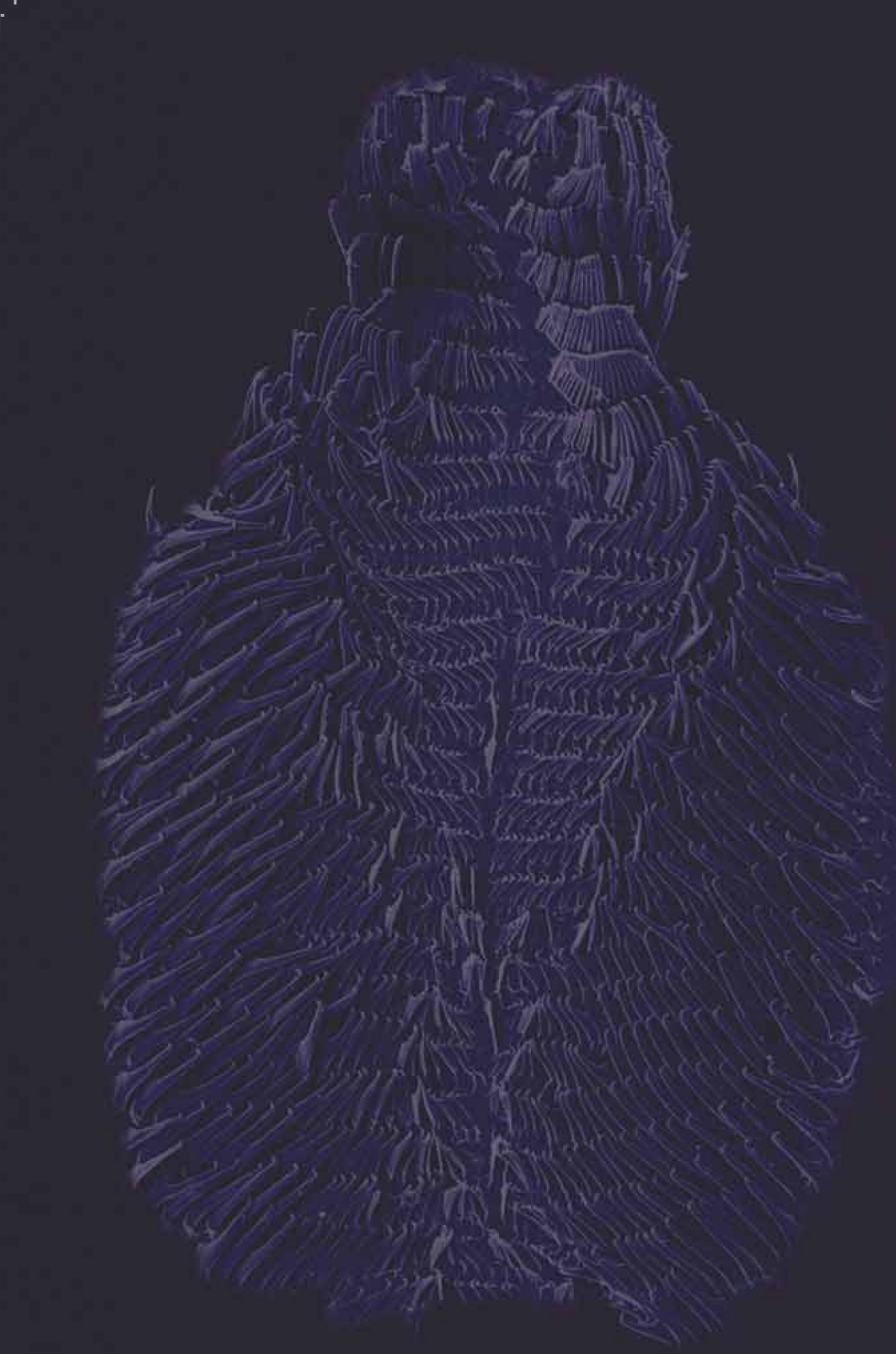
Adriaan Gittenberger

The evolutionary history of parasitic gastropods and their coral hosts



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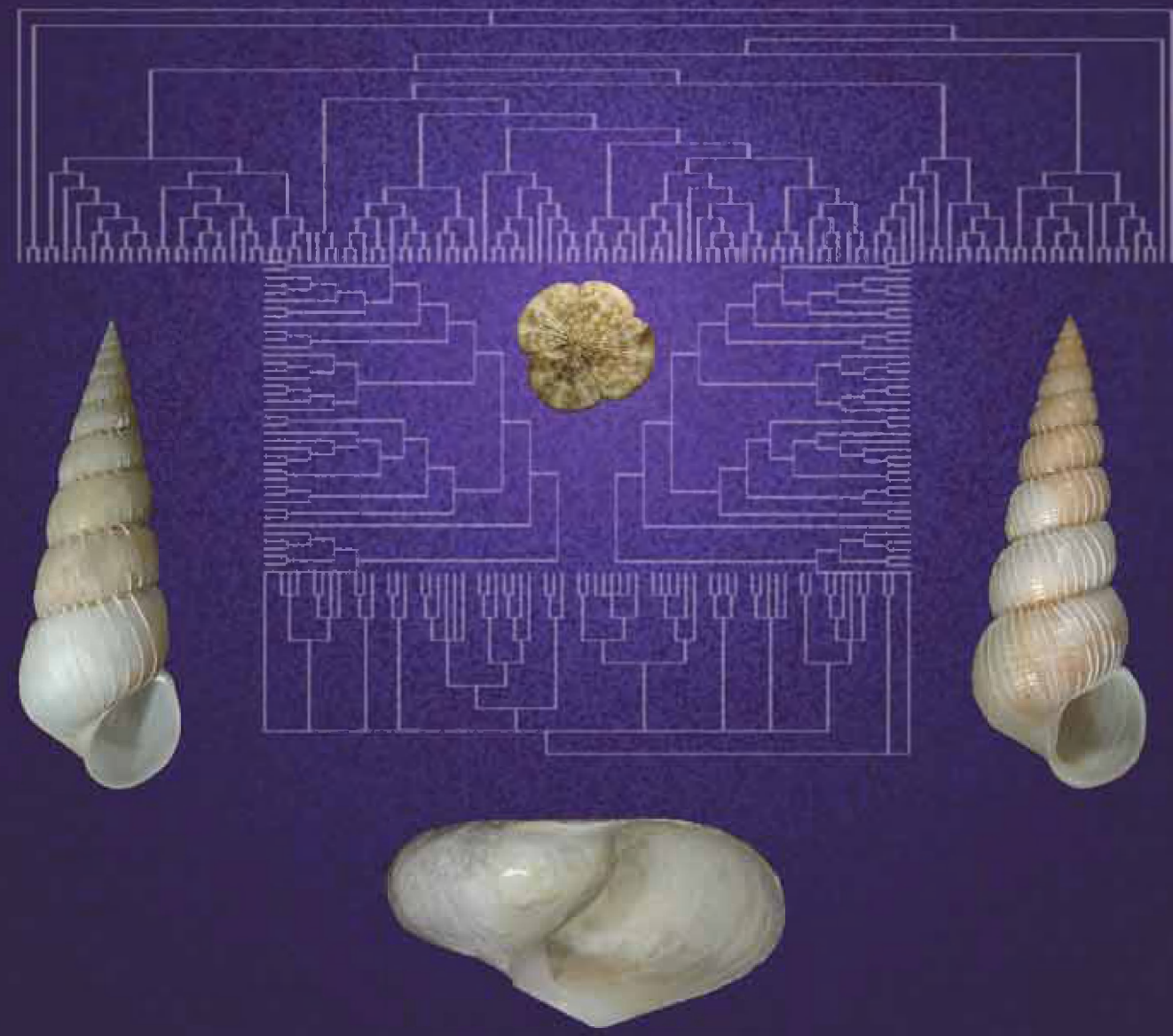

The coral *Tubastrea* spec., host of the wentletrap species *Epidendrium aureum* and *E. sordidum*. Photo A. Gittenberger.

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Voorkant: De schelpjes van *Epifungium adgranulosa*, *E. marki* en *Leptoconchus inpleuractis* gerangschikt om het koraal *Fungia* (*Cycloseris*) *sinensis*. Fylogenetische bomen van de Epitoniidae, Fungiidae en Coralliophilidae.
Achterkant: Radula van de wenteltrap *Cirsotrema varicosa.*
Opmaak: M. Rensing & A. Gittenberger

ISBN 90-9021100-4

The evolutionary history of parasitic gastropods and their coral hosts in the Indo-Pacific

Proefschrift

ter verkrijging van

de graad van Doctor aan de Universiteit Leiden,

op gezag van de Rector Magnificus Dr. D.D. Breimer,

hoogleraar in de faculteit der Wiskunde

en Natuurwetenschappen en die der Geneeskunde,

volgens besluit van het College voor Promoties

te verdedigen op woensdag 29 november 2006

klokke 15:00 uur

door

Adriaan Gittenberger

geboren te Leiden

in 1976

Promotiecommissie:

Promotor:	Prof. dr. P.M. Brakefield (Universiteit Leiden) Prof. dr. E. Gittenberger (Universiteit Leiden)
Co-promotor:	Dr. B.W. Hoeksema (Nationaal Natuurhistorisch Museum 'Naturalis', Leiden)
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De totstandkoming van dit proefschrift werd financieel mogelijk gemaakt door

Nederlandse Organisatie voor Wetenschappelijk Onderzoek (WOTRO beurs W82-249)
Nationaal Natuurhistorisch Museum 'Naturalis'

Alida M. Buitendijk Fonds
Jan Joost ter Pelkwijkfonds
Leids Universiteits Fonds
Koninklijke Nederlandse Akademie van Wetenschappen

Voor mijn ouders, en voor oma

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De evolutionaire geschiedenis van parasitaire slakken en hun gastheer koralen in de Indo-Pacific

Nederlandse inleiding en samenvatting

Nederlandse inleiding en samenvatting

In en om Indonesië, waar de Indische en Pacifische oceanen samenkomen, concentreert zich de hoogste diversiteit van mariene diersoorten ter wereld. Deze buitengewoon hoge biodiversiteit is mogelijk ontstaan doordat veel soorten uit de Indische of de Pacifische oceaan in hun verspreidingsgebieden een 'overlap' in dit gebied hebben. Bovendien hebben veel van deze soorten complexe symbiotische en parasitaire relaties wat waarschijnlijk de soortvorming kan versnellen en de diversiteit nog verder kan verhogen.

Hierbij komen uiteenlopende vragen aan de orde: [1] Vindt soortvorming meestal plaats in allopatrie of sympatrie? [2] Leiden complexe symbiotische relaties tussen mariene organismen tot co-evolutie, co-speciatie en dus inderdaad tot een verhoogde diversiteit? [3] Hoe kan bij soorten met grote verspreidingsgebieden gene-flow over grote afstanden in stand gehouden worden waardoor geen verdere differentiatie optreedt?

Op dergelijke vragen kan alleen een bevredigend antwoord gevonden worden als afzonderlijke soorten duidelijk beschreven zijn en hun fylogenetische relaties zijn vastgesteld.

Daarop concentreert zich dit proefschrift. De paddenstoelkoralen (Fungiidae) en de parasitaire slakken (Epitoniidae en Coralliophilidae) die op en in deze koralen te vinden zijn, werden bestudeerd als model organismen om deze onderzoeksvragen te behandelen. Hiervoor zijn ontogenetische, morfologische, ecologische, moleculaire en bio-geografische gegevens verzameld. De eerste resultaten van dit onderzoek vormen het grootste deel van dit proefschrift.

Ruim 800 uur werd onder water doorgebracht, waarbij ongeveer 60.000 koralen (Fungiidae, Dendrophylliidae en Euphylliidae) werden bekeken op zoek naar endo- (Coralliophilidae) en ectoparasitaire (Epitoniidae) slakken. Het onderzoek concentreerde zich in de Indo-West-Pacific, van Egypte (Rode zee), de Malediven, Thailand, Maleisië, Japan, Palau, de Filippijnen, Indonesië en Australië tot Hawaii. Op de meeste locaties werd een week tot een maand aan veldwerk besteed. In de Spermonde archipel bij Makassar, SW Sulawesi, Indonesië, werd een jaar aan veldwerk besteed aangezien de diversiteit en dichtheid van koralen rondom Sulawesi hoger is dan waar ook ter wereld. Omdat vrij levende paddenstoelkoralen (Fungiidae) het verbindende element in dit onderzoek vormden, is geprobeerd om alle soorten binnen deze familie te vinden, in het bijzonder ook de minder algemene. Die in collecties zeldzamere soorten leven vaak in voor duikers onaantrekkelijke gebieden met zandbodems of sterke stromingen, of op grote diepte.

Er werden ongeveer 4000 parasitaire slakken gevonden in associatie met koralen. Hierbij werd telkens de locatie, met diepte, microhabitat, parasiet en gastheersoort genoteerd. Het DNA van 600 van deze parasitaire slakken en 100 paddenstoelkoralen werd onderzocht en de resultaten werden gebruikt voor het reconstrueren van de fylogenieën. Deze analyses brachten twee verrassend soortenrijke, cryptische, adaptieve radiaties van parasitaire slakken aan het licht. Zo bleken er veel meer endo- en ectoparasitaire gastropoden van paddenstoelkoralen te zijn dan voorheen werd gedacht, omdat de meeste parasitaire soorten niet onmiskenbaar geïdentificeerd kunnen worden op basis van hun schelp. Moleculaire (DNA), ecologische (de gastheer) en anatomische (radula en kaak) kenmerken bleken bruikbaarder te zijn voor identificaties. Verder bleek dat de relatie tussen de parasieten en hun gastheersoorten veel exclusiever is dan tot dusver algemeen geaccepteerd werd.

De moleculaire fylogenie reconstructie van de paddenstoelkoralen komt sterk overeen met de indeling die alleen gebaseerd is op morfologische gegevens (Hoeksema, 1989). De verschillen zijn meestal terug te voeren op convergente evolutie. Het voorouderlijke kenmerk om vast te blijven zitten aan het substraat, in plaats van los te breken in een jong stadium, blijkt verschillende keren te zijn 'teruggekomen' in deze koralenfamilie waarvan de meeste soorten vrijlevend zijn.

Een vergelijking tussen de fylogenie reconstructies van de paddenstoelkoralen, en die van hun endo- en ectoparasitaire slakken, laat zien dat de evolutionaire geschiedenissen van deze taxa nauw aan elkaar

gerelateerd zijn. Zo geven de resultaten aan dat wenteltrapjes maar één keer in hun evolutie een 'overstap' van zeeanemonen naar harde koralen hebben gemaakt. De soorten die bij harde koralen worden gevonden behoren namelijk allemaal tot dezelfde monofyletische groep.

De fylogenieën van de gastheren en hun parasieten suggereren dat de meeste onderzochte slakkensoorten ontstaan zijn door sympatrische soortvorming. Een realistisch scenario van allopatrische soortvorming ontbreekt. In het verleden zijn kennelijk populaties met voorkeuren voor verschillende gastheersoorten ontstaan. De hier onderzochte parasitaire slakken paren en leggen eieren bij hun gastheer, wat een differentiatie en specialisatie vergemakkelijkt. In enkele gevallen werden aanwijzingen voor co-evolutie gevonden.

1

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

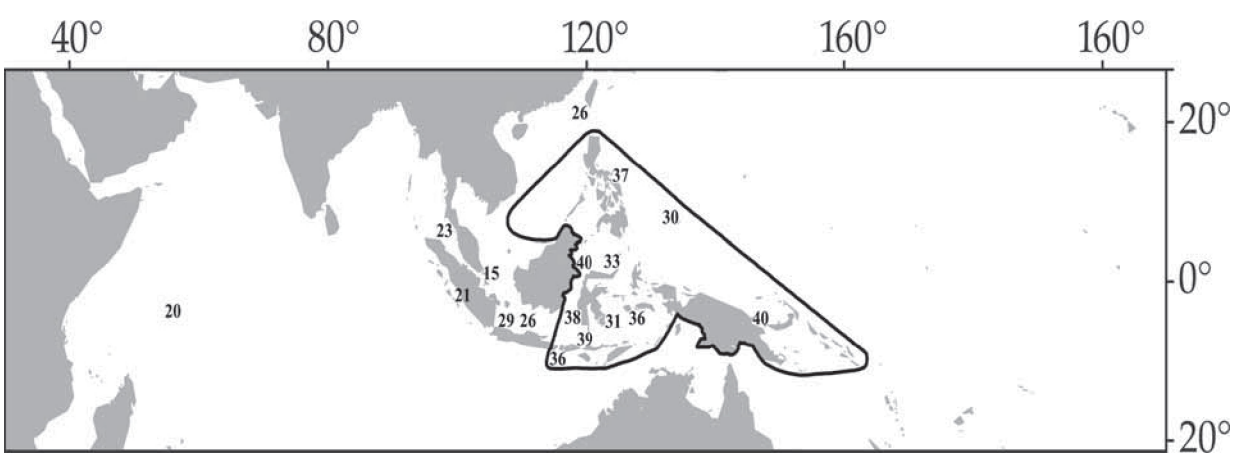

Fig. 1. The Indo-West Pacific, illustrating the numbers of Fungiidae in various areas that were intensively studied (Hoeksema, in press).

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, microhabitat, 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 know. 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.

2

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

Adriaan Gittenberger and Bert W. Hoeksema

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

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Key words: eco-phenotype; plasticity; allozymes; river outlets; mushroom corals; Fungiidae; *Cycloseris*; Indonesia

Abstract

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 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 separate coral morphs should be considered three species. Eventually it was concluded that there are only two species, 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.

Contents

Introduction

Intraspecific variation in scleractinian corals is a classic problem in their taxonomy, both in regard to recent and fossil species (Best et al., 1999; Knowlton and Budd, 2001). Habitat-induced variability has been observed in coral species distributed along depth ranges, in which the specimens from the deeper sites used to be flatter than those from shallower places. The former ones exposing more surface area in order to compensate for less light penetration at greater depths (Wijsman-Best, 1972, 1974; Hoeksema, 1993). Other environmental factors of importance in coral shape plasticity may be sedimentation, salinity and water temperature, turbulence and flow; in addition to coral morphology also the pigmentation in the soft tissue may be affected (Bruno and Edmunds, 1997; Todd et al., 2002a, 2002b, 2004b, 2004c). Coral damage and subsequent regeneration also have specific effects on shape, which may impede taxonomy and easy identification (Hoeksema, 1989, 1991b, 1993; Oren et al., 1997; Nagelkerken and Bak, 1998).

For no obvious reason, most of the research on intraspecific coral variation has been performed on massive faviids, both in the Atlantic (Dustan, 1975; Foster, 1977, 1979; Lasker, 1981; Graus and Macintyre, 1982; Dodge, 1992; Beltran-Torres and Carricart-Gavinet, 1993; Amaral, 1994; Manica and Carter, 2000) and the Indo-Pacific (Wijsman-Best, 1972, 1974; Miller, 1994; Oren et al., 1997; Todd et al., 2001, 2002a, 2002b, 2004a, 2004b, 2004c). Mushroom corals (Fungiidae), which are endemic to the Indo-Pacific, have mainly been studied in relation with light penetration, sedimentation, and traumatic damage (Hoeksema, 1989, 1991b, 1993; Hoeksema and Moka, 1989). A physiological difference with regard to vulnerability to elevated temperature has also been shown among individuals of the same mushroom coral species within close range of each other (Hoeksema, 1991a).

During earlier taxonomic and morphological studies on mushroom corals three different morphs of *Fungia* (*Cycloseris*) spp. were distinguished (Hoeksema, 1989; Hoeksema and Moka, 1989). Two of these were considered separate species, viz.*Fungia* (*Cycloseris*) *costulata* Ortmann, 1889 (figs 1-2), and *F.* (*C.*) *tenuis* Dana, 1864 (figs 7-8); the third one was seen as a morph of the first (figs 3-6; Hoeksema and Moka, 1989: fig. 12). *Fungia* (*C.*) *tenuis* has much rougher costae and usually a slightly different coloration (dark brown stomatal ends) as compared to *F.* (*C.*) *costulata*. The two are usually observed on the same reefs. However, *F.* (*C.*) *costulata* may also be present on reefs that are more nearshore, in more sediment-rich water, and they may occur deeper when found on the same reef as *F.* (*C.*) *tenuis*. The alleged separate morph of *F.* (*C.*) *costulata* is thinner and shows an evenly brown-olive green color (figs 3-6). It occurs on nearshore reefs, either on patch reefs near river outlets or inside deep bays and estuaries. The three morphs cannot always be distinguished easily. Therefore, in order to investigate the taxonomic implications of the morphological differences, several allozymes of the morphs were compared. Allozyme electrophoresis has successfully been used to solve similar taxonomical problems (Gittenberger et al., 2001; Sanjuan et al., 1997). The three morphs will be referred to as morphs A, B and C for respectively *Fungia* (*Cycloseris*) *costulata*, *F.* (*C.*) *tenuis* and *F.* (*C.*) cf *costulata*.

Material and methods

Sampling

Specimens of morphs A, B and C were found sympatrically at Bone Baku reef, off Makassar, Sulawesi, Indonesia. Twelve specimens of each morph were collected within an area of about 200 m^2 at depths between 2 and 12 meters. They were coded A1-12, B1-12 and C1-12. To make sure that no clones were included, only individuals that differed in polyp coloration were selected. While diving, the specimens were individually put into separate plastic bags and transported to the laboratory in a bucket with seawater. They were kept alive in two 30 liter aquariums with two air-pumps each. To reduce the pollution in the aquariums, the water was taken a few kilometers off the coast and filtered through a coffee filter. Before the allozyme electrophoresis, all corals were digitally photographed on both sides with a Fujifilm MX-2700 camera.

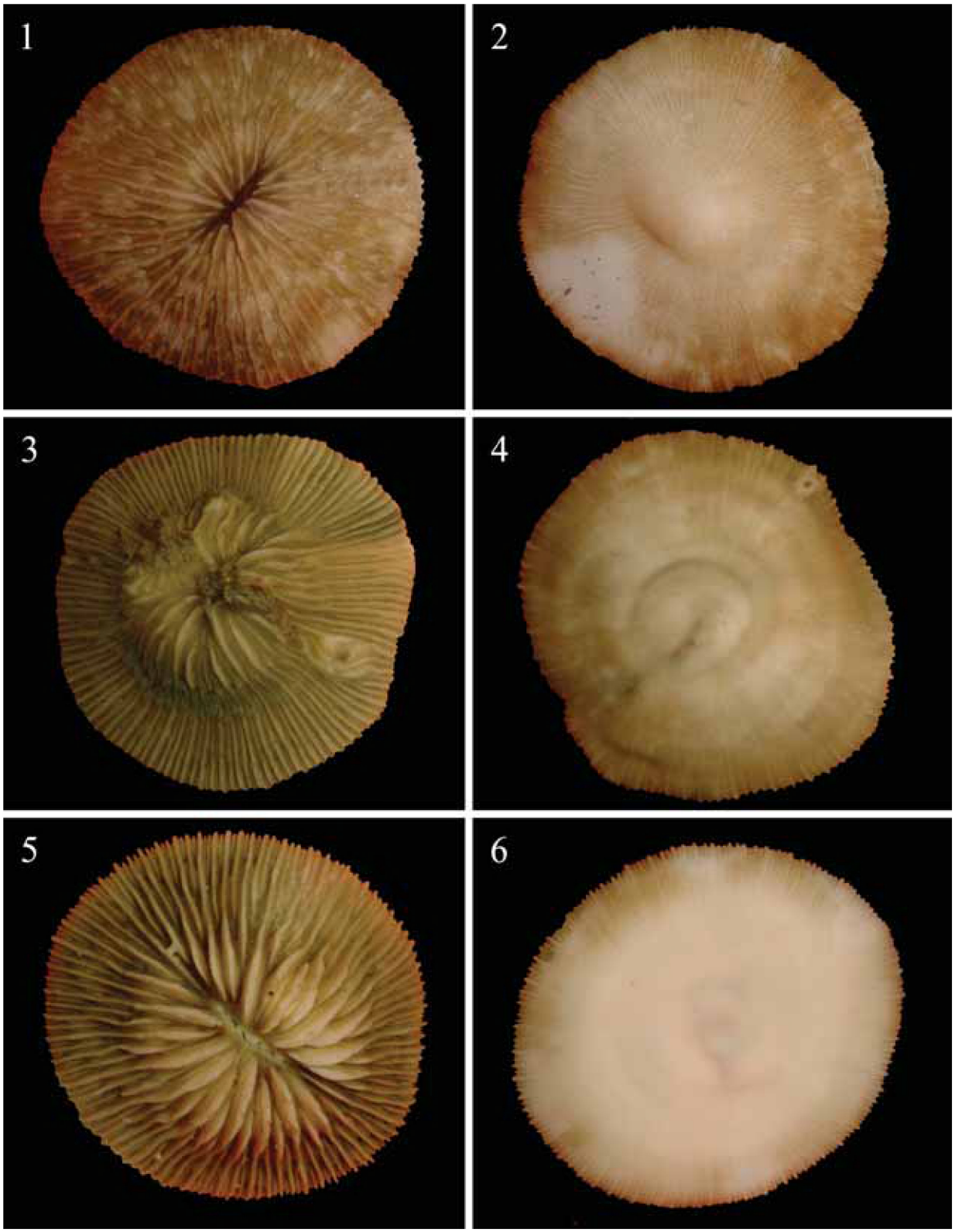
Allozyme electrophoresis

Each coral was taken out of the aquarium. After that half a 1.5 ml test-tube of coral tissue mixed with small pieces of skeleton was rasped of the septae with a scalpel, and 0.050 ml of homogenizing buffer (0.01M Tris, 0.001 M NaEDTA, 0.01 M Maleic acid and 0.001 M MgCl2) was added. The mixture was ground with a micro-pestle and put on ice. The damaged specimens were digitally photographed on both sides and conserved in 96% alcohol, as reference material. To create a centrifuge, the blades of a small table-ventilator were removed and the tubes were stuck to the spindle with heavy duty tape. Each sample was centrifuged for 30 seconds at maximum speed. The supernatants were extracted with a 0.100 ml pipette and added to a new tube, which was centrifuged for 30 seconds and put on ice.

Occasionally the supernatant was too slimy (highly viscose and sticky) to be extracted into a 0.100 ml pipette point. In that case, the top of this pipette point was cut off with a scalpel to enable the extraction of the "slimy" supernatant into a new tube. An additional 0.050 ml homogenization buffer was added and everything was mixed by sucking it up and down into the cut pipette point. After centrifuging this mixture at maximum speed for 30 seconds, the supernatant could be extracted with a 0.100 ml pipette point. It was added to a new tube and put on ice.

The slots of a well-plate were filled with 0.010 ml supernatant each. An applicator was used to load and apply the supernatant to a cellulose acetate gel (Hillis et al., 1987). Supernatants of all samples were run on a gel for 25 minutes and on an additional gel for 40 minutes. The electrophoresis was performed in a refrigerator at 4°C.

To test which allozyme systems in combination with which running buffers work best for Fungiidae, i.e. show polymorphic loci with a good resolution and activity, a preliminary study was done in the Netherlands. In total 10 allozyme systems were tested on two specimens of *Heliofungia actiniformis* (Quoy and Gaimard, 1833) and two specimens of



Figs 1-6. Upper and lower surfaces of mushroom corals. 1-2, *Fungia* (*Cycloseris*) *costulata*. 3-6, *Fungia* (*Cycloseris*) cf *costulata*. Scale = 1:1.

Fungia (*Verrillofungia*) *repanda* Dana, 1846, viz. apartate aminotransferase (sAAT 2.6.1.1), alcohol dehydrogenase (ADH, 1.1.1.1), glucose dehydrogenase (GCDH, 1.1.1.118), glucose 6 phosphate dehydrogenase (G6PDH, 1.1.1.49), hexokinase (HK, 2.7.1.1), L-iditol dehydrogenase (IDDH, 1.1.1.14), isocitrate dehydrogenase (IDH, 1.1.1.42), malate dehydrogenase (MDH, 1.1.1.37), glucose-6-phosphate isomerase (GPI, 5.3.1.9), and phospho-glucomutase (PGM, 5.4.2.2). The nomenclature and IUBNC numbers are according to those of the standard of the International Union of Biochemistry (IUBNC, 1984). All allozyme systems were tested in combination with three buffers (Saccheri, 1995), i.e. TG (pH 8.5, 25mM Tris, 192 mM Glycine), TM (pH 7.8, 50 mM Tris, 20 mM Maleic acid) and P (pH 7.0, 11.6 mM Na2HPO4.2H2O, 8.4 mM NaH2PO4.H2O). The loci of the allozyme systems G6PDH, HK, MDH and GPI were polymorphic, with a good activity and a reasonable resolution using TM, TM, TG and P buffer respectively. The chemicals to test these allozyme systems were either bought in Indonesia or imported ice-packs from the Netherlands. These allozyme system-buffer combinations also gave good results during an additional test in Indonesia for specimens of *Herpolitha limax* (Esper, 1797), *Zoopilus echinatus* Dana, 1846, *Fungia* (*Danafungia*) *fralinae* Nemenzo, 1955, *F.* (*D.*) *scruposa* Kluzinger, 1879, *F.* (*Pleuractis*) *gravis* Nemenzo, 1955, *F.* (*Verrillofungia*) *repanda* Dana, 1846 and *F.* (*V.*) *scabra* Döderlein, 1901. A spider extract was used as a reference and positive control in all analyses. It showed a good activity and resolution for the allozyme system-buffer combinations described above. Unexpectedly, none of the specimens of morphs A, B or C showed any clear bands. Therefore, the allozyme system-buffer combinations were tested again for these corals. A good activity and reasonable resolution was only seen for the PGI allozyme system in combination with TG buffer. It showed one polymorphic and one homomorphic locus and was studied for the three morphs. The spider extract showed 4 bands with a high activity and good resolution and was used as a reference.

Data analyses

The resulting bands for each specimen were scored independently on two gels which had run for 20 and 40 minutes respectively. The bands that were scored twice were used for further analysis. The package of Swofford and Selander (1981), BIOSYS-1, was used to analyse the data. The exact probability test was used to test for Hardy-Weinberg at the polymorphic locus.

Morphological investigations

All the corals used in the experiment were investigated and identified morphologically in the field and, independently, from the photographs.

Results

Morphology

Except for the morphological differences described in the introduction, two additional characters distinguishing between A and B on the one hand, and C on the other hand were noticed.

It took about 2 minutes per specimen of the morphs A and C to scrape off sufficient tissue mixed with septal skeleton pieces to fill half a 1.5 ml tube, while it only took about 15 seconds for each specimen of B, indicating that the skeletal structure of B was weaker. Furthermore, all specimens of only the morphs A and C had slimy mucous for which the protocol had to be adjusted (see "Material and methods section").

Allozyme electrophoresis

The frequencies of the 6 alleles found for the polymorphic locus of PGI are shown in Table 1. The alleles A, D and F, accounting for 77% of all alleles scored for morph B, are not present in A and C. The alleles B and C, accounting for respectively 100% and 90% of the alleles in the samples in morphs A and C, account for only 9% of the alleles in morph B.

None of the three samples A, B and C (respectively $p = 0.57$, 1.00 and 0.48) was significantly ($\alpha = 0.05$) deviating from Hardy-Weinberg. However, when pooling the samples, the frequencies of the alleles were significantly ($p = 0.02$) deviating for the

Table 1 Frequencies of the alleles for the PGI allozyme system.

	Sample		
Allele	***F.* (*C.*) *costulata***	***F.* (*C.*) cf *costulata***	***F.* (*C.*) *tenuis***
(N)	10	9	11
A	0.000	0.000	0.045
B	0.300	0.500	0.045
C	0.600	0.500	0.045
D	0.000	0.000	0.591
E	0.100	0.000	0.136
F	0.000	0.000	0.136

sample A+B+C, almost significantly (respectively p = 0.06 and p = 0.12) for A+B and B+C, and not (p= 0.35) for A+C. This indicates that the samples A, B, C and A+C can each be considered representatives of single demes, while the samples in which morph B was pooled with the morphs A and C cannot.

Nei's genetic distances (D), ranging between 0.02 and 0.32, and Rogers' genetic distances, ranging between 0.087 and 0.317, are shown in table 2. The dendrogram (fig. 9) resulting from an UPGMA on Rogers' genetic distances has a very high cophenetic correlation (0.99), indicating that it accurately reflects the pattern of genetic variation in the matrix of genetic distances (Sneath and Sokal, 1973). An UPGMA using Nei's genetic distances gave similar results.

Discussion

The fact that the allozyme system buffer combinations that work best for *Fungia* (*Danafungia*) *fralinae*, *F.* (*D.*) *scruposa*, *F.* (*Pleuractis*) *gravis*, *F.* (*Verrillofungia*) *repanda* and *F.* (*V.*) *scabra* do not give any clear results for the *Fungia* (*Cycloseris*) specimens, could be an indication that the allozymes of the latter taxon differ considerably from those of the former taxa. Therefore it might be more appropriate

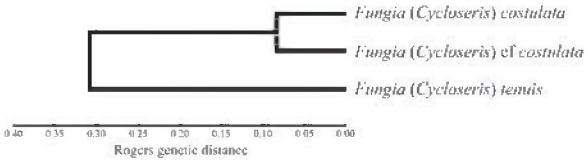


Fig. 9. UPGMA dendrogram based on Rogers' genetic distances for the three samples (cophenetic correlation = 0.99).

to refer to *Cycloseris* as a genus. DNA-analyses of Fungiidae also support this view (Chapter 3).

A significant deviation of Hardy Weinberg was found when the alleles of all the specimens were pooled. This indicates that they should not be considered representatives of a single panmictic population. No proof was found for a reproduction barrier between *F.* (*C.*) *costulata* offshore morphs and *F.* (*C.*) *costulata* nearshore morphs. Pooling their alleles, no deviation of Hardy Weinberg was found. They should therefore be referred to as phenotypes within *F.* (*C.*) *costulata*.

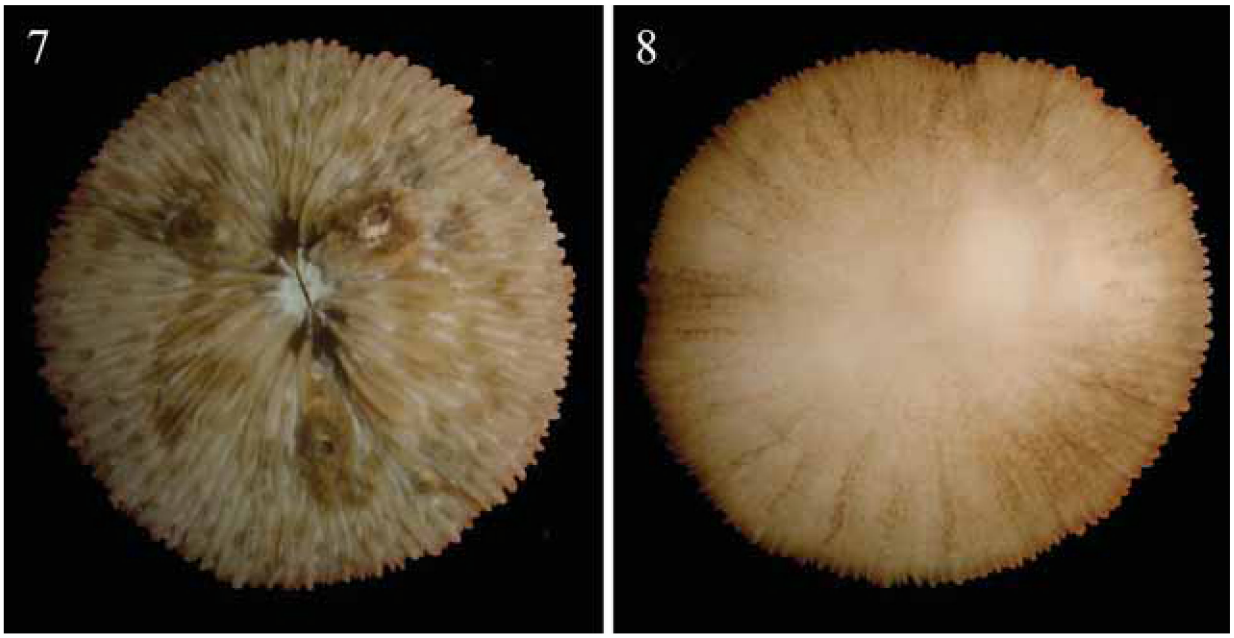
Nei's and Rogers' genetic distances and the resulting dendrogram (fig. 9) clearly show that there is very little to no gene flow between *F.* (*C.*) *tenuis* and *F.* (*C.*) *costulata* at Bone Baku reef. In total 77% of all alleles scored for *F.* (*C.*) *tenuis* were not present in the specimens of both forms of *F.* (*C.*) *costulata*, and vice versa 95% of the alleles scored for *F.* (*C.*) *costulata* were only accounting for 9% in *F.* (*C.*) *tenuis*. These results combined with the morphological differences, i.e. the roughness of the costae, the mouth coloration, skeletal strength and sliminess of the mucus, support the view that *Fungia* (*Cycloseris*) *costulata* Ortmann, 1889, and *F.* (*C.*) *tenuis* Dana, 1864, are two valid species; and that *F.* (*C.*) *costulata* has a nearshore ecomorph that may be related to low-salinity sea water.

Acknowledgements

We would like to thank drs P. v. Bragt from the Hoge Laboratorium School, Breda, the Netherlands, for pro-

Table 2 Rogers' (below diagonal) and Nei's (above diagonal) genetic distances between the samples.

Sample	***F.* (*C.*) *costulata***	***F.* (*C.*) cf *costulata***	***F.* (*C.*) *tenuis***
F.* (*C.*) *costulata	0	0.02	0.30
F.* (*C.*) cf *costulata	0.09	0	0.32
F.* (*C.*) *tenuis	0.31	0.32	0



Figs 7-8. Upper and lower surface of *Fungia* (*Cycloseris*) *tenuis*. Scale = 1:1.

viding the space and equipment to do the preliminary allozyme electrophoresis study in the Netherlands. Dr. A. Noor is thanked for his help concerning the permits and facilities enabling research off Makassar, Indonesia. This study was supported by WOTRO (grant nr. W 82-249).

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3

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

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

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Key words: coral reefs; Scleractinia; Fungiidae; *Fungia*; taxonomy; Cytochrome Oxidase I; Internal Transcribed Spacer I & II; Indo-Pacific

Abstract

DNA samples from fungiid corals were used to reconstruct the phylogeny of the Fungiidae (Scleractinia), based on the markers COI and ITS I & II. In some cases coral DNA was isolated and sequenced from parasitic gastropods that have eaten from their host corals, by using fungiid-specific primers. Even though the present molecular phylogeny reconstructions largely reflect the one based on morphological characters by Hoeksema (1989), there are some distinct differences. Most of these are probably linked to parallel or convergent evolution. Most fungiid coral species live fixed to the substrate in juvenile stage and become detached afterwards. A loss of this ability to become free-living, appears to have induced similar reversals independently in two fungiid species. These species express ancestral, plesiomorphic character states, known from the closest relatives of the Fungiidae, like encrusting and multistomatous growth forms. Consequently, they were both placed in the genus *Lythophyllon* by Hoeksema (1989). However, the present 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 various cladograms that were based on either of the two markers. This may have been caused by one or more bottleneck events in the evolutionary history of that species, which resulted in a much faster average DNA mutation rate in *Ctenactis crassa* as compared to the other fungiid species. Furthermore, it was investigated whether the exclusion of intraspecifically variable base positions from molecular data sets might improve the phylogeny reconstruction. For COI and ITS I&II in fungiid corals this has three positive effects: (1) it raised the support values of most branches in the MrBayes, Parsimony and Neighbor Joining consensus trees, (2) it lowered the number of most parsimonious trees, and (3) it resulted in phylogeny reconstructions that more closely resemble the morphology-based cladograms. Apparently, the exclusion of intraspecific variation may give a more reliable result. Therefore, the present hypotheses about the evolutionary history of the fungiid corals are based on analyses of both the data sets with and without intraspecific variation.

Contents

Introduction

Most coral species (Scleractinia) show much ecophenotypical variation. Because of this and the low number of plesiomorph characters states, phylogeny reconstructions based on morphology are troublesome. Molecular analyses have helped to

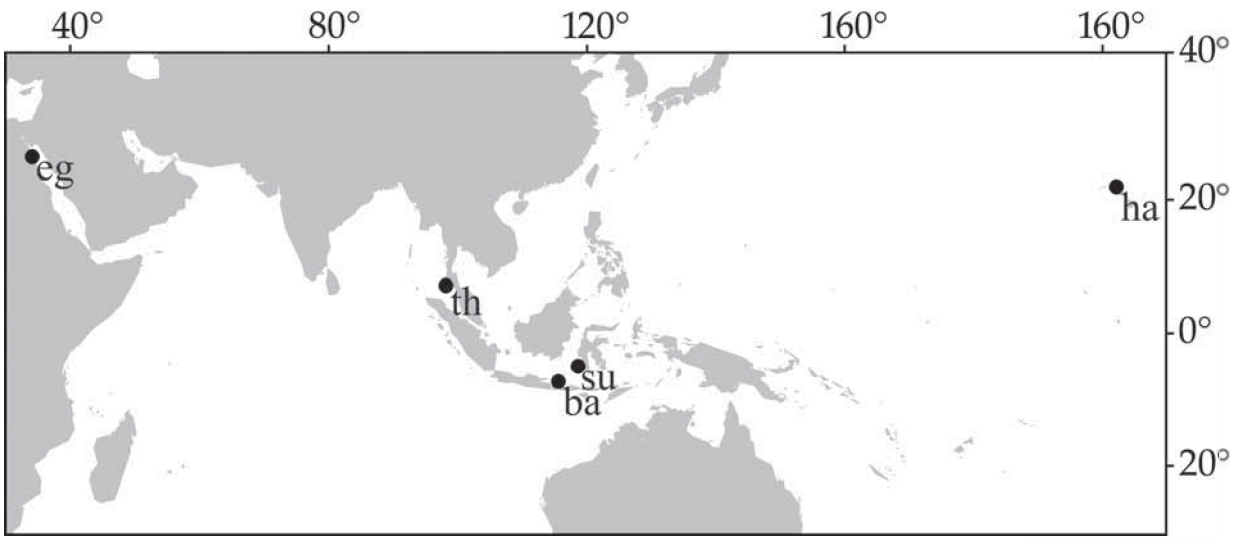

Fig. 1. The Indo-Pacific region, from the Red Sea to the Hawaiian Archipelago, illustrating the localities of the material used in this study (table 1). Abbreviations: ba, Bali, Indonesia [3]; ha, Oahu, Hawaii [5]; eg, Egypt (Red Sea) [1]; su, Sulawesi, Indonesia [4]; th, Phiphi Islands, Thailand [2].

shed more light upon their evolutionary history. Discrepancies between coral phylogeny reconstructions based on either morphological or molecular data are frequently found (Fukami et al., 2004). Even though such incompatible results have been found in various animal taxa, so-called reticulate evolution has been used most predominantly as the most likely explanation in corals (Diekmann et al., 2001). Other evolutionary history scenarios, like homeostasis, parallel or convergent evolution, and bottleneck events are considered less frequently. Such scenarios may at least partly be the cause of different mutation speeds in sister taxa or data saturation in general. The possibility of misidentifications because of e.g. the presence of cryptic species is usually also neglected.

Characters that are variable within species and within populations are commonly used in molecular phylogeny reconstructions. Even characters varying within individuals are usually included, like the base positions varying between the copies of ITS sequenced from one specimen. Such characters are often excluded in morphology-based phylogeny reconstructions. Therefore we have analysed the data sets both with and without intraspecifically variable base positions.

Material and methods

Sampling

The fungiid corals of which a DNA-sample was analysed, were collected during various expeditions in the Indo-Pacific conducted over the last thirty years by either the National Museum of Natural History Naturalis or by affiliated institutes. To get a good representation of intraspecific molecular variation, the specimens that were included for each species were preferably taken from populations far apart (fig. 1), i.e. Egypt (Red Sea), Thailand (Indian Ocean), Indonesia (Sulawesi and Bali: border of Indian and Pacific Oceans) and Hawaii (Pacific Ocean). The coral samples were preserved on ethanol 70% or 96%. All corals were identified twice, after photographs and/or specimens, independently by B.W. Hoeksema and A. Gittenberger.

DNA extraction and sequencing

Small pieces of coral tissue and skeleton were scraped off each specimen with a sterile scalpel to fill about

half a 1.5 ml tube. A mixture of 0.003 ml proteinase K (20 mg/ml) and 0.5 ml CTAB buffer, i.e. 2% CTAB, 1.4 M NaCl, 0.2% mercapto-ethanol, 20 mM EDTA and 100 mM TRIS-HCl pH8, was added to the tube for incubation at 60° C, for c. 15 hours. After incubation the solution was mixed with 0.5 ml Chloroform/ Isoamyl alcohol, and centrifuged for 10' at 8000 rpm. The supernatant was extracted, mixed with 0.35 ml isopropanol, put aside for c. 15 hours at 4° C and finally centrifuged for 10' at 8000 rpm to precipitate the DNA. The supernatant was discarded and the remaining DNA-pellet was washed at room temperature with 0.5 ml of an ethanol/ammonium-acetate solution for 30'. After centrifugation for 10' at 8000 rpm, this solution was discarded. The pellet was dried in a vacuum centrifuge and than dissolved in 0.020 ml MilliQ. The DNA quality and quantity were tested by electrophoresis of the stock-solution through an agarose gel and by analysing a 1:10 dilution of the stock in a spectrophotometer.

The ITS (Internal Transcribed Spacer I & II) and COI (Cytochrome Oxidase I) regions of the samples in table 1 were amplified using the primers and annealing temperatures (AT) as specified in table 2. Fungiid DNA specific COI primers were made by developing internal primers on the basis of fungiid sequences that were retrieved with Folmer Universal COI primers. The fungiid specific primer sequences were checked against the COI sequences (A. Gittenberger and E. Gittenberger, 2005; A. Gittenberger et al., chapter 8) of their epitoniid ecto-parasites (Mollusca: Gastropoda: Epitoniidae) and their coralliophilid endo-parasites (Mollusca: Gastropoda: Coralliophilidae) to make sure that they would not fit on the COI region of these gastropods. Although the DNA-extract of fungiids was used for most sequences, we also successfully sequenced the fungiid COI region using the DNA-extract of their parasitic gastropods. This was done to get data from localities where only the gastropods could be collected and no fungiid DNA material was available. Knowing the fungiid species with which the snails are associated, the retrieved sequences were checked with those of the same fungiid species from other localities. The PCR was performed in a Peltier Thermal Cycler PTC-200, using the following PCR- program: 1 cycle of 94°C for 4' and 60 cycles of 94°C for 5"; AT (Annealing Temperature; table 2) for 1'; 0.5°C/s to 60°C; 72°C for 1'. The optimalized PCR reaction mix consisted of 0.0025 ml PCR buffer (10x), 0.0005 ml MgCl2 (50 mM), 0.0010 ml forward primer (10 pM), 0.0010 ml reverse primer (10 pM), 0.0005 ml dNTP's (10 mM), 0.0003 ml Taq polymerase (5 units / 0.001 ml), 0.0132 ml MilliQ and 0.0010 ml 1:10 DNA stock-solution (= c. 100 ng DNA). For amplifying the ITS region, 0.0020 ml Qsolution (QIAGEN) was used instead of the 0.0020 ml MilliQ. After the PCR, the samples were kept on 4° C until purification by gel extraction using the QIAquick Gel Extraction Kit (QIAGEN). The samples were kept on 4°C until cycle sequencing. Cycle sequencing was done in both directions of the amplified region, with a program consisting of 45 cycles of 96°C for 10", 50°C for 5" and 60°C for 4'. The reaction mix used contained 0.0020 ml Ready Reaction Mix (Big DyeTM by PE Biosystems), 0.0020 ml Sequence Dilution-buffer, 0.0005 ml primer (5 pM forward or reverse primer solution) and 0.0055 ml amplified DNA (= half the PCR-product, evaporated to 0.0055 ml by vacuum centrifugation). The cycle sequence products were purified with Autoseq G50 columns (Amersham Pharmacia Biotech) and kept on 4°C until they were run on an ABI 377 automated sequencer (Gene Codes Corp.), using the water run-in protocol as described in the User Bulletin of the ABI Prism 377 DNA Sequencer (PE Biosystems, December 7, 1999). The consensus sequences that were used in further analyses, were retrieved by combining the forward and reverse sequences in Sequencher 4.05 (Genes Codes Corp.). The consensus sequences were checked against sequences from GenBank, i.e. the National Centre for Biotechnology Information (NCBI), as a check for contamination.

Sequence alignment and phylogenetic analyses

The COI and ITS sequences were aligned with ClustalW Multiple alignment, which is implemented in BioEdit 7.0.1 (Hall, 1999). The default parameters of these programs were used. Because MacClade 4. ClustalW had some difficulties aligning the ITS data set due to multiple gaps, some manual insertions, manual modifications were made in the resulting alignment. Afterwards the COI alignment was checked for stopcodons with MacClade 4.0 (Maddison and Maddison, 2000). Alignments are available from the authors.

Table 1. Specimens of which the COI and/or ITS marker was successfully sequenced. Locality data and availability of voucher specimen or photo is indicated.

Sequenced specimens	Locality [locality nr. fig.1]	Voucher Specimen or Photo	COI	ITS
Ctenactis albitentaculata	Indonesia, South Sulawesi, Spermonde Archipelago [4]	Spec	X	X
Ctenactis crassa	Thailand, Krabi, Phiphi Islands [2]	Photo	X	X
Ctanactis crassa	Indonesia, South Sulawesi, Spermonde Archipelago [4]	Spec	X	X
Ctenactis echinata	Egypte, Red Sea, Marsa Nakari [1]	Photo	X	X
Ctenactis echinata	Indonesia, South Sulawesi, Spermonde Archipelago [4]	Spec	X	X
Fungia (*Cycloseris*) *costulata*	Egypte, Red Sea, Marsa Nakari [1]	Photo	X	X
Fungia (*Cycloseris*) *costulata*	Thailand, Krabi, Phiphi Islands [2]	Photo	X	X
Fungia (*Cycloseris*) *costulata*	Indonesia, South Sulawesi, Spermonde Archipelago [4]	Spec	X	X
Fungia (*Cycloseris*) *cyclolites*	Thailand, Krabi, Phiphi Islands [2]	Photo	X	X
Fungia (*Cycloseris*) *fragilis*	Thailand, Krabi, Phiphi Islands [2]	Photo	X	
Fungia (*Cycloseris*) *fragilis*	Indonesia, South Sulawesi, Spermonde Archipelago [4]	Spec	X	
Fungia (*Cycloseris*) *sinensis*	Indonesia, South Sulawesi, Spermonde Archipelago [4]	Spec	X	X
Fungia (*Cycloseris*) *tenuis*	Thailand, Krabi, Phiphi Islands [2]	Photo	X	X
Fungia (*Cycloseris*) *tenuis*	Indonesia, South Sulawesi, Spermonde Archipelago [4]	Spec	X	
Fungia (*Cycloseris*) *vaughani*	Thailand, Krabi, Phiphi Islands [2]	Photo	X	X
Fungia (*Cycloseris*) *vaughani*	Indonesia, South Sulawesi, Spermonde Archipelago [4]	Spec	X	
Fungia (*Danafungia*) *fralinae*	Indonesia, South Sulawesi, Spermonde Archipelago [4]	Spec	X	X
Fungia (*Danafungia*) *scruposa*	Indonesia, South Sulawesi, Spermonde Archipelago [4]	Spec	X	X
Fungia (*Danafungia*) *horrida*	Indonesia, South Sulawesi, Spermonde Archipelago [4]	Spec		X
Fungia (*Fungia*) *fungites*	Indonesia, South Sulawesi, Spermonde Archipelago [4]	Spec	X	X
Fungia (*Lobactis*) *scutaria*	Egypte, Red Sea, Marsa Nakari [1]	Photo	X	X
Fungia (*Lobactis*) *scutaria*	Indonesia, South Sulawesi, Spermonde Archipelago [4]	Spec	X	
Fungia (*Lobactis*) *scutaria*	United States of America, Hawaii, Kaneohe Bay [5]	Spec	X	X
Fungia (*Lobactis*) *scutaria*	United States of America, Hawaii, Kaneohe Bay [5]	Spec	X	
Fungia (*Pleuractis*) sp. A (see A. & E. Gittenberger, 2005)	Egypte, Red Sea, Marsa Nakari [1]	Photo	X	X
Fungia (*Pleuractis*) *gravis*	Indonesia, South Sulawesi, Spermonde Archipelago [4]	Spec	X	X
Fungia (*Pleuractis*) *moluccensis*	Thailand, Krabi, Phiphi Islands [2]	Photo	X*	
Fungia (*Pleuractis*) *moluccensis*	Indonesia, South Sulawesi, Spermonde Archipelago [4]	Spec		X
Fungia (*Pleuractis*) *paumotensis*	Thailand, Krabi, Phiphi Islands [2]	Photo	X*	
Fungia (*Pleuractis*) *paumotensis*	Indonesia, South Sulawesi, Spermonde Archipelago [4]	Spec	X	X
Fungia (*Pleuractis*) *taiwanensis*	Indonesia, Bali, Tanjung Benoa [3]	Spec		X
Fungia (*Verrillofungia*) *concinna*	Thailand, Krabi, Phiphi Islands [2]	Photo	X*	

Fungia (*Verrillofungia*) *concinna*	Indonesia, South Sulawesi, Spermonde Archipelago [4]	Spec	X	X
Fungia (*Verrillofungia*) *repanda*	Thailand, Krabi, Phiphi Islands [2]	Photo	X*	
Fungia (*Verrillofungia*) *scabra*	Indonesia, South Sulawesi, Spermonde Archipelago [4]	Spec	X	X
Fungia (*Verrillofungia*) *scabra*	Indonesia, South Sulawesi, Spermonde Archipelago [4]	Spec	X	
Fungia (*Verrillofungia*) *scabra*	Indonesia, South Sulawesi, Spermonde Archipelago [4]	Spec	X	
Fungia (*Verrillofungia*) *spinifer*	Indonesia, South Sulawesi, Spermonde Archipelago [4]	Spec	X	X
Fungia (*Wellsofungia*) *granulosa*	Egypte, Red Sea, Marsa Nakari [1]	Photo		X
Fungia (*Wellsofungia*) *granulosa*	Indonesia, South Sulawesi, Spermonde Archipelago [4]	Spec	X	X
Halomitra clavator	Indonesia, South Sulawesi, Spermonde Archipelago [4]	Spec	X	X
Halomitra pileus	Thailand, Krabi, Phiphi Islands [2]	Photo	X*	
Halomitra pileus	Indonesia, South Sulawesi, Spermonde Archipelago [4]	Spec	X	X
Halomitra pileus	Indonesia, South Sulawesi, Spermonde Archipelago [4]	Spec	X	.
Heliofungia actiniformis	Indonesia, South Sulawesi, Spermonde Archipelago [4]	Spec	X	X
Heliofungia actiniformis	Indonesia, South Sulawesi, Spermonde Archipelago [4]	Spec	X	
Heliofungia actiniformis	Indonesia, South Sulawesi, Spermonde Archipelago [4]	Spec	X	
Heliofungia actiniformis	Indonesia, South Sulawesi, Spermonde Archipelago [4]	Photo	X**	
Herpolitha limax	Egypte, Red Sea, Marsa Nakari [1]	Photo	X*	
Herpolitha limax	Thailand, Krabi, Phiphi Islands [2]	Spec	X	X
Herpolitha limax	Indonesia, South Sulawesi, Spermonde Archipelago [4]	Spec	X	X
Lithophyllon undulatum	Indonesia, South Sulawesi, Spermonde Archipelago [4]	Spec	X	X
Lithophyllon undulatum	Indonesia, South Sulawesi, Spermonde Archipelago [4]	Spec	X	X
Lithophyllon mokai	Indonesia, South Sulawesi, Spermonde Archipelago [4]	Spec	X	X
Lithophyllon mokai	Indonesia, South Sulawesi, Spermonde Archipelago [4]	Spec	X	
Lithophyllon mokai	Indonesia, South Sulawesi, Spermonde Archipelago [4]	Spec	X	
Podabacia sp. A	Thailand, Krabi, Phiphi Islands [2]	Photo	X	
Podabacia sp. B	Thailand, Krabi, Phiphi Islands [2]	Photo	X	X
Podabacia crustacea	Indonesia, South Sulawesi, Spermonde Archipelago [4]	Spec	X	X
Podabacia crustacea	Indonesia, South Sulawesi, Spermonde Archipelago [4]	Spec	X	
Podabacia motuporensis	Indonesia, South Sulawesi, Spermonde Archipelago [4]	Spec	X	X
Podabacia motuporensis	Indonesia, South Sulawesi, Spermonde Archipelago [4]	Spec	X	
Polyphyllia talpina	Indonesia, South Sulawesi, Spermonde Archipelago [4]	Spec	X	X
Sandalolitha dentata	Thailand, Krabi, Phiphi Islands [2]	Photo	X	X
Sandalolitha dentata	Indonesia, Bali, Tanjung Benoa [3]	Spec		X
Sandalolitha dentata	Indonesia, South Sulawesi, Spermonde Archipelago [4]	Spec	X	X
Sandalolitha robusta	Indonesia, South Sulawesi, Spermonde Archipelago [4]	Spec	X	X
Zoopilus echinatus	Indonesia, South Sulawesi, Spermonde Archipelago [4]	Spec	X	X

* Sequence obtained from DNA extract of *Epitonium* spec. ** Sequence obtained from DNA extract of *Leptoconchus* spec.

Table 2. Primer sequences, annealing temperatures and sources.

Primer	Annealing temp.	Primer seq.	Primer length	Reference
COI Folmer Universal primer (LCO-1490)	53	5`-GGT CAA CAA ATC ATA AAG ATA TTG G-3`	25-mer	Folmer *et al.*, 1994
COI Folmer Universal primer (HCO-2198)	53	5`-TAA ACT TCA GGG TGA CCA AAA ATC A-3`	25-mer	Folmer *et al.*, 1994
COI mod F (FungCO1for1)	53	5`-CTG CTC TTA GTA TGC TTG TA-3`	20-mer	Newly developed primer
COI mod R (FungCO1rev2)	53	5`-TTG CAC CCG CTA ATA CAG -3`	18-mer	Newly developed primer
TW5 (ITS F)	45	5`-CTT AAA GGA ATT GAC GGA AG-3`	20-mer	White *et al.*, 1990
JO6 (ITS R)	45	5`-ATA TGC TTA AGT TCA GCG GGT-3`	21-mer	Diekmann *et al.*, 2001
ITS mod F (ITS-F-Bastian)	45	5`-AGA GGA AGT AAA AGT CGT AAC AAG-3`	24-mer	Our lab

The phylogenetic analyses were performed on six data sets, i.e. the full COI data set, the ITS data set and the combined COI+ITS data set, and finally these three data sets without the intraspecifically varying base positions. The latter three data sets were included to get an idea of the amount of "false" versus "good" phylogenetic signal that may be present in relatively fast mutating base-positions. To get a better idea of which positions vary intraspecifically, we included conspecific samples from distant localities like e.g. Indonesia and the Red Sea (table 1; fig. 1).

The data sets were analysed with Paup 4.0b10 (Swofford, 2002). The homogeneity of base frequencies in the sequences was tested with chi-square for the full data sets of ITS and COI, and additionally for COI for the first, second and third codon positions separately. To test for the presence of phylogenetic signal we performed the G1 skewness statistic based on 1000 random trees (Hillis and Huelsenbeck, 1992) and the permutation test (Archie, 1989; Faith and Cranston, 1991) with 100 replicates, a full heuristic search, TBR algorithm, steepest descent and 1000 random addition replicates per replicate.

PAUP 4.0b10 was used for maximum parsimony and neighbor joining analyses. MrBayes 3.0B4 (Ronquist and Huelsenbeck, 2003) was used for a Bayesian inference analysis. To find the most parsimonious tree(s), a full heuristic search was done with 1000 random addition replicates, TBR algorithm and steepest descent. In addition a non-parametric parsimony bootstrap analysis was done with a full heuristic search, 1000 bootstrap replicates, a maximum duration of one hour per replicate, one random addition per replicate and TBR algorithm. A Neighbor Joining bootstrap analysis was done with 10,000 bootstrap replicates. Bayesian inference was performed in MrBayes 3.0B4 with five incrementally (T=0.20) heated Markov chains and a cold one, which were run 4,000,000 generations and sampled once every 50 generations, using the best-fit model for nucleotide substitution, i.e. HKY+I+G. The best-fit model was calculated by both the likelihood ratio test and the Akaike information criterion in MrModeltest 2.1 (Nylander, 2004) based on the calculated likelihood scores of 24 models of nucleotide substitution. To determine the burnin, the loglikelihoods of saved trees were plotted in a Microsoft Excel graph to see from where on they become stationary.

Results

The COI data set (table 1) consist of 63 sequences of 500 bases each. The data set does not include any gaps or stopcodons. The ITS data set (table 1) consists of 45 sequences with lengths varying between 604 and 618 bases. The length varies due to multiple gaps. Results from the statistical analyses are represented in the tables 3-4. The parsimony analyses are

Table 3. Results from parsimony analyses (heuristic search, 1000 random addition sequences, TBR swapping algorithm with steepest descent) for the data sets that were analysed.

Data set	Number of most parsimonious trees	Tree score	Consistency index	Rescaled consistency index	Parsimony informative base positions
COI with intraspecific variation	226	92	0.783	0.652	23
COI without intraspecific variation	112	83	0.807	0.652	18
ITS with intraspecific variation	241	300	0.530	0.367	77
ITS without intraspecific variation	176	105	0.705	0.518	29
COI & ITS with intraspecific variation	791	377	0.589	0.439	95
COI & ITS without intraspecific variation	36	220	0.695	0.583	61

presented in table 3 together with the number of informative base positions for both kinds of data sets (with and without intraspecifically varying base positions). For the ITS alignment without intraspecific variation, the likelihood ratio test and the Akaike information test resulted in different substitution models when analysed by Mr Modeltest. We use the result from the likelihood ratio test, because it is in congruence with the result obtained by both the likelihood ratio test and the Akaike information test on the data set without intraspecific variation. Base frequencies in the complete data set and in the first, second and third codon positions separately, are not significantly inhomogeneous across taxa, i.e. $P = 1.00$ in all cases.

In all cases the consistency index of the most parsimonious trees was higher for the data set without the intraspecifically variable base positions (table 3). The data sets without these positions resulted in less most parsimonious trees than the data sets with intraspecifically variable base positions included. The combined COI+ITS data set without intraspecific variation results in the lowest number of most parsimonious trees, i.e. 36 instead of 791 when intraspecific variation is included (table 3). This supports the positive effect of [1] excluding intraspecific variation and [2] including more than one marker in the analysis. The found lower tree-scores do not necessary have anything to do with a false or good phylogenetic signal in the excluded positions, because one expects them to be lower in any data set with fewer characters.

The phylogeny reconstructions based on the six data sets, i.e. the full COI data set, the ITS data set and the combined COI+ITS data set, and these three data sets without the intraspecifically varying base positions, are illustrated in figures 2-7. Here, we only present the results of the MrBayes analyses. Neighbor joining, maximum parsimony and parsimony bootstrap analyses gave similar results, which will be provided by the authors on request.

General discussion

Our discussion starts from the six molecular phylogeny reconstructions that result from the Bayesian analysis (figs 2-7). Because the maximum parsimony and neighbor joining analyses gave similar results, they support the conclusions that are made below. In this study we have focussed on the following questions:

[1] can a gastropod parasite successfully be used as a source for both its own DNA and that of its coral host;

[2] what is the effect of excluding all intraspecifically variable base positions when reconstructing a molecular phylogeny;

Table 4. Results of Chi-square-, G1 skewness- and permutation- tests to check for phylogenetic signal and consistency of the analysed data sets.

	Chi square test				
Type of data set	**X^2**	**df**	**P**	**G1 skewness test**	**Permutation test**
COI with intraspecific variation	4.0	75	1.00	-0.627	P<0.01
COI without intraspecific variation	3.7	63	1.00	-0.761	P<0.01
ITS with intraspecific variation	12.5	141	1.00	-0.529	-*
ITS without intraspecific variation	4.5	105	1.00	-0.372	-*
COI & ITS with intraspecific variation	7.1	123	1.00	-0.536	-*
COI & ITS without intraspecific variation	4.0	99	1.00	-0.570	-*

* We were not able to obtain this result due to extremely long calculation times.

[3] what is the most likely phylogeny of the fungiid corals, taking all kinds of data into account;
[4] do all the genera and subgenera of the Fungiidae that are recognized in the literature represent monophyletic taxa;
[5] what classification of the Fungiidae represents the phylogeny of that family best and how should the nomenclature be adapted to reflect this?
One source for two sequences

By using specific primers, DNA of the coral and that of its parasite could be amplified successfully with certainty (table 1). Since the entire body of the snails were used, it remains unclear whether the coral DNA was isolated from the stomach of the snail, or from other parts of the parasite that are in frequent intensive contact with the coral.

Excluding intraspecific variation

There are differences in the phylogeny reconstructions based on the COI and ITS data sets with intraspecifically variable base positions (figs 2, 4) in comparison to those constructed with these positions excluded (figs 3, 5). The "better" phylogeny reconstruction is here assumed to be the one that is most similar to the phylogenies that were based on other, unrelated data sets, e.g. on another marker or on morphology.

In phylogenies resulting from the molecular analyses of the ITS data sets and the combined COI+ITS data sets, the sequence of *Verrillofungia concinna* clusters far away from the sequences of the other *Verrillofungia* species and *Lithophyllon undulatum* when intraspecifically variable base positions are included (figs 2, 6). When these are excluded, all *Verrillofungia* and *Lithophyllon undulatum* form a monophyletic group, with support values of 51 and 100, based on respectively the ITS (fig. 3) and the combined COI+ITS data set (fig. 7). This result is also supported by the analyses of the COI data set (figs 4-5) and gives an indication of what error may happen when intraspecifically variable base positions are included in molecular analyses.

A similar phenomenon seems to have influenced the position of *Heliofungia fralinae* in the phylogeny reconstruction based on the ITS data set with intraspecifically variable base positions included. There this species clusters with a significant support value of 65 (fig. 2) as the sister species of *Verrillofungia concinna*. In the analysis of the ITS data set without these base positions (fig. 3), it clusters much more closely to the *Heliofungia actiniformis* sequence, with which it forms a strongly supported monophyletic group in the other molecular analyses (figs 4-7), i.e. with support values of 64, 74, 96 and 100, respectively.

A final example of the misleading effect of the use of intraspecifically variable base positions in phylogeny reconstruction is the position of the clade with *Pleuractis granulosa*, *P. paumotensis*, *P. taiwanensis* and *P. moluccensis*. These species seem to be distantly related to *Pleuractis gravis*, *P.* spec. A and the *Cycloseris* in the phylogeny based on ITS including the intraspecific variation (fig. 2), while it forms a significantly supported monophyletic group with these species in all other analyses (figs 3-7).

Table 5. Proposed classification of the Fungiidae.

Genus	Species
Fungia	*F. fungites*
Cycloseris [used to be *Fungia* (*Cycloseris*)]	*C. costulata; C. cyclolites; C. curvata; C. distorta; C. fragilis; C. hexagonalis; C. mokai* [used to be *Lithophyllon mokai*]; *C. sinensis; C. tenuis; C. somervillei; C. vaughani*
Danafungia [used to be *Fungia* (*Danafungia*)]	*D. horrida; D. scruposa*
Lobactis [used to be *Fungia* (*Lobactis*)]	*L. scutaria*
Pleuractis [used to be *Fungia* (*Pleuractis*)]	*P. granulosa* [used to be *Fungia* (*Wellsofungia*) *granulosa*]; *P. gravis; P. moluccensis; P. paumotensis*
Verrillofungia [used to be *Fungia* (*Verrillofungia*)]	*V. concinna; V. repanda; V. spinifer; V. scabra*
Cantharellus	*C. doederleini; C. noumeae*
Ctenactis	*C. albitentaculata; C. crassa; C. echinata*
Halomitra	*H. clavator; H. pileus*
Heliofungia	*H. actiniformis; H. fralinae* [used to be *Fungia (Danafungia) fralinae*]
Herpolitha	*H. limax*
Lithophyllon	*L. undulatum*
Podabacia	*P. crustacea*
Polyphyllia	*P. novaehiberniae; P. talpina*
Sandalolitha	*S. dentata; S. robusta*
Zoopilus	*Z. echinatus*

Even though the COI data set has less intraspecifically variable base positions than the ITS data set, these positions do seem to induce a similar error (figs 4-5). Most monophyletic groups that are strongly supported by the analyses of the other data sets (see the genus discussions for details) have higher support values, or are only present in the COI based phylogeny reconstruction, when the intraspecific variation is excluded (fig. 5). Excluding characters with a good phylogenetic signal would logically result in lower bootstrap values and a more random final tree, which, because of the many possible trees, is very unlikely to become more similar to the morphological phylogeny only by chance.This is shown for the clades [1] *Halomitra* spp. and *Danafungia scruposa*, [2] *Heliofungia actiniformis* and *Heliofungia fralinae*, and [3] *Cycloseris* spp., *Lithophyllon undulatum*, and *Pleuractis* spp., which are supported by values of 74, 64 and 74, respectively, in figure 4, and by 82, 74 and 81 in figure 5. In one case, a clade that is supported by the other data sets, has a distinctly lower support value in figure 4 in comparison to figure 3. This concerns the clade with *Verrillofungia* spp. and *Lithophyllon undulatum*, of which the support value of 71 (fig. 4) drops to 37 when intraspecific variation is excluded (fig. 5).

Even though the support values are low, there are two clades in figure 5 that are absent in figure 4, which are strongly supported by the analysis of the morphological data set (fig. 8; Hoeksema, 1989) and/or the other molecular data sets (figs 2-3, 6-7). This concerns the clade in figure 4 where *Halomitra clavator* is more closely related to *Danafungia scruposa* than to *Halomitra pileus*, making *Halomitra* paraphyletic. In figure 5 and in all other molecular and morphological analyses *Halomitra* is monophyletic. A second case is the clade with *Herpolitha limax*, *Ctenactis albitentaculata* and *C. echinata*, which does not form a monophyletic group with the clade containing *Polyphyllia talpina* and *Ctenactis crassa* in figure 4, while it forms a monophyletic group in figure 5. Even though *C. crassa* is not even closely related to *Ctenactis albiten-*

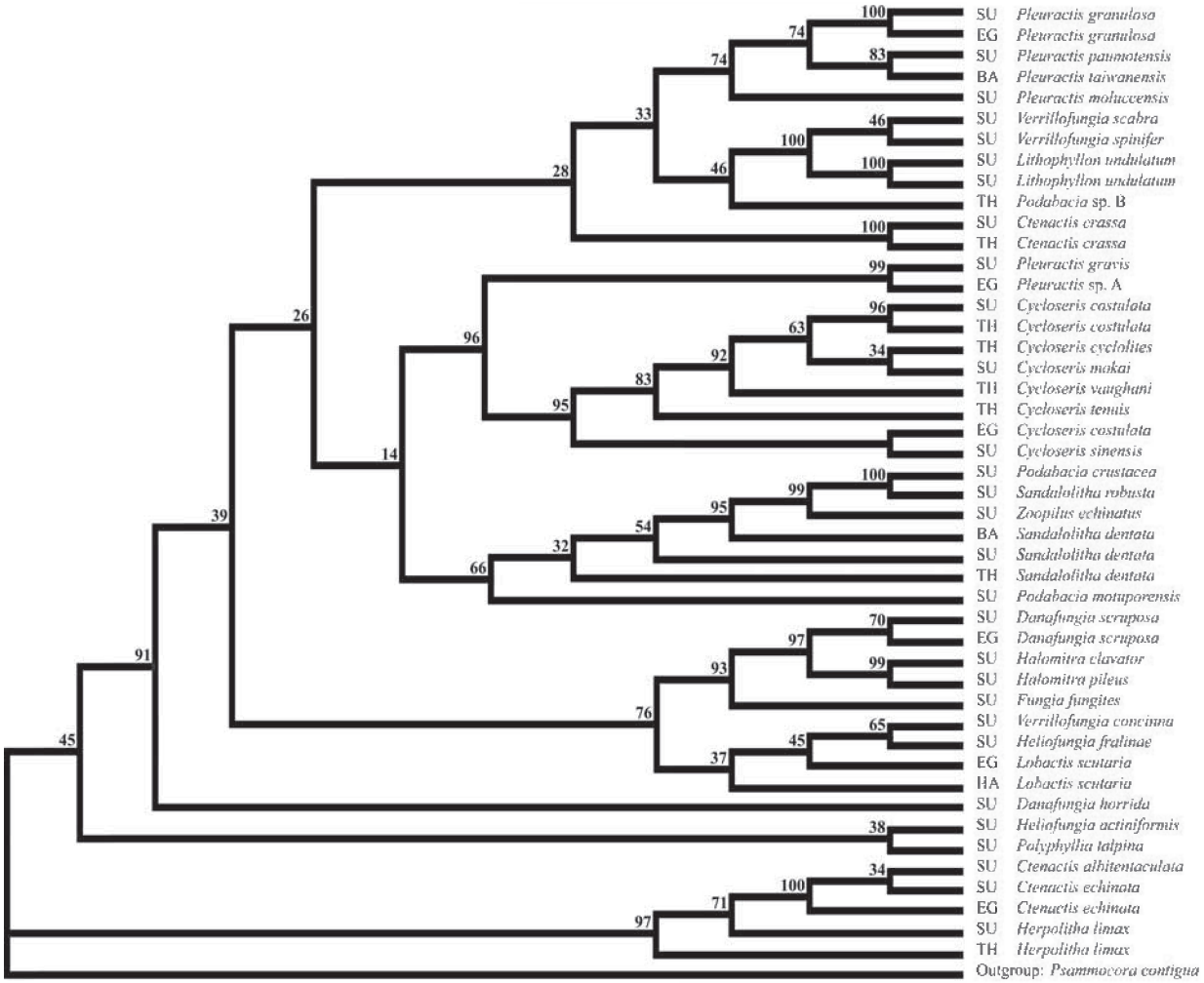

Fig. 2. Bayesian analysis of ITS data set with intraspecific variation: 50% majority rule consensus tree with compatible groupings. Locality abbreviations (fig. 1): ba, Bali, Indonesia; ha, Oahu, Hawaii; eg, Egypt (Red Sea); su, Sulawesi, Indonesia; th, Phiphi Islands, Thailand. Taxonomy as in proposed classification (table 5).

taculata and *C. echinata* in all other molecular phylogenies, it forms a sister clade (together with *Polyphyllia talpina*) of the clade with *C. albitentaculata* and *C. echinata* in figure 5. As is discussed in its genus description, *C. crassa* seems to have gone through a period with an accelerated mutation rate in comparison to the other fungiid species, resulting in its inconsistent position in the molecular phylogeny reconstructions.

Some of the above mentioned "errors" were resolved when the COI and ITS data sets were combined before analysing them (figs 6-7). One could expect this effect because autapomorphic character states, which are often present in saturated base positions, have more influence in small data sets than in large ones. In the latter case they may be neutralized while supporting incongruent results. Characters or base positions that support a similar hierarchy will than automatically gain influence.

Even though the molecular phylogeny reconstructions of the Fungiidae calculated without intraspecific variation seem to be more reliable in general, excluding this variation may also have disadvantages. It is advisable to analyse molecular data sets both with and without intraspecifically variable base positions to acquire the optimal informative contents. Furthermore the analysis of a data set that includes two markers instead of a single one, may result in a phylogeny reconstruction that has higher support

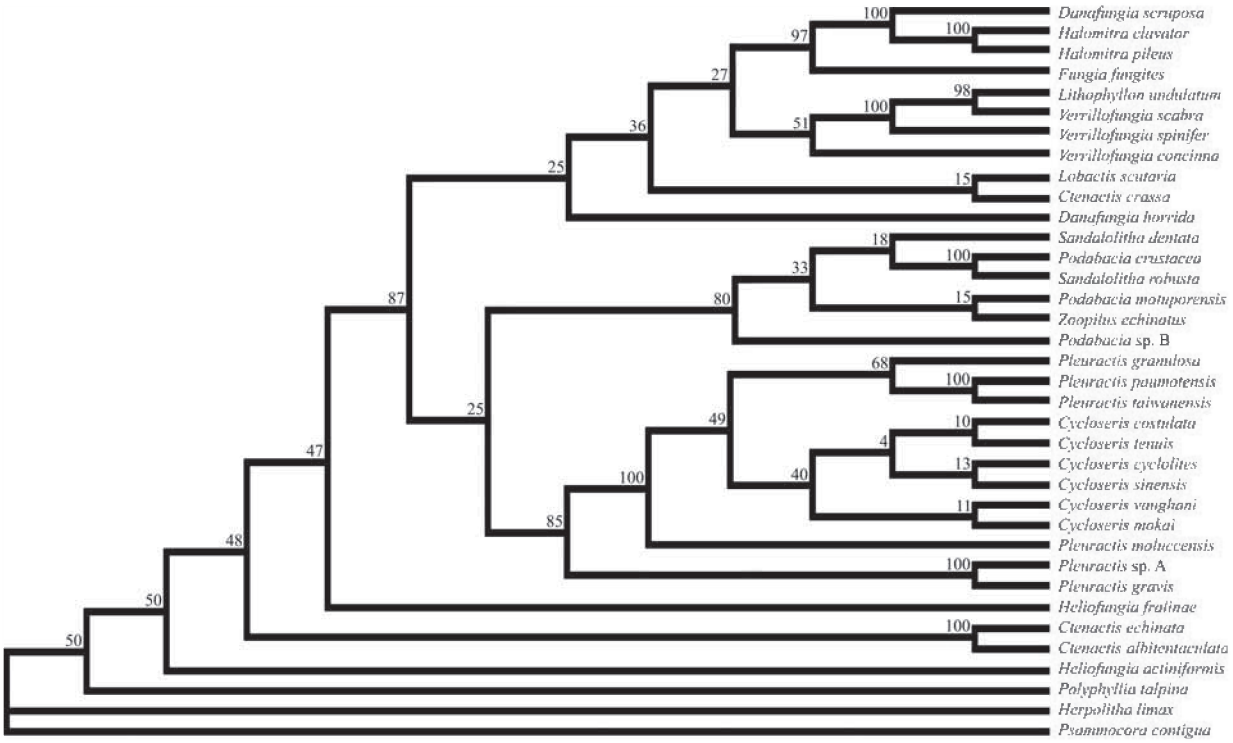

Fig. 3. Bayesian analysis of ITS data set without intraspecific variation: 50% majority rule consensus tree with compatible groupings. Taxonomy as in proposed classification (table 5).

values and has relatively more in common with a phylogeny based on morphology.

A classification of the Fungiidae

None of the taxa of the genus group that were accepted by Hoeksema (1989), i.e. *Ctenactis*, *Fungia*, *Halomitra*, *Lithophyllon*, *Podabacia*, and subgenera, i.e. *Cycloseris*, *Danafungia*, *Verrillofungia*, *Pleuractis*, comes out as monophyletic in all phylogeny reconstructions when more than one species was included in the analyses (table 1) (figs 2-7). This can be explained by a misinterpretation of morphological data, a misinterpretation of molecular data, or by the low amount of interspecific genetic variation in the studied markers. Here we discuss all the redefined (sub)genera on the basis of the newly acquired molecular data and the morphological analyses published by Hoeksema (1989). We focus on those nominal taxa that turn out as paraphyletic in one or more of the reconstructed phylogenies. The taxonomical revisions that are necessary to make the taxa in the Fungiidae monophyletic are summarized in table 5. Each of these revisions is discussed in the following paragraphs.

Genus *Cantharellus* Hoeksema and Best, 1984

Type species: *Cantharellus noumeae* Hoeksema and Best, 1984.

Molecular analysis: No specimens were available for DNA-analyses.

Genus description: The description of Hoeksema (1989: 209) remains sufficient.

Genus *Ctenactis* Verrill, 1864

Type species (by original designation): *Madrepora echinata* Pallas, 1766.

Molecular analysis: In all molecular phylogeny reconstructions (figs 2-7) *Ctenactis echinata* and *C. albi-*

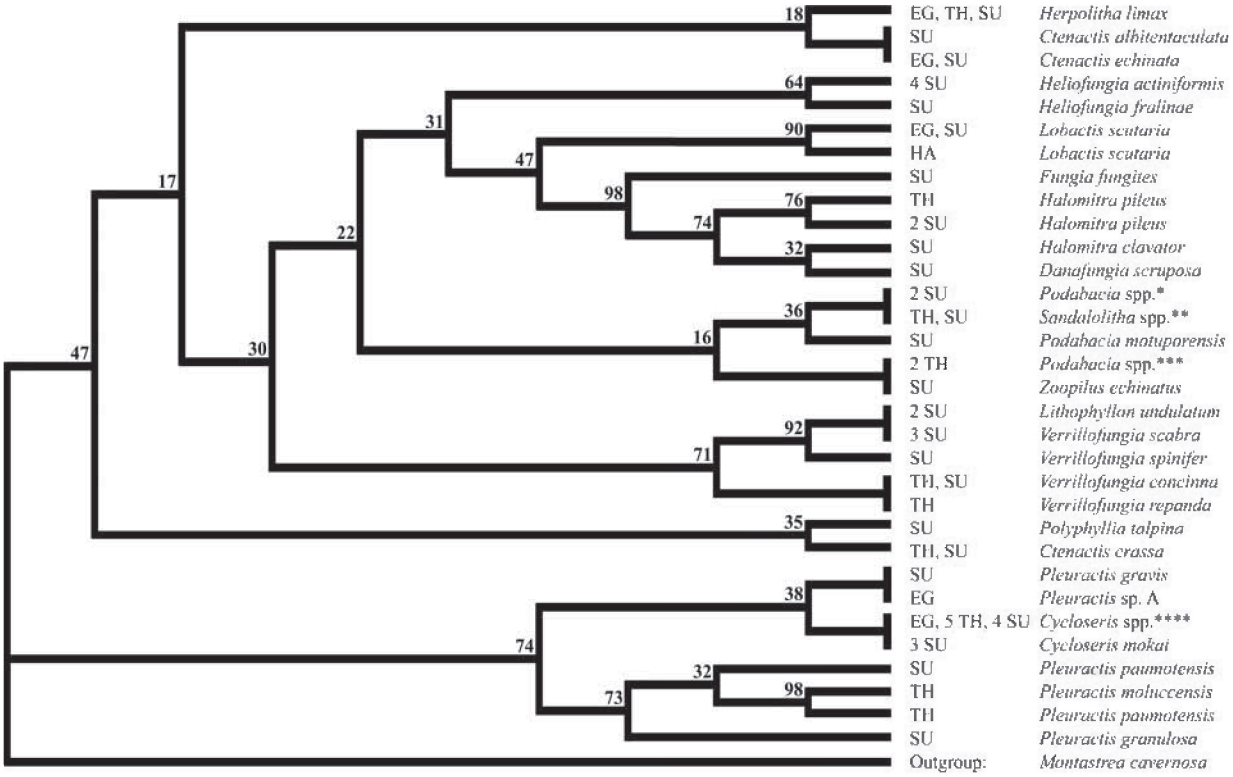

Fig. 4. Bayesian analysis of COI data set with intraspecific variation: 50% majority rule consensus tree with compatible groupings. Locality abbreviations (fig. 1): ba, Bali, Indonesia; ha, Oahu, Hawaii; eg, Egypt (Red Sea); su, Sulawesi, Indonesia; th, Phiphi Islands, Thailand. Taxonomy as in proposed classification (table 5).
Numbers with localities refer to the number of identical sequences.
* *Podabacia crustacea* (su), *P. motuporensis* (su)
** *Sandalolitha dentata* (th & su), *S. robusta* (su)
*** *Podabacia* sp. A (th), *P.* sp. B (th)
**** *Fungia* (*Cycloseris*) *costulata* (eg, th), *F.* (*C.*) *cyclolites* (th), *F.* (*C.*) *fragilis* (th, su), *F.* (*C.*) *sinensis* (th), *F.* (*C.*) *tenuis* (th, su), *F.* (*C.*) *vaughani* (th, su)

tentaculata cluster together with strong support values. In no case these two species form a monophyletic group with *Ctenactis crassa*. These results do not necessarily indicate that *Ctenactis* is paraphyletic however. The position of *C. crassa* in the molecular phylogenies is much less consistent and poorly supported than the position of any of the other fungiid species that were included. These inconsistencies in the results of the analyses of the COI and ITS data sets may be related to the fact that much more mutations have occurred in the *C. crassa* clade than in any of the other clades (the data and alignments that illustrate these high mutation numbers can be obtained from the authors). The average mutation rate in the *C. crassa* clade is much higher than in all other clades and may have caused the inconsistencies. Because the DNA of the studied markers of *C. crassa* has evolved distinctly different from the DNA in the other fungiid species, the position of *C. crassa* in these phylogenies is unreliable. Therefore and on the basis of the morphology of the three species (Hoeksema, 1989: 154-166) we here conclude that the nominal genus *Ctenactis* refers to a monophyletic group. Possibly the *C. crassa* population has gone through one or more bottleneck events, which could explain the relatively high number of mutations in the COI and ITS regions.

Except for the sequences of *Ctenactis crassa*, the sequences of the genera *Ctenactis*, *Herpolitha* and *Polyphyllia* cluster in one monophyletic group or relatively close to each other (fig. 7). In general they cluster as the most basal lineages of the Fungiidae. These results suggest that the elongated form, the

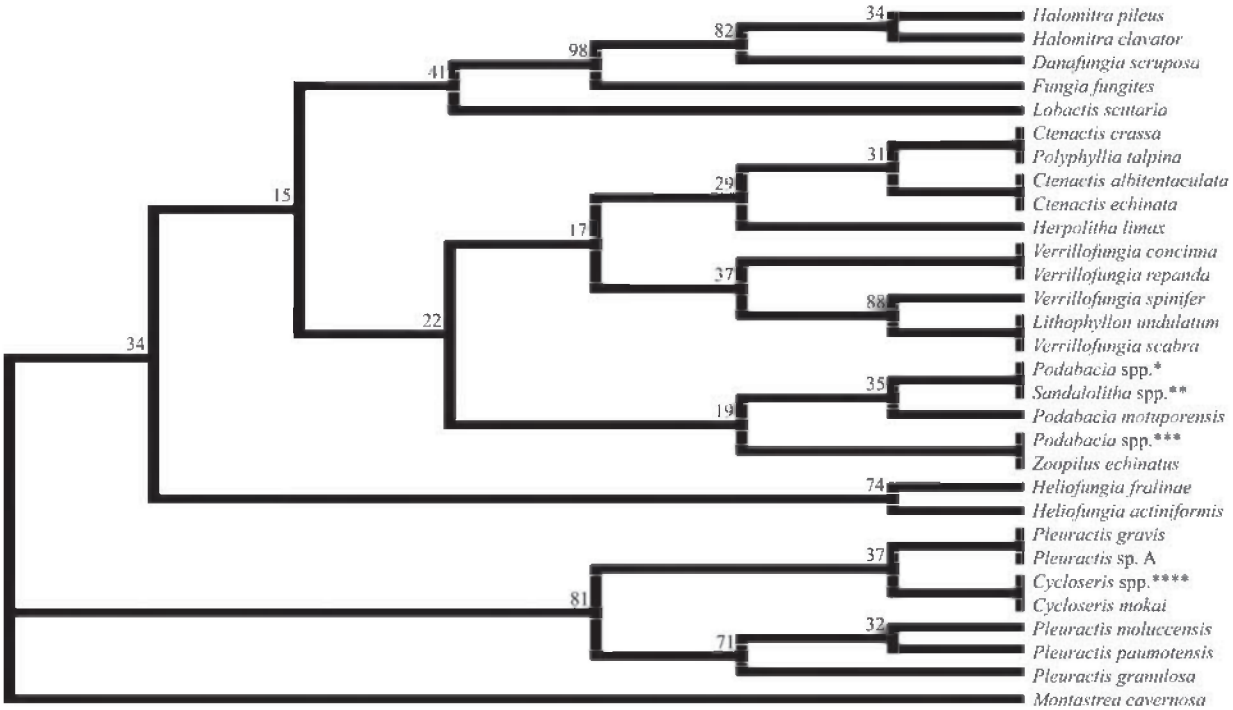

Fig. 5. Bayesian analysis of COI data set without intraspecific variation: 50% majority rule consensus tree with compatible groupings. Taxonomy as in proposed classification (table 5).
* *Podabacia crustacea*, *P. motuporensis*
** *Sandalolitha dentata*, *S. robusta*
*** *Podabacia* sp. A, *P.* sp. B
**** *Fungia* (*Cycloseris*) *costulata*, *F.* (*C.*) *cyclolites*, *F.* (*C.*) *fragilis*, *F.* (*C.*) *sinensis*, *F.* (*C.*) *tenuis*, *F.* (*C.*) *vaughani*

relatively long central burrow and the potential to form several stomata in this burrow, are plesiomorph character states. These character states are considered to be autapomorphies in the phylogeny based on morphology (fig. 8) by Hoeksema (1989), with *Herpolitha* and *Polyphyllia* forming a clade to which *Ctenactis* is only very distantly related.

Genus description: The description of Hoeksema (1989: 153-154) remains sufficient.

Genus *Fungia* Lamarck, 1801

Type species: *Fungia fungites* (Linnaeus, 1758)

Molecular analysis: In all molecular phylogenies (figs 2-7) *Fungia fungites* clusters as a sister taxon of a clade with *Halomitra pileus*, *H. clavator* and *Fungia* (*Danafungia*) *scruposa*, making *Fungia* paraphyletic.

The molecular results also consistently imply that *Fungia* is more closely related to the genera *Lithophyllon*, *Podabacia*, *Sandalolitha* and *Zoopilus*, than to its alleged subgenera *Wellsofungia*, *Pleuractis* and *Cycloseris*, making *Fungia* polyphyletic. These molecular results are fully supported by morphology (fig. 8; Hoeksema, 1989). To make *Fungia* monophyletic we suggest that its so-called subgenera are upgraded to the genus level.

Genus description: The description of this genus is similar to that of its type species (see Hoeksema, 1989: 116).

Genus *Cycloseris* Milne Edwards and Haime, 1849 (= upgraded subgenus; see the molecular analysis of the "Genus *Fungia*")

Type species: *Fungia cyclolites* Lamarck, 1815.

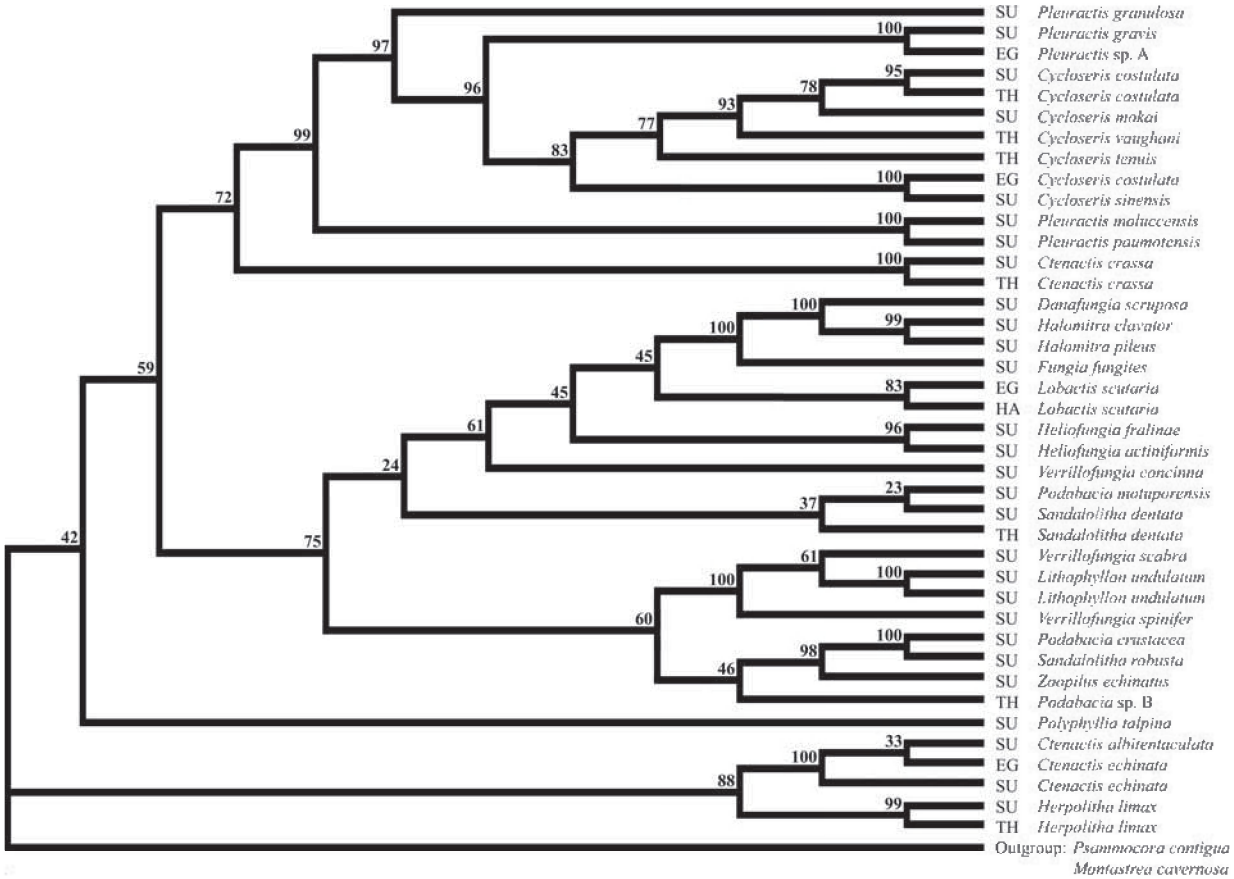

Fig. 6. Bayesian analysis of the combined ITS & COI data set with intraspecific variation: 50% majority rule consensus tree with compatible groupings. Locality abbreviations (fig. 1): ba, Bali, Indonesia; ha, Oahu, Hawaii; eg, Egypt (Red Sea); su, Sulawesi, Indonesia; th, Phiphi Islands, Thailand. Taxonomy as in proposed classification (table 5).

Molecular analysis: In all molecular phylogenies (figs 2-7) the *Cycloseris* sequences cluster together with the sequences of *Lithophyllon mokai*. Analyses based on the ITS and the combined data sets of COI and ITS (figs 2-3, 6-7) indicate that *L. mokai* is not a basal lineage in the *Cycloseris* clade. It may even be the sister species of the type species of *Cycloseris*, i.e. *Fungia* (*Cycloseris*) *cyclolithes*. We therefore conclude that *Lithophyllon mokai* Hoeksema, 1989 should be named *Cycloseris mokai* (Hoeksema, 1989).

Specimens of the species *Cycloseris mokai* have a stronger stem than the other species in the genus and therefore do not break loose from the substrate. This may have resulted in encrusting specimens which are poly-stomatous, instead of free-living and monostomatous as in all other *Cycloseris* species. This hypothesis is supported by the morphology of *Lithophyllon undulatum*, another fungiid species with encrusting, polystomatous specimens, similar to those in *Cycloseris mokai*. The sister species of *L. undulatum* (figs 2-7), viz. *Verrillofungia* species, also have free-living, monostomatous specimens. This is a classic example of convergent evolution. In both cases, becoming sessile may have caused the corals to become encrusting and polystomatous. Hoeksema (1989: 258) already predicted for Fungiidae on the basis of morphology, that reversals like species that loose their ability to detach themselves from the substrate, may be difficult to recognize because they represent a multistate character (i.e. a series of successive character states) in which the final state resembles the initial one. This seems to have happened independently in the species "*Lithophyllon*" *mokai* and *Lithophyllon undulatum*. The

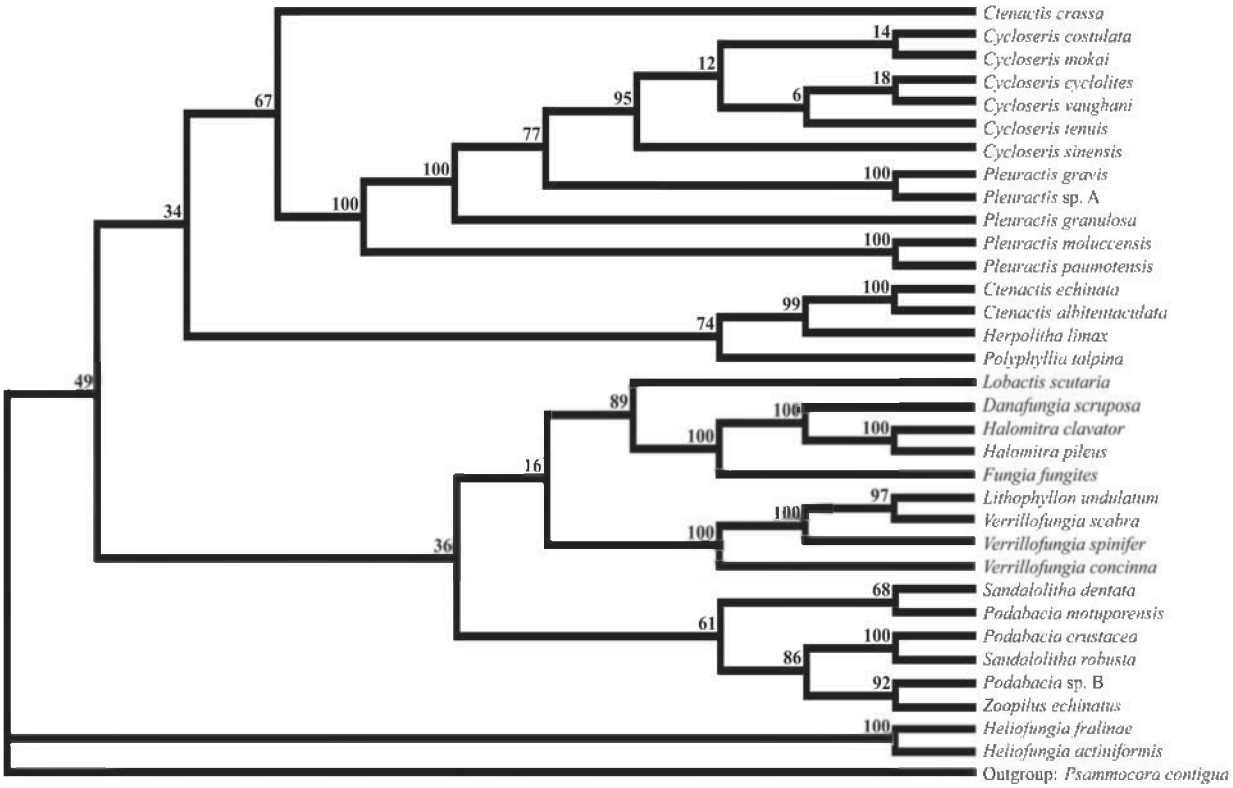

Fig. 7. Bayesian analysis of the combined ITS & COI data set without intraspecific variation: 50% majority rule consensus tree with compatible groupings. Taxonomy as in proposed classification (table 5).

resulting autapomorphies are inappropriate for phylogeny reconstruction, which may at least partly explain the conflicting views that were published by Wells (1966: fig. 3), Cairns (1984: fig. 3) and Hoeksema (1989)(fig. 8) when constructing a Fungiidae phylogeny based on morphology. See also the remarks on the molecular analyses of *Lithophyllon* and *Verrillofungia*.

Genus description: The following should be added to the description of *Cycloseris* by Hoeksema (1989: 30): One species, i.e. *Cycloseris mokai* (Hoeksema, 1989), differs from the other *Cycloseris* species in being encrusting, polystomatous, and irregularly shaped instead of free-living, monostomatous and circular to oval.

Genus *Danafungia* Wells, 1966
(= upgraded subgenus; see the molecular analysis of the "Genus *Fungia*")

Type species: *Fungia danai* Milne Edwards and Haime, 1851, sensu Wells, 1966 [= *Fungia scruposa* Klunzinger, 1879].

Molecular analysis: The phylogenies based on the COI data sets support that *Heliofungia actiniformis* and *Danafungia fralinae* are sister species with values of 64 and 74 respectively in figures 4 and 5. Even though the ITS data sets do not seem to support this result when analysed separately from the COI data sets (figs 1-2), the support values for this relationship become very high when the COI and ITS data sets are combined, i.e. 96 and 100 respectively in figures 6 and 7. All molecular phylogenies (figs 2-7) strongly support that *Danafungia fralinae* does not form a monophyletic group with the type species of *Danafungia*, *D. scruposa*. We therefore conclude that *Danafungia fralinae* Nemenzo, 1955, should be named *Heliofungia fralinae* (Nemenzo, 1955). In the analyses of the ITS data sets *Danafungia horrida* does not cluster together with the

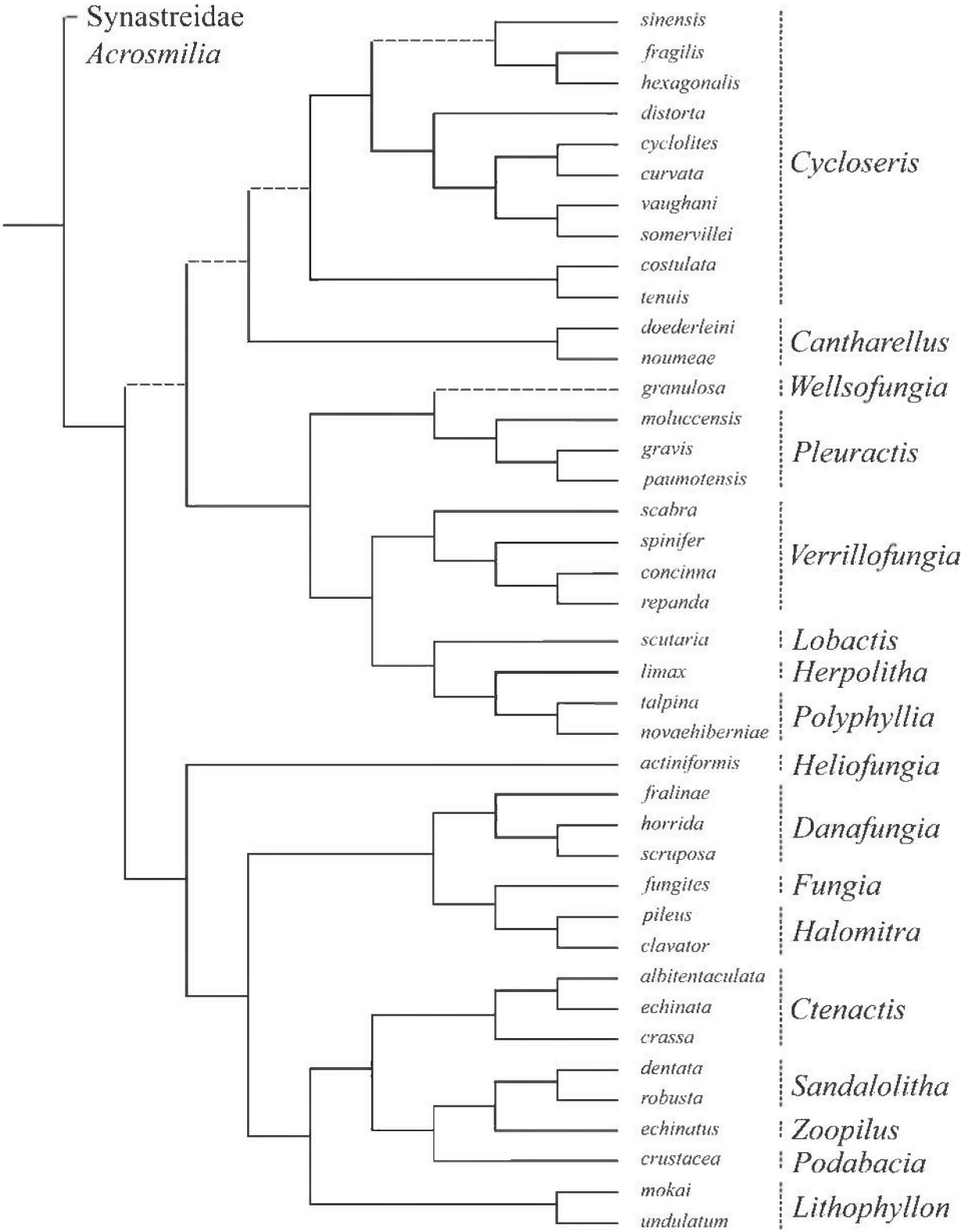

Fig. 8. A cladogram of the Fungiidae based on morphological characters; after Hoeksema (1989: 256).

type species *D. scruposa* (figs 2-3). This result is not strongly supported however, because it is based on a single ITS sequence of *D. horrida* that clusters at two totally different places in the two reconstructed phylogenies (figs 2-3). Therefore and on the basis of the morphology of the two species (Hoeksema 1989: 101-115), we conclude that *D. horrida* should remain in the nominal genus *Danafungia*.

Genus description: The description of Hoeksema (1989: 96-97) remains sufficient with the adjustment that two instead of three species are recognized within this genus.

Genus *Lobactis* Verrill, 1864
(= upgraded subgenus; see the molecular analysis of the "Genus *Fungia*")

Type species: *Fungia dentigera* Leuckart, 1841 (= *Fungia scutaria* Lamarck, 1801).

Molecular analysis: In most of the phylogenies (figs 3-7) and especially in the analyses of the combined COI + ITS data sets (figs 6-7), the sequences of the type and only species in the genus, i.e. *Lobactis scutaria* (Lamarck, 1801), cluster with low support at the basis of a clade with the genera *Danafungia*, *Fungia* and *Heliofungia*. In the phylogeny based on morphology by Hoeksema (1989) (fig. 8) it is situated basally from *Herpolitha* and *Polyphyllia*, however. This difference can be explained by parallel or convergent evolution by which the oval coral form that placed *Lobactis* basally to a clade with *Herpolitha* and *Polyphyllia*, has evolved twice.

Genus description: The description of Hoeksema (1989: 129) remains sufficient.

Genus *Pleuractis* Verrill, 1864
(= upgraded subgenus; see the molecular analysis of the "Genus *Fungia*")

Type species: *Fungia scutaria* Lamarck, 1801, sensu Verrill, 1864 [= *Fungia paumotensis* Stutchbury, 1833].

Molecular analysis: In all phylogeny reconstructions (figs 2-7) the *Pleuractis* sequences cluster together with the sequences of *Wellsofungia granulosa*, the type and only species of *Wellsofungia*. The analyses furthermore strongly indicate that *Wellsofungia granulosa* is more closely related to *Pleuractis moluccensis* and *P. paumotensis*, than the latter two species are related to *P. gravis* and *P.* spec. A. Hoeksema (1989: 255), when describing the subgenus *Wellsofungia* on the basis of morphology, stated: "*Wellsofungia* is separated from *Pleuractis* because it does not contain species that show an oval corallum outline (apomorph character state 28). Phylogenetically such groups of which the monophyly cannot be demonstrated by the presence of synapomorphies are of a reduced interest". Based on this statement, the morphology of the species, and the molecular data presented here, we conclude that *Wellsofungia granulosa* should be called *Pleuractis granulosa*. The nominal genus *Wellsofungia* has hereby become a synonym of *Pleuractis*.

A clade with *Cycloseris* sequences clusters within the clade with the *Pleuractis* sequences in all molecular phylogenies (figs 2-7) indicating that the latter genus may be paraphyletic. Some of these reconstructions support that *P. moluccensis*, *P. paumotensis* and *P. granulosa* are more closely related to the *Cycloseris* species than *P. gravis* and *P.* spec. A (figs 3, 6-7), while other data (figs 2, 4-5) indicate that *P. gravis* and *P.* spec. A are more closely related to *Cycloseris* spp. Because of these inconsistent results it cannot be said which of the two hypotheses is more likely and therefore it also remains uncertain whether *Pleuractis* is paraphyletic in the first place. Based on these inconsistent results and the morphological analyses in Hoeksema (1989), we keep on considering *Pleuractis* to be monophyletic.

Genus description: Adult animals are free-living and monostomatous. Their outline varies from oval to elongate. The corallum wall is perforated in adults. The blunt costal spines are either simple and granular or fused and laterally compressed. The septal dentations vary from fine and granular to coarse and angular. The septa are usually solid, but in some species they are perforated. The granulations on the septal sides are either irregularly arranged or they form rows or ridges parallel or perpendicular to the septal margins.

Genus *Verrillofungia* Wells, 1966
(= upgraded subgenus; see the molecular analysis of the "Genus *Fungia*")

Type species: *Fungia repanda* Dana, 1846.

Molecular analysis: In the paragraph "Excluding intraspecific variation" (p. 44) the *Verrillofungia concinna* sequence is discussed in detail. Its position in the phylogenies that were based on the ITS data set with intraspecifically variable base positions (figs 2, 6) appears to be incorrect because it differs strongly from its position in the other phylogenies (figs 3-5, 7). In all molecular phylogenies (figs 2-7) *Verrillofungia* sequences cluster with the sequences of *Lithophyllon undulatum*, the type species of the genus *Lithophyllon*. All analyses furthermore strongly indicate that *L. undulatum* is not on a basal lineage in the *Verrillofungia* clade. Based on these results, and the fact that *Lithophyllon* Rehberg, 1892, has priority over *Verrillofungia* Wells, 1966, one may suggest to consider *Verrillofungia* simply a junior synonym of *Lithophyllon*. This would cause much confusion however, because the generic name *Lithophyllon* is generally known as referring to species, which are encrusting and polystomatous, and all *Verrillofungia* species are free-living and mono-stomatous. In this exceptional case we therefore accept a paraphyletic genus, *Verrillofungia*, with species of which the individuals are free-living and monostomatous. See also the remarks on the molecular analysis of *Cycloseris* and *Lithophyllon*.

Genus *Halomitra* Dana, 1846

Type species: *Fungia pileus* Lamarck, 1801 [= *Halomitra pileus* (Linnaeus, 1758)].

Molecular analysis: In five out of the six molecular phylogenies (figs 2-3, 5-7), the *Halomitra* species *H. clavator* and *H. pileus* form a monophyletic group. Even though the COI data set with intraspecifically variable base positions indicates that *Halomitra clavator* clusters with *Danafungia scruposa* (fig. 4), the support value of this clade is very low, i.e. 32. In contrast, the support values for the *H. clavator* and *H. pileus* clades in the phylogenies based on the ITS and the combined data sets are very high, i.e. 99, 100, 99 and 100, respectively (figs 2-3, 6-7). Therefore we conclude that *Halomitra* is a monophyletic taxon.

Genus description: The description of Hoeksema (1989: 199-200) remains sufficient.

Genus *Heliofungia* Wells, 1966

Type species: *Fungia actiniformis* Quoy and Gaimard, 1833.

Molecular analysis: See the remarks on the molecular analysis of *Danafungia*.

Genus description: Adult animals are free-living and monostomatous. Their outline varies from circular to slightly oval. The corallum wall is solid and granulated. The polyps are fleshy, with extended tentacles that are relatively long, i.e. up to at least 2 cm.

Genus *Herpolitha* Eschcholtz, 1825

Type species: *Herpolitha limacina* (Lamarck) (= *Madrepora limax* Esper, 1797). Designated by Milne Edwards and Haime, 1850.

Molecular analysis: See the remarks on the molecular analysis of *Ctenactis*.

Genus description: The description of Hoeksema (1989: 167-168) remains sufficient.

Genus *Lithophyllon* Rehberg, 1892

Type species: *Lithophyllon undulatum* Rehberg, 1892.

Molecular analysis: See the remarks on the molecular analysis of *Cycloseris* and *Verrillofungia*.

Genus description: The description of this genus is similar to that of this type species (see Hoeksema 1989: 216).

Genus *Podabacia* Milne Edwards and Haime, 1849

Type species: *Agaricia cyathoides* Valenciennes, ms., Milne Edwards and Haime, 1849 [= *Podabacia crustacean* (Pallas, 1766)].

Molecular analysis: In the phylogeny based on morphology (fig. 8) by Hoeksema (1989), and in all molecular phylogenies, the sequences of *Podabacia*, *Sandalolitha* and *Zoopilus* cluster as a monophyletic group or at least close to each other. We can only conclude on the basis of morphology that these three nominal genera are separate entities. The individual *Sandalolitha*, *Podabacia* and *Zoopilus* sequences vary too little to distinguish these taxa. The support values within the clades are generally low and, whenever they are higher, give conflicting results in the various analyses.

Genus description: The description of Hoeksema (1989: 226) remains sufficient.

Genus *Polyphyllia* Blainville, 1830

Type species: *Fungia talpa* Lamarck, 1815 [=*Polyphyllia talpina* (Lamarck, 1815)].

Molecular analysis: See the remarks on the molecular analysis of *Ctenactis* and *Podabacia*.

Genus description: The description of Hoeksema (1989: 176) remains sufficient.

Genus *Sandalolitha* Quelch, 1884

Type species: *Sandalolitha dentata* Quelch, 1884.

Molecular analysis: See the discussion on the molecular results of *Podabacia*.

Genus description: The description of Hoeksema (1989: 186) remains sufficient.

Genus *Zoopilus* Dana, 1846

Type species: *Zoopilus echinatus* Dana, 1846.

Molecular analysis: See the discussion on the molecular results of *Podabacia*.

Genus description: The description of Hoeksema (1989: 195) remains sufficient.

Acknowledgements

We are grateful to Prof. Dr. E. Gittenberger (Leiden) for critically discussing the manuscript. Dr. C. Hunter is thanked for her help in providing material from Hawaii. We are also grateful to Prof. Dr. Alfian Noor (Hasanuddin University, Makassar) for his support in Makassar. This research project was supported by WOTRO (grant nr. W 82-249) with additional funding by the Schure-Beijerinck-Popping Fonds (KNAW), the Alida Buitendijk Fonds (Leiden University), and the Jan Joost ter Pelkwijkfonds (Leiden). The research in Indonesia was generously sponsored by the Indonesian Institute of Sciences (LIPI).

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4

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

Adriaan Gittenberger and Edmund Gittenberger

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

This text is not issued for purposes of zoological nomenclature (see ICZN Art. 8.2.)

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Key words: parasitic snails; coral reefs; coral/mollusc associations; Coralliophilidae; *Leptoconchus*; Scleractinia; Fungiidae; Indo-Pacific

Abstract

A large, cryptic, adaptive radiation is revealed. Fourteen *Leptoconchus* species (Gastropoda: Coralliophilidae) that live associated with a variety of mushroom coral species (Scleractinia: Fungiidae) are provisionally described as new to science, i.e. *Leptoconchus inactiniformis*, *L. inalbechi*, *L. incrassa*, *L. incycloseris*, *L. infungites*, *L. ingrandifungi*, *L. ingranulosa*, *L. inlimax*, *L. inpileus*, *L. inpleuractis*, *L. inscruposa*, *L. inscutaria*, *L. intalpina*, *L. massini*. [These names will be made available in the near future.] Although their identities as separate gene pools are convincingly demonstrated by molecular data, most of these species cannot be identified unequivocally on the bases of only conchological characters. Shell shape and sculpture are only partially diagnostic because of the interspecifically strongly overlapping character states and the large phenotypic plasticity. Environmental conditions, sexual dimorphism and probably protandry may affect shell size, shape and sculpture in ways that are still insufficiently known. However, in accordance with the molecular data, the ecological data, i.e. host species preferences, do reveal the identity of the various gastropod parasite species that were found to be associated with only one or a restricted number of fungiid species and have large ranges, similar to those of their hosts. None of the host coral species was found to be associated with more than one *Leptoconchus* species.

Contents

Introduction

Within the gastropod family Coralliophilidae Chenu, 1859, the genus *Leptoconchus* Rüppell, 1834, is extreme in various ways. The snails live in bore-holes in corals, locked up there for most of their lives. A host specificity was mentioned already by Deshayes (1863: 124), but several taxa were introduced in the past without any details on the associated coral host species. That means that a potential clue to their identity is not always available. This is essential since

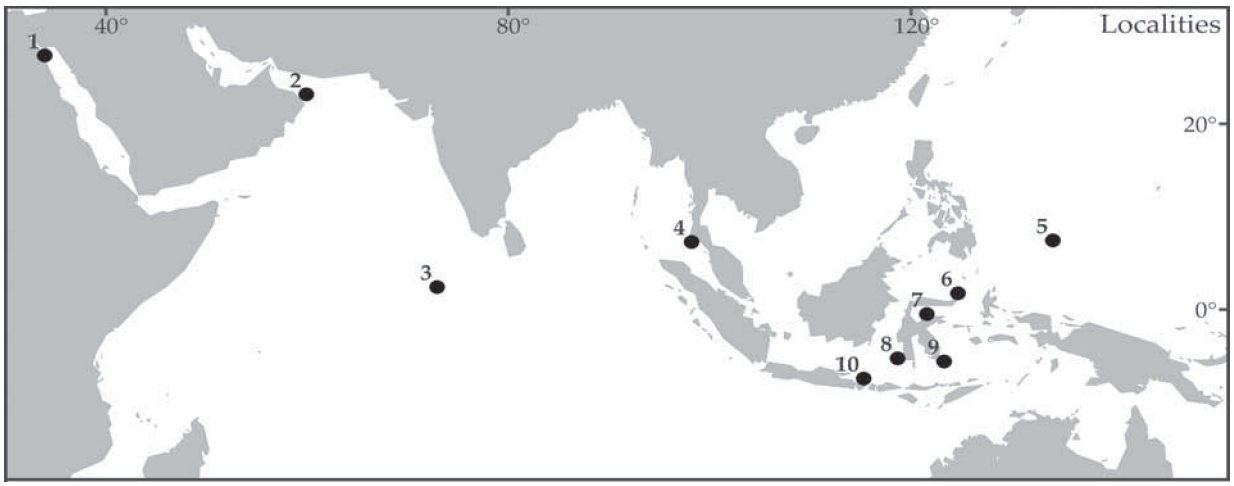


Fig. 1. The Indo-Pacific region, from the Red Sea to the Hawaiian Archipelago, illustrating the research localities 1-10. 1, Marsa Nakari, c. 350 km S of Hurghada, Egypt (Red Sea); 2, Oman; 3, Vilamendhoo Island, Ari Atoll, Maldives; 4, Phiphi Islands, Krabi, Thailand; 5, Palau; 6, Siladen and Bunaken Islands, N Sulawesi, Indonesia; 7, Togian Islands, E Sulawesi, Indonesia; 8, Spermonde Archipelago, SW Sulawesi, Indonesia; 9, Wakatobi, SE Sulawesi, Indonesia; 10, Bali, Indonesia.

in the course of evolution from free-living to boring snails, the shells have lost most potentially diagnostic characters of shape, sculpture or colour pattern. Apart from that, there seems to be a great phenotypic plasticity in relation to environmental factors like size and other characters of the coral host. We observed a conspicuous sexual dimorphism. The variation in conchological characters might be even more confusing when *Leptoconchus* species are protandric hermaphrodites indeed, as was convincingly suggested by Richter and Luque (2004).

The animals have to be collected with a hammer, since only by breaking the coral hosts to pieces they become available for study. This implies that for both technical and ethical reasons large series of specimens, which are a prerequisite to study the variation in shell shape, could not be acquired. As a consequence of all this, the genus is still poorly known, despite the fact that Massin (1982, 1983) published some useful reviews of our current knowledge on *Leptoconchus* and closely related genera.

This paper deals mainly with the *Leptoconchus* species that are associated with mushroom corals (Fungiidae). On the basis of general shell shape, i.e. height/width ratio, the shell surface, which is either smooth or not, the presence versus absence of an operculum, and the location of the bore-hole, on either the upside or the basis of the mushroom coral disc, some species or species groups have been distinguished by Massin and Dupont (2003). These authors, while summarizing the state of the art in *Leptoconchus* systematics and ecology, distinguished nine so-called Operational Taxonomic Units (OTUs 1-9), without clarifying the taxonomic status of these entities.

Since only shell morphology and anatomy do not result in unequivocal results, an additional discriminating tool had to be introduced. Here we describe the results of a molecular analysis, on the basis of DNA sequencing data for many snails that were identified as *Leptoconchus* spec. This research material was collected from several fungiid hosts, in a vast range, from the Red Sea in the west to Palau in the east (fig. 1). It turned out that the OTU's distinguished by Massin and Dupont (2003) are not always equivalent to separate gene pools, i.e. species. In several cases an OTU turned out to be composed of more than one species, which are often not even sister taxa or monophyletic groups. It has to be concluded that *Leptoconchus* is much more diverse than hitherto thought. On the basis of our results we may additionally conclude that most probably a relatively high number of species remains to be discovered and described.

For the moment being, not all the *Leptoconchus* species that emerge from the molecular analyses can be characterized morphologically. Here we illustrate and describe the shell of the future holotype, which is always a relatively large, in all probability female

snail. Whenever possible the associated, smaller, male shell is also described and the largest shell measurements found are added. The intraspecific variation remains unknown.

At present, nearly all species, and their holotypes, can only be distinguished unequivocally on the basis of molecular data and their associated coral hosts. These species will be formally named, since their taxonomic status is no matter of dispute. They may be widespread. Several of these cryptic species occur sympatrically, with broadly overlapping ranges but, if so, associated with different coral hosts.

Large series of shells are not available for study and a more detailed analysis of the anatomical characters of the *Leptoconchus* species is seriously hampered by the conservation of the specimens in hand, which are in alcohol 96% and withdrawn into their shells. For the obvious reasons mentioned before, a substantial increase in better research material is not to be expected. That is why we prefer not to postpone calling attention for this adaptive radiation.

Material and methods

Morphology:

Dissection turned out to be hardly possible with the strongly contracted specimens that are conserved in alcohol 96%. A superficial analysis did not result in the discovery of species specific anatomical details. Because the snails do not possess a radula or jaws, that potential source of diagnostic character states is not available here.

The animals show a conspicuous sexual dimorphism. Frequently, a large and a small specimen were found together in a single fungiid. Inside the coral the separate bore-holes of a couple were connected by a narrow window. In such cases, the large individual, which was usually associated with eggs, was considered a female and the small one, without eggs, a male. It turned out to be impossible in practice to confirm this assumption in all cases by anatomical verification, but the dimorphism was obvious.

Fieldwork:

Approximately 60,000 mushroom corals (Scleractinia, Fungiidae) were searched for *Leptoconchus* snails in the Indo-West Pacific of Egypt, Maldives, Thailand, Palau and Indonesia (fig. 1). While scuba-diving, fungiids were carefully inspected at both sides, looking for the tiny holes with protruding siphons of the snails. When the presence of a bore-hole was discovered, its location was registered, the coral disc was broken, and the snail inside the boring cavity was collected. To enable regeneration of the coral, its fragments were left in the original habitat. In total 685 snails were collected from 327

Table 1. Samples of which the ITS2 region was sequenced. The locality codes refer to those indicated in fig. 1.

Species	Coral Host	Sampe localities (fig. 1)
Leptoconchus incycloseris	*Fungia* (*Cycloseris*) *costulata*	5, 5, 9
Leptoconchus infungites	*Fungia* (*Fungia*) *fungites*	5, 5, 6, 7, 7, 8, 8, 8, 10
Leptoconchus ingrandifungi	*Sandalolitha dentata*	10
Leptoconchus ingranulosa	*Fungia* (*Wellsofungia*) *granulosa*	7
Leptoconchus inlimax	*Herpolitha limax*	3
Leptoconchus inpileus	*Halomitra pileus*	3, 5, 8
Leptoconchus inpleuractis	*Fungia* (*Pleuractis*) *gravis*	8
	Fungia (*Pleuractis*) *moluccensis*	8
	Fungia (*Pleuractis*) *paumotensis*	6, 7
Leptoconchus massini	*Fungia* (*Verrillofungia*) *concinna*	4, 5, 8
	Fungia (*Verrillofungia*) *repanda*	1, 3, 4, 5, 10

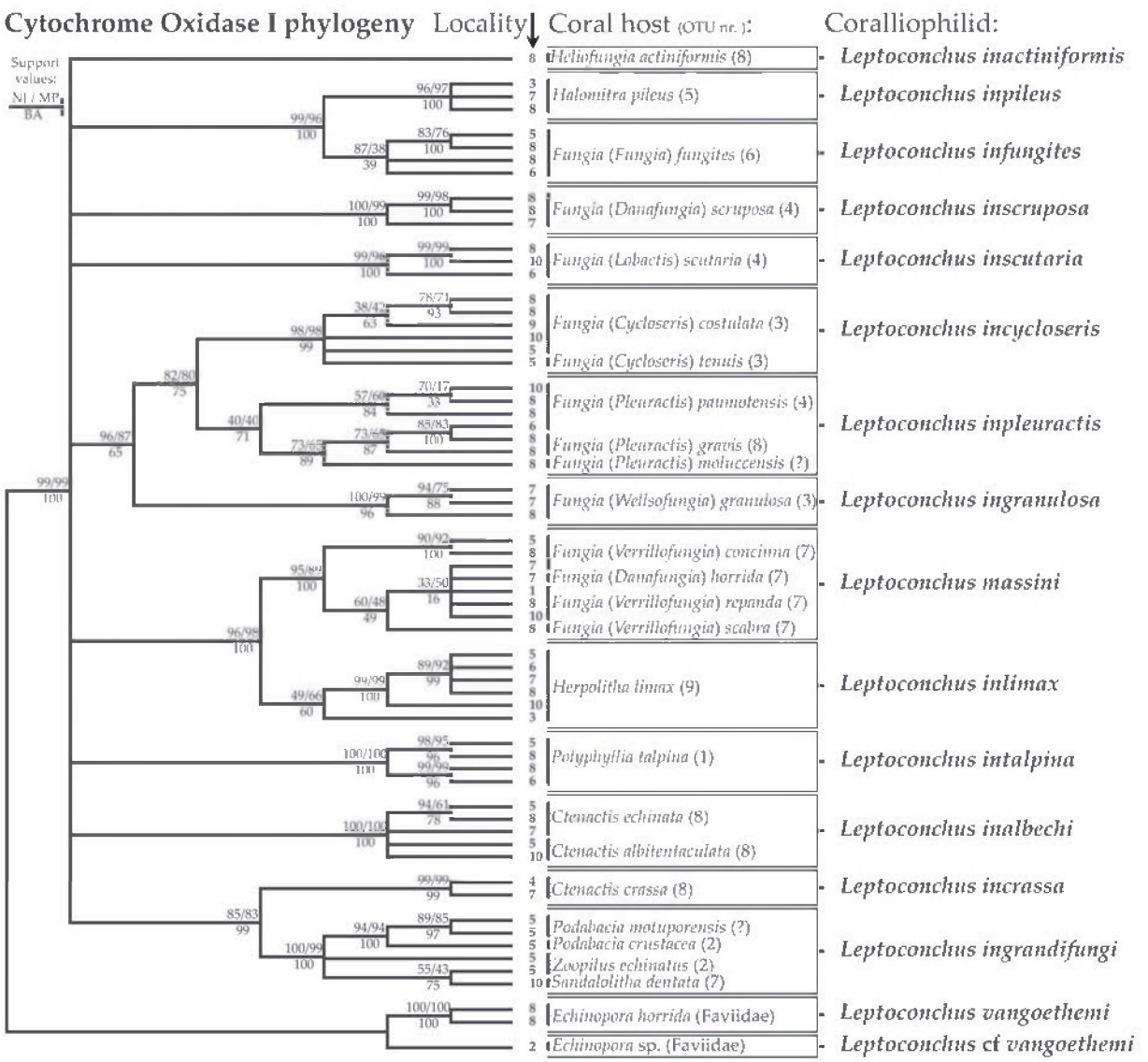


Fig. 2. Cytochrome Oxidase I phylogeny of fungiid associated *Leptoconchus* spp., i.e. the strict consensus tree of the 50% consensus trees with compatible groupings that resulted from [1] the Bayesian inference analysis, [2] the Neighbor Joining bootstrap analysis, [3] the Parsimony bootstrap analysis, and [4] the Heuristic search for the most parsimonious tree(s). The locality numbers refer to those indicated in fig. 1.

hosts. The fungiid hosts were identified twice, from photographs and/or specimens, independently by A. Gittenberger and B.W. Hoeksema. Three specimens of *Leptoconchus vangoethemi* Massin, 1983, which were collected out of corals of *Echinopora horrida* Dana, 1846, and *Echinopora* sp. (Scleractinia, Faviidae), were included in the molecular analyses to function as outgroup taxa (fig. 2).

DNA extraction and sequencing

The snails of which the DNA was successfully sequenced (fig. 2, table 1), were conserved in either ethanol 96%, ethanol 70%, or (the specimens from Thailand) in a 1:1 mixture of rum (c. 40% alcohol) and 70% ethanol. On one occasion, accidentally the coral host, i.e. *Heliofungia actiniformis* (Quoy and

Gaimard, 1833), was sequenced instead of the snail. To reduce the chance of DNA contamination, a thin layer of the outer surface of the snail's foot was removed with a scalpel, before cutting the slice that was used for extraction. This slice was dissolved by incubation at 60° C, for c. 15 hours, in a mixture of 0.003 ml proteinase K (20 mg/ml) and 0.5 ml CTAB buffer, i.e. 2% CTAB, 1.4M NaCl, 0.2% mercapto-ethanol, 20mM EDTA and 100mM TRIS-HCl pH8. After incubation the solution was mixed with 0.5 ml Chloroform/Isoamyl alcohol, and centrifuged for 10'at 8000 rpm. The supernatant was extracted, mixed with 0.35 ml isopropanol, put aside for c. 15 hours at 4° C and finally centrifuged for 10' at 8000 rpm to precipitate the DNA. The supernatant was discarded and the remaining DNA-pellet was washed at room temperature with 0.5 ml of an ethanol/ammonium-acetate solution for 30'. After centrifugation for 10' at 8000 rpm, this solution was discarded. The pellet was dried in a vacuum centrifuge and then dissolved in 0.020 ml MilliQ. The DNA quality and quantity were tested by electrophoresis of the stock-solution through an agarose gel, and by analysing a 1:10 dilution of the stock in a spectrophotometer. The ITS2 and COI regions were amplified using the primers and annealing temperatures (AT) as specified in table 2 in a Peltier Thermal Cycler PTC-200, which has a temperature change speed of c. 3° C /s. The optimised PCR-program consists of 1 cycle of 94° C for 4' and 60 cycles of 94° C for 5"; AT (Annealing Temperature) for 1'; 0.5° C/s to AT + 5° C; 72° C for 1'. After the PCR, the samples were kept on 4° C until purification by gel extraction using the QIAquick Gel Extraction Kit from QIAGEN. The PCR reaction mix consisted of 0.0025 ml PCR buffer (10x), 0.0005 ml MgCl2 (50mM), 0.0010 ml forward primer (10 pM), 0.0010 ml reverse primer (10 pM), 0.0005 ml dNTP's (10 mM), 0.0003 ml Taq polymerase (5 units / 0.001 ml), 0.0132 ml MilliQ and 0.0010 ml 1:10 DNA stock-solution (= c. 100 ng DNA). The samples were kept on 4° C until cycle sequencing. Cycle sequencing was done in both directions of the amplified region, with a program consisting of 45 cycles of 96°C for 10", 50°C for 5" and 60°C for 4'. The reaction mix used was 0.0020 ml Ready Reaction Mix (Big DyeTM by PE Biosystems), 0.0020 ml Sequence Dilution-buffer, 0.0005 ml primer (5 pM forward or reverse primer solution) and 0.0055 ml amplified DNA (= half the PCR-product, evaporated to 0.0055 ml by vacuum centrifugation). The cycle sequence products were purified with Autoseq G50 columns (Amersham Pharmacia Biotech) and kept on 4°C until they were run on an ABI 377 automated sequencer (Gene Codes Corp.), using the water run-in protocol as described in the User Bulletin of the ABI Prism 377 DNA Sequencer (PE Biosystems, December 7, 1999). The consensus sequences were retrieved by combining the forward and reverse sequences in Sequencher 4.05 (Genes Codes Corp.).

Sequence alignment and phylogenetic analyses

The COI sequences were aligned with MacClade 4.0 (Maddison and Maddison, 2000) using the default parameter settings. In MacClade 4.0 there were some difficulties in aligning the ITS2 data set because of the presence of 54 gaps. Manual corrections were done without much problems because most of the gaps were related to repeats of up to three bases. (Alignments are available from the authors.)

The data sets were analysed with Paup 4.0b10 (Swoford, 2002). The homogeneity of base frequencies in the sequences was tested with chi-square for the complete data set, and for the first, second and third codon positions separately in the COI alignment. To test for the presence of phylogenetic signal we did the G1 skewness statistic based on 1000 random trees (Hillis and Huelsenbeck, 1992) and the permutation test (Archie, 1989; Faith and Cranston, 1991) with

Table 2. Primers and annealing temperatures used for amplification of the DNA regions analysed.

Region	Forward primer (5'-3')	Reverse primer (5'-3')	AT
ITS2	GGCGGCCTCGGGTCCATCC (Uit de Weerd and Gittenberger, 2005)	TTCCCGCTTCACTCGCCGTTACTG (Uit de Weerd and Gittenberger, 2005)	61°C
COI	GGTCAACAAATCATAAAGATATTGG (LCO-1490 in Folmer et al., 1994)	TAAACTTCAGGGTGACCAAAAAATCA (HCO-2198 in Folmer et al., 1994)	45°C

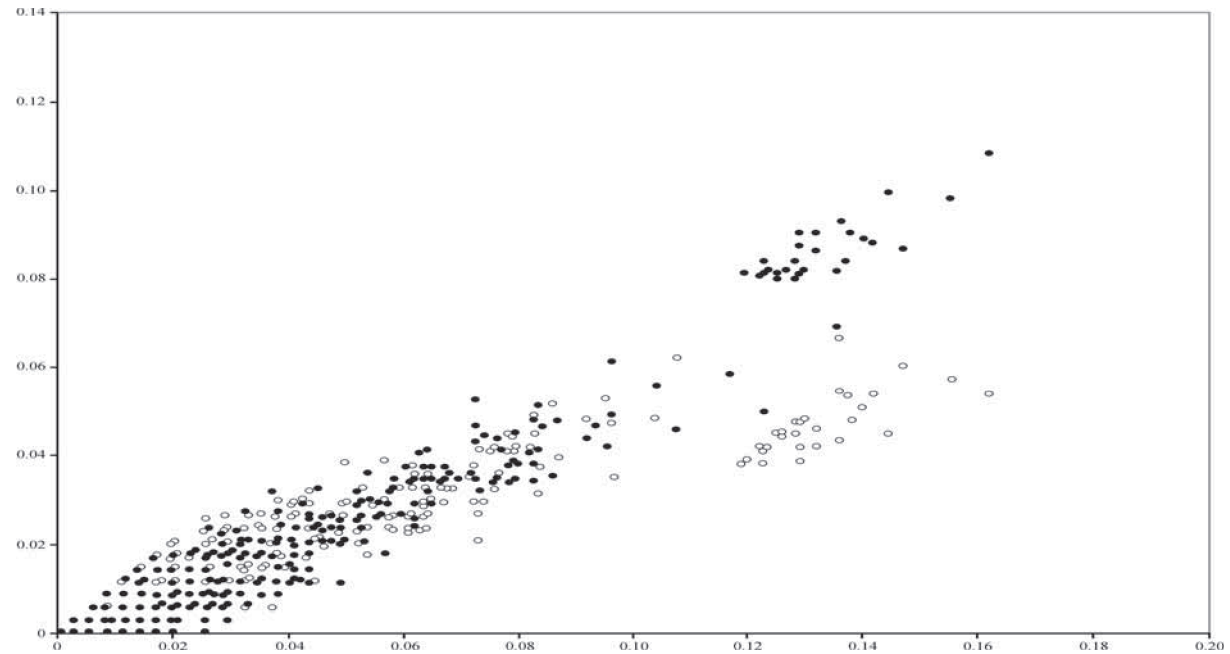


Fig. 3. Tranversional (dots) and transitional (circles) rates (Y-axis) in pairwise comparisons between the ITS2 sequences (table 1), plotted against the rate of all substitutions (X-axis). The rates were calculated with Paup 4.0b10 (Swofford, 2002).

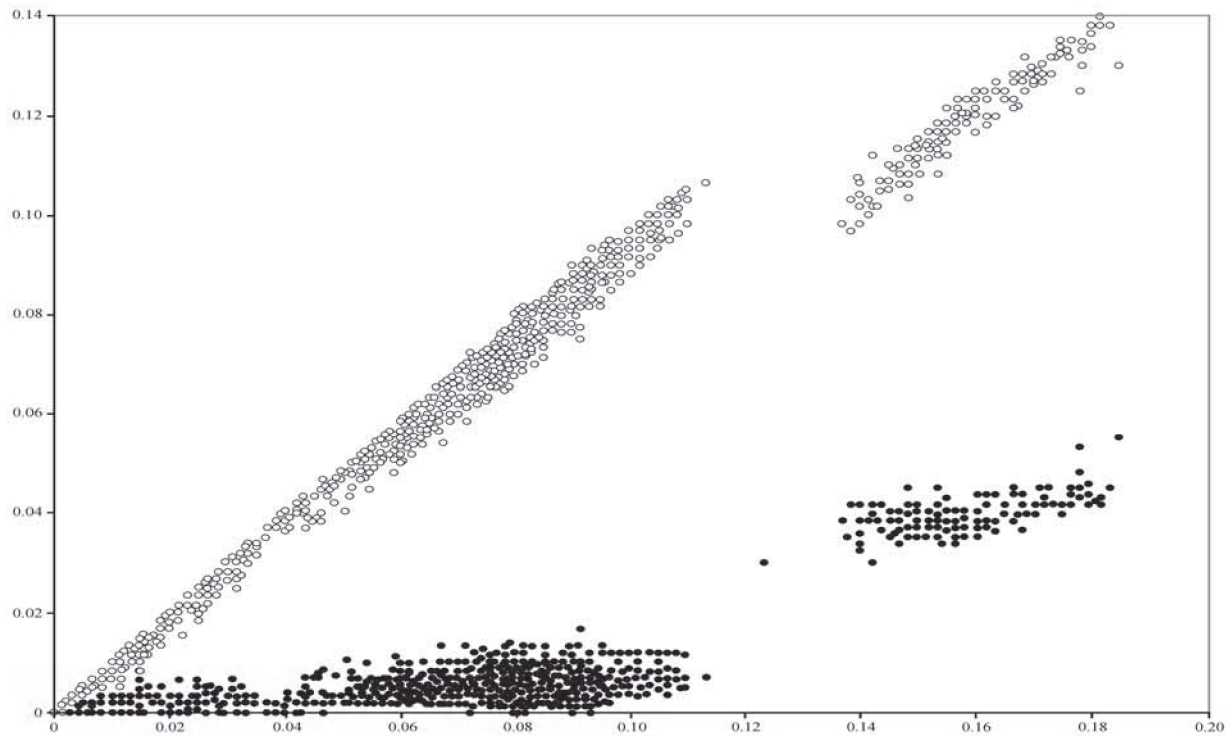


Fig. 4. Tranversional (dots) and transitional (circles) rates (Y-axis) in pairwise comparisons between the COI sequences (fig. 2), plotted against the rate of all substitutions (X-axis). The rates were calculated with Paup 4.0b10 (Swofford, 2002).

500 replicates, a full heuristic search, TBR algorithm, steepest descent and 10 random addition replicates per replicate.

When transversion rates in pairwise comparisons between the sequences are equal to or higher than the transition rates, a data set has to be considered highly saturated (e.g. Yang and Yoder, 1999). To test for saturation, the transitional and transversional rates were plotted against the rate of all substitutions. The rates were calculated with Paup 4.0b10 (Swofford, 2002).

Only the COI alignment was used for phylogeny reconstruction because the ITS2 data set was considered unsuitable to study the species concerned (see 'Results'). PAUP 4.0b10 was used for maximum parsimony and neighbor joining analyses. MrBayes 3.0B4 (Ronquist and Huelsenbeck, 2003) was used for a Bayesian inference analysis.

To find the most parsimonious tree(s), a full heuristic search was done with 1000 random addition replicates, TBR algorithm and steepest descent. In addition a non-parametric parsimony bootstrap analysis was performed with a full heuristic search, 4000 bootstrap replicates, a maximum duration of one hour per replicate, one random addition per replicate and TBR algorithm. A Neighbor Joining bootstrap analysis was executed with 10,000 bootstrap replicates. Bayesian inference was performed with five incrementally (T=0.20) heated Markov chains and a cold one, which were run 4,000,000 generations and sampled once every 50 generations, using the best-fit model for nucleotide substitution, i.e. HKY+I+G, which was indicated by both the likelihood ratio test and the Akaike information criterion in MrModeltest 2.1 (Nylander, 2004) for use in MrBayes 3.0B4, on the basis of the by PAUP 4.0b10 calculated likelihood scores of 24 models of nucleotide substitution. To determine the burnin, the loglikelihoods of the saved trees were plotted in a Microsoft Excel graph to see from where on they become stationary.

The conclusions are based on the strict consensus tree (fig. 2) of the 50% consensus trees with compatible groupings that resulted from [1] the Bayesian inference analysis, [2] the Neighbor Joining bootstrap analysis, [3] the Parsimony bootstrap analysis, and [4] the Heuristic search for the most parsimonious tree(s).

To test whether COI sequences of *Leptoconchus vangoethemi* may be used for outgroup comparison, the Bayesian inference analysis and the Neighbor Joining bootstrap analysis were repeated including a COI sequence (Genbank accession nr. U86331) of the coralliophilid snail species *Coralliophila abbreviata* (Lamarck, 1816). In both analyses the *L. vangoethemi* sequences clustered outside a clade of the fungiid-associated *Leptoconchus* species, confirming that they may be used as an outgroup. Further results of these two analyses are not presented here.

Systematic descriptions

The species are described in phylogenetic order, i.e. following their arrangement from top to bottom in the molecular phylogeny reconstruction (fig. 2). The shells were photographed by the first author using a Canon EOS 300D camera with a ring flash.

The research material is rather diverse, with male and female specimens, and the latter sometimes with egg-capsules. The following abbreviations are used: e, egg-capsules; f, female; f+e, female with egg-capsules; m, male; sh, shell; sn, snail. Two snails, a male and a female with egg-capsules, is indicated as follows: 2sn:m&f+e. In the descriptions of the shells, H = height and W = width.

Results

Molecular analyses

The ITS2 alignment consists of 413 base positions within which there are 54 gaps of one or more bases, 101 variable non-informative positions excluding the gaps and 25 informative sites, of which 13 were informative for grouping together two sequences only. Assuming that one coral species is never associated with more than one species of *Leptoconchus*, as is suggested by the COI data set, almost all the gaps and the variable base-positions, vary within species. This high degree of intraspecific genetic variation is especially apparent when focusing solely on the nine sequences of the *Leptoconchus* snails that were collected out of *Fungia (F.) fungites* corals. The alignment of these sequences has 370 base positions, among which 23 gaps varying in size and position, and 55 variable base positions of which 5 potentially

parsimony informative. These 5 positions do not cluster specimens per locality however. The complete ITS2 data set is furthermore considered to be highly saturated since the transversional rates are equal to higher than the transitional rates in almost all pairwise comparisons (fig. 3; Yang and Yoder, 1999).

These results indicate that the ITS2 region is at least unsuitable for studying the *Leptoconchus* species concerned at a species- or higher taxonomical level. It may only be suitable for population genetic research in Coralliophilidae, as was done by Oliverioi and Mariottini (2001) for *Coralliophila meyendorffii* (Calcara, 1845).

In contrast, the analysis of the COI data set indicated that this marker can be very suitable for studying Coralliophilidae at the species level, or at least to distinguish *Leptoconchus* species that are associated with fungiids. The aligned segment of 600 bases contained 219 variable positions of which 177 are potentially parsimony informative. The data set does not include any gaps or stop codons. The data set has a highly significant phylogenetic signal, as is indicated by the permutation test, i.e. $P = 0.002$, and the G1 skewness test, i.e. $P < 0.01$ ($g1 = -0.432616$). Base frequencies in the complete data set and in the first, second and third codon positions separately, are not significantly inhomogeneous across taxa, i.e. $P = 1.00$ in all cases. There are no indications for saturation in the data set because the transversional rates are much lower than the transitional rates in all pairwise comparisons (fig. 4). As is to be expected, these rates differ less in the comparisons between the ingroup and outgroup sequences, which are clearly visible in figure 4 as the two aggregations of transition and transversion dots, respectively, on the right.

There are two most parsimonious trees (score = 612; CI = 0.452; rescaled CI = 0.361). These two trees and the three 50% consensus trees with compatible groupings trees based on the Parsimony bootstrap, Neighbor Joining bootstrap and Bayesian inference analyses, are all very similar. The strict consensus of these trees (fig. 2) shows all clades that were supported with a value of more than 50% in any of the consensus trees, with the exception of a clade in which *Leptoconchus inscruposa*, *L. inscutaria* and *L. intalpina* cluster together with *L. inpileus* and *L. infungites*. This clade is supported in the Bayesian consensus tree with 64% and in the Neighbor Joining consensus tree with 20%, and is also present in the two most parsimonious trees. In the Parsimony bootstrap consensus tree however, the *L. inscruposa* clade does not cluster with *L. inscutaria*, *L. intalpina*, *L. inpileus* and *L. infungites*. Because of this, the strict consensus tree (fig. 1) does not show any relationship between the *L. inscruposa*, *L. inscutaria*, *L. intalpina*, and the *L. inpileus* and *L. infungites* clades.
When possible, the taxa in the strict consensus tree (fig. 2) are arranged in phylogenetic order of the host corals.

Taxonomical implications

Although the strict consensus tree (fig. 2) does not show much basal resolution, it strongly supports 14 clades that cluster *Leptoconchus* specimens by host species and not by locality. Therefore we now consider these clades to represent 14 species. They are described in the systematic part below. Because it remains uncertain whether the COI region is variable enough to distinguish between very closely related species, some of these clades may even include more than one species.

Systematic part

Coralliophilidae Chenu, 1859
Magilidae Thiele, 1925

A discussion about the systematics of the entire family Coralliophilidae would be premature because of a lack of reliable data.

Leptoconchus Rüppell, 1834

Leptoconchus Rüppell, 1834: 105. Type species (designated by Rüppell, 1835, after ICZN Art. 69.3): *Leptoconchus striatus* Rüppell, 1835.
Magilopsis Sowerby (3rd), 1919: 77. Type species (by original designation): *Leptoconchus lamarckii* Deshayes, 1863.

The genus

For the moment being, Massin (1982, 1983) is followed in separating *Leptoconchus* Rüppell, 1834

[not 1835], from *Magilus* Montfort, 1810, mainly on the basis of the absence versus presence of an irregular, calcareous tube, protruding from the shell aperture towards the surface of the coral in *Magilus*. In *Leptoconchus* species the operculum may either cover the entire aperture (not in any of the species associated with fungiids that are discussed in this article) or be rudimentary, i.e. much smaller, or maybe even lacking completely (which might be an artefact, however). The shells have less than five whorls, rapidly increasing in size, which results in a relatively large last whorl with a large aperture; the whorls may be rather glossy, with inconspicuous, fine wrinkles, or dull, with a roughly wrinkled, calcareous surface. The spire varies from elevated to strongly depressed or flat. There is no umbilicus. There may be a large, shining parietal-columellar shield. The shell height/width indexes vary strongly intra-specifically (see e.g. *Leptoconchus incrassa* [figs 77, 83]) and are not species specific. Female and male specimens may differ considerably is shell shape and size. Here only the height and the width of the shell of the holotype, always a female, and the illustrated male, are given. The animals possess neither a radula nor jaws.

Lamarck (1818: 374) introduced *Magilus peronii* for what he considered a juvenile *Magilus* with only the spiral part of the shell (".. la spirale seulement.."). Later on, Massin (1990) selected a lectotype for *"Leptoconchus" peronii* from among shells supposed to be syntypes, referring to *Leptoconchus striatus* (Rüppell, 1835) as a junior synonym. However, *Leptoconchus peronii* was originally described as associated with "une astrée" (Lamarck, 1818: 374), which is "*Favites* (autrefois *Astraea*)" according to Massin (1982: 21). Rüppell (1835: 259) reported that his *L. striatus*, the type species of *Leptoconchus*, occurs nearly always with a species of "*Meandrina* (*Meand. Phrygia*)". Massin (1982, 1990) listed a variety of coral hosts for *Leptoconchus striatus*. However, in view of the results of our molecular analyses we now hypothesize that several cryptic *Leptoconchus* species, associated with different hosts, are united in the literature under a single name. Consequently, because of their apparently quite different host species (also when taking the subjective interpretation of the taxon names over time into account), we doubt the synonymy of *L. peronii* and *L. striatus*, and we do not accept *L. striatus* as a parasite of a fungiid coral.

According to Deshayes (1863: 124), the *Leptoconchus* species occur mainly associated with "Méandrines", with only *L. lamarckii* as the exception to that rule, while living with "*madrepora*" (".. le seul *Leptoconchus lamarckii* fait exception à cette règle et vit dans un *madrepora*."). Apart from that, Deshayes (1863: 124) mentioned that the collector Maillard observed that the *Leptoconchus* species are host-specific (".. vivent dans une espèce particulière de polypier.."). Therefore, on the basis of the data in the original description of the species, we have to accept that the coral hosts of *Leptoconchus cumingii* Deshayes, 1863, *L. cuvieri* Deshayes, 1863, *L. maillardi* Deshayes, 1863, and *L. rueppellii* Deshayes, 1863, are *Meandrina* species (sensu Deshayes, 1863), whereas *L. lamarckii* Deshayes, 1863, occurs with *Madrepora* (sensu Deshayes, 1863). Since Lamarck (1816) already distinguished *Meandrina*, *Madrepora* and *Fungia*, there is no reason to assume that Deshayes' views differ so much from the more modern interpretations that he might not have recognized fungiid corals as a separate taxon. There may be additional coral hosts, as indicated for *L. cumingii* and *L. lamarckii* by Massin (1982: 14, 17), but as long as the *Leptoconchus* species cannot be identified more reliably on the basis of morphological characters, these are not accepted here unreservedly.

Massin (1982) listed the coral hosts of most *Leptoconchus* species described by Deshayes (1863) as unknown. Massin (1982: 15) made clear that *L. expolitus* Shikama, 1963, cannot easily be interpreted after its original description and figures; especially also because of its coral hosts, we assume that this is not one of the species dealt with here in detail. Also because of its coral host, i.e. *Madrepora* spec., *L. rostratus* A. Adams, 1864, is not further discussed in this paper. We agree with Massin (1982: 15) that the data on *L. djedah* (Chenu, 1843), *L. ellipticus* (Sowerby, 1830), *L. globulosus* (Sowerby, in Reeve, 1872), *L. noumeae* Risbec, 1953, *L. serratus* (Sowerby, in Reeve, 1872), and *L. solidiusculus* (Sowerby, in Reeve, 1872), are insufficient to recognize what species are actually involved. Stabilizing the status of these problematic nominal taxa is impossible without defining them anew. Here they are neglected.

Based on anatomical and ecological characters, Massin and Dupont (2003) distinguished nine "Operational Taxonomic Units (OTUs)" in *Leptoconchus*,

all of which infesting mushroom corals (Fungiidae). It turned out that these OTU's cannot be considered equivalent to species.

The species

Leptoconchus inactiniformis

Type locality. INDONESIA. SW Sulawesi, Spermonde Archipelago, W Samalona island, 05°07'31"S 119°20'31"E.

Material (paratypes, unless stated otherwise; all hosted by *Heliofungia actiniformis*).

INDONESIA. SW Sulawesi, Spermonde Archipelago: type locality, RMNH 87884/holotype, 1sh:f+e [e: RMNH 102741], 102544/1sh:m (with holotype), 87880/1sn:f+e, 87881/1sn:f+e, 87882/2sn:m&f, 87885/1sn:f+e, 1sh:f, 90040/2sn:f&m, 90117/2sn: m&f+e; W Bona Baku reef, 05°07'56"S 119°21'39"E (RMNH 90054/2sn:m&f+e, 90056/1sn:f); W Kudingareng Keke island, 05°06'09"S 119°17'09" (RMNH 90057/1sn:f+e); W Kapodasang reef, 05°05'35"S 119°15'20"E (RMNH 87818/1sn:f, 87846/1sh:f, 90068/3sn:m&2f+e, 90074/2sn:m&f+e, 90075/3sn:m&2f+e, 90080/2sn:m&f+e, 90081/2sn: m&f+e, 90082/2sn:m&f+e, 1sh:f, 90083/2sn:m&f+e, 90103/1sb:f). Central Sulawesi, Tomini Bay, Togian islands, S Talatakoh island, 00°28'22"S 122°08'22"E (RMNH 102545/1sn). Bali, SE Tulamben beach, drop-off, 08°16'40"S 115°35'45"E (RMNH 102546/2sn:2f+e, 102548/3sn:m&2f+e, 102549/2sn: m&f+e, 102550/3sn:3f+e).

PALAU. E of Koror, KB Channel, S of Itelblong island, 07°19'40"N 134°32'26"E (RMNH 102551/3sn: m&2f+e, 102552/1sn:f); Malakal harbor, NW of Ngederrak reef, E of Dolphin Bay, 07°18'40"N 134°27'10"E (RMNH 102547/3sn:m&2f+e); N of Ngeremdiu, Lighthouse reef, backreef, 07°17'11"N 134°27'26"E (RMNH 102553/1sn:m).

Shell. Holotype (figs 5-7) female: H 15.1 mm, W 23.4 mm. The whitish shell has a roughly wrinkled, calcareous surface; the smooth and glossy columellar callus is broadly expanded, covering most of the surface of the last whorl in frontal view. The outer lip is regularly curved, its lower half gradually passing into the remaining basal part of the shell. The height and the width of the largest female shell are 23.0 mm and 30.5 mm, respectively, versus 15.4 mm and 16.8 mm for the largest male. The shell of a male snail (figs 8-10), found with the holotype in the same host, measures H 10.8 mm, W 10.7 mm. In frontal view, the apical part of female shells is not or only slightly protruding above the apertural edge (fig. 5), whereas the apex of male shells protrudes distinctly (fig. 8).

Operculum. Operculum maybe absent.

Habitat. The snails and their egg-capsules were found at 4-18 m, with exclusively the mushroom coral species *Heliofungia actiniformis* (Quoy and Gaimard, 1833). The siphon pores are located on the underside of the corals.

Distribution. When all specimens looking similar in morphology and found associated with *Heliofungia actiniformis* represent *Leptoconchus inactiniformis* indeed, that species may be reported from Indonesia, off SW Sulawesi and Bali, as well as from NE Papua New Guinea (Massin, 1992: OTU8).

Etymology. This species is named after its restricted habitat. It was found exclusively in corals of *Heliofungia actiniformis*.

Leptoconchus inalbechi

Type locality. INDONESIA. SW Sulawesi, Spermonde Archipelago, NW Lumulumu island, 04°58'13"S 119°12'35"E.

Material (paratypes, unless stated otherwise). Samples that were hosted by *Ctenactis albitentaculata* or *Ctenactis echinata*, are coded Ca or Ce, respectively.

INDONESIA. SW Sulawesi, Spermonde Archipelago: type locality, RMNH 90066/holotype Ce/ 1sh:f+e [e: RMNH 102717], 102718 Ce/1sh:m (with holotype); W Samalona island, 05°07'31"S 119°20'31"E (RMNH 90115 Ce/1sn:f, 3sh:f); NW Kapodasang reef, 05°05'38"S 119°14'45"E (RMNH 90071 Ce/1sn:f); W Kapodasang reef, 05°05'35"S 119°15'20"E (RMNH 90076 Ce/2sn:m&f+e, 90102 Ce/2sh:m&f).Central Sulawesi, Tomini Bay, Togian islands, barrier reef, S Waleabahi island, 00°26'16"S

122°15'57"E (RMNH 102719/2sn:m&f+e). Bali: Tulamben beach, "Temple Bay", 08°16'43"S 115°35'49"E (RMNH 102720 Ce/3sn:2m&f, 102721 Ca/4sn:2m&2f+e, 2sh:m&f); NE Nusa Lembongan, Tanjung Jangka, 08°39'46"S 115°28'06"E (RMNH 102722 Ce/1sn:f+e).

PALAU: NE of Ngeremdiu, Lighthouse reef, forereef, 07°16'30"N 134°27'25"E (RMNH 102723 Ca/1sn:f+e, 102724 Ce/2sn:m&f+e); Lighthouse reef, forereef, 07°16'14"N 134°27'21"E (RMNH 102794/3sn:m&2f+e); Lighthouse reef, forereef, 07°16'47"N 134°27'50"E (RMNH 102795 Ca/2sn: m&f+e); S of Garreru, Uchelbeluu reef, inner side barrier reef, 07°16'04"N 134°32'26"E (RMNH 102796 Ce/2sn:m&f+e, 1sh:m); SW of Ubelsechel, N of Toachel Ra Ngel,07°18'03"N 134°29'44"E (RMNH 102798 Ce/1sn:m); E of Babelthuap, E of Arudowaishi Pt., Uchelbeluu reef, backreef, 07°21'20"N 134°36'22"E (RMNH 102797 Ca/ 5sn:2m&3f+e).

Shell. Holotype (figs 71-73), the largest female: H 20.3 mm, W 25.5 mm. The whitish shell has a roughly wrinkled, calcareous surface; the smooth and glossy columellar callus is broadly expanded, covering most of the surface of the last whorl in frontal view. In female shells, the straight basal part of the outer lip forms an obtuse angle with the remaining part of the shell base. In male shells the outer lip is curved more regularly. The largest male shell (figs 74-76), found with the holotype in the same host, measures H 12.3 mm, W 11.6 mm. In frontal view, the apical part of female shells is distinctly protruding above the apertural edge (fig. 71), whereas the apex of male shells protrudes slightly less above the edge (fig. 74).

Operculum. Operculum rudimentary.

Habitat. The snails and their egg-capsules were found at 3-17 m, with the mushroom coral species *Ctenactis echinata* (Pallas, 1766) and *Ctenactis albitentaculata* Hoeksema, 1989. The siphon pores are located on the underside of the corals.

Distribution.When all specimens looking similar in morphology and found associated with either *Ctenactis albitentaculata* or *C. echinata* represent *Leptoconchus inalbechi* indeed, its range extends from Indonesia to Palau.

Etymology. This species is named after its restricted habitat. The epithet is a combination of *in* with parts of the epithets of the host coral's species names, i.e. *alb* and *echi*.

Leptoconchus incrassa

Type locality. PALAU. NE of Ngeremdiu, Lighthouse reef, backreef, 07°17'11"N 134°27'26"E.

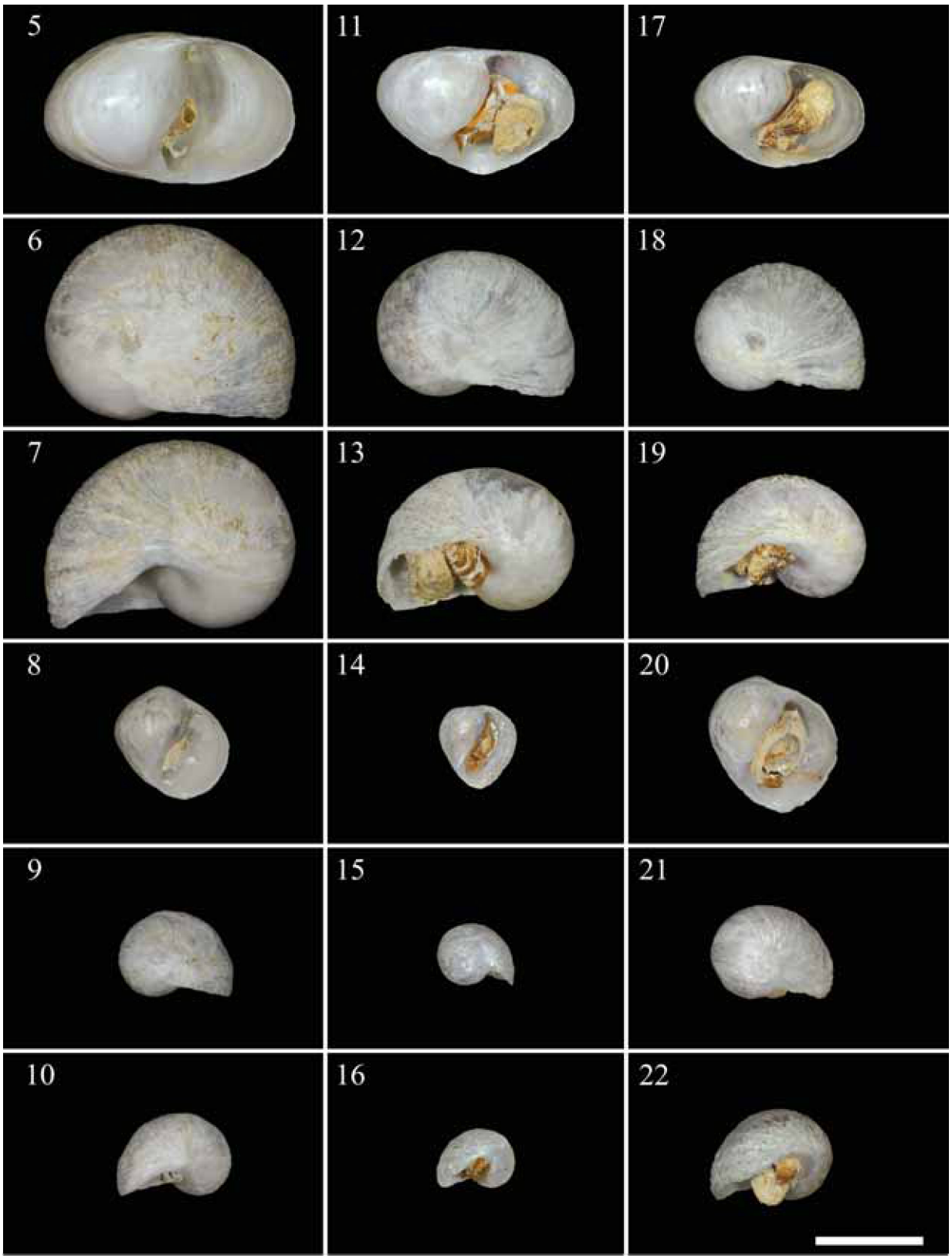
Material (paratypes, unless stated otherwise; all hosted by *Polyphyllia talpina*).

PALAU. NE of Ngeremdiu: type locality, RMNH 102726/holotype, 1sh:f+e [e: RMNH 102727], 102728/1sn:m (with holotype), RMNH 102729/1sn: f, 102730/1sh:f, 102731/2sn:m&f 1sh:f); SE of Ngederrak reef, *Halimeda* flat, 07°17'21"N 134°29'04"E (RMNH 102732/1sn:f+e 1sh:f).

THAILAND. Phiphi islands: NE Ko Phi Phi Le, Pi Le Bay, near cave, 07°41'43"N 98°45'57"E (RMNH 95886/1sn:f 2sh:2f); S Ko Phi Phi Le, Loh Samah, 07°40'28"N 98°46'10"E (RMNH 95978/2sn: m&f+e); Hin Daeng, 07°08'59"N 98°49'25"E (RMNH 95983/1sn:f); E Koh Phi Phi Don, Poh Cape, Hin Phae, 07°43'30"N 98°47'17"E (RMNH 96015/2sn:m&f+e); S Koh Phi Phi Don, S Tongsai Bay, 07°43'14"N 98°46'13"E (RMNH 96006/1sn:f 1sh:f).

INDONESIA. NE Kalimantan, Berau islands, SW Derawan island, 02°16'18"N 118°15'08"E (RMNH 102733/1sn:f). N Sulawesi, SW Gorontalo, 00°21'31"N 124°03'14"E (RMNH 102734/2sn: m&f+e 3sh:sf).

Shell. Holotype (figs 77-79) female: H 15.7 mm, W 22.1 mm. The whitish shell has a roughly wrinkled, calcareous surface; the smooth and glossy columellar callus is not conspicuously expanded. In male shells the columellar callus is more broadly expanded, covering most of the last whorl in frontal view. The palatal and the basal part of the outer lip form a regularly curved entity. The height and the width of the largest female shell (figs 83-85) are 23.1 mm and 29.0 mm, respectively, versus 10.3 mm and 10.7 mm for the largest male shell (figs 80-82), which was found with the holotype in the same host. In frontal view, the apical part of female shells protrudes somewhat above the apertural edge (figs 77, 83),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whereas the apex of male shells protrudes only slightly or not at all (fig. 80).

Operculum. Operculum maybe absent.

Habitat. The snails and their egg-capsules were found at 8-31 m, with exclusively the mushroom coral species *Ctenactis crassa* (Dana, 1846). The siphon pores are located on the underside of the corals.

Distribution. When all specimens looking similar in morphology and found associated with *Ctenactis crassa* represent *Leptoconchus incrassa* indeed, the range of that species extends from Thailand to Palau and Indonesia.

Etymology. This species is named after its restricted habitat. It was found exclusively in corals of *Ctenactis crassa.*

Leptoconchus incycloseris

Type locality. PALAU, NE of Ngeremdiu, Lighthouse reef, forereef, 07°16'30"N 134°27'25"E.

Material (paratypes, unless stated otherwise) Samples that were hosted by *Fungia costulata* or *Fungia tenuis*, are coded Fc or Ft, respectively.

PALAU. Type locality, RMNH 102613/holotype, Fc/1sh:f+e [e: RMNH 102614], 102615/1sh:m (with holotype); SW of Ubelsechel, N of Toachel Ra Ngel, 07°17'50"N 134°29'08"E (RMNH 102616 Ft/1sn: f+e).

INDONESIA. NE Kalimantan, Berau islands, SW Baliktaba reef, N Panjang island, 02°34'43"N 118°00'48"E (RMNH 102617 Fc/2sn:m&f). SW Sulawesi, Spermonde Archipelago: W Kudingareng Keke island, 05°06'09"S 119°17'09"E (RMNH 87830 Fc/1sn:f+e, 87833 Fc/1sn:f, 90051/1sn:f); SW Kudingareng Keke island, 05°06'21"S 119°17'03"E (RMNH 90105 Fc/1sn:f+e); W Badi island, 04°58'05"S 119°16'54"E (RMNH 90037 Fc/1sh:f); SW Bone Tambung, 05°02'12"S 119°16'19"E (RMNH 87860 Fc/1sn:f 1sh:f). Bali: Tulamben beach, 08°16'36"S 115°35'37"E (RMNH 102618 Fc/2sn:m&f+e); Tulamben beach, SE end, drop-off, 08°16'40"S 115°35'45"E (RMNH 102619 Fc/1sn:f).

Shell. Holotype (figs 35-37) female: H 10.7 mm, W 10.7 mm. The whitish shell has a roughly wrinkled, calcareous surface; the smooth and glossy columellar callus is broadly expanded, covering more than half of the surface of the last whorl in frontal view. The lower part of the outer lip and the remaining part of the shell base form an obtuse angle. The height and the width of the largest female shell are 18.9 mm and 19.1 mm, respectively, versus 9.4 mm and 6.1 mm for the largest male. The shell of a male snail (figs 38-40), found together with the holotype, measures H 6.9 mm, W 5.5 mm. In frontal view, the apex of both female and male shells protrudes distinctly above the apertural edge (figs 35, 38).

Operculum. Operculum rudimentary.

Habitat. The snails and their egg-capsules were found at 5-24 m, with the mushroom coral species *Fungia (Cycloseris) costulata* Ortmann, 1889, and *F. (C.) tenuis* Dana, 1846. The siphon pores are located on the upper side of the corals. Massin (2002) reports a *Leptoconchus* specimen associated with the coral *Fungia (Cycloseris) vaughani* Boschma, 1923, from Papua New Guinea. This specimen may belong to *Leptoconchus incycloseris* as well.

Distribution. When all specimens looking similar in morphology and found associated with either *Fungia (Cycloseris) costulata* or *F. (C.) tenuis* represent *Leptoconchus incycloseris* indeed, the range of that species extends from Indonesia to Palau.

Etymology. This species is named after its restricted habitat. It was found exclusively in corals of *Fungia (Cycloseris) costulata* and *F. (C.) tenuis*.

Leptoconchus infungites

Type locality. INDONESIA. Bali, NW Nusa Penida, Toyapakeh, 08°40'56"S 115°28'56"E.

Figs 5-22. Frontal, apical and basal views of shells. 5-10, *Leptoconchus inactiniformis* spec. nov.: 5-7, holotype, female; 8-10, male. 11-16, *Leptoconchus inpileus* spec. nov.: 11-13, holotype, female; 14-16, male. 17-22, *Leptoconchus infungites* spec. nov.: 17-19, holotype, female; 20-22, male. 5-13, Sulawesi, Indonesia; 14-22, Bali, Indonesia.

Material (paratypes, unless stated otherwise; all hosted by *Fungia fungites*).

INDONESIA. Bali: type locality, RMNH 102562/holotype, 1sh: f+e [e: RMNH 102563], 102564/1sh: m (with holotype); Sanur, Jeladi Willis, 08°40'59"S 115°16'03" (RMNH 102565/2sn:m&f+e, 102566/1sn: f 0); Sanur, Penjor Point, 08°41'36"S 115°16'20" (RMNH 102567/3sn:2m&1f+e, 102568/2sn:m&f+e, 102569/2sn:m&f+e, 102570/2sn:m&f+e); Sanur, Penjor Point, 08°42'04"S 115°16'18" (RMNH 102571/1sn:f+e); Sanur, off Kesumasari Beach, Palung Semawang, 08°42'31"S 115°15'59" (RMNH 102572/3sn:2m&1f+e); Bali, NE Pulau Serangan, 08°44'03"S 115°15'05" (RMNH 102573/2sn:m&f+e 3sh:m); Tanjung Benoa, Loloan Benoa, 08°45'46"S 115°14'01" (RMNH 102574/2sn:m&f, 102575/1sn: f+e, 102576/1sn:m); Tulamben beach, 08°16'36"S 115°35'37" (RMNH 102577/1sn:f+e, 102578/2sn: m&f); SE Tulamben beach, drop-off, 08°16'40"S 115°35'45" (RMNH 102579/3sn:2m&f+e); N Nusa Penida, of Desa Ped, 08°40'28"S 115°30'50" (RMNH 102580/2sn:m&f+e, 102581/2sn:m&f+e, 102582/1sn:f, 102583/2sn:m&f, 102584/1sn:m); N Nusa Penida, of Tukad Adegan, 08°40'32"S 115°31'18" (RMNH 102585/1sn:f+e, 102586/1sn: f+e, 102587/1sn:f+e).

NE Kalimantan, Berau islands: N Maratua island, 02°14'51"N 118°37'48" (RMNH 102588/1sn:f+e, 102589/2sn:m&f+e); SE Derawan island, 02°16'18"N 118°15'08" (RMNH102590/2sn:f). N Sulawesi: Bunaken island, 01°36'23"N 124°46'59" (RMNH 90048/1sn:f+e, 90049/1sn:f+e); Bunaken island, 01°37'50"N 124°46'14" (RMNH 90062/1sn:f, 90063/2sn:m&f+e); SW Gorontalo, 00°27'00"N 124°28'43" (RMNH 102591/4sn:2m&2f+e 3sh:2m&1f, 102592/2sn:m&f+e, 102593/3sn: 1m&2f+e 2sh:f, 102594/3sn:2m&1f+e, 102595/6sn: 4m&2f+e 1sh:f); SW Gorontalo, 00°21'31"N 124°03'14" (RMNH 102596/2sn:m&f+e).Central Sulawesi, Tomini Bay, Togian islands, S Batudaka island, 00°35'25"S 121°41'38" (RMNH 102597/1sn: f+e, 102598/3sn:2m&1f+e, 102599/2sn:m&f, 102600/4sn:2m&2f+e, 102750/2sn:m&f+e). SW Sulawesi, Spermonde Archipelago, W Samalona island, 05°07'31"S 119°20'31" (RMNH 90033/1sn: f); W Bone Lola reef, 05°06'09"S 119°17'09" (RMNH 90023/1sn:f); W Bone Tambung island, 05°02'05"S 119°16'16" (RMNH 90110/1sn:f); SW side of Bone Tambung, 05°02'12"S 119°16'19" (RMNH 87879/1sn:f); W Badi island, 04°58'05"S 119°16'54" (RMNH 90030/2sn:m&f+e, 90031/1sn: f, 90112/2sh:m&f).

PALAU. N Ngeremdiu, Lighthouse reef, backreef, 07°17'11"N 134°27'26" (RMNH 102751/2sn: m&f+e); W Babelthuap, Toachel Mlengui, 07°32'31"N 134°28'24" (RMNH 102752/2sn:f+e).

Shell. Holotype (figs 17-19) female: H 16.0 mm, W 25.9 mm. The whitish shell has a roughly wrinkled, calcareous surface; the smooth and glossy columellar callus is broadly expanded, covering most of the surface of the last whorl in frontal view. The outer lip passes into the remaining basal part of the shell with a vague angle. The height and the width of the largest female shell are 24.3 mm and 27.0 mm, respectively, versus 13.5 mm and 11.6 mm for the largest male shell. The shell of a male snail (figs 20-22), found with the holotype in the same host, measures H 13.0 mm, W 11.5 mm. In frontal view, the apical part of female shells is slightly protruding above the apertural edge (fig. 17); the apex of male shells protrudes distinctly above the apertural edge (fig. 20).

Operculum. Operculum rudimentary.

Habitat. The snails and their egg-capsules were found at 4-18 m, with exclusively the mushroom coral species *Fungia (Fungia) fungites* (Linnaeus, 1758). The siphon pores are located on the upper side of the corals.

Distribution. When all specimens looking similar in morphology and found associated with *Fungia (F.) fungites* represent *Leptoconchus infungites* indeed, that species is distributed from Indonesia to Palau. Massin (1992: OTU6) reported it from the Red Sea and the Maldives.

Etymology. This species is named after its restricted habitat. It was found exclusively in corals of *Fungia (Fungia) fungites*.

Leptoconchus ingrandifungi

Type locality. PALAU. NE of Ngeremdiu, Lighthouse reef, forereef, 07°16'30"N 134°27'25"E.

Material (paratypes, unless stated otherwise). Samples that were hosted by *Podabacia crustacea, Podabacia motuporensis*, *Sandalolitha dentata*, *Sandalolitha robusta* or *Zoopilus echinatus*, are coded Pc, Pm, Sd, Sr or Ze, respectively.

PALAU. NE of Ngeremdiu: type locality, RMNH 102805/holotype, Pm/1sh:f+e [e: RMNH 102800], 102801 Pm/3sn:2m&f (with holotype), 102802 Pc/2sn:m&f+e; NE of Ngeremdiu, Lighthouse reef, forereef, 07°16'47"N 134°27'50"E (RMNH 102803 Pm/2sn:m&f+e, 102804 Pm/1sn:f+e, 1sh:m); E of Mecherchar, N of Bkul a Chememiich, inside of barrier reef, 07°09'20"N 134°24'08"E (RMNH 102805 Pm/1sn:m).

INDONESIA. SW Sulawesi, Spermonde Archipelago: W Bone Lola reef, 05°06'09"S 119°17'09"E (RMNH 87824 Sr/1sh:f); W Bone Tambung island, 05°02'05"S 119°16'16"E (RMNH 87861 Pc/1sn:f). Bali, Sanur, Penjor Point, 08°42'04"S 115°16'18"E (RMNH 102806 Sd/1sn:f).

Shell. Holotype (figs 86-88) female: H 6.6 mm, W 11.7 mm. The whitish shell has a roughly wrinkled, calcareous surface; the smooth and glossy columellar callus is broadly expanded, covering most of the surface of the last whorl in frontal view. The symmetrical outer lip passes gradually into the remaining part of the slightly curved shell base. The height and the width of the largest female shell are 15.7 mm and 18.4 mm, respectively, versus 9.1 mm and 10.7 mm for the largest male shell. The figured male shell (figs 89-91) measures H 8.8 mm, W 9.1 mm. In frontal view, the apical part of female shells is in line with the apertural edge or located slightly below it (fig. 86), whereas the apex of male shells protrudes slightly (fig. 89).

Operculum. Operculum maybe absent.

Habitat. The snails and their egg-capsules were found at 12-29 m, with mushroom corals of the species *Podabacia motuporensis* Veron, 1990, *P. crustacea* (Pallas, 1766), *Zoopilus echinatus* Dana, 1846, and Sandalolitha dentata Quelch, 1884. The siphon pores are located on the underside of the corals.

Distribution. When all specimens looking similar in morphology and found associated with one of the host species mentioned, represent *Leptoconchus ingrandifungi* indeed, the range of that species extends from Palau to Indonesia.

Etymology. This species is named after its restricted habitat. It was found exclusively in association with fungiid species of which the individuals can become larger than those of most other fungiid species.

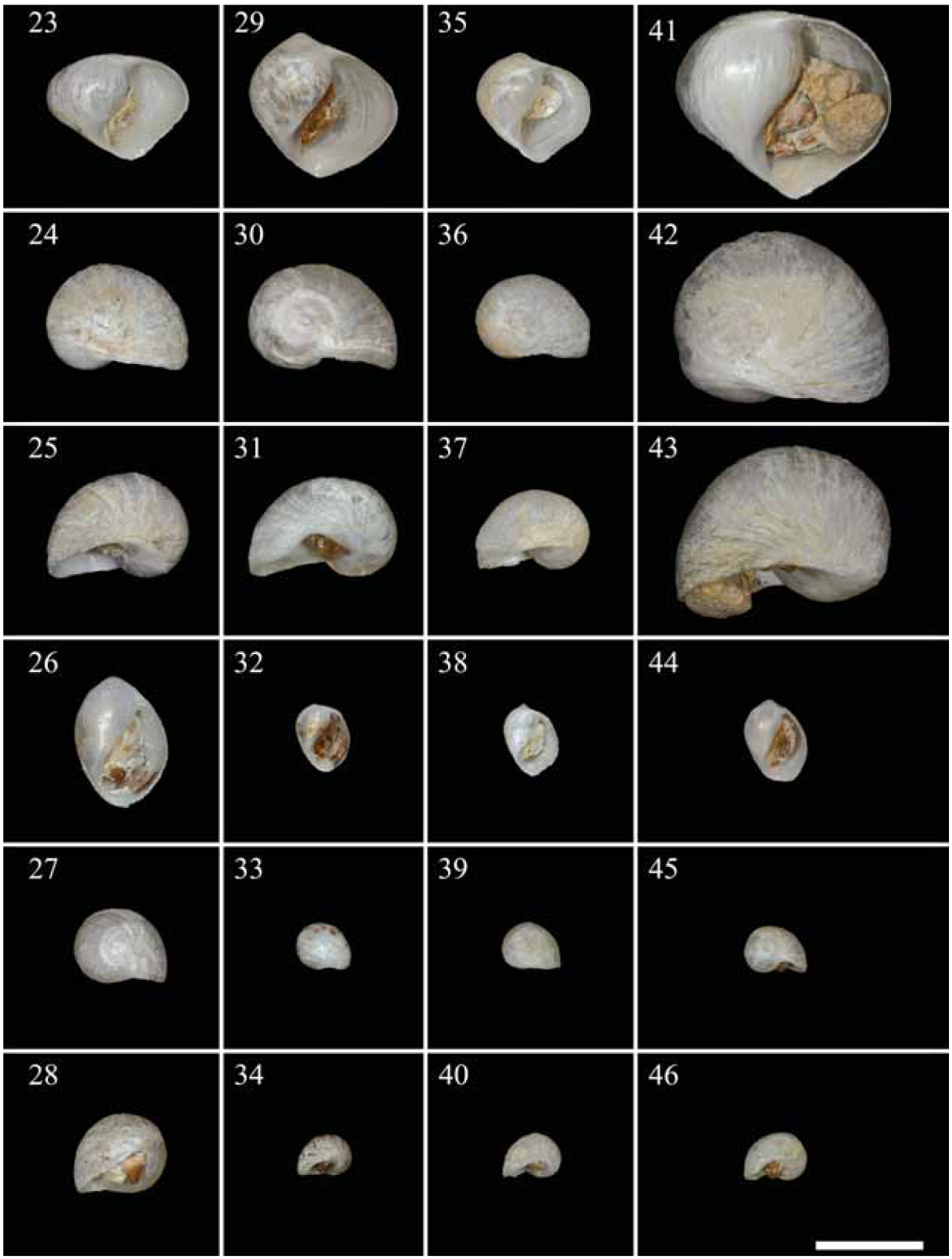
Leptoconchus ingranulosa

Type locality. INDONESIA. Bali, N Nusa Penida, of Tukad Adegan, 08°40'32"S 115°31'18"E.

Material (paratypes, unless stated otherwise; all hosted by *Fungia (Wellsofungia) granulosa*).

INDONESIA. Bali: type locality, RMNH 102769/holotype, 1sh:f, 102770/1sn:m 1sn:f+e (with holotype), 102776/2sn:m&f+e; Tanjung Benoa, Loloan Benoa, 08°45'46"S 115°14'01"E (RMNH 102771/2sn:m&f+e, 102772/1sn:m); Tulamben beach, SE end, drop-off, 08°16'40"S 115°35'45"E (RMNH 102773/1sn:f&e, 102774/2sn:m&f 3sh:m&2f). N Sulawesi, SW of Gorontalo, 00°27'00"N 124°28'43"E (RMNH 102775/2sn:m&f+e). Central Sulawesi, Tomini Bay, Togian islands: barrier reef S of Waleabahi island, 00°26'16"S 122°15'57"E (RMNH 102777/2sn:m&f+e); S Talatakoh island , 00°28'22"S 122°08'22"E (RMNH 102778/1sn:m); Barrier reef S of Talatakoh island, 00°29'39"S 122°04'21"E (RMNH 102779/1sn:f 1sh:m); S Togian island, 00°25'31"S 122°00'11"E (RMNH 102780/2sn:m&f+e, 102781/1sn:m 2sh:f, 102782/2sn:m&f+e 3sh:f); N Togian island, 00°21'13"S 121°50'38"E (RMNH 102783/3sn:m&3f 2sh:f). SW Sulawesi, Spermonde Archipelago: W Kudingareng Keke island, 05°06'09"S 119°17'09"E (RMNH 90027/1sn:m, 90052/1sn:f); SW Kudingareng Keke island, 05°06'21"S 119°17'03"E (RMNH 87858/2sn:m&f); W Bone Lola reef, 05°03'07"S 119°21'09"E (RMNH 90021/1sn:f 1sh:m); W Barang Lompo island, 05°02'51"S 119°19'44"E (RMNH 90024/1sn:f); W Badi island, 04°58'05"S 119°16'54"E (RMNH 90029/1sn:f&e); NW Lumulumu island, 04°58'13"S 119°12'35"E (RMNH 90067/1sn:f); W Kapodasang reef, 05°05'35"S 119°15'20"E (RMNH 90095/1sn:f).

PALAU. NE of Ngeremdiu, Lighthouse reef, forereef, 07°16'30"N 134°27'25"E (RMNH 102784/3sn:m&2f+e 1sh:f, 102785/1sn:m 1sh:f, 102786/1sn:f2sh:f, 102787/4sn:3m&f); Lighthouse reef, forereef,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07°16'14"N 134°27'21"E (RMNH 102788/2sn: m&f+e, 102789/1sn:f); Lighthouse reef, backreef, 07°17'11"N 134°27'26"E (RMNH 102790/2sn:m&f).

Shell. Holotype (figs 47-49): female H 11.3 mm, W 12.2 mm. The whitish shell has a roughly wrinkled, calcareous surface; the smooth and glossy columellar callus is broadly expanded, covering most of the surface of the last whorl in frontal view. In female shells, the outer lip is regularly curved, its lower half gradually passing into the remaining basal part of the shell; in male specimens there is a basal angle. The height and the width of the largest female shell are 16.0 mm and 17.2 mm, respectively, versus H 8.1 mm and W 7.0 mm for the largest male (figs 50-52), which was found with the holotype in the same host. In frontal view, the apical part of female shells is distinctly protruding above the apertural edge (fig. 47); the apex of male shells protrudes hardly or not above the apertural edge (fig. 50).

Operculum. Operculum rudimentary.

Habitat. The snails and their egg-capsules were found at 5-20 m, with exclusively the mushroom coral species *Fungia (Wellsofungia) granulosa* Klunzinger, 1879. The siphon pores are located on the upper side of the corals.

Distribution. When all specimens looking similar in morphology and found associated with *Fungia (Wellsofungia) granulosa* represent *Leptoconchus ingranulosa* indeed, its range extends from Indonesia to Palau.

Etymology. This species is named after its restricted habitat. It was found exclusively in corals of *Fungia (Wellsofungia) granulosa.*

Figs 23-46. Frontal, apical and basal views of shells. 23-28, *Leptoconchus inscruposa* spec. nov.: 23-25, holotype, female; 26-28, male. 29-34, *Leptoconchus inscutaria* spec. nov.: 29-31, holotype, female; 32-34, male. 35-40, *Leptoconchus incycloseris* spec. nov.: 35-37, holotype, female; 38-40, male. 41-46, *Leptoconchus inpleuractis* spec. nov.: 41-43, holotype, female; 44-46, male. 23-28, Sulawesi, Indonesia; 29-34, Bali, Indonesia; 35-46, Palau.

Leptoconchus inlimax

Type locality. INDONESIA. SW Sulawesi, Spermonde Archipelago, W Samalona island, 05°07'31"S 119°20'31"E.

Material (paratypes, unless stated otherwise; all hosted by *Herpolitha limax*).

INDONESIA. SW Sulawesi, Spermonde Archipelago: type locality, RMNH 90045/holotype, 1sh:f, 102679/1sn:f 1sh:m (with holotype), 90053/1sn:f 1sh:f; SW Samalona, 05°07'42"S 119°20'31"E (RMNH 90109/1sn:f); W Bona Baku reef, 05°07'56"S 119°21'39"E (RMNH 90016/1sn:f); W Kudingareng Keke island, 05°06'09"S 119°17'09"E (RMNH 90026/1sn:f); NW Kapodasang, 05°05'38"S 119°14'45"E (RMNH 90069/1sn:f, 90073/1sn:f); W Bone Batang, 05°00'42"S 119°19'31"E (RMNH 90034/1sn:f, 90036/1sn:m). N Sulawesi, SW Gorontalo, 00°21'31"N 124°03'14"E (RMNH 102680/1sn:f). Central Sulawesi, Tomini Bay, Togian islands: barrier reef, S Waleabahi island, 00°26'16"S 122°15'57"E (RMNH 102681/2sn:m&f); S Talatakoh island, 00°28'22"S 122°08'22"E (RMNH 102682/3sn:2m&f+e 1sh:f); S Batudaka island, 00°35'25"S 121°41'38"E (RMNH 102683/2sn:m&f). Bali: Sanur, Penjor Point, 08°41'36"S 115°16'20"E (RMNH 102684/2sn:f); Sanur, Loloan Batu Agung, 08°43'31"S 115°15'57"E (RMNH 102685/6sn: 3m&3f+e, 102686/3sn:1m&2f+e 1sh:m, 102687/1sn: f, 102688/4sn:2m&2f+e); Tulamben beach, 08°16'36"S 115°35'37"E (RMNH 102689/2sn: m&f+e); Tulamben beach, 08°16'40"S 115°35'45"E (RMNH 102690/1sn:f+e); N Nusa Penida, off Desa Ped, 08°40'28"S 115°30'50"E (RMNH 102691/2sn: m&f); NE Nusa Lembongan, Tanjung Jangka, 08°39'46"S 115°28'06"E (RMNH 102692/2sn: m&f+e). NE Kalimantan, Berau islands, Karang Pinaka, NW Samama island, 02°11'22"N 118°17'25"E (RMNH 102693/3sn:2m&1f+e).

PHILIPPINES, Cebu Strait, SW of Bohol, S of Panglao, NE Balicasag island, 09°30'N 123°41'E (RMNH 102694/ 2sn:m&f+e).

PALAU. NE of Ngeremdiu, Lighthouse reef, forereef, 07°16'30"N 134°27'25"E (RMNH 102695/2sn:m&f+e, 102696/2sh:f, 102697/1sn:f, 102698/2sn:m&f+e); NE of Ngeremdiu, Lighthouse reef, backreef, 07°17'11"N 134°27'26"E (RMNH 102699/2sn:m&f+e); S of Garreru, Uchelbeluu reef, inner side barrier reef, 07°16'04"N 134°32'26"E

(RMNH 102700/1sn:f+e 1sh:m, 102701/2sn:m&f+e); S of Ubelsechel, NE of Toachel Ra Ngel, 07°18'28"N 134°30'23"E (RMNH 102702/1sn:f).

MALDIVES. Ari Atoll, Vilamendhoo island (RMNH 102703/1sn:f).

Shell. Holotype (figs 59-61) female: H 19.1 mm, W 22.8 mm. The whitish shell has a roughly wrinkled, calcareous surface; the smooth and glossy columellar callus is broadly expanded, covering most of the surface of the last whorl in frontal view. The lower part of the outer lip forms an obtuse angle with the remaining basal part of the shell.The height and the width of the largest female shell are 20.3 mm and 22.1 mm, respectively, versus H 13.2 mm and W 10.6 mm for the largest male (figs 62-64), which was collected with the holotype in the same host. In frontal view, the apical part of female shells is slightly protruding above the apertural edge (fig. 59); the apex of male shells protrudes distinctly above the apertural edge (fig. 62).

Operculum. Operculum rudimentary.

Habitat. The snails and their egg-capsules were found at 5-24 m, with exclusively the mushroom coral species *Herpolitha limax* (Esper, 1797). The siphon pores are located on the underside of the corals.

Distribution. When all specimens looking similar in morphology and found associated with *Herpolitha limax* represent *Leptoconchus inlimax* indeed, the range of this species extends from the Philippines and Palau to Indonesia.

Etymology. This species is named after its restricted habitat. It was found exclusively in corals of *Herpolitha limax*.

Leptoconchus inpileus

Type locality. INDONESIA. SW Sulawesi, Spermonde Archipelago, W Kapodasang reef, 05°05'35"S 119°15'20"E.

Material (paratypes, unless stated otherwise; all hosted by *Halomitra pileus*).

INDONESIA. SW Sulawesi, Spermonde Archipelago: type locality, RMNH 90078/holotype, 1sh: f+e [e: RMNH 102554], 90077/1sn:f+e, 90079/2sn:m&f+e; W Kudingareng Keke island, 05°06'09"S 119°17'09"E (RMNH 90088/1sn:f+e); W Badi island, 05°58'05"S 119°16'54"E (RMNH 90041/1sn:m); W Bone Tambung island, 05°02'05"S 119°16'16"E (RMNH 90116/1sn:f, 90118/2sn:m&f+e). Central Sulawesi, Tomini Bay, Togian islands: Walea Lighthouse, 00°25'19"S 122°26'08"E (RMNH 102555/1sn:m, 1sh:m); Barrier reef, N Batudaka island, 00°25'20"S 121°40'54"E (RMNH 102556/1sn:f).
NE Kalimantan, Berau islands (RMNH 102557/2sn: m&f+e, 102558/2sn:m&f). Bali, Nusa Penida, 08°40'28"S 115°30'50"E (RMNH 102559/1sh:m).

MALDIVES. Ari Atoll, Vilamendhoo island (RMNH 102749/1sn:f).

Shell. Holotype (figs 11-13) female: H 12.1 mm, W 18.5 mm. The whitish shell has a roughly wrinkled, calcareous surface; the smooth and glossy columellar callus is broadly expanded, covering most of the surface of the last whorl in frontal view. The lower half of the outer lip forms an obtuse angle with the remaining basal part of the shell. The height and the width of the largest female shell are 21.6 mm and 22.6 mm, respectively, versus 12.3 mm and 10.8 mm for the largest male. The shell of a male snail (figs 14-16), found with the holotype in the same host, measures H 8.5 mm, W 7.3 mm. In frontal view, the apical part of female shells is not or hardly protruding above the straight uppermost part of the apertural edge (fig. 11); the apex of male shells is situated in line with the apertural edge or slightly lower (fig. 14).

Operculum. Operculum rudimentary.

Habitat. The snails and their egg-capsules were found at 8-18 m, with exclusively the mushroom coral species *Halomitra pileus* (Linnaeus, 1758). The siphon pores are located on the upper side of the corals.

Distribution. When all specimens looking similar in morphology and found associated with *Halomitra pileus* represent *Leptoconchus inpileus* indeed, that species in known from the Maldives, off Vilamendhoo island, and Indonesia, off Kalimantan, Sulawesi and Bali. Massin (1992: OTU5) reported it from NE Papua New Guinea.

Etymology. This species is named after its restricted habitat. It was found exclusively in corals of *Halomitra pileus.*

Leptoconchus inpleuractis

Type locality. PALAU, W of Babelthuap, Toachel Mlengui, 07°32'31"N 134°28'24"E.

Material (paratypes, unless stated otherwise). Samples that were hosted by *Fungia gravis*, *F. moluccensis* or *F. paumotensis*, are coded Fg, Fm or Fp, respectively.

PALAU: type locality, RMNH 102621/holotype, Fp/1sn:f+e [e: RMNH 102622], 102623 Fp/1sn:m (with holotype); NE of Ngeremdiu, Lighthouse reef, forereef, 07°16'30"N 134°27'25"E (RMNH 102624 Fp/2sn:m&f+e, 102625 Fp/2sn:f); Lighthouse reef, forereef, 07°16'47"N 134°27'50"E (RMNH 102626 Fp/2sn:m&f+e); SW Ngeream, patch reef in KB channel, 07°20'22"N 134°31'05"E (RMNH 102627 Fp/1sn:m); S of Garreru, Uchelbeluu reef, inner side barrier reef, 07°16'04"N 134°32'25"E (RMNH 102628 Fp/3sn:m&2f).

PHILIPPINES. Cebu Strait, SW of Bohol, S of Panglao, NE Balicasag island, 09°31'N 123°41'E (RMNH 102629 Fg/1sn:f).

INDONESIA. NE Kalimantan, Berau islands: E Derawan island, 02°17'32"N 118°15'43"E (RMNH 102630 Fg/2sn:f); NE Buliulin, S Samama island, 02°07'07"N 118°20'32"E (RMNH 102631 Fg/1sn:f). N Sulawesi: Bunaken island, 01°36'23"N 124°46'59"E (RMNH 90047 Fp/3sn:m&2f+e); Bunaken island, 01°39'09"N 124°42'17"E (RMNH 90058 Fp/2sn:m&f+e); Bunaken island, 01°37'50"N 124°46'14"E (RMNH 90064 Fp/2sn:m&f+e); Lembeh Strait, 01°27'35"N 125°13'34"E (RMNH 102632 Fp/2sn:m&f); SW Gorontalo, 00°21'31"N 124°03'14"E (RMNH 102633 Fp/2sn:m&f+e, 102634 Fg/2sn:m&f+e). Central Sulawesi, Tomini Bay, Togian islands, N Togian island, 00°18'41"S 121°58'45"E (RMNH 102635 Fp/1sn:m, 102636 Fp/3sn:m&2f+e). SW Sulawesi, Spermonde Archipelago: W Bona Baku reef, 05°07'56"S 119°21'39"E (RMNH 90055 Fp/1sn:f+e, 90091 Fm/1sn:m); W Samalona island, 05°07'31"S 119°20'31"E (RMNH 90017 Fp/1sn:m 2sh:m&f, 90018 Fm/1sn:f+e, 90042 Fp/2sn:m&f+e, 90046 Fp/1sn:f+e); SE Samalona island, 05°07'39"S 119°20'38"E (RMNH 90044 Fp/2sn:m&f+e); W Kudingareng Keke island, 05°06'09"S 119°17'09"E (RMNH 87827 Fg/1sh:f, 87828 Fg/1sn:f 1sh:f, 87832 Fg/1sn:f, 87835 Fp/2sn:m&f+e, 87836 Fp/1sn:f 1sh:f, 87837 Fg/1sn:m 2sh:f, 90111 Fg/1sn:m 2sh:f); SW Kudingareng Keke island, 05°06'21"S 119°17'03"E (RMNH 87848 Fm/1sn:f+e, 87850 Fm/1sn:m, 87855 Fp/1sn:m, 87856 Fm/2sn:m&f+e, 87869 Fp/1sn:f 1sh:f, 87870 Fp/1sn:f 1sh:f, 87875 Fg/2sn:m&f+e, 87876 Fp/1sh:f, 87877 Fm/2sn:m&f, 90107 Fg/1sn:f); W Kapodasang reef, 05°05'35"S 119°15'20"E (RMNH 90101 Fp/1sn:f, 90104 Fp/3sn:2m&1f+e 1sh:f); W Bone Lola reef, 05°03'07"S 119°21'09"E (RMNH 87820 Fm/1sh:f, 87822 Fm/1sn:m, 87825 Fg/2sn:m&f+e 1sh:f, 87823 Fg/2sh:m&f); NW Bone Tambung island, 05°02'05"S 119°16'16"E (RMNH90020 Fp/2sn:m&f); W Badi island, 04°58'05"S 119°16'54"E (RMNH 90028 Fm/1sn:f, 90113 Fg/1sh:f). Bali: Sanur, Penjor Point, 08°41'36"S 115°16'20"E (RMNH 102637 Fg/2sn:m&f+e); Penjor Point, 08°31'11"S 115°30'37"E (RMNH 102638 Fg/1sn:m); Tulamben beach, drop-off, 08°16'40"S 115°35'45"E (RMNH 102639 Fg/1sn:f 1sh:m, 102640 Fg/2sn:m&f+e 1sh:m, 102641 Fg/1sn:f 1sh:f); Tulamben beach, 08°17'05"S 115°36'11"E (RMNH 102644 Fg/1sn:f 2sh:m&f, 102645 Fg/1sn:f+e, 102646 Fg/1sn:f+e, 102647 Fg/1sn:f 1sh:m, 102648 Fg/2sn:m&f+e, 102643 Fg/2sn:m&f+e); Tulamben beach, Temple Bay, 08°16'43"S 115°35'49"E (RMNH 102743 Fg/1sn:f); N Nusa Penida, of Desa Ped, 08°40'28"S 115°30'50"E (RMNH 102649 Fg/1sn:f+e); NE Nusa Lembongan, Tanjung Jangka, 08°39'46"S 115°28'06"E (RMNH 102650 Fg/2sn:m&f+e); NW Nusa Penida, Toyapakeh, 08°40'56"S 115°28'56"E (RMNH 102651 Fp/1sn:f+e); N Nusa Penida, of Tukad Adegan, 08°40'32"S 115°31'18"E (RMNH 102642 Fg/1sn:f+e).

Shell. Holotype (figs 41-43), the largest female shell: H 18.6 mm, W 20.1 mm. The whitish shell has a roughly wrinkled, calcareous surface; the smooth and glossy columellar callus is broadly expanded, covering most of the surface of the last whorl in frontal view. The lower part of the outer lip and the remaining part of the shell base form a distinct angle in the female shell. The figured male snail (figs 44-46), found with the holotype in the same host, measures H 8.3 mm, W 5.9 mm. The largest male shell measures H 10.0 mm, W 8.3 mm. In frontal view, the apical part of female shells is slightly protruding above the

apertural edge (fig. 41), whereas the apex of male shells protrudes distinctly (fig. 44).

Operculum. Operculum rudimentary.

Habitat. The snails and their egg-capsules were found at 3-20 m, with the mushroom coral species *Fungia (Pleuractis) paumotensis* Stutchbury, 1833, *F. (P.) gravis* Nemenzo, 1955, and *F. (P.) moluccensis* Van der Horst, 1919. The siphon pores are located on the upper side of the corals.

Distribution. When all specimens looking similar in morphology and found associated with one of the three coral host species mentioned represent this species indeed, its range extends from the Philippines to Indonesia and Palau.

Etymology. This species is named after its restricted habitat. It was found exclusively in corals of the subgenus *Pleuractis*.

Leptoconchus inscruposa

Type locality. INDONESIA. N Sulawesi, Lembeh Strait, 01°27'35"N 125°13'34"E.

Material (paratypes, unless stated otherwise; all hosted by *Fungia scruposa*).

INDONESIA. N Sulawesi: type locality, RMNH 102601/holotype, 1sh:f, 102602/1sh:m (with holotype). Central Sulawesi, Tomini Bay, Togian islands: Walea Lighthouse, 00°25'19"S 122°26'08" (RMNH 102603/6sn:3m&3f+e); Barrier Reef, N Batudaka island, 00°25'20"S 121°40'54" (RMNH 102604/3sn:1m&2f+e, 102605/1sn:f+e, 2sh:m&f, 102606/3sn:2m&f+e, 1sh:f, 102607/2sn:m&f+e); Patch reef, S Batudaka island, 00°35'25"S 121°41'38" (RMNH 102608/2sn:m&f+e, 1sh:f, 102609/1sn:f); S Talatakoh island, 00°28'22"S 122°08'22" (RMNH 102610/2sn:m&f, 102611/2sn:m&f+e). SW Sulawesi, Spermonde Archipelago: W Kudingareng Keke island, 05°06'09"S 119°17'09" (RMNH 90106/2sn:m&f); W Bone Lola reef, 05°06'09"S 119°17'09" (RMNH 87817/1sh, f); W Bone Batang, 05°00'42"S 119°19'31" (RMNH 90035/2sn:m&f); W Badi island, 04°58'05"S 119°16'54" (RMNH 90032/2sn:m&f+e, 90038/2sn:m&f+e, 90114/3sh:1m&2f). NE Kalimantan, Berau islands, Karang Pinaka, NW Samama island, 02°11'22"N 118°17'25" (RMNH 102612/6m&5f+e). Bali, Tulamben beach, Coral garden, 02°11'22"N 118°17'25" (RMNH 102753/1sn:f+e; SE Tulamben beach, drop-off, 08°16'40"S 115°35'45" (RMNH 102754/1sh:f; N Nusa Penida, of Desa Ped, 08°40'28"S 115°30'50" (RMNH 102755/1sn:m, 102756/4sn:2m&2f+e); Nusa Lembongan, E Selat Ceningan, seagrass and mangrove, 08°41'03"S 115°27'43" (RMNH 102757/1sn:m).

PHILIPPINES, Cebu Strait, SW of Bohol, S of Panglao, NE Balicasag island, 09°30'N 123°41' (RMNH 102758/1sn:f).

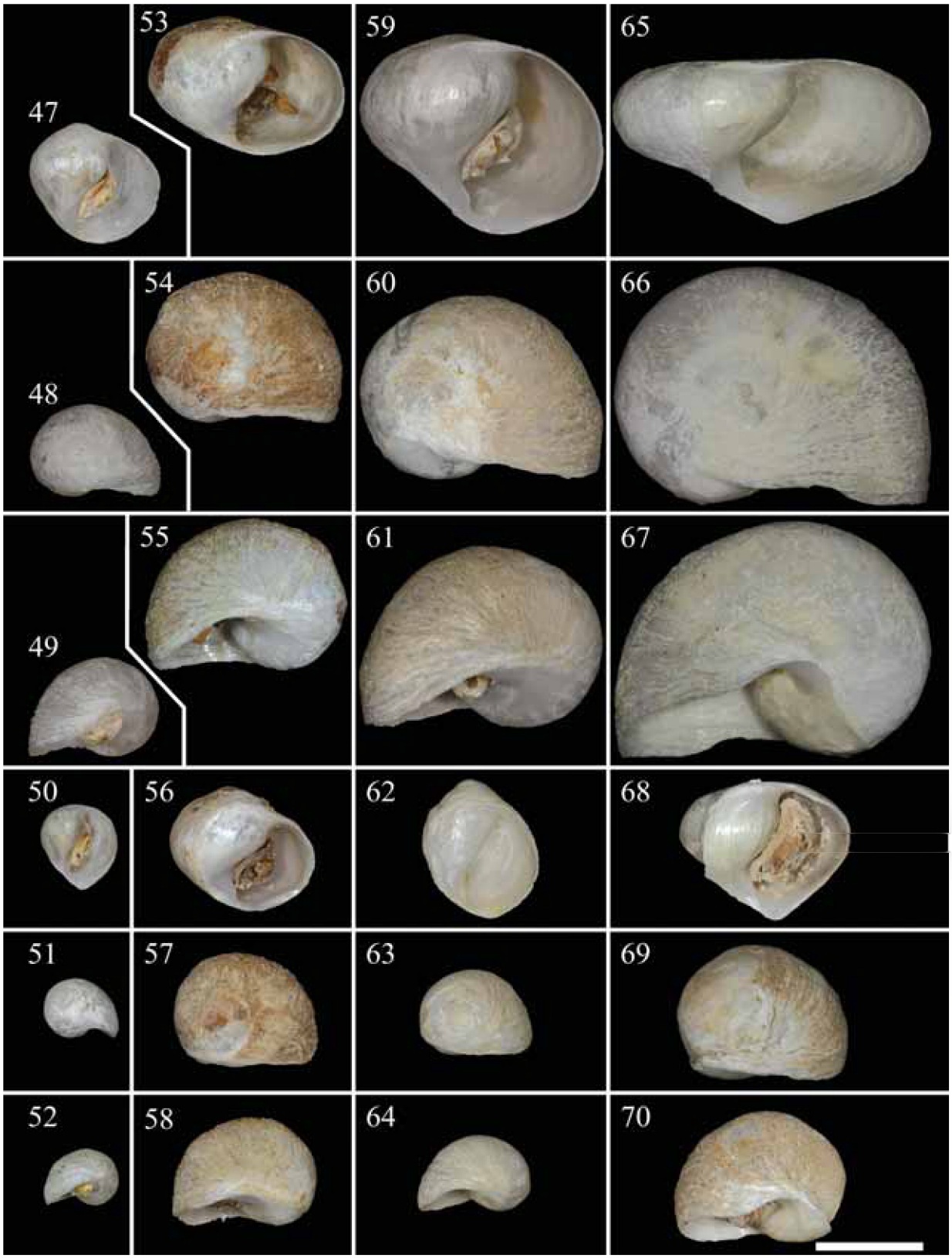
Shell. Holotype (figs 23-25) female: H 19.7 mm, W 23.3 mm. The whitish shell has a roughly wrinkled, calcareous surface; the smooth and glossy columellar callus is broadly expanded, covering most of the surface of the last whorl in frontal view. The lower half of the outer lip forms an obtuse angle with the remaining basal part of the shell. The largest female is the holotype. The figured male shell (figs 26-28), found with the holotype in the same host, is the largest male specimen known, measuring H 12.3 mm, W 8.7 mm. In frontal view, the apical part of female shells hardly protrudes above the apertural edge (fig. 23), whereas the apex of male shells protrudes distinctly (fig. 26).

Operculum. Operculum maybe absent.

Habitat. The snails and their egg-capsules were found at 5-18 m, with exclusively the mushroom coral species *Fungia (Danafungia) scruposa* Klunzinger, 1879. The siphon pores are located on the upper side of the corals.

Distribution. When all specimens looking similar in morphology and found associated with *Fungia (Danafungia) scruposa* represent *Leptoconchus inscruposa* indeed, that species extends from Indonesia to the

Figs 47-70. Frontal, apical and basal views of shells. 47-52, *Leptoconchus ingranulosa* spec. nov.: 47-49, holotype, female; 50-52, male. 53-58, *Leptoconchus massini* spec. nov.: 53-55, holotype, female; 56-58, male. 59-64, *Leptoconchus inlimax* spec. nov.: 59-61, holotype, female; 62-64, male. 65-70, *Leptoconchus inpleuractis* spec. nov.: 65-67, holotype, female; 68-70, male. 47-52, Bali, Indonesia; 53-58, Phiphi Islands, Thailand; 59-64, 68-70, Sulawesi, Indonesia; 65-67, Palau.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Phillipines. Massin (1992: OTU4) reported it from the Red Sea and the Maldives.

Etymology. This species is named after its restricted habitat. It was found exclusively in corals of *Fungia (Danafungia) scruposa*.

Leptoconchus inscutaria

Type locality. INDONESIA. Bali: Nusa Penida, N of Tukad Adegan, 08°40'32"S 115°31'18"E.

Material (paratypes, unless stated otherwise; all hosted by *Fungia scutaria*).

INDONESIA. Bali: type locality, RMNH 102759/ holotype, 1sh:f; Sanur, Penjor Point, 08°41'36"S 115°16'20"E (RMNH 102760/1sh:m, 102761/ 3sn:2m&f+e, 102762/1sn:m); Nusa Dua, E, of Club Med Hotel, N of channel, 08°47'06"S 115°13'57"E (RMNH 102763/1sh:f); Tanjung Benoa, Loloan Benoa, 08°45'46"S 115°14'01"E (RMNH 102764/ 1sn:f+e, 102765/1sn:m, 1sh:f); Tulamben beach, "Coral garden", 08°16'36"S 115°35'37" (RMNH 102766/3sn:m&2f+e); Tulamben beach, SE end, drop-off, 08°16'40"S 115°35'45"E (RMNH 102767/ 1sn:f+e). W Nusa Penida, Teluk Penida, 08°42'54"S 115°27'26"E (RMNH 102768/1sn:f+e). N Sulawesi: off Manado, Siladen island, 01°37'37"N 124°48'01"E (RMNH 90050/1sn:f+e); off Manado, Bunaken island, 01°37'37"N 124°48'01"E (RMNH 90065/1sn: f+e); N Lembeh Strait, E Lembeh island, 01°30'01"N 125°15'39"E (RMNH 102742/6sn:3m&3f+e). SW Sulawesi, Spermonde Archipelago, W Bone Tambung island, 05°02'05"S 119°16'16"E (RMNH 90019/1sn:f).

Shell. Holotype (figs 29-31) female: H 13.9 mm, W 15.9 mm. The whitish shell has a roughly wrinkled, calcareous surface, the smooth and glossy columellar callus is broadly expanded, covering most of the surface of the last whorl in frontal view. The lower part of the outer lip and the remaining basal part of the shell form an obtuse angle. Some female shells and most male ones have brownish dots. The height and the width of the largest female shell are 17.0 mm and 17.5 mm, respectively, versus 11.6 mm and 7.4 mm for the largest male. The figured male specimen (figs 32-34) measures H 7.3 mm, W 5.1 mm. In frontal view, the apical part of female shells distinctly protrudes above the apertural edge (fig. 29); the apex of male shells protrudes less conspicuously above the apertural edge (fig. 32).

Operculum. Operculum rudimentary.

Habitat. The snails and their egg-capsules were found at 5-15 m, with exclusively the mushroom coral species *Fungia (Lobactis) scutaria* Lamarck, 1801. The siphon pores are located on the upper side of the corals.

Distribution. When all specimens looking similar in morphology and found associated with *Fungia (Lobactis) scutaria* represent *Leptoconchus inscutaria* indeed, that species occurs in Indonesia, from Sulawesi to Bali. Massin (1992) mentioned it as OTU4 from NE Papua New Guinea.

Etymology. This species is named after its restricted habitat. It was found exclusively in corals of *Fungia (Lobactis) scutaria*.

Leptoconchus intalpina

Type locality. PALAU. NE of Ngeremdiu, Lighthouse reef, forereef, 07°16'30"N 134°27'25"E.

Material (paratypes, unless stated otherwise; all hosted by *Polyphyllia talpina*).

PALAU. Type locality, RMNH 102712/holotype, sh:f, 102713/1sn:f+e 2sh:m (with holotype), 102714/ 4sn:1m&3f+e; NE of Ngeremdiu, Lighthouse reef, forereef, 07°16'14"N 134°27'21"E (RMNH 102715/ 3sn:2m&1f+e); NE of Ngeremdiu, Lighthouse reef, forereef, 07°16'47"N 134°27'50"E (RMNH 102716/ 2sn:m&f+e).

INDONESIA. N Sulawesi, of Manado, Bunaken island, 01°39'09"N 124°42'17"E (RMNH 90059/1sn: m). SW Sulawesi, Spermonde Archipelago: W Bona Baku reef, 05°07'56"S 119°21'39"E (RMNH 87863/ 1sh:f, 87865/1sn:m 1sh:f, 87866/1sn:f, 87867/1sn:f, 90084/1sn:f, 90085/2sn:2f&e 1sh:m, 90086/1sn:f); W Samalona island, 05°07'31"S 119°20'31"E (RMNH 90043/2sn:m&f+e); SW Kudingareng Keke island, 05°06'21"S 119°17'03"E (RMNH 90094/1sn: f 1sh:m); NW Kapodasang reef, 05°05'38"S 119°14'45"E (RMNH 90070/1sn:f).

Shell. Holotype (figs 65-67), the largest female: H 16.2 mm, W 29.6 mm. The whitish shell has a roughly wrinkled, calcareous surface, the smooth and glossy columellar callus is broadly expanded, covering about half the surface of the last whorl in frontal view. In shells of both female and male snails, the V-shaped basal segment of the outer lip has a short part at the columellar side and a longer part at the palatal side. The largest male shell (figs 68-70), which has a slightly protruding columellar shield, measures H 13.9 mm, W 16.0 mm. In frontal view, the apical part of female shells is situated in line with the apertural edge or lies slightly below it (fig. 65), whereas the apex of male shells may protrude slightly above the apertural edge (fig. 68).

Operculum. Operculum rudimentary.

Habitat. The snails and their egg-capsules were found at 5-14 m, with exclusively the mushroom coral species *Polyphyllia talpina* (Lamarck, 1801). The siphon pores are located on the upper side of the corals.

Distribution. When all specimens looking similar in morphology and found associated with *Polyphyllia talpina* represent *Leptoconchus intalpina* indeed, the range of that species extends from Palau to Indonesia.

Etymology. This species is named after its restricted habitat. It was found exclusively in corals of *Polyphyllia talpina*.

Leptoconchus massini

Type locality. THAILAND. Phiphi islands, NE Ko Phiphi Le, Pi Le Bay, near cave, 07°41'43"N 98°45'57"E.

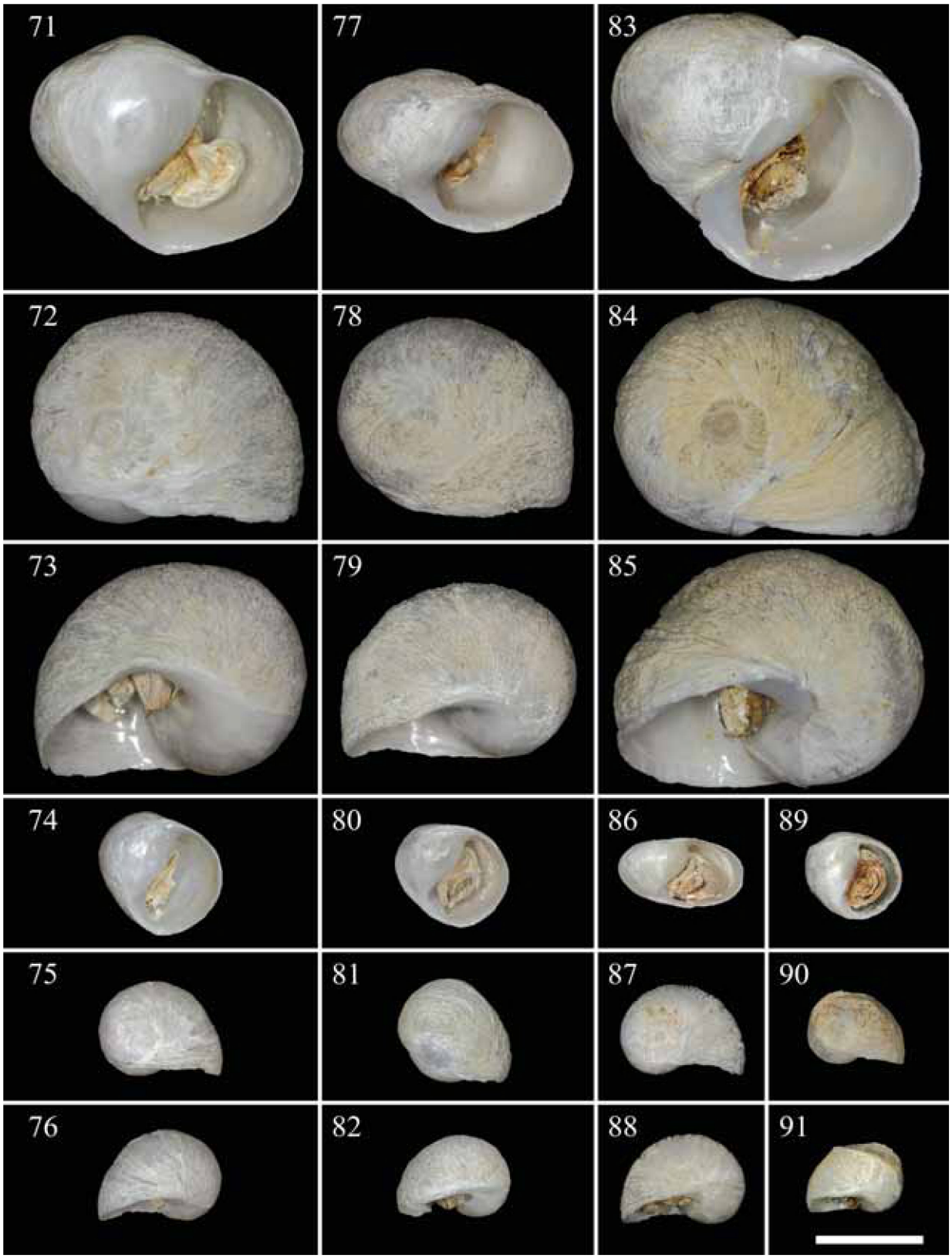
Material (paratypes, unless stated otherwise). Samples that were hosted by *Fungia concinna*, *Fungia repanda*, *Fungia scabra* or *Fungia horrida*, are coded Fc, Fr, Fs or Fh, respectively.

THAILAND. Phiphi islands: type locality, RMNH 95888/holotype, Fc/1sh:f+e [e: RMNH 102652], 102653 Fc/1sn:f+e 1sh:m (with holotype), 95887 Fc/1sn:f+e 1sh:f, 95889 Fc/2sn:m&f+e, 95890 Fc/1sn:f, 95891 Fc/2sn:m&f; S Ko Phiphi Le, Loh Samah, 07°40'28"N 98°46'10"E (RMNH 95979 Fr/2sn:f); S Ko Phiphi Don, 07°43'07"N 98°46'16"E (RMNH 95874 Fc/2sn:m&f+e, 95873 Fc/2sn:m&f+e); E Ko Phiphi Don, 07°44'59"N 98°47'09"E (RMNH 95935 Fc/1sn:f, 95936 Fc/2sn:m&f+e 1sh:f).

EGYPT. Red Sea, 350 km S of Hurghada (RMNH 102654 Fr/1sn:f+e).

PALAU. NE of Ngeremdiu, Lighthouse reef, forereef, 07°16'30"N 134°27'25"E (RMNH 102655 Fc/1sn:m 1sh:f, 102657 Fr/2sn:m&f+e); S of Garreru, Uchelbeluu reef, inner side barrier reef, 07°16'04"N 134°32'26"E (RMNH 102657 Fr/2sn:m&f, 102658 Fr/2sn:m&f+e).

INDONESIA. NE Kalimantan, Berau islands, E Derawan island, 02°17'32"N 118°15'43"E (RMNH 102659 Fr/1sn:f 1sh:f). N Sulawesi, SW of Gorontalo, 00°21'31"N 124°03'14"E (RMNH 102660 Fh/3sn:2m&1f+e, 102661 Fr/3sn:2m&1f+e). Central Sulawesi, Tomini Bay, Togian islands: Walea Lighthouse, 00°25'19"S 122°26'08"E (RMNH 102662 Fr/1sn:f 2sh:m&f, 102663 Fr/2sn:m&f+e); S Walea-bahi island, barrier reef, 00°26'16"S 122°15'57"E (RMNH 102664 Fr/2sn:m&f+e, 102665 Fc/2sn:m&f); S Talatakoh island, barrier reef, 00°29'39"S 122°04'21"E (RMNH 102666 Fr/1sn:f 1sh:f, 102667 Fr/3sn:2m&1f); S Togian island, patch reef, 00°25'31"S 122°00'11"E (RMNH 102668 Fr/1sn:f 1sh:f); S Batudaka island, patch reef, 00°35'25"S 121°41'38"E (RMNH 102669 Fh/3sn:1m&2f+e 2sh:f); W Batudaka island, Copatana Cape, 00°35'50"S 121°37'13"E (RMNH 102670 Fr/3sn:2m&1f+e). SW Sulawesi, Spermonde Archipelago: W Bona Baku reef, 05°07'56"S 119°21'39"E (RMNH 90087 Fs/2sn:m&f+e); W Bone Lola reef, 05°03'07"S 119°21'09"E (RMNH 90022 Fr/2sn:m&f+e); SW Kudingareng Keke island, 05°06'21"S 119°17'03"E (RMNH 87868 Fr/1sh:f, 87871 Fr/2sn:m&f, 87872 Fc/2sn:m&f+e, 87873 Fc/2sn:m&f+e, 87874 Fc/1sn:f); NW Kapodasang reef, 05°05'38"S 119°14'45"E (RMNH 90072 Fr/2sn:m&f+e); W Kapodasang reef, 05°05'35"S 119°15'20"E (RMNH 90089 Fr/2sn:m&f+e, 90090 Fr/1sn:m 1sh:f, 90096 Fr/2sn:m&f, 90097 Fr/1sn:f 2sh:f, 90098 Fc/1sn:f, 90099 Fr/2sn:m&f+e, 90100 Fc/2sn:m&f); NW Bone Tambung island, 05°02'05"S 119°16'16"E (RMNH 90093 Fc/2sn:m&f); SW Bone Tambung, 05°02'12"S 119°16'19"E (RMNH 87862 Fc/1sn:m 1sh:f); W Badi island, 04°58'05"S 119°16'54"E (RMNH 90039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Fc/3sn:1m&2f+e). Bali: Padang Bai, Tanjung Sari, 08º31'11"S 115º30'37"E (RMNH 102671 Fr/1sn: f+e, 102672 Fr/2sn:f+e); Tulamben beach, 08º16'36"S 115º35'37"E (RMNH 102673 Fr/2sn:2f+e); Tulamben beach, 08º16'43"S 115º35'49"E (RMNH 102674 Fr/1sn:f+e, 102675 Fr/2sn:m&f+e, 102677 Fr/2sn: m&f+e).

Shell. Holotype (figs 53-55) female: H 13.5 mm, W 18.4 mm. The whitish shell has a roughly wrinkled, calcareous surface; the smooth and glossy columellar callus is broadly expanded, covering more than half of the surface of the last whorl in frontal view. The outer lip is regularly curved, its lower half gradually passing into the remaining basal part of the shell. The height and the width of the largest female shell are 14.1 mm and 22.5 mm, respectively, versus H 11.8 mm and W 13.5 mm (figs 56-58) for the largest male shell, which was found with the holotype. In frontal view, the apical part of female shells is slightly protruding above the apertural edge (fig. 53), whereas the apex of male shells protrudes distinctly (fig. 56).

Operculum. Operculum rudimentary.

Habitat. The snails and their egg-capsules were found at 5-16 m, with the mushroom coral species *Fungia (Verrillofungia) concinna* Verrill, 1864, *F. (V.) repanda* Dana, 1846, *F. (V.) scabra* Döderlein, 1846, and *Fungia (Danafungia) horrida* Dana, 1846. The siphon pores are located on the upper side of the corals.

Distribution. When all specimens looking similar in morphology and found associated with one of the host species mentioned here, represent *Leptoconchus massini* indeed, the range of this species extends from the Red Sea to Thailand, Palau and Indonesia.

Etymology. This species is named after Claude Massin, who contributed substantially to our knowledge of these hidden snails.

Figs 71-91. Frontal, apical and basal views of shells. 71-76, *Leptoconchus inalbechi* spec. nov.: 71-73 holotype, female; 74-76, male. 77-85, *Leptoconchus incrassa* spec. nov.: 77-79 holotype, female; 80-82, male; 83-85, female. 86-91, *Leptoconchus ingrandifungi* spec. nov.: 86-88, holotype, female; 89-91, male. 71-76, Sulawesi, Indonesia; 77-91, Palau.

Discussion and conclusions

The results that are generated by analysing the DNA sequencing data make sense in that snails that are found with the same host coral species cluster together even when they were collected at locations that are far apart. Snails from a single locality, but from different host species, may cluster far apart even when their shells can hardly or not be distinguished. This becomes especially clear in the COI phylogeny reconstruction (fig. 2) in which the DNA sequences of snails that were collected out of sixteen different fungiid species, occurring at a single locality, i.e. locality 8 (fig. 1), cluster far apart. The emerging pattern indicates the presence of many more or less widespread gastropod species that may occur sympatrically but, if so, always with different coral host species. As a consequence, some species are described as new to science that cannot, or not yet at least, be recognized unequivocally on the basis of only morphological characters of either the shell or the soft parts of the animals.

In their seminal paper, Massin and Dupont (2003) have already discussed the poverty in morphological characters in *Leptoconchus*. Here we show that the cryptic adaptive radiation in *Leptoconchus* is even more speciose that hitherto thought. That implies that previous morphological descriptions may refer to more than a single species, so that variability may be confused with overlapping species specific character states.

Several morphological characters that were discussed by Massin and Dupont (2003) turned out to be unreliable for species identifications. Only five of the nine OTU's that were described by Massin and Dupont (2003) could be recognized also on the basis of the DNA sequencing results, i.e. their OTU's 1, 2, 5, 6 and 9, that represent *Leptoconchus intalpina*, *L. ingrandifungi*, *L. inpileus*, *L. infungites* and *L. inlimax*, respectively. The OTU's 3, 4, 7 and 8 do not refer to monophyletic groups. OTU 3 includes *Leptoconchus incycloseris* and *L. ingranulosa*; OTU 4 includes *L. inscutaria*, *L. inscruposa* and *L. inpleuractis*; OTU 7 includes *L. massini* and *L. ingrandifungi*; OTU 8 includes *L. inpleuractis*, *L. inalbechi*, *L. incrassa* and *L. inactiniformis*

Some of the character states used by Massin and Dupont (2003) to distinguish particular OTU's turned out to be not diagnostic and should be referred to as

intraspecific variability. This is seen in *Leptoconchus inpleuractis*, which is represented in OTU 4 and 8, and *L. ingrandifungi*, which is recognised in both OTU 2 and 7.

It should be emphasized that the presence versus absence of a rudimentary operculum cannot be considered a reliable character. The very small operculum may indeed be 'no longer firmly attached to the foot' (Massin and Dupont, 2003: 122), so that its absence should be considered a potential artefact instead of a reliable, diagnostic character state. Only the size of the operculum relative to the shell aperture may be used to characterize taxa, as is done by Massin and Dupont (2003).

The conchological characters that are used in the literature turned out to be even more unreliable for species recognition than initially thought. In general, the shells of female (phase) snails have a greater relative width than male (phase) ones, whereas in sculpture and colour male and female shells are similar, which is in agreement with the suggested protandry (Richter and Luque, 2004). Maybe the shape of the columellar shield of the shell, the position of the apex in relation to the apertural edge, and the shape of the shell base can be used to characterise species or species groups. At present however, there is still no alternative for reliable species recognition other than DNA sequencing or host species identification. Obviously there are many more species in Leptoconchus than hitherto accepted and the parasite-host relationships are more strict than previously thought.

Acknowledgements

We thank especially Dr. David G. Reid (London) for critical reading and commenting on the text. We are also grateful to Merijn Bos, Michel Claereboudt, Pat Colin, Rachel Colin, Bert W. Hoeksema, Bas Kokshoorn, Claude Massin, Alfian Noor, Niels Schrieken and D.R. Uit de Weerd for their help in providing information and material used in this study. This research project was supported by WOTRO (grant nr. W 82-249) with additional funding by the Schure-Beijrinck-Popping Fonds (KNAW), the Alida Buitendijkfonds, and the Jan Joost ter Pelkwijkfonds. The research in Indonesia was sponsored by the Indonesian Institute of Sciences (LIPI).

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5

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

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Also in: The Nautilus 114(1): 1-13 [2000].

The Nautilus, 114(1) 1-13 (2000)

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

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Key words: parasitic snails; coral reefs; coral/mollusc associations; egg-capsules; Indo-Pacific

Abstract

At least six species of the genus *Epitonium sensu lato* are found associated with mushroom corals (Fungiidae) off Ujung Pandang, Sulawesi, Indonesia. Revised descriptions of *E. costulatum* (Kiener, 1838) and *E. ulu* Pilsbry, 1921 based on type specimens and additional material are given. Four new species are described: *E. hoeksemai*, *E. ingridae*, *E. lochi*, and *E. twilae*. The true identity of *E. bullatum* (Sowerby, 1844), a species not associated with corals and not found in Sulawesi and nearby areas, is clarified. Examination of type specimens made possible the characterization of nominal species that appear to be either identical with or closely related to the fungiid-associated epitoniids found off Sulawesi.

Contents

Introduction

Several epitoniid species are known to live in association with sea anemones (phylum Cnidaria, order Actiniaria) (Robertson, 1963; 1983a, b; 1993; Vecchio, 1964; Salo, 1977; Perron, 1978; Kay, 1979; Schimek, 1986; Hartog, 1987; Dushane, 1988a-c; Yamashiro, 1990; Nakayama, 1991; Mienis, 1994). Less commonly, epitoniids are found associated with stony corals (phylum Cnidaria, order Scleractinia), in particular with species of the free-living Fungiidae or mushroom corals (Robertson, 1963, 1970; Bosch, 1965; Hadfield, 1976; Kay, 1979; Bratcher, 1982; Loch, 1982; Sabelli and Taviani, 1984; Bell, 1985; Dushane, 1988a-c; Loo and Chou, 1988; Page and Willan, 1988; Hoeksema, 1988, 1989; Yamashiro, 1990; Mienis, 1994; Oliverio et al., 1997). Only three *Epitonium* species are usually mentioned in the literature in association with fungiids; in one case (Loch, 1982) a fourth species is reported but not named. This paper deals mainly with the taxonomy of the surprisingly high number of species of *Epitonium* found associated with mushroom corals during a survey in a relatively restricted area in Indonesia, off Ujung Pandang (Sulawesi). Four of these species proved to be new to science, although at least one of them had frequently been cited and illustrated under an incorrect name. The shells of these species are very fragile, which might explain why they are mostly poorly represented or not represented at all in most institutional collections. These species are only known from live-collected specimens: it is very unlikely that empty shells will be found washed ashore without being seriously damaged or unrecognizable. A more elaborate analysis of the ecological data collected during the project is being prepared (Gittenberger, A., unpublished data).

The systematic and evolutionary importance of variable characters such as egg-capsules (Figures 36-38), eggs (Figure 41) and mucous threads (Figures

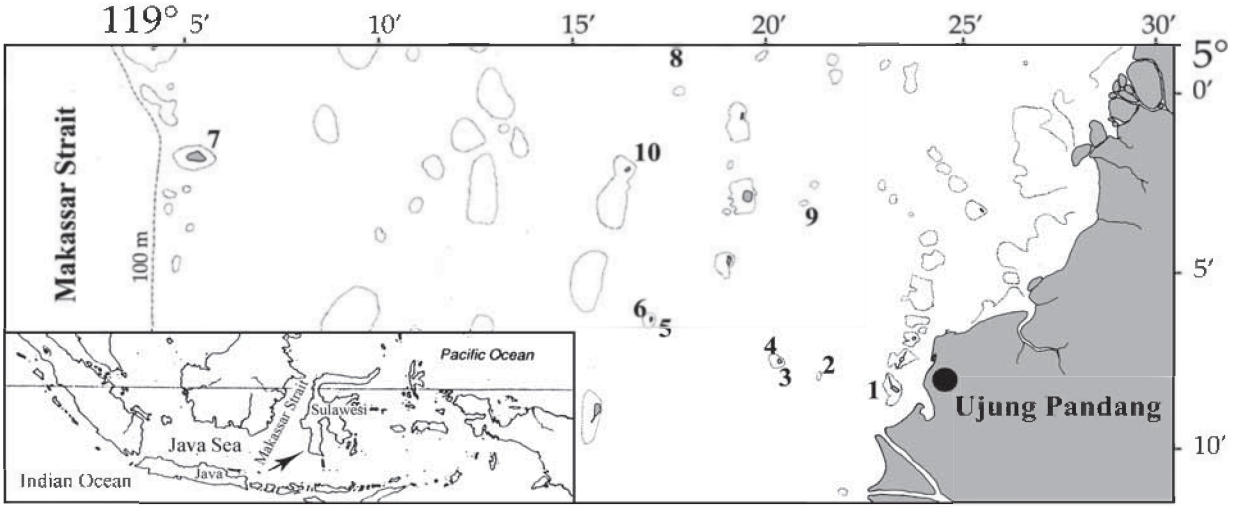


Figure 1. Surveyed area off Ujung Pandang, S. Sulawesi, Indonesia. The coral reefs investigated in particular are: 1, W. (Pulau) Lae-Lae; 2, W. Bone Baku; 3, E. (Pulau) Samalona; 4, W. (Pulau) Samalona; 5, E. and ESE (Pulau) Kudingareng Keke; 6, W. (Pulau) Kudingareng Keke; 7, NW Lan[g]kai; 8, Pulau Badi; 9, Bone Lola; 10, (Pulau) Bone Tambung.

43-47), which can be either straight or twisted, is still poorly known. We observed, however, that populations of the different species may differ in these characters. With exception of one article by Oliverio *et al.* (1997), the literature is scanty in respect to these characters. Oliverio et al., while discussing the coral-associated epitoniid *Epitonium billeeanum* Dushane and Bratcher, 1965, figured the egg-capsules, eggs, mucous threads (of the twisted type) and shells of veliger larvae. We did not observe a difference in sculpture or well-defined transition between the protoconch 1, formed by the shell gland of the larva inside the egg-capsule, and protoconch 2, secreted by the velum of the swimming veliger between hatching and settling. The protoconchs (Figures 16, 25-29, 42, 48) turned out to be very uniform among the various species studied here, all of which apparently have planktotrophic development. Sclerites of at least one species of soft coral, probably of the genus *Sinularia* May, 1898 (subclass Octocorallia, order Alcyonacea, family Alcyoniidae) (L. P. van Ofwegen, NNM) were found associated with the egg-capsules of some species (Figures 39-40).

In a monograph on Epitoniidae from southern Africa and Mozambique, Kilburn (1985: 240) stated that "epitoniid taxonomy remains in a chaotic state, particularly above the species level." Kilburn observed that the classification of the genus *Epitonium* is (p. 280) "very tentative and is aimed solely at grouping together similar species for convenience sake." Clench and Turner (1951) and Bouchet and Warén (1986) followed a similar approach in their revision of eastern Atlantic Epitoniidae. Because we could not unequivocally classify all Indonesian species within one or more of the 19 subgenera used by Kilburn (1985) or the 39 subgenera listed by Wenz (1940) under "*Scala*" (= *Epitonium*), we decided to refrain from following any subgeneric classification. The epitoniid species described in this study live associated with mushroom corals and at least some of them are so similar that they seem to be closely related phylogenetically. They point to possible adaptive radiation within a single clade. Adequate phylogenetic analyses including other species of *Epitonium* co-occurring with different hosts in the same general area could help clarify whether these species found in association with fungiid corals form a monophyletic group.

Material and methods

Samples were collected off the coast of Ujung Pandang, Sulawesi, Indonesia. The fungiid fauna of the area (Figure 1) is relatively well known; see Hoeksema (1989) for details. During the period April-June, 1997, 9 coral reefs were inspected, to a depth of 18 m (rarely 24 m). Approximately 10^4 mushroom corals,

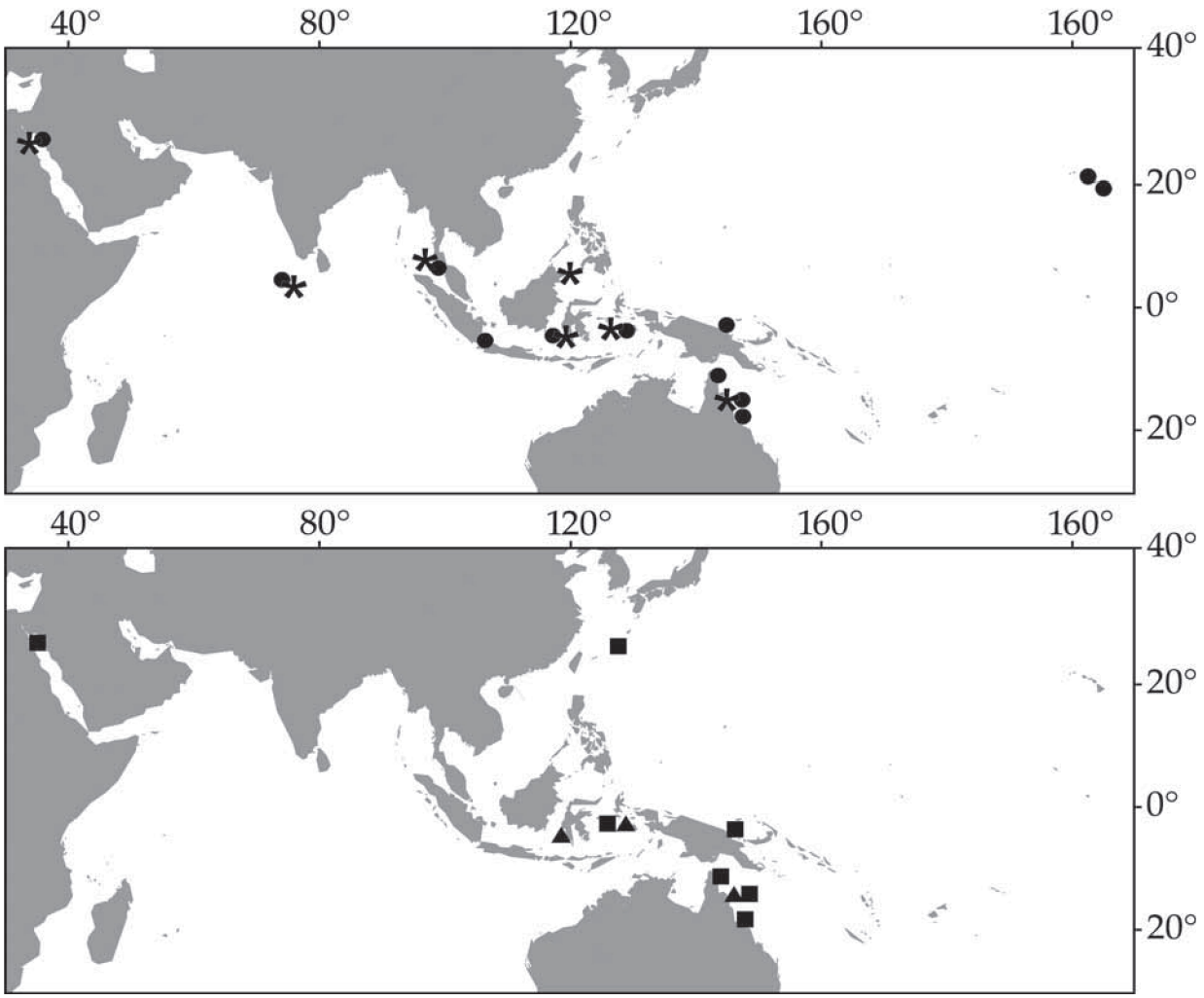
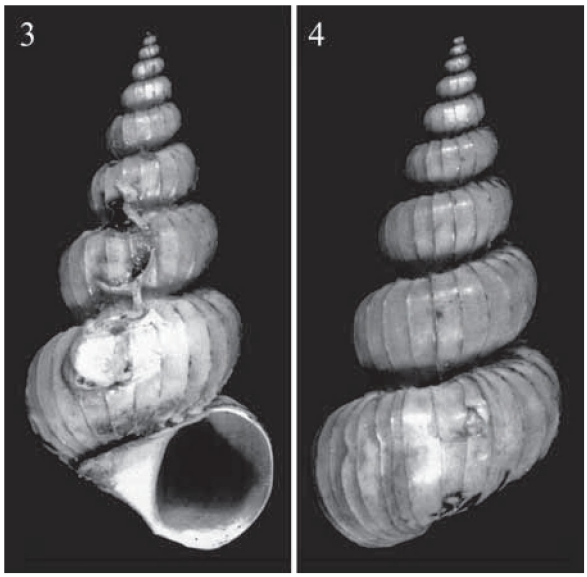


Figure 2. Maps of the Indo-Pacific Region, from the Red Sea to the Hawaiian Archipelago, showing records of the *Epitonium* species in this study known from more than two localities: *Epitonium costulatum* (Kiener, 1838) (stars), *E. ingridae* new species (triangles), *E. twilae* new species (squares) and *E. ulu* Pilsbry, 1921 (circles).

belonging to about 30 species of free-living Fungiidae, were searched for epitoniids and their eggs. Beneath these corals, about 10^3 specimens of *Epitonium*, some of which with egg-capsules, were collected. The identifications of the coral species were made or at least checked by Dr. B. W. Hoeksema. The snails were classified into morphological categories according to characters of shell, egg-capsules, and proboscis. Secondarily, the species thus distinguished were analysed ecologically for preferential depths, hosts, and substrates. The ecological data will be discussed in a future article (Gittenberger & Hoeksema, chapter 9).

The various *Epitonium* species recorded during the survey were identified by review of the literature, consultation with specialists, and by comparison with material deposited in several collections; this includes comparison with type specimens of conchologically similar taxa. These types are mentioned in the systematic treatment of each species.

From the about 10^3 specimens collected, only shells with more than 4 mm length were measured. The number of specimens (n) measured in the calculation of mean values is mentioned at the beginning of the descriptions. Means are indicated between the extremes (minimum-mean-maximum). To allow for



Figures 3-4. Epitonium costulatum (Kiener 1838), holotype (MHNG 1152/16). Shell length 3.3 cm.

better comparisons, shell sculpture is described for both the fifth teleoconch whorl and where the teleoconch is 5 mm in width, a part of the spire that is in part independent of the actual whorl number. The term protoconch refers to the protoconchs 1 + 2. The maximum diameter of protoconch 1 was measured in two shells for each species (except for *E. lochi* because of insufficient material), using SEM photographs of specimens prepared from egg- capsules (Figures 30-31); because very similar values were consistently found, no more measurements were taken. Shells of *Epitonium* species cannot be recognized as fully grown or not. Comparative informal observations indicate that when the snails start laying eggs they have not yet reached maximum size. No minimum values are included in the descriptions but only the largest specimen and the largest number of whorls. After removal from 70% ethanol, egg-capsules without embedded sand quickly collapsed; these could not be photographed. Unless stated otherwise, all descriptions refer to material from off Ujung Pandang.

The following institutional abbreviations are used: AMS, Australian Museum, Sydney; ANSP, Academy of Natural Sciences, Philadelphia; BMNH, The Natural History Museum, London; LACM, Natural History Museum of Los Angeles County, Los Angeles; MHNG, Muséum d'Histoire Naturelle, Genève; MNHN, Muséum national d'Histoire naturelle, Paris; MZB, Museum Zoologicum Bogoriense, Bogor, Indonesia; NNM, National Museum of Natural History, Leiden. Numbers following a slash after collection numbers refer to number of shells in relevant lots.

Systematics

Family Epitoniidae Berry, 1910
Genus *Epitonium* Röding, 1798

Epitonium costulatum (Kiener, 1838)
(Figures 2-6, 22, 25, 38-41, 47)

Scalaria costulatum Kiener, 1838: pl. 2, fig. 4; 1838: 5.
Epitonium costulatum Robertson, 1963: 57, pl. 5, fig. 4; 1970: 45; Loch, 1982: 4, 1 fig.; Dushane, 1988a: 30, figs. 1, 2.

Description:

Shell (Figures 3-6, 22, 25.) (n = 7): Fragile (large specimens) to very fragile, moderately elongate-conical, creamy white, reaching 32 mm in length, with at least 1 damaged specimen (from Ambon) measuring 41.2 mm. Length/width ratio 1.6-1.9-2.2. Protoconch whorls 3 3/8; maximum protoconch 1 diameter 0.14 mm (n = 2). Protoconch with numerous fine, incised, axial lines. Teleoconch with up to 10 whorls, separated by very deep (fenestrated) suture. Successive whorls are almost detached. Teleoconch with evenly spaced, orthocline, thin costae, damaged in all examined specimens. Over most of their length, the costae appear to be curved abaperturally at the outer margin. Costae adapically relatively high and erect, not coronate, becoming short towards columella. Costae mostly continuous, but touching only slightly those of adjoining whorls. Very weak spiral lines present. Fifth teleoconch whorl (width 4.9 mm) with 16-18.4-26 costae. Five mm width whorl (whorl 4, 5, or 6) with 16-17.4-20 costae. Aperture subcircular. Apertural length/shell length ratio 0.3. Umbilicus moderately wide.

Egg-capsules (Figures 38, 39, 40, 47): Embedded with sand and closely connected along a straight,

longitudinally striated, mucous thread (Figure 47). Capsules asymmetrical, somewhat conical with a circular widest part. Capsules 3.0-3.3-3.5 mm in length and 1.5-1.6-2.0 mm in width (n = 8). One egg-capsule contains 70-175-335 eggs (n = 5).

Proboscis: With some irregularly interrupted, longitudinal, white zones, which are as wide as the transparent interspaces.

Type material (Figures 3-4): Holotype MHNG 1152/16.

Type locality: Unknown.

Other material examined: NNM, Indonesia, Ambon, Hitu, outer part of Ambon Bay, E. and W. sides of Laha, A. Fortuin and J. C. den Hartog leg.; LACM 124505, Thailand, Phuket Island.

Records in the literature: Australia: Queensland, Thetford Reef off Cairns (Loch, 1982: 4). Philippines: Bongao Channel, Sanga Sanga (Robertson, 1963: 57-58, pl. 5, fig. 4). Thailand: Raya Island (Dushane, 1988a: 32). Maldives, Little Hiva (Dushane, 1988a: 32). Red Sea: Straits of Than (Dushane, 1988a: 30-31); Sinai, Thomas Reef, 27°59`N, 34°27`E (Dushane, 1988a: 32).

Distribution (Figure 2): Australia (Queensland), Indonesia (Sulawesi), Philippines, Thailand, and Egypt (Red Sea).

Habitat: Snails were recorded at 6-12 m depth. Coral hosts were *Ctenactis echinata* (Pallas, 1766), and *Herpolitha limax* (Esper, 1797). Groups of one to four snails were found in the sand (sometimes buried) under a single coral with sometimes close to a few hundreds egg-capsules.

Remarks: The data provided by Sherborn and Woodward (1901) are insufficient to indicate the exact year of publication of the new taxa in Kiener`s monograph on the `Genre Scalaire`. We follow Troschel (1839), who listed Kiener`s undated work, with the new species in it, in his `Report on the achievements in zoology during the year 1838. V. Mollusca` [in German]. The names are printed both on the plates and in the main text of Kiener`s work.

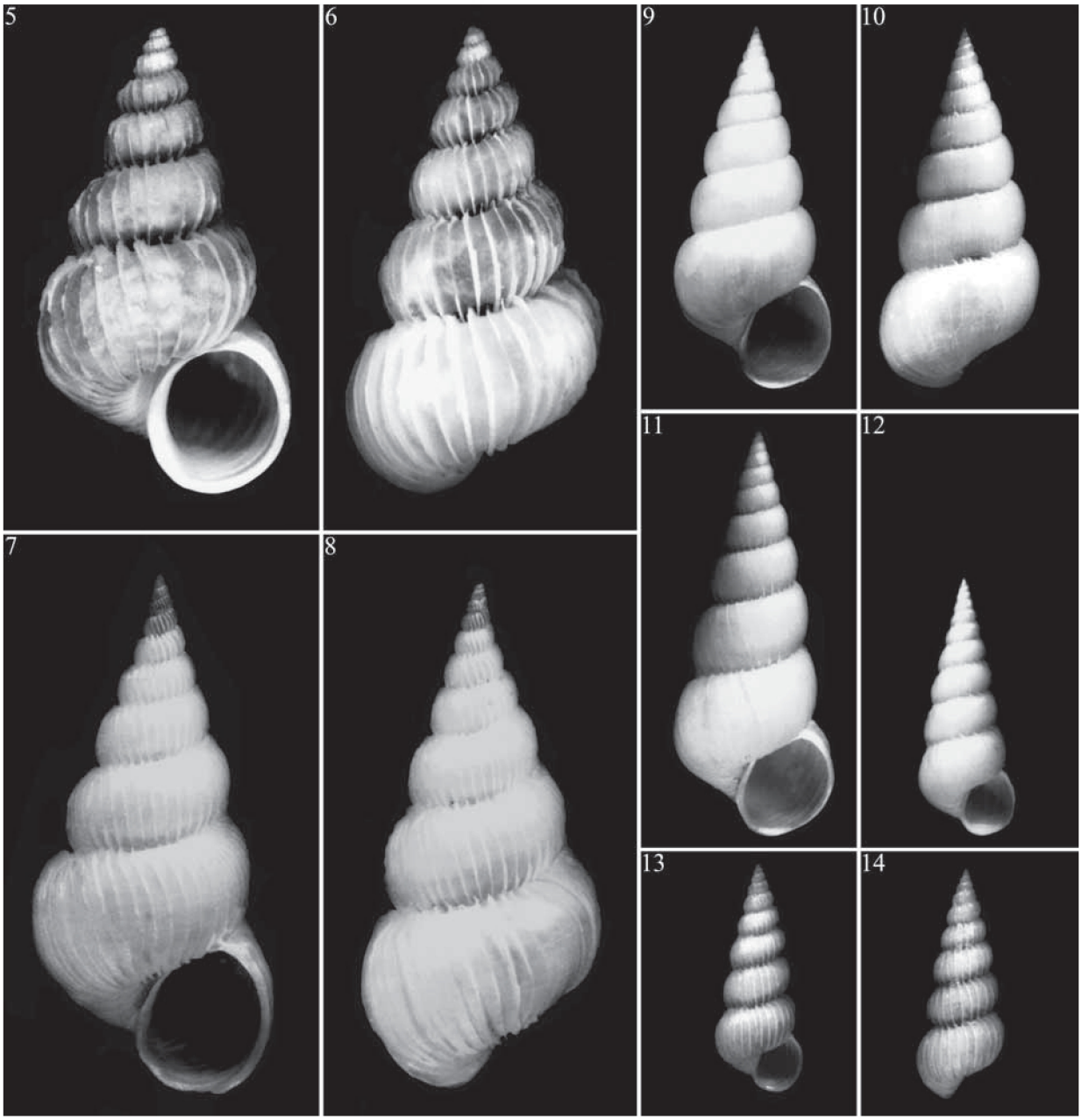
The severely damaged holotype of this species (Figures 3-4) is a relatively elongate shell. Shells of this species are most similar to those of *Epitonium pallasii* (Kiener, 1838), a species originally described from an unknown locality, but now known from the Indo-West Pacific (Kaicher, 1980: 2382; Eisenberg, 1981: pl. 37, fig. 9; Wilson, 1993: 278, pl. 44, fig. 6a-b). According to Kiener (1838) and in agreement with Wilson`s description ("about ten costae on the last whorl") and the figures in the literature, *E. pallasii* differs from *E. costulatum* by the stronger shells with thicker costae, which are more widely spaced. Dushane (1988a: 30, fig. 2) figured very similar egg-capsules of this species, reporting two connecting threads for material from the Red Sea.

Epitonium hoeksemai A. Gittenberger and Goud new species
(Figures 9-10, 18, 20, 26, 43)

Description:

Shell (Figures 9-10, 18, 20, 26) (n=9): Very fragile, elongate-conical, creamy white, reaching 19 mm in length. Length/width ratio 1.6-1.9-2.4. Protoconch whorls 3. Maximum protoconch 1 diameter 0.13 mm (n = 2). Protoconch with numerous very fine, incised, axial lines. Teleoconch whorls up to 9 1/8, separated by a moderately deep suture. Teleoconch sculpture (Figures 18, 20) of somewhat unevenly spaced, orthocline, relatively low costae, and low spiral threads that become conspicuously more numerous and variable on the abapical whorls. Costae on entire teleoconch more prominent than spiral sculpture. Third teleoconch whorl has ca. 12 spiral threads, fifth ca. 25. Costae not always continuous, touching the adjoining whorls, where they are curved adaperturally. Fifth teleoconch whorl (width 2.1 mm) with 24-27-29 costae. Five mm width whorl (whorl 8, 9 or 10) with 32-35-38 costae. Aperture subcircular. Apertural length/shell length ratio 0.28-0.29-0.30. Umbilicus very narrow.

Egg-capsules (Figure 43): Sub-spherical, white, transparent, with protuberances but no embedded sand. Capsules closely connected to each other along a twisted mucous thread.



Figures 5-14. Species of *Epitonium* associated with mushroom corals off Ujung Pandang. 5-6, *E. costulatum* (Kiener, 1838), length 2.8 cm; 7-8, *E. ingridae* new species, holotype, NNM 59088, length 2.0 cm; 9-10 *E. hoeksemai* new species, holotype, NNM 59074, length 1.3 cm; 11-12. *E. ulu* Pilsbry, 1921, length 1.6 cm and 1.0 cm, respectively; 13-14. *E. lochi* new species, holotype, NNM 59094, length 0.9 cm.

Habitat: This species was recorded at 5-15 m depth. Coral hosts were *Heliofungia actiniformis* (Quoy and Gaimard, 1833) and *Fungia fungites* (Linnaeus, 1758). One to 5 specimens were found attached by mucous threads to the underside of a coral near a few hundreds egg-capsules.

Type material: Holotype NNM 59074, from type locality. Paratypes: NNM 59081/1, Indonesia, Sulawesi, off Ujung Pandang, W. Lae-Lae, 9

m; NNM 59079/1, MZB/1, W. Bone Baku, 6 m; NNM 59080/1, 59082/1, 9 m; NNM 59086/2, type locality; NNM 59076/1, 6 m; NNM 59077/5, 12 m; NNM 59083/1, E. Kudingareng Keke, 3 m; W. Kudingareng Keke, 12 m; NNM 59075/1, 14 m; NNM 59084/1, NW Lankai, 6 m; NNM 59087/2, Bone Lola, 15 m; NNM 59085/1, Bone Tambung, 6 m.

Type locality: Indonesia, Sulawesi, off Ujung Pandang, W. Samalona, 5 m depth.

Distribution: Only known from Indonesia, off Sulawesi

Etymology: This species is named after Dr. B. W. Hoeksema, who supervised the field portion of this project.

Remarks: Shells of this species resemble those of *Epitonium ulu*, but differ by a length/width ratio of ca. 1.9 instead of ca. 2.6. Because most examined specimens are damaged, the fine structure of the costae could not be observed. The teleoconch sculpture appears always obsolete to the naked eye. The number of spiral threads increases more conspicuously in *E. hoeksemai*, with ca. 13 spiral threads added between the third and the fifth whorl. In *E. lochi* new species (see below), on the other hand, there is a more clearly reticulate sculpture on the early teleoconch whorls.

Epitonium ingridae A. Gittenberger and Goud new species
(Figures 2, 7-8 23-24, 27, 30, 36, 46)

Description:

Shell (Figures 7-8, 23-24, 27, 30) (n = 5): Very fragile, moderately slender conical, creamy white; reaching 20.8 mm in length. Length/width ratio 2.0-2.2-2.3. Protoconch whorls ca. 3. Protoconch with three whorls; with numerous fine, incised, axial lines. Maximum diameter of protoconch 1, 0.14-0.15 mm (n = 2) (Figure 30). Teleoconch whorls up to 10, separated by deep suture. Teleoconch sculpture of evenly spaced, orthocline, thin, lamellate costae, and numerous very fine spiral threads (>100 on the 9th whorl), superimposed on somewhat coarser spiral cordlets (ca. 15 on fifth teleoconch whorl). Initial whorls with multiple, lamellate costae, fused together to form thicker ones (Figures 23, 24). Coarser spiral cordlets are most prominent on initial teleoconch whorls, where they are superimposed on costae (Figure 24); coarser cordlets become obsolete on most abapical whorls. Costae are more or less damaged in all specimens; better preserved costae coronate. Particularly below the periphery, costae somewhat curved abaperturally at their free margins, whereas adapically more erect and slightly curved abaperturally or adaperturally near suture, depending on position of costa on adjoining whorl. Costae mostly continuous, but hardly touching each other. Fifth teleoconch whorl (width 3.8 mm) with 20-24-31 costae. Five mm width whorl (whorl 6 or 7) with 23-30-33 costae. Aperture subcircular. Apertural length/shell length ratio 0.3. Umbilicus very narrow.

Egg capules (Figures 36, 46) (n = 8): Oval (Figure 36), embedded with sand and closely connected along straight, longitudinally striated, mucous thread (Figure 46). Capsules 3.0-3.3-3.5 mm in length and 1.5-1.6-2.0 mm in width. Capsules contain 93-120-173 white eggs.

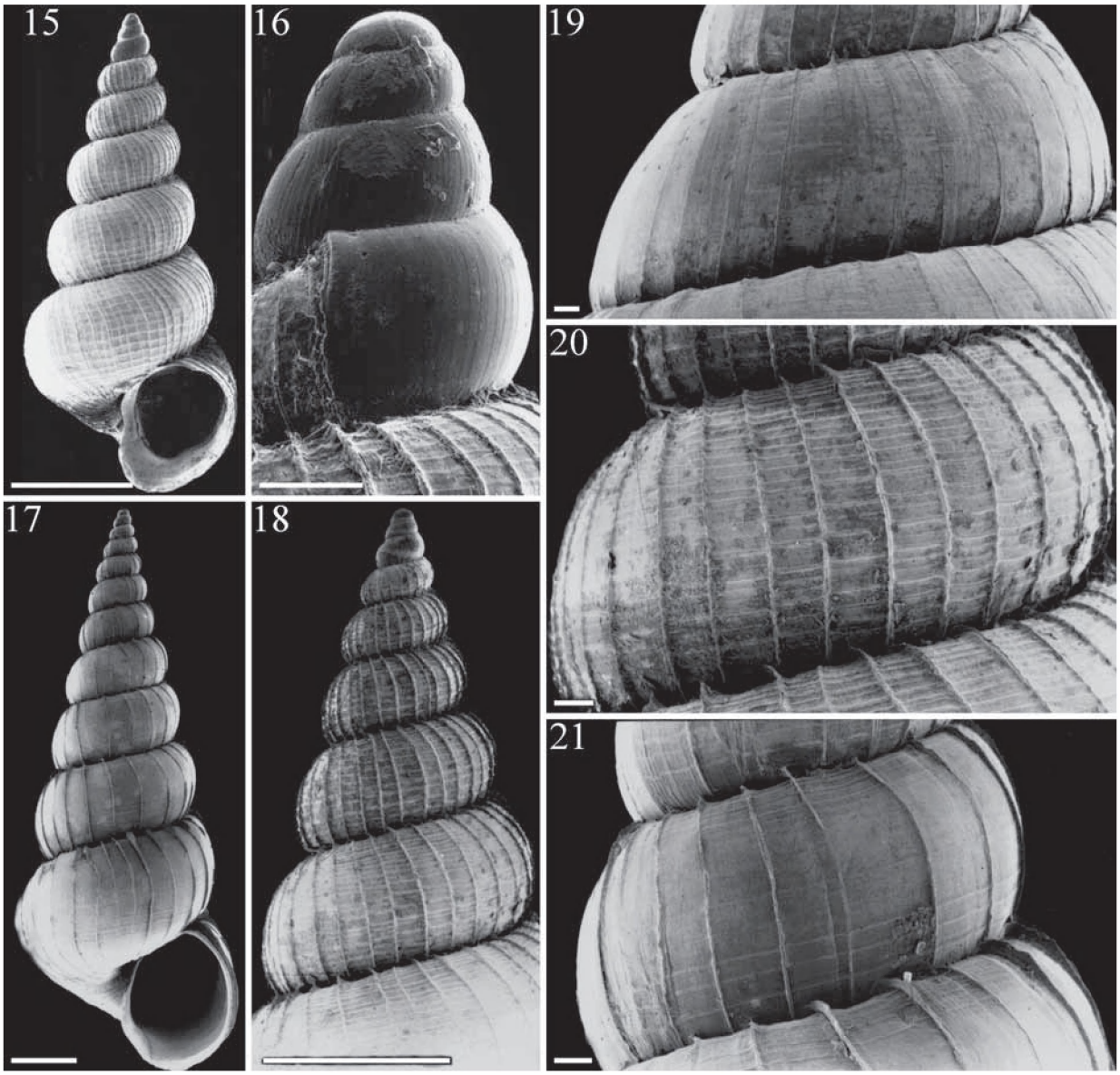
Proboscis: Whitish.

Type material: Holotype NNM 59088, from type locality. Paratypes: NNM 59089/1, Indonesia, Sulawesi, off Ujung Pandang, W. Kudingareng Keke, 12 m; NNM 59090/2, 59092/1, E. Samalona, 9 m; NNM 59091/1, 24 m; NNM 59093/1, Bone Tambung, 7 m.

Type locality: Indonesia, Sulawesi, off Ujung Pandang, ESE. Kudingareng Keke, 15 m.

Other material examined: AMS 329657, Australia, Queensland, off Macgillivray Bay, Lizard island, 14°39`S, 145°29`E, 10 m, I. Loch leg.; NNM unnumbered, 1 shell, Indonesia, Ambon, Hitu, outer part of Ambon Bay, eastern Laha, J. C. den Hartog leg.

Distribution (Figure 2): Australia, Queensland; Indonesia, Ambon, and Sulawesi.



Figures 15-21. SEM micrographs of species of *Epitonium* associated with mushroom corals off Ujung Pandang. 15-16, *E. lochi* new species; 15, Shell. Scale line = 1 mm. 16, Protoconch. Scale line = 0.1 mm. 17, *E. ulu* Pilsbry, 1921, shell. Scale line = 1 mm. 18, *E. hoeksemai* new species, apical whorls. Scale line = 1 mm. 19, *E. twilae* new species, teleoconch whorl sculpture. Scale line = 0.1 mm. 20, *E. hoeksemai* new species, teleoconch sculpture. Scale line = 0.1 mm. 21, *E. ulu* Pilsbry, 1921, teleoconch whorl sculpture. Scale line = 0.1 mm.

Habitat: Specimens of this species were found at 7-24 m depth. Coral hosts were *Fungia concinna* Verrill, 1864, *F. fungites*, *Heliofungia actiniformis*, *Herpolitha limax* and *Polyphyllia talpina* (Lamarck, 1801). Specimens were found attached by mucous threads to the underside of a coral: one or two specimens were found associated with up to a few hundreds egg-capsules.

Etymology: This species is named after Ms. Ingrid van der Loo, Leiden.

Remarks: Conchologically this species resembles the 'probable holotype' (Kaicher, 1951: 3036) of *Epitonium dubium* Sowerby, 1844 (BMNH 1981234) from the Philippines, which is an imperfect shell with a broken aperture and several

apical whorls missing. Its length could have been ca. 20 mm. Costae of adjacent whorls are continuous, slightly curved toward aperture adapically and away from aperture abapically, not projecting over suture. The holotype of *Epitonium dubium* most clearly differs from *E. ingridae* by its less prominent teleoconch sculpture and thicker, not lamellate costae. The specimen figured by De Boury (1912: pl. 7, fig. 4, *Scala dubia*), which might represent *E. dubium* (*cf.* Kilburn, 1985: 327) has more oblique costae. The identity of *Scalaria grayi* Nyst, 1871, (*nomen novum* for *Scalaria striata* Gray, 1847, not Defrance, 1827) is unclear; Tryon (1887: 60, as *S. striata*) and De Boury (1912: 95, as *S. striata* and *S. grayi*) considered this nominal taxon a synonym of *S. dubia.* Kilburn (1985: 327) questioned this synonymy. The shell of *S. grayi* figured by Tryon (1887: pl. 12, fig. 68, as *S. striata*) has a more shallow suture and relatively larger aperture when compared to *E. ingridae*. The new species also resembles *Epitonium friabilis* (Sowerby, 1844) from Western Australia, Swan River. The hototype (BMNH 1966653), figured by Kaicher (1980: 2329), is 16 mm in length and 7 mm in width, with ten whorls. It differs most conspicuously from *E. ingridae* by its closed umbilicus and absence of spiral threads. The species described and illustrated from Sydney Harbour as *Foliaceiscala barissa* by Iredale (1936: 300, pl. 22, fig. 15) seems to be similar in shape and size, but the costae are described as "of different strength, some fine, others large and recurved, while still others approach varices in size."

Epitonium lochi A. Gittenberger and Goud new species
(Figures 13-16, 37, 45)
?*Epitonium* species 4: Loch, 1982: 4-5. 1 fig. (see remarks below).

Description:

Shell (Figures 13-16) (n = 4): Very fragile, elongate-conical, creamy white, reaching 8.5 mm in length. Length/width ratio 2.0.-2.3-2.7. Protoconch whorls 3 1/4. Maximum diameter of protoconch 1, 0.12 mm (n = 1). Protoconch with numerous fine, incised, axial lines. Teleoconch whorls up to 8, separated by a very deep suture. Teleoconch with evenly spaced, orthocline, lamellate costae, crossing low spiral threads that are approximately a half to a fifth as wide as the interspaces (Figure 15). Reticulate pattern present on most adapical whorls, replaced by spiral threads on later whorls. Third whorl with ca. 13 spiral threads, fifth one with ca. 15; spiral threads equally prominent throughout whorl. Costae usually not continuous, lamellar but rather low, barely touching preceding whorl. Due to damage in most specimens, fine structure of costae could not be examined. Fifth teleoconch whorl (width 1.3 mm) with 24-25-26 costae and 12-13-15 spiral threads. Aperture subcircular. Apertural length/shell length ratio 0.22-0.23. Umbilicus absent.

Egg-capsules (Figures 37, 45): The roundish, white, egg-capsules (Figure 37) are mixed with sand, and closely connected to each other along a straight mucous thread without well-defined sculpture (Figure 45).

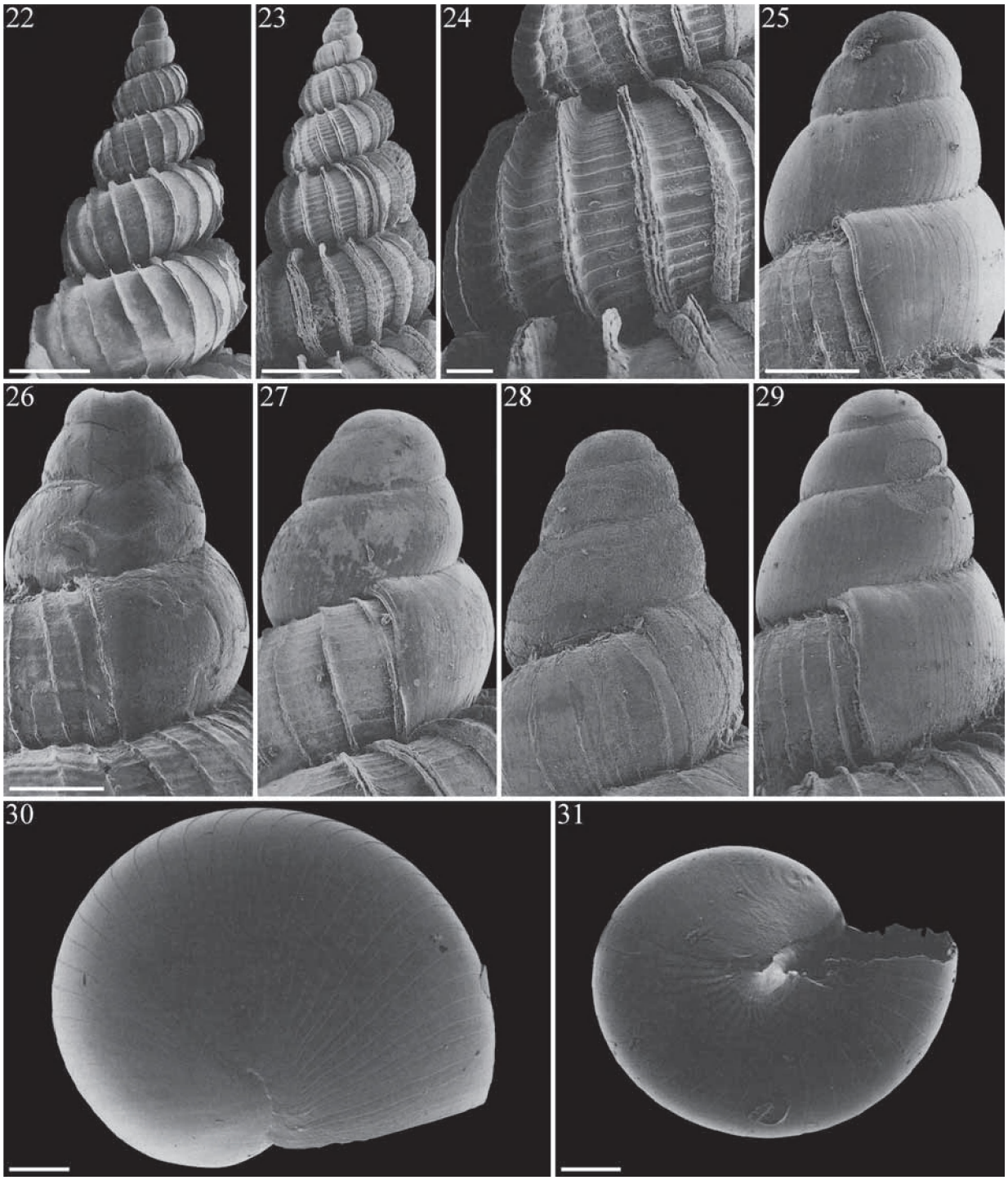
Type material: Holotype NNM 59094, from type locality. Paratypes: NNM 59095/2, 59096/1, Indonesia, Sulawesi, off Ujung Pandang, MZB/1, type locality; 16 m; NNM 59098/1, 18 m; NNM 59099/1, E. Kudingareng Keke, 3 m; 59100/1, 12 m; 59102/1, 18 m; NNM 59101/2, ESE Kudingareng Keke, 15 m; 59103/1, Pulau Badi, 24 m. See also Remarks.

Type locality: Indonesia, Sulawesi, off Ujung Pandang, W. Kudingareng Keke, 12 m.

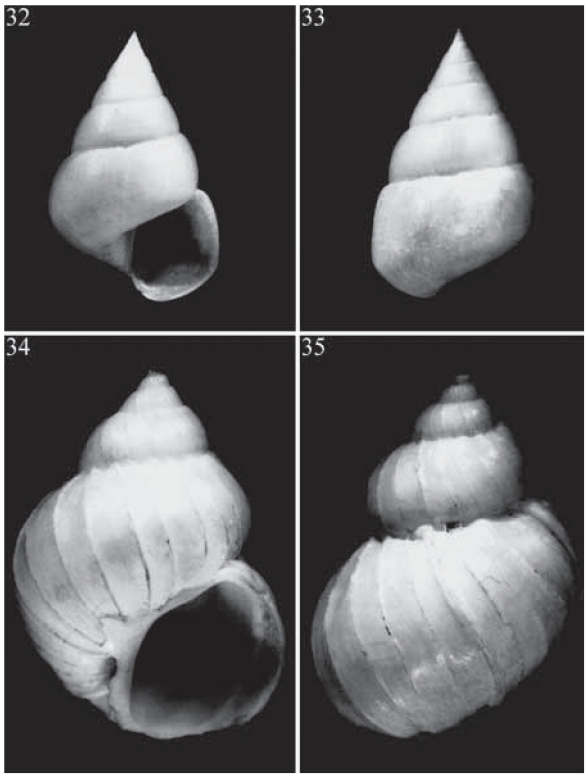
Other material examined: AMS 329687/2, Australia, Queensland, Lizard Island, Watsons Bay, 14°40'S, 145°27'E, 24 m, I. Loch leg.; AMS 329688/1, 329689/1, Granite Bluff, 14°39'S, 145°27'E, 23 m, I. Loch leg. (see Remarks below).

Distribution: Indonesia and probably Australia.

Habitat: The snails were found at 3-24 m depth. *Fungia costulata* Ortmann, 1889, and *F. tenuis* Dana, 1846, were coral hosts. If the Australian record really proves to refer to this species, *Fungia cyclolites* Lamarck, 1816, should be included as an additional host (Loch, 1982: 4). One to 4 specimens were found attached by a straight mucous thread (Figure 45) to the underside of a coral accompanied by up to a few hundreds egg-capsules.



Figures 22-31. SEM micrographs of species of *Epitonium* associated with mushroom corals off Ujung Pandang (unless stated otherwise). 22, *E. costulatum* (Kiener, 1838), Indonesia, Ambon, Hitu, outer parts of Ambon Bay, W. Laha, apical whorls. Scale line = 0.5 mm; 23-24, *E. ingridae* new species. 23, Apical whorls. Scale line = 0.5 mm. 24, Teleoconch whorl sculpture. Scale line = 0.1 mm. 25-29, Protoconch; 25, *E. costulatum* (Kiener, 1838) (same shell as figure 22). Scale line = 0.1 mm; 26, *E. hoeksemai* new species; 27, *E. ingridae* new species. 28, *E. twilae* new species. 29, *E. ulu* Pilsbry, 1921. Scale line = 0.1 mm. 30-31, Protoconch 1; 30, *E. ingridae* new species. 31, *E. twilae* new species. Scale line = 0.02 mm.



Figures 32-35. Species of *Epitonium* often confused in the literature. 32-33, *E. twilae* new species, holotype, NNM 59104, length 1.5 cm. 34-35, *E. bullatum* (Sowerby, 1844), holotype, BMNH 198136, length 2.0 cm.

Etymology: This species is named after Mr. Ian Loch, who described this or a very similar species from Australia, without naming it.

Remarks: Loch (1982) referred to and figured an unnamed 'species 4' from Australia, distinguishing it from *E. ulu*. We were able to compare that material with the specimens collected off Ujung Pandang. In the Australian specimens, the spiral threads are somewhat more prominent, which could represent some degree of intraspecific variation. The limited amount of material does not allow for conclusions on the identity of the Australian specimens; this prevented their inclusion as paratypes.

Conchologically this species is most similar to *Epitonium zatrephes* Melvill, 1910 (holotype BMNH 191281683), from the Mekran coast. This shell is figured by Kaicher (1980: 2377); it differs by having continuous costae and by the more narrowly spaced spiral threads, which are about as wide as their interspaces.

The holotype of *Epitonium obliqua* (Sowerby, 1844) [*Scalaria*] (BMNH 1981231) also resembles *E. lochi*, but differs in having a clearly open, though narrow, umbilicus, and continuous costae.

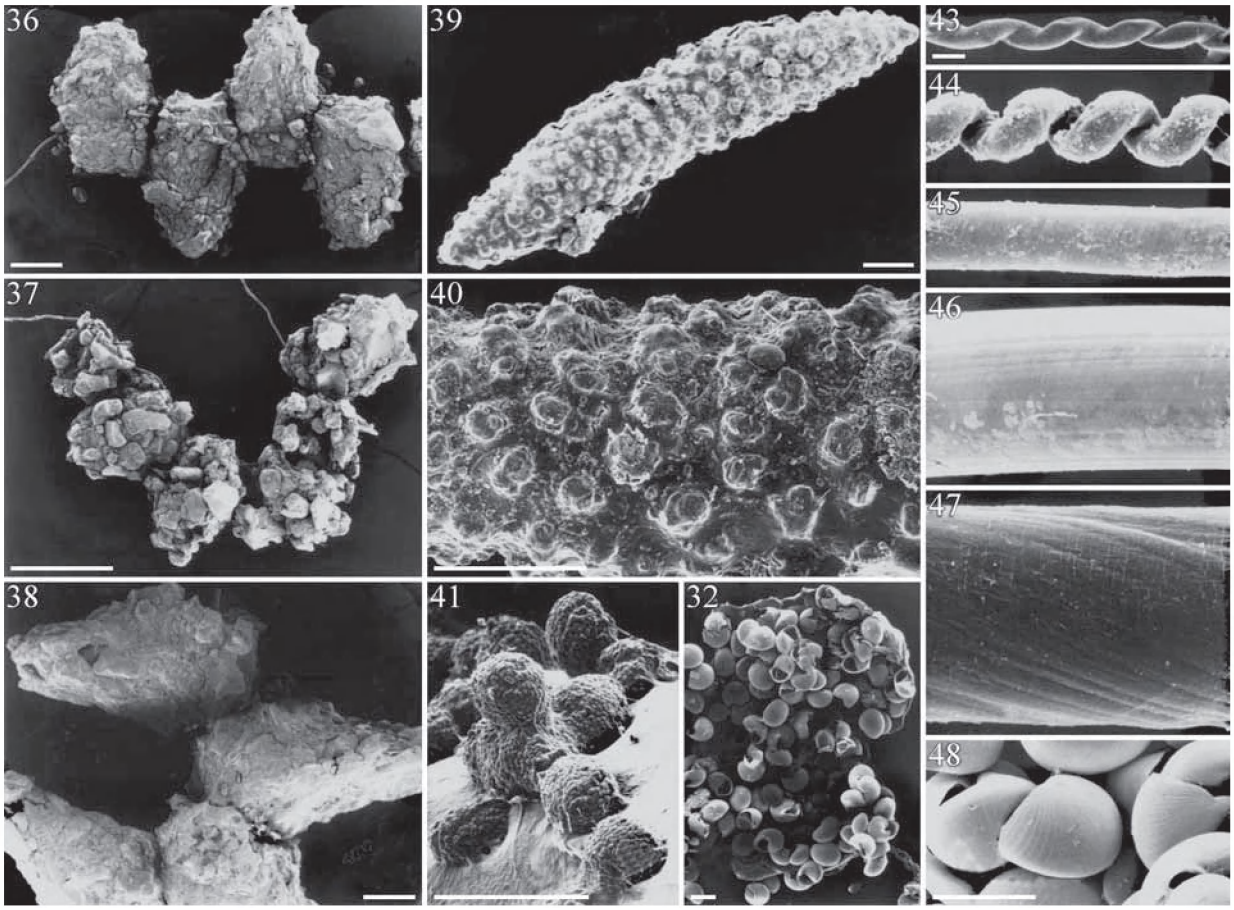
The holotype of *Epitonium deflersi* (Jousseaume, 1911) [*Tenuiscala*] (MNHN De Boury-2706) from Aden, which has a broken aperture and missing apical whorls, can notwithstanding be distinguished from *E. lochi* by the relatively small shell length/width ratio (only ca. 1.9) and the presence of some varices. This holotype is also figured by Kaicher (1981: 3116).

Epitonium twilae A. Gittenberger and Goud new species
(Figures 2, 19, 28, 32-33, 48)

Epitonium bullatum (Sowerby, 1844): Dushane. 1988: 30, figs. 5, 6. Yamashiro, 1990: 299 figs. 1-6. Not *Scalaria bullatum* Sowerby, 1844.
Epitonium species 2: Loch. 1982: 3-4, 1 fig.
Epitonium sp.: Bratcher, 1982: 3, fig. 1.

Description:

Shell (Figures 19, 28, 31, 32-33, 48) (n = 20): Very fragile, broad-conical, creamy white, reaching 17 mm in length. Length/width ratio 1.2-1.4-1.6. Protoconch whorls 3. Protoconch with numerous very fine, incised, axial lines. Maximum protoconch 1 diameter 0.12-0.13 mm (n = 2). Teleoconch whorls up to 9, straight-sided, separated by a shallow suture. Teleoconch sculpture (Figure 19) of unevenly spaced, fine, orthocline, more or less obsolete costae, not or only in part lamellate, and numerous low spiral threads that are separated by interspaces that vary from as wide as the spiral threads to three times as wide. Costae not continuous, not curved, barely touching adjacent whorls. Fifth teleoconch whorl (width = 2.5 mm) with 19-24.4-30 costae. Five mm width whorl (whorl 6 or 7) with 24-31-36 costae. Aperture subcircular. Apertural length/shell length ratio 0.37-0.44-0.52. Umbilicus very narrow.



Figures 36-48. Species of *Epitonium* associated with mushroom corals off Ujung Pandang. 36-38, Egg-capsules. 36, *E. ingridae*. Scale line = 1 mm. 37, *E. lochi* new species. Scale line = 1 mm. 38, *E. costulatum* (Kiener, 1838). Scale line 1 mm. 39, Sclerite of alcyoniid octocoral found in association with egg-capsules of *E. costulatum*. Scale line = 0.1 mm; 40, Detail of figure 39. Scale line = 0.1 mm. 41, *E. costulatum*, eggs within a capsule. 42, *E. ulu*, egg-capsule with protoconchs 1. Scale line = 0.1 mm. 43-47, Mucous threads. Scale line, with figure 43, = 0.01 mm. 43, *E. hoeksemai*. 44, *E. ulu*. 45, *E. lochi*. 46, *E. ingidae*. 47, *E. costulatum*. 48, *E. twilae*, larval shells (= protoconchs 1). Scale line = 0.1 mm.

Egg-capsules (n = 10): Egg-capsules roundish, white, transparent, with protuberances, without embedded sand, closely connected along straight mucous thread. Egg-capsules 1.2-1.4-1.6 mm diameter, with 342-425-532 white eggs per capsule.

Type material: Holotype NNM 59104, from type locality. Paratypes: NNM 59149/1, Indonesia, Sulawesi, off Ujung Pandang: W. Lae-Lae, 7 m; NNM 59148/2, 9 m; NNM 59145/1, type locality, 3 m; NNM 59105/1, 59138/3, 6 m; NNM 59127/1, 59129/1, 59141/10, 59147/1, 59150/2, 9 m; NNM 59126/1, 59142/1, 59143/1, 12 m; MNM 59146, 15 m; NNM 59139, ESE Samalona, 5 m; NNM 59131/4, 12 m; NNM 59140/5, 13 m; NNM 59116/1, 59117/1, 59132/3, 59133/2, 59134/1, 59135/1, W. Samalona, 9 m; NNM 59121/1, 59122/1, 12 m; NNM 59118/1, 15 m; NNM 59151/1, E. Kudingareng Keke, 9 m; NNM 59106/1, 59107/1, W. Kudingareng Keke, 9 m; NNM 59115/3, 10 m; NNM 59113/1, 59114/1, 12 m; NNM 59108/1, 59109/1, 59110/1, 59111/2, 59112/1, 15 m; NNM 59123/1, 59124/1, 18 m; NNM 59152/1, 59153/1, 24 m; NNM 59137/1, NW Lankai, 12 m; NNM 59159/5, Pulau Badi, 25 m; NNM 59161/2, Bone Lola, 8 m; NNM 59160/1, 9 m; NNM 59154/2, 59155/2, 59156/2, 59163/1, Bone Tambung, 5 m;

NNM 59157/1, 22 m. Only the specimens from off Ujung Pandang are considered the type series (see Distribution below).

Type locality: Indonesia, Sulawesi, off Ujung Pandang, W. Bone Baku, 6 m.

Other material examined: AMS 329653/1, Australia, Queensland (see also Loch, 1982: 3, 4, 1 fig.): No. 5 Sandbank Reef, 13°45'S, 144°16'E, 9 m, I. Loch leg.; AMS 099803/2, 0998041, 099805/1, 098806/1, 100188/14, 329680/1, 329683/2, off Lizard Island, 14°39'-14°42'S, 145°23'-145°28'E, 2-11 m, P. H. Colman, I. Loch and W. F. Ponder leg.; AMS 329672/1, Opal Reef, N. of Cairns, 16°15'S, 145°50'E, 9 m, I. Loch leg.; AMS 096575/2, 101238/2, 147334/2, 329676/4, 329679/3, 329670/1, E-NE of Townsvile, 18°46'-18°57'S, 147°31'-147°44'E, 9-18 m, I. Loch leg. NNM unnumbered, Indonesia, Ambon, Hitu, outer part of Ambon Bay, W. Laha, J. C. den Hartog leg.; NNM unnumbered, Sulawesi, off Ujung Pandang.

Records in the literature: Papua New Guinea, Nagada (16 km N. of Madang) (Bratcher, 1982: 3, 1 fig.). Japan, Sesoko Island, Okinawa (Yamashiro, 1990: 299-305, figs. 1-6). Egypt, Red Sea, Sinai, Thomas Reef, 27°59'N, 34°27'E (Dushane, 1988a: 31, figs. 5, 6).

Distribution (Figure 2): Australia (Queensland), Papua New Guinea, Indonesia, Japan, and Egypt (Red Sea).

Habitat: This species was found from 3 m to the maximum diving depth of 24 m. In the literature that might refer to this species a depth of 45 m was mentioned (Loch, 1982). The following coral host species were recorded: *Ctenactis echinata, Herpolitha limax, Sandalolitha dentata* Quelch, 1884, *S. robusta* (Quelch, 1886) and *Zoopilus echinatus* Dana, 1846. Clung with mucous threads to the underside of a coral, one to fourteen specimens were found accompanied by up to a few hundreds of egg-capsules.

Etymology: This species is named after Mrs. Twila Bratcher, of Los Angeles, California, USA, who first differentiated the new taxon from *E. bullatum*.

Remarks: This species has been misidentified by various authors (Dushane, 1988a; Yamashiro, 1990; Mienis, 1994, conditionally) as *Epitonium bullatum* (Sowerby, 1844), a species associated with sea anemones (Kilburn and Rippey, 1982; Kilburn, 1985; Mienis, 1994). The badly damaged holotype of *E. bullatum* (Figures 34, 35) has a more globular, far less fragile shell with convex whorls, costae occasionally forming a varix, and only about 5 teleoconch whorls at a length of 19 mm (several apical whorls are missing). The specimens illustrated by Jousseaume (1921: pl. 3, fig. 2), Azuma (1962: fig. 2, as *Globiscala kashiwajimensis*), Kilburn and Rippey (1982: pl. 11, fig. 15), Kilburn (1985: 330, figures 160-163) and Wilson (1993: p1. 44, fig. 9) exemplify the variability of *E. bullatum*. Although *E. twilae* differs conspicuously in shape from the other *Epitonium* species in this study, its protoconch (Figures 28, 31, 48) cannot be distinguished from that of these other species.
Yamashiro (1990) published various data on the life history of *E. twilae* (as *E. bullatum*). That author described the egg-capsules as elliptical, 0.88 mm in length and 0.75 mm in width, containing 38-98 eggs each. These data differ from our results. Based on very similar shell morphologies, however, we consider his specimens and the ones examined in this section to be conspecific.
Despite the fact that *E. twilae* differs markedly in shell morphology from *E. ulu*, the protoconchs of these species are very similar.

Epitonium ulu Pilsbry, 1921
(Figures 2, 11-12, 17, 21, 29, 44)

Epitonium ulu Pilsbry, 1921: 376, fig. 11c; Bosch, 1965: 267, fig. 1; Robertson, 1970: 45; Hadfield, 1976: 135, Table 1; Taylor, 1977: 253, 258, fig. 7; Kay, 1979: 156, fig. 53a, b; Loch, 1982: 3, 1 fig.; Bell, 1985: 159, figs. 1-6; Dushane, 1988a: 31, figs. 3, 4; 1988c: 9, 1 fig.; Wilson, 1993: 273.

Description:

Shell (Figures 11-12, 17, 21, 29) (n = 20): Very fragile, elongate-conical, creamy white; reaching 16 mm in length. Length/width ratio 2.3-2.6-3.6. Protoconch whorls 3. Maximum protoconch 1 diameter 0.13 mm (n = 2). Protoconch with

numerous, very fine, incised, axial lines. Teleoconch whorls up to 12, separated by moderately deep suture. Teleoconch sculpture varying in intensity from well-defined to obsolete. Costae unevenly spaced, orthocline, more or less lamellate or obsolete, not continuous, relatively prominent adapically and clearly encroaching on adjacent whorl, curved in adapertural direction (Figure 21). Spiral threads vary in strength on a single whorl; spiral threads only slightly increasing in number on later whorls. Fifth teleoconch whorl (width 2.0 mm) with 15-23-28 costae and 9-11-15 spiral threads. Five mm width whorl (between whorl 8 and 11) with 19-28-33 costae and 10-14-25 spiral threads. Aperture circular to somewhat oval. Apertural length/shell length ratio 0.20-0.26-0.29. Umbilicus very narrow to closed.

Egg-capsules (Figure 44): Egg-capsules roundish to oval, white, granulated, sometimes embedded with sand. Egg-capsules closely connected along a twisted mucous thread (Figure 44); Dushane (1988a: 32) reported 3 twisted threads. Capsule diameter 0.8-1.3-1.7 mm (n = 5). One capsule contains 67-225-405 eggs. Dushane (1988a: 32) reported 400-600 eggs within a capsule, which she described as papillose, with softly rounded papillae. Kay (1979: fig. 53B) figures the egg-capsules as elliptical, 1.1 mm in width and ca. 1.6 mm in length. See Bell (1982; 1985) and Dushane (1988a) for further data on egg-capsules, life history, and other relevant aspects.

Proboscis: Whitish, with some transversal, transparent bands.

Type material: Holotype ANSP 127818, from type locality.

Type locality: USA, Hawaii, Hilo.

Other material examined: ANSP 127818, USA, Hawaii, Big Island, Hilo; AMS 138321/1, Australia, Queensland (see also Loch, 1982: 3, 1 fig.), Eel Reef, 12°24`S, 143°22`E, 4-8 m, I. Loch leg.; AMS 329660/1, Long Sandy Reef, 12°29`S, 143°46`E, 10 m, I. Loch, leg.; AMS 099801/3, 099802/2, 100821/1, 329656/3, near Lizard Island, 14°40`-14°42`S, 145°23`-145°28`E, 1.5-14 m, P. H. Colman and I. Loch leg.; AMS 138320/1, S. Escape Reef, 15°53`S, 145°49`E, 18 m, I. Loch, leg.; AMS 096573/7, 329649/2, 329650/1, 329651/1, 329652/1, 329655/2, 329658/7, E-NE of Townsville, 18°46`-18°57`S, 147°31`-147°44`E, 6-15 m, I. Loch leg.; NNM unnumbered, Indonesia: Ambon, Hitu, outer part of Ambon Bay, E. and W. Laha, A. Fortuin and J. C. den Hartog leg.; LACM 86-163, Java, off Jakarta, Kepulauan Seribu (= Thousand Islands), Pulau Pelangi and Pulau Putri; AMS 138318/1, Malaysia: Pulau Singa Besar, Pulau Langkawi, 6°14`S, 99°44`E, 1 m, I. Loch, leg.

Records in the literature: USA, Hawaii, Oahu, Kaneoke Bay (Bell, 1985: 159-164, figs. 1-6); Papua New Guinea (Dushane, 1988a: 32); Maldives (Dushane, 1988a: 32); Egypt (Red Sea), Straits of Tiran, Tiran Island and Sinafir Island (Dushane, 1988a: 31, 32, figs. 3, 4); Sinai, Thomas Reef, 27°59`N, 34°27`E (Dushane, 1988a: 31, figs. 5, 6).

Distribution (Figure 2): Hawaii, Australia (Queensland), Indonesia, Malaysia, Maldives, and Egypt (Red Sea).

Habitat: This species was recorded at 3-24 m depth. Coral hosts were *Fungia spinifer* Claereboudt and Hoeksema, 1987, *F. scabra* Döderlein, 1901, *F. concinna*, *F. horrida* Dana, 1846, *F. scruposa* Klunzinger, 1879, *F. fungites*, *F. granulosa* Klunzinger, 1879, *F. scutaria* Lamarck, 1801, *F. moluccensis* Van der Horst, 1919, *F. gravis* Nemenzo, 1955, and *F. paumotensis* Stutchbury, 1833. One to 11 specimens, free or accompanied by up to a few hundreds of egg-capsules, were observed on the individual corals, attached with mucous threads to the underside or on the substrate of these hosts.

Remarks: Shells of this species vary considerably in length/width ratio, intensity of teleoconch sculpture and number of costae. They differ from *E. hoeksemai* by a length/width ratio of ca. 2.6 instead of ca. 1.9 and by the presence of less than 20 spiral threads on the fifth teleoconch whorl. It is the most common epitoniid species associated with Fungiidae in the study area.

Acknowledgements

We are particularly grateful to Dr. B. W. Hoeksema for his most valuable assistance in collecting and identifying the fungiid corals examined in this article and for contributing his expertise on corals. We thank all who allowed us to examine material in the molluscan collections under their care: Dr. P. Bouchet (MNHN), Mr. I. Loch (AMS), Dr. Y. Finet (MHNG), Dr. J. H. McLean (LACM), Dr. C. Rosenberg (ANSP), and Mrs. K. Way (BMNH). We also thank Mr. A. Weil and Mrs. L. Brown, who contributed expertise on epitoniids, and Dr. L. P. van Ofwegen (NNM), who identified the sclerites associated with some egg-capsules. Some photographs were taken by A 't Hooft (University of Leiden Institute of Evolutionary and Ecological Sciences, Leiden). This project was subsidized by the Royal Dutch Academy of Sciences, the Stichting Jan Joost ter Pelkwijkfonds and the Leiden University Foundation.

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At the time the manuscript was being sent for typesetting, the authors received the following book:

Weil, A., L. Brown and B. Neville. 1999. The wentletrap book. Guide to the Recent Epitoniidae of the world. Evolver srl, Roma, 246 pp.

This work apparently does not contain data that could substantially add or change the contents of the present article.

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

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Also in: Zoologische Verhandelingen Leiden 345: 139-150 [2003].

Zoologische Verhandelingen Leiden, 345 139-150 (2003)

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Key words: parasitic snails; coral reefs; coral/mollusc associations; egg-capsules; veligers; Epitoniidae; *Epitonium*; larval development; radulae; jaws; Euphyllidae; *Plerogyra*; Indo-Pacific

Abstract

This is the first record of an association between a wentletrap species (Gastropoda: Epitoniidae) and coral species of the Euphylliidae (Scleractinia), i.e. *Plerogyra simplex* and *P. diabolotus*. While describing *Epitonium hartogi* spec. nov., special attention is given to the ontogenetic development within the egg-capsules, the structure and microsculpture of the opercula, the radulae, and the microsculpture on the radular jaws. These characters proved to be at least partly diagnostic in the epitoniid species *Epitonium albidum*, *E. billeeanum*, *E. costulatum*, *E. hoeksemai*, *E. ingridae*, *E. lochi*, *E. millecostatum*, *E. pyramidalis*, *E. twilae*, *E. ulu* and *Nitidiscala tincta*. Spiculae-like crystals covering the epitoniid egg-capsules are described; such crystals are also present within the tentacles of the *Plerogyra* host.

Contents

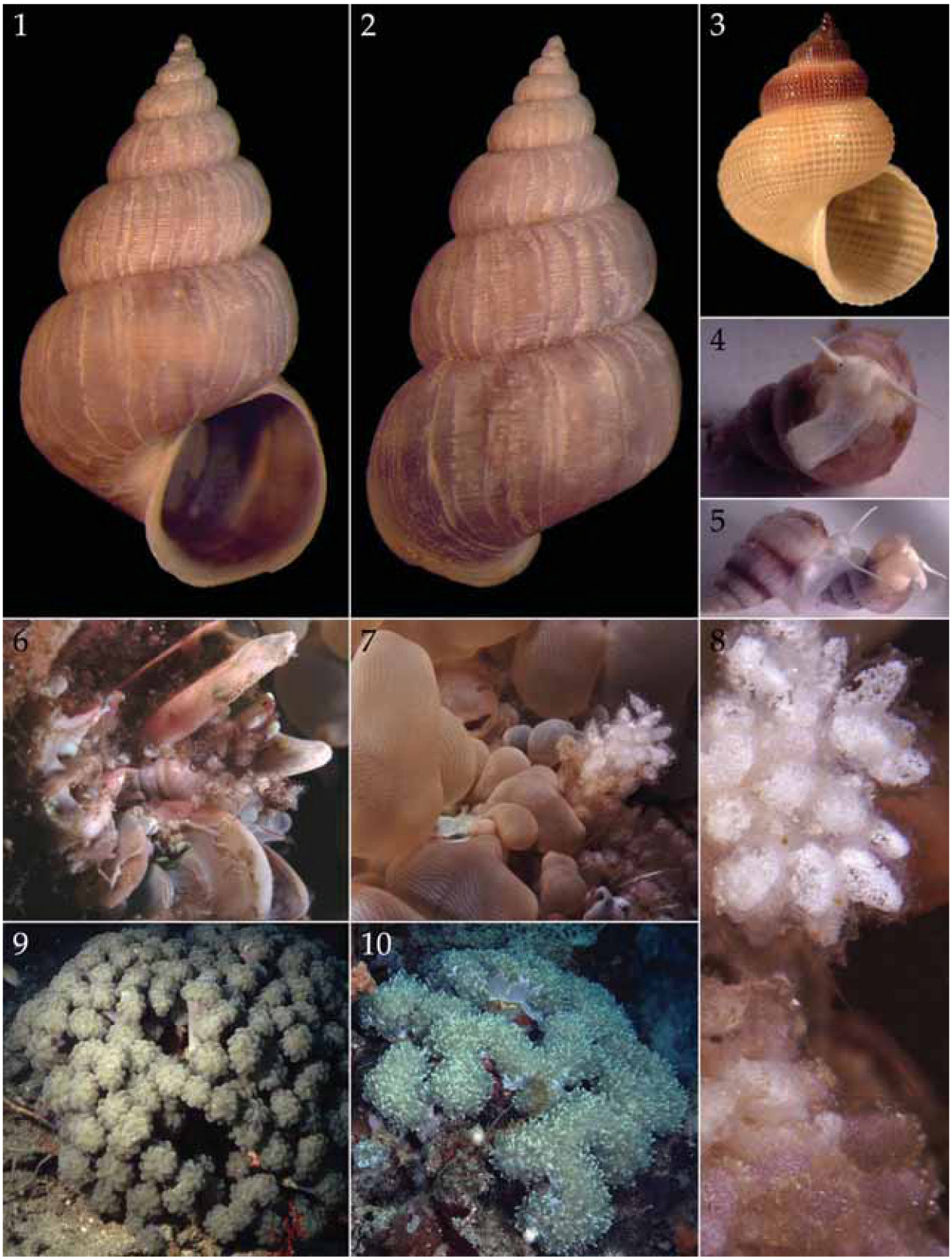
Introduction

Most *Epitonium* species (>100) are found associated with sea anemones (Actiniaria). Less commonly, these snails are found with corals (Scleractinia). More specifically, seven epitoniid species are known to be hosted by coral species of the Fungiidae (Gittenberger et al., 2000; Bonfitto and Sabelli, 2000) and two by species of the Dendrophylliidae (Dushane and Bratcher, 1965; Bouchet and Warén, 1986). The present article describes the first record of an epitoniid associated with corals of the Euphylliidae. A new *Epitonium* species was found associated with bubble corals of *Plerogyra simplex* Rehberg, 1892, and *P. diabolotus*, Ditlev, 2003. It is reported from off Makassar, Sulawesi, Indonesia and off Ko Phiphi Don island, Krabi, Thailand.

Material and methods

Wentletraps were collected in 2001 at the coral reefs surrounding the islets Samalona, Kudingareng Keke and Bone Tambung, off Makassar, SW Sulawesi, Indonesia. One specimen, with egg-capsules, was collected off Ko Phiphi Don island, Krabi, Thailand. The identifications of the coral hosts were made on the basis of photographs by Dr. H. Ditlev and Dr. B.W. Hoeksema. In total, off Makassar, 4 colonies of *P. simplex* Rehberg, 1892, 8 colonies of *P. diabolotus* Ditlev, 2003, and 40 colonies of *P. sinuosa* (Dana, 1846), were searched for snails. The snails were conserved in 96% alcohol. Some egg-capsules were kept in an aquarium. Each day some of those were cut open in a drop of sea-water on a glass-slide, in such a way that the embryos and/or veligers were alive during the observations. While doing so, the larval developmental stages were studied through a microscope and photographed with a digital camera (Fujifilm MX-2700).

The number of specimens is indicated after the slash following the collection number. Only shells with a height of more than 4 mm have been measured. The number of specimens used (n) is mentioned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between brackets behind the values. Means are indicated between the extremes (minimum-mean-maximum). The morphology of the operculae, radulae, jaws, protoconchs, costae, spiral ribs, egg-capsules and the mucus threads, was studied with a SEM. The SEM was also used to study the sharp spiculae-like crystals that were found on the egg-capsules.

In the present article some morphological characters of the new species which are rarely mentioned in the epitoniid literature are compared with those of *E. albidum* (Orbigny, 1842), *E. costulatum* (Kiener, 1838), *E. hoeksemai* Gittenberger and Goud, 2000, *E. ingridae* Gittenberger and Goud, 2000, *E. lochi* Gittenberger and Goud, 2000, *E. millecostatum* (Pease, 1860), *E. pyramidalis* (Sowerby, 1844), *E. twilae* Gittenberger and Goud, 2000, *E. ulu* Pilsbry, 1921, and *Nitidiscala tincta* (Carpenter, 1865). The conchologically similar "golden wentletrap", i.e. *Epitonium billeeanum* (Dushane and Bratcher, 1965) (fig. 3), which occurs associated with corals of the family Dendrophylliidae, is compared in more detail.

Abbreviations: RMNH, National Museum of Natural History, Leiden (formerly Rijksmuseum van Natuurlijke Historie).

Systematics

Family Epitoniidae Berry, 1910
Genus *Epitonium* Röding, 1798

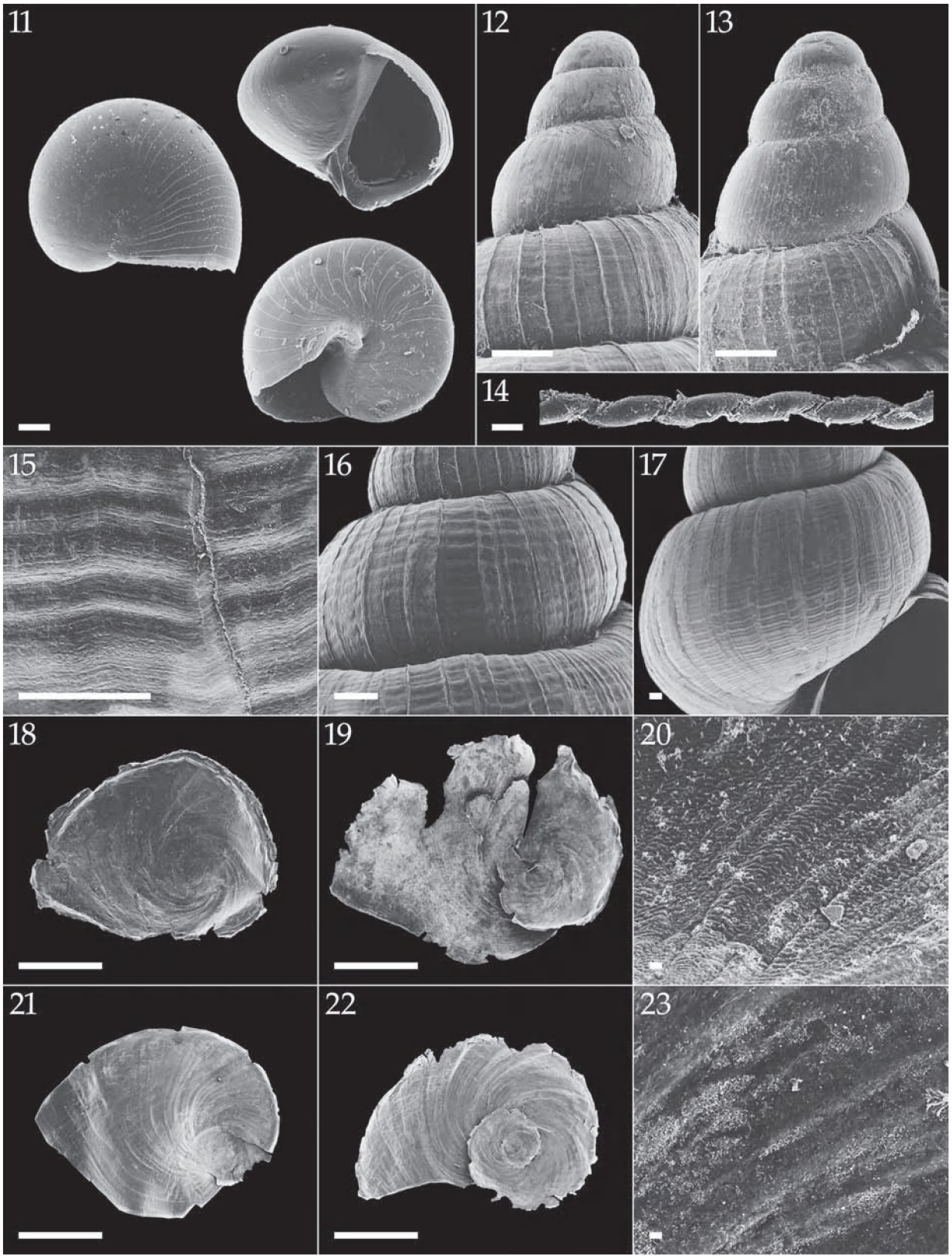
Epitonium hartogi spec. nov.

Material: Indonesia, Sulawesi, off Makassar. Holotype, snail (RMNH 94924) with egg-capsules (RMNH 94934): W Samalona Island (05°07'31"S/ 119°20'31"E), hosted by *Plerogyra simplex*. Paratypes: type locality, with the holotype, snail (RMNH 94925/1); type locality, also hosted by *P. simplex*, 4 snails (RMNH 94926/1, RMNH 94927/3), snails with egg-capsules (RMNH 94928/3); type locality, hosted by *Plerogyra diabolotus*, 9 snails with egg-capsules (RMNH 94932/2, RMNH 94933/7); W Kudingareng Keke (05°06'09"S / 119°17'09"E), hosted by *P. diabolotus*, 4 snails with egg-capsules (RMNH 94930/1, RMNH 94931/3); W Bone Tambung Island (05°02'05"S / 119°16'16"E), 1 snail with egg-capsules (RMNH 94929/1).

Thailand, Krabi, NW Ko Phiphi Don, La Nah Bay (07°46'01"N/ 98°45'42"E), paratype, snail with egg-capsules (RMNH 95989/1), hosted by *P. diabolotus*.

Shell: Shell (figs 1, 2) very fragile, elongate-conical, whitish but coloured purple by the mucus (fig. 5) of its host coral (which can be removed). The inside of the shell, except for the apertural border in front of the operculum in situ, has an irregularly purplish colour (which cannot be removed), especially when wetted (figs 4-6). The holotype measures 7.0 x 4.1 mm. One damaged specimen reaches at least 8.2 mm in height. Height/width ratio 1.4-1.6-1.8 (n = 13). Apart from the smooth apical part, the protoconch is sculptured with evenly spaced, very fine, incised, radial lines, c. 14 per 0.2 mm on the third whorl (fig. 12). Protoconch as in *Epitonium costulatum*, *E. ingridae*, *E. lochi*, and *E. ulu* s. lat., all with c. 15 lines per 0.2 mm (Gittenberger et al., 2000); differing from *E. billeeanum* with c. 21 lines per 0.2 mm (fig. 13). Protoconch 1 + 2 with 3½ whorls (fig. 12). Protoconch 1 consisting of c. ½ whorl (fig. 11). With up to at least 6 (damaged specimen) teleoconch whorls, separated by a deep suture. Teleoconch sculptured with orthocline, usually not continuous, lamellar, low costae without any particular notches or processes, barely touching the preceding whorl, and less prominent, low spiral ribs, covered by numerous very fine, incised spiral lines (fig. 15). One specimen showed continuous spiral ribs more prominent than the costae. Second teleoconch whorl (fig. 16) with 20-22.8-26 (n = 23) rather irregularly spaced costae, and 9-10.3-12 (n = 22) evenly spaced, mostly continuous, spiral ribs. Fifth teleoconch whorl (fig. 17) with 32-37.3-40 (n = 8) very unevenly spaced, irregular, and often split costae, and 29-34.3-40 (n = 12) somewhat unevenly spaced spiral ribs,

Figs 1-10. Material from off Makassar, SW Sulawesi, Indonesia. Figs 1, 2, 4, 5-8, *Epitonium hartogi* spec. nov. 1, 2, holotype (height 7.0 mm); 4, head with proboscis (shell height 6.9 mm); 5, crawling snails partly covered by purple mucus from the coral host (largest shell height 6.9 mm); 6, snail between retracted tentacles within polyp (shell height 6.9 mm); 7, egg-capsules on polyp (capsule length 1.6 mm); 8, egg-capsules with white undifferentiated eggs (upper) and ones with fully grown veligers (lower) appearing purple because of pigmented mantle organs (capsule length 1.6 mm). Fig. 3, *Epitonium billeeanum* (height 6.0 mm). Fig. 9, *Plerogyra simplex* (colony diameter c. 35 cm). Fig. 10, *Plerogyra diabolotus* (colony diameter c. 30 cm). Photos: A. Gittenberger.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mostly not continuous, ending on top or in front of the costae. Apertural height/shell height ratio 0.34-0.38- 0.43 (n = 10). Umbilicus narrow.

Operculum (n = 4): Operculum paucispiral. The coils either interconnected (two of four) to form the shield-like operculum most common in prosobranchs (fig. 18), or scalaroid (loosely) coiled (two of four) (fig. 19), as is also found in e.g. some hydrobiids (Solem, 1974: 129, 130). This dimorphism is also present in *E. billeeanum* (figs 21, 22). On the outside there are numerous, very fine but prominent, wavy line segments, running at about 80° in between irregularly spaced growth-lines (fig. 20). Bonfitto and Sabelli (2000) illustrate a similar pattern in *Epitonium oliverioi*, where the growth-lines are regularly spaced. In *E. billeeanum* (n = 4) such wavy lines are lacking (fig. 23). Although the microsculpture of the operculum can easily be studied by SEM photography, and seems at least to be specific for the species mentioned above, it is hardly ever described in the literature.

Anatomy: The soft parts of the animal are whitish, with small, dark eye-spots (figs 4, 5). There is a pattern of white, non-transparent dots on the transparent whitish proboscis (fig. 4). It was concluded that the adult snails have a pigmented mantle organ, because they released purplish dye when they were collected. Because the epitoniids were conserved in alcohol 96%, the tissue had hardened which hampered dissection.

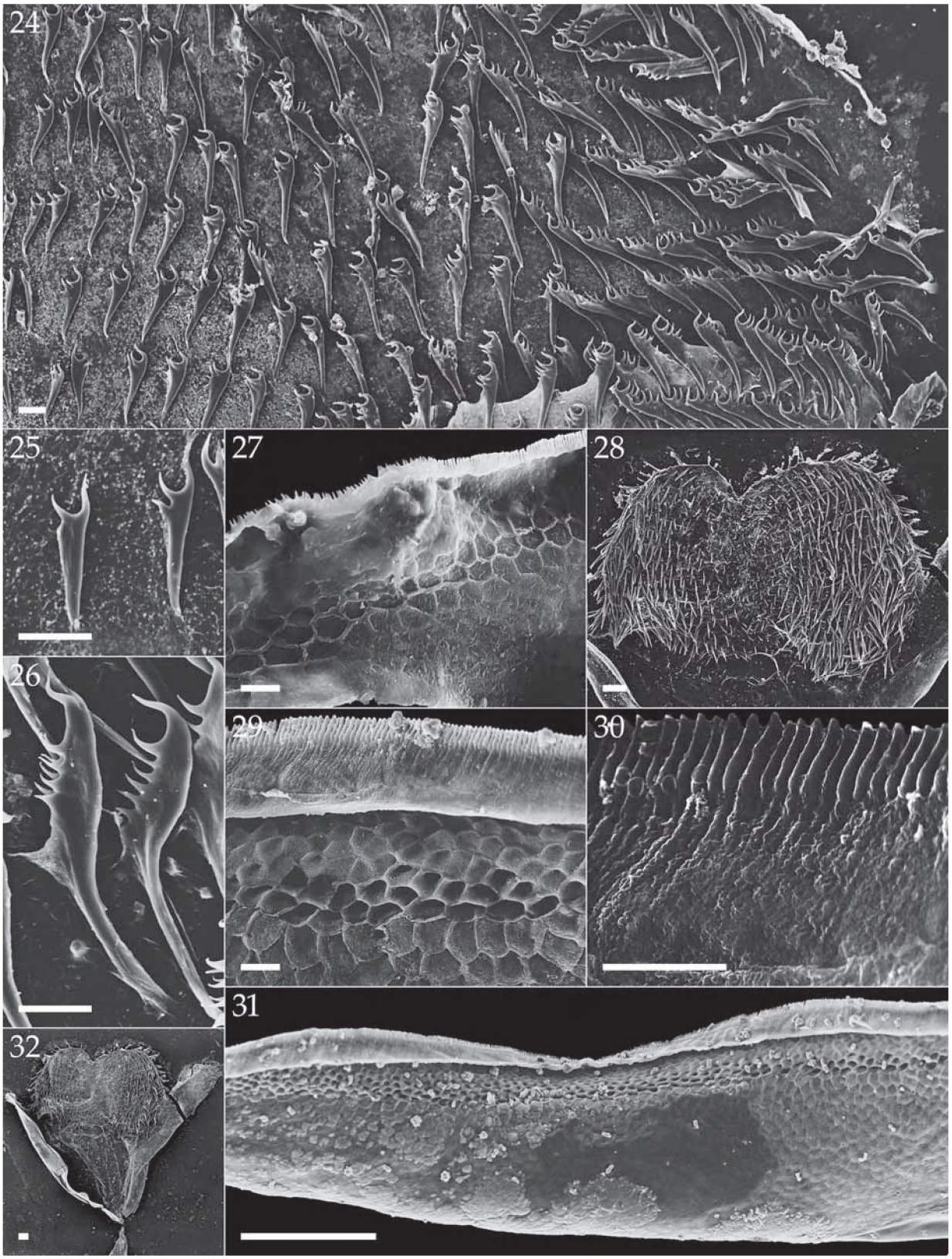
Radulae: Epitoniids have a ptenoglossan radula without a rachidian (Graham, 1965; Boss, 1982; Bandel, 1984; Page and Willan, 1988). In *E. billeeanum* the radula changes when a male grows and becomes a female (Page and Willan, 1988). It is unknown whether this occurs more generally in epitoniids. The three radulae that were investigated are from relatively large specimens, with shell heights of 5.4, 6.9 and 7.4 mm, respectively. These snails were found within a cluster of egg-capsules, without any other large wentletraps nearby, suggesting that they are females. Two of the radulae were damaged while preparing them, making it impossible to accurately count the number of teeth in a row. The radula that was not damaged is described here. It belongs to the specimen with a shell height of 5.4 mm. In half a row (fig. 24) 25 teeth are present, which cannot be distinguished as laterals and marginals, because they change in size and number of cusps gradually, from the centre to the margin of the radula. The innermost teeth (fig. 25, left one) measure about 22 µm in length and the penultimate ones (fig. 26, right one) 50 µm. The most marginal teeth have a reduced length of c. 40 µm. The teeth have an acute primary cusp at the top and 1 to 6 equally sharp, shorter, secondary ones somewhat lower along the blade. In half a row the innermost tooth has one secondary cusp, followed by four teeth with two, seven with three, seven with four, four with five, one tooth with six and the ultimate tooth with two secondary cusps. The three radulae that were investigated resembled each other closely, although the numbers of teeth with a certain number of secondary cusps slightly varied (one more or less). As a malformation, some teeth are split, having a double number of cusps (fig. 26, left one). For nearly 2/3 of its length each tooth is attached to the radular plate, i.e. up to just before the lowest cusp (fig. 26).

In *E. billeeanum* (figs 28, 32) the morphology of the radular teeth is quite different. Especially the size difference between the inner teeth (c. 30 µm long) and the penultimate teeth (about 150 µm long) is apparent. In general, there are fewer cusps on a tooth as well.

Jaws: Epitoniid snails have jaws, flanking the radula, as is shown in fig. 32 (*E. billeeanum*). Because the jaws on the SEM photographs (figs 27, 29-32) are dried, their actual sizes in situ will be somewhat larger.

The dried jaw of *E. hartogi* measures about 525 x 115 µm. The edge of the side where the jaw is attached to the radular plate is relatively smooth. On the other side the edge is provided with about 13 per

Figs 11-23. Material from off Makassar, SW Sulawesi, Indonesia. Figs 11, 12, 14-20, *Epitonium hartogi*. 11, protoconch 1, i.e. hatching veliger shell; 12, protoconch; 14, twisted mucus thread; 15, spiral ribs and lines; 16, second teleoconch whorl; 17, fifth teleoconch whorl; 18, operculum, interconnected coils; 19, operculum, scalaroid; 20, operculum, microsculpture. Figs 13, 21-23, *Epitonium billeeanum*. 13, protoconch; 21, operculum, interconnected coils; 22, operculum, scalaroid; 23, operculum, microsculpture. Scale: 20, 23 = 10 µm; 12-13, 15-17 = 100 µm; 11, 14 = 20 µm; 18, 19, 21, 22 = 1 mm. SEM photos: J. Goud.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10 µm, 4 µm long, sharp tooth-like processes (fig. 27). The jaw surface is smooth to slightly granulated on the inside, facing towards the radula. On the outside, three vaguely delimited zones parallel to the edge can be distinguished. The denticulated edge is followed by a zone, c. 20 µm broad, with a smooth surface, a second zone, c. 10 µm broad, with a pattern of erect edges forming about two rows of irregular penta- or hexagonals, and a third zone, where the irregular penta- or hexagonals gradually become obsolete towards the smooth edge. The third zone is characterized by the presence of small perforations.

In *E. billeeanum* the jaws look quite different. In that species, a jaw (figs 29-32) has about 8 per 10 µm, 6 µm long, lamellar sharp processes on a granulated edge, which is c. 19 µm broad (fig. 30). There is an adjoining first zone with three to four rows of irregular penta- or hexagonals on a finely perforated surface, a second zone of 1 to 2 rows of irregular, deepened, penta- or hexagonals on a slightly granulated surface, and a third zone in which the penta- or hexagonals gradually become obsolete on a surface with perforations, slightly larger than the ones in the first zone (figs 29, 31). The structure of the jaws is described here in considerable detail. Since only a single jaw or pair of jaws could be studied for both species, the amount of intraspecific variation remains unknown. It may be hypothesized that the conspicuous differences in jaw structure observed here, refer at least partly to species level variation. This is also supported by the figure of the marginal processes on the jaw of the epitoniid *Nitidiscala tincta* in Collin (2000), which do not resemble those in *E. hartogi* and *E. billeeanum*.

In epitoniids, the jaws probably function as attachment surfaces for muscles, aiding in keeping the esophagus open for the reception of food. Therefore, Clench and Turner (1952: 353) argue that they should be referred to as "esophageal plates".

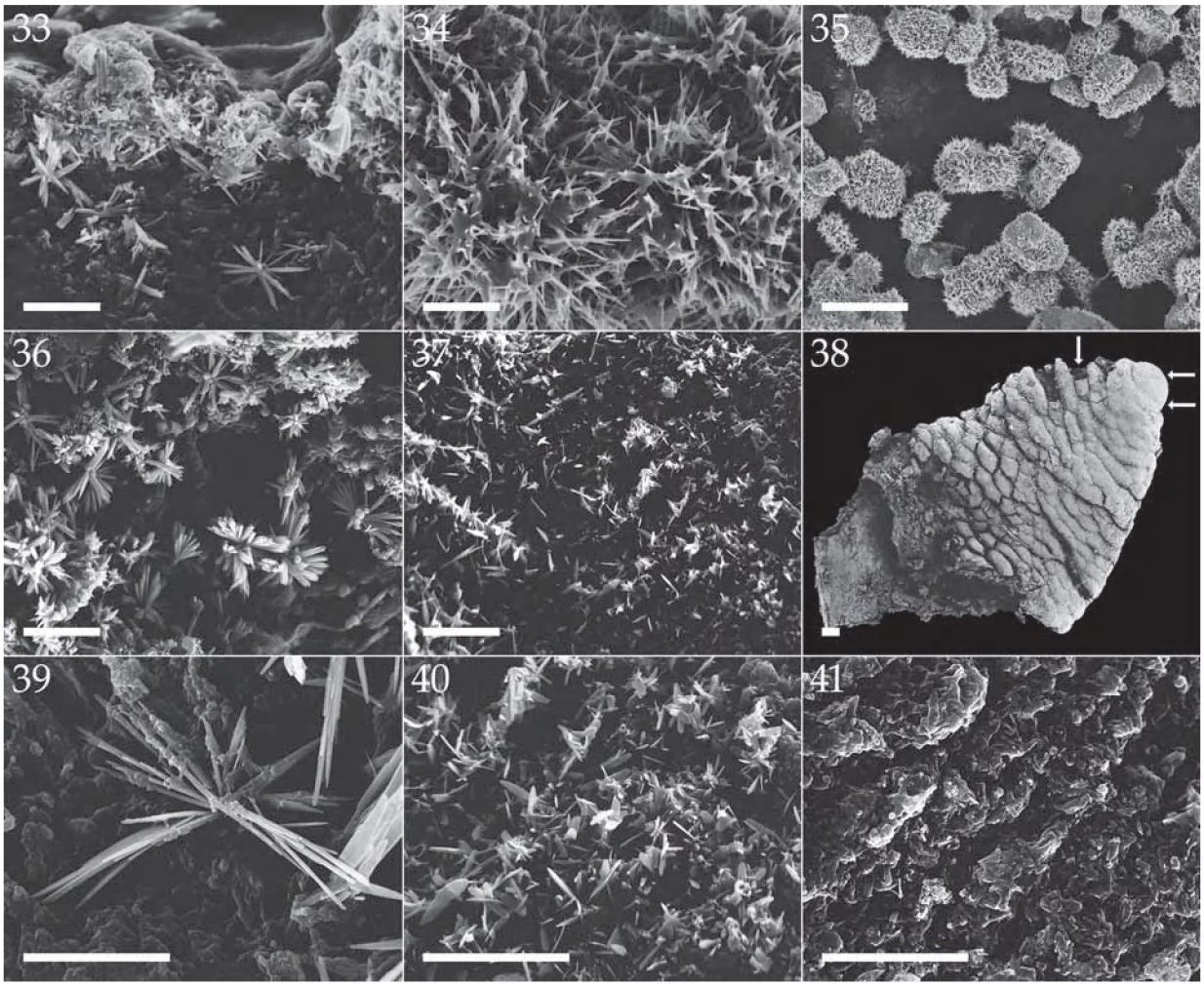
Figs 24-32. Material from off Makassar, SW Sulawesi, Indonesia. Figs 24-27, *Epitonium hartogi.* 24, half a row of radular teeth; 25, inner tooth (left one); 26, penultimate tooth with six secondary cusps (right one), tooth with split cusps (left one); 27, detail outside jaw. Figs 28-32, *Epitonium billeeanum.* 28, rows of radular teeth; 29, detail outside jaw; 30, lamellar processes at edge of jaw; 31, overview outside jaw; 32, radular teeth and laws. Scale: 23-27, 29, 30 = 10 µm; 28, 31, 32 = 100 µm. SEM photos: J. Goud.

Egg-capsules: The ovoid egg-capsules (figs 7, 8), with conspicuous protuberances, are 1.55-1.56-1.57 mm long and 1.12-1.19-1.25 mm broad (n = 4). They are interconnected along a twisted mucus thread (fig. 14) and contain 230-328-415 (n = 6) eggs each. The uncleaved eggs are 39-40-41 µm in diameter (n = 20).

The wall of an egg-capsule is covered with small spiculae-like crystals (fig. 33) and small grains (figs 34, 35), apparently consisting of a mixture of such crystals. When a tentacle (fig. 38) of the host coral was dried and its surface and inside (holes were made with a needle) studied with a SEM, very similar crystals were seen. On top of a tentacle (figs 37, 40) crystals are seen which are much smaller than the ones of the egg-capsules. Just underneath the top (fig. 41) no such crystals were observed on the outside. Inside the tentacle, in particular near the top, many crystals were present with the same size as the ones on the egg-capsules (figs 36, 39). How these crystals can be present both inside tentacles of the coral and on the outside of the egg-capsule of the snail is unclear. The fact that the wentletraps eat coral tissue is probably relevant here.

"The crystals appear to be aragonitic and extracellular. They seem to be the result of a physico-chemical process in which crystal deposition occurs spontaneously in an enriched calcium environment with sufficient carbonate ions available. Using a TEM, this process, which is not necessarily biologically-regulated, was also observed for other coral species" (Hayes, personal communication; see also Hayes and Goreau, 1977).

Veliger growth within the egg-capsules: In *Epitonium hartogi*, all larvae within a single egg-capsule develop more or less synchronously, as in other Epitoniidae studied (Collin, 2000; A. Gittenberger, unpublished data). By opening the egg-capsules along a mucus thread, the larvae were found ordered by developmental stage. The duration of each of these stages could not be studied, but it was observed that undifferentiated eggs develop into hatchlings in about 5 days, in a sea-water aquarium under laboratory conditions. In two cases, mucus threads were found with many egg-capsules, together showing the entire developmental trajectory, i.e. with undifferentiated eggs in capsules on one end, and empty capsules on the other end of the thread, where the veligers had



Figs 33-41. Material from off Makassar, SW Sulawesi, Indonesia. Fig. 33, egg-capsule wall, *Epitonium hartogi.* Figs 33, 34 grains consisting of crystals, from egg-capsule wall, *Epitonium hartogi.* 34, detail; 35, overview. Figs 36-41, *Plerogyra simplex.* 36, 39, crystals inside tentacle; 37, 40, crystals on surface tentacle top; 38, overview tentacle, arrows indicating location of detailed figs 36, 37, 39-41, vertical one: figs 36, 39, horizontal ones: figs 27, 40 (upper) and fig. 41 (lower); 41, surface just underneath tentacle top (without crystals). Scale: 33, 34, 36, 37, 39-41 = 10 µm; 35, 38 = 100 µm. SEM photos: A. Gittenberger and J. Goud.

apparently hatched already; see fig. 8 for one of these cases.

The early larval developmental stages resemble those described for the epitoniid species *Nitidiscala tincta* by Collin (2000) and *Epitonium albidum* by Robertson (1983, 1994). The descriptions in this paper are based on a total of 456 photographs of the larvae. Because most organs are minute and translucent at first, they can easily be overlooked and, therefore, their real order of development might slightly differ from what is described here. A zygote first goes through three synchronous cleavages (fig. 42a), followed by many asynchronous ones, resulting in a round blastula that changes by epiboly into a gastrula that actively swims around, using minor cilia on an "early" velum (fig. 42b). After becoming slightly oval, the pigmented mantle organ begins to form, in order of recognizable development followed by, the foot, the shell (fig. 42c), the operculum, the visceral muscle, the digestive gland, the velar lobes, the statocysts, the eyes (fig. 42d), the larval heart, the columellar muscle, the stomach and finally the right cephalic tentacle with small sensorary cilia on top (fig. 42e, h). Before the veliger hatches, the proto-

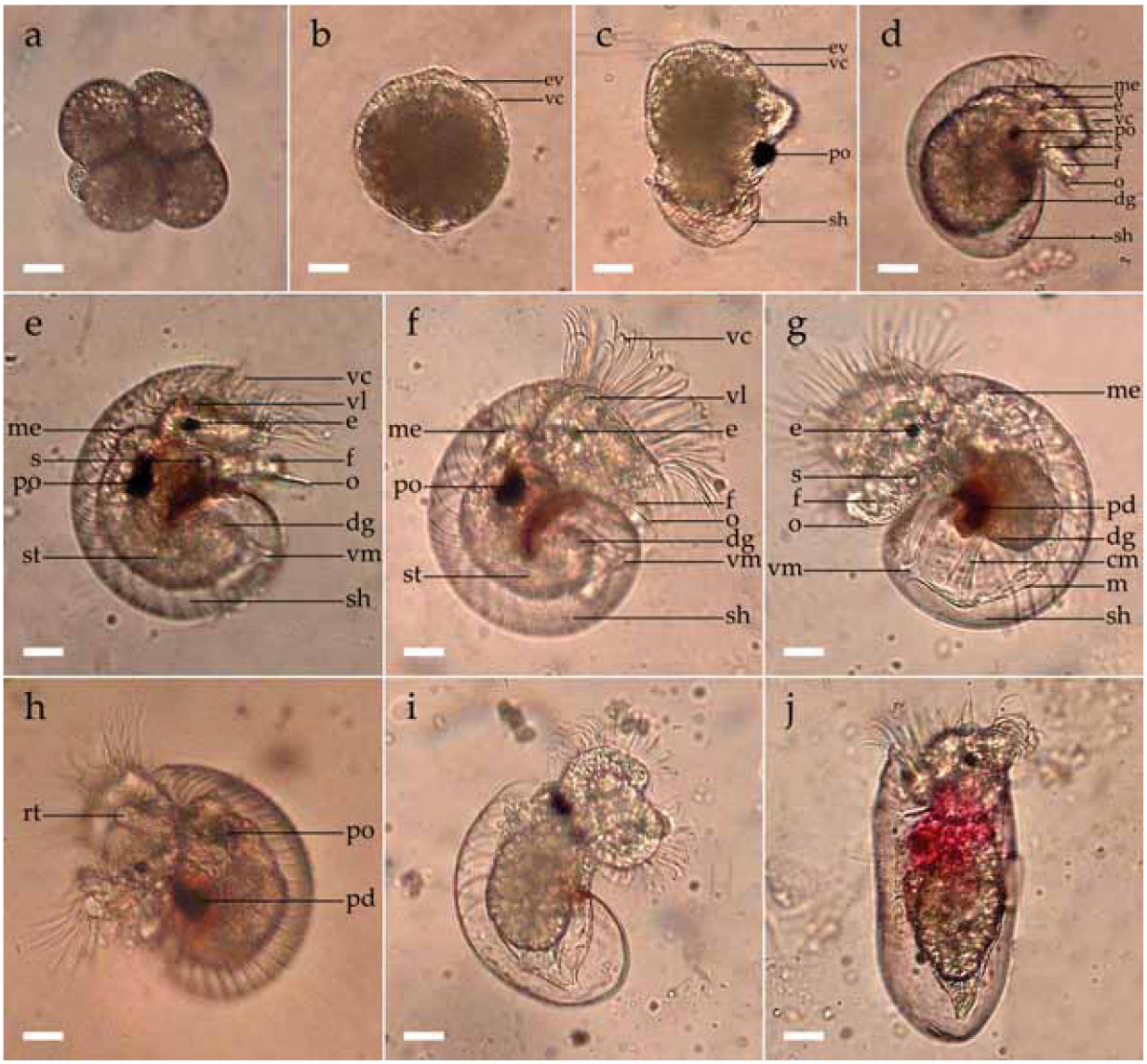


Fig. 42. Material from off Makassar, SW Sulawesi, Indonesia. Veliger development of *Epitonium hartogi* spec. nov. a, 3rd cleavage of cells; b, gastrula; c, first shell growth, black dot is purple dye excreted by the here invisible small pigmented mantle organ; d, early veliger, right lateral view; e, later veliger, right lateral view; f, hatched veliger, right lateral view; g, hatched veliger, left lateral view; h, hatched veliger with right tentacle, left lateral/dorsal view; i, malformed veliger, ventral view; j, malformed veliger, ventral view. Scale = 20 µm. Abbreviations (mainly after Robertson, 1983): cm, columellar muscle; dg, digestive gland; e, eye; ev, early velum; f, foot; m, mantle; me, mantle edge; o, operculum; pd, cavity with purple dye; po, pigmented mantle organ; rt, right tentacle; sh, shell; s, statocyst; st, stomach; v, velar lobe; vc, velar cilia; vm, visceral muscle (?). Photos: A. Gittenberger.

conch shell, the velar lobes and cilia will grow little more (fig. 42f, g). Its left tentacle becomes visible c. one day after hatching. Asymmetric tentacle growth was also found for the "coral-associated" wentletraps *Epitonium billeeanum*, *E. costulatum*, *E. hoeksemai*, *E. ingridae*, *E. ulu* Pilsbry, 1921 (A. Gittenberger, unpublished data) and *E. twilae* (fig. 43a), and for some wentletrap species associated with sea-anemones, i.e. *E. albidum* (see Robertson, 1983, 1994), *E. millecostatum* (see Robertson, 1980), *E. pyramidalis* (fig. 43b, c) and *Nitidiscala tincta* (see Collin, 2000). This asymmetric growth seems to be characteristic for

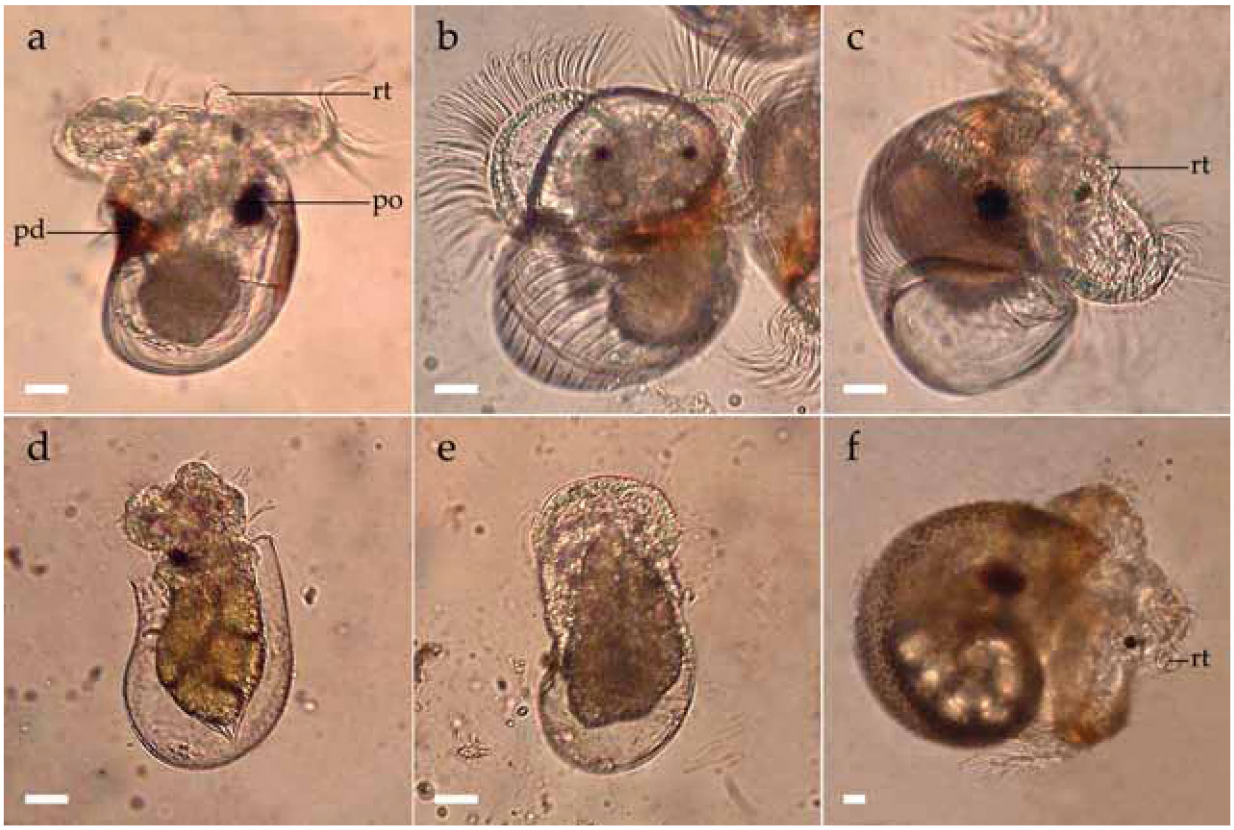


Figure 43. Material from off Makassar, SW Sulawesi, Indonesia. Prosobranch veligers. a, hatching veliger of *Epitonium twilae*, dorsal view; b, c, hatching veliger of *Epitonium pyramidalis*, ventral view (b), lateral/dorsal view (c); d, malformed veliger of *Epitonium billeeanum*, ventral view; e, malformed veliger of *Epitonium costulatum*, dorsal view; f, hatching veliger of *Leptoconchus exopolitus*, right lateral/dorsal view. Scale = 20 µm. Abbreviations: pd, cavity with purple dye; po, pigmented mantle organ; rt, right tentacle. Photos: A. Gittenberger.

epitoniid veligers in general. It was also present in the larvae of a *Leptoconchus exopolitus* Shikama, 1963 (Coralliophilidae) specimen collected off Makassar, SW Sulawesi, Indonesia by the author (fig. 43f), and it was described for *Concholepas concholepas* (Bruguière, 1789)(Muricidae) by DiSalvo (1988), and for *Thais haemastoma* (Linnaeus, 1767) (Muricidae) by D'Asaro (1966). Asymmetric tentacle growth might even be a character common to prosobranch veligers in general, as was postulated by D'Asaro (1966).

The developmental stage, at which an epitoniid veliger hatches, can differ between species. The veligers of *E. pyramidalis*, another sea-anemone associate, hatch from their egg-capsules with 2 tentacles, the left one of which is the smallest, further developed organs and a protoconch consisting of about 1 whorl (fig. 43b, c).

About one percent of the c. 1200 veligers of *Epitonium hartogi* studied has almost uncoiled shells (n = 12)(fig. 42i, j). Such specimens can survive at least until hatching. Similar malformations were found in *E. billeeanum* (fig. 43d) and *E. costulatum* (fig. 43e), collected off SW Sulawesi.

Habitat: *Epitonium hartogi* was recorded at 9-18 m depth, associated with bubble corals (*Plerogyra* spp.). The specimen from Thailand was found on *P. diabolotus*. Off Makassar, the wentletraps were found on all four colonies of *P. simplex* (fig. 9) that were investigated and five of eight colonies of *P. diabolotus* (fig. 10). None of the 40 colonies of *P. sinuosa*, by far the most common *Plerogyra* species present off Makassar, was found with epitoniid parasites. Most of the

wentletraps were completely submerged within the mouth cavity or in between the septae of a polyp (fig. 6). Their presence is indicated by egg-capsules laid on the coral polyp or by some "bubble-tentacles" that can be recognised as damaged (fig. 7). However, it is not unlikely that many specimens also remain within completely healthy looking polyps. After poking the bubbles until they retracted or by breaking away a bit of coral skeleton, the snails were discovered. Only the first specimen ever recorded was not hidden, but crawled over the coral stem of a *P. simplex* colony.

Etymology: This species is named after Jacobus Cornelis den Hartog, former curator of Coelenterata et al., National Museum of Natural History, who died in October 2000.

Acknowledgements

I am grateful to Dr. H. Ditlev (Aarhus, Denmark) and Dr. B.W. Hoeksema (Leiden, The Netherlands) for checking the identification of the host coral *Plerogyra* species and to Dr. R.L. Hayes (Washington, USA) for his information about the crystals. Dr. Claude Massin (Brussels, Belgium) is thanked for his help identifying *Leptoconchus exopolitus*. I would also like to thank Dr. E. Gittenberger (Leiden, The Netherlands) for critically discussing the manuscript, Dr. R. Robertson (Philadelphia, USA), for reviewing it, J. Goud (Leiden, The Netherlands), for making SEM photographs, and Dr. Lisa-Ann Gershwin (Berkeley, USA) for her advice on photographing with a microscope and digital camera. Dr. A. Noor (Makassar, Indonesia) is thanked for his help concerning the permits and facilities enabling the research off Makassar, Indonesia. This study was supported by WOTRO (grant nr. W 82-249).

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7

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

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Also in: Contributions to Zoology 74 (1/2): 125-203 [2005].

Contributions to Zoology, 74 (1/2) 125-203 (2005)

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

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Keywords: Indo-Pacific; parasites; coral reefs; coral/mollusc associations; Epitoniidae; *Epitonium*; *Epidendrium*; *Epifungium*; *Surrepifungium*; new species; new genera; Scleractinia; Fungiidae; *Fungia*

Abstract

Twenty-two epitoniid species that live associated with various hard coral species are described. Three genera, viz. *Epidendrium* gen. nov., *Epifungium* gen. nov., and *Surrepifungium* gen. nov., and ten species are introduced as new to science, viz. *Epidendrium aureum* spec. nov., *E. sordidum* spec. nov., *Epifungium adgranulosa* spec. nov., *E. adgravis* spec. nov., *E. adscabra* spec. nov., *E. marki* spec. nov., *E. nielsi* spec. nov., *E. pseudolochi* spec. nov., *E. pseudotwilae* spec. nov., *Surrepifungium patamakanthini* spec. nov., and '*Epitonium*' *crassicostatum* spec. nov. and '*E.*' *graviarmatum* spec. nov. 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 alone. The shell shape and sculpture are only partially diagnostic because of interspecifically overlapping character states. In most of these cases, the operculum, jaw structure, radula, spawn and/or the habitat do reveal the identity. 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.

Contents

Introduction

The vernacular name "wentletraps" refers to a large group of snail species with usually slender conical shells, often ornamented with more or less prominent axial riblets. As far as known, the animals live as parasites, associated with coelenterates, either corals (Dushane, 1988a; A. Gittenberger *et al.*, 2000), zoanthids (Robertson, 1981; Zahn, 1980) or sea anemones (den Hartog, 1987; Perron, 1978; Robertson, 1963, 1966, 1983a; Schimek, 1986). During this research project it turned out that these associations are restricted even more than initially thought. Some conchologically variable, alleged *Epitonium* species, e.g. "*Epitonium ulu* Pilsbry, 1921", were revealed to be groups of separate species with more or less broadly overlapping shell character states. Consequently, the species described in this paper cannot

always be sharply diagnosed conchologically. The existence of several of these species became especially obvious while trying to characterize the wentletrap species that are associated with corals with molecular markers in an attempt to reconstruct their phylogeny. The data obtained by DNA sequencing (A. Gittenberger *et al.*, in prep.) clearly indicate that there are a much larger number of separate gene pools than previously thought. Some of these species are widespread and several of them may occur sympatrically, though with different coral hosts. Single specimens could not always be identified without molecular data. However, when the identity of the coral host species was known for sure, with the locality where it was found, the identity of the associated epitoniid, determined also by DNA sequencing, could be predicted correctly in all cases.

This is the third contribution in a series of papers aiming at a better knowledge of the epitoniid species (Gastropoda: Epitoniidae) associated with corals (Scleractinia). For a more general introduction to the systematics, morphology and ecology of the large 'convenience genus' *Epitonium*, which ought to be split into smaller units, see also A. Gittenberger *et al.* (2000) and A. Gittenberger (2003).

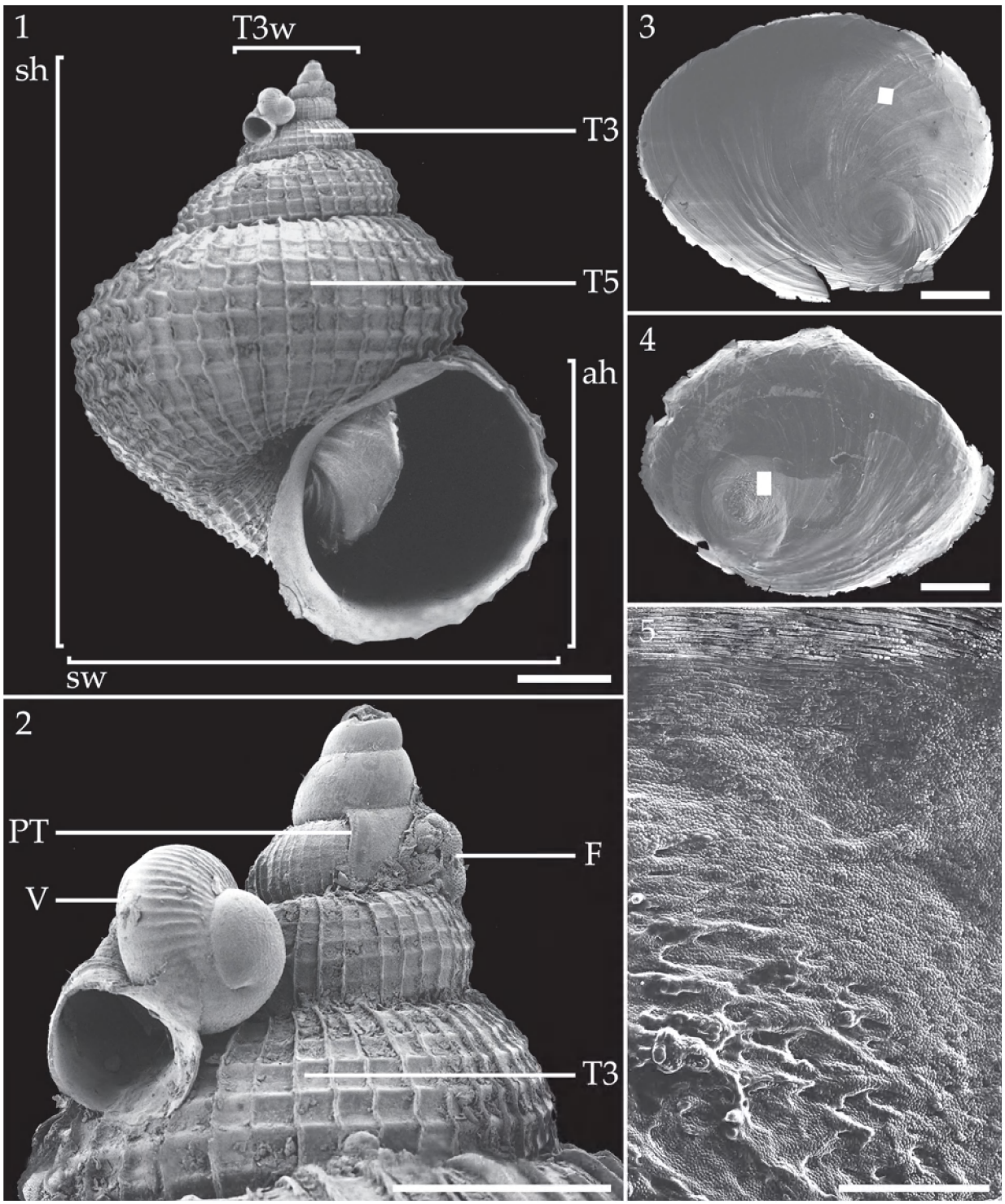
Material and methods

Approximately 60,000 stony corals of the families Fungiidae, Dendrophyllidae and Euphyllidae were searched for epitoniids in the Indo-West Pacific off Egypt, Maldives, Thailand, Malaysia, Japan, Palau, Philippines, Indonesia and Australia. The fungiid hosts were usually identified twice from photographs and/or specimens, independently by A. Gittenberger and B.W. Hoeksema. H. Ditlev identified the euphyllids from photographs. The dendrophyllids were not identified. Most of the specimens used in this study were collected in a three years period (2001-2003) while scuba-diving in Indonesia and Palau during several excursions organized by the National Museum of Natural History Naturalis. This material was preserved in ethanol 96% to enable DNA-analyses. Additional research material from the Red Sea, Maldives, Thailand, Philippines, Australia, Hawaii and the Gulf of California, came partly from other institutes (see the institutional abbreviations below). To give an indication of the intraspecific variation, conspecific specimens are figured for several species. When mean values are indicated, the extremes and the number (n) of items measured are added.

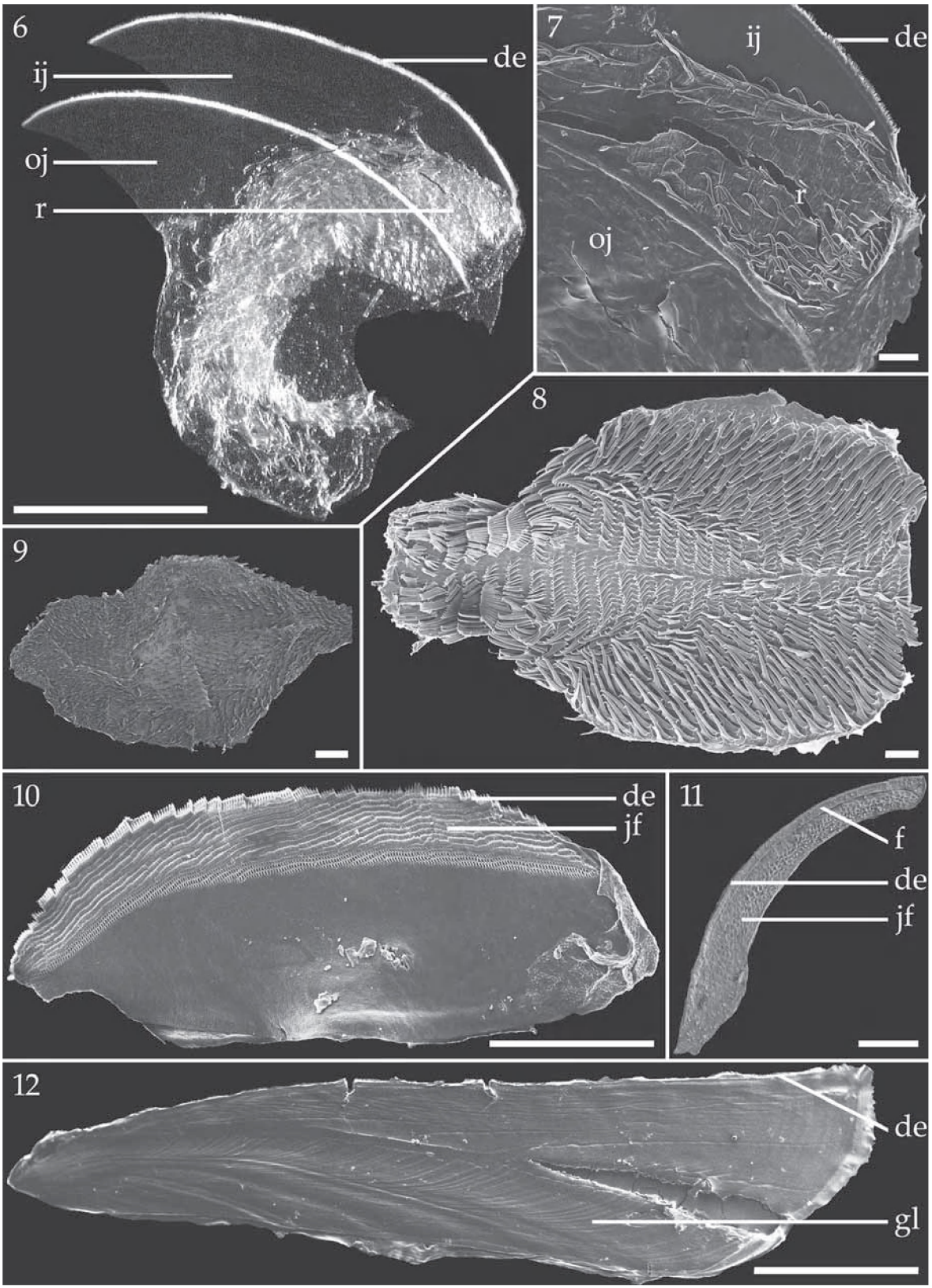
The sculpture on the shells and the opercula, the structure of the mucus threads that connect the egg-capsules, and the morphology of the radulae and jaws were investigated and photographed with a scanning electron microscope (= SEM). The complete shells were photographed with a digital camera (Fujifilm FinePix50i); those smaller than one cm, and the egg-capsules, were photographed with this camera through a microscope, without using additional devices. Most of the epitoniid snails, their egg-capsules and the coral hosts were photographed in situ with a Sea & Sea SX-1000 underwater camera. Unless stated otherwise, all photographs were taken by A. Gittenberger.

The shell height was measured as the length of a line (fig. 1: sh), running parallel to the columella, from the top of the protoconch to the most basal point of the aperture; the apertural height is the distance (fig. 1: ah) between the uppermost and the most basal point of the aperture. The shell width was measured perpendicular to the columella, as the distance (fig. 1: sw) between the left and the right side at the periphery of the shell; the width of teleoconch whorl T3 (figs 1-2: T3, T3w) is the distance between the left and the right side of teleoconch whorl 2¾-3¼. It can only be measured when the protoconch-teleoconch border (PT) is centred, as is illustrated in figure 2. This character was routinely measured in *Epitonium ulu* Pilsbry, 1921, and conchological siblings, where it turned out to be discriminating to some extent. The 'shell height / shell width' (= H/W) and 'apertural height / shell height' (= A/H) values were only calculated for shells that are higher than 5 mm, to allow for better comparisons. Specimens shorter than 5 mm were also studied, especially for the umbilical region.

In most cases the protoconch and the teleoconch whorls could easily be distinguished. The border between protoconch 1 (developed within an egg-capsule) and protoconch 2 (developed after hatching, before the settling stage) is not visible in epitoniid species. Protoconch 1 and 2 are therefore not described separately. In some species almost all protoconchs are badly damaged or broken away and no sculpture can be described for them. Usually the embryonic whorls remain relatively intact, however, still showing the characteristic sculpture of axial



Figs 1-5. Shell and opercula, Palau. 1-2, *Epidendrium sordidum* spec. nov.; 1, shell; 2, protoconch and teleoconch whorls T1-T3. 3-5, *Surrepifungium patamakanthini* spec. nov.; 3, operculum, the outside (white square: detail in Fig. 138); 4, operculum, the inside (white square: detail in Fig. 5); 5, operculum, detail of the inside. Scale bars: 1, 3, 4 = 1 mm; 2 = 0.5 mm; 5 = 0.1 mm. Abbrev.: ah, apertural height; F, foraminifer; PT, protoconch–teleoconch border; sh, shell height; sw, shell width; T3, teleoconch whorl 2¾ - 3¼; T3w, width of T3; T5, teleoconch whorl 4¾ - 5¼; V, vermetid shell. SEM photos.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lines. The initial teleoconch whorls are referred to as whorls 1-3. A quantitative description of the shell sculpture is given for the 2nd and the 5th teleoconch whorl and, whenever relevant, also for the 3rd.

When there are over 20 spiral threads on a whorl, they are referred to as 'numerous'.

Although an epitoniid operculum can have a micro-sculpture on both its inside (figs 4-5) and outside (figs 3, 132-151), not enough material was available to study both sides for all species. We concentrated on the outside, because it has turned out to be species-specific for at least some epitoniids (Bonfitto and Sabelli, 2001; A. Gittenberger, 2003). On all SEM photographs (figs 132-151) the growth lines, which are clearly seen in e.g. figure 132, run from the lower left to the upper right corner (fig. 3). The sculpture, which can be more or less obsolete, is the same all over the outside of the operculum.

Jaws and radulae were studied for most species. They were prepared from specimens with a shell height exceeding 5 mm.

Although the micro-sculpture on epitoniid jaws appears to be valuable for species identification, it has only rarely been described (A. Gittenberger, 2003). Jaws and/or radulae are here compared between 13 of the epitoniid species that are associated with Scleractinia, i.e. *Epidendrium aureum* spec. nov., *E. sordidum* spec. nov., *Epifungium adgravis* spec. nov., *E. hartogi* (A. Gittenberger, 2003), *E. hoeksemai* (A. Gittenberger and Goud, 2000), *E. lochi* (A. Gittenberger and Goud, 2000), *E. nielsi* spec. nov., *E. pseudotwilae* spec. nov., *E. ulu* (Pilsbry, 1921), *Surrepifungium costulatum* (Kiener, 1838), *S. ingridae* (A. Gittenberger and Goud, 2000), *S. oliverioi* (Bonfitto and Sabelli, 2001) and *S. patamakanthini* spec. nov., and 7 species that are associated with Actiniaria in the eastern Atlantic, i.e. *Gyroscala lamellosa* (Lamarck, 1822), *Epitonium clathrus* (Linnaeus, 1758) and *E. clathratulum* (Kanmacher, 1798), and the Indo-Pacific, i.e. *E. ancillottoi* T. and V. Cossignani, 1998, *E. pyramidalis* (Sowerby, 1844), *E.* spec. 1 and *Cirsotrema varicosa* (Lamarck, 1822). *Epitonium* spec. 1 occurs sympatrically with *E. ancillottoi* in Indonesia and resembles it very closely in conchology. It was added here to illustrate that jaw and radula characters are valuable for distinguishing epitoniids in general. *Epitonium* spec. 1 will be described as new to science in an article about wentletraps associated with Actiniaria (Kokshoorn *et al.*, in prep.). Some comparisons are made with the radular teeth of *Janthina janthina* (Linnaeus, 1758) (Gastropoda: Janthinidae) (fig. 16).

Two jaws flank the epitoniid radula (fig. 6). They are largely transparent, with a relatively smooth, lower edge and a whitish, denticulate, upper edge (figs 6-7, 10-12). These denticles can be acute, needle-like (figs 27-28), blunt (figs 25-26, 30-32) or lamellar (fig. 29). On the outside (figs 6-7: oj; figs 10-11), facing away from the radula, most denticles are somewhat convex (figs 25, 27, 30-31), while, on the inside (figs 6-7: ij; fig. 12), they are usually concave (fig. 26) to flat (fig. 32) and often pitted (figs 26, 32). On the outside, some denticles have a kind of buttress (figs 30-31: b) against an inner plate (figs 20-32: ip). Adjunct to the denticles, a pattern of arch-like (figs 17-19), pentagonal (figs 21-22), oval (fig. 20), square (fig. 32), or irregularly formed (figs 23-24) figures may be present. On the outer surface of the jaw, the centre of each figure is either raised (figs 17, 23) or sunken (figs 18-22) in comparison to its border. On the inner surface, the figures are engraved (figs 24, 32). On both sides pits (figs 21-24, 32) and holes (fig. 20) may be present. On the outside, just below the denticles, a jaw-flap may be present, which covers parts of the pattern (figs 11, 220, 226, 228-230, 234, 236-237, 240-244, 253-259: f). The pattern is revealed when this flap lies loose and is curved away, which is sometimes the case after SEM preparation (figs 219, 245, 250: f). Only then is the flap also visible from the inside (figs 249, 252-252: f). The denticles and figures are similar in size, parallel to the denticulate edge of the jaw, independent of the size of the snail (figs 243-244). Growth lines, which are rarely visible on the jaw (fig. 12: gl), indicate that growth proceeds in one direction, i.e. to the right in figure 12.

An epitoniid tooth is attached to the radular plate along its bases (figs 13-15: ba). The part of the tooth

Figs 6-12. Radulae and jaws. 6-7, *Surrepifungium patamakanthini* spec. nov., radula in between the largely transparent [no SEM] jaws, Thailand; 6, overview, lateral view; 7, detail. 8-9, radulae; 8, *Epifungium hartogi*; 9, *Cirsotrema varicosa*. 10-11, jaws, outer surface; 10, *C. varicosa*; 11, *Epifungium hoeksemai*. 12, jaw, inner surface, *Epitonium ancillottoi*. 8-12, Sulawesi, Indonesia. Abbrev.: de, denticulated jaw edge; f, flap; gl, growth lines; ij, inner surface of jaw; jf, jaw figures; oj, outer surface of jaw. Scale bars: 6, 10, 12 = 1 mm; 7-9, 11 = 0.1 mm. Photos: through binoc. (6) and with SEM (7-12).


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along the bases is called the stem, versus the part that is loose, the blade (figs 13-15: st, bl). A basal denticle is often present in between (figs 13-14: bd). Although the stem and the blade may be equally broad (fig. 13), the stem is usually more slender (fig. 15). Along the blade, which always ends with an apical cusp, secondary cusps may be present (figs 13-15: ac, sc). Split cusps (fig. 14: ssc) may be a malformation (fig. 209; A. Gittenberger, 2003), or a consistent character in a species (figs 14, 175). The length of a tooth is measured as the distance between the anterior end of the bases and the tip of the apical cusp (figs 13-15: tl).

Epitoniids have a ptenoglossan radula without a rachidian (Graham, 1965; Boss, 1982; Bandel, 1984; Page and Willan, 1988). No distinction can be made between marginal and lateral teeth. On an epitoniid radula the teeth may differ in size and number of secondary cusps. Half a row of teeth is described from the centre to the margin, by the number of teeth with a specific number of secondary cusps (table 2) and the sizes of the innermost, the largest, the penultimate and the ultimate (outermost) teeth (table 2). Additionally the position of the largest tooth is noted and a description is given of the morphology of the stem and the blade of a tooth (figs 13-15).

Because most of the epitoniids were conserved in alcohol 96%, the tissue of these specimens was hardened which hampered dissection and further anatomical analyses.

The egg-capsules were photographed and measured submerged in ethanol. Although the ethanol may extract water, no clear difference in egg-capsule height and width was found when comparing photographs in ethanol and in situ.

The mucus threads that connect the egg-capsules are indicated as either straight or twisted. While scoring this character, a single mucus-thread, about 0.5 mm long, in between two egg-capsules, should be studied at about 500×. In general, in a mucus thread that is considered to be 'straight', up to two twists per 0.5 mm may still be present. In contrast, in a 'twisted' mucus-thread, at least five, and usually many more, twists are present. Often two straight mucus threads were found twisted around each other, giving the appearance that they are twisted themselves. Apart from this, pulling on a twisted mucus thread may strongly reduce the number of twists.

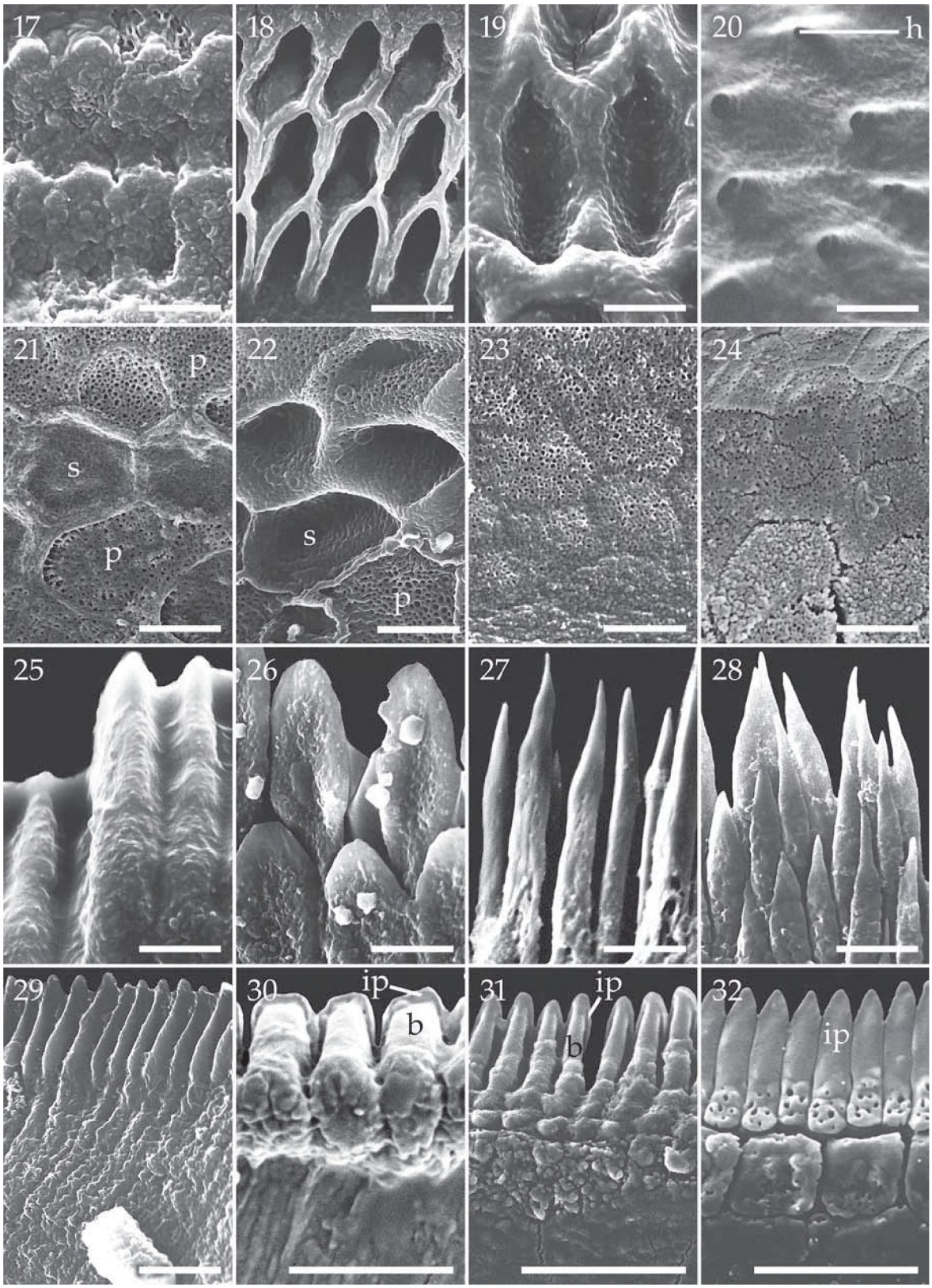
Figs 13-16. Radular teeth. 13, *Surrepifungium patamakanthini* spec. nov., Palau. 14-15, *Cirsotrema varicosa* (14) and *Epifungium adgravis* spec. nov. (15), Sulawesi, Indonesia. 16, *Janthina janthina*, South Africa. Abbrev.: ac, apical cusp; ba, bases; bl, blade; bd, basal denticle; sc, secondary cusps; ssc, split secondary cusp; st, stem; tl, tooth length. Scale bars: 13-15 = 0.01 mm; 16 = 0.1 mm. SEM photos.

In Makassar, SW Sulawesi, Indonesia and Koror, Palau, egg-capsules of the species *Epidendrium aureum* spec. nov., *Epifungium adgravis* spec. nov., *E. hartogi*, *E. hoeksemai*, *E. lochi*, *E. nielsi* spec. nov., *E. twilae* (A. Gittenberger and Goud, 2000), *E. ulu*, *Surrepifungium costulatum*, *S. ingridae and S. patamakanthini* spec. nov. were kept in an aquarium. Each day, some capsules were cut open in a drop of seawater on a glass-slide, in such a way that the embryos and/or veligers were alive during observations. The developmental stages were studied then through a microscope and photographed with a digital camera or filmed with a video camera. Part of the results of this experiment was already published in the species description of *E. hartogi* (A. Gittenberger, 2003: 147, fig. 42). The development of the other species will here be compared with that of *E. hartogi* as described by A. Gittenberger (2003). The results will be described in more detail in a note about the development of epitoniid veligers in general (A. Gittenberger and Reijnen, in prep.).

Each examined sample from the Leiden Museum is cited as RMNH, followed by the institutional registration number. After a slash the material in question is specified in more detail, using the abbreviations sh (number of empty shells), sn (preserved snails), +e (with egg-capsules), r (preserved radula), and d (with DNA-extract). For example "RMNH 95082/2sh, 3sn+e, r, 2d" refers to a sample with RNMH registration no. 95082, containing two empty shells, 3 snails with egg-capsules preserved in ethanol, one preserved radula and two DNA-extracts (of two snails). In the section Material, the type locality is listed first, followed by the countries and localities sorted by geological position, from West to East and from North to South. Because the material came from a variety of sources, not all the locality descriptions are equally detailed.

Unless stated otherwise, all specimens cited for the new species have to be considered paratypes.

In the text, the genera are dealt with in phylogenetic order, based on unpublished molecular (A. Gittenberger *et al.*, in prep.), or on conchological data when molecular data are absent, viz. first *Surrepifungium*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gen. nov., then *Epitonium* Röding, 1798, s.l., and finally *Epidendrium* gen. nov. and *Epifungium* gen. nov. The species are arranged alphabetically.

In general, the full (sub)genus name is used only for the first species name in a paragraph; in all following names with the same (sub)genus, it is abbreviated. When two genera with the same first letter are mentioned in one paragraph, the full name may be repeated to avoid confusion. The first time a snail species is mentioned and in the header of its description, the author(s) are added; most of these species are first mentioned in this materials and methods section. The author(s) of the coral species are only added in the "habitat" paragraphs.

Character states that are shared by all species of a genus, i.e. several "soft parts" and "spawn" characters, are only mentioned in the genus description.

Institutional abbreviations: AMS, Australian Museum, Sydney; ANSP, Academy of Natural Sciences, Philadelphia; BMNH, The Natural History Museum, London; CAS, California Academy of Sciences, San Francisco; MHNG, Muséum d'Histoire Naturelle, Genève; MZB, Zoological Museum of the University of Bologna, Italy; RMNH, National Museum of Natural History, Leiden (formerly Rijksmuseum van Natuurlijke Historie); WAM, Western Australian Museum, Perth.

Figs 17-32. Jaw patterns and denticle types. 17-23, patterns on jaw, outer surface; 17, raised arch figures; 18-19, sunken arch figures; 20, oval figures with hole (h); 21-22 sunken +/- pentagonal figures; 23, pitted, raised, irregular figures. 24, 32, patterns on jaw, inner surface; 24, pitted, engraved, irregular figures; 32, slightly pitted, engraved, square-like figures. 25-32, jaw denticle types; 25, 27, 29-31, jaw, outer surface; 25, 31, convex, blunt denticles; 27, acute, needle-like denticles; 29, lamellar denticles; 30, broad, blunt denticles. 26, 28, 32, jaw, inner surface; 26, two rows of concave, pitted, blunt denticles; 28, several rows of acute, needle-like denticles; 32, flat, basally pitted, slender, blunt denticles. 17, 18, 25, *Cirsotrema varicosa*. 19, 26, *Gyroscala lamellosa*. 20 *Epidendrium sordidum* spec. nov. 21, 24, 31-32, *Epifungium ulu*. 22, 29, *Epidendrium aureum* spec. nov. 23, *Epitonium ancillottoi*. 27-28, *Surrepifungium costulatum*. 30, *Epitonium* spec. 1. 17-18, 20-25, 27-32, Sulawesi, Indonesia; 19, 26, Canary Islands, Spain. Abbrev.: b, buttress; h, hole; p, pitted; s, smooth; ip, inner plate. Scale bar = 0.005 mm. SEM photos.

Systematics

Epitoniidae Berry, 1910

In general, shells of epitoniids that are associated with corals are fragile, i.e. most of the protoconchs, the apertures, and the costal ribs are badly damaged already in life. Shells in other epitoniid species are usually more strongly built.

Surrepifungium gen. nov.

Type species. *Epitonium ingridae* A. Gittenberger and Goud, 2000.

Other species. *Scala costulatum* Kiener, 1838; *Surrepifungium patamakanthini* spec. nov.; *Epitonium oliverioi* Bonfitto and Sabelli, 2001.

Shell (table 1). Initial teleoconch whorls with multiple, lamellate costae, which are either fused to form broader ribs, as in *Surrepifungium ingridae* and *S. patamakanthini* spec. nov. (figs 95-96, 98, 113-114, 116; A. Gittenberger and Goud, 2000: 8, figs 23-24), or single, as in *S. costulatum* and *S. oliverioi*. A spiral sculpture is discernible on the teleoconch, either on all the whorls or gradually becoming obsolete. The latter is the case in *S. costulatum* (fig. 112), *S. oliverioi* (fig. 115) and *S. patamakanthini* spec. nov. The shells are fragile and usually most of the costal ribs are badly damaged (figs 33-41).

Operculum. Nine to twenty wavy threads per 0.1 mm, running about perpendicular to the growth lines over the outside of the operculum (figs 136-139; Bonfitto and Sabelli, 2001: 271, fig. 2B). The threads are segmented by line fragments, which are convex towards the operculum edge.

Radula (table 2). All single teeth have a distinct basal denticle, an acute apical cusp and occasionally an inconspicuous, secondary cusp (figs 184-188, 204-208). The teeth in a row differ distinctly only in size.

Jaw (table 2). The denticulate edge consists of several rows of acute, slender, pitted denticles, best visible from inside (figs 27, 28, 226-235). Usually

Table 1. Shell dimensions and number of costal and spiral ribs on the teleoconch. The extremes and the mean value are followed by a semicolon and the number (n) of specimens when n >1. Abbrev.: A/H, apertural height / shell height; C2, C3, C5, number of costal ribs on teleoconch whorls two, three and five; H/W, shell height/width index; obs., number of specimens in which costal or spiral ribs are obsolete; num., number of specimens in which costal or spiral ribs are numerous (>20); S2, S3, S5, number of spiral ribs on teleoconch whorls two, three and five; T3, width of teleoconch whorl 2¾ - 3¼ in mm.

Species	H/W; n	T3; n	A/H; n	C 2; n	S 2; n	C 3; n	S 3; n	C 5; n	S5; n
Surrepifungium costulatum	1.6-2.2	?	0.28-0.33	16-20	5-8	?	?	16-26	10 obs.
	1.9; 11		0.29; 10	17.7; 10	6.3; 10			18.3; 10	
Surrepifungium ingridae	1.9-2.7	?	0.29-0.31	15-19	7-9	?	?	20-31	10-16
	2.2; 10		0.31; 10	16.5; 10	8.2; 10			24.6; 10	13.1; 10
Surrepifungium patamakanthini	1.8-2.8	?	0.24-0.35	13-20	5-9	?	?	13-20	7-11
	2.3; 22		0.28; 21	15.8; 23	6.1; 19			16.1; 23	8.2; 17
Surrepifungium oliverioi	1.6-2.0	?	0.30-0.39	14-16	4-7	?	?	14-16	10 obs.
	1.8; 10		0.35; 10	14.9; 10	5.9; 10			14.9; 10	
Epitonium crassicostatum	2.2	?	0.27	11	obs.	11	17	11	17
Epitonium graviarmatum	1.7	?	0.40	8	obs.	8	obs.	8	obs.
Epidendrium aureum	1.3-2.0	?	0.31-0.44	35-50	6-9	40-63	7-9	57-93	8-12
	1.6; 18		0.38; 17	39.8; 11	7.1; 12	47.5; 13	7.7; 12	70.0; 13	9.9; 12
Epidendrium billeeanum	1.5-1.7	?	0.34-0.44	25-41	6-6	31-49	6-8	42-64	6-10
	1.6; 5		0.39; 5	30.8; 4	6; 4	36.0; 4	7; 4	55.5; 4	8.3; 4
Epidendrium dendrophylliae	1.8	?	0.35	20	5	20	7	19	12
Epidendrium sordidum	1.1-1.8	?	0.32-0.49	25-36	4-7	29-43	5-7	30-74	7-9
	1.3; 17		0.41; 17	31.5; 13	5.9; 14	33.4; 13	6.9; 14	46.3; 14	8.5; 15
Epifungium adgranulosa	2.0-3.2	0.63-0.80	0.23-0.33	18-31	2-8	19-32	4-10	18-32	6-17
	2.5; 27	0.71; 36	0.28; 19	23.0; 33	5.8; 13	24.1; 33	7.4; 17	25.2; 33	11.5; 25
Epifungium adgravis	2.3-3.0	0.77-0.92	0.23-0.30	23-29	4-6	23-32	5-10	22-31	5-12
	2.7; 14	0.83; 21	0.27; 10	24.8; 18	5.2; 13	25.6; 19	6.4; 13	25.4; 19	8.9; 15
Epifungium adscabra	1.9-2.3	0.66-0.75	0.25-0.37	16-22	5-5	16-25	5-10	17-26	7-19
	2.0; 14	0.70; 11	0.31; 12	19.2; 10	5.0; 9	19.5; 10	6.8; 6	20.2; 9	11.0; 7
					2 obs.		5 obs.		2 obs.
									1 num.
Epifungium hartogi	1.4-1.8	?	0.34-0.43	20-26	9-12	?	?	32-40	29-40
	1.6; 13		0.38; 10	22.8; 23	10.3; 22			37.3; 8	34.3; 12
Epifungium hoeksemai	1.6-2.4	0.63-0.83	0.27-0.38	21-30	5-9	23-32	6-13	27-47	12-26
	2.0; 25	0.74; 18	0.31; 15	24.7; 18	6.9; 17	26.7; 18	8.9; 18	32.7; 18	17.0; 18
Epifungium lochi	2.3-3.1	0.71-0.78	0.23-0.37	20-29	5-9	20-29	6-11	21-35	8-15
	2.7; 9	0.74; 9	0.27; 9	23.1; 9	6.9; 9	24.6; 9	8.0; 9	26.3; 9	11.0; 9
Epifungium marki	2.4-2.9	0.81-0.82	0.25-0.32	23-23	5-6	23-25	6-6	23-31	7-8
	2.7; 4	0.82; 4	0.28; 4	23.0; 4	5.3; 4	24.0; 4	6; 4	26.0; 4	7.8; 4
Epifungium nielsi	2.0-3.1	0.65-0.82	0.22-0.34	16-28	4-7	23-34	6-10	17-39	6-17
	2.5; 26	0.73; 37	0.25; 15	22.0; 36	5.8; 22	23.8; 35	7.7; 27	25.6; 35	11.0; 30
Epifungium pseudolochi	2.4-3.0	0.71-0.74	0.25-0.27	23-24	6-6	24-25	8-9	26-27	10-10
	2.7; 2	0.73; 2	0.26; 2	23.5; 2	6; 2	24.5; 2	8.5; 2	26.5; 2	10; 2
Epifungium pseudotwilae	1.2-2.2	0.83-1.03	0.34-0.65	17-23	5-6	18-24	10 obs.	22-39	10 obs.
	1.3; 19	0.91; 15	0.38; 12	19.9; 19	5.5; 2	22.1; 19		29.7; 19	
					8 obs.				
Epifungium twilae	1.0-1.7	0.91-1.14	0.33-0.59	22-30	5-6	24-30	12 obs.	26-57	12 obs
	1.4; 18	0.97; 15	0.42; 15	25.6; 14	5.5; 2	26.5; 14		39.3; 14	
					10 obs.				
Epifungium ulu	1.7-3.3	0.62-0.78	0.21-0.36	17-26	3-8	17-27	3-8	17-27	5-8
	2.3; 26	0.69; 23	0.27; 20	20.1; 24	4.0; 10	20.7; 24	4.9; 15	21.0; 23	5.9; 19
					14 obs.		9 obs.		5 obs.

Table 2. Radula and jaw. Half a radular row is described from the innermost to the outermost tooth. The lengths of the smallest, largest, penultimate and ultimate tooth are given in mm; the position of the largest tooth is indicated between brackets. The Radular formula N/s indicates the number of teeth (N) with s secondary cusps. Abbrev.: Loc., Locality; SH, shell height in mm; d/.05, denticles per 0.05 mm; Max d, maximum denticle size in mm; Fl W, maximum flap width in mm. Localities: Bali = Bali, Indonesia; Berau = Berau islands, Kalimantan, Indonesia; Mald = Vilamendhoo island, Ari Atoll, Maldives; Palau = Koror, Palau; Phil = Cebu, Philippines; S Sul = Spermonde archipelago, Sulawesi, Indonesia; Thai = Phiphi Islands, Krabi, Thailand. Hosts: Ccra, *Ctenactis crassa*; Cech, *C. echinata*; Den, Dendrophyllidae; Fcon, *Fungia concinna*, Ffun, *F. fungites*; Fgra, *F. gravis*; Fhor, *F. horrida*; Frep, *F. repanda*; Fpau, *F. paumotensis*; Fscu, *F. scutaria*; Hlim, *H. limax*, Psim, *P. simplex*; Sden, *S. dentata*; Srob, *S. robusta*.

Specimen				Radula		Jaw		
Species	Loc.	Host	SH	Teeth lengths (mm)	Radular formula	d/.05	Max d	Fl W
Surrepifungium costulatum	Palau	Cech	26.1	0.030 0.195(20) 0.195 0.120	1/1 18/0 1/1 1/0	14	0.020	0.019
	S Sul	Cech	31.6	0.065 0.130(7) 0.108 0.082	1/1 22/0	14	0.030	0.020
Surrepifungium ingridae	Palau	Frep	20.4	0.021 0.142(14) 0.092 0.061	2/1 17/0 2/1	19	0.022	0.040
	S Sul	Srob	18.3	0.016 0.124(13) 0.085 0.062	2/1 16/0 2/1	20	0.021	0.052
Surrepifungium oliverioi	Palau	Hlim	10.0	0.030 0.135(17) 0.135 0.053	1/1 17/0	?	?	?
	Palau	Hlim	17.1	0.033 0.190(19) 0.190 0.175	1/1 21/0	?	?	?
	Mald	Hlim	18.1	0.049 0.227(18) 0.227 0.169	1/1 18/0	16	0.008	0.012
Surrepifungium patamakanthini	Palau	Ffun	19.0	0.030 0.150(11) 0.150 0.102	1/1 11/0	17	0.022	0.020
	Palau	Ccra	23.0	0.037 0.171(11) 0.171 0.126	1/1 11/0	16	0.022	?
	Mald	Fhor	20.6	0.032 0.155(12) 0.153 0.155	1/1 11/0	18	0.020	?
Epidendrium aureum	Thai	Den	14.5	0.031 0.119(21) 0.062 0.042	1/1 29/0	46	0.0048	?
	S Sul	Den	11.8	0.021 0.127(13) 0.095 0.086	1/1 29/0	38	0.0070	0.026
	S Sul	Den	12.3	0.030 0.143(22) 0.084 0.061	1/1 33/0	?	?	0.026
Epidendrium sordidum	S Sul	Den	16.0	0.041 0.108(46) 0.076 0.074	1/1 1/2 3/3 7/4 9/5 4/6 1/9 2/7 … 8/5 9/4 3/5 2/3 (59 teeth in total)	30	0.0063	0.0163
	Phil	Den	13.1	?	At least 55 teeth	31	0.0080	0.0189
	S Sul	Den	12.0	0.044 ? ? ?	At least 50 teeth, max. 9 sec. cusps / tooth			
Epifungium nielsi	Berau	Fpau	14.0	0.035 0.056(12) 0.048 0.037	1/1 1/2 2/3 5/4 1/5 2/6 6/5 1/4 1/1	71	0.0030	0.0142
Epifungium adgravis	Bali	Fgra	12.4	0.020 0.042(10) 0.036 0.022	1/1 2/3 2/4 4/5 1/6 2/4 1/2 1/1	?	?	?
	S Sul	Fgra	10.0	?	?	56	0.0033	0.010
Epifungium hoeksemai	Palau	Ffun	11.5	0.018 0.027(18) 0.027 0.022	1/1 9/2 1/3 8/2	58	0.0032	0.0120
	Palau	Ffun	12.4	0.018 0.028(17) 0.028 0.025	1/1 17/2	64	0.0030	0.0074
Epifungium lochi	S Sul	Fcos	9.3	0.018 0.034(8) 0.034 0.028	3/2 2/3 4/4 1/5 1/4 1/3	72	0.0018	0.0060
Epifungium ulu	S Sul	Fscu	9.1	0.029 0.049(7) 0.038 0.028	1/2 2/3 8/4 1/3 3/2	?	?	?
	S Sul	Fscu	10.0	0.028 0.050(8) 0.039 0.028	1/2 3/3 9/4 1/5 1/3	65	?	?
	S Sul	Frep	14.0	?	?	58	0.0042	0.0131
	Bali	Ffun	28.2	?	?	50	0.0038	0.0135
Epifungium pseudotwilae	Bali	Sden	13.2	0.029 0.041(5) 0.032 0.028	2/2 1/3 2/4 1/3 1/2 4/3	?	?	?
Epifungium hartogi	S Sul	Psim	5.4	0.022 0.047(24) 0.047 0.040	1/1 4/2 7/3 7/4 4/5 1/6 1/2	65	0.0035	0.018

no particular structure is visible on the inner surface (figs 228-235), but rarely there is a vague, irregular pattern (figs 227-232). On the outer surface, along the line where the jaw-flap merges with the jaw, a pattern of sunken figures (resembling figs 21-22), which are usually pentagonal and pitted, is present (figs 226, 228, 230-231, 234); underneath this line, the pattern is vague or obsolete.

Soft parts. The animal is whitish, with small, dark eyespots.

Spawn. Egg-capsules irregular pentagonal, drop-shaped, and covered with coral-sand grains. A straight mucus thread, finely sculptured with longitudinal lines, connects the capsules along their bases (on the left in figs 264, 266, 268, 270). When veligers hatch, an egg-capsule breaks open at the apical side (on the right in figs 264, 266, 268, 270). The uncleaved eggs are 0.077 mm (n = 10 per species) in diameter. The development from eggs to veligers in the egg-capsules of *Surrepifungium costulatum*, *S. ingridae* and *S. patamakanthini* spec. nov. resembles that described for *Epifungium hartogi* by A. Gittenberger (2003: 147, fig. 42); no data are available for *S. oliverioi*.

Habitat. The snails live at the surface of the sand or buried within it, underneath fungiid corals (Fungiidae). They were never found on the corals themselves. In contrast, snails belonging to *Epifungium* gen. nov. were seen nearby, but crawling on the coral surface.

Etymology. *Surrepifungium* is composed after "*surrepi*", Latin for "to creep or crawl up from below", and "*fungium*", referring to the coral host family "Fungiidae". The name can also be read as "*surr*", a wrong inflection of "sub", standing for "below" and "*epifungium*", after *Epifungium* gen. nov. The gender is neuter, i.e. with the ending "ium".

Differentiation. No shell characters are consistently present in *Surrepifungium* gen. nov. spp., which can distinguish them from all species in *Epitonium* and *Epifungium* gen. nov. The fused, lamellate costae and the fading spiral sculpture are both characteristic, but not present in all *Surrepifungium* gen. nov. species. Most epitoniids of other genera have spiral sculpture on all teleoconch whorls and do not have fused, lamellate costae.

A similar operculum sculpture of wavy threads, running about perpendicular to the growth lines, is present in *Epifungium* gen. nov. (figs 140-151). In that genus, however, twenty to forty threads per 0.1 mm are present instead of nine to twenty in *Surrepifungium* gen. nov. In *Epidendrium aureum* spec. nov. (figs 132-133), *E. sordidum* spec. nov. (fig. 134) and *Epitonium pyramidalis* (fig. 135), no operculum sculpture is present, except for the growth lines. The operculum sculpture of other epitoniids is unknown.

In several species of other epitoniid genera, similar teeth with a distinct basal denticle, an acute apical cusp and occasionally an inconspicuous, secondary cusp are present, viz. in *Acirsa subdecussata* (Cantraine, 1835) (in Bouchet and Warén, 1986: 470, fig. 1098), *Cirsotrema varicosa* (figs 152, 195), *Epidendrium aureum* spec. nov. (figs 160-161, 183, 203), *Epitonium celesti* (in Bouchet and Warén, 1986: 470, fig. 1099), *E. clathrus* (fig. 156) and *E. pyramidalis* (figs 157, 180, 200). Even in *Janthina janthina* (fig. 16) (Janthinoidea Lamarck, 1810 [= Epitoniacea Berry, 1910], Janthinidae) similar teeth occur, but these can be about twenty times larger than the largest ones found in *Surrepifungium* gen. nov.

The structure of the jaws appears to be most clearly diagnostic for the genus. In *Epitonium ancillottoi* and *E.* spec. 1 (figs 30, 219-222), which both resemble *Surrepifungium ingridae* conchologically, and in epitoniids of *Epifungium* gen. nov. (figs 243-263), which are associated with the same coral host species as the *Surrepifungium* gen. nov. species, there is only a single row of blunt denticles on the jaw-edge instead of several rows of acute ones. In *Cirsotrema varicosa* and *Gyroscala lamellosa* (figs 215-217), which differ clearly by their strong shells with a rough surface, there are multiple rows of denticles. These two species closely resemble each other in jaw structure, differing from the *Surrepifungium* gen. nov. species by relatively blunt denticles, no jaw-flap and a distinct, outside jaw-pattern with arch-like, raised and sunken figures (figs 17-19, 215-216).

Instead of the drop-shaped egg-capsules known from *Surrepifungium* gen. nov., most epitoniids have oval to roundish ones. *Epitonium clathrus* (L., 1758), a sea-anemone-eating, Atlantic epitoniid, also has drop-like capsules (Vestergaard, 1935). These egg-capsules however, are triangular instead of pentagonal. *Epitonium clathrus* further differs from *Surrepifun-*

gium gen. nov. species by its strong shell and ribs, and always has some radular teeth with more than one secondary cusp (figs 156, 179, 199).

The habitat is partly shared with several *Epifungium* gen. nov. species, which occasionally occur on the bottom underneath fungiids. When they were found together (n = 24), the snails of *Epifungium* gen. nov. were on the coral and those of *Surrepifungium* gen. nov. on or in the sand underneath. This is more likely due to a dislike of sand by the snails of *Epifungium* gen. nov., than due to interspecific competition (A. Gittenberger and Hoeksema, in prep.). The habitat seems not to be shared with any other epitoniids.

Surrepifungium costulatum (Kiener, 1838)

Scalaria costulatum Kiener, 1838: 5, pl. 2 fig. 4.
Epitonium costulatum (Kiener, 1838); Robertson, 1963: 57, pl. 5 fig. 4; 1970: 45; Loch, 1982: 4, 1 fig.; Dushane, 1988a: 31, figs 1, 2; A. Gittenberger *et al.*, 2000: 3, 4, figs 3-6, 22, 25, 38-41, 47.

Material. Holotype: MHNG 1152/16. MALDIVES. Ari Atoll, off Vilamendhoo Island (hosted by *Herpolitha limax*), 2sn/sh+e, d. THAILAND. Krabi, Phiphi Islands (hosted by *Ctenactis echinata, H. limax, Fungia (Fungia) fungites*), 26sn/sh+12e, 5d. INDONESIA. SW Sulawesi, Spermonde archipelago (hosted by *C. echinata, H. limax*), 31sn/sh+11e, 7d, 2r. Bali (hosted by *C. echinata, H. limax, Sandalolitha dentata, S. robusta*), 16sn/sh+4e. Ambon (hosted by *C. echinata*), 1sn/sh, d. PALAU. Off Koror (hosted by *Ctenactis albitentaculata, C. crassa, C. echinata, H. limax, S. robusta*), 53sn/sh+23e, 10d.

Type locality. Unknown.

Shell (figs 34-35, 94, 112; table 1). Most shells are coiled relatively tightly (figs 34-35), but some are almost completely scalaroid as in *Surrepifungium oliverioi* (figs 36-37). For dimensions and number of costal and spiral ribs on the 2nd and the 5th teleoconch whorls, see table 1. A new maximum shell height of 44 mm was recorded in a sample collected off SW Sulawesi, Indonesia. The protoconch (fig. 94) has 3¼-3½ whorls (n = 10); apart from its smooth apical part, it is sculptured with regularly spaced, very fine, incised, axial lines, 21-24 (mean = 22.5, n = 2) per 0.2 mm on protoconch whorl 2¼-2¾. A. Gittenberger *et al.* (2000) reported very weak spiral lines on the teleoconch whorls. Such spiral lines are distinct on the 1st and 2nd teleoconch whorl (fig. 94) only, usually becoming obsolete from the 4th whorl onwards (n = 20); they are not discernible on the 5th whorl (fig. 112).

Operculum (fig. 136). Operculum paucispiral, with interconnected coils as in *Surrepifungium patamakanthini* spec. nov. (fig. 3). At the outside of the operculum there are 16 wavy threads per 0.1 mm (n = 2), running about perpendicular to the growth lines. These threads are divided into segments, which are convex towards the operculum edge.

Radula (figs 163-164, 184-185, 204-205; table 2). Two radular types were found in *Surrepifungium costulatum*. One in a specimen from Indonesia, (type 1) and the other one in a specimen from Palau (type 2). These two snails were found underneath the same coral species, i.e. *Ctenactis echinata* (Pallas, 1766), and their shells are indistinguishable. In both types the stem and the blade of each tooth are similar in width and merge gradually.

In type 1 (fig. 163), the innermost tooth (fig. 185, left) and the penultimate one (fig. 205) both have an inconspicuous, blunt, secondary cusp, which is absent in all other teeth. Starting from the innermost, smallest tooth, with a height of 0.065 mm, the teeth gradually increase in size to twice that height, i.e. 0.130 mm, up to the 7th tooth, after which they gradually become smaller again until the ultimate, i.e. 23rd tooth, which is 0.082 mm high (table 2). All teeth are attached to the radular plate along the bases up to the basal denticle.

In type 2 (fig. 164), the innermost tooth (fig. 184, left) has an inconspicuous, blunt, secondary cusp, which is absent in all other teeth. Starting from the innermost, smallest tooth, with a height of 0.030 mm, the teeth gradually become elongated and very slender, increasing in size to almost seven times that height, i.e. 0.195 mm, up to the penultimate tooth (fig. 204). After that the smaller, usually malformed, 0.120 mm high 21st tooth follows (table 2). In some of the largest teeth, the bases of the stem become partly detached from the radular plate, just below the basal denticle.

Jaw (figs 226-227; table 2). The jaws associated with both the radular types are similar. The denticulate edge consists of three or four irregular rows of basally pitted, slender, acute denticles, best visible from the inside of the jaw (fig. 227). The denticles in the

Figs 33-37. Shells. 33, 36-37, *Surrepifungium oliverioi*; 33, "*Epitonium oliverioi*", paratype, Madagascar; 36, Egypt; 37, Thailand. 34-35, *S. costulatum* (Kiener, 1838), Palau. Scale bar = 1 cm.

Figs 38-41. Shells. 38-39, *Surrepifungium patamakanthini* spec. nov.; 38, paratype, Maldives; 39, holotype, Palau. 40-41, *S. ingridae*, Palau. Scale bar = 1 cm. ▶


38
39
40
41

upper row are usually the largest ones, i.e. 0.020-0.030 mm (n = 2) in height. Seen from the outside (fig. 226), 14-14 denticles per 0.05 mm (n = 2) extend above a 0.019-0.020 mm (n = 2) broad, relatively smooth to slightly granulated jaw-flap, which merges with the jaw along a zone with a distinct pattern of deeply sunken, pitted, irregular to pentagonal figures. Underneath the jaw-flap, a pattern of irregular to pentagonal figures quickly becomes obsolete. On the inner surface (fig. 227) no pattern is present.

Spawn (figs 264-265). The irregularly pentagonal, drop-shaped egg-capsules are covered with sand. They are 5.0–6.1 mm (mean = 5.3, n = 20) in diameter, e.g. measured horizontally, from left to right in figure 264, and contain 70-345 eggs (mean = 180, n = 10). A straight mucus thread (fig. 265), finely sculptured with longitudinal lines, connects the egg-capsules along their bases (on the left in fig. 264).

Habitat. The snails and their egg-capsules were found at 3-38 m, associated with *Ctenactis albitentaculata* Hoeksema, 1989, *C. crassa* (Dana, 1797), *C. echinata* (Pallas, 1766), *Herpolitha limax* (Esper, 1797), *Sandalolitha robusta* (Quelch, 1886) and *S. dentata* Quelch, 1884. These mushroom coral species occur both on sand and on a more solid substratum, but the snails with the egg-capsules were found on or in the sand (sometimes buried) only.

Distribution (fig. 42). The species is known from the Indo-West Pacific, from Egypt (Red Sea), Maldives, Thailand, Palau and Indonesia to NE Australia. The authors studied material from various localities (fig. 42), relying on data from the literature for the records from the Red Sea (Dushane, 1988a: 30-32), Philippines (Robertson, 1963: 57-58) and Australia (Loch, 1982: 4).

Differentiation. Shells of this species most closely resemble those of *Surrepifungium oliverioi* (Bonfitto and Sabelli, 2001) and *S. patamakanthini* spec. nov. See the differentiation of those species for details.

Remarks. For a photograph of the holotype, a more detailed description of the shell and the proboscis, and a comparison with *Epitonium pallasii* (Kiener, 1838), see A. Gittenberger *et al.* (2000). Here some additional data are given, with notes that may be relevant for the differentiation of this species. See also the remarks on *S. oliverioi*.

Surrepifungium ingridae (A. Gittenberger and Goud, 2000)

Epitonium ingridae A. Gittenberger and Goud, 2000: 7, 8, figs 7-8, 23-24, 27, 30.

Material. INDONESIA (hosted by *Ctenactis echinata*, *Fungia* (*Fungia*) *fungites*, *F.* (*Verrillofungia*) *repanda*, *Sandalolitha robusta*). SW Sulawesi, Spermonde archipelago, holotype (hosted by *F.* (*F.*) *fungites*): RMNH 59088, 6 paratypes+5e: RMNH 59090-59093, 11sn/sh+5e, 4d, 2r. MALAYSIA. East Malaysian peninsula, Tioman and Perhentian islands (hosted by *F.* (*F.*) *fungites*, *S. robusta*), 10sn/sh+3e, 5d. PALAU. Off Koror (hosted by *Ctenactis albitentaculata*, *C. crassa*, *C. echinata*, *F.* (*F.*) *fungites*, *F.* (*V.*) *repanda*, *S. robusta*), 40sn/sh+19e, 10d.

Type locality. INDONESIA. SW Sulawesi, Spermonde archipelago.

Shell (figs 40-41, 95, 113). Shell shapes vary between broad and relatively slender conical (figs 40-41; shell height/width index in table 1). For dimensions and number of costal and spiral ribs on the 2nd and the 5th teleoconch whorls, see table 1. A new maximum shell height of 27 mm (fig. 40) was recorded in a sample collected off Koror, Palau. The protoconch (fig. 95) has 2¾-3 whorls (n = 10); apart from its smooth apical part, it is sculptured with regularly spaced, very fine, incised, axial lines, 25-26 (mean = 25.3, n = 3) per 0.2 mm on protoconch whorl 1¾-2¼.

Operculum (fig. 137). Operculum paucispiral, with interconnected coils as in *Surrepifungium patamakanthini* spec. nov. (fig. 3). At the outside of the operculum there are 14-16 wavy threads per 0.1 mm (mean = 15.0, n = 4), running about perpendicular to the growth lines. These threads are divided into segments, which are convex towards the operculum edge.

Radula (figs 166, 186, 206, table 2). Two radulae could be studied (table 2). The stem and the blade of each tooth are similar in width and merge gradually. All teeth (fig. 166) are attached to the radular plate along the bases up to the basal denticle. The two innermost teeth (fig. 186) and the two outermost ones

(fig. 206) usually have an inconspicuous, acute to blunt, secondary cusp each, which is absent in all other teeth. Starting from the innermost, smallest tooth, with a height of 0.016-0.021 mm (n = 2), the teeth gradually increase in size to about seven times that height, i.e. 0.124-0.142 mm (n = 2), up to the 13th-14th tooth, after which they gradually become smaller again until the ultimate, i.e. 20th-21st tooth, which is 0.061-0.062 mm (n = 2) high (table 2).

Jaw (figs 228-230; table 2). The denticulate edge consists of three to five irregular rows of basally pitted, slender, acute denticles, best visible from the inside of the jaw (figs 228-229). The denticles in the upper row are usually the largest ones, i.e. 0.021-0.022 mm (n = 2) in height. Seen from the outside (figs 228-230), 19-20 denticles per 0.05 mm (n = 2) extend above a 0.040-0.052 mm (n = 2) broad, relatively smooth (fig. 228) to vaguely vertically sculptured (fig. 230) jaw-flap, which merges with the jaw along a zone with a distinct pattern of deeply sunken, pitted, irregular to pentagonal figures. Underneath the jaw-flap, a pattern of sunken, pentagonal figures gradually becomes obsolete (figs 228-229). On the inner surface (fig. 228) no pattern is present.

Spawn (figs 266-267). The irregularly pentagonal, drop-shaped egg-capsules are covered with sand. They are 3.4-3.9 mm (mean = 3.6 mm, n = 20) in diameter, e.g. measured horizontally, from left to right in figure 266, and contain 93-173 eggs (mean = 120, n = 8). A straight mucus thread (fig. 267), finely sculptured with longitudinal lines, connects the egg-capsules along their bases (on the left in fig. 266).

Habitat. The snails and their egg-capsules were found at 1-26 m, associated with *Ctenactis albitentaculata* Hoeksema, 1989, *C. crassa* (Dana, 1797), *C. echinata* (Pallas, 1766), *Fungia* (*Fungia*) *fungites* (Linnaeus, 1758), *F.* (*Verrillofungia*) *repanda* Dana, 1846, *Heliofungia actiniformis* (Quoy and Gaimard, 1833), *Sandalolitha robusta* (Quelch, 1886). One dead specimen was found underneath *Polyphyllia talpina* (Lamarck, 1801). These mushroom coral species occur both on sand and on a more solid substratum, but the snails with the egg-capsules were found on or in the sand (sometimes buried) only.

Distribution (fig. 43). The species is known from the West Pacific, from the west of Peninsula Malaysia and Indonesia to Palau.

Differentiation. Shells of this species most closely resemble those of *Surrepifungium patamakanthini* spec. nov. They differ most clearly in having 20-31 (mean = 24, n = 5) costal ribs on the 5th teleoconch whorl instead of 13-20 (mean = 16.1, n = 23), and by a radula with more than 19, instead of 12 teeth in half a row. For comparisons with the epitoniid species *Epitonium dubium* Sowerby, 1844, *E. friabilis* (Sowerby, 1844), *Scalaria grayi* Nyst, 1871 and *Foliaceiscala barissa* Iredale, 1936, see A. Gittenberger *et al.* (2000).

Remarks. For a more detailed description of the shell and the proboscis, see A. Gittenberger *et al.* (2000). Here some additional data are given, with notes that may be relevant for the differentiation of this species.

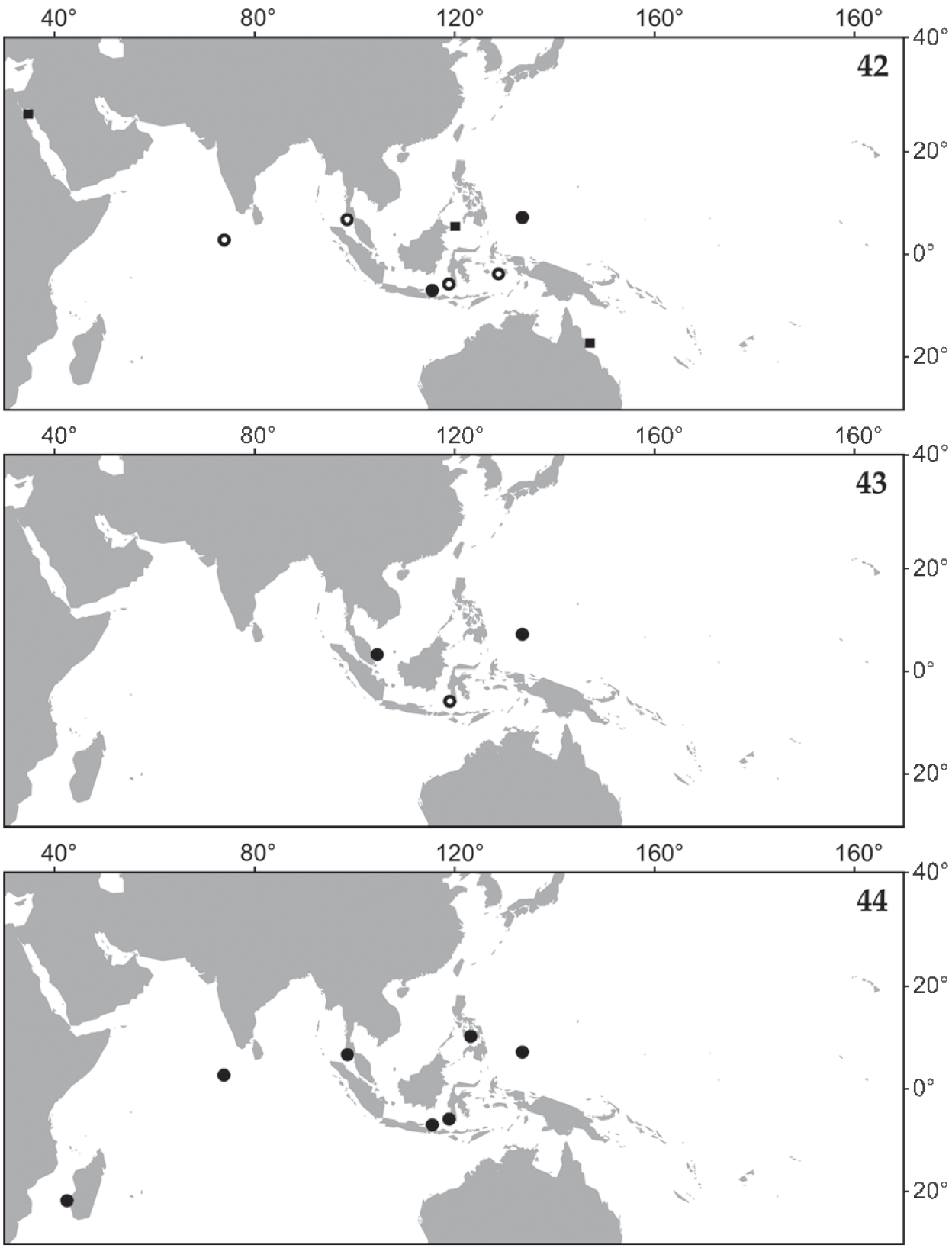
Surrepifungium oliverioi (Bonfitto and Sabelli, 2001)

Epitonium oliverioi Bonfitto and Sabelli, 2001: 269.

Material. EGYPT. Red Sea, 350 km S of Hurghada (hosted by *Herpolitha limax*), 9sn+e, 2d. MADAGASCAR. Nosy Vé Island (hosted by *Fungia* cf (*Verrillofungia*) *repanda*), 3 paratypes: MZB 14026-14027 + "Paratype 4" as in Bonfitto and Sabelli (2001: 270) MALDIVES. Ari Atoll, off Vilamendhoo Island (hosted by *H. limax*), 2sh, 1sn+e, o, 2d. THAILAND. Krabi, Phiphi Islands (hosted by *H. limax*), 1sn+e. INDONESIA. Bali (hosted by *Fungia* (*Fungia*) *fungites*), 1sn+e. PALAU. Off Koror (hosted by *S. robusta* and *H. limax*), 8sn+3e.

Type locality. MADAGASCAR. Nosy Vé Island.

Shell (figs 33, 36-37, 49, 97, 115). Most shells are almost scalaroid (figs 36-37), but some are coiled relatively tightly (fig. 33) as in *Surrepifungium costulatum* (figs 34-35). For dimensions and number of costal and spiral ribs on the 2nd and the 5th teleoconch whorls, see table 1. A new maximum shell height of 20.1 mm was recorded in a sample collected off Koror, Palau. The protoconch (fig. 97) has 3¼-3½ whorls (n = 10); apart from its smooth apical part, it is sculptured with regularly spaced, very fine, incised, axial lines, 25 (n = 1) per 0.2 mm on protoconch


40°
80°
120°
160°
160°
40°
20°
0°
20°
42
43
44

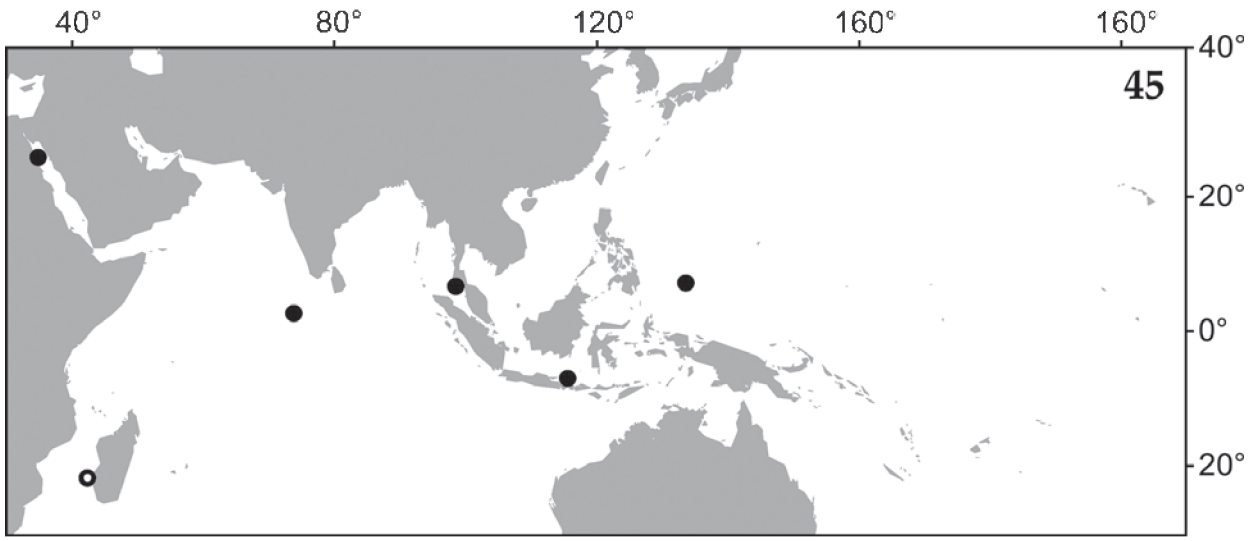


Fig. 45. The Indo-Pacific region, from the Red Sea to the Hawaiian archipelago, with the range of *Surrepifungium oliverioi*. New records (dots) and personally studied material (circles).

whorl 2¼-2¾. The teleoconch has up to 9¼ whorls, separated by a very deep suture, sometimes scalaroid from about the 7th teleoconch whorl onwards; it is sculptured with mostly regularly placed, orthocline, lamellar, moderately high costae, which are usually continuous on the first six teleoconch whorls only. Although damaged costae may seem somewhat coronate (fig. 115), clearly undamaged ones do not have a coronation (fig. 49). Most costae were badly broken in all specimens studied. The teleoconch is additionally sculptured with very low, inconspicuous, regularly spaced, spiral threads on the initial whorls (fig. 97), becoming obsolete from about the 4th teleoconch whorl onwards (fig. 115). Aperture subcircular. There is a distinct umbilicus.

Operculum (fig. 139). Operculum paucispiral, with interconnected coils as in *Surrepifungium patamakanthini* spec. nov. (fig. 3). At the outside of the operculum there are 20 wavy threads per 0.1 mm (n = 1), running about perpendicular to the growth lines. These threads are divided into segments, which are convex towards the operculum edge.

Figs 42-44. The Indo-Pacific region, from the Red Sea to the Hawaiian archipelago, illustrating *Surrepifungium* species ranges. New records (dots) and previously published records (squares = based on photographs only; circles = personally studied material); 42, *Surrepifungium costulatum*; 43, *S. ingridae*; 44, *S. patamakanthini* spec. nov.

Radula (figs 165, 188, 208; table 2). Three radulae could be studied, i.e. of a female (found while laying egg-capsules) and a probable male snail (smaller individual found together with this female) from Palau, and a female from the Maldives. The stem and the blade of each tooth are similar in width and merge gradually. The innermost tooth (fig. 188, left) has an inconspicuous, blunt, secondary cusp, which is absent in all other teeth. Starting from the innermost, smallest tooth, with a height of 0.030-0.049 mm (mean = 0.037, n = 3), the teeth gradually become elongated and very slender, increasing in size to about five times that height, i.e. 0.135-0.227 mm (mean = 0.184, n = 3), up to usually the penultimate tooth (fig. 208). After that the smaller, usually malformed, ultimate, 0.053-0.175 mm high 18th-22nd tooth follows (table 2). In some of the largest teeth, the bases of the stem become partly detached from the radular plate, just below the basal denticle.

Jaw (figs 234-235; table 2). Only one pair of jaws was studied (table 2). The denticulate edge consists of two or three rows of basally scarcely pitted, slender, somewhat drop-shaped, acute denticles, best visible from the inside of the jaw (fig. 235). The denticles in the upper row are usually the largest ones, i.e. up to 0.008 mm in height. Seen from the outside, 16 denticles per 0.05 mm extend above a 0.012 mm broad, relatively smooth to slightly granulated jaw-flap, which merges

with the jaw along a zone with a distinct pattern of deeply sunken, pitted, pentagonal figures. Underneath this zone, no distinct pattern is present. On the inner surface (fig. 235) no pattern is present.

Spawn (figs 270-271). The irregularly pentagonal, drop-shaped egg-capsules are covered with sand. They are 2.5-3.5 mm (mean = 3.2, n = 10) in diameter, e.g. measured horizontally, from left to right in figure 270, and contain 135-160 eggs (mean =149, n = 10). A straight mucus thread (fig. 271), finely sculptured with longitudinal lines, connects the egg-capsules along their bases (on the left in fig. 270).

Habitat. The snails and their egg-capsules were found at 4-38 m depth, associated with *Fungia* (*Fungia*) *fungites* (Linnaeus, 1758), *F.* cf (*Verrillofungia*) *repanda* Dana, 1846, *Herpolitha limax* (Esper, 1797) and *Sandalolitha robusta* (Quelch, 1886). These mushroom coral species occur both on sand and on a more solid substratum, but the snails with the egg-capsules were found on or in the sand (sometimes buried) only.

Distribution (fig. 45). The species is known from the Indo-West Pacific, from Egypt (Red Sea), Madagascar, Maldives and Indonesia to Palau.

Differentiation. Conchologically this species most closely resembles *Surrepifungium costulatum* (figs 34-35). The radula of *S. oliverioi* is similar to the "type 2" radula of *S. costulatum* (see the description of that species; figs 164, 184, 204). Furthermore the DNA-sequences (Cytochrome Oxidase I) found for eight *S. costulatum* and four *S. oliverioi* specimens are very similar and therefore not diagnostic (A. Gittenberger *et al.*, in prep.). In general, the species can be distinguished by their shells, which are usually somewhat more loosely coiled in *S. oliverioi* (figs 36-37) than in *S. costulatum* (figs 34-35) and by their egg-capsule sizes, which are 2.5-3.5 mm in *S. oliverioi* versus 5.0-6.1 mm in *S. costulatum*. These differences may also represent intraspecific variation, suggesting that *S. oliverioi* and *S. costulatum* are conspecific. *Surrepifungium costulatum* however, is the only species that was found to have two types of radula. This may indicate the presence of an additional, cryptic species instead of a dimorphism within the species. If so, a name may be available already. Because of this uncertainty, *Surrepifungium costulatum* and *S. oliverioi* are here still considered separate species. Future analyses of additional molecular markers and the jaws of a larger number of specimens, can resolve this issue. Shells of *S. oliverioi* also resemble those of *S. patamakanthini* spec. nov., but differ in having solely "single" (figs 97, 115) instead of fused lamellate costae (figs 96, 114) on the initial teleoconch whorls, in not having distinct coronations on the costae (figs 49-50), in having a spiral sculpture becoming obsolete from c. the 4th instead of the 6th teleoconch whorl (figs 114-115) on. Specimens of *S. oliverioi* can also be distinguished from *S. patamakanthini* spec. nov. by their radulae with about 20 (fig. 165) instead of 12 teeth (fig. 167) in half a row.

Remarks. The description given above has to differ from that by Bonfitto and Sabelli (2001), because some paratypes were found to be not conspecific with the holotype. Three paratypes were studied. Their heights are 17.0, 15.8 and 9.1 mm (fig. 33). They correspond with paratypes 1 (MZB 14026), 2 (MZB 14027) and 4 (BMNH ?) in Bonfitto and Sabelli (2001). Paratype 1 (MZB 14026) was identified as *Surrepifungium patamakanthini* spec. nov. (fig. 50). The other two paratypes were found to be conspecific with the holotype. The description and photograph of the holotype in Bonfitto and Sabelli (2001) indicate that it is 19 mm in height and has 19 costal ribs on the body whorl. Two *S. oliverioi* specimens from Thailand and Palau, with shell heights of 19.2 mm (fig. 37) and 20.1 mm, have 19 and 20 ribs respectively on the body whorl and therefore resemble the holotype. In *S. patamakanthini* (figs 38-39) however, the shells have at least 21 costal ribs on the body whorl at a height of 16-19 mm, i.e. 21-25 costal ribs (mean = 22.6, n = 15). Paratype 1 (fig. 50) of "*Epitonium oliverioi*" that was identified as *S. patamakanthini* also falls within this range, with a shell height of 17.0 mm and 21 ribs.

Surrepifungium patamakanthini spec. nov.

Material. Samples that were hosted by *Ctenactis echinata*, *C. crassa*, *Sandalolitha robusta*, *Heliofungia actiniformis*, *Fungia* (*Fungia*) *fungites*, *F.* (*Danafungia*) *horrida*, *F.* (*Verrillofungia*) *concinna* and *F.* (*V.*) *repanda* are coded Ce, Cc, Sr, Ha, Ff, Fh, Fc and Fr, respectively. PALAU. SW Ubelsechel, N of Toachel

Ra Ngel (07°17'50"N 134°29'08"E), holotype RMNH 95373 Ff/1sh, with egg-capsules RMNH 100220; paratypes: type locality, RMNH 95374 Ff/1sn, 1sh; SW Ubelsechel, N Toachel Ra Ngel (07°18'03"N 134°29'44"E), RMNH 95376 Fr/1sn+e; S Ubelsechel, NE Toachel Re Ngel (07°18'28"N 134°30'23"E), RMNH 95375 Sr/3sh+e, 3o, r; E Koror, SW Ngeream, patch reef in KB channel (07°20'22"N 134°31'05"E), RMNH 95363 Fc/1+e; N of Ngeremdiu, Lighthouse reef, backreef, (07°17'11"N 134°27'26"E), RMNH 95364 Ff/1sn+e; NE of Ngeremdiu, Lighthouse reef, forereef (07°16'30"N 134°27'25"E), RMNH 95369 Cc/1sh, 95370 Ce/1sn+e, 95365 Fc/1sn, 95372 Ff/1sn; NE of Ngeremdiu, Lighthouse reef, forereef (07°16'47"N 134°27'50"E), RMNH 95371 Ff/1sn; NE of Ngeremdiu, Lighthouse reef, forereef, sandy slope (07°16'14"N 134°27'21"E), RMNH 95379 Cc/1sh+e, 95380 Cc/2sh+e, d, 95381 Cc/1sh, r, d, 95382 Ff/2sh+e, o, 2d, 95378 Ff/1sn+e; S of Ngeremdiu, Rael Dil, backreef (07°15'04"N 134°27'02"E), RMNH 95366 Ff/1sn. MADAGASCAR. Nosy Vé Island, paratype of *Surrepifungium oliverioi*: MZB 14026, 1sh from *Fungia* cf *repanda*. MALDIVES. Ari Atoll, Vilamendhoo Island: House reef, (03°38'N 72°57'E), RMNH 100216 Fr/2sn+e, 100217 Fh/1sh, o, d. THAILAND. Southern Phuket Islets, RMNH 100218 1sn, host unknown; Krabi, Phiphi Islands: Ko Bida Nok (07°39'14"N 98°45'58"E), RMNH 95906 Ce/1sn+e, d; SE Ko Bida Nai (07°39'27"N 98°37'38"E), RMNH 95893 Ce/1sn+e. PHILIPPINES. Cebu Strait: Cabilao Island (off Bohol), La Estrella Resort, RMNH 100219 Ha/1sh. INDONESIA. SW Sulawesi, Spermonde archipelago, SW Kudingareng Keke Island (05°06'21"S 119°17'03"E), RMNH 95295 Ff/2sn, 1sh, d. Bali: Tanjung Benoa, Loloan Benoa (08°43'31"S 115°15'57"E), RMNH 95247 Fr/1sn+e; SE Tulamben beach, Drop-off (08°16'40"S 115°35'45"E), RMNH 95249 Fh/1sn+e.

Type locality. PALAU. SW Ubelsechel, N of Toachel Ra Ngel (07°17'50"N 134°29'08"E).

Shell (figs 38-39, 50, 96, 114; table 1). Shell (figs 38-39) fragile, moderately elongated conical, with convex whorls, creamy white; reaching 22.8 mm in height. For dimensions and number of costal and spiral ribs on the 2nd and the 5th teleoconch whorls, see table 1. The holotype (fig. 39) measures 22.8 ×10.4 mm. The protoconch (fig. 96) has 3¼-3½ whorls (n = 10); apart from its smooth apical part, it is sculptured with regularly spaced, very fine, incised, axial lines, 23 (n = 1) per 0.2 mm on protoconch whorl 2¼-2¾. The teleoconch (figs 38-39, 50, 114) has up to 11½ whorls, separated by a very deep suture; it is sculptured with mostly regularly placed, orthocline, lamellar, moderately high costae, which are usually continuous on the initial teleoconch whorls only. Costae touching the adjoining whorls and usually curving adaperturally at the preceding whorl. Shortly before the preceding whorl is reached, the costae increase abruptly in height, forming a distinct coronation (fig. 114). Initial whorls usually with multiple, lamellate costae, which are fused to form broader ones (figs 96, 114). The number of costae on the initial five teleoconch whorls remains approximately the same, i.e. about 16 ribs per whorl (table 1); it only increases on the younger whorls, with 21-25 (mean = 22.6, n = 15) costal ribs on the 8th -10th teleoconch whorl in shells with a height of 16-19 mm, and even up to 46 costae on the 10th whorl in a shell of 21.0 mm in height. The teleoconch is additionally sculptured with very low, inconspicuous, randomly placed, spiral threads (figs 96, 114), which become obsolete from about the 6th teleoconch whorl onwards. Aperture subcircular. There is a narrow but distinct umbilicus.

Operculum (figs 3-5, 138). Operculum paucispiral, with interconnected coils (fig. 3). At the outside of the operculum (fig. 138) there are 9-10 wavy threads per 0.1 mm (n = 2), running about perpendicular to the growth lines. These threads are divided into segments, which are convex towards the operculum edge. Except for the muscle scar and growth lines, no micro-sculpture was found on the inside of the operculum. The muscle scar is irregular, varying from a roughly dotted surface to a relatively smooth, densely dotted or striped surface (fig. 5).

Radula (figs 6-7, 13, 167, 187, 207; table 2). Three radulae could be studied, i.e. from a snail from the Maldives and two snails from Palau. The stem and the blade of each tooth are similar in width and merge gradually (fig. 13). All teeth (fig. 167) are attached to the radular plate along the bases up to the basal denticle. The innermost tooth (fig. 187, left) in a row has an inconspicuous, pointed, secondary cusp, which is absent in all other teeth. Starting from the innermost, smallest tooth, with a height of 0.030-0.037 mm (mean = 0.033, n = 3), the teeth quickly increase in size to about four times that height up to the 3rd tooth, after which they gradually become somewhat larger still, up to the largest, 0.150-0.171 mm (mean = 0.159, n = 3) high tooth, which is either the penultimate or the ultimate one, i.e. the 12th. In two radulae, the ultimate tooth was c. 0.050 mm smaller, i.e. 0.102-0.126 mm high, than the 0.150-0.171 mm high penultimate one. In the third radula the ultimate tooth was slightly larger, i.e. 0.155 mm, than the penultimate one, i.e. 0.153 mm (table 2).

Jaw (figs 6-7, 231-233; table 2). The denticulate edge consists of three to five irregular rows of basally pitted, slender, acute denticles, best visible from the inside (figs 232-233). The denticles in the upper row are usually the largest ones, i.e. 0.020-0.022 mm (mean = 0.021, n = 3) in height. At the outside (fig. 231), 16-18 denticles per 0.05 mm (mean = 17, n = 3) extend above a 0.020 mm (n = 1) broad, densely pitted jaw-flap, which merges with the jaw along a zone with a pattern of slightly raised, scarcely pitted, irregular to pentagonal figures. Underneath the jaw-flap, a vague pattern of pentagonal figures quickly becomes obsolete. On the inner surface (fig. 232) no pattern is present.

Spawn (figs 268-269). The irregularly pentagonal, drop-shaped egg-capsules are covered with sand. They are 2.7-3.1 mm (mean = 2.9, n = 10) in diameter, e.g. measured horizontally, from left to right in figure 268, and contain 280-480 eggs (mean = 382.2, n = 10). A straight mucus thread (fig. 269), finely sculptured with longitudinal lines, connects the egg-capsules along their bases (on the left in fig. 268).

Habitat. The snails and their egg-capsules were found at 5-18 m, associated with *Ctenactis echinata* (Pallas, 1766), *C. crassa* (Dana, 1846), *Sandalolitha robusta* (Quelch, 1886), *Heliofungia actiniformis* (Quoy and Gaimard, 1833), *Fungia* (*Fungia*) *fungites* (Linnaeus, 1758), *F.* (*Danafungia*) *horrida* Dana, 1846, *F.* (*Verrillofungia*) *concinna* Verrill, 1864 and *F.* (*V.*) *repanda* Dana, 1846. These mushroom coral species occur both on sand and on a more solid substratum, but the snails with the egg-capsules were found on or in the sand (sometimes buried) only.

Distribution (fig. 44). The species is known from the Indo-West Pacific, from Madagascar, Maldives, Thailand, Philippines and Indonesia to Palau.

Differentiation. Conchologically and in habitat preference, this species resembles *Surrepifungium costulatum*, *S. oliverioi* and *S. ingridae*. It differs from these three species in having 12 instead of more than 17 radular teeth in half a row (table 2). It can furthermore be distinguished from *S. costulatum* and *S. oliverioi* by the presence of fused lamellae forming thick costal ribs on the initial whorls and the coronations on the ribs. It differs from *S. ingridae* in having 13-20 (mean = 16.1, n = 23) costae instead of 20-31 (mean = 24, n = 5) costae on the 5th teleoconch whorl (see table 1) and by the lack of a distinct spiral sculpture from about the 6th teleoconch whorl onwards.

Etymology. This species is named in appreciation of Mr Somnuk Patamakanthin, for his hospitality at the Phuket Shell Museum and the donation of specimens of *Surrepifungium costulatum* and *S. patamakanthini* from Thailand.

Epitonium Röding, 1798, s.l.

Type species. *Turbo scalaris* L., 1758 (design.: Suter, 1913: 319).

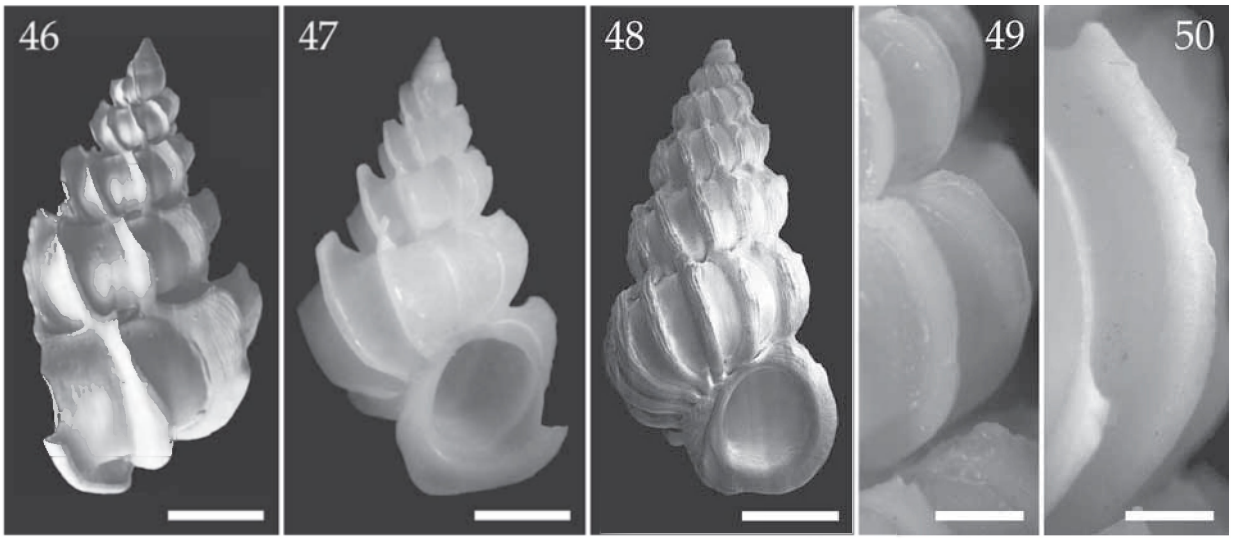
New species. Pending additional data, the following two species are provisionally classified in *Epitonium*, calling attention to these forms by describing, illustrating and naming them.

Epitonium crassicostatum spec. nov.

Material (hosted by *Fungia* (*Cycloseris*) *costulata*). INDONESIA. Bali, Sanur, Jeladi Willis, S of channel entrance (08°40'59"S 115°16'03"E), holotype RMNH 100214/1sh.

Type locality. INDONESIA. Bali, Sanur, Jeladi Willis, S of channel entrance (08°40'59"S 115°16'03"E).

Shell (figs 48, 98, 116; table 1). Shell fragile, elongate-conical, with convex whorls, white. The holotype (figs 48, 98, 116) measures 4.8 × 2.2 mm. The protoconch, broken in the holotype, has at least 2¼ whorls; it is sculptured with regularly spaced, very fine, incised, axial lines, 22 per 0.2 mm on the penultimate protoconch whorl. The teleoconch has up to at least 5½ whorls, separated by a moderately deep suture. Teleoconch sculptured with multiple, lamellate costae, which are fused to form thicker ones. The number of lamellate costae that are connected to form a thicker costal rib, increases gradually from two on the 1st teleoconch whorl (fig. 98) to six on the 6th whorl (fig. 116). Eleven orthocline, continuous, regularly placed, thick costal ribs per whorl are fused together with the ribs on the adjoining whorls (figs 48, 116). All costae have a small coronation just above the centre of the whorl (fig. 116). On the initial



Figs 46-50. Shells. 46-47, *Epitonium graviarmatum* spec. nov., holotype, Maldives. 48, *Epitonium crassicostatum* spec. nov., holotype, Bali, Indonesia. 49-50, "*Epitonium oliverioi*", paratypes, Madagascar; 49, *Surrepifungium oliverioi*, detail costal rib on 5th teleoconch whorl; 50, *Surrepifungium patamakanthini* spec. nov., paratype, not *S. oliverioi*, detail costal rib on 6th teleoconch whorl. Scale bars: 46-48 = 1 mm; 49-50 = 0.5 mm. Photos: through binoc. (46, 48-49) and with SEM, using uncoated material (45, 47).

teleoconch whorls the spiral threads are obsolete. From the 3rd whorl onwards, about 17, very low, spiral threads become discernible. Aperture subcircular, its columellar margin relatively thick, formed by a fusion of several lamellae. Apertural height / shell height = 0.27. Umbilicus closed.

Operculum, Radula, Jaw and Spawn. Unknown.

Habitat. One empty shell was found on sand beneath the mushroom coral *Fungia* (*Cycloseris*) *costulata* Ortmann, 1889, at a depth of 9 m.

Distribution. Off Jeladi Willis, Sanur, Bali, Indonesia.

Etymology. *Crassicostatum* is composed after "*crassi*", Latin for "thick", and "*costatum*", Latin for "having ribs".

Differentiation. This species differs from all other epitoniids in the position of the coronations on the costae, just above the periphery of the whorls. A similar sculpture of an increasing number of fused lamellate costae, forming thick costal ribs up to at least the 6th teleoconch whorl, has also been found in some specimens of *Surrepifungium ingridae* (fig. 113; A. Gittenberger *et al.*, 2000: 8, figs 23-24, 27) and *S. patamakanthini* spec. nov. (fig. 114).

Remarks. The shell height could not be measured accurately because of the missing protoconch whorls. Therefore the indexes based on this height, cannot be accurate either. This species could also be classified with *Surrepifungium* gen. nov., because of the fused, lamellate, thick costal ribs and its association with a fungiid coral.

Epitonium graviarmatum spec. nov.

Material (hosted by *Fungia* (*Cycloseris*) *vaughani*). Maldives. Ari Atoll, Vilamendhoo island, (03°38'N 72°57'E), holotype RMNH 100215/1sh.

Type locality. MALDIVES. Ari Atoll, Vilamendhoo island, (03°38'N 72°57'E).

Shell (figs 46-47, 99, 117; table 1). Shell fragile, conical, with convex whorls, white with a thin, dark, purple line along the upper margin of the initial four protoconch whorls. The holotype (figs 46-47, 99, 117) measures 4.8 × 2.9 mm. The protoconch (fig. 99) has 5 whorls; it is sculptured from c. the 1st whorl onwards with regularly spaced, very fine, incised,

axial lines, 20 per 0.2 mm on protoconch whorl 3¾-4¼, and from about the 2nd whorl onwards with regularly spaced, very fine, incised, spiral lines, 7 per 0.1 mm on protoconch whorl 3¾-4¼. The teleoconch (fig. 117) has up to four whorls, separated by a deep suture; each whorl is sculptured with eight, regularly placed, continuous, orthocline, lamellar, very high costae. Costae fusing with or only touching the costae on the adjoining whorls (fig. 117). Shortly before the preceding whorl is reached, the costae increase abruptly about five times in height, forming a large coronation. On both sides of a costal rib, up to five, evenly placed, fine lines, run parallel to the margin (fig. 117). No spiral sculpture is present on the teleoconch. Aperture subcircular. Apertural height / shell height = 0.31. Umbilicus closed.

Operculum, Radula, Jaw and Spawn. Unknown.

Habitat. One empty shell was found, on the sandy substratum, underneath the mushroom coral *Fungia* (*Cycloseris*) *vaughani* Boschma, 1923, at a depth of 35 m.

Distribution. Off Vilamendhoo island, Maldives.

Etymology. *Graviarmatum* is composed after "*gravi*", Latin for "heavily", and "*armatum*", Latin for "defensively armed".

Differentiation. This species resembles *Epitonium alatum* (Sowerby, 1844). It differs from the holotype (Dushane, 1987a: 1, fig. 3) and the descriptions and photographs in Dushane (1987a: 1, 4, figs 3-4) and Weil *et al.* (1999: 90-91, fig. 272) in having much higher costal ribs and 5 instead of 2 protoconch whorls. The epitoniid identified as *E. alatum* by Nakayama (2003: 48, figs 22-24) closely resembles this species, but is described as having minute spiral striae in between the costae. Such striae are missing in *E. graviarmatum* spec. nov., which seems to have less than 4, instead of 5 protoconch whorls. In *E. alatum* specimens there is an open umbilicus (Dushane, 1987a: 4; Weil *et al.*, 1999: 90; Nakayama, 2003: 48) instead of a closed one.

Remarks. This species might in fact belong to *Surrepifungium* gen. nov., because of the lack of a spiral sculpture on the teleoconch and its association with a fungiid coral.

Epidendrium gen. nov.

Type species. *Epidendrium sordidum* spec. nov.

Other species. *Scalina billeeana* Dushane and Bratcher, 1965; *Epitonium dendrophylliae* Bouchet and Warén, 1986; *Epidendrium sordidum* spec. nov.

Shell (table 1). The fragile shells have a distinct teleoconch sculpture of low, costal ribs and spiral threads. Among the four *Epidendrium* gen. nov. species the shell shapes vary between very broad and relatively slender conical (figs 1, 51-57; table 1; Bouchet and Warén, 1986: 522, figs 1217, 1218). Both slender and broad shells were found in samples collected from the same host. Both forms were found laying egg-capsules, so that the variation cannot be explained by differences in sex.

Operculum. Except for growth lines, no micro-sculpture is present on the outside of the opercula of *Epidendrium aureum* spec. nov. and *E. sordidum* spec. nov. The opercula of *E. billeeanum* and *E. dendrophylliae* could not be studied.

Soft parts. The animal is yellowish, with small, dark eyespots.

Radula (table 2). All single teeth have an acute apical cusp, and no to seven secondary cusps; an inconspicuous basal denticle is absent on the innermost, and present on the outermost teeth within a row (figs 160-162, 182-183, 202-203; Dushane and Bratcher, 1965: 24, fig. 3a-b; Page and Willan, 1988: 224-225, figs 2-3; Richter and Luque, 2004: 100, fig. 1c-d).

Jaw (table 2). The denticulate jaw-edge consists of a single row of slender to lamellar denticles (figs 29, 237-241). Underneath these denticles, a prominent jaw-flap lies loosely on the outer surface of the jaw, partly covering the pattern there (figs 236-237, 240-242).

Spawn. Oval, yellowish, slightly transparent egg-capsules with protuberances (figs 272, 274), connected by a straight (figs 273, 275) to twisted (like fig. 299; Oliverio *et al.*, 1997: 8, figs 14-15) mucus thread. The uncleaved eggs are 0.077 mm (n = 10 / species) in diameter. The eggs and egg-capsules of

Epidendrium billeeanum and *E. dendrophylliae* could not be studied. The development from eggs to veligers in the egg-capsules of *E. aureum* spec. nov. resembles that described for *E. hartogi* by A. Gittenberger (2003: 147, fig. 42); no data are available for *E. billeeanum*, *E. dendrophylliae* and *E. sordidum* spec. nov.

Habitat. The snails live on, or in the vicinity of their dendrophylliid host corals (Scleractinia: Dendrophylliidae).

Etymology. The name *Epidendrium* is composed after "*epi*", Greek for "on", and "*dendrium*", referring to the coral host family "Dendrophylliidae". The gender is neuter, i.e. with the ending "ium".

Differentiation. A similar teleoconch sculpture of distinct low costal ribs and spiral threads is present in some *Epifungium* gen. nov. species, e.g. *E. hoeksemai*, *E. lochi* and *E. pseudolochi* spec. nov. (figs 104-105, 108, 124-125, 128), and in *Epitonium* species, e.g. *E. striatissimum* (Monterosato, 1878) (Bouchet and Warén, 1986: 522, fig. 1216). The relatively large range in the shell height/width indexes within *Epidendrium* gen. nov. species, is uncommon in epitoniids, but also present in the coral-associated species *Epifungium hoeksemai* (figs 75-76), *E. ulu* (figs 70-72) and *Surrepifungium ingridae* (figs 40-41).

The lack of an operculum sculpture of threads, running about perpendicular to the growth lines, distinguishes this genus, or at least *Epidendrium aureum* spec. nov. (figs 132-133) and *E. sordidum* spec. nov. (fig. 134), from the other two epitoniid genera that are associated with corals, viz. *Epifungium* gen. nov. (figs 140-151) and *Surrepifungium* gen. nov. (figs 136-139). *Epitonium pyramidalis* (fig. 135) also lacks this sculpture.

Similar radular teeth are present in all epitoniid genera studied, viz. in *Cirsotrema* (figs 152, 195), *Epifungium* gen. nov. (189-194, 209-214), *Epitonium* (figs 178-180, 198-200), *Gyroscala* (figs 181, 201) and *Surrepifungium* gen. nov. (figs 184-188, 204-208). In *Janthina janthina* (fig. 16) (Janthinoidea Lamarck, 1810 [= Epitoniacea Berry, 1910], Janthinidae) similar teeth as in *Epidendrium aureum* spec. nov. occur, but these can be about twenty times larger.

The jaws, with a single row of denticles and a jaw-flap (figs 236-242), closely resemble those of *Epifungium* gen. nov. species (figs 11, 243-263); they differ from other epitoniid genera, like *Cirsotrema* (figs 10, 215), *Epitonium* (figs 218-225), *Gyroscala* (figs 216-217) and *Surrepifungium* gen. nov. (figs 226-235), in denticle form, the presence of a jaw-flap, and/or the number of denticle rows.

The oval, slightly transparent egg-capsules, with protuberances, are also known from several *Epifungium* gen. nov. species, which are usually found on the surface of their coral host, viz. *E. adgranulosa* spec. nov. (fig. 276), *E. hartogi* (fig. 282), *E. hoeksemai* (fig. 284), *E. nielsi* spec. nov. (fig. 290) and *E. ulu* (fig. 298). Most epitoniids live on and in the sand however, and have drop-shaped, oval or round capsules, which are covered with sand and do not have any protuberances, e.g. *Cirsotrema varicosa*, several *Epifungium* gen. nov. species (figs 278, 280, 286, 288, 292), *Epitonium ancillottoi*, *E. clathrus* (in Vestergaard, 1935) and species of *Surrepifungium* gen. nov. (figs 164, 266, 268, 270).

The habitat seems not to be shared with any other epitoniid species.

Remarks. Because specimens of the two Indo-West Pacific species *Epidendrium aureum* spec. nov. and *E. sordidum* spec. nov. were repeatedly confused with the East Pacific *Epitonium billeeanum* Dushane and Bratcher, 1965, the data presented on allegedly that species by several authors (Debelius, 1996a; Debelius, 1996b; A. Gittenberger, 2003; Loch, 1982; Oliverio *et al.*, 1997; Robertson and Schutt, 1984; Page and Willan, 1988) should be treated with care.

Page and Willan (1988) concluded that snails of *E. billeeanum* from the Great Barrier Reef, Australia, change sex between 8.6 and 12.7 mm shell length, and that their radulae go through an ontogenetic change while doing so. The two radula-types that are described for males and females of *E. billeeanum*, are similar to those of *E. sordidum* spec. nov. and *E. aureum* spec. nov., respectively. Probably Page and Willan (1988) have misidentified their specimens as *E. billeeanum*, a species that, according to our data, only occurs in the East Pacific. Shells of *E. sordidum* spec. nov. and *E. aureum* spec. nov. often occur sympatrically, in large numbers, on the same host colony. In general the shells of *E. sordidum* spec. nov. are smaller than those of *E. aureum* spec. nov., explaining the association Page and Willan (1988)

found between shell size and radular type. See also the remarks on *E. aureum* spec. nov.

Epidendrium aureum spec. nov.

Scalina billeeana Dushane and Bratcher, 1965: Oliverio *et al.*, 1997: 3-10, figs 1-21; Robertson and Schutt, 1984: 4, 2 figs; Debelius, 1996a: 150-151, 2 figs; Debelius, 1996b: 72-73, figs 1-6; A. Gittenberger, 2003: 140-144, figs 3, 13, 20, 28-32. Not *Scalina billeeana* Dushane and Bratcher, 1965.

Material (all hosted by *Tubastrea* or *Dendrophyllia* species). PALAU. W Ulong, W of barrier reef, Tsey's tunnel (07°18'40"N 134°13'30"E), holotype RMNH 95287/1sh; paratypes: type locality, RMNH 95286/6sn; W Babelthuap, Toachel Mlengui, North side of West Passage (07°32'31"N 134°28'24"E), RMNH 95288/2sn, d; E Babelthuap, E of Arudowaishi Pt., Uchelbeluu reef, backreef (07°18'40"N 134°13'30"E), RMNH 95284/1sh, 95285/1sn; SW Ngerchaol, N of entrance Malakal Harbor, Beduliases, (07°20'12"N 134°26'10"E), RMNH 95283/1sn; NE Ngeremdiu, Lighthouse reef, forereef (07°16'30"N 134°27'25"E), RMNH 95282/1sn+e. EGYPT. Off Marsa Shagra, about 300 km S of Hurghada, RMNH 95241/1sn, r, 95242/1sn, 95243/1sn, 95244/3sn, d; Off Marsa Nakari, about 350 S of Hurghada, RMNH 95245/19sn+e, d. SEYCHELLES. E of Mahé, near Sainte Anne Island, Beacon islet (04°37'S 55°31'E), RMNH 100199/1sn. MALDIVES. Ari Atoll, Vilamendhoo Island: House reef, (03°38'N 72°57'E), RMNH 100197/2sn, d, 100196/2sn+e, d, 100178/1sn, 100177/1sn, 100337/1sn. THAILAND. Krabi, Phiphi Islands: Hin Mu Sang, Shark point Phuket (07°48'17"N 97°37'38"E), RMNH 95885/1sn, d; Ko Bida Nok, (07°39'14"N 98°45'58"E), RMNH 95905/11sn, d, 95998/2sn; Hin Daeng (07°08'59"N 98°49'25"E), RMNH 95980/7sn+e, r. PHILIPPINES. Cebu Strait, W Bohol: Cabilao Island, La Estrella Resort, RMNH 100179/8sn, d; W Cabilao Island, S-side fish sanctuary (09°52'37"N 123°45'38"E), RMNH 83485/23sn+e, d; S Cabilao Island, Cabacungan Point (09°51'30"N 123°45'57"E), RMNH 83486/1sh, 15sn, r, d. INDONESIA. NE Kalimantan, Berau Islands, N lighthouse-1 reef, S of Derawan Island (02°16'02"N 118°14'23"E), RMNH 100175/1sn. N Sulawesi: Selat Lembeh, between Tanjungnanas and Teluk Kungkungan (01°28'N 125°15'E), RMNH 100195/4sh, 13sn+e, d, 100194/14sn; N Lembeh Strait, W Lembeh Island (01°30'01"N 125°15'39"E), RMNH 100203/3sn+e; Off Manado, Bunaken: (01°36'23"N 124°46'59"E), RMNH 100176/1sn, 100204/3sn+e; (01°39'09"N 124°42'17"E), RMNH 100206/1sn+e; (01°36'45"N 124°44'22"E), RMNH 100205/1sn+e; (01°37'50"N 124°46'14"E), RMNH 100201/2sn+e, 100202/1sn; (01°37'10"N 124°46'55"E), RMNH 100207/1sn. SW Sulawesi, Spermonde archipelago: SW Samalona Island (05°07'42"S 119°20'31"E), RMNH 95238/1sn+e, r, 95240/1sh; W Kudingareng Keke Island (05°06'09"S 119°17'9"E), RMNH 95233/1sn, r, d; W Badi Island (04°58'05"S 119°16'54"E), RMNH 95235/18sn+e, 95236/4sn+e, 95237/1sn; NW Bone Tambung Island (05°02'05"S 119°16'16"E), RMNH 95234/1sn. Sulawesi, Wakatobi National Park, Karang Kapota NW, outer reef, RMNH 100198/1sh, d. Komodo: Selat Linta, NE Pulau Tatawa (08°30'39"S 119°38'36"E), RMNH 95289/4sn+e; S of Tanjung Toro Langkoi, Manta Ally (08°44'12"S 119°24'42"E), RMNH 95290/6sn; Gili Lawa Laut, 100200/6sn. Bali: E Nusa Dua, Off Club Med Hotel, N of channel (08°47'06"S 115°13'57"E), RMNH 95227/2sn, 95228/2sn+e, 1sh, r, 95229/1sn; NW Nusa Penida, Toyapakeh (08°40'56"S 115°28'56"E), RMNH 95232/1sn+e. AUSTRALIA. Western Australia, Shark Bay, Cleft Bernier I, South of Carnarvon (24°45'32"S 113°09'57"E), WAM/2sh.

Type locality. PALAU. W Ulong, W of barrier reef, Tsey's tunnel (07°18'40"N 134°13'30"E).

Shell (figs 51-52, 92, 118; table 1). The shell height/width indexes vary considerably (table 1), resulting in shells varying from broad-conical (fig. 52) to relatively slender-conical (fig. 51). Shell (figs 51-52) fragile, with convex whorls; reaching 20.1 mm in height. For dimensions and number of costal and spiral ribs on the 2nd and the 5th teleoconch whorls, see table 1. The holotype (fig. 51) measures 20.1 × 10.7 mm. The protoconch is entirely coloured with a dark, purplish red pigment, which continues on the teleoconch whorls, where this colouring is most conspicuous below the periphery, gradually fading out and not visible anymore from about the 5th teleoconch whorl onwards. The remaining parts of the teleoconch are white to yellowish. The protoconch (fig. 92) has 3¼-3½ whorls (n = 10); apart from its smooth apical part, it is sculptured with regularly spaced, very fine, incised, axial lines, 21-22 (mean = 21.7, n = 3) per 0.2 mm on protoconch whorl 2¼-2¾. The teleoconch (figs 51-52, 118) has up to 8¾ whorls, separated by a moderately deep suture; it is sculptured with mostly regularly placed, discontinuous, orthocline, lamellar, not or slightly curved, low costae, not or hardly touching the adjoining whorls. The number of costae on the 2nd, 3rd, 5th and younger teleoconch whorls usually increases quickly, up to 164 costae on the 7th whorl in a shell of 12.0 mm in height. The teleoconch is additionally sculptured with regularly placed, relatively thick, spiral threads. The number of prominent spirals on the 2nd, 3rd, 5th teleoconch whorls slowly increases, usually remaining approximately the same from the 6th whorl onwards; there are up to 35 spirals on a whorl. The lamellar costae increase slightly in height when running over the spiral threads. Aperture subcircular. There is a moderately wide umbilicus.

Operculum (figs 132-133). Operculum paucispiral. The coils are either interconnected, as in *Surrepifungium patamakanthini* spec. nov. (fig. 3), or scalaroid (see A. Gittenberger, 2003: 142, fig. 22). Except for growth lines, no micro-sculpture (figs 132-133) is discernable on the outside of the opercula (n = 4).

Radula (figs 160-161, 183, 203; table 2). Three radulae could be studied, i.e. one from a snail from Thailand and two from Indonesian snails. The stem and the blade of each tooth are similar in width and merge gradually. All teeth (figs 160-161) are attached to the radular plate along the bases up to the inconspicuous, small, basal denticle (fig. 203). The innermost tooth (fig. 183, left) in a row has an acute secondary cusp, which is absent in all other teeth. This secondary cusp is about half the size of the apical cusp. Starting from the innermost, smallest tooth, with a height of 0.021-0.031 mm (mean = 0.027, n = 3), the teeth gradually become elongated and very slender, increasing in size to about four to five times that height, i.e. 0.119-0.143 mm (mean = 0.130, n = 3), up to the 13th-21st tooth (mean = 18.7, n = 3), after which they gradually become smaller again until the ultimate, usually malformed, 0.042-0.086 mm (mean = 0.063, n = 3) high 30th-34th tooth (table 2).

Jaw (figs 22, 29, 236-238; table 2). The denticulate edge consists of a row of lamellar denticles (figs 22, 236-237), which are densely pitted basally, on the inside (fig. 238). They have a maximum size of 0.0048-0.0070 mm (n = 2). Seen from the outside (figs 22, 236-237), 38-46 denticles (n = 2) per 0.05 mm extend above a 0.026-0.026 mm (n = 2) broad, granulated jaw-flap (fig. 22), which lies loosely over part of the jaw-pattern (figs 29, 236-237). This pattern, as far as visible under the jaw-flap, consists of two or three rows of somewhat sunken, densely pitted, pentagonal figures, followed further on by one or two rows of deeply sunken, scarcely pitted, pentagonal figures, and after that by more or less unclear rows of somewhat sunken, scarcely pitted, pentagonal to irregular figures that occasionally have holes (fig. 237; as in *Epidendrium sordidum* spec. nov., fig. 20). Away from the denticulate edge, the pattern gradually becomes obsolete (fig. 236). On the inner surface of the jaw (fig. 238), below the denticles, there are three to five rows of engraved, scarcely pitted, square-like figures, followed by an area that is somewhat granulated to smooth.

Spawn (figs 272-273). Egg-capsules (fig. 272) ovoid, yellowish, somewhat transparent, with conspicuous protuberances, not embedded with sand, 1.46-3.14 mm (mean = 2.17, n = 8) in diameter, e.g. measured horizontally, from left to right in figure 272, containing 270-630 eggs (mean = 521.3, n = 8) each. The mucus threads that connect the egg-capsules, are either straight (fig. 273) or twisted (as in *Epifungium hartogi*, fig. 284; Oliverioi *et al.*, 1997: 8, figs 14-15), and either smooth (fig. 273) or sculptured with longitudinal lines (as in *Epidendrium sordidum* spec. nov., fig. 275).

Habitat. The snails and their egg-capsules were found at 2-28 m, associated with *Tubastrea* and *Dendrophyllia* corals. They usually live on, or in the vicinity of their dendrophylliid hosts, attached to the surface of the substrate with mucus threads. The host corals occur most commonly fixed to the underside of large boulders, in crevices, on the ceilings of caves or on the steep walls of drop-offs. Shells of this species are often found together with those of *Epidendrium sordidum* spec. nov. with the same coral host colony.

Distribution (fig. 58). The species is known from the Indo-West Pacific, from the Red Sea, Seychelles, Maldives, Thailand, Japan, Philippines, Palau and Indonesia to West and East Australia. The authors studied material from various localities (fig. 58), relying on data from the literature for some of the records from the Red Sea (Oliverioi *et al.*, 1997: 6-9, figs 1-8) and Australia (Page and Willan, 1988: 223, fig. 1). The species was observed, but not collected, by the first author in Japan, Okinawa, off Akajima island, and in NE Australia, off the 3rd ribbon reef and off Osprey reef.

Differentiation. The shells of this species most closely resemble those of *Epidendrium billeeanum* Dushane and Bratcher, 1965. They differ in having a dark purplish red instead of a white to yellowish protoconch. Another difference concerns the radula. In *E. aureum* spec. nov. there is no distinct secondary cusp on the elongated, slender radular teeth, as was figured for *E. billeeanum* by Dushane and Bratcher (1965: pl. 24, fig. 3a). The largest teeth are the 12th-22th in half a row of 30-34 teeth in *E. aureum* spec. nov. (table 2), while according to Dushane and Bratcher (1965: 161), the outermost radular teeth

are the largest in *E. billeeanum*. Shells of *E. aureum* spec. nov. also resemble those of *E. sordidum* spec. nov.; they can easily be distinguished, however by the teleoconch sculpture of ribs that do not distinctly vary in height, instead of ribs that abruptly become two to three times higher, forming distinct protuberances, where running over the spiral threads.

Etymology. This species is named after its in situ brightly yellow colour, which gives it a golden hue.

Remarks. The morphological differences between shells of *Epidendrium billeeanum* from the type locality in Baja California, and the epitoniid species here described as *E. aureum* spec. nov. and *E. sordidum* spec. nov. from the Indo-West Pacific, were regarded as intraspecific variation in the literature, mainly because of the absence of sufficient material for study (e.g. Oliverio *et al.*, 1997; Loch, 1982). With hundreds of specimens from the Red Sea, Maldives, Thailand, Philippines, Indonesia and Palau available, it became obvious that these shells from the Indo-West Pacific are consistently different from the 10 shells that were studied from Baja California. Thus, the commonly used vernacular name "Golden Wentletrap" refers to three species, i.e. *E. aureum* spec. nov., *E. billeeanum* and *E. sordidum* spec. nov. These findings and the data obtained by a DNA-analysis (A. Gittenberger *et al.*, in prep.) convincingly show that the Indo-West Pacific specimens represent two species that are both new to science, viz. *E. aureum* spec. nov. and *E. sordidum* spec. nov. Although *E. sordidum* spec. nov. is only slightly less common than *E. aureum* spec. nov. and occurs sympatrically with it at most localities, recognizable photographs of golden wentletraps from the Indo-West Pacific, always show *E. aureum* spec. nov. This is probably because in *E. aureum* spec. nov. the shells are usually somewhat larger and not as dirty as in *E. sordidum* spec. nov. Golden wentletraps on photographs from the Galapagos islands (various internet sources), do not show pigmented protoconchs. Therefore, they are considered conspecific with *E. billeeanum* (fig. 56), which was also cited from the Galapagos islands by Dushane and Bratcher (1965: 161).

Epidendrium billeeanum (Dushane and Bratcher, 1965)

Scalina billeeana Dushane and Bratcher, 1965: 87-88.

Material (hosted by *Tubastrea tenuilamellosa*). MEXICO. Gulf of California, SW Cerralvo Island, holotype CAS 63823/1sh, BMNH paratype/1sh, RMNH 100427/8sn+e.

Type locality. MEXICO. Gulf of California, SW Cerralvo Island.

Shell (fig. 56). The fragile shell (fig. 56) is rather broad-conical and entirely white to yellowish, no distinction can be made between the colour of the protoconch and teleoconch; reaching 14.1 mm in height. For dimensions and number of costal and spiral ribs on the 2nd and the 5th teleoconch whorls of the holotype (fig. 56), see table 1. The holotype measures 6.2 × 4.0 mm. The teleoconch is sculptured with mostly regularly placed, discontinuous, orthocline, lamellar, not or slightly curved, low costae, not or hardly touching the adjoining whorls, and regularly placed, relatively thick, spiral threads. The lamellar costae increase slightly in height when running over the spiral threads.

Operculum. Unknown.

Radula (table 2). Dushane and Bratcher (1965: pl. 24, fig. 3a-b) figured the c. 0.076 mm high, slender, elongated teeth of the holotype, which have either a single, acute or no secondary cusps (where these teeth are situated in a row is not indicated). According to Dushane and Bratcher (1965) the holotype has an indefinite number of these teeth, the outermost of which are the largest. Similar slender, elongated teeth without secondary cusps are known from *Epidendrium aureum* spec. nov. (fig. 203).

Jaw. Unknown.

Spawn. Egg-capsules (as in *Epidendrium aureum* and *E. sordidum*, figs 272, 274) ovoid, yellowish, somewhat transparent, with conspicuous protuberances, not embedded with sand, 2.45-2.60 mm (mean = 2.55, n = 2) in maximum diameter, containing 403-470 eggs (mean = 436.5, n = 2) each. The mucus threads that connect the egg-capsules, are twisted (as in

Epifungium hartogi, fig. 284). The yellow "eggs" that are described by Dushane and Bratcher (1965: 161) are probably egg-capsules.

Habitat. The snails and their egg-capsules were found at about 2-4 m, under rocky ledges, attached to their dendrophylliid host corals, i.e. *Tubastrea tenuilamellosa* (Milne-Edwards and Haime, 1848), by mucus threads (Dushane and Bratcher, 1965).

Distribution. The species is known from the Gulf of California and the Galapagos archipelago.

Differentiation. See the differentiation of *Epidendrium aureum* spec. nov.

Remarks. For a more detailed description, see Dushane and Bratcher (1965). Here some additional data are given, with notes that may be relevant for the differentiation of this species. See also the remarks on *Epidendrium aureum* spec. nov.

Epidendrium dendrophylliae (Bouchet and Warén, 1986)

Epitonium dendrophylliae Bouchet and Warén, 1986: 502, 522-523, figs 1175, 1217-1218; Richter and Luque, 2004: 99-101, fig. 1.

Material. SPAIN. Malaga, collection Frank Swinnen, 1sh.

Type locality. SPAIN, Madeira.

Shell (fig. 57). Shell shapes (table 1) vary between moderately broad (fig. 59; Bouchet and Warén, 1986: 522, fig. 1218) to relatively slender-conical (Bouchet and Warén, 1986: 522, fig. 1217) as is also found in e.g. *Epidendrium aureum* spec. nov. (figs 51-52) and *E. sordidum* spec. nov. (figs 53-55). The fragile shell is white to yellowish. For dimensions and number of costal and spiral ribs on the 2nd and the 5th teleoconch whorls of the specimen studied (fig. 57), see table 1. The protoconch of the holotype (Bouchet and Warén, 1986: 502, fig. 1175) has 3¼-3½ whorls; apart from its smooth apical part, it is sculptured with regularly spaced, very fine, incised, axial lines, 25 per 0.2 mm on protoconch whorl 2¼-2¾.

Operculum. Unknown.

Radula. The radular teeth as described and figured by Richter and Luque (2004: 99-100, fig. 1c-d) have two to six acute, secondary cusps. The apical cusp is about 1½ to 2 times larger than the secondary cusp(s) underneath it. The secondary cusps resemble each other in size.

Jaw. The denticulate jaws have a reticulate pattern on the surface (Richter and Luque, 2004: 99).

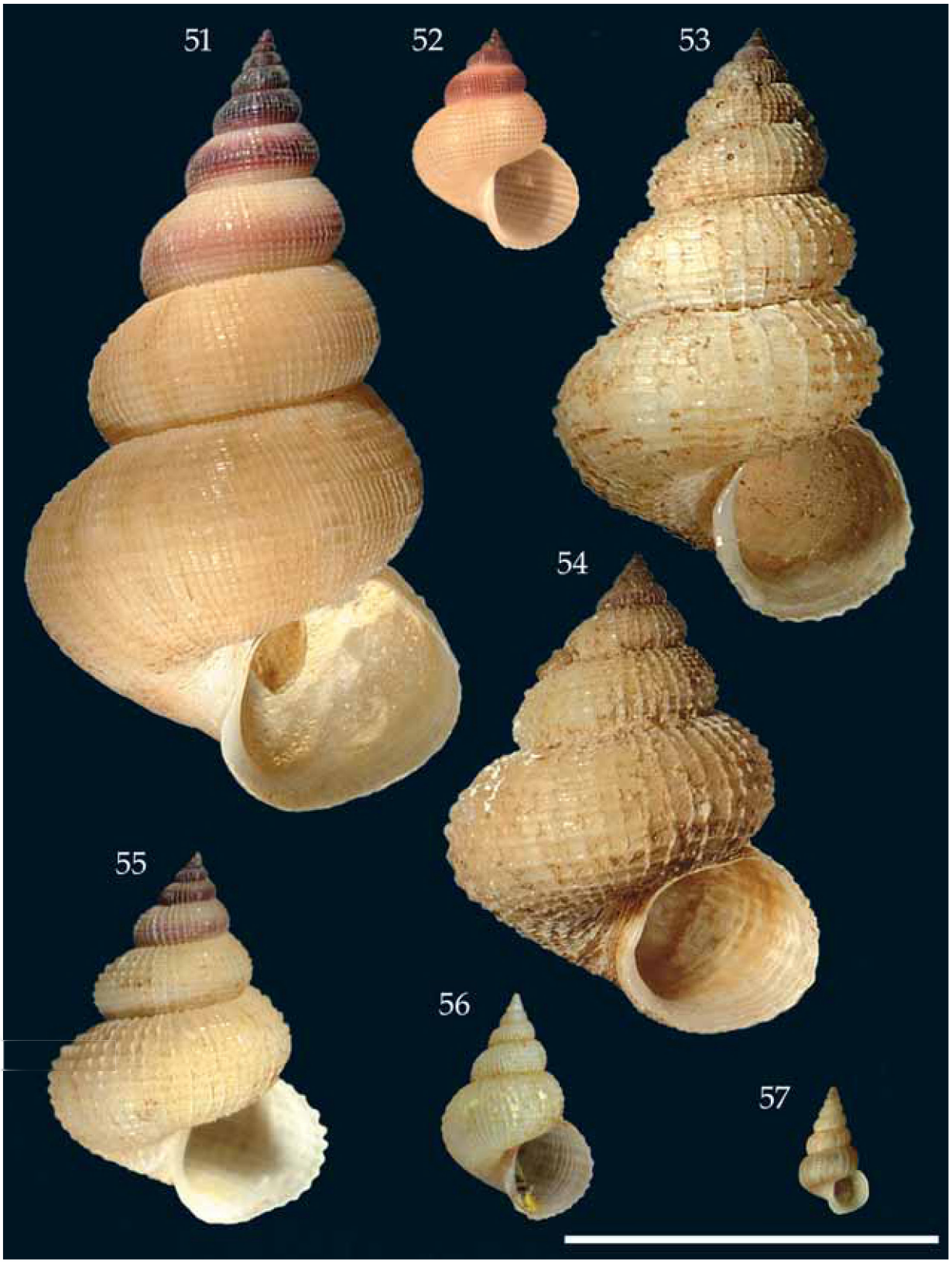
Spawn. Unknown.

Habitat. The snails are found on dendrophylliid corals. Although they usually occur deeper than 40 m and in association with the coral genera *Dendrophyllia* and *Balanophyllia*, Richter and Luque (2004) recorded one specimen from 19 m on *Astroides calycularis* (Pallas, 1766).

Distribution. The species is known from the eastern Atlantic and the western Mediterranean (Richter and Luque, 2004).

Differentiation (figs 1, 2). The shells resemble those of *Epidendrium aureum* spec. nov., *E. billeeanum* and *E. sordidum* spec. nov., but differ in having a closed instead of an open umbilicus, and by less costal ribs on the 2nd, 3rd and 5th teleoconch whorl, i.e. 20, 20 and 19, respectively (table 1), and about 28 on the 5th teleoconch whorl of the holotype (Bouchet and Warén, 1986: 522-523, fig. 1218), versus *E. aureum* spec. nov., *E. billeeanum* and *E. sordidum* spec. nov. with at least 25, 29 and 30 ribs on the 2nd, 3rd and 5th teleoconch whorls and usually many more (table 1). The radular teeth of *E. dendrophylliae* most closely resemble those of *E. sordidum* spec. nov. (figs 162, 182, 202), differing most clearly in having secondary cusps that resemble each other in size, instead of becoming gradually smaller down the blade of a tooth (fig. 202) and by a smaller apical cusp, which is 1½-2 instead of 2-3 times longer than the secondary cusp underneath it.

Remarks. For a detailed description and a comparison with *Epitonium striatissimum* (Monterosato, 1878) see Bouchet and Warén (1986) and Richter and Luque (2004). Here some additional data are given, with notes that may be relevant for the differentiation of this species. See also the remarks on *Epidendrium aureum* spec. nov.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Epidendrium sordidum spec. nov.

Material (all hosted by *Tubastrea* or *Dendrophyllia* spp). INDONESIA.N Sulawesi: Selat Lembeh, between Tanjungnanas and Teluk Kungkungan (01°28'N 125°15'E), holotype RMNH 100208/1sh; N Lembeh Strait, W Lembeh Island (01°30'01"N 125°15'39"E), 100209/2sh; Off Manado, Bunaken (01°35'55"N 124°46'01"E), 100181/1sn+e, 100211/1sn; Off Manado, Siladen (01°37'37"N 124°48'01"E), 100182/1sn. SW Sulawesi, Spermonde archipelago: SW Samalona Island (05°07'42"S 119°20'31"E), RMNH 95239/1sn; W Badi Island (04°58'05"S 119°16'54"E), RMNH 100186/2sn, 100187/1sn, 100188/1sn+e. Sulawesi, Wakatobi National Park, Karang Kapota NW, outer reef, RMNH 100180/5sn+e, d. Bali, Tulamben beach, Liberty wreck (08°16'26"S 115°35'28"E), RMNH 95230/1sn+e. Komodo, S of Tanjung Toro Langkoi, Manta Ally (08°44'12"S 119°24'42"E), RMNH 100192/2sh. MALDIVES. Ari Atoll, Vilamendhoo Island: House reef, (03°38'N 72°57'E), RMNH 100212/1sn, d, 100210/1sn, d. PHILIPPINES. Cebu Strait, W Bohol: Cabilao Island, La Estrella Resort, RMNH 100213/3sn, 2d; W Cabilao Island, S-side fish sanctuary (09°52'37"N 123°45'38"E), RMNH 100183/16sn, d; S Cabilao Island, Cabacungan Point (09°51'30"N 123°45'57"E), RMNH 100185/21sn, 7sh, 2r, o, d. PALAU. W Ulong, W of barrier reef, Tsey's tunnel (07°18'40"N 134°13'30"E), RMNH 100189/3sn+e, 2sh, d; W Babelthuap, Toachel Mlengui, North side of West Passage (07°32'31"N 134°28'24"E), RMNH 100191/2sn, d; E Babelthuap, E of Arudowaishi Pt., Uchelbeluu reef, backreef (07°18'40"N 134°13'30"E), RMNH 100193/2sn.

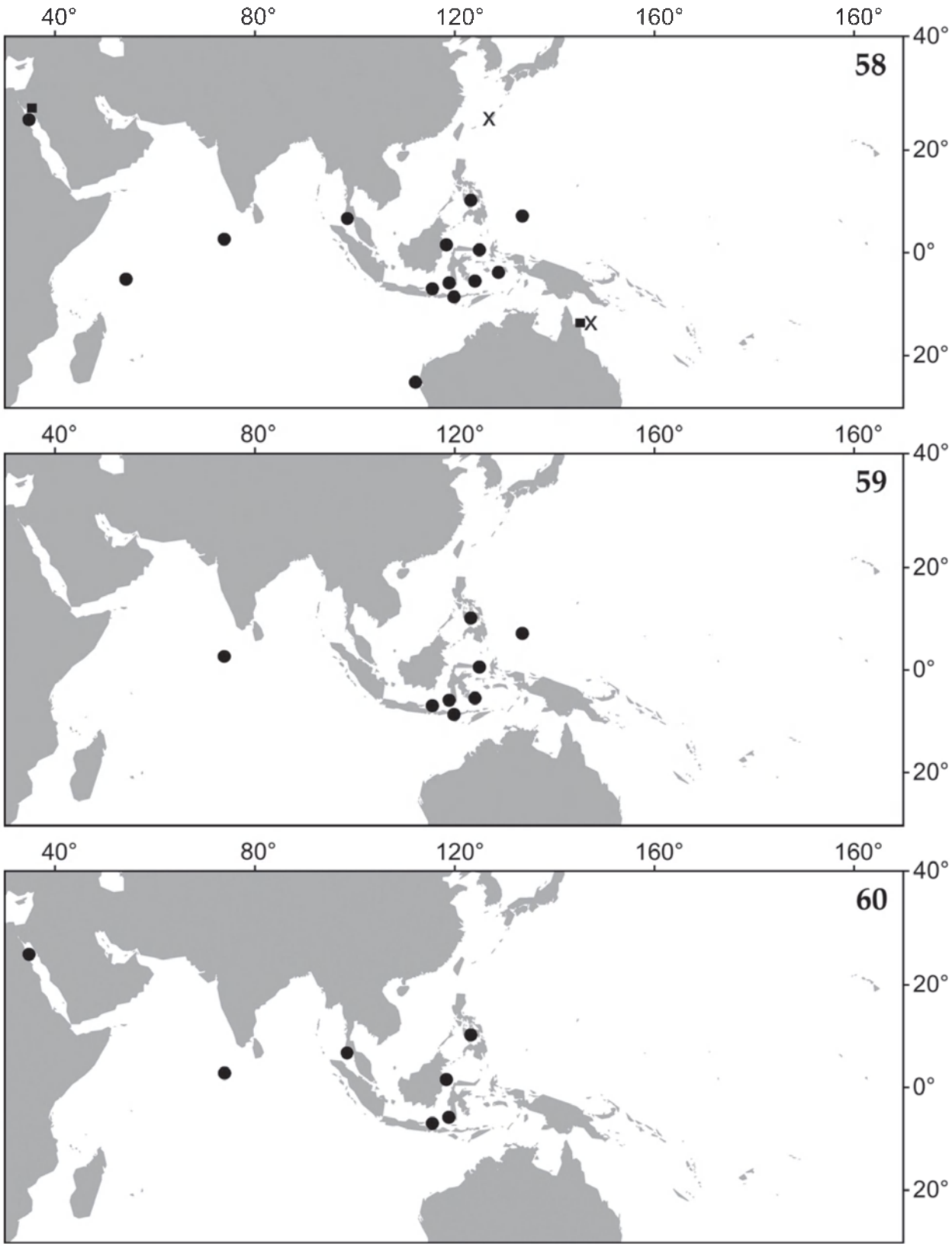
Type locality. INDONESIA. N Sulawesi: Selat Lembeh, between Tanjungnanas and Teluk Kungkungan (01°28'N 125°15'E).

Shell (figs 1-2, 53-55, 93, 119; table 1). The shell height/width indexes (table 1) vary considerably, from 1.1 to 1.8, resulting in shells varying from broad-conical (figs 54-55) to relatively slender-conical (fig. 53). Shell (figs 1-2, 53-55) fragile, with convex whorls; reaching 16.0 mm in height. For dimensions and number of costal and spiral ribs on the 2nd and the 5th teleoconch whorls, see table 1. The protoconch is entirely coloured with a dark, purplish red pigment, which continues on the teleoconch whorls, where it is most conspicuous below the periphery, gradually fading out and not visible anymore from about the 4th teleoconch whorl onwards. The remaining parts of the teleoconch are white to yellowish. The holotype (fig. 53) measures 16.0 × 9.0 mm. The protoconch (fig. 93) has 3¼-3½ whorls (n = 10); apart from its smooth apical part, it is sculptured with regularly spaced, very fine, incised, axial lines, 20-25 (n = 2) per 0.2 mm on protoconch whorl 2¼-2¾. The teleoconch (figs 1-2, 53-55, 119) has up to 7 whorls, separated by a moderately deep suture; it is sculptured with mostly regularly placed, discontinuous, orthocline, lamellar, not or slightly curved, low costae, not or hardly touching the adjoining whorls. The number of costae on the 2nd, 3rd, 5th and younger teleoconch whorls increases quickly, up to 80 costae on the 6th whorl in a shell of 7.0 mm in height. The teleoconch is additionally sculptured with regularly placed, relatively thick, spiral threads. The number of prominent spiral threads on the 2nd, 3rd, and 5th teleoconch whorl slowly increases at first, usually remaining approximately constant from the 6th whorl onwards; there are up to 10 spirals on a whorl. The low costal ribs increase abruptly two to three times in height when crossing a spiral thread, forming distinct protuberances on the shell's surface. Mucus threads, dirt and sand are caught in between these protuberances; small bivalves, vermetid gastropods, polychaetes and foraminifers, often settle on them (figs 1-2); small circular holes of unknown origin, are commonly found in between the costae (see teleoconch whorls 4-5 of the holotype, fig. 53). Therefore, when collecting the snails in the field, they are usually so dirty that the whorls cannot be distinguished. Cleaning takes some effort and normally results in shells that still look worn and dirty (figs 53-54), and only rarely "clean" (fig. 55). Aperture subcircular. There is a moderately wide umbilicus.

Operculum (fig. 134). Operculum paucispiral, with interconnected coils as in *Surrepifungium patamakanthini* spec. nov. (fig. 3). Except for growth lines, no micro-sculpture (fig. 134) is discernable on the outside of the opercula (n = 4).

Radula (figs 162, 182, 202; table 2). Three radulae could be studied, i.e. one from a specimen from the Philippines and two from Indonesian snails (table 2). The stem and the blade of each tooth are similar in width and merge gradually; the blade has 1-9 acute,

Figs 51-57. Shells. Figs 51-52, *Epidendrium aureum* spec. nov.; 51, holotype, Palau; 52, paratype, Egypt. 53-55, *E. sordidum* spec. nov.; 53, holotype, Sulawesi, Indonesia; 54, paratype, relatively broad specimen, Palau; 55, paratype, exceptionally clean specimen, Sulawesi, Indonesia. 56, *E. billeeanum*, holotype, Gulf of California, USA. 57, *E. dendrophylliae*, Malaga, Spain. Scale bar = 1 cm. Photos: A. Gittenberger (51-55, 57) and J. Goud (56).


40°
80°
120°
160°
160°
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0°
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58
59
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secondary cusps. The teeth (figs 160-161) are attached to the radular plate along the bases up to an inconspicuous, small, basal denticle (fig. 202). The number of secondary cusps gradually increases from 1 on the innermost tooth (fig. 182, left) to 9 on the teeth about halfway, after which the number gradually decreases to 2 on the ultimate tooth. The apical cusp is about two to three times larger than the secondary cusp underneath it. Secondary cusps gradually become smaller further down the blade of a tooth (fig. 202). Only the radula of the holotype (figs 162, 183, 203) could be prepared good enough to accurately measure and count all teeth. It looks similar to the other two radulae that were studied. Starting from the innermost, smallest tooth, with a height of 0.041-0.044 mm (n = 2), the teeth gradually increase in size to somewhat more than twice that height, i.e. 0.108 mm (n = 1), up to the 46th tooth, after which they gradually become smaller again until the ultimate, 0.074 mm (n = 1) high 59th tooth (table 2).

Jaw (figs 20, 239-242; table 2). The denticulate edge consists of a row of slender, blunt denticles, which are densely pitted basally, on the inside (fig. 239). They have a maximum size of 0.0063-0.0080 mm (n = 2). Seen from the outside (figs 240-242), 30-31 denticles (n = 2) per 0.05 mm extend above a 0.016-0.019 mm (n = 2) broad, granulated jaw-flap (figs 240-241), which lies loosely over part of the jaw-pattern (figs 240, 242). Sometimes this pattern is obsolete under the jaw-flap (fig. 241). When it is not (figs 240, 242), it consists of two or three rows of somewhat sunken, scarcely pitted, pentagonal figures (fig. 240), followed further on by more or less unclear rows of somewhat sunken, scarcely pitted, pentagonal or oval to irregular figures that occasionally have holes (figs 20, 242). Away from the denticulate edge, the pattern gradually becomes obsolete (fig. 241). On the inner surface of the jaw (fig. 239), below the denticles, there are three or four rows of engraved, scarcely pitted, irregularly square-like figures, followed by an area that is somewhat granulated to smooth.

Figs 58-60. The Indo-Pacific region, from the Red Sea to the Hawaiian archipelago, illustrating epitoniid species ranges. Records of collected material (dots), observed, but not collected material (crosses) and based on photographs only (squares); 58, *Epidendrium aureum* spec. nov.; 59, *Epidendrium sordidum* spec. nov.; 60, *Epifungium adgranulosa* spec. nov.

Spawn (figs 274-275). Egg-capsules (fig. 274) ovoid, yellowish, somewhat transparent, with conspicuous protuberances, not embedded with sand, 1.57-2.00 mm (mean = 1.79, n = 9) in diameter, e.g. measured horizontally, from left to right in figure 274, containing 240-530 eggs (mean = 382.0, n = 9) each. The mucus threads that connect the egg-capsules, are either straight (fig. 275) or twisted (as in *Epifungium hartogi*, fig. 284), and either smooth (as in *Epidendrium aureum* spec. nov., fig. 273) or sculptured with longitudinal lines (fig. 275).

Habitat. The snails and their egg-capsules were found at 3-35 m, associated with *Tubastrea* and *Dendrophyllia* corals. They usually live on, or in the vicinity of their dendrophylliid hosts, attached to the surface of the substrate with mucus threads. The host corals occur most commonly fixed to the underside of large boulders, in crevices, on the ceilings of caves or on the steep walls of drop-offs. The snails are often found together with those of *Epidendrium aureum* spec. nov. with the same coral host colony.

Distribution (fig. 59). The species is known from the Indo-West Pacific, from Maldives, Philippines and Indonesia to Palau.

Differentiation. See the differentiation of *Epidendrium aureum* spec. nov.

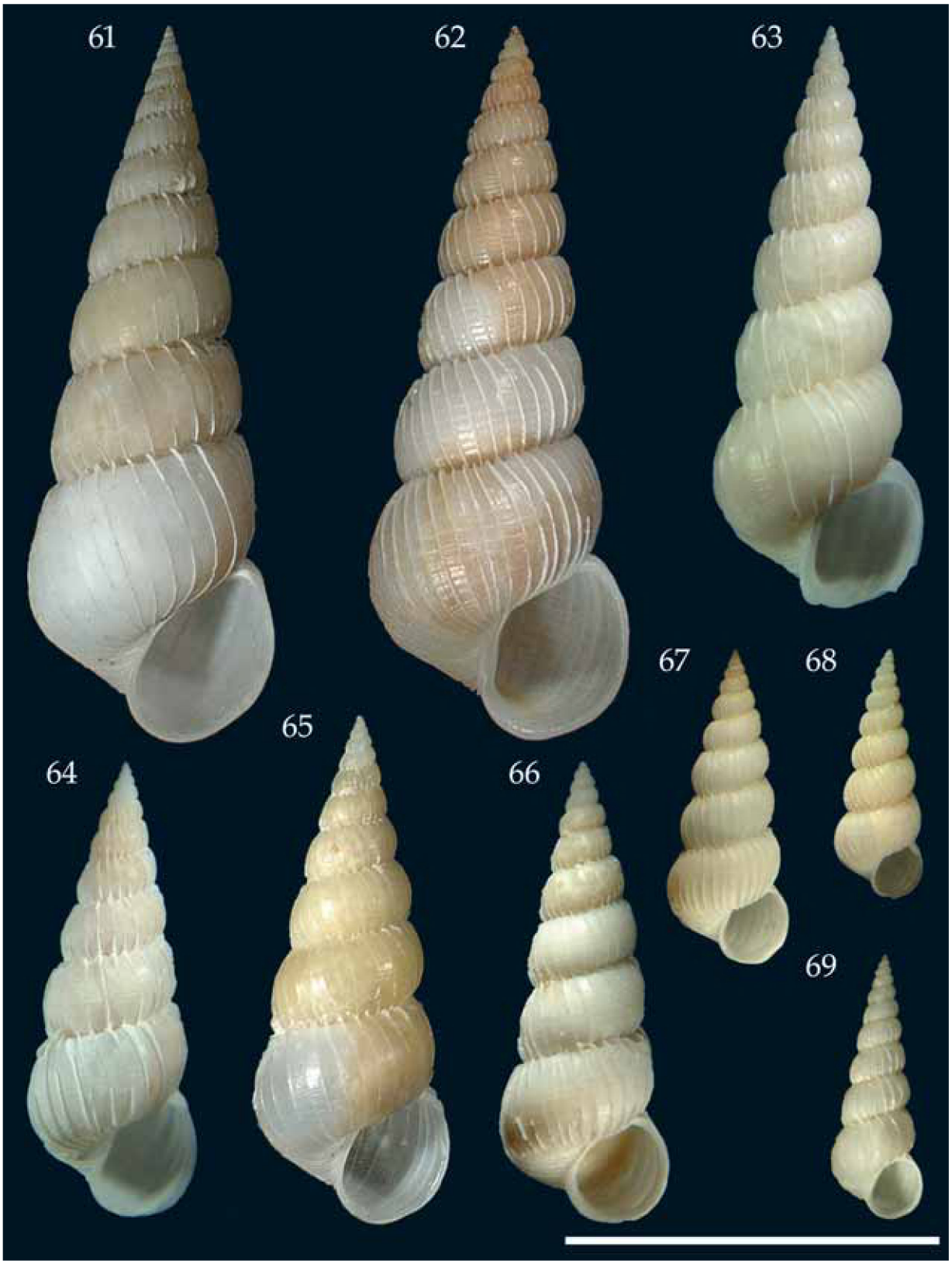
Etymology. This species is named after its appearance. Most shells, even of alive specimens, look worn and "dirty", i.e. "*sordidum*" in Latin.

Remarks. According to Dr. R. Bieler (pers. comm., 2005) the attached vermetid shell illustrated in figs 1-2, might be of a very young *Dendropoma* spec. (Gastropoda, Vermetidae). See the remarks on *Epidendrium aureum* spec. nov.

Epifungium gen. nov.

Type species. *Epitonium ulu* Pilsbry, 1921

Other species. *Epifungium adgranulosa* spec. nov.; *Epifungium adgravis* spec. nov.; *Epifungium adscabra* spec. nov.; *Epitonium hartogi* A. Gittenberger, 2003; *Epitonium hoeksemai* A. Gittenberger and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Goud, 2000; *Epitonium lochi* A. Gittenberger and Goud, 2000; *Epifungium marki* spec. nov.; *Epifungium nielsi* spec. nov.; *Epifungium pseudolochi* spec. nov.; *Epifungium pseudotwilae* spec. nov.; *Epitonium twilae* A. Gittenberger and Goud, 2000.

Shell (table 1). The fragile, whitish shells have a teleoconch sculpture of low costal ribs and spiral threads.

Operculum. Twenty to forty wavy threads per 0.1 mm, running about perpendicular to the growth lines over the outside of the operculum (figs 140-151).

Soft parts. The animal is whitish, with small, dark eyespots.

Radula (table 2). All teeth have an acute apical cusp and one to six secondary cusps; no basal denticle is present (figs 15, 169-174, 189-194, 209-214).

Jaw (table 2). The denticulate jaw-edge consists of a single row of slender, blunt denticles (figs 31-32, 243-263). Underneath these denticles, there is a prominent, usually loose jaw-flap, partly covering the outside jaw-pattern (figs 243-245, 249-259).

Spawn. The egg-capsules are oval to round, with or without protuberances, transparent or covered with sand. They are connected by a straight or twisted mucus thread (figs 276-299). The uncleaved eggs are 0.077 mm (n = 10 / species) in diameter. The development from eggs to veligers in the egg-capsules resembles that described for *E. hartogi* by A. Gittenberger (2003: 147, fig. 42). This development was studied for all *Epifungium* gen. nov. species, except *E. adscabra* spec. nov., *E. marki* spec. nov., *E. pseudolochi* spec. nov. and *E. pseudotwilae* spec. nov.

Habitat. The snails live under fungiid hosts (Fungiidae) on the coral itself or on the substratum underneath, with the exception of *Epifungium hartogi*, which is found on or in the vicinity of euphyllid hosts (Euphyllidae). When the snails are not on the coral surface, they are usually found on a hard substratum, like coral rubble and only rarely on sand.

Figs 61-69. Shells. 61, *Epifungium adgranulosa* spec. nov., holotype, Thailand. 62, *E. marki* spec. nov., holotype, Egypt. Figs 63-64, *E. adgravis* spec. nov.; 63, holotype, Kalimantan, Indonesia; 64, paratype, Sulawesi, Indonesia. Fig. 65, *E. nielsi* spec. nov., holotype, Maldives. Figs 66-67, *E. lochi*, Sulawesi, Indonesia; 66, paratype; 67, holotype. Fig. 68, *E. pseudolochi* spec. nov., holotype, Egypt. Fig. 69, *E. adscabra* spec. nov., holotype, Sulawesi, Indonesia. Scale bar = 1 cm.

Etymology. The name *Epifungium* is composed after "*epi*", Greek for "on", and "*fungium*", referring to the coral host family "Fungiidae". The gender is neuter, i.e. with the ending "ium".

Differentiation. A similar teleoconch sculpture of low costal ribs and spiral threads is present in *Epidendrium* gen. nov. (figs 1-2, 51-57, 92-93, 118-119) and some *Epitonium* species, e.g. *E. striatissimum* (Monterosato, 1878) (Bouchet and Warén, 1986: 522, fig. 1216).

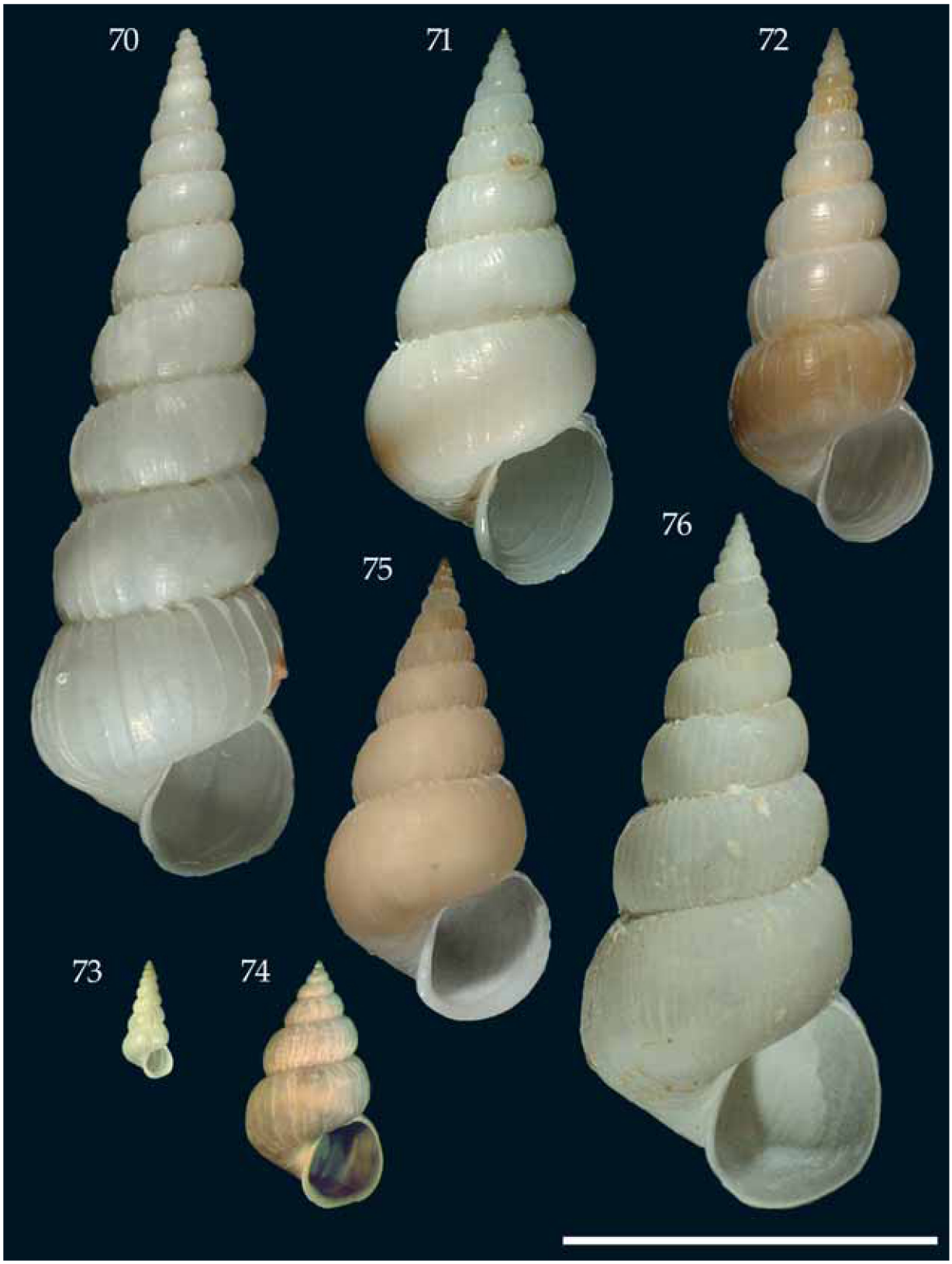
A similar operculum sculpture of wavy threads, running about perpendicular to the growth lines, is present in *Surrepifungium* gen. nov. (figs 136-139). In that genus however, nine to twenty threads per 0.1 mm are present instead of twenty to forty in *Epifungium*. In *Epidendrium aureum* spec. nov. (figs 132-133), *E. sordidum* spec. nov. (fig. 134) and *Epitonium pyramidalis* (fig. 135), no operculum sculpture is present, except for the growth lines. The sculpture on the opercula of other epitoniids, if any, is unknown.

Most epitoniids have at least some teeth on their radula with a distinct basal denticle (e.g. figs 175-176, 178-180, 184-188, 195-196, 198-200, 205-207). Such a denticle is missing in *Epifungium* (figs 15, 189-194, 209-214), however.

The jaws, with a single row of denticles and a jaw-flap (figs 11, 243-263), closely resemble those in *Epidendrium* gen. nov. species (figs 236-242), but differ from the jaws in other epitoniid genera, i.e. *Cirsotrema* (figs 10, 215), *Epitonium* (figs 218-225), *Gyroscala* (figs 216-217) and *Surrepifungium* gen. nov. (figs 226-235), in denticle form, the presence of a jaw-flap, and/or the number of denticle rows.

Similar, round to oval egg-capsules are found in species of most epitoniid genera, with the exception of *Surrepifungium* gen. nov., in which only pentagonal, drop-shaped egg-capsules are present.

The habitat is partly shared with *Surrepifungium* gen. nov. species, which live in or on the sand underneath fungiid host corals. When they were found together (n = 24), the snails of the *Epifungium* gen. nov. species were on the coral and *Surrepifungium* gen. nov.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was found on or in the sand underneath. This is most likely due to a dislike of sand in *Epifungium* gen. nov. species, and not a matter of interspecific competition (A. Gittenberger and Hoeksema, in prep.). The habitat seems not to be shared with any other epitoniids.

Epifungium adgranulosa spec. nov.

Material (always hosted by *Fungia* (*Wellsofungia*) *granulosa* Kluzinger, 1879). THAILAND. Krabi, Phiphi Islands: Hin Bida, "Shark Point Phiphi"(07°38'01"N 98°48'54"E), holotype RMNH 95961/1sh, with egg-capsules RMNH 100335; paratypes: type locality, RMNH 100336/1sh, found together with holotype; E Ko Phiphi Son, Poh Cape, Hin Phae (07°43'30"N 98°47'17"E), RMNH 96010/1sh, d. EGYPT. Off Marsa Shagra, about 300 km S of Hurghada, RMNH 95088/4sn+e, 95087/2sn+e, 95091/1sn, 95093/7sn+e, d; Off Marsa Nakari, about 350 km S of Hurghada, RMNH 95094/1sn, 95097/1sn+e. MALDIVES. Ari Atoll: Haamigili Beru reef, (03°28'N 72°50'E), RMNH 100128/1sn; Vilamendhoo Island, house reef, (03°38'N 72°57'E), RMNH 100127/1sn, 100129/5sn+e, d. 100130/3sn+e. PHILIPPINES. Cebu Strait: Cabilao Island (off Bohol), La Estrella Resort, RMNH 62357/5sn, d; Gilutongan Island, RMNH 62353/4sn+e; Sulpa Island, RMNH 62355/7sn+e, 62356/1sn+e. INDONESIA. NE Kalimantan, Berau Islands, Berau delta, Lighthouse-2 reef (02°09'34"N 118°10'11"E), RMNH 100126/1sh. SW Sulawesi, Spermonde archipelago: W Kudingareng Keke Island (05°06'09"S 119°17'9"E), RMNH 43163/1sn+e, 95030/1sn; ESE Kudingareng Keke Island (05°06'S 119°17'E), RMNH 43295/1sn. Bali: N Nusa Penida Island, off Tukad Adegan (08°40'32"S 115°31'18"E), RMNH 95027/1sh, o, r, d, 1sn; Padang Bai, E Tanjung Sari (08°31'11"S 115°30'37"E), RMNH 95004/1sn.

Type locality. THAILAND. Krabi, Phiphi Islands: Hin Bida, "Shark Point Phiphi"(07°38'01"N 98°48'54"E).

Shell (figs 61, 100, 120; table 1). Shell fragile, elongate-conical, with slightly convex whorls, creamy white; reaching 19.5 mm in height. For dimensions and number of costal and spiral ribs on the 2nd and the 5th teleoconch whorls, see table 1. The holotype (fig. 61) measures 19.5 × 7.0 mm. The protoconch (fig. 100) has 3¼-3½ whorls (n = 10); apart from its smooth apical part, it is sculptured with regularly spaced, very fine, incised, axial lines, 19 (n = 1) per 0.2 mm on protoconch whorl 2¼-2¾. The teleoconch (fig. 120) has up to 10 whorls, separated by a shallow suture; it is sculptured with mostly regularly placed, usually discontinuous, orthocline, lamellar, low costae, touching the adjoining whorls, curving adaperturally at the preceding whorl. Just before reaching the preceding whorl the costae usually become about four times higher, forming a coronation. Although the number of costae on the 2nd, 3rd, 5th and younger teleoconch whorls remains approximately the same (adjoining whorls differing +/- 2) in about half of the specimens, this number may strongly increase or decrease on two or three whorls after which it remains constant again. There are up to 37 costae on a whorl, as was counted on the 9th whorl in a shell of 8.5 mm in height. The teleoconch is additionally sculptured with very low, inconspicuous, spiral threads, randomly placed over each whorl. On the initial whorls the spiral threads are usually obsolete. Towards the younger whorls additional, low, spiral threads become apparent, usually (27 out of 31) becoming numerous from about the 7th teleoconch whorl onwards. In some rare cases, 16 spiral threads are present on the 7th teleoconch whorl (2 out of 33) or the spiral sculpture becomes obsolete on the younger whorls (2 out of 33). Aperture subcircular. Most specimens (30 out of 36) have a very narrow umbilicus, visible in oblique view only. Six specimens have a closed umbilicus. The relative umbilical width is not correlated with the shell-size.

Figs 70-76. Shells. Figs 70-73, *Epifungium ulu*; 70, largest specimen (28.2 mm), Bali, Indonesia; 71, broad specimen, Thailand; 72, slender specimen, Palau; 73, small specimen, Palau. Fig. 74, *E. hartogi*, Sulawesi, Indonesia. Figs 75-76, *E. hoeksemai*; 75, broad specimen, Sulawesi, Indonesia; 76, largest specimen (18.8 mm), Palau. Scale bar = 1 cm.

Operculum (fig. 140). Operculum paucispiral, with interconnected coils as in *Surrepifungium patamakanthini* spec. nov. (fig. 3). At the outside of the operculum (fig. 140) there are 24 wavy, segmented threads per 0.1 mm (n = 1), running about perpendicular to the growth lines.

Radula and Jaw. Unknown.

Spawn (figs 276-277). Egg-capsules (fig. 276) ovoid, with conspicuous protuberances, somewhat transparent when not embedded with sand, 1.00-1.69 mm (mean = 1.24, n = 15) in diameter, e.g. measured horizontally, from left to right in figure 276, containing 120-445 eggs (mean 183.2, n = 15) each. The mucus threads that connect the egg-capsules are strongly twisted and not sculptured (fig. 277).


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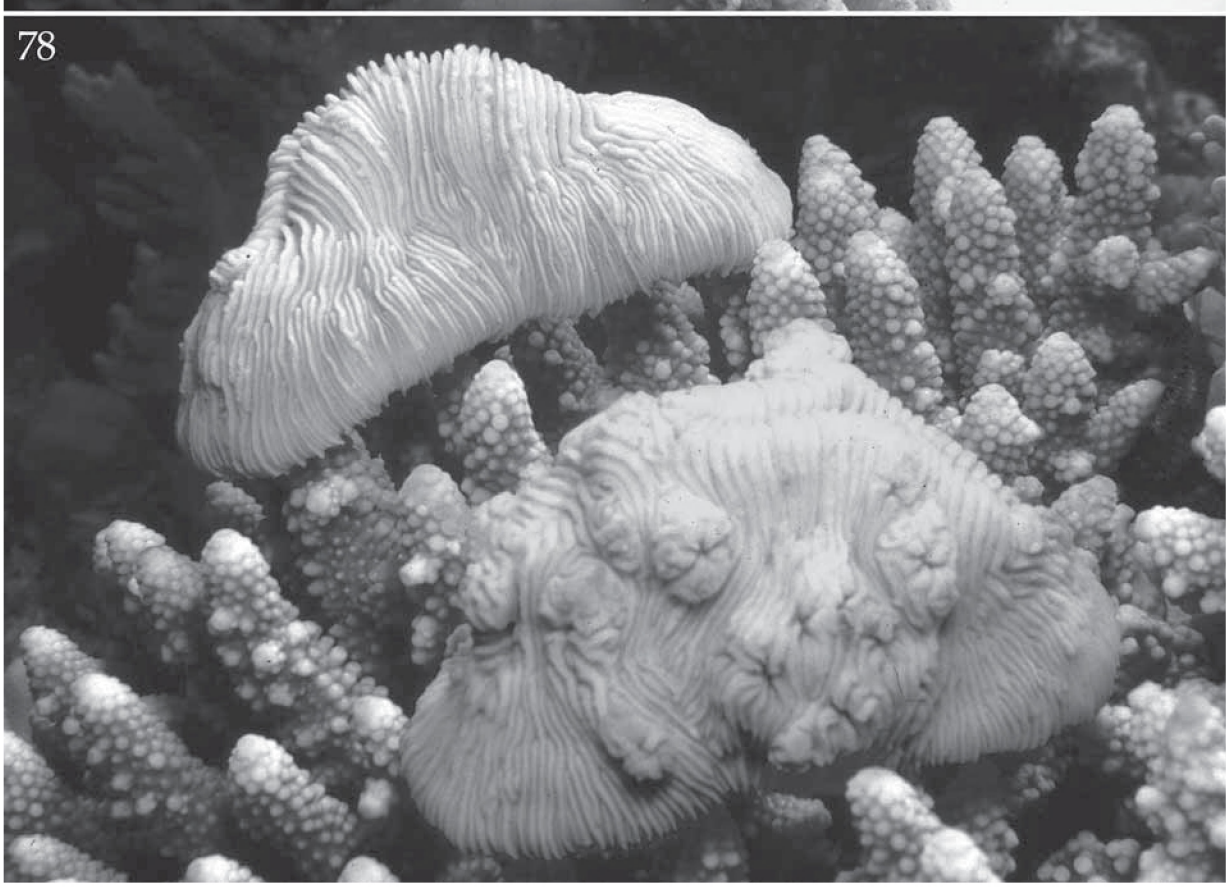
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Habitat. The snails and their egg-capsules were found at 3-18 m, associated with exclusively the mushroom coral species *Fungia* (*Wellsofungia*) *granulosa* Kluzinger, 1879. The snails usually live attached with their mucus threads to the underside of their hosts or to hard substrata underneath. Most host corals were found on coral slopes.

Distribution (fig. 60). The species is known from the Indo-West Pacific, from Egypt (Red Sea), Maldives and Thailand to Indonesia. Also off Palau, many specimens of the host coral species *F.* (*W.*) *granulosa* were thoroughly inspected for wentletraps but no *Epifungium* gen. nov. species were found there.

Differentiation. Conchologically this species resembles *Epifungium adgravis* spec. nov., *E. marki* spec. nov. and *E. nielsi* spec. nov. most. It differs from these species most clearly by its only slightly convex, instead of distinctly convex whorls and by the costal ribs touching the preceding whorls while curving adaperturally. *Epifungium adgranulosa* spec. nov. is the only epitoniid species that is known to be associated with *Fungia* (*Wellsofungia*) *granulosa*.

Etymology. This species is named after its restricted habitat. It was found exclusively on corals of *Fungia* (*Wellsofungia*) *granulosa*.

Remarks. See the remarks on *Epifungium ulu*.

Epifungium adgravis spec. nov.

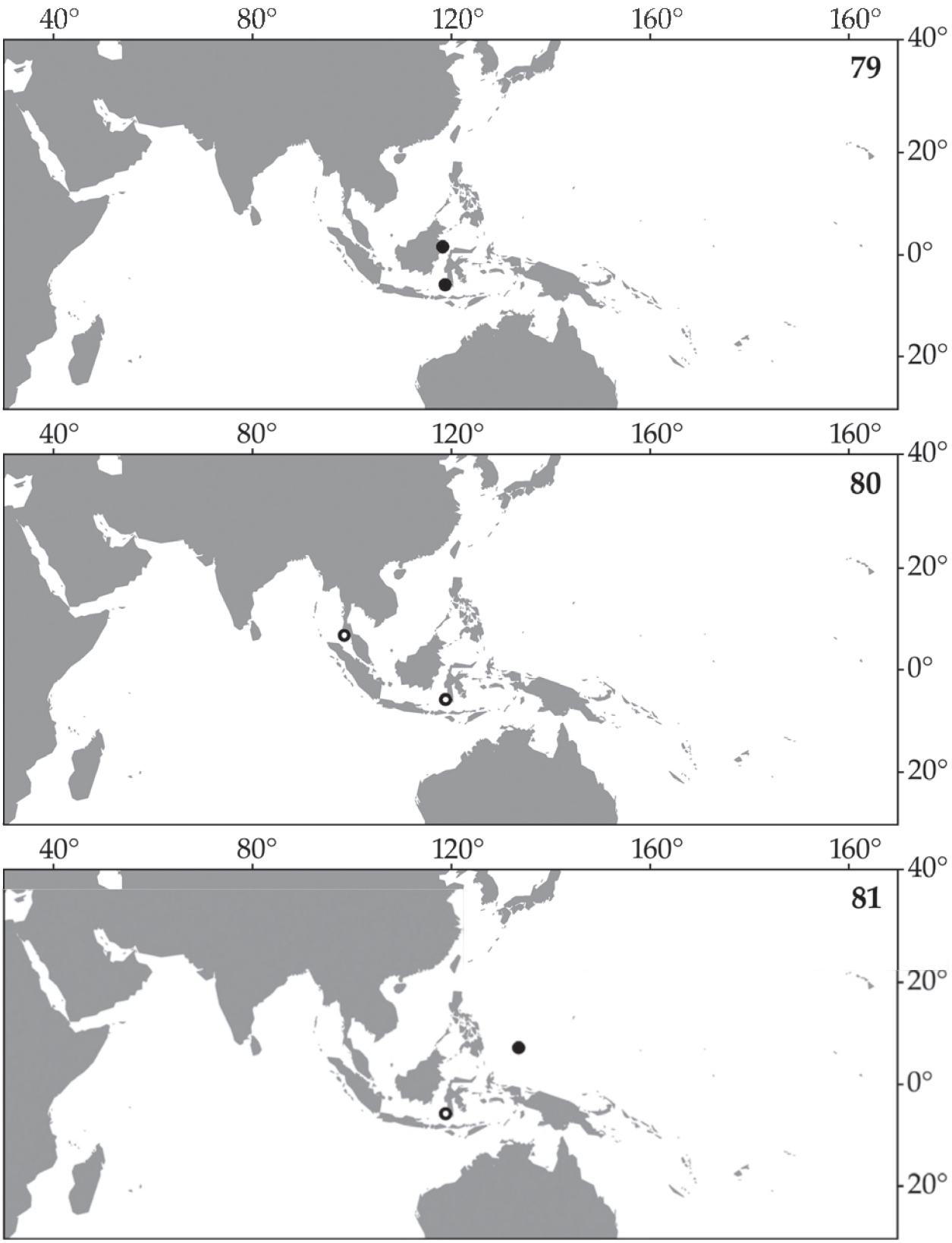
Material (always hosted by *Fungia* (*Pleuractis*) *gravis*). INDONESIA. NE Kalimantan, Berau Islands: S Derawan Island, jetty Derawan Dive Resort (02°17'03"N 118°14'49"E), holotype RMNH 100135/1sh, with egg-capsules RMNH 100434; paratypes: type locality, RMNH 100132/3sn; SW Baliktaba reef, N of Panjang Island (02°34'43"N 118°00'48"E), RMNH 100131/1sn; E Derawan Island, Coral Garden (02°17'32"N 118°15'43"E), RMNH 100136/1sh, 1sn+e; Karang Pinaka reef, NW Samama Island (02°11'22"N 118°17'25"E), RMNH 100134/1sn; N Maratua Island, lagoon near entrance (02°14'53"N 118°37'36"E), RMNH 100133/2sn+e. N Sulawesi, Selat Lembeh, between Tanjungnanas and Teluk Kungkungan (01°28'N 125°15'E), RMNH 43347/1sh+e, r, d. SW Sulawesi, Spermonde archipelago: W Lae Lae Island (05°08'09"S 119°23'13"E), RMNH 95053/1sn; NW Bona Baku reef (05°07'56"S 119°21'39"E), RMNH 95051/1sn, 95050/1sn+e; SW Samalona Island (05°07'42"S 119°20'31"E), RMNH 95077/4sn, 95078/2sn+e; W Bone Lola reef (05°03'07"S 119°21'09"E), RMNH 95046/2sn+e; SW Barang Lompo Island (05°03'S 119°20'E), RMNH 43352/1sn; NW Kudingareng Keke Island (05°06'08"S 119°17'17"E), RMNH 43356/1sh+e, o, 43357/1sn+e; W Kudingareng Keke Island (05°06'09"S 119°17'09"E), RMNH 43276/1sn, 43308/1sn+e, 43165/1sn+e, 43368/3sn+e, 43369/1sn+e, 95031/1sn+e; SW Kudingareng Keke Island (05°06'21"S 119°17'03"E), RMNH 43365/1sn; S Kudingareng Keke Island (05°06'S 119°17'E), RMNH 43361/1sn, 43362/2sn+e; W Badi Island (04°58'05"S 119°16'54"E), RMNH 43371/1sh, o, r, d, 95060/3sn+e; NW Bone Tambung Island (05°02'05"S 119°16'16"E), RMNH 43318/1sn+e, 95055/1sh; 1sn+e. Sulawesi, Wakatobi national park, Pasar Wajo, Buton (05°31'S 122°51'E), RMNH 100137/1sn. Moluccas, Ambon, Hitu, Ambon bay, outer bay, E Laha, up to and including Tawiri, RMNH 43343/1sn+e. Bali: SE-end Tulamben beach (08°16'40"S 115°35'45"E), RMNH 95014/2sn+e; Tulamben area, "Temple bay" (08°16'43"S 115°35'49"E), RMNH 95021/1sn; E Tanjung Sari (08°31'11"S 115°30'37"E), RMNH 95002/1sh+e, o, r, d, 95003/1sh+e; NE Serangan Island (08°44'03"S 115°15'05"E), RMNH 94998/1sn; N Nusa Penida, off Tukad Adegan (08°40'32"S 115°31'18"E), RMNH 95026/1sn; N Nusa Penida, off Desa Buyuk (08°40'25"S 115°32'37"E), RMNH 95028/1sn. W of Flores, NW Rinca, W Teluk Lehokkima (08°38'54"S 119°39'58"E), RMNH 95150/1sn. NE Komodo, NE side of cape, S Gililawa Darat Island (08°28'50"S 119°33'13"E), RMNH 95151/1sn.

Type locality. INDONESIA. NE Kalimantan, Berau Islands: S Derawan Island, jetty Derawan Dive Resort (02°17'03"N 118°14'49"E).

Shell (figs 63-64, 101, 121). Shell fragile, elongate-conical, with convex whorls, creamy white; reaching 15.6 mm in height. For dimensions and number of costal and spiral ribs on the 2nd and the 5th teleoconch whorls, see table 1. The holotype (fig. 63) measures 15.6 × 5.5 mm. The protoconch (fig. 101) has 3¼-3½ whorls (n = 10); apart from its smooth apical part, it is sculptured with regularly spaced, very fine, incised, axial lines, 18 (n = 1) per 0.2 mm on protoconch whorl 2¼-2¾.

The teleoconch (fig. 121) has up to 10 whorls, separated by a deep suture; it is sculptured with mostly regularly placed, usually discontinuous, orthocline, lamellar, not to slightly curved, low costae, not

Figs 77-78. Epifungium marki spec. nov. and its host coral *Fungia* (*Pleuractis*) spec. A, off Marsa Shagra (Red Sea), Egypt. 77, *E. marki*, holotype (largest specimen, shell height = 19.2 mm) with egg-capsules in situ; 78, *F.* (*P.*) spec. A, the two corals were collected on a sandy bottom and placed next to each other for better comparison; upper left specimen (coral length = 15 cm), host of *E. marki* holotype; lower right specimen, morph with many secondary mouths, host of several *E. marki* paratypes.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or hardly touching the adjoining whorls. Just before reaching the preceding whorl the costae become slightly coronate. The number of costae on the 2nd, 3rd, 5th and younger teleoconch whorls remains approximately the same (adjoining whorls differing in about two costae) in most cases; in a few specimens this number strongly increases or decreases on only two or three whorls. There are up to 31 costae on a whorl; on the 10th whorl in a shell of 14.0 mm in height. Very fine, irregularly placed, incised, axial lines and/or split costae are present from the 7th-9th teleoconch whorl onwards. The teleoconch is additionally sculptured with irregularly placed, relatively thick, spiral threads. From the 6th-9th teleoconch whorl onwards, there are irregularly spaced, thin, spiral threads and incised spiral lines in between them and on the major spiral threads. There are usually less spiral threads above the periphery than below it; on the initial whorls they are usually obsolete above the periphery. The number of major spiral threads increases from the 2nd to the 5th whorl, after which it remains almost constant. From the 7th-9th whorl onwards, some of the incised spiral lines or low threads may gradually change into thick spiral threads. Aperture subcircular. In most specimens that are less than about 5 mm high (with 5-6 teleoconch whorls), the umbilicus is closed. Larger specimens have a very narrow umbilicus, visible in oblique view only.

Operculum (fig. 141). Operculum paucispiral, with interconnected coils as in *Surrepifungium patamakanthini* spec. nov. (fig. 3). At the outside of the operculum (fig. 141) there are 21-22 wavy, segmented threads per 0.1 mm (n = 2), running about perpendicular to the growth lines.

Radula (fig. 15; table 2). Two radulae from Indonesian snails could be studied. Both radulae curled and got damaged during SEM-preparation. Therefore it was hard to count the teeth in a row and as a consequence the numbers given below may not be accurate. Each tooth (fig. 15) consists of a moderately broad stem and a somewhat broader blade, which merge gradually; the blade has 1-6 acute, secondary cusps.

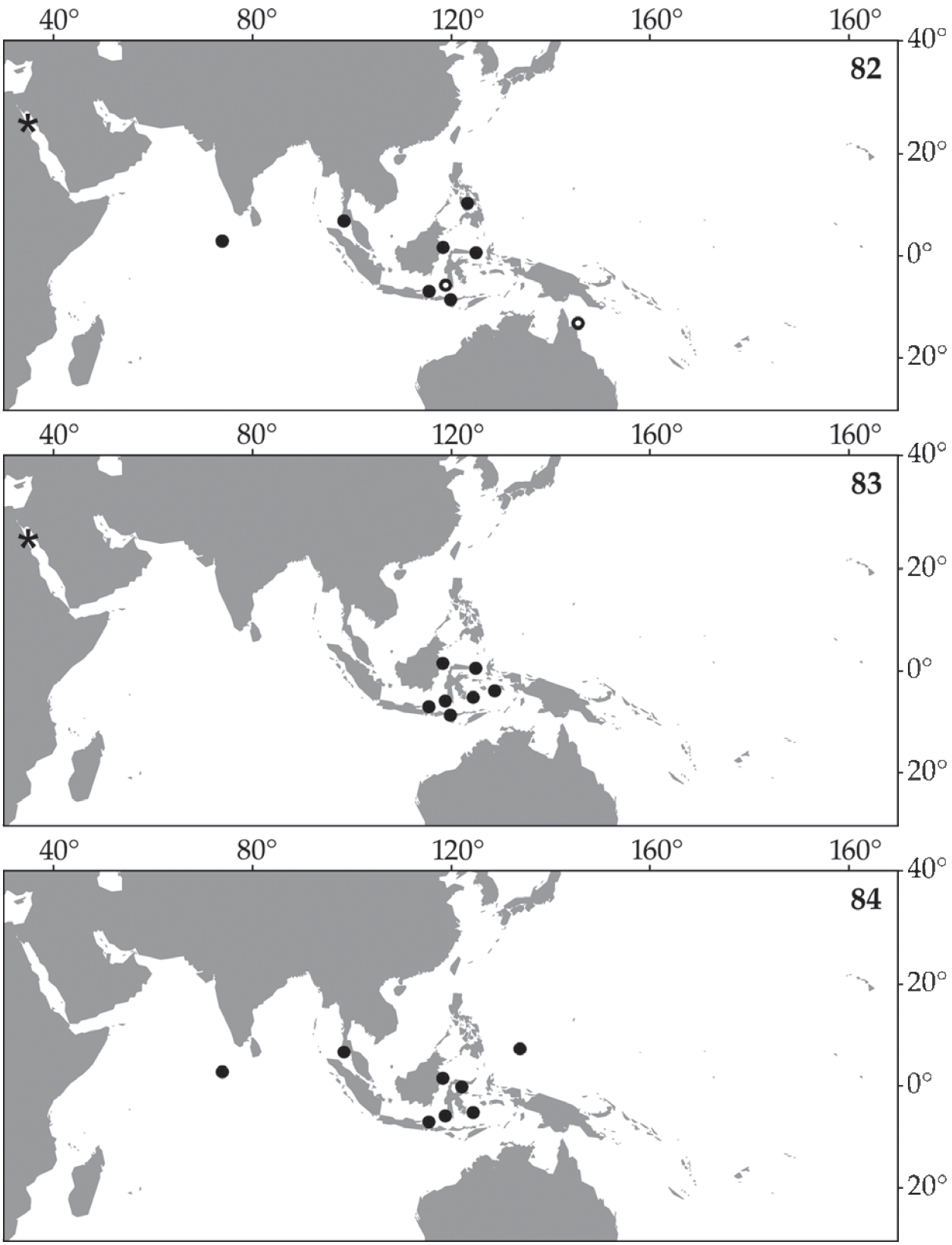
Figs 79-81. The Indo-Pacific region, from the Red Sea to the Hawaiian archipelago, illustrating *Epifungium* species ranges. New records (dots) and personally studied material (circles); 79, *Epifungium adscabra* spec. nov.; 80, *E. hartogi*; 81, *E. hoeksemai*.

The teeth (fig. 15) are attached to the radular plate along the bases, which takes about half of the length of a tooth. The number of secondary cusps (table 2) gradually increases from 1 on the innermost tooth to 6 on the 10th tooth (fig. 15, indicated by "sc"), after which the number gradually decreases to 1 on the ultimate, i.e. 14th tooth. The apical cusp and the secondary cusp directly underneath it are usually similar in size and somewhat curved towards each other; all other secondary cusps are slightly smaller, similar to each other in size, and usually not curved (fig. 15). Starting from the innermost, smallest tooth, with a height of 0.020 mm (n = 1), the teeth gradually increase in size to about two times that height, i.e. 0.042 mm (n = 1), up to the 10th tooth, after which they gradually become somewhat smaller until the penultimate, 0.036 mm high 13th tooth, which is followed by the much smaller 14th ultimate tooth, with a height of 0.022 mm (table 2).

Jaw (fig. 253; table 2). Only the outer surface of one jaw could be studied. The denticulate edge consists of a row of slender, blunt denticles (fig. 253). They have a maximum size of 0.0033 mm. Seen from the outside (fig. 253), 56 denticles per 0.05 mm extend above a 0.0100 mm broad, slightly granulated jaw-flap, which lies merged with the jaw over part of the jaw-pattern. This pattern, as far as visible under the jaw-flap, consists of two or three rows of somewhat sunken, densely pitted, pentagonal figures, under which the pattern is obsolete.

Spawn (figs 278-279). Egg-capsules (fig. 278) ovoid, without any protuberances, sometimes embedded with sand, 0.69-1.58 mm (mean = 1.22, n = 15) in diameter, e.g. measured horizontally, from left to right in figure 278, containing 161-272 eggs (mean = 219.6, n = 13) each. The mucus threads that connect the egg-capsules are straight and not sculptured (fig. 279).

Habitat. The snails and their egg-capsules were found at 6-30 m, associated with exclusively the mushroom coral species *Fungia* (*Pleuractis*) *gravis* Nemenzo, 1955. The snails usually live attached with their mucus threads to the underside of their hosts. Most host corals were found deeper than 20 meters, on a sandy, nearly flat bottom, situated along the lower border of a steeper coral slope.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160°
160°
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20°
0°
20°
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83
84

Distribution (fig. 83). The species is known from Indonesia only.

Differentiation. *Epifungium adgravis* spec. nov. is distributed throughout the Indo-Malayan area (fig. 83). It is the only epitoniid species that is known to be associated with *Fungia* (*Pleuractis*) *gravis*. Conchologically this species (figs 63-64, 101, 121) most closely resembles *E. marki* spec. nov. (figs 62, 77, 106, 126), which is endemic to the Red Sea (fig. 83). *Epifungium adgravis* spec. nov. differs from *E. marki* spec. nov. in having 23-31 costae (mean = 25.8, n = 6) instead of 30-38 costae (mean = 33.3, n = 3) on the 9th-10th teleoconch whorl, 18 (n = 1) instead of 31 (n = 1) axial lines on protoconch whorl 2¼-2¾ (figs 101, 106) and in having 21-22 wavy, segmented threads per 0.1 mm (n = 2) on the operculum instead of 34 per 0.1 mm (n = 1) (figs 141, 146). In *E. marki* spec. nov. the shells also have a somewhat deeper suture (figs 62-64). The shells of *E. adgravis* spec. nov. also resemble those of *E. nielsi* spec. nov. (figs 65, 107, 127), differing especially by the more convex, somewhat broader whorls, which becomes apparent when the width of about the 3rd teleoconch whorl is measured (table 1). Both major and minor spiral threads can be distinguished in most shells of *E. adgravis* spec. nov., but not in *E. nielsi* spec. nov. The spiral threads on the initial teleoconch whorls are usually obsolete above the periphery in *E. adgravis* spec. nov., where they are usually clearly discernible in *E. nielsi* spec. nov. The egg-capsules of *E. adgravis* spec. nov. and *E. nielsi* spec. nov. differ in being smooth (fig. 278) versus with many protuberances (fig. 290), connected to each other by a straight (fig. 279) versus a strongly twisted mucus thread (fig. 291), and by containing over 161 versus less than 137 eggs each.

Etymology. This species is named after its restricted habitat, being found exclusively on *Fungia* (*Pleuractis*) *gravis* Nemenzo, 1955.

Figs 82-84. The Indo-Pacific region, from the Red Sea to the Hawaiian archipelago, illustrating *Epifungium* species ranges. New records (dots and stars) and personally studied material (circles); 82, dots and circles = *Epifungium lochi*, star in the Red Sea = *E. pseudolochi* spec. nov.; 83, dots = *E. adgravis* spec. nov., star in the Red Sea = *E. marki* spec. nov.; 84, *E. nielsi* spec. nov.

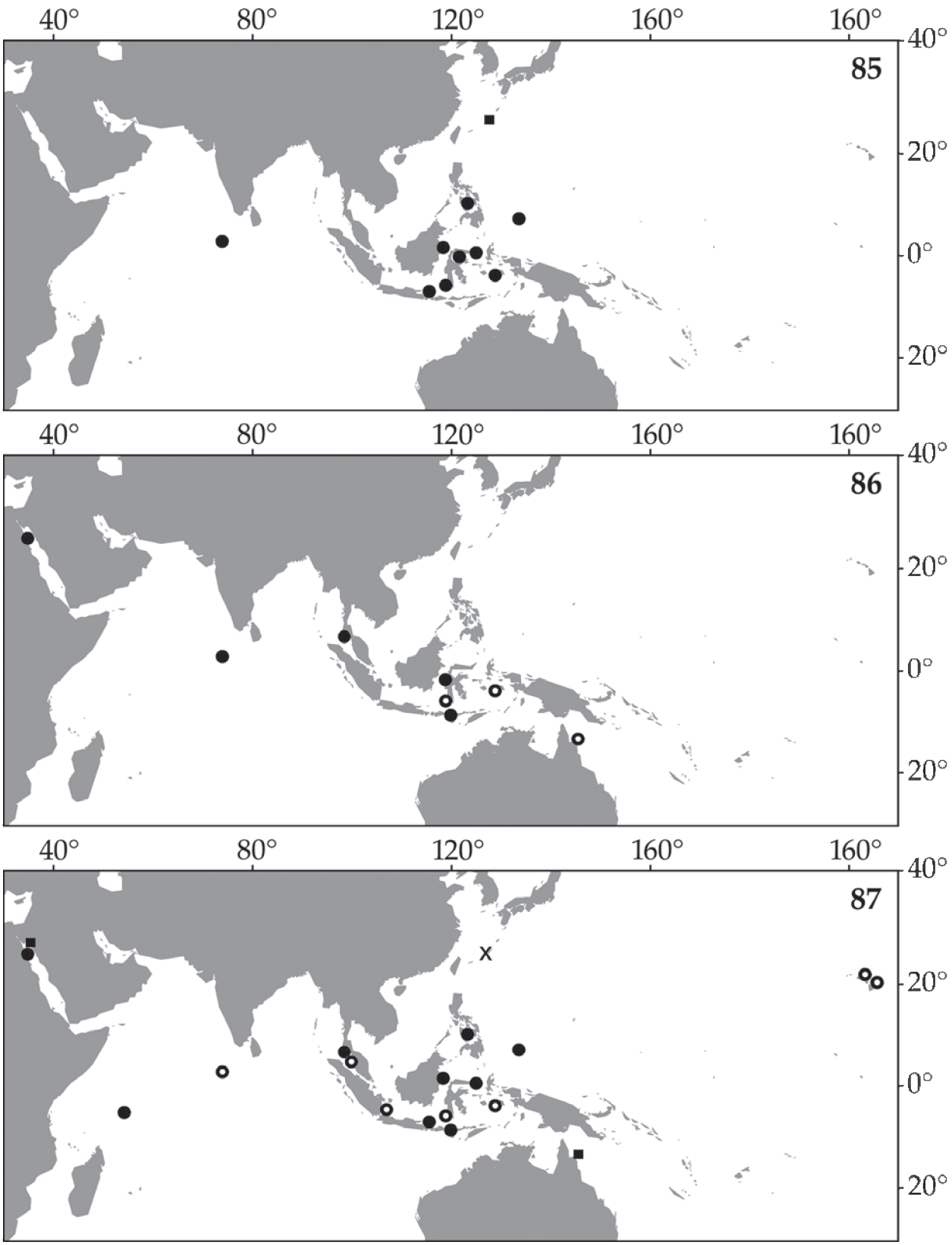
Remarks. Molecular analyses (A. Gittenberger *et al.*, in prep.) indicate that *Epifungium adgravis* spec. nov. and *E. adscabra* spec. nov. (fig. 69) are sister species although they differ considerably conchologically. In shell characters *E. adgravis* spec. nov. is most similar to *E. marki* spec. nov., the sister species of *E. pseudolochi* spec. nov. These two species couples are sister groups again. See also the remarks on *E. pseudolochi* spec. nov.

Epifungium adscabra spec. nov.

Material (always hosted by *Fungia* (*Verrillofungia*) *scabra*). INDONESIA. SW Sulawesi, Spermonde archipelago: W Kudingareng Keke Island (05°06'09"S 119°17'09"E), holotype RMNH 95034/1sh, d with egg-capsules RMNH 100332; paratypes: type locality, RMNH 100333/1sn, 1sh, o, found together with holotype, RMNH 43178/1sh, 43225/1sh, 43225/1sh, 43174/1sh; E Kudingareng Keke Island (05°06'S 119°17'E), RMNH 43279/1sh, 43281/1sh, 43283/1sh, 43286/1sh, 43296/1sh, 43288/1sh, 43297/1sh, 43306/1sh; W Bona Baku reef (05°07'56"S 119°21'39"E), RMNH 43277/1sh, 43267/1sh; W Samalona Island (05°07'31"S 119°20'31"E), RMNH 43229/1sh; E Samalona Island (05°07'28"S 119°20'38"E), RMNH 43249/7sh, 43244/1sh, 43251/2sh. NE Kalimantan, Berau Islands, W Panjang Island (02°21'17"N 118°11'13"E), RMNH 100138/2sn, 1sh, o, d.

Type locality. INDONESIA. SW Sulawesi, Spermonde archipelago: W Kudingareng Keke Island (05°06'09"S 119°17'09"E).

Shell (figs 69, 102, 122; table 1). Shell fragile, elongate-conical, with convex whorls, creamy white; reaching 7.2 mm in height. For dimensions and number of costal and spiral ribs on the 2nd and the 5th teleoconch whorls, see table 1. The holotype (fig. 69) measures 7.2 × 3.8 mm. The protoconch (fig. 102) has 3¼-3½ whorls (n = 10); apart from its smooth apical part, it is sculptured with regularly spaced, very fine, incised, axial lines, 23 (n = 1) per 0.2 mm on protoconch whorl 2¼-2¾. The teleoconch (fig. 122) has up to 9¼ whorls, separated by a moderately deep suture; it is sculptured with mostly regularly placed, usually continuous, orthocline, lamellar, low costae, touching the adjoining whorls, slightly curving adaperturally at the preceding whorl. Costae usually not coronate; some costae become slightly coronate, just before reaching the preceding whorl. The number of costae on the 2nd, 3rd, 5th and younger teleoconch whorls remains approximately the same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(adjoining whorls differing in about two costae). There are up to 23 costae on a whorl; on the 6th whorl in a shell of 6.8 mm in height. The teleoconch is additionally sculptured with very low, inconspicuous, spiral threads. On some teleoconch whorls the spiral threads are obsolete; on the initial whorls they are usually obsolete above the periphery. Although the number of spiral threads approximately doubles between the 2nd and the 5th teleoconch whorl, it usually remains the same afterwards. In some specimens the number of spiral threads keeps on increasing strongly, resulting in numerous spirals from about the 7th whorl onwards. Aperture subcircular. Half of the specimens (7 out of 14) have a very narrow umbilicus, visible in oblique view only. The other seven specimens have a closed umbilicus. The size of the umbilicus is not correlated with shell-size.

Operculum (fig. 142). Operculum paucispiral, with interconnected coils as in *Surrepifungium patamakanthini* spec. nov. (fig. 3). At the outside (fig. 142) there are 28 wavy, segmented threads per 0.1 mm (n = 1), running about perpendicular to the growth lines.

Radula and Jaw. Unknown.

Spawn (figs 280-281). Egg-capsules (fig. 280) ovoid, smooth, without any protuberances, embedded with sand, 0.75-0.91 mm (mean = 0.82, n = 4) in diameter, e.g. measured horizontally, from left to right in figure 280, containing 25-33 eggs (mean = 28.3, n = 4) each. The mucus threads that connect the egg-capsules are straight and not sculptured (fig. 281).

Habitat. The snails and their egg-capsules were found at 3-18 m, associated with exclusively the mushroom coral species *Fungia* (*Verrillofungia*) *scabra* Döderlein, 1901. They usually live attached with their mucus threads to the underside of their hosts, close to the outer edge of the coral. Most host corals were found on coral slopes.

Figs 85-87. The Indo-Pacific region, from the Red Sea to the Hawaiian archipelago, illustrating *Epifungium* species ranges. New records based on collected material (dots) and observed, but not collected material (crosses). Published records, based on personally studied material (circles), photographs only (squares); 85, *Epifungium pseudotwilae* spec. nov.; 86, *E. twilae*; 87, *E. ulu*.

Distribution (fig. 79). The species has a relatively small range. It is only known from Indonesia.

Differentiation. The shells of this species resemble those of *Epifungium adgravis* spec. nov. and *E. marki* spec. nov., from which they can be distinguished by the much smaller width of the 5th teleoconch whorl (figs 121-122, 126), the presence of on average 19-20 instead of 24-26 costal ribs on the 2nd, 3rd and 5th teleoconch whorls (table 1), and an average shell height/width index of 2.0 instead of 2.9 (table 1). *Epifungium adscabra* is the only epitoniid species that is known to be associated with *Fungia* (*Verrillofungia*) *scabra*.

Etymology. This species is named after its restricted habitat. It was found exclusively on corals of *Fungia* (*Verrillofungia*) *scabra*.

Remarks. See the remarks of *Epifungium adgravis* spec. nov. and *E. ulu*.

Epifungium hartogi (A. Gittenberger, 2003)

Epitonium hartogi A. Gittenberger, 2003: 139.

Material. INDONESIA (hosted by either *Plerogyra simplex* or *P. diabolotus*). SW Sulawesi, Spermonde archipelago: holotype (hosted by *P. simplex*) RMNH 94924 and RMNH 94925-94933 (22 paratypes, with 6 clutches of egg-capsules, 1 r, 3 d). THAILAND (hosted by *P. diabolotus*). Krabi, Phiphi Islands: 1 paratype with egg-capsules (RMNH 95989).

Type locality. INDONESIA. SW Sulawesi, Spermonde archipelago.

Shell (figs 74, 103, 123). Shell fragile, elongate-conical, with convex whorls, purplish to creamy white; reaching 8.2 mm in height. For dimensions and number of costal and spiral ribs on the 2nd and the 5th teleoconch whorls, see table 1. The protoconch (fig. 103) has 3¼-3½ whorls (n = 10); apart from its smooth apical part, it is sculptured with regularly spaced, very fine, incised, axial lines, 15 (n = 1) per 0.2 mm on protoconch whorl 2½-3. From the 5th teleoconch whorl onwards, the shell is sculptured with irregularly spaced, irregularly placed, mostly split, usually not continuous, orthocline, low costae, without any particular notches or processes, barely


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touching the adjoining whorls, and numerous low spiral ribs (fig. 123).

Operculum (fig. 143). Operculum paucispiral, with interconnected coils as in *Surrepifungium patamakanthini* spec. nov. (fig. 3). At the outside of the operculum (fig. 143) there are 23-24 wavy, segmented threads per 0.1 mm (mean = 23.8, n = 4), running about perpendicular to the growth lines.

Radula (figs 169, 189, 209; table 2). Three radulae from Indonesian snails could be studied (A. Gittenberger, 2000: 143). The teeth could be counted accurately in one radula only (table 2). Each tooth (figs 169, 189, 209) consists of a slender stem and broad blade, which merge gradually; the blade has 1-6 acute, secondary cusps. The teeth (fig. 169) are attached to the radular plate along the bases, which takes about half of the length of a tooth. The number of secondary cusps (table 2) gradually increases from 1 or 2 on the innermost tooth (fig. 189, left) to 6 on the penultimate, i.e. 24th tooth (fig. 209, right), after which the ultimate, i.e. 25th tooth follows with 2 secondary cusps (fig. 169, right). The apical cusp and the secondary cusp directly underneath it are usually similar in size and somewhat curved upward, away from the stem; all other secondary cusps are slightly smaller, similar to each other in size, and usually not curved (figs 169, 209). Starting from the innermost, smallest tooth, with a height of 0.022 mm, the teeth gradually increase in size to about two times that height, i.e. to 0.047 mm in the penultimate tooth, which is followed by the ultimate, usually malformed 25th tooth, with a height of 0.040 mm (table 2).

Jaw (fig. 254; table 2). Only one jaw was studied (A. Gittenberger, 2000: 145). The denticulate edge consists of a row of slender, blunt denticles (fig. 254). They have a maximum size of 0.0035 mm. Seen from the outside (fig. 254), 65 denticles per 0.05 mm extend above a 0.0179 mm broad, smooth to granulated jaw-flap, which lies merged with the jaw over part of the jaw-pattern. The pattern under the jaw-flap consists of three or four rows of somewhat sunken, pentagonal figures, of which the lower two rows are densely pitted. Underneath this pattern the surface is smooth to granulate. The inner surface of the jaw is unknown.

Spawn (figs 282-283). Egg-capsules (fig. 282; A. Gittenberger, 2003: 140, fig. 8) ovoid, somewhat transparent, with conspicuous protuberances, not embedded with sand, 1.55-1.57 mm (mean = 1.56, n = 4) in diameter, e.g. measured horizontally, from left to right in figure 282, containing 230-415 eggs (mean = 328, n = 6) each. The mucus threads that connect the egg-capsules are strongly twisted and not sculptured (fig. 283).

Habitat. The snails and their egg-capsules were found at 9-18 m, attached with mucus threads to the corals *Plerogyra simplex* Rehberg, 1892, and *P. diabolotus* Ditlev, 2003 (Scleractinia, Euphyllidae).

Distribution (fig. 80). The species is known from Thailand and Indonesia.

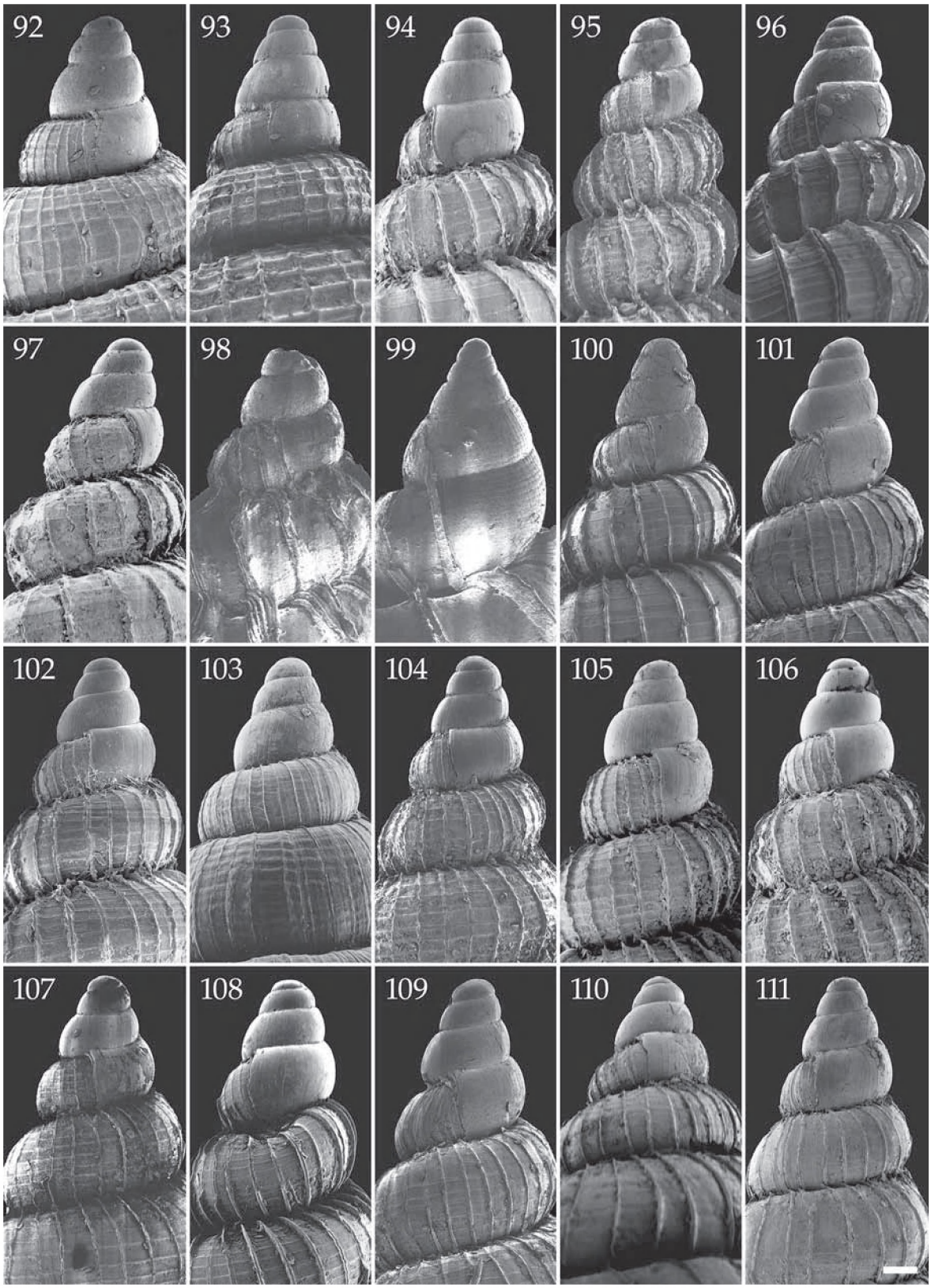
Differentiation. *Epifungium hartogi* is the only epitoniid species that is known to be associated with euphyllid corals. The shells differ from those of the similar species *E. adgravis* spec. nov., *E. hoeksemai*, *E. marki* spec. nov., *E. nielsi* spec. nov. and *E. ulu*, in their purplish colour and by the very irregularly spaced, irregularly placed, mostly split, low costae that are present from about the 5th teleoconch whorl onwards. See A. Gittenberger (2003), for comparisons with the epitoniid species *Epifungium hoeksemai*, *E. lochi*, *E. twilae*, *E. ulu*, *Epitonium albidum* (Orbigny, 1842), "*Epitonium billeeanum*" (= *Epidendrium aureum* spec. nov.), *E. millecostatum* (Pease, 1860), *E. pyramidalis*, *Surrepifungium costulatum*, *S. ingridae*, and *Nitidiscala tincta* (Carpenter, 1865).

Remarks. See A. Gittenberger (2003), for a more detailed description. Here some additional data are given, with notes that may be relevant for the differentiation of this species.

Epifungium hoeksemai (A. Gittenberger and Goud, 2000)

Epitonium hoeksemai A. Gittenberger and Goud, 2000: 4-6, figs 9-10, 18, 20, 26, 43.

Figs 88-91. Shells. 88-89, *Epifungium twilae*, SW Sulawesi, Indonesia; 88, paratype; 89, holotype. 90-91, *E. pseudotwilae* spec. nov.; 90, holotype, Palau; 91, paratype, Kalimantan, Indonesia. Scale bar = 1 cm.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Material. INDONESIA (hosted by either *Heliofungia actiniformis* or *Fungia (Fungia) fungites*). SW Sulawesi, Spermonde archipelago: holotype (hosted by *F. (F.) fungites*): RMNH 59074 and 20 paratypes, viz. RMNH 59075-59087, with 4 clutches of egg-capsules. Additionally studied material: 40 specimens, 11 clutches of egg-capsules, 3 d. PALAU (all hosted by *F. (F.) fungites*). Off Koror: 12 specimens, 7 clutches of egg-capsules.

Type locality. INDONESIA. SW Sulawesi, Spermonde archipelago.

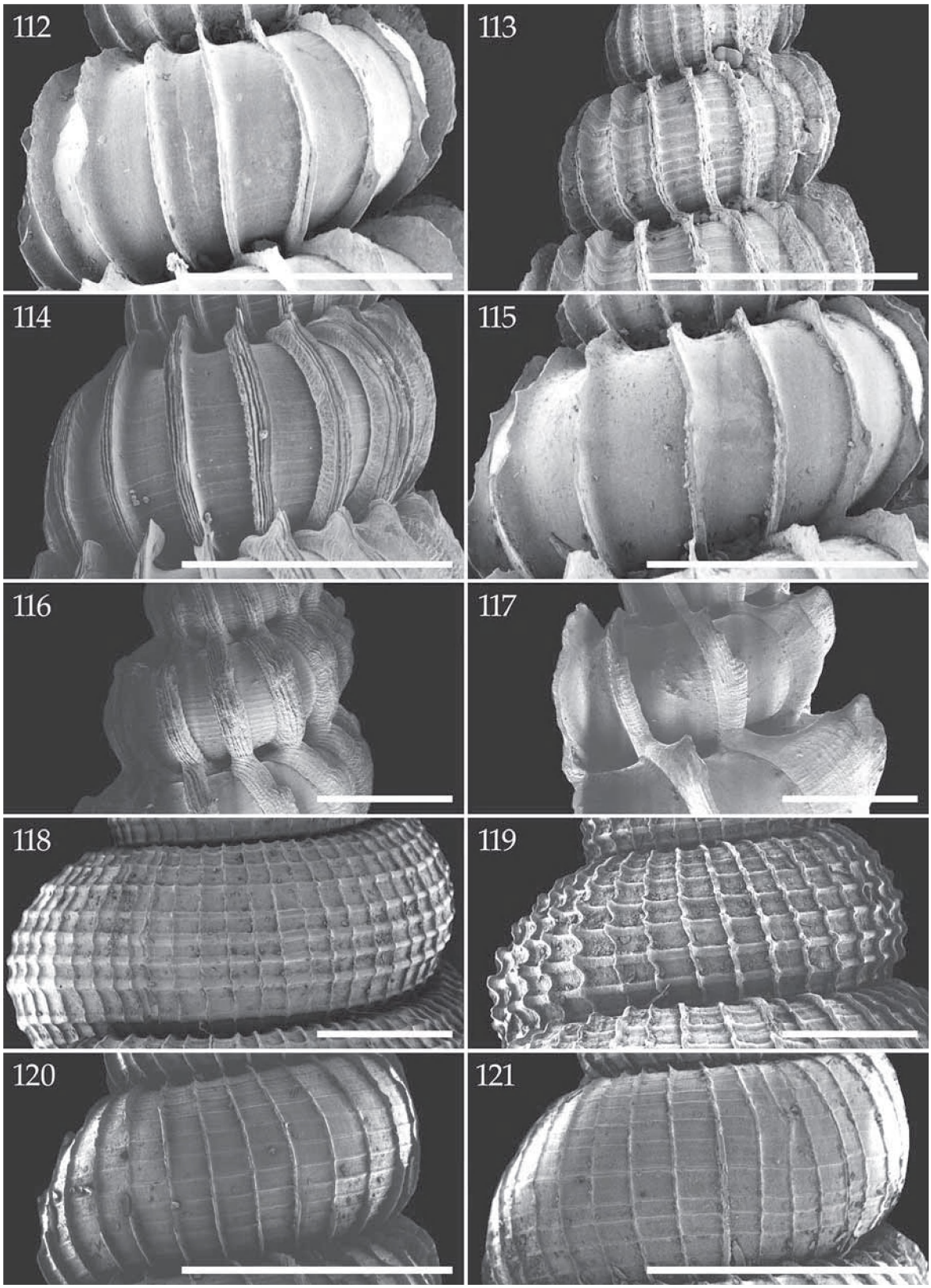
Shell (figs 75-76, 104, 124; table 1). Shell fragile, elongate-conical, with convex whorls, creamy white; reaching 19.0 mm in height. For dimensions and number of costal and spiral ribs on the 2nd and the 5th teleoconch whorls, see table 1. The holotype measures 13.0 × 5.6 mm. The protoconch (fig. 104) has 3¼-3½ whorls (n = 10); apart from its smooth apical part, it is sculptured with regularly spaced, very fine, incised, axial lines, 22 (n = 1) per 0.2 mm on protoconch whorl 2¼-2¾. The teleoconch (fig. 124) has up to 11 whorls, separated by a moderately deep suture; it is sculptured with mostly regularly placed, usually discontinuous, orthocline, lamellar, low costae, not or barely touching the adjoining whorls, slightly curving adaperturally at the preceding whorl. Just before reaching the preceding whorl the costae become slightly coronate. The number of costae on the 2nd, 3rd, 5th teleoconch whorls increases quickly (table 1). Usually this number remains approximately the same (adjoining whorls differing in about two costae) from the 6th whorl onwards (14 of 18 specimens). However, in some shells (4 of 18) it keeps on increasing, and then the number of costae per whorl approximately doubles between the 5th and the 8th teleoconch whorl, reaching up to 79 on the 10th whorl in a shell of 18.8 mm in height. The teleoconch is additionally sculptured with very low, distinct, evenly distributed spiral threads. The number of spiral threads strongly increases towards the younger teleoconch whorls, becoming numerous from about the 6th whorl onwards. Aperture subcircular. The shells have a narrow umbilicus, which is usually visible in oblique view only.

Figs 92-111. Protoconchs. 92, *Epidendrium aureum*; 93, *E. sordidum*; 94, *Surrepifungium costulatum*; 95, *S. ingridae*; 96, *S. patamakanthini*; 97, *S. oliverioi*; 98, *Epitonium crassicostatum*; 99, *E. graviarmatum*; 100, *Epifungium adgranulosa*; 101, *E. adgravis*; 102, *E. adscabra*; 103, *E. hartogi*; 104, *E. hoeksemai*; 105, *E. lochi*; 106, *E. marki*; 107, *E. nielsi*; 108, *E. pseudolochi*; 109, *E. pseudotwilae*; 110, *E. twilae*; 111, *E. ulu*. 92, 94, 98, 100-104, 109, Indonesia; 93, 95-97, Palau; 99, Maldives; 105, 107, 110, 111, Thailand; 106, 108, Egypt. Scale bar = 0.1 mm. SEM Photos.

Operculum (fig. 144). Operculum paucispiral, with interconnected coils as in *Surrepifungium patamakanthini* spec. nov. (fig. 3). At the outside of the operculum (fig. 144) there are 30 wavy, segmented threads per 0.1 mm (n = 1), running about perpendicular to the growth lines.

Radula (figs 170, 190, 210; table 2). Two radulae from specimens from Palau could be studied (table 2). Each tooth has an irregularly triangular shape, starting very narrow and gradually becoming very broad towards the apical part (fig. 170). The stem and the blade merge gradually; the blade has 1-3 acute, secondary cusps. The teeth are attached to the radular plate along the bases, which takes about ¾ of the length of a tooth (figs 170, 190, 210). The innermost tooth has one secondary cusp while all other teeth usually have two; the 11th tooth of one of the radulae has 3 secondary cusps (table 2). The straight, acute, secondary cusps are somewhat smaller than the acute, apical cusp, which is slightly curved upwards, away from the stem (figs 170, 190, 210). Starting from the innermost, smallest tooth, with a height of 0.018 mm (n = 2), the teeth gradually increase in size to about 1½ times that height, i.e. 0.027-0.028 mm (n = 2), up to the penultimate, i.e. 17th-18th tooth (n = 2), after which the ultimate, somewhat smaller, 18th-19th tooth, with a height of 0.022-0.025 mm (n = 2) follows (table 2).

Jaw (figs 11, 255-256, 261; table 2). The denticulate edge consists of a row of slender, blunt denticles, which are basally pitted on the inside (fig. 261). They have a maximum size of 0.0030-0.032 mm (n = 2). Seen from the outside (figs 255-256), 58-64 denticles per 0.05 mm (n = 2) extend above a 0.0074-0.0120 mm (n = 2) broad, smooth to granulated jaw-flap, which lies loosely over part of the jaw-pattern. The pattern under the jaw-flap consists of rows of pitted, sunken, pentagonal figures, gradually becoming obsolete away from the denticulate edge. On the inner surface of the jaw (fig. 261), just below the denticles, there is a row of engraved, scarcely pitted, irregularly square-like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figures, followed by an area that is somewhat granulated to smooth.

Spawn (figs 284-285). Egg-capsules (fig. 284) ovoid, with distinct protuberances, sometimes embedded with sand, 1.11-1.85 mm (mean = 1.45, n = 6) in diameter, e.g. measured horizontally, from left to right in figure 284, containing 136-350 eggs (mean = 215.8, n = 6) each. The mucus threads that connect the egg-capsules are strongly twisted and not sculptured (fig. 285).

Habitat. The snails and their egg-capsules were found at 1-20 m depth, associated with *Heliofungia actiniformis* (Quoy and Gaimard, 1833) and *Fungia* (*Fungia*) *fungites* (Linnaeus, 1758). They usually live attached with their mucus threads to the underside of these mushroom corals or to the hard substrata underneath. Sometimes the snails occur buried in the sand underneath the host. Most host corals were found on coral slopes.

Distribution (fig. 81). The species is known from Indonesia and Palau.

Differentiation. Conchologically this species resembles *Epifungium adgravis* spec. nov., *E. marki* spec. nov., *E. nielsi* spec. nov. and *E. ulu.* It differs most clearly from these species by the sculpture of spiral lines, which are distinct instead of sometimes obsolete on the initial teleoconch whorls, evenly distributed instead of more prominent underneath the periphery of a whorl and increasingly more numerous in between the 2nd and the 5th teleoconch whorl (table 1). On average the number of spiral threads on the 5th teleoconch whorl is much higher and the shell height/width index is lower than in the most similar species (table 1).

Remarks. For a more detailed description of the shell and the proboscis, see A. Gittenberger *et al.* (2000).

Figs 112-121. T5 teleoconch whorls (see Fig. 1). 112, *Surrepifungium costulatum*; 113, *S. ingridae*; 114, *S. patamakanthini*; 115, *S. oliverioi*; 116, *Epitonium crassicostatum*; 117 *E. graviarmatum*; 118, *Epidendrium aureum*; 119, *E. sordidum*; 120, *Epifungium adgranulosa*; 121, *E. adgravis*. 112, 116, 118, 120-121, Indonesia; 113-115, 119, Palau; 117, Maldives. Scale bars = 1 mm. SEM Photos.

Here some additional data are given, with notes that may be relevant for the differentiation of this species. See also the remarks on *Epifungium ulu*.

Epifungium lochi (A. Gittenberger and Goud, 2000)

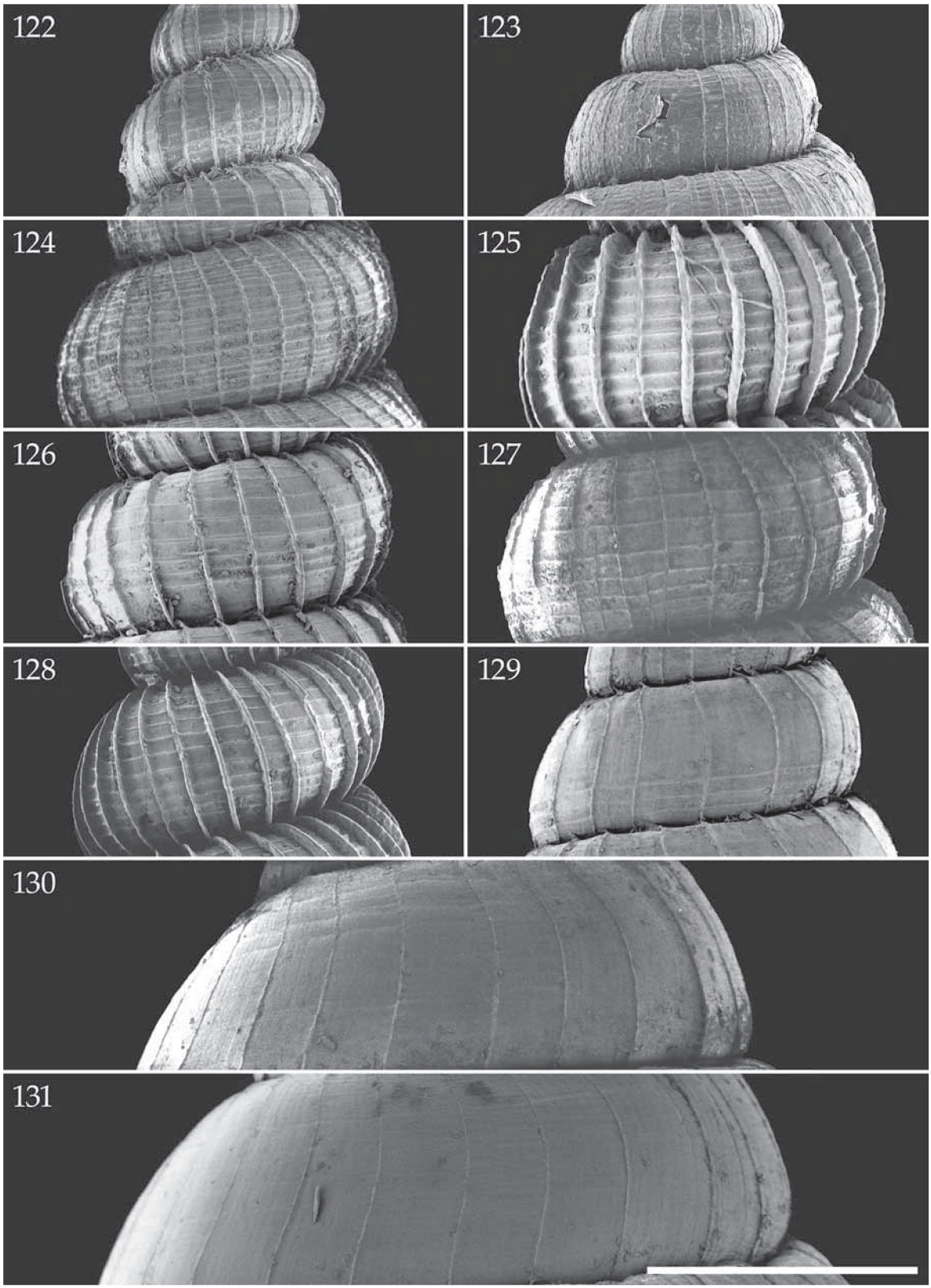
Epitonium lochi A. Gittenberger and Goud, 2000: 9-10, figs 13-16, 37, 45.

?*Epitonium* species 4: Loch, 1982: 4-5, 1 fig. (see differentiation below).

Material. INDONESIA. SW Sulawesi, Spermonde archipelago (hosted by *Fungia* (*Cycloseris*) *costulata*, *F. (C.) sinensis*, *F. (C.) somervillei*, *F. (C.) tenuis*, *F. (C.) vaughani*), holotype (hosted by *F.* (*C.*) *costulata*): RMNH 59094 and 10 paratypes with 2 clutches of egg-capsules: RMNH 59095-59103. Additionally studied material: 19 specimens, 4 clutches of egg-capsules, 1 d. N Sulawesi (hosted by *Fungia* (*C.*) *costulata*), 1 specimen. NE Kalimantan, Berau Islands (hosted by *F.* (*C.*) *fragilis*), 1 specimen, 1 clutch of egg-capsules. Bali (hosted by *Fungia* (*C.*) *costulata*, *F. (C.) distorta*, *F. (C.) fragilis*, *F. (C.) somervillei*, *F. (C.) tenuis*), 15 specimens, 3 clutches of egg-capsules, 1 d. NE Komodo (hosted by *F. (C.) fragilis*, *F. (C.) vaughani*), 2 specimens, 1 d. MALDIVES. Ari Atoll, off Vilamendhoo Island (hosted by *F.* (*C.*) *tenuis*), 1 specimen. THAILAND. Krabi, Phiphi Islands (hosted by *F.* (*C.*) *fragilis* and *F.* (C.) *vaughani*), 11 specimens, 4 clutches of egg-capsules, 2 d. PHILLIPPINES. Cebu (hosted by *F.* (*C.*) *costulata*), 7 specimens, 1 clutch of egg-capsules. AUSTRALIA. Queensland, Lizard Island (hosted by *F.* (*C.*) spp.), from the Australian Museum, Sydney (AMS 329687-329688), 4 specimens, 1 clutch of egg-capsules.

Type locality. INDONESIA. SW Sulawesi, Spermonde archipelago.

Shell (figs 66-67, 105, 125; table 1). Shell fragile, elongate-conical, with convex whorls, creamy white; reaching 13.1 mm in height. For dimensions and number of costal and spiral ribs on the 2nd and the 5th teleoconch whorls, see table 1. The holotype (fig. 67) measures 8.5 × 3.7 mm. The protoconch (fig. 105) has 3¼-3½ whorls (n = 10); apart from its smooth apical part, it is sculptured with regularly spaced, very fine, incised, axial lines, 20 (n = 1) per 0.2 mm on protoconch whorl 2¼-2¾. The teleoconch (fig. 125) has up to 9½ whorls, separated by a very deep suture; it is sculptured with mostly regularly placed, usually discontinuous, orthocline, lamellar, not or slightly curved, low costae, not or hardly touching the adjoining whorls. Just before reaching the preceding whorl the costae become slightly coronate. In 3 out of 10 specimens the number of costae increases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from the 3rd teleoconch whorl onwards, whereas this number decreases in the remaining 7 shells, usually on the 6th and 7th whorl, after which it remains approximately the same. There are up to 26 costae on a whorl; on the 8th whorl in a shell of 8.9 mm in height. The teleoconch is additionally sculptured with very low, distinct, evenly distributed spiral threads. The number of spiral threads gradually increases towards the younger teleoconch whorls, but only rarely becomes numerous. Aperture subcircular. The umbilicus is closed.

Operculum (fig. 145). Operculum paucispiral, with interconnected coils as in *Surrepifungium patamakanthini* spec. nov. (fig. 3). At the outside of the operculum (fig. 145) there are 24-29 wavy, segmented threads per 0.1 mm (n = 2), running about perpendicular to the growth lines.

Radula (figs 168, 171, 191, 211; table 2). Only one radula from an Indonesia snail could be studied (figs 168, 171). The stem and the blade of each tooth are very slender, similar in width and merge gradually; the blade has 2-5 acute, secondary cusps. The teeth (figs 171, 191, 211) are attached to the radular plate along the bases, which takes about half of the length of a tooth. The number of secondary cusps (table 2) gradually increases from 2 on the innermost tooth (fig. 191, left) to 4 on the 5th-10th teeth, after which the penultimate and the ultimate, i.e. 12th tooth, follow with 3 and 2 secondary cusps, respectively (fig. 211, right). The apical cusp and the secondary cusp directly underneath it are usually similar in size and somewhat curved towards each other; all other secondary cusps are slightly smaller, similar to each other in size, and curved upwards to the preceding secondary cusp (fig. 212). Starting from the innermost, smallest tooth, with a height of 0.018 mm, the teeth gradually increase in size to two times that height, i.e. 0.034 mm, up to the 8th, after which they remain the same until the penultimate tooth, which is followed by the smaller, 12th tooth with a height of 0.028 mm (table 2).

Figs 122-131. T5 teleoconch whorls (see Fig. 1). 122, *Epifungium adscabra*; 123, *E. hartogi*; 124, *E. hoeksemai*; 125, *E. lochi*; 126, *E. marki*; 127, *E. nielsi*; 128, *E. pseudolochi*; 129, *E. ulu*; 130, *E. pseudotwilae*; 131, *E. twilae*. 122-124, Indonesia; 125, 127, 129, 131, Thailand;126, 128, Egypt; 130, Palau. Scale bar = 1 mm. SEM Photos.

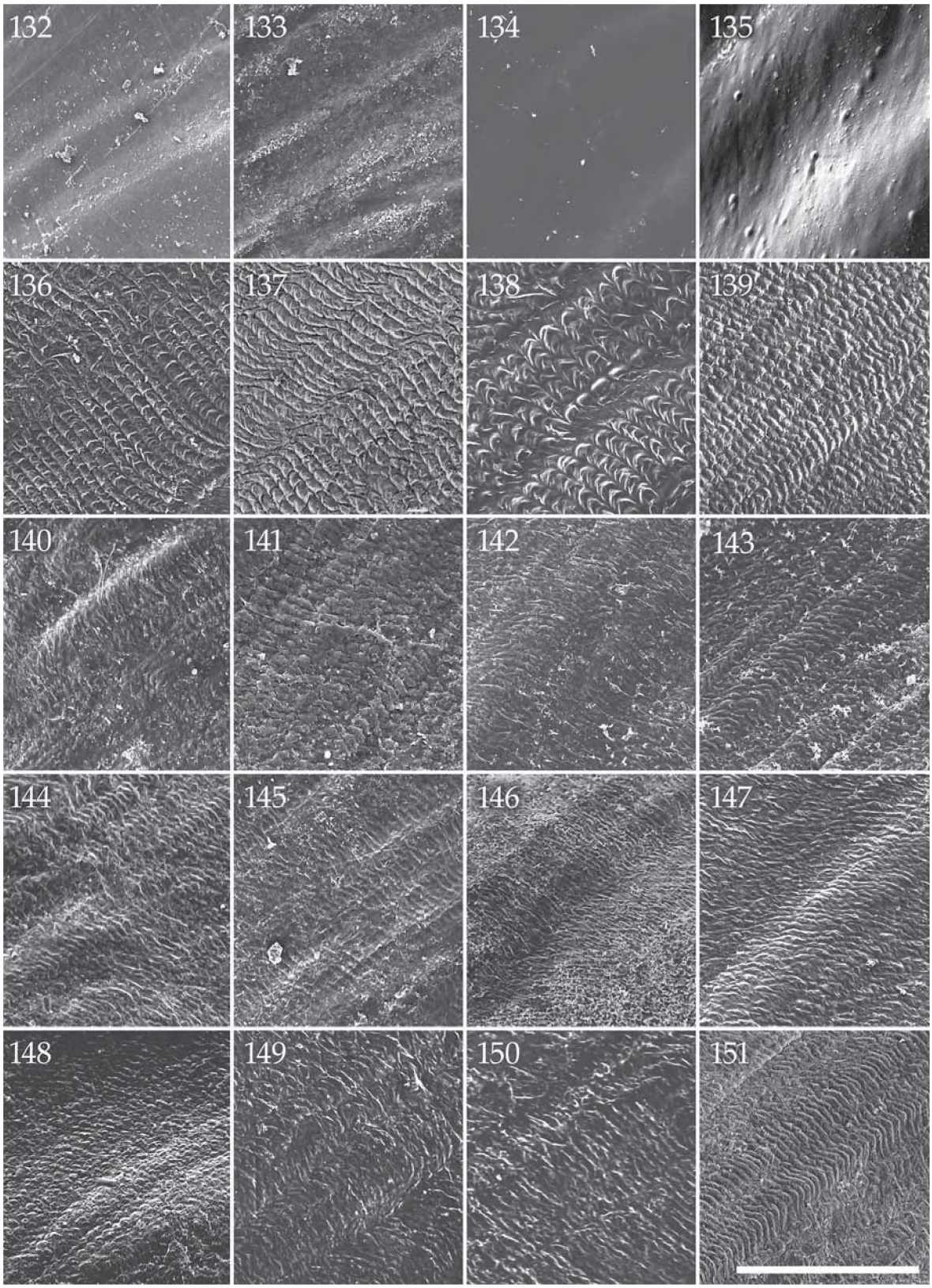
Jaw (figs 257, 262; table 2). The two jaws flanking the studied radula were studied. The denticulate edge consists of a row of slender, blunt denticles, which are basally pitted on the inside (fig. 262). They have a maximum size of 0.0018 mm. Seen from the outside (fig. 257), 72 denticles per 0.05 mm extend above a 0.0060 mm broad, granulated jaw-flap, which lies loosely over part of the jaw-pattern. The pattern under the jaw-flap is vague, but seems to consist of at least several rows of somewhat sunken, pentagonal figures. Most of the jaw is densely pitted, but no pits are discernable directly under the jaw-flap. On the inner surface of the jaw (fig. 262), just below the denticles, there is a row of inconspicuous, engraved, scarcely pitted, irregularly square-like figures, followed by an area that is somewhat granulated to smooth.

Spawn (286-287). Egg-capsules (fig. 286) round to ovoid, without any protuberances, embedded with sand, 0.77-1.40 mm (mean = 1.05, n = 12) in diameter, e.g. measured horizontally, from left to right in figure 286, containing 39-170 eggs (mean = 86, n = 12) each. The mucus threads that connect the egg-capsules are straight and either smooth as in *Epifungium pseudotwilae* spec. nov. (fig. 295) or sculptured with longitudinal lines (fig. 287).

Habitat. The snails and their egg-capsules were found at 3-27 m, associated with *Fungia* (*Cycloseris*) *costulata* Ortmann, 1889, *F. (C.) distorta* Michelin, 1842, *F. (C.) fragilis* (Alcock, 1893), *F. (C.) sinensis* (Milne Edwards and Haime, 1851), *F. (C.) somervillei* Gardiner, 1909, *F. (C.) tenuis* Dana, 1846, or *F. (C.) vaughani* Boschma, 1923. They usually live attached with their mucus threads to the underside of these mushroom corals. Most host corals were found on a sandy, nearly flat bottom, situated along the lower border of a steeper coral slope.

Distribution (fig. 82). The species is known from the Indo-West Pacific, from the Maldives, Thailand, Philippines and Indonesia to Australia.

Differentiation. The shells of this species most closely resemble those of *Epifungium pseudolochi* spec. nov., but differ in having a less deep suture between the teleoconch whorls (figs 66-68, 105, 108, 125, 128), and by costae, which become slightly higher, i.e. coronate, before the preceding whorl (fig.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125), instead of remaining equally high and thus not at all coronate (fig. 128). *Epifungium lochi* also resembles *E. adscabra* spec. nov., *E. adgravis* spec. nov., *E. marki* spec. nov., *E. nielsi* spec. nov. and *E. ulu* spec. nov. in shell characters, but differs by the distinct spiral threads on all teleoconch whorls, combined with a closed umbilicus. It is associated with *Fungia* (*Cycloseris*) spp. The only other epitoniid species found in association with these hosts are *Epitonium crassicostatum* spec. nov. and *E. graviarmatum* spec. nov. For comparisons with *Epitonium deflersi* (Jousseaume, 1911), *E. oblique* (Sowerby, 1844), *E. zatrephes* Melvill, 1910, and *E. ulu* Pilsbry, 1921, see A. Gittenberger *et al.* (2000).

Remarks. For a more detailed description of the shell and the proboscis, see A. Gittenberger *et al.* (2000). Here some additional data are given, with notes that may be relevant for the differentiation of this species.

Epifungium marki spec. nov.

Material (always hosted by *Fungia* (*Pleuractis*) spec. A). EGYPT. Off Marsa Shagra, about 300 km S of Hurghada, holotype RMNH 95082/1sh, d, with egg-capsules RMNH 100331; paratypes: type locality, RMNH 100329/2sn, found together with the holotype; off Marsa Nakari, about 350 km S of Hurghada, RMNH 95099/1sn, 95100/1sn.

Type locality. EGYPT. Off Marsa Shagra, about 300 km S of Hurghada.

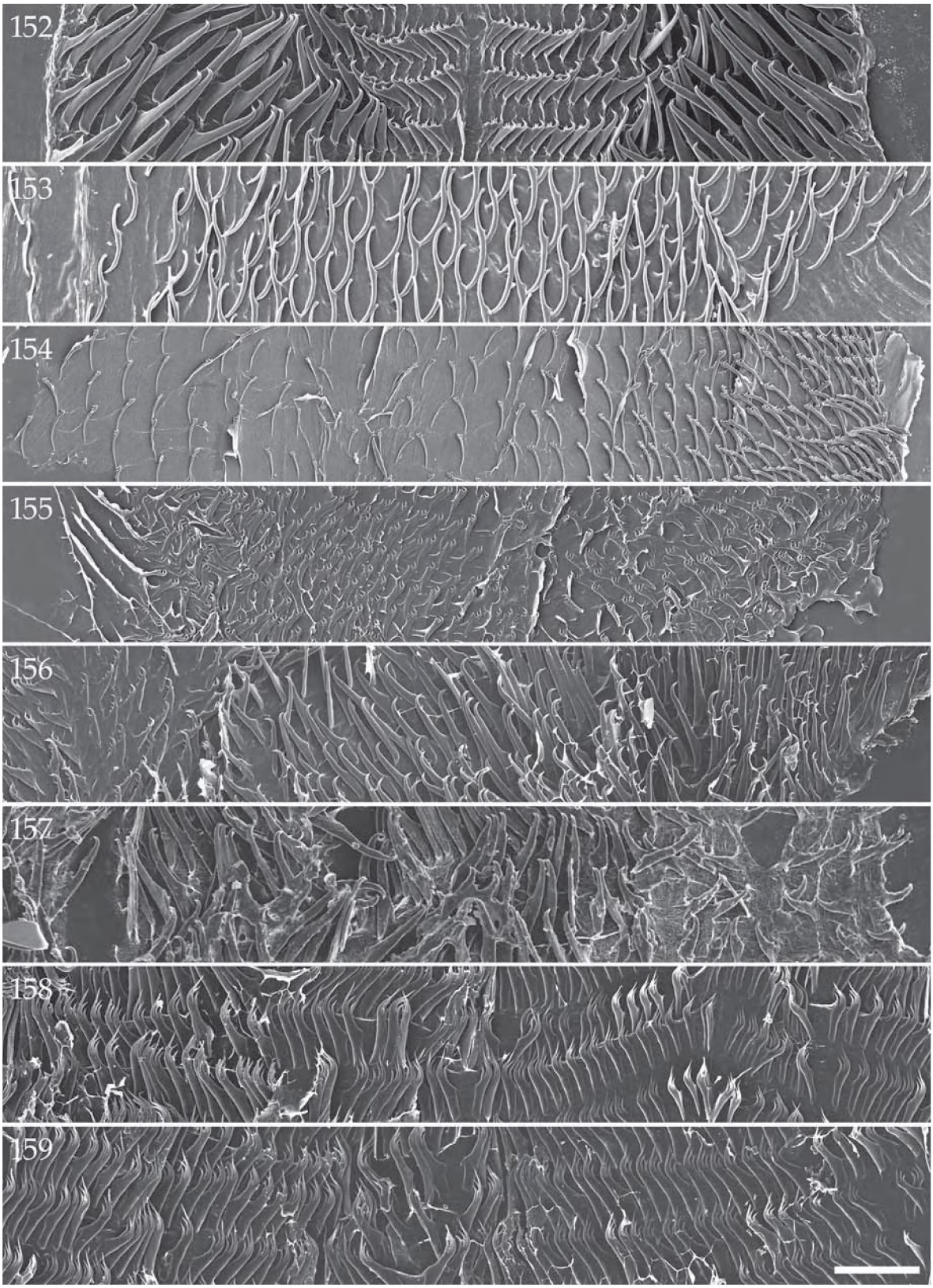
Shell (figs 62, 77-78, 106, 126; table 1). Shell fragile, elongate-conical, with convex whorls, creamy white; reaching 19.2 mm in height. For dimensions and number of costal and spiral ribs on the 2nd and the 5th teleoconch whorls, see table 1. The holotype (fig. 62) measures 19.2 × 6.6 mm. The protoconch (fig. 106) has 3¼-3½ whorls (n = 5); apart from its smooth apical part, it is sculptured with regularly spaced, very fine, incised, axial lines, 31 (n = 1) per 0.2 mm on protoconch whorl 2¼-2¾. The teleoconch (fig. 126) has up to 10.5 whorls, separated by a very deep suture; it is sculptured with mostly regularly placed, usually discontinuous, orthocline, lamellar, not to slightly curved, low costae, not or hardly touching the adjoining whorls. Just before reaching the preceding whorl the costae become slightly coronate. The number of costae on the 2nd, 3rd, 5th and younger teleoconch whorls remains approximately the same in 3 out of 4 specimens (adjoining whorls differing in about two costae); in the fourth specimen this number increases from 24 to 31 on teleoconch whorls 4 and 5. There are up to 38 costae on a whorl; on the 10th whorl of the holotype. Very fine, irregularly placed, incised, axial lines and/or split costae are present from the 7th-9th teleoconch whorl onwards. The teleoconch is additionally sculptured with irregularly placed, relatively thick, spiral threads. From the 6th-9th teleoconch whorl onwards, there are irregularly spaced, thin, spiral threads and incised spiral lines in between and on the major spiral threads. The number of major spiral threads increases from the 2nd to the 5th whorl, after which it remains almost constant. From the 7th-9th whorl onwards, some of the minor spirals may gradually change into thick spiral threads. Aperture subcircular. In the 5 mm high specimen with 5½ teleoconch whorls, the umbilicus is closed; in the other four, larger specimens the umbilicus is very narrow, visible in oblique view only.

Operculum (fig. 146). Operculum paucispiral, with interconnected coils as in *Surrepifungium patamakanthini* spec. nov. (fig. 3). At the outside of the operculum (fig. 146) there are 34 wavy, segmented threads per 0.1 mm (n = 1), running about perpendicular to the growth lines.

Radula and Jaw. Unknown.

Spawn (figs 77, 288-289). Egg-capsules (figs 77, 288) round to ovoid, without any protuberances, embedded with sand, 1.48-1.74 mm (n = 2) in diameter, e.g. measured horizontally, from left to right in figure 288, containing 260-270 eggs (n = 2) each. The mucus threads that connect the egg-capsules are straight and not sculptured (fig. 289).

Figs 132-151. Opercula. 132, 133, *Epidendrium aureum*; 134, *E. sordidum*; 135, *Epitonium pyramidalis*; 136, *Surrepifungium costulatum*; 137, *S. ingridae*; 138, *S. patamakanthini*; 139, *S. oliverioi*; 140, *Epifungium adgranulosa*; 141, *E. adgravis*; 142, *E. adscabra*; 143, *E. hartogi*; 144, *E. hoeksemai*; 145, *E. lochi*; 146, *E. marki*; 147, *E. nielsi*; 148, *E. pseudolochi*; 149, *E. pseudotwilae*; 150, *E. twilae*; 151, *E. ulu*. 132, 134, 136-138, 144, Palau; 133, 141-143, 145, 147,151, Indonesia; 135, 149, Philippines; 139, Maldives; 140, 146, 148, Egypt; 150, Thailand. Scale bar = 0.1 mm. SEM Photos.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Habitat (figs 77-78). The snails and their egg-capsules were found at 15-28 m, attached with mucus threads to the underside of their hosts, which usually lay on the sand just below the lower border of a coral slope. They are associated with *Fungia* (*Pleuractis*) spec. A (figs 77-78), a mushroom coral resembling *Fungia* (*Pleuractis*) *gravis* Nemenzo, 1955, by its discs with a high oral hump and by preferring a similar habitat, i.e. usually deeper than 20 meters, on a sandy, nearly flat bottom, along the lower border of a steeper coral slope. Still *F.* (*P.*) spec. A differs from *F.* (*P.*) *gravis*, resembling other species of the subgenus *Pleuractis*, by the somewhat sinuous septae and the presence of numerous mouths in some specimens (fig. 78). The question how to interpret these differences, which are relevant at least for the epitoniids, is beyond the scope of this paper.

Distribution (fig. 83). The species is known from the Red Sea coast off Egypt.

Differentiation. *Epifungium marki* spec. nov. is the only epitoniid species that is known to be associated with *Fungia* (*Pleuractis*) spec. A. Conchologically it most closely resembles *E. adgravis* spec. nov. (see the differentiation of that species). Shells of *E. marki* spec. nov. also resemble those of *E. nielsi* spec. nov., but differ in more convex, somewhat broader whorls, which becomes apparent when the width of about the 3rd teleoconch whorl is measured (table 1). Both major and minor spiral threads can be distinguished in *E. marki* spec. nov., but not in *E. nielsi* spec. nov. The egg-capsules of *E. marki* spec. nov. and *E. nielsi* spec. nov. differ in being smooth (fig. 288) versus with many protuberances (fig. 290), in straight (fig. 289) versus strongly twisted mucus threads (fig. 291), and by over 260 versus less than 137 eggs in a single egg-capsule.

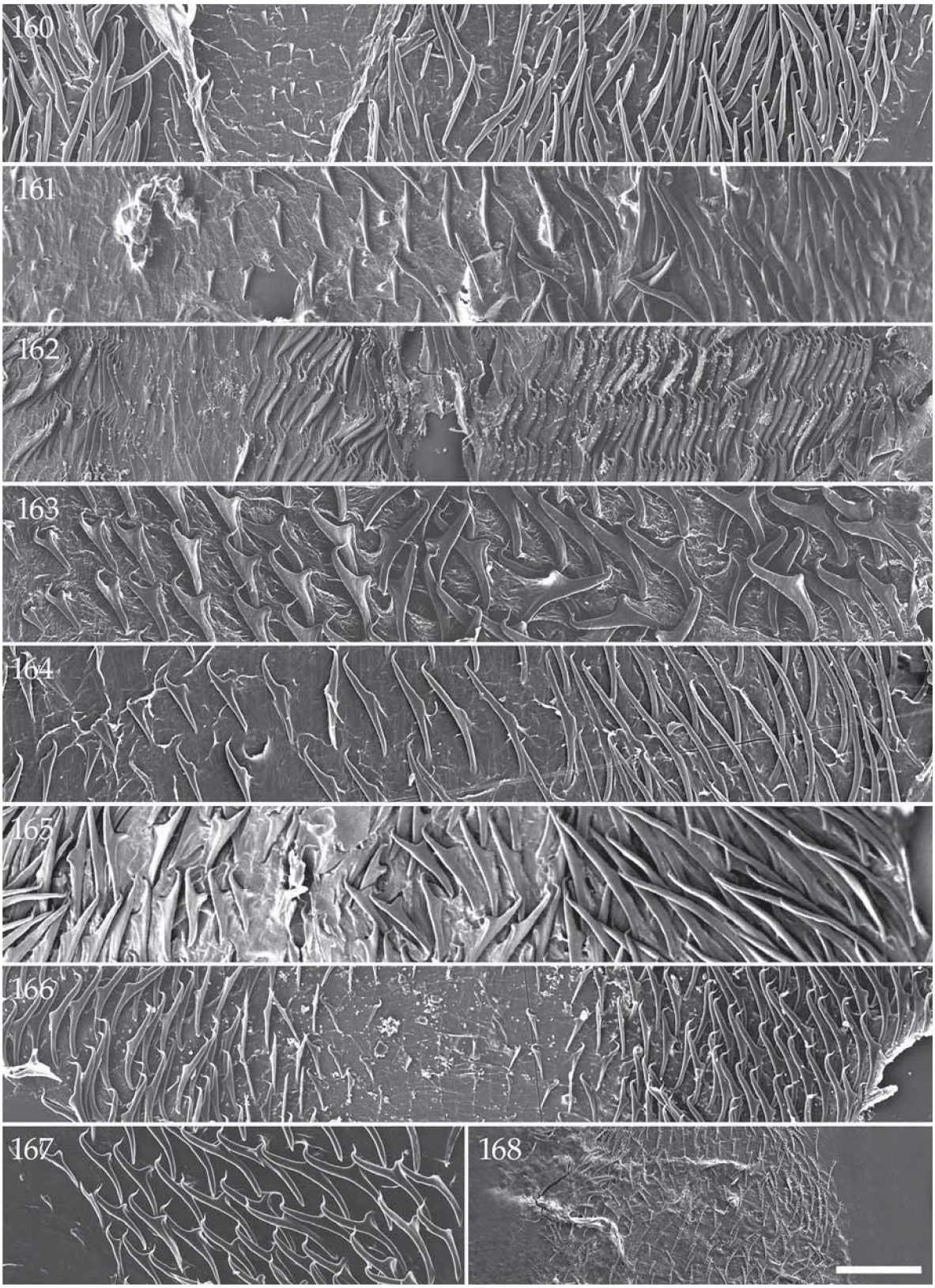
Etymology. This species is named after Mark de Vries, a friend, biologist and pool specialist.

Figs 152-159. Radulae, showing at least half a row of teeth from the innermost, usually the smallest, to the ultimate teeth on the right. 152, *Cirsotrema varicosa*; 153, *Epitonium ancillottoi*; 154, *E.* spec. 1; 152-154, Sulawesi, Indonesia; 155, *E. clathratulum*, off Côte Basque, France; 156, *E. clathrus*, The Netherlands; 157, *E. pyramidalis*, Philippines; 158-159, *Gyroscala lamellosa*, Fig. 158 continues in Fig. 159, Canary Islands, Spain. Scale bar = 0.1 mm. SEM Photos.

Remarks. The *Epitonium* spec. recorded from the Red Sea off Saudi Arabia by Sabelli and Taviani (1984: 91-93, figs 1-3), is probably *Epifungium marki* spec. nov. or *E. nielsi* spec. nov. The photograph of the shell is not sufficiently detailed to decide. The figured coral host (Sabelli and Taviani, 1984: fig. 2) closely resembles *Fungia* (*Pleuractis*) spec. A, but it could also be either *F.* (*P.*) *moluccensis* or *F.* (*P.*) *seychellensis* too, fungiid coral species known to be associated with *E. nielsi* spec. nov. See also the remarks on *E. adgravis* spec. nov. and *E. ulu*.

Epifungium nielsi spec. nov.

Material. Samples that were hosted by *Fungia* (*Pleuractis*) *moluccensis*, *F.* (*P.*) *paumotensis*, or *F.* (*P.*) *seychellensis* are coded Fm, Fp or Fs, respectively. MALDIVES. Ari Atoll, Vilamendhoo Island: House reef, (03°38'N 72°57'E), holotype RMNH 100152 Fs/1sh; paratypes: type locality, RMNH 100151 Fs/1sn, found together with holotype; Type locality, RMNH 100147 Fs/2sn, 100149 Fm/2sn+d, 100148 Fm/1sn, 100141 Fs/1sn+d, 100146 Fs/1sn, 100150 Fs/2sn+e, d, 100144 Fs/4sn, 100143 Fs/3sn, 100145 Fm/1sn, d. INDONESIA. NE Kalimantan, Berau Islands, Derawan Island, E-side, Coral Garden (02°17'32"N 118°15'43"E), RMNH 100153 Fp/1sh, 3sn+e. E Sulawesi, Tomini Bay, Togian Islands, N Togian Island (00°18'41"S 121°58'45"E), RMNH 62508 Fp/1sn+e. SW Sulawesi, Spermonde archipelago: W Bone Baku reef (05°07'56"S 119°21'39"E), RMNH 95052 Fm/2sn, 43264 Fp/1sn+e, 43272 Fp/1sn+e, 43265 Fp/1sn, 43271 Fp/1sn+e, 43270 Fp/5sn+e; W Samalona Island (05°07'31"S 119°20'31"E), RMNH 43202 Fp/1sn+e, 43203 Fp/2sn+e, 43226 Fp/2sn+e, 1sh; SW Samalona Island (05°07'42"S 119°20'31"E), RMNH 43378 Fp/1sn+e, 95079 Fp/1sn+e; E Samalona Island (05°07'39"S 119°20'38"E), RMNH 43250 Fm/1sn; W Kudingareng Keke Island (05°06'09"S 119°17'09"E), RMNH 43292 Fm/1sn; S Kudingareng Keke Island (05°06'21"S 119°17'03"E), RMNH 43360 Fp/1sn; W Bone Lola reef (05°03'07"S 119°21'09"E), RMNH 43341 Fp/1sn+e, 95043 Fp/1sn, 95039 Fp/1sn+e, 95041 Fp/1sn+e, 95047 Fp/1sn+e; W Badi Island (04°58'05"S 119°16'54"E), RMNH 95061 Fm/2sn; Lankai Island, RMNH 43261 Fp/1sn, 43262 Fp/1sn; NW Sumpangbinangae Island (04°22'S 119°35'E), RMNH 43370 Fm/2sn+e. Sulawesi, Wakatobi National Park, Atoll outside SW Karang Kaledupa (05°49'28"S 123°39'02"E), RMNH 100140/1sn+d. Bali: NE Serangan Island (08°44'03"S 115°15'05"E), RMNH 94997 Fm/1sn; SE-end Tulamben beach (08°44'03"S 115°15'05"E), RMNH 95015 Fm/1sn, 95017 Fm/1sn+e. THAILAND. Krabi, Phiphi Islands: NW Ko Phiphi Don Island, La Nah Bay (07°46'01"N 98°45'42"E), RMNH 95993 Fp/2sn, 95995 Fp/1sn; E Ko Phiphi Don Island, Poh Cape, Hin Phae (07°43'30"N 98°47'17"E), RMNH 96009 Fp/2sn, 95933 Fm/1sh, d, 96012 Fm/2sn+e; E Ko Phiphi Don Island, Ran Tee Bay (07°44'59"N 98°47'09"E), RMNH 95932 Fp/3sn+e, 95925 Fp/6sn, d, 95929 Fp/1sn+e; S Ko Phiphi Don, cape S of Tongsae Bay (07°43'07"N 98°46'16"E), RMNH 95867 Fm/1sn+e, 95872 Fp/6sn+e, 95875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Fp/6sn+e; NW Ko Phiphi Le, Palong bay (07°41'21"N 98°45'58"E), RMNH 95879 Fp/1sh; NE Ko Phiphi Le, Pi Le Bay, near cave (07°41'43"N 98°45'57"E), RMNH 95882 Fp/4sn, 95878 Fp/2sn+e; W Ko Phiphi Le, N Maya Bay (07°40'53"N 98°45'47"E), RMNH 95962 Fp/2sn; W Ko Phiphi Le, S Maya Bay (07°40'45"N 98°45'49"E), RMNH 96005 Fm/1sn; S Ko Phiphi Le, Loh Samah (07°40'28"N 98°46'10"E), RMNH 95963 Fp/1sn, 95964 Fp/1sn, 95965 Fp/1sn, 95966 11sn+e, 95971 Fp/3sn+e, 95973 1sn+e, 95974 2sn, 95975 1sn+e, 95976 3sn, 96004 Fp/2sn; Hin Bida, Shark point Phiphi (07°38'01"N 98°48'54"E), RMNH 95956 Fm/2sn+e, 95960 Fm/1sn; Ko Bida Nok, (07°39'14"N 98°45'58"E), RMNH 95911 Fm/1sn+e, 95912 Fp/2sn+e, 95913 Fp/1sn, 95914 Fp/1sn, 95915 Fp/1sn; Hin Klai, Garang Heng (07°41'32"N 98°48'35"E), RMNH 95856 Fm/1sh, 95861 Fm/3sn+e, 95863 Fm/3sn, 95855 Fm/1sn, 95858 Fm/1sn, 95859 Fp/1sn+e, 95860 Fp/2sn+e, d, 95866 Fm/1sn+e. PALAU. NE of Ngeremdiu, Lighthouse reef, forereef (07°16'30"N 134°27'25"E), RMNH 95108 Fp/1sn, 95114 Fp/1sn, 95133 Fp/1sn.

Type locality. MALDIVES. Ari Atoll, Vilamendhoo Island.

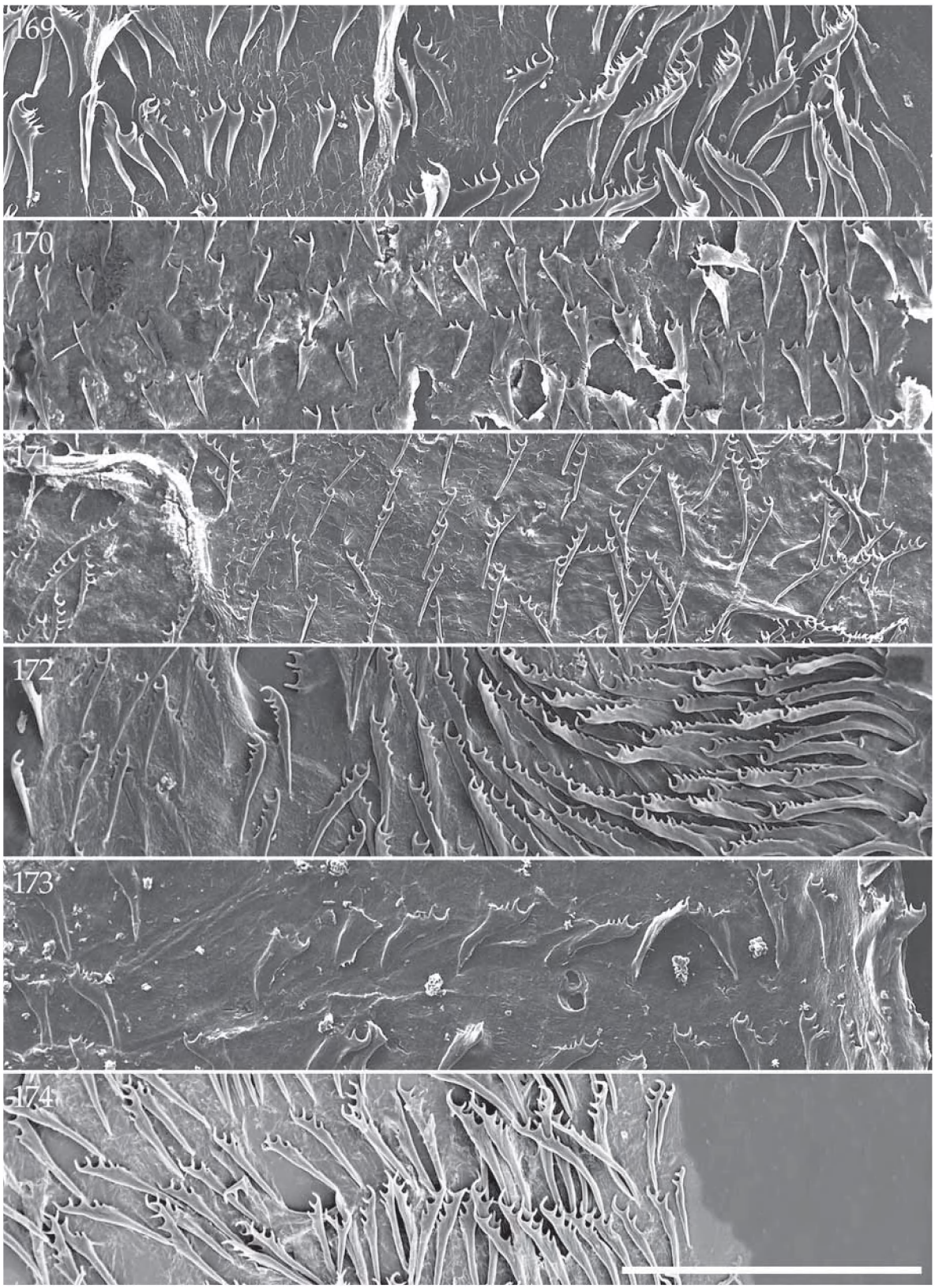
Shell (figs 65, 107, 127; table 1). Shell fragile, elongate-conical, with rather convex whorls, creamy white; reaching 17.5 mm in height. For dimensions and number of costal and spiral ribs on the 2nd and the 5th teleoconch whorls, see table 1. The holotype (fig. 65) measures 14.0 × 5.9 mm. The protoconch (fig. 107) has 3¼-3½ whorls (n = 10); apart from its smooth apical part, it is sculptured with regularly spaced, very fine, incised, axial lines, 22 (n = 1) per 0.2 mm on protoconch whorl 2¼-2¾. The teleoconch (fig. 127) has up to 11 whorls, separated by a moderately deep suture; it is sculptured with mostly regularly placed, usually not continuous, orthocline, lamellar, not or slightly curved, low costae, not or hardly touching the adjoining whorls. Shortly before reaching the preceding whorl the costae become slightly coronate. The number of costae on the 2nd, 3rd, 5th and younger teleoconch whorls usually remains approximately the same (adjoining whorls differing in about two costae); it only increases on the younger whorls in about a third of the shells, up to 41 costae on the 10th whorl in a shell of 14.0 mm in height. The teleoconch is additionally sculptured with randomly placed, low, spiral threads, which are obsolete on the 1st and 2th teleoconch whorl in about a third of the specimens. Towards the younger whorls, additional low, spiral threads become apparent. In about one third of the specimens they are numerous from about the 8th teleoconch whorl onwards. Aperture subcircular. Most specimens (n = 31) have a very narrow umbilicus, visible in oblique view only. Only one specimen has the umbilicus closed.

Figs 160-168. Radulae, showing at least half a row of teeth from the innermost, usually the smallest, to the ultimate teeth on the right; sh = shell height. 160-161, *Epidendrium aureum* spec. nov.; 160, sh = 11.8 mm, Sulawesi, Indonesia; 161, sh = 14.9 mm, Thailand; 162, *E. sordidum* spec. nov., holotype, sh = 16.0 mm, Indonesia; 163-164, *Surrepifungium costulatum*; 163, sh = 31.6 mm, Sulawesi, Indonesia; 164, sh = 26.1 mm, Palau; 165, *S. oliverioi*, sh = 18.1 mm, Maldives; 166, *S. ingridae*, Sulawesi, Indonesia; 167, *S. patamakanthini* spec. nov., Palau; 168, *Epifungium lochi*, Sulawesi, Indonesia. Scale bar = 0.1 mm. SEM Photos.

Operculum (fig. 147). Operculum paucispiral, with interconnected coils as in *Surrepifungium patamakanthini* spec. nov. (fig. 3). At the outside of the operculum (fig. 147) there are 28-29 wavy, segmented threads per 0.1 mm (n = 2), running about perpendicular to the growth lines.

Radula (figs 172, 192, 212; table 2). Only one radula could be studied (fig. 172; table 2). Each tooth (figs 172, 192) consists of a moderately slender stem and a somewhat broader blade, which merge gradually; the blade has 1-6 acute, secondary cusps. The teeth (figs 160-161) are attached to the radular plate along the bases, which takes about half of the length of a tooth (fig. 202). The number of secondary cusps (table 2) gradually increases from 1 on the innermost tooth (fig. 192, left) to 6 on the 11th and the 12th tooth, after which the number gradually decreases to 1 on the ultimate, i.e. 20th tooth (fig. 172, upper right corner). The apical cusp and the secondary cusp directly underneath it are usually similar in size and somewhat curved towards each other; all other secondary cusps are slightly smaller, similar to each other in size, and usually not curved (fig. 212). Starting from the innermost, smallest tooth, with a height of 0.035 mm, the teeth gradually increase in size to about 1½ times that height, i.e. 0.056 mm, up to the 12th tooth, after which they gradually become somewhat smaller until the penultimate, 0.048 mm high 19th tooth, which is followed by the, usually malformed, much smaller ultimate tooth, with a height of 0.037 mm (table 2).

Jaw (figs 258, 263; table 2). Only one jaw was studied. The denticulate edge consists of a row of slender, blunt denticles, which are basally pitted on the inside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(fig. 263). They have a maximum size of 0.0030 mm. Seen from the outside (fig. 258), 71 denticles per 0.05 mm extend above a 0.0142 mm broad, granulated jaw-flap, which lies loosely over part of the jaw-pattern. The pattern under the jaw-flap consists of at least 11 rows of somewhat sunken, pentagonal figures, of which the upper four to five rows are densely pitted, while the others are not. On the inner surface of the jaw (fig. 263), just below the denticles, there is a row of engraved, scarcely pitted, irregularly square-like figures, followed by an area that is somewhat granulated to smooth.

Spawn (figs 290-291). Egg-capsules (fig. 290) ovoid, with distinct protuberances, sometimes embedded with sand, 0.66-1.34 mm (mean = 1.06, n = 18) in diameter, e.g. measured horizontally, from left to right in figure 290, containing 75-137 eggs (mean = 105.5, n = 17) each. The mucus threads that connect the egg-capsules are strongly twisted and not sculptured (fig. 291).

Habitat. The snails and their egg-capsules were found at 4-36 m, associated with *Fungia moluccensis* Van der Horst, 1919, *F. paumotensis* Stutchbury, 1833, and *F. seychellensis* Hoeksema, 1993. They usually live attached with their mucus threads to the underside of these mushroom corals or to a hard substratum underneath. Most host corals were found on coral slopes. Rarely they were also seen on the sandy substratum underneath a coral slope.

Distribution (fig. 84). The species is known from the Indo-West Pacific, from Maldives, Thailand and Indonesia to Palau.

Differentiation. Conchologically this species resembles *Epifungium adgravis* spec. nov. and *E. marki* spec. nov. See the differentiation of those species.

Etymology. This species is named after Niels Schrieken, a friend, scuba-diver and biologist, who assisted in the fieldwork and collected many of the specimens of this new species.

Remarks. See the remarks on *Epifungium adgravis* spec. nov., *E. marki* spec. nov. and *E. ulu*.

Figs 169-174. Radulae, showing at least half a row of teeth from the innermost, usually the smallest, to the ultimate teeth on the right. 169, *Epifungium hartogi*; 170, *E. hoeksemai*; 171, *E. lochi*; 172, *E. nielsi* spec. nov.; 173, *E. twilae*; 174, *E. ulu*. 169-174, Indonesia; 169-171, 173-174, Sulawesi; 172, Kalimantan. Scale bar = 0.1 mm. SEM Photos.

Epifungium pseudolochi spec. nov.

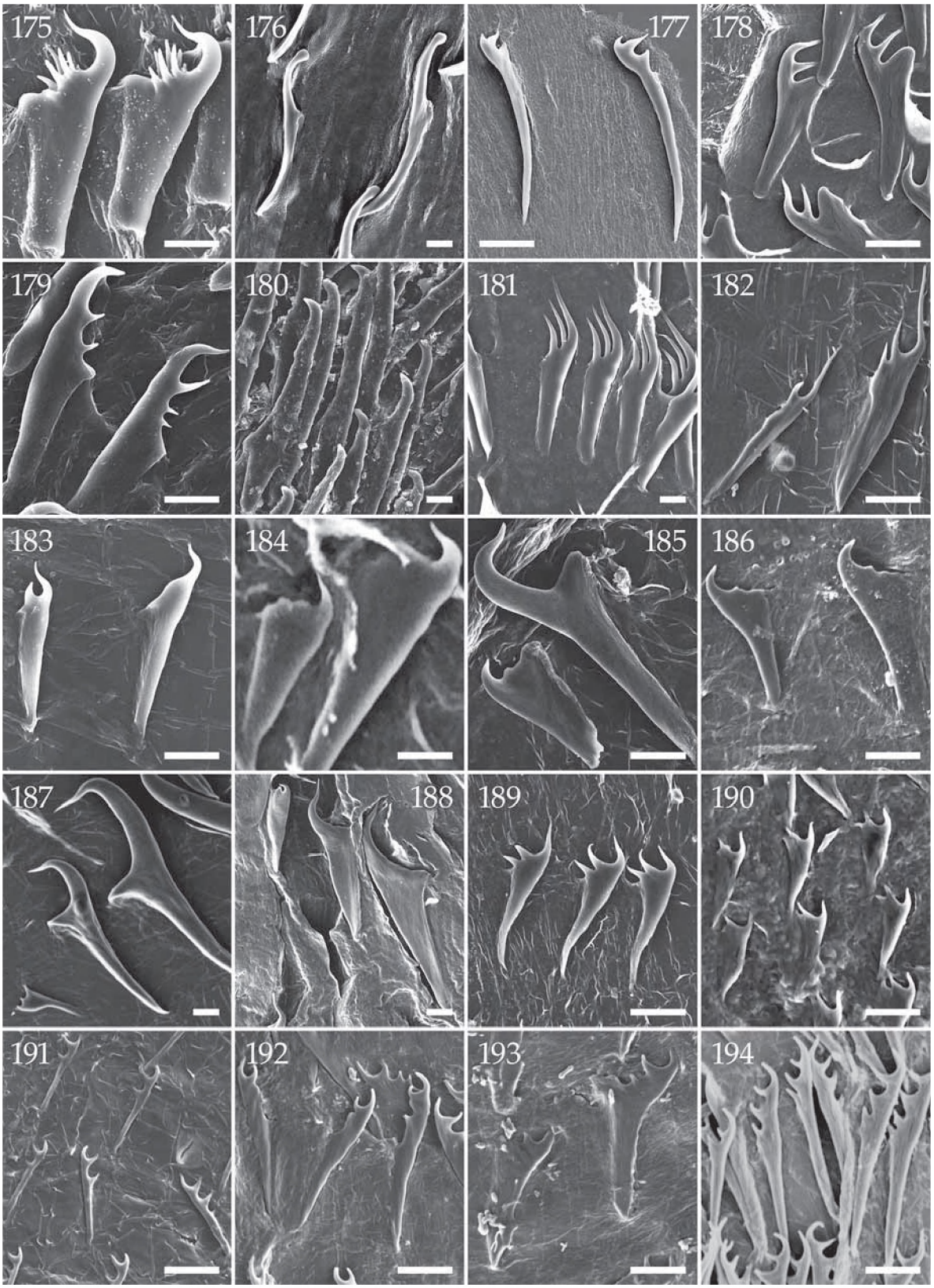
Material (always hosted by *Fungia* (*Cycloseris*) *costulata* Ortmann, 1889). EGYPT. Off Marsa Nakari, about 350 km S of Hurghada, holotype RMNH 95358/1sh, d, with egg-capsules RMNH 100328; paratypes: type locality, RMNH 95355/1sn, 95356/1sn, 95357/1sn+e, 95259/1sn.

Type locality. EGYPT. Off Marsa Nakari, about 350 km S of Hurghada.

Shell (figs 68, 108, 128; table 1). Shell fragile, elongate-conical, with convex whorls, creamy white; reaching 6.6 mm in height. For dimensions and number of costal and spiral ribs on the 2nd and the 5th teleoconch whorls, see table 1. The holotype (fig. 68) measures 6.6 × 2.2 mm. The protoconch (fig. 108) has 3¼-3½ whorls (n = 5); apart from its smooth apical part, it is sculptured with regularly spaced, very fine, incised, axial lines, 23 (n = 1) per 0.2 mm on protoconch whorl 2¼-2¾. The teleoconch (fig. 128) has up to 7½ whorls, separated by a very deep suture; it is sculptured with mostly regularly placed, usually discontinuous, orthocline, lamellar, not or slightly curved, low costae, not or hardly touching the adjoining whorls. The costal ribs remain similar in height along the entire whorl. The number of costae is similar on all whorls (table 1). There are up to 27 costae on a whorl; on the 7th whorl in a shell of 6.6 mm in height. The teleoconch is additionally sculptured with very low, distinct, evenly distributed spiral threads. The number of spiral threads gradually increases towards the younger teleoconch whorls (table 1). Aperture subcircular. The umbilicus is closed.

Operculum (fig. 148). Operculum paucispiral, with interconnected coils as in *Surrepifungium patamakanthini* spec. nov. (fig. 3). At the outside of the operculum (fig. 148) there are 25 wavy, segmented threads per 0.1 mm (n = 1), running about perpendicular to the growth lines.

Radula and Jaw. Unknown.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Spawn (figs 292-293). Egg-capsules (fig. 292) round to ovoid, without any protuberances, embedded with sand, 0.92-0.97 mm (n = 2) in diameter, e.g. measured horizontally, from left to right in figure 292, containing 45-45 eggs (n = 2) each. The mucus threads that connect the egg-capsules are straight and not sculptured (fig. 293).

Habitat. The snails and their egg-capsules were found at 20-30 m, associated with exclusively the mushroom coral species *Fungia* (*Cycloseris*) *costulata* Ortmann, 1889. The snails live attached with their mucus threads to the underside of their hosts. The host corals were found on a sandy, nearly flat bottom, situated along the lower border of a steeper coral slope.

Distribution (fig. 82). The species is known from the Red Sea coast off Egypt.

Differentiation. The shells most closely resemble those of *Epifungium lochi*. See the differentiation of that species.

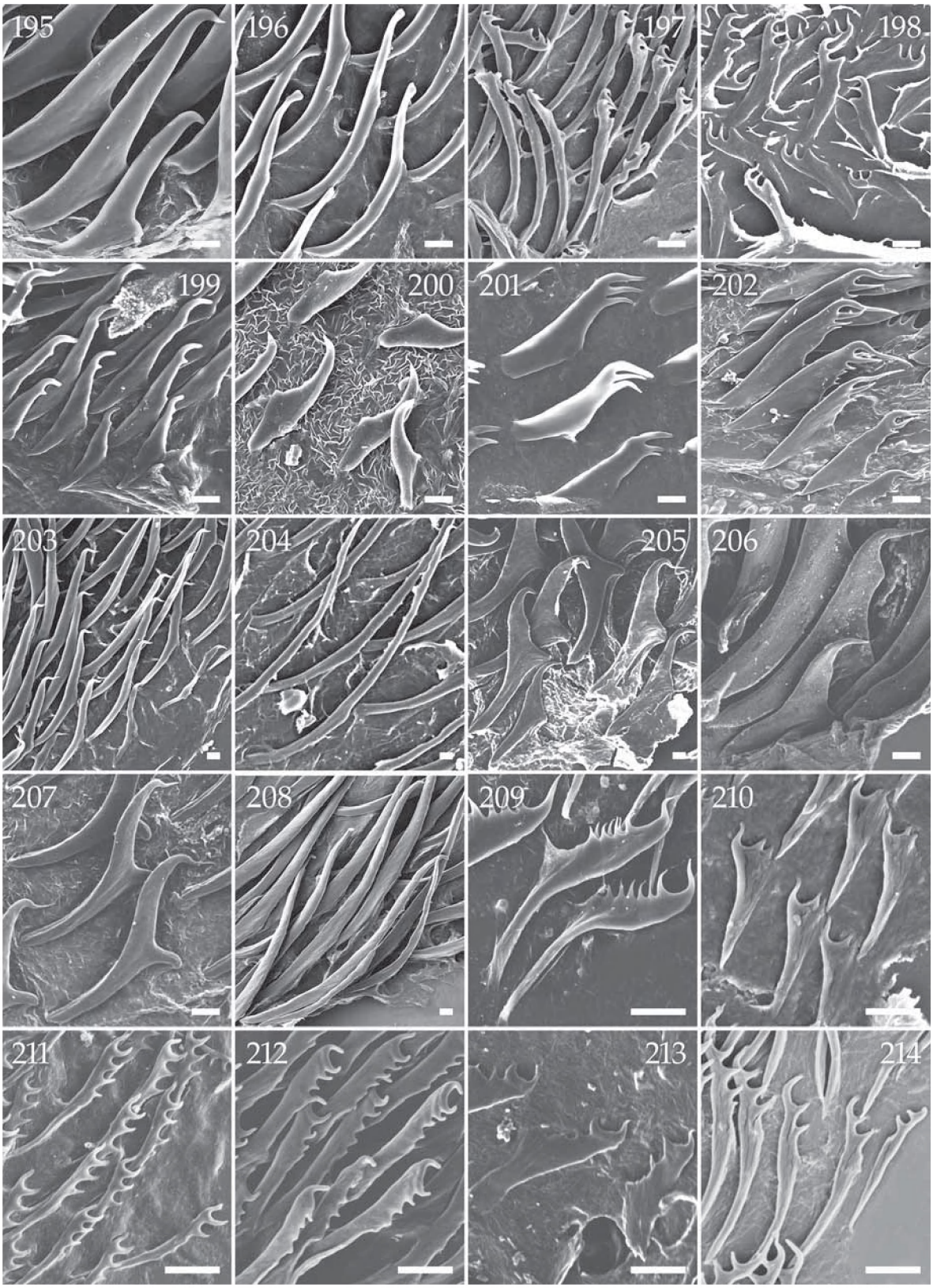
Remarks. Even though its shells most closely resemble those of *Epifungium lochi*, molecular analyses (A. Gittenberger *et al.*, in prep.) indicate that *E. pseudolochi* spec. nov. is more closely related to *E. adgravis* spec. nov., *E. adscabra* spec. nov., *E. marki* spec. nov. and *E. nielsi* spec. nov., than to *E. lochi*.

Epifungium pseudotwilae spec. nov.

Epitonium bullatum (Sowerby, 1844); Yamashiro, 1990: 299, figs 1-6. Not *Scalaria bullatum* Sowerby, 1844.

Material. Samples that were hosted by *Podabacia crustacea*, *Sandalolitha dentata*, *S. robusta*, or *Zoopilus echinatus* are coded Pc, Sd, Sr, or Ze, respectively. PALAU. NE of Ngeremdiu, Lighthouse reef, forereef (07°16'30"N 134°27'25"E), holotype RMNH 95190 Sr/1sh; paratypes: type locality, RMNH 95181 Sr/1sn+e, 95183 Sr/1sn, 95184 Sr/1sh, 1sn, 95190 Sr/1sn+e; N of Ngeremdiu, Lighthouse reef, backreef (07°17'11"N 134°27'26"E), RMNH 95182 Sr/1sn; SW of Ngemelachel Passage, S of Ngchesechang, off mangrove (07°23'35"N 134°35'30"E), RMNH 95187 Sr/1sn; E of Babelthuap, E of Arudowaishi Pt., Uchelbeluu, backreef (07°21'20"N 134°36'22"E), RMNH 95188 Sr/1sn+e. MALDIVES. Ari Atoll, Vilamendhoo Island: House reef, (03°38'N 72°57'E), RMNH 100162 Sd/1sn, 100163 Sd/2sn, 100174 Sd/2sn. PHILIPPINES. Cebu Strait: Olango Channel, E Olanga Island (10°15'32"N 124°04'11"E), RMNH 100164 Sd/2sn+e; W Bohol, NW Cabilao Island, Baluarte Point (9°53'N 123°45'E), RMNH 100156 Sr/3sn+e, r; W Bohol, SW Sandingan Island (09°50'36"N 123°47'17"E), RMNH 100155 Sr/1sn. INDONESIA. NE Kalimantan, Berau Islands: E Derawan Island, Coral Garden (02°17'32"N 118°15'43"E), RMNH 100158 Ze/1sn; S Derawan Island, jetty Derawan Dive Resort (02°17'03"N 118°14'49"E), RMNH 100159 *Podabacia* spec./2sn+e; N Maratua Island, lagoon near entrance (02°14'53"N 118°37'36"E), RMNH 100173 Sr/3sn+e; N Sangalaki Island (02°05'25"N 118°24'16"E), RMNH 100157 Sd/1sn+e; Panjang Island, S of Sharkpoint (02°18'34"N 118°15'16"E), RMNH 100161 Ze/4sn; N Panjang Island, NE Baliktaba reef (02°35'15"N 118°00'35"E), RMNH 100160 Ze/1sn. N Sulawesi, Off Manado, Siladen Island (01°37'37"N 124°48'01"E), RMNH 100154 Sr/1sn. E Sulawesi, Tomini Bay, Togian Islands: N Togian Island (00°18'41"S 121°58'45"E), RMNH 100166 Sr/2sn, 100167 Sr/2sn, 100169 Sr/1sh, 1sn, 100168 Sr/3sn; S Togian Island (00°20'10"S 121°59'00"E), RMNH 100170 Sr/2sh. SW Sulawesi, Spermonde archipelago: W Lae Lae Island (05°08'09"S 119°23'13"E), RMNH 59148 Sr/2sn+e, 59149 Sr/1sn; NW Bona Baku reef (05°07'56"S 119°21'39"E), RMNH 43380 Sr/1sn, 95166 Pc/2sn, 95167 Sr/1sn+e; W Samalona Island (05°07'31"S 119°20'31"E), RMNH 59117 Sr/1sn+e, 59136 Sr/1sh; SW Samalona Island (05°07'42"S 119°20'31"E), RMNH 95176 Sr/1sn+e; E Samalona Island (05°07'28"S 119°20'38"E), RMNH 59131 Sr/4sn, 59139 Sr/1sn+e, 59140 Sr/1sh, 4sn+e. W Bone Lola reef (05°03'07"S 119°21'09"E), RMNH 59161 Sr/2sn+e, 95162 Sr/3sn+e, 95163 Sr/6sn+e, 100165 Sr/1sn, o. SW Barang Lompo Island (05°03'S 119°20'E), RMNH 100171 Sr/2sn+e, 100172 Sr/1sn+e; NW Kudingareng Keke Island (05°06'08"S 119°17'17"E), RMNH 43389 Sd/2sn, 59152 Ze/1sn; W Kudingareng Keke Island (05°06'09"S 119°17'09"E), RMNH 59106 Sr/1sh, 59124 Sr/1sh, 59115 Sr/3sn+e, 59110 Ze/1sn, 59111 Ze/2sn+e, 59112 Ze/1sn; SE Kudingareng Keke Island (05°06'S 119°17'E), RMNH 59151 Sr/1sh; W Badi Island (04°58'05"S 119°16'54"E), RMNH 43390 Ze/1sn, 95171 Ze/2sn, 59159 Sd/5sn+e; NW Bone Tambung Island (05°02'05"S 119°16'16"E), RMNH 59119 Ze/1sh, 59155 Ze/2sh, 59157 Sd/1sh; SW Bone Tambung Island (05°02'12"S 119°16'19"E), RMNH 43388 Ze/2sn, 59154 Ze/2sn, 59156 Ze/1sn, 59158 Ze/1sn+e; W Lankai Island, 59137 Sr/1sh. Moluccas, Ambon, Hitu, Ambon bay, outer bay, N coast, W of Sahuru (03°40'S 128°09'E), RMNH 83488 host unknown/2sn+e. Bali, off Sanur: Loloan Batu Agung (08°43'31"S 115°15'57"E), RMNH 95156 Sd/1sn, 95155 Sd/1sn; Penjor Point (08°42'04"S 115°16'18"E), RMNH 95153 Sd/1sn, 95152 Sd/1sn, 95154 Sd/1sn.

Figs 175-194. Innermost teeth of radulae in Figs 152-174. 175, *Cirsotrema varicosa*; 176, *Epitonium ancillottoi*; 177, *E.* spec. 1; 178, *E. clathratulum*; 179, *E. clathrus*; 180, *E. pyramidalis*; 181, *Gyroscala lamellosa*; 182, *Epidendrium sordidum*; 183, *E. aureum*; 184-185, *Surrepifungium costulatum*; 184, radula in Fig. 164; 185, radula in Fig. 163; 186, *S. ingridae*; 187, *S. patamakanthini*; 188, *S. oliverioi*; 189, *Epifungium hartogi*; 190, *E. hoeksemai*; 191, *E. lochi*; 192, *E. nielsi*; 193, *E. twilae*; 194, *E. ulu*. Scale bars = 0.01 mm. SEM Photos.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Type locality. PALAU. NE of Ngeremdiu, Lighthouse reef, forereef (07°16'30"N 134°27'25"E).

Shell (figs 90-91, 109, 130; table 1). Shell fragile, more broadly conical than most other epitoniid shells, with flattened to slightly convex whorls, creamy white; reaching 18.5 mm in height. For dimensions and number of costal and spiral ribs on the 2nd and the 5th teleoconch whorls, see table 1. The holotype (fig. 90) measures 14.2 × 10.0 mm. The protoconch (fig. 109) has 3¼-3½ whorls (n = 10); apart from its smooth apical part, it is sculptured with regularly spaced, very fine, incised, axial lines, 17 (n = 1) per 0.2 mm on protoconch whorl 2¼-2¾. In almost all shells the protoconch is seriously damaged, with missing whorls, or very strongly eroded. Protoconchs that still show axial lines are rare (1 out of 40). The teleoconch (fig. 130) has up to 8½ whorls, separated by a somewhat indented suture; it is sculptured with mostly regularly placed, usually discontinuous, orthocline, lamellar, not or slightly curved, very low costae, which are not or hardly touching the adjoining whorls. The number of costae on the 2nd, 3rd, 5th and younger teleoconch whorls usually increases considerably. There are up to 65 costae on a whorl; on the 8th whorl in a shell of 14.2 mm in height. The teleoconch is additionally sculptured with numerous, inconspicuous spiral threads, which are usually obsolete on the initial whorls. Aperture rather roundish, its border curved in such a way that the parietal interruption is shorter than each of the three other sides, i.e. the palatal, basal and columellar side, which very gradually change into one another. Umbilicus clearly open, quickly narrowing inside.

Operculum (fig. 149). Operculum paucispiral, with interconnected coils as in *Surrepifungium patamakanthini* spec. nov. (fig. 3). At the outside of the operculum (fig. 149) there are 22 wavy, segmented threads per 0.1 mm (n = 1), running about perpendicular to the growth lines.

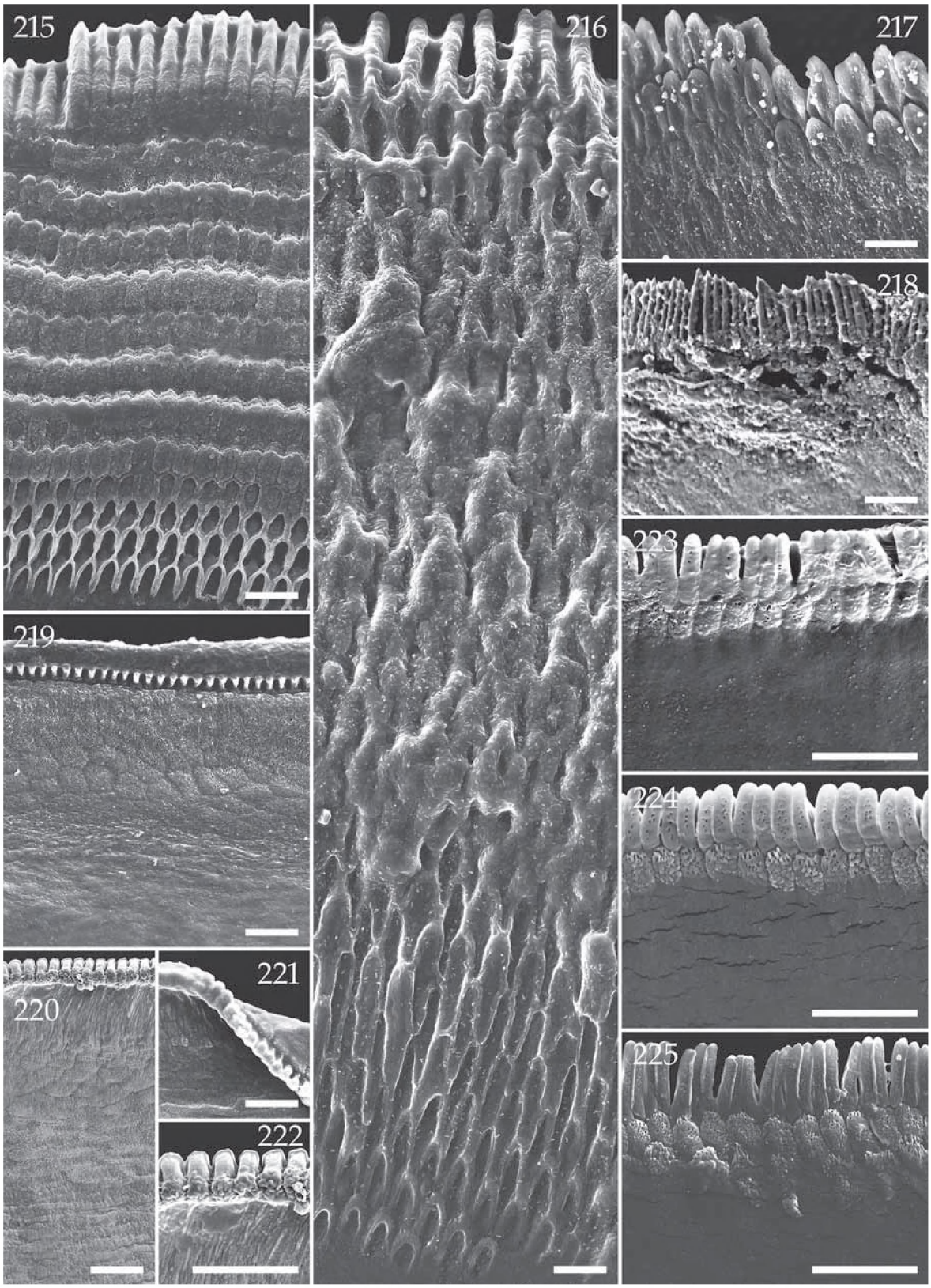
Radula (figs 173, 193, 213; table 2). Only one radula could be studied (fig. 173; table 2). Each tooth (figs 193, 213) consists of a moderately broad stem and a somewhat broader blade; the blade has 2-4 acute, secondary cusps. Where the stem and the blade merge, the blade usually curves away, standing almost perpendicular to the radular plate (fig. 193, right). The teeth (figs 173, 193, 213) are attached to the radular plate along the bases, which takes half to two third of the length of a tooth (fig. 202). The number of secondary cusps (table 2) gradually increases from 1 on the innermost tooth (fig. 193, left) to 4 on the 4th and 5th teeth, after which the number gradually decreases to 2 on the 7th tooth, which is followed by the 8th-11th teeth with 3 secondary cusps (fig. 213). The apical cusp and the secondary cusp directly underneath it are usually similar in size and somewhat curved towards each other; all other secondary cusps are slightly smaller, similar to each other in size, and usually not curved (fig. 173). Starting from the innermost, smallest tooth, with a height of 0.029 mm, the teeth gradually increase in size to almost 1½ times that height, i.e. 0.041 mm, up to the 5th tooth, after which they gradually become somewhat smaller until the ultimate, i.e. 11th tooth, measuring 0.028 mm in height (table 2).

Jaw. Unknown.

Spawn (figs 294-295). Egg-capsules (fig. 294) ovoid, somewhat transparent, smooth or with small protuberances, not embedded with sand, 1.08-2.15 mm (mean = 1.62, n = 17) in diameter, e.g. measured horizontally, from left to right in figure 294, containing 250-650 eggs (mean = 434.4, n = 15) each. The mucus threads that connect the egg-capsules are straight and not sculptured (fig. 295).

Habitat. The snails and their egg-capsules were found at 4-25 m depth, associated with *Podabacia crustacea* (Pallas, 1766), *Sandalolitha robusta* (Quelch, 1886), *S. dentata* Quelch, 1884 and *Zoopilus echinatus* Dana, 1846. They usually live on the underside of these mushroom corals, attached with their mucus

Figs 195-214. Outermost teeth of radulae in Figs 152-174. 195, *Cirsotrema varicosa*; 196, *Epitonium ancillottoi*; 197, *E.* spec. 1; 198, *E. clathratulum*; 199, *E. clathrus*; 200, *E. pyramidalis*; 201, *Gyroscala lamellosa*; 202, *Epidendrium sordidum*; 203, *E. aureum*; 204-205, *Surrepifungium costulatum*; 204, radula in Fig. 164; 205, radula in Fig. 163; 206, *S. ingridae*; 207, *S. patamakanthini*; 208, *S. oliverioi*; 209, *Epifungium hartogi*; 210, *E. hoeksemai*; 211, *E. lochi*; 212, *E. nielsi*; 213, *E. twilae*; 214, *E. ulu*. Scale bars = 0.01 mm. SEM Photos.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threads. The host corals were found on a coral slope or on a sandy bottom bordering a coral slope.

Distribution (fig. 85). This species is known from the Indo-West Pacific, from Maldives, Philippines and Indonesia to Palau.

Differentiation. Conchologically *Epifungium pseudotwilae* spec. nov. closely resembles *E. twilae*, from which it differs however, in having on average 20 instead of 26 costae on the 2nd teleoconch whorl, an average T3 value of 0.91 versus 0.97 mm, and not more than 65 costae on a whorl instead of over 80 from the 7th teleoconch whorl onwards. There is a slight difference also in the form of the aperture, i.e. the parietal, palatal, basal and columellar sides are about equally long in *E. twilae* (figs 88-89), while the parietal side is relatively shorter in *E. pseudotwilae* spec. nov. (figs 90-91). Their habitat preferences also differ; *E. pseudotwilae* spec. nov. is associated with *Podabacia crustacea*, *Sandalolitha robusta*, *S. dentata* and *Zoopilus echinatus*, while *E. twilae* is associated with *Ctenactis crassa*, *C. echinata* and *Herpolitha limax*.

Etymology. Conchologically this species very much resembles *Epifungium twilae*, hence the epitheton *pseudotwilae*.

Remarks. It seems that in both *Epifungium pseudotwilae* spec. nov. and *E. twilae*, there are many more broken and strongly eroded protoconchs than in the other epitoniids that are associated with corals.

All paratypes of *E. twilae* that were found associated with *Sandalolitha robusta* and *Zoopilus echinatus*, have now been identified as *E. pseudotwilae* spec. nov. The epitoniid species collected in the Red Sea off Thomas Reef, Sinai, and identified as *E. bullatum* by Dushane (1988a: 30, figs 5, 6) is either *E. twilae* or *E. pseudotwilae* spec. nov. (see also A. Gittenberger *et al.*, 2000); because the host species is unknown and since the specimen could not be studied in detail, it is impossible to conclude to which of these two species it belongs. See A. Gittenberger *et al.* (2000) for a comparison of "*Epitonium twilae*" with *Epitonium bullatum*.

Figs 215-225. Details of jaws flanking radulae in Figs 152-155, 157-159. 215, *Cirsotrema varicosa*; 216-217, *Gyroscala lamellosa*; 218, *Epitonium pyramidalis*; 219, *E. ancillottoi*; 220-222, *E.* spec. 1; 223-225, *E. clathratulum*. 215-216, 218-223, jaw, outer surface; 217, 224-225, jaw, inner surface; 221, lower left: outer surface of jaw, upper right: inner surface. Scale bars = 0.01 mm. SEM Photos.

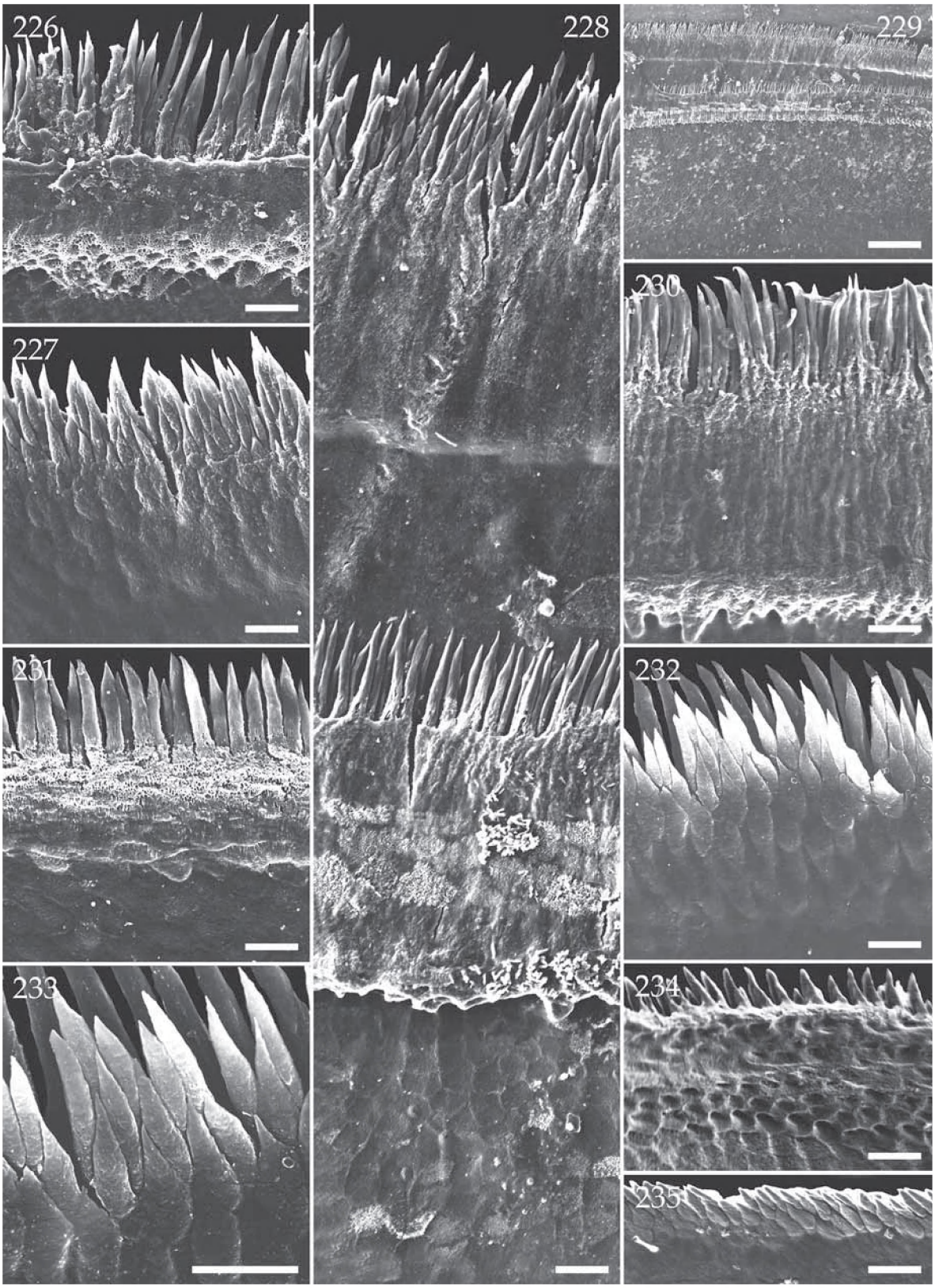
Epifungium twilae (A. Gittenberger and Goud, 2000)

Epitonium twilae A. Gittenberger and Goud, 2000: 10-11, figs 19, 28, 32-33, 48.

Material. INDONESIA (hosted by *Ctenactis crassa*, *C. echinata* and *Herpolitha limax*). SW Sulawesi, Spermonde archipelago: holotype (hosted by *H. limax*) RMNH 59104 and 43 paratypes with 10 clutches of egg-capsules: RMNH 59105, 59107-59109, 59113, 59114, 59116, 59118, 59121-59123, 59126, 59127, 59129, 59132-59135, 59138, 59141-59143, 59145-59147, 59150, 59153, 59160, 59163. Additionally studied material: 17 specimens, 12 clutches of egg-capsules, 4 d, 1 r. Central Sulawesi, Donggala, Pasikewa, W of Towale: 1 specimen, 1 clutch of egg-capsules. NE Komodo: 1 specimen, 1 d. Moluccas, Ambon (hosted by *H. limax*), 3 specimens, 1 clutch of egg-capsules, 2 d. EGYPT (hosted by *H. limax*). Off Marsa Shagra, about 350 km S of Hurghada: 5 specimens, 3 clutches of egg-capsules, 2 d. MALDIVES. Ari Atoll, off Vilamendhoo Island (hosted by *H. limax*), 10 specimens, 1 clutch of egg-capsules, 1 d. THAILAND. Krabi, Phiphi Islands (hosted by *C. crassa*, *C. echinata* and *H. limax*), 47 specimens, 14 clutches of egg-capsules, 1 d. AUSTRALIA. Queensland, Lizard Island (hosted by *H. limax*), from the Australian Museum, Sydney (AMS 99806), 1 specimen.

Type locality. INDONESIA. SW Sulawesi, Spermonde archipelago.

Shell (figs 88-89, 110, 131; table 1). Shell fragile, more broadly conical than most other epitoniid shells, with slightly convex whorls, creamy white; reaching 20.8 mm in height. For dimensions and number of costal and spiral ribs on the 2nd and the 5th teleoconch whorls, see table 1. The holotype (fig. 89) measures 14.4 × 9.0 mm. The protoconch (fig. 110) has 3¼-3½ whorls (n = 10); apart from its smooth apical part, it is sculptured with regularly spaced, very fine, incised, axial lines, 24 (n = 1) per 0.2 mm on protoconch whorl 2¼-2¾. In almost all shells the protoconch is very badly damaged, with missing whorls, or at least very strongly eroded. Protoconchs still showing some axial lines are rare (1 out of 44). The teleoconch (fig. 131) has up to 8¼ whorls, separated by an indented suture; it is sculptured with mostly regularly placed, discontinuous, orthocline, lamellar, not or slightly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curved, very low costae, not or hardly touching the adjoining whorls. The number of costae on the 2nd, 3rd, 5th and younger teleoconch whorls usually increases quickly, exceeding 80 costae on the 7th whorl and >100 on the 8th whorl. There are up to 130 costae on a whorl; on the 8th whorl in a shell of 20.8 mm in height. The teleoconch is additionally sculptured with numerous, inconspicuous, spiral threads, which are usually obsolete on the initial whorls. Aperture with about equally long parietal, palatal, basal and columellar sides, which are gradually changing into one another. There is a narrow umbilicus.

Operculum (fig. 150). Operculum paucispiral, with interconnected coils as in *Surrepifungium patamakanthini* spec. nov. (fig. 3). At the outside of the operculum (fig. 150) there are 24 wavy, segmented threads per 0.1 mm (n = 1), running about perpendicular to the growth lines.

Radula and Jaw. Unknown.

Spawn (figs 296-297). Egg-capsules (fig. 296) ovoid, somewhat transparent, smooth or with small protuberances, not embedded with sand, 1.31-2.88 mm (mean = 1.98, n = 10) in diameter, e.g. measured horizontally, from left to right in figure 296, containing 480-820 eggs (mean = 618.2, n = 10) each. The mucus threads that connect the egg-capsules are straight and not sculptured as in *Epifungium pseudotwilae* spec. nov. (fig. 295) or with a distinct pattern of engraved, diagonal lines (fig. 297).

Habitat. The snails and their egg-capsules were found at 5-38 m, associated with *Ctenactis crassa* (Dana, 1846), *C. echinata* (Pallas, 1766) and *Herpolitha limax* (Esper, 1797). They usually live attached to the underside of these mushroom corals with their mucus threads. The host corals were found on a coral slope or on a sandy bottom bordering a coral slope.

Figs 226-235. Jaw details. 226-227, *Surrepifungium costulatum*, radula in Fig. 163; 228-230, *S. ingridae*; 228-229, Sulawesi, Indonesia; 230, Palau; 231-233, *S. patamakanthini*, radula in Fig. 167; 234-235, *S. oliverioi*, radula in Fig. 165. 226, 230-231, 234, jaw, outer surface; 227, 232-233, 235, jaw, inner surface; 228-229, outer surface jaw on top of inner surface second jaw; Scale bars = 0.01 mm. SEM Photos.

Differentiation. Conchologically this species strongly resembles *Epifungium pseudotwilae* spec. nov. See the differentiation of that species.

Remarks. See the remarks on *Epifungium pseudotwilae* spec. nov.

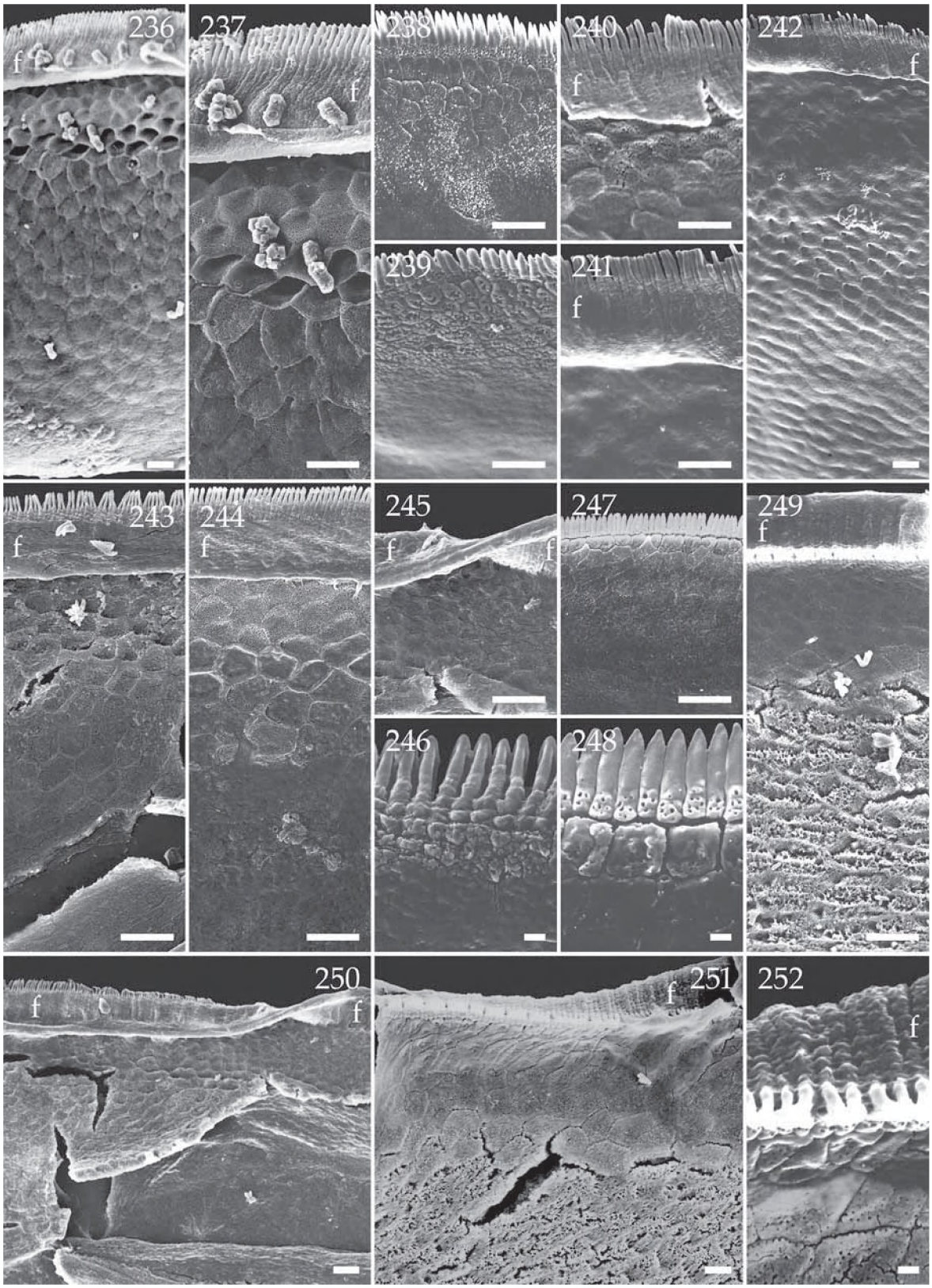
Epifungium ulu (Pilsbry, 1921)

Epitonium ulu Pilsbry, 1921: 376, fig. 11c; Bosch, 1965: 267, fig. 1; Robertson, 1970: 45; Hatfield, 1976: 135, table 1; Taylor, 1977: 253, 258, fig. 7; Kay, 1979: fig. 53a, b; Loch, 1982: 3, 1 fig.; Bell, 1985: 159, figs 1-6; Dushane 1988a: 31, figs 3, 4; 1988b: 9, 1 fig.; Wilson, 1993: 273; A. Gittenberger *et al.*, 2000: 11-12, figs 11-12, 17, 21, 29, 44.

Material. USA. Hawaii (hosted by *Fungia* (*Lobactis*) *scutaria*): holotype ANSP 127818. Additionally studied material: 9 specimens, 1 clutch of egg-capsules. EGYPT. Red Sea, 300-350 km S of Hurghada (hosted by *Ctenactis echinata*, *Fungia* (*Danafungia*) *horrida*, *F.* (*Fungia*) *fungites* and *F.* (*Verrillofungia*) *repanda*), 39 specimens, 3 clutches of egg-capsules, 3 r, 5 d. SEYCHELLES. W St. Francois atoll (fungiid host unknown), 1 specimen. MALDIVES. Ari Atoll, Off Vilamendhoo Island (hosted by *F.* (*V.*) *concinna* and *F.* (*V.*) *repanda*), 14 specimens, 2 d. THAILAND. Krabi, Phiphi Islands (hosted by *F.* (*V.*) *concinna* and *F.* (*V.*) *repanda*), 4 specimens, 1 clutch of egg-capsules, 3 d. PHILIPPINES. Cebu (hosted by *F.* (*V.*) *repanda*), 1 specimen. INDONESIA. NE Kalimantan, Berau Islands (hosted by *F.* (*D.*) *scruposa*), 3 specimens, 1 clutch of egg-capsules. N Sulawesi (hosted by *F.* (*V.*) *repanda*), 1 specimen. SW Sulawesi, Spermonde archipelago (hosted by *F.* (*D.*) *horrida*, *F.* (*D.*) *scruposa*, *F.* (*F.*) *fungites*, *F.* (*L.*) *scutaria*, *F.* (*V.*) *concinna*, *F.* (*V.*) *repanda*, *F.* (*V.*) *spinifer*, *Halomitra pileus*, *Herpolitha limax* and *Sandalolitha robusta*), 247 specimens, 91 clutches of egg-capsules, 11 d. Moluccas, Ambon (hosted by *F.* (*F.*) *fungites* and *F.* (*V.*) *repanda*), 2 specimens, 1 d. Bali (hosted by *C. echinata*, *F.* (*D.*) *horrida*, *F.* (*F.*) *fungites* and *F.* (*V.*) *repanda*), 28 specimens, 6 clutches of egg-capsules, 2 d. PALAU. Off Koror (hosted by *C. echinata*, *F.* (*D.*) *horrida*, *F.* (*F.*) *fungites*, *F.* (*V.*) *concinna*, *F.* (*V.*) *repanda*, *H. pileus* and *S. robusta*), 40 specimens, 12 clutches of egg-capsules.

Type locality. USA. Hawaii.

Shell (figs 70-73, 111, 129; table 1). Shell fragile, with convex whorls, creamy white. The shell height/width indexes (table 1) vary considerably, from 1.7 to 3.3 (n = 26), resulting in shells varying from moderately broad-conical (fig. 71) to slender-conical (figs 70, 72-73). For dimensions and number of costal and spiral ribs on the 2nd and the 5th teleoconch whorls, see table 1. Most specimens that were found are about 4 mm in height (e.g. fig. 73). Most adult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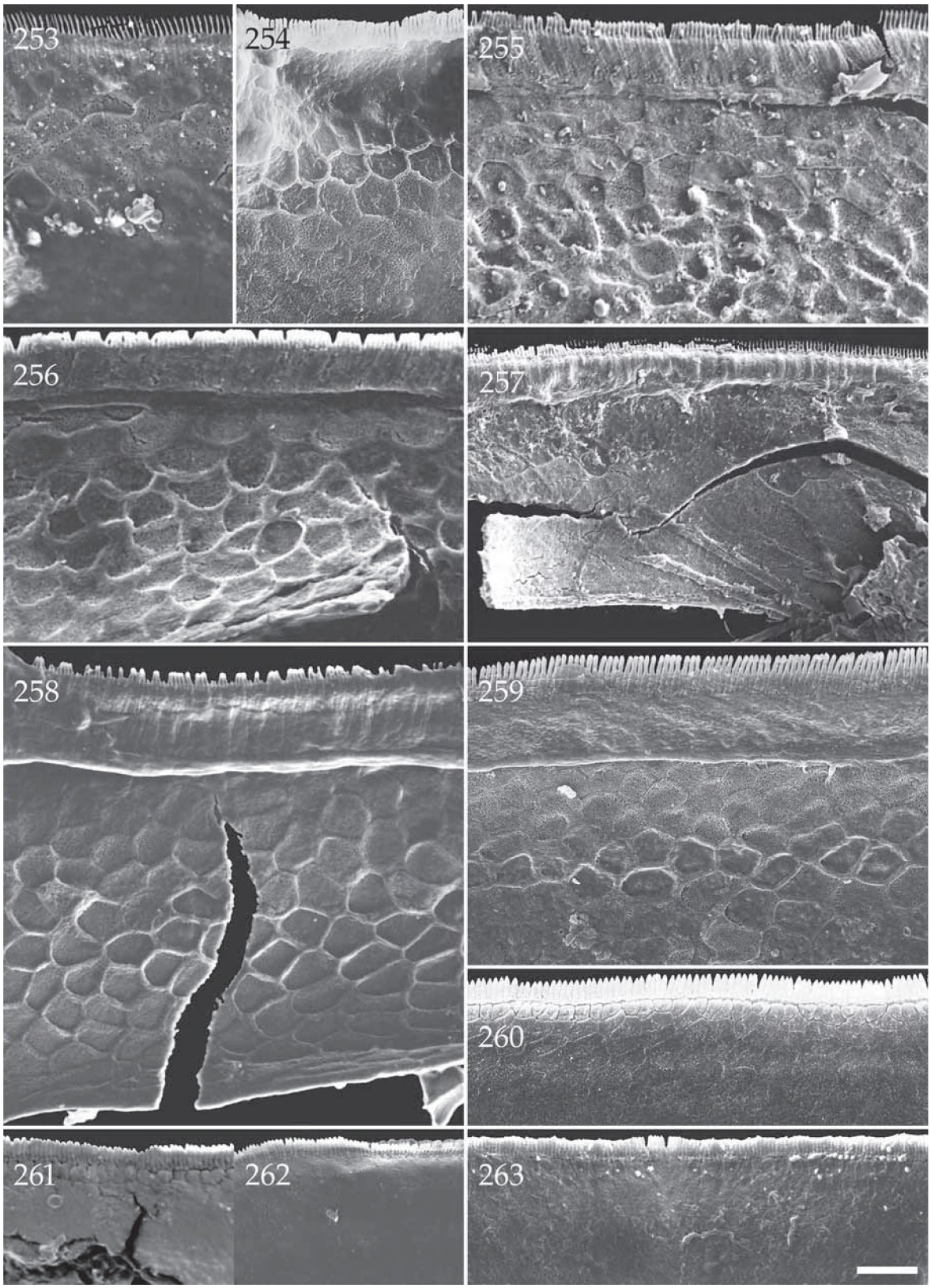
(with egg-capsules) specimens that were found are 8-12 mm in shell height, with about 15 mm for the largest shells. However, an exceptionally large specimen (fig. 70), collected off Bali, Indonesia, reaches 28.2 mm in height. The holotype, missing the protoconch and the initial teleoconch whorl or whorls, measures 14.2 × 5.7 mm. The protoconch (fig. 111) has 3¼-3½ whorls (n = 10); apart from its smooth apical part, it is sculptured with regularly spaced, very fine, incised, axial lines, 25 (n = 1) per 0.2 mm on protoconch whorl 2¼-2¾. The teleoconch (fig. 129) has up to 12¾ whorls, separated by a moderately deep suture; it is sculptured with mostly regularly placed, usually discontinuous, orthocline, lamellar, low costae, touching the adjoining whorls. From about the 5th teleoconch whorl onwards, the costae usually become slightly coronate just before reaching the preceding whorl; they curve adaperturally while touching it. In most specimens the number of costae remains approximately the same on all whorls, with adjoining whorls differing in about two costae at most. One shell with a height 21.6 mm, has 21, 21, 21 and 22 costae on the 2nd, 3rd, 5th and 11th teleoconch whorl, respectively; on the 12th teleoconch whorl however, there are 39 costae, the highest number recorded for *Epifungium ulu*. Very fine, irregularly placed, incised, axial lines are present from about the 6th teleoconch whorl onwards. The teleoconch is additionally sculptured with very low, inconspicuous, spiral threads, which are randomly placed on the whorls and are usually obsolete on the initial whorls. Although the number of spiral threads on the 2nd, 3rd, and 5th teleoconch whorls remains approximately the same (adjoining whorls differing in about two), this number usually increases slowly towards the younger whorls, sometimes becoming numerous from about the 9th teleoconch whorl onwards. Aperture subcircular. About half of the specimens (14 out of 25) have a closed umbilicus; in the remaining 11 shells the umbilicus is very narrow, visible in oblique view only. The presence of either a closed or an open umbilicus is not correlated with shell size.

Figs 236-252. Jaw details. 236-238, *Epidendrium aureum* spec. nov., radula in Fig. 160; 239-242, *E. sordidum* spec. nov., Philippines; 243-252, *Epifungium ulu*; 243, 245, 249-252, shell height = 14.0 mm, radula in Fig. 174; 244, 246-248, shell height = 28.2 mm, shell in Fig. 70. 236-237, 240-246, 250, jaw, outer surface; 238-239, 247-249, 251-252, jaw, inner surface. 245, 249-252, illustrating upturned jaw flap (f). Scale bars = 0.01 mm. SEM Photos.

Operculum (fig. 151). Operculum paucispiral, with interconnected coils as in *Surrepifungium patamakanthini* spec. nov. (fig. 3). At the outside of the operculum (fig. 151) there are 27 wavy, segmented threads per 0.1 mm (n = 1), running about perpendicular to the growth lines.

Radula (figs 174, 194, 214; table 2). The radulae of four Indonesian snails with shell heights of 9.1, 10.0, 14.0 and 28.2 mm, respectively, were studied (figs 174, 194; table 2). The radulae of the two largest snails could not be accurately counted (table 2). No distinct differences in form and/or size of the teeth, related to the size of the snails, were found. Each tooth (figs 174, 194, 214) consists of a moderately slender stem and a somewhat broader blade, which merge gradually; the blade has 2-5 acute, secondary cusps. The teeth (figs 174) are attached to the radular plate along the bases, which takes ½ to ¾ of the length of a tooth (figs 194, 214). The number of secondary cusps (table 2) gradually increases from 2 on the innermost tooth (fig. 194, left) to 4-5 in between the 4th-14th tooth, after which the number decreases to 2-3 on the ultimate, i.e. 15th tooth (fig. 214, right). The apical cusp and the secondary cusp directly underneath it are usually similar in size and somewhat curved towards each other; all other secondary cusps are usually similar in size and somewhat curved upwards, away from the stem (figs 174, 194). Starting from the innermost, smallest tooth, with a height of 0.028-0.029 mm (n = 2), the teeth gradually increase in size to almost two times that height, i.e. 0.049-0.050 mm (n = 2), up to the 7th-8th tooth, after which they gradually become smaller until the penultimate, i.e. 14th, 0.038-0.039 mm (n = 2) high tooth, which is followed by the somewhat smaller, usually malformed, ultimate tooth, with a height of 0.028 mm (n = 2) (table 2).

Jaw (figs 21, 24, 31-32, 243-252, 259-260; table 2). Three jaws from three specimens from Indonesia were studied (table 2). The denticulate edge consists of a row of slender, blunt denticles (figs 31, 246, 243-244, 259), which are basally pitted on the inside (figs 32, 248, 260). They have a maximum size of 0.0038-0.0042 mm (n = 2). Seen from the outside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(figs 243-244, 259), 50-65 denticles (mean = 57.7, n = 3) per 0.05 mm extend above a 0.0038-0.0042 mm (n = 2) broad, granulated jaw-flap (figs 243-244), which lies loosely over part of the jaw-pattern. That the jaw-flap lies loose, is distinct when it turns over, becoming visible from the inside of the jaw (figs 249, 252-252) and revealing the jaw-pattern that is usually beneath it, from an outside view of the jaw (figs 245, 250). The pattern, as far as visible under a jaw-flap that has not turned over (figs 243-244, 259), consists of rows of sunken, pentagonal figures (fig. 21); the upper two or three rows are densely pitted, followed further on by one or two rows that are not pitted and after that by rows, which are scarcely pitted and gradually become obsolete away from the denticulate jaw-edge. On the inner surface of the jaw, just below the denticles, there is a row of engraved, scarcely pitted, irregularly square-like figures (fig. 248), followed further on by several rows of densely pitted, engraved, irregular figures (figs 24, 251-252, 260), gradually becoming obsolete away from the denticulate edge, sometimes changing in a rough surface with relatively large holes (figs 249, 251).

Spawn (298-299). Egg-capsules (fig. 299) ovoid, without distinct protuberances, sometimes embedded with sand, 1.00-1.60 mm (mean = 1.27, n = 20) in diameter, e.g. measured horizontally, from left to right in figure 298, containing 120-330 eggs (mean = 193.9, n = 20) each. The mucus threads that connect the egg-capsules are strongly twisted and not sculptured (fig. 299).

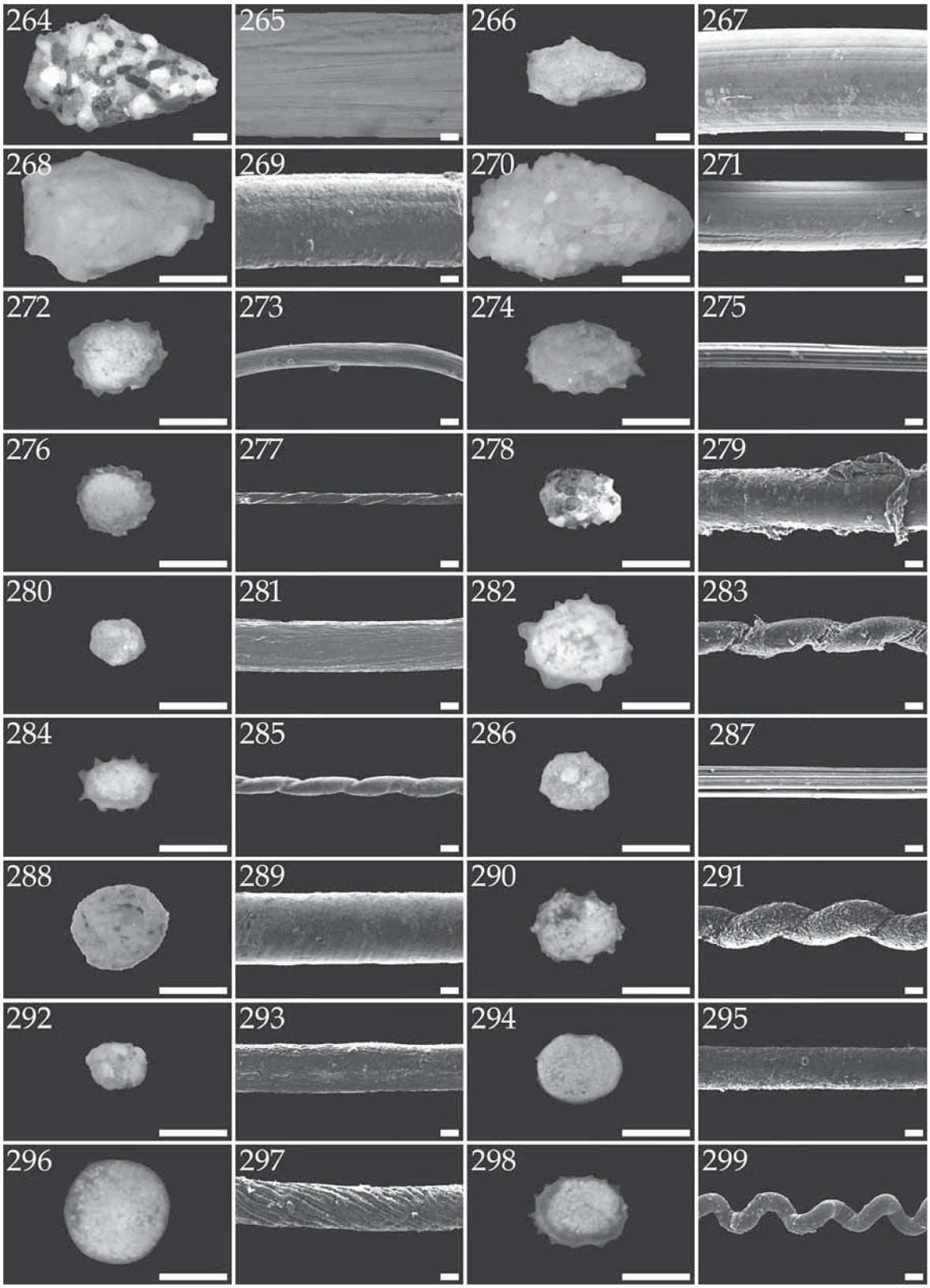
Habitat. The snails and their egg-capsules were found at 1-35 m, associated with *Ctenactis echinata* (Pallas, 1766), *Fungia* (*Danafungia*) *horrida* Dana, 1846, *F.* (*D.*) *scruposa* Kluzinger, 1879, *F.* (*Fungia*) *fungites* (Linnaeus, 1758), *F.* (*Lobactis*) *scutaria* Lamarck, 1801, *Fungia* (*Verrillofungia*) *concinna* Verrill, 1864, *F.* (*V.*) *repanda* Dana, 1846, *F.* (*V.*) *spinifer* Claereboudt and Hoeksema, 1987, *Halomitra pileus* (Linnaeus, 1758), *Herpolitha limax* (Esper, 1797), *Sandalolitha robusta* (Quelch, 1886). They usually live attached with their mucus threads to the underside of these mushroom corals or to hard substrata underneath. Most host corals were found on coral slopes. Taylor (1977: 253) notes that snails of *E. ulu*, in an aquarium, can also feed on the sea-anemone *Aiptasia* spec.

Figs 253-263. Jaw details. 253, *Epifungium adgravis*, radula in Fig. 15; 254, *E. hartogi*, radula in Fig. 169; 255-256, 261, *E. hoeksemai*; 256, 261, radula in Fig. 170, shell height = 14.5 mm, Sulawesi, Indonesia; 255, shell height = 11.9 mm, Palau; 257, 262, *E. lochi*, radula in Fig. 171; 258, 263, *E. nielsi*, radula in Fig. 172; 259-260, *E. ulu*, shell in Fig. 70. 253-259, jaw, outer surface; 260-263, jaw, inner surface. Scale bar = 0.01 mm. SEM Photos.

Distribution (fig. 87). The snails and their egg-capsules were found in the Indo-West Pacific, from Egypt (Red Sea), Seychelles, Maldives, Thailand, Philippines, Indonesia and Palau to Australia.

Differentiation. The shells resemble those of *Epifungium adgranulosa* spec. nov., *E. adgravis* spec. nov., *E. adscabra* spec. nov., *E. hoeksemai*, *E. marki* spec. nov. and *E. nielsi* spec. nov. They differ in having a relatively low number of costal ribs and spiral threads on the 2nd, 3rd and 5th teleoconch whorl (table 2), the lowest average T3 value, i.e. 0.69 mm (table 2), and in being associated with other host species (see the habitat descriptions), with the exception of *Fungia* (*Fungia*) *fungites*, which is associated with both *E. ulu* and *E. hoeksemai*. See the differentiation of *E. hoeksemai*.

Remarks. According to Hoeksema (pers. comm.), off Hawaii, the type locality of *Epifungium ulu*, the only common mushroom coral species is *Fungia* (*Lobactis*) *scutaria*. The only epitoniid species that is associated with this host species is *E. ulu*. Therefore, specimens described as *E. ulu* from Hawaii are most probably correctly identified. At other Indo-Pacific localities the host species of *E. adgranulosa* spec. nov., *E. adgravis* spec. nov., *E. adscabra* spec. nov., *E. hoeksemai*, *E. marki* spec. nov. or *E. nielsi* spec. nov. may also be present (see the habitat descriptions of those species). Therefore all the references in the literature to "*Epitonium ulu*" Pilsbry, 1921, from other localities than Hawaii, should be treated with great care, because other species might be involved. The description of "*Epitonium ulu*" in A. Gittenberger *et al.* (2000: 11-12, figs 17, 21) is at least partly based on *E. adgranulosa* spec. nov., *E. adgravis* spec. nov., *E. adscabra* spec. nov., and *E. nielsi* spec. nov., but the two figures do show *E. ulu* indeed. The epitoniids collected off North Queensland with *Fungia* spp. and *Heliofungia actiniformis*, and identified as *E. ulu* by Loch (1982), probably belong to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a variety of species. Those found associated with the fungiid *Heliofungia actiniformis*, may be *E. hoeksemai*. The shell figured by Loch (1982: 3, on the right) is here considered to represent *E. ulu*. The *Fungia* host species of the epitoniids *E. adgranulosa* spec. nov., *E. adgravis* spec. nov., *E. adscabra* spec. nov. and *E. nielsi* spec. nov., are all known from off North Queensland (Hoeksema, 1989). Because these four epitoniid species closely resemble *E. ulu* in shell shape and sculpture, they may be partly represented in the material recorded by Loch (1982). The two shells of "*E. ulu*" figured by Dushane (1988a: 31, figs 3, 4) from the Red Sea, off Tiran Island, Straits of Tiran, and off Sinafir Island, Saudi Arabia, resemble *E. ulu* and *E. adgranulosa* spec. nov.

General discussion

Even though Bouchet and Waren (1986: 469) argue that the low amount of variation within epitoniids in general may reflect a low degree of specialization, many coral-associated, conchologically poorly differentiated epitoniids have specialized on only one or a restricted number of host species, and have large ranges, similar to those of their hosts. This adaptive radiation of coral-associated epitoniids was not noticed before because most species cannot easily or not at all be identified unequivocally on the basis of conchological characters alone. Their identities as separate gene pools are convincingly demonstrated by molecular data, however. Shell shapes and sculpture are only partially diagnostic because of interspecifically overlapping character states. In most cases, the operculum, the jaw, the radula, the spawn and/or the habitat do tell more about the identity of the species involved. These characters can also be very valuable for distinguishing between at least the newly described genera.

Many (sub)generic names of Epitoniidae are available (see e.g. Kilburn, 1985; Wenz, 1940). Still we found it necessary to introduce three more genus level taxa, viz. *Epidendrium* gen. nov., *Epifungium* gen. nov. and *Surrepifungium* gen. nov. The DNA-data indicate that these three new genera are monophyletic and most closely related to each other, indicating that a host-shift from sea-anemones to corals or vice versa has occurred only once in their evolutionary history (A. Gittenberger *et al.*, in prep.). These new taxa are given a generic instead of a subgeneric status, because molecular data indicate that the genetic distance between the two *Epitonium* species *E. clathrus* and *E. clathratulum* versus the *Cycloscala* species *C. crenulata* (Pease, 1867) is smaller than the genetic distance between the three new coral-associated genera. Another reason to introduce three genera instead of a single new genus with three subgenera, is that no morphological character is known to unequivocally distinguish the combined three taxa from other epitoniid genera. The only non-molecular character known, is the association with hard corals instead of sea anemones and zoanthids.

It was repeatedly argued in literature (e.g. Richter and Luque, 2004) that '*Epitonium*' *billeeanum* and '*E.*' *dendrophylliae* should not be placed in *Epitonium* because these species distinctly differ from the type species *Epitonium scalare* (Linnaeus, 1758). This suggestion was not followed however, because of a lack of data, e.g. molecular data, and the uncertainties in epitoniid classification in general. Another reason why these three generic taxa have not been recognized before is that 16 of the 20 species involved were unknown prior to 2000 (A. Gittenberger *et al.*, 2000; Bonfitto and Sabelli, 2001; A. Gittenberger, 2003). A final argument in favour of introducing new genera is that most type species of epitoniid genera in the literature, are either distinctly different in morphology and/or clearly not associated with coral species, because no corals are present within their ranges and/or their hosts are known to be sea-anemones. No epitoniid species is known to be associated with both corals and sea-anemones. Dushane (1988a), Yamashiro (1990) and Mienis (1994) indicated that *Epitonium bullatum* may be related to both cnidarian taxa, but A. Gittenberger *et al.* (2000) have demonstrated that here the coral-associated epitoniids are in fact *Epifungium twilae*.

Figs 264-299. Egg-capsules and mucus threads. 264-265, *Surrepifungium costulatum*; 266-267, *S. ingridae*; 268-269, *S. patamakanthini*; 270-271, *S. oliverioi*; 272-273, *Epidendrium aureum*; 274-275, *E. sordidum*; 276-277, *Epifungium adgranulosa*; 278-279, *E. adgravis*; 280-281, *E. adscabra*; 282-283, *E. hartogi*; 284-285, *E. hoeksemai*; 286-287, *E. lochi*; 288-289, *E. marki*; 290-291, *E. nielsi*; 292-293, *E. pseudolochi*; 294-295, *E. pseudotwilae*; 296-297, *E. twilae*; 298-299, *E. ulu*. Scale bars: even numbers = 1 mm; odd numbers = 0.01 mm. Photos: through binoc. (even numbers & 265) and with SEM (odd numbers except for 265).

Species that are sympatric from a geographical perspective are usually found with different host coral species; whenever they share a host species they are not entirely syntopic, occurring at different positions on or below the host coral.

Most (sub)genera in the family Epitoniidae have been introduced and described on the basis of teleoconch shell characters only, with a special focus on shell shape, the costal and spiral sculpture, the umbilicus and the suture (see e.g. Weil *et al.*, 1999; Nakayama, 2003). Convergent or parallel evolution in these characters may be common among epitoniids in general (Kilburn, 1985: 241) and has certainly played an important role in the origin of the 22 species that are described here.

Shell shapes often vary between very broad and relatively slender conical within species and within genera, as for example in *Epidendrium* (figs 51-55) and *Epifungium* (figs 61-76, 88-91). Within *Surrepifungium*, the shells of *S. ingridae* and *S. patamakanthini* spec. nov. have coronate costal ribs (figs 38, 40), while the ribs in *S. costulatum* and *S. oliverioi* are more regularly curved (figs 33-37). A spiral sculpture may be present on the entire teleoconch in some species, as in e.g. *Surrepifungium ingridae* (fig. 113) and *Epitonium celesti* (in Bouchet and Waren, 1986: 509), while it is obsolete or absent in closely related species, i.e. *Surrepifungium patamakanthini* spec. nov. and *Epitonium graviarmatum* spec. nov. (fig. 117). The number of ribs is variable within many epitoniid species and can even differ strongly between the whorls of a single shell (table 1; Robertson, 1983b: 116). Within species, shells with and without an open umbilicus are present, i.e. in *Epifungium adgranulosa* spec. nov., *E. adgravis* spec. nov., *E. adscabra* spec. nov., *E. marki* spec. nov., *E. nielsi* spec. nov. and *E. ulu*. In *Epifungium* the suture is very deep to almost fenestrate in *E. marki* spec. nov. and *E. pseudolochi* spec. nov., while it is shallow to somewhat indented in *E. adgranulosa* spec. nov., *E. pseudotwilae* spec. nov. and *E. twilae*.

Because teleoconch characters, like the ones referred to above, are still commonly used to characterize or identify epitoniid genera or subgenera within a very speciose genus *Epitonium*, (e.g. Weil *et al.*, 1999: Appendix II; Bonfitto and Sabelli, 2001; Nakayama, 2003), "epitoniid taxonomy remains in a chaotic state, particularly above the species level" (Kilburn, 1985: 240) and the classification of the genus *Epitonium* is "very tentative and is aimed solely at grouping together similar species for convenience sake" (Kilburn, 1985: 280).

While comparing molecular, conchological, anatomical, ecological and geographical data of the species described here we found that several characters, which are rarely used in the literature, are more robust for making classifications in the Epitoniidae than are most conchological characters. Kilburn (1985: 241) indicated that the protoconch morphology can be used. We found that the protoconchs of almost all species that are associated with corals consist of 2½-3½ whorls, with a sculpture of fine, axial lines; this can only be used to recognize the combined three genera that are described here. However, in *Epitonium graviarmatum* spec. nov., which may also be hosted by corals, there is a different protoconch, consisting of five whorls and a sculpture of costal and spiral lines. No teleoconch characters were found which enable an unequivocal recognition or a differentiation between the genera *Epidendrium* gen. nov., *Epifungium* gen. nov. and *Surrepifungium* gen. nov. The micro-sculpture on the operculum may turn out to be diagnostic, since in the species that are described here it consists of different numbers of wavy threads, running c. perpendicular to the growth lines, i.e. 9 to 20 in *Surrepifungium* (figs 136-139), versus 20 to 40 in *Epifungium* (figs 140-151), and none in *Epidendrium* (figs 132-134). However, *Epitonium pyramidalis* also has no operculum sculpture (fig. 135). Bouchet and Waren (1986: 472) noted that the opercula of several species of *Opalia* and *Cirsotrema* are "minutely beaded" (Bouchet and Waren, 1986: 474, fig. 1116) and "smooth" in *Acirsa*, *Acrilloscala*, *Cyclindriscala*, *Eccliseogyra*, *Epitonium*, *Gregorioiscala*, *Iphitus* and *Periapta* (Bouchet and Waren, 1986: 473-474, figs 1106-1115, 1117-1118).

The radular morphology is at least partly diagnostic for *Epifungium*, since in that genus the snails have teeth without a clear basal denticle and with one to six secondary cusps (figs 169-174). The radula cannot be used to identify *Epidendrium*, *Surrepifungium* and most other epitoniid genera. The alleged, sex-related, ontogenetic changes in the structure of the epitoniid radulae (Page and Willan, 1988) are most probably based on a misidentification of two species that were regarded as a single species (see the remarks on *Epidendrium* gen. nov.). Many wentletraps have teeth with a distinct basal denticle, an acute apical

cusp (fig. 13) and occasionally an inconspicuous, secondary cusp. These teeth are typical for some *Epidendrium* and *Surrepifungium* species (figs 160-161, 163-167), but also for *Acirsa subdecussata* (in Bouchet and Waren, 1986: 470, fig. 1098), *Cirsotrema varicosa* (figs 152, 195), *Epidendrium aureum* spec. nov. (figs 160-161, 183, 203), *Epitonium celesti* (in Bouchet and Waren, 1986: 470, fig. 1099), *E. clathrus* (fig. 156), *E. pyramidalis* (figs 157, 180, 200) and even *Janthina janthina* (fig. 16), a species of still unclear affinities, classified with the Janthinidae, Janthinoidea Lamarck, 1810 [= Epitoniacea Berry, 1910].

The characters of the jaws seem to be much more useful to identify the genera of the species that are studied here. More specifically the shapes of the denticles at the denticulate edge, the structure of the jaw-flap and the pattern on both the inner and the outer surface of the jaw, are informative regarding the coral-associated species studied. The structure of the jaw may prove to be useful for other epitoniid genera as well. For example, *Epitonium ancillottoi* and *E.* spec. 1 have distinctly different radular teeth (figs 153-154, 176-177, 196-197) but similar jaws (figs 219-222), which may be considered indicative of being closely related, as is also indicated in this case by molecular and conchological data. In both *Cirsotrema varicosa* and *Gyroscala lamellosa* the jaws have multiple rows of slender, blunt denticles, without a jaw-flap, and with a pattern of raised and sunken arch-like figures (figs 17-19, 215-217). They differ distinctly from the jaws known from *E. pyramidalis*, *E. ancillottoi*, *E.* spec. 1 and *E. clathratulum* (figs 218-225). In *Gyroscala* the shells more closely resemble *Epitonium* (see e.g. Dushane, 1987b: 12) than *Cirsotrema* species, differing in having a basal cord, which is missing in *Epitonium* and present in *Cirsotrema*. Kilburn (1985: 241), who treats *Gyroscala* as a genus (as do we), noted that Thiele (1929) and Fretter and Graham (1982) classified *Gyroscala* as a subgenus of *Cirsotrema*, whereas Americans (e.g. Abbott, 1974) considered *Gyroscala* a subgenus of *Epitonium*. The presence versus absence of a basal cord is the most frequently used shell character in epitoniid taxonomy (Kilburn, 1985: 241). Both jaw morphology and molecular data (A. Gittenberger *et al.*, in prep.) indicate that *Gyroscala* is more closely related to *Cirsotrema* than to *Epitonium*, which is in conformity with the view that the presence of a basal cord is a more informative character state than most other teleoconch characters.

Also in Nudibranchia there may be two jaws flanking the radula. Surprisingly, some of these jaws (e.g. Rudman and Avern, 1989; Smith and Gosliner, 2003), which are often described in literature, may closely resemble those of epitoniids, in having a denticulate edge with several rows of blunt denticles as in figure 217. No pattern seems to be present on the inner surface of nudibranch jaws and it is unclear whether the outer surface is sculptured. In a preliminary literature study, we only found jaws figured from the inside.

Most epitoniids have ovoid to roundish egg-capsules. Therefore, the irregular, pentagonal egg-capsules that are known from *Surrepifungium* can be used to distinguish these species from conchologically similar species in other genera, like for example *Epitonium ancilottoi* and *E.* spec. 1, which have roundish egg-capsules.

It has to be concluded that most monophyletic groups of Epitoniidae associated with coral species cannot unequivocally be identified on the basis of teleoconch characters only, because of a large amount of convergence or parallel evolution. A combination of molecular data, morphological data of the protoconch, the operculum, the jaws and the spawn, is necessary identifying the clades present. Unfortunately such data sets are not yet available for most epitoniid taxa. A more detailed discussion on the evolutionary history of the epitoniid species, especially those occurring associated with coral species, will be given in an article presenting a phylogeny reconstruction based on the DNA marker CO-I (A. and E. Gittenberger, in prep.).

Acknowledgements

We are grateful to Merijn Bos, Pat Colin, Rachel Colin, Hans Ditlev, Mark Erdmann, Jeroen Goud, Victor de Grund, Bert W. Hoeksema, Bas Kokhoorn, Alfian Noor, Somnuk Patamakanthin, Somwang Patamakanthin, Carlos A. Sánchez, Niels Schrieken, Frank Swinnen and Nicole de Voogd for their help in providing information and material used in this study. In particular we thank Dr David G. Reid (London) for the many constructive comments which enabled us to improve the manuscript. The research

in Indonesia was sponsored by the Indonesian Institute of Sciences (LIPI). This research project was supported by WOTRO (grant nr. W 82-249) with additional funding by KNAW, the Alida Buitendijkfonds, and the Jan Joost ter Pelkwijkfonds.

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Received: 18 July 2005
Accepted: 1 August 2005

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

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

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Key words: parasitic snails; coral reefs; coral/mollusc associations; Epitoniidae; *Epitonium*; *Epidendrium*; *Epifungium*; *Surrepifungium*; Scleractinia; Fungiidae; *Fungia;* Indo-Pacific

Abstract

Since 2000, eighteen epitoniid species that were found in association with corals, were described as new to science in addition to the four such species that were already known. Three genera of coral-associated epitoniids were also described as new. Most of these taxa could only be diagnosed by their ecology and by the morphology of the radulae, jaws, opercula and egg-capsules. Using 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.

Contents

Introduction

This is the fourth contribution in a series of papers aiming at a better knowledge of epitoniid species (Gastropoda: Epitoniidae) associated with corals (Scleractinia). For an introduction about the ontogeny and ecology of these snails, and detailed descriptions of the morphology of their shells, radulae, jaws, opercula and egg-capsules, see also A. Gittenberger (2003), A. Gittenberger and E. Gittenberger (2005), A. Gittenberger and Hoeksema (chapter 10) and A. Gittenberger et al. (2000). The snails and shells that were examined in this study came from many localities (fig. 1).

Before 2000, only four epitoniid species were known to be associated with corals (Scleractinia: Fungiidae or Dendrophyllidae), i.e. *Epidendrium billeeanum* (Dushane and Bratcher, 1965), *Epidendrium dendrophylliae* (Bouchet and Warén, 1986), *Epifungium ulu* (Pilsbry, 1921) and *Surrepifungium costulatum* (Kiener, 1838). Since then, eighteen additional species were found in association with corals. All of these were described as new to science (Bonfitto and Sabelli, 2001; A. Gittenberger, 2003; A. Gittenberger and E. Gittenberger, 2005; A. Gittenberger et al., 2000). Three genera of coral-associated species were described as new to science, i.e. *Epidendrium*, *Epifungium* and *Surrepifungium* (A. Gittenberger and E. Gittenberger, 2005). Most of these species and genera cannot be identified on the basis of conchological characters alone, because of the apparent parallel or convergent evolution in shell shape, size and sculpture (A. Gittenberger and E. Gittenberger, 2005). Most of these taxa can be diagnosed by their ecology and by the morphology of the radulae, jaws, opercula and egg-capsules, however.

Using an original molecular data set, we discuss in this paper the following research questions: [1] do the molecular data support the existence of the recently described, coral-associated species as separate gene pools; [2] are the so-called genera of the Epitoniidae that are associated with corals monophyletic groups;

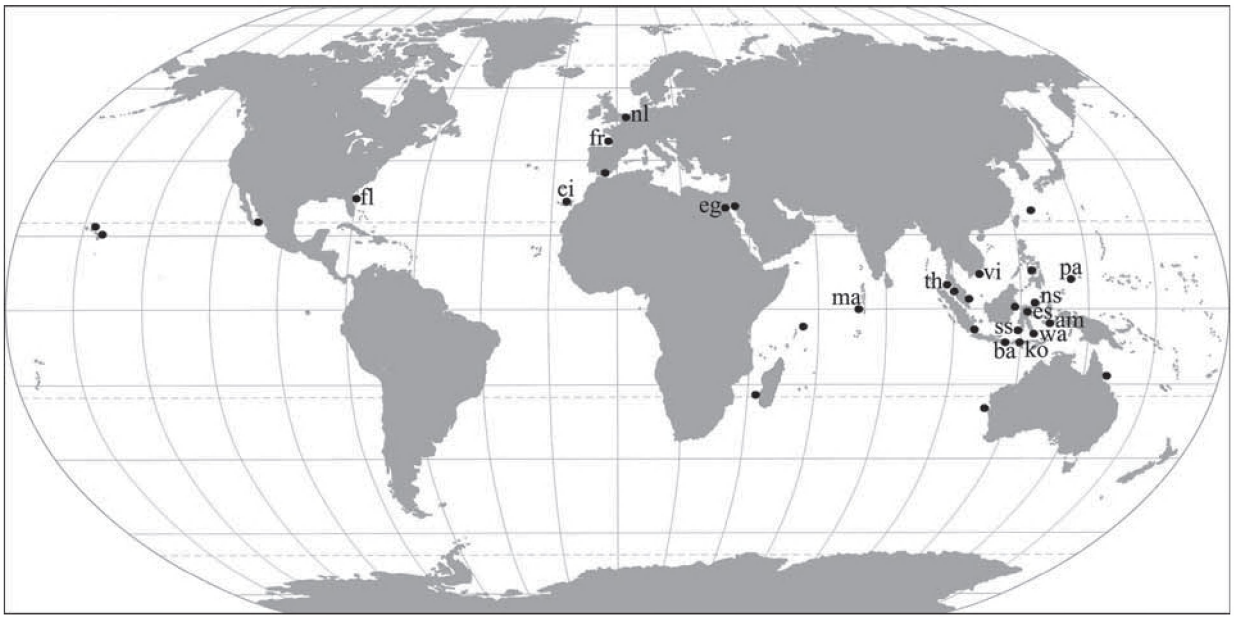


Fig. 1. World map. Black dots indicate localities of which snails and/or shells were examined by the authors. The dots accompanied by the two letter abbreviations, indicate localities from which epitoniid snails were successfully sequenced (see also fig. 2). Abbreviations: am, Ambon, Indonesia; ba, Bali, Indonesia; ci, Canary Islands; eg, Egypt (Red Sea); es, east Sulawesi, Indonesia; fl, Florida, USA; fr, France; nl, The Netherlands; ns, north Sulawesi, Indonesia; ko, Komodo, Indonesia; ma, Maldives; pa, Palau; ss, south Sulawesi, Indonesia; th, Thailand; vi, Vietnam; wa, Wakatobi, Indonesia.

[3] what can be concluded about the status of the nominal genus *Epitonium*; [4] what evolutionary mechanisms, like co-evolution, may have played a prominent role in the evolutionary history of the associations between wentletraps and their coelenterate hosts?

Material and methods

Fieldwork

All snails used in the molecular analyses were identified by the first author. The ones that are associated with corals are described in detail in A. Gittenberger and E. Gittenberger (2005). They were collected by searching approximately 60,000 stony corals of the families Fungiidae, Dendrophylliidae and Euphylliidae for gastropod parasites in the Indo-West Pacific off Egypt, Maldives, Thailand, Malaysia, Japan, Palau, Philippines, Indonesia and Australia. The fungiid hosts were usually identified twice, from photographs and/or specimens, independently by A. Gittenberger and B.W. Hoeksema. H. Ditlev identified the euphylliids from photographs. The dendrophylliids were not identified. Most of the specimens used in this study were collected in a three years period (2001-2003) while scuba-diving in Indonesia and Palau during several excursions organized by the National Museum of Natural History Naturalis. This material was preserved in ethanol 96% to enable DNA-analyses. For making comparisons, epitoniid species that are known to be associated with sea anemones, were also included in the molecular analyses. These snails are found in both the Atlantic and the Indo-Pacific Ocean. The localities from which material was used for the molecular analyses are indicated in figure 1.

DNA extraction and sequencing

Until DNA-extraction, most snails were preserved in ethanol 96%, some in ethanol 70%, and the specimens from Thailand in a 1:1 mixture of rum (c. 40% alcohol) and 70% ethanol. In relatively small specimens, the complete snail without its shell was used for the

extraction. In larger specimens a piece of the foot tissue was cut off with a scalpel. A minute, curved needle, stuck into a wooden match, was used to pull the snails out of their shells without breaking them. The tissue sample was dissolved by incubation at 60° C, for c. 15 hours, in a mixture of 0.003 ml proteïnase K (20 mg/ml) and 0.5 ml CTAB buffer, i.e. 2% CTAB, 1.4M NaCl, 0.2% mercapto-ethanol, 20mM EDTA and 100mM TRIS-HCl pH8. After incubation the solution was mixed with 0.5 ml Chloroform/Isoamyl alcohol, and centrifuged for 10' at 8000 rpm. The supernatant was extracted, mixed with 0.35 ml isopropanol, put aside for c. 15 hours at 4° C and finally centrifuged for 10' at 8000 rpm to precipitate the DNA. The supernatant was discarded and the remaining DNA-pellet was washed at room temperature with 0.5 ml of an ethanol/ ammonium-acetate solution for 30'. After centrifugation for 10' at 8000 rpm, this solution was discarded. The pellet was dried in a vacuum centrifuge and than dissolved in 0.020 ml MilliQ. The DNA quality and quantity were tested by electrophoresis of the stock-solution through an agarose gel, and by analyzing a 1:10 dilution of the stock in a spectrophotometer.

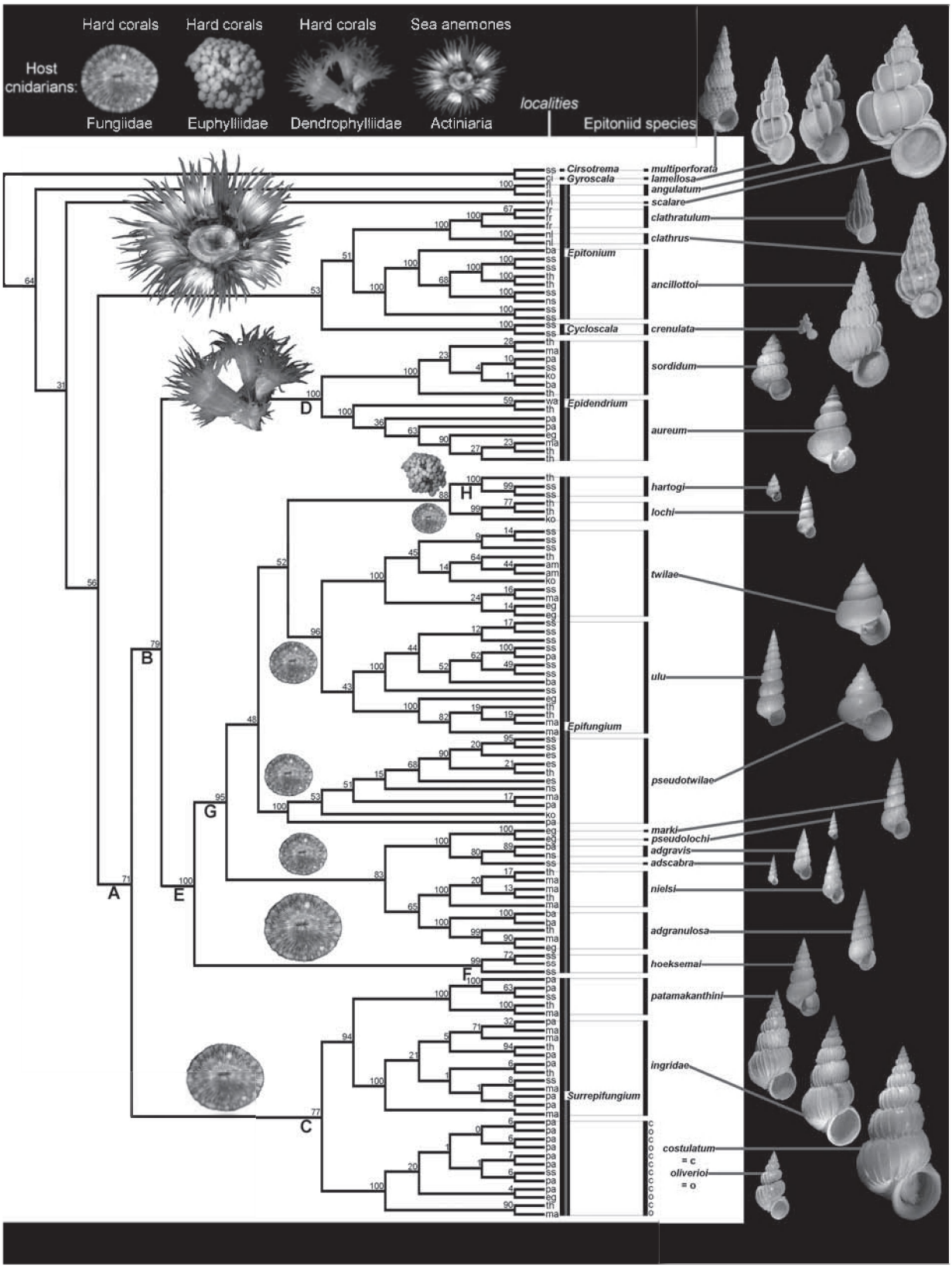
The COI region was amplified using the primers and annealing temperatures (AT) as specified in table 1 in a Peltier Thermal Cycler PTC-200. The epitoniid specific COI primers were developed on the basis of 15 wentletrap sequences retrieved using Folmer Universal COI primers (table 1). The sequences of these primers were made wentletrap-specific by comparing them with the Folmer COI-sequences (A. Gittenberger, Reijnen and Hoeksema, chapter 3) of their fungiid hosts, making sure that the primers would not fit on the COI-region of these corals. The optimized PCR-program consisted of 1 cycle of 94° C for 4' and 60 cycles of 94° C for 5"; AT for 1'; 0.5° C/s to AT + 5° C; 72° C for 1'. After the PCR, the samples were kept on 4° C until purification by gel extraction using the QIAquick Gel Extraction Kit from QIAGEN. The PCR reaction mix consisted of 0.0025 ml PCR buffer (10x), 0.0005 ml MgCl2 (50mM), 0.0010 ml forward primer (10 pM), 0.0010 ml reverse primer (10 pM), 0.0005 ml dNTP's (10 mM), 0.0003 ml Taq polymerase (5 units / 0.001 ml), 0.0132 ml MilliQ and 0.0010 ml 1:10 DNA stock-solution (= c. 100 ng DNA). The samples were kept at 4° C until cycle sequencing. Cycle sequencing was done in both directions of the amplified region, with a program consisting of 45 cycles of 96°C for 10", 50°C for 5" and 60°C for 4'. The reaction mix used was 0.0020 ml Ready Reaction Mix (Big DyeTM by PE Biosystems), 0.0020 ml Sequence Dilution-buffer, 0.0005 ml primer (5 pM forward or reverse primer solution) and 0.0055 ml amplified DNA (= half the PCR-product, evaporated to 0.0055 ml by vacuum centrifugation). The cycle sequence products were purified with Autoseq G50 columns (Amersham Pharmacia Biotech) and kept on 4°C until they were run on an ABI 377 automated sequencer (Gene Codes Corp.), using the water run-in protocol as described in the User Bulletin of the ABI Prism 377 DNA Sequencer (PE Biosystems, December 7, 1999). The consensus sequences that were used in further analyses, were retrieved by combining the forward and reverse sequences in Sequencher 4.05 (Genes Codes Corp.).

Sequence alignment and phylogenetic analyses

The COI sequences were imported in BioEdit v7.0.5 (Hall, 1999) and subsequently aligned using the

Table 1. Primers used for amplifying COI in Epitoniidae

Primers for COI region	AT	Primer seq.	Primer length	Reference
Folmer Universal primer Forward: LCO-1490	45	5'-GGT CAA CAA ATC ATA AAG ATA TTG G-3'	25-mer	Folmer et al., 1994
Folmer Universal primer Reverse: HCO-2198	45	5'-TAA ACT TCA GGG TGA CCA AAA ATC A-3'	25-mer	Folmer et al., 1994
Wentletrap specific primer Forward: WenCOI-for	51	5'-TAT AAT GTA ATT GTA ACT GCT CA-3'	23-mer	Newly developed primer
Wentletrap specific primer Reverse: WenCOI-rev	51	5'-GGG TCA AAA AAT GAA GTA TT-3'	23-mer	Newly developed primer


Hard corals
Hard corals
Hard corals
Sea anemones
Host cnidarians:
Fungiidae
Euphylliidae
Dendrophylliidae
Actiniaria
localities
Epitoniid species
Cirsotrema
Gyroscala
multiperforata
lamellosa
angulatum
scalare
clathratulum
clathrus
Epitonium
ancillottoi
Cycloscala
crenulata
Epidendrium
sordidum
aureum
hartogi
lochi
twilae
ulu
Epifungium
pseudotwilae
marki
pseudolochi
adgravis
adscabra
nielsi
adgranulosa
hoeksemai
patamakanthini
Surrepifungium
ingridae
costulatum
= c
oliverioi
= o
A
B
C
D
E
F
G
H

Clustal-W plugin in the default parameter settings. The alignment was than exported in nexus format and MacClade 4.0 (Maddison and Maddison, 2000) was used for manual editing of the alignment. The codon positions were identified by checking the amount of variation. The positions were than calculated. A translation to amino acids was made using the *Drosophila* genetic code and the protein sequence was checked for stop codons. The alignment is available from the authors. The only samples included in this data set that may be miss-identified, because the shells in question closely resemble each other (A. Gittenberger and E. Gittenberger, 2005), are those of *Surrepifungium costulatum* and *S. oliverioi*.

The homogeneity of base frequencies in the sequences was tested. Paup* 4.0b10 (Swoford, 2002) was used to perform a chi-square for the complete data set, and for the first, second and third codon positions separately. To test for the presence of phylogenetic signal we did the G1 skewness statistic based on 1000 random trees (Hillis and Huelsenbeck, 1992). MrModeltest 2.2 (Nylander, 2004) was used to calculate a best fitting model for the data. Likelihoods for 24 models of evolution were calculated using PAUP* and the command file provided with MrModeltest. MrBayes 3.1 (Ronquist and Huelsenbeck, 2003) was used for Bayesian inference analysis.

Bayesian inference was performed with five incrementally (T = 0.20) heated Markov chains and a cold one, which were run 4,000,000 generations and sampled once every 50 generations, using the best-fit model for nucleotide substitution as suggested by MrModeltest output. Standard deviations (SD) between posterior probabilities of both simultane runs were observed to identify the burnin of suboptimal trees. SD value below 1% was considered significant convergence. The remaining trees were than imported in PAUP* and a majority rule consensus tree with compatible groupings was calculated.

Fig. 2. Majority rule consensus tree with compatible groupings, resulting from a Bayesian inference analysis. The ancestral species A-H are indicated underneath the branches. Hosts are indicated as photos on those lineages that do not show a mayor host switch, i.e. a switch between coral families or corals and sea anemones, assuming maximum parsimony. See fig. 1 for locality abbreviations: fr, France; nl, The Netherlands; ns, north Sulawesi, Indonesia; ko, Komodo, Indonesia; ma, Maldives; pa, Palau; ss, south Sulawesi, Indonesia; th, Thailand; vi, Vietnam; wa, Wakatobi, Indonesia.

Results and discussion

The COI alignment of a stretch of 503 bases contains 211 variable positions 201 of which are potentially parsimony informative. The data set showed no stop codons. A single triplet gap was found in the sequence of *Epifungium twilae* from the Spermonde archipelago, Indonesia. The data set has a highly significant phylogenetic signal, as is indicated by the G1 skewness test, i.e. g1= -0.509. Base frequencies in the complete data set and in the first and second codon positions, are significantly homogeneous across taxa, i.e. P = 1 in all cases. The third codon position has a strong AT bias as is shown in base frequencies (A = 0.35, C = 0.06, G = 0.13, T = 0.46). The best fit model of nucleotide substitution proved to be the General Time Reversal model, including the proportion of invariant sites and gamma shape parameter (GTR + I + G). Bayesian analysis showed a convergence (SD < 0.01) of both simultaneous runs after approximately 3.5 billion generations.

The molecular analyses (fig. 2) support the three nominal, epitoniid genera *Epidendrium*, *Epifungium* and *Surrepifungium* as monophyletic groups. Furthermore, the identification of the individual snails on the basis of the criteria published by A. Gittenberger and E. Gittenberger (2005) was paralleled by the results of the analyses of the DNA sequences. Except for *Epifungium ulu*, all clades representing a species or a genus were supported by 100% or in rare cases by bootstrap values of at least 82%. The *E. ulu* sequences form a clade in the 50% consensus tree with compatible groupings (fig. 2), which is not significantly supported however, i.e. with a value of 43%, and should be considered therefore a "compatible grouping". The two sister clades that are combined here as *E. ulu* are supported by 100% each, however. These two clades represent exclusively specimens from Pacific Ocean localities, i.e. Indonesia and Palau, versus Indian Ocean localities, i.e. Maldives, Thailand and Egypt (Red Sea). Within these two clades a geographical pattern cannot be recognized. There seem to be two allopatric population groups of *E. ulu*, i.e. two panmictic gene pools that are separated by a geological barrier, with little or no gene-flow in between.

With very low support values (less than 60%) the epitoniid genera *Cycloscala*, *Epidendrium*, *Epifungium* and *Surrepifungium*, cluster within the *Epitonium*

clade, indicating that the latter taxon does not represent a monophyletic group in the actual interpretation in the literature. On the basis of such low support values in a Mr Bayes analysis, taking into account that many more alleged *Epitonium* species are known from shells only, additional conclusions on the status of this nominal genus would be premature. The most parsimonious, molecular phylogeny reconstruction (fig. 2) indicates that the ancestor of the Epitoniidae dealt with here was associated with sea-anemones, whereas only once in evolutionary history an epitoniid species switched to hard corals. That is surprising in view of the fact that it could be demonstrated experimentally, that at least under artificial circumstances in an aquarium the coral-associated species *Epifungium ulu* may switch its diet to sea-anemones when no corals are available (Bell, 1985). This induced change in host species was not accompanied by any clear disadvantages, the snails still completed an entire life cycle within 36 days (Bell, 1985). What mechanism[s] kept epitoniids from switching from sea-anemone to coral host species more often in evolutionary history remains unclear.

In conformity with A. Gittenberger and Hoeksema (chapter 10), the recent epitoniid species and their suggested ancestors are referred to as either specialists or generalists, dependent on being associated with either (1) only one or a monophyletic group of host species, or (2) some distantly related hosts. For a molecular phylogeny reconstruction of the coral host species, see A. Gittenberger, Reijnen and Hoeksema (chapter 10).The here molecular phylogeny reconstruction (fig. 1) indicates that ancestors [A], [B], [C], [E] and [F] have been generalists associated with Fungiidae. All species in the *Surrepifungium* lineage, descending from ancestor [C], have remained generalists associated with Fungiidae. The descendants of ancestor [F], i.e. the *Epifungium hoeksemai* lineage, also remained generalists associated with Fungiidae. The ancestor of the sister group of the *E. hoeksemai* clade, i.e. species [G], also remained associated with Fungiidae, but changed its life-history strategy in comparison to its ancestor [E] by becoming a specialist. All descendants of ancestor [G] remained specialists. Remarkably, ancestor [H] and its descendants, i.e. the *Epifungium hartogi* clade, changed from Fungiidae to Euphylliidae as coral hosts.

Like its ancestor [B], ancestor [D] was a generalist. It switched from an association with the Fungiidae to the Dendrophylliidae, however. All descendants of ancestor [D], i.e. the species in the *Epidendrium* clade, have remained generalists associated with Dendrophylliidae.

Here we refer to co-evolution as the evolutionary mechanism in which the evolution of one taxon, e. g. the family Epitoniidae, is influenced by the evolution of another, unrelated taxon, e.g. the phylum Cnidaria, and not necessarily vice versa. Co-evolution may have played a role in the evolutionary history of the clade including *Epifungium marki* and *E. adgravis* and the clade including *E. nielsi* and *E. adgranulosa.* The epitoniid sister species *E. marki* and *E. adgravis* are associated with *Fungia* spec. A and *Fungia gravis*, which are also sister species (A. Gittenberger, Reijnen and Hoeksema, chapter 3). Similarly, the sister species *E. nielsi* and *E. adgranulosa* are associated with two closely related fungiid clades, which may be sister clades (A. Gittenberger, Reijnen and Hoeksema, chapter 3), i.e. *Fungia* (*Pleuractis*) spp. and *Fungia* (*Wellsofungia*) *granulosa.* In both cases an application of the molecular clock model, combined with the phylogeny reconstructions of both the parasites and their hosts, would give more certainty. It could indicate to what extent the speciation events in both the corals and the snails are interdependent in time. However, at present no data are available to calibrate such a molecular clock for both phylogenies.

The conchological similarities between the coral- and sea-anemone-associated wentletraps indicate that parallel or convergent evolution has played a mayor role in the evolutionary history of this group (A. Gittenberger and E. Gittenberger, 2005). In some cases, as for example in *Epifungium twilae* and *E. pseudotwilae*, this convergent evolution is clearly adaptive. The shells of these two species are very similar in all aspects, and conspicuously broader than those of all other *Epifungium* species. With a support value of 98% molecular analyses indicate that *E. twilae* is more closely related to *E. ulu* than to *E. pseudotwilae*, however (fig. 2). The broad shells of *E. twilae* and *E. pseudotwilae* might have evolved in both species independently because of selection pressure by fish predators (A. Gittenberger and Hoeksema, chapter 10). Snails with broad shells may be more difficult to grasp, depending on the size of the mouths of the potential predator fishes. *Epifungium twilae* and *E. pseudotwilae* in general encounter more

of these predators than do the other *Epifungium* species because they are hosted by corals that have the potential of becoming relatively large, leaving space for fishes to get underneath them.

After the generically separate classification of the coral-associated, epitoniid taxa, the remaining so-called genus *Epitonium*, with *E. scalare* (L., 1758) as its type species, became more than ever an unsatisfactory clustering of species, next to somewhat better defined taxa, like *Cycloscala* Dall, 1889, *Cirsotrema* Mörch, 1852, and *Gyroscala* de Boury, 1887, all of which represented by at least one species in the molecular phylogeny reconstruction (fig. 2). This is also illustrated by the positions of the eastern Atlantic species *E. clathrus* (L., 1758) and *E. clathratulum* (Kanmacher, 1798), the type species of the nominal taxa *Clathrus* Oken, 1915, and *Hyaloscala* de Boury, 1890, respectively. These species look quite different in shell characters and are placed in separate subgenera by several authors (Fretter and Graham, 1982). They show up as sister species in the molecular phylogeny analysis (fig. 2), however. Obviously, far more species should be studied to achieve a more convincing, phylogenetically based classification of the Epitoniidae.

Acknowledgements

We are grateful to Bill Frank, Merijn Bos, Pat Colin, Rachel Colin, Hans Ditlev, Mark Erdmann, Jeroen Goud, Victor de Grund, Bert W. Hoeksema, Bas Kokshoorn, Alfian Noor, Somnuk Patamakanthin, Somwang Patamakanthin, Carlos A. Sánchez, Niels Schrieken, Frank Swinnen and Nicole de Voogd for their help in providing information and material used in this study. The research in Indonesia was sponsored by the Indonesian Institute of Sciences (LIPI). This research project was supported by WOTRO (grant nr. W 82-249) with additional funding by KNAW, the Alida Buitendijkfonds, and the Jan Joost ter Pelkwijkfonds.

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

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

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Key words: parasitic snails; coral reefs; coral/mollusc associations; Epitoniidae; *Epitonium*; *Epifungium*; *Epidendrium*; *Surrepifungium*; Scleractinia; Fungiidae; Indo-Pacific

Abstract

By a search of about 60,000 corals for wentletrap infestations, this study revealed several distinctly different epitoniid life strategies in the Indo-West Pacific. The 20 species that were found to be coral-associated were either generalists or specialists. They differed also in their position relative to their hosts, in their substrate preferences and in their host-size preferences. No preferences for depth were found.

Infestation rates are negatively correlated with coral densities, which may indicate that epitoniid veligers can actively find and go to their preferential hosts.

Indirect proof was found that burrowing shrimps with burrows underneath mushroom corals, 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 moment they were exposed artificially.

Contents

Introduction

Wentletraps (Gastropoda: Epitoniidae) in general are permanent ectoparasites or foraging predators that are mostly associated with Actiniaria (Robertson, 1963, 1966, 1983; Perron, 1978; Schimek, 1986; den Hartog, 1987), and less commonly with Zoanthidea (Robertson, 1981; Zahn, 1980) or scleractinian corals (Dendrophylliidae, Euphylliidae, Fungiidae) (A. Gittenberger and E. Gittenberger, 2005). Usually, the exact nature of the various associations is not clear. The snails may use their coelenterate hosts as a food source, for shelter against predators and turbulence, or as a relatively safe spawning site. Due to their hidden position, observations of actual feeding epitoniid snails are scarce (den Hartog, 1987; Perron, 1978), although the presence of nematocysts in their gut contents serves as direct proof for predatory or parasitic behaviour (Perron, 1978). Apparently, the nematocyst venom does not act as a fatal poison for the specialized snails.

The life-cycle of epitoniids starts within an egg-capsule with the development from an undifferentiated egg to a hatching individual, followed by a free-swimming veliger stage, and eventually the settling as a crawling snail (Robertson, 1983, 1994; Bell, 1985; Collin, 2000; A. Gittenberger, 2003). *Epifungium ulu* (Pilsbry, 1921) can go through a complete life-cycle within 36 days (Bell, 1985).

For a good understanding of the biodiversity and ecological complexity of reef communities, species

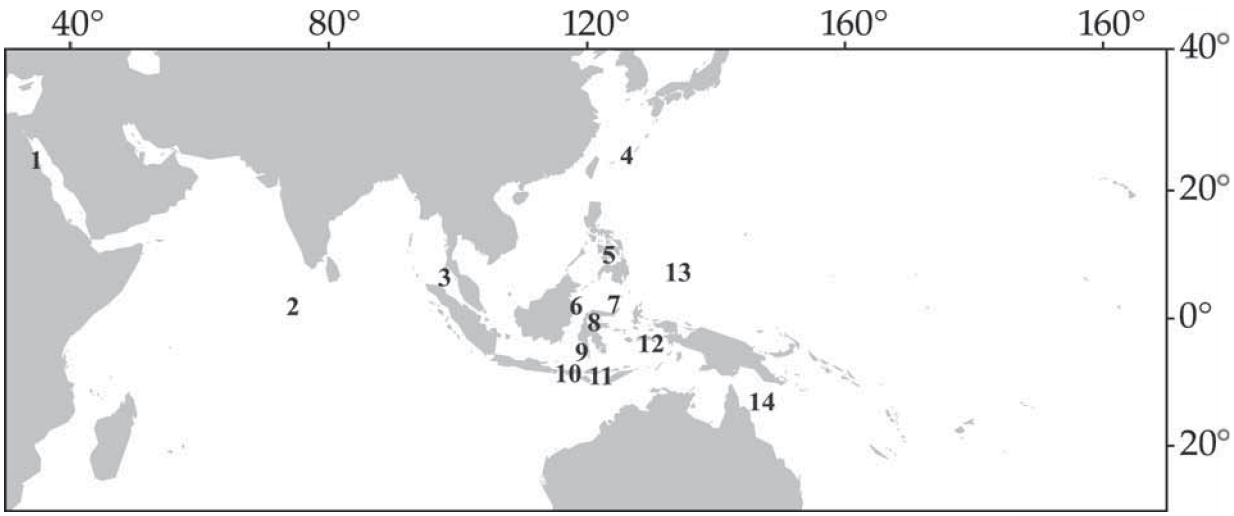


Fig. 1. The Indo-West Pacific region, from the Red Sea to the Hawaiian Archipelago. Research localities are indicated: 1. Marsha Shagra and Marsa Nakari, c. 350 km S of Hurghada, Egypt; 2. Vilamendhoo Island, Ari Atoll, Maldives; 3. PhiPhi Islands, Krabi, Thailand; 4, Okinawa, Rykyu Islands, S Japan; 5. Cebu, Visayas, Central Philippines; 6. Berau Islands, E Kalimantan, Indonesia; 7. Siladen and Bunaken Islands, N Sulawesi, Indonesia; 8. Togian Islands, Central Sulawesi, Indonesia; 9. Spermonde Archipelago, SW Sulawesi, Indonesia; 10. Bali, Indonesia; 11. Flores, Indonesia; 12. Ambon, Indonesia; 13. Palau; 14. Great Barrier Reef, Australia.

interdependencies and their evolutionary histories should be investigated. Hard corals and their parasitic wentletraps are ideal models to study such aspects. Morphological, molecular (A. Gittenberger et al., chapter 8) and ecological studies have shown that a large, partly cryptic, adaptive radiation has taken place among these epitoniids, most of which are highly specialized ecto-parasites (A. Gittenberger et al., 2000; A. Gittenberger, 2003; A. Gittenberger and E. Gittenberger, 2005). Although their identities as separate gene pools can be demonstrated convincingly by molecular data (A. Gittenberger et al., chapter 8), shell shape and sculpture are only partially diagnostic for these gastropod species because of sometimes broadly overlapping character states. In several cases, the habitat and additional morphological characters of the operculum, the jaw, the radula and the spawn, characterize the conchologically cryptic species much better than the more easily accessible shell characters (A. Gittenberger and E. Gittenberger, 2005). These findings contradict the hypothesis of Bouchet and Warén (1986: 469) that a low amount of variation among epitoniids in general may reflect a low degree of specialization. Coral-associated epitoniids are more diverse than previously thought and their cryptic adaptive radiation has remained unnoticed for a long time. Taking recent taxonomic results into account, this article aims at a better insight in the ecological differentiation of coral-associated epitoniids and their evolutionary history in the Indo-West Pacific.

We focus on the following research questions: [1] Where are the epitoniid snails found, relative to their coral hosts? [2] Is there a relationship between the infestation percentages and the upside down or right side up position of the mushroom corals? [3] Is the substratum on which the coral is found related to the chance of it being infested? [4] Which coral species are associated with particular gastropod parasites? [5] What are the infestation percentages of the coral species populations? [6] Are infestation percentages related to depth? [7] Are infestation percentages, parasite sizes and presence/absence of egg-capsules related to host-sizes? [8] What are natural predators of the epitoniids? [9] What, if any, conchological characters may be linked to the adaptive radiation of the various epitoniid species?

Habitat preferences are described for the 20 species of coral-associated epitoniids that are known, viz. *Epidendrium aureum* A. Gittenberger and E. Gittenberger, 2005; *E. sordidum* A. Gittenberger and E. Gittenberger, 2005; *Epifungium adgranulosa* A. Gittenberger and E. Gittenberger, 2005, *E. adgravis* A. Gittenberger and E. Gittenberger, 2005, *E. adscabra* A. Gittenberger and E. Gittenberger, 2005, *E. hartogi*

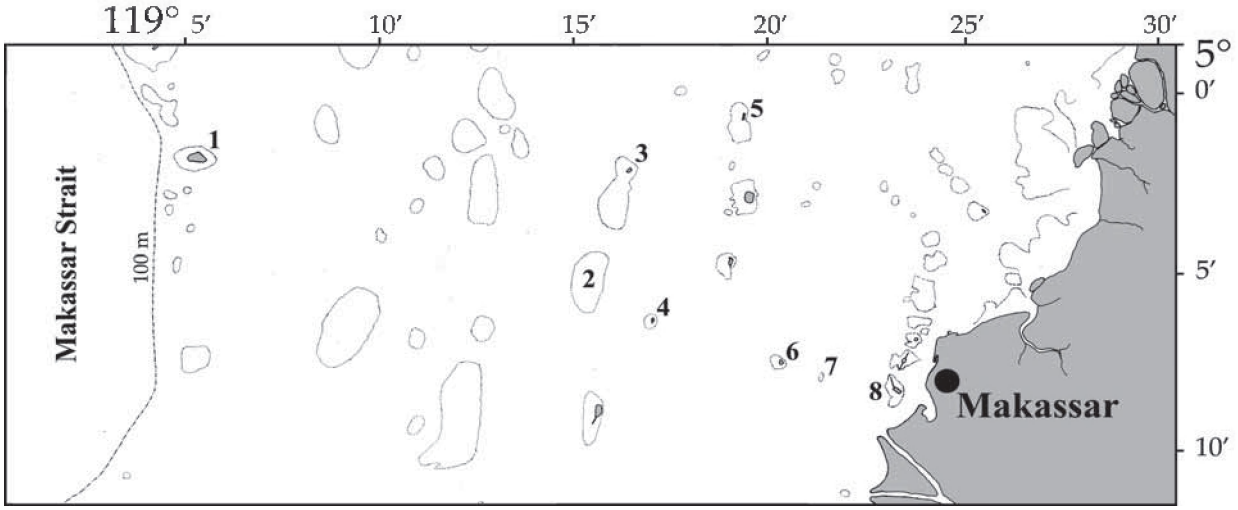
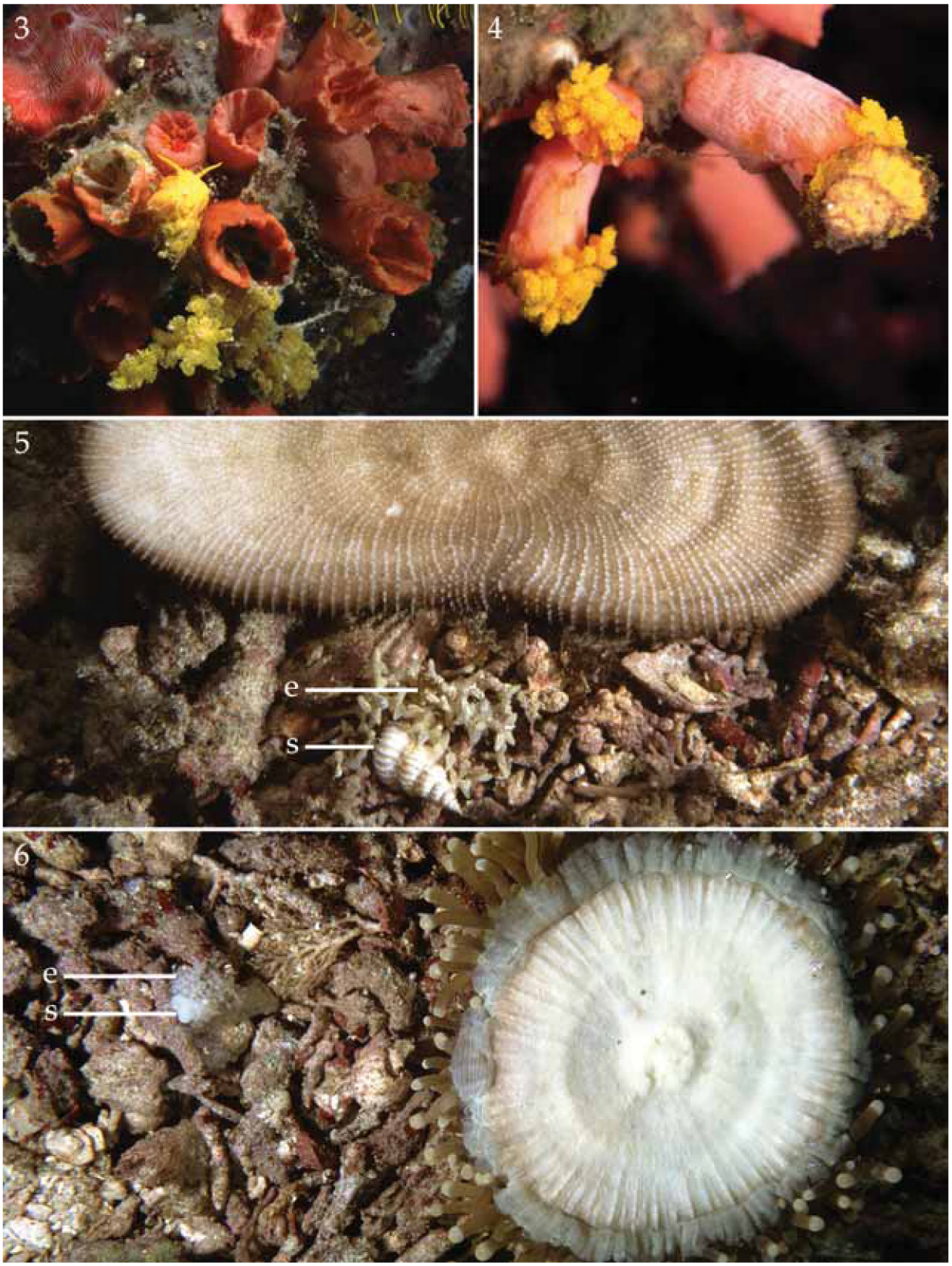


Fig. 2. The southern part of the Spermonde Archipelago, SW Sulawesi, Indonesia, consisting of patch reefs and a barrier reef: Research sites: 1. Langkai Island; 2. Kapodasang (shoal); 3. Bone Tambung Island; 4. Kudingareng Keke Island; 5, Bone Batang Island; 6. Samalona Island; 7, Bone Baku (shoal); 8. Lae-Lae Island.

(A. Gittenberger, 2003), *E. hoeksemai* (A. Gittenberger and Goud, 2000), *E. lochi* (A. Gittenberger and Goud, 2000), *E. marki* A. Gittenberger and E. Gittenberger, 2005, *E. nielsi* A. Gittenberger and E. Gittenberger, 2005, *E. pseudolochi* A. Gittenberger and E. Gittenberger, 2005, *E. pseudotwilae* A. Gittenberger and E. Gittenberger, 2005, *E. twilae* (A. Gittenberger and Goud, 2000), *E. ulu* Pilsbry, 1921, *Epitonium crassicostatum* A. Gittenberger and E. Gittenberger, 2005, *E. graviarmatum* A. Gittenberger and E. Gittenberger, 2005, *Surrepifungium costulatum* (Kiener, 1839), *S. ingridae* (A. Gittenberger and Goud, 2000), *S. oliverioi* (Bonfitto and Sabelli, 2001) and *S. patamakanthini* A. Gittenberger and E. Gittenberger, 2005. Most of these species are associated with only one or a restricted number of coral species and are widespread. Their distributions are similar to those of their hosts, i.e. ranging from the Red Sea or the Maldives, Thailand, Indonesia and Palau to Australia (A. Gittenberger and E. Gittenberger, 2005). Only *S. ingridae* seems to be an exception to this rule. That species is very common in the West Pacific, off the eastern coast of the West Malaysian peninsula, Palau and Sulawesi, but it is not known from anywhere in the Indian Ocean. In contrast, the closely related *S. costulatum*, *S. patamakanthini* and *S. oliverioi* do show more widespread Indo-West Pacific distributions (A. Gittenberger and E. Gittenberger, 2005).

Most coral-associated wentletrap species are found with mushroom corals (Fungiidae), which were the main focus of the present research project. Fungiids have various advantages over other coral groups as model organisms for field studies. The family consists of over 45 species and is abundant throughout the Indo-West Pacific (Hoeksema, 1989b, 1993a, 1993b, 1993d; Hoeksema and Putra, 2002). These corals seem to have a high survival rate during bleaching events (Hoeksema, 1991a), which is also important for the occurrence of associated animals that depend on their survival.

Most mushroom corals are free-living in the adult stage due to their breakage from an early attachment stalk. As a result of the detachment, they may tumble downward along slopes, bottom-dwelling animals may push them, currents and waves may transport them, and they may even move themselves (Hubbard, 1972; Jokiel and Cowdin, 1976; Chadwick, 1988; Chadwick-Furman and Loya, 1992; Yamashiro and Nishihira, 1995; Plusquelllec et al., 1999). This mobility may help mushroom corals to disperse in order to reach favourable habitats, it may prevent burial in soft sediments, and it may have a function in avoiding competition for space (Hoeksema, 1989a, 1993c, 2004; Chadwick, 1988; Chadwick-Furman and Loya, 1992; Yamashiro and Nishihira 1995). The mobility depends on the weight and size of the free-living corals (Hoeksema, 1991b). The mobility of the host may also have implications for the survival of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the ecto-parasitic snails. Movements may cause the parasitic snails occurring underneath to become temporarily more exposed to predators. On the other hand, mobility may also prevent a burial in sediment which would be lethal to both the coral host (Gilmour, 2002a) and its associates. Large corals cannot move easily and offer more surface area for parasites.

These detached corals can easily be handled for the inspection for parasites without causing damage to the corals themselves and their environment.

Material and methods

Fieldwork localities and general methods

About 800 hours scuba-diving were spent underwater by the authors, searching approximately 60,000 stony corals for epitoniids in the Indo-West Pacific, i.e. off Egypt (Red Sea), the Maldives, W Thailand (Andaman Sea), W Malaysia (South China Sea), S Japan, Palau, the Philippines, Indonesia and Australia (fig. 1). Most fieldwork periods lasted one week to a month. In 1997 and 2001 research took place in periods of three and nine months, respectively, in the Spermonde Archipelago off Makassar, SW Sulawesi, Indonesia (fig. 2). This area is located in the centre of maximum marine biodiversity (Hoeksema, 1993d, 2004a; Hoeksema and Putra, 2002). Off Makassar the coral diversity and densities were higher than at any of the other study localities. Therefore that archipelago was considered the most suitable place for more detailed field studies. Concentrating on free-living mushroom corals, a special effort was made to search all species within this family, including rare or less common ones like the *Fungia* (*Cycloseris*) species, *F.* (*Danafungia*) *fralinae* Nemenzo, 1955, *F.* (*Verrillofungia*) *spinifer* Claereboudt and Hoeksema, 1987, *Heliofungia actiniformis* (Quoy and Gaimard, 1833), *Sandalolitha dentata* Quelch, 1884, *Halomitra clavator* Hoeksema, 1989, and *Zoopilus echinata* Dana, 1846. Most of these species live in environments that are usually avoided by divers, e.g. at relatively deep (up to 45 meter) or shallow (< 2 meter) slopes and flats, in areas with strong currents or murky water, or on sandy bottoms.

Figs 3-6. Habitats of Epitoniidae encountered. 3, *Epidendrium aureum*, snail with egg-capsules on substrate next to dendrophylliid coral host; 4, *Epidendrium sordidum*, shell overgrown with hydroids, together with egg-capsules on dendrophylliid coral host; 5, *Surrepifungium costulatum*, snail with egg-capsules on substrate, revealed by turning the host coral upside down, i.e. a specimen of *Ctenactis echinata*; 6, *Epifungium hoeksemai*, snail with egg-capsules on substratum, revealed by turning the host coral upside down, i.e. a specimen of *Heliofungia actiniformis*. 3-4, Ari Atoll, Maldives; 5-6, SW Sulawesi, Indonesia. Abbreviations: e, egg-capsules; s, snail.

Sampling

The snails were collected and conserved in 70% or 95% ethanol for morphological or molecular analyses, respectively. Most associations were photographed in detail with a Sea & Sea SX-1000 SLR camera with a 50 mm macro lens. A white PVC board and a graphite pencil were used underwater to note observations related to the infestations, i.e. depth, host species, substratum characteristics, and position of the parasite relative to its host. The fungiids were identified twice, independently by both authors, after photographs and/or specimens. Dr. H. Ditlev identified the euphylliids from photographs. The dendrophylliids (*Tubastrea* and *Dendrophyllia* species) were not identified to species level. The first author identified the epitoniid species. The position of a parasite was recorded as 'buried in sand' (no illustration), 'on the coral host' (figs 3-4, 8-9), or 'on the substrate underneath the coral' (figs 5-7). Regarding the size-dependent mushroom coral mobility (Hoeksema, 1989a, 1991b, 2004b), an upside down position of the fungiid host (figs 5-9, 11, 13-14, 16-17) was recorded opposite the more regular orientation (figs 10, 12), since the former position may minimize the survival of snails because of their exposure to predators. The substratum was characterized as (1) 'flat' for an even bottom of sand, coral or stone, without any holes or crevices (fig. 12; to the right of the fungiid coral), as (2) 'burrow' when there was at least one circular burrow (figs 11, 13-14), possibly made by a crustacean (e.g. fig. 15), or as (3) 'holes' where holes and crevices occurred but no burrows (fig. 6).

Transect studies

In the Spermonde Archipelago (fig. 2; locality 9 in fig. 1) mushroom corals were searched for epitoniids


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along horizontal transects at 3, 6, 9, 12, 15 and 18 m depth. This was done at seven sites on five coral reefs, at various distances from the coastline, i.e. at W Lae-Lae Island, W Bone Baku reef, E Samalona Island, W Samalona Island, E Kudingareng Keke Island, W Kudingareng Keke Island and NW Langkai Island, respectively (fig. 2). A transect line was marked by a measuring tape, attached to the bottom at 3, 6, 9, 12, 15 and 18 m depth. Mushroom corals were counted within a distance of one meter at both sides along the tape guided by a 1 m long aluminium rod. When less than 100 corals were observed along the first 100 m, the transect length was extended to reach this number. For each transect and site fungiid densities and infestation percentages were calculated. The infestation percentages were plotted against the fungiid densities. To get an indication of mushroom coral species composition for each locality and depth, about 4500 fungiids were identified and counted along the transects. Based on the resulting species compositions and the total number of corals in the transects, an approximate number of specimens that was searched for each fungiid species was calculated. These approximate numbers were used to calculate the infestation percentages for the most common epitoniid species, i.e. *Epifungium ulu*, *E. pseudotwilae* and *E. twilae*.

Measuring coral-sizes

During the three-months fieldwork period in 1997 in the Spermonde Archipelago, the size of all infested corals was measured. This was done by comparing these with the outlines of surfaces of 10, 25, 50, 100, 150, 200 and 300 cm^2, drawn on boards, after which the specimens were recorded as belonging to one of those size-classes. To fit all fungiid shapes, five boards were made for corals varying from round to elongated, i.e. with length/width indexes of 1, 1.5, 2, 3 and 4. Off W Kudingareng Keke Island, the surface size of all specimens of *Fungia* (*Verrillofungia*) *concinna*, *F.* (*V.*) *repanda* and *Herpolitha limax* at 3-18 m depth, was measured to get an indication of the size distributions within their populations. These three species were chosen because they were abundant at all locations and the most common hosts of the abundant epitoniids *Epifungium ulu* and *E. twilae*. The null-hypothesis, infestations by *E. ulu* and *E. twilae* are not related to coral-size, was tested with Chi-square against three alternative hypotheses, i.e. [1] coral-size influences the probability of being infested; [2] host-size is positively correlated with parasite-size; [3] host-size is positively correlated with the percentage of cases of infestation with egg-capsules present.

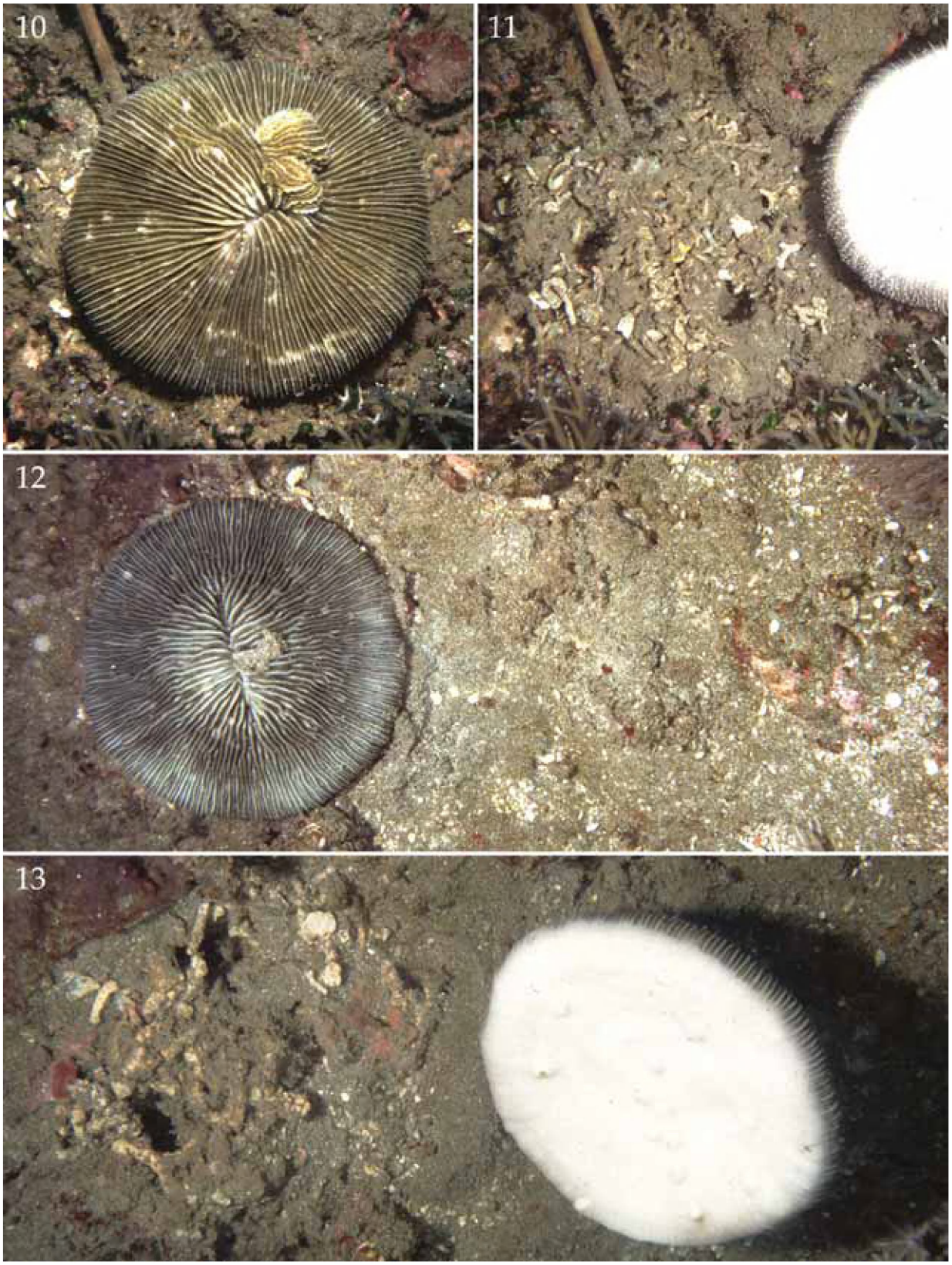
Figs 7-9. Habitats of Epitoniidae encountered (continued). 7, *Epifungium nielsi*, snail with egg-capsules on substratum, revealed by overturning the host coral, i.e. *Fungia paumotensis*; 8, *Epifungium pseudolochi*, snail with egg-capsules on coral, revealed by overturning the host, i.e. *Fungia costulata*; 9, *Epifungium twilae*, snail with egg-capsules on coral, revealed by overturning the host, i.e. *Herpolitha limax*. 7, Ari Atoll, Maldives; 8, Marsa Nakari, 350 km S of Hurghada, Egypt; 9, SW Sulawesi, Indonesia.

Turned over hosts and epitoniid predators

Free-living fungiid corals are known to occasionally turn around (see e.g. Hoeksema, 2004b). To investigate how this overturning may affect epitoniid snails that live hidden underneath the corals, 16 hosts with snails and/or egg-capsules of *Epifungium ulu* were carefully turned upside down NW of Langkai Island (for site, see fig. 2), preventing accidental detachment of the parasites. After two hours and after two days the numbers of epitoniids and egg-capsule clutches that were still on their hosts were counted.

Two corals with snails and egg-capsules of *Epifungium ulu* and one with snails and egg-capsules of *E. twilae* were placed upside down, next to each other, off W Kudingareng Keke Island (for site, see fig. 2). The specimens were observed from a distance of about 3 meters for 30 minutes to check which animals would attack them. These epitoniid species were selected since their shells are similar in height but not in width, i.e. shells of *E. twilae* are relatively much broader (fig. 9; A. Gittenberger and E. Gittenberger, 2005). Snails with broader shells might be more difficult to grasp depending on the size of the mouths of the potential predator fishes. Additionally, all animals that were seen eating or attacking epitoniids at any time during one of the field surveys were recorded and photographed whenever possible.

It has been hypothesized that the overturning of a fungiid coral from an upright position to upside down and back again, depends upon its size and form (Hoeksema, 1989a). The rate at which this may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happen was studied experimentally in the Spermonde Archipelago, using populations of 12 species, varying in shape from circular, viz. *Fungia (D.) horrida*, *F. (D.) scruposa*, *F. (F.) fungites*, *F. (V.) concinna*, *F. (V.) repanda* and *F. (V.) scabra*, and oval, viz. *F. (L.) scutaria*, *F. (P.) gravis* and *F. (P.) paumotensis*, to elongated, viz. *Ctenactis echinata*, *Herpolitha limax* and *Polyphyllia talpina*.

With a waterproof pen, 360 squares of 22 × 25 cm, 24 squares of 30 × 30 cm, 24 squares of 20 × 35 cm and 24 squares of 25 × 40 cm, were drawn and numbered on two orange, plastic cloths, which were fastened with pegs to the sea-bottom, at a depth of 18 m, on a slope of on average 15°, at W Kudingareng Keke Island (see fig. 2). For each of the 12 species, 24 specimens (size-class 25-100 cm^2) were put in upright position in the 22 × 25 cm squares. Additionally, 24 corals of *Fungia* (*Verrillofungia*) *repanda* (size-class 100-150 cm^2) were placed in 30 × 30 cm squares, 24 *Herpolitha limax* corals (size-class 100-200 cm^2) in 20 × 35 cm squares, and 24 *H. limax* specimens (size-class 200-300 cm^2) in 25 × 40 cm squares. The corals that proved to have turned after three and after ten days were scored. The experiment was repeated with all corals in upside down position at the start and after four hours and after two days it was recorded how many had turned back. Then the corals were temporarily taken from the water in buckets to measure the length/width ratio and wet weight, after which they were returned to the reef.

More than 100 specimens of each of the 23 most common fungiid species in the Spermonde Archipelago were checked to calculate the percentages of the coral populations that are lying upside down under natural conditions.

Results

General results

About 1.5% of all mushroom corals that were searched (n=60,000) was found with epitoniids. Among the various species the number of infestations varied from a single one to 103. For each of the 20 epitoniid species the number is indicated between brackets: *Surrepifungium costulatum* (103), *S. ingridae* (43), *S. oliverioi* (10) and *S. patamakanthini* (27), *Epidendrium aureum* (52), *E. sordidum* (22), *Epifungium adgranulosa* (20), *E. adgravis* (38), *E. hoeksemai* (34), *E. lochi* (36), *E. nielsi* (83), *E. ulu* (191), *E. adscabra* (22), *E. hartogi* (10), *E. marki* (4), *E. pseudolochi* (5), *E. pseudotwilae* (68), *E. twilae* (98), *Epitonium crassicostatum* (1) and *E. graviarmatum* (1). Of the 870 observed cases of infestation, 283 (32.5%) included egg-capsules. In total 1657 epitoniid specimens were collected, that is on average about two snails per host. Of the c. 2,500 fungiids found upside down, only one was infested and that by epitoniid egg-capsules only. In the transects off SW Sulawesi, 3.7% of all corals (n=7219) were found in association with an epitoniid species, viz. *Epifungium adgranulosa*, *E. adscabra*, *E. hoeksemai*, *E. lochi*, *E. marki*, *E. nielsi*, *E. pseudotwilae*, *E. twilae*, *E. ulu*, *Surrepifungium costulatum*, *S. ingridae* or *S. patamakanthini*.

Figs 10-13. Burrow substrata, SW Sulawesi, Indonesia. 10-11, *Fungia repanda*; 10, in situ; 11, overturned, i.e. revealing two circular burrows; 12-13, *Fungia granulosa*; 12, in situ; 13, overturned, i.e. revealing two circular burrows.

Coral species and their hosted wentletraps

For the associations that were found per species, see table 1. When a single host coral was found associated with both an *Epifungium* and a *Surrepifungium* wentletrap species, the *Epifungium* was always on the coral while the *Surrepifungium* was on the substratum underneath or had burrowed inside the sediment.

The infestation percentages of the mushroom coral populations in the Spermonde Archipelago, by *Epifungium ulu*, *E. pseudotwilae* and *E. twilae*, are indicated in table 2. Throughout the Indo-West Pacific, *E. ulu* was found to have infested seven, two, one and six corals of *Ctenactis echinata*, *Halomitra pileus*, *Herpolitha limax* and *Sandalolitha robusta*, respectively, while about 8,000, 2,000, 5,000 and 2,000 specimens of these host species were searched. This indicates that the infestation percentages are in general less than 0.3%. The *Halomitra* and *Sandalolitha* infestations were found in Indonesia and Palau, while the *Ctenactis* hosts were predominantly found in Egypt (Red Sea), Indonesia and Palau. The *Herpolitha* infestation was recorded in


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Table 1. Epitoniid species and their associated fungiid host species. Abbreviations: FCcos, *Fungia* (*Cycloseris*) *costulata*; FCdis, *F.* (*C.*) *distorta*; FCfra, *F.* (*C.*) *fragiles*; Fcsin, *F.* (*C.*) *sinensis*; FCsom, *F.* (*C.*) *somervillei*; FCten, *F.* (*C.*) *tenuis*; FCvau, *F.* (*C.*) *vaughani*; FWgra, *F.* (*Wellsofungia*) *granulosa*; FPspA, *F.* (*Pleuractis*) sp. A; FPgra, *F.* (*P.*) *gravis*; FPmol, *F.* (*P.*) *mollucensis*; FPpau, *F.* (*P.*) *paumotensis*; FVsca, *F.* (*Verrillofungia*) *scabra*; FVcon, *F.* (*V.*) *concinna*; FVrep, *F.* (*V.*) *repanda*; FVspi, *F.* (*V.*) *spinifer*; FDhor, *F.* (*Danafungia*) *horrida*; FDscr, *F.* (*D.*) *scruposa*; FLscu, *F.* (*Lobactis*) *scutaria*; FFfun, *F.* (*Fungia*) *fungites*; Hpile, *Halomitra pileus*; Hacti, *Heliofungia actiniformis*; Calbi, *Ctenactis albitentaculata*; Ccras, *C. crassa*; Cechi, *C. echinata*; Hlima, *Herpolitha limax*; Srobu, *Sandalolitha robusta*; Sdent, *S. dentata*; Pcrus, *Podabacia crustacea*; Zechi, *Zoopilus echinatus*.

Epitoniid species	Fungiid host species																												
	FCcos	FCdis	FCfra	FCsin	FCsom	FCten	FCvau	FWgra	FPspA	FPgra	FPmol	FPpau	FVsca	FVcon	FVrep	FVspi	FDhor	FDscr	FLscr	FFfun	Hpile	Hacti	Calbi	Ccras	Cechi	Hlima	Srobu	Sdent	Pcrus	Zechi
Epifungium:																														
pseudolochi	X																													
lochi	X	X	X	X	X	X	X																							
adgranulosa								X																						
marki									X																					
adgravis										X																				
nielsi											X	X																		
adscabra													X																	
ulu														X	X	X	X	X	X	X	X				X	X	X			
hoeksemai																				X		X								
twilae																								X	X	X				
pseudotwilae																											X	X	X	X
Epitonium:																														
crassicostatum	X																													
graviarmatum							X																							
Surrepifungium:																														
costulatum																							X	X	X	X	X	X		
ingridae															X					X			X	X	X		X			
oliverioi															X					X						X	X			
patamakanthini														X	X		X			X		X		X	X		X			

Indonesia. A special effort was made to find as many epitoniid species as possible, for each locality, during the time that was available. Because most *Fungia* species are associated with only one epitoniid species, whereas most *Ctenactis*, *Halomitra*, *Herpolitha*, and *Sandalolitha* species have several associates, specimens of the latter group of coral genera were searched more intensively at all localities, except for the Spermonde Archipelago where fungiids were randomly searched, independent of species.

In total 31 species of free-living fungiid species were found at the research locations (fig. 1), i.e. *Fungia* (*Cycloseris*) *costulata*, *F.* (*C.*) *distorta*, *F.* (*C.*) *fragilis*, *F.* (*C.*) *sinensis*, *F.* (*C.*) *somervillei*, *F.* (*C.*) *tenuis*, *F.* (*C.*) *vaughani*, *F.* (*Wellsofungia*) *granulosa*, *F.* (*Pleuractis*) sp. A, *F.* (*P.*) *gravis*, *F.* (*P.*) *moluccensis*, *F.* (*P.*) *paumotensis*, *F.* (*Verrillofungia*) *scabra*, *F.* (*V.*) *concinna*, *F.* (*V.*) *repanda*, *F.* (*V.*) *spinifer*, *F.* (*Danafungia*) *horrida*, *F.* (*D.*) *scruposa*, *F.* (*Lobactis*)

Figs 14-17. Possible predators of epitoniids in Indonesia. 14, *Fungia fungites*, overturned, revealing a circular burrow; 15, *Alpheus frontalis*, from underneath fungiid, i.e. a specimen of *Ctenactis echinata;* 16, a wrasse, *Halichoeres melanurus*, checking out overturned fungiids; 17, a damselfish, *Plectroglyphidodon lacrymatus*, checking out an overturned fungiid. 14, Bali; 15-17, SW Sulawesi.

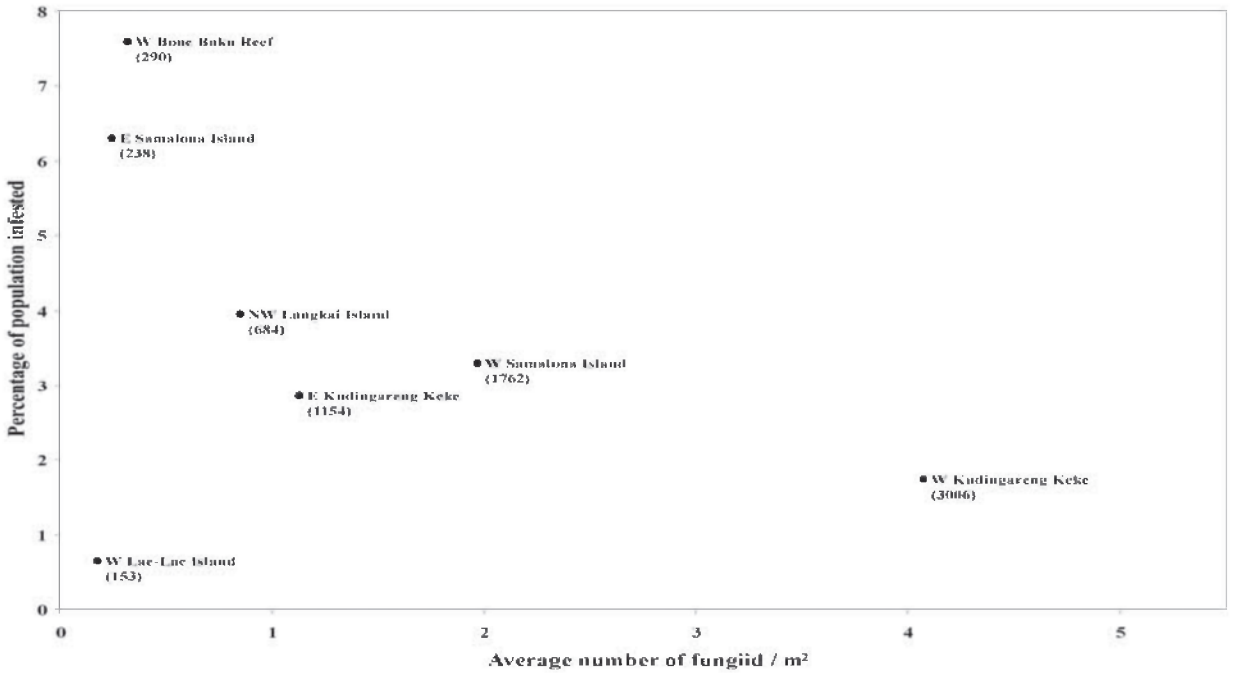

Fig. 18. Mushroom coral densities of the coral reef localities in the Spermonde Archipelago, SW Sulawesi, Indonesia, plotted against epitoniid infestation percentages. Sites (fig. 2) and n-values are indicated next to data points

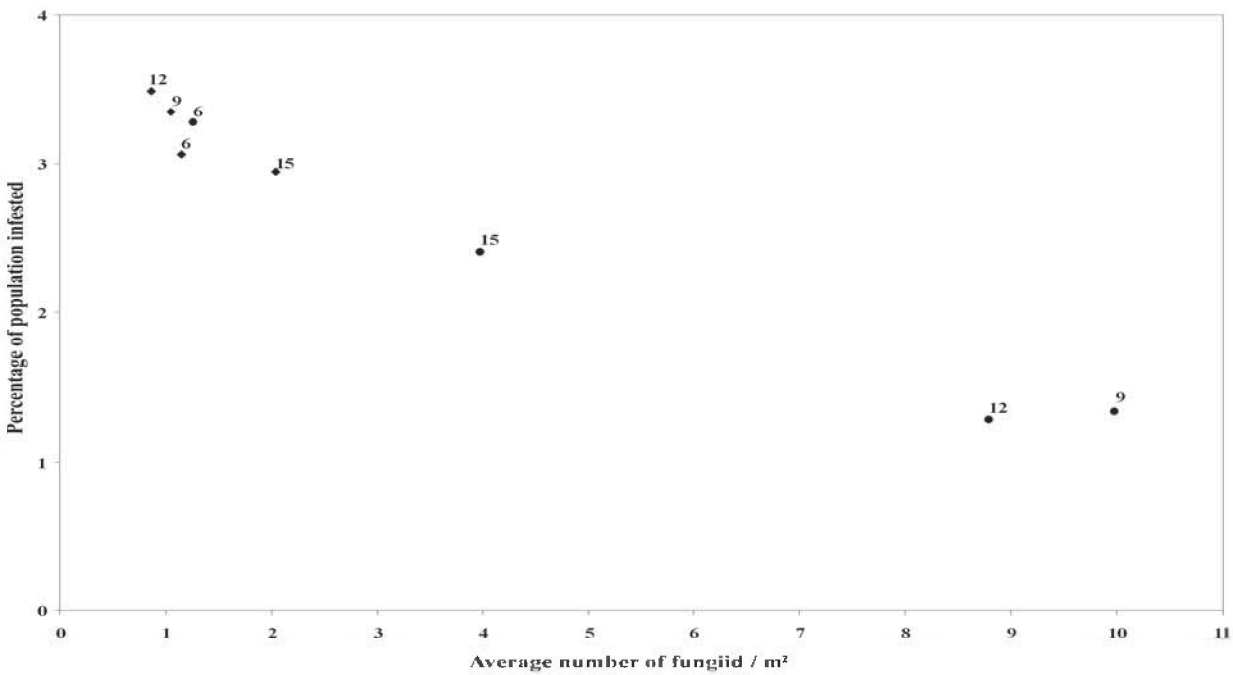

Fig. 19. Mushroom coral densities at 6, 9, 12 and 15 m depth transects on the east (diamonds) and west (circles) side of Kudingareng Keke Island, Spermonde Archipelago, SW Sulawesi, Indonesia (fig. 2), plotted against infestation percentages by *Epifungium ulu*. Total n = 3671 corals; a minimum number of 172 corals per transect. Transect depth is indicated next to the data points.

scutaria, *F.* (*Fungia*) *fungites*, *Halomitra pileus*, *Heliofungia actiniformis*, *Ctenactis albitentaculata*, *C. crassa*, *C. echinata*, *Herpolitha limax*, *Sandalolitha dentata*, *S. robusta*, *Zoopilus echinatus*, *Polyphyllia talpina* and *Fungia* (*Danafungia*) *fralinae*. Only *P. talpina* and *F.* (*D.*) *fralinae*, were never found in associations with wentletraps, even though over 1000 specimens of each of these species were inspected. Only two of the three euphylliid species that were investigated, i.e. *Plerogyra diabolotus* Ditlev, 2003, and *P. simplex* Rehberg, 1892, were found in association with an epitoniid species, i.e. *Epifungium hartogi* (A. Gittenberger, 2003). *Plerogyra sinuosa* (Dana, 1846), by far the most common euphylliid at most localities, was never found to be infested. At most places where dendrophylliid corals were found in association with epitoniids, i.e. in the Maldives, the Philippines, Palau and Indonesia, *Epidendrium aureum* and *E. sordidum* occurred both sympatrically and syntopically, directly next to or on the corals, in mixed populations, infesting the same specimens (A. Gittenberger and E. Gittenberger, 2005: figs 58-59).

Coral densities and infestation percentages

The relative numbers of infestations vary significantly over localities (X^2=63.4, p<0.001) and transects (X^2=21.7, p<0.025). At nearly all sites, with the exception of W Lae-Lae Island (fig. 18), the coral densities and the infestation percentages of the fungiid populations are negatively correlated, i.e. r = -0.43. When the W Lae-Lae Island record is excluded the correlation becomes stronger, i.e. r = -0.80. A similar negative correlation, i.e. r = -0.98, was found for the coral densities and the percentages of infestation by *Epifungium ulu* along the transects (fig. 19) off E and W Kudingareng Keke Island. Only these transects were used in this analysis, because only there more than a hundred corals could be searched in the four transects, at 6, 9, 12 and 15 m depth, respectively. These findings are in agreement with observations made in Egypt, the Maldives, Thailand and Palau. In those areas, infestation percentages of over 50% were repeatedly found at sites where only 10 mushroom corals or less could be found during a dive, so that we may conclude that the fungiid density was very low there. Dives with over 100 records of inspected corals never yielded infestation percentages higher than 5%.

Depths

No correlations between infestation percentages and depths were found in the transect study (fig. 19). In general, at all investigated Indo-West Pacific localities no epitoniid species shows a preference for depth as such. Species like *Epifungium lochi*, *E. adgravis*, *E. marki* and *E. pseudolochi*, usually occur deeper than others, but in those cases the coral hosts have a preference for greater depth. When their hosts were occasionally found in shallower water, the epitoniids

Table 2. Infestation percentages of fungiid populations in the Spermonde Archipelago, SW Sulawesi, Indonesia, by *Epifungium ulu*, *E. pseudotwilae* and *E. twilae*.

Epitoniids / Fungiids	***Epifungium ulu***	***Epifungium pseudotwilae***	***Epifungium twilae***
Fungia (*D.*) horrida (n = 280)	0.71 %	0.00 %	0.00 %
Fungia (*D.*) *scruposa* (n = 401)	1.00 %	0.00 %	0.00 %
Fungia (*F.*) *fungites* (n = 759)	1.45 %	0.00 %	0.00 %
Fungia (*L.*) *scutaria* (n = 125)	1.60 %	0.00 %	0.00 %
Fungia (*V.*) *concinna* (n = 791)	3.67 %	0.00 %	0.00 %
Fungia (*V.*) *repanda* (n = 2098)	2.24 %	0.00 %	0.00 %
Ctenactis echinata (n = 415)	0.24 %	0.00 %	0.96 %
Herpolitha limax (n = 393)	0.00 %	0.00 %	6.62 %
Sandalolitha robusta (n = 173)	0.00 %	4.05 %	0.00 %
Zoopilus echinatus (n = 136)	0.00 %	7.35 %	0.00 %

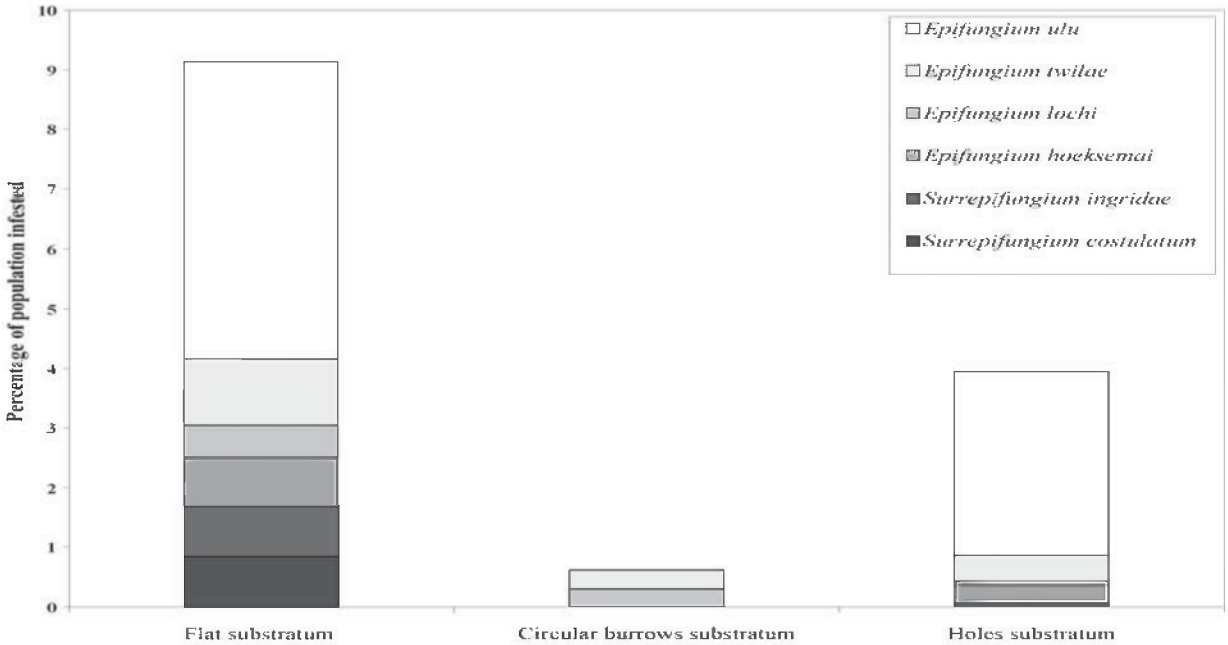

Fig. 20. Percentages of fungiid corals lying on either evenly flat sediment (n = 362), on circular burrows (n = 329) or on holes (n = 1620) substratum that were infested by *Surrepifungium costulatum* (n = 3), *S. ingridae* (n = 5), *Epifungium adgranulosa* (n = 1), *E. adgravis* (n = 2), *E. adscabra* (n = 9), *E. hoeksemai* (n = 4), *E. lochi* (n = 4), *E. nielsi* (n = 9), *E. pseudotwilae* (n = 5), *E. twilae* (n = 7) and *E. ulu* (n = 47).

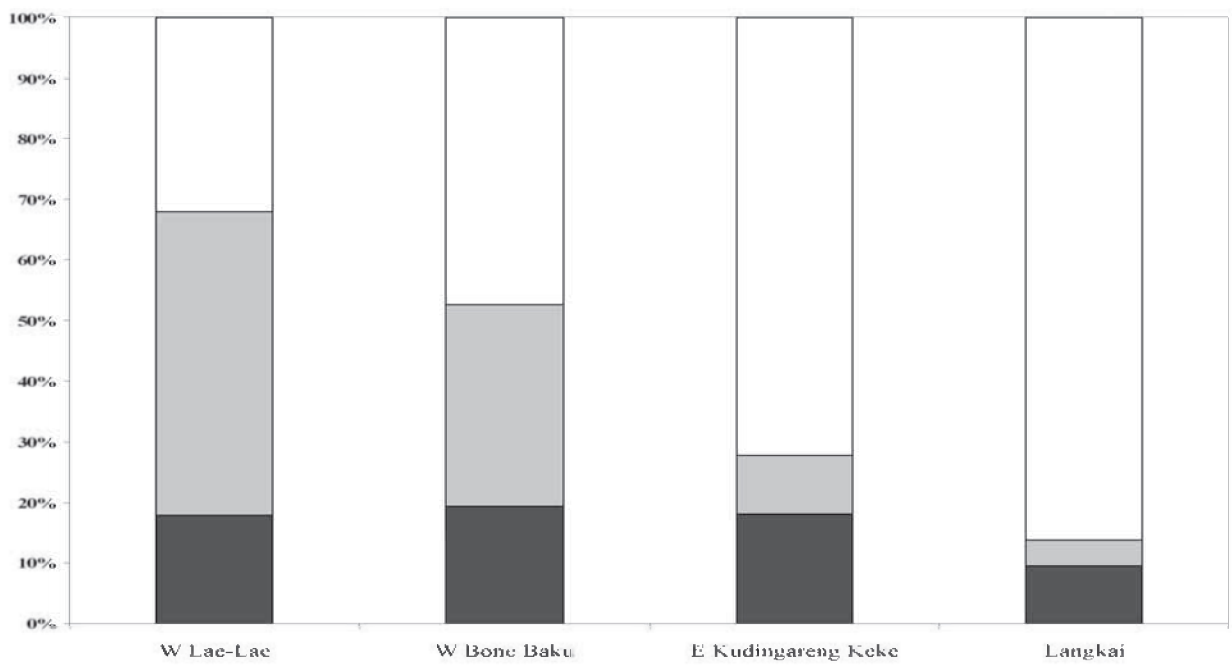

Fig. 21. Percentages of fungiids at the sites W Lae-Lae (n = 184), W Bone Baku (n = 289), E Kudingareng Keke (n = 1154) and Langkai (n = 684), either lying on flat sediment (white), substrata with burrows (grey) or with holes (black).

were usually found there as well. The only exception that is known concerns some populations of *E. twilae* from the Red Sea. None of the 107 samples of that species found in the Maldives, Thailand and Indonesia, came from more than 24 m depth, but the four samples from the Red Sea were found at 30, 35, 35 and 40 m, respectively. The absence of *E. twilae* deeper than 24 m in the Maldives, Thailand and Indonesia, may be related to the fact that specimens of the preferred host species, i.e. *Ctenactis crassa*, *C. echinata* and *Herpolitha limax*, were rare at those depths. At the Red Sea locality, *Ctenactis* species were not present, but *H. limax* was common at 6-45 m depth. Although > 50 specimens of *H. limax* from less than 30 meter of depth were inspected, none of these was found to be infested, whereas 4 of the 12 specimens that were found deeper hosted *E. twilae*.

Table 3. Depth range and positions of epitoniid shells relative to the coral host.

Epitoniid species	Position relative to the host			Depth (meter)
	Buried in substratum	On sub-stratum	On coral	
Epidendrium:				
aureum		X	X	2-28
sordidum		X	X	3-35
Epifungium:				
adgranulosa		X	X	3-18
adgravis		X	X	3-30
hoeksemai	X	X	X	1-20
lochi		X	X	3-27
nielsi		X	X	4-36
ulu		X	X	1-35
adscabra			X	3-18
hartogi			X	9-18
marki			X	15-28
pseudolochi			X	20-30
pseudotwilae			X	4-25
twilae			X	5-38
Epitonium:				
crassicostatum	?	?	?	9
graviarmatum	?	?	?	35
Surrepifungium:				
costulatum	X	X		3-18
ingridae	X	X		1-26
oliverioi	X	X		4-38
patamakanthini	X	X		5-18

Substrata

The structure of the substratum has implications for the occurrence of corals and their infestation by epitoniids. Figure 20 shows the infestation percentages of corals found on flat, holes and burrow substrata, respectively, in the Spermonde Archipelago. Corals that lie on a flat substratum have significantly the highest chance of being infested (X^2=14.9, p<0.001), whereas corals that are found on a burrow substratum significantly have the lowest chance of acting as a host (X^2=14.8, p<0.001). Specimens of some epitoniid species, i.e. *Epifungium adgranulosa*, *E. adgravis*, *E. hoeksemai*, *E. lochi*, *E. nielsi* and *E. ulu*, can be found both on the substratum and on the underside of their fungiid host (table 3). When there is a flat substratum below its host, *Epifungium ulu* is found significantly more often attached to the coral (n=25) than lying on the substratum (n=1)(X^2=22.2, p<0.001). When a substratum with holes is present, no significant preference is found (X^2=1.2, p=0.3), although relatively more specimens (n=37) are found on the substratum than on the coral itself (n=29).

The relative numbers of corals lying on either a flat, a burrow or a holes substratum vary significantly between localities off SW Sulawesi (fig. 21; X^2=412.4, p<0.001). Although the number of corals on a flat substratum remains similar, a burrow substratum is found more often at localities closer to the coast and a holes substratum is found more often away from the coast.

At all Indo-West Pacific localities investigated (fig. 1) mushroom corals were found also on burrow substrata, but except for two cases of infestation in the Spermonde Archipelago, they did not host any epitoniids in such a habitat. Burrows are found more often underneath mushroom corals than around them, which suggests that their occurrence is correlated.

Occasionally gobies (Gobiidae) and goby-shrimps (Alpheidae) were seen hyding away underneath mushroom corals that, after being turned over, revealed one or two burrows. Two shrimp species that are known to live in burrows were found associated with gobies. The shrimps were caught be pushing the

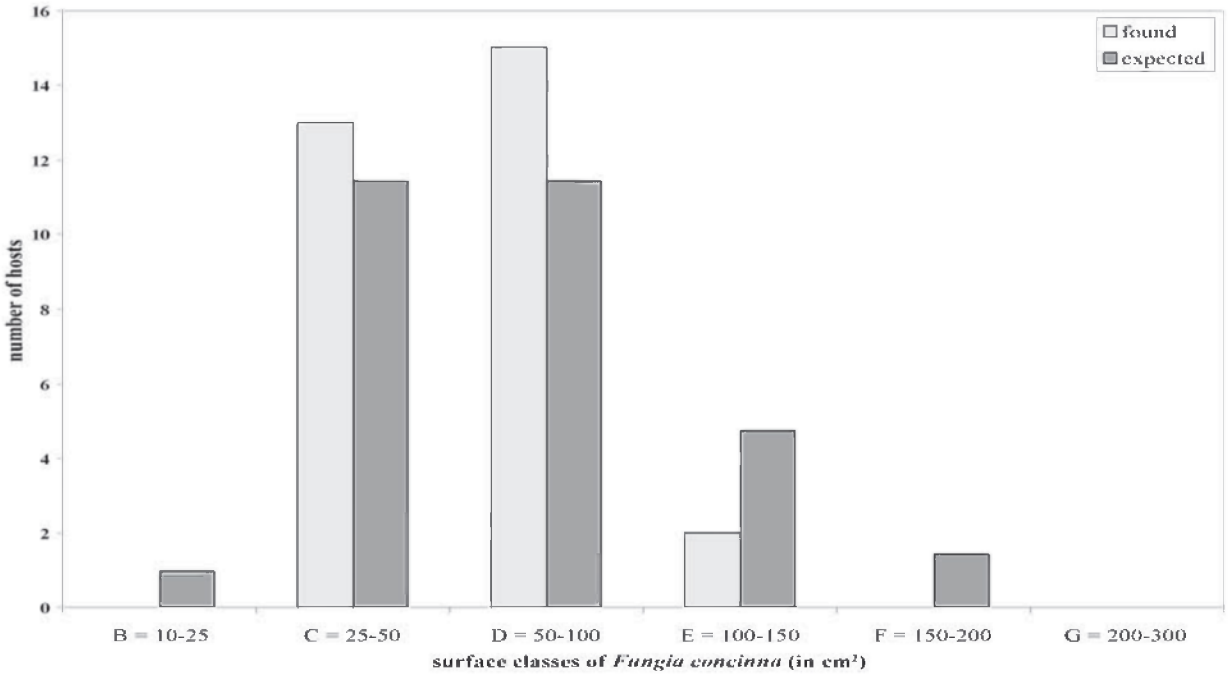

Fig. 22. Number of specimens of *Fungia concinna* in the size classes 10-25, 25-50, 50-100, 100-150, 150-200 and 200-300 cm² that was found infested by *Epifungium ulu* in the Spermonde Archipelago, SW Sulawesi, Indonesia (see fig. 2), next to the number that is expected when infestations are random, based on the coral size distribution of *Fungia concinna* specimens off W Kudingareng Keke, Spermonde Archipelago (n = 63).

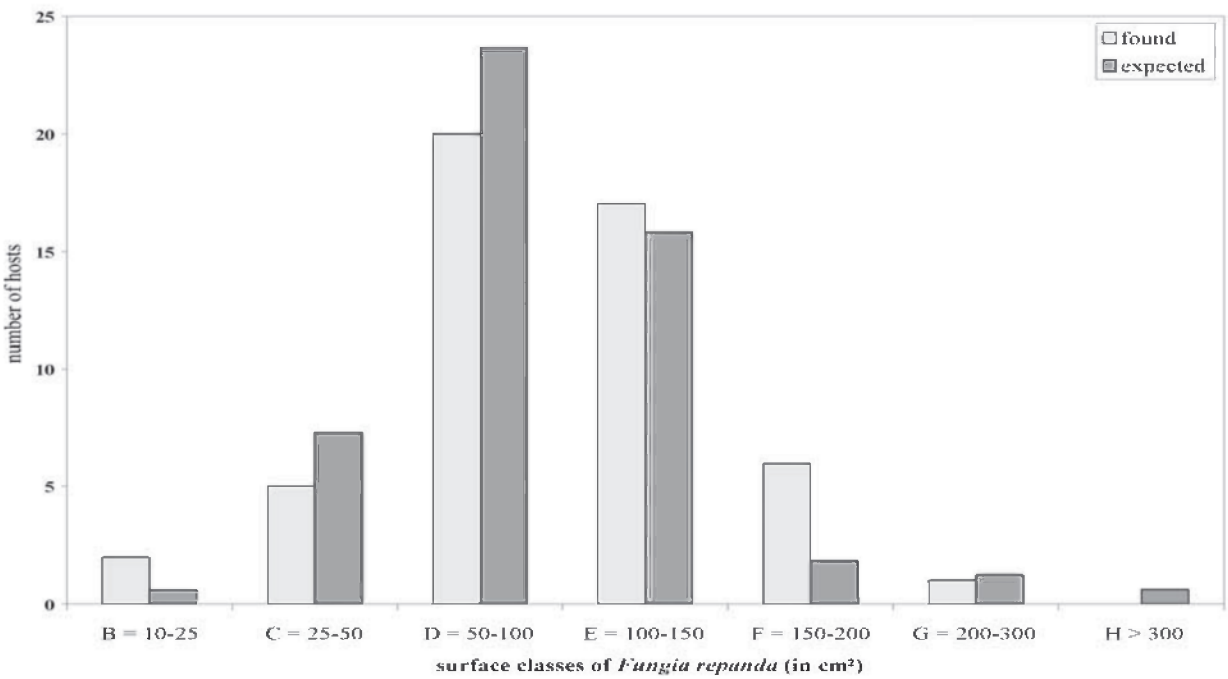

Fig. 23. Number of specimens of *Fungia repanda* in the size classes 10-25, 25-50, 50-100, 100-150, 150-200, 200-300 and >300 cm² that was found infested by *Epifungium ulu* in the Spermonde Archipelago, SW Sulawesi, Indonesia (see fig. 2), next to the number that is expected when infestations are random, based on the coral size distribution of *Fungia repanda* specimens off W Kudingareng Keke, Spermonde Archipelago (n = 84).

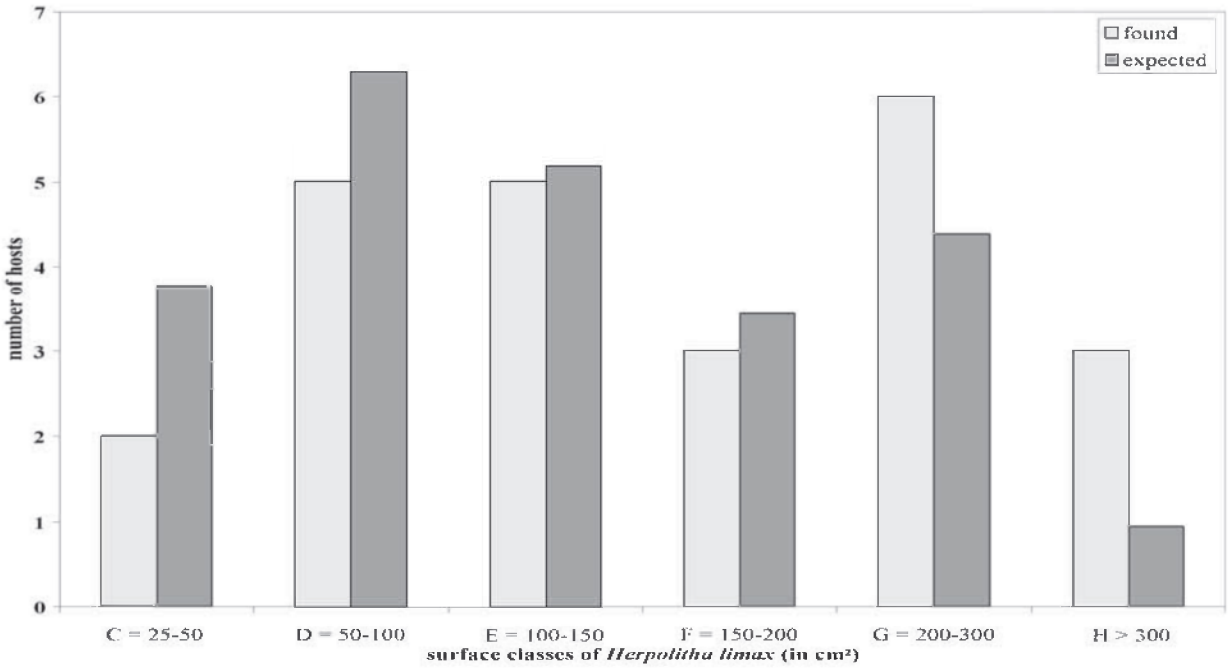

Fig. 24. Number of specimens of *Herpolitha limax* in the size classes 10-25, 25-50, 50-100, 100-150, 150-200, 200-300 and >300 cm² that was found infested by *Epifungium twilae* in the Spermonde Archipelago, SW Sulawesi, Indonesia (see fig. 2), next to the number that is expected when infestations are random, based on the coral size distribution of *Herpolitha limax* specimens off W Kudingareng Keke, Spermonde Archipelago (n = 153).

mushroom-coral quickly over the sand, blocking their escape routes. This concerned *Alpheus frontalis* H. Milne Edwards, 1837 (Caridea: Alpheidae; fig. 15), found underneath *Ctenactis echinata* at Palau, and *Axiopsis* sp. (Thalassinidea: Axiidae) found underneath *Herpolitha limax* off SW Sulawesi.

Both the shells and the egg-capsules are usually attached to the substrate by one or two, or by numerous mucus threads. By coincidence it turned out that these threads may be elastic and strong enough to pull some of the collected specimens out of the collection tube, back to their habitat over distances of up to about 50 cm. This unforeseen experiment made clear that the snails may be strongly connected to the substratum

Coral-sizes

At W Kudingareng Keke Island, 63, 84 and 153 specimens of *Fungia* (*Verrillofungia*) *concinna*, *F.* (*V.*) *repanda* and *Herpolitha limax*, respectively, were collected to study the size distributions within

Table 4. The size distributions of *Epifungium ulu* and *Epifungium twilae* samples with egg-capsules versus samples without egg-capsules (grey), found on corals in the size classes 0-50 cm², 50-150 cm² and >150 cm² in the Spermonde Archipelago, SW Sulawesi, Indonesia.

Coral size class:	**10-50 cm²**		**50-150 cm²**		**>150 cm²**	
***Epifungium ulu* samples**	**percentage**	**N**	**percentage**	**N**	**percentage**	**N**
with egg-capsules	26%	16	42%	35	60%	6
without egg-capsules	74%	46	58%	48	40%	4
***Epifungium twilae* samples**	**percentage**	**N**	**percentage**	**N**	**percentage**	**N**
with egg-capsules	17%	3	29%	4	65%	11
without egg-capsules	83%	15	71%	10	35%	6

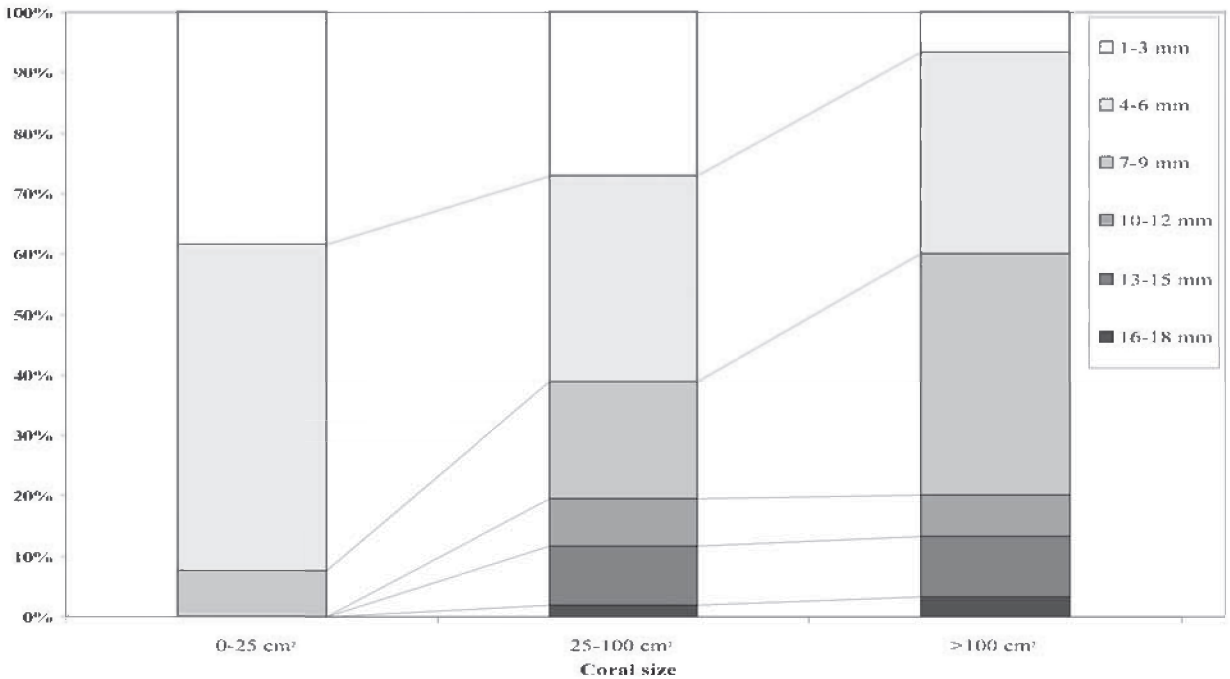

Fig. 25. The maximum shell heights found in *Epifungium ulu* samples (n= 146) and their distribution in the size classes 0-25 (n = 13), 25-100 (n = 103) and >100 cm² (n = 30) of their coral hosts, in the Spermonde Archipelago, SW Sulawesi, Indonesia.

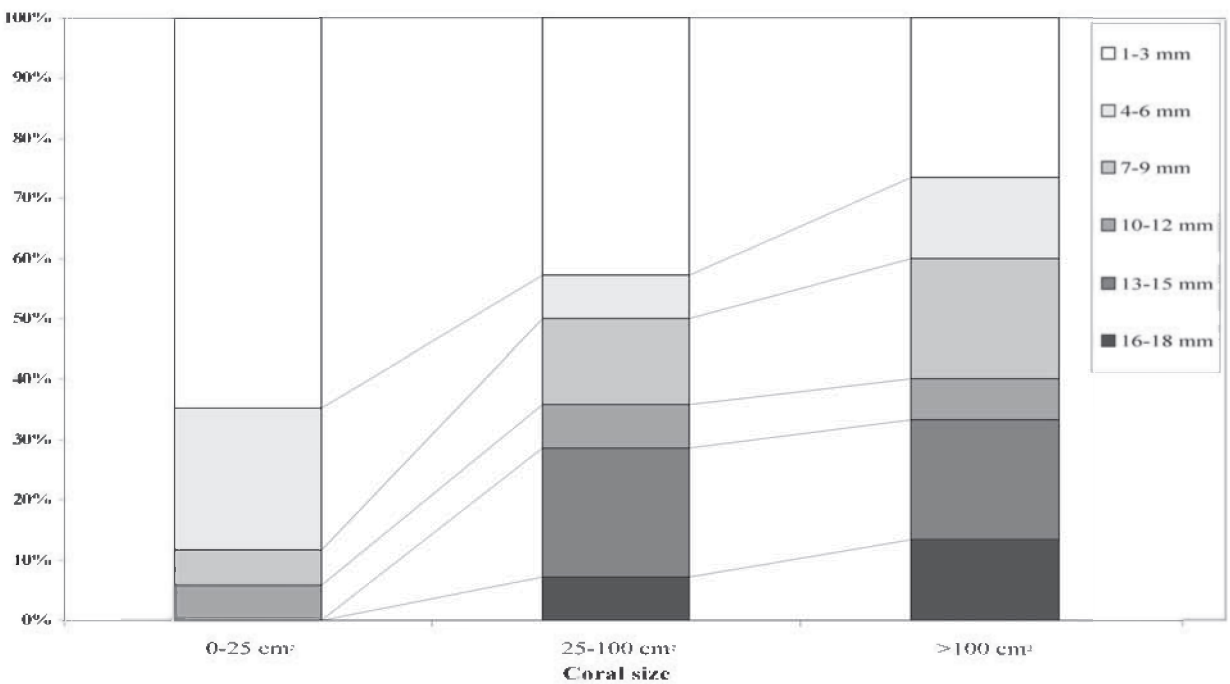

Fig. 26. The maximum shell heights found in *Epifungium twilae* samples (n= 46) and their distribution in the size classes 0-25 (n = 17), 25-100 (n = 14) and >100 cm² (n = 15) of their coral hosts in the Spermonde Archipelago, SW Sulawesi, Indonesia.

populations (figs 22-24) and the infestations by *Epifungium ulu* (figs 22-23) and *E. twilae* (fig. 24) in various size classes. *Epifungium ulu* specimens were found significantly more often underneath relatively large specimens of *Fungia repanda* (fig. 23; X^2=14.4, p<0.001). *Epifungium ulu* specimens were found less than expected on larger *Fungia concinna* corals, but this difference is not significant (fig. 22; X^2=1.8, p=0.20). *Epifungium twilae* specimens were found significantly more often with larger hosts (fig. 24; X^2=4.7, p<0.05). Furthermore, larger corals are infested significantly more frequently by relatively large specimens of *E. ulu* (fig. 25; X^2=11.2, p<0.025) and *E. twilae* (fig. 26; X^2=67.1, p<0.001). Under larger host corals, specimens of *Epifungium ulu* (table 4; X^2=4.7, p<0.05) and *E. twilae* (table 4; X^2=10.3, p<0.05) are found significantly more often with egg-capsules than without.

Turned over hosts and epitoniid predators

Only a single coral among c. 2000 that were found in upside down position was infested by epitoniid egg-capsules and none with one or more snails. Figure 27 illustrates the fate of 28 epitoniids and 7 clutches of egg-capsules that were initially attached to 16 coral hosts. The coral discs were placed upside down and checked after two hours and once again after two days. While turning the corals, some snails were immediately pulled from their hosts by the currents or by fish, mainly Labridae [e.g. fig. 16: *Halichoeres melanurus* (Bleeker, 1851)] and Pomacentridae [e.g. fig. 17: *Plectroglyphidodon lacrymatus* (Quoy and Gaimard, 1825)]. One of the two corals that still hosted epitoniids after two days had returned to an upright position, whereas the other coral was lying somewhat hidden in a hole, out of the current.

In the experiment in which three hosts were laid upside down, i.e. two with specimens and egg-capsules of *Epifungium ulu* and one with *E. twilae*, all *Epifungium ulu* were eaten or removed within 30 minutes by wrasses and damselfishes, while *E. twilae* survived.

In general, predation by fishes varies strongly over time and place. Some fishes had to be scared away before turning over a fungiid. Otherwise, they would most probably have speeded forward to snatch any epitoniids revealed. Small, slender fishes like wrasses were often encountered hiding below large fungiids, like convex corals of *Herpolitha*, *Sandalolitha* and *Ctenactis*. A substratum with holes or an irregular substratum is usually present in these cases, creating an entrance for the fishes under the coral margin. If a flat substratum is present and the coral is not convex but also flat, there is not enough room for a fish to get below it.

No significant differences were found between the corals in the turn-over rate experiment, because only 3 of the 360 fungiids, i.e. 360 = (12 species × 24 specimens) + (3 larger size-classes × 24 specimens), had turned over within the 10 days of the experiment. The number of specimens that had regained an upward position within 2 days after being turned over at the start, did differ significantly between the twelve species (X^2=58.3, p<0.001), viz. *Fungia* (*Danafungia*) *horrida*, *F.* (*D.*) *scruposa*, *F.* (*Fungia*) *fungites*, *F.* (*Verrillofungia*) *concinna*, *F.* (*V.*) *repanda*, *F.* (*V.*) *scabra*, *F.* (*Lobactis*) *scutaria*, *F.* (*Pleuractis*) *gravis*, *F.* (*P.*) *paumotensis*, *Ctenactis echinata*, *Herpolitha limax* and *Polyphylia talpina*, and the size classes of *F.* (*V.*) *repanda* and *H. limax*. The turn back ratios are shown in table 5.

In the Spermonde Archipelago, 1,109 out of 26,277 fungiids, i.e. 4.2%, were observed as upside down under natural conditions. These percentages differ significantly between the species (fig. 28; X^2=202.1, p<0.001).

Discussion and conclusions

Coral species and their hosted wentletraps

Epifungium and *Surrepifungium* species are here referred to as either specialists or generalists, dependent on being associated with only one or a monophyletic group of host species, versus an association with some distantly related hosts (coral phylogeny based on molecular data: A. Gittenberger et al., chapter 8). After these definitions, most *Epifungium* species, i.e. *E. adgranulosa*, *E. adgravis*, *E. adscabra*, *E. hartogi*, *E. lochi*, *E. marki*, *E. nielsi*, *E. pseudolochi*, *E. pseudotwilae* and *E. twilae*, are to be called specialists (table 1). The hosts of *E. pseudotwilae*, i.e. *Sandalolitha*, *Podabacia* and *Zoopilus* species, and the hosts of *E. twilae*, i.e. *Herpolitha* and *Ctenactis* species, do

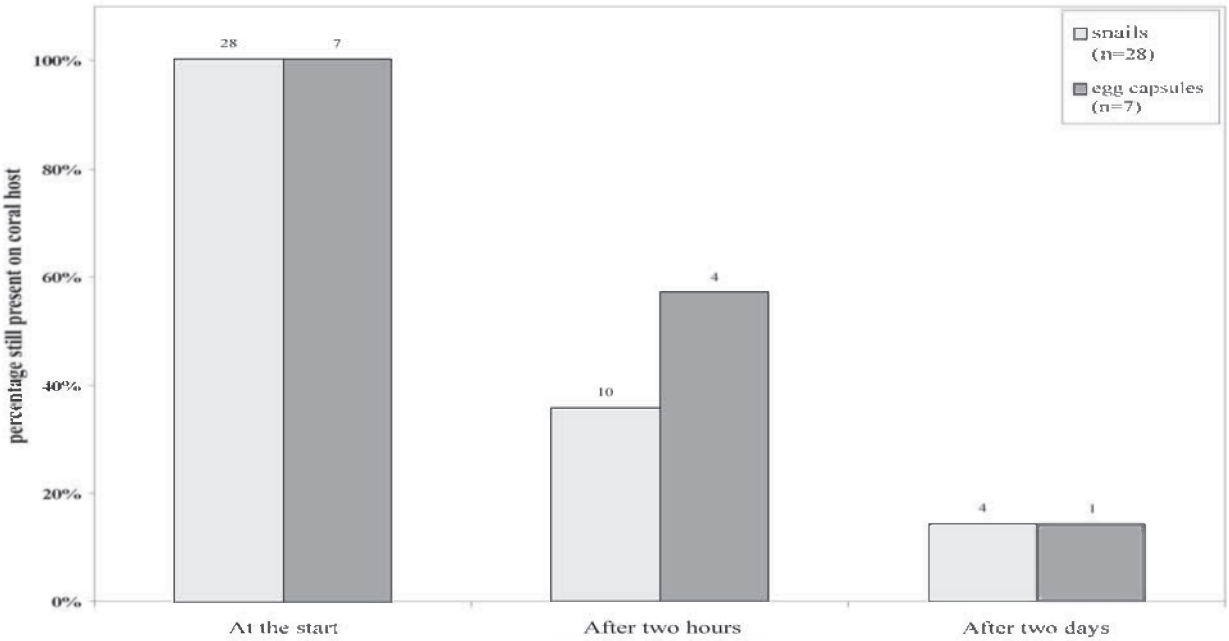

Fig. 27. The numbers of shells and egg-capsule clutches of *Epifungium ulu* that remained on the underside of the host corals even though they were overturned; after two hours and after two days, off W Langkai, Spermonde Archipelago, SW Sulawesi, Indonesia (see fig. 2).

not form two clades in the Fungiidae phylogeny reconstruction based on morphology by Hoeksema (1989b). However, anticipating the publication of a revised, molecular phylogeny reconstruction of the Fungiidae, we consider *E. pseudotwilae* and *E. twilae* specialists (A. Gittenberger et al., chapter 3).

All fungiid species, except *Fungia* (*Cycloseris*) *costulata*, are associated with only one *Epifungium* specialist (table 1). The two species that have specialized on *F.* (*C.*) *costulata* may have been able to do so because of their allopatry, since *Epifungium pseudolochi* is restricted to the Red Sea, while *E. lochi* is found in the Indo-West Pacific, from the Maldives, Indonesia, Australia to Palau (A. Gittenberger and E. Gittenberger, 2005).

Epifungium hartogi is exceptional in being the only *Epifungium* species that is associated with euphylliid corals. The snails are hidden deep inside the mouth cavity (the stomach) of their host (A. Gittenberger, 2003), which has been illustrated before for a zoanthid-associated wentletrap species (Zann, 1980: 132, upper fig.). Because the snails are invisible then from outside and since they may only need to leave their shelter for spawning, many more epitoniids living in similar habitats where they are easily overlooked might await discovery.

The four *Surrepifungium* species, viz. *S. costulatum*, *S. ingridae*, *S. oliverioi* and *S. patamakanthini*, and the two *Epifungium* species, viz. *E. hoeksemai* and *E. ulu*, may be considered generalists. *Surrepifungium* species and *E. hoeksemai* resemble most epitoniids associated with sea-anemones, and differ from other coral-associated species by their ability to bury themselves into the sand. The feeding behaviour of the *Surrepifungium* species has not yet been observed. Maybe the snails extend their proboscis towards the coral tissue while remaining protected against the nematocysts on the substrate underneath. A similar behaviour has been observed in sea-anemone-associated epitoniids like *Epitonium clathratulum* (Kanmacher, 1797); these snails may extend their proboscis to up to three times the shell-length towards the stem or the tentacles of their host (e.g. Perron, 1978: 65; Robertson, 1983: 4; den Hartog, 1987: 105).

Occasionally an *Epifungium* species may share its host with an epitoniid of the genus *Surrepifungium* (table 1). If so, the *Epifungium* is found on the coral itself while the *Surrepifungium* occurs on or in the substratum underneath. In *Surrepifungium* the snails are never found on their hosts, opposite to what is

usually observed in *Epifungium*. In the latter case the snails are closest to their food but constantly within reach of the particular coral species' nematocysts. The *Epifungium* species have to be adapted to more extreme environments, which might explain why they are more strictly specialized to their hosts than the *Surrepifungium* species.

The habitat preferences of *Epifungium hoeksemai* are unusual for coral-associated epitoniids. These snails differ from other coral-associated epitoniids in being able to bury in the sand, or crawl on the substratum below their hosts, or over the coral's surface (table 3). *Epifungium hoeksemai* further differs from the other generalists in being associated with only two host species, i.e. *Fungia* (*F.*) *fungites* and *Heliofungia actiniformis*, instead of at least four and usually more than six (table 1). These two coral species differ conspicuously, both morphologically (Hoeksema, 1989b) and genetically (A. Gittenberger et al., chapter 3). *Fungia* (*F.*) *fungites* is exceptional among the 21 *Fungia* species that are known to be associated with epitoniids in that it may be found with two *Epifungium* species. All the other *Fungia* species, except for *F.* (*C.*) *costulata*, are known to be associated with only a single wentletrap species (table 1). The second host of *E. hoeksemai*, i.e. *H. actiniformis*, is unusual by its fleshy tentacles (fig. 6) that are at least ten times longer than those of other fungiids. *Heliofungia actiniformis*, *Fungia (Danafungia) fralinae* (see Hoeksema, 2004b) and *Polyphyllia talpina* have the longest tentacles among the fungiids. The latter two species are the only free-living mushroom coral species that were never found associated with epitoniids, even though more than 1000 specimens of each were searched. Only tentacle length distinguishes them as a couple from the other fungiids. However, the association between *E. hoeksemai* and *H. actiniformis* contradicts the hypothesis that relatively long tentacles in general prevent wentletraps from settling on a particular fungiid.

Even though *Epifungium ulu* does infest *Ctenactis*, *Halomitra*, *Herpolitha* and *Sandalolitha* populations, with population infestation percentages of less than 0.3%, there seems to be a preference for *Fungia* species that are not associated with any other *Epifungium*, with the exception of *E. hoeksemai* (table 1). This is at least suggested by the infestation percentages of 0.7-3.7% of the populations of such *Fungia* species in the Spermonde Archipelago (table

Table 5. Results of turn back rate experiment off W Kudingareng Keke, SW Sulawesi, Indonesia. All data are based on 24 specimens for each species and size class. The fungiid species are ordered by the turn back rate of 24 specimens in the size class 25-100 cm².

fungiid species:	Coral size-class (cm^2)	Average of length / width	Average weight (gram)	Number of corals (n = 24) that turned back after 2 days
Polyphyllia talpina	25-100	3.6	142	20
Herpolitha limax	25-100 100-200 >200	2.2 3.1 3.4	127 302 754	11 11 1
Fungia scutaria	25-100	1.6	135	9
Fungia gravis	25-100	1.6	251	7
Fungia paumotensis	25-100	1.7	131	5
Fungia repanda	25-100 100-150	1.1 1.1	127 326	5 0
Ctenactis echinata	25-100	2.2	94	4
Fungia scruposa	25-100	1.1	127	3
Fungia scabra	25-100	1.1	75	3
Fungia concinna	25-100	1.2	110	1
Fungia horrida	25-100	1.0	163	1
Fungia fungites	25-100	1.1	93	0

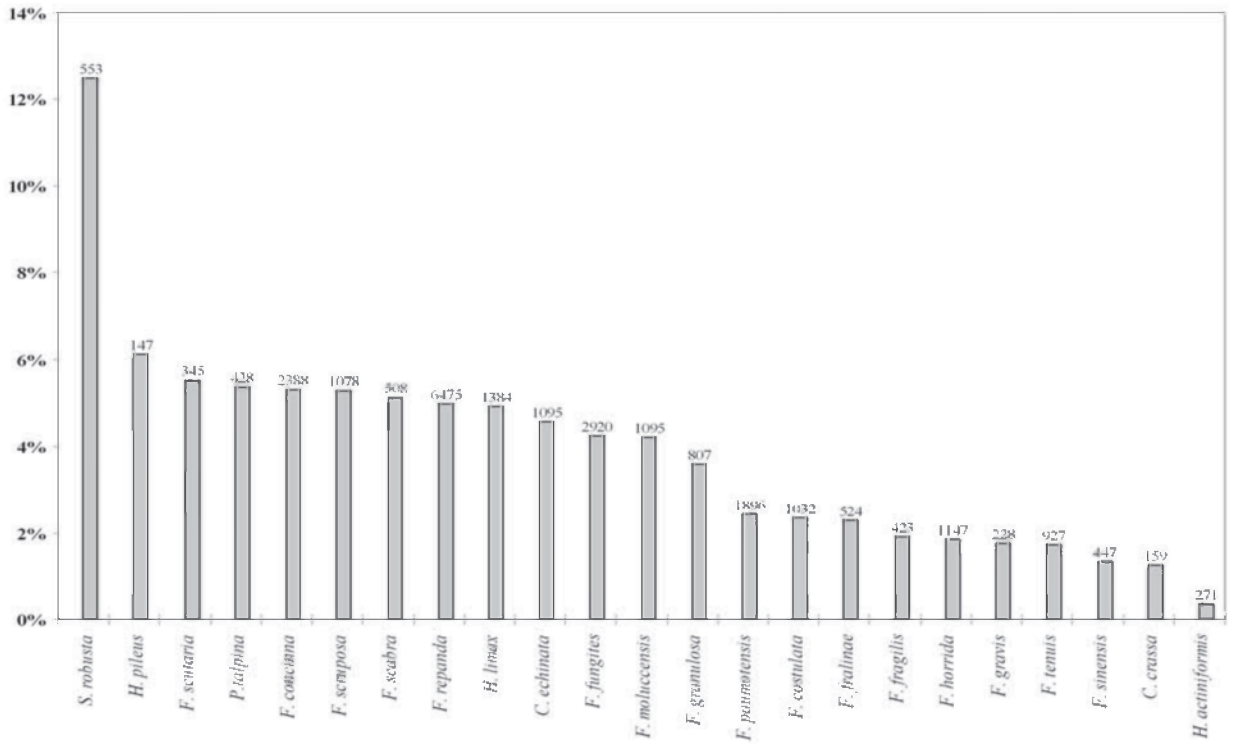

Fig. 28. Percentages of fungiid species populations that were observed in upside down position in the Spermonde Archipelago, SW Sulawesi, Indonesia. The n-values are indicated above the columns.

2). At none of the fieldwork localities (fig. 1) in the Indo-Pacific, any indication was found for local, divergent preferences of *E. ulu*. *Halomitra* and *Sandalolitha* infestations were rarely found in both Indonesia and Palau, and the *Ctenactis* infestations are rare in Egypt (Red Sea), Indonesia and Palau. The infestation percentages of *Fungia* populations seem to be much higher at all fieldwork localities.

The host preferences of *Epitonium crassicostatum* and *E. graviarmatum* cannot be indicated because both species are known from one empty shell only, found with *Fungia* (*Cycloseris*) *costulata* and *F.* (*C.*) *vaughani*, respectively.

In general, sister species do not occur sympatrically and syntopically, but *Epidendrium aureum* and *E. sordidum* are found together on the same host species without any obvious niche differentiation. There may be differences however, since *Epidendrium sordidum* is the only epitoniid species with shells that are usually completely overgrown by other organisms, like hydroids (fig. 4), forams and vermetids (A. Gittenberger and E. Gittenberger, 2005), during their lifetime. As a consequence, these snails are better camouflaged and possibly somewhat better protected against predators, as compared to *Epidendrium aureum* (fig. 3). The life-strategies of these two species seem to be very similar in all other aspects and a realistic mechanism that might have triggered sympatric speciation cannot be indicated.

Trophic aspect of mollusc-coral relationship

Unlike endoparasitic molluscs of the families Coralliophilidae and Mytilidae (Bouillon et al., 1980; Massin, 1989, 1992; Hoeksema and Achituv, 1993; Hoeksema and Kleemann, 2002; Kleemann and Hoeksema, 2002; Massin and Dupont, 2003), the ectoparasitic epitoniids do not appear to inflict serious visible damage to their coral hosts. The thick layer of mucus secreted by most mushroom corals may be defensive and in itself is believed to have high food quality (Krupp, 1982, 1984, 1985; Chadwick, 1988). Mushroom corals are very successful in regenerating

and repairing their tissue (Chadwick and Loya, 1990; Kramarsky-Winter and Loya, 1996; Chadwick-Furman et al., 2000). Fragmented mushroom corals are also known for their regenerative capacity and survival, which may result in large areas covered by these free-living corals (Hoeksema, 1989b; Chadwick and Loya, 1990; Littler et al., 1997; Yamashiro and Nishihira, 1998). Just before they die, adult polyps may even generate complete new buds from their soft tissue (Gilmour, 2002a, 2002b, 2004a, 2004b; Hoeksema, 1989b, 2004b; Kramarsky-Winter and Loya, 1996, 1998). Hence, infestations by epitoniids may slightly harm individual fungiids, but is not likely to have any lethal effect on mushroom coral populations. There are also no indications that infested mobile mushroom corals may actively turn themselves upside down to expose their parasites for removal by potential predators.

Coral densities

Low epitoniid infestation percentages in relatively high fungiid densities were observed in Egypt (Red Sea), the Maldives, Thailand, Indonesia and Palau. The infestation percentages by *Epifungium ulu* in the transects at 6, 9, 12 and 15 m off W and E Kudingareng Keke Island, are independent of depth and also negatively correlated with coral density (fig. 19). Among the seven reefs that were studied in the Spermonde Archipelago, only the Lae-Lae Island had an exceptionally low infestation percentage in combination with its number of potential coral hosts, diverging from the general trend. The relatively low number of infestations in this case may be caused by the fact that the water at Lae-Lae Island is murky because of its position close to the land, the city Makassar, and a river outlet (fig. 2). The fungiids here were also lying relatively more often on substrata with burrows than at the other localities (fig. 21) and fungiids with burrows underneath are almost never infested (fig. 20).

The negative correlation between coral density and infestation percentage supports the hypothesis that before settlement, a certain number of veligers are evenly dispersed over coral reefs and depths. Apart from that it has to be accepted that the veligers can actively go for a suitable host. Host species recognition by chemotaxis was already described for epitoniids by Bell (1985), Perron (1978) and Salo (1977). It explains the relatively high infestation percentages when few suitable fungiid hosts are present. Exceptional are those reef areas that are covered almost entirely by corals of a single fungiid species that is immune to epitoniids, e.g. *Fungia* (*Danafungia*) *fralinae* (see Hoeksema, 2004b).

Depth ranges

In general coral-associated epitoniids do not show any preference for depth (e.g. fig. 19). The species that are usually found in deep waters, like *Epifungium lochi*, are related to corals, like *Fungia* (*Cycloseris*) species, with a preference for those depths. The only exception to this rule is an *Epifungium twilae* population in the Red Sea, off Marsa Nakari, Egypt. Infestations (n=4) only occurred deeper than 29 meters, even though suitable hosts were present at all depths. This may be related to the unusually heavy rainfall in the year previous to the fieldwork, which formed some freshwater lakes in the desert. One of these lakes formed a small canal towards the coast, flowing into the sea at the fieldwork locality, with much dirt and sand, which made the shallow water very murky for several months. The visibility remained good only at greater depths (local dive guides, pers. comm.). Indirect evidence for epitoniids disliking murky waters was also found off Lae-Lae Island in the Spermonde Archipelago (see fig. 2), where infestation percentages were much lower than expected (fig. 18).

Substrata

A significantly higher number of epitoniids was found on corals living on flat substrata than on those from a substratum with holes (fig. 20). This may be explained by the fact that in the latter case potential predators, like fish, can reach below a fungiid disc, making use of such holes, as was observed in the field repeatedly. This might also explain why in *Epifungium ulu* most snails are observed on the substratum (like *Epifungium hoeksemai* in fig. 6) instead of on the coral`s surface when there are holes below the coral. Under those conditions the snails might be more easily overlooked by fish. Alternatively, when the underground is flat, the snails are found

significantly more often on the coral itself.

Snails of *Surrepifungium* species are never found on the coral's surface. In contrast to *Epifungium* species, except for *E. hoeksemai*, they may bury themselves into the sand (table 3), to be protected against potential threads like fishes and currents.

Most of the burrows that were found under mushroom corals (figs 11, 13-14) are probably made by shrimps, like the ones that were caught, i.e. *Alpheus frontalis* (fig. 15) and *Axiopsis* sp., and the goby-shrimps and gobies that were seen below fungiids in the field. These shrimps or gobies may remove and eat any epitoniid that tries to settle above its home, i.e. the burrow. This may explain why a significantly low number of epitoniid snails was found with fungiids lying on substrata containing burrows.

Coral-sizes

Coral-size matters in relation to infestation with epitoniid snails. The presence of *Epifungium ulu* and *E. twilae*, with their egg-capsules, is clearly related to host-size since [1] the snails are more frequently found underneath larger than smaller hosts (figs 23-24), [2] larger snails are more often observed with larger hosts (figs 25-26) and [3] epitoniids are relatively more often found together with egg-capsules underneath larger hosts (table 4). These results can be explained by a combination of factors.

Larger host-corals are heavier than smaller ones and will be overturned less easily. Consequently, they constitute a more stable environment for snails that cannot survive on upside down mushroom corals. Since larger usually also means older, the largest corals have been the longest period of time exposed to infestation. An individual coral may be a host for years and maybe generations of snail parasites. In fact, up to 20 snails, with a large variety of shell-heights, indicative of different generations, have been found on a single coral. It remains to be investigated whether these are successive generations, i.e. whether some veligers stay and settle below their parents' coral, not leaving their place of birth.

The preference of epitoniids for larger hosts may also be related to the convex (domed) shape of some free-living mushroom corals, leaving more living space for epitoniids in between the disc and the substratum. This is especially relevant for snails that cannot bury into the sand, i.e. most *Epifungium* species (table 3), or have broad shells (height/width 1.0-1.2), i.e. *Epifungium pseudotwilae* and *E. twilae* (fig. 9; A. Gittenberger and E. Gittenberger, 2005). These wentletraps are only found associated with fungiids that are or can become relatively large, i.e. species of *Ctenactis*, *Herpolitha*, *Podabacia*, *Sandalolitha* and *Zoopilus* (see Hoeksema, 1989b, 1991b). Epitoniids with more slender shells (height/width >2.0), like *Epifungium adgranulosa*, *E. adscabra*, *E. marki*, *E. nielsi* (fig. 7), *E. lochi* (fig. 8) and *E. pseudolochi*, are associated either with small fungiids, i.e. *Fungia* (*Cycloseris*) species, *F.* (*Wellsofungia*) *granulosa* (fig. 12), or *F.* (*Verrillofungia*) *scabra*, or with fungiids that have oval discs which are not or rarely convex, e.g. the *Fungia* (*Pleuractis*) species (fig. 7).

Epifungium hoeksemai (fig. 6) and *E. ulu*, the only two generalists in *Epifungium*, have moderately broad-conical to slender-conical shells with H/W indexes of 1.6-2.4 and 1.7-3.3, respectively (A. Gittenberger and E. Gittenberger, 2005: figs 70-73, 75-76). In *E. hoeksemai* the snails may bury into the substrate; maybe they do so when the space under a host is limited. This behaviour is not known from any other *Epifungium* species. Most of the coral hosts of *E. hoeksemai* and *E. ulu* have discs that are at least slightly convex, i.e. *Ctenactis echinata*, *Fungia* (*Danafungia*) species, *F.* (*Lobactis*) *scutaria*, *F.* (*Fungia*) *fungites*, *Halomitra pileus*, *Heliofungia actiniformis*, *Herpolitha limax* and *Sandalolitha robusta*.

Turned over hosts and epitoniid predators

Epitoniids are hardly ever found on fungiids that lie upside down. Usually the wentletraps are removed from their host within hours or days after the coral disc has been turned over (fig. 27). Snails that become abruptly exposed to the open water will either be eaten by fishes (figs 16-17) or be removed from their food-source and shelter by the water turbulence. Maybe the latter alternative was underscored during the fieldwork, because corals were always turned upside down carefully. Under natural conditions the coral discs will be turned around much more abruptly, by the then relatively strong currents. The egg-capsules may 'survive' somewhat longer than the

snails because their clutches are attached to the substrate by many mucus threads instead of only one or two that hold the shells of the snails themselves.

The frequencies of overturning differ conspicuously between the various fungiid species (table 5), as do the numbers of specimens lying upside down under natural conditions (fig. 28). It may be assumed that being associated with hosts that do not easily turn over enhances the survival rate for the wentletraps, but a preference of epitoniids for the most 'stable' host species was not noticed.

Epifungium pseudotwilae and *E. twilae* are associated with fungiids that may be relatively large, e.g. *Ctenactis*, *Herpolitha*, *Sandalolitha* and *Zoopilus* species. Wrasses, damselfish and gobies are more frequently found below such large corals and may therefore be more threatening to *E. pseudotwilae* and *E. twilae* than to the other *Epifungium* species. According to molecular data (A. Gittenberger et al., chapter 8), despite their conchological similarity, *E. pseudotwilae* and *E. twilae* are not sister species. Their shells are conspicuously broader than those of the other *Epifungium* species, which have far more slender shells (A. Gittenberger and E. Gittenberger, 2005). The broadly conical shell shape in both *E. pseudotwilae* and *E. twilae* might have originated by parallel evolution, resulting from a selection pressure by fish predators. Small fishes that may reach the underside of the coral discs may not be able to get hold of the broad *E. pseudotwilae* and *E. twilae*, simply because their mouths are too small. This hypothesis is supported by the observation that damselfishes and wrasses only ate the slender specimens of *Epifungium ulu*, without attacking the relatively broad, large *E. twilae*.

Acknowledgements

We are grateful to Prof. Dr. Edmund Gittenberger (Leiden) and Dr. David G. Reid (London) for critically discussing the manuscript. Merijn Bos, Pat Colin, Rachel Colin, Hans Ditlev, Mark Erdmann, Jeroen Goud, Victor de Grund, Bas Kokshoorn, Somnuk Patamakanthin, Somwang Patamakanthin, Niels Schrieken, and Dr. Nicole J. de Voogd are thanked for their help in providing information and material used in this study. Dr. Charles H. J. M. Fransen (Leiden) is thanked here for identifying the burrowing crustaceans. We are also grateful to Prof. Dr. Alfian Noor (Hasanuddin University, Makassar) for his support in Makassar.

This research project was supported by WOTRO (grant nr. W 82-249) with additional funding by the Schure-Beijerinck-Popping Fonds (KNAW), the Alida Buitendijkfonds (Leiden University), and the Jan Joost ter Pelkwijkfonds (Leiden). The research in Indonesia was generously sponsored by the Indonesian Institute of Sciences (LIPI).

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Curriculum Vitae

Curriculum Vitae

Adriaan Gittenberger was born March 17th, 1976, in Leiden. After his education at the city gymnasium (ß), he started studying Biology at Leiden University in 1994. He acquired his MSc in 1999 (cum laude), with a specialization in taxonomy, ecology and molecular biology and a preference for marine biology. To increase his abilities, he followed from 1997-1998 lectures in 'Computer Science' at Leiden University. Additional courses that were attended are: 'Linnaeus II', by the Expert Centre for Taxonomic Identification, Amsterdam (1999); "Implementing SQL 7.0 & Java 2.0, SUN certified programmer", by AtosOrigin, Utrecht (2000); 'Marine Biodiversity Data Management', by UNESCO, MARBEF & IODE, Flanders Marine Institute, Ostend, Belgium (2006) ; "Course in Taxonomy and Biology of Tunicates", by The Smithsonian Tropical Research Institute, Bocas Research Station, Bocas del Toro, Panama (2006).

Before the research project that resulted in the present thesis could begin, he worked for one year (1999-2000) as Project Leader & Software Engineer with AtosOrigin, Utrecht, on the development of the Configuration Management Database for the Philips Global Network.

In the period 1999-2006 he worked as a researcher on a variety of short term projects related to marine invasive species and/or marine biodiversity for the ANEMOON foundation, Expert Centre for Taxonomic Identification, European Invertebrate Survey, Institute of Environmental Sciences, Central Bureau of Statistics, National Museum of Natural History Naturalis, Paris National Museum of Natural History, and the Smithsonian Marine Invasions Laboratory (Smithsonian Environmental Research Center).

A grant of the WOTRO foundation gave the opportunity to acquire a position at the National Museum of Natural History Naturalis to work on the subject of this thesis from 2000 on. Additional grants were received from: (1997) KNAW, Jan Joost ter Pelkwijkfonds, LUF and LUSTRA; (2000) KNAW; (2004) Jan Joost ter Pelkwijkfonds and Alida M. Buitendijk Fonds; (2005) Woodshole Oceanographic Institution, and NWO.

Since 2005 he is a Researcher at the National Museum of Natural History Naturalis for the EU-funded MarBEF and BioCoMBE projects (www.Marbef.org & www.Biocombe.org).

Most of his activities and functions are in one way or another related to the marine environment:

Coordinator (since 1998) of the Marine Monitoring Projects MOO (since 1998) and SETL (since 2006) of the ANEMOON Foundation (www.anemoon.org). The MOO-project was honoured with the Dutch Underwater Sports Association NOB 2000 Science award. The SETL project is an international fouling community study organized in cooperation with the Marine Invasions Laboratory of the Smithsonian Environmental Research Institution, USA, the National Museum of Natural History Naturalis, Leiden, and the Institute of Environmental Sciences, Leiden University.

Board member of the SeaFoundation (since 2006). With its multidisciplinary methodology the Seafoundation focuses on combining the hydrographical, biological, environmental, chemical and technological knowledge present in universities, schools, research institutes, fisheries, industrial companies and other foundations. As such the SeaFoundation works as an intermediate and promoter of projects concerning the marine environment worldwide, keeping the People, Planet, Profit concept in mind.

Webmaster (since 2000) of the websites on Gastropod Parasites and their Coral Hosts (since 2000) (www.ascidians.com/oio/corals.htm) and The Dutch Ascidians Homepage (since 2000) (www.ascidians.com)

President (2003-2006), secretary (1999-2000) and CMAS dive-instructor (since 2000) of the Scuba Diving Club "LOV Calypso", Leiden, The Netherlands.

Organizer (since 2006) of the Flora & Fauna Square at the annual National scuba-diving fair "Duikvaker", representing Dutch organizations and institutes with a marine research department, (ANEMOON Foundation, North Sea Foundation, Underwater Biology Foundation, National Museum of Natural History

Naturalis, Leiden University, Groningen University and Rotterdam Zoo) and the Sea Day Symposium for the European Invertebrate Survey (EIS), The ANEMOON Foundation and the National Museum of Natural History Naturalis (2006).

Active membership of the National Exotic Species Workgroup (since 2005) of The Netherlands Flemish Ecological Society & Workgroup Ecological Water Management and a member of the steering committee of the KaBar project (since 2005) of the Flemish institute for technological research (VITO), Belgium. (http://www.vito.be/english)

His special interest in ascidians, demonstrated in for example the Dutch Ascidians Homepage, resulted in contacts with: Lawrence Berkeley National Laboratory, California, USA; University of Rhode Island, Graduate School of Oceanography, Narragansett, Rhode Island, USA; Nori Satoh Lab, Division of Molecular and Evolutionary Developmental Biology, Kyoto, Japan; Department of Ecology and Evolutionary Biology, Cornell University, Corson Hall, Ithaca, USA; Department of Neuroscience, Uppsala University, Sweden; Jyväskyla University, Department of Biological and Environmental Sciences, Jyväskyla, Finland; Marine Biology Section, Marine Department, Ghent University, Belgium; Laboratory of Biochemistry and Molecular Biology, Stazione Zoologica "Anton Dohrn", Napoli, Italy.

His underwater photos, mainly but far from exclusively of ascidians, were used in popular and scientific journals, like Cell (2001), De Ingenieur (2005), Duiken (2006), Duikkrant (2001), Duikmagazine (2005, 2006), Mare (2005), Médécine Sciences (2003, 2006), Naturwissenschaftliche Rundschau (2003) and Vita Malacologica (2004), in books by R. Leewis (2002, 2005) and R.P. Olinsji (2006), and in calendars of Bureau Waardenburg (2001, 2002, 2003).

His interests and expertise extend from fieldwork, as a licensed, 2 star CMAS Dive Instructor, to the practical and theoretical work for molecular phylogeny reconstruction.

For a varied audience of both amateurs, students and scientists 20 lectures on various aspects of marine biodiversity were given during the period 2004-2006. The first price for the best student oral presentation was awarded at the World Congress of Malacology, Perth, Australia (2004), and the distinction for best oral presentation was granted at the PhD-Day of the Research School Biodiversity, Leiden (2004). For publications that are not incorporated in this thesis, and posters, see below.

Publications, not incorporated in this thesis

Gmelig Meyling, A.W., R.H. de Bruyne, A. Gittenberger & N. Schrieken, 1999. Using Scuba diving: Data analyses of faunal research by scuba divers in the coastal waters of the province Zeeland; period 1994-1998, pp. 275, 4 appendices. ANEMOON Foundation, Bennebroek, The Netherlands [in Dutch].

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Posters

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A biogeographical study of parasitic gastropods and their coral hosts in the Indo-West Pacific. At:
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