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Phylogenetic position and taxonomy of *Cycloseris explanulata* and *C. wellsi* (Scleractinia: Fungiidae): lost mushroom corals find their way home

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Abstract

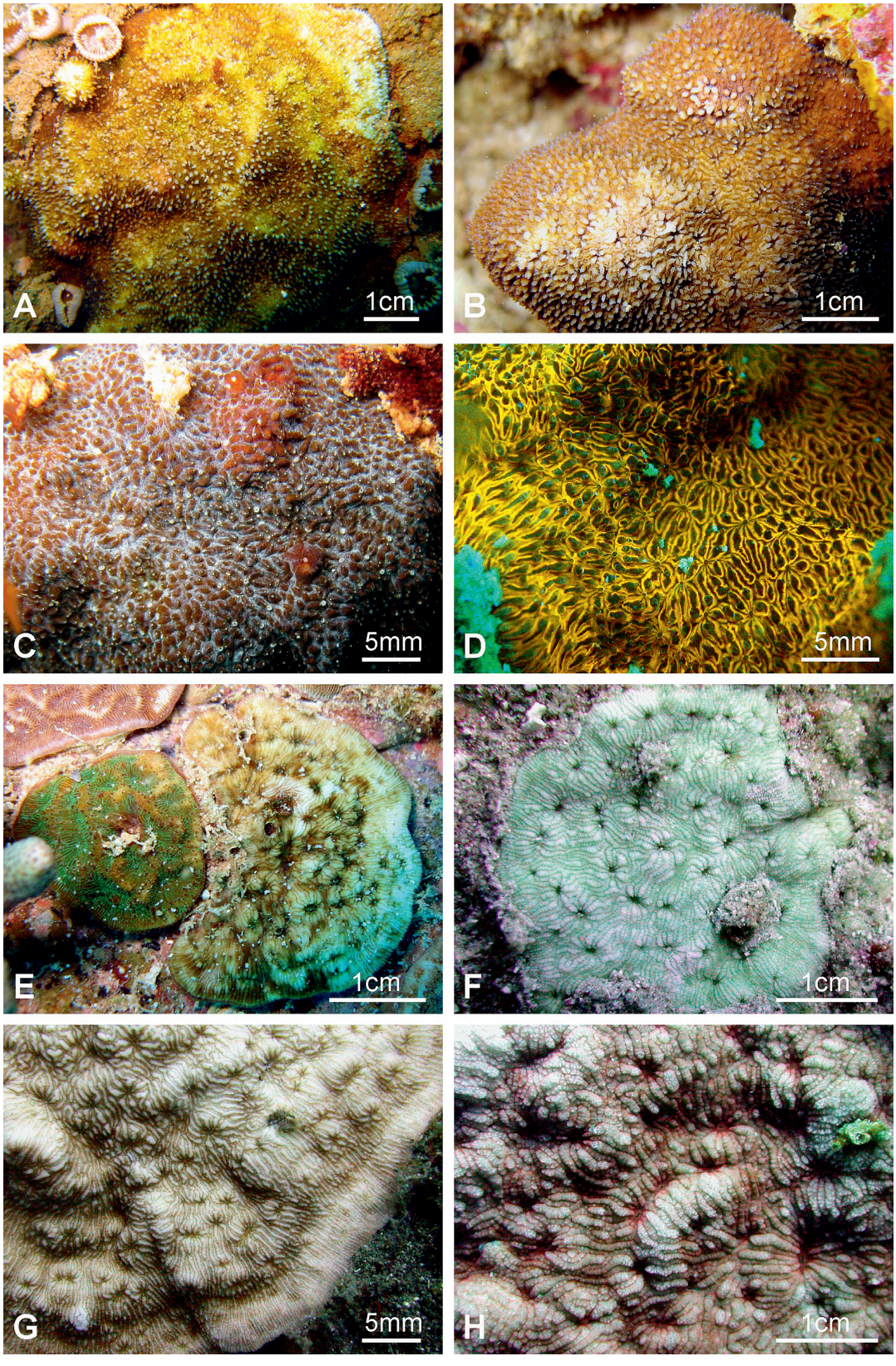
The scleractinian species *Psammocora explanulata* and *Coscinaraea wellsi* were originally classified in the family Siderastreidae, but in a recent morpho-molecular study it appeared that they are more closely related to each other and to the Fungiidae than to any siderastreid taxon. A subsequent morpho-molecular study of the Fungiidae provided new insights regarding the phylogenetic relationships within that family. In the present study existing molecular data sets of both families were analyzed jointly with those of new specimens and sequences of *P. explanulata* and *C. wellsi*. The results indicate that both species actually belong to the *Cycloseris* clade within the family Fungiidae. A reappraisal of their morphologic characters based on museum specimens and recently collected material substantiate the molecular results. Consequently, they are renamed *Cycloseris explanulata* and *C. wellsi*. They are polystomatous and encrusting like *C. mokai*, another species recently added to the genus, whereas all *Cycloseris* species were initially thought to be monostomatous and free-living. In the light of the new findings, the taxonomy and distribution data of *C. explanulata* and *C. wellsi* have been updated and revised. Finally, the ecological implications of the evolutionary history of the three encrusting polystomatous *Cycloseris* species and their free-living monostomatous congeners are discussed.

Contents

Introduction

The taxonomy of scleractinian corals is undergoing a revolution. Molecular analyses have indicated that this anthozoan order is divided over two major clades (Robust and Complex) and a basal clade consisting of various para- and polyphyletic genera and families (Romano and Palumbi, 1996; Romano and Cairns, 2000; Chen *et al*., 2002; Fukami *et al*., 2004, 2008; Le Goff-Vitry *et al*., 2004; Kerr, 2005; Nunes *et al*., 2008; Kitahara *et al*., 2010; Huang *et al*., 2011; Stolarski *et al*., 2011). Molecular data have corrected or supported old taxonomic views based on morphological characters and have lead to new insights, some of which are supported by re-examined morphological characters regarding skeletal microstructures (Fukami *et al*., 2000; Stolarski and Roniewicz, 2001; Benzoni *et al*., 2007, 2010, 2011; Stefani *et al*., 2007, 2008, 2011; Wallace *et al*., 2007; Huang *et al*., 2009; Budd *et al*., 2010).

In the monophyletic Indo-Pacific coral family Fungiidae Dana, 1846, 40 out of 50 species are free-living and 10 are attached (Hoeksema, 1989, 2009,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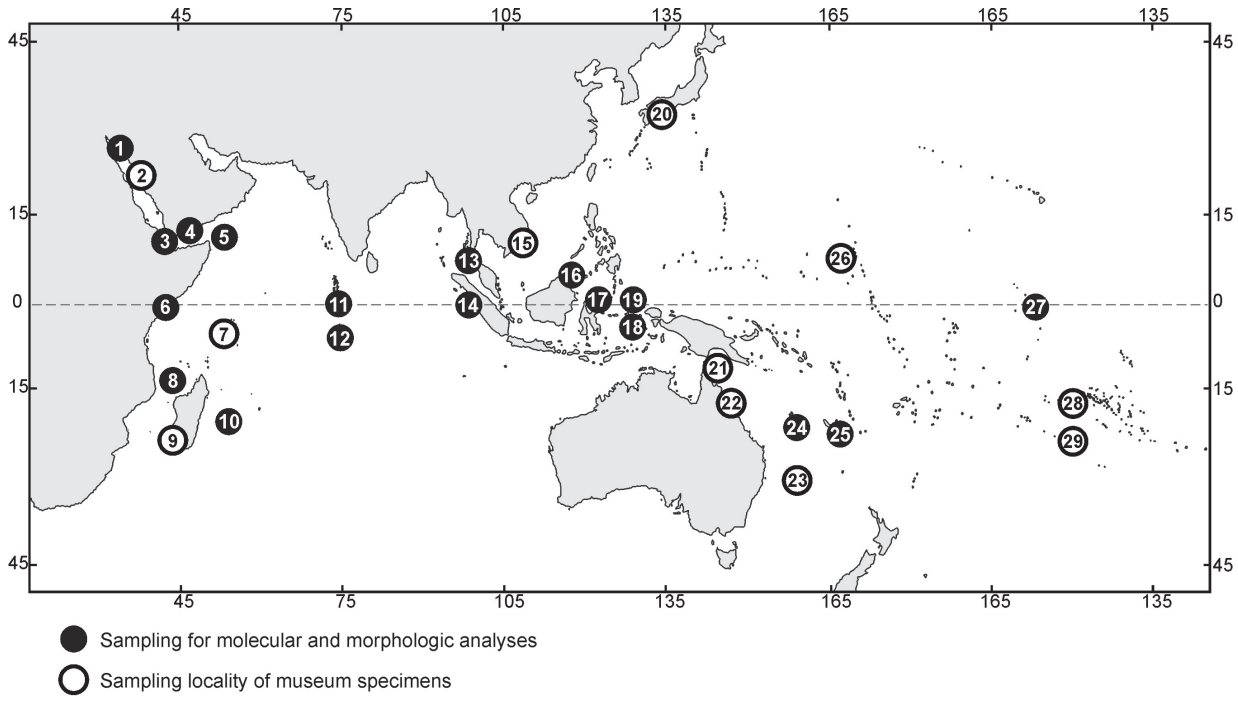

Fig. 2. Map of the sampling localities (black dots) and for examined museum specimens (white dots). Numbers within each circle correspond to the following localities: 1 = Gulf of Aqaba; 2 = Saudi Arabia, Red Sea; 3 = Djibouti; 4 = Yemen (Gulf of Aden); 5 = Socotra Island; 6 = Kenya; 7 = Seychelles; 8 = Mayotte Island; 9 = Madagascar; 10 = La Réunion; 11 = Maldives; 12 = Chagos, BIOT; 13 = Thailand (Andaman Sea); 14 = Sumatra, Indonesia; 15 = Vietnam; 16 = Sabah, Malaysia; 17 = Manado, Indonesia; 18 = Ambon, Indonesia; 19 = Ternate, Indonesia; 20 = Shikoku, Japan; 21 = Murray Islands, Australia; 22 = from Palm Island to Lizard Island, Australia; 23 = Lord Howe Island, Australia; 24 = Middleton Reef, Australia; 25 = Chesterfield Islands, New Caledonia; 26 = Marshall Islands; 27 = Line Islands, Kiribas; 28 = Society Islands, French Polynesia; 29 = Austral Islands, French Polynesia.

2012b; Gittenberger *et al*., 2011). Many species have large coralla that occur abundantly in mixed assemblages on shallow reefs (Claereboudt, 1988; Hoeksema and Moka, 1989; Hoeksema, 1991a, 2012a; Goffredo and Chadwick-Furman, 2000; Elahi, 2008; Hoeksema and Koh, 2009; Hoeksema and Matthews, 2011). Some species may form monospecific aggregations as a result of asexual reproduction by budding or fragmentation (Nishihira and Poung-In, 1989; Yamashiro and Nishihira, 1998; Hoeksema, 2004; Hoeksema and Gittenberger, 2010; Hoeksema and Waheed, 2011; Hoeksema and Yeemin, 2011). Owing to their remarkable life histories, ecology, and striking appearances, the Fungiidae have received much attention with regard to their evolutionary history, which resulted in phylogeny reconstructions based on morphological characters and life history traits (Wells, 1966; Cairns, 1984; Hoeksema 1989, 1991b, 1993; Hoeksema *et al*., 2012).

Recent molecular studies gave new insights with regard to the phylogeny of the Fungiidae. The encrusting polystomatous species *Lithophyllon mokai* Hoeksema, 1989 appears to be most closely related to *Cycloseris*, a genus otherwise consisting of free-living monostomatous species (Gittenberger *et al*., 2011), whereas based on morphology it was considered a sister taxon of the attached foliaceaous species *L. undulatum* Rehberg, 1892 (Hoeksema, 1989, 1991b, 2009).

◀ *Fig. 1. Psammocora explanulata* (A-D) and *Coscinaraea wellsi* (E-H) *in situ*. A) HS 1769, Cap Bourail, New Caledonia; B) HS 1397, Côte Oubliée, New Caledonia; C) Al Mukallah, Yemen; D) Mayotte Island; E) *Coscinaraea monile* (left) and *C. wellsi* (right), Burum, Yemen; F) UNIMIB S061 Ras Nosrani, South Sinai, Egypt; G) UNIMIB I 080 Mapia House Reef, Manado, Sulawesi, Indonesia; H) UNIMIB I 108 Negheri, Manado, Sulawesi, Indonesia.

Table 1. List of specimens from which sequences and morphological data were obtained. For each specimen the code, identification, sampling locality, and Genbank accession code for sequences generated in this study are provided. * For sampling details, see lists of examined material.

code	*Genus*	*species*	Locality*	COI	rDNA
UNIMIB BA 116	*Psammocora*	*explanulata*	Balhaf, Yemen	HE600143	HE599790
UNIMIB CHA 520	*Psammocora*	*explanulata*	Chagos		HE599791
UNIMIB CHA 524	*Psammocora*	*explanulata*	Chagos	HE600145	HE599792
UNIMIB CHA 540	*Psammocora*	*explanulata*	Chagos		HE599793
UNIMIB I 080	*Coscinaraea*	*wellsi*	Manado, Indonesia	HE600144	
UNIMIB KE 403	*Coscinaraea*	*wellsi*	Kenya		HE599794
UNIMIB KE 404	*Coscinaraea*	*wellsi*	Kenya	HE600149	HE599795
UNIMIB KE 405	*Coscinaraea*	*wellsi*	Kenya		HE599796
UNIMIB MA 465	*Coscinaraea*	*wellsi*	Mayotte Island	HE600150	HE599797
UNIMIB MU 102	*Coscinaraea*	*wellsi*	Al Mukallah,Yemen	HE600151	HE599798
IRD HS 1397	*Psammocora*	*explanulata*	New Caledonia	HE600146	HE599799
UNIMIB RE 513	*Psammocora*	*explanulata*	La Réunion	HE600147	HE599800
UNIMIB S 061	*Coscinaraea*	*wellsi*	Sharm el Sheikh, Egypt		HE599801
UNIMIB S 062	*Coscinaraea*	*wellsi*	Sharm el Sheikh, Egypt	HE600152	HE599802
UNIMIB SO 051	*Coscinaraea*	*wellsi*	Socotra Island, Yemen	HE600153	HE599803
UNIMIB SO 138	*Psammocora*	*explanulata*	Socotra Island, Yemen	HE600148	
COCSTER25	*Coscinaraea*	*wellsi*	Ternate, Indonesia	HE600154	

Furthermore, two encrusting polystomatous species classified with the Siderastreidae Vaughan and Wells, 1943, *Psammocora explanulata* Van der Horst, 1922 (Fig. 1A-D), and *Coscinaraea wellsi* Veron and Pichon, 1980 (Fig. 1E-H), appear to be more closely related to one another and to some Fungiidae than to the original congeners. These hypotheses are supported by morphological investigations, which reveal that these two species display typical fungiid skeletal structures which had not been previously noted in these taxa (Benzoni *et al*., 2007). However, so far these species have not yet been formally revised and their closest relatives among the Fungiidae have remained unknown.

Molecular and morphological hypotheses are often in conflict suggesting that the taxonomic positions of the taxa need to be revised. However, the taxonomic consequences of the genetic results are often not formalized from a taxonomic point of view. The molecular phylogeny of *Psammocora explanulata* and *Coscinaraea wellsi* has revealed a taxonomic misplacement, which constitutes a historical constraint as long as they remain in the genus or family to which they were originally assigned based on a misinterpreted morphology. Hence, in lack of a proper study of their type specimens and other collected material, and of supporting field observations, their taxonomic revision stagnates. Therefore, in the present study, the phylogenetic positions of these two species within the Fungiidae are re-examined based on newly obtained mitochondrial COI and nuclear rDNA sequences from material collected throughout the Indo-Pacific and the joint datasets from Benzoni *et al*. (2007) and Gittenberger *et al*. (2011). Furthermore, the molecular hypothesis was tested by re-examining the morphological characters of the species in question. Hence, on the basis of the genetic results and of morphological studies, their taxonomic positions are revised. Finally, the study of historical museum material and illustrated specimens allows a reappraisal of their morphologic variability and geographic distribution, which has become increasingly relevant since coral species may have disappeared from areas where they previously occurred (Hoeksema and Koh, 2009; van der Meij *et al*., 2010; Hoeksema *et al*., 2011; van der Meij and Visser, 2011).

Material and methods

Sampling

Sampling took place at various localities in the Indo-Pacific (Fig. 2). Specimens were collected for molecular analyses in Egypt (Gulf of Aqaba, Red Sea), Yemen (Gulf of Aden), Socotra Island, Kenya, Mayotte Island,

La Réunion, Chagos (Indian Ocean), Indonesia, and New Caledonia (Pacific Ocean). Digital images of living corals in the field were taken with a Canon G9 in an Ikelite underwater housing. Coral specimens were collected, labelled, and fragments of ca 1 cm^2 were subsampled and preserved in absolute ethanol for molecular analysis. The remaining corallum was placed in sodium hypochlorite for 48 hours to remove all soft tissue, rinsed in freshwater and dried for microscopic examination. Images of cleaned skeletons were taken with a Canon G9 digital camera.

Museum collections and other examined specimens

Type material and specimens examined for this study are deposited in the following institutes.

Abbreviations:

AIMS	Australian Institute of Marine Science, Townsville, Australia
BMNH	The Natural History Museum (formerly British Museum of Natural History), London, UK
EPA	Environment Protection Authority, Sana'a and Socotra, Yemen
IRD	Institut de Recherche pour le Développement, Nouméa, New Caledonia
MNHN	Museum National d'Histoire Naturelle, Paris, France
MTQ	Museum of Tropical Queensland, Townsville, Australia
RMNH	Netherlands Centre for Biodiversity Naturalis (former Rijksmuseum van Natuurlijke Historie collection), Leiden, the Netherlands
UNIMIB	Università degli Studi di Milano-Bicocca, Milan, Italy
USNM	United States National Museum of Natural History, Washington, USA
ZMA	Netherlands Centre for Biodiversity Naturalis (former Zoölogisch Museum Amsterdam collection), Leiden, the Netherlands

Type specimens of *Psammocora explanulata* were examined in the BMNH and ZMA collections. Three of them (BMNH 1937.11.17.116, ZMA Coel. 1072, and ZMA Coel. 1071) are indicated as 'Syntype' on their label, while for specimen BMNH 1937.11.17.69 the indication 'Type' is given. The holotype of *Coscinaraea wellsi* USNM 44818 was examined, as well as the specimens of *C. wellsi* at MTQ that are depicted with the original species description (Veron and Pichon, 1980).

Specimen identification

The specimens were identified by use of the original descriptions and illustrations of *Psammocora explanulata* and *Coscinaraea wellsi* by Van der Horst (1922) and Veron and Pichon (1980), respectively. Species descriptions and illustrations in other widely used references were also examined (Wells, 1954; Veron and Pichon, 1976; Scheer and Pillai, 1983; Veron, 1986, 2000; Sheppard and Sheppard, 1991; Hoeksema and van Ofwegen, 2004; Fenner, 2005; Dai and Horng, 2009; Pichon *et al*., 2010). The morphological terms used follow the terminology explained and illustrated by Hoeksema (1989).

DNA extraction, COI and rDNA amplification and sequencing

Analyses of sequences from the mitochondrial cytochrome *c* oxidase subunit I gene (COI, partially) and a selection of nuclear rDNA (the entire ITS1, 5.8S, ITS2 and a fragment of 18S and 28S) were used to infer phylogenetic relationships between the examined taxa. COI and rDNA were both amplified from most, but not for all, specimens of *Psammocora explanulata* and *Coscinaraea wellsi* analyzed in this study. The list of examined samples and successful amplifications is reported in Table 1. Both markers have been previously used to assess evolutionary relationships among the Anthozoa (Benzoni *et al*., 2007, 2010; Stefani *et al*., 2008; Forsman *et al*., 2009; Gittenberger *et al*., 2011). The DNA was extracted from ethanol-preserved tissues using a DNeasy® Tissue Kit (QIAGEN, Qiagen Inc., Valencia, CA, USA). Each extract was quantified using a Nanodrop 1000 spectrophotometer (Thermo Scientific).

A COI fragment of *ca*. 500 bp was amplified using fungiid-specific COI primers fungCOIfor1 (5'- CTG CTC TTA GTA TGC TTG TA -3') and fungCOIrev2 (5'- TTG CAC CCG CTA ATA CAG -3') by Gittenberger *et al*. (2011). A PCR mix (50 μl) consisted of 1X Buffer, 2 mM $MgCl_2$, 0.2 μM of forward and reverse primer, 0.1 mM dNTPs, 2 units of Taq DNA polymerase and ~30 ng DNA. The protocol was 94°C (4 min), followed by 30 cycles of 94°C (1 min), 53°C (30 sec) and 72°C (1 min), followed by 72°C (5 min). An approximately 800 bp long region of rDNA was amplified and sequenced with the universal primer ITS4

(5'- TCC TCC GCT TAT TGA TAT GC -3') (White *et al*., 1990) and coral-specific primer A18S (5'- GAT CGA ACG GTT TAG TGA GG -3') (Takabayashi *et al*., 1998). Amplifications were performed in a 50 μl volume, using 1X Buffer, 2 mM $MgCl_2$, 0.4 μM of forward and reverse primer, 0.1 mM dNTPs, 2 units of Taq DNA polymerase and ~30 ng DNA. PCR cycling was as follows: 96°C (2 min), followed by 30 cycles of 96°C (10 sec), 50°C (30 sec) and 72°C (4 min), followed by 72°C (5 min). PCR products were purified and directly sequenced using an automated 3730x1 DNA Analyzer (Applied Biosystem, Foster City, CA, USA). Sequences obtained in this study have been deposited in GenBank, and accession numbers are listed in Table 1.

Phylogenetic analyses

The obtained COI and rDNA sequences were aligned with other available homologues from the families Siderastreidae and Fungiidae (Benzoni *et al*., 2007; Gittenberger *et al*., 2011). In particular all the genera of the former family, and 14 out of 15 of the latter were included in the analyses, thus excluding only the genus *Cantharellus* Hoeksema and Best, 1984. Among the 11 species currently recognized in the genus *Cycloseris*, only the six analyzed by Gittenberger *et al*. (2011) were included in the present analyses. Sequences were viewed, edited and assembled using CodonCode Aligner 2.0.6 (CodonCode Corporation, Dedham, MA, USA). Multiple alignments were finally adjusted using

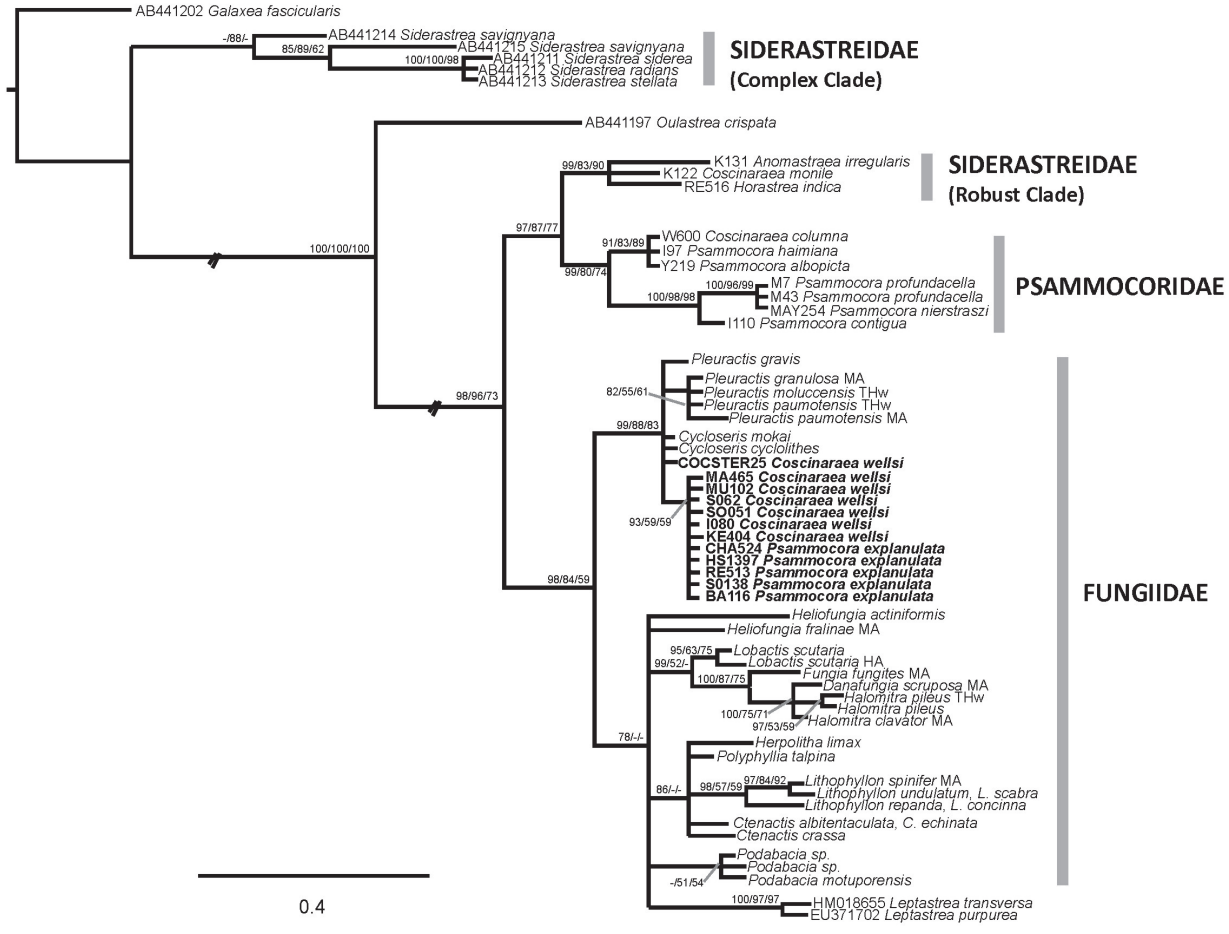

Fig. 3. Phylogenetic tree based on the mitochondrial gene COI inferred by Bayesian inference. The clade support values are *a posteriori* probabilities transformed to a percentage (BI), bootstrap values from maximum parsimony (MP) and bootstrap values from maximum likelihood (ML), in this order. Sequences generated in this study are in bold.

BioEdit 7.0.9.1 (Hall, 1999). Identification of invariable, polymorphic and parsimony informative sites was conducted with DnaSP 5.10.01 (Librado and Rozas, 2009). Intra and interspecific pairwise distances (uncorrected *p*-distances) were calculated in MEGA 4.0.2 (Tamura *et al*., 2007).

Phylogenetic relationships were reconstructed using Maximum Parsimony (MP), Maximum Likelihood (ML) and Bayesian Inference (BI). For both markers MP analyses were performed with PAUP* 4.0b10 (Swofford, 2003) using a heuristic search with starting trees obtained by random stepwise addition, with 10 replicates, and the tree bisection-reconnection (TBR) branch swapping algorithm. Bootstrap replicates (n=500) were used to assess the robustness of the internal nodes of the trees. For the ML and BI analyses, nucleotide substitution model parameters were determined by using MrModeltest2.3 (Nylander, 2004). Based on arguments presented by Posada and Buckley (2004), we used the Akaike Information Criterion (AIC) to select best-fit models. The model GTR+I+G (gamma=0.4791 and p-invar=0.4595) was suggested as best fit for COI, and for the rDNA, the model SYM+I+G (gamma=0.6387 and p-invar=0.5340) was selected instead. ML reconstructions were performed with PhyML 3.0 (Guindon and Gascuel, 2003) using the default parameters. The reliability of the ML tree was assessed by bootstrap analyses, with 500 replications. BI analyses were conducted with MrBayes 3.1.2 (Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003), using the previously determined models of nucleotide evolution. In the case of COI, a Markov Chain Monte Carlo analysis was applied with four chains running for 1,500,000 generations, saving the current tree every 10 generations. Subsequently, a consensus tree was produced (with a burnin of 37500 trees) indicating the Bayesian posterior probabilities of each node. The rDNA phylogeny was obtained on the basis of 6,000,000 generations, sampling trees every 100 generations. The first 30,000 trees were discarded as burnin. Convergence of parameters estimates were monitored using Tracer 1.5 (Drummond and Rambaut, 2007) and by using the statistics provided by MrBayes.

Results

COI phylogeny

Seven COI sequences for *Coscinaraea wellsi* and five for *Psammocora explanulata* were obtained. All sequences for *Coscinaraea wellsi* except the one from Ternate, Indonesia, shared the same haplotype. After alignment, 455 base pairs were obtained for the COI fragment, containing 329 invariable, 17 uninformative, and 109 parsimony informative base pairs with a total of 170 mutations. No indels were detected. *Galaxea fascicularis* (clade V and Complex group) was selected as outgroup due to its divergence from *Siderastrea* (clade IX and Complex group) and clade XI (Robust group) based on the mitochondrial tree proposed by Fukami *et al*. (2008).

All phylogenetic methods (BI, MP, ML) provided trees with the same overall topology, *i.e*. all specimens were assigned to the same clades, and the relationships among these clades were stable (Fig. 3). *Siderastrea* de Blainville, 1830, the type genus of the family Siderastreidae, is highly divergent from the other Siderastreidae (*sensu* Veron, 2000) as already shown in previous molecular studies (Benzoni *et al*., 2007; Fukami *et al*., 2008; Kitahara *et al*., 2010). The genera *Coscinaraea* Milne Edwards and Haime, 1848, *Psammocora* Dana, 1846, *Horastrea* Pichon 1971, and *Anomastraea* Marenzeller, 1901, form a strongly supported group including the Siderastreidae and Psammocoridae clades in Fig. 3. This, together with the Fungiidae and the genera *Oulastrea* Milne Edwards and Haime, 1848, and *Leptastrea* Milne Edwards and Haime, 1848 (both traditionally ascribed to the Faviidae) form a larger and well supported clade (Fig. 3). All the taxa in this larger clade were assigned to clade XI by Fukami *et al*. (2008). However, in our analysis *Oulastrea crispata* (Lamarck, 1816) appears to be highly distinctive and basal to the remainder of this clade (Fukami *et al*., 2008). Two main subclades are evidenced in clade XI. One subclade comprises the remaining siderastreids, with the exception of *C. wellsi* and *P. explanulata*. The other subclade includes all fungiids, all specimens of *C. wellsi* and *P. explanulata*, and *Leptastrea*. Moreover, *C. wellsi* and *P. explanulata* are closely related to each other together with the genera *Cycloseris* Milne Edwards and Haime, 1849 and *Pleuractis* Verrill, 1864. This group is also well supported by different phylogenetic analyses (posterior probability=99, MP bootstrap=88, ML bootstrap=83). The close relationships between *C. wellsi* and *P. explanulata* among the *Cycloseris* species are also supported by pairwise distances. The genetic distance of *C. wellsi* and *P. explanulata* compared to the *Cycloseris* species is very low (0.1 ± 0.04% in both cases). Conversely, significantly higher values are evidenced between *C. wellsi* and its congeners *Coscinaraea monile* (Forskål, 1775)

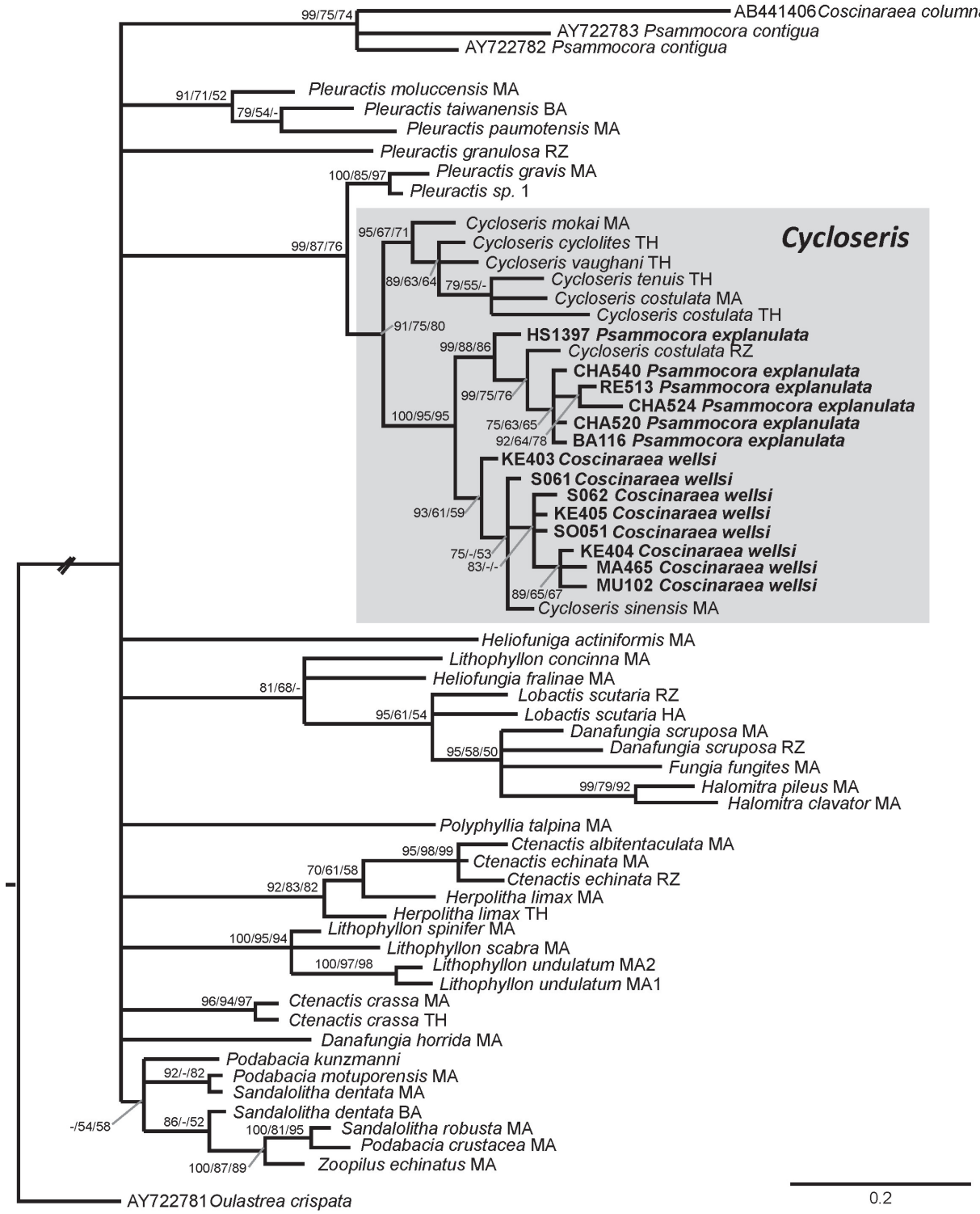

Fig. 4. Phylogenetic tree based on rDNA (spanning the entire ITS1, 5.8S, ITS2 and a portion of 28S and 18S) inferred by Bayesian inference. The clade support values are *a posteriori* probabilities transformed to a percentage (BI), bootstrap values from maximum parsimony (MP) and bootstrap values from maximum likelihood (ML), in this order. Sequences generated in this study are in bold.

(3.1 ± 0.8%) and *C. columna* (Dana, 1846) (3.0 ± 0.8%), and between *P. explanulata* and the other *Psammocora* species (3.9 ± 0.8%).

rDNA phylogeny

A total of eight sequences of *C. wellsi* and six of *P. explanulata* were obtained for the rDNA locus. Direct sequencing produced reliable electropherograms and no ambiguous nucleotide peaks. The aligned matrix was 678 base pairs long, 419 positions were constant, 128 positions were polymorphic, and 64 base pairs potentially parsimony-informative. Finally, 127 indel sites were found, and they were treated as a fifth character in phylogenetic analyses. *Oulastrea crispata* was selected as outgroup owing to its high divergence within clade XI *sensu* Fukami *et al*. (2008) based on mitochondrial phylogeny (Fig. 3), and because sequences from other outgroups were not available for this marker.

The general topology of the phylogeny reconstructions obtained with MP, ML and Bayesian procedures was congruent (Fig. 4), with minor differences in the relationships among sequences in the terminal clades and reflecting the same topology as observed in COI phylogeny.

Two main subclades within clade XI *sensu* Fukami (2008) are partially recognizable. *Coscinaraea columna* (Dana, 1846) and *Psammocora contigua* (Esper, 1794) form a well-supported group, separated from *C. wellsi* and *P. explanulata*. The average distance of *C. wellsi* from *C. columna* is 5.5 ± 0.9%, while genetic divergence between *P. explanulata* and *P. contigua* is 5.0 ± 0.8%. Thus, even in this case, the two species are distantly related to their supposed congeners. The Fungiidae and *C. wellsi* and *P. explanulata* form an unresolved clade due to a large basal polytomy. Nevertheless, all monophyletic groups represented by more than one species are the same as those recovered in the nuclear phylogeny of Fungiidae by Gittenberger *et al*. (2011) and therefore not discussed again. All the examined specimens of *C. wellsi* and *P. explanulata* are in a well-supported group including *Pleuractis gravis* (Nemenzo, 1955), *P.* spec. 1 and all *Cycloseris* species. These two species show a close phylogenetic relationship to *Cycloseris*, as corroborated by average distances between *C. wellsi* and *Cycloseris* (1.4 ± 0.4%) and between *P. explanulata* and *Cycloseris* (1.7 ± 0.4%). *C. wellsi* and *P. explanulata* form two resolved but not monophyletic lineages due to the presence of *Cycloseris sinensis* Milne Edwards and Haime, 1851 in the *C. wellsi* clade, and of *Cycloseris costulata* (Ortmann, 1889) in the *P. explanulata* clade.

A reappraisal of the morphology and distribution of *Cycloseris explanulata* and of *C. wellsi* is given in the Appendix. Based on the aforementioned molecular evidence and morphologic observations discussed hereafter, the taxonomic position of the two species is revised and both are formally assigned to the genus *Cycloseris* within the family Fungiidae.

Discussion

Phylogeny, taxonomy, and distribution of Cycloseris explanulata *and* Cycloseris wellsi

The joint analyses of the databases of Benzoni *et al*. (2007) and Gittenberger *et al*. (2011), and the study of a large collection of specimens of *Cycloseris wellsi* and *C. explanulata* (Appendix) confirmed that both species are genetically and structurally more related to each other and to the Fungiidae than to *Coscinaraea* or *Psammocora*, the genera to which they originally belonged, respectively (Benzoni *et al*., 2007). Both species share typical structural characters typical for the Fungiidae (*i.e*. interstomatous septa, tentacular lobes, fulturae) and which are not found in any other of the taxa ascribed to the Siderastreidae. Conversely, they lack typical structures found in the genera to which they were originally assigned. For example, in both *Cycloseris wellsi* and *C. explanulata* the structure of the colony wall is septothecal, the septa are joined by fulturae, and the costae developed, whereas in *Psammocora* and *Coscinaraea* the corallum wall is synapticulothecal, the septa are joined by synapticulae and costae are not developed (Benzoni *et al*., 2007). Furthermore, both these attached and polystomatous taxa share a combination of morphologic characters that are typical of *Cycloseris*, *i.e*. a solid corallum wall, the presence of fine and sharp septal margin and lateral septa ornamentation, and of costae covered by fine protuberances (Hoeksema, 1989). Moreover, both the mitochondrial (Fig. 3) and the nuclear marker (Fig. 4) indicate that among the fungiids *C. wellsi* and *C. explanulata* are most closely related to species in the monophyletic genus *Cycloseris*. In particular, all examined specimens of *C. wellsi* were recovered in the same clade as *Cycloseris cyclolites* (Lamarck, 1816), the type species of the genus. The phylogenetic trees in Figs. 3 and 4 show complementary information with no conflicting signals. Indeed no species or species

groups are found in different or contrasting clades. The only differences concern the resolution of some species groups detected in COI rather than in rDNA trees. In general, the COI phylogenies resolve evolutionary relationships at a more basal taxonomic level detecting four well-supported clades in these corals, namely the Siderastreidae (Complex clade), Siderastreidae (Robust clade), Psammocoridae, and Fungiidae clades. This is in agreement with the well known slow substitution rate of COI in corals (Hellberg, 2006; Huang *et al*., 2008). On the contrary, rDNA phylogeny does not recover the monophyly of Fungiidae clade but it is useful to investigate phylogenetic relationships at genus and species level within this clade. While in the mitochondrial cladogram *Psammocora explanulata* and *Coscinaraea wellsi* are grouped together with no genetic differentiation in the mitochondrial tree (Fig. 3), in the rDNA cladogram the position of these two species is well-resolved (Fig. 4) due to the higher resolution of ITS1 and ITS2 regions (Chen *et al*., 2004; Wei *et al*., 2006).

Despite having been traditionally assigned to two different genera, *C. wellsi* and *C. explanulata* are morphologically very similar (Veron and Pichon, 1980; Veron, 2000) (Figs. 1, 6, 8). In the taxonomic literature the former species has been confused with the latter (see the synonymies above) and one of the 'syntypes' of *C. explanulata* (ZMA Coel. 1071, Fig. 8F) is actually a specimen of *C. wellsi* (cf. UNIMIB KE 404, Fig. 8E). This is not surprising considering the morphological similarity and the co-occurrence of both species in similar environments (also shared with *C. mokai*) and their overlapping wide Indo-Pacific distribution ranges (Figs. 7 and 9). This being said, *C. wellsi* has

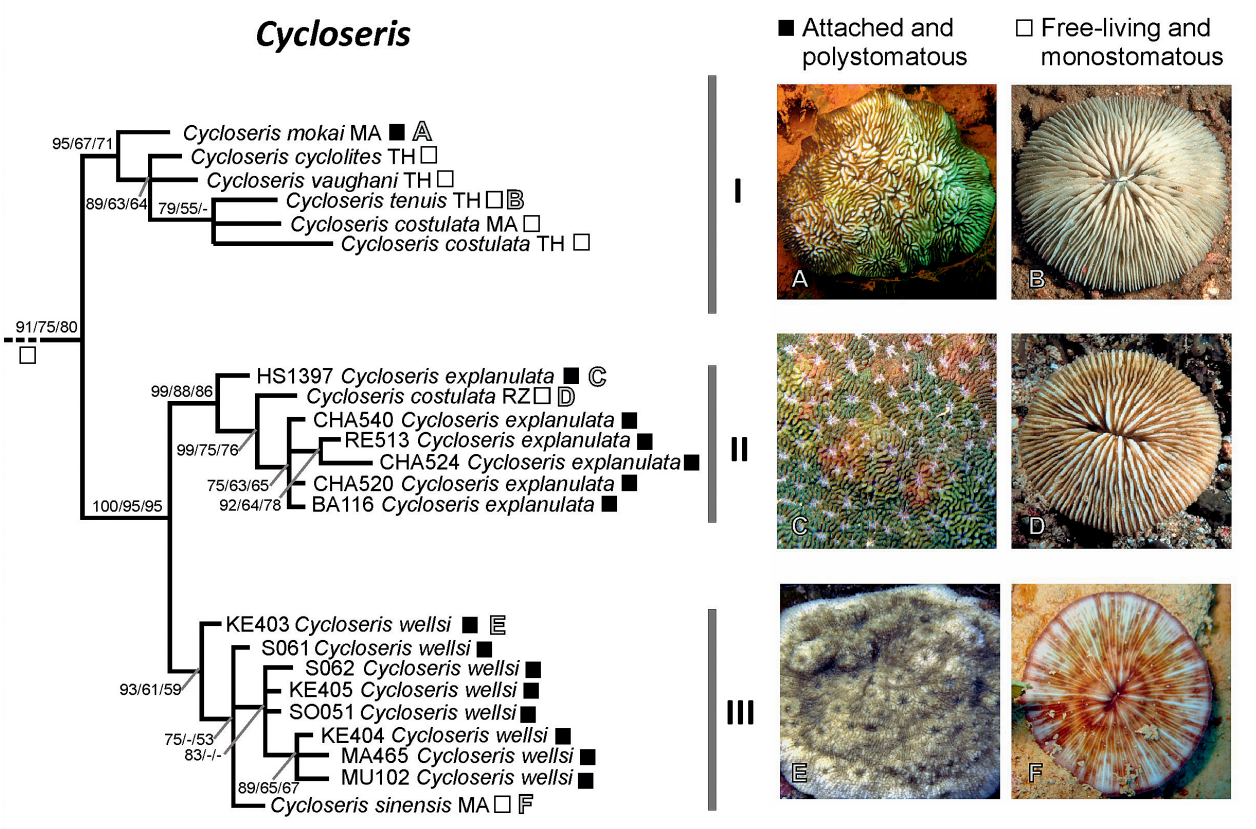

Fig. 5. Detail of the rDNA phylogeny showing the *Cycloseris* clade (highlighted in grey in Fig. 3) modified to indicate the presence of attached and polystomatous species and free-living and monostomatous species in each of its main lineages (I – III). A) *Cycloseris mokai*, Prony Bay, New Caledonia, new geographic record (image from the IRD Nouméa Lagplon archive); B) *C. tenuis*, Sulawesi, Indonesia (photo BWH); C) *C. explanulata*, Mayotte Island; D) *C. costulata*, Bali, Indonesia (photo BWH); E) *C. wellsi*, Bali, Indonesia (photo BWH); F) *C. sinensis*, Banc Gail, New Caledonia (image from the IRD Nouméa Lagplon archive). Black squares indicate attached and polystomatous taxa, white squares free-living and monostomatous ones. Please note that letters placed after the squares in the tree on the left hand side of the figure correspond to the photo labels on the right hand side.

larger calices, more septa reaching the fossa, longer and more winding interstomatous septa, and longer enclosed petaloid septa. Finally, in daytime *C. explanulata* tentacles are mostly extended (Fig. 1A-D) whilst *C. wellsi* polyps are mostly retracted (Fig. 1E-H).

On the basis of the examined material, the known geographic distribution ranges of *C. explanulata* and *C. wellsi* are updated and extended when compared to those presented by Veron (2000). The distribution ranges of both species show much overlap, extending from eastern Africa and the Red Sea to Hawaii and French Polynesia (Figs. 7, 9). New records for *C. wellsi* are from the Gulf of Aden (Djibouti and Socotra Island) Kenya and French Polynesia and for *C. explanulata* from Vietnam, the Line Islands, and New Caledonia (Appendix).

Attached and polystomatous Cycloseris *species*

Attached species among the Fungiidae appear to be more common than previously assumed (Hoeksema, 1989, 2009). They belong to the genera *Cantharellus*, *Lithophyllon*, *Podabacia*, and *Cycloseris* (Gittenberger *et al*., 2011). The phylogenetic and taxonomic position of *Cantharellus* with three small monostomatous species is uncertain but it is probably closely related to *Cycloseris* (Hoeksema, 1989; Gittenberger *et al*., 2011). The genera *Lithophyllon* and *Podabacia* consist of polystomatous species, which are foliaceaous and may attain large sizes (Hoeksema, 1989, 1991b, 2009). With the present inclusion of *C. explanulata* and *C. wellsi* in the Fungiidae, the number of ten attached species among 50 mushroom coral species (Gittenberger *et al*., 2011) has increased to 12 among 52.

The earlier inclusion of the encrusting polystomatous species *C. mokai* in *Cycloseris* by Gittenberger *et al*. (2011) was unexpected because *Cycloseris* originally used to consist of free-living monostomatous species. Specimens of *C. mokai* are usually found in lower reef slope habitats, mostly above sandy bottoms, where they live attached to the vertical sides of rocks, which may help to prevent burial (Hoeksema, 2012a). The possession of multiple mouths may spread the risk of mouth clogging and feeding obstruction in conditions of heavy sedimentation (Hoeksema, 1991b). From a phylo-ecological perspective, *C mokai* may be derived from an ancestor that lived on sediment but because it lost the capacity to detach itself (a morphological or life history character state reversal), its vertical distribution range became shallower (an ecological character state reversal) (Hoeksema, in prep.).

Cycloseris explanulata and *C. wellsi* belong to separate lineages within *Cycloseris* (Figs. 4 and 5) and their ancestors may have undergone a similar fate as those of *C. mokai*. According to the present phylogeny reconstruction it appears that all three species had free-living ancestors that lived on sandy substrates in the proximity of lower reef slopes, where they may have settled as planula larvae (see *e.g*. Hoeksema, 2012a). Moreover, the three species belong to three separate lineages within the genus *Cycloseris*, each comprising both attached and polystomatous species in addition to free-living and monostomatous corals (Fig. 5). The three attached *Cycloseris* species are usually small and have many mouths in close proximity to each other, which may be an advantage in conditions of limited substratum surface (Hoeksema, 1991b). The present scenario confirms that homoplasy (convergence), including character reversals from both morphological and ecological perspective, is a common phenomenon among mushroom corals (Hoeksema, 1991b; Gittenberger *et al*., 2011).

The present study confirms the utility of re-examining morphological characters in the light of new molecular data as already demonstrated by previous studies (*e.g*. Budd and Stolarski 2009, 2011; Benzoni *et al*., 2011). This allowed the re-assignment of two misclassified mushroom corals to the family Fungiidae, based on the re-examination of historical museum material and analyses of new specimens with DNA samples recently collected by the authors (*e.g*. Djibouti, Kenya, the Line Islands, New Caledonia, Sabah, Yemen). This confirms that historical and new collections of skeletons and DNA are of paramount importance for the development of our knowledge of the diversity, phylogeny, and biogeography of hard corals and other marine organisms (Hoeksema *et al*., 2011; Karsenti *et al*., 2011).

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Appendix

A reappraisal of the morphology and distribution of Cycloseris explanulata *and* Cycloseris wellsi

Family Fungiidae Dana, 1846
Genus *Cycloseris* Milne Edwards and Haime, 1849
For a complete diagnosis of this genus refer to Hoeksema (1989).

Cycloseris explanulata (van der Horst, 1922)

Psammocora explanulata van der Horst (1922: *partim* pl. 32, figs. 7-8); Wells (1954: pl. 157, figs. 9-10); Veron and Pichon (1976: 28-30, figs. 27-32); Scheer and Pillai (1983: 20, pl. 1, fig. 9); Sheppard and Sheppard (1991: 81, fig. 69, pl. 48); Veron (1986: 277); Veron (2000); Fenner (2005: 72); Pichon *et al*. (2010: 212-213, figs. 1-4); Turak and DeVantier (2011: p. 105).
Lithophyllon mokai - sensu Hoeksema and van Ofwegen (2004) *partim*; Veron (2000: 306).
Psammocora sp. Hoeksema and van Ofwegen (2004) *partim*

Examined material
Type material: BMNH 1937.11.17.69 (Lectotype, present designation) Providence, Seychelles (coll. J.S. Gardiner) 91.5-142 m; BMNH 1937.11.17.116 (Paralectotype) Providence, Seychelles (coll. J.S. Gardiner) 53 m; ZMA Coel.1072 (Paralectotype) Providence, Seychelles, 106-142.6 m.
Other material: **Egypt**, AIMS unregistered (coll. J.E.N. Veron). **Saudi Arabia**, NHM 1991.6.4.67 Yambu (coll. C.R.C. Sheppard) 15 m; MTQ G 57709 Sharm Jozai, Duba (26°57.6' N 35°58.0' E) 07.vii.1998 (coll. E. Turak, L. Devantier). **Yemen**, UNIMIB BU018 Burum (14°19.710' N 48°59.903' E) 22.iii.2008 (coll. F. Benzoni, M. Pichon); UNIMIB BU067 Burum (14°18.421' N 48°58.068' E) 19.iii.2009 (coll. F. Benzoni, M. Pichon); UNIMIB BA116 Sikha Island, Bir Ali (13°55.648' N 48°23.234' E) 22.xi.2008 (coll. F. Benzoni, S. Montano) 20 m. **Socotra**, EPA/Senckenberg C138S Kal Farun (12°26.4' N 52°08.9' E) 11.iv.1999; MTQ G 57712 Kal Farun (12°26.4' N 52°08.9' E) 11.iv.1999 (coll. L. Devantier); UNIMIB SO079 Hawlaf (12°40.808' N 54°04.504' E) 14.iii.2010 (coll. F. Benzoni, A. Caragnano); UNIMIB SO138 Qeso shore (12°40.212' N 53°26.893' E) 18.iii.2010 (coll. F. Benzoni, A. Caragnano) 7 m. **Seychelles**, RMNH Coel.19095 Bird Island (03°42' S 55°12' E) 21.xii.1992 (coll. B.W. Hoeksema) 8-21 m; RMNH Coel.19096 Alphonse Atoll (07°00' S 52°43' E) 03.i.1993 (coll. B.W. Hoeksema); RMNH Coel.19094 Aride Island (04°13' S 55°40' E 18/19.xii.1992) (coll. B.W. Hoeksema); RMNH Coel.19097 Alphonse Atoll (07°02' S 52°44' E) 04.vi.1993 (coll. B.W. Hoeksema) 8 m. **Mayotte**, MNHN 20360 Banc de la Zélée, (12°25.6' S 46°16.2' E) 09.iv.1973 (coll. G. Faure) 32-52 m; UNIMIB MA 243, 2004 (coll. F. Seguin); UNIMIB MA 447 (12°47.602' S 44°58.860' E) 16.iv.2005 (coll. F. Benzoni); UNIMIB MA 449 Banc de Boa (12°41.178' S 45°02.296' E) 18.iv.2005 (coll. F. Benzoni) 16 m; UNIMIB MA 451B (12°50.183' S 44°56.488' E) 19.iv.2005 (coll. F. Benzoni) 17 m; UNIMIB MA 453 Moutsoumbatsou (12°50.183' S 44°56.488' E) 19.iv.2005 BA (coll. D. Obura) 22 m; UNIMIB MA 454 Moutsoumbatsou (12°50.183' S 44°56.488' E) 19.iv.2005 (coll. F. Benzoni) 19 m; UNIMIB MA 461 Faro Boueni (12°54.684' S 44°58.089' E) 22.iv.2005 (coll. F. Seguin); UNIMIB MA463 Faro Boueni (12°54.684' S 44°58.089' E) 22.iv.2005 (coll. F. Benzoni) 12 m; UNIMIB TO MY124 (12°52.534' N 45°16.834' E) 06.vi.2010 (coll. F. Benzoni); UNIMIB TO MY138 (12°53.980' N 45°15.416' E) 07.vi.2010 (coll. F. Benzoni); UNIMIB TO MY142 (12°53.980' N 45°15.416' E) 07.vi.2010 (coll. F. Benzoni). **La Réunion**, MNHN 20357 St. Gilles, 14.ix.1973 (coll. G. Faure); MNHN 20358 St. Gilles, 26.viii.1976 (coll. G. Faure); UNIMIB REU513 Petit Moteur, St. Gilles, 01.xi.2005 (coll. F. Benzoni, M. Pichon); MNHN 20359 (coll. G. Faure). **Madagascar**, MNHN 20389, Tuléar (coll. M. Pichon). **Maldives**, UNIMIB M014 Bulhalafushi 27.iv.2004 (coll. F. Benzoni) 15 m. **Chagos**, NHM TWCMS H11910 Ile de Coin, Peros Banhos, 1978, 22 m; NHM TWCMS H11916 Ile de Coin, Peros Banhos, 1978; NHM TWCMS H11925 Ile de Coin, Peros Banhos, 1978; NHM TWCMS C14748, 1975, 38 m; UNIMIB CHA521 I. Diamant, Peros Banhos, 11.iii.2006 (coll. D. Obura) 20 m; UNIMIB CHA522 I. Diamant, Peros Banhos, 11.iii.2006 (coll. D. Obura) 20 m; UNIMIB CHA524 I. Puole, Peros Banhos, 12.iii.2006 (coll. D. Obura) 20 m; UNIMIB CHA525 Eagle Islands 13.iii.2006 (coll. D. Obura) 21 m; UNIMIB CHA540 I. Passe, Peros Banhos 10.iii.2006 (coll. D. Obura) 19 m. **Thailand**, NHM 1977.2.25.17, Pangah Bay, 19.ix.1975 (coll. H. Ditlev) 10 m. **Indonesia**, RMNH Coel.33609 S coast of Erie, Ambon (03°45' S 128°08' E) 12.xi.1996 (coll. B.W. Hoeksema); RMNH Coel.33643 Ambon (03°43' S 128°16' E), (coll. B.W. Hoeksema) 15-20 m; MTQ G 57718 Bunaken Island, Sulawesi (01°38' N 124°45' E)

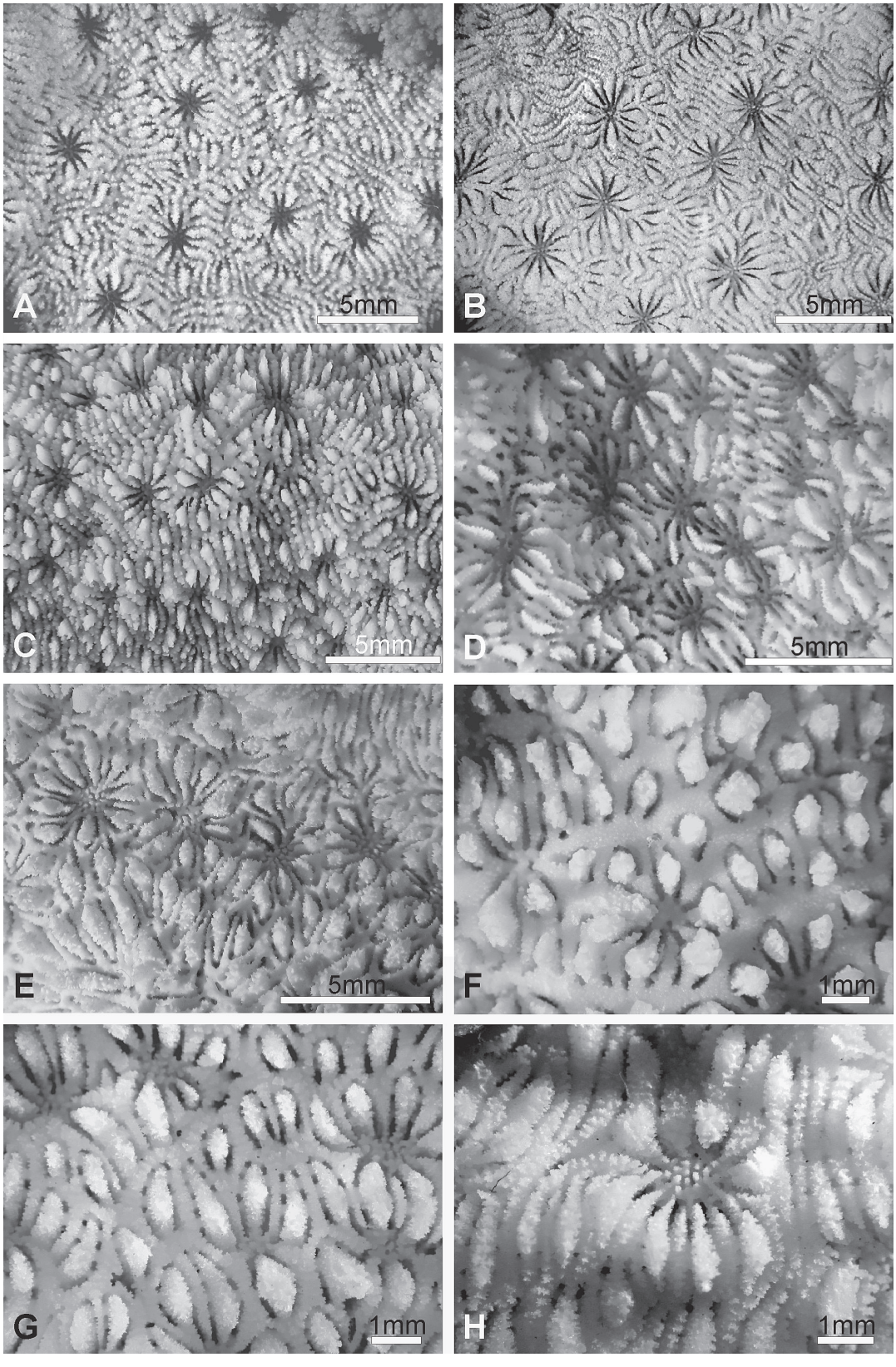
22.vii.2002 (coll. E. Turak); MTQ G 57719 Manado Tua, Sulawesi (01°38' N 124°43' E) 21.vii.2003 (coll. E. Turak); RMNH Coel.23308 Padang, Sumatra, 27.iv.1995 (coll. B.W. Hoeksema). **Australia**, AIMS 1813 Orpheus, Palm Island (coll. J.E.N. Veron); AIMS 1804 Orpheus, Palm Island (coll. J.E.N. Veron); JCU 3243 Lizard Island (coll. M. Pichon). **New Caledonia**, IRD HS 1397 N'Goë, Toupeti, Côte Oubliée (21°37.4117' S 166°26.7299' E) 17.iii.07 (coll. F. Benzoni, G. Lasne) 10-15 m; IRD HS 1769 Cap Goulevin (21°32.294' S 165°14°286' E) 01.xi.2007 (coll. F. Benzoni, G. Lasne) 33 m. **Marshall Islands**, USNM 44820 Bikini, 1954 (coll. J. Wells); MTQ G 57309 Dog tooth point, Rongelap (11°46.7' N 166°86.6' E) 13.vii.2003 (coll. Z. Richards); MTQ G 56300 Rongelap (11°31. 2' N 166°50.5' E) 02.viii.2002 (coll. Z. Richards); RMNH Coel.14545 Enewetak Atoll, xii.1976. **Line Islands**, UNIMIB LI490 Kiritimati Kir-09, 08.viii.2005 (coll. D. Obura) 10-17 m; UNIMIB LI493 Kiritimati Kir-11, 09.viii.2005 (coll. D. Obura) 10-17 m. **French Polynesia**, MNHN 20326 Baie d'Opunohu, Moorea, Society Islands (coll. J.P. Chevalier).

Morphology. Animals polystomatous. Corallum attached, generally thinly encrusting and following the underlying substrate (Fig. 1A-D). Colonies irregular in outline although smaller colonies can be circular (Fig. 1A). Calices scattered over the corallum surface without any particular arrangement (Fig. 6), they can be more closely packed (Fig. 6D) or more distant (Fig. 6B). Calice diameter between 2.6 and 3.1 mm. Thicker and more exsert septa (five to seven) alternate with thinner septa flush with the corallum surface. The former are mostly petaloid in shape (Fig. 6). Continuous septa going from one fossa to the other between adjacent calices, previously referred to as septocostae (Van der Horst, 1921, 1922; Veron and Pichon, 1976), can be observed in some specimens (Fig. 6A-D; Veron and Pichon, 1976, Figs 28, 31-32). These are actually interstomatous septa (Benzoni, 2007) homologous to those found in the Fungiidae (*sensu* Hoeksema, 1989). Enclosed petaloid septa derived from the alternate fusion of lower and higher order septa are found between calices like in the genus *Psammocora* Dana, 1846 (Benzoni *et al*., 2007, 2010). They range from 1.4 to 1.7 mm in length (Benzoni, 2007). Morphologic affinities between the pattern of septa fusion in *C. explanulata* and in the fungiid genus *Polyphyllia* Blainville, 1830 have been remarked by Van der Horst (1922) in the original species description. While enclosed septa with a petaloid outline are always observed in *C. explanulata*, interstomatous septa are developed in some specimens (Fig. 6E-H), and are mostly found between closely neighboring corallites (Veron and Pichon, 1976, Figs 31-32), *i.e*. less than one calice away from each other. Exsert tentacular lobes are typically found on top of thicker septa and enclosed petaloid septa in this species (Fig. 6). Septal margins are ornamented by ridges composed of short series of minute granules oriented transversally to the septal plane forming distinct septal paddles (Benzoni *et al*. 2007, Fig. 3G). Septal sides are ornamented by minute granules. Septa in *C. explanulata* are connected by buttress-like structures developing below the septal edge and joining the septa sides (Benzoni *et al*. 2007, Fig. 5B). These structures defined as fulturae are typical for the Fungiidae (see Gill, 1980, pl.1:1 for *Fungia* Lamarck, 1801; Hoeksema, 1989, Fig. 652 for *Herpolitha* Eschscholtz, 1824; Fig. 656 for *Sandalolitha* Quelch, 1884; Fig. 664 for *Lithophyllon* Rehberg, 1892). Fulturae differ from the synapticulae found, *inter alia*, in the Siderastreidae which are typically isolated from each other and are often developed near the septal edge (Gill, 1980). Columella always present, papillary, and formed by six to 15 tightly packed vertical processes all of the same size (Fig. 6H). Colony wall septothecal and compact. Costae are found on the lower side of the corallum, they are small and ornamented by minute rounded granulations. Unfortunately, they are often obscured due to the attached growth mode, and by the incrustations of crustose coralline algae and invertebrates. These are small and ornamented by minute rounded granulations.

Geographical distribution. *Cycloseris explanulata* occurs throughout the Indo-Pacific. Based on the present material and published illustrations it is recorded from Egypt, Saudi Arabia, Yemen, Socotra Island, Maldives, Chagos, Seychelles, Mayotte, Madagascar, La Réunion, Thailand, Indonesia, Vietnam, Papua New Guinea, Australia, New Caledonia, the Marshall Islands, Hawaii, the Line Islands, and French Polynesia (Fig. 7).

Cycloseris wellsi (Veron and Pichon, 1980)

Psammocora explanulata Van der Horst, 1922 *partim*; Veron (2000: p. 156, Figs. 1-2)
Coscinaraea ostraeformis - sensu Wells (1954: pl. 155, Figs 5-6), *not* van der Horst (1922)
Coscinaraea wellsi Veron and Pichon (1980); Nishihira and Veron (1995); Veron (1986: p. 284); Veron (2000: p. 167); Hoeksema and van Ofwegen (2004);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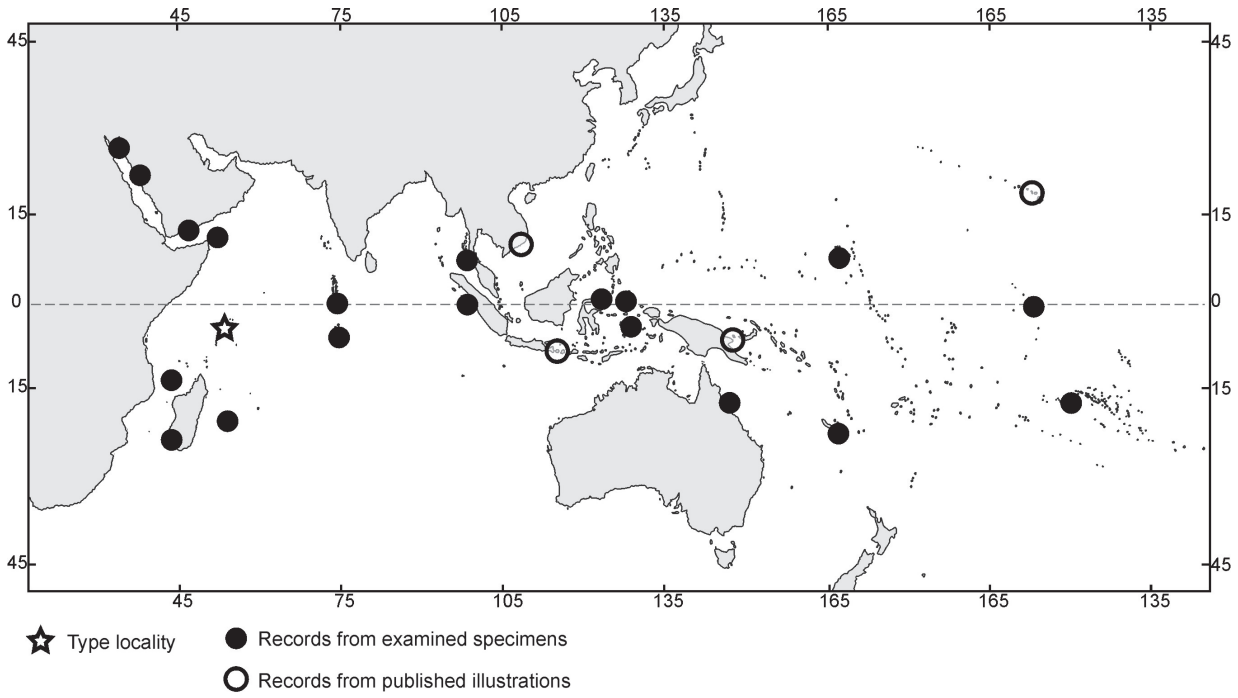
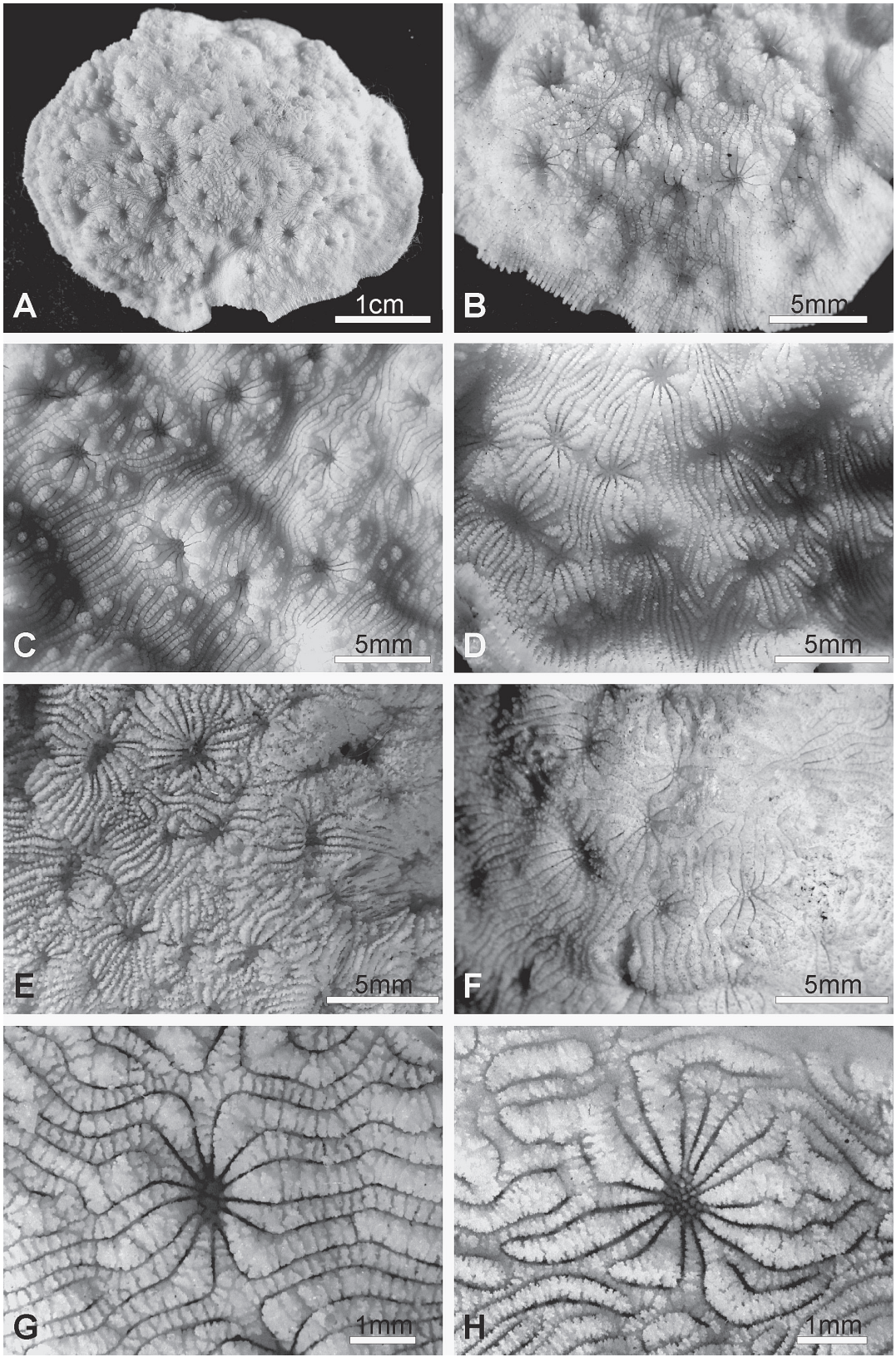


Fig. 7. Records of *Cycloseris explanulata*. The star indicates type locality, grey circles indicate records from specimens examined in this study, and empty circles figures from published illustrations.

Fenner (2005: 71); Turak and DeVantier (2011: p. 110)
Lithophyllon mokai - sensu Hoeksema and van Ofwegen (2004) *partim*

Examined material
Type material: USNM 44818 (Holotype) Bikini Atoll, Ralik Chain, Marshall Islands, 14.viii.1947 (coll. J.W. Wells) 53.38-76.25 m.
Other material: **Egypt**, UNIMIB S 060 Ras Nosrani, South Sinai (27°57.989' N 34°25.190' E) 16.v.2004 (coll. F. Benzoni) 20 m; UNIMIB S 061 Ras Nosrani, South Sinai (27°57.989' N 34°25.190' E) 16.v.2004 (coll. F. Benzoni) 24 m; UNIMIB S 062 Ras Nosrani, South Sinai (27°57.989' N 34°25.190'E) 16.v.2004 (coll. F. Benzoni) 23.5 m. **Israel**, RMNH Coel.24180 Eilat, Gulf of Aqaba 20.iv.1996 (coll. S. Goffredo) 45 m. **Djibouti**, UNIMIB TO DJ043 Oblal (11°51.680' N 43°06.480' E) 28.i.2010 (coll. F. Benzoni) 10 m; UNIMIB TO DJ099 Kalaf, Ablali (11°43.787' N 42°46.417' E) 29.i.2010 (coll. F. Benzoni) 15 m; UNIMIB TO DJ176 Maskali (11°43.064' N 43°09.359' E) 01.ii.2010 (coll. F. Benzoni) 18 m. **Yemen**, UNIMIB MU095 Al Mukallah (14°31.067' N 49°10.335' E) 18.iii.2007 (coll. F. Benzoni, M. Pichon); UNIMIB MU102 Al Mukallah (14°31.067' N 49°10.335' E) 18.iii.2007 (coll. F. Benzoni, M. Pichon); UNIMIB MU164 Al Mukallah (14°30.793' N 49°10.339' E) 20.iii.2007 (coll. F. Benzoni, M. Pichon) 18 m; UNIMIB BU017 Burum (14°19.710' N 48°59.903' E) 22.iii.2008 (coll. F. Benzoni, M. Pichon). **Socotra**, UNIMIB SO051 Ras Adho (12°38.672' N 54°16.043' E) 13.iii.2010 (coll. F. Benzoni, M. Pichon). **Kenya**, UNIMIB KE403 Kiunga, 14.iii.2005 (coll. D. Obura); UNIMIB KE404 Cha Chano, 12.iii.2005 (coll. D. Obura); UNIMIB KE405

◀ *Fig. 6.* Morphology and variability of skeletal structures in *Cycloseris explanulata* A) Lectotype (NHM 1937.11.17.69) Providence, Seychelles (91.5-142 m); B) Paralectotype (ZMA Coel. 1072) Providence, Seychelles (106-142.6 m); C) specimen IRD HS 1769 from Cap Goulevin, New caledonia (33 m) (same specimen as in Fig. 4B); D) specimen UNIMIB LI490 Kiritimati, Line Islands; E) specimen MNHN 20358 St. Gilles, La Réunion; F) specimen NHM TWCMS H11910 from Ile de Coin, Peros Banhos, Chagos (22 m); G) specimen UNIMIB MA 451B from Mayotte; H) specimen UNIMIB MA 461 from Faro Boueni, Mayotte.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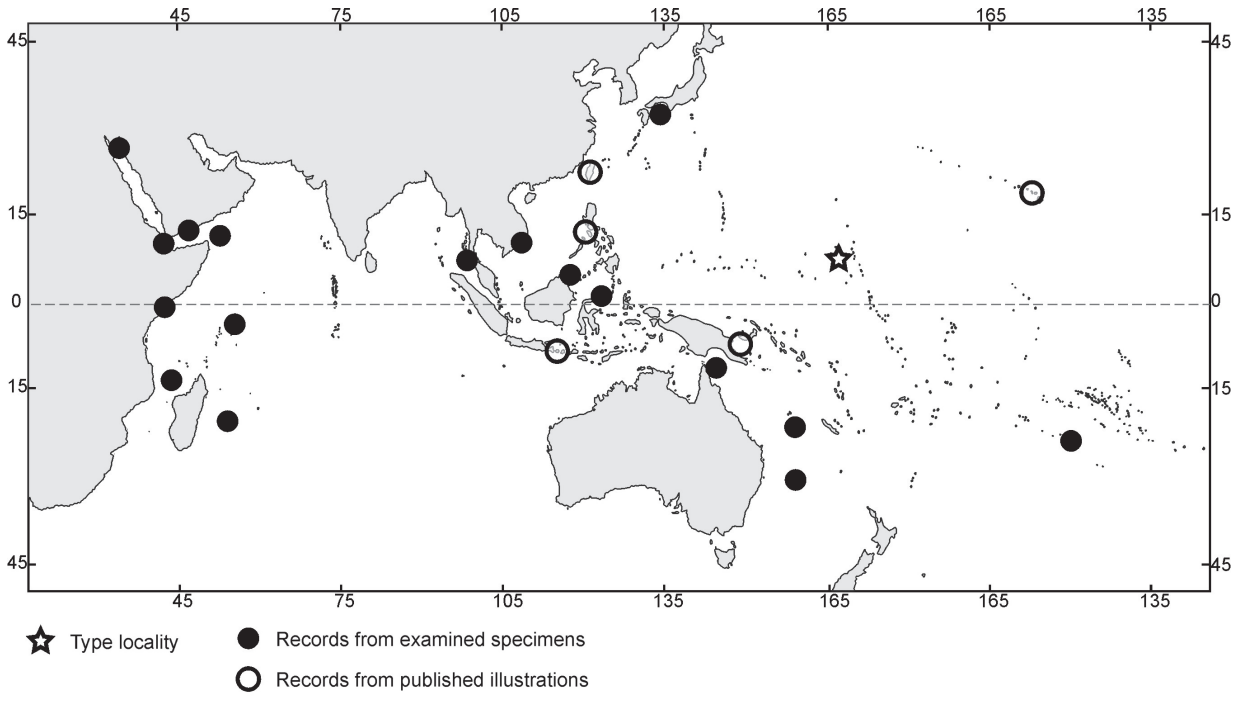

Fig. 9. Records of *Cycloseris wellsi*. The star indicates type locality, grey circles indicate records from specimens examined in this study, and empty circles figures from published illustrations.

Kiunga, 12.iii.2005 (coll. D. Obura). **Seychelles**, ZMA Coel.1071 (Syntype of *Psammocora explanulata*) Amirante, Seychelles, 11.x.1905, >36.5 m. **Mayotte**, UNIMIB MA 452B (12°50.183' S 44°56.488' E) 19. iv.2005 (coll. F. Benzoni, M. Pichon); UNIMIB MA 465 Passe Bateaux (12°59.530' S 44°59.136' E) 23. iv.2005 (coll. F. Benzoni, D. Obura); UNIMIB MA 478 pointe Paskélé (13°00.350' S 45°07.208' E) 26.iv.2005 (coll. D. Obura); UNIMIB TO MY123 (12°52.534' N 45°16.834' E) 06.vi.2010 (coll. F. Benzoni) 22 m. **La Réunion**, MNHN 470 (*partim*, only larger specimen), 1841 (coll. L. Rousseau). **Thailand**, UNIMIB LP 191 Laem Pakarang, Khao Lak (08°43.612' N 98°13.121 E) 12.xii.2006 (coll. F. Benzoni, D. Basso) 16 m. **Vietnam**, AIMS unregistered 27 (coll. J.E.N. Veron). **Malaysia**, RMNH Coel.39965 Singamata Pancang, Semporna region, eastern Sabah (04°31.350'N 118°37.001' E) 12. xii.2010 (coll. B.W. Hoeksema) 20 m. **Indonesia**, UNIMIB I 080 Mapia House Reef, Manado, Sulawesi (01°27.527' N 124°46.007' E) 08.vi.2004 (coll. F. Benzoni) 23 m; UNIMIB I 108 Negheri, Manado Tua, Sulawesi (01°36.902' N 124°42.020' E) 17.vi.2004 (coll. F. Benzoni) 38 m; UNIMIB I 114 Molas Ship Wreck, Molas, Sulawesi (01°31.906' N 124°49.518' E) 18. vi.2004 (coll. F. Benzoni). **Japan**, AIMS 12017 Tosashimizu, Shikoku (coll. J.E.N. Veron). **Australia**, MTQ G 59726 Lord Howe Island (31°28' S 159°09' E); MTQ G 45740 Murray Islands, Queensland (09°55' S 144°05' E) 10-25 m; MTQ G 45737 Maer Island, Murray Islands, Queensland (09°55' S 144°05' E) 0-15 m; AIMS (BOX45) unregistered, Elizabeth Middleton Reef loc. 474. **New Caledonia**, IRD HS 2081 Ile Longue ST1159, Chesterfield Islands (19°52.710' S 158°18.720' E) 11. vii.2008 (coll. G. Lasne) 65 m. **French Polynesia**, MNHN unregistered, Tubua'i, Austral Islands, v.1979 (coll. J.P. Chevalier) 100 m («Marara» dredging).

◀ *Fig. 8*. Morphology and variability of skeletal structures in *Cycloseris wellsi* A-B) Holotype (USNM 44818) Bikini Atoll, Marshall Islands (53.38-76.25 m); C) specimen IRD HS 2081 Chesterfield Islands, New Caledonia; D) specimen UNIMIB MU102 Al Mukallah, Yemen; E) specimen UNIMIB KE 404 Kiunga, Kenya; F) ZMA Coel. 1071 ('Syntype' of *Psammocora explanulata*) Amirante, Seychelles (> 36.5 m); G) specimen UNIMIB S 061 Ras Nosrani, South Sinai, Egypt (24 m); specimen UNIMIB I 080 Mapia House Reef, Manado, Sulawesi (23 m).

Morphology. Animals polystomatous. Corallum attached (Fig. 1E-H). Colonies are encrusting and with a circular or oval outline (Fig. 1E-F), their margins sometimes detached from the substratum (Fig. 1E, G). Calices scattered over the corallum surface or in a serial arrangement especially towards the margins (Fig. 1F, G; Fig. 8). Calice diameter between 3.5 and 5.1 mm. Septa unequal and alternating, thicker septa may be more exsert than thinner ones (Fig. 8C). Six to 10 thicker septa may reach the fossa (Fig. 8). Interstomatous septa between calices up to 1.3 calices away from each other. In some corallites all septa reaching the fossa can be interstomatous (Fig. 8G). Elongated enclosed petaloid septa running parallel to interstomatous septa over the corallum surface are also commonly observed. These can be short and straight (Fig. 8C-E) or long and attain irregular shapes (Fig. 8H). Exsert tentacular lobes are typically observed on top of thicker septa and of enclosed petaloid septa, and at both ends of interstomatous septa in the holotype and in many specimens (Fig. 8B-C). However, they can be reduced and barely visible in other specimens (Fig. 8D-F). Septal margins are ornamented by septal paddles (Benzoni *et al*., 2007, Fig. 4B). Septal sides are ornamented by minute granules. Septa in *C. wellsi* are connected by fulturae (Benzoni *et al*., 2007, Fig. 5C). Columella always present, papillary, and formed by nine to 21 tightly packed vertical processes of equal size (Fig. 8H). Colony wall septothecal and compact, ornamented by fine costae (Veron and Pichon, 1980). Costae in *C. wellsi* and their ornamentation are very similar to those of *Lithophyllon mokai* (Hoeksema, 1989: Fig. 594).

Distribution. *Cycloseris wellsi* occurs throughout the Indo-Pacific. Based on the present material and published illustrations *C. wellsi* has been recorded from Egypt, Djibouti, Yemen, Socotra Island, Kenya, Seychelles, Mayotte, La Réunion, Thailand, Indonesia, Vietnam, Malaysia, Philippines, Taiwan, Japan, Papua New Guinea, Australia, New Caledonia, Hawaii, and French Polynesia (Fig. 9).