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General introduction and summary

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The central Indo-Pacific hosts the world's richest marine fauna. For this extraordinarily high level of biodiversity two main explanations can be given. (1) Most Indo-West Pacific species are widespread, with most distributions overlapping in the Indo-Malayan centre of maximum diversity. (2) Many species have complex symbiotic and parasitic relationships that may accelerate speciation and promote diversity.

Various questions still wait for answers, like for example: (1) Has speciation usually occurred in allopatry, so that the areas of overlap between sister taxa should be seen as a result of secondary range-shifts (related to the complex geological history of the area, with varying currents and water/land distributions related to plate tectonics and sea-level changes)? (2) How can gene flow be maintained over very long distances in putatively widespread species, whose pelagic larvae are supposed to be relatively short-lived? (3) Do complex symbiotic relationships among marine organisms lead to co-evolution, co-speciation, and hence elevated biodiversity?

These questions can only be answered when the species themselves are clearly diagnosed and when their phylogenetic relationships have been unraveled. In the present study, mushroom corals (Fungiidae) and their gastropod parasites (Epitoniidae and Coralliophilidae) were studied as model organisms to contribute to answering the more general research

questions. Morphological, ecological, molecular and distributional data were collected and analysed to be able to reach this goal. The primary results of this approach form the largest part of this thesis.

For my research on the evolutionary and ecological relationships between scleractinian corals (Fungiidae, Dendrophylliidae, Euphylliidae) and their gastropod symbionts (Coralliophilidae, Epitoniidae), about 800 hours were spent underwater with the help of SCUBA. Approximately 60,000 stony coral specimens were searched for endoparasitic and ectoparasitic snails in various parts of the Indo-West Pacific, i.e. coastal areas of Egypt (Red Sea), Maldives, Thailand, Malaysia, Japan, Palau, Philippines, Indonesia and Australia. At most localities the fieldwork lasted one week to a month. Additional periods of three and nine months (in 1997 and 2001, respectively) were spent in the Spermonde Archipelago, off Makassar, SW Sulawesi, Indonesia, which is situated in the centre of maximum diversity. The coral diversity here is among the highest in the world (fig. 1). The family of the mushroom corals (Fungiidae) was used as a model taxon for the study on host specificity in associated gastropods. A special effort was made to search all species within this family, in particular also the less commonly observed ones, which live in environments that are usually avoided by divers, such

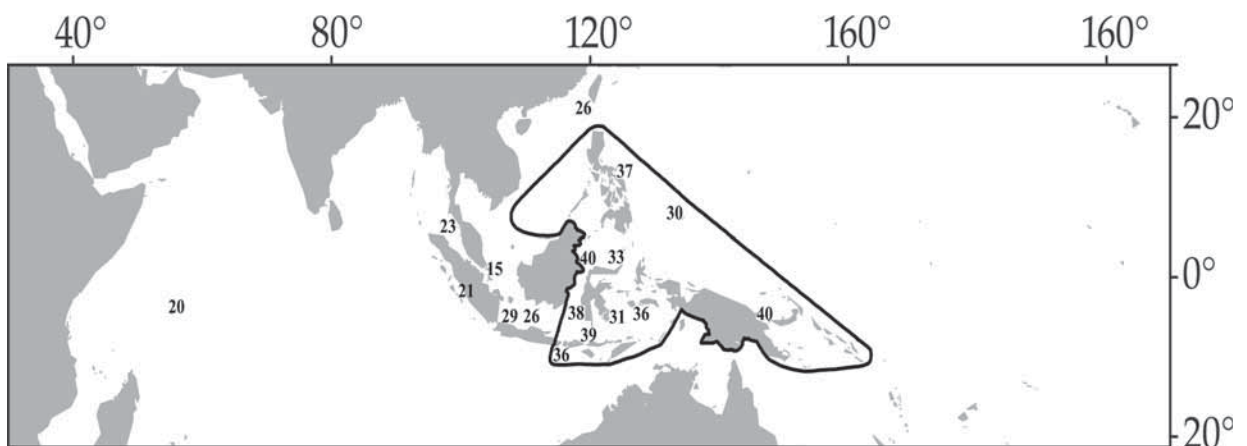


Fig. 1. The Indo-West Pacific, illustrating the numbers of Fungiidae in various areas that were intensively studied (Hoeksema, in press).

as sandy reef bases, shallow reef flats, areas with strong currents, or murky water.

During the study, in total about 1000 individual coralliophilid and 3000 epitoniid snails were found in association with the corals examined. For most of these coral infestations the locality, depth, micro-habitat, parasite species and host species were noted. Subsequently, the DNA of about 600 parasitic gastropods and mushroom corals was sequenced and used for phylogeny reconstructions. The genetic analyses made clear that both families of associated gastropods showed a surprisingly speciose, cryptic, adaptive radiation. There appeared to be many more endo- and ectoparasitic gastropod species associated with fungiid corals than previously thought on the basis of shell characters only. Furthermore, the associations between parasites and their host species are far more exclusive than hitherto perceived. In associations where parasitic species cannot unequivocally be identified on the basis of their shell morphology, molecular data (DNA sequences), host species preferences, and the structure of radulae and jaws, turned out to be much more useful in species distinctions.

The phylogeny reconstruction of the mushroom corals, based on molecular data, in general resembles the one based on morphological data (Hoeksema, 1989). The most conspicuous deviation is caused by a misleading case of convergent evolution, associated with a reversal to an ancestral character state (the loss of the ability to detach from the substrate).

A comparison between the phylogeny reconstructions of the fungiid corals, the epitoniids and the *Leptoconchus* species, respectively, indicates that the phylogenetic histories of these three species groups are clearly interlinked. For outgroup comparisons also epitoniids not associated with corals were collected in the field. The phylogenetic analyses indicate that the ancestors of the recent coral-associated wentletraps were parasites of sea-anemones and that a host shift from sea-anemones (Actiniaria) to hard corals (Scleractinia) has occurred only once in their evolutionary history, since the coral-associated epitoniids form a monophyletic group.

Abstracts

Chapter 2

Phenotypic plasticity revealed by molecular studies on reef corals of *Fungia* (*Cycloseris*) spp. (Scleractinia: Fungiidae) near river outlets

On a patch reef off Makassar, Sulawesi, Indonesia, corals identified as *Fungia* (*Cycloseris*) *costulata*, *Fungia* (*Cycloseris*) *tenuis* and *Fungia* (*Cycloseris*) cf. *costulata* were collected, down to a maximum depth of 10 m. The corals lived sympatrically. Mushroom coral clones resulting from fragmentation can easily be recognized by their equal coloration and close proximity. Therefore, to ensure that no clones were collected, corals of dissimilar colors were selected at a mutual distance of 5 m. The corals were kept alive in two 30-liter sea-water aquariums with an air-pump. They were photographed in detail. Using allozyme electrophoresis in a laboratory close to the field area, it was tested whether the three coral morphs should be considered separate species. Eventually it was concluded that there are only two species involved, i.e. *F. (C.) costulata* and *F. (C.) tenuis*, of which *F. (C.) costulata* has two distinct morphs, one of which may be an eco-phenotype occurring on reefs off river outlets or inside estuaries.

Chapter 3

A molecular analysis of the evolutionary history of mushroom corals (Scleractinia: Fungiidae) and its consequences for taxonomic classification

DNA samples from fungiid corals were used to reconstruct the phylogeny of the Fungiidae (Scleractinia). In some cases the coral DNA was isolated and sequenced from the parasitic gastropods that were eating these corals, by using fungiid-specific primers. The molecular phylogeny reconstruction is similar to the morphology-based one, except for some differences that are probably caused by parallel or convergent evolution. Most fungiid corals are fixed to the substrate in a young stage to break loose afterwards. Apparently, the loss of this ability to become unattached, induced similar reversals independently in two fungiid species. As a consequence, these were both placed in the genus *Lithophyllon* by Hoeksema

(1989). However, the molecular analysis indicates that these species are not even closely related. Another discrepancy is formed by the separate positions of *Ctenactis crassa*, away from its congeners, in the various cladograms. This may have been caused by one or more bottleneck events in the evolutionary history of that species, which resulted in much faster average DNA mutation rate as compared to the other fungiid species. It turned out that excluding intraspecifically variable base positions from molecular data sets may improve the resulting phylogeny reconstruction, lowering the number of most parsimonious trees and indicating phylogenies that more closely resemble those suggested by morphology. In rare cases, however, this loss of data had a negative effect. Therefore, the hypotheses about the evolutionary history of the fungiid corals are based on analyses of both the data sets with and without intra-specific variation.

Chapter 4

A largely cryptic, adaptive radiation of parasitic snails: sibling species in *Leptoconchus* (Gastropoda: Caenogastropoda: Coralliophilidae) associated with specific coral hosts (Scleractinia: Fungiidae)

A cryptic, adaptive radiation of 16 coralliophilid species, provisionally classified here with *Leptoconchus*, is unravelled. Up to eight species were found sympatrically in the same geographic area, but associated with different scleractinian host species. They are described mainly on the basis of molecular and habitat (host preference) data since most species so far cannot be identified on the basis of their shells or anatomical characters. The species have large ranges throughout the Indo-West Pacific, obviously depending on the distribution of their associated host coral species.

Chapter 5

***Epitonium* (Gastropoda: Epitoniidae) associated with mushroom corals (Scleractinia: Fungiidae) from Sulawesi, Indonesia, with the description of four new species**

From off Ujung Pandang (= Makassar), Sulawesi, Indonesia, at least six sympatric, epitoniid species

are reported that are associated with mushroom corals. Four of these wentletrap species were described as new to science. The status of three more, nominal *Epitonium* species is clarified.

Chapter 6

The wentletrap *Epitonium hartogi* spec. nov. (Gastropoda: Epitoniidae), associated with bubble coral species, *Plerogyra* spec. (Scleractinia: Euphylliidae), off Indonesia and Thailand

For a majority of epitoniid snails, only conchological data are known. In the description of *Epitonium hartogi*, a species associated with bubble corals (Scleractinia: Euphylliidae: *Plerogyra* spec.), many more details of promising other characters are added in an attempt to create a new standard for diagnoses in epitoniids. The structure of the opercula, the radulae and the jaws, studied with a SEM, contains diagnostic elements that hitherto have been neglected. To enable comparisons at a higher taxonomic level, the ontogenetic development within the egg is also described.

Chapter 7

A hitherto unnoticed adaptive radiation: epitoniid species (Gastropoda: Epitoniidae) associated with corals (Scleractinia)

Twenty-two epitoniid species that live associated with various hard coral species are described. *Epidendrium* gen. nov., *Epifungium* gen. nov., and *Surrepifungium* gen. nov., and ten species, are described as new to science. Although their identities as separate gene pools are convincingly demonstrated by molecular data, some of these species cannot be identified unequivocally on the basis of conchological characters only. Shell shape and sculpture are only partially diagnostic because of interspecifically overlapping character states. However, the morphology of the operculum, the jaw, the radula, and the spawn and/or the habitat make clear that separate species are involved. Most of these species are associated with only one or a restricted number of coral host species, and have large ranges, similar to those of their hosts.

Chapter 8

A molecular phylogeny of Epitoniidae (Mollusca: Gastropoda), focusing on the species associated with corals

Since 2000, 18 epitoniid species that were found in association with corals have been described as new to science in addition to only four such species that were already known. Together, these species belong to four genera, three of which were also described as new. Most of these taxa can only be diagnosed by their host preference and by the morphology of the radulae, jaws, opercula and egg-capsules. By use of an original molecular data set, it is demonstrated that these data support the existence of the recently described, coral-associated species as separate gene pools and the alleged genera as monophyletic groups. The nominal genus *Epitonium*, as it shows up in most of the recent literature, turns out to be polyphyletic. To some extent, co-evolution has played a role in the evolutionary history of the associations between wentletraps and their coelenterate hosts.

Chapter 9

Habitat preferences of 20 Indo-West Pacific wentletrap species (Gastropoda: Epitoniidae) associated with scleractinian corals

Based on observations of about 60,000 corals and their infestation by epitoniid snails, several distinctly different life strategies of these wentletraps in the Indo-West Pacific are described. The 20 gastropod species that were found to be coral-associated are either generalists or specialists. They differed also in their position relative to their hosts and in preferences for substrate and host size. No preferences for depth were found. The infestation rates are negatively correlated with the coral densities, which may indicate that epitoniid veligers actively search for their preferential hosts. Burrowing shrimps living underneath a mushroom coral, may eat or at least remove any epitoniid that they come across. Fishes, like wrasses and damselfishes, were seen speeding towards epitoniids to eat them, the very moment that they were artificially exposed by turning the fungiid coral-disc upside down.

