

Sponge Systematics by Starfish: Predators Distinguish Cryptic Sympatric Species of Caribbean Fire Sponges, *Tedania ignis* and *Tedania klausii* n. sp. (Demospongiae, Poecilosclerida)

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Abstract. *Tedania ignis* (Duchassaing and Michelotti, 1864), the fire sponge, is common throughout the tropical western Atlantic, and is a popular species for studies of ecology, larval biology, and chemistry. *T. ignis* is readily consumed by seagrass-dwelling starfish, and so finding sponges similar to this species in a seagrass meadow provoked closer scrutiny. A variety of ecological, morphological, and molecular traits consistently and unambiguously distinguish *T. ignis* from a cryptic sympatric congener, here described as *Tedania klausii*, n. sp. Starfish that consume *T. ignis* reject *T. klausii*, and angelfish consume *T. klausii* less quickly. In Belize, *T. ignis* individuals transplanted to a seagrass meadow inhabited by *T. klausii* were consumed by starfish, and individuals of *T. klausii* transplanted to a mangrove-lined creek in which *T. ignis* flourishes, died. In Panama, many individuals of *T. klausii* were diseased in May 2004, while adjacent individuals of *T. ignis* were unaffected. Spicule types are the same in the two forms, and sizes overlap; but within individuals, the relative sizes of styles and tylotes differ in a pattern that distinguishes the two forms. Comparison of DNA sequences for mitochondrial cytochrome *c* oxidase subunit I (COI) revealed that 8 single nucleotide mutations consistently differ between the two forms regardless of habitat (seagrass *vs.* mangrove) and geographically separated sites (Belize *vs.* Panama).

Introduction

Failure to distinguish cryptic species can confound our understanding of ecological and evolutionary processes.

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Meaningful answers to questions relating to (1) biodiversity and ecosystem function, (2) species diversity and community stability, (3) density-dependence of pathogen spread, and (4) population-size-dependent vulnerability to extinction depend on knowing how many species are present, which individuals fall into which species, and how large the populations of each species are. Predictions about shifts in distribution patterns or losses of biodiversity that result from changing environmental conditions are very different for a single morphologically variable generalist species with a large population than for two specialized species with smaller populations. Evolutionary questions, including those relating to modes of speciation, are raised when similar sympatric species play different roles, have different physiological capacities, and interact differently with competitors or predators. For instance, recent distinction of three species among individuals of what had been known as the common Caribbean coral *Montastraea annularis* has challenged accepted ideas about mechanisms of reproductive isolation, interactions with photosynthetic symbionts, and use of morphological characters to distinguish coral species (*e.g.*, Weil and Knowlton 1994; Toller *et al.*, 2001; Levitan *et al.*, 2004; Fukami *et al.*, 2004), and demonstrates how answers to ecological and evolutionary questions can be derailed if we base them on inaccurate distinction among key species (*e.g.*, Knowlton, 2001).

Sponges are among the most abundant and diverse sessile animals in many hard substratum marine habitats, including coral reefs, mangrove roots, rock walls, and caves. Their conspicuous diversity of colors and growth forms superficially make identification seem clear-cut, but the relative paucity of quantifiable morphological characters, and the malleability of overall form, makes sponge systematics par-

ticularly challenging. Many sponge species have gone through series of name changes and movement among families and even orders of Demospongiae (e.g., Hooper and van Soest, 2002). Measurements and descriptions of skeletal elements have been the mainstay of species distinctions, but closer scrutiny with information derived from microscopy, chemistry, and molecular techniques has demonstrated that some species that had long been considered to be cosmopolitan, or morphologically variable, are actually more than one species (e.g., Boury-Esnault *et al.*, 1992, 1993, 1999; Solé-Cava *et al.*, 1992; Klautau *et al.*, 1994; Solé-Cava and Boury-Esnault, 1999; Boury-Esnault and Solé-Cava, 2004).

A few species have distinctive characteristics that have allowed apparently unambiguous identification for more than a century. *Tedania ignis* (Duchassaing and Michelotti), the common Caribbean fire sponge, is one of these species. The genus *Tedania*, which is distributed worldwide, has recently received much attention in the systematics literature. It has been placed in a separate family (Tedaniidae) within the Order Poecilosclerida (Bergquist and Fromont, 1988; Hooper and Wiedenmayer, 1994; Desqueroux-Faúndez and van Soest, 1996), and recent descriptions of new species have provided impetus for reinterpretation of previous species assignments in Brazil (Mothes *et al.*, 2000), the southeastern Pacific (Desqueroux-Faúndez and van Soest, 1996), the western Pacific (Kennedy and Hooper, 2000), and the Iberian Peninsula (Cristobo, 2002). Throughout this period of scrutiny, *T. ignis* has remained undisturbed, although a number of specimens previously regarded as other species are now considered to be *T. ignis* (e.g., Mothes *et al.*, 2000). *T. ignis* was described as *Thalysias ignis* by Duchassaing and Michelotti in 1864 and was moved to *Tedania* by Verrill (1907). It is a conspicuous sponge, with a bright saturated orange color and a characteristic spicule complement and growth form, and it causes contact dermatitis in humans. As one of the most common, readily collected, and easily manipulated species in the tropical western Atlantic, it has provided fertile material for chemistry (e.g., Schmitz *et al.*, 1984; Garson, 1993; Monks *et al.*, 2002), larval biology (e.g., Jaeckle, 1995; Maldonado and Young, 1996; Maldonado, 1998), and ecology (e.g., Sutherland, 1980; Bingham and Young, 1991; Wulff, 1995, 2005; Ellison *et al.*, 1996; Dunlap and Pawlik, 1996; Nunez *et al.*, 1999).

In June 2001 I first noticed sponges similar to *T. ignis*, and with the same spicule complement, living in seagrass meadows near Twin Cays, Belize. Their subtle differences in morphology and coloration could have been attributed to environmental differences in the seagrass meadow, relative to the nearby mangrove roots on which *T. ignis* is abundant, but for one observation: experiments investigating sponge feeding by the large, common, seagrass-dwelling starfish *Oreaster reticulatus* had demonstrated that it readily consumes *T. ignis* collected from mangrove roots, but consis-

tently rejects most seagrass-dwelling sponge species (Wulff, 1995). The starfish rapidly find and consume edible sponges that wash into seagrass beds from reefs or that fall off of mangrove roots (Wulff, 1995, 2000). Thus *T. ignis* in a seagrass bed inhabited by *Oreaster* was a clear anomaly. Once the possibility of a cryptic *Tedania* species was raised, individuals of the unusual form were also readily distinguishable among individuals of the normal *T. ignis* on nearby mangroves. In January 2002, I also noticed the unusual form growing on mangrove roots, along with *T. ignis, sensu stricto*, in Bocas del Toro, Panama.

Spicules of the two forms are indistinguishable by shape and overlap in sizes, so molecular characters and ecological attributes were analyzed as well. Experimental manipulations evaluated "common garden" growth rates, survival of transplantation among habitats, and consumption by starfish, angelfish, and parrotfish. Field experiments and other analyses were duplicated, as much as possible, in Twin Cays, Belize, and Bocas del Toro, Panama, providing a biogeographic perspective on ecological as well as molecular and morphological attributes.

Materials and Methods

Ecological distinction between forms

Predation by angelfish, parrotfish, and starfish on both forms was studied in Belize and Panama. In the field, pieces of both forms of *Tedania* were attached, using narrow beaded cable ties, to the plastic bases of cages (30 × 35 × 15 cm, with meshes 5 × 7 cm), along with sponges of other species (5 species per trial). One individual of the starfish *Oreaster reticulatus* (Linnaeus), with radius between 11 and 13 cm, was placed in each cage and allowed to feed for 24 h. Small pieces of both forms of *Tedania* were also attached to pieces of coral rubble on stakes that could be inserted into the reef to observe feeding by angelfish, *Pomacanthus arcuatus* (Linnaeus), and parrotfish, *Sparisoma aurofrenatum* (Cuvier and Valenciennes). Data recorded included the number of bites on each specimen during the first hour, the time elapsed when a specimen was completely consumed, and the net result of consumption after 24 h. To make the interactions as natural as possible, sponge pieces were protected inside cages to allow their cut surfaces to regenerate before they were made available to the predators.

Habitat distribution patterns were quantified in the course of complete censuses of 10 mangrove roots or root clusters at each of three sites: Sponge Haven and Hidden Creek, both in Twin Cays, Belize; and across the bay from the Smithsonian Tropical Research Institute marine station in Bocas del Toro, Panama. Seagrass meadows and coral reefs in Bocas del Toro and Belize were also surveyed for the two forms.

Growth rates and development of the overall growth form of *Tedania ignis* from mangrove roots ($n = 10$), and the

unusual form from both mangroves ($n = 10$) and seagrass meadows ($n = 10$), were compared by attaching small pieces (6–13 cm³, all cut to the same oblong shape, with length approximately twice the width) with cable ties to lengths of pre-conditioned PVC pipe suspended among mangrove roots at Sponge Haven, Twin Cays, Belize. The volume of each piece was recorded at the start and after 6 months.

To determine if absence from a habitat indicated inability to live there rather than lack of colonization, in Belize transplants were made to habitats in which one or the other form was not found. *Tedania ignis*, *sensu stricto*, which was only found on mangroves, was transplanted from mangrove roots to seagrass, 250 m away ($n = 12$); and the unusual form was transplanted from mangrove roots at one site where it was abundant (Sponge Haven) to mangrove roots at another site, 330 m away (Hidden Creek), from which it was absent ($n = 12$). Controls for manipulation effects (*i.e.*, cutting, transporting by boat, and reattaching with cable ties) were transplantation of *T. ignis* from mangroves at Sponge Haven to mangroves at Hidden Creek, where it is common ($n = 12$), and of the unusual form from mangroves at Sponge Haven to the seagrass meadow, where it is common ($n = 10$). Transplants to the seagrass meadow were randomly spaced along three transect lines, and transplants to mangrove roots were placed wherever they would not be in immediate contact with prior residents.

Morphological distinction between forms

Spicule preparations were made from specimens of each *Tedania* form from both Panama and Belize. Individuals of the unusual form were collected on mangrove roots at both locations, and also in seagrass beds in Belize. Individuals of *T. ignis* were collected on mangrove roots in Panama and Belize, and also at geographically distant sites where the unusual form was not found: on mangrove roots in the Florida Keys (Zane Grey Creek, Long Key), and on very low intertidal rocks on the coast of Brazil near Recife. For each spicule type, 25 length measurements and 10 width measurements were made for each individual.

Whole skeletons were cleaned for examination by macerating the tissue. Architectural features were compared by light microscopy. In the field, overall growth form was quantified by measuring heights and widths of individual volcano-shaped mounds.

Molecular distinction between forms

Comparisons of the DNA sequence of the mitochondrial cytochrome *c* oxidase subunit I gene (COI) between each form of *Tedania* and other genera representing the order Poecilosclerida that were available in GenBank were made to determine if the unusual form of *Tedania* could be genetically distinguished from *T. ignis*. COI sequences from

four other poecilosclerid species were used: *Iotrochota birotulata* (AY561963), *Diacarnus spinipoculum* (AY561975), *Crambe crambe* (AF526297 and AF526298), and *Microciona prolifera* (AJ704978). Small samples (3 × 4 mm) were excised from three individuals of each form of *Tedania* from mangroves, from two individuals of the unusual form from seagrass, in Belize, and from one individual of each form from mangroves in Bocas del Toro, Panama. Samples were preserved in 100% ethanol and, after several changes of the ethanol to relieve dilution, transported to the laboratory and stored at –80 °C.

Total nucleic acid was extracted from small subsamples using a cetyl-trimethyl-ammonium bromide extraction technique (Doyle and Doyle, 1987) and amplified by PCR using the primers and protocols of Folmer *et al.* (1994). PCR products were purified using the ExoSAP-IT kit (USB Corporation, Cleveland, OH) and were directly sequenced in both the forward and reverse directions using the amplification primers. Forward and reverse sequences were edited and assembled using Sequencher 4.0.5 (Gene Codes Co., Ann Arbor, MI). PCR products yielding ambiguous sequences were amplified and sequenced for a second time from the original extraction and used to create a majority consensus sequence using all four sequences (two forward and two reverse). In cases where no clear consensus could be reached, the International Union of Pure and Applied Chemistry (IUPAC) ambiguity codes were applied. An alignment of all sequences was made using the default settings in Clustal × 1.81 (Thompson *et al.*, 1997) and adjusted manually in Bioedit 5.0.9 (Hall, 1999). Pairwise genetic distances were calculated with the DNADIST 3.5c accessory application in Bioedit, using the default settings.

Results

Ecological distinction among forms

Consumption by predators. Starfish in Bocas del Toro, Panama, and Twin Cays, Belize, distinguished the two forms unambiguously, entirely consuming *Tedania ignis* in 20 of 20 trials, but only partially consuming the unusual form collected on mangroves in Bocas del Toro and Belize in 4/21 trials, and the unusual form collected in seagrass meadows in Belize in 0/25 trials (Table 1, difference between the forms is significant by the *G* test at $P < 0.001$). Gray angelfish, *Pomacanthus arcuatus*, consumed both forms, but consumed *T. ignis* more quickly. *T. ignis* collected from mangroves was consumed within 1 h (generally within 10 min) in all 16 of 16 trials, but the unusual form was consumed within 1 h in only 12/21 trials when collected from mangroves, and in 8/12 trials when collected from seagrass (Table 1, difference between the forms is significant by the *G* test at $P < 0.001$). Individuals of the unusual form that remained after 1 h were all consumed within 24 h.

Table 1

Summary of ecological experiments and observations, in the field, of *Tedania ignis* and *T. klausi* in Twin Cays, Belize, and Bocas del Toro, Panama

Result or observation	<i>T. ignis</i>	<i>T. klausi</i>
Consumed by starfish within 24 h	20/20	4/46
Consumed by angelfish on coral reefs within 1 h	16/16	20/34
Diseased on mangroves in Bocas del Toro	0/63	9/22
Survival of transplantation from main channel to tidal creek, 12 mo	12/12	0/12
Survival of transplantation from seagrass to mangrove, 6 mo	—	10/10
Survival of transplantation from mangrove to seagrass, 6 mo	0/12	10/10

T. ignis does not inhabit seagrass meadows, so transplantation of this species from seagrass to mangrove was not possible. All comparisons between forms are significantly different by the *G* test at $P < 0.001$.

Parrotfish, *Sparisoma aurofrenatum*, which are known to consume other mangrove sponge species, declined to consume both forms of *Tedania*.

Habitat distribution. In Belize, the unusual form constituted 31% of the 29 individuals of *Tedania* spp. on 10 mangrove roots or root clusters that were completely censused at Sponge Haven, but no individuals of the unusual form were found on mangrove roots at Hidden Creek. Neither form was found on shallow coral reefs in Belize or Panama; and *T. ignis* was never found in seagrass meadows. In the seagrass meadow at Twin Cays, Belize, the unusual form is one of the four most common sponge species by total volume, but was not found in seagrass meadows in Bocas del Toro, Panama. The unusual form was not found on mangrove roots in San Blas, Panama; Pelican Cays, Belize; or in the Florida Keys. On mangrove roots in Bocas del Toro, Panama, the unusual form constituted 12% of the 17 individuals of *Tedania* spp. on 10 clusters of completely censused mangrove roots. In May 2004, some individuals of the unusual form appeared to be diseased in Bocas del Toro. In a stretch of mangrove roots 15 m long, tissue was almost completely macerated from 5/18 individuals of the unusual form; an additional 4 individuals had lost all live tissue and their skeletons were deteriorating (*i.e.*, a total of 9/22 individuals were affected). By contrast, all 63 individuals of *T. ignis* appeared to be healthy.

Growth rates and development of overall form. Growth rates of the two forms were similar on PVC pipes suspended

among mangrove roots, with mean specific growth rates (*i.e.*, size increase/original size) over 6 months of 4.51 (SE = 0.74), for *T. ignis* of 5.41 (SE = 0.63) for the unusual form from mangroves, and of 4.28 (SE = 0.46) for the unusual form from seagrass. Sample sizes were, respectively, 5, 7, and 6, as only individuals that increased in size were included in these growth rate estimates.

Overall morphologies that developed during the 6 months were strikingly different for the two forms. All individuals of *T. ignis* grew as low mounds, extending evenly in all lateral directions. By contrast, all individuals of the unusual form, from both the mangroves and seagrass, developed one to three (in most cases two) tall and relatively narrow, volcano-shaped mounds (dimensions of the four largest mounds, as height by width [midway between base and peak], were 4.5×2.4 cm, 5.2×2.0 cm, 8.0×2.1 cm, 5.8×2.9 cm), each surmounted by a single osculum. Three of the 10 individuals of *T. ignis* did not survive, while all 10 individuals of the unusual form from the mangroves and all 10 from the seagrass survived. The basis for this distinction may lie in differences in initial attachment to the PVC pipes. Within 2 days, all individuals of the unusual form had started to spread in a thin crust over the pipes, creating a very stable attachment. All individuals of both forms were firmly attached after 10 days, but individuals of *T. ignis* had not spread over the PVC, so their grip was not as resistant to being dislodged.

Transplantation among habitats. Transplants of all 10 individuals of the unusual form from the seagrass to mangroves at Sponge Haven survived. Of 12 individuals of the unusual form transplanted from mangroves at Sponge Haven to mangroves at Hidden Creek, a distance of only 330 m, no individuals survived (previously reported in Wulff, 2004). The transplanted sponges had readily reattached and appeared to be thriving at the end of 10 days, so their disappearance during the subsequent 12 months suggested that this tidal creek had episodes of abiotic conditions that were intolerable to the unusual form but not to *T. ignis*. All 12 transplants of *T. ignis* from Sponge Haven to Hidden Creek (*i.e.*, the controls for manipulation and transportation effects) survived (Table 1). When *T. ignis* was transplanted into seagrass meadows at Twin Cays ($n = 12$ individuals), 250 m from their home mangrove roots at Sponge Haven, all individuals were consumed by the starfish *Oreaster reticulatus* within 5 days. All 10 individuals of the unusual form transplanted from Sponge Haven mangroves to the seagrass (*i.e.*, the controls for manipulation and transportation effects) survived (Table 1).

Morphological distinction among forms

Spicule types did not differ between the forms. Both had smooth, slightly curved styles; straight tylotes with micro-

Table 2

Mean lengths (μm) of 25 spicules of each type, and mean widths (μm) of 10 styles and 10 tylotes, for each specimen

Species	Collection location	Styles	Tylotes	Onychaetes, large	Onychaetes, small	
<i>Tedania ignis</i>	Belize, Twin Cays: mangroves	251.4 \times 5.5	227.7 \times 3.4	206.7	57.7	
		269.8 \times 5.2	226.3 \times 3.2	211.1	60.2	
		263.6 \times 5.3	223.1 \times 3.2	222.6	65.2	
		264.2 \times 9.8	230.5 \times 4.0	237.9	77.6	
		260.4 \times 6.6	229.2 \times 3.2	195.5	62.0	
	Panama, Bocas del Toro: mangroves	260.6 \times 5.3	224.9 \times 3.2	206.4	54.3	
		262.3 \times 5.6	223.1 \times 3.2	212.5	56.6	
	Brazil, Pernambuco: intertidal rocks	252.7 \times 7.3	231.6 \times 4.0	190.1	54.9	
		220–240 ^a	210–225	180	50	
		USA, Florida Keys: mangroves St. Thomas				
<i>Tedania klausii</i>	Belize, Twin Cays: mangroves	234.1 \times 4.8	230.4 \times 3.6	160.1	63.1	
		242.9 \times 5.2	240.6 \times 3.1	160.4	56.5	
		239.3 \times 5.0	232.8 \times 3.2	162.2	54.1	
		246.4 ^d \times 4.8	244.9 \times 3.1	164.7	52.3	
		237.1 ^e \times 5.0	230.4 \times 3.6	155.6	60.3	
	Belize, Twin Cays: seagrass	246.8 \times 4.6	245.4 \times 3.1	175.3	61.3	
		242.3 \times 4.9	248.5 \times 2.9	174.9	56.1	
		253.9 \times 4.9	252.3 \times 3.0	176.1	52.9	
		250.4 ^d \times 5.3	252.2 \times 3.2	187.5	50.1	
		259.5 ^f \times 5.3	253.8 \times 3.4	168.6	63.8	
		238.2 \times 7.5	241.7 \times 3.7	188.2	55.8	
	Panama, Bocas del Toro: mangroves	237.7 \times 8.3	232.5 \times 4.6	183.4	52.4	
	<i>T. cf. ignis</i>	Guam	177.5 ^c \times 5.2	219.6 \times 2.6	199.1	54.8
	<i>T. cf. ignis pacifica</i>	Hawaii	188.2 ^b \times 5.0	194.5 \times 3.2	125.2	35.4
		Palau, Koror	257.7 ^b \times 5.3	230.1 \times 3.1	210.8	62.0

All specimens of *Tedania ignis* and *T. klausii* were collected by the author, with the exception of the St. Thomas specimen of *T. ignis* (a), which is the paralectotype of Duchassaing & Michelotti, 1864, ZMA POR.2373, as reexamined by van Soest (1984); and specimens of *T. cf. ignis pacifica* (b) from Hawaii (USNM 22744) and Palau (USNM 22921), which were both collected by de Laubenfels in 1947–1949. The specimen of *T. cf. ignis* from Guam (c), was collected by Gustav Paulay, Florida Museum of Natural History, Univ. Florida. Two specimens of *T. klausii* (d) one from the mangrove and one from the seagrass, were grown on the same PVC pipe for 6 months before bits were collected for spicule preparations. Spicule measurements are also included for the type specimens of *T. klausii*: the holotype specimen (e), collected from a mangrove root, USNM 1083267; and the paratype specimen (f), collected from the seagrass meadow, USNM 1083268.

spined ends; and two classes of very thin, straight onychaetes, microspined along their entire lengths (e.g., Wiedenmayer, 1977; van Soest, 1984; Zea, 1987). Dimensions of each of the four spicule types overlap between the two forms, although styles of the unusual form tend to be slightly shorter (Table 2). To ensure that spicule size comparisons were not confounded by possible mixtures of the two forms in previous literature reports, I compared the spicule dimensions of sponges I had collected since I became aware of the possibility of a cryptic *Tedania* species. For all of these samples, spicule lengths of individuals of *T. ignis* did not differ among sponges collected in Belize, Panama, Brazil, and the Florida Keys (Table 2).

Spicules of the unusual form were consistent among specimens collected from the same habitat, regardless of geographic location, but spicules of individuals collected from seagrass tended to be longer (differences are only significant for tylotes, by ANOVA, $P < 0.005$, for the specimens included in Table 2). Two individuals that were

collected in seagrass and mangroves and grown next to each other on the same PVC pipe (suspended among mangrove roots) for 6 months maintained this difference, with spicule lengths longer in the specimen originally collected from the seagrass (Table 2). Since both specimens increased in size at least 5-fold while on the pipe, this indicates inherent (vs. habitat-controlled) differences in spicule dimensions.

Although the lengths of spicules *per se* do not differentiate these species unambiguously, the ratios of lengths of spicules of different types do. Within individual specimens of the unusual form, the tylotes and styles were consistently very similar in size; in *T. ignis* the styles were longer than the tylotes in every specimen (Table 2). The mean percent difference in length between tylotes and styles for the 8 specimens of *T. ignis* represented in Table 2 is 12.8% (range 8.3%–16.1%), contrasting with the mean percent difference in length between tylotes and styles for the 12 specimens of the unusual form of only 1.6% (range 0.6%–2.8%). The difference between the forms in the relative sizes of tylotes

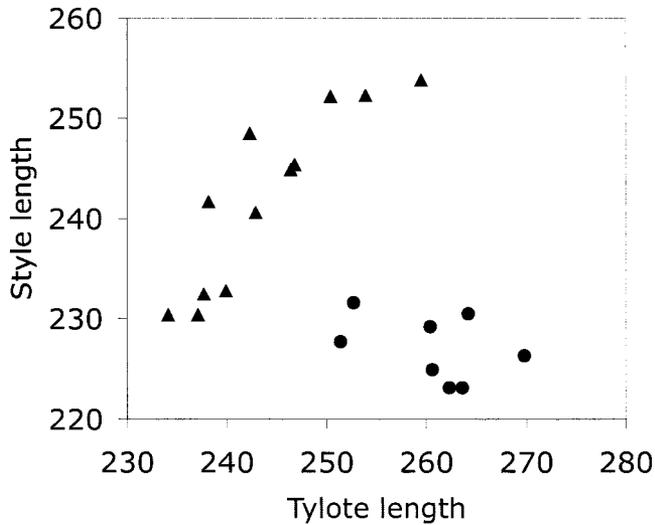


Figure 1. Distinction between the relative sizes of styles and tylotes in *Tedania ignis* (circles) and *T. klausii* (triangles). Each symbol represents the mean of the lengths (in μm) of 25 spicules of each category for one sponge individual (data are in Table 2). The mean percent by which styles are longer than tylotes is 12.8% for *T. ignis* and 1.6% for *T. klausii*, and this difference is significant by the Wilcoxon two-sample test ($P < 0.001$).

and styles is significant by the Wilcoxon two-sample test ($P < 0.001$), and this clear morphospace separation between the forms is depicted in Figure 1.

The two *Tedania* forms can be readily distinguished in the field by shape, surface skeletal features, color, and consistency. Skeletal construction in the unusual form is very focused on narrow ridges running up the sides of the mounds. The dermal membrane covering the canals between the ridges is almost translucent and is clearly inflated when the sponge is pumping (Fig. 2A), imparting a vertically striped appearance to the mounds in life. The surface often has small white flecks in it (Fig. 2A–D). By contrast, the surface of *T. ignis* is opaque saturated orange, and more uniformly corrugated. Relative to *T. ignis*, the unusual form is softer, more compressible, and slightly pinker and paler (Fig. 2B). The mounds of the unusual form are almost chimney-like (*i.e.*, tall and narrow), distinct from the rounded mounds of *T. ignis* (Fig. 2A, B). Each tall mound in the unusual form is surmounted by a single osculum, whereas oscula in *T. ignis* can be more generally scattered. The oscula of the unusual form are ringed by a thin, transparent membrane (Fig. 2A–C), which is not a feature of *T. ignis*. All of the oscula in a confluent individual of the unusual form may be completely closed when the sponge is disturbed (*e.g.*, by sediment deposited after a storm, or a large ophiuroid crawling over the sponge), because the rim collapses, along with the thin ectosome covering the surface canals, during lulls in pumping (Fig. 2D). When the oscula are closed and the canals deflated, the mounds appear

pleated due to the deep crevices between the narrow ridges (Fig. 2D).

Molecular distinction among forms

Ten *Tedania* COI sequences (GenBank accession numbers: DQ133896–DQ133905) were included in a 658-character alignment of 15 total poecilosclerid sequences. Pairwise comparisons of genetic distances between the 5 poecilosclerid genera represented in GenBank reveal an average genetic distance between genera of 0.1787 and a within-species genetic distance of 0.0019 (for *Crambe crambe*). The average genetic distance between all individuals of both forms of *Tedania* (0.0093) falls between these generic and specific distances. Average distances within individuals of the typical *T. ignis* form (0.0016) and average distances within individuals of the unusual *Tedania* form (0.0030) are similar to the within-species distance for *Crambe crambe*. Genetic distances within forms are similar regardless of geographic distance or habitat type.

The genetic distance between individuals of the same *Tedania* form is due to nucleotide substitutions that are not shared among all individuals, while the genetic distance between forms is mostly due to mutations shared among all individuals sampled of each form. There are 8 single nucleotide mutations dispersed throughout the alignment that are specific to each form of *Tedania* and are present in all individuals of that form sequenced, regardless of site or habitat, creating a genetic signature of each form (Table 3).

Systematics: Tedania (Tedania) klausii new species

Material examined. Holotype: USNM 1083267 Twin Cays, Belize (from a mangrove root at Sponge Haven); Paratype: USNM 1083268 Twin Cays, Belize (from the seagrass meadow); and numerous other specimens of *T. ignis* and *T. klausii* from mangroves and seagrass meadows in Belize and mangroves in Panama.

Description. Large specimens are clusters of tall volcano-shaped mounds, each mound surmounted by a single osculum; smaller specimens consist of a single tall, narrow, volcano-shaped mound rising from a wider base. In mangrove specimens, the mounds tend to be at least twice as tall as they are wide (Fig. 2A, B), and in seagrass specimens adjacent mounds may become partially fused (Fig. 2C). Skeletal construction is very focused on narrow ridges running up the sides of the mounds. The crevices between the ridges are 3–8 mm wide, when measured midway between the base and peak of each mound, and at least as deep. In life this imparts a vertically striped appearance to the mounds, as the dermal membrane covering the canals between the ridges is almost translucent and is clearly inflated when the sponge is pumping (Fig. 2A). The dermal membrane also provides a rim (1–3 mm wide) around the edge of

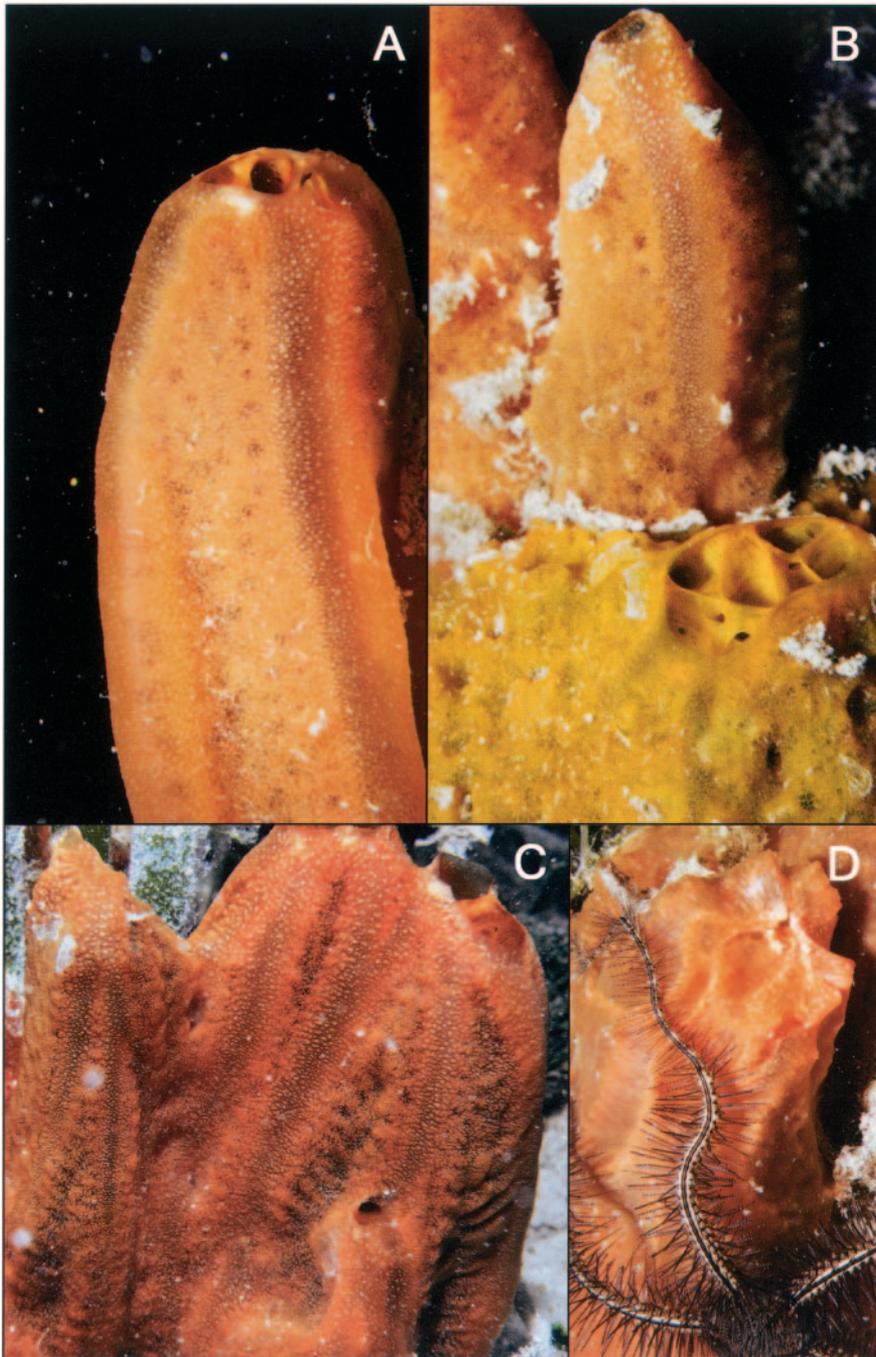


Figure 2. *Tedania ignis* and *T. klausii* on mangrove roots and in a seagrass meadow at Twin Cays, Belize. (A) A mangrove specimen of *T. klausii*, illustrating the membranous oscular rim and the vertically striped appearance of the inflated canals. (B) Contrast in color and mound shape between *T. ignis* (lower specimen) and *T. klausii* (upper specimen) on a mangrove root. This is an extreme example of the difference between the tall narrow mounds of *T. klausii* and the low wide mounds of *T. ignis*; as well as the translucent vertical stripes on *T. klausii*, where the dermal membrane is stretched over canals, vs. the uniformly opaque, saturated orange color of *T. ignis*. (C) A portion of a large seagrass specimen, illustrating how adjacent mounds are sometimes fused together. (D) Deep crevices between narrow ridges of the skeleton are evident in *T. klausii* when the osculae are closed and the dermal membranes over the canals are deflated, in this case in response to the ophiuroid crawling over the sponge.

Table 3

Mutations in the COI DNA sequences at 15 positions in 10 specimens of *Tedania* spp.

Specimens		Positions of mutations														
		2	4	8	0	2	3	4	4	4	5	5	5	6	6	6
Habitat	Country	8	6	9	6	8	5	5	2	7	3	5	6	5	7	1
<i>T. ignis</i>																
Mangrove																
	Belize	T	A	T	T	A	T	T	C	T	A	T	A	T	G	A
	Belize
	Belize
	Panama	C	G
<i>T. klausii</i>																
Mangrove																
	Panama	.	.	.	G	G	C	A	G	A	G	.	G	.	.	G
	Belize	G	C	A	G	A	G	.	G	.	.	G
	Belize	G	C	A	G	A	G	.	G	A	.	G
	Belize	.	.	A	.	G	C	A	G	A	G	C	G	A	A	G
Seagrass																
	Belize	G	C	A	G	A	G	.	G	A	.	G
	Belize	G	C	A	G	A	G	.	G	.	A	G

At 8 of the positions (# 208, 325, 415, 432, 457, 553, 556, and 631), mutations consistently differentiate specimens of *T. ignis* from *T. klausii*, regardless of habitat (mangroves vs. seagrass meadow) or geographic location (Panama vs. Belize). The entire sequences are available in GenBank, with accession numbers DQ133896–DQ133905.

each osculum (Fig. 2). During lulls in pumping, the membrane collapses, closing the osculum and making the vertical ridges sharply evident (Fig. 2D). The consistency is highly compressible, and the color is orange, with a slightly pink tint. White flecks are often scattered in the ectosome (Fig. 2).

Spicules. Ectosomal tyloles are terminally microspined, with the shafts very straight and the ends slightly inflated. Choanosomal styles are smooth and slightly curved, with the curved portion about a third of the way from the head to the pointed end. Onychaetes are very narrow, microspined along their entire lengths, and of two distinct size classes. Spicule dimensions are given as minimum – mean – maximum for lengths ($n = 25$) and widths ($n = 10$) in each category. Type specimen (mangrove root): tyloles 218 – 230.4 – 240 $\mu\text{m} \times 3.2$ – 3.6 – 4.0 μm ; styles 214 – 237.1 – 250 $\mu\text{m} \times 4.8$ – 5.0 – 5.3 μm ; large onychaetes 126 – 155.6 – 172 $\mu\text{m} \times 1.4$ – 1.6 – 1.8 μm ; small onychaetes 45 – 60.3 – 78 $\mu\text{m} \times 0.6$ – 0.9 – 1.0 μm . Paratype specimen (seagrass meadow) tyloles 230 – 253.8 – 266 $\mu\text{m} \times 3.2$ – 3.4 – 3.8 μm ; styles 252 – 259.5 – 272 $\mu\text{m} \times 4.8$ – 5.3 – 6.4 μm ; large onychaetes 124 – 168.6 – 195 $\mu\text{m} \times 1.5$ – 1.6 – 1.8 μm ; small onychaetes 48 – 63.8 – 99 $\mu\text{m} \times 0.5$ – 0.7 – 0.8 μm . Within individual specimens styles and tyloles were always very similar in length (within 0.6%–2.8%).

Spicule dimensions were very similar in mangrove specimens from Belize and Panama (Table 2). Spicules were slightly longer in seagrass specimens.

Distribution. To date, *T. klausii* has been identified only in Panama and Belize. In Panama it inhabits mangrove roots in Bocas del Toro; and in Twin Cays, Belize, it inhabits both seagrass meadows and mangrove roots. Although it was searched for on mangroves in the Pelican Cays in Belize, and in the Florida Keys, where the similar *T. ignis* can be common, it was not found at these sites. If some of the seagrass meadow and lagoon specimens referred to *T. ignis* in previous literature reports and guidebooks represent this newly described species, its geographic distribution is greater than recognized here.

Etymology. The species name honors Klaus Rützler of the U.S. National Museum of Natural History, Smithsonian Institution, for his many years of creative and path-making contributions to sponge science, bridging the fields of ecology, systematics, functional morphology, and cell biology; and for his generous encouragement of colleagues; and—through development and maintenance of the Caribbean Coral Reef Ecosystem Program and the Carrie Bow Cay field station on the Belize Barrier Reef—for his facilitation of studies of sponges and all other groups of organisms

inhabiting the coral reefs, mangroves, and seagrass meadows of Belize.

Discussion

Distinguishing cryptic species by ecological characteristics

Many cryptic species are being discovered in sponges (e.g., Boury-Esnault *et al.*, 1992, 1993, 1999; Solé-Cava *et al.*, 1992; Klautau *et al.*, 1994; Boury-Esnault and Solé-Cava, 2004), particularly within species that had appeared to be geographically widespread, or variable in color or morphology. In many cases the focus has been on biochemical and other differences that can be used to reliably distinguish similar allopatric species. When cryptic species are sympatric, recognition may depend on identification of specific ecological differences. In this case, the clue that a common, conspicuous, and apparently unambiguously identifiable species is actually two species was provided by starfish that are capable of exerting control over habitat distributions of sponges by their feeding preferences. Although ecological characters might simply represent phenotypic responses to environmental variables and alone cannot distinguish species, they can suggest genetic distinctions that are testable by transplant experiments and genetic analyses. Ecological differences between similar species may also suggest mechanisms of speciation, especially in the case of sympatric species.

Consequences of ecological differences between cryptic species

Distinguishing cryptic species has ramifications beyond systematics. Differences between *Tedania ignis* and *T. klausii* in palatability to potential predators and in susceptibility to abiotic extremes and disease have consequences for habitat distributions, potential invasiveness, and disease dynamics. Ready consumption of *T. ignis* by the large (up to 19 cm in radius), common, seagrass-dwelling starfish *Oreaster reticulatus* suggests that some seagrass meadow specimens referred to *T. ignis* (e.g., Wiedenmayer, 1977; Humann, 1992) may actually be *T. klausii*. Ecological conclusions based on designation of *T. ignis* as a habitat generalist (e.g., Diaz *et al.*, 2004) may require reevaluation, although it is possible that continued loss of predators from seagrass meadows and coral reefs could allow *T. ignis* to expand its habitat distribution. *T. ignis* is one of two mangrove species most readily consumed by reef-dwelling angelfishes (Dunlap and Pawlik, 1996; Wulff, 2005). Unusually great palatability to reef and seagrass-dwelling predators appears to constrain *T. ignis* to living on mangrove roots or in intertidal or cryptic spaces, raising the possibility that ecological speciation within the Caribbean has generated a seagrass meadow version, *T. klausii*.

The possibility that a species might become invasive if introduced outside its normal range is of increasing importance in marine systems, and differences in susceptibility to predators and abiotic factors are relevant to this concern. Because it is unusually palatable, *T. ignis* would not be predicted to be invasive, but *T. klausii*, which might be mistaken by humans for its more edible congener, would be less likely to be kept in check by predators. On the other hand, *T. klausii* may be more constrained by abiotic factors, as evidenced by its inability to inhabit Hidden Creek in Belize, where *T. ignis* is abundant.

Disease influenced these similar-looking species differently in Bocas del Toro, Panama, in early summer 2004. Many *T. klausii* individuals were lost, with no effect on *T. ignis* individuals growing immediately adjacent to them. Disease in sponges has generally been reported to influence only one or a few of the species in diverse communities (e.g., Smith, 1941; Reiswig, 1973; Rützler, 1988; Wulff, 1997, 2006; Goreau *et al.*, 1998; Pansini and Pronzato, 1990; Pronzato *et al.*, 1999; Nagelkerken *et al.*, 2000; Williams and Bunkley-Williams, 2000). The possibility that disease is caused by species-specific pathogens provides additional impetus for distinguishing cryptic species. If pathogen transmission is density-dependent, spread of disease would be predicted to be more rapid for a large population of a single common species than for sparser populations of two species, only one of which is vulnerable.

Morphological and molecular distinction among sponge species

Heavy reliance on morphological characters in sponge systematics may reflect what characters are readily available rather than confidence in their reliability. The possibility that simple comparisons of spicule measurements and shapes cannot be used for definitive species identification has been raised for *T. ignis* before (e.g., de Laubenfels, 1950a,b; Lehnert and van Soest, 1996; Kennedy and Hooper, 2000), and for sponges generally (e.g., Klautau *et al.*, 1999). When de Laubenfels (1950a) wondered if Bermuda *Tedania* specimens that he could consistently distinguish from *T. ignis* by subtle differences in the field, and by smaller spicules and tylostyles rather than styles, represented a different species, he opted to provide a new name (*T. tora*), but remarked “We may grant that *tora* is distinctly different from the abundant *Tedania*s that surround it, but argue that it represents some pathological modification, like finding a few hunchbacks among a crowd of people, all the others being normal as to spine.”

The spicule complement of *T. ignis* is shared by *Tedania anhelans*, the type species of the genus, with the exception of the two classes of onychaetes in *T. ignis*. Many specimens throughout the tropical world oceans have been referred to *T. anhelans*, but reexamination of those collected

in Brazil (Hechtel, 1976; van Soest, 1987; Mothes *et al.*, 2000) placed them in *T. ignis*, and questions have been raised about other specimens as well (*e.g.*, de Laubenfels 1950a, b). The spicule dimensions of specimens of *T. ignis* that I have collected since I became aware of the possibility of a cryptic *Tedania* species show very little difference over a large geographic range (from Brazil, the Florida Keys, Panama, and Belize) and between mangrove roots or intertidal rocks (Table 2). Perhaps some of the more varied dimensions reported in the literature reflect mixtures of specimens of *T. ignis* and *T. klausii*, which could easily be confounded because they share the same spicule types, and lengths of spicules of each type overlap. New ways of using measurements of skeletal elements for species distinction are suggested by the clear distinction between *T. ignis* and *T. klausii* in the relative lengths of two categories of spicules within individual sponges (Fig. 1).

What molecular tools will be most useful in helping to distinguish among sponge taxa at different levels, and in different groups of sponges, is still being determined. An analysis of studies in which allozymes have been used to distinguish cryptic species revealed the intriguing pattern that genetic identities for some sponge genera are unusually large between species, in others they are similar to those in other invertebrate taxa, and in still others both patterns are present (Solé-Cava and Boury-Esnault, 1999). Analysis of COI sequences has been successfully applied on the interspecific level, to test hypothesized cospeciation of sponge species in the order Halichondrida with bacterial symbionts (Erpenbeck *et al.*, 2002), but COI sequences for four species in two genera of freshwater sponges in Lake Baikal were found to be identical (Schröder *et al.*, 2003). Although COI variability was found to be low for *Crambe crambe* in the western Mediterranean and eastern Atlantic, it has provided evidence for intraspecific population structure over distances ranging from 20 to 3000 km (Duran *et al.*, 2004). In the present study, COI variability was also low, but the same eight nucleotides distinguished *T. ignis* and *T. klausii* regardless of habitat and over a geographic distance of at least 1200 km—a pattern congruent with all of the ecological and morphological data collected.

Biogeographic aspects of Tedania klausii and Tedania ignis

T. ignis has been reported from much of the coast of Brazil (Mothes *et al.*, 2000), and throughout the wider Caribbean region: from Venezuela (Sutherland, 1980; Diaz *et al.*, 1985), Colombia (Zea, 1987), and Panama (Wulff, 1994), to Belize (Ellison *et al.*, 1996; Rützler *et al.*, 2000; Wulff, 2005), Jamaica (Hechtel, 1965), Cuba (Alcolado, 1980), and the Bahamas (Wiedenmayer, 1977), to the Indian River Lagoon (Maldonado and Young, 1996), northern

Gulf of Mexico (Storr, 1976; pers. obs.), and Bermuda (de Laubenfels, 1950a; Rützler, 1986).

Reports have not been confined to the tropical western Atlantic. De Laubenfels (1950b) collected what he referred, with some qualms, to *T. ignis*, in Kaneohe Bay in Hawaii. Re-examination of his specimen USNM 22744 confirmed that the spicules are shorter than those of Caribbean *Tedania* examined for this study (Table 2), and the lengths of tyloles and styles are similar to each other. These characteristics are reminiscent of *T. ignis* identified by de Laubenfels (1950a) in Bermuda, raising questions about possible spicule differences in northern extremes of the range, as well as of geographic distributions and cryptic species. Spicule dimensions of an Iwayama Bay, Koror, Palau specimen, referred by de Laubenfels (1954) to *T. ignis* (USNM 22921), are remarkably similar to those of Caribbean *T. ignis* (Table 2). His chief concern about the Palau specimen was that it was tucked into a semi-cryptic space instead of living exposed; but this might be expected for a sponge species that is as readily consumed as *T. ignis* (*e.g.*, Dunlap and Pawlik, 1996; Wulff, 2005). The misgivings that de Laubenfels had were significant enough for him to suggest that his specimens from both Hawaii and Palau be regarded as belonging to a subspecies, *T. ignis pacifica* (de Laubenfels, 1954).

These are not the only *Tedania* specimens raising Caribbean-tropical Pacific biogeography questions that merit further study. Like the Hawaii specimen of de Laubenfels, a sponge recently collected in Guam and identified as *T. ignis* (pers. comm.; G. Pauly, Florida Museum of Natural History) has small spicules (Table 2) relative to Caribbean *Tedania*; but further exploration of ecological and molecular characters may tell an interesting biogeography story of this genus. The volcano-shaped mounds, translucent inflated vertical canals, and white flecks in the ectosome of this navigation-buoy-dwelling sponge from Guam match the external characteristics of *T. klausii*, raising the contrasting possibilities that this previously undescribed species may have recently colonized the Caribbean from the tropical Pacific; or *vice versa*.

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