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PHYLOGENY AND VICARIANCE BIOGEOGRAPHY OF NORTH ATLANTIC CHALINIDAE (HAPLOSCLERIDA, DEMOSPONGIAE)

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ABSTRACT

The present paper consists of a phylogenetic and historical biogeographic analysis of the North Atlantic shallow-water Haplosclerida (Porifera, Demospongiae), and of the Chalinidae in particular. The monophyly of the Haplosclerida is founded on five assumed apomorphous (derived) characters. Six related outgroups, viz. the Esperiopsidae, Desmacellidae, Mycalidae, Myxillidae, Microcionidae, and Axinellida s.l. have been used for establishing the character polarity within the Haplosclerida. A key to the haplosclerid families, the Chalinidae, Niphatidae, Callyspongiidae, Petrosiidae and Oceanapiidae, and a hypothesis on the phylogenetic relationships of the families is presented.

Within the Chalinidae, eight monophyletic species groups are distinguished on the basis of assumed apomorphous characters. Two of these groups belong to the nominal genera *Acervochalina* and *Dendroxea*, the other six to the genus *Haliclona*. A key to the species groups and a hypothesis on the phylogenetic relationships of the groups is presented. Subsequently, each individual species group is analyzed phylogenetically. The obtained species cladograms and the distributional types of the species within the North Atlantic Ocean are used for the construction of a general area cladogram, representing a hypothesis on the historical relationships of areas of endemism in the North Atlantic Ocean. The analysis is based on the component-compatibility and parsimony methods as developed by Zandee & Roos (1987). For generation of the general area cladogram the computer program CAFCA (Zandee, 1987) has been used. Three main vicariance events can be recognized from the general area cladogram, viz. the Cretaceous separation of South America and Africa, a subsequent separation of the Boreal area from the south-eastern part of the North Atlantic and the Mediterranean, and the Miocene (Messinian) salinity crisis in the Mediterranean basin. The individual species area cladograms are evaluated in order to establish which show "vicariance fit" with the general area cladogram, and which species have deviating distribution patterns needing the most parsimonious "ad hoc" explanations, like dispersal or extinction.

CONTENTS

INTRODUCTION

In previous papers dealing with the taxonomy of the Haplosclerida, the species of the north-eastern Atlantic shallow-water (0-200 m) area have been taxonomically revised and redescribed (de Weerdt, 1985, 1986, in press a; de Weerdt & van Soest, 1986, 1987). In the present paper the phylogenetic relationships of the Haplosclerida are analyzed according to the principles of phylogenetic systematics, or cladistics, with emphasis on the Chalinidae. The cladistic analysis includes all the well-known chalinid species of the entire North Atlantic down to the equator, amounting to 57 species; a few ill-known species have been left out of consideration. This study has been possible because the North Atlantic chalinid sponge fauna may now be sufficiently (although not comprehensively) known, as a result of regional taxonomic studies by different authors (Griessinger, 1971, Mediterranean; van Soest, 1980, West Indies; de Weerdt, 1985, 1986, North East Atlantic; de Weerdt & van Soest, 1986, south-eastern part of the North Atlantic; van Lent & de Weerdt, 1987, Banyuls, Mediterranean).

In sponge systematics it is still rather unusual to analyze species or higher taxa in a cladistic way, i.e. to search for synapomorphous (shared derived) characters for characterizing monophyletic groups. Van Soest (1980) was the first to present a cladogram as a hypothesis about the phylogenetic relationships of the haplosclerid families, and he has recently evaluated possible phylogenetic classifications of the Demospongiae as a whole (van Soest, 1987). Zea (unpublished) has demonstrated how computerized cladograms can be obtained, using outgroup analysis and parsimony in a phylogenetic analysis of the genus *Siphonodictyon* (= *Aka*) (Haplosclerida).

The present paper starts with the demonstration of the monophyly of the Haplosclerida, after which the phylogenetic relationships of the five families is analyzed. Finally, a phylogenetic and historical biogeographic analysis of the North Atlantic Chalinidae is presented. The obtained taxon cladograms of the chalinid species groups and the distributional types of the species within the North Atlantic are used to construct a general area cladogram, representing the assumed historical relationships of areas of endemism within the North Atlantic.

A previous attempt to achieve these goals was part of my PhD thesis which has a limited distribution (de Weerdt, 1987); since then, significant methodological progress has been made (notably by Zandee & Roos, 1987), and the present analysis is the first serious application of the new methods, moreover it is the first historical biogeographic study involving marine areas of endemism.

MATERIAL AND METHODS

The phylogenetic analysis of the Chalinidae is based on the following material: species occurring in the north-eastern part of the North Atlantic Ocean have been taxonomically revised and redescribed by the present author (de Weerdt, 1986). All the type and other authentic material has been studied, supplied with freshly collected sponges from several localities; this material is deposited in the collection of the Zoölogisch Museum, Amsterdam (ZMA).

Species occurring in the Mediterranean have been revised by Griessinger (1971); part of his type material, which is present in the Muséum National d'Histoire Naturelle, Paris (MNHN) has been studied. Schizotypes, kindly donated by N. Boury-Esnault (MNHN) are deposited in the ZMA collection.

Van Lent & de Weerdt (1987) recorded several chalinids from Banyuls, Mediterranean, including one new species. The material is deposited in the ZMA collection.

Species occurring in the south-eastern and south-central parts of the North Atlantic have been redescribed by de Weerdt & van Soest (1986). The material was collected by the CANCAP-expeditions organized by the Rijksmuseum van Natuurlijke Historie (RMNH), Leiden. It is incorporated in the collections of RMNH.

Chalinids occurring in the Caribbean have been redescribed by van Soest (1980). In addition the present author has recently collected several specimens from Curaçao and Bonaire, which are incorporated in the collections of ZMA. One undescribed species, collected by S. Zea in the Colombian Caribbean, has been included in the phylogenetic analyses. It will be referred to as *Haliclona* n.sp.

The phylogenetic analyses are based on the principles of phylogenetic systematics, as they are formulated by, e.g., Hennig (1966), Wiley (1981) and Eldredge & Cracraft (1980). Cladograms have been constructed following the two-step procedure of outgroup comparison (in order to polarize characters into apomorphous (derived) and plesiomorphous (primitive)), and parsimony (finding a cladogram with a minimal number of evolutionary steps) (cf. Watrous & Wheeler, 1981; Maddison et al., 1984; Wiley, 1987a). The characters used for the analyses are confined to morphological characters of the mature sponges, e.g. the habit, presence of fistular outgrowths, consistency, colour, ectosomal and choanosomal skeletal architecture, size and shape of the spicules, amount of spongin, etc. Many of these characters are not confined to haplosclerids, but occur outside the group as well. Parallelism may quite well be a common feature in sponges, at least when such simple characters as consistency and colour are concerned. Reversals and homoplasious developments of all character states have therefore been accepted, except for the microscleres. Microscleres are assumed to be characters which are lost easier than gained (cf. Ross, 1974; Farris, 1977; Felsenstein, 1985; Pimentel & Riggins, 1987). All the haplosclerid microscleres (sigmata, toxa, rhaphides, microxea) occur also outside the group, and absence is therefore consistently treated as the derived state.

Analysis of character evolution within the Chalinidae was done using the computer program TreeTools (Ellis, 1986). This program has been used because it permits all possible transformation series of multistate characters, including closed loops, i.e., no a priori assumptions about the relations between the various character states are needed (cf. Ellis, 1986, and also Mickevich, 1982). Because of the simplicity of most of the characters used in the present analyses it seemed most objective to apply the "closed loops option". TreeTools utilizes Wagner parsimony only (reversals of all character states are allowed), which seemed to be no problem with the above mentioned assumptions concerning the microscleres.

For the generation of a general area cladogram, representing the assumed historical relationships of the endemic areas within the North Atlantic, the computer program CAFCA (Zandee, 1987) has been used. This program has been developed by Zandee & Roos (1987) and is based on component-compatibility and parsimony methods. In the vicariance biogeography section of the present paper the procedure leading to a general area cladogram following these methods will be expalined into detail. For more information and criticisms one is referred to, e.g., Zandee & Roos (1987), Wiley (1987a) and a recent issue of Systematic Zoology (e.g., Page, 1988).

PHYLOGENY

MONOPHYLY AND CHARACTER POLARITY OF THE HAPLOSCLERIDA

At present there is still little consensus about the family classification of the Haplosclerida. Van Soest (1980) proposed five families in the order, viz. the Haliclonidae (= Chalinidae, cf. de Weerdt, 1986), Callyspongiidae, Niphatidae, Oceanapiidae and Petrosiidae, the latter three of which were established by him in that article. His tentative hypothesis on the phylogenetic relationships of the families was based on skeletal and morphological characters. Bergquist (1980, 1985) and Bergquist & Warne (1980) placed the Oceanapiidae and Petrosiidae separate from the other families on the basis of solid spicule skeletons, oviparous reproduction and biochemical properties. Bergquist (1980) established the order Nepheliospongida for these families and the fossil family Nephelio-

spongiidae. In my paper dealing with the Oceanapiidae and Petrosiidae of the north-eastern Atlantic (de Weerdt, 1985), I followed van Soest's (l.c.) classification and kept the two families within the Haplosclerida. Hartman (1982) and van Soest (1987) use the name Petrosiida Boury-Esnault & van Beveren (1982) in favour of Nepheliospongida but, like Bergquist, they keep the Oceanapiidae and Petrosiidae in a separate (although closely related) order. Whether the Oceanapiidae and Petrosiidae belong to the Haplosclerida or not, they are generally accepted as sister-groups. Through five apomorphous characters (see below) they form a monophyletic group. The taxonomic rank to which each monophyletic subset should be raised (or lowered) is a classification problem, rather than a phylogenetic problem.

For the assessment of the monophyly and character polarity within the Haplosclerida s.l., six closely related outgroups have been used. These outgroups are derived from the phylogenetic analysis of the Demospongiae by van Soest (1987). They are the Esperiopsidae (the sister-group of the Haplosclerida s.l.) (cf. van Soest, in press), the Desmacellidae and Mycalidae, which are sister-groups, the Myxillidae and Microcionidae (cf. van Soest, in press), which are also sister-groups, and the Axinellida s.l. Together with the Haplosclerida they form a monophyletic subset, with the presence of rhaphides and a plumoreticulate skeletal architecture as synapomorphous characters. In fig. 1 the phylogenetic relationships of these groups, as hypothesized by van Soest (1987) is given, slightly simplified with his permission. The synapomorphous character uniting the Haplosclerida with the Esperiopsidae is the presence of small (100-250 μm) diactines. For the other characters of the outgroups one is referred to van Soest (1987).

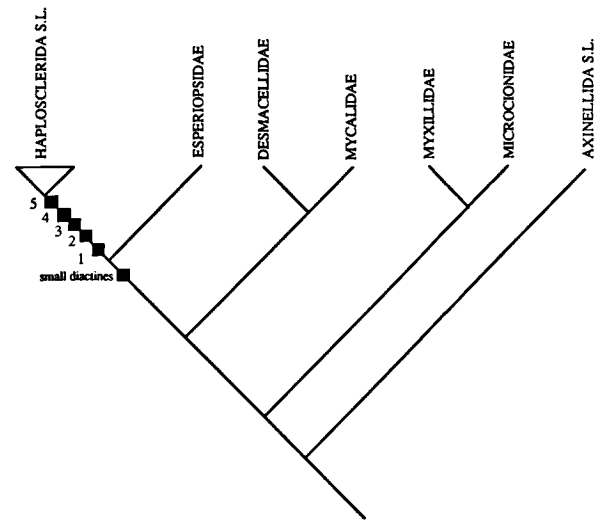


Fig. 1. Cladogram representing the hypothesized phylogenetic relationships of the Haplosclerida s.l. and six related outgroups (partly after van Soest, 1987). For explanation of characters see text.

APOMORPHOUS CHARACTERS OF THE HAPLOSCLERIDA *S.L.*

1. A regular, unispicular, tangential ectosomal skeleton. In the outgroups and the remaining Demospongiae the ectosomal skeleton is confused, or non-tangential.

2. Toxa sharply bent in the middle and with sharply recurved apices. The presence of toxa is considered primitive for the Haplosclerida, because of the widespread occurrence in many other sponge groups. The form, although not present in all species, is typical.

3. Sigmata centrangulated. Like the toxa, sigmata are very common outside the Haplosclerida, and therefore considered primitive. The centrangulated form is typical.

4. Absence of chelae. It is assumed that chelae, like all other sponge microscleres, are much easier lost than gained. According to van Soest (1987, fig. 2) chelae developed in the ancestor of the monophyletic group consisting of the Haplosclerida, Esperiopsidae, Desmacellidae + Mycalidae and Myxillidae + Microcionidae. The loss of chelae in the Haplosclerida, as well as in the Desmacellidae, may therefore be considered as a homoplasious evolutionary step in these lines.

5. Megascleres only diactines (loss of monactines). In the sister-group of the Haplosclerida, the Esperiopsidae, and in most of the other out-

groups both monactines and diactines occur simultaneously. The Mycalidae and Microcionidae have only monactines. The exclusive occurrence of diactines in the Haplosclerida is considered as an evolutionary step involving the loss of monactines.

PHYLOGENY OF THE HAPLOSCLERID FAMILIES

In fig. 2 the phylogenetic relationships of the families is inferred, based on the following synapomorphous characters:

1. Ectosomal skeleton organized. It is confused in the outgroups, and also (although slightly less so) in some oceanapiids and petrosiids. It is always organized in the Chalinidae, Callyspongiidae and Niphatidae.

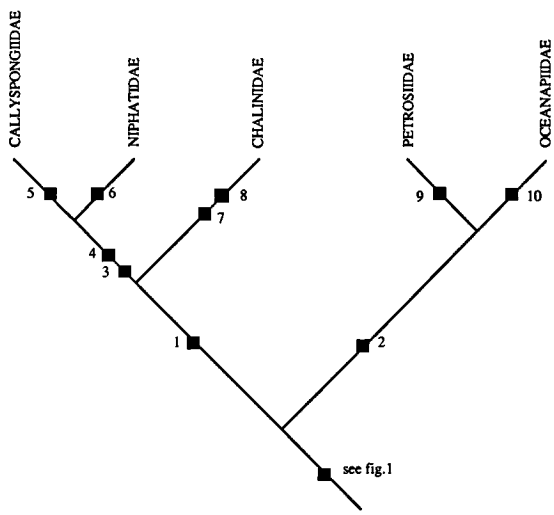


Fig. 2. Cladogram representing the hypothesized phylogenetic relationships of the haplosclerid families. For explanation of characters see text.

2. Choanosomal skeleton isotropic. In the outgroups and in the Chalinidae, Callyspongiidae and Niphatidae the choanosomal skeleton is always more or less organized into a reticulation of primary and secondary fibres. It is isotropic in the Oceanapiidae and Petrosiidae.

3. Ectosomal skeleton multispicular. In the Niphatidae and Callyspongiidae there is a trend towards a multispicular ectosomal skeleton.

4. Peripheral condensation of the choanosomal skeleton. This is a synapomorphy uniting the Callyspongiidae and Niphatidae.

In addition, the following autapomorphous characters can be recognized:

5. Ectosomal skeleton double-meshed. Autapomorphy of the Callyspongiidae.

6. Choanosomal skeleton consisting of thick, multispicular primary lines. Autapomorphy of the Niphatidae.

7. Unispicular secondary lines. Autapomorphy of the Chalinidae.

8. Paucispicular primary lines. Autapomorphy of the Chalinidae.

9. Choanosomal skeleton consisting of a regular system of pauci- to multispicular tracts which form a circular pattern, superimposed on an isotropic reticulation of single spicules. Autapomorphy of the Petrosiidae.

10. An irregular system of reinforcing spicule tracts in the choanosome. Autapomorphy of the Oceanapiidae

The cladogram of the haplosclerid families differs from the one given by van Soest (1980) in that the Oceanapiidae and Petrosiidae are now assumed to be sister-groups, based on the synapomorphy of character 2 (isotropic skeleton). It confirms the current opinion that the Oceanapiidae and Petrosiidae are more closely related to each other than each of them is to the other families.

KEY TO THE FAMILIES OF THE HAPLOSCLERIDA

1 a. Ectosomal skeleton, if present, organized 2
b. Ectosomal skeleton rather dense and confused . 4
2 a. Ectosomal skeleton double-meshed .... Callyspongiidae
b. Ectosomal skeleton single-meshed or absent..... 3
3 a. Choanosomal skeleton a coarse reticulation of thick, multispicular primary lines, connected by secondary lines of variable thickness . Niphatidae
b. Choanosomal skeleton a delicate reticulation of uni-, pauci- or rarely multispicular primary lines ..... Chalinidae

4 a. Choanosomal skeleton a unispicular, isotropic or subisotropic reticulation added to which there is an irregular system of spicule tracts ... Oceanapiidae
b. Choanosomal skeleton a regular, subisotropic reticulation of spicule tracts ..... Petrosiidae

PHYLOGENY OF THE CHALINID SPECIES GROUPS

In the study area, I have distinguished eight monophyletic species groups within the Chalinidae, on basis of assumed phylogenetic characters. Six of these groups belong to the nominal genus *Haliclona* Grant, the other groups are the genera *Acervochalina* Ridley and *Dendroxea* Griessinger. Especially the genus *Haliclona* offers problems in the large number of described genera which are considered synonymous with it. Although it is fully admitted that study of the type-species of each described genus is necessary, I would still like to mention the genera which are thought to be synonymous with *Haliclona*. These are: *Adocia* Gray, *Amorphina* Schmidt, *Asychis* Gray, *Chalina* Grant, *Diplodemia* Bowerbank, *Euchalinopsis* Lendenfeld, *Gellius* Gray, *Halichoclona* de Laubenfels, *Kallypilidion* de Laubenfels, *Katiba* de Laubenfels, *Lessepsia* Keller, *Nara* de Laubenfels, *Neoadocia* de Laubenfels, *Orina* Gray, *Pellinella* Thiele, *Pellinula* Czerniavsky, *Philotia* Gray, *Prianos* Gray, *Reniera* Schmidt, *Reniclona* de Laubenfels, *Rhaphisia* Topsent, *Rhizoniera* Griessinger, *Sigmadocia* de Laubenfels, *Toxadocia* de Laubenfels, *Toxiclona* de Laubenfels, and *Veluspa* Miklucho-Maclay. For an enumeration of the type-species and authors I may refer to de Weerdt (1987). Part of these genera have already been treated in my earlier taxonomic studies (e.g., de Weerdt, 1986), but quite a few have been described on basis of material from outside the Atlantic, and need further examination.

The six assumed monophyletic species groups within *Haliclona*, established on basis of North Atlantic material, have received a tentative name of a characteristic species, viz. the *oculata* group, *aquaeducta* group, *fistulosa* group (species currently known under the invalid genus name *Pellina*, which is a synonym of *Halichondria*, cf. de Weerdt, 1986), *angulata* group, *arenata* group, and *rosea* group.

Until the validity of these groups has been tested by other characters and by material from elsewhere, no nomenclatorial implications have been made and all the groups are treated as having the same taxonomic rank. Species included in the analyses are listed below. The order is according to their distribution patterns. Species which have not been included because they are insufficiently known are also enumerated and tentatively assigned to a species group. For purely taxonomic studies of the species included in the analyses I may refer to de Weerdt, 1986, in press a; de Weerdt & van Soest, 1986; van Lent & de Weerdt, 1987).

oculata group:

Haliclona oculata (Pallas, continuous amphi-Atlantic), *H. urceolus* (Rathke & Vahl, Arctic-eastern Boreal), *H. simulans* (Johnston, Mediterranean-Atlantic), *H. laevis* (Griessinger, Mediterranean), *H. reptans* (Griessinger, Mediterranean), *H. cribrata* (Pulitzer-Finali, Mediterranean), *H. varia* Sarà (Mediterranean), *H. venata* Sarà (Mediterranean), and *H.* n.sp. (Caribbean).

acervochalina group:

Acervochalina loosanoffi (Hartman, North West Atlantic, Netherlands, one record from South Ireland), *A. limbata* (Montagu, Mediterranean-Atlantic), *A. fertilis* (Keller, Mediterranean-Atlantic), *A. parasimulans* (Lévi, Canary Islands, West Africa), *A. nigra* (Boury-Esnault & Lopes, Azores), and *A. molitba* (de Laubenfels, Caribbean).
Not included is *A. crassiloba* sensu de Laubenfels (as *Haliclona*, Caribbean).

aquaeducta group:

Haliclona primitiva (Lundbeck, Arctic), *H. cinerea* (Grant, Mediterranean-Atlantic), *H. aquaeducta* (Schmidt, Mediterranean-Atlantic), *H. citrina* (Topsent, Mediterranean-Atlantic), *H. cratera* (Schmidt, Mediterranean-Atlantic), *H. mediter-*

ranea Griessinger (Mediterranean-Atlantic), *H. neens* (Topsent, Azores, West Africa), *H. abbreviata* (Topsent, West Africa), *H. subtilis* Griessinger (Mediterranean), *H. griessingeri* van Lent & de Weerdt (Mediterranean), and *H. hogarthi* Hechtel (Caribbean).
Not included are *H. coerulescens* (Topsent, West Africa) and *H. flavescens* (Topsent, Mediterranean).

fistulosa group:

Haliclona fistulosa (Bowerbank, Mediterranean-Atlantic), *H. fulva* (Topsent, Mediterranean-Atlantic), *H. perlucida* (Griessinger, Mediterranean-Atlantic), *H. magna* (Vacelet, Mediterranean), *H. semitubulosa* sensu Topsent (Mediterranean), and *H. implexiformis* (Hechtel, Caribbean).
Not included is *H. albifragilis* (Hechtel, Caribbean).

angulata group:

Haliclona angulata (Bowerbank, Mediterranean-Atlantic), *H. fibulata* (Schmidt, Mediterranean-Atlantic), *H. rava* (Stephens, Mediterranean-Atlantic). *H. lacazei* (Topsent, Mediterranean-Atlantic), *H. binaria* (Topsent, Azores, Canary Islands), *H. laxa* (Topsent, Mediterranean), and *H. piscaderaensis* (van Soest, Caribbean).
Not included are: *H. laurentina* (Lambe, ?Arctic), *H. uncinata* (Topsent, Mediterranean), *H. microsigma* (Babic, Mediterranean), *H. tenuisigma* (Babic, Mediterranean), *H. dubius* (Babic, Mediterranean), *H. aperta* (Sarà, Mediterranean), *H. calcinea* Burton (Caribbean), and *H. tenerrima* Burton (Caribbean).

arenata group:

Haliclona xena de Weerdt (Netherlands), *H. valliculata* (Griessinger, Mediterranean-Atlantic), *H. implexa* (Schmidt, Mediterranean-Atlantic), *H. mucosa* (Griessinger, Mediterranean), *H. arenata* (Griessinger, Mediterranean), *H. mamillata* (Griessinger, Mediterranean), *H. tubifera* (George & Wilson, Caribbean), *H. curacaoensis* (van Soest, Caribbean), and *H. caerulea* (Hechtel, Caribbean).

rosea group:

Haliclona rosea (Bowerbank, Arctic-eastern Boreal), *H. indistincta* (Bowerbank, eastern Boreal), *H. viscosa* (Topsent, Mediterranean-Atlantic), *H. grossa* (Schmidt, Mediterranean), *H. sarai* (Pulitzer-Finali, Mediterranean), *H. rhizophora* (Vacelet, Mediterranean), and *H. canaliculata* Hartman (North West Atlantic).

dendroxea group:

Dendroxea lenis (Topsent, Mediterranean-Atlantic) and *D. carmabi* (van Soest, Caribbean).

In fig. 3 the cladogram representing the hypothesized phylogenetic relationships of the chalinid species groups is presented, based on the following characters:

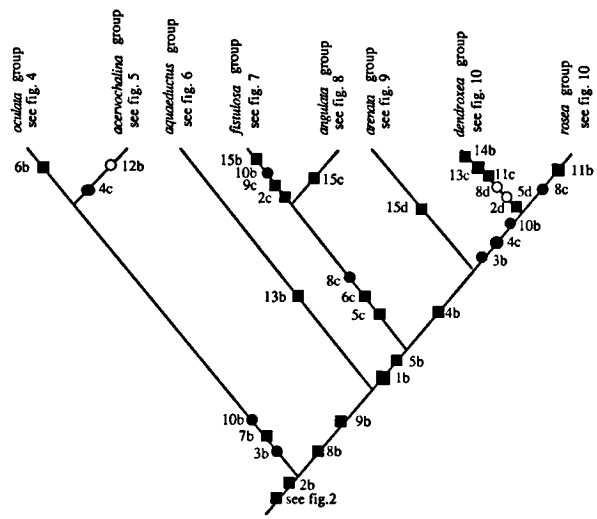


Fig. 3. Cladogram representing the hypothesized phylogenetic relationships of the chalinid species groups. For explanation of characters see text. ■ = character without homoplasious development, ● = character with one or more homoplasious developments, ○ = reversal.

1. Architecture of the secondary lines. The plesiomorphous state 1a is secondary lines (more or less) at right angles to the primary lines. The derived state 1b is "confused" secondary lines, i.e. the majority of the secondary spicules has an oblique position with respect to the primary lines (cf. de Weerdt,

1985, fig. 2, and de Weerdt, 1986, figs. 1, 3, 5). State 1a is found in the Callyspongiidae, Niphatidae, and in the *oculata* and *aquaeducta* groups. State 1b is a synapomorphy of the *fistulosa*, *angulata*, *arenata*, *rosea* and *dendroxea* groups.

2. Habit. It is difficult to assess which type of growth form is the primitive one, because the Chalinidae and also the outgroups are rather polymorphous. Some trends can however be observed. The form occurring most commonly in the Niphatidae and Callyspongiidae, and also in the Petrosiidae is tubular-lobate-ramose. This habit, which is quite rare within the Chalinidae, is therefore assumed to be plesiomorphous and has been assigned to the hypothetical outgroup as state 2a. One form is quite typical for chalinids, viz. massively encrusting with oscular mounds or "chimneys" (state 2b). Except for the *fistulosa* and *dendroxea* groups, this form is encountered in all the species groups, albeit most frequently in the *acervochalina* and *aquaeducta* groups. A massive form (2c) is very common in the *fistulosa* group. Finally, thinly encrusting (state 2d) is the form invariably occurring in the two species of the *dendroxea* group. The assumed transformation series of the character states is d - a - b - c, b - d. Probably because of the polymorphism in many groups, state 2b has been generated at the root of the cladogram. State 2c is an autapomorphy of the *fistulosa* group, state 2d an autapomorphy of the *dendroxea* group.

3. Form and size of the oscules. Small (1 mm or less) oscules, which are flush with the surface, is a typical feature of species of the *dendroxea*, *oculata* and (although slightly less so) *acervochalina* groups (state 3b). The assumed plesiomorphous state 3a is elevated oscules (situated at the top of the "chimneys"). State 3b has been generated as a synapomorphy of the *oculata* and *acervochalina* groups, with a homoplasious development in the ancestor of the *rosea* and *dendroxea* groups.

4. Ectosomal skeleton. A unispicular ectosomal skeleton is a synapomorphy of the Haplosclerida, and therefore plesiomorphous for the Chalinidae (state 4a). The following trends within the Chalinidae are considered apomorphous: state 4b is a trend towards a diminishing in the cohesion between the spicules which form the ectosomal skeleton (see de Weerdt, 1985, fig. 1e). There are many open spaces between the spicules, in which there is a high concentration of pores in the ectosomal membrane (see also Griessinger, 1971, for a detailed description of this type of ectosomal skeleton). This step is hypothesized to have taken place in the ancestor of the monophyletic subset *arenata* and *rosea* + *dendroxea* groups. The next trend (state 4c) is a complete loss of the tangential spicules in the ectosomal membrance, which occurred in the ancestor of the *rosea* and *dendroxea* groups. There is a homoplasious loss of the ectosomal skeleton in the *acervochalina* group. The assumed transformation series of these character states is a - b - c, a - c.

5. Spicula length. This is a variable character, but certain trends can be observed. A length between 80 and 120 μm is assumed to be plesiomorphous (state 5a), because it is the most common size in all the outgroups. Within the Chalinidae there is a trend towards longer spicula (state 5b: 120-170 μm, and state 5c: > 170 μm). The assumed transformation series of these character states is a - b - c. State 5b has been generated as a step on the stem down from the *fistulosa* and *angulata* groups. State 5c is a synapomorphy of the *fistulosa* and *angulata* groups. In the *dendroxea* group there is a reversal of small spicula (in the cladogram re-coded as the new state 5d).

6. Spicula form. The form occurring most commonly in the outgroups and also within the Chalinidae is slender and fusiform, which is therefore considered the plesiomorphous state (state 6a). In all the species of the *oculata* group the oxea are typically short and rather fat ("cigar"-shaped), which is an autapomorphy of this group (state 6b). In the *fistulosa* and *angulata* groups they are robust "needles" (state 6c), which is an synapomorphy of these groups. The assumed transformation series of these character states is a - b, a - c.

7. "Parallel spicules". When several spicula make a line or reinforcing tract, they are lying

abreast, not alternately overlapping (see de Weerdt, 1986, fig. 3 and Griessinger, 1971, fig. 13a). The latter state is considered plesiomorphous (state 7a). "Parallel spicules" (state 7b) is a synapomorphy of the *oculata* and *acervochalina* groups.

8. Amount of spongin. The Niphatidae and Callyspongiidae have abundant spongin, the Oceanapiidae and Petrosiidae much less. It is assumed that there has been a trend in the ancestor of the Chalinidae and the Callyspongiidae + Niphatidae towards abundant spongin, which state is therefore plesiomorphous within the Chalinidae (state 8a). The next trend within the Chalinidae is towards a diminishing in the amount of spongin (spongin "intermediate", state 8b). The following trend is towards very scarce spongin (state 8c). The assumed transformation series of these character states is a - b - c. State 8b has been generated as a step on the stem down from the *aquaeducta* group. State 8c is a synapomorphy of the *fistulosa* and *angulata* groups, with a homoplasious development in the *rosea* group. In the *dendroxea* group there is a reversal towards abundant spongin (in the cladogram re-coded as the new state 8d).

9. Consistency. The consistency in the outgroups is as follows: the Niphatidae are generally though, the Callyspongiidae resilient, the Oceanapiidae firmly friable and the Petrosiidae firm to stony. The soft/resilient and firm/resilient consistency of most species of the *acervochalina* and *oculata* groups is therefore considered the plesiomorphous state (state 9a). The very soft to limp consistency (state 9b) of practically all species of the *aquaeducta*, *angulata*, *rosea* and *dendroxea* groups is considered a synapomorphy of these groups. In the *fistulosa* group there is a trend towards a firmly friable consistency (state 9c). The assumed transformation series of these character states is a - b, a - c.

10. Microscleres. Present (state 10a) is plesiomorphous (see above); absent is state 10b. The absence is a homoplasious synapomorphy of the *acervochalina* + *oculata* and the *rosea* + *dendroxea* sister-groups, and a homoplasious autapomorphy of the *fistulosa* group. In the other species groups there are species with microscleres.

In addition the following autapomorphous characters, which do not contribute to the cladogram topology, have been recognized:

11. Architecture of the primary lines. The plesiomorphous state 11a is "straight" primary lines, state 11b is "wavy" primary lines, state 1c dendritic primary lines. All possible transformations between the character states are assumed. State 11a is found in the outgroups, but especially in the Callyspongiidae and Niphatidae. Within the Chalinidae straight primary lines occur in the *oculata*, *aquaeducta*, *fistulosa*, *angulata* and (although slightly less so) in the *arenata* group. Wavy primary lines is an autapomorphy of the *rosea* group, dendritic primary lines an autapomorphy of the *dendroxea* group.

12. Number of spicula in the secondary lines. All the chalinid species groups, except for the *acervochalina* group, have unispicular secondary lines (see also fig. 2, character 7). In the *acervochalina* group the secondary lines are always more than one spiculum long, which is the state most commonly present in the other haplosclerid families, and therefore considered plesiomorphous (state 12a). This state has been generated as a reversal in the *acervochalina* group (in the cladogram re-coded as the new state 12b).

13. Number of spicula in the primary lines. Paucispicular primary lines have earlier been established as an autapomorphy of the Chalinidae (see character 8 of fig. 12). At this taxonomic level the same character turns to plesiomorphous (state 13a). Within the Chalinidae there is a trend towards unispicular primary lines, which is exclusively found in the *aquaeducta* group (state 13b). In the *dendroxea* group there is a "new" trend towards multispicular primary lines (state 13c). The assumed transformation series of these character states is a - b, a - c.

14. Multispicular basal layer (state 14b). Autapomorphy of the *dendroxea* group. In the

other species groups no such basal layer is present.

15. Architecture of the choanosomal skeleton. The following states are considered apomorphous: state 15b is a rather dense, subisotropic reticulation, with high spicula amount, but usually with many subdermal and choanosomal spaces, which is an autapomorphy of the *fistulosa* group (see de Weerdt, 1986, fig. 9). State 15c is a subhalichondroid reticulation, which is an autapomorphy of the *angulata* group (see de Weerdt, 1986, fig. 17). State 15d is a reticulation in which the primary lines are somewhat irregular and ill-defined, irregularly connected by the secondaries, which is an autapomorphy of the *arenata* group (see de Weerdt, 1986, fig. 11).

Within the chalinid species groups there are five homoplasious developments and three reversals. The homoplasies are found in the following character states:

1. Character state 3b (oscules flush). Homoplasious development in the ancestor of the *acervochalina* and *oculata* groups and in the ancestor of the *rosea* and *dendroxea* groups.

2. Characters state 4c (no ectosomal skeleton). Homoplasious development in the ancestor of the *rosea* and *dendroxea* groups and in the *acervochalina* group.

3. Character state 8c (scarce spongin). Homoplasious development in the ancestor of the *fistulosa* and *angulata* groups and in the *rosea* group.

4 + 5. Character state 10b (no microscleres). Homoplasious development in the ancestor of the *acervochalina* and *oculata* groups, in the *fistulosa* group and in the ancestor of the *rosea* and *dendroxea* groups.

The reversals are:

1. Character state 5d (spicula length of 80-120 μm). Reversal in the *dendroxea* group.

2. Character state 8d (abundant spongin). Reversal in the *dendroxea* group.

3. Character state 12b (secondary lines more than one spiculum long). Reversal in the *acervochalina* group.

The phylogenetic analyses of the Chalinidae have resulted in the hypothesis that the family is monophyletic by three apomorphous characters (paucispicular primary lines, unispicular secondary lines and a habit consisting of a massively encrusting base with oscular mounds or "chimneys"), and that the *oculata* and *acervochalina* groups, the *fistulosa* and *angulata* groups, and the *rosea* and *dendroxea* groups are sister-groups.

Each group is hypothesized to be monophyletic by one or more apomorphous characters, although most of these are not unique trends. Summarizing, the following characters are considered "uniquely" derived: the cigar-shaped oxea of the *oculata* group (character state 6b), a very delicate unispicular skeleton with primary lines which are consistently unispicular (character state 13b) in the *aquaeducta* group, the subisotropic skeleton (character state 15b) in the *fistulosa* group, the subhalichondroid skeleton (character state 15c) in the *angulata* group, the irregular skeleton with ill-defined primary and secondary lines in the *arenata* group (character state 15d), the multispicular basal layer (character state 14b) and dendritic primary lines (character state 11c) in the *dendroxea* group, and the wavy primary lines (character state 11b) in the *rosea* group. The *acervochalina* group is quite characteristic, but unfortunately its most characteristic feature (secondary lines more than one spiculum long, character state 12b) has to be considered as a reversal.

The here presented hypothesis on the phylogenetic relationships within the Chalinidae and the proposed species groups which are the result of the analyses, are in strong contrast with the current use of chalinid genus names. To mention one of the many problems which will be encountered when the groups will have to receive a proper name: *Reniera* Schmidt is, unfortunately, described on basis of material which has been mis-used by the author, and it is well-known that the original specimen of the type-species, *Reniera aquaeductus* Schmidt, has probably to be considered "lost" (although there are specimens in musea labeled "*Reniera aquaeductus* Type" in Schmidt's handwriting).

There is, however, general agreement about the identity of the Mediterranean-Atlantic *H. aquaeducta* (pro *aquaeductus*), and the species is fortunately quite characteristic. The genus *Reniera* is one of the most problematic genera and the tendency to keep it as a valid genus has led to many different definitions by authors (e.g., Griessinger, 1971). It may turn out to be a valid genus (or subgenus) name, but again a re-definition should be needed, based on the assumed phylogenetic character "skeleton always unispicular". However, when one of the other described genera within the Chalinidae (see above) turns out to be based on a species exhibiting the same skeletal architecture, the priority rules have to be applied. Van Soest's (1980) definition of *Reniera* fits with the *arenata* group, as well as does *Sigmadocia* sensu van Soest (l.c.). This has already been suggested by him (l.c.) and this confirmed by my studies of "*Sigmadocia*" species.

Many similar problems will be encountered when the species groups will have to receive a proper nomenclatorial treatment in the future. It is very obvious that this stage has not been reached yet, and that testing of the here presented hypotheses is urgently needed by study of other characters and material from outside the North Atlantic.

KEY TO THE SPECIES GROUPS OF THE CHALINIDAE

1 a. A multispicular layer is present at the basis of the sponge. The choanosomal skeleton consists of dendritic multispicular primary lines, which become paucispicular towards the surface ..... *dendroxea* group

b. No multispicular layer at the basis. The choanosomal skeleton is a reticulation of primary and secondary lines or (sub)istotropic 2

2 a. The secondary interconnecting lines are more than one spiculum long. No ectosomal skeleton. Spongin abundant. No microscleres. Sponges generally hispid ..... *acervochalina* group

b. Connections between primary lines always one spiculum long, sponges not strongly hispid 2

3 a. Choanosomal skeleton a reticulation of primary and secondary lines, or more confused (subhalichondroid) 4

b. Choanosomal skeleton mainly or completely isotropic 9

4 a. Choanosomal skeleton subhalichondroid, i.e. dense and rather confused. An ectosomal skeleton may be present. Spongin very scarce or absent. Oxea are robust needles, generally over 250-300 µm long. Microscleres (toxa, sigmata, rhaphides) commonly present. Sponges friable ..... *angulata* group

b. Choanosomal skeleton a more or less, regular reticulation of primary and secondary lines, spicula less robust 5

5 a. Choanosomal skeleton very regular, consisting of straight uni-paucispicular primary lines, which are very regularly connected by the secondary spicules. An ectosomal skeleton may be present 6

b. Choanosomal skeleton less regular, but not subhalichondroid. Primary lines pauci- or multispicular. Secondary spicula rather confused, often in an oblique position 8

6 a. Spongin abundant, especially towards the stalk, if this is present. Oxea proportionally short (80-120 µm), fat, cigar-shaped. Sponges resilient or firm, but not friable. Oscula numerous, small, regularly distributed (except in tubular forms) ..... *oculata* group

b. Spongin not very abundant, may be even absent. Sponges soft or firm, but than very friable; spicula 120 µm or longer; oscules not so small and numerous 7

7 a. Sponges soft. Spongin clearly present, but confined to the nodes of the spicula. Spicula fusiform, brevipointed or strongylote. The form is cushion-shaped with oscular mounds or chimneys, rarely delicately ramose ..... *aquaeducta* group

b. Sponges firm, friable. Spongin very scarce or absent. Oxea are robust needles, over 170-200 µm long. Sponges massive, often with fistular outgrowths ..... *fistulosa* group

8 a. No ectosomal skeleton. Primary lines pauci- or multispicular, wavy. Secondary spicula rather confused, often in an oblique position. Spongin scarce, confined to the nodes of the spicula. No microscleres. Habit thickly encrusting or massive ..... *rosea* group

b. An ectosomal skeleton is always present. It consists of an irregular, but coherent reticulation of spicula, with many open spaces. In these spaces there is a high concentration of pores. Oxea fusiform. Microscleres may be present. The habit is thickly encrusting, cushion-shaped with oscular mounds or coalescent tubes ..... *arenata* group

9 a. Sponges soft. Spongin clearly present, but confined to the nodes of the spicula. Spicula fusiform, brevipointed or strongylote. The form is cushion-shaped with oscular mounds or tubes, rarely delicately ramose ..... *aquaeducta* group

b. Sponges firm, friable. Spongin very scarce or

absent. Oxea are robust needles, over 170-200 µm long. Sponges massive, often with fistular outgrowths ..... *fistulosa* group

PHYLOGENY OF THE *OCULATA* GROUP

In fig. 4 the cladogram representing the hypothesized phylogenetic relationships of the species of the *oculata* group is presented, based on the following characters:

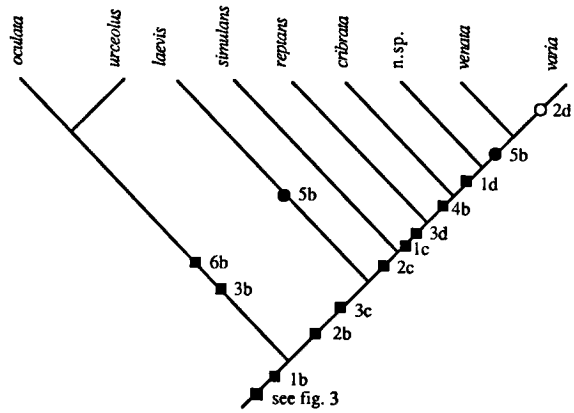


Fig. 4. Cladogram representing the hypothesized phylogenetic relationships in the *oculata* group. For explanation of characters see text. ■ = character without homoplasious development, ● = character with a homoplasious development, ○ = reversal.

1. Colour. Within the *oculata* group the following colour variations are found: brown (state 1b), yellow (state 1c) and white (state 1d). The colour purple is not present in the *oculata* group, but because of the widespread occurrence of this colour in the other species groups and also in the other haplosclerids, purple is considered as the plesiomorphous state (1a) and has been assigned to the hypothetical outgroup. The assumed transformation series is a - b - c - d, a - d, b - c. State 1b (brown) has been generated at the root of the cladogram; it evolved to yellow (state 1c) in the ancestor on the stem down from *Haliclona reptans*, and in white (state 1d) in the ancestor on the stem down from *H.* n.sp. Within the group there are no homoplasies.

2. Consistency. The following states are recognized: resilient (plesiomorphous, state 2a), firm, compressible (state 2b) and firm, incompressible (state 2c). The assumed transformation series is a - b - c. State 2b evolved in the ancestor on the stem down from *H. laevis*, state 2c on the stem down from *H. simulans*. In *H. varia* there is a reversal to a firm but still compressible consistency (in the cladogram recoded as the new state 2d).

3. Habit. "Oscular mounds" is consistently treated as the plesiomorphous state (state 3a) and this state has been assigned to the hypothetical outgroup. Within the *oculata* group the following states are considered apomorphous: state 3b is the development of a stalk (synapomorphy of *H. oculata* and *H. urceolus*), state 3c is repent ramose, which form evolved in the ancestor on the stem down from *H. laevis*. State 3d is thinly encrusting which evolved in the ancestor on the stem down from *H. reptans*. The assumed transformation series is a - b, a - c - d, a - d. There are no homoplasies within the group.

4. Amount of spongin. Abundant spongin (state 4a) is plesiomorphous for the *oculata* group. There is a trend towards scarce spongin (state 4b) in the ancestor of *H. cribrata*, *H.* n.sp., *H. varia* and *H. venata*. There are no homoplasies within the group, but it is not a unique trend.

5. Subectosomal aquiferous canals strongly developed, and clearly visible (state 5b). It is a synapomorphy of *H. venata* and *H. varia*, with a homoplasious development in *H. laevis*.

6. Absence of an ectosomal skeleton (state 6b). Plesiomorphous is the presence of a unispicular, tangential ectosomal skeleton (state 6a). The absence is a synapomorphy of *H. oculata* and *H. urceolus*. There are no homoplasies.

Within the *oculata* group there is one homoplasious development and one reversal. Character state 5b (strongly developed subectosomal canal system) developed homoplasious in the ancestor of *H. venata* and *H. varia* and in *H. laevis*. The reversal is character state 2d (firm, compressible consistency) in *H. varia*.

PHYLOGENY OF THE *ACERVOCHALINA* GROUP

In fig. 5 the cladogram representing the hypothesized phylogenetic relationships of the species of the *acervochalina* group is presented, based on the following characters:

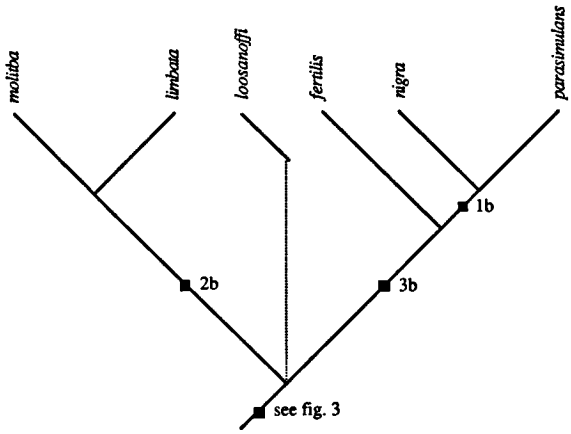


Fig. 5. Cladogram representing the hypothesized phylogenetic relationships in the *acervochalina* group. For explanation of characters see text.

1. Habit. Plesiomorphous is oscular mounds (state 1a). State 1b is a ramose habit, which is a synapomorphy of *Acervochalina nigra* and *A. parasimulans*.

2. Extreme variability in spicule width and the amount of spongin (state 2b). Synapomorphy of *A. limbata* and *A. molitba* (cf. also van Soest, 1980).

3. Spicula length. Plesiomorphous is a spicula length of 80-120 μm. There is a trend towards longer spicula (> 120 μm, state 3b) in *A. nigra*, *A. parasimulans* and *A. fertilis*.

The cladogram of the *acervochalina* group is not very robust, since each group is united by single character states. Furthermore the cladogram contains an unresolved trichotomy.

PHYLOGENY OF THE *AQUAEDUCTA* GROUP

In fig. 6 the cladogram representing the hypothesized phylogenetic relationships of the species of the *aquaeducta* group is presented, based on the following characters:

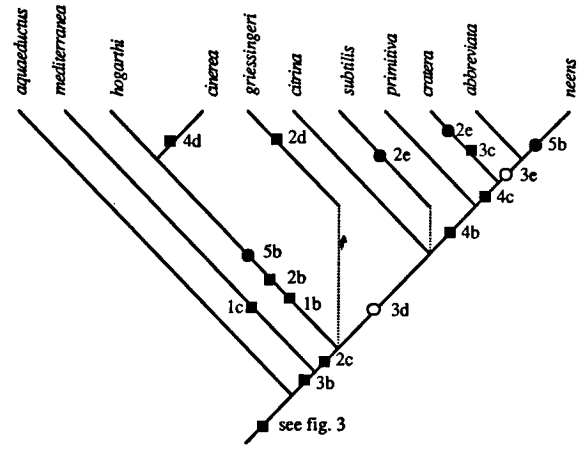


Fig. 6. Cladogram representing the hypothesized phylogenetic relationships in the *aquaeducta* group. For explanation of characters see text. ■ = character without homoplasious development, ● = character with a homoplasious development, ○ = reversal.

1. Habit. The plesiomorphous state (1a) is thickly encrusting with oscular mounds and tubes (see fig. 3). *Haliclona cinerea* and *H. hogarthi* are commonly repent ramose (state 1b), which form is considered a synapomorphy of the two species. State 1c is tubes, which is an autapomorphy of *H. mediterranea*. The assumed transformation series is a - b - c, a - c.

2. Colour. Purple is plesiomorphous (state 2a). *H. hogarthi* is usually purple, but it may also be brown (pers. obs.). *H. cinerea* is usually brown, but it may turn to purplish under certain circumstances. The trend towards a brown colour (state 2b) is considered a (weak) synapomorphy of *H. cinerea* and *H. hogarthi*. In addition, the following states are recognized: state 2c is yellow, state 2d grey and state 2e orange. The assumed transformation series include all possible transformations between the different character states. State 2c (yellow) has been generated on the stem down from *H. cinerea* and *H. hogarthi*. State 2d (grey) is an autapomorphy of *H. griessingeri*. State 2e (orange) developed homoplasious in *H. subtilis* and *H. cratera*.

3. Spicula length. It is not possible to assign

a state at the root, which means that the character state distribution within the *aquaeducta* group is based on parsimony only. A spicula length of 120-170 μm is coded 3a. The most parsimonious distribution is to place state 3b (80-120 μm) on the stem down from *H. mediterranea*. The trend towards larger spicula (120-170 μm) has been generated as a reversal on the stem down from *H. citrina* (in the cladogram re-coded as state 3d). The small spicula in *H. abbreviata* and *H. neens* has been generated as a reversal of state 3b (in the cladogram re-coded as state 3e). The very long spicula of *H. cratera* (over 300 μm, state 3c) is an autapomorphy. The assumed transformation series of the character states is a - b, a - c.

4. Spicula form. The following states are recognized: fusiform (plesiomorphous, state 4a), brevipointed (state 4b), strongylote (state 4c), and "cigar"-shaped (stated 4d). The assumed transformation series is a - b - c, a - d. State 4b evolved in the ancestor on the stem down from *H. primitiva*. Strongylote oxea (state 4c) is a synapomorphy of *H. cratera*, *H. abbreviata* and *H. neens*. In *H. cinerea* the oxea are typically "cigar"-shaped, a feature which is very common in the *oculata* group. Possibly it is an "underlying synapomorphy" (cf. Sæther, 1983). Within the *aquaeducta* group this character state (state 4d) is an autapomorphy of *H. cinerea*.

5. Slime strands (collagen fibres which are observable when pieces of the living sponge are torn apart). Presence is considered as the apomorphous state 5b. To my knowledge, slime strands are within the Chalinidae restricted to species of the *aquaeducta* group. They have been observed in *H. cinerea* (pers. observ.), *H. hogarthi* (pers. observ.), *H. neens* (cf. Topsent, 1918) and *H. coerulescens* (Topsent, 1918, not included in the phylogenetic analysis). State 5b has been generated as a synapomorphy of *H. cinerea* and *H. hogarthi*, with a homoplasious development in *H. neens*.

There are two homoplasious developments and two reversal in the *aquaeducta* group. The homoplasies are:

1. Character state 2e (orange colour). Homoplasious development in *H. subtilis* and in *H. cratera*.

2. Character state 5b (slime strands). Homoplasious development in the ancestor of *H. cinera* and *H. hogarthi* and in *H. neens*.

The reversals are character state 3d, reversal of spicula of 120-170 μm on the stem down from *H. citrina*, and state 3e, reversal of small spicula (80-120 μm) in the ancestor of *H. abbreviata* and *H. neens*.

There are two unresolved trichotomies in the cladogram of the *aquaeducta* group.

PHYLOGENY OF THE *FISTULOSA* GROUP

In fig. 7 the hypothesized phylogenetic relationships of the species of the *fistulosa* group are presented, based on the following characters:

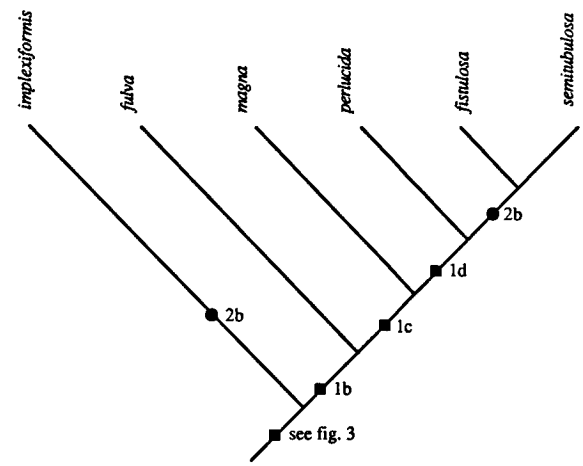


Fig. 7. Cladogram representing the hypothesized phylogenetic relationships in the *fistulosa* group. For explanation of characters see text. ■ = character without homoplasious development, ● = character with a homoplasious development.

1. Colour. Purple is plesiomorphous (state 1a). State 1b is orange-red, state 1c light-orange, state 1d whitish. The assumed transformation series of the character states is a - b - c - d. State 1b has been generated on the stem down from *Haliclona fulva*. State 1c evolved in

the ancestor on the stem down from *H. magna*. State 1d evolved on the stem from *H. perlucida*.

2. Fistular outgrowths (state 2b). Fistules have evolved in a homoplasious fashion, viz. in the ancestor of *H. fistulosa* and *H. semitubulosa*, and in *H. implexiformis*.

There is one homoplasy, viz. in character state 2b (fistular outgrowths).

PHYLOGENY OF THE *ANGULATA* GROUP

In fig. 8 the cladogram representing the hypothesized phylogenetic relationships of the species of the *angulata* group is presented, based on the following characters:

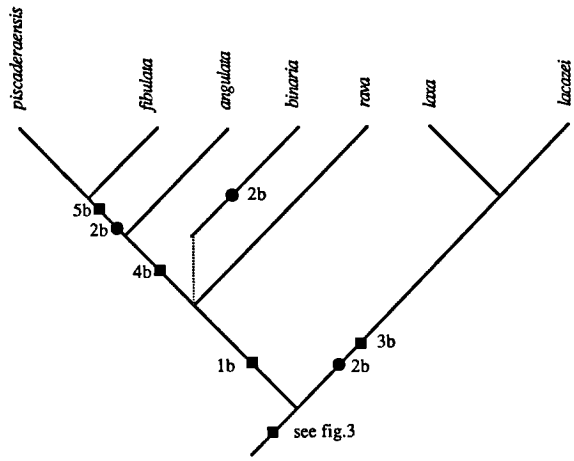


Fig. 8. Cladogram representing the hypothesized phylogenetic relationships in the *angulata* group. For explanation of characters see text. ■ = character without homoplasious development, ● = character with a homoplasious development.

1. Absence of rhaphides (state 1b). *Haliclona lacazei* and *H. laxa* have rhaphides, which is considered plesiomorphous. The absence is a weak synapomorphy of the other species.

2. Absence of toxa (state 2b). State 2b shows three homoplasious developments within the *angulata* group. It is a synapomorphy of *H. lacazei* and *H. laxa*, and of *H. fibulata* and *H. piscaderaensis*, and an autapomorphy of *H. binaria*.

3. Absence of sigmata (state 3b). Synapomorphy of *H. lacazei* and *H. laxa*.

4. Fistular processes (state 4b). Synapomorphy of *H. angulata*, *H. piscaderaensis* and *H. fibulata*.

5. Surface strongly reticulate (state 5b). Plesiomorphous is a smooth, or slightly punctate surface. It is a synapomorphy of *H. fibulata* and *H. piscaderaensis*.

Within the *angulata* group there are three homoplasious developments, all restricted to character state 2b (absence of toxa). The cladogram contains one unresolved trichotomy.

PHYLOGENY OF THE *ARENATA* GROUP

In fig. 9 the cladogram representing the hypothesized phylogenetic relationships of the species of the *arenata* group is presented, based on the following characters:

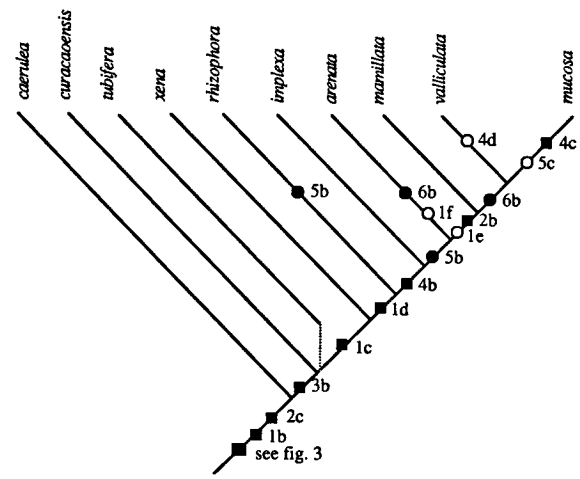


Fig. 9. Cladogram representing the hypothesized phylogenetic relationships in the *arenata* group. For explanation of characters see text. ■ = character without homoplasious development, ● = character with a homoplasious development, ○ = reversal.

1. Habit. Like always, oscular mounds have been coded as the plesiomorphous state 1a. In addition, the following states have been recognized: state 1b is tubular-ramose, state 1c coalescent tubes, and state 1d tubes arising from a common stalk. The assumed transfor-

mation series of these character states is a - b, a - c - d. State 1b has been generated at the root of the cladogram, and state 1a as a reversal on the stem down from *Haliclona mamillata* (in the cladogram re-coded as the new state 1e). State 1c evolved in the ancestor on the stem down from *H. xena*. This state transformed into state 1d in the ancestor on the stem down from *H. rhizophora*. In *H. arenata* there is a reversal to coalescent tubes (in the cladogram re-coded as the new state 1f).

2. Pore areas. The plesiomorphous state (state 2a) is pores which are equally distributed in the ectosomal membrane. In the *arenata* group the pores are centralized in certain areas. These areas may be undivided (see Griessinger, 1971, figs. 5a1 & 5c1), or they may be divided by spicula into smaller, secondary areas (see Griessinger, 1971, figs. 5b1 & 5d). The latter state has been coded as state 2b, the state "pore areas undivided" as state 2c. The assumed transformation series is a - b - c, a - c. By parsimony, state 2c has been generated at the root of the cladogram, state 2b as a development in the ancestor on the stem down from *H. mamillata*. There are no homoplasious developments.

3. Absence of microscleres (state 3b). *H. caerulea* is the only species with microscleres (sigmata). State 3b has therefore been generated as a development in the ancestor on the stem down from the trichotomy formed by *H. curacaoensis* and *H. tubifera*.

4. Slime. The same states occur as in the *rosea* and *dendroxea* groups, viz. absent (state 4a), scarce (state 4b) and copious (state 4c). The assumed transformation series is a - b - c. Copius slime occurs only in *H. mucosa*, and is therefore an autapomorphy of this species. State 4b developed in the ancestor on the stem down from *H. implexa*. In *H. valliculata* there is a reversal to absence of slime (in the cladogram re-coded as the new state 4d).

5. Aquiferous system. The plesiomorphous state 5a is a "normal" development of the aquiferous system, state 5b is a strong development. State 5b has been generated as a synapomorphy of *H. arenata*, *H. mamillata* and *H. valliculata*, with a homoplasious development in *H. rhizophora*. In *H. mucosa* there is a reversal towards a normal development of the aquiferous system (in the cladogram re-coded as the new state 5c).

6. Surface. The plesiomorphous state 6a is a regular, smooth surface. State 6b, which is found in *H. arenata*, *H. mucosa* and *H. valliculata* is a very irregular surface with many depressions, grooves and pits. The pore fields (see character 2) are often centralized in the depressions. State 6b is a synapomorphy of *H. valliculata* and *H. mucosa*, with a homoplasious development in *H. arenata*.

There are two homoplasious developments in the *arenata* group and four reversals. The homoplasies are:

1. Character state 5b (strongly developed aquiferous system). Homoplasious development in *H. rhizophora* and in the ancestor on the stem down from *H. arenata*.

2. Character state 6b (irregular surface). Homoplasious development in *H. arenata* and in the ancestor of *H. valliculata* and *H. mucosa*.

The reversals are:

1. Character state 1e (habit oscular mounds). Reversal in the ancestor on the stem down from *H. mamillata*.

2. Character state 1f (habit coalescent tubes). Reversal in *H. arenata*.

3. Character state 4d (absence of slime). Reversal in *H. valliculata*.

4. Character state 5c (normally developed aquiferous system). Reversal in *H. mucosa*.

The cladogram of the *arenata* group contains one unresolved trichotomy.

PHYLOGENY OF THE *ROSEA* AND *DENDROXEA* GROUPS

The *rosea* and *dendroxea* groups are treated in the same phylogenetic analysis, because the *dendroxea* group is represented only by two species. In fig. 10 the cladogram representing the hypothesized phylogenetic relationships of the groups is presented, based on the following characters:

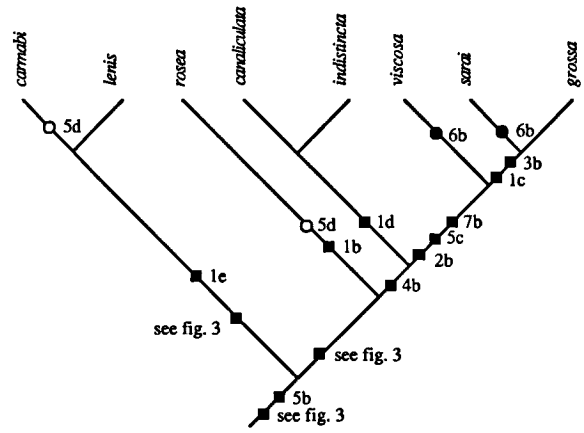


Fig. 10. Cladogram representing the hypothesized phylogenetic relationships in the *rosea* and *dendroxea* groups. For explanation of characters see text. ■ = character without homoplasious development, ● = character with a homoplasious development, ○ = reversal.

1. Habit. Plesiomorphous (state 1a) is a massively encrusting base with oscular mounds. This form occurs only in *Haliclona viscosa*. State 1b is irregularly cushion-shaped, which is an autapomorphy of *H. rosea*. State 1c is massive, and a synapomorphy of *H. sarai* and *H. grossa*. State 1d is thickly encrusting, and a synapomorphy of *H. canaliculata* and *H. indistincta*. State 1e is a thin sheet, and a synapomorphy of *Dendroxea lenis* and *D. carmabi*. The assumed transformation series of the character states is a - b - c - d, a - c, a - d, b - d, d - e.

2. Oscules. The state oscules "flush" is a synapomorphy of the *rosea* and *dendroxea* groups (see character state 3b of fig. 3). Within the group there is a trend towards oscules "elevated", which has been generated as a new step (state 2b) in the ancestor on the stem down from *H. viscosa*.

3. Spicula length. A spicula length of 120-170 μm is the plesiomorphous state for the *rosea* group (see fig. 3). The small spicules in *Dendroxea lenis* and *D. carmabi* have earlier been generated as a reversal (see character state 5d of fig. 3). The large spicules (over 170 μm) of *Haliclona grossa* and *H. sarai* may be considered as a new state (state 3b), evolved in their common ancestor.

4. Tendency to reach large size (state 4b). This (very weak) trend is a synapomorphy of *Haliclona indistincta*, *H. canaliculata*, *H. viscosa*, *H. sarai* and *H. grossa*.

5. Slime. The absence of slime is coded as the plesiomorphous state 5a, but no state could be assigned to the hypothetical ancestor (for the same reason as in the *arenata* group). State 5b is scarce slime, state 5c copious slime. The assumed transformation series of these states is a - b - c. State 5b has been generated as the state occurring at the root of the cladogram. State 5a (absence of slime) which was primarily considered plesiomorphous, has been generated as a reversal in *Dendroxea carmabi* and *Haliclona rosea* (in the cladogram re-coded as state 5d). State 5c has been placed on the stem down from *H. viscosa*.

6. Consistency. Soft is the plesiomorphous state (state 6a, see also fig. 3). *H. viscosa* and *H. sarai* are firmly friable (state 6b). This state has been generated as a homoplasious development in the two species, but it is equally parsimonious to place this step on the stem down from *H. viscosa*.

7. Surface. A smooth surface is plesiomorphous (state 7a). In *H. sarai* and *H. viscosa* the surface is rather irregular (state 7b). This state is assumed to have evolved in the ancestor of *H. viscosa*, *H. sarai* and *H. grossa*.

Within the *rosea* and *dendroxea* groups there are two homoplasious developments and two reversals.

The homoplasies are:

1. Character state 5d (absence of slime). Homoplasious development in *H. rosea* and *Dendroxea carmabi*.

2. Character state 6b (firm consistency). Homoplasious development in *H. viscosa* and *H. sarai*.

The reversals are found in the same character states, viz. state 5d (absence of slime) in *H. rosea* and *Dendroxea carmabi*.

It is evident that in all the species groups only a few characters are left for a sound phylogenetic analysis, but nevertheless these provide

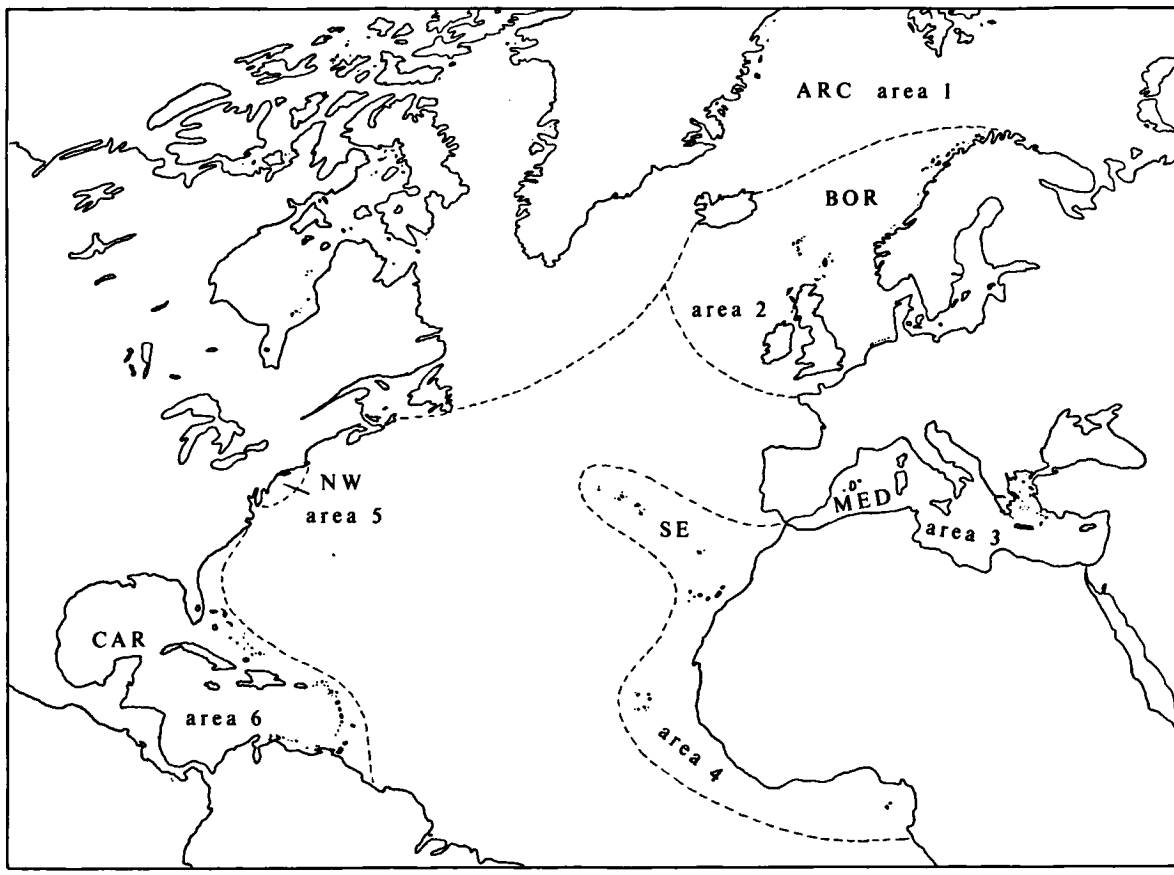


Fig. 11. Areas of endemism within the North Atlantic. Area 1 = Arctic, area 2 = Boreal, area 3 = Mediterranean, area 4 = south-eastern parts of the North Atlantic, area 5 = North West Atlantic, area 6 = Caribbean, area 7 = Netherlands.

sufficient tools for application of cladistic principles. It will hereafter be shown that, despite the fact that the cladograms are not "robust", the analyses may be used as a basis for analytical biogeographical studies.

DESCRIPTIVE BIOGRAPHY

Areas of endemism. In table I the North Atlantic distribution of the chalinid species is presented. The distribution patterns conform largely to the endemic areas as established by Ekman (1953) and Briggs (1974) for different marine evertebrates and fishes (see Boury-Esnault & Lopes, 1985, for distributions of sponges). These are (fig. 11):

Area 1. Arctic. The eastern part of the Arctic area borders the eastern Boreal area; its southern limit lies at a relatively high latitude (North Norway and North Iceland) because of the warm North Atlantic Current which reaches as far north as these latitudes. At the western side the southern limit of the Arctic reaches as far south as Nova Scotia. This low latitude is caused by the cold Labrador Current, which comes from the North. Two chalinids have an Arctic distribution, viz. *Haliclona laurentina* (ill-known) and *H. primitiva*. The latter species is known from the White Sea, and South and West Greenland (see de Weerdt, 1986, fig. 2).

Area 2. Boreal. The northern limit of the eastern Boreal area lies at North Norway; to the west the boundary is formed by the Faroe Islands, and South and West Iceland; at the

south the limit is at the southern entrance of the English Channel. Only one chalinid has a purely Boreal distribution, viz. *H. indistincta* (see de Weerdt, 1986, fig. 10).

Area 3. Mediterranean. The known high endemism in the Mediterranean (e.g., Briggs, 1974; Vacelet, 1980) is reflected also by the distribution of the chalinid sponges. Twenty-two chalinids are apparently restricted to the Mediterranean. However, this number includes also the ill-known species.

Taking only the better known species into account, there are still 15 species which have not been recorded outside the Mediterranean. These are: *Haliclona laevis*, *H. reptans*, *H. cribrata*, *H. venata*, *H. varia*, *H. griessingeri*, *H. subtilis*, *H. magna*, *H. semitubulosa* sensu Topsent, *H. laxa*, *H. rhizophora*, *H. arenata*, *H. mamillata*, *H. sarai*, and *H. grossa*.

Area 4. The Azores, Madeira, Canary Islands, Cape Verde Islands, and West Africa from Morocco south to the Gulf of Guinea (south-central and south-eastern part of the North Atlantic). This area comprises thus both the Mauritanian and Senegalanian regions as recognized by Ekman (1953) and Boury-Esnault & Lopes (1985), as well as the Azores which were included in the Lusitanian region by Boury-Esnault & Lopes (1985). The distribution of *Haliclona neens* is reponsible for this, because it has been recorded from the Azores and from São Tomé (Gulf of Guinea). *Acervochalina parasimulans* is known from the Canary Islands and also from Guinea (São Tomé, Principe and Annabon). Quite probably this area as used here is artificial, but the known distribution of the chalinid species does not allow for a smaller subdivision.

Five species are endemic to this part of the North Atlantic Ocean, viz. *Haliclona neens*, *H. abbreviata* (São Tomé), *H. binaria* (Azores, Canary Islands), *Acervochalina parasimulans*, and *A. nigra* (Azores).

Area 5. North West Atlantic (western Boreal). This area borders the Arctic area at Newfoundland in the North, and ends at Cape Hatteras in the south. *Haliclona canaliculata* is the only endemic species of this area. It is known from the Long Island Sound (Connecticut) only (Hartman, 1958, and pers. comm.), and this distribution falls within the region between Cape Hatteras and Cape Cod ("Middle Atlantic Seabord") which is considered a separate endemic area by authors (cf. Briggs, 1974). According to Briggs (1974) the data are too scanty to justify this point of view, and he considers this area as the southern part of the western Atlantic Boreal.

Area 6. Caribbean. The name Caribbean is here used in the widest sense, and comprises in the present study the whole tropical and subtropical part of the western Atlantic, from Cape Hatteras (North Carolina) south to Trinidad, and including Bermuda. Boury-Esnault & Lopes (1985) extend the Caribbean "Province" south to the equator, but that the southern border ends at Trinidad seems to be sufficiently established (Briggs, 1974). Briggs (l.c.) subdivided the area into smaller endemic units, and recognized for instance a separate West Indian Province for Bermuda, the Bahamas, and the Greater and Lesser Antilles south to Grenada. With the present, still rather poor knowledge of the distribution of the chalinids within the Caribbean s.l., it is not possible to follow Briggs' (l.c.) subdivisions.

Thirteen species are endemic to the Caribbean, four of which are ill-known. The other nine species are *Haliclona hogarthi*, *H.* n.sp., *H. implexiformis*, *H. piscaderaensis*, *H. caerulea*, *H. curacaoensis*, *H. tubifera*, *Acervochalina molitba* and *Dendroxea carmabi*. Of these, *H. tubifera* seems to be restricted to the Carolina region and Bermuda (van Soest, 1980). This distribution corroborates Brigg's (1974) establishment of a separate Carolina region.

Area 7. The Netherlands. This is not an endemic area, because the Netherlands do not harbour a historically determined sponge fauna. However, *H. xena*, which has quite certainly been introduced with oysters, occurs

Table I. North Atlantic distribution of the Chalinidae. Species marked with an asterisk * are included in the phylogenetic analyses. Arc = Arctic, Bor = Boreal, Neth = Netherlands, Lus = Lusitanian, Az = Azores, Can = Canary Islands, Mad = Madeira, CV = Cape Verde Islands, W-Afr = West Africa, Med = Mediterranean, NW = North West Atlantic, Car = Caribbean.

species	distribution											
	Arc	Bor	Neth	Lus	Az	Can	Mad	CV	W-Afr	Med	NW	Car
oculata group												
*Haliclona oculata**	×	×	×								×	
*Haliclona urceolus**	×	×										
*Haliclona simulans**		×			×	×	×			×		
*Haliclona laevis**										×		
*Haliclona reptans**										×		
*Haliclona cribrata**										×		
*Haliclona varia**										×		
*Haliclona venata**										×		
Haliclona n.sp.*												×
acervochalina group												
*Acervochalina limbata**		×		×		×				×		
*Acervochalina loosanoffi**			×								×	
*Acervochalina fertilis**					×	×				×		
*Acervochalina parasimulans**						×			×			
*Acervochalina nigra**					×							
*Acervochalina molitba**												×
Acervochalina crassiloba sensu de Laubenfels												×
aquaeducta group												
*Haliclona primitiva**	×											
*Haliclona cinerea**		×			×							
*Haliclona aquaeducta**					×					×		
*Haliclona citrina**					×					×		
*Haliclona neens**					×				×			
*Haliclona cratera**								×		×		
*Haliclona abbreviata**									×			
*Haliclona mediterranea**					×					×		
*Haliclona subtilis**										×		
*Haliclona griessingeri**										×		
*Haliclona hogarthi**												×
Haliclona coerulescens									×			
Haliclona flavescens										×		
fistulosa group												
*Haliclona fistulosa**		×		×	×					×		
*Haliclona fulva**						×				×		
*Haliclona perlucida**					×	×				×		
*Haliclona magna**										×		
*Haliclona semitubulosa** sensu Topsent										×		
*Haliclona implexiformis**												×
Haliclona albifragilis												×
angulata group												
*Haliclona angulata**		×		×	×	×	×	×		×		
*Haliclona fibulata**		×			×	×				×		
*Haliclona rava**		×								×		
*Haliclona binaria**					×	×						
*Haliclona lacazei**									×	×		

Table I (continued)

species	distribution											
	Arc	Bor	Neth	Lus	Az	Can	Mad	CV	W-Afr	Med	NW	Car
*Haliclona laxa**										×		
*Haliclona piscaderaensis**												×
Haliclona laurentina	×											
Haliclona tenuisigma										×		
Haliclona uncinata										×		
Haliclona marismedi										×		
Haliclona dubia										×		
Haliclona microsigma										×		
Haliclona aperta										×		
Haliclona tenerrima												×
Haliclona calcinea												×
arenata group												
*Haliclona xena**			×									
*Haliclona valliculata**					×	×				×		
*Haliclona implexa**					×	×	×			×		
*Haliclona mucosa**						×				×		
*Haliclona arenata**										×		
*Haliclona mamillata**										×		
*Haliclona tubifera**												×
*Haliclona curacaoensis**												×
*Haliclona caerulea**												×
rosea group												
*Haliclona rosea**	×	×										
*Haliclona indistincta**		×										
*Haliclona viscosa**		×		×						×		
*Haliclona grossa**										×		
*Haliclona sarai**										×		
*Haliclona rhizophora**										×		
*Haliclona canaliculata**											×	
dendroxea group												
*Dendroxea lenis**					×	×	×			×		
*Dendroxea carmabi**												×

exclusively in the Netherlands. The species has been included in the phylogenetic analyses. The species cladograms will later on be converted in area cladograms (see below). In order to be consistent in the use of the cladograms, without changing the cladogram topology obtained from the phylogenetic analyses, *H. xena* has been left at its place in the cladogram. Consequently, the Netherlands have to receive a "number". In the further biogeographical analyses it will be left out of consideration.

Widespread species

There are quite a few species which occupy more than one of the above mentioned endemic areas. The following distribution patterns of these widespread species can be observed.

1. *Continuous amphi-Atlantic distribution. Haliclona oculata* is the only species with this distribution pattern (see de Weerdt, 1986, fig. 2). Its range starts at the eastern Atlantic side as far south as the west coast of Portugal. It is very

common in the entire eastern Boreal area, the Arctic (with records as far east as the Kara Sea), and the North West coast of America south to North Carolina. It occurs probably in the entire Arctic and subarctic region (e.g., Koltun, 1959). A continuous amphi-Atlantic distribution is known from several marine invertebrates (Ekman, 1953), and also from sponges (for instance *Halichondria panicea*, cf. Vethaak et al., 1982).

2. *Disjunct amphi-Atlantic distribution. Acervochalina loosanoffi* has this distribution pattern. The species has originally been described from North America (from Connecticut to Maryland, cf. Hartman, 1958), but it is known also from the Netherlands and South Ireland (only one locality, viz. Lough Ine, cf. de Weerdt, 1986, fig. 22). It has quite certainly been introduced in the Netherlands by import of oysters, because it lives on oysters in the States as well as in the Netherlands.

3. *Arctic-eastern Boreal distribution. Haliclona urceolus* (cf. de Weerdt, 1986, fig. 2) and *H. rosea* (cf. de Weerdt, 1986, fig. 14) occur both in the Arctic and the eastern Boreal part of the North Atlantic Ocean. The most western Arctic record of *H. urceolus* is at West Greenland, and of *H. rosea* at the east coast of Baffin Island. *H. rosea* has its southern limit in the eastern Boreal a little more south than *H. urceolus*, viz. at the south coast of Brittany, whilst no records of *H. urceolus* south of Ireland are known. However, these data apply for the latter species only to the shallow-water parts of the ocean. *H. urceolus* has recently been collected from Mauritania at a depth of 300-400 m by R. W. M. van Soest, and tropical submergence is therefore possible. The same behaviour may be exhibited by *H. rosea*, because there are several Antarctic records of a chalinid species remarkably similar to *H. rosea* This may indicate a bipolar distribution with tropical submergence, although tropical deep-water records of *H. rosea* are still lacking.

4. *Mediterranean-Atlantic distribution.* Seventeen chalinid species occur in the Mediterranean as well as in the eastern parts of the North Atlantic. Within this distribution three patterns may be distinguished:

a. The first includes the Mediterranean, the Lusitanian and the Mauritanian regions (including the Macaronesian Islands). Species with this wide range are *Haliclona simulans* (cf. de Weerdt, 1986, fig. 6), *H. cinerea* (cf. de Weerdt, 1986, fig. 6, and de Weerdt & Stone, in prep.), *H. fistulosa* (cf. de Weerdt, 1986, fig. 10), *H. angulata* (cf. de Weerdt, 1986, fig. 18), *H. fibulata* (cf. de Weerdt, 1986, fig. 18), and *Acervochalina limbata* (cf. de Weerdt, 1986, fig. 22).

b. The second pattern is restricted to the Mediterranean and Lusitanian region. Two species have this distribution pattern, viz. *H. rava* (cf. de Weerdt, 1986, fig. 18) and *H. viscosa* (cf. de Weerdt, 1986, fig. 10).

c. The third pattern is restricted to the Mediterranean and Mauritanian region. Seven species conform to this distribution pattern, viz. *H. aquaeducta*, *H. mediterranea*, *H. citrina*, *H. cratera*, *H. fulva*, *H. perlucida* and *A. fertilis*. These three Mediterranean-Atlantic distribution patterns are well-known (Ekman, 1953; Briggs, 1974; Vacelet, 1980; Boury-Esnault & Lopes, 1985), and are confirmed by the distribution of the chalinid species.

It appears that all the widespread North Atlantic chalinid species occur only in contiguous areas of endemism. In the vicariance biogeography section of this paper these distribution patterns will be discussed in greater detail. The lack of widespread species in disjunct areas of endemism within the North Atlantic corroborates the theory that sponges are no good dispersers (with exceptions, of course). Sponge larvae have never been recorded by Scheltema (1977, 1986) in his studies of long-distance dispersal by benthic invertebrates. They do furthermore not show teleplanic characters and are known to settle within hours or a few days at the most. The conclusion that long-distance dispersal in sponges must be considered as a highly excep-

tional event (see also Boury-Esnault & Lopes, 1985) seems well justified.

In the next chapter it will be shown that the chalinid species cladograms and the distribution patterns of the species can be used to apply recently developed methods in vicariance biogeography.

VICARIANCE BIOGRAPHY

Vicariance biogeography is a method of analytical historical biogeography which uses the hypothesized phylogenies of organisms and their distribution patterns to infer historical relationships of areas of endemism. The principles of vicariance biogeography have been formulated for the first time by Platnick & Nelson (1978), and a few years later in greater detail by the same authors (Nelson & Platnick, 1981). A first methodological application to Central American poeciliid fishes was published by Rosen (1978). Since then, the subject is getting increasing interest, and many papers dealing with newly developed methods, including computer programs, criticisms, etc. have been published recently (e.g., Wiley, 1987b, 1988; Humphries & Parenti, 1986; Zandee & Roos, 1987; Cracraft, 1988; Meyers, 1988; Page, 1988). Applications of the methods of vicariance biogeography based on real data are still very rare, however, and the present study is, to my knowledge, the first effort dealing with marine organisms and areas of endemism. It seems therefore useful to give a short introduction to the principles of vicariance biogeography and to review the conditions required for application of these principles (see also de Weerdt, in press b).

In vicariance biogeography the distribution patterns of organisms are viewed in light of the idea that geographical fragmentation of an ancestral biota is the prime cause of speciation (vicariance) (e.g., Rosen, 1976; Wiley, 1981). Speciation by dispersal (founder speciation) is not excluded, but dispersal hypotheses offer no general explanation for the repeated occurrence of various animal and plant groups of related taxa in widely separated areas. Furthermore, dispersal hypotheses cannot be falsified (since individual historical dispersal events cannot be witnessed), whereas vicariance hypotheses can be falsified by the recognition of conflicting distribution patterns of unrelated groups (e.g., Platnick & Nelson, 1978; Wiley, 1981; Humphries & Parenti, 1986).

The same philosophy forms the background of phylogenetic systematics, where relationships of organisms are thought to be the result of common ancestry. Shared derived characters are the tools for inferring the phylogenetic relationships, and the cladogram is the figurized hypothesis of these relationships. Because phylogenetic systematics and vicariance biogeography are based on the same principles, cladograms of species or higher taxa can be used to construct cladograms of areas, when the distributions of the taxa are known. *Area cladograms* are obtained by replacing the taxon names by the distribution patterns of the taxa, and these figures indicate the relative recency of their common ancestral biota. When more than one area cladogram of different groups of organisms, inhabiting the same endemic areas, are available, they can be combined into a *general area cladogram*. A general area cladogram is a hypothesis on the historical relationships of the areas of endemism, which can be corroborated by general area cladograms obtained from other taxonomic groups, and by geological data (Platnick & Nelson, 1978).

Usually there are many incongruences between the individual area cladograms, due to natural processes as extinction or primitive absence (causing "missing areas"), and dispersal or absence of speciation after a vicariance event (causing widespread species and "redundant areas"). The procedure leading to the construction of a general area cladogram is strongly biased by assumptions concerning these incongruent patterns and no general agreement has yet been obtained (e.g., Nelson & Platnick, 1981; Humphries & Parenti, 1986; Wiley, 1987b; Zandee & Roos, 1987; Page, 1988). Assumptions concerning the widespread species problem are currently known as "Assumption 1", "Assumption 2" and "Assumption 0".

The first two assumptions have been developed by Nelson & Platnick (1981). "Assumption 1" is the assumption that when a widespread species (occupying more than one endemic area) turns out to be polytypical, the resulting two species do not necessarily have to be sister-species, but each of them may be more closely related to a third, phylogenetically most closely related species. "Assumption 2" goes even further than that, because it allows the resulting two species to be more closely related to every other member of the same monophyletic group than to each other. As a result of both assumptions, the relationships between the endemic areas inhabited by these widespread species are allowed to be ambiguous, which may result in partly or completely unresolved general area cladograms (cf. Zandee & Roos, 1987).

"Assumption 0", originally developed by Brooks (1981, cf. Wiley, 1987b), is the assumption that when a widespread species turns out to be polytypical, the resulting two species will always be more closely related to each other than each of them will be to another species. The same applies to the areas inhabited by them. In other words, the taxon phylogenies are primarily considered unambiguous. General area cladograms constructed on basis of "Assumption 0" are usually fully resolved (cf. Zandee & Roos, 1987).

Apart from these assumptions which have a large impact on the topology of the general area cladogram, a few conditions for application of the methods of vicariance biogeography need to be taken into consideration. The main conditions are:

1. Biogeographic analyses must be based on sound phylogenetic studies (Humphries & Parenti, 1986: 67). The cladograms of the chalinid species groups presented here are not robust, in the sense that many species are united by single, often weak synapomorphies. However, they represent "the state of art" in chalinid phylogenetic analyses. Fortunately, the taxonomic status of the included species is stable as a result of recent revisional studies (Griessinger, 1971; de Weerdt 1985, 1986; de Weerdt & van Soest, 1986, 1987; van Lent & de Weerdt, 1987). Species of uncertain taxonomic status have been left out of consideration (see table I); this is especially important in the *angulata* group, which certainly needs more attention in the future. Many of the species belonging to the *angulata* group are however predominantly deep-water species, and the present revision and analysis has focused on shallow-water (0-200 m) species.

2. At least two and preferably more phylogenetic analyses of unrelated taxa must be available for the same set of areas (Humphries & Parenti, 1986: 33). I find the word "unrelated" somewhat confusing, because all organisms are related in a way. Rosen's (1978) example implied two genera of poeciliid fishes, and my study concerns eight species groups within one family. One group (the *dendroxea* group) consists at present only of two species and is therefore combined with the analysis of its sister-group (the *rosea* group), which reduces the group cladograms to seven. The groups are thought to be of the same taxonomic rank, which implies that the same vicariance events are assumed to be responsible for speciation within each group. The species groups are considered "unrelated enough" to justify the historical biogeographic analysis.

3. Three-taxon statements are the most basic possible units of biogeographic (as well as phylogenetic) analysis (Platnick & Nelson, 1978: 1). The number of cladograms (seven) and the number of areas of endemism (six) conform to this requirement.

4. The groups used for the analysis must be monophyletic (Humphries & Parenti, 1986: 31). All the chalinid species groups are hypothesized as monophyletic groups, by one or more synapomorphous characters.

5. The areas used for the analysis must be areas of endemism, containing at least two endemic taxa of some rank (Platnick & Nelson, 1978: 15). This condition is necessary because only other endemic taxa can be used for testing hypotheses about the historical relationships of areas. The areas used in the present analysis are all generally recognized areas of endemism (Ekman, 1953; Briggs, 1974; Boury-Esnault &

Lopes, 1985), which means that the here presented hypotheses can be tested by cladistic analyses of other, endemic, "unrelated" taxa.

Summarizing, it may be concluded that it is justified to perform vicariance biogeography with the obtained cladograms of the chalinid species groups. This effort completely follows the component-compatibility and parsimony methods of Zandee & Roos (1987), for which the computer program CAFCA (Zandee, 1987) is available. The methods can be applied using the three "Assumptions" (see above), but the following analyses are based on "Assumption 0".

Components are recent and ancestral distributional types (areas). Although Nelson & Platnick (1981) use the word component, to my knowledge, for composite areas only, it makes more sense to me to follow Zandee & Roos (1987) and the dictionaries and to use the word component in the meaning of "ingredient" (this word has not been used by Zandee & Roos (l.c.); they use the word "building blocks"). Both single areas and composite areas are the components ("building blocks") for the construction of a general area cladogram. Composite areas are derived from present-day distributions of widespread species, and from ancestral distributional types. The latter are obtained by adding together the distributions of daughter taxa of a hypothesized ancestral taxon (e.g., Wiley, 1987b; Zandee & Roos, 1987). This is an easy procedure once the taxon cladograms are converted into area cladograms by replacing the taxon names by the distributions of the taxa.

The component-compatibility method aims at the recognition of the largest sets of mutually in- or exclusive composite distributional types ("maximal cliques"). Usually there are several maximal cliques, i.e. several alternative general area cladograms. The choice for the "best" general area cladogram is determined by the number of components of the individual taxon area cladograms fitting with components of the general area cladogram, and the number of not-fitting components. Distributional types which do not fit with the general area cladogram need ad hoc explanations like extinction, primitive absence, no response to a vicariance event, etc. The most parsimonious solution between fitting and not-fitting components determines the choice for the "best" general area cladogram.

In fig. 12 the individual taxon area cladograms of the chalinid species groups are presented. The species names have been left at their place, but their distributions have been added to the cladograms. Both the recent and ancestral species (the internal nodes) have received a number, printed in plain style. The numbers of the areas are printed in italic. The composite areas at the internal nodes are the sum of the areas of recent species and of ancestors "higher up" in the cladograms. A few extra ancestors had to be added to the cladograms containing unresolved polytomies. By doing this, all possible solutions have been included (this step seems to be justified according to Zandee, pers. comm.). In table II all the components derived from the recent and ancestral species are shown. When combining the components into maximal cliques, 19 alternative general area cladograms are obtained. These are:

1. (((((1,2)5)3)6)4)
2. (((((1,2)5)3)4)6)
3. (((((2,3)4)6)5)1)
4. (((((2,3)5)1)6)4)
5. (((((2,3)5)1)4)6)
6. (((((3,4)1)2)6)5)
7. (((((3,4)1)6)2)5)
8. (((((3,4)2)6)1)5)
9. (((((3,4)5)6)2)1)
10. (((((3,4)5)2)6)1)
11. (((((3,4)6)2)1)5)
12. (((((2,5)1)3)4)6)
13. (((((2,5)1)3)6)4)
14. (((((3,6)4)1)2)5)
15. (((((3,6)4)2)1)5)
16. (((1,2)(3,4)6)5)
17. (((1,2)(3,6)4)5)
18. (((3,4)(2,5)6)1)
19. (((2,5)(3,6)4)1)

It is evident that the use of a computer is

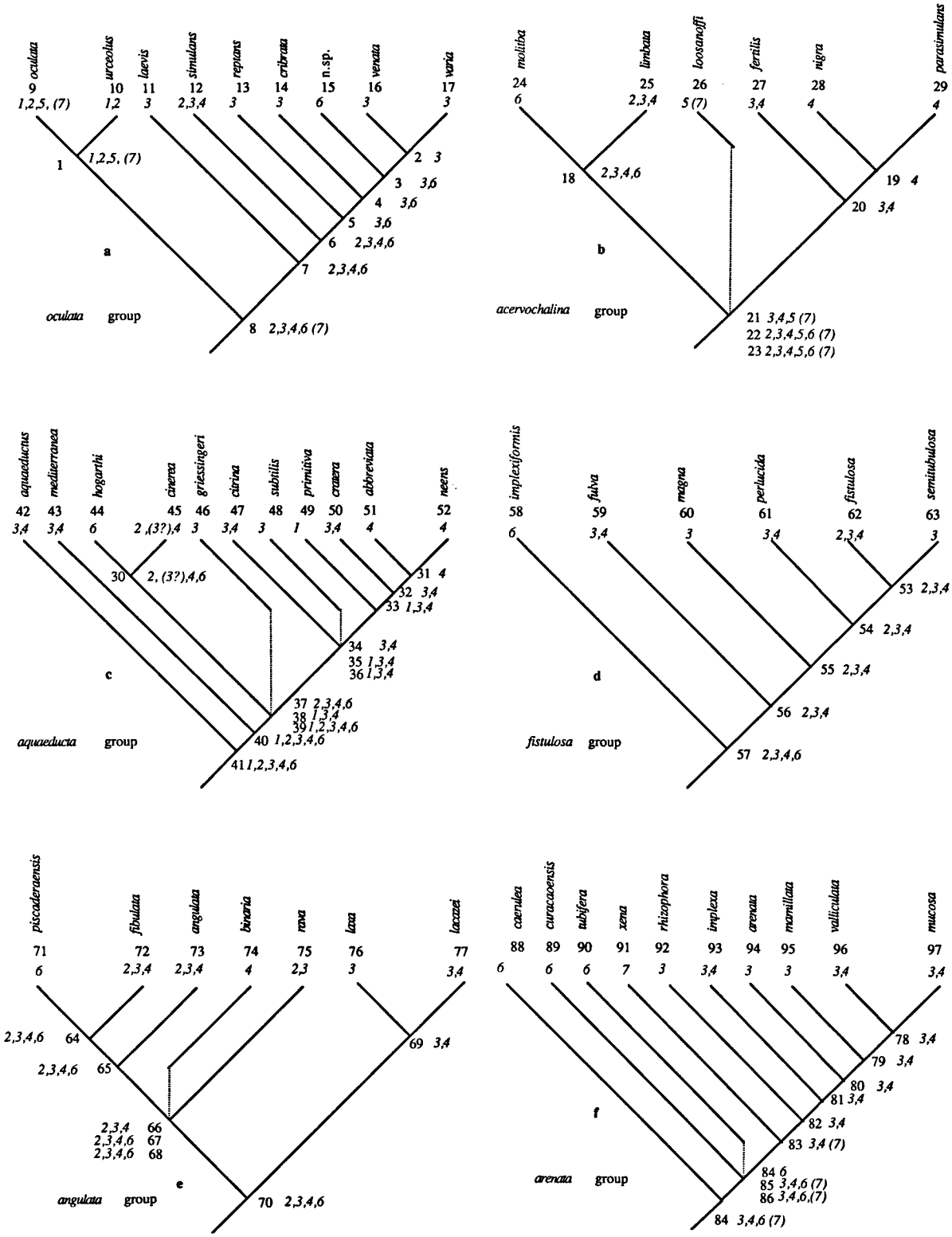
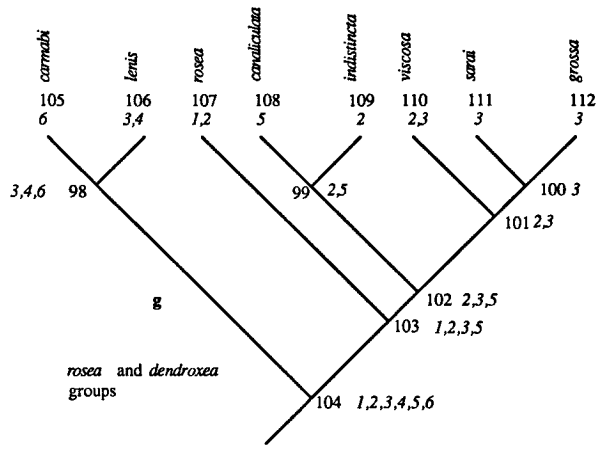


Fig. 12. Taxon area cladograms of the chalinid species groups. Species numbers are printed in plain style, area numbers in italic. Area numbers are similar to those of fig. 11. For explanation see text.



highly desirable to calculate all the fitting and not-fitting components of the individual taxon area cladograms for each of the 19 alternative general area cladograms (see de Weerdt, in press b, for a manually elaborated analysis of a reduced data set). The most parsimonious general area cladogram, generated by CAFCA, is number eight. In fig. 13 this cladogram is shown in the more currently used presentation. Internally, this general area cladogram consists of the following components of table II:

a. component 9 = area 3 + 4 (Mediterranean + south-eastern part of the North Atlantic)
b. component 14 = area 2 + 3 + 4 (Boreal + Mediterranean + south-eastern part of the North Atlantic)
c. component 19 = area 2 + 3 + 4 + 6 (Boreal + Mediterranean + south-eastern part of the North Atlantic + Caribbean)
d. component 20 = area 1 + 2 + 3 + 4 + 6 (Arctic + Boreal + Mediterranean + south-eastern part of the North Atlantic + Caribbean)
e. component 22 = area 1 + 2 + 3 + 4 + 5 + 6 (Arctic + Boreal + Mediterranean + south-eastern part of the North Atlantic + Caribbean)

Through comparison of the general area cladogram with palaeogeographical data, it is possible to recognize the ancestral area of component 22 as the western Tethys Sea, before the separation of South America and Africa (Dietz & Holden, 1970; Sclater et al., 1977). The widening of the South Atlantic during the Cretaceous period is assumed to be represented by the branching point down from component 14. This vicariance event is generally accepted as the major event causing the existence of closely related species at both side of the Atlantic (e.g., Rosen, 1976; Pielou, 1979).

The separation of component 14 into component 2 (Boreal) and component 9 may be the late Cretaceous—early Tertiary climatological detoriation which has led to faunal shifts in the

Table II. Components (distributional types) which can be derived from the species area cladograms. Area 1 = Arctic, area 2 = Boreal, area 3 = Mediterranean, area 4 = south-eastern part of the North Atlantic, area 5 = North West Atlantic, area 6 = Caribbean.

component #	distributional type	species #
1	1	49
2	2	109
3	3	2, 11, 13, 14, 16, 17, 46, 48, 60, 63, 76, 92, 94, 95, 100, 112
4	4	19, 28, 29, 31, 51, 52, 74
5	5	108
6	6	15, 24, 44, 58, 71, 88, 89, 90, 105
7	1,2	10, 107
8	2,3	53, 75, 101
9	3,4	20, 27, 32, 34, 42, 43, 47, 50, 59, 61, 69, 77, 78, 79, 80, 81, 82, 93, 96, 97, 106
10	2,5	99
11	3,6	3, 4, 5
12	1,3,4	33, 35, 36, 38
13	1,2,5	1, 9
14	2,3,4	12, 25, 45, 53, 54, 55, 56, 62, 66, 72, 73
15	2,3,5	102
16	3,4,5	21
17	3,4,6	87, 98
18	1,2,3,5	103
19	2,3,4,6	6, 7, 18, 30, 57, 64, 65, 67, 68, 70
20	1,2,3,4,6	39, 40, 41
21	2,3,4,5,6	22, 23
22	1,2,3,4,5,6	104

North Atlantic (e.g., Ekman, 1953; Kauffman, 1973). The separation of component 9 into component 3 (Mediterranean) and component 4 (south-eastern part of the North Atlantic) is assumed to be the temporary closure of the Atlantic-Mediterranean connection during the Miocene (Messinian) salinity crisis in the Mediterranean basin. Before the closure, the passage through the present Strait of Gibraltar was much wider than after that period (Ekman, 1953), and dispersal from both directions possibly less strongly influenced by prevalent current directions. It is assumed that speciation has occurred at both sides of the Gibraltar bridge during the salinity crisis.

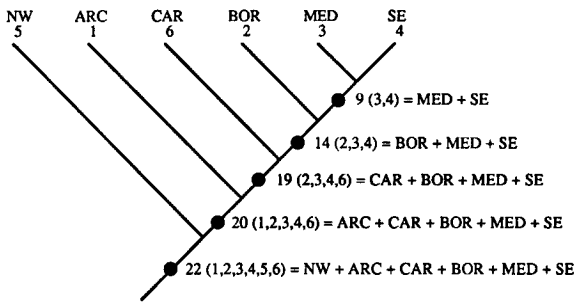


Fig. 13. General area cladogram representing the hypothesized historical relationship between the North Atlantic areas of endemism. For explanation see further text. MED = Mediterranean, SE = south-eastern part of the North Atlantic, BOR = Boreal, CAR = Caribbean, ARC = Arctic, NW = North West Atlantic.

The ancestral area consisting of components 3 and 4 may, however, not have included the Macaronesian Islands. The exact age of the islands seems to be part of controversial theories (cf. Ridley et al., 1974; Schmincke, 1976; Stock & Rondé-Broekhuizen, 1986), but the main volcanic activities leading to the present island areas are estimated to have taken place in the Miocene-Quarternary period for the Azores (Ridley et al., 1974), Miocene-Pliocene for the Canary Islands (Dillon & Sougy, 1974), and Miocene-Quarternary for the Cape Verde Islands (Dillon & Sougy, 1974). Thus, because the volcanic activities took place more or less simultaneously with the salinity crisis, it is doubtful whether colonization of the islands was already possible during or prior to this period. It may be that the sponge population was restricted to the shelf sea of the Iberian and African coasts, and that colonization of the islands has taken place from these coasts and the Mediterranean shortly after the opening of the Gibraltar Strait. Present-day conditions inhibit dispersal of sponge larvae from the Mediterranean to the islands because of the eastward surface current at Gibraltar (cf. also Boury-Esnault & Lopes, 1985). During a certain period after the opening of the Gibraltar Strait in the early Quarternary, the surface current has been westward, however, as a response to the sudden decrease in salinity of the Mediterranean water (Maldonado, 1985). Those parts of the newly originated islands which were already relatively quiet with respect to volcanic activities might have been populated by chalinid sponge species during this period.

If this would be true, the scenario consists of a first separation of a former continuous Mediterranean-Iberian-African chalinid sponge fauna into two faunas at both sides of the Gibraltar landbridge, followed by speciation at both sides. After the opening of the Strait of Gibraltar there has been a short-term westward flow of sponge larvae, consisting of a mixture of closely related Mediterranean and African-Iberian species, towards the newly formed, accessible parts of the Macaronesian islands. Later, the Mediterranean could be invaded by species, which were originally endemic to the south-eastern parts of the North Atlantic. This scenario may explain the present-day combination of endemic species in the Mediterranean as well as in the Macaronesian islands, and the large amount of species common to both areas.

Concerning the Mediterranean, it is assumed that survival and speciation of chalinid sponges was possible during the salinity crisis. It is known that the situation in the Mediterranean during the salinity crisis was extremely complex, and that there may have been fluctuations in the Mediterranean seawater level, as well as in salinity (Maldonado, 1985). Euryhaline coral species (*Porites*, *Siderastrea*), *Halimeda*, red

algae, vermetid gastropods, bryozoans, serpulid worms, as well as boring sponges flourished well in the western part of the Mediterranean during the salinity crisis (Esteban, 1979 [1980]; Esteban et al., 1978; Chevalier, 1961). It is, therefore, quite possible that (euryhaline) chalinid sponges were also able to survive the extreme conditions during this period.

Components 5 (North West Atlantic) and 1 (Arctic), as well as the internal component 20 do not contribute to the present hypothesis on the historical relationships of areas of endemisms of the North Atlantic. This is due to the low number of species responsible for these components. Arctic species are, furthermore, assumed to be more closely related to North Pacific than to North Atlantic species because of the recent (Pleistocene) openings and closures of the Bering Strait (see also Lindstrom, 1987).

EVALUATION OF THE INDIVIDUAL SPECIES AREA CLADOGRAMS

The last step of the procedure is comparison of the individual species area cladograms with the general area cladogram in order to establish which speciation events show vicariance fit and which need ad hoc explanations because of deviating distribution patterns of certain species.

OCULATA GROUP (fig. 12a)

The distributions of the sister-species *H. oculata* and *H. urceolus* do not fit with the general area cladogram. The partly sympatric distribution of the species is difficult to explain, when only the Atlantic-Arctic geographical history is taken in concern. Through the absence of a land barrier between the Arctic and the North Atlantic, the latter area has been severely effected by the Pleistocene glaciations. The climatological changes have caused repeated latitudinal faunal shifts in the North Atlantic, and adaptations as well as extinctions may have played an important role in the formation of the present-day faunal units (Ekman, 1953; Pielou, 1979). The North Pacific has much less suffered from the Pleistocene climatological detoriations, because the eustatic (worldwide) lowering of the sea level during the glaciations created the Beringia landbridge, which prevented the cool Arctic water to flow into the Pacific. At the same time, however, this landbridge was responsible for complete isolation of the Arctic and North Pacific faunas. Vicariant sister-species are, therefore, more likely to be of Arctic-North Pacific, than of Arctic-North Atlantic origin.

Both *H. oculata* and *H. urceolus* have a very wide Arctic distribution (see de Weerdt, 1986, fig. 2), viz. from Canada to Siberia, and it is possible that they occur in the entire Arctic region. In the North Atlantic, *H. oculata* has a wider range than *H. urceolus*. It is continuous amphi-Atlantic, and the most southern record is from Portugal. *H. urceolus* is restricted to the eastern Boreal part of the North Atlantic, with a southern limit at South Ireland and the Netherlands. It has, however, recently been collected from Mauritania at a depth of 300-400 m by R.W.M. van Soest (material in ZMA collection), and it is possible that the species shows tropical submergence (see also above). Both species are quite certainly good survivors, which appears from many characteristics. First, they possess gemmulae which are situated at the basis of the stalk. Both species have a growth form consisting of upright branches arising from a stalk,with which it is attached to stones, mussels, etc. This means that they may be moved quite easily through wave actions, etc. They may not be able to survive displacement themselves, but the gemmulae will. Both species are very variable with respect to growth form and spicule size (cf. Hartman, 1958; de Weerdt, 1986), and, finally, *H. oculata* can tolerate brackish water. All these factors make them good dispersers, and it is therefore entirely possible that their present Atlantic occurrence is the result of dispersal from the North Pacific (*H. oculata*) and Arctic (*H. urceolus*).

Interpretation of the remaining parts of the cladogram is quite difficult, because the distributions of ancestral species 5, 4 and 3 do not fit with the general area cladogram, and the

similar distributions of ancestral species 8, 7 and 6 suggest unknown vicariance events which may have taken place before the Tethys break-up. Because of the incompatibility of the distribution of ancestral species 5, 4 and 3 with the general area cladogram, the distributions of these species have been generated as homoplasies, thus as parallelisms (independant arrivals in the Mediterranean (area 3) and the Caribbean (area 6). The occurrence of the recent species 6 (*H.* n.sp.) in area 6 (Caribbean) is responsible for this situation. It seems premature to elaborate a scenario to explain these distribution patterns.

ACERVOCHALINA GROUP (fig. 12b)

The distribution of the sister-species *A. molitba* and *A. limbata* conforms to the separation of South America and Africa, thus to the branching point down from component 14 in the general area cladogram. Their common ancestor, species 18, is assumed to have had a Tethyan distribution.

The distributional types of ancestral species 19 and 20, and of the recent species *A. fertilis*, *A. nigra* and *A. parasimulans* conform to the supposed vicariance events during the Miocene salinity crisis (the branching point dividing component 9 into areas 3 and 4). *A. fertilis* may not have responded to this vicariant event, but it may also have dispersed from the Mediterranean (area 3) to the Azores and Canary Islands, in the period after the salinity crisis when there was a temporary eastward current from the Mediterranean (Maldonado, 1985). The latter assumption is less parsimonious, however.

AQUAEDUCTA GROUP (fig. 12c)

When the Arctic distribution of *H. primitiva* is left out of consideration (see discussion general area cladogram), all the distribution patterns of the species of the *aquaeducta* group are compatible with the general area cladogram. The cladogram is interpreted as representing a series of unknown vicariance events prior to the Tethys break-up, speciation of the Tethyan ancestral species 30 into the Caribbean species *H. hogarthi* and the eastern Atlantic species *H. cinerea* as a result of the opening of the South Atlantic, and a series of speciations in the Mediterranean and eastern Atlantic areas during and after the salinity crisis.

The supposed Mediterranean distribution of *H. cinerea* is somewhat problematic, because former Mediterranean records of the species seem to be reliable (Topsent, e.g., 1925, and material in the MNHN; Griessinger, 1971, as *H. elegans*), but the species has not been found since, despite collecting activities of van Lent in Bayuls (cf. van Lent & de Weerdt, 1987) and of the present author in Spain (Estartit). There is, furthermore, only one record from the south-eastern part of the North Atlantic, viz. from the Azores (de Weerdt & van Soest, 1986). If the sister-species *H. hogarthi* and *H. cinerea* are, indeed, the result of the Tethys break-up, the mainly Boreal distribution of *H. cinerea* could be the result of disappearance (although not entirely) from areas 3 and 4.

FISTULOSA GROUP (fig. 12d)

All the distributional types in the *fistulosa* group are compatible with the general area cladogram. Speciation of ancestral species 57 into the Caribbean species *H. implexiformis* and ancestral species 56 matches with the early Tertiairy opening of the South Atlantic. The other speciation events are assumed to have taken place during the Miocene salinity crisis.

ANGULATA GROUP (fig. 12e)

Except for the distribution of *H. rava*, all the ancestral and recent distributional types of the species of the *angulata* group are compatible with the general area cladogram. It is tentatively assumed that *H. rava* has become extinct from area 4, but it is also possible that the species has not yet been found in this area.

ARENATA GROUP (fig. 12f)

The cladistic sequence and distributional types of the species of the *arenata* group fit quite

well, although not perfectly, with the general area cladogram. Unknown vicariance events, either prior to the Tethys break-up or during Pleistocene Caribbean events, are assumed to be responsible for the speciations of *H. caerulea*, *H. curacaoensis* and *H. tubifera*. The Caribbean Chalinidae are presently under revision by the author, and Caribbean-eastern Pacific relationships will receive the necessary attention in the near future.

H. xena has been introduced in the Netherlands by oysters, and does not contribute to the analysis (area 7, the Netherlands is, therefore, placed within brackets). All the other speciations may be placed in the Miocene salinity crisis. It is most parsimonious to assume that *H. implexa*, *H. valliculata* and *H. mucosa* have not responded to this vicariance event.

DENDROXEA AND *ROSEA* GROUPS
(fig. 12g)

Dendroxea carmabi and *D. lenis* are the only species with a distribution pattern compatible with the general area cladogram. Their distributions and sister-species relationship fit with the Tethys break-up, but with the assumption that *D. lenis* has become extinct from area 2 (Boreal). *Haliclona rosea* is an Arctic-Boreal species, and may have close relatives in the North Pacific (see above). A bipolar distribution with tropical submergence is also possible (see above).

The distribution of the North Atlantic species *H. canaliculata* and its Boreal sister-species *H. indistincta* may be explained by Pleistocene isolations of the two areas (see also Vethaak et al., 1982)

It is most parsimonious to assume that both ancestral species 101 and *H. viscosa* have become extinct from area 4. *H. sarai* and *H. grossa* are assumed to have speciated during the Miocene salinity crisis.

DISCUSSION

The analyses of the historical relationships of areas of endemism within the North Atlantic ocean, here presented based on phylogenetic analyses of chalinid sponges, are a first attempt at cladistic biogeography with marine organisms, and also the first application of the component-compatibility method as developed by Zandee & Roos (1987). They have led to the hypothesis that speciation processes within the Chalinidae can be matched with late Cretaceous and Miocene vicariance events. The geological age of demosponges (Cambrium, e.g., Finks & Hill, 1967) and their slow evolutionary rate do not conflict with this hypothesis.

The analyses are based on a single group of organisms only, and were furthermore restricted to (largely contiguous) areas of endemism within the North Atlantic. Chalinids outside the North Atlantic are still in need of revision, and could therefore not be included. It is realized that it is likely that the Caribbean fauna is probably more closely related to the eastern Pacific than to the eastern Atlantic fauna, because the Pliocene closure of the Atlantic-Pacific connection through the Panama land bridge is a more recent vicariant event than the widening-up of the Central Atlantic. The same holds true for the Arctic fauna, which is probably more closely related to the North Pacific than to the North Atlantic fauna. Furthermore the Mediterranean area is treated as one biogeographic unit, whilst it is known that the eastern and western parts have very different and complex histories. However, since we lack enough data on the chalinids of the eastern Mediterranean, we cannot elaborate on this problem. The general area cladogram here presented is, thus, far from complete.

The Chalinidae are, furthermore, certainly not the ideal tools for such analyses, because of the scarcity and simplicity of their morphological characters. The reason why I used them is the mere reason that I am most familiar with these sponges through my earlier taxonomic revisions. These revisions were necessarily based on characters which could be studied on preserved (including type) specimens and freshly collected material, and the same characters have been used for the analyses. It is well

justified to make a phylogenetic analysis on whatever characters available, but it is evident that testing of the here presented hypotheses on the phylogenetic relationships of the chalinid species by other characters (derived from histological and biochemical studies) is urgently needed.

During all the procedures leading to the general area cladogram quite a few decisions had to be taken, and the assumption that microscleres are lost easier than gained may need some discussion here. Many different options concerning microscleres may be applied, because their ontogeny is still poorly known (Garrone et al., 1981), and their structure varies from very simple to very complex. Sigmatose microscleres and rhaphides are of a widespread and unstable occurrence, and it could be assumed that they have envolved independently in the different lines. These homoplasious developments could be parallelisms (same genes involved) or convergences (different genes involved), and it would be unrealistic to exclude these possibilities entirely. However, it seems more likely that they have evolved only once, and that they have been lost "here and there". Justification of this point of view is the fact that activation of the microsclerocytes seems to be dependent on favourable conditions (cf. Hartman, 1981), but also the apparent evolutionary trend in sponges in general towards simplicity (Vacelet, 1985). Sponge microscleres, even the relatively simple toxa, sigmata and rhaphides are, furthermore, considered "complex enough" to make homoplasious losses more reasonable than homoplasious gains (e.g., Ross, 1974; Wiley, 1981).

Despite the imperfections, the present study has shown that the component-compatibility method may be succesfully employed for historical biogeographic analyses of marine areas of endemism using sponges, but no doubt also other organisms, as tools. Methodological problems in combining conflicting area cladograms seem to be solved satisfactorily by the Zandee-Roos (1987) solution. However, smaller problems may still be encountered, e.g. the treatment of (genuine) polytomies.

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