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Remarks about the Relations of the Floras of the Northern Atlantic, the Polar Sea, and the Northern Pacific.

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It is a fact, known already for a long time, that a great many species of the northern hemisphere have a circumpolar distribution. An interpretation of this circumstance became possible first when geologists had come to know the Glacial Period and its effects. After similar views had been advanced in the works of Forbes, Lyell and others, Darwin in Origin of species (12) shows how the iceage must have driven the old tertiary plants of the districts around the pole, or their descendants, from the territories they once occupied, southwards into the continents of our time, where they found an asylum during the glaciation. At the time when the ice again melted away they began slowly to wander back, interspersed with alpine elements from the districts where they had survived the iceage. At the same time they also left tribes in their temporary homesteads, which contributed to a new colonization of the southern mountains. In such a manner the great number of circumpolar species is accounted for and likewise that contingent of species, which every arctic district has in common with the alpine region of the mountains south of it, but not with other districts.

This theory, further developed by Sir Joseph Hooker in his Outlines of distribution of arctic plants (24) and by later authors, is now universally adopted and doubtless well founded. Still it has as yet mostly been brought to bear only upon the higher plants, or at most upon the landvegetation as a whole. As far as marine algae are concerned only few writers have tried to make use of this point of view for the explication of the present distribution of species and genera. However, some suggestions are made by Kjellman (30) and Reinke (40).

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Hawing been occupied with other similar researches I have come to consider the question, if analogous features could be detected in the distribution of the marine algae. A priori it should seem probable that the same cause — the advancing and afterwards again retreating glaciation — would have the same effect in the case of the marine flora as in that of the land-plants, but it must be remembered, that for instance a land-connection that could make a retreat possible for the vegetation of a landdistrict, could easily cause the destruction of the inhabitants of the sea to the north by barring their way southwards. However it seems that the influence of the iceage has been on the whole the same for the distribution of species as well in the sea as on the land, and I think that in the same measure as our knowledge of the flora of the different districts becomes more complete, similar causes and results shall appear in both cases. The following only presumes to be a preliminary attempt to throw light upon some points of the problem, a complete treatment would require a rather great preparatory work, that I have no occasion to undertake at present, notwithstanding I should be very much inclined to do it later.

It is the swedish arctic work that has enabled us to gain a stricter knowledge of the flora at least of some parts of the Polar Sea, and Kjellman has in his fundamental work (30) treated as well all the rich material brought home by himself and others from different parts of the arctic regions visited by the swedish expeditions as also many other collections, and he has likewise tried to make use of the statements of elder writers. But it is now more than twenty years since his great work was published, other parts of the arctic regions have been carefully explored, in many cases the limits of species have been altered, old statements, which Kjellman thought right to adopt, have become improbable in the light of newer investigations on both sides of the arctic circle. I therefore feel justified in undertaking a revision of the list of species that ought to be counted as arctic.[1]) I give it below (Table I); it is limited to the *Phaeophycaee* and *Rhodophyceae* on account of the highly uncertain synonymic of the others groups, which makes all comparisons unprofitable, a fact already pointed out by several writers, as I have quoted in a paper about a comparative investigation of the relation of the marine flora of the Faeroe Islands to the other northatlantic floras (38). As for the boundaries of the arctic regions, I do not think that any part of the coast of Norway can rightly be reckoned as arctic, as Kjellman also has pointed out (30, p. 4) and furthermore accentuated (30, p. 67) when he says: 'On this account, the Norwegian Polar Sea ought not to be comprehended within

[1]) When I speak of arctic species, I always only will signify such as now live under arctic conditions.

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the region of the arctic Flora, but, the greater part of the elements of its Flora being natives of the northern Atlantic and having been transplanted from there to the north and north-west coast of Norway, it should be referred to the region of the Atlantic Flora'. About the western Murman Sea and White Sea I have been rather doubtful, as its climate and iceconditions can hardly be called true arctic. Still I have counted it as such. With a better right perhaps northeast Iceland could be reckoned as arctic and also the part of the american coast from Hudson Strait down to New Foundland, but still it seems more natural to let them pass as temperate.

Kjellman at first (30, p. 34—40) gives a list of 196 species (104 red and 92 brown algae; the numbers here and in the following always have reference to these groups only), but, by excluding such species as only on the norwegian coast pass the polar circle northward, he reduces the number to 134 (66 brown, 68 red), which enter the Polar Sea proper. Still this list must undergo some further reductions. Kjellman has 4 species as doubtful, but I think more must be excluded, viz., 1:ly such as are doubtless wrongly determined by the collectors or authors or have come into the list by some other mistake, 2:ly species known only from old sources and never found again, 3:ly such species as are not recognized by later writers, who have studied them in connection with a greater material. Even if the specific distinction is upheld, they can hardly be used to prove an arctic endemism dating long time back. The species I think necessary to cancel are:

Lithothamnion polymorphum
Melobesia Lejolisii
Polysiphonia elongata
— *fastigiata*
— *atrorubescens*
Delesseria rostrata
— *corymbosa*
Nitophyllum punctatum
Cruoria pellita
Hydrolapathum sanguineum
Halosaccion saccatum
Callophyllis laciniata
Callymenia septentrionalis
Gigartina mamillosa
Rhodochorton spinulosum
Porphyra abyssicola
Fucus edentatus
— *linearis*
— *distichus*
Haplospora globosa
Phyllaria lorea
Laminaria atrofulva

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Laminaria fissilis
Asperococcus bullosus
Elachista lubrica
Myrionema strangulans
Scytosiphon attenuatus
Phloeospora pumila
Cladostephus spongiosus
Stupocaulon scoparium
Gleothamnion palmelloides.

When these 31 species are excluded the number of arctic species should consequently only be 103 (51 brown and 52 red), but we now know 159 species (84 brown, 75 red) from the arctic regions, as can be seen in the following list (Table I). This is mostly due to Rosenvinge, who in his works about the marine algae of Greenland (42, 43) has treated all the rich collections brought home from that country by the numerous danish investigators of later years. Smaller but still important contributions are made by Wille (53), Asa Gray (23), Farlow (18), Ostenfeld (37) and Jónsson (27, 28). My own small collections from Jones Sound, made during the second Norwegian Polar Expedition I regret not to have had time to determine as yet. Still I hardly think there will be any considerable additions to the flora of the Polar Sea as a whole, only some species not previously found in the american part of it.

As the result of the theoretical studies of Kjellman it appears, that the Polar Sea has its own characteristic flora, notwithstanding the appearence of most of its species also outside the arctic seas, and that the original home of the present arctic marine flora must be sought in the very ice-abounding Polar Sea itself. As far as I can understand, he thinks that the algae, or most of them at least, have, even if their southern limit became very much expanded during the iceage, never entirely quitted the present arctic regions. About the migration of the flora during the iceage he says very little, as also about its relation to the tertiary flora of the same area. I must especially point out this fact as later writers seem to have quite misunderstood him. The most important of these is Reinke (40), who gives a clear specification of the different stages in the evolution of the floras of the Polar Sea and the Atlantic. He speaks of a highly uniform flora that lived during most of the tertiary time in the northern Atlantic, as is unquestionably proved by the small differences that prevail even now on both sides of that ocean. This flora had its northern limit at a landbridge that lay along the line now marked by its remnants the Faeroes and Iceland. North of this land existed another flora, even that probably uniform, in the present arctic sea. But in tertiary time there also ruled a warmer climate, and, when against the end of the tertiary period the bridge was broken, a mixing of the two floras began. How far this interchange of

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species proceeded before the incipient glaciation began to press first the polar flora and gradually also the north one atlantic southwards, can not be determined. All this is not mentioned by Kjellman, but about the next stage there is a marked difference between him and Reinke. The latter thinks it very likely, that the old polar flora was totally exstirpated in its original homestead and only could survive by migrating southwards. Yet Reinke seems not to have observed Kjellman's opinion in this point, as he does not object against it and only refers to Warming's (52) theory about the landflora of Greenland. Afterwards, when the ice melted away, the algae gradually came back, but it now was a flora, mixed of polar and atlantic elements. Kjellman only regards the atlantic species as new immigrants. This difference between the opinions of Kjellman and Reinke seems to have totally escaped Börgesen (8, p. 102), who gives, what he himself calls a very condensed report („— — mit Referat er jo meget kortfattet", 9, p. 248) of their theories. The curious assertion, that the flora of the northern area was arctic already during the existence of the landbridge (8, p. 102) he has retracted afterwards (9, p. 248—49).

In the following list of arctic algae I have included all the species that are found along the coast from the Kola Peninsula to Bering Strait, along the northern coast of America, in the Arctic-american Archipelago, at the coasts of Greenland, Jan Mayen, Spitzbergen, Beeren Island and Novaja Semlja, i. e. in the regions that can be called true arctic (cf. Kjellman, 30, p. 4 and 68). The division of the area is somewhat altered from that of Kjellman, in as much as western Greenland has been separated from the American province because of the very different degree in which these tracts are investigated and the Kara Sea is transferred to the Siberian Polar Sea. In the column of the Spitzbergen-province, that perhaps is less uniform than Kjellman thought, I have marked occurrence in Spitzbergen itself with „s", in east Greenland with „g", and in other parts (Murman Sea) with „e". In the column of the northern Pacific I have made no separate mention of the occurrence in different parts, as nearly all species are found in the best explored, that is to say the northwestern coast of America. As for the temperate european area, entered in the table, northern Norway and the Iceland-Faeroe-district have got separate columns. If I had had newer and better information at my disposal about the northern portion of the american east coast, I should have given it a separate column, now most species indicated are from the United States after Farlow (17) and Collins (11), even if some are admitted on other authority. The

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works consulted are to be found in the following list of literature. The arrangement of the table is after Engler u. Prantl, Die natürlichen Pflanzenfamilien (Kjellman, Schmitz—Hauptfleisch—Falkenberg). I have also used De Toni's Sylloge for the arrangement, partly for the synonymics and limitation, of the species, but only in a few cases concerning the geographical distribution, as he seems not always to have been quite so successful as desirable in excluding old and unreliable sources.

Table I.

	North atlantic coast of America	Northwestern Europe	Faeroes and Iceland	Northern Norway	West coast of Greenland	Spitzbergen province	Siberian Polar Sea	American Polar Sea	Northern Pacific
Pylaiella litoralis (L.) Kjellm.	×	×	×	×	×	gse	×	×	×
varia Kjellm.	×	×	×	×	×	gs	×		×
Ectocarpus pycnocarpus Rosenv.					×	g			
penicillatus (Ag.) Kjellm.	×	×	×	×	×				
siliculosus (Dillw.) Lyngb.	×	×	×	×	×	g			
confervoides (Roth) Le Jol.	×	×	×	×	×	gse			×
ovatus Kjellm.	×	×		×	×	gs			
Streblonema Pringsheimi Reinke		×			×				
tomentosoides (Farl.) De Toni	×	×	×		×				
Stilophorae Crouan		×	×		×				
aecidioides Rosenv.	×	×	×	×	×	g			
helophorum (Rosenv.) Batt.		×				g			
Microsyphar Polysiphoniae Kuck.		×	×		×				
Phycocelis globosa (Reinke) De Toni	×	×	×		×	g			
Dermatocelis Laminariae Rosenv.			×		×				
Symphyocarpus strangulans Rosenv.		×			×	g			
Phaeostroma pustulosum Kuck.		×	×		×				
Isthmoplea sphaerophora (Harv.) Kjellm.	×	×	×	×	×	ge			
Sphacelaria olivacea (Engl. Bot.) Ag.		×	×	?	×				
cirrosa (Roth) Ag.	×	×	×	×				×	×
racemosa Grev.		×		×	×	gse	×	×	×
radicans Harv.		×	×		×				
brittannica Sauv.		×	×		×	g			

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	North atlantic coast of America	Northwestern Europe	Faeroes and Iceland	Northern Norway	West coast of Greenland	Spitzbergen province	Siberian Polar Sea	American Polar Sea	Northern Pacific
Chaetopteris plumosa (Lyngb.) Kütz.	×	×	×	×	×	gse	×	×	×
Punctaria plantaginea (Roth) Grev.	×	×	×	×	×	gse		×	×
Lithosiphon Laminariae (Lyngb.) Harv.		×	×	×		e ?			
Coilodesme bulligera Strömf.			×	×	×	g			×
Omphalophyllum ulvaceum Rosenv.	×		×		×	g			
Phaeosaccion Collinsii Farl.	×	×		×	×				
Physematoplea attenuata Kjellm.	×	×		×	×	g			
Pogotrichum filiforme Reinke		×	×		×				
Scytosiphon lomentarius (Lyngb.) J. Ag.	×	×	×	×	×	ge		×	×
Phyllitis fascia (Muell.) Kütz.	×	×	×	×	×	ge		×	×
zosterifolia Reinke	×	×	×		×				
Kjellmania subcontinua Rosenv.					×				
Coelocladia arctica Rosenv.					×				
Phloeospora subarticulata Aresch.		×		×		se			×
tortilis (Rupr.) Aresch.		×	×	×	×	gse	×	×	×
Desmarestia viridis (Müll.) Lamour.	×	×	×	×	×	gse		×	×
aculeata (L.) Lamour.	×	×	×	×	×	gse	×	×	×
Dictyosiphon corymbosus Kjellm.			×	×	×	e			
hispidus Kjellm.	×	×			×	gse			
hippuroides (Lyngb.) Kütz.	×	×	×	×	×	se			×
foeniculaceus (Huds.) Grev.	×	×	×	×	×	gse		×	×
Chordaria Aresch.	×	×	×	×	×				×
Leptonema fasciculatum Reinke	×	×	×	×	×	g			
Elachista fucicola (Vell.) Aresch.	×	×	×	×	×	gse	×	×	×
Eudesme virescens (Carm.) J. Ag.	×	×	×	×	×	e			×
Myriocladia callitricha Rosenv.					×				
Mesogloia vermiculata (Engl. Bot.) Le Jol.	×	×		×		e			
Chordaria flagelliformis (Müll.) Ag.	×	×	×	×	×	gse	×	×	×

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	North atlantic coast of America	Northwestern Europe	Faeroes and Iceland	Northern Norway	West coast of Greenland	Spitzbergen province	Siberian Polar Sea	American Polar Sea	Northern Pacific
Ralfsia verrucosa (Aresch.) J. Ag.	×	×	×	×	×				×
deusta (Ag.) J. Ag.	×	×	×	×	×	ge		×	×
clavata (Carm.) Farl.	×	×	×		×	g			×
ovata Rosenv.			×		×				
Chorda Filum (L.) Lamour.	×	×	×	×	×	gse		×	×
tomentosa Lyngb.	×	×	×	×	×				
Phyllaria dermatodea (De la Pyl.) Le Jol.	×		×	×	×	gse			×
Alaria esculenta (Lyngb.) Grev.	×	×	×	×		s ?			×
Pylaii (De la Pyl.) J. Ag.	×		×	×	×	g			×
membranacea J. Ag.				×	×	gse			
grandifolia J. Ag.				?		gse			
dolichorachis Kjellm.							×	?	×
flagellaris Strömf.	×		×			g			
oblonga Kjellm.							×		
elliptica Kjellm.							×		
Agarum Turneri Post. et Rupr.	×				×	g		×	×
Laminaria nigripes J. Ag.			×	×	×	gse	×		×
digitata (L.) Lamour.	×	×	×	×	×	gse	×		?
longicruris De la Pyl.[1])	×		×		×	g		×	×?
cuneifolia J. Ag.					×	e?	×	×	×
groenlandica Rosenv.					×	g			
solidungula J. Ag.					×	gse	×	×	?
saccharina (L.) Lamour.	×	×	×	×		ge			×
Agardhii Kjellm.						(g)se	?		
Lithoderma fatiscens Aresch.		×	×	×	×	gse	×		×
Sorapion Kjellmani (Wille) Rosenv.			×		×	ge			
Scaphospora arctica Kjellm.	×?	×		×		gse			
Fucus inflatus Vahl.	×		×	×	×	gse	×	×	×
ceranoides L.	×	×		×		s			
vesiculosus L.	×	×	×	×	×	ge	×		×
serratus L.	×	×	(×)	×		se			

[1]) inclusive *L. faeroensis* Börges.

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	North atlantic coast of America	Northwestern Europe	Faeroes and Iceland	Northern Norway	West coast of Greenland	Spitzbergen province	Siberian Polar Sea	American Polar Sea	Northern Pacific
Pelvetia canaliculata (L.) Dcsne et Thur.	?	×	×	×		e			
Ascophyllum nodosum (L.) Le Jol.	×	×	×	×	×	g(s)e		×	
Bangia fuscopurpurea (Dillw.) Lyngb.	×	×	×	×	×				×
Porphyra umbilicalis (L.) Kütz.	×	×	×	×	×	e			×
miniata (Ag.) J. Ag.	×	×	×	×	×	gse		×	×
Conchocelis rosea Batt.		×	×	×	×	g			
Chantransia efflorescens (J. Ag.) Kjellm.		×	×	×		gse	×		
secundata (Lyngb.) Thur.	×	×	×	×	×	e			×
virgatula (Harv.) Thur.	×	×	×	×	×				×
microscopica (Kütz.) Fosl.		×		×	×	g			
Harveyella mirabilis (Reinsch) Rke et Schmitz	×	×	×	×		g			
Phyllophora Brodiaei (Turn.) J. Ag.		×	×	×	×	se	×		×
interrupta (Grev.) J. Ag.				×	×	gse	×	×	
Actinococcus subcutaneus (Lyngb.) Rosenv.	×	×	×		×	g			
Ceratocolae Hartzii Rosenv.			×		×	g			
Callymenia Schmitzii Hauptfl.	×				×				
Ahnfeltia plicata (Huds.) Fr.	×	×	×	×		se	×	×	×
Cystoclonium purpurascens (Huds.) Kütz.	×	×	×	×		e			
Turnerella Pennyi (Huds.) Schmitz		×	×	×	×	gse		×	
rosacea (J. Ag.) Schmitz						s			
Euthora cristata (L.) J. Ag.	×	×	×	×	×	gse	×	×	×
Rhodophyllis dichotoma (Lepech.) Gobi	×		×	×	×	gse		×	×
Rhodymenia pertusa (Post. et Rupr.) J. Ag.						s			×
palmata (L.) Grev.	×	×	×	×	×	ge	?	×	×
Halosaccion ramentaceum (L.) J. Ag.	×		×	×	×	gse	×	×	×

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	North atlantic coast of America	Northwestern Europe	Faeroes and Iceland	Northern Norway	West coast of Greenland	Spitzbergen province	Siberian Polar Sea	American Polar Sea	Northern Pacific
Delesseria sinuosa (Good. et Woodw.) Lamour.	×	×	×	×	×	gse	×	×	×
Baerii (Post. et Rupr.) Rupr.	×			×	×	gse		×	×
spinulosa (Rupr.) J. Ag.	×				×	g ?			×
Polysiphonia urceolata (Lightf.) Grev.	×	×	×	×	×	e			×
Schübeleri Fosl.				×	×				
arctica J. Ag.			×	×	×	gse	×	×	×
nigrescens (Dillw.) Grev.	×	×	×	×		e			×
Rhodomela lycopodioides (L.) Ag.		×	×	×	×	gse	×	×	×
Larix (Turn.) Ag.								×	×
Odonthalia dentata (L.) Lyngb.	×	×	×	×		s	×	×	×
Ptilota plumosa (L.) Ag.		×	×	×		se			×
pectinata (Gunn.) Fosl.	×		×	×	×	gse	×	×	×
asplenioides (Turn.) Ag.							×		×
Antithamnion boreale (Gobi) Kjellm.	×	×	×	×	×	gse	×	×	×
floccosum (Müll.) Kleen	×	×	×	×	×				×
americanum (Harv.) Farl.	×							×	×
Pylaisii (Mont.) Kjellm.	×	×		×	×			×	×
Ceramium arcticum J. Ag.				×		s			
rubrum (Huds.) Ag.	×	×	×	×	×	se			×
Rhodochorton Rothii (Turt.) Näg.	×	×	×	×	×	gse		×	×
intermedium Kjellm.						s			
sparsum (Carm.) Kjellm.	×	×		×	?			×	
spetsbergense Kjellm.						s			
penicilliforme (Kjellm.) Rosenv.			×	×	×	gse	×		
membranaceum Magn.	×	×	×	×	×	g			
Dumontia filiformis (Fl. Dan.) Grev.		×	×	×		e			×
Dilsea integra (Kjellm.) Rosenv.						gse	×	×	×
edulis Stackh.		×	×	×		se			
Furcellaria fastigiata (L.) Lamour.		×	×	×		se	×		
Polyides rotundus (Gmel.) Grev.	×	×	×	×		e			

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	North atlantic coast of America	Northwestern Europe	Faeroes and Iceland	Northern Norway	West coast of Greenland	Spitzbergen province	Siberian Polar Sea	American Polar Sea	Northern Pacific
Petrocelis polygyna (Kjellm.) Schmitz						g	×		
Cruoria arctica Schmitz			×		×	g			
Cruoriella Dubyi (Crouan) Schmitz	×	×	×	×			×		
Peysonellia Rosenvingii Schmitz	×			×	×	g			
Rhododermis elegans Crouan		×	×		×	g			
Clathromorphum compactum (Kjellm.) Fosl.	×		×	×	×	se			×
circumscriptum (Strömf.) Fosl.	×		×	×	×	g			×
Lithothamnion arcticum (Kjellm.) Fosl.							×		
Lenormandi (Aresch.) Fosl.		×	×	×		e			
laeve (Strömf.) Fosl.	×	×	×	×	×	g			
investiens Fosl.				×		g			
thophiforme Unger		×	×	×	×				
foecundum Kjellm.	×		×	×	×		×		
varians Fosl.				×		g			
colliculosum Fosl.	×	×	×	×	×	s			
flabellatum Rosenv.	×	×		×	×	g			
botrytoides Fosl.					×				
fruticulosum (Kütz.) Fosl.	×	×	×	×	×				
glaciale Kjellm.		×	×	×	×	gse		?	×
flavescens Kjellm.			×	×		se			
Corallina officinalis L.	×	×	×	×		e			×
Hildenbrandtia rosea Kütz.	×	×	×	×	×	gse			×

The number of species here counted as arctic, *Phaeophyceae* 84, *Rhodophyceae* 75, together 159, gives a relation between the numbers of the groups, that is more in accordance with the fact that the former increase, the latter diminish northwards. The above numbers give 53 brown and 47 red algae in a hundred, while the numbers of Kjellman give resp. 49 and 51 for the arctic regions. In Northern Norway the percentage is 41 to 59, in Iceland 47 to 53, in the Faeroes 45 to 55 and in Scotland 42 to 58 (Simmons, 38, p. 227 and 228). Farther southwards the relative number of *Phaeophyceae* becomes still smaller.

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As it is rather troublesome to see of the table I how many species are found in each district, the following summary must be made:

Table II.

Districts	Phaeo-phyceae	Rhodo-phyceae	Total
Asiatic Polar Sea	18 (19)	19 (20)	37 (39)
American — —	21 (22)	22 (23)	43 (45)
West coast of Greenland	67	46 (47)	113 (114)
Spitzbergen province (together)	58 (61)	59	117 (120)
Thereof only in East Greenland	17	16	33
— — — Spitzbergen	1 (2)	7	8 (9)
— — — the Murman and White Sea	5 (6)	9	14 (15)
— — — E. Greenl. and Spitzb.	2	0	2
— — — — Murm. a. Wh. S.	7	1	8
— — — Spitzberg. — —	3	8	11
— East Greenland (total)	49 (50)	35	84 (85)
— Spitzbergen —	29 (31)	33	62 (64)
— Murman a. White Sea (total)	38 (40)	36	74 (76)

The two sets of numbers are due to the entering in table I of some species, whiche have only with doubt been accepted as citizens of the arctic regions or some part of them. They are marked in the table by a „?“. I will have to come back to some of them at least later.

Among the districts that of Spitzbergen shows the greatest number of species. This must be due in part to favourable conditions of life, which have made it possible for a number of atlantic algae to enter the eastern portion of it. The warm waters of the Gulfstream must be the principal factor in so bringing up the number for the Murman and White Sea and also for Spitzbergen. On the other hand the careful exploration effected in the latter country by the swedish expeditions and in the first named part by russian, swedish and other investigators plays a great part. As for east Greenland it must principally be the diligent work of danish and other explorers that has brought up the number so far as 84. Next in number comes the coast of Danish Greenland, which although the smallest of the four districts has still not less than 113 species. Even if favourable conditions take a part in this result it is mostly due to the assiduous work of the danish investigators

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and collectors, who have brought the knowledge about this part of the arctic regions far beyond that we have of most others. The scantiness of the list from the Siberian Polar Sea doubtless is caused in a great measure by the nature of the coast, that is unfavourable for the growth of algae (cf. Kjellman, 30, p. 7, 20 etc.), but then this long coast is almost only explored during one sole voyage, the Vega-expedition. On the american side I think only exploration is lacking; many parts of the coast of the continent as well as of the islands are favourable enough, but here a great work is still left undone.

However, for the investigation here contemplated, there is another point of view of still greater importance than the numbers of species in the different districts. That is the distribution of the species in those districts, which is summarized in the following table.

Table III.

Distribution of species	Phaeophyceae	Rhodophyceae	Total
1. In all arctic districts	9 (10)	8 (9)	17 (19)
2. W. Greenl., Spitzb. prov., Asiatic Pol. Sea	5	2	7
3. — — — Amer. — —	10	5 (6)	15 (16)
4. — Asiat. Pol. Sea — — —	0	0	0
5. Spitzb. prov. — — — — — —	0	3	3
6. W. Greenland. Spitzbergen prov.	23	19	42
7. — Amer. Polar Sea	0	1 (2)	1 (2)
8. — Asiat. — —	0	1	1
9. Spitzbergen prov. — — —	0 (1)	3	3 (4)
10. — — Amer. — —	0	0	0
11. Asiatic Polar Sea — — —	0 (1)	0	0 (1)
12. W. Greenland	19	8	27
13. Spitzbergen province	11 (12)	17	28 (29)
14. Asiatic Polar Sea	2	2	4
15. American — —	1	3	4
	84	75	159

I have here also included such combinations of distribution, as, although theoretically possible, are not found in reality. It is however of some importance to observe as well the lacking of these as also the number of species for each existing combination.

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The species common to all the four arctic districts are very few, only 17 (19), giving 12 per ct. of the whole number, which seems to speak against the looking upon the present flora of the Polar Sea as old and directly descending from the former flora of the regions it now occupies. The 19 species under 1. (table III) are:

**Pylaiella litoralis*
**Sphacelaria racemosa*
**Chaetopteris plumosa*
**Phloeosphora tortilis*
**Desmarestia aculeata*
**Elachista fucicola*
**Chordaria flagelliformis*
Laminaria cuneifolia
" solidungula
**Fucus inflatus*
Phyllophora interrupta
**Euthora cristata*
**Rhodymenia palmata*
**Halosaccion ramentaceum*
**Delesseria sinuosa*
**Polysiphonia arctica*
**Rhodomela lycopodioides*
**Ptilota pectinata*
**Antithamnion boreale.*

Of these the species marked with * are found in the northern part of the Atlantic as well as of the Pacific, and some of them are still wider distributed. Only *Laminaria cuneifolia* and *L. solidungula* do not go down into the Atlantic, but the former at least seems to have been found in the Pacific. *Phyllophora interrupta* is a decidedly arctic form, notwithstanding its being found also on atlantic coasts, where it is else substituted by *Ph. Brodiaei.* However the above list will, as I have already alluded to, probably get considerable additions, when we get a bet-knowledge of the american and asiatic Polar Sea. Yet, even if all species not found only in one of the least explored districts, a number of about 20, were distributed, all over the arctic regions, we would still get only about 25 per ct. of the whole flora. Indeed, the groups, 6, 12, 13, containing the numbers of species from the best known districts show a total of 98 species, but it is very improbable that the majority of these will ever be found in the other regions. If some will, it surely must be some of the species that are common to the whole area north of the Atlantic, but it must be remembered, that it is not only through the better exploration, that western Greenland and at least some parts of the Spitzbergen province show so much greater figures than the other districts, but that also the natural conditions of those coasts play their part, and that the neighbourhood of atlantic, richly stocked districts has facilitated immigration of southern forms. Thus I think it will always be necessary to uphold the assertion, that the present arctic marine flora is no unity and that its origin can hardly be in the regions it now occupies. I will give further reasons for this opinion later, but now the flora of the Spitzbergen district must be studied some what closer. The 120 species of that area are distributed as follows:

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Table IV.

Distribution of species	Phaeo-phyceae	Rhodo-phyceae	Total
East coast of Greenland	17	16	33
Spitzbergen	2	7	9
Murman and White Sea	6	9	15
East Greenland and Spitzbergen	2	0	2
— — Murman and White Sea	7	1	8
Spitzbergen — — — —	3	8	11
In the whole province	24	18	42

Among the 42 species that are indicated as spread over the whole province we find again the widely distributed species of 1. in table III with two exceptions, *Laminaria cuneifolia*, only found (?) in the White Sea, and *Rhodymenia palmata* not known from Spitzbergen. Most of the others are widely spread. Of special interest however are *Alaria grandifolia* and *Laminaria Agardhii*, which perhaps are confined to this area and *Scaphospora arctica* that only here enters the arctic regions.

Of the species which enter the arctic Sea along the north coast of Europe 5, viz., *Dictyosiphon corymbosus*, *Eudesme virescens, Porphyra umbilicalis*, *Chantransia secundata*, and *Polysiphonia urceolata* are also found in western Greenland. It certainly is due to the favourable conditions of immigration, that these mostly atlantic algae here have reached so far north, as is also the case with: *Mesogloia vermiculata, Pelvetia canaliculata, Cystoclonium purpurascens, Polysiphonia nigrescens, Dumontia filiformis, Polyides rotundus, Lithothamnion Lenormandi, Corallina officinalis*, all species that nowhere else belong to the arctic regions, likewise as with *Lithosiphon Laminariae*, if that alga is really found on the coast of Novaja Semlja. On the other side *Laminaria cuneifolia*, an arctic-pacific species, here should have its limit, if the plant found in the White Sea is rightly determined by Gobi.

Among the 9 species indicated only for Spitzbergen 3 are endemic, viz., *Turnerella rosacea*, *Rhodochorton intermedium, Rh. spetsbergense. Ceramium arcticum,* lately described by Agardh (6), is also known from northern Norway. *Alaria esculenta* is dubious and perhaps also *Rhodymenia pertusa*, which is a pacific species nowhere found in arctic waters. Rosenvinge (42, p. 811) has shown, that Greenland-specimens conveyed by Kjellman to this species are *Rh. palmata,* and the same perhaps is the case with the Spitzbergen specimens. It also would be astounding if the latter, common species there should be substituted by such a traveller from afar. *Fucus ceranoides* only here enters

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the arctic region, *Odonthalia dentata* and *Lithothamnion colliculosum* are found also in other arctic provinces.

Of the 11 species found as well in Spitzbergen as in the Murman Sea but not on the east coast of Greenland 7 are also absent from the western coast of that country. The 4 others, *Dictyosiphon hippuroides, Phyllophora Brodiaei, Ceramium rubrum, Clathromorphum compactum,* in all probability will be found there yet. The two species, *Pylaiella varia* and *Ectocarpus ovatus*, that are only found in east Greenland and Spitzbergen but not in the southeastern part of the province, probably also will be detected there. The 8 species from east Greenland and the southeastern district are not very arctic. With one exception, *Laminaria saccharina* (var.) they are found also in western Greenland. 5 of them, *Scytosiphon lomentarius, Phyllitis fascia, Ralfsia deusta, Fucus vesiculosus, Rhodymenia palmata* are found only in the southern part of the east Greenland-coast, two others, *Isthmoplea sphaerophora* and *Sorapion Kjellmani* are not found there yet. Lastly there are 33 species only found in east Greenland; most of these are also known from the western coast of that country.

The 120 species of the Spitzbergen-province are distributed as follows: east Greenland has 85, Spitzbergen 64, the Murman and White Sea 76. If a comparison of the East-Greenland-flora with those of the others parts of the province is made after the method I have previously (38, p. 219) proposed, the result will be the following:

Table V.

	East Greenland	Common	Spitzbergen	Total	East Greenland	Common	Spitzbergen Murman and White Sea	Total
Number of species	41	44	20	105	33	52	35	120
Per ct of total number	39	42	19		28	43	29	
Number of species	1	12	57	70	1	12	89	102
Per ct of total number	2	17	81		1	12	87	

The series of figures below I have taken from Kjellman (30), to show how far our knowledge of the East-Greenland-flora has advanced since his work was written. It is easily understood, in looking at these figures, why Kjellman could say: „The scanty notices, that we possess on the marine vegetation on

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the east coast of Greenland, point to its being like that of Spitzbergen". But, when more comprehensive collections were brought home from east Greenland (by Hartz from Scoresby Sound and by Bay from Angmagsalik) Rosenvinge who studied them came to another result. He has given especial attention to the question about the relation of the East-Greenland-flora to that of Spitzbergen in consequence of the idea of Kjellman, quoted above, and he comes to the conclusion, that the flora is nearer related to that of the western coast of Greenland than to that of Spitzbergen (44, p. 154—57, 176—79). „All in all the marine flora of east Greenland seems to show a considerable correspondence with that of western Greenland" he says (p. 178). Notwithstanding this, the latest author who has treated the flora of east Greenland, Jónsson (28), says: „Thus the latest collections from the eastern coast furthermore confirm Rosenvinges statement as to the difference between the marine flora of East and West Greenland" (p. 2). Indeed Rosenvinge speaks of differences between the east and west coast (as also between different parts of the latter) but, as the sentence quoted above stands together with a reflexion about the resemblance of the marine flora of east Greenland to that of Spitzbergen, one must get the impression, that Rosenvinge thinks the East-Greenland-flora nearest related to that of Spitzbergen. Also (p. 3) Rosenvinge is quoted instead of Kjellman (cf. above), Rosenvinge in the passage referred to (44, p. 154) speaks about the entire Greenland flora.

The easiest method to make a comparison between the floras on both coasts of Greenland will be the same as used above, and by such a proceeding also the relative resemblance with the Spitzbergen-flora will appear:

	East Greenl.	Common	West. Gr.	Total
Number of species	12	73	41	126
Per ct of total number	9	58	33	

The 12 East-Greenland-species, not found on the western coast are:

Streblonema helophorum
Alaria flagellaris
„ *grandifolia*
Laminaria saccharina
„ *Agardhii*
Scaphospora arctica
Chantransia efflorescens
Harveyella mirabilis
Dilsea integra
Petrocelis polygyna
Lithothamnion investiens
„ *varians.*

Some of these are small algae or such that may on other accounts easily escape the collector, and which can perhaps still be found on the west coast, but for the great *Alaria*- and *Laminaria*-species at least we must seek another way to account for their being found only on the east coast. At all events it is evident, that the flora of east Greenland is not by far so nearly

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related to that of Spitzbergen as Jónsson thinks, on the contrary we must agree with Rosenvinge that it is very closely allied to that of the western coast.

But here a new question arises: is the flora of east Greenland uniform all along the coast? To get an answer to this question I have noted how far southwards on the coast those species grow, which are not found on the west side. None of them reaches to the south of 65°, for several the southern limit, as far as known at present, lies to the north of the 70th parallel. On the other hand several more or less common West-Greenland-algae do not from Cape Farewell reach further up on the east coast than to the 66th parallel or there about. I have here only taken into consideration such species as are, within the arctic regions, only found in Greenland, as these seem most fit to throw light upon the problem about the uniformity of the east-coast-flora. At least 10 such species are only found in southern East Greenland, viz.:

Ectocarpus pycnocarpus
— *siliculosus*
Coilodesme bulligera
Physematoplea attenuata
Alaria Pylaii
Agarum Turneri
Laminaris longicruris
— *groenlandica*
Delesseria spinulosa
Rhodochorton membranaceum.[1])

If a comparison is made by means of the previous method, we find:

	Southern East-Greenl.	Common	Northern East-Greenl.	Total
Number of species	10	63	12	85
Per ct. of total number	12	74	14	

Through taking into consideration also the distribution within the Greenland-area of more widely spread algae, the percentage of southern species would be still more augmented at the cost of the species common to the whole coast, but I think the difference between the northern and southern flora will appear as clearly, if only the distribution of the *Laminariaceae* is considered. The distinctly american species *Laminaria longicruris*[2]) and *Agarum Turneri* do not reach above 66° and about the same latitude also the endemic *Lam. groenlandica*, and *Alaria Pylaii*, arctic only in Greenland, have their limit. On the other hand *Laminaria saccharina* (var.) and *L. Agardhii* (dubious) have their southern limit, the former at 69°, the latter at 74° (?). Unquestionably this remarkable mode of distribution must somehow stand in connection with the former landbridge between Iceland and Greenland, that has reached the Greenland coast between the 65th and 69th parallel, as is still pointed out by the submarine ridge in the Denmark Strait. That two species, *Alaria*

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[1]) Also found at Jan Mayen.

[2]) As it is only found at one point and not (yet?) farther south, too great importance must not be attached to it.

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grandifolia and *A. flagellaris*, go so far south as about 65° does not contend against this view, as they can perhaps have wandered other ways or more swiftly. At all events this distribution can hardly date back to preglacial time but must have been effected after the maximal glaciation. If the land-bridge had been broken for ever already in tertiary time, even with the slow progress that these algae probably are capable of, there would have been time enough for them to blend throughout the whole coast line. Also it seems impossible, with the help of preglacial factors, to explain how *Laminaria saccharina*, a decidedly temperate alga, has come to grow far up on the East Greenland coast but not in the southern parts of it, when at the same time extremely arctic species as *Laminaria longicruris* and *Agarum Turneri* are found to the south of its area.

There is another feature of the distribution of arctic algae, left almost quite out of consideration as yet, that must however be examined, namely the distribution of the arctic species outside the Polar Sea. The following table (VI) gives a summary of the most important points thereof.

Table VI.

Distribution of species	Phaeophyceae	Rhodophyceae	Total Number	Total Per ct.
Atlantic-arctic-pacific	34	30	64	40
Atlantic-arctic	39	35	74	47
Pacific-arctic	2	4	6	4
Arctic, endemic	9	6	15	9

It may perhaps be needed to remark, that I always use the words atlantic, etc. only to signify species growing in the Atlantic, resp. Polar Sea, etc., not as terms with any other meaning. The same species therefore very well can be called as well arctic as atlantic, resp. pacific. The case is, that I can not see there has been anything won with the division of the northatlantic and arctic floras, introduced by Reinke (40, p. 94—95). The author says himself, that he only for shortness sake speaks of an arctic, an hemiarctic, a subarctic, and an atlantic series of algae, but, since almost every author, working with an atlantic or arctic marine flora has felt obliged to use those terms, they have only led to confusion. The name hemi-arctic is never used, as far as I know, but Kuckuck (34, p. 10) has created in its stead a northatlantic series. As the

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referring of a species to one of the groups or another is solely based upon how far southwards or northwards the writer thinks it to be found, there must be an everlasting interchange of species between the groups, especially the northatlantic and the subarctic series, as is easily seen by comparing the lists in the above mentioned treatises and those of Rosenvinge (44) and Börgesen (8). Comparisons of percentage of species, referred to those series, such as are to be found in the papers quoted. can not be of the slightest interest, as it is selfevident that, if species that have their distribution chiefly far northwards are called arctic, those with a somewhat more southerly area, subarctic, a. s. o., a coastline further to the north will always show a greater percentage of „arctic" species, than one farther southwards, and vice versa — if not some special circumstance plays in. Börgesen (8) for instance devotes several pages to such examinations and comparisons, as the „result" of which it appears, that in the flora of the Faeroes (lying in the northern Atlantic) there is a very great percentage of „northatlantic species".

The table (VI) shows, that most of the arctic algae are also found in some parts of the Atlantic (87 per ct.). Of these again 64 (40 per ct. of total number) are also spread to the northern part of the Pacific. Among these we will find most of the species, which have a wide distribution in the arctic seas and also a few species with a very wide range, such as are found again in the southern temperate region or even in the antarctic, and also such as are spread even to the warmer parts of the oceans. The species common to the arctic flora and that of the Pacific are much fewer than those, which the former has in common with the atlantic one, 70 species (44 per ct.). Of these 6 only are not found even in the northern Atlantic, namely *Alaria dolichorachis*, **Laminaria cuneifolia*. **Rhodymenia pertusa, Rhodomela larix, Ptilota asplenioides*, **Dilsea integra*. Hereto comes further *Laminaria solidungula* if that species really grows in the Pacific and not only young specimens of *Cymathere triplicata* are taken for it as Setchell (49, p. 260) thinks. Of the six species three, marked with *are found also in parts of the Polar Sea lying north of the Atlantic. Kjellman (30, p. 53) sees in the existence of such a distribution a proof for the assumption of a centre of dispersion in the Polar Sea itself. I will not deny, that so may have been, only I think the continuity of the evolution within the Polar Sea very doubtful. There also are atlantic species that reach far into the arctic area, even north of Asia and America. Such are: *Chantransia efflorescens, Turnerella Pennyi. Rhodochorton penicilliforme, Lithothamnion foecundum:* more dubious are *Laminaria digitata, L. longicruris, Rhodochorton sparsum. Cruoriella Dubyii.* I do not however think there is too much stress to be laid on this fact. The three pacific-arctic species, which only go a short way into the arctic sea from Bering Strait, viz. *Alaria dolichorachis. Rhodomela larix. Ptilota asple-*

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nioides, doubtless are rather late immigrants from the Pacific, where they have their principal area of distribution.

A group of species that must be discussed in detail, is that of the endemic forms in the Polar Sea. Kjellman has 27 such species (30, p. 74—75), but about them it has come true to a greater degree than he has thought probable himself, what he says (30, p. 49): — — „it is thus certainly possible that some one or other of them, attention being now drawn to it, may prove to go southward — —". When such are withdrawn, together with the forms now not upheld as species, we should get only 8 or 9 arctic-endemic species. Still some new have been found, and consequently the list of such algae now contains the following 15:

Ectocarpus pycnocarpus
Kjellmania subcontinua
Coelocladia arctica
Myriocladia callitricha
Alaria grandifolia (?)
— *oblonga*
— *elliptica*
Laminaria groenlandica
— *Agardhii.*
Callymenia Schmitzii
Turnerella rosacea
Rhodochorton intermedium
— *spetsbergense*
Petrocelis polygyna
Lithothamnion arcticum.

If those species (9 per ct. of the whole arctic flora) should without restriction be standing for the future as endemic in the arctic regions, this doubtless would give a momentous support to the opinion of Kjellman, that the arctic flora is old in its present area, but I think that, by submitting them to a thorough scrutiny, we will get a somewhat different view of them. Most of the species are hitherto only known from the original locality or a rather small area and will probably gradually be found to have a much wider dispersion, as has already been the case with several of Kjellman's and Rosenvinge's new species, or to be nearly allied to species of southern waters. *Coelocladia arctica* is the representative of a monotypic genus, the only one that is endemic in the arctic regions. Even if it is hardly restricted to the west coast of Greenland, there is nothing to be said about it at present. *Kjellmania subcontinua* and *Myriocladia callitricha* have their nearest relatives in the northern Atlantic. Of the three *Alarias* one, *A. grandifolia*, is found in the neighbourhood of the northatlantic area of dispersion of the genus and probably also grows within that district, the two others, seen only at one point near Bering Strait, probably will be found also in the northern Pacific, where the genus shows its greatest development and is represented by a considerable number of species, or at least these two may be regarded as immigrants from the Pacific, which have become differentiated after their transplantation to the Polar Sea. The two *Laminarias* seem to be bound to the arctic sea nearest to the Atlantic, where they have their relations. On the other

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hand, if the extremely arctic, wide spread *L. solidungula* does not grow in the Pacific, as seems most probable after the before mentioned statement of Setchell, we should there have a true arctic species, that would give a certain support to the theory of Kjellman, as it is among the algae who can perhaps with a better right than most others be set up as survivors of the glacial period in the Polar Sea itself.

All the *6 Rhodophyceae* must be said to be little known and pertaining to genera, as yet too insufficiently studied, to be apt to be used to prove anything about the history of the arctic flora. Moreover one, *Rhodochorton intermedium*, is said to be identic with *Rh. Rothii* (Jónsson, 28, p. 2). I think already what is hitherto said, will be almost enough to prove that we can not have any right to conclude from the endemism in the Polar Sea, that there has been a long-continued evolution of species, having their original homestead in those ice-encumbered waters, and never having quitted them even during the most unfavorable times of the iceage.

The great number of species (64, 40 per ct.) common to the north Atlantic, the Polar Sea and the northern Pacific could certainly also seem to support the above mentioned view of Kjellman, but, if this circumstance is examined together with another, I think it will sooner prove quite a different course of development. I mean the fact that a number of species, not growing in the Polar Sea, are notwithstanding found in the northern parts as well of the Atlantic as of the Pacific. J. G. Agardh has been the first algologist to draw the attention to the question about the appearance in widely different parts of the world of the same species. When he first commented upon it in 1862 (2) he was most inclined to think, that botanists, who profess to have found common european species in far away seas, have been missled by some outward likeness; corresponding but not identic species have been found. Where still the same species occur in different regions, the distribution is due to the currents; thus he speaks of an american-european floral province within the range of the colder part of the Gulfstream, and of a circum-american province that is characterized by *Agarum* and by other *Laminaria*-species than the former. Even the latter should have got its limits through currents. This view is again discussed and upheld in another paper (4, p. 8—9 and 11) 1872, but in the mean time Agardh has himself identified an alga from Spitzbergen with a species described from California (*Fucus Harveyanus*) in a treatise published 1868 (3, p. 10) and here he also speaks of the joint appearance of many species of algae in the Atlantic and Pacific. He thinks that this is due to a current that transports algae from New Foundland and Spitzbergen to northwestern America and Kamshatka. But as Kjellman (30, p. 55) points out, such a current is never ob-

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served, on the contrary he speaks of quite a net of currents in the Polar Sea, where an alga must move from one stream to another if it should make such a voyage. Kjellman rightly observes that such a complicated drift can hardly be thought possible, and he therefore seeks the solution of the problem in the former disposition of land and water and in altered hydrographic conditions. As to the supposition of Agardh, that it will probably appear by more scrupulous examination, that the number of species widely spread or at least common to the Atlantic and Pacific is much smaller than hitherto presumed, Kjellman is most disposed to assent to his opinion. However in the latest careful work about the flora of the northwestern coast of America (49), the only part of the north-pacific coastlines that can be said to be comparatively well known, Setchell and Gardner have, even if some old statements about the occurrence of atlantic species are cancelled, also identified some algae, formerly regarded as representative species, with atlantic ones, or at least only given them rank of varieties. Consequently the number of atlantic-arctic-pacific species has become as great as previously mentioned and also the group of atlantic-pacific species has sooner become augmented than diminished.

In the following table (VII) the latter algae are enumerated. I have here also inserted separate columns for the Bering Sea and for the northern part of the east coast of Asia, although nearly all species are stated only from the american side.

Table VII.

	Northern Norway	Iceland and Faeroes	Northwestern Europe	Atlantic coast of America	Pacific coast of America	Bering Sea	North eastern coast of Asia
Pylaiella macrocarpa Fosl.	×				×		
Ectocarpus terminalis Kütz.	×		×			×	
granulosus (Engl. Bot.) Ag.		×	×	×	×		
* *tomentosus* (Huds.) Lyngb.	×	×	×	×	×		
Phycocelis baltica (Reinke) Fosl.			×	×	×		
Sphacelaria Plumula Zanard.			×		×		
Cladostephus verticillatus (Lightf.) Ag.			×	×	?		
Desmotrichum undulatum (J. Ag.) Reinke		×	×	×	×		
Punctaria latifolia Grev.		×	×	×	×	×	×
Striaria attenuata (Ag.) Grev.			×	×	×		

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	Northern Norway	Iceland and Faeroes	Northwestern Europe	Atlantic coast of America	Pacific coast of America	Bering Sea	Northeastern coast of Asia
**Desmarestia ligulata* (Lightf.) Lamour.		×	×		×		
Myrionema vulgare (Thur.) Sauv.	×	×	×	×	×		
Castagnea divaricata (Ag.) J. Ag.	?		×	×	×		
Leathesia difformis (L.) Aresch.	×	×	×	×	×	×	×
Carpomitra Cabrerae (Clem.) Kütz.			×		×	.	
Lithoderma lignicola Kjellm.	×				×		
Erythrotrichia ceramicola (Lyngb.) Aresch.	×	×	×	×	×		
Porphyra leucosticta Thur.		×	×	×	×		
Choreocolax Polysiphoniae Reinsch		×	×	×	×		
Chondrus crispus (L.) Stackh.	×	×	×	×	×	×	×
Gigartina mammillosa (Good. et Woodw.) J. Ag.	×	×	×	×	×	×	×
Callophyllis laciniata (Huds.) Kütz.	×	×	×		×		
**Callymenia reniformis* (Turn.) J. Ag.			×	×	×		
Agardhiella tenera (J. Ag.) Schmitz				×	×		
**Gracilaria confervoides* (L.) Grev.			×		×		
**Hypnea musciformis* (Wulf.) Lamour.			×	×	×	×	
Rhodymenia Palmetta (Esp.) Grev.			×		×		
Lomentaria ovalis (Huds.) Endl.			×		×		
**Plocamium coccineum* (Huds.) Lyngb.	×	×	×	×	×		
Delesseria alata (Huds.) Lamour.	×	×	×	×	×		×
Laurencia pinnatifida (Gmel.) Lamour.		×	×		×		
Chondria atropurpurea Harv.				×	×		
**Polysiphonia atrorubescens* (Dillw.) Grev.	×	×	×	×	×		
Callithamnion polyspermum Ag.	×	×	×	×	×		
Baileyi Harv.				×	×		
Ceramium tenuissimum (Lyngb.) J. Ag.			×	×	×		
Petrocelis Middendorfi (Rupr.) Kjellm.	×				×		×
Lithothamnion Sonderi Hauck			×		×		

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A few (7) species in the list are marked with *: these are such as have also a more southern distribution, either in the warmer seas or as well in the southern as in the northern temperate zone. For them the possibility of a southern way of immigration must be admitted, perhaps also their origin dates far back in the tertiary period. Still of the 16 *Phaeophyceae* and 22 *Rhodophyceae* in the table 31 species have a distribution that can hardly be accounted for otherwise than through assuming their original home to have been in the present arctic regions.

Indeed it is no great number compared to the total of the atlantic or pacific flora, but then we also must remember the 64 atlantic-arctic-pacific species from table VI. Thus a number of about 100 algae, common to the northern parts of the oceans on both sides of America is reached, at all events a rather considerable part of the total figures. Moreover the numbers in table VII could with a good right be increased by transferring from table VI such species as are found in the Arctic Sea only in a limited region immediately beyond the northern border of the Atlantic as here defined. Among these are: *Polysiphonia nigrescens*, *Dumontia filiformis*, *Corallina officinalis* from the Murman or White Seas; *Alaria esculenta* from Spitzbergen and further some species, found either in western Greenland alone or besides also at the european northcoast, but not in other arctic districts. Even about these it holds true, that if they have now for the first time entered the Polar Sea, it becomes impossible to give any reason for their appearance also in the Pacific. On the other hand if we think species with such a distribution to be what I will call tertiary-polar species, i. e. such as have had their former home in the sea around the pole, it becomes natural, that they should have been driven southwards by the glaciation both into the Atlantic and the Pacific and there have got their present distribution.

We now must go back to what we know about the tertiary flora of the polar regions, and to the conclusions that can be drawn from that knowledge. In the miocene time there has been a rather warm climate far up in the present arctic regions, as is shown by the plantfossils found not only about 70° on both coasts of Greenland but also to the north of the 80th parallel in Grinnelland. If at all there existed then a flora that could be called arctic, it must have had a very limited area. For the present research it can however be left out of consideration if there already so long ago were any algae that lived under arctic conditions or if the arctic species were formed first during the preglacial period, that is when the deterioration of climate began. Species that were not able to adapt themselves to the gradually less and less favorable conditions of life, must then either have been exstirpated or driven southwards

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from the Polar Sea through the openings between the continents. If Bering Strait was already then a narrow sound. while there were wider entrances to the Atlantic, such a distribution of land and water must have made it very much easier for the tertiary polar algae to retreat to the latter ocean than to the Pacific, which would consequently not get as many citizens from the tertiary polar flora as the Atlantic. At first the less hardy algae migrated southwards and totally left their former homestead, then, in the same measure as the glaciation went forward, also the arctic forms, which now must have existed. began to wander southwards into the upper parts of the oceans, which were gradually cooled down, until during the maximal glaciation an arctic flora grew along the coasts far beyond its present limit. Here arises the question. if the arctic flora then held not only the present temperate region but also its present area besides. The opinion of Kjellman is, that it has never left the Polar Sea, as it appears from his discussion of the history of the flora, and from the summary (30, p. 61): „The Flora has had its centre of development in the Arctic Sea. Its area was more extensive during the glacial period than at present. It has been recruited in later times by more southern species."

To me its seems impossible, that the Polar Sea can have offered the necessary conditions of life for the greater part of its present inhabitants during the maximum of glaciation. Even the coast of Norway, now temperate, then must have been almost or perhaps entirely destitute of vegetation. because the great inlandice formed the entire coastline. The same must have been the case with most parts of Greenland and also other arctic lands. Along a glacierfront of such a thickness as it is here the question of there can of course not have been any vegetation, the ice protruded to depths where all algae are wanting. Indeed there must have been places here and there where the coast was formed of rocks, but here the seaice made the existence of a vegetation impossible at least in the littoral region. Even now the icefoot lies unbroken from year to year in many parts of the arctic coasts, and this must have been the rule during the iceage, when the climate was still more unfavorable than now. Consequently the littoral vegetation must have been totally extinct in the polar regions during the maximal glaciation. For the sublittoral algae the conditions can perhaps have been somewhat more favorable, at least locally. But even for them it must have been extremely difficult to hold the ground. The sea has been icecovered for most part of the year, in some places perhaps always. and even at points, where there has been some open water in the summer, they have had to fight against still stronger enemies than now. We see how in the present arctic seas the rock-bottom is rubbed and almost polished far down in the sublittoral region by the driftice, and the mud- or gravel-bottom ploughed up so that hardly any algae can take stand there. The most luxuriant vegetation is always to be found in the sheltered

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nooks of fjords and bays, but such localities are also most apt to hold their icesheat even in summertime. During the iceage a breaking up of the ice in such places can hardly have occured regularly, and consequently they can not have housed any considerable vegetation. I will not go so far as to assert, that there can have been no vegetation at all in the Polar Sea proper during the iceage, still I can come to no other conclusion but that it must have been a very scanty one; all littoral species were necessarily driven away or exstirpated, and of the sublittoral only a very limited number can have survived in some comparatively favorable localities. Among species that I am especially inclined to reckon as such possible survivors are *Phyllophora interrupta*, found even on the upploughed mudbottom in front of smaller glaciers, and the widely spread arctic *Laminaria solidungula*. Some other common arctic species perhaps also could come into consideration, but I think it rather unprofitable to speculate upon this question, as the present distribution can be as easily accounted for in another way. Of course those species, who were most able to stand the arctic conditions, were only driven a shorter way southwards than others and they followed the melting ice closely on their way back. Therefore they came first into the Polar Sea again and took possession of most parts of it. Doubtless this took place as well from the atlantic side as, perhaps in a smaller degree, also from the pacific. If the species in question were able to hold their ground against the new immigration of southern forms, they also stayed as citizens of the now again warmer regions, where they had outlived the glacial period. Especially this has been the case where the nature still affords conditions of life somewhat similar to those of the arctic regions, or where immigration from the south was difficult because the way southwards was early broken for instance at the coast from Labrador down and in Iceland. It must be remembered, that there has been a long time for these migrations, which are doubtless still in progress along the coasts as far as hydrographic and other conditions allow. That the currents do not exercise such an influence upon the vegetation, as attributed to them especially by Agardh, clearly appears from the fact, that nothwithstanding the stream that sets in from the Bering Sea, there is only a very small number of pacific species that has come into the Polar Sea by way of Bering Strait, and that not a single representative of the many peculiar pacific genera, especially the numerous *Laminariaceae*, has entered here although some of them grow far north as well on the asiatic as on the american side. On the other hand a current can greatly influence the vegetation of a coast by altering the climate and other conditions of life, as is clearly shown by the arctic features of the vegetation on the northern atlantic coast of America and by the almost purely atlantic flora along the coast of northern Norway. Of course I consider the Gulfstream as a factor of the greatest importance for the phy-

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siognomy of the vegetation at the parts of the european coast washed by its waters, but only by its influence upon the conditions of life, not directly as a bearer of new immigrants, where the necessary ways for the migration of algae are broken. This view is supported, f. i., by the flora of the Faeroes, that, in spite of very favorable conditions of life, shows a more northerly character in the proportion of brown and red algae (45 and 55 per ct.) than even the northernmost portion of the norwegian coast (41 and 59 per ct.) Even the west Greenland coast has a great number of southern forms, that do not enter other parts of the arctic area (23 species), and here no drift-theories can be brought into action.

It is previously mentioned that the flora of the Polar Sea has a very much greater affinity to that of the Atlantic than to that of the Pacific, the percentage being 87 and 44 resp. This doubtless will be attributed by the partisans of the drift-theory to the mighty influence of the Gulfstream, for my part I seek the solution of this problem in the present or former existence of a greater number of coast-ways for immigration and further in the previously mentioned circumstance, that a much greater number of the preglacial-polar (the original arctic) species here had found an asylum, while the Bering Strait-way was the only one for the migration to and from the Pacific.

The mere species-statistics and the few hints about other points of view hitherto given, are not sufficient however to get a clear understanding of the degree of affinity between the different floras, it also must be examined how the families and genera are distributed outside the area here in question.

In the following table (VIII) all families are entered (after Engler & Prantl) and their distribution in different seas indicated. Families not present in our area are set in ( ). For the others even the genera represented within this area are entered with their distribution (after De Toni, some dubious statements however excluded, as also genera not represented by identic species in the north Atlantic and Pacific). Monotypic genera are marked with 1., 1? indicates that some species more is referred with doubt to the same genus. Genera not present in the Polar Sea, but with identic species in the northern parts as well of the Atlantic as of the Pacific are marked with*.

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Table VIII.

Families and genera	North Atlantic	Warmer Atlantic	North Pacific	Warmer Pacific	Indian Ocean	South temperate and antarctic Seas
Phaeophyceae.						
Ectocarpaceae	—	—	—	—	—	—
Pylaiella	×	×	×		×	×
Ectocarpus	×	×	×	×	×	×
Streblonema	×		×	?		
Microsyphar 1.	×					
Phycocelis	×		×			
Dermatocelis 1.	×					
Symphyocarpus 1.	×					
Phaeostroma	×					
Isthmoplea 1?	×					
(Choristocarpaceae)	—[1]					
Sphacelariaceae	—	—	—	—	—	—
Sphacelaria	×	×	×	×	×	×
Chaetopteris 1.	×	?	×			
* *Cladostephus*	×	×	×		×	×
Encoeliaceae	—	—	—	—	—	—
* *Desmotrichum*	×		×			
Punctaria	×		×			
Lithosiphon	×					
Coilodesme	×		×			
Omphalophyllum 1.	×					
Phaeosaccion 1.	×					
Physematoplea 1.	×					
Pogotrichum 1?	×					
Scytosiphon	×		×	×		×
Phyllitis	×		×		×	×
Striariaceae	—	—	—		—	—
Kjellmania	×					
Coelocladia 1.	[2]					
Phleospora	×	×	×		?	×
* *Striaria* 1.	×		×			
Desmarestiaceae	—	—	—	—	—	—
Desmarestia	×		×	×	×	×
Dictyosiphonaceae	—		—			—
Dictyosiphon	×		×			?
(Myriotrichiaceae)	—	—				
Elachistaceae	—	—	—		—	
Leptonema 1.	×					
Elachista	×	×	×		×	
Chordariaceae	—	—	—	—	—	—
* *Myrionema*	×		×	×	×	
Eudesme	×		×		?	
* *Castagnea*	×	×	×			
Myriocladia	×	×			×	×
* *Leathesia*	×		×		?	

[1]) Only mediterranean.
[2]) Endemic in Greenland.

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Families and genera	North Atlantic	Warmer Atlantic	North Pacific	Warmer Pacific	Indian Ocean	South temperate and antarctic Seas
Mesogloia	×	×	×		×	×
Chordaria	×		×		×	
(Stilophoraceae)	—					
(Spermatochnaceae)	—				?	
Sporochnaceae	—	—	—	—	—	—
* *Carpomitra*	×	×	×	×	×	×
Ralfsiaceae	—	—	—		—	
Ralfsia	×	×	×		×	
Laminariaceae	—	—	—	—	—	—
Chorda	×		×			
Phyllaria	×	×	×			
Alaria	×		×			
Agarum	×		×			
Laminaria	×	×	×			
Lithodermataceae	—	?	—			
Lithoderma	×	?	×			
Sorapion	×					
(Cutleriaceae)	—	—		—	—	
Tilopteridaceae	—					
Scaphospora	×					
Fucaceae	—	—	—	—	—	—
Fucus	×	×	×		?	
Pelvetia 1?	×		?		?	
Ascophyllum 1?	×	×				

Families and genera	North Atlantic	Warmer Atlantic	North Pacific	Warmer Pacific	Indian Ocean	South temperate and antarctic Seas
Rhodophyceae.						
Bangiaceae	—	—	—	—	—	—
Bangia	×	×	×		×	
Porphyra	×	×	×	×	×	×
* *Erythrotrichia*	×		×			?
Conchocelis 1.	×					
(Rhodochaetaceae)	[1]					
Helminthocladiaceae	—	—	—	—	—	—
Chantransia	×	×	×	×	×	×
(Chaetangiaceae)	—	—	—	—	—	—
Gelidiaceae	—	—	—	—	—	—
* *Choreocolax*	×		×			×
Harveyella 1.	×					
(Acrotylaceae)	-				—	
Gigartinaceae	—	—	—	—	—	—
* *Chondrus*	×		×	×		
* *Gigartina*	×	×	×	×	×	×
Phyllophora	×	×	×			
Actinococcus	×	×			×	
Ceratocolax 1.	×					
* *Callophyllis*	×	×	×	×	×	×
Callymenia	×	×	×	×	×	×
Ahnfeltia	×	×	×	×		×
Rhodophyllidaceae	—	—	—	—	—	—
Cystoclonium	×	×	×			

[1]) Only mediterranaen.

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Families and genera	North Atlantic	Warmer Atlantic	North Pacific	Warmer Pacific	Indian Ocean	South temperate and antarctic Seas
* *Agardhiella* 1.	×	×	×			
Turnerella	×		×			
Euthora	×		×			
Rhodophyllis	×		×	×	×	×
Sphaerococcaceae	—	—	—	—	—	—
* *Gracilaria*	×	×	×	×	×	×
* *Hypnea*	×	×	×	×	×	
Rhodymeniaceae	—	—	—	—	—	—
Rhodymenia	×	×	×	×	×	×
* *Lomentaria*	×	×	×		×	
* *Plocamium*	×	×	×	×	×	×
Halosaccion	×		×			
Delesseriaceae	—	—	—	—	—	—
Delesseria	×	×	×		×	×
(Bonnemaisoniaceae)	—	—	—	—	—	—
Rhodomelaceae	—	—	—	—	—	—
* *Laurencia*	×	×	×	×	×	×
* *Chondria*	×	×	×	×	×	×
Polysiphonia	×	×	×	×	×	×
Rhodomela	×		×		?	?
Odonthalia	×		×			
Ceramiaceae	—	—	—	—	—	—
* *Callithamnion*	×	×	×	×	×	×
Ptilota	×		×			
Antithamnion	×	×	×	×	×	×
Ceramium	×	×	×	×	×	×
Rhodochorton	×		×	?	?	×
(Gloiosiphoniaceae)	—	—	—			—
(Grateloupiaceae)	—	—	—	—	—	—
Dumontiaceae	—	—	—		—	—
Dumontia 1.	×		×			×
Dilsea	×		×			
Nemastomaceae	—	—	—	—	—	—
Furcellaria 1.	×					
Rhizophyllidaceae	—	—	—	—	—	
Polyides 1.	×					
Squamariaceae	—	—	—	—	—	
Petrocelis	×		×			
Cruoria	×	×	×			
Cruoriella	×					
Peysonellia	×	×		×	×	
Rhododermis	×					
Corallinaceae	—	—	—	—	—	—
Clathromorphum	×		×			
Lithothamnion	×	×	×	×	×	×
Corallina	×	×	×	×	×	×
Hildenbrandtia	×	×	×		×	×

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For convenience I have used different signs to mark the distribution of families (—) and genera (×).

Before going into detail with the conclusions that can be drawn from the above table, it will be useful to summarize the distribution of the families as follows:

Table IX.

	Arctic				Not arctic				Total
	Atlantic	Atlantic-pacific	In most Seas	Northern and southern temperate and cold Seas	Atlantic	Atlantic pacific and southern	In most Seas	Only Indian Ocean	
Phaeophyceae	1	1	10	1	4	—	2	—	19
Rhodophyceae	—	—	14	—	1	1	4	1	21
Together	1	1	24	1	5	1	6	1	40

Out of 40 (marine) families 27 are represented in the Arctic Sea and of these again 24 have a wide distribution in most parts of the oceans. As the families, mostly at least, represent very old types it is natural that they should have spread so far. About the age of the few families, that have a more narrow area, it is hardly possible to have any opinion, but for the three arctic ones it seems most probable that the following preglacial homesteads must be supposed: for *Lithodermataceae* the Polar Sea, for *Tilopteridaceae* the sea south of the tertiary landbridge. That the *Dictyosiphonaceae* have been represented in the tertiary Polar Sea can hardly be doubted, but on the other hand they have another area of distribution in the south, probably also old, as they are represented there not only by a *Dictyosiphon* (?) but also by an endemic genus *Scytothamnus*.

Of the 13 families not present in the arctic regions 6 have a wide distribution, and 5 others only are represented in the atlantic area. The latter are all such as only have a very limited number of species. Probably these lead their origin from the tertiary-atlantic flora. One family, *Gloiosiphoniaceae*, has a distribution somewhat similar to that of the *Dictyosiphonaceae* and may perhaps have been present in the tertiary Polar Sea, although it is now entirely wanting in those waters. As can be seen of the table IX, there is only a single family, *Acrotylaceae*, that is entirely absent from the Atlantic. Perhaps this ocean really is richer in different algae than other seas, most probably however this apparent greater abundance of forms is due in a great measure to the better exploration of those waters. Future researches perhaps will make it necessary to take another view upon the history of some of the above-

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mentioned families, but in the light of our present knowledge I think it can hardly be regarded otherwise.

An inspection of the table VIII further corroborates the opinion already pronounced, that there is a very near affinity between the floras of the Arctic Sea and the northern Atlantic, so close indeed, that it seems dubious, if not the marine floras of most parts of the arctic regions are to be looked upon as merely provinces of the atlantic flora, nothwithstanding the great differences that must have prevailed between the preglacial vegetations among whom their ancestors are to be sought. It is pointed out previously that the number of species that can without restrictions, be regarded as endemic in the arctic regions is all but considerable, and that only few species are distributed all over the arctic area. If the present arctic flora was the result of a long unbroken development within the area it now occupies, there would in all probability exist a number of endemic genera, and these as well as a greater number of endemic species must also be spread over great parts of the area. Now only one endemic, monotypic genus exists, that has a very narrow limit, as far as hitherto known, and the endemic species mostly have a distribution only within a small area. Most of them moreover pertain to genera, where there has been doubtless of late a lively production of new forms, or where probably such generation is still in progress, as is shown by the many closely allied or hardly distinguished species of such genera as *Laminaria*, *Alaria*, *Rhodochorton*, described from the arctic regions. Such a fact does not speak against the assumption, that the arctic marine flora has immigrated in postglacial time, likewise as the atlantic flora, f. i. at the norwegian coast, and the landfloras of the former glaciated areas in general, as is shown by the existence in those areas of such genera as *Hieracium*, *Taraxacum* and perhaps others, including many local species.

Kjellman speaks of the great number of monotypic genera as proving the considerable age of the arctic flora. Now the number of genera is 80 (43 of *Phaeophyceae*, 37 of *Rhodophyceae*), all with a single exception also present in the Atlantic. Among them are 15 (19) monotypic ones, which indeed is a great number, but except *Coelocladia*, as formerly mentioned, they are all also atlantic, and most of them have their principal distribution south of the Arctic Sea. Some, f. i. *Pelvetia*, *Dumontia*, *Furcellaria*, *Polyides*, beyond doubt are to be reckoned as tertiary-atlantic, consequently I cannot in their existence see any cause for the supposition of a long development within the Polar Sea. Of the 42 genera of brown algae (*Coelocladia* excepted) 16 are atlantic-arctic, 14 atlantic-arctic-pacific, 12 have a wider distribution. Of the 37 genera of *Rhodophyceae* 7 are atlantic-arctic, 12 atlantic-arctic-pacific, 18 have a wider range. Consequently even here the affinity between the atlantic and the arctic flora is expressed, the atlantic genera of the arctic flora beeing 99 in a hundred, the pacific ones only 66.

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There is another series of genera entered in the table VIII left aside as yet, viz. such as are represented by the same species in the Atlantic and the Pacific but wanting in the Polar Sea. Of those 4 brown and 2 red ones are only found in the northern parts of both oceans, 3 brown and 11 red genera have a wider distribution. Some of the former 6 at least must be reckoned as once pertaining to the polar flora. but not having been able to stand arctic conditions, they have. once driven away, never returned to their former home, likewise as most of the species in table VII. There also are genera represented in both oceans, but by different species. Among them also there probably are descendants from the preglacial-polar flora, but as it can hardly be asserted for most of them that their origin is such, I have abstained from enumerating them.

Hitherto the researches made here have always been in accordance with the theories of *Reinke* (40) quoted above (p. 4—5) but there is another point, where something more can doubtless be done than he thought possible. As his work has the baltic flora and its history for its only object, he has left the relation of the atlantic and arctic algae to those of the Pacific quite out of consideration. Still I think that if he had drawn the latter flora into his comparisons, he would not have come to any such result as (40, p. 98): — —„mögen auch mehrere der nach jetzigem Befunde als atlantisch angesprochenen Species doch vielleicht ihren Ursprung nördlich der Landbrücke genommen haben und erst später nach Süden gewandert sein. während manche wegen ihrer Verbreitung bis über den Polarkreis hinaus jetzt zu den subarktischen gerechnete Art südlich der Landbrücke entstanden und erst später in den arktischen Ozean eingewandert ist. Dies läßt sich für den Einzelfall nicht unterscheiden".

Such species as are spread from the Atlantic through the Polar Sea to the northern Pacific but not southwards must doubtless in tertiary time have had their home in the seas around the pole. Consequently we here have found a way to determine where genera and species have had their origin as far as the tertiary period is concerned. Indeed we know nothing about the preglacial limit between the polar and the pacific flora. but it seems necessary to think that there has at least not existed any broader and easier connection then, on the contrary perhaps there has been still less possibility of interchange of species than by way of the present Bering Strait. Else it would be impossible to explain the fact, that not a single pacific genus is represented in the Polar Sea and the north Atlantic. Had pacific genera entered the Polar Sea we would have found some of their species also in the northern Atlantic, at least if they had had time to spread northward before the glaciation, and it would not be so apparent, that there only has been an immigration of tertiary-polar algae to both oceans during glacial time.

Indeed it would be an unprofitable task to try to determine

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the tertiary origin of every species and genus of the present floras of the regions in question, as in many cases our present knowledge of their distribution will probably prove incomplete, but in many other instances I think it must be possible to settle already now the question about the tertiary area.

At first I will take into consideration such genera as must have had their sole home or at least have been principally represented in the tertiary Polar Sea, as can be concluded from Table VIII.

Such are:

Streblonema
Phycocelis
Chaetopteris
Desmotrichum
Punctaria
Coilodesme
Phleospora
Striaria
Dictyosiphon
Eudesme
Castagnea
Leathesia (?)
Ralfsia (?)
Chorda
Phyllaria
Alaria
Agarum
Laminaria
Lithoderma
Fucus
Phyllophora
Cystoclonium
Agardhiella
Turnerella
Euthora
Halosaccion
Rhodomela
Odonthalia
Ptilota
Dilsea.

Genera that can in consequence of their present distribution hardly have been anything but tertiary-atlantic are:

Sorocarpus
Dichosporangium
Isthmoplea
Halopteris
Physematoplea
Delamarea
Pogotrichum
Arthrocladia
Gobia
Leptonema
Halothrix
Cutleria
Tilopteris
Scaphospora
Himanthalia
Pelvetia
Ascophyllum
Halidrys
Naccaria
Sphaerococcus
Grinnellia
Halurus
Compsothamnion
Dudresnaya
Furcellaria
Polyides.

Of course the above lists cannot have any claim to be reckoned as complete, probably still more genera could be added to the former, and as to the latter there is always some doubt left if not their tertiary home can still have been on the north side of the landbridge (cf. the above quotation from Reinke), but then we must either suppose that they have been destroyed by the progress of glaciation on their way to Bering Strait or also alter the previous supposition that the flora in the old Polar Sea has been a uniform one, a theory that is rather

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well supported by the distribution of species. For such genera as *Pelvetia, Ascophyllum, Halidrys, Himanthalia, Furcellaria, Polyides,* which have a wide area in the northern Atlantic, and are only represented by a single species, it seems however hardly possible to presume an origin elsewhere, they must have had their tertiary home in the same region. As for species of other genera which could be counted as citizens of the tertiary-polar flora, I think it will be enough to refer to the tables I, VI, and VII.

But still there are more algae, which probably have had their origin in the same area. Indeed it is difficult to form an absolute opinion about such as are at present distributed principally in the immediate neighbourhood of the limit between the Polar Sea and the Atlantic, f. inst. in northern Norway and Iceland or somewhat further to the south and besides in some arctic district to the north of the Atlantic. Algae such as species of *Microsyphar*, *Dermatocelis*, *Symphyocarpus*, *Phaeostroma*, *Omphalophyllum*, *Phaeosaccion*, *Kjellmania*, *Sorapion*, a. o., most probably have grown in the Polar Sea of tertiary times, and are there now for the second time, but on the other hand it cannot be denied, that as far as the present distribution is known, it also allows to think of an origin south of the land-bridge. At least a 100 species or somewhat more in the present floras of the Atlantic, the Arctic Sea and the north Pacific after all probability can be traced back to the tertiary Polar Sea. However I cannot agree with Kjellman (30, p. 56) that we must seek the origin of such species, as are now atlantic-pacific, in a glacial sea. Doubtless they are descendants of the old tertiary flora of the Polar Sea, that was not arctic. When the arctic conditions began to make existence difficult for that flora, its place was filled up by the first arctic one, that may have lived previously far north or first appeared in the preglacial time as a result of the altered conditions of life. Lastly even the arctic species began a migration southwards into both oceans, but came back again afterwards.

Still there are some algae that must be treated more in detail, namely the *Fucaceae* and *Laminariaceae*. Kjellman (30, p. 11—12) also speaks of these as especially characteristic for the Polar Sea. The third family he mentions, the *Corallinaceae,* must be left aside as too little known, notwithstanding its prominence in the most arctic parts of the Polar Sea. There also the *Laminariaceae*, represented by the genera *Laminaria*, *Agarum* and *Alaria* take a very great part in forming the vegetation, so as to qualify the arctic waters for the name „the sea of the *Laminariaceae*". The *Fucaceae* on the other hand are, as Kjellman also points out, mostly restricted to the less arctic parts of the Polar Sea, only there they are able to hold extensive parts of the bottom. It is also natural, that the *Fucaceae*, as mostly litoral algae, should have their principal area south of the arctic regions.

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The genus *Fucus* itself however is represented in the arctic seas by 4 species, or by 11 if the disposition of De Toni (14, III, p. 193—209) is followed. Still more species are described but the later authors have reduced the number considerably. If the definition of species is followed, that Rosenvinge (42) has proposed (I have used it above) we have one widely spread arctic species, *F. inflatus*, with numerous varieties, found also as well some way down in theAtlantic as in the Pacific. The other species reported from the latter ocean is perhaps not quite sure (as it is excluded by Setchell and Gardner (49) from the flora of northwestern America). It is *F. vesiculosus*, the most common in the Atlantic, that although entering the Polar Sea is not extremely arctic. The two others, *F. ceranoides* and *F. serratus* are northatlantic species, that only enter the Spitzbergen district a little way northward. Further we have one species, *F. spiralis*, in the northern Atlantic and one (2 or 3?) that goes down to southern Europe (*F. virsoides* in the Mediterranean). It cannot be denied that there is a possibility to seek the tertiary origin of the genus as well in the Polar Sea as in the Atlantic, but I am more inclined to think, that it first entered the latter sea as a fugitive before the glaciation, else it should have more representatives in the Atlantic. In the northern Pacific the *Fucaceae* are very scantily represented. Setchell (49) has besides the abovementioned *Fucus*-species only one *Cystophyllum* and with doubt a *Cystoseira*. Farther south in the Pacific many genera are represented, such as have a great distribution to the south in general. The Atlantic as previously mentioned has its own genera of Fucaceae, limited to the northern part.

A still greater interest attaches to the *Laminariaceae*. As pointed out especially by Setchell (48) the family is distributed principally in two widely separated areas, one arctic and circumpolar in the northern seas, another circumpolar in the southern hemisphere, including also the antarctic regions as far as the conditions there allow a vegetation of higher algae to exist. There is however a very marked difference between these two areas of distribution, especially when the Arctic Sea and the northern Atlantic are compared with the southern district. The former area is characterised by 6 genera, of which one only is (perhaps) represented within the southern range of distribution. On the other hand the forms, that give the character to the southern area are entirely absent from the abovementioned parts of the northern one, but are represented in the northern Pacific by allied genera and species or even by identic ones.

Setchell (48) gives a table of distribution to which must be referred for particulars. Even if some new species are added since and the area for some has got additions, the differences are not so great as to make a new survey necessary, especially as the alterations do not apply to the genera to which the special interest for this research attaches. In the above quoted treatise Setchell divides the *Laminariaceae* into three tribes:

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Laminariideae. *Lessoniideae* and *Alariideae*. All are present in the northern Pacific, but the *Lessoniideae* are totally wanting in the Polar Sea and the northern Atlantic, where we only have the genera *Chorda*, *Phyllaria*, *Saccorhiza* (not arctic) and *Laminaria* of the subtribe *Laminarieae*, *Agarum* of the subtribe *Agareae*, and *Alaria* of the subtribe *Alarieae*. *Chorda* is only with reservation referred to the family (cf. also Reinke, 41), but that is a question of minor interest here. Of the three species in the genus one is only found in the Baltic, the two others indeed are found in the Arctic Sea. *Ch. Filum* at a good many different points, but not very far to the north, *Ch. tomentosa* only in western Greenland. This could speak for an atlantic origin, but as *Ch. Filum* is also found in the northern Pacific, there can hardly be thought of any other original home than the Polar Sea.

Laminaria. Of this genus De Toni (14, III) enumerates 28 species (excl. *Hedophyllum*), of which 16 are indicated for the northern Pacific, 8 for the northern Atlantic. In the Polar Sea 8 species should grow as indicated in table I. Of these *L. groenlandica*, *L. Agardhii*, and perhaps *L. solidungula* are only arctic, the other species are *L. nigripes* and *L. saccharina*, atlantic-pacific: *L. digitata* and *L. longicruris*, somewhat dubious as pacific plants: *L. cuneifolia* only pacific and arctic. The atlantic species, that do not go into the Polar Sea, however are mostly restricted to the northern parts of the european coast (*L. hyperborea*, *Gunneri*, *(discolor)*, *hieroglyphica)*. One species, *L. Rodriguezii* is only found in the Mediterranean, two species in South Africa (*L. pallida* also at St. Paul and the Crozet Islands.) The Pacific on the other hand has not less than 10 species of its own, also with a northern distribution. Indeed it cannot be denied that such a distribution can have its cause in the circumstance that the genus was widely spread already before the iceage, but then it becomes difficult to explain, why not a single species goes farther down in the Pacific (one species, *L. himanthophylla*, indeed is mentioned from southern South America by Postels and Ruprecht (39), but it is never found again, and De Toni has it among „species maxime dubiae"). The fact that the *Laminariae* are entirely absent from the tropic seas also points to a northern origin. From there the few southern forms must have strayed during the iceage (cf. Setchell. 48, p. 363).

But why do we not have any atlantic-pacific species, wanting in the Polar Sea? I think the answer must be: because there are different species formed from the phylembryons that have occupied the tertiary Polar Sea and been driven southward into different areas. That a lively formation of new species has taken place lately, or is still in progress, cannot be doubted when the great number of nearly allied species is taken into consideration, that has been distinguished by different authors (cf. Setchell. 48 p. 339). If the later writers are right, who have ranged a great many of them as synonyms under comparatively

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few species, is not easily decided, at all events the number of forms that stand very near to each other is considerable and must be accounted for by assuming a cleaving of the previous species within a near period. The species that are found farther to the south must have been among the first to leave the preglacial Polar Sea (or their ancestors have done it). That *L. Rodriguezii* can have come into the Mediterranean during the iceage is not in the least improbable. Somewhat more difficult it is to explain the existence of *Laminaria*-species at the coast of South Africa.

Phyllaria also is probably a tertiary-polar genus, as it has a species common to both northern oceans, and also some way enters the Polar Sea. That two species reach south of the Strait of Gibraltar does not contend against such an assumption.

Saccorhiza has a distribution that seems to point to an origin in the Atlantic, but I am inclined to think, that it too has come from the tertiary Polar Sea, together with the other *Laminarieae*.

Agarum. This genus is represented on the whole coast of northern America and also on the Pacific coast of Asia, but not in the european and asiatic parts of the Polar Sea. As all the 4 other genera of the *Agareae* are solely northpacific, there perhaps could be some reason for assuming the Bering-Sea-region to be their original home, but that would not account for the occurrence of *Agarum Turneri* as far as Greenland (even on the southern part of the east coast) and the Atlantic shores of America. That genus at least must have been tertiary polar (cf. Setchell, 48, p. 373). Perhaps also the other genera have originated north of Bering Strait, but only been spread within a smaller area before they were driven southwards by the glaciation.

That the *Lessoniideae* are of pacific origin cannot be doubted, and most probably they also have had their first home in the northern parts of that ocean, as most of them are still found there. They must have during the iceage passed the warmer seas and reached the southern temperate and antarctic waters, where especially *Macrocystis pyrifera* now has a great area.

Among the *Alariideae* there are forms of so widely different distribution, that it is hardly possible to form any opinion about the origin of the whole tribe. Most of them indeed are northpacific, *Ecklonia* however is principally distributed in the southern and even in warmer seas. The genus of greatest interest here is *Alaria* that shows a considerable correspondence with *Laminaria* (cf. Setchell, 48, p. 366), as well in the distribution as in the existence of a great many closely allied forms, by some authors classified as species, by others reduced to varieties. Setchell (48, p. 347) speaks of this confusion and gives the number of species as 15 or 20. In his table there are 18 species (De Tony has one more, *A. musaefolia*). I prefer to

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follow Setchell as to the specific distinction. There are two areas, where the *Alariae* are especially numerous, viz., the northern Pacific and the border-regions between the Polar Sea and the Atlantic. The type of the genus, *A. esculenta*, is widely spread in the northern Atlantic, where it reaches down to the coast of France, it is hardly arctic anywhere (Spitzbergen?) but appears again in the northern Pacific (?).

A. Pylaii comes in within the northern parts of the range of the former species (Norway, Faeroes, Maine, Bering Sea) but is as far as known at present not distributed very far into the arctic regions. Three species, *A. membranacea, A. grandifolia*, and *A. flagellaris* are northatlantic-arctic. One, *A. dolichorhachis*, is pacific with an arctic range in the neighbourhood of Bering Strait. As previously mentioned the two species that stand as arctic-endemic probably are to be found also outside that sound. This gives us 8 species, the ninth, *A. linearis*, is only found in Iceland (Jónsson (26) has it under *A. esculenta*), all the other 9 species are northpacific. It is apparent that such a distribution must doubtless point to a centre of dispersion in the tertiary Polar Sea, and to a cleaving into new forms in very late periods.

The name „Sea of the *Laminariaceae*" for the Polar Sea, must have been still more appropriate in tertiary times than now (cf. Setchell 48, p. 373), as the family has probably been restricted to that area, with a few exceptions only.

It must now be examined how far the views here stated are in accord with the ideas of Reinke (41) about the phylogenesis of the *Laminariaceae*. The simplest form of all is after his opinion (p. 51) *Laminaria solidungula* (Setchell has *L. Phyllitis*) and that species is not only the primitive type („die ideelle und embryologische Grundform") of the family, but he also accepts the hypothesis, that it is the original form („die Urform des *Laminariaceen*typus") from which all the different *Laminariaceae* have sprung. This again he thinks derived from the *Flagellatae*, and as far as is indicated in the treatise he seems to assume a direct descendance from the *Flagellatae*, so far as none of the phylembryons of *Laminaria solidungula* should live now, all the intermediate members of the chain should be exstirpated without leaving any trace, as they, likewise as the *Laminariaceae* now living, have been unfit for preservation in a fossil state. He further has a discussion of the probabilities for and against a monophyletic origin of the family, but as already intimated, not the least that points to an assumption that more *Phaeosphoreae* also could have the same ancestor among the *Flagellatae*, i. e. that the *Laminariaceae* could descend from another now existing family of brown algae, or at least have the same origin as some or other of these. I cannot see why not the theory of Kjellman (Engler & Prantl, I. 2, p. 253) should be at least quite as acceptable. that the *Laminariaceae* have branched off from the *Encocliaceae*. Indeed this is a question

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that can hardly ever be solved, as the most important evidence, the extinct forms, from which the now living *Phaeosphoreae* are derived, will never be brought forward, but for the present object it is of less importance. Otherwise it is with the question about the monophyletic or polyphyletic origin of the *Laminariaceae*.

Reinke thinks that a monophyletic origin must most probably be assumed for them, even if he admits that rather weighty arguments can be advanced against it, such as the fact, that a *Laminaria* is quite as well adapted for its conditions of life as f. inst. a *Lessonia*, and that the different types grow together, especially in the Pacific. The most important evidence for the monophyletic origin is that all other forms during their ontogenesis have to pass a „*Laminaria*-stage". But there are facts, not mentioned by Reinke, that must be taken into consideration, and which in my opinion turn the balance in favour of the polyphyletic origin of the family.

If the genus *Laminaria* was the original one, from which all the others are derivates, it must be assumed that *Laminaria* has several times given birth to new types, while as well the primeval *L. solidungula* as other *Laminaria*-species, that have through „explosion" (Reinke) given rise to new species and genera still live, notwithstanding the very long ages that must have passed since the differentiation from *L. solidungula* of f. inst. the phylembryons of *Macrocystis* or *Lessonia* took place. Indeed such a thing cannot be declared impossible, but mostly those old types will be found to stand rather isolated, as we see in the case of such plants as can be followed some way back in the geological record, f. inst. the *Gymnospermae*, the *Amentaceae* and others. The genera usually are well defined, the species likewise, and mostly the latter are few or there is only one species to the genus. I think there can hardly be brought forward any evidence of an old type, that has for ages lived besides its heterogenous offspring and than abruptly entered a new period of mutation. But that decidedly should be the case with *Laminaria* if Reinke was right; there we at present have a rather great number of little differentiated species, that cannot very long ago have branched off from their common progenitors. Moreover it can hardly be thought, especially when the distribution of the genus *Laminaria* as it now is, is taken into consideration, that a species that is now exclusively arctic should be the ancestor of all the genera of *Laminariaceae* now living solely outside the arctic regions, or even restricted to southern waters alone.

It seems to me quite impossible to assume a monophyletic origin for the whole family from *Laminaria solidungula*. On the contrary I am inclined to look upon the highly organised genera, or at least their hypothetical *Laminaria*-like ancestors, as much older than any now existing *Laminaria*. How far back we must go to find the common phylembryons of *Laminaria*

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and the other genera must rest a matter of speculation, at all events *Laminaria* must be regarded as a young genus, where the differentiation of species has not yet reached its end. That *L. solidungula* really is the first *Laminaria* may be possible, even if there are other species that can be regarded as equally primitive, but the ancestor of the whole family it can hardly be. It must be assumed that the origin of the *Laminariaceae* is polyphyletic as far back as we have any possibility to follow their phylembryons — of course their lineage will converge somewhere down against the base of organic life, perhaps among the *Flagellatae*.

Having now tried to show how the two families, which are especially characteristic for the northern waters contribute with regard to their distribution in an unmistakeable manner to confirm the opinion previously arrived to by examination of greater parts of the floras, I will summarize the results as follows.

The now existing joint appearance of species in the North Atlantic and the North Pacific must be due to the emigration to both sides from the tertiary Polar Sea. Only in very few cases this community of species allows another explication.

The history of the floras of the northern seas must be summarized as follows:

In the early tertiary time there was a distinct flora in the Polar Sea, limited by a now disappeared landbridge from the atlantic flora — probably also barred from the Pacific, as the great difference from the present flora of that ocean indicates, or at least possessing very small possibilities for an interchange of species with that sea. Then the landbridges were broken and the algae of the Polar Sea got possession of ways of migration to the south. This migration was accelerated in the preglacial time and the Atlantic received a considerable number of new citizens from the north, the Pacific a smaller one. When the Iceage came the progress of glaciation drove still more and more species out from the Polar Sea, which became, if not entirely void of algae, at least very poor in species. After the maximal glaciation was over the algae again wandered into the polar regions, and this migration must still be in progress as far as the natural conditions allow. Many of the tertiary-polar genera and species have not again been able to enter their old homesteads, as the present conditions there are averse to it. Consequently we have a number of algae, now purely atlantic or besides also pacific and also some solely pacific ones, which have their original home in the Polar Sea but are now lacking there. On the other hand there were old atlantic algae, that during the Iceage had adapted themselves to glacial conditions and after the end of the glaciation entered the Polar Sea together with the reimmigration of the tertiary-polar species. On the pacific side this kind of species seems entirely lacking, but notwithstanding the result must be that the present flora

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of the Polar Sea shows a very near analogy to the floras of the arctic lands. That such isolated colonies are lacking as the landplants have left in southern mountains, must be a necessary consequence of the absence of such ways southwards for the algae as the mountainridges have formed for the landplants, and also thereof that in the oceans there are no isolated areas with conditions like those of the arctic regions.

Now it is left to try to trace some of the different stages in the postglacial reimmigration of algae to the northern seas, especially to the present Arctic Sea. We know that changes as well in the climate as in the level of sea have taken place in postglacial time. Such different periods ought to have left some marks in the present features of the floras. The tertiary polar flora was rather uniform, even if there are some facts that seem to indicate certain differences already before the glacial period between different parts of the Polar Sea. The present arctic marine flora is less uniform, as the above tables of distribution show, and therefore an attempt to trace the immigration back is rather tempting. But it would hardly be possible at present to carry out such an investigation into detail, and I must restrict myself to try an elucidation of a few points.

The warm postglacial time, that we know from many evidences in northern Europe, even from Spitzbergen, must doubtless have greatly influenced the migration of algae. This period of warmer climate in connection with an upheaval of the land, that brought Spitzbergen in continuity with northern Europe, has, as Nathorst (36) shows, materially contributed to the colonization of that archipelage with landplants. Of course also the algae have wandered along the then existing coast, and there are some species in the Spitzbergen-flora, which have in all probability reached so far just at that time. Such are *Alaria esculenta* (?), *Fucus ceranoides*, *F. serratus*, and the now extinct *Pelvetia canaliculata*, that has been found together with *Mytilus edulis* and *Cyprina islandica*, which now also are found only in a subfossil state. Probably there have at that time been more southern species and perhaps also the distinctly temperate forms of the Murman and White Sea date back to the same period.

That the *Laminaria saccharina* of northeastern Greenland has come thither during equally favourable conditions can hardly be doubted. Still it is not to be explained with regard only to the present distribution of land and water why it should be restricted to the coast north of 69°. I have previously pointed out the interesting disposition of the *Laminariaceae* in east Greenland, that seems decidedly to show the influence of a postglacial barrier south of Scoresby Sound, i. e., the old now submarine ridge has been above sealevel in postglacial time, as the distribution of the *Laminariaceae* and especially of *Lam. saccha-*

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rina does not allow to think of preglacial causes for its present appearance.

Indeed there has been a great contest about the assuming of a postglacial landbridge over the northern Atlantic, and it is likely to be continued for some time yet. There have been brought forward many arguments for and against the theory from geological as well as from botanical and zoological point of view. Geologists at present mostly seem averse to it, but as far as I can judge, they have not produced any conclusive evidence against the possibility of the postglacial upheaval of the tertiary landconnection, or at least considerable parts of it, which would be enough to form ways of immigration at least for the marine algae, probably also for the flora of the lands in question. Thoroddsen indeed has lately (Ymer 1904, h. 4) thought fit to give an advice to botanists to explain the immigration out from the present conditions, but as he has given no convincing proof of the impossibility of the landconnection and has besides shown himself to be totally ignorant about some of the most important botanical facts on which the opposite opinion is based, I cannot see that he is justified in giving any such prescription.

As it cannot be thought of quoting all the many works where the question of the landbridge is treated, I will only refer to one more of the latest, that is rather well in accord with the view I have adopted. It is the great memoir of Nansen about the bathymetrical features of the northern seas (35). The result of the author, reached through comparison of a great many observations, regarding the sculpture of the bottom of the Atlantic and the Polar Sea, is that great oscillations of sea-level must be assumed in different geological periods, even so late as at least at the end of the iceage. How late an upheaval has taken place is not distinctly said, and to judge from part of a letter from the author, that Börgesen (10) has published, he seems not to assume an emergence of land so late as during the warm postglacial time. But I cannot see, that his researches contend against such a supposition, especially when viewed in connection with the above mentioned statements of Nathorst. If the oscillations have been synchronical, we must assume, that about the same time when Spitzbergen was connected with northern Europe and Asia, also great parts of the old submarine ridge were above sealevel, and as this took place in the warm period of the postglacial time, there must then have ruled the conditions required for immigration of a temperate flora northward. Moreover Nansen (35, p. 71, 75, 123—126) points out that the absence of a typical coast-platform at the Faeroes and most part of the coast of Iceland indicates a recent submergence. The loose basaltic rocks of those islands are very much subject to be cut down by the waveaction and still caves do only appear at present sealevel, postglacial marine sediments are absent above the present shoreline of the Faeroes, which also

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points to the same conclusion, that a submergence in a very near period is probable, or that at least no emergence has lately taken place.

As I have elsewhere discussed the features of the marine flora of the Faeroes compared with those of neighbouring shores, that speak for a landconnection in postglacial time, I shall not here repeat that discussion. Further research about the question of the ways and means of migration must be left to another occasion.

Lund, march 1905.

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