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Study on *Leptoconchus* species (Gastropoda, Coralliophilidae) infesting Fungiidae (Anthozoa : Scleractinia). 1. Presence of nine Operational Taxonomic Units (OTUs) based on anatomical and ecological characters

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ABSTRACT. This paper deals with the *Leptoconchus* infesting Fungiidae. A dichotomous key based on five characters, and sustained by a multivariate analysis (canonical discriminant analysis) based on 11 characters allows clear separation into nine *Leptoconchus* Operational Taxonomic Units (OTUs). The nine OTUs are provisionally labelled OTU1, OTU2,…, OTU9. A single *Leptoconchus* OTU infests several fungiid species whereas a single fungiid species is never infested by different *Leptoconchus* OTUs. Some *Leptoconchus* OTUs infest closely related coral species, whereas other infest distantly related species.

KEY WORDS : *Leptoconchus*, Fungiidae, taxonomy, coral host specificity.

INTRODUCTION

Most species belonging to the genus *Leptoconchus* Rüppell, 1835 have whitish shells, without characteristic sculptures such as spines, nodules, cords, ribs, costae or columellar folds. Adults secrete deposits that cover their protoconch. Despite the lack of characteristic shell sculptures, Sowerby 2nd (1830), Deshayes (1863), and Sowerby 2nd (in Reeve, 1872) distinguished several species of *Leptoconchus* (see Massin, 1982) based mainly on shell shape (globose, lenticular, turbinate, etc). The lack of shell characteristics to separate different species led Sowerby 3rd (1919) to consider that nearly all *Leptoconchus* species represent juveniles of *Magilus* and that the genus *Magilus* Montfort, 1810 includes only one species, i.e., *Magilus antiquus* Montfort, 1810. This view was not shared by subsequent authors (Gohar & Soliman, 1963; Shikama, 1963; Massin, 1982, 1983, 1990; Kosuge & Suzuki, 1985; Zibrowius & Arnaud, 1995) who have since recognised different species based on shell shape, shell aperture, shell surface (smooth or not), presence/absence of an operculum, and coral host.

Shells of *Leptoconchus* species are said to be highly variable depending on the coral they are infesting. However, several ecological studies have shown that these molluscs are host-specific (Robertson, 1970; Massin, 1989, 1990, 2000) and that the coral host had little (Massin, 1990 : Faviidae) or no influence (Massin, 2000 : Fungiidae) on shell morphology.

According to Bouillon et al. (1983) Fungiidae are infested by a single species of *Leptoconchus*. Zibrowius & Arnaud (1995) mentioned also one species of *Leptoconchus* (*L. striatus* Rüppell, 1835) in Fungiidae from the Seychelles. Several other papers (Hoeksema, 1993a, b; Hoeksema & Achituv, 1993) mention the presence of *Leptoconchus* snails in Fungiidae but without referring to (a) given species.

In contrast, evidence from Massin (2000), including burrow observations (location within the coral, opening on oral/aboral side of Fungiidae), the number of adjoining *Leptoconchus* individuals in a coral (pair/cluster) and the deformation of the coral skeleton, suggests that several species of *Leptoconchus* infest Fungiidae. In a first step we will separate the *Leptoconchus* specimens studied into several Operational Taxonomic Units (OTUs) based on anatomical and ecological characters. Then we will try to see, among the Fungiidae, if a single *Leptoconchus* OTU infests more than one coral species, and if the hypothesis holds that a coral species is never infested by two or more *Leptoconchus* OTUs. These phenomena have already been observed for *Leptoconchus* species associated with Faviidae (Massin, 1983).

MATERIAL AND METHODS

Several discriminant characters were selected. Most of these characters were studied only for females. Males were rarely taken into account because the selected characters show few, if any, variations.

Selected characters :

1. Opening of the *Leptoconchus* burrow on coral surface. *Oral surface : 0; aboral surface : 1.* Depending on the *Leptoconchus* species, the opening of the burrow is located on the oral or aboral surface of the fungiid. This character is highly discriminant and corresponds to a different ecology. *Leptoconchus* species with the opening of the burrow on the oral surface of the coral are unable to

achieve lateral movements, whereas those with the opening on the aboral surface can achieve lateral movements only for a short distance after settlement.

2. Female shell height (H) in mm.
3. H/W : ratio of shell height (H) and shell width (W). This character has been used for females (multivariate analysis) and for males and females (dichotomous key).
4. Operculum. *Operculum absent : 0; operculum present : 1*. If present, the operculum is usually reduced, translucent and difficult to observe. It may be easily overlooked or lost; when very reduced, it is no longer firmly attached to the foot.
5. Ho/H : ratio of operculum height (Ho) and shell height (H). This character has been used for females (multivariate analysis) and for males and females (dichotomous key). Ho often represents less than 20% of H.
6. Foot secretion. A*bsent : 0; weak but present : 1*; *well developed : 2*. The burrow is not lined with calcareous secretions from the molluscs except at the level of the foot where an oval calcareous plate is variously developed, and at the level of the short funnel, which connects the burrow with the outside. However, this character has not been taken into account because it is always present.
7. Deformation of coral skeleton. *No deformation : 0; weak deformation : 1; strong deformation : 2*. Several infested corals show no deformation of the coral skeleton (some *Fungia (Danafungia) scruposa* Klunzinger, 1879 and *F. (Lobactis) scutaria* Lamarck, 1801) on either the oral or aboral surfaces. The presence of *Leptoconchus* snails can also induce a week deformation of the septae and/or the costae (*F. (F.) fungites* (Linnaeus, 1758), *F. (Verrillofungia) concinna* Verrill, 1864), or a strong deformation, sometimes with the presence of a prominent bump (*Halomitra pileus* (Linnaeus, 1758), some *F. (D.) scruposa*).
8. Position of the *Leptoconchus* in the coral. DB/R x 100; Ratio between the distance to the coral mouth (DB) and the radius of the coral (R). For round corals, (monostomatous and polystomatous), DB is the distance from the centre of the coral to the burrow opening and R is the radius of the coral. For elongate (oval) corals (monostomatous with a very long mouth slit or polystomatous), DB is the shortest distance (perpendicular) from the opening of the burrow to the long axis of the oval, and R is the half of the short axis of the oval.
9. Number of *Leptoconchus* individuals in a coral. *Leptoconchus specimens alone : 0; Leptoconchus specimens in pair : 1; Leptoconchus specimens in cluster (three and more) : 2*. Generally, there are at least two *Leptoconchus specimens* together (male and female) to ensure reproduction (there is an internal fecundation). In some species, isolated female specimens have been observed over long time periods. Clusters (up to 15 specimens) have also been observed (*Halomitra pileus* (Linnaeus, 1758), *Heliofungia actiniformis* (Quoy & Gaimard, 1833)). If one coral harbours several pairs (two-three) of *Leptoconchus* individuals it will be noted as "1".
10. Shell top. *Shell top flat : 0 : shell top with a visible spire but reduced : 1; shell top with a prominent spire : 2.* Most of the female *Leptoconchus* individuals living in Fungiidae have a flat shell top, although some (living in thick corals or living in the prominent bumps of a coral) present a more or less well-developed spire.
11. Rostrum. *Rostrum absent : 0; rostrum present : 1*. The rostrum (attenuated extremity of last whorl) is sometimes prominent as for the *Leptoconchus* specimens infesting *Fungia (Danafungia) scruposa* or *Halomitra pileus* corals. However, most of the time it is reduced or absent. The *Leptoconchus* specimens infesting *F. (F.) fungites* corals are highly variable regarding the presence/absence of a rostrum.

Three hundred seventy eight female snails infesting 303 corals, coming from Papua New Guinea and the Maldives, have been observed and included in the matrix. The following fungiid species are included in the present work :

Fungia (Cycloseris) costulata Ortmann, 1889, *F. (C.) fragilis* (Alcock, 1893), *F. (C.) tenuis* Dana, 1846, *F. (Wellsofungia) granulosa* Klunzinger, 1879, *F. (Pleuractis) gravis* Nemenzo, 1955, *F. (P.) paumotensis* Stutchbury, 1833, *F. (Verrillofungia) concinna* Verrill, 1864, *F. (V.) repanda* Dana, 1846, *F. (V.) spinifer* Claereboudt & Hoeksema, 1987, *F. (Lobactis) scutaria* Lamarck, 1801, *Herpolitha limax* (Esper, 1797), *Polyphyllia talpina* (Lamarck, 1801), *P. novaehiberniae* (Lesson, 1831), *Heliofungia actiniformis* (Quoy & Gaimard, 1833), *F. (Danafungia) horrida* Dana, 1846, *F. (D.) fralinae* Nemenzo, 1955, *F. (D.) scruposa* Klunzinger, 1879, *F. (F.) fungites* (Linnaeus, 1758), *Halomitra pileus* (Linnaeus, 1758), *Ctenactis albitentaculata* Hoeksema, 1990, *C. crassa* (Dana, 1846), *C. echinata* (Pallas, 1766), *Sandalolitha dentata* Quelch, 1884, *S. robusta* (Quelch, 1886), *Zoopilus echinatus* Dana, 1846, and *Podabacia crustacea* (Pallas, 1766). Relationships between these corals are based on the cladogram of Hoeksema (1989 : fig. 673).

Leptoconchus snails known only from one to two females (e.g. in *Fungia (Pleuractis) seychellensis* Hoeksema, 1993 from the Seychelles; Hoeksema, 1993b; in *Lithophyllon undulatum* Rehberg, 1892 from Indonesia; Massin 2000) or from traces (burrow openings) in a single coral (*Cantharellus jebbi* Hoeksema, 1993 from Papua New Guinea; Hoeksema, 1993a) were not taken into account in the present work.

The dichotomous key is based on the study of more than 1000 *Leptoconchus* specimens (males and females) coming from 430 corals collected in Papua New Guinea, Indonesia and the Maldives. Corals from the Maldives included basically only *Fungia (Fungia) fungites*. They have been summed with the *F. (F.) fungites* from Papua New Guinea because for characters 3 and 5, statistically, they did not show differences (see table 1).

Characters 1, 3, 4, 5 and 9 have been taken into account for the dichotomous key. The coral host is only used as an added value and not as a discriminant character.

This key was tested using multivariate analysis. Simple linear regression models were used to test that there was no correlation between the 11 variables. Tests were also used to check that the data represent a random sample from a normal distribution using the Shapiro & Wilk (1965) statistic. A canonical discriminant analysis was used to separate the different Operational Taxonomic Units (OTUs), a classification variable, using characters 1

TABLE 1

Measures of characters 3 and 5 for the *Leptoconchus* specimens infesting *Fungia (Fungia) fungites* (LINNAEUS, 1758) from the Maldives and PNG. F.(F.)f. = *F. (F.) fungites*; H : shell height; Ho : operculum height; PNG = Papua New Guinea; W : shell width.

Character	F.(F.)f. Maldives	F.(F.)f. PNG	F.(F.)f. Maldives + PNG
3 (H/W shell ♀)	0.79 ± 0.09 (n = 143)	0.84 ± 0.11 (n= 48)	0.80 ± 0.10 (n= 191)
3 (H/W shell ♂)	1.37 ± 0.20 (n= 131)	1.32 ± 0.16(n= 36)	1.36 ± 0.20 (n= 167)
5 (Ho/H ♀ X 100)	8.58 ± 2.71 (n= 120)	7.64 ± 2.05 (n= 35)	8.40 ± 2.60 (n= 155)

to 11 as quantitative variables (KSHIRSAGAR, 1972). Mahalanobi's distances were computed and species were hierarchically clustered using UPGMA method. All analyses were performed using SAS/STAT® software's capabilities (SAS INSTITUTE INC., 1990).

RESULTS

Taking into account the most discriminant characters observed, nine *Leptoconchus* OTUs can be distinguished. They will be provisionally numbered as OTU1, OTU2,…, OTU9.

The dichotomous key allows separation of the nine OTUs. Some of them are very closely related to each other (e.g. OTU8 and OTU9, and OTU5 and OTU6). The most discriminant characters are 1, 3 and 4. Except for OTU7, *Leptoconchus* individuals are infesting either polystomatous or monostomatous corals but not both (Fig. 1).

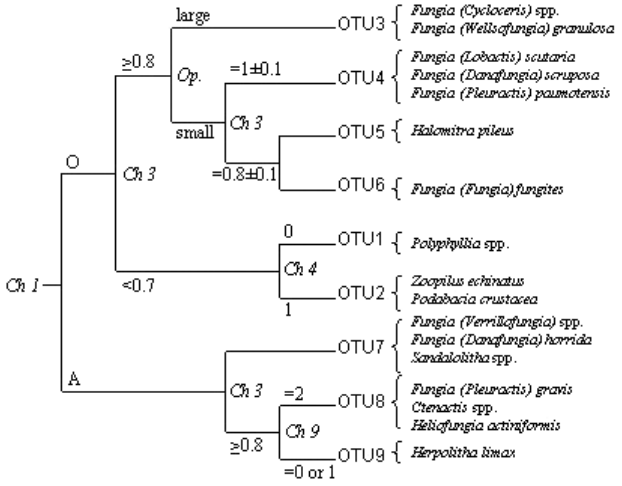

Fig. 1. – Key of the nine *Leptoconchus* species associated with Fungiidae. Ch: character; op: operculum.

Character one allows separation into two groups of *Leptoconchus* : group 1 (OTUs1-6) versus group 2 (OTUs7-9).

In group 1 (with an oral opening of the siphon), OTUs1-6 can be distinguished by characters 3, 4, 5 and 9. Once again, the first discriminant character used is character 3, which separates two groups of *Leptoconchus* : OTU1 and OTU2 versus OTUs3-6.

The lenticular shells with H/W <0.7 (OTU1 and OTU2) are separated by character 4. OTU1 and OTU2 are also separated by their coral hosts (Fig. 1) : OTU1 infests *Polyphyllia talpina* and *P. novaehiberniae* whereas OTU2 infests *Zoopilus echinatus* and *Podabacia crustacea*.

The globose shells with H/W≥0.8 (OTUs3-6) are close to each other but can be separated by characters 3, 4, 5 and 9. OTU3 is clearly separated from OTUs4-6 using characters 4 and 5. Character 3 separates OTU4 from OTU5 and OTU6, whereas character 9 separates OTU5 from OTU6. However, if we are dealing with an early infestation of OTU5, only one or two mollusc specimens will be present in the coral host and the distinction between OTU5 and OTU6 is no longer possible unless the coral host is known (Fig. 1).

In group 2 (with an aboral opening of the siphon), OTUs7-9 can be distinguished by characters 3, 4, 5 and 9. OTU7 is lenticular, whereas OTU8 and OTU9 are globose. OTU8 and OTU9 are very close to each other, but are separated by character 9 and by the coral host (Fig. 1) : OTU8 is found in *Fungia (Pleuractis) gravis*, *Ctenactis albitentaculata, C. crassa, C. echinites* and *Heliofungia actiniformis* whereas OTU9 is exclusive to *Herpolitha limax.*

The key has been established without taking the coral host into account. If coral hosts are listed for each *Leptoconchus* OTU (Fig. 1), it must be noted that a *Leptoconchus* OTU can infest several coral species but that a coral species is never infested by different *Leptoconchus* OTUs. Moreover, a single *Leptoconchus* OTU can infest closely related corals or distantly related corals (see Table 2). For Fungiidae relationships see HOEKSEMA, 1989.

TABLE 2

Operational Taxonomic Units (OTUs) associated with closely related and distantly related corals

	OTU	Coral species
OTU infesting closely related corals	2	*Zoopilus echinatus*, *Podabacia* spp.
	3	*F. (Cycloseris)* spp., *F. (Wellsofungia) granulosa*
	5-6	*Halomitra pileus, F. (Fungia) fungites*
OTU infesting distantly related corals	4	*F. (Danafungia) scruposa, F. (Lobactis) scutaria, F. (Pleuractis) paumotensis*
	7	*F. (Verrillofungia)* spp., *F. (Danafungia) horrida, Sandalolitha* spp.
	8	*F. (Pleuractis) gravis*, *Ctenactis* spp., *Heliofungia actiniformis*

Three canonical discriminant analyses were performed. Using all the eleven characters, the nine OTUs are significantly separated into two clusters ($p<0.01$) : group 1 (OTUs1-6) and group 2 (OTUs7-9). The discrimination between these clusters is based on the opening of the burrow on the fungiid surface (character 1). All characters except 1, 4 and 5 were then used to perform further canonical discriminant analyses on each group. Characters 4 and 5 were removed due to the few data available (Table 3). For group 1, 5 new clusters were significantly discriminated ($p<0.01$) on the basis of characters 3 and 7 (Fig. 2). The character 3 aimed to significantly separate 3 clusters in group 2 (Fig. 3). Fig. 4 presents the UPGMA tree inferred from Mahalanobi's distances computed at the three levels of the analysis. This tree presents a structure similar to the dichotomous key (Fig. 1). Differences were observed in the relations between the OTUs4-6 and for the positions of OTU1 and OTU2.

TABLE 3

Quantity of data available for the multivariate analysis.
OTU : Operational Taxonomic Unit

OTU	N (all data)	N (without Ch4 & Ch5)
1	1	10
2	1	1
3	6	20
4	4	43
5	5	16
6	30	73
7	53	60
8	30	39
9	11	11
Total	140	273

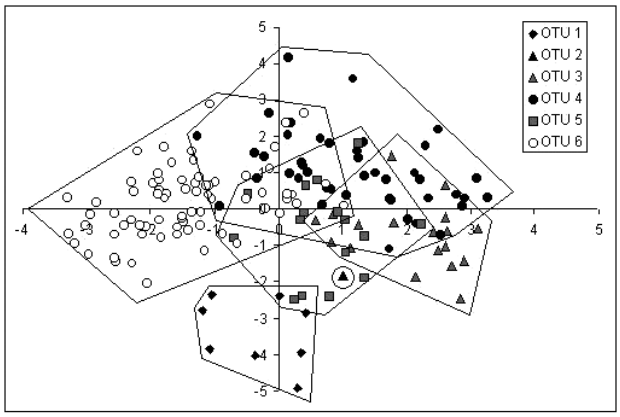

Fig. 2. – Canonical discriminant analysis of the OTUs 1 to 6 using characters 2 to 4 and 7 to 11. (can1=-0.25*ch2+3.60*ch3-0.89*ch6+1.53*ch7-0.02*ch8+0.73*ch9+0.35*ch10-0.32*ch11; can2=0.23*ch2+6.21*ch3+0.43*ch6-0.43*ch7-0.01*ch8-0.18*ch9-0.39*ch10-0.09*ch11)

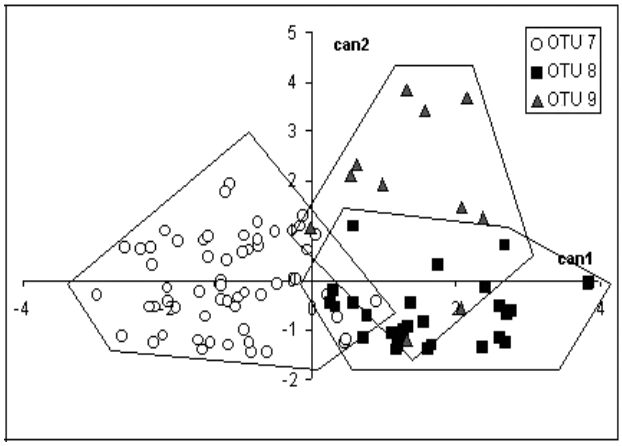

Fig. 3. – Canonical discriminant analysis of the OTUs 7 to 9 using characters 2 to 4 and 7 to 11. (can1=0.29*ch2+5.74*ch3-0.43*ch6-0.44*ch7-0.02*ch8+0.58*ch9-0.24*ch10-0.001*ch11; can2=-0.02*ch2+3.20*ch3+0.52*ch6+1.16*ch7-0.002*ch8-0.74*ch9*0.14*ch10+1.56*ch11)

DISCUSSION

Character 1 is the most discriminant, and allows separation of OTUs1-6 (group 1) from OTUs7-9 (group 2), no matter which analysis is used.

Some small discrepancies appear in group 1 between the key and the UPGMA tree. In the key OTU1 and OTU2 are closely related but clearly separated from each other by the presence/absence of an operculum. In the UPGMA tree OTU2 appears as an outgroup versus OTU1 and OTUs3-6. This is most probably due to the fact that very few data are available for OTU2 and particularly for character 4 (presence/absence of an operculum). Consequently, character 4 has not been taken into account in the UPGMA tree.

In the key, OTU5 and OTU6 are closely related and only the presence of a cluster of molluscs versus presence of a pair of molluscs allows their separation. In the UPGMA tree, using character 7 (deformation of coral skeleton) OTU5 and OTU6 are clearly separated, OTU5 being even closer to OTU4 than to OTU6.

In group 2, canonical discriminant analysis and the UPGMA tree provide the key ordination, separating OTU8 and OTU9.

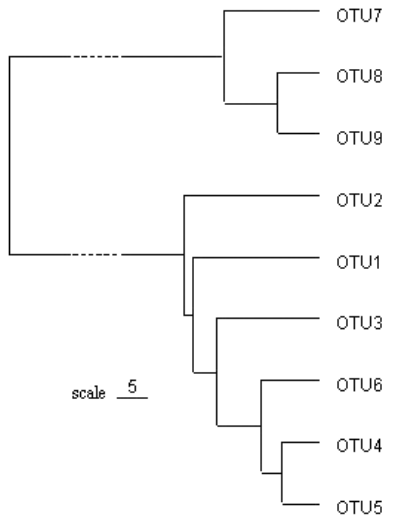

Fig. 4. – UPGMA tree inferred from Mahalanobi's distances computed at the three levels of the analysis.

The dichotomous key has been established using a maximum of characters linked to the molluscan anatomy (characters 3, 4, and 5). The two other anatomical characters (10 and 11) are highly variable and not very discriminant (see canonical analysis of group 1). The emphasis on anatomical characters is dictated by the fact that ecological characters are seldom available from museum collections. For the usefulness of the key it is better to take into account a maximum of anatomical characters. Nevertheless, many ecological data are very discriminant (mainly characters 1, 7, and 9) and allow separation of OTUs in the key as well as in the canonical discriminant analysis and the UPGMA tree.

The nine *Leptoconchus* OTUs selected here present enough discriminant characters to be easily separated from each other. Their taxonomic status will be discussed in a forthcoming paper.

The study of the *Leptoconchus* specimens infesting Fungiidae has shown that a single *Leptoconchus* OTU can infest several corals, whereas a single coral is never infested by several *Leptoconchus* OTUs. This is very similar to the observations done on *Leptoconchus* specimens infesting Faviidae (Massin 1983). Other molluscs infesting living colonies of Scleractinia as *Lithophaga* species (Kleeman, 1980; Morton, 1983) are less selective in their coral/host relationships. For these bivalves, several species can be present in a single coral host. Different *Epitonium* species associated with Fungiidae are also able to infest a single coral host : e.g. *Epitonium costulatum* (Kiener, 1838), *E. ingridae* Gittenberger & Goud, 2000 and *E. twilae* Gittenberger & Goud, 2000 are associated with *Herpolitha limax* (see Gittenberger et al., 2000).

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REFERENCES

Bouillon, J., C. Massin & J. Van Goethem (1983). *Fungiacava eilatensis* Soot-Ryen (Bivalvia, Mytilidae) et *Leptoconchus striatus* Rüppell (Gastropoda, Coralliophilidae) mollusques perforant des *Fungia* (Anthozoa, Fungiidae) récoltés en Papouasie Nouvelle-Guinée. *Bull. Séanc. Acad. r. Sci. Outre-mer, Cl. Sci. nat. méd.,* 4 : 549-570.

Deshayes, G.P. (1863). Catalogue des Mollusques de l'île de la Réunion. In : Maillard (ed.), *Notes sur l'île de la Réunion,* Paris : 1-144.

Gittenberger A., J. Goud & E. Gittenberger (2000). *Epitonium* (Gastropoda : Epitoniidae) associated with mushroom corals (Scleractinia : Fungiidae) from Sulawesi, Indonesia, with the description of four new species. *The Nautilus*, 114(1) : 1-13

Gohar, H.A.F. & G.N. Soliman (1963). On the biology of three coralliophilids boring in living corals. *Publ. mar. biol. Stat. Ghardaqa,* 12 : 99-126.

Hoeksema, B.W. (1989). Taxonomy, phylogeny and biogeography of mushroom corals (Scleractinia : Fungiidae). *Zool. Verhandl.*, 254 : 1-295.

Hoeksema, B.W. (1993a). Mushroom corals (Scleractinia : Fungiidae) of Madang Lagoon, northern Papua New Guinea : an annotated check-list with the Description of *Cantharellus jebbi* spec. nov. *Zool. Mededel*., 67 : 1-19.

Hoeksema, B.W. (1993b). Historical biogeography of *Fungia (Pleuractis)* spp. (Sceractinia : Fungiidae), including a new species from the Seychelles. *Zool. Mededel*., 67 : 639-654.

Hoeksema, B.W. & Y. Achituv (1993). First Indonesian record of *Fungiacava eilatensis* Goreau et al., 1968 (Bivalvia : Mytilidae), endosymbiont of *Fungia* spp. (Scleractinia : Fungiidae). *Basteria*, 57 :131-138.

Kleeman, K.H. (1980). Boring bivalves and their host corals from the Great Barrier Reef. *J. Moll. Stud*,. 46(1) : 13-54.

Kosuge, S. & M. Suzuki (1985). Illustrated catalogue of *Latiaxis* and its related groups. Family Coralliophilidae. *Inst. Malac. Tokyo, Spec. Publ.*, 1 : 1-83.

Kshirsagar, A.M. (1972). *Multivariate Analysis.* Marcel Dekker, Inc., New York.

Massin, C. (1982). Contribution to the knowledge of two boring gastropods with an annotated list of the genera *Magilus* Montfort, 1810 and *Leptoconchus* Rüppell, 1835. *Bull.Inst. r. Sci. nat. Belgique, Biol.*, 53(17) : 1-28.

Massin, C. (1983). Note on the genus *Leptoconchus* Rüppell, 1835 (Mollusca, Gastropoda, Coralliophilidae) with the description of two new species, *Leptoconchus vangoethemi* sp. n. and *Leptoconchus cyphastreae* sp. n. from Papua New Guinea. *Bull. Inst. r. Sci. nat. Belgique, Biol.*, 55(1) : 1-16.

Massin, C. (1989). Boring Coralliophilidae (Mollusca, Gastropoda) : coral host relationship. *Proc. 6th Inter. Coral Reef Symp.,* J.C. Choat et al. (eds), 6th Int. Coral Reef Symp. Executive Committee, 3 : 177-184.

Massin, C. (1990). Biologie et écologie de *Leptoconchus peronii* (Lamarck, 1818) (Gastropoda, Coralliophilidae) recolté en Papouasie Nouvelle-Guinée avec une redescription de l'espèce. *Bull. Inst. r. Sci. nat. Belgique, Biol.*, 60 : 23-33.

Massin, C. (2000). Ecology of the *Leptoconchus* spp. (Gastropoda, Coralliophilidae) infesting Fungiidae (Anthozoa, Madreporaria). *Bull. Inst. r. Sci. nat. Belgique, Biol.,* 70 : 235-252.

Morton, B. (1983). Coral-Associated Bivalves of the Indo-Pacific. In *The Mollusca*, K.M. Wilbur (ed.), vol. 6 Ecology : 139-224, Academic Press, New York.

Reeve, L. (1872). Monograph of the genus *Magilus*. In *Conchologia iconae*, vol. 10, London.

Robertson, R. (1970). Review of the predator and parasites of stony corals, with special reference to symbiotic prosobranch Gastropods. *Pacific Sci.*, 24(1) : 43-54.

SAS Institute Inc. (1990). S*AS/STAT User's guide, Version 6, Fourth edition, vol 1*. SAS Institute Inc., North Carolina, United States.

Shapiro, S.S. & M.B. Wilk (1965). An analysis of variance test for normality (complete samples). *Biometrika,* 52 : 591-611.

Shikama, T. (1963). On Some Noteworthy Marine Gastropoda from Southwestern Japan. *Sci. Rep. Yokoyama natn. Univ., sect. 2, biol. geol. Sci.*, 10 : 61-66.

Sowerby, G.B. (2nd of the name). (1830). *Genera of Recent and Fossil Shells*. London.

Sowerby, G.B. (3rd of the name). (1919). Notes on *Magilus* and its allies, substituting the generic name *Magilopsis* for *Leptoconchus lamarckii* Deshayes. *Proc. malac. Soc. London*, 13 : 75-77.

Zibrowius, H. & M. Arnaud. (1995). New records of molluscs (*Leptoconchus*, *Lithophaga*, *Fungiacava*) that bore Indo-Pacific reef corals and their interactions with their hosts. *Bull. Mus. natl. Hist. nat.*, Paris 4e sér., 16 (section A) : 231-244.

ANNEX

	Key for the *Leptoconchus* OTUs (Operational Taxonomic Units) infesting Fungiidae.	
	- *Leptoconchus* with the burrow opening on the oral side of the coral	1
	- *Leptoconchus* with the burrow opening on the aboral side of the coral	2
1 -	H/W females <0.7	3
-	H/W females ≥0.8	4
3 -	Operculum absent, often in group >2	OTU1
-	Operculum present, alone or in pair	OTU2
4 -	Operculum present, >10% of shell height for females and >14% for males	OTU3
-	Operculum present or absent, if present <10% of shell height (males & females)	5
5 -	H/W females 1.00 ± 0.10	OTU4
-	H/W females 0.80 ± 0.10	6
6 -	H/W males 1.13 ± 0.18, 50% of the examined specimens living in groups >3	OTU5
-	H/W males 1.35 ± 0.21, never living in group >3	OTU6
2 -	H/W females 0.70 ± 0.10, H/W males 1.00 ± 0.10, operculum always present, >15% of shell height	OTU7
-	H/W females ≥0.80 ± 0.10, H/W males ≥1.10 ± 0.10, operculum present or absent, if present (less than 20% of the specimens examined) <12% of shell height	7
7 -	H/W females 0.80 ± 0.10, H/W males 1.10 ± 0.10, very often in groups >3	OTU8
-	H/W females 0.90 ± 0.10, H/W males 1.22 ± 0.10, nearly always alone or in pair (90% of the specimens examined)	OTU9

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