Biogeography of the marine red algae of the South African West Coast: a molecular approach

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Abstract

This study investigates the hypothesis that a major portion of the present red algal flora of the South African West Coast and Namibia (Benguela Marine Province) originated in Australasia (Australia and New Zealand) and was dispersed across West Antarctica, followed by its isolation with the establishment of the West Wind Drift as a permanent oceanic feature. Phylogenetic hypotheses are inferred for six species clusters, and pairwise base differences are calculated for additional selected taxa based on analyses of *rbc*L sequences. These are compared to the history of tectonic, paleoclimatic and paleoceanographic events that may have influenced the distribution of red algae to the South African West Coast.

Abbreviations: pbd – pairwise base distance

Introduction

The South African West Coast composes part of the Benguela Marine Province, a biogeographic region that extends from Cape Agulhas at the southernmost tip of Africa to Cape Fria in Namibia and intermittently further north. Its southern boundary is marked by convergence of the Benguela Upwelling System with the Agulhas Current that flows westward along the east and south coasts of South Africa as far as Cape Agulhas. It extends northward from the Cape peninsula to the limits of upwelling in Namibia and Angola. Mean annual sea temperatures for the region range from 12°C to 16°C and are thus transitional between cold- and warm-temperate phytogeographic provinces. Upwelling along the West Coast may have begun as early as 12 million years ago, but the present fully developed Benguela system came into being in the last 2 million years (Stegenga *et al.*, 1997 and included references).

Prior to the publication of 'Seaweeds of the South African West Coast' by Stegenga *et al.* (1997), the algal flora of this region was known only from scattered reports in the literature. This volume expands the list of described seaweeds by nearly 60% to approximately 400 species of which 274, or 68%, are red algae (Rhodophyta). Of these, 58% are said to be endemic to southern Africa (from the border of Angola to the border of Mozambique). While red algal species endemism is unusually high for the region, generic endemism is low. If one excludes some small ceramiaceous and parasitic genera, only the monotypic genus *Heringia* stands out as a South African endemic. The rest can, for the most part, be assigned to genera found elsewhere in the Southern Hemisphere or in the world at large.

Hommersand (1986) proposed that a large percentage of red algal taxa found along the west coast of South Africa (Benguela Marine Province) belong to genera and species clusters that originated in the Pacific Ocean on the eastern side of Australasia (New Zealand, Tasmania and southern Australia). These were said to have been dispersed through a seaway across West Antarctica during periods of minimal glaciation during Oligocene and Miocene and to have been distributed by high latitude ocean currents to South Africa (Fig. 1). A second com-

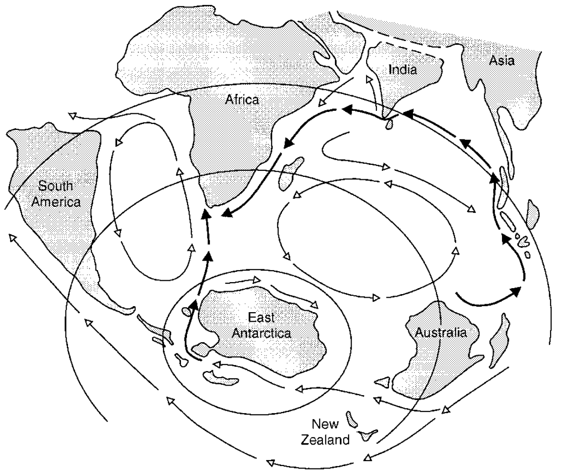

Figure 1. Proposed pathway of algal migration from high latitudes in the antiboreal Pacific Ocean through West Antarctica to South Africa during Oligocene and Miocene and from West Australia to southern Africa through the North Indian Ocean from Miocene to the present (coarse arrows). Lighter arrows show the presumed direction of oceanic currents in Miocene. Map adapted from Barron & Harrison (1980), Frakes (1979), Tchernia (1980), Ciesielski *et al.* (1982) and Scherer *et al.* (1998).

ponent of the flora was postulated to have originated in the South Indian Ocean on the western side of Australia and to have been distributed to East and South Africa by prevailing currents through the North Indian Ocean (Fig. 1). The present study tests this model by investigating phylogenies for five clusters of genera and species known primarily from South Africa and Australasia, and additional pairwise base differences calculated for selected species pairs based on analyses of *rbc*L sequences. (See Hommersand 1986 for background information on the relevant plate tectonic, paleoclimatic and paleoceanographic history.)

Materials & Methods

Algal samples used in molecular studies were desiccated in silica gel. Methods of DNA extraction, amplification and sequencing of *rbc*L followed the procedures and conditions described in Fredericq *et al.* (1999). Parsimony analyses of *rbc*L sequence data were performed using the PAUP computer program (v. 4.0b4a*: Swofford 2000) under the conditions described in Hommersand *et al.* (1999). Sister taxa identified in global searches of over 500 rhodophytan species were selected as outgroup taxa for each data set. Bootstrap support (BP) for nodes in the parsimony trees were based on 1,000 resampling replications. Pairwise base differences (pbd) were calculated in % between selected sister and nearest neighbour taxa using the Tamura-Nei correction (Tamura & Nei 1993).

Results & Discussion

Table 1 contains a list of selected families and genera found in the Benguela Upwelling Province in South Africa that are represented by related species in Australia and New Zealand, or South America. The number of species per genus is tabulated for each of ten biogeographic provinces based on reports in the literature. Most of the genera listed in Table 1 were discussed previously by Hommersand (1986), and only those taxa for which molecular data are provided are covered here. Phylogenies were inferred for five *rbc*L data sets containing taxa distributed primarily between Australasia and South Africa (Fig.s 2–6), and *rbc*L sequence divergence values expressed as pairwise base differences were calculated in % for selected species pairs (Table 2).

Trematocarpus/Sarcodia clade (Sarcodiaceae) (Fig 2)

Trematocarpus and *Sarcodia* formed two strongly supported sister clades (BP = 97, 100) with *Plocamium* serving as an outgroup (Fredericq *et al.*, 1996). *'Kallymenia' antarctica*, a species incorrectly assigned to *Kallymenia*, was resolved in basal position (BP = 87) in the *Trematocarpus* group and *T. dichotomus* from Chile was basal (BP = 93) to a terminal clade containing *T. flabellatus* and *T. fragilis* from South Africa. *Sarcodia montagnei* from New Zealand, *S. marginata* and S. sp. form a clade (BP = 96) sister to a clade containing *S. ceylanica* from Taiwan and *S. dentata* from South Africa (BP = 100). The tree topology suggests that *Trematocarpus* was initially distributed across the antiboreal Pacific Ocean in Gondwanaland and only later was distributed to South Africa. The cluster of *Sarcodia* species from New Zealand and

	Australia	New Zealand	South Africa	South America	West Antarctica	West Wind Drift	Pacific North America	Japan	Western Europe	North Indian Ocean
Balliaceae										
Ballia*1	2	2	2	2		2				
Hildenbrandiaceae										
Hildenbrandia*2	1	2	1	1		1				
Liagoraceae										
Helminthora	2	2	1	1			1		1	
Galaxauraceae										
Gloiophloea	1									
Scinaia*3	2	2	1	2			1	1	1	
Nothogenia	1	3	2	1		1				
Bonnemaisoniaceae										
Delisea	4	4	1		1	1		1		
Ptilonia	2	2		2		1		1		
Halymeniaceae										
Gratekiyoua*4	1	1	1	1			1	1		
Gratekiyoua*5	1	1		1			1			
Aeodes	1	1	2							
Pachymenia	2	3	2	1						
Polyopes	2		1					2+		2
Kallymeniaceae										
Pugetia	1	1	1	1			1			
Thamnophyllis	1	1	2							
Kallymenia	7	1	3				?	9	1	2
Plocamiaceae										
Plocamium	10	7	7	3		2	3	5	1	2
Sarcodiaceae										
Trenatocarpus	2	1	2	1	1			1		
Sarcodia	3	3	1					2		3
Nemastomataceae										
Tsengia*6	3	3	2	?				2	?	

	Australia	New Zealand	South Africa	South America	West Antarctica	West Wind Drift	Pacific North America	Japan	Western Europe	North Indian Ocean
Schizymeniaceae										
Schizymenia	1	1	1	1			1	1	1	
Phyllophoraceae										
Gymnogongrus*7	4	4	6	8	2	2	10	12	4	7
Gigartinaceae										
Gigartina	9	5	4						1	
Sarcothalia	2	5	1	3	2					
'Sarcothalia'		2	1							
Iridaea				2	1	2				
Rhodymeniaceae										
Cenacrum		1	1		1	1				
Rhodymenia*8	9	7	5	11		1	8	7	5	4
Hymenocladia	6	1	1							
Ceramiaceae										
Pterothamnieae	7	4	2	2	2	2	7	3	4	
Ceramieae										
Ceramium*9	1	2	2	1						
Ceramium*10	1	2	1							
Euptilota-group	2	2	1	1	1			1		2
Euptilota	1	2	1					1		2
Calithamnieae										
Carpothamnion	1		1							
Spyrideae	5	2	5				2	3	1	4
Delesseriaceae										
Apoglossum	3	2	2				1		1	1
Paraglossum	1	1	1	3	1	?				
Schizoseris	2	5?	1	2		1	?	1		
Haraldiophyllum	2	1	1	1			9		1	
Rhodomelaceae										
Streblocladia		2	2	1					1	

Table 1. List of families and genera found predominantly in the Southern Hemisphere, giving the number of species reported in temperate biogeographic provinces. [1]*Ballia* (Balliales, see Choi *et al.*, 2000), [2]*Hildenbrandia* (= *H. lecanellierii*), [3]*Scinaia* (= species previously referred to *Pseudogloiophloea*), [4]*Grateloupia* (= foliose species referred to *G. doryphora*), [5]*Grateloupia* (= *'Grateloupia' intestinalis*-type), [6]*Tsengia* (including some species assigned to *Nemastoma*), [7]*Gymnogongrus* (including *Ahnfeltiopsis*, see Fredericq & Ramírez, 1996, Fredericq *et al.*, 2001). [8]*Rhodymenia* (including *Epymenia* and *Dendrymenia*). [9]*Ceramium* (= *C. planum* group), [10]*Ceramium* (= *C. rubrum* group). Species distributions were drawn from the following sources: west coast of South Africa (Stegenga *et al.*, 1997); Australia (Huisman, 2000); southern Australia (Womersley, 1994, 1996, 1998); New Zealand (Adams, 1994); Chile (Ramírez & Santelices, 1991); Antarctic and subantarctic (Papenfuss, 1964, Ricker 1987); Pacific North America (Scagel *et al.*, 1989, Abbott & Hollenberg, 1976, González-González *et al.*, 1996); Japan (Yoshida, 1998); Atlantic Europe (Guiry, 1997); Indian Ocean (Silva *et al.*, 1996), and recent papers on special groups.

Australia may be basal; however, additional species must be sequenced from Australasia and the Indian Ocean to achieve resolution. *Sarcodia dentata* just reaches southern South Africa west of Cape Agulhas, and is the easternmost representative of the seemingly widespread *S. ceylonica* group. Species referred to *S. montagnei* in the Indian Ocean are probably misidentified. The position of *Trematocarpus dichotomous* from Chile basal to *T. fragilis* and *T. flabellatus* from South Africa, stands in the absence of sequence data for species of *Trematocarpus* that are recorded from Australia and New Zealand. Evaluation of pairwise base distances between *Sarcodia ceylonica* from Japan and *S. den-*

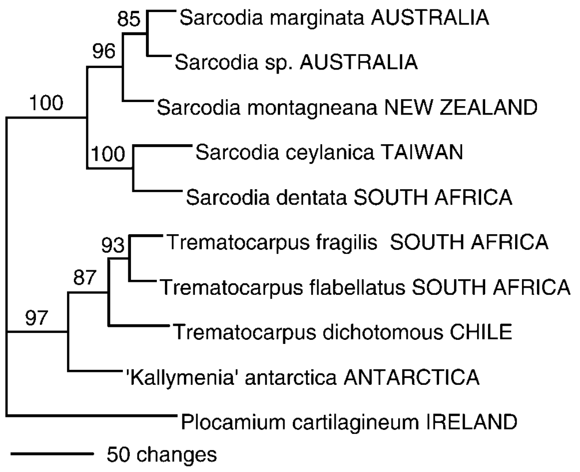

Figure 2. Single maximum parsimony tree of length = 577 (CI = 0.7679, RI = 0.6923) resulting from parsimony search of *rbc*L data for nine Sarcodiaceae and one outgroup species. Branch lengths are proportional to the number of mutational changes and bootstrap proportion values are shown for branches with support >50 %.

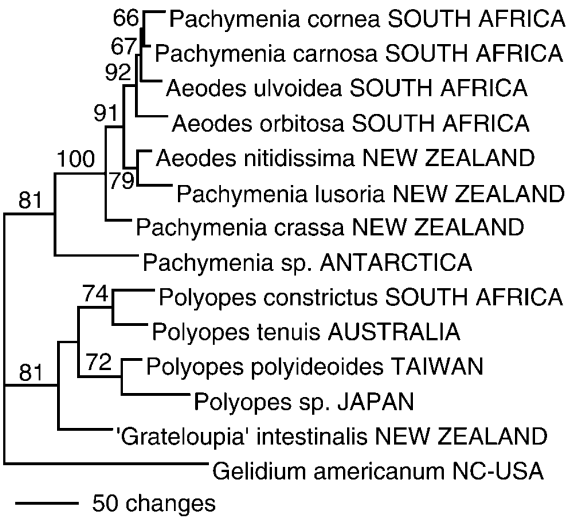

Figure 3. Single maximum parsimony tree of length = 913 (CI = 0.6673, RI = 0.6089) resulting from parsimony search of *rbc*L data for thirteen Halymeniaceae belonging to the *Polyopes* and Aeodes groups and two outgroup species. Conditions as in Fig. 2.

tata from South Africa (pbd = 4.9 %) require investigation of additional *Sarcodia* species from the North Indian Ocean.

Polyopes/Pachymenia clades (Halymeniaceae) Fig 3

Chiang (1970) identified a cluster of genera in the Cryptonemiaceae (= Halymeniaceae) that included *Polyopes, Pachymenia, Dermocorynus* and *Aeodes*, in which the auxiliary cell ampullae (systems of filaments that bear the auxiliary cells) were multiply branched. These were referred to as '*Aeodes*-type' ampullae. In our studies, species having *Aeodes*-type ampullae fall into two non-sister clades (data for non-sister relationship not shown): a *Polyopes* and a *Pachymenia* clade, each with 81 % bootstrap support. The *Polyopes* clade is represented by one species of *Polyopes* in South Africa, and the *Pachymenia* clade by two South African species each of *Pachymenia* and *Aeodes*.

The *Polyopes* clade contains *'Grateloupia' intestinalis* from New Zealand, a species incorrectly assigned to *Grateloupia*, and two additional clades: one containing *Polyopes constrictus* from South Africa and *P. tenuis* from Australia (BP = 74), and another containing *P. polyideoides* from Taiwan and an unidentified species from Japan (BP = 72). Material of the type species of *Polyopes, P. constrictus* from Australia, was unavailable. Additional species of *Polyopes* have been identified from the Indian Ocean; however, the data suggest that the plant known as *P. constrictus* in South Africa is related more closely to the Australian species (pbd = 6.0%) than to those from the Indo-Pacific Ocean (pbd = 7.0% to 12.0%). Additional samples will need to be sequenced to resolve questions concerning the biogeography of *P. constrictus* in South Africa.

An undescribed species from Antarctica was resolved at the base of the *Pachymenia* clade (BP = 100) that included three New Zealand species, (*P. crassa, P. lusoria* and *Aeodes nitidissima*) and four South African species, (*A. orbitosa, A. ulvoidea, P. carnosa* and *P. cornea*). Our molecular data demonstrate that the orbicular genus *Aeodes* (type species: *A. nitidissima* J. Ag., 1876, p. 678 from New Zealand) and the strap-shaped genus *Pachymenia* (type species *P. carnosa* J. Ag., 1876, p. 143, from South Africa) belong in a single genus. Bootstrap support for the tree topology in Figure 3, in which the South African cluster formed a well-supported terminal clade (BP = 92), argues for a biogeographical hypothesis in which the *Aeodes/*

'Gigartina' skottsbergii Chile	1.8 %	'Gigartina' skottsbergii Antarctica
Iridaea cordata Chile	3.4 %	Iridaea cordata Antarctica
Gigartina pistillata South Africa	2.2 %	Gigartina muelleriana Australia
Sarcothalia stiriata South Africa	2.2 %	Sarcothalia livida New Zealand
Mazzaella convoluta South Africa	2.3 %	Mazzaella membrancea Chile
'Sarcothlia' scutellata South Africa	3.2 %	'Sarcothalia' decipiens New Zealand
Epymenia obtusa South Africa	3.2 %	Epymenia wilsonis New Zealand
Hymenena venosa South Africa	3.3 %	Hymenena multipartita Australia
Gigartina bracteata South Africa	3.6 %	Gigartina muelleriana Australia
Rhodophyllis reptans South Africa	3.8 %	Rhodophyllis divaricata France
Aeodes orbitosa South Africa	4.4 %	Aeodes nitidissima New Zealand
Trematocarpus fragilis South Africa	4.9 %	Trematocarpus dichotomus Chile
Sarcodia dentata South Africa	4.9 %	Sarcodia ceylonica Taiwan
Botryoglossum platycarpum South Africa	5.0 %	Hymenena multipartita Australia
'Delesseria' papenfussii South Africa	5.3 %	'Delesseria' species Antarctica
Polyopes constrictus South Africa	6.0 %	Polyopes tenuis Australia
Rhodophyllis reptans South Africa	6.3 %	Rhodophyllis membranacea New Zealand

Table 2. Pairwise base differences (pbd) between sister and nearest neighbour species calculated from rbcL data sets published here and in Hommersand *et al.* (1999) and Lin *et al.* (2002).

Pachymenia group radiated first in Australasia and was only later distributed to South Africa. The pairwise base distance between nearest neighbours *Aeodes nitidissima* (New Zealand) and *Aeodes orbitosa* (South Africa) was 4.4 %.

Epymenia/Rhodymenia clade (Rhodymeniaceae) (Fig 4)

Two genera of Rhodymeniaceae are represented in the South African West Coast, Australia and New Zealand: *Hymenocladia* and *Epymenia*. The first of these was not investigated and the second is often subsumed under *Rhodymenia*. When accepted as a separate genus, *Epymenia* is distinguished by the presence of superficial fertile proliferations. In the present study, the three *Epymenia* species and two *Dendrymenia* species from the Southern Hemisphere formed a separate clade (BP = 100) sister to two Northern Hemisphere species of *Rhodymenia*. The basal position of *E. wilsonis* from New Zealand was supported (BP = 59) relative to the groups containing two species of *Epymenia* from South Africa (BP = 97) and two of *Dendrymenia* from South America (BP =100). Womersley (1996) recognized a single species, *Rhodymenia obtusa* (Greville) Womersley from

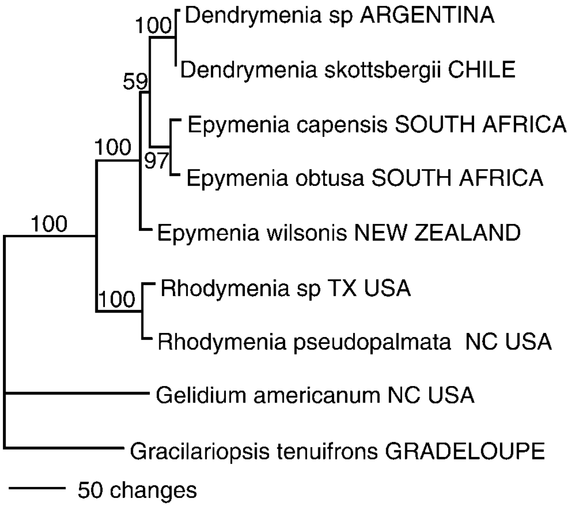

Figure 4. Single maximum parsimony tree of length = 522 (CI = 0.8678, RI = 0.7629) resulting from parsimony search of *rbc*L data for seven Rhodymeniaceae placed in *Rhodymenia, Epymenia* of *Dendrymenia* and two outgroup species. Conditions as in Fig. 2.

Australia and the other three regions. The South African and South American species are almost equally distant from *Epymenia wilsonis* from New Zealand (pbd = 3.2 % to 3.6 %). We favour an origin of the complex in Australasia and its subsequent dispersal to South Africa and South America. Alternatively, the group originated in South America and has a subantarctic distribution along the West Wind Drift. Reports of *E. obtusa* from Îles Kerguelen (Papenfuss, 1964) should be reinvestigated.

Rhodophyllis/Craspedocarpus/Calliblepharis/Hypnea (Rhodophyllidaceae, Hypneaceae) (Fig 5)

The genera *Rhodophyllis, Craspedocarpus* and *Calliblepharis* are usually placed in the family Cystocloniaceae. Our unpublished studies, however, show that this assemblage is not closely related to *Cystoclonium* and we recognized the family Rhodophyllidaceae for this group. The Caulacanthaceae are a basal group in global searches of the family cluster that we have referred to as the 'Solieriaceae complex' (Fredericq *et al.*, 1996, 1999), and the Hypneaceae form a terminal clade that is not separable from the Rhodophyllidaceae.

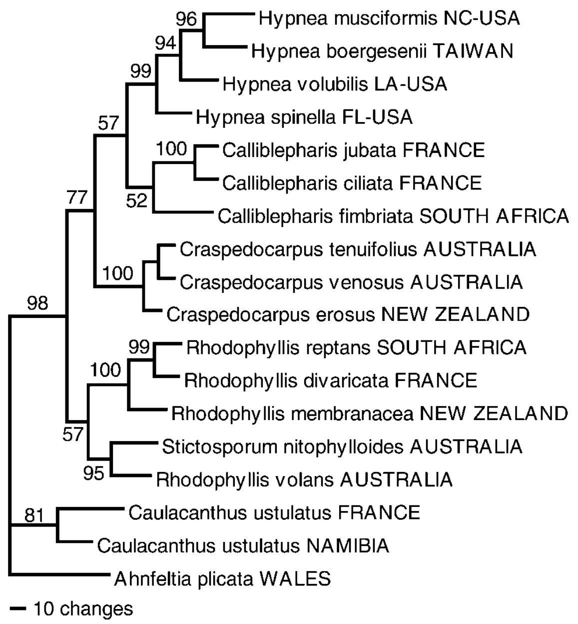

Figure 5. One of three minimal trees of length = 896 (CI = 0.4621, RI = 0.5092) resulting from parsimony search of *rbc*L data for fifteen species belonging to the Rhodophyllidaceae/ Hypneaceae clade and three outgroup species. Conditions as in Fig. 2.

Selecting two *Caulacanthus* species as outgroup taxa produced an assemblage having strong bootstrap support (BP = 98) that contained two principal clades, a *Rhodophyllis* clade (BP = 57), including *Stictosporum*, and a clade that contained the remaining genera (BP = 77). Three genera were identified in the second clade: *Craspedocarpus* (BP =100), *Calliblepharis* with no bootstrap support (BP = 52) and *Hypnea* (BP = 99). The position of the South African species, *Rhodophyllis reptans*, was well supported (BP = 100) in a cluster that also included *R. membranacea* from New Zealand and *R. divaricata* from France. The topological position of the plant known as *Calliblepharis frimbriata* from South Africa was unsupported in *rbc*L trees.

The *Rhodophyllis* assemblage may have originated on the eastern side of Gondwanaland in what is now New Zealand and Tasmania and been dispersed across the antiboreal Pacific Ocean to South Africa, as indicated by the large pairwise base distance between *R. membranacea* and *R reptans* (pbd = 6.3 %). *R. divaricata*, the type species of *Rhodophyllis*, probably reached western Europe by amphitropical distribution in Miocene or Pliocene (*R. reptans/R.divaricata*, pbd = 3.8 %). The record of the South African species, *R. reptans*, from St. Paul Island in the southern Indian Ocean fits the hypothesis of long range dispersal along the boundary of the subtropical/subantarctic convergence proposed by Hommersand (1986).

The *Craspedocarpus/Calliblepharis* group almost certainly followed a different pathway with dispersal through the North Indian Ocean. This hypothesis is supported by the discovery of a new species of *Calliblepharis, C. celatospora* Kraft, in Western Australia that is related to *C. fimbriata* from South Africa (Chiovitti *et al.* 1998), and the presence of similar species in the North Indian Ocean (Silva *et al.* 1996). The geographical range of this group extends to the Atlantic Ocean with the recognition of *Calliblepharis fimbriata* in Brazil (Guimarães & Pereira 1993) and *Craspedocarpus humilis* in North Carolina (Schneider 1988). A pattern of distribution through the North Indian Ocean to South Africa (Fig. 1), and from there to western South and North America by way of the South Equatorial and Guiana currents, as proposed by Hommersand (1986, Fig. 3), is favoured. A close connection between the Cystocloniaceae (including the Rhodophyllidaceae) and the Hypneaceae was proposed earlier by Hommersand and Fredericq (1990) based on similarities in cystocarp development. Recognition of the family Hypneaceae is not supported by the *rbc*L data.

Gigartina clade (Gigartinaceae) (Fig. 6)

The phylogenetic systematics and biogeography of the Gigartinaceae was investigated by Hommersand et al. (1994, 1999). Four genera are represented in South Africa: *Gigartina, Mazzaella, Sarcothalia* and '*Sarcothalia*', the last of these being unnamed. Here, we add six additional taxa belonging to *Gigartina* and examine the biogeographic relationships of each.

'Gigartina' alveata from New Zealand was resolved in basal position (BP = 100) adjacent to a clade containing *'Gigartina' radula* and *'G.' atropurpurea* (BP = 100). The topological position of the remaining fourteen *Gigartina* taxa was unresolved. South African species clustered together in a terminal clade, but without bootstrap support. Pairwise base differences among the three South African species ranged from (pbd = 1.7 % to 4.5%), or approximately the same as the range for all true *Gigartina* species in the tree. These results suggest that an assemblage of *Gigartina* species radiated at about the same time in the antiboreal Pacific Ocean in the vicinity of Australasia and that one or more species reached South Africa. We favour dispersal to South Africa via West Antarctica, however, there is no bootstrap support for this biogeographical hypothesis.

Three other gigartinacean genera in South Africa are treated in Hommersand *et al.* (1999). *Sarcothalia livida* from New Zealand was once thought to be the same as S. stiriata from South Africa and their sister relationship is close (pbd = 2.2%). Another pair of sister species, *'Sarcothalia' decipiens* from New Zealand and *'S.' scutellata* from South Africa (pbd = 2.5%), and a pair of *Mazzaella* species, *M. membranacea* from Chile and *M. convoluta* from South Africa (pbd = 2.5%) are separated by similar pairwise base differences. Species of all three genera may have been distributed to South Africa at approximately the same time by way of West Antarctica.

Apoglosseae, Cryptopleureae, Schizoserideae and Myriogrammeae (Delesseriaceae)

Recent studies by Lin *et al.* (2001) have shed light on the phylogenetic systematics of members of the Delesseriaceae. Several tribes and genera occur primarily in the Southern Hemisphere, including Apoglosseae (*Apoglossum, Paraglossum*), Cryptopleureae (*Botryoglossum, Hymenena, Acrosorium*), Schizoserideae (*Schizoseris*) and Myriogrammeae (*Myrogramme, Haraldiophyllum*), which are represented in South Africa. *Delesseria papenfussii* from South Africa belongs in *Paraglossum* J. Ag., a genus that has gone unrecognized until recently. *Delesseria (Paraglossum) papenfussii* is sister to an undescribed species of *Paraglossum* from Antarctica (pbd = 5.6%) and clearly separate from *Delesseria (Paraglossum) crassinervia* from New Zealand and three other

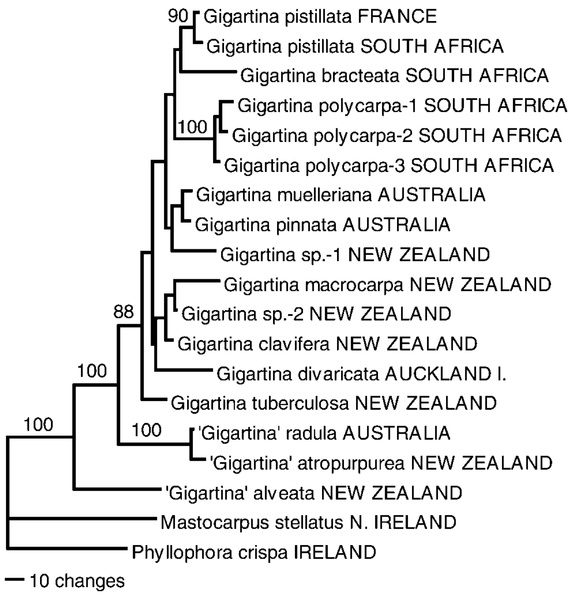

Figure 6. One of four minimal trees of length = 583 (CI = 0.7273, RI = 0.6103) resulting from parsimony search of *rbc*L data for fourteen taxa belonging to *Gigartina* and five outgroup species. Conditions as in Fig. 2.

species from South America and the subantarctic islands. In a limited survey of members of the tribe Cryptopleureae, *Botryoglossum platycarpum* from South Africa stood closest to *Hymenena multipartita* from southern Australia (pbd = 5.0%). *Hymenena venosa*, the type species of *Hymenena* from South Africa, was nearly equidistant from *H. falklandica* from the Falkland Islands (3.5%), *H. multipartita* from Australia (3.3%) and *Acrosorium venulosum* from Wales (3.2%). The plant known correctly as *Nitophyllum (Polyneura) venosum* and incorrectly as *Myriogramme livida* from South Africa belongs in *Schizoseris*, a widely distributed genus in the Southern Ocean. Two other genera, *Myriogramme* and *Haraldiophyllum*, that are also widespread in the Southern Ocean, are represented in South Africa. Further investigations of species of Delesseriaceae will contribute significantly to our understanding of the biogeography of South African red algae.

Vicariance events leading to the establishment of the South African red algal flora

Except during periods of extensive glaciation, West Antarctica consisted of exposed islands, with the Antarctic Peninsula wholly or partly connected to the South American continent (Fig. 1). Paleoclimatologists disagree as to the extent of glaciation in Antarctica during Oligocene (34 to 20 million years ago); however, periods of maximum Antarctic ice were apparently experienced in Miocene at 15, 10.2, 8.9, 6.4 and 2.4 million years ago. According to Ciesielski *et al.* (1982), the West Antarctic ice sheet did not form until after nine million years ago, and the Ross and Weddell Seas were ice free prior to that time. Scherer *et al.* (1998) concluded, based on an analysis of fossil marine diatom deposits, that the West Antarctic ice sheet collapsed several times during Pleistocene creating a seaway across parts of West Antarctica, perhaps as recently as 11,400 years ago. The West Antarctic ice sheet cannot, then, have been the limiting factor for the dispersal of marine algae from the antiboreal Pacific Ocean to South Africa.

At the present time, the phytogeographic province of the South African West Coast is isolated from a connection with Antarctica by the persistence of the West Wind Drift. The final barrier to the formation of the modern West Wind Drift was the connection between South America and West Antarctica. Initiation of the Shackleton Fracture Zone beginning at 29 million years ago, led to formation of the Drake Passage by 22 million years ago, and the opening of the east Scotia Sea (Barker & Burrell 1977). However, widening of Drake Passage may have taken place slowly and the West Wind Drift may not have reached its present strength until a time of maximum Antarctic glaciation at six million years ago, or perhaps later. The Benguela Upwelling System is a more recent development, said to have evolved concomitant with changes in oceanic circulation associated with the closing of the sinus of Panama in the last three million years (Marlow *et al.*, 2000).

At some point in time, the West Wind Drift must have begun to act as an effective barrier to the dispersal of species from the Pacific Ocean in eastern Australia and New Zealand to South Africa. Since none of the South African species investigated were identical to species found in other biogeographic provinces, it is unlikely that man is responsible for transporting any of these to South Africa within historical times. To investigate the likelihood that a vicariance event isolated the South African flora from distant biogeographic provinces, we examined pairwise base differences between sister and nearest neighbour species within and outside South Africa. These ranged from 2.2% to 6.4% (Table 2). In our opinion, the establishment of the West Wind Drift as a permanent barrier would also have isolated species found in southern South America from those occurring across Drake Passage in the region of the Antarctic Peninsula. Hommersand *et al.* (1999, Fig. 1) investigated the phylogenetic relationships of two species of Gigartinaceae from Ancud, Chile, and the South Shetland Islands, Antarctica, each of which had received the same names. We interpret the pairwise base differences for *Iridaea cordata* (pdb = 3.4%) and *Gigartina skottsbergii* (pbd = 1.8%) as minimal values related to the vicariant event we associate with the establishment of the West Wind Drift. We would expect pairwise base differences to be the same or greater for species pairs in which one of the species is found in South Africa and this appears to be the case (Table 2). Too few examples were analyzed to test the hypothesis that red algal taxa that originated in western Australia were later distributed to southern Africa through the North Indian Ocean by means of the North Equatorial current. Such a test will require phylogenetic studies of Indian Ocean species.

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Appendix 1

Ahnfeltia plicata (Hudson) Fries, Broadhaven, Pembrokeshire, Wales, coll. CA Maggs, 9.ii.1993 (U04168, 99%)

Aeodes nitidissima J. Agardh, Hangliton Bay, North Island, New Zealand, coll. W Nelson, 24.iii.2000 (AF385637, 95%)

Aeodes orbitosa (Suhr) Schmitz, Blaubergstrand, Table Bay, Cape Province, South Africa, coll. MH Hommersand 16.vii.1993 (U21599, 83%)

Aeodes ulvoidea Schmits, Haga, Haga, Cape Province, South Africa, coll. O DeClerck, 16.x.1999 (AF385638, 83%)

Calliblepharis ciliata (Hudson) Kützing, dredged, Pighuet, Brittany, France, coll. J Cabioc'h, 22.vi.1993 (AF385653, 98%)

Calliblepharis fimbriata (C. Agargh) Kützing, Sharks Bay, Port Alfred, South Africa, coll. MH Hommersand, 19.vii.1993 (AF385654, 92%)

Calliblepharis jubata (Goodenough et Woodward) Kützing, Penmarch, Brittany, France, coll. MH Hommersand 21.vi.1993 (U04189, 81%)

Caulacanthus ustulatus (Turner) Kützing, Carentec, Brittany, France, [introduced species, see Rueness (1997)] coll. J Cabioc'h, 22.vi.1993 (U04188, 69%)

Caulacanthus ustulatus (Turner) Kützing, Swakopmund, Namibia, coll. MH Hommersand, 7.xi.1995 (AF099687, 93%)

Craspedocarpus erosus (J.D. Hooker et Harvey) Schmitz, Lyall Bay, Wellington, New Zealand, coll. WA Nelson, 21.iv.1994 (AF385657, 99%)

Craspedocarpus tenuifolius (Harvey) Min-Thein et Womersley, D'Estrees Bay, Kangaroo I. South Australia, coll. MH & FC Hommersand 7.ix.1995 (AF385655, 86%)

Craspedocarpus venosus (Kutzing) Min-Thein et Womersley, Port MacDonnell, South Australia, coll. MH Hommersand & G.T. Kraft, 15.vii.1995 (AF385656, 94%)

Epymenia capensis (J. Agardh) Papenfuss, Kommetjie, Cape Peninsula, South Africa, coll. O DeClerck, 24.i.2001 (AF385646, 98%)

Epymenia obtusa (Greville) Kützing, Kommetjie, Cape Peninsula, South Africa, coll. MH Hommersand, 9.xi.1993 (AF385647, 97%)

Epymenia sp. (Rhodymenia skottsbergii?), Isla Negra, prov. San Antonio, Chile, coll. S Fredericq & M.E. Ramírez, 26.i.1994 (AF385648, 75%)

Epymenia sp., Isla Despar, Tierra del Fuego, Argentina, coll. ML Mendoza, 8.xii.1999 (AF385649, 80%)

Epymenia wilsonis Sonder, Island Bay, Wellington, New Zealand, coll. WA Nelson, 12.x.2000 (AF385650, 79%)

Gelidium americanum (W.R. Taylor) Santelices, Radio Island, Carteret Co., NC, USA, coll. DW Freshwater, 16.ii.1991 (L22459, 100%)

'Gigartina' alveata (Turner) J. Agardh, Tauranga Bay, North I., New Zealand, coll. WA Nelson, ii.1993 (U03422, 93%)

'Gigartina' atropurpurea (J. Agardh) J. Agardh, Island Bay, Wellington, New Zealand, coll. WA Nelson, 23.v.1993 (U03423, 94%)

Gigartina bracteata (Gmelin) Setchell et Gardner, Oudekraal, Cape Peninsula, South Africa, coll. J Bolton, 28.ii.1993 (AF385662, 97%)

Gigartina clavifera J. Agardh, Princess Bay, Wellington, New Zealand, coll. WA Nelson, 23.v.1993 (U03424, 92%)

Gigartina divaricata J. D. Hooker et Harvey, Adams is., Survey Bay, Auckland Is., coll. T Grant, 11.xii.1996 (AF146204, 94%)

Gigartina macrocarpa J. Agardh, Bream Head, Northland, New Zealand, coll WA Nelson & G Knight, 6.x.1995 (AF386529, 99%)

Gigartina muelleriana Setchell et Gardner, Flinders Jetty, Victoria, Australia, coll. GW Saunders & GT Kraft (U03427, 92%)

Gigartina pinnata J. Agardh, Port MacDonnell, South Australia, coll. MH Hommersand, 15.vii.1995 (AF385663, 93%)

Gigartina pistillata (S.G. Gmelin) Stackhouse, Smitswinkel Bay, False Bay, Cape Peninsula, South Africa, coll. J Bolton, 4.vi.1993. (U03430, 54%)

Gigartina pistillata S.G. Gmelin) Stackhouse, Santec, Brittany, France, coll. J Cabioc'h, 6.iv.1993 (U03429, 90%)

Gigartina polycarpa (Kützing) Setchell et Gardner-1, Kommetjie, Cape Peninsula, South Africa, coll. J Bolton, 24.ii.l993 (U03431, 90%)

Gigartina polycarpa (Kützing) Setchell et Gardner-2, Blaubergstrand, Table Bay, Cape Province, South Africa, coll. MH Hommersand, 16.vii.1993 (AF386531, 75%)

Gigartina polycarpa (Kützing) Setchell et Gardner-3, 2nd sister, Riet River Port Alfred, South Africa, coll. MH Hommersand, 20.vii.1993 (AF385664, 93%)

'Gigartina' radula (Esper) J. Agardh, Evans Cave, Cape Lannes, S Australia, Australia, coll. MH Hommersand, 11.ix.1995 (AF146205, 99%)

Gigartina sp.-1, Manawa tawhi, Tasman Bay, Three Kings Is., New Zealand, coll. M Francis & WA Nelson, 25.xi.1998 (AF385665, 94%)

Gigartina sp.-2, 12 mile, West Coast, South I. New Zealand, coll. WA Nelson, 25.ix.1995 (AF386530 99%)

Gigartina 'tuberculosa' sensu Lindauer, Stewart I., New Zealand, coll. WA Nelson, viii.1994 (AF385666, 96%)

Gracilariopsis tenuifrons (Bird et Oliveira) Fredericq & Hommersand, Petit Havre, Grande-Terre, Guadeloupe, F.W.I., coll. A Renoux, 9.xi.1993 (U04171, 82%)

'Grateloupia' intestinalis (J.D. Hooker et Harvey) Setchell ex Parkinson, Qaro, New Zealand, coll. WA Nelson, 19.ix.93 (AF385639, 97%)

Hypnea boergesenii Tanaka, Long Tung Park, NE Taiwan, coll. S Fredericq & S-M Lin, 12.viii.1993 (AF385634, 94%)

Hypnea musciformis (Wulfen) Lamouroux, Fort Fisher, New Hanover Co., NC, USA, coll. DW Freshwater, iii.1990 (U04179, 97%)

Hypnea spinella (C. Agardh) Kützing, Layton, Drive, Long Key, Florida Keys, Florida, USA, coll. F Gurgel, 17.ix.1998 (AF385635, 98%)

Hypnea volubilis Searles, 30 m, Sonnier Banks, Louisiana, USA, coll. S Fredericq & B Gavio, 30.vi.1999 (AF385636, 97%)

Mastocarpus stellatus (Stackhouse) Guiry, Bally Castle, Co. Antrim, Northern Ireland, coll. CA Maggs, 20.i.1992 (U29920, 100%)

'Kallymenia' antarctica Hariot, Pta Collins, Bahía Fildes, King George I., South Shetland Is., Antarctica, coll. S Fredericq & J Rodríguez, 15.ii.1994 (U21698, 97%)

Pachymenia carnosa, Kommetjie, Cape Peninsula, South Africa, coll. O DeClerck, 9.xi.1999 (AF385640, 97 %)

Pachymenia cornea (Kützing) Chiang, Buffles Bay, Cape Peninsula, South Africa, coll. MH Hommersand, 14.vii.1993 (U21588, 89%)

Pachymenia crassa Lindauer, Northwest Bay, Great I., Three Kings Is., New Zealand, coll. V Staines, 18.I.1994 (U21598, 88%)

Pachymenia lusoria (Greville) J. Agardh, Aramaara, North Island, New Zealand, coll. WA Nelson, 19.iii.1994 (AF385641, 94%)

Pachymenia sp., Pta Peñon, Bahía Fildes, King George I., South Shetland Is., Antarctica, coll. S Fredericq & J Rodríguez, 14.ii.1994 (U22096, 97%)

Phyllophora crispa (Hudson) Dixon, Spiddal, Co. Galway, Ireland, coll. MD Guiry, 7.iii.1993 (U02990, 97%)

Plocamium cartilagineum (Linnaeus) Dixon, Spiddall Co., Galway, Ireland, coll. MD Guiry, 28.ii.1993. (U21701, 90%)

Polyopes constrictus (Turner) J. Agardh, Kommetjie, Cape Peninsula, South Africa, coll. R Anderson & J Bolton, 31.i.2001 (AF385642, 98%)

Polyopes polyideoides Okamura, Makang Harbor, N.E. Taiwan, coll. S Fredericq & J Lewis, 11.viii.1993 (AF385643, 91%)

Polyopes sp. (as Prionitis af. angusta), Murroran, Hokkaido, Japan, coll. S Fredericq & K Kogame, 6.ix.1993 (AF385644, 83%)

Polyopes tenuis Womersley et Lewis, Williamstown, Victoria, Australlia, coll. GT Kraft, 6.iii.97 (AF385645, 77%)

Rhodophyllis divaricata (Stackhouse) Papenfuss, Carantec, Brittany, France, coll. J Cabioc'h, 22.vi.1993 (AF385658, 92%)

Rhodophyllis membranacea (Harvey) J.D. Hooker et Harvey, Papatouri, North Island,New Zealand, coll. WA Nelson, 18.ii.1996 (AF385659, 94%)

Rhodophyllis reptans (Suhr) Papenfuss, Glencairn, near Simonstown, False Bay, Cape Peninsula, South Africa, coll. R Anderson, 18.i.1994 (AF385660, 93%)

Rhodophyllis volans Harvey, Port MacDonnell, South Australia, Australia, coll. MH Hommersand, 15.vii.1995 (AF38628, 94%)

Rhodymenia pseudopalmata (Lamouroux) P. Silva, Wrightsville, Beach, New Hanover Co., NC, USA, coll. DW Freshwater, vi.91 (U04184, 98%)

Rhodymenia sp., Port Aransas Channel, Port Aransas, TX-USA, coll. S Fredericq & F Gurgel, 17.v.1998 (AF385651, 97%)

Sarcodia ceylanica Harvey ex Kützing, Long-Shia Dong, Hsiao Liuchiu I., Taiwan, coll. S Fredericq, 23.vii.1993 (U26819, 98%)

Sarcodia dentata (Suhr) R.E. Norris, The Kowie, Port Alfred, South Africa, coll, MH Hommersand 10.vii.1993 (U26816, 98%)

Sarcodia marginata J. Agardh, Warrnambool, Victoria, Australia, coll. MH Hommersand, 13.vii.95 (AF212193, 98%)

Sarcodia montagneana (J. Hooker & Harvey) J. Agardh, Taipa, North I. New Zealand, coll. W Nelson, 2.xii.93, (U21705, 88%)

Sarcodia sp., 20 m., The Docks, Jervis Bay, New South Wales, Australia, coll. A Millar & D Hardin, 25.x.1995 (AF212194, 89%)

Stictosporum nitophylloides (Harvey) J. Agardh, Tarcoola Beach, Geraldton, Western Australia, coll. MH & FC Hommersand, 21.ix.1995 (AF385661, 88%)

Trematocarpus dichotomus Kützing, Horcón, Prov. Valparaíso, Chile, coll. S Fredericq & ME Ramírez, 27.i.1994 (U26814, 98 %)

Trematocarpus flabellatus (J. Agardh) G.B. DeToni, Kommetjie, Cape Peninsula, South Africa, Kommetjie, Cape Peninsula, South Africa, coll. MH Hommersand & S. Fredericq, 28.i.2001 (AF385652, 95%)

Trematocarpus fragilis (C.A. Agardh) G.B. DeToni, Buffles Bay, Cape Peninsula, South Africa, coll. MH Hommersand 14.vii.1993 (U26815, 97%)