

SPECIES DIAGNOSTICS IN *TRIPOLIUM* GENUS (ASTERACEAE) WITH A VIEW TO HETEROCARPY

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Tripolium genus is represented by the only species *Tripolium pannonicum* (Jacq.) Dobrocz. The individuals of this species feature variable morphological characters due to wide distribution area of the species covering vast territory from the Atlantic coast of Europe through the Pacific Ocean. As a typical halophyte, it grows in azonal communities of several latitude zones. The study was based on the analysis of morphological characters which used to be diagnostic in distinguishing between the closely related taxa: *T. pannonicum* (Jacq.) Dobrocz. subsp. *tripolium* (L.) Greuter. (*T. vulgare* s. str.) and *T. pannonicum* (Jacq.) Dobrocz. subsp. *pannonicum*. The significance of morphological diagnostic characters in protologs and subsequent botanical literature is discussed. Such morphological characters as presence/absence of heterocarpy and stem branching pattern are stated to be independent of geographical distribution of populations. They rather represent an adaptive character of propagation in annual plants of *Tripolium pannonicum* (Jacq.) Dobrocz. under variable environmental conditions of under flooding zone.

Key words: carpology, halophyte, heterocarpy, morphology, taxonomy, *Tripolium vulgare*, *T. pannonicum*.

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INTRODUCTION

Tripolium Nees genus belongs to the tribe Astereae, subtribe Asterinae (Cass.) Dumort. (family Asteraceae). According to Nesom and Robinson (2007), the subtribe includes 13 genera and about 270 species. The recent studies involving molecular methods showed that Galatella group (incl. *Galatella*, *Tripolium* and *Bellis*) is formed of a well-defined, monophyletic clade, with a clear separation but uncertain position of *Tripolium* (Li et al., 2012; Jafari et al., 2015, Korolyuk et al., 2015).

We consider that *Tripolium* genus is represented by the only species *Tripolium pannonicum* (Jacq.) Dobrocz. s. l. (which in the most part of Russian publications was incorrectly identified for the Asian territory as *T. vulgare* Nees). This is an annual halophyte growing in azonal communities. Due to specific ecology and wide distribution area covering several latitudinal zones, these plants possess variable morphological characters. The species is distributed in the temperate belt of Europe and Asia. Previously, it was considered that they grew also in North America (Novopokrovsky, 1922; Tamamshyan, 1959). According to Nesom (1994), the North American specimens are adventitious. The “Flora of China” also reports *T. pannonicum* as growing both in Asia, Europe and North Africa (Chen et al., 2011).

The taxonomical treatment of the species is still disputable due to specific ecology, wide distribution area, and variable morphological characteristics in the specimens. Moreover, the undescriptive diagnoses of ‘Linnaeus’s species’ also contribute to the nomenclature problems (Linnaeus 1753: 872).

Below we discuss the possible split of the species into two species or subspecies accepted by some specialists. The populations confined to inland saline habitats belong to *T. pannonicum* (Jacq.) Dobrocz. subsp. *pannonicum*, while the Atlantic coastline populations are attributed to *T. pannonicum* (Jacq.) Dobrocz. subsp. *tripolium* (L.) Greuter. In addition to geographical distribution, in 19–20th centuries the following morphological characteristics were also offered for taxa distinguishing: stem branching, phyllary tip peculiarities, and heterocarpy. Persistence of the latter character made it to be most reliable for many Brassicaceae and Asteraceae species groups (Voitenko, 1969, 1970; Levina, 1981). The ‘heterocarpic’ plants in *Tripolium* genus feature an expressed difference in cypselae size, and it is true for the Atlantic coastline populations (Table 1). The study targeted to estimate the possibility to use these morphological characters, especially heterocarpy, in *Tripolium* genus diagnostics based on the material collected across the territory from the Atlantic through the Pacific coastlines.

Table 1

Differences in morphology (1) and distribution area (2) between *Tripolium vulgare* and *T. pannonicum* (according to Tsvelev, 1994)

Различия в морфологии (1) и распространении (2) между *Tripolium vulgare* и *T. pannonicum* (согласно Цвелеев, 1994)

No.	<i>T. vulgare</i> Nees s. str. (as realized by Tsvelev N.N., 1990, 1994)	<i>T. pannonicum</i> (Jacq.) Dobrocz. s. str.
1	Cypselas 2.6–4 mm long, indistinctly differing in size within one capitulum. Stems usually branched in upper part	Cypselas of outer flowers of capitulum 1.6–2.5 mm long, with pappus 6–9 mm long; cypselas of inner flowers noticeably different in size: 2.8–4 mm Stems usually branched nearly from the base; leaves less carnose in average
2	Atlantic coastal area	Inland coastlines of Pontic-Pannonian region

MATERIAL AND METHODS

For *T. pannonicum* (Jacq.) Dobrocz., the samples of various Herbaria (BRNU, DE, KW, LE, LISU, NS, NSK, P, PE, TASH, TK) and personal collections from different regions where the species grows were studied. Fruiting plants for comparative morphology were collected in 17 natural populations growing in Russia: the Republics of Kalmykia, Khakassia, Tyva, the Samara, Leningrad and Novosibirsk Regions, Primorsky Krai and Crimea; as well as in Europe (Austria, Hungary) and Xinjiang Uygur Autonomous region (China) (Fig. 1, Table 2). For heterocarpy analysis we selected the dried samples with seeds both from Herbarium and personal collections. The latter are stored at I.M. Krasnoborov Herbarium, Russia, Novosibirsk (NS) and at Herbarium of the University of Debrecen, Hungary, Debrecen (DE).

In total, we measured the size in over 100 capitula (ca. 2000 cypselas) from 22 inland and 11 coastal populations. Of them, 73 were estimated at minimum one capitulum per specimen). Additionally, 39 capitula were analyzed in one inland specimen to show the presence and variability of heterocarpy.

The microphotographs of samples were made by "Discovery.V12" stereomicroscope and digital image

processing software "Axio vision 4.8". Heterocarpy was evaluated for every sample. In this particular case, 'heterocarpy' means markedly different cypselas size: inner cypselas are elongate and 1.5–2 times longer than outer ones. Uniform-sized cypselas in a capitulum mean the absence of heterocarpy. When making quantitative estimations, the size difference of 1.5 mm was considered as the absence of heterocarpy, while 1.5–2.0 mm indicated the indistinct heterocarpy.

The microphotographs show distinct size-wise grouping of cypselas. However, we built histograms for each studied capitulum. The histograms show the polymodal distribution of a continuously varying quantitative character (cypselas size). Varying cypselas sizes yield two modal classes and discontinuities between sub-samplings on a graph stating, thus, the presence of heterocarpy.

Though all estimation results are given in Table 2 (with the exception of 38 capitula from one specimen: no. 20.1.2–20.1.39**), only two examples were illustrated to show the expressed and absent heterocarpy.

All the photos, with the exception of the sample from Buryatia, were made by the authors.



Fig. 1. The map of distribution of the studied populations of *Tripolium pannonicum*.

Рис. 1. Карта распространения изученных популяций *Tripolium pannonicum*.

Table 2

Comparative table of the studied cypselas showing the presence/absence of heterocarpny in capitula in *T. pannonicum* samples of various geographical origin
Сравнительная таблица изученных образцов, показывающая присутствие/отсутствие гетерокарпии семянок в корзинках *T. pannonicum*
из популяций разного географического происхождения»

Population No; (*) the IDs of the field sampled populations	Locality, date and collector, acronym	Number of estimated capitula in a population	Capitulum number per specimen (population counting number, specimen counting number, capitulum counting number)	Number of cypselas per capitulum	Length of cypselas mean \pm SD mm		heterocarpny presence (H)/ absence (Ab); indistinct (I)
					3	4	
1*	Intracontinental populations Russia, the Republic of Kalmykia, Tselinny Raion, 30 km away of the highway to Volgograd. Saline meadow at small ravine bottom. 46°39'51.51"N, 44°26'08.01"E. 30 IX 2012. M.N. Lomonosova (NS), No. 959	1	1.1.1 1.2.2	39 32	1.46–3.65 $\Delta = 2.19$	H	H
2*	Russia, the Samara Region, Stavropol Raion, Sancheyevo settlement vicinities. Forb- <i>Puccinellia-Artemisia</i> alkaline meadow 53°6'73.172"N, 49°21'09.52"E. 22 IX 2013. M.N. Lomonosova (NS) No. 1061	2	2.1.1 2.2.2	13 34	1.36–3.57 $\Delta = 2.21$	H	Ab
3*	Russia, the Republic of Khakassia, Altai Raion, 7 km SW of Novomikhailovka settlement, Trekhoberki area. Alkaline land. 53°25'43.48"N, 91°25'43.48"E. 08.09.2013. E.A. Korolyuk, A.Yu. Korolyuk (NS), No. 107	3	3.1.1 3.2.2 3.3.3	18 31 32	1.73–2.93 $\Delta = 1.2$	Ab	I
4*	Austria. Burgelland, Neusiedl am See district. In the vicinities of Hoelle, saline meadow. 47°9'33.841"N, 16°8'41.541"E. 31 X 2015. M.N. Lomonosova (NS), No. 164	3	4.1.1 4.2.2 4.2.3 4.3.4	41 19 26 46	2.2–2.8 $\Delta = 0.6$	I	I
5*	Russia, the Novosibirsk Oblast, Cherepanovo Raion, Iskitim settlements vicinities. Wet habitat. 54°6'10.022"N, 83°33'30.292"E. 08 X 2015. E.A. Korolyuk (NS), 84EK	2	5.1.1 5.1.2 5.2.1	21 33 28	1.62–4.16 $\Delta = 2.54$	H	H
6*	Russia, the Republic of Tyva, Erzin Raion, 12 km SW of Erzin settlement. Southern side of Duskholt Lake, alkaline lands. 50°3'37.5"N, 94°8'62"E. 03 IX 2013. A.Yu. Korolyuk, E.A. Korolyuk (NS), 468AK	2	6.1.1 6.2.2 6.2.3	22 17 33	1.41–3.4 $\Delta = 2$	Ab	H

Continued Table 2

		2	3	4	5	6	7
1	7*	China, Xinjiang Uygur Autonomous region, Altai province, Altai town vicinities. 47.83°N, 88.120°E, 22 IX 2012. D.N. Shaulo, A. Smirnov, A.S. Erst (NS), s.n.	2	7.1.1	50	1.49–3.39 Δ = 1.9	H
8*	Russia, Tyumen' Oblast, Tyumen', 11 th km of the Salair Highroad. Sandy shore of Verkhneye Krivoye Lake, 57°22'N, 65°47'E, 15 IX 2018. A.A. Krasnikov (NS), s.n.	1	7.1.2	33	1.71–4.54 Δ = 2.83	H	
9*	[Hungary] Hortobágy: Újszentrőmargita, margin of the forest "Margitárdő". 47.73334°N, 21.09358°E, 19 X 2017. A. Takács (DE), s.n.	1	9.1.1	56	3: 1.91–3.79 Δ = 1.88	I	
10	[Hungary] In pratis salsis inter Siófok et Fokszabadi. 46.905°N, 18.061°E, 04 VIII 1922. S. Polgár (DE), s.n.	1	10.1.1	39	0.65–2.41 Δ = 1.76	I	
11	[Czech Republic] Moravia Meridionalis, Hustopeč: in salsis prope pagum Velké Němciče. 48.944°N, 16.733°E. X 1924. J. Podpéra & V. Tomeš (DE), s.n.	2	11.1.1	23	1.96–3.34 Δ = 1.38	I	
			11.1.2	44	1.44–3.57 Δ = 2.13	H	
12	[Hungary] cott. Győr, in pascuis natronatis pr. opp. Győr-Nádorváros. 47.683°N, 17.638°E. 09 IX 1898. S. Polgár (DE), s.n.	1	12.1.1	32	0.87–2.93 Δ = 2.06	I	
13	[Czech Republic] Nikolslouř: in pratis salsis pr. 48.805°N, 16.637°E. IX 1935. H. Laus (DE), s.n.	1	13.1.1	63	1.36–2.8 Δ = 1.44	I	
14	[Hungary] Budapest: In pratis subsalsis territ. Kelenföld. 47.430°N, 19.145°E. 27 IX 1910. J. Szurák (DE), s.n.	1	14.1.1	66	1.34–2.99 Δ = 1.56	H	
			14.1.2	47	1.71–3.09 Δ = 1.38	I	
15	[Hungary] Mezőzombor, saline pasture "Fecskés". 48.152°N, 21.261°E. 26 IX 2003. Cs. Molnár (DE), s.n.	1	15.1.1	56	1–3.66 Δ = 2.66	H	
16	[Hungary] cott. Hajdú, ad silvam in pratis pseudonatronatis pr. predium Ohat. 47.623°N, 20.950°E. 23 IX 1932. R. Soó (DE), s.n.	1	16.1.1	24	1: 0.73–2.18 Δ = 1.45	Ab	
			16.1.2	43	1.17–3.52 Δ = 2.35	H	
17	Hungary, Békés county. Kardoskút. Fehér-tó. 46.495°N, 20.70°E. 04 X 2000. Virág V. (DE)	1	17.1.1	73	1.18–3.26 Δ = 2.08	H	
18	Uzbekistan, Tashkent Oblast, Mirzachul Raion, Krupskaya settlement, dry lake bottom, 40°69'N, 68°06'E. 1938 г. Vasilkovskaya. (TASH), s.n.	18.1	23	1.99–3.13 Δ = 2.83	Ab		
19*	Russia, Altai Krai, Kulunda Raion, 8 km south of Kulunda settlement, southern shore of Ulkenkol Lake, alkaline meadow. 52°48'N, 78°90'E. 20 IX 2009. E.A. Korolyuk (NS)	1	19.1.1	33	1.67–3.86 Δ = 2.19	H	
			19.1.2	26	2–4.11 Δ = 2.11	H	
			19.1.3	28	2–3.1 Δ = 2.1	Ab	

20*	Russia, Novosibirsk Oblast, Karasuk Raion, 3 km south of Rasskazovo settlement, Gorkoye Lake side, dry solonets. 53°62'295"N, 77°93'332"E, alt = 119 m. 26 IX 2020. A.Yu. Korolyuk, E.A. Korolyuk (NS), 15-20EK	20.1; 20.1.2-20.1.39**	20.1;	35	1.55-4.12 $\Delta = 2.57$	H
21*	Russia, Altai Krai, Kamensk Raion, Kormilovo settlement vicinities, alkaline meadow. 53°51'9291"N, 81°085'094"E. 16 IX 2005. A.Yu. Korolyuk (NS)	21.1	25 (40 along with under-ripe seeds)	25	1.85-4.6 $\Delta = 2.75$	Ab
22*	53.519291°N, 81.085094°E Altai Territory, Kamensk Raion, 5 km NNE of Lugovoye settlement, solonchak. 15.09.2009. E.A. Korolyuk (NS)	1	22.1.1	35	1.7-3.63 $\Delta = 1.93$	H
23*	Russia, Crimea, Kerch, Primorskoye settlement, coastline. 45°15'1096"N, 35°49'9369"E. 09 X 2016. O.N. Demina, L. Rogal (NS), s.n.	4	23.1.1 23.1.2 23.1.3 23.1.4 23.1.5 23.2.6 23.2.7 23.3.8 23.3.9 23.3.10 23.3.11 23.4.12. 23.4.13 23.4.14	(23, 20) 31 36 31 26 22 20 32 30 25 27 13 16 33	1.5-4.4 $\Delta = 3.35$ 1.26-4.5 $\Delta = 3.24$ 1.12-4.84 $\Delta = 3.72$ 1-4.17 $\Delta = 3.17$ 0.7-2.46 $\Delta = 1.86$ 1.45-5.08 $\Delta = 3.63$ 0.49-2.85 $\Delta = 2.36$ 1.25-4.4 $\Delta = 3.15$ 1.33-3.42 $\Delta = 2.09$ 1.84-5.23 $\Delta = 3.39$ 1.46-3.94 $\Delta = 2.48$ 0.13-4.93 $\Delta = 4.08$ 1.14-2.1 $\Delta = 0.5$ 1.45-4.3 $\Delta = 2.85$ 1.4-2.53 $\Delta = 1.13$ 1.6-2.6 $\Delta = 1$ 1.8-2.8 $\Delta = 1$	H H H H H H H H H H H H H H I Ab Ab
24*	Russia, Primorsky Krai, Nakhodka Raion, Avangard settlement. River firth. 43°27'57.36"E, 133°22'04.6"N. 19 IX 2015. M.N. Lomonosova, I.A. Gorbunova (NS) No. 1247	2				

Continued Table 2

1	2	3	4	5	6	7
25*	Russia, Primorsky Krai. Chukotsk Raion. Rechitsa settlement vicinities. Dry valley, wet area along the road. 43°12'N, 132°23'E. 22 IX 2015. M.N. Lomonosova (NS), s.n.	2	25.1.1	20	1:1.32–2.29 Δ = 0.87	Ab
26*	Russia, Leningrad Oblast, Vyborg Raion, Krestovskiy Peninsula, south-western shoreline, Gulf of Finland coast, at the water's edge. 60.51337°N, 28.22507°E. 28 VII 2019. E.A. Glazkova (LE) No. 1740	1	26.1.1	31	1.14–2.2 Δ = 1.06	H
27	Russia, Arkhangelsk Governorate, Kemsk Uezd, island in the Knyazhy Bay, on the shore. Wet habitat. 66.88°N, 32.52°E. 09 VII 1917. M.A. Bychkov (LE), No. 212	1	26.1.2	25	1.75–4.4 Δ = 2.65	H
28	Italy, Prov. di Venezia: Fusina, in argillosis salsis barene dictis, copiosus. 45.68°N, 12.42°E. 10 X 1908. A. Beguinot (LE), s.n.	1	27.1.1	39	1.88–4.24 Δ = 2.36	I
			27.1.1	25	2.21–4.61 Δ = 2.4	H
29	Attica: in humidis salsuginosis halipedi ad Phalerum. 37.92°N, 23.70°E. 9 Novemb. 1887. de Heldresih (LE)	2	28.1.1	52	1.96–7.05 Δ = 5.09	H
			28.1.2	26	2–7.05 Δ = 5	H
			28.1.3	30	2.01–7.07 Δ = 5.06	H
30	Zelande, îla de Walkeren, port de Flessingen, 51.45°N, 3.38°E. 25 Septembre 1849. (LE)	1	29.1.1	48	1.34–2.81 Δ = 1.53	I
31	Herbarium Britannicum. Sussex: Cooden Beach. 50.83°N, 0.43°E. 14.09.1932. Ballard F. (LE), No. 643	1	30.1.1	27	1.71–4.06 Δ = 2.9	H
32	Ad oras Oceani atl in Extremad cape Costa de Gale, Setuval. 38.48°N, -8.88°E. Oct. 1839. (LISU), s.n.	1	31.1.1	48	2.27–5.04 Δ = 2.77	H
			31.1.1	36	1.98–4.3 Δ = 2.32	I
			32.1.1	20	2.24–3.88 Δ = 1.64	I
33	Arredores de Lisboa: Praia de Cascaes. Coll. A. Richardo de Conha. 38.69°N, -9.41°E. Outubro de 1890 (LISU), s.n.	2	32.1.2	31	2.46–4.19 Δ = 1.73	I
			33.1.1	13	3.36–5 Δ = 1.64	Ab
			33.2.3	33	1.63–5.12 Δ = 3.49	H
			33.2.3	22	2.26–5.75 Δ = 3.49	H

** – for population 20, 39 capitula were studied, all with visually detected heterocarp. The table contains the measurements only for capitulum 20.1.1, the data on the rest of capitula (20.1.2–20.1.38) are not given here.

RESULTS AND DISCUSSION

Taxonomic history and nomenclature

As a rule, the 'old' species, described in the 18th century (e. g. by C. Linnaeus) and growing widely, represent a minefield as regards both taxonomical issues and the apprehension of this species' volume. First, the protologs of old diagnoses are very uninformative. It may impede the author's material interpretation during further lectotypification. Second, for a long time, due to some political reasons, many monographs hadn't had an opportunity to compare the material covering wide distribution areas of the species and used only regional samples and available published data. It resulted in splitting 'old' species into smaller taxa, and further species' volume revision yielded numerous synonyms. *Tripolium* genus is an illustrative example.

Aster tripolium L. was described by Linnaeus (1753) with the following diagnosis: "foliis lanceolatis integrerrimis carnosis glabris, ramis inaequatis, floribus corymbosis. Habitat in Europae littoribus maritimus & ad Sibiriae lacus salsas". There are two specimens stored at Linnaeus' herbarium collection in London. Grierson (1982) chose one of them (LNN 997.15) as a lectotype for *Aster tripolium* L. However, as this specimen has not *Species plantarum* number, it probably was later added to the herbarium (Jarvis, Thurland, 1998), thus Jarvis & Thurland (l.c.)



Fig. 2. A herbarium sample of *Aster tripolium* L. 997.14. (LNN) from Linnaeus collections (taken from http://linnean-online.org/cgi/search/linnaean_herbarium_simple).

Рис. 2. Гербарный образец *Aster tripolium* L. 997.14. (LNN) из коллекций Линнея (заимствовано: http://linnean-online.org/cgi/search/linnaean_herbarium_simple).

designated the other one (LNN 997.14) as lectotype. This herbarium sample represents the upper part (i. e. the flowering branches) of an individual (Fig. 2).

Twenty years after Linnaeus' description, Jacquin (1770-1771) described *Aster pannonicus* Jacq. as a separate species from Nyitra county of the former Hungarian Kingdom (western part of the present-day Slovakia). The author did not mention in protolog its close relation to *Aster tripolium* L. The protolog contains a picture and a brief description: "Ex radice perenni quotannis caules plures prodeunt, uti tota planta, glaberrimi, teretes, suberecti, toti foliis ramisque onusti. Illa funt ex lanceolato linearia, integrerima, acuta, sessilia. Rami numerosi eandem ferme altitudinem attingunt cum ipso caule, unde flores evadunt corymbose. Hi ex caeruleo purpurascunt. Ab Astere acri, cui Proximus; diftinctum puto foliis min-

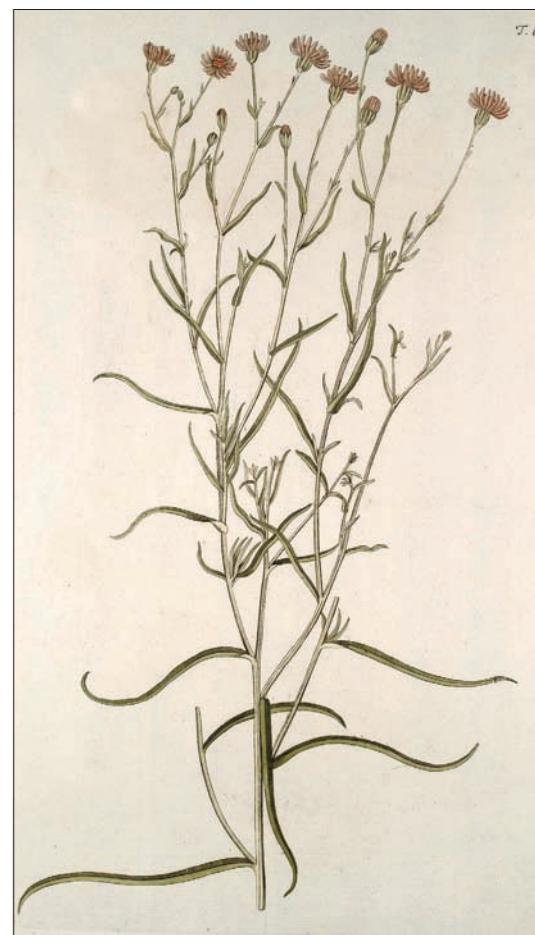


Fig. 3. A picture of *Aster pannonicus* Jacq. From protolog (Jacquin N. 1770-1771, Hort Bot. Vindob. I: 3, t. 8).

Рис. 3. Изображение из протолога *Aster pannonicus* Jacq. (Jacquin N. 1770-1771, Hort Bot. Vindob. I: 3, t. 8).

ime strictis, sed potius omnium flexilissimis, tum etiam saepe nullatenus acri. Septembri florere incipit". The picture depicts the upper part of a stem with inflorescences (Fig. 3). So far, we have not found original herbarium materials for this protolog.

Despite the sketchy information in protologs and a strong similarity between two species, they have long been treated as different taxa in various publications.

Some authors split *T. pannonicum* (Jacq.) Dobrocz. s. l. (non auct.) (= *T. vulgare* Nees s. l. = *Aster tripolium* L.) into two subspecies, which, in turn, are often interpreted as separate species. The main distinguishing factors are considered to be the populations' geographical distribution (inland saline habitats / coastline habitats of the Atlantic Ocean basin) and some morphological characters (stem branching, phyllary tip peculiarities, and heterocarpy).

Confusion should be noticed that has existed in nomenclature since the times of Nees (1832–1833). The name *T. vulgare* Nees. appeared to be excessive (nomen superfluum). Up to 2003 (before the work by Greuter), this epithet was used in many treatments and keys of Asia. According to nomenclature rules, Dobrochaeva (1962) offered a correct combination in the "Flora of Ukraine", though she interpreted it as a part based on basionym *Aster pannonicus* Jacq. Thus, if we accept two species, a new combination should be formed for the independent species derived from the upgraded rank of *Tripolium pannonicum* (Jacq.) Dobrocz. subsp. *tripolium* (L.) Greuter.

What are the distinctions on which such closely related taxa based? And who offered these distinctions?

Thus, for two related taxa, we have at our disposal rather brief protologs, one herbarium sheet which was lectotyped as a type for *Aster tripolium* L., and the absence of this for *Aster pannonicus* Jacq., though there is a picture of it in its protolog. Based on this material, the main morphological character that distinguishes these related taxa is a capitulescence form: whether it is corymbose or branching starts from the base forming a panicle.

R. Soo (1925) was the first who combined these two separate taxa into one species. However, he distinguished them at the subspecies level. He did not point out any morphological differences. All he did was a new nomenclature combination *A. tripolium* L. subsp. *pannonicum* (Jacq.) Soo. There he also offers a combination for a white-flower form (*f. tauschieri* Soo). Later, the clearly defined complex of morphological characters appeared in the Soviet botanical literature distinguishing two related halophytic taxa. D.N. Dobrochaeva (1962) considered geographical distribution and branching character to be the main distinguishing factors for the related taxa. N.N. Tsvelev (1990, 1994) dis-

tinguished two species emphasizing "that differences between them though insignificant but quite stable" (Table 1). Besides, he assumes that ecological-geographical differences correlate with morphological characters, primarily with heterocarpy. Characterizing the general geographic distribution of *T. vulgare* s. str., Tsvelev (1994) assumed occurrence of the species both in the coastline area of Scandinavia, Atlantic region, Middle Europe, North America, and in the European part of the USSR (Leningrad, Pskov). This statement enhances the ill-defined geographical distinction of relative species. Alongside the whole continental part of Eurasia, he mentions the southern territory of the Russian Far East, Japan and China for *T. pannonicum* (Jacq.) Dobrocz. If a geographical factor is given a priority when plants are divided into coastal populations and those growing in continental azonal solonchak and solonetzi habitats, then how to treat the plants of coastal and littoral populations of the Russian Far East, Japan and China?

We consider it necessary to give a detailed nomenclature citation that proves the complicated taxonomical history of the species.

***Tripolium* Nees.** 1832, Gen. Sp. Aster.: 152. – *Aster* L. sect. *Tripolium* (Nees) Benth., 1873, Benth. et Hook. fil. Gen. Pl. 2: 273; Mot. Ito et Soedjima, 1995, Fl. Jap. 3b: 61.

Genus type: *Tripolium pannonicum* (Jacq.) Dobrocz. (*Tripolium vulgare* Nees. nom. illeg.).

***Tripolium pannonicum* (Jacq.) Dobrocz.** Euro+Med (2006-): Euro+Med PlantBase – the information resource for Euro-Mediterranean plant diversity. Published on the Internet <http://ww2.bgbm.org/EuroPlusMed>; Nesom & Robinson, 2007, in Compositae: 320; Chen Yilin & L. Brouillet, 2011, in Fl. China, 11: 559.

INCL: *T. pannonicum* (Jacq.) Dobrocz. subsp. *pannonicum* Euro+Med (2006-): Euro+Med PlantBase – the information resource for Euro-Mediterranean plant diversity. Published on the Internet <http://ww2.bgbm.org/EuroPlusMed>. – *T. pannonicum* (Jacq.) Dobrocz. s. str., 1962, in Fl. URSR 11: 63; Tsvelev, 1990, in Novost. Sist. Vysh. Rast. 27: 145 – *T. pannonicum* (Jacq.) Dobrocz. subsp. *maritimum* Holub., 1973, Folia Geobot. Phytotax. 8, 2: 177, nom. illeg.; Tsvelev, 1990, in Novost. Sist. Vysh. Rast. 27: 145; 1994, in Fl. Evrop. Ch. ССР, 7: 188, in syn. *T. pannonicum* Schur., 1853, Enum Pl. Transs.: 304.

b a s i o n y m – *Aster pannonicus* Jacq., 1770, Hort Bot. Vindob. I: 3, t. 8. – *A. tripolium* L. subsp. *pannonicum* (Jacq.) Soo, 1925, Bot. Kozlem. 22: 64; Merxm. ab Schreib., 1976, Fl. Europ. 4: 115. – *Galatella pannonica* (Jacq.) Galasso, Bartolucci & Ardenghi, comb. nov., 2017, Italian Botanist 3: 34, urn:lsid:ipni.org:names:60474383-2.

Tripolium pannonicum (Jacq.) Dobrocz. subsp. ***tripolium*** (L.) Greuter, Willdenowia 33(1): 47. 2003; Euro+Med (2006-): Euro+Med PlantBase – the information resource for Euro-Mediterranean plant diversity. Published on the Internet <http://ww2.bgbm.org/EuroPlusMed> – *T. maritimum* Leveille, 1842, Demid. Voy. Russ. Mer. 2:192, (236, 237?) – *T. vulgare* Nees, 1832, Gen. Spec. Aster.:152 nom. superfl. (nom.illeg.); DC., 1836, Prodr. 5: 253; Ledeb., 1845, Fl. Ross. 2: 477; Novopokrovsky, 1922, in Sched. Herb. Fl. Ross. 8: 189, N 2763a; Pavlov, 1938, Fl. Tsentr. Kazakhst. 3: 223; Terekhova, 1965, in Fl. Kazakhst. 8: 338; Tamamshyan, 1959, in Fl. SSSR 25:184; Krasnoborov, 1984, Opred. rast. Tuv. ASSR: 223; Petrovsky, 1987, in Arkt. Fl. SSSR 10: 70; Barkalov, 1992, in Sosud. Rast. Sov. DV: 91, p.p.; Tsvelev, 1994, in Fl. Evrop. Ch. SSSR 7: 188, p.p.; Gubanov, 1995, in Konsp. Fl. Vnesh. Mongolii: 109; Korolyuk, 1997, in Fl. Sib. 13: 35 – *T. vulgare* Nees var. *typicum* Trautv., 1866, Enum. Pl. Songoricarum, v. Bull. Mosc. a. 2: 338; Novopokrovsky, 1922, in Sched. Herb. Fl. Ross. 8: 189, N 2763a, 2763b.

basionym – *A. tripolium* L., 1753, Sp. Pl.:872, 2039; Ledeb., 1833, Fl. Alt. 4: 98; Reichenberg, 1854, Icon. Fl. Germ. 16, tab. 16.; Shmalg., 1897, in Fl. Sr. i Yuzhn. Ros. 2: 41; Krylov, 1904, Fl. Altaya 3:590; Komarov, 1907, Fl. Manchzh. 3:604; Kitam., 1937, Mem. Coll. Sci. Kyoto Univer. ser. B., 13: 376; Sergievskaya, 1949, Fl. Zap. Sib. 11: 2669; Mot. Ito et Soejima, 1995, Fl. Japan 3b: 60. – *A. tripolium* var. *integrifolium* Miyabe et Kudo, 1915, in Miyabe & Miyake, Fl. Saghal.:

240. – *Aster* sp. Gmelin, 1749, Fl. Sib. 2:187 – *A. maritimus* Salisb., 1796, Prodr. : 198 – *Galatella pannonica* (Jacq.) Galasso, Bartolucci & Ardenghi subsp. *tripolium* (L.) Galasso, Bartolucci & Ardenghi, comb. nov., 2017, Italian Botanist 3: 34, urn:lsid:ipni.org:names: 60474384-2.

Diagnostic characters and taxonomical role of heterocarpy

Annual or biennial plants, stems grooved, hollow, glabrous, 10 to 100–120 cm tall, branched from the base. Leaves carious, cuspidate, glabrous, lower leaves petiolate, oblong-ovate or lanceolate. Middle and upper leaves linear-lanceolate or linear, sessile, their margins entire or serrate. Capitula are heterogamous, about 2 cm in diameter, organized in cymose-panicked capitulecence. Involucral leaflets smooth, grassy, reddish at tips. Outer series short, ovate, 3–4 times shorter than inner leaflets, oblong-linear with rounded tips. Involucre tubular. Marginal flowers ray, pistillate, fertile, blue, pinkish or white, 12–18 mm long and 1–1.5 mm wide. Disk flowers tubular, bisexual, yellow, puberulous. Cypselas (achenes) glabrous or pubescent, compressed laterally, with 2 conducting bundles, 1.5–7 mm long. As a rule, inner cypselas are 2.8–7 mm long and outer 1.5–2.5 mm long. Pappus white, multi-rowed, 10–15 mm long.

On alkaline lands, alkaline meadows, sea coasts. Eurasian polyzonal halophytic species. Flowering in July–October (Fig. 4), fruiting in August–October



Fig. 4. *Tripolium pannonicum* dominated communities. Altai Krai, july, 2020, flowering plants. Photo by E.A. Korolyuk.

Рис. 4. Сообщества с доминированием *T. pannonicum* в Алтайском крае, июль 2020 г., цветущие особи. Фото Е.А. Королюк.



Fig. 5. *T. pannonicum* dominated communities in Novosibirsk Oblast. Late September, 2020, fruiting and flowering plants at the same time. Photo by E.A. Korolyuk.

Рис. 5. Сообщества с доминированием *T. pannonicum* в Новосибирской области, конец сентября 2020 г., плодоносящие особи. Фото Е.А. Королюк.

(Fig. 5). Officinal (traditional medicine), meliferous, fodder plant for cattle, horses and rabbits, ornamental.

This species is a typical halophyte (Fig. 6). Analyzing the specimens of the genus from the vast territory of the former USSR, Tamamshyan (1959) noticed that transition from the coastline to drier continental conditions was followed by some changes in plant habitus though their major distinctive features remained constant. She emphasized that such changes were not related to any distribution area and were observed in different geographic regions. Detailed studies of the anatomy of vegetative organs and root system prove adaptive characteristics for surviving in the given environment (Berću et al., 2012; Karanović et al., 2015).

Annuals (and short-lived perennials) have a remarkable plasticity in their morphology. Thus, such characters – as branch pattern and leaf thickness – are too arbitrary for taxa distinguishing. These are depending on the variable water conditions during the growing season. For instance, in case of summer overwetting, water in temporary water bodies can stay for considerable time. Hence, plants overgrow in height and start branching at the top to form corymbose capitulescences. In case of quick drying out of water bodies, often accompanied with overgrazing, branching is developed all over the central stem forming panicle capitulescence.

Presence/absence of ray flowers in a capitulum is one of the distinguishing characters of *T. pannonicum* s. str. and *T. pannonicum* subsp. *tripolium* according to

European authors (Wagenitz, 1964; Merxmüller et al., 1976). However, the study of Sterk and Wijnands (1970) state the wide variability of morphological characters associated with different flower types in capitula. The same is true for marginal flowers in a capitulum. Some populations feature the forms with ray flowers of varying colour shades, like in Buryat population shown in Figure 7.

It is often stated that heterocarpy is one of the ways of adaptive seed propagation in angiosperms and is determined by the differentiation of heteromorphic diaspores by distribution distance and seed germination peculiarities. The results of different studies (Levina, 1981; Voitenko, 1969, 1970; Mandak, Pyšek, 2001) showed a specific feature of different-sized (or having other adaptations like various ballistic ones) seeds: the seeds of barochorous diaspores (remaining close to a parent plant) are characterized by a deep and prolonged dormant period, while the remotely dispersed seeds germinate instantly or quickly exit the dormancy.

In case of *Tripolium* genus, all the cypselas in the studied populations and herbarium samples (regardless of their size) had the pappuses as an adaptation for distribution. Hence, cypselas size and, probably, their weight, could have a great impact on the distance of seed dispersion from a parent plant.

Heterocarpy in *Tripolium*, expressed as cypselas size (for significant differences see No. 28 in Table 2, Fig. 8), is, probably, associated with physiological differences in heterocarpic diaspores as well. Thus, ger-

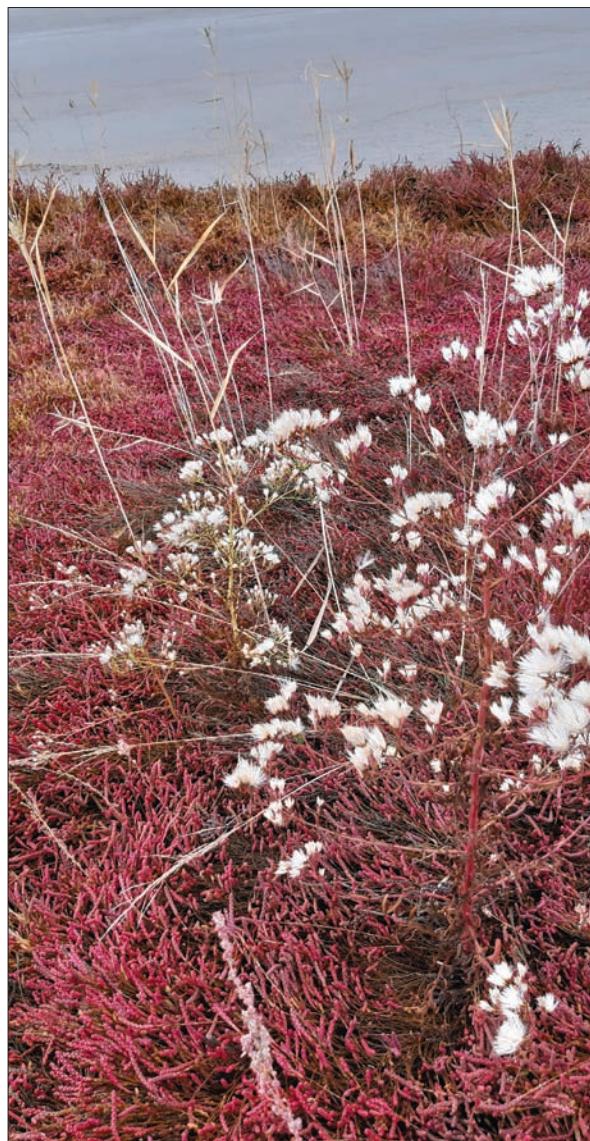


Fig. 6. Novosibirsk Oblast, a typical halophytic community with *Salsola* and *Tripolium*. Late September, 2020. Photo by E.A. Korolyuk.

Рис. 6. Новосибирская область, типичное галофитное сообщество с доминантами солянками и триполиумом (*Salsola* и *Tripolium*). Конец сентября, 2020 г. Фото Е.А. Королюк.

minating the seeds under laboratory conditions, we observed instant germination of small seeds, while large seeds did not break dormancy for 2–3 months. Besides, we also recorded a varying ratio of “large” and “small” cypselas per capitulum in different plants. The largest cypselas were observed in populations of southern locations of the distribution range (Italy, Uzbekistan) characterized by a long and favorable period for flowering and fruiting. This is a disputable question whether it is genetically fixed as a species characteris-

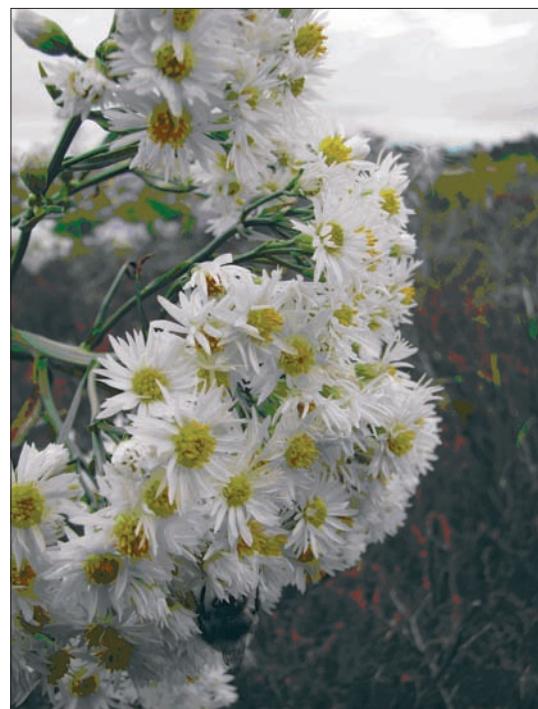


Fig. 7. White-flower specimens in *T. pannonicum* population (Buryatia). Photo by A.Yu. Korolyuk.

Рис. 7. Белоцветковые особи в популяции *T. pannonicum* (Бурятия). Фото А.Ю. Королюка.

tic feature or not. There are the data proving both dependence of seed productivity on changing abiotic conditions over the years and significant fluctuations in seed mass per specimen in natural environment and in culture over the years (Kurochkina, 2016).

In our study, the sampling was random and we targeted to find valid material for revealing the presence or absence of heterocarpy under various geographic conditions and to understand whether this character is reliable for distinguishing closely related taxa. However, the problem of heterocarpy in widely distributed species with narrow ecology is of great interest and requires further investigation. The plants of *Tripolium* genus can be used as a model object for such studies.

Unfortunately, it is very problematic to find reliable material to study heterocarpy. Cypselas in live plants and, even more, in herbarium samples are often absent. If herbarium was not treated with fumigators, even after one year of storage, the samples with ripe seeds could be damaged by insects, which would result in loss of both cypselas and capitula.

We first estimated cypela size (heterocarpy) as related to stem branching and capitula ratio on the branches of various order. For this purpose, we studied all 39 capitula of one specimen from the inland popu-

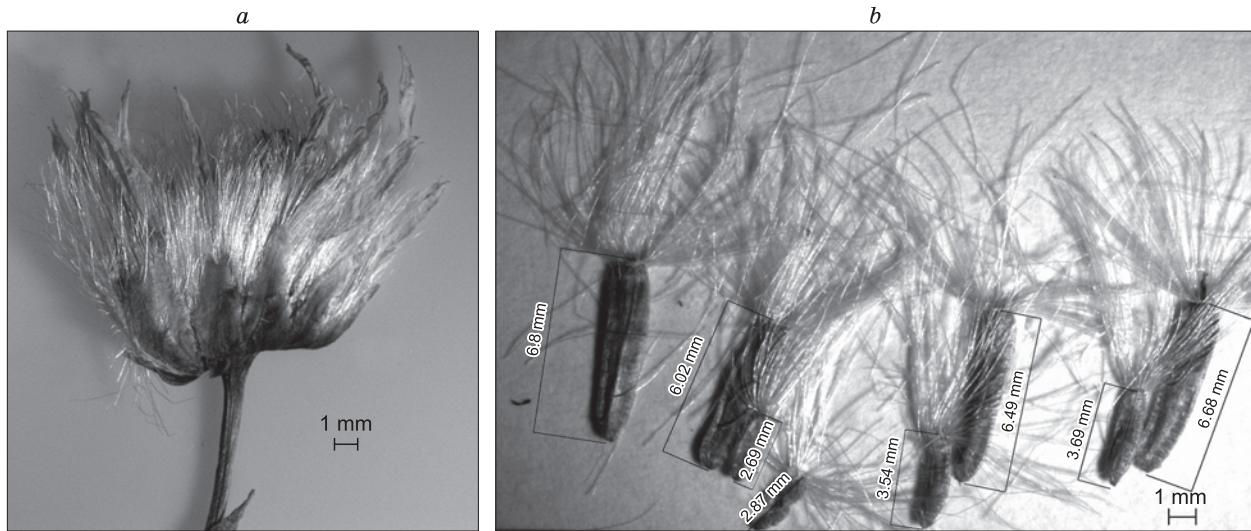


Fig. 8. Capitulum (*a*) and cypselas of varying size (*b*) (фрагмент; образец из приморской популяции № 28.1.2, табл. 2).

Рис. 8. Корзинка (*a*) и разные по величине семянки (*b*) (фрагмент; образец из приморской популяции № 28.1.2, табл. 2).

lation of Novosibirsk Oblast (Table 2, No. 20.1.2–20.1.39 Fig. 5). Each capitulum featured heterocarpy, i.e. the inner cypselas were noticeably larger than outer ones. The difference in cypselas size in this plant did not correlate with the temporal difference of inflorescence development, which is characteristic for some Apiaceae representatives.

The average number of cypselas per capitulum was 27 varying from 20 to 30 in most capitula. However, sometimes much lower (6–8) or higher (up to 73) number of cypselas was recorded. High variation of

cypselas number might appear within population or even within individuals (Table 2).

Cypselas also varied in size within specimens both from inland and coastal populations. Besides, the heterocarpy was observed in capitula of all plants with ripe cypselas. Cypselas length ranged from 1 to 7 mm. The difference in cypselas sizes in a capitulum was clearly observed in most cases.

Of 22 inland populations, the largest population number (7) showed the presence of heterocarpy (No. 1, 8, 9, 15, 17, 20, 22 in Table 2; Fig. 9). Four po-

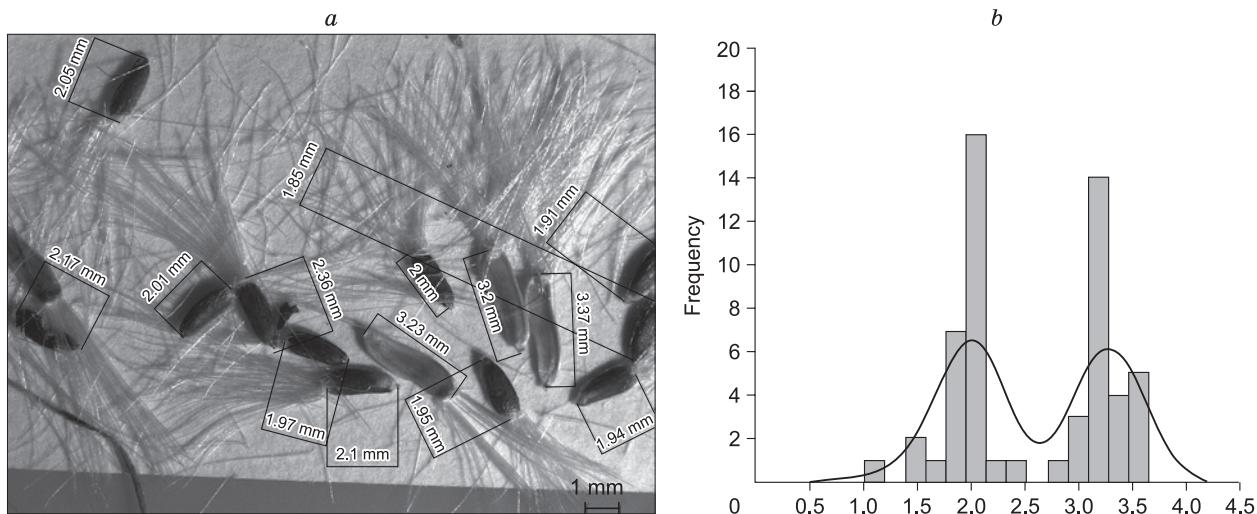


Fig. 9. Гетерокарпия в корзинке *T. pannonicum*, внутренеконтинентальная популяция (№ 15, табл. 2): *a* – семянки из корзинки (№ 15.1.1, фрагмент); *b* – гистограмма распределения с двумя характерными пиками.

Рис. 9. Гетерокарпия в корзинке *T. pannonicum*, внутренеконтинентальная популяция (№ 15, табл. 2): *a* – фото семян из корзинки (№ 15.1.1, фрагмент); *b* – гистограмма распределения с двумя характерными пиками.

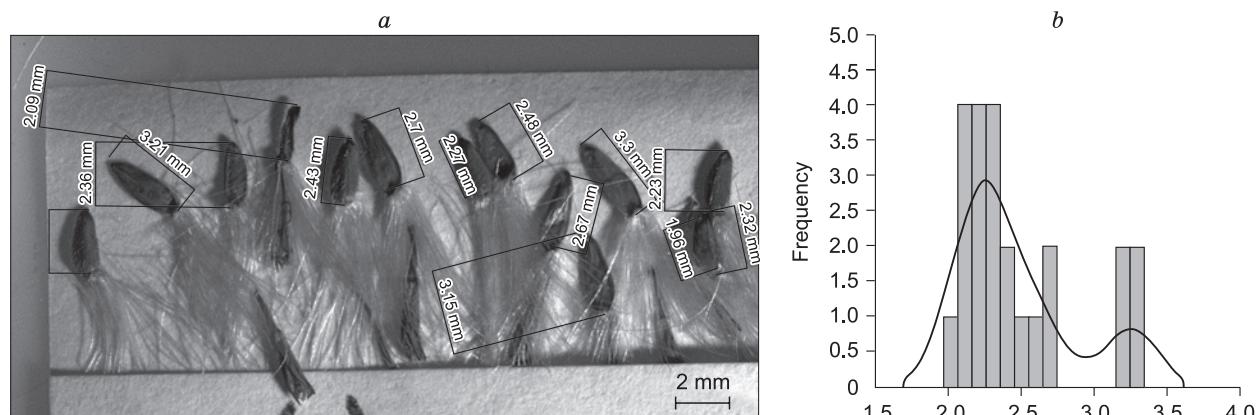


Fig. 10. No heterocarpy in capitula of *T. pannonicum* from the interior population (Russia, Samara, No. 2): *a* – cypselas from capitulum (No. 2.1.1, fragment); *b* – distribution histogram.

Рис. 10. Отсутствие гетерокарпии из внутриконтинентальной популяции *T. pannonicum* (Россия, Самарская область, № 2): *a* – фото семян из корзинки (№ 2.1.1, фрагмент); *b* – гистограмма распределения.

pulations featured both clear and indistinct heterocarpy (No. 3, 7, 11, 14 in Table 2). The same population number (three for each) demonstrated the absence (No. 2, 18, 21 in Table 2, Fig. 10), presence and absence (No. 5, 16, 19 in Table 2), or indistinct heterocarpy (No. 10, 12, 13 in Table 2). One population showed all the variants (No. 6 in Table 2). Such scatter in variants is rather due to various ripeness levels.

Eleven coastal populations included old samples from the coastal area of Portugal, Greece, Italy, and Great Britain (LISU, LE) as well as new samples from the North Sea area (LE). Besides, we studied two populations from the Pacific coastland. Three populations, all from the western part of the range, showed the presence of heterocarpy (No. 27, 28, 30 in Table 2). Clear and indistinct heterocarpy was recorded in other three populations (No. 23, 26, 29 in Table 2). Of them, 'Kerch' population (No. 23 in Table 2) demonstrated the heterocarpy in 14 capitula of all the studied 4 specimens, and only two capitula of different specimens showed indistinct heterocarpy due to unripe cypselas. The capitula in "Far East" populations featured indistinct and absent heterocarpy (No. 24 in Table 2) or both its presence and absence (No. 25 in Table 2). 'Presence/absence' combination was also recorded in one western population (No. 33 in Table 2).

Thus, we consider that the 'presence/absence of heterocarpy' does not correlate with geographical distribution of plants being rather the matter of ripe cypselas number in a capitulum.

CONCLUSIONS

Based on the studied samples, we state that those morphological characters used for distinguishing *T. pannonicum* (Jacq.) Dobrocz. subsp. *tripolium* (L.)

Greuter (*T. vulgare* Nees s. str.) from *T. pannonicum* (Jacq.) Dobrocz. subsp. *pannonicum* for the plants growing both in inland or coastal territories do not correlate with their geographic distribution. By the opinion of Venable et al. (1993), 'heteromorphism' or varying cypselas size is often characteristic for annual plants under conditions of arid or variable environment. This is rather an adaptation to reproduction and distribution of such plants.

As to the habitus of annual plants growing in variable environment, it often depends on substrate moisture conditions and growth phase. Cypselas of *T. pannonicum* (Jacq.) Dobrocz. are accumulated in the seed soil bank and often germinate throughout the growing season depending on flooding duration. Hence, plants coming up in different months and different latitudinal conditions would differ in height, shoot and capitula number, leaf size and other quantitative characteristics. Thus, we consider that *Tripolium* genus is represented by one halophytic species *T. pannonicum* (Jacq.) Dobrocz. covering a wide distribution area, while such morphological characters as heterocarpy and branching pattern do not strongly correlate with geographical distribution.

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ДИАГНОСТИКА ВИДА В РОДЕ *TRIPOLIUM* (ASTERACEAE) В СВЯЗИ С ГЕТЕРОКАРПИЕЙ

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В данном исследовании проанализированы проблемы видоспецифичности и связанные с этим проблемы выделения надежных диагностических признаков. Род *Tripolium* Nees в ряде случаев считается монотипным, представленным одним видом *Tripolium pannonicum* (Jacq.) Dobrocz. Некоторые авторы признают подвидовое деление: *T. pannonicum* (Jacq.) Dobrocz. subsp. *tripolium* (L.) Greuter. (*T. vulgare* s. str.) и *T. pannonicum* (Jacq.) Dobrocz. subsp. *pannonicum*. В ряде случаев эти таксоны признают в качестве самостоятельных видов, поскольку растения имеют изменчивые морфологические особенности, широкий ареал от Атлантического побережья Европы до Тихого океана, пересекающий несколько широтных зон, где они (растения) произрастают вazonальных сообществах и являются типичными галофитами. В работе обсуждается значимость морфологических диагностических признаков, приведенных для этих таксонов в протологах и последующей ботанической литературе. Анализируется корреляция морфологических признаков – присутствие/отсутствие гетерокарпии и характер ветвления с географическим распределением популяций. Считаем, что эти признаки носят приспособительный характер для однолетних растений в переменчивой экологической среде (зона подтопления), каким является *Tripolium pannonicum*.

Ключевые слова: галофит, гетерокарпия, кариология, морфология, таксономическое значение, *Tripolium vulgare*, *T. pannonicum*.

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