New, resurrected and redefined species of *Mastocarpus* (Phyllophoraceae, Rhodophyta) from the northeast Pacific

SANDRA C. LINDSTROM1*, JEFFERY R. HUGHEY2 AND PATRICK T. MARTONE1

1Department of Botany, 3529-6270 University Blvd, University of British Columbia, Vancouver V6T 1Z4, Canada
2Division of Science and Mathematics, Hartnell College, Salinas, California 93901, USA


Recent molecular phylogenetic investigations of the red algal genus *Mastocarpus* from the northeast Pacific resolved numerous cryptic species. Although species were clearly defined through genetic analyses, the correct names to apply to the species remained unclear due to both morphological variability within species and morphological similarity between species. To determine the appropriate name for each entity, we analyzed DNA from type material of taxa previously ascribed to *Mastocarpus*. In combination with this analysis, an updated phylogeny based on a broad range of geographical and morphological collections is presented that includes data from nuclear (ribosomal internal transcribed spacers [ITS]), chloroplast (*rbcL*) and mitochondrial [cytochrome oxidase I (COI)] genomes. By analyzing partial ITS region sequences of type specimens, we are able to match currently accepted names (*Mastocarpus papillatus*, *M. pacificus* and *M. jardinii*) to modern collections. We resurrect the following specific epithets and propose the new combinations *Mastocarpus cristatus*, *Mastocarpus latissimus* and *Mastocarpus agardhii*, and we create new species for which we were unable to verify an existing name: *Mastocarpus alakensis*, *Mastocarpus intermedius*, *Mastocarpus vancouveriensis*, *Mastocarpus californianus* and *Mastocarpus rigidus*. The species formerly included in *M. papillatus* are now identified as *Mastocarpus alakensis*, *M. papillatus*, *Mastocarpus intermedius*, *Mastocarpus cristatus*, *Mastocarpus vancouveriensis* and *Mastocarpus latissimus*. The name *M. jardinii* applies to a species thus far collected only from Moss Beach in San Mateo County and the Monterey Peninsula, both in California.Specimens other than the type previously assigned to *M. jardinii* are now separated into three species: *Mastocarpus rigidus*, *Mastocarpus californianus* and *Mastocarpus agardhii*. *Mastocarpus cristatus* represents a species closely allied to Clade 3 (*Mastocarpus intermedius*), and *M. pacificus* represents Clade 7. Morphological and anatomical diagnoses, along with vertical distributions and geographic ranges, are provided for each species.

**KEY WORDS**: Biogeography, COI, ITS, *Mastocarpus*, Pacific North America, Phylogeny, *rbcL*, Rhodophyta, Species, Taxonomy, Type material

INTRODUCTION

The genus *Mastocarpus* Kützing 1843 was originally established to accommodate four cartilaginous ‘Gigartinae’ with stipitate, frequently divided thalli and protruding cystocarpic papillae. Kützing’s proposal, however, was dismissed by J. Agardh (1851, 1876, 1899), who retained all of the *Mastocarpus* species in Gigartina Stackhouse 1809. Setchell & Gardner (1933) later resurrected the name but at the rank of subgenus, as *Mastocarpus* (Kützing) Setchell & N.L. Gardner, effectively lectotypifying the Kützing genus when they chose *Gigartina mamillosa* (Goodenough & Woodward) J. Agardh as the ‘typical species’. *Mastocarpus* went without treatment until Guiry et al. (1984) reinstated the genus based on morphological, life history and biochemical features. These features included ‘channelled’ gametophytic thalli with female reproductive structures and carposporophytes borne in papillae and a heteromorphic (or direct) life history with the crustose *Petrocelis*-like tetrasporophyte phase producing tetrasporangia singly. The reinstatement has been supported by molecular analyses (Fredericq & Lopez-Bautista 2002; Lindstrom 2008a; LeGall & Saunders 2010).

The number of *Mastocarpus* species recognized worldwide at the time of Setchell & Gardner (1933, as subgenus *Mastocarpus*) was 17. Of those, 12 were distributed in Pacific North America. Abbott (1972) reduced all but two names (*Gigartina agardhii* Setchell & N.L. Gardner, *Gigartina jardinii* J. Agardh) into synonymy under *Gigartina papillata* (C. Agardh) J. Agardh. In support of this reduction, she noted that intermediate characters between the different species were common, and sometimes characters attributed to more than one species appeared on a single thallus. West et al. (1978) recognized *Gigartina papillata* as a distinct entity and on the basis of priority placed *Gigartina agardhii* into synonymy under *Gigartina jardinii*.

Recent molecular studies on species of *Mastocarpus* from the northeast Pacific (Lindstrom 2008a) identified five distinct *Mastocarpus papillatus* clades (species) and a single, strongly supported clade containing *Mastocarpus jardinii*. Unfortunately, no reliable morphological distinctions were discernible among the species identified as *Mastocarpus papillatus*, and although a lengthy list of names extending back to *Sphaerococcus papillatus* C. Agardh (1821) was provided, it was unclear which names to apply to which clades (Lindstrom 2008a). The present study expands on the northeast Pacific data set of Lindstrom (2008a) by...
including more samples from a wider geographic area and sequences of the chloroplast large subunit of the ribulose-1, 5-bisphosphate carboxylase/oxygenase (\textit{rbcL}) gene, the mitochondrial cytochrome oxidase I (COI) gene and the nuclear internal transcribed spacer region (ITS1, 5.8S rRNA gene and ITS2). Here we assign names to clades by performing genetic analyses on type material (Hughes et al. 2001, 2002). In addition, we present distributional, ecological and morphological data to aid in the delineation and identification of the northeast Pacific species of \textit{Mastocarpus}.

**MATERIAL AND METHODS**

**DNA analysis of newly collected material**

DNA extraction, amplification and sequencing of ITS and \textit{rbcL} genes followed the procedures in Lindstrom (2008a). The primer pair ITS1-J60 was used to amplify and sequence the complete ITS region including the 5.8S rRNA gene (Lindstrom 2008a), and the primer pair F57-RbcSst was used to produce 1356 bp of the \textit{rbcL} gene (Freshwater \\& Ruinen 1994). Amplification and sequencing of 665 bp at the 5' end of the COI gene followed Saunders (2005) using primers GazF1 and GazR1. Polymerase chain reaction (PCR) products were sequenced using the ABI Applied Biosystems (Foster City, California, USA) Big Dye Terminator V.3.1 cycle sequencing kit by the Nucleic Acid Protein Service Unit (University of British Columbia, Vancouver, British Columbia, Canada).

**DATA ANALYSIS:** Fully alignable ITS, \textit{rbcL} and COI sequences from the specimens listed in Table 1 were concatenated and then subjected to maximum parsimony (MP), neighbour-joining (NJ) and maximum likelihood (ML) analyses using PAUP* 4.0b10 (Swofford 2002) following Lindstrom \\& Fredericq (2003). The generalized time-reversible model + I + G was determined to be the appropriate model of evolution for the ML analysis using the Akaike Information Criterion in Modeltest 3.7 (Posada \\& Crandall 1998). Model parameters included nucleotide frequencies $A = 0.2878$, $C = 0.1814$, $G = 0.2041$; substitution rates $A > C$ 1.7580, $A > G$ 6.5293, $A > T$ 0.6466, $C > G$ 1.1034, $C > T$ 12.9896; gamma shape parameter (G) = 0.6719 and proportion of invariable sites (I) = 0.5819. Bootstrap proportions were determined based on 10,000 replicates for MP, 1000 replicates for NJ and 100 replicates for ML. Because the specimens in the concatenated analysis represented a random assortment for which all three parts of the genome had been sequenced, we also analyzed all unique ITS genotypes (Table 1) using MP, NJ and ML analyses to determine whether the concatenated results were consistent with a much larger taxon sample. The transversion model + I + G was determined to be the appropriate model for this ML analysis with the following parameters: nucleotide frequencies $A = 0.2688$, $C = 0.2195$, $G = 0.2179$ and substitution rates $A > C$ 1.7592, $A > G$ 3.5976, $A > T$ 0.8863, $C > G$ 1.1063, $C > T$ 3.5976, $G = 0.7453$ and I = 0.3408.

**DNA analysis of type material**

**DNA EXTRACTION:** All extractions and amplifications of type material (Table 2) were performed in a laboratory at Hartnell College, Salinas, California, in which modern DNA from \textit{Mastocarpus} has not been analyzed. Standard negative controls were processed in parallel with type material to monitor for contamination from exogenous DNA. Extractions were carried out using the DNeasy Blood \\& Tissue Kit (Qiagen, Valencia, California, USA). Approximately 15 mg of dried tissue (~5 mm\textsuperscript{2} in size) was preincubated for 30 min at 56°C in a 1.7 ml microcentrifuge tube in a solution of 270 µl of Buffer A and 30 µl of Proteinase K. Partially digested samples were then ground with the wooden end of sterile swab and further incubated for 30 min to 2 h. Samples were centrifuged for 3 min at 8000 rpm to separate cellular debris from the supernatant. Two hundred microlitres of the supernatant (including any precipitate) was transferred to a new microcentrifuge tube containing 200 µl of ethanol (96–100%) and 200 µl Buffer AL. The resulting sample was mixed by pipetting, transferred to the DNeasy Mini spin column and then centrifuged for 90 s at 8000 rpm. For cases in which phycocollodids inhibited the flow-through of the supernatant, extended centrifugation at the same rate was carried out. The spin column was removed and placed in a new 2 ml collection tube and washed with 500 µl of Buffer AW1 by centrifugation for 1 min at 8000 rpm. The column was then placed in a new 2 ml collection tube and washed with 500 µl of Buffer AW2 by centrifugation for 3 min at 14,000 rpm. The DNA was eluted with 70 µl of Buffer AE for 5 min followed by centrifugation for 1 min at 8000 rpm.

**DNA AMPLIFICATION PROTOCOL:** For all PCR reactions, 6 µl of stock or 6 µl of diluted DNA (10-fold) served as template for 50 µl reactions following the protocol outlined in the TopTa\textsuperscript{TM} PCR Handbook using 10 µl of 5X Q-Solution (Qiagen). To eliminate competition from nonspecific fungal contaminants, a \textit{Mastocarpus} specific forward ITS 1 primer 5’ GGACATTTCGTAGTGGGATAGT 3’ was used in conjunction with the universal ITS 2 reverse primer (GCTGCGTTCTTCTCATCGATGC) designed by White et al. (1990). Reactions were run on a Perkin Elmer Cetus DNA Thermal Cycler (Waltham, Massachusetts, USA) with the following parameters: 94°C for 90 s, followed by 40 cycles of 94°C for 25 s, 53°C for 30 s and 72°C for 60 s and final extension of 72°C for 5 min. PCR products were purified using the QIAquick PCR Purification Kit following the manufacturer’s instructions (Qiagen). The samples were sequenced using both forward and reverse primers by Functional Biosciences, Inc. (Madison, Wisconsin, USA) and edited using Chromas Lite Version 2.01 (Technelysium Pty Ltd, Queensland, Australia).

**RESULTS**

Phylogenetic analysis of concatenated ITS, COI and \textit{rbcL} sequence data representing 43 ingroup and two outgroup taxa generated the ML phylogram in Fig. 1. With the
Table 1. Specimens of *Mastocarpus* sequenced, including extract number, collection data and GenBank and voucher accession numbers. Specimens for which all three genomes (COI, ITS and rbcL) were analyzed were used to construct Fig. 1. Sequences in brackets are from other studies.

<table>
<thead>
<tr>
<th>Extract number</th>
<th>Collection site and habitat</th>
<th>Date</th>
<th>Collector</th>
<th>COI acc.</th>
<th>ITS acc.</th>
<th>rbcL acc.</th>
<th>Voucher</th>
</tr>
</thead>
<tbody>
<tr>
<td>M5</td>
<td>Sunshine Cove, AK, high boulder</td>
<td>24 Jun. 2002</td>
<td>SCL</td>
<td>HQ437761</td>
<td>UBC A85244</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M8</td>
<td>Birch Bay, WA, mid to high cobble</td>
<td>03 Nov. 2001</td>
<td>SCL</td>
<td>DQ872469</td>
<td>UBC A85238</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M25</td>
<td>Rosario Beach, WA, mid</td>
<td>24 Jan. 2002</td>
<td>SCL</td>
<td>HQ437762</td>
<td>UBC A85253</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M42</td>
<td>Sunshine Cove, AK, high</td>
<td>24 Jun. 2002</td>
<td>SCL</td>
<td>HQ437769</td>
<td>UBC A85244</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M53</td>
<td>Moses Point, BC, high cobble</td>
<td>27 Apr. 2002</td>
<td>SCL</td>
<td>DQ872472</td>
<td>UBC A85239</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M57</td>
<td>Glencoe Cove, BC, high</td>
<td>27 Apr. 2002</td>
<td>SCL</td>
<td>HQ437763</td>
<td>UBC A85246</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M65</td>
<td>Port Hardy, BC, high intertidal</td>
<td>16 May 2003</td>
<td>SCL</td>
<td>HQ437708 DQ872670</td>
<td>UBC A85240</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M68</td>
<td>Miracle Beach, BC, high rock in sand</td>
<td>16 May 2003</td>
<td>SCL</td>
<td>DQ872471</td>
<td>UBC A85355</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M72</td>
<td>Sayward, BC, mid</td>
<td>18 May 2003</td>
<td>SCL</td>
<td>HQ437764</td>
<td>UBC A85245</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M134</td>
<td>Sitka, AK, low cobble</td>
<td>27 Jul. 2003</td>
<td>SCL</td>
<td>HQ437751</td>
<td>UBC A85254</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M136</td>
<td>Lantzville, BC, high</td>
<td>16 May 2003</td>
<td>SCL</td>
<td>HQ437765</td>
<td>UBC A85264</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M137</td>
<td>Hornby Island, BC, mid to high</td>
<td>29 Feb. 2004</td>
<td>VR</td>
<td>HQ437770</td>
<td>UBC A85249</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M161</td>
<td>Second Priest Rock, AK, high</td>
<td>05 Aug. 2004</td>
<td>SCL</td>
<td>HQ437770</td>
<td>UBC A85817</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M168</td>
<td>Triple Islets, BC, high</td>
<td>14 Sep. 2004</td>
<td>LG</td>
<td>HQ437752</td>
<td>UBC A88733</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M180</td>
<td>Beaver Harbour, BC, high mid</td>
<td>18 May 2003</td>
<td>SCL</td>
<td>HQ437753</td>
<td>UBC A85290 UBC A85291</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M181</td>
<td>Miracle Beach, BC, high rock in sand</td>
<td>16 May 2003</td>
<td>SCL</td>
<td>HQ437748</td>
<td>UBC A85355</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M187</td>
<td>Glencoe Cove, BC, high</td>
<td>27 Apr. 2002</td>
<td>SCL</td>
<td>DQ872468</td>
<td>UBC A85317</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M188</td>
<td>Birch Bay, WA, mid to high cobble</td>
<td>03 Nov. 2001</td>
<td>SCL</td>
<td>HQ437749</td>
<td>UBC A85238</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M191</td>
<td>Dupont, AK, mid</td>
<td>23 Jun. 2002</td>
<td>SCL</td>
<td>HQ437769</td>
<td>UBC A85288</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M193</td>
<td>Chugach Bay, AK, high</td>
<td>09 Jul. 2002</td>
<td>SCL</td>
<td>HQ437771</td>
<td>UBC A88736</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M200</td>
<td>Second Priest Rock, AK, high</td>
<td>05 Aug. 2004</td>
<td>SCL</td>
<td>HQ437772</td>
<td>UBC A85817</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M201</td>
<td>Second Priest Rock, AK, high</td>
<td>05 Aug. 2004</td>
<td>SCL</td>
<td>HQ437758</td>
<td>UBC A85817</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M255</td>
<td>Cape Ilktugtak, AK, mid</td>
<td>13 Jun. 2003</td>
<td>SCL</td>
<td>HQ437759</td>
<td>UBC A85284</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M261</td>
<td>Passage Island, AK, high intertidal</td>
<td>30 Jun. 2003</td>
<td>MRL</td>
<td>HQ437709 HQ437768</td>
<td>UBC A85281</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M263</td>
<td>Judith Island, AK</td>
<td>28 Jun. 2003</td>
<td>MRL</td>
<td>HQ437773</td>
<td>UBC A88740</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M292</td>
<td>NW Olympic Peninsula, WA, mid boulder</td>
<td>31 May 2003</td>
<td>SCL</td>
<td>EU186040</td>
<td>UBC A85279</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M298</td>
<td>Monashka Bay, AK, high</td>
<td>19 May 2005</td>
<td>SCL</td>
<td>HQ437774</td>
<td>UBC A88741</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M299</td>
<td>Afognak Island, AK, high</td>
<td>25 May 2005</td>
<td>SCL</td>
<td>HQ437754</td>
<td>UBC A85350</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M305</td>
<td>Near Island, AK, mid boulder</td>
<td>20 May 2005</td>
<td>SCL</td>
<td>HQ437775</td>
<td>UBC A85347</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M317</td>
<td>Spruce Island, AK, high</td>
<td>29 May 2005</td>
<td>SCL</td>
<td>HQ437776</td>
<td>UBC A88742</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M354</td>
<td>Tigalda Bay, AK</td>
<td>02 Jul. 2006</td>
<td>MRL</td>
<td>HQ437755</td>
<td>UBC A88743</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M361</td>
<td>Peacock Point, AK</td>
<td>14 Jul. 2006</td>
<td>MRL</td>
<td>HQ437777</td>
<td>UBC A85833</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M362</td>
<td>Tigalda Bay, AK</td>
<td>02 Jul. 2006</td>
<td>MRL</td>
<td>HQ437778</td>
<td>UBC A88536</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M382</td>
<td>Butze Rapids, BC, low intertidal</td>
<td>17 Jun. 2007</td>
<td>SCL</td>
<td>HQ437710 HQ437750</td>
<td>UBC A88520</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M394</td>
<td>Harpso Point, AK, high</td>
<td>29 Jun. 2007</td>
<td>MRL</td>
<td>HQ437759</td>
<td>UBC A85838</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M459</td>
<td>Akun Bay, AK, low boulder</td>
<td>13 Jun. 2008</td>
<td>SCL</td>
<td>HQ437760</td>
<td>UBC A88503</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M462</td>
<td>Sunset Beach, OR, high</td>
<td>06 Apr. 2008</td>
<td>SCL</td>
<td>HQ437781</td>
<td>UBC A88493</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M463</td>
<td>Sunset Beach, OR, mid</td>
<td>06 Apr. 2008</td>
<td>SCL</td>
<td>HQ437782</td>
<td>UBC A88498</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M464</td>
<td>Sunset Beach, OR, high</td>
<td>06 Apr. 2008</td>
<td>SCL</td>
<td>HQ437783</td>
<td>UBC A88497</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M468</td>
<td>Crescent City, CA, high</td>
<td>06 Apr. 2008</td>
<td>SCL</td>
<td>HQ437789</td>
<td>UBC A88503</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M500</td>
<td>Pearse Island, BC, high</td>
<td>24 May 2009</td>
<td>SCL</td>
<td>HQ437766</td>
<td>UBC A87901</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M511</td>
<td>Malcolm Island, BC, mid boulder</td>
<td>28 May 2009</td>
<td>SCL</td>
<td>HQ437767</td>
<td>UBC A88459</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M516</td>
<td>Walter’s Island, Kyuquot Sound, BC</td>
<td>26 May 2009</td>
<td>PTM</td>
<td>HQ437756</td>
<td>UBC A88756</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M528</td>
<td>Trinidad, CA, mid boulder</td>
<td>14 Feb. 2010</td>
<td>SCL</td>
<td>HQ437757</td>
<td>UBC A88465</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*Mastocarpus papillatus* (Clade 2)

<table>
<thead>
<tr>
<th>Extract number</th>
<th>Collection site and habitat</th>
<th>Date</th>
<th>Collector</th>
<th>COI acc.</th>
<th>ITS acc.</th>
<th>rbcL acc.</th>
<th>Voucher</th>
</tr>
</thead>
<tbody>
<tr>
<td>M1</td>
<td>Clover Point, BC, mid</td>
<td>27 Apr. 2002</td>
<td>SCL</td>
<td>EU186041</td>
<td>UBC A85272</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M10</td>
<td>Baker Beach, Humboldt County, CA, high intertidal</td>
<td>25 May 2002</td>
<td>SCL</td>
<td>HQ437711 HQ437784</td>
<td>UBC A85271</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Extract number</td>
<td>Collection site and habitat</td>
<td>Date</td>
<td>Collector</td>
<td>COI acc.</td>
<td>ITS acc.</td>
<td>rbcL acc.</td>
<td>Voucher</td>
</tr>
<tr>
<td>----------------</td>
<td>----------------------------</td>
<td>------</td>
<td>-----------</td>
<td>----------</td>
<td>----------</td>
<td>-----------</td>
<td>---------</td>
</tr>
<tr>
<td>M104</td>
<td>Seppings Island, BC, mid</td>
<td>18 Apr. 2003</td>
<td>SCL</td>
<td>HQ437776</td>
<td></td>
<td>UBC A85120</td>
<td></td>
</tr>
<tr>
<td>M156</td>
<td>Low Arch, SW Farallon Island, CA</td>
<td>14 Apr. 2004</td>
<td>KD</td>
<td>HQ437772</td>
<td>EU186044</td>
<td>UBC A85820</td>
<td></td>
</tr>
<tr>
<td>M210</td>
<td>Agate Beach, CA</td>
<td>13 Jan. 1973</td>
<td>ARP</td>
<td>HQ437778</td>
<td></td>
<td>UC 1471472</td>
<td></td>
</tr>
<tr>
<td>M238</td>
<td>Baker Beach, CA, mid</td>
<td>25 May 2002</td>
<td>SCL</td>
<td>HQ437781</td>
<td>DQ872478</td>
<td>UBC A85318</td>
<td></td>
</tr>
<tr>
<td>M284</td>
<td>Golden Gardens, Seattle, WA, high riprap</td>
<td>30 May 2003</td>
<td>SCL</td>
<td>HQ437784</td>
<td>DQ872466</td>
<td>UBC A85276</td>
<td></td>
</tr>
<tr>
<td>M469</td>
<td>Crescent City, CA, high</td>
<td>06 Apr. 2008</td>
<td>SCL</td>
<td>HQ437786</td>
<td></td>
<td>UBC A88489</td>
<td></td>
</tr>
<tr>
<td>M471</td>
<td>Humboldt Bay jetty, CA, high</td>
<td>07 Apr. 2008</td>
<td>SCL</td>
<td>HQ437789</td>
<td></td>
<td>UBC A88487</td>
<td></td>
</tr>
<tr>
<td>M476</td>
<td>Cape Mendocino, CA, high</td>
<td>08 Apr. 2008</td>
<td>SCL</td>
<td>HQ437790</td>
<td></td>
<td>UBC A88495</td>
<td></td>
</tr>
<tr>
<td>M526</td>
<td>Moss Beach, San Mateo County, CA, high intertidal at rock/sand interface</td>
<td>16 Nov. 2009</td>
<td>KAM &amp; PTM</td>
<td>HQ437713</td>
<td>HQ437879</td>
<td>UC 1944776</td>
<td></td>
</tr>
<tr>
<td>M527</td>
<td>Moss Beach, CA</td>
<td>16 Nov. 2009</td>
<td>KAM</td>
<td>HQ437791</td>
<td></td>
<td>UC 1944779</td>
<td></td>
</tr>
<tr>
<td>M529</td>
<td>Trinidad, CA, mid boulder</td>
<td>14 Feb. 2010</td>
<td>SCL</td>
<td>HQ437792</td>
<td></td>
<td>UBC A88466</td>
<td></td>
</tr>
<tr>
<td>M357</td>
<td>Fort Bragg, CA, mid rock in sand</td>
<td>15 Feb. 2010</td>
<td>SCL</td>
<td>HQ437793</td>
<td></td>
<td>UBC A88437</td>
<td></td>
</tr>
<tr>
<td>M358</td>
<td>Point Arenas, CA, mid</td>
<td>16 Feb. 2010</td>
<td>SCL</td>
<td>HQ437794</td>
<td></td>
<td>UBC A88474</td>
<td></td>
</tr>
<tr>
<td>M359</td>
<td>Bodega Head, CA, high</td>
<td>16 Feb. 2010</td>
<td>SCL</td>
<td>HQ437795</td>
<td></td>
<td>UBC A88475</td>
<td></td>
</tr>
<tr>
<td>M360</td>
<td>Bodega Head, CA, mid</td>
<td>16 Feb. 2010</td>
<td>SCL</td>
<td>HQ437796</td>
<td></td>
<td>UBC A88476</td>
<td></td>
</tr>
<tr>
<td>M361</td>
<td>Bodega Head, CA, mid</td>
<td>16 Feb. 2010</td>
<td>SCL</td>
<td>HQ437797</td>
<td></td>
<td>UBC A88477</td>
<td></td>
</tr>
<tr>
<td>M362</td>
<td>Bodega Head, CA, mid</td>
<td>16 Feb. 2010</td>
<td>SCL</td>
<td>HQ437798</td>
<td></td>
<td>UBC A88478</td>
<td></td>
</tr>
<tr>
<td>M363</td>
<td>Bodega Head, CA, mid</td>
<td>16 Feb. 2010</td>
<td>SCL</td>
<td>HQ437799</td>
<td></td>
<td>UBC A88480</td>
<td></td>
</tr>
<tr>
<td>M364</td>
<td>Cambria, CA, mid</td>
<td>18 Feb. 2010</td>
<td>SCL</td>
<td>HQ437800</td>
<td></td>
<td>UBC A88481</td>
<td></td>
</tr>
<tr>
<td>M365</td>
<td>Pescadero State Beach, CA, high rock in sand</td>
<td>17 Feb. 2010</td>
<td>SCL</td>
<td>HQ437801</td>
<td></td>
<td>UBC A88508</td>
<td></td>
</tr>
</tbody>
</table>

*Mastocarpus intermedius* (Clades 3A & 3B)

<table>
<thead>
<tr>
<th>Extract number</th>
<th>Collection site and habitat</th>
<th>Date</th>
<th>Collector</th>
<th>COI acc.</th>
<th>ITS acc.</th>
<th>rbcL acc.</th>
<th>Voucher</th>
</tr>
</thead>
<tbody>
<tr>
<td>M2</td>
<td>Barkley Sound, BC, mid to low</td>
<td>10 Aug. 2002</td>
<td>SCL</td>
<td>HQ437819</td>
<td></td>
<td>UBC A85324</td>
<td></td>
</tr>
<tr>
<td>M11</td>
<td>Baker Beach, Humboldt County, CA, low intertidal boulder</td>
<td>25 May 2002</td>
<td>SCL</td>
<td>HQ437723</td>
<td>DQ872481</td>
<td>DQ872502</td>
<td>UBC A85235</td>
</tr>
<tr>
<td>M174</td>
<td>Triple Island, BC, mid intertidal</td>
<td>01 Sep. 2004</td>
<td>LG</td>
<td>HQ437724</td>
<td>EU186047</td>
<td>HQ437886</td>
<td>UBC A85833</td>
</tr>
<tr>
<td>M234</td>
<td>Birch Bay, WA, low</td>
<td>04 Jul. 2004</td>
<td>SCL</td>
<td>HQ437820</td>
<td></td>
<td>UBC A88739</td>
<td></td>
</tr>
<tr>
<td>M245</td>
<td>Whiffin Spit, BC, low intertidal boulder</td>
<td>03 Feb. 2002</td>
<td>SCL</td>
<td>HQ437825</td>
<td>EU186031</td>
<td>UBC A85823</td>
<td></td>
</tr>
<tr>
<td>M288</td>
<td>NW Olympic Peninsula, WA, low</td>
<td>31 May 2003</td>
<td>SCL</td>
<td>HQ437826</td>
<td></td>
<td>UBC A85296</td>
<td></td>
</tr>
<tr>
<td>M344</td>
<td>Cape Kaguayak, AK, low</td>
<td>25 Jun. 2005</td>
<td>SCL</td>
<td>HQ437821</td>
<td></td>
<td>UBC A88513</td>
<td></td>
</tr>
<tr>
<td>M375</td>
<td>Ventura Beach, CA, low intertidal riprap</td>
<td>10 Nov. 2007</td>
<td>SCL</td>
<td>HQ437826</td>
<td>HQ437815</td>
<td>HQ437887</td>
<td>UBC A88510</td>
</tr>
<tr>
<td>M378</td>
<td>Ventura Beach, CA, low intertidal riprap</td>
<td>10 Nov. 2007</td>
<td>SCL</td>
<td>HQ437727</td>
<td>HQ437816</td>
<td>HQ437888</td>
<td>UBC A88510</td>
</tr>
<tr>
<td>M407</td>
<td>Hopkins Marine Station, Pacific Grove, CA, mid intertidal</td>
<td>07 Jan. 2008</td>
<td>PTM</td>
<td>HQ437817</td>
<td>HQ437890</td>
<td>UBC A88558</td>
<td></td>
</tr>
<tr>
<td>M440</td>
<td>Pacific Grove, CA, high</td>
<td>31 Dec. 2007</td>
<td>PWG</td>
<td>HQ437822</td>
<td></td>
<td>UBC A88548</td>
<td></td>
</tr>
<tr>
<td>M473</td>
<td>Cape Mendocino, CA, upper mid</td>
<td>08 Apr. 2008</td>
<td>SCL</td>
<td>HQ437804</td>
<td></td>
<td>UBC A88483</td>
<td></td>
</tr>
<tr>
<td>M474</td>
<td>Mussel Rock, Cape Mendocino, CA, low intertidal boulder</td>
<td>08 Apr. 2008</td>
<td>SCL</td>
<td>HQ437818</td>
<td>HQ437893</td>
<td>UBC A88485</td>
<td></td>
</tr>
<tr>
<td>M479</td>
<td>Van Damme State Park, CA, upper mid</td>
<td>09 Apr. 2008</td>
<td>SCL</td>
<td>HQ437824</td>
<td></td>
<td>UBC A88482</td>
<td></td>
</tr>
<tr>
<td>M550</td>
<td>Ensenada, Mexico</td>
<td>24 Feb. 2010</td>
<td>PWG</td>
<td>HQ437825</td>
<td></td>
<td>UBC A88550</td>
<td></td>
</tr>
</tbody>
</table>

*Mastocarpus cristatus* (Clade 3C)

<table>
<thead>
<tr>
<th>Extract number</th>
<th>Collection site and habitat</th>
<th>Date</th>
<th>Collector</th>
<th>COI acc.</th>
<th>ITS acc.</th>
<th>rbcL acc.</th>
<th>Voucher</th>
</tr>
</thead>
<tbody>
<tr>
<td>M406</td>
<td>Hopkins Marine Station, Pacific Grove, CA, high intertidal</td>
<td>07 Jan. 2008</td>
<td>PTM</td>
<td>HQ437728</td>
<td>HQ437804</td>
<td>HQ437889</td>
<td>UBC A88557</td>
</tr>
<tr>
<td>M408</td>
<td>Hopkins Marine Station, Pacific Grove, CA, low intertidal</td>
<td>07 Jan. 2008</td>
<td>PTM</td>
<td>HQ437730</td>
<td>HQ437805</td>
<td>HQ437891</td>
<td>UBC A88745</td>
</tr>
<tr>
<td>M410</td>
<td>Hopkins Marine Station, Pacific Grove, CA, low intertidal</td>
<td>07 Jan. 2008</td>
<td>PTM</td>
<td>HQ437731</td>
<td>HQ437806</td>
<td>HQ437892</td>
<td>UBC A88746</td>
</tr>
<tr>
<td>M416</td>
<td>Pacific Grove, CA, mid</td>
<td>07 Jan. 2008</td>
<td>PTM</td>
<td>HQ437807</td>
<td></td>
<td>UBC A88561</td>
<td></td>
</tr>
<tr>
<td>M417</td>
<td>Pacific Grove, CA, mid</td>
<td>07 Jan. 2008</td>
<td>PTM</td>
<td>HQ437808</td>
<td></td>
<td>UBC A88561</td>
<td></td>
</tr>
<tr>
<td>M421</td>
<td>Pacific Grove, CA, mid</td>
<td>07 Jan. 2008</td>
<td>PTM</td>
<td>HQ437809</td>
<td></td>
<td>UBC A88562</td>
<td></td>
</tr>
<tr>
<td>M426</td>
<td>Pacific Grove, CA, high</td>
<td>07 Jan. 2008</td>
<td>PTM</td>
<td>HQ437810</td>
<td></td>
<td>UBC A88557</td>
<td></td>
</tr>
<tr>
<td>Extract number</td>
<td>Collection site and habitat</td>
<td>Date</td>
<td>Collector</td>
<td>COI acc.</td>
<td>ITS acc.</td>
<td>rbcL acc.</td>
<td>Voucher</td>
</tr>
<tr>
<td>---------------</td>
<td>-----------------------------</td>
<td>------------</td>
<td>-----------</td>
<td>----------</td>
<td>----------</td>
<td>-----------</td>
<td>-----------</td>
</tr>
<tr>
<td>M427</td>
<td>Pacific Grove, CA, mid</td>
<td>07 Jan. 2008</td>
<td>PTM</td>
<td>HQ437811</td>
<td>UBC A88563</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M429</td>
<td>Pacific Grove, CA, mid</td>
<td>07 Jan. 2008</td>
<td>PTM</td>
<td>HQ437812</td>
<td>UBC A88563</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M431</td>
<td>Pacific Grove, CA, mid</td>
<td>07 Jan. 2008</td>
<td>PTM</td>
<td>HQ437813</td>
<td>UBC A88564</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><strong>Mastocarpus vancouveriensis</strong> (Clade 4)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>M50</td>
<td>Fishboat Bay, BC, mid boulder</td>
<td>29 Apr. 2002</td>
<td>SCL</td>
<td>DQ872483</td>
<td>UBC A85234</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M63</td>
<td>Sandy Beach, Sitka, AK, mid intertidal boulder/cobble</td>
<td>20 Apr. 2000</td>
<td>SCL</td>
<td>HQ437718</td>
<td>EU186048</td>
<td>HQ437882</td>
<td>UBC A85325</td>
</tr>
<tr>
<td>M224</td>
<td>China Beach, BC, low intertidal boulder</td>
<td>29 Apr. 2002</td>
<td>SCL</td>
<td>HQ437719</td>
<td>UBC A88738</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M287</td>
<td>Tongue Point, WA, low mid rock in sand</td>
<td>01 Jun. 2003</td>
<td>SCL</td>
<td>EU186050</td>
<td>UBC A85297</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M477</td>
<td>Cape Mendocino, CA, low rock near sand</td>
<td>08 Apr. 2008</td>
<td>SCL</td>
<td>HQ437827</td>
<td>UBC A88486</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><strong>Mastocarpus latissimus</strong> (Clade 5)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>M44</td>
<td>Chance Cove, AK</td>
<td>12 Jul. 2002</td>
<td>MRL</td>
<td>HQ437831</td>
<td>UBC A85338</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M66</td>
<td>Lantville, BC, mid</td>
<td>16 May 2003</td>
<td>SCL</td>
<td>DQ872492</td>
<td>UBC A85230</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M106</td>
<td>Shakun Islets, AK</td>
<td>16 Jun. 2003</td>
<td>SCL</td>
<td>HQ437832</td>
<td>UBC A85331</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M108</td>
<td>Kiukpaklik Island, AK, low</td>
<td>16 Jun. 2003</td>
<td>SCL</td>
<td>DQ872491</td>
<td>UBC A85231</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M109</td>
<td>Shakun Islets, AK</td>
<td>16 Jun. 2003</td>
<td>SCL</td>
<td>HQ437833</td>
<td>UBC A85329</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M110</td>
<td>Shakun Islets, AK, low</td>
<td>16 Jun. 2003</td>
<td>SCL</td>
<td>HQ437834</td>
<td>UBC A85330</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M129</td>
<td>Halibut Point, AK, low</td>
<td>02 Aug. 2003</td>
<td>SCL</td>
<td>HQ437835</td>
<td>UBC A85334</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M185</td>
<td>Sombrio Beach, BC, low</td>
<td>30 Apr. 2002</td>
<td>SCL</td>
<td>HQ437836</td>
<td>UBC A88734</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M189</td>
<td>Brockton Point, BC</td>
<td>08 Feb. 2002</td>
<td>CI7</td>
<td>HQ437837</td>
<td>UBC A88735</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M235</td>
<td>Baker Beach, CA, mid</td>
<td>25 May 2002</td>
<td>SCL</td>
<td>HQ437838</td>
<td>UBC A85319</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M241</td>
<td>Knoll Head, AK, low</td>
<td>28 Aug. 2004</td>
<td>SCL</td>
<td>HQ437839</td>
<td>UBC A85308</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M291</td>
<td>NW Olympic Peninsula, WA, low intertidal boulder</td>
<td>31 May 2003</td>
<td>SCL</td>
<td>HQ437820</td>
<td>HQ437828</td>
<td>EU186036</td>
<td>UBC A85298</td>
</tr>
<tr>
<td>M309</td>
<td>Cape Sitkinak, AK, low</td>
<td>24 Jun. 2005</td>
<td>SCL</td>
<td>EU186054</td>
<td>UBC A85352</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M386</td>
<td>Big Beach, Ucluelet, BC, low mid intertidal</td>
<td>18 May 2007</td>
<td>SCL</td>
<td>HQ437722</td>
<td>HQ437830</td>
<td>HQ437885</td>
<td>UBC A88504</td>
</tr>
<tr>
<td>M490</td>
<td>La Desembocadora de Bio Bio, Chile, mid</td>
<td>09 Nov. 2008</td>
<td>PWG</td>
<td>HQ437840</td>
<td>NCU 588649</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><strong>Mastocarpus rigidosus</strong> (Clade 6A)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>M3</td>
<td>Botany Bay, BC, mid intertidal</td>
<td>30 Apr. 2002</td>
<td>SCL</td>
<td>HQ437735</td>
<td>DQ872496</td>
<td>DQ872504</td>
<td>UBC A85227</td>
</tr>
<tr>
<td>M7</td>
<td>Baker Beach, CA</td>
<td>25 May 2002</td>
<td>SCL</td>
<td>DQ872495</td>
<td>UBC A85385</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M38</td>
<td>Fishboat Bay, BC, mid boulder</td>
<td>29 Apr. 2002</td>
<td>SCL</td>
<td>DQ872497</td>
<td>UBC A85228</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M64</td>
<td>Halibut Point, AK, lower mid</td>
<td>20 Apr. 2000</td>
<td>SCL</td>
<td>HQ437847</td>
<td>UBC A85340</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M73</td>
<td>Cape Palmerston, BC, mid intertidal boulder</td>
<td>17 May 2003</td>
<td>SCL</td>
<td>HQ437736</td>
<td>HQ437841</td>
<td>HQ437896</td>
<td>UBC A85341</td>
</tr>
<tr>
<td>M293</td>
<td>NW Olympic Peninsula, WA, mid intertidal boulder</td>
<td>31 May 2003</td>
<td>SCL</td>
<td>HQ437737</td>
<td>EU186057</td>
<td>HQ437897</td>
<td>UBC A85316</td>
</tr>
<tr>
<td>M307</td>
<td>Cape Kaguyak, AK, low</td>
<td>25 Jun. 2005</td>
<td>SCL</td>
<td>EU186059</td>
<td>UBC A85354</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M379</td>
<td>Dundas Island, BC, mid intertidal</td>
<td>19 Apr. 2007</td>
<td>SCL</td>
<td>HQ437738</td>
<td>HQ437842</td>
<td>HQ437898</td>
<td>UBC A88744</td>
</tr>
<tr>
<td>M454</td>
<td>Outside Chernofoiski Harbor, Unalaska Island, AK, high intertidal</td>
<td>11 Jun. 2008</td>
<td>SCL</td>
<td>HQ437742</td>
<td>HQ437843</td>
<td>HQ437902</td>
<td>UBC A88463</td>
</tr>
<tr>
<td>M460</td>
<td>Clover Point, BC, mid intertidal</td>
<td>02 Mar. 2008</td>
<td>SCL</td>
<td>HQ437743</td>
<td>HQ437844</td>
<td>HQ437903</td>
<td>UBC A88517</td>
</tr>
<tr>
<td>M465</td>
<td>Sunset Beach, OR, mid intertidal rock</td>
<td>06 Apr. 2008</td>
<td>SCL</td>
<td>HQ437744</td>
<td>HQ437845</td>
<td>HQ437904</td>
<td>UBC A88494</td>
</tr>
<tr>
<td>M466</td>
<td>Sunset Beach, OR, mid intertidal rock</td>
<td>06 Apr. 2008</td>
<td>SCL</td>
<td>HQ437745</td>
<td>HQ437846</td>
<td>HQ437905</td>
<td>UBC A88492</td>
</tr>
<tr>
<td>M505</td>
<td>Plumper Island, BC</td>
<td>25 May 2009</td>
<td>SCL</td>
<td>HQ437848</td>
<td>UBC A88755</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M531</td>
<td>Trinidad, CA, mid boulder</td>
<td>14 Feb. 2010</td>
<td>SCL</td>
<td>HQ437849</td>
<td>UBC A88468</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M534</td>
<td>Humboldt Bay jetty, CA, mid</td>
<td>15 Feb. 2010</td>
<td>SCL</td>
<td>HQ437850</td>
<td>UBC A88506</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Extract number</td>
<td>Collection site and habitat</td>
<td>Date</td>
<td>Collector</td>
<td>COI acc.</td>
<td>ITS acc.</td>
<td>rbcL acc.</td>
<td>Voucher</td>
</tr>
<tr>
<td>---------------</td>
<td>-----------------------------</td>
<td>------------</td>
<td>-----------</td>
<td>----------</td>
<td>----------</td>
<td>-----------</td>
<td>-----------</td>
</tr>
<tr>
<td><strong>Mastocarpus californianus</strong> (Clade 6B)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>M475</td>
<td>Mussel Rock, Cape Mendocino, CA, low intertidal boulder</td>
<td>08 Apr. 2008</td>
<td>SCL</td>
<td>HQ437746</td>
<td>HQ437851</td>
<td>HQ437906</td>
<td>UBC A88483</td>
</tr>
<tr>
<td>M480</td>
<td>Van Damme State Park, CA, mid intertidal</td>
<td>09 Apr. 2008</td>
<td>SCL</td>
<td>HQ437747</td>
<td>HQ437852</td>
<td>HQ437907</td>
<td>UBC A88462</td>
</tr>
<tr>
<td>M543</td>
<td>Bodega Head, CA, mid</td>
<td>16 Feb. 2010</td>
<td>SCL</td>
<td>HQ437748</td>
<td>HQ437853</td>
<td>HQ437908</td>
<td>UBC A88479</td>
</tr>
<tr>
<td><strong>Mastocarpus agarathi</strong> (Clade 6C)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>M436</td>
<td>Hopkins Marine Station, Pacific Grove, CA, mid intertidal</td>
<td>07 Jan. 2008</td>
<td>PTM</td>
<td>HQ437739</td>
<td>HQ437854</td>
<td>HQ437899</td>
<td>UBC A88565</td>
</tr>
<tr>
<td>M438</td>
<td>Hopkins Marine Station, Pacific Grove, CA, mid intertidal</td>
<td>07 Jan. 2008</td>
<td>PTM</td>
<td>HQ437740</td>
<td>HQ437855</td>
<td>HQ437900</td>
<td>UBC A88567</td>
</tr>
<tr>
<td>M439</td>
<td>Hopkins Marine Station, Pacific Grove, CA, high intertidal</td>
<td>07 Jan. 2008</td>
<td>PTM</td>
<td>HQ437741</td>
<td>HQ437856</td>
<td>HQ437901</td>
<td>UBC A88526</td>
</tr>
<tr>
<td><strong>Mastocarpus pacificus</strong> (Clade 7)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>M35</td>
<td>Kurumoishi, Hokkaido, Japan</td>
<td>28 Jul. 2002</td>
<td>SCL</td>
<td>HQ437857</td>
<td></td>
<td></td>
<td>UBC A88732</td>
</tr>
<tr>
<td>M49</td>
<td>Kurumoishi, Hokkaido, Japan, mid</td>
<td>28 Jul. 2002</td>
<td>SCL</td>
<td>DQ872486</td>
<td></td>
<td></td>
<td>UBC A85274</td>
</tr>
<tr>
<td>M52</td>
<td>Kurumoishi, Hokkaido, Japan, mid intertidal</td>
<td>28 Jul. 2002</td>
<td>SCL</td>
<td>HQ437716</td>
<td>EU186060</td>
<td>DQ872506</td>
<td>UBC A88732</td>
</tr>
<tr>
<td>M56</td>
<td>Kukak Bay, AK, mid intertidal</td>
<td>14 Jun. 2003</td>
<td>SCL</td>
<td>HQ437717</td>
<td>DQ872487</td>
<td>DQ872507</td>
<td>UBC A85229</td>
</tr>
<tr>
<td>M312</td>
<td>Akhiok Island, AK, low</td>
<td>21 Jun. 2005</td>
<td>SCL</td>
<td>DQ872488</td>
<td></td>
<td></td>
<td>UBC A85359</td>
</tr>
<tr>
<td>M324</td>
<td>Shearwater Bay, AK, low pebble</td>
<td>26 Jun. 2005</td>
<td>SCL</td>
<td>HQ437858</td>
<td></td>
<td></td>
<td>UBC A88546</td>
</tr>
<tr>
<td><strong>Mastocarpus stellatus</strong> (Clade 8)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>M154</td>
<td>Ormhilleren, Oygarden, Norway, mid intertidal</td>
<td>23 Jun. 2004</td>
<td>SCL</td>
<td>[DQ191350]</td>
<td>DQ872485</td>
<td>DQ872508</td>
<td>UBC A85222</td>
</tr>
<tr>
<td>(Clade 9, included in <strong>Mastocarpus papillatus</strong>)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>M437</td>
<td>Hopkins Marine Station, Pacific Grove, CA, mid intertidal</td>
<td>07 Jan. 2008</td>
<td>PTM</td>
<td>HQ437714</td>
<td>HQ437802</td>
<td>HQ437880</td>
<td>UBC A88566</td>
</tr>
<tr>
<td>M443</td>
<td>Foot of 15th Street, Pacific Grove, CA, low</td>
<td>31 Dec. 2007</td>
<td>PWG &amp; PTM</td>
<td>HQ437715</td>
<td>HQ437803</td>
<td>HQ437881</td>
<td>UBC A88525</td>
</tr>
<tr>
<td><strong>Mastocarpus jardini</strong> (Clade 10)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>M405</td>
<td>Hopkins Marine Station, Pacific Grove, CA, low</td>
<td>07 Jan. 2008</td>
<td>PTM</td>
<td>HQ437733</td>
<td>HQ437859</td>
<td>HQ437894</td>
<td>UBC A88556</td>
</tr>
<tr>
<td>M409</td>
<td>Pacific Grove, CA, low</td>
<td>07 Jan. 2008</td>
<td>PTM</td>
<td>HQ437734</td>
<td>HQ437860</td>
<td>HQ437895</td>
<td>UBC A88574</td>
</tr>
<tr>
<td>M411</td>
<td>Pacific Grove, CA, low</td>
<td>07 Jan. 2008</td>
<td>PTM</td>
<td>HQ437735</td>
<td>HQ437861</td>
<td>HQ437896</td>
<td>UBC A88574</td>
</tr>
<tr>
<td>M413</td>
<td>Hopkins Marine Station, Pacific Grove, CA, mid</td>
<td>07 Jan. 2008</td>
<td>PTM</td>
<td>HQ437736</td>
<td>HQ437862</td>
<td>HQ437897</td>
<td>UBC A88574</td>
</tr>
<tr>
<td>M525</td>
<td>Moss Beach, San Mateo County, CA, low</td>
<td>16 Nov. 2009</td>
<td>KAM</td>
<td>HQ437863</td>
<td></td>
<td></td>
<td>UC 1944777</td>
</tr>
<tr>
<td><strong>Mastocarpus pachanica</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>M312</td>
<td>Various</td>
<td>26 Jun. 2005</td>
<td>SCL</td>
<td>HQ437858</td>
<td></td>
<td></td>
<td>UBC A88546</td>
</tr>
<tr>
<td><strong>Mastocarpus yendoi</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>M312</td>
<td>Various</td>
<td>26 Jun. 2005</td>
<td>SCL</td>
<td>HQ437858</td>
<td></td>
<td></td>
<td>UBC A88546</td>
</tr>
<tr>
<td><strong>Ahnfeltiopsis paradox</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>M437</td>
<td>Various</td>
<td>07 Jan. 2008</td>
<td>PTM</td>
<td>HQ437714</td>
<td>HQ437802</td>
<td>HQ437880</td>
<td>UBC A88566</td>
</tr>
<tr>
<td><strong>Ahnfeltiopsis leptophylla</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>M437</td>
<td>Various</td>
<td>07 Jan. 2008</td>
<td>PTM</td>
<td>HQ437714</td>
<td>HQ437802</td>
<td>HQ437880</td>
<td>UBC A88566</td>
</tr>
</tbody>
</table>

1 Habitat is bedrock unless stated otherwise.


3 Specimens with only ITS accession numbers represent unique genotypes that contributed to the construction of Fig. 2.

4 n/a = not available.
inclusion of additional taxa beyond those in Lindstrom (2008a), particularly specimens from California, and the addition of another gene (COI) to the analysis, 12 northeast Pacific species were resolved. *Mastocarpus* species received robust bootstrap support, ranging from 96% to 100% for all analyses. The only exception to this support was *Mastocarpus papillatus* (see below). *Mastocarpus alaskensis* and *M. papillatus* occurred on a strongly supported branch, as did *Mastocarpus intermedius* and *Mastocarpus cristatus*. *Mastocarpus rigidus* and *Mastocarpus californianus* also showed a strong sibling relationship, as did these two species to *Mastocarpus agardhii*; finally, these three species were clearly related to *Mastocarpus latissimus*. The remaining species showed no clear relationships with other species and occurred alone on their own robustly supported branches.

Sequence analysis of the ITS regions of 382 specimens of *Mastocarpus* resulted in the identification of 128 unique ribotypes. Maximum likelihood and maximum parsimony analyses of these unique ribotypes generated phylograms that were congruent with the concatenated tree, with the exception of *Mastocarpus cristatus*, which was nested within a branch containing *Mastocarpus intermedius* (Fig. 2). Separate analyses on 68 COI and 66 *rbc* L gene sequences, representing all known *Mastocarpus* clades, supported similar relationships as those found in Fig. 1 (data not shown).

Within species variation in *rbc* L ranged from 0% among many conspecifics to a maximum of 0.7% in *M. pacificus* (between Japanese and Alaskan specimens) and 1.3% among some specimens retained in *M. papillatus*. This latter figure was more than the level of difference between *Mastocarpus intermedius* and *Mastocarpus cristatus* (0.6–0.7%) and similar to the level of difference between *M. papillatus* and its sibling species *Mastocarpus alaskensis* (1.0–1.5%) and among the closely related *Mastocarpus rigidus*, *Mastocarpus californianus* and *Mastocarpus agardhii* (1.0–1.7%). For the COI gene, within species variation ranged from 0% among many conspecifics, to 1.7% for *M. pacificus* and up to 5.5% for specimens retained in *M. papillatus*. In contrast to the *rbc* L gene, which indicated little distance between *Mastocarpus intermedius* and *Mastocarpus cristatus*, there was significant distance in the COI gene (3.5–4.5%) between these species. *Mastocarpus rigidus* and *Mastocarpus californianus* were separated by a modest distance (2.2–2.3%), and both showed a similar and shorter distance to *Mastocarpus latissimus* (2.0–3.2%) than to *Mastocarpus agardhii* (8.6–9.1%).

Below we provide details of our identification of these clades with existing species names, and we create new species that cannot be matched with existing names. We follow Lindeberg & Lindstrom (2010, fig. 4) in the application of the habitat descriptors high, mid and low intertidal. In general, high intertidal is at the elevation of Balanus glandula Darwin and Endocladia maricata (Endlicher) J. Agardh and near the upper limit of Fucus distichus subsp. evanescens (C. Agardh) H.T. Powell, where these species occur. The mid intertidal zone is the elevation dominated by *Ficus distichus* and Semibalanus cariosus (Pallas). The low intertidal zone is often dominated by green or red algae at more sheltered sites and by kelps on
more exposed shores. Species descriptions are based on our collections.

**Mastocarpus papillatus** (C. Agardh) Kützing 1843: 398

Gametophytic thallus upright, crisp, up to 9 cm tall. Stipe terete, unbranched, 1–3 mm in length, expanding slightly into a flattened apophysis 6–15 mm long and 2–18 mm wide, then into blades 3–10 mm wide and 300–500 μm thick. Thallus uniformly reddish black. Margin of apophysis slightly swollen, giving thallus its canaliculate character; margin of blade slightly wavy, rarely proliferous. Branching highly variable, generally subdichotomous, to three orders, occasionally unbranched. Apices rounded, crenate, or irregular. In section, cortex of 6–8 cell layers, occupying about half the width of the section. Male thalli smooth, without papillae. Female thalli with simple papillae, initially nipple-like, becoming subspherical at maturity; papillae restricted to blade surface (not along margins); larger papillae occurring on older (lower) parts of the thallus in discrete patches (Figs 24, 25). Distinguished from other *Mastocarpus* species by molecular sequence differences.

**Basionym:** *Sphaerococcus papillatus* C. Agardh 1821: pl. 19.

**Homotypic Synonym:** *Gigartina papillata* (C. Agardh) J. Agardh 1846: pl. 19.
HETEROTYPIC SYNONYMS: *Petrocelis franciscana* Setchell & N.L. Gardner in N.L. Gardner 1917: 391, pl. 33, fig. 1; *Gigartina obovata* J. Agardh 1899: 25.

TYPE: Golden Gate, San Francisco, California, *Leg. Chamisso*, 1816, LD! [Herbarium Agardh (Hb. Ag.) 23883] (http://botany.ubc.ca/sandral/Sphae-pap.jpg). We select the specimen in the upper right as lectotype.

ITS sequence of Hb. Ag. 23883: Clade 2 (Lindstrom 2008a). This 220 bp fragment at the 5’ end of the nuclear small subunit rDNA (nSSU) ITS1 region of the type specimen differed from the 41 other sequenced specimens in this clade by 0–6 nucleotides and 0–12 indels. The type specimen was identical to a 120 bp fragment from Agate Beach, California, 13 January 1973 (UC 1471472), to a 218 bp fragment from the holotype of *Petrocelis franciscana* (UC 188973, Fort Point, San Francisco, California) and to a 203 bp fragment from the type of *Gigartina obovata* (Hb. Ag. 23840, Golden Gate, California, *Leg. Berggren*, see Setchell & Gardner 1933: 288, pl. 62). We designate the upper specimen, which is larger, as lectotype of *Gigartina obovata*.

Assignment of the type material of *Mastocarpus papillatus* to Clade 2 solves a long-standing uncertainty as to the provenance of this collection. The herbarium sheet bears the note: ‘*e mari Atlantico Chamisso*’. In his description, C. Agardh (1821) wrote: ‘*Ad insulam O-wai-hee [Hawaii] Chamisso, in cujus collectione specimina vidi*’. Setchell & Gardner (1933) concluded that the type locality was in error, stating ‘both specimens and plate agree perfectly with specimens from the Pacific coast of North America’. It had even been surmised that the specimen might have come from Unalaska, Alaska, one of the stops on Chamisso’s voyage (M.J. Wynne, personal communications).

The occurrence of this species on the Monterey Peninsula, California, is debatable. We provisionally include high intertidal specimens of *Mastocarpus*, represented by Clade 9 (this study), in *M. papillatus*. Clade 9 is thus far known only from the Monterey Peninsula. This clade is separated from other specimens of *M. papillatus sensu stricto* (Clade 2) on a branch with high bootstrap support in separate analyses of the individual genes as well as the concatenated data (Fig. 1). However, its relationship with Clade 2 is paraphyletic in these analyses. To our knowledge, there are no previously existing names for Clade 9. Further study of *M. papillatus* in this region is required to understand how many species of this high intertidal entity should be recognized. Verified distribution: Cambria, San Luis Obispo County, California, to Cape Palmerston, northern Vancouver Island, British Columbia (Fig. 42).

Fig. 2. Maximum likelihood tree (*−2ln L = 3499.2610*) of all unique *Mastocarpus* ITS sequences. The size of the datafile precluded bootstrap analyses.
Mastocarpus jardini (J. Agardh) J.A. West in Guiry, West, Kim & Masuda 1984: 57

Gametophytic thallus upright, crisp, up to 9 cm tall. Stipe terete, unbranched, 1–3 mm in length, expanding slightly into a flattened apophysis 8–10 mm long and 2–5 mm wide, then into blades 4–10 mm wide and 250 μm thick. Thallus uniformly dark reddish black. Margin of apophysis and blade slightly swollen, giving thallus its canaliculate character; margin of blade straight, not wavy. Branching divaricate, up to three orders. Apices tapered and crenate or irregular. In section, cortex of 6–8 cell layers, occupying about half the width of the section. Papillae simple or becoming branched, sessile or cylindrical in shape, centrally or terminally enlarged, occurring on surfaces of blades as well as along margins; some papillae becoming bladelike (Figs 40, 41). Distinguished from other Mastocarpus species by molecular sequence differences.


Type: Bering Island, Commander Islands, Russia, Leg. F.R. Kjellman, 14–19 August 1879, Vega Expedition, UPS! S! (http://botany.ubc.ca/sandral/Gigar-pac.jpg).

Heterotypic synonym: Chondrus mamillosus var. unalascensis Ruprecht 1850: 126 (type locality: Unalaska, Alaska, Leg. Wosnessenski) = Gigartina unalascensis (Ruprecht) J. Agardh 1899: 11 (the latter name was first used by Kjellman 1889: 31, but he neither indicated that it was a new combination nor cited the basionym) = Mastocarpus unalascensis (Ruprecht) Makienko in Klochkova 1996: 191 (http://botany.ubc.ca/sandral/Chond-mam-una.jpg).

ITS sequences of type specimens in S: Mazzaella sp. and Clade 7 (Lindstrom 2008a). These sequences come from the upper right and upper left specimens of the S syntype collection, respectively (http://botany.ubc.ca/sandral/Gigar-pac.jpg). (UPS, where additional type material is housed, would not provide type material for sequencing.) The 225 bp fragment at the 5' end of the nSSU ITS1 region from the Mastocarpus specimen differed by up to 2 indels from the two specimens in this clade we have sequenced from northern Japan. It was identical to all specimens from Russia and Alaska and to syntype material of Chondrus mamillosus var. unalascensis in S. We designate the upper left specimen of the S syntype as lectotype of Gigartina pacifica, and we designate the central specimen of the S syntype (http://botany.ubc.ca/sandral/Chond-mam-una.jpg) as lectotype of Chondrus mamillosus var. unalascensis since these are the specimens we obtained sequences from.

The type material of Mastocarpus pacificus has channelled, spreading, dichotomous, papillate blades and looks like a typical species of Mastocarpus, whereas all Clade 7 specimens that we sequenced were flat rather than canaliculate and lacked papillae. Ohno et al. (1982) previously noted that broad thalli with both surface and marginal papillae dominated in summer and narrow thalli with only marginal papillae dominated in winter. Because of this alternation in forms, they dubbed this species ‘Gigartina pacifica-ochotensis’.

Kjellman (1889) reported this species, from Bering Island, Commander Islands, Russia, to be quite abundant and gregarious on upper subtidal rock. Based on our collections, this species occurs intertidally, not subtidally. We have collected it on both emergent rock and in tidepools. Most if not all of the sites where we collected our smooth, linear specimens experience some shore ice during the winter. Ours were all summer collections, however, suggesting that this species does not alternate forms between summer and winter, as it does in Japan.
Mastocarpus latissimus (Harvey) comb. nov.

Gametophytic thallus upright, crisp, up to 40 cm tall but usually smaller. Stipe terete, unbranched, 4–12 mm in length, expanding slightly into an apophysis 20 mm long, then into blades up to 40 mm wide and 250 µm thick. Thallus uniformly red to reddish black. Margin of apophysis slightly swollen, giving thallus its canaliculate character; margin of blade slightly wavy. Branching dichotomous, subdichotomous, or arising as proliferations from the apophysis, with proliferations becoming subdichotomous. Apices rounded or crenate. In section, cortex of 6–7 cell layers, occupying about half the width of the section. Male thalli with few, small, nipple-like papillae. Female thalli with mostly simple papillae, initially nipple-like, becoming spherical with cystocarps growing out laterally. Some papillae proliferous and bladelike, occurring on surface and along margins of thallus (Figs 32, 33). Distinguished from other Mastocarpus species by molecular sequence differences.

Basionym: Gigartina mamillosa var. latissima Harvey 1862: 172 [=G. latissima (Harvey) Eaton in J. Agardh 1899: 32].


Heterotypic synonym: Gigartina dichotoma N.L. Gardner 1927: 333, pl. 59 (type locality: Duxbury Reef, Marin County, California, Leg. N.L. Gardner 6212, UC 296705).

ITS sequence of lectotype of G. latissima: Clade 5 (Lindstrom 2008a). The 221 bp fragment at the 5′ end of the nSSU ITS region of this specimen was identical to 12 sequences from Alaska and northern California. The 221 bp fragment of the right-hand specimen of Hb. Ag. 23855 was identical to most of the remaining specimens from Alaska and British Columbia except for a single unique transition.

ITS sequence of the holotype of G. dichotoma also belonged to Clade 5. The 223 bp fragment at the 5′ end of the nSSU ITS1 region of the type specimen was identical to two specimens (from La Desembocadora de Bio Bio, near Concepción, Chile, Leg. Paul Gabrielson). These sequences differed from other Clade 5 sequences by a 1 bp indel. Although the Chilean sequences differed from other Clade 5 sequences at up to five other nucleotide positions, either indels or base pair substitutions, across the 728 bp ITS region, these differences were uncommon among the 63 sequences compared. Habitat: mid to low intertidal on bedrock and boulders. Verified distribution: Moss Beach, San Mateo County, California, north to Attu Island, Aleutian Islands, Alaska; Chile (Fig. 42).

Mastocarpus agardhii (Setchell & N.L. Gardner) comb. nov.

Gametophytic thallus upright, cartilaginous, up to 15 cm tall. Stipe and apophysis terete, branched or unbranched, 25–55 mm in length, constituting a third to half the height of the thallus, expanding into narrow blades of uniform width (~3 mm) and 450–500 µm thick. Thallus uniformly dark reddish black. Margin of apophysis and blade slightly swollen, giving thallus its canaliculate character. Branching more or less dichotomous or divaricate, up to six orders. Apices narrowly rounded on female thallus to slightly crenate on male thalli. In section, cortex of 10–11 cell layers, occupying about half the width of the section. Papillae vermiform (Fig. 39), on blade surface and submarginal. Cystocarpic papillae with long stalks (pedicellate), each with a swollen subterminal cystocarp (Fig. 38). Distinguished from other Mastocarpus species by molecular sequence differences.


Holotype: Pyramid Point, Monterey County, California, Leg. W.A. Setchell, 1686, 18 May 1897, UC 93733. Isotypes distributed as Phycotheca Boreali-Americana (PB-A) 427 (Setchell & Gardner 1933: 290, as ‘cotypes’).

ITS sequence of UC 93733 (holotype): Clade 6C (Lindstrom 2008a; this study). The 218 bp fragment at the 5′ end of the nSSU ITS1 region from the type specimen is identical to extracts M78, 381, 503 and 513 from Vancouver Island, British Columbia, and M436, 438 and 439 from the Monterey Peninsula, California.

Mastocarpus agardhii (Clade 6C) is one of three species formerly and erroneously referred to as M. jardinii. In contrast to M. jardinii, which occurs in the low intertidal, Mastocarpus agardhii grows on the rocks in the high to mid intertidal ‘between the 3.5- and 1.0-foot tide levels’ on the Monterey Peninsula (Smith 1944: 284) and in the mid intertidal elsewhere.

This species was first described as Gigartina papillata f. dissecta Setchell on the label to PB-A 427. Later Setchell & Gardner (1933) elevated the taxon to specific rank, adopting the epithet agardhii. Setchell & Gardner noted that the species was incorrectly identified by J. Agardh (1899: 24) as Gigartina batrachopus [batrachopus] Bory (1828: 153, pl. 19, fig. 2), a species now considered to be referable to Laurencia (www.algaebase.org, visited 15 January 2010). Rather than illustrating their type specimen, however, they provided photos of Agardh’s material, identifying it as Gigartina agardhii but with the misleading label, ‘Type sheet of G. batrachopus’. Mastocarpus agardhii was included as a synonym of Mastocarpus jardinii by Guiry et al. (1984). The present work clearly indicates that the two species are distinct.

The specimens identified as Mastocarpus agardhii from Vancouver Island, based on nSSU ITS sequences, show either evidence of hybridization with other, closely related species or evidence of chimeric thalli due to coalescence (Santelices et al. 1999). M78 has the ITS sequence of Mastocarpus agardhii, a rbCL sequence allopying it to Clade 6B (Mastocarpus californianus; see below) and a COI sequence allopying it to Clade 5 (Mastocarpus latissimus). In contrast, M381, which also has the ITS sequence of Mastocarpus agardhii, has the COI sequence of Clade 6A (Mastocarpus rigidus; see below) and the rbCL sequence of Clade 6B. Compared with Clade 6A, Clade 6C (Mastocarpus agardhii) occurs slightly higher in the intertidal zone where the two species co-occur on Vancouver Island.
Verified distribution: Monterey Peninsula, California; north and west Vancouver Island, British Columbia (Fig. 42).

_Mastocarpus cristatus_ (Setchell) comb. nov.

Gametophytic thallus upright, crisp, flabellate, up to 8 cm tall, terete at base, stipe unbranched, 3–5 mm in length, expanding slightly into an apophysis 5–15 mm long, then into blades mostly less than 8 mm wide and 250–300 μm thick (but often appearing thicker due to dense covering of papillae). Thallus uniformly reddish black. Margin of apophysis swollen, giving it a distinctive canaliculate appearance. Branches subdichotomous, to five orders, with crenate apices. In section, cortex of 6–8 cell layers, occupying at least half the width of the section. Papillae occurring on both male and female thalli and on both surfaces and margins of blades, including near the base of the thallus, often very dense (Figs 30, 31). Female papillae compound, uniform in size and shape along the length of the thallus. Male papillae initially elongate and acute, becoming proliferous and elliptical in shape. Distinguished from other _Mastocarpus_ species by molecular sequence differences.


_Holotype:_ Pyramid Point, Monterey County, California, Leg. W.A. Setchell, 1665, 18 May 1897, UC 93707. Isotypes distributed as PB-A No. 426.

ITS sequence of UC 93707 (holotype): Clade 3C (Lindstrom 2008a; this study). The 227 bp fragment at the 5' end of the nSSU ITS1 region from this type specimen differed by 1 indel from some specimens of this species and by the indel and a single additional nucleotide difference from other specimens. All specimens were collected from the Monterey Peninsula, the only area where this species is currently known to occur (Fig. 42). Specimens grew on bedrock from 0.25 m to 1.0 m (mid intertidal).

_New species of Northeast Pacific Mastocarpus_

**CLADE 1:** Known to occur from Trinidad, Humboldt County, California, to Attu Island, Alaska, and possibly further west, this may be the most abundant species of _Mastocarpus_ based on its broad geographic range and local dominance in the mid to high intertidal. A potentially available name for this species is Gigartina stichensis. However, since we have been unable to obtain type material of _Gigartina stichensis_ from LE, we propose the name _Mastocarpus alaskensis_ for this taxon because it is the common high intertidal species in Alaska.

_Mastocarpus alaskensis_ sp. nov.

Figs 3–6, 22, 23

_Thallus gametophyticus erectus crispus usque ad 15 (ad 21) cm altus_ (Fig. 3). _Stipes teres eramosus 1–3 mm longus, leviter expansus in apophysim 6–14 mm longam 4–10 mm latam, deinde in laminas 4–35 mm latas usque ad 350 μm crassas. Thallus rubroniger brunneoruber vel rubrobrunneus, decoloratus fusce roseus. Apophysis margine leviter tumido, thallum canaliculatum faciens; lamina margine leviter undulato raro profloro. Ramification subdichotoma vel flabellata, ad quatuor ordines, thallus interdom um eramosus. Apices crenati dissecti vel irregulariter lobati. Cortex in sectione transversali e stratis cellularum sex ad octo (ad 12) constare visus, circiter dimidiam partem sectionis occupans (Figs 4, 5). Thalli masculi laeves sine papillis (Fig. 6). Thalli foemini papillis simplicibus, primum barbatuliformibus dein cylindricis postremo subsphaericis, ad superficiem laminae (non ad margines) restrictis (Figs 22, 23); papillis majoribus in partibus thalli senioribus (inferioribus). Ab aliis speciebus Mastocarpi ordinibus nucleotidorum distinguendus."

Gameopathic thallus upright, crisp, up to 15 (to 21) cm tall (Fig. 3). Stipe terete, unbranched, 1–3 mm in length, expanding slightly into an apophysis 6–14 mm long and 4–10 mm wide, then into blades 4–35 mm wide and up to 350 μm thick. Thallus uniformly reddish black, brownish red, reddish brown, fading to dusky rose. Margin of apophysis slightly swollen, giving thallus its canaliculate character; margin of blade slightly wavy, rarely proliferous. Branching subdichotomous to flabellate, to four orders, occasionally unbranched. Apices crenate, dissected, or irregularly lobed. In section, cortex of six to eight (to 12) cell layers, occupying about half the width of the section (Figs 4, 5). Male thalli smooth, without papillae (Fig. 6). Female thalli with simple papillae, stubble-like at first, becoming cylindrical and then subspherical; papillae restricted to blade surface (not along margins; Figs 22, 23); larger papillae occurring on older (lower) parts of the thallus. Distinguished from other _Mastocarpus_ species by molecular sequence differences.

_Holotype:_ Left specimen (Fig. 3), UBC A88537, high intertidal bedrock, north of Deep Bay, Atka Island, Aleutian Islands, Alaska, 15 July 2007, Leg. Mandy R. Lindeberg (ALEUT07_387). DNA extract M392.

_Habitat:_ Occurring on rock, usually in the mid to high intertidal zone. Where they co-occur, this species can be slightly lower than _M. papillatus_.

_Verified distribution:_ Trinidad, Humboldt County, California, north to Attu Island, Aleutian Islands, Alaska (Fig. 42).

_CLADE 3:_ Is divided into two distinct, well supported clades (Fig. 1). As noted above, one of these is assignable to _Mastocarpus cristatus_; a species thus far known only from the Monterey Peninsula. We propose the name _Mastocarpus intermedius_ for the other clade because it shares many characters with other species in the genus.

_Mastocarpus intermedius_ sp. nov.

_Figs 7–10, 28, 29_

_Thallus gametophyticus erectus crispus usque ad 9 cm altus_ (Fig. 7). _Stipes teres eramosus 1–8 mm longus sensim expansus in apophysim 10–20 mm longam, deinde in laminas plerunque ad 20 mm latas 175–350 μm crassas. Thallus uniformiter rubroniger. Apophysis margine tumido, thallum
distincte canaliculatum faciens. Ramificatio subdichotoma flabellata vel prolifera, usque ad quatuor ordines, vel thallus eramosus. Apices rotundati vel irregulares. Cortex in sectione transversali e stratis cellularum 8–15 constare visus, plus quam dimidiam partem sectionis occupans (Figs 8-10). Papillae in thallis maturis masculis foeminisque et in utraque superficie laminae, et prope basin frondis (Figs 7, 28, 29); papillae foeminae primum hemisphaericae, dein compositae interdum vermiformes (convolutissimae); papillae masculae ligulatae, dein magnificantes proliferantes. Ab aliis speciebus *Mastocarpus* ordinibus nucleotidorum distinguendus.

Gametophytic thallus upright, crisp, up to 9 cm tall (Fig. 7). Stipe terete, unbranched, 1–8 mm in length, expanding gradually into an apophysis 10–20 mm long, then into blades mostly to 20 mm wide and 175–350 μm thick. Thallus uniformly reddish black. Margin of apophysis swollen, giving it a distinctive canaliculate appearance. Branching subdichotomous, flabellate or proliferous, up to four orders, or unbranched. Apices rounded to irregular in shape. In section, cortex 8–15 layers, occupying more than half the section (Figs 8-10). Papillae occurring on both mature male and female thalli and on both surfaces and margins of blades, including near the base of the frond (Figs 7, 28, 29). Female papillae initially hemispheric, becoming compound and sometimes veriform (very convoluted). Male papillae ligulate, becoming large and proliferous. Distinguished from other *Mastocarpus* species by molecular sequence differences.

**HOLOTYPE:** Leftmost specimen (Fig. 7), UBC A88558, epilithic, near coarse sand at base of boulders, +0.5 m above mean lower low water (MLLW), Hopkins Marine Station, Pacific Grove, Monterey County, California, 7 January 2008, Leg. Patrick T. Martone (Z). DNA extract M407.

**HABITAT:** Occurring on rock usually in the mid to low intertidal zone.

**VERIFIED DISTRIBUTION:** Ensenada, Baja California, Mexico, north to northern British Columbia; Cape Kaguyak, Kodiak Island, Alaska (Fig. 42).

**CLADE 4:** Is clearly distinguished in all analyses (Figs 1, 2). We propose the name *Mastocarpus vancouveriensis* for this species because its distribution is centred on Vancouver Island.

*Mastocarpus vancouveriensis* sp. nov.

Figs 11–14, 26, 27

*Thallus gametophyticus erectus aliquot flaccidus usque ad 8 cm altus, basi teres. Stipes eramosus 3–5 mm longus leviter*
expansus in apophysim 10–15 mm longam 2–3 mm latam (Fig. 11). Thallus fusce ruber vel rubroniger. Apophysis margin leviter tumido, thallum canaliculatum faciens. Ramificatio prolifera ex apice apophysis, interdum subdichotoma, ad tres ordines. Laminae proliferae ad 1.5 cm latae 3 cm longae, primum orbiculares vel ellipticae, dein cordatae, stipite angustissimo affixa. Apices rotundati. Cortex in sectione transversali e stratis cellularum sex ad octo constare visus, plus quam dimidiam partem latitudinis sectionis (200 μm) vix occupans (Figs 12, 13). Spermatangia in superficie laminarum (Fig. 14). Thalli foeminae papillis plerumque simplicibus, subsphaericis, interdum ramis duo globularis instructis, sparsis, ad partes seniores thalli restrictis (Figs 26, 27). Ab aliis speciebus Mastocarpi ordinibus nucleotidorum distinguendus.

Gametophytic thallus upright, somewhat flaccid, up to 8 cm tall, terete at base, stipe unbranched, 3–5 mm in length, expanding slightly into an apophysis 10–15 mm long and 2–3 mm wide (Fig. 11). Thallus dark red to reddish black. Margin of apophysis slightly swollen, giving thallus its canaliculate character. Branching proliferous from apex of apophysis, occasionally subdichotomous, to three orders. Proliferous blades to 1.5 cm wide and 3 cm long, initially orbicular to elliptical, becoming cordate, attached by a very narrow stipe. Apices rounded. In section, cortex of six to eight cell layers, occupying slightly more than half the

Figs 7–10. Mastocarpus intermedius type material.
Fig. 7. Holotype (left) and isotypes of Mastocarpus intermedius (UBC A88558).
Fig. 8. Cross section of blade.
Fig. 9. Detail of cortex (and medulla) in cross section.
Fig. 10. Spermatangia in blade cross section.

Fig. 11. Holotype (lower centre) and isotypes of *Mastocarpus vancouveriensis* (UBC A85326).

Fig. 12. Cross section of blade.

Fig. 13. Detail of cortex (and medulla) in cross section.

Fig. 14. Spermatangia in blade cross section.
200 μm width of the section (Figs 12, 13). Spermatangia on blade surface (Fig. 14). Female thalli with mostly simple papillae, subspherical, occasionally with two globular-shaped branches; sparse, restricted to older parts of thallus (Figs 26, 27). Distinguished from other Mastocarpus species by molecular sequence differences.

**HOLOTYPE:** Bottom centre specimen (Fig. 11), UBC A85326, high intertidal bedrock in sand, Brady’s Beach, Barkley Sound, British Columbia, Canada, 17 April 2003, Leg. S.C. Lindstrom (SCL 10719). DNA extract M91.

**HABITAT:** Occurring on rock usually in the mid to high intertidal zone often surrounded by sand.

**VERIFIED DISTRIBUTION:** Cape Mendocino, California, north to Sitka, Alaska (Fig. 42).

**CLADE 6A AND 6B:** Share a habit of clustered, narrow, cartilaginous thalli with Clade 6C (Mastocarpus agardhii). These two species are more closely related to each other than either is to Mastocarpus agardhii as noted above. However, Clades 6A and 6B are sufficiently distinct to warrant recognition as separate species (Figs 1, 2), and we propose the names Mastocarpus rigidus for Clade 6A because of the upright, rigid character of this species and Mastocarpus californianus for Clade 6B because it is currently known only from northern California.

**Mastocarpus rigidus sp. nov.**

Figs 15–18, 34, 35

*Thallus gametophyticus erectus cartilagineus usque ad 9 cm altus (Fig. 15). Stipes apophysisque teres (Fig. 18) eramosa*
20–35 mm longa, partem tertiam vel dimidiam altitudinis thalli attingens, expansa in laminas 5 mm latas in thallis foeminis, 12 mm latas in thallis masculis, 275 μm crassas. Thallus unicolor: rubroniger. Apophysis margine leviter tumido, thallum canaliculatum faciens. Ramificatio plus minusve dichotoma, usque ad quatuor ordines. Apices anguste rotundati vel crenato-fimbriati. Cortex in sectione transversali e stratis cellularum septem ad novem constare visus, dimidiam partem latitudinis sectionis occupans (Fig. 16). Papillae simplices in superficie marginibusque, hemisphaericae vel irregulares sed interdum proliferantes (laminiformes; Figs 34, 35), papillis senioribus majoribus basalius, junioribus minoribus distalius. Spermatangia et in papillis et in superficie laminae (Fig. 17). Ab aliis speciebus Mastocarpus ordinibus nucleotidorum distinguendus.

Gametophytic thallus upright, cartilaginous, up to 9 cm tall (Fig. 15). Stipe and apophysis terete (Fig. 18), unbranched, 20–35 mm in length, constituting a third to half the height of the thallus, expanding into blades 5 mm wide on female thalli, 12 mm wide on male thalli and 275 μm thick. Thallus uniformly reddish black. Margin of apophysis slightly swollen, giving thallus its canaliculate character. Branching more or less dichotomous, up to four orders. Apices narrowly rounded to crenate/fimbriate. In section, cortex of seven to nine cell layers, occupying half the width of the section (Fig. 16). Papillae simple, on surface and margins, hemispheric to irregular in shape but can become proliferous (bladelike; Figs 34, 35). Older, larger papillae basal; smaller, younger papillae distal. Spermatangia on both papillae and blade surface (Fig. 17). Distinguished from other Mastocarpus species by molecular sequence differences.

**Holotype:** Leftmost specimen (Fig. 15), UBC A88570, on mid intertidal bedrock with *Fucus distichus* subsp. *evanescens* and *Saccharina sessilis*, Botanical Beach, Vancouver Island, British Columbia, Canada, 11 July 2010, Leg. Patrick T. Martone (PTM 184). DNA extract M559.
Habitat: Occurring on rock usually in the (lower) mid intertidal zone. Where they co-occur, this species can be slightly lower than Mastocarpus agardhii. Thalli often occur in clumps of 15–50 individuals.

Verified distribution: North Jetty, Humboldt Bay, California, north to Atka Island, Aleutian Islands, Alaska (Fig. 42).

*Mastocarpus californianus* sp. nov.

Figs 19–21, 36, 37

Thallus gametophyticus erectus cartilagineus usque ad 8 cm altus (Fig. 19). Stipes apophysisque teres eramosa 15–35 mm longa, usque ad partem dimidiam altitudinis thalli attingens sed plerumque brevior, 2–3 mm lata, expansa in laminas proliferas 1–3 mm lata 350 μm crassas. Thallus unicolor: rubroniger. Apophysis margin leviter tumido, thallum canaliculatum faciens. Ramificatio irregularis, interdum prope basin thalli. Apices cordati vel crenati. In sectione transversali e stratis cellularum 10–11 constare visus, circiter dimidiam partem longitudinis sectionis occupans (Figs 20, 21). Papillae simplices in superficie marginibusque, interdum proliferantes (laminiformes; Figs 36, 37). Ab aliis speciebus Mastocarpi ordinibus nucleotidorum distinguendus.

Gametophytic thallus upright, cartilaginous, up to 8 cm tall (Fig. 19). Stipe and apophysis terete, unbranched, 15–35 mm in length, constituting up to half the height of the thallus but often considerably less, 2–3 mm wide, expanding into proliferous blades 1–3 mm wide and 350 μm thick. Thallus uniformly reddish black. Margin of thallus slightly swollen, giving it a canaliculate character. Branching irregular, can occur near base of thallus. Apices cordate to crenate. In section, cortex of 10–11 cell layers, occupying about half the width of the section (Figs 20, 21). Papillae simple, on surface and margins, some becoming proliferous (bladelike; Figs 36, 37). Distinguished from other *Mastocarpus* species by molecular sequence differences.

Holotype: Leftmost specimen (Fig. 19), UBC A88483, low intertidal boulder, ~0.3 m above MLLW, ‘Mussel Rock’, Cape Mendocino, Humboldt County, California, 8 April 2008, Leg. S.C. Lindstrom (SCL 13349). DNA extract M475.

Habitat: Occurring on rock usually in the (lower) mid intertidal zone. Thalli often occur in clumps of 15–50 individuals.

---

Figs 22–41. Characteristic shapes of papillae near the centre of blades on their surfaces (left) and at their margins (right). Scale bars = 1 mm.

Figs 22, 23. Mastocarpus alaskensis (UBC A88520).
Figs 24, 25. Mastocarpus papillatus (UBC A88477).
Figs 26, 27. Mastocarpus vancouveriensis (UBC A85326).
Figs 28, 29. Mastocarpus intermedius (UBC A88510).
Figs 30, 31. Mastocarpus cristatus (UBC A88562).
Figs 32, 33. Mastocarpus lattissimus (UBC A88534 left; UBC A88504 right).
Figs 34, 35. Mastocarpus rigidus (UBC A88494 left; UBC A88542 right).
Figs 36, 37. Mastocarpus californianus (UBC A88483).
Figs 38, 39. Mastocarpus agardhii (UBC A88526 left; UBC A88565 right).
Figs 40, 41. Mastocarpus jardinii (UBC A88747).
VERIFIED DISTRIBUTION: Bodega Head to Cape Mendocino, California (Fig. 42).

Names of North Pacific species of Mastocarpus that have not yet been assigned to contemporary specimens

Petrocelis middendorfii (Ruprecht) Kjellman 1883: 190

BASIONYM: Cruoria middendorfii Ruprecht 1850: 137.

TYPE: Asa Island, Sea of Okhotsk, Russia.

We have been unable to obtain type material of this species. If we are able to acquire this material, it is possible that this specific epithet will replace an existing or a proposed name, most likely M. pacificus, given its provenance.

Mastocarpus ochotensis (Ruprecht) Makienko in Klochkova 1996: 191

BASIONYM: Chondrus mamillulosus var. ochotensis Ruprecht 1850: 126.

HOMOTYPIC SYNONYMS: Gigartina ochotensis (Ruprecht) Yendo 1916: 57. (The name was first used by Kjellman 1889: 31 but without indicating it was a new combination, nor citing the basionym.)

TYPE: Sea of Okhotsk.

We have been unable to obtain type material of this species. It is possible that this specific epithet will replace a proposed name but we expect that this species is a synonym of M. pacificus, which has nomenclatural priority.

Gigartina sitchensis (Ruprecht) Yendo 1916: 57

This name was first used by Kjellman 1889: 31 but without indicating it was a new combination, nor citing the basionym.

BASIONYM: Chondrus mamillulosus var. sitchensis Ruprecht 1850: 126.

TYPE: Presumably Sitka, Alaska.

As noted above, we have been unable to obtain type material of this species. It is possible that this is an older name for Mastocarpus alaskensis, although other species of Mastocarpus are also known to occur in the Sitka area. Moreover, we have encountered a number of instances of misapplication of provenance to old Russian material, so we are reluctant to predict to which species this might belong.

DISCUSSION

These results underscore earlier observations that there are more species of Mastocarpus in the northeast Pacific than previously acknowledged (Lindstrom 2008a; Le Gall & Saunders 2010). Inclusion of mitochondrial COI sequence data supports earlier conclusions derived from nuclear ITS and chloroplast rbcL sequences (Lindstrom 2008a). Sequences from additional specimens from California indicate that even more species than those originally identified by Lindstrom (2008a) required names.

Small fragments of type material from public herbaria provided unambiguous ITS sequences that allowed us to match unequivocally these types with our own modern collections. These results highlight the importance of sequencing type material, where possible, to determine the correct application of existing names to cryptic species identified using molecular techniques. However, we acknowledge that this is often not as easy with other taxa as it has been with Mastocarpus. Mastocarpus is a genus for which many types are available in herbaria; many of the species are well-adapted to tough intertidal conditions (extended periods of desiccation, burial by sand), which may 'predispose' them to enhanced preservation compared with thalli from other environments.

Despite the success of this study, we were unable to find morphological features that would allow us to unequivocally identify many species. Nevertheless, Mastocarpus species show distinct geographic ranges and preferred habitats. However, even these observations require caveats since ranges may shift through time or by human-mediated activities. Mastocarpus pacificus, which is represented by the type of M. unalascensis from the Aleutian Islands from nearly 200 years ago, is much less common there now than Mastocarpus alaskensis, which appears to be absent from early Aleutian collections. Although Mastocarpus alaskensis is usually found in the mid to high intertidal zone, we have occasionally found it lower on the shore in areas with otherwise sparse algal cover. We were surprised to find specimens of Mastocarpus agarthii on Vancouver Island with sequences identical to those from the Monterey Peninsula more than 1000 km away and with no apparent geographically intermediate populations. Moreover, these Vancouver Island populations are odd because specimens with ITS of Mastocarpus agarthii have organelle sequences from other species as noted above. (Zuccarello et al. 2005 also observed mixed genotypes in European Mastocarpus, with asexual thalli having the plastid haplotype of the breeding group and the mitochondrial haplotype of the southern breeding group.) The occurrence of Mastocarpus latissimus in Chile, with little genetic differentiation from some California specimens, also raises the possibility of modern, anthropogenic dispersal.

These results support the hypothesis that biogeography is a major driver of speciation among seaweeds in the northeast Pacific (Lindstrom et al. 1996; Lindstrom 2006, 2008a, b). Sister species recognized in this paper show clear geographic differentiation, although sometimes with present-day overlap. Mastocarpus alaskensis is the northern counterpart of M. papillatus, although they overlap from northern Vancouver Island to northernmost California; where they co-occur, M. papillatus is slightly higher in the intertidal, as one might expect in a more southerly species. Mastocarpus rigidus and Mastocarpus californianus also show geographic differentiation, with Mastocarpus rigidus known to occur from Humboldt Bay to the Aleutian Islands, and Mastocarpus californianus thus far known only from Bodega Head to Cape Mendocino. These two species are in turn sister species to Mastocarpus agarthii, which occurs on the Monterey Peninsula, California.

This study does not address the fascinating question of the relationship between apomictic and sexual upright thalli in Mastocarpus spp., a phenomenon widely published in the genus (e.g. Polanshek & West 1977; Ohno et al. 1982; Fierst
et al. 2010) and discussed in Lindstrom (2008a). The sequence data from this study do provide the means for identifying individuals to determine whether they represent different species or even different genotypes of the same species in studies of apomixis and sexual reproduction in the genus. Nor do we address the relationship between the Petrocelis (sporophytic) phase and the gametophytic phase, such as whether all species have a Petrocelis phase and whether that phase occurs at the same elevation as its gametophyte. The type of Petrocelis franciscana had a sequence identical to the type of Mastocarpus papillatus. Field observations (Lindstrom, unpublished observations) confirmed the presence of a Petrocelis crust in the vicinity of at least some individuals of Mastocarpus alaskensis, Mastocarpus latissimus and Mastocarpus pacificus. We suspect that a Petrocelis phase occurs for most if not all the species.

Although we initially assumed that all Mastocarpus species were dioecious, we observed spermatangia on thalli of Mastocarpus alaskensis, Mastocarpus intermedius, Mastocarpus vancouveriensis and Mastocarpus rigidus that also bore what appeared to be cystocarpic papillae. This phenomenon requires further investigation. The frequency of spermatangia may suggest that individuals are protandrous. We often encountered distinct, pale, nonpapillate male thalli in populations of Mastocarpus alaskensis and M. papillatus. We don’t know whether these thalli eventually produce cystocarpic papillae.

It is likely that at least some of the species of Mastocarpus in the northeast Pacific are more widely distributed than our collections indicate. We hope this work provides the necessary framework for others to determine the range of morphological plasticity and details of their reproductive anatomy, ecology, physiology and geography.

We offer the following key to the gametophytic phase of species of Mastocarpus occurring in the northeast Pacific with a caveat: it will not work for all specimens. Most species of Mastocarpus are highly variable in their shape, particularly the widely distributed low intertidal species Mastocarpus intermedius and Mastocarpus latissimus, and it is impossible to account for that amount of polymorphism and still provide a useable key. To help cope with some of this variation, we refer the reader to Table S1 in Lindstrom (2008a) and to http://botany.ubc.ca/sandral/M[species epithet].jpg, where images of representatives of each species are posted. To help narrow the range of possible identifications, a map of the known distributions of northeast Pacific species of Mastocarpus discussed in this paper is presented in Fig. 42.

| 1. Thalli often of similar sizes and growing in clusters; stipe usually a third to three-quarters the height of the thallus; apophysis and most branches narrow, to ~2 mm wide, of more or less uniform width, except distal ends of branches, which may become bladelike | 2. Thalli not clustered, or if clustered, of different sizes; stipe mostly one quarter or less the height of the thallus; apophysis and branches mostly >2 mm wide, broadening distally | 3. Thalli to 15 cm tall; papillae present on cystocarpic thalli | 4. Branching more or less dichotomous, with orderly, slender branches that are four or more times dichotomous; from central California to the Aleutian Islands, Alaska | 5. Thalli up to 15 cm tall, divided up to six orders; papillae vermiform and pedicellate, generally not proliferous; occurring in the mid to high intertidal; known only from northern California (Cape Mendocino to Bodega Head) | 6. Branches or blades 4–10 mm wide, slender in appearance; papillae cylindrical, centrally or terminally enlarged; occurring in the low intertidal; known only from northern California to northern Southeast Alaska | 7. Vegetative blades stiplate, arising from the apex of the apophysis (occasionally subdichotomous); papillae sparse, mostly simple, restricted to older parts of the surface of female thalli; occurring on rock in the mid to high intertidal, often associated with sand; known from northern California to northern Southeast Alaska | 8. Vegetative blades part of a more or less dichotomous axis, proliferous branches when present not arising solely from the apophysis; papillae, habitats and distributions various |

| 5. Thalli up to 9 cm tall, divided up to four orders; papillae simple and sessile, becoming proliferous; occurring in the low to mid intertidal; known from Humboldt Bay, California, north to the Aleutian Islands, Alaska | 6. Branches or blades greater than 10 mm wide, bladelike in appearance; papillae, habitats and distributions various | 7. Branches of blades stiplate, arising from the apex of the apophysis (occasionally subdichotomous); papillae sparse, mostly simple, restricted to older parts of the surface of female thalli; occurring on rock in the mid to high intertidal, often associated with sand; known from northern California to northern Southeast Alaska | 8. Vegetative blades part of a more or less dichotomous axis, proliferous branches when present not arising solely from the apophysis; papillae, habitats and distributions various |

1 This species was described by Le Gall and Saunders (2010) from the west coast of Vancouver Island; it is also known from central California (Hughey, personal observations). Its morphological similarity to Ahnfeltiopsis leptophylla suggests it is more widely distributed than just these two areas. Habitat information included here was provided by Saunders (personal communication, 10 August 2010).
8. Blades irregularly dichotomous or proliferous, sometimes constricted; papillae on both surfaces and margins of blades and on both female and male thalli, male papillae can become proliferous; usually occurring in the mid to low intertidal ................................. 9
8. Blades more or less regularly dichotomous, rarely proliferous or constricted; papillae only on female thalli, mostly solely on surface of blades, male papillae lacking; usually found in the mid to high intertidal ................................. 11
9. Vegetative blades mostly narrow (< 8 mm wide); papillae diffuse on both female and male thalli, becoming branched or bladelike; known only from the Monterey Peninsula, California .............................................. M. cristatus
9. Vegetative blades very narrow (< 2 mm wide) to 30 mm broad; widely distributed. ................................................. 10
10. Female thalli with hemispheric to verrucose papillae, which can become very convoluted; known from Baja California, Mexico, to northern British Columbia and from a single site on Kodiak Island, Alaska .............................................. M. intermedium
10. Female thalli with simple papillae; known from Moss Beach, San Mateo County, California, north to Attu Island, Aleutian Islands, Alaska; Chile .............................................. M. latissimus
11. Papillae congested on margins of female plants, surfaces generally smooth; known from Kodiak Island, Alaska, to northern Japan .............................................. M. pacificus (pacificus form)
11. Papillae often stubble-like, restricted to older parts of the surface of the female thalli; known from California to the Aleutian Islands, Alaska ......... 12
12. Blades up to 15 (to 21) cm tall and up to 350 μm thick; mid to high intertidal but lower than M. papillatus where they co-occur; known from northern California to the Aleutian Islands, Alaska .............................................. M. alaskensis
12. Blades up to 9 cm tall and up to 500 μm thick; high intertidal, higher than M. alaskensis, where they co-occur; known from central California to northern Vancouver Island, British Columbia ................................................................. M. papillatus

ACKNOWLEDGEMENTS

We would like to thank the following people for making collections for us or for facilitating the collecting trips: Simona Augyte, Corban Bristow, Don Canestro, Amy Deveau, Kathleen Dickey, Paul Gabrielson, Larry Golden, Gayle Hansen, Jochen Halfar, Chris Harley, Max Hommersand, Jon Houghton, Gail Irvine, Emily Jones, Denis Kushnerak, Mandy Lindeberg, Kathy Ann Miller, Scott Pilcher, Vera Roningen, Susan Sauge, Frank Shaughnessy, Kathryn Springman and Andrew Weltz; Kathy Ann Miller (UC) and Marianne Hamnede (S) for supplying snippets of type material for sequencing and Patrik Frödén and Arne Thell (LD) for loaning material from the Herbarium Agardh; Jelena Pistolic, Vera Roningen, Juliana Kwan, Vida Omidvar, Tina Chen and Shadi Shadbahr for help in the laboratory; Gary Saunders for providing additional information on Mastocarpus pachynicus. An NSERC grant to SCL covered laboratory and some collecting expenses.

REFERENCES


Received 28 October 2010; accepted 12 April 2011

Associate editor: Giuseppe Zuccarello