BOTANIKA INSTITUTI HUZURIDAGI ILMIY DARAJALAR BERUVCHI DSc.05/2025.27.12.B.23.01.M RAQAMLI ILMIY KENGASH

BOTANIKA INSTITUTI

YUSUPOV ZIYOVIDDIN OLIMJON O‘G‘LI

ALLIUM L. (AMARYLLIDACEAE) TURKUMINING FILOGENIYASI, BIOGEOGRAFIYASI VA EVOLYUTSIYASI (MARKAZIY OSIYO MISOLIDA)

03.00.05 – Botanika

BIOLOGIYA FANLARI BO‘YICHA FAN DOKTORI (DSc) DISSERTATSIYASI AVTOREFERATI

Toshkent – 2026

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Yusupov Ziyoviddin Olimjon o‘gli
Allium L. (Amaryllidaceae) turkumining filogeniyasi, biogeografiyasi va evolyutsiyasi (Markaziy Osiyo misolida) 3

Yusupov Ziyoviddin Olimjon ugli
Molecular phylogeny, biogeography and evolution of *Allium* L. (Amaryllidaceae) with a focus on Central Asia 27

Юсупов Зиёвиддин Олимжон угли
Молекулярная филогения, биогеография и эволюция *Allium* L. (Amaryllidaceae) с акцентом на Центральную Азию 51

E’lon qilingan ishlar ro‘yhati
Список опубликованных работ
List of published *w*orks 55

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Toshkent – 2026

Biologiya fanlari bo'yicha fan doktori (DSc) dissertatsiyasi mavzusi O'zbekiston Respublikasi Oliy ta'lim, fan va innovatsiyalar vazirligi huzuridagi Oliy attestatsiya komissiyasida B2025.2.DSc/B267 raqam bilan ro'yxatga olingan.

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Dissertatsiya himoyasi Botanika instituti huzuridagi DSc.05/2025.27.12.B.23.01.M raqamli Ilmiy kengashning 2026 yil "10" mart kuni soat 14:00 dagi majlisida bo'lib o'tadi. (Manzil: 100125, Toshkent shahri, Do'rmon yo'li ko'chasi, 32-uy. Botanika instituti majlislar zali. Tel.: (+99871) 262-37-95, E-mail: botany@academy.uz).

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Dissertatsiya avtoreferati 2026 yil «24» fevral kuni tarqatildi.

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KIRISH (fan doktori (DSc) dissertatsiyasi annotatsiyasi)

Dissertatsiya mavzusining dolzarbligi va zaruriyati. Hozirgi kunda biologiya fanining ustuvor yo‘nalishlaridan biri o‘simliklarning filogenetik aloqalari, evolyutsion tarixi va biogeografik shakllanish qonuniyatlarini zamonaviy molekulyar-genetik hamda filogenomik yondashuvlar asosida o‘rganishdan iboratdir. Genom texnologiyalarining jadal rivojlanishi, yuqori aniqlikdagi DNK sekvensiyalash usullarining keng qo‘llanilishi va bioinformatik tahlil imkoniyatlarining ortib borishi o‘simliklar evolyutsiyasining murakkab jarayonlarini yanada chuqurroq va ishonchliroq talqin etish imkonini bermoqda. Bu esa an’anaviy morfologik va anatomik belgilarga asoslangan tasniflarni qayta ko‘rib chiqish, turkum va tur darajasidagi filogenetik munosabatlarni aniqlashtirish zaruratini yuzaga keltirmoqda.

Markaziy Osiyo hududi o‘simliklar xilma-xilligi va taksonomik murakkabligi bilan ajralib turadigan muhim biogeografik mintaqalardan biri bo‘lib, hudud geologik rivojlanish tarixining murakkabligi, tog‘ va cho‘l ekotizimlarining uyg‘unlashuvi hamda tarixiy paleoiqlimiy jarayonlar, jumladan oxirgi muzli davri turkumlari va turkumosti taksonlarning evolyutsion shakllanishi, diversifikatsiyasi va areallarining qayta tuzilishida muhim rol o‘ynagan. Ushbu mintaqa florasini to‘liq turkum va turkumosti darajasida filogenetik, morfologik hamda molekulyar-genetik yondashuvlar asosida to’liq o‘rganish yuqori taksonlar darajasidagi evolyutsion munosabatlarni aniqlashtirish, morfologik belgilar va adaptiv xususiyatlarning evolyutsion shakllanishini talqin etish hamda ekologik omillar bilan bog‘liq moslashuv mexanizmlarini tushuntirish imkonini beradi. Bu esa zamonaviy botanika va evolyutsion biologiya fanlari uchun muhim ilmiy ahamiyat kasb etadi.

O‘zbekiston Respublikasida biologik xilma-xillikni o‘rganish va saqlab qolishga alohida e’tibor qaratilmoqda. Respublika hududi o‘simliklarini zamonaviy molekulyar-genetik yondashuvlar asosida inventarizatsiya qilish floraning tuzilishi va evolyutsion aloqalarini aniqlash uchun muhim ilmiy asos yaratadi. Molekulyar va filogenetik ma’lumotlar iqlim o‘zgarishi sharoitida hudud florasini monitoring qilish, tezkor va ishonchli tur identifikatsiyasini amalga oshirish hamda biologik resurslarni muhofaza qilishga qaratilgan harakatlar strategiyasini ilmiy jihatdan ta’minlashda muhim ahamiyat kasb etadi.

O‘zbekiston Respublikasi Prezidentining 2017-yil 4-sentyabrdagi PQ-3256-son «O‘zbekiston Respublikasi Fanlar Akademiyasi Botanika instituti va Zoologiya instituti faoliyatini tashkil etish chora-tadbirlari to‘g‘risida»gi Qarori[1], O‘zbekiston Respublikasi Prezidentining 2022-yil 20-maydagi PQ-251-son «Dorivor o‘simliklarni madaniy holda yetishtirish va qayta ishlash hamda davolashda ulardan keng foydalanishni tashkil etish chora-tadbirlari to‘g‘risida»gi Qarori[2], O‘zbekiston

[1] O‘zbekiston Respublikasi Prezidentining 2017-yil 4-sentyabrdagi PQ-3256-son «O‘zbekiston Respublikasi Fanlar Akademiyasi Botanika instituti va Zoologiya instituti faoliyatini tashkil etish chora-tadbirlari to‘g‘risida»gi Qarori.

[2] O‘zbekiston Respublikasi Prezidentining 2022-yil 20-maydagi PQ-251-son «Dorivor o‘simliklarni madaniy holda yetishtirish va qayta ishlash hamda davolashda ulardan keng foydalanishni tashkil etish chora-tadbirlari to‘g‘risida»gi Qarori

Respublikasi Konstitutsiyasining (yangi tahrirdagi) 49 va 115 moddalarida oid ayrim vazifalar hamda boshqa me‘yoriy-huquqiy hujjatlarda belgilangan vazifalarni amalga oshirishda ushbu dissertatsiya tadqiqoti muayyan darajada xizmat qiladi.

Tadqiqotning respublika fan va texnologiyalari rivojlanishining asosiy ustuvor yo‘nalishlariga mosligi. Mazkur tadqiqot respublika fan va texnologiyalar rivojlanishining V. «Qishloq xo‘jaligi, biotexnologiya, ekologiya va atrof-muhit muhofazasi» ustuvor yo‘nalishiga muvofiq bajarilgan.

Dissertatsiya mavzusi bo‘yicha xorijiy ilmiy-tadqiqotlar sharhi. *Allium* L. turkumini o‘rganish bo‘yicha klassik va zamonaviy tadqiqotlar dunyo bo‘ylab yetakchi ilmiy markazlar va oliy ta’lim muassasalarida olib borilgan bo‘lib, bu turkumining taksonomiyasi, molekulyar filogeniya, biogeografiya va evolyutsiyasini tushunishga katta hissa qo‘shgan. Ushbu tadqiqotlarda ishtirok etgan taniqli universitetlar va ilmiy tashkilotlar quyidagilardan iborat: O‘simlik genetik resurslarining taksonomiyasi bo‘limi - Leibniz instituti (IPK), Germaniya; Osnabruk universitetining botanika bog‘i (Germaniya); Sichuan universiteti (Xitoy); Changvon milliy universiteti (Koreya Respublikasi); Xishuangbanna Tropical botanika bog’i (Xitoy); Moskva davlat universiteti (Rossiya); Kunming Botanika instituti (Xitoy).[3]

Allium turkumining molekulyar taksonomiyasi oid jahonda olib borilgan tadqiqotlar natijasida qator, jumladan, quyidagi natijalar olingan: turkum ITS geni asosida o‘rganilib, turkumostilar va seksiyalar darajasida tasniflangan (Germaniya, Osnabrück University), Keyinchalik 39 ta turining to‘liq xloroplast genomlari asosida filogenomik tahlillar o‘tkazilib, turkumning kelib chiqish yoshi 34–47 mln yil deb aniqlangan (Xitoy, Sichuan University). Biogeografik tadqiqotlar *Allium* turlarining Eski dunyodan Yangi dunyoga Sharqiy Osiyo va Yevropa orqali tarqalganligini ko‘rsatgan (Xitoy, Sichuan University; Germaniya, Leibniz Institute), Shuningdek, urug‘ epidermis hujayralarining mikromorfologiyasi O‘rta Osiyoga mansub 48 ta tur misolida o‘rganilib, uning taksonomik ahamiyati isbotlangan (Koreya, Changwon University).

Bugungi kunda *Allium* turkumining molekulyar taksonomiyasi, evolyutsiyasi va biogeografiyasi bo‘yicha xorijiy ilmiy tadqiqotlar asosan quyidagi ustuvor yo‘nalishlarda olib borilmoqda: filogenomik yondashuvlar asosida (to‘liq xloroplast genomlari va yadro genomlari) turkum ichidagi evolyutsion munosabatlarni aniqlash; molekulyar va morfologik belgilarni integratsiyalash orqali taksonomik nomuvofiqliklarni bartaraf etish; biogeografik modellashtirish yordamida *Allium* turlarining kelib chiqishi va tarixiy migratsiya yo‘llarini rekonstruksiya qilish; mikromorfologik belgilar (urug‘ shakli va epidermis hujayralari) ning taksonomik ahamiyatini aniqlash; gibridizatsiya va poliploidiya jarayonlarining *Allium* evolyutsiyasiga ta’sirini baholash.

Muammoning o‘rganilganlik darajasi. *Allium* turkumining ilmiy o‘rganilishi XVIII asrga borib taqaladi. Uning taksonomik asoslari dastlab C. Linnaeus (1753)

[3] Dissertatsiyaning mavzusi bo’yicha ilmiy tadqiqotlar sharhi http://www.works.doklad.ru, http://www.works.doklad.ru, http://www.dissercat.com, http://www.researchgate.net, http://webofscience.com va boshqa manbalar asosida ishlab chiqilgan.

tomonidan yaratilgan. Keyingi davrlarda J.G. Baker (1874, 1875, 1892); E. Regel (1879); P.E. Boissier (1882); E. Regel & A. Herder (1884); A. Engler (1892); A.A. Grossheim (1940); V.I. Grubov (1955); R.V. Kamelin (1973); P. Hanelt (1992); N. Friesen (2007); F.O‘. Hassanov (2008) va boshqa tadqiqotchilar tomonidan *Allium* turkumiga mansub turlarning tasniifi va tipifikatsiyasi tizimli ravishda amalga oshirilgan. Ushbu ishlarda piyozcha va ildizpoya tuzilishi, barg morfologiyasi, gulkosa va gulqo‘rg‘on elementlari, changchi hamda urug‘ belgilari kabi asosiy diagnostik morfologik xususiyatlar majmuasi asosida turkumning ichki tasnifi shakllantirilib, turkumosti va seksiyalar darajasida turli klassifikatsiya modellari taklif etilgan.

Keyingi bosqichlarda *Allium* turkumiga mansub turlarning turli geografik mintaqalarda tarqalishi, ularning molekulyar filogeniyasi, biogeografik shakllanishi va evolyutsion rivojlanish yo‘nalishlari an’anaviy morfologik yondashuvlar bilan bir qatorda zamonaviy molekulyar-genetik va filogenomik usullar asosida keng o‘rganilgan. Ushbu tadqiqotlarda yadroviy va plastid genom markerlari asosida turlararo filogenetik munosabatlar, asosiy evolyutsion liniyalar hamda tarixiy migratsiya va diversifikatsiya jarayonlarini talqin etishga alohida e’tibor qaratilgan (Hanelt, 1992; Fritsch & Friesen, 2002; Friesen et al., 2006, 2014; Gurushidze et al., 2008, 2010; Blattner et al., 2008; Li et al., 2010, 2016; Cheryomushkina, 2012; Nguyen et al., 2013; Xie et al., 2019; Yusupov et al., 2021; Han et al., 2022; Zhou et al., 2023).

Markaziy Osiyo misolida *Allium* turkumining filogeniyasi, biogeografiyasi va evolyutsiyasini o‘rganishga qaratilgan tadqiqotlarda ham mintaqa florasiga oid muhim ilmiy adabiyotlardan keng foydalanilgan. Xususan, Markaziy Osiyo hududida tarqalgan *Allium* turlarining taksonomik tuzilishi (Kamelin, 1973; Khassanov, 2008, 2018, 2022; Tojibaev et al., 2014; Fritsch, 2016); evolyutsion aloqalari (Qin et al., 2010; Friesen et al., 2006, 2014, 2024, 2025; Choi et al., 2012; Tan et al., 2017; Basamunkh et al., 2020; Dong et al., 2022) va tarixiy tarqalishini yorituvchi klassik va zamonaviy ishlar morfologik hamda molekulyar-filogenetik talqinlar uchun muhim metodologik asos bo‘lib xizmat qilgan (Cheryomushkina, 2004; Friesen et al., 2007; Gurushidze et al., 2008, 2010).

Shu bilan birga, hozirgi kungacha Markaziy Osiyo florasidagi tarqalgan *Allium* turkumiga mansub turlar ishtirokida tuzilgan filogenetik rekonstruksiyalar va ularga integratsiya qilingan morfologik belgilar turlar sonining yetarli darajada qamrab olinmaganligi sababli mintaqa florasining evolyutsion va biogeografik rivojlanish jarayonlarini to‘liq ochib bera olmagan. Mazkur holat Markaziy Osiyoda tarqalgan *Allium* turlarini keng qamrab olgan kompleks filogenetik va evolyutsion tadqiqotlarni amalga oshirish zaruratini ko‘rsatadi. Bunday yondashuv zamonaviy molekulyar usullar asosida *Allium* turkumining filogenetik tuzilishi, evolyutsion rivojlanish yo‘nalishlari hamda turli geologik davrlarda yuz bergan divergentsiya jarayonlarini chuqur va ishonchli tahlil qilish uchun mustahkam ilmiy poydevor yaratib, ilmiy va amaliy ahamiyat kasb etadi.

Tadqiqotning dissertatsiya bajarilayotgan ilmiy-tadqiqot muassasining ilmiy-tadqiqot ishlari rejalari bilan bog‘liqligi. Mazkur dissertatsiya tadqiqoti Fanlar akademiyasi Botanika instituti Molekulyar filogeniya va biogeografiya

laboratoriyasi tomonidan amalga oshirilgan “PFI-5 Hayot daraxti: O‘zbekiston bir urug‘pallalilari” (2020-2024) va Xalqaro O‘zbekiston-Belorussiya ilmiy-texnik dasturi "Belorussiya va O‘zbekistonning kamyob va yo‘qolib ketish xavfi ostida bo‘lgan turlarining genetik inventarizatsiyasi DNK barkodlash texnologiyasidan foydalanib o‘tkazish" (Loyiha raqami: MRB-AN-2019-30) davlat fundamental davlat dasturlari hamda Toshkent va Kunming botanika bog‘larida “Global *Allium* Garden (Tashkent-Kunming centers)” tashkil etilishi bo‘yicha amaliy loyihalar doirasida amalga oshirilgan.

Tadqiqotning maqsadi *Allium* turkumiga mansub turlar o‘rtasidagi evolyutsion aloqalar, filogenetik tuzilma va diversifikatsiya jarayonlarini aniqlash hamda ularning mikromorfologik belgilari asosida taksonomik tizimda qo‘llash imkoniyatlarini asoslashdan iborat.

Tadqiqotning vazifalari:

urug‘ mikromorfologiyasini o‘rganish asosida *Allium* turkumi turlari uchun yangi aniqlagich kalitni ishlab chiqish va olingan morfologik belgilarni turkumning molekulyar filogenetik daraxtiga integratsiya qilish;

molekulyar tahlillar va urug‘ morfologiyasi bo‘yicha ma’lumotlarni integratsiya qilish asosida *Allium* turkumi turlarining biogeografik kelib chiqishi haqida yangi gipotezani ishlab chiqish;

molekulyar ma’lumotlar asosida *Cepa* seksiyasi turlarining evolyutsion va filogenetik yaqin qarindoshlarini aniqlash hamda Markaziy Osiyo piyoz turlarining madaniylashish jarayonidagi rolini baholash;

yadro va xloroplast asosida *Cepa* seksiyasi uchun tuzilgan filogenetik daraxtlar nomuvofiqliklarini tahlil qilish va sabablarini aniqlash hamda turlar orasidagi gibridlanish jarayonlarini ochib berish;

Markaziy Osiyoda keng tarqalgan *Allium* ostturkumiga mansub turlararo plastom genom tahlillarini amalga oshirish va filogenetik munosabatlarni aniqlash;

plastom genomlaridagi yagona nukleotid polimorfizmlarini (SNP) tahlil qilish va aniqlangan o‘zgaruvchan hududlar bo‘yicha *Allium* ostturkumi va *Alluim* turkumi turlari uchun barkoding markerlar anilqash;

Allium turlari uchun sinapomorfik belgilarning evolyutsion o‘zgarishini aniqlash va tahlil qilish;

Allium turkumi ichidagi asosiy evolyutsion liniyalarning (EL1–EL3) yadro va plastid genomlari asosida shakllanish vaqtini aniqlash hamda ularning biogeografik kelib chiqishini rekonstruksiya qilish.

Tadqiqotning obyekti. *Allium* turkumiga mansub *Allium* turkumosti turlari va *Cepa* seksiyasi turlari.

Tadqiqotning predmeti. Filogenetik munosabatlar, evolyutsion rivojlanish yo‘nalishlari, biogeografik shakllanish qonuniyatlari hisoblanadi.

Tadqiqotning usullar. Dissertatsiyada ishini bajarishda morfologik, skanirlovchi elektron mikroskopiya, filogenetik, filogeografik va statistik metodlardan foydalanilgan.

Tadqiqotning ilmiy yangiligi quyidagilardan iborat:

Allium turlarini farqlashda urug‘ epidermis hujayralarining periklinal yuzasi va hujayralararo masofasi muhim yangi diagnostik belgi sifatida aniqlangan;

ITS geniga asoslangan filogenetik daraxt hamda urug‘ mikromorfologiyasiga tayangan tahlillar natijasida dastlabki ajdod turlar Markaziy Osiyo–Eron–Kavkaz mintaqasida shakllanganini, keyinchalik esa *Allium* turlarining Shimoliy Osiyo orqali “Eski dunyo” turlarining “Yangi dunyo” hududiga Bering bo‘g‘ozi orqali tarqalganligi ochib berilgan;

xloroplast genomlariga asoslangan tahlillar natijasida *Cepa* seksiyasi turlari uchun filogenetik daraxt rekonstruksiya qilinib, unda Markaziy Osiyoga xos *A. oschaninii, A. praemixtum* va *A. pskemense* turlarining Shimoliy va Sharqiy Osiyo guruhlari o‘rtasida o‘zaro gibridizatsiya natijasida yuz bergan xloroplast o‘zlashtirilishi jarayonlari orqali shakllangani isbotlangan;

molekulyar tadqiqotlar natijasida *Allium* turlari filogenetik daraxtlarini qurishda qo‘llash uchun *rpoC2, ycf1, ndhF, matK, ndhD* kabi yuqori o‘zgaruvchan genlar DNK-barkod markerlar sifatida aniqlangan;

turkumning dastlabki ajdod turlarida diagnostik ahamiyatga ega bo‘lgan asosiy sinapomorfik belgilar sifatida piyoz qobig‘ining qog‘ozsimon tuzilishi, kichik o‘lchamli haqiqiy piyozlarning mavjudligi, chang iplarida tishchalarning yo‘qligi, shuningdek pushti va oq rangli gul shakllarining ustunligi aniqlandi;

Allium turkumining dastlabki evolyutsion liniyasi (EL1) Markaziy Osiyo va unga tutash hududlarda (Kavkaz, Eron va Markaziy Osiyo oralig‘i) shakllangan hamda keyinchalik diversifikatsiyaga uchragani aniqlangan;

Allium turkumi ichidagi asosiy evolyutsion yo‘nalishlarning ajralib chiqishi taxminan 30,9 mln yil avval, ya’ni Oligotsen–Miotsen davrlariga to‘g‘ri kelishi asoslangan.

Tadqiqotning amaliy natijalari quyidagilardan iborat:

Allium turkumiga mansub 95 ta tur uchun urug‘ epidermis hujayralarining turlarni ajratishda muhim bo‘lgan diagnostik belgilariga asoslangan mukammal taksonomik kalit ishlab chiqilgan;

Markaziy Osiyoda tarqalgan *Allium* turkumosti turlarining 59 turi uchun gul ichki tuzilishi (chang iplarining turlari va shakllari) bo‘yicha to‘liq morfologik tahlil, shuningdek *Allium* turkumining 80 ta turi uchun piyoz shakllari va gul ichki tuzilishiga oid illustratsiyalar amalga oshirilgan;

Markaziy Osiyoga xos *Allium* turkumining 77 ta turi uchun to‘liq xloroplast genomlari hamda 110 ga yaqin yadroviy DNK (ITS geni) ketma-ketliklari aniqlangan va xalqaro GenBank (NCBI) ma’lumotlar bazasiga joylashtirilgan;

yangi filogeografik va taksonomik tadqiqotlar uchun muhim bo‘lgan molekulyar markerlar (*ycf1, ndhF, rpoC2, matK* va *ndhD* genlari) aniqlangan hamda ular noyob va muhofaza qilinadigan *Allium* turlarini ishonchli identifikatsiya qilish uchun universal DNK-barkod markerlari sifatida qo‘llanilishi asoslangan.

Tadqiqot natijalarining ishonchliligi zamonaviy va ilmiy jihatdan tan olingan usullarni qo‘llash orqali ta’minlandi. Urug‘ morfologiyasi skanerlovchi elektron mikroskopiya (SEM) yordamida, xloroplast genomlari esa kompleks molekulyar-filogenetik tahlillar asosida o‘rganildi. Olingan filogenetik natijalar kladistik tahlil qilinib, jamoatchilikka ochiq bo‘lgan ITS va to’liq chloroplast geomlari ketma-ketliklari bilan taqqoslandi, bu esa xulosalarning mustahkamligini ta’minladi. Tadqiqotning asosiy natijalari milliy va xalqaro ilmiy konferensiyalarda taqdim

etilib, soha mutaxassislari tomonidan ijobiy baholandi. Molekulyar filogenetik tahlil natijalari nufuzli ilmiy jurnallarda chop etilgan bo‘lib, DNK ketma-ketliklari xalqaro GenBank ma’lumotlar bazasiga joylangan (https://www.ncbi.nlm.nih.gov/), bu esa olingan natijalarning ochiqligi, tekshiriluvchanligi va qayta foydalanish imkoniyatini ta’minlaydi.

Tadqiqot natijalarining ilmiy va amaliy ahamiyati.

Ushbu tadqiqotning ilmiy ahamiyati *Allium* turkumining evolyutsion liniyalari Oligotsen va Miotsen davrlarida shakllanganini biogeografik yondashuv asosida ilmiy jihatdan asoslab berilishi, urug‘ epidermisi hujayralarining mikromorfologik belgilariga tayangan holda turlarni diagnostika qilishning yangi yondashuvi ishlab chiqilishi, 110 ta *Allium* turiga oid plastid genomlari asosida morfologik ma’lumotlar bilan integratsiyalangan molekulyar filogenetik daraxtlar qurilishi hamda turkumning ostturkumlari va seksiyalarini tasniflash, xususan *Cepa* seksiyasi turlari doirasida gibridizatsiya va xloroplast genomlarining o‘zlashtirilishi jarayonlari ochib berilganligi bilan izohlanadi..

Tadqiqot natijalari yovvoyi *Allium* turlarini genetik resurs va seleksiya obyekti sifatida baholash, gibridlanish va xloroplast o‘zlashtirilishi jarayonlarini hisobga olgan holda ulardan amaliy foydalanish imkonini berdi. Shuningdek, turlarni tezkor va ishonchli identifikatsiya qilish uchun DNK-barkod markerlari hamda urug‘ mikromorfologiyasiga asoslangan diagnostik kalitlarni ishlab chiqish *Allium* turlarini muhofaza qilish, genofondni saqlash va biologik xilma-xillikni baholashda muhim amaliy asos bo‘lib xizmat qiladi.

Tadqiqot natijalarining joriy qilinishi.

Allium (Amaryllidaceae) turkumining filogeniyasi, biogeografiyasi va evolyutsiyasi (Markaziy Osiyo misolida) ni o‘rganish bo‘yicha olingan natijalar asosida:

Allium turkumining 77 dan ortiq turlarining to‘liq xloroplast genomlari va nrDNK(ITS geni) to‘liq tahlili, o‘simlik turlarini laboratoriya sharoitida tur identifikatsiyasi va hududiy kelib chiqishini ekspress aniqlash usullari O‘zbekiston Respublikasi Fanlar akademiyasi Botanika instituti, Molekulyar filogeniya va biogeografiya laboratoriyasida 2021-2024 yillarda bajarilgan “Hayot daraxti: O‘zbekiston bir urug‘pallalilari” fundamental loyiha dasturiga joriy etilgan (O‘zbekiston Respublikasi Fanlar akademiyasining 2025-yil 20-iyundagi №4/1255-1522-son ma’lumotnomasi). Natijada, turkumning eng qadimgi vakillarini kelib chiqish va O‘rta Osiyodagi vakillari ichidan “qadimiy gibridlangan” turlarni aniqlash, madaniylashtirish jarayonlarida qo‘llash imkonini bergan;

molekulyar — filogenetik tahlillar asosida 77 ta tur 105 namuna uchun olingan DNK ketma-ketliklari (xloroplast genomlari, ITS) xalqaro NCBI GenBank (https://www.ncbi.nlm.nih.gov/)da NC_044411, NC_044412, NC_068792, NC_068793, NC_068794, NC_068796, OP642457, OP643522, PQ308296, PQ308298 raqamlari ostida saqlangan. Integratsiyalashgan ushbu ma’lumotlar *Allium* turkumining molekulyar taksonomiyasi bo‘yicha yangi ma’lumotlarni olish imkonini bergan, bu nafaqat mahalliy turlar xilma-xilligini sezilarli darajada boyitdi, balki Markaziy Osiyo florasiga oid filogenetik va biogeografik qarashlarni kengaytirdi hamda fan uchun noma’lum bo‘lgan yangi turlarni aniqlash imkonini

bergan;

O‘zbekiston va Sharqiy Osiyo florasiga mansub *Allium* turlari o‘rtasidagi molekulyar-filogenetik va biogeografik munosabatlarni aniqlash, SEM usuli asosida urug‘ning makro va mikromorfologik xususiyatlari hamda morfologiyasini tahlil qilish orqali labaratoriya sharoitida tur aniqlash usuli Xitoy Fanlar Akademiyasi Kunming Botanika institutida amalga oshirilgan “Global *Allium* Garden” (U1802232, 2018–2022 yy) xalqaro loyiha faoliyatiga joriy qilingan (Xitoy Fanlar akademiyasining 2025-yil 5-fevraldagi ma’lumotnomasi). Natijada, *Allium* turlari o‘rtasidagi evoluytsion munosabatlarni aniqlash, taksonomiyasiga oid yangi ilmiy qarashlarni shakllantirish, turlarni aniqlashning zamonaviy taksonomik kalitini ishlab chiqish imkonini bergan.

Tadqiqot natijalarining approbatsiyasi. Mazkur tadqiqot natijalari 2 ta xalqaro va 2 ta respublika ilmiy-amaliy anjumanlarida muhokamadan o‘tkazilgan.

Tadqiqot natijalarining e’lon qilinishi. Dissertatsiya mavzusi bo‘yicha jami 16 ta ilmiy ish nashr etilgan, O‘zbekiston Respublikasi Oliy Attestatsiya Komissiyasining doktorlik disertatsiyalari asosiy ilmiy natijalarini chop etishga tavsiya etilgan ilmiy nashrlarda 11 ta ilmiy maqola, jumladan, 3 ta respublika va 8 ta xorijiy jurnallarda nashr etilgan.

Dissertatsiyaning tuzilishi va hajmi. Dessertatsiya tarkibi kirish, 5 ta bob, xulosa, foydalanilgan adabiyotlar ro‘yxati va ilovadan iborat. Dessertatsiya hajmi 182 betni tashkil etadi.

DISSERTATSIYANING ASOSIY MAZMUNI

Kirish qismida dissertatsiya ishining dolzarbligi va uning zaruriyati asoslab berilgan, tadqiqotning ilm-fan va texnologiyalar rivojlanishining ustuvor yo‘nalishlariga uyg‘unligi ko‘rsatilgan. Shuningdek, dissertatsiya mavzusi bo‘yicha respublikadagi va xorijdagi ilmiy-tadqiqot ishlariga oid sharhlar, muammoning o‘rganilganlik darajasi, tadqiqotning asosiy maqsadi, vazifalari, obyekti va predmeti haqida batafsil ma’lumotlar keltirilgan. Tadqiqot natijalarining amaliyotga tatbiq etilganligi, chop etilgan ishlar va dissertatsiyaning tuzilishi ham bayon etilgan.

Dissertatsiyaning “***Allium* L. taksonomiyasining tarixi va hozirgi qabul qilingan tasnifi”** nomli birinchi bobi *Allium* turkumining taksonomik tarixi va hozirgi davrda qabul qilingan taksonomik tahlil qilingan. *Allium* turkumi 1000 dan ortiq turga ega bo‘lib, bir urug‘pallalilar orasida eng yirik taksonlardan biri sanaladi. Turkum turlari morfologik tuzilishining xilma-xilligi, turli ekologik sharoitlarga yuqori darajada moslashuvchanligi va iqtisodiy jihatdan katta ahamiyati tufayli uzoq vaqt davomida botaniklarning qiziqishini uyg‘otgan. Bosh piyoz (*A. cepa)*, sarimsoq (*A. sativum*) kabi muhim o‘simliklar, bu turkumning qishloq xo‘jaligi va oziq ovqat sohalaridagi global ta’sirini ko‘rsatadi (Burba va Galmarini, 1994; Wheeler et al., 2013). Ularda achchiq hidi va ta’mini beruvchi sulfid birikmalari borligi *Allium* turlarini boshqa turlardan yanada ajratib turadi (Fritsch va Friesen, 2002). Xalqaro ekologik taqsimoti nuqtai nazardan Markaziy va Sharqiy Osiyo, O‘rta Yer Dengizi havzasi va Shimoliy Amerika kabi *Allium* ning xilma-xillik markazlari mavjud (Khassanov, 2018).

Allium ning taksonomik o‘rganilishi, XVIII-asrda Linney (1763) tomonidan changchilar soni va tuzilishi asosida olib borilgan dastlabki morfologik tasniflashlar bilan boshlandi. 1745-yilda Halleir, 1832-yilda Don va 1837-yilda Koch kabi olimlar tasniflash tizimlarini takomillashtirishgan, so‘ngra 1875 va 1887-yillarda Regel, 1935-yilda Vvedensky va 1968-yilda Traub tomonidan yirik tahrirlar amalga oshirilgan. Ikki asrdan ortiq muddat davomida olib borilgan tadqiqotlar natijasida shakllangan bilimlar asosida turkumning tasnifi yanada takomillashtirilib, turkum turlari yuzlab taksonomik birliklarga bo‘lingan, osttukum va seksiyalarga ajratilgan (Kamelin, 1973; Hanelt, 1990). 20-asrning oxirlarida molekulyar ma'lumotlarning integratsiyasi taksonomiyani inqilobiy ravishda o‘zgartirdi: Hanelt va boshqalar (1992) hamda Gregory va boshqalar (1998) ostturkumlar va sektsiyalar doirasini rivojlantirdilar, natijada Friesen va boshqalar (2006) tomonidan 15 ta ostturkum va 72 ta seksiyalar taklif qilindi. Ular shuningdek molekulyar dalillar asosida uchta yirik evolyutsion liniyalarni aniqladilar (Friesen va boshqalar, 2006; Fritsch va Friesen, 2002).

Morfologik murakkablik hali ham qiyinchiliklarni keltirib chiqaradi, chunki urug‘ning epidermis hujayralari tuzilishi yoki piyozning qobig‘i shakli kabi muhim xususiyatlar gerbariy namunalarida ko‘pincha mavjud bo’lmay, bu tez-tez noto‘g‘ri identifikatsiyalarga olib keladi (Hanelt va boshqalar, 1992; Khassanov va Fritsch, 1994). Sitologik tadqiqotlar, *Allium* larda x=8 asosiy xromosoma sonining ustunligini ko‘rsatdi, ammo sezilarli o‘zgarishlar va keng miqyosdagi poliploidiya, turkumning ichida moslashish va turlanishning asosiy omili bo‘lib qolmoqda (Traub va Traub, 1968; Ohri va boshqalar, 1998; Wu va boshqalar, 2010). Poliploidiya, ko‘pincha atrof-muhitning stressiga moslashish bilan bog‘liq bo‘lib, *Allium* turlarining Miotsen va Pliotsen davrlarida iqlim o‘zgarishlari ostida diversifikatsiyalanishiga olib kelgan (Han va boshqalar, 2020; Mayrose va boshqalar, 2010).

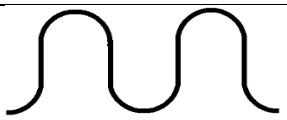
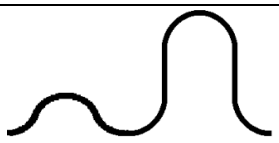
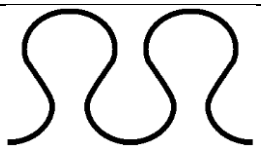
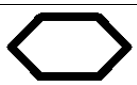
So‘nggi filogenetik tadqiqotlar, yadro (ITS) va plastid ma'lumotlari asosidagi filogeniya cheklangan yechimlar ko‘rsatgan (Xie va boshqalar, 2020). Ushbu yondashuvlar, evolyutsion aloqalar, ajralish vaqtlarini va morfologik innovatsiya bilan atrof-muhitga moslashuv o‘rtasidagi o‘zaro aloqalarni aniqlashda yanada aniqroq bo‘lishi mumkin. Shunday qilib, *Allium* taksonomiyasining tarixi nafaqat botanika fanining rivojlanishini — morfologiyadan molekulyar filogenetikaga — balki tukumning poliploidiya, moslashish va diversifikatsiya jarayonlarini o‘rganishdagi rolini ham aks ettiradi.

Dissertatsiyaning “***Allium*** **turkumining makro-morfologik va mikro-morfologik urug‘ xususiyatlari**” nomli ikkinchi bobda *Allium* urug‘larining makro- va mikromorfologiyasini hozirgi kungacha eng keng qamrovli o‘rganilishi ko’rsatilgan. Tadqiqotda 14 ta ostturkum va 58 ta seksiyaga mansub 95 ta tur (98 ta namunaning) o‘rganilib, skanerlovchi elektron mikroskopiya (SEM) yordamida 10 ta epidermis hujayrasining periklinal devor yuzasi maydoni, hujayralar orasidagi masofa, hujayra shakllari, antiklinal va periklinalal devorlarning tuzilishi kabi xususiyatlar tahlil qilingan. Natijalar shuni ko‘rsatdiki, ushbu tadqiqotda birinchi

marta o‘rganilgan 10 ta epidermis hujayrasining periklinal devor yuzasi maydoni va ular orasidagi masofa *Allium* turkumida turlarni ajratishda foydali ekanligi aniqlandi. Urug‘ xususiyatlariga asoslanib, taksonomik kalitlar va *Allium* evolyutsiyasining ilk bosqichlaridagi migratsiya yo‘nalishlarining taxminiy rekonstruktsiyalari taqdim etdildi. Tadqiqotda, epidermis hujayralari shakllari turli *Allium* turlaridagi evolyutsiya jarayonining bosqichlarini ko‘rsatadi. Hujayralar joylashuvining bo‘shlig’i, kichik yoki mavjud bo‘lmagan verrukalar (tugunlarga o‘xshash), botiq periklinal devorlar, to‘g‘ri yoki yoy shaklidagi antiklinal devorlar va keng tuxumsimon urug‘lar qadimiy, primitiv xususiyatlar sifatida qaraldi. O‘rtacha rivojlanish bosqichi xususiyatlariga retikulyar, to‘rga o‘xshash hujayralar joylashuvi, o‘rtacha kattalikdagi verrukalar, tekis periklinal devorlar, yoy yoki S-tipidagi antiklinal devorlar va tor tuxumsimon urug‘lar kiritildi. Eng rivojlangan xususiyatlar esa zichroq joylashgan hujayralar, yirik verrukalar, gumbazsimon periklinal devorlar, U va Ω-tiplaridagi, shuningdek tuxumsimon yoki yassi tuxumsimon shakldagi urug‘lar bilan ajralib turdi.

1-jadval

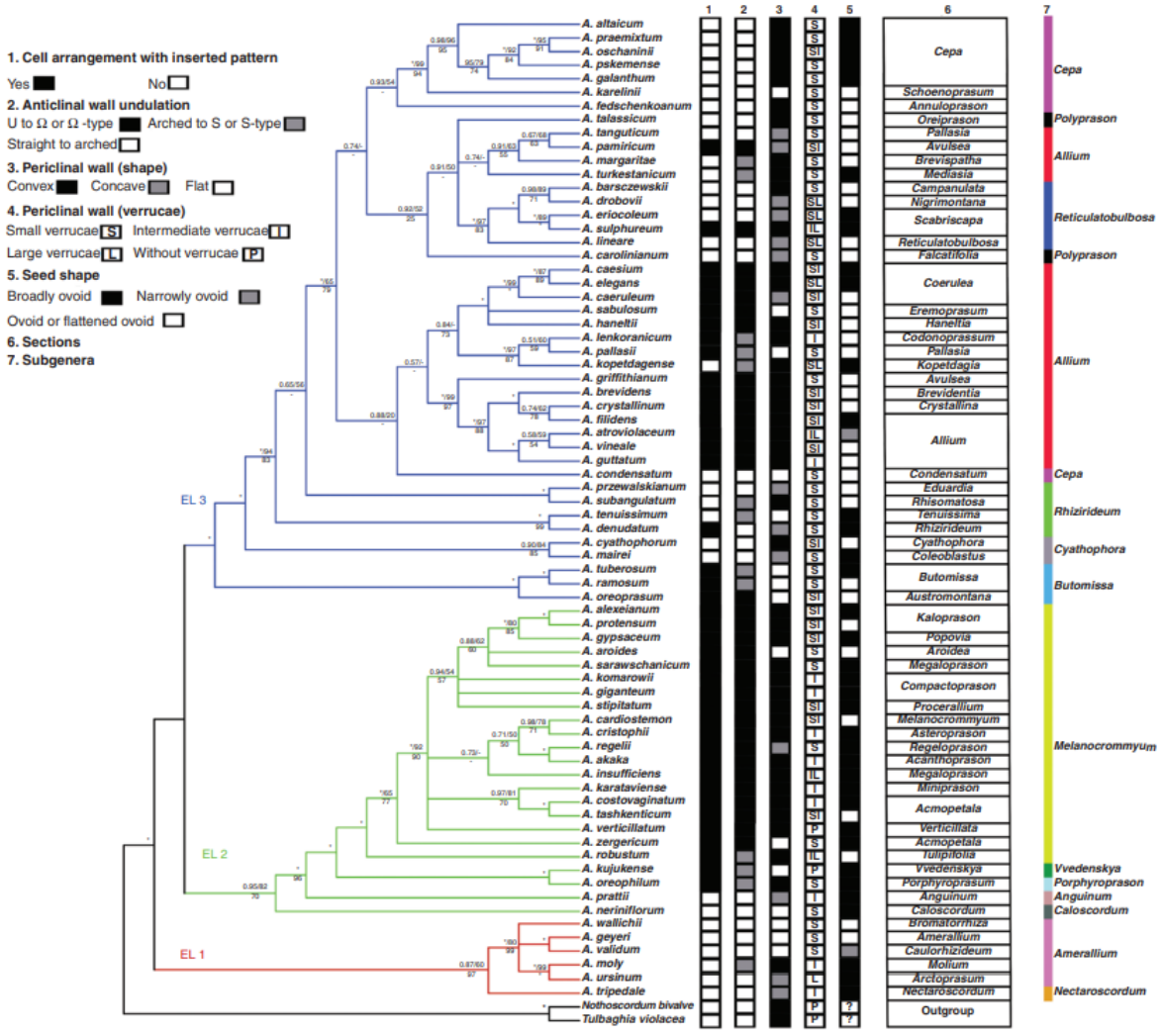
Allium turlarida urug‘epidermis hujayrasi antiklinal devori va hujayra shaklining dominant egrilik turlari

A. Antklinal devor: dominant egrilik turlari:			B. Hujayra shakllari:		
	To‘g‘ri–Egri	7		Dumaloq	1
	S-tip	6		Elliptik	2
	Egri-S-tip	5		Cho‘zinchoq	3
	U-tip	4		To‘rtburchak	4
	S-U-tip	3		5 qirrali	5
	Ω-tip	2		6 qirrali	6
	U - Ω-tip	1			

Morfologik belgilar ITS ketma-ketliklariga asoslangan filogenetik daraxtga joylashtirilganda (1-rasm), bu hujayra xususiyatlari *Allium* ichidagi uchta asosiy

evolyutsion yo‘nalishlarni (EL1, EL2, EL3) qo‘llab-quvvatladi (2-rasm).

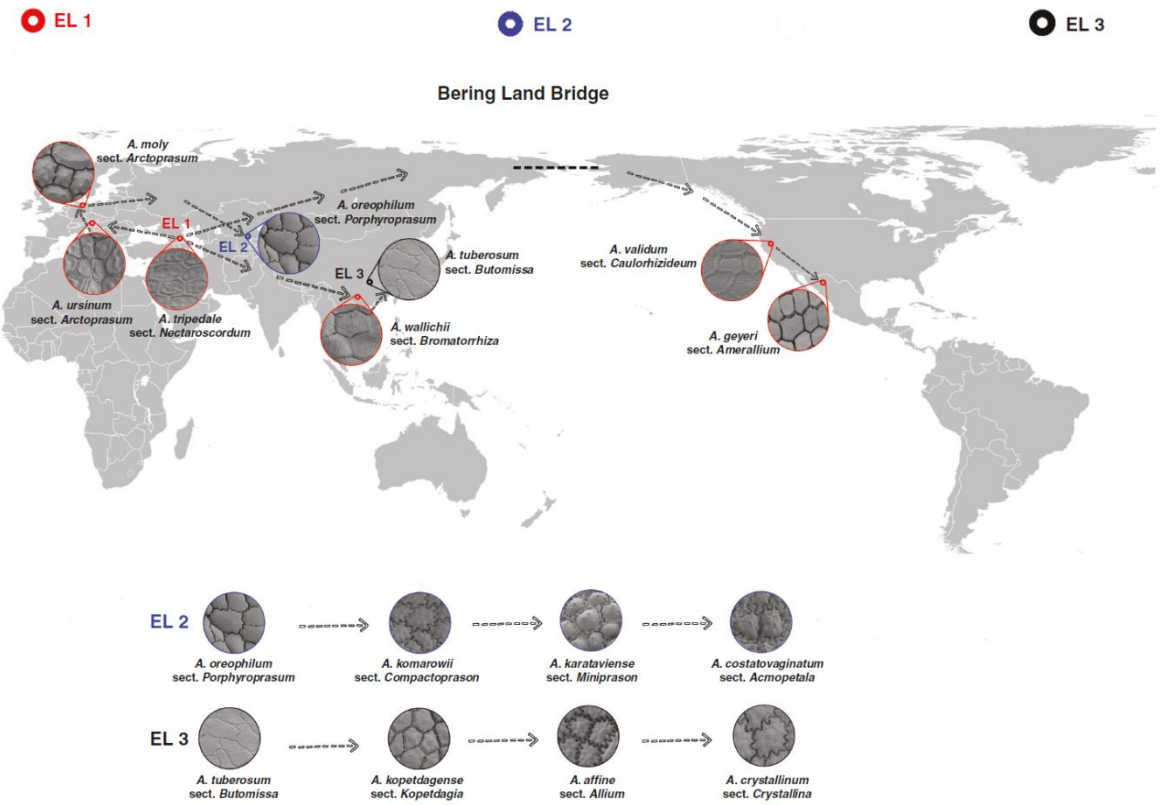
Birinchi evolyutsion yo‘nalish (EL1) turlari va tashqi guruh turlari eng primitiv urug‘ epidermis xususiyatlarini ko‘rsatdi. Ikkinchi evolyutsion yo‘nalishdagi taksonlar asosan o‘rtacha xususiyatlarga ega bo’lib, bundan *Melanocrommyum* ostturkumi a’zolari mustasno bo‘lib, ular rivojlangan xususiyatlarni namoyish etdi. Uchinchi evolyutsion yo‘nalishda ko‘pchilik turlar primitiv hujayra xususiyatlarini saqlab qolgan, bundan *Allium* ostturkumi vakillari istisno qilib, ular asosan rivojlangan xususiyatlarga ega edi. *Allium* ajdodlari Kavkaz, Markaziy Osiyo va Eron bilan chegaralangan hududda paydo bo‘lgan, deb taxmin qilindi. Ushbu hududdan birinchi evolyutsion yo‘nalishdagi taksonlar janubiy Yevropa va Sharqiy O‘rta Yer Dengizi tomon yoki Sharqiy Osiyo va Uzoq Sharqqa qarab harakat qilgan.



1-rasm. ITS ketma-ketliklargiga asoslangan filogenetik daraxtning urug‘ epidermis xususiyatlari bilan bog‘liqligi.

Misol uchun, eng primitiv epidermis hujayralari xususiyatlarini ko‘rsatgan *Nectaroscordum* ostturkumi a’zolari g‘arbiy yo‘nalish bo‘ylab harakat qilgan deb taxmin qilinadi. Periklinal devorlarining shakli va antiklinal devorlarining burmalanishi - *Allium* turkumi urug‘ epidermis xususiyatlarining evolyutsiyasini belgilovchi ikki asosiy omillari deb qaraladi. Primitiv turlar botiqsimon periklinal

devorlari va to‘g‘ri yoki yoy shaklidagi antiklinal devorlarga ega bo‘lsa, rivojlangan taksonlar bo’rtiq periklinal devorlar va to‘lqinli (S-tip, U-tip, U-Ω-tip, Ω-tip) antiklinal devorlarga ega. Xulosa qilib aytganda, *Allium* urug‘larining makro- va mikromorfologiyasini keng qamrovli o‘rganish ushbu yirik va iqtisodiy ahamiyatli turkumdagi taksonomik, evolyutsion va biogeografik aloqalar bo‘yicha qimmatli ma’lumotlarni taqdim etadi. Urug‘ epidermis xususiyatlari nafaqat turlarni ajratish uchun foydali ekanligini, balki *Allium* da tan olingan turli evolyutsion bosqichlarni ham aks ettirishi mumkinligini ko‘rsatdi. Taklif etilgan migratsiya yo‘nalishlari va urug‘ epidermisi xususiyatlarining evolyutsiyasi ushbu turkumning Kavkaz, Markaziy Osiyo va Eron hududlariga asoslangan biogeografik tarixini tushunish uchun asos bo‘lib xizmat qiladi.

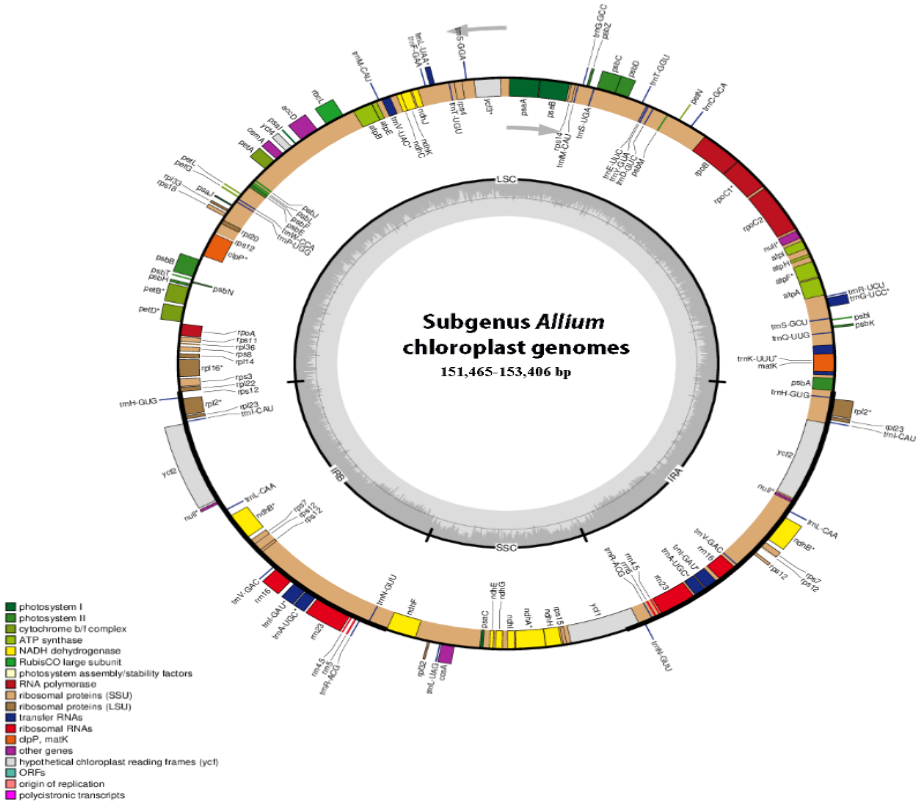


2-rasm. Dunyo miqyosida *Allium* turkumining urug’ epidermis xususiyatlariga asoslangan holda tarqalish migratsiyasi. Turlarni xaritada joylashishi va tarmoqlanishi gerbariy ma'lumotlariga va ITS ketma-ketliklariga asoslangan filogenetik daraxtdagi o‘rniga mos ravishda joylashtirilgan..

Dissertatsiyaning **“Markaziy Osiyoda *Allium* turkumi *Allium* turkumostisining (Amaryllidaceae) filogenomikasi va morfologik evolyutsiyasi”** nomli uchinchi bobida ostturkumga tegishli o’simliklarningning xloroplast genomi tuzilishi, genetik xilma-xillik va filogenetik munosabatlarni keng qamrovli tahlili amalga oshirilgan. Natijalar xloroplast genomi umumiy o‘lchami 151,465 juftlikdan 153,406 juftlikgacha o‘zgarib turishini ko’rsatdi (3-rasm). SSR lar tahlili ichki transkripsiya hududlarida muhim polimorfizmni ochib berdi, bu hududlar oqsil kodlovchi ketma-ketliklarga nisbatan yuqori nukleotid xilma-xilligini ko‘rsatdi.

Yangi sekvenslangan o‘nta *Allium* turi, *Allium* ostturkumining olti sektsiyasi

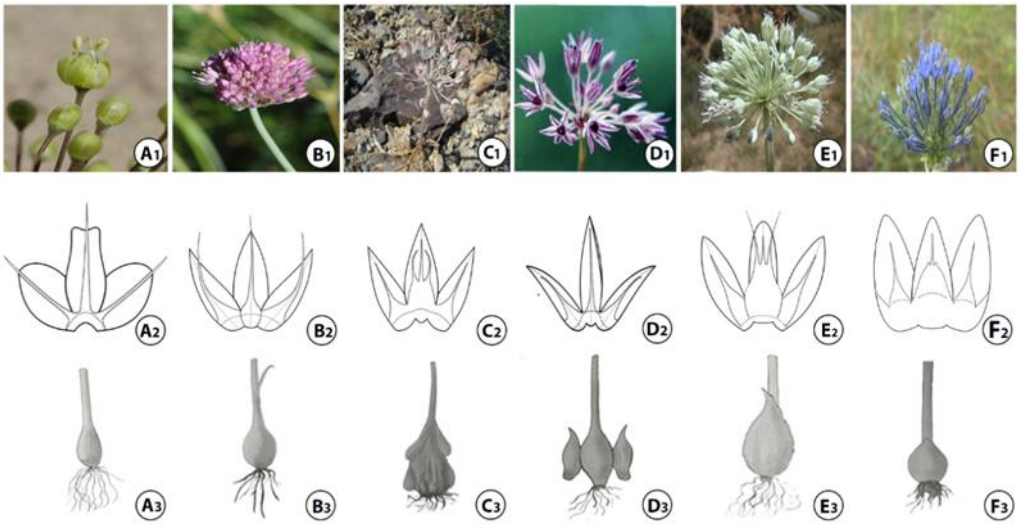
vakillari bo‘lib, turkumning filogeniya va xloroplast genom strukturasiga yangi o’zgarishlarni kiritdi. Ushbu turlar quyidagi bo‘limlarga mansub: *Allium* seksiya (*A. filidens*), *Brivedentia* seksiya (*A. michaelis* va *A. nikolai*), *Coerulea* seksiya (*A. caesium* va *A. glomeratum*), *Eremoprasum* seksiya (*A. confragosum* va *A. sabulosum*), *Haneltia* seksiya (*A. haneltii*) va *Pallasia* seksiya (*A. pallasii* va *A. tanguticum*). Qiziqarli tomoni, *Pallasia* seksiyasining oxirgi ikki turi (*A. pallasii* va *A. tanguticum*) Xie va boshqalar (2020b) tomonidan ham xloroplast genomining to‘liq sekanslanishi orqali tahlil qilingan bo‘lib, ular har ikki tadqiqotda (bizning tadqiqotimizda ham) filogenetik daraxtda bir xil o‘rinda emas, balki boshqa molekulyar kladda o’rin olgan. Shunga o‘xshash tarqalish *Coerulea* seksiyasidan *A. caesium* va *A. glomeratum* turlarida, *Eremoprasum* seksiyasidan *A. confragosum* va *A. sabulosum* turlarida ham kuzatildi.



3-rasm. *Allium* ostturkumi turlarining xloroplast genom tuzilishi.

O’tkazilgan filogenetik tahlillar, turlar filogenetik daraxtdagi joyi va ularning taksonomik joylashuvi o‘rtasida sezilarli nomuvofiqliklarni ochib berdi. Masalan, *A. confragosum* morfologik xususiyatlarga asoslanib *Eremoprasum* seksiyasiga kiritilgan bo‘lsa-da, filogenetik daraxtda *A. confragosum Eremoprasum* ning tipik turi bo‘lgan *A. sabulosum* bilan bir xil kladada joylashmagan. Aksincha, u *A. caesium*, *A. haneltii* va *A. caeruleum* kabi turlar bilan birga klasterlashgan. Khassanov (2018) *A. confragosum* va *A. sabulosum* ni bir xil seksiyaga joylashtirgan edi, chunki ular ichki changchilarning uch qismga bo‘linishi va ostki qismidagi qobig’i tishli bo‘lishi kabi o‘xshash xususiyatlarga ega. Biroq, *A. confragosum A. sabulosum* dan farq qiladi, chunki uning to‘pgul o‘rovchi qoplamasi doimiy saqlanib qoladi. *A. confragosum* gul ochilishidagi to’pgul o’rovchi qoplamaning doimiy

saqlanishi bilan *A. haneltii*, *A. caeruleum* va *A. caesium* ga o‘xshashdir. Ushbu dalil, ilgari *Allium* ostturkumdagi seksiyalarni belgilashda ishlatilgan morfologik xususiyatlarning ahamiyatini qayta ko‘rib chiqishni talab qiladi (4-rasm). Bizning tadqiqotimiz, *Allium* ostturkumining to’liq xloroplast genomi asosidagi filogeniyasiga oid 18 turdan foydalanilgan birinchi keng qamrovli tahlil bo‘lib, bu *Allium* turkumining mavjud seksiyalar klassifikatsiyasi bilan mos kelmasligini ko‘rsatdi.



4-rasm. *Allium* ostturkumiga mansub turlarning gullarining morfologik belgilari, changchi ipchalari va piyozlari. (A) *A. sabulosum* (*Eremoprasum* seksiyasi, V. Epiktetov rasmi); (B) *A. pallasii* (*Pallasia* seksiyasi, V. Epiktetov rasmi); (C) *A. michaelis* (*Brivedentia* seksiyasi, G. Lazkov rasmi); (D) *A. haneltii* (*Haneltia* seksiyasi, F. Khassanov rasmi); (E) *A. filidens* (*Allium* seksiyasi, G. Lazkov rasmi); (F) *A. caesium* (*Coerulea* seksiyasi, L. Valdshmit rasmi).

To’liq xloroplast genomi ma'lumotlari asosida qurilgan filogenetik daraxtda ko‘pchilik kladlarda boshqa ostturkumlar vakillari, masalan, *Polyprason*, *Reticulatobulbosa* va *Cepa* ostturkumlaridan ma’lum turlar mavjud bo‘lib, faqat bir kladda barcha vakillar *Allium* ostturkumiga tegishli bo‘lgan. Bu, Friesen va boshqalar (2006) tomonidan tuzilgan ITS asosidagi filogenetik daraxtga qarama-qarshi, unda *Allium* ostturkumi alohida klad hosil qilgan edi.

Shuningdek, tadqiqotda *Allium* turlarining xloroplast genom strukturasidagi farqlar tahlil qilingan. To’liq xloroplast genomlarda ko‘pincha psevdogen (genlarning funksional vazifasini yo’qotishi) yoki genlarning to‘liq yo‘qolishi kuzatildi (Haberle et al., 2008; Guisinger et al., 2011; Schwarz et al., 2015). Biz *rpl22* genining yo‘qolishi, *rps2*, *accD*, *psaI*, *rpl20*, *rpl23*, *rpl32* va ndh guruhidagi genlarning psevdogen holatiga o’tishi, shuningdek *rps16* va *infA* genlarining yo‘qolishi yoki psevdogen holatiga o’tishini aniqladik. Avvalgi tadqiqotlarda (Xie va boshqalar, 2019; Scobeyeva va boshqalar, 2021) *Allium* da *rps16*, *rps2*, *infA* va *rpl32* genlari yo‘qolishi yoki psevdogen holatiga o’tishini ko‘rsatilgan edi. Shuningdek, biz *A. ovalifolium*, *A. ochotense* va *A. paradoxum* turlarida *psaI*, *rpl20* va *rpl22* genlaridagi yangi psevdogen holatiga o’tishi yoki yo‘qolishini aniqladik. *Allium* dagi avvalgi tadqiqotlar (Huo et al., 2019; Xie et al., 2020b) bilan taqqoslaganda, IR/SSC va IR/LSC chegaralarining taqqoslanishi o‘xshash

xususiyatlarga ega bo‘lib, faqat *rpl22*, *rps19*, *ycf1* va *ndhK* genlarining joylashuvi bo‘yicha kichik farqlar mavjud. Shuningdek, barcha o‘rganilgan turlarda *trnH-rps19* klasteri *Allium* ostturkumi turlarining IR hududlarida joylashganligini aniqladik, bu esa Wang va boshqalar (2008) tomonidan tavsiflangan IR/LSC juftliklarining kengayishi va qisqarishlariga mos keladi. Bu natijalar, *Allium* ostturkum turlarining genom tuzilishini tushunishda katta yordam beradi.

Filogenetik tahlillar ushbu turlar joylashuvi ko‘pincha ularning hozirgi taksonomik tasniflariga zid kelishini ko‘rsatdi, bu esa avvalgi seksiyalarni belgilashda ishlatilgan morfologik xususiyatlarni qayta ko‘rib chiqish zarurligini taklif qiladi. Tadqiqot shuningdek, to’liq xloroplast genomi asosida qurilgan filogenetik daraxt morfologiyaga asoslangan tasniflar va avvalgi molekulyar tadqiqotlar, masalan, ITS ketma-ketliklarini ishlatganlar bilan muhim farqlarni ko‘rsatdi. Masalan, morfologiyaga asoslangan holda *Eremoprasum* seksiyasiga kiritilgan *A. confragosum* filogenetik daraxtda boshqa seksiyadagi turlar bilan bir klasterda joylashganligi aniqlangan, bu esa hozirgi tasnif tizimida muammolar mavjudligini ko‘rsatadi. Umuman olganda, natijalar *Allium* ostturkumining filogeniyasi avvalgi tushunchalardan ko‘ra murakkabroq ekanligi ko’rsatadi.

Dissertatsiyaning **“*Allium* turkumi *Cepa* seksiyasi filogenomikasi: Markaziy Osiyoda bosh piyozning madaniylashtirilishi bo‘yicha yangi ilmiy qarashlar.”** nomli to‘rtinchi bobida *Cepa* seksiyasi iqtisodiy jihatdan muhim o‘simliklarni o‘z ichiga olgan bo‘lib, uning filogenetik munosabatlarini tushunish har doim qiyin bo‘lganligi, ushbu tadqiqotda, to‘rt (*Allium oschaninii, A. praemixtum, A. pskemense* va *A. galanthum*) *M*arkaziy Osiyo turining to‘liq xloroplast genomlarini sekvens qilish orqali bu munosabatlarni aniqlash maqsadi qo’yilgan.

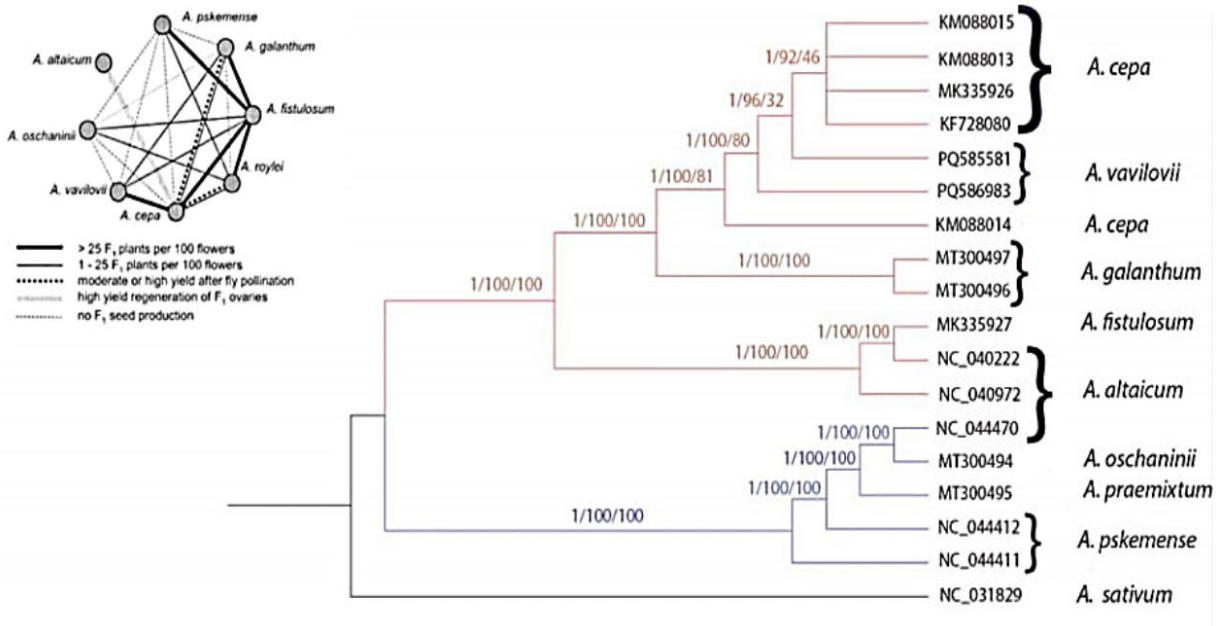
Tahlil natijalari seksiya ichida ikkita alohida kladni ko‘rsatdi (5-rasm). Birinchi klad *A. oschaninii, A. praemixtum* va *A. pskemense* ni o‘z ichiga olgan bo‘lsa, ikkinchi klad *A. galanthum, A. altaicum* va ikki madaniy tur, ya'ni *Allium cepa* va *Allium fistulosum* larni o‘z ichiga oldi. Ushbu natijalar, avvalgi yadro DNK va morfologik ma'lumotlarga asoslangan filogenetik tadqiqotlar bilan ziddiyatda bo‘lib, turlararo gibridizatsiya va xloroplast o’zlashtirish (chloroplast capture) jarayonlari bu munosabatlarni shakllantirishda muhim rol o‘ynaganligini ko‘rsatadi.

Tadqiqot natijalari shuni ko‘rsatadiki, *A. galanthum, A. cepa* bilan yaqinroq genetik o’xshashlikda bo‘lishiga qaramay, piyozning madaniy navlarini hosil bo’lishida rol o‘ynamagan bo’lishi mumkin. Ushbu xulosa, bu turlar o‘rtasida sezilarli morfologik va yadro DNK farqlari mavjudligi bilan tasdiqlanadi. Ushbu natijalar, Markaziy Osiyo turlarining madaniy piyozning eng yaqin yovvoyi qarindoshlari ekanligi haqidagi keng tarqalgan fikrni qarshi chiqadi. Buning o‘rniga, *A. cepa* ning madaniy sharoitida yetishtirilishi boshqa joylarda sodir bo‘lgan bo‘lishi mumkin va bu muhim o‘simlikning haqiqiy yovvoyi ajdodlarini aniqlash uchun qo‘shimcha tadqiqotlar o’tkazish zarurligi ta’kidlaydi.

Shuningdek, tahlil *rpoC2* xloroplast genining *filogeniyada* ahamiyatliligini ta'kidlaydi, bu gen 80 ta oqsil kodlovchi genlar, to‘liq xloroplast genomlar, xloroplastning SSC va LSC qismlari asosida qurilgan filogenetik daraxt bilan bir xil tuzilishdagi filogenetik daraxtlarni ishlab chiqardi. Ushbu filogenetik moslik, *rpoC2*

genini *Allium* turlaridagi kelajakdagi filogeografik va filogenetik tadqiqotlar uchun qimmatli gen sifatida belgilaydi.

Birgina genning kengroq genetik ma'lumotlar bilan mos kelishi, filogenetik tahlillarni kuchaytiradi va bu o‘simliklarning evolyutsion tarixini yanada aniqroq tushunishga yordam beradi.



5-rasm. *Cepa* seksiyasining 16 ta to’liq xloroplast genomining 80 ta oqsil kodlovchi genlariga asoslangan filogenetik daraxti.

Biroq, tadqiqotda shuningdek, bir qator turlar, jumladan *A. rhabdotum, A. roylei, A. farctum, A. asarense* turlari uchun xloroplast genomlarining mavjud emasligi *Cepa* seksiyasi ichidagi filogenetik munosabatlarni to‘liq tushunishni qiyinlashtiradi. Ushbu bo‘shliqlar, seksiya ichidagi evolyutsion dinamikani to‘liq tushunishni qiyinlashtiradi va kelajakdagi tadqiqotlar ushbu bo‘shliqlarni to‘ldirish zarurligini anglatadi. Ushbu bo‘shliqlarni bartaraf etish orqali *Allium* turlarining evolyutsiyasi va madaniy sharoitida yetishtirilishi haqida yanada to‘liq tasavvurga ega bo‘lishlari mumkin bo’ladi.

Xulosa qilib aytganda, ushbu tadqiqot *Cepa* seksiyasi ichidagi filogenetik munosabatlar haqida yangi tushunchalar beradi, avvalgi taxminlarni inkor etadi va uning evolyutsion tarixining murakkabligini ta'kidlaydi. Olingan natijalar, o‘simliklar evolyutsiyasi va madaniy sharoitida yetishtiriladigan *A. cepa* turini yanada chuqurroq tushunish uchun bir nechta genetik ma'lumot manbalarini birlashtirishning ahamiyatini ko‘rsatadi

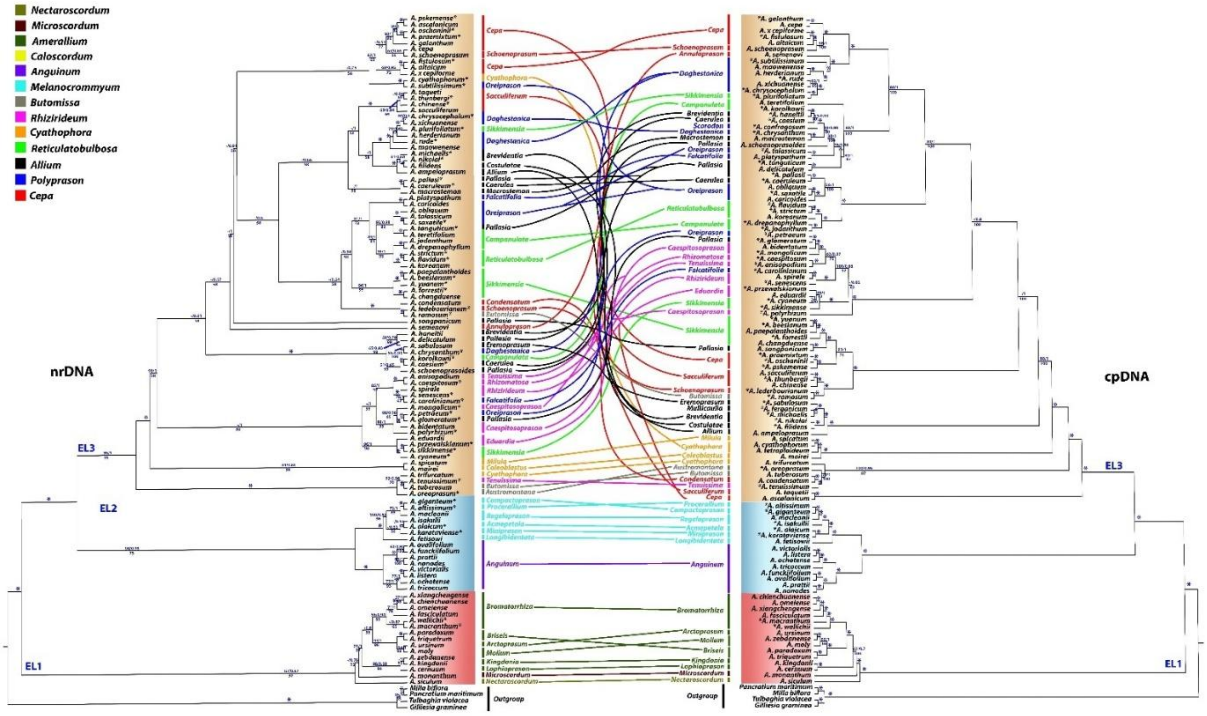
Dissertatsiyaning **“*Allium* L. (Amaryllidaceae) turkumining murakkab evolyutsiyasining qiyosiy filogenomikasi”** nomli beshinchi bobida *Allium* ning murakkab evolyutsion tarixini keng qamrovli filogenomik tahlil orqali aniqlash maqsad qilgan. Tadqiqotda, *Allium* turlari o‘rtasidagi filogenetik munosabatlarni xloroplast genomi ma'lumotlari va ribosomal DNK (ITS) ketma-ketliklari yordamida tiklashga qaratilgan. Tadqiqot molekulyar ma'lumotlarni morfologik xususiyatlar bilan birlashtirib, ushbu turkumining xilma-xilligini shakllantirgan

evolyutsion jarayonlar haqida tushuncha berishga harakat qiladi. Tadqiqot 110 ta *Allium* turini o‘z ichiga olib, bu 50 ta seksiya va 13 ta ostturkumlarni ifodalaydi. Ushbu tanlov strategiyasi turkum ichidagi genetik xilma-xillikni qamrab olishni maqsad qiladi. O’simliklar tabiiy populyatsiyalaridan yangi barg namunalarini to‘plandi. Tadqiqotda 58 ta *Allium* turining to‘liq xloroplast genomi ketma-ketliklari sekvenslandi va Milliy Biotexnologiya Ma'lumot Markazidan (NCBI) identifikatsion raqamlar olindi. Xloroplast genom ketma-ketliklarini tahlil qilish bir nechta o‘zgaruvchan joylarni aniqladi, bu esa *Allium* turlari o‘rtasidagi filogenetik muammolar yechimini yechishda salmoqli hissa qo‘shadi. Ribosomal DNK (ITS) ketma-ketliklar va xloroplast ma'lumotlari bir-birini to‘ldiruvchi ma'lumotlarni taqdim etib, ba'zi kladlar ikkala ma'lumot to‘plami tomonidan yaxshi qo‘llab-quvvatlanayotgan bo‘lsada, boshqalari biroz nomuvofiqlikni ko‘rsatdi. Ushbu nomuvofiqlik *Allium* turkumining evolyutsion tarixini shakllantirishda gibridizatsiya va xloroplast o’tkazish jarayonlarining muhim rol o‘ynashi mumkinligini ko‘rsatdi, bu esa filogenetik munosabatlarni talqin qilishni murakkablashtiradi.

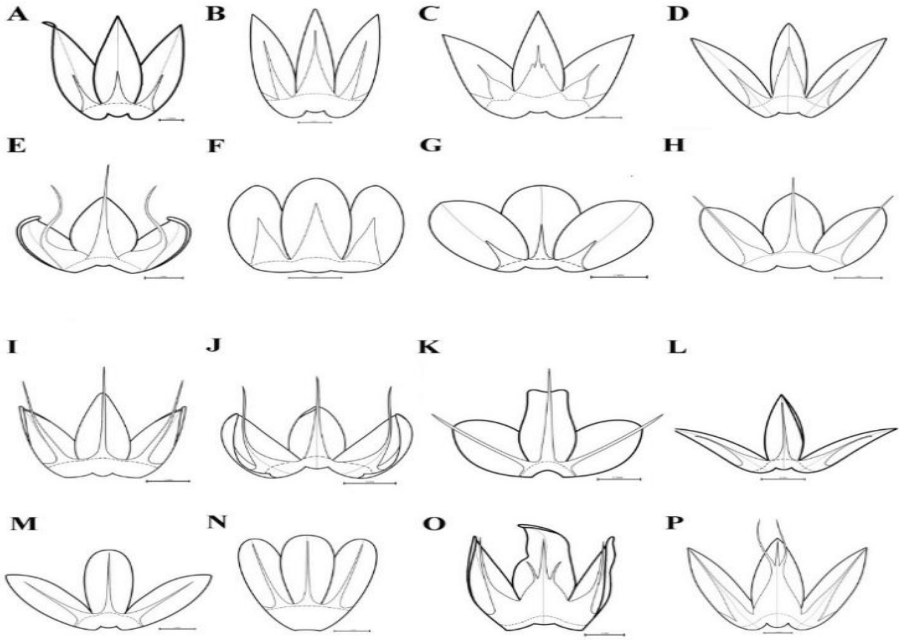
Filogenetik tahlillar *Allium* turkumi ichida birinchi va ikkinchi evolyutsion liniyalarda (EL1 va EL2) aniq evolyutsion chiziqlarni ko‘rsatdi (6-rasm). Ushbu chiziqlar monofiletik, bu esa ularning turkumining evolyutsion tarixida muhim tarmoqlarni ifodalashini ko‘rsatadi. Olingan natijalar, ushbu liniyalar *Allium* evolyutsiyasining dastlabki bosqichlarida ajralib chiqqanligini, ehtimol, bu esa atrof-muhit omillari va moslashuvchanlik jarayonlari orqali amalga oshirilganligini takidlaydi. Ushbu evolyutsion liniyalarga tegishli asosiy morfologik xususiyatlarni aniqlash, ularning xilma-xilligini shakllantirgan evolyutsion omillar haqida tushuncha beradi. Bunga qarama-qarshi ravishda, uchinchi evolyutsion liniya (EL3) ko‘proq murakkab munosabatlarni ko‘rsatdi, bir nechta turlar, polifiletik tarzda joylashadi. Ushbu natijalar, L3 liniyasida muhim evolyutsion jarayonlar, masalan, gibridizatsiya va gen oqimi jarayoni sodir bo‘lganligi, bu esa EL3 liniyasidagi turli guruhlarda o‘xshash morfologik xususiyatlarning paydo bo‘lishiga olib keladi. Ushbu liniyaning ribosomal DNK (ITS) ketma-ketliklari va xloroplast asosidagi filogeniyalaridagi nomuvofiqligi, evolyutsion mexanizmlarni, jumladan, atrof-muhit omillarining turlararo ta'sirlari va ular xilma-xilligining shakllantirishdagi potentsial rolini yanada chuqurroq o‘rganish zarurligini ta'kidlaydi.

Tadqiqot, shuningdek, *Allium* turlarining morfologik evolyutsiyasini o‘rganib, filogenetik munosabatlarni asosiy morfologik xususiyatlar bilan bog‘laydi. Tahlillar, ba'zi xususiyatlar, masalan, piyoz hajmi va barg shakli, ma'lum evolyutsion liniyalarga bog‘liqligini ko‘rsatdi. Ushbu natijalar *Allium* ichidagi morfologik xilma-xillikning tasodifiy o‘zgarishlar natijasi emas, balki atrof-muhit sharoitlariga moslashuvchanlik mexanizmlari bilan bog‘liq ekanligini taklif qiladi. Ushbu qonuniyatlarni tushunish, turkumining ekologik va evolyutsion dinamikalari haqida qimmatli tushunchalar berishi mumkin. *Allium* turlarining changchilari tuzilishi ham, ushbu turkumining filogenetik munosabatlarini tushunishda muhim rol o‘ynaydi. Taqqoslash filogenomik tahlilida turlicha changchi turlari turli xil turlarda kuzatilgan bo‘lib, bu turlarni tasniflash va evolyutsion tadqiqotlar uchun zarurligi takidlaydi.

Tadqiqotda ko‘plab *Allium* turlarida uchta tishli ichki changchilar mavjudligi aniqlangan (7-rasm), bu esa lateral (yon) qirralar markaziy qirralardan uzunroq bo‘lgan changchilar bilan tavsiflanadi. Ushbu morfologik xususiyat, turlarni farqlashda muhim ahamiyatga ega bo‘lib, evolyutsion moslashuvchanlikni ko‘rsatishi mumkin.



6-rasm. Xloroplastning 78 ta oqsil kodlovchi genlari DNK ketma-ketliklari asosidagi (o‘ngda) va yadroviy ribosomali DNK (ITS) asosidagi daraxtlar (chapgda) o‘rtasidagi topologik nomuvofiqlik.



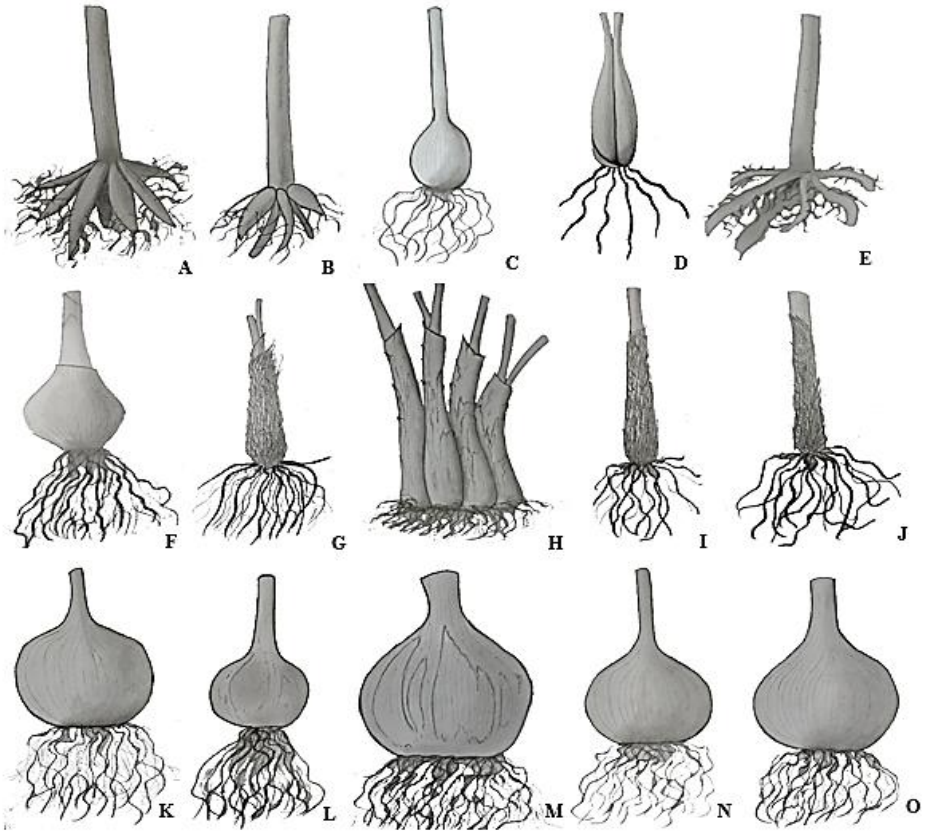
7-rasm. *Coerulea seksiyasiga mansub turlarning changchi shakllari*: A. *A. svetlanae*; B. *A. taciturnum*; C. *A. caeruleum*; sect. *Kopetdagia*: D. *A. kopetdagense*; *Eremoprasum* seksiyasi: E. *A. confragosum*; F. *A. incrustatum*; G. *A. jaxarticum*; H. *A. popovii*; I. *A. scrobiculatum*; J. *A. transvestiens*; K. *A.*

sabulosum; *Haneltia* seksiyasi: L. *A. haneltii*; *Codonoprasum* seksiyasi: M. *A. convallarioides*; N. A. *lenkoranicum*; *Multicaulia* seksiyasi: O. *A. ferganicum*; P. *A. rinae*.

Shuningdek, ba'zi turlarda oddiy tashqi changchilar mavjud bo‘lib, ular ba'zan kichik lateral qirralarga ega bo‘lishi mumkin, bu esa turkum ichidagi changchi tuzilmalarining xilma-xilligik darajasi yuqori ekanligini ko’rsatadi. Filogenetik daraxt bo‘ylab changchi turlarini o‘rganish morfologik evolyutsiya qonuniyatlarini ochib beradi va *Allium* turlarining ekologik moslashuvlari haqida ma'lumot beradi. Masalan, changchi tuzilmasidagi farqlar ma'lum ekologik sharoitlar yoki changlatish strategiyalari bilan bog‘liq bo‘lishi mumkin, bu esa ushbu xilma-xil turkumining evolyutsiyasida morfologiya va ekologiya o‘rtasidagi murakkab o‘zaro ta'sirni ko’rsatadi. Umuman olganda, changchi turi *Allium* turkumining filogenetik tahlilida asosiy morfologik xarakter sifatida xizmat qiladi, evolyutsion liniyalarni tiklashda yordam beradi va turkumining xilma-xilligi va moslashuv mexanizmlarini tushunishni oshiradi. Xulosa qilib aytganda, ushbu bob *Allium* turkumining keng qamrovli filogenomik tahlilini taqdim etadi, murakkab evolyutsion munosabatlarni ochib beradi va molekulyar va morfologik ma'lumotlarni birlashtirishning ahamiyatini ta'kidlaydi.

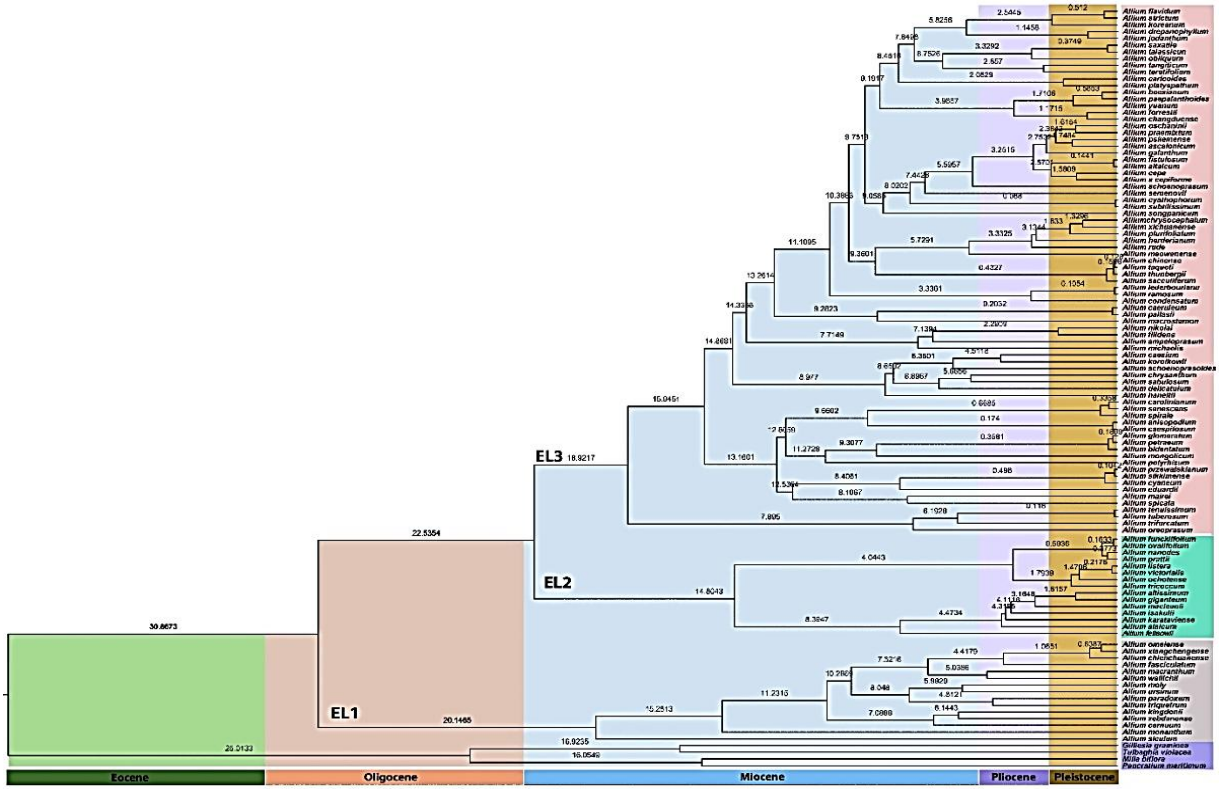
Piyoz po‘st tuzulishining tolali va to‘rli tuzilmalargacha bo‘lgan evolyutsiyasi, bu turkumning qurib qolish va mexanik shikastlanish kabi jismoniy bosimlarga moslashish qobiliyatini ko‘rsatadi. Tolali va to‘rli po‘stlar(qobiqlar), ya’ni piyoz usti hosila belgilar, har xil sharoitlarda, masalan, qurg‘oqchil hududlar yoki baland tog‘li muhitlarda yaxshiroq himoya tizimini ta’minlashi taxmin qilinadi (7-8-rasmlar). Bu Li va boshq. (2010) tomonidan bildirilgan fikrlar bilan hamohang bo‘lib, ular piyoz po‘stusti morfologiyasi *Allium* turlarining yashash joyiga moslashuvi bilan chambarchas bog‘liq ekanligini ta’kidlaganlar. Piyoz po‘stust tuzilmalarining xilma-xilligi ushbu belgilarning ma’lum ekologik bosimlarga javoban evolyutsiyalashganini ko‘rsatadi va turkumning keng hududlarni egallash qobiliyatiga hissa qo‘shadi. Yaqin qarindosh guruhlar ichida bir nechta po‘st turlarining mavjudligi esa, bu belgilar o‘xshash ekologik chaqiriqlarga mustaqil ravishda paydo bo‘lganini bildiradi. *Allium* turkumida changchi ipchalar evolyutsiyasi, xususan oddiydan uch tishli ipchalarga o‘tish jarayoni, turkum ichidagi ko‘payish strategiyalari va changlanish mexanizmlariga oid qimmatli ma’lumotlarni taqdim etadi. Oddiy ipchalar ehtimol ajdodiy belgi bo‘lib, umumiyroq tuzilmani ifodalaydi, uch tishli ipchalar esa hosila belgi bo‘lib, ma’lum changlatuvchi bosimlarga javoban paydo bo‘lgan bo‘lishi mumkin. Uch tishli morfologiya, murakkabroq va tarmoqlangan tuzilishi bilan ajralib turib, chang tuzulishini chiroyliroq ko’rsatish yoki uning changlanish jarayonini oshirishi mumkin, ayniqsa maxsus changlatuvchilarga tayanadigan turlarda. Bu Huang va boshq. (2014) ishlarida qayd etilgan bo‘lib, ular *Allium* turkumida chang ipi morfologiyasining ko‘payish biologiyasidagi ahamiyatini ta’kidlaganlar. Ma’lum guruhlarda uch tishli ipchalarning mavjudligi shuni ko‘rsatadiki, bu turlar o‘ziga xos changlatuvchilarni jalb qilish yoki ma’lum ekologik sharoitlarda ko‘payish samaradorligini optimallashtirish uchun moslashgan bo‘lishi mumkin. *Allium*

turkumining evolyutsion tarixi, geologik voqealari va iqlim o‘zgarishlari ta’sirida shakllangan filogenetik tafovut va biogeografik tarqalish o‘rtasidagi dinamik o‘zaro ta’sir sifatida namoyon bo‘ladi. Yadro (ITS) va plastid DNK ma’lumotlar to‘plamlariga asoslangan natijalarimiz *Allium* ning uchta asosiy evolyutsion kladlar (EL1, EL2 va EL3) ga diversifikatsiyalanganini isbotlovchi kuchli dalillarni beradi.



8-rasm. *Amerallium* ostturkumiga mansub bo‘lgan turlarining piyoz shakllari (15 ta tur): **A.** *A. fasciculatum*; **B.** *A. macranthum*; **C.** *A. paradoxum*; **D.** *A. ursinum*; **E.** *A. wallichii*; subgen. *Caloscordum*: **F.** *A. neriniflorum*; subgen. *Anguinum*: **G.** *A. nanodes*; **H.** *A. ovalifolium*; **I.** *A. prattii*; **J.** *A. victorialis*; subgen. *Melanocrommyum*: **K.** *A. alaicum*; **L.** *A. altissimum*; **M.** *A. giganteum*; **N.** *A. isakulii;* **O.** *A. macleanii*.

BEAST tahlili orqali yaratilgan xronogrammalar (9-rasm) *Allium* ning dastlabki radiatsiyasi Eotsen oxiri – Oligotsen boshiga, taxminan 30 mln yil avvalga to‘g‘ri kelishini ko‘rsatadi. Bu davr global sovish jarayonlari bilan mos keladi va ehtimol diversifikatsiyaning asosiy harakatlantiruvchi omili bo‘lgan bolishi mumkin (Friesen va boshq., 2006; Li va boshq., 2010). RASP dasturida BBM (Bayesian Binary MCMC) va S-DIVA (Statistical Dispersal-Vicariance Analysis) modellaridan foydalangan holda o‘tkazilgan ajdodlar arealni rekonstruksiya qilish *Allium* turkumining biogeografik kelib chiqishi va tarqalish qonuniyatlariga oid muhim ma’lumotlarni beradi(10-rasm). Natijalar *Allium* ning Markaziy Osiyo va unga qo‘shni hududlarda (A hududi) paydo bo‘lganini qat’iy ko‘rsatadi. Bu gipoteza mazkur mintaqaning *Allium* uchun biologik xilma-xillik markazi sifatida tan olingan maqomi bilan yaxshi asoslangan (Fritsch va Friesen, 2002).

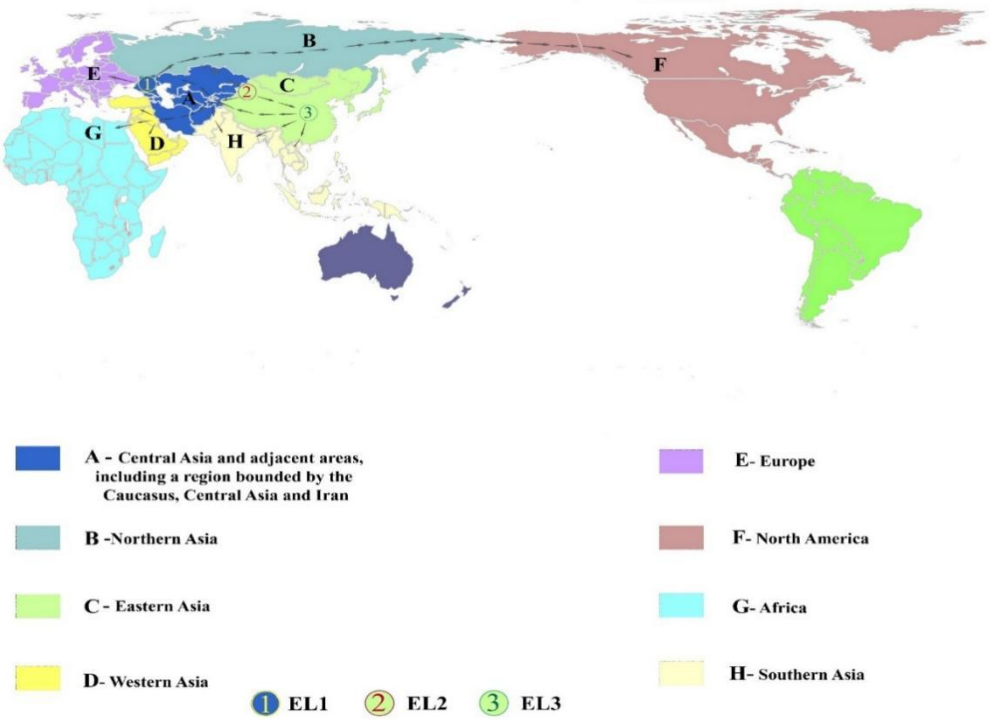


9-rasm. *Allium* turkumining ribosomal DNK (ITS) ma'lumotlar to'plamiga asoslangan holda BEAST dasturi orqali olingan xronogramma. Bu yerda o'rtacha (mean) qiymatlar ko'rsatilgan va *Allium* turkumining uchta evolyutsion liniyalar (EL1–EL3) filogeniyasi aks ettirilgan.

Markaziy Osiyo – Kavkaz, Markaziy Osiyo yondosh hududlari va Eronni qamrab olgan holda – qurg'oqchil cho'llardan tortib mo'tadil tog'li hududlargacha bo'lgan turli ekologik sharoitlarga ega bo'lib, *Allium* ning dastlabki diversifikatsiyasi uchun qulay muhit yaratgan. Mintaqaning murakkab relyefi va iqlim o'zgaruvchanligi ko'plab ekologik nishalarni yuzaga keltirgan, bu esa turlanish va turkumning ilk vakillarining shakllanishini osonlashtirgan.

Markaziy Osiyo (A hududi) ning ajdod areal sifatida yuqori ehtimollik darajasi (BBM 45–47%, S-DIVA 50%) turkumning kelib chiqishi va dastlabki diversifikatsiyasida mintaqaning muhim o'rin tutganini ko'rsatadi. Bu xulosa ilgari olib borilgan tadqiqotlar bilan uyg'un bo'lib, ular ham Markaziy Osiyoni *Allium* ning asosiy xilma-xillik markazi sifatida qayd etgan (Friesen va boshq., 2006).

Mintaqaning o'ziga xos iqlimiy va geologik xususiyatlari, jumladan tog' tizmalari va qurg'oqchil hududlarning mavjudligi, turkumning dastlabki radiatsiyasi uchun zarur sharoitlarni yaratgan bo'lishi mumkin. *Allium* ning Markaziy Osiyodagi dastlabki diversifikatsiyasi, shuningdek, mintaqaning iqlimiy beqarorlik davrlarida "refugium" sifatidagi roli bilan ham qo'llab quvvatlangan. Bu esa turlarning uzoq vaqt davomida saqlanishi va diversifikatsiyasiga imkon yaratgan.



10-rasm. RASP dasturining BBM va S-DIVA usullari yordamidagi o'tkazilgan tahlillari. *Allium* turkumining ITS ketma-ketliklari asosidagi dastlabki evolyutsiyasi davridagi taxminiy tarqalish yo'nalishlari keltirilgan.

XULOSALAR

"*Allium* L. (Amaryllidaceae) turkumining filogeniyasi, biogeografiyasi va evolyutsiyasi (Markaziy Osiyo misolida)" mavzusidagi fan doktori (DSc) dissertatsiyasi doirasida olib borilgan tadqiqotlar natijasida quyidagi xulosalar taqdim etildi:

1. Ilk bor *Allium* turkumining 14 ta ostturkum va 58 ta seksiyaga mansub 95 turida aniqlangan urug' epidermisining antiklinal devor tuzilishi (7 xil), epidermis hujayralari shakllari (6 xil), periklinal devor yuzasidagi verrukalar, hujayra naqshlari hamda qo'shni hujayralar orasidagi masofa kabi morfologik belgilar tur va seksiya darajasida ishonchli diagnostik mezonlar ekanligi aniqlandi. Ushbu belgilar asosida umumiy turkum doirasida turlarni ishonchli aniqlash imkonini beradigan taksonomik kalit ishlab chiqildi va amaliy qo'llash imkonini beradi.

2. *Allium* turlarining evolyutsion tarixi va biogeografik kelib chiqishiga ko'ra, EL-1 dastlabki evolyutsion liniya vakillarida olti burchakli epidermis hujayra shakli va periklinal yuzaning verrukalardan xoli bo'lishi kabi primitiv belgilar ustun bo'lgan. EL-2 va EL-3 liniyalarda esa epidermis hujayra devorining burmalanishi hamda periklinal yuzalarda verrukalarning rivojlanishi *Melanocrommyum* va *Allium* ostturkumlari vakillarining qurg'oqchil Miotsen davri uchun morfologik adaptatsiyasini ko'rsatadi.

3. Ribosomal DNK ning ITS ketma-ketliklari asosida qurilgan filogenetik daraxtlar hamda urug' makro- va mikromorfologik belgilariga tayangan filogenetik tahlillar *Allium* turlarining kelib chiqishi Markaziy Osiyo va unga tutash hududlar — Kavkaz, Eron va Markaziy Osiyo oralig'i bilan chambarchas bog'liq ekanligini

ishonchli ravishda ko‘rsatdi. Urug‘ epidermisi morfologiyasining molekulyar kladlar bilan yuqori darajada mos kelishi, ayniqsa, Markaziy Osiyo taksonlarining *Allium* turkumi evolyutsiyasida markaziy o‘rin tutganini tasdiqlaydi. Ushbu ma’lumotlar “Eski dunyo”ga mansub evolyutsion liniyalar dastlab Markaziy Osiyo–Eron–Kavkaz mintaqasida shakllanganini, keyinchalik esa *Allium* turlarining Shimoliy Osiyo orqali “Yangi dunyo” hududlariga, xususan Bering bo‘g‘ozi orqali tarqalganligini asoslaydi.

4. Olingan filogenetik daraxt rekonstruksiya natijalariga ko‘ra, *Cepa* seksiyasi turlari Shimoliy Osiyo va Markaziy Osiyo turlarini o‘z ichiga olgan ikkita alohida molekulyar guruhga ajraldi. Bu holat Markaziy Osiyoga xos turlarining Shimoliy va Sharqiy Osiyo guruhlari o‘rtasida o‘zaro gibridizatsiya orqali xloroplast o‘zlashtirilishi jarayonlari natijasida shakllangan “qadimiy gibrid taksonlar” ekanligini hamda seksiya evolyutsiyasida gibridlanish muhim evolyutsion omil bo‘lganini tasdiqlaydi.

5. *Allium* ostturkumi turlarining xloroplast genomlariga xos xususiyatlarga ko‘ra, faqat ushbu ostturkumda kuzatiladigan gen yo‘qolishlari (*rpl22, rps16, infA*) hamda faol psevdogenlashuv holatlari (*rps2, accD, psaI, rpl20, rpl23, rpl32, rps16* va *infA*) aniqlangan. Ushbu genomik o‘zgarishlar *Allium* ostturkumi xloroplast genomlarini boshqa ostturkumlardan farqlab, ularning o‘ziga xos evolyutsion yo‘nalishga ega ekanligini ko‘rsatadi. Shuningdek, xloroplast genomlaridagi *matK* va *rpoC2* oqsil kodlovchi genlar eng yuqori o‘zgaruvchan hududlar sifatida aniqlanib, filogenetik daraxtlar topologiyasiga mos keladi hamda *Allium* turkumining barcha turlari uchun DNK-barkodlash va filogeografik tadqiqotlarda universal barkodlar sifatida tavsiya etiladi.

6. Morfologik va filogenetik tahlillar *Allium* turkumining dastlabki ajdod liniyalarida sinapomorfik belgilar, jumladan qog‘ozsimon qobiqli, kichik haqiqiy piyozli, tishsiz chang ipli hamda pushti va oq rangli gullarga ega shakllar ustun bo‘lganini ko‘rsatdi. Biroq Markaziy Osiyoda kechgan keyingi evolyutsion jarayonlar davomida *Allium* turlarida ushbu belgilar bilan bir qatorda yirik piyozli va rizomli, tishli chang ipli, sariq va ko‘k rangli gullarga ega shakllarning paydo bo‘lishi kuzatilib, bu holat hududda ikkilamchi morfologik diversifikatsiya (*secondary diversification*) yuz berganidan dalolat beradi.

7. *Allium* turkumi ichidagi asosiy evolyutsion liniyalarning ajralishi Oligotsen–Miotsen davrlariga to‘g‘ri keladi. Yadroviy genomlar asosida o‘tkazilgan vaqt-kalibrlangan filogenetik tahlillar natijasida birinchi evolyutsion liniya (EL-1) Oligotsen davrida (taxminan 30,9 mln yil avval) Markaziy Osiyo va unga tutash hududlarda (Kavkaz–Eron–Markaziy Osiyo mintaqasi) shakllangani aniqlandi hamda keyinchalik ushbu hududdan Yevropa va Shimoliy Amerika tomon diversifikatsiyalangan. Ikkinchi evolyutsion liniya (EL-2) Erta Miosenda (taxminan 22,5 mln yil avval) Sharqiy Osiyoda, uchinchi evolyutsion liniya (EL-3) esa Erta Miosenda (taxminan 18,9 mln yil avval) Markaziy Osiyo va unga tutash hududlarda yuz berib, faol diversifikatsiya jarayonlarini boshdan kechirgan. Plastid genomlari asosidagi tahlillar esa dastlabki evolyutsion liniya (EL-1) yoshi yadroviy genomlar bo‘yicha olingan baholarga nisbatan taxminan 4 mln yilga farq qilishini ko‘rsatdi.

SCIENTIFIC COUNCIL DSc.05/2025.27.12.B.23.01.M ON AWARD OF SCIENTIFIC DEGREES AT THE INSTITUTE BOTANY

INSTITUTE OF BOTANY

YUSUPOV ZIYOVIDDIN OLIMJON UGLI

MOLECULAR PHYLOGENY, BIOGEOGRAPHY AND EVOLUTION OF *ALLIUM* L. (AMARYLLIDACEAE) WITH A FOCUS ON CENTRAL ASIA

03.00.05 – Botany

DISSERTATION ABSTRACT OF THE DOCTOR OF SCIENCE (DSc) ON BIOLOGICAL SCIENCES

Tashkent – 2026

The title of the doctoral dissertation (DSc) has been registered by the Supreme Attestation Commission at the Ministry of higher education, science and innovations of the Republic of Uzbekistan with the registration number of B2025.2.DSc/B267.

The dissertation has been carried out at the Institute of Botany.

The abstract of the dissertation is posted in three languages (Uzbek, English, Russian (resume)) on the webpage of the Scientific Council (www.botany.uz) and on the website of the Information-educational portal "ZiyoNET" (www.ziyonet.uz).

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The defense will be held on «10» March 2026 at 14:00 at the meeting of the Scientific Council DSc.05/2025.27.12.B.23.01.M on award of scientific degrees at the Institute of Botany (Address: 32 Durmon yuli str., Tashkent, 100125, Uzbekistan. Conference hall of the Institute of Botany. Phone.: (99871) 262-37-95; Fax: (+99871) 262-79-38; E-mail: botany@academy.uz).

The dissertation has been registered at the Informational Resource Centre of the Institute of Botany under № 86 (Address: 32 Durmon yuli str., Tashkent, 100125, Uzbekistan. Phone.: (+99871 262-37-95).

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INTRODUCTION (abstract of DSc thesis)

Actuality and importance of the topic of the dissertation. At present, one of the priority areas in the field of biology is the study of the phylogenetic relationships, evolutionary history, and biogeographical formation patterns of plants based on modern molecular-genetic and phylogenomic approaches. The rapid development of genomic technologies, the widespread application of high-precision DNA sequencing methods, and the growing potential of bioinformatic analyses make it possible to interpret the complex processes of plant evolution in a deeper and more reliable manner. This progress necessitates the revision of traditional classifications based on morphological and anatomical features, as well as the clarification of phylogenetic relationships at the genus and species levels.

Central Asia represents an important biogeographical region characterized by high plant diversity and taxonomic complexity. The region's intricate geological structure, the convergence of mountain and desert systems, and historical paleoclimatic changes have played a significant role in the evolutionary formation, diversification, and range restructuring of plant genera and infrageneric taxa. Comprehensive studies of the flora of this region at the genus and infrageneric levels, based on phylogenetic, morphological, and molecular-genetic approaches, allow for a clearer understanding of evolutionary relationships among higher taxa, interpretation of the evolutionary formation of morphological traits and adaptive characteristics, and explanation of adaptation mechanisms linked to ecological factors. These investigations are of great scientific significance for modern botany and evolutionary biology.

In the Republic of Uzbekistan, special attention is devoted to the study and conservation of biological diversity. The inventory of the country's plant species based on modern molecular-genetic approaches provides a fundamental scientific basis for identifying the structural and evolutionary relationships of the flora. Molecular and phylogenetic data are of great importance for monitoring regional flora under conditions of climate change, ensuring rapid and reliable species identification, and scientifically supporting strategies aimed at conserving biological resources.

This dissertation research contributes, to a certain extent, to the implementation of tasks set forth in the Resolution of the President of the Republic of Uzbekistan dated September 4, 2017, No. PQ-3256, *"On measures for organizing the activities of the Institute of Botany and the Institute of Zoology of the Academy of Sciences of the Republic of Uzbekistan"*; the Presidential Resolution dated May 20, 2022, No. PQ-251, *"On measures for the cultivation, processing, and extensive use of medicinal plants in therapeutic practice"*; as well as Articles 49 and 115 of the newly revised Constitution of the Republic of Uzbekistan and other relevant normative and legal documents.

Compliance with national scientific and technological priorities.

This research corresponds to one of the key priority areas identified in the national strategy for the development of science and technology in the Republic of Uzbekistan, namely Priority Area V: "Agriculture, Biotechnology, Ecology, and

Environmental Protection."

Overview of international research on the dissertation topic.

Classical and modern studies on the genus *Allium* L. have been conducted at leading scientific centers and higher education institutions worldwide, contributing significantly to understanding its taxonomy, molecular phylogeny, biogeography, and evolution. Leading universities and research institutions participating in these studies include the Leibniz Institute of Plant Genetics and Crop Plant Research (IPK), Germany; the Botanical Garden of Osnabrück University, Germany; Sichuan University, China; Changwon National University, Republic of Korea; the Xishuangbanna Tropical Botanical Garden, China; Lomonosov Moscow State University, Russia; and the Kunming Institute of Botany, China.

As a result of worldwide studies on the molecular taxonomy of the genus *Allium*, a number of important findings have been obtained. In particular, the genus was studied based on the ITS gene and classified at the subgenus and section levels (Germany, Osnabrück University). Subsequently, phylogenomic analyses based on complete chloroplast genomes of 39 species were conducted, and the age of origin of the genus was estimated to be 34–47 mln years (China, Sichuan University). Biogeographic studies have shown that *Allium* species dispersed from the Old World to the New World via East Asia and Europe (China, Sichuan University; Germany, Leibniz Institute). In addition, the micromorphology of seed epidermal cells was investigated in 48 species from Central Asia, and its taxonomic significance was demonstrated (Korea, Changwon University).

At present, international research on the molecular taxonomy, evolution, and biogeography of the genus *Allium* is mainly focused on the following priority directions: determining evolutionary relationships within the genus using phylogenomic approaches (complete chloroplast genomes and nuclear genomes); resolving taxonomic inconsistencies through the integration of molecular and morphological characters; reconstructing the origin and historical migration routes of *Allium* species using biogeographic modeling; assessing the taxonomic significance of micromorphological characters (seed shape and epidermal cell structure); and evaluating the impact of hybridization and polyploidy processes on the evolution of *Allium*.

Degree of study of the problem. The scientific study of the genus *Allium* dates back to the eighteenth century, with its taxonomic foundations initially established by C. Linnaeus (1753). In subsequent periods, the description and typification of *Allium* species were systematically carried out by J.G. Baker (1874, 1875, 1892); E. Regel (1879); P.E. Boissier (1882); E. Regel & A. Herder (1884); A. Engler (1892); A.A. Grossheim (1940); V.I. Grubov (1955); R.V. Kamelin (1973); P. Hanelt (1992); N. Friesen (2007); F.O‘. Hassanov (2008) and other researchers. In these studies, the internal classification of the genus was developed based on a comprehensive set of diagnostic morphological characters, including bulb and rhizome structure, leaf morphology, perianth and floral elements, stamens, and seed traits, and various classification models at the subgeneric and sectional levels were proposed.

In later stages, the distribution of *Allium* species across different geographic regions, their molecular phylogeny, biogeographic formation, and evolutionary

trajectories were extensively investigated using modern molecular-genetic and phylogenomic approaches alongside traditional morphological methods. These studies placed particular emphasis on elucidating interspecific phylogenetic relationships, major evolutionary lineages, and historical migration and diversification processes based on nuclear and plastid genome markers (Hanelt, 1992; Fritsch & Friesen, 2002; Friesen et al., 2006, 2014; Gurushidze et al., 2008, 2010; Blattner et al., 2008; Li et al., 2010, 2016; Cheryomushkina, 2012; Nguyen et al., 2013; Xie et al., 2019; Yusupov et al., 2021; Han et al., 2022; Zhou et al., 2023).

Studies focusing on Central Asia have likewise drawn extensively on key scientific literature concerning the regional flora in investigations of the phylogeny, biogeography, and evolution of the genus *Allium*. In particular, classical and contemporary works addressing the taxonomic structure, evolutionary relationships, and historical distribution of *Allium* species occurring in Central Asia have provided an essential methodological framework for morphological and molecular-phylogenetic interpretations (Cheryomushkina, 2002, 2012; Hassanov, 2008, 2018, 2022; Qin et al., 2010; Friesen et al., 2006, 2014, 2024, 2025; Choi et al., 2012; Tan et al., 2017; Basamunkh et al., 2020; Dong et al., 2022; Gurushidze et al., 2008, 2010; Tojibaev et al., 2014).

Nevertheless, phylogenetic reconstructions constructed to date that include *Allium* species distributed in Central Asia, together with integrated morphological datasets, have not fully elucidated the evolutionary and biogeographic development of the regional flora due to insufficient taxon sampling. This circumstance highlights the need for comprehensive phylogenetic and evolutionary studies encompassing a broad representation of *Allium* species from Central Asia. Such an approach, based on modern molecular methodologies, provides a robust scientific foundation for in-depth and reliable analyses of the phylogenetic structure, evolutionary trajectories, and divergence events of the genus *Allium* across different geological periods, and thus possesses both scientific and practical significance [1].

Connection of the research with the research plans of the scientific research institution where the dissertation is being carried out.

This dissertation research was conducted within the framework of state-funded fundamental research programs, including the project “PFI-5 Tree of Life: Monocotyledons of Uzbekistan” (2020–2024) implemented by the Laboratory of Molecular Phylogeny and Biogeography of the Institute of Botany, as well as the international Uzbekistan–Belarus scientific and technical program “Genetic inventory of rare and endangered species of Belarus and Uzbekistan using DNA barcoding technology” (Project No. MRB-AN-2019-30). In addition, the research was carried out within applied projects related to the establishment of the “Global *Allium* Garden (Tashkent–Kunming Centers)” at the Tashkent and Kunming Botanical Gardens.

The aim of the research is to determine the evolutionary relationships,

[1] http://www.works.doklad.ru, http://www.dissercat.com, http://www.researchgate.net, http://www.webofscience.com, and other sources.The review of scientific research related to the topic of the dissertation has been developed based on materials from

phylogenetic structure, and diversification processes among species of the genus *Allium*, and to substantiate the applicability of their micromorphological characters in the taxonomic system.

The objectives of the research:

to study the seed micromorphology and, based on the identified micromorphological characteristics of seeds, to develop a morphological taxonomic key for distinguishing the species of the genus *Allium*;

to integrate seed morphological data into the molecular phylogenetic tree;

to develop a biogeographical origin hypothesis for the species of the genus *Allium* based on data obtained from seed morphology and preliminary molecular analyses;

to identify the evolutionary and phylogenetic closest relatives of *Allium cepa* within the section *Cepa* using molecular data, and to evaluate the role of Central Asian species in the domestication process;

to analyze and determine the causes of inconsistencies between phylogenetic trees constructed based on nuclear and chloroplast data in the section *Cepa*, and to reveal the hybridization processes occurring among species;

to conduct plastome genome analyses of interspecific taxa belonging to the subgenus *Allium* widely distributed in Central Asia, and to determine their phylogenetic relationships;

to analyze single nucleotide polymorphisms (SNPs) in plastome genomes and identify barcoding markers for the species of the subgenus *Allium* and the entire genus based on the detected variable regions;

to determine and analyze the evolutionary changes of synapomorphic characters specific to *Allium* species;

to identify the formation time of the main evolutionary lineages (EL1–EL3) within the genus *Allium* based on nuclear and plastid genomes, and to reconstruct their biogeographical origins.

Research object: Species of the subgenus *Allium* and section *Cepa* belonging to the genus *Allium* (Amaryllidaceae).

Research subject comprises the phylogenetic relationships, evolutionary development pathways, and biogeographic formation patterns..

Research methods: field investigations, scanning electron microscopy, phylogenetic, phylogeographic, and statistical methods were employed in the dissertation.

The scientific novelty of the research is as follows:

in distinguishing *Allium* species, the periclinal surface of seed epidermal cells and the intercellular distance have been identified as important new diagnostic characters;

based on analyses combining the ITS gene phylogenetic tree and seed micromorphological data, it has been revealed that the ancestral *Allium* species originated in the Central Asia–Iran–Caucasus region, and later dispersed from the "Old World" to the "New World" through the Bering Strait via Northern Asia;

analyses based on chloroplast genomes have reconstructed the phylogenetic tree for the section *Cepa*, demonstrating that Central Asian species such as *A.*

oschaninii, *A. praemixtum*, and *A. pskemense* originated through chloroplast capture processes resulting from hybridization events between Northern and Eastern Asian groups;

molecular studies have identified highly variable genes such as *rpoC2*, *ycf1*, *ndhF*, *matK*, and *ndhD* as effective DNA barcode markers for constructing phylogenetic trees of *Allium* species;

in the early ancestral *Allium* species, synapomorphic characters have been identified, including the presence of papery bulb tunics, small true bulbs, toothless filaments, and flowers with pink or white coloration;

the earliest evolutionary lineage of the genus *Allium* (EL1) was formed in Central Asia and adjacent territories (the Caucasus, Iran, and the Central Asian transitional zone) and subsequently underwent diversification;

the divergence of the main evolutionary lineages within the genus *Allium* occurred approximately 30.9 mln years ago, corresponding to the Oligocene–Miocene epochs.

The practical results of the research:

A comprehensive taxonomic key has been developed for 95 species belonging to the genus *Allium*, based on diagnostic characteristics of seed epidermal cells that are important for distinguishing species;

for 59 species of the subgenus *Allium* distributed in Central Asia, a complete morphological analysis of floral internal structures (types and shapes of filaments) has been carried out, and for 80 species of the genus *Allium*, detailed illustrations of bulb morphology and floral structures have been produced;

complete chloroplast genomes for 77 Central Asian *Allium* species and approximately 110 nuclear DNA (ITS gene) sequences have been determined and deposited in the international GenBank (NCBI) database;

molecular markers significant for new phylogeographic and taxonomic studies (*ycf1*, *ndhF*, *rpoC2*, *matK*, and *ndhD* genes) have been identified, and their application as universal DNA barcode markers for the reliable identification of rare and protected *Allium* species has been substantiated.

The reliability of the research esults was ensured through the application of modern and scientifically recognized methods. Seed morphology was studied using scanning electron microscopy (SEM), while chloroplast genomes were analyzed using comprehensive molecular phylogenetic approaches. The obtained phylogenetic results were subjected to cladistic analysis and compared with publicly available ITS sequences and whole chloroplast genomes, which strengthened the robustness of the conclusions. The main findings of the study were presented at national and international scientific conferences and were positively evaluated by subject-area specialists. The results of the molecular phylogenetic analyses were published in leading scientific journals, and the DNA sequences were deposited in the international GenBank database (NCBI; https://www.ncbi.nlm.nih.gov/), ensuring data transparency, verifiability, and the possibility of reuse.

Scientific and practical significance of the research results.

The scientific significance of this research is demonstrated by the biogeographic justification of the formation of evolutionary lineages of the genus

Allium during the Oligocene and Miocene periods, the development of a novel approach to species diagnosis based on micromorphological characters of seed epidermal cells, the construction of molecular phylogenetic trees integrated with morphological data using plastid genomes from 110 *Allium* species, as well as the clarification of subgeneric and sectional classification within the genus, particularly revealing processes of hybridization and chloroplast genome capture within species of section *Cepa*.

The practical significance of the research is reflected in the applicability of the phylogenomic trees constructed on the basis of identified molecular-phylogenetic and morphological characters for breeding programs, especially in the development of new cultivars of onion (*Allium cepa*) involving closely related wild relatives, as well as in the development of DNA barcodes and diagnostic keys based on seed micromorphology for accurate and rapid species identification.

Implementation of the research results.

Based on the results obtained from the study of the phylogeny, biogeography, and evolution of the genus *Allium* (Amaryllidaceae) with reference to Central Asia, the following outcomes were achieved::

Comprehensive analyses of complete chloroplast genomes and nrDNA (ITS region) from more than 77 *Allium* species were conducted. The developed approaches for laboratory-based species identification and rapid determination of geographic origin of plant taxa were implemented within the fundamental research program **"**Tree of Life: Monocotyledons of Uzbekistan" (2021–2024) carried out at the Laboratory of Molecular Phylogeny and Biogeography, Institute of Botany, Academy of Sciences of the Republic of Uzbekistan (Certificate No. 4/1255-1522, dated June 20, 2025, Academy of Sciences of the Republic of Uzbekistan). As a result, it became possible to identify the most ancient lineages of the genus and to detect "ancient hybridized" taxa among Central Asian representatives, with potential applications in domestication and breeding processes..

Based on molecular-phylogenetic analyses, DNA sequence data (chloroplast genomes and ITS regions) obtained from 105 samples representing 77 species were deposited in the international NCBI GenBank database (https://www.ncbi.nlm.nih.gov/) under accession numbers NC_044411, NC_044412, NC_068792, NC_068793, NC_068794, NC_068796, OP642457, OP643522, PQ308296, and PQ308298. The integration of these data provided new insights into the molecular taxonomy of the genus *Allium*, significantly enriching knowledge of local species diversity, expanding phylogenetic and biogeographic perspectives on the flora of Central Asia, and enabling the identification of taxa previously unknown to science..

Furthermore, the approach for laboratory-based species identification through the assessment of molecular-phylogenetic and biogeographic relationships between *Allium* species from Uzbekistan and East Asia, combined with SEM-based analyses of seed macro- and micromorphological characters, was implemented within the international project **"**Global *Allium* Garden" (U1802232, 2018–2022**)** conducted at the Kunming Institute of Botany, Chinese Academy of Sciences (Certificate dated February 5, 2025, Chinese Academy of Sciences). This implementation facilitated

the clarification of evolutionary relationships among *Allium* species, the development of new taxonomic concepts, and the creation of modern taxonomic identification keys for the genus.

Approval of the research results.

The results of this research have been discussed at 2 international and 2 national scientific-practical conferences.

Publication of the research results.

A total of 16 scientific works have been published on the dissertation topic. Among these, 11 articles appeared in journals recommended by the Higher Attestation Commission of the Republic of Uzbekistan for publishing key scientific results of doctoral dissertations, including 3 articles in national journals and 8 in international journals.

Structure and volume of the dissertation.

The dissertation consists of an introduction, 5 chapters, a conclusion, a list of references, and an appendix. The total volume of the dissertation is 182 pages.

MAIN CONTENT OF THE DISSERTATION

The Introduction section justifies the relevance and necessity of the dissertation work, highlighting ITS alignment with the priority directions of scientific and technological development. It also provides a detailed review of scientific research conducted both in the Republic and abroad on the dissertation topic, the level of study of the problem, as well as the main objectives, tasks, object, and subject of the research. Additionally, the practical implementation of the research results, the published works, and the structure of the dissertation are described.

The first chapter of the dissertation, titled "**History of *Allium* L. taxonomy and currently accepted taxonomy**" analyzes the taxonomic history of the genus *Allium* and the currently accepted taxonomic framework. The genus *Allium*, one of the largest among petaloid monocots with over 1000 identified species, has long fascinated botanists due to ITS remarkable morphological diversity, ecological adaptation, and economic significance. Important crops such as onion (*A. cepa*), garlic (*A. sativum*), leek (*A. ampeloprasum*), and bunching onion (*A. fistulosum*) exemplify the genus's global impact in agriculture and cuisine (Burba & Galmarini, 1994; Wheeler et al., 2013). The characteristic sulfur compounds responsible for their pungent odor and flavor further distinguish *Allium* species (Fritsch & Friesen, 2002). Centers of diversity lie in Central and Eastern Asia, the Mediterranean Basin, and North America, reflecting a wide ecological distribution (Khassanov, 2018). Taxonomic studies of *Allium* began with early morphological classifications based on floral filaments (Linnaeus, 1763). Through the 18th and 19th centuries, scholars like Halleir (1745), Don (1832), and Koch (1837) refined classification schemes, followed by major revisions by Regel (1875, 1887), Vvedensky (1935), and Traub (1968). As knowledge expanded, classifications fluctuated between a few dozen species and several hundred, grouped into multiple subgenera and sections (Kamelin, 1973; Hanelt, 1990). The integration of molecular data in the late 20th century

revolutionized taxonomy: Hanelt et al. (1992) and Gregory et al. (1998) advanced a framework of subgenera and sections, culminating in Friesen et al. (2006) who proposed 15 subgenera and 72 sections encompassing ~780 species. They also identified three major evolutionary lineages supported by molecular evidence (Friesen et al., 2006; Li et al. 2010).

Morphological complexity continues to pose challenges, as critical traits like seed testa structure or bulb tunic form are often obscured in herbarium specimens, leading to frequent misidentifications (Hanelt et al., 1992; Khassanov & Fritsch, 1994). Cytological studies revealed a predominance of basic chromosome number x=8, but with considerable variation and extensive polyploidy, a key driver of adaptation and speciation within the genus (Traub & Traub, 1968; Ohri et al., 1998; Wu et al., 2010). Polyploidy, often linked to environmental stress adaptation, has allowed *Allium* species to diversify under shifting climatic conditions from the Miocene to Pliocene (Han et al., 2020; Mayrose et al., 2010).

Recent phylogenomic studies employing nuclear genomic and plastid data aim to resolve longstanding ambiguities, as ITS-based phylogenies have shown limited resolution (Xie et al., 2020). These approaches promise greater clarity on evolutionary relationships, divergence times, and the interplay between morphological innovation and environmental adaptation. Thus, the history of *Allium* taxonomy reflects both the progression of botanical science—from morphology to molecular phylogenetics—and the genus's role as a model for studying polyploidy, adaptation, and diversification in monocots.

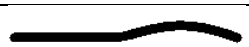
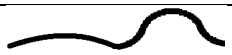
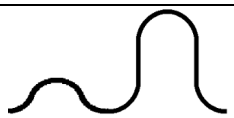
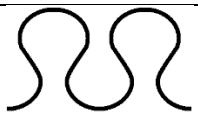
In the second chapter of the dissertation, titled "**Macro- and Micromorphological Seed Characteristics of the Genus *Allium*,**" the most comprehensive study to date of the macro- and micromorphology of *Allium* seeds has been conducted. The research examined 95 species (98 samples) belonging to 14 subgenera and 58 sections, using scanning electron microscopy (SEM) to analyze characteristics such as the surface area of the periclinal walls of 10 seed coat cells, the distances between the cells, cell shapes, and the arrangement and structure of anticlinal and periclinal walls.

The results showed that, for the first time, the surface area of the periclinal walls of 10 seed coat cells and the distances between them were found to be useful in distinguishing species within the genus *Allium* Based on seed characteristics, a taxonomic key and a hypothesized reconstruction of early migration routes during the initial stages of *Allium* evolution were proposed. The study revealed that the shapes of seed coat cells reflect different evolutionary stages within *Allium*

Loose cell arrangement, small or absent verrucae (wart-like structures), concave periclinal walls, straight or arc-shaped anticlinal walls, and broadly ovate seeds were considered primitive characteristics. Intermediate evolutionary traits included reticulate or net-like cell patterns, moderately developed verrucae, flat periclinal walls, arc or S-type anticlinal walls, and narrowly ovate seeds. The most advanced traits were characterized by closely packed cells, large verrucae, convex periclinal walls, U-type and Ω-type anticlinal walls, and ovate or flattened ovate seeds.

Table 1.

Dominant curvature types of anticlinal wall and dominant testa cell shapes

A. Anticlinal wall: dominant curcave type:			B. Dominant testa cell shapes:		
	Straight to Arched	7		Orbicular	1
	S-type	6		Elliptic	2
	Arched to S-type	5		Oblong	3
	U-type	4		Rectangular	4
	S to U-type	.3		5 edged	5
	Ω-type	2		6 edged	6
	U to Ω-type	1			

When these morphological traits were mapped onto a phylogenetic tree based on ITS (internal transcribed spacer) sequences (Figure 1), the cell features largely supported the existence of three major evolutionary lineages (EL1, EL2, EL3) within *Allium* (Figure 2).

The members of the first evolutionary lineage and the outgroup species exhibited the most primitive seed coat characteristics. Taxa in the second evolutionary lineage generally possessed intermediate traits, except for members of the subgenus *Melanocrommyum*, which displayed advanced features. In the third evolutionary lineage, most species retained primitive seed coat traits, with the exception of representatives of the subgenus *Allium*, which predominantly showed advanced characteristics.

It is hypothesized that the ancestors of *Allium* originated in a region bordered by the Caucasus, Central Asia, and Iran. From this area, taxa belonging to the first evolutionary lineage likely migrated either toward southern Europe and the eastern Mediterranean or toward East Asia and the Far East. For example, members of the subgenus *Nectaroscordum*, which displayed the most primitive seed coat cell characteristics, appear to have moved westward. The evolution of *Allium* seed coat characteristics is thought to be primarily influenced by two factors: the shape of the periclinal walls and the type of undulation in the anticlinal walls. Primitive species exhibit concave periclinal walls and straight or arc-shaped anticlinal walls, whereas more advanced taxa possess convex periclinal walls and undulating anticlinal walls (S-type, U-type, U-Ω-type, or Ω-type).

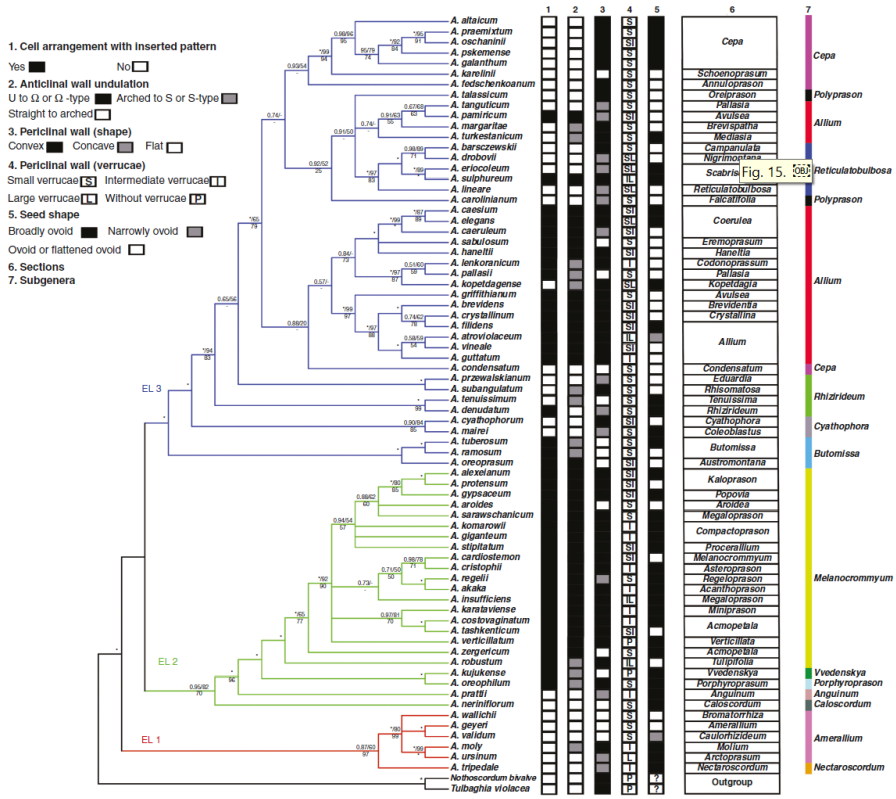


Figure 1. Phylogenetic tree based on ITS sequences linked with seed cell shapes.

In conclusion, the comprehensive study of the macro- and micromorphology of *Allium* seeds provided valuable insights into the taxonomic, evolutionary, and biogeographic relationships within this large and economically important genus. Seed coat traits were shown to be not only useful for distinguishing species but also reflective of the recognized evolutionary stages within *Allium* The proposed migration routes and the evolution of seed coat traits form a basis for understanding the biogeographic history of the genus, rooted in the regions of the Caucasus, Central Asia, and Iran.

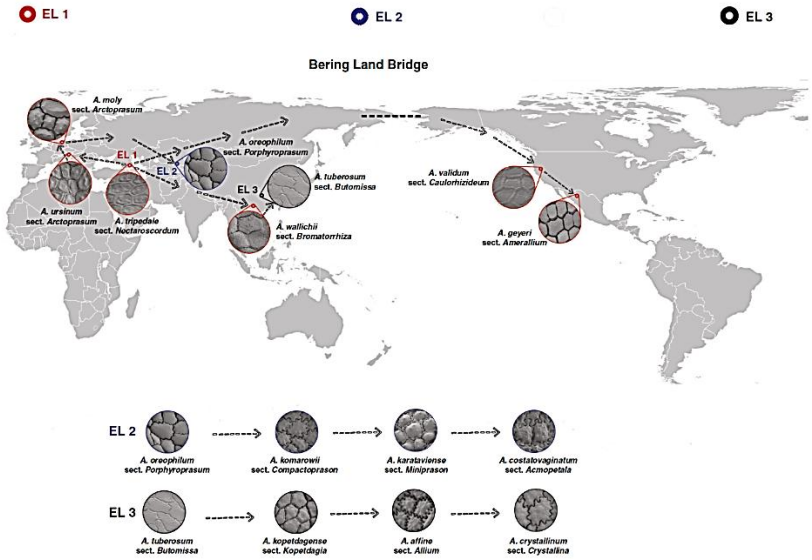


Figure 2. Global distribution of *Allium* based on testa cell characteristics of seeds. The placement and branching of species on the map were carried out according to herbarium data and their positions on the ITS-based phylogenetic tree.

The third chapter of the dissertation, titled "**Phylogenomics and morphological evolution of *Allium* Subgenus *Allium* (Amaryllidaceae) in Central Asia**" presents a comprehensive analysis of the chloroplast genome structures, genetic diversity, and phylogenetic relationships of ten species. The results showed that the total size of the chloroplast genomes ranged from 151,465 bp to 153,406 bp (Figure 3). SSR analysis revealed significant polymorphism in the intergenic spacer regions, which exhibited higher nucleotide diversity compared to protein-coding sequences. The ten newly sequenced species of the subgenus *Allium* belong to six sections: sect. *Allium* (*A. filidens*), sect. *Brivedentia* (*A. michaelis* and *A. nikolai*), sect. *Coerulea* (*A. caesium* and *A. glomeratum*), sect. *Eremoprasum* (*A. confragosum* and *A. sabulosum*), sect. *Haneltia* (*A. haneltii*), and sect. *Pallasia* (*A. pallasii* and *A. tanguticum*).

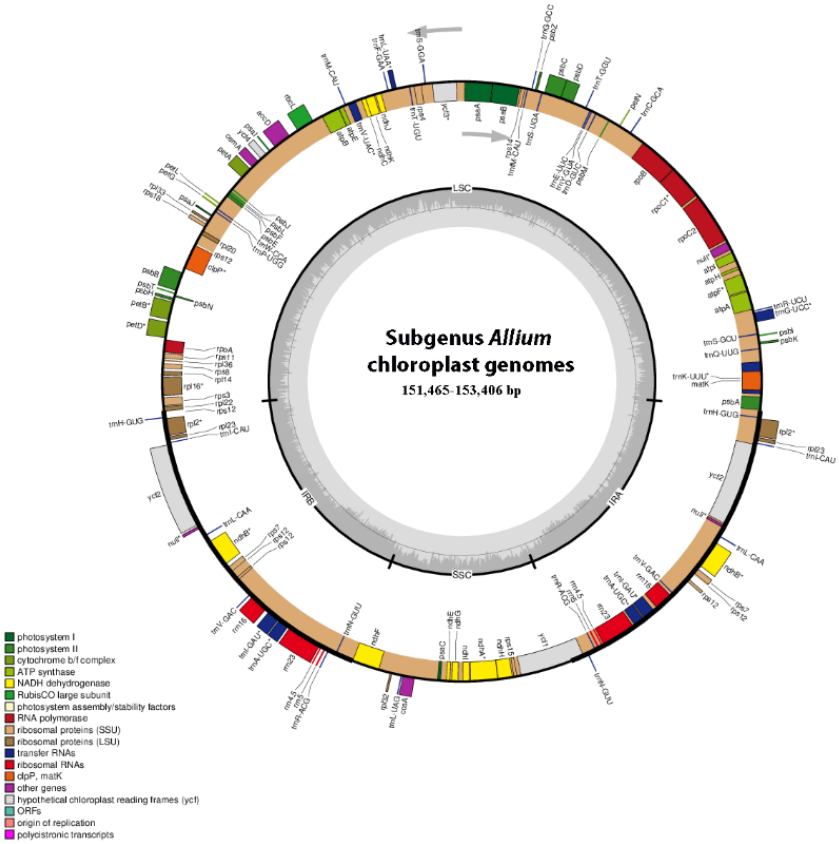


Figure 3. Chloroplast genome structure of species from the subgenus *Allium*.

Genes shown outside the circular genome map are oriented clockwise, while those insides are oriented counterclockwise. Genes are color-coded according to their functional group (refer to the key at the bottom left). The positions of the large single-copy (LSC), small single-copy (SSC), and inverted repeat (IR: IRA and IRB) regions are indicated in the inner circles.

Phylogenetic analysis revealed that the placement of these species often contradicts their current taxonomic classification, suggesting a need to re-evaluate the morphological traits previously used to define sections. The study also showed that the phylogenetic tree constructed using the complete chloroplast genome differs

significantly from both morphology-based classifications and previous molecular studies that relied on ITS sequences.

The ten newly sequenced species of *Allium*, representing six sections within the subgenus *Allium*, provide fresh insights into the phylogeny and chloroplast genome structure of the genus. These species belong to the following sections: sect. *Allium* (*A. filidens*), sect. *Brivedentia* (*A. michaelis* and *A. nikolai*), sect. *Coerulea* (*A. caesium* and *A. glomeratum*), sect. *Eremoprasum* (*A. confragosum* and *A. sabulosum*), sect. *Haneltia* (*A. haneltii*), and sect. *Pallasia* (*A. pallasii* and *A. tanguticum*). Interestingly, the last two species from sect. *Pallasia* (*A. pallasii* and *A. tanguticum*) were also analyzed by Xie et al. (2020b) using the whole chloroplast genome, showing similar phylogenetic positions, but not clustered together, instead scattered across the tree. This scattering pattern was similarly observed in the present study with *A. caesium* and *A. glomeratum* from sect. *Coerulea* and *A. confragosum* and *A. sabulosum* from sect. *Eremoprasum*.

The phylogenetic analysis revealed significant discrepancies between species positions in the phylogenetic tree and their taxonomic classification. For instance, *A. confragosum* was classified into sect. *Eremoprasum* based on morphological traits but clustered in the phylogenetic tree with species from different sections, such as *A. caesium*, *A. haneltii*, and *A. caeruleum*. The morphology-based classification of *A. confragosum* with *A. sabulosum*, based on shared features like tripartite inner filaments and basal tunic splitting with crests, was contradicted by the phylogenetic analysis, which places *A. confragosum* with species that have persistent spathes, resembling *A. haneltii* and *A. caesium* (Figure 4). These results suggest the need for reevaluation of the morphological traits traditionally used for section classification in subgenus *Allium*.

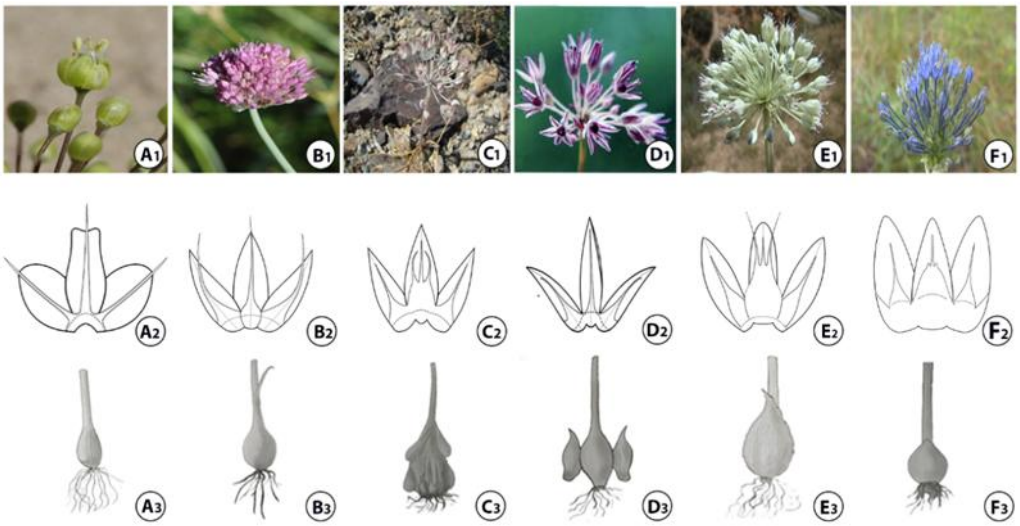


Fig. 4. The flower morphological characters, filaments, and bulbs of subgenus *Allium* species. **(A)** *A. sabulosum,* (sec. *Eremoprasum*, photo by V. Epiktetov); **(B)** *A. pallasii* (sec. *Pallasia*, photo by V. Epiktetov); **(C)** *A. michaelis* (sec. *Brivedentia*, photo by G. Lazkov); **(D)** *A. haneltii* (sec. *Haneltia*, photo by F, Khassanov); **(E)** *A. filidens* (sec. *Allium* photo by G. Lazkov); **(F)** *A. caesium* (sec. *Coerulea* photo by L. Valdshmit).

This study provides the first comprehensive phylogenetic analysis of 18 species using whole plastome data for subgenus *Allium*, revealing that the phylogenetic relationships among *Allium* species do not align with the current sectional classification, and even challenge the validity of the subgenera recognized in the genus. In contrast to previous studies, the phylogenetic tree constructed from plastome data showed that in most clades, species from different subgenera were intermingled, with only one clade containing all members from subgenus *Allium*. This contradicts the previous ITS-based phylogenetic tree by Friesen et al. (2006), where subgenus *Allium* formed a distinct clade, suggesting that ITS markers may provide a more robust reflection of morphological classifications than plastid markers.

In addition to the phylogenetic analysis, the study also examined the chloroplast genome structure of *Allium* species. The loss or pseudogenization of several genes, including *rpl22*, *rps2*, *accD*, and ndh, was identified in the plastomes. These findings align with previous studies on *Allium* plastomes, but also introduce new instances of pseudogenization and gene loss, particularly for *psaI*, *rpl20*, and *rpl22* in specific species like *A. ovalifolium*, *A. ochotense*, and *A. paradoxum*. Furthermore, comparisons of the IR/SSC and IR/LSC boundaries revealed that all studied species share similar characteristics, with minor variations in the positions of genes like *rpl22*, *rps19*, *ycf1*, and ndhK. The trnH-*rps19* cluster, located in the IR regions, was consistent with type III expansion and contraction of the IR/LSC junctions, as described by Wang et al. (2008). These insights into the plastome structure of *Allium* species provide valuable information for understanding the genome organization and evolutionary dynamics of this genus.

For example, *A. confragosum*, which was classified under sect. *Eremoprasum* based on morphological features, was found to cluster with species from a different section in the chloroplast-based phylogenetic tree highlighting inconsistencies in the current classification system. Overall, the findings emphasize that the phylogeny of the subgenus *Allium* is more complex than previously understood.

In the *fourth chapter* of the dissertation titled "**Phylogenomics of *Allium* sect. *Cepa* (Amaryllidaceae) Provides New Insights into the Domestication of Onion in Central Asia**" which includes economically important plants, has always been difficult to understand in terms of ITS phylogenetic relationships. This study aimed to clarify these relationships by sequencing the complete chloroplast genomes of four Central Asian species (*Allium oschaninii*, *A. praemixtum*, *A. pskemense*, and *A. galanthum*).

The analysis results revealed two distinct clades within the section (Figure 5). The first clade contained *A. oschaninii*, *A. praemixtum*, and *A. pskemense*, while the second clade included *A. galanthum*, *A. altaicum*, and two cultivated species, *Allium cepa* and *Allium fistulosum*. These findings contradict previous phylogenetic studies based on nuclear DNA and morphological data, suggesting that interspecific hybridization and chloroplast capture played significant roles in shaping these relationships.

The results also indicated that, despite ITS close genetic relationship with *A. cepa*, *A. galanthum* has not contributed to the domestication of onion. This

conclusion is supported by the significant morphological and nuclear DNA differences between these species. These findings challenge the common belief that Central Asian species are the closest wild relatives of cultivated onion. Instead, the domestication of *A. cepa* may have occurred elsewhere, highlighting the need for further research to identify the true wild ancestors of this important crop.

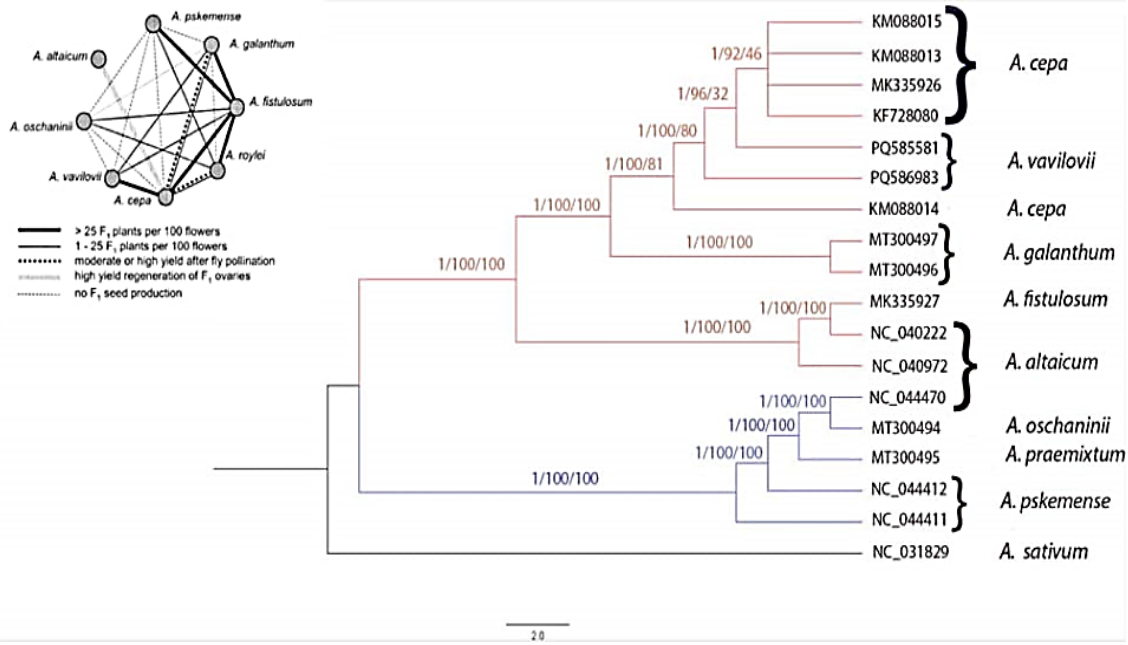


Figure 5. Phylogenetic tree based on 80 protein-coding genes of 16 plastomes of the genus *Allium*

The analysis also highlights the utility of the plastid gene *rpoC2*, which produced a tree topology consistent with the phylogenetic tree based on 80 protein-coding genes, complete plastome genomes, and the SSC and LSC regions. This alignment designates *rpoC2* as a valuable gene for future phylogeographic and phylogenetic studies in the genus *Allium*. The correspondence of a single gene with broader genetic data enhances phylogenetic analyses and helps provide a clearer understanding of the evolutionary history of these plants.

However, the study also identified the absence of chloroplast genomes for several species, including *A. rhabdotum*, *A. roylei*, *A. farctum*, *A. asarense*, and *A. vavilovii*, which complicates the complete understanding of the phylogenetic relationships within *Allium* sect. *Cepa*. These gaps make it difficult to fully grasp the evolutionary dynamics within the section, and future research should focus on filling these gaps. By addressing these gaps, a more complete understanding of the evolution and domestication of *Allium* species can be achieved.

In conclusion, this study provides new insights into the phylogenetic relationships within *Allium* sect. *Cepa*, challenges previous assumptions, and emphasizes the complexity of ITS evolutionary history. The findings highlight the importance of integrating multiple genetic data sources for a deeper understanding of plant evolution and domestication.

The fifth chapter of the dissertation, titled "**Comparative Phylogenomics reveals the Complex Evolution of the Genus *Allium* (Amaryllidaceae)**" aims to determine the complex evolutionary history of *Allium* through a comprehensive

phylogenomic analysis. The study focuses on reconstructing the phylogenetic relationships among *Allium* species using chloroplast genome data and nuclear ribosomal internal transcribed spacer (nrITS) sequences. By combining molecular data with morphological characteristics, the research attempts to provide insights into the evolutionary processes that have shaped the diversity of this genus.

The study included 110 *Allium* species, representing 50 sections and 13 subgroups. This selection strategy aimed to capture the genetic diversity within the genus. New leaf samples were collected from natural populations. A total of 58 *Allium* species' complete chloroplast genomes were sequenced, with additional data obtained from the National Center for Biotechnology Information (NCBI).

The analysis of plastome sequences identified several variable sites that contributed to the phylogenetic resolution of *Allium* species. The nrITS and chloroplast data provided complementary information, with some clades being well-supported by both datasets, while others showed discrepancies. These discrepancies suggest that hybridization and chloroplast capture may have played a significant role in shaping the evolutionary history of *Allium*, complicating the interpretation of phylogenetic relationships.

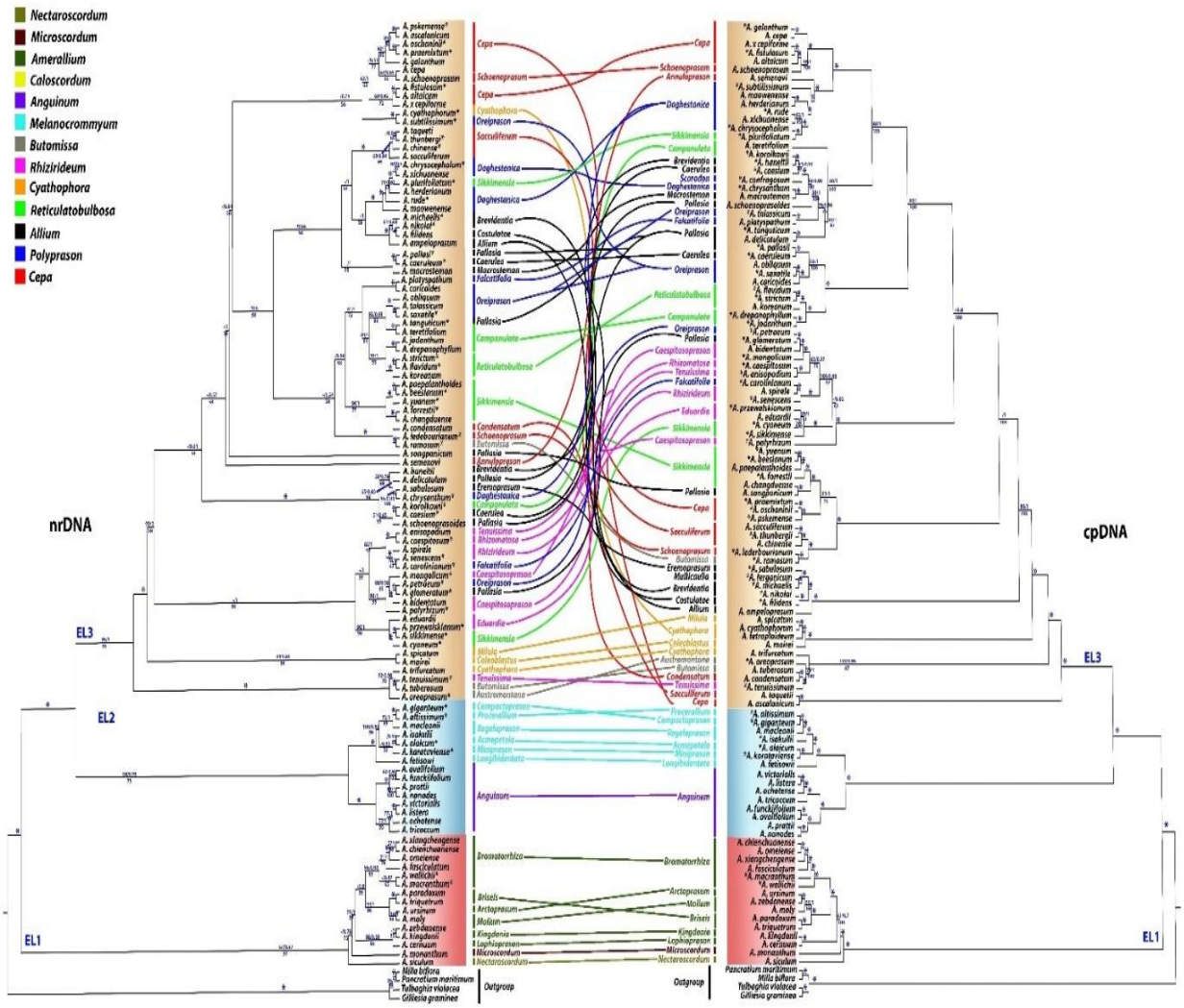


Figure 6. Topological incongruence between trees based on 78 chloroplast protein-coding genes (right) and nuclear ribosomal DNA (ITS) (left).

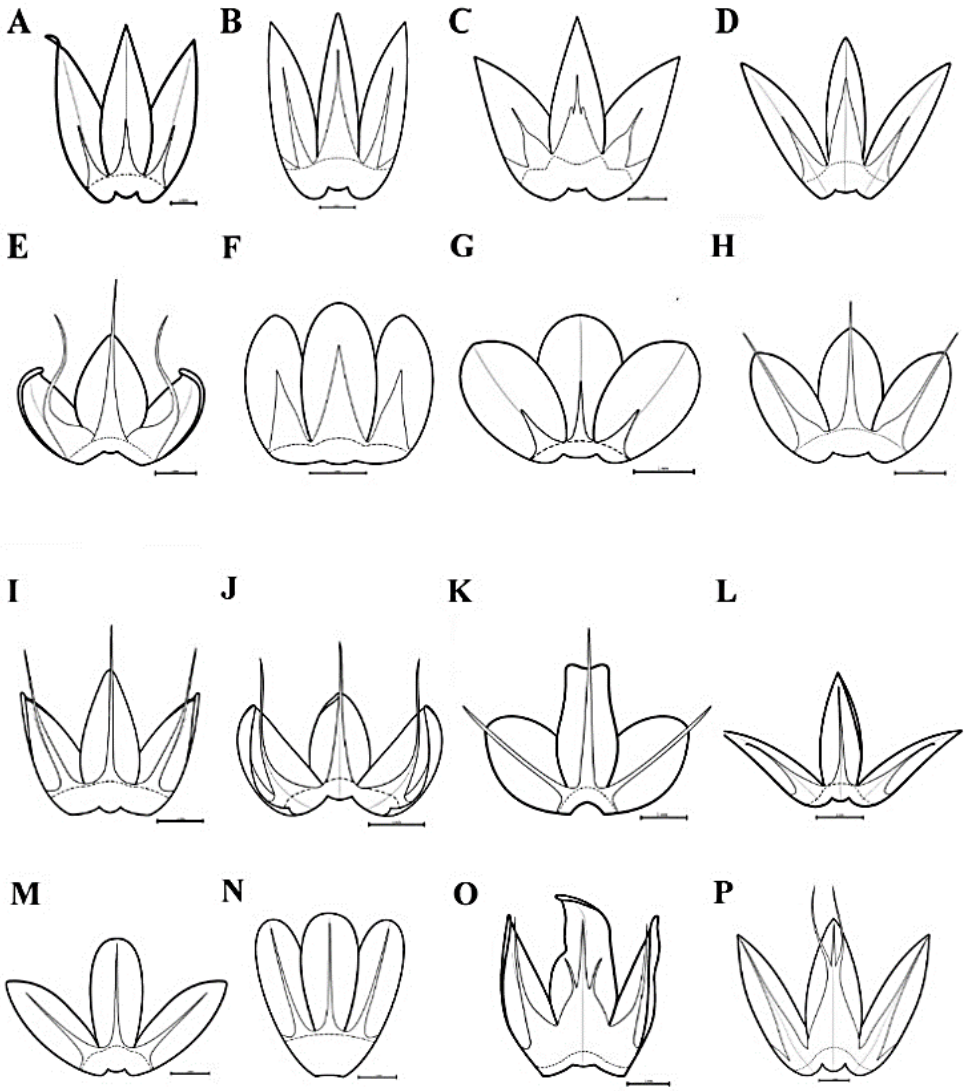


Figure 7. sect. *Coerulea*: A. *A. svetlanae*; B. *A. taciturnum*; C. *A. caeruleum*; sect. *Kopetdagia*: D. *A. kopetdagense*; sect. *Eremoprasum*: E. *A. confragosum*; F. *A. incrustatum*; G. *A. jaxarticum*; H. *A. popovii*; I. *A. scrobiculatum*; J. *A. transvestiens*; K. *A. sabulosum*; sect. *Haneltia*: L. *A. haneltii*; sect. *Codonoprasum*: M. *A. convallarioides*; N. *A. lenkoranicum*; sect. *Multicaulia*: O. *A. ferganicum*; P. *A. rinae*.

The phylogenetic analysis revealed distinct evolutionary lineages in the first and second evolutionary pathways (L1 and L2) within *Allium* (Figure 6). These lineages are monophyletic, indicating that they represent significant branches in the evolutionary history of the genus. The results suggest that these pathways diverged during the early stages of *Allium* evolution, likely driven by environmental factors and adaptive dispersal. Identifying the key morphological traits associated with these evolutionary pathways provides insights into the evolutionary pressures that shaped their diversity. In contrast, the third evolutionary pathway (L3) displayed more complex relationships, with several species clustering in a polyphyletic manner.

This finding suggests that important evolutionary processes, such as hybridization and gene flow, have occurred in L3, leading to the emergence of similar morphological traits across different lineages. The incongruence between

nrITS and chloroplast phylogenies in this lineage highlights the need for further investigation into evolutionary mechanisms, including the potential role of environmental factors in interspecies interactions and the shaping of biodiversity. The study also links the morphological evolution of *Allium* species to phylogenetic relationships, with the analysis showing that some traits, such as bulb size and leaf shape, are associated with specific evolutionary lineages. These findings suggest that morphological diversity within *Allium* is not a result of random variation but rather linked to adaptive responses to environmental conditions. Understanding these correlations could provide valuable insights into the ecological and evolutionary dynamics of the group. The filament type of *Allium* species plays a key role in understanding the phylogenetic relationships of the group. Comparative phylogenomic analysis revealed that different filament types were observed across various species, underscoring their importance for classification and evolutionary studies.

The study identified the presence of three-edged internal filaments in many *Allium* species (Figure 7), characterized by filaments with lateral edges that are longer than the central edge. This morphological feature is of significant importance in species differentiation and may indicate evolutionary adaptations. Additionally, some species possess simple external filaments, which may occasionally have small lateral edges, contributing to the diversity of filament structures within the genus. Studying the filament types across the phylogenetic tree reveals patterns of morphological evolution and provides insights into the ecological adaptations of *Allium* species. For example, differences in filament structure could be related to specific ecological conditions or pollination strategies, highlighting the complex interactions between morphology and ecology in the evolution of this diverse group. Overall, filament type serves as a key morphological character in the phylogenetic analysis of the genus *Allium*, aiding in the reconstruction of evolutionary lineages and enhancing our understanding of the genus's diversity and adaptation mechanisms. In conclusion, this chapter presents a comprehensive phylogenomic analysis of the genus *Allium*, uncovers complex evolutionary relationships, and emphasizes the importance of integrating molecular and morphological data.

The evolution of bulb tunics, ranging from papery to fibrous and reticulate structures, highlights the genus's ability to adapt to physical stresses such as herbivory, desiccation, and mechanical damage. Fibrous and reticulate tunics, which are derived traits, likely provide enhanced protection in harsh environments, such as arid regions or high-altitude habitats (Figs. 7-8).

This is consistent with the work of Li et al. (2010), who suggested that bulb tunic morphology is closely linked to habitat preferences in *Allium* species. The diversity in bulb tunic structures suggests that these traits have evolved in response to specific ecological pressures, contributing to the genus's ability to colonize a wide range of environments. The presence of multiple tunic types within closely related lineages further indicates that these traits may have evolved independently in response to similar environmental challenges.

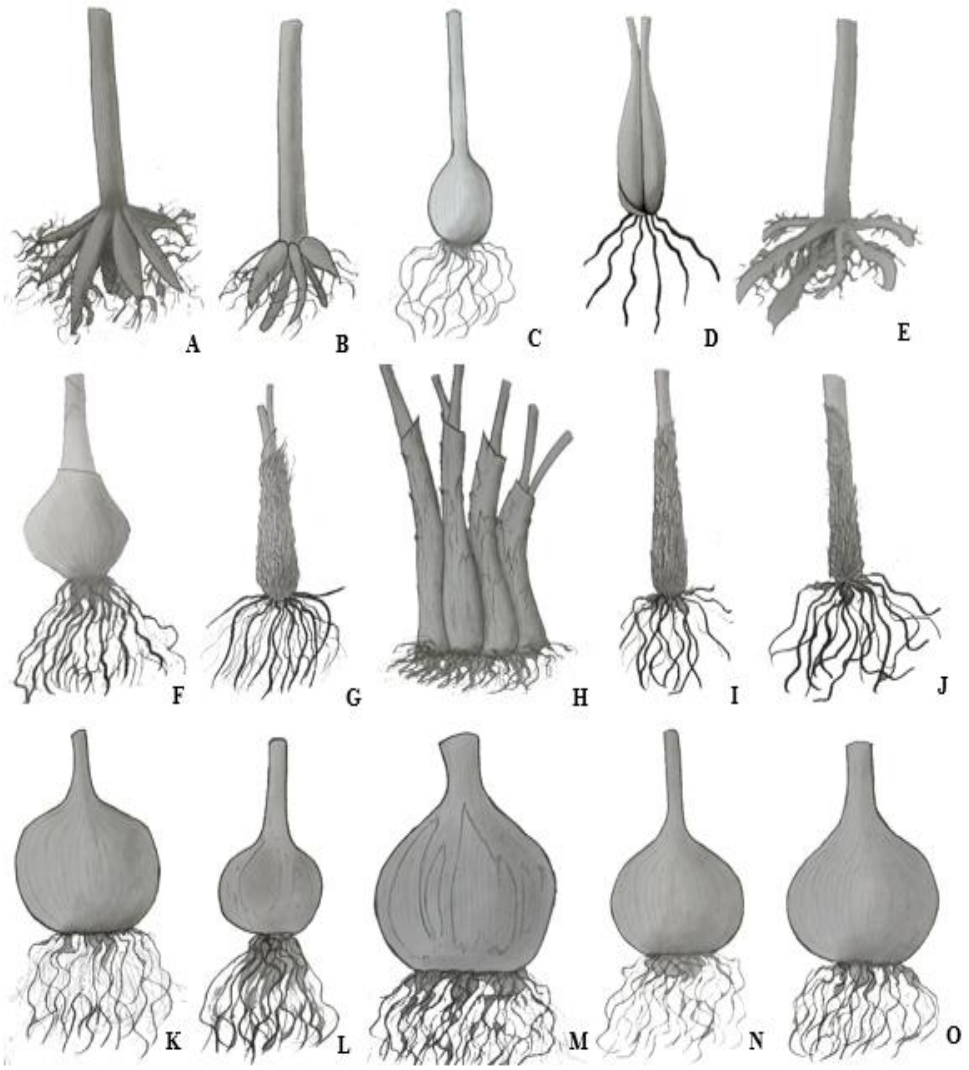


Fig. 8. Shape of bulbs of fifteen *Allium species* belonging to subg. *Amerallium* : **A.** *A. fasciculatum*; **B.** *A. macranthum*; **C.** *A. paradoxum*; **D.** *A. ursinum*; **E.** *A. wallichii*; subgen. *Caloscordum*: **F.** *A. neriniflorum*; subgen. *Anguinum*: **G.** *A. nanodes*; **H.** *A. ovalifolium*; **I.** *A. prattii*; **J.** *A. victorialis*; subgen. *Melanocrommyum*: **K.** *A. alaicum*; **L.** *A. altissimum*; **M.** *A. giganteum*; **N.** *A. isakulii;* **O.** *A. macleanii*.

The evolution of filament types in *Allium*, specifically the transition from simple to tricuspidate filaments, offers valuable insights into the reproductive strategies and pollination mechanisms within the genus. Simple filaments are likely the ancestral condition, representing a more generalized structure, while tricuspidate filaments are a derived trait that may have evolved in response to specific pollination pressures. The tricuspidate morphology, characterized by a more complex and branched structure, could enhance pollen presentation or improve the precision of pollen transfer, particularly in species that rely on specialized pollinators. This finding is consistent with the work of Huang et al. (2014), who highlighted the significance of filament morphology in the reproductive biology of *Allium* The presence of tricuspidate filaments in certain lineages suggests that these species may have adapted to exploit specific pollinators or to optimize reproductive efficiency in particular ecological settings.

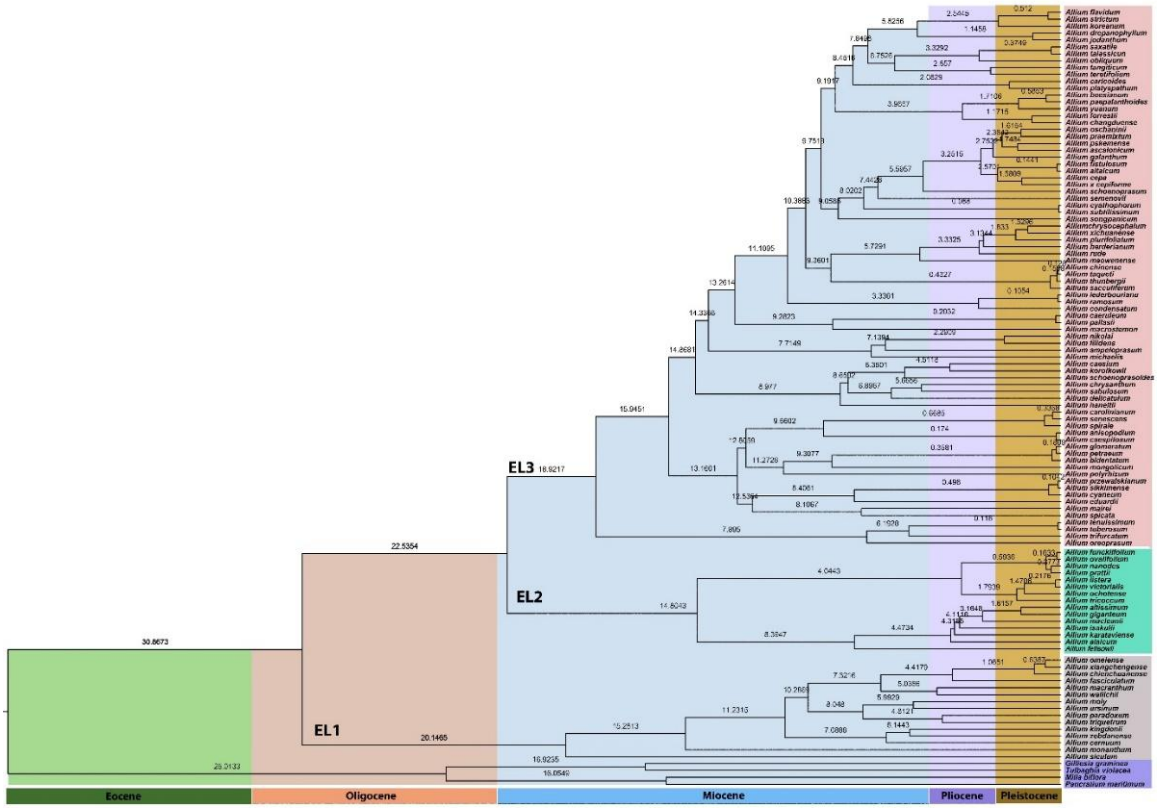


Fig. 9. BEAST-derived chronogram with the mean value of *Allium* based on the nuclear DNA (ITS) data set. Phylogeny of three evolutionary lineages of *Allium*: EL1–EL3.

The evolutionary history of *Allium* unfolds as a dynamic interplay between phylogenetic divergence and biogeographic dispersion, shaped by geological events and climatic shifts. Our findings, derived from nuclear (ITS) and plastid DNA datasets, provide compelling evidence for the diversification of *Allium* into three major evolutionary lineages (EL1, EL2, and EL3). The chronograms generated through BEAST analysis (Fig. 9) suggest that the initial radiation of *Allium* traces back to the late Eocene–early Oligocene transition, approximately 30 mln years ago, coinciding with significant global cooling events that likely acted as a driver of diversification (Friesen et al., 2006; Li et al., 2010). The ancestral range reconstruction using RASP under the BBM (Bayesian Binary MCMC) and S-DIVA (Statistical Dispersal-Vicariance Analysis) models provides critical insights into the biogeographic origins and dispersal patterns of the genus *Allium* (Fig. 10). The results strongly suggest that *Allium* originated in Central Asia and ITS adjacent regions (Area A), a hypothesis that is well-supported by the region's status as a biodiversity hotspot for the genus (Fritsch & Friesen, 2002). Central Asia, encompassing areas such as the Caucasus, Central Asia, and Iran, is characterized by diverse ecological conditions, ranging from arid deserts to temperate mountain ranges, which likely provided the ideal environment for the early diversification of *Allium* This region's complex topography and climatic variability created numerous ecological niches, facilitating speciation and the establishment of the genus's early lineages. The high probabilities assigned to Central Asia (Area A) as the ancestral area for *Allium* (BBM 45-47%, S-DIVA 50%) underscore the region's importance as

a center of origin and early diversification for the genus. This finding aligns with previous studies that have identified Central Asia as a major center of diversity for *Allium* (Friesen et al., 2006). The region's unique combination of climatic and geological features, including the presence of mountain ranges and arid basins, likely provided the necessary conditions for the genus's initial radiation. The early diversification of *Allium* in Central Asia may have been further facilitated by the region's role as a refugium during periods of climatic instability, allowing for the persistence and diversification of lineages over time.

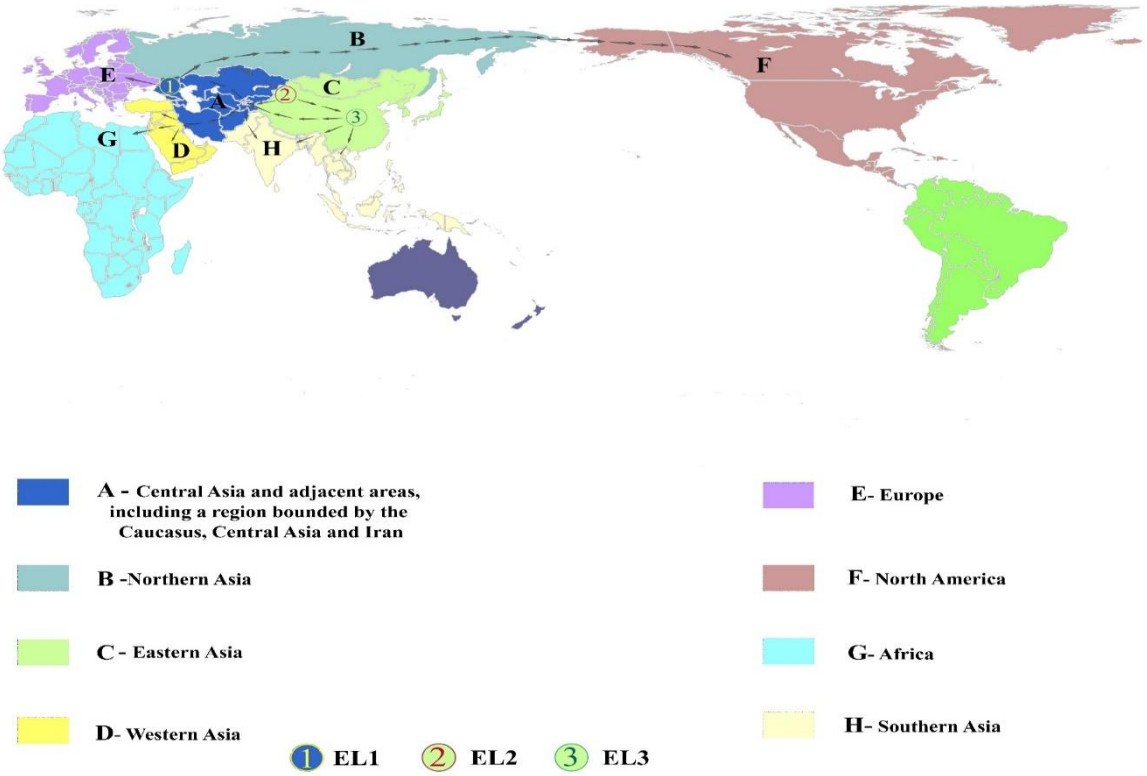


Fig. 10. Estimated directions of the genus *Allium* during ITS early evolution infered by using RASP (BBM and S-DIVA methods). Phylogeny of three evolutionary lineages of *Allium*: EL1–EL3

CONCLUSIONS

The following conclusions were made in the DSc dissertation on the topic "Molecular Phylogeny, Biogeography, and Evolution of the genus *Allium* with a focus on Central Asia (Amaryllidaceae) ":

1. In 95 species belonging to 14 subgenera and 58 sections of the genus *Allium*, seed epidermal morphological characters—including anticlinal wall structure (7 types), epidermal cell shape (6 types), verrucae on the periclinal wall surface, cell surface patterns, and distances between adjacent cells—were identified as reliable diagnostic characters at both species and sectional levels. Based on these characters, a taxonomic key was developed that enables reliable identification of species within the genus and provides practical applicability;

2. With respect to the evolutionary history and biogeographic origin of *Allium*

species, representatives of the earliest evolutionary lineage (EL-1) were characterized by primitive traits such as hexagonal epidermal cell shapes and smooth periclinal surfaces lacking verrucae. In contrast, EL-2 and EL-3 lineages exhibited increased anticlinal wall undulation and the development of verrucae on the periclinal surface, reflecting morphological adaptations of representatives of the subgenera *Melanocrommyum* and *Allium* to the arid conditions of the Miocene epoch.

3. Phylogenetic trees constructed based on ribosomal DNA ITS sequences, together with phylogenetic analyses relying on seed macro- and micromorphological characters, convincingly demonstrated that the origin of *Allium* species is closely associated with Central Asia and adjacent regions, including the Caucasus and Iran. The strong correspondence between seed epidermal morphology and molecular clades particularly confirms the central role of Central Asian taxa in the evolution of the genus *Allium*. These findings support the hypothesis that the "Old World" evolutionary lineages initially originated in the Central Asia–Iran–Caucasus region and subsequently dispersed into the "New World" via Northern Asia, most likely through the Bering land bridge.

4. According to reconstructed phylogenetic trees, species of section *Cepa* were separated into two distinct molecular groups comprising taxa from Northern Asia and Central Asia. This pattern indicates that Central Asian species represent "ancient hybrid taxa" formed through chloroplast capture resulting from intergroup hybridization between Northern and Eastern Asian lineages, confirming that hybridization played a significant evolutionary role in the evolution of section *Cepa*.

5. Comparative analyses of chloroplast genomes revealed that species of subgenus *Allium* possess unique genomic features, including gene losses (*rpl22, rps16, infA*) and extensive pseudogenization (*rps2, accD, psaI, rpl20, rpl23, rpl32, rps16,* and *infA*), which are not observed in other subgenera. These genomic changes distinguish chloroplast genomes of subgenus *Allium* and indicate a distinct evolutionary trajectory. In addition, the protein-coding genes *matK* and *rpoC2* were identified as the most highly variable regions, showing strong congruence with phylogenetic tree topologies and are therefore recommended as universal DNA barcodes for phylogenetic and phylogeographic studies across all *Allium* species.

6. Morphological and phylogenetic analyses demonstrated that early ancestral lineages of *Allium* were characterized by synapomorphic traits, including papery tunics, small true bulbs, filamentous stamens lacking teeth, and pink or white flowers. However, subsequent evolutionary processes in Central Asia led to the emergence of forms with large bulbs or rhizomes, toothed filaments, and yellow or blue flowers, indicating the occurrence of secondary morphological diversification within the region.

7. The divergence of the major evolutionary lineages within the genus *Allium* occurred during the Oligocene–Miocene periods. Time-calibrated phylogenetic analyses based on nuclear genomes revealed that the first evolutionary lineage (EL-1) originated during the Oligocene (approximately 30.9 mln years ago) in Central Asia and adjacent regions (Caucasus–Iran–Central Asia) and subsequently diversified toward Europe and North America. The second evolutionary lineage (EL-

2) emerged in the Early Miocene (approximately 22.5 mln years ago) in East Asia, whereas the third evolutionary lineage (EL-3) originated during the Early Miocene (approximately 18.9 mln years ago) in Central Asia and neighboring regions, undergoing active diversification. Analyses based on plastid genomes indicated that age estimates for the earliest evolutionary lineage (EL-1) differ by approximately 4 mln years compared with estimates derived from nuclear genome data.

НАУЧНЫЙ СОВЕТ DSc.05/2025.27.12.B.23.01.M ПО ПРИСУЖДЕНИЮ УЧЕНЫХ СТЕПЕНЕЙ ПРИ ИНСТИТУТЕ БОТАНИКИ

ИНСТИТУТ БОТАНИКИ

ЮСУПОВ ЗИЁВИДДИН ОЛИМЖОН УГЛИ

МОЛЕКУЛЯРНАЯ ФИЛОГЕНИЯ, БИОГЕОГРАФИЯ И ЭВОЛЮЦИЯ *ALLIUM* L. (AMARYLLIDACEAE) С АКЦЕНТОМ НА ЦЕНТРАЛЬНУЮ АЗИЮ

03.00.05 – Ботаника

АВТОРЕФЕРАТ ДИССЕРТАЦИИ ДОКТОРА НАУКА (DSc) ПО БИОЛОГИЧЕСКИМ НАУКАМ

Ташкент – 2026

Тема диссертации доктора наук (DSc) по биологическим наукам зарегистрирована в Высшей аттестационной комиссии при Министерстве высшего образования, науки и инноваций Республики Узбекистан за номером B2025.2.DSc/B267

Диссертация выполнена в Институте ботаники.

Автореферат диссертации на трех языках (узбекский, английский и русский (резюме)) размещён на веб-странице Научного совета по адресу www.botany.uz и в Информационно-образовательном портале «ZiyoNet» по адресу www.ziyonet.uz.

Научный консультант:	**Тожибаев Комилжон Шаробитдинович** доктор биологических наук, академик
Официальные оппоненты:	**Каримов Фарход Исомиддинович** доктор биологических наук, профессор
	Кушанов Фахриддин Неъматуллаевич доктор биологических наук, профессор
	Ронг Ли PhD, профессор
Ведущая организация:	**Институт биологии и биотехнологии растений** (Алматы, Республика Казахстан)

Защита диссертации состоится «10» марта 2026 года в 14:00 часов на заседании Научного совета DSc.05/2025.27.12.B.23.01.M при Институте ботаники (Адрес: 100125, г. Ташкент, ул. Дурмон йули, дом 32. Актовый зал Института ботаники. Тел.: (+99871) 262-37-95, факс (+99871) 262-79-38, E-mail: botany@academy.uz

С диссертацией можно ознакомиться в Информационно-ресурсном центре Института ботаники (зарегистрировано за номером № 86). Адрес: 100125, г. Ташкент, ул. Дурмон йули, дом 32. Тел.: (+99871) 262-37-95.

Автореферат диссертации разослан «24» февраля 2026 года.
(реестр протокола рассылки № 25 от «19» февраля 2026 года).

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ВВЕДЕНИЕ (аннотация диссертации доктора наук (DSc)

Цель исследования является выявление эволюционных связей, филогенетической структуры и процессов диверсификации между видами рода *Allium* L., а также научное обоснование возможности использования их микроморфологических признаков в таксономической системе.

Объект исследования: Виды подрода *Allium* и секции *Cepa*, относящиеся к роду *Allium* (Amaryllidaceae).

Научная новизна исследования:

установлено, что периклинальная поверхность клеток эпидермиса семени и расстояние между соседними клетками являются важными диагностическими признаками при дифференциации видов рода *Allium*;

на основе филогенетического анализа, выполненного по последовательностям гена *ITS*, и исследований микроморфологии семян выявлено распространение видов «Старого Света» на территорию «Нового Света» через Берингов пролив;

по результатам анализа хлоропластных геномов реконструировано филогенетическое дерево видов секции *Cepa*, в котором выделены две самостоятельные молекулярные группы, соответствующие видам Северной и Центральной Азии;

установлено наличие процессов хлоропластного захвата (chloroplast capture) и гибридизации среди видов секции *Cepa*;*;*

по результатам молекулярных исследований определены высоковариабельные гены *rpoC2, ycf1, ndhF, matK, ndhD*, рекомендованные в качестве ДНК-баркодных маркеров для построения филогенетических деревьев видов рода *Allium*;

выявлены синапоморфные признаки у ранних предковых видов *Allium*, включающие бумаговидные покровные чешуи, мелкие истинные луковицы, нитеобразные тычиночные нити без зубцов, а также цветки розовой и белой окраски;

установлено, что первая эволюционная линия рода *Allium* (EL1) сформировалась в Центральной Азии и прилегающих регионах (Кавказ, Иран и Центральная Азия) с последующей активной диверсификацией;

обосновано, что расхождение основных эволюционных направлений внутри рода *Allium* произошло около 30,9 млн лет назад, что соответствует олигоцен–миоценовому времени..

Внедрение результатов исследования:

Результаты исследования полных хлоропластных геномов и ITS-участков видов рода *Allium*, полученные в Лаборатории молекулярной филогении и биогеографии Института ботаники Академии наук Республики Узбекистан, были использованы при построении филогенетического древа однодольных в рамках фундаментального проекта ПФИ-5 «Дерево жизни: однодольные растения Узбекистана» (2021–2024 гг.) (справка Академии наук Республики Узбекистан №4/1255-1522 от 20 июня 2025 г.);

Все полученные ДНК-последовательности (хлоропластные геномы, ITS)

77 видов и 105 образцов загружены и хранятся в международной базе данных GenBank NCBI (https://www.ncbi.nlm.nih.gov/). Эти данные предоставили новые возможности для молекулярной таксономии рода *Allium*, существенно дополнили сведения о местном разнообразии видов, расширили современные представления на региональном (Центральная Азия) уровне и позволили выявить новые виды, ранее неизвестные науке;

Результаты исследования были использованы в международном проекте «Global *Allium* Garden» (U1802232, 2018–2022 гг.), реализованном Институтом ботаники Куньминь, Академии наук Китая, для изучения молекулярно-филогенетических и биогеографических связей видов *Allium* Узбекистана и Восточной Азии. Кроме того, на основе анализа макро- и микроморфологических особенностей семян методом сканирующей электронной микроскопии (SEM) был разработан новый универсальный таксономический ключ (справка Академии наук Китая от 5 февраля 2025 г.).

Структура и объём диссертации:

Диссертация состоит из введения, 5 глав, заключения, списка использованной литературы и приложения. Общий объём диссертации составляет 182 страниц.

E’LON QILINGAN ILMIY ISHLAR RO‘YHATI
СПИСОК ПУБЛИКУЕМЫХ РАБОТ
LIST OF PUBLISHED WORK

I бўлим (I часть; Part I)

1. Khassanov F.O., Yusupov Z. Taxonomical Revision of Genus *Allium* L. (Amaryllidaceae) in the Flora of Middle Asia // In Biodiversity, Conservation and Sustainability in Asia: Volume 2: Prospects and Challenges in South and Middle Asia. - Cham: Springer International Publishing - 2022. - 2, -P. 403-433. (Book, Monograph).

2. Khassanov F.O., Yusupov Z. Revision of the Genus *Allium* L. (Amaryllidaceae) in the Flora of India // In Biodiversity, Conservation and Sustainability in Asia: Volume 2: Prospects and Challenges in South and Middle Asia. - Cham: Springer International Publishing - 2022. - 2, -P. 377-402. (Book, Monograph).

3. Yusupov Z., Deng T., Volis S., Khassanov F., Makhmudjanov D., Tojibaev K., Sun H. Phylogenomics of *Allium* section *Cepa* (Amaryllidaceae) provides new insights on domestication of onion // Plant Diversity. – 2021. –43(2). –P. 102-110. (Scopus, Cite Score 8,3).

4. Yusupov Z., Ergashov I., Volis S., Makhmudjanov D., Dekhkonov D., Khassanov F., Tojibaev K., Deng T., Sun H.. Seed macro-and micro-morphology in *Allium* (Amaryllidaceae) and ITS phylogenetic significance // Annals of Botany. – 2022. - 129 (7). -P. 869–911. (Scopus, CiteScore: **7.9).**

5. Khassanov F.O., Pulatov S., Asatulloev T., Ergashov I., Tojibaev K.S., Yusupov Z. *Allium sunhangii*–a new species from section *Brevidentia* FO Khass. & Iengal.(Amaryllidaceae) from Southern Pamir-Alay, Uzbekistan // PhytoKeys – 2023. – 219. – P. 35-48. (Scopus, Cite Score 2,6).

6. Jang J.E., Baasanmunkh S., Nyamgerel N., Oh S.Y., Song J.H., Yusupov Z., Tojibaev K., Choi H.J. Flower morphology of *Allium* (Amaryllidaceae) and ITS systematic significance // Plant Diversity. – 2024. –46(1). –P. 3-27. (Scopus, Cite Score 8,3).

7. Ergashov I., Yusupov, Z., Toshtemirov J., Mamajonov S., Akbarova M., Marupov A., Yusupova Z., Esankulova D., Esankulov A. Evaluating the vulnerability of endangered *Allium* species (Amaryllidaceae) to climate change in Central Asia // Analele Universităţii din Oradea, Fascicula Biologie. – 2025. –32(1). –P. 87-105. (Scopus, Cite Score 0,5).

8. Ergashov I., Yusupov Z., Dolatyari A., Khorasani M., Eker, I., Turdumatova N., Lazkov G., Rasulov F., Sun H., Deng T., Tojibaev K. New insights into the molecular phylogeny and biogeographical history of *Allium* subgenus *Melanocrommyum* (Amaryllidaceae) based on plastome and nuclear sequences // Plant Diversity. – 2025. –47(4). –P. 28-49. (Scopus, Cite Score 8,3).

9. Yusupov Z. *Allium* sect. *Cepa* (mill.) Prokh. seksiyasining O‘rta Osiyo hududida tarqalishi. Namangan davlat universiteti ilmiy axborotnomasi. – 2025. – №1. – B. 117-120 (03.00.00; №17)

10. Azimova D., Esanqulova D., Sharipova M., Sindorov A., Rahmataliyev A., Yusupov.Z. Study of the distribution of endemic species of the genus *Allium* L. in the Nuratau mountain range // Namangan davlat universiteti ilmiy axborotnomasi. – 2025. – №3. – B. 233-235 (03.00.00; №17)

11. Ergashov I., Zohidov G., Turdibekov M., Yusupov Z., Davidov M. The comparative morphological analysis of the subgenus *Melanocrommyum* (Amaryllidaceae, Allioideae) In Uzbekistan // Scientific journal of the Fergana State University. -2025. – №3. – B. 136-145 (03.00.00; №22)

II бўлим (II часть; Part II)

12. Munavvarov A., Yusupov Z., Ergashov I., Tojibaev K.S., Deng T., Sun H. Complete chloroplast genomes of ten species from subgenus *Allium* (*Allium*, Amaryllidaceae) // Plant Diversity of Central Asia. – 2022. - 1 (2). -P. 67–81.

13. Alieva K.B., Hamidova M.H., Yusupov Z.O. Comparison of ecology between the main agricultural crop of *Allium sativum and Allium longicuspus* // Proceedings of the international scientific and practical conference “Innovation in Life Sciences”. Navoi, Uzbekistan. 2022. –P. 21-24.

14. Yusupov Z.O. *Allium* diversity and seed morphology studies in Central Asia // 2nd International Conference Conservation of biological diversity in Central Asia: problems, solutions and prospects - Namangan. 2025. - P. 751-752.

15. Yusupov Z.O., Ergashov.I. The complete chloroplast genome of *Allium sabulosum* from section *Eremoprasum* (Amaryllidaceae) // International and Practical Conference - “Innovation And Partnership In Sustainable Development: Biodiversity, Green Economy And Ecology”. – Osh, Kyrgyzstan. 2025. - P. 266-271.

16. Ergashov I., Toshtemirov J., Yusupov Z.O. The complete chloroplast genome of *Allium majus* (Amaryllidaceae) : An endemic species from Uzbekistan // VII International Symopsium – “Innovation in Life Sciences”. Belgorod, Russia. 2025. –P. 479-481.

17. Ergashov I., Yusupov Z.O., Mingboev F.N., Yuldashev H. Plastome structure and hybrid compatibility of *Allium vavilovii* (Amaryllidaceae, Allioideae) a valuable resource for onion improvement Uzbekistan // International Scientific and Practical Conference on “Prospects and Challenges for the Development of Botany in Uzbekistan”, dedicated to the 75th Anniversary of the Botanist V. Mahmudov. Ferghana, Uzbekistan. 2025. –P. 44-49.

Avtoreferat «O‘zbekiston biologiya jurnali» jurnali tahririyatida tahrirdan o‘tkazilib, o‘zbek, rus va ingliz tillaridagi matnlar o‘zaro muvofiqlashtirildi.

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Bichimi: 84x60 $^{1}/_{16}$. «Times New Roman» garniturasi.
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