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EVOLUTIONARY DEVELOPMENT OF THE GENUS *POPULUS* L. (*SALICACEAE* MIRB.) IN WESTERN KAZAKHSTAN

This article examines the origin, evolution, and phylogenetic relationships of the genus *Populus* L. (poplars) within the family Salicaceae, with a focus on species occurring in Western Kazakhstan. An integrative analysis of paleobotanical, morphological, and ecological data reveals the main pathways of species formation and adaptation mechanisms of poplars in steppe and semi – desert environments.

Paleobotanical evidence shows that *Populus* L. diverged from its closest relative, *Salix*, in East Asia at the end of the Cretaceous period (approximately 68 – 67 million years ago). In the study region, the sections Leucoides, Tacamahaca, and Aigeiros were already established by the early Paleocene, with some fossil remains dating to around 63 million years. From the Paleocene onward, poplars dispersed into North America via high-latitude land bridges. The Trepidae subsection emerged between 15 and 3.5 million years ago, during the Miocene – Pliocene. These data confirm the key role of East Asia as the primary center of origin and diversification of the genus.

Archaeological excavations near Taksai (Western Kazakhstan) uncovered *Populus* L. wood fragments dated to 500 – 401 BC, demonstrating the long-term persistence of poplar floodplain ecosystems in the region. Notably, *P.* × *canescens* is identified as one of the oldest natural hybrids of the genus, known since the late Pliocene (about 3.5 million years ago).

The unique geomorphological and climatic features of Western Kazakhstan promote high ecological plasticity, hybridization, and genetic diversity among *Populus* L. species. This makes the region an important natural model for studying evolutionary processes, hybrid dynamics, and adaptive strategies within the genus. The findings highlight the significance of local poplar populations for understanding long-term environmental stability and provide a valuable basis for future studies on conservation, reforestation, and the management of floodplain ecosystems.

Keywords: Evolution of *Populus*, *Populus* systematics, paleobotany, Salicaceae, Western Kazakhstan.

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Батыс Қазақстандағы *Populus* L. (*Salicaceae* mirb.) туысының даму эволюциясы

Мақалада зерттеу *Populus* L. (терек) туысының шығу тегі мен эволюциялық даму үдерістерін, Salicaceae тұқымдасының филогенетикалық орны мен тарихи-географиялық таралу ерекшеліктерін талдауға бағытталған. Жұмыста Батыс Қазақстанның табиғи флорасында таралған түрлерге ерекше назар аударылып, палеоботаникалық, морфологиялық және экологиялық деректердің интегративті талдауы негізінде терек түрлерінің қалыптасу жолдары мен дала және шөлейт экожүйелеріне бейімделу тетіктері айқындалды.

Populus L. туысы Солтүстік жарты шардың қоңыржай белдеуінде эволюциялық тұрғыдан табысты таралған таксондарының бірі болып саналады. Палеоботаникалық материалдар *Populus* L. пен оның ең жақын туысы *Salix* (тал) туысының филогенетикалық ажырауы Шығыс Азияда Бор кезеңінің соңында, шамамен 68 – 67 миллион жыл бұрын жүзеге асқанын көрсетеді. Зерттеу аймағында ерте палеоцен кезеңінде терек туысының – Leucoides, Tacamahaca және Aigeiros секциялары қалыптасқан. Осы дәуірге жататын қазба қалдықтарының ішінде ең жасы үлкен шамамен 63 миллион жыл болады.

Палеоценнен бастап теректер құрлық көпірлері арқылы Солтүстік Америка аумағына бірнеше дисперсиялық кезеңдермен таралған.

15-3,5 млн жыл бұрын *Populus* туысының миоцен мен плиоцен кезеңдерінде Trepidae қосалқы секциясы пайда болды. Зерттеу барысында туыстың эволюциялық кезеңдері, филогенети-

калық байланыстары және *Populus* түрлерінің бастапқы шығу және диверсификация орталығы ретінде Шығыс Азияның шешуші рөлі жан-жақты қарастырылды.

Тақсай ауылы маңында (Батыс Қазақстан) жүргізілген археологиялық қазбалар барысында табылған *Populus* ағашының қалдықтары б.з.д. 500 – 401 жылдарға жатқызылды. Бұл деректер аймақтағы теректердің жайылма экожүйелерінің өте ертеден бері сақталып келе жатқанын дәлелдейді. Ерекше маңызға ие түрлердің бірі – P. × canescens, шамамен 3,5 миллион жыл бұрынғы кеш плиоцен кезеңінен белгілі ең көне табиғи гибридтердің бірі екені анықталды.

Батыс Қазақстанның бірегей геоморфологиялық және климаттық жағдайлары жайылма ормандардағы терек туысы түрлернің экологиялық икемділігін, гибридизациясын арттыруға ықпал ететіні көрсетілді. Бұл аймақ *Populus* L. туысының эволюциялық үдерістерін және бейімделу стратегияларын зерттеу үшін маңызды модельдік аумақ болып табылады.

Түйін сөздер: *Populus* эволюциясы, *Populus* систематикасы (жүйеленуі), палеоботаника, Salicaceae, Батыс Қазақстан.

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Эволюционное развитие рода *Populus* L. (*Salicaceae* Mirb.) в Западном Казахстане

В статье исследуются происхождение и эволюционные процессы развития рода *Populus* L. (тополь), филогенетическое положение семейства Salicaceae, а также особенности историко-географического распространения его представителей. Особое внимание уделено видам, распространённым в природной флоре Западного Казахстана. На основе комплексного анализа палеоботанических, морфологических и экологических данных выявлены пути формирования видов тополей и механизмы их адаптации к степным и полупустынным экосистемам.

Род *Populus* L. является одной из эволюционно наиболее успешных групп древесных растений умеренного пояса Северного полушария. Палеоботанические материалы свидетельствуют, что филогенетическое расхождение *Populus* и его ближайшего родственника – рода Salix (ива) – произошло в Восточной Азии в конце мелового периода, примерно 68–67 млн лет назад. На территории исследования в раннем палеоцене сформировались секции рода *Populus:* Leucoides, Tacamahaca и Aigeiros. Среди ископаемых остатков этого периода самые древние датируются приблизительно 63 млн лет.

Начиная с палеоцена, тополя распространялись на территорию Северной Америки через существовавшие сушевые мосты, проходя несколько дисперсионных этапов. В интервале 15–3,5 млн лет назад, в миоцене и плиоцене, сформировалась подсекция Trepidae. В ходе исследования подробно рассмотрены эволюционные этапы рода, его филогенетические связи и ключевая роль Восточной Азии как первоначального центра происхождения и диверсификации *Populus* L.

При археологических раскопках в районе села Таксай (Западный Казахстан) обнаружены фрагменты древесины *Populus*, датируемые 500–401 гг. до н. э. Эти находки подтверждают сохранение устойчивых пойменных тополевых экосистем региона на протяжении многих столетий. Особый интерес представляет вид *Populus* × canescens, один из древнейших известных естественных гибридов, происхождение которого прослеживается до позднего плиоцена – около 3,5 млн лет назад.

Показано, что уникальные геоморфологические и климатические условия Западного Казахстана способствуют повышенной экологической пластичности и гибридизации представителей рода *Populus* в пойменных лесах. Регион является важной модельной территорией для изучения эволюционных процессов и адаптационных стратегий тополей.

Ключевые слова: эволюция *Populus*, систематика *Populus*, палеоботаника, Salicaceae, Западный Казахстан.

Introduction

There are about 110 species of poplars on the globe, of which 15 species of poplars are found in the wild flora of Kazakhstan [1].

The genus *Populus* L. is broadly distributed across the Northern Hemisphere, where numerous species play significant ecological and economic roles. Representatives of the genus are notable for their rapid growth rates, high tolerance to environmental stressors, strong vegetative propagation capacity, and the wide-ranging use of their wood in various industries [3;4].

The genus *Populus* L. belongs to the family Salicaceae, order Salicales Lindley (Salicinales), superorder Dillenianae, subclass Dilleniidae, class

Magnoliatae (Dicotyledones), and the division Magnoliophyta (Angiospermae).

According to studies by A. L. Takhtajan, the simple structure of the flowers in Salicales is a secondary feature that evolved as an adaptation to wind pollination. For this reason, he places this family in the subclass Dilleniidae and the superorder Dillenianae. In his works, Takhtajan – drawing on the research of N. Hallier (1911, 1912, 1918), H.Gobi (1916), A. Cronquist (1957), and M. Gzyryan (1955) – argues that the family Salicaceae originated from Flacourtiaceae, a hypothesis supported by similarities in the wood anatomy and floral morphology of these families [5].

It is believed that the flowers of Salicales evolved from bisexual, insect-pollinated flowers with a normally developed perianth. This hypothesis is supported by pronounced rudimentary processes observed in Salicaceae flowers and by the presence of atavistic abnormalities, including the occasional formation of bisexual flowers. Thus, the reduction of the perianth and the shift to wind pollination are regarded as relatively recent evolutionary changes associated with the specialization of the family.

The family Salicaceae is relatively small in terms of the number of genera and species. It is primarily composed of three genera: the widespread and ecologically important *Populus*, the highly diverse genus *Salix* L., and the small, relict genus *Chosenia* Nakai, which occupies an intermediate position between willows and poplars. These genera share several morphological and anatomical features, including similarities in wood structure, seeds, and reproductive organs.

One of the best-studied and economically important genera of the family is *Populus*. In 1947, the International Poplar Commission approved a division of this genus into five sections: Leuce Duby, Aigeiros Duby, Tacamahaca Spach, Leucoides Spach, and Turanga Bge. For many decades, this classification served as a basis for botanical and forestry research, since the sections reflect both morphological distinctions and ecological specialization among poplar groups.

In the following decades, various attempts were made to clarify the intra- and interspecific relationships within the genus. For example, S. Ya. Sokolov (1951) proposed his own system, dividing *Populus* into three subgenera: Turanga Bge., Leuce Duby, and Eupopulus Dode. His classification incorporated wood and bud morphology as well as biogeographical patterns, which made it convenient for floristic and dendrological studies.

Later, R. V. Kamelin (1973), analyzing the degree of primitiveness and evolutionary advancement of particular traits, recognized five subgenera: Tsavo (Iarn.) R. Kam., Turanga (Bunge) Dode, Tacamahaca (Spach) R. Kam., and *Populus*. Of particular interest is that Kamelin elevated Tsavo to the rank of subgenus, emphasizing the pronounced morphological and evolutionary distinctiveness of this lineage [6]. His approach was based on a broad comparative analysis that included not only morphology but also ecological characteristics.

S. K. Cherepanov, who published an extensive floristic review in 1973, adhered to a more conservative viewpoint and recognized only three subgenera: *Balsamifera Bugala, Populus,* and *Turanga (Bunge) Dode* [7]. His classification prioritized practical floristic usability and taxonomic stability, making it suitable for identification guides and regional botanical treatments.

In the present study, we follow the classification proposed by F. Guinier, which has gained wide acceptance among botanists and foresters and is used by specialists both in Kazakhstan and abroad. Guinier's system is noted for its logical structure and good correspondence with morphological and evolutionary data.

According to Guinier's classification, the genus *Populus* is divided into five sections: – Turanga (Bge.), which includes ancient and xerophytic forms found primarily in arid regions; Leuce Duby (white poplars), characterized by light bark and distinctly white-tomented leaves; Aigeiros Duby (black poplars), widespread along river floodplains and known for their ecological plasticity; Tacamahaca Spach (balsam poplars), distinguished by their aromatic resinous buds and high frost resistance; Leucoides Spach, a relatively rare group notable for its distinctive fruit structure [8].

Thus, the diversity of approaches to the systematics of *Populus* reflects the complexity and ancient history of its evolution, as well as the considerable variability of its morphological traits. Guinier's classification appears most suitable for practical application, as it integrates morphological, biogeographical, and ecological criteria.

The systematics of *Populus* L. remains the subject of ongoing debate, particularly concerning the rank of individual taxa, their nomenclature, and phylogenetic relationships.

These discrepancies are related to the high variability of *Populus* L. species across different geographical regions, which greatly complicates the establishment of clear morphological boundaries between subgenera and sections.

Throughout the twentieth century, numerous classification schemes were proposed, each reflecting attempts to organize the considerable intra- and interspecific diversity of the genus.

V. L. Komarov (1934) distinguished five major taxonomic groups within the genus *Populus*: white poplars (*Leuce* Duby), black poplars (*Aigeiros* Duby), aspens (*Trepidae* Dode), turangas (*Turanga* Bge.), and balsam poplars (*Tacamahaca* Spach) [9]. This system was among the first attempts to integrate morphological, ecological, and geographical characteristics, which made it possible to structure the diversity of the genus to some extent.

Western Kazakhstan represents a unique natural region that combines features of steppe, semi-desert, and floodplain ecosystems. This combination of landscapes makes the area particularly valuable for botanical, biogeographical, and evolutionary studies. Both native poplar species, adapted to local climatic contrasts, and introduced species used in urban landscaping and forest reclamation occur here. Their coexistence creates favorable conditions for studying hybridization, adaptation, introgression, and natural selection within the genus *Populus*. It is especially noteworthy that many species and hybrids in Western Kazakhstan exhibit a high degree of ecological plasticity, making the region a kind of "natural laboratory" for exploring evolutionary processes in the genus.

The origin and geological development of the West Kazakhstan region are closely linked to processes occurring within the Precaspian tectonic depression. This depression, bounded by major fault zones, is the deepest subsiding block of the East European Platform. The geological structure of the region has had a profound impact on its present – day landscape, hydrological network, and vegetation patterns.

Without delving into the full complexity of the region's geological history, we highlight only those aspects most relevant to the formation of its modern landscape. The main features of the surface of West Kazakhstan were established before the Quaternary period, beginning in the Paleogene. During this time, sedimentation, subsidence, and uplift occurred, producing a mosaic of elevations, depressions, ancient terraces, and drainage lines. These geomorphological features played an important role in shaping vegetation distribution, including natural habitats of various poplar species.

Beginning in the Paleogene, several areas of Western Kazakhstan began to rise above sea level, most notably the Obshchiy Syrt and the Podural Plateau. In the Pliocene (upper Neogene), renewed subsidence of part of the Obshchiy Syrt allowed the waters of the extensive Akchagyl Basin of the ancient Caspian Sea – existing roughly 1.7 million years ago – to once again occupy large parts of the region. However, it is believed that the Akchagyl transgression did not inundate the Podural Plateau, as this area was experiencing uplift at the time.

Amid regional neotectonic uplift, local elevations and depressions formed within the plateau as a result of salt-dome activity. Consequently, the surface of the West Kazakhstan region within the Podural Plateau has not been submerged by marine transgressions since the mid-Paleogene and represents the oldest portion of the landscape.

After the retreat of the Akchagyl Sea, a further significant uplift of the Obshchiy Syrt occurred, preventing subsequent Caspian transgressions from reaching this area. As a result, the northern part of the region – lying 80 – 100 meters above sea level – is composed of heavily eroded Mesozoic (mainly Cretaceous) and Paleogene marine deposits.

On the pre-Akchagyl surface along the present – day Ural River valley, a submeridional scarp and a major fault zone can be traced. These structures likely played a decisive role in determining the position of the Ural Valley during the regression of the Lower Khvalyn Basin. Due to Quaternary tectonic movements, an elevated step formed beneath the Obshchiy Syrt, on which the high Lower Khvalyn terrace of the Caspian Sea developed, characterized by thin Quaternary deposits.

The southern part of the region, located along the zero-metre contour, is underlain by an ancient bedrock uplift that determined the shoreline of the Upper Khvalyn Basin. This uplift is also believed to be responsible for the endorheic nature of several small steppe rivers that do not flow into major drainage systems.

The aim of this study is to analyze the origin and evolution of the genus *Populus* L. in the context of the natural conditions of Western Kazakhstan, identify key factors influencing species distribution, ecological plasticity, and variability, and assess the role of hybrid forms in shaping local populations and their adaptation to the geomorphological and climatic features of the region.

Materials and methods

The study is based on an analysis of scientific literature on the systematics, phylogeny, paleobotany, and evolutionary history of the genus *Populus*

L. Sources published between 1905 and 2024 were examined. A comparative and analytical review of different taxonomic approaches and their correspondence to modern molecular-phylogenetic data was carried out. Latin names of vascular plants were verified using the IPNI and POWO databases.

Wood fragments were obtained during archaeological excavations in the village of Taksai, Terektinsky District, West Kazakhstan Region. Samples were collected from a depth of 1.3 – 5.0 m. After preliminary cleaning, the specimens were described and photographed under standardized lighting conditions.

Thin sections (transverse, radial, and tangential) were prepared following the standard IAWA (2004) protocol. Microscopic examination was performed using a Leica DM500 microscope.The following anatomical parameters were measured:vessel diameter ,vessel density (no./mm²); fiber wall thickness, size and height of wood rays.

In this study, no quantitative statistical methods were applied, as the research is analytical and comparative in nature and is based on the examination of published taxonomic, phylogenetic, morphological, and paleobotanical data. Instead of numerical analysis, a qualitative comparative approach was employed to identify points of concordance and divergence among various classification systems of the genus *Populus* L. proposed by different domestic and international researchers over time.

In comparing the works of Dode (1905), Komarov (1934), Sokolov (1951), Kamelin (1973), Cherepanov (1973), Eckenwalder (1996), Skvortsov (2010), as well as modern molecular studies (Cervera et al., Wang et al., Liu et al., Zhang et al., Zong et al.) [10], a structural taxonomic comparison approach was employed. This included: (1) a comparative analysis of taxa of the same rank proposed by different authors, and an evaluation of the stability of taxonomic characters used across various classification systems (leaf morphology, bud structure, wood anatomy, pollen, seeds); and (2) a comparison of historical – biogeographical scenarios of origin, particularly the East Asian versus North American hypotheses.

Particular attention was given to assessing the consistency among different sources of evidence – morphological, paleobotanical, and geographical. This made it possible to integrate the findings into a unified conceptual framework that characterizes the evolutionary development of the genus within the environmental context of Western Kazakhstan.

Results and discussion

A.L. Takhdajian [11] believes that the family Salicaceae is the closest to the family Tamaricales, especially Violates, in the structure of the gynoecium and a number of other features, and could have originated from Flaoourtiaceae, with which it is similar in the anatomical structure of wood and morphology of flowers. Poplar species are characterized by a diploid set of chromosomes (2 n = 3 8), some of them have an autotriploid set (2 n = 5 7) – *P.alba* L., *P. tremula* L., *P. nigra* L.- and even autotetraploid (2 n = 7 6), in *P. x canescens* a form with an allotriploid set of chromosomes 2 n = 57 is known [12].

OECD reports report systematics and genus remains a subject of scientific debate [13]. To date, there are several scientific approaches to the systematics of the genus *Populus*, reflecting both morphological and molecular-genetic diversity of representatives. The most significant classifications were proposed by such researchers as Dode (1905), Komarov (1934, 1936), Kamelin (1973), Zsuffa (1975), Starova (1980), Eckenwalder (1996), and Skvortsov (2010), each of which takes into account the peculiarities of the structure of leaves, buds, flowers, and species ranges [141].

Despite the considerable number of studies devoted to the systematics and phylogeny of *Populus* L., the internal relationships among its major sections and the precise delineation of their taxonomic boundaries remain incompletely resolved. This persistent ambiguity is largely attributable to several complicating factors, including extensive natural and artificial hybridization, pronounced morphological plasticity, and substantial discrepancies in the interpretation of diagnostic characters among different authors. Such inconsistencies are evident in the works of Cervera et al. (2005), Cronk (2005), Wang et al. (2014), Liu et al. (2017), Zhang et al. (2017, 2018), Zhou et al. (2018), and Zong et al. (2019) [15,16].

The question of the actual number of species within the genus *Populus* has likewise long been a matter of scientific debate, with estimates varying widely among researchers. The greatest divergence in opinion is observed in the works of Chinese botanists, who typically recognize a substantially larger number of species than their Western counterparts (Fang et al., 1999; Wan & Zhang, 2013; [17]. As a result, specialists from other regions consider these traits unreliable, which complicates the accurate delimitation of species. At present, two primary hy-

potheses address the origin of the genus *Populus*: the North American hypothesis and the East Asian hypothesis. The North American hypothesis posits that poplars originated in the Eocene of North America and subsequently dispersed into Eurasia by way of Paleogene land bridges (J.M. Murillo, 2004; Manchester et al., 2006; D. Kalivas 2013; A. Sasmaz, 2016) [20]. A key line of evidence is the existence of *Populus mexicana* Wesm. ex DC., the only extant representative of section Abaso, which today is restricted to the warm regions of Mexico. Fossil evidence indicates that ancient members of Abaso were once widely distributed, extending as far north as Alaska. The earliest fossil remains tentatively assigned to *Populus* are derived from Paleocene deposits of North America and date to approximately 58 million years ago. Modern *P. mexicana* shows pronounced morphological affinity to the well-substantiated fossil species *P. wilmattae* Cockrell, discovered in Middle Eocene strata (~48 Ma) of northeastern Utah [21]. This fossil taxon is widely employed as a calibration point in molecular phylogenetic analyses [22].

The early Paleogene fossil floras of Kamchatka likewise contain abundant poplar remains, indicating that the genus was already well established in northern Asia during this period. According to Budantsev (2006), the formation of the Paleogene flora in the western part of Kamchatka, which took place during the Late Paleocene – Early Eocene (approximately 55 – 60 million years ago), was accompanied by the disappearance of several Mesozoic conifer taxa, such as *Ginkgo kamtschatica*, *Metasequoia occidentalis*, and *Trochodendroides arctica*, while certain representatives of the Cretaceous period, particularly *Platanus basicordata*, persisted. During this transitional period into the Cenozoic era, new floristic elements began to appear, including the early representatives of the genus *Populus* [23]. According to modern phylogenetic reconstructions, the fossil remains of Populus discovered in these deposits represent geologically ancient forms that align well with the current understanding of poplar evolution. Molecular and paleobotanical evidence indicates that the divergence between the genera *Populus* and Salix occurred during the Late Cretaceous (approximately 68 – 67 million years ago), marking one of the earliest branching events within the Salicaceae family. This separation coincided with significant global climatic changes and the rapid diversification of angiosperms. Additional biogeographic studies suggest that *Populus* most likely originated in East Asia, which acted as a major evolutionary center for early representatives of temperate woody flora. From this region, ancestral poplar lineages subsequently migrated to North America, Europe, and North Africa, likely using high-latitude land bridges such as Beringia during warmer climatic phases of the Paleogene [23]. Such migrations created conditions for early diversification within the genus and contributed to the formation of several distinct evolutionary lineages. In the works of Du et al. (2022), the section *Populus (Leuce)*, which encompasses the white poplars, is consistently regarded as a monophyletic lineage [24]. This conclusion is supported by concordant data from both morphological characteristics – such as leaf structure, bark texture, and seed morphology – and molecular markers including chloroplast and nuclear DNA. The section is further distinguished by clear reproductive barriers with other sections, indicating long-term evolutionary isolation. Recent phylogenomic analyses also reinforce the early divergence of the *Populus (Leuce*) lineage, suggesting that it may represent one of the oldest surviving branches within the genus. Fossil evidence from the Paleogene of Eurasia, combined with molecular clock estimates, supports the hypothesis that the evolutionary history of the white poplars spans more than 50 million years. This makes the group particularly valuable for understanding long-term patterns of adaptation, hybridization, and biogeographic dispersal within *Populus*.

This section also exhibits near – complete reproductive isolation from the other sections of the genus. The subsection *Albidae* (commonly referred to as the silver poplars; see Table 1) is currently represented by only a single extant Eurasian species, *P.alba* L. In contrast, the North American representatives of this lineage constitute evolutionary derivatives confined primarily to the montane regions of tropical Mexico, within the Madrean floristic subkingdom. It is presumed that their ancestral forms dispersed into North America during the Paleocene–Eocene interval, shortly after the earliest progenitors of the genus *Populus* colonized the continent. Comparable to members of section *Turanga*, the extant taxa of subsection *Albidae* are widely regarded as relict components of the Madrean – Tethyan floristic region, preserving ancient biogeographic signatures that trace back to early Cenozoic vegetation dynamics.

The analysis of biometric traits and fluctuating asymmetry of the leaf blade revealed clear morphological differentiation among the examined sections of *Populus*. The observed patterns of variation provide important insights into their taxonomic rela-

tionships, adaptive strategies, and microevolutionary dynamics.

The consistently larger leaf dimensions recorded for section Aigeiros align with its known ecological association with more mesic environments, where broader and longer leaves contribute to enhanced photosynthetic capacity. In contrast, the smaller leaf sizes characteristic of Trepidae likely reflect adaptation to drier or more continental habitats, where reduced transpiration and smaller lamina surface area are advantageous. The intermediate values found in Albidae suggest ecological flexibility and occupation of transitional environmental niches (Table 1).

Intraspecific variability, expressed through coefficients of variation ranging from 9 to 25%, highlights substantial morphological plasticity within the studied groups. Such variability is important for understanding microevolutionary processes and potential pathways of divergence. The fluctuating asymmetry values, used as an indicator of developmental stability, further support the presence of differential environmental pressures acting upon the taxa.

A notable finding is that the morphometric parameters of Albidae exceed those of the parental species. This pattern can be interpreted as evidence of somatic and adaptive heterosis, reflecting enhanced growth performance and increased ecological fitness. The morphological distinctness of Albidae from both parental forms provides additional support for its taxonomic autonomy and confirms its intermediate but well-defined position within the genus.

The results not only strengthen existing taxonomic concepts but also contribute to understanding the evolutionary trajectories of these groups in the environmental context of Western Kazakhstan.

Table 1 – Biometric characteristics of the leaf blade in the sections Albidae, Trepidae, and Aigeiros

Indicators	Albidae	Trepidae	Aigeiros
Leaf blade length, cm			
Mcp	6,5	4,95	7,14
±m	0,50	0,54	0,3
Kv	9,7	15,0	9,7
Maximum leaf blade width, cm			
Mcp	4,5	4,35	5,65
±m	0,73	0,56	0,60
Kv	18,7	17,2	9,9
Petiole length, cm			
Mcp	6,46	3,01	5,84
±m	2,07	0,39	0,73
Kv	16,9	20,2	12,6
Distance between the widest part of the leaf blade and its base, cm			
Mcp	3,32	1,96	3,52
±m	0,14	0,71	0,3
Kv	10,6	22	2,78

The biometric characteristics of the leaf blade clearly distinguish the sections Albidae, Trepidae, and Aigeiros. The largest leaf dimensions are observed in Aigeiros, reflecting its adaptation to more humid environmental conditions. Albidae occupies an intermediate position across all parameters. The smallest values occur in Trepidae, indicating adaptation to drier or more continental habitats. These differences confirm the diagnostic significance of leaf morphometry in delimiting the sections of the genus *Populus*.

The subsection Albidae (the silver poplars; see Table 2) currently includes only a single modern Eurasian species, *P. alba* L. Their ancestral forms are thought to have entered North America during or shortly after the colonization of the continent by the ancestors of the Abaso lineage in the Paleocene – Eocene. As with representatives of section

Turanga, modern Albidae taxa are regarded as relictual elements of the Madrean – Tethyan floristic region.

Paleobotanical evidence for fossil representatives of the subsection Albidae is sparse, and all currently known occurrences originate from the European sector of Eurasia [25]. From Late Pliocene deposits of Kazakhstan, the species *P. gokhtuniae* Gabrielyan sp. nov. has been described, exhibiting a high degree of morphological similarity to modern *P. alba* (Table 3). *P. alba* itself is reliably documented in the fossil record beginning in the Pliocene, approximately 5 million years ago [26].

Table 2 – Evolutionary timeline of modern species in the genus *Populus*, section *Populus* (Leuce)

Name of taxon	Time of occurrence	Geographical localization of poplars of Kazakhstan
Subsection *Albidae*		
P. alba	Pliocene	Otrogo general syrt, Tobyl-Ishim, Irtysh, Semipalatinsk hog, Aktobe, Zaisan, Balkhash-Alakul.
P. × canescens	Late Pliocene	Semipalatinsk hog, Aktobe, Turgai, Karaganda, Aktogai (Kounradsky), Zaisan, Altai.
Subsection *Trepidae*		
P. tremula	Pliocene	Otrogo Common Syrt, Tobyl-Ishim, Irtysh, Semipalatinsk Hog, Kokchetav, Pre-Caspian, Aktobe, Mugodzhary, Turgai, Western and Eastern Cretaceous, Zaisan, Altai, Tarbagatai, Dzungarian Alatau, Zailin Kungai Alatau, Ketmen-Terskey Alatau.

Research indicates that the hybrid forms within the section *Populus* have a very ancient origin, and this conclusion is increasingly supported by new evidence. Introgressive hybridization is recognized as a key component of the reticulate evolution of the genus *Populus*. However, information regarding the timing of the emergence of modern spontaneous hybrids remains extremely limited and fragmentary. Perhaps one of the few exceptions is *Populus* × *canescens* (Aiton) Sm. – a natural spontaneous hybrid growing in the central floodplain of the Ural River.

P. alba and *P. tremula* species with close variability are known from the late Miocene and early Pliocene, and *P. × canescens* itself is recorded from the late Pliocene about 3.5 million years ago (Table 2) from the territory of modern Armenia [25;27].

The object of the study are fragments of tree trunk found during archaeological excavations conducted by archaeologist Amangeldieva Yana on the territory of Taksai village of Terektinsky district of West Kazakhstan region (GPS-coordinates: 51°19.635′N, 52°17.472′E; 51°19.590′N, 52°17.529′E).

The analysis showed that the morphological features of the specimens allow us to assign them to the genus *Populus* L. In terms of trunk structure and fiber characteristics, these remains are similar to species belonging to the *Albidae* subsection of the *Aigeiros* section (Fig.1). Radiocarbon dating showed that the age of these specimens corresponds to approximately 500 – 401 BC.

Despite the fact that this period belongs to the ancient time in the historical scale, the paleobotanical data testify to the wide distribution of representatives of the poplar genus (*Populus* L.) along the Uralsk since ancient times. These data confirm that floodplain forests in the Uralsk region have been preserved as sustainable bioecological systems for a long time.

The subsection *Trepidae* – Aspidae is relatively richly represented in the fossil record. However, in contrast to other numerous groups, such as Tacamahaca, aspens were not characterized by diversity in the Paleogene; their peak of prosperity was in the Miocene (Table 2).

The peak of evolutionary development within the subsection Trepidae occurred during the Miocene. In the Early Miocene, the species *P. tremulifolia* Sap. was recorded in the territory of Kazakhstan, whose ancestral forms later became widely distributed across Eastern Europe and the Caucasus. Another noteworthy finding within the Early Miocene flora of Kazakhstan is the presence of P. orzhilanensis Kornilova [28].

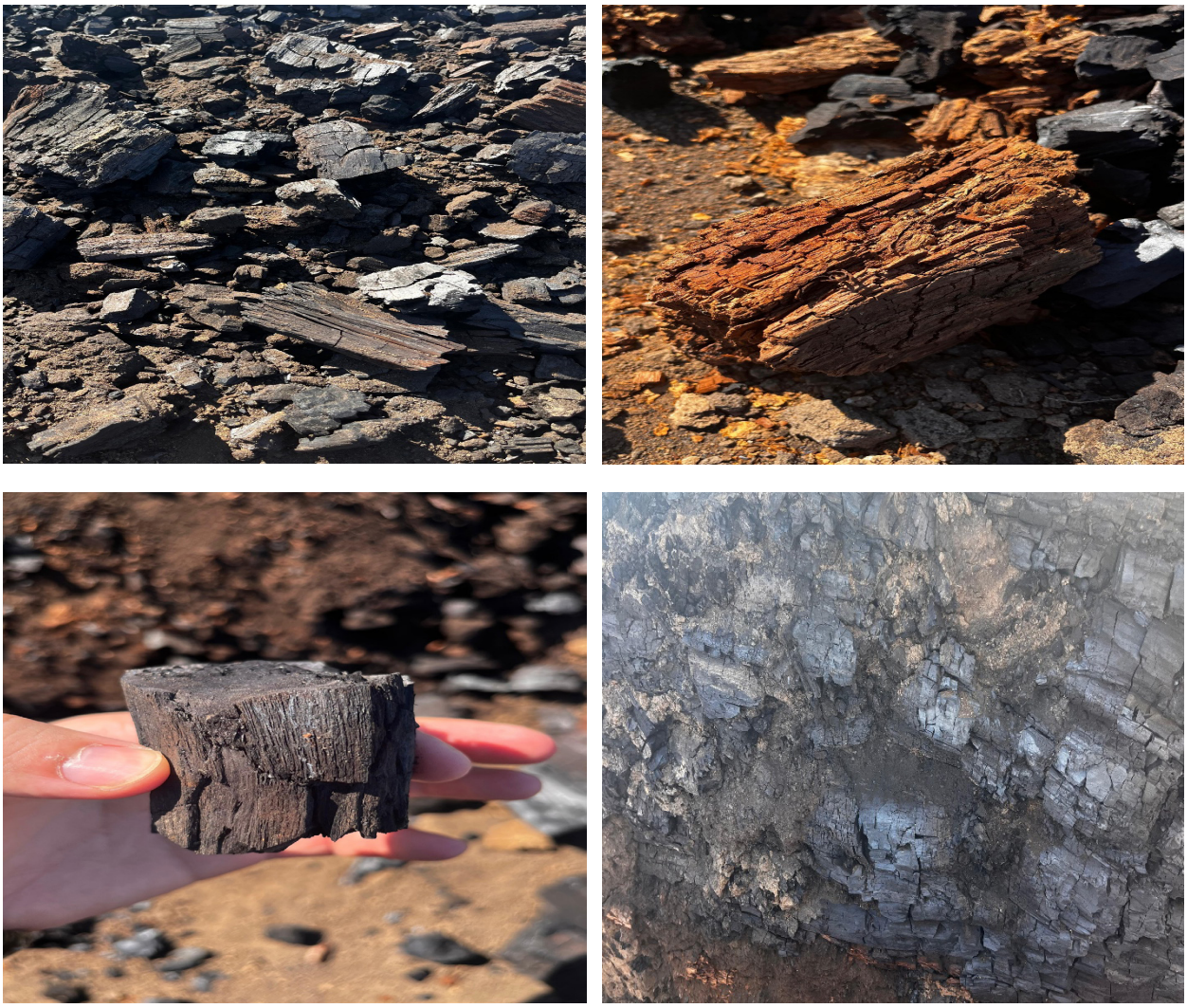

Figure 1 – Samples of *Populus* L. species discovered as a result of the paleobotanical study

Within Eurasia, the youngest representative of this subsection is P. tremula L., whose fossil remains have been identified in Pliocene deposits of Armenia, dated to approximately five million years ago.

In North America, ancestral lineages of modern aspens began to expand across the continent during the second half of the Miocene. By the end of this epoch, these ancestral populations had already diverged into two distinct species – *P. tremuloides* Michaux and *P. grandidentata* Michaux [29].

Long-term studies by Z. S. Wang and colleagues indicate that the section Aigeiros – the black poplars (*Populus nigra* L.) – represents one of the most evolutionarily advanced lineages within the genus *Populus* (Table 3). According to phylogenetic data, the origin of the sections Aigeiros and Tacamahaca is likely hybrid in nature, having formed during the early stages of the genus's evolutionary history [30]. It is assumed that species of section *Aigeiros* emerged as a result of ancient hybridization events involving ancestral lineages of the sections *Populus* and *Tacamahaca*. At the initial stages of divergence, genetic differentiation among these lineages was minimal, which is supported by evidence of ancient plastid capture resulting from interlineage hybridization.

A notable example is *Populus nigra*, whose origin is linked to an ancient hybrid lineage formed through crosses between ancestral black and white poplars. Analyses of chloroplast DNA reveal a high degree of similarity between the plastid genomes of *P. nigra* and species of the section *Populus*, providing strong evidence for an event of ancient plastid capture [31].

Table 3 – Divergence times of modern *Populus* species in the sections Leucoides and Aigeiros

Name of taxon	Time of emergence	Geographical localization of poplars of Kazakhstan
Section *Aigeiros*		
P. nigra	Pliocene	Otrogo general syrt, Tobyl-Ishim, Irtysh, Semipalatinsk hog, Kokchetav., Aktobe, Mugodzhary, Western Shallow Soil, Eastern Shallow Soil, Zaisan, Altai.

At the same time, nuclear DNA markers and morphological characteristics reported by Cervera et al. (2005) and Wang et al. (2014) consistently place *P. nigra* within the section Aigeiros, confirming its distinctiveness and phylogenetic cohesion. It is noteworthy that natural hybridization between representatives of the sections *Aigeiros* and *Populus* no longer occurs under present-day conditions, whereas hybridization among species of the sections *Aigeiros*, *Tacamahaca*, and *Leucoides* is still observed [32].

The earliest fossil remains resembling modern *P. nigra* – designated as *P. cf. nigra* – have been recovered from Miocene deposits in the Kochkor Basin of Kyrgyzstan [33]. Analysis of paleontological materials shows that the fossil remains of P. nigra date back to the Pliocene, with an estimated age of around five million years. Morphologically similar and diagnostically comparable specimens have also been identified in Late Pliocene deposits of Armenia, confirming that ancestral forms of P. nigra were already widely distributed across Eurasia by the end of the Neogene [34]. These findings indicate that the evolutionary lineage of black poplars developed on the Eurasian continent significantly earlier than in North America. In North America, the earliest fossil evidence of representatives of section Aigeiros appears only in Upper Miocene strata, suggesting a later arrival and radiation of this group on the continent.

In recent years, representatives of section Tacamahaca – the balsam poplars – have been increasingly used in the territory of Western Kazakhstan, particularly in urban alleys, parks, and shelterbelt plantations. Globally, this section comprises approximately ten recognized species, many of which exhibit complex clonal or hybrid origins resulting from prolonged natural selection and anthropogenic breeding. The primary center of diversity for Tacamahaca is located in Asia, where most species and endemic forms are concentrated; a considerably smaller number occur in North America.

Evolutionary studies and paleobotanical data indicate that in the past, the Tacamahaca section possessed a much broader geographic range and a higher level of species diversity than at present. This is supported by numerous fossil findings from Oligocene and Miocene deposits of Eurasia, which demonstrate that balsam poplars occupied key ecological niches within ancient forest communities. The reduction of their modern distribution is associated with global climatic shifts during the late Cenozoic and increased competition from more specialized woody taxa.

For Western Kazakhstan, species of the Tacamahaca section hold particular ecological significance: they exhibit high adaptability, including tolerance to drought, frost, and anthropogenic stress, making them promising candidates for urban greening, afforestation, and the restoration of degraded ecosystems. Furthermore, studying their genetic diversity and potential hybrid forms in the region can substantially contribute to understanding adaptive strategies within the genus *Populus* under extreme climatic conditions.

Although such subdivisions can help organize and interpret the substantial variation observed among fossil balsam poplars, this structure is regarded as overly complex for the currently accepted modern species (see Table 4). It tends to be favored mainly by proponents of an extremely broad, monotypic interpretation of the genus *Populus*, who recognize around – or more than – one hundred taxa.

Table 4 – Evolutionary timeline for the origin of contemporary *Populus* species of section *Tacamahaca*

Name of taxon	Time of emergence	Geographical localization of poplars of Kazakhstan
P. balsamifera	Late Miocene	In Kazakhstan it is found in urban plantings in Karaganda, Semipalatinsk and Uralsk.

Fossil evidence from the Late Oligocene of southern Western Siberia (approximately 24.5 million years ago) documents the presence of P. balsamoides Goepp., a species that later became widely distributed in the Miocene floras of Europe.

Assigning the North American representatives of the section Tacamahaca – whether extant or fossil – to any of the three previously discussed series (Laurifoliae, Tacamahaca, Latifolia) is not considered appropriate. In North America, *Populus* species capable of hybridization are phylogenetically much more closely related to one another than to their Eurasian counterparts.

According to studies by Dayanandan (2002) and Eckenwalder (2009), among the modern North American representatives of the section Tacamahaca, the greatest morphological similarity and closest phylogenetic affinity are observed between P. balsamifera and P. trichocarpa [37].

Phylogenetic analyses suggest that the divergence between P. balsamifera and P. trichocarpa may have taken place during the Middle or Late Miocene. However, some studies propose a considerably more recent divergence, suggesting that the two species separated during the Pleistocene glaciation, approximately 74.8 thousand years ago [38].

Conclusion

Representatives of the genus *Populus* L. – including two subsections (*Albidae*, *Trepidae*) and three sections (*Tacamahaca*, *Aigeiros*, *Populus* (*Leuce*)) – have been present in the floodplain forests of the Ural River valley within the studied region since ancient times.

The evolutionary history of the genus *Populus* L. in Western Kazakhstan reflects a long and complex process of phylogenetic, biogeographic, and ecological development. Analysis of paleobotanical and morphological evidence indicates that representatives of the three major sections – *Populus* (Leuce), *Aigeiros*, and *Tacamahaca* – have been present in the Ural River basin since ancient times, forming stable components of the region's floodplain and steppe – forest ecosystems. The earliest known hybrid taxon, *P.* × *canescens*, is recorded from the Late Pliocene, demonstrating that hybridization has long served as an important mechanism supporting genetic diversity within poplar populations.

The unique climatic and geological conditions of Western Kazakhstan create favorable prerequisites for the formation of local populations with high levels of species and genetic variability. The identified patterns of hybridization and adaptation in representatives of *Populus* in this region are of considerable importance both for theoretical botany and for practical applications in reforestation, landscape restoration, and sustainable bioresource management.

Understanding the mechanisms of adaptation, hybridization, and dispersal within the genus *Populus* is crucial for both theoretical botany and evolutionary biology, as well as for practical applications in forestry, landscape restoration, and environmental management. Owing to their high tolerance to drought, soil salinity, and anthropogenic stress, poplar species remain among the most promising candidates for green infrastructure development and the rehabilitation of degraded ecosystems in Western Kazakhstan.

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