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**O‘ZBEKISTONDAGI MELANOCROMMYUM KENJA TURKUMINING
(AMARYLLIDACEAE, ALLIOIDEAE) QIYOSIY MORFOLOGIK ANALIZI****СРАВНИТЕЛЬНЫЙ MORFOЛОГИЧЕСКИЙ АНАЛИЗ ПОДРОДА
MELANOCROMMYUM (AMARYLLIDACEAE, ALLIOIDEAE) В УЗБЕКИСТАНЕ****THE COMPARATIVE MORPHOLOGICAL ANALYSIS OF THE SUBGENUS
MELANOCROMMYUM (AMARYLLIDACEAE, ALLIOIDEAE) IN UZBEKISTAN****Ergashov Ibroximjon Abduvali o‘g‘li¹** ¹mustaqil izlanuvchi**Zohidov G‘iyosiddin G‘ulomiddin o‘g‘li²** ²Namangan davlat universiteti tayanch doktoranti**Turidibekov Mustafobek Ma‘ruf o‘g‘li³** ³Farg‘ona davlat universiteti mustaqil tadqiqotchisi**Yusupov Ziyoviddin Olimjon o‘g‘li⁴** ⁴O‘zbekiston Respublikasi Fanlar Akademiyasi Botanika Instituti katta ilmiy hodimi PhD**Davidov Mahmudjon Adhamovich⁵** ⁵Farg‘ona davlat universiteti dotsenti, PhD**Annotatsiya**

Allium (Amaryllidaceae) turkumi taksonomik jihatdan murakkab va morfologik jihatdan xilma-xil guruh bo‘lib, *Melanocrommyum* kenja turkumi O‘rta Osiyodagi *Allium* turlarining muhim qismini tashkil qiladi. Ushbu tadqiqotda O‘zbekistondagi *Melanocrommyum* turlarining batafsil morfologik tahlili, daladan olingan namunalar va gerbariy namunalarini birlashtirgan holda taqdim etadi. Biz oltita asosiy morfologik xususiyatga e‘tibor qaratib, (changchi ipi uzunligi, gulqo‘rg‘on rangi, gul zichligi, barg ostki qismi uzunligi, barg shakli, to‘pgul zichligi) ikkala molekulyar (ITS va trnL-trnF ketma-ketliklari) ma‘lumotlardan tuzilgan filogeniyaga joylashtirdik. Bizning tahlilimiz turlar bo‘yicha sinapomorfia, gomoplaziya va evolyutsion plastisiya hususiyatlarini ochib berdi. Natijalar taksonomik tasniflarni takomillashtirish va *Melanocrommyum* sistemikasini yanada kengroq tushunishga hissa qo‘shish uchun morfologik belgilar xaritasini molekulyar ma‘lumotlar bilan birlashtirishning foydaliligini ta’kidlaydi.

Аннотация

Род *Allium* (Amaryllidaceae) — таксономически сложная и морфологически разнообразная группа, при этом подрод *Melanocrommyum* представляет значительную часть видов *Allium* Центральной Азии. В этом исследовании представлен подробный морфологический анализ видов *Melanocrommyum* в Узбекистане, объединяющий полевые образцы и гербарные образцы. Мы сосредоточились на шести ключевых морфологических признаках: длине нити, цвете околоцветника, плотности цветка, длине обвертываемого профилля, форме листа и плотности соцветия, отображенных на филогении, построенной как на молекулярных (последовательности ITS и trnL-trnF), так и на морфологических данных. Наш анализ выявляет закономерности синпоморфии, гомоплазии и эволюционной пластичности у разных видов. Результаты подчеркивают полезность объединения картирования морфологических признаков с молекулярными данными для уточнения таксономических классификаций и содействия более полному пониманию систематики *Melanocrommyum*.

Abstract

The genus *Allium* (Amaryllidaceae) is a taxonomically complex and morphologically diverse group, with the subgenus *Melanocrommyum* representing a significant portion of Central Asia's *Allium* species. This study presents a detailed morphological analysis of *Melanocrommyum* species in Uzbekistan, combining field-collected samples and herbarium specimens. We focused on six key morphological traits: filament length, perianth color, flower density, sheathy prophyll length, leaf shape, and inflorescence density mapped onto a phylogeny constructed from both molecular (ITS and trnL-trnF sequences) and morphological data. Our analysis reveals patterns of synapomorphy, homoplasy, and

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evolutionary plasticity across species. The results highlight the utility of combining morphological character mapping with molecular data to refine taxonomic classifications and contribute to a more comprehensive understanding of *Melanocrommyum* systematics.

Kalit so'zlar: *Allium*, Morfologik tahlil, Filogenetik tahlil, morfologik belgi evolyutsiyasi, Sinapomorfiya, Gomoplaziya, Taksonomiya.

Ключевые слова: *Allium*, морфологический анализ, филогенетический анализ, эволюция признаков, синапоморфия, гомоплазия, таксономия.

Key words: *Allium*, Morphological analysis, Phylogenetic analysis, Character evolution, Synapomorphy, Homoplasy, Taxonomy.

INTRODUCTION

In this study, we present a detailed morphological analysis of the subgenus *Melanocrommyum* in Uzbekistan, based on both herbarium specimens and field-collected samples. A matrix of phenotypic characters covering floral and vegetative traits is compiled and coded across representative species. These characters are then mapped and analyzed using Mesquite (Maddison and Maddison, 2019), a software platform for evolutionary analysis of discrete character states. By integrating character state mapping with hierarchical clustering and parsimony-based trait reconstruction, we aim to detect patterns of synapomorphy, homoplasy, and divergence within the subgenus. The objectives of this study are to (1) characterize the morphological diversity of *Melanocrommyum* species in Uzbekistan; (2) identify informative and evolutionarily stable characters for future taxonomic use; (3) visualize and interpret the evolutionary trends in key traits using Mesquite. This analysis not only contributes to the systematics of Central Asian *Allium* species but also provides a framework for future phylogenetic work integrating morphology with molecular data.

LITERATURE REVIEW

The genus *Allium* L. (Amaryllidaceae) comprises one of the largest monocot lineages, with more than 1000 described species exhibiting remarkable morphological and ecological diversity [1: 372]. Among its subgenera, *Melanocrommyum* stands out due to its striking spherical umbels, coriaceous bulb tunics, and colorful perianth segments features that make it both taxonomically challenging and horticulturally significant [2: 4]. This subgenus is especially well represented in arid and montane regions of Central Asia, with Uzbekistan forming a key center of endemism and species radiation [3: 17].

The classification of *Melanocrommyum* species in Uzbekistan has long been complicated by a high degree of morphological convergence and plasticity [3: 17]. Traditional taxonomic keys often rely on overlapping traits such as tepal coloration, inflorescence density, and tunic structure, which may vary within species or populations [4: 8]. This makes it difficult to establish reliable diagnostic features and evolutionary relationships based solely on external morphology. Despite these challenges, a comparative analysis of morphological characters remains essential particularly in regions where molecular data are lacking or incomplete.

METHODOLOGY

All fresh materials collected beyond Uzbekistan during field trips (between 2019 and 2024) and herbariums collected from Uzbekistan were studied from National Herbarium of Uzbekistan (TASH). Morphological descriptions of the species of subg. *Melanocrommyum* in the flora of Uzbekistan were compiled based on the works of Khassanov [3].

To investigate the phylogenetic relationship of the species of the subgenus *Melanocrommyum*, nrDNA (ITS) and chloroplast dataset (*trnL-trnF*) sequences of 37 taxa representing 12 sections were downloaded from NCBI (see Table 1) and integrated to construct a phylogenetic tree. The sequences were aligned using MEGA 7.0 [5]. The best-fitting substitution models for Bayesian inference were selected using MrModeltest 2.3 [6]. Bayesian inference employed MrBayes v.3.2.6 with a Metropolis-coupled Markov chain Monte Carlo approach and maximum likelihood employed RAxML v.8.2.10 [7] in the GTRGAMMA substitution model at the Cipres Portal (Miller et al. 2010). Phylogenetic analyses were also performed with the maximum parsimony method using PAUP* 4.0a169 [8]. The maximum parsimony bootstrap analysis was performed with heuristic search, TBR (tree bisection–reconnection) branch-swapping, 1000

bootstrap replicates, random addition sequence with ten replicates, and a maximum of 1000 trees saved per round.

Table 1

Previously published ITS, tRNA-Leu and tRNA-Phe gene accessions obtained from GenBank.

N	Species name	ITS NCBI numbers	<i>trnL-trnF</i> gene
1	<i>Allium nevskianum</i>	FM177365	FN178131
2	<i>Allium alexeianum</i>	FM177247	FN177920
3	<i>Allium majus</i>	FM177355	FN178110
4	<i>Allium protensum</i>	FM177379	FN178147
5	<i>Allium caspium subsp. baissunense</i>	FM177267	FN177946
6	<i>Allium caspium subsp. caspium</i>	FM177280	FN177962
7	<i>Allium gypsaceum</i>	FM177322	FN178029
8	<i>Allium aroides</i>	FM177259	FN177938
9	<i>Allium sarawschanicum</i>	FM177406	FN178203
10	<i>Allium komarowii</i>	FM177342	FN178083
11	<i>Allium winklerianum</i>	FM177455	FN178323
12	<i>Allium hissaricum</i>	FM177328	FN178034
13	<i>Allium macleanii</i>	FM177351	FN178109
14	<i>Allium giganteum</i>	FM177320	FN178016
15	<i>Allium altissimum</i>	FM177251	FN177925
16	<i>Allium stipitatum</i>	AJ411911	FN178234
17	<i>Allium rosenorum</i>	FM177395	FN178190
18	<i>Allium jesdianum subsp. angustitepalum</i>	FM177253	FN177932
19	<i>Allium lipskianum</i>	FM177348	FN178096
20	<i>Allium aflatunense</i>	FM177239	FN177912
21	<i>Allium alaicum</i>	FM177250	FN177919
22	<i>Allium backhousianum</i>	FM177264	FN177942
23	<i>Allium dodecadontum</i>	FM177461	FN177999
24	<i>Allium schachimardanicum</i>	FM177410	FN178210
25	<i>Allium darwasicum</i>	FM177452	FN177987
26	<i>Allium sewerzowii</i>	FM177403	FN178224
27	<i>Allium tashkentium</i>	FM177434	FN178290
28	<i>Allium severtzovioides</i>	FM177414	FN178216
29	<i>Allium costatovaginatatum</i>	FM177286	FN177974
30	<i>Allium motor (tschimganicum)</i>	FM177364	FN178118
31	<i>Allium karataviense</i>	FM177341	FN178056
32	<i>Allium isakulii subsp. balkhanicum</i>	FM177271	FN177949
33	<i>Allium taeniopetalum</i>	FM177433	FN178115
34	<i>Allium verticillatum</i>	FM177447	FN178318
35	<i>Allium cupuliferum subsp. cupuliferum</i>	FM177292	FN177980
36	<i>Allium suworowii</i>	FM177430	FN178279
37	<i>Allium tulipifolium</i>	FM177442	FN178301
38	<i>Allium oreophilum</i>	AJ411931	FN177902
39	<i>Allium kujukense</i>	AJ411947	FN177898

We traced the evolution of the following most informative taxonomic characters of the subgenus *Melanocrommyum*: 1. The length ratio of filament to tepals (longer; shorter; equal); 2. Perianth color (longer; shorter; equal); 3. Flower density (many-flowered; few-flowered); 4. Sheathy prophyll (long; short; moderately long); 5. Leaves (ovate; oblanceolate; linear-lanceolate; narrowly lanceolate; threadlike) 6. Inflorescence (dense; loose) (**Tables 2-3**). The morphological data were obtained by examining fresh material and herbarium specimens at TASH and from the literature [3; 4; 9; 10; 11]. Analyses were performed using an Mk1 evolutionary model in the software Mesquite

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v.2.0 [12]. The corresponding characteristics were mapped onto the species trees constructed from the ITS and cp integrated dataset.

Table 2

List of morphological characteristics

N	Character	Character state
1	The length ratio of filament to tepals	Longer (0); shorter (1); equal (2)
2	Perianth color	White (0); white or purplish (1); greenish (2); purplish (3)
3	Flower density	Many-flowered (0); few-flowered (1)
4	Sheathy prophyll	long(0); short (1); moderately long (2)
5	Leaves	ovate (0) oblanceolate (1); linear-lanceolate (2); narrowly lanceolate (3); threadlike (4)
6	Inflorescence	Dense (0); loose (1)

Table 3

The morphological character matrix of the species of the subgenus
Melanocrommyum and two outgroup species

No.	Species/Characteristics	1	2	3	4	5	6
1	<i>Allium nevskianum</i> Vved. ex Wendelbo	0	0	2	0	0	1
2	<i>Allium alexeianum</i> Regel	0	0	0	0	1	2
3	<i>Allium majus</i> Vved.	0	0	2	1	1	1
4	<i>Allium protensum</i> Wendelbo	0	1	0	0	1	2
5	<i>Allium caspium</i> (Pall.) M. Bieb.	0	0	1	0	0	2
6	<i>Allium gypsaceum</i> Popov & Vved.	0	1	0	0	1	2
7	<i>Allium aroides</i> Popov & Vved.	0	0	2	2	0	0
8	<i>Allium sarawschanicum</i> Regel	0	1	0	0	1	1
9	<i>Allium komarowii</i> Lipsky	0	0	2	1	1	1
10	<i>Allium winklerianum</i> Regel	0	0	2	0	0	1
11	<i>Allium hissaricum</i> Vved.	0	0	1	2	1	2
12	<i>Allium maclearii</i> J.G. Baker	0	1	0	0	1	0
13	<i>Allium giganteum</i> Regel	0	0	2	1	0	1
14	<i>Allium altissimum</i> Regel	0	1	0	0	0	1
15	<i>Allium stipitatum</i> Regel	0	1	0	0	1	2
16	<i>Allium rosenorum</i> R.M. Fritsch	0	0	1	0	0	1
17	<i>Allium jesdianum</i> subsp. <i>angustitepalum</i> (Wendelbo) F.O. Khass. & R.M. Fritsch	0	0	0	0	1	2
18	<i>Allium lipskianum</i> Vved.	0	0	2	1	1	1
19	<i>Allium aflatunense</i> B. Fedtsch.	0	0	2	2	0	0
20	<i>Allium alaicum</i> Vved.	0	0	1	0	1	1
21	<i>Allium backhousianum</i> Regel	0	0	1	0	0	1
22	<i>Allium dodecadontum</i> Vved.	0	0	2	0	1	1
23	<i>Allium schachimardanicum</i> Vved.	0	0	2	2	0	2
24	<i>Allium darwasicum</i> Regel	0	0	1	0	1	2
25	<i>Allium sewerzowii</i> Regel	0	0	1	0	0	1
26	<i>Allium taschkenticum</i> F.O. Khass	1	1	1	0	0	2
27	<i>Allium severtzovioides</i> R.M. Fritsch	0	1	2	0	1	2
28	<i>Allium costatovaginatatum</i> Kamelin & Levichev	1	1	1	0	0	0
29	<i>Allium tschimganicum</i> B. Fedtsch. ex Popov	2	2	2	2	2	0
30	<i>Allium karataviense</i> Regel	0	1	0	1	1	0
31	<i>Allium isakulii</i> subsp. <i>nuratense</i> (Kamelin) R.M. Fritsch & F.O. Khass.	1	3	1	1	2	1
32	<i>Allium taeniopetalum</i> subsp. <i>taeniopetalum</i> Popov	1	3	0	0	3	1

	& Vved.						
33	<i>Allium verticillatum</i> (Regel) Regel	0	3	0	0	4	1
34	<i>Allium cupuliferum</i> Regel	1	3	1	1	2	1
35	<i>Allium suworowii</i> Regel	1	3	0	1	2	0
36	<i>Allium tulipifolium</i> Ledeb.	1	3	0	1	2	1
37	<i>Allium oreophilum</i> C.A. Mey.	1	3	0	1	1	1
38	<i>Allium kujukense</i> Vved.	1	3	1	1	4	1

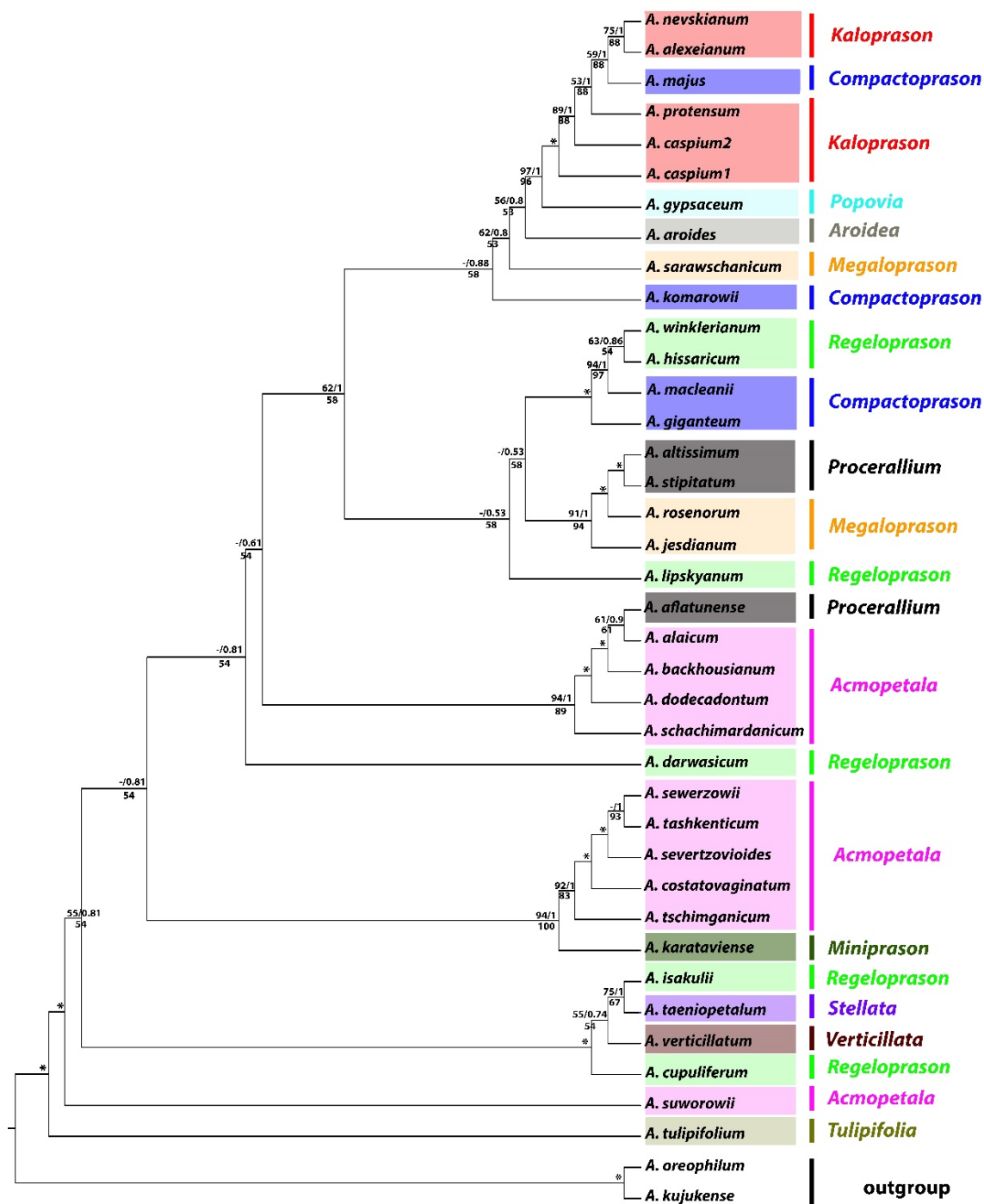


Fig. 1. The tree was inferred from the combination of ITS and *trnL-trnF* gene and was constructed with Maximum likelihood / maximum parsimony, which are given on each branch; Bayesian inference posterior probability is be—low branches. *Maximum support in all three analyses or maximum support value for only one or two methods

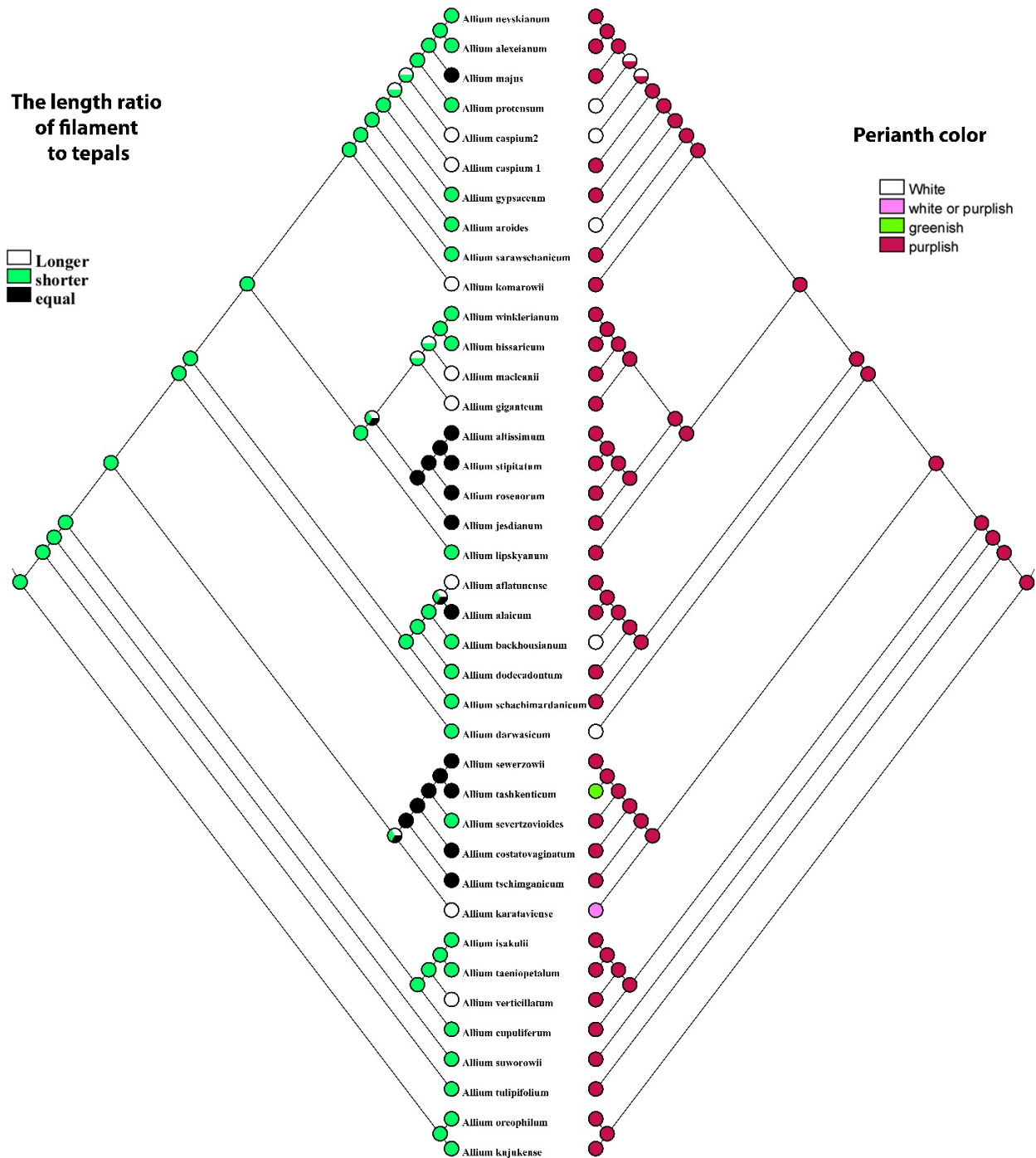


Fig 2. Evolutionary history of characteristics of selected two morphological characters in subg. *Melanocrommyum* based on the Likelihood tree obtained from the cp and nrDNA datasets. The character state at the node of subg. *Melanocrommyum* indicates the ancestral state of subg. *Melanocrommyum*

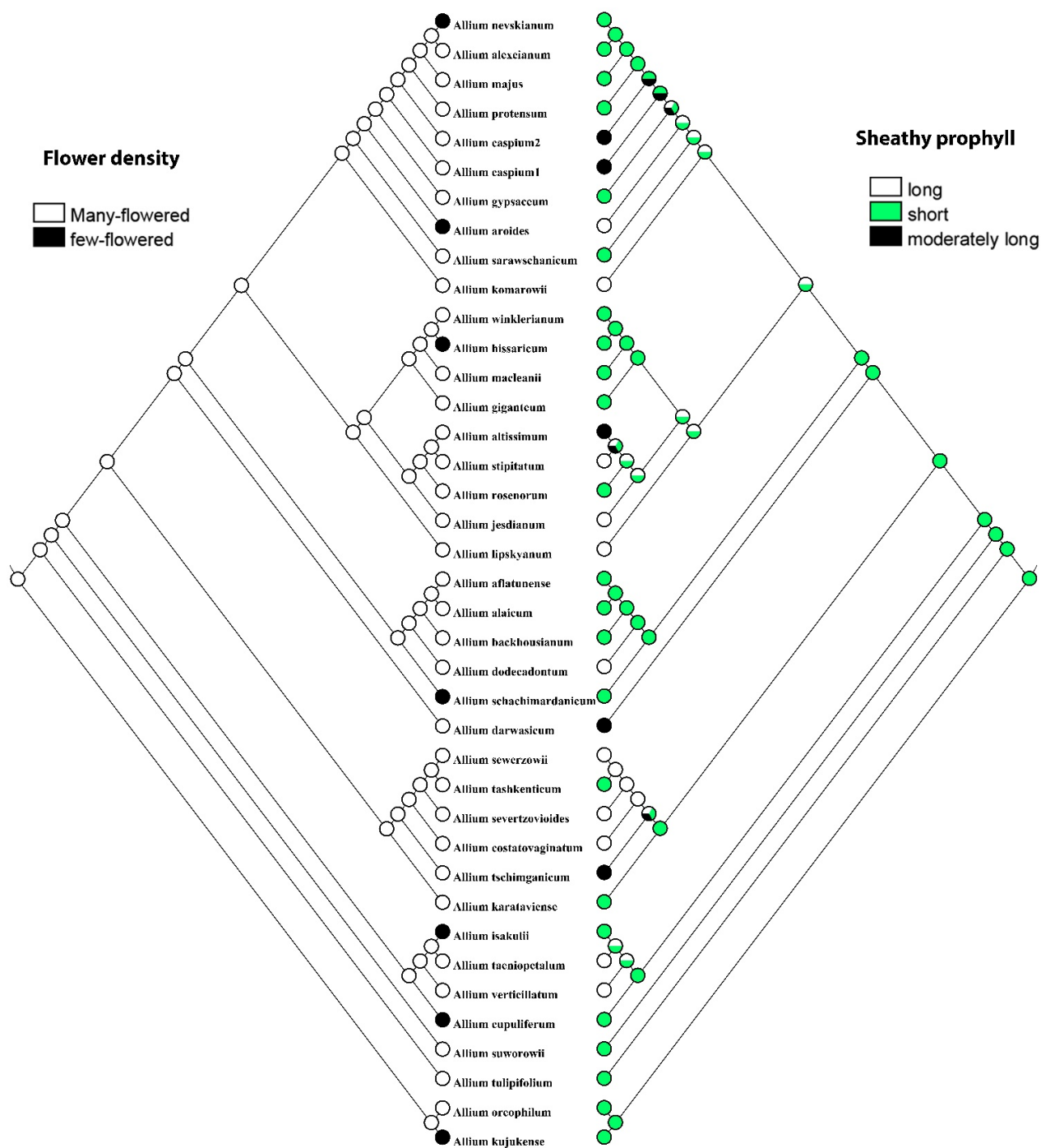


Fig 3. Evolutionary history of characteristics of selected two morphological characters in subg. *Melanocrommyum* based on the Likelihood tree obtained from the cp and nrDNA datasets. The character state at the node of subg. *Melanocrommyum* indicates the ancestral state of subg. *Melanocrommyum*

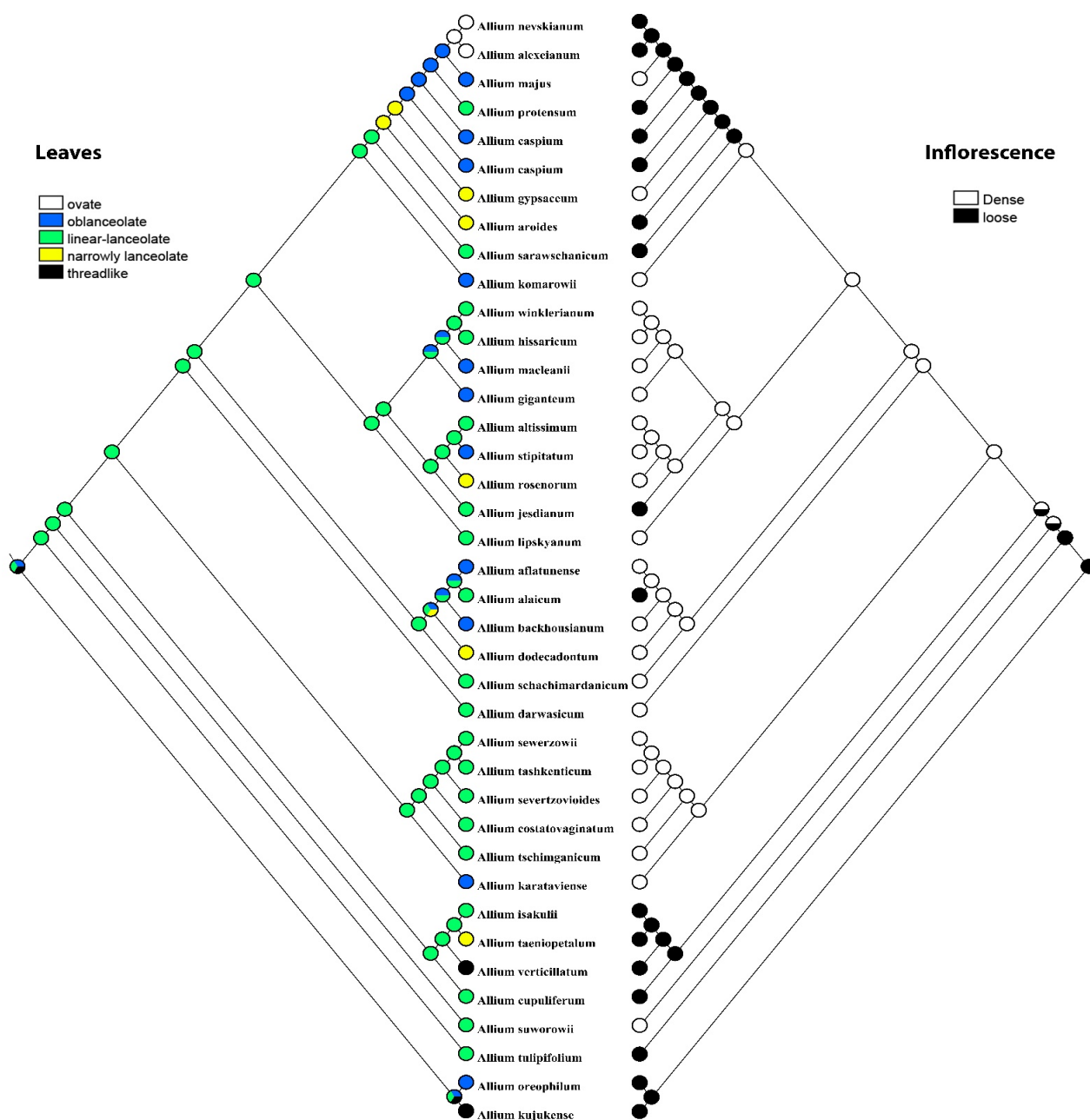


Fig 4. Evolutionary history of characteristics of selected two morphological characters in subg. *Melanocrommyum* based on the Likelihood tree obtained from the cp and nrDNA datasets. The character state at the node of subg. *Melanocrommyum* indicates the ancestral state of subg. *Melanocrommyum*.

RESULTS AND DISCUSSIONS

The cladogram (Fig. 1) presents the phylogenetic relationships among 37 species of the subgenus *Melanocrommyum*, based on a combined morphological character dataset analyzed using parsimony and likelihood methods. The analysis reveals several well-supported clades corresponding to established taxonomic sections within *Melanocrommyum*, while also highlighting areas of morphological convergence and taxonomic ambiguity. According to the previous studies [13; 14] the results from chloroplast *trnL-trnF* sequence analysis showed a congruence with outcome of nuclear rDNA ITS data. Thus, the sequences of nuclear DNA (ITS region) and plastid datasets (*trnL-trnF* gene) were integrated to construct the phylogenetic tree of the species of the subgenus. Gurushidze et al. [13; 14] found the monophyly of the subgenus and most sections were para- or sometimes polyphyletic. In our analysis we also confirm the monophyly of the subgenus and some sections are also para- or polyphyletic for the taxa distributed in Uzbekistan (Fig. 1).

Morphological character evolution across *Allium* subgenus *Melanocrommyum* was analyzed through trait mapping in Mesquite, revealing both conserved and highly labile traits within the species. Six traits—filament length, perianth color, flower density, sheathy prophyll length, leaf shape, and inflorescence density were scored across 39 species and visualized on a reference phylogeny. The findings highlight notable patterns of synapomorphy, convergence, and morphological plasticity that inform both systematics and evolutionary understanding of this taxonomically complex group.

The length ratio of filaments to tepals (Fig. 2, left) exhibits moderate variation across clades. The ancestral state reconstruction suggests that shorter filaments are likely the plesiomorphic state, found in many early-diverging taxa including *A. tulipifolium*, *A. suworowii*. However, the "equal length" state evolved independently multiple times most notably within *Procerallium* and *Acmopetala* lineages (e.g., *A. stipitatum*, *A. altissimum*), indicating parallel evolution. Conversely, longer filaments are a rarer, derived trait present only in a few taxa, such as *A. caspium* and *A. karataviense*. These patterns suggest that filament length may evolve in response to reproductive pressures such as pollinator type or floral architecture (Jang et al., 2008), but its taxonomic utility remains limited due to its homoplastic distribution.

Perianth color (Fig. 2, right) displays a more conservative evolutionary pattern. The purplish perianth state dominates the tree, occurring in the majority of species across different clades, indicating its likely ancestral status. Only a few lineages deviate, such as *A. tashkenticum* (greenish), *A. karataviense* (white/purplish), and *A. aroides* (white). These exceptions may reflect ecological specialization or local adaptation to light conditions and pollinator spectra, as proposed by Fritsch and Friesen [15]. Despite these outliers, perianth pigmentation is largely conserved and phylogenetically informative, aligning well with major clades.

Flower density (Fig. 3, left), categorized as many-flowered or few-flowered, shows relatively limited phylogenetic signal. Most species exhibit many-flowered inflorescences, with a few exceptions such as *A. cupuliferum*, *A. schachimardanicum*, *A. isakulii* which display fewer flowers per umbel. These few-flowered species are scattered across unrelated clades, suggesting independent derivation. This supports previous claims that flower number is often influenced by environmental or physiological factors, making it probably less reliable for systematics [1].

Sheathy prophyll length (Fig. 3, right), scored as short, moderately long, or long, displays intermediate levels of variation. While the long and short categories appear throughout the phylogeny, moderately long prophylls are more restricted and seem to emerge independently in specific groups such as *A. caspium* and *A. altissimum*. The plasticity in this character reduces its diagnostic value, although its variation within clades may still offer supportive characters when used in combination.

One of the most variable and evolutionarily informative traits is leaf shape (Fig. 4, left), categorized into six states: ovate, oblanceolate, linear-lanceolate, narrowly lanceolate, oblong-lanceolate, and threadlike. Threadlike leaves are particularly distinct and restricted to only two taxa *A. verticillatum* and outgroup species, *A. kujukense*, indicating strong character specialization. Linear-lanceolate and narrowly lanceolate leaves occur more broadly but show clade-level consistency, especially within *Procerallium* and *Regeloprason* clusters. The high degree of differentiation and moderate phylogenetic constraint make leaf shape a potentially powerful character in sectional delimitation, consistent with findings by Khassanov & Fritsch [16].

Inflorescence density (Fig. 4, right), scored as dense or loose, exhibits strong evolutionary lability. Loose inflorescences occur across unrelated species, pointing to repeated independent derivation. This character likely responds to ecological variables such as wind exposure or pollinator access and has low taxonomic consistency across clades. As such, while it may carry ecological significance, its role in classification should be cautious and context-dependent. Taken together, these morphological traits reveal that while some characters like perianth color and leaf shape show phylogenetic signal and clade-level conservation, others such as filament length, flower density, and inflorescence structure are evolutionarily labile and homoplastic. These findings echo earlier studies emphasizing the limitations of single-trait taxonomy in *Melanocrommyum* and the importance of multivariate and integrative approaches [14]. Morphological character mapping via tools like Mesquite thus remains essential in highlighting trait stability versus variability, supporting both evolutionary interpretation and careful taxonomic refinement.

CONCLUSION

The phylogenetic and morphological analyses of *Allium* subgenus *Melanocrommyum* underscore both the complexity and evolutionary dynamism of this group. While the monophyly of the subgenus is well supported, several sections remain para- or polyphyletic, reflecting historical taxonomic ambiguities. Trait mapping reveals that certain morphological characters such as perianth color and leaf shape retain strong phylogenetic signals and offer value for sectional delimitation, whereas others like filament length, flower density, and inflorescence density are highly homoplastic and ecologically labile. These findings highlight the necessity of integrating molecular phylogenetics with multivariate morphological analyses to achieve a more robust and nuanced classification framework for this taxonomically intricate lineage.

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