The species was also observed on *L. album* subsp. *crinitum* at all sites at low frequencies (Table 18). In higher elevations, especially in the 3rd station (mountain summit area), the frequency of *B. pascuorum* subsp. *olympicus* declined where *L. album* subsp. *crinitum* was gradually much more abundant than *L. villosifolium*.

Figure 91. *Bombus pascuorum* subsp. *olympicus* on *L. villosifolium*

Figure 92. *B. pascuorum* subsp. *olympicus* on *L. album* subsp. *crinitum*

Apis mellifera (L., 1758)

Apis mellifera (Western honeybee) is native to Europe, Asia and Africa. The commercial value of honey bees come from their pollinator services of crops. Honey bees were the smallest bees among the pollinators (total body length 14.4 mm, n=3). The species was only observed on *L. album* subsp. *crinitum* at 2nd and 3rd station at very low frequencies (Table 18) thus, it was not possible to produce any video recordings to calculate the handling time. The field observations revealed that the species crawl from one flower to the other on the inflorescence of *L. album* subsp.

crinitum. Regarding their relatively small body proportions, the honeybee got into contact with the reproductive surfaces of *L. album* subsp. *crinitum*. The species was loaded with pollen on their head and thorax parts (Figure 135).

Figure 93. *Apis mellifera* on *L. album* subsp. *crinitum* (3rd station)

Figure 94. *Bombylius fulvescens* (Bombyliidae) sucking nectar from flowers of *L. villosifolium*, not touching the reproductive surfaces; pollination was not confirmed.

3.6.4 Morphometric Fitting between flowers and pollinators

- *Lamium villosifolium* provides a large landing place for the pollinators and has a wide flower entrance of 2.69 x 5.66 mm (d_h x d_v). Corolla tube length is 13.14 ± 1.19 mm, but the mean distance from nectar to the flower entrance is 9.85 ± 0.66 mm (Table 19). For a successful pollen transfer process, the insect's body should be long enough to get touched by the pollen sacs and, second, that the proportions of the insect's head (head width) and proboscis fit the flower entrance and corolla tube length.

- All insects pollinating *L. villosifolium* have a body size larger than the length of the long and short anthers (Figure 140; boxplot). The main pollinators have body sizes ranging from 21.68 ± 2.12 mm (*Bombus pascuorum*) to 22.70 ± 1.52 mm (*Bombus lapidarius*) and 25.84 ± 1.40 mm (*Bombus* *argillaceus*), thus being longer than both long and short anthers. The width of flower entrance is 2.72 ± 0.42 mm in *L. villosifolium* (Figure 139). The head width below the eyes of all pollinators observed is wider than the flower tube entrance, indicating that the proboscis length is the limiting factor for reaching the nectar (Figure 138 and 139). Proboscis length was the most variable morphological trait measured among pollinators. The main bee pollinators, *Bombus argillaceus*, *B. pascuorum* and *B. lapidarius* have a proboscis length of 13.54 mm, 10.21 mm, 8.51 mm, respectively; (Figure 138) which fits with the distance from the flower entrance to the nectar cover. It is evident from the observations that, both *Apis mellifera* and *Bombus lucorum* were not observed on *L. villosifolium*, where the proboscis length of *A. mellifera* is not long enough for reaching the nectar cover.

- *Lamium album* subsp. *crinitum* provides a smaller landing place for the pollinators and has a narrower flower entrance of 2.48 x 3.57 mm (dh x dv). Corolla tube length is 6.50 ± 0.54 mm, but the mean distance from nectar to the flower entrance is 5.66 ± 0.71 mm (Table 19). All insects pollinating *L. album* subsp. *crinitum* have a body size larger than the length of the long and short anthers (Figure 140; boxplot). The main pollinators have body sizes ranging from 14.62 ± 0.36 mm (*Apis mellifera*) and 18.83 ± 1.43 (*Bombus lucorum*) to 21.68 ± 2.12 mm (*Bombus pascuorum*) and 22.70 ± 1.52 mm (*Bombus lapidarius*), thus being longer than both long and short anthers.

- The width of flower entrance is 2.38 ± 0.25 in *L. album* subsp. *crinitum* (Figure 137). The head width below the eyes of two pollinators (*Bombus lapidarius* and *Bombus pascuorum*) observed is much wider than the flower tube entrance, indicating that the proboscis length is the limiting factor for reaching the nectar (Figure 138 and 139). The head width below the eyes in *Apis mellifera* is 2.5 mm which is slightly wider than the width of flower entrance. Moreover, the head width below the eyes in *Bombus lucorum* is 2.35 mm, which is slightly shorter than the width of flower entrance.

However, both *A. mellifera* and *B. lucorum* are capable of reaching the nectar cover by the length of their proboscis. Proboscis length was the most variable morphological trait measured among pollinators. The main bee pollinators, *B. lapidarius*, *B. pascuorum*, *B. lucorum* and *Apis mellifera* and have a proboscis length of 8.51, 10.21, 10.05 and 6.85 mm, respectively; (Figure 138) which fits with the distance from the flower entrance to the nectar cover.

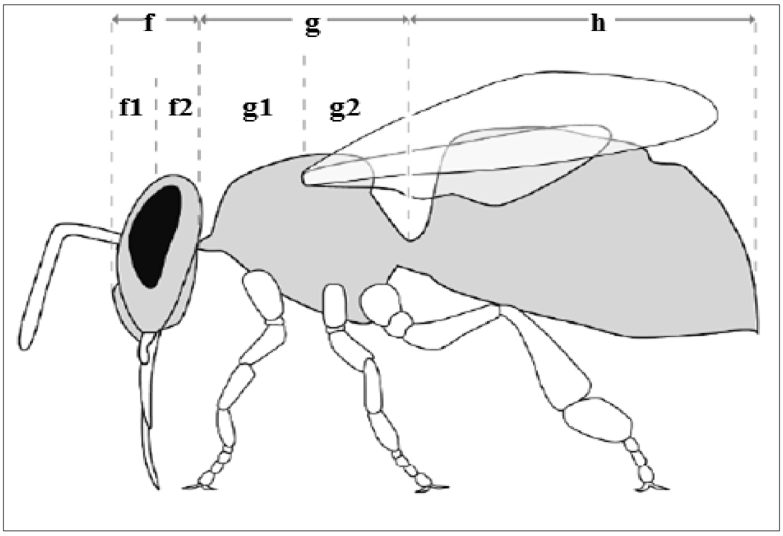


Figure 95. Pollen placement site on the pollinators` body. (f) head length (f1: anterior headvpart, f2: posterior head part), (g) thorax (g1: anterior thorax, g2: posterior thorax), (h) abdomen (Figure from Celep et al., 2014)

Table 19. Morphometric data of flowers of *Lamium* species (mean ± standard deviation, min and max values)

	b	**c**	**d_H**	**d_v**	**e**
L. villosifolium	24.18 ± 1.27 (21.85 – 26.96)	13.14 ± 1.19 (10.42 – 15.06)	2.69 ± 0.41 (2.12 – 3.72)	5.66 ± 0.55 (4.70 – 6.77)	9.85 ± 0.66 (8.71 – 11.00)
L. album subsp. *crinitum*	14.83 ± 0.71 (13.29 – 15.91)	6.50 ± 0.54 (5.45 – 7.39)	2.48 ± 0.26 (1.97 – 2.95)	3.57 ± 0.29 (3.19 – 4.14)	5.66 ± 0.71 (4.56 – 6.73)
	f	**g**	**h**	**i**	**j**
L. villosifolium	18.06 ± 1.35 (14.87 – 20.36)	10.81 ± 1.25 (8.18 – 13.2)	8.66 ± 1.11 (6.71 – 10.32)	2.04 ± 0.19 (1.57 – 2.36)	21.12 ± 1.58 (18.01 – 23.93)
L. album subsp. *crinitum*	9.52 ±1.30 (7.89 – 11.21)	8.11 ± 0.68 (7.24 – 9.56)	6.78 ± 0.50 (5.83 – 7.73)	1.41 ± 0.17 (1.21 – 1.89)	6.70 ± 0.61 (5.51 – 7.81)

Morphometric data of flowers of *Lamium* species (mean ± standard deviation, min and max values); (b) flower length, (c) length of corolla tube, (d) flower entrance – d_H, horizontal; d_V, vertical-, (e) distance flower entrance to nectar cover, (f) distance thecae to nectar cover, (g) length of long anther, (h) length of short anther, (i) theca length, (j) style in natural position, all measurements in mm, (n: 30)

Table 20. Morphometric measurements of pollinator species (all measurements in mm)

Species	**Gender**	**A height of head**	**B length of maxillae**	**C glossa length**	**B+C length of proboscis**	**D head width**	**E head width below eyes**	**F head length**	**G thorax length**	**H abdomen length**	**F+G+H total body length**
L. villosifolium											
Bombus argillaceus	f-w	6.2	9.5	6.1	15.6	5.0	3.3	2.8	8.0	14.5	26.5
Bombus argillaceus	f-w	6.8	8.5	5.0	13.5	5.3	3.0	3.6	7.9	15.0	28.0
Bombus argillaceus	f-w	5.0	6.5	4.4	10.9	4.7	3.0	2.5	7.5	11.0	23.0
Bombus argillaceus	f-w	6.0	8.0	5.5	13.5	5.0	3.1	3.0	8.5	12.0	25.5
Bombus argillaceus	f-w	5.5	8.5	5.7	14.2	4.5	3.1	2.8	8.5	11.5	25.5
Bombus pascuorum	f	6.0	10.0	4.5	14.5	5.2	3.1	2.9	7.6	11.5	25.0
Bombus pascuorum	f	5.2	7.9	3.0	10.9	4.9	2.8	2.5	7.4	10.0	21.0
Bombus pascuorum	f	6.5	8.3	3.0	11.3	4.7	3.2	2.7	8.0	11.0	24.0
Bombus pascuorum	f	4.5	7.2	3.2	10.4	4.7	2.7	2.7	7.3	10.0	21.0
Bombus pascuorum	f	4.9	8.0	2.8	10.8	4.7	2.7	2.9	7.5	10.0	21.0
Bombus pascuorum	f	5.0	6.5	2.3	8.8	4.5	3.7	2.5	7.5	10.5	21.5
Bombus pascuorum	f-w	4.5	5.5	2.0	7.5	4.3	2.5	2.1	6.0	8.0	17.5
Bombus lapidarius	f	4.7	6.6	3.0	9.8	4.5	2.8	2.5	7.6	11.5	23.5
Bombus lapidarius	f	5.0	6.5	3.2	9.7	4.7	3.0	2.7	8.0	9.5	22.5
L. crinitum											
Apis mellifera	f	3.6	3.1	3.8	6.9	4.0	2.6	2.1	3.7	6.0	14.0
Apis mellifera	f	3.5	3.8	4.2	8.0	4.5	2.4	2.0	4.1	6.8	14.8
Bombus lapidarius	f	5.3	6.1	2.7	8.8	5.1	3.0	3.0	7.2	10.5	21.8
Bombus lapidarius	f	4.9	6.5	2.8	9.3	4.7	2.9	2.7	7.5	11.0	22.0
Bombus lapidarius	f	4.5	5.5	2.4	7.9	4.4	2.7	2.6	8.0	14.0	25.5
Bombus lapidarius	f	4.7	4.8	2.1	6.9	4.9	2.9	2.6	8.1	13.0	24.5

Table 20 (cont`d)

Species	**Gender**	**A height of head**	**B length of maxillae**	**C glossa length**	**B+C length of proboscis**	**D head width**	**E head width below eyes**	**F head length**	**G thorax length**	**H abdomen length**	**F+G+H total body length**
L. crinitum											
Bombus lapidarius	f	4.8	6.8	3.0	9.8	4.5	2.8	2.5	7.6	11.5	23.5
Bombus lapidarius	f	4.6	6.3	2.6	8.9	4.5	2.9	2.5	6.4	11.0	22.5
Bombus lapidarius	f	4.6	6.8	3.0	9.8	4.8	3.0	2.7	7.8	11.6	23.5
Bombus lapidarius	f	4.8	5.8	2.5	8.3	5.0	2.7	2.5	8.0	11.5	24.0
Bombus lapidarius	f	4.5	5.7	2.5	8.2	4.6	2.9	2.8	8.5	12.0	24.0
Bombus lapidarius	f	5.4	6.4	2.8	8.2	4.8	2.5	2.7	7.9	13.0	22.0
Bombus lapidarius	f	5.0	5.3	2.3	7.6	4.6	2.7	2.9	6.5	9.0	20.0
Bombus lapidarius	f	5.0	6.5	2.8	8.3	4.7	3.0	2.7	8.0	9.5	22.5
Bombus lapidarius	f-w	4.9	5.9	2.6	7.5	4.5	2.5	2.7	7.4	9.0	20.0
Bombus lapidarius	f-w	4.7	5.7	2.6	7.3	4.5	2.7	2.7	7.1	11.0	22.0
Bombus lucorum	f-w	4.5	6.0	2.7	8.7	4.1	2.3	2.6	6.5	8.0	17.0
Bombus lucorum	f	5.1	8.7	3.8	12.5	4.5	2.3	2.7	7.3	10.0	21.3
Bombus pascuorum	f	5.1	5.5	2.0	7.5	4.7	3.0	2.7	7.5	13.0	22.5

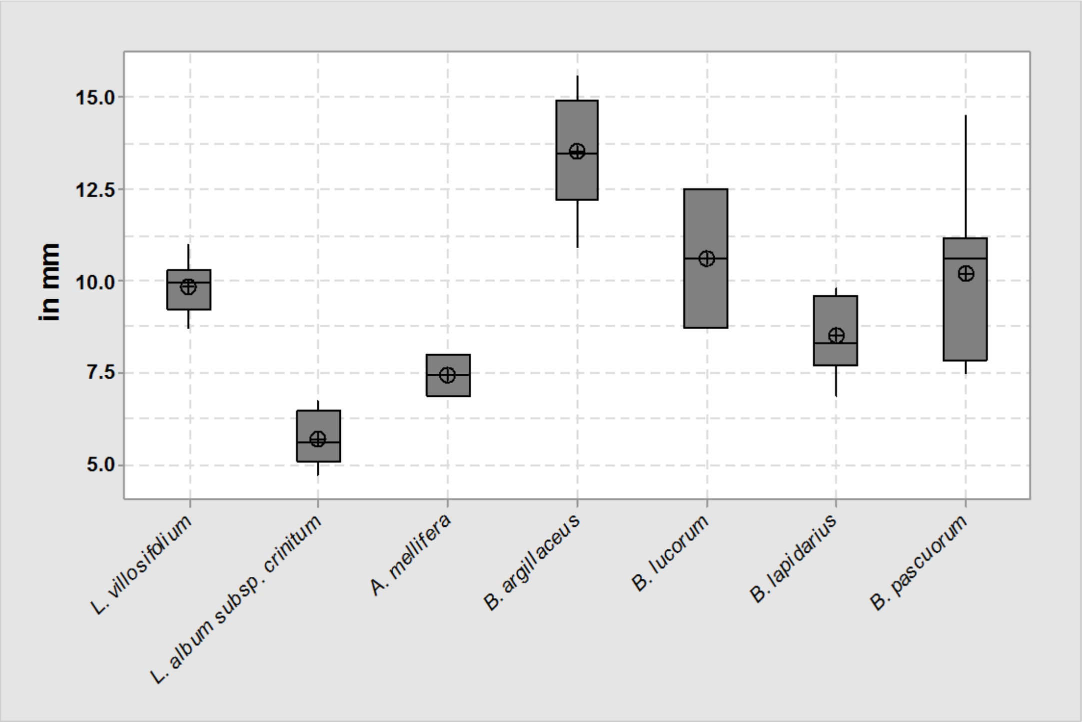


Figure 96. Morphometric fitting between tube proportions in *Lamium* flowers and head proportions (proboscis) of pollinators. Distance flower entrance to nectar cover in *L. villosifolium* and *L. album* subsp. *crinitum* compared with the pollinators' proboscis length. The box plots consist of mean, upper and lower quartiles, and range of measured characters.

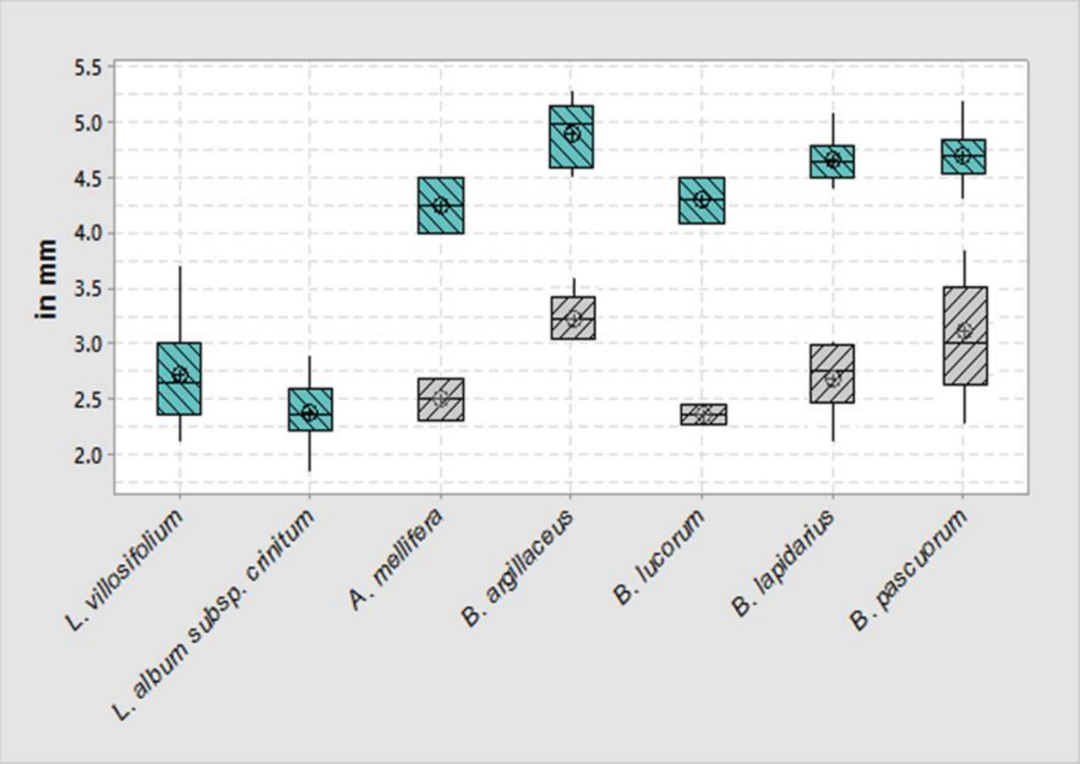


Figure 97. Morphometric fitting between tube proportions in *Lamium* flowers and head proportions of pollinators. Width of floral entrance (d_H) in *L. villosifolium* and *L. album* subsp. *crinitum* compared with width of pollinator heads; below (lower box plots) and above eyes (upper box plots). The box plots consist of mean, upper and lower quartiles, and range of measured characters.

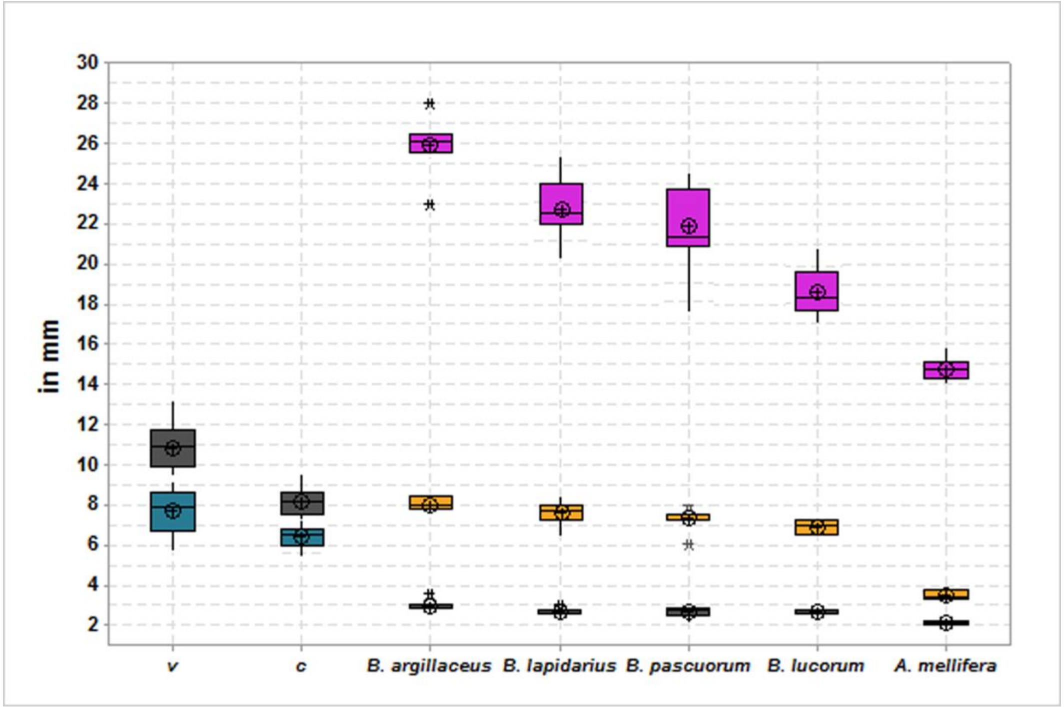


Figure 98. Morphometric fitting between anther length in *Lamium* flowers and the body proportions of pollinators. (v) Length of anthers (long in grey, short in blue) in *L. villosifolium*; (c) Length of anthers (long in grey, short in blue) in *L. album* subsp. *crinitum*. The three boxplots per insect species refer to head length (dark grey), thorax length (yellow), and total body length (purple, compare with Fig. 3F: f–h). Pollinators are arranged according to their total body length; from large to small. The box plots consist of mean, upper and lower quartiles, and range of measured characters.

3.6.5 Estimation of pollen transfer

Pollen load–pollen placement–stigma contact

- *Lamium villosifolium*

According to their specific body proportions, the main pollinators of *L. villosifolium* were loaded with pollen on anterior (f1) and posterior (f2) part of the head (*B. argillaceus*), posterior part of the head and anterior (g1) part of the thorax (*B. lapidarius* and *B. pascuorum*). Voucher specimens of collected pollinators indicated that, main pollinators carried 20-200 pollen grains on their body (Table 21). The average number of pollen grains that pollinators carried was; 80.90 ± 48.70 pollen grains (n:11) for *Bombus argillaceus*, 50 ± 20 pollen grains (n: 6) for *Bombus lapidarius*, 68.75 ± 16.15 pollen grains (n: 9) for *Bombus pascuorum* (Table 21) Regarding the pollen load on each pollinator species, there was no statistical difference among the main pollinators ($F_{2, 24} = 1.36$, $P = 0.27$).

On the basis of morphometric measurements, the initial place of pollen placement is rather precise. However, if a pollinator has already contacted the pollen sacs but continues to move inward, pollen might be slightly spread along the head or thorax. In general, irrespective of the different size of the pollinators, pollen is loaded on the anterior (f1), posterior (f2) part of the head (behind the eyes) and anterior (g1) part of the thorax (Figure 123, 124, 125, 126, 127, 128, 133 and Table 21).

- *Lamium album* subsp. *crinitum*

According to their specific body proportions, the main pollinators of *L. album* subsp. *crinitum* were loaded with pollen on their anterior (f1) part of the head (*B. lapidarius* and *B. pascuorum*), anterior (f1) and and posterior (f2) part of the head (*B. lucorum*) and anterior+posterior part of the head (f1+f2) and anterior (g1) part of the thorax (*A. mellifera*). Voucher specimens of collected pollinators indicated that, main pollinators carried 20-120 pollen grains on their body (Table 21). The average number of pollen grains that pollinators carried was; 55 ± 15.41 pollen grains (n:12) for *Bombus lapidarius*, 50 ± 20 pollen grains (n: 6) for *Bombus pascuorum*, 47.85± 19.97 pollen grains (n: 7), 87.5 ± 25.86 for *Bombus lucorum* (n: 4), 68.33 ± 8.49 for *Apis mellifera* (n: 3) (Table 21). Regarding the pollen load on pollinator species, *B. lucorum* carried significantly more pollen grains than *B. lapidarius* and *B. pascuorum* ($F_{3, 25} = 3.92$, $P = 0.02$).

On the basis of morphometric measurements, the initial place of pollen placement is rather precise. In general, irrespective of the different size of the pollinators, pollen is loaded on the anterior (f1), posterior (f2) part of the head (behind the eyes) and anterior (g1) part of the thorax (Figure 129, 130, 131, 132, 134, 134, 135 and Table 21).

Stigma contact of the pollinator species could not be quantified because of the flower morphology of the *Lamium* species. Both anther and stigma were hidden below the upper lip of corolla, therefore it was not possible to observe and quantify the stigma contact.

3.6.6 Pollinator Behavior at an *inflorescence* and a *flower*;

- Handling time of a single flower-

The bees landed on the lower lip and touched the reproductive surfaces while inserting their proboscis into the flower tube. Video recording of the pollinators revealed that there were differences in handling time of a single flower (Table 21). Among the pollinators of *L. villosifolium*, the handling time of a single flower was; 1.78 ± 0.52 s (n: 32) for *B. argillaceaus*, 2.58 ± 1.52 s (n: 15) for *B. lapidarius,* 2.58 ± 1.23 s (n: 32) for *B. pascuorum*. The handling time of *B. argillaceus* differed significantly among the main pollinators ($F_{2, 76}$ = 5.31, P = 0.007).

The bees landed on the narrower lower lip and touched the reproductive surfaces while inserting their proboscis into the flower tube. Video recording of the pollinators revealed that there were differences in handling time of a single flower (Table 21). Among the pollinators of *L. album* subsp. *crinitum*, the handling time of a single flower was; 2.28 ± 0.67 s (n: 19) for *B. lucorum*, 1.79 ± 0.91s (n: 32) for *B. lapidarius*, 2.28 ± 0.67 s (n: 22) for *B. pascuorum*. The handling time of *B. lapidarius* differed significantly among the main pollinators ($F_{2, 72}$ = 7.53, P = 0.001).

- Duration of stay at an inflorescence-

Bombus argillaceus, the fastest pollinator species for handling the flowers of *L. villosifolium*, stayed on average for 7.87 ± 4.17 s (n: 15) at an inflorescence. Duration of stay at an inflorescence was 6.56 ± 2.71 seconds (n: 6) for *B. lapidarius* and 6.41 ± 6.17 s (n: 15) for *B. pascuorum* (Table 21). Differences in duration of stay at an inflorescence did not differed significantly among the main pollinators of *L. villosifolium* ($F_{2,35}$ = 0.34, P = 0.716).

Bombus lapidarius, the fastest pollinator species for handling the flowers of *L. album* subsp. *crinitum*, stayed on average for 8.70 ± 5.01 s (n: 25) at an inflorescence. Duration of stay at an inflorescence was 10.72 ± 6.55 s (n: 12) for *B. pascuorum* and 13.06 ± 4.57 s (n: 5) for *B. lucorum* (Table 20). Differences in duration of stay at an inflorescence did not differed significantly among the main pollinators of *L. album* subsp. *crinitum* ($F_{2,41}$ = 1.54, P = 0.227).

-Number of flowers visited per inflorescence-

Number of flowers visited per inflorescence was calculated from the video recordings of pollinators. On *L. villosifolium*, *B. argillaceus* visited 2.60 ± 1.49 (n: 15) flowers, whereas, the number of flowers visited was 2.5 ± 0.54 (n: 6) for *B. lapidarius* and 2.6 ± 1.05 (n: 15) for *B. pascuorum* (Table 21). The number of flowers visited did not differed significantly among the main pollinators ($F_{2, 35}$ = 0.02, P = 0.984).

On *L. album* subsp. *crinitum*, *B. lapidarius* visited 4.48 ± 2.82 (n: 25) flowers, whereas, the number of flowers visited was 3.32 ± 1.66 (n: 12) for *B. pascuorum* and 4.6 ± 0.80 (n: 5) for *B. lucorum* (Table 20). The number of flowers visited did not differed significantly among the main pollinators ($F_{2, 41}$ = 1.53, P = 0.228).

3.6.7 Geographic Variation in Pollinator Assemblage in *L. villosifolium*

Field investigations and video recordings revealed that *Lamium villosifolium* was pollinated by 3 bee species from one genus and 3 subgenera (*Bombus*; *Megabombus*, *Melanobombus*, *Thoracobombus*) of Apidae (Table 18). Among the investigated bee species, *Bombus pascuorum*, *Bombus argillaceus*, and *Bombus lapidarius* had visitation frequency values of; 45.45%, 36.36%, 18.18%, respectively (Table 18 and 21). As indicated previously, the population size of the *Lamium* species differed in 3 stations (Table 17). The pollinator assemblage of *L.*

villosifolium differed among populations of 3 stations (Table 18). Although *Bombus pascuorum* and *Bombus argillaceus* were the most frequently observed pollinator species for *L. villosifolium*, their relative abundance gradually declined from the 1st to the 3rd station (lower to higher altitude). Almost no *B. argillaceus* were observed at the 3rd station (Figure 141).

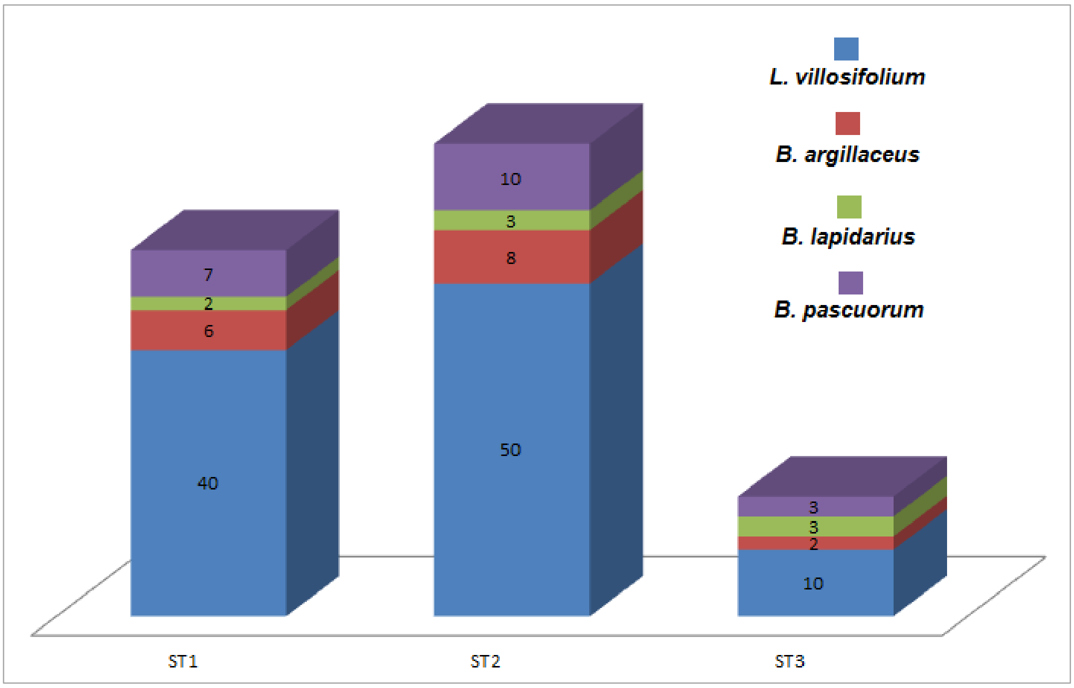


Figure 99. Altitudinal differences in assemblages of pollinators of *L. villosifolium*. Numbers in bar diagrams indicate; the number of individual plants (blue) and number of observed pollinators (red, green, purple) in each station. ST1: Station 1, 1580 m; ST2: Station 2, 1840 m; ST3: Station 3, 2062 m.

3.6.8 Geographic Variation in Pollinator Assemblage in *L. album* subsp. *crinitum*

Field investigations and video recordings revealed that *Lamium album* subsp. *crinitum* was pollinated by 4 bee species from 2 genera and 4 subgenera (*Bombus* and *Apis*; *Melanobombus*, *Bombus*, *Thoracobombus* and *Apis*) of Apidae (Table 18). Among the investigated bee species, *Bombus lapidarius*, *Bombus pascuorum*, *Bombus lucorum*, and *Apis mellifera* had visitation frequency values of; 60.87 %, 23.90 %, 8.7 %, 6.52 %, respectively (Table 18 and 21). As indicated previously, the population size of the *Lamium* species differed in 3 stations (Table 17). The pollinator assemblage of *L. album* subsp. *crinitum* differed among populations of 3 stations (Table 18). *Bombus lapidarius* and *Bombus pascuorum* were the most frequently observed pollinator species for *L. album* subsp. *crinitum*, the relative abundance of *B. lapidarius* gradually increased from the 1st to the 3rd station (lower to higher altitude) whereas the relative abundance of *Bombus pascuorum* declined from the 1st to the 3rd station (lower to higher altitude, Figure 142).

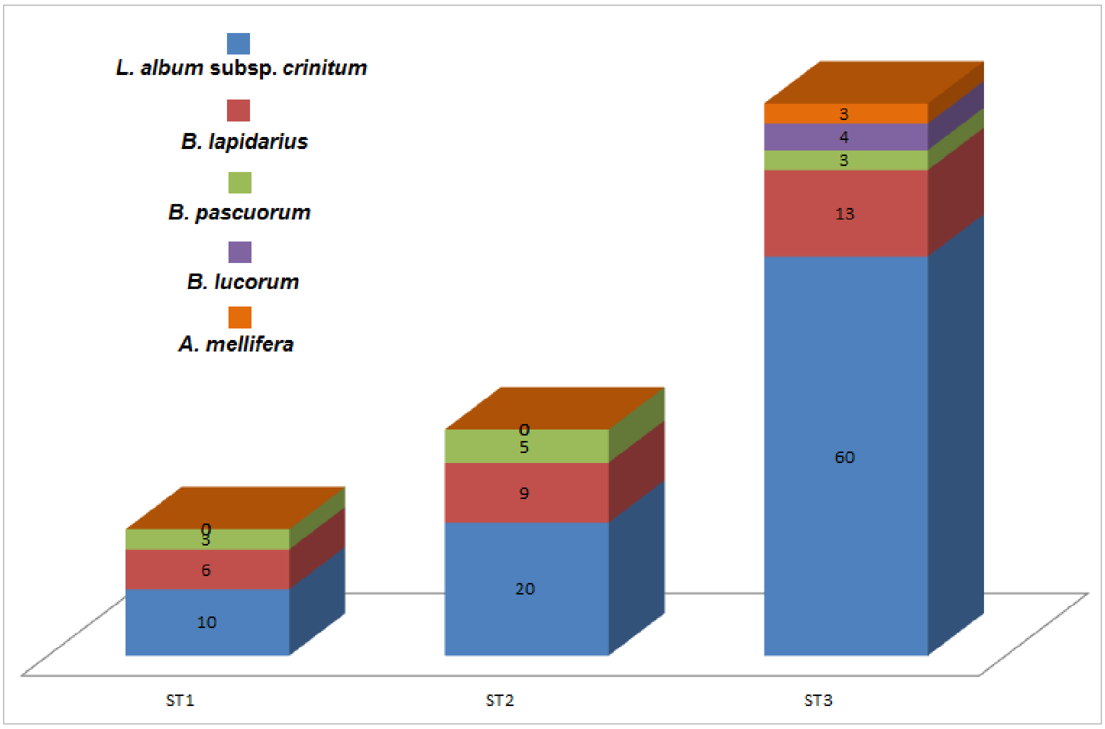


Figure 100. Altitudinal differences in assemblages of pollinators of *L. album* subsp. *crinitum*. (Numbers in bar diagrams indicate; the number of individual plants (blue) and number of observed pollinators (red, green, purple, orange) in each station. ST1: Station 1, 1580 m; ST2: Station 2, 1840 m; ST3: Station 3, 2062 m.

3.6.9 Shared Pollinators

Bombus pascuorum and *Bombus lapidarius* were confirmed as pollinators of both *L. villosifolium* and *L. album* subsp. *crinitum* (Table 21). The two pollinators have body sizes ranging from 21.68 ± 2.12 mm (*B. pascuorum*) and 22.70 ± 1.52 mm (*B. lapidarius*). The pollinators slightly differed in total body size. *B. lapidarius* and *B. pascuorum* had a proboscis length of 8.51 and 10.21 mm, respectively; (Figure 137) whereas the distance from the flower entrance to the nectar cover was 9.85 ± 0.66 for *L. villosifolium* and 5.66 ± 0.71 for *L. album* subsp. *crinitum*). The morphometric measurements indicated that, the proboscis length of *B. lapidarius* and the distance from the flower entrance to the nectar cover of *L. villosifolium* scarcely overlapped. However, the proboscis length of *B. lapidarius* is long enough to suck nectar from *L. album* subsp. *crinitum*. In addition, the proboscis length of *B. pascuorum* was long enough for both *Lamium* species.

Due to the differences in flower morphology of the *Lamium* species, the shared pollinator species were loaded with pollen on different parts of their body. Such that, *B. lapidarius* was loaded with pollen on the posterior head and anterior thorax part (f2 + g1) while visiting *L. villosifolium*, whereas, it was loaded with pollen on the anterior head part (f1) while visiting *L. album* subsp. *crinitum*. In addition, *B. pascuorum* was loaded with pollen on the posterior head and anterior thorax part (f2 + g1) while visiting *L. villosifolium* whereas, it was loaded with pollen on the anterior head part (f1) while visiting *L. album* subsp. *crinitum*.

- Regarding the pollinator behavior, the video recordings and calculations revealed that, the handling time of *B. lapidarius* differed significantly on each *Lamium* species ($F_{1,\,46}$ = 4.88, P = 0.032). However, the handling time of *B. pascuorum* did not differed significantly on each *Lamium* species ($F_{1,\,53}$ = 0.45, P = 0.505). It is evident that, *B. lapidarius* is good at handling the flowers of *L. album* subsp. *crinitum*.

- For *L. villosifolium,* differences in handling time of a single flower did not differed significantly among the main pollinators (*B. lapidarius* and *B.pascuorum*) ($F_{1,\ 46}$ = 0.00, *P* = 1.00). However, for *L. album* subsp. *crinitum*, the handling time of a single flower differed significantly among the main pollinators (*B. lapidarius* and *B.pascuorum*) ($F_{1,\ 53}$ = 12.90, *P* = 0.001). It is again evident that, *B. lapidarius* is good at handling the flowers of *L. album* subsp. *crinitum* compared to *B. pascuorum*.

Table 21. Pollinator behavior analysis

	Bombus argillaceus	n	***Bombus lapidarius***	**n**	***Bombus pascuorum***	n	*Bombus lucorum*	n	*Apis mellifera*	n
L. villosifolium										
Handling time [s]	1.78 ± 0.52	32	**2.58 ± 1.52**	**15**	**2.58 ± 1.23**	32	-	-	-	-
Number of flowers visited/inflorescence	2.60 ± 1.49	*15	**2.5 ± 0.54**	***6**	**2.6 ± 1.05**	*15	-	-	-	-
Duration of stay at an inflorescence [s]	7.87 ± 4.17	*15	**6.56 ± 2.71**	***6**	**6.41 ± 6.17**	*15	-	-	-	-
Pollen deposition site	f1 ± f2	**11	**f2 ± g1**	****6**	**f2 ± g1**	**9	-	-	-	-
Estimation of pollen load	80.90 ± 48.70 (40-200)	**11	**50 ± 20 (20-80)**	****6**	**68.75 ± 16.15 (50-100)**	**9	-	-	-	-
Frequency [%]	36.36	***44	**18.18**	*****44**	**45.45**	***44	0	***44	0	***44
L. album* subsp. *crinitum										
Handling time [s]	-	-	**1.79 ± 0.91**	**32**	**2.81 ± 1.15**	22	2.28 ± 0.67	19	-	-
Number of flowers visited/inflorescence	-	-	**4.48 ± 2.82**	***25**	**3.32 ± 1.66**	*12	4.6 ± 0.80	*5	-	-
Duration of stay at an inflorescence [s]	-	-	**8.70 ± 5.01**	***25**	**10.72 ± 6.55**	*12	13.06 ± 4.57	*5	-	-
Pollen deposition site	-		**f1**	****12**	**f1**	**7	f1± f2	**4	f1± f2 ± g1	**3
Estimation of pollen load			**55 ± 15.41 (30-80)**	****12**	**47.85± 19.97 (20-80)**	**7	87.5 ± 25.86 (50-120)	**4	68.33 ± 8.49 (60-80)	**3
Frequency [%]	0	***46	**60.87**	*****46**	**23.90**	***46	8.7	***46	6.52	***46

n; number of flowers observed, *n; number of inflorescences observed, **n; number of pollinators investigated for pollen load and pollen placement, ***n frequency is based on number of pollinators observed in total. Shared pollinator species of *L. villosifolium* and *L. album* subsp. *crinitum* are in blue. [s]: seconds.

3.6.10 Pollination Biology of Two Sympatric *Lamium* Species

Floral Morphology - Bilabiate structure-

- Floral phenotypes such as; colour, scent, size and shape of the flower, are associated with specific pollinator groups and these associations are known as pollination syndromes (Faegri and van der Pijl, 1979; Fenster et al., 2004). Flowers pollinated by bees are often yellow, blue, purple and white with tubular, campanutale, or zygomorphic shapes and have their nectar presented in the flower tube (Vogel, 1954; Proctor et al., 1996; Harborne, 1997; Wester and Classen-Bockhoff, 2011). This floral construction is interpreted as an adaptation to the morphology and foraging behavior of bees (Fenster et al., 2004) and such bilabiate flowers are nototribic by definition (Westerkamp and Classen-Bockhoff, 2007).

- The investigated *Lamium* species have zygomorphic, bilabiate flowers which provide a landing place and offer nectar at the base of the corolla tube. There are dots and lines on the lower lip of *L. villosifolium* and faint dots on the lower lip of *L. album* subsp. *crinitum* that may attract the pollinator species. There are 4 stamens in two pairs (each stamen is monthecate) and each pair is different in length of their filaments. This anther and theca ornamentation may increase the male reproductive surface of the flowers. The anthers and stigma are hidden below the upper lip of the corolla. The sharp teeth of the lateral lobes support the handling process of the pollinators. Each pollinator visiting the flowers of *Lamium* species, land on the lower lip of the corolla, exert their mouthparts into the corolla tube and get into contact with the reproductive surfaces hidden below the upper lip during the feeding process, from their dorsal side. Such characteristics of the *Lamium* species are consistent with the bee-pollination syndrome. Recently, the pollination syndrome concept has been questioned by some authors (Waser et al., 1996; Ollerton et al., 2007; 2009). Moreover, plant-pollinator interactions should identify the role of primary and secondary pollinators and quantify their relative efficiency and success on plant reproductive success (Rosas-Guerrero et al., 2014).

Pollinators; Pollinator Behavior-Flower Constancy

- Lamiaceae species are predominantly pollinated by social bees (van der Pijl, 1972; Stebbins, 1974; Faegri and Van der Pijl, 1979) as well as solitary bees (Dafni, 1991). *Lamium villosifolium* and *L. album* subsp. *crinitum* are clearly adapted to bees as pollinators. Four different species of bumblebees (*B. argillaceus*, *B. lapidarius*, *B. lucorum* and *B. pascuorum*) and honeybee (*Apis mellifera*) are observed as pollinators. Bumblebees and honeybees are also reported as pollinators of various *Lamium* species (Denisow and Bozek, 2008; Lye et al., 2009; Cozmuta et al., 2012).

- In the hermaphrodite flowers of the two *Lamium* species, the degree of temporal (dichogamy) and spatial (herkogamy) separation of male and female phases should be understood. In both *Lamium* species, there is no spatial separation of anthers and stigma. Both male and female reproductive surfaces are located close to eachother. However, the degree of autogamy might be prevented with temporal separation of male and female phases. Both herkogamy and dichogamy prevent autogamy but are not effective in preventing geitonogamy (Shivanna, 2014). Thus, to understand the degree of geitonogamy, the foraging behavior of the pollinators is important.

- Based on its high visitation frequency, high pollen load and shorter handling time, *Bombus argillaceus* is the most efficient pollinator for *L. villosifolium*. However the species stays on a single inflorescence a little bit longer than the other pollinators. This foraging behavior contributes more to pollen dispersal within an individual which promotes autogamy. The success of *B. argillaceus* is equally followed by *B. pascuorum* based on its higher visitation frequency and shortest stay at an inflorescence, which thereby increases outcrossing.

For *L. album* subsp. *cirnitum*, *B. lapidarius* is by far the most efficient pollinator based on shorter handling time and high visitation frequency. It is followed by *B. pascuorum* and *B. lucorum*. The latter species carried high amounts of pollen compared to the other pollinator species however it has very low visitation frequency. In addition, *B. lucorum* stays longer on an individual plant and might contribute to a high degree of geitonogamy (Karron et al., 2009; Zhang et al., 2011). Based on the lowest visitation frequency, *Apis mellifera* is the least successful pollinator species for *L. album* subsp. *cirnitum*.

- Pollinators often limit their visits to one type of flower while bypassing other equally rewarding ones which is defined as flower constancy (Grant, 1950). Foraging is a difficult activity and it requires certain handling skills for the pollinators per specific plant species, which may lead to flower constancy (Darwin, 1876; Waser, 1986). When bees specialize on a restricted number of flower species, they may manipulate the flowers faster and produce more offspring (Heinrich, 1976; Williams, 1977; Strickler, 1979). The observations indicated that flower constancy may be an effective way for a precise pollination process but it may increase the degree of geitonogamy. *Lamium* species offering many more flowers per verticillaster (i.e. *L. album* subsp. *crinitum*) may be more rewarding to bees in which the pollinators may continuously visit. However, continuous visits on the single inflorescences may lead to geitonogamy in *L. album* subsp. *crinitum*. Geitonogamy is as costly as cross-pollination without providing the genetic benefits of outcrossing (Lloyd and Schoen, 1992). In contrast, due to the fewer number of flowers per inflorescence in *L. villosifolium*, the pollinators visit few numbers of flowers per plant, which may in this case, decrease the degree of geitonogamy.

Morphometric Fit- Pollen Placement- Isolating Mechanisms-

- Two of the pollinators of *L. villosifolium* were also observed as pollinators *L. album* subsp. *crinitum* at the same flowering period and at the same place (during June and early July at 3 stations). Sharing pollinators generally bears the risk of pollen loss and pollen mixture, however variation in the length of the anthers facilitates pollen placement on different areas of the pollinators' bodies (Grant, 1994). Depending on the morphometric differences of two *Lamium* species, shared pollinators are loaded with pollen on different parts of their body. In zygomorphic bilabiate flowers, effective pollen transfer depends on the fitness between flowers and pollinators, in which pollen is protected against pollen-collecting bees (Sargent, 2004; Westerkamp and Classen-Bockhoff, 2007). Following the different flower proportions, pollen grains of *L. villosifolium* and *L. album* subsp. *crinitum* were deposited on different parts of the pollinator's body.

- Proboscis length is another variable character among the pollinator species. The proboscis length of *A. mellifera* is not long enough to reach the nectar cover present in the corolla tube of *L. villosifolium*. Thus, honeybees might be excluded as pollinators in *L. villosifolium*. All other pollinators of both *Lamium* species easily reach to the nectar cover; hence proboscis length is not a limiting factor for rest of the pollinators.

Color-Visual Clues-Nectar

- Both color and fragrance act as attrantants to guide the visitor to the flower (Shivanna, 2014). Bumblebees and honeybees have trichromatic vision with UV, blue and yellow as primary colours and their spectral range extend from about 550 nm to 336 nm. Human vision is also trichromatic (blue, green and red as primary colours) and the spectral range is confined to visible wavelengths (from 400 nm to about 700 nm) (Kevan, 1979; 1983). Many flowers have patterns caused by the absence of ultra-violet from certain regions and these regions are invisible to man however they act as a guide to bees for the available sources. (Proctor & Yeo, 1973). Flowers with hidden nectar generally have contrasting and highly variable patterns on the petal (Medel et al. 2004). Another floral attractant, floral scent is associated with pollinator activity. Maximum amount of floral fragrance coincides with the activities of pollinators (Ando et al. 2001). Kugler (1970) reported that, the lower lip of *L. album* and both lips (lower lip with higher amounts) of *L. maculatum* emit a faint odour, where the nectar indicators are located. In addition, the essential oil is emitted by trichomes on the stamens and inside the corolla tube of *L. album* (Sulborska et al. 2014). Both *L. villosifolium* and *L. album* subsp. *crinitum* have hairy anthers and annulus inside their corolla tube. They also bear nectar guides on the lower lip of their corolla. Moreover, 3 and 4 bee species were oberserved as pollinators of magenta colored *L. villosifolium* and white colored *L. album* subsp. *crinitum*, respectively. No difference is observed in pollinator frequency based on pollinator preference of flower color. However, significant differences on pollinator visiting frequencies were observed between white and violet colored *Salvia* species (Classen-Bockhoff et al., 2004; Atalay, 2011).

- Lamiaceae species are by far the most nectariferous species in volume and sugar content (Faegri and van der Pijl, 1979; Baker and Baker, 1983). The nectar production of *L. villosifolium* and *L. album* subsp. *crinitum* is not indicated in the present study. However, various authors reported that both *L. maculatum* (Marina et al. 2004) and *L. album* (Sulborska et al. 2014) produced high amounts of nectar, that both species were defined as valuable nectar sources for many bee species.

Geographical Variation in Pollinator Assemblage

- The endemic *L. villosifolium* is distributed at elevations ranging from 1500 to 1800 meters. At 1st (1580 m) and 2nd station (1840 m), the population density of the species is high. However, at 3rd station (2062 m), the population density of *L. villosifolium* was very low. The abundance of *L. villosifolium* clearly decreased along the altitudinal gradient, which is accompanied by the decline in its pollinator assemblage. *Lamium album* subsp. *crinitum* prefers rather higher elevations. The species is distributed between 1500-2400 meters. In contrast to *L. villosifolium*, the population density of *L. album* subsp. *crinitum* increased along the altitudinal gradient. Similarly, an increase in the most efficient pollinator abundance for *L. album* subsp. *crinitum* is observed along the altitudinal gradient. It is evident from the observations that, the different population densities determined by the altitudinal preferences of the two *Lamium* species, affected their pollinator assemblages in all stations. Moreover, variations in floral traits (i.e. flower tube length) were not observed in both *Lamium* species along an altitudinal gradient. However, there are various studies indicating an altitudinal variation in floral traits, which is correlated by the pollinator assemblage difference (Hattori et al., 2015; Kuriya et al., 2015). Flower-size variations may be related to the local species composition of flower visitors in *L. album* subsp. *barbatum* (Hattori et al., 2015) and floral traits (size) are under a pollinator-mediated selection regime in *Prunella vulgaris* (Kuriya et al., 2015).

CHAPTER 4

CONCLUSIONS

4.1 The Genus *Lamium* in Turkey

The taxonomic revision of the genus *Lamium* resulted in; two new species (*L. bilgilii*, *L. cappadocicum*, two new subspecies (*L. ponticum* subsp. *anatolicum* and *L. amplexicaule* subsp. *vanense*), one new combination (*L. micranthum*) and one new synonym (*L. vremanii*, syn. of *L. album* subsp. *crinitum*). In conclusion, the country is now home to 36 taxa, 18 of which are endemic.

Besides, 13 taxa (species and subspecies such as; *L. lycium, L. cariense, L. garganicum* subsp. *laevigatum, L. garganicum* subsp. *rectum, L. garganicum* subsp. *lasioclades, L. microphyllum, L. cymbalarifolium, L. sandrasicum, L. armenum* subsp. *armenum, L. armenum* subsp. *sintenisii, L. eriocephalum* subsp. *glandulosidens*, *L. tomentosum* var. *filicaule*, *L. tomentosum* var. *alpestre*) which were regarded as synonyms by Mennema (1989), were resurrected or their previous taxonomic status which were given in the Flora of Turkey were accepted. Taxa (*L. pisidicum, L. tenuiflorum, L. veronicifolium, L. garganicum* subsp. *reniforme, L. garganicum* subsp. *nepetifolium, L. garganicum* subsp. *pulchrum, L. purpureum* var. *aznovourii, L truncatum, L. gundelsheimeri*, *L. leucolophum, L. tomentosum* var. *hakkariense, L. sulphureum ve L. moschatum* var. *rhodium)* that were regarded as synonyms by Mennema (1989) are accepted in their current status.

Lamium microphyllum, L. cymbalarifolium and *L. sandrasicum* are endemic, stoloniferous, dwarf species complex and are adapted to Southwest Anatolian mountain tops. These 3 species resemble *L. garganicum* only on the basis of their corolla morphology. *Lamium armenum* subsp. *armenum* ve *L. armenum* subsp. *sintenisii* are the two endemics that are distributed in the Northeast Anatolian mountain tops.

The inclusion of *L. orientale* and *L. multifidum* (previously recognized in the genus *Wiedemannia*) in the genus *Lamium* is supported. However, the members of the genus *Galeobdolon* are differentiated from the genus *Lamium,* by their corolla morphology, corolla color and glabrous anthers. It is evident that the opinions are divided; taxonomists and molecular biologists take different approaches to this problem. In present study, *Galeobdolon* is excluded from the *Lamium* due to the morphological differences.

The anatomical characteristics of the vegetative organs of the genus *Lamium* have systematic importance, particularly at sectional and species level. The anatomical characteristics of root, stem, leaf and petiole are partly informative for particular `species groups`. It is evident from the gross morphology that, *L. cymbalariifolium* and *L. sandrasicum* (sect. *Lamium*) are only similar to the `*garganicum* complex` (sect. *Lamium*) on the basis of corolla morphology. In addition to the gross morphological characters, variations in the root, stem, leaf and petiole anatomical features are taxonomically significant for these two alpine endemic species. Similarly, root anatomical characteristics of *L. maculatum* and *L. villosifolium,* which belong to sect. *Lamiotypus,* are strongly delimiting these two taxa from the remaining members of sect. *Lamiotypus*. Therefore, in addition to the gross morphological characters, root anatomical data is taxonomically important for these two species. In addition, the anatomical features of the members of sect. *Amplexicaule*; *L. eriocephalum* subsp. *eriocephalum* and *L. eriocephalum* subsp. *glandulosidens,* are strongly delimiting these two taxa from the remaining sect. *Amplexicaule* members. In addition to the gross morphological characters, variations in the anatomical features are taxonomically significant for these two alpine endemic species. *Lamium orientale* and *L. multifidum* were previously assigned to genus *Wiedemannia* (Fischer and Meyer, 1838). Later on, both were included in *Lamium* (Krause, 1903; Ryding, 2003; Harley, 2004; Govaerts et al., 2010). The anatomical properties of *L. orientale* and *L. multifidum* support their inclusion in the genus *Lamium*. Gross morphology of *Lamium galeobdolon* subsp *montanum* supports its transfer to a separate genus. However, the anatomical results support the inclusion of *L. galeobdolon* subsp. *montanum* in the genus *Lamium*. Moreover, the integration of *Galeobdolon* and *Lamium* seems to be legitimate by Bendiksby et al. (2011b) and Krawczyk et al. (2013, 2014) however its taxonomic placement is not settled. Trichome micromorphology provides valuable information at the species level. The indumentum is taxonomically significant, particularly in the `*garganicum* complex` and its close relatives (*L. bilgilii*, *L. cappadocicum, L. armenum*) as well as in distinguishing the alpine endemic *L. eriocephalum.*

Lamium has tricolpate pollen with reticulate, granulate and microreticulate exine sculpturing pattern. Variation in exine sculpturing pattern has systematic importance particularly at sectional level. Our results support the inclusion of *L. orientale* and *L. multifidum* in the genus *Lamium*. In addition, the results support the resurrection of *L. armenum* subsp. *armenum* from *L. garganicum* complex which is also stated by Krawczyk et al. (2014). However, the palynological results are not fully supporting the resurrection of the other species (i.e. taxa in the `*garganicum*` complex) which are treated as synonyms and/or infraspecific taxa by Mennema (1989). Phylogenetic studies on the genus *Lamium*, based on more compherehensive sampling that particularly includes the Turkish endemics will be necessary to illuminate the infrageneric relationships in the genus. The present study provides pollen morphological characters that hopefully will be useful for future systematic and phylogenetic analyses.

The observations on two sympatric *Lamium* species demonstrated that; two species are isolated from each other on the basis of morphological, mechanical and altitudinal aspects. Two *Lamium* species are clearly adapted to pollination by Apiodea. The size match between floral traits and pollinators ensured successful pollen transfer. On the basis of pollinator efficiency, *Bombus lapidarius* is the best pollinator species for *L. album* subsp. *crinitum* whereas *B. argillaceus* and *B. pascuorum* are equally successful for *L. villosifolium*. Relative pollinator efficiency may influence the reproductive success of *Lamium* species. Further analysis on the reproductive system of the *Lamium* species and single-visit experiments will illuminate the differences in pollinator effectiveness. Moreover, a change in the plant population density along the altitudinal gradient clearly indicated the differences in pollinator assemblages.

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FOREIGN LANGUAGES

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PUBLICATIONS

- **Atalay,** Z., Celep, F., Bilgili, B., Doğan, M. (2016). Pollen morphology of the genus *Lamium* L. (Lamiaceae) and its systematic implications. *Flora,* 219: 68–84.

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