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Morphological and molecular evidence for *Osmundea coelenterata* comb. nov. (Ceramiales, Rhodophyta) from the tropical Atlantic Ocean

Evidencias morfológicas y moleculares para *Osmundea coelenterata* comb. nov. (Ceramiales, Rhodophyta) del Océano Atlántico tropical

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ABSTRACT

Background. As part of the monographic studies on the *Laurencia* complex (Rhodomelaceae, Rhodophyta) from Cuba, detailed taxonomic research was carried out on *Laurencia coelenterata*, a diminutive species collected in Santiago de Cuba, in the eastern Cuban archipelago. The vegetative and reproductive features of the species clearly belong to the genus *Osmundea*, a member of the *Laurencia* complex: two pericentral cells per each vegetative axial segment, tetrasporangia cut off randomly from cortical cells, and filament-type spermatangial branches. **Goals**. In this study the morphological characteristics previously unknown to *Laurencia coelenterata* are shown, and in order that their taxonomic position within the *Laurencia* complex is discussed. Furthermore, the global geographic distribution of the *Osmundea* species is analysed. **Methods**. Morphological and molecular analysis of the *rbc*L gene sequences were performed allied with the preparation and interpretation of phylogenetic hypotheses. **Results**. The new morphological analysis of the paratype specimen (# 4451) housed in the Puertorriqueño Marine Herbarium showed that *Laurencia coelenterata* was incorrectly placed in the genus *Laurencia*. The phylogenetic position of the present species was inferred by the analysis of the chloroplast-encoded *rbc*L gene sequences, and the range of the genetic variation found in this analysis also supports the transfer of *Laurencia coelenterata* to the genus *Osmundea*, as *O. coelenterata* (D. L. Ballantine *et* Aponte) M.T. Fujii, Sentíes *et* Areces. **Conclusions**. The morphological and molecular approach in algal taxonomy is allowing consolidate the nomenclatural status of the species, and the new combination for *Laurencia coelenterata* as O*smundea coelenterata* is not an exception.

Key words: *Laurencia* sensu lato, *Osmundea, rbc*L, Santiago de Cuba, taxonomy.

RESUMEN

Antecedentes. Como parte de los estudios monográficos sobre el complejo *Laurencia* (Rhodomelaceae, Rhodophyta) en Cuba, se llevó a cabo la recolecta e investigación taxonómica detallada de una pequeña especie *Laurencia coelenterata*, presente en Santiago de Cuba, región oriental del archipiélago cubano. Los caracteres vegetativos y reproductivos presentes en esta especie y que son exclusivos del género *Osmundea* (miembro del complejo *Laurencia*) son: dos células periacentrales por cada segmento axial vegetativo, los tetrasporangios nacen al azar de las células corticales y las ramas espermatangiales son de tipo “filamento”. **Objetivos**. En este trabajo se describen caracteres morfológicos previamente no conocidos para *Laurencia coelenterata* y se discute su posición taxonómica dentro del complejo *Laurencia*. Además se analiza la distribución geográfica global de las especies de *Osmundea.* **Métodos**. Se realizaron análisis morfológicos y moleculares de secuencias del gen *rbc*L. Complementándose con la elaboración e interpretación de las hipótesis filogenéticas. **Resultados**. El análisis morfológico actual del paratipo (# 4451) resguardado en el Herbario Marino Puertorriqueño mostró que *L. coelenterata* fue ubicado de manera incorrecta dentro del género *Laurencia*. La posición filogenética de esta especie fue inferida por secuencias del gene cloroplástico *rbc*L y el intervalo de variación genética encontrado, también soporta la transferencia de *Laurencia coelenterata* al género *Osmundea*, como *O. coelenterata* (D. L. Ballantine *et* Aponte) M.T. Fujii, Sentíes *et* Areces. **Conclusiones**. La aproximación morfológica y molecular en la taxonomia algal esta permitiendo consolidar el status nomenclatural de las especies, este estudio no es la excepción para la nueva combinación de *Osmundea coelenterata*.

Palabras clave: *Laurencia* sensu lato, *Osmundea, rbc*L, Santiago de Cuba, taxonomía.

INTRODUCTION

Laurencia coelenterata D.L. Ballantine & Aponte (1995) is a diminutive species, originally collected from the Dry Tortugas, Florida, at 9 m depth. According to the authors, the name given to it was due to the superficial resemblance of juvenile plants to an anemone. Despite this characteristic, the species is not easily found in the natural environment because of its small thalli.

The taxonomy of the red algal genus *Laurencia* J.V. Lamouroux sensu lato is extremely complicated because of the large degree of morphological plasticity and worldwide distribution from temperate to tropical oceans. Consequently, the taxonomic position of the species in this group has changed rapidly as new morphological and molecular data are processed. In the roughly two hundred years since the creation of the genus *Laurencia* (Lamouroux, 1813), many changes have been proposed in what we currently refer to as the *Laurencia* complex, made up of seven formally proposed genera: *Laurencia* sensu stricto, *Osmundea* Stackhouse (1809), *Chondrophycus* (Tokida *et* Y. Saito) Garbary & J.T. Harper (1998), *Palisada* (Yamada) K.W. Nam (2007), *Yuzurua* (K.W. Nam) Martin-Lescanne (Martin-Lescanne *et al.*, 2010), *Laurenciella* V. Cassano *et al.* (2012), and most recently *Choronaphycus* Metti, (Metti *et al.*, 2015).

In the Cuban archipelago, the *Laurencia* complex has 17 species, distributed into 3 genera: *Laurencia* sensu stricto (11), *Palisada* (5), and *Yuzurua* (1 with two varieties) (Suárez *et al.*, 2015).

During the *Laurencia* complex expedition to the eastern coast of the Cuban archipelago, *Laurencia coelenterata* was found growing on the consolidated substrata in a biogenic sand beach, with limestone and beds of the seagrass *Thallasia testudinum* Banks ex König at the bottom. The detailed morphological studies carried out on this material revealed vegetative and reproductive characteristics belonging to the genus *Osmundea*, and not to the genus *Laurencia* (Ballantine & Aponte, 1995). In this study, previously unknown morphological features of *L. coelenterata* are revealed that justify its transfer to *Osmundea*. Emendation to the species's original description is provided. The new combination is corroborated by chloroplast-encoded *rbc*L gene-sequence analysis.

MATERIAL AND METHODS

Study area. Samples were collected at the Cazonal beach, Santiago de Cuba (19° 53'39" N and 75° 31'8 .7" W), Cuba. Cazonal is a biogenic sand beach, 60 cm deep, with isolated limestone and beds of the seagrass *Thallasia testudinum* at the bottom. The beach is located 52 km east of the city of Santiago de Cuba.

Morphological study. Transverse and longitudinal hand sections were made with a stainless-steel razor blade and stained with 0.5% aqueous aniline blue solution, acidified with 1N HCl, to highlight the diagnostic morphological features.

The microscopic measurements were obtained using a calibrated ocular micrometer. Photographs were taken with a Panasonic FT3 Lumix digital camera and the photomicrographs were obtained using a Zeiss Axiocan ERC-5S digital camera (Göttingen, Germany) coupled to an Axioskop 2 Zeiss microscope (Göttingen, Germany). The vouchers were deposited at the herbarium of the Instituto de Botânica, at São Paulo, Brazil (SP) and at the phycological collections of the Oriente University, at Santiago de Cuba, Cuba (FCA 191-ah).

Molecular study. Samples for molecular analysis were cleaned, dried, and preserved in silica gel. Total DNA was extracted using a DNeasy Plant Mini Kit (QIAGEN, Valencia, CA, USA), according to the manufacturer's instructions. The *rbc*L gene was amplified in three overlapping fragments with the primer pairs suggested by Freshwater & Rueness (1994), using the Taq polymerase chain reaction (PCR) Core Kit (QIAGEN). All PCR products were analyzed by electrophoresis in 1% agarose to confirm product size. The PCR products were purified with the QIAquick Purification Kit (QIAGEN) according to the manufacturer's recommendations. Cycle sequencing was carried out on an ABI PRISM 3100 Genetic Analyzer (Applied Biosystems, Carlsbad, CA, USA), using the BigDye Terminator Cycle Sequencing Reaction Kit (Applied Biosystems). Primers were used for PCR amplification and cycle sequencing. Sequences were analyzed with Sequence Navigator software, version 1.0.1 (Applied Biosystems).

Phylogenetic analyses. Phylogenetic relationships were inferred with PAUP* version 4.0b10 (Swofford 2002) and MrBayes v.3.0 beta 4 (Huelsenbeck & Ronquist, 2001). Maximum parsimony (MP) trees were constructed by applying the heuristic search option, tree-bisection-reconnection (TBR) branch swapping, with unordered and unweighted characters, and gaps treated as missing data. Modeltest software, version 3.7 (Posada & Crandall, 1998), was used to find the model of sequence evolution least rejected in each data set by a hierarchical likelihood ratio test. Once the evolution model had determined a Maximum Likelihood (ML), searches were performed by applying the estimated parameters (substitution model, gamma distribution, proportion of invariant sites, and frequencies of the bases). Maximum likelihood analysis was then employed to construct the most likely tree from the data set. Maximum Likelihood and MP branch supports were calculated by nonparametric bootstrapping analysis (Felsenstein, 1985), as implemented in PAUP*.

The general time-reversible model of nucleotide substitution with invariant sites and gamma-distributed rates for the variable sites (GTR + I + G) were used for Bayesian analysis (BI). This model was selected based on an ML ratio test implemented by the software Modeltest, version 3.06 (Posada & Crandall, 1998), with a significance level of 0.01. For Bayesian analysis, we ran four chains of Markov Chain Monte Carlo, sampling one tree every 1,000 generations for 4,000,000 generations, starting with a random tree. A 50% consensus tree-majority rule (as implemented by PAUP*) was computed after the burn-in point. The range of *rbc*L divergence values within and between species was calculated using uncorrected "p" distances obtained from PAUP*.

RESULTS

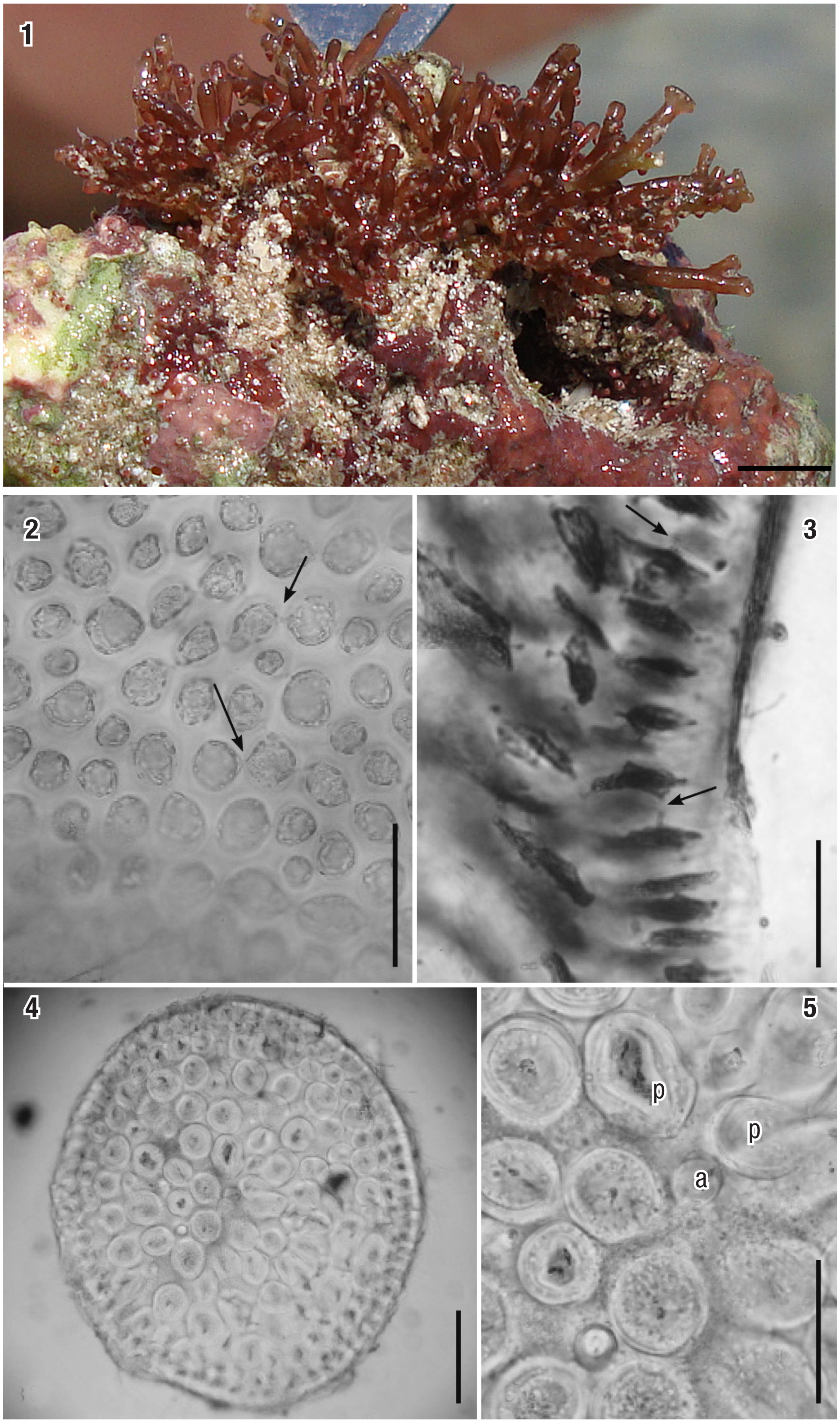
Osmundea coelenterata* (D.L. Ballantine *et* Aponte) M.T. Fujii, Sentíes *et* Areces *comb. nov. (Figs 1-9).

BASIONYM: *Laurencia coelenterata* D.L. Ballantine *et* Aponte, 1995, Bot. Mar. 38: 417-418, figs. 1-2).

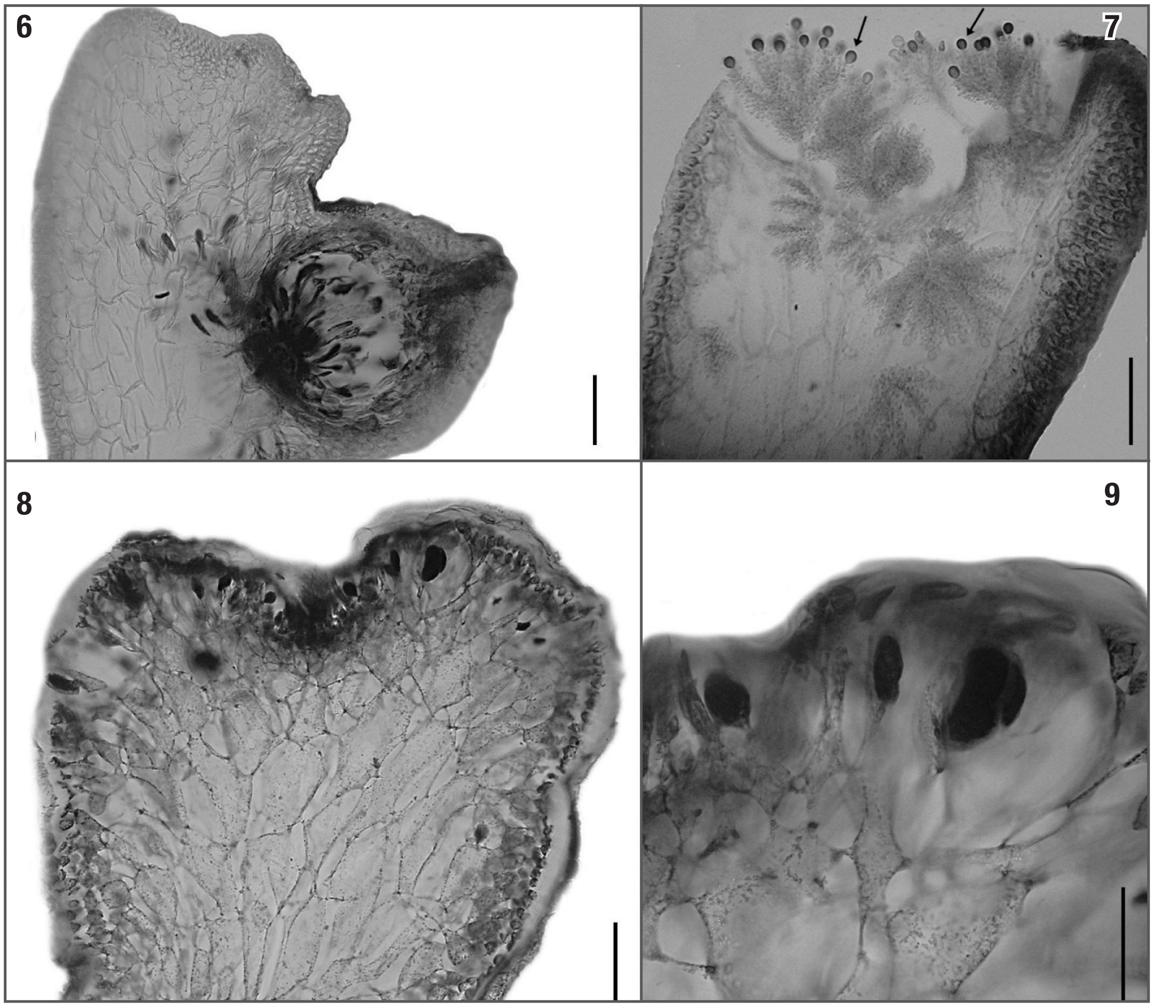
HOLOTYPE: US (D.L. Ballantine # 3908)

PARATYPE: Herbario Marino Puertorriqueño # 4451!

TYPE LOCALITY: Pulaski Shoals, Dry Tortugas, Florida, USA (24°41.661" N, 82°42.296"W).



Figures 1-5. *Osmundea coelenterata* comb. nov. 1 Aspect of a tuft from Cuba on the natural substrate. Scale bar: 2 mm. 2-3) Cortical cells in surface view and in longitudinal section view, respectively. Arrows indicate secondary pit connections. 4) Transverse section of the thallus (note thick-walled medullary cells). 5) Detail of medulla in transverse section, showing an axial cell (a) with two pericentral cells (p). Scale bars = 100 µm (Figs 2, 5), 50 µm (Fig. 3) and 200 µm (Fig. 4).



Figures 6-9. *Osmundea coelenterata* comb. nov. 6) Longitudinal section through a mature cystocarp (note the cystocarp partially immersed in the thallus). 7) Longitudinal section through a cup-shaped spermatangial pit, showing "filament-type" spermatangial branches originated from cortical cells, and terminating in a single vesicular sterile cell (arrows). 8-9) Longitudinal sections through the tetrasporangial branches, with tetrasporangia originated from cortical cells, and showing right angle arrangement in relation to the branch. Scale bars = 100 µm (Figs 6, 8), 50 µm (Figs 7, 9).

Amended diagnosis: vegetative axial segment with two pericentral cells, whose diameters are slightly smaller than those of the surrounding cells; male gametophytes with 'filament type' spermatangial branches originated from apical and cortical cells; tetrasporangia are randomly produced from cortical cells at the apex of the branches.

Habit: plants forming tufts, strongly attached to the substrate by a discoid holdfast, rigid, cartilaginous in texture, not adhering to herbarium paper when dried. The thalli are reddish-brown, the axes terete to slightly compressed, claviform, 3-4 mm high and 500-800 µm diameter. The axes are sparsely branched and the branches are produced alternately. Short branchlets are present in the apical portions of some branches and axes, giving the species a very characteristic appearance (Fig. 1).

Vegetative structures: in surface view, cortical cells are rounded, regularly arranged throughout the thalli, 10-25 µm diameter, with secondary pit connections frequently present between the cortical cells (Fig. 2). *Corps en cerise* absent. In transverse section, thalli with one-two layers of quadratic to slightly radially elongated pigmented cortical cells, not arranged as palisade, 20-35 µm high x 20-30 µm wide in the middle portions of the main axes (Fig. 3). Medullar region with three or four layers of colorless cells, rounded, (50)90-130 µm diameter, where the pericentral cells are smaller than those in the other layers. Medullary cell walls are extremely thick and can almost completely fill the lumen of the cells. However, lenticular thickenings are absent (Figs 4-5). Each vegetative axial segment cuts off two pericentral cells, rounded, 90-130 µm diameter (Fig. 5). In median longitudinal section through a branchlet, cortical cell walls near apices not projecting beyond the surface.

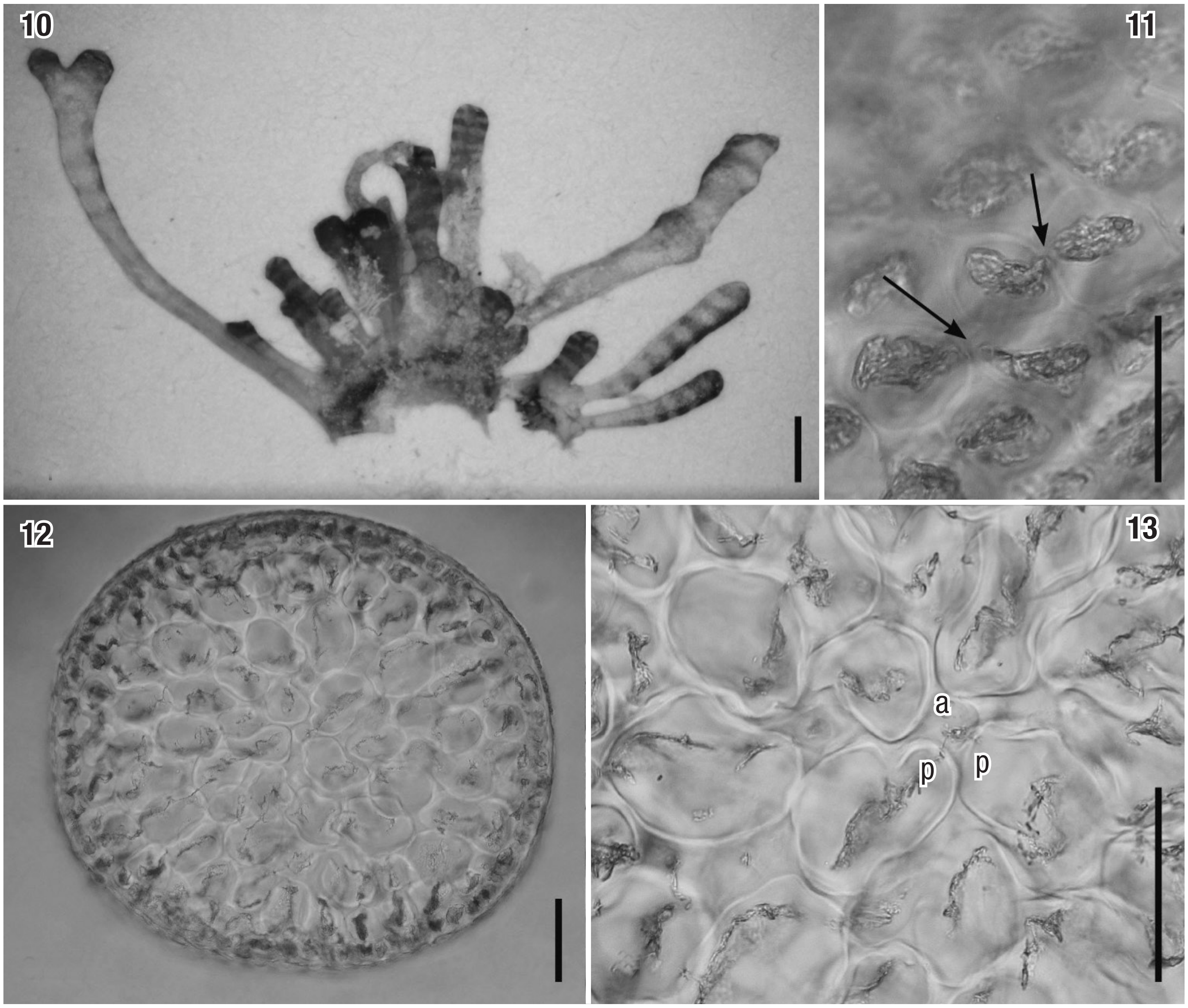
Reproductive structures: female gametophytes are characterized by laterally bearing cystocarps partially immersed in the thalli. The cystocarps are pyriform, 350-500 µm diameter, bearing a prominent carpostome. Carpospores are claviform, 40-45 µm high x 10-15 µm wide, and are produced abundantly (Fig. 6). Male gametophytes have filament-type spermatangial branches originating in cortical cells in the cup-shaped spermatangial pit. Spermatangial branches bear spermatangial mother cells that give rise to several elliptical spermatangia, 4-8 µm diameter, each with a single distally located nucleus, and usually terminating in one elliptical vesicular sterile cell, 7-8.5 µm high x 6.0-6.5 µm wide. (Fig. 7). Tetrasporangia are cut off randomly from the cortical cells at the apex of the branches and have a diameter of 50–80 µm, displaying right-angle arrangement in relation to the longitudinal axes. The fertile pericentral cells cut off two presporangial cover cells distally and the tetrasporangia. The post-sporangial cell was not discernible (Figs. 8-9).

Habitat and distribution: The holotype specimens were collected by SCUBA at 9 m depth at the Dry Tortugas, Florida, USA. In Santiago de Cuba, however, *Osmundea coelenterata* was found growing on the consolidated substrata in a biogenic sand beach, with isolated limestone and beds of the seagrass *Thallasia testudinum* at the bottom.

Material examined: CUBA: IDO-161, Cayo Paredon Grande, Archipiélago Jardines del Rey (intertidal), 21.x.1992, Leg. A. Areces (SP 401499). Santiago de Cuba, Playa Cazonal, 12.xi.2008, Leg. A. Jover Capote, female, male, and tetrasporangial specimens (FCA 191-ah).

Additional material examined: *Laurencia coelenterata*, USA, Dry Tortugas, Pulaski Shoals, 9 m, 17.ix.1991, Leg. David L. Ballantine, (Herbario Marino Puertorriqueño # 4451 - Paratype) (Figs 10-13).

Molecular analyses. A total of 37 sequences were analyzed including five outgroup taxa, *Bostrychia radicans* (Montagne) Montagne,



Figures 10-13. Paratype of *Laurencia coelenterata* (# 4551). 10) Habit of the plant. 11) Cortical cells in surface view, showing a secondary pit-connection between them (arrows). 12) Transverse section of the thallus. 13) Detail of the upper portion of a branch with an axial cell (a) and two pericentral cells (p). Scale bars: 1 mm (Fig. 10), 50 µm (Figs 11 and 13) and 100 µm (Fig. 12).

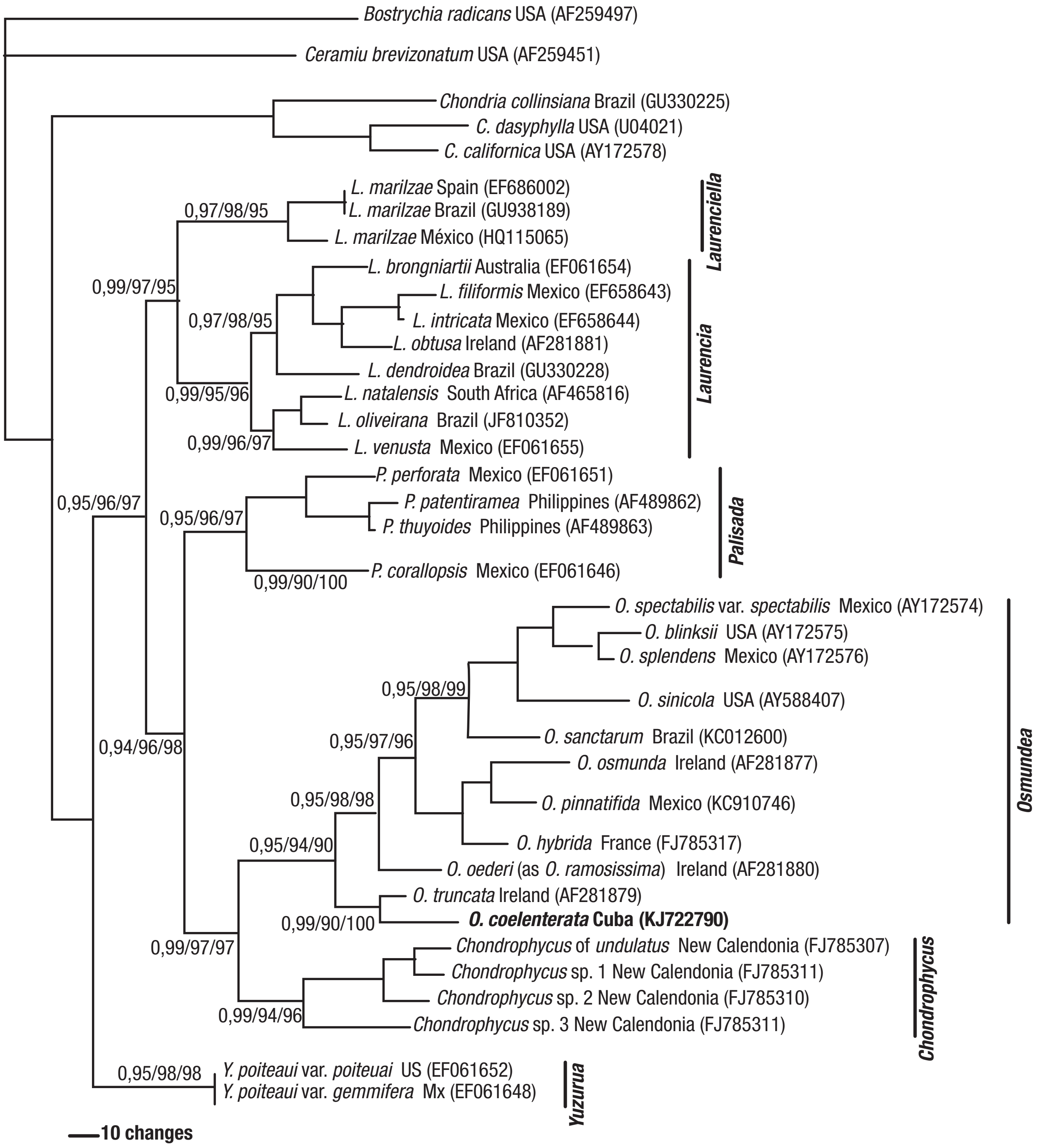


Figure 14. Phylogenetic relationships in the *Laurencia* complex based on Bayesian analysis of *rbcL* DNA sequences. Bayesian posterior probability/MP bootstrap/and ML bootstrap values are indicated at the nodes. Taxa marked in bold indicate newly determined sequence.

Chondria collinsiana M.A. Howe, *C. dasyphylla* (Woodward) C. Agardh, *C. californica* (Collins) Kylin in the Rhodomelaceae, and *Ceramium brevizonatum* H.E. Petersen in the Ceramiaceae. Maximum Parsimony, ML and BI topologies were similar. The first 50 nucleotides and the last 40 bp of all *rbc*L sequences were removed, producing a data set of 1377 base pairs, and the rest of the sequences were aligned without ambiguity.

Intergeneric divergence varied from 9.2 to 13.7% for *Laurencia* and *Osmundea* from 8.5 to 12% for *Chondrophycus* and *Laurencia,* from 9 to 11.5% for *Chondrophycus* and *Osmundea*, from 8 to 10% for *Lau-*

renciella and *Laurencia*, from 8.2 to 10% for *Laurenciella* and *Palisada*, from 10 to 11% for *Laurenciella* and *Chondrophycus*, from 10 to 13% for *Laurenciella* and *Osmundea*, from 9.8 to 10.2% *Laurenciella* and *Yuzurua*, from 7 to 10.5% for *Laurencia* and *Palisada*, from 8.5 to 10% for *Laurencia* and *Yuzurua*, from 8 to 9.2% for *Palisada* and *Chondrophycus*, from 8.5 to 12.5% for *Palisada* and *Osmundea*, from 8 to 10.5% for *Palisada* and *Yuzurua*, from 9.5 to 10.8% for *Chondrophycus* and *Yuzurua*, and from 10.5 to 11.9% for *Osmundea* and *Yuzurua*.

Interspecific divergence obtained for the species of *Laurencia* varied from 1 to 6%, from 1.3 to 6% for *Palisada*, from 1.8 to 7% for *Osmundea*, from 1.3 to 1.5% for *Laurenciella*, 0.5% for *Yuzurua*, and from 1.6 to 6% for those of *Chondrophycus*.

Finally, the divergence of the Cuban specimen from other *Osmundea* species was 3.0-8.5%.

The topology of the majority rule Bayesian tree is shown in Figure 14. The data set consisted of 907 constant characters, 170 parsimony informative sites, and 300 parsimony non-informative sites.

The analyses show a monophyletic *Laurencia* complex with high bootstrap support in relation to the members of the outgroups. The *Laurencia* complex separated into six clades with high bootstrap support, corresponding to the following genera: *Laurencia, Chondrophycus*, *Osmundea*, *Palisada*, *Laurencia*, and *Laurenciella.*

The monophyletic clade that corresponded to the genus *Osmundea* included eleven species. Within the *Osmundea* assemblage, the Cuban specimen formed a well-supported clade with *O. truncata* (Kützing) K.W.Nam *et* Maggs from Ireland.

DISCUSSION

The Cuban specimens formed a well-supported clade with other species of *Osmundea* corroborating the morphological data. The divergence of the Cuban specimen from other *Osmundea* species was high, which confirms that it constitutes an authentic taxonomic entity. The intergeneric and interspecific divergence values obtained in the present work are similar to those reported by other authors for the *Laurencia* complex (McIvor *et al*., 2002; Cassano *et al*., 2012a,b; Machín-Sanchez *et al*., 2014; Metti *et al*., 2015).

The genera *Laurencia* and *Osmundea* are clearly distinguished genetically as well as morphologically. Some features, such as the presence of the secondary pit connections between cortical cells and the presence/absence of lenticular thickening are shared by both genera, but the majority of diagnostic morphological features are distinct, such as four pericentral cells per vegetative segment in *Laurencia* against two in *Osmundea*; the origin of spermatangia and tetrasporangia is random from cortical cells in *Osmundea*, whereas in *Laurencia* it is from a particular fertile pericentral cell.

The tetrasporangial arrangement in superficial view of the branches is parallel in *Laurencia*, whereas it can be parallel or right-angled in *Osmundea*.

Ballantine and Aponte (1995) had already noticed that *L. coelenterata* does not conform to Saito's (1967) concept of the subgenera *Laurencia* and *Chondrophycus*, since the species possesses tetrasporangia with a right-angle arrangement (a character of the subgenus *Chondrophycus*), and secondary pit connections between cortical cells (a character of the subgenus *Laurencia*). Currently, we know that the right-angle arrangement of tetrasporangia is shared mainly by the species of *Chondrophycus*, *Palisada*, and *Yuzurua*, and pit connections between adjacent cortical cells could be present in all members of the *Laurencia* complex (Nam 2006, Cassano *et al.* 2012, Metti *et al.* 2015).

Osmundea truncata from Ireland is the closest species to this species, although their gross morphology is completely distinct. The thallus in *O. truncata* is up to 5 cm high, slightly or strongly compressed and abundantly branched (Machín-Sanchéz *et al*., 2012), whereas in *O. coelenterata* it is smaller (3-4 mm), terete, and branching is rare. In relation to the anatomical comparison, *Osmundea truncata* and *O. coelenterata* have in common the presence of longitudinally arranged secondary pit connections between adjacent cortical cells and cup-shaped spermatangial pit. Lenticular thickenings are present in the former but absent in the latter. Furthermore, the genetic divergence between these species is 1.5%, clearly representing two distinct species of *Osmundea*.

The geographic distribution of the *Osmundea* species was analyzed based on dataset presented by Guiry and Guiry (2015). In this database, there are 24 species (and infraspecific) names, of which 20 have been flagged as currently accepted taxonomically. Eight species (40%) of these occur exclusively in the North American Pacific: *O. blinksii* (Hollenberg *et* I.A. Abbott) K.W. Nam, *O. crispa* (Hollenberg) K.W. Nam, *O. estebaniana* (Setchell *et* N.L. Gardner) J.N. Norris, *O. multibulba* (E.Y. Dawson, Neushul *et* Wildman) K.W. Nam, *O. purepecha* Sentíes, Mendoza-González *et* Mateo-Cid, *O. spectabilis* (Postels *et* Ruprecht) K.W. Nam, and *O. splendens* (Hollenberg) K.W. Nam.

Osmundea lata (M. Howe *et* W.R. Taylor) Yoneshigue-Valentin, M.T. Fujii *et* Gurgel and *O. sanctarum* M.T. Fujii *et* Rocha-Jorge occur only in Brazil and they have restricted and timely distribution in subtidal conditions, under the influence of cold waters of the South Atlantic Central Waters (Howe & Taylor, 1931; Yoneshigue-Valentin *et al*., 1995, 2003; Rocha-Jorge *et al*., 2013).

The Northern hemisphere of the Atlantic Ocean, including the Mediterranean, Adriatic Sea, and Macaronesia houses 50% of the *Osmudea* species known to date: *O. hybrida* (A.P. de Candolle) K.W. Nam, *O. maggsiana* Serio, Cormaci *et* G. Furnari, *O. oederi* (Gunnerus) G. Furnari, *O. osmunda* (S.G. Gmelin) K.W. Nam & Maggs, *O. pedicularioides* (Børgesen) G. Furnari, Serio *et* Cormaci, *O. pelagiensis* G. Furnari, *O. pelagosae* (Schiffner) K.W. Nam, *O. pinnatifida* (Hudson) Stackhouse, *O. truncata* (Kützing) K.W. Nam *et* Maggs, and *O. verlaquei* G. Furnari (Gury & Gury 2015). Except *Osmundea maggsiana* and *O. pelagiensis* that are reported only from the Mediterranean and/or Adriatic Sea (Cormaci *et al.,* 1994; Serio *et al*., 2008), all others are widely distributed in the Northern Atlantic Ocean and beyond but have never occurred in the North American Pacific.

Osmundea pinnatifida is the most widely distributed species in the northern hemisphere of the Atlantic Ocean and also in the Indian and Pacific Oceans (Guiry & Gury, 2015), characterizing the Hommersand's late Tethyan distribution pattern, according to McIvor *et al.* (2002), corroborated by Furnari *et al.* (2004). The reference to this species in Brazil was never confirmed nor was *O. hybrida* (Fujii *et al.,* 2011).

The geographic distribution pattern found for the species of *Osmundea* suggests their affinity to temperate and warm temperate conditions. Therefore, this is the first report of *Osmundea* in the Caribbean, occurring in a typical tropical environment. This fact indicates that further studies are needed in the Caribbean region and in the Western Atlantic.

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