

Short Communication

Taxonomic position of the two sympatric forms of *Chondracanthus chamissoi* (f. *lessonii* and f. *chauvinii*) (Rhodophyta, Gigartinaeae) by using two molecular markers

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ABSTRACT. The red seaweed *Chondracanthus chamissoi* shows high morphological variability. Initially, three species were identified based on the width of the main axis of their blades. Later, all of them were included in a single species with two morphological groups. Recently, quantitative studies demonstrated the existence of two forms in *C. chamissoi*: f. *lessonii* and f. *chauvinii*. It was also shown that these two forms occur in sympatry, growing side by side. These forms were not associated with either a life cycle phase or the sex of the blades. This study aimed to determine whether the two forms could represent different species. We evaluated the forms' taxonomic position using COI and *rbcL* markers, including samples from three localities in southern Chile. All specimens shared a single *rbcL* haplotype, whereas the two COI haplotypes differed by four base pairs and were present in blades of both forms and life cycle phases. The two morphological types correspond to intraspecific forms. This species is of commercial importance, and its main market is aimed at human consumption with a marked preference for f. *lessonii*.

Keywords: *Chondracanthus chamissoi*; seaweed; COI; *rbcL*; forms; sympatric; morphological variability; coexistence

Chondracanthus chamissoi (Rhodophyta, Gigartinaeae) is a red seaweed that extends geographically from Paita, Peru (5°S), to Ancud, Chile (42°S) (Ramírez & Santelices 1991). Recent genetic analyses indicated that this species is also present in Korea and Japan, where it has been confused with *C. teedei* (Yang et al. 2015). In Chile, this species has been harvested and exported for the carrageenan industry (Hoffmann & Santelices 1997) and human consumption, mainly to Asian countries (Bulboa & Macchiavello 2006). Like many red seaweeds, *C. chamissoi* has a Polysiphonia-type, triphasic life cycle, alternating isomorphic gametophytic and sporophytic generations (Hoffmann & Santelices 1997, Avila et al. 2011).

C. chamissoi shows great morphological variability of blades throughout its geographical distribution range (Howe 1914, Dawson et al. 1964, Santelices 1989,

Ramírez & Santelices 1991, Bulboa & Macchiavello 2006, Rodríguez & Otaíza 2018).

Howe (1914) recognized three species based on the width of the blades' main axis in samples from Peru. He named *Gigartina chamissoi* those with intermediate blade width, *G. lessonii* those with more extreme narrow blades, and *G. chauvinii* those with broad main axes. Nevertheless, Howe (1914) admitted that the distinction of these species' morphological limits was difficult to establish. Later, Dawson et al. (1964) included *G. lessonii* and *G. chauvinii* as two morphological groups within *G. chamissoi*, the "*lessonii* group" with the main axis of 3-5 mm in width and the "*chauvinii* group" with the main axis of 20 mm or more. Ramírez & Santelices (1991) retained the distinction into three species until new studies provide more information. Ecological and culture studies have been

done in Chile regarding the high morphological variability of *C. chamissoi* (e.g. González & Meneses 1996, Vásquez & Vega 2001, Bulboa & Macchiavello 2006, Fonck et al. 2008, Sáez et al. 2008, Otaíza & Fonseca 2011, Bulboa et al. 2013, Rodríguez & Otaíza 2018, Arbaiza et al. 2019, Zapatas-Rojas et al. 2020, Oyarzo et al. 2021) but did not distinguish between morphological groups.

In previous studies, morphological variability was solely distinguished based on the width of the main axis. Still, recently Rodríguez & Otaíza (2020) quantitatively characterized more than 1000 thalli, including sporophytic and male and female gametophytic blades collected from three localities in the Biobío Region (southern Chile) and, for one of the localities, blades were collected in two seasons of the year. Their results clearly showed two distinct forms: gametophytes and sporophytes in the three localities and the two seasons. The two forms are discrete entities, differing statistically in four morphological characters. Apart from the narrow central axes, *f. lessonii* was characterized by having thick and curved (i.e., channeled) central axes and few or no spines on the surface (Fig. 1). On the other hand, *f. chauvinii* had wide and thinner central axes, flat, and numerous spines on both surfaces (Rodríguez & Otaíza 2020). Furthermore, their results show that thalli conform two separate groups in multivariate analyses, and there were no individuals with a different combination of characters.

An explanation based on differences among phases of the life cycle (e.g. heteromorphy or sexual dimorphism), as is the case with other species (e.g. Drew 1949, Van der Meer & Todd 1980), is not supported by the results obtained by Rodríguez & Otaíza (2020), who found both forms across gametophytes and sporophytes. Additionally, these authors showed that the forms occurred in sympatry, collected side by side, in the same patches. Sympatric occurrence of two distinct morphological forms is a rare phenomenon. Considering that morphological variability, generally described for red seaweeds like ecotypes or ecomorphs, is the result of growth in different environments, geographically separated (e.g. Gutierrez & Fernández 1992, Brodie et al. 1993, Shaughnessy 1996, Edding et al. 2006, Faria et al. 2017). Howe (1914) suggested one possible explanation: that the two forms correspond to two different species, reproductively isolated.

This study aimed to evaluate the taxonomic position of the two forms documented by Rodríguez & Otaíza (2020) for *C. chamissoi*, to determine whether consistent genetic differences occur by using a genetic characterization using two DNA molecular markers. In

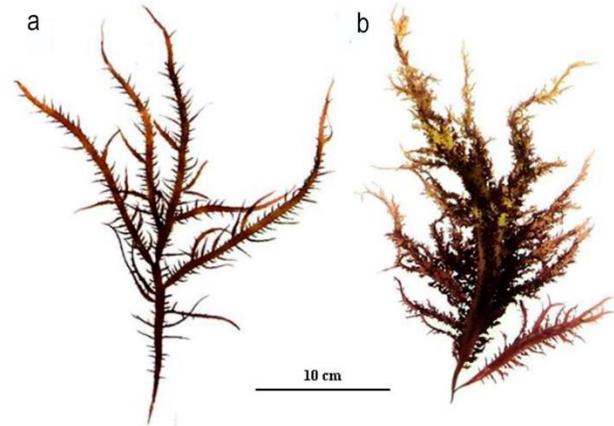


Figure 1. Two forms of *Chondracanthus chamissoi* described by Rodríguez & Otaíza (2020), a) tetrasporophytic blade of *f. lessonii*, b) female blade of *f. chauvinii*. Both specimens were collected from the same patch in summer 2018 in Cocholgüe, Chile.

red seaweeds, the mitochondrial gene cytochrome C oxidase subunit I (COI), and the plastidial *rbcl* gene, corresponds to the large subunit of ribulose-1,5-biphosphate carboxylase/oxygenase (RuBisCo). They have been used together for the identification of taxa at a generic and species level, and even at the intraspecific level (e.g. Gurgel & Fredericq 2004, Kim et al., 2006, Yang et al. 2013, López et al. 2017), including studies on species of the genus *Chondracanthus* (Schneider & Lane 2005, Hughey & Hommersand 2008), and in *C. chamissoi* itself (Yang et al. 2015). The latter study was done using both markers, including samples from Chile, without considering the forms (Yang et al. 2015).

Female gametophytic blades, identified by the presence of cystocarps, were collected randomly from shallow platforms (1-2 m of depth) at three localities in the Biobío Region, southern Chile: Ramuntcho (36°45'06"S, 73°11'04"W), Cocholgüe (36°35'15"S, 72°58'60"W) and Punta Lavapié (37°08'55"S, 73°35'13"W), between October and November 2017. From each clump, a single blade was collected.

Thalli were classified into *f. lessonii* and *f. chauvinii*, according to their morphological characters, as described by Rodríguez & Otaíza (2020). A small fragment without visible reproductive structures was cut from the fresh thalli and preserved in silica gel until the molecular analysis was done from each individual. Fifty-four individuals were analyzed with the mitochondrial partial gene COI, considering 8-11 thalli of each form and locality. Additionally, a subsample of 1-2 thalli of each form and locality was analyzed using the *rbcl* plastidial gene. The DNA extraction was done using a GeneJET Genomic DNA Purification (Thermo Scientific™), following the manufacturer's protocol,

and the resulting DNA was stored at -20°C until it was processed. Amplification of the COI gene was done using the primers designed by Saunders (2005) for red seaweeds (GazF1: 5' TCAACAAATCATAAAGAT ATTGG 3' and GazR2: 5' ACTTCTGGATGTCCA AAAAYCA 3') following the PCR conditions described by Fraser et al. (2009). For the amplification of the *rbcL* gene, the specific primers F7 and R753 (F7: 5' AACTCTGTAGAACGNACAAG 3'; R753: 5' GCT CTTTCATACATATCTTCC 3') (Gavio & Fredericq 2002) were used, with the conditions of the PCR described by Boo et al. (2013). Amplifications of both molecular markers were done using DNA GoTaq polymerase Fermelo Biotec (Promega, Madison, USA), in a Verity (Applied Biosystems, Foster City, USA). PCR products were purified and sequenced by MacroGen Inc. (Seoul, South Korea) using GazR2 primer for COI and F7 for *rbcL*. The edition, alignment of multiple sequences, and identification of polymorphic sites were made with BioEdit 7.2.5 (Hall 1999). The obtained sequences were analyzed using BLAST in GenBank (<https://blast.ncbi.nlm.nih.gov/Blast.cgi>; Altschul et al. 1990) to identify coincidences with other sequences in GenBank, including those published by Yang et al. (2015) for *C. chamissoi*.

Considering 698 base pairs (bp), the nine sequences obtained for *rbcL* corresponded to a single haplotype identical to the sequences of *C. chamissoi* available in GenBank (GenBank access number KP059091.1). The 54 sequences obtained from COI resulted in an alignment of 672 bp, with two haplotypes, named H1 and H2. Both haplotypes coincided (100% similarity) with GenBank sequences of *C. chamissoi* collected in Chile. H1 has been reported from Tarapacá (18°S), and H2 has been reported from Coquimbo (30°S) (GenBank access number KP059067.1 and KP059069.1, respectively, Yang et al. 2015).

In this study, haplotype H2 was detected in all three sampled localities, whereas H1 was found only at Punta Lavapié (Table 1). Interestingly, the two haplotypes reported by Yang et al. (2015) for the Biobío Region (from Cocholgüe and Lebu) were not found in this study despite our samples from nearby localities. On the other hand, both COI haplotypes were obtained from thalli of both forms (Table 1), indicating that morphological, but no genetic, differences exist between them. Furthermore, the divergence between these two haplotypes was only 0.5% (4 bp), whereas interspecific divergence between *C. chamissoi* and its sister species *C. teedei* is between 2.7-3.8% (Yang et al. 2015). Thus, even if the haplotypes had been previously related to the forms (one haplotype = one form), variability between them is lower than the divergence threshold generally considered to discriminate among

Table 1. Summary of the COI sequences of thalli of *Chondracanthus chamissoi* f. *lessonii* and f. *chauvinii* from three localities in southern Chile. The frequency of the H1 and H2 haplotypes is indicated for each locality and form.

Locality	Form	N° of COI sequences	H1 (%)	H2 (%)
Ramuntcho	f. <i>lessonii</i>	8	0	100
Ramuntcho	f. <i>chauvinii</i>	8	0	100
Cocholgüe	f. <i>lessonii</i>	8	0	100
Cocholgüe	f. <i>chauvinii</i>	9	0	100
Punta Lavapié	f. <i>lessonii</i>	10	90	10
Punta Lavapié	f. <i>chauvinii</i>	11	91	9

Gigartinales species (<1% for intraspecific divergence, >1.5% for interspecific divergence, with observed values commonly higher than 9% in the Gigartinales; Le Gall & Saunders 2010).

The genetic data obtained in this and previous studies are limited in quantity and geographical distribution. Even so, they suggest a low genetic diversity in *C. chamissoi*, with haplotypes shared between distant localities in the southeast Pacific (Tarapacá-Biobío: 2359 km of coastline) and low divergence between populations in Chile and Asia (Yang et al. 2015). A phylogeographic study is necessary to reveal the dispersion mechanisms of this species and, in particular, better understand vegetative reproduction's role in its propagation.

It has been shown that *C. chamissoi* has a great capacity for vegetative reproduction by secondary attachment of fragments (Macchiavello et al. 2003, Sáez et al. 2008, Rodríguez & Otaíza 2018). However, the relative frequency with which this type of reproduction occurs compared to the production of new individuals from spores is unknown. Future research should determine whether vegetative reproduction is common in *C. chamissoi*, as it has been reported for *C. pectinatus* and *C. squarulosus* (Pacheco-Ruiz & Zertuche-González 1999, 2005). As vegetative reproduction produces genetically identical new individuals, if this type of reproduction were common, then many thalli could be part of widely distributed clones, which could explain the low intraspecific variability found in *C. chamissoi* (Table 1; Yang et al. 2015).

In sum, differences between phases or sexes (Rodríguez & Otaíza 2020) cannot explain the occurrence of the two forms of *C. chamissoi*. Also, phenotypic differences resulting from exposure to different environmental conditions cannot explain the two forms. At each site, thalli of both forms were collected in the same patches. On the other hand, our results in this study indicate no evidence that the two

forms correspond to phylogenetic species, and genetic differences at the intraspecific level were not found. Rodríguez & Otaíza (2020) propose that the origin of the two forms may be related to the differentiation of the tissues at the tips of the axes associated with the formation of secondary attachment discs. Regrowth after wound healing can produce different morphology types in the same thallus, as has been shown for *Solieria filiformis* (Perrone & Cecere 1997), so axes with a different morphology may grow from the secondary attachment discs differentiated from the apexes.

Identifying the mechanism that originates morphological variants in this species, and in the Gigartineaceae, in general, is important given their economic and ecological value (Graham & Wilcox 2000). The primary market for *C. chamissoi* is as food for humans in Peru and Asian countries, with a marked preference for f. *lessonii*, considered more palatable (F. Tellier *comm. per.*). Resolving the mechanisms that result in the modification of thallus morphology could be incorporated into production techniques, positively impacting this algal resource's added value, which is considered one of the red seaweeds with the highest landings in Chile and Peru (PRODUCE 2017, SERNAPESCA 2017).

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