



Systematic, Morphological and Phylogenetic Features of the Family *Boraginaceae* Juss. and the Genus *Lappula* L.

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Abstract

The family *Boraginaceae* Juss. (Borage family) is one of the most morphologically diverse and large taxa of flowering plants, while the genus *Lappula* L. is among the most taxonomically complex groups in the flora of arid regions. This article summarizes the systematic position, morphological and ecological characteristics of the family *Boraginaceae*, as well as the current taxonomic and phylogenetic status of the genus *Lappula*, and provides a comparative morphological analysis of eight *Lappula* species recorded in the flora of Uzbekistan. Using a comparative-analytical approach based on classical and modern floristic literature, the APG IV system, and international taxonomic databases, the vegetative and generative organs of the genus, fruit (ereme) micromorphology,

gynobasis structure, and ecological adaptations were studied. The species reliably differ from one another primarily in stem branching, leaf shape and indumentum, corolla size, gynobasis type, cicatrix position, and the number, shape, and arrangement of spines on the eremes. *Lappula squarrosa* was found to be the most widespread and ecologically adaptable species; *L. sinaica* and *L. sessiliflora* exhibit pronounced xerophytic characteristics; while heteroeremocarpia was confirmed in *L. microcarpa* and *L. drobovii*. The results improve the diagnostic basis for the identification of the genus *Lappula* in Central Asia and contribute to assessing the systematic significance of the genus and conserving plant diversity in the flora of Uzbekistan.

Keywords: *Boraginaceae*, *Lappula*, systematics, phylogeny, morphology, fruit micromorphology, epizoochory, xerophyte, flora of Uzbekistan

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1 Introduction

The family *Boraginaceae* Juss. (Borage family) is one of the large taxa within flowering plants (*Magnoliophyta*), characterized by evolutionary complexity and considerable morphological diversity. According to modern taxonomic sources, the family comprises 155 genera and 2,686 species [1, 2]. Representatives of the family are widely distributed in temperate, subtropical, and partly tropical regions of the globe, with particularly high species diversity observed in the Mediterranean, Irano-Turanian, Central Asian, Caucasian, and arid regions of North America [3, 4]. Representatives of *Boraginaceae* have high ecological adaptability and consist mainly of xerophytic and semi-xerophytic plants; they are adapted to living under conditions of water scarcity. A thick cuticle, dense indumentum, deep taproot system, and short growing season are manifestations of these adaptations [5, 6].

In recent decades, advances in molecular phylogenetics have made it possible to revise the internal systematics of the family. Studies based on chloroplast and nuclear DNA markers have clarified the relationships among many genera and confirmed the status of the order Boraginales as an independent evolutionary unit [7–9]. The genus *Lappula* L. is one of the morphologically complex and polymorphic groups of the family *Boraginaceae*, and its representatives occupy an important place in the flora of arid regions. In the identification of species of the genus, the structure of the eremes (fruitlets), the shape and arrangement of spines, as well as the morphology of the gynobasis and cicatrix are considered the main diagnostic criteria [10, 11]. Therefore, the genus *Lappula* remains a relevant research subject for systematic botany, floristics, geobotany, and evolutionary biology.

Although the genus *Lappula* is represented by several species in the flora of Uzbekistan, the comparative morphological characteristics of these species, particularly their diagnostic features based on ereme micromorphology and gynobasis structure, have not yet been sufficiently summarized. In the available floristic sources, species descriptions are presented in a scattered manner and are poorly integrated with modern molecular-phylogenetic data. The aim of this article is to summarize the systematic, morphological, and phylogenetic characteristics of the family *Boraginaceae* and the genus *Lappula*, and to conduct a comparative morphological analysis of eight *Lappula* species recorded in the flora of Uzbekistan in order to identify their reliable diagnostic features. The results of the study contribute to assessing the taxonomic status of the genus in Central Asia and to the inventory of the flora of the region.

2 Materials and Methods

The study analyzed classical and modern floristic and monographic sources related to the family *Boraginaceae* and the genus *Lappula*: “*Flora SSSR*” [11], “*Flora Kazakhstana*” [12], “*Flora Iranica*” [3], “*Flora Tadzhikskoi SSR*” [13], “*Opredelitel rasteniy Sredney Azii*” [14], and “*O‘zbekiston floras*” [15], as well as specialized studies devoted to the genus [10]. The systematic position of the family was reviewed based on the APG IV classification system [16] and the modern family classification of the order Boraginales [8, 9]. The nomenclature and distribution of taxa were determined according to international databases — *Plants of the World Online* [2], *Angiosperm Phylogeny Website* [17], and *The Plant List* [18].

Morphological characters were studied using a comparative-analytical method. Vegetative (root system, stem branching and indumentum, leaf shape and size) and generative (inflorescence type, flower structure and size, gynobasis shape) organs were analyzed. Particular attention was paid to the micromorphological characters of the fruit — the dry coenobium and the eremes separated from it — including the disc surface, keel, number, shape and arrangement of spines, tubercles, and cicatrix type, as these have the greatest taxonomic significance in the genus. Morphological terminology was presented based on general botanical sources [19, 20] and specialized studies on fruit morphology [5, 6, 21].

A comparative analysis of the species distributed in the flora of Uzbekistan was conducted based on the descriptions provided in the floristic sources mentioned above; comparative tables were compiled for the species according to life form, vegetative and generative characters, ereme structure, and ecological group. The phylogenetic position and molecular systematics of the genus *Lappula* were described through a comparative synthesis of the results of published studies based on DNA markers [4, 7, 22].

3 Research Results

3.1 General Description of the Family *Boraginaceae*

Representatives of the family *Boraginaceae* include annual, biennial, and perennial herbs, shrubs, subshrubs, and, in some cases, trees. In the flora of Uzbekistan, the family is represented by 32 genera and approximately 120 species [15, 23].

In most representatives, the taproot system is well developed, with the main root penetrating into the deeper layers of the soil and ensuring plant survival under conditions of water scarcity. In the roots of some species, biologically active compounds, including alkaloids, flavonoids, and phenolic compounds, accumulate [5].

The stem is usually erect or semi-erect, with well-developed mechanical tissues. The covering of the stem and leaves with coarse hairs is one of the most characteristic features of the family; the hairs reduce water evaporation and protect the plant from phytophagous insects and herbivorous animals [1].

The flowers are usually bisexual, actinomorphic, and pentamerous. The number of stamens is equal to the number of corolla lobes, and they are attached to the corolla tube; the presence of a superior ovary is

characteristic of the family [24–26].

One of the important evolutionary features of the family is the scorpioid (coiled) inflorescence. In such an inflorescence, the flowers open successively; this increases pollination efficiency and ensures prolonged activity of the generative organs [27].

The division of the fruit into four one-seeded eremes is a principal diagnostic feature of the family. Spines, tubercles, and other micromorphological elements on the surface of the eremes are not only of taxonomic significance but also determine the mode of seed dispersal [6, 21].

3.2 Morphological Description of the Genus *Lappula*

The genus *Lappula* is one of the largest and taxonomically complex genera of the family *Boraginaceae*, with representatives distributed mainly in arid and semi-arid regions; they are annual, biennial, and sometimes short-lived perennial plants [11, 12]. The taproot system is well developed; the root is usually slender and robust, producing numerous lateral roots. In annual species, the root is relatively simple, whereas in biennial species (*L. microcarpa*, *L. drobovii*) it is more strongly developed. The deep root system ensures the uptake of water and mineral nutrients under drought conditions and adaptation to a xerophytic life form [28].

The stem is erect, semi-erect, or spreading; it may branch from the base, middle, or upper part. Branching may be monochasial, dichasial, or much-branched. Height varies from 5–80 cm depending on the species. The stem surface is covered with stiff, coarse, or semi-appressed hairs; the hairs are simple, setose, and sometimes located on small tubercles. Dense indumentum gives the stem a grayish-green color, reduces transpiration, reflects solar radiation, and protects against phytophagous organisms [14].

The leaves are simple, alternate, and exstipulate; their shape is linear, lanceolate, oblong-lanceolate, strap-shaped, or spatulate. Basal leaves often form a rosette. The leaf blade is usually 0.5–7 cm long and 1–14 mm wide; the margin is entire, and the apex is acute or obtuse. The leaf surface is covered with a thick cuticle and dense hairs, which reduce water evaporation; in most species, the leaves are gray or grayish-green [11].

One of the most characteristic features of the

genus is the coiled (scorpioid) inflorescence. The inflorescences are initially spirally coiled, gradually uncoiling during flowering and forming a simple or compound cyme. The fertile cymes are 3–20 cm long; in some species, they elongate considerably during fruiting. Flowering proceeds acropetally [27].



Figure 1. General habit of a representative species of the family *Boraginaceae* Juss.

The flowers are small, bisexual, actinomorphic, and pentamerous. The calyx consists of 5 fused sepals; it is 1–4 mm long during flowering, persists during fruiting, and sometimes enlarges. The petals are fused to form a tubular, campanulate, or funnel-shaped corolla; the color is blue, light blue, azure, white, or pale violet; the length is 1.5–6 mm and the diameter is 2–8 mm. There are 5 stamens, attached to the corolla tube; the anthers are bilocular and dehisce by longitudinal slits; the arrangement of the stamens is of secondary importance in species diagnosis. The gynoecium consists of two carpels; the superior ovary subsequently divides into four lobes, each developing a single seed; the style is slender, and the stigma is bilobed or entire [24].

One of the important structures characteristic of *Boraginaceae* is the gynobasis. In the genus *Lappula*, the gynobasis occurs in conical, narrowly conical, tubular, or porch-shaped forms; its shape, height, and position relative to the eremes are important diagnostic characters at the species level [5].

The fruit is of the dry coenobium type and, when mature, separates into four one-seeded eremes, making it the most important systematic organ of the genus. The eremes are ovate, oblong, triangular, or wedge-shaped, 2–4 mm long. The ereme is differentiated into a disc, keel, spines, tubercles, and cicatrix. The disc surface is smooth or tuberculate; in most species, anchor-shaped (hooked) spines develop along the margin of the disc, and their number, length, and arrangement are considered the main criteria for species identification. Tubercles are small surface projections that sometimes form the bases of spines and are widely used in micromorphological

diagnostics. The cicatrix is the scar at the point where the ereme is attached to the gynobasis; it may be basal, central, rhomboid, or triangular and is of important taxonomic significance in distinguishing *Lappula* species [6, 21].

In some representatives of the genus, heteroeremocarpia — differences in the shape or structure of eremes within a single coenobium — is observed. This characteristic is particularly pronounced in *L. microcarpa* and *L. drobovii* and is regarded as an evolutionary adaptation that ensures the dispersal of seeds by different mechanisms [5].

The following adaptations to arid environments are observed in *Lappula* representatives: dense indumentum, a thick cuticle, narrow or reduced leaves, a deep root system, a short growing season, and eremes with hooked spines adapted for epizoochorous dispersal. This combination of characteristics enables representatives of the genus to survive successfully in desert, semi-desert, and foothill regions [4, 28].

3.3 Phylogenetic Position and Molecular Systematics of the Genus *Lappula*

In traditional systematics, species and genera were distinguished mainly on the basis of morphological characters — the structure of flowers, fruits, and seeds — whereas molecular systematics makes it possible to determine the degree of evolutionary relatedness using genetic markers [7]. The genus *Lappula* has long been regarded as a group closely related to the genera *Cynoglossum*, *Hackelia*, *Eritrichium*, and *Rochelia*; however, because morphological similarity does not always reflect true phylogenetic relationships, the need for molecular studies has arisen [8].

According to the APG IV (2016) system, the family *Boraginaceae* is one of the principal representatives of the order Boraginales [16]. Although the position of this group was not clearly defined in the earlier APG II and APG III systems, subsequent molecular analyses have demonstrated it as an independent evolutionary lineage [17]. Studies based on DNA sequences have shown that the order Boraginales encompasses the families *Boraginaceae* s.s., *Heliotropiaceae*, *Cordiaceae*, *Ehretiaceae*, *Hydrophyllaceae*, and *Lennoaceae*; although these families originated from a common ancestor, they diverged into independent lineages as a result of genetic divergence [9, 22].

Molecular phylogenetic studies have established that the genus *Lappula* belongs to the tribe Cynoglosseae of the family *Boraginaceae*. In phylogenetic trees, *Lappula*

is closely positioned to the genera *Cynoglossum* L., *Hackelia* Opiz, *Eritrichium* Schrad., *Rochelia* Rchb., and *Asperugo* L.; these genera are united by similarities in fruit morphology, gynobasis structure, and the stamen apparatus [7, 22]. According to molecular data, *Lappula* and *Hackelia* diverged from a common ancestor relatively recently, and the hooked spines on the fruit surface are evolutionarily homologous structures [8].

Nuclear and chloroplast genomic markers are primarily used to study the phylogeny of the genus. ITS (Internal Transcribed Spacer) is part of nuclear ribosomal DNA and is the most widely used marker for determining interspecific relationships, intrageneric divergence, and the timing of evolutionary separation; in *Lappula* species, ITS analysis has demonstrated the monophyly of the genus [7]. The *rbcL* gene is located in the chloroplast genome and encodes the RuBisCO enzyme involved in photosynthesis; this marker is effective for determining relationships at higher taxonomic levels, including interfamily and intergeneric relationships [22]. The *matK* gene is a rapidly evolving region of chloroplast DNA and is useful for identifying species-level differences and distinguishing closely related species [22]. The *trnL-F* region, as a non-coding part of the chloroplast genome, is widely used for comparing geographic populations, determining biogeographic history, and conducting phylogenetic reconstructions [22].

Until the end of the 20th century, some representatives of the genus *Lappula* were separated by different authors into independent genera due to significant differences in fruit morphology [10]. Molecular studies, however, have established that the majority of representatives belong to a single monophyletic clade; nevertheless, additional studies on the phylogenetic position of certain species, such as *L. sinaica*, *L. semiglabrata*, and *L. drobovii*, are still ongoing [4].

Fruit micromorphology is of particular importance in the phylogeny of the genus. Studies using scanning electron microscopy (SEM) examine disc structure, tubercle shape, spine arrangement, cicatrix type, and the development of the ventral keel; these characters have been found to show a high degree of correspondence with molecular data [5, 21]. For example, in *L. squarrosa*, multiseriate anchor-shaped spines; in *L. semiglabrata*, wedge-shaped eremes; and in *L. sinaica*, eremes attached along the ventral keel are phylogenetically important diagnostic characters.

Studies based on the molecular clock method indicate that the formation of the genus *Lappula* dates back to

the Paleogene and Neogene periods [4]. The principal centers of evolution of the genus are considered to be Central Asia, the Irano-Turanian region, the Caucasus, Mongolia, and northern China; Central Asia is regarded as a secondary center of species diversification [4, 28]. Geological processes associated with the formation of the Tian Shan, Pamir-Alay, and Gissar ranges led to the emergence of new ecological niches and accelerated species differentiation. Modern next-generation sequencing (NGS) technologies are expanding opportunities for identifying cryptic species and studying speciation processes based on complete chloroplast genomes and SNP markers [22].

3.4 Comparative Analysis of *Lappula* Species in the Flora of Uzbekistan

Although the *Lappula* species recorded in the flora of Uzbekistan are morphologically similar to one another, they differ significantly in their vegetative and generative organs, particularly in the morphology of the eremes. The main diagnostic characters used for species identification include stem branching, leaf shape and indumentum, flower size, gynobasis structure, cicatrix position, and the number and shape of spines on the eremes.

Of the eight species analyzed, six are annuals (*L. squarrosa*, *L. consanguinea*, *L. sessiliflora*, *L. semiglabrata*, *L. sinaica*, *L. patula*), while two (*L. microcarpa*, *L. drobovii*) are biennial plants. In biennial species, the vegetative organs are relatively larger and more strongly developed, which is associated with their longer ontogenetic development.

Stem height and degree of branching are important for distinguishing species (Table 1). The tallest species is *L. squarrosa* (sometimes reaching up to 80 cm), whereas the shortest representatives are *L. consanguinea* and *L. semiglabrata*.

Table 1. Differences in Stem Structure among Representatives of the Genus *Lappula*

Species	Height (cm)	Stem characteristics
<i>L. squarrosa</i>	30–80	Strongly branched
<i>L. consanguinea</i>	5–15	Branched from the base
<i>L. sessiliflora</i>	5–20	Simple or sparsely branched
<i>L. semiglabrata</i>	5–15	Dichasially branched
<i>L. sinaica</i>	10–40	Arching branched
<i>L. patula</i>	10–40	Branched from the middle
<i>L. microcarpa</i>	30–50	Widely branched
<i>L. drobovii</i>	40–50	Highly branched

Leaf shape and indumentum are also important distinguishing characters. The species with lanceolate

leaves are *L. squarrosa* and *L. sinaica*; species with linear leaves are *L. sessiliflora*, *L. patula*, *L. microcarpa*, and *L. drobovii*; species with broadly linear leaves are *L. consanguinea* and *L. semiglabrata*. Although leaf indumentum is dense in all species, *L. semiglabrata* and *L. consanguinea* are distinguished by hairs located on small white tubercles.

The flowers are usually small and blue or white. The species with blue flowers are *L. squarrosa*, *L. consanguinea*, *L. sessiliflora*, *L. semiglabrata*, *L. sinaica*, *L. patula*, and *L. microcarpa*; the only species with white flowers is *L. drobovii*. The largest corolla size is observed in *L. microcarpa* (5–6 mm in diameter).

The structure of the gynobasis is an important diagnostic character from a systematic perspective and is represented in the species as follows: anchor-shaped — *L. squarrosa*; narrowly conical — *L. consanguinea*, *L. sessiliflora*, *L. semiglabrata*; porch-shaped — *L. sinaica*; short-conical — *L. patula*; tubular — *L. microcarpa* and *L. drobovii*. The most complex gynobasis structure is observed in *L. sinaica*.

The principal systematic character of the genus — the eremes — has a species-specific structure; the main diagnostic characters of the species are summarized in Table 2.

Cicatrix is the scar at the point where the ereme is attached to the gynobasis and plays an important role in species diagnosis: a basal cicatrix is observed in *L. microcarpa* and *L. drobovii*, a rhomboid cicatrix in *L. semiglabrata*, and a central cicatrix in *L. squarrosa*, whereas in *L. sinaica* the cicatrix is reduced or completely undeveloped.

Ecologically, all species exhibit xerophytic or semi-xerophytic characteristics. Strongly xerophytic species include *L. sinaica*, *L. sessiliflora*, and *L. semiglabrata*; semi-xerophytic species include *L. squarrosa*, *L. consanguinea*, and *L. patula*; species adapted to foothill and adyr regions include *L. microcarpa* and *L. drobovii* [23, 29].

4 Discussion

The results obtained show that the morphological differentiation of *Lappula* species in the flora of Uzbekistan is manifested primarily in the generative sphere — in fruit (ereme) structure, gynobasis shape, and cicatrix position. This conclusion is consistent with studies emphasizing the high taxonomic significance of fruit micromorphology in the family *Boraginaceae* [5, 6]. Since vegetative characters (stem height, branching,

Table 2. Main Diagnostic Characters of *Lappula* Species in the Flora of Uzbekistan

Species	Life form	Leaf shape	Flower color	Gynobasis type	Diagnostic Features of Eremes and the Cicatrix	Ecological group
<i>L. squarrosa</i>	Annual	Lanceolate	Blue	Anchor-shaped	Multiseriate anchor-shaped spines, strongly developed disc; cicatrix central	Semi-xerophyte
<i>L. consanguinea</i>	Annual	Broadly linear	Blue	Narrowly conical	Tuberculate surface, small conical spines, small eremes	Semi-xerophyte
<i>L. sessiliflora</i>	Annual	Linear	Blue	Narrowly conical	Sessile, eremes attached to the inflorescence axis	Strongly xerophytic
<i>L. semiglabrata</i>	Annual	Broadly linear	Blue	Narrowly conical	Wedge-shaped, glossy-surfaced eremes; cicatrix rhomboid	Strongly xerophytic
<i>L. sinaica</i>	Annual	Lanceolate	Blue	Porch-shaped	Attached to the gynobasis along the ventral keel, with a tuberculate disc; cicatrix reduced or absent	Strongly xerophytic
<i>L. patula</i>	Annual	Linear	Blue	Short-conical	Narrowly lanceolate disc; 4–6 anchor-shaped spines on each side	Semi-xerophyte
<i>L. microcarpa</i>	Biennial	Linear	Blue	Tubular	Small-fruited, with two rows of spines; heteroeremocarpia; cicatrix basal	Foothill and adyr regions
<i>L. drobovii</i>	Biennial	Linear	White	Tubular	Winged and wingless eremes; heteroeremocarpia clearly expressed; cicatrix basal	Foothill and adyr regions

and leaf shape) are often variable and dependent on environmental conditions, they should be regarded as secondary diagnostic criteria.

The development of hooked spines on the eremes is an important functional and evolutionary character of the genus: these structures ensure epizoochorous dispersal and contribute to the colonization of new territories and the survival of species in arid ecosystems [21]. The heteroeremocarpia observed in *L. microcarpa* and *L. drobovii* is interpreted as an adaptation that combines different dispersal strategies within a single plant [5].

The results of the morphological analysis are generally consistent with molecular-phylogenetic data: the position of *Lappula* within the tribe Cynoglosseae, its close relationship with *Hackelia*, and the monophyly of the genus are supported by similarities in fruit and gynobasis characters [7, 8, 22]. At the same time, the boundaries and phylogenetic position of certain species, such as *L. sinaica*, *L. semiglabrata*, and *L. drobovii*, have not been fully clarified; molecular

studies encompassing local populations of these species are necessary [4].

The combination of xerophytic characteristics, such as dense indumentum, a deep root system, narrow leaves, and a short growing season, indicates the high adaptation of representatives of the genus to the desert, semi-desert, and adyr regions of Uzbekistan. The role of Central Asia as a secondary diversification center for *Lappula* [4] explains the high morphological diversity of local species. These results have practical significance for inventorying the flora of the region, developing identification keys, and conserving biodiversity [15, 23].

Certain limitations of the study should also be noted: the analysis relies mainly on floristic sources and published morphological and molecular data. Comprehensive herbarium materials, scanning electron microscopy (SEM) analysis of eremes, and molecular studies based on local specimens are required for the final determination of species boundaries.

5 Conclusions

The *Lappula* species occurring in the flora of Uzbekistan exhibit significant morphological and ecological differences. Among the eight species analyzed, *L. squarrosa* stands out as the most widespread and ecologically adaptable species; *L. sinaica* and *L. sessiliflora* exhibit pronounced xerophytic characteristics; and heteroeremocarpi is observed in *L. microcarpa* and *L. drobovii*. The most informative characters for reliable species differentiation are the number, shape, and arrangement of spines on the eremes, the gynobasis type, and the condition of the cicatrix.

The hooked spines on the fruits of the genus's representatives ensure epizoochorous dispersal; dense indumentum, a deep root system, and a short growing season indicate their adaptation to desert and adyr regions. Thus, the genus *Lappula* L. is of significant scientific importance not only in the systematics of the family *Boraginaceae*, but also in floristics, geobotany, evolutionary botany, and ecology.

Future studies in molecular phylogenomics, population genetics, and ereme micromorphology will contribute to a deeper understanding of the evolutionary history of the genus and the conservation of biodiversity in the flora of Uzbekistan.

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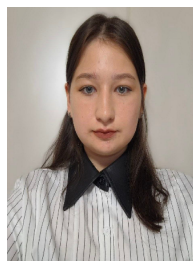
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