# Evolutionary trends in onshore-offshore distribution patterns of mushroom coral species (Scleractinia: Fungiidae)

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## Abstract

A phylogenetically based comparative analysis of onshore-offshore distribution patterns of mushroom coral species (Scleractinia: Fungiidae) was made to reconstruct an evolutionary scenario for differentiation in fungiid shelf habitats. This phyloecological study integrates data on fungiid distribution patterns along environmental gradients on the Spermonde Shelf, SW Sulawesi, with a recently published phylogeny reconstruction of the Fungiidae. A mushroom coral fauna of 34 species was used to compare their distributions by use of 50-m$^2$ belt quadrats in transects (1) from the mainland to the shelf edge, (2) around reefs with regard to predominant wind directions, and (3) over bathymetrical reef zones. Species association ordinations were made for each of the four shelf zones using both abundance and incidence data to examine whether closely related species co-occurred. Some closely related species or even sister species appeared to show very similar distribution patterns and to co-exist in high abundances. These results indicate that there may not be community saturation and competitive exclusion among mushroom corals species, most of which are free-living. In reconstructions of fungiid habitat evolution, offshore reef slopes appear to be original (ancestral), whereas onshore habitats, shallow reef flats, and deep sandy reef bases seem to be derived. The latter is in contrast with an earlier hypothesis, in which deep sandy substrates were considered ancestral mushroom coral habitats.

## Contents

## Introduction

Most studies on biotic changes of marine faunas along onshore-offshore gradients concern the evolution and extinction of taxa as represented in the fossil record. The general scenario is that marine faunas in the Phanerozoic originated in shallow coastal seas and expanded from there into deep offshore ecosystems, but also that some of the younger lineages may have originated in less stable nearshore environments (Jablonski and Valentine, 1981; Jablonski et al., 1983; Valentine and Jablonski, 1983; Jablonski and Bottjer, 1988, 1990; Sepkoski, 1991; Jacobs and Lindberg, 1998). With an increasing availability of phylogeny reconstructions based on molecular methods it is also possible to use recent taxa in studies on evolutionary trends in habitat preferences. Only few examples are known from the marine realm. For instance, Lindner et al. (2008) found that recent stylasterid corals (Hydrozoa: Stylasteridae), the second largest group of hard corals, evolved mainly in the deep sea, and invaded shallow waters from there.

Studies of onshore-offshore distribution patterns of recent coral reef species usually concern shallow, tropical shelf seas, with various examples known from the Great Barrier Reef (Done, 1982; Williams, 1982; Dinesen, 1983; Williams and Hatcher, 1983; Russ, 1984; Wilkinson and Trott, 1985; Preston and Doherty, 1990, 1994; DeVantier et al., 2006) and the

Spermonde Archipelago in southwest Sulawesi (Moll, 1983; de Beer, 1990; Hoeksema, 1990, 2012; Verheij and Prud'homme van Reine, 1993; Troelstra *et al*., 1996; de Voogd *et al*., 1999, 2006; Renema *et al*., 2001; Cleary *et al*., 2005; Becking *et al*., 2006; Cleary and de Voogd, 2007; Hoeksema and Crowther, 2011). To study the evolutionary history of cross-shelf distribution patterns, it would be ideal to use a phylogenetic ecological model in which detailed information on onshore-offshore distributions can be combined with a phylogeny reconstruction of a monophyletic species group abundantly represented in various shelf habitats.

A recent molecular phylogenetic study of 50 mushroom coral species (Scleractinia: Fungiidae) has be-

come available, which enabled an evolutionary study of their life history traits (Gittenberger *et al*., 2011) and their associated fauna (Hoeksema *et al*., 2012). In addition, field data on the cross-shelf bathymetric distribution patterns of 34 mushroom coral species were obtained on the Spermonde shelf (Hoeksema, 2012). Use of their phylogenetic relations may help to clarify the evolution of their habitat preferences along environmental gradients, like depth (reflected in reef zonation) and increasing distance from the mainland in a direction from onshore to offshore.

Mushroom corals are suitable for such studies because most species have an adult free-living (anthocyathus) phase in their life history (Wells, 1966;
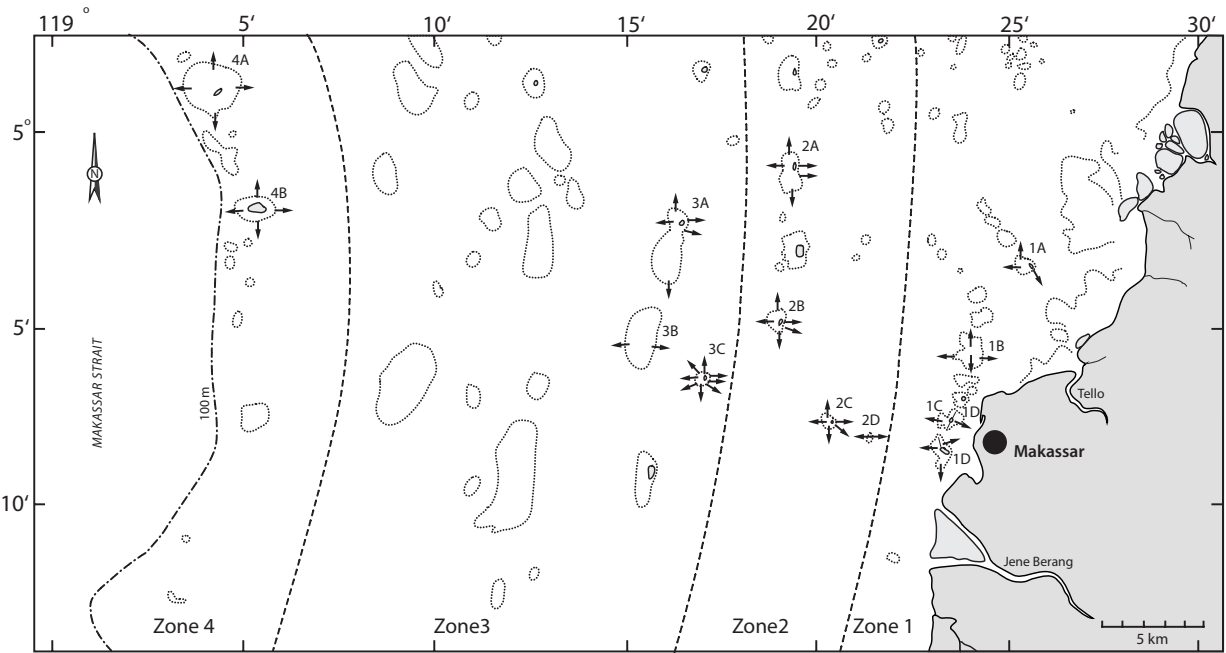


*Fig. 1.* The locations of 52 transects around coral reefs in four zones on the central section of the Spermonde Shelf where mushroom coral abundances were measured. The names of the reefs are listed in Table 1. After Hoeksema (2012).
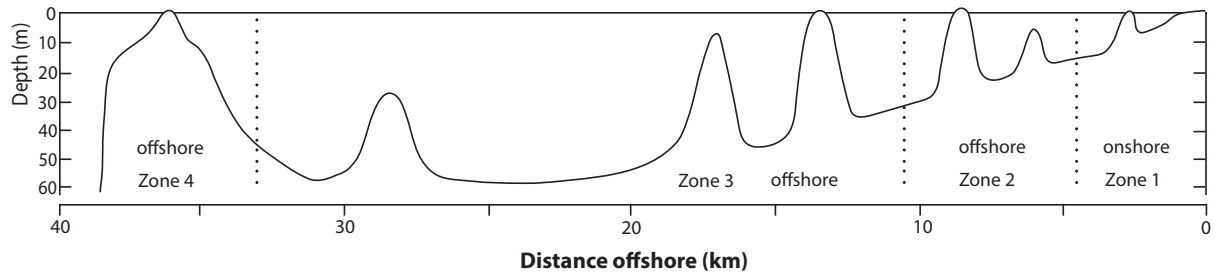


*Fig. 2.* Schematic cross-section of the central Spermonde Shelf (approximately W-E) from the Makassar Strait to the mainland. After Hoeksema (2012).

Hoeksema, 1989), which enables them to inhabit various kinds of substrata, including sandy reef bases (Goreau and Yonge, 1968; Fisk, 1983; Chadwick, 1988; Hoeksema 1988, 2012; Chadwick-Furman and Loya, 1992). Initially, mushroom corals are attached to a hard substratum, but individuals of free-living species eventually detach themselves (Yamashiro and Yamazato, 1987a, b, 1996; Hoeksema, 1989; Hoeksema and Yeemin, 2011). About 20% of all mushroom coral species remain attached after settlement on a solid substrate. They belong to the genera *Cantharellus* (n=3), *Cycloseris* (n=3), *Lithophyllon* (n=2), and *Podabacia* (n=4) (see Hoeksema, 1989, 1993a, 2009; Benzoni *et al*., 2012).

Mushroom corals usually occur in mixed multi-species assemblages (Pichon, 1974; Claereboudt, 1988; Hoeksema and Moka, 1989; Hoeksema 1991b, 2012; Latypov, 2007; Elahi, 2008; Hoeksema and Koh, 2009; Hoeksema and Matthews, 2011). High concentrations of mushroom corals can be the result of either sexual or asexual reproduction (Nishihira and Poung-In, 1989; Yamashiro *et al*., 1989; Krupp *et al*., 1992; Kramarsky-Winter and Loya, 1996; Littler *et al*., 1997; Colley *et al*. 2002; Gilmour 2002, 2004; Hoeksema, 2004; Knittweis *et al*., 2009a; Hoeksema and Gittenberger, 2010; Hoeksema and Waheed, 2011; Hoeksema and Yeemin, 2011). Asexual reproduction strategies are applied by various mushroom coral species on the Spermonde shelf (Hoeksema, 2012).

Data on onshore-offshore distribution patterns within a monophyletic group of sympatrically occurring marine species is rarely available, usually because of identification problems. Therefore a taxonomic revision of the scleractinian mushroom coral family Fungiidae (Hoeksema, 1989), a recent phylogenetic analysis (Gittenberger *et al*., 2011), and a descriptive study of their cross-shelf distributions in the Spermonde Archipelago (Hoeksema, 2012), make them ideal as a model group for a study on the evolution of distribution patterns along onshore-offshore environmental gradients, as reflected in reef zonation (depth) and onshore-offshore distribution patterns.

Based on their (poorly studied) fossil record, small size, simple morphology, and wide geographic range it was assumed that the earliest members of the Fungiidae were *Cycloseris* species, which were known to live on shallow reefs and on sandy bottoms down to about 120 m deep (Wells, 1966). Other genera were considered as derived. The present study, which is based on recent information regarding the phylogeny and ecology of the Fungiidae, will examine whether these habitats could indeed have been representative for the earliest mushroom corals.

## Material and methods

*Study area*

Mushroom coral distribution patterns were studied on the central part of the Spermonde Shelf, off southwest Sulawesi in the southern Makassar Strait, which bears a large group of cay-crowned reefs and shoals known as the Spermonde Archipelago (Fig. 1). The reefs are arranged in parallel rows in N-S direction, in between the coastline of SW Sulawesi and the outer barrier reef, which is situated about 40 km from the mainland in the study area (Hoeksema, 1990, 2012). The shelf can be divided into four zones from the coastline to the westward shelf edge (Figs 1-2). Zone 1 is 5 km wide where the sea floor reaches a maximum depth of 20 m. Zone 2 ranges 5-12.5 km away from the coastline, where the depth of the sea floor varies approximately between 20 and 30 m. Zone 3 is 12.5 to 30 km offshore with a sea floor at 30-50 m depth and many submarine shoals and some reefs that are crowned by sand cays. Zone 4 is the outer rim, which includes the barrier reef, ranging 30 to 40 km away from the shoreline. To the east, the depth reaches 40-50 m, while to the west the submarine contours drop immediately to below 100 m. Some of the reefs on the ridge following the outer shelf edge have islets on top of them.

*Data sampling*

The survey was conducted in 1984-1986 on 13 reefs by snorkeling and SCUBA diving (Hoeksema, 2012). The abundance data of 34 fungiid species was recorded around 13 reefs in the four shelf zones (Tables 1-2). Since the mushroom coral fauna in onshore zone 1 differed distinctly from those of the other three zones (Table 2; Hoeksema, 2012: Fig. 11), corals observed in this particular zone were classified as having an Onshore (On) range, while those in zones 2-4 were categorized as Offshore (Off).

To compare mushroom coral distributions with wind speed frequencies, transect sites were selected around each of the 13 reefs, mainly at the N, W, S and E side in 565 belt quadrats (50×1 m²) over 52 transects (Table 1). If eastward reef sides were generally sandy with little coral cover, additional transects at the ESE or SE were selected in shelf zones 2 and 3.

*Table 1.* List of 13 reefs in four reef zones on the Spermonde Shelf with the position of 52 transects (Fig 1). In each transect mushroom coral abundances were recorded in 50-m2 belt transects with 3 m depth intervals down to the maximum depth where mushroom corals occurred or where the bottom became horizontal.

| Shelf Zone | Reef | Transect direction with maximum depth (m) | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | N | NW | W | SW | S | SE | ESE | E |
| Zone 1 | A. Barang Baringang | 6 | - | 9 | - | - | - | 9 | - |
| | B. Gusung Trabanusu | 9 | - | 15 | - | 15 | - | - | 9 |
| | C. Lae-Lae Keke | - | - | 12 | - | - | - | - | 9 |
| | D. Lae-Lae | - | - | 12 | - | 12 | - | - | 9 |
| Zone 2 | A. Bone Batang | 30 | - | 24 | - | 24 | - | 21 | 24 |
| | B. Barang Caddi | 24 | - | 24 | - | 24 | - | 21 | 27 |
| | C. Samalona | 21 | - | 24 | - | 24 | - | 18 | 24 |
| | D. Bone Baku | - | - | 21 | - | - | - | - | 18 |
| Zone 3 | A. Bone Tambung | 36 | - | 36 | - | 36 | - | 36 | 33 |
| | B. Kapodasang | - | - | 33 | - | - | - | - | 27 |
| | C. Kudingareng Keke | 30 | 30 | 30 | 33 | 36 | 24 | 24 | 24 |
| Zone 4 | A. Lanyukang | 6 | - | 24 | - | 15 | - | - | 18 |
| | B. Langkai | 6 | - | 18 | - | 18 | - | - | 30 |

In each transect, species abundances were measured at various depths. On the reef flats, mushroom coral inventories were conducted at 3 m depth and at 5, 10, 20 and 50 m distance away from the 3 m isobaths in the direction of the reef centre, where the depths were ca. 2.5, 2, 1.5 and 1 m, respectively. On reef slopes and reef bases, inventories were made at 3 m depth intervals, from 6 m deep down to the depth where the bottom became horizontal or no mushroom corals were encountered anymore, which was 39 m deep in the third shelf zone, meaning that depths over 36 m were not included. Northward and southward reef bases in shelf zone 4 were generally shallow as they were based on the barrier, which is mostly covered by fine sand on its top.

For each transect, three reef zones were distinguished, *i.e.*, the reef flat, the reef slope and the reef base (Hoeksema, 2012). The bottom inclination on the reef flats was < 15° and the substratum consisted predominantly of coral and rubble, except for the sandy E sides. The bottom inclination of the reef slopes usually varied between 15° and 45° and the substratum consisted mostly of hard coral. Some westward slopes were partly covered by rubble and most eastward slopes consisted entirely of sand. At the reef base, the inclination was also < 15° and the sea-floor itself consisted of sand or silt and contained little coral cover.

Descriptions of the recorded species (Table 2) are given by Hoeksema (1989) and their updated classification by Gittenberger *et al*. (2011). Corals that could not be identified in situ were collected for further examination and were deposited in the collection (RMNH Coel.) of Naturalis. Two fungiid species were present in the Spermonde Archipelago but they were not clas-

sified as such during the fieldwork, *i.e.*, the encrusting species *Cycloseris explanulata* (van der Horst, 1922), and *C. wellsi* (Veron and Pichon, 1980). Although their position in the Fungiidae was recognized and corrected recently Benzoni *et al*. (2007, 2012), they could not be included in the present analysis without proper distribution data.

Many of the Spermonde reefs are inhabited by people and are situated in close proximity of the capital of South Sulawesi, Makassar, which may have impact on the coral populations here (Knittweis *et al*., 2009b; Knittweis and Wolff, 2010; Ferse *et al*., 2012, in press). Since the survey was conducted in 1984-1986, the distributions may have changed over time due to human impact (Hoeksema and Koh, 2009; van der Meij *et al*., 2010; Hoeksema *et al*., 2011). For the present study such changes are not considered relevant.

*Phylogeny reconstruction*

The cladogram used as basis for the reconstruction of a phylo-ecological scenario involving mushroom corals present in the Spermonde Archipelago has been presented by Gittenberger *et al*. (2011: Fig. 9), for which DNA-samples of mushroom corals were collected at various Indo-Pacific regions. Soft tissue samples were removed from the corals for amplification of the ITS (Internal Transcribed Spacers I & II) and a part (from the 3'-end) of the COI (Cytochrome Oxidase I) regions, for which Fungiid DNA-specific COI primers were made. The COI and ITS sequences were aligned with ClustalW Multiple alignment by use of BioEdit 7.0.1, for which default parameters were used (Hall, 1999). The COI data set consisted of 63 sequences of

*Table 2*. Presence (1) absence (0) data of 34 fungiid species recorded in four parallel shelf zones of the Spermonde Archipelago. The shelf zones were oriented in N-S direction, parallel to the coastline. The onshore-offshore distribution (On-Off) is indicated as well as the predominant reef zonation (F = Flat, S = Slope, B = Base). Numbers of individuals per species are indicated (n) as well as the abundance ranking of each species from most common to most rare (1-34).

| Species | Zone | | | | Onshore-offshore | Reef zone | n | Abundance rank |
|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | | | | |
| 01. *Ctenactis albitentaculata* Hoeksema, 1989 | 0 | 1 | 1 | 1 | -Off | - S - | 66 | 27 |
| 02. *Ctenactis crassa* (Dana, 1846) | 0 | 1 | 1 | 1 | -Off | - S - | 159 | 23 |
| 03. *Ctenactis echinata* (Pallas, 1766) | 1 | 1 | 1 | 1 | On-Off | FS - | 1509 | 5 |
| 04. *Cycloseris costulata* (Ortmann, 1889) | 1 | 1 | 1 | 1 | On-Off | - SB | 1051 | 10 |
| 05. *Cycloseris cyclolites* (Lamarck, 1816) | 0 | 1 | 1 | 0 | -Off | - SB | 17 | 31 |
| 06. *Cycloseris distorta* (Michelin, 1842) | 0 | 0 | 1 | 0 | -Off | - S - | 1 | 34 |
| 07. *Cycloseris fragilis* (Alcock, 1893) | 0 | 1 | 1 | 1 | -Off | - SB | 424 | 17 |
| 08. *Cycloseris mokai* (Hoeksema, 1989) | 0 | 1 | 1 | 1 | --Off | - S - | 254 | 21 |
| 09. *Cycloseris sinensis* (Milne Edwards and Haime, 1851) | 0 | 1 | 1 | 1 | -Off | - SB | 471 | 16 |
| 10. *Cycloseris somervillei* (Gardiner, 1909) | 0 | 1 | 1 | 1 | -Off | - - B | 38 | 30 |
| 11. *Cycloseris tenuis* (Dana, 1846) | 0 | 1 | 1 | 1 | -Off | - S - | 938 | 11 |
| 12. *Cycloseris vaughani* (Boschma, 1923) | 0 | 1 | 1 | 1 | -Off | - - B | 46 | 29 |
| 13. *Danafungia horrida* (Dana, 1846) | 1 | 1 | 1 | 1 | On-Off | FS - | 1256 | 9 |
| 14. *Danafungia scruposa* (Klunzinger, 1879) | 1 | 1 | 1 | 1 | On-Off | FS - | 1264 | 8 |
| 15. *Fungia fungites* (Linnaeus, 1758) | 1 | 1 | 1 | 1 | On-Off | FS - | 3909 | 2 |
| 16. *Halomitra pileus* (Linnaeus, 1758) | 0 | 1 | 1 | 1 | -Off | - S - | 151 | 24 |
| 17. *Heliofungia actiniformis* (Quoy and Gaimard, 1833) | 1 | 1 | 1 | 1 | On-Off | - S - | 342 | 19 |
| 18. *Heliofungia fralinae* (Nemenzo, 1955) | 0 | 1 | 1 | 1 | -Off | - S - | 625 | 13 |
| 19. *Herpolitha limax* (Esper, 1797) | 1 | 1 | 1 | 1 | On-Off | FS - | 1398 | 6 |
| 20. *Lithophyllon concinna* (Verrill, 1864) | 1 | 1 | 1 | 1 | On-Off | FS - | 2904 | 3 |
| 21. *Lithophyllon repanda* (Dana, 1846) | 1 | 1 | 1 | 1 | On-Off | FS - | 6588 | 1 |
| 22. *Lithophyllon scabra* (Döderlein, 1901) | 1 | 1 | 1 | 1 | On-Off | FS - | 556 | 15 |
| 23. *Lithophyllon spinifer* (Claereboudt and Hoeksema, 1987) | 0 | 0 | 1 | 0 | -Off | - SB | 2 | 33 |
| 24. *Lithophyllon undulatum* Rehberg, 1892 | 0 | 1 | 1 | 1 | -Off | - S - | 148 | 26 |
| 25. *Lobactis scutaria* (Lamarck, 1801) | 0 | 1 | 1 | 1 | -Off | FS - | 363 | 20 |
| 26. *Pleuractis granulosa* (Klunzinger, 1879) | 0 | 1 | 1 | 1 | -Off | - S - | 828 | 12 |
| 27. *Pleuractis gravis* (Nemenzo, 1955) | 0 | 1 | 1 | 1 | -Off | - S - | 254 | 22 |
| 28. *Pleuractis moluccensis* (Van der Horst, 1919) | 1 | 1 | 1 | 1 | On-Off | - SB | 1311 | 7 |
| 29. *Pleuractis paumotensis* (Stutchbury, 1833) | 1 | 1 | 1 | 1 | On-Off | FS - | 1907 | 4 |
| 30. *Podabacia crustacea* (Pallas, 1766) | 1 | 1 | 1 | 1 | On-Off | - S - | 150 | 25 |
| 31. *Polyphyllia talpina* (Lamarck, 1801) | 1 | 1 | 1 | 1 | On-Off | FS - | 421 | 18 |
| 32. *Sandalolitha dentata* Quelch, 1884 | 0 | 1 | 1 | 1 | -Off | - S - | 63 | 28 |
| 33. *Sandalolitha robusta* (Quelch, 1886) | 1 | 1 | 1 | 1 | On-Off | FS - | 558 | 14 |
| 34. *Zoopilus echinatus* Dana, 1846 | 0 | 0 | 1 | 0 | -Off | - S - | 7 | 32 |

500 bases each, not including any gaps or stop codons. The ITS data set consisted of 45 sequences with lengths varying between 604 and 618 bases. The phylogenetic analyses were performed on six data sets, *i.e.* the COI data set, the ITS data set and the combined COI+ITS data set, all of which with and without intraspecifically varying base positions. In all cases the consistency index of the most parsimonious trees was higher for the data set without the intraspecifically variable base positions, which resulted in less most parsimonious trees than the data sets with intraspecifi-

cally variable base positions included. The combined COI+ITS data set without intraspecific variation resulted in the lowest number of most parsimonious trees, *i.e.* 36 instead of 791 when intraspecific variation is included. Therefore the latter was selected as basis for the eventual phylogeny reconstruction. To fill in gaps concerning species not included in the molecular analysis, data from a morphology-based cladogram are used, which overall agrees much with the one based on molecular data (Hoeksema 1989, 1991a; Gittenberger *et al.*, 2011).

*Evolution of onshore-offshore and bathymetric distribution ranges*

The onshore-offshore and bathymetric distribution ranges of the mushroom coral species were projected onto a cladogram (phylogeny reconstruction) to explore how frequently invasion of a particular habitat by a species may have resulted from either 1) synapomorphy in a common lineage or 2) homoplasy (convergence), and also 3) whether there were reversals in ecological traits (cf. Hoeksema, 1991a; Gittenberger *et al*., 2011). Each species was assigned a cross-shelf and a reef zonation distribution type, as follows:

Cross-Shelf zonation: Onshore-offshore (On-Off) as derived from the commonly inherited Offshore (Off) only. Onshore (On) only was not observed.

Reef zonation: Flat - Slope (FS), Slope - Base (SB), or Base only (B) as derived from the commonly inherited Slope (S).

These characters were projected onto the cladogram of Gittenberger *et al*. (2011: Fig. 9), which differentiates between lineages with and without molecular support. When an entire clade is restricted to a particular ecological zone (cross-shelf or bathymetric), it may be assumed that it originated within that zone (Davis *et al*., 2005; Ricklefs, 2006).

*Species co-occurrences: cluster analyses of abundance and incidence data*

Multivariate analyses of both abundance and presence/absence data of mushroom coral species were conducted to determine the extent of their co-occurrences in the belt quadrats for each of the four shelf zones using the Plymouth Routines in Multivariate Ecological Research (PRIMER) version 6 software (Clarke and Warwick, 2001; Clarke and Gorley, 2006). Group-averaged hierarchical clustering dendograms were generated from Bray-Curtis resemblance matrices to show the degree of species co-existence. The Bray-Curtis similarity measure was used with regard to species abundance data (square root transformed) and incidence data (presence/absence). In the latter case the Bray-Curtis similarity index is equivalent to the Sorenson similarity index (Clarke and Gorley, 2006). Similarity profiles (SIMPROF) were derived from the dendogram to show significant groupings of the sites.

*Ordination of species co-occurrences*

To study to what degree mushroom coral species co-existed, the presence-absence data of the species in the 50-m$^2$ SUs (sample units = belt quadrats) were analyzed separately for each of the four shelf zones. For every zone, a data matrix was constructed in which the observed species were arranged in columns and the SUs containing fungiids in rows. The data of the four shelf zones were analyzed separately because the zones differ in the number and composition of species and in the number of SUs. An overall analysis of the shelf would be biased by the dominance of the zone with the highest number of SUs. Moreover, separate analyses enable interzonal comparisons of the interspecific affinities.

The R-mode analyses of the ecological species affinities are performed with SPASSOC (Ludwig and Reynolds, 1988), which gives a variance ratio test *VR* for each analysis, which suggests positive overall association when *VR* > 1 and negative net association when *VR* < 1. An accompanying test statistic *W* denotes whether deviations from 1 are significant (Schluter, 1984). Furthermore, the analysis indicates whether the association is positive or negative per species pair and a chi-square statistic is given, which highlights bias caused by a too low species representation. The chi-square is computed from a pair-wise species 2×2 contingency table, which is considered biased when any cell in the table has an expected frequency < 1 or if more than two of the cells have expected frequencies < 5 (Zar, 1974: 49). In case of a biased chi-quadrat value the Yates correction factor for continuity was employed. SPASSOC supplies three interspecific co-occurrence coefficients which serve as measures for the degree of association. In the present study Ochiai's (1957) index, IO, was selected because, compared to other indices it is little affected by the frequency of occurrence (Jackson *et al*., 1989), making interzonal comparisons of species associations more reliable.

Only significant associations, *i.e.* those with (corrected) chi-quadrats > 3.84, were admitted to the analyses. The IO-values representing positive and negative associations were arranged as symbols in trellis diagrams (Green, 1979). Species names listed in the upper right triangle have been reordered in the lower left triangle to achieve the greatest possible number of high similarity values nearest to the principal diagonal (McIntosh, 1978; Legendre and Legendre, 1983). Since each species is arranged next to its closest associates, the concentrations of high associations close to the diagonal resemble clusters. Arranged thus, the sum of the products of each IO-value by its distance to the diagonal (measured by the numbers of intermediate columns and rows) should be minimal. This can be

accomplished by manual pair-wise switching of rows and columns of two species that have neighbouring positions, which has to be continued in each newly re-ordered matrix. Eventually, convergence is obtained when for each species pair the column-row combination closest to the principal diagonal has the highest total of IO-values.

## Results

### Onshore-offshore distributions

Mushroom corals were abundant in multi species assemblages (>500 individuals per 50-m² belt quadrat) in shelf zones 1-3, whereas the highest number counted in zone 4 was only 195 (Hoeksema, 2012). Hence, proximity to the mainland and river outlets *per se* did not limit overall mushroom coral abundance. The highest mushroom coral concentrations were observed in W, N, NW, and SW transects, at the sides most strongly exposed to winds from the west, whereas fungiids were absent from several transects on east-ward reef slopes (E or ESE) with a sand cay nearby, from where sand can easily be transported over the reef flat (Hoeksema, 2012). In contrast, submerged reefs and reefs with breakwaters on their top had high mushroom densities in their eastward transects. Fungi-ids were absent from wide, wave-exposed westward reef flats in shelf zone 4, where storm-driven waves may prevent coral settlement.

Reefs in zone 3 had the greatest vertical ranges of mushroom coral presence, up to 36 m depth (Table 1). For the shallower-based reefs in shelf zones 2 and 1, mushroom corals extended down to 27 m and 15 m depth respectively. The sea floor in zone 1 (15 m) consisted of fine silt (without any life cover) and mushroom corals were only observed down the reef slope to 12 m depth. On zone 4 reefs, fungiids were often relatively sparse, probably because many of the reefs sit on top of a sandy bank (the barrier), but they extend deepest on the reefs of the western margin where the bottom merges into the Makassar Strait drop-off.

Based on detailed results presented earlier (Hoek-sema, 2012) distinction among species can be made with regard to their onshore-offshore distributions by their occurrence in the four reef zones (Table 2). Individuals of species only counted once in a zone were considered exceptional and not included, such as single specimens of *Cycloseris cyclolites*, *Lithophyllon undulatum* and *Lobactis scutaria* in zone 1. Among

the 34 fungiid species recorded in the belt quadrats, 19 were not recorded in zone 1 and were therefore categorized as species with a predominantly offshore distribution (Off), whereas 15 that were also present in zone 1 were categorized as having an onshore-offshore range (On-Off). Likewise, with regard to their bathymetric distributions (Hoeksema, 2012), the zonation patterns of the 34 species (see Table 2) were classified by their occurrence in the reef zones "flat" (F), "slope" (S), and "base" (B), as FS (n=12), S (n=14), SB (n=6), or B (n=2). Apparently there were no species with F or FSB ranges. Furthermore, the total numbers of specimens per species and, consequently, their order of abundance are indicated, with for instance *Lithophyllon repanda*, *Fungia fungites*, *L. concinna*, *Pleuractis paumotensis*, and *Ctenactis echinata* ranking as the five most common species, respectively (Table 2).

### Evolutionary trends in cross-shelf distributions

By plotting the onshore-offshore distribution ranges indicated in Table 2 on the phylogenetic model presented by Gittenberger *et al*. (2011) a scenario can be reconstructed in which evolutionary trends can be discerned (Fig. 3). Since all mushroom coral species on the Spermonde shelf had an offshore component, it is assumed that the common ancestor of the Fungiidae also occurred offshore (cf. Davis *et al*., 2005; Ricklefs, 2006). Offshore habitats remote from terrigenous impact are common on oceanic reefs and have always remained available during sea level fluctuations. In 12 species lineages (represented by 15 species) an on-shore component was found (Fig. 3). This indicates that an onshore-offshore shelf range (with a component of terrigenous impact) appeared to have evolved 12 times from a predominant offshore distribution only. *Herpolitha limax*, *Lithophyllon scabra*, and *Pleuractis paumotensis* were the only species showing their highest concentrations in shelf zone 1 (Hoeksema, 2012). Of these, *L. scabra* was the least abundant on the most offshore reefs in shelf zone 4, while it was a dominant species in some reef zones in shelf zone 1.

Nearly all mushroom coral species on the Spermonde shelf inhabited reef slopes or had sister species (phylogenetically most closely related) with a reef slope distribution. Therefore it is assumed that the common ancestor of the Fungiidae also inhabited reef slopes which, unlike reef flats, remained available during sea level fluctuations. The bathymetric range of nine species lineages (involving 10 species) included reef flats, suggesting that mushroom coral species
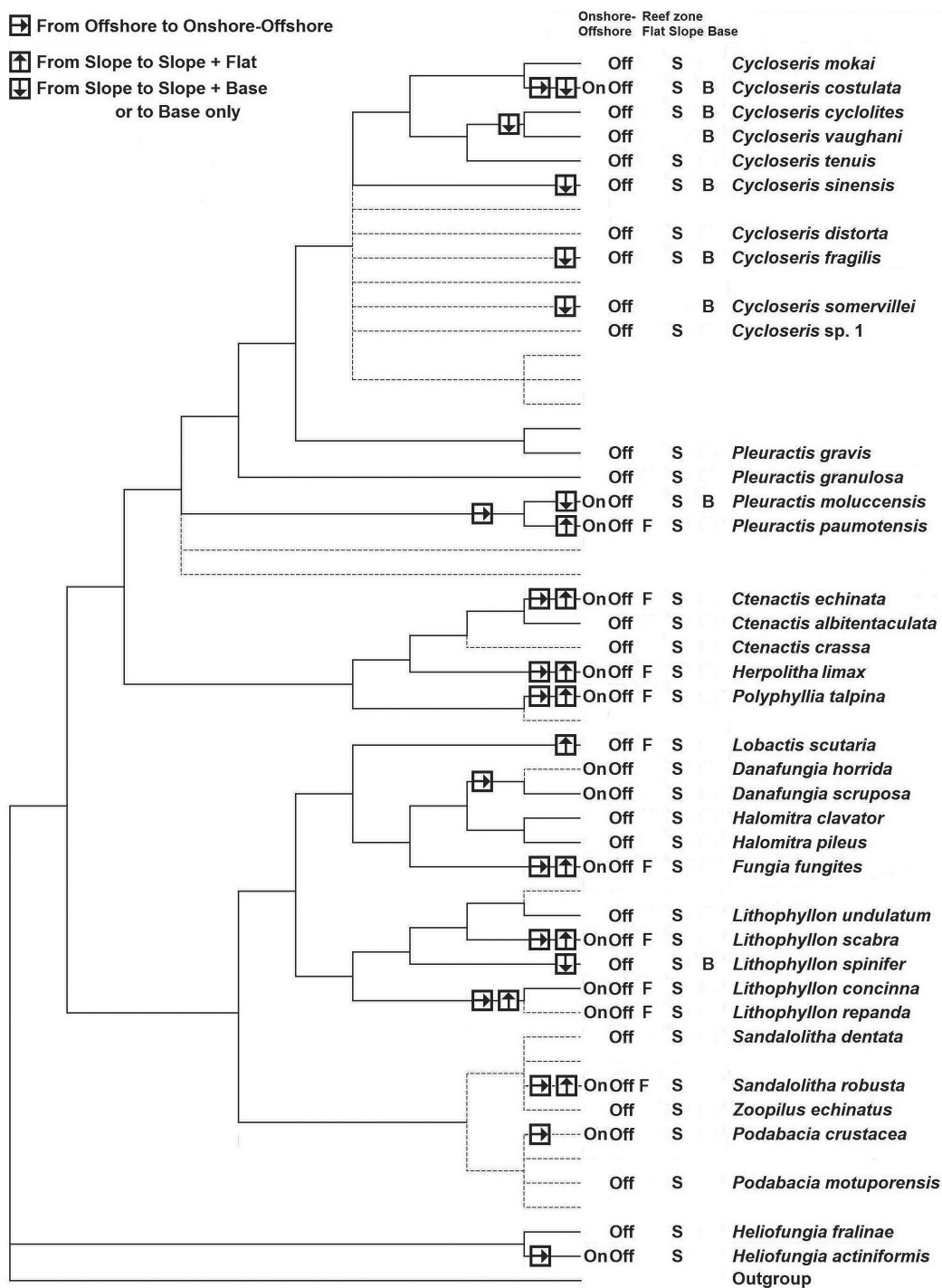
*Fig. 3.* Cladogram of the Fungiidae based on the phylogeny reconstruction by Gittenberger *et al.* (2011: Fig. 9). Species lineages represented by solid lines are supported by molecular analysis, while those that are not supported by the molecular analyses or have remained uncertain are indicated by a broken line. Cross-shelf distributions (onshore-offshore) and reef zonation distributions (indicated in Table 2) have been superimposed on the cladogram and are based on the sharing of these traits by the species within the species lineages. Their appearance in the phylogeny have been reconstructed accordingly: onshore-offshore (On-Off) as derived from offshore only (Off); reef flat - slope (F-S), reef slope - base (S-B), or reef base only (B) as derived from reef slope only (S).
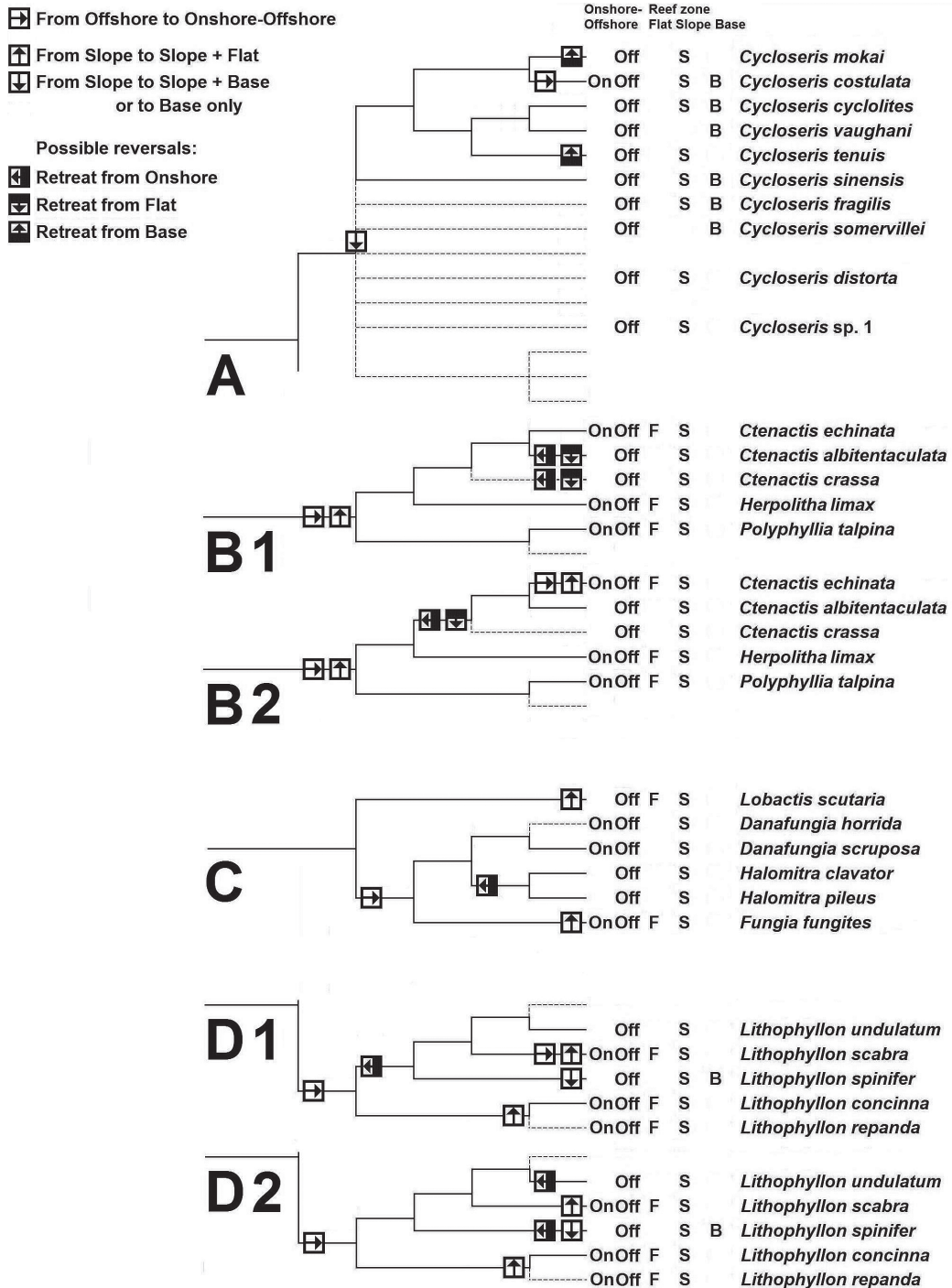
Fig. 4. Alternative evolutionary scenarios of cross-shelf distributions when three kinds of reversals are included: retreat from onshore, retreat from reef flats and retreat from reef bases. A. *Cycloseris* clade is more parsimonious: five reef base colonizations have been reduced to one but two retreats from reef bases have been added. B1-B2. *Ctenactis-Herpolitha-Polyphyllia* clade shows equal numbers of transformations (total six) if besides extensions to onshore habitats and colonization of reef flats also retreat from onshore reefs and reef flats are added. C. *Lobactis-Danafungia-Halomitra-Fungia* clade shows equal number of transformations (total four) if retreat from onshore reefs is added and an extension to onshore is not included. D1-D2. *Lithophyllon* clade shows one supernumerous transformation (six instead of five) if retreat from onshore is built-in and therefore this alternative is considered less plausible.
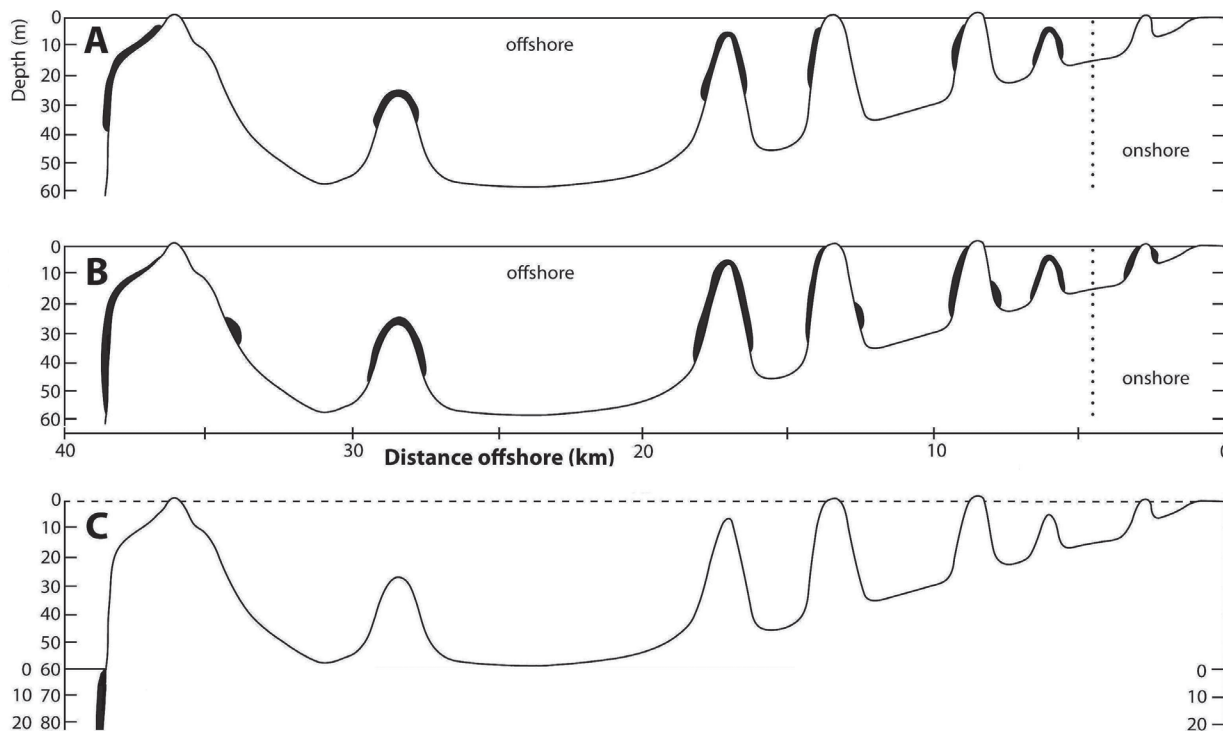
*Fig. 5.* Evolutionary scenario of mushroom coral habitats (marked by thick lines covering reefs) based on the Spermonde Shelf as a model area. A. Original situation in which mushroom corals and/or their ancestors inhabited offshore reef slopes, especially exposed ones. B. Present situation in which mushroom corals also inhabit nearshore reefs, shallow reef flats and deep, sandy reef bases. C. Past situations when the sea level was lower than the shelf during glacial periods and corals lived on fringing reefs that were not shelf-based and possibly more oceanic.

ranges in those lineages expanded from reef slopes into reef flats during periods when these flats were available (Fig. 3). Many of the most common species even showed most of their highest densities in shallow reef zones: *Ctenactis echinata*, *Fungia fungites*, *Herpolitha limax*, *Lithophyllon concinna*, *L. repanda*, *Pleuractis paumotensis*, *Polyphyllia talpina*, and *Sandalolitha robusta* (Hoeksema, 2012). On the other hand, in seven species lineages (involving eight species) reef bases were added to the bathymetrical distribution or even had replaced the reef slope (Fig. 3). The replacement concerns two separate lineages, each with one species, *i.e.*, *Cycloseris somervillei* and *C. vaughani*, both of which showed to be restricted to sandy substrates (Hoeksema, 2012).

Alternative scenarios concerning the evolution of cross-shelf distributions can be considered when three kinds of reversals are included: retreat from onshore, retreat from reef flats and retreat from reef bases (Fig. 4). The *Cycloseris* clade is more parsimonious by two transformations less by the inclusion of reversals: five

reef base colonizations have been reduced to one but two retreats from reef base have been added (Fig. 4A). The *Ctenactis-Herpolitha-Polyphyllia* clade shows equal numbers of transformations (total six) if besides extensions to onshore habitats and colonization of reef flats also retreats from onshore and reef flats are possible, which yields two extra scenarios (Fig. 4A-B). The *Lobactis-Danafungia-Halomitra-Fungia* clade shows equal number of transformations (total four) if retreat from onshore is added and one extension to onshore is excluded (Fig. 4C). The *Lithophyllon* clade shows one extra transformation (six instead of five) if retreat from onshore is built-in; this alternative is considered less parsimonious and therefore less likely (Fig. 4D).

All possible scenarios combined indicate that mushroom corals initially inhabited offshore reef slopes and most abundantly on exposed ones; see Hoeksema, 2012; Fig 5A) and from there evolved into onshore habitats and moved into either shallow or deep reef zones as in the present situation (Fig. 5B). How-

ever, when sealevels were much lower during glacial periods, they could only retreat to the steep outward reef slope on the barrier (Fig. 5C).

*Species co-occurrences based on abundance and incidence data*

Cluster analyses of abundance and incidence data for mushroom coral species recorded in zone 1 show remarkable patterns with regard to co-occurrence or differences among closely related species, especially when sister species pairs are indicated, *i.e.* species that are phylogenetically most closely related (Fig. 6). *Pleuractis gravis*, *Cycloseris cyclolites* and *Lobactis scutaria* were outliers that showed significantly different distribution patterns from the other species because they were rare in zone 1, each represented by a single specimen only (see Hoeksema, 2012):

Some pairs of sister species showed very similar distributions patterns, especially the very abundant species *Lithophyllon concinna* and *L. repanda* for both abundance and incidence data and *Danafungia horrida* and *D. scruposa* for abundance data (Fig. 6). These high similarities in species co-existence were not significant. The sister species *Pleuractis moluccensis* and *P. paumotensis* showed significantly different patterns.

The cluster analyses for species in zone 2 did not show outliers (Fig. 7). Again, *Lithophyllon concinna* and *L. repanda* clustered close together, indicating their very similar distributions, but not significantly. The sister species *Danafungia horrida* and *D. scruposa* clustered close together with regard to their incidence data. Other pairs of closely related species did not show much significant similarity in their distributions.

The cluster analyses for zone 3 showed three rare species that acted as outliers: *Lithophyllon spinifer*, *Cycloseris cyclolites*, and *Zoopilus echinatus* (Fig. 8). The sister species pairs *Lithophyllon concinna - L. repanda* and *Danafungia horrida - D. scruposa* showed much resemblance in abundance distributions. All four species grouped together with regard to incidence data. Other sister species pairs did not show such similarities.

Zone 4 distribution patterns (Fig. 9) showed one outlier among the clusters, *i.e. Cycloseris sinensis*, which occurred in a high abundance in a single belt quadrat all by itself (Hoeksema, 2012). *Danafungia horrida* and *D. scruposa* showed much similarity with regard to both their abundance and incidence distribution data, which cannot be said for other sister species pairs.

Overall it is remarkable that some pairs of sister species appear to show very similar cross-shelf distribution patterns by grouping closely together, although not significantly, in cluster analyses for most of the four shelf zones, especially with regard to the species pairs *Danafungia horrida - D. scruposa* and *Lithophyllon concinna - L. repanda*. Other sister species pairs, such as *Ctenactis albitentaculata – C. echinata*, *Heliofungia actiniformis – H. fralinae* and *Pleuractis moluccensis – P. paumotensis* were consistent by showing dissimilar distributions across all four shelf zones.

*Ordination of species co-occurrences*

The ordination of co-occurrence among species in trellis diagrams based on presence-absence data in the belt quadrats (SUs) for each shelf zone enables direct comparisons of all species directly with each other (Fig. 10). Samples of sister species pairs are indicated and show that within such pairs of very closely related species much overlapping in distribution patterns occurs.

On shelf zone 1, 19 species encountered in 69 SUs (see Hoeksema, 2012) showed 61 pair-wise combinations of significant co-occurrence and three of significant non-co-occurrence (Table 3, Fig. 10A). The highest IO-values (IO > 0.80) were found for the species pairs *Cycloseris cyclolites - Lobactis scutaria*, *Lithophyllon repanda - Ctenactis echinata*, and *Pleuractis paumotensis - Herpolitha limax*. The three species pairs representing negative associations (non-co-occurrence) were *Polyphyllia talpina - Ctenactis echinata*, *P. talpina - Fungia fungites*, and *P. talpina - Lithophyllon concinna*, which clustered along the left margin in the re-arranged diagram (Fig. 10A). Of these, species of the combination *Cycloseris cyclolites - Lobactis scutaria* were each represented by a single specimen co-occurring in the same SU. They did not show significant associations with any other species and therefore became ordered at the end of the sequence. Among the sister species pairs *Danafungia horrida - D. scruposa* (IO> 0.60), *Lithophyllon concinna - L. repanda* (IO> 0.40), and *Pleuractis moluccensis - P. paumotensis* (IO> 0.60) there were no high IO-values for co-occurrences (Fig. 10A).

On shelf zone 2, 31 fungiid species were encountered in 137 SUs containing Fungiidae (Hoeksema, 2012). In the analysis, 264 species pairs showed significantly positive associations and five significantly negative ones (Table 3, Fig. 10B). Thirteen species pairs involving ten species had IO-values > 0.80. *Lithophyllon repanda* and *Danafungia scruposa* were
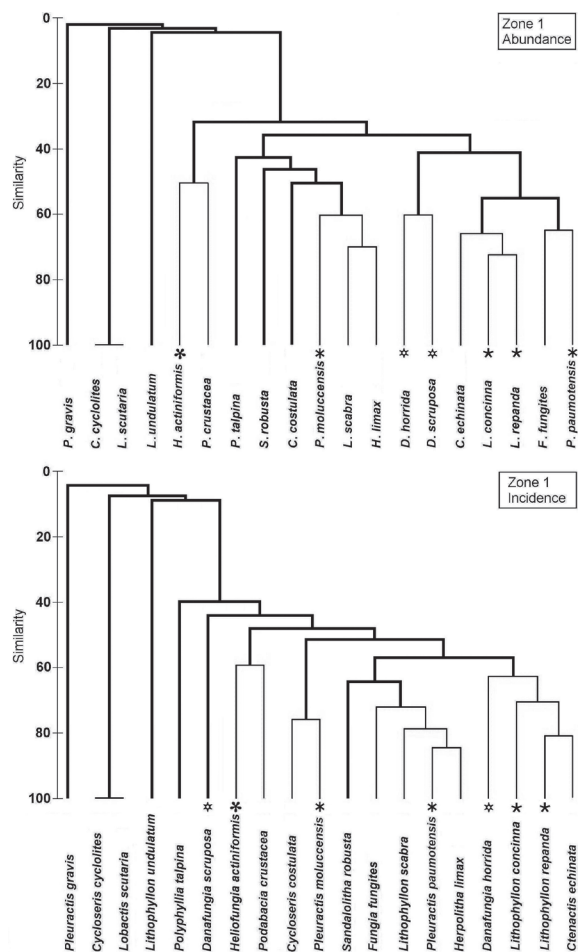
*Fig. 6.* Dendrogram (group average, Bray Curtis similarity) showing clustering of mushroom coral species recorded in belt quadrats in shelf zone 1 based on abundance data by square root transformation and incidence data (presence/absence). Bold lines: significant groupings based on similarity profiles (SIM-PROF). Starlike symbols indicate sister species pairs.

*Fig. 7.* As Fig. 6, but for shelf zone 2.

part of five and four of these pairs, respectively, while *Cycloseris tenuis*, *Danafungia horrida*, *Pleuractis paumotensis* and *Herpolitha limax* were combined in three of such pairs. *Fungia fungites* was highly associated with two species, whereas *Ctenactis echinata*, *Cycloseris costulata*, and *Lithophyllon concinna* were each highly associated with only one other species. The five negative associations involved *Fungia fungites* (2×), *Pleuractis moluccensis* (2×), *Lithophyllon repanda* (1x) and *Sandalolitha dentata* (1×), which in the re-arranged trellis diagram appeared in two columns at the left side (Fig. 10B). Each of the species was positively associated with at least one other. The
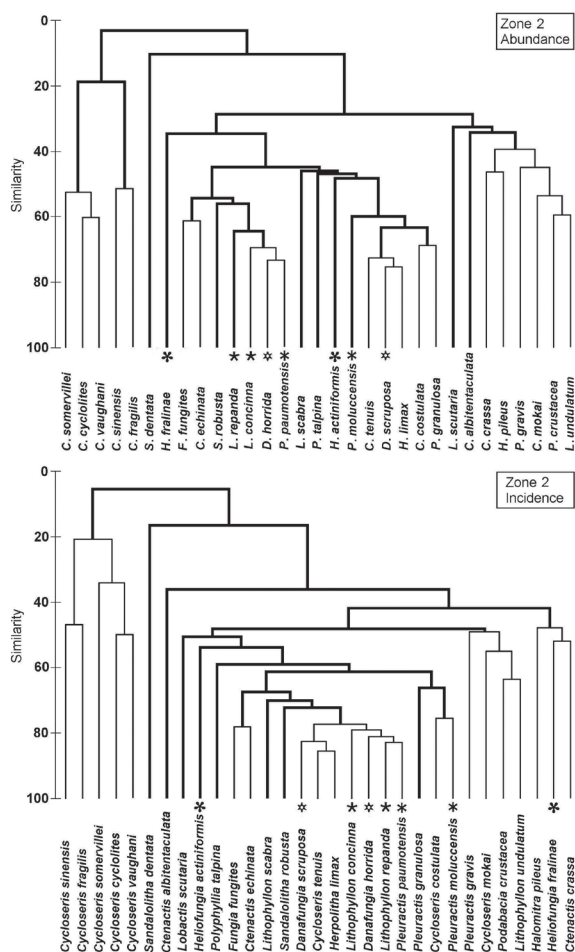
overall species association proved to be positive and highly significant (Table 3). Some sister species pairs showed high IO-values for co-occurrences: *Danafungia horrida - D. scruposa* (IO> 0.80) and *Lithophyllon concinna - L. repanda* (IO> 0.80). The latter became re-arranged close to each other in the trellis diagram (Fig. 10B). Other sister species pairs, such as *Heliofungia actiniformis – H. fralinae* (IO> 0.40) and *Pleuractis moluccensis - P. paumotensis* (IO> 0.50) showed little similarity in their distributions (Fig. 10B).

Shelf zone 3 had the highest species number, 34 in a total of 162 belt quadrats with fungiids (Hoeksema, 2012; Table 3). A total of 311 species pairs showed a significant positive association and 48 displayed a significant negative association (Fig. 10C). The analysis of zone 3 contained 13 species pairs with IO-values > 0.80, involving seven species: *Lithophyllon repanda*

*Fig. 8*. As Fig. 6, but for shelf zone 3.



*Fig. 9*. As Fig. 6, but for shelf zone 4.

(6×), *Herpolitha limax* (5×), *Danafungia scruposa* (4×), *Pleuractis paumotensis* (4×), *Lithophyllon concinna* (3×), *Danafungia horrida* (3×) and *Fungia fungites* (1×). In the negative associations four species were involved: *Cycloseris somervillei* (16×), *C. vaughani* (13×), *C. fragilis* (11×) and *C. sinensis* (6×). In the re-arranged diagram, the negative associations clustered in the left corner below (Fig. 10C). Due to their low abundance, *Cyclo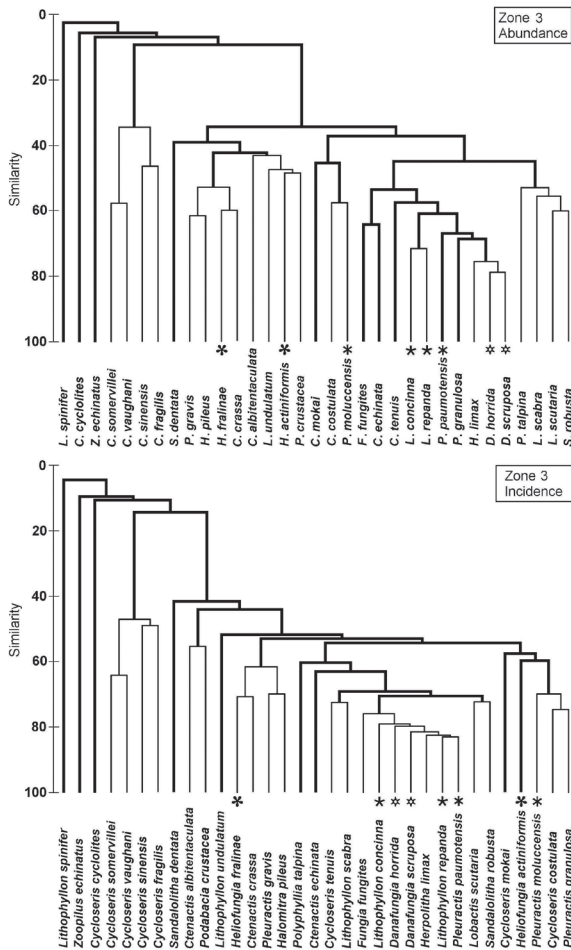seris distorta* and *C. cyclolites* showed no significant association with any other species. The net species association is positive (since *VR* > 1) and highly significant (Table 3).

The sister species pairs *Danafungia horrida - D. scruposa* (IO> 0.80) and *Lithophyllon concinna - L. repanda* (IO> 0.80) showed high IO-values for co-occurrences, and became re-arranged close to each other in the trellis diagram (Fig. 10C). Other sister species
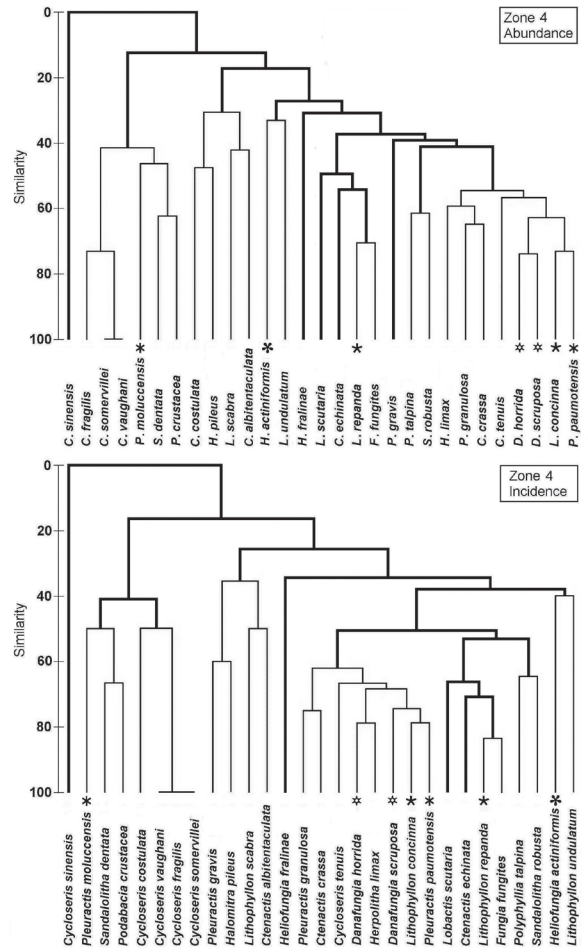
pairs, such as *Heliofungia actiniformis – H. fralinae* (IO> 0.50), showed little similarity in their distributions (Fig. 9-3). The pair *Pleuractis moluccensis - P. paumotensis* showed no significant association.

In shelf zone 4, 49 SUs contained fungiids, which belonged to 29 species (Table 3); 93 species pairs had significant positive associations, while no significant negative associations occurred (Fig. 10D). Ten species pairs showed high IO-values (>0.80), in which seven species were involved: *Cycloseris somervillei* (2×), *C. fragilis* (2×), *C. vaughani* (2×), *Lithophyllon repanda* (1×), *Danafungia horrida* (1×), *Fungia fungites* (1×) and *Herpolitha limax*. *C. sinensis* and *L. scabra* were less common and therefore showed no significant associations with other species. The overall species association was significantly positive (Table 3). The sister species pairs *Danafungia horrida - D. scruposa* (IO> 0.70) and
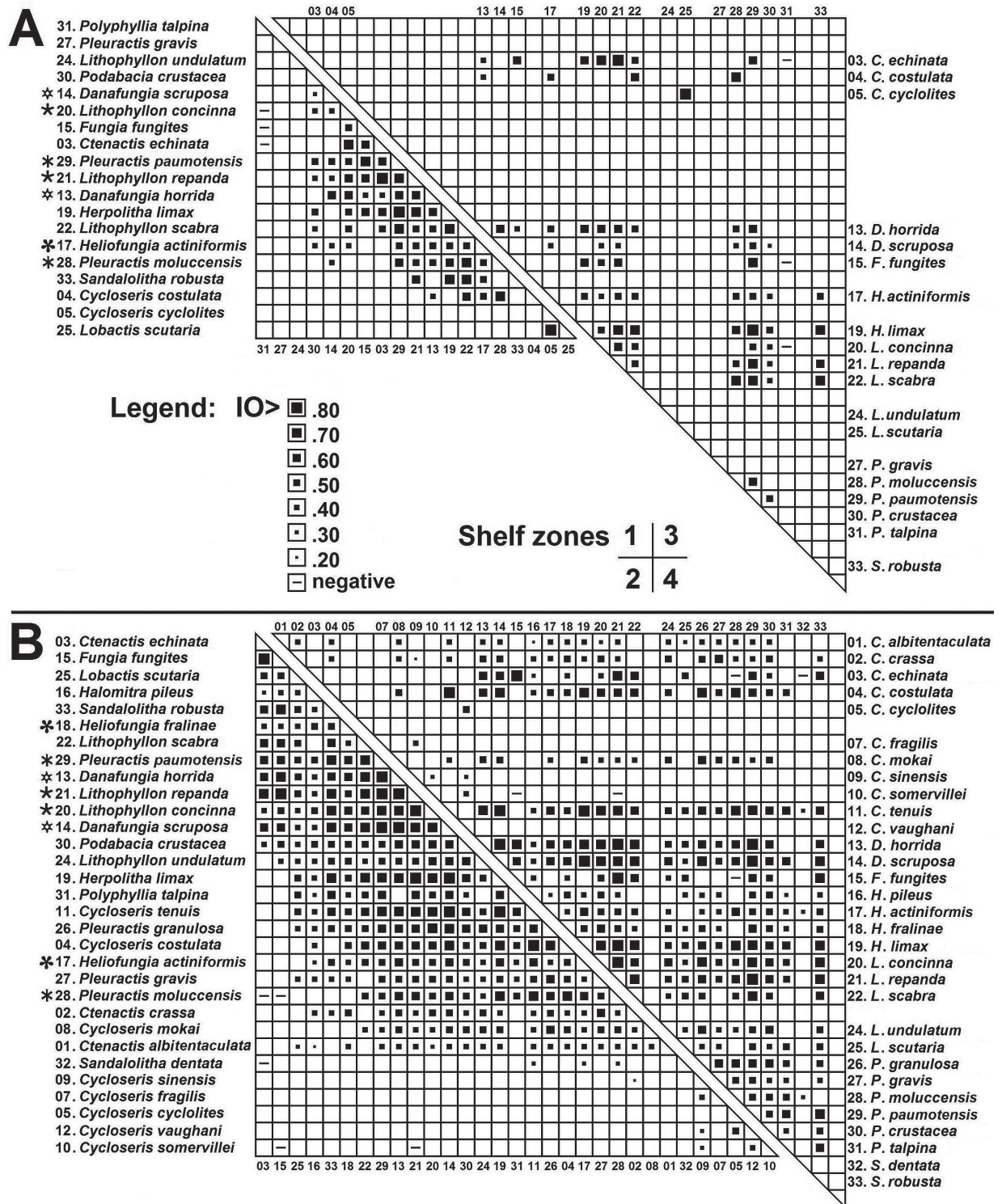
**Fig. 10.** Trellis diagrams with IO-values calculated to indicate significant fungiid species associations. Negative associations are indicated by a minus sign. For each shelf zone (A= zone 1, B = zone 2, C = zone 3, D = zone 4) a set of two matrices is given: the upper right triangle shows species in alphabetical / taxonomic order (gaps indicate absent species); the lower left one is the rearranged similarity matrix with seriated order in species co-occurrences. Star-like symbols indicate sister species pairs.

**C**

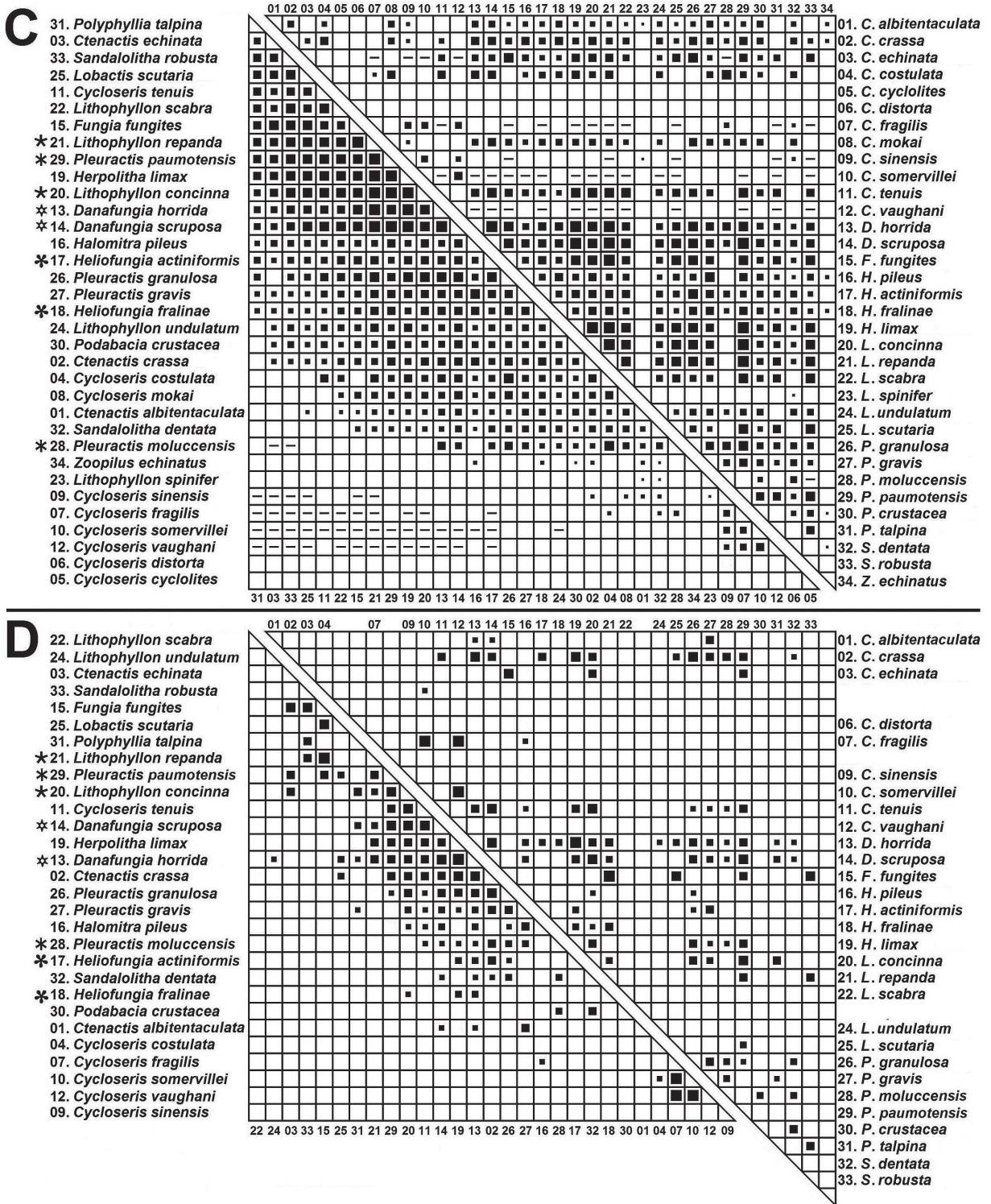| # | Species |
|---|---------|
| 31. | *Polyphyllia talpina* |
| 03. | *Ctenactis echinata* |
| 33. | *Sandalolitha robusta* |
| 25. | *Lobactis scutaria* |
| 11. | *Cycloseris tenuis* |
| 22. | *Lithophyllon scabra* |
| 15. | *Fungia fungites* |
| ✱21. | *Lithophyllon repanda* |
| ✱29. | *Pleuractis paumotensis* |
| 19. | *Herpolitha limax* |
| ✱20. | *Lithophyllon concinna* |
| ✧13. | *Danafungia horrida* |
| ✧14. | *Danafungia scruposa* |
| 16. | *Halomitra pileus* |
| ✱17. | *Heliofungia actiniformis* |
| 26. | *Pleuractis granulosa* |
| 27. | *Pleuractis gravis* |
| ✱18. | *Heliofungia fralinae* |
| 24. | *Lithophyllon undulatum* |
| 30. | *Podabacia crustacea* |
| 02. | *Ctenactis crassa* |
| 04. | *Cycloseris costulata* |
| 08. | *Cycloseris mokai* |
| 01. | *Ctenactis albitentaculata* |
| 32. | *Sandalolitha dentata* |
| ✱28. | *Pleuractis moluccensis* |
| 34. | *Zoopilus echinatus* |
| 23. | *Lithophyllon spinifer* |
| 09. | *Cycloseris sinensis* |
| 07. | *Cycloseris fragilis* |
| 10. | *Cycloseris somervillei* |
| 12. | *Cycloseris vaughani* |
| 06. | *Cycloseris distorta* |
| 05. | *Cycloseris cyclolites* |

01. *C. albitentaculata*
02. *C. crassa*
03. *C. echinata*
04. *C. costulata*
05. *C. cyclolites*
06. *C. distorta*
07. *C. fragilis*
08. *C. mokai*
09. *C. sinensis*
10. *C. somervillei*
11. *C. tenuis*
12. *C. vaughani*
13. *D. horrida*
14. *D. scruposa*
15. *F. fungites*
16. *H. pileus*
17. *H. actiniformis*
18. *H. fralinae*
19. *H. limax*
20. *L. concinna*
21. *L. repanda*
22. *L. scabra*
23. *L. spinifer*
24. *L. undulatum*
25. *L. scutaria*
26. *P. granulosa*
27. *P. gravis*
28. *P. moluccensis*
29. *P. paumotensis*
30. *P. crustacea*
31. *P. talpina*
32. *S. dentata*
33. *S. robusta*
34. *Z. echinatus*

**D**

| # | Species |
|---|---------|
| 22. | *Lithophyllon scabra* |
| 24. | *Lithophyllon undulatum* |
| 03. | *Ctenactis echinata* |
| 33. | *Sandalolitha robusta* |
| 15. | *Fungia fungites* |
| 25. | *Lobactis scutaria* |
| 31. | *Polyphyllia talpina* |
| ✱21. | *Lithophyllon repanda* |
| ✱29. | *Pleuractis paumotensis* |
| ✱20. | *Lithophyllon concinna* |
| 11. | *Cycloseris tenuis* |
| ✧14. | *Danafungia scruposa* |
| 19. | *Herpolitha limax* |
| ✧13. | *Danafungia horrida* |
| 02. | *Ctenactis crassa* |
| 26. | *Pleuractis granulosa* |
| 27. | *Pleuractis gravis* |
| 16. | *Halomitra pileus* |
| ✱28. | *Pleuractis moluccensis* |
| ✱17. | *Heliofungia actiniformis* |
| 32. | *Sandalolitha dentata* |
| ✱18. | *Heliofungia fralinae* |
| 30. | *Podabacia crustacea* |
| 01. | *Ctenactis albitentaculata* |
| 04. | *Cycloseris costulata* |
| 07. | *Cycloseris fragilis* |
| 10. | *Cycloseris somervillei* |
| 12. | *Cycloseris vaughani* |
| 09. | *Cycloseris sinensis* |

01. *C. albitentaculata*
02. *C. crassa*
03. *C. echinata*
06. *C. distorta*
07. *C. fragilis*
09. *C. sinensis*
10. *C. somervillei*
11. *C. tenuis*
12. *C. vaughani*
13. *D. horrida*
14. *D. scruposa*
15. *F. fungites*
16. *H. pileus*
17. *H. actiniformis*
18. *H. fralinae*
19. *H. limax*
20. *L. concinna*
21. *L. repanda*
22. *L. scabra*
24. *L. undulatum*
25. *L. scutaria*
26. *P. granulosa*
27. *P. gravis*
28. *P. moluccensis*
29. *P. paumotensis*
30. *P. crustacea*
31. *P. talpina*
32. *S. dentata*
33. *S. robusta*

*Fig. 10.* (continued).

*Table 3*. Interspecific association of Fungiidae in 50×1 m² SUs in each of the four Spermonde shelf zones. The presence absence data of species are compared by R-mode analysis for SUs having at least one species represented. When VR, the variance ratio, > 1, there is a possible possitive overall association which proves to be significant when the test statistic W approximates a chi-square distribution (Schluter, 1984).

| Shelf zone | SUs with fungiids | Number of species | VR, overall association | W, test statistic | Association (+ or ) |
|---|---|---|---|---|---|
| 1 | 69 | 19 | 4.8 | 329 | + |
| 2 | 137 | 31 | 8.4 | 1153 | + |
| 3 | 162 | 34 | 8.8 | 1424 | + |
| 4 | 49 | 29 | 7.2 | 352 | + |

*Lithophyllon concinna - L. repanda* (IO> 0.50) did not show highest IO-values for co-occurrences (Fig. 10D). Other sister species pairs, such as *Heliofungia actiniformis – H. fralinae* and *Pleuractis moluccensis - P. paumotensis* showed no significant association at all.

It is remarkable that among some sister species, such as *Danafungia horrida* with *D. scruposa*, and *Lithophyllon concinna* with *L. repanda*, distributions patterns appear to be very similar, showing much co-occurrence, especially in shelf zones 2 and 3 where mushroom corals are most abundant. In other sister species pairs, the species show very different patterns and little co-existence.

## Discussion

### Onshore-offshore patterns

Three major environmental gradients are considered important for fungiid distribution patterns on the Spermonde Shelf (1) reefs varying in distance offshore, away from terrigenous impact (2) position of sites around reefs with regard to predominant wind direction, and (3) depth zonation over reef flats, slopes and bases (Hoeksema, 2012). Substantial environmental differences may exist across tropical continental shelves with regard to the physiography of coral reefs (Hopley, 1982; de Klerk, 1983). Consequently, more oceanic, peripheral habitats on a shelf differ physically and biologically from inshore habitats (Done, 1982), such differences being considered of considerable relevance to biogeographic and speciation patterns and processes (Jablonski and Valentine, 1981; Valentine and Jablonski, 1983; Potts, 1983, 1984, 1985).

Fungiid faunas on near-shore reefs on the Spermonde shelf (Zone 1) are distinct from the rest (Hoeksema, 2012). The fungiids here are not nearshore specialists, but rather a subset of species that are widely distributed across the shelf (Table 1; Hoeksema, 2012). For example the predominantly deep-living *Cycloseris* species (rare or absent in zone 1) are mostly restricted to the reef bases of reefs further offshore (Hoeksema, 2012). In zone 1, depths > 15 m do not exist on the reef slope because the sea floor surrounding the reefs is relatively shallow (deepest SU at 15 m) and it consists of fine sediment deposited by fluvial discharge. Therefore, species with predominant deep offshore distributions that prefer oceanic conditions are absent here. Similar patterns of onshore-offshore distributions for particular mushroom coral species were found in northern Papua New Guinea, East Kalimantan and eastern Sabah (Hoeksema, 1993a; Hoeksema *et al.*, 2004; Waheed and Hoeksema, 2013).

Species with a more off-shore biased distribution are best represented in zone 3, and to a minor degree in zone 2. Here, the presence or absence of a sand cay seems to exert an important influence on the fungiid fauna. Shelf zone 4 is less rich in species than zone 3 because the reefs in zone 4 sit upon a shallow sand ridge (the barrier), which lacks dense coral cover, except along some stretches of narrow reef flope (Hoeksema, 2012).

### Spatial partitioning and co-existence

Because many coral species have broad ranges with respect to depth distribution and the location of the reefs they occupy, habitat partitioning is not necessarily important in the maintenance of coral reef diversity (Connell, 1978). With the application of molecular techniques in the taxonomy of reef corals it has been discovered that what used to be considered species may actually consist of species complexes, which may imply that these ecological ranges are split up and narrower than previously assumed (Knowlton and Jackson, 1994). In the present analyses of species co-occurrences on the Spermonde shelf, most fungiids appear to show much overlap regarding their onshore-offshore, circum-reef and depth distributions as presented by Hoeksema (2012).

Among the 34 mushroom coral species encountered in belt quadrats, many show much similarity regarding their presence and abundance over reef flats, slopes and

bases within transects around reefs across the shelf. For a better understanding of niche differentiation and species co-existence it is important to compare distribution patterns of phylogenetically closely related species, preferably sister species. Although there is in general much overlap in distribution patterns of closely related species, their distributions are usually not similar.

Therefore, the co-existence of sister species showing very similar distribution patterns in high densities is exceptional, like *Lithophyllon concinna* with *L. repanda*, and *Danafungia horrida* with *D. scruposa*. These are typical examples of niche conservatism (sensu Wiens and Graham, 2005; Holland and Zaffos, 2011; Mouquet *et al.*, 2012), in which sister species share similar habitat traits that did not change during and after speciation. The co-existence of similar species is not unique though and various ecological explanations have been suggested (Scheffer and van Nes, 2006).

The four mushroom species in question have widely overlapping Indo-West Pacific geographic ranges and a fossil records that can be traced back to either the Miocene or Pliocene (Hoeksema, 1989). Because of their ecological similarities, there is no clear indication for sympatric speciation and if they originated by allopatric speciation, it is unclear where and how that process started. Furthermore, with regard to their associated fauna, only both *Danafungia* species show a clear difference, *i.e.*, the presence of dissimilar endosymbiotic *Leptoconchus* snails (Gittenberger and Gittenberger, 2011; Hoeksema *et al.*, 2011). Spatial partitioning may not have occurred among mushroom corals if there was sufficient geographic and ecological space to expand into, especially in the case of free-living species.

The range overlaps shown by the co-occurrence analyses reflect what also can be seen in dense mixed mushroom coral assemblages *in situ*, with specimens of various species literally being piled on top of each other (Littler *et al.*, 1997; Hoeksema and Matthews, 2010; Hoeksema, 2012). There appears to be no visible effect of community saturation or competitive exclusion, especially because of the ability of many free-living mushroom coral species to occupy different kinds of substrates and to escape burial in sand (Schuhmacher, 1977, 1979; Bongaerts *et al.*, 2012). Furthermore, mushroom corals are known to be aggressive towards other corals (Sheppard 1979, 1981; Cope, 1981; Thomason and Brown, 1986; Hildemann *et al.*, 1975a, b; Chadwick-Furman and Loya, 1992; Jokiel and Bigger, 1994; Abelson and Loya, 1999), but they appear not to harm each other. On the other hand,

it may be risky for mushroom corals to get into contact with sedentary organisms that are known to produce toxins, such as sponges (de Voogd *et al.*, 2005). When that happens, they may use their ability to move away, either by their own force or by wave action (Abe, 1939; Horridge, 1957; Hubbard, 1972; Jokiel and Cowdin, 1976; Chadwick, 1988; Hoeksema, 1988; Chadwick-Furman and Loya, 1992; Yamashiro and Nishira, 1995; Hoeksema and de Voogd, 2012).

*Phylogenetic ecology*

When historical, causal explanations are sought in biological comparisons, a phylogenetic foundation is essential (Bock, 1989), especially since adaptations of an organism to its environment may be limited by phylogenetic constraints (Gans, 1989; McKitrick, 1993). Because of their independence from morphological character state transformations, molecular phylogeny reconstructions are ideal to detect evolutionary trends in morphology, life history traits, and associated fauna of corals (Gittenberger *et al.*, 2011; Hoeksema *et al.*, 2012). In the present study they are applied to detect evolutionary causes for species distributions and abundances.

In evolutionary ecology, historical causes are sought behind ecological adaptations when the autoecologies of species in a community are compared (Orians, 1962; Lack, 1965). However, evolutionary ecology is not necessarily restricted to comparisons within monophyletic groups because it does not take phylogeny reconstructions into account. Hence, for comparative historical ecological studies with a phylogenetic approach the term 'phylogenetic ecology' is used (Hoeksema, 1990; Westoby, 2006), which can also be referred to as 'phylo-ecology' or 'ecophylogenetics'. This approach is gaining support in community ecology, which implies abandoning localized concepts of communities and adopting a historical perspective with respect to the evolution of diversity within larger regions (Losos, 1996; Ricklefs, 1996, 2006; Schluter *et al.*, 1997; Webb *et al.*, 2002; Johnson and Stinchcombe, 2007; Cavender-Bares *et al.*, 2009; Mouquet *et al.*, 2012).

The present evolution models of cross-shelf distributions and depth ranges in the Fungiidae (Figs 3-4) suggest that their ancestral species occurred on offshore reef slopes, which is plausible because they constitute the most diverse habitat for many coral species on the Spermonde Shelf (Moll, 1983; Hoeksema, 2012). The ancestor of the Fungiidae was probably an *Acrosmilia*-like scleractinian, which in overall shape

resembled the attached anthocaulus-stage of the Fungiidae (Wells, 1966). From this coral, displaying a sedentary turbinate shape and a vertical corallum wall, evolved a free-living coral with a more horizontal wall by the broadening of the oral surface and the development of the detachment process (see Yamashiro and Yamazato 1987a, b, 1996; Hoeksema and Yeemin, 2012). This evolutionary sequence resembles the succession in the first post-settlement stages of the fungiid life cycle (Wells, 1966; Hoeksema, 1989). Little is known about the ecology of *Acrosmilia* corals but because of their sedentary attached growth form, they presumably lived on hard substrates, like on reef slopes.

In post-larval stage, ancestral fungiids also settled on such hard substrata but by becoming free-living they were also able to colonize unconsolidated substrates, such as sand and rubble (Wells, 1966). On reef slopes, they could become part of and move with coral debris, decreasing the risk of becoming buried (Hoeksema, 1988). On the other hand, in 12 mushroom coral species the ability to become free-living has been lost and they remain secondarily attached (Hoeksema, 1991a, 2009; Gittenberger *et al.*, 2011; Benzoni *et al.*, 2012). In some areas attached fungiids have become quite common or even dominant (Cope, 1981, 1982; Hoeksema, 2009). However, if corals of these species accidently break, their fragments are able to survive as free-living corals as well. The ultimate reversal towards the sedentary shape is found in three polystomatous encrusting *Cycloseris* species (Gittenberger *et al.*, 2011; Benzoni *et al.*, 2012), some of which inhabit the sides of dead coral at the border of reef slope and reef base where sedimentation may be high. Because of their vertical attached position and the possession of multiple mouths, they may also be adapted to free themselves from sediments (Chadwick-Furman and Loya, 1992; Erftemeijer *et al.*, 2012).

In various species lineages, fungiids have colonized nearshore habitats but they have not become specialized in onshore distributions. They are just more eurytopic, by tolerating the proximity of river mouths, which suggests that they are more resistant to freshwater. Perhaps this was an advantage for populations that remained in isolated sea basins during sea level regressions (McManus, 1985). These seas were probably deprived from oceanic influence and therefore affected by river discharge from the surrounding shores.

In several species lineages, mushroom corals appeared to have migrated upward, which enabled them to live on shallow reef flats (Figs 3-4). Here they can receive more light but they are also more exposed to wave action and temperature fluctuations. *Fungia fungites* is able to reach high densities here and may be best adapted to live in shallow reef habitats. In order to achieve this shallow depth range, the planula larvae have to settle in shallower depth zones. During periods of transgression this could have been an advantage for species that needed to keep pace with the rising sea-level. New species may even have evolved along the outward side of shelves (Fig. 5C) or around oceanic islands that became isolated during transgressions (Potts, 1983, 1984, 1985; Rosen, 1984; Hoeksema, 1989). Furthermore, free-living adults had to maintain shallow positions on steep reef slopes. Many species that expanded upwards in bathymetric range show large septo-costal ornamentations which may provide additional resistance on exposed steep reef slopes and prevent them to slide downwards too quickly (Hoeksema, 1989, 1991a, 1993b). On the other hand, by not departing from deeper reef slopes entirely, species were able to survive during sea level regressions, when shallow shelf habitats disappeared (Fig. 5C; Hoeksema, 2007).

In other lineages, mushroom coral species appeared to have migrated downward, enabling them to colonize deep sandy bottoms offshore (Fig. 3). Some free-living *Cycloseris* species have become specialized in this kind of habitat, which is remote from the ancestral situation. In this way they have become nearly independent from hard substrates, especially when they apply fragmentation as a reproductive mechanism (Yamashiro and Nishihira, 1994, 1998; Colley *et al.*, 2002; Hoeksema and Waheed, 2011). This model is in contrast with a previous evolution scenario (Wells, 1966), in which it was assumed that these small, free-living mushroom corals with simple skeleton structures (*Cycloseris* spp.) were the least evolved and that their deep sandy substrates represented ancestral habitats among Recent fungiids. The present model suggests that these corals have developed a small size and simple structures in order to be more mobile and to be more resistant to sedimentation. Mushroom corals with fine ornamentations on their septa are more capable of shedding sediments (Schuhmacher, 1977, 1979), and it is likely that a fine ornamentation does not hinder their movements over sandy substrates (Hoeksema, 1988, 1993b; Yamashiro and Nishihira, 1995).

Alternative evolutionary scenarios are obtained if reversals are included in the habitat transformations: retreats from onshore reefs, reef flats, and reef bases (Fig. 4). This model is most parsimonious with regard to the *Cycloseris* clade (Fig. 4A). Alternative scenarios

for other clades do not result in more parsimonious solutions when reversals are introduced (Fig. 4B-D). The alternative scenarios do not change the notion that offshore reef slopes were the most likely original mushroom coral habitat.

The application of a phylogenetic model for reconstructing the evolution of mushroom coral habitats over environmental gradients appears to give insight in adaptive shifts that occurred in various independent species lineages over time. The model shows how gradients of species richness could have evolved on shelf-based reef systems through diversification from an ancestral ecological zone of origin (offshore slopes used by Fungiidae ancestors) combined with homoplastic adaptive shifts leading to the colonisation of new ecological zones, *i.e.* onshore habitats, reef flats and reef bases. The present high mushroom coral diversity found on offshore slopes in shelf zone 3, confirms the assumption that cross-shelf gradients of diversity have been established with the highest species richness in environments that are older, more widespread, or less stressful (Ricklefs, 2006). The multiple independent evolutionary developments from offshore to onshore-offshore distributions, and toward shallower and deeper habitats, help to understand how mushroom coral species could colonize new habitats, and also how this could lead to situations in which many closely related species are able to co-exist without outcompeting each other. Ultimately, these scenarios help to clarify the evolution of fungiid species diversity.

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