The Order Palmariales (Rhodophyta) in the North Pacific Area of Russia: Taxonomic Revision of *Halosaccion* Kützing and *Devalereaa* Guiry

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**Author’s contribution**

The sole author designed, analyzed and interpreted and prepared the manuscript.

**ABSTRACT**

Research data on taxonomy of the members of the family Palmariaceae (Palmariales, Rhodophyta) from the Russian Pacific coasts are presented. Special attention is paid to taxonomic status of two genera of palmarialean algae inhabiting the area: *Halosaccion* and *Devalereaa*. The genus *Halosaccion* is presented in the Russian Pacific area by 3 species: *H. glandiforme* (= *H. hydrophorum*), *H. minjaii*, *H. yendoi* (= *D. yendoi*). The first one *H. glandiforme* is proposed herein as a type species of the genus *Halosaccion*, while *H. hydrophorum* is treated as a later taxonomic synonym of *H. glandiforme*. The generic position of *H. yendoi* is hitherto controversial. It was described originally as *H. yendoi*, then transferred to *Devalereaa*, but later on reinstated within *Halosaccion* on the basis of genetic data in spite of anatomy typical of the genus *Devalereaa*. Taxonomic assignment of *Halosaccion firmum* raised doubts as well. It is anatomically close to *Devalereaa* and probably should be transferred to this genus. This supposition, based on anatomical parameters, is supported by preliminary genetic data, so a new combination *Devalereaa firmum* (Postels et Ruprecht) Selivanova is presented herein with the proviso that genetic studies will be continued to confirm our results. At present the genus *Devalereaa* in the studied area is shown to...
include for sure only one species *D. compressa* in addition to *D. firma*. Generic attribution of *D. microspora* (= *H. microsporum*) remains questionable until molecular genetic data are available.

**Keywords:** Rhodophyta; Palmariales; Palmariaeae; Halosaccion; Devaleraea; morphology; taxonomy.

1. **INTRODUCTION**

Red palmarialean algae represent one of the most important components of marine algal flora of the Far Eastern seas of Russia [1]. The order Palmariales Guiry et Irvine in Guiry [2] was segregated from the order Rhodymeniales F. Schmitz on the basis of the peculiarities of formation and development of tetrasporangia. The order was considered for a long time to be monotypic with the only family Palmariaceae Guiry [3]. Describing the family, its author (Guiry [3]) included into it the genera *Palmaria* Stackhouse, *Halosaccion* Kützing and *Leptosarca* A. Gepp et E. Gepp. These three genera differed from the other representatives of the order Rhodymeniales sensu stricto by the absence of the carposporophyte generation and the presence of the stalk-cell in the developing tetrasporangia [3]. Later on, the genus *Leptosarca* was synonymized with the genus *Palmaria* by Ricker [4]. At present there are 5 genera within the family Palmariaceae according to Schneider and Wynne [5], in addition to already mentioned *Palmaria* and *Halosaccion* these are: *Neohalosacciocolax* I.K. Lee et Kurogi, *Devaleraea* Guiry and *Coriophyllum* Setchell et N.L. Gardner in Gardner. In accordance with another viewpoint of Guiry and Guiry [6] there are 4 actual genera in Palmariaceae, whereas the genus *Coriophyllum* is included in the family Rhodophysemataceae Saunders et McLachlan, [7] which also belongs to the order Palmariales. This family was segregated from the family Acrochaetiaeae Fritsch ex W.R. Taylor by the absence of a carposporophyte and monosporangia, presence of a unique stalk sporangial cell integral to the sexual cycle and abundance of cellular fusions. The Rhodophysemataceae was also differentiated from the Palmariaceae by the presence of Rhodophysema-like tetrasporangia and heteromorphic sexual life history [7].

The position of the genus *Coriophyllum* had been uncertain for a long time, but most phycologists referred it to the family Peyssonneliaceae Denizot, within the order Cryptonemiales Schmitz [9]. Now Peyssonneliaceae is considered to belong to a separate order Peyssonneliales D.M. Kayesky, Fredericq et J.N. Norris [10], whereas *Coriophyllum* is transferred to the family Rhodophysemataceae, order Palmariales [6]. Describing *Pseudorhododiscus* the author of the taxon (Masuda [11]) had difficulties in assigning it to a definite family and so left it in the category “genera with uncertain taxonomic position”. At the present time it is included in the family Rhodophysemataceae [6]. In addition, a relatively recently described genus *Rhodonematella* S.L. Clayden et G.W. Saunders was placed in the family Rhodophysemataceae [12]. Other members of the Rhodophysemataceae (Rhodophysema, Rhodophysemopsis) formerly were referred to the order Acrochaetiales by Perestenko [13] but this viewpoint was not shared by foreign phycologists. It should be noted that there were two more members considered to belong to the family Rhodophysemataceae – the genera *Halosacciocolax* S. Lund and *Meiodiscus* G.W. Saunders et McLachlan [7]. The genus *Halosacciocolax* had a very complicated taxonomic history. Initially it had been referred to the family Peyssonneliaceae by Lund [14], then to the family Acrochaetiaeae Fritsch ex Taylor by Cabioch and Guiry [15], later on to Palmariaceae by Hawkes and Scagel [16] and at last to Rhodophysemataceae by Saunders and McLachlan [7]. But at present the genus *Halosacciocolax* has lost its taxonomic independence being merged in synonymy with *Rhodophysema* by Saunders and Clayden [17], the type genus of the family Rhodophysemataceae.
The genus *Meiodiscus* was also placed in the family Rhodophysemataceae by the authors of the genus and the family [7,18]. However, later on another family has been described within the order Palmiales – Meiodiscaceae S.L. Clayden et G.W. Saunders – to include the species of the genus *Meiodiscus* (*M. concrescens* (K.M. Drew) P.W. Gabrielson in Gabrielson et al. and *M. spetsbergensis* (Kjellman) G.W. Saunders et McLachlan) together with a new monotypic genus *Rubrointrusa* S.L. Clayden et G.W. Saunders [12]. Both relatively recently described new genera of palmarialean algae (*Rhodonematella* and *Rubrointrusa*) though referred to different families of the order Palmiales (Rhodophysemataceae and Meiodiscaceae correspondingly) were based on the former representatives of the order Colaconematales: *Colaconema subimmersum* (Setchell et N.L. Gardner) P.W. Gabrielson in Gabrielson et al. (now *Rhodonematella subimmersa* (Setchell et N.L. Gardner) S.L. Clayden et G.W. Saunders) and *Colaconema membranaceum* (Magnus) Woelkerling (now *Rubrointrusa membranacea* (Magnus) S.L. Clayden et G.W. Saunders [12].

One more family was described within the order Palmiales – Rhodothamniellaceae G.W. Saunders in Saunders et al. [8] that contained two genera – *Camontagnea* Pujals and *Rhodothamniella* Feldmann in Christensen [5,6]. Algae of the both genera have uniseriate filamentous structure. In the opinion of Saunders et al. [8] members of this family represent an early genealogical line in the order Palmiales.

Molecular studies of Ragan et al. [19] revealed that members of the order Palmiales had genetic affinity with morphologically distant algae of the orders Acrochaetiales and Nemaliales Schmitz in Engler. In addition to the data on similarity of the pit-plug formation it gave the authors reason to suppose that all three orders had diverged together from main genealogic line in the order Palmiales.

According to the present-day systematic data the order Palmiales consists of 4 families: Palmariaceae, Phodophysemataceae, Meiodiscaceae and Rhodothamniellaceae [6]. Algae of the family Rhodothamniellaceae have not been found on the Russian Pacific coasts up to now, whereas members of the other families are rather numerous. For example, the family Phodophysemataceae in the Far Eastern seas of Russia is presented by 2 genera: *Rhodophysema* (including *R. georgei* Batters, *R. elegans* (P.L. Crouan et H.M. Crouan ex J. Agardh) P.S. Dixon, *R. nagaii* Masuda, *R. odonthaliae* Masuda et M. Ohta) [13] and *Pseudorhododiscus* (*P. nipponicus* Masuda) [20]; the family Meiodiscaceae is presented by *Meiodiscus spetsbergensis* [13]. The majority of them are small-sized epiphytic or parasitic algae in the form of crusts, cushions or felt. The family Palmariaceae also includes a small parasitic alga *Neohalosaccioflex*, but the leading role in this family belongs to three genera of mainly epilithic macroalgae: *Palmaria*, *Halosaccion* and *Devaleraea*, widespread on the Russian Pacific coasts [1,21]. The problems of taxonomy of the genus *Palmaria* were discussed in details in our previous paper [22], the rest 2 genera of palmarialean algae - *Halosaccion* and *Devaleraea* - are in the focus of attention of the present study. Main objective of our work is to clarify taxonomic status of these genera and to reconsider generic position of the species referred to them.

2. MATERIALS AND METHODS

The phycological material used in the present study was collected at the coasts of Eastern Kamchatka from Dezhnev Bay in the north to Lopatka Cape in the south, including Bering Sea, the Commander and Northern Kurile Islands (Fig. 1) during expeditions of the Hydrobiology Laboratory of Kamchatka Branch of the Pacific Geographical Institute from 1986 to 2015. Algae were collected from May through October on the littoral fringe during low tides, and with use of SCUBA from the depths of 1-5 m according to the standard hydrobiological methods. Algae cast ashore were also sampled. Most part of the studied algae was collected by the author of the present paper manually in Avacha Gulf (south-eastern Kamchatka) and Commander Islands in the intertidal zone during low tides. No special instruments were used. Occasionally other collectors also took part in this work. Fresh material was roughly identified visually in the field, put in plastic bags with clean sea water, labeled and brought either to the laboratory or on board a ship. In case of need the material was kept for some time in refrigerator. Then major part of samples was pressed on herbarium paper, dried, labeled and put for storage in the Herbarium of Kamchatka Branch of the Pacific Geographical Institute (Petropavlovsk-Kamchatski, Russia). The processing of collections and identification of algae was conducted at the same Institute.
Fig. 1. A schematic map showing the areas of phycological studies at the coasts of the Eastern Kamchatka

Numbers correspond to the algal collection cités within the studied water area: 1 – Shumshu Island (Northern Kurile Islands); 2 – Cape Lopatka (southern extremity of Kamchatka Peninsula); 3 – Avacha Gulf; 3a – Avacha Bay; 4 – Kronotskii Gulf; 5 – Kamchatskii Gulf; 6 – Ozernoi Gulf; 7 – Karaginskii Island; 8 – Dezhnev Bay; 9 – Commander Islands

The material was sectioned freehand with a razor blade, placed in a drop of fresh water on the slides and examined using light microscopy. The sections were studied unstained. Photos of samples studied were made using photocameras Olympus µ-5010, Olympus SZ-20, Panasonic FS62 Lumix and digital camera for microscope DCM 130.

The following taxonomic and floristic literature was used to identify the plant material involved in this study: Abbott and Hollenberg [9], Hawkes and Scagel [16], Lee [23,24], Guiry [25], Perestenko [13,26,27], Klochkova et al. [28], Lindeberg and Lindstrom [29], Gabrielson et al. [30]. I also consulted AlgaeBase [6].

3. RESULTS

On the total 77 herbarium sheets containing samples of Halosaccion and 58 sheets with samples of Devaleraea were examined (Table 1).

Examination of the samples of palmarialean algae from our collections revealed two species of Halosaccion to grow in the studied area – H. glandiforme and H. minjaii. As it follows from the Table, H. glandiforme is the most widespread species in the studied areas. It has wide geographic range and continuous distribution in contrast to H. minjaii which is relatively rare as compared to H. glandiforme and grows mostly on the islands (Commander, Kurile Islands) [31], being only occasionally met on the continental part of Kamchatka [32]. Nevertheless H. minjaii can form dense thickets in associations with coralline algae in the littoral pools and sometimes even compete with H. glandiforme [31].

The genus Devaleraea is presented by three species. D. firma is distributed mostly in the southern part of the studied area where it is rather abundant and sometimes forms monodominant communities on the rocks and stones in the low intertidal zone. D. firma is also in competitive relations with H. glandiforme [33].
Table 1. The list of palmarialean algae of the genera *Halosaccion* and *Devaleraea* collected in different areas of the Eastern Kamchatka, the Commander and Northern Kurile Islands

| Species names                        | Areas of algal collections (numbers correspond to those presented in the map on Fig. 1) |
|--------------------------------------|--------------------------------------------------------------------------------------|
|                                      | 1 | 2 | 3 | 3a | 4 | 5 | 6 | 7 | 8 | 9 |
| *Halosaccion glandiforme* (Gmelin)  | + | + | + | + | + | + | + | + | + | + |
| Ruprecht                             |   |   |   |   |   |   |   |   |   |   |
| *Halosaccion minjaii* I.K. Lee       | + |   | + |   | + | + | + | + |   |   |
| *Devaleraea firma* (Postels et Ruprecht) Selivanova¹ | + | + | + | + |   |   |   |   |   |   |
| *Devaleraea compressa* (Ruprecht) Selivanova et Kloczcova | + |   |   |   |   |   |   |   |   |   |
| *Devaleraea microspora* (Ruprecht) Selivanova et Kloczcova | + | + | + | + | + | + |   |   |   |   |

¹ *Note*: detailed information concerning taxonomic status of *D. firma* is presented in the section discussion

In most cases the members of the genera *Halosaccion* and *Devaleraea* are well distinguished even in the field. If plants are membranaceous or thin-coriaceous, saccate, single or aggregated, unbranched, reddish purple to yellowish brown, water filled if undamaged – they most likely belong to the genus *Halosaccion*. If thalli of the plants are coriaceous, reddish purple to coral red, flattened, sometimes branched – they probably represent the genus *Devaleraea*. For more detailed identification it is necessary to examine plants anatomy.

A key to genera based on anatomical features is presented below:

1. Large-celled multiseriate cortex with lateral anastomoses and small-celled medulla with stellate proplast – *Halosaccion*.
2. Small-celled cortex without anastomoses and large-celled medulla without stellate proplasts – *Devaleraea*.

A key to genera based on anatomical features is presented below:

1. Plants membranaceous or thin-coriaceous, saccate, with smooth surface, unbranched, reddish purple to yellowish, often water filled – *H. glandiforme*.
2. Plants coriaceous, saccate, dark purple to grayish, frequently with plentiful outgrowths on the surface and so called hieroglyphic zones in fertile samples – *H. minjaii*.

Three species of *Devaleraea* also differ from each other by morphology.

A key to the species of *Devaleraea* based on morphological features:

1. Thallus rigid, coriaceous, of lanceolate or linear-lanceolate form, flattened, unbranched – *D. firma*.
2. Thallus relatively soft, tubular, flattened, sometimes produces plentiful branches – *D. microspora*.
3. Thallus thin-coriaceous, tubular, flattened, narrow-linear, sometimes bipalmate – *D. compressa*.
The discussed taxa are illustrated in the present paper with the only exclusion – pictures of *H. minjai* are not presented herein, however this species was discussed and depicted in our previous work [31]. The illustrations presented in this study are based on freshly collected material. The examined specimens of algae used for pictures are listed below. Numbers on the left indicate registration numbers of the sheets kept in our Herbarium:

*Devaleraea firma* (Postels et Ruprecht) Selivanova, *comb. nov.* (Fig. 2).

No. 5305. June 17, 2016. South-eastern Kamchatka, Avacha Gulf, Avacha Bay, Lagernaya Inlet, low intertidal zone, rocks covered with sand and mussels. Vegetative. Collected by O.N. Selivanova.

*Halosaccion glandiforme* (Gmelin) Ruprecht (Fig. 3).

Nos. 5309-5311. June 17, 2016. South-eastern Kamchatka, Avacha Gulf, Avacha Bay, Lagernaya Inlet, upper intertidal zone, rocks and stones. Vegetative. Collected by O.N. Selivanova.

*Devaleraea compressa* (Ruprecht) Selivanova et Kloczcova (Fig. 4).

Nos. 5306-5308. June 17, 2016. South-eastern Kamchatka, Avacha Gulf, Avacha Bay, Lagernaya Inlet, low intertidal zone, rocks and boulders. Vegetative. Collected by O.N. Selivanova.

4. DISCUSSION

Our previous taxonomic revision of the members of the order Palmariales revealed 7 species of *Palmaria* growing at the Pacific coasts of Russia: *Palmaria callophylloides* Hawkes et Scagel, *P. integrifolia* Selivanova et Zhigadlova, *P. hecatensis* Hawkes, *P. marginicrassa* I.K. Lee, *P. mollis* (Setchell et Gardner) van der Meer et Bird, *P. monilorhiza* (Blinova et Zinova) Perestenko, *P. stenogona* (Perestenko) Perestenko [22]. It seems that *Palmaria* is the only genus of the three genera of macroalgae of the family Palmariaceae that is relatively easy for identification at the generic level.

Taxonomy of the genus *Halosaccion* is not so definite. Palmarialean algae of tubular or saccate form with an inner cavity had been attributed to this genus for a long time. Then M.D. Guiry [25] on the basis of vegetative anatomy of the species of *Halosaccion* showed that they should be divided into two groups. Members of the first group have relatively large-cells multiseriate cortex with lateral anastomoses and relatively small-celled medulla with cytoplasmic outgrowths giving a stellate form to the protoplast. These algae according to Guiry [25] represented the genus *Halosaccion sensu stricto*. Members of the second group have anatomical features close to *Palmaria* – small-celled cortex without anastomoses well distinguished from the medulla which is large-celled and without stellate protoplasts. The algae from the second group were referred to a separate genus *Devaleraea* [25]. *Devaleraea ramentacea* (Linnaeus) Guiry (basionym *Fucus ramentaceus* Linnaeus, homotypic synonym *Halosaccion ramentaceum* (Linnaeus) J. Agardh) was designated as the type species of this genus. Two additional species from the former genus *Halosaccion* were transferred to *Devaleraea*: *D. yendoi* (I.K. Lee) Guiry (basionym *Halosaccion yendoi* I.K. Lee) and *D. arctica* (A.D. Zinova) Guiry (basionym *Halosaccion arcticum* A.D. Zinova) [25]. But at present *D. arctica* is regarded as a taxonomic synonym of *D. ramentacea*.

Later on, after revision of the palmarialean algae from the Russian Pacific coasts two other species of *Halosaccion* were transferred to *Devaleraea* with nomenclatural combinations: *Devaleraea microspora* (Ruprecht) Selivanova et Kloczcova for *Halosaccion microsporum* Ruprecht and *D. compressum* (Ruprecht) Selivanova et Kloczcova for *H. compressum* Ruprecht accordingly [31].

Herein *Halosaccion firmum* (Postels et Ruprecht) Kützing is proposed for the same transfer on the basis of anatomical features typical of *Devaleraea*:

*Devaleraea firma* (Postels et Ruprecht) Selivanova, *comb. nov.*

Basionym: *Dumontia firma* Postels et Ruprecht, *Illustrationes Algarum*: 19. 1840, tab. 35, Fig. B. tab. 40, fig. 82-83.

Synonym: *Halosaccion firmum* (Postels et Ruprecht) Kützing 1843:439.

The decision to transfer *H. firmum* to the genus *Devaleraea* is based on the following features of its anatomy: the presence of 2-3-layered large-celled medulla with the protoplasts adjoining to the cell-walls, absence of stellate protoplasts, abrupt transition from the medulla to the small-celled cortex consisting of 2-3 rows (Fig. 2 C, D) inherent in *Devaleraea*. 

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Fig. 2. Habit and anatomy of *Devaleraea firma* (Postels et Ruprecht) Selivanova
A – algae growing in the intertidal zone; B – fresh samples before pressing on herbarium paper, scale bar = 3 cm; C, D – cross sections of the middle portions of the frond at different magnification power, scale bar = 100 µm

Rightfulness of the attribution of *H. firmum* to *Devaleraea* besides that is supported by preliminary data of molecular-genetic analysis of palmarialean algae from Kamchatka [34]. As it followed from the genetic tree constructed using neighbor-joining method on the basis of ribosomal small subunit DNA sequences, algae referred to *H. firmum* formed common cluster with the species of the genera *Palmaria* and *Devaleraea* and differ from other species of *Halosaccion* [34] (Available at http://lib.komisc.ru/add/conf/algo_2009/wp-content/uploads/2009/06/algoconf_abstr_symvyrar20091.pdf)

Analogous results were shown in genetic tree constructed by the method of maximum parsimony on the basis of ITS1, ITS2 analysis (personal communication of Dr. Han-Gu Choi, Korean Polar Research Institute, Incheon, Korea). However these molecular-genetic studies were not finished and are treated as preliminary. That is why a new combination *Devaleraea firma* (Postels et Ruprecht) Selivanova is presented with the proviso that genetic studies will be continued to confirm our results.

Describing the genus *Devaleraea* M.D. Guiry [25] noted its close resemblance to the genus *Palmaria*. Subsequent studies [35] and preliminary data of molecular-genetic studies of Dr. Han-Gu Choi (personal communication) confirmed this opinion. The genera *Halosaccion* and *Devaleraea* differ from the genus *Palmaria* morphologically by having inner cavity in the blade. However this feature is not reliable for distinguishing the genera. Species of *Palmaria* in some cases can acquire a cavity and so can be identified erroneously as *Devaleraea*, whereas species of *Devaleraea* with small cavity can be mistaken for *Palmaria*. These two genera also have close genetic affinity. But the genus *Halosaccion* according to our data [34] is well
distinguished genetically from Devaleraea and Palmaria.

All species of the genus Palmaria, in spite of considerable morphological differences, have relatively uniform anatomy: solid blade without cavity, large-celled medulla without stellate protoplasts and small-celled cortex without anastomoses.

In spite of some unresolved taxonomic problems the systematics of the genus Palmaria as a whole is more or less defined [22]. This is not the case with two other genera of the family Palmariaceae – Halosaccion and Devaleraea.

It should be noted that the genus Devaleraea was not recognized immediately and unconditionally by all researchers. For example, L.P. Perestenko in her monograph on red algae of the Far Eastern seas of Russia [13] did not mention Devaleraea at all but stated that there were 5 species of Halosaccion in the area: H. microsorum, H. firmum, H. hydrophorum (Postels et Ruprecht) Kützing, H. minjaii I. K. Lee, H. yendoi I.K. Lee.

Note. Actually there is one more species of Halosaccion known from the Russian Pacific – H. tilesii Kjellman that up to now is treated as an independent one (“current” as it is cited in Algaebase [6]). However L.P. Perestenko [13,26] asserted that its description was based on the material representing in fact Palmaria stenogona that often forms a sort of a hollow cavity in the frond filled with water. This phenomenon was observed repeatedly by her on Commander Islands. So she concluded that the species called Halosaccion tilesii did not really exist [26].

In her later work, Perestenko [27] nevertheless recognized the genus Devaleraea, but reduced its volume to the only species D. ramentacea. Some Japanese phycologists also did not recognize Devaleraea [36,37], and continued to cite D. ramentacea and D. yendoi as the species of the genus Halosaccion. Taxonomic status of the latter species H. yendoi (= D. yendoi) in fact remains uncertain up to now. In the Algaebase [6] both names – H. yendoi and D. yendoi – are presented as “current”. However preliminary genetic studies of Dr. Han-Gu Choi (personal communication) are indicative of belonging of this species to the genus Halosaccion.

There is no certainty also with the type species of the genus Halosaccion. Neolecottypification and designation of H. firmum as a type species [25] later on was considered to be erroneous [27].

The problem of lectotypification of the genus Halosaccion is discussed in detail by L.P. Perestenko [27]. She wrote: “There are samples of algae collected by Mertens during F. Litke’s expedition (1826-1829) in Avacha Bay kept in the Herbarium of Komarov Botanical Institute Russian Academy of Sciences. They are signed by Ruprecht “Dumontia firma P. et R., saxis et mytilis”. The samples have linear-lanceolate form with narrow-cuneate base and rounded apex. From these samples I.K. Lee allocated a lectotype specimen with tetrasporangia on August 3, 1979. Examination of the lectotype H. firmum showed that it had anatomical structure typical of Devaleraea” ([27] p.1147).

However Perestenko continues: “the species described and illustrated by I.K. Lee under the name H. firmum, had a typical structure of H. hydrophorum (P. et R.) Kütz. (= H. glandiforme)...” [27] p.1148). So she concluded that the selection of H. firmum as a type species of the genus Halosaccion Kützing made by M. Guiry [25] after Lee was unsuccessful “because it was not based on the type sample but on the description given by I.K. Lee on the material collected on Hokkaido [13]. “Thus if we recognize H. firmum as a lectotype of the genus Halosaccion then the genus Devaleraea becomes a synonym of the genus Halosaccion.” ([27] p. 1148).

Perestenko [27] believed that there was no reason in neolecottypification of the genus Halosaccion and selection of H. firmum as a type species. In her opinion the role of the type species of the genus Halosaccion should belong as before to H. hydrophorum (as it was designated by F. Schmitz [38]. Thus according to Perestenko [27] p. 1149:

Halosaccion Kützing, 1843: 439.
Lectotypus generis: Halosaccion hydrophorum (Postels et Ruprecht) Kützing, 1843: 439 (as H. hydrophora).
Basioniym: Dumontia hydrophora Postels et Ruprecht, 1840: 19, tab. 35, fig. C.
Locus typicus: Kamtschatka, Russia.

However the status of this species (H. hydrophorum) itself remains questionable. As it follows from the historical reference of the same L.P. Perestenko [13,27]: “F. Ruprecht 1850 [39] placed D. hydrophora (including Fucus saccatus sensu Turner) in the synonymy with Ulva...”
glandiformis Gmelin 1768 [40] proposing a combination *Halosaccion glandiforme* (Gmelin) Ruprecht. Consequently the second name (i.e. *H. glandiforme*) became the name of the type species of *Halosaccion*. But as far as a type of *H. glandiforme* (*U. glandiformis*) was lost forever after the October revolution of 1917 (as a whole herbarium of Gmelin, verbal information of A.D. Zinova), there is no reason to keep the epithet *glandiformis* in the presence of the specimen of *H. hydrophorum*, illustrated and referred to by Postels and Ruprecht in their description of *D. hydrophora* that can be considered as a type” ([27] p.1148). The type *H. hydrophorum* is kept in the Herbarium of Komarov Botanical Institute Russian Academy of Sciences, St-Petersburg and according to Perestenko [27] can be treated as a type species of the genus *Halosaccion*. She also came to a conclusion that in this case *Devaleraea* with the type species *H. ramentaceum* (Linnaeus) J. Agardh can be retained as a separate genus ([27] p.1148).

I doubt whether these arguments: the loss of the type sample of *Ulva glandiformis* and reservation of the sample of the later taxonomic synonym *Dumontia hydrophora* (basionym for *Halosaccion hydrophorum*), are enough to consider earlier species epithet *glandiforme* abolished and whether Perestenko’s decision is in agreement with currently effective International Code of Nomenclature for Algae, Fungi and Plants [41]. In any case her proposal obviously contradicts the law of priority.

It is expedient to retain widely used for more than 100 years name - *H. glandiforme*, and to treat *H. hydrophorum* as its synonym, in spite of the loss of the type specimen of *Ulva glandiformis*. In this case *H. glandiforme* (Fig. 3) should be recognized as the type species of the genus *Halosaccion*.

So I suggest lectotypification of the genus *Halosaccion* as follows:

*Halosaccion* Kiitzing, 1843: 439.
Lectotypus generis: *Halosaccion glandiforme* (Gmelin) Ruprecht, Algae Ochotensis, 1850: 87 (100), tab. 16, a-q.
Basionym: *Ulva glandiformis* Gmelin, Historia fucorum, 1768: 232.
Synonyms: *Dumontia hydrophora* Postels et Ruprecht, 1840: 19, pl. 35, fig. C; *Halosaccion hydrophorum* (Postels et Ruprecht) Kützing, 1843: 439.
Locus typicus: Kamtschatka, Russia.

On the other hand, both *H. glandiforme* and *H. hydrophorum* are now recognized as separate (‘current’) species (see: Algaebase [6]). Obviously additional studies are necessary to solve these problems.

Fig. 3. Habit and anatomy of *Halosaccion glandiforme* (Gmelin) Ruprecht
A – algae growing in the intertidal zone; B – fresh samples before pressing on herbarium paper, scale bar = 2 cm; C, D – cross sections of the middle portions of the frond at different magnification power, C - scale bar = 100 µm; D - scale bar = 10 µm
The number of species representing the genera Halosaccion and Devaleraea is the next problem to be solved concerning the algae of the order Palmariales from the Far Eastern seas of Russia. Up to the present day only 2 species in this area are unconditionally recognized within Halosaccion: H. glandiforme (=H. hydrophorum) and H. minjaii. As it was pointed out earlier two species formerly belonging to the genus (H. microsporum and H. compressum) were transferred to Devaleraea by Klochkova and Selivanova [31]. Another Russian phycologist Perestenko [27] did not support this transfer as well as validity of division of the genus Halosaccion into two genera. The following arguments were presented by this author to confirm her position:

1. Type specimen of H. hydrophorum, Dumontia hydrophora Postels et Ruprecht, illustrated by Turner [42] had a stellate protoplast typical of the genus Halosaccion. At the same time there are anatomical features characteristic of Devaleraea. Quite often protoplasm is non-stellate in the cells lining the cavity, and it can be non-stellate or have short extensions in the medulla of the membranaceous fronds. “Asterism” can be expressed to a different extent due to the different length of protoplasm extensions. On the border between cortex and medulla cells of the inner cortex can fuse and in this case the protoplast acquires laciniate form. It should be noted that Perestenko [27] unlike Guiry [25] distinguished stellate and laciniate protoplasts. She supposed that the extensions of a stellate protoplast were formed as a result of thickening of membrane (cell-wall) or other reasons, except cell fusion, whereas a laciniate protoplast was formed only due to cell fusion. So in her opinion Guiry [25] illustrating H. americanum I.K.Lee depicted laciniate protoplasts (cytoplasts) calling them stellate.

2. Anatomical parameters of algae may depend on age, ecology and other factors. It is well known that algae can become reproductive at different stages of ontogeny and sometimes even at an infant age (neoteny). This can happen at seasonal temperature decrease and in spreading of species northwards or southwards from optimal geographic range (in the boreal zone). So it may cause seasonal or geographical morphological variations in different generations of one and the same species. For example, studying age and seasonal changes in the populations of H. hydrophorum (=H. glandiforme) and H. yendoi Peresetenko [27] supposed that H. yendoi represents a form of H. hydrophorum that appeared as a result of pedomorph development (neoteny) of the alga at the southern extremity of the species area. She was not sure whether H. yendoi was a separate species or just a geographical race of H. hydrophorum, still, in her opinion, transfer of H. yendoi to the genus Devaleraea was formal.

3. Two other species transferred to the genus Devaleraea: H. microsporum and H. compressum [31] were also disputed. H. microsporum was described by Ruprecht on the material collected in the Sea of Okhotsk and Avacha Gulf (Kamchatka). Illustrations of this species are given in the table 15 [39]. Perestenko [27] points out that anatomical structure of this species represents the features of both Halosaccion and Devaleraea. The protoplast in the cells of medulla is non-stellate and without outgrowths, however in the outer layer of the medulla it may become laciniate as a result of cell fusion. “Asterism” appears in the type specimen with thickened membranes of the subcortical cells. H. compressum was described by Ruprecht on algae collected by Rieder in Kamchatka [39]. It differs from H. microsporum by unbranched and, as usual, non-proliferating flat frond with a central cavity or without it. Protoplast in the medullar cells is mostly non-stellate but in the external medulla it may be stellate or laciniate. In the type specimen it has extensions (so is stellate).

4. From all said Perestenko [27] concludes that anatomical features are insufficient for exact delineation of the genera Halosaccion and Devaleraea. If morphological criteria are added, i.e. the genus Devaleraea is delimited by the species with tubular frond whereas the genus Halosaccion – by the species with saccate or vesicular fronds, then D. yendoi with a saccate frond of Halosaccion but anatomy of Devaleraea could not be attributed to any of them. It aggravates the problem of delineation of two genera. That is why all known species from the Far Eastern seas were left by
Perestenko [13,27] within the genus Halosaccion.

I disagree with some of her conclusions and my counter-evidence is based mostly on the data of genetic analyses of the species of palmarialean algae from the Russian Pacific coasts [34] though these studies are unfinished and are treated as only preliminary.

1. In spite of overlapping anatomical features, the members of the genus Halosaccion are well distinguished from the species of Devaleraea, forming separate cluster in the genetic tree. More genetic affinity is noted between the species of Palmaria and Devaleraea [34].

2. In case of H. yendoi Perestenko [27] turned out to be right. This species is closer genetically to the genus Halosaccion than Devaleraea, and forms the common cluster with H. glandiforme (H. hydrophorum in the interpretation of Perestenko). However genetic data testify to the independence of two species H. yendoi and H. glandiforme in spite of their close relations. So there are no sufficient grounds for recognition of H. yendoi as a neotenic form of H. hydrophorum (= H. glandiforme) though they probably have common origin. But our long-term studies showed that these 2 species are separated geographically. Within the Russian Pacific sector H. yendoi is widespread in the Sea of Japan, in the south of the Sea of Okhotsk, on Sakhalin and southern Kurile Islands [31] while H. glandiforme is spread in the northern areas: At the coasts of the Eastern Kamchatka and Commander Islands [21]. According to Perestenko [27] the areas of the two species are overlapping only on Kurile Islands, on the rest of the water area they are allopatric species. So on the basis of genetic data (though preliminary) the status of D. yendoi should be reconsidered and the taxon should be reinstated within the genus Halosaccion, in spite of its anatomy typical of Devaleraea.

3. In contrast to the above said, genetic data on Devaleraea compressa (Fig. 4) obviously support the viewpoint of Klochkova and Selivanova [31]. This species was shown to have close genetic relations with the complex Palmaria-Devaleraea and is considerably different from the members of the genus Halosaccion [34].

**Fig. 4. Habit and anatomy of Devaleraea compressa (Ruprecht) Selivanova et Kloczcova**

A – algae growing in the intertidal zone; B – fresh samples before pressing on herbarium paper, scale bar = 2 cm; C, D – cross sections of the middle portions of the frond at different magnification power, scale bar = 100 µm
Unfortunately we had not yet carried out genetic analyses of *D. microspora*. So until more detailed study is done we leave this species as a taxon with uncertain generic position.

5. CONCLUSIONS

This study is a part of multi-year floristic studies on the Pacific coasts of Russia. It showed that red palmarialean algae are well presented there by the genera *Halosaccion* and *Devaleraea* (Palmariales, Palmariaceae). The taxonomic revision of both genera carried out in this study revealed that the genus *Halosaccion* includes for sure 2 species:

1. *H. glandiforme* Gmelin) Ruprecht, *species lectotypica nova proposita*. Note: *H. hydrophorum* (Postels et Ruprecht) Kützing up to now recognized as the type species of the genus *Halosaccion* is treated herein as a taxonomic synonym of *H. glandiforme*.
2. *H. minjaii* I.K. Lee.

One more known species of the genus - *H. yendoi* I.K. Lee needs further taxonomic consideration. Described originally as *H. yendoi* it was later transferred to *Devaleraea* on the basis of anatomical features. But its preliminary genetic data suggest its belonging to the genus *Halosaccion*.

The genus *Devaleraea* includes 3 species:

1. *D. firma* (Postels et Ruprecht) Selivanova, *comb. nov*.
2. *D. compressa* (Ruprecht) Selivanova et Kloczcova.
3. *D. microspora* (Ruprecht) Selivanova et Kloczcova.

All three species have typical anatomy of the genus *Devaleraea*. The belonging of the first two species to this genus is also supported by preliminary genetic data. Generic position of *D. microspora* (*=H. microsporum*) is not so obvious because of the absence of genetic data.

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COMPETING INTERESTS

Author has declared that no competing interests exist.

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