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SOLVING TAXONOMIC AND NOMENCLATURAL PROBLEMS IN PACIFIC GIGARTINACEAE (RHODOPHYTA) USING DNA FROM TYPE MATERIAL[1]

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Molecular data obtained by a procedure for extracting PCR-amplifiable nuclear and chloroplast DNA from old and formalin-fixed red algal herbarium specimens were used to elucidate problems in the systematics of Pacific Gigartinaceae. Correspondence between nucleotide sequences of the internal transcribed spacer 1 region or the RUBISCO spacer from type specimens and modern collections supports the following conclusions. (1) The type of *Fucus cordatus* Turner, now *Iridaea cordata* (Turner) Bory, came from the southern hemisphere (probably from Isla de los Estados, Argentina) rather than from Banks Island, B.C., Canada. (2) The type of *Iridaea heterocarpa* P. et R. [*Mazzaella heterocarpa* (P. et R.) Fred.] represents the tetrasporangial phase of a species of *Chondrus*, possibly *C. crispus* Stackh. (3) The types of *Iridaea lilacina* P. et R., *I. phyllocarpa* P. et R., and *Iridophycus furcatum* S. et G. represent a single species from Alaska, *Mazzaella phyllocarpa* (P. et R.) Perest., currently but incorrectly called *M. heterocarpa*. (4) The type of *Iridophycus oregonum* Doty represents the tetrasporangial phase of the species from southern Alaska to southern California known incorrectly as *M. heterocarpa*. (5) *Mazzaella splendens* (S. et G.) Fred. is more closely related to *M. linearis* (S. et G.) Fred. than it is to *M. flaccida* (S. et G.) Fred. (6) *Iridophycus coriaceum* S. et G. is conspecific with *M. splendens*, whereas *Rhodoglossum coriaceum* E.Y. Dawson is an independent species: *Mazzaella coriacea* (E.Y. Dawson) Hughey. (7) *Iridaea cornucopiae* P. et R. is conspecific with *Mazzaella laminarioides* (Bory) Fred., and the type probably came from Chile rather than from the North Pacific. (8) Plants attributed to *Iridaea cornucopiae* in Pacific North America are referable to *Mazzaella parksii* (S. et G.) comb. nov. (9) *Rhodoglossum parvum* G. M. Smith et Hollenb. is an independent species: *Mazzaella parva* (G. M. Smith et Hollenb.) comb. nov. (10) *Grateloupia squarrulosa* S. et G., *Grateloupia johnstonii* S. et G., and *Gigartina pectinata* E.Y. Dawson represent a single species: *Chondracanthus squarrulosus* (S. et G.) comb. nov.

Key index words: **Chondracanthus; DNA; Gigartinaceae; herbarium specimens; *Iridaea*; ITS 1; *Mazzaella*; PCR; red algae; RUBISCO spacer; type material**

Abbreviations: **ITS, internal transcribed spacer**

Marine macroalgae are preserved and stored today largely as they have been for 300 years. They are spread out on a sheet of mounting paper, sometimes after immersion for varying lengths of time in a formalin solution, and covered with cloth or waxed paper. The wet specimens are then dried between sheets of blotting paper under pressure. Dried specimens usually adhere to the mounting paper with exuded polysaccharide and are resistant to decay when stored in folders in herbaria. Ironically, members of the Gigartinaceae, the family of red algae with which the present article is concerned, together with certain other carrageenophytes, are uniquely predisposed to self-destruct in the herbarium (Nelson and Falshaw 1999). Fortunately, none of the critical specimens used in the present study had undergone visible chemical deterioration.

Type specimens, on which names of species are based, are necessary sources of comparative material for systematic studies. Principle II of the International Code of Botanical Nomenclature states, "The application of names of taxonomic groups is determined by means of nomenclatural types" (Greuter et al. 2000, p. 3). The Gigartinaceae is a family of red algae with approximately 100 currently recognized species, almost all of which have extant type specimens. Although morphological and molecular studies have advanced our understanding of this family at the generic level (Hommersand et al. 1993, 1994, 1999), the taxonomic and nomenclatural status of many of the species remains in doubt, partly because of the high degree of plasticity exhibited by the thallus and the absence of unambiguous diagnostic characters.

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A few reports of the extraction and amplification of nuclear and plastid DNA from herbarium material have been published. Goff and Moon (1993) were successful in using a specimen of *Gracilaria* that had been collected 11 years earlier and not fixed in formalin, whereas Brodie et al. (1998) used specimens of *Porphyra* collected as early as 1926 but of unstated preservation history. Hughey and Hommersand (1999) outlined a procedure that was effective for isolating amplifiable nuclear and chloroplast DNA from very old herbarium specimens (as old as 327 years) and formalin-fixed material. In this study, we compared internal transcribed spacer (ITS 1) and intergenic RUBISCO spacer DNA sequences of type material to those of modern collections to solve some long-standing taxonomic problems in the Gigartinaceae from Pacific North America. The ITS 1 and RUBISCO spacer regions are ideal parts of the genome for determining the identity of red algal type specimens because they are sufficiently variable and short enough that PCR products are consistently obtainable (Maggs et al. 1992, Goff et al. 1994, Van Oppen et al. 1995, Lindstrom et al. 1996, Müller et al. 1998, Rintoul et al. 1999).

MATERIALS AND METHODS

Material used for the DNA analyses consisted of fragments of type specimens and other historically important herbarium collections that were investigated in comparison with recent specimens collected in the vicinity of the type locality. Species investigated are listed in Table 1 and in the Appendix together with their GenBank numbers.

DNA extraction. Approximately 15 mg of dried tissue ($\sim$5 mm^2) was ground in a 1.7-mL microcentrifuge tube with a pellet pestle in 700 μL of extraction buffer (Dellaporta et al. 1983) containing 100 mM Tris (pH 8.0), 50 mM EDTA, 500 mM NaCl, 10 mM 2-mercaptoethanol (added just before use, 7 μL·mL^{-1} extraction buffer), 50 μL of 20% SDS, 10 μL of 0.1 M DTT, 4 mg of lyophilized Proteinase K (Boehringer Mannheim, Indianapolis, IN), and incubated at 65° C for 3 h or overnight. Polysaccharides were removed by adding 250 μL of potassium acetate (5 M), incubating on ice for 30 min, and centrifuging for 30–40 min at 12,000*g* (Dellaporta et al. 1983). The supernatant (750 μL) was extracted once with an equal volume of chloroform in a sterile tube and then centrifuged for 15 min at 12,000*g*. DNA was precipitated from the aqueous phase with two-thirds volume isopropanol for ≥1 h at −20° C, spun for 20–30 min at 12,000*g*, and washed with 450 μL of 70% ethanol. DNA samples were air dried and resuspended in 100 μL of distilled water or TE (10 mM Tris-Cl, 1 mM EDTA, pH 8.0). A working solution of 10:1 (water:DNA) was prepared for PCR in a separate tube. A negative control containing no organic material was performed with each set of extractions. Vortexing was avoided during all steps to prevent shearing the DNA.

DNA amplification protocol. Six to 12 μL of diluted DNA was added to each 50-μL reaction containing 5 μL of 10× reaction buffer (containing 15 mM magnesium chloride), 10 μL of Q-solution, 1–3 μL from each 10 μM primer (Table 2), 200 μM of each dNTP, and 2.5–5.0 units of Taq DNA Polymerase (Qiagen, Valencia, CA). Using Qiagen Taq Polymerase in combination with the manufacturer's buffer and Q-solution, we were able to amplify samples that previously failed. Initially, the ITS region was amplified and sequenced with the ITS 1 forward primer reported in White et al. (1990), but later, to avoid amplification of fungal contaminants common on herbarium specimens, two genus-specific primers were synthesized (Table 2): ITS 1M, *Mazzaella* specific, and ITS 1C, *Chondracanthus* specific. The ITS 2 reverse primer (White et al. 1990) was used for all reactions. The ITS 4 reverse primer (White et al. 1990) was used to amplify the ITS 1, 5.8S, and ITS 2 of *Rhodoglossum parvum*. The RUBISCO spacer was amplified using the F-1467 primer (Table 2) and the R-*rbc*S primer (Hommersand et al. 1994).

Table 1. Concordance of names treated in this article. Names enclosed in quotation marks are misapplied.

Original name	Name in Abbott (1972) or Abbott and Hollenberg (1976)	Name Resulting from this study
Chondrus affinis	*Rhodoglossum affine*	*Mazzaella affinis*
Collinsia californica	*Rhodoglossum californicum*	*Mazzaella californica*
Fucus cordatus	NA	*Iridaea cordata*
Gigartina pectinata	NA	*Chondracanthus squarrulosus*
Grateloupia johnstonii	NA	*Chondracanthus squarrulosus*
Grateloupia squarrulosa	NA	*Chondracanthus squarrulosus*
NA	*"Iridaea cordata"*	*Mazzaella splendens*
Iridaea cornucopiae	NA	*Mazzaella laminarioides*
NA	*"Iridaea cornucopiae"*	*Mazzaella parksii*
Iridaea heterocarpa	NA	*Chondrus cf. crispus*
NA	*"Iridaea heterocarpa"*	*Mazzaella oregona* and *Mazzaella phyllocarpa*
Iridaea laminarioides	NA	*Mazzaella laminarioides*
Iridaea lilacina	*"Iridaea cordata"*	*Mazzaella phyllocarpa*
Iridaea micans	NA	*Iridaea cordata*
Iridaea phyllocarpa	NA	*Mazzaella phyllocarpa*
Iridaea rosea	*Rhodoglossum roseum*	*Mazzaella rosea*
Iridophycus coriaceum	*"Iridaea cordata"* var. *splendens*	*Mazzaella splendens*
Iridophycus flaccidum	*Iridaea flaccida*	*Mazzaella flaccida*
Iridophycus fulgens	*"Iridaea cordata"* var. *splendens*	*Mazzaella splendens*
Iridophycus furcatum	*"Iridaea heterocarpa"*	*Mazzaella phyllocarpa*
Iridophycus lineare	*Iridaea lineare*	*Mazzaella linearis*
Iridophycus oregonum	*"Iridaea cordata" var. splendens*	*Mazzaella oregona*
Iridophycus parksii	*"Iridaea cornucopiae"*	*Mazzaella parksii*
Iridophycus reediae	*"Iridaea cordata"* var. *splendens*	*Mazzaella splendens*
Iridophycus sinicola	*"Iridaea cordata"* var. *splendens*	*Mazzaella splendens*
Iridophycus splendens	*"Iridaea cordata"* var. *splendens*	*Mazzaella splendens*
Rhodoglossum coriaceum	*"Iridaea cordata"* var. *splendens*	*Mazzaella coriacea*
Rhodoglossum parvum	*Rhodoglossum roseum*	*Mazzaella parva*

NA, not applicable.

TABLE 2. Primers used in this study.

Primer	Oligonucleotide sequence	Authority
ITS 1	TCCGTAGGTGAACCTGCGG	White et al. (1990)
ITS 1C	GGACATTCGTAGTGGGATAGC	This paper
ITS 1M	GGACATTCGTAGTGGGATGAC	This paper
ITS 2	GCTGCGTTCTTCATCGATGC	White et al. (1990)
ITS 4	TCCTCCGCTTATTGATATGC	White et al. (1990)
F-1467	CTCCAACAGCTAACGTTTAG	This paper
R-*rbc*S	TGTGTTGCGGCCGCCCTTGTGTTAGTCTCAC	Hommersand et al. (1994)

Primers 5′→3′.

Reactions were cycled in a PTC-100 PCR Thermocycler (MJ Research, Watertown, MA) using the following parameters: 94° C for 3 min, followed by 40 cycles of 95° C for 30 s, 50° C for 90 s, and 72° C for 90 s, and final extension of 72° C for 5 min. PCR products were electrophoresed on 1.5% agarose gels containing EtBr (0.5 $\mu g \cdot mL^{-1}$) and purified using the QIAquick PCR Purification Kit following the manufacturer's instructions (Qiagen). Some PCR amplifications that failed were successfully amplified under 1/2 volume conditions, by increasing the concentration of primers, or by extending the annealing time to 120 s. A negative control was run with each set of PCR reactions to check for contamination. PCR products were sequenced with Big Dye Terminators (ABI Automated 377, PE Applied Biosystems, Foster City, CA).

Precautionary steps to avoid contamination

1. The DNA stocks, PCR reagents, and PCR products were stored in separate cases (see Hummel and Herrmann 1994)
2. To monitor for false positives, a negative control containing no organic material was performed with each set of extractions. The control was run through the entire procedure, from extraction to amplification, and treated under the same conditions as the investigated samples.
3. Specimens were extracted in small batches. No more than two, four, or six samples were processed at one time, reducing the complexity and thus the possibility for error.
4. Samples were processed in alternating order. When two or more samples of one species were extracted in the same batch, they were separated in the rack by a sample belonging to a different taxon. Sample order was maintained throughout the extraction, amplification, and sequencing procedures. For example, if species A was placed in tubes 1 and 3, then species B would be placed in tubes 2 and 4, a third species might be placed in tube 5, whereas tube 6 would be the negative control. This system was adopted as a safeguard to detect the carry-over of DNA from tube to tube during processing. Chromatograms were critically examined and compared for signal, background, and sequence between and within batches for all data that were generated.
5. Reagents were routinely discarded. Reaction buffers, Q-solution, and sterile water were discarded regularly, and small aliquots of dNTPs and primers were exhausted after mixing three to four PCR cocktails.
6. Herbarium specimens of unrelated red algae were analyzed. If rampant contamination was a problem in our current laboratory, then amplifying and sequencing DNA from formalin-fixed herbarium specimens of other red algae would detect spurious Gigartinaceae DNA. To test the possibility that our results were due to foreign contaminants, we sequenced the ITS 1 region of species from selected samples of *Cryptopleura*, *Gelidium*, *Gracilaria*, *Gracilariopsis*, *Palmaria*, *Polysiphonia*, and *Rhodymenia*. All the resulting sequences agreed with those posted for their respective genera in GenBank. None matched any that were posted for Gigartinaceae.

Data Analysis. The boundaries of the ITS 1 region and RUBISCO spacer were determined from published sequences in Goff et al. (1994), Hommersand et al. (1994), and Van Oppen et al. (1995). Sequences were pasted directly into MacDraw Pro 1.5v2 (Claris Corp., Santa Clara, CA) and aligned manually. All reference to the number of base pairs (bp) that differ between sequences included gaps unless otherwise noted.

Abbreviations of authors of scientific names are in accordance with Brummitt and Powell (1992) except as follows: C. Ag. (C. Agardh), J. Ag. (J. Agardh), Fred. (Fredericq), Lamour. (Lamouroux), P. et R. (Postels et Ruprecht), and S. et G. (Setchell et Gardner).

RESULTS

Length and sequence divergences observed for the ITS 1 and RUBISCO spacer in Gigartinaceae were within the ranges generally reported for red algae. Sequences were obtained for the ITS 1 region from holotype, lectotype, or isotype specimens of all species of *Iridophycus* described by Setchell and Gardner (1937) from Pacific North America, including taxonomic (heterotypic) synonyms. Sequences were also obtained from several type specimens of *Mazzaella* from central California (previously attributed to *Rhodoglossum*) and of *Chondracanthus* from the Gulf of California (previously attributed to *Gigartina* or *Grateloupia*). The RUBISCO spacer was sequenced for the type of *Fucus cordatus* Turner because the ITS 1 region failed to amplify in this sample. DNA sequences were compared with each other and with recently collected field material. Our observations (Figs. 1–3) are summarized as follows:

1. A RUBISCO spacer sequence from the type of *Fucus cordatus* [*Iridaea cordata* (Turner) Bory] was identical to that of a recent collection from Isla de los Estados, Argentina and differed from a collection from Chile by 2 bp and from type material of *Iridaea micans* Bory from the Falkland Islands by 3 bp. It differed from specimens attributed to *I. cordata* from British Columbia and Washington by 11–12 bp.
2. An ITS 1 sequence of the type of *Iridaea heterocarpa* P. et R. [*Mazzaella heterocarpa* (P. et R.) Fred.] from Kamchatka, Russia differed from that of *Chondrus crispus* Stackh. from England and Connecticut and from *Chondrus platynus* (C. Ag.) J. Ag. from the Sea of Okhotsk, Russia by 1 bp. It differed from the type of *Iridaea lilacina* P. et R. by 18 bp and from specimens attributed to *M. heterocarpa* from Oregon by 23–24 bp.
3. An ITS 1 sequence of the type of *Iridaea lilacina* P. et R. [*Mazzaella lilacina* (P. et R.) Leister] from Sitka, Alaska was identical to that of the type of *Iri-*

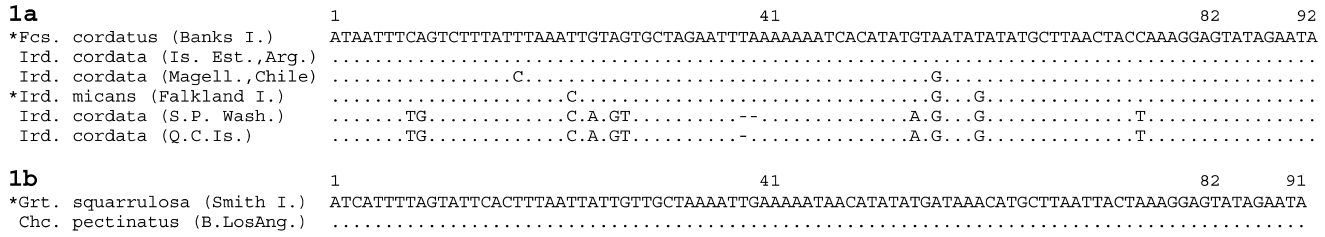

FIG. 1. Aligments of RUBISCO spacer sequences. Abbreviations correspond to names and localities in the Appendix. Dots are identical to uppermost line, dashes indicate gaps, and asterisks (*) indicate type material. (a) *Fucus cordatus, Iridaea micans.* and *I. cordata* sensu Setchell from Pacific North America. (b) *Grateloupia squarrulosa* and *Chondracanthus pectinatus.*

daea phyllocarpa P. et R. [*Mazzaella phyllocarpa* (P. et R.) Perest.] reported as being from Kamchatka, Russia and the type of *Iridophycus furcatum* S. et G. from Sitka, Alaska and differed from other specimens attributed to *Mazzaella heterocarpa* from Alaska by zero to 1 bp. It differed from the type of *Iridophycus oregonum* Doty and from collections attributed to *Mazzaella heterocarpa* from southern Alaska, Oregon, and California by 4–7 bp.

4. An ITS 1 sequence of the type of *Iridophycus splendens* S. et G. [*Mazzaella splendens* (S. et G.) Fred.] differed from that of the types of *I. coriaceum* S. et G., *I. reediae* S. et G., *I. sinicola* S. et G., and recent collections of *M. splendens* from central California by zero to 1 bp and from the type of *I. fulgens* S. et G. from Trinidad, California and a recent collection of *M. splendens* from southern Alaska by 3 bp.
5. An ITS 1 sequence of the type of *Iridophycus lineare* S. et G. [*Mazzaella linearis* (S. et G.) Fred.] was identical to that of recent collections from central California and differed from a sample from British Columbia by 1 bp. It differed from the type of *M. splendens* by 4 bp.
6. An ITS 1 sequence of the type of *Iridophycus flaccidum* S. et G. [*Mazzaella flaccida* (S. et G.) Fred.] was identical to that of a recent collection from California. It differed from type specimens of *M. splendens* and *M. linearis* by 6 bp.
7. An ITS 1 sequence of the type of *Rhodoglossum coriaceum* E.Y. Dawson [*Mazzaella coriacea* (E. Y. Dawson) Hughey] differed from a recent collection from Monterey, California by 3 bp and from a recent collection from La Bufadora, Baja California by 1 bp. It differed from the type of *Iridophycus coriaceum* S. et G. from the Monterey Peninsula by 18 bp.
8. An ITS 1 sequence of the type of *Iridaea cornucopiae* P. et R. [*Mazzaella cornucopiae* (P. et R.) Hommers.], thought to come from the North Pacific Ocean, differed by zero to 3 bp from the type and recent collections of *Mazzaella laminarioides* (Bory) Fred. from central Chile. It differed from the type of *Iridophycus parksii* S. et G. from Trinidad, California and from collections attributed to *M. cornucopiae* from Alaska, Oregon, and California by more than 30 bp. It differed from a specimen attributed to *Iridaea cornucopiae* from the Kurile Islands, Russia by 31 bp.
9. An ITS 1 sequence of the type of *Rhodoglossum parvum* G. M. Smith et Hollenb. from Monterey, California differed by zero to 1 bp from other collections of this species. It differed by 22 bp from *Rhodoglossum roseum* Kylin [*Mazzaella rosea* (Kylin) Fred.] where it had been placed in synonymy, and by 16 bp from *M. affinis* (Harv.) Fred.
10. An ITS 1 sequence of the type of *Gigartina pectinata* E.Y. Dawson [=*Chondracanthus pectinatus* (E.Y. Dawson) L. Aguilar et R. Aguilar] from the Gulf of California was identical to that of *Grateloupia squarrulosa* S. et G. and differed by 1 bp from that of *Grateloupia johnstonii* S. et G. from the same region.

DISCUSSION

To facilitate an understanding of the various taxonomic problems addressed in this study, we preface our discussion of these problems with an account of the relationship among generic names that have been applied to Gigartinaceae in the northeast Pacific. *Chondrus* was established by Stackhouse (1797 [1795–1801], p. xv, xxiv) to accommodate six species previously assigned to *Fucus*, distinguished by having embedded cystocarps that protrude above both surfaces of the thallus. Later, Stackhouse (1801 [1795–1801], p. xxxii) stated that *Chondrus* comprised a single species, *C. crispus* Stackh., from the North Atlantic. *Chondrus* was first attributed to the Pacific coast of North America by Harvey (1841) but excluded from that region by Kylin (1928). The generic revisions of Hommersand et al. (1993, 1994, 1999) restrict the genus to the western North Pacific in addition to the North Atlantic.

Gigartina was established by Stackhouse (1809, pp. 55, 74) on the basis of *Fucus pistillatus* S. G. Gmelin (1768, p. 159, pl. XVIII: fig. 1), of unknown provenance. Unaware of the Stackhouse publication (most copies of the journal were destroyed by fire during Napoleon's occupation of Moscow in 1812), Lamouroux (1813, p. 134) also established a genus named *Gigartina.* As defined by Lamouroux, *Gigartina* included red algae with cylindrical axes bearing spherical or hemispherical tubercles, thus encompassing 30 species representing several different presently recog-

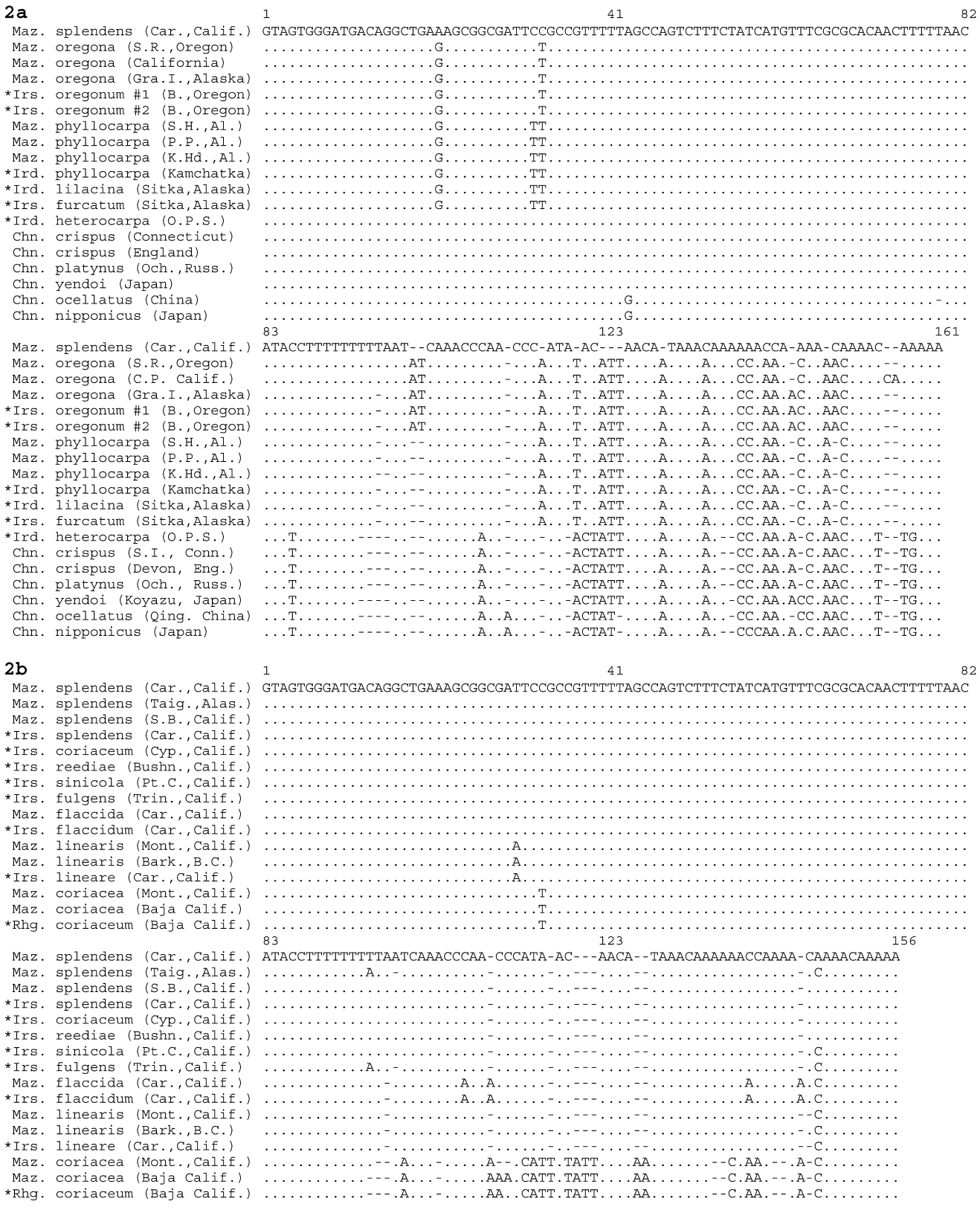

FIG. 2. Alignments of ITS 1 sequences. Abbreviations correspond to names and localities in the Appendix. Dots are identical to uppermost line, dashes indicate gaps, and asterisks (*) indicate type material. (a) *Mazzaella splendens*, *Iridophycus oregonum*, *Iridaea phyllocarpa*, *Iridaea lilacina*, *Iridophycus furcatum*, *Iridaea heterocarpa*, and *Chondrus* spp. (b) *Iridophycus splendens*, *I. coriaceum*, *I. reediae*, *I. sinicola*, *I. fulgens*, *I. flaccidum*, *I. lineare*, and *Rhodoglossum coriaceum*.

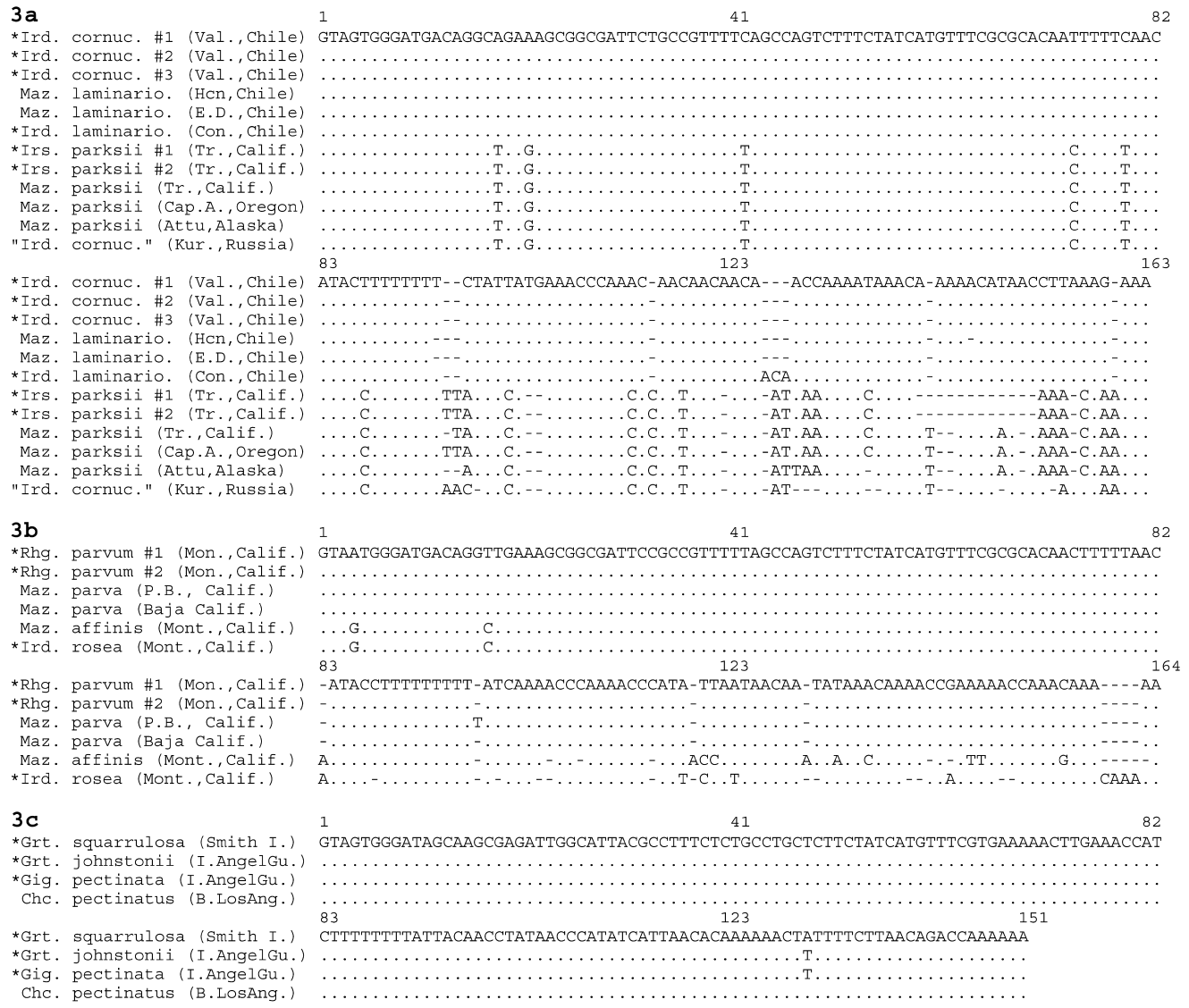

FIG. 3. Alignments of ITS 1 sequences. Abbreviations correspond to names and localities in the Appendix. Dots are identical to uppermost line, dashes indicate gaps, and asterisks (*) indicate type material. (a) *Iridaea cornucopiae*, *I. laminarioides*, and *Iridophycus parksii*. (b) *Rhodoglossum parvum*, *Mazzaella affinis*, and *Iridaea rosea*. (c) *Grateloupia squarrulosa*, *G. johnstonii*, and *Gigartina pectinata*.

nized genera, families, and even orders. Among the original species was *Fucus pistillatus*. Although the two uses of the name *Gigartina* were coincidental, they had a common source: *Fucus gigartinus* Linnaeus (1759, p. 1344), an earlier heterotypic synonym of *Fucus pistillatus*. The epithet is derived from the Greek word *gigarton*, meaning grape seed, and refers to the large tuberculate cystocarps produced by this species. Both Stackhouse and Lamouroux adopted the later of the two synonyms to avoid publishing a tautonym. In accordance with Art. 7.5 of the St. Louis Code (Greuter et al. 2000), *Gigartina* Lamour. must be typified with *F. pistillatus*, the type of *Gigartina* Stackh., a generic name that Lamouroux should have adopted and coincidentally did adopt. In this rare nomenclatural situation, *Gigartina* Lamour. is considered an isonym of *Gigartina* Stackh. Lamouroux's account is treated as if he had attributed the generic name to Stackhouse.

J. Agardh (1842, p. 103; 1851–1863, p. 260; 1876, p. 189) was the architect of the genus as conceived during the 20th century, with emphasis on external tubercular cystocarps. Most recently, Abbott and Hollenberg (1976) recognized 10 species in California. The generic revisions of Hommersand et al. (1993, 1994, 1999), however, exclude *Gigartina* from the Pacific coast of the Americas and Japan. To accommodate Pacific species that had been placed in *Gigartina*, those authors adopted the generic name *Chondracanthus* Kützing (1843, p. 399), which had resided in the synonymy of *Gigartina* for more than a century. Setchell

and Gardner (1933, p. 257) treated *Chondracanthus* as a subgenus of *Gigartina* and lectotypified it with *C. chauvinii* (Bory) Kütz. from Chile.

Iridaea was established by Bory (1826a, p. 15) to accommodate several foliose red algae characterized primarily by their iridescence. Earlier (invalid) uses by Bory of this name and its variant *Iridea*, as well as their subsequent history, are detailed by Parkinson (1981). Bory (1826a, 1826b, 1827–1829) assigned the new genus to his new family Laminariaceae. He was aware that the generic name was preoccupied by *Iridea* Stackhouse (1816) but felt free to use it in a different sense because the earlier homonym was a synonym of *Desmarestia* Lamouroux (1813). Bory was probably not aware, however, that his use of the name was superfluous because the circumscription of the genus included the type species of two previously described genera, *Palmaria* Stackhouse (1801) and *Dilsea* Stackhouse (1809). According to Art. 7.5 of the St. Louis Code (Greuter et al. 2000), *Iridaea* should be typified with the type of the earlier of the two generic names (*Fucus palmatus* Linnaeus, the type of *Palmaria*). In the absence of such a rule, Greville (1830, p. 157) chose *Fucus edulis* Stackhouse (1796), on which *Dilsea* had been based, as the type. Greville also dismissed Bory's placement of *Iridaea* in the Laminariaceae, saying that the two taxa had "absolutely no points in common except a flat frond, and the ocean for its habitation." The genus was placed in the Gigartinaceae by Kützing (1843, p. 395).

In treating South African *Iridaea*, J. Agardh (1848, 1849) removed the types of *Palmaria* and *Dilsea*, among other species, leaving a core of previously and newly published species that defined the genus as generally conceived in the 20th century. He considered *I. cordata* (Turner) Bory (1826a, p. 16) as the type. Schmitz (1889, p. 440), however, designated *I. micans* Bory (1826a, p. 16) as the type.

Setchell and Gardner (1936), in a review of South American representatives of *Iridaea*, were faced with the knowledge that Bory's generic name was a later homonym. In view of the conflicting ways in which *Iridaea* had been typified, they chose to describe a new genus, *Iridophycus*, rather than merely propose a substitute name. They designated *Iridophycus capense* (J. Ag.) S. et G. (*Iridaea capensis* J. Ag. 1848) as type.

Kylin (1941, p. 23) examined type material of *Collinsia californica* J. Agardh (1899, p. 79), the only species of its genus, and found that it was referable to *Iridaea*. Meanwhile, G. DeToni (1936), combing the phycological literature for homonyms, noted that *Collinsia* J. Agardh 1899 was preoccupied by *Collinsia* Nuttall 1817 (Scrophulariaceae) and proposed the substitute name *Mazzaella*, commemorating Angelo Mazza (1844–1929), a minor Italian phycologist.

Papenfuss (1947) pointed out that unless the name *Iridaea* was conserved, it would have to be replaced by *Mazzaella* rather than *Iridophycus* because the former was published a few months earlier than the latter. He wrote, "Unless *Iridaea* were conserved, a comparatively large number of species would thus have to be transferred to the little-known *Mazzaella*." *Iridaea* was subsequently conserved, with the conserved type *I. cordata* (Turner) Bory.

Hommersand et al. (1993, 1994, 1999) reorganized the genera within the Gigartinaceae on the basis of morphology and molecular data. The suite of characters used by those authors to define the genus *Iridaea* was found in species from the southern hemisphere, but not the northern hemisphere. A generic name was thus needed to accommodate those North Pacific species that had been assigned to *Iridaea*. This name was unwittingly provided by G. DeToni when he proposed *Mazzaella* as a substitute for *Collinsia* J. Ag. Thus, Papenfuss' attempt to prevent the adoption of this little-known name was foiled by the vagaries of taxonomy.

Rhodoglossum was established by J. Agardh (1876, p. 183) on the basis of five species from Tasmania and New Zealand. It was said by its author to be closely related to *Iridaea*, from which it differed primarily by the position of the tetrasporangial sori, subcortical in *Rhodoglossum* versus medullary in *Iridaea*. *Rhodoglossum* was treated as a subgenus of *Iridaea* by DeToni (1897, p. 189), but Setchell (in Collins et al. 1898, no. 538) disagreed and attributed the genus to the Pacific coast of North America. *Rhodoglossum* was credited with four species in the California flora by Abbott and Hollenberg (1976). As with *Iridaea* and *Gigartina*, the generic revisions by Hommersand et al. (l.c.) exclude *Rhodoglossum* from Pacific North and South America, assigning those species to *Mazzaella*.

Identity of Fucus cordatus *Turner.* *Fucus cordatus* Turner (1808–1809, p 118, pl. 116), the conserved type of *Iridaea* Bory 1826 *nom. cons.*, was described from a collection made by Archibald Menzies, the surgeon and naturalist of the Vancouver Expedition (1791–1795), allegedly "At Banks' Isles, on the North West coast of North America," and indeed this is the inscription on the backside of the type sheet in the herbarium of the Royal Botanic Garden, Edinburgh (Fig. 4a). There are two specimens on the type sheet, both of which are cystocarpic.

In 1937, the type sheet was lent to Setchell, who removed fragments for sectioning. These fragments remain in UC, but the label does not specify from which of the two specimens they were removed, nor does Setchell provide this information in the published results of his study (Setchell 1940). He noted, however, that the lower specimen was a very close match to Turner's figure. Kim (1976, p. 94), without explaining his choice, designated the lower specimen as lectotype, but Leister (1977, p. 55) pointed out that when Turner's figure is reversed, back to front, it matches the upper specimen almost perfectly.

Setchell (1940) concluded that *Fucus cordatus* was applicable to a species "most probably confined to the shores of northwestern North America, not having been found south of the Straits of Juan de Fuca, and certainly bearing no relation to the South American

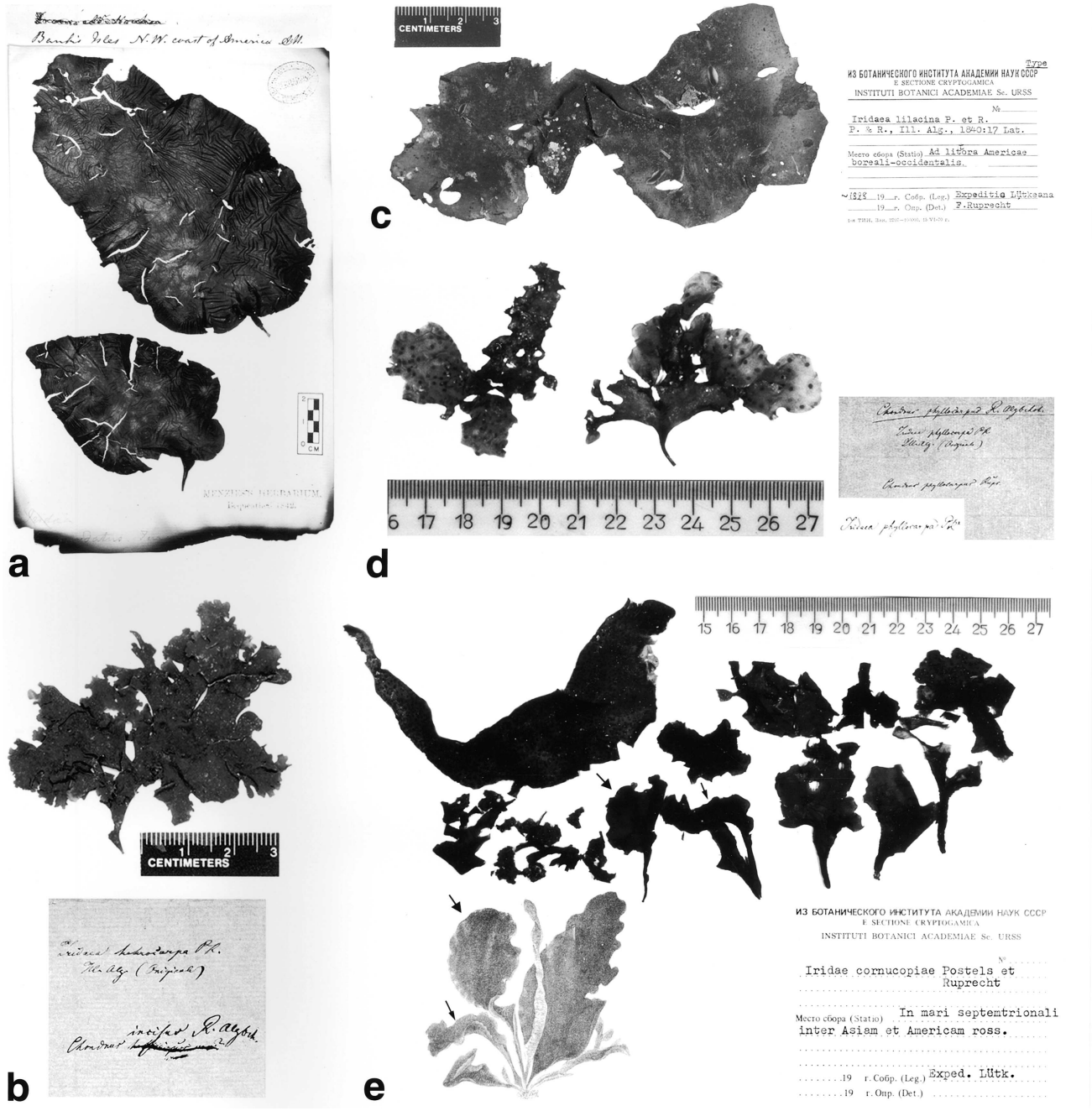

FIG. 4. Habits of type specimens reported from the northeastern Pacific that were DNA sequenced in this study. (a) *Fucus cordatus* Turner (E) (photo by G. L. Leister). (b) *Iridaea heterocarpa* P. et R. (LE). (c) *Iridaea lilacina* P. et R. (LE). (d) *Iridaea phyllocarpa* P. et R. (LE). (e) *Iridaea cornucopiae* P. et R. (LE). Top: Photo by S. Lindstrom. Bottom: Illustration of *Iridaea cornucopiae* in P. et R. (1840, Pl. XXXVIII, fig. b). Broad and narrow arrows indicate correpondence of two blades illustrated by Postels and Ruprecht with specimens in the type collection.

or South African species earlier considered identical with it." In a striking departure from Setchell's conclusion, Leister (1977) found that the type of *F. cordatus* matched in morphological detail the type of *Iridaea micans* Bory (1826a, p. 16), originally described from the Falkland Islands. On the other hand, he found that it differed significantly in cystocarpic and tetrasporangial development from the North American alga previously identified as *I. cordata*. He pointed out the need for a revision of the Gigartinaceae based on "new investigations of morphological and anatomical characters analyzed and interpreted from a developmental perspective." Such investigations were undertaken by Hommersand et al. (1993, 1994, 1999).

In support of his suspicion that the type sheet of *Fucus cordatus* had been assigned an erroneous provenance, Leister noted that the Vancouver Expedition did not anchor in the vicinity of Banks Island (east coast of Hecate Strait, British Columbia, Canada). He thought it probable that the type specimens had been collected by Menzies when he was surgeon on Captain Colnett's *Prince of Wales* on the northern shore of Isla de los Estados, Argentina where the ship anchored from 26 January to 12 February 1787. A dissenting opinion has been provided in a personal communication by Eric W. Groves (Department of Botany, Natural History Museum, London), who has studied Menzies's collections closely. Groves found few labeling errors and is therefore convinced that the type specimens of *F. cordatus* indeed were collected in British Columbia.

To test Leister's hypothesis that the type specimens of *Fucus cordatus* came from the southern rather than the northern hemisphere, we compared DNA sequences of the RUBISCO spacer from several specimens, including the upper specimen on the type sheet, two South American specimens of *Iridaea cordata* (one from Magellanes, Chile, the other from Isla Observatorio, Isla de los Estados, Argentina), the cystocarpic specimen illustrated by Bory 1828 [1827–1829], pl. 13 bis, fig. a) under the name *I. micans* from the Falkland Islands, and two North American specimens of *I. cordata* sensu Setchell (one from Shannon Point, Washington, the other from Striae Point, Queen Charlotte Islands, British Columbia, opposite Banks Island) (Fig. 1a). The DNA sequence obtained for *F. cordatus* was identical to that for *I. cordata* from Isla de los Estados but differed from that of the Chilean specimen by 2 bp and from that of Bory's *I. micans* by 3 bp. In contrast, it differed significantly from the sequences obtained for the North American specimens, by 11 bp in the case of the Queen Charlotte specimen and by 12 bp in the case of the Washington specimen. In our opinion, the latter specimens, which differ between themselves by only 1 bp, are both representative of *Mazzaella splendens* (S. et G.) Fred. (in Hommersand et al. 1994, p. 198, Table IV). These molecular data support Leister's conclusion that *F. cordatus* came from the southern hemisphere and probably from Isla de los Estados, Argentina.

Identities of Iridaea heterocarpa *P. et R.,* Iridaea lilacina *P. et R.,* Iridaea phyllocarpa *P. et R., and* Iridophycus oregonum *Doty.* The plant generally known as *Mazzaella heterocarpa* (P et R.) Fred. (*Iridaea heterocarpa* P. et R.) is said to be widely distributed from Alaska to southern California (Scagel et al. 1989). Setchell and Gardner (1903, p. 299) initially treated *I. heterocarpa* as a probable synonym of *I. cordata* (as *I. laminarioides* f. *cordata*). At that time, the species was known to Setchell and Gardner only from the protologue. In November 1903, Setchell visited St. Petersburg for the purpose of examining the types of the Postels and Ruprecht species. Unfortunately, he did not specify in his notes the reproductive stage of the type of *I. heterocarpa*, merely commenting that "an original Ill. Alg. specimen is a lobed *Ir. lam.* f. *parvula*." Later, in a synopsis of an unpublished monograph on *Iridophycus*, Setchell and Gardner (1937, p. 170) recognized *I. heterocarpum* as an independent species but failed to provide a description. In the unpublished manuscript (in UC), which appears to have been written primarily by Gardner, the genus is treated in full. Their description of *I. heterocarpum* was based on specimens, each with a very short stipe and a blade that was variously lobed or incised and usually broader than tall and that had relatively large cystocarps (up to 3 mm diameter) but variable in size even on the same plant, thus consonant with the epithet bestowed on the species by Postels and Ruprecht. As shown below, however, the epithet probably did not refer to mature cystocarps. Setchell and Gardner's concept of *I. heterocarpum* was adopted by Smith (1944, p. 291) and Abbott (1972, p. 65, figs.18–20), the latter citing *I. furcatum* Setchell et Gardner (1937, p. 171) from Sitka, Alaska as a synonym.

Based on developmental details of the cystocarp of specimens identified as *Iridophycus heterocarpum* but not including the type, Fredericq (in Hommersand et al. 1993, p. 110) referred *Iridaea heterocarpa* to *Mazzaella.* To determine the correctness of the current circumscription of *Mazzaella heterocarpa*, we examined the single specimen constituting the holotype of *Iridaea heterocarpa* Postels et Ruprecht (1840, p. 18), which was lent by LE. According to the protologue, its provenance is "oceano pacifico septemtrionali." On the outside of the envelope is written "*Iridaea heterocarpa* PR., Ill. Alg. (Original), *Chondrus heterocarpus* R. Alg. Och." The word "*heterocarpus*" is crossed out and above it is written "*incisus.*" The envelope contains a single tetrasporangial specimen (Fig. 4b), with a habit that agrees with the original description. The fact that it is tetrasporangial, however, is puzzling because according to the protologue, "sporidia" are lacking.

In interpreting the protologues in Postels and Ruprecht, one must keep in mind that Ruprecht was completely responsible for the text of "*Illustrationes Algarum*" and that he was a 25-year-old grass specialist at the time he was assigned the task. Literature available to him (e.g., Greville 1830) would have taught him that red algae have a double fructification: "spherical or hemispherical capsules, sessile or stalked, and containing a round mass of seeds" (i.e. cystocarps with carposporangia) and "granules (mostly ternate) scattered or collected into little spots (sori) or lines" (i.e. tetrasporangia with tetraspores). Although it was known that the two types of fructification occurred on distinct specimens, their interrelationship in a life history remained a mystery throughout the 19th century. It is important to note that although Greville easily distinguished emergent "capsules" from embedded "granules" in *Gracilaria*, he was confused when dealing with foliose fronds in which both cystocarps and tetrasporangial sori are embedded. *Chondrus*, for example, was considered to have a single fructification,

"subspherical capsules . . . containing a mass of minute free seeds."

Despite Ruprecht's lack of experience, he chose to coin new terms for reproductive structures in red algae. "Capsules" were called "gongyli" and "granules" were called "sporidia." *Iridaea heterocarpa* was said to lack definite sporidia but to have gongyli mixed with rose-colored granules. The gongyli were said to be about 1 mm in diameter ("diametro semilinealibus") and to be either solitary or aggregated into fours, threes, or twos. This statement suggests that Ruprecht was describing a tetrasporangial sorus rather than a cystocarp. The meaning of "heteromorphic" in the phrase "Gongyli crebri, heteromorphi," reflected in the epithet "*heterocarpa*," is not apparent, but it probably refers to some perceived differences among tetrasporangial sori rather than to differences in size among mature cystocarps. It seems that Ruprecht, like Greville, was confused by the reproductive morphology of foliose red algae.

The single specimen at LE, which we are considering the holotype of *Iridaea heterocarpa*, was revisited by Ruprecht after studying the algae of the Okhotsk Sea for a decade. During that period, he learned to distinguish clearly between "Tetrasporenfrucht" (cluster of variously divided tetrasporangia) and "Samenhaufen" (cluster of carposporangia). In reviewing the species of *Iridaea*, Ruprecht (1850, p. 316) transferred *I. heterocarpa* to *Chondrus* Stackh. because its tetrasporangial sorus was thought to agree exactly with that of *C. crispus* Stackh., the lectotype of its generic name. In making the transfer, Ruprecht changed the epithet illegitimately from *heterocarpus* to *incisus* and altered the label on the type specimen accordingly. We made a hand section of the type specimen, which revealed that Ruprecht was correct: the tetrasporangia develop from secondary filaments in the medulla in a manner characteristic of *Chondrus* rather than from primary cortical cells or secondary filaments in the inner cortical region characteristic of *Mazzaella* (Hommersand et al. 1993).

To confirm the assignment of the type of *Iridaea heterocarpa* to *Chondrus*, we compared the ITS 1 region of the type to those of two collections of *C. crispus* (one with broad blades from Connecticut and one with narrow blades from England), a collection of *C. platynus* (C. Ag.) J. Ag. from the Sea of Okhotsk, Russia, one collection each of *C. yendoi* Yamada et Mikami from Japan, *C. nipponicus* Yendo from Japan, *C. ocellatus* Holmes from China, and plants referable to *I. heterocarpa* sensu S. et G. from Alaska (Fig. 2a). The sequence of the type of *I. heterocarpa* was found to differ from that of *C. crispus* and of *C. platynus* by only 1 bp, from that of *C. yendoi* by 2 bp, from that of *C. nipponicus* by 6 bp, and from that of *C. ocellatus* by 7 bp. It differed from that of the Alaskan specimens by 18 bp. These molecular data, coupled with our observations of tetrasporangial development of the type, demonstrate that Ruprecht was correct in transferring *Iridaea heterocarpa* to *Chondrus*. It seems best to place it in the synonymy of *C. crispus* Stackh.

Iridaea lilacina Postels et Ruprecht (1840, p. 17) was originally described from an unspecified locality on the northwest coast of North America. Setchell and Gardner (1903, p. 299) treated *I. lilacina* as a synonym of *I. cordata* (as *I. laminarioides* f. *cordata*). When Setchell visited St. Petersburg he examined the lectotype of *I. lilacina*, and wrote: "= *Ir. lam.* f. *cordata*!!" Later, Setchell and Gardner (1937, p. 170) transferred *I. lilacina* to *Iridophycus*, but a description was not provided. Misled by cystocarpic fragments in the Farlow Herbarium that were spuriously attributed to the type collection of *Iridaea lilacina*, Setchell and Gardner transferred this species to *Schizymenia* in their unpublished manuscript. Abbott (1972, p. 54) treated *I. lilacina* as a synonym of *I. cordata* var. *cordata*, without giving a supporting comment. J. Agardh (1851, p. 254) had suggested this synonymy previously but with a question mark.

Iridaea lilacina appears in Hommersand et al. (1993, p. 110) as an accepted species of *Mazzaella* [*M. lilacina* (P. et R.) Leister], implicitly replacing *Iridaea splendens* (S. et G.) Papenfuss (1958, p. 106), a name previously applied by Leister (1977) to the North American alga incorrectly identified as *I. cordata*. The type of *I. lilacina* was stated to be in LE, but there was no indication that it had been consulted by anyone other than Abbott. Hommersand et al. (1994, p. 199) addressed the issue of *Iridaea lilacina* directly, stating that they had examined the type (Fig. 4c, lent by LE) and confirmed that it belongs in *Mazzaella* but that they were unable to establish its identity with one of the presently recognized species. The type of *I. lilacina* was said by Postels and Ruprecht (1840) to have sporidia, but not gongyli, and our examination of the type specimen confirmed that it is tetrasporangial.

To elucidate the status of *Mazzaella lilacina*, we sequenced the ITS 1 region of the type specimen and found that the sequence (Fig. 2a) was identical to that of three samples from Alaska that had been identified as *M. heterocarpa* in accordance with Abbott (1972, p. 65), including the type of *Iridophycus furcatum* Setchell et Gardner (1937, p. 171) from Sitka, a species merged with *Iridaea heterocarpa* by Abbott (l.c.). The type of *I. lilacina* differed from an additional specimen that had been identified as *M. heterocarpa* from Knoll Head, Alaska by 1 bp.

To determine the limits of *Mazzaella lilacina*, we obtained sequences from an array of forms from Alaska, Oregon, and California that had been identified as *M. heterocarpa*. In addition, we sequenced the type of *Iridaea phyllocarpa* Postels et Ruprecht (1840, p. 18), from Kamchatka (Fig. 4d) and the type of *Iridophycus oregonum* Doty (1947, p. 182) from Brookings, Oregon. The former species was transferred to *Mazzaella* by Perestenko (1994, p. 121), whereas the latter species, which had been compared with *Iridophycus heterocarpum* by its author, was placed in the synonymy of *Iridaea cordata* var. *splendens* by Abbott (1972). The se-

quence from the type of *I. phyllocarpa* was identical to that of the type of *I. lilacina* and to those of all Alaskan specimens sequenced in this study except one from Gravina Island (near Ketchikan), which grouped with specimens from Oregon (Seal Rock and Brookings) and California (Monterey Peninsula) (Fig. 2a). Within this group, which includes the type of *Iridophycus oregonum*, variation was no more than 2 bp, but as a group they differed from the types of *Iridaea lilacina* and *I. phyllocarpa* by 4–7 bp.

Thus, two names are available for the species that comprises the northern populations formerly identified as *M. heterocarpa*. The basionyms (*I. lilacina* and *I. phyllocarpa*) have equal priority so that the choice between *Mazzaella lilacina* (P. et R.) Leister and *Mazzaella phyllocarpa* (P. et R.) Perestenko must be based on other considerations. Because the name *M. lilacina* was treated implicitly by Hommersand et al. (1993, p. 110) as an earlier synonym of *Iridaea splendens*, confusion might arise if it were reassigned to another species. Hence, we adopt *M. phyllocarpa* as the correct name. This species is characterized by simple obovate or undulate blades with ruffled margins or several such blades arising from a proliferous apophysis borne on a stipe of medium length. The medullary filaments are large, thick, and sinuously interwoven and the cortex is composed of densely organized isodiametric cells. Examination of the cystocarp showed that long, densely staining, once or twice segmented terminal tubular filaments radiate from the gonimoblasts.

The entity that ranges from southern Alaska to Ventura County in southern California that differs from *I. phyllocarpa* by at least 4 bp is morphologically distinct. It is characterized by having irregularly shaped to furcate and undulate blades that arise from a small stipe. The medullary filaments are slender and loosely interwoven, and the cortex is composed of small isodiametric cells that are well spaced. Cystocarpic plants of this species lack terminal tubular gonimoblast filaments. Instead, the gonimoblasts are surrounded by short-celled secondary filaments of gametophytic origin, some of which grow inward and connect to the gonimoblast cells. The correct name for the species that comprises the southern populations formerly identified as *M. heterocarpa* is as follows:

Mazzaella oregona (Doty) Hughey, P. C. Silva et Hommersand, comb. nov.

Basionym: *Iridophycus oregonum* Doty (1947, p. 182, pl. 11; fig. C).

Holotype: Brookings, Oregon, Doty 4065, 16.xii.1941 (DS 306918 in UC).

Homotypic synonym: *Iridaea oregona* (Doty) Papenfuss (1958, p. 106).

According to Doty, this species differs from *I. heterocarpum* sensu Smith "in having a much thinner cortex, in having longer, larger, and less-branched medullary cells, in the thinner frond, in the branching, and in the larger tetrasporangia." In our opinion, none of these perceived differences can be used to distinguish *I. oregonum* from specimens from the same area that were determined by Doty as *I. heterocarpum*.

Relationships among Iridophycus flaccidum *S. et G.,* I. lineare *S. et G., and* I. splendens *S. et G., including molecular study of the types of* I. fulgens *S. et G.,* I. reediae *S. et G., and* I. sinicola *S .et G.* In a review of *Iridophycus* in the North Pacific, Setchell and Gardner (1937) recognized 16 species, of which 11 were newly described, including *I. flaccidum*, *I. lineare*, and *I. splendens*. All these three species are referable to *Mazzaella*, and all were collected at Carmel on the Monterey Peninsula, California. The three species were recognized by Smith (1944), who discussed ways to distinguish among them. *Iridophycus lineare* was said to be distinctive by way of its long stipe and linear blade, which is frequently spiraled. *Iridophycus flaccidum* was said to have ovate-lanceolate blades that are three to six times as long as broad, green-olive if growing in the mid-littoral, or deep purple if growing in the lower littoral. *Iridophycus splendens*, on the other hand, was said to have lanceolate blades that are 10 or more times as long as broad, of a rich purple color. According to Smith, living specimens of *I. splendens* could be confused with lower littoral specimens of *I. flaccidum*, but herbarium specimens are uniformly purple whereas those of *I. flaccidum* are purple only at the base.

Abbott (1972), in her monograph of North American species assigned at that time to *Iridaea*, accepted *I. linearis* and *I. flaccida* as independent species but reduced *I. splendens* to varietal status within *I. cordata*. She distinguished *I. flaccida* from *I. cordata* (including var. *splendens*) by its yellowish green color and the presence of a sterile margin on tetrasporangial blades. The nominal variety (var. *cordata*) was said to be common in the northeastern Pacific but uncommon in California. With the knowledge that *I. cordata* is applicable to a southern hemisphere alga, the identity and correct name of the common northeastern Pacific *Mazzaella* became uncertain.

Foster (1982), in both *in situ* and transplant studies of *I. flaccida*, demonstrated that the clear space along the margins of tetrasporangial blades and the color were variable characters. He concluded that these results strongly support the view that *I. flaccida* and *I. "cordata"* are conspecific. Scagel et al. (1989) followed Silva (1979, p. 327) in accepting *I. splendens* as the appropriate name for the common lower intertidal Pacific coast species. They treated *I. flaccida* as a synonym and further suggested that records of *I. linearis* from the Pacific northwest may also be referable to *I. splendens*.

Shaughnessy (1995) transplanted holdfasts of *Mazzaella splendens* and *M. linearis* (S. et G.) Fred. into *in situ* reciprocal common gardens and found consistent differences in the morphology and biomass of the regenerated blades. *Mazzaella linearis* was unable to adapt physiologically to an intertidal site with low and intermediate wave exposure.

Based on *rbc*L sequence analyses, Hommersand et al. (1994, 1999) found *Mazzaella flaccida* to be a distinct species, sister to a terminal clade containing *M. linearis* and *M. splendens*. For further analysis, we sequenced the ITS 1 region of the type specimens of these three taxa and compared them with sequences from appropriately determined recent collections (Fig. 2b). In all instances, the sequences from the types are distinct from one another but identical to those for their recently collected counterparts with the exception of a collection of *M. linearis* from Shaughnessy's study site (Barkley Sound, Vancouver Island, Canada), for which the sequence differed from that of the type of that species by 1 bp. *Mazzaella linearis* and *M. splendens* differed by 4 bp. The sequences generated for *M. flaccida* differed by 6 bp from both *M. linearis* and *M. splendens*. Morphological observations further support the recognition of all three species (Hughey, personal observation).

Our circumscription of *Mazzaella splendens* encompasses both *I. cordata* var. *cordata* sensu Abbott and *I. cordata* var. *splendens*. Abbott and Hollenberg (1976, p. 530) suggested that the two varieties may be mere "ecological variants." To determine whether there are molecular grounds for recognizing two varieties of *M. splendens*, we sequenced the type specimens of three species of *Iridophycus* described from California by Setchell and Gardner (1937), all of which are similar in habit to the type of *I. splendens*. The type of *I. fulgens* came from Trinidad (Humboldt County), that of *I. sinicola* from San Francisco Bay, and that of *I. reediae* from near Point Buchon (San Luis Obispo County). Abbott (1972, pp. 55, 61) described the three type specimens and gave reasons for assigning them to *Iridaea cordata* var. *splendens*.

The ITS 1 sequence generated from the type of *I. reediae* was identical to that from the type of *I. splendens*, whereas the latter differed from the sequence from the type of *I. sinicola* by 1 bp and from the type of *I. fulgens* by 3 bp. The sequence from *I. fulgens* was identical to that of other northern plants (Alaska to northern California) assigned to *Mazzaella splendens* on the basis of habit. These data support the merger of all three species with *M. splendens* and could be used to support taxonomic recognition of two subspecies, northern and southern.

Mention should be made of *Iridophycus agardhianum* S. et G. (1937, p. 170), a substitute name for *Iridaea minor* J. Agardh (1849, p. 86), which is a later homonym of *I. minor* (J. Ag.) Endlicher [now considered a synonym of *Schizymenia dubyi* (Chauvin ex Duby) J. Ag.]. *Iridaea minor* was based on a collection made by David Douglas at Monterey, California (Kylin, 1941, pl. 8: fig. 21). Smith (1944, p. 288) placed it in the synonymy of *I. flaccidum*, whereas Abbott (1972, p. 61, 65) placed it in the synonymy of *Iridaea cordata* var. *splendens*. Molecular data from the type specimen, which we do not have, would settle the question. Regardless of the outcome, the epithet may not displace either *flaccida* or *splendens*. The three epithets have equal priority so that the choice of either *flaccida* or *splendens* over *agardhiana* must be followed (Art. 11.5 of the ICBN).

Relationship between Iridophycus coriaceum *S. et G. and* Rhodoglossum coriaceum *Dawson. Iridophycus coriaceum* Setchell et Gardner (1937, p. 170) was described on the basis of collections from Cypress Point on the Monterey Peninsula, California and said to range from Neah Bay, Washington to Carmel, California. It was recognized as an independent species by Smith (1944) but referred to *Iridaea cordata* var. *splendens* by Abbott (1972, p. 55). *Rhodoglossum coriaceum* Dawson (1946, p. 75, figs. 1, 10, 11) was described on the basis of collections from Pacific Baja California, between Tijuana and Ensenada. It was later (Dawson, 1961, p. 434) said to range from Ventura, California to Punta Maria, Baja California. Dawson initially thought he was dealing with *I. coriaceum* but found that the tetrasporangia were produced by the innermost cortical cells rather than on special branches arising from medullary cells. This difference had been used by Kylin (1928) to distinguish *Rhodoglossum* from *Iridophycus*, and Dawson, following Kylin, thus described his material as a new species of the former genus. *Rhodoglossum coriaceum* was also referred to *Iridaea cordata* var. *splendens* by Abbott (1972, p. 55).

On the basis of *rbc*L sequence analysis and morphological observations of the type, Hughey (in Hommersand et al. 1999, p. 147) transferred *Rhodoglossum coriaceum* to *Mazzaella*. The specimen of *M. coriacea* that was sequenced came from Pacific Grove, Monterey County, California, raising the question whether Smith had any representatives of this species in hand when he wrote "Marine algae of the Monterey Peninsula, California" (1944) and, if so, what name did he apply to them. An examination of the specimens that were used by Smith when writing his book (and which are now housed in UC) shows that five of the six specimens labeled *Iridophycus coriaceum* are representative of *M. coriacea* rather than *I. coriaceum*. Moreover, Smith's illustration of *I. coriaceum* (pl. 71, fig. 4) is clearly referable to *M. coriacea*.

To clarify the confusion, we sequenced the ITS 1 region of an isotype of *Rhodoglossum coriaceum*, two other collections of that species (one from La Bufadora, Baja California, the other from Monterey, California), and the type of *Iridophycus coriaceum* (Fig. 2b). The sequence of the isotype of *R. coriaceum* differed from that of the La Bufadora collection by a single base pair and from that of the Monterey collection by 3 bp. In contrast, the sequence differed by 18 bp from that of the type of *I. coriaceum*, which was found to have a sequence identical to that previously determined for *Mazzaella splendens*. Thus, Abbott's treatment of *I. coriaceum* as a synonym of *I. splendens* (Abbott 1972, p. 55, as *Iridaea cordata* var. *splendens*) is supported by our sequence data. *Iridophycus coriaceum* and *I. splendens* have equal priority, both having been published by Setchell and Gardner in the same paper (1937, p. 170), but even if *I. coriaceum* had priority, it

could not displace *Mazzaella splendens* as the name of this species because of the prior existence of *M. coriacea* (E. Y. Dawson) Hughey.

Mazzaella coriacea can be distinguished from *M. splendens* by its larger cystocarps (1.5–3 mm diam. vs. 1 mm), color (generally brownish red or tan vs. purple), thicker blades (1.5 mm vs. 0.5–0.7 mm), more strongly developed stipe and apophysis, and a preference for heavily exposed intertidal sites (headlands or channels). *Mazzaella coriacea* is distributed from Monterey, California to Punta María, Baja California (Dawson 1961, p. 257), whereas *M. splendens* ranges from southeastern Alaska to northern Baja California (Scagel et al. 1989, p. 295).

Identities of Iridaea cornucopiae *P. et R. and* Iridophycus parksii *S. et G. Iridaea cornucopiae* Postels et Ruprecht (1840, p. 18, pl. XXXVIII, fig. b; pl. XL, figs. 89, 90) was based on an alga allegedly collected on the northwest coast of North America. Kützing (1849, p. 726) placed it in synonymy with *I. laminarioides* Bory (1828 [1827–1829], p. 105, pl. 11: fig. 1), a species based on a Dumont d'Urville collection from Concepción, Chile. J. Agardh (1851 [1851–1863], p. 253) gave it varietal status within the Chilean species. Yendo (1917, p. 78) reported *I. laminarioides* var. *cornucopiae* to be abundant in northern Japan. His collections, however, were later referred to a new species in a different genus, *Chondrus yendoi* Yamada et Mikami (in Mikami 1965, p 236, figs. 31–33). Simultaneously, Mikami (op. cit., p. 259) recognized the presence of "true" *I. cornucopiae* in the Kurile Islands, basing his opinion on an examination of the type collection (Fig. 4e). It had previously been reported from the Kuriles by Yamada (1934, p. 348, with a query; 1935, p. 23, without a query) and Nagai (1941, p. 189, as *Iridophycus cornucopiae*).

In a review of *Iridaea* (as *Iridophycus*), Setchell and Gardner (1937, pp. 170, 173) recognized *I. cornucopiae* as an independent species and included it in a key to northern hemisphere species but without explaining their taxonomic opinion. Abbott (1972, p. 62) treated the species fully, ascribing a range from Hokkaido, Japan through the Aleutian Islands to Humboldt County, California. It was transferred to *Mazzaella* (as *M. cornucopiae)* by Hommersand (in Hommersand et al. 1993, p. 110).

An examination in various herbaria of specimens from the Pacific coast of North America labeled *Iridaea cornucopiae* gave rise to uncertainty as to the application of the name. To obtain pertinent molecular data, we extracted DNA from fragments of the type collection of *I. cornucopiae*, including two packets, each containing a large frond, and loose fragments from a packet containing a collection of smaller fronds (Fig. 4e, top), some of which corresponded in habit to the drawing in Postels and Ruprecht (1840, pl. XXXVIII, b) (Fig. 4e, bottom). The nucleotide sequence of the ITS 1 region from all sources was identical. However, when we compared the sequence obtained from the type material with that obtained from five collections thought to be *Mazzaella cornucopiae* (from Alaska, Oregon, and California), we found that it differed significantly (by more than 30 bp) from these collections, which, however, differ from one another by 1–5 bp (Fig. 3a).

Following earlier authors, who considered *I. cornucopiae* to be conspecific with *I. laminarioides*, we compared sequences obtained from Chilean collections of the latter species. Surprisingly, we found total agreement with the sequence obtained from a juvenile thallus from Horcón and a mature thallus from El Desembocadero de Bío Bío (near Concepción) and only a 3-bp difference (single indel event) compared with the sequence obtained from a mature thallus of the type collection of *I. laminarioides* from Concepción (Bory 1828 [1827–1829], pl. 11, fig. 1d). Considering that the specimens in the type collection of *I. cornucopiae* (Fig. 4e) and those illustrated by Postels and Ruprecht fit comfortably within the morphological spectrum exhibited by *I. laminarioides* in Chile, it seems likely that erroneous labeling is involved. According to the journal of the expedition (Lütke 1835, pp. 34–42), the *Seniavin* under the command of Capt. Lütke anchored at Tomé in Bahía de la Concepción on March 16, 1827. The naturalists visited the immediate vicinity, but the account of the work of the naturalists on the voyage (Kittlitz 1836, pp. 254–257) mentions only zoological observations. Continuing northward, the *Seniavin* stopped at Valparaiso, Chile during the period March 26 to April 15. Kittlitz (1836, p. 261) noted that Carl Friedrich Mertens, the botanist, augmented his collections of intertidal plants and animals during their stay in Valparaiso. This information provides circumstantial evidence that the provenance of the type collection of *I. cornucopiae* was Chile rather than Alaska.

With the elimination of *I. cornucopiae* from the North American flora, the proper name for the entity that has been incorrectly referred to that species remains to be determined. The only available name seems to be *Iridophycus parksii* Setchell et Gardner (1937, p. 172), described from material collected near Trinidad, Humboldt County, California by Harold E. Parks. The furrowed apophyses and blades of the type collection are illustrated by Abbott (1972, fig. 16), who placed *I. parksii* in the synonymy of *I. cornucopiae*.

To confirm that herbarium specimens identified as *I. parksii* on the basis of habit are conspecific with the type of that species, we sequenced the ITS 1 region of these specimens and compared the results with the sequence from two specimens of the holotype collection (one cystocarpic, the other tetrasporangial) (Fig. 3a). A 9-bp indel was present in the type collection that was absent in the other specimens. Treating the indel as a single event or as population variation, type material of *I. parksii* differed from other collections from Pacific North America by 1 bp (Cape Arago, Oregon), 2 bp (Kodiak I., Alaska and Humboldt, California), 3 bp (Trinidad, California), and 5 bp (Attu I., Alaska), all of which are morphologically indistinguishable and appear to belong to a single species.

Mazzaella parksii (S. et G.) Hughey, P. C. Silva et Hommersand, comb. nov.

Basionym: *Iridophycus parksii* Setchell et Gardner (1937, p. 172).

Holotype: UC 507492.

Homotypic synonym: *Iridaea parksii* (S. et G.) Papenfuss (1958, p. 106).

To determine if populations of *I. parksii* from California and Alaska are conspecific with western Pacific populations reported as *I. cornucopiae*, we sequenced the ITS 1 region of the specimen from the Kurile Islands determined as *I. cornucopiae* and pictured by Mikami (1965, pl. VII, fig. 2). A 15-bp difference was found when this sequence was compared with that for two specimens of *I. parksii* from the type collection and a plant from Oregon and a 14-bp difference compared with the Alaskan collection (Fig. 3a). This molecular evidence of taxonomic dissimilarity led us to seek supporting morphological differences.

A preliminary examination of *Mazzaella parksii* shows that tetrasporangial sori extend from the most shallow to the deep parts of the medulla. At maturity, tetraspores are released through a cup-shaped pore. According to Mikami (1965, p. 261, fig. 43A), the tetrasporangial sori of *Iridaea cornucopiae* from the Kuriles are formed "in the comparatively shallow places of the medulla." He did not mention the presence of a pore. In addition, we have observed in the cystocarp of *M. parksii* only about one-fifth the number of "special absorbent filaments" shown by Mikami (1965, p. 262, figs. 44C, 45B). We believe that the molecular and morphological data support recognition of populations in the Kurile Islands previously referred to *I. cornucopiae* as an independent species of *Mazzaella*. We have not yet determined the correct name for the species to which the Kurile specimens belong.

Taxonomic status of Rhodoglossum parvum *G. M. Smith et Hollenberg. Rhodoglossum parvum* G. M. Smith et Hollenberg (1943, p. 216, figs. 15, 16) was described on the basis of a collection from Cypress Point on the Monterey Peninsula, California. It was said to differ from *R. affine* (Harv.) Kylin in its proportionally longer stipe, fewer dichotomies (one to three), and lack of curvature of blade segments. In addition, the cystocarps were described as being only 0.5 mm broad compared with 1–2.5 mm in *R. affine*.

Rhodoglossum parvum was considered by Abbott and Hollenberg (1976) to be a depauperate form of *R. roseum* (Kylin) G. M. Smith (*Iridaea rosea* Kylin), a species in which the blade is simple and the cystocarps are conspicuous (>1 mm diam.).

To elucidate the taxonomic status of *Rhodoglossum parvum*, we sequenced the entire ITS 1, 5.8S, and ITS 2 regions (720 bp) from a specimen on the holotype sheet of this species. We also sequenced the ITS 1 region for two additional collections of *R. parvum* and found that the sequence from one collection (Pebble Beach, Carmel, California) differed from that of the type by 1 bp, whereas the sequence in the other collection (Punta Santo Tomás, Baja California) was identical to that of the type (Fig. 3b). The ITS 1 region of *R. parvum* differed from that of a cystocarpic plant from the holotype sheet of *I. rosea* by 22 bp and from that of a modern collection of *R. affine* by 16 bp. It is clear from this comparison that the three species are distinct. All are referable to *Mazzaella*: *M. affine* (Harv.) Fred., *M. rosea* (Kylin) Fred., and *M. parva* (G.M. Smith et Hollenberg.) comb. nov.

Mazzaella parva (G. M. Smith et Hollenberg) Hughey, P. C. Silva et Hommersand, comb. nov.

Basionym: *Rhodoglossum parvum* G.M. Smith et Hollenberg (1943: 216, figs. 15, 16).

Holotype: DS 306402 in UC.

Identity of Grateloupia squarrulosa *S. et G. and* Grateloupia johnstonii *S. et G. Grateloupia squarrulosa* Setchell et Gardner (1924, p. 780, pls. 81, 82) and *Grateloupia johnstonii* Setchell et Gardner (1924, p. 782, pl. 84) were described from sterile specimens collected in drift by Ivan M. Johnston from the Gulf of California. *Grateloupia squarrulosa* came from Smith Island, where, according to the label on the type sheet, it was found "in unattached tangles between the rocks," whereas *Grateloupia johnstonii* was gathered 3 days later at nearby Isla Angel de la Guarda. Setchell and Gardner concluded that the two species were closely related but noted that they differed "in thickness, color, number and character of the ultimate pinnules, and the angle at which the branches arise." They gave no explanation for assigning these collections to *Grateloupia*.

Dawson (1944, p. 281) included both species in his survey of the marine algae of the Gulf of California but without having seen new material and almost certainly without examining type material. Later, Dawson (1954, pp. 258, 259) expressed doubt about the generic placement of the two species, being particularly puzzled by the presence of medullary filaments of large diameter (10–20 μm in *G. johnstonii*, 20–25 μm in *G. squarrulosa*).

We examined the types of the two species and found that they fit our concept of *Gigartina pectinata* E. Y. Dawson (1944, p. 302, pl. 64: fig. 1), which was also described from Isla Angel de la Guarda and was recently transferred to *Chondracanthus* by L. Aguilar and R. Aguilar (1997, p. 157). The similarity in habit, coupled with our observation that *C. pectinatus* forms tangled clumps in the intertidal (a mode of growth attributed by Johnston to *Grateloupia squarrulosa*), led us to compare the three species.

We obtained DNA from fragments of the types of the three species and a recent collection of *C. pectinatus*. The sequence for the ITS 1 region from the type of *G. squarrulosa* was found to be identical to that from the recent collection of *C. pectinatus*. Morover, it differed from those determined for the types of *G. johnstonii* and *G. pectinata* (which are identical) by only a

single base pair (Fig. 3c). Sequences of the RUBISCO spacer showed no difference between the type of *G. squarrulosa* and the recent collection of *C. pectinatus* (Fig 1b). We conclude that *Grateloupia johnstonii*, *Grateloupia squarrulosa*, and *Gigartina pectinata* are representative of a single species that belongs in the genus *Chondracanthus*. Although the two Setchell and Gardner names have equal priority (1924) over the Dawson name (1944), *Grateloupia johnstonii* may not be used as a basionym within *Chondracanthus* because of the prior existence of *Chondracanthus johnstonii* (E. Y. Dawson) Guiry (in Hommersand et al. 1993, p. 115), based on *Gigartina johnstonii* E. Y. Dawson (1944, p. 302), also from the Gulf of California. We therefore transfer *Grateloupia squarrulosa* to *Chondracanthus*.

Chondracanthus squarrulosus (S. et G.) Hughey, P. C. Silva et Hommersand, comb. nov.

Basionym: *Grateloupia squarrulosa* Setchell et Gardner (1924, p. 780, pls. 81, 82). Holotype: CAS 1368 in UC!; isotypes: UC 221076!, UC 483280!

Heterotypic synonym: *Grateloupia johnstonii* Setchell et Gardner (1924, p. 782, pl. 84). Holotype: CAS 1371 in UC!; isotype: UC 221069!

Heterotypic synonym: *Gigartina pectinata* E.Y. Dawson (1944, p. 302, pl. 64: fig. 1). *Chondracanthus pectinatus* (E.Y. Dawson) L. Aguilar et R. Aguilar (1997, p. 157). Holotype: AHFH 0043 in LAM; isotype: UC 700708! *Dawson 239*, 26 Jan 1940, cast up on north beach, Puerto Refugio, Isla Angel de la Guarda, Gulf of California, Mexico.

CONCLUSIONS

PCR-amplifiable DNA can be isolated from old and formalin-fixed red algal specimens. Nucleotide sequences obtained from type specimens can be used to determine the application of specific names. Interspecific sequence divergences in species distinguished on the basis of morphological criteria differed, with *Chondrus* showing a low rate of divergence (2–7 bp), *Chondracanthus* a moderate rate (3–20 bp), and *Mazzaella* a high rate (4–35 bp). We concluded that a 1- to 3-bp difference in *Mazzaella* equated to populational variation.

Comparisons of nucleotide sequences in the ITS 1 region and the RUBISCO spacer from type specimens and modern collections support the following conclusions:

1. *Iridaea cordata* (Turner) Bory is recognized as a species from southern South America.
2. The type of *Iridaea heterocarpa* P. et R. represents the tetrasporangial phase of a species of *Chondrus*, possibly *C. crispus* Stach.
3. Plants attributed to *Iridaea heterocarpa* P. et R. [*Mazzaella heterocarpa* (P. et R.) Fred.] in Alaska belong primarily in *Mazzaella phyllocarpa* (P. et R.) Perest.; those distributed from southern Alaska to southern California belong in *Mazzaella oregona* (Doty) comb. nov.
4. *Mazzaella splendens* (S. et G.) Fred., *M. linearis* (S. et G.) Fred. and *M. flaccida* (S. et G.) Fred. are distinct species.
5. *Iridophycus coriaceum* S. et G. is conspecific with *M. splendens*, whereas *Rhodoglossum coriaceum* E. Y. Dawson is an independent species: *Mazzaella coriacea* (E.Y. Dawson) Hughey.
6. *Iridaea cornucopiae* P. et R. is conspecific with *Mazzaella laminarioides* (Bory) Fred., and the type probably came from Chile rather than from the North Pacific Ocean. Plants attributed to *Iridaea cornucopiae* in Pacific North America are referable *Mazzaella parksii* (S. et G.) comb. nov.
7. *Rhodoglossum parvum* G.M. Smith et Hollenb. is an independent species: *Mazzaella parva* (G.M. Smith et Hollenb.) comb. nov.
8. Plants attributed to *Gigartina pectinata* E.Y. Dawson [*Chondracanthus pectinatus* (E.Y. Dawson) L. Aguilar et R. Aguilar] from the Gulf of Calfornia, Mexico are referable to *Chondracanthus squarrulosus* (S. et G.) comb. nov.

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APPENDIX

Names and authors, collection and herbarium information, and GenBank accession numbers for species analyzed in this study.

Chondracanthus squarrulosus (S. et G.) Hughey et al. Smith I., Gulf of Calif., Mexico, coll. I.M. Johnston 60, 28.vi.1921 (holotype of *Grateloupia squarrulosa* Setchell et Gardner, CAS 1368 in UC), (ITS- AF401056) (RUBISCO spacer- AF398561)
—Isla Angel de la Guarda, Gulf of Calif., Mexico, coll. I.M. Johnston 88, 1.vii.1921 (holotype of *Grateloupia johnstonii* Setchell et Gardner, CAS 1371 in UC), (ITS- AF401057)
—Isla Angel de la Guarda, Gulf of Calif., Mexico, coll. E.Y. Dawson 239, 27.i.1940 (holotype of *Gigartina pectinata* Dawson, LAM 500907), (ITS- AF401058)
—Bahía de los Angeles, Gulf of Calif., Mexico, coll. J.R. Hughey, 5.vii.1996 (NCU), (ITS- AF401059; RUBISCO spacer- AF398562)

Chondrus crispus Stackh.. Sherwood I. State Park, Fairfield Co., Connecticut., coll. M.H. Hommersand, 6.v.1973 (NCU), (ITS- AF398542)
—Devon, England, coll. J. Brodie, 7.ii.1993 (NCU), (ITS- AF398543)

Chondrus nipponicus Yendo. Oshoro, Shiribeshi, Hokkaido, Japan, coll. M.H. Hommersand, 3–4.viii.1971 (NCU), (ITS- AF398547)

Chondrus ocellatus Holmes. Qingdao, Shandong, Prov., China, coll. M.H. Hommersand, 26.vi.1994 (NCU), (ITS- AF398546)

Chondrus platynus (C. Ag.) J. Ag., Okhotsk Sea, Gijiginskaya Bay, Chaibukha, Russia, coll. L. P. Perestenko, 29.vi.1973 (LE, fragment NCU), (ITS- AF398544)

Chondrus yendoi Yamada et Mikami. Koyazu, Yamadawan, Iwate-ken, Honshu, Japan, coll. M.H. Hommersand, and M. Yoshizaki, 12.vii.1994 (NCU), (ITS- AF398545)

Fucus cordatus (see *Iridaea cordata*)
Gigartina pectinata (see *Chondracanthus squarrulosus*)
Grateloupia johnstonii (see *Chondracanthus squarrulosus*)
Grateloupia squarrulosa (see *Chondracanthus squarrulosus*)

Iridaea cordata (Turn.) Bory. Isla de los Estados, Argentina, coll. A. Menzies, in 1787 (upper specimen on holotype sheet of *Fucus cordatus* Turn., E; Fig. 2, this paper), (RUBISCO spacer- AF398555)
—Isla de los Estados, Argentina, coll. SOSC, Ref. 609, 19.x.1971 (NCU), (RUBISCO spacer- AF398556)
—Punta Daniel Este, Magellanes, Chile, coll. S. Fredericq & M.E. Ramírez, 19.ii.1994 (NCU), (RUBISCO spacer- AF398557)

Iridaea cordata sensu Setchell (see *Mazzaella splendens*)
Iridaea cornucopiae Type (see *Mazzaella laminarioides*)
Iridaea cornucopiae sensu Abbott (see *Mazzaella parksii*)
Iridaea cornucopiae P. et R. sensu Mikami. Urup I., Kurile Is., Russia, coll. Y. Yamada, viii.1933 (SAP 028912; pl. VII, fig. 2 in Mikami 1965), (ITS- AF400062)

Iridaea heterocarpa P. et R. Oceano pacifico septemtrionali ("Camtschat?", Russia), coll. C.H. Mertens, 1826–1829 (lectotype, here designated: LE; Fig. 3, this paper), (ITS- AF398541)

Iridaea lilacina (see *Mazzaella phyllocarpa*)

Iridaea micans Bory. Port Louis, Falkland Is., coll. Dumont d'Urville, 1822–1825 (PC; pl. 13bis, fig. A in Bory 1826–1829), (RUBISCO spacer- AF398558)

Iridaea phyllocarpa (see *Mazzaella phyllocarpa*)
Iridaea rosea (see *Mazzaella rosea*)
Iridophycus coriaceum (see *Mazzaella splendens*)
Iridophycus flaccidum (see *Mazzaella flaccida*)
Iridophycus lineare (see *Mazzaella linearis*)
Iridophycus furcatum (see *Mazzaella phyllocarpa*)
Iridophycus fulgens (see *Mazzaella splendens*)
Iridophycus lineare (see *Mazzaella linearis*)
Iridophycus oregonum (see *Mazzaella oregona*)
Iridophycus parksii (see *Mazzaella parksii*)
Iridophycus reediae (see *Mazaella splendens*)
Iridophycus sinicola (see *Mazzaella splendens*)

Mazzaella affinis (Harv.) Hommers. Pacific Grove, Monterey Co., Calif., coll. M.H. Hommersand, 2.i.1993 (NCU), (ITS- AF401064)

Mazzaella coriacea (E.Y. Dawson) Hughey. Near Punta Descanso, Baja Calif., Mexico, coll. E.Y. Dawson 97–45, 8.iv.1945 (isotype of *Rhodoglossum coriaceum* E.Y. Dawson, UC 696951), (ITS- AY048052)
—La Bufadora, Baja Calif., Mexico, coll. M.H. Hommersand, 6.vii.1996 (NCU), (ITS- AY048051)
—Pacific Grove, Monterey Co., Calif., coll. J.R., P.A., & D.R. Hughey, 14.vii.1996 (NCU), (ITS- AY048050)

Mazzaella flaccida (S. et G.) Fred. Carmel Beach, Monterey Co., Calif., coll. A.V. Manza, 18.vii.1935 (cystocarpic part of holotype of *Iridophycus flaccidum* S. et G., UC 539561), (ITS- AY048046)
—Carmel Beach, Monterey Co., Calif., coll. J.R., P.A., & D.R. Hughey, 13.vii.1996 (NCU), (ITS- AY048045)

Mazzaella laminarioides (Bory) Fred. Concepción, Chile, coll. Dumont d'Urville, 1822–1825 (holotype of *Iridaea laminarioides* Bory, PC; pl. 11, fig. 1D in Bory 1826–1829), (ITS- AF400056)
—Pta. Horcón, Quillota, Aconcagua, Chile, coll. M.H. Hommersand, 29.vii.1994 (NCU), (ITS- AF400054)
—El Desembocadero de Bío Bío, near Concepción, Chile, coll. M.H. Hommersand, 2.i.1995 (NCU), (ITS- AF400055)
—#1 Near Valparaiso, Chile, coll. C.H. Mertens, in 1827 (lectotype of *Iridaea cornucopiae* P. et R. here designated: LE; fig. 4, this paper), (ITS- AF400051)
—#2 Near Valparaiso, Chile, coll. C.H. Mertens, in 1827 (isotype of *Iridaea cornucopiae* P. et R. here designated:11), (ITS- AF400052)
—#3 Near Valparaiso, Chile, coll. C.H. Mertens, in 1827 (isotype *Iridaea cornucopiae* P. et R. here designated: LE), (ITS- 400053)

Mazzaella linearis (S. et G.) Fred. Carmel Beach, Monterey Co., Calif., coll. N.L. Gardner 3330, v.1916 (cystocarpic part of holotype of *Iridophycus lineare* S. et G. UC 507637), (ITS- AY048049)
—Barkley Sound, Vancouver I., B.C., coll. F. Shaughnessy, 24.vi.1994 (NCU), (ITS- AY048048)
—Moss Beach, Monterey Co., Calif., coll. F. Shaughnessy, 23.vii.1996 (NCU), (ITS- AY048047)

Mazzaella oregona (Doty) Hughey et al.#1 Brookings, Curry Co., Oregon, coll. M.S. Doty, 16.xii.1941 (specimen on left of holotype sheet of *Iridophycus oregonum* Doty, DS 306918 in UC), (ITS- AF398533)
—#2 Brookings, Curry Co., Oregon, coll. M.S. Doty, 16.xii.1941 (specimen on upper right of holotype sheet of *Iridophycus oregonum* Doty, DS 306918 in UC), (ITS- AF398534)
—Gravina I., Ketchikan area, Alaska, coll. S.C. Lindstrom 8662, 30.vi.2000 (NCU), (ITS- AF398532)
—Seal Rock, Lincoln Co., Oregon, coll. E. Henry, 24.v.1993 (NCU), (ITS- AF398530)
—Cypress Pt., Monterey Co., California, coll. J.R., P.A., and D.R. Hughey, 12.vii.1996 (NCU), (ITS- AF398531)

Mazzaella parksii (S. et G.) Hughey et al. #1 Two miles N. of Trinidad, Humboldt Co., California, H. E. Parks, v.1933, (cystocarpic part of holotype of *Iridophycus parksii* S. et G., UC 5074921) (ITS- AF400057
—#2 Two miles N. of Trinidad, Humboldt Co., California, H. E. Parks, v.1933, (tetrasporic part of holotype of *Iridophycus parksii* S. *et* G., UC 5074921) (ITS- AF400058)
—Near Trinidad, Humboldt Co., Calif., coll. E.Y. Dawson, 25.vii.1965 (NCU 25398), (ITS- AF400059)
—Attu I., Alaska, coll. K.A. Miller, 19.vi.1987 (UC 1573586), (ITS- AF400061)
—Cape Arago, Coos Co., Oregon, coll. J.R. Hughey, 4.ix.1998, (NCU), (ITS- AF400060)

Mazzaella parva (Smith et Holl.) Hughey et al.. #1. Cypress Pt., Monterey Co., Calif., coll. G.M. Smith 40–178, 28.xi.1940 (part of holotype of *Rhodoglossum parvum* Smith *et* Holl., DS 306402 in UC), (ITS- AF401060)
—#2 Cypress Pt., Monterey Co., Calif., coll. G.M. Smith 40–178, 28.xi.1940 (part of holotype of *Rhodoglossum parvum* Smith et Holl., DS 306402 in UC), (ITS- AF401061)
—Pebble Beach, Monterey Co., Calif., coll. unknown, 7.vi.1901, (UC 94330), (ITS- AF401062)
—Punta Santo Tomás, Baja Calif., Mexico, coll. J.R. Hughey, 2.vii.1996 (NCU), (ITS- AF401063)

Mazzaella phyllocarpa (P. et R.) Perest. "Ad littora Kamtschatica", Russia, coll. C.H. Mertens, 1826–1829 (lectotype of *Iridaea phyllocarpa* P. et R., here designated: LE; Fig. 4, this paper), (ITS- AF398538)
—"Ad littora Americae boreali-occidentalis", coll. C.H. Mertens, in 1828 (lectotype, of *Iridaea lilacina* P. et R., here designated: LE; Fig. 4, this paper), (ITS- AF398539)
—Sitka, Alaska, coll. N.L. Gardner 3999, xii.1917 (part of holotype collection of *Iridophycus furcatum* S. et G., UC 543957), (ITS- AF398540)
—Perevalnie Pass, Kodiak I., Alaska, coll. G. Hansen, 20.viii.1993 (NCU), (ITS- AF398536)
—Snug Harbor, Alaska, coll. S.C. Lindstrom, 24.vi.1994 (NCU), (ITS- AF398535)
—Knoll Head, near Sitka, Alaska, coll. S.C. Lindstrom, 2.vi.1996 (UBC), (ITS- AF398537)

Mazzaella rosea (Kylin) Fred. Pacific Grove, Monterey Co., Calif., coll. H. Kylin, vii.1922 (cystocarpic part of holotype of *Iridaea rosea* Kylin, LD 81/65–5537), (ITS- AF401065)

Mazzaella splendens (S. et G.) Fred. Carmel Beach, Monterey Co., Calif., coll. A.V. Manza, 19.vii.1935 (cystocarpic part of holotype of *Iridophycus splendens* S. et G., UC 539564), (ITS- AF401068)
—Cypress Pt., Monterey Co., Calif., coll. N.L. Gardner 6315, vii.1917 (cystocarpic part of holotype of *Iridophycus coriaceum* S. et G., UC 296589), (ITS- AF401069)
—Bushnell's Beach, San Luis Obispo Co., California, coll. R.S. Reed, vii.1917 (part of holotype collection of *Iridophycus reediae* S. et G., UC 392651), (ITS- AF401070)
—Near Pt. Cavallo, Marin Co., California, coll. N.L. Gardner 7631, 16.xi.1933 (isotype specimen of *Iridophycus sinicola* S. et G., LAM), (ITS- AF401071)
—Near Trinidad, Humboldt Co., California, coll. N.L. Gardner 7867, xii.1934 (isotype specimen of *Iridophycus fulgens* S. et G., LAM), (ITS- AF401072)
—Carmel, Monterey Co., Calif., coll. J.R., P.A., & D.R. Hughey, 13.vii.1996 (NCU), (ITS- 398529)
—Jalama Beach Co. Park, Santa Barbara Co., Calif., coll. M.H. Hommersand, 21.vii.1966 (NCU), (ITS- AF401067)
—Taigud I., Sitka area, Alaska, coll. S.C. Lindstrom, 29.iv.1994 (NCU), (ITS- AF401066)
—Shannon Pt., Skagit Co., Wash., coll. S. Lindstrom, 11.v.1993 (NCU), (RUBISCO spacer- AF398559)
—Queen Charlotte I., British Columbia, Canada, coll. R.F. Scagel, 25.vii.1953 (UBC 2710), (RUBISCO spacer- AF398560)

Rhodoglossum coriaceum (see *Mazzaella coriacea*)

Rhodoglossum parvum (see *Mazzaella parva*)