Identification of a new stony coral host for the anemone shrimp *Periclimenes rathbunae* Schmitt, 1924 with notes on the host-use pattern

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Abstract

Periclimenes rathbunae Schmitt, 1924 is a western Atlantic symbiotic shrimp species mainly associating with anemones. Adult shrimps of *P. rathbunae* are characterised by an orange-white spotted colour pattern. During fieldwork along the coast of Curaçao (2013), morphologically similar, though generally smaller sized shrimps were collected from the stony coral *Dendrogyra cylindrus* Ehrenberg, 1834. These specimens were over-all more translucent. This study elucidates the taxonomic status of the coral-associated specimens in relation to anemone-associated specimens of *P. rathbunae* and related anemone-associated species using one nuclear (histone H3, *H3*), a mitochondrial protein-coding (cytochrome oxidase subunit I, *COI*) and a mitochondrial ribosomal RNA (*16S*) gene. Molecular phylogenetic reconstructions clustered the coral-associated specimens with anemone-associated *P. rathbunae* within a distinct clade, revealing that the aberrant coral-associated shrimp specimens belong to *P. rathbunae*. It can be concluded that 1) the stony coral *D. cylindrus* is a host of *P. rathbunae*, constituting the first record of an association between a scleractinian coral and a palaemonid shrimp species in the Atlantic Ocean; 2) the colour pattern of *P. rathbunae* is a phenotypically plastic characteristic that varies with size and is depending on the host species; and 3) mean body size of *P. rathbunae* is smaller on *D. cylindrus* than on the anemone *Stichodactyla helianthus*. This raises interesting questions about patterns of host use for this species and warrants further in-depth field ecological study for this species.

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Introduction

Counting over 150 species, *Periclimenes* Costa, 1844 is one of the most speciose genera of the caridean shrimp family Palaemonidae Rafinesque, 1815 (De Grave and Fransen, 2011; Mitsuhashi *et al.*, 2012; De Grave, 2014). Its species are dispersed in marine waters all over the world, few are free-living, the majority associates with mostly sessile or slow-moving benthic invertebrates (Bruce, 2007). The ubiquity of cryptic species – generally defined as at least superficially morphologically indistinguishable species (Bickford *et al.*, 2006) – among marine habitats (Knowlton, 1993) casts doubt on *Periclimenes*' current species count.

The present study focuses on the species boundaries of the symbiotic shrimp *Periclimenes rathbunae* Schmitt, 1924. Occurring in shallow, tropical waters of the western Atlantic, *P. rathbunae* is widely reported to associate with anemones (Spotte *et al.*, 1991; Hayes and Trimm, 2008), including *Bartholomea annulata* (Le Sueur, 1817), *Bunodosoma granuliferum* (Le Sueur, 1817), *Condylactis gigantea* (Weinland, 1860), *Homostichanthus duerdeni* (Carlgren, 1900), *Lebrunia danae* (Duchassaing and Michelotti, 1860) (= *Lebrunia neglecta* Duchassaing and Michelotti, 1860), *Stichodactyla helianthus* (Ellis, 1768), and *Exaiptasia pallida* (Agassiz in Verrill, 1864). Furthermore, soft coral *Eunicea tourneforti* Milne Edwards and Haime, 1857 has been documented to host *P. rathbunae* (cf. Hayes and Trimm, 2008). Reports of *P. rathbunae* on other hosts are scarce. From 1982 till 2006, *P. rathbunae* has only been reported to associate with corallimorph *Ricordea florida* Duchassaing and Michelotti,

Fig. 1. *Periclimenes rathbunae* Schmitt, 1924. A, on the stony coral *Dendrogyra cylindrus* Ehrenberg, 1834, Curaçao, Cas Abou (12.227861N, 69.091778W), photograph by S.E.T. van der Meij; B, on the anemone *Stichodactyla heliantus* (Ellis, 1768), (BW0060), Curaçao, Car Wrecks (12.161N, 69.004083W), photograph by C.H.J.M. Fransen.

1860 three times (Ritson-Williams and Paul, 2007). Notably, symbioses with Scleractinia have never been reported for any Atlantic palaemonid shrimp species.

During fieldwork along the coast of Curaçao (2013), shrimps that are morphologically similar to *P. rathbunae* were collected from a scleractinian coral, *Dendrogyra cylindrus* Ehrenberg, 1834. The overall more translucent appearance of the newly obtained specimens clearly differed from the orange-white spotted colour pattern of larger adult *P. rathbunae* as described by Spotte *et al.* (1991) (Fig. 1A, B). Since differences in ecology and colour pattern often function as diagnostics to identify decapod cryptic species living in

sympatry (Knowlton, 1993; Knowlton, 2000), the coral-associated specimens were expected to belong to a yet unidentified cryptic species of *Periclimenes*.

Here, the specimens of *Periclimenes* hosted by *D. cylindrus* are described morphologically and compared to anemone-associated shrimps of *P. rathbunae*. As the original description of the species is rather brief, a detailed re-description has been provided (Appendix).

Using a DNA barcoding approach, the aim of this study was to unravel the phylogenetic relationships of the coral and anemone-associated specimens. Partial sequences of the mitochondrial cytochrome oxidase subunit I (*COI*) gene, the mitochondrial ribosomal

Table 1. Analysed specimens with species name, sample number, collection registration number, sampling locality, host and GenBank

Species	Locality			
	Sample nr	Voucher reg. nr	Name	Coordinates
<i>Ancylomenes pedersoni</i> (Chace, 1958)	BW0010	RMNH.CRUS.D.56996	Hilton Reef	12.121789N, 68.969508W
<i>Ancylomenes pedersoni</i> (Chace, 1958)	BW0020	RMNH.CRUS.D.56997	Playa Forti	12.366139N, 69.15375W
<i>Periclimenes yucatanicus</i> (Ives, 1890)	BW0030	RMNH.CRUS.D.56998	Playa Boka Sami	12.147611N, 68.99875W
<i>Periclimenes yucatanicus</i> (Ives, 1890)	BW0040	RMNH.CRUS.D.56999	Playa Forti	12.366139N, 69.15375W
<i>Periclimenes rathbunae</i> Schmitt, 1924	BW0050	RMNH.CRUS.D.57034	Hilton Reef	12.121789N, 68.969508W
<i>Periclimenes rathbunae</i> Schmitt, 1924	BW0060	RMNH.CRUS.D.57036	Car Wrecks	12.161N, 69.004083W
<i>Periclimenes rathbunae</i> Schmitt, 1924	BW0070	RMNH.CRUS.D.57035	Playa Forti	12.366139N, 69.15375W
<i>Periclimenes rathbunae</i> Schmitt, 1924	BW0170	RMNH.CRUS.D.57032	Cas Abou	12.227861N, 69.091778W
<i>Periclimenes rathbunae</i> Schmitt, 1924	BW0171	RMNH.CRUS.D.57032	Cas Abou	12.227861N, 69.091778W
<i>Periclimenes rathbunae</i> Schmitt, 1924	BW0180	RMNH.CRUS.D.57031	Marie Pampoen	12.090761N, 68.904956W
<i>Periclimenes rathbunae</i> Schmitt, 1924	BW0181	RMNH.CRUS.D.57031	Marie Pampoen	12.090761N, 68.904956W
<i>Periclimenes rathbunae</i> Schmitt, 1924	BW0190	RMNH.CRUS.D.57033	Grote Knip	12.351139N, 69.151917W
<i>Gnathophylloides mineri</i> Schmitt, 1933	BW1050	RMNH.CRUS.D.57000	W Piscadera Baai	12.12275N, 68.970428W
<i>Ascidonia quasipusilla</i> (Chace, 1972)	BW1200	RMNH.CRUS.D.57001	Hilton Reef	12.121789N, 68.969508W

RNA (16S rRNA) gene and the nuclear histone *H3* gene were obtained from anemone-associated *P. rathbunae* shrimp specimens and from the coral-associated resembling shrimps. Additional sequences were obtained from previous studies. By way of character based phylogenetic methods conducted in PAUP 4.0b10 (Swofford, 2002) and MrBayes 3.1.2 (Ronquist and Huelsenbeck, 2003), *COI*, *16S* and *H3* single-gene phylogenies were reconstructed to infer 1) if the coral-associated specimens belong to a novel, cryptic species of *Periclimenes*; or 2) if the specimens belong to the species *Periclimenes rathbunae*, indicating *D. cylindrus* is a new host of *P. rathbunae*. Beside *P. rathbunae*, the two other anemone-associated species *Periclimenes yucatanicus* (Ives, 1891) and *Ancylomenes pedersoni* (Chace, 1958) were added to infer their phylogenetic relations (see supplementary video S1). The sea urchin-associated *Gnathophylloides mineri* Schmitt, 1933 and ascidian associated *Ascidonia quasipusilla* (Chace, 1972) were included as outgroups in the analyses.

Material and methods

Sampling

Shrimps were collected at eight locations near the coast of Curaçao and preserved in ethanol (80%). Photographs and videos were taken with a Nikon D80 digital photo camera and GoPro Hero 4 Silver video camera with a MacroMate Mini 55mm +15 close-up lens

respectively. Eggs or pleopods were collected from 14 shrimps selected for DNA analyses of partial *COI*, *16S* and *H3* sequences (Table 1). Material has been deposited in Naturalis Biodiversity Center (formerly Rijksmuseum van Natuurlijke Historie, RMNH) and the Oxford University Museum of Natural History (OUMNH).

Morphological analysis

A detailed morphological description of the coral-associated specimens was made (Appendix) and compared with anemone-associated specimens. Drawings were made using a Zeiss Discovery.V8 and an Olympus BX53 stereo microscope, both with a drawing tube. Drawings were mounted using Adobe Photoshop CS6 software.

DNA extraction

Total genomic DNA was extracted with the Nucleo-Mag® 96 Tissue kit (Machery-Nagel, Düren, Germany) using a Thermo Scientific KingFisher™ Flex Magnetic Particle Processor. Extraction was performed with 200 µl lysis buffer and 20 µl proteinase K. Incubation took place overnight at 56°C.

Polymerase chain reaction

Partial *COI*, *16S* and *H3* sequences were amplified by polymerase chain reactions (PCR) in a total reaction

accession numbers. * the corresponding shrimp specimen was collected near this probable host.

Host class: subclass: order: species	GenBank accession #		
	<i>COI</i>	<i>16S</i>	<i>H3</i>
Anthozoa: Hexacorallia: Actiniaria: <i>Condylactis gigantea</i> *	KX090106	KX090083	-
Anthozoa: Hexacorallia: Actiniaria: <i>Bartholomea annulata</i> *	KX090107	KX090084	KX090129
Anthozoa: Octocorallia: Holaxonia: <i>Eunicia</i> sp.	KX090108	KX090085	KX090130
Anthozoa: Hexacorallia: Actiniaria: <i>Condylactis gigantea</i>	KX090109	KX090086	KX090131
Anthozoa: Hexacorallia: Actiniaria: <i>Stichodactyla heliantus</i>	KX090110	KX090087	KX090132
Anthozoa: Hexacorallia: Actiniaria: <i>Stichodactyla heliantus</i>	KX090111	KX090088	KX090133
Anthozoa: Hexacorallia: Actiniaria: <i>Condylactis gigantea</i>	KX090112	KX090089	KX090134
Anthozoa: Hexacorallia: Scleractinia: <i>Dendrogyra cylindrus</i>	KX090113	KX090090	KX090135
Anthozoa: Hexacorallia: Scleractinia: <i>Dendrogyra cylindrus</i>	KX090114	KX090091	KX090136
Anthozoa: Hexacorallia: Scleractinia: <i>Dendrogyra cylindrus</i>	KX090115	KX090092	KX090137
Anthozoa: Hexacorallia: Scleractinia: <i>Dendrogyra cylindrus</i>	KX090116	KX090093	KX090138
Anthozoa: Hexacorallia: Scleractinia: <i>Dendrogyra cylindrus</i>	KX090117	KX090094	KX090139
Echinoidea: Euechinoidea: Camarodonta: <i>Lytechinus variegates</i>	KX090118	KX090095	KT224392
Ascidacea: - : Stolidobranchia: <i>Pyura torpida</i> (Sluiter, 1898)	KX090119	KX090096	KX090140

Table 2. Primer information. * M13F primer tail, 5'-TGTAACGACGGCCAG-3'; M13R primer tail, 5'-CAGGAAACAGCTATGAC-3'.

Primer name	Sequence (5' to 3')	Target gene	Reference
M13F-LCOI1490 *	TGTAACGACGGCCAGTGGTCAACAAATCATAAAGATATTGG	<i>COI</i>	Folmer <i>et al.</i> (1994)
M13R-HCO2198 *	CAGGAAACAGCTATGACTAACTTCAGGGTGACCAAAAAATCA	<i>COI</i>	Folmer <i>et al.</i> (1994)
M13F-LepF1 *	TGTAACGACGGCCAGTATTCAACCAATCATAAAGATATTGG	<i>COI</i>	Hebert <i>et al.</i> (2004)
M13R-LepR1 *	CAGGAAACAGCTATGACTAACTTCTGGATGTCCAAAAAATCA	<i>COI</i>	Hebert <i>et al.</i> (2004)
M13F-jgCOI490 *	TGTAACGACGGCCAGTTTTCIACIAAYCAYAARGAYATTGG	<i>COI</i>	Geller <i>et al.</i> (2013)
M13R-jgCO2198 *	CAGGAAACAGCTATGACTAIACYTCIGGRTGICCAARAAYCA	<i>COI</i>	Geller <i>et al.</i> (2013)
16SarF	CGCCTGTTTATCAAAAACAT	<i>16S</i>	Palumbi <i>et al.</i> (1991)
16Sbr	CCGGTCTGAACTCAGATCACGT	<i>16S</i>	Palumbi <i>et al.</i> (1991)
F1	ATGGCTCGTACCAAGCAGACVGC	<i>H3</i>	Colgan <i>et al.</i> (1998)
R1	ATATCCTTRGGCATRATRGTCAC	<i>H3</i>	Colgan <i>et al.</i> (1998)

volume of 25 μ l. Primer sequences are included in Table 2.

A 658 bp fragment of the mitochondrial cytochrome c oxidase subunit I gene (*COI*) was amplified with M13F-LCOI1490 and M13R-HCO2198 universal DNA primers (Folmer *et al.*, 1994) mixed with Lepidoptera M13F-LepF1 and M13R-LepR1 primers (Hebert *et al.*, 2004) in an equal volume ratio (1:1). If the desired 658 bp *COI* fragment could not be amplified using the two above mentioned primer pairs (that is, for sample BW0010, BW0060 and BW1050), alternative M13F-jgCOI490 and M13R-jgHCO2198 *COI* primers were used, redesigned by Geller *et al.* (2013). The PCR reaction was performed with 1.0 μ l forward primer (10 μ mol/l), 1.0 μ l reverse primer (10 μ mol/l), 0.5 μ l dNTP (2.5 mM) (Amersham), 0.25 μ l Taq DNA polymerase (5 U/ μ l) (QIAGEN), 2.5 μ l CoralLoad 10x PCR buffer (QIAGEN) and 1–2 μ l template DNA. The reaction mixtures of sample BW0010, BW0060 and BW1050 included 2.0 μ l template DNA. The rest of the reactions were performed using 1.0 μ l template DNA. Initial denaturation took place for 3 minutes at 94°C, followed by 39 cycles of denaturation, annealing and extension (15 seconds at 94°C; 30 seconds at 50°C and 40 seconds at 72°C respectively). Final extension was performed for 5 minutes at 72°C.

A 500–520 bp fragment of the *16S* mitochondrial ribosomal gene was amplified with 16Sar and 16Sbr rDNA primers (Palumbi *et al.*, 1991). The PCR reaction was performed with 1.0 μ l forward primer (10 μ mol/l), 1.0 μ l reverse primer (10 μ mol/l), 2.5 μ l dNTP (2.5 mM) (Amersham), 0.25 μ l Taq DNA polymerase (5 U/ μ l) (QIAGEN), 2.5 μ l CoralLoad 10x PCR buffer (QIAGEN) and 1 μ l template DNA. The reac-

tion mixture of samples BW0010, BW0170, BW0171, BW0190 and BW1200 included 5.0 μ l 5x Q-solution (QIAGEN). Initial denaturation took place for 3 minutes at 94°C, followed by 39 cycles of denaturation, annealing and extension (10 seconds at 94°C; 1 minute at 50°C and 1 minute at 72°C respectively). Final extension was performed for 5 minutes at 72°C. Annealing temperature of sample BW0010, BW0170, BW0171, BW0190 and BW1200 was set to 57°C to increase annealing specificity.

A 328 bp fragment of the nuclear histone H3 (*H3*) gene was amplified with a F1 and R1 primer pair (Colgan *et al.*, 1998). The PCR reaction was performed with 1 μ l forward primer (10 μ mol/l), 1 μ l reverse primer (10 μ mol/l), 2.5 μ l dNTP (2.5 mM) (Amersham), 0.25 μ l Taq DNA polymerase (5 U/ μ l) (QIAGEN), 2.5 μ l CoralLoad 10x PCR buffer (QIAGEN) and 1 μ l template DNA. The reaction mixture of sample BW0190 included 5.0 μ l 5x Q-solution (QIAGEN). Initial denaturation took place for 3 minutes at 95°C, followed by 39 cycles of denaturation, annealing and extension (10 seconds at 95°C; 1 minute at 48°C and 1 minute at 72°C respectively). Final extension was performed for 5 minutes at 72°C.

Sequencing

Raw PCR products were purified, diluted and sequenced by BaseClear, Leiden. Sanger sequences were obtained with an ABI3730xl DNA Analyzer. M13F and M13R primers were used by BaseClear to sequence *COI* fragments. For sequencing of *16S* and *H3* gene fragments, the same primers as those that were used for PCR were supplied at a concentration of 5.0 pmole/ μ l.

Molecular phylogenetic analyses

Of the 14 specimens selected for this study, 14 *COI* sequences, 14 *16S* sequences and 13 *H3* sequences were obtained (Table 1). Chromatograms were corrected manually using Sequencher (v. 4.10.1) and aligned using ClustalW Multiple alignment (v.1.4.; Thompson *et al.*, 1994) with a gap open penalty of 15 and a gap extension penalty of 6.66. Nine *COI* sequences, nine *16S* sequences, and four *H3* sequences derived from Naturalis Biodiversity Center (Table 3, placed in Appendix) were added to the alignment. *Gnathophylloides mineri* Schmitt, 1933 (BW1050) was selected as outgroup in relation to the anemone- and scleractinian-associated species. To explore the effect of choosing a more closely related outgroup, *Ascidonia quasipusilla* (Chace, 1972) was selected alternatively. Sequences were trimmed to the length of the shortest sequence included in the alignment. All *COI* sequences comprised 658 bp. *16S* fragment length ranged from 506 to 509 bp. Partial *H3* sequences included 328 bp. Stop codons were assumed to indicate pseudogenes had been sequenced. To verify no stop codons were included, *COI* alignments were translated using an invertebrate mitochondrial genetic code. *H3* sequences were translated with a standard genetic code. None of the *COI* and *H3* sequences coded for stop codons. The single-gene alignment based on sequence data derived from the mitochondrial gene encoding cytochrome c oxidase subunit I (*COI*) comprised 21 ingroup sequences and one outgroup sequence. With outgroup *G. mineri* (BW1050), 204 characters of the 632 sites included in this alignment were variable, whereas 149 sites were parsimony informative. The *16S* ribosomal RNA single-gene alignment of 23 ingroup sequences and one outgroup sequence comprised 513 characters, 132 of which were variable. Seventy-nine sites were parsimony informative. The 276 bp histone 3 (*H3*) single-gene alignment contained 15 ingroup sequences and one outgroup sequence. Only 12 out of 50 variable sites were parsimony informative. *COI* and *H3* alignments did not include any indels. Prior to submission to GenBank, the first base pair at the 5' end of the *COI* and the *H3* sequences was removed to adjust the reading frame to reading frame 1.

The best-fitting models for sequence evolution of the *COI* (GTR+I), *16S* (GTR+G) and *H3* (GTR+I) datasets were determined by jModelTest 2.3.1. (Darriba *et al.*, 2012), selected by the AIC (Akaike Information Criterion), and subsequently applied to the maxi-

mum likelihood (ML) analyses with PAUP* 4.0b10 (Swofford, 2003). ML trees were constructed using a heuristic search with tree-bisection-reconnection (TBR) branch-swapping algorithm. For ML analyses, tree reliability was estimated with a bootstrap test of phylogeny comprising 1000 replications. All codon positions, as well as non-coding sites, were examined. Gaps and missing data were ignored.

Bayesian inferences were estimated in MrBayes 3.1.2 (Ronquist and Huelsenbeck, 2003). The programme was run for 5,000,000 generations with a burnin set to 25% for each marker using the most complex GTR+I+G model.

Results

Morphological comparison

A detailed morphological comparison revealed no characters that were different between coral- and anemone-associated specimens. Distinguishing characters in the genus *Periclimenes*, like the shape of the rostrum (Fig. 4C-K) and features on the dactyli of the ambulatory pereopods (Figs. 9, 10), are identical among coral- and anemone-associated specimens. The maximum size of specimens on the stony coral host is much smaller than that of specimens collected from sea anemones, pochl. 2.58 mm versus pochl. 5.25 mm respectively. The median size of stony coral-associated specimens (pocl = 1.88 mm; n = 11) is significantly smaller than that (pocl = 2.60 mm; n = 50) of *P. rathbunae* collected from anemones (Wilcoxon rank sum test, $p < 0.001$). The size of ovigerous females ranges from pochl. 1.78-2.58 in the stony coral associates and between 2.05-5.25 in anemone-associated specimens.

Phylogenetic position of the coral-associated specimens

ML trees based on *COI*, *16S* and *H3* sequence data are presented in Fig. 2A-C respectively. Both anemone- and stony coral-associated *Periclimenes rathbunae* specimens formed a highly supported monophyletic clade. Branching within this clade was poorly supported.

The selection of *Gnathophylloides* as outgroup affected the branching order of clade 1 (*Periclimenes rathbunae* and coral-associated *Periclimenes*), clade 2 (*Ancylomenes pedersoni*), and clade 3 (*Periclimenes yucatanicus*) of Fig. 2. When *Ascidonia quasipusilla*

Fig. 2. Maximum likelihood (ML) trees. Confidence values at the nodes were obtained from 1000 bootstrap replicates of ML trees (first number) and Bayesian Inference (BI) (second number). Only values above 50% are indicated. Scale bars indicate genetic distance. Colours correspond to host species.

(BW1200) was selected alternatively, either *Ancylomenes pedersoni* (in *COI* and *H3* ML phylogenetic reconstructions) or *P. yucatanicus* (in a *16S* ML phylogenetic reconstruction) branched off first, followed by the remaining two species branching off as sister species. However, independent of the chosen outgroup, support for clade 1 was high, while branching support within the clade remained poor.

Discussion and conclusions

Phylogenetic reconstructions based on partial *COI*, *16S* and *H3* sequences clustered the coral-associated *Periclimenes* and *Periclimenes rathbunae* within one clade with very high to maximal statistical support (Fig. 2). This shows that the specimens of coral-associated *Periclimenes* belong to *P. rathbunae*.

The association of *P. rathbunae* with *Dendrogyra cylindrus* identified here is the first report of a scleractinian coral associating with an Atlantic palaemonid shrimp species. While colonies of *D. cylindrus* consti-

tute up to 3 m high, cylindrical pillars, anemones that typically host *P. rathbunae*, like *Bartholomea annulata* (known as ‘ringed anemone’ or ‘corkscrew anemone’) and *Stichodactyla helianthus* (descriptively named ‘Caribbean carpet anemone’), extent no more than approximately 20 cm from the sea floor. Despite this clear difference in the overall shape of both hosts, the surface structure of *D. cylindrus*, comprising relatively long undulating tentacles standing out during daytime, is remarkably similar to that of anemones. Likewise, soft coral *Eunicea tourneforti* and corallimorph *Ricordea florida*, which have also been found to host *P. rathbunae* (Ritson-Williams and Paul, 2007; Hayes and Trimm, 2008), are covered with tentacles, suggesting a surface with tentacles, or at least tentacle-like extensions, is essential to the habitat of *P. rathbunae*.

Hosted by anemones, adult *P. rathbunae* have an orange dominated colour pattern, whereas the species is more translucent with a more olive colour pattern when it is hosted by *D. cylindrus*. Similar colour transformations have been reported to result from centrip-

etal and centrifugal pigment translocation in the cytoplasm of specialised shrimp cells called chromatophores (Fingerman, 1970), located at the skin and at the surface of internal organs. This has been found to enable rapid colour changes, allowing for adaptive processes including camouflaging, aposematic signalling and intraspecific communication (Milograna *et al.*, 2012).

Spotte *et al.* (1991) already noticed that *P. rathbunae* is able to alter its transparency to adapt its colouration to that of the host. Shrimps collected from *Stichodactyla helianthus*, that were observed *in vitro*, had a less intense olive colour than the shrimps occurring in nature. Specimens inhabiting *Condylactis gigantea* didn't have any background colouration. Spotte *et al.* (1991) concluded such transparency allows light from the surface of the anemone to be transmitted through the shrimp body, thereby matching its overall colouration to that of the variably coloured hosts. Moreover, Spotte *et al.* (1991) described the colouration of *P. rathbunae* is age-dependent, with juveniles having an overall clear appearance. In addition to the median size of the shrimp specimens collected from *D. cylindrus*, which was smaller than that of specimens collected from anemones, this suggests *D. cylindrus* hosts more juvenile *P. rathbunae*.

Baeza *et al.* (2001) observed a comparable distribution of the commensal crab *Allopetrolisthes spinifrons* (H. Milne Edwards, 1837) among its hosts. *A. spinifrons* has been documented to associate with sea anemones, gastropods and sea stars. Whereas small life stages of the crab were found to inhabit all of these hosts, adult (mature) crabs were only hosted by sea anemones. Baeza *et al.* (2001) expected habitat restrictions force *A. spinifrons* larvae to settle on alternative non-anthozoan hosts (gastropods and sea stars) that offer protection against predation and possibly provide a food source (mucus) too. During ontogeny, juvenile crabs likely migrate to the preferred host (sea anemones) over short periods of time, resulting in the identified host-use pattern.

Despite the similarity in the host-use patterns of *A. spinifrons* and *P. rathbunae*, the same reasoning cannot fully explain the distribution of *P. rathbunae* between its anemone and stony coral hosts. Beside the small translucent specimens of *P. rathbunae* (probably juvenile shrimps), also ovigerous females were collected from the stony coral host (Table 1). This shows the guest range of *D. cylindrus* is not completely restricted to small juvenile (immature) life stages of *P. rathbunae*. Moreover, in contrast to the anemone hosts

of *A. spinifrons*, that usually host no more than one adult or juvenile crab (Baeza *et al.*, 2001), one anemone can be inhabited by numerous conspecific shrimps. This reduces the probability that habitat (host availability) restrictions occur for *P. rathbunae* in nature, as one host is not fully occupied by the time one, or a few individuals have settled on the host.

Although several studies have questioned (Baeza *et al.*, 2001) or investigated (Levine and Blanchard, 1980; Crawford, 1992; Giese *et al.*, 1996) the effect of sea anemone toxins on their decapod inhabitants, the sensitivity to sea anemone nematocysts has not been linked to host-use patterns before. However, the effect of sea anemones on their inhabitants, which varies between different species of anemones and their inhabitants (Levine and Blanchard, 1980; Elliot and Mariscal, 1996), shows some potential to facilitate ontogenetic habitat-shifts. Levine and Blanchard (1980) found un-acclimated shrimps of *P. rathbunae* that have just moulted are more vulnerable to stinging nematocysts than conspecific shrimps that did not moult prior to the exposure to the anemone (*S. helianthus*). As moulting is required for the growth of (juvenile) shrimps, this might explain why juvenile shrimps occur on alternative, less aggressive hosts like *D. cylindrus*. To test any of these hypotheses, further in-depth field ecological studies for this species will be needed.

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SI. Palaemonid shrimps on diverse hosts. In chronological order: *Periclimenes rathbunae* on *Dendrogyra cylindrus*, *Periclimenes rathbunae* on *Stichodactyla helianthus*, *Periclimenes yucatanicus* on *Condylactis gigantea*, *Ancylomenes pedersoni* on *Bartholomea annulata* and *Gnathophyllodes mineri* on *Lytechinus variegatus*.

Appendix

Systematic account

Family Palaemonidae Rafinesque, 1815

Genus *Periclimenes* Costa, 1844

Periclimenes rathbunae Schmitt, 1924

(Figs. 1, 3–11)

Periclimenes rathbunae Schmitt, 1924: 70, Figs. 5–6; Holthuis, 1951: 58, pl. 17.

Type-locality. Spanish Port, Curaçao, Netherlands Antilles.

Holotype. ZMA DE240829

Material examined. Netherlands Antilles, Curaçao.

Holotype female (pocl. 3.25 mm), ZMA DE240829: Spanish Port, 20.v.1920, collected by C.J. van der Horst.— 2 ovigerous females (pocl. 1.78, 2.18 mm), 3 non-ovigerous females (pocl. 1.43, 1.57, 1.60 mm), RMNH.CRUS.D.57031: stn COA.21, Marie Pampoen, N 12.090761 W 68.904956, 5.xi.2013, depth 10 m, on *Dendrogyra cylindrus* Ehrenberg, 1834, collected by S.E.T. van der Meij, photo COA.21 041-052.— 2 ovigerous females (both pocl. 1.88 mm (drawings)) OUMNH.ZC.2015-02-008, 1 ovigerous female (pocl. 2.13 mm), 1 male (pocl. 1.63 mm), RMNH.CRUS.D.57032: stn COA.17, Cas Abou, N 12.227861 W 69.091778, 3.xi.2013, depth 8 m, on *Dendrogyra cylindrus* Ehrenberg, 1834, collected by S.E.T. van der Meij, photo COA.17 020-025.— 2 ovigerous females (pocl. 2.06, 2.58 mm), RMNH.CRUS.D.57033: COA.22, Grote Knip, N 12.351139 W 69.151917, 6.xi.2013, depth 8 m, on *Dendrogyra cylindrus* Ehrenberg, 1834, collected by C.H.J.M. Fransen, photo COA.22 223-237.— 1 male (pocl. 2.50 mm, P2major regenerating), 1 female (pocl. 1.55 mm) RMNH.CRUS.D.57034: stn COA.01, Hilton Reef, N 12.121789 W 68.969508, 31.x.2013, depth 20 m; on *Stichodactyla helianthus* (Ellis, 1768), collected by C.H.J.M. Fransen, photo COA.01 071-081.— 1 ovigerous female (pocl. 2.51 mm) RMNH.CRUS.D.57035: stn COA.18, Playa Forti, N 12.366139 W 69.15375, 1.xi.2013, depth 15 m, on *Condylactis gigantea* (Weinland, 1860), collected by C.H.J.M. Fransen, photo COA.18 026-032.— 1 ovigerous female (pocl. 4.75 mm), RMNH.CRUS.D.57036: stn COA.05, Car Wrecks, N 12.161 W 69.004083, 3.xi.2013, on *Stichodactyla helianthus* (Ellis, 1768), collected by C.H.J.M. Fransen, photo COA.05 038-053.— 1 female (pocl. 3.35 mm), 1 male (pocl. 1.65 mm)

RMNH.CRUS.D.57037: CUR.01, south coast, Carmabi Reef/Hilton Pier, 12°16'19.2"N 068°58'09.0"W, depth 5.1 m, 26.iv.2005, on *Stichodactyla helianthus*, collected by N. Snijders. g006.— 1 ovigerous female (pocl. 2.60 mm) RMNH.CRUS.D.57038: CUR.01, south coast, Carmabi Reef/Hilton Pier, 12°16'19.2"N 068°58'09.0"W, depth 8 m, 26.iv.2005, on *Lebrunia neglecta*, collected by N. Snijders. g007.— 1 non-ovigerous female (pocl. 2.35 mm) RMNH.CRUS.D.53148: CUR.01: south coast, Carmabi Reef/Hilton Pier, 12°16'19.2"N 068°58'09.0"W, depth 5.2 m, 26.iv.2005, on *Stichodactyla helianthus*, collected by N. Snijders. g014.— 1 non-ovigerous female (pocl. 2.75 mm) RMNH.CRUS.D.53150: CUR.03: south coast, Hilton Reef, 12°07'19.5"N 068°58'07.8"W, depth 5.3 m, 27.iv.2005, on *Stichodactyla helianthus*, collected by N. Snijders. g019.— 1 ovigerous female (pocl. 2.55 mm) RMNH.CRUS.D.57039: CUR.03, south coast, Hilton Reef, 12°07'19.5"N 068°58'07.8"W, depth 4 m, 27.iv.2005, on *Stichodactyla helianthus*, collected by N. Snijders. g020.— 2 females (pocl. 1.85 and 4.35 mm) RMNH.CRUS.D.57040: CUR.03, south coast, Hilton Reef, 12°07'19.5"N 068°58'07.8"W, depth 4 m, 27.iv.2005, on *Stichodactyla helianthus*, collected by N. Snijders. g021.— 1 female (pocl. 2.70 mm), 1 male (pocl. 1.80 mm), RMNH.CRUS.D.57041: CUR.03, south coast, Hilton Reef, 12°07'19.5"N 068°58'07.8"W, depth 4 m, 27.iv.2005, on *Stichodactyla helianthus*, collected by N. Snijders. g022.— 1 female (pocl. 1.80 mm) RMNH.CRUS.D.57042: CUR.03, south coast, Hilton Reef, 12°07'19.5"N 068°58'07.8"W, depth 2.9 m, 27.iv.2005, on *Stichodactyla helianthus*, collected by N. Snijders. g023.— 1 male (pocl. 2.40 mm) RMNH.CRUS.D.57043: CUR.03, south coast, Hilton Reef, 12°07'19.5"N 068°58'07.8"W, depth 2.3 m, 27.iv.2005, on *Stichodactyla helianthus*, collected by N. Snijders. g028.— 1 ovigerous female (pocl. 2.80 mm) RMNH.CRUS.D.57044: CUR.05, south coast, Marie Pampoen/ Carpale, 12°05'42.1"N 068°54'43.0"W, depth 12 m, 1.v.2005, on *Hexacorallia*, collected by N. Snijders. g037, JE-009.— 4 females (pocl. 2.30, 3.85, 4.00 and 4.10 mm) 1 male (pocl. 1.75 mm) RMNH.CRUS.D.57045: CUR.01, south coast, Hilton pier, 12°07'19.2"N 068°58'09.0"W, 3.5 m depth, 2.v.2005, on *Stichodactyla helianthus*, collected by N. Snijders. g042.— 1 ovigerous female (pocl. 2.05 mm) RMNH.CRUS.D.57046: CUR.07, south coast, Vaersenbaai, 12°09'38.3"N 069°08'17.2"W, depth 5.5 m, 03.v.2005, on *Lebrunia neglecta*, collected by N. Snijders. g044.—

Fig. 3. *Periclimenes rathbunae* Schmitt, 1924. Ovigerous female, pocl. 2.18 mm, RMNH.CRUS.D.57031, habitus, lateral view. Scale bar: 2 mm.

1 non-ovigerous female (pocl. 4.05 mm), RMNH. CRUS.D.57047: CUR.03, Hilton Reef, 12°07'19.5"N 068°58'07.8"W, 5.2 m depth, 13.v.2005, on *Stichodactyla helianthus*, collected by N. Snijders, g068.— 1 male (pocl. 1.95 mm) RMNH.CRUS. D.57048: CUR.22, south coast, Superior Producer, 12°05'21.5"N 068°56'35.5"W, depth 4.4 m, 2.vi.2005, on *Stichodactyla helianthus*, collected by N. Snijders. g094.— 1 male (pocl. 2.20 mm), RMNH.CRUS. D.57049: CUR.22, South Coast, Superior Produces, 12°05'21.5"N 068°56'35.5"W, 4.6 m depth, 2.vi.2005, on *Stichodactyla helianthus*, collected by N. Snijders, g097.— 1 ovigerous female (pocl. 3.00 mm), 1 male (pocl. 1.75 mm) RMNH.CRUS.D.37655: Piscadera baai, W side of mouth, between *Rhizophora*, 14.xii.1963, collected by P. Wagenaar Hummelinck, no. 1460.— 2 ovigerous females (pocl. 2.40, 3.30 mm), 2 non-ovigerous females (pocl. 2.35, 2.45 mm) RMNH. CRUS.D.37651: Piscadera baai, 25.vii.1978, on *Bartholomea annulata*, collected by Svoboda.— 2 ovigerous females (pocl. 4.60, 5.25 mm), 3 non-ovigerous females (pocl. 2.60, 2.95, 3.25 mm), 5 males (pocl. 1.45–2.35 mm) RMNH.CRUS.D.30617: Awa di Oostpunt, 1 m depth, 8.viii.1973, on *Stoichactis* sp. in *Thalassia*-bed, collected by J.C. den Hartog.— 4 ovigerous females (pocl. 3.35–4.40 mm) RMNH. CRUS.D.30616: Vaerssen Baai, 1.3–3 m, 25.iv.1973, on *Stichodactyla helianthus*, collected by J.C. den Hartog and R. de Windt.— 1 female (pocl. 2.80 mm), 2 males (pocl. 1.80, 2.60 mm) RMNH.CRUS.D.30618: Awa di Oostpunt, 1.5–3 m, 8.viii.1973, on *Exaiptasia pallida*, collected by J.C. den Hartog and R. de Windt.— 1 ovigerous female (pocl. 3.90 mm) RMNH.CRUS.D.30619:

Vaerssen Baai, 1.5–3 m, 24.vii.1973, on *Stichodactyla helianthus*, collected by J.C. den Hartog and R. de Windt.— 3 females (pocl. 2.80–3.20 mm) RMNH. CRUS.D.26236a: summer 1968, on *Lebrunia neglecta*, collected by F. Nijhout.— 1 ovigerous female (pocl. 3.50 mm), 1 female (pocl. 4.15 mm) RMNH. CRUS.D.26236b: summer 1968, on *Stichodactyla helianthus*, collected by F. Nijhout. **Bonaire**. 2 ovigerous female (pocl. 3.25, 4.25 mm) RMNH.CRUS.D.30620: off Goto Lake, in shallow water, 11.iv.1973, on *Stichodactyla helianthus*, collected by J.C. den Hartog. **Virgin Islands**. 1 female (pocl. 3.75 mm) RMNH. CRUS.D.20809: Tavernier, -ii.1971, collected by N. Ziler. **Florida Keys, U.S.A.** 1 ovigerous female (pocl. 3.00 mm) RMNH.CRUS.D.20810: Lameshur Bay, St. John, 31.vii.1970, 30 ft depth, on *Bartholomea annulata*, collected by R.H. Chesher.

Description. Small sized, rather slender shrimp, with slender pereopods (Fig. 3).

Carapace smooth. Rostrum (Fig. 4A–K) well developed, reaching to end of basal segment of antennular peduncle; lamina deep, lateral carina indistinct, situated near to proximally slightly convex ventral margin with 0–3 (usually 1) very small subdistal teeth; convex posterior part of ventral margin with single row of plumose setae; dorsal margin convex, elevated, strongly compressed, with 5–8 subequal teeth, posteriormost one or two (seldom three) teeth situated posteriorly to level of posterior margin of orbit, proximalmost tooth usually at somewhat larger distance to anterior teeth than distance between teeth on rostrum proper; 2–3 plumose setae just in front of dorsal teeth.

Fig. 4. *Periclimenes rathbunae* Schmitt, 1924. Ovigerous female, pochl. 2.18 mm, RMNH.CRUS.D.57031: A, anterior appendages, lateral view; B, anterior appendages, dorsal view. C-K, rostrum, lateral view; C-G, associated with *Dendrogyra cylindrus* Ehrenberg, 1834, RMNH.CRUS.D.57031; H-K, associated with *Stichodactyla helianthus* (Ellis, 1768). C, ovigerous female, pochl. 2.18 mm; D, female pochl. 1.60 mm; E, female pochl. 1.57 mm; F, female pochl. 1.43 mm; G, ovigerous female pochl. 1.78 mm; H, female pochl. 1.55 mm, RMNH.CRUS.D.57034; I, male pochl. 2.50 mm, RMNH.CRUS.D.57034; J, ovigerous female pochl. 4.75 mm, RMNH.CRUS.D.57036; K, ovigerous female pochl. 2.51 mm, RMNH.CRUS.D.57035. Scale bar: A, B, J = 2 mm; C-I, K = 1 mm.

Supra-orbital spines absent. Inferior orbital angle well developed, produced, rounded in lateral view. Antennal spine small, marginal, situated below inferior orbital angle. Hepatic spine distinctly larger than antennal spine, situated well behind level of posterior orbital margin and slightly below level of antennal spine. Antero-lateral angle of carapace (Figs. 3, 4A, C-K) blunt, not produced.

Abdominal segments (Fig. 3) smooth. Third segment slightly produced posterodorsally. Pleura all broadly rounded. Sixth abdominal segment 1.6 times as long as fifth (relatively longer in smaller specimens), posteroventral angle feebly produced, rounded, posterolateral angle acute.

Telson (Fig. 5A) 1.2 times as long as sixth abdominal segment and 3.1 times longer than anterior width; lateral margins converge posteriorly; two pairs of small sized submarginal dorsal spines present at 0.80 and 0.85 of telson length; posterior margin rounded, 0.43 of anterior width, with three pairs of spines. Lateral spines short, slightly longer than dorsal spines. Intermediate spines well developed, about 0.17 of telson length, 1.8 times length of submedian spines.

Eyes (Fig. 4A, B) well developed. Cornea globular, with distinct accessory pigment spot dorsally. Eye-stalks slightly more than twice as long as proximal width, slightly swollen proximally.

Fig. 5. *Periclimenes rathbunae* Schmitt, 1924. Ovigerous female, pocl. 2.18 mm, RMNH.CRUS.D.57031: A, tailfan, dorsal view. Ovigerous female, pocl. 1.88 mm, OUMNH.ZC.2015-02-008; B, antennula, dorsal view; C, antenna, ventral view. Scale bar: A = 1 mm; B, C = 0.8 mm.

Antennular peduncle (Fig. 5B) exceeding tip of rostrum by distal one or two segments. Proximal segment long, slender, 3.0 times longer than wide; stylocerite slender, acute, reaching almost to middle of segment; lateral margin straight, anterolateral margin produced, angular, with distolateral tooth and row of setae; medial ventral margin without tooth. Statocyst containing granular statolith. Intermediate and distal segments short, together equal to 0.38 of proximal segment length. Upper outer flagellum biramous, with first 4-5 segments fused. Aesthetascs present on distal 4 segments of fused part and short free ramus. Shorter free ramus uni-segmented, longer rami with 6-7 segments.

Lower inner flagellum slender, slightly longer than upper flagellum.

Antennal basicerite (Fig. 5C) with lateral tooth. Ischiocerite and merocerite normal. Carpocerite slender, reaching 0.4 of length of scaphocerite. Scaphocerite long, rather slender, with lamella slightly overreaching distal margin of antennular peduncle. Lateral border straight, ending in acute large distolateral tooth. Lamella extending beyond distolateral tooth, feebly angulated distomedially, about 2.9 times longer than broad, with greatest width at about half of its length.

Epistome and labrum normal.

Second and third thoracic sternites unarmed.

Fig. 6. *Periclimenes rathbunae* Schmitt, 1924, ovigerous female, pocl. 1.88 mm, OUMNH.ZC.2015-02-008: A, right mandible, dorsal view; B, right mandible, ventral view; C, right maxillula, dorsal view; D, right maxilla, dorsal view; E, right first maxilliped, dorsal view. Scale bar: A-E = 0.4 mm.

Fourth thoracic sternite with short medial process and shallow lateral carinae posteromedial of first pereopods.

Fifth thoracic sternite with distinct lateral plates posteromedial of second pereopods.

Sixth to eighth thoracic sternites unarmed.

Mandible (Fig. 6A, B) with cylindrical molar process bearing a few brushes of setae distally. Incisor process slender, with four well developed teeth distally, of which lateralmost slightly enlarged. Mandible without palp.

Maxillula (Fig. 6C) with upper lacinia rectangular with row of few serrulate spines and slender setae me-

dially; lower lacinia more slender, with few serrulate setae distally; palp bilobed, medial lobe with single short recurved simple seta.

Maxilla (Fig. 6D) with short tapering non-setose palp with few plumose setae laterally. Basal endite well developed, not bilobed, with row of about 15 also short, stout and blunt, with about six simple setae distally. Coxal endite obsolete, median margin convex, without setae, medial region slightly convex. Scaphognathite normal, widest centrally, about 23.82 times longer than broad, with marginal plumose setae.

First maxilliped (Fig. 6E) with short, slender, tapering palp without setae. Basal region broad, not dis-

Fig. 7. *Periclimenes rathbunae* Schmitt, 1924, ovigerous female, pocl. 1.88 mm, OUMNH.ZC.2015-02-008: A, right second maxilliped, dorsal view; B, right third maxilliped, dorsal view; C, right first maxilliped, dorsal view; D, idem, chela; E, left major second pereopod; F, idem, chela. Scale bar: A, D, F = 0.4 mm; B, C, E = 1 mm.

tinctly separated from the coxal region. Median margin sparsely provided with setulose and slender simple setae. Caridean lobe distinct, with coarsely setulose plumose marginal setae. Flagellum of exopod well developed with 4 long plumose distal setae and few short subdistal setae. Epipod indistinctly bilobed.

Second maxilliped (Fig. 7A) with dactylar segment narrow, 2.4 times longer than wide, straight medially, densely fringed with with numerous coarsely serrulate, spiniform, and long curled finely serrulate setae medially. Propodal segment longer than dactylar segment, almost twice as long as wide, with a subrectangular distomedial angle not produced, with few long

serrulate setae. Carpus short, unarmed. Meral segment short, not excavate, without setae. Ischium fused to basis. Basis with long slender exopod exceeding length of endopod, with 4 long plumose setae distally and one short plumose seta subdistally. Coxa slightly produced medially, with few small simple setae medially, rounded small oblong epipod laterally.

Third maxilliped (Fig. 7B) slender. Terminal segment 3.4 times longer than proximal width, slightly shorter than length of penultimate segment, with few serrulate and simple setae medially. Penultimate segment slender, 4.4 times longer than wide. Meral segment short, 0.57 of length of penultimate segment,

Fig. 8. *Periclimenes rathbunae* Schmitt, 1924, ovigerous female, pochl. 1.88 mm, OUMNH.ZC.2015-02-008: A, right minor second pereiopod; B, idem, chela; C, right third pereiopod; D, right fourth pereiopod; E, right fifth pereiopod; F, coxa right fourth pereiopod. Scale bar: A, C-E = 1 mm; B = 0.4 mm; F = 0.2 mm.

twice as long as wide, clearly separated from short ischial segment. Ischial segment half length of meral segment, as long as wide, distinctly separated from basal segment. Basal segment oblong, as long as meral segment. Exopod reaching mid length of meral segment, with 4 distal and 2 subdistal plumose setae. Coxa not produced medially, with rounded lateral plate and small rudimentary arthrobranch.

First pereiopod (Fig. 7C) slender, reaching distal margin of scaphocerite. Chela with palm subcylindrical, straight, 2.0 times longer than wide. Fingers (Fig. 7D) as long as palm, straight not subspatulate, with brushes of few setae in distal part, cutting edges entire, tips of fingers hooked. Cleaning setae present proximally on palm and distoventral part of carpus. Carpus 1.0 times length of chela, 5.5 times longer than wide. Merus about as long as carpus, twice length

of ischium. Basis and coxa without special features.

Second pereiopods, subequal in length, usually dissimilar. Major second pereiopod (Fig. 7E) extending beyond antennular peduncle with chela. Chela with palm subcylindrical, straight, about three times as long as wide. Fingers (Fig. 7F) 0.75 of palm length. Dactylus wider than fixed finger, with dorsolateral longitudinal carina in larger specimens, with brushes of setae in distal part, unguis strongly hooked, cutting edge with 0-3 slightly recurved teeth proximally, decreasing in size proximally. Fixed finger with tip strongly hooked, with 0-4 slightly recurved teeth in proximal half, decreasing in size proximally. Carpus, merus and ischium unarmed, their length ratios of 0.5, 1.0 and 0.8 times length of palm. Basis and coxa without special features. Minor second pereiopod (Fig. 8A). Chela with fingers (Fig. 8B) as long as subcylindrical palm,

Fig. 9. *Periclimenes rathbunae* Schmitt, 1924, ovigerous female, pocl. 1.88 mm, OUMNH.ZC.2015-02-008: associated with *Dendrogyra cylindrus* Ehrenberg, 1834: A, dactylus right third pereopod; B, idem, fourth right pereopod; C, idem, fifth right pereopod. Scale bar = 0.2 mm.

fingers distally hooked, cutting edges entire; carpus slightly longer than palm, gradually increasing in distally; merus slightly longer than carpus; ischium as long as carpus.

Ambulatory pereopods (Fig. 8C-E) slender, similar in form, slightly increasing in length from third to fifth. Dactylus (Figs. 9, 10) slender, uniformly tapering, unarmed, about 0.25 of propodus length, 5.5 times as long as proximal width, with slender unguis almost as long as corpus. Propodus about 12-15 times longer than wide, with two distoventral spines in third and fourth and one in fifth pereopod; distoventral spines with fine denticulation on flexor margin. Carpus, merus and ischium 0.47, 1.0 and 0.53 of propodus length, unarmed (Fig. 4C, D). Coxa of fourth pereopod in female with patch of short curved spines proximoven- trally (Fig. 8F).

Endopod of first pleopod in ovigerous female (Fig. 11A) short, 0.25 of length of exopod, with long plumose setae along its entire margin. Endopod of first pleopod in male (Fig. 11B) short, 0.41 times length of exopod, distally rounded, with 3 long plumose setae along lateral margin and one long plumose seta in proximal part of medial margin with one small short seta somewhat more anteriorly. Endopod of second pleopod in male (Fig. 11C), 0.77 times length of exopod. Appendix masculina long and slender, almost twice as long as appendix interna, with five serrate long setae distally.

Uropods (Fig. 5A) extending beyond tip of telson. Protopodite unarmed laterally. Exopod with lateral border almost straight, entire, terminating in a small tooth with small mobile spine medially, about 2.3 times longer than wide, about as long as endopod.

Fig. 10. *Periclimenes rathbunae* Schmitt, 1924, associated with *Stichodactyla helianthus* (Ellis, 1768): A, dactylus right third pereopod, male, post. 2.20 mm, RMNH.CRUS.D.57049; B, idem, male, post. 1.75 mm, RMNH.CRUS.D.57045. Scale bar = 0.2 mm.

Table 3. Additional sequences obtained from Naturalis Biodiversity Center with species name, sample number, voucher registration number,

Species	Locality			
	Sample nr	Voucher reg. nr	Country	Coordinates
<i>Periclimenes rathbunae</i> Schmitt, 1924	G014	RMNH.CRUS.D.53148	Carmabi Reef	12.272000N, 68.969167W
<i>Periclimenes rathbunae</i> Schmitt, 1924	G019	RMNH.CRUS.D.53150	Hilton Reef	12.122083N, 68.968833W
<i>Periclimenes rathbunae</i> Schmitt, 1924	JE-009	RMNH.CRUS.D.57044	Marie Pampoen/ Carpile	12.095028N, 68.911944W
<i>Periclimenes rathbunae</i> Schmitt, 1924	JE-013	RMNH.CRUS.D.57048	Superior Producer	12.089306N, 68.943194W
<i>Periclimenes rathbunae</i> Schmitt, 1924	JE-014	RMNH.CRUS.D.57044	Marie Pampoen/ Carpile	12.095028N, 68.911944W
<i>Periclimenes rathbunae</i> Schmitt, 1924	JE-015	RMNH.CRUS.D.57047	Hilton Reef	12.122083N, 68.968833W
<i>Periclimenes rathbunae</i> Schmitt, 1924	JE-016	RMNH.CRUS.D.57037	Carmabi Reef	12.272000N, 68.969167W
<i>Periclimenes yucatanicus</i> (Ives, 1890)	G015	RMNH.CRUS.D.53149	Carmabi Reef	12.272000N, 68.969167W
<i>Periclimenes yucatanicus</i> (Ives, 1890)	G017	RMNH.CRUS.D.53151	Drielstraat	12.095028N, 68.911944W
<i>Ancylomenes pedersoni</i> (Chace, 1958)	G004	RMNH.CRUS.D.53153	Carmabi Reef	12.272000N, 68.969167W
<i>Ancylomenes pedersoni</i> (Chace, 1958)	G012	RMNH.CRUS.D.53154	Carmabi Reef	12.272000N, 68.969167W
<i>Ancylomenes pedersoni</i> (Chace, 1958)	G010	RMNH.CRUS.D.53147	Carmabi Reef	12.272000N, 68.969167W

Fig. 11. *Periclimenes rathbunae* Schmitt, 1924, RMNH.CRUS.D.57032. A, first right pleopod, ovigerous female, pocl. 2.18 mm; B, first right pleopod, male, pocl. 1.63 mm; right second pleopod, male, pocl. 1.63 mm. Scale bar: A = 0,8 mm; B, C = 0.4 mm.

sampling locality, host, and GenBank accession numbers.

Host class: subclass: order: species	GenBank accession #		
	COI	16S	H3
Anthozoa: Hexacorallia: Actiniaria: <i>Stichodactyla helianthus</i>	KX090120	-	-
Anthozoa: Hexacorallia: Actiniaria: <i>Stichodactyla helianthus</i>	KX090121	-	-
Anthozoa: Hexacorallia: - : -	KX090122	KX090097	KX090141
Anthozoa: Hexacorallia: Actiniaria: <i>Stichodactyla helianthus</i>	-	KX090098	KX090142
Anthozoa: Hexacorallia: - : -	KX090123	KX090099	-
Anthozoa: Hexacorallia: Actiniaria: <i>Stichodactyla helianthus</i>	KX090124	KX090100	KX090143
Anthozoa: Hexacorallia: Actiniaria: <i>Stichodactyla helianthus</i>	KX090125	-	KX090144
Anthozoa: Hexacorallia: Actiniaria: <i>Condylactis gigantea</i>	KX090126	KX090101	-
Anthozoa: Hexacorallia: Actiniaria: <i>Condylactis gigantea</i>	KX090127	KX090102	-
Anthozoa: Hexacorallia: Actiniaria: <i>Bartholomea annulata</i>	KX090128	KX090103	-
Anthozoa: Hexacorallia: Actiniaria: <i>Bartholomea annulata</i>	-	KX090104	-
Anthozoa: Hexacorallia: Actiniaria: <i>Condylactis gigantea</i>	-	KX090105	-

From ca. 30–80 eggs of ca. 0.5 mm in diameter present under abdomen depending on size of female.

Size. Ovigerous females ranging from pocl. 1.75–5.25 mm, maximum size of males 2.60 mm.

Colour. Juveniles are largely transparent. Adult specimens with distinct pattern of red and white dots and lines. For detailed descriptions of juvenile and adult colour patterns see Spotte *et al.* (1991).

Remarks on variation. In the type description no mention is made of teeth on the cutting edges of the dactylus and fixed finger of the major chela of the second pereopods. When checking the holotype (ZMA DE240829) three recurved teeth were observed in the proximal part of both dactylus and fixed finger. Also Holthuis (1951) did not note these teeth as the specimen he described from the Tortugas is lacking the major second pereopod. The armature of the major second chela is rather variable ranging from entire cutting edges to three on the dactylus and four on the fixed

finger. If teeth are present, usually the fixed finger has one more than the dactylus. There is no clear relation of the armature with size. However, in the smallest specimens the number of teeth is usually lower than in adult specimens. In adult specimens though, major second chelae with entire cutting edges are not uncommon. No relation between armature and gender of the specimens was observed.

The dorsolateral flange on the dactylus of the major second pereopod is usually more developed in larger specimens. In those specimens with a very well developed dorsolateral flange, the dactylus is distinctly longer than the fixed finger. However, several of the larger specimens have been observed without a dorsolateral flange. In few specimens with a dorsolateral flange on the major second chela such a flange is also present on the minor second chela.

The major second pereopod is occurring on the right or left side in equal numbers (antisymmetric).