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The name game: morpho-molecular species boundaries in the genus *Psammocora* (Cnidaria, Scleractinia)

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The morphometric and molecular boundaries between twelve *Psammocora* (Cnidaria, Scleractinia) nominal species were addressed. The type specimens of *Psammocora haimiana* Milne Edwards & Haime, 1851, *P. togianensis* Umbgrove, 1940, *P. folium* Umbgrove, 1939, *P. digitata* Milne Edwards & Haime, 1851, *Maeandroseris australiae* Rousseau, 1854, *P. samoensis* Hoffmeister, 1925, *P. superficialis* Gardiner, 1898, *P. profundacella* Gardiner, 1898, *P. nierstraszi* Van der Horst, 1921, *P. verrilli* Vaughan, 1907, and *P. albopicta* Benzoni, 2006, were analysed together with specimens from museum collections, including those depicted in widely cited taxonomic descriptions, and material collected for this study in different parts of the Indo-Pacific. Morphometric analyses of the dimensions of skeletal structures allowed the identification of groups of specimens with similar morphologies. Congruency between these groups and current species whose synonymies and descriptions were found in recent taxonomic references was, hence, investigated and the species revised. Finally, the phylogenetic relationships of a representative subset of specimens were reconstructed based on rDNA and COI, thus allowing a direct link between morphologic and genetic information. Incongruence between type of morphology and literature descriptions was evidenced for some widely recognised species. Based on this integrated approach, five species were unambiguously identified.

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ADDITIONAL KEYWORDS: 5.8S – calice morphometry – enclosed petaloid septa – ITS – phylogeny – *Psammocora haimiana* – *Psammocora vaughani* – Scleractinian coral.

INTRODUCTION

Species in Scleractinia (Cnidaria, Anthozoa) are essentially described on the basis of skeleton morphology. However, the skeletal structures, especially of colonial corals, can be extremely variable and, thus, pose problems for the recognition of intraspecific vs. interspecific morphologic variability (Quelch, 1886; Bell, 1895; Gardiner, 1904; Vaughan, 1907; Veron & Pichon, 1976; Veron *et al*., 1977; Borel Best *et al*., 1984; Van Veghel & Bak, 1993; Wallace, 1999; Wolstenholme *et al*., 2003; Stefani *et al*., 2008b; Todd, 2008). Morphological plasticity, recent divergence between species or phenomena of reticulate evolution have been indicated as factors causing the overlap of intraspecific and interspecific variability. On the one hand, it has been shown that morphologic plasticity can be induced in variable proportions in different taxa by environmental conditions (Willis, 1985; Gittenberger, 2006) or genetic causes (Wallace & Willis, 1994; Knowlton *et al*., 1997; Miller & Babcock, 1997; Szmant *et al*., 1997; Dai *et al*., 2000; Levitan *et al*., 2004). However, the study of species specific skeletal plasticity has been undertaken, to date, for less than 2% of the known coral species (Todd, 2008). On the other hand, hybridisation in corals (Willis *et al*., 1992; Veron, 1995; Odorico & Miller, 1997; van Oppen *et al*., 2000; Vollmer & Palumbi, 2002, 2004; Miller & van Oppen, 2003; Wolstenholme *et al*., 2003) and its consequences for coral species morphology, as well as for

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the coral species concept itself, has proven to be significant in many cases, yet its level of influence is still under debate (Fukami *et al*., 2004). Furthermore, recent divergence between species was hypothesized to be the cause of subtle genetic differentiation and weak morphological differentiation in the genus *Platygyra* (Miller, 1992; Miller & Benzie, 1997; Mangubhai *et al*., 2007), and this is likely to occur in other taxa. Slow rates of molecular evolution, together with large population sizes and long generation times, which obscure the distinction between ancestral polymorphism and recent hybridisation, have been also suggested (Medina *et al*., 1999; van Oppen *et al*., 2000, 2001, 2002, 2004; Diekmann *et al*., 2001; Márquez *et al*., 2002; Wolstenholme *et al*., 2003; McFadden & Hutchinson, 2004). Hence, systematists and taxonomists may be confronted with the challenging task of species boundary delimitation in Scleractinia without knowing the exact extent of the role played by environmental or genetic factors in generating intraspecific morphologic variability. Since molecular techniques have become available, an increasing number of studies have addressed the phylogenetic relationships between hard coral taxa and evaluated their consistency. Suprageneric phylogenetic relationships (Lopez & Knowlton, 1997; Medina *et al*., 1999; van Oppen *et al*., 2000, 2001, 2002, 2004; Diekmann *et al*., 2001; Márquez *et al*., 2002; Wolstenholme *et al*., 2003; McFadden & Hutchinson, 2004; Fukami *et al*., 2008) as well as species boundaries have been pursued using molecular data to question traditional skeleton-based phylogenies. To date, species boundaries have been investigated by means of joint morphologic and molecular analyses in the genera *Montastraea* (Knowlton *et al*., 1992; Weil & Knowlton, 1994; Medina *et al*., 1999), *Acropora* (Wallace, 1999; Wolstenholme *et al*., 2003), *Montipora* (Stobart, 2000), *Platygyra* (Miller, 1994; Miller & Benzie, 1997; Mangubhai *et al*., 2007), *Porites* (Forsman, 2003), *Pocillopora* (Flot & Tillier, 2006), *Seriatopora* (Flot *et al*., 2008) and *Psammocora* (Benzoni *et al*., 2007; Stefani *et al*., 2008a and b) and in the family Fungiidae (Gittenberger, 2006). Concordance between morphologic and molecular taxa boundaries in corals was demonstrated in some cases (Potts *et al*., 1993; Budd *et al*., 1994; Stobart, 2000; Benzoni *et al*., 2007, Stefani *et al*., 2008b). However, in other cases molecular and morphologic investigations led to discordant results. However, another possible cause of the lack of morphologic and molecular congruity has been suggested to be the use of morphologic characters which can be highly variable both within and between species in response, for example, to environmental factors such as, for example, the colony growth form instead of corallite characters (Stefani *et al*., 2008b; Flot *et al*., 2008).

Skeletal structures in the Indo-Pacific coral genus *Psammocora* Dana, 1846, present peculiar features exclusively found in this taxon among the extant Scleractinia (see Benzoni *et al*., 2007, for a review). Species synonymies between some of the 24 nominal species described have been proposed by different authors (Veron & Pichon, 1976; Scheer & Pillai, 1983; Sheppard & Sheppard, 1991; Stefani *et al*., 2008b). Cairns *et al*. (1999) listed 11 valid *Psammocora* species, and Veron (2000) 12. However, synonymies were not indicated nor discussed in either case. Moreover, nomenclatural confusion due to incorrect subsequent spellings (International Code of Zoological Nomenclature art. 33.3) for some species in the genus exists. For example, the species name *P. haimiana,* originally published by Milne Edwards & Haime (1851), has been modified to *P. haimeana,* presumably starting from Klunzinger (1879), and used by several authors since (Veron & Pichon, 1976; Ditlev, 1980; Sheppard & Sheppard, 1991; Scheer & Pillai, 1983; Veron, 1986; Veron, 2000; Stefani *et al*., 2008a; Todd, 2008).

Recently, the validity of nominal species in *Psammocora* has been addressed through a joint morphologic and molecular approach. In a first attempt to study the species boundaries between *Psammocora contigua* (Esper, 1794), *P. digitata* Milne Edwards & Haime, 1851, *P. profundacella* Gardiner, 1898, and *P. haimeana* Milne Edwards & Haime, 1851, Stefani *et al*. (2008a) concluded that *P., digitata* and *P. contigua* were separate molecular and morphometric entities, whereas *P. haimeana* and *P. profundacella* could not be separated based on either corallite morphometrics or molecular analyses. However, although the authors based their specimen identification on widely cited references (Pillai & Scheer, 1976; Veron & Pichon, 1976; Scheer & Pillai, 1983; Sheppard & Sheppard, 1991; Veron, 2000), they did not examine the type material. In a later study Stefani *et al*. (2008b) examined the species boundaries among *P. contigua, P. obtusangula* and *P. stellata* including in their analyses the type specimens of 11 *Psammocora* nominal species characterised by a branching growth form. On the basis of combined and concordant morphometric and molecular evidence, and after type material re-examination, the authors retained two species only, *P. contigua* and *P. stellata*, and revised their synonymies. Finally, in a study of the phylogenetic relationships of the genus *Psammocora* with the rest of the genera currently recognised in the family Siderastreidae, both molecular and morphologic data provided concordant evidence that the species *P. explanulata* van der Horst, 1922, was genetically and structurally more closely related to the family Fungiidae than to any other *Psammocora* nominal species (Benzoni *et al*., 2007) and could, in fact, belong to that

family. Thus, the authors argued that the genus as currently defined including *P. explanulata* is not monophyletic. However, the other examined species in the genus all belonged to the same evolutionary lineage.

In this study we investigated the morphometric and molecular boundaries between the 12 *Psammocora* nominal species which, to date, have not been formally revised since their description. All examined species have been shown to belong to the same monophyletic clade (Benzoni *et al*., 2007) or have been widely synonymised with such species in the literature. Moreover, all present the typical skeletal characters exclusive (enclosed petaloid septa) to the genus. Unfortunately, the monophyly of the examined group of nominal species could not be verified based on type material genetic analyses as no tissue was available for any other type specimen but *P. albopicta*. *Psammocora haimiana* Milne Edwards & Haime, 1851, *Psammocora digitata, Maeandroseris australiae* Rousseau, 1854, *Psammocora folium* Umbgrove, 1939, *Psammocora togianensis* Umbgrove, 1940, *Psammocora superficialis* Gardiner, 1898, *Psammocora profundacella*, *Psammocora verrilli* Vaughan, 1907, *Psammocora nierstraszi* Van der Horst, 1921, *Psammocora samoensis* Hoffmeister, 1925, *P. vaughani* Yabe *et al*., 1936, and *Psammocora albopicta* Benzoni, 2006, type specimens were retrieved and their morphology analysed. *Psammocora* specimens in museum collections, including those depicted in widely cited taxonomic descriptions (Veron & Pichon, 1976; Sheppard & Sheppard, 1991) were studied, and material collected in different parts of the Indo-Pacific was analysed. Through an integrated morpho-molecular approach the following objectives were pursued: 1) the recognition of morphometric boundaries between the 12 nominal species, 2) a match between morphologic and molecular data in the examined taxa, and 3) a taxonomic revision including emended descriptions based on the results of the applied integrated approach.

MATERIAL AND METHODS

In this study museum specimens, including types, and specimens collected *ad hoc* were examined.

Museum abbreviations

BPBM – BP Bishop Museum, Honolulu, Hawaii
FBC – F. Benzoni Collection, Milan, Italy
IGPTU – Institute of Geology and Palaeontology, Tohoku University, Sendai, Japan
IRD – Institut de Recherche pour le Développement
MNHN – Museum National d'Histoire Naturelle, Paris, France
MSNM – Museo di Storia Naturale di Milano, Milan, Italy
MTQ – Museum of Tropical Queensland, Townsville, Australia
NHM – Natural History Museum, London, UK
RMNH – Rijksmuseum van Natuurlijke Historie, Leiden, the Netherlands
USNM – United States National Museum of Natural History, Washington, USA
ZMA – Instituut Voor Taxonomische Zoölogie (Zoölogisch Museum), Amsterdam, the Netherlands

Examined museum material

The type material of 10 described nominal *Psammocora* species, namely *Psammocora nierstraszi* (Figure 1A), *Psammocora verrilli* (Figure 1B), *Psammocora albopicta* (Figure 1D), *Psammocora samoensis* (Figure 1F), *Psammocora superficialis* (Figure 1G), *Psammocora profundacella* (Figure 1H), *Psammocora haimiana* (Figure 1I), *Psammocora togianensis* (Figure 1J), *Psammocora folium* (Figure 1K), and *Psammocora digitata* (Figure 1L) was examined. The holotype of *Maeandroseris australiae* (Figure 1E), designated as the type specimen of the subgenus *Plesioseris* Duncan, 1884, and later synonymised with *Psammocora* (Veron & Pichon, 1976), was also studied (Table 1). The type specimens of *P. vaughani* (IGPTU 44975, IGPTU 44971) were declared lost (Nemoto Yun, *in litteris*) and could not be examined. However, a very clear illustration of the holotype was given in the original species description. Part of the holotype picture in Yabe *et al*. (1936) is reproduced in Figure 1C. Three specimens collected in Hawai'i and registered at the Bishop Museum and identified as *P. vaughani* were included in this study. Specimens collected and identified by J.P. Chevalier from New Caledonia and Vanuatu registered at the MNHN were also analysed.

The *Psammocora* specimens in the AIMS Monograph Coral Collection at MTQ, on which Veron & Pichon (1976) based their landmark publication, were examined and photographed in 2004 with particular attention to the specimens shown in the monograph figures. *Psammocora* specimens depicted in Sheppard & Sheppard (1991) and deposited at the NHM were examined and photographed during a visit to the museum collections in 2005.

The term nominal species in this paper refers to taxa described based on skeleton morphology for which type material was deposited in a museum. All original descriptions of the nominal species examined were retrieved and studied.

Specimen collection

Corals for this study were collected while SCUBA diving between 2 and 30 m depth at different

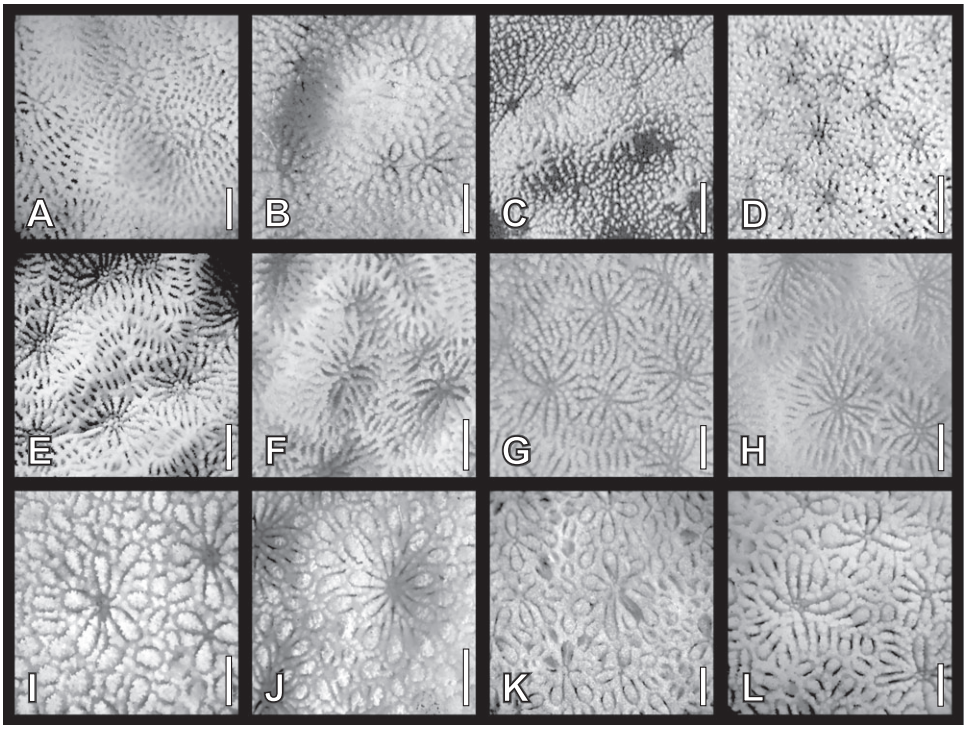


Figure 1. Type specimen corallite morphology of the *Psammocora* nominal species examined in this study: (A) ZMA COE 01078 *Psammocora nierstraszi* holotype; (B) USNM, 21637, *P. verrilli* holotype; (C) IGPTU 44975, *P. vaughani* holotype, reproduced from Yabe *et al*. (1936); (D) MSNM 332, *P. albopicta* holotype; (E) MNHN 521, *Maeandroseris australiae* holotype; (F) USNM 68209, *P. samoensis* syntype; (G) UMZC unnumbered, *P. superficialis* holotype; (H) UMZC unnumbered, *P. profundacella* holotype; (I) MNHN 535, *P. haimiana* holotype; (J) RMNH Coel. 10195, *P. togianensis* syntype; (K) RMNH Coel. 9360, *P. folium* holotype; (L) MNHN 533, *P. digitata* holotype. White scale bar = 1 mm.

Table 1. *Psammocora* type specimens analysed for this study

Genus species	Taxonomic authority	Museum No.	Type status	Code
Psammocora haimiana	Milne Edwards & Haime, 1851	MNHN 535	Holotype	haimi.
Psammocora digitata	Milne Edwards & Haime, 1851	MNHN 533	Holotype	digi.
Psammocora superficialis	Gardiner, 1898	UMZC unnumbered	Holotype	sup.
Psammocora profundacella	Gardiner, 1898	UMZC unnumbered	Holotype	prof.
Psammocora verrilli	Vaughan, 1907	USNM 21637	Syntype	verr.
Psammocora nierstraszi	Van der Horst, 1921	ZMA COE 01078	Holotype	nie.
Psammocora samoensis	Hoffmeister, 1925	USNM 68209	Syntypes	sam. a
		USNM 68210		sam. b
Psammocora folium	Umbgrove, 1939	RMNH Coel. 9360	Holotype	fol.
Psammocora togianensis	Umbgrove, 1940	RMNH Coel. 10195	Syntypes	tog. a
		RMNH Coel. 10196		tog. b
		RMNH Coel. 10197		tog. c
		RMNH Coel. 10198		tog. d
		RMNH Coel. 10199		tog. e
		RMNH Coel. 10200		tog. f
Psammocora albopicta	Benzoni, 2006	MSNM 332	Holotype	albo. a
		MSNM 333	Paratype	albo. b
		MSNM 335	Paratype	albo. c
Maeandroseris australiae	Rousseau, 1854	MNHN 521	Holotype	austr.

Taxonomic authority, type specimen registration numbers, type status and the code used in Figure 3 are given for each specimen.

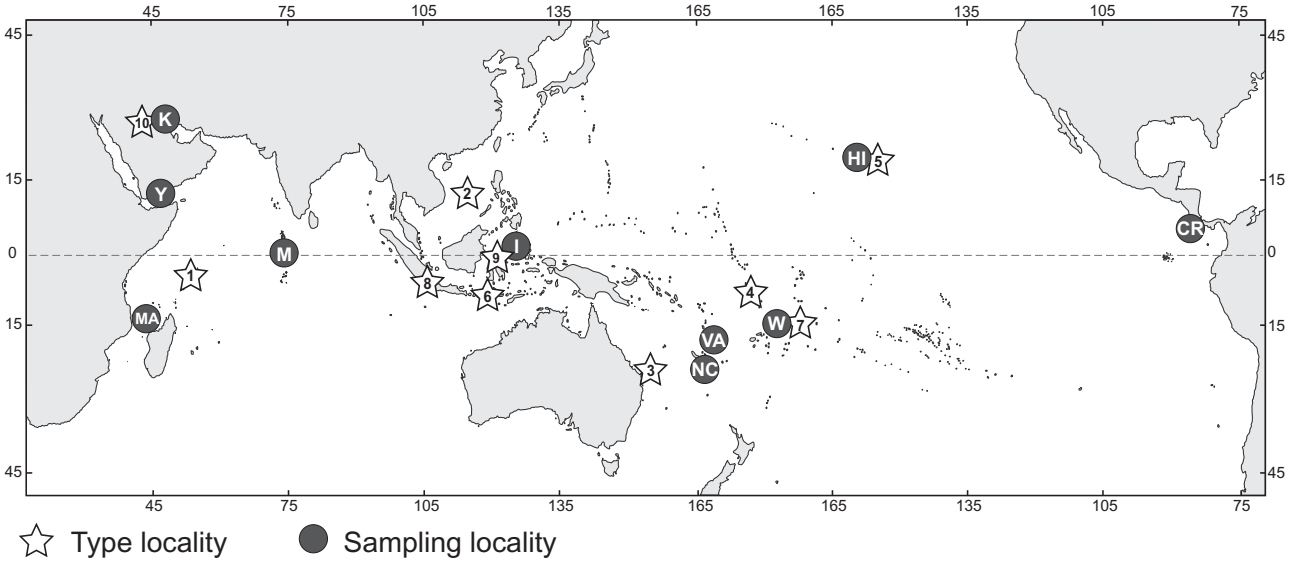


Figure 2. Map showing type localities (stars) of the examined nominal species and sampling localities (gray filled circles) of the specimens collected for this study (Table 2). Code for sampling localities: CR = Costa Rica; HI = Hawai'i; I = North Sulawesi, Indonesia; K,= Kuwait; M = Maldives; MA = Mayotte Island; NC = New Caledonia; W = Wallis Island; Y = Yemen. Numbers in the stars refer to type localities in Table 2.

localities in Kuwait, Yemen, Mayotte Island, Maldives, North Sulawesi (Indonesia), New Caledonia and Wallis Island (Figure 2). The specimen of *P. superficialis* from Costa Rica was collected and kindly provided by Jorge Cortés, and the specimen of *P. explanulata* from the Line Islands by David Obura. The list of all the *Psammocora* specimens examined is given in Table 2.

Coral specimens were collected, tagged and, for each specimen, 1 cm^2 was broken off the colony and preserved in absolute ethanol for molecular analysis. The remaining corallum was left for 48 hours in a 50% sodium hypochlorite solution at ambient temperature to remove all soft parts, rinsed in freshwater and dried for microscope observation.

Character measurement

Macrophotographs of the skeletons were taken with a Canon Powershot A620 camera through a Soligor B-52 Adapter Tube mounted on a Zeiss Stemi DV4 stereomicroscope. Five 20x and 10x non-overlapping digital images were shot. A 1-cm^2 ocular graticule was used as a reference scale. A corallite suitable for sampling of morphometric characters was defined for the purpose of this study as the largest corallite in a frame which was not undergoing any budding process.

Eight linear variables were measured on five different corallites for each examined specimen using Image Tool 3.00 (Wilcox *et al*., 1986–2001): m1 = minimum distance between calices within the enclosed series (from columella to columella); m2 = minimum distance between calices belonging to neighbouring enclosed series (from columella to columella); m3 = calice diameter; m4 = columella diameter; m5 = maximum width of petaloid septa reaching the fossa; m6 = maximum length of petaloid septa reaching the fossa; m7 = maximum width of enclosed petaloid septa; m8 = maximum length of enclosed petaloid septa. For a review of the unique septa arrangement and terminology of the genus *Psammocora* refer to Benzoni *et al*. (2007). Morphometric characters m1 and m2 were measured on 10x digital images, characters m3 to m8 on 20x frames.

Variables were log-transformed and tested for normality (Shapiro–Wilk's *W*-test) and homogeneity of variance (Levene's test). For each character the specimen mean was calculated from five replicates for each specimen.

Morphometric analyses and specimen identifications

The data set of the 19 type specimens (Table 1) was explored by means of multivariate statistics. The objective of the analyses was to identify groups of types sharing similar dimensions regardless of the synonymies proposed in the literature. The Primer v.5.2.9 (Primer-E Ltd. Plymouth, UK) statistical package was used to calculate and plot an unweighted pair group method with arithmetic mean (UPGMA) agglomerative hierarchical cluster analysis based on

Table 2. Material examined in this study through corallite morphometric and molecular analyses

Code	Species	Locality	TCM	rDNA	COI
K118	*albopicta*	Kuwait	B	AM230614	
K140	*albopicta*	Kuwait	B	FM986358	
K141	*albopicta*	Kuwait	B	FM986359	
K142	*albopicta*	Kuwait	B		
K154	*albopicta*	Kuwait	B		
K161	*albopicta*	Kuwait	B		
K162	*albopicta*	Kuwait	B		
MSNM 332	*albopicta*	Kubbar Island, Kuwait (10)	B		
MSNM 333	*albopicta*	Umm Al-Maradem, Kuwait	B		
MSNM 335	*albopicta*	Balhaf, Yemen	B		
Y219	*albopicta*	Balhaf, Yemen	B	FM986360	FM865871
Y221	*albopicta*	Balhaf, Yemen	B		
Y223	*albopicta*	Balhaf, Yemen	B		FM865872
Y226	*albopicta*	Balhaf, Yemen	B		
MNHN 20325	*digitata*	Belep, New Caledonia	E		
MNHN 20324	*digitata*	Belep, New Caledonia	E		
HS1376	*digitata*	Côte Oubliée, New Caledonia	E	FM986361	FM865873
HS1379	*digitata*	Côte Oubliée, New Caledonia	D	FM986362	
HS1746	*digitata*	Côte Oubliée, New Caledonia	E	FM986363	
HS1802	*digitata*	Côte Oubliée, New Caledonia	E	FM986364	
HS1818	*digitata*	Côte Oubliée, New Caledonia	E	FM986365	
I102	*digitata*	North Sulawesi, Indonesia	D	AM230609	AM494857
I87	*digitata*	North Sulawesi, Indonesia	D	FM986366	
I93	*digitata*	North Sulawesi, Indonesia	D	FM986367	
I97	*digitata*	North Sulawesi, Indonesia	D	FM986368	AM494856
M16	*digitata*	Maldives	D	AM749205	
M26	*digitata*	Maldives	D	AM749206	AM494855
M35	*digitata*	Maldives	D	AM230610	
M38	*digitata*	Maldives	D	AM749207	
MNHN 533	*digitata*	China Seas (2)	E		
MNHN 535	*digitata*	Seychelles (1)	D		
NC588	*digitata*	Côte Oubliée, New Caledonia	D	FM986369	FM865874
NC92	*digitata*	Côte Oubliée, New Caledonia	D		
MNHN 20322	*digitata*	Ile des Pins, New Caledonia	D		
MNHN 20323	*digitata*	Port Vila, Vanuatu	D		
RMNH Coel. 10195	*digitata*	Togian, Sulawesi, Indonesia (9)	D		
RMNH Coel. 10196	*digitata*	Togian, Sulawesi, Indonesia (9)	D		
RMNH Coel. 10197	*digitata*	Togian, Sulawesi, Indonesia (9)	D		
RMNH Coel. 10198	*digitata*	Togian, Sulawesi, Indonesia (9)	D		
RMNH Coel. 10199	*digitata*	Togian, Sulawesi, Indonesia (9)	D		
RMNH Coel. 10200	*digitata*	Togian, Sulawesi, Indonesia (9)	D		
RMNH Coel. 9360	*superficialis*	Jakarta, Indonesia (8)	D		
W534	*digitata*	Wallis Island	E		
W536	*digitata*	Wallis Island	E		
W546	*digitata*	Wallis Island	E		
W570	*digitata*	Wallis Island	E		
W612	*digitata*	Wallis Island	E	FM986370	FM865875
W613	*digitata*	Wallis Island	E	FM986371	FM865876
W615	*digitata*	Wallis Island	E	FM986372	FM865877
W616	*digitata*	Wallis Island	E	FM986373	
I82	*haimeana*	North Sulawesi, Indonesia	C		
I96	*haimeana*	North Sulawesi, Indonesia	C	FM986374	
M5	*haimeana*	Maldives	C	AM749219	
M17	*haimeana*	Maldives	C	AM749216	

Table 2. *Continued*

Code	Species	Locality	TCM	rDNA	COI
M27	*haimeana*	Maldives	C	AM749222	
M28	*haimeana*	Maldives	C	AM749217	
M30	*haimeana*	Maldives	C	AM749218	
M33	*haimeana*	Maldives	C	AM749221	
I107	*nierstraszi*	North Sulawesi, Indonesia	A		
I83	*nierstraszi*	North Sulawesi, Indonesia	A	FM986375	
I84	*nierstraszi*	North Sulawesi, Indonesia	A	FM986376	
I88	*nierstraszi*	North Sulawesi, Indonesia	A		
I89	*nierstraszi*	North Sulawesi, Indonesia	A	FM986377	
I90	*nierstraszi*	North Sulawesi, Indonesia	A	FM986378	
I95	*nierstraszi*	North Sulawesi, Indonesia	A	FM986379	
M36	*nierstraszi*	Maldives	A		
M42	*nierstraszi*	Maldives	A	FM986380	
M43	*nierstraszi*	Maldives	A	AM230606	FM865878
MA234	*nierstraszi*	Mayotte	A	FM986381	
MA250	*nierstraszi*	Mayotte	A		
W135	*nierstraszi*	Wallis Island	A		
W144	*nierstraszi*	Wallis Island	A		
ZMA COE 01078	*nierstraszi*	Sumbawa, Indonesia (6)	A		
I100	*profundacella*	North Sulawesi, Indonesia	C		
I113	*profundacella*	North Sulawesi, Indonesia	C	FM986382	
I91	*profundacella*	North Sulawesi, Indonesia	C	AM230615	
I98	*profundacella*	North Sulawesi, Indonesia	C		
M10	*profundacella*	Maldives	C	AM230616	
M15	*profundacella*	Maldives	C	AM749215	
M18	*profundacella*	Maldives	C	AM230619	FM865879
M31	*profundacella*	Maldives	C	AM749224	
M34	*profundacella*	Maldives	C	AM749225	
M6	*profundacella*	Maldives	C	AM749223	
M7	*profundacella*	Maldives	C	AM230617	AM494853
M9	*profundacella*	Maldives	C	AM230618	
MNHN 521	*profundacella*	Australia (3)	C		
CR335	*superficialis*	Costa Rica	C	FM986383	
UMZC unnumbered	*profundacella*	Funafuti, Tuvalu (4)	C		
UMZC unnumbered	*superficialis*	Funafuti, Tuvalu (4)	C		
USNM 68209	*profundacella*	Tutuila, Samoa (7)	C		
USNM 68210	*superficialis*	Tutuila, Samoa (7)	C		
MA489	*superficialis*	Mayotte Island	A		
MA254	*superficialis*	Mayotte Island	A		AM494850
MA245	*superficialis*	Mayotte Island	A		
MA240	*superficialis*	Mayotte Island	A	FM986384	
MA239	*superficialis*	Mayotte Island	A	FM986385	
M54	*superficialis*	Maldives	A	FM986386	
USNM 21637	*verrilli*	Molokai,Hawai'i (5)	A		
BM SC207	*verrilli*	Molokai,Hawai'i	C		
BM SC1105	*verrilli*	Oahu, Hawai'i	A		
BM SC1104	*verrilli*	Oahu, Hawai'i	C		

For each *Psammocora* specimen code, species identification based on published morphologic descriptions or current synonymy for type specimens, sampling locality, type cluster morphology (TCM) identification, the presence and the EMBL codes of ITS and COI sequences are given. The number in brackets after the sampling locality for type specimens refers to the nominal species type localities in Figure 2.

the Bray-Curtis distance. Principal component analysis (PCA) was performed with Statsoft Statistica (v. 4). The skeleton morphology of the type specimens that were grouped together based on the morphometric analysis results was then described, and the term type cluster morphology (TCM) used. Each TCM was coded with the same capital letter used to identify the cluster it was typical of. No a *priori* assumptions were made with regard to either nominal species or TCMs being monophyletic or reproductively isolated biological entities.

The 101 specimens in Table 2, thus including both type and non-type specimens, were examined and independently identified twice as follows: the first time based on the TCM described in this study and the second time based on the skeleton morphology described and illustrated in widely cited taxonomic descriptions. In addition to the original descriptions, several publications containing descriptions and illustrations of the *Psammocora* species under investigation were examined (Klunzinger, 1879; Pillai & Scheer, 1976; Veron & Pichon, 1976; Ditlev, 1980; Faure, 1982; Scheer & Pillai, 1983; Veron, 1986; Sheppard & Sheppard, 1991; Nishihira & Veron, 1995; Veron, 2000; Fenner, 2005). Most of the species morphologies described and illustrated in the different publications were concordant with each other, with the one main exception being Sheppard & Sheppard (1991). Hence, based on completeness of the species treated and quality of skeleton illustration, as well as the fact that the illustrated specimens could be studied, it was decided to refer to Veron & Pichon (1976) and Veron (2000). Discrepancies between these two references and Sheppard & Sheppard (1991) are treated in the discussion. For specimens deposited in collections the identification on the museum label was verified with literature and then used as literature-based identification.

No photographic sampling for morphometric analysis was performed on either MTQ or NHM specimens published in Veron & Pichon (1976) and Sheppard & Sheppard (1991), respectively. However, since detailed photographic documentation including the scale of the specimens was accumulated at the time of the museum visits, specimens could be re-identified based on TCM.

Multivariate analyses were performed on the whole data set, including type and non-type specimens, and maintaining in parallel both identifications. Corallite morphometric data of all the specimens (Table 2) were explored by means of PCA. The biplot of the first two principal components was examined to verify whether any distinct group of specimens could be distinguished. The congruency between groups of specimens found in the PCA plot and groups based on the taxonomic literature as well as TCM was hence examined. The data set was then subjected to discriminant analysis (DA) using the General Discriminant Analysis module of Statsoft Statistica (v. 4). The analysis was performed twice using different a *priori* groups: the first time using literature-based species identifications and the second time using TCMs. Correlations between discriminant functions and initial variables and the classification success rate of DA were calculated in both analyses.

A multivariate analysis of variance (MANOVA) was performed using Statsoft Statistica (v. 4) to test for significant differences between groups of specimens. Then, separate analyses of variance and *post-hoc* comparisons of means were performed to interpret the MANOVA results for each variable. Turkey's test for unequal sample size (Spjotvoll & Stoline, 1973) was used for *post-hoc* comparisons of means. Alpha values were adjusted using the Bonferroni correction for multiple tests taking into account the average variable correlation (Simes, 1986).

Molecular analyses

Total DNA was extracted and purified from each colony using the DNAeasy® Tissue kit (QIAGEN, Qiagen Inc., Valencia, California, USA) reagents.

Two molecular markers, a portion of rDNA and a portion of mtDNA COI gene, were selected in order to build phylogenetic relationships. The two selected markers have proved informative at different and complementary phylogenetic levels. In scleractinian corals rDNA is better suited for phylogenetic inference at intrageneric and intraspecific level (Chen *et al*., 2004; Wei *et al*., 2006). Conversely, COI showed better resolution at a higher systematic level due to the intrinsic slow evolutionary rate of mtDNA (Shearer *et al*., 2002; Hellberg, 2006; Shearer & Coffroth, 2008; Huang *et al*., 2008). Equilibration of the extracted DNA solutions was performed at about 3 ng/µl. A fragment of ~700 bp of the rDNA spanning a portion of the 5.8S gene, the entire ITS1, 5.8S, ITS2 regions, and a portion of the 28S gene was amplified by PCR using the primers A18S (Takabayashi *et al*., 1998) and ITS4 (White *et al*., 1990). Reactions were conducted in a 50 µl PCR mix consisting of 1X PCR buffer, 2 mM MgCl2, 0.4 mM of each primer, 0.1 mM of each dNTP, 2 U Taq DNA polymerase (Sigma-Aldrich Co., St. Louis, Montana, USA) and 8 µl of DNA solution. The thermal cycle included an initial denaturation phase at 96 °C for 2′, followed by 30 cycles composed of three steps – (1) 10″ at 96 °C (2) 30″ at 50 °C (3) 4′ at 72 °C – and, finally, an extension phase at 72 °C for 5′. A portion of 458 bp of the mtDNA COI gene was amplified using either the primers FungCOIfor and FungCOIrev (Gittenberger, 2006) or the primers MCOIF and MCOIR (Fukami

et al., 2004). Reactions were set up in a 50 μl PCR mix containing 1X PCR buffer, 2mM $MgCl_2$, 0.4 mM of each primer, 0.01 mM dNTP, 5 U of Taq polymerase and 8 μl of equilibrated DNA solution. The thermal cycle consisted of an initial phase at 94 °C for 4′, followed by 45 cycles composed of three steps – (1) 10″ at 94 °C (2) 1′ at 53 °C (3) 1′ at 72 °C – and, finally, an extension phase at 72 °C for 5′.

The amplified samples were purified using commercial kits. Sequencing reactions were carried out in both directions using a dideoxy-dye-terminator method (CEQ™ DTCS-Quick Start kit, Beckman Coulter) and a Beckman Coulter CEQ™ apparatus, using the same primers employed in PCR.

The rDNA sequences were aligned with other homologous ones obtained from previous work (Stefani *et al*., 2008b, Benzoni *et al*., 2007) in order to enlarge the specific data set. Consequently, only a portion of the 320 homologue positions, spanning part of the 5.8S gene (141 bp) and part of the ITS2 region (179 bp), was used for phylogenetic inference. Alignment was conducted via the software ClustalX (Thompson *et al*., 1997) and then manually checked and adjusted with BioEdit 5.0.9 (Hall, 1999). Identification of polymorphic and parsimony informative sites was conducted using DnaSP 3.52 software (Rozas & Rozas, 2001).

In order to confirm the monophyly of the *Psammocora* species examined in this study COI sequences of *P. explanulata* (AM494878), *Horastrea indica* (AM494864), *Fungia seychellensis* (AM230627), *Coscinaraea monile* (AM494858) and *Anomastraea irregularis* (AM494870) of the same specimens used for the rDNA analyses in Benzoni *et al*. (2007) were included. *Siderastrea* was not included as the genus has been shown to belong to the Complex clade while *Psammocora, Coscinaraea* and *Fungia* to the Robust clade (Romano & Palumbi, 1996; Fukami *et al*., 2008), therefore monophyly of the *Psammocora* species examined in this study was analysed referring to the most closely related taxa (Benzoni *et al*., 2007).

Prior to phylogeny reconstruction, the best sequence evolution model for both data sets was selected using Modeltest 3.06 (Posada & Crandall, 1998) according to a likelihood ratio test (LRT). Phylogenetic relationships were inferred under Bayesian (Huelsenbeck *et al*., 2001; Huelsenbeck & Ronquist, 2001) and maximum likelihood approaches. Bayesian analysis was run by starting four Markov chains from random trees and running them for 3000 000 (1000 000 for the COI data set) generations, with the first 2900 000 (900 000 for COI data set) generations discarded as the burn-in. The analysis was run independently four times and monitored to ensure that the standard deviation of split frequencies was < 0.01. ML analysis was performed using a heuristic search with random addition sequence, based on branch swapping with tree-bisection-reconnection (TBR), using PAUP4b10 (Swofford, 2001). The ML starting tree was obtained via stepwise addition and replicated 10 times, starting each replicate with a random input order of sequences. A bootstrap procedure with 1000 replications was applied to estimate confidence in the nodes of the ML trees using a heuristic search (TBR branch swapping, random addition sequence). Two matrixes of p- distances among the nominal species were generated for both data sets.

Terminology

In this paper we have deliberately decided to use the Milne Edwards & Haime (1851) name *P. haimiana* when referring to the species holotype and its morphology, and *P. haimeana* when referring to literature-based identification.

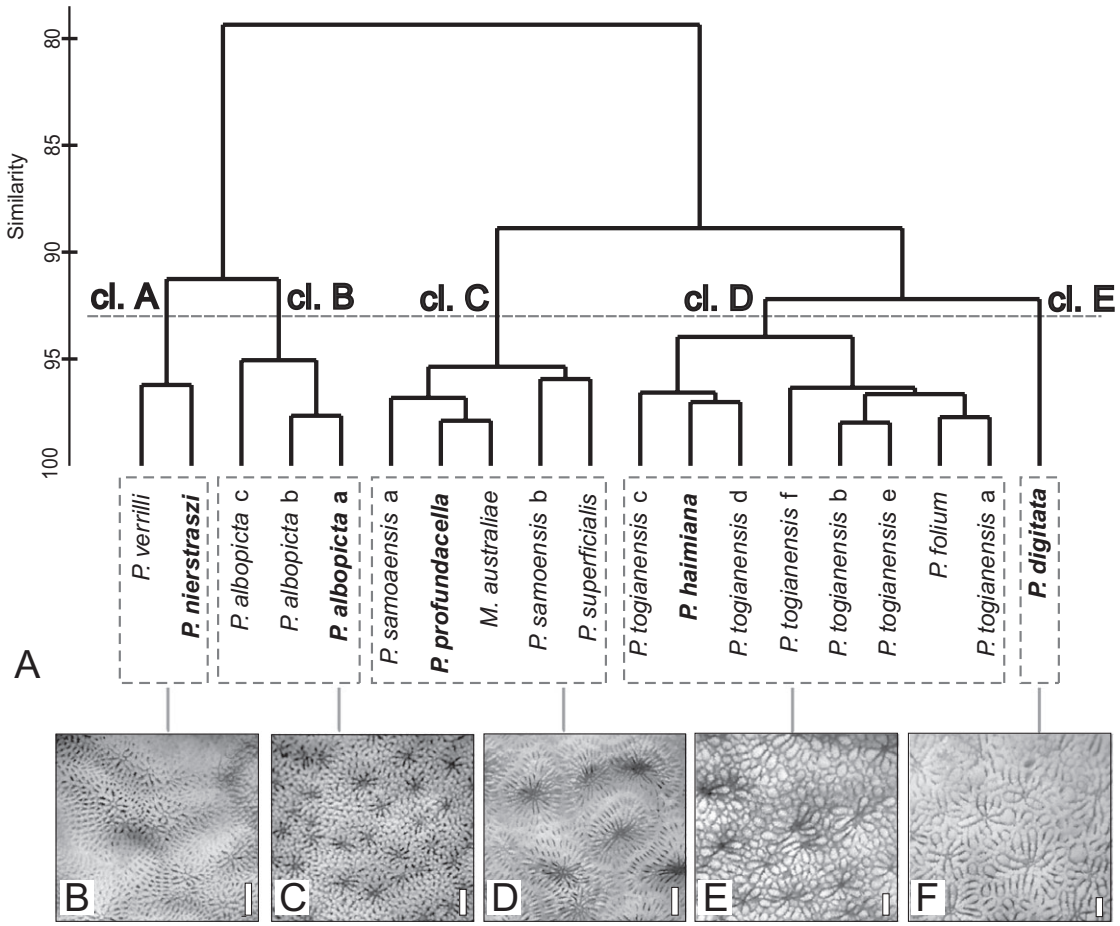
RESULTS

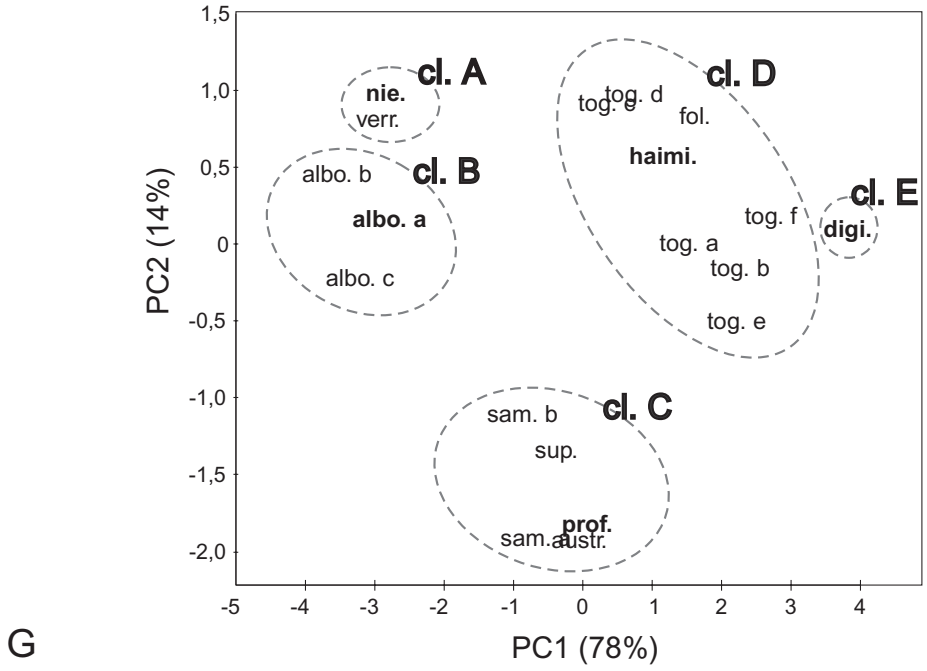
Type specimen grouping based on morphometric analyses

Multivariate exploration of the type material data set by hierarchical cluster analysis allowed grouping together of type specimens with similar corallite dimensions (Figure 3A). The dendrogram was arbitrarily cut off at 93% similarity to include in the same group all the syntypes of *P. togianensis*. Five discrete clusters (cl.) coded by the capital letters A to E were identified (Figure 3A). The type cluster morphology is described hereafter.

Cluster A – *Psammocora nierstraszi* (Figure 1A) and *P. verrilli* (Figure 1B) holotypes. Both specimens present small calices (0.8–0.9 mm in diameter), up to 3 petaloid septa reaching the fossa and a styliform columella. Calices are arranged in series up to 6 or more calices long, and up to 16 enclosed petaloid septa apart (Figure 3B). Acute ridges often separate parallel series and can sometimes form hydnophoroid protuberances (Figure 1B).

Cluster B – The holotype and two paratypes of *P. albopicta* (Figure 1D) form this cluster (Figure 3A). Although the calice size is similar to that of cluster A specimens (0.9–1 mm), all specimens present a maximum of 2 series of enclosed petaloid septa around each calice. Up to 4 septa reaching the fossa are petaloid, but often the petaloid shape is less marked than in the other cluster morphologies. Hence, in cluster B specimens (Figure 3C) the calices are closer to each other than in cluster A specimens (Figure 3B). Calices are never arranged in long series, and sometimes the serial arrangement is not visible (Figure 3C). Ridges between series of calices seldom occur and are never acute but rounded.


Similarity
80
85
90
95
100
cl. A
cl. B
cl. C
cl. D
cl. E
P. verrilli
P. nierstraszi
P. albopicta c
P. albopicta b
P. albopicta a
P. samoaensis a
P. profundacella
M. australiae
P. samoensis b
P. superficialis
P. togianensis c
P. haimiana
P. togianensis d
P. togianensis f
P. togianensis b
P. togianensis e
P. folium
P. togianensis a
P. digitata
A
B
C
D
E
F


cl. A
nie.
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cl. B
albo. b
albo. a
albo. c
cl. D
tog. d
tog. c
fol.
haimi.
tog. f
cl. E
digi.
tog. a
tog. b
tog. e
cl. C
sam. b
sup.
prof.
sam.a
austr.
PC2 (14%)
PC1 (78%)
1,5
1,0
0,5
0
-0,5
-1,0
-1,5
-2,0
-5
-4
-3
-2
-1
0
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2
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G

Figure 3. Morphometric analyses of the *Psammocora* type specimens examined and type clusters definition. (A) Hierarchical Cluster Analysis dendrogram; Clusters (cl.) identified by capital letters from A to E. Groups of type specimen names belonging to the same cluster are delimited by a dashed line filled in grey. Type specimens in bold indicate the nominal species described first in each cluster and whose corallite morphology is illustrated in the pictures: (B) cl. A, *P. nierstraszi* ZMA COE 01078; (C) cl. B, *P. albopicta* MSNM 332; (D) cl. C, *P. profundacella* UMZC unnumbered; (E) cl. D, *P. haimiana* MNHN 535; (F) cl. E, *P. digitata* MNHN 533. All white scale bars = 1 mm. (G) Principal component analysis plot of the first two PC. Percentages of variance are given next to each PC in brackets. Dashed ellipses filled in grey include type specimens belonging to the clusters defined in A) as indicated by the letter code. Specimen codes in the PCA plot are listed in Table 1.

Cluster C – *Maeandroseris australiae* (Figure 1E), both *P. samoensis* syntypes (Figure 1F), *P. superficialis* (Figure 1G), and *P. profundacella* (Figure 1H) holotypes are grouped in this cluster. Calices are between 1.4 and 1.7 mm in diameter, the columella is made of one central process surrounded by 4–6 granules positioned at the inner end of the septa and up to 6 septa reaching the fossa are petaloid. Calices occur singly or in short series enclosed by 2–5 enclosed petaloid series (Figure 1E–H, 3D), and ridges between calice series are acute forming a characteristic 'ladder pattern' (Veron & Pichon, 1976; Stefani *et al*., 2008a).

Cluster D – The holotypes of *P. haimiana* (Figure 1I), *P. folium* (Figure 1K) and all syntypes of *P. togianensis* (Figure 1J) are grouped in cluster D. Calices are 1.9–2.3 mm in diameter, with up 6 petaloid septa reaching the fossa. The columella is formed from 1 to 4 granules. Specimens present a maximum of 2 series of enclosed petaloid septa around each calice. Calices are never arranged in long series, but sometimes short (2–4 calices) series are visible (Figure 3E). Ridges between series of calices seldom occur and are never acute but rounded.

Cluster E – *Psammocora digitata* holotype (Figure 1L) forms a singleton in the cluster analysis dendrogram (Figure 3A). However, as shown by the PCA plot, this specimen is closer to the rest of the specimens grouped in cluster D than to any other examined specimen. The main features of this specimen are that it has the largest calice diameter among all examined type specimens (2.9 mm on average) (Figure 3F) and that there are up to 8 petaloid septa reaching the fossa, more than in any other type specimen. The columella is made up of 1–5 processes. The calices are seldom arranged in series, and ridges between series of calices are absent. When series occur they are a maximum of 4 calices long (Figure 3E).

The same groups of type specimens obtained by cluster analysis could be recognised on the PCA plot of the first two principal components (Figure 3G). Principal component 1 (PC1) and principal component 2 (PC2) accounted for 92% of the total data set variance, thus suggesting that the information was redundant for most of the characters used in the analysis. PC1 was highly correlated with all the variables examined ($r > 0.5$ for each variable). The strongest correlations occurred with the calice diameter (m3, $r = 0.97$) and the lengths of both petaloid septa and of the enclosed petaloid septa (m6 and m8, $r = 0.95$). PC2 was positively correlated to the diameter of the columella (m4, $r = 0.75$) and negatively to the maximum width of the petaloid septa reaching the fossa (m5, $r = -0.55$).

Specimens identifications

Each examined specimen was identified twice: first based on taxonomic descriptions (Veron & Pichon, 1976; Veron, 2000) and second on TCM descriptions given in the previous section (Table 2). For type specimens, species synonymies proposed in the taxonomic literature (Veron & Pichon, 1976; Veron, 2000) instead of the identifications based on taxonomic descriptions are given. The literature-based identifications matched the type specimens cluster-based identifications in some cases. Each specimen identified as *P. nierstraszi*, *P. albopicta* or *P. profundacella* was assigned to TCM A, B or C, respectively. However, of the eight specimens identified as *P. superficialis,* six were identified as TCM A and two as TCM C. Two specimens identified as *P. verrilli* (BM SC207 and BM SC1104 J. Wells *id*.) were identified as TCM C and one (BMSC, 1105, J. Wells *id*.) as TCM A, like the species holotype. Specimens identified as *P. digitata* showed either type cluster D or E morphology. Surprisingly, each specimen identified as *P. haimeana* based on literature descriptions showed TCM C morphology, unlike the holotype which fell in type cluster D (Figure 3A) together with *P. togianensis* and *P. folium* type specimens.

In the case of specimens described and illustrated in Veron & Pichon (1976) and Sheppard & Sheppard (1991), the original authors' and the TCM identifications are given in Table 3. In most cases, except *P. profundacella* specimens, the species identifications given by the authors and the TCM identifications based on type material examined in this study did not match (* in Table 3). In other words, the species

Table 3. Examined *Psammocora* specimens used to describe species morphologies in recent taxonomic descriptions

Code	Original identification	Ref.	Published figure	TCM
AIMS 624b	*P. nierstraszi*	1	Figs 23, 24	C*
MTQ G 57726	*P. nierstraszi*	1		A
NHM 1991.6.4.63	*P. haimeana* with '*nierstraszi*' characters	2	Fig. 67a	C*
MTQ G 35076	*P. superficialis*	1		C
MTQ G 57723	*P. superficialis*	1		A*
MTQ G 57724	*P. superficialis*	1		A*
NHM 1991.6.4.65	*P. haimeana* with '*superficialis*' characters	2	Fig. 67c	A*
MTQ G 35070	*P. profundacella*	1		C
MTQ G 35072	*P. profundacella*	1		C
MTQ G 35073	*P. profundacella*	1		C
MTQ G 35074	*P. profundacella*	1		C
MTQ G 35075	*P. profundacella*	1		C
MTQ G 46773	*P. profundacella*	1		C
MTQ G 46776	*P. profundacella*	1		C
MTQ G 46779	*P. profundacella*	1		C
MTQ G 46782	*P. profundacella*	1		C
MTQ G 57722	*P. profundacella*	1		C
AIMS 5340	*P. haimeana*	1	Figs 39, 40	C*
MTQ G 35060	*P. digitata*	1		D*
MTQ G 35064	*P. digitata*	1		D*
MTQ G 35065	*P. digitata*	1		D*
MTQ G 35066	*P. digitata*	1		D*
MTQ G 35068	*P. digitata*	1		D*
NHM 1991.6.4.64	*P. haimeana* with '*haimeana*' characters	2	Fig. 67b	C*

For each specimen registration code, species identification based on the published description, published reference, illustration in which it is depicted, and type cluster morphology (TCM) identification based on the results of this study are given. 1 = Veron & Pichon, 1976; 2 = Sheppard & Sheppard, 1991.
*indicates that the specimen TCM identification is different from the nominal species type material morphology.

names were used to describe specimens displaying skeleton morphologies different from the type material upon which the original description of the nominal species was based.

The specimen depicted in Veron & Pichon (1976) and identified as *P. nierstraszi* (AIMS 624b) displayed a typical TCM C, unlike the species holotype which has TCM A. However, another specimen identified by the same authors as *P. nierstraszi* (MTQ G 57726) showed TCM A skeletal features. Sheppard & Sheppard (1991) synonymised *P. haimeana*, *P. profundacella* and *P. nierstraszi* and gave a good illustration of specimen NHM, 1991.6.4.63 as a typical example of *P. haimeana* with '*nierstraszi*' characters. However, the specimen displayed TCM C features. Specimens identified as *P. superficialis* by Veron & Pichon (1976) showed either TCM A or C (like the holotype) characters. The specimen depicted in Sheppard & Sheppard (1991) and identified as *P. haimeana* with '*superficialis*' characters was identified as TCM A. All the examined specimens identified as *P. profundacella* and *P. haimeana* by Veron & Pichon (1976), as well as Sheppard & Sheppard's (1991) *P. haimeana* with '*haimeana*' characters, presented TCM C morphology (Table 3). However, the TCM of *P. haimiana* holotype is D. Finally, all MTQ specimens identified as *P. digitata* by Veron & Pichon (1976) showed TCM D characters, unlike the species holotype (TCM E).

Morphometric analyses of types and collected specimens

Eight morphometric variables were scored from 101 specimens. Hence, morphometric data for 505 corallites were collected for a total of 4040 measurements. PCA biplots of the averaged morphometric data for the examined specimens and the type specimens are shown in Fig. 4A and B. The first two principal components accounted for 87% of the total variance. Four groups of specimens were visible in the PCA plot (dashed grey ellipses numbered from 1–4 in Figure 4A and B). Each morphometric variable was strongly positively correlated with the first principal component (all correlation coefficients > 0.75 except for m4), thus also indicating correlation among linear variables. The strongest correlations were found

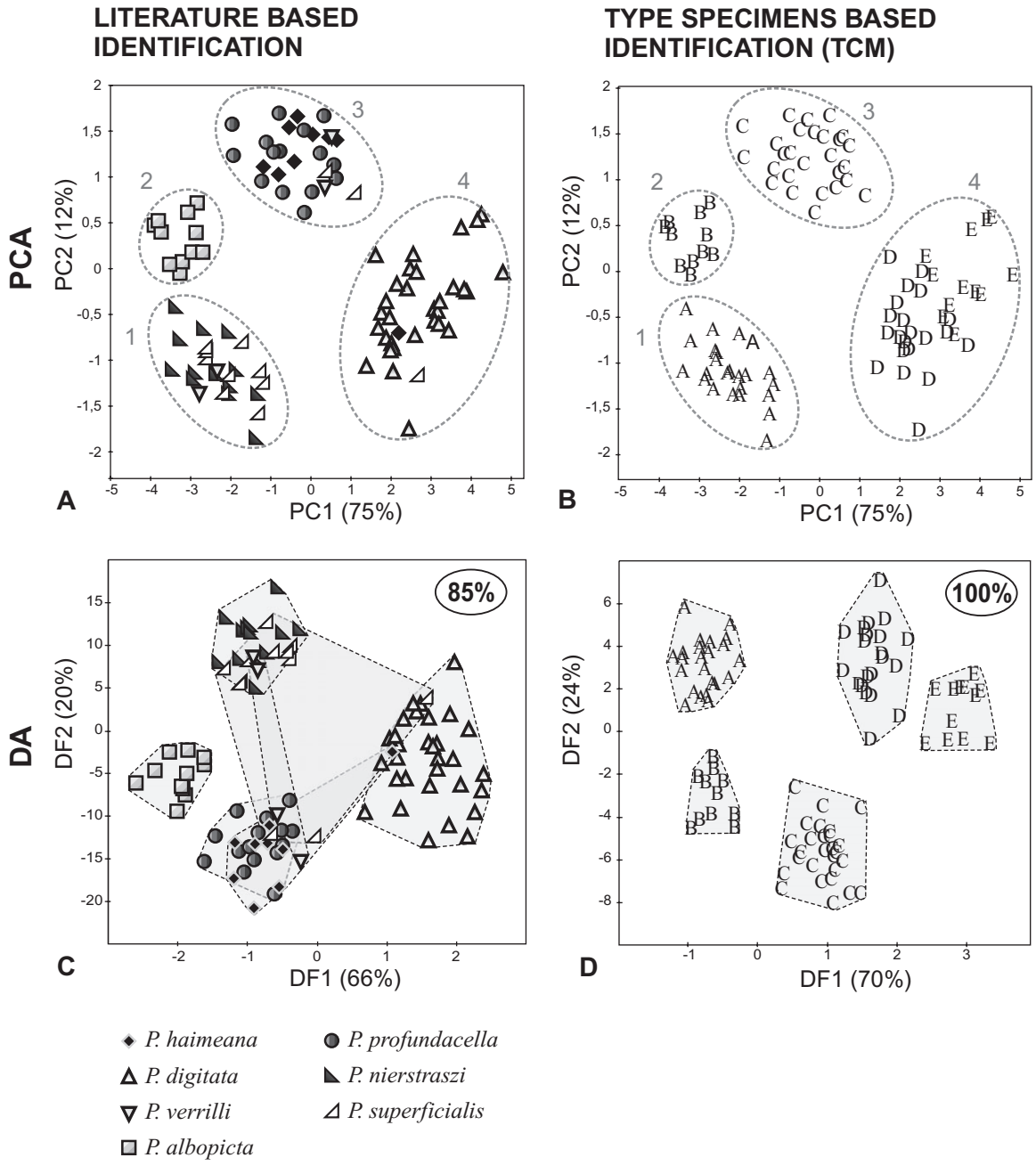


Figure 4. Morphometric analyses of all examined *Psammocora* specimens including types (Table 2). Each symbol or capital letter represents a specimen (average of 5 replicates). (A) and (B) are plots of the first two principal components (PC) showing the ordination of the specimens based on corallite morphometric variables. Each specimen is represented in the plot by (A), a symbol for species identifications based on the taxonomic literature, and (B), a capital letter corresponding to the type cluster morphology (Table 2). Groups of specimens visible in the plot are encircled by dashed ellipses and numbered arbitrarily from 1–4. (C) and (D) depict discriminant analysis of the same data set using as a *priori* groups (C), species identifications based on the taxonomic literature, and (D), type cluster morphology identifications. Grey filled dashed polygons include all specimens belonging to the same a *priori* group. The percentages of variance for each discriminant function (DF) are given in brackets. The overall correct classification rate for DA is in the oval at the top right corner of the plot. Legends for each symbol and capital letter are given in the figure.

between PC1 and variables such as the calice diameter (m3, r = 0.95), the length of the petaloid septa (m6, r = 0.95), the length of the enclosed petaloid septa (m8, r = 0.93) and the minimum distance between calices within the enclosed series (m1, r = 0.93). Correlations between initial variables and PC2 were very weak to modest. Only the diameter of the fossa (m4) presented a correlation coefficient strongly positively correlated with PC2 (r = 0.75).

Based on literature identifications, specimens of the same species were either concentrated in one group only or spread between two or three groups in the PCA plot (Figure 4A). Each specimen identified as *Psammocora nierstraszi*, *P. albopicta*, *P. profundacella* or *P. digitata* was found in group 1, 2, 3 or 4, respectively (Figure 4A). *Psammocora verrilli* specimens were split between groups 1 (the holotype and one specimen) and 3 (two specimens), *P. haimeana* between groups 3 (all specimens but the holotype) and 4 (the holotype). Finally, *P. superficialis* specimens were found in groups 1 (all non type specimens), 3 (the holotype) and 4 (*P. folium* holotype synonymised in the literature with *P. superficialis*).

Based on TCM a better match between specimen identifications and PCA groups was evident. Specimens with TCM C, A or B were found in group 1, 3 or 4, respectively (Figure 4B). In other words, each TCM of specimens corresponded to one group in the PCA plot with the exception of type cluster D and E morphologies, which were found in group 4 together (Figure 4B). However, within group 4, specimens showing TCM E and D could be separated in two sub-groups that only partially overlapped (Figure 4B).

Discriminant analysis of the corallite variables data set using literature-based identification as a *priori* groups yielded a correct classification rate of 85% (Figure 4C). For *P. profundacella*, *P. albopicta*, *P. nierstraszi* and *P. digitata* the correct classification rate was 100%, but *P. haimeana*, *P. verrilli* and *P. superficialis* had poor classification rates (Figure 4C). However, using type clusters as a *priori* groups increased the overall classification success to 100% (Figure 4D). Thus, TCM-based identifications better reflected the morphologic discontinuities in the database than literature-based identifications. Moreover, specimens characterised by TCM E and D were in two separated groups in the DA plot (Figure 4D). Characters most strongly correlated with DF1 using type cluster morphologies as a *priori* groups were calice diameter (m3, r = 0.87) and the enclosed petaloid septa length (m10, r = 0.85), indicating that the first discriminant function was strongly correlated with the corallites' size. The second discriminant function was positively correlated with enclosed petaloid septa thickness (m7, r = 0.53).

The multivariate analysis of variance result indicated that overall differences among groups was statistically highly significant ($p < 0.0001$). The analyses of variance between groups of specimens based on TCM identifications (Table 3) showed that significant differences between TCMs were found for each variable. However, pair-wise comparisons indicated that statistically significant differences existed between each pair-wise comparison for m8 only (Table 3). The ANOVA of each linear variable between specimens displaying TCM E and D showed that significant differences existed for all characters (m4 at $p < 0.05$; m1, m2 and m8 at $p < 0.01$; m3 and m6 at $p < 0.001$) except for the petaloid (m5) and enclosed petaloid septa width (m7). Specimens with TCM E were significantly larger than those with TCM D in all dimensions measured except m5 and m7.

Molecular boundaries

Molecular analysis provided reliable sequences for both markers. Polymorphism was not visible in rDNA electropherograms, yet intraindividual variability could not be ruled out since samples were not cloned and screened. Alignment of the rDNA portion was conducted on a total of 51 *Psammocora* specimens (Table 1) and one *Coscinaraea columna* (Dana, 1846) (W600) and two *Coscinaraea monile* (Forskål, 1775) sequences (CM5 and K122) as outgroups. A total of 29 polymorphic sites, 16 of which are parsimony informative, were identified. As expected, most of the variation was concentrated on the ITS2 fragment (27 variable positions, 15 of which are parsimony informative). A total of 32 haplotypes were identified, 7 of which are associated with multiple specimens. Among these, according to the literature-based specimen identification, haplotypes I96 (FM986374) and M6 (AM749223) were shared by specimens identified as *P. haimeana* and *P. profundacella*. However, based on TCM identifications, all haplotypes shared by multiple specimens were associated with a single type cluster morphology (Table 2).

Considering the high difference in evolutionary rates between 5.8S and ITS2 fragments, a partition was imposed on the dataset and different evolutionary models were associated with each fragment. In particular, a simple JC model was associated with the 5.8S fragment by hLRT, while according to AIC a K80 model was selected (Kimura, 1980). Differently, an HKY model (gamma correction = 0.2772) was selected by hLRT (Hasegawa *et al.*, 1985) for the ITS2 portion, while AIC criterion suggested a trasversional model (gamma correction = 0.3062). The analysis were performed using both the options and yielded congruent results. Bayesian and ML phylogeny reconstruction were performed to account for this partition and dif-

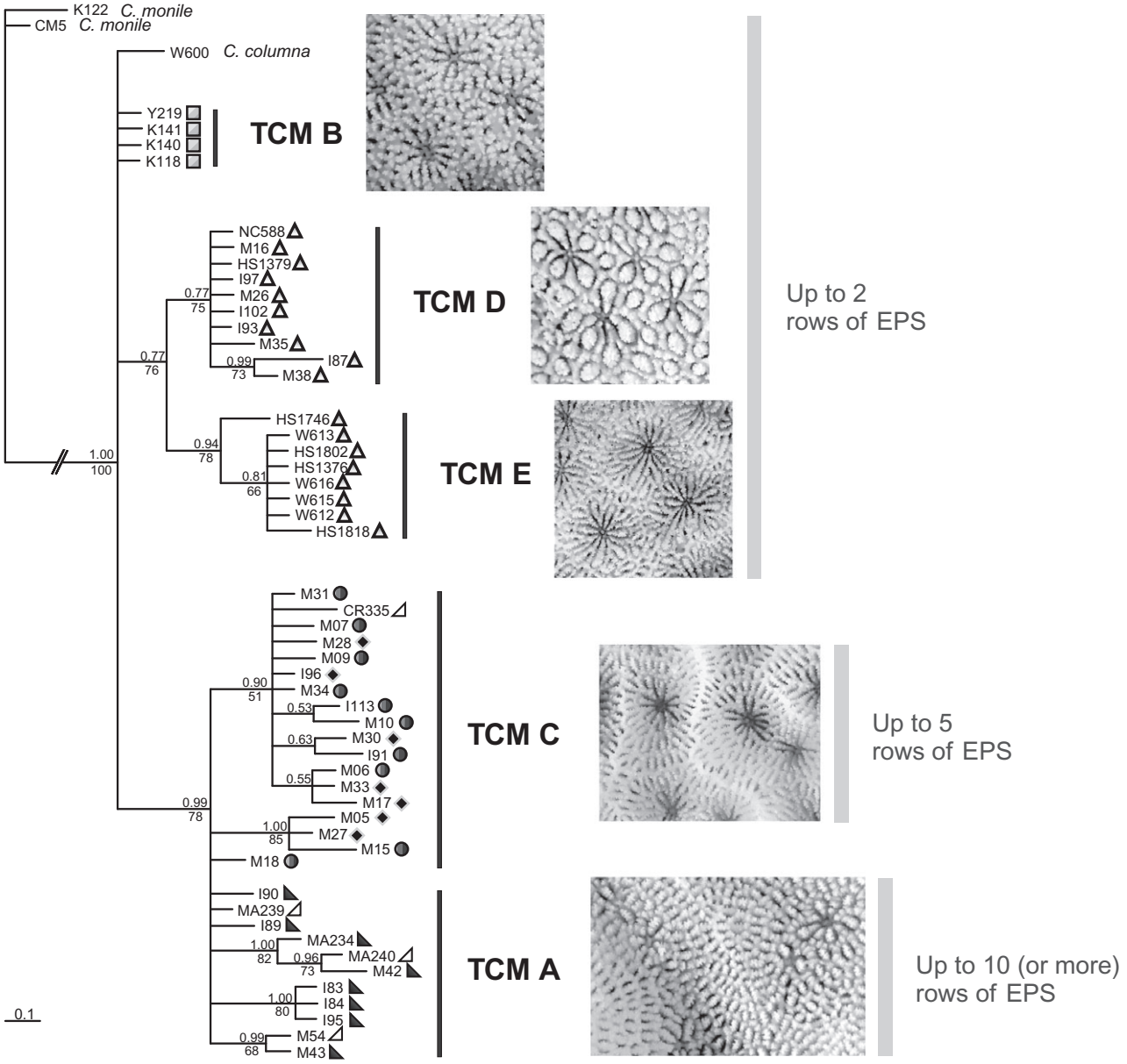


Figure 5. Phylogenetic relationships among the 51 rDNA *Psammocora* sequences, as obtained from Bayesian and ML analyses. At each node the a *posteriori* probabilities of the Bayesian analysis (above) and the bootstrap percentages (below) are reported. Species symbols are the same as in Figure 4. Type cluster morphology (TCM) descriptions are given in the text and illustrations in Figure 3.

ferent evolutionary patterns. Both analyses produced the same tree topology (Figure 5). Two main clades were evidenced, but different levels of support both by bootstrap and a *posteriori* probability were detected along the main nodes. One of the main clades included sequences associated with specimens all identified as *P. digitata* based on literature-based identification (Table 2; Figure 5). The same specimens, however, were identified as TCM E or D based on type cluster morphology (Table 2; Figure 5). Interestingly, in this first clade TCM E and D were shown to be reciprocally monophyletic, even though monophyly of clade TCM D is not strongly supported by a *posteriori* probability. Thus, the internal divergence in the clade seemed to match the differences between the two TCM also evidenced by the DA (Figure 4D) as well as by the analysis of variance on morphometric characters. The second main clade in the phylogeny showing extensive polytomy-related sequences of specimens was identified as TMC A or C. Internal sub-clades existed in this

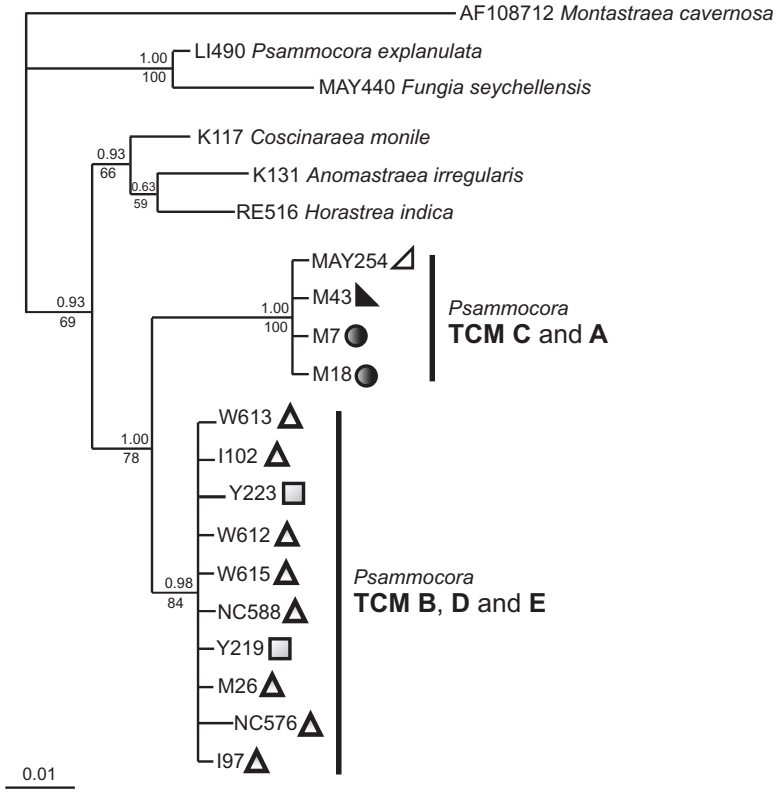


Figure 6. Phylogenetic relationships among the 14 COI *Psammocora* sequences, and sequences of *P*, *explanulata*, *Coscinaraea monile*, *Anomastraea irregularis*, *Horastrea indica*, and *Fungia seychellensis*, as obtained from Bayesian and ML analyses. At each node the a *posteriori* probabilities of the Bayesian analysis (above) and the bootstrap percentages (below) are reported. Species symbols are the same as in Figure 4. Type cluster morphology (TCM) descriptions are given in the text and illustrations in Figure 3.

clade, but no reciprocal monophyly. In particular, one main sub-clade was related to most of the TCM C sequences (Figure 5). All the TMC A sequences, plus the remaining four TCM C sequences, were organised in minor distinct sub-clades. According to literature-based identifications, specimens identified as *P. profundacella*, *P. haimeana*, *P. superficialis* and *P. nierstraszi* (Table 2) were included in this clade, in an unresolved and polyphyletic structure (Figure 5). Finally, TCM B sequences resulted paraphyletic and basal to the other clades. Hence, a better correspondence was attained between the molecular phylogeny and identifications based on TCM rather than on literature descriptions, even though a lack of strong resolution showed by some of the main clades, probably related to the low number of informative positions, was observed.

Mean intraspecific and minimum interspecific p-distances (Meier *et al*., 2008) were then calculated according to literature-based species identifications and to TCM (Table 5, supplementary material). The mean intraspecific distance of each species was lower than respective interspecific comparisons in 90% of cases when referred to TCM, while this percentage lowered to 47% when referred to literature-based species. Mean interspecific distances were significantly higher than mean intraspecific ones (Mann-Whitney test, $p < 0.05$) in both the cases. However, for TCM the intraspecific distances were lower (range 0.25–1.27) than for the literature-based species identifications (range of 0.81–1.46 excluding the monomorphic *P. albopicta*). Finally, the two main clades identified were 3.15 ± 0.51 (SD) divergent.

Alignment of the mtDNA COI fragment was conducted on 15 sequences of the studied *Psammocora* (Table 2), also including sequences of *P. explanulata*, *Horastrea indica*, *Fungia seychellensis*, *Coscinaraea monile* and *Anomastraea irregularis*, and of *Montastraea cavernosa* (AF108712) as an outgroup. Excluding the outgroup, a total of 39 polymorphic sites (23 parsimony informative) were detected, while no gaps were identified. The HKY model was selected by both hLRT and AIC criteria and phylogenetic reconstruc-

tion, which was performed according to Bayesian and ML criteria, yielded congruent results (Figure 6). Two main clades can be observed, the first one including *P. explanulata* and *F. seychellensis*, and a second one including *A. irregularis*, *H. indica*, *C. monile*, and the *Psammocora* species examined in this study (Figure 6) which resulted monophyletic. Within the subclade formed by the *Psammocora* species addressed in this study four haplotypes characterised the alignment, and were shared according to both the literature-based and TCM identifications (Table 2). In the first case, haplotype W613 was shared between *P. digitata* and *P. albopicta* (TCM B, D and E), while haplotype MA254 was shared between *P. superficialis*, *P. profundacella* and *P. nierstraszi* (TCM A and C). Within each clade, no resolution at species level could be observed. This was reflected in the mean values of intraspecific and the minimum interspecific distances (supplementary material), which were low or null, as in the case of the divergence between TMC A and TMC C. The divergence between the two main clades was estimated as 2.26 ± 0.069.

A phylogenetic analysis concatenating both datasets was also performed after having verified their congruence through a partition homogeneity test in Paup 4b10. In this case, only 12 combined sequences were available, and *P. superficialis* was not represented. The analysis confirmed the distinction of the two main lineages as identified by both the markers. In detail, within one clade the divergence of TCM E and TCM D clades was strongly supported (*a posteriori* probability > 0.90, bootstrap percentage > 90%), while TCM A and TCM C were unresolved in a single clade (data not shown).

DISCUSSION

The well documented intraspecific variability of skeletal characters in corals (Veron & Pichon, 1976; Veron, 1995; Todd, 2008) contributes to the complex and problematic picture of species name multiplication. It has been surmised that the holotype system is inadequate for characterising population level variability, and that in a population-based approach the holotype serves as an abstraction of the organism (Mayr, 1970). Despite its limitations, zoological nomenclature is still universally used, and well serves its purpose; however, the problems with the different nominal species which have been described still need to be addressed for the majority of Scleractinia. The advent of molecular phylogenetic analyses seems to have led some to think that species boundaries in corals should rely heavily on molecular markers, regardless of the still unsolved problems in a morphology-based taxonomy. Unfortunately, the molecular techniques developed during recent decades cannot assist in the study of type, and name bearing, specimens since only skeletal structures were traditionally preserved. Hence, the only means (also used in molecular phylogenies) of making comparisons between different type specimens of a genus and between them and other specimens is to refer to the variability of their skeletal structures via a morphometric approach. The need for studies integrating type material re-examination with the definition of morphologic boundaries in coral species based on variability quantification over large collections of specimens still poses a challenge in some taxa. The monographs by Veron & Pichon (1976; 1980; 1982), Veron and Wallace (1984) and Veron *et al*. (1977) represent the stepping stones for this integration. Studies tackling the revision of coral taxa through the examination of representative collections and referring to type material have been published so far on the genera *Leptoseris* (Dinesen, 1980), *Porites* (Jameson, 1997), *Montastraea* (Weil & Knowlton, 1994), *Acropora* (Wallace, 1999), *Montipora* (Stobart, 2000), *Psammocora* (Stefani *et al*., 2008b) and on the family Fungiidae (Hoeksema, 1989).

Given the morphologic plasticity of hard corals, the intra- and interspecies variability of the taxonomically informative skeletal characters should be assessed through a quantification of such variability. Morphometric studies undertaken to verify the statistical significance of morpho-species separation based on skeletal character dimensions have been conducted among the extant taxa on the *Montastraea annularis* species complex (Budd, 1993; Weil & Knowlton, 1994; Manica & Carter, 2000), on the *Acropora humilis* group (Wolstenholme *et al*., 2003), on two species in the genus *Montipora* (Stobart, 2000), on part of the genus *Porites* (Budd *et al*., 1994; Jameson, 1997), on the genus *Platygyra* (Miller, 1994; Miller & Babcock, 1997; Miller & Benzie, 1997), for three species in the genus *Pavona* (Maté, 2003) and for the branching species in the genus *Psammocora* (Stefani *et al*., 2008b). Although morpho-species have been, and still are, described based on skeletal morphology, measurements of the characters used in the descriptions are seldom published, the exceptions being few (Wallace, 1999; Maté, 2003; Benzoni, 2006). In fact, which morphologic characters should be considered for species level studies of various taxa is still unclear and needs further study. However, recent evidence seems to indicate that dimensions at the corallite level, rather than the corallum level, are the most informative and also show the best correlation with molecular phylogenies (Stefani *et al*., 2008a; Flot *et al*., 2008; Budd & Stolarski, 2009).

UNRAVELLING THE *PSAMMOCORA* NAME GAME

In this study of the boundaries between nominal species in the genus *Psammocora*, the morphometric analysis of type specimens and of a collection of museum and collected specimens unveiled the intricate name game which has been going on for more than a century in the taxonomic literature, and which we try to unravel here.

The morphometric study of calice and septa dimensions of examined *Psammocora* nominal species type material and of a large collection of specimens allowed us to pinpoint five clusters of types corresponding to five statistically distinct groups of specimens. The analysis of type material provided two different kinds of incongruence between the type morphology, on the one hand, and the current synonymies and species morphology descriptions on the other hand. First, as expected in any revision, currently recognised synonymies between species contrasted with the evidence of very different morphologies. Second, and more unexpected, the species holotype morphology and the same species morphology as commonly described in the current taxonomic literature had nothing in common.

Psammocora albopicta was the only straightforward case among those examined. The type cluster morphology (TCM B) described based on the species type material matched the morphology of the other specimens examined, and the differences between *P. albopicta* and similar species discussed in the original taxon description (Benzoni, 2006) were confirmed by morphometric (Figure 4) analyses in this study although based on molecular results it was unresolved (Figure 5). Morphologic affinities between *P. albopicta* and nominal species showing TCM coded as A (Figure 3), namely *P. nierstraszi* and *P. verrilli*, were also indicated by the non-statistically significant differences in some calice and septa dimensions (Table 4). However, overall the distinction of *P. albopicta* from other similar species was strongly supported. It is fair to say that *P. albopicta* is the most recently described species in the genus, and that its formal taxonomic description stemmed from an extensive study of the genus *Psammocora* (Benzoni, 2007) which also partially served as a reference for the present work.

Affinities between *P. nierstraszi* and *P. verrilli* have never been discussed in the literature before. However, in this study the holotypes of the two nominal species were grouped together in the same cluster (TCM A) (Figure 3). The use of type cluster morphology for the identification of examined material revealed a statistically supported group of specimens with homogeneous character dimensions (Figure 4), thus indicating that the two species names could refer to the same morphologically defined taxonomic unit. *Psammocora verrilli* was described in Hawai'i and is considered a rare species, endemic to the archipelago (Maragos, 1977; Veron, 2000; Fenner, 2005). Illustrations *in vivo* of *P. verrilli* specimens (Veron, 2000; Fenner, 2005) are scarce and do not show the characteristic skeletal features that should differentiate the species from the others. Illustrations of the skeleton are equally rare in the literature (Maragos, 1977; Veron, 2000) and are mostly limited to pictures of the type specimen. According to Veron (2000), *P. verrilli* is most similar to *P. superficialis* but the author did not mention any morphologic affinity between *P. verrilli* and *P. nierstraszi*. Curiously, the same author published corallite drawings of smaller corallites with a typically styliform columella as *P. superficialis*, and larger corallites with a complex columella as *P. nierstraszi*. Hence, in the corallite drawings Veron (2000) swapped the type material morphology between the two species. Specimens identified as *P. verrilli* in the examined museum collections are also limited. Besides the holotype only three specimens from the Bishop Museum could be studied. These revealed that under this species name have been grouped specimens with different morphologies ascribable to both typical TCM A

Table 4. One-way ANOVA results for differences between type cluster morphologies (TCM) defined in this study

	F	p	A–B	A–C	A–D	A–E	B–C	B–D	B–E	C–D	C–E	D–E
m1	92.0	***	n.s.	***	***	***	***	***	***	***	***	*
m2	49.2	***	***	n.s.	**	***	***	***	***	***	***	*
m3	505.1	***	n.s.	***	***	***	***	***	***	***	***	***
m4	49.2	***	**	***	***	***	***	***	***	***	n.s.	*
m5	94.2	***	*	n.s.	***	***	*	***	***	***	***	n.s.
m6	190.6	***	n.s.	***	***	***	***	***	***	***	***	***
m7	199.5	***	***	n.s.	***	***	***	***	***	***	***	n.s.
m8	107.6	***	***	***	***	***	***	***	***	***	***	*

* = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$; n.s. = not significant.

Table 5. Mean interspecific genetic distances between the five TCM identified (codes as defined in Figure 4), both for rDNA (% p-distances) and COI markers (% K2P distance)

	A	B	C	D	E
rDNA					
A	1.27 (0.64)				
B	2.17 (0.39)	0.00 (0)			
C	2.12 (0.49)	1.90 (0.26)	1.17 (0.76)		
D	3.28 (0.54)	0.92 (0.43)	2.95 (0.48)	0.32 (0.40)	
E	3.47 (0.45)	1.12 (0.30)	3.12 (0.43)	1.21 (0.34)	0.25 (0.31)
COI					
A	0.000 (0.000)				
B	0.110 (0.118)	0.220 (–)			
C	2.243 (0.005)	2.242 (0.006)	0.000 (0.000)		
D	2.239 (0.000)	2.237 (0.002)	0.000 (0.000)	0.00 (–)	
E	0.040 (0.087)	0.165 (0.156)	2.300 (0.105)	2.295 (0.104)	0.110 (0.121)

Standard deviation has been estimated and indicated in brackets when more than one comparison was available. Along the diagonal, intraspecific estimates are also reported.

and C (Figure 4A and C). The same was evidenced for specimens identified as *P. nierstraszi* based on, or described in, taxonomic descriptions (Figure 4A and C). For example, Veron & Pichon (1976) were correct when giving their description of *P. superficialis* in stating, 'We include in this species a series of specimens with a heterogeneous appearance'. The specimen they depicted as *P. nierstraszi* shows corallite characters typical of cluster B specimens (Table 3), but another specimen studied by the same authors in their monograph (MTQ G 57726) displays TCM A, like the species holotype (Table 3). In addition, Faure (1982) in his treatment of *P. superficialis* described the typical TCM A skeletal features of *P. nierstraszi*. Another example of confusion between TCM A and C in the literature is that of the *P. nierstraszi* morphology according to Sheppard & Sheppard (1991). The authors argued that *P. nierstraszi*, *P. haimeana*, *P. profundacella* and *P. superficialis* are all the same species with characters encompassing 'those of all four species as redescribed in Veron & Pichon (1976)' (Sheppard & Sheppard, 1991: 80). However, the specimen with '*nierstraszi*' characters displayed the typical TCM C morphology (Table 3). Conversely, the only specimen with TCM A in the same reference is that identified as having '*superficialis*' characters. This confusion is most likely due to the fact that *P. superficialis* and *P. nierstraszi* colonies with poorly developed walls and a rather smooth appearance may look similar to the naked eye. However, calice size, serial arrangement of the corallites and the number of rows of enclosed petaloid septa leave no doubt as to the separation of the two species. The results obtained in this study are, hence, in agreement with Scheer & Pillai's (1983) decision to keep *P. nierstraszi* separated from *P. haimeana*, *P. profundacella*, and *P. superficialis*.

Although the type material of *P. vaughani* has been declared lost (Benzoni *et al*., 2007) and could not be included in the morphometric analyses of types in this paper, the good illustrations of the specimens described by Yabe *et al*. (1936) allow some comments on the morphologic affinities between the lost type and those we examined. As shown in Figure 1, *P. vaughani* displays the typical morphology of TCM A like *P. nierstraszi* and *P. verrilli*. The authors themselves referred to the strong corallite similarities, despite the different colony growth form, between their new species type material and *Psammocora obtusangula* (Lamarck, 1816), a branching species recently synonymised with *Psammocora contigua* (Esper, 1794) by Stefani *et al*. (2008b). The corallite morphology and the dimensions of *P. contigua* and of the species characterised as TCM A in this study are very similar, and it cannot be excluded that further studies including all these species may show scarce morphometric differences between them, or none. *Psammocora vaughani* was also synonymised with *P. contigua* by other authors (Veron & Pichon, 1976; Scheer & Pillai, 1983), and with *P. superficialis* (Veron & Pichon, 1976). Finally, Veron (2000) re-established the species as a valid one. This being said, the corallite drawing and Figure 3 of the *P. vaughani* description in Veron (2000) illustrate a coral devoid of the typical *Psammocora* skeletal characters, namely the enclosed petaloid septa, which does not match either the original description or illustrations. The author himself states that the specimens he

identified as *P. vaughani* present '*Coscinaraea*-like' skeletal characters, and that he retained the species in the genus *Psammocora* 'only because of the small corallite size'. The illustrations of *P. vaughani* in Nishihira & Veron (1995) also show atypical morphology. Specimens of this species seem to be rare also in museum collections. Three specimens deposited at the MSNM (80277, 80282 and 81262) from Australia identified as cf. *vaughani* by Yabe, Sugyiama and Eguchi (http://nhb-acsmith1.si.edu/emuwebizweb/pages/nmnh/iz/DtlQuery.php) were later identified as *P. superficialis* by Hoeksema.

As a result of this study, showing the strong similarities between the holotypes of *P. verrilli*, *P. nierstraszi* and *P. vaughani*, and based on the fact that the group of specimens identified as TCM A was statistically significantly different from the rest of the groups identified, it is proposed that the three nominal species characterised by TCM A be synonymised. *Psammocora nierstraszi* and *P. vaughani* are junior synonyms of *P. verrilli*. However, since *P. verrilli* is, as mentioned, currently considered a Hawaiian endemic species, the use of its name would cause confusion and *P. nierstraszi* is preferred according to Article 23.9.3 of the International Code of Zoological Nomenclature.

Type specimens of *P. profundacella*, *P superficialis*, *P. samoensis* and *M. australiae* (Figure 1) share similar corallite and septa morphology and were all included in type cluster C (Figure 3). The morphometric analyses of a larger set of specimens identified as TCM C showed that all the type and non-type specimens formed together a distinct group in the PCA plot (Figure 4B) with 100% classification success rate in the DA (Figure 4D). The holotype of *M. australiae* is possibly the first specimen showing TCM C described in the literature. Duncan (1884) based on it his description of the subgenus *Plesioseris*, later synonymised with *Psammocora* (Veron & Pichon, 1976). The synonymy of *M. australiae* with *P. profundacella* was already accepted by Veron & Pichon (1976). Likewise, morphologic affinities between *P. profundacella* and *P. samoensis* appeared evident to Scheer & Pillai (1983). Veron & Pichon (1976) synonymised *P. samoensis* with *P. nierstraszi,* as already suggested by Wells (1954). Morphologic similarities between the specimen they illustrate as *P. nierstraszi* (AIMS 624b, Table 3) and *P. samoensis* syntypes (Figure 1) are evident. However, as discussed above, the *P. nierstraszi* specimen in question does not show the typical species characters previously described and displays TCM C. Finally, although some consider the two nominal species to be distinct taxa (Veron & Pichon, 1976; Ditlev, 1980; Veron, 2000; Fenner, 2005), the skeletal affinities between *P. superficialis* and *P. profundacella* have been deemed by others to be strong enough to consider the two nominal species as one polymorphic taxonomic entity (Matthai, 1948; Burchard, 1979; Scheer & Pillai, 1983; Wells, 1983; Sheppard & Sheppard, 1991; Reyes-Bonilla, 2002).

Based on the strong similarity between the holotypes of *P. profundacella*, *P superficialis*, *P. samoensis* and *M. australiae*, and on the fact that the group of specimens identified as TCM C was statistically significantly different from the rest of the groups identified in this study, the four nominal species characterised by TCM C are placed in synonymy. According to the ICZN rules *Meandroseris australiae* is the senior synonym of *P. profundacella*, *P superficialis* and *P. samoensis*. However, since the name has not been used in the scientific community for more than 50years since its original proposal, the more recent name *P. profundacella* which is in common use is considered *nomen protectum*, and hence valid, while *M. australiae* is considered *nomen oblitum* (Article 23.9.2).

As discussed, *P. profundacella* is, according to the morphometric data obtained in this study, a very distinctive and well-defined species so far as the calice and septa dimensions are concerned (TCM C). The same holds true for *P. nierstraszi* (TCM A). Where, then, does the morphologic variability which has caused so much nomenclatural confusion in the literature (Table 3) lie? Both species are characterised by the presence of a variably developed synapticulothecal wall and by the arrangements of the calices in series on the corallum surface. The degree of development of the synapticulothecal walls can be very different in both species and can give the corallum either an even or ridged appearance. The highly variable number of calices arranged in series once led to the definition of different subgenera based on this character, namely *Plesioseris* Duncan, 1884, predominantly monocentric, and *Psammocora*, predominantly polycentric. However, as Veron & Pichon (1976) remarked, the subdivision of *Psammocora* into subgenera 'does not appear to improve the taxonomy of the genus, or to be useful for the classification of species'. Finally, several species examined in this study were monocentric in parts of the colony and polycentric in other parts, or presented a smooth and a ridged side, as also shown by Todd (2008). Environmental factors, such as different exposure to light of different parts of the same colony, could play an important role in the high variability of these characters at the colony as well as the population level. Hence, the use of macroscopic but non-informative characters (wall ridge formation and series of calices) instead of smaller and less readily observable but informative characters (calice and septa dimensions) is likely to be the main cause of the nomenclatural confusion within and between *P. profundacella* and *P.*

nierstraszi. However, although *P. profundacella* (TCM B) and *P. nierstraszi* (TCM C) specimens examined in this study could be fully distinguished based on morphology, they were indistinguishable in the molecular analyses (Figure 5 and 6). Hence, the morphologic similarities of some characters that have led to the confusion between these two species in the literature could actually be explained based on their genetic affinities.

An even more challenging name game is that between the nominal species displaying TCM D, namely *P. haimiana*, *P. togianensis* and *P. folium*, and *P. digitata* (TCM E). To begin with, *Psammocora haimiana* Milne Edwards & Haime, 1851 and *Psammocora haimeana* (*sensu* Klunzinger, 1879) are not simply two spellings of the same species name as Veron & Pichon (1976) reported. The holotype of *P. haimiana* described by Milne Edwards & Haime (1851) was later illustrated by Rousseau (1854) (Figure 7A). The colony was depicted faithfully in its superficial shape though a reference scale was missing. The type specimen re-examination in this study revealed that the large massive type specimen colony shape (Figure 7B) resulted from the fusion of the distal ends of markedly claviform digitations typically found in specimens currently identified as *P. digitata* (Figure 7D). This was easily observed because the holotype was broken, hence showing the internal structure of the colony (Figure 7D). Corallite characters of the *P. haimiana* holotype (Figure 1I, 3E, and 7C) were in every respect similar to those of specimens showing TCM D and referred to in the literature as *P. digitata* (Veron & Pichon, 1976; Ditlev, 1980; Veron, 1986; Veron, 2000; Benzoni *et al*., 2007; Stefani *et al*., 2008a). Unfortunately, none of the specimens described as *P. haimeana* in the literature or in this study, following widely cited taxonomic references, bear any similarity to the species holotype (Figure 4, Table 3). Possibly Klunzinger (1879) was the first to identify massive and predominantly monocentric morphs of *P. profundacella* (TCM C) from the Red Sea as *P. haimeana*, thus introducing not only a new spelling of the species name, but also a taxonomic error which has been passed on from publication to publication until today. According to Van der Horst (1922: 426) several *P. haimeana* specimens collected during the Percy Sladen Trust Expedition to the Indian Ocean were all typical 'according to Klunzinger's excellent description'. Also Vaughan (1918: 141) referred to Klunzinger (1879) stating that the specimens he examined from Cocos Keeling were 'so precisely like those figured by Klunzinger that no further description is needed'. The first to report *P. profundacella* in the Red Sea were Scheer & Pillai (1983) who considered *P. superficialis* and *P. profundacella* synonyms but still recognised *P. haimeana* as a different and valid species. The corallite characters used by different authors to separate *P. haimeana* from *P. profundacella* are sometimes not very clear and seem to differ strongly depending on the author (Veron & Pichon, 1976; Veron, 2000; Fenner, 2005). Moreover, the morphologic affinities between specimens identified and published in illustrations as *P. haimeana* and those of *P. profundacella* are obvious (Veron & Pichon, 1976; Ditlev, 1980; Faure, 1982; Veron, 1986; Veron, 2000). Finally, intermediate morphologies (Stefani *et al*., 2008a) as well as specimens showing both morphologies in different parts of the same colony have been reported (Todd, 2008). The possible synonymy of *P. profundacella* and *P. haimeana* discussed by Matthai (1948) and proposed by Scheer & Pillai (1983) and Sheppard & Sheppard (1991) is hence supported by our results because the morphologic entity the authors considered under the

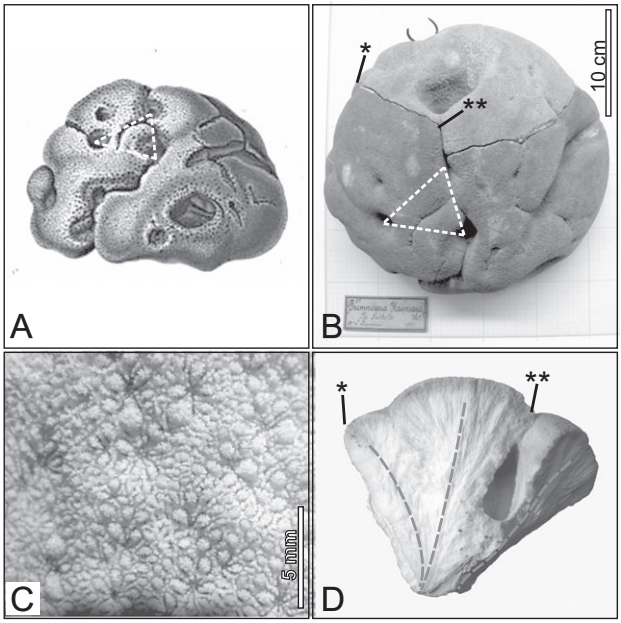


Figure 7. (A) Illustration of *P. haimiana* holotype in Rousseau (1854); (B) MHNH535; (C) detail of the corallites arrangement and the typical '*gros grains oblongs au milieu de granulations beaucoup plus petites*' mentioned by Milne Edwards (Milne Edwards & Haime, 1851: 68) in the original species description; (D) lateral view of a holotype fragment revealing that the colony was primarily columnar and that the claviform digitations coalesced forming a secondary massive growth form (grey dashed arrows indicate growth directions of adjacent digitations); * and ** indicate the positions shown by the arrows of the same points on the specimen surface in its different illustrations in the plate. White dashed triangles in A) and B) indicate the position of the same points in the specimen illustration and in its picture, respectively.

name of *P. haimeana* is actually distinct from the *P. haimiana* of Milne Edwards & Haime (1851) and similar to that of the other species that display TCM C. The aforementioned phenotypic plasticity of *P. profundacella* and the confusion which was generated from it might have led several authors to classify the different morphologies of one very variable morphospecies as separate species. Clearly, both the fact that the *P. haimiana* holotype illustration by Rousseau (1854) gave poor details of the corallites and lacked a reference scale and, more surprisingly, that the holotype seems to have never been re-examined since the description of Milne Edwards & Haime (1851) contributed to the perpetuation of an incorrect identification.

As mentioned above, the typical corallite morphology of *P. haimiana* is the same as that of specimens commonly described in the literature under the name of *P. digitata*, an apparently well defined and readily identified species (Veron & Pichon, 1976; Ditlev, 1980; Veron, 1986; Veron, 2000; Benzoni *et al*., 2007; Stefani *et al*., 2008a). Nevertheless, once more, the study of the holotype morphology provided some interesting and unexpected results. In the type cluster analysis, the holotype of *P. digitata* formed a singleton (TCM E) (Figure 3) despite affinities to the type material grouped in cluster D presented in the results. All examined specimens corresponding to the typical *P. digitata* (TCM E) corallite morphology formed a univocally defined group readily separated from all the other species in the genus (Figure 4). Moreover, molecular analyses revealed that *P. digitata* (TCM E) is clearly distinct from specimens with TCM D (Figure 5).

The widely accepted synonymy between *P. digitata* and *P. togianensis* (Van der Horst, 1922; Veron & Pichon, 1976) cannot be confirmed given that the morphology of the *P. digitata* specimens which the synonymy was based on was, in fact, at least in the case of Veron & Pichon (1976), that of *P. haimiana* (Table 3). However, the study of the whole type series of *P. togianensis* and of *P. haimiana* as well as of the non-type material in this study showed that the former species should be considered a junior synonym of the latter. *Psammocora folium* has been largely disregarded in the literature since its description and, because of its flat growth form and smooth corallum surface, was never synonymised with any of the other species in type cluster D, which are typically digitate to claviform in growth form. Nevertheless, the morphometric analysis of the holotype calices and septa showed that the specimen is affine to the other specimens with TCM D. Moreover, flat, foliose, or encrusting TCM D colonies have been commonly recognised as well, though under the name of *P. digitata* (Veron & Pichon, 1976; Veron, 2000).

In conclusion, following the results obtained and discussed in this study, *P. folium* and *P. togianensis* are considered junior synonyms of *P. haimiana* (not *P. haimeana*), thus restoring the original name spelling.

Finally, *P. digitata* (TCM E) is recognised as a valid species but its name has been erroneously extensively used to identify specimens with the typical *P. haimiana* morphology (TCM D).

Description of taxa

A detailed taxonomic account of four of the five species resulting from this study as discussed above is given. For a detailed description of *Psammocora albopicta,* see the original description (Benzoni, 2006).

Family Psammocoridae Chevalier and Beauvais, 1987

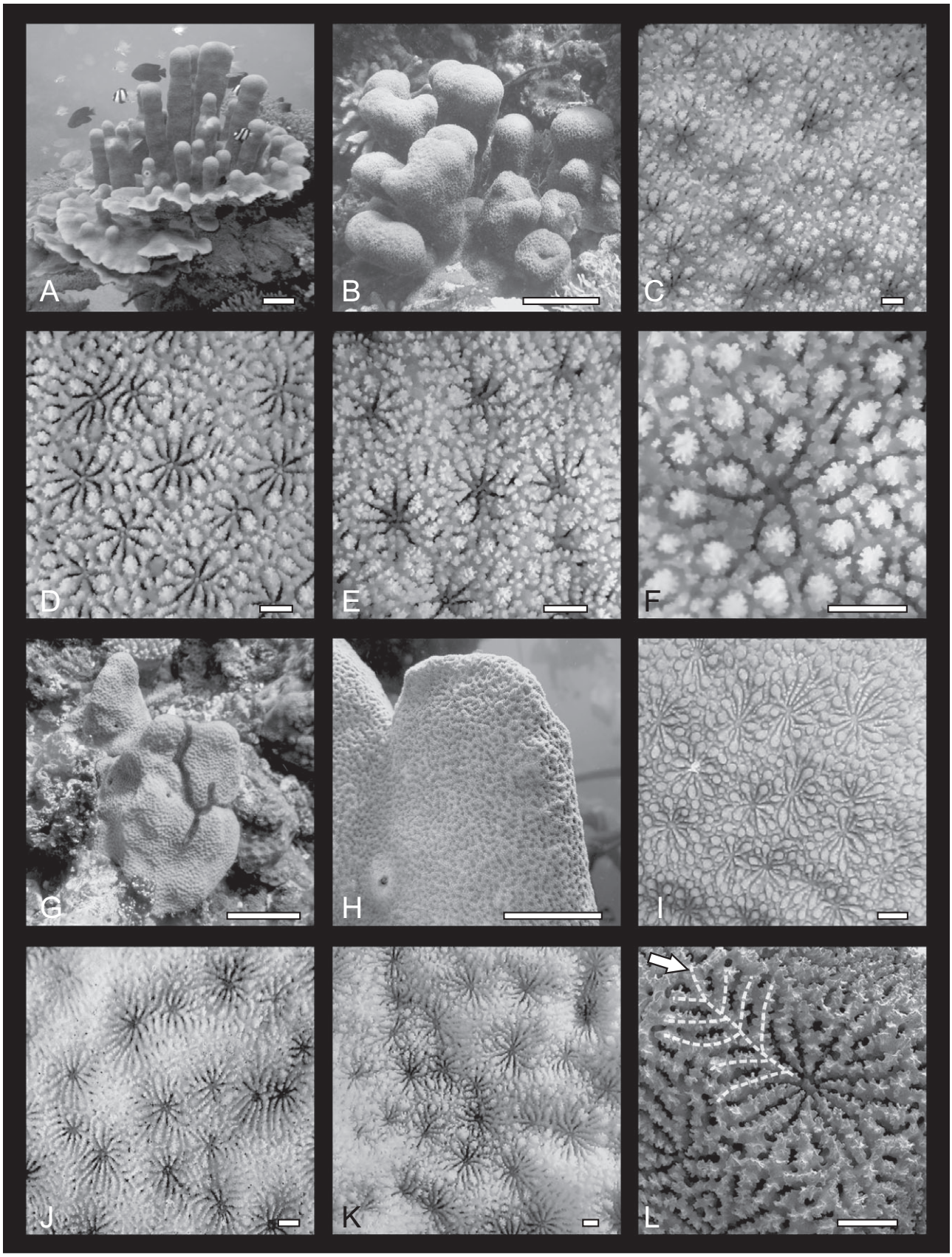
Genus *Psammocora* Dana 1846

Psammocora haimiana Milne Edwards & Haime, 1851

(Figure 1I, J, K; 3E; 8A–F)

Psammocora haimiana Milne Edwards & Haime, 1851 p. 68

Figure 8. *Psammocora haimiana* (A) living colony with the typical columnar digitations and a foliose base, Côte Oubliée, New Caledonia (10 m), scale bar = 10 cm; (B) *in vivo* image of a colony with claviform digitations (specimen I102), Indonesia (2 m), scale bar = 10 cm; (C) calice arrangement in specimen M35, exert septa are visible over the colony surface, scale bar = 1 mm; (D) specimen HS1379 with the typically small fossa and columella made of one styliform process scale bar = 1 mm; (E) specimen NC588 with larger fossa and columella surrounded of small granules, scale bar = 1 mm; (F) detail of a typical calice surrounded by EPS in specimen M16, scale bar = 1 mm. *Psammocora digitata* (G) living colony at 5 m depth in Wallis and Futuna, scale bar = 10 cm; (H) typical shape of the digitations (specimen HS1376), scale bar = 5 cm; (I) detail of specimen W613 surface *in vivo*, scale bar = 1 mm; (J) calice arrangement in specimen W570, scale bar = 1 mm; (K) calice arrangement in specimen HS1802, scale bar = 1 mm; (L) scanning electron microscope image of a calice of specimen HS1818, the white arrow indicates the typical petaloid septa arrangement of the species whereby septa fuse forming a feather of alternating petaloid and non-petaloid septa on both sides of a central axis (dashed white lines), scale bar = 1 mm (SEM image courtesy of Paolo Gentile).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Psammocora exesa Gardiner, 1905 p. 952, Pl. XCII. Figure 22; Yabe, Sugiyama and Eguchi, 1936 p. 59–60, Pl. XLIV, Figure 3, 4; Dai & Horng, 2009 p. 57, not skeleton picture

Psammocora folium Umbgrove, 1939 p. 52, Pl. XIV, Figures 3a-3b, and Pl. XVI Figure 1, 2

Psammocora togianensis Umbgrove, 1940 p. 299, Pl. XXIX Figure 3, Pl. XXX Figure 1, Pl. XXXI Figure 3, 4; Wells, 1954 p. 410, Pl. 156 Figure 6, 7; Pillai & Scheer, 1976 p. 19, Pl. 1 Figure 1

Psammocora digitata Veron & Pichon, 1976 p. 30–33, Figure 33, 34, 35, 36, 37, 38; Ditlev, 1980 p. 51, Figure 209, 210; Veron, 1986 p. 270–271, Figure 1, 2, p. 272 Figure 1, not skeleton picture; Veron, 2000 p. 154–155 Vol.2, not skeleton drawing; Stefani *et al*., 2008a, Figure 2a; Dai & Horng, 2009 p. 51

Type material examined. Holotype MNHN 535 Seychelles (type locality); *Psammocora folium* holotype RMNH Coel. 9360; *Psammocora togianensis* syntypes RMNH Coel. 10195, Coel. 10196, Coel. 10197, Coel. 10198, Coel. 10199, Coel. 10200.

Other material examined. **MALDIVES** FBC M16 (27/04/2004 F. Benzoni and F. Stefani) Bulhalafushi; M26 (28/04/2004 F. Benzoni and F. Stefani) Eboodhoo; M35 (29/04/2004 F. Benzoni and F. Stefani) Dega Thila; M38 (29/04/2004 F. Benzoni and F. Stefani) Dega Thila. **'INDIAN SEA'** MNHN 534. **INDONESIA** I87 (09/06/2004 F. Benzoni) Mapia House Reef, Manado, North Sulawesi; I93 (10/06/2004 F. Benzoni) Likuan III, Bunaken, North Sulawesi; I97 (11/06/2004 F. Benzoni) Bualo, Manado Tua, North Sulawesi; I102 (12/06/2004 F. Benzoni) Raymond Reef, Bunaken, North Sulawesi. **AUSTRALIA** MTQ G 35060 (M. Pichon and J.E.N. Veron) Sue Island, Great Barrier Reef; MTQ G 35064 (J.E.N. Veron) Tijou, Great Barrier Reef; MTQ G 35065 (J.E.N. Veron) Keeper Reef, Great Barrier Reef; MTQ G 35066 (J.E.N. Veron) Electra Head, Great Palm Island, Great Barrier Reef; MTQ G 35068 (M. Pichon and J.E.N. Veron) Thursday Island, Great Barrier Reef. **NEW CALEDONIA** IRD HS1379 (17/03/07 F. Benzoni and G. Lasne) IRD ST1064 N'Goë, Toupeti, Côte Oubliée; FBC NC588 (23/03/07 F. Benzoni) IRD ST1078, N'Goë, Côte Oubliée; FBC NC 92 (27/03/07 F. Benzoni) IRD ST, 1085, Ouinné, Côte Oubliée; MNHN 20322 (J.P. Chevalier) Ile des Pins; MNHN 20356 (28/04/1978 G. Faure) Ile aux Goelands. **VANUATU** MNHN 20323 (15/10/1962 J.P. Chevalier) Ile Pelé, Vaté, Port Vila.

Revised description: Corallum. Colony growth form can be variable but most commonly is digitiform. Digitations columnar (Figure 8A) to claviform (Figure 8B) up to 30 cm in height. Base of colonies can be encrusting or have free margins and become foliose (Figure 8A). Digitations do not anastomose but, if claviform, can grow very close at top (Figure 8B). Digitations circular to oval in section with rounded ends.

Corallites. Calice diameter 1.9–2.2 mm (Figure 8C, D, E, F). Fossa diameter 0.4–0.5 mm. Columella 0.2–0.3 mm in diameter, typically made of one styliform process (Figure 8D). In the largest calices 2–4 very small granules can form at the inner end of the petaloid septa (Figure 8E). Six to 8 septa reach the fossa, 3–5 of them are petaloid (Figure 8F). Petaloid septa 0.3–0.4 mm wide and 0.8–1 mm long. Non-petaloid septa (0.1–0.2 mm wide) reaching the fossa furcate fuse, enclosing petaloid septa to form a compact mesh with reduced interseptal spaces (Figure 8C, D, E). Enclosed petaloid septa 0.3–0.4 mm wide and 0.5–0.6 mm long (Figure 8F). Occasionally, larger and rounded enclosed petaloid septa can be found as in the holotype (Figure 7C). Up to two rows of enclosed petaloid septa can be found between adjacent calices (Figure 8C); generally one complete row is present (Figure 8D, E). Short series of calices can form but are seldom more than 3–4 calices long. Distance between two calices within the same series is 1.8–2.3 mm. The nearest calices of two parallel series are 2.5–3.4 mm apart. A synapticulothecal wall is present but it is seldom visible unless slightly raised from the colony surface (Figure 8C) and forming a rounded ridge, never acute.

Living polyps. Polyps and extrapolypal tentacles (Matthai, 1948; Benzoni *et al*., 2007) commonly extended at daytime and giving the corallum surface a furry appearance (Figure 8B). Tentacles and extrapolypal tentacles are tapering, brown to pale beige in colour, and end with a rounded tip paler than the rest of the tentacle. The number of extrapolypal tentacles corresponds to the number of enclosed petaloid septa.

PSAMMOCORA DIGITATA MILNE EDWARDS & HAIME, 1851
(FIGURE 1L; 3E; 8G-L)

Psammocora digitata Milne Edwards & Haime, 1851 p. 68; Veron, 1986 p. 272, skeleton picture

Psammocora sp. Laboute & Richer de Forges, 2004

Type material. Psammocora digitata Holotype MNHN 533 China Seas (type locality)

Other material examined. **AUSTRALIA** MTQ G 35066 (J.E.N. Veron) Electra Head, Great Palm Island, Great Barrier Reef; MTQ G 41913 Maer Island; MTQ G 46700 Lizard Island, Great Barrier Reef; MTQ G 46768 Lizard Island, Great Barrier Reef; MTQ G 46788 Lizard Island, Great

Barrier Reef. **NEW CALEDONIA** IRD HS1376 (17/03/2007 F. Benzoni and G. Lasne) IRD ST1064, Cap Toupeti; IRD HS1746 (31/10/2007 F. Benzoni and G. Lasne) IRD ST1119, Cap Goulevin; IRD HS1802 (01/11/2007 F. Benzoni and G. Lasne) IRD ST1121 Cap Goulevin; HS1818 (02/11/2007 F. Benzoni and G. Lasne) IRD ST1125 Cap Goulevin; MNHN 20324 (27/09/1962 J.P. Chevalier) Ile Art, Bélep Islands; MNHN 20325 (26/09/1962 J.P. Chevalier) Ogumboa, Bélep Islands. **WALLIS AND FUTUNA** FBC W534 (20/04/2007 F. Benzoni and M. Pichon) ST. 18; W536 (20/04/2007 F. Benzoni and M. Pichon) ST. 18; W546 (21/04/2007 F. Benzoni and M. Pichon) ST. 20; W570 (21/04/2007 F. Benzoni and F. Seguin) ST. 21; W612 (24/04/2007 F. Benzoni and F. Seguin) ST. 24; W613 (24/04/2007 F. Benzoni and F. Seguin) ST. 24; W615 (25/04/2007 F. Benzoni and F. Seguin) ST. 26; W616 (25/04/2007 F. Benzoni and F. Seguin) ST. 26.

Revised description: Corallum. Colony growth form massive (Figure 8G) to digitiform, with columnar digitations most commonly rastremating from the base, rounded at the tip and oval in section (Figure 8H). Colonies can attain large sizes and exceed 50 cm in diameter.

Corallites. Calice diameter 2.4–3.2 mm (Figure 8I, J, K, L). Fossa diameter 0.3–0.5 mm. Columella 0.2–0.4 mm in diameter, typically made of one styliform process, sometimes in the largest calices 3–6 very small granules can form around it at the inner end of the petaloid septa. Seven to 12 septa reach the fossa. Of the septa in the calice 6–12 are petaloid, elongated and with a round and often exert distal end (Figure 8I, L). Petaloid septa 0.3–0.4 mm wide and 1.1–1.5 mm long. Some of the petaloid reach the fossa, others fuse with non-petaloid ones. Non-petaloid septa are 0.2 mm wide. In larger calices a typical septal arrangement can be found. A long non-petaloid septum forms the axis (Figure 8L). Septa fuse forming a feather of alternating petaloid and non-petaloid septa on both sides of a central axis (Figure 8L). Calices presenting this septal arrangement have a comet shape with the comet tail being the feather septal system (Figure 8L). This pattern is found in the holotype (central corallite in Figure 1D) as well as in the other examined specimens but not in the other species. Enclosed petaloid septa 0.3–0.4 mm wide and 0.6–0.7 mm long. Up to two rows of enclosed petaloid septa can be found between adjacent calices (Figure 8J), generally one complete row is present around larger calices (Figure 8K). Short series of calices can form where budding processes take place and are seldom more than 2–3 calices long (Figure 8J, K). Distance between two calices within the same series can vary from 1.8–3 mm. The nearest calices of two parallel series are 3–3.7 mm apart. A synapticulothecal wall is present but it is seldom visible unless slightly raised from the colony surface and forming a rounded ridge (Figure 8K), never acute.

Living polyps. Polyps and extrapolypal tentacles commonly extended at daytime though shorter and less obvious than in *P. haimiana* (Figure 8H, I). Tentacles and extrapolypal tentacles are tapering, light brown to pale green in colour, and ending with a small rounded tip of the same colour as the rest of the tentacle. The number of extrapolypal tentacles corresponds to the number of enclosed petaloid septa.

Remarks. This species is currently known from relatively few locations within the central and western Pacific only, namely Australia, New Caledonia, Wallis Island and the unfortunately vague type location, the 'China Seas'. However, re-examination of existing museum collections and additional sampling could provide new geographic records. The species might have been confused with *Coscinaraea exesa* (Dana, 1846) which has a different septal pattern.

PSAMMOCORA PROFUNDACELLA GARDINER, 1898 (FIGURE 1E, F, G, H; 3D; 9A–E)

Maeandroseris australiae Rousseau, 1854, Pl. 28

Psammocora haimeana Klunzinger, 1879 p. 81, Pl. IX, Figure 5; Veron & Pichon, 1976 p. 34, Figure 39, 40; Ditlev, 1980, p. 51 Figure 215; Sheppard & Sheppard, 1991 p. 80, Figure 67a, 67b, Pl. 47; Scheer & Pillai, 1983 p. 19, Pl. 1, Figure 7, 8; Veron, 1986 p. 276, Figure 1 and corallite drawing, not Figure 2; Veron, 2000 p. 152 Vol 2, Figure 1, 2, 3, 4, not skeleton drawing; Stefani *et al*., 2008a, Figure 2c; Todd, 2008 p. 329, Fig. 9A

Psammocora superficialis Gardiner, 1898 p. 537, Pl. XLV. Figure 2; Yabe, Sugiyama and Eguchi, 1936 p. 60, Pl. XLI, Figure 4, 5; Veron & Pichon, 1976 p. 27, Figure 25; Todd, 2008 p. 329, Figure 9C; Dai & Horng, 2009 p. 54 skeleton picture

Psammocora profundacella Gardiner, 1898 p. 537, Pl. XLV, Figure 3; Yabe, Sugiyama and Eguchi, 1936 p. 60, Pl. XLV, Figure 4, 5, 7, 8; Veron & Pichon, 1976 p. 35–37, Figure 41, 42, 43, 44; Scheer & Pillai, 1983 p. 19, Pl. 1, Figure 5, 6; Stefani *et al*., 2008a, Figure 1b, 2d, 2e; Dai & Horng, 2009 p. 53

Psammocora samoensis Hoffmeister, 1925 p. 46, Pl. 5, Figures 3a-3b-3c

Psammocora nierstraszi Veron & Pichon, 1976 p. 25–26, Figure 23, 24; Scheer & Pillai, 1983 p. 19, Pl. 1, Figure 3, 4; Veron, 1986 p. 277, skeleton picture; Nishihira & Veron, 1995 p. 198

Psammocora verrilli Veron, 2000 p. 151 Vol 2, Figure 6; Fenner, 2005, p. 76 both figures

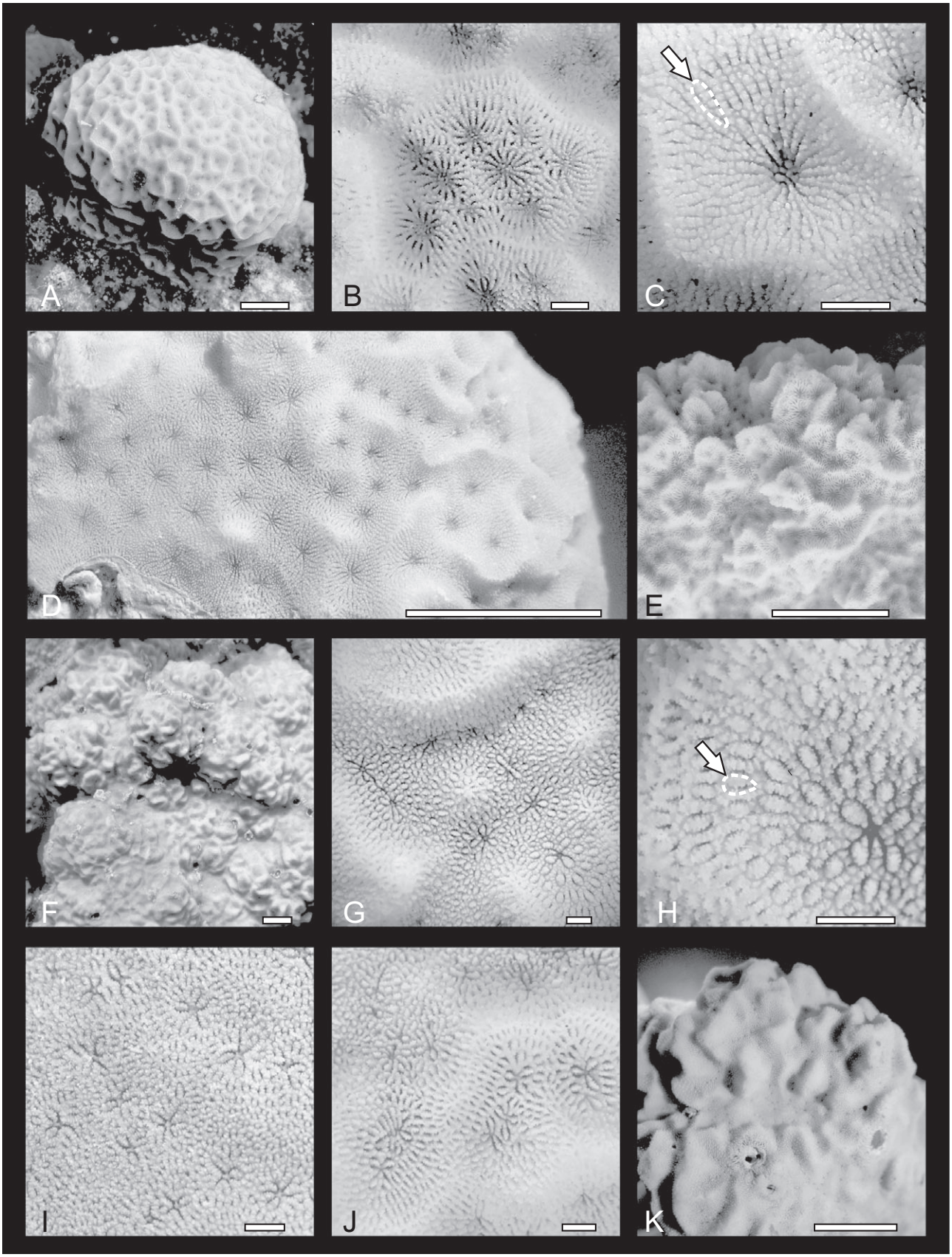
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Figure 9. *Psammocora profundacella* (A) living colony with a massive growth form, North Sulawesi, Indonesia (7 m), scale bar = 1 cm; (B) calices enclosed by a common synapticulothecal wall (M18), scale bar = 1 mm; (C) single calice surrounded by series of enclosed petaloid septa (EPS) (I113), white arrow indicates a single rice-grain shaped EPS (outlined by the dashed white line), scale bar = 1 mm; (D) a specimen from the Maldives displaying a smooth (on the left) and a ridged (on the right) side, scale bar = 1 mm; (E) a specimen (I100) with well developed ridges, scale bar = 1 mm. *Psammocora nierstraszi* (F) living colony showing the typical encrusting growth form, Mayotte (10 m), scale bar = 10 cm; (G) view of specimen M43 showing serial calices arrangement, ridges and hydnophoroid formations, scale bar = 5 cm; (H) single calice of the same specimen surrounded by series of EPS, white arrow indicates a single apple-seed shaped EPS (outlined by the dashed white line), scale bar = 1 mm; (I) smooth side of specimen I89, scale bar = 1 mm; (J) ridged side of the same specimen, scale bar = 1 mm; (K) a specimen (I88) with well developed ridges, scale bar = 1 mm.

Psammocora digitata Veron, 2000 p. 155 Vol 2, skeleton drawing

Type material examined. Holotype UMZC unregistered, Funafuti, Tuvalu (type locality); *Maeandroseris australiae* holotype MNHN 521, Australia; *Psammocora superficialis* holotype UMZC unregistered, Funafuti, Tuvalu; *Psammocora samoensis* syntypes USNM 68209, 68210 Pago Pago Harbour, Tutuila, Samoa

Other material examined. **SAUDI ARABIA (Red Sea)** NHM 1991.6.4.63 (C.R.C. Sheppard and A.L.S. Sheppard) Yanbu; NHM 1991.6.4.64 (C.R.C. Sheppard and A.L.S. Sheppard) Yanbu. **MALDIVES** M5 (27/04/2004 F. Benzoni and F. Stefani) Dangheti; M6 (27/04/2004 F. Benzoni and F. Stefani) Dangheti; M7 (27/04/2004 F. Benzoni and F. Stefani) Dangheti; M9 (27/04/2004 F. Benzoni and F. Stefani) Dangheti; M10 (27/04/2004 F. Benzoni and F. Stefani) Dangheti; M15 (27/04/2004 F. Benzoni and F. Stefani) Bulhalafushi; M17 (27/04/2004 F. Benzoni and F. Stefani) Bulhalafushi; M18 (27/04/2004 F. Benzoni and F. Stefani) Bulhalafushi; M27 (28/04/2004 F. Benzoni and F. Stefani) Eboodhoo; M28 (28/04/2004 F. Benzoni and F. Stefani) Eboodhoo; M30 (28/04/2004 F. Benzoni and F. Stefani) Eboodhoo; M31 (28/04/2004 F. Benzoni and F. Stefani) Eboodhoo, M33 (28/04/2004 F. Benzoni and F. Stefani) Eboodhoo; M34 (28/04/2004 F. Benzoni and F. Stefani) Eboodhoo. **INDONESIA** FBC I82 (09/06/2004 F. Benzoni) Mapia House Reef, Manado, North Sulawesi; I91 (10/06/2004 F. Benzoni) Likuan III, Bunaken, North Sulawesi; I95 (10/06/2004 F. Benzoni) Celah Celah, Bunaken, North Sulawesi; I96 (11/06/2004 F. Benzoni) Bualo, Manado Tua, North Sulawesi; I98 (11/06/2004 F. Benzoni) Bualo, Manado Tua, North Sulawesi; I100 (12/06/2004 F. Benzoni) Mandolin, Bunaken, North Sulawesi; I113 (18/06/2004 F. Benzoni) Molas Ship Wreck, Manado, North Sulawesi. **AUSTRALIA** AIMS 624b (J.E.N. Veron and M. Pichon) Orpheus, Palm Island, Great Barrier Reef; AIMS 5340 (27/11/1974J.E.N. Veron and M Pichon) between S. Yule and Triangle, Great Barrier Reef; MTQ G, 35070 (coll. M Pichon) Tijou reef, Great Barrier Reef; MTQ G 35072 (J.E.N. Veron and M. Pichon) Darnley Island, Great Barrier Reef; MTQ G 35073 (J.E.N. Veron) Solitary Islands, Great Barrier Reef; MTQ G 35074 (M. Pichon) Lizard Island, Great Barrier Reef; MTQ G 35075 (M. Pichon) Low Woody Islets, Great Barrier Reef; MTQ G 35076 Robinson Beach, Great Palm Island, Great Barrier Reef; MTQ G 46773 Lizard Island, Great Barrier Reef; MTQ G 46776 Lizard Island, Great Barrier Reef; MTQ G 46779 Lizard Island, Great Barrier Reef; MTQ G 46782 Lizard Island, Great Barrier Reef; MTQ G 57722 Great Barrier Reef. **HAWAII** BM SC207 (1904 J.E. Duerden and Stokes) Kalaeloa, Molokai; BM SC1104 (01/11/1971 R. Kinzie) Waikiki, Oahu. **COSTA RICA** CR335 (01/02/2005 J. Cortés) Isla del Caño.

Revised description: Corallum. Encrusting to submassive and massive (Figure 9A). Colonies never exceed 15–20 cm in diameter and, on average, tend to be between 5 and 10 cm wide. Free-living colonies can form on mixed sandy and rubble substrates and are commonly found in shallow and exposed environments.

Corallites. Calice diameter 1.4–1.7 mm (Figure 9B, C, D). Fossa diameter 0.4–0.5 mm. Columella 0.2–0.4 mm in diameter, typically made of one styliform process surrounded by 3–6 smaller granules forming at the proximal end of the septa (Figure 9B, C). Ten to 13 septa reach the fossa, 3–6 of them are petaloid with a rice grain shape (Figure 9C) and 0.1–0.2 mm wide and 0.5–0.7 mm long. Non-petaloid septa reaching the fossa are 0.1 mm wide. They furcate and fuse enclosing petaloid septa and forming a compact mesh with reduced interseptal spaces. Enclosed petaloid septa 0.1–0.2 mm wide and 0.3–0.5 mm long. Up to six rows of enclosed petaloid septa can be found between calices (Figure 9B, C), generally at least one or two complete rows are present around non-budding calices. Series of calices can form, their length being very variable even within different parts of the same colony (Figure 9B, D). Distance between two calices within the same series is 1.2–1.8 mm. The nearest

calices of two parallel series are 2.1–2.9 mm apart. The synapticulothecal wall is clearly visible when raised from the colony surface to form an acute ridge surrounding calices and/or series of calices (Figure 9A, B, C, D, E).

Living polyps. Polyps and extrapolypal tentacles commonly extended at daytime. Tentacles and extrapolypal tentacles are tapering, ending with a rounded whitish tip (figured in Benzoni *et al.*, 2007), and mostly transparent although in some colonies they can be brightly coloured (e.g. green or pink) and the oral disc can have a different colour from the tentacles. The number of extrapolypal tentacles corresponds to the number of enclosed petaloid septa.

Remarks. Psammocora profundacella is a widespread species throughout the Indo-Pacific. Although not a major reef builder, rarely forming colonies larger than 15 cm in diameter, and never dominant, this species is commonly found on reefs from shallow reef flats to deeper outer reef slopes.

PSAMMOCORA NIERSTRASZI VAN DER HORST, 1921 (FIGURE 1A, B, C; 3B; 9F–K)

Psammocora verrilli Vaughan, 1907 p. 144, Pl. XLIV, Figures 1-1a; Maragos, 1977 p. 235, Figure 117; Veron, 2000 p. 151 Vol 2, skeleton picture

Psammocora nierstraszi van der Horst, 1921 p. 34, Pl. II, Figure 3, 4; Veron, 2000 p. 153 Vol. 2, Figure 5, 6, 7, 8, not skeleton drawing; Fenner, 2005, p. 74

Psammocora vaughani Yabe & Sugiyama, 1936 p. 60, Pl. XLI, Figure 6, 7

Psammocora haimeana Sheppard & Sheppard, 1991 p. 80, Figure 67c; Nishihira & Veron, 1995 p. 201, all three figures; Dai & Horng, 2009 p. 52

Psammocora superficialis Veron & Pichon, 1976 p. 27, Figure 26; Veron, 1986 p. 274, Figure 2 and skeleton picture; Nishihira & Veron, 1995 p. 199, *in vivo* picture at the bottom; Veron, 2000 p. 150–151 Vol. 2, Figure 3, 4, 5; Dai & Horng, 2009 p. 54 not skeleton picture

Type material examined. Holotype ZMA COE 01078 Sumbawa, Indonesia (type locality); *Psammocora verrilli* holotype USNM 21637 Kalaeloa, Molokai, Hawai'i.

Other material examined. **SAUDI ARABIA (Red Sea)** NHM 1991.6.4.65 (C.R.C. Sheppard and A.L.S. Sheppard) Yanbu. **MALDIVES** M36 (29/04/04 F. Benzoni and F. Stefani) Dega Thila; M42 (30/04/04 F. Benzoni and F. Stefani) Faanu Madugau; M43 (30/04/04 F. Benzoni and F. Stefani) Faanu Madugau; M54 (01/05/04 F. Benzoni and F. Stefani) Mushi Mas Minghili. **MAYOTTE** FBC MA234 (2004 F. Seguin); FBC MA250 (2004 F. Seguin); FBC MA239 (2004 F. Seguin); FBC MA240 (2004 F. Seguin); FBC MA245 (2004 F. Seguin); FBC MA254 (2004 F. Seguin); FBC MA489 (26/04/05 F. Benzoni and D. Obura) BA22. **INDONESIA** FBC I83 (09/06/04 F. Benzoni) Mapia House Reef, Manado, North Sulawesi; I84 (09/06/04 F. Benzoni) Mapia House Reef, Manado, North Sulawesi; I88 (10/06/04 F. Benzoni) Likuan III, Bunaken, North Sulawesi; I89 (10/06/04 F. Benzoni) Likuan III, Bunaken, North Sulawesi; I90 (10/06/04 F. Benzoni) Likuan III, Bunaken, North Sulawesi; I95 (10/06/04 F. Benzoni) Celah Celah, Bunaken, North Sulawesi; I107 (15/06/04 F. Benzoni) Likuan III, Bunaken, North Sulawesi. **AUSTRALIA** MTQ G 57723 Great Barrier Reef; MTQ G 57724 Great Barrier Reef; MTQ G 57726 Great Barrier Reef. **WALLIS AND FUTUNA** FBCW135 (30/05/2002 M. Pichon and F. Benzoni) ST. 3; W144 (30/05/2002 M. Pichon and F. Benzoni) ST. 3. **HAWAII** BM SC1104 (14/11/1971 R. Kinzie) Kahe Pt., Oahu.

Revised description: Corallum. Colony growth form encrusting (Figure 9F) to submassive tending to follow the underlying substrate and up to 1.5 m in diameter. Free living forms are commonly found (e.g. the species holotype). Colony surface varies from smooth to ridged and is typically finely beaded (Figure 9F).

Corallites. Calice diameter 0.9–1 mm (Figure 9G, H, I, J). Fossa diameter 0.2 mm. Columella 0.1 mm in diameter, typically made of a single styliform process (Figure 9H, I, J). Five to 8 septa reach the fossa, 2–3 of them are petaloid with an apple seed shape (Figure 9H), 0.1–0.2 mm wide and 0.3–0.4 mm long. Non-petaloid septa reaching the fossa 0.1–0.2 mm wide. They divide and fuse enclosing petaloid septa in the fashion typical of the genus. Enclosed petaloid septa are 0.2 mm wide and 0.3 mm long. Up to 10 rows of enclosed petaloid septa, or even more, can be found between calices (Figure 9G, H, J, K). Enclosed petaloid septa are often exert above the corallum surface and give the colony surface a typical spiky appearance (Figure 9G, K). Calices are arranged in series of variable length and never delimited by the wall (Figure 9G, J, K). Distance between two calices within the same series 0.9–1.2 mm. The nearest calices of two parallel series are 2.2–2.8 mm apart. The synapticulothecal wall is clearly visible when raised from the colony surface to form an acute ridge surrounding calices and/or series of calices (Figure 9F, G, J, K). At times ridges can be so acute and developed as to form crests (Figure 1I, J, K, 3B, and 5 as TCM A; Figure 9K). Hydnophoroid formations are also commonly observed (Figure 9G).

Living polyps. Polyps and extrapolypal tentacles commonly extended at daytime. Tentacles and extrapolypal tentacles are short and end with a rounded whitish tip. The living parts besides the minuscule tentacle tips are uniformly coloured throughout the colony, and colour can vary from light brown to dark green. Oral discs never have a different colour from the tentacles. The number of extrapolypal tentacles corresponds to the number of enclosed petaloid septa.

Molecular phylogenies and the morpho-molecular match

Whether morphologically defined taxa correspond, or not, to an underlying systematic order, and to what extent the morpho-molecular match applies, can be addressed thanks to the availability of molecular techniques. Perhaps not surprisingly, studies on the molecular characterisation of species boundaries in corals have shown that morphological differences between species in Scleractinia do not necessarily match genetic differences. Morphometric variation and genetic differences were reconciled within the *Montastraea annularis* species complex (Knowlton *et al*., 1992; Weil & Knowlton, 1994), for the *Acropora humilis* group (Wolstenholme *et al*., 2003), for two species in the genus *Montipora* (Stobart, 2000), for part of the genus *Porites* (Budd *et al*., 1994) and for three species in the genus *Pavona* (Maté, 2003). However, no genetic differences could be found, for example, between morphometrically distinct species in the genus *Platygyra* (Miller & Babcock, 1997; Miller & Benzie, 1997). Finally, in the case of the largely polyphyletic (Fukami *et al*., 2008) family Faviidae only Huang *et al*. (2009) have studied phylogenetic relationships between species using molecular and morphologic phylogenies, and their analyses revealed incongruence between morphologic and molecular trees.

In this study an almost complete agreement between corallite morphometry and molecular analyses was obtained. In general, the delineation of species boundaries on the basis of the joint results of morphologic and molecular analysis largely agreed with the main results obtained from the type material morphometric analysis based on corallite structure dimensions. Moreover, the COI analysis confirmed the monophyly of the examined *Psammocora* species all characterised by the presence of enclosed petaloid septa (Benzoni *et al*., 2007), as well as the close phylogenetic relationships between *P. explanulata* and a fungiid, both characterised by the presence of fulturae.

Comparison of the results obtained via the two molecular markers used provided sufficient resolution to evidence deep, past and shallow, recent phylogenetic traits. Despite some striking differences, both approaches clearly showed the presence of a marked divergence within the genus *Psammocora*, separating TCM B (*P. albopicta*), D (*P. haimiana*) and E (*P. digitata*) from TCM A (*P. nierstraszi*) and C (*P. profundacella*). The magnitude of this divergence is relevant if compared to analogous estimates produced for other genera and families of Scleractinia. The use of ITS as a reliable marker for phylogenetic analysis was first questioned (Vollmer & Palumbi, 2004), and then re-evaluated, at least for the taxa in the Robust clade (Chen *et al*., 2004; Romano & Cairns, 2000), to which *Psammocora* belongs. An exhaustive analysis of rDNA variability in several coral genera (Wei *et al*., 2006) reported mean values ranging from 1.95 to 3.10 for genera within the Robust clade (excluding the peculiar case of *Platygyra*). Divergences among the studied TCM of the genus *Psammocora* fall within this range when comparing TCM within each of the two main identified clades. However, comparisons between TCM of different clades resulted in distances out of this range, and the mean divergence between the two clades was, consequently, higher than the normal interspecific divergence. The same pattern was evidenced when comparing the distance estimate derived from the COI marker with respect to values from the literature (Shearer & Coffroth, 2008; Shearer *et al*., 2002). Most of the genetic distances between congeners drawn from 17 different genera from different families were < 2% while, in this study, all comparisons between TCM of different clades resulted in values higher than 2%. In fact, intraspecific divergences, together with interspecific distances within the same clade, clearly confirmed the limits of this marker at low systematic level. Together, both inferences revealed the presence of previously undetected distinctions within the genus *Psammocora*.

Ribosomal DNA showed different levels of distinction of TCM clades. TCM D (*P. haimiana*) and TCM E (*P. digitata*) clades were well resolved, matching the type cluster morphology-based identifications of specimens all identified as *P. digitata* based on the taxonomic literature descriptions. TCM B (*P. albopicta*) was not completely resolved, while TCM C (*P. profundacella*) and TCM A (*P. niestraszi*) were partially resolved, though strongly related. From the first case to the latter, a gradient of lineage sorting, related to presumptive different time points of species origin, can be hypothesised. *P. digitata* and *P. haimiana* seem to have completed the process of lineage sorting, although a more variable markers is needed to definitively solve this question. Conversely, in *P. niestraszi* and *P. profundacella*, though showing clear morphological distinction, the process of lineage

sorting driven by concerted evolution may still be incomplete, although clear morphological distinctions exist between the two species. An alternative hypothesis explaining the lack of resolution of these two species emphasises the potential role of hybridisation (Diekmann *et al*., 2001; Vollmer & Palumbi, 2004). Yet, the absence of intraindividual polymorphism in rDNA sequences and the lack of morphological overlapping weaken the likelihood of this hypothesis.

The enclosed petaloid septa (EPS) corresponding to extrapolypal tentacles surrounding the polyp (Benzoni *et al*., 2007) are typical of and unique to the genus *Psammocora*. These structures have been indicated to be systematically informative at the genus and also at the species level. Their relevance for species boundary delimitation has already been underlined by Benzoni *et al*. (2007) and Stefani *et al*. (2008a, b). The combined morphologic and molecular results provided in this paper suggest that not only are the EPS dimensions informative in defining and recognising species boundaries, but also their degree of development seems to relate to the age of the taxon examined. In other words, older species have less developed EPS, while younger and less resolved species have the highest known development of EPS, as shown in Figure 5. Under this hypothesis, *P. albopicta* could be considered the most likely ancestral candidate. Conversely, the corallite size which has been indicated by some to be an informative character (Kerr, 2005) seems not to be correlated, at least in *Psammocora*, to the taxon degree of evolution.

The taxa basal and in the top half of the ITS-based phylogeny (Figure 5) are also found in one of the two divergent clades of the COI phylogeny (Figure 6). They are *P. albopicta*, *P. haimiana* and *P. digitata,* and all show 1 or 2 rows of enclosed petaloid septa surrounding calices, with the second, and more external, row being most often incomplete. Conversely, taxa found in the second clade in both ITS and COI phylogenies are characterised by a number of EPS series which are up to 5 complete rows for *P. profundacella* (TCM C) and up to 10 complete series, or more, in *P. nierstraszi* (TCM A) (Figure 5). Moreover, the calices in these species tend to be arranged in series separated by acute ridges and the highest number of EPS rows is found between parallel series of calices. Hence, along the succession of speciation events in the ITS phylogeny, the number of EPS rows seems to be a highly informative character. This holds true also when looking at the COI phylogeny (Figure 6). One of the two strongly supported clades includes specimens with a maximum of 1 or 2 rows of enclosed petaloid septa surrounding the calices and the other specimens with a higher number of EPS rows.

This study results complement and partially complete those obtained by Stefani *et al*. (2008a) (Table 6). The authors based their analyses on rDNA and corallite morphometrics as in the present study. However, they used literature based identifications of specimens without referring to the type material. For this reason some of the species names of the taxa they investigated appear completely or partially different from those presented in this paper. However, based on the nomenclatural changes resulting from this revision, all the species analysed by Stefani *et al*. (2008a) except *P. contigua* were also studied in this paper (Table 6). Moreover, the morphometric and molecular results found by these authors based on corallite dimensions and rDNA are congruent with those presented here. According to both sets of authors *P. haimiana*, identified as *P. digitata* by Stefani *et al*. (2008a), is morphometrically and molecularly distinguished from *P. profundacella*, then partially identified as *P. haimeana*. In the other published paper on the species boundaries in the genus *Psammocora* (Stefani *et al*., 2008b) the authors addressed the nominal species characterised by branching colony growth form. They concluded that both based on genetic (β-tubulin) and morphometric data *P. contigua* and *P. stellata* could be separated, but that *P. obtusangula*, a valid species according to Veron (2000) is a synonym of *P. contigua* (Table 6). Unfortunately, different species were examined by Stefani *et al*. (2008b) and in the present study, and different genes were used (Table 6). Hence, the species boundaries and phylogenetic relationships between the species examined in both studies remain to be investigated. Specifically, *P. stellata* should be analysed together with *P. haimiana*, *P. digitata*, *P. profundacella*. *P. nierstraszi*, and *P. albopicta*, while the relationships between *P. contigua* and *P. digitata*, *P. nierstraszi*, and *P. albopicta* are still to be addressed (Table 6). Stefani *et al*. (2008a) showed that *P. contigua* and *P. profundacella* could be separated based on corallite morphometry but not based on rDNA. Interestingly, the same conclusion was reached in the present study in the case of *P. profundacella* and *P. nierstraszi*. Moreover, besides different colony growth form corallite dimensions of *P. contigua* (Stefani *et al*., 2008a, b) and *P. nierstraszi* (Benzoni, 2006; this study) are very similar. Hence, although species boundaries between *P. contigua* and *P. nierstraszi* have not been specifically investigated yet, further study could actually show that neither morphologic nor genetic differences are found between these two nominal species. Finally, the status of *P. explanulata* and its position within the Fungiidae as hypothesized by Benzoni *et al*. (2007) and this study should be definitively addressed and formalised in a study including both Psammocoridae and Fungiidae.

Table 6. List in chronological order of the nominal *Psammocora* species examined in Stefani *et al*. (2008a, b) and this study

	Performed analyses and main results		
Nominal species	Stefani *et al*., 2008a	Stefani *et al*., 2008b	This study
P. contigua	rDNA‡ Mophometrically distinguished by the other examined species, genetically not from *P. profundacella*	βtub*†‡ Valid species	
P. phrygiana		Synonym of *P. contigua*†*	
P. obtusangula		βtub*†‡ Synonym of *P. contigua*	
P. plicata = *P. frondosa*		Synonym of *P. contigua*†*	
P. planipora		Synonym of *P. stellata*†*	
P. haimiana	rDNA (identified as *P. digitata*) Morphometrically and genetically distinguished by the other examined species‡		rDNA, COI*†‡ Morphometrically but not genetically entirely separable from *P. digitata*
P. digitata			rDNA, COI*†‡ Valid species but genetically not entirely separable from *P. haimiana*
P. stellata		βtub*†‡ Valid species	
P. gonagra		Synonym of *P. contigua*†*	
P. ramosa		Synonym of *P. contigua*†*	
P. superficialis			rDNA, COI*†‡ Synonym of *P. profundacella*
P. profundacella	rDNA (partially identified as *P. haimeana*)‡ Mophometrically distinguished by the other examined species, genetically not from *P. profundacella*		rDNA, COI*†‡ Valid species but genetically indistinguishable from *P. nierstraszi*
P. divaricata		Synonym of *P. stellata*†*	
P. brighami		Synonym of *P. stellata*†*	
P. verrilli			Synonym of *P. nierstraszi*†‡*
P. nierstraszi			rDNA, COI*†‡ Valid species but genetically indistinguishable from *P. profundacella*
P. samoensis			Synonym of *P. profundacella*†*
P. vaughani			(on holotype illustration)* Synonym of *P. nierstraszi*
P. decussata		Synonym of *P. contigua*†*	
P. folium			Synonym of *P. haimiana*†*
P. togianensis			Synonym of *P. haimiana*†*
P. albopicta			r DNA, COI*†‡ Valid species but genetically not entirely resolved

For each nominal species the analyses performed and main results relevant to the systematics and taxonomy of the genus obtained in the mentioned papers are reported. Valid nominal species in after the revision in either Stefani *et al*. (2008b) or this study are in bold.
EPS, enclosed petaloid septa; –, species not examined.
*Type material examined.
†Type material morphometry.
‡Non-type specimens morphometry.

CONCLUSIONS

In general, the delineation of species boundaries on the basis of the joint results of morphologic and molecular analyses largely agreed with the results obtained from the morphometric analysis of calice and septa dimensions of the 12 examined *Psammocora* nominal species type material. Extending the analyses from type specimens to a data set as much as possible representative of the different nominal species morphologic variability allowed quantification of characters of five distinct morphologic species, namely *P. haimiana*, *P. digitata*, *P. profundacella*, *P. nierstraszi* and *P. albopicta*. Finally, the combination of the morphometric and molecular results allowed verification that the morphologic differences between species were largely representative of an underlying phylogeny, and that the typical skeletal features of the genus (the enclosed petaloid septa) are informative in species boundary distinction as well as in reconstructing the evolution of the genus.

The name game results allowed matching of species described in the literature with the type morphology and name of different species as well as the establishment of synonymies between supposed endemics and widely distributed taxa. Thus, in addition to the relevance of the taxonomic revision resulting from this study, the synonymies established call for a redefinition of the geographic distribution of the examined *Psammocora* species which may have important consequences at the biogeographic (Sheppard, 1998) and ecologic (Bortolus, 2008) levels. In the case of *Psammocora* this was already discussed by Stefani *et al*. (2008b) in referring to branching species.

In the early days of coral taxonomy scientists were limited by a number of factors in their understanding of species boundaries. Today, with extensive sampling, underwater observation and excellent *in vivo* images, we have a much wider knowledge of coral morphology and its variability. However, as species names are used to identify such entities, it is still necessary to refer to the type material characteristics when a species name is used. Problems can arise with species descriptions and synonymies proposed in the literature only referring to other author's identifications, or to the interpretation of what the species looks like in the field, without having examined the type material. This fact was evidenced in this paper thanks to the study of both type material and museum specimens published in widely cited taxonomic descriptions of the examined species. The multidisciplinary evidence gathered highlighted a lack of correspondence between the species names used to identify the specimens in the reference literature and the typical type morphology of most species.

Although it is evident that the holotype system is inadequate for characterising the population level variability in scleractinian corals, the need for a permanent and objective reference for any nominal species described remains. Nowadays, a type series of different specimens displaying the widest possible range of variability as well as matching voucher specimens for genetic studies and illustrations of the organism in its natural environment are unquestionable requirements for the description of a new species. Moreover, when exploring species boundaries in corals, the central role played by existing museum collections as well as direct field observation and sampling should be kept in mind. Museum collections are, and will remain, a fundamental tool for understanding both the morphologic plasticity range of a taxon as well as its geographic distribution. A large part of this information residing in several collections around the world has only been partially analysed and is waiting to be re-discovered.

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