РОССИЙСКАЯ АКАДЕМИЯ НАУК
РУССКОЕ БОТАНИЧЕСКОЕ ОБЩЕСТВО

РАСТИТЕЛЬНОСТЬ РОССИИ

ОБЩЕРОССИЙСКИЙ
ГЕОБОТАНИЧЕСКИЙ ЖУРНАЛ

2

Санкт-Петербург
2001

Растительность России. СПб., 2001.
№ 2. С. 87—98.

Vegetation of Russia. St. Petersburg, 2001.
N 2. P. 87—98.

SURVEY OF COMMUNITIES OF THE CLASS *SALICORNIETEA FRUTICOSAE*

ОБЗОР СООБЩЕСТВ КЛАССА *SALICORNIETEA FRUTICOSAE*

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The revision of the high-rank classification units of the cl. ***Salicornietea fruticosae*** has been carried out. Two subclasses are included into the renewed system of syntaxa of this class: ***Arthrocnemenea*** uniting Mediterranean (usually coastal) communities of perennial hyperhalophytes and ***Kalidienea*** including mainly inland East-European and Asian communities. New orders, ***Artemisio-Puccinellietalia, Kalidietalia caspici*** and ***Kalidietalia gracilis***, and a number of alliances and suballiances have been proposed. It is shown that the ord. ***Limonietalia*** should be displaced from the cl. ***Salicornietea fruticosae*** and referred to a more glycophytic class.

The northern distribution limits of communities of the cl. ***Salicornietea fruticosae*** seems to coincide well with that of the Ancient Mediterranean region of M. G. Popov.

Key words: *Braun-Blanquet approach, halophytic communities, nomenclature, syntaxonomy,* ***Salicornietea fruticosae.***
Ключевые слова: *система Браун-Бланке, галофитные сообщества, номенклатура, синтаксономия,* ***Salicornietea fruticosae.***

Nomenclatural sources: Cherepanov, 1995; Flora Europaea, 1964—1993; Gubanov, 1996.

INTRODUCTION

The peculiarity of syntaxonomic constructions according to the Braun-Blanquet approach is that of their regular revision which is usually performed when these constructions are supplemented with the material obtained from the new regions.

The main purpose of the present paper is the revision and review of the higher syntaxa of the cl. ***Salicornietea fruticosae*** which communities of predominant perennial succulent hyperhalophytes are related to. The revision of the lower classification units (associations and subassociations) has not been carried out since it would greatly increase the volume of work and also of the present article but give nothing significant to the achievement of the main purpose.

The description of the plant cover of the vast territory of the former USSR started approximately 20 years ago, and the realization of such a project as Survey of the Vegetation of Europe as well following the Braun-Blanquet approach makes the revision of classification schemes necessary (Pignatti, 1990; Rodwell et al., 1997; Mirkin et al., 2000).

MATERIALS AND METHODS

The sphere of our revision was primarily restricted to Eurasia. Moreover, we probably cover only the northern part of the distribution area of communities of the cl. ***Salicornietea fruticosae*** on this continent, since the most significant number of relevés of these communities made following the Braun-Blanquet approach is given only for these ranges. It is obvious that communities of this class should be widely represented within the whole area of Northern Africa, both inland and coastal. (A small number of community relevés of the cl. ***Salicornietea fruticosae*** on the Tunisia coast has been included in our processing).

As an initial material for the survey of communities of the cl. ***Salicornietea fruticosae*** in Eurasia, the 260 lower syntaxonomic units (associations and subassociations) identified for ranges from the Atlantic Ocean to the Gobi desert were reviewed. The identification of these units was based on 2349 relevés. All the material was accumulated in the database created with the help of the TURBO(VEG) software package (Hennekens, 1996a) and

then processed with the MEGATAB visual editor for phytosociological tables (Hennekens, 1996b) [with the program TWINSPAN (Hill, 1979) included] which is intended for hierarchical construction. The program TWINSPAN carries out the cluster analysis algorithms.

Computer processing resulted in a series of tables characterizing the lower syntaxonomic units, with the total number of columns equal to that of syntaxa included in the analysis. As the associations and subassociations were distinguished while working on relevés, a small number of syntaxa of intermediate and transitional character (14 columns totally) was rejected in the tables.

As far as the table of lower syntaxonomic units would take a great deal of space in the paper, we present the synoptic tables of higher syntaxa only. However, the initial data can be sent via e-mail to anyone who takes interest in them.

When revising the syntaxonomy, the authors followed the ICPN. One of the results of this work was the identification of syntaxa names which disagreed with the ICPN rules and hence were subject to rejection with proper citations from the ICPN articles and principles..

The identification of diagnostic taxa (Dt) was based only upon the material included in the database. The syntaxa distribution maps were also compiled using this database. Hence the established composition of diagnostic taxa for units of a subclass/order rank within the areas mentioned can be modified with the inclusion of data from any new regions in the analysis.

Nomenclatural types (Nt) are identified for all the higher syntaxa, and the most probable dominants (Dm) are mentioned for characterization of the alliances. In case the lectotype has not been chosen by the authors, reference to publication where it was established is given.

It was found suitable to use superspecies and aggregations of ecologically close species as diagnostic taxa. This method was employed in the revision of high-rank syntaxa of the cl. ***Asteretea tripolium*** for the area of the former USSR and Mongolia (Golub, 1994) where the detailed arguments for proper use of species in wide meaning (*sensu lato*), superspecies and aggregations of species in syntaxonomic revisions covering large territories were given. The alike approach gained the support and has been already used in the other regions (Babalonas et al., 1995). All the species groups are named as supraspecific taxa.

The botanists working in different regions from Portugal to Mongolia have different views on the plant species volume which makes a revision of the system of the cl. ***Salicornietea fruticosae*** difficult. While composing the relevés, the problem of plant name unification also arose, as names of many species have been changed for purely nomenclatural reasons since the publication of some manuscripts was made. In the process of work a consolidated list of plant taxa (species, subspecies, variants) registered in the relevés of communities of the cl. ***Salicornietea fruticosae*** was made. The vascular plant names are given following Flora Europaea (Tutin et al., 1964—1993) mostly. If species weren't found there, the monograph of S. K. Cherepanov (1995) and then the publication of I. A. Gubanov (1996) were used subsequently.

All the taxa with constancy higher than 20 % in communities of the syntaxa studied are listed in Tables 1—4. The constancy of diagnostic taxa is given in percentage. The taxa which act as dominants in more than 50 % relevés of a given syntaxon are printed in bold type. Species included in the supraspecific taxa are absent in the tables but mentioned in the text.

Results

(Survey and revision of the higher syntaxa)

Class ***Salicornietea fruticosae*** Br.-Bl. et Tx. ex de Bolòs y Vayreda 1950 : 86

Salicornietea fruticosae Br.-Bl. et Tx. 1943 (Art. 8) : 8
Salicornietea fruticosae Br.-Bl. et Tx. in Br.-Bl. et al. 1952 (Art. 31) : 101
Arthrocnemetea fruticosi *sensu auct.* (Art. 30)
Sarcocornietea fruticosae *sensu auct.* (Art. 30)
Kalidietea Mirkin in Kashapov et al. 1988 (Art. 1) : 26
Kalidietea Mirkin et al. 1988 (Art. 8) : 83

Dt: species of the tribe *Salicornieae* (*Arthrocnemum fruticosum*, *A. perenne*, *A. macrostachyum*, *Kalidium caspicum*, *K. foliatum*, *K. gracile*, *Halocnemum strobilaceum*, *Halostachys belangeriana*) (Tab. 1).

Nt: ***Salicornietalia fruticosae*** Br.-Bl. 1933 (lectotypus).

These are floristically poor communities with the dominance of perennial low shrub and dwarf-semishrub (chamaephytic and nanophanerophytic) succulent hyperhalophytes, spread over the area of Eurasia and Northern Africa.

Subclass ***Arthrocnemenea*** subclass nova

Dt: species of the genera *Arthrocnemum* (*A. fruticosum, A. macrostachyum, A. perenne*), *Limonium* (*L. aragonense, L. auriculae-ursifolium, L. bellidifolium, L. biflorum, L. binervosum, L. caesium, L. cossonianum, L. cymuliferum* s. l., *L. delicatulum* s. l., *L. densiflorum, L. densissimum, L. diffusum, L. echioides, L. ferulaceum,*

Table 1

Diagnostic taxa of the subclasses of the cl. *Salicornietea fruticosae*

Диагностические таксоны подклассов кл. ***Salicornietea fruticosae***

Syntaxa names	*Arthrocnemenea*	*Kalidienea*
Number of associations and subassociations included in the syntaxon	**132**	**65**
Dt of subcl. *Arthrocnemenea*		
Parapholis C.E. Hubb.	26	-
Inula L.	33	-
Halimione portulacoides	65	-
Juncus L.	41	2
Puccinellia Parl.	31	17
Limonium Mill.	61	26
Dt of cl. *Salicornietea fruticosae*		
Tribe *Salicornieae* Moq.	**99**	**85**
Dt of subcl. *Kalidienea*		
Petrosimonia Bunge	1	40
Salsola L.	2	57
Other taxa		
Suaeda Forssk. ex Scop.	28	52
Aeluropus Trin.	17	34
Frankenia L.	10	29
Salicornia europaea s.l.	16	26
Sphenopus divaricatus	8	28

Dt of the class Dt of the subclasses

L. giacominii, L. girardianum, L. gmelinii, L. graecum, L. latebracteatum, L. narbonense s. l., *L. oleifolium* s. l., *L. ramosissimum* s. l., *L. vulgare* s. l.), *Juncus* (*J. acutus, J. anceps, J. bufonius, J. gerardii, J. hybridus, J. littoralis, J. maritimus, J. pygmaeus, J. subulatus*), *Inula* (*I. crithmoides, I. mediterranea*), *Puccinellia* (*P. distans, P. fasciculata, P. festuciformis* s. l., *P. maritima*), *Parapholis* (*P. filiformis, P. incurva, P. strigosa*) and *Halimione portulacoides* (Tab. 2).

Nt: ***Salicornietalia fruticosae*** Br.-Bl. 1933.

As a rule, these are mainly coastal communities of succulent hyperhalophytes which occur in relatively mild climatic conditions of the Mediterranean Sea and the Atlantic coasts, often with a sound participation of hemicryptophytes of non-succulent character.

Order ***Salicornietalia fruticosae*** Br.-Bl. 1933 : 12
Salicornietalia Br.-Bl. 1931 (Art. 2b): 38

Table 2

Diagnostic taxa of the orders of the cl. *Salicornietea fruticosae*
Диагностические таксоны порядков кл. ***Salicornietea fruticosae***

Syntaxa names	*Salicornietea fruticosae*			
	Kalidienea			*Arthrocnemenea*
	Kalidietalia gracilis	*Kalidietalia caspici*	*Halimionetalia verruciferae*	*Salicornietalia fruticosae*
Number of associations and subassociations included in the syntaxon	**4**	**39**	**22**	**132**
Reaumuria songarica	50	-	-	-
Achnatherum splendens	50	-	-	-
Haloxylon ammodendron	50	-	-	-
Nitraria sibirica	**50**	-	-	-
Phragmites australis	**75**	5	9	9
Dt of subcl. *Kalidienea*				
Petrosimonia sibirica + *P. glauca*	-	39	-	-
P. oppositifolia	-	-	41	
P. brachiata	-	-	14	
Salsola L. (excluding section *Climacoptera*)	25	21	14	2
Section *Climacoptera* Botsch. of genus *Salsola* L.	-	74	23	-
Dt of cl. *Salicornietea fruticosae*				
Kalidium caspicum	-	**36**	-	-
K. gracile	**100**	-	-	-
K. foliatum	100	-	5	17
Halocnemum strobilaceum	-	**72**	**59**	17
Halostachys belangeriana	-	**44**	-	-
Dt of subcl. *Arthrocnemenea*				
Arthrocnemum fruticosum	-	-	-	**69**
A. macrostachyum	-	-	-	**56**
A. perenne	-	-	-	**31**
Halimione portulacoides	-	-	-	65
Inula L.	-	-	-	33
Parapholis C.E. Hubb.	-	-	-	26
Juncus L.	-	-	5	41
Puccinellia Parl.	-	3	46	31
Limonium Mill.	-	3	73	61
Salicornia europaea s.l.	-	13	55	16
Artemisia santonicum	-	-	32	1
Halimione verrucifera	-	-	50	-
Other taxa				
Psylliostachys spicata + *P. suworowii*	-	28	-	-
Sphenopus divaricatus	-	46	-	8
Aeluropus Trin.	-	36	36	17
Frankenia L.	-	18	50	10
Suaeda Forssk. ex Scop.	-	51	59	28

Dt of the class Dt of the subclasses Dt of the orders

Arthrocnemetalia fruticosi Br.-Bl. 1931 corr. de Bolòs 1967 (Art. 30) : 30

Sarcocornietalia fruticosi Br.-Bl. 1931 corr. Castroviejo et Cirujano 1980 (Art. 30) : 144

Dt order = dt subclass.

Nt: ***Salicornion fruticosae*** Br.-Bl. 1933 (lectotypus — Rivas-Martínez et Costa 1984).

The characters of this order coincide with those of the subclass.

Alliance ***Arthrocnemion perennis*** (Rivas-Martínez in Rivas-Martínez et al. 1980) stat. nov.

Arthrocnemenion perennis Rivas-Martínez in Rivas-Martínez et al. 1980 (basionymum) : 51

Halimionion portulacoidis J.-M. Géhu 1976 (Art. 5) : 397

Puccinellio maritimae—Halimionion portulacoidis J.-M. Géhu 1994 (Art. 5): 194

Dt: *Puccinellia maritima*, *Aster tripolium*, *Bostrychia scorpioides* (Hudson) Montagne (red alga). The absence of *Arthrocnemum macrostachyum* is also characteristic for community composition in this alliance (Tab. 3).

Nt: ***Puccinellio maritimae—Arthrocnemetum perennis*** (Arenes 1933) J.-M. Géhu 1976 (lectotypus — Rivas-Martinez et Costa 1984).

Dm: *Arthrocnemum fruticosum*, *A. perenne*.

These are communities of the Atlantic coast spread from the Strait of Gibraltar to the English Channel and the southern coast of England. The habitats of communities are well-moistened and very often located under the direct influence of the sea tides. On the Pyrenean Peninsula coast communities of this alliance interact with those of the all. ***Salicornion fruticosae,*** forming transitional phytocoenoses.

Alliance ***Salicornion fruticosae*** Br.-Bl. 1933 : 15

Salicornion fruticosae Br.-Bl. 1931 (Art. 2b) : 38

Arthrocnemion fruticosi Br.-Bl. 1931 corr. de Bolòs 1967 (Art. 30) : 30

Arthrocnemion glauci Rivas-Martínez et Costa 1984 (syntax. syn.) : 18

Dt: species of the genera *Arthrocnemum* (*A. fruticosum*, *A. macrostachyum*, *A. perenne*), *Limonium* (*L. aragonense*, *L. bellidifolium*, *L. biflorum*, *L. caesium*, *L. cos-*

Table 3

Diagnostic taxa of the alliances of the subcl. *Arthrocnemenea* and adjacent syntaxa

Диагностические таксоны союзов субкл. ***Arthrocnemenea*** и ближайших синтаксонов

Syntaxa names	*Arthrocnemion perennis*	*Salicornion fruticosae*	*Limoniastrion monopetali*	Syntaxa not included in the cl. *Salicornietea fruticosae*	
				Limonietalia	*Suaedion brevifoliae*
Number of associations and subassociations included in the syntaxon	**14**	**113**	**5**	**10**	**20**
Puccinellia maritima	57	-	-	-	-
Aster tripolium	50	8	-	-	5
Bostrychia scorpioides	59	2	-	-	-
Dt of ord. *Salicornietalia fruticosae* = dt of subcl. *Arthrocnemenea*					
Arthrocnemum perenne	**64**	**27**	20	-	-
A. fruticosum	**57**	**70**	80	20	10
A. macrostachyum	-	**62**	80	20	20
Halimione portulacoides	100	60	80	20	30
Juncus L.	7	43	40	30	35
Inula L.	14	35	40	40	35
Parapholis C.E. Hubb.	-	27	60	70	25
Limonium Mill.	57	59	100	**100**	90
Puccinellia festuciformis s.l.	-	26	20	10	20
Limoniastrum monopetalum	-	1	**100**	10	-
Other taxa					
Senecio auriculata	-	-	-	30	-
Artemisia caerulescens s.l.	7	9	20	50	5
Plantago L.	14	13	-	80	55
Lygeum spartum L.	-	2	20	**40**	50
Sphenopus divaricatus	-	9	20	10	30
Aeluropus littoralis	-	17	-	10	30
Salsola vermiculata	-	-	-	-	25
Suaeda vera	7	12	-	-	**100**

Dt of the class; Dt of the subclass and the order; Dt of the alliances; Non-characteristic species of the cl. ***Salicornietea fruticosae***

sonianum, L. cymuliferum s. l., *L. delicatulum* s. l., *L. densiflorum, L. densissimum, L. echioides, L. ferulaceum, L. giacominii, L. girardianum, L. gmelinii, L. graecum, L. latebracteatum, L. narbonense, L. oleifolium, L. ramosissimum, L. vulgare* s. l.), *Juncus* (*J. acutus, J. anceps, J. bufonius, J. gerardi, J. hybridus, J. littoralis, J. maritimus, J. pygmaeus, J. subulatus*), *Inula* (*I. crithmoides, I. mediterranea*), *Parapholis* (*P. filiformis, P. incurva, P. strigosa*), *Halimione portulacoides* and *Puccinellia festuciformis* s. l.

Nt: ***Salicornietum fruticosae*** Br.-Bl. 1933 (lectotypus).

Dm: species of the genus *Arthrocnemum* and (much less often) *Halocnemum strobilaceum*.

These are mainly coastal, less often inland communities of the Mediterranean and the Atlantic coasts of the Pyrenean Peninsula. They occur in the habitats subject to periodical flooding. The phytocoenologists of Western Europe distinguished 4 suballiances, diagnosing these syntaxa by the predominance of different species of the tribe *Salicornieae* Moq.

Suballiance ***Sarcocornienion alpini*** Rivas-Martínez et al. 1990 : 93

Dt: *Arthrocnemum perenne* s. l. (Dm).

Nt: ***Halimiono portulacoidis-Sarcocornietum alpini*** Rivas-Martínez et Costa 1984 (holotypus).

On the Mediterranean coast communities of this suballiance occupy the lowest level of the saline marshes greatly subjected to the sea-water influence among all those of the all. ***Salicornion fruticosae***.. On the Atlantic coast they occur at higher levels than those of the all. ***Arthrocnemion perennis***. Communities of this suballiance were described for the coast of the Pyrenean Peninsula by Rivas-Martínez et al. (1990), Peinado et al. (1992). These authors indicated the particular subspecies *Arthrocnemum perenne* [identified by them as *Sarcocornia perennis* (Miller) A. J. Scott subsp. *alpini* (Lag.) Castroviejo (Rivas-Martínez et al., 1990)] as characteristic for communities of the suballiance. Insofar we can judge, the corresponding nomenclatural combination in the genus *Arthrocnemum* has not been published yet (cf. «The Plant Names Project», 2000).

Suballiance ***Arthrocnemenion fruticosi***

Arthrocnemenion fruticosi Rivas-Martínez in Rivas-Martínez et al. 1980 (Art. 28) : 51

Sarcocornienion fruticosae Rivas-Martínez et al. 1990 (Art. 30) : 91—92

Dt: *Arthrocnemum fruticosum* (Dm).

They are coastal communities of the Mediterranean Sea and the Atlantic coasts which are located at a higher bank level than those of the suball. ***Sarcocornienion alpini*** and the all. ***Arthrocnemion perennis*** but still exist under the strong sea influence.

Suballiance ***Arthrocnemenion glauci*** Rivas-Martínez et Costa in Rivas-Martínez et al. 1980 : 51

Arthrocnemenion macrostachyi Peinado et al. 1992 (Art. 30) : 286

Dt: *Arthrocnemum macrostachyum* (Dm).

Nt: ***Sphenopo divaricati—Arthrocnemetum glauci*** Br.-Bl. (1928) 1933 (lectotypus — Rivas-Martínez et Costa 1984).

These are the Mediterranean coastal, sometimes inland communities. They occupy the highest and hence driest locations on the coast, if compared to those of the previous suballiances, and are more rich in their floristic composition than the latter.

Suballiance ***Halocnemenion*** Géhu et Costa in Géhu et al. 1984 : 362

Dt: *Halocnemum strobilaceum* (Dm).

Nt: ***Arthrocnemo glauci—Halocnemetum strobilacei*** Oberd. 1952 (holotypus).

Communities with the dominance of *Halocnemum strobilaceum* are inclined to the eastern part of the Mediterranean. The westernmost point where they were described is the coast of Tunisia (Géhu, Géhu-Frank, 1991).

Alliance ***Limoniastrion monopetali*** Pignatti 1953 : 176

Dt: *Limoniastrum monopetalum*.

Nt: ***Limonio densissimi—Limoniastretum monopetali*** Pignatti 1953 (lectotypus — Rivas-Martínez et Costa 1984).

These are coastal communities with the dominance of low bushes of *Limoniastrum monopetalum*. Their locations are more remote from the water level than those of the all. ***Salicornion fruticosae***. In comparison with the latter, these communities are developed on drier and less salinized soils which are usually not subject to sea flooding. They are transitional from the communities of the ord. ***Salicornietalia fruticosae*** to those of the ord. ***Limonietalia*** Br.-Bl. et. de Bolòs 1957. Described in the western part of the Mediterranean region from Sicily and Tunisia to Spain (Braun-Blanquet et al., 1952; Géhu, Géhu-Frank, 1991; Curcó, 1996) and also from the southern coast of Portugal westward from Gibraltar (Rivas-Martínez et al., 1980).

Subclass ***Kalidienea*** subcl. nov.

Dt: species of the genera *Kalidium* (*K. caspicum, K. foliatum, K. gracile*), *Salsola* (*S. aralensis, S. crassa, S. lanata, S. transoxana, S. turcomanica, S. acutifolia, S. arbuscula, S. dendroides, S. foliosa, S. kali, S. nitraria, S. orientalis, S. passerina, S. paulsenii, S. soda*), *Petrosimonia* (*P. brachiata, P. glauca, P. oppositifolia, P. sibirica, P. triandra*) and *Halocnemum strobilaceum*. The absence of species of the genus *Arthrocnemum* is also an apparent diagnostic feature of the subclass.

Nt: ***Kalidietalia caspici*** ord. nov. hoc loco.

These are mainly inland communities of perennial succulent hyperhalophytes of the south of Eastern Europe, Kazakhstan, the Middle Asia, Iran and Mongolia which occur in different types of salty marshes. The coastal communities of the subclass usually occur near lakes of the marine origin or deeply cut-in gulfs, limans, etc., not along the open seashore.

Order ***Halimionetalia verruciferae*** ord. nov.

Halostachyetalia Ţopa 1939 (Art. 3f, Art. 3f) : 64—65

Dt: *Halimione verrucifera, Artemisia santonicum, Petrosimonia oppositifolia, Salicornia europaea* s. l., species of the genera *Limonium* (*L. gmelinii, L. meyeri, L. bellidifolium, L. suffruticosum, L. iranicum*), *Puccinellia* (*P. fominii, P. distans*).

Nt: ***Artemisio santonici—Puccinellion fominii*** Shelyag-Sosonko et al. 1989 (holotypus).

Such coastal and inland communities are spread from the western part of the Black Sea area to the west of the Caspian Lowland, obviously including the Transcaucasus.

This order may be considered transitional to the subcl. ***Arthrocnemenea***, which can be seen from the high constancy of species of the genera *Puccinellia* and *Limonium*.

The latter ones are typical of communities of the subcl. ***Arthrocnemenea*** (see Tab. 1).

Alliance ***Artemisio santonici—Puccinellion fominii*** Shelyag-Sosonko et al. 1989 : 8

Halocnemion Korzhenevskiy et Klyukin 1990 (Art. 1, Art. 8) : 12

Halimionion Atri et al. 1995 (Art. 8) : Tab. 2.

Halimionio-Petrosimonion triandrae Coldea 2000 (syntax. syn.): 208.

Dt of the alliance = dt of the order.

Nt: ***Puccinellio fominii—Halimionetum verruciferae*** Shelyag-Sosonko et al. 1989 (holotypus).

Dm: *Halocnemum strobilaceum*, *Halimione verrucifera*.

The characters of this alliance correspond to those of the order.

Suballiance ***Artemisio santonici—Puccinellienion fominii*** suball. nov.

Dt suballiance = dt alliance (Tab. 4).

Nt: ***Puccinellio fominii—Halimionetum verruciferae*** Shelyag-Sosonko et al. 1989.

They are communities of the alliance in the northern part of the Black Sea area.

Suballiance ***Climacoptero-Suaedienion acuminatae*** (Golub et Čorbadze 1989) stat. nov. nom. corr. hoc loco.

Climacoptero-Suaedion Golub et Čorbadze 1989 : 120 (basionymum)

Dt: *Salsola crassa*. A sharp fall of the species constancy in the genera *Limonium* and *Puccinellia* and also in *Artemisia santonicum* is also typical for the composition of communities of this suballiance.

Nt: ***Kalidietum foliati*** Golub et Čorbadze 1989 (holotypus).

These communities, developed in the western part of the Caspian Lowland and Western Iran, are transitional from those of the ord. ***Halimionetalia verruciferae*** to the ord. ***Kalidietalia caspici***.

Climacoptero-Suaedion Golub et Čorbadze 1989 was transferred to the level of a suballiance. When establishing the alliance, it was implied that the second part of its name is derived from the taxon *Suaeda salsa*. However, it was revealed during the field works of 1996 that this species was mentioned erroneously for the communities of the ass. ***Kalidietum foliati*** (nomenclatural type of the alliance). *Suaeda acuminata* is more frequent in the habitats of this association. According to Art. 43 of the ICPN, correction of the alliance name is considered necessary (see above).

Order ***Kalidietalia caspici*** ord. nov.

Dt: *Halostachys belangeriana*, *Kalidium caspicum* and species of section *Climacoptera* Botsh. of genus *Salsola* (*S. aralensis*, *S. crassa*, *S. lanata*, *S. transoxana*, *S. turcomanica*).

Nt: ***Kalidion caspici*** all. nov. hoc loco.

They are communities of the perennial succulent hyperhalophytes in the Iranian-Turanian area, according to the phytogeografic subdivision of the world by A. L. Takhtajan (1978).

Table 4

Diagnostic taxa of the alliances and orders of subcl. *Kalidienea*

Диагностические таксоны союзов и порядков субкл. ***Kalidienea***

Syntaxa names	*Artemisio santonici-Puccinellion fominii*	*Kalidion caspici*	*Climacopterion lanatae*	*Aeluropodion littoralis*	*Kalidion gracilis*
Number of associations and subassociations included in the syntaxon	**22**	**19**	**14**	**6**	**4**
Dt of ord. *Halimionetalia verruciferae*					
Halimione verrucifera	**50**	-	-	-	-
Salicornia europaea s.l.	**55**	16	7	17	-
Limonium Mill.	73	-	-	17	-
Puccinellia Parl.	46	-	-	17	-
Artemisia santonicum	32	-	-	-	-
Petrosimonia oppositifolia	41	-	-	-	-
Petrosimonia sibirica + *P. glauca*	-	16	**79**	17	-
Sphenopus divaricatus	-	11	100	33	-
Eremopyrum triticeum	-	16	36	-	
E. orientale	-	16	29	-	-
Malcolmia africana	-	11	29	-	
Tetradiclis tenella	-	5	29	-	
Psylliostachys spicata + *P. suworowii*	-	-	79	-	-
Aeluropus littoralis	36	5	14	**100**	-
A. lagopodioides	-	16	21	33	-
Polygonum acetosum	-	5	7	33	-
Karelinia caspicum	-	-	-	33	-
Scirpus maritimus s.l.	-	-	-	33	-
Tamarix hispida	-	5	-	33	-
Dt of ord. *Kalidietalia caspici*					
Sect. Climacoptera Botsch. of genus *Salsola* L.	23	68	**100**	33	-
Dt of cl. *Salicornietea fruticosae*					
Halostachys belangeriana		26	50	83	-
Kalidium caspicum		**53**	**29**	-	-
Halocnemum strobilaceum	**59**	**68**	**79**	**67**	-
Dt of ord. *Kalidietalia gracilis*					
Kalidium gracile	-	-	-	-	**100**
K. foliatum	5	-	-	-	50
Phragmites australis	9	-	-	33	**75**
Nitraria sibirica	-	-	-	-	**50**
Reaumuria songarica	-	-	-	-	50
Achnatherum splendens	-	-	-	-	50
Haloxylon ammodendron	-	-	-	-	50
Other taxa					
Suaeda Forssk. ex Scop.	59	58	36	67	-
Frankenia hirsuta	50	11	21	33	-
Salsola L. (*excluding* sect. *Climacoptera*)	14	42	-	-	25

Dt of the class Dt of theorders Dt of the alliances

Alliance ***Kalidion caspici*** all. nov.

Halostachyion Atri et al. 1995 (Art. 8) : Tab. 2.

Dt alliance = dt order.

Nt: ***Kalidietum caspici*** Tschernova et Golub in Golub 1995 (holotypus).

Dm: *Halocnemum strobilaceum* and *Kalidium caspicum*. These communities, extremely poor in floristic regard, are mainly spread in the desert area of the Iranian-Turanian region.

Suballiance ***Kalidienion caspici*** suball. nov.

Dt suballiance = dt alliance.

Nt: ***Kalidietum caspici*** Tschernova et Golub in Golub 1995.

The characters of this suballiance correspond to those of the alliance.

Suballiance ***Halocnemo-Haloxylenion aphylli*** (Berdiev et Golub in Golub 1995) status nov.

Halocnemo-Haloxylion aphylli Berdiev et Golub in Golub 1995: 5 (basionymum).

Dt: *Haloxylon aphyllum*.

Nt: ***Haloxylo-Kalidietum caspici*** Berdiev et Golub in Golub 1995 (holotypus).

These communities are developed on residually salinized and takyr-like soils which are often covered with a thin layer of sand, with the level of ground water bedding up to 4 m deep. They are transitional to those with a dominance of the woody species *Haloxylon aphyllum*. Described from the area of the South-Western Turkmenistan and the lower Amu Darya River (Berdiev et Golub, 1992; Bakhiev et al., 1994).

Alliance ***Climacopterion lanatae*** Berdiev et Golub in Golub 1995 : 3

Frankenio-Aeluropodion repentis Rukhlenko 1997a (Art. 1) : 3

Climacopterion longipistillatae Rukhlenko 1997b (Art. 1) : 8

Climacopterion glaberrimae Rukhlenko 1997b (Art. 1) : 2

Dt: *Petrosimonia sibirica* + *P. glauca*, *Sphenopus divaricatus*, *Psylliostachys spicata* + *P. suworowii*, *Eremopyrum orientale*, *E. triticeum*, *Malcolmia africana*, *Tetradiclis tenella*.

Nt: ***Tetradiclido-Petrosimonietum glaucae*** Berdiev et Golub in Golub 1995 (holotypus).

Dm: *Halocnemum strobilaceum*, *Salsola lanata*, *Petrosimonia sibirica*.

These are communities of the dry subtropical zone of South-Western Turkmenistan, mainly described in the Atrek River valley.

Communities of the all. ***Kalidion caspici*** which are more poor in their floristic composition may occur in the same region but in conditions of less moisture and more toxic soil salinization.

Alliance ***Aeluropodion littoralis*** Berdiev et Golub in Golub 1995: 5

Phragmito-Halostachyion Golub et E. Kuzmina ex Bakhiev et Golub 1995 (syntax. syn.) : 17

Dt: *Aeluropus littoralis*, *A. lagopodioides*, *Polygonum acetosum*, *Karelinia caspicum*, *Scirpus maritimus*, *Tamarix hispida*, *Phragmites australis*.

Nt: ***Spergularietum sperguloidis*** Berdiev et Golub in Golub 1995 (holotypus).

Dm: *Halostachys belangeriana* (the upper layer), *Aeluropus littoralis* and (less often) *Halocnemum strobilaceum* (the lower layer).

These communities are widespread in the river valleys of the Middle Asia, on locations well-moistened through most of the vegetation period. The typical soils are meadow solonchaks, salt-affected soils, and residual solonchaks, usually with a heavy texture. The salt content in the upper soil horizons reaches 4 %.

Communities of the alliance are neighboring the halophytic phytocoenoses with dominant hemicryptophytes (close to the cl. ***Festuco-Puccinellietea*** Soó 1968) and bushes (***Nerio-Tamaricetea*** Br-Bl. et de Bolòs 1957).

Order ***Kalidietalia gracilis*** Mirkin ord. nov.

Kalidietalia Mirkin in Kashapov et al. 1988 (Art. 1, Art. 8) : 4, 26

Kalidietalia gracilis Mirkin et al. 1988 (Art. 8) : 79, 83

Dt: *Kalidium gracile*, *K. foliatum*, *Reaumuria songarica*, *Achnatherum splendens*, *Phragmites australis*, *Haloxylon ammodendron*, *Nitraria sibirica*. The absence of *Halocnemum strobilaceum* is a characteristic feature of the communities of the order.

Nt: ***Kalidion*** Mirkin all. nov. hoc loco.

Dm: *Kalidium gracile*, *Phragmites australis*, *Nitraria sibirica*.

These are communities of the perennial hyperhalophytes of Mongolia. They are distinguished by their pronounced floristic poorness. The order and subordinated alliance are established on the basis of a small number of the relevés by Hilbig (1987) and Kashapov et al. (1988). The level of their knowledge is insufficient.

Alliance ***Kalidion gracilis*** Mirkin all. nov.

Kalidion Mirkin in Kashapov et al. 1988 (Art. 1, Art. 8) : 4, 26

Kalidion Mirkin et al. 1988 (Art. 8) : 79, 83

Dt alliance = dt order.

Nt: ***Salsolo passerinae—Kalidietum foliati*** Kashapov et al.1988 ass. nov. hoc loco (nomenclatural type is given in the Appendix).

Dm: *Kalidium gracile*, *Phragmites australis*, *Nitraria sibirica*.

The characters of this alliance coincide with those of the order.

Discussion

The diagnostic group of taxa of the cl. ***Salicornietea fruticosae*** comprises closely related perennials of the family *Chenopodiaceae* referred to the tribe *Salicornieae* (Moquin-Tandon, 1849; Pratov, 1987) or the subfamily *Salicornioideae* (Ulbrich, 1934). Thus, the diagnostic taxon of the cl. ***Salicornietea fruticosae*** may be regarded as a group of perennial species of the tribe *Salicornieae* Moq. (*Arthrocnemum fruticosum*, *A. perenne*, *A. macrostachyum*, *Kalidium caspicum*, *K. foliatum*, *K. gracile*, *Halocnemum strobilaceum*, *Halostachys belangeriana*). It should be noted that the genus *Halimione* Aell. (typical of some syntaxa of the cl. ***Salicornietea fruticosae***) is also sometimes included in the tribe *Salicornieae* (Williams, Ford-Lloyd, 1974). However, according to the more traditional view, the genus *Halimione* should be placed in the tribe *Atripliceae* or even included in the genus *Atriplex* (see Stace, 1997).

None of the above-mentioned species of this tribe *Salicornieae* is spread over the total ranges of the cl. ***Salicornietea fruticosae***. These species are gradually replacing each other in the meridional direction, and their areas are considerably overlapping. For instance, *Halocne-*

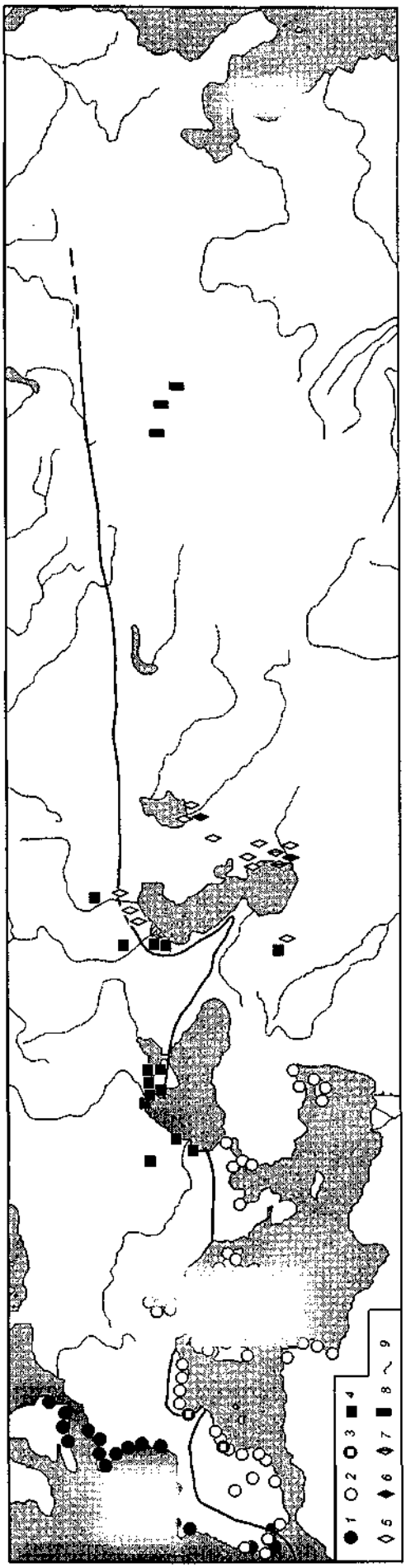
mum strobilaceum, typical for the Middle-Asian and East-European communities of the class, is seldom or rare in the Mediterranean up to the eastern coast of Spain (where it occurs in combination with the species of the subcl. ***Arthrocnemenea***). This species can also be referred to the genus *Kalidium* whose main area is located in Central and Middle Asia. But *Kalidium foliatum* is to be found in several points of the southern Spain after a great disjunction in its area (from the Northern Caspian Lowland to the Iberian Peninsula; Jalas, Suominen, 1980).

West-European phytocoenologists often refer communities of the ord. ***Limonietalia*** Br.-Bl. et de Bolòs 1957 to the cl. ***Salicornietea fruticosae*** (Braun-Blanquet, Bolòs, 1957; Géhu, Géhu-Frank, 1984; Rivas-Martínez, 1984; Rivas-Martínez, Costa, 1984; Peinado et al., 1992). But, as follows from the taken analysis, this decision seems wrong for several reasons. Firstly, though species of the diagnostic «nucleus» of the class (taxa of the tribe *Salicornieae*) occur in communities of the ord. ***Limonietalia***, they do not dominate in these phytocoenoses. On the contrary, their constancy and abundance in the latter decrease sharply. Secondly, they are not succulent chamaephytes or nanophanerophytes but hemicryptophytes (mostly various cereals, also the species of genera *Limonium*, *Plantago*, etc.) which dominate the communities of the ord. ***Limonietalia***. Some of these hemicryptophytes have thick leaves (species of the genus *Limonium*), but they can't be considered succulents. Thirdly, communities of the ord. ***Limonietalia*** are much more rich in their floristic composition than those of the ord. ***Salicornietalia fruticosae***. Eventually, the habitats of communities of the ord. ***Limonietalia*** are never flooded, the latter occupy more dry and less salinized locations than those of the ord. ***Salicornietalia fruticosae***. In other words, communities of the ord. ***Limonietalia*** strongly differ from those of succulent perennial hyperhalophytes both floristically, ecologically and physiognomically. Probably, the most appropriate place for the ord. ***Limonietalia*** is the cl. ***Festuco-Puccinellietea*** Soó 1968.

Communities of the all. ***Suaedion brevifoliae*** Br.-Bl. et de Bolòs 1957 are also represented on the Pyrenean Peninsula. They have been attributed to the ord. ***Salicornietalia fruticosae*** (Castroviejo, Cirujano, 1980; Ladero et al., 1984; Rivas-Martínez, Costa, 1984) and sometimes to the ord. ***Limonietalia*** (including the latter in the cl. ***Salicornietea fruticosae***; Rigual, 1968; Costa, Boira, 1981; Peinado et al., 1984). However, despite the fact the perennial succulent *Suaeda vera* dominates the associations of this alliance, these communities have just a few in common with typical phytocoenoses of the ord. ***Salicornietalia fruticosae*** according to all the other characters. Species of the tribe *Salicornieae* (namely those of the genus *Arthrocnemum*) are insignificantly represented in them. We are sure that communities of the all. ***Suaedion brevifoliae*** shouldn't be included in the ord. ***Salicornietalia fruticosae.*** Still it is the problem which needs further elaboration.

The degree of division of communities of the subcl. *Arthrocnemenea* into alliances and suballiances is higher than that in the subcl. ***Kalidienea***. This is connected with a higher level of knowledge of these communities by West-European vegetation scientists.

Communities of the cl. ***Salicornietea fruticosae*** [together with those of the cl. ***Thero-Salicornietea*** (S. Pignatti 1953) R. Tx. in R. Tx. et Oberd. 1958 are the most halophytic phytocoenoses in Eurasia. In the specific landscapes they refer to the borderline points on the axes of soil salinity gradients, as any of the high plants become



The distribution syntaxa of class *Salicornietea fruticosae*.
Распространение сообществ класса ***Salicornietea fruticosae***.
Subcl. ***Arthrocnemenea*** ord. ***Salicornietalia fruticosae***: *1* — all. ***Arthrocnemion perennis***, *2* — all. ***Salicornion fruticosae***, *3* — all. ***Limoniastrion monopetali***. Subcl. ***Kalidienea***, ord. ***Halimionetalia verruciferae***: *4* — all. ***Artemisio santonici—Puccinellion fominii***; ord. ***Kalidietalia caspici***: *5* — all. ***Kalidion caspici***, *6* — all. ***Climacopterion lanatae***, *7* — all. ***Aeluropodion littoralis***; ord. ***Kalidietalia gracilis***: *8* — all. ***Kalidion gracilis***. *9* — the northern boundary of Ancient Mediterranean according to M. G. Popov (1950).

eliminated with further increase of salt concentration in soil solutions. For instance, maximal salt content in soils under communities dominated by *Halocnemum strobilaceum* is equal to 4—7 % in the north of the Caspian Lowland under the chloride-sulphate or sulphate-chloride soil salinity conditions (Tarasov et al., 1983; Grebenyuk, 1988; Grebenyuk, Kashchenko, 1988; Golub, Čorbadze, 1989). Approximately the same values are indicated in the South-Western Turkmenistan (Berdiev, 1986) and in the Aral Sea area (Bakhiev, 1979) for the chloride type of soil salinity.

Comparing the community distribution of the cl. ***Salicornietea fruticosae*** to different variants of florogenetic division of the Holarctic (Popov, 1929, 1950; Lavrenko, 1962; Mattic, 1964; Takhtajan, 1978; Razumovsky, 1999), it is evident to see that the northern ranges of communities of the cl. ***Salicornietea fruticosae*** up to the Atlantic Ocean coincide with those of the Ancient Mediterranean region as outlined in the last works of M. G. Popov (including the territory of Mongolia; Popov, 1950). Communities of the class have spread much further to the north of this limit only along the European coast of the Atlantic (see figure). Unfortunately, we cannot compare the southern ranges of the Ancient Mediterranean to the area of the cl. ***Salicornietea fruticosae***, as the reliable vegetation data are absent from along this boundary (see the unit «Materials and Methods» above). It can be only noted that in the African and Asian coastal areas between the tropics they are replaced by the mangroves.

The communities close to the cl. ***Salicornietea fruticosae*** were described also from the coasts of America (Peinado et al., 1994, 1995). It is important to note that in California and the adjacent part of Mexico the climatic conditions are similar to those of the Mediterranean region, and M. G. Popov (1950) even included these areas in his wide concept of the Ancient Mediterranean. The comparative analysis of the Old and the New Worlds' communities with perennial species of the tribe *Salicornieae* may be the subject of a special study based on extensive material.

It may be suggested that communities of the cl. ***Salicornietea fruticosae*** originated at the coasts of the ancient Tethys Ocean. They seem to mark the northern boundary of this ancient water reservoir and, moreover, they still bear the ecological features of coastal communities even when being particularly inland. In the coastal zones they are formed under the influence of both ground and surface salty sea-water. In the continental areas they are confined to various kinds of depressions and river valleys where salty ground waters lie close to the surface, and the community locations are subject to surficial flooding in moist seasons as well as along the marine coast.

It may be also suggested that the driving force of the evolution of species of the tribe *Salicornieae*, the «nucleus» of communities of the cl. ***Salicornietea fruticosae***, was the adaptation to increasing continentality of the climate as the Ancient Tethys regressed.

Thus, it is reasonable to consider the cl. ***Salicornietea fruticosae*** Ancient Mediterranean, not Mediterranean and thermo-atlantic as it is often interpreted (e.g. Mucina, 1997). The appearance of analogous communities of the cl. ***Salicornietea fruticosae*** in Australia (Bridgewater, 1982; Bridgewater, Cresswell, 1993) is probably connected with the subsequent penetration of diaspores of a species close to the genus *Arthrocnemum* into the inland and coastal marshes of this continent from the Ancient Mediterranean source.

Acknowledgements

We thank Dr. S. Rivas-Martínez, Dr. J.-M. Géhu, and Dr. F. Alcaraz for the information support of our work, Dr. H. Freitag for valuable advice and comments. The financial support from the Russian Foundation for Fundamental Research (grant 01-04-48008) is also appreciated. We also thank S. M. Hennekens for the assignment of the program package and I. V. Volgina for her assistance in translating the article into English.

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Appendix

Ass. ***Salsolo passerinae—Kalidietum foliati*** [Tab. 15 in the paper of Kashapov R. Sch. et al. (1988)]

Relevé number	1	2	3	4	5	6	7	8	9	10	
Total projective cover, %	2	2	4	2	2	1	5	5	5	2	**C**
Number of species	3	3	3	4	4	3	4	4	4	3	
Salsola passerina	+	+	+	+	+	+	+	+	+	+	V
Kalidium foliatum	+	+	+	+	+	+	+	+	+	+	V
Reaumuria soongorica	+	+	+	+	+	+	+	+	+	+	V
Kalidium gracile	-	-	-	+	-	-	+	+	+	-	II
Haloxylon ammodendron	-	-	-	-	+	-	-	-	-	-	I

Note. 1—10 — South-Gobi Aimak, Bulgan-somone, plain 1 km north-east from the top 1117.8 m in the Khanain-Khira place (15.08.1971). Relevés were made by B. M. Mirkin. Relevé N 8 is the nomenclatural type of the association.

Резюме

Проведены обзор и ревизия высших синтаконов класса ***Salicornietea fruticosae*** Br.-Bl. et Tx. ex de Bolòs y Vayreda 1950 в Евразии. В качестве исходного материала было рассмотрено 260 низших синтаксономических единиц (ассоциаций и субассоциаций), выделенных на территории от Атлантического океана до пустыни Гоби. Установление этих единиц базировалось на 2349 геоботанических описаниях. Весь материал собирался в базе данных «Turboveg», а затем обрабатывался с помощью пакета программ «Megatab», с включенной в него программой TWINSPAN, предназначенной для иерархических построений.

При ревизии синтаксонов авторы строго следовали «Международному кодексу фитосоциологической номенклатуры» (Weber et al., 2000). Одним из результатов этой работы явилось выявление синонимов, которые со ссылками на статьи и положения этого кодекса были отвергнуты.

Показано, что диагностическими таксонами кл. ***Salicornietea fruticosae*** можно считать группу видов многолетников трибы *Salicornieae* Moq. (*Arthrocnemum fruticosum, A. perenne, A. macrostachyum, Kalidium caspicum, K. foliatum, K. gracile, Halocnemum strobilaceum, Halostachys belangeriana*). Ни один из указанных видов не распространен на всей территории ареала кл. ***Salicornietea fruticosae***. Указанные виды постепен-

но замещают друг друга в меридиональном направлении. При этом их ареалы очень сильно перекрываются.

В результате ревизии выделено два подкласса: ***Arthrocnemenea*** и ***Kalidienea***. Степень дробления на союзы и подсоюзы сообществ первого подкласса выше, чем второго. Это связано с большей изученностью сообществ подкласса ***Arthrocnemenea*** геоботаниками.

Сообщества кл. ***Salicornietea fruticosae*** (наряду с сообществами кл. ***Thero-Salicornietea***) — наиболее галофитные фитоценозы на территории Евразии. В конкретных ландшафтах они располагаются на оси градиента засоления почвы в точках, далее которых (при дальнейшем нарастании концентрации солей в почвенном растворе сообщества) высшие растений уже отсутствуют.

При сопоставлении размещения сообществ кл. ***Salicornietea fruticosae*** с различными вариантами флорогенетического районирования Голарктики было установлено, что северная граница распространения сообществ этого класса до Атлантического океана хорошо совпадает с такой же границей области Древнего Средиземья, причем с более поздним вариантом ее выделения, когда в эту область была включена территория Монголии (Попов, 1950). И только вдоль европейского побережья Атлантики сообщества класса распространились значительно севернее этой границы.

Можно полагать, что сообщества кл. ***Salicornietea fruticosae*** начали формироваться еще на берегах древнего Тетиса. И они не только маркируют северную границу этого древнего водоема, но и до сих пор сохранили в своей экологии черты приморских сообществ, даже если они являются сугубо внутриконтинентальными. В приморской зоне они формируются под влиянием соленых морских вод, как поверхностных, так и грунтовых. В континентальных областях — приурочены к различного рода депрессиям и долинам рек, где неглубоко залегают соленые грунтовые воды. Причем во влажные сезоны года эти местоположения, так же как и на берегу моря, могут затапливаться с поверхности.

Таким образом, целесообразно считать кл. ***Salicornietea fruticosae*** не средиземноморским и термоатлантическим, как это нередко трактуется (например, L. Mucina (1997)), а древнесредиземноморским.