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BIOGEOGRAPHY OF *NITRARIA* L.

Nitraria is a halophyte shrub, which grows in arid, semi-arid areas and particularly in saline deserts and salt marshes. The genus belongs to family Nitrariaceae and includes 10(12) species all over the world with unusual disjointed distribution. These shrubs are used in the protective afforestation for enhancing sand deposits and banks and reducing soil salinity and concentration of organic substances. The genus *Nitraria* L. is an old, Tertiary Period's relict plant which initially was described in Komarov's investigations and given main hypothesis about its origin and distribution centers in Chinese and Mongolian floristic geography. The probability that *Nitraria* L. is a very ancient genus, having its origins in Central Asia, is found as a theme of discussion of many researchers. The wide separateness between *N. billardieri* in Australia and the closely related *N. schoberi* in Eastern Europe and Asia has been difficult to explain. Recent molecular phylogenetic studies and methods have given new findings on systematics of the genus and new hypotheses on distribution pattern and time of origin. In this article, we discuss hypotheses about origin and distribution of *Nitraria* L.

Key words: *Nitraria* L., origin place, historical biogeography, ancestral area reconstruction

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Нитрарияның (*Nitraria* L.) биогеографиясы

Нитрария құрғақ және жартылай құрғақ аймақтарда өсетін, әсіресе тұзды шөлдер мен тұзданған батпақтарда таралған галофитті бұта болып табылады. *Nitraria* L. туысы Nitrariaceae жанұясына кіреді және оның дүние жүзінде ерекше жекеленіп таралған 10 (12) түрі бар. Бұл бұталар құмды аймақтар мен жағалауларды бекіту үшін қорғаныс ретінде, сондай-ақ топырақтың тұздылығы мен ондағы органикалық заттардың концентрациясын азайту үшін отырғызылады. *Nitraria* L. туысы бұл ежелгі үштік дәуірдің реликті өсімдігі, алғаш рет Комаровтың зерттеулерінде сипатталды, ал бұл Қытай және Монғол флористикалық географиясында оның шығу тегі мен таралу орталықтары жайлы негізгі гипотезаларды қалыптастырды. *Nitraria* L. өте ежелгі өсімдік туысы ретінде отаны Орталық Азия болып есептелу ықтималдылығы көптеген зерттеушілердің талдау тақырыбына айналды. *N. billardieri* түрінің Австралияда оқшау дамығандығын және онымен өте ұқсас *N. schoberi* түрінің Шығыс Еуропа мен Азияда таралуын түсіндіру қиын. Соңғы молекулярлық-филогенетикалық зерттеулер мен әдістер туыстың систематикасы туралы жаңа мәліметтер, оның таралу ерекшеліктері мен пайда болу уақыты туралы жаңа гипотезалар алуға мүмкіндік берді. Мақалада *Nitraria* L. шығу тегі мен таралуы жайлы гипотезалар қарастырылған.

Түйін сөздер: Нитрария (*Nitraria* L.), пайда болған жері, тарихи биогеография, байырғы аумақты реконструкциялау.

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Биогеография нитрарии (*Nitraria* L.)

Нитрария (*Nitraria* L.) представляет собой галофитовый кустарник, который растет в засушливых и полувзасушливых районах, особенно распространен в засоленных пустынях и на соляных болотах. Род *Nitraria* L. принадлежит к семейству Nitrariaceae и включает 10 (12) видов во всем мире, характеризующихся необычно разрозненным распределением. Эти кустарники используются в защитном облесении для укрепления песчаных отложений и берегов, а также для уменьшения засоленности почв и концентрации в них органических веществ. Род *Nitraria* L. – это древнее реликтовое растение третичного периода, которое впервые было описано в исследованиях Комарова, что сформировало основную гипотезу об источниках его происхождения и центрах распространения в китайской и монгольской флористической географии. Вероятность того, что *Nitraria* L. является очень древним родом растений, родиной которого считается Центральная Азия, является темой обсуждения для многих исследователей. Сложно объяснить обособленность *N. billardieri* в Австралии и нахождение тесно связанной с ней *N. schoberi* в Восточной Европе и Азии. Последние молекулярно-филогенетические исследования и методы способствовали получению новых данных о систематике рода, гипотез об особенностях его распределения и времени возникновения. В данной статье рассмотрены гипотезы о происхождении и распространении *Nitraria* L.

Ключевые слова: Нитрария (*Nitraria* L.), место происхождения, историческая биогеография, реконструкция исконной территории.

Introduction

Nitraria from Nitrariaceae family (formerly Zygophyllaceae) are shrubs of 0.5 – 2 m height, with entire, alternate, fleshy leaves. They grow in great abundance and produce salty-sweet edible fruits, which are important as a food (Komarov, 1908, 1947; Pan et al., 1999; Noble and Whalley, 1978a; Sheahan, 2011). *Nitraria* consists of 10 to 12 species with a worldwide distribution including Southeast Europe, Southwest and Central Asia (Usturt, Turan, Turgai, Kazakh uplands and partially mountains Kopetdag, Pamir-Alai, Tian Shan, Dzungar Alatau, Saur and Tarbagatai), Mongolia and China, North Africa, and Australia (Fig. 1) (Table 1). The name Nitre-bush is from the Latin word for saltpeter, nitrate, indicating its whereabouts at the bitter salt lakes. These shrubs are used in the protective afforestation for enhancing sand deposits and banks, and reducing soil salinity and the concentration of organic substances (Noble and Whalley, 1978b; Parida and Das, 2005; Vysochina et al., 2011). The taxonomy of *Nitraria* has been the subject of disagreement among different botanists for a long time. Despite of many dissimilarities in anatomy, embryology, biochemistry and plastid type, genus *Nitraria* was often included in Zygophyllaceae in the past. More recently, molecular phylogenetic studies have shown that Nitrariaceae is closely

related to Sapindales, where *Nitraria*, *Peganum*, *Malacocarpus* and *Tetradiclis* form a clade, with *Nitraria* sister to the other three genera, and *Tetradiclis* close to *Peganum* + *Malacocarpus* (Sheahan and Chase 1996; Savolainen et al. 2000; Muellner et al. 2007). Separation of *Nitraria* and *Peganum* (and *Malacocarpus*) from the family Zygophyllaceae and define them as distinct families was proposed by several authors (Sheahan and Cutler 1993; Ronse Decraene et al., 1996 and Bachelier et al., 2011).

Distribution of the *Nitraria* had attracted the special attention of researchers during long time. They tried to explain the origin of the genus. There were different hypotheses on the origin of the genus. Komarov (1908) suggested *Nitraria* originated from Africa, as an origin of tropical and western, and penetrated to Mongolia through the Aral-Caspian basin during its drying; Ilyin (1944) and Vassilchenko (1982) supported this opinion. According to Komarov (1908) the original location of *N. schoberi* were, in all probability, the seashore. Pan et al. (1999) also thought African and Australian species are primitive whereas Central Asian species are derived with respect to the pollen characters. Popov (1927) suggested the opposite concept of Komarov reminding the antiquity of the flora of Central Asian deserts. He insisted that «Mongolia and the desert country of Tien Shan had their own, older than the Miocene-Pliocene, the

sources of desert forms, some of which, after drying of the Aral-Caspian (Turan) plain began to penetrate there from north-east, moving to south-west». His opinion was fully accepted by Korovin (1935), later almost completely agreed by Bobrov (1946). While Grubov (1963) thought it should be native origin, i.e. from Central Asia, because the area is reach in endemic species and had ancient transformative geological events. Based on the ploidy variation, Pan et al. (2003) speculated the place with the primitive diploid species should be the origin place of *Nitraria*, namely, Tethys seacoast, presently Africa and the Mediterranean. Yang (2006) also thought an African origin likely, however, dispersal to Australia was assumed to have been a migration via Asia.

Recent molecular investigations have improved the generic classification, species relationship and distribution pattern of *Nitraria* (Zhang 2006; Su and Zhang 2013; Temirbayeva and Zhang 2015).

Methods

Modern biogeographical analysis is conducted by several steps of molecular methods: taxon sampling and DNA sequencing (using DNA fragments of *nrDNA* and *cpDNA*) following by

Bayesian phylogenetic analysis and divergence time estimation (implemented in BEAST) and ancestral area reconstruction (conducted by S-DIVA approach implemented in RASP) (Temirbayeva and Zhang 2015; Zhang et al 2015).

Discussion and Conclusions

Initially Komarov (1908) proposed two predictions about its center of origin. First, it would be Gondwana. *Nitraria* grows in Australia and Africa, but it does not exist in the Indian subcontinent, Madagascar and South Africa. Its absence in the Indian subcontinent is especially indicative. Second, it would be Angara continent. In general, it's poor not only with *Nitraria*, but also with its relatives. Moreover, Malpighiaceae and Zygophyllaceae do not have the original types here, which would have prevented them here generally considered by later invaders. Finally, he thought that *Nitraria* is the origin of tropical and western and penetrated into Mongolia via the Aral-Caspian basin as it is drying up. The habitat of *Nitraria* in Australia was explained only by assuming the hypothesis that the plant in its history was connected with the continent of Gondwana, unless, of course, as it was a random element.



Figure 1 – Distribution of the *Nitraria* in the World

Table 1 – Classification and distribution of species in the genus *Nitraria* L.

Species	Denominated year	Habitat and distribution
<i>N. schoberi</i> L.	1753	Salinized low lands in Europe along Mediterranean, the Caspian and Xinjiang, China, Kazakhstan
<i>N. sibirica</i> Pall.	1784	Salinized low lands and drought hillslope in northern China and the Siberia, Kazakhstan, Mongolia
<i>N. senegalensis</i> Lam.	1797	Desert in northwestern Africa
<i>N. tridentate</i> Chev.	1798	Desert in northern Africa and adjacent regions of Arabia
<i>N. billardieri</i> D.C.	1828	Savannah and desert in southwestern Australia
<i>N. retusa</i> Aschers.	1876	Desert in northern Africa
<i>N. sphaerocarpa</i> Maxim.	1883	Desert in northwestern China and Mongolia
<i>N. roborowskii</i> Kom.	1908	Margin of desert or basin in northwestern China, Mongolia, Russia
<i>N. komarovii</i> Ili. et Lav.	1944	Margin of desert or basin along the Caspian
<i>N. tangutorum</i> Bobr.	1946	Salinized low lands and margin of desert in northwestern China
<i>N. praevisa</i> Bobr.	1965	Sands in Gansu, Ninxia and Inner-Mongolia, China
<i>N. pamirica</i> Vas.	1974	Drought hillslope in Pamirs with altitude 3800-4300 m
<i>N. sinensus</i> Kitag.	1979	Sands along the sea of the Liadong Peninsula, China

The most mysterious is the complete isolation of the Australian *Nitraria* from Asian, and it still has not yet been found on the plains of Hindustan, even in the Indus Basin. Maksimovic (Enum. Pl. Mongoliae) suggests that the reason for this is the drift of Mongolian seeds to Australia by migratory birds. Against this opinion says, however, a strong prevalence of *Nitraria* in Australia (Swan River to the west, New South Wales on the east side of the sea in South of Australia and Victoria and the Murray River) seems exciting and the entire of central desert this country (Komarov, 1947).

Scatter of general area of distribution is extremely mysterious. Maksimovic Opinion on the transfer of the plant fruit by birds, wandering from Central Asia to Australia and back, causing two objections. First, how much time should be delayed, though retaining the ability to germinate in the intestines of birds, these are quite large and heavy seeds, so as not to be dropped by during the flight, the duration of which is very significant. Secondly, in case of accidental drift by birds apparently single seeds, whether plant may spread as widely as is the case in our Australian plants. Furthermore, if we accept identity and the Senegalese plant of Oliver and for him to take the same explanation, is it not the birds fly from Syria to Senegal and back, and why not sown *N. Schoberi* in the Sahara, lying as if on the way. There is no also *Nitraria* in the deserts of the Indian subcontinent; therefore, it is necessary

to prove that the birds that would fly away for the winter of Qaidam to the banks of the Indus, does not exist (Komarov, 1908; 1947).

In recent studies (Temirbayeva and Zhang 2015; Zhang et al 2015) eight species of *Nitraria* (nine species of Nitrariaceae family) were sampled from China, Middle East, North Africa and Australia to reconstruct phylogeny, using sequences of nrDNA and cpDNA regions and test the monophyly of the species within the genus; and use the phylogenetic trees generated from these data to examine previous biogeographic hypotheses about origin of the genus. To test these biogeographical hypotheses, the robust methodology of molecular clock and ancestral areas reconstruction, developed in the last decades, are used to investigate *Nitraria* origin and evolution, and reconstruct the biogeographical history of *Nitraria* disjunct distribution and speciation. (Fig. 2).

The dating result showed that *Nitraria* is in reality an ancient taxon, originating in early Paleocene to Cretaceous, yet diversification within *Nitraria* is dated to late Miocene 8.96 Ma forward. Except for *N. sphaerocarpa* and African *N. retusa*, most of the species nodes or clades of the genus are young, less than 9 Ma, late Miocene to Pliocene.

Five areas were used in ancestral area reconstruction. Central Asia includes mainly desert and steppe regions, as well as some significant mountains. In term of floristic divisions, two parts, Mongolia and the Junggar-Turan province 21, or the

Junggar and Kashgar subkingdoms 58, here named eastern and western Central Asia, can be designated within Central Asia (Fig. 2). *Nitraria* also occurs in Siberia, generally in Siberian steppe, which is distinct from the Central Asian desert. Thus, five areas are divided for *Nitraria*, **A**: eastern Central Asia, also including North China-Northeast China of East Asia, **B**: western Central Asia, as well as Iran, Turkey, and Eastern Europe, **C**: Siberian steppe, **D**: Africa, northern Africa and adjacent regions of the Middle East, **E**: Australia.

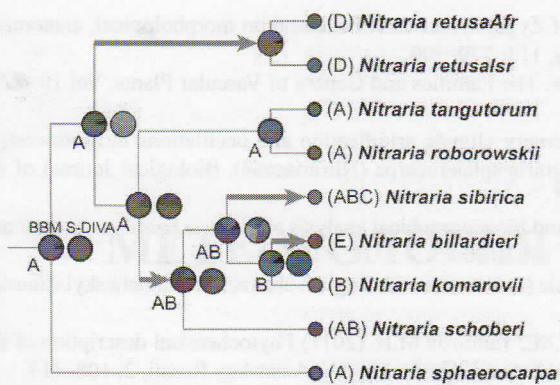


Figure 2 – Biogeographical ancestral optimization performed with S-DIVA and BBM, implemented in RASP (Zhang et al., 2015)

According to ancestral area reconstruction of S-DIVA analyses eastern Central Asia (A) is confirmed to be the origin place of the genus *Nitraria*, and then four dispersals occurred in the evolutionary history of *Nitraria*.

Eastern Central Asia, located along the eastern Tethys, was an ancient land that in early

Tertiary, from Paleocene to Oligocene, had an arid subtropical flora and vegetation which could have fostered the growth and development of ancient arid lineages such as *Nitraria*. Antiquity of the eastern Central Asian flora can be evidenced from pollen complexes in several regions such as Kashgar, the Zaidam Basin, and the Hexi Corridor in China, particularly *Nitraria* pollen found in Paleocene strata at Keche county, Xinjiang province (located on the southern slope of the Tianshan Mts. and pertaining to the Kashgar flora); and the late Eocene (Paleocene-Cretaceous) at Xining, Qinghai province, having old arid vegetation and arid endemic genera. Eastern Central Asia could be regarded as the ancestral area because of the richness of *Nitraria* species there, with six endemic species, and with *N. sphaerocarpa* being located at a basal position on the phylogenetic tree (Zhang et al., 2015).

N. retusa – is North African species, settling eastward to Palestine. As it turned out, there is in the «continuation» of its type much further east: in 1974 L.I. Vasilyeva published a new species (*N. pamirica*) from South-Eastern Pamirs, having a grid (not armored) structure of the endocarp. This is a great discovery allowing ranking *N. pamirica* to relict species, which in the southeast corner of the Pamirs, they grow in abundance (Lukanenkova, 1964). In contrast to the tall-stem shrub species of the genus *Nitraria*, plants of Pamir type are flattened and pinned to the ground, and perhaps are fixed juvenile form of some ancient species. In previous studies, all researches were done not including *N. pamirica* species, so further work is needed to collect this sample and establish the full phylogenetic, biogeographical, phylogeographical analysis of *Nitraria* genus.

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