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Historical biogeography in tropical Atlantic populations of *Cladophoropsis membranacea* and related species

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SUMMARY OF CONCLUSIONS

The Tethys was an equatorial sea that came into existence some 200 million years ago and closed about 12 million years ago thereby fragmenting the pan-tropical marine flora. The tropical provinces of the eastern Pacific, the Indo-West Pacific, the eastern Atlantic, and the Caribbean are today's isolated remnants. Because the tropics have remained relatively stable with respect to temperature throughout long periods of geologic time, it is the least complicated place in which to test a Tethyan vicariance hypothesis. Species and lineages occurring in today's provinces are hypothesized to have shared an evolutionary heritage of ancestor-descendant relationships that can be recovered in a phylogeny and reflects their earlier coalescence. This thesis explores the link between historical biogeographic pattern and phylogeny in the tropical intertidal alga *Cladophoropsis membranacea* and related species in the Siphonocladales-Cladophorales complex.

The central conclusions of this research are that intraspecific phylogenetic reconstruction of widely separated isolates of *C. membranacea* reflect a strong Tethyan vicariance imprint, that at least two additional dispersal events have occurred, and that vicariance has had the greater structuring influence on biogeographic pattern in comparison to dispersal.

Results from scDNA-DNA hybridization data and rDNA-ITS sequence comparisons support four principal clades in *C. membranacea*: one in the Pacific (Okinawa and Hawaii), one in the Red Sea and eastern Mediterranean Sea, one in the eastern tropical Atlantic (Canary Islands, Cape Verde Islands) and one in the Caribbean (Curaçao, Bonaire and St. Croix). In addition, two overlying dispersal events were discovered. One of these events has occurred between the Canary Islands and Cape Verde Islands, reflected by the fact that three isolates from the Cape Verde Islands shared identical ITS sequences with all isolates obtained from the Canary Islands. This is further supported by allozyme data. The more surprising discovery was the close relationship between two isolates from the Cape Verde Islands and the Mauritanian isolate with all isolates from the Caribbean, here supporting a trans-Atlantic dispersal. This trend is strongly supported by both molecular data sets and by the allozyme data, and confirms traditional floristic observations of a significant Caribbean imprint on the eastern tropical and subtropical islands in the Atlantic Ocean.

The evidence for a greater role for vicariance is shown in these results by a resolved phylogenetic structure based on genetic distance and ITS sequence divergence. Heteroduplex thermostabilities ($dTm_{(e)}$) and nucleotide substitution rates within ITS sequences are still relatively conservative in an evolutionary context. If contemporary dispersal events were the major or only structuring factor, $dTm_{(e)}$ values of up to 2.5 °C and ITS sequence variation of up to 4% would not have been detected.

In addition to the biogeographic conclusions, a number of insights were gained about phylogenetic relationships among species and genera, as well as about modes of reproduction in some of these species. Comparisons among six species in four genera of the Siphonocladales-Cladophorales complex confirmed an extremely close relationship among *Boodlea coacta*, *C. membranacea* and *Struvea anastomosans* (*Chamaedoris peniculum* as outgroup) and detected two cases of nonmonophyly. Although this has no consequences for the biogeographic analyses it has resulted in a change in thinking about species concepts and evolutionary strategies in these algae.

Flexibility of life histories in terms of sexual and asexual reproduction (including parthenogenetic development of zoospores and gametes) is well-documented in the laboratory but very difficult to determine in the field due to isomorphic, free-living haploid and diploid plants. Low amounts of genetic variation and the preponderance of heterozygous genotypes detected in allozyme banding pattern comparisons showed that asexual reproduction plays a strong role in *C. membranacea*, whereas sexual reproduction was predominant in *S. anastomosans* (at least in the only population sampled).

A number of workers have suggested the possibility of hybrids based on field observations of intermediate morphological forms. Results from the sequencing studies in this research further suggest that introgressive speciation might be a possibility. Species concepts may be more fluid than currently recognized and quantitative information over its extent would help to elucidate speciation processes and maintenance of genetic variation as an evolutionary strategy which are different from most standard "biological" species models.

In conclusion, *C. m* cosmopolitan, tropical line vicariance and some dispersal understood in marine alga history strategies and possibly focused on in future research biogeography also on a m

SAMENVATTING

De Tethys Oceaan was e geleden afgesloten werd continent. (Zie de omslag oppervlakte-water in de n ontstaan van een opening gebeurtenissen moeten o gebieden van zeeieren nu aantreffen in zowel he kust en in het Caribisch-bewoners van de Tethys

Met name in het F dan nu, maar de kusten min of meer constant klim mariene milieu dat vicari evolutionaire verwantsch er van uit dat zeeieren oceaan verspreiden. De ondanks de grote afstand kan worden ontdekt tus

De biota in de te geschikt voor het tester gedurende het Pleistoc soorten in deze zone h geïsoleerde refugia. Da breedten veel dichter b door middel van disper

In conclusion, *C. membranacea* is a representative of an old, formerly cosmopolitan, tropical lineage, whose present-day distribution is best explained by vicariance and some dispersal. The dynamics of long range dispersal are poorly understood in marine algae but must certainly be facilitated by flexibility in life history strategies and possible hybridization. This is an area that needs to be focused on in future research by investigating population structure and biogeography also on a more detailed regional scale.

SAMENVATTING

De Tethys Oceaan was een pantropische oceaan die ongeveer twaalf miljoen jaar geleden afgesloten werd door de botsing van het Afrikaanse en Euraziatische continent. (Zie de omslag van dit proefschrift). In diezelfde periode koelde het oppervlakte-water in de noordelijke Atlantische Oceaan sterk af als gevolg van het ontstaan van een opening naar de noordelijke poolzee. Door deze vicariante gebeurtenissen moeten de tot dan aaneengesloten, pantropische verspreidingsgebieden van zeewieren uiteengevallen zijn. De tropische zeewiersoorten die we nu aantreffen in zowel het Indo-Westpacifische gebied als aan de Westafrikaanse kust en in het Caribisch-Braziliaanse kustgebied, zijn dus van oorsprong al bewoners van de Tethys Oceaan geweest.

Met name in het Pleistoceen zijn de tropen veel minder uitgebreid geweest dan nu, maar de kusten rond de evenaar hebben gedurende het hele Tertiair een min of meer constant klimaat gekend. Daarom verwachten we juist in het tropische mariene milieu dat vicariante gebeurtenissen worden weerspiegeld in de moleculair evolutionaire verwantschappen van ver uiteengelegen populaties. Daarbij gaan we er van uit dat zeewieren zich niet gemakkelijk over grote afstanden door de open oceaan verspreiden. De nul-hypothese is dat zeewieren dit juist wel kunnen en dat ondanks de grote afstanden en barrières geen enkel moleculair evolutionair verschil kan worden ontdekt tussen de ver uiteengelegen populaties.

De biota in de tegenwoordig gematigde klimaatzones zijn veel minder geschikt voor het testen van de vicariantie hypothese. Gematigde breedten hebben gedurende het Pleistoceen zeer heftige klimaatsveranderingen ondergaan. Veel soorten in deze zone hebben zich dus herhaaldelijk moeten terugtrekken in geïsoleerde refugia. Daarbij komt nog dat de kustgebieden in de gematigde breedten veel dichter bij elkaar liggen dan die in de tropen hetgeen rekolonisatie door middel van dispersie vereenvoudigd.