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Morphological and Molecular Evidences Within Osmundea (Ceramiales, Rhodophyta) from the Canary Islands, Eastern Atlantic Ocean

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Morphological and molecular evidences within Osmundea (Ceramiales, Rhodophyta) from the Canary Islands, eastern Atlantic Ocean

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The genus Osmundea is a strongly supported monophyletic group within the Laurencia complex and shows a disjunct distribution occurring in the North-East and South-West Pacific, the Indian and Atlantic oceans and the Mediterranean Sea. Its phenotypic plasticity on the Canary Islands may be the result of the high ecological variability partially due to the particular oceanographic characteristics in this region. The combination of molecular analyses based on the comparison of the plastid-encoded rbcL sequences and morphological data allowed us to delimit three distinct taxa from the coasts of the Canarian Archipelago: Osmundea pinnatifida, Osmundea truncata and an unidentified species, Osmundea sp. Moreover, the high value of genetic divergence between Osmundea sp. and the rest of the Osmundea species suggests that this taxon should be assigned to a new species within the Osmundea genus. Occurrence of O. hybrida and O. oederi (synonym: O. ramosissima) has not been confirmed. Our results also suggest a possibly questionable record of the taxa O. hybrida and O. oederi on the Canary Islands.

Keywords: Laurencia complex, phylology, rbcL, taxonomy

Introduction

The genus Osmundea Stackhouse, resurrected by Nam et al. (1994), is segregated from the other four genera of the Laurencia complex [Laurencia sensu stricto J.V. Lamouroux, Chondrophycus (Tokida and Saito) Garbary and Harper, Palisada (Yamada) KW Nam, and Yuzurua (KW Nam) Martin-Lescanne] by a set of vegetative and reproductive characters. Some of these characters are unique to the genus Osmundea, not being shared with any other genera of the complex, such as the tetrasporangial production from random cortical cells and filament-type spermatangial development (Nam et al. 1994). Osmundea is further distinguished from Laurencia s.s. by presenting two pericentral cells in each vegetative axial segment, whereas Laurencia s.s. possesses four pericentral cells per axial segment (Nam et al. 1994, Garbary and Harper 1998, Nam 1999).

Osmundea has been considered the only genus of the Laurencia complex that has a disjunct distribution (Mclvor et al. 2002). Previous phylogenetic studies based on rbcL gene sequencing showed a clear divergence between the Spectabilis group from the North-East Pacific formed by O. blinkii (Hollenberg and I.A. Abbott) Nam, O. sinicola (Setchell and Garnder) Nam, O. spectabilis and O. splendens, and the other one from the North Atlantic and the Mediterranean coasts formed by O. hybrida (A.P. de Candolle) Nam, O. osmunda (S.G. Gmelin) Nam and Maggs, the type species of the genus, O. pinnatifida (Hudson) Stackhouse, O. oederi (Gunnerus) G. Furnari [as O. ramosissima (Oeder) Athanasiadis] and O. truncata (Kützing) Nam and Maggs (Mclvor et al. 2002, Abe et al. 2006, Fujii et al. 2006, Martin-Lescanne et al. 2010).

Four species of the genus Osmundea have been described for the Canarian Archipelago: O. hybrida, O. oederi, O. pinnatifida and O. truncata (Gil-Rodríguez et al. 2003). Nonetheless, due its phenotypic plasticity, the occurrence of the genus Osmundea in the Canary Islands has been most likely overestimated.


For the purpose of completing the taxonomic and phylogenetic overview on the genus Osmundea on the Canary Islands, the present study had the following three objectives: (1) identify the actual representation of the genus Osmundea on the Canaries; (2) assess its distribution; and (3) define the morphological and phylogenetic characteristics of its members (inferred from their rbcL sequences).

Material and methods

Between 2007 and 2011, samples of Osmundea were collected
from 12 intertidal locations on the Islands of La Palma (La Fajana de Barlovento 28R 0227347/3193712, Las Salinas-Cancajos 28R 0230568/3171968, Bco. de La Herradura 28R 0229635/3191032), La Gomera (Charco del Conde 28R 0270268/3108917), Tenerife (Punta del Hidalgo 28R 0369850/3161577, Puerto de la Cruz 28R 0348346/3146402, La Barranquera 28R 0363281/3157675, Playa Paraiso 28R 0325227/3111777), Gran Canaria (Quintanilla 28R 0446622/3113614, Punta de Gáldar 28R 0437424/3116437), and Fuerteventura (Corralejo 28R 0607498/3181158, El Viejo Rey-La Pared 28R 0575584/3120754) (Canary Islands, Spain) (Figure 1).

Morphological observations
Anatomical studies were carried out on both fresh specimens and plants were fixed in 4% formalin seawater. A minimum of 20 specimens of O. truncata and O. pinnatifida, and five specimens of Osmundea sp. were studied. Sections for microscopic observations were made by hand using a stainless steel razor blade under a Leica MZ 12.5 stereo-scopic dissection microscope (Wetzlar, Germany) and stained with 0.5% aqueous aniline blue solution acidified with 1 N HCl (Tsuda and Abbott 1985). Photomicrographs were taken with a Leica DFC290 digital camera coupled to a Leica DM 2000 microscope (Wetzlar, Germany). Voucher specimens were deposited in the herbarium TFC (University of La Laguna). For the purpose of comparison, additional specimens from the Canary Islands provided by the Netherlands Centre for Biodiversity Naturalis (section NHN) (L) and the herbarium of the University of Las Palmas de Gran Canaria (BCM) were examined. Herbarium abbreviations follow the online Index Herbariorum (Thiers [continuously updated]). Specimens examined are listed in the Appendix.

DNA analyses
DNA and phylogenetic analyses were carried out using the methodologies described in Gili-Rodriguez et al. (2009). Samples used for molecular analyses were dried in silica gel. Specimens including their GenBank access numbers are shown in Table 1. Total DNA was extracted by using the DNeasy Plant Mini Kit (Qiagen Inc., Valencia, California) according to the manufacturer’s instructions. A total of 1,467 base pairs of the rbcL gene was amplified in three fragments with the primer pairs FrbcLstart-R753, F577-R1150 and F753-RrbrcS (Freshwater and Rueness 1994) by using the Taq PCR Core Kit (Qiagen). All PCR products were analysed by electrophoresis in 1% agarose to confirm product size. The PCR products were purified with the Qiagen QIAquick Purification Kit according to the manufacturer’s instructions. Cycle sequencing was carried out using the BigDye Terminator Cycle Sequencing Reaction Kit (Applied Biosystems, Princeton, New Jersey) on an ‘ABI PRISM 3100 Genetic Analyzer’ (Applied Biosystems). The primers used for PCR amplification were also used for the sequencing reactions. Sequences were analysed with the Sequence Navigator software (Applied Biosystems).

Phylogenetic analyses
Phylogenetic relationships were inferred with PAUP* version 4.0b10 (Swofford 2002) and MrBayes version 3.0 beta 4 (Huelsenbeck and Ronquist 2001). Maximum parsimony (MP) trees were constructed by using the heuristic search option, tree-bisection-reconnection (TBR) branch swapping, unordered and unweighted characters. Branch length was optimised by using delayed transformation (DELTRAN), which favours parallelisms over reversals. Support values for the relationships discovered in this analysis were calculated by performing bootstrap (Felsenstein 1985) analysis, as implemented in PAUP*. Ten thousand heuristic search replicates were executed by using the TBR branch-swapping algorithm. The model used in the Bayesian analysis 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 based on maximum likelihood (ML) ratio test implemented by the software Modeltest version 3.06 (Posada and Crandall 1998) with a significance level of 0.01. For Bayesian analysis, we ran four chains of the Markov chain Monte Carlo, sampling one tree every one thousand generations for three million 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 rbcL divergence values within and among species was calculated using uncorrected ‘p’ distances resulting from PAUP*.

Results
Morphological analyses
Osmundea truncata (Kützing) Nam et Maggs (Nam et al. 1994:393).
Basionym: Laurencia truncata Kützing (1865:19, pl.51c).
Holotype: Pius Titius; L 941.99.271 (Maggs and Hommersand 1993)
Type locality: Pirano, Croatia (Maggs and Hommersand 1993).
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<th>Species</th>
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<th>GenBank accession number</th>
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<td>Centroceras sp. [as C. clavatum (C. Agardh) Montagne]</td>
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<td>Ceramium brevizonatum H. E. Petersen</td>
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<td>Laurencia caduciramusolosa Masuda et Kawaguchi</td>
<td>Spain, Canary Islands, Tenerife, Punta del Hidalgo, 6 May 2008 (this study)</td>
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<td>Laurencia dendroidea J. Agardh</td>
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<td>Osmunda osmunda (S.G. Gmelin) Nam et Maggs</td>
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<td>Osmunda spectabilis var. spectabilis (Postell et Ruprecht) Nam</td>
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<td>Osmunda splendens (Hollenberg) Nam</td>
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**Morphology** — Thallus erect, up to 5 cm high, terete in the basal region, slightly or strongly compressed in the middle and apical regions of the axes, ultimate branches cylindrical, truncated at the apices (Figure 2a). Reddish-brown in colour, cartilaginous in texture and main axis in the middle is 25–55 mm long × 0.3–0.5 mm wide. It grows individually or in tufts over rocks, attached by discoid holdfast (Figure 2b). Thalli irregularly ramified with four orders of branches, 0.4–1.5 mm long × 0.2–0.3 mm wide, branches irregularly alternate. Branchlets with subdichotomy (Figure 2a). Presence of few, dense hyaline trichoblasts in the apical depressions located in the pit of the branchlets. Alternately arranged buds can be frequently observed on the main axis (Figure 2c).

**Vegetative structures** — In surface view, cortical cells in the middle region of the thalli are polygonal to elongated, 11–24 μm long × 10–17 μm wide, and connected to one another by numerous secondary pit connections (Figure 3a). *Corpus en cerise* were absent in living material. Transverse sections of the thallus (Figure 3b) show two cortical layers of heavily pigmented cells. Outer cortical cells are rectangular, 14–19 μm long × 8–14 μm wide, not arranged in palisades. Secondary pit connections are present between adjacent outer cortical cells (Figure 3d). Inner cortical cells are rounded. Medullary cells are 28–47 μm long × 25–53 μm wide. Annular (Figure 3e) and lenticular (Figure 3f) thickenings are present. Discernible axial segments are found in the apical pit of branchlets. Each vegetative axial segment cuts off two periaxial cells, 26–52 μm long × 16–44 μm wide (Figure 3c). In longitudinal sections of the ultimate branches, outer cortical cells walls near apices do not project beyond the surface, but expose secondary pit connections between adjacent cortical cells (Figure 3g).

**Reproductive structures** — Fertile male branches with cup-shaped spermatangial pits, which are located in the apex and/or at the bifurcation of the branchlets (Figure 4a). Spermatangial branches of filament-type. Spermatangial branches are unbranched, 43–85 μm long, and usually terminate in an apical, vesicular, sterile cell of 20–42 × 20–33 μm (Figure 4b). Clusters of 2–3 or even 4–6 apical, vesicular, sterile cells can also be found (Figure 4c). Ovoid spermatangia, 8–12 μm long × 3–6 μm wide, each with a single apical nucleus. Female gametophyte with cystocarps located sub-apical in the fertile branches. Sessile and ovoid cystocarps, 0.6 mm long × 0.7 mm wide, with a protruding ostiole (Figure 4d). Carposporangia are ovoid, 71 μm long × 41 μm wide (Figure 4e). Tetrasporophyte with simple cylindrical branches, 0.8–1.7 mm long × 0.4–0.5 mm wide, with mature tetrasporangia present in the last two orders of branching, arranged parallel to the stichidal axis (Figure 4f). Tetrasporangia are randomly born on cortical cells. The two presporangial cover cells are arranged parallel to the stichidal axis in surface view. The postsporangial cover cell divides and thus contributes to cortex formation around the tetrasporangia (Figure 4g, h, i).
Distribution and habitat in the Canary Islands — La Palma, Tenerife, Lanzarote (Haroun et al. 2002), La Gomera, and Fuerteventura as new records (Figure 1); in the borderline of mid-intertidal rock pools, hidden among species of Cystoseira C. Agardh. Specimens were also collected from crevices and large boulders in the lower intertidal.

Osmundea pinnatifida (Hudson) Stackhouse (1809:79)
Basionym: Fucus pinnatifidus Hudson (1762:473).
Lectotype: No. 405, Herb. Petiver, British Museum.
Nomenclatural synonyms: Laurencia pinnatifida (Hudson) J.V. Lamouroux (1813:42), Gledium pinnatifidum (Hudson) Lyngbye (1819:40), Chondria pinnatifida (Hudson) C. Agardh (1822:337).
Type locality: Harwich, Essex, England (Maggs and Hommersand 1993)

Morphology — Thallus erect, up to 4 cm high, strongly compressed, cartilaginous in texture, brownish-purple colour, main axis 0.3–0.7 mm wide in the middle (Figure 5a). Erect fronds pinnate, attached to substratum by stolonal branches and basal crust (Figure 5b). Thallus has three orders of branches, branching irregularly alternate-distichous (Figure 5a). Branches compressed, 0.1–1.5 mm long × 0.3–0.5 mm wide, ultimate branchlets terete. Fresh plants have a strong chemical smell and flavour.

Vegetative structures — In surface view, morphology of the outer cortical cells in the middle of the thall are polygonal, pentagonal or hexagonal, 10–24 μm long × 7–19 μm wide, not connected by secondary pit connections (Figure 5c). Corps en cérise were absent in living material. Transverse sections of the thallus show two different layers of cortical cells (Figure 5e). Outer cortical cells are hyaline, rectangular, small, 15–23 μm long × 12–20 μm wide, not arranged in palisades. Secondary pit connections are absent between adjacent outer cortical cells (Figure 5e). Inner cortical cells are pigmented, larger than external cells, 16–25 μm long × 16–18 μm wide. Medullary cells are rounded, large, 26–43 μm long × 27–42 μm wide and with thickened walls. Annular and lenticular thickenings can be present or absent (Figure 5f, g). Axial segments are discernible in the apical pit of the branchlets. Each vegetative axial segment cuts off two pericentral cells, 24–35 μm long × 17–24 μm wide (Figure 5d). In longitudinal sections of the ultimate branches, outer cortical cells walls near apices do not project beyond the surface.

Reproductive structures — Fertile male branches with pocket-shaped spermatangial pits, located at the bifurcations of the ultimate branchlets or laterally in series, 0.3–0.4 mm long × 0.1–0.2 mm wide (Figure 6a). Pocket-shaped has a narrow apical pore (Figure 6b). Spermatangial branches of filament-type, terminating in a vesicular, sterile cell, 18 μm × 12 μm. Ovoid spermangia, 5–11 μm long × 2–5 μm wide, each with a single apical nucleus. Female gametophyte with cystocarps laterally located, mainly in the second-order branches, sessile, slightly ovoid, 0.5 mm long × 0.4 mm wide, with a non-protruberant ostiole (Figure 6c). Tetrasporophyte has simple or composed cylindrical branches, 0.8–0.9 mm long × 0.2–0.4 mm wide. Tetrasporangia are randomly born on cortical cells. In surface view, the two presporangial cover cells are

Figure 2: Osmundea truncata from the Canary Islands: (a) habit of a plant; (b) detail of dicoid holdfast; (c) detail of buds alternately arranged in main axis, new branches originating from damages produced by loss of old branches
arranged parallel to the stichidal axis. The postsporangial cover cell divides and thus contributes to cortex formation around the tetrasporangia (Figure 6d, e, f).

**Distribution and habitat in the Canary Islands** — El Hierro, La Palma, La Gomera, Tenerife, Gran Canaria, Fuerteventura, and Lanzarote (Haroun et al. 2002) (Figure 1), growing on basaltic substratum in the lower intertidal zone of exposed coasts.

**Osmundea sp.**

**Morphology** — Thallus erect, up to 3 cm high, main axes cylindrical in the basal and the middle region, slightly compressed in the apical region. Reddish-pink in colour, cartilaginous in texture, main axis in the middle is 0.3–0.8 mm wide. It is growing isolated, not tufted, attached by a discoid holdfast. Branching is irregularly alternate. Axes denuded in lower part and with 1–2 orders of branches in the upper third of the main axis. Branches 0.2–2 mm long × 0.3–0.6 mm wide, with truncated apices in which dense tufts of hyaline trichoblasts are inserted (Figure 7a).

**Vegetative structures** — In surface view, cortical cells in the middle region of the thalli are polygonal, pentagonal or hexagonal, 11–22 μm long × 7–14 μm wide, with secondary pit connections between adjacent cells (Figure 7e). *Corps en cerise* were absent in living specimens. Transverse sections of the thallus have two layers of pigmented cortical cells (Figure 7b). Outer cortical cells are rectangular, 20 μm long × 14 μm wide, not arranged in palisades. Secondary pit connections are present between adjacent outer cortical cells. Inner cortical cells are rounded and larger than external cells, 19–33 μm long × 16–28 μm wide. Medullary cells are round,
38–62 μm in diameter, with thick walls, annular thicken-
ings are present (Figure 7b). Axial segments are discern-
ible in the apical pits of the branchlets. Each vegetative
axial segment cuts off two periaxial cells, 43–56 μm long ×
39–43 μm wide (Figure 7c).

Reproductive structures — Tetrasporophyte with simple
cylindrical branchlets, 0.4–0.6 mm long × 0.3–0.5 mm
wide, with mature tetrasporangia arranged parallel to the
axial axis. Tetrasporangia are randomly born on cortical
cells. The two presporangial cover cells are arranged
parallel to the stichidial axis in surface view. The postsporo-
gangial cover cell divides to contribute to the formation of
the cortex around the tetrasporangia. (Figure 7e, f). Male
and female gametophytes were not observed.

Distribution and habitat in the Canary Islands — Osmun-
dea sp. was collected in La Punta de Gáldar, a very exposed
coast north-west of the Island of Gran Canaria (Figure 1),
growing epilithically in crevices of basaltic platforms in the
lower intertidal zone.

Molecular analyses

Variation in the rbcL sequences — We sequenced the
rbcL gene for 13 specimens of the Laurencia complex:
one specimen of Laurencia caduciramulosa Masuda and
Kawaguchi, three of O. pinnatifida, eight of O. truncata
and one of Osmundea sp. A total of 47 sequences was
analysed, including Ceramium brevzonatum H.E. Petersen
and Centroceras sp. [as C. clavatum (C. Agardh in Kunth)
Montagne in Durieu de Maisonneuve] as outgroups.
Intergeneric divergence variations are shown in Table 2.

Phylogeny — The dataset consisted of 802 constant
characters and 90 parsimony non-informative sites.
Maximum parsimony produced two trees of 1 060 steps
(CI = 0.8, HI = 0.2). The topology of the majority rule
Bayesian tree with bootstrap and posterior probability
values is shown in Figure 8. The analysis shows a
monophyletic Laurencia complex with high bootstrap
values in relation to members of the outgroups. The
Laurencia complex separated into five monophyletic

Figure 4: Reproductive structures of Osmundea truncata from the Canary Islands: (a–c) male gametophyte — (a) cup-shaped spermatangial
receptacles located in the apical region of the branches and/or at the bifurcations of the branchlets, (b) spermatangial filaments terminating in
by 1–3 sterile, vesicular cells, (c) spermatangial filaments terminating in 4–6 sterile, vesicular cells, (d–e) female gametophyte — (d) sessile
cystocarps with protruding ostioles, (e) large clavate carposporangia; (f–i) tetrasporophyte with conspicuous tetrasporangia — (f) tetraspo-
grangial branchlets showing parallel arrangement of tetrasporangia, (g–h) transverse section of a tetrasporangial branchlet — note a post-
sporangial cell [post], a stichidial cell [st] and two presporangial cover cells [pre] arranged parallel (arrows) to the stichidial axis and (i) prespo-
rangial cover cells in surface view (arrows)
clades with high bootstrap support, corresponding to the genera that form the group: Chondrophycus, Laurencia, Osmundea, Palisada and Yuzurua. The earliest diverging clade, the genus Laurencia included five taxa: L. viridis, L. oblusa, L. intricata, L. dendroidea and L. caduciramulosa. The monophyletic clade that corresponded to the genus Palisada also included five taxa: P. perforata, P. flagellifera, P. cf. cruciata, P. cf. robusta and P. corallopsis. The genera Palisada and Yuzurua turned out to be sister groups forming a clade with high bootstrap support and posterior probability values. The monophyletic clade corresponding to the genus Yuzurua included one taxon: Y. poiteaui. The Chondrophycus clade included four taxa: C. cf. undulatus, C. sp.1, C. sp. 2 and C. sp. 3. Finally, the genera Osmundea assemblage included two sister groups. The earliest diverging clade included four taxa from the North-East Pacific region: O. spectabilis var. spectabilis, O. blinksii, O. splendens and O. sinicola. The
other sister clade was resolved into two sister lineages that included several taxa from the North Atlantic coast. One subclade included three taxa: *O. truncata*, *O*. sp. and *O. oederi*; the other subclade included three taxa: *O. osmundae*, *O. hybrida* and *O. pinnatifida*.

Discussion

Similar to the other species of the marine habitat of the Canary Islands, the genus *Osmundea* is characterised by its diversification, high spatial variability, and by constituting generally small populations, both in biomass and in distribution. These features are likely the result of the particular oceanographic characteristics at the meso- as well as macro-scale, which usually occur in the bodies of water surrounding the islands (Haroun et al. 2009). The species referred to in this study populate a great variety of habitats in the intertidal zone, generally located in the north, north-west and north-east of the archipelago, all of them being exposed to strong, high-energy waves. Specimens were
Figure 7: Habit, vegetative and reproductive structures of *Osmundea* sp.: (a) habit, showing erect axes borne on discoid holdfast — note 1–2 orders of branches in the upper third of the main axis; (b–c) transverse section of the upper portion of a branch — (b) medullary cells with annular thickenings (arrow), (c) vegetative axial segment with an axial cell [a] and two pericentral cells [p]; (d) longitudinal section of cortex showing two layers of pigmented cortical cells — note outer cortical cells with secondary pit connections (arrows); (e) surface view of tetrasporophyte — detail of cortical cells with secondary pit connections (arrow) and two presporangial cover cells (pre) arranged parallel to the stichidal axis; (f) transverse section of a tetrasporangial branchlet, showing the post-sporangial cell [post], the stichidal cell [st] and the two presporangial cover cells [pre] (arrows)

normally collected in shady zones of intertidal rock pools, basaltic, littoral-platform surfaces, and in deep crevices of rocks located in the lower intertidal zone.

Morphological comparisons among the species of *Osmundea* are shown in Table 3. Collected specimens of *O. truncata* revealed two morphotypes. In the Canary Islands, specimens of *O. truncata* were generally located in pools of the mid-intertidal zone, hidden between thalli of the genus *Cystoseira* C. Agardh; some specimens, however, were found in large crevices of the lower intertidal zone. These samples exhibited only two orders of branches instead of four or five, prevalent in *O. truncata* (Maggs and Hommersand 1993). Also, they exhibited male gametophytes with spermatangial filaments terminating in a cluster of sterile, apical cells and not in a single one, which is commonly observed in *O. truncata* (Nam et al. 2000). The two located morphotypes are most likely the result of the ecological conditions which characterise the habitat.

In the Canary Islands, the occurrence of *O. truncata* had been reported for La Palma, Tenerife and Lanzarote (Haroun et al. 2002). Our morphological findings, however, extended the distribution area of the taxon, including, for the first time, the islands of La Gomera and Fuerteventura. Our results additionally confirmed the occurrence of *O. pinnatifida* in the intertidal zone of particularly exposed rocky coasts and also revealed several differences. The population of *O. pinnatifida* assessed in Puerto de la Cruz (Tenerife) exhibited smaller and less robust thalli than the specimens collected in Quintanilla, Arucas, Island of Gran Canaria. Moreover, the samples from Tenerife typically had very few and sometimes no lenticular thickenings. Again, these differences in morphology could be the result of the habitat they occupied.
Table 2: The intergeneric divergence and interspecific divergence values obtained for rbCL sequences in this work and values reported by others workers for the Laurencia complex

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Intergeneric divergence values for rbCL sequences (%)</th>
<th>Values reported by other authors (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chondrophycus-Laurencia</td>
<td>9.0–11.3</td>
<td>–</td>
</tr>
<tr>
<td>Chondrophycus-Osmundea</td>
<td>9.2–11.9</td>
<td>11.28–12.85 (Mcvor et al. 2002)</td>
</tr>
<tr>
<td>Chondrophycus-Palisada</td>
<td>9.2–11.1</td>
<td>–</td>
</tr>
<tr>
<td>Chondrophycus-Yuzuru</td>
<td>10–11.8</td>
<td>–</td>
</tr>
<tr>
<td>Laurencia-Osmundea</td>
<td>8.6–12.8</td>
<td>10.56–10.59 (Mcvor et al. 2002)</td>
</tr>
<tr>
<td>Laurencia-Palisada</td>
<td>9.1–11.7</td>
<td>10–12 ([Palisada as Chondrophycus] Diaz-Larrea et al. 2007); 6–10  (Cassano et al. 2009)</td>
</tr>
<tr>
<td>Laurencia-Yuzuru</td>
<td>7.9–10.8</td>
<td>9–11 (Martin-Lescanne et al. 2010)</td>
</tr>
<tr>
<td>Osmundea-Palisada</td>
<td>9.6–12.8</td>
<td>10–13 ([Palisada as Chondrophycus] Diaz-Larrea et al. 2007); 9–12  (Cassano et al. 2009)</td>
</tr>
<tr>
<td>Osmundea-Yuzuru</td>
<td>9.5–13.5</td>
<td>–</td>
</tr>
<tr>
<td>Osmundea</td>
<td>3.1–6.9</td>
<td>–</td>
</tr>
<tr>
<td>Laurencia</td>
<td>3.3–5.9</td>
<td>6–8 (Diaz-Larrea et al. 2007); 3–8  (Cassano et al. 2009)</td>
</tr>
<tr>
<td>Osmundea</td>
<td>4.0–9.8</td>
<td>4.6–5.5 (Nam et al. 2000); 2.04–8.9 (Mcvor et al. 2002)</td>
</tr>
<tr>
<td>Palisada</td>
<td>2.8–5.8</td>
<td>6–8 ([Palisada as Chondrophycus] Diaz-Larrea et al. 2007); 4–10  (Cassano et al. 2009)</td>
</tr>
<tr>
<td>Yuzuru</td>
<td>2.3–5.9</td>
<td>0.01–0.02 ([Yuzuru as C. gemmiferus and C. poiteau] Diaz-Larrea et al. 2007); 0.2 (Martin-Lescanne et al. 2010)</td>
</tr>
<tr>
<td>Osmundea sp.–O. truncata</td>
<td>6.8–7.7</td>
<td>–</td>
</tr>
<tr>
<td>Osmundea sp.–O. pinnatifida</td>
<td>7.7–9.0</td>
<td>–</td>
</tr>
<tr>
<td>Osmundea sp.–O. oederi</td>
<td>4.5</td>
<td>–</td>
</tr>
</tbody>
</table>

In Tenerife, the population was found on small surfaces, in rocky, abrupt zones, semi-protected from the impact of the strong waves. In contrast, the population of O. pinnatifida is widely spread in Gran Canaria, inhabiting the vertical, highly wave-exposed areas of large clumps of rock. The observed morphotypes could represent the result of adaptation to diverse ecological conditions.

Our results indicate a new taxonomic unit for the Canary Islands, Osmundea sp. However, taxonomic determination was not possible as all of the collected specimens turned out to be sterile or tetrasporophytes. The fact that no gametophyte was found in the collections restricted identification to morphologic characterisation.

Osmundea hybrida and O. oederi have been reported for the Canary Islands by Gil-Rodríguez et al. (2003). The record of these two taxa in the islands was based on the before-mentioned citations of Laurencia hybrida and Osmundea ramosissima (as L. platycephala) (Gil-Rodríguez and Haroun 1993).

In the past, there have been many errors in species identification in the genus Osmundea on the European coasts, particularly with O. hybrida, O. pinnatifida, O. oederi and O. truncata, which has led to taxonomic confusions (Maggs and Hommersand 1993, Nam et al. 1994, 2000).

Osmundea hybrida and O. oederi were not collected in our study, although the sites of previous records of both species, such as Gran Canaria, Tenerife and La Palma, were sampled. However, specimens of these two taxa previously collected in the Canaryies and deposited in the herbaria TFC, BCM and L were examined for comparison. Our analyses revealed that this material had been misidentified. In some cases, the study specimens showed morphological characters of O. truncata or O. pinnatifida, others exhibited morphological features of the genus Laurencia. Thus, all of this material is considered to be incorrectly determined.

The intergeneric divergence values obtained in our work for rbCL sequences are comparable to those reported by other workers for the Laurencia complex (Table 2). The interspecific divergence values reported here are also comparable with those reported previously for the genus Osmundea (Table 2).

Our phylogenetic analyses confirmed the results obtained by Martin-Lescanne et al. (2010), inferring the Laurencia complex as a monophyletic group that includes five genera. Bayesian topology (Figure 8) demonstrated that the samples identified as O. truncata for seven Canarian localities (Los Cancajos and La Fajana de Barlovento, island of La Palma; Charco del Conde, island of La Gomera; La Barranquera, Puerto de la Cruz and Playa Paraiso, island of Tenerife; Corralejo, island of Fuerteventura) were grouped in the clade that included the O. truncata sequence from GenBank (Ireland). Our results confirmed the presence of the taxonomic entity O. truncata in the Canarian Archipelago and confirm with records obtained by Haroun et al. (2002) who published on the islands of La Palma and Tenerife. Also, the presence of O. truncata for La Gomera and Fuerteventura in our study is the first record of this species for these islands.

The sample from the locality of Quintanilla, Gran Canaria, identified as O. pinnatifida, was grouped in the same clade as the O. pinnatifida sequences from GenBank. Our results are in agreement with Haroun et al. (2002) who recorded O. pinnatifida for the island of Gran Canaria based on morphological evidence. The sequences of the species of O. truncata and O. pinnatifida from the Canary Islands were resolved into two subclades which correspond to the observed morphotypes. This could be the result of speciation
Table 3: Comparative morphological data of *Osmundea* spp.

<table>
<thead>
<tr>
<th>Species</th>
<th>Vegetative structures</th>
<th>Male structures</th>
<th>Female structures</th>
<th>Geographic distribution</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Thallus</td>
<td>Type of attachment</td>
<td>Secondary pit connection</td>
<td>Lenticular thickening</td>
<td>Spermatangial pit</td>
</tr>
<tr>
<td><em>O. blinkai</em> (Hollenberg et Abbott) Nam</td>
<td>Compressed</td>
<td>Spreading crust</td>
<td>Absent</td>
<td>Absent</td>
<td>Pocket-shaped</td>
</tr>
<tr>
<td><em>O. crispa</em> (Hollenberg) Nam</td>
<td>Angular to terete</td>
<td>...</td>
<td>Absent</td>
<td>Absent</td>
<td>Pocket-shaped</td>
</tr>
<tr>
<td><em>O. hybrida</em> (A.P. de Candolle) Nam</td>
<td>Terete</td>
<td>Discoid holdfasts</td>
<td>Absent</td>
<td>Absent</td>
<td>Cuplike</td>
</tr>
<tr>
<td><em>O. lata</em> (M. Howe &amp; W.R. Taylor) Yoneshigue-Valentin, M.T. Fuji &amp; Gurgel Nam</td>
<td>Compressed</td>
<td>Discoid holdfasts</td>
<td>Present</td>
<td>Absent</td>
<td>Cuplike</td>
</tr>
<tr>
<td><em>O. maggsiana Serio, Cormaci &amp; G. Furnari</em></td>
<td>Terete</td>
<td>Discoid holdfasts</td>
<td>Absent</td>
<td>Absent</td>
<td>Cuplike</td>
</tr>
<tr>
<td><em>O. multibulba</em> (Dawson, Neushul et Wildman) Nam</td>
<td>Compressed</td>
<td>...</td>
<td>Absent</td>
<td>Absent</td>
<td>Pocket-shaped</td>
</tr>
<tr>
<td><em>O. pelagiasis</em> G. Furnari</td>
<td>Compressed</td>
<td>Basal crust</td>
<td>Absent</td>
<td>Absent</td>
<td>Cuplike</td>
</tr>
<tr>
<td><em>O. pelagosa</em> (Schiffner) Nam</td>
<td>Compressed</td>
<td>Discoid holdfasts</td>
<td>Present</td>
<td>Present</td>
<td>Pocket-shaped</td>
</tr>
<tr>
<td><em>O. pinnatifida</em> (Hudson) Stackhouse</td>
<td>Compressed</td>
<td>Stolonous</td>
<td>Absent</td>
<td>Absent/ present</td>
<td>Pocket-shaped</td>
</tr>
<tr>
<td><em>O. oederi</em> (Gunnerus) G. Furnari</td>
<td>Suberete</td>
<td>Discoid holdfasts</td>
<td>Present</td>
<td>Absent</td>
<td>Cuplike</td>
</tr>
<tr>
<td><em>O. sinicola</em> (Setchell &amp; Gardner) Nam</td>
<td>Compressed</td>
<td>...</td>
<td>?</td>
<td>Present</td>
<td>Pocket-shaped</td>
</tr>
<tr>
<td>Osmundea sp.</td>
<td>Suberete</td>
<td>Discoid holdfasts</td>
<td>Present</td>
<td>Absent</td>
<td>?</td>
</tr>
<tr>
<td><em>O. spectabilis</em> (Postels et Ruprecht) Nam</td>
<td>Suberete</td>
<td>Discoid holdfasts</td>
<td>Present</td>
<td>Absent</td>
<td>Pocket-shaped</td>
</tr>
<tr>
<td><em>O. splendidens</em> (Hollenberg) Nam</td>
<td>Compressed</td>
<td>...</td>
<td>Absent</td>
<td>Absent</td>
<td>Pocket-shaped</td>
</tr>
<tr>
<td>*O. trunca (Kützing) Nam et Maggs</td>
<td>Suberete</td>
<td>Compressed</td>
<td>Discoid holdfasts</td>
<td>Present</td>
<td>Present</td>
</tr>
<tr>
<td><em>O. verlaquei</em> (G. Furnari</td>
<td>Compressed</td>
<td>Basal crust</td>
<td>Present</td>
<td>Absent</td>
<td>Cuplike</td>
</tr>
</tbody>
</table>

* Denotes a specific reference for the character, which is detailed in the Source column.
Figure 8: Phylogenetic relationships of the Laurencia complex based on Bayesian analysis of rbcl DNA sequences. Pairs of numbers at the nodes reflect the bootstrap (top) and Bayesian posterior probability (bottom) values.
events, which are common in islands’ ecosystems (Whittaker and Fernández-Palacios 2007).

Osmunda sp. diverged from O. oederi in highly uncorrected p-distance values (4.5%). The sister clade, which includes O. truncata samples, also diverged from Osmunda sp. with p-distance values of 6.8%–7.7%, as well as O. pinnatifida samples (7.7%–9%). These data suggest that Osmunda sp. constitutes a distinct entity and should be assigned to a new taxon within the genus Osmunda.

In summary, this work provides the first citations of O. truncata on the islands of La Gomera and Fuerteventura and confirms the presence of O. pinnatifida in Gran Canaria. These two species both exhibit distinct morphotypes which could be the result of adaptation to ecological factors of their particular environment. Furthermore, O. hybrida and O. oederi appear to be dubious records for the Canary Islands. Finally, the high degree of genetic variation between Osmunda sp. from the rest of the Osmunda species suggests that this species should be assigned to a new taxon within the Osmunda genus from the Atlantic region (Canary Islands).

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Appendix: Taxa used for morphological study


**Osmunda sp.** Fresh specimens. Gran Canaria island: Punta de Gáldar (TFC Phyc. 14025).
