

Petal and Sepal Epidermal Micromorphology of Six *Lathyrus* Taxa (*Fabaceae*) and their Systematic Value

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Abstract

In this study, the epidermal types and their distribution on dorsal and lateral petals, the trichome types and their density on sepals of *Lathyrus chloranthus*, *L. digitatus*, *L. laxiflorus* subsp. *laxiflorus*, *L. roseus* subsp. *roseus*, *L. sativus*, and *L. tuberosus*, belonging to sections *Lathyrus*, *Lathyrostylis*, *Pratensis*, and *Orobon* of the genus *Lathyrus* in Turkey were investigated using light microscopy (LM) and scanning electron microscopy (SEM), and the systematic significance of these characters was evaluated. These taxa, except *L. sativus*, are studied for the first time under aspects of the petal and sepal micromorphology. Three major epidermal types were recognized on the petal: tabular rugose striate cells (TRS), areolate cells with more or less striations (AS), and papillose conical striate cells (PCS). TRS and AS were further subdivided into three subtypes. TRS was found on the dorsal and lateral petals of *L. chloranthus*, *L. sativus*, and *L. tuberosus*; the dorsal petals of *L. roseus* subsp. *roseus* and the lateral petals of *L. laxiflorus* subsp. *laxiflorus*, while AS was present on the dorsal and lateral petals of *L. digitatus* and the lateral petals of *L. roseus* subsp. *roseus*. PCS was found only on the dorsal petals of *L. digitatus*. Three main types of trichomes on the sepal were observed: peltate glandular, capitate glandular, and nonglandular trichomes. The capitate glandular and nonglandular trichomes were further subdivided into three subtypes. The peltate glandular trichomes were present only in *L. chloranthus*, but absent in the others. The capitate glandular trichomes were found in *L. chloranthus*, *L. laxiflorus* subsp. *laxiflorus*, *L. roseus* subsp. *roseus*, and *L. tuberosus*. The nonglandular trichomes were always present in *L. chloranthus* and *L. laxiflorus* subsp. *laxiflorus*. The present results show that the petal and sepal micromorphology can be used in delimitation of the taxa based on petal and sepal micromorphology.

Keywords: *Fabaceae*, *Lathyrus*, micromorphology, petal, sepal, Turkey

Introduction

Lathyrus L. (*Fabaceae*) is the largest genus in the economically important tribe *Fabeae* of the subfamily *Papilionoideae*, with approximately 170 species worldwide (ILDIS, 2010; Lewis *et al.*, 2005). The eastern Mediterranean region is the main center of diversity for the genus, which is less diversified in North and South America (Kupicha, 1983). Many species of the genus are found throughout the temperate northern hemisphere (Asmussen and Liston, 1998; Kupicha, 1983). Moreover, a few species are distributed in the tropical zones and the highlands of East Africa (Davis, 1970; Kenicer *et al.*, 2005; Senn, 1938). *Lathyrus* species are economically important as food and fodder crops, ornamentals, soil nitrifiers, dune stabilizers, significant agricultural weeds, and model organisms for genetic and ecological research (Chittenden, 1951; Kenicer *et al.*, 2005).

Most researchers separate *Lathyrus* into 12 or 13 sections (Asmussen and Liston, 1998; Czefranova, 1971; ILDIS, 2002; Kupicha, 1983; Leht, 2009). Kupicha's (1983) infrageneric classification is the only worldwide treatment of the genus. She divided it into 13 sections based on morphological traits: *Orobus*, *Lathyrostylis*,

Lathyrus, *Orobon*, *Pratensis*, *Aphaca*, *Clymenum*, *Orobastrum*, *Viciopsis*, *Linearicarpus*, *Nissolia*, *Neurolobus* and *Notolathyrus*. Since Kupicha's (1983) monograph, Doğan *et al.* (1992) have carried out a phenetic analysis of 54 *Lathyrus* species in Turkey and clustered them into 9 sections. Most recent molecular phylogenetic studies (Croft *et al.*, 1999; Kenicer *et al.*, 2005) generally support Kupicha's (1983) classification.

In Turkey, the genus is represented by 76 taxa (66 species) (Davis, 1970; Davis *et al.*, 1988; Güneş and Özhatay, 2000; Genç and Şahin, 2011) belonging to 11 sections according to the infrageneric system of Kupicha (1983). These sections are *Orobus*, *Lathyrostylis* (*Platystylis*), *Lathyrus* (syn. *Cicercula*), *Orobon*, *Pratensis*, *Aphaca*, *Clymenum*, *Orobastrum*, *Viciopsis*, *Linearicarpus*, and *Nissolia* (Kupicha, 1983). Turkey is a major center of diversity for the genus in Eurasia with a high number of species.

The epidermal surface of petals is significant in pollination because it affects the way that pollinators perceive and interact with the flower (Ojeda *et al.*, 2009). Many legume species have a specialized flower morphology that promotes pollinator specificity (Ojeda *et al.*, 2009). In *Compositae* (Baagoe, 1977, 1980; Hansen, 1991) and *Fabaceae*

(Stirton, 1981) the properties of the petal epidermal types have been used for taxonomic and phylogenetic analyses.

Studies on the petal and sepal epidermal micromorphology of leguminous species are rather limited (Christensen and Hansen, 1998; Hammett *et al.*, 1994; Ojeda *et al.*, 2009; Stirton, 1981). Stirton (1981) examined the lateral petals of the papilionoids. Hammett *et al.* (1994) reported the epidermal type of the dorsal and lateral petals in 2 *Lathyrus* species, and Ojeda *et al.* (2009) reported the epidermal types on the dorsal, lateral, and ventral petals of 7 species of the same genus. Except for *L. sativus*, the petal, and sepal micromorphology of *L. chloranthus*, *L. digitatus*, *L. laxiflorus* subsp. *laxiflorus*, *L. roseus* subsp. *roseus*, and *L. tuberosus* have not been analyzed previously. Therefore, this study aims to investigate the epidermal types and their distribution on dorsal, and lateral petals and the trichome types and their density on sepals of these six taxa from four sections, namely *Lathyrus*, *Lathyrostylis*, *Pratensis*, and *Orobon* distributed in Turkey, and to evaluate the systematic value of these characters.

Material and methods

Specimens of the six *Lathyrus* taxa studied were collected from their natural habitats in Central Anatolia, Turkey. The collected specimens were deposited in the herbarium of Department of Biological Sciences, Middle

East Technical University (METU), Ankara. The voucher specimens are listed in Tab. 1.

Petals and sepals of fully opened flowers were investigated using a Leica DM1000 LM and a QUANTA 400F SEM. After a number of specimens had been compared under LM, three to six petals and sepals were examined for each species under SEM. Two kinds of petals (a dorsal petal, called a 'standard' and two lateral petals or 'wings') were examined. The epidermal types of the petals were classified based on cell size, shape (the primary sculpture), and on the fine relief of the cell wall, using the terminology of Barthlott (1977) and Kay *et al.* (1981). To investigate trichomes on the sepals, sections were made by hand using commercial razor blades. The trichome types and densities are described. The general trichome terminology follows Metcalfe and Chalk (1957) and Kahraman *et al.* (2010).

Results

Petal micromorphology

In the *Lathyrus* taxa studied, three main epidermal cell types were determined: tabular rugose striate cells (type 1), areolate cells with more or less striations (type 2) and papillose conical striate cells (type 3) (Fig. 1-16, Tab. 2).

Type 1. Tabular rugose striate cells (TRS): This type was further subdivided into three subtypes based on several properties, such as cell size, shape and density of striations.

Tab. 1. Collection data of the *Lathyrus* specimens examined

Section	Taxon	Collection data
<i>Lathyrus</i>	<i>L. chloranthus</i> Boiss. and Balansa	B4 Kırşehir: Kaman, Kalehöyük, 1050 m, 33°45'578"E -39°20'155"N, 20.06.2010, Çildir 184.
	<i>L. sativus</i> L.	A4 Ankara: near Lalahan, 39°58'443"N-33°07'216"E, 1100 m, 06.05.2009, Çildir 121a.
	<i>L. tuberosus</i> L.	A4 Ankara: Çubuk, Karagöl, 1512 m, 40°24'775"N-32°54'706"E, 30.05.2010, Çildir 132a. B6 Sivas: Yıldızeli, near Kızılırmak River, 1368 m, 39°51'230"N-36°32'246"E, 23.06.2010, Çildir 172.
<i>Lathyrostylis</i>	<i>L. digitatus</i> (Bieb.) Fiori	A4 Ankara: Çubuk, Karagöl, 1515 m, 40°24'825"N-32°54'710"E, 30.05.2010, Çildir 133; Ankara: Çubuk to Karagöl, 1208 m, 40°23'417"N-32°56'663"E, 30.05.2010, Çildir 128.
		Çankırı: Eldivan road, 1381 m, 40°29'724"N-32°29'875"E, 27.06.2010, Çildir 179a.
		B3 Eskişehir: Mihalıççık, 1435 m, 39°53'588"N-31°27'731"E, 16.06.2010, Çildir 146. B4 Ankara: Kıbrıs village, 1050 m, 39°52'247"N-33°00'092"E, 12.06.2010, Çildir 145.
<i>Pratensis</i>	<i>L. laxiflorus</i> (Desf.) Kuntze subsp. <i>laxiflorus</i>	B3 Eskişehir: Mihalıççık, roadside, 1435 m, 59°53'588"N-31°27'731"E, 16.06.2010, Çildir 149; Eskişehir: Yukarı Kalabak village, 1127 m, 39°32'617"N-30°17'614"E, 27.06.2009, Çildir 108.
	<i>L. roseus</i> Stev. subsp. <i>roseus</i>	B6 Sivas: Zara to Şerefiye, 1639 m, 39°58'281"N-37°43'434"E, 22.06.2010, Çildir 162a.

Tab. 2. Distribution of the epidermal types in the dorsal and lateral petals of the taxa examined

Section	Taxon	Dorsal petal	Lateral petal
<i>Lathyrus</i>	<i>L. chloranthus</i>	TRS ⁱ	TRS ⁱ
	<i>L. sativus</i>	TRS ⁱ	TRS ⁱ
	<i>L. tuberosus</i>	TRS ⁱ	TRS ⁱ
<i>Lathyrostylis</i>	<i>L. digitatus</i>	AS ⁱ	AS ⁱⁱ
<i>Pratensis</i>	<i>L. laxiflorus</i> subsp. <i>laxiflorus</i>	PCS	TRS ⁱⁱⁱ
	<i>L. roseus</i> subsp. <i>roseus</i>	TRS ⁱ	AS ⁱ

Subtype TRSⁱ: Elongated cells with dense striations. Observed in the dorsal and lateral petals of *L. sativus* (Fig. 13-14), the dorsal petals of *L. roseus* subsp. *roseus* (Fig. 9-10) and *L. tuberosus* (Fig. 15). *Subtype TRSⁱⁱ*: More or less isodiametric cells with dense striations. Observed in the dorsal and lateral petals of *L. chloranthus* (Fig. 1-2) and the lateral petals of *L. tuberosus* (Fig. 16). *Subtype TRSⁱⁱⁱ*: Elongated cells with less-dense striations. Observed in the lateral petals of *L. laxiflorus* subsp. *laxiflorus* (Fig. 7, 8).

Type 2. Areolate cells with more or less striations (AS): This type was further subdivided into three subtypes based

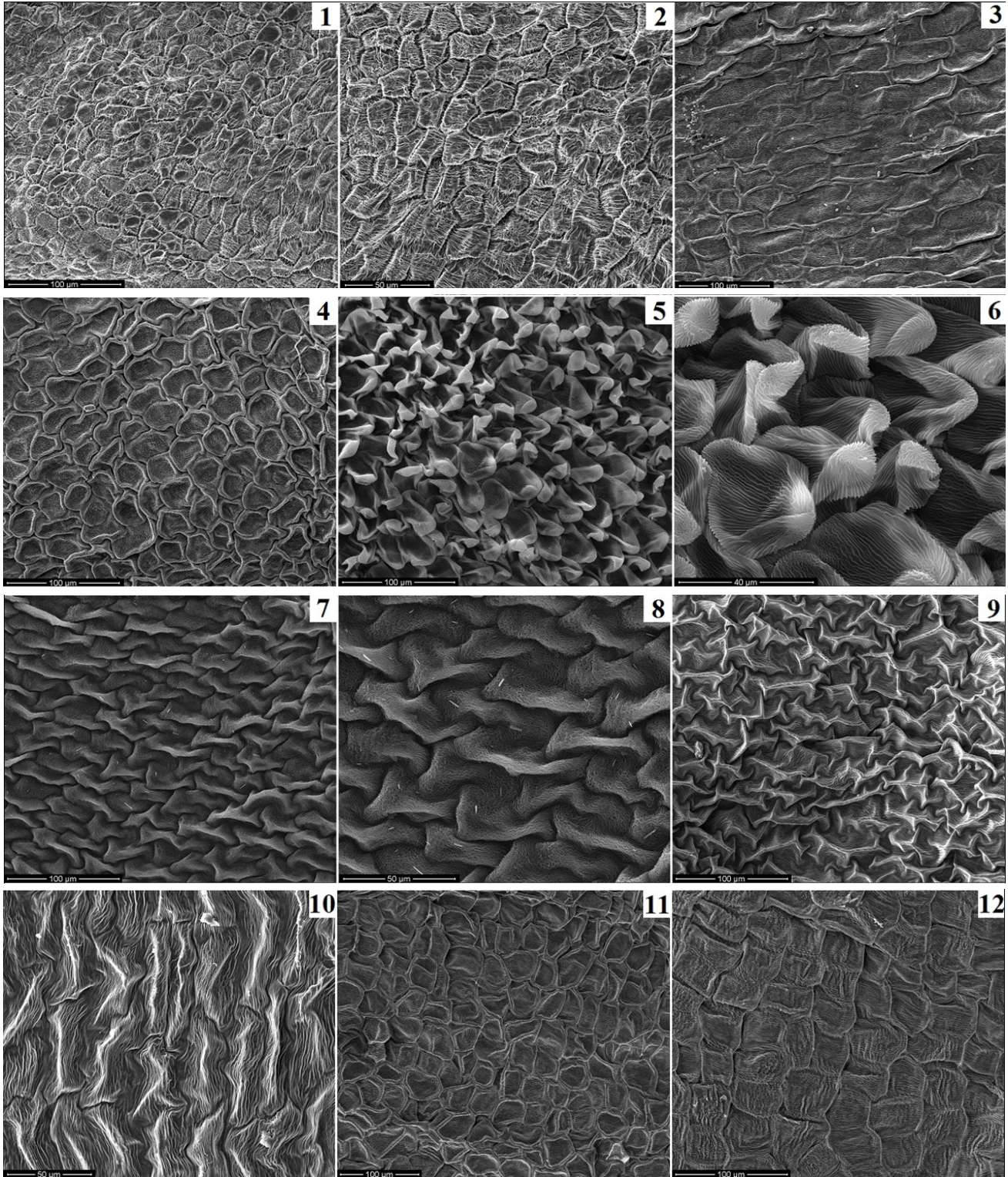


Fig. 1-12. SEM micrographs showing the petal epidermal micromorphology of the *Lathyrus* taxa studied. Dorsal petals of (1) *L. chloranthus*, (3) *L. digitatus*, (5, 6) *L. laxiflorus* subsp. *laxiflorus* and (9, 10) *L. roseus* subsp. *roseus*. Lateral petals of (2) *L. chloranthus*, (4) *L. digitatus*, (7, 8) *L. laxiflorus* subsp. *laxiflorus* and (11, 12) *L. roseus* subsp. *roseus*

on several properties, such as cell size, shape and waviness of the cell margin.

Subtype ASⁱ: Elongated cells with straight anticlinal walls. Observed in the dorsal petals of *L. digitatus* (Fig. 3). *Subtype ASⁱⁱ*: Isodiametric cells with straight or weakly

curved anticlinal walls. Observed in the lateral petals of *L. roseus* subsp. *roseus* (Fig. 11-12). *Subtype ASⁱⁱⁱ*: Isodiametric cells with curved anticlinal walls. Observed in the lateral petals of *L. digitatus* (Fig. 4).

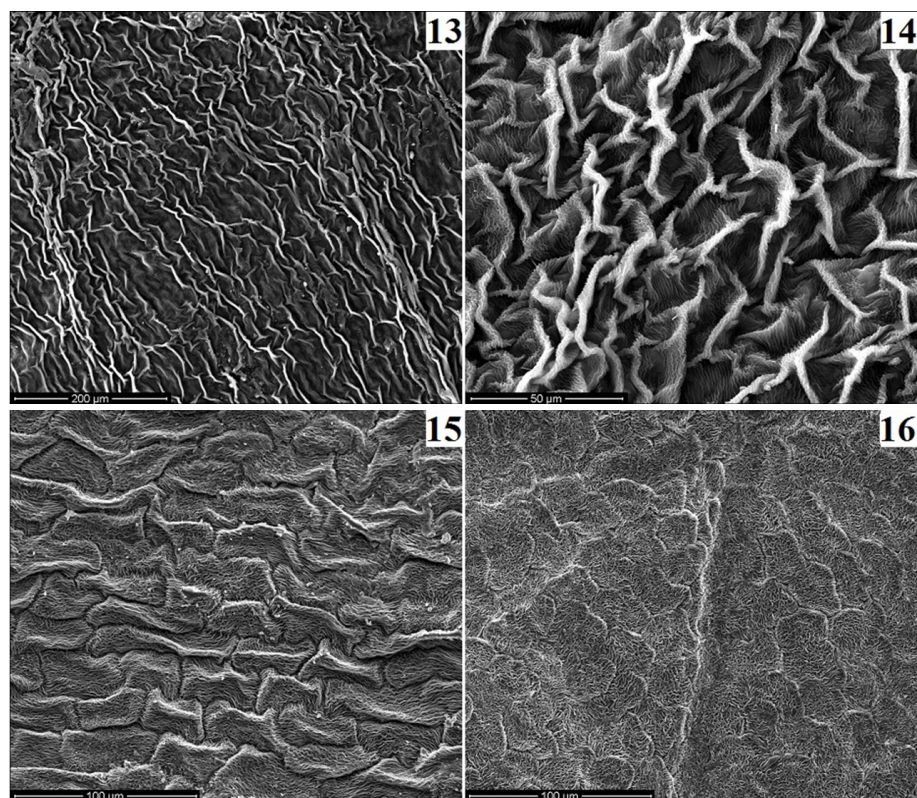


Fig. 13-16. SEM micrographs showing the petal epidermal micromorphology of the *Lathyrus* taxa studied. Dorsal petals of (13) *L. sativus* and (15) *L. tuberosus*. Lateral petals of (14) *L. sativus* and (16) *L. tuberosus*

Tab. 3. Distribution of the trichome types and density on sepals of the taxa examined

Section	Taxon	Peltate glandular	Capitate glandular		Nonglandular	
			Subtype i	Subtype ii	Subtype i	Subtype ii
<i>Lathyrus</i>	<i>L. chloranthus</i>	+	+	-	±	+
	<i>L. sativus</i>	-	-	-	-/±	-
	<i>L. tuberosus</i>	-	-	+	-/±	-
<i>Lathyrostylis</i>	<i>L. digitatus</i>	-	-	-	-/±	-
<i>Pratensis</i>	<i>L. laxiflorus</i> subsp. <i>laxiflorus</i>	-	-	+	±	+
<i>Orobon</i>	<i>L. roseus</i> subsp. <i>roseus</i>	-	-	+	-/±	-

(-) absent, (±) scarce, (+) present

Type 3. Papillose conical striate cells (PCS): This type was observed only in the dorsal petals of *L. laxiflorus* subsp. *laxiflorus* (Fig. 5-6).

Sepal micromorphology

The sepals of the studied taxa had irregular cells with undulated to sinuated anticlinal walls. Three different trichome types on the epidermal cells were observed: peltate, capitate glandular, and nonglandular trichomes (Fig. 17-28, Tab. 3).

The peltate glandular trichomes had a basal epidermal cell, one neck cell and multicellular secretory head. They were found in the grooves of the calyces of *L. chloranthus* (Fig. 17, 18), but absent on those of the others.

The capitate glandular trichomes had a basal epidermal cell, unicellular stalk, a neck cell and a cutinized secretory

head. They were subdivided into two subtypes on the basis of their structure: (i) composed of a unicellular globose secretory head. This subtype was found only in *L. chloranthus* (Fig. 17-19). (ii) composed of a multicellular oval secretory head. This subtype was mainly situated on the sepal teeth of *L. roseus* subsp. *roseus* and *L. tuberosus* and the sides of the sepal ribs of *L. laxiflorus* subsp. *laxiflorus* (Fig. 22-25, 27, 28).

The nonglandular trichomes were subdivided into two subtypes on the basis of their structure: (i) composed of short acicular epidermal cells. This subtype was always present in *L. chloranthus* and *L. laxiflorus* subsp. *laxiflorus*, but very rare or absent in the others; (ii) composed of long filamentous epidermal cells. They were situated on the teeth and ribs of the calyces of *L. chloranthus* and *L. laxiflorus* subsp. *laxiflorus* (Fig. 17-20, 22).

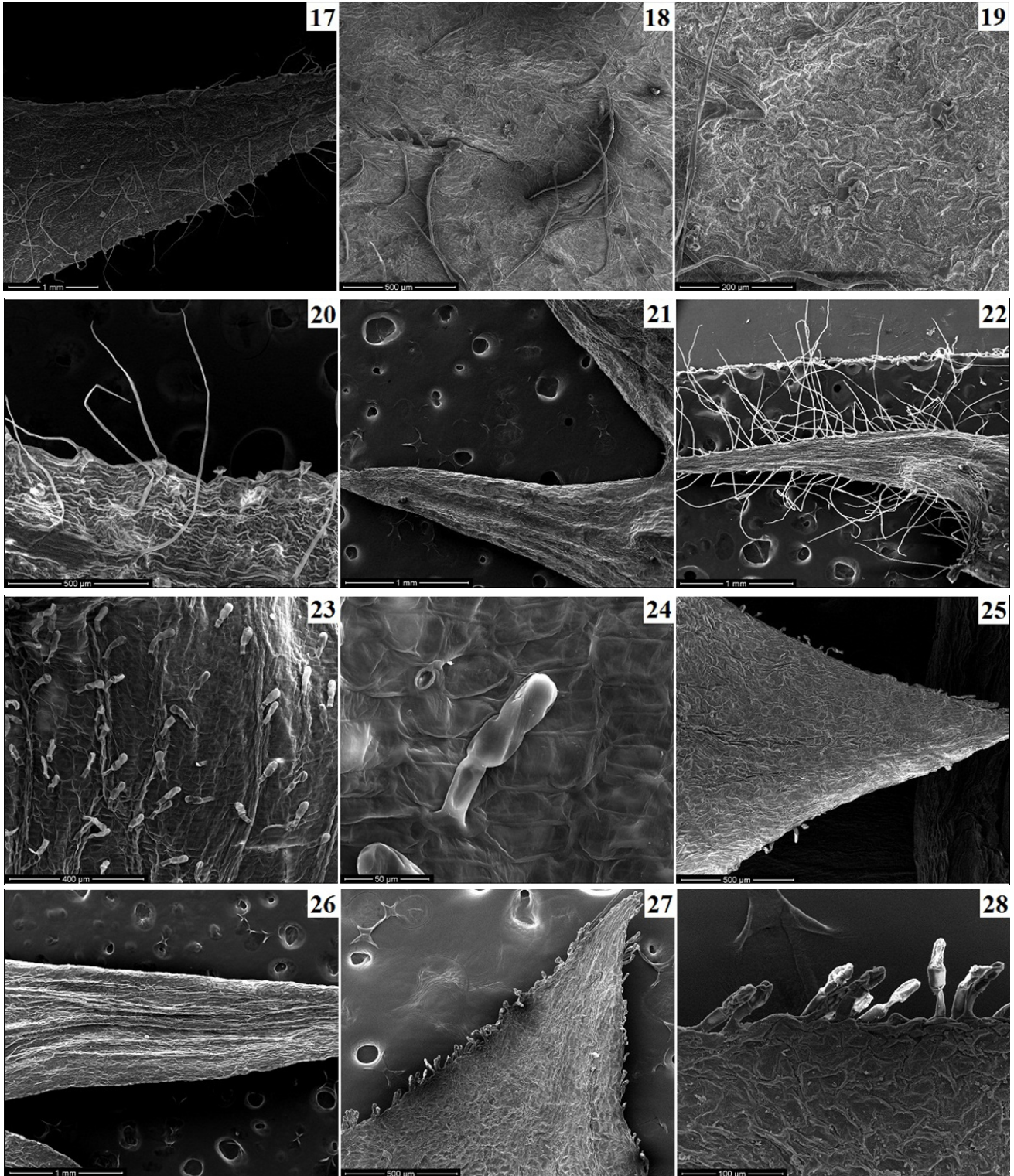


Fig. 17-28. SEM micrographs showing trichomes and epidermal micromorphology of sepals of the *Lathyrus* taxa studied. (17-20) *L. chloranthus*, (21) *L. digitatus*, (22-24) *L. laxiflorus* subsp. *laxiflorus*, (25) *L. roseus* subsp. *roseus*, (26) *L. sativus*, and (27-28) *L. tuberosus*

Discussion

The micromorphological data play significant role in the modern classification of angiosperms (Heywood, 1971). Petal micromorphology represents an important

character in separation of taxa (Metcalf and Chalk, 1957). Ojeda *et al.* (2009) analyzed the epidermal types and their distribution within the family *Fabaceae* and concluded that papilionoids had a high degree of petal micromorphological variation, and great differences between the dorsal,

lateral, and ventral petals occurred, but found only smaller differences among *Lathyrus* species. TRS was found on the three petal types of some species, such as *L. japonicus*, *L. latifolius*, *L. sativus*, and *L. sylvestris*. In *L. venatus*, the dorsal and lateral petals had papillose knobby rugose cells (PKR), whereas the ventral petals had TRS. In *L. vernus*, the dorsal and ventral petals had TRS while the lateral petals had PKR. The present study showed that there was micromorphological variation between the dorsal and lateral petals of the taxa. TRS was the dominant epidermal type in the dorsal and lateral petals of the taxa. PCS and AS epidermal types were observed in *L. digitatus*, *L. laxiflorus* subsp. *laxiflorus*, and *L. roseus* subsp. *roseus*, but PKR was not recognized in any taxa. The dorsal and lateral petals of *L. chloranthus*, *L. digitatus*, *L. sativus*, and *L. tuberosus* had the same major micromorphology. However, this was not the case in *L. laxiflorus* subsp. *laxiflorus* with PCS on the dorsal petal and TRS on the lateral petal; and *L. roseus* subsp. *roseus* with TRS on the dorsal petal and AS on the lateral petal.

L. chloranthus, *L. sativus*, and *L. tuberosus* had the same main epidermal type (TRS) on their dorsal and lateral petals, however, minor differences in cell size, shape (isodiametric or elongated), and density of striations allow clear petal micromorphological identification of these taxa. TRS was subdivided into three subtypes: TRS^i , TRS^{ii} and TRS^{iii} . TRS^i was found on the dorsal and lateral petals of *L. sativus* and the dorsal petals of *L. tuberosus*, but TRS^{ii} was found on the dorsal and lateral petals of *L. chloranthus* and the lateral petals of *L. tuberosus*.

Among the taxa *L. digitatus* and *L. roseus* subsp. *roseus* had AS cell type, which was differentiated by cell size, shape (isodiametric or elongated), and waviness of the cell margin. AS^i was subdivided into three subtypes: AS^i , AS^{ii} and AS^{iii} . AS^i was observed on the dorsal petal of *L. digitatus*, AS^{ii} on the lateral petal of *L. roseus* subsp. *roseus* and AS^{iii} on the lateral petal of *L. digitatus*.

Molecular genetic studies show that each petal in a papilionoid legume flower has a distinct molecular identity that may be marked by epidermal type (Cronk, 2006; Weng et al., 2011). Many studies have focused on the molecular genetics of PCS cell type. MIXTA, a MYB transcription factor, is responsible for the differentiation of PCS in *Anthirrinum majus* and in some species of Solanaceae (Glover and Martin, 2002; Noda et al., 1994). However, there is not yet any evidence that MIXTA plays a role in PCS differentiation in legumes (Ojeda et al., 2009). In *Lotus japonicus*, the genes, CYCLOIDEA 2 (LjCyc2) and KEEL WING 1 (KEW1 or LjCyc3) are associated with dorsal and lateral petal identity, respectively (Weng et al., 2011). Now, there is no information about the precise pathway by which petal identity genes promote the differentiation of the epidermal types described in this study.

Legumes show a variety of uni- and multicellular trichomes, both secretory and nonsecretory, on the vegetative (Franceschi and Giaquinta, 1983; Retallack and

Willson, 1988; Shaheed and Illoh, 2010) and floral organs (Bernard and Singh, 1969; de Freitas Mansano and de Pádua Teixeira, 2008; Guard, 1931; Gunasinghe et al., 1988; Healy et al., 2005; Lersten and Burubaker, 1987; Tucker, 1997). The present study agrees with the findings of the previous studies conducted on the legumes. Only the calyxes of *L. chloranthus* carried peltate glandular trichomes. The capitate glandular and non-glandular trichomes differed in structure. Whereas *L. chloranthus* had unicellular globose-headed capitate trichomes (capitate subtype i), *L. laxiflorus* subsp. *laxiflorus*, *L. roseus* subsp. *roseus*, and *L. tuberosus* had the multicellular oval-headed capitate trichomes (capitate subtype ii). The short acicular (nonglandular subtype i) and long filamentous nonglandular trichomes (nonglandular subtype ii) were always found in *L. chloranthus* and *L. laxiflorus* subsp. *laxiflorus*.

Conclusions

Little is known of the petal and sepal micromorphology of the genus *Lathyrus*. Therefore, the present study provides a more extensive knowledge of petal and sepal surface properties of the genus. *Lathyrus* taxa can be separated on the basis of the petal and sepal micromorphology. Different petals within a flower of *Lathyrus* can also be separated micromorphologically.

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