

World-wide latitudinal and longitudinal seaweed distribution patterns and their possible causes, as illustrated by the distribution of Rhodophytan genera*

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ABSTRACT: The degree of similarity between red algal generic floras in each pair of 22 climatically defined biogeographic regions was established on a world-wide scale by Jaccard's similarity index and by an hierarchical clustering with an agglomerative centroid method. Two clusterings were carried out, the first one on the basis of all 637 genera, and the second one on the basis of genera not occurring in the tropics and non-endemic to any one of the 22 regions (145 genera). This latter clustering served to detect better the relationships among non-tropical floras. The results indicate the following division of the earth's rhodophytan seaweed floras: (1) A rich tropical-warm temperate "Tethyan" group including the rich tropical Indo W Pacific and W Atlantic floras, and the rich warm temperate NW Pacific and NE Atlantic floras; (2) the depauperate extensions of the above group (the tropical E Pacific and E Atlantic floras, and the warm temperate NW and SW Atlantic floras); (3) a cold temperate and a warm temperate N Pacific group; (4) an Arctic-cold temperate N Atlantic group and a NE Atlantic warm temperate flora; (5) an Antarctic-cold temperate southern hemisphere group including the cold temperate SE Pacific, SW Atlantic, SE Atlantic floras, and the Antarctic flora; (6) the two highly individual, but slightly related warm temperate SE Atlantic flora (S. Africa) and SW Pacific flora (Southern Australia and Northern New Zealand); (7) the depauperate warm temperate SE Pacific flora. Although the northern and southern hemisphere temperate and polar floras are quite unrelated (on the basis of genera lacking in the tropics), they share nonetheless a number of cool water genera which apparently have succeeded in passing the adverse tropical belt. The rich tropical-warm temperate group is thought to consist of vicariant portions of a formerly continuous Tethyan flora. The N Pacific and N Atlantic temperate floras are thought to have developed independently since the Oligocene ($\sim 40.10^6$ y) deterioration of the climate and to have partially mixed their cool water genera only after the Pliocene inundation (2.10^6 y) of the Bering Land Bridge. The warm-temperate floras of S Africa and southern Australia probably owe their richness and individuality to a very long isolation (already at the start of the Cenozoicum) and a continued residence in warm temperate conditions with small seasonal fluctuations.

INTRODUCTION

It is a well-known fact that the coasts in different climatic zones, and those situated in climatically similar zones but in different oceans or hemispheres, are inhabited by dissimilar seaweed floras. An impressive overview over the world's seaweed floras and

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vegetations will be given in Lüning's forthcoming book on marine botany (Lüning, 1985). Nonetheless these floras share smaller or larger numbers of seaweed species and genera, and are consequently more or less similar.

In the course of the last ten years several studies were devoted to an analysis of the different degrees of similarity, or relatedness, among seaweed floras inhabiting more or less restricted portions of the world's seacoasts, and to efforts to relate the resulting patterns to present and past environmental conditions.

Examples of such studies covering larger areas are my own investigation on the seaweed biogeography of the northern Atlantic Ocean (van den Hoek, 1975), and those of Lawson (1978) and Santelices (1980) on the floras of the tropical to subtropical Atlantic Ocean, and the temperate coast of Pacific South America, respectively.

To my knowledge, comparable analyses of seaweed floras on a world-wide scale have not yet been undertaken. The present study is a first attempt at such an analysis, which is limited to the distributions of rhodophytan genera (637 genera in total). Genera were chosen (and not species) for two reasons: firstly because generic distribution patterns were thought to possibly reflect events and conditions in the geologic past better than species distributions, and secondly because more taxonomic tangles and uncertainties were expected on the species than on the genus level. Furthermore, if world-wide trends do exist on the generic level, they can be also expected on the species level (not necessarily the other way round).

Some of the questions which can be asked are: Can tropical, warm temperate, cold temperate, antarctic and arctic floras really be distinguished from one another on the basis of generic distributions, and do such floras differ between Pacific and Atlantic Oceans? If patterns do emerge, can these be interpreted on the basis of present and past conditions and configurations of the oceans? And can these patterns be interpreted on the basis of either dispersal or vicariance or both?

MATERIAL AND METHODS

For the purpose of this study the world's coasts were divided into 22 regions, namely the Arctic Region, four cold temperate northern hemisphere regions, four warm temperate northern hemisphere regions, four tropical regions, four warm temperate southern hemisphere regions, four cold temperate southern hemisphere regions, and the Antarctic Region (see Fig. 1 and Table 1). These regions were defined by their temperature regimes (Table 2) and are comparable to those distinguished by Michanek (1979), Lüning (1985), and Briggs (1974). In the North Atlantic Ocean the interregional latitudinal boundaries coincide with floristic discontinuities, where many "southern" species more or less suddenly disappear (van den Hoek, 1975) polewards and are only replaced by few "northern" species. As such discontinuities reflect temperature discontinuities or substrate discontinuities along uninterrupted coastlines, the latitudinal boundaries used here need not coincide with floristic discontinuities. For instance, along the NW American coast the most pronounced floristic discontinuity is situated at Point Conception at c. 35°N, coinciding with a temperature discontinuity (Scagel, 1963; Murray & Littler, 1981), whereas the boundary between the cold temperate and warm temperate NE Pacific Regions is situated at 40°N (Cape Mendocino) in the present study. In Japan, the boundary between the cold temperate and warm temperate NW Pacific Regions appa-

Table 1. Phytogeographic regions (cf. Fig. 1 and Table 2). WS₂ includes Juan Fernandez Isl. and Galapagos Isl.; WS₃ includes S. Africa, Tristan da Cunha and Gough Island; CS₁ includes southern New Zealand, Stewart Isl., Chatham Isl., Bounty Isl., Antipodes Isl., Auckland Isl., Campbell Isl., Macquarie Isl.; CS₃ includes Lindsay Isl., Bouvet Isl., Marion Isl., Prince Edward Isl., Crozet Isl., Kerguelen Isl., McDonald Isl., Heard Isl.; CS₄ includes southern SE America, Falkland Isl., S. Georgia, S. Shetland Isl., S. Orkneys

Region	Approximate latitudinal extent
AR = Arctic Region	
CN ₁ = Cold temperate NW Pacific Region	55°N–40°N (Japan) and 35°N (Korea)
CN ₂ = Cold temperate NE Pacific Region	65°N–40°N
CN ₃ = Cold temperate NE Atlantic Region	70°N–55°N
CN ₄ = Cold temperate NW Atlantic Region	52°N–40°N
WN ₁ = Warm temperate NW Pacific Region	40°N–30°N (25°N in mainland China)
WN ₂ = Warm temperate NE Pacific Region	40°N–25°N
WN ₃ = Warm temperate NE Atlantic Region	55°N–20°N
WN ₄ = Warm temperate NW Atlantic Region	40°N–30°N
T ₁ = Tropical Indo-W Pacific Region	30° (25°)N–30°S
T ₂ = Tropical E Pacific Region	25°N–5°S (0° on Galapagos Isl.)
T ₃ = Tropical E Atlantic Region	20°N–10°S
T ₄ = Tropical W Atlantic Region	30°N–25°S
WS ₁ = Warm temperate SW Pacific Region	30°S–45°S
WS ₂ = Warm temperate SE Pacific Region	5°S–45°S
WS ₃ = Warm temperate SE Atlantic Region	10°S–45°S
WS ₄ = Warm temperate SW Atlantic Region	25°S–40°S
CS ₁ = Cold temperate SW Pacific Region	45°S–55°S
CS ₂ = Cold temperate SE Pacific Region	45°S–60°S
CS ₃ = Cold temperate SE Atlantic Region	45°S–50°S
CS ₄ = Cold temperate SW Atlantic Region	40°S–60°S
AN = Antarctic Region	

Table 2. Interregional latitudinal boundaries and the isotherms with which they approximately coincide. A winter isotherm is a February isotherm on the northern hemisphere and an August isotherm on the southern hemisphere. A summer isotherm is an August isotherm on the northern hemisphere and a February isotherm on the southern hemisphere

Latitudinal boundaries between regions	Boundary on, or halfway between	
	winter isotherm	summer isotherm
AR and CN ₁₋₄	0°C	8°C
CN ₁₋₄ and WN ₁₋₄	10°C	15°C
WN ₁₋₄ and T ₁₋₄	20°C	25°C
T ₁₋₄ and WS ₁₋₄	20°C	25°C
CS ₁₋₄ and WS ₁₋₄	10°C	15°C
AN and CS ₁₋₄	0°C	8°C

rently coincides with a distinct floristic discontinuity (Funahashi, 1973). Along the coasts of SW America the boundary between the Cold temperate SE Pacific Region and the Warm temperate SE Pacific Region, as well as that between the Warm temperate SE Pacific Region and the Tropical E Pacific Region do coincide with floristic discontinuities

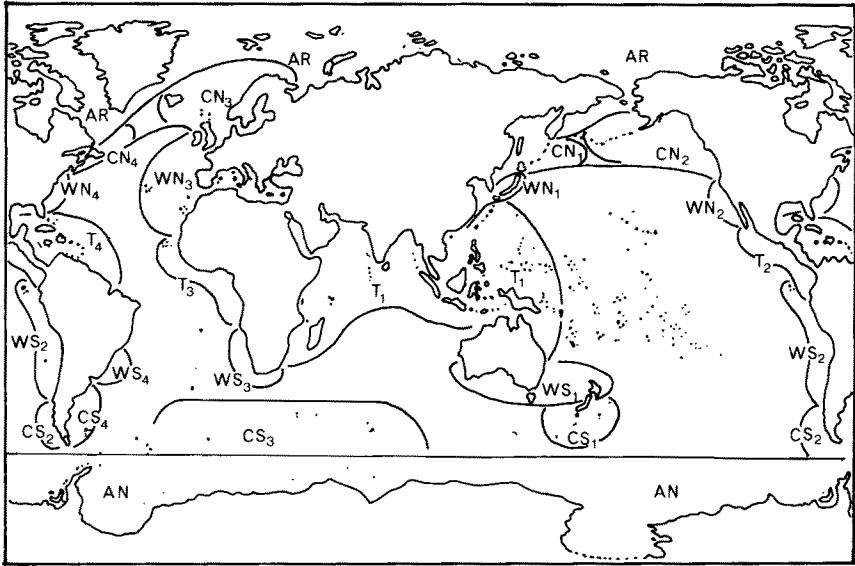


Fig. 1. The world's 22 phylogeographic seaweed regions. For abbreviations, see Table 1. (For the positions of interregional boundaries, see Table 2)

which are mainly characterized here by decreases in species numbers towards the equator (Santelices, 1980). Along the coast of SE America, the boundary between the Cold temperate SW Atlantic Region and the Warm temperate SW Atlantic Region also coincides with an equatorwards decrease in species numbers (Kühnemann, 1972). For most regions the detailed analyses necessary to establish floristic discontinuities are not available.

The degree of similarity in red algal generic floras between each pair of the 22 biogeographic regions was established by Jaccard's similarity index. Only the presence or absence of the 637 rhodophytan genera included in this study were noted for each region. A hierarchical clustering of the rhodophytan generic floras was carried out with an agglomerative centroid method (see van den Hoek, 1975, for application of these methods to algal biogeography). The results are presented in a dendrogram (Fig. 2). At a later stage, a clustering was carried out on the basis of genera lacking in the tropics and of non-endemic genera, in an effort to get a better insight into the relationships between non-tropical floras (145 genera). The results are given in the dendrogram of Fig. 3.

The relationships between non-tropical floras was further investigated by arranging the distributions of 118 of the above 145 non-tropical and non-endemic genera along series of regions which may serve at present, or may have served in the past, as dispersal routes for cool water genera ("almost" endemic genera restricted to pairs of adjacent cold- and warm temperate regions were also excluded, e.g. those restricted to the cold and the warm temperate NE Pacific regions). Uninterrupted coastlines or series of islands were taken to be, or to have been, the most likely dispersal routes. The two wide tropical belts of the Tropical W Pacific and W Atlantic regions are thought to have always been serious barriers to the dispersal of cool water genera, as well as continents

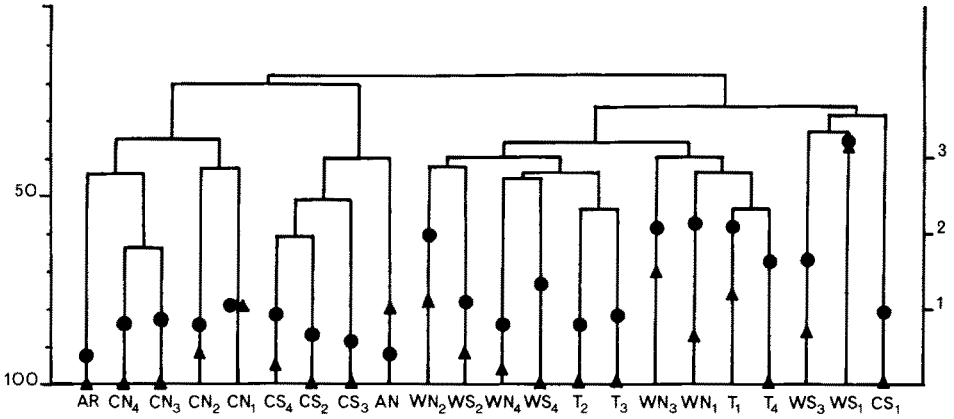


Fig. 2. Dendrogram depicting similarities of rhodophytan generic floras of the world's 22 phyto-geographic seaweed regions. For abbreviations denoting regions, see Table 1. Left vertical axis: percentage similarity. Right vertical axis: number of genera \times 100 (dots); percentage endemism \times 10 (triangles)

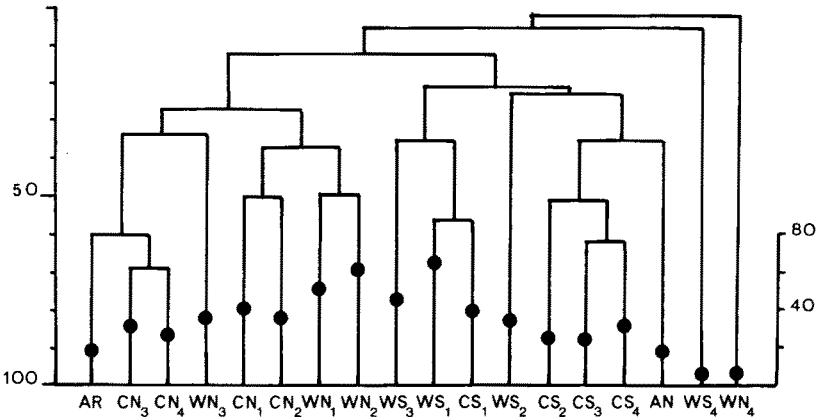


Fig. 3. Dendrogram depicting similarities of rhodophytan generic floras of the world's 18 non-tropical phyto-geographic seaweed regions, based on genera not occurring in the tropics and non-endemic to one region. Parasitic genera are also excluded. For abbreviations denoting regions, see Table 1. Left vertical axis: percentage similarity. Right vertical axis: number of genera (dots)

and wide ocean stretches. The following series of coastal stretches were included in this approach (cf. Fig. 1): 1) NW Pacific – NE Pacific – (tropical E Pacific) – SE Pacific + SW Atlantic – SE Atlantic – SW Pacific (Table 3); in this series the West Wind Drift in the southern hemisphere, or the Gondwana land connection, were included as possible dispersal routes; 2) NW Atlantic – NE Atlantic – (tropical E Atlantic) – SE Atlantic – SW Pacific (Table 4); 3) NW Pacific – (tropical W Pacific) – SW Pacific – SE Atlantic – SW Atlantic (Table 5).

This latter series was included to accommodate several genera with a widely disjunct Japanese – southern Australian / northern New Zealand distribution, and which are not connected by NE and SE Pacific occurrences.

Several genera with unusual disjunctions and which could not be arranged in Tables 1–3 are separately tabulated (Table 6).

For each of the 22 regions the numbers of tropical, tropical-warm temperate, warm temperate-arctic/antarctic, warm temperate – cold temperate, warm temperate, cold temperate – arctic/antarctic, antarctic, tropical-cold temperate, and tropical-arctic/antarctic genera were determined (Fig. 4).

The distributions of the 637 genera over the 22 regions were determined using the following publications: Abbott (1979), Abbott & Doty (1960), Abbott & Hollenberg (1976), Abbott & Yoshizaki (1981), Acléto (1973), Adey & MacIntyre (1973), Ardré (1970), Baardseth (1941), Ballisteros & Martinengo (1982), Børgesen (1934, 1942, 1943, 1944, 1945, 1949, 1950, 1951, 1952, 1953, 1954, 1957), Boudouresque & Perret (1977), Chamberlain (1965), Chapman (1969a+b, 1979), Chapman & Dromgoole (1970), Chapman & Parkinson (1974), Chihara (1975), Christensen & Thomsen (1974), Coppejans (1983), Dawson (1946), Dawson et al. (1964), Dixon & Irvine (1977), Earle (1969), Edelstein (1964), Fan (1961), Feldmann (1939, 1946, 1954), Feldmann & Magne (1964), Funahashi (1973), Funk (1955), Gayral (1958), Giaccone (1969), Giaccone & Longo (1976), Gordon (1972), Hackett (1975), Hawkes et al. (1978), van den Hoek (1978, 1982a, 1982b), van den Hoek & Donze (1967), Irvine (1982, 1983), Islam (1976), Itono (1977), Jaasund (1976,

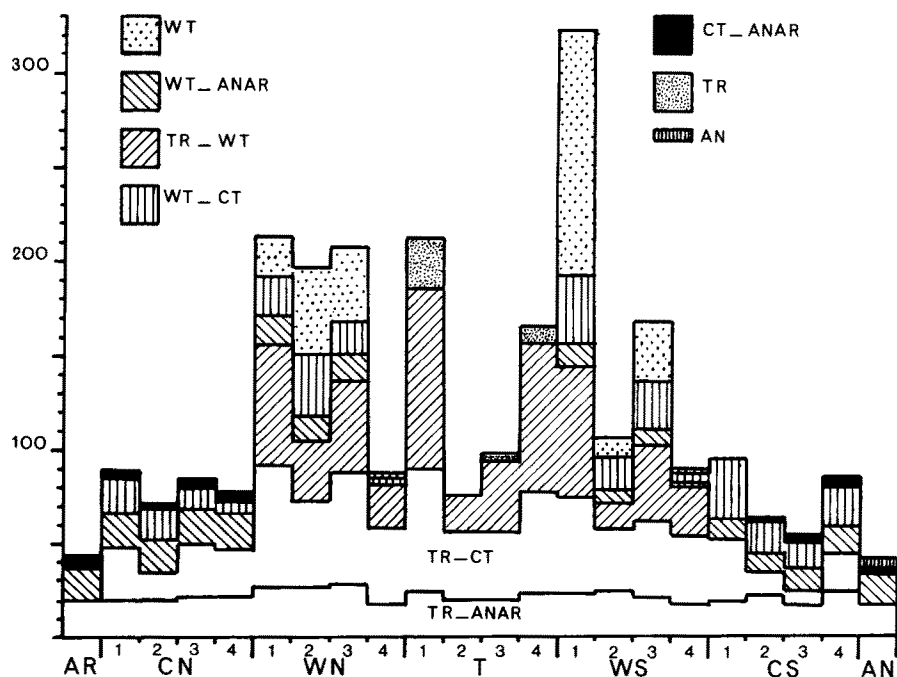


Fig. 4. Numbers of genera with different distribution types composing the rhodophytan generic floras of the world's 22 phylogeographic seaweed regions. For abbreviations denoting seaweed regions (horizontal axis), see Table 1. Left vertical axis: number of genera. WT = warm temperate; WT-ANAR = warm temperate to arctic/antarctic; TR-WT = tropical to warm temperate; WT-CT = warm temperate to cold temperate; CT-ANAR = cold temperate to arctic/antarctic; TR = tropical; AN = antarctic; TR-CT = tropical to cold temperate; TR-ANAR = tropical to arctic/antarctic

Table 3. Non-tropical (= cool water), non-endemic genera along coasts of the NE Atlantic (NEA), the Arctic Ocean (AR), The NW Pacific (NWP), the NE Pacific (NEP), the E Pacific tropics (TR), the SE Pacific (SEP), the SE Atlantic (SEA), the SW Pacific (SWP), Antarctic coasts (ANT). c = cold temperate, w = warm temperate

Taxa		NEA	AR	NWP	NEP	TR	SEP*	SEA	SWP	ANT
<i>Dumontia</i>	c	+	+	+						
	w	+		+						
<i>Neodilsea</i>	c	+	+	+						
	w			+						
<i>Mikamiella</i>	c			+	+					
	w									
<i>Tokidadendron</i>	c			+	+					
	w									
<i>Fimbrifolium</i>	c	+	+	+	+					
	w									
<i>Devalaerea</i>	c	+	+	+	+					
	w									
<i>Pantoneura</i>	c	+	+	+	+		+			wide N-S disjunction
	w									
<i>Odonthalia</i>	c	+	+	+	+					
	w			+	+					
<i>Turnerella</i>	c	+	+	+	+					
	w			+	+					
<i>Clathromorphum</i>	c	+	+	+	+					
	w			+	+					
<i>Halosaccion</i>	c	+	+	+	+					
	w			+	+					
<i>Ptilota</i>	c	+	+	+	+					
	w			+	+				+	queer N-S disjunction
<i>Nemalion</i>	c	+		+	+				+	N-S link through
	w	+		+	+			+	+	Atlantic? (Table 4)
<i>Membranoptera</i>	c	+	+	+	+					
	w	+		+	+					
<i>Palmaria</i>	c	+	+	+	+					
	w	+		+	+					
<i>Rhodomela</i>	c	+	+	+	+					
	w	+		+	+					
<i>Gloiosiphonia</i>	c	+		+	+					
	w	+		+	+					
<i>Dilsea</i>	c	+		+						
	w	+		+						
<i>Gloiopeltis</i>	c			+	+					
	w			+	+					
<i>Calliarthron</i>	c			+	+					
	w			+	+					
<i>Serraticardia</i>	c			+	+					
	w			+	+					
<i>Constantinea</i>	c			+	+					
	w				+					
<i>Neoptilota</i>	c			+						
	w			+	+					
<i>Farlowia</i>	c			+						
	w			+	+					
<i>Nienburgia</i>	c			+	+					
	w			+	+					
<i>Polyneura</i>	c			+						N-S link through
	w	+		+	+			+		Atlantic? (Table 4)
<i>Bonnemaisonia</i>	c	+								N-S link through
	w	+		+	+				+	Atlantic? (Table 4)
<i>Aeodes</i>	c			+					+	N-S link through
	w	+		+	+			+	+	Atlantic? (Table 4)
<i>Haraldiophyllum</i>	c									amphioceanic E-W
	w	+		+	+					disjunction
<i>Stenogramme</i>	c								+	N-S link through
	w	+		+	+				+	Atlantic? (Table 4)

Table 3 (continued)

Taxa		NEA	AR	NWP	NEP	TR	SEP*	SEA	SWP	ANT	
<i>Rhodoptilum</i>	c										
	w			+	+						
<i>Sorella</i>	c										
	w			+	+						
<i>Binghamia</i>	c										
	w			+	+						
<i>Pikea</i>	c										
	w			+	+						
<i>Neopolyporolithon</i>	c										
	w			+	+						
<i>Yamadaea</i>	c										
	w			+	+						
<i>Coeloseira</i>	c										also in warm SW Atlantic
	w			+	+						
<i>Bossiella</i>	c			+	+		+				
	w			+	+		+				
<i>Scagelia</i>	c				+						
	w				+		+				
<i>Leptocladia</i>	c										
	w				+		+				
<i>Sciadophycus</i>	c										
	w				+		+				
<i>Anisocladella</i>	c						+				
	w				+		+				
<i>Chondrus</i>	c	+		+	+		+			+	
	w	+		+	+		+				
<i>Phycodrys</i>	c	+	+	+	+		+	+	+	+	
	w	+		+	+		+				
<i>Delesseria</i>	c	+		+	+		+	+	+	+	also N-S link through Atlantic (Table 4)
	w	+		+	+		+	+	+		also N-S link through Atlantic (Table 4)
<i>Rhodochorton</i>	c	+	+	+	+		+	+	+	+	
	w	+		+	+		+	+	+		
<i>Leptophytum</i>	c	+	+	+	+		+	+	+	+	
	w	+		?	+		?	?	+		
<i>Rhodoglossum</i>	c			+	+		+	+	+	+	
	w			+	+		+	+	+		
<i>Iridaea</i>	c			+	+		+	+	+	+	
	w			+	+		+	+	+		
<i>Branchioglossum</i>	c			+							also in warm NW Atlantic
	w			+	+		+		+		
<i>Prionitis</i>	c			+						+	
	w			+	+		+	+			
<i>Erythroglossum</i>	c			+	+		+	+			
	w	+		+	+		+		+		
<i>Porphyropsis</i>	c	+									
	w	+		+	+		+		+		
<i>Hymenena</i>	c			+	+		+	+	+		
	w			+	+		+	+	+		
<i>Schimmelmannia</i>	c										also N-S link through Atlantic (Table 4)
	w	+		+	+		+	+			
<i>Platythamnion</i>	c				+						
	w			+	+		+		+		
<i>Tayloriella</i>	c							+			
	w				+		+	+			
<i>Botryoglossum</i>	c						+	+			
	w				+			+	+		
<i>Pugetia</i>	c									+	
	w				+		+	+	+		
<i>Acanthococcus</i>	c						+	+			also in warm SW Atlantic
	w						+	+			
<i>Aristothamnion</i>	c						+	+			
	w						+	+			
<i>Pseudophycodrys</i>	c						+				* Tristan da Cunha
	w							+	*		

Table 3 (continued)

Taxa		NEA	AR	NWP	NEP	TR	SEP*	SEA	SWP	ANT	
<i>Pseudolaingia</i>	c						+	+			
	w						+				
<i>Cladodonta</i>	c						+	+			
	w						+	+			
<i>Polyporolithon</i>	c						+	+	+		* Tristan da Cunha
	w										
<i>Ballia</i>	c						+	+	+	+	
	w						+	+	+		
<i>Chaetangium</i>	c						+	+	+		
	w						+	+	+		
<i>Platyclinia</i>	c						+	+			
	w						+		+		
<i>Lophurella</i>	c						+	+	+		
	w							+	+		* Tristan da Cunha
<i>Pseudolithophyllum</i>	c						+	+	+	+	
	w						+	+	+		
<i>Pachymenia</i>	c								+		
	w						+	+	+		
<i>Epymenia</i>	c						+	+	+		
	w							+	+		
<i>Mychodea</i>	c						+		+		
	w							+	+		
<i>Curdiea</i>	c						+	+	+	+	
	w								+		
<i>Perithamnion</i>	c						+	+	+	+	
	w								+		
<i>Carradoria</i>	c										also in warm SW Atlantic
	w							+	+		
<i>Hemineura</i>	c										
	w							+	+		
<i>Pseudoanemonia</i>	c										
	w							+	+		
<i>Aphanocladia</i>	c						+		+		also in warm SW Atlantic
	w								+		
<i>Leptosarca</i>	c						+		+		
	w								+		
<i>Cladhymenia</i>	c							+	+		
	w								+		
<i>Hymenocladia</i>	c								+		
	w							+	+		
<i>Kuetzingia</i>	c										
	w							+	+		
<i>Episporium</i>	c										
	w							+	+		
<i>Dictymenia</i>	c										
	w							+	+		
<i>Glaphyrymenia</i>	c										
	w							+	+		
<i>Erythrymenia</i>	c										
	w							+	+		
<i>Erythroclonium</i>	c										
	w							+	+		
<i>Metamastophora</i>	c										
	w							+	+		
<i>Dicurella</i>	c										
	w							+	+		
<i>Ptilophora</i>	c										
	w							+	+		
<i>Thamnophyllis</i>	c										
	w							+	+		
<i>Spongoclonium</i>	c									+	
	w								+		

* including cool SW Atlantic

Table 4. Non-tropical (= cool water), non-endemic genera along coasts of the NE Pacific (NEP), the NW Pacific (NWP), the Arctic (AR), the NW Atlantic (NWA), the NE Atlantic (NEA), the E Atlantic tropics (TR), the SE Atlantic (SEA), the SW Atlantic (SWA), the SW Pacific (SWP), Antarctic coasts (ANT). c = cold temperate, w = warm temperate

Taxa		NEP	NWP	AR	NWA	NEA	TR	SEA	SWA	SWP	ANT	
<i>Neodilsea</i>	c		+	+	+							
	w		+									
<i>Odonthalia</i>	c	+	+	+	+	+						
	w	+	+									
<i>Clathromorphum</i>	c	+	+	+	+	+						
	w	+	+									
<i>Ptilota</i>	c	+	+	+	+	+						wide N-S disjunction
	w	+	+							+		
<i>Halosaccion</i>	c	+	+	+		+						
	w	+	+									
<i>Turnerella</i>	c	+	+	+	+	+						
	w	+	+									
<i>Fimbrifolium</i>	c	+	+	+	+	+						
	w											
<i>Devalaerea</i>	c	+	+	+	+	+						
	w											
<i>Pantoneura</i>	c	+	+	+	+	+						
	w								+			
<i>Palmaria</i>	c	+	+	+	+	+						
	w	+	+									
<i>Rhodomela</i>	c	+	+	+	+	+						
	w	+	+									
<i>Dumontia</i>	c		+	+	+	+						
	w		+									
<i>Membranoptera</i>	c	+	+	+	+	+						
	w	+										
<i>Polyides</i>	c			+	+	+						
	w											
<i>Gloiosiphonia</i>	c	+	+		+	+						
	w	+	+									
<i>Cystoclonium</i>	c		+		+	+						
	w											
<i>Dilsea</i>	c	+				+						
	w	+										
<i>Plumaria</i>	c				+	+						
	w											
<i>Furcellaria</i>	c				+	+						
	w											
<i>Compsothamnion</i>	c					+						
	w				+	+						
<i>Rhodochorton</i>	c	+	+	+	+	+		+	+	+	+	also N-S link through Pacific (Table 3)
	w	+	+					+	+	+	+	N-S link rather through Pacific (Table 3)
<i>Phycodrys</i>	c	+	+	+	+	+		+	+	+	+	N-S link rather through Pacific (Table 3)
	w	+	+									
<i>Leptophytum</i>	c	+	+	+	+	+		+	+	+	+	
	w	+										
<i>Phyllophora</i>	c			+	+	+			+	+	+	wide N-S disjunction
	w											
<i>Delesseria</i>	c	+	+			+		+	+	+	+	also N-S link through Pacific (Table 3)
	w	+	+					+		+	+	N-S link rather through Pacific (Table 3)
<i>Nemalion</i>	c	+	+		+	+						
	w	+	+					+	+	+		
<i>Chondrus</i>	c	+	+		+	+			+		+	N-S link rather through Pacific (Table 3)
	w		+									N-S link rather through Pacific (Table 3)
<i>Porphyropsis</i>	c				+	+						N-S link rather through Pacific (Table 3)
	w	+	+		+	+				+		wide N-S disjunction
<i>Bonnemaisonia</i>	c					+						wide N-S disjunction
	w	+	+							+		
<i>Aeodes</i>	c		+									
	w	+	+			+		+		+		

Table 4 (continued)

Taxa		NEP	NWP	AR	NWA	NEA	TR	SEA	SWA	SWP	ANT	
<i>Apoglossum</i>	c						+					
	w						+	+		+		
<i>Schimmelmannia</i>	c											also N-S link through Pacific (Table 3)
	w	+	+				+	+				
<i>Polyneura</i>	c		+									
	w	+	+				+	+				
<i>Alsidium</i>	c											
	w						+	+				
<i>Streblocladia</i>	c										+	
	w						+	+				
<i>Erythroglossum</i>	c							+				
	w	+	+				+					
<i>Stenogramme</i>	c										+	widely disjunct
	w	+	+				+			+		

Table 5. Non-tropical (= cool water), non-endemic genera along coasts of the NW Pacific (NWP), the W Pacific tropics (TR), the SW Pacific (SWP), the SE Atlantic (SEA), the SW Atlantic (SWA), Antarctic coasts (ANT). c = cold temperate, w = warm temperate

Taxa		NWP	TR	SWP	SEA	SWA	ANT	
<i>Tylotus</i>	c							
	w	+		+	+			
<i>Trematocarpus</i>	c			+		+		also in NWA (warm) and SEP (warm)
	w	+		+	+			
<i>Schizoseris</i>	c	+		+	+	+		
	w	+		+	+			
<i>Ptilonia</i>	c	+		+	+	+	+	
	w	+		+				
<i>Delisea</i>	c			+	+	+	+	
	w	+		+	+			
<i>Dasyclonium</i>	c			+				
	w	+		+	+			
<i>Marionella</i>	c			+				
	w	+		+	+			
<i>Rhodopeltis</i>	c							
	w	+		+				
<i>Cirrucarpus</i>	c			+				
	w	+		+				

1977), Johansen (1981), Joly (1967), Jónsson (1912), Kapraun (1980), Kraft (1981), Kraft & Woelkerling (1981), Kühnemann (1972), Kylin (1956), Lawson & John (1977, 1982), Lee (1980), Levring (1960, 1974), Lund (1951, 1959), Makienko (1975), Meñez & Mathieson (1981), Munda (1972, 1979), Nizamuddin et al. (1979), Nizamuddin & Gessner (1970), Norris (1957), Oliveira Filho (1977), Papenfuss (1964, 1968), Parke & Dixon (1976), Parsons (1975), Pedersen (1976), Perestenko (1980), Perez-Cirera (1975), Pham-Hoàng Hô (1969), Pielou (1978), Rueness (1977), Santelices (1980), Santelices & Abbott (1978), Scagel (1953, 1957), Schneider et al. (1979), Schnetter & Meyer (1982), Searles (1968), Searles & Schneider (1978), Segawa (1965), Shepherd & Womersley (1981), Simons

Table 6. Non-tropical (= cool water), non-endemic genera with irregular disjunct distributions. (For explanation of abbreviations, see texts to Tables 3–5)

Taxa		AR	NWP	NEP	NWA	NEA	TR	SWP	SEP	SWA	SEA	AN
<i>Cruoria</i>	c	+			+	+						
	w		+			+						
<i>Pseudoscinaia</i>	c											
	w			+				+				
<i>Petroglossum</i>	c											
	w			+	+							
<i>Holmesia</i>	c											
	w			+								+
<i>Dermocorynus</i>	c											
	w			+								
<i>Brongniartella</i>	c					+			+			
	w					+			+			
	w		+									+
<i>Haraldiophyllum</i>	c											
	w		+	+		+						

(1976), South (1976), South & Hooper (1980), Sparling (1957), Svendsen (1959), Taylor (1945, 1957, 1960, 1971), Tokida (1954), Tsuda & Wray (1977), Velasquez et al. (1975), Vozžinskaja (1964, 1965), Wagner (1954), Weber-van Bosse (1928), Wilce (1959), Woelkerling (1980), Wollaston (1979), Womersley (1965, 1981), Womersley & Abbott (1968), Womersley & Bailey (1970), Womersley & Norris (1971), Wynne (1983), Zaneveld (1966), Zinova (1955).

RESULTS

In the dendrogram (Fig. 2) depicting the overall similarities of the rhodophytan generic floras of the 22 regions the six following clusters can be distinguished on the 40–45 % similarity-level:

- (1) an Arctic-cold temperate N Atlantic cluster (AR, CN₄ and CN₃, Fig. 1);
- (2) a cold temperate N Pacific cluster (CN₁ and CN₂, Fig. 1);
- (3) an Antarctic-cold temperate southern hemisphere cluster (CS₂, CS₄, CS₃, AN, Fig. 1);
- (4) a warm temperate E Pacific cluster, including northern and southern hemisphere E Pacific warm temperate floras (WN₂ and WS₂);
- (5) a poor tropical-warm temperate cluster, including the E Pacific and E Atlantic tropical floras, as well as the NW Atlantic and SW Atlantic warm temperate floras (T₂, T₃, WN₄, WS₄); cluster 5 is linked to cluster 4 on the 40 % level;
- (6) a rich tropical-warm temperate cluster, including the Indo W Pacific and W Atlantic tropical floras, as well as the NE Atlantic and NW Pacific warm temperate floras (T₁, T₄, WN₃, WN₁).

The following three floras stand apart and have a high individuality:

- (7) the warm temperate SW Pacific flora of southern Australia and northern New Zealand (WS₁);
- (8) the warm temperate SE Atlantic flora of southern Africa (WS₃);

(9) the cold temperate SW Pacific flora of southern New Zealand and adjacent islands (CS₁).

The above six clusters and three floras with high individuality are indicated in Fig. 5 by areas with different types of hatching.

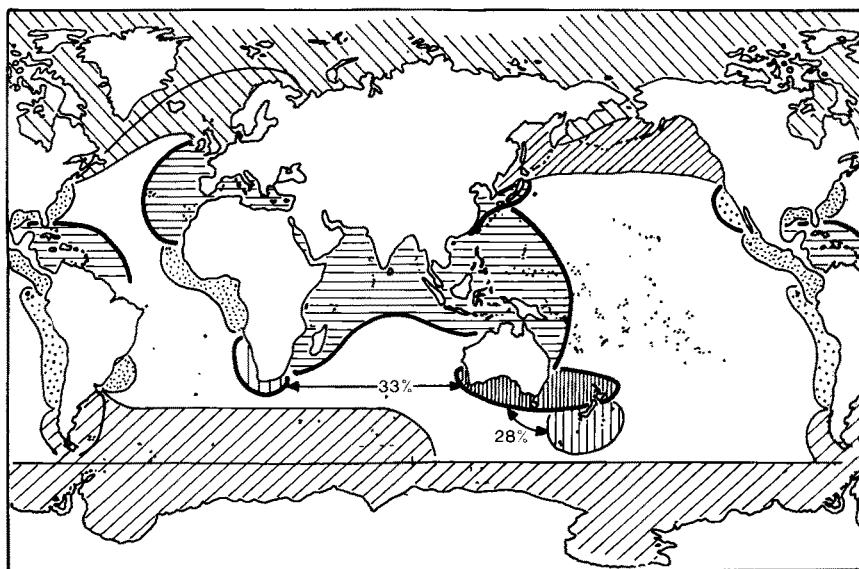


Fig. 5. Map illustrating clusters of regions on the 40–45 % similarity level in Fig. 2. Regions with the same type of hatching are in one cluster (compare with Fig. 1 for regions). The Warm temperate SE Atlantic Region (WS₃), the Warm temperate SW Pacific Region (WS₁) and the Cold temperate SW Pacific Region (CS₁) form a cluster (at about the 30 % level, cf. Fig. 2). Thick lines delimit rich floras (> 150 genera), thin lines poor floras (< 110 genera)

In Fig. 2, two broad “superclusters” at the 20 to 25 % similarity level encompass the cold temperate, arctic and antarctic floras on the one hand, and the warm temperate and tropical floras on the other hand. This second supercluster also includes the cold temperate SW Pacific flora.

For the second clustering only genera lacking in the tropics and not endemic to one of the regions were used. In this clustering the tropical regions are of course not included. For practical reasons, parasitic genera were also excluded, as they are irregularly represented in the floristic accounts consulted. In this way 145 genera remained of the total of 637. The total number of cool water genera (including non-tropical endemics) amounts to 307. This difference indicates that the majority of rhodophyten genera do occur in the tropics. The results of the second clustering, which are given in the dendrogram of Fig. 3, enhance some of the results of the first clustering, especially by distinguishing the following clusters on the 50–60 % similarity level:

- (1) an Arctic-cold temperate N Atlantic cluster (AR, CN₃, CN₄, cf. Fig. 1);
- (2) a cold temperate N Pacific cluster (CN₁, and CN₂);
- (3) a cold temperate southern hemisphere cluster (CS₂, CS₃, CS₄, see Fig. 1) which is linked to the Antarctic flora at the 35 % similarity level.

The removal, from this clustering, of genera with broad tropical to warm temperate, tropical to cold temperate, and tropical to arctic/antarctic distributions (in short: with tropical to cool water distributions) (see Fig. 4) apparently stresses the fact that cold temperate floras of both hemispheres differ markedly from one another in their cool water rhodophytan genera, although they apparently share a number of (amphiequatorial) genera. This removal of broadly occurring genera even stresses the distinct individuality of the Arctic-cold temperate N Atlantic cluster versus the cold temperate N Pacific cluster. However, Fig. 6 demonstrates that the large majority of the cool-water

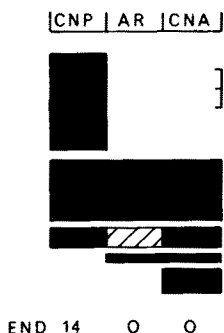


Fig. 6. Numbers of non-endemic genera not occurring in the tropics shared by the Cold temperate N Pacific regions (CNP), the Arctic Region (AR) and the Cold temperate N Atlantic regions (CNA).
END = number of endemic genera

genera in the Arctic and cold temperate N Atlantic Regions are shared by the cold temperate N Pacific Regions (21 of 29 genera). The difference between both pairs of regions is apparently caused in the first place by the large number (39) of temperate genera present in the N Pacific but absent in the Arctic and N Atlantic.

At about the 50–60 % similarity level, two more clusters can be distinguished which were not present in the first clustering (compare Fig. 3 with Fig. 2):

- (4) a warm temperate N Pacific cluster (WN₁ and WN₂, Fig. 1), which is linked to the cold temperate N Pacific cluster at the 36 % similarity level;
- (5) a warm to cold temperate SW Pacific cluster (WS₁ and CS₁, Fig. 1), uniting the southern Australian and the New Zealand floras; this cluster is linked to the warm temperate SE Atlantic flora (southern Africa, WS₃) at the 33 % similarity level.

The above five clusters at the 50–60 % level, and several separate floras, are illustrated in Fig. 7 by areas with different types of hatching.

Genera with a broad tropical-arctic/antarctic, tropical-cold temperate and tropical-warm temperate distribution form the majority of rhodophytan genera in the two N Pacific warm temperate floras (73 % of the warm temperate NW Pacific flora and 53 % of the warm temperate NE Pacific flora, respectively; cf. Fig. 4). Exclusion of these broadly distributed genera results in clustering of both floras on the 50 % similarity level, which means that they have a high relatedness with regard to their cool-water genera.

In the N Atlantic Ocean the situation is quite different: here the warm temperate floras on both sides of the ocean (WN₃ and WN₄, Fig. 1) are unrelated (Figs 2, 3). Both floras do predominantly consist of broadly distributed tropical to cool-water genera: the

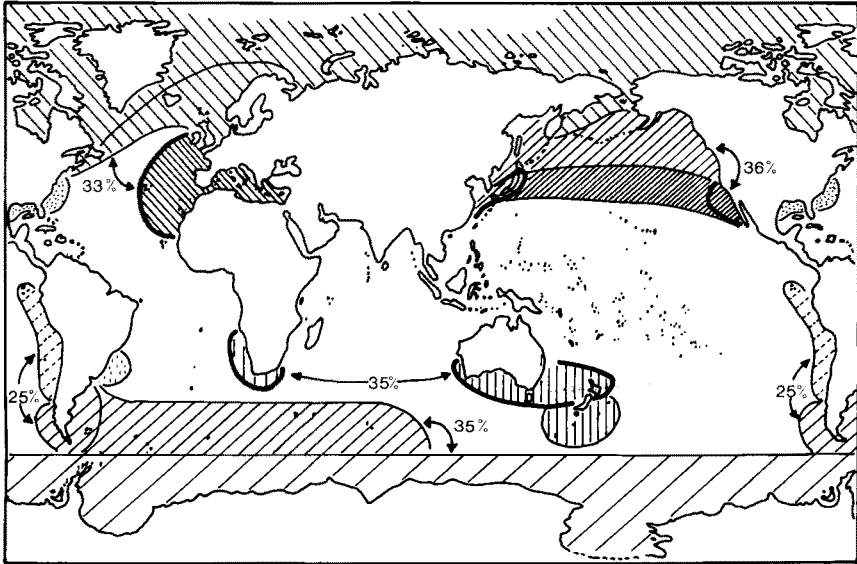


Fig. 7. Map illustrating clusters of non-tropical regions on the 50–60 % similarity level in Fig. 3, which is based on genera not occurring in the tropics and non-endemic to one region. Regions with the same type of hatching are in one such cluster (compare with Fig. 1 for regions). Clusterings on lower similarity levels are indicated by connecting arrows. The Warm temperate NW Atlantic Region (WN_4) and the Warm temperate SW Atlantic Region (WS_4) are highly unrelated here to anyone of the other regions. Thick lines delimit rich floras (> 150 genera), thin lines poor floras (< 110 genera)

warm temperate NE Atlantic flora (WN_3) for 66 %, the warm temperate NW Atlantic flora (WN_4) even for 97 %. Exclusion of the above broadly distributed genera in the second clustering will of course strongly enhance the difference between both floras. The warm temperate NW Atlantic flora is apparently a depauperate extension of the rich tropical W Atlantic Flora, whereas the warm temperate NE Atlantic flora has a strong individuality with regard to its cool-water genera. Fig. 8 further illustrates this difference between the warm temperate floras of the N Pacific and N Atlantic. In the N Pacific the warm temperate floras on the western and eastern sides of the ocean are highly related (with regard to cool-water genera), as they share 39 genera, of which 22 are disjunct as they are lacking in one or both cold temperate regions. In the N Atlantic, on the other hand, the warm temperate floras on the western and eastern sides of the ocean are highly unrelated, as they share only 2 genera (one of which has a disjunct distribution).

In both the N Pacific and the N Atlantic Ocean the warm temperate and cold temperate floras are mutually related at about the 35 % level (except for the warm temperate NW Atlantic flora) (Figs 3, 7), when they are clustered on the basis of genera lacking in the tropics and of non-endemic genera. This clustering also reveals an individuality of the N Pacific temperate flora versus that of the Arctic-N Atlantic temperate flora.

Above, the high proportion has been mentioned of more or less broadly distributed tropical to cool water genera in the warm temperate floras of the northern hemisphere:

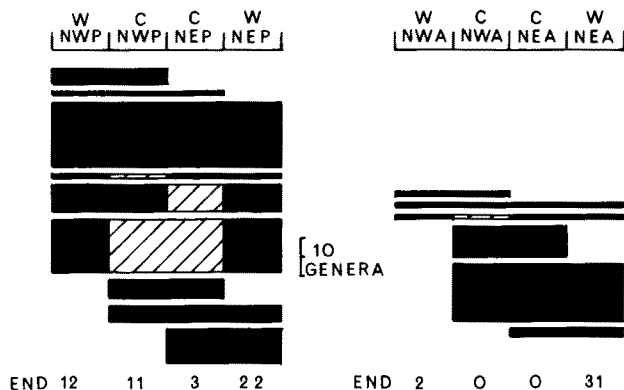


Fig. 8, left: Numbers of non-endemic genera not occurring in the tropics shared by the Warm temperate NW Pacific region (WNWP), the Cold temperate NW Pacific region (CNWP), the Cold temperate NE Pacific region (CNEP), and the Warm temperate NE Pacific region (WNEP). END = numbers of endemic genera. Fig. 8, right: Numbers of non-endemic genera not occurring in the tropics shared by the Warm temperate NW Atlantic region (WNWA), the Cold temperate NW Atlantic region (CNWA), the Cold temperate NE Atlantic region (CNEA), and the Warm temperate NE Atlantic region (WNEA)

73 % of the warm temperate NW Pacific flora (of 216 genera in total); 53 % of the warm temperate NE Pacific flora (of 202 genera in total); 97 % of the warm temperate NW Atlantic flora (of 85 genera in total); and 66 % of the warm temperate NE Atlantic flora (of 208 genera in total). These tropical to cool water genera play an important role in determining the similarities among these floras and the tropical floras, as established in the first overall clustering (Figs 2, 5). Two "rich" (c. 210 genera) northern hemisphere warm temperate floras (NW Pacific, NE Atlantic) with high proportions of tropical to cool water genera form the previously mentioned "rich tropical-warm temperate cluster" together with the Indo W Pacific and the W Atlantic tropical floras (WN₃, WN₁, T₁, T₄; cf. Figs 1 and 5). As exclusion of these tropical to cool water genera results in a clustering (Fig. 3) which stresses the separateness of the temperate N Pacific and N Atlantic floras, their presence must be responsible for the constitution of this "rich tropical-warm temperate cluster". This latter cluster does not encompass the rich (c. 200 genera) warm temperate NE Pacific flora (WN₂). The proportion of tropical to cool water genera in this latter flora (53 %), however, is distinctly lower than in the warm temperate NW Pacific flora (73 %) and the warm temperate NE Atlantic flora (66 %). Also the absolute number of cool water genera (= not occurring in the tropics) is distinctly higher in the warm temperate NE Pacific flora than in the warm temperate NE Atlantic and NW Pacific floras (Fig. 4). In other words: the warm temperate NE Pacific flora has a more temperate character than both other rich northern hemisphere warm temperate floras.

Two tropical floras, the tropical E Pacific flora and the tropical E Atlantic flora, form the previously mentioned "poor tropical-warm temperate cluster", together with the warm temperate NW Atlantic and SW Atlantic warm temperate floras (Figs 2, 5). These four floras are characterized by low numbers of genera (c. 75–95, cf. Fig. 4) which almost all have wide tropical to cool water distributions. These floras apparently differ from the two rich tropical floras by the absence of numerous genera, mainly tropical and tropical

to warm temperate ones. Both the warm temperate NW and SW Atlantic floras (WN_4 and WS_4 , Fig. 1) occupy marginal positions in the second clustering (Fig. 3) as these two floras consist almost entirely of tropical to cool water genera, which are not included in this second clustering. This indicates that both these floras are depauperate extensions of the rich tropical W Atlantic flora.

In the second clustering the cold temperate SW Pacific flora (CS_1 ; southern New Zealand and adjacent islands) and the warm temperate SW Pacific flora (WS_1 , southern Australia and northern New Zealand) are quite narrowly related (55 %, Figs 3, 7), and this is in contrast to the first clustering (Figs 2, 5) where they are much more distantly related. Obviously the exclusion, in the second clustering, of the numerous tropical to cool water genera and warm temperate endemic genera has greatly reduced the difference between both floras. The remaining numbers of warm temperate-arctic/antarctic genera and warm temperate-cold temperate genera are approximately equal (c. 45) in both floras (compare WS_1 and CS_1 in Fig. 4), and only these are compared in the second clustering. As in the first clustering, the nearest related flora (on the 33 % level) is the warm temperate SE Atlantic flora (WS_3 , southern Africa). Both clusterings stress the separate but interrelated positions of the temperate floras of southern Africa, southern Australia and New Zealand. The warm temperate flora of southern Australia and northern New Zealand (the warm temperate SW Pacific flora, WS_1) has certainly the highest individuality of all 22 benthic seaweed floras here distinguished, with its high numbers of rhodophytan genera (328) and of endemic rhodophytan genera (105) (Figs 2, 4).

The warm temperate SE Pacific flora stands quite apart in the second clustering (Figs 3, 7), where it is distantly linked, only on about the 22 % level, with the cluster of the cold temperate, southern hemisphere floras (CS_2 , CS_3 , CS_4) and Antarctica (AN) (Fig. 3). The 43 % similarity, in the first clustering (Fig. 2), with the warm temperate NE Pacific flora is apparently mainly caused by the widely distributed tropical-cool water genera.

The relationships among the southern hemisphere temperate floras are further illustrated by Fig. 9; 46 of the 82 non-endemic cool water genera are widely distributed over cold temperate as well as warm temperate regions in the southern hemisphere, 5 are restricted to cold temperate regions (2 also occur in Antarctica), and 32 to the warm temperate regions. Of these, 16 are restricted to both the warm temperate SE Atlantic Region (S Africa) and the warm temperate SW Pacific Region (southern Australia and northern New Zealand). These latter two regions also share 16 cool water genera with wide distributions. The above 32 cool water genera shared by the floras of southern Africa and southern Australia plus New Zealand are mainly responsible for a certain measure of relatedness between both floras, whereas their high numbers of endemic genera (especially of the warm temperate SW Pacific flora) set them apart from other southern hemisphere temperate floras.

Fig. 9 shows that, in contrast to especially the warm temperate SW Pacific flora, the warm temperate SE Pacific flora does not have a pronounced individuality, although it stands quite apart in the second clustering (Fig. 3); 21 of the 35 cool water genera are shared with other southern hemisphere temperate regions, and of these 18 have a wide cold and warm temperate distribution. There are only 4 endemic genera, and 4 genera which are only shared with the warm temperate NW Pacific Region. In short, the warm

temperate SE Pacific flora of rhodophyтан genera can be characterized as a depauperate southern hemisphere warm temperate flora.

A considerable number (47) of cool water rhodophyтан genera (i.e., genera absent from the tropics) occur on both the northern and the southern hemisphere. Of these, 24



Fig. 9. Numbers of non-endemic genera not occurring in the tropics shared by the Antarctic Region, the cold temperate and warm temperate regions of the southern hemisphere. AN = Antarctic; SWA = SW Atlantic; SEA = SE Atlantic; SWP = SW Pacific; SEP = SE Pacific. END = number of endemic genera. Bar = 10 genera

seem to "jump" the tropics along E Pacific coasts, 11 along E Atlantic coasts (of these, 3 also "jump" the E Pacific tropics), whereas 9 seem to "jump" the wide tropics along W Pacific coasts (Fig. 10, which summarizes Tables 3, 4 and 5). Still another 6 amphiequatorial genera have irregular distributions (Table 6); 71 cool water non-endemic genera are restricted to either the northern hemisphere (37), or the southern hemisphere (34). The total number of cool water genera (including endemic genera, and "near-endemic" genera restricted to adjacent cool- and warm temperate regions) which are restricted to either the northern hemisphere or the southern hemisphere, amounts to 307. Of these, 131 are restricted to the northern hemisphere and 176 to the southern hemisphere (of this latter group 105 are endemic genera of the warm temperate SW Pacific region).

Thus only a comparatively small proportion (15 %) of all cool water rhodophyтан genera (= not occurring in the tropics) has an amphiequatorial distribution. However, quite a large proportion (40 %) of more or less widely distributed (non-endemic) cool water genera occur on both sides of the equator.

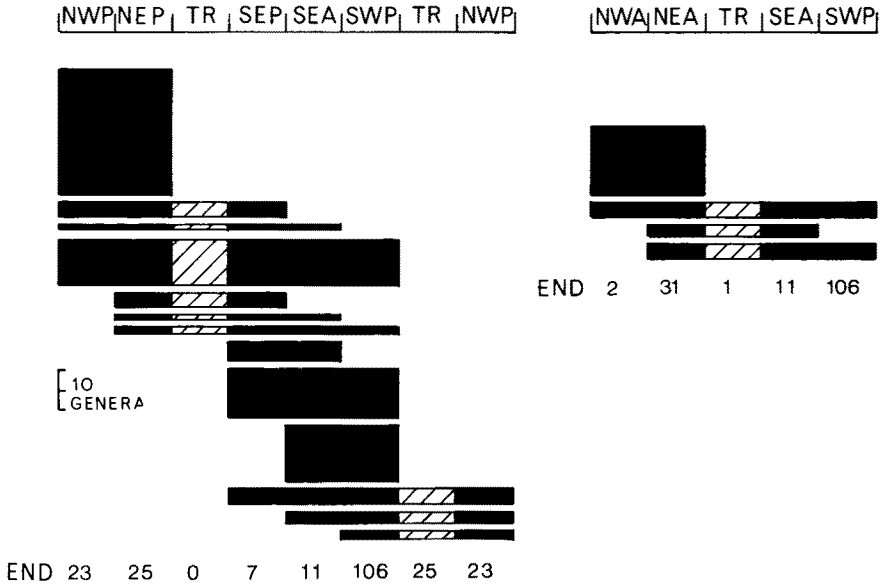


Fig. 10, left: Numbers of non-endemic genera not occurring in the tropics shared by the NW Pacific (NWP), NE Pacific (NEP), SE Pacific (SEP), SE Atlantic (SEA) and SW Pacific (SWP). END = numbers of endemic genera. Fig. 10, right: Numbers of non-endemic genera not occurring in the tropics shared by the NW Atlantic (NWA), NE Atlantic (NEA), the SE Atlantic (SEA) and the SW Pacific (SWP)

12 of the 21 genera, shared by the NW Pacific and the SW Pacific regions, occur all along the "route" NW Pacific – NE Pacific – SE Pacific + SW Atlantic – SE Atlantic – SW Pacific (Fig. 10). This suggests that these genera may have crossed the E Pacific tropics. However, the remaining 9 genera shared by the NW Pacific and the SW Pacific regions do not occur along this indirect "route" and seem to have directly crossed the wide Indo-W Pacific tropical belt.

DISCUSSION

Apparently rhodophytan genera are not distributed across the world's oceans in a haphazard way, but according to certain patterns. Fig. 5, which illustrates the results of the first overall clustering, stresses the relatedness of the rich tropical Indo W Pacific flora, the rich tropical W Atlantic flora, and the rich warm temperate NW Pacific and NE Atlantic floras. These four floras form the "rich tropical-warm temperate cluster" on the 40–50 % similarity level (Fig. 2). Within this cluster, the two rich tropical floras have a similarity of c. 55 %. This cluster is highly disjunct, as it is traversed, in N-S direction, by the African-Asian landmass and by the Atlantic Ocean. It can possibly be interpreted as being composed of vicariant portions of an originally continuous tropical to warm temperate Tethyan flora of rhodophytan genera. This interpretation pertains of course only to the genera shared by the four floras. The definitive closure of the Tethys by relative uplift in the Middle East separated the Indo W Pacific and Atlantic floras at

about the middle Miocene ($\sim 18.10^6$ y; Hallam, 1981). Towards the end of the Miocene the remnant of the Tethys Ocean, the Mediterranean became also separated from the Atlantic and subsequently more or less evaporated (Messinian salinity crisis, $\sim 5.10^6$ y). After that it was refilled with Atlantic seawater and biota. Separation of the E and W Atlantic portions of the Tethys started already in the late Cretaceous ($\sim 80.10^6$ y) with the opening of the S Atlantic along its whole length. However, in the north uninterrupted coastlines and stepping stone archipelagos have connected the W and E Atlantic up into the Eocene ($\sim 40.10^6$ y) when the Greenland-Scotland Ridge across the opening N Atlantic separated the Atlantic Ocean from the Arctic Ocean. At that time the climate in the whole N Atlantic Ocean was tropical to warm temperate so that exchange of tropical to warm temperate genera between the W and E Atlantic along this ocean's northern coasts was possible (Frakes, 1979).

This situation may have existed again, after a cooler period, in the late Oligocene ($\sim 30.10^6$ y), and once again (after another period of cooling) in the early Miocene ($\sim 20.10^6$ y) (Frakes, 1979) when the Greenland-Scotland Ridge had gradually subsided to a series of islands across the northern N Atlantic (Thiede & Eldholm, 1983).

In Eocene W Europe, as a result of the high sea levels, was an intricate archipelago with ever changing configurations in the course of geologic time; this possibly promoted rich quasi-sympatric speciation (cf. Pielou, 1977, 1978) of the warm temperate and tropical seaweed floras.

The question now arises whether recent transoceanic dispersal of seaweed species between Caribbean and warm temperate Europe and W Africa cannot better explain the similarity between the floras of their rhodophyten genera. However, the strong relatedness (55 % level) between the highly disjunct rich tropical floras of the W Atlantic and Indo W Pacific Oceans favours vicariance as an explanation, without excluding the possibility of additional transoceanic dispersal in the Atlantic. Even strictly tropical species may show this highly disjunct and possibly vicariant distribution (van den Hoek, 1982a).

A second tropical-warm temperate cluster is the "poor tropical-warm temperate cluster", composed of the E Pacific and E Atlantic tropical floras, as well as the NW Atlantic and SW Atlantic warm temperate floras (Fig. 5, finely stippled areas; see also Fig. 2). These four floras have comparatively low numbers of rhodophyten genera (about half the number present in the floras of the previous cluster), and almost no endemic genera (Fig. 2; Fig. 4). Fig. 4 shows that they are predominantly composed of widely distributed tropical to arctic/antarctic and tropical to cold temperate genera, and of fair numbers of tropical to warm temperate genera which are, however, much lower than those in the floras of the previous cluster. Other distributional categories are hardly represented. Apparently this "poor tropical-warm temperate cluster" differs from the "rich tropical-warm temperate cluster" by the absence of numerous genera, mainly tropical-warm temperate ones. Various causes may be invoked for the depauperate condition of these four floras. The warm temperate NW Atlantic flora occurs along the vast sediment coasts of the SE USA which are inhospitable to benthic algae. Inshore waters have high seasonal temperature fluctuations. Scattered offshore reefs which are bathed by tropical Gulf Stream water with more even temperatures are inhabited by an impoverished Caribbean flora (Searles, 1984; Searles & Schneider, 1980; van den Hoek, 1975). The warm temperate SW Atlantic flora is separated from the Caribbean flora as

well as the cold temperate SW Atlantic flora by vast sediment coasts. Contractions of the tropical belt during the Pleistocene glaciations may have enforced migrations of this flora which could not "escape" without losses towards the Caribbean over the barrier formed by the sediment coasts which also hindered remigration during the interglacials. Such Pleistocene flora-migrations may have also added to the impoverishment of the warm temperate NW Atlantic flora. Fig. 3, which clusters the floras on the basis of cool water genera (i.e., genera absent from the tropics), stresses the point that both the NW and SW warm temperate Atlantic floras hardly contain strictly cool water genera and are consequently both depauperate extensions of the rich tropical W Atlantic flora. Comparable reasons may be, and have been, invoked (van den Hoek, 1975, 1982a) for the depauperate nature of the tropical E Atlantic flora: that is, the occurrence of long sediment coasts with relatively few rocky outcrops in combination with Pleistocene temperature fluctuations and concomitant flora migrations. However, the impoverishment of the E Atlantic portion of the former Tethys flora may have started during the steep cooling trend in late Miocene ($\sim 10\text{--}5.10^6$ y; cf. Thunell & Belyea, 1982). Comparable reasons may be invoked for the depauperate nature of the westernmost portion of the former Tethys-flora, the tropical E Pacific flora which became definitely isolated from the rich tropical W Atlantic flora by the Pliocene uplift of the Central American isthmus (2.10^6 y). In general, it is likely that the tropical east sides of the Pacific and Atlantic Oceans have been subject to much more unstable climatic conditions during the geologic past than the west sides where the tropical belts are much broader and conditions more even as a consequence of the general oceanic circulation patterns.

Fig. 4 shows that apart from the depauperate tropical and warm temperate floras, the tropical and warm temperate floras contain more than twice the number of rhodophyten genera present in the cold temperate floras, which, in their turn, are roughly twice as rich as the Arctic and Antarctic floras. These differences in generic richness can be interpreted as reflecting the much greater age of the tropical and warm temperate floras than that of the cold temperate, arctic and antarctic floras. In early Tertiary (Paleocene and Eocene, $\sim 65\text{--}40.10^6$ y), the climate varied from tropical at the equator to warm temperate at the poles. Two precipitous temperate drops occurred, one in the early Oligocene ($\sim 35.10^6$ y), the other in the middle Miocene ($\sim 10.10^6$ y). The first is generally associated with the opening of Drake's Passage (between Fuegia and the Antarctic Peninsula) and the initiation of the Circum Antarctic Current isolating Antarctica from heat influx from the tropics. After that the gradually increasing glaciation of Antarctica could have helped to steepen the latitudinal temperature gradient (Frakes, 1979). In the early Oligocene also, cold water could have started to flow from the Arctic Ocean into the N Atlantic Ocean over the subsiding Greenland-Scotland Ridge (McKenna, 1983).

These Cenozoic temperature drops may have promoted the evolution of cold temperate floras from warm temperate floras. Fig. 4 suggests that this was partly realized by the origin of new species within existing genera and partly by the origin of new cold water genera. Unfortunately few red algae fossilize. The calcareous red algae, however, have left abundant fossils which are attributed to 17 fossil genera and 15 extant genera which are also reported as fossils (Johansen, 1981). Of these latter 15 genera, the earliest fossils are *Lithoporella*, *Lithothamnion* and *Sporolithon* from the late Jurassic (140.10^6 y); the earliest fossils of *Lithophyllum*, *Amphiroa*, *Arthrocardia*, *Jania*, and *Pneophyllum* (cf. Chamberlain, 1983) from the Cretaceous ($130\text{--}65.10^6$ y); the earliest

fossils of *Mesophyllum* from the Paleocene ($\sim 55.10^6$ y); of *Corallina* and *Tenarea* from the Eocene ($\sim 45.10^6$ y); of *Melobesia* from the Oligocene ($\sim 35.10^6$ y); and of *Calliarthron*, *Neogoniolithon* and *Porolithon* from the Miocene ($\sim 20.10^6$ y). 14 of these 15 genera now have wide tropical to cool water distributions. Only *Calliarthron* has a warm to cold temperate distribution in the N Pacific. *Porolithon* and *Neogoniolithon* on the other hand, have a tropical to warm temperate distribution. These latter two mainly tropical genera are thought to have evolved rather recently in association with highly increased fish grazing in coral reefs (Steneck, 1983). 12 of the above 14 genera of the Corallinaceae with wide present tropical-to-temperate distributions are indeed very old (Jurassic to Eocene). Two other recent calcified rhodophyтан genera with tropical to cool water distributions, *Ethelia* and *Peyssonellia* are known as fossils from the lower Cretaceous (130.10^6 y) and the Paleocene (60.10^6 y), respectively (Tappan, 1980). These fossil records therefore support the idea that at least a large proportion of the extant rhodophyтан genera with tropical-to-temperate distributions existed already in the Eocene ($55\text{--}50.10^6$ y) when the climate varied from tropical at the equator to warm temperate at the poles (with surface water temperatures of c. $15\text{--}20^\circ\text{C}$ at the poles, and $20\text{--}30^\circ\text{C}$ at the equator) (Frakes, 1979; p. 193). According to this reasoning, the genera with strict temperate and temperate to arctic/antarctic distributions are of more recent date, and evolved in response to the step-wise steepening latitudinal temperature gradient. In accordance with this viewpoint is the extremely low number of cold temperate to arctic/antarctic genera, which probably evolved after the steep middle Miocene temperature drop ($\sim 10.10^6$ y) which developed during the Pliocene (2.10^6 y) into temperature conditions comparable to the present ones.

Fig. 7 illustrates the relationships, on the 50–60 % level of similarity, among the non-tropical floras on the basis of rhodophyтан genera which do not occur in the tropics, that is on the basis of genera of presumably relatively "recent" origin (younger than Eocene: 40.10^6 y). In order to stress resemblances endemic genera have also been omitted. In Fig. 7 the rich warm temperate floras of the NE Atlantic and the NW Pacific, after being freed from the overriding influence of the tropical to cool water genera, show distinctly other patterns of relatedness than in the first clustering (Fig. 5). In the N Pacific, the warm temperate NW and NE Pacific floras are apparently closely related on the basis of their cool water rhodophyтан genera and stand apart, at the same time, from all other warm temperate floras. The nearest related flora is the cold-temperate N Pacific flora (at the 36 % similarity level). Apparently a Tethyan connection between the Pacific and Atlantic Oceans is suggested predominantly on the basis of genera occurring in the tropics, and not on the basis of genera excluded from the tropics.

The high similarity (50 %) between the warm temperate NW and NE Pacific floras of rhodophyтан genera reflects the high number of 39 cool water genera which they share. Of these, 22 are highly disjunct and are lacking along cold temperate northern Pacific shores (Fig. 8). This highly disjunct group of warm temperate genera can possibly be explained as being composed of two vicariant NW and NE Pacific portions of a once continuous warm temperate flora along the northern coasts of the N Pacific Ocean, which was separated from the Arctic Ocean by the Bering Land Bridge during most of the Tertiary. This situation may have existed during a relatively warm period in the early Miocene ($\sim 25\text{--}15.10^6$ y), and also in earlier warm periods in the Oligocene and Eocene (Frakes, 1979).

An alternative explanation for the above disjunction would be recent dispersal of warm temperate species from Japan across the Pacific Ocean, by the Kuro Shio Current.

In the N Atlantic Ocean the situation differs completely from that in the N Pacific Ocean. The two N Atlantic warm temperate floras are not at all related. Both floras share only one highly disjunct warm temperate genus (Fig. 8). Nonetheless, uninterrupted coastlines and an island chain in the north (the subsiding Greenland-Scotland Ridge) could be invoked to explain exchange of warm temperate genera between NW and NE Atlantic coasts during warm early Miocene and possibly still earlier warm periods. If a rich warm temperate NW Atlantic flora has ever existed, its disappearance could be explained by the present and Pleistocene nature of the SE USA coasts, where long sediment shores are inhospitable to benthic algal growth and where scattered offshore reefs are inhabited by an impoverished extension of the rich NW Atlantic tropical flora. Flora migrations enforced by the Pleistocene glaciations could have enhanced this impoverishment (see also above).

Both in the overall clustering (Figs 2, 5) and the clustering based on the cool water genera (Figs 3, 7), the rich warm temperate SE Atlantic and SW Pacific floras take distinctly individual positions although they are mutually related on about the 35 % level in both clusterings. One may wonder why these two warm temperate floras do not belong to the warm temperate "Tethyan cluster" (the tropical W Atlantic and Indo-W Pacific, and the warm temperate NE Atlantic and NW Pacific floras), with which they are contiguous. The difference is reflected by their higher proportions of genera not occurring in the tropics, that is, cool water genera (the warm temperate SE Atlantic with 40 % and the warm temperate SW Pacific with 55 % versus the warm temperate NE Atlantic with 34 % and the warm temperate NW Pacific with 27 %; cf. Fig. 4). This more pronounced "temperate" character of the warm temperate SE Atlantic and SW Pacific floras possibly reflects their very long isolation (~ early Cretaceous, 100.10⁶ y) and their very long residence in warm temperate conditions, as they moved from a position at about 50° S latitude in Eocene towards 30° S latitude at present and stayed, in this way, in about the same climatic zone during the Cenozoic steepening of the latitudinal temperature gradient. Especially for the warm temperate SW Pacific flora this is an attractive explanation. This flora, which is contiguous with the rich tropical Indo-W Pacific flora, contains about the same absolute number of tropical-cool water genera as warm temperate NW Pacific and NE Atlantic floras, but distinctly more cool water genera most of which are endemic as well to this region (Fig. 4).

The rich warm temperate NE Pacific flora has also a relatively high proportion of cool water genera (46 %) and consequently a pronounced temperate character. This is possibly related to the fact that it is, and has been for a very long time (since early Oligocene?) contiguous with the poor E Pacific tropical flora (Fig. 4, compare WN₂ with T₂).

The poor warm temperate SE Pacific flora takes quite an isolated position, especially in the clustering based on cool water genera and non-endemic genera (Figs 3, 7). It is mainly composed of genera with a wide southern hemisphere cold- and warm temperate distribution (Fig. 9) and differs from the rich warm temperate SE Atlantic and SW Pacific floras mainly by the *absence* of numerous genera. On the species level this flora (phaeophytes and chlorophytes included) is also comparatively poor. It contains a considerable proportion of cool water southern hemisphere ("subantarctic") species,

apart from a fair proportion (32 %) of endemic species (which contrasts with the low proportion – 4 % – of endemic rhodophytan genera) (Santelices, 1980).

Towards the north, the species number gradually decreases in the warm temperate SE Pacific Region (Santelices, 1980). This agrees with my observation that the adjacent tropical East Pacific flora is distinctly poorer in rhodophytan genera (Fig. 4) because of the northward disappearance of the cool water genera. One reason for this relative poverty in comparison to the warm temperate SW Pacific and SE Atlantic floras may be that the cool northward Peru Current which extends the warm temperate SE Pacific Region as far north as 4° S latitude, may be aperiodically replaced by warm tropical surface water ("el Niño") as far as 30° S latitude. This phenomenon which has a catastrophic effect on fish and intertidal life (Stephenson & Stephenson, 1972; Smith, 1983) may have occurred over long geologic periods, as it is associated with the general oceanic circulation pattern and its small deviations.

The clustering patterns (Figs 5, 7) of the four warm temperate southern hemisphere floras do not support the concept of a formerly continuous warm temperate Gondwana flora. These four floras differ greatly from one another, and the two most related floras (on the 35 % level) are those of southern Australia and South Africa the latter of which was the first area to separate from the Antarctic-Australian block (already in the middle Cretaceous, ~ 100.10⁶ y). However, the distribution of the 16 rhodophytan genera shared by and restricted to the warm temperate SE Atlantic and SW Pacific regions (Fig. 9) may be explained by either dispersal (by the West Wind Drift) or by vicariance.

The wide distribution, in the southern oceans, of the majority of non-endemic cool water genera over the warm temperate and cold temperate regions (with the exclusion of the warm temperate SW Atlantic Region which can be better conceived of as a depauperate extension of the tropical W Atlantic Region) rather suggests dispersal as its cause, particularly as these genera also occur on widely scattered subantarctic islands which are partly on continental chunks, and partly of later volcanic origin. Therefore, these regions must have been colonized by algae arriving from elsewhere. However, it is quite conceivable that cold to warm temperate genera evolved along the coasts of Antarctica after the Oligocene opening of the Drake Passage (35.10⁶ y) and the ensuing cold period. With increasing severity of the polar climate, these cold to warm temperate genera could retreat to southern America and the subantarctic islands, and leave the Antarctic coasts to the further development of the poor Antarctic flora (Fig. 4). This latter scenario accords with the high similarity between the cold temperate SE Pacific, SW Atlantic and SE Atlantic floras and their relatedness with the Antarctic flora (Figs 5, 7).

The high individuality of the two rich warm temperate floras in the southern hemisphere (i.e. the SE Atlantic and the SW Pacific floras) as compared with the much greater relatedness, to other floras, of the three rich warm temperate floras of the northern hemisphere, points to the long isolation (since at least Cretaceous, ~ 100.10⁶ y) of these southern floras and the effectiveness of the wide oceans as barriers to dispersal. In the northern hemisphere, on the other hand, tropical to warm temperate genera could be exchanged between the Atlantic and Pacific Oceans along the coasts of the Tethys Ocean up to the closure of the Tethys in the Miocene (~ 18.10⁶ y), and along the northern coasts of these oceans as late as the early Miocene (20.10⁶ y).

Exchange of cool temperate genera between the N Pacific Ocean and the N Atlantic Ocean, through the Arctic Ocean, could have started after the late Pliocene (3–2.10⁶ y)

inundation of the Bering Land Bridge. This is evidenced by the passage of many N Pacific elements into the N Atlantic, via the Arctic (McKenna, 1983). There are two distinct clusters: The Arctic-cold temperate N Atlantic cluster and the cold temperate N Pacific cluster (Figs 2, 3, 5, 7). The difference is mainly caused by the much greater number of strictly N Pacific cool water genera rather than of strictly N Atlantic cool water genera (Fig. 6). Also on the species level (including phaeophytan and chlorophytan species as well) the cold temperate N Pacific floras are much richer than the cold temperate N Atlantic floras (van den Hoek, 1975). The cold temperate N Pacific also harbours the great majority of cool water genera present in the cold temperate N Atlantic and the Arctic. This greater richness of the cold temperate N Pacific can possibly be attributed to the less severe Pleistocene climatic fluctuations and the concomitant more limited flora migrations and extinctions in the Pacific than in the Atlantic Ocean. During the Pleistocene glaciations the Bering Land Bridge reemerged because of the lowering (~ 130 m) of the sea level so that the Pacific became separated again from the Arctic Ocean; whereas the Atlantic Ocean remained in wide open contact with the Arctic Ocean and experienced in consequence considerably more severe climatic deteriorations (McIntyre, 1976). This possibly caused more extinctions in the N Atlantic than in the N Pacific (van den Hoek, 1975).

Of all floras included in this study, the cold temperate NE and NW Atlantic floras and the Arctic flora are the most narrowly related (Figs 2, 3, 8). Possibly this group originated as one flora in the early Oligocene Arctic Ocean which was highly isolated by the Bering Land Bridge and the Scotland-Greenland Land Bridge. Later this flora could have penetrated into the N Atlantic Ocean over the subsiding Greenland-Scotland Ridge. The cold temperate NW and NE Atlantic floras remained connected up into the Miocene ($10 \cdot 10^6$ y) (McKenna, 1983) or even perhaps the Pliocene ($3 \cdot 10^6$ y) (Thiede & Eldholm, 1983) by northern Atlantic coastlines and a series of stepping stones formed by the chain of islands on the subsiding Greenland-Scotland Ridge. During the glaciations the N Atlantic cold temperate floras were forced to considerable southward displacements i.e. in Europe approximately to the coasts of Spain and NW Africa, in America to the Carolina coasts. Were the Carolina coasts during the glaciations with their much lower sealevels (~ 130 m) as inhospitable to seaweeds as they are now? In that case the southward retreating cold temperate NE American flora was doomed to (near) extinction so that the NW Atlantic coast had to be repopulated during the interglacials from the NE Atlantic, European coasts. This is somewhat difficult to imagine, as this would imply transoceanic dispersal against the SW-to-NE direction of the currents (Gulfstream and North Atlantic Drift). Therefore, the high resemblance between the cold temperate NE and NW Atlantic floras can possibly be best explained by conceiving them as vicariant portions of a once – i.e. in Miocene and Pliocene – continuous flora. Their geologically rather recent separation and isolation (Pliocene, $\sim 2 \cdot 10^6$ y) could explain their high degree of resemblance.

The above account implies that from the tropical Tethyan seaweed flora different temperate and cold water floras evolved into the cooling northern hemisphere and the cooling southern hemisphere. Nonetheless, both hemispheres share a number (47; 15 %) of the total number of cool water rhodophytan genera (307), that is, of genera not occurring in the tropics. Apparently the tropical belt is a formidable barrier against dispersal of cool water seaweeds, but nonetheless a number have succeeded in passing

this filter since the evolution of the northern and southern hemisphere cool water floras which probably started at the end of Eocene ($\sim 40.10^6$ y). Fig. 10 suggests that the least difficult tropical barrier to pass has been the E Pacific Tropical Region where 24 genera "jumped" the tropics. This can be understood as here the tropical belt is relatively narrow (cf. Fig. 1) and probably underwent intermittent late Cenozoic lowerings of temperature. For a comparable reason the "jumping" of the E Atlantic tropics by 11 genera can be understood (Fig. 10). However, 9 genera with widely disjunct distributions in the warm temperate NW and SW Pacific regions seem to have directly "jumped" the wide tropical Indo-W Pacific belt (Fig. 10), and for this hardly a reasonable explanation can be given. Are they perhaps tropical-to-warm temperate genera whose tropical populations have not yet been discovered, for instance because they occur in rarely investigated deep water habitats? Or are they composed of vicariant species which were formerly linked by now extinct tropical species? A direct dispersal over the Indo-W Pacific, however, would seem highly improbable.

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