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

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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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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.

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Introduction

Within the gastropod family Coralliophilidae Chenu, 1859, the genus *Leptoconchus* Ruppell, 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

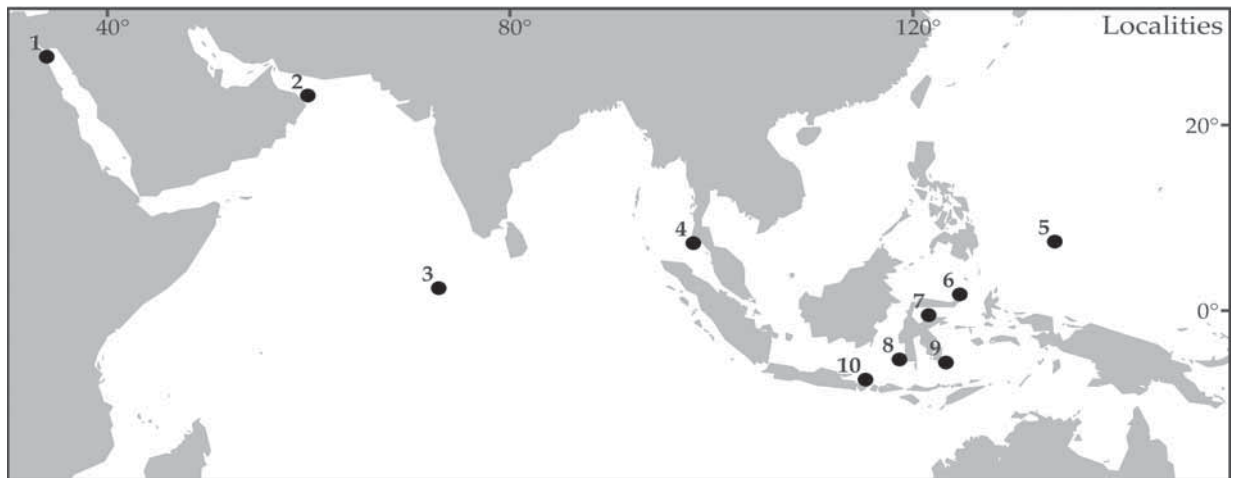


Fig. 1. The Indo-Pacific region, from the Red Sea to the Hawaiian Archipelago, illustrating the research localities 1-10. 1, Marsa Nakari, c. 350 km S of Hurghada, Egypt (Red Sea); 2, Oman; 3, Vilamendhoo Island, Ari Atoll, Maldives; 4, Phiphi Islands, Krabi, Thailand; 5, Palau; 6, Siladen and Bunaken 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)
<i>Leptoconchus incycloseris</i>	<i>Fungia (Cycloseris) costulata</i>	5, 5, 9
<i>Leptoconchus infungites</i>	<i>Fungia (Fungia) fungites</i>	5, 5, 6, 7, 7, 8, 8, 8, 10
<i>Leptoconchus ingrandifungi</i>	<i>Sandalolitha dentata</i>	10
<i>Leptoconchus ingranulosa</i>	<i>Fungia (Wellsofungia) granulosa</i>	7
<i>Leptoconchus inlimax</i>	<i>Herpolitha limax</i>	3
<i>Leptoconchus inpileus</i>	<i>Halomitra pileus</i>	3, 5, 8
<i>Leptoconchus inpleuractis</i>	<i>Fungia (Pleuractis) gravis</i>	8
	<i>Fungia (Pleuractis) moluccensis</i>	8
	<i>Fungia (Pleuractis) paumotensis</i>	6, 7
<i>Leptoconchus massini</i>	<i>Fungia (Verrillofungia) concinna</i>	4, 5, 8
	<i>Fungia (Verrillofungia) repanda</i>	1, 3, 4, 5, 10

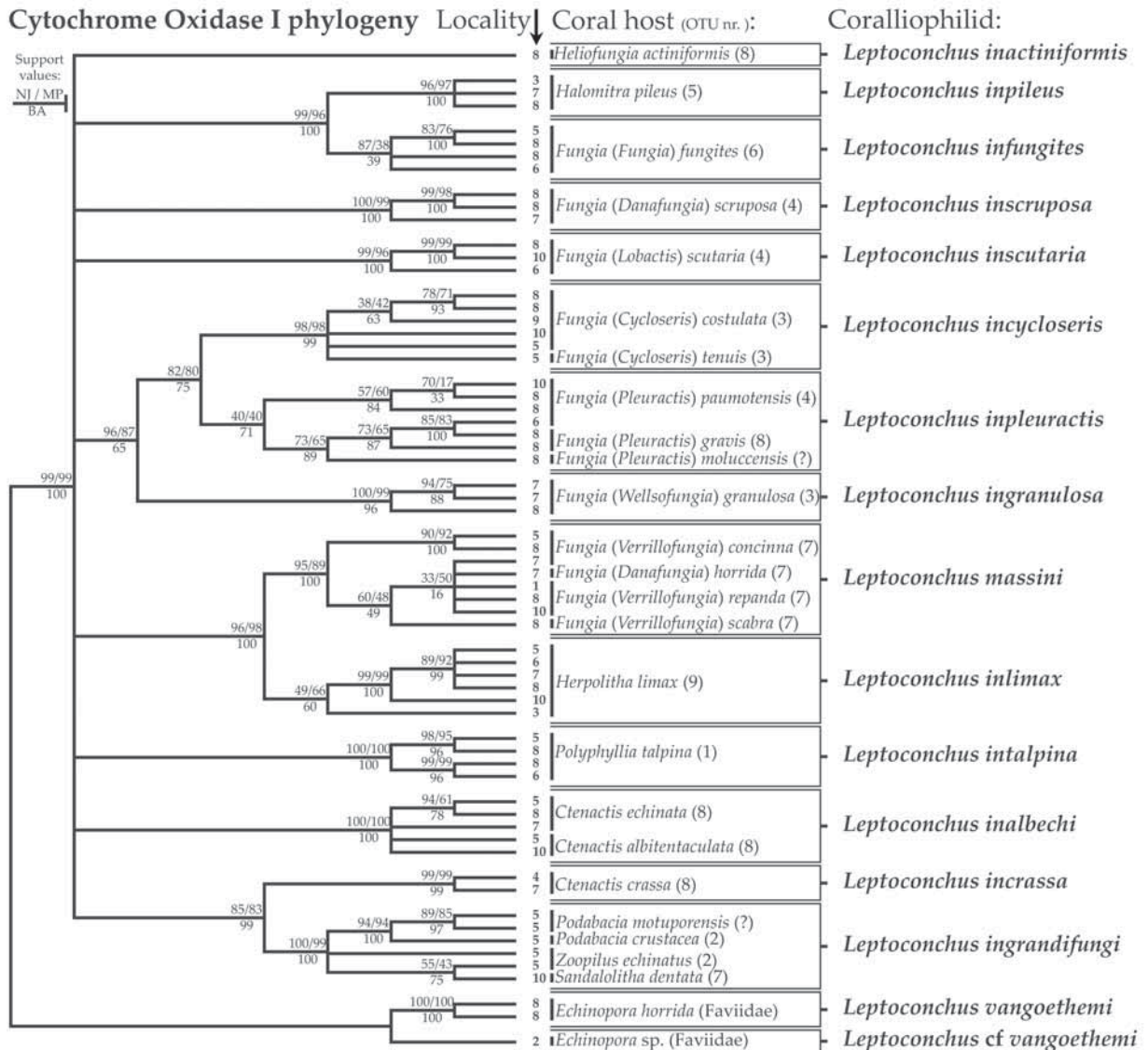


Fig. 2. Cytochrome Oxidase I phylogeny of fungiid associated *Leptoconchus* spp., i.e. the strict consensus tree of the 50% consensus trees with compatible groupings that resulted from [1] the Bayesian inference analysis, [2] the Neighbor Joining bootstrap analysis, [3] the Parsimony bootstrap analysis, 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 Dye™ 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 (Swofford, 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)	TAAACTCAGGGTGACCAAAAAATCA (HCO-2198 in Folmer et al., 1994)	45° C

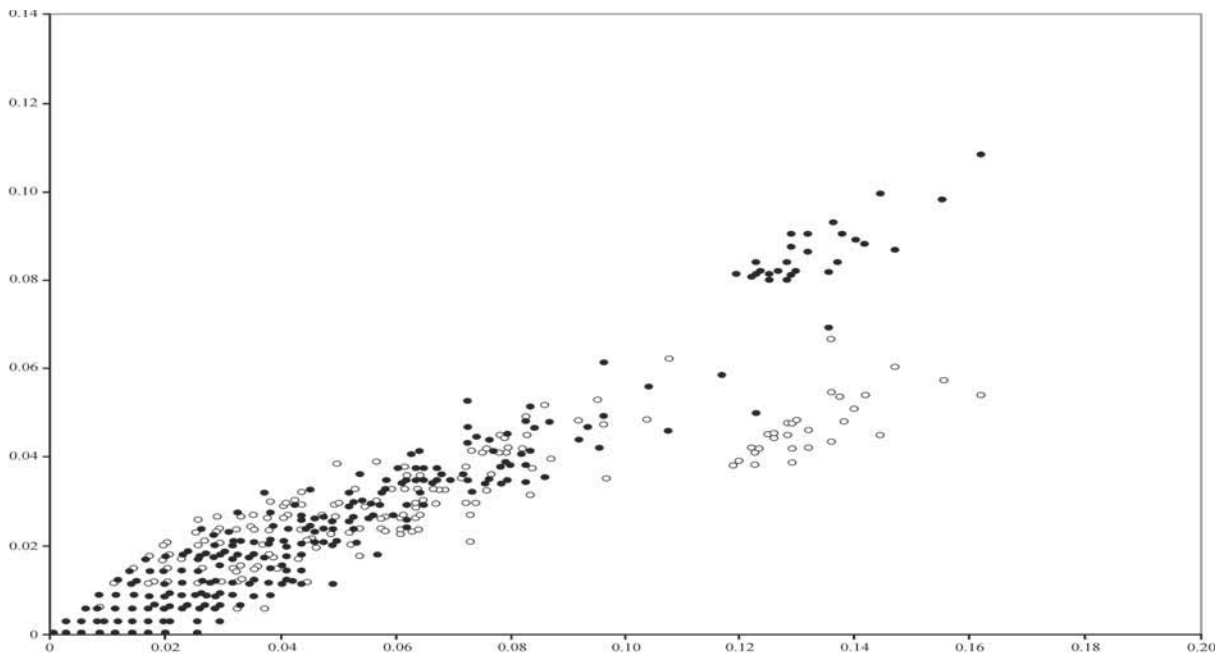


Fig. 3. Transversal (dots) and transitional (circles) rates (Y-axis) in pairwise comparisons between the ITS2 sequences (table 1), plotted against the rate of all substitutions (X-axis). The rates were calculated with Paup 4.0b10 (Swofford, 2002).

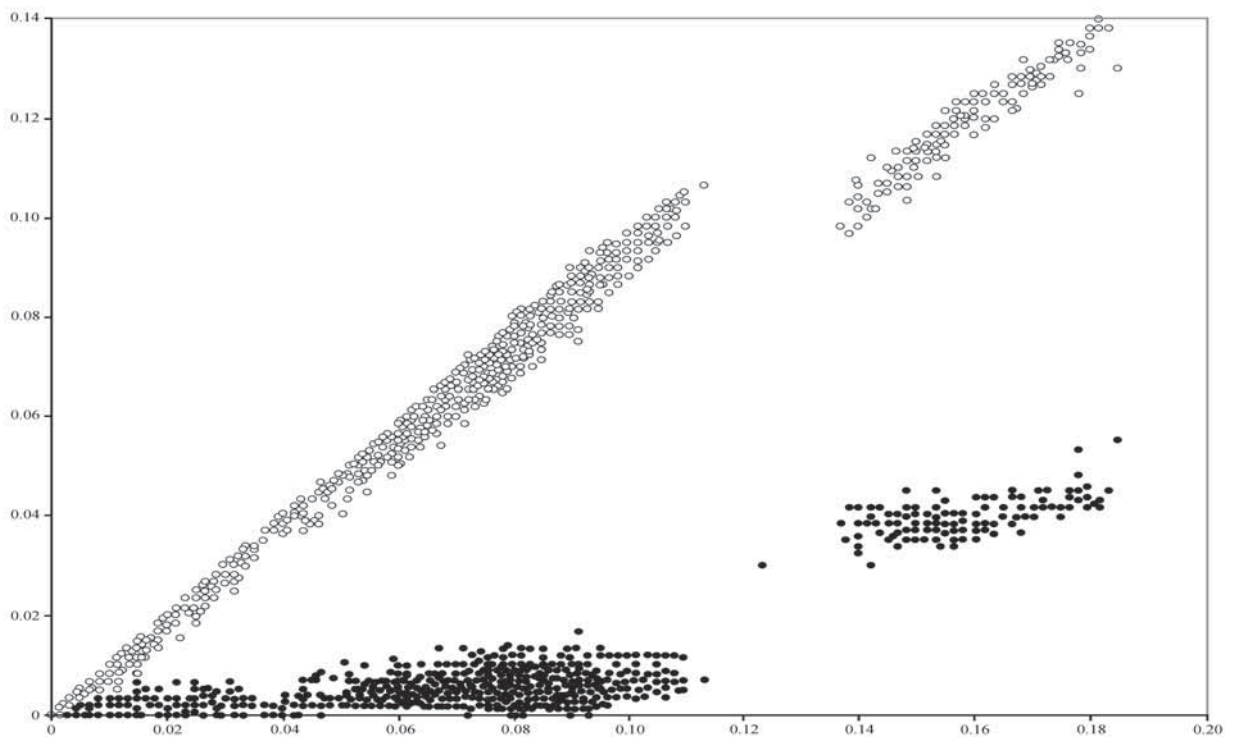


Fig. 4. Transversal (dots) and transitional (circles) rates (Y-axis) in pairwise comparisons between the COI sequences (fig. 2), plotted against the rate of all substitutions (X-axis). The rates were calculated with Paup 4.0b10 (Swofford, 2002).

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 transversal 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 Oliverio 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 transversal 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 in 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 "Méandrine", 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. expositus* 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.

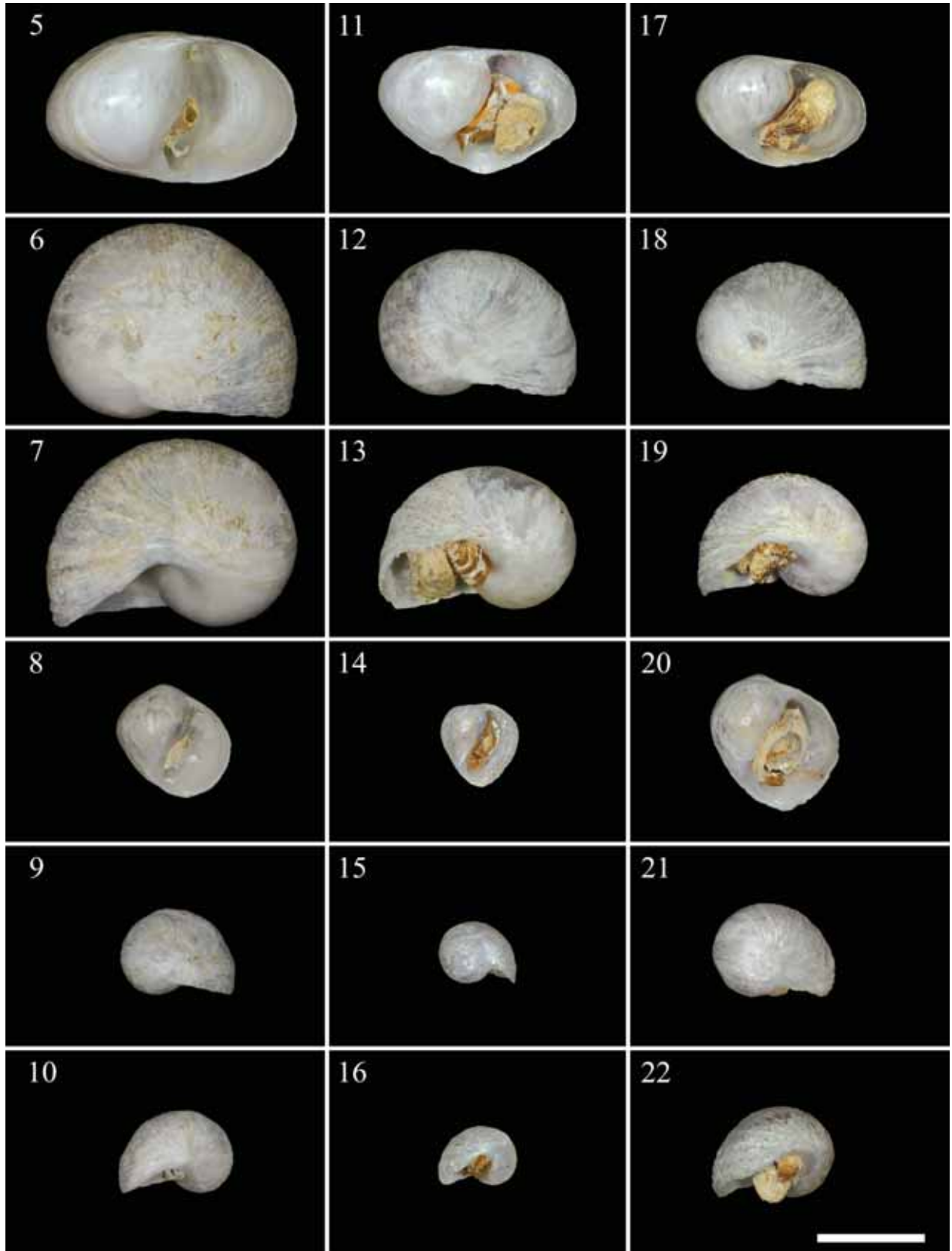
Material (paratypes, unless stated otherwise; all hosted by *Polyphyllia talpina*).

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 Tong sai 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),



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,

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.

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.

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" (RMNH 102590/2sn: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,



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 Ngei, 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 is 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 (RMNH 90020 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).

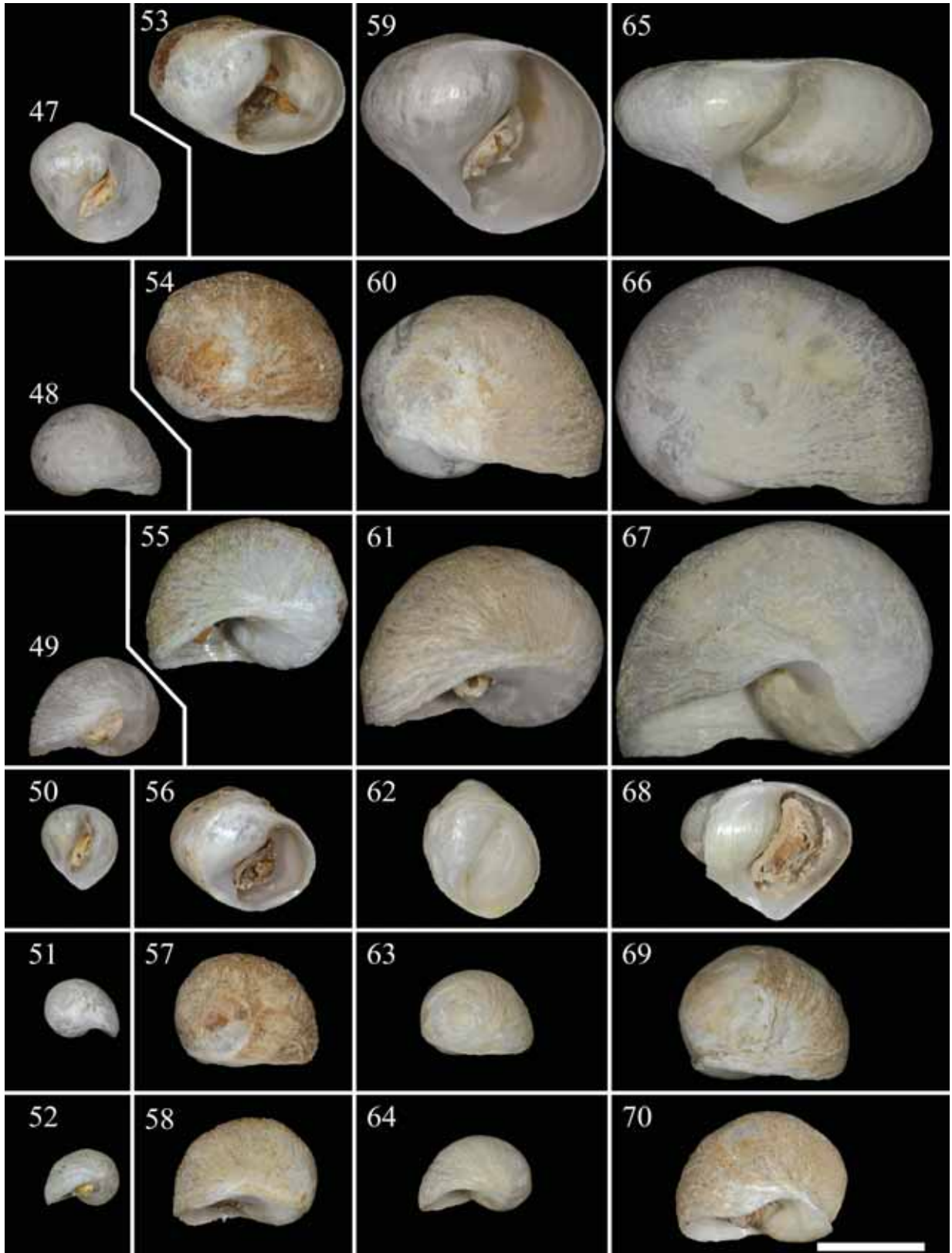
Shell. Holotype (figs 23–25) female: H 19.7 mm, W 23.3 mm. The whitish shell has a roughly wrinkled, calcareous surface; the smooth and glossy columellar callus is broadly expanded, covering most of the surface of the last whorl in frontal view. The lower half of the outer lip forms an obtuse angle with 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.



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 Bena, Loloan Bena, 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.

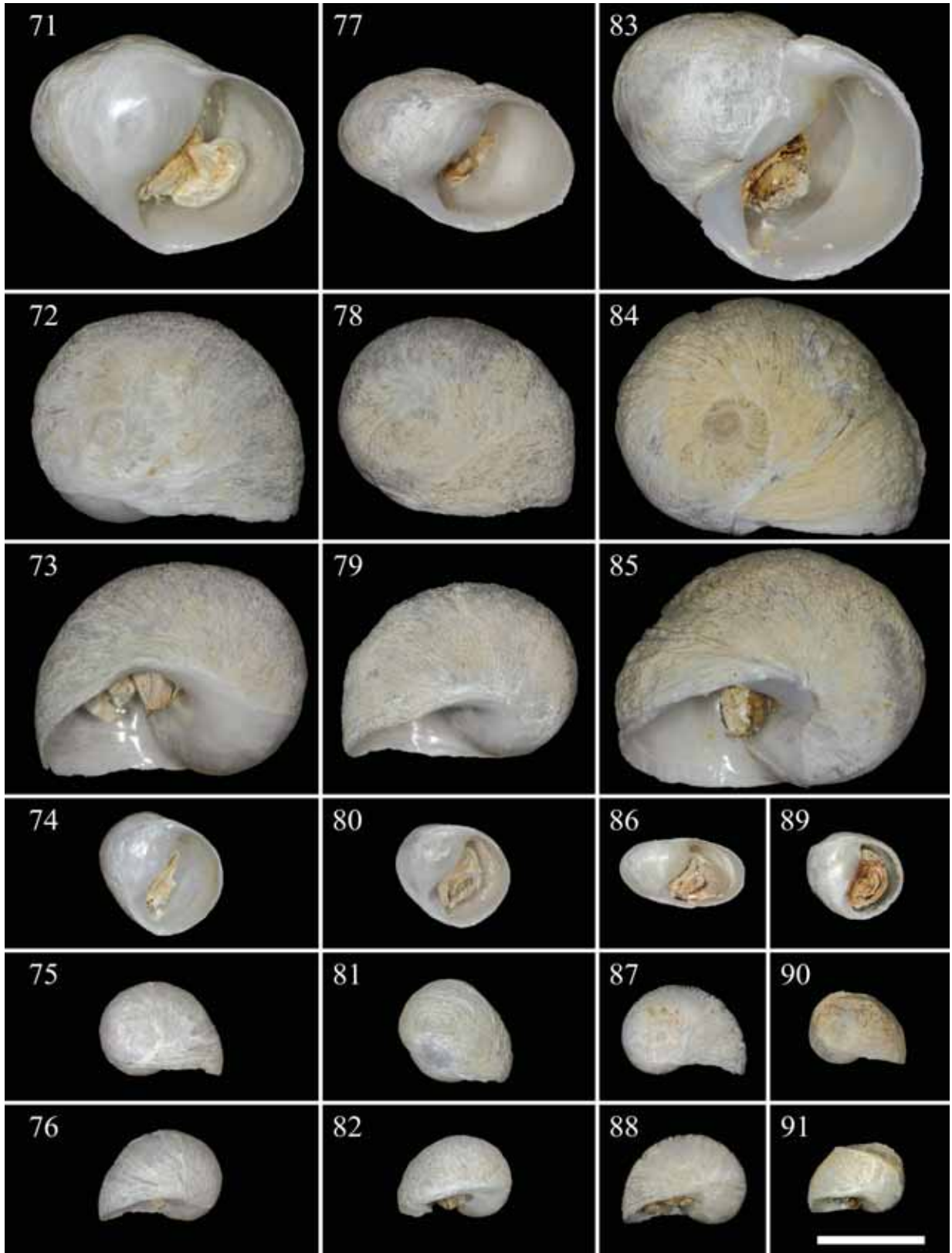
THAILAND. Phiphi islands: type locality, RMNH 95888/holotype, Fc/1sh:f+e [e: RMNH 102652], 102653 Fc/1sn:f+e 1sh:m (with holotype), 95887 Fc/1sn:f+e 1sh:f, 95889 Fc/2sn:m&f+e, 95890 Fc/1sn:

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 Waleabahi 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



Fc/3sn:1m&2f+e). Bali: Padang Bai, Tanjung Sari, 08°31'11"S 115°30'37"E (RMNH 102671 Fr/1sn:f+e, 102672 Fr/2sn:f+e); Tulamben beach, 08°16'36"S 115°35'37"E (RMNH 102673 Fr/2sn:2f+e); Tulamben beach, 08°16'43"S 115°35'49"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 than 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.

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