Phylogenetic ecology of octocoral - gastropod associations

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Summary

Octocorals, most commonly represented by soft corals and gorgonians, live in all oceanic basins and continental shelves, in shallow and deep water. The majority of the species can be found on tropical and temperate coral reefs, where they may act as a host to associated taxa such as shrimps, echinoderms, fish, worms, and snails. The focus of this PhD thesis is on the association between symbiotic snails of the family Ovulidae and their octocoral hosts. These snails are mostly found on the branches of gorgonians and on the body of massive soft corals. They are either remarkably well-camouflaged or flamboyantly coloured. Such interspecific relations raise the question how these associations have evolved and how species have adapted their appearance as trait to enable survival on their host.

In **chapter 1**, the associations between Caribbean octocorals and Ovulidae were studied. The results showed that *Cyphoma gibbosum* is a generalist symbiont found on 21 octocorals species, belonging to nine genera, whilst *Cymbovula acicularis* is a specialist species. The latter was only found on closely related species of the genera *Gorgonia* and *Pseudopterogorgia* (= nowadays *Antillogorgia*). In addition, the phylogeny of Atlantic Ovulidae was reconstructed based on 16S and COI sequences. The sequence data of 13 specimens belonging to four nominal Caribbean ovulid species was combined with sequence data of Indo-Pacific ovulids to get insight into the interspecific relationships. A specimen of *Simnialena uniplicata* clustered within the clade of *C. gibbosum*. Shell morphological features of different growth stages of *C. gibbosum* were compared with the shell of *S. uniplicata* to seek for morphological evidence for this seemingly aberrant clustering. Based on this comparison it was hypothesised that *S. uniplicata* exemplifies a case of paedomorphosis. In **chapter 2,** the results of chapter 1 are revisited with molecular data from four loci (16S, COI, H3 and 28S), and an additional 23 specimens belonging to five nominal species and an undescribed morphotype. The newly acquired data showed that the mantle patterns in Ovulidae, which were thought to be diagnostic at species level, are not indicative in case of the *Cyphoma* species. Morphological results from earlier studies were in agreement with these results, and consequently the species' names *C. signatum* and *C. mcgintyi* are synonymised with *C. gibbosum*. The black morph (previously identified as *S. uniplicata*) should also be referred to as *C. gibbosum*. Three hypotheses were opted (rapid divergence, supergenes, and recent speciation) to explain the differences in the mantle colour pattern and the lack of molecular differentiation. In **chapter 3** an experimental approach was used to identify the bioactivity of the host corals of Ovulidae and Cryptochiridae (coral-dwelling crabs) to detect if bioactivity of host species is a possible trigger in symbiont speciation. A luminometer with light emitting *Aliivibrio fisheri* bacteria was used to investigate the bioactivity, by means of EC_{50}-values, for the host corals (stony corals [=Scleractinia] and octocorals). It showed that investigated octocorals were more bioactive than the examined scleractinians. Among the Octocorallia, studied species of the genera *Antillogorgia* and *Gorgonia* were the most bioactive and *Madracis auretenra* for the Scleractinia. When bioactivity values and the associated symbionts were plotted on the host cladograms, the most bioactive octocoral genera appeared to have most (two) symbionts. Host coral bioactivity is therefore most probably unrelated to the snail's host preference. In contrast, cryptochirid

crabs were not found on the most bioactive scleractinian, but were found in association with less bioactive coral hosts, implying that bioactivity might be an evolutionary driver. Speciation linked to host shifts, however, cannot be ruled out as the evolutionary mechanism.

In **Chapter 4** the phylogenetic relationships among five *Crenavolva* species are discussed. This chapter discussed the second record for the species *C. chiapponii* and concerned a sample from shallow water, whereas this species previously was considered to be restricted to deep water. This was also the first time that *Acanthogorgia* sp. was identified as its host species. The phylogenetic relationships of *C. chiapponii* with its congeners *C. aureola*, *C. striatula, C. tokuoi* and *C. trailli* were assessed based on two molecular markers (16S and COI) in combination with GenBank data available for two of the *Crenavolva* species. The phylogram showed that *C. chiapponii* did not genetically differ from *C. aureola*. This was supported by a lack of diagnostic morphological features separating these nominal species and therefore *C. chiapponii* was synonymised with *C. aureola*.

In the next chapter, **chapter 5**, a large-scale molecular data set was presented to investigate the traditional subfamily division within the family Ovulidae. It appeared that the subfamilies Aclyvolvinae and Simniinae are paraphyletic. Especially the species within the Aclyvolvinae (n = 8) have been troublesome in their identification; with a four-marker dataset (16S, COI, H3 and 28S) the phylogenetic relationships between these species was re-assessed. The type species of two of the three genera (*Hiatavolva depressa* and *Aclyvolva lanceolata*) did not cluster together with other species in these genera. *Hiatavolva depressa* was retrieved in the subfamily Prionovolvinae and did not cluster with its congeners. Instead, the congeners *H. rugosa* and *H. coarctata,* cluster with the type and other species of the genus *Aclyvolva* and were therefore moved to that genus. Molecular and morphometric results show that *A. lamyi* and *A. nicolamassierae* are synonyms of *A. lanceolata* and that *A. rugosa* (n. comb.) is a synonym of *A. coarctata* (n. comb.). The genus *Kuroshiovolva* could not be retrieved in a fixed phylogenetic position within the Aclyvolvinae, but did not cluster with *Hiatavolva depressa* or *Aclyvolva* spp. Its taxonomic position therefore remains uncertain. Photographs of type species are provided in this chapter, as well as new information on the geographical distribution and host species of Aclyvolvinae. In **chapter 6** an approach as in chapter 5 was used, but instead of ovulids the speciose octocoral family Melithaeidae - host to many ovulid species - was investigated. The taxonomic position of six genera (*Asperaxis*, *Acabaria*, *Clathraria*, *Melithaea*, *Mopsella*, *Wrightella*) divided over two subfamilies were reviewed and reassessed. Material collected from the Central Pacific, Red Sea and Indian Ocean (as far south as South Africa) was used for sequencing of four different loci, both mitochondrial (COI, mtMutS, ND6) and nuclear (28S rDNA). A combination of molecular and morphological data revealed that all former so-called genera, except for the monotypic genus *Asperaxis* and the genus *Wrightella,* are paraphyletic. Moreover, molecular data on the two subfamilies in the Melithaeidae (Asperaxinae and Melithaeinae) indicated that the family is also paraphyletic. Furthermore, it was observed that species did not cluster according to their present morphology-based classification, but instead clustered according to a biogeographical pattern. Melithaeid species from the Red Sea, Indian Ocean and Central Pacific, grouped each into well-supported clades related to their respective distribution ranges. Consequently, we did not find morphological or molecular phylogenetic support to maintain the generic names *Acabaria*, *Clathraria*, *Mopsella* and *Wrightella*. These names are synonymised with the oldest available generic name: *Melithaea*. As a result, six secondary homonyms originated and were renamed, viz. *Melithaea hendersoni* nom. nov., *Melithaea kukenthali* nom. nov., *Melithaea mcqueeni* nom. nov., *Melithaea shanni* nom. nov., *Melithaea thorpeae* nom. nov., and *Melithaea wrighti* nom. nov. Additionally, neotype specimens were selected for *Melithaea ochracea* to stabilize the genus *Melithaea*, and for *Acabaria rubra*. **Chapter 7** is the all-enfolding chapter in which all available data on the associations between Octocorallia and Ovulidae was combined to investigate coevolutionary scenarios on large molecular and host species association datasets. A tanglegram, identifying all known associations between Octocorallia and Ovulidae, was constructed and subsequently subjected to coevolutionary analyses in Jane 4 and CoRe-PA. To create the tanglegram, phylogeny reconstructions of the Ovulidae and Octocorallia were made, each based on four loci (16S, 28S, COI, H3 and 28S, igr-COI, mtMutS, ND6, respectively). Statistical tests show that the number of coevolutionary events was higher than expected by chance alone, thereby indicating a coevolutionary scenario between Octocorallia and Ovulidae. For a coevolutionary or cospeciation scenario the phylogenies are expected to be mirror images with identical branch lengths. To estimate these speciation times, molecular dating was carried out on the octocoral and ovulid datasets in BEAST2. Fossil data for the Octocorallia and Ovulidae was used to calibrate the nodes in their respective phylogeny reconstructions. The molecular clock analyses showed that diversification in the Octocorallia started before diversification in the Ovulidae (100-50 mya vs. 40-15 mya). Diversification in the Ovulidae corresponds with diversification of other gastropod groups from the Indo-Pacific, and is linked to the collision of the Australian plate with the southeast boundary of the Eurasian plate approximately 25 million years ago. This resulted in an increase in shallow-water areas, which possibly fostered the diversification of gastropods and zooxanthelate (octo)corals. The discrepancy between the diversification times excludes coevolution or cospeciation as evolutionary scenario. Most probably sequential evolution, where the host affects the symbiont but not vice versa, is the evolutionary scenario explaining the intrinsic association between Octocorallia and Ovulidae.