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Molecular-assisted taxonomic study on the *Sargassum* C.Agardh (Fucales, Phaeophyceae) in northwestern Luzon, Philippines

Wilfred John E. SANTIAÑEZ
John Michael L. LASTIMOSO
G.T. Velasquez Phycological Herbarium and The Marine Science Institute, College of Science, University of the Philippines Diliman, Quezon City, 1101 (Philippines)
wjsantianez@msi.upd.edu.ph (corresponding author)
jmlastimoso@msi.upd.edu.ph

Masakazu HOSHINO
Department of Natural History Sciences, Graduate School of Science, Hokkaido University, Sapporo, 060-0810 (Japan)
and Research Center for Inland Seas, Kobe University, Rokkodai 1-1, Nadaku, Kobe 657-8501 (Japan)
mhoshino.sci@gmail.com

Brix Nester Q. VILLAFUERTE
G.T. Velasquez Phycological Herbarium and The Marine Science Institute, College of Science, University of the Philippines Diliman, Quezon City, 1101 (Philippines)
bnvillafuerte@msi.upd.edu.ph

Kazuhiro KOGAME
Department of Biological Sciences, Faculty of Science, Hokkaido University, Sapporo, 060-0810 (Japan)
kogame@sci.hokudai.ac.jp

Gavino C. TRONO, Jr
G.T. Velasquez Phycological Herbarium and The Marine Science Institute, College of Science, University of the Philippines Diliman, Quezon City, 1101 (Philippines)
gctrono@yahoo.com

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ABSTRACT
The diversity of the brown algal genus *Sargassum* C.Agardh in the Philippines is the highest in the tropical western Pacific Ocean. However, most studies on Philippine *Sargassum* are based on morpho-anatomies and the assumption that the genus is very diverse in the country has never been tested based on molecular information. Considering that many *Sargassum* species are highly polymorphic and the recent advance on *Sargassum* systematics facilitated by molecular phylogenetic studies, we believe that the species of *Sargassum* from the Philippines should now be reassessed with the tools of molecular taxonomy. We present here the results of our molecular-assisted taxonomic studies on the *Sargassum* of the northern Philippines, particularly along the coasts of four coastal provinces in northwestern Luzon (i.e., Ilocos Norte, Ilocos Sur, La Union, and Pangasinan). We recognized three distinct species

lineages, namely, *Sargassum aquifolium* (Turner) C.Agardh, *Sargassum ilicifolium* (Turner) C.Agardh, and *Sargassum polycystum* C.Agardh based on our molecular analyses of 74 specimens from our study areas. Our morphological observations on the range of characters of these species also suggest that several common *Sargassum* taxa in the Philippines have been misidentified. Particularly, specimens previously attributed to *S. kushimotense* Yendo should be referred as *S. aquifolium* while the widely distributed and highly plastic *S. ilicifolium* is often confused and identified in the Philippines under several names including *S. crassifolium* J.Agardh, *S. cristaefolium* C.Agardh, and *S. turbinarioides* Grunow. Taken together, our results suggest that *Sargassum* biodiversity in the Philippines may have been inflated by misidentifications, and, that species diversity is actually much lower than initially thought.

KEY WORDS
Pacific Ocean,
Philippines,
Sargassaceae,
Fucales.

RÉSUMÉ
Étude des Sargassum *(Fucales, Phaeophyceae) dans le nord-ouest de Luzon, Philippines au moyen des outils de la taxonomie moléculaire.*
La diversité du genre d'algues brunes *Sargassum* C.Agardh aux Philippines est la plus élevée de l'océan Pacifique tropical occidental. Cependant, la plupart des études sur les *Sargassum* des Philippines sont basées sur de la morpho-anatomie, et l'hypothèse selon laquelle le genre est très diversifié dans le pays n'a jamais été vérifiée sur la base d'informations moléculaires. Étant donné que de nombreuses espèces de *Sargassum* sont hautement polymorphiques et que les études phylogénétiques moléculaires ont récemment permis de faire progresser la systématique, nous pensons que les espèces de *Sargassum* des Philippines devraient maintenant être réévaluées au moyen d'outils de la taxonomie moléculaire. Nous présentons ici les résultats de nos études taxonomiques moléculaires sur les sargasses du nord des Philippines, en particulier le long des côtes de quatre provinces côtières du nord-ouest de Luzon (Ilocos Norte, Ilocos Sur, La Union et Pangasinan). Nous avons reconnu trois lignées d'espèces distinctes, à savoir *Sargassum aquifolium* (Turner) C.Agardh, *Sargassum ilicifolium* (Turner) C.Agardh, et *Sargassum polycystum* C.Agardh, sur la base d'analyses moléculaires de 74 spécimens provenant de nos zones d'étude. Nos observations morphologiques sur la gamme de caractères de ces espèces suggèrent également que plusieurs taxons communs de *Sargassum* aux Philippines ont été mal identifiés. En particulier, les spécimens précédemment attribués à *S. kushimotense* Yendo devraient être appelés *S. aquifolium*, tandis que *S. ilicifolium*, largement répandue et très plastique, est souvent confondue et identifiée aux Philippines sous plusieurs noms, dont *S. crassifolium* J.Agardh, *S. cristaefolium* C.Agardh et *S. turbinarioides* Grunow. Nos résultats suggèrent que la biodiversité des sargasses aux Philippines pourrait avoir été gonflée par des erreurs d'identification et que la diversité des espèces est en fait beaucoup plus faible qu'on ne le pensait initialement.

MOTS CLÉS
Océan Pacifique,
Philippines,
Sargassaceae,
Fucales.

INTRODUCTION

The genus *Sargassum* C.Agardh (Fucales, Phaeophyceae) is a habitat-forming brown seaweed that dominates most of the wave-exposed reefs and/or rocky areas of the Philippines. Species of *Sargassum* are important component of the benthos, supporting biodiversity and life histories of various marine organisms. Aside from the use of *Sargassum* as animal fodder and plant fertilizer, among others, by coastal dwellers in the Philippines (Montaño *et al.* 2006), they are prized for their high-value natural products such as fucoxanthin and alginates (Narsico *et al.* 2018), and they hold good potential as feedstock for a sustainable alternative source of energy, i.e., biomethane (Marquez *et al.* 2014; De Ramon N'Yeurt & Iese 2015).

Sargassum is most biodiverse in the Pacific (Phillips 1995), with the Philippines having the highest number of recorded species and varieties in the tropical western Pacific (Ganzon-Fortes 2012; Ang *et al.* 2013; Lastimoso & Santiañez 2021), although the identities of these Philippine taxa have never been confirmed based on molecular-assisted taxonomic studies. The first report of *Sargassum* in the Philippines was made by Bory de Saint-Vincent in 1834 when he described *S. belangeri* Bory de Saint-Vincent (Belanger & Bory de Saint-Vincent 1834). In the 1800s until the early part of the 1900s, significant contributions on the diversity and distribution of *Sargassum* of the Philippines were made by foreign phycologists using materials collected during various oceanographic explorations (Modelo & Umezaki 1995; see Ganzon-Fortes 2012 for details). Taxonomic studies on seaweeds collected during those explorations resulted in the description of some new species, varieties, and forms with the Philippines as their type localities such as *Sargassum philippinense* Grunow, *Sargassum cystophyllum* Montagne, and *Sargassum filiforme* Montagne (Montagne 1842, 1844; Grunow 1915, 1916). Meanwhile, the first comprehensive list of *Sargassum* in the country was integrated in the catalog by Silva *et al.* (1987), where a total of 72 taxa were recorded, including infraspecific names. Trono (1992), however, pointed out that much of the taxa listed by Silva *et al.* (1987) are questionable and he encouraged a detailed work on the taxonomy of *Sargassum* flora of the Philippines.

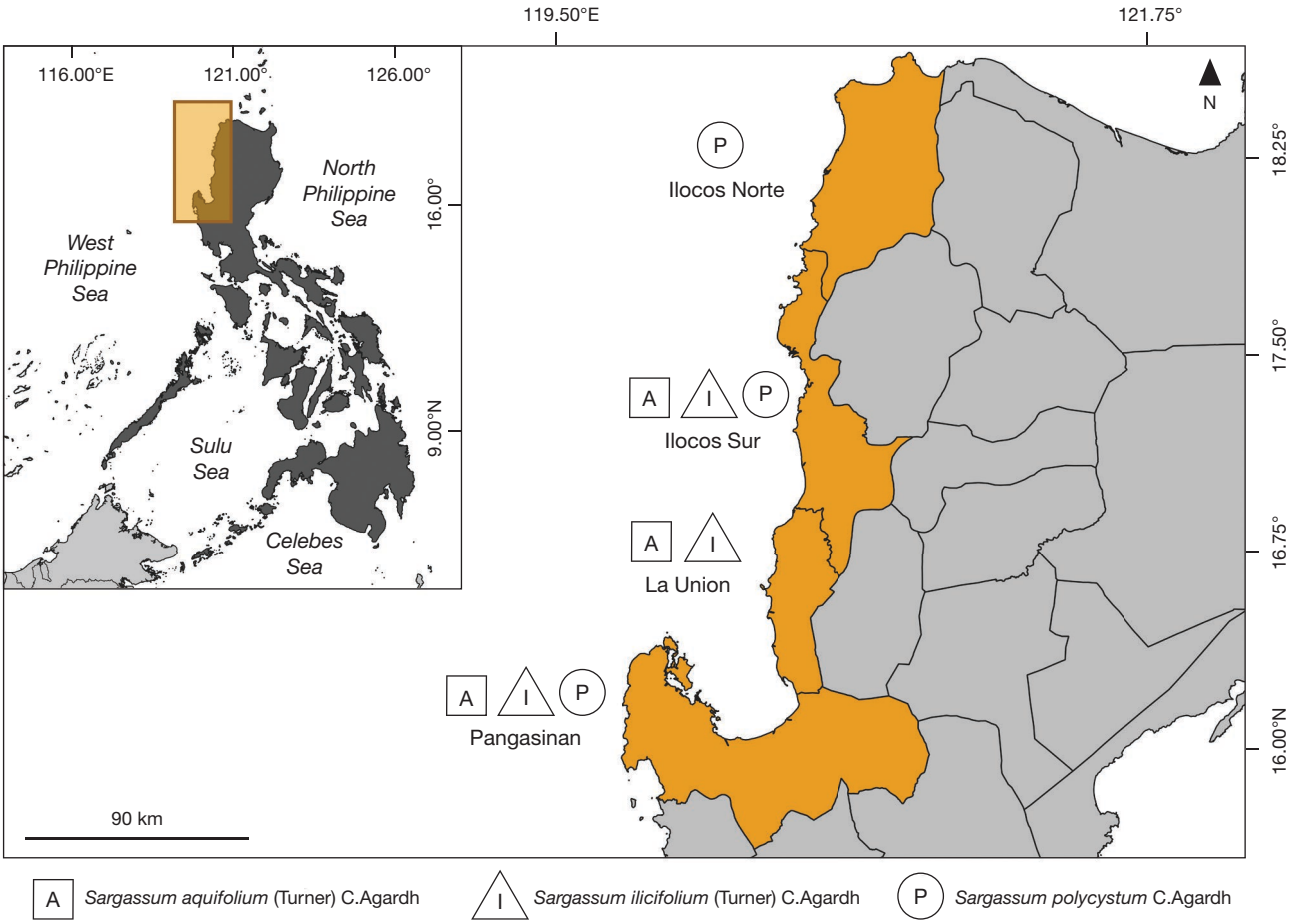

Fig. 1. — Map of the Philippines showing collection localities and distribution of specimens of *Sargassum* C.Agardh used in this study.

The years 1980s to the early 1990s can be considered as the 'golden years' for the genus *Sargassum* in the Philippines. During this period, significant advances on research on the diversity (taxonomy), biology, and ecology of *Sargassum* were made in many parts of the country as a response to the growing interest of using *Sargassum* as a potential resource for industrial and commercial applications. The first detailed taxonomic study of the genus *Sargassum* in the country was made by Ang & Trono (1987) where they reported and described eight species from Calatagan, Batangas. A more comprehensive study was conducted by Trono (1992) using reproductive materials collected from various localities in the country that were deposited at the Gregorio T. Velasquez Herbarium (MSI), Marine Science Institute, University of the Philippines. Trono (1992) confirmed the presence of ten species listed in the catalog published by Silva *et al.* (1987) and added five species as new records for the Philippines. Trono (1994) considered 12 of the unidentified *Sargassum* species that he described in 1992 as species new to science, all of which were deemed endemic to the Philippines (Modelo & Umezaki 1995; Santiañez & Trono 2013). Building on the efforts of the latter, Modelo & Umezaki (1995) worked on *Sargassum* materials from the Philippines that were deposited in the National Museum of the Philippines as well as in various herbaria around the world and they reported 20 species, six of which were added as new records to the country. These include *S. acinaciforme* Montagne, *S. angustifolium* C.Agardh, *S. glaucescens* J.Agardh, *S. henslowianum* C.Agardh, *S. herporhizum* Setchell & Gardner and *S. parvivesiculosum* Tseng & Lu (Modelo & Umezaki 1995). Three years later, a new species, *Sargassum corderoi* Modelo, Umezaki & Liao, was also added to the increasing list of *Sargassum* in the country (Modelo *et al.* 1998). Recent updates on the list of the *Sargassum* of the Philippines included that of Ganzon-Fortes (2012), Ang *et al.* (2013) and Lastimoso & Santiañez (2021). A total of 73 *Sargassum* species was listed by Ganzon-Fortes (2012), but some of the recent nomenclatural changes on the taxa were not incorporated in the report (Santiañez & Trono 2013). Ang *et al.* (2013) verified the various records of the seaweed species in the Philippines, accounting for the most recent nomenclatural changes, and reported 85 *Sargassum* taxa, including infraspecific names. Both reports did not include the study made by Modelo & Umezaki (1995), but these have been accounted for by the most recent listing by Lastimoso & Santiañez (2021) where 100 *Sargassum* taxa (including infraspecific names) were reported. Of these, 10 species are known to be endemic in the Philippines (i.e., *Sargassum abbottiae* Trono, *Sargassum angii* L.M.Liao, *Sargassum*

curimaoense Trono, *Sargassum bataanense* Trono, *Sargassum ohnoi* Trono, *Sargassum samarense* Trono, *Sargassum sullivanii* Trono, *Sargassum umezakii* Trono, *Sargassum velasquezii* Trono, *Sargassum yoshidae* Trono [Trono 1992, 1994]), four of which are known to only occur in their type localities in the northern West Philippine Sea region.

Molecular-assisted alpha-taxonomic (MAAT) studies in the last two decades confirmed that *Sargassum* species are extremely polymorphic and alluded that the diversity of the genus may have been overestimated; in some of these works, several species and varieties have been relegated to a single species (e.g. Mattio *et al.* 2008, 2009, 2010; Mattio & Payri 2010). As such, it is likely that *Sargassum* diversity in the Philippines has been inflated and that some, if not many, have been misidentified. Documenting *Sargassum* biodiversity and distribution in the Philippines is pressing considering that several of these are endemic and populations are threatened by unmanaged wild harvesting. In addition, consistent identification of the different *Sargassum* species is crucial for resource development especially as locally adapted cultivation technology for biomass production advances (Aaron-Amper *et al.* 2020; Largo *et al.* 2020).

In this study, we contribute to the understanding of *Sargassum* diversity and distribution in the Philippines by integrating molecular data with morphological information. We envision that the basic biodiversity knowledge provided in this work will facilitate advances in *Sargassum* resources management and conservation, not only in northwestern Philippines but also at the regional level.

MATERIAL AND METHODS

Preparation of voucher specimens

Sargassum specimens (n = 74; Appendix 1), were collected by snorkeling at the intertidal to upper subtidal areas in four provinces in northwestern Luzon, Philippines (i.e., Ilocos Norte, Ilocos Sur, La Union, and Pangasinan; Fig. 1) in September-October 2018 and March 2019. All samples were sorted and pressed using standard herbarium techniques. Prior to pressing, subsamples were obtained from the apical portions of the thallus (i.e., young blades and/or receptacles) of voucher specimens and were dried in silica gel for subsequent DNA extraction and sequencing. Voucher specimens were deposited at the Gregorio T. Velasquez Phycological Herbarium (MSI), Marine Science Institute, University of the Philippines, Diliman, Quezon City, Philippines.

DNA extraction and molecular analyses

Total genomic DNA was extracted from a small fragment of silica gel-preserved *Sargassum* specimens using Gencheck® DNA Extraction Reagent (FASMAC, Atsugi, Japan) as described in Hoshino *et al.* (2020). The PCR was performed using Tks GflexTM DNA Polymerase (Takara Bio Inc., Otsu, Japan). The primers used were CAF4A and CAR4A (Kogame *et al.* 2005) or SarF (5-'GTGATGTTTACATGGTGG-3') and SarR (5'-CCCCACCAGTAAATAGTC-3') for *cox*3. The PCR program consisted of a denaturation step at 94°C for one minute, followed by 35 cycles of 98°C for ten seconds, 50°C for 15 seconds and 68°C for 30 seconds, and a final elongation step at 68°C for seven minutes. DNA sequencing was conducted according to the method described in Hoshino *et al.* (2020). Newly generated *cox*3 sequences were aligned with GenBank-available *cox*3 sequences of other members of *Sargassum* subgenus *Sargassum* from previous MAAT work on the genus (e.g. Mattio *et al.* 2009; Dixon *et al.* 2012; Yip *et al.* 2018) together with *Turbinaria ornata* (Turner) J.Agardh and *Turbinaria gracilis* Sonder (as outgroup) using MUSCLE in MEGA 6 (Tamura *et al.* 2013). Molecular phylogenetic analyses of the aligned sequences under the Maximum Likelihood (ML) were conducted in RAxML v8 (Stamatakis 2014) through the Cipres Phylogenetic Portal (Miller *et al.* 2010) as described in Santiañez *et al.* (2018). Additional ML branch support values were calculated in IQTREE 2 v.2.2.0 (Minh *et al.* 2020), for which ultrafast bootstrap (UFBS; Hoang *et al.* 2018) and Shimodaira-Hasegawa approximate likelihood ratio test percentages (aLRT; Guindon *et al.* 2010) with 1000 replicates were assessed. Moreover, Bayesian inference analyses were performed with MrBayes v.3.2.7a (Ronquist *et al.* 2012) with 25 million generations until a frequency of 0.01 was reached. We computed sequence divergences (*p*-distances) between and among *Sargassum* taxa included in this study similar to those of Santiañez & Wynne (2020).

Morphological descriptions and comparisons

Morphologies of the samples for each of the species lineages were examined based on the characters outlined in Santiañez & Trono (2013). Measurements were made using a caliper and/or ruler under a Ken-A-Vision VisionScope T2600-230 stereomicroscope (Ken-A-Vision, Inc., Kansas City, United States) or with a hand lens, and subsequent photographs were taken using a Nikon D5300 digital camera (Nikon, Tokyo, Japan). Morphological observations were then compared to published reports describing the *Sargassum* resources of the Philippines (Ang & Trono 1987; Trono & Ganzon-Fortes 1988; Trono 1992, 1994; Modelo & Umezaki 1995; Calumpong & Meñez 1997; Santiañez & Trono 2013) and other localities within the Central Indo-Pacific region, such as Thailand (Noiraksar & Ajisaka 2008; Coppejans *et al.* 2010, 2017; Kantachumpoo *et al.* 2015), Malaysia (Wong *et al.* 2008), Vietnam (Nguyen *et al.* 1993), Singapore (Yip *et al.* 2018) and Taiwan (Yoshida 1988).

RESULTS

Diversity and distribution of *Sargassum* in northwestern Luzon inferred from cox3 data

A total of 74 *cox*3 sequences (383-582 bp) were newly generated from *Sargassum* specimens collected along the coasts of four provinces (i.e., Ilocos Norte, Ilocos Sur, La Union, and Pangasinan) in northwestern Luzon, Philippines. Our

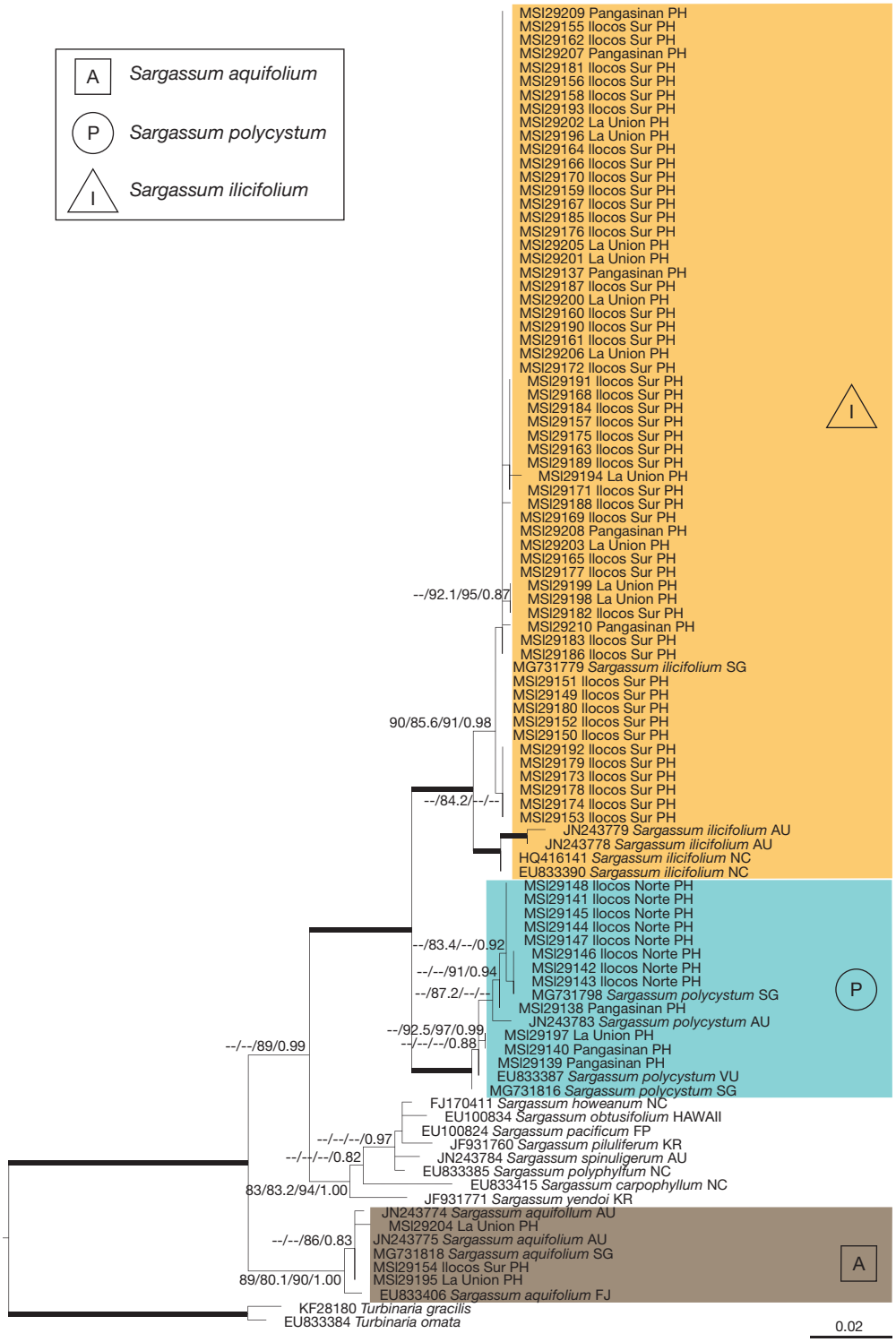

FIG. 2. — Maximum likelihood tree of *Sargassum* C.Agardh from northwestern Philippines based on *cox*3 sequence data. Support values in the form of non-parametric bootstrap (NPBS), approximate likelihood ratio test percentages (aLRT), ultrafast bootstrap (UFBS) and Bayesian posterior probabilities (BPP) are shown at each branch. **Thickened lines** indicate highly supported nodes (NPBS: ≥90%; aLRT: ≥90%; UFBS: ≥95%; and BPP: ≥0.90). Values <80% (NPBS), <80% (aLRT), <80% (UFBS), and <0.80 (BPP) are removed. Specimen codes correspond to those listed in Appendix 1. Abbreviations: **AU**, Australia; **FP**, French Polynesia; **KR**, Korea; **NC**, New Caledonia; **PH**, Philippines; **SG**, Singapore; **VU**, Vanuatu.

*cox*3-gene tree (Fig. 2) showed that our specimens were recovered into three distinct clades, and, by integrating molecular information with morpho-anatomical observations, we attributed these different clades to *Sargassum aquifolium* (Turner) C.Agardh, *Sargassum ilicifolium* (Turner) C.Agardh, and *S. polycystum* C.Agardh. Most of our samples

(n = 59) clustered within the *S. ilicifolium* clade, 12 were within the *S. polycystum* clade, and three were within the *S. aquifolium* clade. Based on these clustering, *S. ilicifolium* appeared to be the most widely distributed species, occurring in all coastal areas sampled (Fig. 1). *Sargassum polycystum* was also confirmed to be present in all areas except in La Union. Specimens of *S. polycystum* from northwestern Philippines were recovered together with their conspecifics in Singapore, Australia, and Vanuatu (*p*-distance: 0-0.012). *Sargassum aquifolium* was only recovered in La Union and Ilocos Sur, but the species formed a clade with specimens from other areas in the Pacific such as Singapore, Fiji and Australia (*p*-distance: 0-0.005). Interestingly, all *S. ilicifolium* from the Philippines formed a distinct cluster together with those from Singapore (*p*-distance: 0-0.005), while their conspecifics in the southern Pacific (i.e., New Caledonia and Australia; *p*-distance: ≤ 0.031) were recovered in a different clade. Interspecific divergences between taxa included in this study ranged from 0.005 to 0.088.

Morphology of *Sargassum* species from northwestern Luzon, Philippines

Family Sargassaceae Kützing
Genus *Sargassum* C.Agardh

Sargassum aquifolium (Turner) C.Agardh

Fucus aquifolius Turner, *Fuci sive plantarum fucorum generi a botanicis ascriptarum icones descriptiones et historia*: 111 (Turner 1807).

Sargassum kushimotense sensu Trono (1992, 1997); Santiañez & Trono (2013), non *Sargassum kushimotense* Yendo.

Type locality. — **Indonesia**. Sunda Strait (Silva *et al.* 1996).

Specimens examined. — **Philippines**. Ilocos Sur, San Esteban, Apatot, 26.IX.2018, leg. W.J.E. Santiañez (MSI[MSI29154]); La Union, Balaoan, Almeida, 27.IX.2018, leg. W.J.E. Santiañez (MSI[MSI29195]); La Union, Balaoan, Paraoir, 27.IX.2018, leg. W.J.E. Santiañez (MSI[MSI29204]).

Distribution in northwestern Luzon. — Ilocos Sur, La Union, and Pangasinan (Fig. 1).

Description

Thallus golden brown when fresh (Fig. 3A), drying dark brown, to 42 cm long, attached to the substrate by a conical to discoid holdfast (Fig. 3B, C). Main axes smooth, slightly compressed, short, to 3 mm long, giving rise to several compressed secondary axes, 2.5 mm wide (Fig. 3C). Blades linear-lanceolate to linear-oblanceolate, narrowed towards blunt or acute apices, mostly less than 36 mm long, 8 mm wide; margins serrate-dentate; stalk short, base asymmetrical; midrib apparent, slightly elevated, fading near the tips; cryptostomata prominent, elevated, scattered but tending to be arranged in rows in narrow blades (Fig. 3B, D). Vesicles large, ovoid to obovoid, 5 mm wide, 7 mm long; tips rounded to pointed, some mucronate; stalks compressed, winged to foliaceous, often as long as vesicles (Fig. 3D). Young receptacles densely clustered, short, compressed to slightly flattened (some somewhat triquetrate, others twisted), often with sharp teeth.

Sargassum ilicifolium (Turner) C.Agardh

Fucus ilicifolius Turner, *Fuci sive plantarum fucorum generi a botanicis ascriptarum icones descriptiones et historia*: 113 (Turner 1807).

Sargassum aquifolium sensu Coppejans *et al.* (2017), non *Sargassum aquifolium* (Turner) C.Agardh.

Sargassum crassifolium sensu Ang & Trono (1987); Trono (1992, 1997); Noiraksar & Ajisaka (2008); Coppejans *et al.* (2010); Santiañez & Trono (2013), non *Sargassum crassifolium* J.Agardh.

Sargassum cristaefolium sensu Ang & Trono (1987); Trono (1992, 1997); Modelo & Umezaki (1995), non *Sargassum cristaefolium* C.Agardh.

Sargassum turbinarioides sensu Trono (1997), non *Sargassum turbinarioides* Grunow.

Type locality. — **Indonesia**. Sunda Strait (Silva *et al.* 1996: 676).

Specimens examined. — **Philippines**. Pangasinan, Bolinao, Malilnep, 9.III.2019, leg. A.C. Calaguing (MSI[MSI29137]); Ilocos Sur, San Esteban, Apatot, 26.IX.2018, leg. W.J.E. Santiañez (MSI[MSI29151, MSI29152, MSI29156, MSI29160]); Ilocos Sur, Santiago, Ambucao, 26.IX.2018, leg. W.J.E. Santiañez (MSI[MSI29174, MSI29176, MSI29186, MSI29187, MSI29189]); La Union, Balaoan, Almeida, 27.IX.2018, leg. W.J.E. Santiañez (MSI[MSI29196]); La Union, Balaoan, Paraoir, 27.IX.2018, leg. W.J.E. Santiañez (MSI[MSI29199, MSI29200, MSI29201]); La Union, San Fernando, Lingsat-MPA, 27.IX.2018, leg. W.J.E. Santiañez (MSI[MSI29206]).

Distribution in northwestern Luzon. — Ilocos Sur, La Union, and Pangasinan (Fig. 1).

Description

Thallus golden to dark brown in color, to 45 cm long, holdfast conical to discoid (Fig. 4). Main axes terete to slightly compressed, to 3 mm in diameter, warty, usually covered with epiphytes; secondary axes also terete or slightly compressed, smooth, slightly thinner than main axes (Fig. 4C). Blades vertically attached, to 4 cm long, somewhat leathery or crisp when dried (Fig. 4D); blade shape highly variable but mostly lanceolate to oblanceolate in vegetative branches (Fig. 4C, D, G), those in reproductive branches oblanceolate to obovate; apex often attenuate or acute, sometimes round or obtuse (Fig. 4E-G); base usually asymmetrically cuneate; margin serrate to biserrate, sometimes erose or repand; some blades in terminal portion of the axes with duplicated apices perpendicular to the surface, some appearing turbinarioid (Fig. 4C'; Fig. 4G: arrowhead); midrib thin, apparent from to ⅔ of the blade length, sometimes percurrent; cryptostomata embedded and randomly scattered on the surface of the blade; petiole short to 3 mm long, flattened or cylindrical, with occasional spine-like protrusions. Vesicles smooth, globose, to 5.4 mm in diameter, sometimes ribbed to mucronated or phyllocystic with few cryptostomata; stalks short, to 3 mm long (Fig. 4D, F). Dioecious, receptacles closely associated with blades and vesicles, arranged racemosely (Fig. 4E, F); female receptacles compressed to flattened with dentate margin (Fig. 4E), male receptacles cylindrical and lumpy (Fig. 4F).

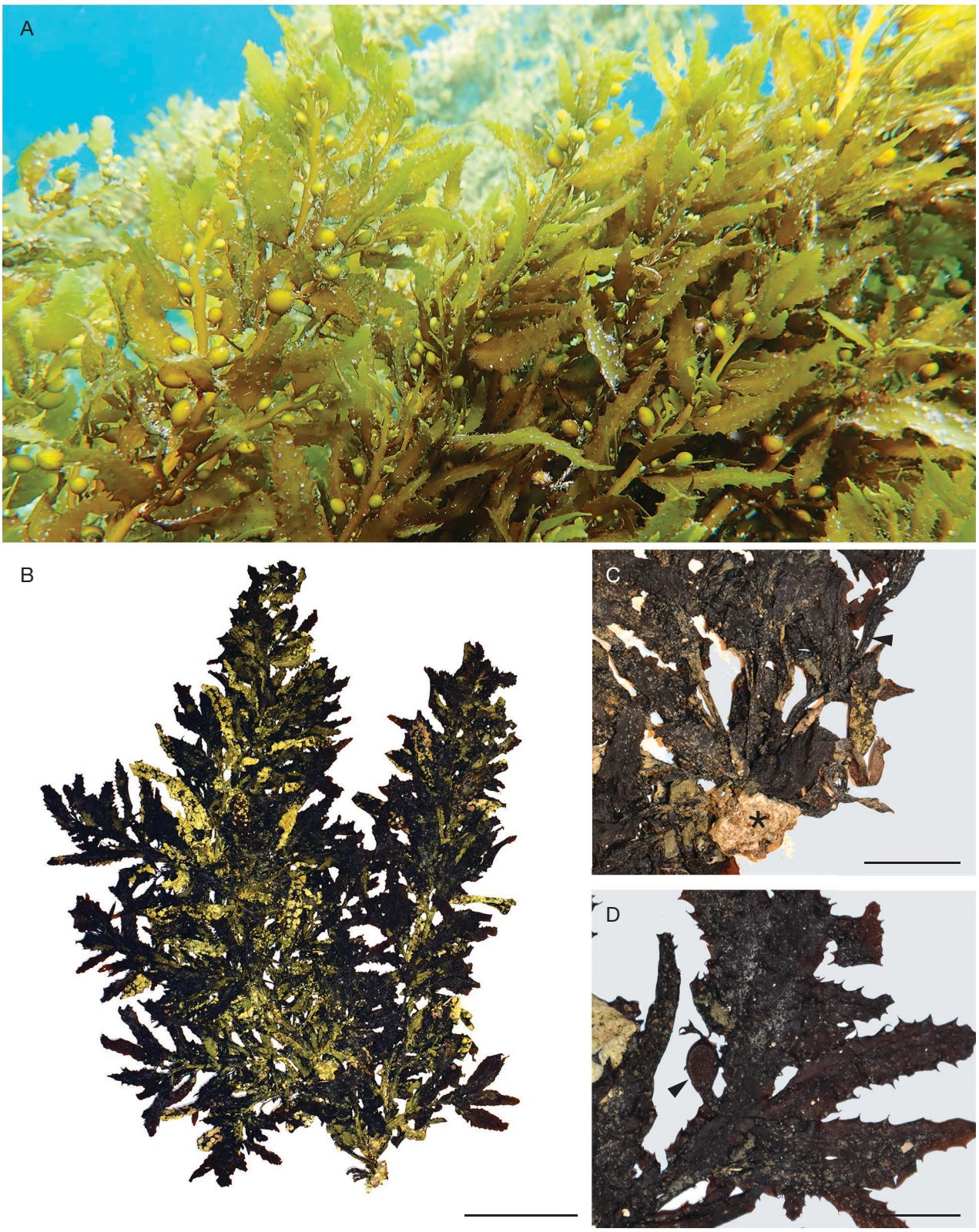

Fig. 3. — *Sargassum aquifolium* (Turner) C.Agardh from northwestern Philippines: **A**, *in situ* photograph of *S. aquifolium* growing in the shallow subtidal of Bolinao, Pangasinan; **B**, habit of *S. aquifolium* showing holdfast, short main axis, the several compressed secondary axes, and linear-lanceolate to linear-oblanceolate blades with sharply serrate-dentate margins; **C**, closer view of the basal portion of the thallus showing holdfast (**asterisk**) and the compressed axes (**arrowheads**) arising from the short stem; **D**, portion of an axis showing a ribbed vesicle with foliaceous mucro and compressed stalk (**arrowhead**) and blades marked with toothed margins. Scale bars: B, 5 cm; C, D, 1 cm.

Sargassum polycystum C.Agardh

Systema algarum: 304 (Agardh 1824).

Sargassum myriocystum sensu Santiañez & Trono (2013), non *Sargassum myriocystum* J.Agardh.

TYPE LOCALITY. — **Indonesia**. Sunda Strait (Silva *et al.* 1996: 694).

SPECIMENS EXAMINED. — **Philippines**. Pangasinan, Bolinao, Dos Hermanos, 9.III.2019, leg. A.C. Calaguing (MSI[MSI29138, MSI29139]); Pangasinan, Bolinao, Malilnep, 9.III.2019, leg. A.C. Calaguing (MSI[MSI29140]); Ilocos Norte, Burgos, Bayog, 25.IX.2018, leg. W.J.E. Santiañez (MSI[MSI29141, MSI29142, MSI29143, MSI29144, MSI29148]); La Union, Balaoan, Almeida, 27.IX.2018, leg. W.J.E. Santiañez (MSI[MSI29197]).

DISTRIBUTION IN NORTHWESTERN LUZON. — Ilocos Norte, Ilocos Sur, La Union, Pangasinan (Fig. 1).

DESCRIPTION

Thallus golden (when fresh) to dark brown (when dried) in color, to 57 cm long, holdfast discoid. Main axis terete, warty, short, usually to 5 mm long (rarely to 18 mm long), bearing several secondary axes, some of which are modified into stoloniferous holdfast (Fig. 5A-C). Secondary axes with numerous short protuberances, these either densely aggregated or sparsely distributed throughout the surface (Fig. 5A, D); secondary axes of some specimens smooth (Fig. 5E). Blades on vegetative branches large, to 60 mm long, 13 mm wide, oblong to oblanceolate, base asymmetrical, margin serrate-dentate, apices acute to rounded, cryptostomata elevated and scattered, midrib distinct, disappearing before the tip; those in fertile branches considerably smaller, less than 15 mm long, 6 mm wide, obovate, some oblong to somewhat oblanceolate, base asymmetrical, margin serrate dentate, midrib usually not apparent, but only occur in the basal ⅓ of the blades when present, apices rounded to obtuse. Vesicles small, generally less than 2 mm long and 1.5 mm wide, numerous, spherical to ovoid, often with a short and thin or foliaceous mucro, subtended by short (sometimes as long as vesicles) and thin stalks (Fig. 5D, E). Plant dioecious (Fig. 5F, G), receptacles closely associated with vesicles and/or blades (zygocarpic), racemosely arranged; female receptacles toothed, compressed (rarely triquetrous) to flattened towards the tip, sometimes somewhat twisted, generally less than 2.5 mm long, 1 mm at the widest (Fig. 5F); male receptacles smooth, filiform, to 5 mm long, cylindrical in cross-section, to 0.5 mm in diameter (Fig. 5G).

DISCUSSION

Our current study suggests that only three *Sargassum* species inhabit the coast of northwestern Philippines. Of the 18 *Sargassum* reported from this region (Appendix 2), we only confirmed the presence of *S. aquifolium*, *S. ilicifolium*, and *S. polycystum* from Ilocos Norte down to Pangasinan (see the Key). Based on our molecular studies, *S. ilicifolium* is the most widely distributed while based on our morpho-anatomical works, the species also exhibited the most variable morphologies.

We were only able to sequence and observe three specimens of *S. aquifolium* from Ilocos Sur and La Union, which clustered with *S. aquifolium* from Fiji in the South Pacific (GenBank[EU833406]; identified based on the authority of Mattio *et al.* [2009]). Based on our morpho-anatomical analyses, our *S. aquifolium* specimens closely resemble the *S. kushimotense* reported by previous works from several areas in Luzon (e.g. Trono 1992, 1997; Santiañez & Trono 2013). While we were not able to sequence *S. aquifolium* specimens from Bolinao, Pangasinan, we commonly observed this species (although not abundant) in the area and is referred to as *S. kushimotense sensu* Trono (1992). Yendo (1907) originally described *S. kushimotense* based on materials from Kushimoto, Wakayama, Japan (Yoshida *et al*. 2004). Although only based on vegetative thalli, *S. kushimotense* was distinguished from other *Sargassum* with compressed axes in having blades that are thin and papyraceous coarsely dentate margins, 5-10 cm long and 1.5-2 cm wide, and its typically spherical vesicles subtended by a long, flattened stalk and possess a foliaceous mucro (Yendo 1907). When compared to the original description and illustration of *S. kushimotense* (Yendo 1907: pl. XVI, fig. 20), the Philippine materials identified as *S. kushimotense* are different in having a more pronounced compressed axes, shorter but narrower blades, and its vesicles are elliptical, have shorter stalks, and usually lack the foliaceous mucro typical to *S. kushimotense* from Japan. As such, we believe the records of *S. kushimotense sensu* Trono (1992, 1997) and others from the Philippines are misidentified and should be considered as *S. aquifolium*. The common and widely distributed tropical species *S. oligocystum* (Noro *et al.* 1994) can also be confused with *S. aquifolium*. The former is distinguished from the latter in having flattened axes (vs compressed axes in *S. aquifolium*), longer and broader blades with shallow serrate-dentate margins, smaller spherical to obovate vesicles subtended by short terete to flattened stalks and apices that are usually rounded or with occasional spine or teeth.

Our integrative taxonomic work on *S. ilicifolium* suggested that the species exhibits very high phenotypic plasticity. That is, it encompasses several characteristics of other closely related taxa, especially those *Sargassum* taxa possessing 'duplicated' blades that we have observed and described in our previous studies. These include taxa previously identified in the Philippines as *S. crassifolium* (*sensu* Trono 1992, 1997; Santiañez & Trono 2013), *S. cristaefolium* (*sensu* Trono 1992, 1997; Modelo & Umezaki 1995; Santiañez & Trono 2013) and *S. turbinarioides* (*sensu* Trono 1997). Blade duplication in *S. ilicifolium* collected in northwestern Philippines has also been observed and illustrated in specimens of *S. cristaefolium* (Santiañez & Trono 2013: fig. 2) and *S. crassifolium* (Santiañez & Trono 2013: fig. 3) from Alabat Island in the northeastern Philippines, and in specimens observed and illustrated by Modelo & Umezaki (1995) as *S. crassifolium* (pl. 4a, b) and *S. cristaefolium* (pl. 3a) from several areas in the Philippines. Ang & Trono (1987) and Trono (1992) have noted the similarities between *S. crassifolium* and *S. cristaefolium*, and

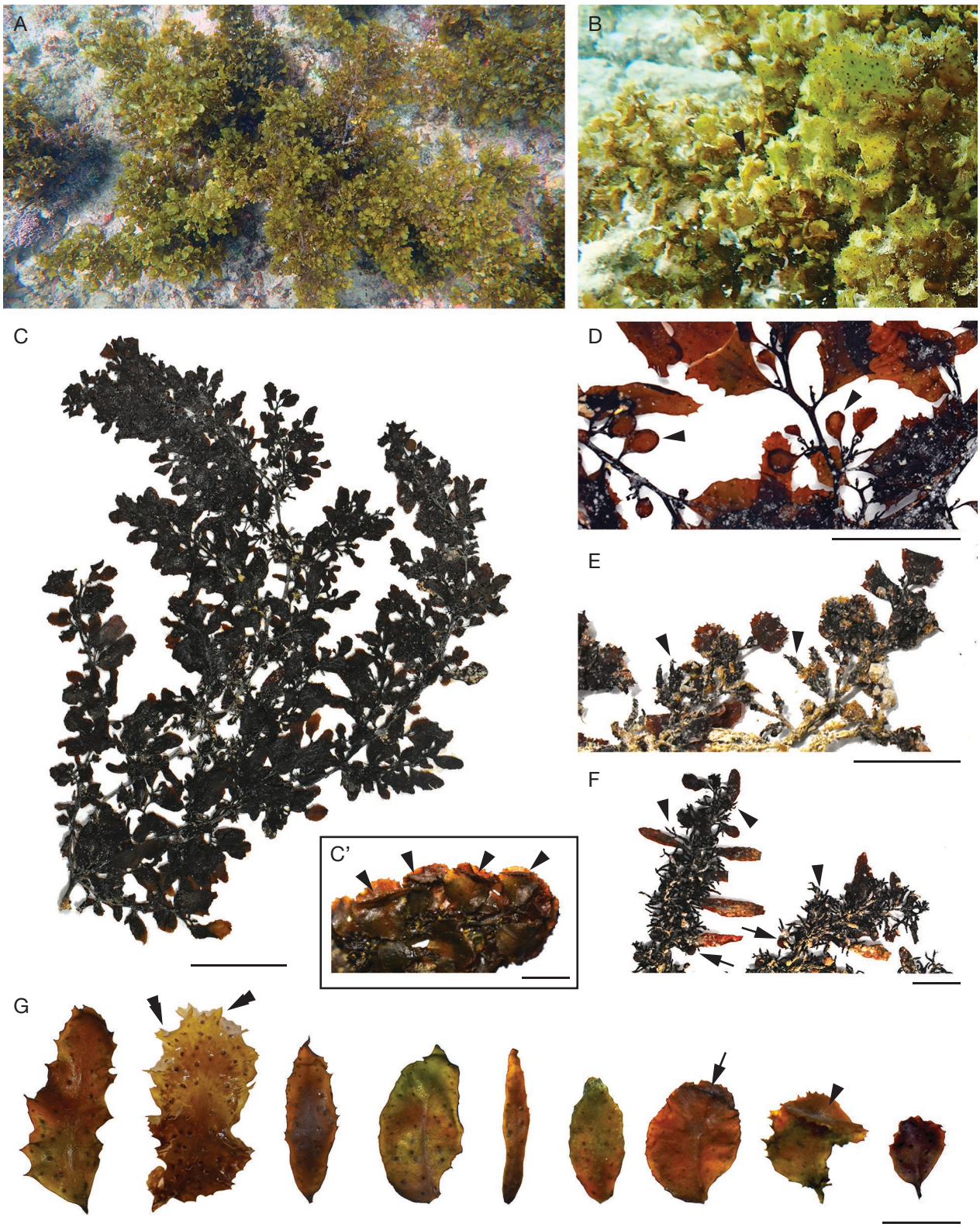

Fig. 4. — *Sargassum ilicifolium* (Turner) C.Agardh from northwestern Philippines: **A**, top view of some *S. ilicifolium* thalli growing in the shallow subtidal of Arosan, Bolinao, Pangasinan; **B**, *in situ* photograph of a young *S. ilicifolium* thalli showing the wavy and toothed and occasionally "duplicated" blades (**arrowhead**); **C**, pressed herbarium specimen of *S. ilicifolium* from Ilocos Sur, Philippines. Portion of an axis showing several turbinariod blades (**C'**: **arrowheads**); **D**, portion of an axis showing small, ribbed vesicles (**arrowheads**) growing together with blades of various shapes; **E**, fertile portion of a female plant showing the compressed to flattened and toothed female receptacles (**arrowheads**) that are closely associated with blades; **F**, portion of a male plant showing terete receptacles (**arrowheads**) that are closely associated with vesicles (**arrows**) and blades; **G**, variability of shape and form of *S. ilicifolium* blades, those with double rows of teeth, duplicated apical margins, and with cup-shaped/turbinarioid apices are indicated with **double arrowheads**, **arrow**, and **arrowhead**, respectively. Scale bars: C, 5 cm; C', E-G, 1 cm; D, 2 cm.

Key to the confirmed species of *Sargassum* C.Agardh in northwestern Luzon, Philippines

1. Thallus typically with stoloniferous holdfasts; branches terete, usually with numerous branched protuberances; vesicles small, numerous, spherical to ovoid ..... *Sargassum polycystum* C.Agardh
— Thallus without stoloniferous holdfasts; branches smooth, terete, slightly compressed, to compressed; vesicles large, globose to obovoid, ribbed, sometimes mucronated 2

2. Branches smooth and compressed; blades linear-lanceolate to linear oblanceolate, distinctly serrate-dentate; vesicles large, ovoid to obovoid, to 7 mm long ..... *Sargassum aquifolium* (Turner) C.Agardh
— Branches smooth, terete to slightly compressed; blades highly variable in shape, margins serrate to biserrate, 'duplicated' especially towards the apices, duplication sometimes appearing turbinarioid; vesicles globose, to 5.4 mm in diameter ..... *Sargassum ilicifolium* (Turner) C.Agardh

the likelihood of misidentification of one with the other in other reports. In distinguishing *S. cristaefolium* from *S. crassifolium* in the Philippines, Ang & Trono (1987) and Trono (1992) mentioned that the doubling of blades in *S. crassifolium* involved only the doubling of marginal teeth rows (Ang & Trono 1987: fig. 1d) while in *S. cristaefolium* it involved the doubling of blades (Trono 1992: figs 12, 14). These characters – especially the doubling of marginal teeth rows (Fig. 4G: double arrowheads), the doubling of apical blades margins (Fig. 4G: arrow) and the turbinarioid blades (Fig. 4C: arrowhead; Fig. 4G) – are within the range of characters found in our *S. ilicifolium* from northern Luzon; hence, we consider the above-mentioned taxa, i.e., *S. crassifolium* (*sensu* Ang & Trono 1987; Trono 1992, 1997; Santiañez & Trono 2013) and *S. cristaefolium* (*sensu* Ang & Trono 1987; Trono 1992, 1997; Modelo & Umezaki 1995; Santiañez & Trono 2013) as misidentifications and should be considered as *S. ilicifolium*. Our findings on the wide range of morphologies of *S. ilicifolium* from the Philippines also suggest that *Sargassum* taxa previously identified as *S. aquifolium*, *S. crassifolium* and *S. cristaefolium* in other areas within the tropical western Indo-Pacific region may have been misidentified. Particularly, *S. aquifolium sensu* Coppejans *et al.* (2017) in Andaman Sea, Thailand and *S. crassifolium sensu* Noiraksar & Ajisaka (2008) and Coppejans *et al.* (2010) from the Gulf of Thailand are attributable to *S. ilicifolium*. In describing and identifying their *S. crassifolium* from the Gulf of Thailand, Noiraksar & Ajisaka (2008) and Coppejans *et al.* (2010) referred to *S. crassifolium sensu* Trono (1997), which we consider here as a synonym of *S. ilicifolium*. Accordingly, Thai species of *S. crassifolium* sometimes possess double serrulate apices/margins (Noiraksar & Ajisaka 2008: fig. 5b) or two-edged/duplicated margins (Coppejans *et al.* 2010: fig. 105a, b). In their later work, Coppejans *et al.* (2017) considered *S. crassifolium* as a junior synonym of *S. aquifolium* and described the latter species as very similar to their *S. crassifolium* from the Gulf of Thailand (Coppejans *et al.* 2010). That is, *S. aquifolium* from Andaman Sea was described as having two-edged/duplicated margin and the accompanying photographs (Coppejans *et al.* 2017: fig. 70a-c) closely resembled those found in our *S. ilicifolium* specimens (Fig. 4A, B). The results of our molecular phylogenetic works showed two distinct clades of *S. ilicifolium* – the Philippines-Singapore clade and southern Pacific clade. We were not able to scrutinize the morpho-anatomies of specimens used by Mattio & Payri (2009) but their morphological description and photographs (Mattio & Payri 2009: fig. 8) of the *S. ilicifolium* from New Caledonia (which belongs to the latter clade) closely resemble the specimens that we examined in this study. Hence, we consider these clades as a single taxon, which we identify as *S. ilicifolium*, based on the authority of Mattio *et al.* (2009).

The morphologies of *S. polycystum* specimens we examined in this study were similar to those in previous studies (e.g. Chiang *et al.* 1992; Trono 1992, 1997; Noiraksar & Ajisaka 2008; Mattio *et al.* 2009; Yip *et al.* 2018), especially the presence of secondary holdfasts and muricate axes. We noted that sexual dimorphism in *S. polycystum* is apparent not only in their receptacles but also in the shape and nature of the vesicles (Fig. 5) and blades of fertile branches. That is, blades of fertile branches in female individuals are shorter and obovate (Fig. 5F) as opposed to the elongated, oblanceolate blades of male individuals (Fig. 5G); meanwhile female vesicles are often ovoid and with a short mucro (Fig. 5F) while male vesicles are spherical and with smooth apices (Fig. 5G). We also observed some specimens that lack the typical secondary holdfast derived from the secondary axes; some specimens also had secondary axes with few spinose protuberances, while others had smooth surfaces. These observations on the absence of secondary holdfast and spinose axes are similar to those reported by Noiraksar & Ajisaka (2008) for *S. polycystum* populations in Thailand. Populations of Thai *S. polycystum* are also confused with *S. baccularia* but Noiraksar & Ajisaka (2008) noted that these two species can be distinguished based on the shape and nature of their vesicles and receptacles. That is, *S. polycystum* possesses spherical to obovate vesicles and its female receptacles are terete to slightly compressed; meanwhile, *S. baccularia* has spherical to elliptical vesicles and its female receptacles are triquetrous. In our current studies, we observed that the vesicles of *S. polycystum* can be elliptical and their female receptacles triquetrous especially near the tip. As such, we believe that *S. baccularia sensu* Noiraksar & Ajisaka (2008) is a misapplied name and that the specimens are referable to *S. polycystum*. Kantachumpoo *et al.* (2015) provided molecular evidence based on ITS sequences for the distinction of *S. baccularia* and *S. polycystum* from Thailand and illustrated both taxa using the same specimens found in Noiraksar & Ajisaka (2008). However, *S. baccularia* specimen of Kantachumpoo *et al.* (2015) clustered with *S. oligocystum*, a species known to have distinctly compressed to flattened axes (Trono 1992, 1997; Calumpong & Meñez 1997; Noiraksar &

FIG. 5. — *Sargassum polycystum* C.Agardh from northwestern Philippines: **A**, habit of a typical muricate *S. polycystum* showing stoloniferous holdfast (**s**) arising from the main axes, these having several cauline blades (**ca**); **B**, habit of a female specimen of *S. polycystum*; **C**, habit of a male *S. polycystum* with few secondary axes, some areas showing filiform receptacles; **D**, portion of an axis showing short protuberances typical to *S. polycystum*; **E**, portion of a female *S. polycystum* specimen showing a smooth surface and numerous, often densely aggregated mucronate vesicles; **F**, terminal portion of an axis showing young, flattened receptacles (**arrowheads**) closely associated with ovoid vesicles with short mucro, each vesicle also having long stalks; **G**, terminal portion of an axis of a male specimen showing branching filiform receptacles (**arrowhead**) that are closely associated with spherical vesicles with short stalks. Scale bars: A-C, 5 cm; D, E, 1 cm; F, G, 0.25 cm.

Ajisaka 2008; Wong *et al.* 2008). Kantachumpoo *et al.* (2015) did not provide detailed comparisons between the species among their materials. Although it is unclear whether the material used by Kantachumpoo *et al.* (2015) is the same as that described in Noiraksar & Ajisaka (2008), it is likely that the *S. baccularia sensu* Kantachumpoo *et al.* (2015) has been misidentified. In Malaysia, Wong *et al.* (2004) also noted the confused taxonomies of *S. baccularia* and *S. polycystum* and showed that *S. polycystum* and *S. baccularia* can be distinguished based on random amplified polymorphism DNA (RAPD) and morphology. For the latter, they suggested that the absence of secondary holdfasts derived from secondary axes distinguishes *S. baccularia* from *S. polycystum*. According to our studies and those of Noiraksar & Ajisaka (2008), these secondary holdfasts may also be absent in *S. polycystum*. Nonetheless, we suggest further studies to verify whether these species should be considered as distinct.

Taking all our findings into consideration, our current efforts suggest that the *Sargassum* diversity in the northwestern Philippines may have been grossly overestimated. Furthermore, our results call for the need to revisit the taxonomy of the reported 99 *Sargassum* taxa in the country – in particular the 18 species that have their type locality in the archipelago. Lastly, we call not only for a reassessment of the taxonomy of Philippine *Sargassum* species, but also of those found in the Indo-Pacific region.

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APPENDICES

APPENDIX 1. — Collection details, herbarium code, and GenBank accession numbers of Philippine *Sargassum* C.Agardh specimens examined in this study.

Species and collection details	Voucher	GenBank
Sargassum aquifolium (Turner) C.Agardh		
Ilocos Sur, San Esteban, Apatot, 17°18'50.86"N, 120°25'29.28"E, 26.IX.2018	MSI29154	OR640017
La Union, Balaoan, Paraoir, 16°48'17.27"N, 120°19'32.60"E, 27.IX.2018	MSI29204	OR640019
La Union, Balaoan, Almeida, 16°49'11.19"N, 120°19'45.25"E, 27.IX.2018	MSI29195	OR640018
Sargassum ilicifolium (Turner) C.Agardh		
Pangasinan, Bolinao, Malilnep, 16°26'46.82"N, 119°56'23.41"E, 9.III.2019	MSI29137	OR639958
Ilocos Sur, San Esteban, Apatot, 17°18'50.86"N, 120°25'29.28"E, 26.IX.2018	MSI29149	OR639959
Ilocos Sur, San Esteban, Apatot, 17°18'50.86"N, 120°25'29.28"E, 26.IX.2018	MSI29150	OR639960
Ilocos Sur, San Esteban, Apatot, 17°18'50.86"N, 120°25'29.28"E, 26.IX.2018	MSI29151	OR639961
Ilocos Sur, San Esteban, Apatot, 17°18'50.86"N, 120°25'29.28"E, 26.IX.2018	MSI29152	OR639962
Ilocos Sur, San Esteban, Apatot, 17°18'50.86"N, 120°25'29.28"E, 26.IX.2018	MSI29153	OR639963
Ilocos Sur, San Esteban, Apatot, 17°18'50.86"N, 120°25'29.28"E, 26.IX.2018	MSI29155	OR639964
Ilocos Sur, San Esteban, Apatot, 17°18'50.86"N, 120°25'29.28"E, 26.IX.2018	MSI29156	OR639965
Ilocos Sur, San Esteban, Apatot, 17°18'50.86"N, 120°25'29.28"E, 26.IX.2018	MSI29157	OR639966
Ilocos Sur, San Esteban, Apatot, 17°18'50.86"N, 120°25'29.28"E, 26.IX.2018	MSI29158	OR639967
Ilocos Sur, San Esteban, Apatot, 17°18'50.86"N, 120°25'29.28"E, 26.IX.2018	MSI29159	OR639968
Ilocos Sur, San Esteban, Apatot, 17°18'50.86"N, 120°25'29.28"E, 26.IX.2018	MSI29160	OR639969
Ilocos Sur, San Esteban, Apatot, 17°18'50.86"N, 120°25'29.28"E, 26.IX.2018	MSI29161	OR639970
Ilocos Sur, San Esteban, Apatot, 17°18'50.86"N, 120°25'29.28"E, 26.IX.2018	MSI29162	OR639971
Ilocos Sur, San Esteban, Apatot, 17°18'50.86"N, 120°25'29.28"E, 26.IX.2018	MSI29163	OR639972
Ilocos Sur, San Esteban, Apatot, 17°18'50.86"N, 120°25'29.28"E, 26.IX.2018	MSI29164	OR639973
Ilocos Sur, San Esteban, Apatot, 17°18'50.86"N, 120°25'29.28"E, 26.IX.2018	MSI29165	OR639974
Ilocos Sur, San Esteban, Apatot, 17°18'50.86"N, 120°25'29.28"E, 26.IX.2018	MSI29166	OR639975
Ilocos Sur, San Esteban, Apatot, 17°18'50.86"N, 120°25'29.28"E, 26.IX.2018	MSI29167	OR639976
Ilocos Sur, San Esteban, Apatot, 17°18'50.86"N, 120°25'29.28"E, 26.IX.2018	MSI29168	OR639977
Ilocos Sur, San Esteban, Apatot, 17°18'50.86"N, 120°25'29.28"E, 26.IX.2018	MSI29169	OR639978
Ilocos Sur, San Esteban, Apatot, 17°18'50.86"N, 120°25'29.28"E, 26.IX.2018	MSI29170	OR639979
Ilocos Sur, San Esteban, Apatot, 17°18'50.86"N, 120°25'29.28"E, 26.IX.2018	MSI29171	OR639980
Ilocos Sur, San Esteban, Apatot, 17°18'50.86"N, 120°25'29.28"E, 26.IX.2018	MSI29172	OR639981
Ilocos Sur, Santiago, Ambucao, 17°18'18.62"N, 120°25'17.09"E, 26.IX.2018	MSI29173	OR639982
Ilocos Sur, Santiago, Ambucao, 17°18'18.62"N, 120°25'17.09"E, 26.IX.2018	MSI29174	OR639983
Ilocos Sur, Santiago, Ambucao, 17°18'18.62"N, 120°25'17.09"E, 26.IX.2018	MSI29175	OR639984
Ilocos Sur, Santiago, Ambucao, 17°18'18.62"N, 120°25'17.09"E, 26.IX.2018	MSI29176	OR639985
Ilocos Sur, Santiago, Ambucao, 17°18'18.62"N, 120°25'17.09"E, 26.IX.2018	MSI29177	OR639986
Ilocos Sur, Santiago, Ambucao, 17°18'18.62"N, 120°25'17.09"E, 26.IX.2018	MSI29178	OR639987
Ilocos Sur, Santiago, Ambucao, 17°18'18.62"N, 120°25'17.09"E, 26.IX.2018	MSI29179	OR639988
Ilocos Sur, Santiago, Ambucao, 17°18'18.62"N, 120°25'17.09"E, 26.IX.2018	MSI29180	OR639989
Ilocos Sur, Santiago, Ambucao, 17°18'18.62"N, 120°25'17.09"E, 26.IX.2018	MSI29181	OR639990
Ilocos Sur, Santiago, Ambucao, 17°18'18.62"N, 120°25'17.09"E, 26.IX.2018	MSI29182	OR639991
Ilocos Sur, Santiago, Ambucao, 17°18'18.62"N, 120°25'17.09"E, 26.IX.2018	MSI29183	OR639992
Ilocos Sur, Santiago, Ambucao, 17°18'18.62"N, 120°25'17.09"E, 26.IX.2018	MSI29184	OR639993
Ilocos Sur, Santiago, Ambucao, 17°18'18.62"N, 120°25'17.09"E, 26.IX.2018	MSI29185	OR639994
Ilocos Sur, Santiago, Ambucao, 17°18'18.62"N, 120°25'17.09"E, 26.IX.2018	MSI29186	OR639995
Ilocos Sur, Santiago, Ambucao, 17°18'18.62"N, 120°25'17.09"E, 26.IX.2018	MSI29187	OR639996
Ilocos Sur, Santiago, Ambucao, 17°18'18.62"N, 120°25'17.09"E, 26.IX.2018	MSI29188	OR639997
Ilocos Sur, Santiago, Ambucao, 17°18'18.62"N, 120°25'17.09"E, 26.IX.2018	MSI29189	OR639998
Ilocos Sur, Santiago, Ambucao, 17°18'18.62"N, 120°25'17.09"E, 26.IX.2018	MSI29190	OR639999
Ilocos Sur, Santiago, Ambucao, 17°18'18.62"N, 120°25'17.09"E, 26.IX.2018	MSI29191	OR640000
Ilocos Sur, Santiago, Ambucao, 17°18'18.62"N, 120°25'17.09"E, 26.IX.2018	MSI29192	OR640001
Ilocos Sur, Santiago, Ambucao, 17°18'18.62"N, 120°25'17.09"E, 26.IX.2018	MSI29193	OR640002
La Union, Balaoan, Almeida, 16°49'11.19"N, 120°19'45.25"E, 27.IX.2018	MSI29194	OR640003
La Union, Balaoan, Almeida, 16°49'11.19"N, 120°19'45.25"E, 27.IX.2018	MSI29196	OR640004
La Union, Balaoan, Paraoir, 16°48'17.2656"N, 120°19'32.5992"E, 27.IX.2018	MSI29198	OR640005
La Union, Balaoan, Paraoir, 16°48'17.2656"N, 120°19'32.5992"E, 27.IX.2018	MSI29199	OR640006
La Union, Balaoan, Paraoir, 16°48'17.2656"N, 120°19'32.5992"E, 27.IX.2018	MSI29200	OR640007
La Union, Balaoan, Paraoir, 16°48'17.2656"N, 120°19'32.5992"E, 27.IX.2018	MSI29201	OR640008
La Union, Balaoan, Paraoir, 16°48'17.2656"N, 120°19'32.5992"E, 27.IX.2018	MSI29202	OR640009
La Union, Balaoan, Paraoir, 16°48'17.2656"N, 120°19'32.5992"E, 27.IX.2018	MSI29203	OR640010
La Union, San Fernando, Lingsat-MPA, 16°38'31.42"N, 120°18'21.56"E, 27.IX.2018	MSI29205	OR640011
La Union, San Fernando, Lingsat-MPA, 16°38'31.42"N, 120°18'21.56"E, 27.IX.2018	MSI29206	OR640012
Pangasinan, Bolinao, Patar, 16°18'0"N, 119°46'34.32"E, 26.X.2018	MSI29207	OR640013
Pangasinan, Bolinao, Patar, 16°18'0"N, 119°46'34.32"E, 26.X.2018	MSI29208	OR640014
Pangasinan, Bolinao, Patar, 16°18'0"N, 119°46'34.32"E, 26.X.2018	MSI29209	OR640015
Pangasinan, Bolinao, Estanza, 16°21'41.76"N, 119°50'26.7"E, 26.X.2018	MSI29210	OR640016

Appendix 1. — Continuation.

Species and collection details	Voucher	GenBank
Sargassum polycystum C.Agardh		
Pangasinan, Bolinao, Dos Hermanos, 16°25'46.46"N, 119°55'48.18"E, 9.III.2019	MSI29138	OR639946
Pangasinan, Bolinao, Dos Hermanos, 16°25'46.46"N, 119°55'48.18"E, 9.III.2019	MSI29139	OR639947
Pangasinan, Bolinao, Malilnep, 16°26'46.82"N, 119°56'23.41"E, 9.III.2019	MSI29140	OR639948
Ilocos Norte, Burgos, Bayog, 18°31'1.63"N, 120°35'4.33"E, 25.IX.2018	MSI29141	OR639949
Ilocos Norte, Burgos, Bayog, 18°31'1.63"N, 120°35'4.33"E, 25.IX.2018	MSI29142	OR639950
Ilocos Norte, Burgos, Bayog, 18°31'1.63"N, 120°35'4.33"E, 25.IX.2018	MSI29143	OR639951
Ilocos Norte, Burgos, Bayog, 18°31'1.63"N, 120°35'4.33"E, 25.IX.2018	MSI29144	OR639952
Ilocos Norte, Burgos, Bayog, 18°31'1.63"N, 120°35'4.33"E, 25.IX.2018	MSI29145	OR639953
Ilocos Norte, Burgos, Bayog, 18°31'1.63"N, 120°35'4.33"E, 25.IX.2018	MSI29146	OR639954
Ilocos Norte, Burgos, Bayog, 18°31'1.63"N, 120°35'4.33"E, 25.IX.2018	MSI29147	OR639955
Ilocos Norte, Burgos, Bayog, 18°31'1.63"N, 120°35'4.33"E, 25.IX.2018	MSI29148	OR639956
La Union, Balaoan, Almeida, 16°49'11.19"N, 120°19'45.25"E, 27.IX.2018	MSI29197	OR639957

Appendix 2. — Reported *Sargassum* C.Agardh species found in the northwestern area of the Philippines according to previous published literature.

Species	Ilocos Norte	Ilocos Sur	La Union	Pangasinan	
Sargassum acinaciforme Montagne	–	–	–	×	Modelo & Umezaki 1995
Sargassum angii L.M.Liao	×	–	–	–	Trono 1994
Sargassum angustifolium C.Agardh	×	–	–	×	Modelo & Umezaki 1995
Sargassum aquifolium (Turner) C.Agardh	×	–	–	×	As *S. crassifolium*: Trono & Lluisma 1990; Trono & Tolentino 1993 Modelo & Umezaki 1995; Ortiz & Trono 2000
Sargassum balingasayense Trono	–	–	–	×	Trono 1994
Sargassum carpophyllum J.Agardh	×	–	–	–	Modelo & Umezaki 1995; Hurtado & Ragaza 1999
Sargassum currimaoense G.C.Trono	×	–	–	–	Trono 1994
Sargassum feldmannii Pham-Hoàng Hô	–	–	–	×	Trono 1997
Sargassum glaucescens J.Agardh	×	–	×	–	Modelo & Umezaki 1995
Sargassum granuliferum C.Agardh	–	–	–	×	Modelo & Umezaki 1995
Sargassum hemiphyllum (Turner) C.Agardh	–	–	–	×	Trono 1997
Sargassum henslowianum C.Agardh	×	–	–	–	Modelo & Umezaki 1995
Sargassum herporhizum Setchell & N.L.Gardner	–	–	×	×	Modelo & Umezaki 1995
Sargassum ilicifolium (Turner) C.Agardh	×	–	–	×	Modelo & Umezaki 1995; Trono 1997; as *S. cristaefolium*: Trono & Lluisma 1990; Trono & Tolentino 1993; Modelo & Umezaki 1995; Hurtado & Ragaza 1999; Ortiz & Trono 2000; as *S. sandei*: Modelo & Umezaki 1995
Sargassum kushimotense Yendo	–	–	–	×	Trono 1992, 1997
Sargassum oligocystum Montagne	×	–	×	×	Trono & Lluisma 1990; Trono & Tolentino 1993; Modelo & Umezaki 1995; Trono 1997
Sargassum polycystum C.Agardh	×	–	×	×	Trono & Lluisma 1990; Trono 1992, 1997; Modelo & Umezaki 1995; Ortiz & Trono 2000; as *S. myriocystum*: Modelo & Umezaki 1995
Sargassum siliquosum J.Agardh	×	×	×	×	Trono 1992, 1997; Modelo & Umezaki 1995; Hurtado & Ragaza 1999