Marine algae of the Sulu Sea islands, Philippines III. Taxonomic account of the Gracilariaceae (Rhodophyta) from the Cuyo Islands

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ABSTRACT

The Cuyo Islands lie on the northern fringes of the vast Sulu Sea straddling between the westernmost Philippine island of Palawan and the central portion of the archipelago. A recent study revealed a high diversity of the benthic brown algae (Phaeophyceae) there. However, records of other algal groups like the green and red algae have been sporadic and few. This study is a survey of the representatives of the Gracilariaceae, a group of economically-important red algal species valued for its agar content. Collections were made by snorkeling and Scuba diving from shallow-water and subtidal habitats from 16 stations in six islands. Results revealed a total of five species of the Gracilariaceae distributed throughout the Cuyo Islands. As these species constitute a significant but untapped marine resource for commercial exploitation, the results of this survey will serve to provide useful baseline information for resource management, eventually contributing towards better livelihood generation and options in coastal villages.

Keywords: *Gracilaria*, *Gracilariocolax*, *Hydropuntia*, Palawan, seaweed, taxonomy

INTRODUCTION

Numerous islands, atolls and reefs are scattered throughout the vast expanses of the Sulu Sea on the western fringes of the Philippine archipelago. The most well-known among these are the uninhabited Tubbataha Reefs, a pair of pristine atolls lying close to the geographic center of the Sulu Sea. Their biological importance as habitats for diverse marine life led to their inscription as a UNESCO World Heritage Site in 1993 and their inclusion in the Ramsar List of Wetlands of International Importance in 1999. On the other hand, the other island groups in the Sulu Sea are populated by people of varied ethnolinguistic backgrounds who mainly depend on the sea for daily subsistence through such activities as seaweed farming and fishing.

A historical account of seaweed taxonomic studies in the Sulu Sea islands covering the latter half of the 20th century was provided by Liao and Young (2002) who also compiled a comprehensive synoptic list of seaweeds from the Tubbataha Reefs. Since that first survey, two latter studies have been added. Liao et al. (2013) studied 17 species of benthic brown algae (Phaeophyceae) from the Cuyo Islands, many of them typical reef-dwelling species of the Dictyotaceae and the massive tropical species of *Sargassum* that frequently form extensive beds. Later, Santiañez et al. (2015) reported 176 species of seaweeds from another group of islands collectively called the Balabac Marine Biodiversity Conservation Corridor (BMBCC) located on the westernmost flanks of the Sulu Sea just off the southern tip of Palawan Island. Adjacent to the BMBCC is Bugsuk Island where an earlier seaweed survey was conducted and published by Trono and Ang (1982).

The Gracilariaceae is a large cosmopolitan group of marine red algae that is predominantly tropical in distribution. It consists traditionally of eight genera including both free-living and parasitic representatives, with the total number fluctuating and bloating to 13 genera in recent times due to continuing revisions based on morphological and molecular grounds (Liao and Hommersand 2003; Iyer et al. 2005; Yang and Kim 2015). Agar is the main commercial polysaccharide extracted from the cell wall of species of the Gracilariaceae and finds its use in the food and biotechnology industry. This has resulted in extensive efforts to harvest raw materials from natural stocks or its cultivation particularly near estuarine habitats around Southeast Asia (Guanzon and De Castro 1992).

This study serves to document the diversity and distribution of species of the Gracilariaceae found in the Cuyo Islands by providing morphological information that will help with species identification. The information represents a contribution towards producing a list of species with potential economic importance that can guide resource management planning. The same information will also contribute data to the knowledge of the taxonomy and phytogeography of the Gracilariaceae in the Philippines.

METHODS

Study Sites

The Cuyo Islands form part of the political province of Palawan and is comprised of three municipalities namely, Agutaya, Cuyo and Magsaysay. Six islets were visited, and 16 sampling stations were established. The details of the collecting sites and dates can be found in Liao et al. (2013).

Collection and Identification

Samples were collected by snorkeling and Scuba diving and taken to the laboratory for processing. Part of the samples were pressed to make herbarium specimens while some were preserved in 5% formalin-seawater solution for anatomical studies. Hand sections with double-edged razor blades were made to observe internal anatomy under a compound microscope. All prepared voucher specimens (herbarium materials) were distributed for permanent deposition in ten Philippine and foreign herbaria. For the complete list, refer to Liao et al. (2013). Various taxonomic references and authentic herbarium materials were examined for comparison. Specimens are assigned distinctive code numbers following the designated collecting site numbers as described earlier in Liao et al. (2013). For example, 78EM-43 (68-73) means materials were obtained from station 78EM-43 and consisted of six samples numbered serially from 68 to 73.

RESULTS AND DISCUSSION

Taxonomic Account

Artificial key to the species of the Gracilariaceae of the Cuyo Islands

1A Plants pustulate, occurring on surfaces of larger algae,
parasitic
1B Plants erect, attached to substrate by holdfast, free living 2
2A Thalli bearing distinct constrictions along the main axis
2B Thalli smooth throughout, without distinct constrictions
3A Thalli filiform, with faint constrictions at the base of
branches
3B Thalli robust, with prominent constrictions throughout the thalli, issued at
relatively uniform intervalsGracilaria salicornia
4A Branching prominently dichotomous, diameter of segments relatively uniform
throughout, up to 3 mm in diameter Gracilaria canaliculata
4B Branching irregular, becoming secund distally, diameter at the base
up to 5 mm, tapering into acute and bent tips Gracilaria arcuata

Gracilaria arcuata Zanardini

Zanardini 1858: 265, pl. 5, fig. 2 (type locality: Mari Rubro, or the Red Sea); Weber-van Bosse 1928: 429, fig. 173; Cordero 1977: 124, pl. XX, B, fig. 101; Cordero 1981: 55, fig. 18A; Trono et al. 1983: 32, fig. 7; Trono 1997: 208, fig. 133; Hurtado et al. 2006: 10, middle figure.

Illustrative materials: Tsutsui et al. 2005: 194, figs. 1-3; Lin 2009: 10, figs. 2a-c; Wang et al. 2015: 92.

Plants forming low tufts, to 7 cm tall, with some parts repent, attached to rocks and reef debris at several points; fronds terete, 4-5 mm in diameter at the base where faint constrictions may be observed occasionally, becoming slightly narrowed distally and markedly arcuate towards the tips; branching dichotomous to irregular, sometimes secund near the acute apices, intricate; medulla made up of loose cells, cuboidal, thin-walled, to 600 μ m in diameter; cortical cells two layers, oblong, arranged side by side on their longer sides.

Specimens examined: 78EM-14 (98-104); 78EM-16 (101-104); 78EM-18 (283-290, 517-523); 78EM-20 (277-279); 78EM-43 (68-73); 78EM-45 (183, 184)

Remarks: Materials examined are of two forms. One is the more common form that is well-branched, with distinctly arcuate and intricate tips like 78EM-14 (98-104) and 78EM-20 (277-279). This is the var. *snackeyi* Weber-van Bosse first described from Indonesia. The other form is less branched at the distal portions, with acute or round tips and inconspicuously arcuate like 78EM-16 (101-104) and 78EM-43 (68-73), thus approaching var. *arcuata*. The latter form was originally described from the Red Sea, and recorded mainly from the western Indian Ocean and the Mediterranean. It is much slender and elongated (as observed in authentic materials from Tunisia) than the Cuyo materials under study. It appears then that var. *snackeyi* is the most common form encountered in the East Indies.

Chang and Xia (1976) observed both forms in materials from the South China Sea. However, their text-fig. 13-1 labelled as var. *typica* (=arcuata) is no different from the var. *snackeyi* as illustrated by Weber-van Bosse (1928), while text-fig. 13-2 identified as var. *snackeyi* f. *rhizophora* Børgesen resembles closely var. *arcuata* except for its thicker diameter.

Gracilaria canaliculata Sonder

Sonder 1871: 56 (type locality: Wagap, New Caledonia); Calumpong and Meñez 1997: 179, middle figure; Trono 2004: 81, fig. 134.

Synonym: *Gracilaria crassa* Harvey ex J. Agardh 1876: 417; Cordero 1977: 127, figs. 108-110; Cordero 1981: 56, fig. 20A

Illustrative materials: Hurtado et al. 2006: 10, bottom figure; Coppejans et al. 2009: 168, figs. 10D, 23D, 135; Lin 2009: 14, figs. 4a, b.

Thalli consists of erect and prostrate portions, the latter appressed to small rocks and coral fragments and closely attached by hapters at many points; fronds terete, to 3 mm in diameter, marked by many faint

constrictions here and there, segments between constrictions smooth, segment tips tend to be slightly swollen and blunt; branching di- to trichotomous and irregular, angle of branching usually wide, between 60-90° with point of branching rarely marked off by constrictions; medullary cells polygonal in cross-section, to 500 μm across, diminishing in size towards the peripheries; cortical layer composed of small cells, ovoid, tightly packed, to 10 μm in diameter.

Specimens examined: 78EM-18 (291-296, 425, 515, 516)

Remarks: In the Philippines, this plant has almost always been reported under the name *Gracilaria crassa* Harvey ex J. Agardh, a name now considered as a junior synonym of *Gracilaria canaliculata* Sonder. The latter name, however, is not the earliest name given to this plant. Kützing (1868: 29) had first applied the name *Sphaerococcus canaliculatus* Kützing to it which unfortunately turned out to be a latter homonym of *S. canaliculatus* C. Agardh (1822: 260). Realizing this, Sonder (1871) proposed the present name which rendered the specific name of Kützing invalid and unusable.

Dawson (1954: 438) remarked about the constrictions in *G. canaliculata* (as *G. crassa*) saying that "younger stages" are "without regular constrictions, but develop as the plant matures, and these become more pronounced and the segments more elongated..." approaching the form of *Gracilaria salicornia* (C. Agardh) Dawson.

The first published report of *G. canaliculata* from the Philippines was made by Cantoria et al. (1951) in connection with a study on the pharmacopoeial properties of some marine algae. Upon examining the unpublished thesis of the first author on which this report was based, the specimens referred to as *G. canaliculata* are actually materials of *Hydropuntia eucheumatoides* (Harvey) Gurgel and Fredericq as shown in the photographs.

Gracilaria salicornia (C. Agardh) Dawson

Dawson 1954: 4, fig. 3 (type locality: Manila Bay); Galutira and Velasquez 1964: 506, pl. 5, figs. 15a, b, pl. 8, figs. 32a, b; Velasquez et al. 1971: 30, pl. 13, fig. 62; Cordero 1977: 132, pl. XIX, C, figs. 116-118; Vannajan and Trono 1978: 22, fig. 24; Cordero 1981: 57: pl. 38, fig. 22A; Trono et al. 1983: 23, figs. 3, 4b; Hurtado et al. 2006: 12, middle figure.

Basionym: Sphaerococcus salicornia C. Agardh 1820: pl. 8, figs. 1-4.

Synonyms: *Corallopsis salicornia* (C. Agardh) Greville 1830: 53. *Gracilaria cacalia* (J. Agardh) Dawson 1954: 2. *Corallopsis cacalia* J. Agardh 1852: 583.

Illustrative materials: Tsutsui et al. 2005: 197, top figures; Ohba et al. 2007: 93, top figures; Lee et al. 2015: 170, middle figures; Wang et al. 2015: 96, bottom figure.

Plants erect, up to 6 cm tall, attached by a single holdfast; fronds generally terete throughout, to 1.6 mm in diameter, the basal parts show inconspicuous constrictions at random portions, reclined, parts touching substrate developing short disc-tipped hapters, distal portions markedly constricted, composed of almost uniformly sized segments, clavate, with sharply tapered bases and inflated distal portions, to 4 mm in diameter, the broad apices depressed or lacunate, issuing 1-3 new branches from there, dichotomous or irregular; medulla composed of uniformly thin-walled cells, ovoid, 250-300 µm in diameter, progressively smaller distally; cortical cells composed of 2-3 layers, ovoid, 7-10 µm in diameter.

Specimens examined: 78EM-12 (105-112); 78EM-13 (170-176); 78EM-20 (272-276); 78EM-45 (185-195)

Remarks: This species is distinctive among species of *Gracilaria* in having well-defined deep constrictions spaced apart along the main axis, producing a series of clavate segments. This unique feature was used to erect a segregate genus Corallopsis within the Gracilariaceae with C. salicornia as its type species. However, upon examination of vegetative and reproductive structures of *C. salicornia*, it was concluded that they are similar with those found in the generitype of *Gracilaria*, *G. compressa* and thus should remain within the genus (Liao and Hommersand 2003). G. cacalia is often regarded as an intermediate form between G. canaliculata and G. salicornia, distinguished only by the degree of constrictions on the thallus, i.e., faint constrictions in the former while deep and well-defined constrictions in the latter. Lin (2009: 24, figs. 8a-b) studied a sample from southern Taiwan identified as G. salicornia but which resembled the form of G. cacalia as did Coppejans et al. (2009: 172, fig. 139) in samples from Sri Lanka. Another species G. minor (Sonder) Durairatnam is characterized by fronds that are "stalked below soon becoming constricted and articulated above" (Durairatnam 1961: 64). Some phycologists have recognized G. minor as a variety under G. salicornia, while others have suggested the conspecificity of the two (Womersley and Bailey 1970). Xia (1986) listed several species as synonyms of G. salicornia including G. cacalia, G. minor, among others.

Trono and Ganzon-Fortes (1980) described two ecological forms of *G. salicornia* from Batangas: one form inhabiting areas with strong water

movement shows less prominent constrictions approaching the morphology of *G. cacalia*, while another one growing in calmer waters show strong constrictions typically seen in *G. salicornia*. It is clear that this species shows morphological plasticity contributing to its complicated taxonomic history.

Gracilariocolax sp.

Illustrative materials: Yamamoto 1986: 281 (as *Congracilaria babae*); Yamamoto 1991: 381 (as *Congracilaria babae*); Lin 2009: 6, figs. 1a-c (as *Congracilaria babae*).

Plants minute, parasitic, attached to the surface of host alga ($Gracilaria\ salicornia$) in random places, but more commonly on older parts; irregularly globose, mushroom-shaped, often in loose aggregates, pigmented, subtended by short stalks which are up to 700 μ m in diameter.

Specimens examined: 78EM-13 (170-176)

Remarks: This adelphoparasitic species is widely reported around Southeast Asia as *Congracilaria babae* Yamamoto (Yamamoto 1991; Yamamoto and Phang 1997; Kongkittayapun and Chirapart 2011) growing on a specific host alga, *Gracilaria salicornia*. It has also been reported to occur on *Hydropuntia edulis* (S.G. Gmelin) Gurgel and Fredericq (=*Gracilaria edulis*) collected from Indonesian waters (Gerung et al. 1999) and on *Hydropuntia* sp. from East Malaysia (Ng et al. 2014).

Weber-van Bosse (1928) established the new genus *Gracilariocolax* to accommodate a parasitic species associated with Gracilaria collected from Java. In addition, she described a few other parasitic species under the genus Gracilariophila. Very little is known about parasitic species on Gracilaria until Yamamoto (1986) described another species under his newly proposed genus Congracilaria which he recognized as being distinct because of the production of bisporangia as opposed to tetrasporangia in *Gracilariocolax*, among other characters. Later, Ng et al. (2013) noted that the distinction between bisporangia and tetrasporangia in Congracilaria Gracilariocolax was superfluous. Furthermore, molecular analysis revealed that Congracilaria was nestled within the Gracilaria sensu stricto clade, and supported its recognition as a species of *Gracilaria* by Ng et al. (2014), effectively subsuming the genus Congracilaria under Gracilaria.

Gerung and Yamamoto (2002) opined that the genus *Gracilariophila* is restricted to the western coasts of North America and specifically growing on species of *Gracilariopsis*. They went on to transfer all previously described species of *Gracilariophila* from Indonesia into *Gracilariocolax*, a move that is supported here. As a result, all parasitic species on *Gracilaria* at least in

Southeast Asia should be recognized as species of *Gracilariocolax*. The placement of the samples from Cuyo Islands cannot be ascertained within the genus *Gracilariocolax* and must await further morphological studies.

Hydropuntia edulis (S.G. Gmelin) Gurgel and Frederica

Silva 1952: 293; Cordero 1977: 128, fig. 111; Trono 1997: 210, fig. 134; Hurtado et al. 2006: 11, bottom figure.

Basionym: *Fucus edulis* S.G. Gmelin 1768: 113 (type locality: East Indies, probably Ambon in Maluku province, Indonesia)

Synonyms: Gracilaria edulis (S.G. Gmelin) Silva 1952: 293.

Gracilaria coronopifolia of Filipino authors [not J. Agardh 1852: 592]; Galutira and Velasquez 1964: 508, pl. 5, fig. 14, pl. 9, fig. 34; Cordero 1977: 127, pl. XX, A, figs. 104, 104a; Trono et al. 1983: 20, figs. 2, 9b

Gracilaria verrucosa of Filipino authors [not (Hudson] Papenfuss 1950: 195, rejected name (=Gracilariopsis longissima (S.G. Gmelin) Steentoft, Irvine & Farnham)]; Galutira and Velasquez 1964: 507, pl. 4, fig. 13, pl. 8, fig. 33; Villones and Magdamo 1968: 29, fig. 29; Velasquez et al. 1971: 30, pl. 13, fig. 61; Cordero 1977: 135; Vannajan and Trono 1978: 22, fig. 18; Cordero 1981: 59, fig. 39; Trono et al. 1983: 17, figs. 1, 4a

Gracilaria confervoides (Linnaeus) Greville 1830: liv, 123; illegitimate name; Montagne 1844: 662

Illustrative materials: Calumpong and Meñez 1997: 178, bottom figure (as *Gracilaria verrucosa*); Lin 2009: 33, figs. 11a-d (as *Hydropuntia edulis*); Lee et al. 2015: 169, middle figures (as *Hydropuntia edulis*); Wang et al. 2015: 94.

Plants bushy, erect, sometimes entangled, 8-15 cm tall, attached by single disc-like holdfasts; fronds terete, to 1.5 mm in diameter, to 300 μm broad at the ultimate branchlets, branching irregular, often essentially dichotomous or secund, more pronounced and frequent towards the tips, often resulting in crowded corymbose apical portions, commonly of uniform diameter, tapering gently towards the apical parts, at times with inconspicuous and shallow constrictions at the base; branchlets fine and filiform issued randomly on main axis, widely scattered, more evident near the tips; medullary cells thin-walled, ovoid, 200-260 μm in diameter, decreasing in size abruptly towards the peripheries; cortical cells forming 2-3 layers, elongate to cuboidal, arranged side by side, to 10 μm across.

Specimens examined: 78EM-12 (101-104); 78EM-13 (150-165); 78EM-20 (280-295, 295A)

Remarks: For the longest time, species of Gracilaria that are uniformly slender and terete and exhibiting hair-like thalli have been identified as Gracilaria verrucosa (Hudson) Papenfuss for lack of better diagnostic characters and for reasons of convenience. As a result, G. verrucosa was considered a cosmopolitan species that occurs in virtually all localities in the tropical and temperate regions, until Steentoft et al. (1995) examined historic materials as well as fresh materials obtained from the type locality in the U.K. Today G. verrucosa is a rejected name and materials formerly associated with this name are recognized under Gracilariopsis longissima (S.G. Gmelin) Steentoft, Irvine & Farnham with its distribution limited to western Europe. For a full discussion of this complicated nomenclatural history, see Steentoft et al. (1995). Species from East and Southeast Asia and the Pacific formerly known as G. verrucosa have now been renamed as Hydropuntia edulis (S.G. Gmelin) Gurgel and Frederica or described as new species.

Gracilaria coronopifolia J. Agardh is a species first described from Hawaii and has been reported from many Philippine localities. These previous reports should be carefully re-examined. It resembles *G. edulis* in having uniformly slender main axes that are branching repeatedly into acute tips. *G. coronopifolia* branches more frequently in distal portions resulting to a corymbose shape as seen by Cordero (1977: 127, pl. XX, A) in one sample from Siquijor which needs to be re-studied. Yamamoto et al. (1999) observed spermatangial conceptacles from cultured samples of Philippine materials identified as *G. coronopifolia* and found them to be different from those in materials from Hawaii which is the type locality of *G. coronopifolia*. They concluded that *G. coronopifolia* does not occur in the western Pacific region and may be restricted only to the Hawaiian archipelago. Furthermore, authentic *G. coronopifolia* may not be present in the Philippines as it was not among the species recorded in the treatise of Trono (1997, 2004).

GENERAL DISCUSSION

Among the three previous records of the Gracilariaceae from the Cuyo Islands (Liao et al. 2013), only one species, *Gracilaria blodgettii* Harvey, was not encountered in the present study. *G. blodgettii* was first reported by Cordero (1977) based on samples collected from Catadman Sound on Cuyo Island by G.T. Velasquez. To the current list of three species of the Gracilariaceae are added three new records: *G. canaliculata*, *Hydropuntia edulis* and *Gracilariocolax* sp., bringing the total number of known species to six.

The Gracilariaceae marine flora of the Cuyo Islands is relatively poor compared to nearby areas. Hurtado et al. (2006) recorded 11 species of Gracilariaceae from 11 sites around Panay Island about 150 km directly east

of the Cuyo Islands. Across the vast Sulu Sea about 650 km to the southwest of the Cuyo Islands lie Balabac island and a few islets around it. Santiañez et al. (2015) conducted a comprehensive survey there and found at least nine species of the Gracilariaceae. In another survey on two sites off the town of Bulusan, Sorsogon on mainland Luzon island, at least 14 species were documented by Kraft et al. (1999), one of the highest number recorded for a specific locality in the Philippines, and probably anywhere in Southeast Asia.

It seems that most species of the Gracilariaceae are euryhaline (Bird and McLachlan 1986) with many species better adapted to estuarine conditions where they have been found to produce high biomass. This euryhaline trait enabled some species like *Gracilaria vermiculophylla* (Ohmi) Papenfuss to become successful species for aquaculture and pollution management (Yokoya et al. 1999), and conferring invasive species traits to it. Furthermore, it was found to be highly resistant to desiccation, sand burial and herbivory further contributing to its colonizing and invading success (Thomsen and McGlathery 2007). As a matter of fact, *G. vermiculophylla* has dispersed into many habitats in Europe and on both the Pacific and Atlantic coasts of North America where it had colonized with much success.

While there are many euryhaline species of Gracilariaceae, it is not unlikely that there may also be stenohaline ones. This could partly explain the different species composition found in specific areas. For instance, G. salicornia may be characterized as a true marine species having been recorded from many truly marine habitats throughout its geographic range but conspicuously absent from areas subjected to wide salinity fluctuations, although Chirapart (2016) has observed that this species is remarkably tolerant to various environments. Many of the finer filiform species of Gracilaria like G. tenuistipitata Zhang and Xia, G. fisheri (Xia and Abbott) Abbott, Zhang and Xia and Gracilariopsis heteroclada Zhang and Xia, are more adapted to lower and fluctuating salinities commonly found in estuaries. The estuaries of the Asian continent, for example, in the Indo-Chinese region are particularly suitable for the growth of these species where there is a thriving industry based on harvesting biomass from natural stocks as well as from aquaculture. Such environments are not present in small islands like the Cuyo Islands where there are practically no large river systems that can create estuarine habitats. On larger islands like neighboring Panay and Luzon islands, some limited estuarine conditions might exist to allow the growth of these commercially-important species. The relatively low species number found in the Cuyo Islands may be partly attributed to the truly marine conditions occurring there that only allow stenohaline, marine species to grow. However, many species of the Gracilariaceae, just like other seaweed species, also show vulnerability to deteriorating environmental conditions. In Thailand, Chirapart (2016) noted that the diversity and biomass of some species of *Gracilaria* have declined as a result of environmental degradation.

The waters around the Cuyo Islands provide a truly marine environment free of large salinity (and temperature) fluctuations due to their isolated geographic position that is far away from the diluting influence of river systems usually associated with large islands and continental masses. The six species of Gracilariaceae thus far recorded from the Cuyo Islands have been documented from similar island environments that support more stable salinity and temperature regimes conducive for the growth and survival of stenohaline marine species.

The present report dealt with historical collections from about four decades ago. In addition, the collections were made during a short visit during the dry season months. It is therefore recommended that a year-round or at least seasonal collection be made to compare species found during the dry and rainy months as local microclimate conditions affecting marine communities may play an important role in the occurrence of species. It will also be of interest in this era of rapid environmental change to compare species diversity over the past decades (Liao and Bataan 2016) with collections from the present times providing telling indicators of the combined impact of natural and anthropogenic effects. In the Cuyo Islands, however, it is expected that the former would exert greater impact as the level of human activity there has not increased appreciably over the years to significantly and adversely alter the relatively pristine state of the marine environment observed there four decades ago. The information generated in this study can also provide baseline information useful for the management of economically-important species of the Gracilariaceae which are potential sources of agar. Combined with biomass and seasonality data, the harvest and culture of these species may be proposed as a feasible economic activity.

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REFERENCES

- Agardh CA. 1820. Species Algarum. Vol. 1, part 1. Lund., 1-168.
- Agardh CA. 1822. Species Algarum. Vol. 1, part 2. Lund., 169-398.
- Agardh JG. 1852. Species Genera et Ordines Algarum. Volumen Secundum: Algas Florideas Complectens. Part 2, fasc. 2. Lund., 505-700.
- Agardh JG. 1876. Species Genera et Ordines Algarum. Volumen Tertium: de Florideis curae posteriors. Part 1. Leipzig, 1-724.
- Bird CJ and McLachlan J. 1986. The effect of salinity on the distribution of *Gracilaria* Grev. (Rhodophyta, Gigartinales): An experimental assessment. Botanica Marina, 29: 231-238.
- Calumpong HP and Meñez EG. 1997. Field Guide to the Common Mangroves, Seagrasses and Algae of the Philippines. Bookmark, Makati City. 197pp.
- Cantoria MG, Velasquez GT and Valenzuela P. 1951. Pharmacopial properties of agar from three Philippine seaweeds. Journal of the Philippine Pharmaceutical Association, 38: 187-190.
- Chang JF and Xia BM. 1976. Studies on Chinese species of *Gracilaria*. Studia Marina Sinica (in Chinese, with English abstract), 11: 91-166.
- Chirapart A. 2016. Transition of species composition, abundance and distribution of the gracilarioid seaweeds (Rhodophyta) in coastal areas of the upper Gulf of Thailand observed from 2004 to 2007. Natural History Bulletin of the Siam Society, 61: 71-88.
- Coppejans E, Leliaert F, Dargent O, Gunasekara R and De Clerck O. 2009. Sri Lankan seaweeds, methodologies and field guide to the dominant species. ABC Taxa, 6: 1-265.
- Cordero PA. 1977. Studies on Philippine marine red algae. Special Publications from the Seto Marine Biological Laboratory, Kyoto University, 4: 1-258.
- Cordero PA. 1981. Taxonomy and distribution of Philippine useful seaweeds. National Research Council of the Philippines Bulletin, 81: 1-78.
- Dawson EY. 1954. Notes on tropical Pacific marine algae. Bulletin of the Southern California Academy of Sciences, 53: 1-7.
- Durairatnam M. 1961. Contribution to the study of marine algae of Ceylon. Fisheries Research Station, Ceylon, Bulletin, 10: 1-181.
- Galutira EC and Velasquez GT. 1964. Taxonomy, distribution and seasonal occurrence of edible marine algae in Ilocos Norte, Philippines. Philippine Journal of Science, 92: 483-522.
- Gerung GS, Terada R, Yamamoto H and Ohno M. 1999. An adelphoparasite on *Gracilaria edulis* (Gracilariaceae Rhodophyta) from Manado, Indonesia. In: Abbott IA (ed). Taxonomy of Economic Seaweeds with Reference to Some Pacific Species, vol. VII. California Sea Grant College System, University of California, La Jolla,131-136.
- Gerung GS and Yamamoto H. 2002. The taxonomy of parasitic genera growing on *Gracilaria* (Rhodophyta, Gracilariaceae). In: Abbott IA

- and McDermid K (eds). Taxonomy of Economic Seaweeds with Reference to Some Pacific Species, vol. VIII. California Sea Grant College Program, University of California, San Diego, La Jolla, 209-213.
- Gmelin SG. 1768. Historia Fucorum. St. Petersburg. 239pp.
- Greville RK. 1830. Algae Britannicae. Edinburgh. 218pp.
- Guanzon NG and De Castro TR. 1992. The effects of different stocking densities and some abiotic factors on cage culture of *Gracilaria* sp. (Rhodophyta, Gigartinales). Botanica Marina, 35: 239-243.
- Hurtado AQ, Luhan MRJ and Guanzon NG. 2006. Seaweeds of Panay, 2nd ed. Aquaculture Department, Southeast Asian Fisheries Development Center, Tigbauan, Iloilo. 50pp.
- Iyer R, Tronchin EM, Bolton JJ and Coyne VE. 2005. Molecular systematics of the Gracilariaceae (Gracilariales, Rhodophyta) with emphasis on southern Africa. Journal of Phycology, 41: 672-684.
- Kongkittayapun N and Chirapart A. 2011. Morphometric and molecular analysis of *Gracilaria salicornia* and its adelphoparasite in Thailand. Science Asia, 37: 6-16.
- Kraft GT, Liao LM, Millar AJK, Coppejans EGG, Hommersand MH and Freshwater DW. 1999. Marine benthic red algae (Rhodophyta) from Bulusan, Sorsogon province, southern Luzon, Philippines. Philippine Scientist, 36: 1-50.
- Kützing FT. 1868. Tabulae Phycologicae, Vol. 18. Nordhausen. 35pp.
- Lee AC, Baula IU, Miranda LN and Sin TM. 2015. A Photographic Guide to the Marine Algae of Singapore. Tropical Marine Science Institute, National University of Singapore, Singapore. 201pp.
- Liao LM and Bataan DAU. 2016. Reclaiming the past in understanding the present: Documenting environmental change in coastal ecosystems using seaweed herbarium specimens. In: Proceedings of the International Symposium of Human, Culture and Nature Explored with University Museum Collections, Vietnam National University, Hanoi, 73-76.
- Liao LM, Belleza DFC and Geraldino PJL. 2013. Marine algae of the Sulu Sea Islands, Philippines II: Annotated list of the brown seaweeds (Phaeophyceae) from the Cuyo Islands. Phytotaxa, 152: 1-17. DOI: http://dx.doi.org/10.11646/phytotaxa.152.1.1.
- Liao LM and Hommersand MH. 2003. A morphological study and taxonomic reassessment of the generitype species in the Gracilariaceae. Journal of Phycology, 39: 1207-1232.
- Liao LM and Young JG. 2002. Marine algae of the Sulu Sea Islands, Philippines I: Introduction, historical account and additional records from the Tubbataha reefs. Philippine Scientist, 39: 15-35.
- Lin SM. 2009. Marine Benthic Macroalgal Flora of Taiwan, Part I. Order Gracilariales (Rhodophyta). National Taiwan Ocean University, Keelung. 50pp.

- Montagne C. 1844. Plantae cellulares quas in insulis Philippinensibus a cl. Cuming collectae recensuit, observationibus non nullis descriptionibusque illustravit C. Montagne, D.M. London Journal of Botany, 3: 658-662.
- Ng P-K, Lim P-E, Kato A and Phang SM. 2013. Molecular evidence confirms the parasite *Congracilaria babae* (Gracilariaceae, Rhodophyta) from Malaysia. Journal of Applied Phycology, 26: 1287-1300.
- Ng P-K, Lim PE and Phang SM. 2014. Radiation of the red algal parasite *Congracilaria babae* onto a secondary host species, *Hydropuntia* sp. (Gracilariaceae, Rhodophyta). PLOS One, 9(5): e97450. DOI: 10.1371/journal.pone.0097450.
- Ohba H, Victor S, Golbuu Y and Yukihara H. 2007. Tropical Marine Plants of Palau. Palau International Coral Reef Center, Koror. 153pp.
- Papenfuss GF. 1950. Review of the genera of algae described by Stackhouse. Hydrobiologia, 2: 181-208.
- Santiañez WJE, Sariego RS and Trono GC. 2015. The seaweed flora of the Balabac Marine Biodiversity Conservation Corridor (BMBCC), southern Palawan, western Philippines. Plant Ecology and Evolution 148: 267-282. DOI: http://dx.doi.org/10.5091/plecevo. 2015.973.
- Silva PC. 1952. A review of nomenclatural conservation in the algae from the point of view of the type method. University of California Publications in Botany, 25: 241-323.
- Sonder OG. 1871. Die algen des tropischen Australiens. Abhandlungen aus dem Gebiete der Naturwissenschaften herausgegeben von dem Naturwissenschaftlichen Verein in Hamburg, 5: 33-74.
- Steentoft M, Irvine LM and Farnham WF. 1995. Two terete species of *Gracilaria* and *Gracilariopsis* (Gracilariales, Rhodophyta) in Britain. Phycologia, 34: 113-127.
- Thomsen MS and McGlathery KJ. 2007. Stress tolerance of the invasive macroalgae *Codium fragile* and *Gracilaria vermiculophylla* in a softbottom turbid lagoon. Biological Invasions, 9: 499-513.
- Trono GC. 1997. Field Guide and Atlas of the Seaweed Resources of the Philippines. Bookmark, Makati City. 306pp.
- Trono GC. 2004. Field Guide & Atlas of the Seaweed Resources of the Philippines, Vol. 2. Bureau of Agricultural Research and Marine Environment and Resources Foundation, Quezon City. 261pp.
- Trono GC and Ang PO. 1982. Marine benthic marine algae from Bugsuk Island and vicinity, Palawan, Philippines. Kalikasan, Philippine Journal of Biology, 11: 1-26.
- Trono GC, Azanza-Corrales R and Manuel D. 1983. The genus *Gracilaria* (Gigartinales, Rhodophyta) in the Philippines. Kalikasan, Philippine Journal of Biology, 12: 15-41.
- Trono GC and Ganzon-Fortes ET. 1980. An Illustrated Seaweed Flora of Calatagan, Batangas. Filipinas Foundation, Makati, Metro Manila. 114pp.

- Tsutsui I, Huynh QN, Nguyen HD, Arai S and Yoshida T. 2005. The Common Marine Plants of Southern Vietnam. Japan Seaweed Association, Tosa, Kochi. 250pp.
- Vannajan S and Trono GC. 1978. The marine benthic algae of Manila Bay. II. Phaeophyta and Rhodophyta. Kalikasan, Philippine Journal of Biology, 7: 7-30.
- Velasquez GT, Cornejo DF, Santiago AE and Arcega LB. 1971. Algal communities of exposed and unprotected marine waters of Batangas and Bataan. Philippine Journal of Science, 100: 1-40.
- Villones AI and Magdamo LG. 1968. A checklist of the littoral marine algae at Bagong Silang, Calatagan, Batangas. Philippine Biota, 3: 9-16, 24-30.
- Wang W-L, Liu SL and Li TH. 2015. Seaweeds of Dongsha Atoll in the South China Sea. Marine National Park Headquarters, Kaohsiung. 200pp.
- Weber van Bosse A. 1928. Listes des algues du Siboga. IV. Rhodophyceae. Troisième partie. Gigartinales et Rhodymeniales et tableu de la distribution des Chlorophycées, Phaeophycées at Rhodophycées de l'Archipel Malaisien. Siboga-Expeditie Monographie, 59d: 393-533.
- Womersley HBS and Bailey A. 1970. Marine algae of the Solomon Islands. Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences, 259: 257-352.
- Xia B. 1986. On *Gracilaria salicornia* (C. Agardh) Dawson. Chinese Journal of Oceanology and Limnology, 4: 100-106.
- Yamamoto H. 1986. *Congracilaria babae* gen. et sp. nov. (Gracilariaceae), an adelphoparasite growing on *Gracilaria salicornia* of Japan. Bulletin of the Faculty of Fisheries, Hokkaido University, 37: 281-290.
- Yamamoto H. 1991. Observation of the adelphoparasite *Congracilaria babae* Yamamoto (Gracilariaceae, Rhodophyta) of the Philippines. Sorui, Japanese Journal of Phycology, 39:381-384.
- Yamamoto H and Phang SM. 1997. An adelphoparasitic alga growing on *Gracilaria salicornia* from Malaysia. In: Abbott IA (ed). Taxonomy of Economic Seaweed Species with Reference to some Pacific and Caribbean Species. Vol. VI. California Sea Grant College Program, La Jolla, California, 91-96.
- Yamamoto H, Terada R and Muraoka D. 1999. On so-called *Gracilaria* coronopifolia from the Philippines and Japan. In: Abbott IA (ed). Taxonomy of Economic Seaweeds with Reference to some Pacific Species, vol. VII. California College Sea Grant System, University of California, La Jolla, 89-97.
- Yang MY and Kim MS. 2015. Molecular analyses for identification of the Gracilariaceae (Rhodophyta) from the Asia-Pacific region. Genes and Genomics, 37: 775-787. DOI:10.1007/s13258-015-0306-1.
- Yokoya NS, Kakita H, Obika H and Kitamura T. 1999. Effects of environmental factors and plant growth regulators on growth of the red alga *Gracilaria vermiculophylla* from Shikoku island, Japan. Hydrobiologia, 398: 339-347.

Zanardini G. 1858. Plantarum in mari Rubro hucusque collectarum enumeration (juvante A. Figari). Memorie del Reale Istituto Veneto di Scienze, Lettere ed Arti, 7: 209-309.

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