

POSSIBLE SYNONYMY OF THE WESTERN ATLANTIC ANEMONE SHRIMPS *PERICLIMENES PEDERSONI* AND *P. ANTHOPHILUS* BASED ON MORPHOLOGY

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ABSTRACT

The anemone shrimp *Periclimenes pedersoni* Chace, 1958 occurs in south Florida and throughout the West Indies. *Periclimenes anthophilus* Holthuis and Eibl-Eibesfeldt, 1964 closely resembles *P. pedersoni* but is believed to be endemic to Bermuda. Morphological analysis of specimens from the type locations (50 each from Bermuda and the Bahamas, 60 possible variables) revealed no important differences, and *P. anthophilus* should perhaps be considered a junior synonym of *P. pedersoni*.

Holthuis and Eibl-Eibesfeldt (1964) described *Periclimenes anthophilus* as a new species of anemone shrimp from Bermuda based on 11 specimens collected in association with the sea anemones *Actinia bermudensis* McMurrich, 1889 and *Condylactis gigantea* Weinland, 1860. No specimens were found on the anemone *Bartholomea annulata* Duchassaing and Michelotti, 1866.

Holthuis and Eibl-Eibesfeldt declared *P. anthophilus* to be distinct from *P. pedersoni* Chace, 1958 despite the striking similarity in color pattern and only minor differences in morphology. According to their assessment, morphological variation was restricted mainly to pereopods 2 and location of the first dorsal rostral tooth with respect to the hepatic spine. In *P. pedersoni* the hepatic spine was reported to be level with, or behind, the first dorsal rostral tooth; in specimens of *P. anthophilus* examined by Holthuis and Eibl-Eibesfeldt the hepatic spine was anterior to it. The propodi of pereopods 2 of *P. pedersoni* were considered to be proportionately narrower, the carpus proportionately longer (nearly as long as the propodus), and the dactyls triangular in cross section instead of cylindrical.

Chace (1972) reviewed these differences, remarking that in *P. pedersoni* the dactyls of pereopods 2, like those of *P. anthophilus*, are triangular in cross section, an observation omitted accidentally from his original description (Chace, 1958). He concluded that the different host associations of *P. anthophilus* (*P. pedersoni* associates primarily with *B. annulata*) and proportionately shorter carpus of its major pereopod 2 were adequate justification for retaining species distinctions. Further doubts that *P. anthophilus* and *P. pedersoni* are distinct were echoed by Levine and Blanchard (1980), and by Williams (1984). Nizinski (1989) argued for retaining separation based mainly on behavioral considerations. More recently, Wicksten (1995b) proposed that *P. anthophilus* be considered a junior synonym of *P. pedersoni* but offered no supporting data.

P. pedersoni occurs in south Florida and throughout the West Indies (Spotte et al., 1991). In contrast, *P. anthophilus* is thought to be endemic to Bermuda (Chace, 1972; Williams, 1984), although Criales (1984) and Stanton (1977) reported having seen *P. anthophilus* (or *P. cf. anthophilus*) elsewhere (see Discussion).

Here I test the null hypothesis of species synonymy using taxonomic methods and discuss purported differences in social structure, behavior, and color pattern. Although the principal objective was to attempt to falsify the null hypothesis of taxonomic synonymy, salient features of within-species differences were not ignored. For convenience,

“symbiont” refers to the smaller and “host” to the larger of two organisms living together sensu Castro (1988). For clarity, the original specific names of the shrimp have been retained.

MATERIALS AND METHODS

BERMUDAN COLLECTIONS, AUGUST 1994 (~32°20'N, 64°43'W).—Shrimp were obtained at depths of 1–5 m; all were associated with *C. gigantea*. Eleven specimens came from a single location in Harrington Sound within a radius of ~50 m. These were transported alive to Connecticut and maintained in 30-L aquariums. Sea anemones (*C. gigantea*) purchased from local pet shops were placed three to an aquarium. The anemones had been collected in south Florida or the West Indies.

BAHAMIAN COLLECTIONS, DECEMBER 1994 (~23°46'N, 76°06'W).—Shrimp were collected in Exuma Sound, Exuma Cays, Bahamas, at depths of 1–8 m within ~3 km of Lee Stocking Island. All shrimp were collected from specimens of *B. annulata* except one obtained from the bivalve mollusk *Lima scabra* Schumacher, 1817. Because the Bahamas are the type location of *P. pedersoni* (Chace, 1958), I felt reasonably assured that the null hypothesis of synonymy in *P. anthophilus* and *P. pedersoni* could be tested directly without first demonstrating that *P. pedersoni* is taxonomically homogeneous throughout its range.

OBSERVATIONS.—Specimens in the U.S. National Museum of Natural History were examined to make superficial comparisons. For purposes here, only my own material was used because the procedure was destructive, requiring removal of body parts for measurement. In addition, the statistical analyses demanded relatively large and consistent sample sizes from each location. Data were obtained from 50 specimens each of *P. anthophilus* and *P. pedersoni*. From every shrimp I recorded 74 continuous and 13 discrete variables (Table 1). Observations were made with aid of a stereoscopic microscope fitted with an ocular micrometer. I also prepared wet mounts of an upper antennular flagellum from each shrimp and counted segments of the fused and unfused rami under high magnification. In addition, one of the second pleopods was removed from nonovigerous specimens, placed in a wet mount, and examined under high magnification for an appendix masculina. All specimens possessed a well developed appendix interna; consequently, those without an appendix masculina were recorded as females. Based on this criterion, male/female proportions in the sample populations were similar: *P. anthophilus* (19 males, 31 females = 0.62), *P. pedersoni* (18 males, 32 females = 0.56). Whether these proportions extend to the populations at large is unknown.

CONTINUOUS VARIABLES.—The two shortest pereopod segments (coxa and basis) were not measured. Within-species comparisons of the remaining five paired segments (left vs right) were performed with dependent t-tests (two-tailed); missing data were deleted casewise. Significant differences were not apparent in the *P. anthophilus* data. Exceptions in the *P. pedersoni* data were pereopods 1 dactyls ($t_{49} = -2.83$, $P < 0.01$), pereopods 2 dactyls ($t_{46} = -2.52$, $P < 0.05$), and pereopods 4 carpus ($t_{49} = 2.38$, $P < 0.05$). Data for left and right segments of all pereopods were combined, reducing the number of possible continuous variables to 47. Tied and missing values were omitted when assessing between-species differences in carpus length of the major pereopod 2. To compute estimated embryo volume I measured the lengths and widths of 33 embryos from every ovigerous shrimp before applying a derived formula for an oblate spheroid (Bauer, 1991; Mashiko et al., 1991; Spotte, 1997). The main data sets for *P. anthophilus* and *P. pedersoni* contained, respectively, three and 14 ovigerous specimens. Damaged embryos from one specimen of *P. pedersoni* were counted but not measured.

OUTLIERS.—Raw values of the continuous variables were examined by species for outliers using linear least-squares regression and scatterplots with carapace length as independent variable. When necessary, data were analyzed three times in succession. Individual body parts were remeasured after each of the first two analyses if their values exceeded ± 3 SD of the raw regression residuals (Spotte et al., 1994; also see Spotte, 1997), and erroneous entries in the data were corrected prior to

Table 1. Possible variables ($n = 60$) used in comparing the morphology of *P. anthophilus* and *P. pedersoni*. Units of continuous variables are in mm except embryo volume, which is in mm^3 .

Continuous variables	Discrete variables
Carapace length	Dorsal rostral teeth
Antennal scale length, width	Ventral rostral teeth
Antennular scale length, width	Antennular flagellum (fused rami)
Antennal peduncle length	Antennular flagellum (unfused rami)
Antennular peduncle length	Bands on antennae
Cornea length	Appendix masculina spines
Eyestalk length	Total embryos
Somite 1–6 lengths	Carapace upturned or horizontal
Somite 5/somite 6 proportion	Rostrum upturned or horizontal
Telson length	Extension of rostrum to cornea
Spinule 1/spinule 2 distance	Position of first rostral tooth
Embryo volume	Position of second rostral tooth
Propodus width, pereopods 1, 2	Sex
Dactyl lengths, pereopods 1–5	
Propodus lengths, pereopods 1–5	
Carpus lengths, pereopods 1–5	
Merus lengths, pereopods 1–5	
Ischium lengths, pereopods 1–5	
Carpus length, major pereopod 2	

the next analysis. Only outliers remaining after the third analysis were discarded (five from the original *P. anthophilus* data set of $n = 3373$, 17 from the original *P. pedersoni* set of $n = 3486$).

DATA TRANSFORMATIONS.—Continuous variables were divided by carapace length to reduce size effects (Gibson et al., 1992; Turner et al., 1989). As defined here, carapace length is the distance from the posterior margin of the ocular orbit to the posterior margin of the carapace. Carapace length was chosen as the variable indicating body size because in decapods it is relatively unaffected by variations induced during growth and maturation (Finney and Abele, 1981; Gray and Newcombe, 1938; Lovett and Felder, 1989). Square roots of the resultant proportions were arcsin-transformed (Zar, 1984) with exception of somite 3 and the left and right propodus of pereopods 2. Proportions for these variables were arctan-transformed instead because several exceeded unity. Two sets of data already in proportional form were retained as untransformed values. The first of these was the somite 5 to somite 6 length proportion; the second was a distance proportion involving the two pairs of dorsal spinules on the telson, both distances measured from the telson's proximal end.

DISCRETE VARIABLES.—Discrete data were recorded as counts or simply coded. Some entries in Table 1 require further description. Recorded were whether (1) the carapace was upturned or horizontal; (2) the rostrum was upturned or horizontal; (3) the rostrum fell short of, extended to, or extended past the cornea; (4) the first dorsal rostral tooth was posterior to, even with, or anterior to the hepatic spine; and (5) the second dorsal rostral tooth was anterior or posterior to the posterior margin of the ocular orbit. Type II errors (errors of β) could not be computed in tests involving chi-square (see the Results) because doing so requires that the alternative hypothesis contain a specific value similar to that of a mean or variance.

RESULTS

CONTINUOUS VARIABLES.—To assess size differences between and within species I used independent t-tests (two-tailed) on untransformed carapace lengths. *Periclimenes anthophilus* males vs females: $t_{48} = -3.39$, $P < 0.01$; males (mean = 2.28 ± 0.41 mm), females (mean = 2.78 ± 0.54 mm). *P. pedersoni* males vs. females: $t_{48} = -4.37$, $P < 0.001$; males (mean = 3.18 ± 0.48 mm), females (mean = 4.26 ± 0.98 mm). The null hypothesis was rejected in both analyses, confirming known sexual dimorphism (Chace, 1958; Nizinski, 1989). Significant within-species results disallowed the pooling of data to assess between-species differences. However, specimens of *P. pedersoni* were clearly larger than those of *P. anthophilus*. An independent t-test (two-tailed) also was used to assess comparative mean embryo volumes. Species differences were significant: $t_{559} = -31.15$, $P < 0.0001$ (for *P. anthophilus*, $n = 3$, mean = 0.05 ± 0.02 mm³; for *P. pedersoni*, $n = 14$, mean = 0.11 ± 0.02 mm³).

Within-species analyses of untransformed proportional data were performed nonparametrically using Mann-Whitney's U-test. For somite 5/somite 6 proportions the null hypothesis was accepted for *P. anthophilus*, indicating no difference between sexes ($U = 264.5$, $Z = -0.60$, $P > 0.05$). The *P. pedersoni* data, however, revealed marked sexual dimorphism ($U = 105.0$, $Z = -3.70$, $P < 0.001$), confirming an earlier observation of Chace (1958) that somite 6 is proportionately longer in males (mean = 0.48) than in females (mean = 0.52). The null hypothesis was accepted for both species in analyses involving spinules 1/spinules 2 proportions ($U = 221.5$ – 274.5 , $Z = -1.19$ to -0.22 , $P > 0.05$).

The remaining 45 continuous variables were evaluated using discriminant analysis. This procedure measures the extent that each variable contributes uniquely to prediction of group membership (Fisher, 1936). Groups compared were *P. anthophilus* and *P. pedersoni* (sexes combined by species). Results are displayed in descending order of discriminatory power (Table 2). Variables not shown lacked the capacity to discriminate and were excluded from the model. As seen from partial Wilks's λ values and standardized canonical coefficients, the ischium of pereopods 5 was the strongest discriminatory variable.

DISCRETE VARIABLES.—Some results are summarized in Table 3. Banded antennae were common among specimens of *P. anthophilus* but occurred in only two specimens of *P. pedersoni*. Antennal band counts in *P. anthophilus* were tested for possible size and sex effects using the original 50 shrimp plus data from an additional four males and seven females. Size effects are depicted in Figure 1. Sex effects were analyzed using Mann-Whitney's U-test ($n = 61$, $U = 179.0$, $Z = -3.83$, $P < 0.001$). Males had significantly more bands than females: males ($n = 23$, range = 1–8, mean = 5 ± 1.78); females ($n = 38$, range = 0–6, mean = 2.84 ± 2.00).

Table 2. Discriminant analysis (45 continuous variables), between-species results after 4 forward steps adjusted to high sensitivity ($F_{\text{enter}} = 1.00$). Wilks's $\lambda = 0.013$, $F_{(4,4)} = 73.53$, $P < 0.001$, $n = 50$ for both groups.

Discriminating variables retained in the model	Partial Wilks's λ	$F_{(1,4)\text{-remove}}$	P	Standardized canonical coefficients
Pereopods 5 ischium	0.2089	15.15	0.0177	-1.65
Somite 3	0.3173	8.61	0.0426	-1.29
Pereopods 4 dactyls	0.3465	7.54	0.0516	-1.15
Somite 6	0.4458	4.97	0.0896	-1.05

Table 3. Between-species comparison of some discrete variables (Mann-Whitney's U-test). Absence of significance is at $P > 0.05$. Segments are those of the upper antennular flagellum. Unequal sample sizes were used in the analysis of total embryos ($n = 3$ for *P. anthophilus*, $n = 14$ for *P. pedersoni*).

Variable	U	Z	P	<i>P. anthophilus</i> , <i>P. pedersoni</i> , range	range
Dorsal rostral teeth	529.0	-4.97	<0.001	4-8	2-7
Ventral rostral teeth	948.0	-2.08	<0.050	0-4	0-5
Unfused rami	293.0	-6.60	<0.001	5-19	6-15
Fused rami	1,203.0	-0.32	n. s.	1-9	2-7
Appendix masculina spines	111.5	-1.81	n. s.	4-8	3-8
Total embryos	1.0	-2.52	<0.050	33-80	78-221

I constructed 2×2 contingency tables to test (1) carapace orientation (upturned or horizontal), (2) rostrum orientation (upturned or horizontal), and (3) placement of the second rostral tooth (anterior or posterior to the posterior margin of the ocular orbit) for *P. anthophilus* males vs females, *P. pedersoni* males vs females, and *P. anthophilus* vs *P. pedersoni* (sexes combined by species). The null model could not be rejected by any test involving carapace orientation ($\chi^2 = 0.04-1.98$, $P > 0.05$) or placement of the second rostral tooth ($\chi^2 = 0.16-2.35$, $P > 0.05$). The alternative model could be accepted in two analyses involving rostrum orientation ($\chi^2 = 0.36-1.17$, $P > 0.05$) but not in the third: *P. pedersoni* males vs females ($\chi^2 = 4.43$, $P < 0.05$). Horizontal rostrums seem less common in males of *P. pedersoni* than in females, confirming an original observation of Chace (1958). Carapace orientation is similar in the sexes, contradicting Chace's observation. Failure to reject the null model for position of the second dorsal rostral tooth (males vs females) is inconsistent with original descriptions of both species.

Log-linear models were used to test the null hypothesis of independence between location of the first dorsal rostral tooth relative to the hepatic spine, and between the relative locations of the rostrum and cornea (Table 4). Significant within-species differences disallowed the pooling of data for between-species assessment.

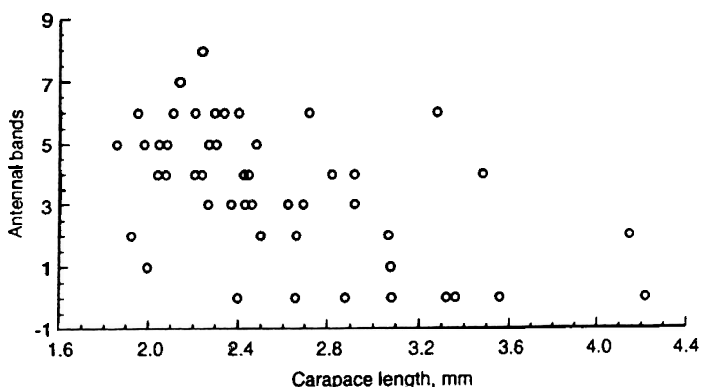


Fig. 1. *Periclimenes anthophilus*, scatterplot of antennal bands vs. carapace length (untransformed data). The negative trend indicates that the number of bands decreases with growth. Band counts and carapace length show significant correlation: Spearman's rank correlation test ($n = 61$, $r = -0.49$, $t_{59} = -4.31$, $P < 0.001$).

Table 4. Results of log-linear analyses (some discrete variables) with n for each sex shown in the columns. Numbers at tops of columns: first dorsal rostral tooth (1) anterior to, (2) even with, or (3) posterior to the hepatic spine, and rostrum (1) falls short of, (2) extends to, or (3) extends past the cornea.

Species	Sex	First dorsal rostral tooth vs. hepatic spine				Rostrum vs. cornea			
		1	2	3	Pearson's χ^2	1	2	3	Pearson's χ^2
<i>P. anthophilus</i>	M	8	6	5	0.81, P > 0.05	19	0	0	45.97, P < 0.001
	F	11	8	12	Fail to reject the null	1	0	30	Reject the null
<i>P. pedersoni</i>	M	15	3	0	10.10, P < 0.01	2	16	0	33.22, P < 0.001
	F	12	16	4	Reject the null	1	4	27	Reject the null

SOCIAL STRUCTURE.—I compared relative numbers of shrimp of each species per sea anemone and also looked for clumping patterns that might have indicated whether proportions of males and females differ by species. Relative numbers (41 anemones with 62 specimens of *P. anthophilus*, 11 anemones and one bivalve mollusk with 54 specimens of *P. pedersoni*) were assessed using an independent t-test (two-tailed). The dependent variable was number of shrimp per host divided casewise by the sum of n hosts: $t_{51} = -9.45$, $P < 0.001$. For *P. anthophilus*, mean = 0.038 (± 0.025). For *P. pedersoni*, mean = 0.375 (± 0.229). The distributions differed significantly (i.e., there were comparatively fewer specimens of *P. anthophilus* per host). I then constructed log-linear models and used Pearson's χ^2 to assess the null model of independence between relative numbers of males and females occupying a host. The species were tested separately. The null model could not be rejected for either ($\chi^2 = 37.88$ and 13.41, $df = 40$ and 11, $P > 0.05$), indicating independence in the relative numbers of males and females occupying an anemone and confirming indirectly the findings of Nizinski (1989) for *P. anthophilus*.

DISCUSSION

MORPHOLOGY.—Assessing a large array of morphological characters lessens the likelihood that different results might be obtained if additional characters are measured at some future time (Sneath and Sokal, 1973). In this study, raw data from 50 specimens each of *Periclimenes anthophilus* and *P. pedersoni* were collected in the form of 87 variables. The final analyses used 60 possible variables: ovigerous females, 59 variables (appendix masculina spines omitted); nonovigerous females, 57 variables (appendix masculina, embryo volume, total embryos omitted); males, 58 variables (embryo volume, total embryos omitted).

Only a few variables revealed potentially valid between-species differences: untransformed carapace length, the continuous variables in Table 2, and possibly four discrete variables in Table 3. Manipulating the discriminant analysis by forcing F_{enter} upward in stepwise increments yielded a changing mosaic of discriminatory variables retained in the model. No continuous variable evaluated proved reliably diagnostic of either species (i.e., none contributes uniquely to prediction of group membership). Embryo volume, although significantly different, was not retained in any of the models.

None of the between-species differences posited by Holthuis and Eibl-Eibesfeldt (1964) proved valid: pereopods 2 propodi of *P. pedersoni* are not proportionately narrower than those of *P. anthophilus*, nor is the carpus proportionately longer. Location of the first

dorsal rostral tooth with respect to the hepatic spine is a sexually dimorphic character in *P. pedersoni* (Table 4) but not in *P. anthophilus*. Holthuis and Eibl-Eibesfeldt did not draw a distinction between the major and minor pereopods 2 when referring to width of the propodus and length of the carpus. Chace (1972) interpreted their comments about carpus length to mean the major pereopod 2. The discriminant analysis tested proportionate carpus length both ways. Neither variable was retained in the model (i.e., the null could not be rejected).

Chace (1972) speculated that *P. pedersoni* might be smaller than *P. anthophilus*, but the reverse proved true in my samples. If the size disparity reported here is later shown not to have been an artifact, a weak argument can be made for retaining two species based on four discreet variables. These are listed in Table 3 as showing significance. All, however, correlate positively with carapace length and therefore are manifestations of growth. Thus, larger shrimp can be expected to have greater numbers of rostral teeth, more unfused rami of the antennular flagella, and even bigger brood masses.

ASSOCIATIONS.—*Periclimenes anthophilus* reportedly associates with the actinarian *Actinia bermudensis*, although only Holthuis and Eibl-Eibesfeldt (1964) seem to have observed it. The typical host of *P. anthophilus* is *C. gigantea* (Crawford, 1992; Levine and Blanchard, 1980; Nizinski, 1989; this report). As reviewed by Spotte (1996), *P. pedersoni* associates with a number of hosts, including *Aiptasia pallida* Verrill, 1864, *B. annulata*, *Bunodosoma granulifera* Lesueur, 1817, *C. gigantea*, *Heteractis lucida* Duchassaing and Michelotti, 1860, *Lebrunia danae* Duchassaing and Michelotti, 1860, an unidentified species of *Cerianthus* Chiaje, 1830, the rhizostome scyphozoan *Cassiopea xamachana* Bigelow, 1892, the bivalve mollusk *Lima scabra*, and the antipatharian *Antipathes pennacea* Pallas, 1766.

The fact that *P. anthophilus* apparently associates only with *C. gigantea* and never with *B. annulata* at Bermuda—but that *B. annulata* apparently is the preferred host of *P. pedersoni* in south Florida and the West Indies—has been mentioned as a suitable criterion for differentiation (Chace, 1972; Nizinski, 1989). No evidence, however, points to *P. anthophilus* having developed an exclusive affinity with *C. gigantea* as a consequence of reproductive isolation, nor has anyone tested for differences in the actual or potential hosts (i.e., examined the null hypothesis that the systematics of *B. annulata* and *C. gigantea* at Bermuda and in the West Indies are not significantly dissimilar). At minimum, such a test must show that any differences are unimportant from the standpoint of host selection by the shrimp. In sea anemones, huge genetic differences can exist among similar morphs (Monteiro et al., 1997).

Either of two hypotheses might explain the apparent obligate association of *P. anthophilus* with a single species of anemone. *Hypothesis 1*: If, in the western North Atlantic, *B. annulata* is genetically homogeneous but "*C. gigantea*" at Bermuda is different from *C. gigantea* elsewhere, then *P. anthophilus* has shifted to a new host (*sensu* Bush, 1975 and Feder et al., 1990), abandoned its previous facultative existence, and become an obligate symbiont of "*C. gigantea*." *Conclusion*: A host shift has occurred, and the apparent "host specificity" is positive evidence of ecological divergence. *Hypothesis 2*: If, in the western North Atlantic, *C. gigantea* is genetically homogeneous but "*B. annulata*" at Bermuda is different from *B. annulata* elsewhere, then *P. anthophilus* has retained one of its associations from the West Indies but become an obligate symbiont by not adapting to the different "*B. annulata*." *Conclusion*: A host shift has not occurred, and the apparent "host specificity" is negative evidence of ecological divergence.

Specimens of *P. anthophilus* kept alive in laboratory aquariums associated in <3 d with specimens of *C. gigantea* obtained at locations other than Bermuda. Bush (1975) noted that host shifts are most likely to occur when both hosts (old and new) occupy the range throughout which the symbiont (in Bush's example, a parasite) is dispersed. Host shifts precede speciation, and the confirmation of host shifting is not necessarily evidence that speciation has occurred.

BEHAVIOR, SOCIAL STRUCTURE, COLOR PATTERN.—Nizinski (1989) favored retention of species distinctions based on what she perceived to be important differences in host specificity, behavior on the host, social structure within aggregations of shrimp, and degree of dependence on "cleaning" of fishes. She proposed that *P. anthophilus* and *P. pedersoni* differ in numbers of individuals typically occupying an anemone, but without making a direct test of this hypothesis. Only data for *P. anthophilus* were presented. She nonetheless stated that the large group sizes in her study "were more common than implied in accounts of other species of *Periclimentes*." Findings here, in contrast, suggest a strongly clumped distribution for *P. pedersoni* in the Exuma Cays, unlike the more uniform distribution of *P. anthophilus* at Bermuda where 28 of 62 shrimp were observed alone on anemones.

Adequate experiments that might reveal different comparative social structures and use of space on the host have not been done. Stanton (1977) reported that *P. pedersoni* associating with *Lebrunia danae* at Grand Bahama were most often seen stationed to one side of the anemone or hovering over its fronds. Herrnkind et al. (1976), in discussing *L. danae* at the same location, wrote that *P. pedersoni* "typically stood on the substrate [sic] within a few cm of the anemone," although on other occasions the shrimp "rested atop the flattened, dichotomous fronds." Behavior was not quantified in either report. Nizinski (1989) cited these publications as evidence that *P. pedersoni* uses the space on its host differently than the *P. anthophilus* in her experiments, which roamed freely among the tentacles of their hosts. However, the host species in her experiments was *C. gigantea*, not *L. danae*. Different hosts might elicit different behaviors.

"Cleaning" behavior has been observed in both *P. anthophilus* (Sargent and Wagenbach, 1975) and *P. pedersoni* (review of Spotte, 1998). Nizinski (1989) suggested that *P. anthophilus* is a "facultative cleaner," a categorical term that is merely inclusive: in the western North Atlantic where no species of *Periclimentes* is known to be an obligate "cleaner" of fishes, the term might not even apply (Spotte, 1998). Nizinski offered by way of contrast the behavior of *P. pedersoni* as described by others. Laboratory studies have demonstrated that *P. pedersoni* spends <2% of its time at "cleaning" and "cleaning"-related activities (Jonasson, 1987), but these results were criticized by Wicksten (1995a). Nizinski's alternative suggestion was that *P. anthophilus* mimics other "cleaner" shrimp, although prospective candidates are not known to exist in Bermudan waters.

Knowlton (1993: table 1) listed *P. anthophilus* as a "sibling species" (presumably of *P. pedersoni*) and stated that its color pattern was different. A quantitative comparison has not, to my knowledge, been published. Color pattern might be a reliable taxonomic character in some snapping shrimps (Knowlton and Keller, 1985), but its usefulness for distinguishing closely related species of *Periclimentes* still awaits confirmation (Spotte et al., 1994).

Pigmentation increases with size in both *P. anthophilus* and *P. pedersoni* (Spotte, unpublished data), a characteristic of some other *Periclimentes* spp. (Nöel, 1983; Spotte et al., 1991). Specimens of *P. anthophilus* were less densely pigmented than *P. pedersoni* of

comparable size. Purplish areas on *P. anthophilus* sometimes tended toward rose; in *P. pedersoni*, the common trend was toward violet. The two specimens of *P. pedersoni* with banded antennae, however, more closely resembled *P. anthophilus* in color pattern. Specimens of *P. pedersoni* later collected in the lower Florida Keys were less densely pigmented than the Bahamian shrimp, their purplish areas were rosier, and most possessed banded antennae (Spotte, unpub. data). In terms of color pattern, the Florida Keys and Bermudan specimens were similar.

Criales (1984) and Stanton (1977) used the presence of bands on the antennal flagella to distinguish *P. anthophilus* (or *P. cf. anthophilus*) from *P. pedersoni* in the field, implying that *P. anthophilus* ranges beyond Bermuda. Even assuming *P. anthophilus* to be a valid species, antennal banding is unreliable by not being diagnostic. In their original description of *P. anthophilus*, Holthuis and Eibl-Eibesfeldt (1964) wrote: "In some specimens [sic] the antennae are completely white, but in others these white markings are interrupted by reddish violet zones." A half-tone photograph labeled *P. pedersoni* in Limbaugh (1961) and credited to F. M. Bayer shows a shrimp with banded antennae. The photograph was taken in the Florida Keys (F. M. Bayer, pers. comm., 13 August 1994). Specimens of *P. pedersoni* with red antennal bands have been reported from the Caribbean coast of Colombia (Criales, 1984), the west coast of Florida (Limbaugh et al., 1961), Florida Keys (Gwaltney and Brooks, 1994; this report), and Bahamas (Stanton, 1977; this report).

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