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Taxonomy of some species of Papilionoideae (Fabaceae) based on micromorphological and microanatomical characteristics

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ABSTRACT: This study evaluated the taxonomic significance of selected micromorphological and microanatomical characters for distinguishing nineteen species belonging to nine genera representing six tribes of the subfamily Papilionoideae (Fabaceae) in Iraq. The investigated characters included indumentum, calcium oxalate crystal types, leaflet venation patterns, and anatomical features of fruit cross-sections. Considerable interspecific variation was observed in the type, density, and distribution of glandular and non-glandular trichomes, as well as in papillae morphology. Druse crystals were recorded exclusively in *Colutea cilicica*, whereas prismatic crystals occurred in most of the remaining taxa. Leaf venation patterns also showed diagnostic variation; the semicraspedodromous pattern was exclusive to *Pisum sativum*, while the acrodromous pattern characterized *Scorpiurus muricatus*. In addition, anatomical features observed in fruit cross-sections, including pericarp organization, vascular bundle arrangement, and seed-coat structure, provided valuable characters for distinguishing genera and species, particularly within *Onobrychis*. These findings demonstrate that the integration of micromorphological and microanatomical characters provides reliable complementary evidence for the taxonomy of Papilionoideae and enhances the delimitation of closely related genera and species when used alongside conventional morphological characters. Furthermore, *Astragalus rhodosemius* Boiss. & Hausskn. is reported as a new record for the flora of Iraq.
Keywords: fruit anatomy; leaf venation; micromorphology; trichomes.

Taxonomia de algumas espécies de Papilionoideae (Fabaceae) com base em características micromorfológicas e microanatômicas

RESUMO: Este estudo avaliou o significado taxonómico de caracteres micromorfológicos e microanatómicos seleccionados para distinguir dezanove espécies pertencentes a nove géneros, que representam seis tribos da subfamília Papilionoideae (Fabaceae) no Iraque. Os caracteres investigados incluíram o indumento, os tipos de cristais de oxalato de cálcio, os padrões de venação dos folíolos e as características anatómicas dos cortes transversais dos frutos. Observou-se uma variação interespecífica considerável no tipo, na densidade e na distribuição dos tricomas glandulares e não glandulares, bem como na morfologia das papilas. Os cristais do tipo drusa foram registados exclusivamente em *Colutea cilicica*, enquanto que os cristais prismáticos ocorreram na maioria dos restantes taxa. Os padrões de venação foliar também apresentaram variação diagnóstica; o padrão semicraspedódromo foi exclusivo de *Pisum sativum*, ao passo que o padrão acródromo caracterizou *Scorpiurus muricatus*. Além disso, as características anatómicas observadas em cortes transversais dos frutos, incluindo a organização do pericarpo, a disposição dos feixes vasculares e a estrutura do tegumento da semente, forneceram caracteres valiosos para distinguir géneros e espécies, particularmente no âmbito de *Onobrychis*. Estes resultados demonstram que a integração de caracteres micromorfológicos e microanatómicos fornece evidências complementares fiáveis para a taxonomia de Papilionoideae e melhora a delimitação de géneros e espécies estreitamente relacionados quando utilizada em conjunto com caracteres morfológicos convencionais. Ademais, *Astragalus rhodosemius* Boiss. & Hausskn. é relatado como um novo registo para a flora do Iraque.
Palavras-chave: anatomia do fruto; venação foliar; micromorfologia; tricomas.

1. INTRODUCTION

The subfamily Papilionoideae (Fabaceae) is the largest and most diverse lineage within the legume family, comprising approximately 503 genera and more than 14,000 species distributed worldwide. Recent phylogenetic studies have considerably improved the classification of the subfamily; however, the circumscription of several genera and species remains challenging because of extensive morphological variation and overlap among diagnostic characters (LPWG, 2017; AROGUNDADE et al., 2019).

Traditional taxonomic studies of Papilionoideae have relied primarily on external morphological features such as floral structure, fruit morphology, and vegetative characters. Nevertheless, many of these characters are influenced by environmental conditions and phenotypic plasticity, reducing their reliability for species delimitation (MYRTSI et al., 2023; JASSIM et al., 2024). Consequently, micromorphological and anatomical characters have become increasingly important as complementary sources of taxonomic evidence (ANIZ; JASSIM, 2024; CASTILLÓN et al., 2025).

Characters including trichome morphology, papillae, calcium oxalate crystal types, leaf venation architecture, and fruit anatomy have proven valuable for distinguishing taxa at different taxonomic levels within Fabaceae. These characters are generally more stable than external morphological features and have been successfully applied in systematic and taxonomic investigations of several genera of Papilionoideae (OGBOLE et al., 2023; NUNES et al., 2024).

In Iraq, the subfamily Papilionoideae is represented by numerous genera and species occupying diverse ecological habitats. Although the Iraqi Flora provides comprehensive morphological descriptions (Townsend, 1974), comparative studies integrating micromorphological and microanatomical characters across multiple genera remain limited. Consequently, the diagnostic value of these characters for species identification and taxonomic delimitation within the Iraqi representatives of Papilionoideae has not been fully evaluated extracts (MOHAMMED et al., 2024).

Therefore, the present study aimed to evaluate the taxonomic significance of selected micromorphological and microanatomical characters, including indumentum, calcium oxalate crystals, leaf venation patterns, and fruit anatomy, in nineteen species belonging to nine genera of Papilionoideae occurring in Iraq. The study also sought to identify the most reliable diagnostic characters for distinguishing species, genera, and tribes and to document the occurrence of *Astragalus rhodosemius* as a new record for the flora of Iraq.

2. MATERIAL AND METHODS

2.1. Plant material and identification

Nineteen species representing nine genera belonging to six tribes of the subfamily Papilionoideae were investigated in this study (Table 1). Plant specimens were collected from different regions of Iraq, including Erbil, Karbala, and Babylon. Additional herbarium specimens were examined when necessary to verify species identity. Identification was carried out using Flora of Iraq (Townsend, 1974) and other relevant taxonomic references.

Table 1. Taxonomic list of the investigated Papilionoideae species included in the present study.
Table 1. Taxonomic list of the investigated Papilionoideae species included in the present study.

Tribe	Genus	Species, Variety or Subspecies
Astragaleae (Adans.) Hutch.	*Astragalus* L. (1753)	*Astragalus kahiricus* DC. (1825)
		Astragalus rhodosemius Boiss. & Hausskn. (1872)
	Glycyrrhiza L. (1753)	*Glycyrrhiza glabra* var. *glandulifera* (Waldst. & Kit.) Regel & Herder (1966)
Coronilleae (Adans.) Hutch.	*Coronilla* L. (1753)	*Coronilla scorpioides* (L.) W.D.J. Koch (1837)
	Hippocrepis L. (1753)	*Hippocrepis unisiliquosa* subsp. *bisiliqua* (Forssk.) Bornm. (1928)
	Scorpiurus L. (1753)	*Scorpiurus muricatus* var. *subvillosus* (L.) Lam. (1779)
Coluteae (Benth.) Hutch.	*Colutea* L. (1753)	*Colutea cilicica* Boiss. & Balansa (1856)
Loteae Benth.	*Hymenocarpos* Savi (1798)	*Hymenocarpos circinnatus* (L.) Savi (1798)
Hedysareae DC.	*Onobrychis* Mill. (1754)	*Onobrychis acaulis* Bornm. (1906)
		Onobrychis caput-galli (L.) Lam. (1779)
		Onobrychis crista-galli (L.) Lam. (1779)
		Onobrychis carduchorum C.C. Towns. (1968)
		Onobrychis megataphros Boiss. (1843)
		Onobrychis haussknechtii Boiss. (1872)
		Onobrychis galegifolia Boiss. (1843)
		Onobrychis ptolemaica (Delile) DC. (1825)
		Onobrychis schahuensis Bornm. (1914)
Vicieae (Adans.) DC.	*Pisum* L. (1753)	*Pisum sativum* (M. Bieb.) Asch. & Graebn. (1910)

2.2. Micromorphological and microanatomical investigations

The study was designed to evaluate the taxonomic significance of selected micromorphological and microanatomical characters. Four groups of diagnostic characters were investigated:

- Indumentum (trichomes and papillae)
- Calcium oxalate crystal types
- Leaf and leaflet venation patterns
- Fruit transverse anatomy

Each character was examined in the plant organ where it naturally occurs, including stems, leaves, leaflets, petioles, sepals, petals, fruits, and seeds, depending on organ availability.

2.2.1. Indumentum

The indumentum of different vegetative and reproductive organs was examined using a Zeiss light microscope. Trichome type, distribution, density, and length were recorded and measured with an ocular micrometer. Selected structures were documented using scanning electron microscopy (SEM). The terminology used in this study follows Metcalfe; Chalk (1950, 1979), Esau (1965), Khdhair et al. (2024) and Radford et al. (1974).

2.2.2. Calcium oxalate crystals

Calcium oxalate crystals were investigated in different plant organs, including leaves, fruits, sepals, and other tissues where crystals were present. Crystal type and distribution were recorded and photographed for comparative taxonomic evaluation.

2.2.3. Leaf venation

Leaf and leaflet venation architecture was examined using cleared leaves. Primary, secondary, and tertiary veins, areoles, marginal venation, and veinlets were described following Hickey (1973), Melville (1976), and Ash et al. (1999).

2.2.4. Fruit anatomy

Transverse sections of mature fruits were prepared using the paraffin embedding technique to examine the anatomical organization of the pericarp and seed coat.

Fruit anatomical observations were restricted to species for which mature fruits were available. Several taxa, particularly those naturally distributed in northern Iraq, could not be included because suitable mature fruits were unavailable during the sampling period.

3. RESULTS

3.1. Indumentum Study

The indumentum of the studied species exhibited considerable variation in trichome type, length, surface ornamentation, density, and distribution. Both non-glandular and glandular trichomes, as well as papillae, were observed on different vegetative and reproductive organs (Figures 1–7).

Figure 1. A: Non-glandular hairs: Uniserate: short hairs in; 1: *O. galgifolia*; 2: *O.schabuensis*; 3: *Astragalus*; 4: *H. unisiliquosae*; 5: *S. muricatus*; B: Non-glandular hairs: Uniserate: Long hairs in; 6: *H. circinnatus*; 7: *H. circinnatus* + *O. caput galli*; 8-9: *O.caput galli*; 10-11: *O. haussknechtii*; 12-13: *O. acaulis*; 14-15: *G. glabra*.

Figura 1. A: Pelos não glandulares: Uniserados: pelos curtos em; 1: *O. galgifolia*; 2: *O.schabuensis*; 3: *Astragalus*; 4: *H. unisiliquosae*; 5: *S. muricatus*; B: Pelos não glandulares: Uniserado: Pelos longos em; 6: *H. circinnatus*; 7: *H. circinnatus* + *O. caput galli*; 8-9: *O.caput galli*; 10-11: *O. haussknechtii*; 12-13: *O. acaulis*; 14-15: *G. glabra*.

3.1.1. Non-glandular trichomes

A. Uniseriate trichomes

Uniseriate trichomes occurred in several forms and lengths among the studied species. Short trichomes (32.5–217 µm) were observed on the sepal surface of *Onobrychis galegifolia* and *O. schabuensis*. In *O. galegifolia*, these trichomes were densely distributed on the basal stem, petiole, and leaflets (Figure 1).

Long uniseriate trichomes (500–1500 µm) were recorded on different organs of *Hippocrepis circinnatus*, *Scorpiurus muricatus*, *Onobrychis caput-galli*, *O. crista-galli*, and the two investigated *Astragalus* species, whereas the leaves of

Astragalus rhodosemius were glabrous (Figure 1). The highest trichome density was observed on the stem of *H. circinnatus*.

Uniseriate trichomes measuring 97.5–1575 µm were recorded on the sepals, the outer surface of the standard petal, and other vegetative organs of *O. acaulis*, *O. galegifolia*, *O. haussknechtii*, *O. ptolemaica*, and *O. schahuensis*. These trichomes formed dense, interwoven indumentum on the sepal epidermis of *O. acaulis*, *O. galegifolia*, and *O. schahuensis* (Figures 1, 5 and 6).

Smooth-surfaced uniseriate trichomes (62.5–150 µm) were observed on different organs of *Glycyrrhiza glabra* var. glandulifera (Figure 1), whereas granular-surfaced uniseriate trichomes (120–1675 µm) were recorded on the sepals and fruit surface of *H. circinnatus* (Figure 1).

Simple unicellular trichomes were observed at the base of the staminal filaments of *S. muricatus* (Figure 1). In addition, uniseriate trichomes with a papillary surface were recorded in *Hedysarum unisiliquosum* subsp. bisiliqua and in most of the investigated *Onobrychis species* (Figures 5 and 6).

Whip trichomes (long, interwoven trichomes) were distributed on the outer surface of the fruits of *O. acaulis*, *O. galegifolia*, *O. megataphros*, and *O. schahuensis*. These trichomes were more densely distributed in *O. galegifolia* than in *O. schahuensis* and *O. megataphros* (Figure 6).

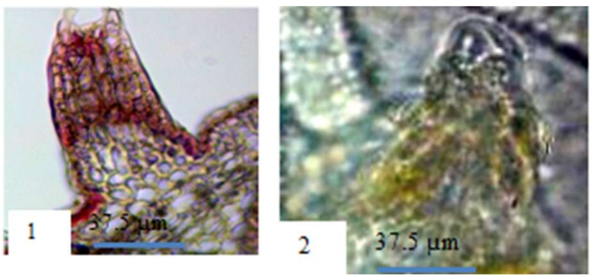


Figure 2. Non-glandular hairs, multicellular, multiseriate (Shaggy); 1: in G. glabra; 2: all studied *Onobrychis* species and *H. circumnatus*.
Figura 2. Tricomas não glandulares, multicelulares, multisseriados (do tipo Shaggy); 1: em *G. glabra*; 2: em todas as espécies de *Onobrychis* estudadas e em *H. circumnatus*.

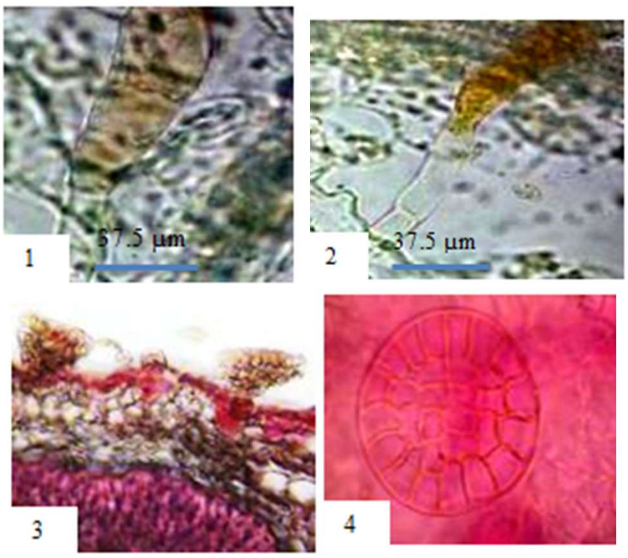


Figure 3. Glandular hairs: 1-2: *P. sativum*; 3-4: Peltate hair in *G. glabra*.
Figura 3: Tricomas glandulares: 1-2: *P. sativum*; 3-4: Tricoma peltado em *G. glabra*.

B. Multiseriate multicellular (shaggy) trichomes

Multiseriate multicellular (shaggy) trichomes were observed on the stem of *G. glabra* var. glandulifera. They were also present on the fruits of all investigated *Onobrychis* species, *S. muricatus*, and along the margins of the fruit of *H. circinnatus* (Figures 2 and 6).

3.1.2. Glandular trichomes

Three forms of glandular trichomes were recognized (Figures 3 and 7).

A. Short-stalked uniseriate glandular trichomes were observed on the sepals of *Pisum sativum*.
B. Short-stalked multiseriate glandular trichomes with peltate glands were recorded in *G. glabra* var. *glandulifera*.
C. Multiseriate glandular trichomes with long or short stalks and a semi-striated surface were observed on the fruit epidermis of *H. unisiliquosum* subsp. *bisiliqua*.

3.1.3. Papillae

Three types of papillae were recognized (Figures 4 and 7).

A. Small, rounded papillae were observed on the stigmatic surface of *Colutea cilicica*, *Coronilla scorpioides*, *H. unisiliquosum* subsp. *bisiliqua*, *H. circinnatus*, *S. muricatus*, and *G. glabra* var. *glandulifera*.
B. Conical papillae were recorded on the inner surface of the corolla in the same species.
C. Dense semicircular papillae were observed on the fruit surface of *H. unisiliquosum* subsp. *bisiliqua* (Figures 4 and 7).

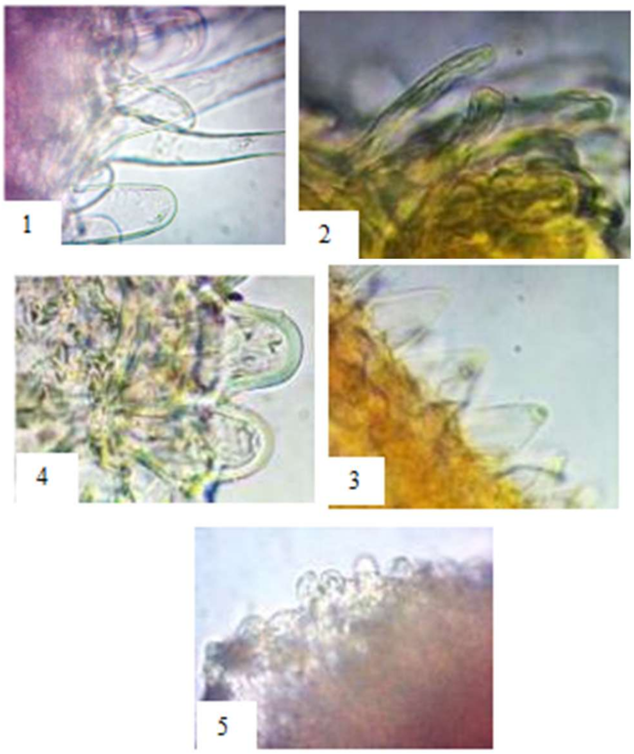


Figure 4. Some of the papillae recorded in some of the studied species; 1: *C. scorpioides*, *H. unisiliquosa*, *S. muricatus*, *H. circinnatus*, *C. cilicica* e *G. glabra*; 2: *A. kahiricus*; 3: *H. circinnatus*, *S. muricatus*; 4: *H. unisiliquosa*; 5: *P. sativum*.
Figura 4. Algumas papilas registradas em algumas das espécies estudadas; 1: *C. scorpioides*, *H. unisiliquosa*, *S. muricatus*, *H. circinnatus*, *C. cilicica* e *G. glabra*; 2: *A. kahiricus*; 3: *H. circinnatus*, *S. muricatus*; 4: *H. unisiliquosa*; 5: *P. sativum*.

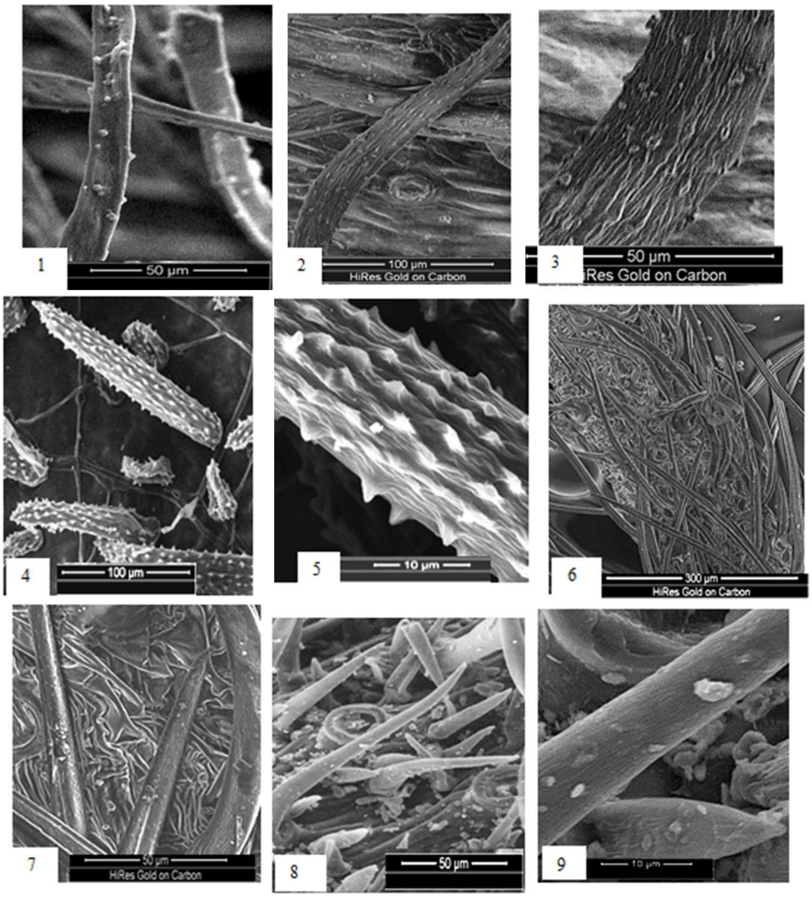
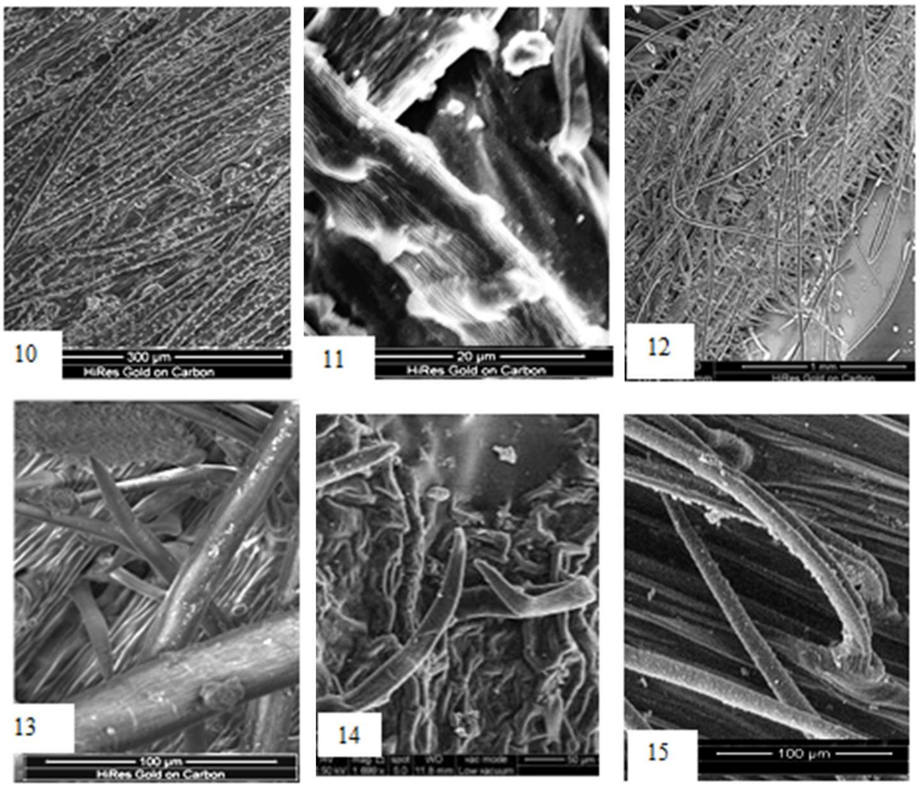


Figure 5. Some types of non-glandular hairs under a scanning electron microscope distributed in different parts of the genus *Onobrychis*; 1: *O. acaulis*; 2-3: *O. carduchorum*; 4-5: *O.c aput-galli*; 6-7: *O. crista-galli*; 8-9: *O. galegifolia.*
Figura 5. Alguns tipos de tricomas não glandulares observados em microscopia eletrônica de varredura, distribuídos em diferentes partes de espécies do gênero *Onobrychis*; 1: *O. acaulis*; 2-3: *O. carduchorum*; 4-5: *O. caput-galli*; 6-7: *O. crista-galli*; 8-9: *O. galegifolia.*



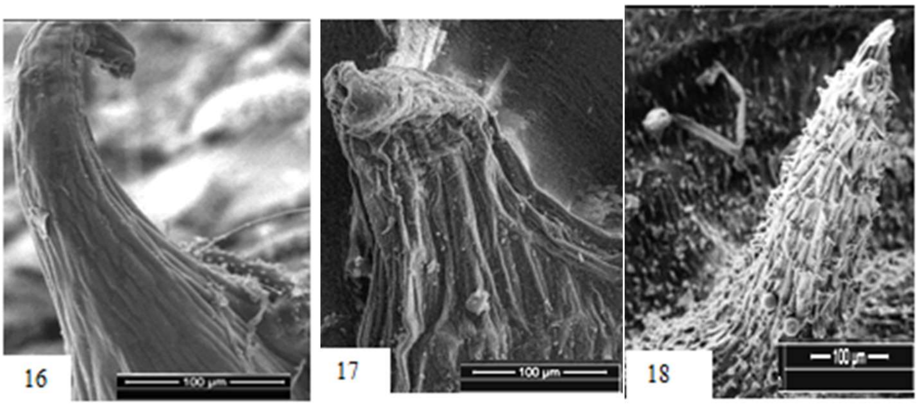


Figure 6. Some types of non-glandular hairs under a scanning electron microscope; 10-11: *O. megataphros*; 12-13: *O. schahuensis*; 14: *G. glabra*; 15: *H. circinnatus*; Shaggy hairs: 16: *O. caput-galli*; 17: *H. circinnatus*; 18: *S. muricatius*.
Figura 6. Alguns tipos de tricomas não glandulares sob microscópio eletrônico de varredura; 10-11: *O. megataphros*; 12-13: *O. schahuensis*; 14: *G. glabra*; 15: *H. circinnatus*; Tricomas lanosos: 16: *O. caput-galli*; 17: *H. circinnatus*; 18: *S. muricatius*.

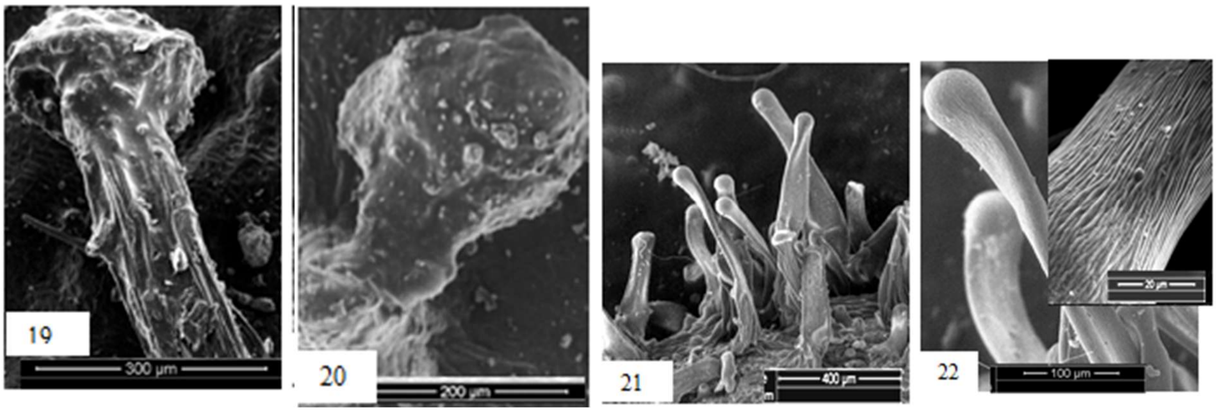


Figure 7. Some glandular hairs under a scanning electron microscope: 19-20: *G. glabra*; 21-22: *H.unisiliquosa*.
Figura 7. Alguns tricomas glandulares sob microscópio eletrônico de varredura: 19-20: *G. glabra*; 21-22: *H. unisiliquosa*.

3.2. Crystal Types

The anatomical examination of different vegetative and reproductive organs revealed the presence of two types of calcium oxalate crystals, namely druse and prismatic crystals (Figure 8).

3.2.1. Druse crystals

Druse crystals were observed exclusively in the fruit epidermis of *Colutea cilicica* and were absent in all other investigated genera (Figure 8).

3.2.2. Prismatic crystals

Prismatic crystals exhibited different shapes and distribution patterns among the studied taxa. They were observed along the leaf veins of the investigated *Onobrychis* species and *Pisum sativum*. In addition, prismatic crystals occurred in the epidermal cells of the fruit of *Coronilla scorpioides* and in the calyx epidermis of the studied *Onobrychis* species. They were also recorded in the fruit endocarp of most investigated genera. Furthermore, prismatic crystals were present in the leaf mesophyll of all studied genera, particularly above the vascular bundle of the midrib (Figure 8).

3.3. Leaf Venation Pattern

Leaf venation analysis revealed two principal venation patterns among the investigated species: acrodromous and pinnate (Figures 9–12).

A. Acrodromous pattern

The acrodromous venation pattern was observed only in *Scorpiurus muricatus*. Three perfect basal primary veins originated from the leaf base and extended towards the leaf apex. The areoles were irregular in shape, whereas the veinlets were either absent or simple, occasionally branching once and terminating in swollen ends (Figure 12).

B. Pinnate pattern

The pinnate venation pattern was recorded in the remaining studied species. In this pattern, the midrib represented the primary vein, while the laterally arranged veins constituted the secondary veins. Two subtypes of pinnate venation were recognized.

3.3.1. Camptodromous–brochidodromous pattern

This pattern was observed in the investigated species of *Astragalus*, *Glycyrrhiza*, *Colutea*, *Hippocrepis*, *Hymenocarpos*, and in *Onobrychis crista-galli*, *O. galegifolia*, *O. haussknechtii*, and *O. ptolemaica* (Figures 9–12). Secondary veins were interconnected by distinct arches, whereas tertiary veins formed a randomly reticulate network in all species except *Astragalus rhodosemius*, where they exhibited an orthogonal reticulate arrangement.

The areoles were generally polygonal, consisting of five or more sides, whereas quadrangular areoles were recorded in *Hippocrepis unisiliquosa* subsp. bisiliqua (Figure 10). Marginal venation was incomplete but looped in *A. rhodosemius*, *Colutea cilicica*, and *H. circinnatus* (Figures 9 and 10).

Veinlets also exhibited variation among the studied taxa. They were simple or branched once in *Glycyrrhiza glabra* var. *glandulifera*, *Hymenocarpos circinnatus*, and *O. ptolemaica*; branched once or twice with swollen ends in *A. rhodosemius* and *O. haussknechtii*; and branched into more than three orders in *Astragalus kahiricus* and *O. haussknechtii*.

3.3.2. Camptodromous–cladodromous pattern

This venation pattern was recorded in the remaining investigated species of *Onobrychis*. The primary vein was prominent and gradually tapered towards the leaf apex, whereas the secondary veins extended towards the leaf margin. Tertiary veins exhibited a randomly reticulate arrangement, and the areoles were polygonal with four to five or more sides. Veinlets terminated in swollen ends and branched once in *O. caput-galli* and *O. megataphros*, whereas they branched twice or more in *O. carduchorum* (Figure 10).

3.3.3. Semicraspedodromous pattern

The semicraspedodromous venation pattern was observed exclusively in *Pisum sativum* (Figure 11). In this pattern, each secondary vein divided near the margin, with one branch terminating at the leaf margin and the other joining the adjacent secondary vein. Tertiary veins formed a randomly reticulate network, and the areoles consisted of four to five sides.

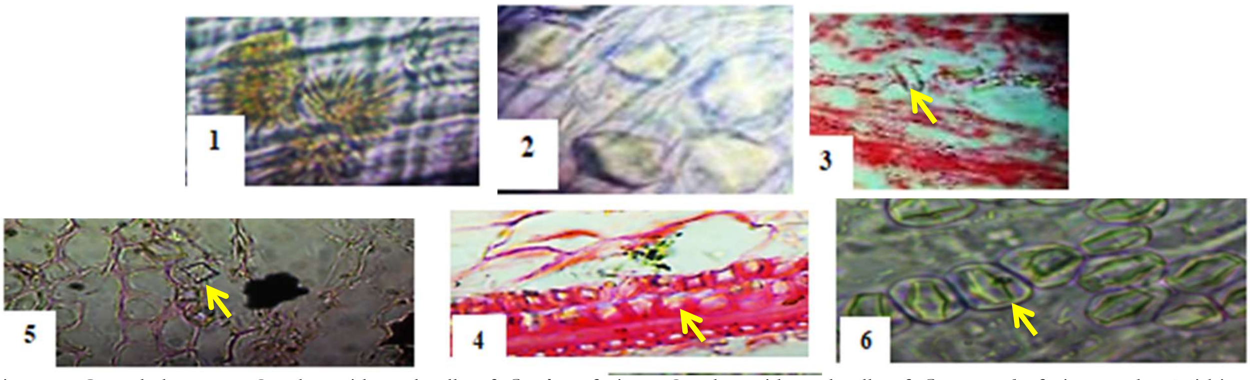


Figure 8. Crystal shapes: 1: On the epidermal cells of *C. cilicica* fruit; 2: On the epidermal cells of *C. scorpioides* fruit; 3 and 4: Within the sclerenchyma cells of the fruit endocarp of most of the studied genera; 5: In the midrib of *P. sativum* leaflets; 6: and in the midrib of the leaflets and on the epidermal cells of the sepals of *Onobrychis* species.
Figura 8. Formas de cristais: 1: Nas células epidérmicas do fruto de *C. cilicica*; 2: Nas células epidérmicas do fruto de *C. scorpioides*; 3 e 4: No interior das células do esclerênquima do endocarpo do fruto da maioria dos gêneros estudados; 5: Na nervura central dos folíolos de *P. sativum*; 6: e na nervura central dos folíolos e nas células epidérmicas das sépalas de espécies de *Onobrychis*.

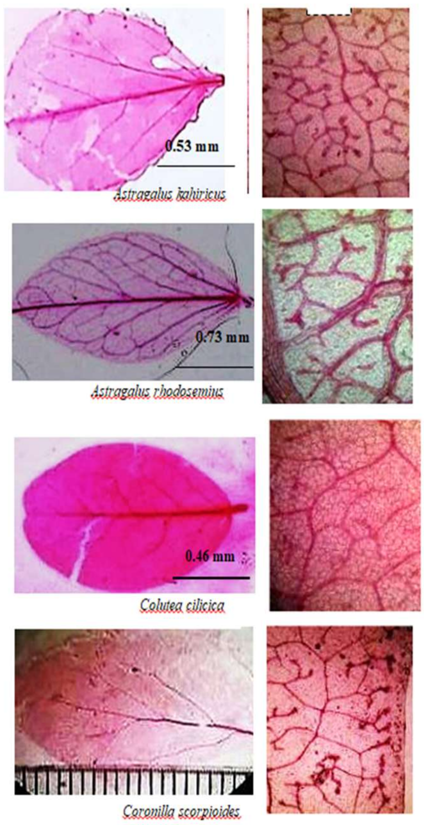
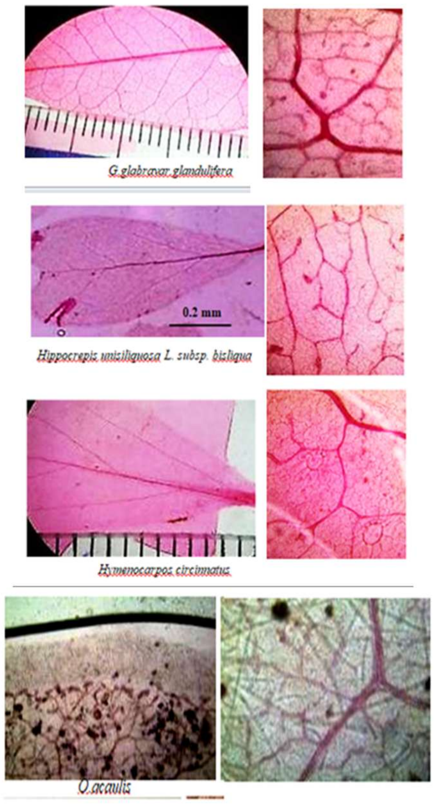


Figura 9. The variations in the characteristics of the venation patterns: A: Venation type; B: Veinlets.
Figura 9. Variações nas características dos padrões de nervação, A: Tipo de nervação; B: Vênulas.



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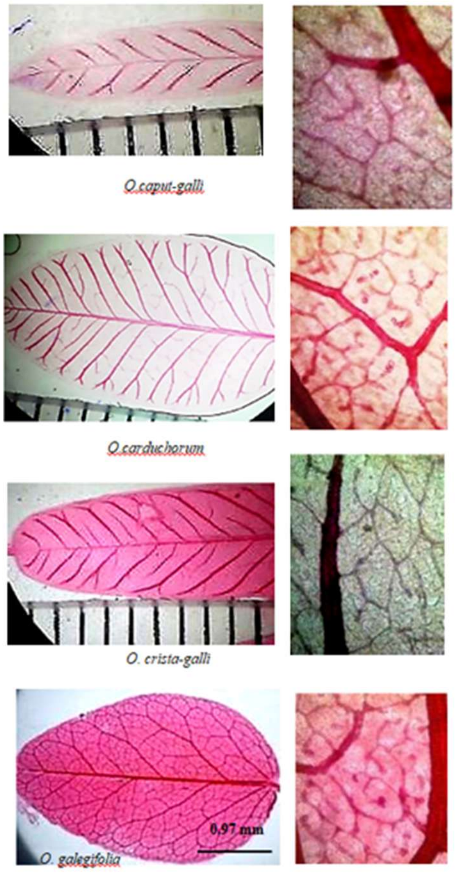

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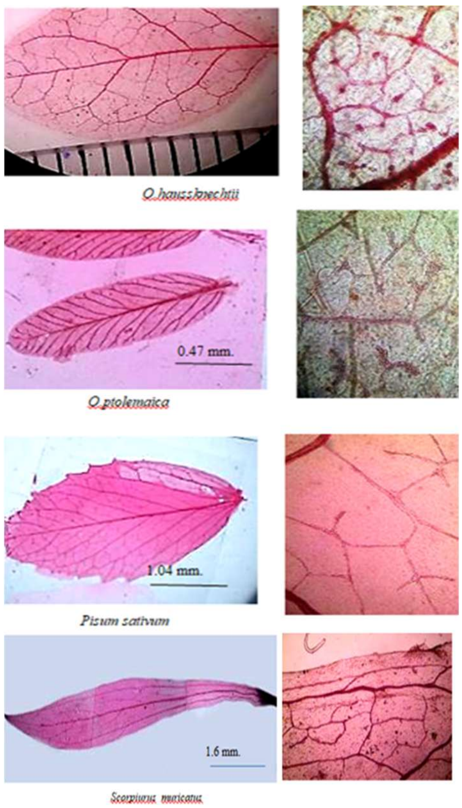

Figura 12. The variations in the characteristics of the venation patterns: A: Venation type; B: Veinlets.
Figura 12. Variações nas características dos padrões de nervação, A: Tipo de nervação; B: Vênulas.

3.4. Cross Sections of Fruits

The study included the anatomical characteristics of cross-sections of the fruit. It included specific aspects such as the general shape of the section and the layers of the pericarp. (Table 2). The exocarp in all species was characterized by a single layer of thin-walled epidermal cells, and there was variation in the average length and thickness of these cells.

Fahn (1982) explained that the general structure of the pod is uniform in most genera of the Leguminosae family. The difference may be in the thickness of the pericarp tissue, and this is what was observed in the results of the study. The pod wall, like that of other fruits, is characterized by three parts: exocarp, mesocarp and endocarp. In all studied species, the exocarp is characterized by a single layer of thin-walled epidermal cells, sometimes including hypodermis cells. The minimum cell length was 13.75 µm in *G. glabra*, and the maximum was 52.5 µm in *P. sativum.*

The mesocarp layer consists of parenchyma cells arranged in several layers. The average thickness of this region ranged from a minimum of 70 µm in *C. cilicica* to 560 µm in *G. glabra*. (Table 2). The lateral and dorsal bundles were distinguished in the fruits of some studied species, and this characteristic was of taxonomic importance in distinguishing the genera of the tribe Coronilleae as well as separating some species of the genus *Onobrychis* (Table 2).

Endocarp: This forms the lining of the pod wall cavity. The endocarp cells have thin walls, though they may be thick in some species, or the cells may be fibrous. This characteristic was identified in *Onobrychis* species and *S. muricatus*, which helped distinguish these genera from the other studied genera. Also, found that the average thickness of the endocarp is of taxonomic importance in differentiating members of the tribe Coronilleae and dividing the studied *Onobrychis* species into two groups (Table 2).

As for the structure of the seed coat. The structure of the seed coat has shown taxonomic importance in separating the species *P. sativum, H. circinnatus, S. muricatus* and among the studied species of the genus *Onobrychis* based on the length of macro-sclereids and osteosclereids found in the seed coat. (Table 2).

4. DISCUSSION

The present study demonstrated that indumentum characters constitute valuable micromorphological markers for the taxonomic discrimination of the investigated species of Papilionoideae. Variations in trichome type, length, surface ornamentation, density, and distribution among vegetative and reproductive organs provided useful diagnostic characters for distinguishing taxa at both the generic and specific levels. These findings support the view that indumentum characters represent stable taxonomic features and have long been recognized as important criteria in the classification of Leguminosae (METCALFE; CHALK, 1950; FAHN, 1982).

The investigated species exhibited considerable diversity in non-glandular trichomes, including differences in length, surface ornamentation, and distribution. Such variation agrees with previous anatomical studies indicating that trichome morphology is genetically controlled and has significant systematic value in the delimitation of closely related taxa (METCALFE; CHALK, 1950; WERKER, 2000).

In the present study, the dense and interwoven non-glandular trichomes observed on the sepals of several

Onobrychis species, together with the occurrence of whip trichomes on the fruit surface, proved to be useful diagnostic characters for distinguishing species within the genus. (PENG et al., 2022). Differences in trichome surface ornamentation also contributed to species discrimination. Smooth-surfaced trichomes were restricted to *Glycyrrhiza glabra var.* glandulifera, whereas granular-surfaced trichomes characterized *Hippocrepis circinnatus*. Similarly, papillary uniseriate trichomes were recorded in *Hippocrepis unisiliquosa* subsp. bisiliqua and most investigated Onobrychis species, indicating that trichome surface morphology provides additional taxonomic evidence when evaluated together with other micromorphological characters (FEITOZA; LIMA, 2021).

The results were consistent with the studies of Weland (1968), Hickey (1973) and Melville (1976), as well as the study of Ash et al. (1999) and confirm the importance of the venation system in the leaf as taxonomic evidence in separating genera and species. The occurrence of glandular trichomes further increased the taxonomic value of indumentum characters. The presence of peltate glandular trichomes in *G. glabra* var. *glandulifera* agrees with the observations of Metcalfe; Chalk (1950), while differences in stalk length and gland structure among the studied taxa provide additional diagnostic features that facilitate species identification. Papillae also exhibited noticeable variation in shape and distribution. Rounded papillae were consistently observed on the stigmatic surface of several genera, whereas conical papillae characterized the inner surface of the corolla. In contrast, the dense semicircular papillae covering the fruit surface of *H. unisiliquosa* subsp. *bisiliqua* represent a distinctive micromorphological feature that supports the separation of this taxon from the remaining investigated species. Although several indumentum characters were shared among different genera, the combined evaluation of trichome morphology, papillae, and their distribution patterns considerably enhanced the taxonomic resolution of the investigated taxa. Therefore, these characters should be interpreted collectively rather than individually to achieve a more reliable delimitation of species within Papilionoideae (ROTH, 1977; FAHN, 1982; WANG; GRUSAK, 2005; FEITOZA; LIMA, 2021).

The occurrence and distribution of calcium oxalate crystals have long been regarded as valuable anatomical characters in plant taxonomy because they are generally under strong genetic control and are less affected by environmental conditions than many external morphological traits (METCALFE; CHALK, 1950; FAHN, 1982). In the present study, two crystal types, namely druse and prismatic crystals, were recorded among the investigated taxa, demonstrating considerable variation in both crystal morphology and distribution (FEITOZA; LIMA, 2021).

Table 2. Comparative microanatomical characteristics of the fruit wall in the investigated Papilionoideae taxa.
Tabela 2. Características microanatômicas comparativas da parede do fruto nos táxons de Papilionoideae investigados.

Species	Exocarp thickness (μm)	No. of vascular bundles	Mesocarp thickness (μm)	Epidermal thickness (μm)	Mesocarp cell shape	Endocarp cell shape	Macrosclereid thickness (μm)	Osteosclereid thickness (μm)	Seed coat structure
Astragalus spp.	NA	NA	NA	NA	NA	NA	NA	NA	NA
Colutea cilicica	50–300	2L	NA	NA	Elongate	Unclear	12.5–25	75–162	NA
Coronilla scorpioides	62.5–225	3L + 15D	20–25	17.5–42.5	Elongated	Pentagonal	10–25	35–125	50–100
Glycyrrhiza glabra var. *glandulifera*	400–800	3D*	3.75–7.5	5–13.75	Elongated–oval	Spindle-shaped	17.5–25	87.5–175	80–130
Hippocrepis unisiliquosa subsp. *bisiliqua*	20–250	4L + 13D	10–30	17.5–55.5	Various	Winged spherical	10–52.5	22.5–70	20–250
Hymenocarpos circinnatus	42.5–250	2L + 35D	17.5–45	27.5–100	Various	Fusiform	12.5–22.5	13–27.5	25–162.5
Onobrychis acaulis	NA	NA	NA	NA	NA	NA	NA	NA	NA
Onobrychis caput-galli	NA	3L	NA	NA	Elongated	Semi-oval with spines	20–62.5	50–75	20–150
Onobrychis carduchorum	35–437.5	3L	5–20	5–30	Elongated	Semi-oval with spines	10–50	25–137.5	50–262.5
Onobrychis crista-galli	95–737.5	3L	5–12.5	10–20	Semi-spherical	Semi-oval with spines	12.5–20	27.5–37.5	NA
Onobrychis galegifolia	12.5–650	2L	15–25	15–75	Oval–elongated	Fusiform with spines	NA	NA	37.5–125
Onobrychis haussknechtii	NA	NA	NA	NA	NA	NA	NA	NA	NA
Onobrychis megataphros	NA	NA	NA	NA	NA	NA	NA	NA	NA
Onobrychis ptolemaica	250–737.5	3L	15–27.5	NA	Semi-spherical	Semi-oval with spines	12.5–37.5	30–75	45–62.5
Onobrychis schahuensis	17.5–750	NA	7.5–12.5	5–30	Elongated	Fusiform with spines	NA	NA	45–125
Pisum sativum	112.5–475.5	4–6L + 27–33D	15–35	10–87.5	Elongated	Fusiform	15.5–50	175–200	50–87.5
Scorpiurus muricatus	87.5–337.5	NA	17.5–35	15–45	Oval–elongated	Oval with spines	32.5–92.5	35–100	25–167.5

Druse crystals were restricted to the fruit epidermis of *Colutea cilicica*, making this character particularly useful for distinguishing this species from the remaining investigated taxa. The occurrence of druse crystals in only one of the studied genera suggests that this feature has potential diagnostic value at the generic level. Similar observations have been reported in previous anatomical studies, which considered crystal morphology an informative taxonomic character in Leguminosae and several other angiosperm families (SETIA et al.,1987). In contrast, prismatic crystals exhibited a wider distribution and were recorded in several vegetative and reproductive organs, including the leaf veins, calyx epidermis, fruit epidermis, endocarp, and leaf mesophyll. Their widespread occurrence among the investigated genera indicates that this crystal type is a common anatomical feature within Papilionoideae. However, differences in their distribution among organs may still provide useful supplementary characters when combined with other micromorphological and anatomical features (AL-AMERY; AL-BERMANI, 2011).

Figure 13. Characteristics of the cross-section of the fruits of some of the studied species,ac.s. = Macrosclereids, L.v.b. = Lateral vascular bundle, D.v.b. = Lateral vascular bundle, Par.t. = Parenchyma tissue, S.c.t. = Sclerenchyma tissue, G.h. = Gland hair, Ost. S. = Osteosclereids, Epi. = Epidermis cells.
Figura 13. Características da seção transversal dos frutos de algumas das espécies estudadas. Mac. = Macroesclereides; F.v.l. = Feixe vascular lateral; F.v.d. = Feixe vascular dorsal; T. par. = Tecido parenquimático; T. escl. = Tecido esclerenquimático; P. gl. = Pelo glandular; Ost. = Osteosclereides; Epi. = Células da epiderme.

The present findings indicate that crystal morphology alone is insufficient for reliable taxonomic identification because some crystal types are shared among several taxa. Nevertheless, integrating crystal characteristics with indumentum features, leaf venation patterns, and fruit anatomical characters considerably improves the discrimination of closely related genera and species within Papilionoideae (FUGARASTI et al., 2020). Leaf venation has long been recognized as one of the most stable anatomical characters in plant taxonomy because venation architecture is generally less influenced by environmental conditions than many external morphological traits. Consequently, venation characters have been widely used to distinguish taxa and to support systematic relationships within angiosperms (HICKEY, 1973; MELVILLE, 1976).

The present investigation revealed three distinct venation patterns among the studied taxa, namely acrodromous, camptodromous (brochidodromous and cladodromous), and semicraspedodromous venation. The diversity observed in these venation patterns confirms their taxonomic significance for distinguishing closely related genera and species within Papilionoideae (JORDÃO et al., 2020).

The acrodromous venation pattern was restricted to *Scorpiurus muricatus*, indicating that this character is of considerable diagnostic value for recognizing this species within the investigated taxa. Likewise, the exclusive occurrence of the semicraspedodromous venation pattern in *Pisum sativum* further demonstrates the usefulness of leaf venation as a reliable taxonomic character at the species level(KHDHAIR et al., 2024).

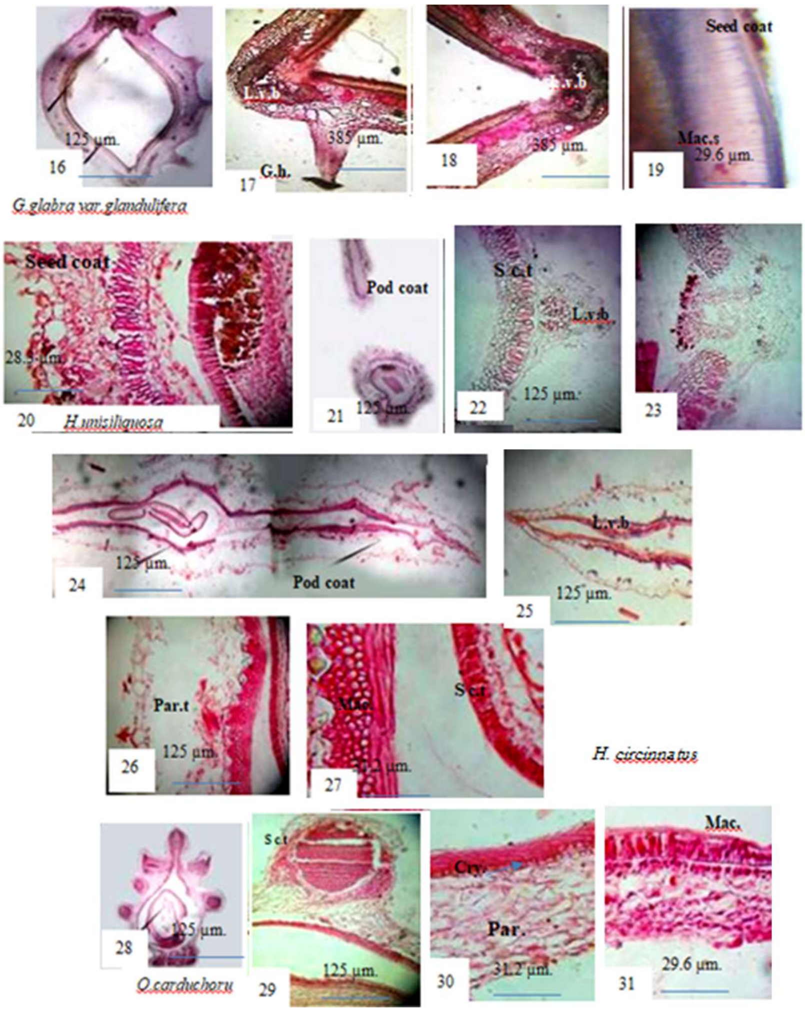

Figure 14. Characteristics of the cross-section of the fruits of some of the studied species, Mac.s.= Macrosclereids; L.v.b. = Lateral vascular bundle, D.v.b. = Lateral vascular bundle, Par.t. = Parenchyma tissue, S.c.t. = Sclerenchyma tissue, G.h. = Gland hair, Ost.S. = Osteosclereids, Epi= Epidermis cells.

Figura 14. Características da seção transversal dos frutos de algumas das espécies estudadas. Mac.s. = Macroscleređdes; L.v.b. = Feixe vascular lateral; D.v.b. = Feixe vascular lateral; Par.t. = Tecido parenquimático; S.c.t. = Tecido esclerenquimático; G.h. = Tricoma glandular; Ost.S. = Osteosclereídes; Epi = Células da epiderme.

The camptodromous venation pattern was the predominant type among the investigated taxa; however, considerable variation was observed in the arrangement of tertiary veins, the shape of areoles, marginal venation, and veinlet branching. These characters provided additional evidence for distinguishing species within the genera *Astragalus* and *Onobrychis*. In particular, the orthogonal reticulate tertiary venation observed in Astragalus rhodosemius, together with differences in veinlet branching patterns among *Astragalus* and *Onobrychis* species, proved to be informative diagnostic features (AL-KAHFAJI et al., 2023).

The present findings agree with the concepts proposed by Hickey (1973) and Melville (1976), who emphasized that characters such as tertiary venation, areole configuration, and veinlet termination possess considerable systematic value when used collectively. Similarly, recent anatomical studies on Papilionoideae have demonstrated that leaf venation provides reliable taxonomic evidence, particularly when integrated with other micromorphological and anatomical characters (YOUSEF; JASSIM, 2026).

Although some venation patterns were shared by several taxa, the combined evaluation of venation architecture, veinlet morphology, and areole characteristics substantially increased the taxonomic resolution achieved in the present study. Therefore, leaf venation should be regarded as a complementary diagnostic character and interpreted together with indumentum, crystal morphology, and fruit anatomical features for a more robust taxonomic assessment of Papilionoideae (ABDULAZEEM; JASSIM, 2018; OYEBANJI et al., 2020).

Fruit anatomical characters have long been recognized as reliable taxonomic markers in Leguminosae because they are generally stable and less influenced by environmental conditions than external morphological features (METCALFE; CHALK, 1950; FAHN, 1982; HASSAN et al., 2025). The present investigation demonstrated considerable variation in the anatomical organization of the fruit wall among the investigated taxa, particularly in the structure of the exocarp, mesocarp, endocarp, vascular bundles, and supporting tissues (AL-AMERY et al., 2024a; HASSAN et al., 2026).

The observed differences in the thickness and arrangement of the pericarp layers, together with the distribution of sclerenchymatous tissues and vascular bundles, provided valuable anatomical evidence for distinguishing the investigated genera. These structural differences are consistent with previous anatomical studies, which have emphasized that fruit anatomy represents an important source of taxonomic information in Fabaceae and contributes to species delimitation when evaluated alongside other anatomical and morphological characters (AL-AMERY et al., 2024b).

Although several anatomical features were shared among the investigated taxa, variations in tissue organization and the degree of development of the fruit wall supplied additional diagnostic characters for separating closely related species. Such observations indicate that fruit anatomy complements other micromorphological characters, particularly trichome morphology, crystal distribution, and leaf venation patterns.

It should be noted that fruit anatomical observations were conducted only for the taxa in which mature fruit material was available. Consequently, anatomical comparisons could not be extended to all investigated species. Nevertheless, the available data clearly demonstrate the taxonomic usefulness of fruit anatomical characters and support their application as complementary evidence in systematic studies of Papilionoideae (AJAO; MOTEETEE, 2020).

The integration of fruit anatomical characters with the micromorphological features investigated in the present study provides a more comprehensive basis for species identification and taxonomic delimitation than reliance on a single character alone.

5. CONCLUSIONS

The present study demonstrated that the integration of micromorphological and microanatomical characters provides a reliable basis for the taxonomic discrimination of the investigated species of Papilionoideae. Among the examined characters, indumentum, crystal morphology, leaf venation, and fruit anatomy showed different levels of taxonomic significance and collectively improved species delimitation.

Several characters proved to be particularly diagnostic. Druse crystals were recorded exclusively in the fruit epidermis of *Colutea cilicica*, whereas the semicraspedodromous venation pattern was restricted to *Pisum sativum*. Likewise, the acrodromous venation pattern was unique to Scorpiurus muricatus. Within *Onobrychis*, differences in trichome morphology, density, and distribution, together with variation in leaf venation architecture, provided valuable characters for distinguishing closely related species. In addition, fruit anatomical features supplied complementary evidence that supported the identification of the investigated taxa.

Although some characters were shared among several genera, the combined evaluation of all investigated micromorphological and microanatomical features resulted in a more robust taxonomic interpretation than the use of any single character alone. Therefore, the present study highlights the importance of integrating multiple anatomical and micromorphological datasets in taxonomic studies of Papilionoideae and provides useful diagnostic information for future systematic investigations of the subfamily.

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Data availability: The data used to verify this study's findings can be obtained by contacting the corresponding author upon request.

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