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Ligia Collado-Vides
Department of Biological Sciences and Southeast Environmental Research Center, Florida International University, colladol@fiu.edu

Alain Duran
Department of Biological Sciences, Florida International University, alduran@fiu.edu

Elizabeth Armenis
Department of Biological Sciences, Florida International University, earmenis@fiu.edu

Valéria Cassano
Universidade de São Paulo

Deron Burkepile
University of California, Santa Barbara

See next page for additional authors

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Authors

Ligia Collado-Vides, Alain Duran, Elizabeth Armenis, Valéria Cassano, Deron Burkepile, Andrew A. Shantz, Laura Palma, Jhoana Díaz-Larrea, and Abel Sentíes

SEASONAL RECRUITMENT AND SURVIVAL STRATEGIES OF *PALISADA CERVICORNIS* COMB. NOV. (CERAMIALES, RHODOPHYTA) IN CORAL REEFS [1]

Ligia Collado-Vides[2]
Department of Biological Sciences and Southeast Environmental Research Center, Florida International University, Miami, FL, 33199 United States
Phone 305 348 22 74 Fax 305 438 1986 and Cell 305 7901219
Alain Duran, Elizabeth Armenis
Department of Biological Sciences, Florida International University, Miami, FL, 33199 United States
Valéria Cassano
Departamento de Botânica, Universidade de São Paulo, Rua do Matão 277, São Paulo 05508-900, Brazil
Deron Burkepile, Andrew A. Shantz
Department of Ecology, Evolution, & Marine Biology and Marine Science Institute, University of California, Santa Barbara, CA, 93106 United States
Laura Palma
Department of Biological Sciences, Florida International University, Miami, FL, 33199 United States
Jhoana Díaz-Larrea, Abel Sentíes
Departamento de Hidrobiología, Universidad Autónoma Metropolitana-Iztapalapa, Apdo. Postal 55-535, México D.F, 09340, México
and *Mutue Toyota Fujii*

Núcleo de Pesquisa em Ficologia, Instituto de Botânica, Av. Miguel Estéfano, 3687 – 04301-902
São Paulo, Brazil

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[2]Author for correspondence: email colladol@fiu.edu

Running title: Survival strategies of *Palisada cervicornis* comb. nov.

Abstract

As marine tropical ecosystems deteriorate and lose biodiversity, their communities are shifting to dominance of a few species, altering ecosystem's functioning and services. Macroalgae are are becoming dominant on coral reefs, and frequently observed outcompeting corals. Turf algal assemblages are the base of energy flow in these systems and one of the most abundant types of macroalgae on coral reefs, but little is known about their biology and diversity. Through molecular and morphological analyses, we established the proper identity of the turf-forming species *Laurencia cervicornis*, and by studying seasonal recruitment and the impact of herbivorous fishes on its abundance, we describe its survival strategy. The molecular analyses using a total of 45 *rbc*L gene sequences including eight current genera within the *Laurencia* complex and two new sequences of *L. cervicornis*, strongly support the new combination of *Palisada cervicornis* comb. nov. In addition, a detailed morphological characterization including the description of reproductive structures, is provided. *P. cervicornis* was seen recruiting in all seasons but was typically in low abundance. Specimens grown on tiles in fish exclosure cages were devoured in less than 4 hours when offered to fishes. Even though many species of the *Laurencia* complex have chemicals that deter herbivory, species within the genus *Palisada* lack

feeding deterrents and are highly palatable. We suggest that *P. cervicornis* is a palatable species that seems to survive in the community by obtaining a size-refuge from herbivory within turf communities..

Key words: Algal recruitment, Florida, herbivory, *Laurencia cervicornis*, *Palisada cervicornis*, phylogeny, *rbc*L gene, Rhodomelaceae, taxonomy, turf algae.

Abbreviations: BI, Bayesian inference; bp, base pairs; ML, maximum likelihood; NJ, neighbor joining; *rbc*L gene, large subunit of the Ribulose 1,5-bisphosphate carboxylase/oxygenase gene.

Introduction

Tropical coastal ecosystems are exposed to major anthropogenic stressors that are causing a shift in dominance and/or composition of species, altering the ecosystem's diversity andfunctioning (Duarte 2000, McGlathery 2001). Particularly on coral reefs, reduced grazing pressure and increases in nutrients have facilitated a shift from coral-to macroalgae-dominated systems (Hughes 1994, Gardner et al. 2003, Doropoulos et al. 2013). Field monitoring and experimental studies (e.g. Artmitage et al. 2005, Collado-Vides et al. 2007, Mumby 2009, Duran et al. 2016) have reported that different groups of macroalgae have the ability to dominate coral reefs depending upon nutrient availability and levels of herbivory.

Marine macroalgae encompass over 10,000 species globally (Guiry, 2012). For the Caribbean Sea, Littler and Littler (2000) described around 553 species of macroalgae, and more recently Dawes and Mathieson (2008) described 693 algal species in Florida alone. This vast taxonomic and morphological diversity has resulted in a relatively low taxonomic resolution of most ecological studies. The vast majority of studies reporting shifts of species dominance are carried out using the word ‘macroalgae’ as their unit of measurement, while other studies use form-functional groups as their measurement unit (Bruno et al. 2009, Suchley et al. 2016), and still fewer studies have reported results at the genus and species level (Burkepile 2009, Ceccarelli et al. 2011, Duran et al. 2016). However, particular macroalgal species can have profound effects on coral-algae interactions; for example, crustose coralline algae (CCA) are known to be an important group of algae related with coral settlement; however, only a few CCA species actually facilitate coral recruitment (Harrington et al. 2004). Moreover, it is expected that future changes in temperature and CO_2 will affect the composition of macroalgae and their interactions with corals due to species-specific physiological tolerances and increasing algal allelopathic strength (Ober et al. 2016, Del Monaco et al. (2017).).

Macroalgal turf, a loosely defined assemblage of aggregated compact small algae (Connell et al. 2014 for a review of the term), likely play important roles in coral reef communities, such as primary producers, structure providers, nitrogen fixers, and facilitate the accumulation of sediments (McCook 1999 for a review). Moreover, algal turfs can have both positive and negative effects on coral recruits (Arnold et al. 2010, Venera-Ponton et al. 2011), and through direct contact, turfs can negatively affect coral growth (Wild et al. 2014). Turfs in the Caribbean Sea are composed of species from such genera as: *Laurencia* J.V. Lamouroux, *Sphacelaria* Lyngbye, and *Gelidium* J. V. Lamouroux, and small filamentous species of all four algal phyla and cyanobacteria (Hay 1981, Carpenter 1986, Littler and Littler 2013). In the Florida Keys coral reefs, species of the *Laurencia* complex are frequently observed , but their abundance falls into the lower end of the dominant groups of algae, while brown algae such as

Dictyota spp., *Lobophora* spp. and the green calcareous *Halimeda* spp. occupy more of the reef (Yñiguez et al. 2015). However, recruitment and successional studies in the area show that *Laurencia* species are more abundant than previously recognized (Duran et al. 2016) but difficult field identification and consistent removal via high grazing pressure limit their recognition. Furthermore, because *Laurencia* spp. are turf-forming, their abundance might be frequently underestimated. Thus, studies may frequently overlook species with potentially important roles on coral reefs.

Regulation of algal abundance has been related to the abundance of herbivorous fishes. Several experimental studies demonstrate that fish grazing can substantially influence the abundance of different macroalgal species (e.g. Bellwood et al. 2006, Blanco et al. 2011). However, algae can avoid grazing by producing biologically active compounds that deter herbivory (Gressler et al. 2010, 2011). *Laurencia* spp. are some of the most chemically defended seaweeds and produce a large number of secondary metabolites (Pereira et al. 2003, Manilal 2011), 400 of which might have some deterrent effect on fishes (Hay et al. 1988). This might explain why herbivory is relatively low for some *Laurencia* species (Loffler et al. 2014). However, some species within the genus contain similar secondary compounds that do not affect grazing (Hay et al. 1988). Furthermore, some species, such as *Laurencia intricata* J.V. Lamouroux, are nutritionally rich in lipids, protein, amino acids and fatty acids (Gressler et al. 2010) making them highly palatable. Although species-level identification of algae is difficult and often requires specialized methods that go beyond morphological characterization, proper identification of species provides important information about many characteristics of organisms that clarify their role in the ecosystem (Knowlton and Jackson 1994, De Clerck et al. 2013, Fong and Fong 2014).

The taxonomy of the red algal genus *Laurencia* is extremely complicated due to the large degree of morphological plasticity, the worldwide distribution from temperate to tropical oceans, and the diversity of environments in which it is observed (Fujii et al. 2011). Consequently, the taxonomic position of species within the *Laurencia* complex has rapidly changed as new morphological and molecular data are recognized. Over the past two hundred years, since the establishment of the genus *Laurencia* (Lamouroux 1813), many taxonomic changes have been proposed resulting in the current *Laurencia* complex. Currently, it is composed of eight formally proposed genera: *Laurencia* J.V. Lamouroux *sensu stricto*, *Osmundea* Stackhouse (1809), *Chondrophycus* (Tokida & Y. Saito) Garbary & J.T. Harper (Garbary and Harper 1998), *Palisada* (Yamada) K. W. Nam (Nam 2007), *Yuzurua* (K.W. Nam) Martin-Lescanne (Martin-Lescanne et al. 2010), *Laurenciella* Cassano, Gil-Rodríguez, Sentíes, Díaz-Larrea, M. C. Oliveira & M. T. Fujii (Cassano et al. 2012a), *Coronaphycus* Metti (Metti et al. 2015), and the most recently established *Ohelopapa* F. Rousseau, Martin-Lescanne, Payri & L. Le Gall (Rousseau et al. 2017). Within this complicated taxonomic reality, it is difficult to come up with proper identification of this important complex of species on coral reefs, causing potential underestimation of their diversity and abundance.

In this study, taxonomists and ecologists joined forces to properly identify a turf-forming species in coral reefs, and understand the causes of its low abundance. During a recruitment and successional study of macroalgae in the Florida Keys (Duran et al. 2016), we noticed the presence of a unique tiny turf-forming species that we identified as *Laurencia cervicornis* Harvey. This tiny (< 1 cm tall) species was previously merged by Howe with *Laurencia corallopsis* (Howe 1918), now known as *Palisada corallopsis* (Montagne) Sentíes, M.T. Fujii & Díaz-Larrea (Sentíes and Díaz-Larrea 2008); however, Littler and Littler (2000), and Wynne *et* *al.* (2005) did not recognize this merger, keeping both species: *L. cervicornis* and *P. corallopsis* as taxonomically distinct entities. Furthermore, the previously known *Laurencia coelenterata* D. L. Ballantine & Aponte, now established as *Osmundea coelenterata* (D. L. Ballantine & Aponte) M. T. Fujii, Sentíes & Areces (Fujii et al. 2016), is also a small species that in the field can easily be confused with *L. cervicornis* or *P. corallopsis* unless clear iridescence is observed. We were able to identify and study this species only by growing it on tiles kept in the laboratory under controlled conditions in the total absence of grazers. Therefore, the first goal of this study was to determine the taxonomic identity of our specimens and provide a detailed morphological and molecular analysis of this species. Secondly, to understand the forces controlling the extremely low abundance of *Laurencia cervicornis* in the Florida Keys, we asked the following questions: 1) Is *L. cervicornis* regularly recruiting? And if so, how frequent is this species recruiting in the study site? 2) If recruitment is frequent, why is the species not abundantly present? We expected to find recruits of *L. cervicornis* throughout the year, but its abundance would be rapidly controlled by herbivores, which could explain the extremely low abundance of this species in the field.

Materials and Methods

Study site

This study was conducted in the Florida Reef Track, near Pickles Reef (Key Largo, Florida 25°00’05” N, 80°24’55” W) in a spur and groove reef at a mid-depth area (5-6 m). Parrotfish and surgeonfish are the dominant herbivorous fishes on Pickles Reef with an average abundance of 5087.17 g per 100 m^2 while the long-spined urchin, *Diadema antillarum* Philippi (1845), is present, only at very low densities (<1 individual per 50 m^2) (Duran et al. 2016). Water temperature varies seasonally ranging from 24 ºC in winter (December and January) to 30 ºC during summer. Collection of material and experiments were conducted with the approval of the Florida Keys National Marine Sanctuary (permits: FKNMS-2009-047 and FKNMS-2011-090).

Taxonomic approach

Samples of *Laurencia cervicornis* were collected from Pickles Reef, Key Largo, Florida, USA (Table S1).

Molecular analyses

The samples used for molecular analysis were dried in silica gel. The total DNA was extracted, using the DNeasy Plant Mini Kit (Qiagen, Valencia, CA, USA) according to the manufacturer's instructions. DNA was amplified by polymerase chain reaction (PCR) using the reaction mix of the Promega® (Madison, WI, USA) in a final volume of 25 µL. The samples were amplified in three overlapping parts with the primer pairs: FrbcLstart - R753, F492 - R1150 and F993 - RrbcS (Freshwater and Rueness 1994). Successfully amplified products were purified with the column MicroSpin™ S-300 HR (GE Healthcare, Buckinghamshire, UK) following the manufacturer's protocol. Sequencing reactions were performed with BigDye™ Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems, Foster City, USA) on an ABI PRISM 3100 Genetic Analyzer (Applied Biosystems). The primers used for sequencing were the same used for the PCR amplification.

Sequence alignments and phylogenetic analysis

DNA sequences were analyzed and manually edited in BioEdit v7.0.9.0 (Hall 1999). Identity of generated sequences was checked through BLAST available at the NCBI website (http://www. ncbi.nlm.nih.gov).

The model used in the Bayesian inference (BI) and maximum likelihood (ML) analyses was the general-time-reversible model of nucleotide substitution with invariant sites and gamma distributed rates for the variable sites (GTR + I + G). This model was selected using jModeltest 2.1.10 (Darriba et al. 2012) under the Akaike information criterion (AIC) as implemented on the CIPRES Science Gateway v3.3. For Bayesian inference analysis, two runs of four chains of the Markov chain Monte Carlo (one hot and three cold) of 10,000,000 generations, with sampling every 1,000 generations, and the initial 10,000 generations in both runs were discarded as 'burn in' to build the consensus tree using MrBayes (v3.2) (Ronquist et al. 2012) implemented on the CIPRES portal. Maximum Likelihood (ML) was performed with PhyML (Guindon and Gascuel 2003) using TOPALi v2.5 graphical interface (Milne et al. 2004) under heuristic search with 100 bootstrap replicates. Neighbor-Joining (NJ) analysis was performed under heuristic search with 2,000 bootstrap replicates using PAUP 4.0b8 (Swofford 2002). Pairwise distances were calculated using the uncorrected 'p' distances in PAUP.

Morphology

Voucher specimens and material for morphological studies were fixed in 4% formalin/seawater solution or pressed as herbarium sheets. Transverse and longitudinal hand-sections were obtained with a razor blade and stained with 0.5% aqueous aniline blue solution acidified with dilute 1N HCl. The microscopic measurements were obtained from the middle portions of the thallus using a calibrated ocular micrometer. Photomicrographs were obtained using a Zeiss Axiocam ERC-5S digital camera (Göttingen, Germany) coupled to an Axio skop 2 Zeiss microscope (Göttingen, Germany) and Stemi SV6 Zeiss stereomicroscope (Göttingen, Germany). The vouchers were deposited in the herbaria of the Botanical Institute, São Paulo (SP), Brazil, of the University of São Paulo (SPF), and Fairchild Tropical Botanical Garden

Herbarium (FTG 167768). Abbreviations follow on-line Index Herbariorum: http://sciweb.nybg.org/science2/IndexHerbariorum.asp (Thiers 2017, continuously updated).

Ecological approach

Recruitment experiment

Eight experimental plots (9 m^2: 3 x 3 m) were established in June 2009 to examine the effects of herbivory on benthic community dynamics. Briefly, within each plot we established 2 1 x 1m herbivore exclusion cages and 2 exclusion cage controls made of three walls to mimic the effects on flow but an open top to allow herbivores access (for a detailed explanation of methods see Zaneveld et al. 2016). Recruitment of *Laurencia cervicornis* was assessed using 10 x 10 cm limestone tiles (obtained from quarried South Florida Pleistocene limestone) attached to plastic mesh with plastic cable ties and secured to the ground with galvanized staples. Two tiles were placed in each exclosure cage (n = 8 plots x 2 exclusion cages x 2 exclusion control cages = 32 tiles) and left in the field for three months. To assess seasonal variability, tiles were collected and replaced with new tiles every three months. A total of three deployments covering three seasons: fall (September - December 2011), winter (December 2011 - March 2012) and spring (March - June, 2012) were accomplished. Collected tiles were brought to the laboratory and placed in individual aquaria to allow algae to grow to a size that allowed species identification. Aquaria were previously prepared to replicate optimal conditions (12:12 light-dark period, salinity: 35-36 PSU, temperature: 25-28 ºC, constant water circulation and air pump). Within a week of collection, the percent cover of *L. cervicornis* was visually quantified and sorted out into the following categories: 0.1 % for a single individual occupying <0.5% of the tile; 0.5% for less than three sparse individuals that occupied <1% cover; 1% for >1 individuals that occupied <5%

cover; and then multiples of 5 were used from 5 to 100% coverage. After inspection, tiles were returned to their corresponding aquaria and maintained for three more months to promote growth and to discover reproductive structures in the recruited specimens.

The average percent cover of the two tiles placed within each cage for the eight plots was used to calculate seasonal abundance and compared across seasons using ANOVA. All analyses were conducted using R program from R Development Core Team (2012), version 3.2.2.

Impact of herbivorous fishes on Laurencia cervicornis *experiment*

Feeding assays were used to assess herbivory impact on the abundance of *L. cervicornis*. In May 2015, 50 limestone tiles (similar to those described above) were deployed for 6 months within a single 2 x 1 x 0.5 m (length x width x height, mesh size 2.5 cm diameter) cage at a 12 m depth to study recruitment and growth of macroalgae, including *L. cervicornis*. The cage was located off Key Largo (24.9500° N, 80.4540° W), approximately 50 m from the Aquarius Reef Base. From November 9-13 of 2015, nine tiles per day were removed from the exclosure and exposed to herbivorous fishes each day. Divers surveyed and photographed each tile at 4-hour intervals. The first photographs were taken as soon as the tiles were removed from the cage and were employed as a baseline in the morning at ~08:00 (initial t = 0). Additional photographs were taken midday (~12:00; t = +4 hours) and late afternoon (~16:00; t = +8 hours). We calculated the percent cover of *L. cervicornis* from photos at each time point using Vidana spatial ecology software (http://www.marinespatialecologylab.org/resources/vidana/). Percent cover was averaged within time points (initial, noon and evening) and repeated measurement ANOVA was used to compare removal rate of *Laurencia cervicornis* within the treatment day. All analyses were conducted using the R program (R Development Core Team 2012, version 3.2.2).

Results

Laurencia cervicornis is a tiny iridescent species living intermingled with other small turf-forming species. In the study area, turfs were frequently covered by sediments making it difficult to distinguish species. We discovered *L. cervicornis* in recruitment tiles kept in aquaria in the laboratory. In the field, it was necessary to flush the sediments covering turfs in order to detect some small iridescent tips intermingled with the rest of turf-forming species. Accordingly, it was impossible to estimate *L. cervicornis* abundance in the field and the results presented here are restricted to observations from our recruitment tiles.

Molecular analysis

A total of 45 *rbc*L gene sequences were used in this study, including three newly generated sequences, two of *L. cervicornis* and one of *P. corallopsis* from Florida, US. The remaining sequences were obtained from GenBank. Two species of Rhodomelaceae were used as outgroups, *Chondria collinsiana* M. Howe and *C. dasyphylla* (Woodward) C. Agardh (Table S1). The final *rbc*L gene alignment consisted of 1,446 bp. The topology of the consensus tree is shown in Fig. 1. The *Laurencia* complex was resolved as monophyletic with full support based on the models applied to the sequences analyzed. Species of the *Laurenci*a complex were separated into eight clades corresponding to the current genera of the complex: *Chondrophycus*, *Coronaphycus*, *Laurencia*, *Laurenciella*, *Palisada*, *Osmundea*, *Ohelopapa* and *Yuzurua*, with high to moderate support values, except *Ohelopapa* that joined the *Palisada* but without support. Within the *Palisada* assemblage, two main subclades were recognized, both with high support. The two samples of *L. cervicornis* grouped with full support and the intraspecific divergence was 0.2%. *L. cervicornis* is closest phylogenetically to *P. furcata* and *P. corallopsis* from which it diverged by 3.1-3.5% and 2.7-3.3%, respectively. *Palisada corallopsis* from Florida diverged from the sample from Mexico by 0.4%, indicating that both are the same taxonomic entity. The interspecific divergence within the *Palisada* clade ranged from 1.4% (*P*. cf. *perforata* and *P*. cf. *cruciata* from New Caledonia) to 6.8 % (*P*. *corallopsi*s from Mexico and *P*. *perforata* from the Canary Islands).

Our phylogenetic analyses strongly support the transfer of *Laurencia cervicornis* to the genus *Palisada*, and the nomenclatural change is proposed here:

Palisada cervicornis (Harvey) Collado-Vides, Cassano et M. T. Fujii **comb. nov**.

Basionym: *Laurencia cervicornis* Harvey, Smithsonian Contributions to Knowledge 5(5): 73, pl. 18C, 1853.

Morphology

Plants grown in aquaria were erect, forming reddish brown tufts or hemispherical clumps up to 5-6 cm high but were never observed over 1 cm high in the field. The plant exhibits blue iridescent rings throughout the thalli (Fig. 2A). The thalli are terete, cartilaginous in texture, and are 0.7-1.2 mm in diameter. Erect axes arise from a single discoid holdfast. Upright branches are scarcely ramified; branching is irregular to dichotomous usually with 1-2 orders of branches (Fig. 2A). Cells in surface view are polygonal, isodiametric, 22-48 μm long and 16-34 μm wide. Secondary pit connections between cortical cells are present (Fig. 2B). In the transverse section, the thalli have one or two layers of pigmented cortical cells 17-23 μm long and 19-32 μm in diameter, and four or five layers of colorless medullary cells, rounded or slightly radially elongated, 51-101 μm long and 30-83 μm wide. Medullary cell walls are uniformly thickened, but lenticular thickenings are absent. Each vegetative axial segment produces two pericentral cells (Fig. 2C). Tetrasporangial branchlets are cylindrical, simple or compound, 1.0–2.7 mm long and 0.5–1.2 mm wide. The arrangement of the tetrasporangia is in a right-angle pattern in relation to fertile branchlets. Mature tetrasporangia are tetrahedrally divided, 38-91 μm in diameter. In female thalli, cystocarps are conical with a protuberant ostiole, developed at the subapical portions, partly immersed in the branches, 578-852 μm in diameter. Carposporangia are clavate, 78-113 μm long and 24-95 μm in diameter (Fig. 2D). Male branches are characteristically swollen, 0.5-1.2 mm in diameter. In longitudinal section through a fertile branchlet, the spermatangial pits are cup shaped, and an axial cell row is discernible at the base (Fig. 2E). Spermatangial trichoblasts arise from axial cells, consisting of fertile and sterile branches (Fig. 2F); the fertile branches produce many ovoid spermatangia, 7-10 μm long and 3.5-5.8 μm in diameter, and terminate in vesicular sterile cells, 19-30 μm long and 13-21 μm in diameter; each spermatium possesses an apical nucleus (Fig. 2F).

Ecological approach

Recruitment and seasonality

Palisada cervicornis recruited to each of the 32 tiles throughout the study period; no significant differences were found between exclosure and control treatments (ANOVA, $F_{1,69} = 0.011$, $p = 0.917$). Seasonal differences in recruitment were significant with highest abundance in spring compared with fall and winter (Fig. 3; ANOVA, $F_{2,69} = 4.499$, $p = 0.014$; Tukey posthoc,, spring ≠ (fall = winter), p = 0.013)..

Herbivory impact on Palisada cervicornis *abundance:*

After six months growing inside an exclosure cage, all 50 recruitment tiles were colonized by *P. cervicornis,* with an average of 5% percent cover. As soon as the tiles were exposed to fish grazing, the abundance of *P. cervicornis* rapidly decreased , with the maximum reduction occurring in the first 4 hours of exposure (ANOVA, $F_{2,111}= 43.361$, $p < 0.0001$, Tukey posthoc, p

< 0.0001, am ≠ (noon = afternoon)); when total consumption of *P. cervicornis* was observed (Fig. 4).

Discussion

Discovering a tiny, inconspicuous species during an ecological study provided us with the opportunity to address taxonomic and ecological questions in a combined effort. Using molecular tools, we properly identified the species and readjusted its nomenclature status, and through field and laboratory experiments we identified survival strategies of *Palisada cervicornis* in a Florida coral reef.

Taxonomic approach

The samples from the Florida Reef Track, clearly grouped in the *Palisada* clade distant from the *Laurencia* and *Chondrophycus* clades. Therefore, the sequences from Florida strongly support the new combination here proposed. Intraspecific divergence was minimal (0.2%) and within the range of other *Laurencia* complex species that had divergences of 0.01% to 0.02% for *Palisada poiteaui* (Díaz-Larrea et al. 2007), 0%-0.4% for *Palisada perforata* (Cassano et al. 2009), and 0%-0.9% for *Laurencia dendroidea* (Cassano et al. 2012b). Furthermore, the divergence between *P. cervicornis* and *P. corallopsis* (2.7-3.3%) establish these two species as separate taxonomic entities, solving the previously proposed merger of those species (Howe 1918). Even though the type locality for *Palisada cervicornis* is Key West and the samples for this study come from the upper Keys, this sequence can be representative for the type locality as it belongs to the Florida Reef Track. As for *P. corallopsis*, this is the first reported sequence for the species in Florida, differing by only 0.4% from the sequence reported for the Mexican Caribbean (Díaz-Larrea et al. 2007). The sequenced sample of *P. corallopsis* is from a region near its type locality, which is Cuba (Howe 1918). Therefore, we consider this sequence as representative of the species.

Although *Palisada cervicornis* (as *Laurencia cervicornis*) has been reported in several sites around the world, many of those reports do not include a morphological description (Suárez 2005, Wynne et al. 2005, Wynne 2011, Tsuda and Walsh 2013); or the descriptions are for juvenile organisms (Littler and Littler 2000, Dawes and Mathieson 2010). Thanks to the cultivation of the specimens of *P. cervicornis* in aquaria, we were able to describe the morphology, including for the first time a detailed description of its reproductive structures and other observations allowing us to differentiate this species from other similar species in the region.

Morphologically, *Palisada cervicornis* is easily confused with *Osmundea coelenterata* (originally described as *Laurencia coelenterata*), *Yuzurua iridescens* (M.J. Wynne & D.L. Ballantine) Sentíes & M.J. Wynne and *P. corallopsis* due to the compact and small thalli and their turf-forming habit. All four species share morphological features such as, two pericentral cells per vegetative axial segment, and arrangement of the tetrasporangia at a right-angle. Furthermore, three of the four species show secondary pit connections between adjacent cortical cells, with the exception being *P. corallopsis*. However, each one possesses its own distinctive characteristics; for example, *Osmundea coelenterata* has the filament-type of spermatangial branches originating from cortical cells, and tetrasporangia are cut off randomly from the cortical cells, both typical of *Osmundea* (Fujii et al. 2016). *Yuzurua iridescens* possesses all generic features established by Nam (1999, as subgenus *Yuzurua*) (Sentíes et al. 2015), and differs from *P. cervicornis* by the presence of cortical cell walls near apices markedly projecting with apiculate tips. *P. cervicornis* and *P. corallopsis* both form small turfs, but *P. corallopsis* presents a height of up to 8 cm and no iridescence. *O. coelenterata* shows a partial iridescence in the apical section of the branchlets (*in situ* observations), and very small size (to 4 mm), while *P. cervicornis* is larger (2.5 cm in the field, but grows larger in the tanks) and exhibits iridescence along all branches. An examination of a paratype specimen of *O. coelenterata* (as *L. coelenterata*) from Puerto Rico (#4551) revealed iridescent rings throughout the thalli, the same as *P. cervicornis*; however, the differences in both species are at the genus level. The results of the molecular analyses, and the in-depth morphological observations obtained in the present study corroborate the current taxonomic position of these closely related species of the *Laurencia* complex.

Ecological aspects of the turf-forming alga Palisada cervicornis.

Coral reef systems have been characterized as grazing controlled ecosystems (Burkepile et al. 2013), where highly productive algal turfs support large grazer communities (Poulin and Klumpp 1992). In turn, these herbivores often affect the abundance and diversity of the algal species present (Hay 1981, Duran et al. 2016) and their productivity (Carpenter 1986, Russ 2013). We show that although *Palisada cervicornis* is inconspicuous, it is a common member of the turf community in the Florida Keys that recruits year-round. However, when allowed to grow in herbivore exclusion cages, large *P. cervicornis* are promptly consumed upon exposure to herbivorous fishes (100% consumption after 4 hours of exposure to grazing). In general, the survival of species within the *Laurencia* complex is attributed to the chemical deterrents the algae produce (Hay et al. 1988, Pereira et al. 2003, Malinal 2011). For example, *Laurencia dendroidea* (as *L. obtusa*) produces elatol, which significantly deters herbivory and has been found in *Laurencia* species worldwide (Pereira et al. 2003). Importantly, not all species in the *Laurencia* complex show similar chemical characteristics, particularly species of the genus

Palisada, which lack elatol, as well as terpenes and acetogenins that are present in all *Laurencia* species tested so far (Fujii et al. 2011). Thus, *P. cervicornis* seems to persist in the community by obtaining a size-refuge from herbivory within turf communities rather than through chemical defenses commonly found in *Laurencia* species (*e.g.* Carpenter 1986; Verges 2011).

Integration

Understanding species interactions and their consequences for ecosystem dynamics remains a challenge. On coral reefs, herbivore control of macroalgae has been one of the most important and well-studied interactions, with direct consequences on management and the development of strategies to protect and facilitate the recovery of these important ecosystems (Hughes et al. 2010, Mumby 2009).

Through the combined efforts of taxonomists and ecologists, we are able to explain the rapid consumption of what was previously believed to be, a heavily-defended *Laurencia* species. Further, our recruitment experiments showed that *P. cervicornis* recruits year round; thus helping explain how such a palatable species is able to persist in a heavily grazed system. In an era in which biodiversity loss is a major environmental crisis (Rockstrom et al. 2009), our report of a new taxonomic combination and first molecular sequence near the type locality of the species, sheds light on the ecology of *P. cervicornis* and furthers our knowledge of the algal biodiversity on the Florida Reef track.

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Legend of Tables and Figures

Table S1. Taxa used in this study for phylogenetic analysis.

FIG. 1. Consensus tree derived from Neighbor-Joining analysis of *rbc*L gene sequences. Bootstrap supports for NJ (2000 replicates) and ML (100 replicates) (>60%) and Bayesian posterior probabilities (>0.6) are shown at the nodes; - indicates lack of support; * indicates full support (99-100% bootstrap value for NJ/ML, and 1.00 for PP). Taxa marked in bold indicate newly generated sequences.

FIG. 2. Morphological features of *Palisada cervicornis* comb. nov. (A) Habit of a specimen, scale bar = 3 mm. (B) Cortical cells in surface view, showing secondary pit-connections (arrows), scale bar = 20 µm. (C) Transverse section of the upper portion of a branch showing an axial cell (a) and two pericentral cells (p), scale bar = 25 µm. (D) Longitudinal section through a female branchlet showing immersed cystocarp, scale bar = 100 µm. (E) Longitudinal section through a male branchlet showing spermatangial branches in cup-shaped tips, scale bar =

100 μm. (F) Detail of spermatangial branches on trichoblast with two laterals, sterile (arrow) and spermatangial (arrowhead) branches on its suprabasal cell (sbt). Note spermatangia with an apical nucleus, scale bar = 25 μm.

FIG. 3- Seasonal abundance of *Palisada cervicornis* in recruitment tiles.

FIG. 4- Experimental herbivory impact on *Palisada cervicornis.*