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Genetic Divergence and Polyphyly in the Octocoral Genus *Swiftia* [Cnidaria: Octocorallia], Including a Species Impacted by the *DWH* Oil Spill

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Abstract: Mesophotic coral ecosystems (MCEs) are recognized around the world as diverse and ecologically important habitats. In the northern Gulf of Mexico (GoMx), MCEs are rocky reefs with abundant black corals and octocorals, including the species *Swiftia exserta*. Surveys following the *Deepwater Horizon* (*DWH*) oil spill in 2010 revealed significant injury to these and other species, the restoration of which requires an in-depth understanding of the biology, ecology, and genetic diversity of each species. To support a larger population connectivity study of impacted octocorals in the GoMx, this study combined sequences of *mtMutS* and nuclear 28S rDNA to confirm the identity of *Swiftia* sea fans in the GoMx, compare these markers for different polyp colors in the GoMx and Atlantic, and examine the phylogeny of the genus. Two *mtMutS* haplotypes were identified, one seemingly endemic to the northern GoMx. Compared to other North Atlantic *Swiftia*, *S. exserta*, the type of the genus was found to be extremely divergent and distinct from the two other *Swiftia* at both loci, with strong evidence of polyphyly in the genus. This information refines our understanding of the geographical distribution of injured coral and highlights how little is known about MCEs. Substantial taxonomic revisions may be needed for several taxa injured by the *DWH* oil spill.

Keywords: *Swiftia*; *mtMutS*; 28S; phylogenetics; DNA barcoding; *Deepwater Horizon*

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1. Introduction

Mesophotic coral reefs along the continental shelf of the northern Gulf of Mexico (GoMx) serve as essential habitat for a diverse array of marine organisms, including commercially and recreationally managed fish species. These reefs are typically found within 50–200 m depth and receive roughly 1–10% of sunlight compared to their shallow-water tropical counterparts [1]. The Pinnacles Trend, a reef tract consisting of nine deep-water "drowned" rocky reefs, occurs on the outer continental shelf of northeastern GoMx between the Mississippi River Delta and Pensacola, FL at depths of 60–90 m [2–4]. Corals growing on these mesophotic reefs are predominantly heterotrophic scleractinians, black corals, and gorgonian octocorals [2–4]. Coral growth rates are slow [4–7], less than 6 cm/yr among temperate mesophotic octocorals [6,7]. These taxa rely on nutritional input from surface waters [8,9], thus making them especially vulnerable to pollution. One of the most destructive examples of this was the *Deepwater Horizon* (*DWH*) oil spill of 2010.

Several mesophotic reefs in the Pinnacles Trend region were situated under the oil slick from the *DWH* oil spill for a period of 24–45 days [2]. Post-spill surveys of two of the largest Pinnacles reefs, Alabama Alps (AAR) and Roughtongue (RTR), revealed large

octocoral colonies below the oil slick showed significantly more injury than in years before the spill, with about one-third of large sea fans exhibiting injury in the form of overgrowth, broken branches, and bare branches [2]. Furthermore, Silva et al. [10] found oil levels in coral tissues and sediments exceeded baseline values at both AAR and RTR. Among the injured sea fans was a conspicuous *Swiftia* (Duchassaing and Michelotti, 1860) [11] species that occurs at similar depths as a morphologically similar northwestern Atlantic species: *Swiftia exserta* (Ellis and Solander, 1786) [12], the type species of the genus (Figure 1).

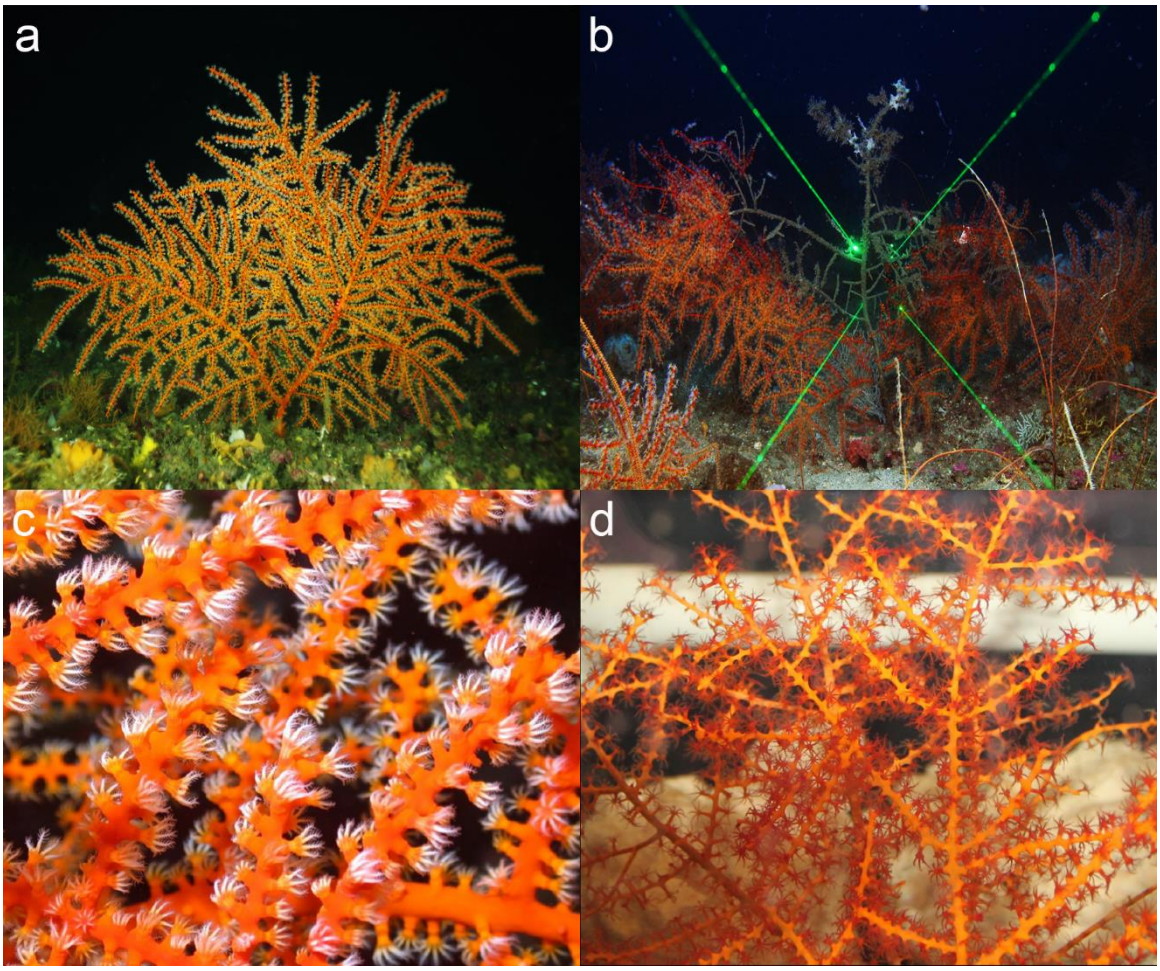

Figure 1. (**a**) Healthy *Swiftia* sp. from northern Gulf of Mexico with white polyps. (**b**) Injured *Swiftia* sp. from northern Gulf of Mexico. (**c**) Close-up of white polyps (NOAA/FGBNMS). (**d**) Close-up of *Swiftia exserta* from Riviera Beach, FL (Atlantic Ocean) with red polyps. Panels a and b are reprinted with permission from Etnoyer et al., 2016.

Swiftia exserta is an azooxanthellate bright red-orange gorgonian octocoral broadly distributed in the western Atlantic Ocean from shallow depths of about 18 meters off the coast of southeast Florida, down to 494 meters in the GoMx [13,14] (Figure 1). It was originally described by Ellis and Solander [12] from a specimen collected in the Caribbean, and named *Gorgonia exserta*. The genus *Swiftia* was later erected in 1860 by Duchassaing and Michelotti. There are currently 20 accepted species of *Swiftia* [15], and it is unclear whether the Pacific and Atlantic species belong in the same genus [16,17]. Goldberg [13] was the first to summarize and report on *S. exserta's* wide geographical distribution, noting its occurrence from the West Indies. He was also the first to examine its morphology in detail, describing and comparing the diagnostic sclerites of colonies in SE Florida to those in Brazil. The composition and sizes of coenenchymal and calycular sclerites of *S. exserta* are very different from the other *Swiftia* species in the northwestern Atlantic [13,18].

Across the species' range there appears to be heterogeneity in polyp color; the polyps in individuals from the Atlantic coast of Florida are predominately red and polyps in individuals from more northern reaches (northern GoMx and off the Carolinas) are predominately white (Frometa personal observations). Therefore, as part of an experimental study to document the effects of oil and dispersants on *Swiftia* colonies [19], DNA sequences of the octocoral barcode gene *mtMutS* from presumed *S. exserta* individuals from the GoMx (white polyps) were compared to reference sequences from *S. exserta* individuals from the Caribbean provided by the Smithsonian National Museum of Natural History (NMNH), courtesy of Dr. Herman Wirshing. New sequences from *S. exserta* (red polyps) samples collected from the same locale off SE Florida as described by Goldberg [13] were also included. Preliminary results from the injured white-polyp *S. exserta* from the GoMx indicated a 100% match to sequences of both newly generated sequences from red-polyp individuals from SE Florida, and to reference sequences of Caribbean *S. exserta* obtained from the NMNH. [20]. While we acknowledge the limitations placed on analyses using solely mitochondrial DNA markers, these data failed to provide any evidence suggesting that the white-polyp color morph is anything but a conspecific of *S. exserta*. Additionally, these results revealed no close homologies on GenBank (<89% identity), bringing its relationship to other taxa in the *Swiftia* genus into question.

The aforementioned *mtMutS* marker has been successfully used as a DNA barcode to identify some octocoral species, but it has shown more success at resolving genus and family level relationships [21,22]. Whereas mitochondrial DNA evolves more rapidly than nuclear DNA in most animals, this is not generally the case for octocorals and other anthozoans; slow nucleotide substitution rates thus result in low variation among species [23,24]. In the case of octocoral mitochondrial genomes, the slow substitution rate could be explained by the putative DNA mismatch repair function of *mtMutS* [25].

In contrast, some nuclear genes in octocorals show higher levels of variation in anthozoans, even when mitochondrial variation is low, providing an alternative independent measure to test for relatedness [23,24,26,27]. Combining nuclear and mitochondrial loci to form a multilocus barcode provides a powerful approach that has been shown to be more effective at delimiting morphospecies than single-gene barcodes [28–32]. Of these, the nuclear 28S rDNA locus has been commonly used in combination with mitochondrial genes for resolving octocoral phylogenetics [28,30,31,33–35]

A database of accurate species-specific DNA barcodes is necessary to better understand biodiversity and distribution of octocorals worldwide [31]. Such information is critical to properly manage and effectively restore the injured corals in the GoMx. For restoration efforts to be successful, it is crucial to not only understand the biology and ecology of impacted species, but to also preserve their genetic diversity [36,37]. Successful restoration also requires detailed monitoring, which can only happen if we understand the ecosystem to be restored and the taxa present. A larger collaborative study funded by the NOAA RESTORE Science Program [38] is currently examining the distribution and population connectivity of *Swiftia* sea fans in the GoMx by utilizing high-throughput restriction site associated DNA (RAD) sequencing, in order to inform upcoming restoration efforts.

The objective of this study was to sequence the commonly used DNA barcodes for octocorals, *mtMutS* and nuclear 28S, in order to confirm the identity of *S. exserta* samples collected throughout the northern GoMx for the larger NOAA RESTORE study. We expand our barcoding analyses to include other members of the *Swiftia* genus and Plexauridae to provide phylogenetic context and to test whether the *Swiftia* genus is monophyletic. This study presents novel molecular barcodes for *Swiftia exserta* and reveals new phylogenetic relationships among a sample of individuals from the *Swiftia* genus.

2. Materials and Methods

2.1. Sampling and Region of Study

A total of 240 samples of white-polyp *S. exserta* were collected from 11 sites in the northern GoMx (60–98 m deep), the two oil spill-impacted reefs in the Pinnacles Trend and

nine other sites, including the Flower Garden Banks National Marine Sanctuary (FGBNMS) (Figure 2, Table S1). These surveys occurred during three research cruises (OP17, MT17, MT18) in 2017–2018, aboard the Oceaneering ship *MSV Ocean Project* and NOAA ship *R/V Manta*, as part of the NOAA RESTORE project. Coral tissue samples were collected using two remotely operated vehicles (ROVs), *Comanche* (Oceaneering) and *Mohawk* (UNCW), respectively. All samples were georeferenced and accompanied by in situ and ex situ images of each coral. Occurrence data are publicly available at the NOAA National Database of Deep Sea Corals and Sponges [39] and used to generate the map in Figure 2.

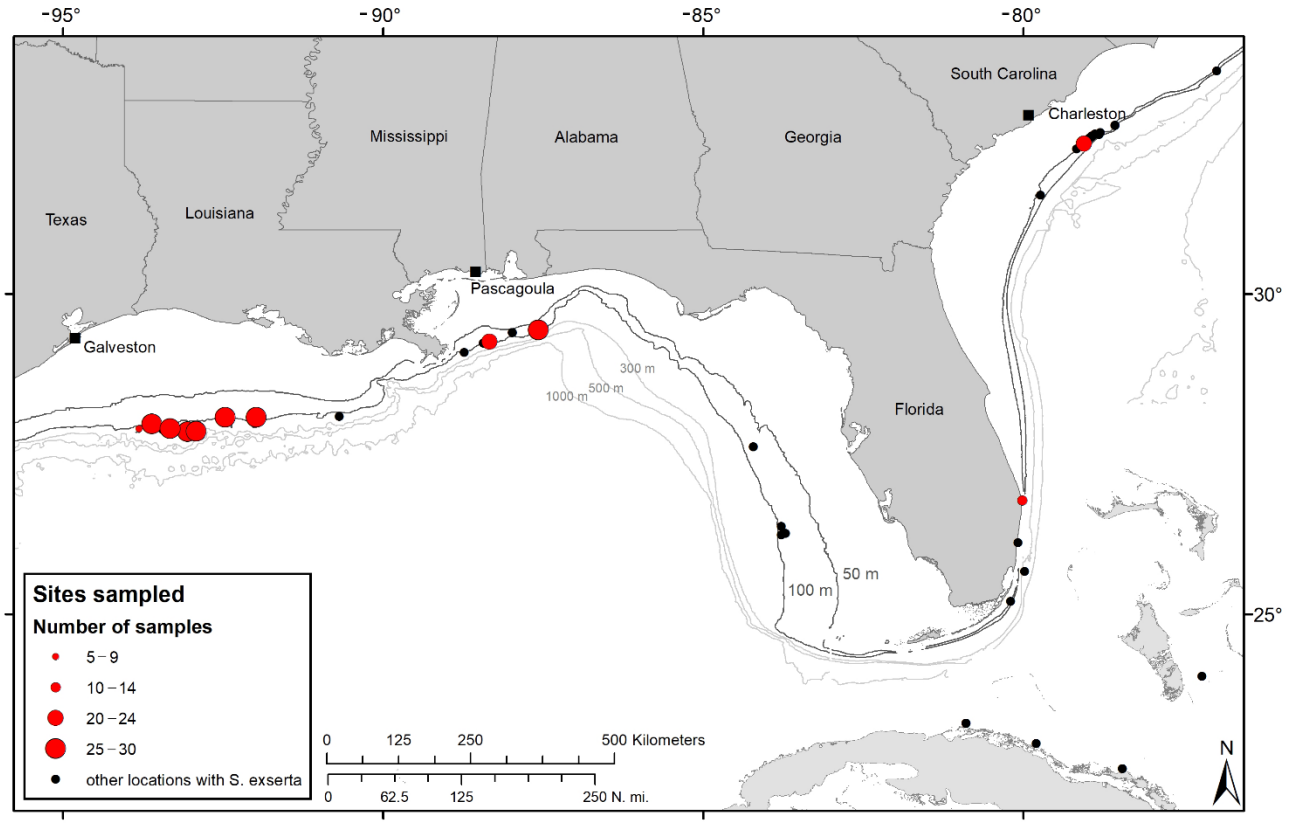

Figure 2. Sampling locations and number of *S. exserta* samples collected. Other known locations of *S. exserta* are shown in black circles [39]. The depth range of samples was 18–200 m, but most were between 50 and 100 m isobaths. See Table S1 for details.

Additional samples of white-polyp *S. exserta* from South Carolina (n = 20, 48–61 m deep) and red-polyp *S. exserta* samples from off the coast of SE Florida (n = 10, 18 m deep) were added to analyses to examine any regional variation that could be considered in restoration planning. Samples off the coast of Charleston, South Carolina were provided by John Reed (Harbor Branch Oceanographic Institute), and collected from the Edisto Island Marine Protected Area (MPA) in 2018, aboard the NOAA ship *Pisces* using ROV Mohawk. *Swiftia exserta* samples from SE Florida were collected by Henry Feddern (Tavernier, FL) via scuba off the coast of Riviera Beach. Additional samples of *Swiftia* spp. from the West Atlantic (*S. casta*, *S. pallida*, and *S. koreni*), were accessed through collaborators at the Smithsonian NMNH. All unique sequences generated from this study were deposited into the NCBI GenBank database. Sample information can be found on Table S1.

2.2. Molecular Procedures

DNA was extracted from coral tissue (2–5 polyps) using a DNeasy blood and tissue kit following manufacturer protocol (Qiagen Corporation, Germantown, MD, USA). DNA concentrations used in polymerase chain reactions (PCR) varied depending on quality

of DNA, ranging from 1.6–313 ng/µL. The *mtMutS* gene region was amplified using primers ND42599F (5′- GCCATTATGGTTAACTATTAC -3′) [40] and MUT3458R (5′- TSGAGCAAAAGCCACTCC -3′) [41]. The thermal cycling profile employed was as follows: 98 °C for 30 s, 36 cycles of 98 °C for 10 s, 55 °C for 30 s, 72 °C for 30 s, and a final extension step at 72 °C for 5 min. 28S rDNA was amplified with primers 28S-Far (5′- CACGAGACCGATAGCGAACAAGTA -3′) [33] and 28S-Rar (5′- TCATTTCGACCCTAAGACCTC-3′) [33]; thermal cycling profile followed protocols from Mcfadden et al. [22] with a modification in the denaturing temperature of 98 °C from 95 °C. All PCR reactions contained 15.8 µL PCR-grade water, 5 µL 5× Phusion HF Buffer (New England BioLabs, Inc., Ipswich, MA, USA), 1.25 µL of each primer (10 mM), 0.5 µL dNTPs (2.5 mM each), 0.2 µL Phusion HF polymerase (1 units/50 µL PCR, New England BioLabs), and 1 µL of sample DNA for a total reaction volume of 25 µL. Negative controls (all of the above without DNA) were amplified for every PCR reaction.

All PCR reactions were visualized on a 0.7% agarose gel stained with ethidium bromide to confirm targeted amplicon size and to check for contamination. Successful amplified products were cleaned using the ExoSap (exonuclease I and shrimp alkaline phosphatase) standard protocol. Briefly, 1 µL of ExoSap mix (3:1 Sap:Exo) was added to 4 µL of each product. Products were incubated for 15 min at 37 °C, followed by 15 min at 80 °C. Cleaned products were sequenced (Sanger) in both directions using amplification primers and Applied Biosystems BigDye® Terminator v3.1 (Thermo Fisher Scientific, Waltham, MA, USA). Cycle sequencing reactions consisted of 2 µL of the cleaned PCR template, 3.4 µL of water, 2 µL of 5× sequencing buffer, 1 µL of BigDye® Terminator v3.1 Ready Reaction Mix, and 1.6 µL of primer. The cycling protocol employed was 40 s at 96 °C, followed by 5 s at 50 °C, and 4 min at 60 °C. Resultant fragments were precipitated with Ethanol/EDTA/Sodium acetate and separated on an Applied Biosystem 3130×l genetic analyzer at the NOAA National Centers for Coastal Ocean Sciences (NCCOS) lab in Charleston, SC. All *mtMutS* sequences were visually inspected, edited and concatenated using Sequencher [42]. Geneious Prime 2020.1.1 [43] was used for cleaning and editing 28S sequences. Geneious Prime was also used to concatenate forward and reverse reads for individual samples and generate consensus sequences for the 28S marker.

2.3. Phylogenetic Inference

New sequences were aligned with sequences obtained from previous studies of octocorals in the Gulf of Mexico [44,45] and Caribbean [41,46], as well as sequences of other *Swiftia* spp. and closely related taxa downloaded from GenBank (NCBI). All sequences downloaded from GenBank are listed in Table S2.

Sequences were aligned using the MAFFT v7.45 [47,48] plug-in on Geneious Prime. The L-INS-i algorithm was used for both gene regions, with a scoring matrix of 200PAM/k = 2 and default settings for gap open penalty and offset value.

The larger *mtMutS* phylogeny included *Swiftia* spp. from both the Atlantic and Pacific oceans, whereas 28S sequences were only available for the Atlantic *Swiftia* spp. (*S. casta*, *S. pallida*, and *S. koreni*). For the cases where data for both loci were available from the same individual, we tested for phylogenetic congruence between data sets using a partition homogeneity test as implemented in PAUP4 [49]. Nuclear 28S and *mtMutS* sequences failed the test for phylogenetic congruence so they were analyzed independently.

For both nuclear and mtDNA data sets, we conducted both Bayesian and maximum likelihood (ML) analyses to examine phylogenetic relationships among the selected taxa. JModelTest 2.1.10 [50,51] was used to determine the most appropriate evolutionary model for nucleotide substitutions. The General-Time-Reversible model plus gamma distribution (GTR + G) was chosen as the best model for *mtMutS* (AICc = 10991.41) and the Tamura-Nei model plus invariable sites with a gamma distribution (TRN + I + G) was chosen for 28S (AICc = 14623.82).

Bayesian analyses were performed using BEAST (V2.6.3) [52]. BEAUTi (v2.6.3) was used to construct input files for BEAST. Default model parameters were used for both

nuclear 28S and *mtMutS*, with the exception of a Yule model of speciation and random local clock model as tree priors. Ten million generations were run with the first one million discarded (burn-in). Data and trees were sampled every 1000 generations. Convergence of the parameters were verified with Tracer V1.7.1 [53]. A maximum clade credibility (MCC) tree was visualized with the program FigTree (v1.4.4).

Maximum likelihood estimates were performed in RAxML-NG (v1.0.1) using the aforementioned substitution models for nuclear and mtDNA loci. Support for nodes was tested using 200 bootstrap replicates. A midpoint-rooted ML tree was used to plot node support values using both bootstrap and Bayesian posterior probabilities. Pairwise uncorrected p-distances were calculated for both genes using MEGA X software [54] and provided in Table 1.

Table 1. Pairwise uncorrected p-distances (%) for all *Swiftia* species at (**a**) mitochondrial mutS and (**b**) nuclear 28S.

	Swiftia exserta	***Swiftia casta***	***Swiftia kofoidi***	***Swiftia koreni***	***Swiftia pacifica***	***Swiftia pallida***	***Swiftia simplex***
(**a**)							
S. casta	14.9						
S. kofoidi	15.1	9.2					
S. koreni	13.5	7.1	3.9				
S. pacifica	14.6	8.8	2.1	3.2			
S. pallida	13.3	6.4	4.5	2.1	3.7		
S. simplex	13.3	6.4	4.2	1.8	3.4	1.1	
S. spauldingi	14.4	7.1	5.9	3.5	4.9	2.7	2.7
(**b**)							
S. casta	13.7						
S. koreni	12.2	8.1					
S. pallida	13.2	8.2	—-	1.7			

3. Results

3.1. Haplotype Variation in Swiftia exserta

The *mtMutS* (710 bp) gene region was successfully sequenced for 165 samples of *Swiftia exserta* from 11 study locations (Table S1). Only one polymorphic site at position 248 was found within this marker, representing two haplotypes. These haplotypes matched those from samples identified as *S. exserta* by taxonomic experts at the Smithsonian NMNH [20]. The most common haplotype (designated as T) was observed at every site, including those off the coasts of South Carolina and Florida. The minor haplotype (C) was only observed at three sites in the Gulf of Mexico, all at depths between 60–80 m; these included both impacted sites AAR and RTR, and a bank proposed for protection in the NW GoMx, Alderdice Bank (Figure 3). Both variants of *S. exserta*, those with red polyps and those with white polyps, shared haplotype T.

The 28S rDNA gene (655 bp) was successfully sequenced for 90 samples of *S. exserta* from 10 out of the 11 locations (Table S1). A total of 10 polymorphic sites were identified across all *S. exserta* 28S sequences, regardless of locality or polyp color. An insertion of two bases was present in all sequences, which made calling bases for the variable sites difficult in some cases. Alleles were deemed heterozygotes if two peaks were present and their height ratio was $\geq$50%. Both homozygous alleles were sampled for 6 out of the 10 variable sites. In these cases, the IUPAC degenerate nucleotide codes were applied. For the four sites in which only one of the homozygous alleles was sampled, an N was applied.

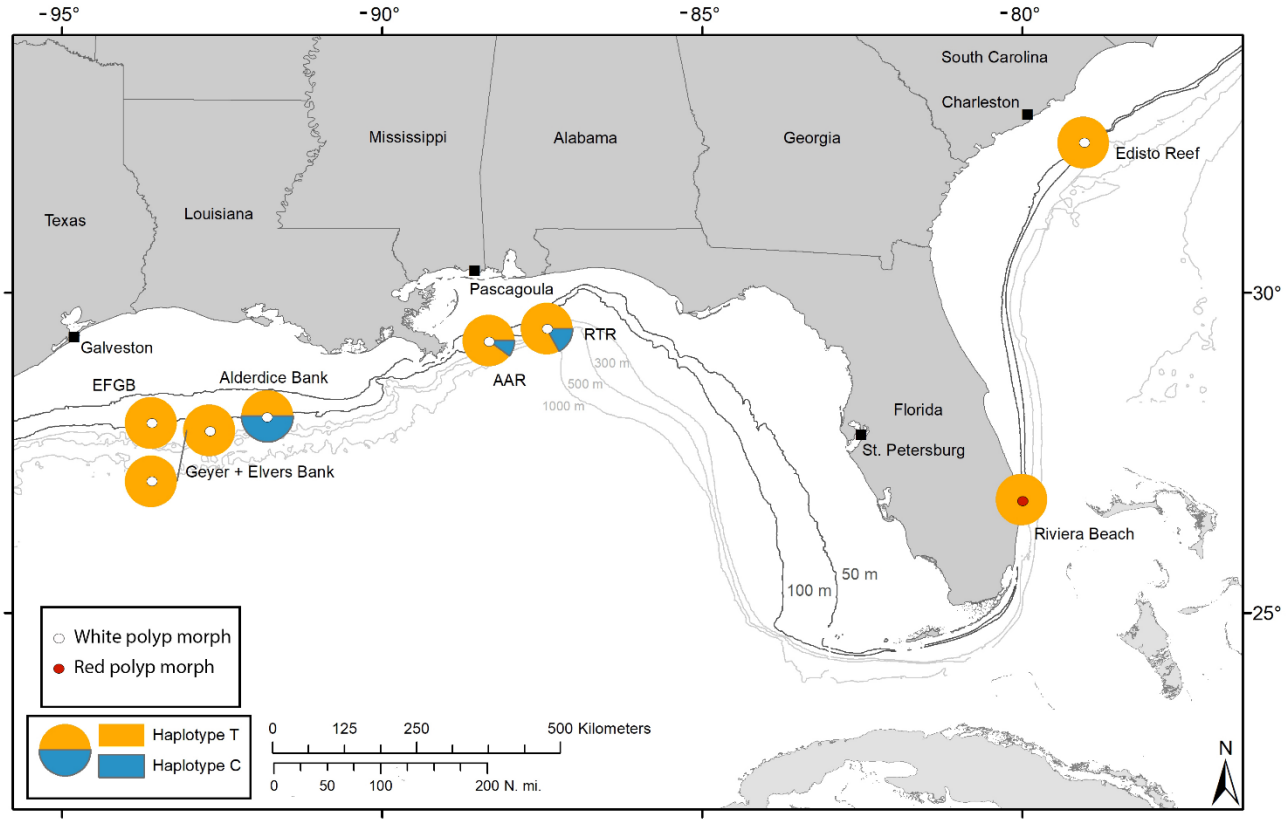

Figure 3. Distribution of mitochondrial mutS haplotypes of *Swiftia exserta*. Haplotype C was only observed at impacted sites AAR and RTR, and Alderdice Bank in NW Gulf of Mexico.

3.2. Haplotype Variation in Swiftia casta

A total of six samples of *S. casta* were successfully sequenced (Table S1) for the *mtMutS* region (710 bp). Two haplotypes were defined by a single polymorphic base, an A to C transition at position 547, with the A haplotype occurring in 5 out of 6 individuals. The 28S rDNA gene (710 bp) was also successfully sequenced for the same six samples. All sequences were observed to be monomorphic.

3.3. Phylogenetic Analysis

The final alignment of *mtMutS* contained 35 sequences (32 unique sequences) and covered 728 nucleotides. The final alignment of 28S sequences contained 24 unique sequences and covered 727 nucleotides. Both gene trees were largely congruent, recovering the same intrageneric groupings for the *Swiftia* genus. The *mtMutS* region of *S. exserta* allowed us to examine phylogenetic relationships for taxa in which we were unable to obtain 28S rDNA sequences.

Both phylogenies (Figures 4 and 5) recover *S. exserta* individuals in a clade with other plexaurids of the *Muricea*, *Plexaura*, and *Pseudoplexaura* genera, but they differ in the position of *S. exserta*. The *mtMutS* sequences of *S. exserta* are highly divergent from other members of the *Swiftia* genus (~11% uncorrected p-distance from other *Swiftia* species, Table 1) and are more genetically similar to *Muricea* spp. (Figure 4). Similarly, the 28S sequences of *S. exserta* are highly divergent from other members of the *Swiftia* genus (>12% uncorrected p-distance from other *Swiftia* species, Table 1) and are more closely related to the sister *Plexaura–Pseudoplexaura* clade (Figure 5). The two gene genealogies also recovered the same groupings for the other *Swiftia* species. In both phylogenies, *Swiftia* is polyphyletic with *S. exserta* and *S. casta* falling outside of the monophyletic clade of the other *Swiftia*

species included in this study. These results suggest the *Swiftia* genus is polyphyletic with three distinct clades: *S. exserta*, *S. casta*, and the rest of the *Swiftia* species.

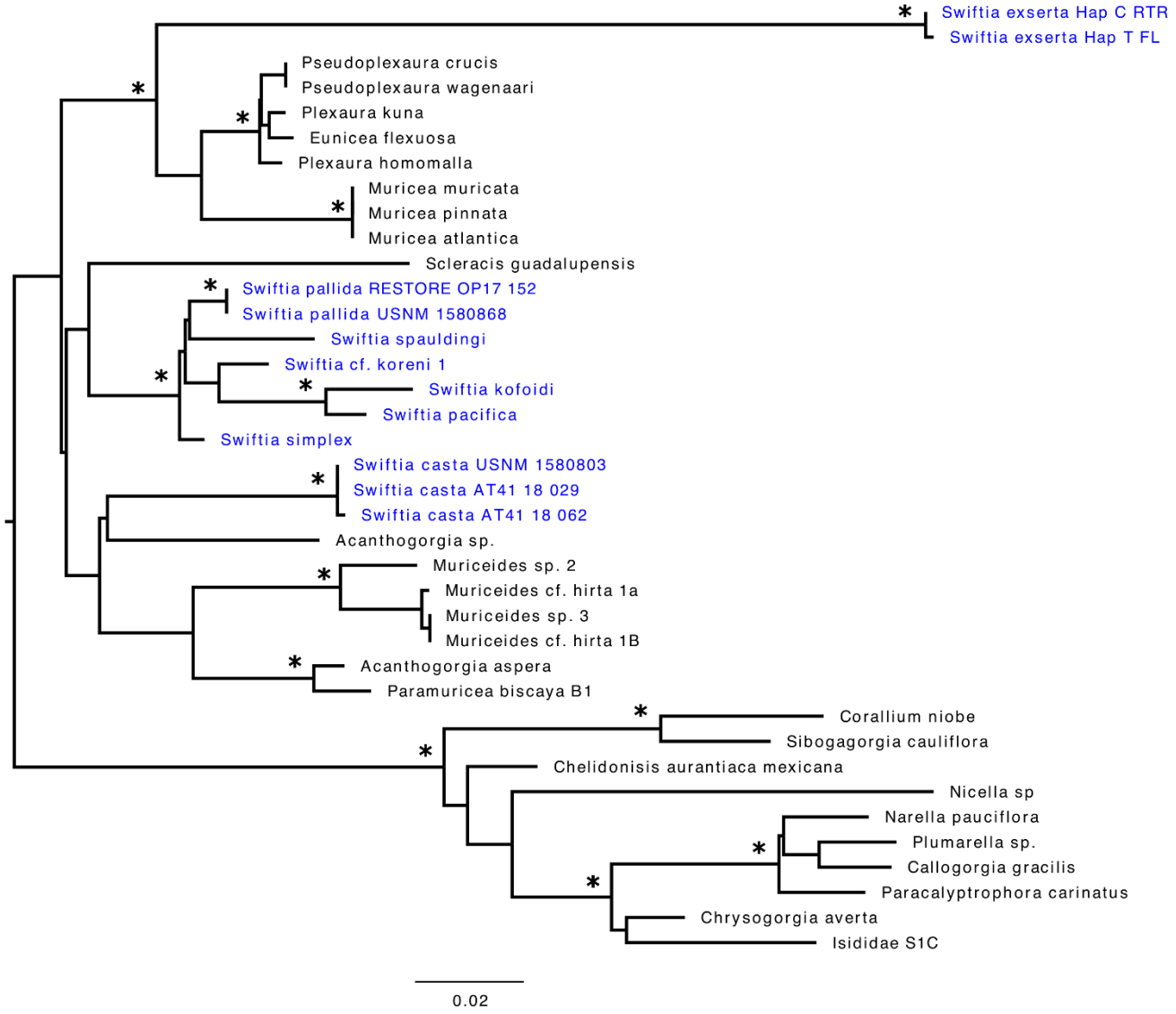

Figure 4. Midpoint-rooted Maximum Likelihood (ML) phylogeny of mitochondrial barcode *mtMutS*, including all Atlantic *Swiftia* species (blue). Asterisks represent bootstrap support above 80% and posterior probability greater than 0.99.

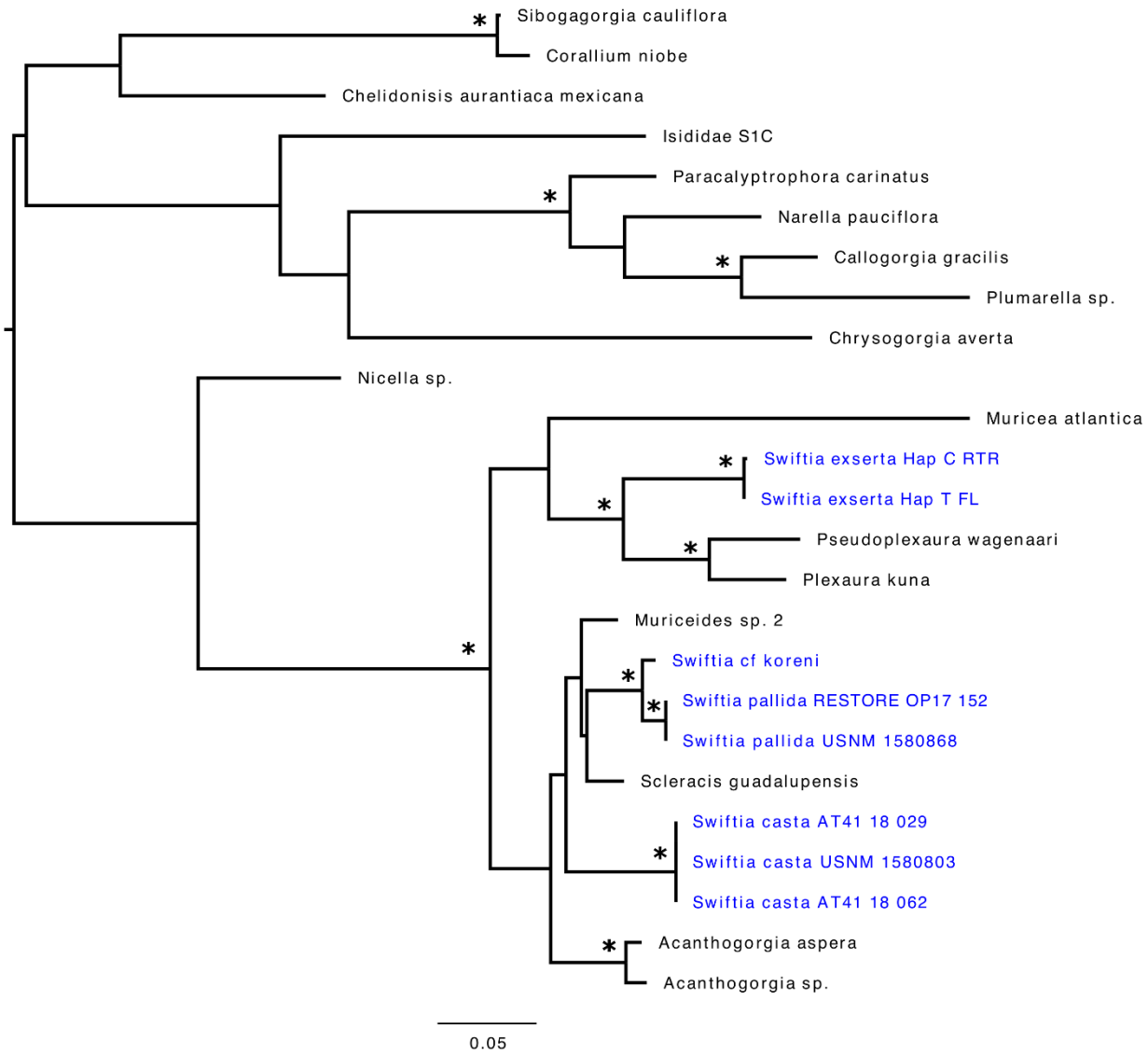

Figure 5. Midpoint-rooted ML phylogeny of nuclear barcode 28S rDNA, with all *Swiftia* species in blue. Asterisks represent bootstrap support above 80% and posterior probability greater than 0.99.

4. Discussion

The impetus for this molecular study was to identify *Swiftia exserta* sea fans in the Gulf of Mexico impacted by the *DWH* oil spill and explore potential genetic differences between polyp morphotypes (red and white). The *mtMutS* sequences of hundreds of *S. exserta* specimens collected in the Gulf of Mexico and the Atlantic were identical to sequences from specimens identified as *S. exserta* by taxonomic experts at Smithsonian NMNH. Furthermore, we compared both nuclear and mitochondrial DNA sequences of impacted white-polyp *Swiftia exserta* to red-polyp *S. exserta* from Florida and found no consistent evidence of species-level divergence.

Studies over the last decade have shown that a combined multi-locus phylogenetic and morphological approach is imperative to properly delineate species of deepwater corals [55]. Unfortunately, like many octocorals, the original description of *S. exserta* was morphological, and based on samples that can no longer be sampled for quality DNA. A preliminary morphological examination of sclerites from *Swiftia exserta* phenotypes was conducted using scanning electron microscopy and the results suggested no significant difference in sclerite morphology and composition, spindle size (ANOVA $p = 0.97$), or

capstan size (ANOVA $p = 0.61$) between the two morphotypes [13,20]. Thus, we proceed with the hypothesis that the impacted species of *Swiftia* with white polyps in the GoMx is in fact a conspecific of *S. exserta*, exhibiting phenotypic plasticity, a phenomenon that is very common among octocorals [28,35,56–58]. The red-polyp variant of *S. exserta* has only been observed at shallower depths (~10–30 m), while the white-polyp variant occurs at mesophotic depths from 50–200 m, and they share a haplotype of *mtMutS*. This pattern may indicate the difference in polyp color could be a result of different temperature or nutrition source.

Additionally, and perhaps of greater importance, the placement of *Swiftia* in a phylogeny with other Holaxonians revealed extreme genetic divergence and a need for major revisions to the genus. We found *S. exserta* to be 12.8–15.1% genetically divergent (uncorrected p-distances) from the rest of the *Swiftia* spp. at the *mtMutS* locus and 11.4–12.2% divergent from other Atlantic *Swiftia* spp. for 28S (Table 1). These divergence values are strikingly higher than the minimum genetic distances previously reported for congeneric octocoral species (France and Hoover, 2002: 0–2.8%; McFadden et al., 2011: 0–7.12, mean 2.2). McFadden [22] also reported a mean minimum genetic distance of 0.31% among sister taxa in the same clade.

Bayesian and maximum likelihood gene tree topologies of *mtMutS* were congruent and placed *S. exserta* as sister to a well-supported clade of shallow-water *Muricea*, *Plexaura*, *Pseudoplexaura*, and *Eunicea*, all of which co-occur with *S. exserta* off the coast of Florida [59]. The inferred relationships in this clade are identical to those reported in previous studies [41,46]. The placement of *S. exserta* sister to a clade consisting of shallow-water plexaurids does not seem unusual; *S. exserta* is only one of two known *Swiftia* species that can be found as shallow as 18 meters [13,60]. The gene tree of the 28S gene region also placed *S. exserta* in a clade with *Pseudoplexaura*, *Plexaura* and *Muricea*, with it sister to a clade formed by both *Pseudoplexaura wagenaari* and *Plexaura kuna*. This discrepancy between the gene trees can be due to the smaller sample size of the 28S dataset or to different evolutionary histories of each gene.

All tree topologies, regardless of gene or evolutionary model, show three distinct clades of *Swiftia*—one consisting of only *S. exserta*, another consisting of *S. casta* among other plexaurids, and the third including the remainder of the western Atlantic *Swiftia* species. The third larger clade consists of *Swiftia* spp. sister to another plexaurid, *Scleracis guadalupensis*. This relationship is consistent with previous studies using *mtMutS* [44,46].

It is not surprising that *Swiftia* taxonomy appears problematic; previous studies have suggested the genus needs revision [46,60,61]. The gene genealogies in this study suggest that the genus *Swiftia* is likely a construct founded in morphological similarities rather than evolutionary relatedness, a major issue that has made revisions of octocoral taxonomy and systematics challenging [28–30]. Bayer [62] placed *Swiftia* under the family Paramuriceidae, noting that although Deichmann [63] assigned it to Gorgoniidae, he believed it had more in common with the paramuriceids and plexaurids. It was later placed in the family Plexauridae, where it currently lies [64]. We also recognize *S. exserta* was originally called *Gorgonia exserta* by Ellis and Solander [12]. It was later synonymized by Duchassaing and Michelotti [11], and this may have led to the polyphyly of the genus we document here.

While the placement and divergence of *S. exserta* is striking, this divergence within genera is not uncommon among octocorals [22,34,35]. Species delimitation of octocorals can be equivocal when only using morphology or only DNA barcoding data. For example, a newly discovered *Swiftia* sp. from off the Costa Rican margin matches sequences from GenBank of *Swiftia simplex* with 100% similarity, but their morphology differs [61]. The study noted that the taxonomic status of *S. simplex* needs revision and, therefore, the *S. simplex* specimen could have been misidentified. This discordance between morphological and molecular data is very common among octocorals [28,35,55,65]. Additionally, the lack of molecular barcode sequences for museum-vouchered *Swiftia* spp. in GenBank has hindered the ability to resolve issues within the genus. Although other studies suggest the *Swiftia* genus to be monophyletic, their phylogenies never included sequences from

S. casta or *S. exserta*. The phylogeny presented by Breedy et al. [61] included a sequence from GenBank (COI: KC984618; mutS: KC984582) misidentified as *S. exserta*, which has since been modified to *Swiftia* sp. (A. Quattrini). This only further highlights the dire need for reliable DNA barcodes with taxonomic accuracy.

Cryptic speciation is an alternative theory that could account for the extreme divergence presented here. As *S. exserta* was first described in the Caribbean, it is possible that we have not sampled the true *S. exserta*, but rather a new species with similar morphology. However, we compared our sequences to sequences obtained from samples identified as *S. exserta* [20] (USNM #s 1018489, 1021359, and 1021503) by taxonomist Ted Bayer (Smithsonian NMNH) and found 100% similarity. Nevertheless, samples of *S. exserta* from the type locality in the Caribbean must also be obtained and studied to clarify this issue.

Phylogenies are useful tools to understand taxonomy and biodiversity, but they can also be a powerful tool for distinguishing conservation priorities. Phylogenetic diversity, rather than haplotypic diversity, is a measure of evolutionary legacy and biodiversity defined as the sum of the branch lengths in the phylogeny of a given taxon [66,67]. This approach for measuring biodiversity has shown that organisms on long branches such as *S. exserta* are at higher risk for extinction, and so are their closest relatives [67,68]. With no apparent close relatives in the Gulf of Mexico, this unique lineage of *Swiftia* at impacted sites AAR and RTR warrants attention. Furthermore, accurately documenting species identities and distributions is fundamental information for generating habitat assessments and predictive models, two overarching aims for restoration in the GoMx. The results from the larger NOAA RESTORE population connectivity study on *S. exserta* will be key to understanding gene flow in the species and the best methods for restoration and conservation, including designation of marine protected areas of impacted coral communities.

This study also provides the first publicly available nuclear barcodes for the taxon referred to as *S. exserta* in the Gulf of Mexico. *S. exserta* is considered the "type species" for the genus *Swiftia*, so this addition to GenBank is critically important, as well as somewhat confounding. One of the major problems hindering biodiversity conservation is lack of knowledge. This study stemmed from a need for accurate species identifications to inform resource management, conservation and restoration. *Swiftia exserta* was not the only octocoral severely impacted by the *DWH* oil spill, as several deep-sea species, particularly *Paramuricea biscaya*, were also impacted [69]. Our study highlights the need to revisit and confirm species identities, distributions, and phylogenetic relationships of several impacted octocoral species. Before the spill, the identity and distribution of *Swiftia* sea fans was uncertain, and this remains the case for other injured octocoral species. The phylogenetic results of this study are novel and undoubtedly warrant a major revision of the *Swiftia* genus. It is imperative that an approach combining morphology and phylogenetics be undertaken to resolve taxonomic issues and gain a better understanding of the biology and ecology of these extremely vulnerable, poorly studied ecosystem engineers.

Supplementary Materials: The following are available online at https://www.mdpi.com/article/10.3390/d13040172/s1, Table S1: Sample information for all sequences generated for this study, Table S2: Sequences downloaded from GenBank and used in phylogenetic analyses.

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