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Diversity and specificity of Caribbean sponge–zoanthid symbioses: a foundation for understanding the adaptive significance of symbioses and generating hypotheses about higher-order systematics

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The diversity and specificity of symbiotic associations may be useful in revealing the underlying ecology of symbioses and evolutionary relationships of symbiotic species. Symbioses between coral reef sponges and zoanthids are widespread and common in the greater Caribbean region, although the diversity and specificity of the species involved have only been explored at a few sites and the adaptive significance has only been examined for three combinations. We identified extensive diversity among sponges that associate with zoanthids by compiling sponge–zoanthid species associations from field surveys, the literature, and museum collections, and examined the patterns of specificity at multiple levels of sponge and zoanthid taxonomy. The results obtained indicate that facultative sponges are highly specific to the species of their partners whereas obligate zoanthids are not. The patterns of specificity among sponges and zoanthids suggest that many of these associations are not likely to be parasitic. Sponges harbouring photosynthetic endosymbionts associate at a disproportionately high frequency with zoanthids that harbour photosynthetic endosymbionts. Zoanthids embed in the surfaces of sponges to various degrees, resulting in a range of intimacy that negatively correlates with the number of hosts and polyp volume of zoanthids. Dendrograms based on the similarity among associations are largely consistent with current hypotheses of sponge higher-order systematics, but inconsistent with the current hypotheses of zoanthid systematics, and they highlight the potential utility of ecological characters in systematic analyses. © 2007 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2007, **92**, 695–711.

ADDITIONAL KEYWORDS: coral reefs – Demospongia – epibiont – Macrocnemina – mutualism – parasitism – photosynthetic endosymbionts – similarity analysis – symbiont intimacy – symbiont size.

INTRODUCTION

Two related aspects of symbiotic interactions that can contribute to our understanding of the ecology and evolution of symbiotic species are the diversity of species involved in symbiotic relationships and the specificity of those species to their symbiotic partners. Specificity in symbiotic associations can be examined at the level of less-inclusive clades (e.g. genotypes, ecotypes, or species) and at the level of more-inclusive clades (e.g. genera, families, or orders), with each level of analysis being useful for revealing different information about the ecology and evolution of symbioses. Examining specificity at the level of less-inclusive clades can give an indication of the adaptive significance of symbiosis and the mechanisms by which the association is mediated; for example, the specificity of gall forming wasps to distinct host trees suggests that biochemical interactions or other correlates of chemistry may be important to this parasitism (Abrahamson *et al*., 2003). Examining specificity at the level of more-inclusive clades may inform hypotheses about the evolutionary relationships of symbiotic species that cannot be inferred from other analyses; for example, different communities of gall-forming insects are associated with different hybrid species (Floate & Whitham, 1995) and clades of species (Abrahamson *et al*., 1998).

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Caribbean sponge–zoanthid associations provide a profitable system in which to study the diversity and specificity of symbioses because of the heterogeneity of species associations that suggest hypotheses about: (1) the adaptive significance of the symbioses and (2) the notoriously challenging (due to simple morphology) higher-level systematics of sponge and zoanthid taxa. Sponges (phylum Porifera, class Demospongiae), which perform unique functional roles in marine ecosystems independent of their symbionts, are known to form symbioses with a great diversity of taxa (Wulff, 2006). However, sponge symbioses with zoanthids (phylum Cnidaria, class Anthozoa, order Zoanthidea, suborder Macrocnemina) are among the most common and widespread. Sponge-symbiotic zoanthids can be found living on coral reef sponges throughout the tropics, and in the wider Caribbean region the incidence rates can be very high (i.e. all individuals in a host-sponge population may be associated with zoanthids; Crocker & Reiswig, 1981). However, the diversity of symbiotic species involved in sponge–zoanthid associations has only been reported from two locations, Puerto Rico (West, 1979) and Barbados (Crocker & Reiswig, 1981), with a combined total of 21 sponge and six zoanthid species.

The functional roles of sponge–zoanthid symbioses appear to vary with the particular species combination and the context of the interaction. Caribbean sponge-symbiotic zoanthids are obligate symbionts, although one species of zoanthid has been reported to rarely live on bare substratum (West, 1979; Crocker & Reiswig, 1981). Sponges are facultative hosts, although some sponges are only occasionally found without zoanthid symbionts (Crocker & Reiswig, 1981). Zoanthids live embedded, to various degrees, in the pinacoderm of sponges (West, 1979) and, in at least one species combination, the host coralline sponge physically reacts to the zoanthid by reorganizing skeletal elements around the base of polyps and coenenchyme (Willenz & Hartman, 1994). In another combination of species, the zoanthid appears to be effective in reducing spongivorous fish predation on a host sponge (West, 1976) but does not deter feeding by spongivorous seastars (Wulff, 1995) or deter nonspongivorous fish from feeding on pelleted sponge (and zoanthid) extracts (Pawlik *et al*., 1995). In a third combination of species, the zoanthid does not reduce spongivorous fish predation on the host, but may reduce water flow through the host (Lewis, 1982).

In the present study, we expand the diversity of species observed in sponge–zoanthid symbioses in the wider Caribbean to include a more than four-fold greater number of sponge species than previously reported, and use the observed specificity to less-inclusive clades to inform hypotheses about the adaptive significance of some species combinations, and the observed specificity to more-inclusive clades to inform hypotheses about the higher-order systematics of Demospongiae and Macrocnemina.

MATERIAL AND METHODS

To determine the diversity and specificity of sponge and zoanthid species involved in symbioses, we conducted roving diver surveys on coral reefs off of Holetown, Barbados (13°10′N, 59°38′W); Salisbury, Dominica (15°23′N, 61°25′W); Navassa Island, USA (18°24′N, 75°00′W); Bocas del Toro, Panama (9°16′N, 82°14′W; 9°19′N, 82°13′W; 9°20′N, 82°12′W; 9°21′N, 82°16′W); Charlotteville, Tobago (11°19′N, 11°18′W; 11°18′N, 60°30′W); and on hard bottom communities off of the gulf coast of Florida, USA (29°39′N, 84°22′W; 29°53′N, 84°32′W) and Georgia, USA (31°36′N, 80°47′W). Additional specimens were sampled from the live collections at Gulf Specimen Marine Laboratory in Panacea, Florida, USA. From 2002 to 2005, we collected small samples of each sponge species observed hosting a zoanthid and isolated spicules using the sodium hypochlorite centrifugation protocol of Rützler (1978). We identified sponge species by microscopic examination of spicules and skeletal architecture, and zoanthid species by colony and polyp morphology. Field survey data were supplemented with species combinations published in the sponge and zoanthid literature, and captured in the Porifera and Cnidaria collections of the United States National Museum of Natural History (USNM).

We ranked the degree that zoanthids embed in the surface of sponges from a combination of species descriptions (West, 1979), photographs and thin-sections loaned to us by Dr Henry Reiswig (University of Victoria), photographs and observations made during field surveys, and dissections of each zoanthid species sampled from associations with several different sponges.

We estimated the size of zoanthid polyps by calculating the volume of a cylinder using the length and diameter of the polyp column as reported by West (1979); except in the case of *Epizoanthus* sp. nov. *sensu* Crocker & Reiswig (1981) for which dimensions were estimated using the average diameter of polyps in histological preparations loaned to us by Dr Henry Reiswig and the length of the next largest zoanthid species (which is apparently much larger).

We assessed the similarity of sponge and zoanthid species in terms of their symbiotic associations by constructing similarity dendrograms based on the occurrences of their symbiotic partners, which we then compared with the recently published systematics of sponges and zoanthids to evaluate congruency between clades based on symbiotic associations and clades based on traditional taxonomy. We grouped sponges by their common zoanthid associations and zoanthids by their common sponge associations in distance analyses that are analogous to the hierarchical cluster analysis of Abrahamson *et al*. (1998). We created binary character matrices of the observed presence/absence of sponge and zoanthid taxa using MacClade, version 4.0 and treated the occurrence of species as characters in constructing similarity dendrograms.

Because zoanthid species associate with multiple sponge species, a small number of zoanthid 'characters' are sufficient to provide shared occurrences to calculate similarity. By contrast, each sponge species almost exclusively associates with a single zoanthid species and therefore zoanthids rarely share specific sponges, restricting our ability to estimate similarity by using sponge species as characters. The higher-level systematics of sponges provided additional shared characters to assess similarities among zoanthids (e.g. two zoanthid species may share a genus or family of sponge hosts). However, an individual association between a zoanthid and sponge may be represented in multiple hierarchical taxonomic levels and therefore the characters (taxa) will not all be independent. We mitigated the effects of non-independent characters by disregarding more-inclusive sponge taxa with character states identical to their less-inclusive taxa in order to retain unique shared characters from all taxonomic levels while eliminating repeated characters and provide a more conservative estimate of similarity. Similarity among sponge genera is based on six symbiotic-zoanthid species; and similarity among zoanthid species is based on 84 sponge taxa (species, genera, and families). We constructed similarity dendrograms in PAUP* 4.0b10 (Swofford, 2002) using minimum-evolution analyses with the total character difference as the distance criterion. Trees were found using a heuristic search algorithm, equal weight for all characters, and tree-bisection–reconnection branch swapping. Where computationally possible, we estimated support by 50 000 pseudoreplicates of nonparametric bootstrapping.

RESULTS

DIVERSITY

Ninety-two species of sponges (Table 1) and six species of zoanthids [*Epizoanthus cutressi* West, *Epizoanthus* sp. nov. *sensu* Crocker & Reiswig (1981), *Parazoanthus catenularis* (Duchassaing & Michelotti), *Parazoanthus parasiticus* (Duchassaing & Michelotti), *Parazoanthus puertoricense* West, and *Parazoanthus swiftii* (Duchassaing & Michelotti)] were observed associated with sponges in the wider Caribbean region.

SPECIFICITY TO LESS-INCLUSIVE CLADES AND THE ADAPTIVE SIGNIFICANCE OF SYMBIOSES

The surveys of zoanthid and sponge species combinations revealed that most sponge species host a single species of zoanthid, a few host two, and none host more. Zoanthid species were observed to associate with as few as three and as many as 51 different species of sponges (Table 1).

At least nine species of host-sponges have photosynthetic endosymbionts (cyanobacteria or dinoflagellates) and three species of symbiotic-zoanthids have photosynthetic dinoflagellates (Table 1). The occurrence of zoanthid and sponge species combinations in which both partners either have or do not have photosynthetic endosymbionts outnumbered combinations in which only one partner had photosynthetic endosymbionts 55–20. A contingency table of the numbers of observed species-combinations in which partners have and do not have photosynthetic endosymbionts (Table 2) demonstrates that the occurrence of photosynthetic endosymbionts in sponge–zoanthid associations are not independent ($G = 20$, d.f. = 1, $P < 0.001$). Additionally, the specificity of sponges with photosynthetic endosymbionts to zoanthids with photosynthetic endosymbionts is almost absolute, whereas the specificity of zoanthids with photosynthetic endosymbionts to sponges with photosynthetic endosymbionts is much less strict (Table 2).

The various degrees that zoanthids embed in the surface of sponges results in a wide range in intimacy of associations, from species that live entirely on the surface of sponges to species that live completely beneath the surface of sponges (Fig. 1A). The degree that zoanthids live embedded in sponges is inversely correlated (Kendall's rank correlation: $\tau = 0.966$, d.f. = 5, $P = 0.013$) with number of host-sponge species observed for each zoanthid (Fig. 1B) (i.e. zoanthids that live deeply embedded in sponges have few hosts, and zoanthids that live on the surface of sponges have many hosts). The degree that zoanthid colonies are embedded in sponges is also inversely correlated (Kendall's rank correlation: $\tau = 0.929$, d.f. = 5, $P = 0.019$) with the volume of zoanthid polyps (Fig. 1C) (i.e. zoanthids that live deeply embedded in sponges have smaller polyp volumes, and zoanthids that live on the surface of sponges have larger polyp volumes).

SPECIFICITY TO MORE-INCLUSIVE CLADES AND SIMILARITY AMONG ASSOCIATIONS

Sponge species associate with only one or two zoanthid species. When sponges associate with two zoanthids, the zoanthids tend to be congeners; with the exception of two sponge species (*Cribrochalina*

Table 1. Symbiotic associations of sponge and zoanthid species

	P. c.[a]	*P. pa.*[a]	*P. pu.*	*P. s.*	*E. c.*[a]	***E.* sp. nov.**
Homosclerophorida						
Plankinidae						
Plakortis angulospiculatus (Carter)						6
Plakortis zyggompha (de Laubenfels)						6
Plakortis sp.						C&R
Hadromerida						
Clionaidae						
Cliona aprica Pang[b]		(Z&W)				
Cliona caribbaea Carter[b]		PA, 4, USNM-31605				
Cliona celata Grant		USNM-39614				
Cliona delitrix Pang		C&R, 4, 5, USNM-49564				
Cliona lampa de Laubenfels		USNM-32890				
Cliona tenuis Zea & Weil		(Z&W)				
Cliona varians (Duchassaing & Michelotti)[b]		HI, USNM-48485				
Cliona cf. *vermifera*		4				
Cliona spp.		WE, USNM-34200				
Spheciospongia vesparium (Lamark)[b]		WE, 2, USNM-32955				
Spirastrellidae						
Spirastrella cf. *coccinea*		2				
Poecilosclerida						
Microcionina						
Acarnidae						
Acarnus annominatus Gray				C&R		
Damiria sp.				C&R		
Microcionidae						
Clathria (Axosuberites) obliqua (George & Wilson)				USNM-33445		
Clathria (Axosuberites) sp.				USNM-33389		
Clathria (Clathria) prolifera (Ellis & Solander)				7, 8		
Clathria (Microciona) spinosa (Wilson)				USNM-33375		

Table 1. *Continued*

	P. c.[a]	*P. pa.*[a]	*P. pu.*	*P. s.*	*E. c.*[a]	***E.* sp. nov.**
Clathria (Microciona) spp.				C&R, USNM-49156		
Clathria (Thalysias) juniperina (Lamarck)				WE, 5, USNM-31497		
Clathria (Thalysias) schoenus (de Laubenfels)				1		
Clathria (Thalysias) cf. *schoenus*				1		
Clathria (Thalysias) vasiformis (de Laubenfels)				USNM-48219		
Clathria spp.				3, USNM-48224		
Raspailiidae						
Ectyoplasia ferox (Duchassaing & Michelotti)				C&R		
Endectyon (Hemectyon) pearsei (Wells & Wells)				USNM-32183		
Thrinacophora funiformis Ridley & Dendy				USNM-1084839		
Myxillina						
Desmacididae						
Desmapsamma anchorata (Carter)				C&R, 2, 5		
Iotrochotidae						
Iotrochota birotulata (Higgin)				WE, 1–5, USNM-31599		
Iotrochota cf. *birotulata*				4		
Iotrochota imminuta Pulitzer-Finali				(P)		
Tedaniidae						
Tedania (Tedania) ignis (Duchassaing & Michelotti)				1		
Mycalina						
Desmacellidae						
Biemna sp.				USNM-49089		
Halichondrida						
Axinellidae						
Axinella corrugata (George & Wilson)				USNM-39875		

Table 1. *Continued*

	P. c.[a]	*P. pa.*[a]	*P. pu.*	*P. s.*	*E. c.*[a]	***E.* sp. nov.**
Axinella meandroides Alvarez, van Soest & Rützler				(A) USNM-42800		
Axinella polycapella de Laubenfels				7		
Axinella waltonsmithi (de Laubenfels)				USNM-32202		
Axinella sp.				USNM-48017		
Dragmacidon reticulata (Ridley & Dendy)				(A), USNM-34155		
Dragmacidon lunecharta (Ridley & Dendy)				(P)		
Dragmacidon sp.				(NMNH-48262)		
Ptilocaulis walpersi (Duchassaing & Michelotti)				1		
Desmoxyidae						
Higginsia striglata (Lamarck)				USNM-33246		
Higginsia sp.				USNM-1015523		
Dictyonellidae						
Dictyonella cf. *madeirensis*				USNM-1084838		
Svenzea zeai (Alvarez, van Soest, & Rützler)[c]			R, 2, 3, 4, USNM-42805			
Halichondriidae						
Epipolasis spp.				C&R, USNM-39378		
Hymeniacidon spp.			C&R, USNM-32321	C&R		
Topsentia bahamensis Diez, Pomponi, & van Soest				(D)		
Topsentia ophiraphidites (de Laubenfels)				1, 3 (D)		
Topsentia cf. *ophiraphidites*				1		
Topsentia spp.				2, 3, 4, USNM- 31606		
Agelasida						
Agelasiidae						

Table 1. *Continued*

	P. c.[a]	*P. pa.*[a]	*P. pu.*	*P. s.*	*E. c.*[a]	***E.* sp. nov.**
Agelas dispar Duchassaing & Michelotti			USNM-32345	2, 4		
Agelas clathrodes (Schmidt)				3		
Agelas conifera (Schmidt)			2, 4, USNM-31830			
Agelas inaequalis Pulitzer-Finali				(P)		
Agelas sceptrum (Lamark)			4			
Agelas sventres Lehnert & van Soest			(L&S)	3		
Agelas tubulata Lehnert & van Soest				(L&S)		
Agelas spp.			WE, C&R, 2, 3, 5	C&R, 2, 3		
Astroscleridae						
Stromatospongia vermicola Hartman			WE			
Haplosclerida						
Haplosclerina						
Callyspongiidae						
Callyspongia (Cladochalina) amigera (Duchassaing & Michelotti)		(P), 1				
Callyspongia (Cladochalina) vaginalis (Lamark)		WE, 1, 2, 6, USNM-31519				
Callyspongia (Cladochalina) villosa (Pallas)		USNM-31532				
Callyspongia spp.		C&R, USNM-31842				
Chalinidae						
Haliclona virdis (Duchassaing & Michelotti)		USNM-50286				
Haliclona sp.		USNM-49737				
Niphatidae						
Cribrochalina vasculum (Lamark)[b]	(WI), 4, 5,				4, 5	
Cribrochalina dura (Wilson)[b]	3, USNM-31601				2, 4, USNM-31608	
Niphates digitalis (Lamarck)		H, 2, 4, USNM-32233				
Niphates caycedoi (Zea & van Soest)		1				

Table 1. *Continued*

	P. c.[a]	*P. pa.*[a]	*P. pu.*	*P. s.*	*E. c.*[a]	***E.* sp. nov.**
Niphates erecta Duchassaing & Michelotti		C&R, 1–5, USNM-31900				
Petrosina						
Petrosiidae						
Neopetrosia proxima (Duchassaing & Michelloti)	(C), 1, 2	1				
Neopetrosia subtriangularis (Duchassaing)[b]	(S), 1, 2					
Petrosia pellasarca (de Laubenfels)	(Z), 2					
Petrosia weinbergi van Soest	(S)					
Petrosia sp.	3, 5					
Xestospongia deweerdtae Lehnert & van Soest	(S&W)					
Xestospongia dominicana Pulitzer-Finali	(P)					
Xestospongia muta (Schmidt)[b]	WE, 4, USNM 41535				WE	
Xestospongia rampa (de Laubenfels)	(L&S)					
Xestospongia rosariensis Zea & Rützler[b]	1	1				
Xestospongia spp.	C&R, WE, USNM 32338				C&R, WE	
Calcifibrospongiidae						
Calcifibrospongia actinostromarioides Hartman					(W&H)	

Sponges arranged into higher taxa according to Systema Porifera (Hooper & van Soest, 2002a). Sponge–zoanthid species combinations culled from the literature are listed by author and designated by a letter (A, Alvarez, van Soest & Rützler, 1998; C, Campos *et al*., 2005; C&R, Crocker & Reiswig, 1981; D, Diaz, Pomponi & van Soest, 1993; HI, Hill, 1998; L&S, Lehnert & van Soest, 1996; PA, Pang, 1973; P, Pulitzer-Finali, 1986; R, Rützler, van Soest & Alvarez, 2003; S, van Soest, 1980; S&W, van Soest & de Weerdt, 2001; WE, West, 1979; WI, Wiedenmayer, 1977; W&H, Willenz & Hartman, 1994; Z, Zea, 1987; Z&W, Zea & Weil, 2003), combinations observed in the field are listed by geographical location designated by a number (1, Panama; 2, Dominica; 3, Tobago; 4, Navassa Island; 5, Barbados; 6, Florida; 7, Gulf Specimen Marine Laboratory; 8, Grey's Reef National Marine Sanctuary), and combinations observed in the collections of the USNM are designated by their museum specimen numbers. Parenthetical entries are our estimation of the zoanthid species identities from sources where the sponge species are expertly identified, but zoanthid species are incompletely described. The presence of photosynthetic endosymbionts in zoanthids or sponges is listed by publication designated by superscript letters after species names ([a]West, 1979; [b]Vicente, 1990; [c]Rützler *et al*., 2003).

E. c., *Epizoanthus cutressi* West; ***E.* sp. nov.**, ***Epizoanthus* sp. nov.** *sensu* Crocker & Reiswig (1981); *P. c.*, *Parazoanthus catenularis* (Duchassaing & Michelotti); *P. pa.*, *Parazoanthus parasiticus* (Duchassaing & Michelotti); *P. pu.*, *Parazoanthus puertoricense* West; *P. s.*, *Parazoanthus swiftii* (Duchassaing & Michelotti).

Table 2. Contingency table of associations of zoanthid species with and without photosynthetic endosymbionts by sponge species with and without photosynthetic endosymbionts

	Zoanthid photosynthetic endosymbionts	
Sponge photosynthetic endosymbionts	Symbionts reported	No symbionts reported
Symbionts reported	13	1
No symbionts reported	19	42

Only sponges that could be identified to species were included.

vasculum and *Cribrochalina dura*) that associate with zoanthids that represent separate genera and families (Table 1).

Zoanthids colonize 3–51 different species of sponges and each zoanthid species colonizes a different taxonomic scope of sponges, ranging from specialists of a single sponge genus to more diffuse associations with several different sponge orders (Table 1). A *G*-test of the number of species combinations in a zoanthid-species by sponge-order contingency table (Table 3) demonstrates that zoanthid symbioses are not independent of sponge ordinal level systematics ($G = 122$, d.f. = 25, $P << 0.001$) and each zoanthid species is restricted to a limited portion of the Caribbean sponge diversity.

Similarity dendrograms were used to group sponges and zoanthids based on the occurrence of their symbiotic partners. The dendrogram of sponge genera was constructed using six zoanthid species as characters and is the strict consensus of the 500 000 best trees. This analysis distinguished four clusters of sponge genera (Fig. 2) that closely correspond to the taxonomic orders of sponges as defined by Systema Porifera (Hooper & van Soest, 2002a): (1) Hadromerida with Haplosclerida (suborder Haplosclerina without genus *Cribrochalina*); (2) Haplosclerida (suborder Petrosina with the addition of *Cribrochalina*); (3) Poecilosclerida and Halichondrida (without genera *Svenzea* and *Hymeniacidon*); and (4) Agelasida (with Halichondrida genera *Svenzea* and *Hymeniacidon*). The genus *Plakortis* (order Homosclerophorida) was assigned to the outgroup because of independent data that suggest that Homosclerophorida are different from all other orders of Demospongiae (Muricy & Díaz, 2002; Boury-Esnault, 2006).

The dendrogram of zoanthid species was constructed using 84 sponge-host taxa (species, genera, and families) and is the single best tree. Mitigating the effects of non-independent characters had no effect on the resulting topology of the zoanthid dendrogram, the identical topology was found if only species were included or if all 140 taxa ranging from species to orders were included. This analysis distinguished three clades of zoanthid species by their sponge-host taxa (Fig. 3): (1) *P. swiftii* with *P. puertoricense*; (2) *E. cutressi* with *P. catenularis*; and (3) *P. parasiticus* basal to the *E. cutressi* and *P. catenularis* group. *Epizoanthus* sp. nov. was assigned to the outgroup because it shares no sponge-host taxon below the level of class with any other zoanthid species.

DISCUSSION

DIVERSITY

Sponge species associated with zoanthids represent nearly half (six out of 14) of the extant orders of Demospongiae (Hooper & van Soest, 2002a) and 14% of the total described sponge species diversity of the region (640 sponge species from all depths and habitats within the Caribbean region; van Soest, 1994). The six sponge-associated zoanthid species constitute all of the previously reported Caribbean sponge-symbiotic zoanthids (Crocker & Reiswig, 1981).

SPECIFICITY TO LESS-INCLUSIVE CLADES AND THE ADAPTIVE SIGNIFICANCE OF SYMBIOSES

Sponges are highly specific to zoanthid species and zoanthids are not specific to sponge species. The disparity between the specificity of facultative sponges and the specificity of obligate zoanthids suggests that zoanthids can obtain the benefit that they derive from associating with sponges from any of several different sponge species whereas the costs or benefits that sponges derive from associating with zoanthids are more particular, regardless of the exact effects of symbiosis on sponges.

In a distinct pattern that cuts across sponge and zoanthid taxonomic groups, sponges that host photosynthetic endosymbionts are almost exclusively associated with zoanthid species that also host photosynthetic endosymbionts (Table 2). The high degree of specificity of sponges to zoanthids with photosynthetic endosymbionts suggests a shared strategy for maximizing exposure to sunlight or more complex interactions between hosts and the endosymbionts of zoanthids (e.g. Saffo, 1990) or between sponge and zoanthid endosymbionts. The high degree of specificity of sponges to zoanthids with photosynthetic endosymbionts is in contrast to the lack of specificity of zoanthids to sponges with photosynthetic endosymbionts. Slightly more than half of the species combinations in which zoanthids host photosynthetic endosymbionts are with sponges that do not

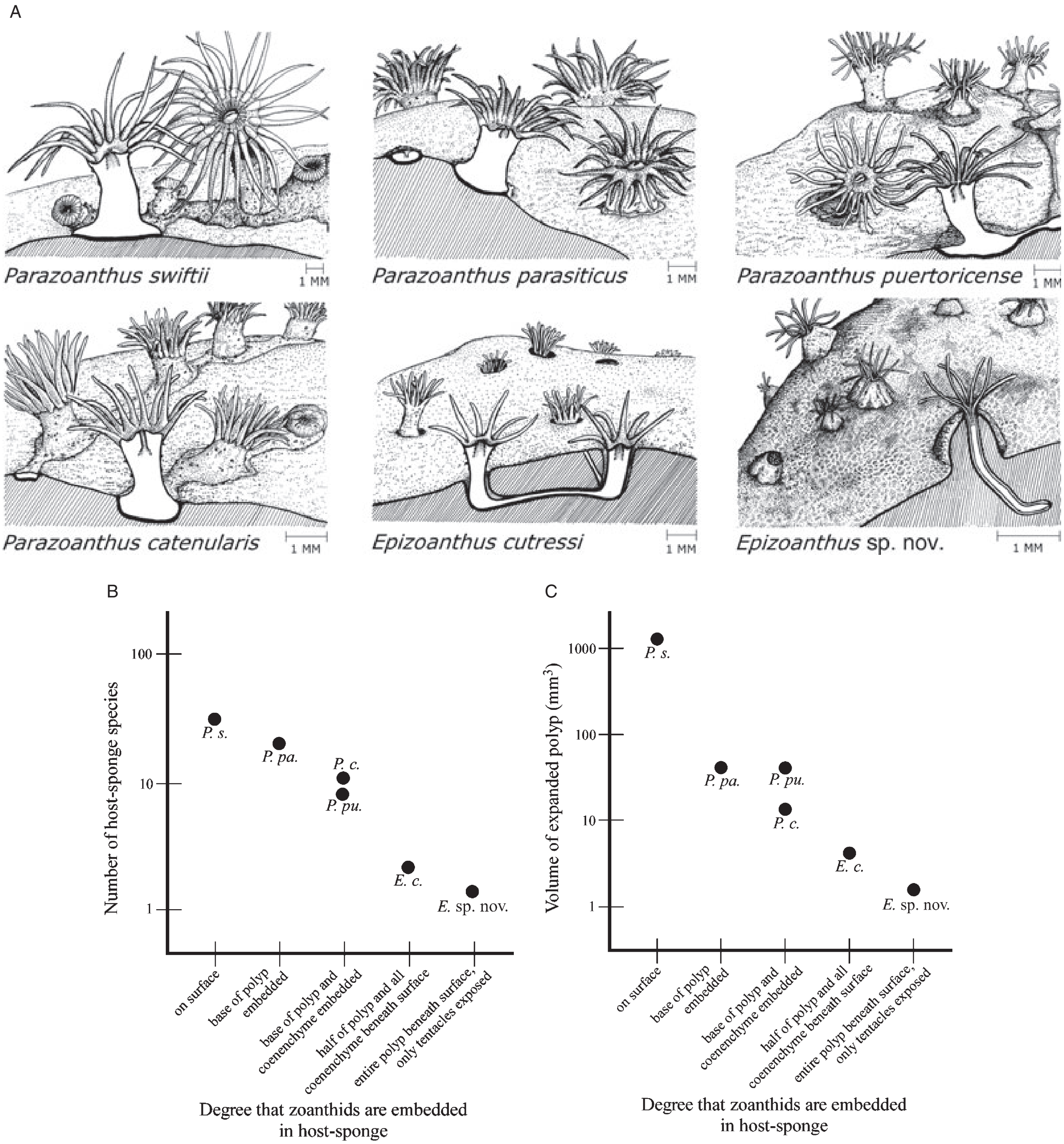

Figure 1. A, line drawings of symbiotic-zoanthids showing the degree that each species embeds in host sponges (intimacy). Species arranged according to the intimacy of the associations. Drawings by J. Putnam H. of Florida State University. B, Correlation between the degree that zoanthids embed in sponges and the number of host-sponge species. C, correlation between the degree that zoanthids embed in sponges and the volume of expanded zoanthid polyps. *E. c.*, *Epizoanthus cutressi* West; ***E.* sp. nov.**, ***Epizoanthus* sp. nov.** *sensu* Crocker & Reiswig (1981); *P. c.*, *Parazoanthus catenularis* (Duchassaing & Michelotti); *P. pa.*, *Parazoanthus parasiticus* (Duchassaing & Michelotti); *P. pu.*, *Parazoanthus puertoricense* West; *P. s.*, *Parazoanthus swiftii* (Duchassaing & Michelotti).

Table 3. Contingency table of observed symbiotic associations arranged by zoanthid species and sponge order

	Zoanthid species					
Sponge orders	*Parazoanthus catenularis*	*Parazoanthus parasiticus*	*Parazoanthus puertoricense*	*Parazoanthus swiftii*	*Epizoanthus cutressi*	***Epizoanthus* sp. nov.**
Homosclerophorida						3
Hadromerida		12				
Poecilosclerida				23		
Halichondrida			3	21		
Agelasida			7	7		
Haplosclerida	14	12			6	

(Table 2), suggesting that (in at least some species combinations) matching ecological strategies is not crucial for zoanthids to be successful symbionts of sponges.

Caribbean sponge-symbiotic zoanthids are obligate symbionts and therefore must receive some net benefit from forming associations with sponges. Sponges are facultative hosts of zoanthids and previous research has indicated that the relationships may include mutualisms (West, 1976) and parasitisms (Lewis, 1982; Willenz & Hartman, 1994). Zoanthids appear to be able to successfully associate with many species of sponges, whereas sponges are quite specific about which zoanthid species are acceptable partners and about matching the presence of photosynthetic endosymbionts with their zoanthid partners. Disparity between the relative specificity of hosts and symbionts is common and, at least in mutualistic symbioses, generally in favour of higher relative specificity of hosts for their symbionts (Smith & Douglas, 1987). Reviews of specificity data by other authors have suggested a general trend for parasites to be highly specific (Adamson & Caira, 1994), mutualists to not be highly specific (Hoeksema & Bruna, 2000), and parasites to be relatively more specific than mutualists (Law, 1985; Smith, 1992). The low degree of specificity of most zoanthid species to sponges and the disparity between the relative specificity of zoanthids and sponges suggest that most sponge–zoanthid symbioses are not likely to be parasitic associations; however, specificity can be determined by several other factors (e.g. Desdevises, Morand, & Legendre, 2002) and may be influenced by relative intimacy and size of zoanthids. The net outcomes of the actual interactions between sponges and zoanthids remain to be tested experimentally, but perhaps the associations at the extremes of specificity represent good comparisons with which to start.

Specificity among zoanthids positively correlates with the degree that zoanthids embed in the surface of sponges and negatively correlates with polyp size. The hypothesis that we favour for this pattern is that the degree that zoanthids embed in sponges restricts the number of hosts (i.e. symbionts with more intimate relationships have fewer hosts; Borowicz & Juliano, 1991) and the relative size of polyps (i.e. deeply embedded zoanthids occupy space within sponges and smaller zoanthids may require less reorganization of sponge skeletal elements). However, the alternative hypothesis that polyp size determines the number of hosts (i.e. large polyps may be better at adapting to novel hosts) and dictates the degree that zoanthids can embed in the surface of sponges (i.e. large polyps cannot embed in the surface of hosts) appears equally parsimonious.

The direct physical and chemical interactions between zoanthids and sponges have received little attention (but see Crocker & Reiswig, 1981; Willenz & Hartman, 1994); however, the interaction probably involves traits that are neither simple nor interchangeable for use with unfamiliar hosts and therefore restrict zoanthid species to groups of similar sponges. Host-specific traits involved in zoanthid-sponge symbioses may include traits that control recognition of hosts (larval chemotaxis), traits that control colonization of hosts (cell-surface structure and biochemistry), and traits that control the persistence of the symbiosis, regardless of the specific effects on sponges or zoanthids.

There are rare examples of nonspecific associations by *P. swiftii* with sponges that are not typical *P. swiftii* hosts (e.g. *Callyspongia* sp.), with sponges that are not normal hosts of any zoanthid [e.g. *Aplysina longissima* (Carter)], and of bare substratum (Crocker & Reiswig, 1981). Nonspecific associations seem to be possible because of the apparently unique ability of *P. swiftii* to migrate between adjacent hosts (Crocker & Reiswig, 1981). However, because nonspecific associations are almost always observed when a typical host of *P. swiftii* (usually *Iotrochota birotulata*) is adherent to the unusual host (Crocker & Reiswig,

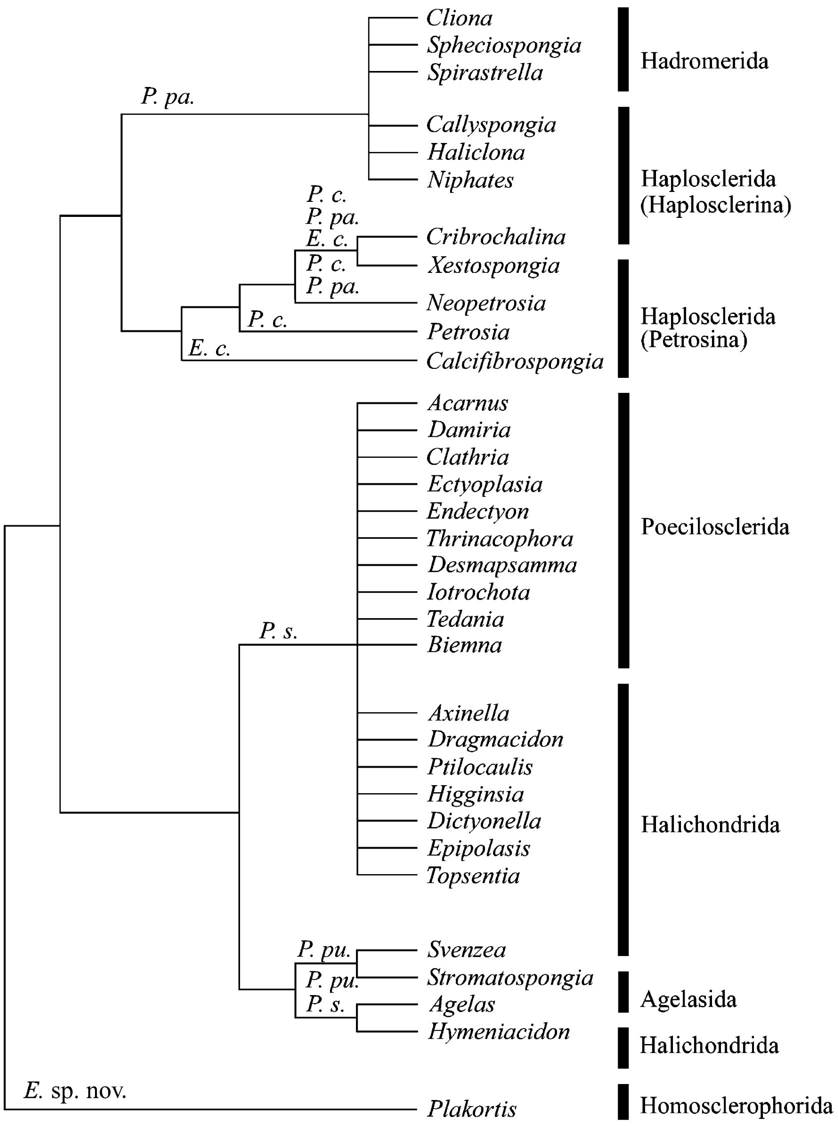

Figure 2. Sponge genera clustered by similarity of zoanthid symbioses. Similarity dendrogram of sponge genera based on binary presence/absence data for six zoanthid species and is the strict consensus of the 500 000 best trees. Zoanthid species abbreviations shown over branches of host-sponge clades. *E. c.*, *Epizoanthus cutressi* West; ***E.* sp. nov.**, ***Epizoanthus* sp. nov.** *sensu* Crocker & Reiswig (1981); *P. c.*, *Parazoanthus catenularis* (Duchassaing & Michelotti); *P. pa.*, *Parazoanthus parasiticus* (Duchassaing & Michelotti); *P. pu.*, *Parazoanthus puertoricense* West; *P. s.*, *Parazoanthus swiftii* (Duchassaing & Michelotti).

1981), these associations may represent ephemeral expansions of a colony that are not independently viable.

The only other group of symbiotic zoanthids for which host/symbiont specificity data are available are the deep-sea zoanthid-pagurid crab symbioses. The patterns of specificity observed in the crab–zoanthid symbioses are the opposite of the sponge–zoanthid symbioses in that the zoanthids are relatively specific to crab species and crabs are less specific to zoanthid species (Ates, 2003: table 1). The relatively low specificity of crabs to zoanthids may reflect the less intimate associations between pagurid crabs and their symbiotic-zoanthids which live on the surface of occupied gastropod shells, replace the shell with a carcinoecium, or are held near the carapace (with modified limbs) of crab-hosts. The relatively high specificity of zoanthids to pagurid crabs may also reflect host behaviour-mediated mating opportunities that result from associations with mobile deep-sea crabs (similar examples are reviewed in Williams & McDermott, 2004).

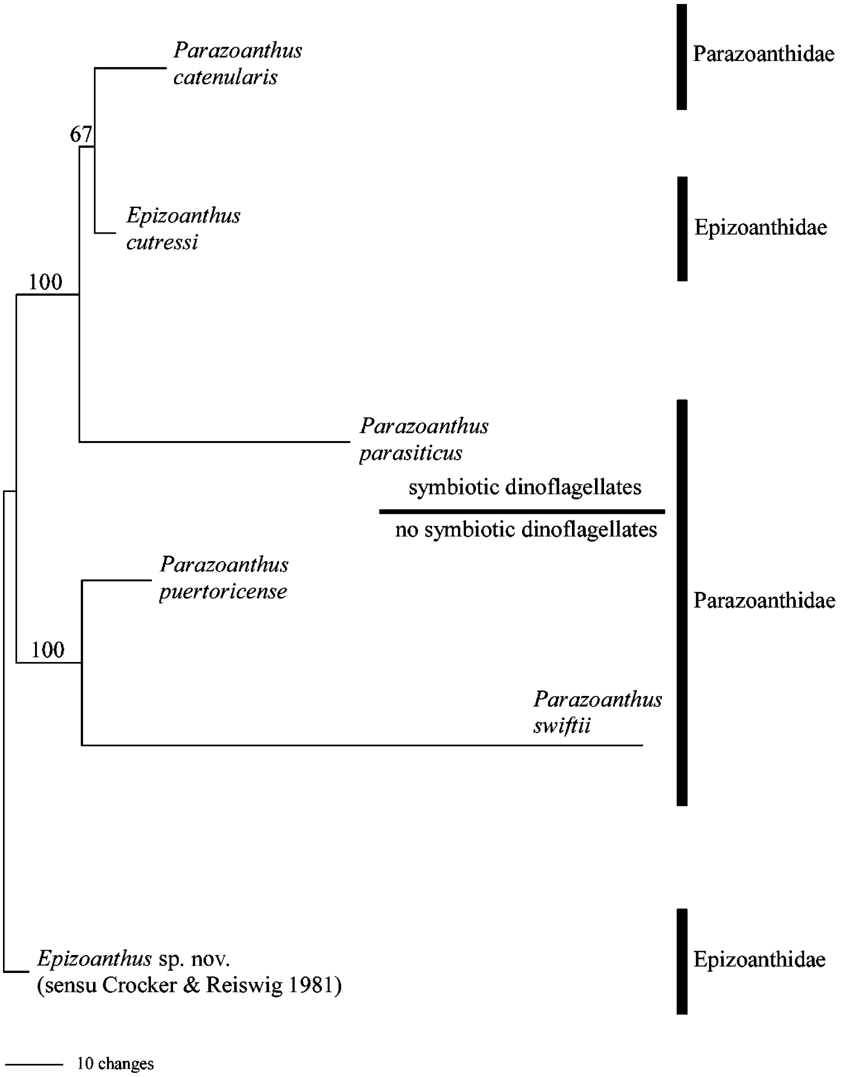

Figure 3. Zoanthid species clustered by similarity of sponge symbioses. Similarity dendrogram of zoanthid species based on binary presence/absence data for 84 unique sponge taxa (species, genera, and families) and is the single best tree with estimates of branch support calculated by 50 000 pseudoreplicates of nonparametric bootstrapping.

SPECIFICITY TO MORE-INCLUSIVE CLADES

The diversity of zoanthids associated with any one sponge species is restricted by the relatively high specificity of sponges to zoanthids; however, when a sponge species is observed to associate with two different zoanthid species, they are usually congeneric. Closely-related sponges were also observed to associate with zoanthids that are congeneric, both in this and in previous morphological (Duerden, 1898; West, 1979) and molecular (Sinniger *et al.*, 2005) studies. The only apparently distantly related zoanthids (from different genera and families) that we observed associated with a single sponge species are *P. catenularis* and *E. cutressi*.

The relatively diffuse specificity of zoanthids allows a high diversity of sponges to associate with individual zoanthid species. Each zoanthid species associates with a different taxonomic level of sponges, ranging from zoanthids that specialize on one sponge genus to zoanthids that specialize on several sponge orders (Table 1).

SIMILARITY AMONG ASSOCIATIONS AND IMPLICATIONS FOR SPONGE SYSTEMATICS

Although the grouping of sponges by their symbiotic associations (Fig. 2) is not a representation of phylogenetic relatedness *per se*, patterns of similar associations are almost perfectly congruent with the currently accepted systematics of sponges (Hooper & van Soest, 2002a) that are based on shared morphology, chemistry, cytology, or development. In addition, the few instances where the similarity of zoanthid symbioses differ from the current sponge systematics involve taxa in which there are documented uncertainties (discussed below) with respect to their systematic position; suggesting that zoanthid-symbioses may be informative for sponge systematics.

Zoanthid species distinguish between order Haplosclerida suborder Petrosina (with genus *Cribrochalina*) and orders Hadromerida and Haplosclerida suborder Haplosclerina (without genus *Cribrochalina*; Fig. 2). The concept of order Haplosclerida has undergone repeated revisions but, in the most recent configuration, this order encompasses two marine suborders: Haplosclerina and Petrosina (Hooper & van Soest, 2002b). The two suborders are distinguished by viviparous reproduction and an 'organized' ectosomal skeleton in Haplosclerina, and oviparous reproduction and a 'confused' ectosomal skeleton in Petrosina (Hooper & van Soest, 2002b). It has been suggested (Hooper & van Soest, 2002b; McCormack, Erpenbeck & van Soest, 2002) that reproduction and skeletal organization may be poor characters for distinguishing between Haplosclerina and Petrosina because each character is found in other distantly related sponges, the descriptions of skeletal characters are considered 'vague', and the suborders are not distinguished by chemical or molecular data. Similarly, genus *Cribrochalina* has had a controversial history and the current systematic position of this genus remains tentative (Desqueyroux-Faúndez & Valentine, 2002). *Cribrochalina* was previously thought to be allied with suborder Petrosina; however, the current systematics places *Cribrochalina* in suborder Haplosclerina (with the caveat that some *Cribrochalina* species may more closely fit the concept of suborder Petrosina: Desqueyroux-Faúndez & Valentine, 2002). *Cribrochalina dura* and *C. vasculum* host both *P. catenularis* and *E. cutressi*, which only associate with sponges in the suborder Petrosina (with the exception of *Cribrochalina*). The specialization of *P. catenularis* and *E. cutressi* to sponges of suborder Petrosina supports the hypothesis that *C. dura* and *C. vasculum* also belong in suborder Petrosina, and supports the hypothesis of two marine suborders in order Haplosclerida (i.e. suborder Haplosclerina is exclusively associated with *P. parasiticus* and sponges of suborder Petrosina are the only hosts of *P. catenularis* and *E. cutressi*).

Zoanthid species also distinguish between order Agelasida (with order Halichondrida genera *Svenzea* and *Hymeniacidon*) and orders Poecilosclerida and Halichondrida (excluding *Svenzea* and *Hymeniacidon*; Fig. 1). The taxonomic history of all three orders contains controversial reorganizations, with order Agelasida generally considered to be part of order Poecilosclerida until 1980 (van Soest & Hooper, 2002a), and recent molecular and chemical evidence suggesting that parts of order Halichondrida are most closely related to species in order Agelasida (Borchiellini *et al*., 2004; Erpenbeck, Breeuwer & van Soest, 2005a, b; Nichols, 2005; Erpenbeck *et al*., 2006; van Soest & Hooper, 2002b). The specificity of zoanthids supports the hypothesis that parts of order Halichondrida (genera *Svenzea* and *Hymeniacidon*) are more closely related to species of order Agelasida (hosts of *P. puertoricense* and *P. swiftii*), but does not distinguish between orders Poecilosclerida and Halichondrida (exclusively hosting *P. swiftii*).

SIMILARITY AMONG ASSOCIATIONS AND IMPLICATIONS FOR ZOANTHID SYSTEMATICS

The associations of zoanthids with particular sponges have historically been used to inform zoanthid systematics because of the depauperate morphological character set of zoanthids; for example, Pax & Müller (1962) define the subspecies of *Parazoanthus axinellae* by the frequency of colonization of sponges in the genus *Thenea*. Recent molecular phylogenetics (Sinniger *et al*., 2005) also suggests that patterns of host taxa associations are informative for zoanthid systematics.

Sponge taxa distinguish between clades of zoanthid species (*P. swiftii* with *P. puertoricense*, and *P. parasiticus* basal to *E. cutressi* and *P. catenularis*), dividing the zoanthids by species that host endosymbiotic dinoflagellates and species that do not (Fig. 2). The grouping of *E. cutressi* with species of genus *Parazoanthus* is not congruent with the current morphology-based taxonomy, which arranges genera *Epizoanthus* and *Parazoanthus* into separate sister families (Epizoanthidae and Parazoanthidae) within the zoanthid suborder Macrocnemina (Ryland & Muirhead, 1993). There is molecular evidence that the genus *Parazoanthus* may be paraphyletic; however, genus *Epizoanthus* and families Epizoanthidae and Parazoanthidae are apparently monophyletic (Sinniger *et al*., 2005). The zoanthid species included in the analysis of Sinniger *et al*. (2005) included examples of species with similar hosts across genera within family Parazoanthidae, but species with different hosts (or species which are asymbiotic) across families. If symbioses are informative about evolutionary relationships, then the diversity of symbioses sampled by Sinniger *et al*. (2005) would inadvertently bias the results to find monophyletic families and hide mixed family clades defined by their symbioses. The similarity of sponge-hosts of *E. cutressi* and *P. catenularis* support the hypothesis that genus *Parazoanthus* is paraphyletic, but also suggests novel hypotheses that genus *Epizoanthus* and the families Epizoanthidae and Parazoanthidae may be paraphyletic as well.

CONCLUSIONS

This study compiles data collected over 4 years of field surveys of the wider Caribbean, a review of the available literature, and a comprehensive examination of the Cnidaria and Porifera collections at the USNM; however, additional species combinations are certain to be discovered lurking in the vast literature of sponge biology, in new sponge species that are constantly being described, and in the unexplored regions and depths. With the data collected thus far, we offer the following conclusions:

1. Sponges representing at least 14% of the total described Caribbean sponge diversity and nearly half of the extant orders of Demospongiae associate with symbiotic-zoanthids.
2. Sponges are highly specific to zoanthid species (no one sponge species hosts more than two zoanthid species) and zoanthids are much less specific to sponge species (zoanthid species are associated with 3–51 different sponge species).
3. Sponges from disparate taxonomic groups that host photosynthetic endosymbionts almost exclusively associate with zoanthids that also host photosynthetic endosymbionts, suggesting that the adaptive significance of this subset of symbioses includes a shared strategy for maximizing photosynthetic potential.
4. The low degree of specificity of most zoanthids to sponges and the disparity between zoanthid and sponge specificity may indicate that most sponge–zoanthid associations are generally not parasitic.
5. The degree that zoanthid species are embedded in sponges is negatively correlated with the number of host sponge species and the volume of zoanthid polyps, suggesting that intimacy with the host may constrain the specificity and size of zoanthids.
6. Although zoanthids form associations with many sponge species, they are specific to more-inclusive clades of sponges at various taxonomic levels (from one sponge genus to groups of sponge orders).
7. The similarity of symbiotic associations among sponge genera is almost entirely consistent with current sponge systematics. Zoanthid symbioses support generally accepted hypotheses dividing the sponge order Haplosclerida into suborders Petrosina and Haplosclerina, separating order Agelasida from order Poecilosclerida, and reassigning parts of the order Halichondrida to order Agelasida; but also support the less accepted hypothesis that some species in genus *Cribrochalina* belong in suborder Petrosina.
8. The similarity of symbiotic associations among zoanthid species supports molecular evidence that suggests genus *Parazoanthus* is paraphyletic, but also makes the new suggestion that genus *Epizoanthus* and families Epizoanthidae and Parazoanthidae are also paraphyletic.

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