

A Biogeographical Study of *Laurencia* and *Hypnea* Species of the Macaronesian Region

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2 Figures, 5 Tables

Most of the Macaronesian islands, except the Cape Verde Islands, were included by FELDMANN (1946) in the Lusitano-African region. In more recent studies, VAN DEN HOEK (1984) included the Azorean archipelago in the Warm Temperate NE Atlantic region and the Azores flora is also incorporated in the list of benthic marine algae of the North Atlantic Ocean (SOUTH & TITLEY 1986). PRUD'HOMME VAN REINE (1988) assigned to the Azores an intermediary position between the subtropical Macaronesian islands (Madeira, Salvages and Canaries) on the one side and the warm temperate Eurafrian coasts on the other side. On the contrary, the Cape Verdean seaweed flora is characterized as tropical on account of the predominance of algal species with a tropical distribution (FELDMANN 1946; VAN DEN HOEK 1975, 1984). LAWSON & JOHN (1987), however, on the basis of an ordination (reciprocal averaging) of a large number of tropical and subtropical seaweed floras around the Atlantic Ocean, concluded that the Cape Verde Islands belong to the Warm Temperate African flora, including also the Canarian, the Mauritanian and the Senegalese floras. PRUD'HOMME VAN REINE & VAN DEN HOEK (1988), however, found out

a separate and individual position, with a distinct E America imprint for the Cape Verdean seaweed flora. Thus, additional studies are needed to better understanding the biogeographical position of the seaweed floras present in the Macaronesian archipelagos.

In the Macaronesian region the assembled seaweed flora of each archipelago is clearly dominated by members of Rhodophyta (PRUD'HOMME VAN REINE 1988; LEVRING 1974; GIL-RODRÍGUEZ & AFONSO-CARRILLO 1980; PRUD'HOMME VAN REINE & VAN DEN HOEK 1988). Among those red algae, the genera *Laurencia* and *Hypnea* have several species, mainly in intertidal and shallow sublittoral habitats. Nevertheless, it is possible to find an latitudinal gradient in the respective florula size and composition for each archipelago. This fact provides a sound opportunity to study the biogeographical relationships within the different Macaronesian archipelagos and with surrounding areas.

The present study is carried out to determine the taxonomical status of several species of these two genera and to further contribute to the biogeographical relationships of the Macaronesian archipelagos seaweed floras.

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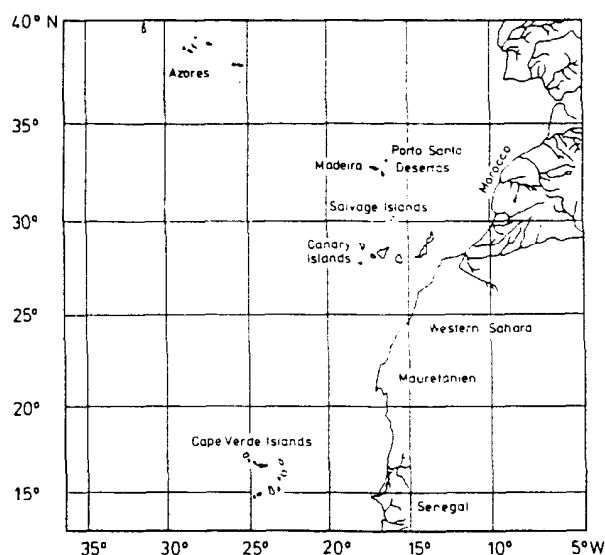


Fig. 1. Macaronesian archipelagos and north-western Africa.

Material and Methods

Species of *Laurencia* and *Hypnea* collected during different expeditions in the Macaronesian archipelagos were identified (Fig. 1). Most of the samples came from the CANCAP Expeditions of the Netherlands Commission for Sea Research (NRZ) and are deposited in the Rijksherbarium Leiden (L). Fresh and dried samples from local collections in La Laguna University Herbarium (TFC) were also observed.

The species of *Laurencia* were identified following the criteria of SAITO (1967, 1969, 1982), SAITO & WOMERSLEY (1974) and GIL-RODRIGUEZ & HAROUN (in press). Hypneaceae were identified following the often conflicting criteria of LAWSON & JOHN (1987), BODARD (1968), BOERGESEN (1915-1920), MSHIGENI (1978) and DAWSON (1961). More than 300 samples of *Laurencia* and 250 samples of *Hypnea* species have been studied. Most specimens were identified up to the specific level, but specially the specimens of *Laurencia* species from Cape Verde Islands still needs more careful determinations.

The new data have been compared to records from literature and have been used in combination. The florulas of both genera recorded from the Azores, Madeira, Salvages, Canaries and Cape Verde Islands have been compared with lists prepared for a number of selected geographical areas:

- 1) The tropical E Atlantic region as defined by VAN DEN HOEK (1984) (excluding the Cape Verde Islands) or Tropical West Africa as defined by LAWSON & JOHN (1987).
- 2) The tropical and subtropical coasts of the Americas as defined by WYNNE (1986), an area roughly similar to the Caribbean area by VAN DEN HOEK (1984).
- 3) The temperate North Atlantic coasts as defined by SOUTH & TITTELY (1986).

Besides, the mean surface temperature of the sea in °C of different selected areas were considered,

both in summer and winter months during the last glaciations (18,000 years ago) and at present (Table 1; cf. CROWLEY 1981; MCINTYRE & KIPP 1976; PRELL et al. 1976; SARNTHEIN et al. 1982).

Other geographical and historical parameters, as surface area and geographical spreading of each archipelago, distances to the nearest continent and age of the islands, were compiled from several sources (Table 2; cf. MITCHELL-THOME 1976; ROTHE 1982; SCHMINCKE 1982) and are compared with the assembled seaweed floras of each of the archipelagos (SCHMIDT 1931; AUDIFFRED & PRUD'HOMME VAN REINE 1985; LEVRING 1974; AUDIFFRED & WEISSCHER 1984; GIL-RODRIGUEZ & AFONSO-CARRILLO 1980; AFONSO-CARRILLO et al. 1984; GIL-RODRIGUEZ et al. 1985, and unpublished records from CANCAP-Expeditions).

Table 1. Mean surface temperature of the sea in °C. - LG = last glaciation (c. 18.000 years ago).

Area	T in summer		T in winter	
	LG	Recent	LG	Recent
WM		21.5-25.0		12.0-14.0
SCWT	12-19	17.5-21.5	4-12	12.5-18.0
AZO	18-20	21.0-23.0	12-15	15.0-17.5
MAD	22-23	21.5-23.0 *	14-16	16.0-18.0 *
SAL	21-23	21.0-22.5 *	12-15	17.0-18.0 *
L/F	18-20	20.5-22.0 *	12-14	17.0-18.0 *
OC	19-22	21.5-22.5 *	12-14	18.0-19.5 *
Subtr.Afr.	19-24	21.0-26.0	12-17	17.5-20.5
CVI	23-25	24.5-26.0	17-20	21.0-24.0
Tr.Afr.	22-26	24.0-27.0	16-26	19.0-28.0

WM = Western Mediterranean; SCWT = Southern cooler warm temperate subregion; AZO = Azores; MAD = Madeira; SAL = Salvages; L/F = Lanzarote, Fuerteventura and the small eastern Canary islets; OC = other Canaries except L/F; Subtr.Afr. = Subtropical Africa; CVI = Cape Verde Is.; Tr.Afr. = Tropical Africa; * = Macaronesia s.s.

Table 2. Geographical characteristics and assembled seaweed floras of Macaronesian archipelagos.

	AZO	MAD	SAL	CAN	CVI
No. seaweed spp.	189	292	193	460	223
Surface area (km ²)	2304	796	4	7273	4030
No. islands	9	2 (+4)	3	7 (+3)	10 (+2)
Archip. width (km)	615	100	24	520	330
Distance nearest Continent (km)	1450	610	350	100	460
Age (M.y.a.)	1-5	2-3	-	17-20*1	10-15
				2-14*2	

AZO = Azores; MAD = Madeira; SAL = Salvages; CAN = Canaries; *1 = Lanzarote & Fuerteventura; *2 = other Canary Islands; CVI = Cape Verde Islands.

Results

Taxonomic remarks

Although specimens are easily identified up to the generic level, the taxonomic status of some samples, specially of members of the genus *Laurencia*, are in much confusion. Therefore, a sound taxonomic research is actually carried up by members of the Phycology Section of La Laguna University (c.f. GIL-RODRIGUEZ & HAROUN, in press), with close collaboration from the staff of the Rijksherbarium of Leiden.

The species of *Hypnea* are more easily identified, but some taxonomic questions still remain unsolved:

1) In some dredging samples of the CANCAP expeditions near Cape Verde Islands, we have found several specimens of an unknown species growing on calcareous algae substrate between 30 to 80 m depth. The external morphology of the plants is rather similar to that of *H. musciformis* (WULF.) LAMOUROUX, with some hook-like tips, but often the tips of branchlets end in small discoid holdfasts. Besides, its internal structure is different from *H. musciformis*; the deep-water species T.S. shows 1 large central cell surrounded by 6-7 pericentral cells and a cortex of quadrangular cells. Only sterile specimens of the deep-water species have been collected, so further taxonomic determination is not possible yet.

2) The samples of the CANCAP expeditions reported until now as *Hypnea spinella* (C. AG.) J. AG. or *H. cervicornis* J. AG. were carefully studied. The internal structure of the thalli is the same in both species: 1 small central cell surrounded by 5 (-6) large pericentral cells and a layer of small cortical cells. Besides, the dimensions of the axis and branchlets shows a clear overlap, with plants showing *H. spinella* morphology on the one side, but dimensions of *H. cervicornis* on the other side. The reverse case was also found.

On basis of the specimens studied, a distinct transition from typical *H. spinella* into typical *H. cervicornis* has been found, and thus these two taxa can be considered to be a single one. The only main diverging character between both taxa is their habitat (Fig. 2). Plants with *H. spinella* morphology are more abundant in the intertidal platforms, with some individuals also present in the tide-pools and in shallow water. On the contrary, plants with *H. cervicornis* morphology are mainly found in permanently submerged habitats, while almost no plants occurs on the intertidal platforms. It seems that *H. spinella* is only a compact growth-form of habitats with rough wave action, whereas *H. cervicornis* is a more elongate growth-form of habitats with less wave action.

During the detailed study of *Hypnea* specimens we observed parasitic plants growing on several *Hypnea* species. The plants are small globular bodies with several papillae, less pigmented than the host and scattered along the host thallus. This bodies has been recognized as *Hypneocolax stellaris* BOERGENSEN, an adelphoparasite first described for the Virgin Islands (formerly West Danish Indies).

Hypneocolax stellaris was found growing on *Hypnea spinella* (C. AG.) J. AG., *H. flagelliformis* GREV. ex J. AG. and *H. valentiae* (TURNER) MONTAGNE from the intertidal zones of some southern localities of the Canary Islands and also from the Cape Verde Islands.

This species has so far only been recorded from the Caribbean, Baja California, Hawaii and Indonesian coasts. This is thus the first record for the E Atlantic Ocean.

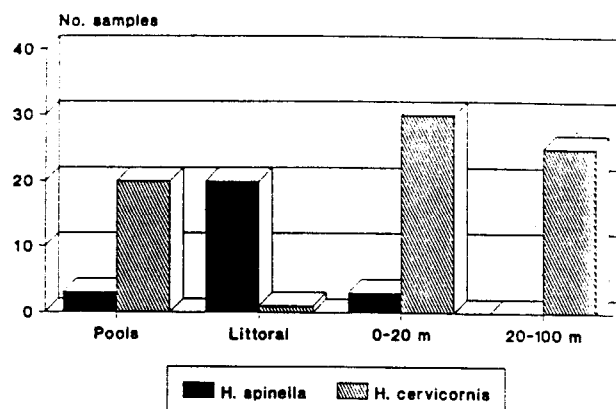


Fig. 2. Habitat distribution of *Hypnea spinella* and *H. cervicornis* from CANCAP expeditions.

Biogeographical aspects

The distributional patterns of *Hypnea* spp. and *Hypneocolax stellaris* in the different archipelagos are represented in Table 3. There is a clear increase in the number of species present in the southern islands compared to the Azores. The analysis of the *Laurencia* species is not yet finished, specially not for the Cape Verde specimens. Nevertheless, it can be observed that the species composition changes towards the southern islands.

The Azores florula has a clear North Atlantic imprint [with *L. hybrida* (DC) LENORMAND ex DUBY, *L. platycephala* KUTZING, *L. pinnatifida* (HUDSON) LAMOUROUX and *L. obtusa* (HUDSON) LAMOUROUX], whereas in the Canary Islands the genus *Laurencia* possesses a more subtropical character [with *L. majuscula* (HARVEY) LUCAS, *L. corrallopsis* HOWE, *L. perforata* (BORY) MONTAGNE]. In Cape Verde Islands

Table 3. Distribution of *Hypnea* spp. and *Hypneocolax stellaris* in the Macaronesian region.

	AZO	MAD	SAL	CAN	CVI
<i>H. musciformis</i>	+	+	+	+	+
<i>H. spinella/cerv.</i>	(+)	+	+	+	+
<i>H. valentiae</i>	-	-	-	+	+
<i>H. flagelliformis</i>	-	-	-	+	+
<i>H. arbuscula</i>	-	-	-	-	+
<i>H. cenomyce</i>	-	-	-	-	+
<i>H. sp. 1</i>	-	-	-	-	+
<i>H. stellaris</i>	-	-	-	+	+

AZO = Azores; MAD = Madeira; SAL = Salvages; CAN = Canary Islands; CVI = Cape Verde Islands.

the florula is mainly of tropical to subtropical affinity [*L. papillosa* (FORSK.) GREVILLE]. Besides, *L. microcladia* KÜTZING has recently been identified from the Azores, Madeira, Canaries and also from the Cape Verde Islands; this species is so far only known from the W Atlantic side (Caribbean area and Bermudas); therefore, this is the first record for the E Atlantic side.

Table 4. Numbers of *Hypnea* and *Laurencia* species present in nearby floras.

	<i>Hypnea</i>	<i>Laurencia</i>
North Atlantic Ocean SOUTH & TITTLLEY (1986)	1	4
Trop. & Subtropical Americas WYNNE (1986)	6	22
Tropical West Africa LAWSON & JOHN (1987)	7	12

In Table 4 are represented the numbers of *Laurencia* and *Hypnea* species present in the North Atlantic Ocean, Tropical and Subtropical America (Caribbean area) and Tropical West Africa, considered here as potential donor areas. Only one species of *Hypnea* (*H. musciformis*) is recorded in the North Atlantic flora and only 4 *Laurencia* species. In warmer waters the numbers of species of both genera are larger. Although, an almost similar number of *Hypnea* species occurs in the Caribbean area and in the Tropical West Africa area, the number of *Laurencia* species in the latter area is only half that of the former area, reflecting the less rich tropical flora of the African coasts.

The numbers of common species shared by the Macaronesian archipelagos with the above mentioned potential donor areas are represented in Table 5. Towards the south an increase of species shared by each Macaronesian Archipelago with the Tropical West Africa area is observed and the same holds for the western Atlantic area.

Discussion

Taxonomic comments

According to most authors, *H. spinella* and *H. cervicornis* are closely related species (BOERGESEN 1915-20; DANGEARD 1949; LAWSON & JOHN 1987) and probably synonymous, but no-one made the decision, whether to unite them or not. We have shown, on basis of the specimens studied, a distinct transition from typical loosely branched and elongated *H. cervicornis* into typical compact *H. spinella*. This is probably the result of wave action in the habitats, and thus we consider these two taxa to be a single one. DAWSON (1961, p. 235) considered *H. esperi* KÜTZING to be a "small variant of *H. cervicornis*", but MSHIGENI (1978, p. 876) cited *H. esperi* as a synonym of *H. spinella*. Both authors also cited the other names (*H. spinella* and *H. cervicornis* respectively) as independent separate species. The correct name for the alga is *Hypnea spinella* (C. AGARDH) J. AGARDH (1847, p. 14), not KÜTZING 1849. Basyonym is *Sphaerococcus spinellus* C. AGARDH (1822, p. 323). Lectotype in LD is herb. Ag. 33888, "Vestindien". For *H. cervicornis* J. AGARDH (1852, p. 451) the lectotype (in LD) is herb. Ag. 33878, *Sphaerococcus spinellus* var. *laxior*, "In litore maris prope Bahian, legit et misit Martius".

Biogeographical comments

The marked differences between disjunct floras have been attributed to historical factors such as the configuration of oceans and continents in the geological past and paleoclimatic events (VAN DEN HOEK 1984; BREEMAN 1988). Although all the Macaronesian archipelagos are of volcanic origin, other geographic characteristics, specially their distance to the nearest continent and their age, are different. The impoverished *Laurencia* and *Hypnea* florula present in the Azores compared to other Macaronesian archipelagos seems largely due to the isolated position of the former area, which is located at considerable distance from other shores. In this respect, the seaweed flora of this archipelago has been characterized as chance survivors of chance invasions by long-range dispersal (VAN DEN HOEK 1987; PRUD'HOMME VAN REINE 1988).

Table 5. Numbers of *Hypnea* or *Laurencia* species common to Macaronesian and nearby florulas.

	<i>Hypnea</i>					<i>Laurencia</i>				
	AZO	MAD	SAL	CAN	CVI	AZO	MAD	SAL	CAN	CVI
N. Atl. Oc.	1	1	1	1	1	4	3	3	3	1?
Tr. Subtr. A.	2	2	2	3	3	2	2	2	5	6?
Tr. W. Afr.	2	2	2	3	6	2	2	3	8	6?

AZO = Azores; MAD = Madeira; SAL = Salvages; CAN = Canary Islands; CVI = Cape Verde Islands; N.Atl.Oc. = North Atlantic Ocean; Tr.Subtr.A. = Tropical & Subtropical Americas; Tr.W.Afr. = Tropical West Africa.

In the warm temperate flora of North America there are few *Laurencia* and *Hypnea* species (WYNNE 1986; KAPRAUN 1980). The drastic temperature changes, sometimes more than 30°C in each year, have been pointed as a plausible explanation of the depauperate flora of the North American coasts (VAN DEN HOEK 1975 & 1984; SEARLES 1984). Thus, few species now present in the Azores seem to originate from that area. The record of *L. microcladia*, known from American Atlantic coasts but not from Eurafri-can coasts, in the Azores and also in the other Macaronesian archipelagos, is the only example. Long range dispersal it is probably more difficult from the european side of the North Atlantic Ocean to the Azores due to the adverse current system; however, the *Laurencia* florula composition is almost similar in both Azores and the North Atlantic European coasts.

The geographic distribution boundaries of benthic algal species can be defined according to limiting temperatures (VAN DEN HOEK 1982; BREEMAN 1988), either as a growth (or reproduction) limit in the growing season and/or as a lethal limit in the adverse season. It is important to point out the close similarity of the temperature values for the Madeira, Salvages, and Canary Islands considered here as Macaronesian s.s. (c.f. PRUD'HOMME VAN REINE & VAN DEN HOEK, l.c.). In summer months the temperature in Azores waters is almost the same as in the other and more southern islands, but during winter much lower values are recorded in the former archipelago. Most probably winter temperature is a lethal limit for most subtropical species. The temperature regimen in Cape Verde Islands is always much higher than in the rest of the Archipelagos. Therefore, higher numbers of tropical to subtropical species are encountered in this Archipelago (*L. papillosa*, e.o.).

The larger numbers of species present in the Macaronesian s.s. islands seem to be results of their closer vicinity to donor areas and/or a warmer temperature regime. The richness of the Macaronesian s.s. seaweed flora may have resulted from its lesser susceptibility to extinction by lowered coenozoic temperatures and the presence of more diverse coastlines (PRUD'HOMME VAN REINE & VAN DEN HOEK, l.c.). Even in the tiny Salvage Islands there are more *Laurencia* and *Hypnea* species than in Azores. In the Canary Islands there is a sharp increase in the number of species of both genera; the new species appearing are often shared with the Cape Verde Islands.

The tropical portion and also the tropical to subtropical portion of the assembled seaweed flora of the Cape Verde Islands have a distinct E America (largely Caribbean) imprint (PRUD'HOMME VAN REINE & VAN DEN HOEK, l.c.). As an example, *L. papillosa* is only recorded from Caribbean and Cape Verdean coasts. Besides, Cape Verde Islands assembled seaweed flora is slightly more related to the Canary Islands flora (OC-portion) than to the Subtropical and Tropical West Africa floras (PRUD'HOMME VAN REINE & VAN DEN HOEK, l.c.). The canarian flora also appeared as the nearest relative of the Cape Verde Islands flora in LAWSON & JOHN (l.c.). The number of species of Hypneaceae and *Laurencia* which the Canary Islands and the Cape Verde Islands have in common and also share with the Tropical and Subtropical Americas, perhaps reflect their affinities as Tethyan remaining florulas on both sides of the Atlantic Ocean. Paleoclimatic changes and the subsequent flo-

ra-migrations, however, may have impoverished the warm temperate and tropical E Atlantic floras (VAN DEN HOEK 1984), thus the lower number of *Laurencia* species in the eastern Atlantic can be explained.

The composition of the florula of both genera in the Canary Islands supports its intermediate position between the tropical to subtropical imprint of the southern Cape Verde Islands and the warm temperate imprint of the northern Azores. Besides, the new records of *Hypneocolax stellaris* only in southern localities of the Canaries and in Cape Verde enhanced their subtropical to tropical affinities with the western Atlantic assembled seaweed flora.

Summary

Species of *Laurencia* and *Hypnea* mainly collected during the CANCAP expeditions (Netherlands Commission for Sea Research) were identified. A distinct transition from typical *H. spinella* (C. AG.) J. AG. growth-form into typical *H. cervicornis* J. AG. growth-form was observed based on different wave action. Thus, following the nomenclatural rules *H. cervicornis* must be considered to be a synonyme of the older name *H. spinella*. Besides, *Hypneocolax stellaris* BOERGESEN, an adelphoparasite, is recorded for the first time in the E Atlantic Ocean. The same holds for *L. microcladia* KÜTZING, of which collected specimens have now been identified for Azores, Madeira, Canaries and Cape Verde Islands.

The new floristic data has been compared to records from literature and have been used in combination to find the distributional pattern of both genera in the Macaronesian archipelagos. There is a clear increase in the number of species present towards the southern archipelagos. The new species appearing are often shared by Canary and Cape Verde Islands. The Canary Islands florulas can be characterized as intermediate between the warm temperate imprint of northern Azores and the tropical to subtropical character of Cape Verde Islands.

The number of species of Hypneaceae and *Laurencia* species which the Canary Islands and the Cape Verde Islands have in common and also share with the Tropical and Subtropical America, seems to reflect their affinities as Tethyan remaining florulas on both sides of the Atlantic Ocean.

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