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Genetic and morphological variation in corallivorous snails (*Coralliophila* spp.) living on different host corals at Curaçao, southern Caribbean

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Abstract

Snails of the genus *Coralliophila* (Muricidae: Coralliophilinae) are common corallivores in the Caribbean, feeding on a wide range of host species. In the present study, the morphological and genetic variation in *C. galea* and *C. caribaea* were studied in relation to their association with host coral species at Curaçao. Differences in shell shape among snails living on different hosts were quantified using geometric morphometric and phylogenetic relationships were studied using two mitochondrial markers (12S and COI). Based on these analyses, a new species, *C. curacaoensis* sp. nov., was found in association with the scleractinian coral *Madracis auretenra*. Both *C. galea* and *C. caribaea* showed host-specific differences in shell shape, size, and shell allometry (i.e. changes in morphological development during growth). Shell spire variability contributed foremost to the overall variation in shell shape. In *C. caribaea* minor genetic differences existed between snails associated with scleractinian and alcyonacean corals, whereas in *C. galea* such intraspecific variation was not found. These results shed more light on morphological and genetic differences among coral-associated fauna living on different host species.

Contents

Introduction

Shallow tropical coral reefs are known as the world's most diverse marine ecosystems, with estimates of global species numbers ranging to over one million, constituting a large portion of marine species (Reaka-Kudla, 1997; Plaisance *et al.*, 2011; Appeltans *et al.*, 2012; Fisher *et al.*, 2015). Many coral-associated species depend on their host for food, shelter or recruitment (Scott, 1987; Stella *et al.*, 2010, 2011; Hoeksema *et al.*, 2012, 2017). Currently, 51 invertebrates are known that feed on live scleractinian corals, of which 17 are obligate corallivores (Rotjan and Lewis 2008), while many other species prey on coral species other than scleractinians (Schiaparelli *et al.*, 2005; Reijnen *et al.*, 2010; Wolf *et al.*, 2014; Sánchez *et al.*, 2016). New cases of corallivory, involving new records of predator-prey combinations, are still being reported regularly (e.g., Berumen and Rotjan, 2010; Vermeij, 2010).

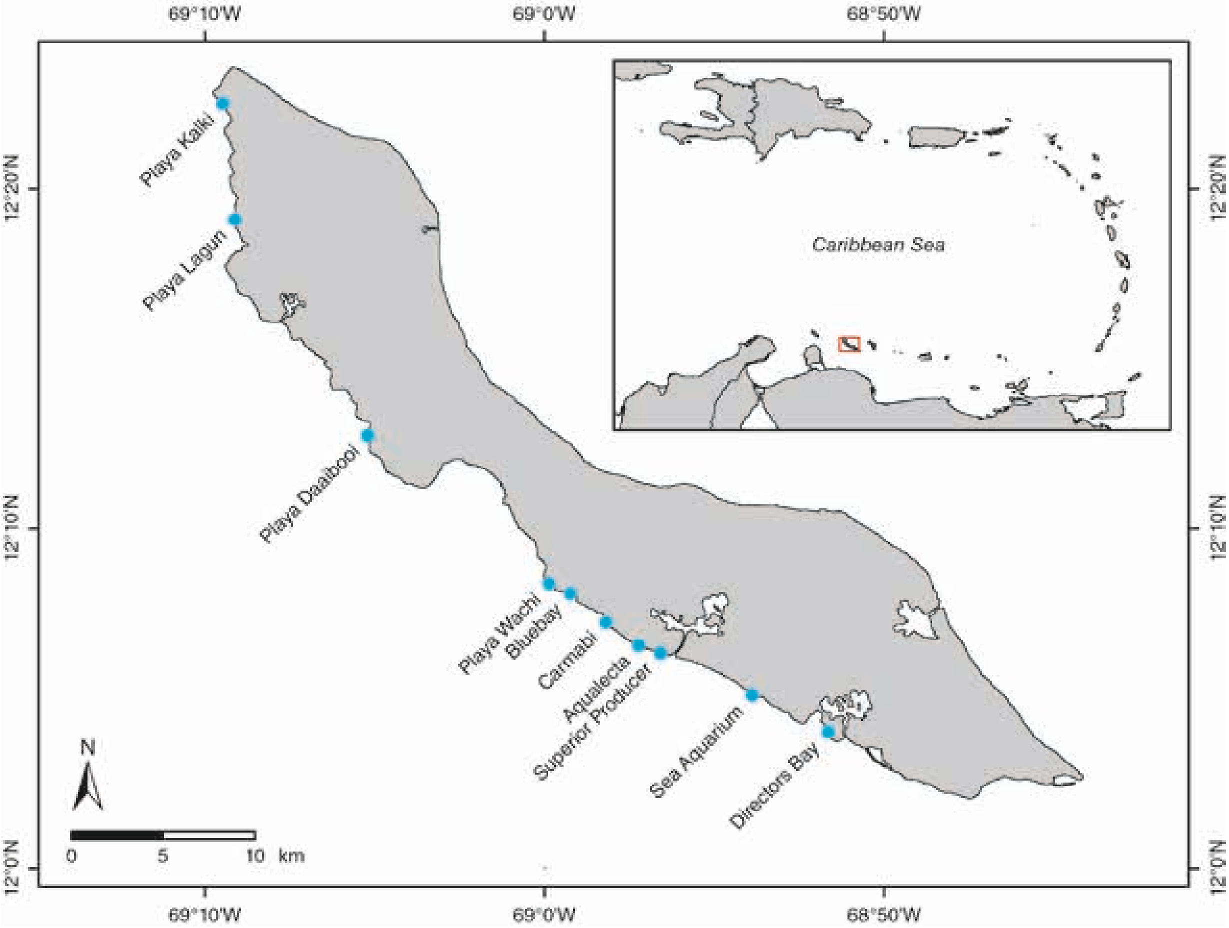

Fig. 1. Map of the localities along the coast of Curaçao where *Coralliophila* spp. were collected.

Snails belonging to the subfamily Coralliophilinae (Gastropoda: Muricidae), with 200-250 species described worldwide, are corallivores that feed on anthozoan host species (Oliverio and Mariottini, 2001a; Oliverio, 2008; Oliverio *et al*., 2009). Within this subfamily, species of the genus *Coralliophila* Adam and Adams, 1853 are common corallivores found on reefs in the Caribbean and Brazil, with *C. galea* (Dillwyn, 1823) and *C. caribaea* Abbott, 1958 as the most abundant species. These species associate with a wide range of anthozoan host species belonging to the hexacoral orders Scleractinia, Zoantharia or Coralliomorpharia, and/or the octocoral order Alcyonacea (Robertson, 1970; Miller, 1981; Dias and Gondim, 2016). Overlap in host species has been reported for *C. galea* and *C. caribaea*, involving hosts belonging to the Scleractinia, Zoantharia and Coralliomorpharia, but host partitioning has also been observed whereby *C. caribaea* only preyed on alcyonaceans (Robertson, 1970; Miller, 1981), whereas *C. galea* preferred scleractinians (Miller, 1981).

In the ecological literature, the most common *Coralliophila* species in the Caribbean, *C. galea,* has often been misidentified as *C. abbreviata* (Lamarck, 1816) (see Bouchet, 2015; Netchy *et al*., 2016). *Coralliophila abbreviata* is a junior synonym of *C. erosa* (Röding, 1798), a species exclusively known from the Indo-Pacific (Oliverio, 2008). Predation by *Coralliophila galea* can negatively impact coral communities (Baums *et al*., 2003a). Bruckner *et al*. (1997), for example, measured a mean tissue consumption per snail of 1.9 cm^2 day^{-1}, with a maximum of 6.5 cm^2 day^{-1} on *Acropora palmata* (Lamarck, 1816). *C. galea* predation also prevented the recovery of *Acropora cervicornis* (Lamarck, 1816) populations from damage caused by a hurricane (Knowlton *et al*. 1988, 1990).

Host-specific differences in morphological and ecological traits may arise in both *Coralliophila* species, like host-related size structuring (Hayes, 1990a; Bruckner *et al*., 1997; Baums *et al*., 2003a; Johnston and Miller, 2006, Johnston *et al*., 2012) and timing of sex change in *C. galea* (Baums *et al*., 2003a; Johnston and Miller, 2006). Host-associated cryptic species also occur among coral-associated gastropods in the Indo-Pacific. Gittenberger and Gittenberger (2011) reported on an adaptive, host-associated radiation among endolithic snails of the genus *Leptoconchus* Rüppell, 1834 (Coralliophilinae), consisting of 14 cryptic species living inside the skeletons of 24 species of mushroom coral hosts (Scleractinia: Fungiidae). A similar adaptive radiation was found among 22 snails of the family Epitoniidae divided over 34 host coral species (Gittenberger and Gittenberger, 2005; Gittenberger and Hoeksema, 2013). In *C. galea*, only a weak genetic divergence existed between snails associated with the scleractinians *Acropora palmata* and *Orbicella* spp. (Johnston *et al*., 2012).

In the present study, host-specific differences in size, shell shape and allometric patterns as well as genetic differences in both *C. galea* and *C. caribaea* were found in response to living of different scleractinian and alcyonacean host species. To study shell morphology independent of shell size, landmark-based geometric morphometrics were used to model shell shape (see e.g., Stone, 1998; Carvajal-Rodríguez *et al*., 2005; Queiroga *et al*., 2011; Mariani *et al*., 2012; Burridge *et al*., 2015; Liew and Schilthuizen, 2016). Host-related size structuring has been observed for *C. galea*, and was consequently also expected for *C. caribaea* in addition to host-associated differences in shell shape and allometry.

Two mitochondrial markers (12S rRNA and cytochrome *c* oxidase subunit I) were used to assess intraspecific host-associated genetic divergence in *C. galea* and *C. caribaea* across the whole range of their host species at Curaçao, extending the results of Johnston *et al*. (2012). Based on Johnston *et al*. (2012), who found high gene flow across the Caribbean and weak host-associated divergence within *C. galea*, we expect genetic divergence among host species to be low or absent for both *C. galea* and *C. caribaea*. By combining morphological and genetic methods, additional information has been obtained regarding the evolutionary and ecological relations between corallivorous snails and their hosts. Lastly, a new species, *C. curacaoensis* Potkamp and Hoeksema sp. nov., was found and described (see Appendix).

Materials and methods

Snails were collected in January-March 2015 from coral colonies at ten localities along the leeward coast of Curaçao, southern Caribbean (Fig. 1). Colonies of scleractinians and alcyonaceans were haphazardly selected and searched for snails during SCUBA dives. As the sampling effort was not equal among localities and localities were < 50 km apart from each other, locality was not used as a factor in statistical analyses. Aforementioned surveys of invertebrates associated with corals appear to be effective, as they have previously resulted in new host records for Curaçao and the Caribbean in for example ovulid snails on octocorals (Reijnen *et al*., 2010), gall crabs in scleractinians (Van der Meij, 2014) and serpulids in reef corals (Hoeksema *et al*., 2015; Hoeksema and Ten Hove, 2017).

All snails associated with a colony were collected and stored in one plastic sampling bag per host colony. Host corals were photographed and their identity, depth and locality were recorded. If present, feeding scars were photographed as well. After sampling, snails were put in 96% ethanol (in a few cases 70% ethanol) until further processing. All specimens have been deposited in the collections of Naturalis Biodiversity Center, Leiden, the Netherlands (catalogued under numbers coded RMNH). In the case of snails associated with alcyonaceans, a small sample of the distal part of host colonies was also collected for species identification. Alcyonacean sclerites were isolated by dissolving the coenchymal tissue in sodium hypochlorite (4% household bleach solution). Alcyonaceans were identified to the genus level using photographs and light microscopy slides of the sclerites, using the keys by Bayer (1961).

Morphology

Shell length of the snails was measured with a digital calliper to the nearest 0.01 mm. Of 60 snails (7% of total), only the shell length was measured with a Vernier calliper to the nearest 0.05 mm. Shell length was defined as the length from the tip of the apex to the tip of the aperture (end of the anterior canal) (Fig. 2). To determine any measurement error that could arise from inconsistencies in the orientation of the shell between the calliper blades, the shell length of 65 snails was measured in triplicate. The measurement error was defined as the average distance to the mean of the three replicate measurements of each shell. The error for shells measured with the Vernier calliper was not calculated. Shell lengths and widths were log-transformed

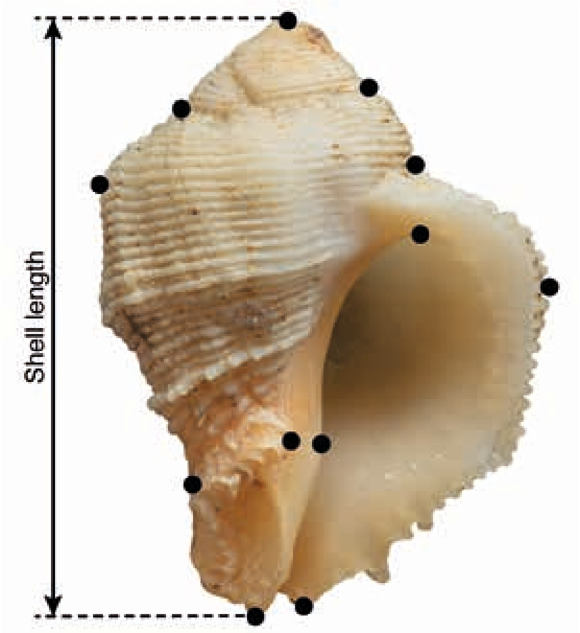

Fig. 2. Shell length as used to measure all shells. Twelve black points represent the 12 landmarks used in the geometric morphometric analysis.

in all statistical analysis to achieve normal distributions and homogeneity of variance. Differences in shell length were tested using ANOVA models and in some cases using Kruskall-Wallis rank sum tests.

Landmark-based geometric morphometrics were used to assess the shape of each shell. After measuring shell length, the ventral side (aperture facing upwards) was photographed with a Nikon D7000 DSLR camera equipped with a Sigma 105 mm macro lens. The locations of 12 landmarks were recorded on each photo (Fig. 2) and chosen to capture the observed variation in shell shape during shell measurements. Most of these landmarks have been used before in the morphometrics of gastropods (Zelditch *et al*., 2004; Hollander *et al*., 2006; Mariani *et al*., 2012). Shells covered by encrusting algae were excluded from this analysis because their landmarks were hidden. To align landmarks and remove the effect of size, a generalized Procrustes superimposition was applied to the data (Gower, 1975; Rohlf and Slice, 1990). Replication errors landmark data were calculated as well. See Online Supplementary Material 1 for the methods followed.

To statistically test for differences in shell shape and potential relationships between shell shape and shell size, snail host species or depth (as well as the interactions between host species and both shell size and depth), distance-based Procrustes ANOVA models were used that are equivalent to other distance-based ANOVA methods, like PerMANOVA (Goodall 1991; Anderson 2001; Adams and Otárola-Castillo 2013). For all Procrustes ANOVA models, significance of the different factors was tested against 10,000 permutations. Host-associated differences in shell shape were tested through pairwise comparisons of the effect of host species in a full model (with all tested factors included) against a reduced model (with all factors except host species included). To account for multiple tests, *p*-values were corrected using a Bonferroni correction.

To define allometric patterns, a common allometric component (CAC) was calculated from the landmark data to express allometric patterns as one variable (Mitteroecker *et al*., 2004). Host-specific regressions between CAC and shell length were made (excluding hosts having less than five specimens with morphometric data). The vectors of shell length of snails associated with different host species were compared to reveal differences in allometric patterns in the amount of change in shell shape per unit of growth (corresponding to the distance among vectors of shell length) and the direction of shell shape change (corresponding to the correlation among vectors of shell length). Pairwise comparisons of both the distance and correlation among the vectors of shell length were made between a full model and a reduced model without the interaction between the factors host species and shell length (see Online Supplementary Material 2). As before, the *p*-values were corrected with a Bonferroni correction.

To visualize variation in shell shape, a principal component analysis (PCA) was performed using the landmark data. To separate real variation in shell shape from noise resulting from the error described above and calculate repeatability of axes, landmark data of the three replicated photos was included in the PCA. Intraclass correlation coefficients (ICC, model 2,1) were calculated between the PCA-scores of triplicates on all PCA-axes. An axis was considered repeatable when the ICC was higher than 0.80 (Burridge *et al*., 2015). To visualize differences in allometric patterns among snails associated with different host species, linear regressions between PCA scores and shell length were used to predict PCA scores (and therefore shell shape) of shells of specific lengths associated with specific host species

After the morphometric analysis, shells were crushed to remove the snail from its shell. Using a dissecting microscope, the sex of each snail was determined by presence or absence of a penis just above the left eye-

Table 1. Sequences of forward (F) and reverse (R) primers for the amplification of two mitochondrial markers, 12S rRNA (12S) and cytochrome *c* oxidase subunit I (COI). All primers are as in Barco *et al*. (2010).

Marker	**Primer**	**Sequence (5'-3')**[a]	**Reference**
12S	12S-I (F)	TGC CAG CAG YCG CGG TTA	Oliverio and Mariottini (2001)
	12S(-) (R)	AGA GYG RCG GGC GAT GTG T	Bandyopadhyay *et al*. (2008)
COI	LCO1490 (F)	GGT CAA CAA ATC ATA AAG ATA TTG G	Folmer *et al*. (1994)
	HC02198 (R)	TTA ACT TCA GGG TGA CCA AAA AAT CA	Modified from Folmer *et al*. (1994)

[a]: R = A, G; Y = C, T

stalk. Differences in sex ratios among snails associated with different host species were assessed using Fisher's exact tests. For tests on larger tables (to test for differences among host species), *p*-values were computed using Monte Carlo simulations, with 1 million replications. Pairwise differences among host species were assessed using pairwise Fisher's exact tests; *p*-values were corrected using a Bonferroni correction. Linear regressions were made between sex ratio and mean shell length, and between mean male and female shell length. Individual points (corresponding to a single host species) were weighed according to the number of specimens. Only host species with more than five specimens were included in the analyses comparing snails among host species.

All statistics were done in R, using the package Geomorph 2.1.5 for all morphometric analyses (Adams and Otárola-Castillo, 2013; Adams *et al*., 2015; R Core Team, 2015).

Genetics

A small piece of tissue was removed from the foot of a selection of snails for genetic analysis. Two mitochondrial markers were amplified and sequenced: a fragment the 12S rRNA (12S) gene and a fragment of the cytochrome *c* oxidase subunit 1 gene (COI). Both markers have been used extensively and proven informative in closely related gastropods (Oliverio and Mariottini, 2001a, 2001b; Barco *et al*., 2010; Gittenberger and Gittenberger, 2011). DNA was extracted on a KingFisher Flex magnetic particle processor (Thermo Scientific), using the Nucleospin Tissue kit (Macherey-Nagel, Düren, Germany). PCR reaction mixtures consisted for both markers of 0.25 μL QIAGEN Taq DNA polymerase (5 units μL^{-1}), 0.5 μL dNTPs (2.5 mM) and 1.0 μL of both the forward and reverse primers, as well as 0.5 μL 100 mM Promega BSA, 0.5 μL 25 mM $MgCl_2$, 2.5 μL 10x PCR buffer (QIAGEN) and 15.8 μL milli-Q water. In the PCR, an annealing temperature of 50°C was used for both 12S and COI. PCR products were sequenced using Sanger sequencing by BaseClear (Leiden, the Netherlands). Primers were used as in Barco *et al*. (2010) (Table 1). Five previously published sequences were used in the phylogenetic analysis (Table 2).

Forward and reverse sequences were assembled automatically and edited by hand in Sequencher 5.4 (Gene Codes Corporation, Ann Arbor, MI, USA). Sequences were aligned using the MAFFT algorithm on the GUIDANCE2 server (Katoh *et al*., 2005; Sela *et al*., 2015). The appropriate substitution model for either marker was determined based on the Akaike information criterion (AIC) in both the jModelTest 2.1.7 and MrModeltest 2 software packages (Nylander, 2004; Darriba *et al*., 2012). Both software packages agreed on the best substitution model to be used in MrBayes. The GTR + Γ (Tavaré 1986) model was used for 12S, the HKY85 + Γ + I (Hasegawa *et al*., 1985) model was used for COI. A phylogenetic tree was constructed based on both markers separately as well as a concatenated dataset using Bayesian inference with the (parallel) Metropolis coupled Markov chain Monte Carlo ($(MC)^3$) method in MrBayes 3.2 (Altekar *et al*., 2004; Ronquist *et al*., 2012). In MrBayes, the $(MC)^3$ analysis was run in duplicate, for a length of 25,000,000 generations for the concatenated dataset and a length of 15,000,000 generation for the trees based on single markers. Trees were sampled every 100 generations. Burn-in was determined by looking at the deviation of split frequencies, trees sampled before this deviation dropped below 0.01 were discarded. For the concatenated analysis, the burn-in was determined to be 1.49 million generations, almost 6% of the total length of the analysis. For the trees based on 12S and COI separately, burn-in was determined to be 555,000 and 1,155,000 generations respectively. Sequences of the muricid species *Drupella rugosa* (Born, 1778), previously published by Claremont *et al*. (2011), were used as an outgroup.

Table 2. Specimens used in phylogenetic analysis with their voucher numbers (RMNH) and GenBank accession numbers.

		Accession numbers	
Species / Host taxon	**Voucher**	**12S**	**COI**
***Coralliophila galea* (Dillwyn, 1823)**			
Host: Subclass Hexacorallia, Order Scleractinia			
Acroporidae			
Acropora palmata (Lamarck, 1816)	RMNH.5004294	KY829357	KY818778
	RMNH.5004295	—	KY818777
	RMNH.5004296	—	KY818776
Agariciidae			
Agaricia agaricites (Linnaeus, 1758)	RMNH.5004297	KY829360	KY818784
	RMNH.5004298	KY829359	KY818783
	RMNH.5004299	—	KY818782
Agaricia humilis Verrill, 1901	RMNH.5004300	—	KY818781
Agaricia lamarcki Milne Edwards and Haime, 1851	RMNH.5004301	—	KY818780
	RMNH.5004302	KY829358	KY818779
Astrocoeniidae			
Madracis auretenra Locke, Weil and Coates, 2007	RMNH.5004306	KY829354	KY818772
	RMNH.5004307	KY829353	KY818771
	RMNH.5004308	KY829352	KY818770
Meandrinidae			
Meandrina meandrites (Linnaeus, 1758)	RMNH.5004309	KY829350	KY818768
	RMNH.5004310	KY829349	KY818767
Merulinidae			
Orbicella annularis (Ellis and Solander, 1786)	RMNH.5004312	KY829348	KY818766
	RMNH.5004313	KY829347	KY818765
	RMNH.5004314	KY829346	KY818764
Orbicella faveolata (Ellis and Solander, 1786)	RMNH.5004315	KY829345	KY818763
	RMNH.5004316	KY829344	KY818762
Orbicella franksi (Gregory, 1895)	RMNH.5004317	KY829343	KY818761
	RMNH.5004318	KY829342	KY818760
Montastraeidae			
Montastraea cavernosa (Linnaeus, 1767)	RMNH.5004311	KY829351	KY818769
Mussidae			
Colpophyllia natans (Houttuyn, 1772)	RMNH.5004303	—	KY818775
Diploria labyrinthiformis (Linnaeus, 1758)	RMNH.5004304	KY829356	KY818774
	RMNH.5004305	KY829355	KY818773
Pseudodiploria clivosa (Ellis and Solander, 1786)	RMNH.5004320	—	KY818759
	RMNH.5004321	—	KY818786
Pseudodiploria strigosa (Dana, 1846)	RMNH.5004322	KY829361	—
Poritidae			
Porites porites (Pallas, 1766)	RMNH.5004319	—	KY818785
***Coralliophila caribaea* Abbott, 1958**			
Host: Subclass Hexacorallia, Order Scleractinia			
Agariciidae			
Agaricia lamarcki Milne Edwards and Haime, 1851	RMNH.5004274	—	KY818724
Meandrinidae			
Meandrina meandrites (Linnaeus, 1758)	RMNH.5004278	KY829309	—
Montastraeidae			
Montastraea cavernosa (Linnaeus, 1767)	RMNH.5004279	KY829323	KY818739
	RMNH.5004280	KY829322	KY818738
	RMNH.5004281	KY829321	KY818737
Mussidae			
Colpophyllia natans (Houttuyn, 1772)	RMNH.5004275	KY829310	—
	RMNH.5004276	—	KY818755
Diploria labyrinthiformis (Linnaeus, 1758)	RMNH.5004277	KY829338	KY818754
Mycetophyllia ferox Wells, 1973	RMNH.5004282	KY829320	KY818736
Pseudodiploria strigosa (Dana, 1846)	RMNH.5004290	—	KY818728

		Accession numbers	
Species / Host taxon		**Voucher**	**12SCOI**
Poritidae			
Porites astreoides Lamarck, 1816	RMNH.5004283	—	KY818735
	RMNH.5004284	KY829319	KY818734
	RMNH.5004285	KY829318	KY818733
Porites porites (Pallas, 1766)	RMNH.5004286	KY829316	KY818731
	RMNH.5004287	KY829315	KY818730
	RMNH.5004288	KY829314	KY818729
	RMNH.5004289	KY829317	KY818732
Siderastreidae			
Siderastrea siderea (Ellis and Solander, 1768)	RMNH.5004291	KY829313	KY818727
	RMNH.5004292	KY829312	KY818726
	RMNH.5004293	KY829311	KY818725
Host: Subclass Octocorallia, Order Alcyonacea			
Gorgoniidae			
Antillogorgia sp.	RMNH.5004260	KY829336	KY818752
	RMNH.5004261	KY829334	KY818750
	RMNH.5004262	KY829332	KY818748
	RMNH.5004263	KY829331	KY818747
	RMNH.5004264	KY829325	KY818741
Gorgonia sp.	RMNH.5004268	KY829337	KY818753
Plexauridae			
Eunicea sp.	RMNH.5004265	KY829333	KY818749
	RMNH.5004266	KY829327	KY818743
	RMNH.5004267	KY829324	KY818740
Pseudoplexaura sp.	RMNH.5004269	KY829335	KY818751
	RMNH.5004270	KY829330	KY818746
	RMNH.5004271	KY829329	KY818745
	RMNH.5004272	KY829328	KY818744
	RMNH.5004273	KY829326	KY818742
***Coralliophila curacaoensis* Potkamp and Hoeksema sp. nov.**			
Host: Subclass Hexacorallia, Order Scleractinia			
Astrocoeniidae			
Madracis auretenra Locke, Weil and Coates, 2007	RMNH.5004323	KY829340	KY818757
	RMNH.5004324	KY829339	KY818756
	RMNH.5004325	KY829341	KY818758
***Coralliophila fontanangioyae* Smriglio and Mariottini, 2000**			
Host: Subclass Hexacorallia, Order Scleractinia			
Astrocoeniidae			
Madracis asperula Milne Edwards and Haime, 1849	—	FN391972[a]	—
***Coralliophila meyendorffii* (Calcara, 1845)**			
Host: Subclass Hexacorallia, Order Scleractinia			
Dendrophylliidae			
Balanophyllia europaea (Risso, 1826)	—	AJ297519[b; c]	FN651936[c]
***Coralliophila mira* (Cotton and Godfrey, 1932)**			
—	—	FN651853[c]	FN651937[c]
***Leptoconchus* sp.**			
—	—	FN391979[c]	FN651939[c]
***Drupella rugosa* (Born, 1778)**			
—	—	FR854011[d]	FR853848[d]

Previously published sequenches: [a] Oliverio *et al*. (2009); [b] Oliverio and Mariottini (2001); [c] Barco *et al*. (2010); [d] Claremont *et al*. (2011).

Table 3. Number of specimens of *Coralliophila* spp. collected from different hosts species (C) and the number of specimens used in the morphometric analyses (M). Numbers between brackets indicate the number of host colonies from which snails were collected.

	Coralliophila galea		***Coralliophila caribaea***		***Coralliophila curacaoensis* sp. nov.**	
Host species	**C**	**M**	**C**	**M**	**C**	**M**
Subclass Hexacorallia, Order Scleractinia						
Acroporidae						
Acropora palmata (Lamarck, 1816)	7 (3)	4				
Agariciidae						
Agaricia agaricites (Linnaeus, 1758)	66 (12)	59				
Agaricia humilis Verrill, 1901	49 (17)	29				
Agaricia lamarcki Milne Edwards and Haime, 1851	24 (7)	20	3 (3)	—		
Astrocoeniidae						
Madracis auretenra Locke, Weil and Coates, 2007	8 (2)	—			10 (3)	7
Meandrinidae						
Meandrina meandrites (Linnaeus, 1758)	55 (8)	39	5 (3)	1		
Merulinidae						
Orbicella annularis (Ellis and Solander, 1786)	224 (29)	138				
Orbicella faveolata (Ellis and Solander, 1786)	55 (9)	32				
Orbicella franksi (Gregory, 1895)	22 (5)	15				
Montastraeidae						
Montastraea cavernosa (Linnaeus, 1767)	1 (1)	—	5 (2)	2		
Mussidae						
Colpophyllia natans (Houttuyn, 1772)	34 (11)	20	7 (5)	4		
Diploria labyrinthiformis (Linnaeus, 1758)	29 (10)	16	1 (1)	—		
Mycetophyllia ferox Wells, 1973			1 (1)	—		
Pseudodiploria clivosa (Ellis and Solander, 1786)	7 (2)	2				
Pseudodiploria strigosa (Dana, 1846)	107 (12)	68	3 (3)	—		
Poritidae						
Porites astreoides Lamarck, 1816			7 (3)	4		
Porites divaricata Le Sueur, 1820			1 (1)	—		
Porites furcata Lamarck, 1816			3 (2)	1		
Porites porites (Pallas, 1766)	1 (1)	—	18 (6)	8		
Siderastreidae						
Siderastrea siderea (Ellis and Solander, 1768)	1 (1)	—	27 (6)	21		
Subclass Octocorallia, Order Alcyonacea						
Gorgoniidae						
Antillogorgia sp.			16 (7)	3		
Gorgonia sp.			5 (3)	—		
Plexauridae						
Eunicea sp.			13 (5)	2		
Plexaura sp.			2 (1)	—		
Pseudoplexaura sp.			22 (6)	9		

Finally, an automatic barcode gap discovery analysis (ABGD) based on Kimura two-parameter (K2P) model on the marker COI was used to assess species delineation on the phylogenetic tree and to identify Molecular Operational Taxonomic Units (MOTUs) (see Kimura, 1980; Blaxter, 2004; Puillandre *et al*., 2012; Barco *et al*., 2013). Sequences from coralliophiline snails previously published by Harasewych *et al*. (1997), Puillandre *et al*. (2009), Barco *et al*. (2010), Claremont *et al*. (2011) and Gittenberger and Gittenberger (2011) were included in this analysis (Online Supplementary Material 3), while the outgroup was excluded.

To further assess host-associated genetic divergence, a haplotype network was built for both *C*. *galea* and *C*. *caribaea*, using both markers separately. Networks were calculated using an infinite site model based on uncorrected distances between haplotypes. To statistically assess intraspecific genetic divergence, an AMOVA (*p*-values calculated based on 100,000 permutations) with host species or host order for both *C. galea* and *C. caribaea* was used on both markers. Statistics on genetic data and the calculation of the haplotype networks were performed in R using the packages APE 3.4 and pegas 0.8-2 (Paradis *et al*., 2004; Paradis, 2010; R Core Team, 2015).

Results

Across all sampled localities along the coast of Curaçao, a total of > 500 colonies of Scleractinia and > 70 colonies of Alcyonacea were searched for snails. Three species of *Coralliophila* were found associated with either Scleractinia or Alcyonacea. Besides *C. galea* and *C. caribaea*, a new species, *C. curacaoensis* Potkamp and Hoeksema sp. nov. was found (described in Appendix).

A total of 690 specimens of *C. galea*, 139 specimens of *C. caribaea* and 10 specimens of *C. curacaoensis* sp. nov. were found on a total of 157 scleractinian colonies and 22 gorgonians (Table 3; voucher numbers RMNH.5004260-5004370). *Coralliophila caribaea* occurred on both host species groups, whereas the other two *Coralliophila* species were only found on scleractinians. In 10 out of 157 associations, *C. galea* co-existed on the same host colony with either *C. caribaea* or *C. curacaoensis* sp. nov. (on two colonies). *Coralliophila* snails were found in association with 20 host species in total, belonging to ten scleractinian genera (Table 3): *C. galea* occurred on 16 hosts species (Fig. 3), *C. caribaea* on 12 hosts species (Fig. 4), and *C. curacaoensis* sp. nov. on a single host species (Fig. 5). In addition, *C. caribaea* occurred on five alcyonacean taxa (Fig. 4). *Coralliophila galea* and *C. caribaea* shared seven host species, whereas *C. curacaoensis* sp. nov. shared its single host species, *Madracis auretenra* Locke, Weil and Coates, 2007, with *C. galea* (Table 3).

In case of scleractinian hosts, both *C. galea* and *C. caribaea* were usually found at the edge of living coral tissue. On corals with a massive or plate-like growth form, snails were usually found at or underneath the edge of their host (Figs. 3d-e; 3h-i; 3k; 4a; 4d-e). Some snails occurred inside crevices and in between ridges of the host colony, in case of for example *C. galea* on *Pseudodiploria strigosa* (Dana, 1846) (Fig. 3l) and *C. caribaea* on *Siderastrea siderea* (Ellis and Solander, 1768) (Fig. 4g). On large coral colonies of *Orbicella annularis* (Ellis and Solander, 1786), *C. galea* commonly clustered together in groups in crevices between the columns that make up the host colonies, again at the edge of living coral tissue (Fig. 3f). Snails on branching corals were found on the branches themselves, such as *C. curacaoensis* sp. nov. on *M. auretenra* (Figs. 3g; 3j; 4b-c; 5).

Snails on alcyonacean hosts were usually found at the base of the colonies (Fig. 4h) but also on the branches, usually on a dead patch (Fig. 4f). Some snails situated underneath the edge of the coral base were almost endofaunal (Figs. 4i-k). Snails sometimes occurred in small aggregations, tightly stacked on top of each other (Figs. 4i-j). Predation on host colonies was visible as damage to the soft surface tissue or its complete removal, leaving bare skeleton behind (Fig. 6). Damage on coral tissue seemed minimal for most host species, despite the occurrence of snail aggregations, except for a few host colonies showing more severe damage (e.g., Fig. 3a). In absence of long-term monitoring of coral colonies, it was unclear whether such damage is indeed the result of predation by *Coralliophila* spp. or if it was already present when the snails arrived.

Shell dimensions

Shell length of *C. galea* and *C. caribaea* ranged from 3.4 to 38.9 mm and 4.3 to 25.8 mm respectively. In both species, a clear host-associated size structuring of shell length existed ($F = 13.6$; $p < 0.0001$ and $F = 5.8$; $p < 0.0001$ for *C. galea* and *C. caribaea*, respectively (Fig. 7). The mean length of *C. galea*, snails differed among host species (29 combinations of host pairs, post-hoc Tukey HSD test), compared to a total of for *C. caribaea* (Tables S2-S3 in Online Supplementary Material 4). *C. caribaea* (nine pairs of hosts) associated with alcyonacean host species that were larger (based on shell length) than snails associated with scleractinian hosts (including all specimens; $F = 23.8$; $p < 0.0001$; Fig. 7).

C. curacaoensis sp. nov. was on average smaller (shell length 2.5-8.9 mm) than *C. galea* and *C. caribaea*. However, *C. curacaoensis* sp. nov. was only found on *Madracis auretenra*, which was also a host of *C. galea*. *Coralliophila galea* individuals associated with *M. auretenra* (shell length 5.4-9.7 mm) were not different in size compared to specimens of *C. curacaoensis* sp. nov. ($F = 4.07$; $p = 0.061$).

Shell shape

Landmarks could be recorded from a total of 504 out of 631 photographed specimens (60.1% of all collected

Fig. 3. In-situ photos of *Coralliophila* galea, associated with various host species: *Agaricia agaricites* (a); *A. humilis* (b); *A. lamarcki* (c); *Colpophyllia natans* (d-e); *Orbicella annularis* (f); *Madracis auretenra* (g); *Meandrina meandrites* (h); *Diploria labyrinthiformis* (i); *Porites porites* (j); *Pseudodiploria clivosa* (k); *P. strigosa* (l). One of the snails has its proboscis extended into the mouth of a polyp (b). Arrows: hidden snails.

specimens): 442 shells of *C. galea*, 55 of *C. caribaea* and seven of *C. curacaoensis* sp. nov. (Table 3). Principal component analysis on landmark data of all three species revealed six axes, explaining 71.0% of all observed variance, with an ICC > 0.80 that could therefore be considered repeatable. While overlap in shell

Fig. 4. In-situ photos of *Coralliophila caribaea*, associated with various host species: *Mycetophyllia ferox* (a); *Porites porites* (b-c); *Colpophyllia natans* (d); *Montastraea cavernosa* (e); *Antillogorgia* sp. (f); *Siderastrea siderea* (g); *Gorgonia* sp. (h); *Pseudoplexaura* sp. (i-k). Some snails have their proboscis extended into the mouth of a polyp (c-e). Two individuals of *C. caribaea* co-occurred with a single individual of *C. galea* (d: arrow). The tight clustering of some snails on a single coral colony is shown by removal of the snail on top (i-j). Arrows: hidden snails.

shape between species existed, all three species were separated on the first and third PC axis, which explained 31.2% and 10.4% of all variances in shell shape (Fig. 8). On the first PC axis, *Coralliophila galea* shells separated from both *C. caribaea* ($p < 0.0001$) and *C. curacaoensis* sp. nov. ($p < 0.0001$). On the third PC

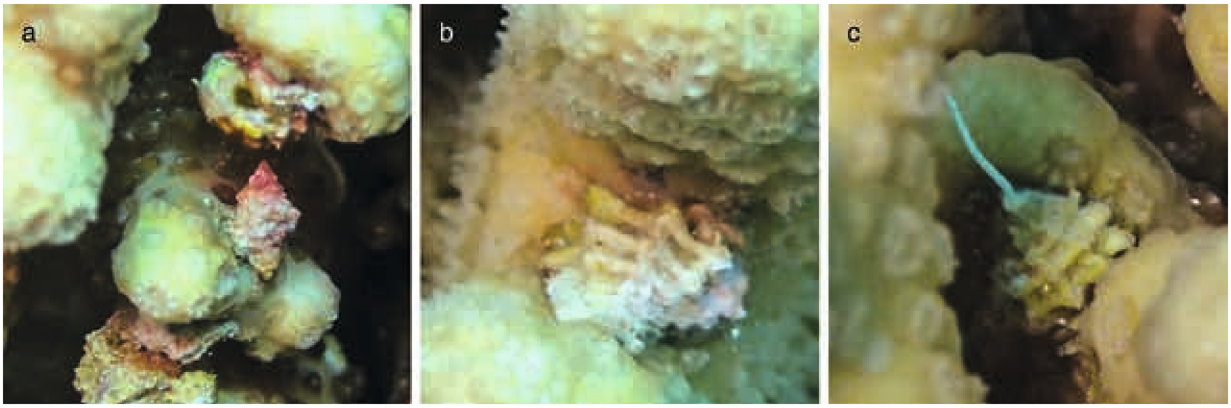

Fig. 5. In-situ photos of *Coralliophila curacaoensis* sp. nov. in association with *Madracis auretenra*. One snail has its proboscis extended into the mouth of a polyp (c).

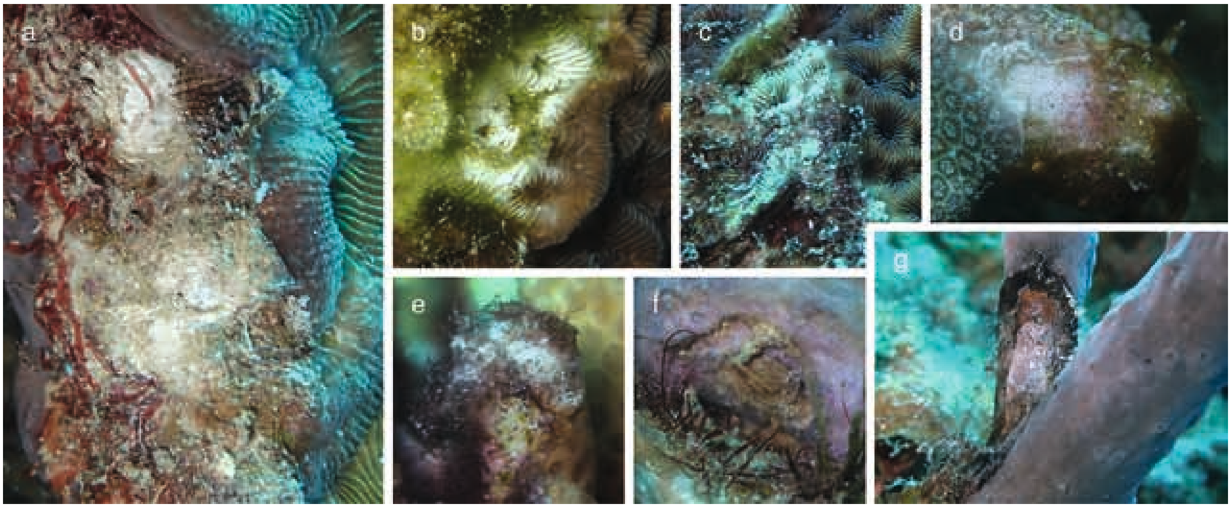

Fig. 6. Removed coral tissue of various host coral species underneath *Coralliophila* individuals: *Colpophyllia natans* (a); *Agaricia agaricites* (b-c); *Porites furcata* (d); *Madracis auretenra* (e); *Pseudoplexaura* sp. (f); *Eunicea* sp. (g).

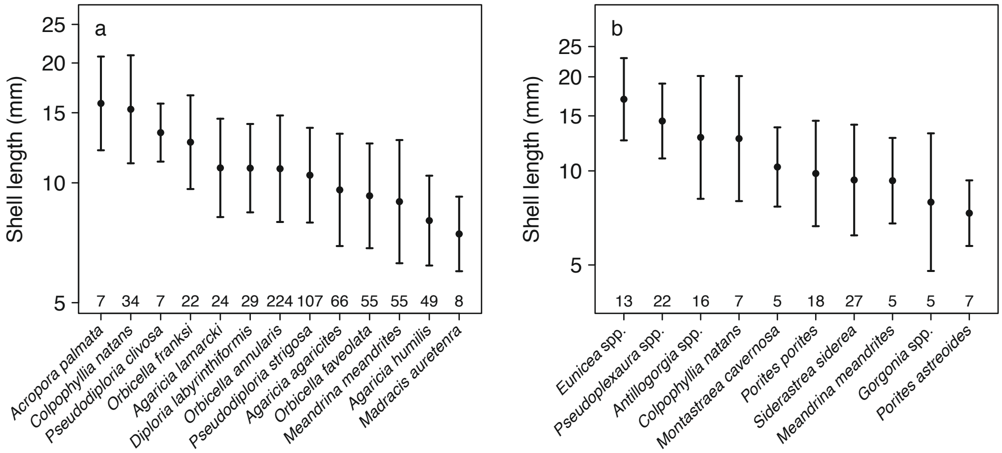

Fig. 7. Host-dependent size structuring of *Coralliophila galea* (a) and *C. caribaea* (b). Error bars represent one standard deviation. Shell length is plotted on a logarithmic scale; numbers above axis represent sample sizes. For significant differences, see Tables S2 and S3 for *C. galea* and *C. caribaea*, respectively (Online Supplementary Material 4).

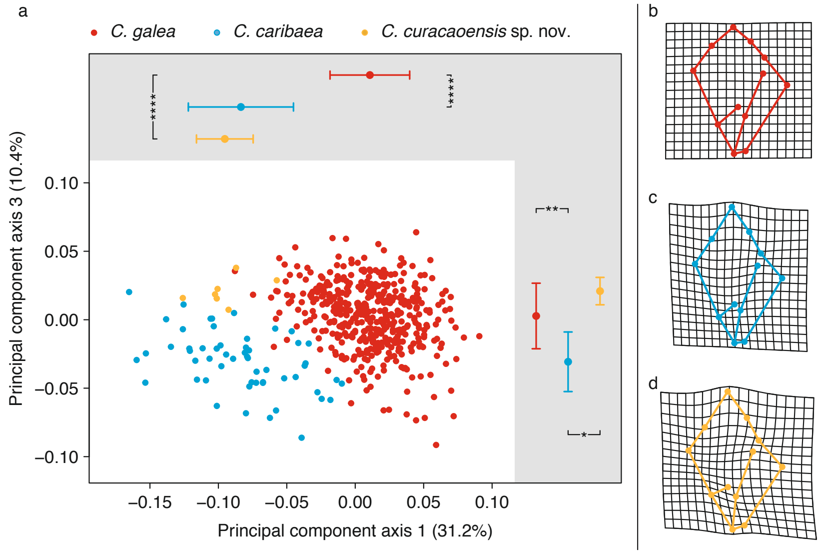

Fig. 8. Interspecific variation in shell shape of three *Coralliophila* spp. by principal component analysis (a). The first and third axes of the PCA are plotted. Mean principal component scores of *Coralliophila* spp. are shown in the margins. Error bars represent one standard deviation. Significant differences: *: $p < 0.05$; **: $p < 0.01$; ****: $p < 0.0001$. Mean shell shapes of the three species are shown (b-d), grids are warped against the mean shell shape of *Coralliophila* spp.

	Coralliophila galea			***Coralliophila caribaea***		
	R²	**F**	***p***	**R²**	**F**	***p***
Shell length	0.072	37.72	0.001	0.041	3.13	0.038
Host order	—	—	—	0.093	7.17	0.001
Host species	0.069	3.30	0.001	0.183	1.76	0.013
Depth	0.006	2.90	0.002	0.031	2.35	0.023
Host species × Shell length	0.046	2.20	0.001	0.133	1.46	0.004
Host species × Depth	0.030	1.75	0.001	0.092	2.36	0.001
Residuals	0.777	—	—	0.429	—	—

Table 4. Factors used in the models of shell shape of both *Coralliophila galea* and *C. caribaea*. Shell length was transformed with the natural logarithm; *p*-values are based on 1,000 permutations.

axis, shells from *C. curacaoensis* sp. nov. were also separated from *C. caribaea* shells ($p = 0.016$). In total, species identity accounted for 19.5% of all observed variance in shell shape.

Intraspecific variation in shell shape of both *C. galea* and *C. caribaea* was high (Figs. 9-10). For *C. galea*, principal component analysis again revealed five repeatable axes (ICC > 0.80, explaining 62.3% of variance in shell shape). For *C. caribaea*, four repeatable axes were found (ICC > 0.80, explaining 72.2% of variation) by the principal component analysis. Compared to *C. galea*, the first two PC axes of *C. caribaea* explained more of the intraspecific variance in shell shape. Most of the intraspecific variation on the repeatable PC axes of both species was related the shape and relative size of the shell spire. Despite high intraspecific variation, no distinct ecotypes could be distinguished in either species, as all specimens clustered together into one cloud without gaps.

For both *C. galea* and *C. caribaea*, all factors and interactions had a significant influence on shell shape (Procrustes ANOVA model; Table 4). Though all tested factors contributed to shell shape, the explained variance in shell shape by any factor was low ($R^2 < 0.20$ for all factors and interactions) and residual variance was high ($R^2 = 0.777$ for *C. galea* and $R^2 = 0.429$ for *C. caribaea*).

Host-associated differences in shell shape accounted for some of the intraspecific variation in shell shape of *Coralliophila* spp. In *C. galea*, differences in host species explained 6.9% of variance in shell shape (Table 4). Among snails from different hosts species, eleven pairwise differences in shell shape were found (Table S4 in Online Supplementary Material 4), that, even though statistically significant, were subtle, and strong overlap in shell shape existed among snails from different host species (Figs. 9-10).

Shell shape of *C. caribaea* also differed among host

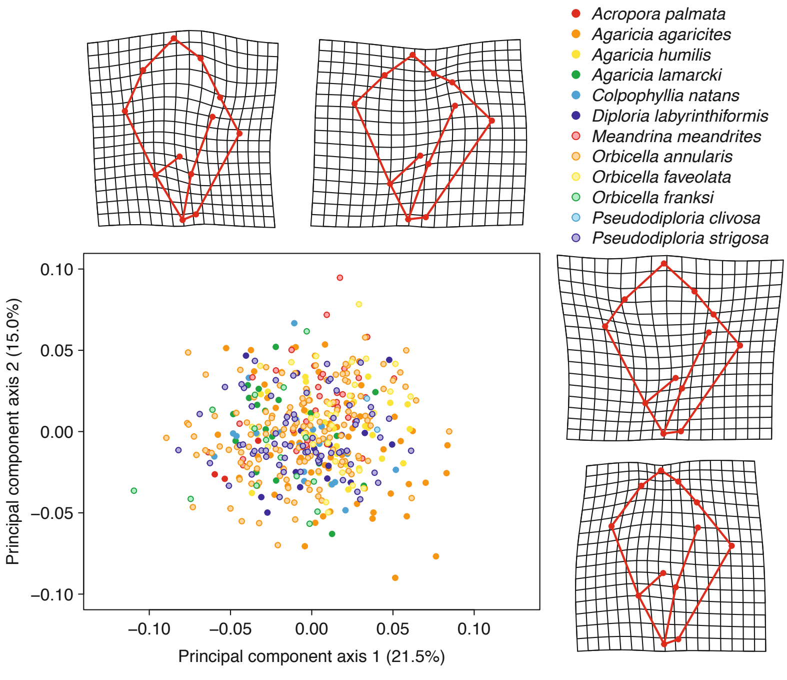

Fig. 9. Intraspecific variation of shell shape in *Coralliophila galea*. The first two axes of the principal component analysis are plotted, with colours coding for host species. Warped grids represent the extreme values of the first and third PC-axis. Grids are warped against the mean shell shape of *C. galea*.

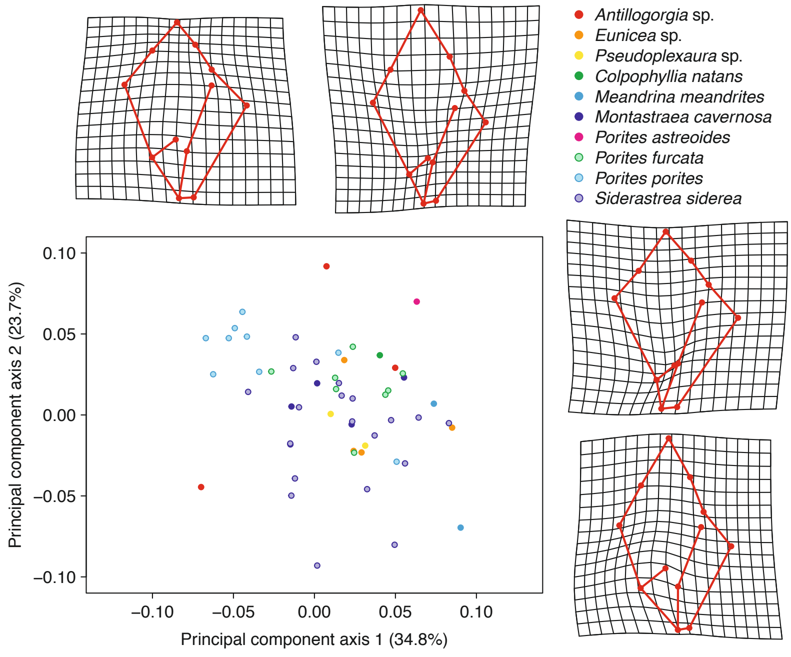

Fig. 10. Intraspecific variation of shell shape in *Coralliophila caribaea*. The first two axes of the principal component analysis are plotted, with colours coding for host species. Warped grids represent the extreme values of the first and third PC-axis. Grids are warped against the mean shell shape of *C. caribaea*.

species. Firstly, snails originating from hosts of the order Alcyonacea and snails from Scleractinia differed in shell shape, which accounted for 9.3% of the observed variance in shell shape (Table 4). At the host genus level, two pairwise differences were significant (Table S5).

Depth had a small, though significant, effect on shell shape in both *C. galea* and *C. caribaea* (Table 4). On top of an overall effect of depth, and a small host-specific effect of depth was observed in both *C. galea* and *C. caribaea*.

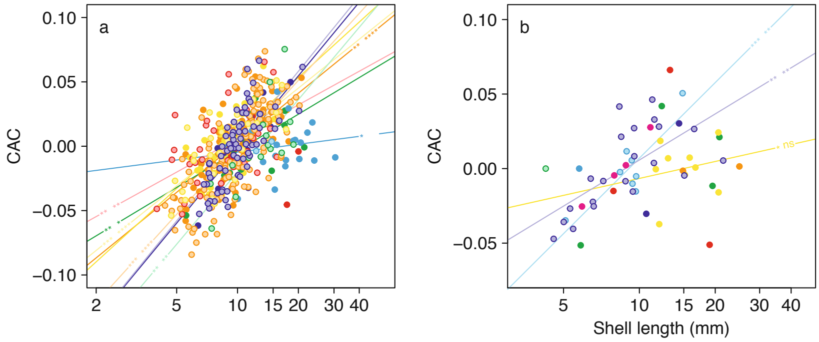

Fig. 11. Allometric patterns in *Coralliophila galea* (a) and *C. caribaea* (b). Common allometric component (CAC) is plotted against shell length (a). Separate regressions for host species with five or more specimens are plotted, symbols on the lines represent the R^2-value (first symbol) and *p*-value (second symbol) of the regression: ns: $p > 0.05$; *: $R^2 < 0.1$, $p < 0.05$; **: $R^2 \geq 0.1$, $p < 0.01$; ***: $R^2 \geq 0.5$, $p < 0.001$; ****: $R^2 \geq 0.75$, $p < 0.0001$. Points and regression lines per host are colour-coded as in Figs. 9-10. Shell length is plotted on a logarithmic scale.

Since *C. curacaoensis* sp. nov. only occurred on *M. auretenra*, host-related differences could not be assessed. Shell length did not contribute to intraspecific variations in shell shape within this species (F = 2.1; $p = 0.070$).

Allometry

Allometric patterns were important in determining the shell shape in both *C. galea* and *C. caribaea*. In both species, shell length explained minor variation in shell shape ($R^2 = 0.072$; $p = 0.001$ and $R^2 = 0.041$; $p = 0.049$ for *C. galea* and *C. caribaea*, respectively), and these relationships depended on the host on which snails were found (shell length and host species interaction, $R^2 = 0.046$; $p = 0.001$ and $R^2 = 0.133$; $p = 0.004$ for *C. galea* and *C. caribaea*, respectively). The presence of such host-associated differences was also implied by the regressions between the CAC and shell length, where the slope of these linear regressions varied among snails associated with different host species (regressions were only done for hosts with ≥ 5 specimens; Fig. 11). Post-hoc tests further confirmed the presence of host-associated differences in allometric patterns in both *C. galea* and *C. caribaea*. Predicting the hypothetical shell shape of shells associated with a certain host species for a specific shell length, based on linear regressions of PC scores against shell length, clearly showed these differences (Fig. 12). Allometric patterns were subtler in *C. caribaea* compared to *C. galea*. In case of *C. galea*, both the distance (i.e., amount of change per unit of growth) and correlation (i.e., the direction of change) among vectors of shell length were, after Bonferroni corrections (*n* = 45), different for six pairs of host species (Fig. 12a; Table S6 in Online Supplementary Material 4). In *C. caribaea*, the correlation of vectors differed for a single pair of host species, while no differences were observed in the distances among vectors (Fig. 12b; Table S7 in Online Supplementary Material 4).

Replication error in morphometric data

Shell lengths of a random selection of snails (*n* = 65) were measured in triplicate. Average distance from the mean of these three measurements was 0.03 mm for shell length. Error in landmark data was assessed based on 53 out of the 65 specimens (47 specimens of *C. galea*, six specimens of *C. caribaea*). Replication errors were slightly higher for *C. galea* than for *C. caribaea*. Error in digitizing landmarks was 3.6% in *C. galea* compared to 1.7% in *C. caribaea*. The total error, which included inconsistencies in parallax as well, was 11.4% in *C. galea* and 4.0% in *C. caribaea*. Replication error in *C. curacaoensis* sp. nov. was not calculated.

Sex ratios

Sex could be determined for 609 specimens of *C. galea* and 115 specimens of *C. caribaea*. In *C. galea*, 74.4% were male. With 64.3%, the fraction of males in *C. caribaea* was lower ($p = 0.030$). Females were larger than males in both *C. galea* ($\chi^2 = 133.9$; $p < 0.0001$) and *C. caribaea* (F = 35.1; $p < 0.0001$). Both males and females were found on all but one host species (*C. caribaea* on *Porites furcata* Lamarck, 1816, on which only female specimens were found). Sex ratios within *C. galea* differed among snails associated with different host species ($p = 0.0004$; only including hosts with ≥ 5 specimens; Fig. 13a). After Bonferroni correction of *p*-values (*n* = 78) one pair remained significant: snails associated with *Agaricia humilis* Verrill, 1901 had a higher male to female ratio than snails associ-

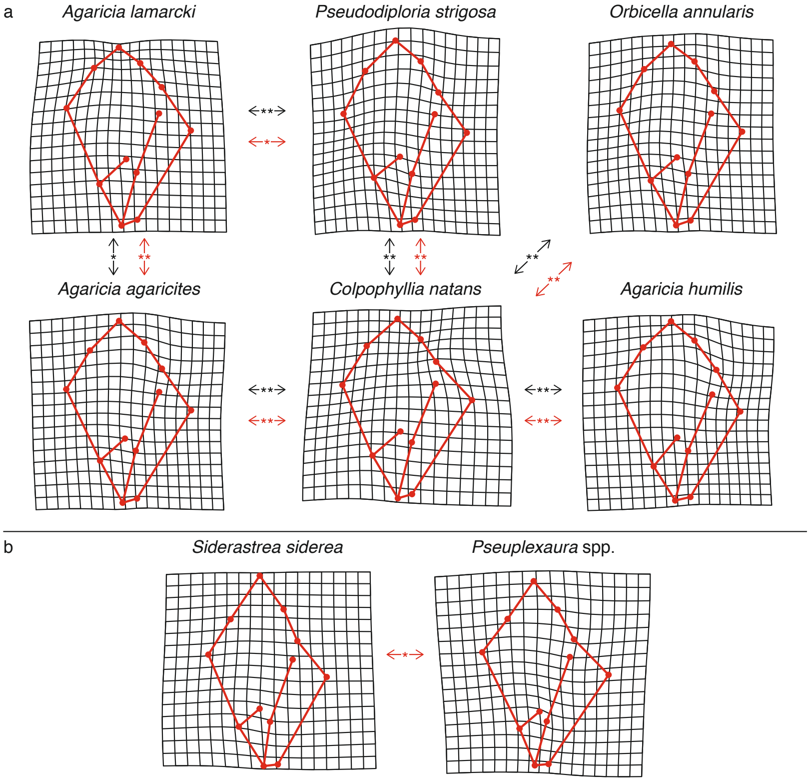

Fig. 12. Predicted shell shape of *Coralliophila galea* (a) and *C. caribaea* (b) shells of different shell lengths associated with different host species, based on principal component scores of repeatable axes. Grids show the predicted shape of the largest specimen collected from the respective host, warped against the predicted shape of the smallest specimen collected. Black arrows indicate significant differences in the amount of change in shell shape per unit of growth, red arrows indicate significant differences in the direction of change in shell shape. Significant differences: *: $p < 0.05$; **: $p < 0.01$.

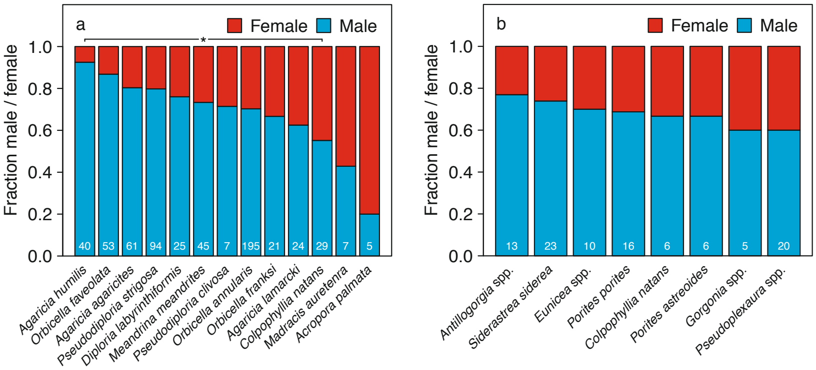

Fig. 13. Sex ratios of *Coralliophila galea* (a) and *C. caribaea* (b) associated with different host species. Host species are ranked based on the fraction of males. After Bonferroni correction for multiple pairwise comparisons, no significant differences remained in *C. caribaea*. Significant differences: *: $p < 0.05$.

ated with *Colpophyllia natans* (Houttuyn, 1772) ($p = 0.032$). Within *C. caribaea*, no variation in sex ratios between host species existed ($p = 0.975$; only including hosts with ≥ 5 specimens; Fig. 13b). Sex ratio of *C. caribaea* associated with alcyonaceans (66.0% male) and scleractinians (63.1% male) was similar as well ($p = 0.845$).

Within *C. galea*, mean length of females per host species correlated with the mean length of males ($R^2 = 0.707$; $p = 0.0002$) (Fig. 14a). The same was observed in *C. caribaea* ($R^2 = 0.614$; $p = 0.011$) (Fig. 14b).

Genetics

The three Caribbean *Coralliophila* species clustered into three well-supported, separate clades on the phylogenetic tree (posterior probability (PP) = 0.997-1.000; Fig. 15). Phylogenetic trees constructed for both markers separately showed the same pattern (Online Supplementary Material 5). No monophyletic Caribbean cluster was found: *Coralliophila curacaoensis* sp. nov. is the sister species of a group consisting of both *C. fontanangioyae* Smriglio and Mariottini, 2000 and *C. meyen-*

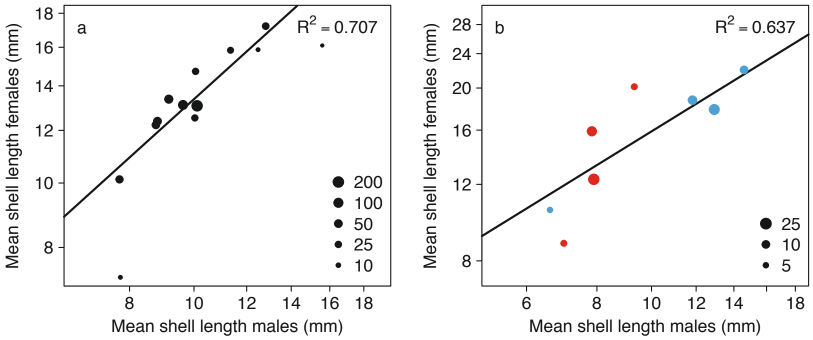

Fig. 14. Mean shell length against the proportion of male snails per host species of *Coralliophila galea* (a) and *C. caribaea* (b). Regression was not significant for *C. caribaea* (b). In the linear regression, individual points were weighed per number of observations per host species. Number of observations is represented by the size of points. Points are coloured by host order (b), blue for Alcyonacea, red for Scleractinia.

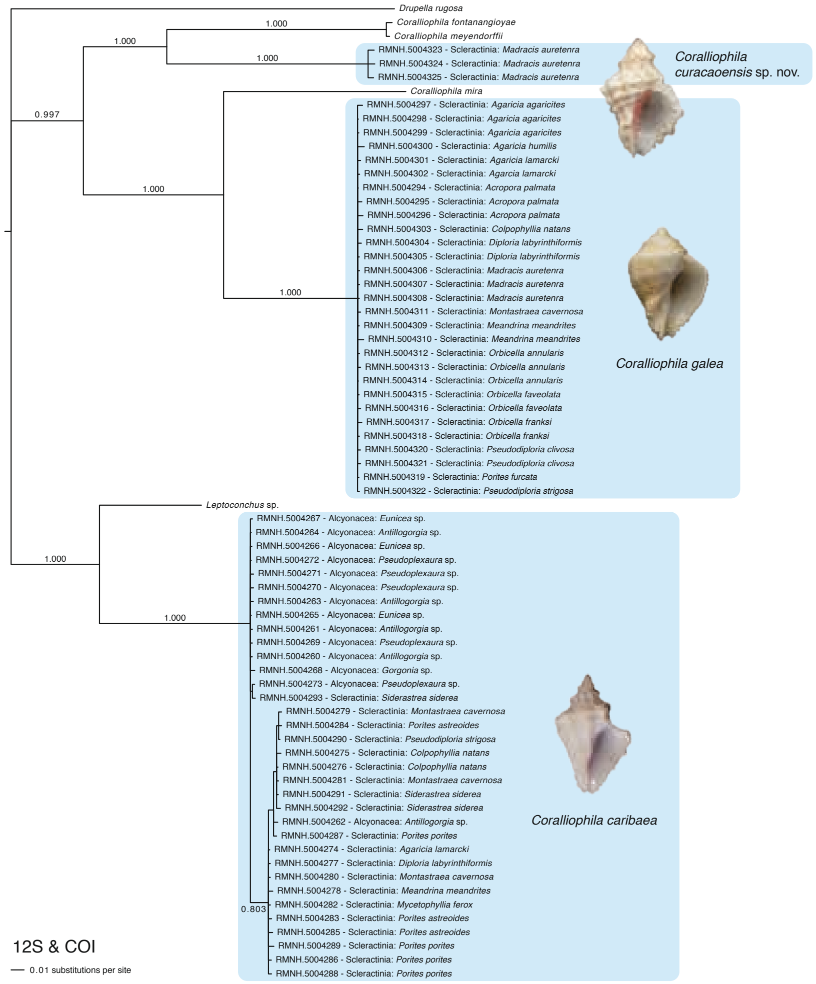

Fig. 15. Phylogenetic tree based on the 12S rRNA (12S) and cytochrome *c* oxidase subunit I (COI) markers of a selection of the collected *Coralliophila* spp. specimens. The three shaded clades represent the three species of *Coralliophila* found in the present study. Within the shaded clusters, tip labels represent the host order and host species with which the snail was associated. Specimens outside the shaded cluster are previously published sequences. Branch labels are posterior probabilities (PP). Intraspecific PP-values are not shown (except for the main clade within *C. caribaea*) and were all lower than 0.90. Scale bar: 0.01 substitutions per site.

dorffii (Calcara, 1845) from the Eastern Atlantic and the Mediterranean; *C. galea* is sister of *C. mira* (Cotton and Godfrey, 1932) from the Indo-Pacific, and *C. caribaea* is sister of the Indo-Pacific *Leptoconchus* sp. Hence, the genus *Coralliophila* is also not monophyletic.

No host-associated genetic divergence was found within *Coralliophila galea* ($p = 0.458$ and $p = 0.342$ for 12S and COI, respectively). In *C. caribaea* on the other hand, a small divergence (mean uncorrected distance of 0.6% for 12S and 2.9% for COI) was

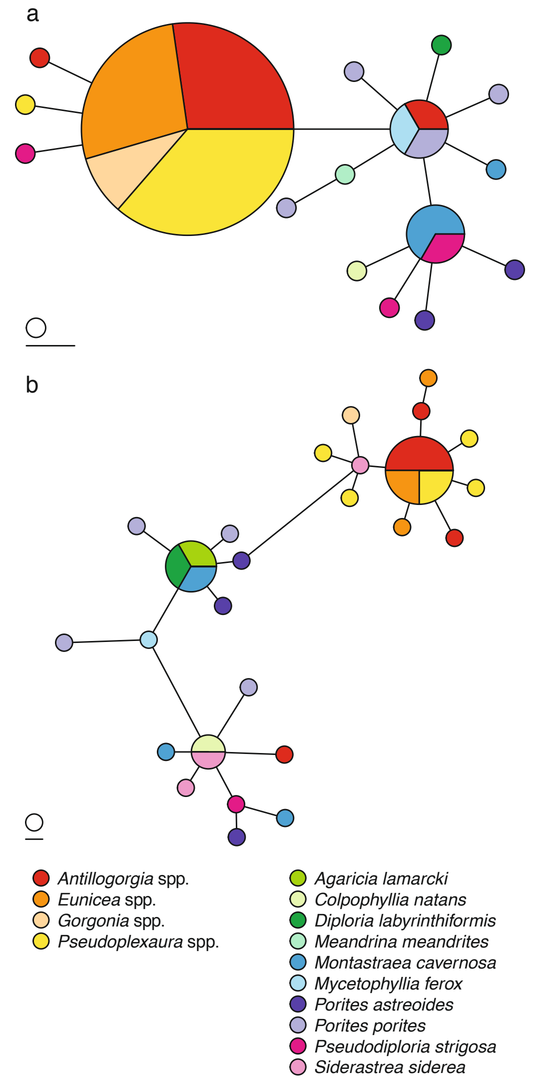

Fig. 16. Haplotype networks based on an infinite site model (using simple, uncorrected distances) of the sequenced specimens *C. caribaea*, both for the markers 12S rRNA (12S) (a) and cytochrome *c* oxidase subunit I (COI) (b). Haplotype are coloured based on host species with which the haplotypes were associated, size represents the frequency of haplotypes. Length between haplotypes is based on the number of mutations between haplotypes. Circles and lines in the bottom left of each figure represent a frequency of one and one mutation between haplotypes respectively.

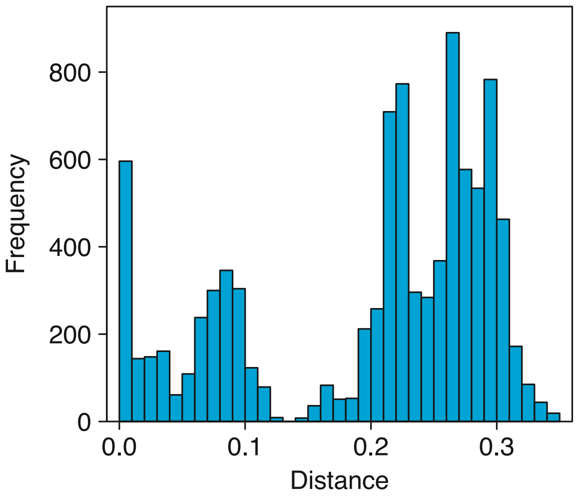

Fig. 17. Automatic Barcode Gap Discovery analysis based on Kimura two-parameter distances of a dataset of coralliophiline cytochrome *c* oxidase subunit I (COI) sequences, including the *Coralliophila* spp. specimens sequenced in the present study.

found between snails associated with Alcyonacea and those associated with Scleractinia ($p < 0.0001$ for both 12S and COI). This genetic structuring within *C. caribaea* was also visible on the phylogenetic tree, as *C. caribaea* collected from Scleractinia cluster all on a single branch (with one exception), although the support value for this branch was low (PP = 0.803). There was no host-associated divergence within *C. caribaea* from scleractinian corals ($p = 0.213$ and $p = 0.971$ for 12S and COI, respectively) or alcyonacean hosts ($p = 0.941$ and $p = 0.945$ for 12S and COI, respectively).

The small divergence among *C. caribaea* individuals associated with either scleractinians or alcyonaceans was also observed in the haplotype networks constructed for both markers (Fig. 16). With one exception for COI, haplotypes were unique to snails associated with hosts from either Scleractinia or Alcyonacea. In addition, haplotypes of snails associated with alcyonaceans mostly (with one exception for both markers) clustered together on a single branch in the haplotype network. Snails associated with scleractinians formed (again, with one exception for both markers) the other branches in the networks. The two clusters were separated by two mutations for 12S and eight mutations for COI. No clear correlation between host species and haplotype was present within *C. galea*.

The ABGD analysis based on COI, using a more extensive dataset of coralliophiline snails, proposed nine different groupings of specimens into MOTUs, depending on the a priori boundary between intra- and interspecific divergence. A histogram of the frequencies of pairwise Kimura two-parameter (K2P) distances revealed a multimodal distribution, with the lowest minimum frequency around a K2P distance of 0.05 (Fig. 17). Using this value as a boundary between intra- and interspecific divergence, the coralliophiline dataset can be subdivided into 16 MOTUs. At this value, the specimens of *C. galea*, *C. caribaea* and *C. curacaoensis* sp. nov. are clustered into three different MOTUs, in agreement with the phylogenetic tree. The divergence within *C. caribaea* was confirmed to be intraspecific, not revealing any cryptic species, using this boundary value of 0.05.

Discussion

Most of the host species associations for *Coralliophila galea* and *C. caribaea* found in the present study have been previously recorded (Miller, 1981; Brawley and Adey, 1982; Hayes, 1990a; Bruckner *et al.*, 1997; Del Monaco *et al.*, 2010; Potkamp *et al.*, 2017). Feeding of *C. galea* on *Orbicella annularis* was found to be infrequent around 1970 (Robertson, 1970; Ott and Lewis, 1972), but later clearly impacted reef communities (Brawley and Adey, 1982; Knowlton *et al.*, 1988, 1990; Hayes, 1990a; Bruckner *et al.*, 1997; Baums *et al.*, 2003b). Predation pressure by *Coralliophila* spp. may depend on prey preference. Multiple studies concluded that *C. galea* can cause much damage to *Acropora* spp., and to a lesser extent to *Orbicella* spp. (Brawley and Adey, 1982; Knowlton *et al.*, 1988, 1990; Baums *et al.*, 2003b). On some host species, such as *O. annularis*, large aggregations of *C. galea* snails can be found. Aggregations of *C. caribaea* were generally smaller. Large aggregations of snails of the genus *Drupella* Thiele, 1925 (Muricidae: Ergalataxinae) can have a damaging effect on Indo-Pacific reef corals (Hoeksema *et al.*, 2013; Moerland *et al.*, 2016; Scott *et al.*, 2017; references herein), suggesting that large *C. galea* aggregations are harmful as well, confirming earlier findings (Bruckner *et al.*, 1997; Knowlton *et al.*, 1988, 1990; Hayes, 1990a; Baums *et al.* (2003a, 2003b). Predation on Alcyonacea by *C. caribaea* is also relevant, as gorgonians represent a large part of Caribbean and Brazilian reef communities (e.g. Preston and Preston, 1975; Sánchez *et al.*, 1998, 2003; Dias and Gondim, 2016; Lau, 2016). However, few studies have been conducted on the ecology and prey preference of *C. caribaea*.

The physiology of coralliophilines, with a proboscis used in feeding, helps to optimally exploit energy from their hosts (Ward, 1965; Robertson, 1970). The Indo-Pacific *C. violacea* (Kiener, 1836), which usually, like its Caribbean congeners, also feeds along the coral margin, has adopted a prudent feeding strategy by exploiting energy sinks along the margin of its hosts, thereby causing minimal damage (Oren *et al.*, 1998). Similar behaviour in Caribbean *Coralliophila* spp., combined with an absence of large feeding scars on most host species, suggests that *C. galea* and *C. caribaea* employ similar strategies (Martin *et al.*, 2014). If so, the high feeding rates of *C. galea* on *Orbicella* spp. calculated by Baums *et al.* (2003b), which were based on the energetic requirements of *C. galea* rather than on feeding scars, might be an overestimation of the actual feeding rates. *Coralliophila curacaoensis* sp. nov. also used its proboscis for feeding on its only known host, *Madracis auretenra*. As this coral is common across the Caribbean, it is likely that this new snail species will also be discovered at other localities.

Morphology

A large range in shell sizes was observed within *Coralliophila* spp. Females were on average larger than males, which is consistent with the fact that *C. galea* is a protandrous hermaphrodite (Baums *et al.*, 2003a; Johnston and Miller, 2006). The same pattern was observed within *C. caribaea*, suggesting a similar life history, which has been suggested to be a synapomorphous trait among the Coralliophilinae (Richter and Luque, 2002, 2004). In addition, host-associated size structuring existed within both *C. galea* and *C. caribaea* populations. Differences in shell length related to host species have been observed before within *C. galea* (Hayes, 1990a; Bruckner *et al.*, 1997; Baums *et al.*, 2003a; Johnston and Miller, 2006). Ecotypes with distinctive shell lengths have also been observed in their Mediterranean congener *C. meyendorffii*, where small snails are associated with scleractinian hosts and large snails are associated with sea anemones (Oliverio and Mariottini, 2001b;Kružić *et al.*, 2013). The results of the present study confirm and expand this pattern of host-associated size structuring in *C. galea*, and show that it also exists in *C. caribaea*.

Migration between host species with age could induce host-associated size structuring. In the Indo-Pacific corallivorous snail *Drupella cornus* (Röding, 1798), prey preference seems to change as snails age (Black and Johnson, 1994; McClanahan, 1997; Schoepf *et al.*, 2010; Moerland *et al.*, 2016). Age-dependent host preference would result in a clear host-associated size structuring as seen within *Coralliophila* spp. However, no evidence exists to support that *C. galea* or

C. caribaea migrate between host species. As both male and female snails were found on all but one host species (for which more than one specimen was collected) of *C. galea*, it seems unlikely that size-related migration between specific host species also occurs in *C. galea*, i.e., that juvenile snails (which would all be males) are associated with different host species than adults.

Another potential mechanism behind host-associated size structuring can result from size-dependent susceptibility to predation (Johnston and Miller, 2006). Selective predation on larger snails, which on some host colonies are more exposed than smaller snails, would result in host-associated size structuring. Wells and Lalli (1977) hypothesized further that brooding females of *C. galea* are, compared to *C. caribaea*, more vulnerable to predation because of the placement of egg capsules in the mantle cavity. Predation on larger snails would therefore decrease mean shell size and skew the male to female ratio. Variation in male to female ratios, as observed in *C. galea*, would be expected in case of size-specific predation. However, information on predation on *Coralliophila* spp. is limited, resulting from laboratory experiments or anecdotal observations (Goldberg 1971; Wells and Lalli, 1977; Baums *et al*., 2003a; Sharp and Delgado, 2015).

Besides a large range in shell size, high intraspecific variation in shell shape was found in both *C. galea* and *C. caribaea*. Despite this high intraspecific variation, no distinct ecotypes based on shell shape could be identified within either species, though weak host-associated differences in mean shell shape and allometric patterns existed in both *C. galea* and *C. caribaea*. Differences in shell shape were subtle with strong overlap among snails associated with different host species. Tested factors explained little of the observed variation in the models of shell shape suggesting the presence of factors not considered here.

Differences in growth rate could also explain host-dependent size structuring as well as the intraspecific variation in shell shape and allometry (Kemp and Bertness, 1984; Boulding and Hay, 1993; Chiu *et al*., 2002; Urdy *et al*., 2010a, 2010b). While growth rate has not been measured in the present study, the strong correlation between average male and female size separated by host species (assuming sex-change occurs at the same relative age) is consistent with the idea that growth rates differ among snails associated with different host species, confirming previous studies (Baums *et al*., 2003b; Johnston and Miller, 2006). Such differences in growth rate may result from, for example, differences in nutritional quality of host tissue (Szmant *et al*., 1990), anti-predatory mechanisms of host species (Barnes, 1970; Brauer *et al*., 1970; Moore and Huxley, 1976; Glynn and Krupp, 1986; Pawlik *et al*., 1987; Harvell *et al*., 1988; Harvell and Fenical, 1989; Van Alstyne and Paul, 1992; Pawlik, 1993; O'Neal and Pawlik, 2002; Gochfeld, 2004; Lages *et al*., 2010), predation pressure on snails (Fraser and Gilliam, 1992; Connell, 1998; Nakaoka, 2000) or intraspecific competition (Williamson *et al*., 1976; Cameron and Carter, 1979), among other factors. Baums *et al*. (2003b) suggested that differences in environment or nutrition (and by extension, host species) played a role in the growth rate of *C. galea*, Johnston and Miller (2006) suggested a role for nutritional quality and secondary metabolites, as well as intraspecific competition in the population structure of *C. galea*. Shell morphology has also been related to vulnerability to predation (Ebling *et al*., 1964; Kitching *et al*., 1966; Vermeij, 1974, 1993; Cotton *et al*., 2004). Variation of these factors across the range of hosts species, with vastly different colony shapes, may therefore result in host-dependent variation in shell size, shape and allometry as observed in the present study. However, little is known about the extent to which these factors play a role in corallivores in general or in *Coralliophila* spp. specifically. The mechanisms behind the observed patterns in shell size and shape remain therefore largely unknown.

Genetics

No host-associated genetic divergence was observed within *C. galea*: specimens failed to cluster by host species in the Bayesian analysis and genetic distances in snails were not significantly larger between host species than the distances within host species. Haplotypes were not correlated with host species. Johnston *et al*. (2012) also did not observe host-specific clustering in genetic data and only found a small genetic divergence between *C. galea* snails associated with *Acropora palmata*, *Orbicella* spp. and *Mycetophyllia* spp. Two ecotypes of the Mediterranean congener *C. meyendorffii*, which are associated with different host species, are also not genetically divergent (Oliverio and Mariottini, 2001b).

In contrast to *C. galea*, a host-associated genetic divergence was found within *C. caribaea*. Snails associated with alcyonaceans were genetically distinct from snails associated with scleractinians with one exception either way. The genetic divergence within *C. caribaea* was however relatively small. On the phylogenetic tree, the support value for the branch with nearly all snails associated with scleractinians was low. Haplotypes differed on a few loci between snails associated with scleractinians and alcyonaceans (two mutations between the haplotype cluster mostly associated with alcyonaceans and the other haplotypes for 12S, eight mutations for COI), and correlation of haplotypes with host order was not perfect. The K2P distance between specimens associated with alcyonaceans and scleractinians fell below the threshold between interspecific and intraspecific divergence as determined in the ABGD analysis. These observations all indicate that the divergence within *C. caribaea* is of relatively recent origin. Genetically diverged host races have mostly been described in insects (e.g. Feder *et al*., 1988; McPheron *et al*.; 1988; Powell *et al*., 2014), but also in sponge-associated shrimp species (Duffy, 1996). Formation of host races may be the first stage of sympatric speciation (Maynard Smith, 1966; Berlocher, 1998). Isolation among host races is required for full speciation to occur, as the host races will revert to a panmictic population in absence of reproductive isolation (Jaenike, 1981). While the genetic divergence observed in the present study suggest some reproductive isolation, more analyses are needed to assess the degree of reproductive isolation between the two putative host races found within *C. caribaea* (Jaenike, 1981).

Mathematical models suggested that host-associated selective forces are critical for snails to specialize (Kawecki, 1996, 1997). The absence of host-associated genetic divergence within *C. galea* is therefore consistent with the results from earlier prey-preference experiments, where only a weak preference for the native host species was found (Hayes, 1990b). This is especially true for species whose pelagic larval stage is long, as a long larval stage favours generalists and promotes plasticity instead of divergence and speciation (Sotka, 2005). The larval ecology of snails is therefore relevant too. Larval development varies among coralliophillid species, with planktotrophic development being considered the plesiomorphic state within the Coralliophillinae, while some evidence indicates a prolonged intracapsular or lecithotrophic development in several species (Richter and Luque, 2002; Oliverio, 2008). Veliger shells of both *C. galea* and *C. caribaea* have been illustrated by Abbott (1958) and Wells and Lalli (1977) (only *C. galea*). Both species are thought to have planktotrophic development, but the duration of the planktonic stage remains unknown, and is expected to be > 30 days for *C. galea* (Wells and Lalli, 1977; Richter and Luque, 2002; Johnston *et al*., 2012). Studies on the protoconch of snails may provide more insight in the larval ecology of Caribbean *Coralliophila* spp. (Oliverio, 2008).

For genetic divergence to be established, selection pressures must be strong enough to overcome homogenizing processes that increase gene flow between populations (Schluter, 2009; Johnston *et al*., 2012). The difference in host-associated genetic divergence between *C. galea* and *C. caribaea* suggests that selection pressures to specialize to either scleractinian or alcyonacean host species might be higher than the selection pressures to specialize to specific (groups of) species within these orders. Anti-predatory mechanisms of gorgonians might play a role here. Some generalist predators, such as the facultatively corallivorous polychaete *Hermodice carunculata* (Pallas, 1766), do feed on gorgonians (Marsden 1962; Preston and Preston 1975; Lasker 1985; Rotjan and Lewis 2008; Wolf *et al*., 2014), but most other species feeding on gorgonians, such as ovulid gastropods of the genus *Cyphoma* Röding, 1798, are specialized to this diet (Birkeland and Gregory 1975; Harvell and Suchanek 1987; Lasker and Coffroth, 1988; Lasker *et al*., 1988; Van Alstyne and Paul 1992; Burkepile and Hay, 2007; Chiappone *et al*., 2003; Reijnen *et al*., 2010; Schärer *et al*., 2010; Pinto *et al*., 2017; Reijnen and Van der Meij, 2017). Selection to overcome these mechanisms within *C. caribaea* might therefore have been strong enough to induce genetic divergence.

While specialization to (a group of) host species might have played a role in the intraspecific divergence observed within *C. caribaea*, the absence of a monophyletic Caribbean *Coralliophila* clade on the phylogenetic tree suggests that host-associated divergence was not the mechanism behind the divergence among species and that their common ancestor originated outside of the modern Caribbean. A similar pattern has been observed in the shrimp family Palaemonidae (Horká *et al*., 2016). Therefore, more extensive phylogenetic and phylogeographic analyses of *Coralliophila* spp. are needed to unravel the biogeographic patterns of this genus in the Caribbean.

The phylogenetic analyses in the present study suggest that the genus *Coralliophila* is polyphyletic, as *C. caribaea* seems to be closer related to the Indo-Pacific genus *Leptoconchus* than its own congeners (Fig. 15; Oliverio and Mariottini, 2001a; Oliverio *et al*., 2002, 2009). The genus *Coralliophila* is therefore in need of a taxonomic revision (Oliverio and Gofas, 2006; Oliverio, 2008; Oliverio *et al*., 2009).

Some overlap was observed between the distributions of intraspecific and interspecific divergence in the

ABGD analysis, which is indicative of the absence of a universal threshold within the Coralliophilinae (Collins and Cruickshank, 2013). Only one other threshold value based on an ABGD analysis for muricid gastropods was found in literature: Barco *et al*. (2013) reported a threshold K2P distance between 0.020 and 0.025 based on a dataset of COI sequences of the genus *Ocinebrina* Jousseaume, 1880, which is lower than the value found in the present study. In addition, with the threshold value used in the present study, many of the *Leptoconchus* species included in the ABGD analysis could not be distinguished as separate species. This reinforces the lack of a universal threshold between intraspecific and interspecific divergence.

Phenotypic plasticity and genetic differentiation

While no host-associated genetic divergence has been observed within *C. galea*, adaptive genetic polymorphisms may still play a role, and the relative importance of both a genetic basis and phenotypic plasticity to variation in morphology remains unknown (Johnston *et al*., 2012). Both mechanisms are not mutually exclusive, as both genetic differentiation and phenotypic plasticity are thought to play a role in the adaptation of the snail *Littorina saxatilis* (Olivi, 1792) to the local habitat (Janson, 1983; Johannesson and Johannesson, 1996; Hollander *et al*., 2006). Reciprocal transplant experiments of *C. galea* among different host species showed that current host species was a more important determinant for growth than the native host species, suggesting that phenotypic plasticity plays at least some role in the morphological variation of *C. galea* (Baums *et al*., 2003b). Johnston *et al*. (2012) also attributed difference in growth rates at least partly to phenotypic plasticity. These results suggest that within *C. galea,* habitat-related phenotypic plasticity is more important than evolutionary divergence, although the intraspecific genetic variation observed within *C. caribaea* does not preclude a role for phenotypic plasticity within this species.

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Online Supplementary Material

1. Methods used to calculate replication error in landmark data.
2. Hypothetical example of analyses of allometric patterns.
3. Table S1 with previously published sequences included in the Automated Barcode Gap Discovery analysis.
4. Tables S2-S7 with pairwise statistics for morphometric analyses.
5. Figs. S1-S2 with phylogenetic trees constructed for 12S and COI separately.

Appendix

Systematics of *Coralliophila* spp. at Curaçao

In this appendix, a formal description of *Coralliophila curacaoensis* sp. nov. is presented, together with diagnostic descriptions of two common congeners occurring in Curaçao: *C. caribaea* Abbott, 1958 and *C. galea* (Dillwyn, 1823) (see also De Jong and Coomans 1988).

Systematics

Family Muricidae Rafinesque, 1815.
Subfamily Coralliophilinae Chenu, 1859
Genus ***Coralliophila*** Adams and Adams, 1853

For description and synonymy, see Oliverio (2008: 485). The genus *Coralliophila*, with which *C. curacaoensis* sp. nov. has been classified, is used here in a wide sense (*Coralliophila s.l.*), as strong evidence exists for polyphyly within this genus as currently defined (Oliverio and Mariottini, 2001a; Oliverio *et al*. 2002, 2009; Oliverio 2008). A taxonomic revision of the genus, limiting its use only to the clade that includes the Indo-Pacific type species *Coralliophila violacea* (Kiener, 1836), might classify the other species into a separate genus.

Coralliophila caribaea Abbott, 1958

Fig. 18.

Diagnosis. Shell angular, rhomboidal in shape. High conical spire, sutures incised. Aperture oval. Teleoconch sculptured with spiral cords, densely packed with small scales. On the body whorl, higher and lower spiral cords set alternately. Six to seven axial ribs per whorl. Umbilical area moderately narrow, fasciole imbricated, umbilical furrow closed. Colouration operculum deep red to violet. Associated with alcyonacean and scleractinian host species. Also recorded from zoantharians and coralliomorpharians (Miller, 1981).

Coralliophila galea (Dillwyn, 1823)

Fig. 19.

Synonym. *Coralliophila abbreviata* auct. non Lamarck, 1816 (see Bouchet, 2015)

Diagnosis. Globose, inflated shell. Short conical spire, sutures not incised. Aperture oval, wide. Teleoconch sculptured with numerous low spiral cords, densely packed with small scales. One larger spiral cord on the body whorl, located close to the anterior end of the shell. Umbilical area wide, with imbricated fasciole and open umbilical furrow. Yellow to transparent operculum. Associated with a range of scleractinian host species. Also recorded from Zoantharia and Coralliomorpharia (Miller, 1981).

Coralliophila curacaoensis sp. nov. Potkamp and Hoeksema

Fig. 20.

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Etymology. Named after the island of Curaçao, the type locality of *C. curacaoensis* sp. nov.

Type material. Holotype RMNH.5004326 (Figs. 20a-f) and nine paratypes RMNH.5004323-5004325 (only molecular sequences deposited), RMNH.5004327-5004328, RMNH.5004329-5004332 (only soft tissue deposited) (Figs. 20g-y).

Type locality. Leeward coast of Curaçao, Playa Daaibooi, 12°13'N, 69°05'W, 11 m depth (holotype RMNH.5004326 and paratypes RMNH.5004323 and RMNH.5004327-5004332). Playa Kalki, 12°22'N, 69°09'W, 8 m depth (paratype RMNH.5004324) and 10 m depth (paratype RMNH.5004325).

Distribution. Only recorded from the type locality, Curaçao, southern Caribbean. Specimens were found in association with corals of the scleractinian species *Madracis auretenra* Locke, Weil and Coates, 2007.

Diagnosis. Small size, shell angular, rhomboidal in shape. Aperture oval, elongated. Cone-shaped spire with incised sutures. Teleoconch sculptured with spiral cords, on the body whorl relatively high and widely set. Two high imbricated spiral cords around the shoulder, spiral cords decreasing in size towards the anterior end. Eight to nine varices per whorl, giving the shell a latticed appearance. Umbilical area moderately wide, with imbricate fasciole and narrowly open umbilical furrow. Operculum transparent to pale red.

Description. Small shell size compared to its congeners: largest specimen with a length of 8.9 mm, width 5.8 mm. Shell rhomboidal in shape with teleoconch consisting of 3+ whorls. Protoconch eroded on holotype. Spire cone-shaped, sides angular to almost flat, sutures moderately incised. Body whorl more than half

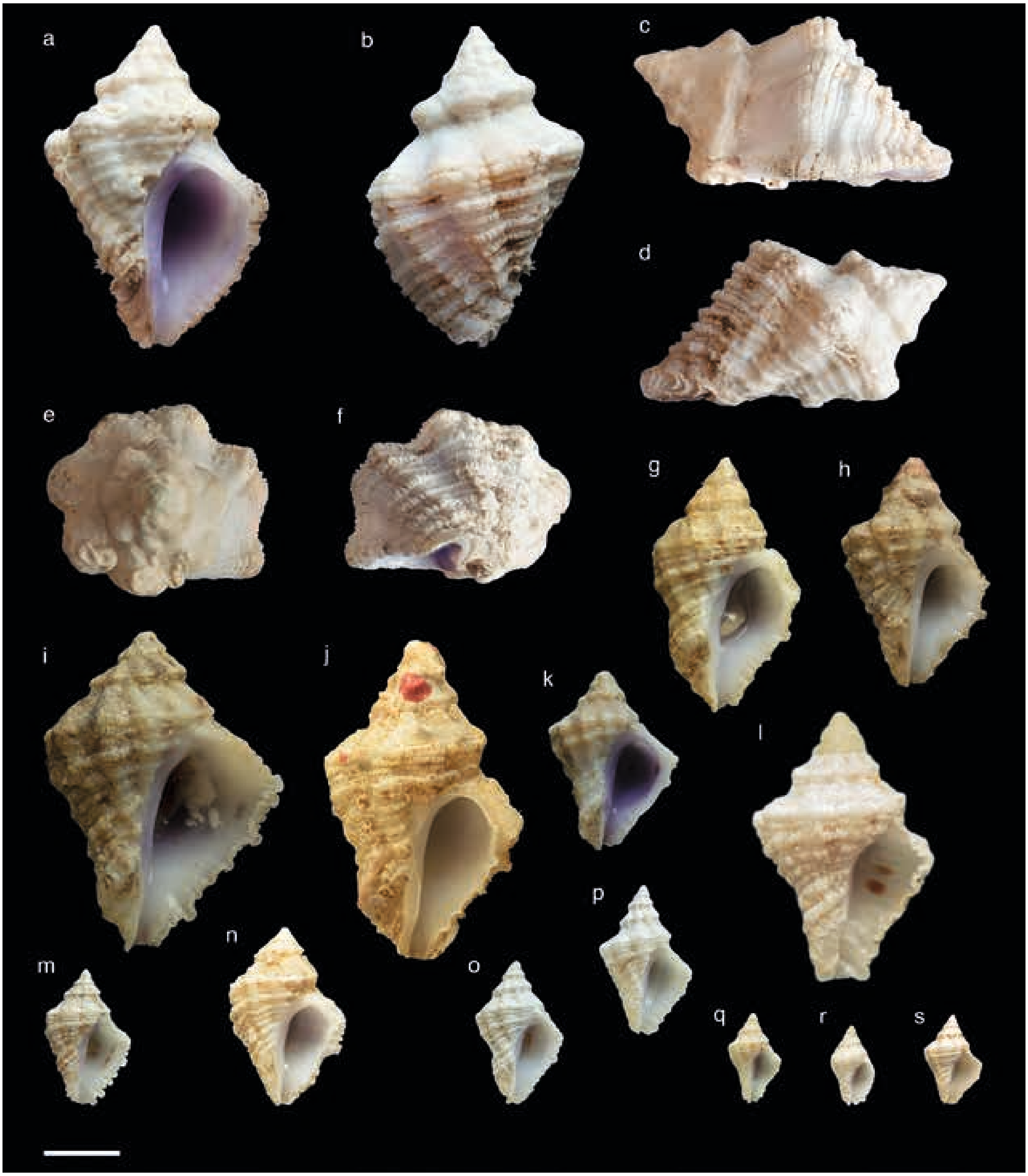

Fig. 18. *Coralliophila caribaea*. Ventral, dorsal, both lateral, posterior and anterior views of a single shell, respectively (a-f). Examples of intraspecific variation in shell size and shape (g-s). An egg capsule is visible in one shell aperture (g). Scale bar: 1 cm.

Fig. 19. Coralliophila galea. Ventral, dorsal, lateral, posterior and the anterior views of a single shell, respectively (a-f). Examples of intraspecific variation in shell size and shape (g-q). Scale bar: 1 cm.

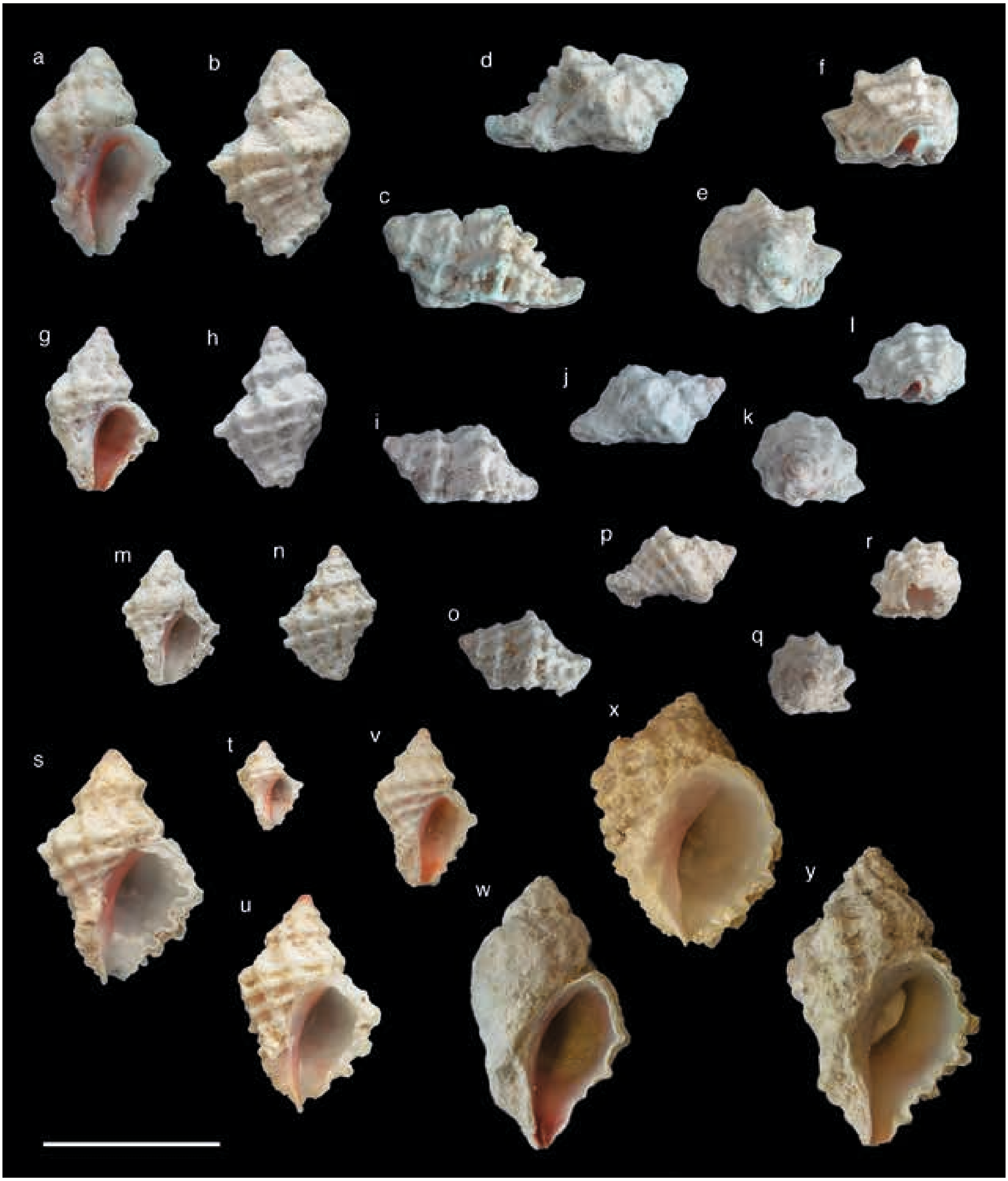

Fig. 20. Coralliophila curacaoensis sp. nov. Different views of shells of holotype RMNH.5004326 (a-f) and paratypes RMNH.5004327 (g-l) and RMNH.5004328 (m-r), as well as the ventral side of shells of paratypes RMNH.5004329 (s), RMNH.5004332 (t), RMNH.5004330 (u), RMNH.5004331 (v), RMNH.5004324 (w), RMNH.5004325 (x) and RMNH.5004323 (y). Some shells are photographed in a slightly different orientation (w-y). Scale bar: 1 cm.

of the total shell length, basal outline sharply curving at the shoulder, anterior to the shoulder straight, in some specimens more inflated. Aperture long, oval. Outer lip fimbriated; inner lip gently arcuate. Siphon canal broadly open, relatively long at around one fifth of the total shell length; umbilical area moderately wide, fasciole imbricate, umbilical furrow narrowly open.

Teleoconch sculptured with widely set spiral cords. Two high spiral cords on the body whorl, the first one located at the shoulder, the second directly anterior, widely spaced. Several, also widely spaced, smaller cords anterior to the two large cords (three on the holotype), decreasing in size. Spiral cords with relatively large imbricated scales, clearest at the intersection between varices and spiral cords. On the holotype, five small cords posterior to the shoulder on the body whorl, more closely set compared to cords anterior to the shoulder. Eight to nine varices per whorl, three of which very large on the body whorl of the holotype.

Shell colour ivory white. Operculum transparent to pale red.

Remarks. Among its Caribbean congeners, *C. curacaoensis* sp. nov. is the smallest species. It has only been found in association with *M. auretenra*. The mitochondrial marker 12S rRNA of *C. curacaoensis* differs at on average 17.1% of positions from *C. caribaea* and 18.6% of positions from *C. galea*. For the COI marker, 24.6% of positions are on average different in *C. caribaea* compared to *C. curacaoensis*, and 21.9% of positions compared to *C. galea*.

Coralliophila curacaoensis sp. nov. resembles most *C. caribaea*, but it differs from that species in that the spiral cords on the body whorl are smaller on *C. curacaoensis* and more numerous and closely set on *C. caribaea*. Consequently, *C. caribaea* lacks the strongly fimbriated outer lip of *C. curacaoensis*. The colour of the operculum of *C. caribaea* is a deeper red than the operculum of *C. curacaoensis*. Sutures are generally less incised in *C. caribaea*.

Coralliophila galea, differs mainly from *C. curacaoensis* sp. nov. in having a more globose shell, having more numerous, closely set, spiral cords, lacking the high spiral cords and a fimbriated outer lip. The spire of *C. galea* is shorter and sutures are not incised as in *C. curacaoensis*.

Several other species of the genus *Coralliophila* are known from the western Atlantic, two of which resemble *C. curacaoensis* sp. nov.: *C. pacei* Petuch, 1987 and *C. richardi* (Fischer, 1882). *Coralliophila pacei* has only been found in shallow water along the southeastern coast of Florida (Petuch and Myers, 2014). It shows two large spiral cords on the body whorl, with two small cords in between, which are absent in *C. curacaoensis*. The large cords on *C. curacaoensis* are more widely spaced, decreasing in size anterior to the large cords. Furthermore, varices on *C. curacaoensis* are not as low as on *C. pacei*.

Coralliophila richardi is a deep-water species found on cold-water reefs formed by the scleractinians *Lophelia pertusa* (Linnaeus, 1758) and *Madrepora oculata* Linnaeus, 1758, across the North Atlantic (Bouchet and Warén 1985; Oliverio and Gofas, 2006; Schembri *et al*., 2007; Taviani *et al*., 2008, 2009). *Coralliophila richardi* lacks the high, imbricate spiral cords and therefore the fimbriated outer lip, which are shown by *C. curacaoensis*.

Coralliophila fontanangioyae Smriglio and Mariottini, 2000 is known from the Canary Islands in the Eastern Atlantic. It is relatively closely related but genetically distinct from *C. curacaoensis* sp. nov. (Fig. 15). Oliverio *et al*. (2009) published a 12S rRNA sequence from *C. fontanangioyae*, which differs on average at 21.1% of positions from the newly sequenced 12S rRNA sequences of *C. curacaoensis*. Morphologically, *C. fontanangioyae* resembles *C. curacaoensis* in shell ornamentation but its whorls have less sharper edges than those of *C. curacaoenis* (Gofas, 2005). *Coralliophila fontanangioyae* occurs in association with the deep-water scleractinian *Madracis asperula* Milne Edwards and Haime, 1849 (Smriglio and Mariottini, 2000; Oliverio *et al*., 2009), whereas *C. curacaoenis* and *C. galea*, have been found in association with colonies of *Madracis auretenra*.

Coralliophila meyendorffii (Calcara, 1845), the sister species of *C. fontanangioyae* (Fig. 15), has a much finer ornamentation and its spirals have edges that are less sharp than those of *C. curacaoenis* sp. nov. (see Oliverio and Gofas, 2006). It has an East Atlantic - Mediterranean distribution over a wide depth range that includes the Adriatic Sea (Oliverio and Mariottini, 2001; Oliverio and Gofas, 2006; Kružić *et al*., 2013). It predates on the scleractinians *Balanophyllia europaea* (Risso, 1826) or *Cladocora caespitosa* (Linnaeus, 1767) (Oliverio and Mariottini, 2001b; Kružić *et al*., 2013), while it is also known as an associate of sea anemones (Oliverio and Mariottini, 2001b; Oliverio and Gofas, 2006).

Other East Atlantic *Coralliophila* species are predominantly known from deep water and have not been recorded from the West Atlantic and not as associates of either scleractinians or alcyonaceans (Pons-Moyà *et al*. 2001; Oliverio and Gofas, 2006; Oliverio *et al*., 2009).