Received: 23 July 2020 | Revised: 15 July 2021 | Accepted: 18 August 2021

DOI: 10.1111/jwas.12849

FUNDAMENTAL STUDIES

Journal of the World Aquaculture Society Open Access | WORLD AQUACULTURE Society | WILEY

The widely distributed, edible seaweeds in Peru, *Chondracanthus chamissoi* and *Chondracanthus chamissoi* f. *glomeratus* (Gigartinaceae, Rhodophyta), are morphologically diverse but not phylogenetically distinct

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Funding information
Consejo Nacional de Ciencia, Tecnología e Innovación Tecnológica, Grant/Award Number: Convenio de Subvención Nro. 017-2016-FONDECYT

Abstract

Chondracanthus chamissoi is part of the diet of coastal people from Peru and is exported dehydrated to Asian countries for direct consumption. Although it is considered endemic to Peru and Chile, its range has extended to distant regions, such as Korea, Japan, and France. Using morphological and molecular approaches, we examined specimens from Peru assigned to *C. chamissoi* (including the taxon of uncertain status *Chondracanthus glomeratus*) to improve phylogenetic and geographical information and characterize its morphological variability. Twenty-one localities on the Peruvian coast were sampled, obtaining 102 COI and 27 *rbc*L sequences. To differentiate both entities, morphological characters such as thallus size, consistency, arrangement of main and secondary axes,

branching patterns and location of reproductive structures, were analyzed on 46 specimens. While morphological characteristics are clearly contrasting among the two groups, both COI and *rbc*L phylogenies revealed a well-supported clade with no genetic differentiation between the two morphologies. Therefore, the phylogenies indicate that *C. chamissoi* and *C. glomeratus* form a single taxonomic entity with high morphological variability, large geographic distribution and at least two morphological forms. The smaller form of *C. chamissoi* can be identified as *C. chamissoi* f. *glomeratus*. Such morphological variability can be of interest for future aquaculture development.

KEYWORDS
Gigartina, morphology, phylogeny, yuyo

1 | INTRODUCTION

Chondracanthus chamissoi (C. Agardh) Kützing, a red algae known in Peru as "yuyo" or "mococho," is distributed in South America from Paita, Peru (5°S) to Ancud, Chile (42°S) (Ramírez & Santelices, 1991). It is the only species consumed in a fresh state, serving as an accompaniment in typical coastal dishes or as a main ingredient as in salads (Ávila, Piel, Cáceres, & Alveal, 2011; PRODUCE, 2016). This seaweed seems to have been part of the Peruvian diet since prehispanic times, as indicated by arqueobotanical records from the Nazca and Paracas culture and by the algal representation on ceramics of the Moche culture (Aldave, 1971). Recently, its fresh and dehydrated form has enjoyed growing demand in Asian countries, in which *C. chamissoi* is consumed in soups and salads (Macchiavello et al., 2012). A few years ago, *C. chamissoi* was offered at the fishing terminals, markets, and supermarkets for the purchase of marine products, and later sold for $ 0.5 US dollars/kg. Today, the price fluctuates between 3 and 4 US dollars/kg in the supermarket. The price of dried seaweed is 9 US dollars/unit (approximately 200 g) (Villena, pers. com.). Also, this species synthesizes carrageenans, polysaccharides with binding properties, emulsifiers, thickeners, gelling agents, which are used in the formulation of various foods such as ice cream, chocolate milk, cheese, creams, and hams (Ávila et al., 2011; Kradolfer, 2007). *Chondracanthus chamissoi* is thus used locally for human consumption, as well as exported for human food and for the hydrocolloid industry.

In Peru, as in Chile, this resource is obtained from natural populations through direct extraction by artisanal fishermen, an activity that sustains many families economically and contributes to the country's food security (Flores, Zavala, Donayre, Guardia, & Sarmiento, 2015). With rising demand for high-quality products and evidence of overexploitation of the natural resource, aquaculture development has been increasingly considered as a viable alternative. Attempts to cultivate *C. chamissoi* in Peru occurred in early 2000 (Hayashi, Bulboa, Kradolfer, Soriano, & Robledo, 2013). Production from cultivation decreased from 131 tons in 2012 to 2 tons in 2014 (FAO, 2018a), and ceased entirely in 2015 (FAO, 2018b). Meanwhile, in Chile, cultivation techniques for *C. chamissoi* were improving (Ávila et al., 2011; Bulboa, Macchiavello, Véliz, & Oliveira, 2010; Correa, Beltrán, Buschmann, & Westermeier, 1999; Fonck, Martínez, Vásquez, & Bulboa, 2008), but there are still many challenges to solve before commercial cultivation (e.g. epiphytism) (Bulboa, Macchiavello, Véliz, Macaya, & Oliveira, 2007). Currently, the effort for the commercial cultivation of *C. chamissoi* has concentrated on strategies for vegetative propagation (Bulboa et al., 2013; Macchiavello et al., 2018; Sáez & Macchiavello, 2018). Despite the cultural and economic relevance of the "yuyo" in Peru, the basic biological and ecological aspects of the species are poorly known. Most studies have focused on

distributional data and morphological characterization (Acleto, 1986; Calderón, Ramírez, & Bustamante, 2010) and more recently on cultivation techniques (Arbaiza, Gil-Kodaka, Arakaki, & Alveal, 2019). Importantly, no genetic information has been published in scholarly journals, except three sequences from plastidial DNA published during 2020 (Calderón, Bustamante, & Boo, 2020); this nearly complete lack of basic genetic information may limit future development strategies for aquaculture, such as selection of local wild variants for agronomic trait improvement (Camus, Faugeron, & Buschmann, 2018; Valero et al., 2017).

The taxonomic status of *C. chamissoi* has changed over the years, being described as *Sphaerococcus chamissoi* C. Agardh, of material collected in Chiloé, Chile, transferred to *Gigartina chamissoi* (C. Agardh) J. Agardh, and subsequently assigned as *Chondracanthus chamissoi* (C. Agardh) Kützing. In Peru, *C. chamissoi* has been reported in the northern and central coast (Piura, La Libertad, Áncash, Lima, Callao, and Ica; Figure 1; Dawson, Acleto, & Foldvik, 1964, Ramírez & Santelices, 1991); while in Chile, it has been found from the Tarapacá Region (Iquique) to the Los Lagos Region (Chiloé, type locality) (Ramírez & Santelices, 1991; Silva, Basson, & Moe, 1996). The other species of the genus *Chondracanthus*, cited for Peru and Chile, is *Chondracanthus glomeratus* (M. Howe) Guiry (Hommersand, Guiry, Fredericq, & Leister, 1993), previously described as *Gigartina glomerata* M. Howe from San Lorenzo Island, Peru (Howe, 1914) and known in Peru as "yuyo clavo" (IMARPE, 2018). This species has a restricted distribution in Peru, where it has been reported only in Lima and Callao (San Lorenzo Island, type locality) (Dawson et al., 1964; Howe, 1914), while in Chile it has been found in the Regions of Tarapacá (Iquique) and Los Lagos

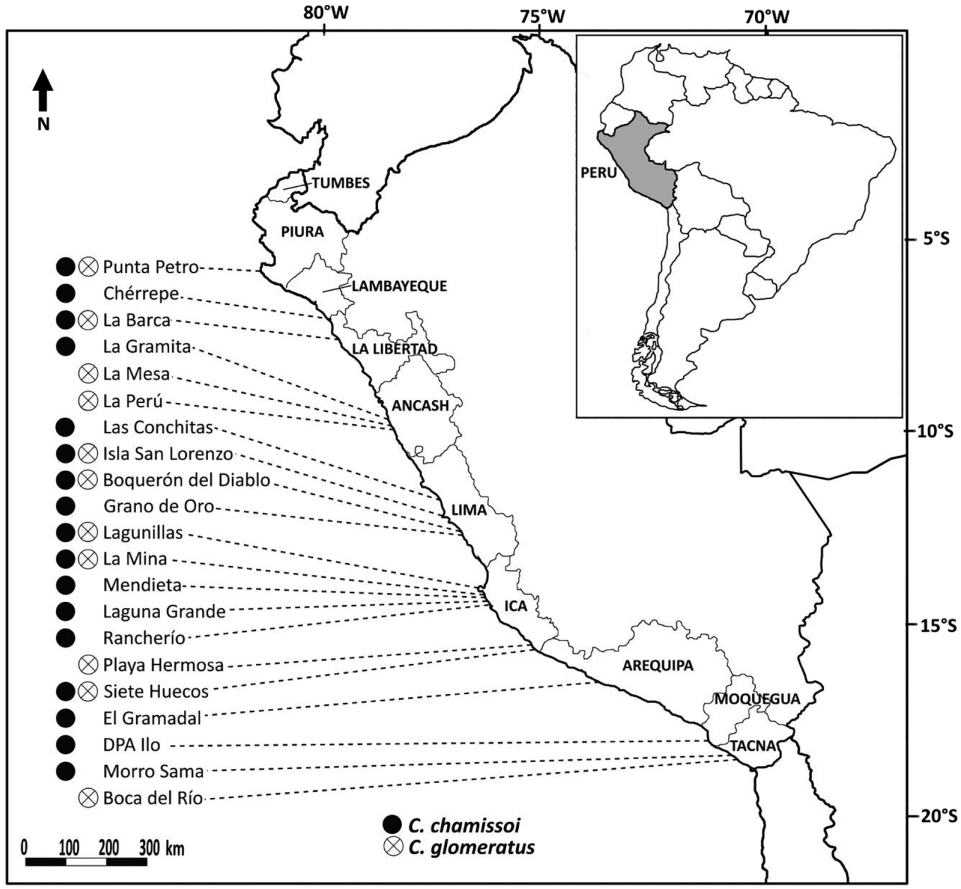

FIGURE 1 Map of the Peruvian coast showing the collection localities of *Chondracanthus chamissoi* and *C. glomeratus*

(Chiloé) (Ramírez & Santelices, 1991). Growth characterizations have shown a higher biomass for "yuyo" (*C. chamissoi*), with an estimation of 651 t in La Libertad Region, northern Peru, as compared to only 3.53 t for "yuyo clavo" (*C. glomeratus*) (IMARPE, 2018).

The morphology of *C. chamissoi* is highly variable (Acleto, 1986). Two species were previously recognized to be closely related to *C. chamissoi* (as *Gigartina chamissoi*): *Gigartina lessonii* (Bory) J. Agardh, which included the narrow forms of its fronds, and *Gigartina chauvinii* (Bory) J. Agardh, which included the wide forms (Howe, 1914). Subsequently, the two "species" were considered as *C. chamissoi*, with mention that within this species two morphological groups exist and cohabit (Dawson et al., 1964). Morphological descriptions of *C. chamissoi* from Peru and Chile coincide that this species can reach up to 50 cm and have one or more flattened main axes with lateral branches that are similar to the main axes. Additionally, small branches called pinnules, alternately or dystically arranged, are found on the margins of the main axes or lateral branches where the cystocarps and tetrasporangial sori are located (Acleto, 1986; Calderón et al., 2010; Otaíza & Cáceres, 2015). In a recent study performed in Southern Chile, Biobío Region, Rodríguez and Otaíza (2020) separated *C. chamissoi* into two distinct morphological groups of thalli, one group identified as *C. chamissoi* f. *lessonii* C.Y. Rodríguez & Otaíza (with narrow, thick, and curved blades, with few spines) and another group identified as *C. chamissoi* f. *chauvinii* C.Y. Rodríguez & Otaíza (with broad, thin, and flat blades, with many spines). On the other hand, *C. glomeratus* grows in dense tufts, with a height of 3–5 cm. Unlike *C. chamissoi*, its main axes give rise to the lateral branches, both with a cylindrical complanate diameter. These pinnules are concentrated in the apical part of its ramifications, housing the tetrasporangial cystocarps and sori, giving it an agglomerated appearance (Howe, 1914).

The taxonomic identification of red algae using only morphological characters is insufficient because of the algae's high plasticity (Saunders, 2005; see also for recent examples Guillemin et al., 2016; Núñez-Resendiz, Dreckmann, Sentíes, Wynne, & León-Tejera, 2019 and Díaz-Tapia, Maggs, Nelson, Macaya, & Verbruggen, 2020). Specimens identified morphologically as *C. chamissoi* from Chile, *C. teedei* (Mertens ex Roth) Kützing from South Korea and Japan, and *Chondracanthus* sp. from France have proven to be *C. chamissoi*, when they were phylogenetically evaluated with mitochondrial and plastidial DNA sequences (Yang, Macaya, & Kim, 2015). Therefore, the known distribution of *C. chamissoi* has undergone changes and is no longer considered endemic to Peru and Chile. The presence of *C. chamissoi* in the North-East Atlantic is beyond the scope of our study, but see Mineur, Le Roux, Stegenga, Verlaque, and Maggs (2012) for their discussion regarding possible origin and vectors of introduction in the Gulf of Morbihan, France, and the study of Yang et al. (2015). Using the same DNA markers, a recent study also revealed no genetic differentiation among specimens from f. *lessonii* and f. *chauvinii* sampled in southern Chile (Rodríguez, Tellier, Pérez-Araneda, & Otaíza, 2021). Also recently, through a phylogenetic analysis of *rbc*L DNA sequences, Calderón et al. (2020) suggested the other species of the genus *Chondracanthus*, *C. glomeratus*, as a synonym for *C. chamissoi*; however, their conclusions are limited by the small sampling, which included only two Peruvian specimens morphologically identified as *C. glomeratus* (from the same locality) and one *C. chamissoi* specimen from Peru, and other countries (Calderón et al., 2020). While the one-marker approach suggests the species are conspecific, we aimed to resolve the designation of *C. glomeratus* through a more integrative approach, considering Peruvian specimens assigned to *C. chamissoi* and *C. glomeratus*, throughout the Peruvian coast and including localities where the two species coexist. This study using both qualitative and morphometric characters and two molecular markers allows to increase the taxonomic, phylogenetic, and distributional information of this resource.

2 | MATERIALS AND METHODS

2.1 | Sample collection

Specimens assigned to *C. chamissoi* and *C. glomeratus* were collected between 2016 and 2017 in the low intertidal zone and the subtidal zone up to 5 m deep, or attached to buoys and ropes of artisanal fishing vessels. The sampling

took place in 21 localities throughout the Peruvian coast, from Punta Petro (Piura, 05°47′S) to Boca del Rio (Tacna, 18°09′S) (Table 1, Figure 1; see also Table A1). At all but three localities, we collected up to three specimens of each species. At three localities where the two species could be found in sympatry (Punta Petro, La Barca, and Boquerón del Diablo), we collected between 11 and 14 specimens per species. Portions of specimens were preserved in silica gel for molecular analysis. Associated material was herborized, photographed with a digital camera or scanned, and conserved in the Scientific Collection of the Instituto del Mar del Perú—IMARPE.

2.2 | Molecular analysis

DNA extraction followed the protocol of the GF-1 Plant DNA Extraction Kit (Vivantis, Malaysia). PCR reactions followed the modified method of Saunders and Kucera (2010), using the mitochondrial COI primers GazF1 and GazR1 (Saunders, 2005), and the plastidial *rbc*L primers F57, R753, F577, R-rbcLstart (Freshwater & Rueness, 1994; Gavio & Fredericq, 2002). All PCR products were amplified using *Taq* DNA polymerase of Applied Biological Materials (abm) Inc. (Vancouver, Canada), and purified and sequenced by Macrogen Inc. (Seoul, South Korea). The sequences were edited with CodonCode Aligner 7.1.2. and aligned with MUSCLE (Edgar, 2004). During this study, we generated 102 COI sequences (600 base pairs, bp), corresponding to 52 *C. chamissoi* and 48 *C. glomeratus* specimens (Table 1, see also Table A2). Additionally, we obtained *rbc*L sequences (1,250 bp) for a subsample of 27 specimens (17 *C. chamissoi* and 10 *C. glomeratus*; see Tables 1 and A2).

Each data set included the newly obtained sequences from the Peruvian samples, published sequences from *C. chamissoi* (13 COI sequences from Chile, South Korea, and Japan; 21 *rbc*L sequences from Chile, Peru, South Korea, Japan, and France), and published sequences from other species of *Chondracanthus* worldwide. Additionally, we included the following external groups: *Chondrus crispus* and *Mazzaella laminarioides* for COI, *Gigartina grandifida*, *Rhodoglossum gigartinoides*, and *Mazzaella laminarioides* for *rbc*L. Table A3 indicates specimen collection information and GenBank accession numbers for all non-Peruvian sequences.

Phylogenetic reconstructions considered one sequence per *C. chamissoi*/*C. glomeratus* haplotype. New COI and *rbc*L haplotypes are deposited in GenBank (Accession Numbers: are indicated in Table A2). Maximum likelihood (ML) phylogenetic trees were built with W-IQ-TREE (Trifinopoulos, Nguyen, von Haeseler, & Minh, 2016). We selected the nucleotide substitution model using the Akaike information criterion (Akaike, 1973) implemented in jModelTest 2.1.10 (Darriba, Taboada, Doallo, & Posada, 2012). The selected model was GTR + I + G for both data sets. Relative phylogenetic support for each node was estimated using 1,000 bootstrap replicates (Felsenstein, 1985). Bayesian inference was performed using MrBayes v3.2.6 (Ronquist et al., 2012). Two independent analyses were run with three chains each for 15 million generations. Trees and parameters were sampled every 1,000 generations. The first 25% of the sampled trees were discarded as "burn-in" to ensure stabilization. The remaining trees were used to compute a consensus topology and posterior probability values.

Inter- and intraspecific genetic distances were calculated in MEGA v 7.0 (Kumar, Stecher, & Tamura, 2016) using Kimura 2-parameter model (Kimura, 1980) with 1,000 replicates for both markers (COI and *rbc*L). Interspecific measures correspond to the pairwise distances between the *Chondracanthus* specimens used in the tree reconstruction (Tables A4 and A5).

2.3 | Morphological analysis

We photographed and analyzed morphologically 41 herborized specimens: 25 identified as *C. chamissoi*, from 17 localities, and 16 identified as *C. glomeratus*, from 11 localities (Table 1). Fertile material (gametophytes, tetrasporophytes) was also considered. For each specimen, we registered or measured qualitative (reproductive phase,

TABLE 1 *Chondracanthus chamissoi* and *C. glomeratus* from the Peruvian coast: sampling localities, frequency of COI and *rbc*L haplotypes and specimens considered for the morphological analyses

		Haplotypes		Morphological analyses	
Locality	**Species**	**COI (*n*)**	***rbc*L (*n*)**	***n***	**Fig. 3**
Punta Petro, Sechura, Piura	*C. chamissoi*	H1 (7), H7 (5)	R1 (1)	1	a11
	C. glomeratus	H1 (6), H2 (2), H3 (1), H4 (1), H7 (4)	R1 (1)	2	b7, b9
Chérrepe, Pueblo Nuevo, La Libertad	*C. chamissoi*	H1 (1)	R1 (1)	1	a2
La Barca, Malabrigo, La Libertad	*C. chamissoi*	H1 (10)	R1 (1)	2	a13
	C. glomeratus	H1 (11)	R1 (1)	1	b12
La Gramita, Casma, Ancash	*C. chamissoi*	H1 (2)	R3 (1)	2	a7
La Mesa, Casma, Ancash	*C. glomeratus*	H5 (2), H6 (1)	R1 (1)	3	b13, b14, b15
La Perú, Culebras, Ancash	*C. glomeratus*	H1 (1)	R2 (1)	1	b4
Las Conchitas, Ancon, Lima	*C. chamissoi*	H1 (1)	R2 (1)	1	a12
Isla San Lorenzo, La Punta, Callao	*C. chamissoi*	H1 (1)	R1 (1)	1	a5
	C. glomeratus	H1 (1)	R2 (1)	1	b1
Boquerón del Diablo, Pucusana, Lima	*C. chamissoi*	H1 (12)	R1 (1)	2	a1
	C. glomeratus	H1 (12)	R1 (1)	2	b10, b11
Grano de Oro, Pucusana, Lima	*C. chamissoi*	H1 (1)	ND	1	—
Lagunillas, Paracas, Ica	*C. chamissoi*	H1 (1)	R2 (1)	1	—
	C. glomeratus	H1 (1)	R2 (1)	1	b5
La Mina, Paracas, Ica	*C. chamissoi*	H1 (1)	R2 (1)	1	—
	C. glomeratus	H1 (1)	R2 (1)	1	b2
Mendieta, Paracas, Ica	*C. chamissoi*	H1 (1)	R1 (1)	1	—
Laguna Grande, Paracas, Ica	*C. chamissoi*	H7 (1)	R2 (1)	1	a13
Ranchería, Paracas, Ica	*C. chamissoi*	H1 (1)	R2 (1)	1	—
Playa Hermosa, Marcona, Ica	*C. glomeratus*	H1 (2)	R2 (2)	2	b3, b6
Siete Huecos, Marcona, Ica	*C. chamissoi*	H1 (2), H4 (1)	R1 (2)	3	a6, a15
	C. glomeratus	H4 (1)	ND	1	—
Gramadal, Atico, Arequipa	*C. chamissoi*	H1 (2)	R1 (1)	2	a4, a9
DPA Ilo, Ilo, Moquegua	*C. chamissoi*	H1 (2)	R1 (1)	2	a3, a10
Morro Sama, Sama, Tacna	*C. chamissoi*	H1 (2)	R1 (1)	2	a8
Boca del Río, Sama, Tacna	*C. glomeratus*	H1 (1)	ND	1	b8
	C. chamissoi	54	17	25	—
	C. glomeratus	48	10	16	—
Total (21 localities)		102	27	41	—

Notes: H1–H7, COI haplotypes; R1–R3, *rbc*L haplotypes. *n*, number of specimens showing each haplotype or considered for morphological analyzed. ND, nondetermined; —, not shown. Fig. 3, reference to the specimen photograph from Figure 3.

color, texture, location of the pinnules, location of the reproductive structures, branching pattern), and morphometric characters (height and length from holdfast to first division).

To compare specimen height between species, we used a Welch's *t*-test instead of a student's *t*-test as sample sizes differed. Assumptions of normality and homoscedasticity were tested prior to analysis, using Shapiro–Wilk's

and Levene's tests. Height data were log transformed. All statistical analyses were run using the R statistical software (R Development Core Team, 2020).

3 | RESULTS

3.1 | Distribution on the Peruvian coast

Based on morphological characteristics, we assigned the 102 collected specimens to *C. chamissoi* or *C. glomeratus*. Both morphologies could be found throughout the Peruvian coast, from the northernmost locality (Punta Petro, 05°47′S) to the two southernmost localities (Morro Sama, 18°00′S for *C. chamissoi*; Boca del Rio, 18°09′S for *C. glomeratus*; Table 1 and Figure 1).

3.2 | COI and *rbc*L haplotypes distribution

Eleven COI haplotypes were found in *C. chamissoi* and *C. glomeratus* specimens (Figure 2). Two of these haplotypes were restricted to the North West Pacific coast (Japan and South Korea). On the South East Pacific coast (SEP), two haplotypes were restricted to Chilean *C. chamissoi* specimens, four were restricted to (Peruvian) *C. glomeratus* specimens, and the last three haplotypes were shared among specimens assigned to *C. glomeratus* and specimens assigned to *C. chamissoi* from both Chile and Peru (Table 1; Figure 2). The haplotypes specific to *C. glomeratus* were observed at low frequency and at a single location (Punta Petro for H2 and H3; La Mesa for H5 and H6). On the other hand, the dominant haplotype, H1, was found in *C. chamissoi* specimens from northern Peru (Punta Petro; 05°47′S) to southern Chile (Cocholgüe, 36°37′S), as well as in *C. glomeratus* specimens from the northernmost (Punta Petro) to the southernmost (Boca del Rio, 18°09′S) localities where the species was found.

Additional COI sequencing has been done for three localities where the two species coexist, revealing that at La Barca and Boquerón del Diablo all specimens shown H1, independently of their morphology. At Punta Petro, all *C. chamissoi* specimens presented H1 or H7, haplotypes also dominating among *C. glomeratus* specimens of this locality (of a total of 14 specimens, 6 presented H1 and 4 shown H7).

Nine *rbc*L haplotypes were found among all *C. chamissoi* and *C. glomeratus* specimens, of which three were restricted to Asia (one also found in France) and two restricted to Chilean *C. chamissoi* specimens (Figure 2). R3 haplotype was found exclusively in a single specimen (*C. chamissoi* from Peru), while R1 and R2 were found in Peruvian specimens assigned both to *C. chamissoi* or *C. glomeratus*. R1 was the dominant haplotype, with a wide distribution from Punta Petro (05°47′S) in Peru to Chonchi (42°40′S), in Chile.

3.3 | Phylogenetic analyses

The phylogenetic maximum likelihood (ML) COI tree showed that all specimens of *C. chamissoi* (from this study and GenBank) and those considered as *C. glomeratus* form a highly supported monophyletic clade (ML = 95, Bayesian posterior probabilities PP = 99). Haplotypes found in Peruvian samples were forming a well-supported clade together with another haplotype from Chile (ML = 88, PP = 93), while GenBank haplotypes that corresponded to specimens of *C. chamissoi* from Japan and South Korea were placed in a sister clade.

Similarly, the phylogenetic ML *rbc*L tree resolved that all *C. chamissoi* and *C. glomeratus* sequences (from this study and GenBank) were grouped in a highly supported monophyletic clade (ML = 96, PP = 100). The three haplotypes detected in Peruvian samples were grouped with another Chilean sequence in a highly supported clade (ML = 94, PP = 100).

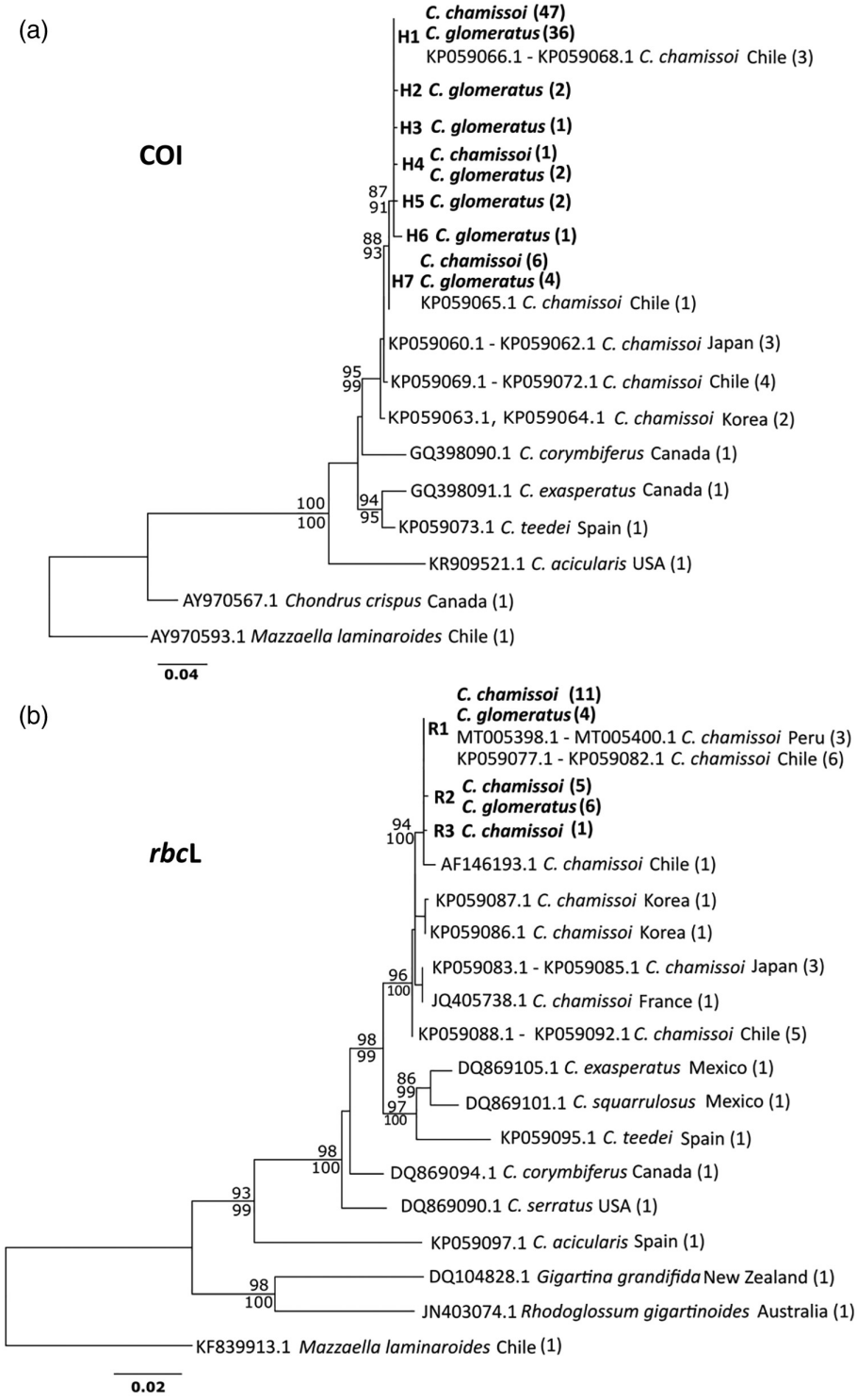

FIGURE 2 Phylogenetic ML trees of COI (a) and *rbc*L (b) sequences of *Chondracanthus* species, including *C. chamissoi* from Peru and other countries, and *C. glomeratus* from Peru; numbers ≥70, above and below branches, correspond to maximum likelihood bootstraps and Bayesian posterior probabilities (PP), respectively

The values of intraspecific distance genetic of *C. chamissoi* for both markers were very low (COI = 0.005 and *rbc*L = 0.004) compared to the interspecific distance with other species of the genus *Chondracanthus*.

3.4 | Morphological analyses

A total of 41 herborized specimens was considered for morphological analyses, 25 of them distinctive and morphologically recognized as *C. chamissoi* morphotypes (COI haplotypes H1, H2, and H7, *rbc*L haplotypes R1 and R2; Table A2) and 16 recognized as *C. glomeratus* morphotypes (COI haplotypes H1, H5, and H6; *rbc*L haplotype: R1). Qualitative and morphometric characters of both forms, *C. chamissoi* and *C. glomeratus*, including their sexual/asexual phases (gametophytes or tetrasporophytes specimens), showed the distinction of both morphologies along the Peruvian coast (Table 2, Figure 4).

The external morphology of selected specimens of *Chondracanthus* has been measured, photographed and labeled as two morphological groups: *chamissoi* form (Figure 3a) and *glomeratus* form (Figure 3b). The *C. chamissoi* specimens along the Peruvian coast, despite sharing the same haplotype (H1), showed specimens entire (Figure 3a3, a4), densely branched (Figure 3a6, a8), thin (Figure 3a9, a12, a14), notorious and wide central axis (Figure 3a3, a6), wide pinnules covering the central axis (Figure 3a4), interrupted pinnules (Figure 3a9), short narrow pinnules (Figure 3A14), and pinnules of different sizes (Figure 3a13). Specimens belonging to haplotype H4 had dense pinnules (Figure 3a15), whereas specimens having H7 lacked a central axis (Figure 3a13) and showed proliferations like short thick pinnules (Figure 3a11, a13).

Specimen heights were significantly different between species (Welch's *t*-test: $t = 8.2838$, $p < .001$), with specimens identified as *C. glomeratus* being smaller than those identified as *C. chamissoi* (Figure 4).

Considering morphological distinctiveness among specimens assigned to *C. glomeratus* and *C. chamissoi*, which cannot be molecularly distinguished in *rbc*L and COI phylogenies, we propose the recognition of the following new form:

Chondracanthus chamissoi f. *glomeratus* (M. Howe) S. A. Suárez *comb. et stat. nov.*

Basionym: *Gigartina glomerata* M.Howe, *Memoirs of the Torrey Botanical Club* 15: 103, pl. 39; pl. 40: figs 1–11, 1914.

Homotypic synonym: *Chondracanthus glomeratus* (M. Howe) Guiry (in Hommersand et al.) *Proceedings of the International Seaweed Symposium* 14:115, 1993.

4 | DISCUSSION

The morphological evidence and the combined analysis of COI and *rbc*L sequences of the species *C. chamissoi* and *C. glomeratus* of the Peruvian coast support the notion that both entities represent a single genetic species, *C. chamissoi*, with high morphological variability. *Chondracanthus chamissoi* has taxonomic priority and, accordingly, we validate that *C. glomeratus* is a taxonomic synonym, and propose *Chondracanthus chamissoi* f. *glomeratus*. This study clarifies the species distribution and reports the first results on the genetic diversity of *Chondracanthus* populations from Peru.

In the phylogenetic analyses of COI and *rbc*L sequences, the sequences of the specimens considered as *C. glomeratus* and those recognized as *C. chamissoi* on the Peruvian coast were resolved as monophyletic (ML = 80 for COI, 96 for *rbc*L). These specimens were assigned previously as *C. chamissoi* (54 COI and 17 *rbc*L sequences) and as *C. glomeratus* (48 COI and 10 *rbc*L sequences). Our results also confirm that specimens identified morphologically as *C. chamissoi* from Chile share haplotypes with specimens from Peru, and are closely related (ML = 96, intraspecific distance = 0.005) to *C. chamissoi* from South Korea and Japan in the COI analysis (Figure 1), and to *C. chamissoi* from South Korea, Japan, and France in the *rbc*L analysis (Figure 2). Therefore, the present study completes the

TABLE 2 Qualitative and morphometric characters of *C. chamissoi* and *C. glomeratus* according to the literature information and our results

Character	*C. chamissoi* form This study (Figure 3a)	*C. chamissoi* Acleto (1986) Calderón et al. (2010)	*C. glomeratus* form This study (Figure 3b)	*C. glomeratus* Howe (1914)
N	25	—	16	—
Height (cm)	32	36–40	8	3–5
Distance from holdfast to first division (cm)	3–7	—	3	Naked for 1–2.5 cm in basal and median parts
Texture	Cartilaginous	Cartilaginous, membranous	Cartilaginous, coriaceous	Firm and rigid (with formalin), corneous (dry)
Color	Dark green, brown, red, purple, iridescence	Purple iridescence, Red to dark green	Dark green, brownNo iridescence	—
Thallus	Flat	Flat	Terete	Subterete, compressed
Branching pattern	Subdichotomous	Subdichotomous	SubdichotomousFinal portion of main axes	SubdichotomousAt first subdistichous, later irregularly polystichous, short, simple or compound branches
Pinnules (location)	On main and lateral axes, continuous or discontinuous	Main and lateral axes	On lateral axes, discontinuous	On simple or compound branches
Pinnules (orientation)	Alternate/ in two opposite rows	Alternate/in two opposite rows	Alternate	Subrotate or coronate verticil of branchlets, or irregularly fasciculate-ramose
Pinnules (shape)	Narrow/thick, long/short	Long/short, depending on the size of the specimen	Narrow, short	Obtuse or acute, acuminate, ovoid or short-digitiform
Reproductive female structures (location)	On pinnules	On pinnules of primary and secondary proliferations	On pinnules, aggregated (glomerulus-like)	Aggregated or solitary, variously disposed on ultimate ramuli

Note: *N*, number of specimens analyzed; –, unavailable information.

mitochondrial and plastidial phylogenetic analyses by Yang et al. (2015) where material from Chile, Japan, and France were proven to be *C. chamissoi*. Additionally, three (H1, H4, and H7) of the seven COI haplotypes found on the Peruvian coast and two (R1 and R2) of the three *rbc*L haplotypes were shared among specimens identified as *C. chamissoi* and as *C. glomeratus*. The other haplotypes appeared as specific to *C. chamissoi* or *C. glomeratus*; however, these are rare haplotypes and a larger sampling is required to elucidate the possible specificity to one or the other morphological groups. So far, a case of conspecificity has been reported within the genus *Chondracanthus* using

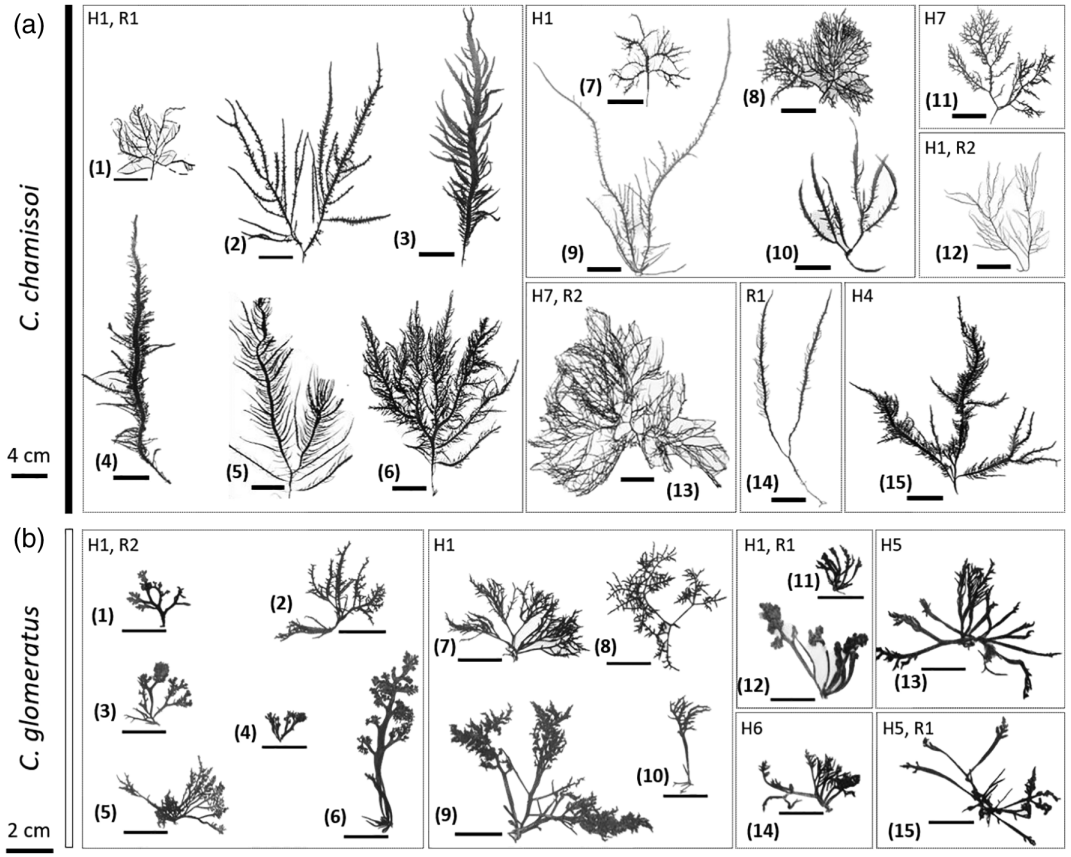

FIGURE 3 Herbarium specimens assigned to *Chondracanthus chamissoi* (a) or *C. glomeratus* (b) based on their morphology (note the different scales), showing morphological diversity and haplotype (H for COI and R for *rbc*L); corresponding sampling localities are indicated on Table 1

mitochondrial markers. Yang et al. (2015), through a COI phylogeny, found that specimens considered as *C. teedei* from Japan and South Korea actually belong to *C. chamissoi*. The *C. teedei* specimens had been misidentified and confused with specimens of *C. teedei* from the NE Atlantic and Mediterranean because of the similarity of some morphological characteristics of the thallus (Dixon & Irvine, 1977). In the study by Yang et al. (2015), the specimens of *C. teedei* from Japan and South Korea have different haplotypes but are very close to those of *C. chamissoi*, so that both taxa are included in a highly supported clade, suggesting conspecificity. Because of the shared haplotypes observed among Peruvian specimens of *C. chamissoi* and *C. glomeratus*, the species undergoes at least some current or recent gene flow, and we propose to consider them as a single taxonomic unit. This is well-supported by the intraspecific distance values of all *C. chamissoi* haplotypes. Nevertheless, an ongoing, recent evolutionary divergence cannot be totally excluded, requiring further population genetics analyses with highly variable molecular markers.

The phenotypic plasticity exhibited by the species of the genus *Chondracanthus* (Hughey & Hommersand, 2008) and the species of the family Gigartinaceae in general (Hommersand et al., 1993) constitutes an important cause of taxonomic nomenclatural confusions. Within the Gigartinaceae family and the genus *Chondracanthus*, cases of taxonomic synonyms were detected after phylogenetic reconstruction using different plastidial markers, for example, Hughey and Hommersand (2008), by inferring the phylogeny of North Pacific *Chondracanthus* with the *rbc*L gene.

The genus *Chondracanthus*, with two known species in Peru had been reported as *C. chamissoi* in Piura (Talara and Paita), La Libertad (Chicama and Pacasmayo), Áncash (Chimbote), Lima (Ancón, San Bartolo and Pucusana), Callao

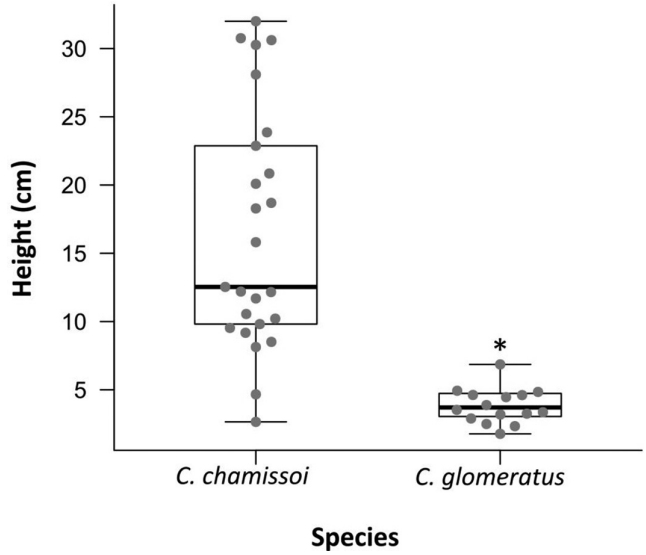

FIGURE 4 Height of the Peruvian specimens assigned to *Chondracanthus chamissoi* and *C. glomeratus* in base of their morphological characteristics; on the boxplot, data points are reported along with the median, in order to enhance visualization of dispersion

(Isla San Lorenzo) and Ica (Lagunillas, Mendieta, and Laguna Grande) (Dawson et al., 1964; Ramírez & Santelices, 1991), and as *C. glomeratus* in Lima (San Bartolo, Pucusana, Herradura, Miraflores, Barranco, Islas Pescadores, Chancay) and Callao (Isla San Lorenzo) (Howe, 1914; Ramírez & Santelices, 1991). In this study, we add new records of distribution along the Peruvian coast as well as showing the range of morphological variability, evaluating forms previously known as *C. chamissoi* and *C. glomeratus*. From 21 localities evaluated from 5°47′S (Punta Petro, Piura) to 18°09′S (Boca del Río, Tacna), the *chamissoi* form is distributed in 17 localities along the coast of Peru, and the *glomeratus* form in 11 localities. Both morphologies are present in seven localities from Piura, La Libertad, Callao, Lima, and Ica. The genetic data obtained provide an initial overview of the geographic structure of the genetic diversity of this species. These results are a contribution for future phylogeographic and population genetics studies.

The qualitative and morphometric characterization revealed a higher morphological variability among the 26 specimens from *C. chamissoi* morphotype, compared to the 16 specimens from *C. glomeratus* form. Particularly, the forms differed significantly regarding specimen height. Within the *chamissoi* form, the specimens differed in their central axis morphology, ranging from entire to densely branched axis, and from a thin or even absent central axis to a notorious and wide axis. Variability in pinnules was also observed among *chamissoi* specimens, with dense pinnules covering central axis or interrupted pinnules, and varying form and size of pinnules.

The diversity of forms of *Chondracanthus chamissoi* (as *Gigartina chamissoi*) was previously reported. Howe (1914) indicated that two entities from Peru could not be clearly differentiated from *G. chamissoi* from Chile (type locality), and then they were recognized as *Gigartina lessonii* with a narrow frond and *Gigartina chauvinii* with a wide frond. Subsequently, the two "species" from Peru were considered as *C. chamissoi*, indicating two morphological groups with narrow and broad fronds (Dawson et al., 1964). A study published recently (Rodríguez & Otaíza, 2020) presents a detailed morphological characterization of these *lessonii* and *chauvinii* forms of *C. chamissoi*, thus confirming the morphological differentiation, at least in the studied localities of southern Chile; additionally, the two forms shared COI and *rbc*L haplotypes, with no genetic differentiation (Rodríguez et al., 2021).

On the other hand, specimens identified as *C. glomeratus* show considerably less morphological diversity along the Peruvian coast. As Howe (1914) distinctly remarked, *glomeratus* has a cespitose (growing as dense turf appearance), unlike the *chamissoi* form, the pinnules are concentrated in the apical part of their ramifications, housing the

cystocarps and sori, giving it that glomerulus-like appearance. Howe (1914) described the habit of *C. glomeratus* with material from San Lorenzo Island (type locality, Callao). In the present study, only one specimen of *C. glomeratus* from San Lorenzo Island was included and it corresponds to the most frequent COI haplotype (H1). Additionally, two sequences of *C. glomeratus*, obtained by Calderón et al. (2020) from the same locality, correspond to the most frequent *rbc*L haplotype (R1). Although, qualitative and morphometric characters of other specimens of *C. glomeratus* that have haplotypes H1, H5, and H7 coincide with the habits described by Howe (1914) and Dawson et al. (1964), 3–5 cm in height and a leathery texture, and a pompous form of the thallus and cystocarps added to its branches.

The habitats of *C. glomeratus* have not been related to ecological factors, only Howe (1914) indicated that this species is attached to shells or mussels on rocks, or barnacles. The specimens considered as *C. glomeratus* in this study were collected in the low intertidal and subtidal (3 m) on mollusks shells or rocks, most of them under high wave-exposition regimen. In contrast, the specimens considered as *C. chamissoi* were collected from different habitats: low intertidal, subtidal, ropes of artisan vessels, and buoys. Macroalgae can be affected by water motion, nutrient acquisition, and loss of biomass or injury of thallus as a result of mechanical fatigue. There are numerous examples of environmentally induced forms as in highly plastic Phaeophyceae, with optimal morphologies that are favored in high wave-exposed areas, drag reduction (small size, streamlined shape, and flexibility) and increase strength (thickness and aggregation) (see Hodge, Buchanan, & Zucarello, 2011). Therefore, wave-exposition regimen can provide insights into environmental selection and plasticity in *C. chamissoi* form, and explain the small size and tufted form of *C. glomeratus*. In contrast, Rodríguez and Otaíza (2020) reported that the *lessonii* and *chauvinii* forms of *C. chamissoi* are observed in very close proximity, thus leading the authors to exclude phenotypic plasticity induced by environmental variables, and to propose alternative mechanisms.

Chondracanthus glomeratus was previously proposed as conspecific with *C. chamissoi* by Calderón et al. (2020). The authors first corroborated that two specimens recently collected of *C. glomeratus* from Isla San Lorenzo (Callao) correspond with the original description and images of the paratype (NY900141) deposited in The New York Botanical Herbarium (Calderón et al., 2020, figure 5E). Simultaneously, they showed that based on a molecular analysis, *rbc*L sequences of both specimens were identical to one specimen of *C. chamissoi* from Yacila (Piura) (Calderón et al., 2020, Figure 2b). Based on our morphological results, we confirm that specimens of *C. glomeratus* collected in Peru revealed forms that coincide with the original description and images of the type. Thus, our results show that a distinct morphological form of *C. chamissoi* is present and can be identified as *C. chamissoi* f. *glomeratus* (Figures 3, 4, and Table A4). This form is characterized by small blades of 3–8 cm in length with an aggregated (glomerulus-like) form of the thallus, having terete blades, cartilagineous or coriaceous texture, and lacking pinnules on the portion between holdfast and first division. In addition to two co-occurring forms described for *C. chamissoi* based mainly on blade width, *C. chamissoi* f. *lessonii*, and *C. chamissoi* f. *chauvinii* (Rodríguez & Otaíza, 2020), we propose a new form based mainly on blade size.

Further studies are needed to understand the drivers of the genetic and phenotypic diversity observed in *C. chamissoi* from the South East Pacific coast. Because the species is considered as candidate for commercial production, there is a need for a detailed characterization of the genetic diversity, thus allowing both to conserve the genetic variability of natural populations and to help future breeding strategies and local variant selection for interesting agronomic traits, as recommended by Valero et al. (2017).

5 | CONCLUSIONS

The genus *Chondracanthus* is represented by only one species, *C. chamissoi* in Peru. This species includes the entities previously named *C. chamissoi* and *C. glomeratus*. We provided a first estimate of the haplotype diversity for the Peruvian part of the species distribution. The presence of only one species, *C. chamissoi*, and its distribution along the Peruvian coast was genetically confirmed from 5°S to 18°S. In addition, two morphological groups are designated

to reflect the extreme diversity of forms that contain this species: *chamissoi* and *glomeratus* forms. The smaller form of *C. chamissoi* can be identified as *Chondracanthus chamissoi* f. *glomeratus* S.A.Suárez f. nov.

ACKNOWLEDGMENTS

We thank the Biodiversity Research Functional Area from the Marine Institute of Peru (Área Funcional de Investigaciones en Biodiversidad del Instituto del Mar del Perú) for providing their facilities for the analysis of specimens of the Scientific Collection. The valuable comments from one anonymous referee and the editor were very helpful in improving the original manuscript. We also wish to thank Michael Guiry for his kind assistance in writing the nomenclatural proposal. We are grateful to Victoria Hinojosa for checking the language of the final manuscript.

CONFLICT OF INTEREST

All authors approve the submitted version of this manuscript and declare that they have no conflicts of interest. This article has not been published before and is not concurrently being considered for publication elsewhere, all authors agree to its submission and the corresponding author has been authorized by co-authors. Also, this article does not violate any copyright or other personal proprietary right of any person or entity, and it contains no abusive, defamatory, obscene, or fraudulent or any other statements that are unlawful in any way.

AUTHOR CONTRIBUTIONS

The authors' contribution was as follows: Natalia Arakaki, Sigfried Suárez-Alarcón, Patricia Gil-Kodaka, and Florence Tellier participated in the conception and design of the work. All authors did the sampling. Natalia Arakaki, Florence Tellier, Sigfried Suárez-Alarcón, and Diego Márquez-Corigliano led the collection and analysis of genetic and morphological data. Natalia Arakaki and Florence Tellier drafted the manuscript. All authors contributed to the interpretation of the data and critical reviews of the manuscript.

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How to cite this article: Arakaki, N., Suárez-Alarcón, S., Márquez-Corigliano, D., Gil-Kodaka, P., & Tellier, F. (2021). The widely distributed, edible seaweeds in Peru, *Chondracanthus chamissoi* and *Chondracanthus chamissoi* f. *glomeratus* (Gigartinaceae, Rhodophyta), are morphologically diverse but not phylogenetically distinct. *Journal of the World Aquaculture Society*, *52*(6), 1290–1311. https://doi.org/10.1111/jwas.12849

APPENDIX

TABLE A1 Collection information of *Chondracanthus* species from Peru

Locality	Department	Latitude	Longitude	Date	Habitat
Punta Petro, Sechura	Piura	05°47′02.10″S	81°04′01.90″W	October 16, 2017	Low intertidal
Chérrepe, Pueblo Nuevo	La Libertad	07°10′20.50″S	79°41′27.90″W	September 23, 2017	Low intertidal
La Barca, Malabrigo	La Libertad	07°42′19.20″S	79°27′07.70″W	September 23, 2017	low intertidal
La Gramita, Casma	Ancash	09°42′47.50″S	78°17′40.70″W	September 21, 2017	Low intertidal
La Mesa, Casma	Ancash	09°46′33.70″S	78°14′41.80″W	September 21, 2017	Low intertidal
La Perú, Culebras	Ancash	09°56′30.81″S	78°13′44.18″W	May 30, 2016	Low intertidal
Las Conchitas, Ancon	Lima	11°45′33.90″S	77°10′18.20″W	May 14, 2016	Subtidal (3 m)
Isla San Lorenzo, La Punta	Callao	12°03′41.30″S	77°14′20.60″W	June 16, 2017	Subtidal (4 m)
Boquerón del Diablo, Pucusana	Lima	12°28′55.00″S	76°48′02.20″W	June 17, 2017	Low intertidal
Grano de Oro, Pucusana	Lima	12°29′25.40″S	76°47′55.80″W	November 14, 2016	Low intertidal
Lagunillas, Paracas	Ica	13°53′49.50″S	76°18′45.10″W	December 9, 2016	Low intertidal
La Mina, Paracas	Ica	13°54′40.50″S	76°19′04.20″W	April 3, 2016	Low intertidal
Mendieta, Paracas	Ica	14°02′49.60″S	76°15′54.50″W	May 27, 2017	Subtidal (5 m)
Laguna Grande, Paracas	Ica	14°08′28.20″S	76°15′50.30″W	October 8, 2016	Low intertidal
Ranchería, Paracas	Ica	14°09′06.60″S	76°15′02.80″W	April 3, 2016	Low intertidal
Playa Hermosa, Marcona	Ica	15°21′21.10″S	75°10′12.10″W	October 23, 2016	Low intertidal
Siete Huecos, Marcona	Ica	15°23′07.10″S	75°09′32.70″W	April 8, 2017	Low intertidal
Gramadal, Atico	Arequipa	16°13′48.80″S	73°38′12.00″W	September 29, 2017	Ropes of AFV
DPA Ilo, Ilo	Moquegua	17°38′38.60″S	71°20′49.70″W	August 31, 2017	Buoys of AFV
Morro Sama, Sama	Tacna	18°00′01.80″S	70°53′11.40″W	September 1, 2017	Low intertidal
Boca del Río, Sama	Tacna	18°09′20.80″S	70°41′08.50″W	December 9, 2017	Low intertidal

Note: AFV, artisanal fishing vessels.

TABLE A2 Voucher number and GenBank accession numbers of *C. chamissoi* individuals from Peru

	Specimen	Locality	COI	*rbc*L
1	ccha_ppe_1	Punta Petro	—	MW924601
2	cglo_ppe_1	Punta Petro	MW924525	MW924602
3	cglo_ppe_2	Punta Petro	MW924504	—
4	ccha_ppe_3	Punta Petro	MW924499	—
5	cglo_ppe_3	Punta Petro	MW924526	—
6	ccha_ppe_4	Punta Petro	MW924518	—
7	cglo_ppe_4	Punta Petro	MW924528	—
8	ccha_ppe_5	Punta Petro	MW924501	—
9	cglo_ppe_5	Punta Petro	MW924505	—
10	ccha_ppe_6	Punta Petro	MW924519	—
11	cglo_ppe_7	Punta Petro	MW924506	—
12	ccha_ppe_8	Punta Petro	MW924500	—
13	cglo_ppe_8	Punta Petro	MW924527	—
14	ccha_ppe_9	Punta Petro	MW924502	—
15	ccha_ppe_10	Punta Petro	MW924503	—
16	cglo_ppe_10	Punta Petro	MW924507	—
17	cglo_ppe_11	Punta Petro	MW924515	—
18	ccha_ppe_11	Punta Petro	MW924522	—
19	ccha_ppe_12	Punta Petro	MW924521	—
20	ccha_ppe_13	Punta Petro	MW924520	—
21	cglo_ppe_13	Punta Petro	MW924530	—
22	ccha_ppe_15	Punta Petro	MW924523	—
23	cglo_ppe_15	Punta Petro	MW924529	—
24	ccha_ppe_16	Punta Petro	MW924524	—
25	ccha_che_1	Chérrepe	MW924541	MW924603
26	ccha_che_2	Chérrepe	MW924540	—
27	ccha_che_5	Chérrepe	MW924539	—
28	ccha_che_8	Chérrepe	MW924531	—
29	ccha_che_13	Chérrepe	MW924538	—
30	ccha_lba_1	La Barca	—	MW924604
31	cglo_lba_2	La Barca	MW924548	MW924605
32	ccha_lba_3	La Barca	MW924533	—
33	cglo_lba_3	La Barca	MW924543	—
34	ccha_lba_4	La Barca	MW924534	—
35	cglo_lba_4	La Barca	MW924547	—
36	cglo_lba_5	La Barca	MW924544	—
37	ccha_lba_6	La Barca	MW924536	—
38	cglo_lba_6	La Barca	MW924546	—
39	ccha_lba_7	La Barca	MW924537	—
40	cglo_lba_7	La Barca	MW924549	—
41	cglo_lba_8	La Barca	MW924552	—

(Continues)

TABLE A2 (Continued)

	Specimen	Locality	COI	*rbc*L
42	ccha_lba_10	La Barca	MW924532	—
43	cglo_lba_11	La Barca	MW924542	—
44	cglo_lba_12	La Barca	MW924550	—
45	ccha_lba_13	La Barca	MW924535	—
46	cglo_lba_13	La Barca	MW924545	—
47	cglo_lba_14	La Barca	MW924551	—
48	ccha_lgr_1	La Gramita	MW924553	MW924606
49	ccha_lgr_2	La Gramita	MW924554	—
50	cglo_lme_1	La Mesa	—	MW924607
51	cglo_lme_2	La Mesa	MW924512	—
52	cglo_lme_6	Siete Huecos	MW924514	—
53	cglo_lme_10	Siete Huecos	MW924513	—
54	cglo_LPR_1	La Peru	MW924555	MW924623
55	ccha_CAS_1	Las Conchitas	MW924556	MW924626
56	ccha_isl_1	Isla San Lorenzo	—	MW924608
57	ccha_isl_6	Isla San Lorenzo	MW924557	—
58	cglo_ISL	Isla San Lorenzo	MW924558	MW924624
59	chsp1_bdd_1	Boquerón del Diablo	MW924567	MW924609
60	chsp2_bdd_1	Boquerón del Diablo	MW924576	MW924610
61	chsp1_bdd_2	Boquerón del Diablo	MW924566	—
62	chsp2_bdd_2	Boquerón del Diablo	MW924571	—
63	chsp2_bdd_3	Boquerón del Diablo	MW924582	—
64	chsp2_bdd_4	Boquerón del Diablo	MW924578	—
65	chsp1_bdd_5	Boquerón del Diablo	MW924570	—
66	chsp1_bdd_6	Boquerón del Diablo	MW924565	—
67	chsp2_bdd_6	Boquerón del Diablo	MW924581	—
68	chsp1_bdd_7	Boquerón del Diablo	MW924568	—
69	chsp2_bdd_7	Boquerón del Diablo	MW924572	—
70	chsp1_bdd_8	Boquerón del Diablo	MW924564	—
71	chsp2_bdd_8	Boquerón del Diablo	MW924573	—
72	chsp1_bdd_9	Boquerón del Diablo	MW924569	—
73	chsp2_bdd_9	Boquerón del Diablo	MW924574	—
74	chsp1_bdd_10	Boquerón del Diablo	MW924560	—
75	chsp2_bdd_10	Boquerón del Diablo	MW924575	—
76	chsp1_bdd_11	Boquerón del Diablo	MW924563	—
77	chsp2_bdd_11	Boquerón del Diablo	MW924579	—
78	chsp1_bdd_12	Boquerón del Diablo	MW924562	—
79	chsp1_bdd_13	Boquerón del Diablo	MW924559	—
80	chsp2_bdd_13	Boquerón del Diablo	MW924580	—
81	chsp1_bdd_14	Boquerón del Diablo	MW924561	—
82	chsp2_bdd_14	Boquerón del Diablo	MW924577	—

TABLE A2 (Continued)

	Specimen	Locality	COI	*rbc*L
83	cglo_MNA_1	Las Minas	MW924586	MW924619
84	ccha_MNA_2	Las Minas	MW924587	MW924620
85	ccha_men_1	Mendieta	MW924588	MW924611
86	ccha_men_4	Mendieta	MW924516	—
87	ccha_men_5	Mendieta	MW924517	—
88	ccha_RIO	Rancherio	MW924591	MW924625
89	ccha_RIO	Rancherio	—	MW924627
90	ccha_LGD_1	Laguna Grande	MW924508	—
91	cglo_PHM_1	Playa Hermosa	MW924589	MW924621
92	cglo_PHM_2	Playa Hermosa	MW924590	MW924622
93	ccha_sh_C2	Siete Huecos	MW924509	—
94	cglo_sh_C1	Siete Huecos	MW924510	—
95	cglo_sh_C4	Siete Huecos	MW924511	—
96	ccha_sh_N2	Siete Huecos	MW924592	MW924612
97	ccha_sh_C1	Siete Huecos	MW924593	MW924613
98	ccha_gmd_1	Gramadal	—	MW924614
99	ccha_gmd_2	Gramadal	MW924595	—
100	ccha_gmd_5	Gramadal	MW924594	—
101	ccha_ilo_1	Ilo	MW924597	MW924615
102	ccha_ilo_3	Ilo	MW924596	—
103	ccha_mor_1	Morro Sama	MW924598	MW924616
104	cccha_mor_3	Morro Sama	MW924599	—
105	cglo_BRO	Boca del Río	MW924600	—
106	ccha_GDO_1	Grano de Oro	MW924583	—
107	cglo_LAS_1	Lagunillas	MW924584	MW924617
108	ccha_LAS_2	Lagunillas	MW924585	MW924618

TABLE A3 Sequences from GenBank for phylogenetic analyses, including other specimens of *C. chamissoi*, other species of the *Chondracanthus* genus and external groups

Species	Locality	Accession number		References
		COI	*rbc*L	
C. acicularis	Sebastian Inlet, Florida, USA	KR909521.1	—	Yang and Kim (2016)
	Roche, Andalusia, Spain	—	KP059097.1	Yang et al. (2015)
C. chamissoi	Chile	KP059065.1-KP059072.1	KP059077.1-KP059082.1; KP059088.1-KP059092.1	Yang et al. (2015)
		—	AF146193.1	Hughey and Hommersand (2008)
	Peru	—	MT005398.1-MT005400.1	Calderón et al. (2020)
	Korea	KP059063.1, KP059064.1	KP059086.1-KP059087.1	Yang et al. (2015)
	Japan	KP059060.1-KP059062.1	KP059083.1-KP059085.1	Yang et al. (2015)
	France	—	JQ405738.1	Mineur et al. (2012)
C. corymbiferus	Canada	GQ398090.1	—	Le Gall and Saunders (2010)
	Indian Island, Washington, USA	—	DQ869094.1	Hughey and Hommersand (2008)
C. exasperatus	Canada	GQ398091.1	—	Le Gall and Saunders (2010)
	Bahía Colnett, Baja California, Mexico	—	DQ869105.1	Hughey and Hommersand (2008)
C. serratus	Mission Bay, California, USA	—	DQ869090.1	Hughey and Hommersand (2008)
C. squarrulosus	Los Angeles Bay, Gulf of California, Mexico	—	DQ869101.1	Hughey and Hommersand (2008)
C. teedei	San Fernando, Andalusia, Spain	KP059073.1	KP059095.1	Yang et al. (2015)
Chondrus crispus	Peggy's Cove, Nova Scotia, Canada	AY970567.1	—	Saunders (2005)
Mazzaella laminarioides	Chacao, Los Lagos, Chile	AY970593.1	—	Saunders (2005)
	Chiloé, Chile	—	KF839913.1	Saunders and Millar (2014)
Gigartina grandifida	Waitangi West, Chatham Islands, New Zealand	—	DQ104828.1	Nelson and Broom (2008)
Rhodoglossum gigartinoides	Flinders Jetty, Victoria, Australia	—	JN403074.1	Schneider, Chengsupanimit, and Saunders (2011)

TABLE A4 Genetic distances between *Chondracanthus* species for the COI marker (below the diagonal)

		1	2	3	4	5	6
1	*C. chamissoi*	**0.005**	0.013	0.009	0.010	0.009	0.017
2	*C. acicularis*	0.089		0.014	0.014	0.013	0.017
3	*C. corymbiferus*	0.047	0.101		0.010	0.009	0.017
4	*C. exasperatus*	0.047	0.093	0.058		0.007	0.016
5	*C. teedei*	0.045	0.091	0.05	0.027		0.015
6	*C. crispus*	0.129	0.141	0.131	0.125	0.111	

Note: Standard deviations are shown above the diagonal and intraspecific distance of *C. chamissoi* in the diagonal.

TABLE A5 Genetic distances between *Chondracanthus* species for the *rbc*L marker (below the diagonal). Standard deviations are shown above the diagonal and intraspecific distance of *C. chamissoi* in the diagonal

		1	2	3	4	5	6	7	8	9	10	11	12	13
1	*C. chamissoi*	0.004	0.009	0.007	0.010	0.006	0.006	0.005	0.007	0.008	0.007	0.006	0.006	0.009
2	*C. acicularis*	0.071	—	0.009	0.009	0.010	0.009	0.008	0.009	0.009	0.009	0.009	0.009	0.008
3	*C. bajacalifornicus*	0.047	0.071	—	0.010	0.006	0.008	0.006	0.002	0.009	0.003	0.008	0.008	0.009
4	*C. chapmanii*	0.076	0.071	0.074	—	0.010	0.010	0.009	0.009	0.008	0.010	0.009	0.010	0.009
5	*C. corymbiferus*	0.036	0.070	0.034	0.072	—	0.007	0.005	0.006	0.009	0.006	0.007	0.008	0.009
6	*C. exasperatus*	0.030	0.068	0.048	0.072	0.037	—	0.006	0.008	0.009	0.008	0.005	0.006	0.009
7	*C. harveyanus*	0.028	0.056	0.032	0.064	0.023	0.026	—	0.006	0.008	0.006	0.006	0.006	0.008
8	*C. kjeldsenii*	0.044	0.065	0.005	0.068	0.034	0.043	0.029	—	0.009	0.003	0.008	0.008	0.009
9	*C. saundersii*	0.061	0.064	0.068	0.054	0.067	0.060	0.059	0.063	—	0.009	0.009	0.009	0.008
10	*C. serratus*	0.042	0.068	0.007	0.071	0.032	0.043	0.027	0.005	0.066	—	0.008	0.008	0.009
11	*C. squarrulosus*	0.033	0.069	0.055	0.072	0.043	0.017	0.029	0.050	0.063	0.050	—	0.007	0.009
12	*C. teedei*	0.038	0.065	0.061	0.072	0.051	0.033	0.038	0.056	0.062	0.056	0.036	—	0.009
13	*C. tenellus*	0.063	0.061	0.065	0.063	0.067	0.064	0.058	0.06	0.043	0.063	0.069	0.066	—