**Saccharina compla(nada?) Species**

Determining the validity of *S. complanata* as a distinct species

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**Abstract**

The kelp species *Saccharina complanata* (order Laminariales, family Laminariaceae) originally described as *Saccharina latissima f. complanata*, is a poorly understood species, often overlooked in studies involving other *Saccharina* species, such as S*accharina latissima,* commonly known as 'sugar kelp'. *S. complanata* is morphologically distinguished from *S. latissima* through a longer, complanate stipe (typically >30 cm). Owing both to the morphological plasticity of *Saccharina* species and a paucity of morphological and genetic data surrounding *S. complanata*, many phycologists continue to question the validity of *S. complanata* as a species. To address this I sequenced the nuclear-encoded rRNA internal transcribed spacer (ITS) 1 & 2 regions of over 20 alga that presented morphologically as *S. latissima* or *S. complanata* and compared them to existing ITS sequences of species within order Laminariales using a maximum likelihood phylogenetic tree. Here I show that, unexpectedly, *S.complanata* shares a close genetic relation to the kelp *Pleurophycus gardneri* (family Alariaceae). I debate whether the genetic similarities of the ITS 1 & 2 regions of *P. gardneri* and *S.complanata* indicate *complanata* as a new *Pleurophycus* species or variational form of *P. gardneri*. This preliminary data strongly suggests that deeper genetic investigations and potential reorganizations of the *Pleurophycus* genus to include *S. complanata* are necessary.

**Introduction**

Brown algae of the order Laminariales, commonly known as 'kelp', are a diverse group of macroalgae species found in all 11 marine regions of the world (Bolton 2010). They are generally characterized by large thalli differentiated into holdfast, stipe, and blade (Taylor 1957), and play a critical multi-faceted role in marine ecosystems (Teagle et al., 2017).

One of the Laminariales genera, *Saccharina* (family Laminariaceae), displays diverse morphological characteristics as a result of environmental and other external factors (Diehl et al., 2023;Zhu et al., 2021). Temperature alone has been shown to modify *Saccharina* species' bullation pattern, cell size, and blade thickness (Druehl, 1968). Such morphological variance is exemplified in the case of *Saccharina latissima* vs *Sacarhina complanata*, two species whose similar and often overlapping characteristics make it difficult to distinguish them by eye. In addition, the history of the genus Saccharina and origins of *S. complanata* further complicates the identification and baseline understanding of these species (Fig. 1).

The genus *Saccharina* was first described by Stackhouse in 1809, though promptly renamed *Laminaria*, a commonly used synonym, in 1812 (Stackhouse, 1809). A year later, J.V. Lamouroux presented the species *Laminaria saccharina*, described as having a single long, undivided ruffled blade, with occasional bullations, and a short terete stipe with a branching holdfast (Lamouroux ,1813; Scagel, 1971). In 1903, Setchell and Gardner described a new form of the species, *L. saccharina f. complanata*, distinguished by a long, flattened stipe and found only in San Juan Island (Fig. 2). They collected the type specimen for *L. saccharina f. complanata* in the San Juan Islands of Washington State located in the Salish Sea and the Eastern North Pacific (Setchell and Gardner, 1903). Nine years later, in a report on fertilizer resources in the United States, Setchell raised *L. saccharina f. complanata* to species status, declaring it *Laminaria complanata* (United States. et al., 1912). Muenscher's 1917 key (Fig. 3) attempted to clear up any residual confusion between *L. complanata* and *L. saccharina* with a visual depiction (Muenscher, 1917).

Development of modern DNA sequencing techniques gave phycologists the ability to reexamine *Laminaria* as a genus through a genetic lens. Molecular phylogenetic studies of the

Laminariales order found results strongly at odds with historical, morphologically-based phylogenies. In 2006 Lane et al. sequenced over 6000 bp from 42 taxa within the Laminarales order resulting in the split of the *Laminaria* genus and the resurrection of the name *Saccharina* to form two genera *Laminaria* and *Saccharina* (Lane et al., 2006). *Laminaria saccharina* was transferred to the *Saccharina* genus as *S.latissima* to avoid a tautonym. Finally in 2012, *Laminaria complanata* was reclassified to its current name, *Saccharina complanata* (Gabrielson, 2012).

The last twenty years have produced numerous studies attempting to reorganize the taxonomy of the laminariales family and utilize genetic techniques to study saccharina species (Lane et al., 2006). However, due in part to the convoluted taxonomic evolution of the species and its limited locality, *Saccharina complanata* is absent from a majority of these studies. No known genetic sequences of *S. complanata* can be identified and its appearance in modern literature is limited to morphological observations and footnote speculations. In his 2012 publication "Keys to the seaweeds and seagrasses of southeast Alaska, British Columbia, Washington, and Oregon", Gabrielson noted that further investigation into *S. complanata* is required to confidently establish distinction from *S. latissima* (Gabrielson, 2012). The historical distinction of *S. latissima* and *S. complanata* based solely on small variations in stipe morphology, especially within a genus known for rather extreme morphological variation, leads me to hypothesize that *S. complanata* and *S. latissima* are the same species. Therefore through DNA sequence analysis of *S. complanata* and *S. latissima*, I expect to find little to no genetic difference between the species, and, like Setchell and Gardners original description, *Saccharina complanata* is best described as a form of *S. latissima*.

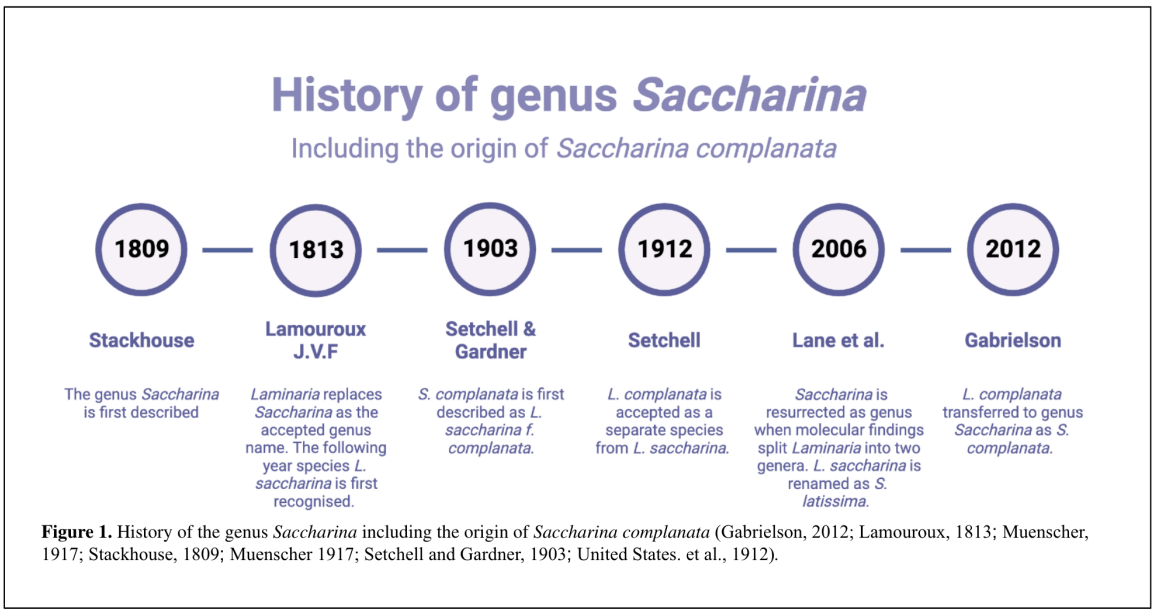


**Figure 1.** History of the genus *Saccharina* including the origin of *Saccharina complanata* (Gabrielson, 2012; Lamouroux, 1813; Muenscher, 1917; Stackhouse, 1809; Muenscher 1917; Setchell and Gardner, 1903; United States. et al., 1912).

**Laminaria saccharina** f. **complanata** Setchell and Gardner f. nov.

Stipe long, up to 50 cm., terete below, soon flattened (20 mm. wide and 3 mm. thick about two-thirds the way up), without mucilage ducts. Blade 80–100 cm. long, 40–50 cm. wide just above the base, ample, ruffled, with base decidedly cordate. Mucilage ducts in the blade large and extremely abundant, just under the surface layer of cells.

Found in a single locality, growing on piles, in quiet water, just below low water mark. Friday Harbor, San Juan Island, Wash., *N.L.G.*, No. 682!

A very distinct form, easily recognized by its decidedly flattened stipe.

**Figure 2.** Original description of *L. saccharina f. complanata* from the *Algae of Northwestern America* (Setchell and Gardner, 1903).

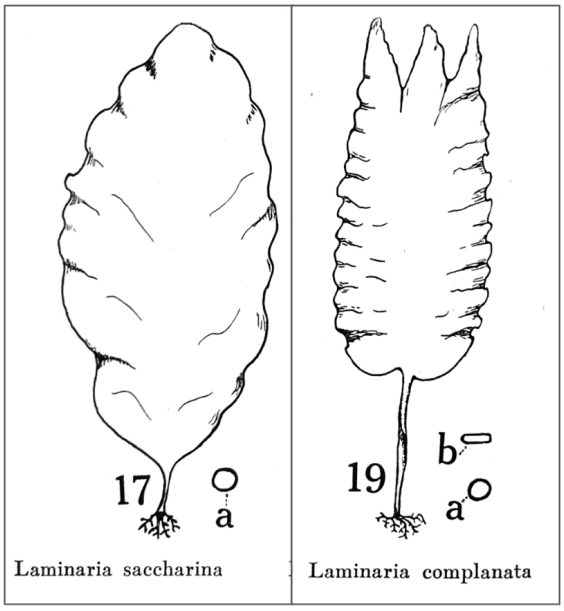


**Figure 3.** Drawings of *L. saccharina* and *L. complanata* (Muenscher, 1917)

## Methods

### Collection and Preservation

A total of 27 specimens were collected from various sites around San Juan Island from June 22nd-27th, 2023 (Table 1). Care was taken during collection to keep the entire stipe and holdfast of the alga intact for accurate morphological comparisons. Three additional voucher specimens with accompanying blade tissue, preserved in silica gel, were donated by Dr. Tom Mumford and Arden Litcher. Upon returning from the field, fresh specimens were photographed and tissue from the blade was excised for genetic analysis. Whole thalli images were uploaded to GoodNotes (GoodNotes Limited 2023) where the background was smoothed and image cropped in order to obtain a clear and focused picture of the specimen. Vouchers were created by pressing the entire alga, including the holdfast/stipe, on herbarium paper. Donated herbarium specimens were photographed, and the blade clippings removed from their corresponding silica gel samples for DNA sequencing. Cross sections of the blades and stipes were mounted on slides and preserved with 50% karo for future morphological comparisons. Vouchers of all specimens collected for this experiment are accessioned in the University of Washington Burke Herbarium (WTU).

### DNA Extraction and Sequencing

DNA was extracted using a modified protocol of the Bioline Extract- PCR Kit (Bioline, Memphis, TN, USA). Small clippings of healthy blade tissue were placed in 50 µL of the extraction buffer and incubated at 75ºC for ~ 60 minutes. At several points during the primary incubation period the samples were ground using plastic microtube pestles. Samples were then incubated at 95ºC for 10 minutes to halt the enzymatic reaction. The extraction solution was run through One-Step PCR Inhibitor Removal Kit columns (Zymo Research, Irvine, CA, USA) and

stored at -20ºC. PCR reactions were carried out using 4.25 µL $dH_2O$, 6.25 µL MyTaq HS Red Mix (Bioline), 1 µL template DNA, and 0.5 µL of each primer (10µM). P1F and KG4 (Cite) primers were used to target the nuclear-encoded rRNA internal transcribed spacer 1 (ITS1), 5.8 ribosomal RNA gene, and ITS 2. The thermocycler was programmed with an initial denaturation at 95ºC for 2:45 followed by 35 cycles of 90ºC for 0:15, 45ºC for 0:45, and 72ºC for 1:00 with a final extension period of 5:00. 5 µl of the PCR product were loaded onto a test electrophoresis gel to check for successful amplification (as defined by clear, bright bands). PCR reactions of each sample were run with several extraction dilutions (1:1, 1:10, 1:100, 1:200, 1:1000) with the 1:100 and 1:200 dilutions having the highest rate of successful amplification. PCR products were cleaned using ExoSap (Thermo Fisher Scientific, Waltham, MA, USA) and sequenced commercially by Genewiz (Azenta Life Sciences, Burlington, MA, USA).

Individual sequence reactions were edited and contigs assembled using Sequencher (Gene Codes Corp., Ann Arbor, MI, USA). Separate analysis of the two ITS regions was necessary due to the presence of a single base repeat in the ITS2 that prevented the assembly of the forward and reverse sequence reactions in some specimens. An additional 14 sequences of a variety of Laminariales species were mined from GenBank to aid in phylogenetic comparisons, including ones from Lane et al. (2006). Multiple sequences of *S. latissima* and *H. nigripes* from different locations were also downloaded and the sequences compared to assess any genetic variability within the ITS regions between specimens of the same species. A majority of the sequences were trimmed according to preexisting annotations of the 18S, ITS1, 5.8S, ITS2, and 26S regions. ITS regions of the collected specimens and GenBank sequences that were not annotated were cut using a *S. latissima* sequence as a template (Fig. 4). The last 5 bp (CATTA) in the 18S region of each sequence were included to aid with alignments of ITS-1. An identical

technique was employed to isolate the ITS2 regions using the 26s and 5.8s sequences of the same *S. latissima* sequence. The high level of conservation of these rRNA genes allowed for confident identification and trimming of the ITS regions

Phylogenetic Analysis

The Multiple Alignment using Fast Fourier Transform (MAFFT) program was used for sequence alignment. Maximum likelihood trees were constructed using MEGA11: Molecular Evolutionary Genetics Analysis version 11 (Tamura, Stecher, and Kumar 2021) using a general time reversible model of evolution and gamma distribution among sites. Support for branches was determined based on 100 bootstrap replications of the maximum likelihood searches.

**Table 1**

| Specimen/GenBank ID | Suspected Species | Species based on genetics | Collection location |
|---|---|---|---|
| EDM 02 | *S. latissima* | *H. nigripes* | Deadman Bay, San Juan, WA, USA |
| EDM 06 | *S. latissima* | *H. nigripes* | Deadman Bay, San Juan, WA, USA |
| EDM 07 | *S. latissima* | *S. latissima* | Reuben Tarte, San Juan, WA, USA |
| EDM 11 | *S. latissima* | *S. latissima* | Reuben Tarte, San Juan, WA, USA |
| EDM 12 | *S. latissima* | *S. latissima* | Reuben Tarte, San Juan, WA, USA |
| EDM 13 | *S. complanata* | Complanata group | Mosquito Pass, San Juan, WA, USA |
| EDM 14 | *S. complanata* | *S. latissima* | Mosquito Pass, San Juan, WA, USA |
| EDM 15 | *S. latissima* | *S. latissima* | Friday Harbor Lab Dock, San Juan, WA, USA |
| EDM 19 | *S. complanata* | Complanata group | Friday Harbor Town Dock, San Juan, WA, USA |
| EDM 20 | *S. complanata* | Complanata group | Friday Harbor Town Dock, San Juan, WA, USA |
| EDM 21 | *S. latissima* | *S. latissima* | Friday Harbor Town Dock, San Juan, WA, USA |
| EDM 23 | *S. complanata* | Complanata group | Mosquito Pass, San Juan, WA, USA |
| EDM 24 | *S. complanata* | Complanata group | Mosquito Pass, San Juan, WA, USA |

| | | | |
|---|---|---|---|
| EDM 25 | *S. latissima* | Complanata group | Mosquito Pass, San Juan, WA, USA |
| EDM 27 | *S. latissima* | Complanata group | Mosquito Pass, San Juan, WA, USA |
| FHL23-44 | *P. gardneri* | Complanata group | Eagle Cove, San Juan, WA, USA |
| FJ042746 | *S. latissima* | *S. latissima* | Vivian Island, BC, Canada |
| AF319021 | *S. gyrata* | *S. gyrata* | Akkeshi, Japan |
| AY857891 | *S. angustata* | *S. angustata* | Muroran, Hokkaido, Japan |
| AY857896 | *S. sessilis* | *S. sessilis* | Cape Beale, Bamfield, BC, Canada |
| AY851509 | *N. luetkeana* | *N. luetkeana* | Cape Beale, Bamfield, BC, Canada |
| AY857879 | *C. costata* | *C. costata* | Whiffen Spit, Sooke, BC, Canada |
| AY857880 | *A. clathratum* | *A. clathratum* | Grand Mannan Is., NB, Canada |
| AY857878 | *E. fistulosa* | *E. fistulosa* | Seldovia Point, AL, USA |
| AY857875 | *P. californica* | *P. californica* | Cape Beale, Bamfield, BC, Canada |
| AY857874 | *L. littoralis* | *L. littoralis* | Frank Island, Uculet, BC, Canada |
| AF362997 | *A. marginata* | *A. marginata* | Seal Rock, OR, USA |
| KM019204 | *H. nigripes* | *H. nigripes* | Schoodic Point, ME, USA |
| AY857876 | *P. gardneri* | *P. gardneri* | Pachena Beach, Bamfield, BC, Canada |
| AY857873 | *U. pinnatifida* | *U. pinnatifida* | l'Etang de Thau, France |

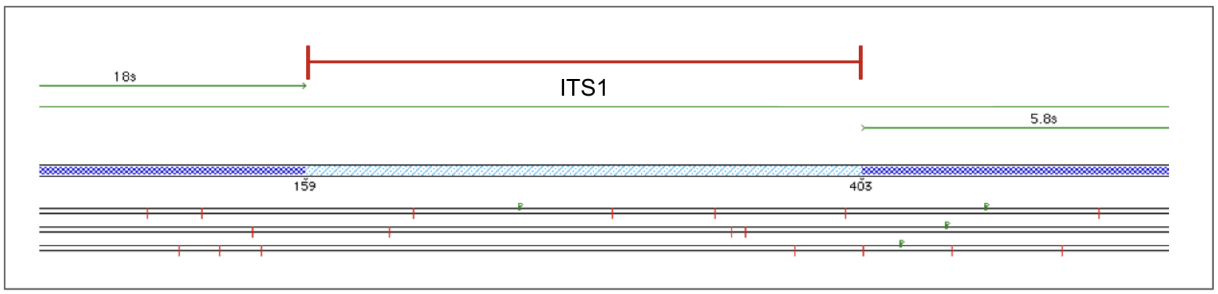


**Figure 4.** Visual of 18s through 26s regions**,** represented by snapshots of Sequencher alignments *S. latissima*

## Results

Twenty-seven specimens were collected and classified based on morphological features as either *S. latissima* or *S. complanata* using the Gabrielson 2018 keys. Of these twenty-seven specimens, I obtained sequence data from fourteen. Within these specimens, sequence data revealed 3 genetically distinct groups, *S. latissima*, *H. nigripes*, and a species not matching any preexisting ITS sequence data (Fig. 5). Six specimens (EDM 07, 11, 12, 14, 15, 21) were identified as *S. latissima* with ITS regions identical to sequences of *S.latissima* sourced from Genbank (Fig. 5a). EDM02 and EDM06 matched sequences of *H. nigripes*, and were found to have mucilage ducts in their stipes, a key feature that separates *H. nigripes* from *S. latissima* and other *Saccharina* species (Fig. 5b). Seven specimens (EDM 13, 19, 20, 23, 24, 25, 27, FHL23-44) had ITS 1 regions that, although consistent between themselves, revealed no close homology to any *Saccharina* GenBank sequences (Fig. 5c). These seven specimens are henceforth referred to as the complanata group.

Sequence alignments showed high levels of conservation between the ITS1 regions of specimens within the same species (Fig. 6). One donated alga, FHL23-44, presented the

morphology of a classic *P. gardneri*, with a distinct thick, broad midrib, however its ITS region was identical to specimens in the complanata group (Fig. 5c, 6).

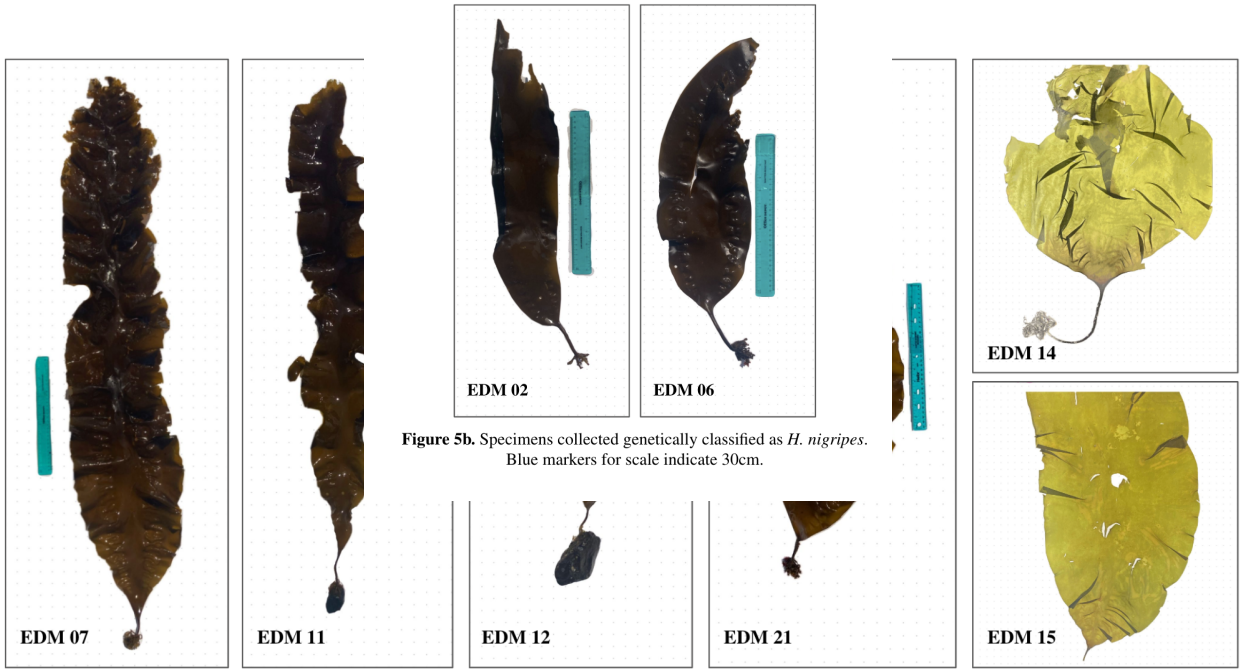


**Figure 5b.** Specimens collected genetically classified as *H. nigripes*. Blue markers for scale indicate 30cm.

**Figure 5a.** Specimens collected genetically classified as *S. latissima.* Blue markers for scale indicate 30cm. EDM 14/15 are photographs of voucher pressings, not the fresh specimens.


**Figure 5c.** Specimens collected falling into the category of complanata group. Blue markers for scale indicate 30cm, clear/white markers indicate 15cm. EDM 13/FHL23-44 are photographs of voucher pressings, not fresh specimens

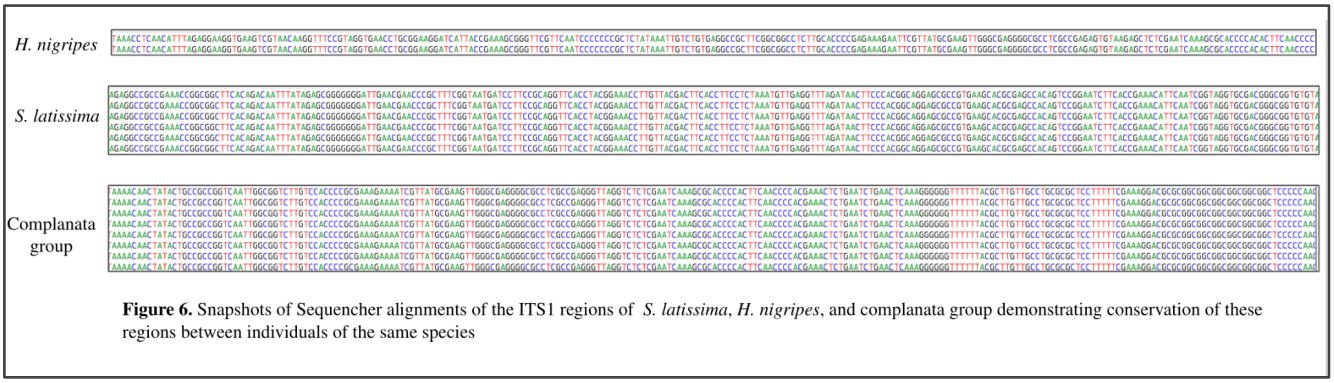


**Figure 6.** Snapshots of Sequencher alignments of the ITS1 regions of *S. latissima*, *H. nigripes*, and complanata group demonstrating conservation of these regions between individuals of the same species

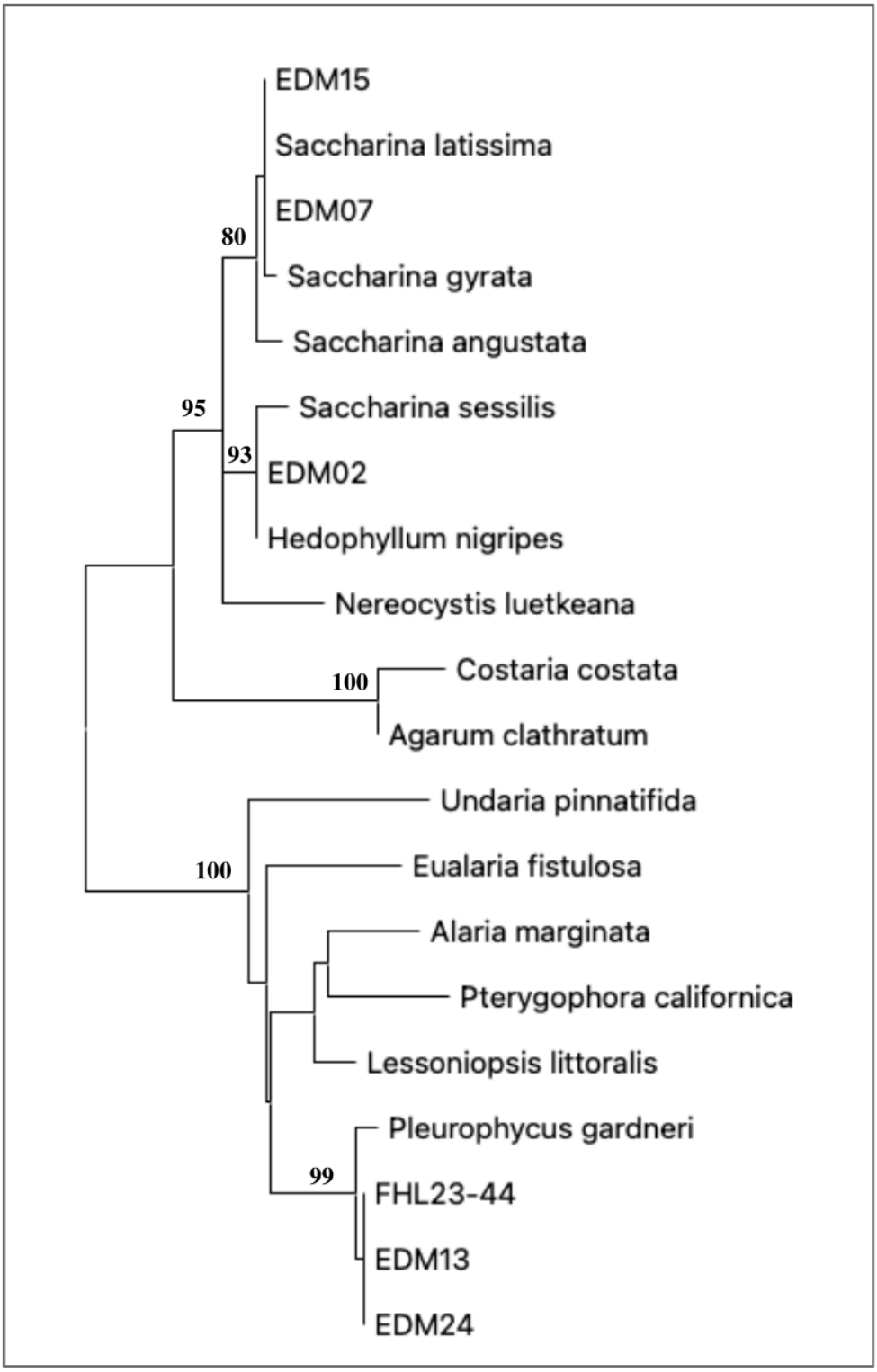


**Figure 7.** Maximum likelihood tree of ITS 1 regions using a general time reversal model of evolution and gamma distribution. Bootstrap values under 80 were removed from the tree.

The maximum likelihood tree resolved three major clades representing the families Costariaeceae, Laminaraceae, and Alariaceae (Fig. 7). Specimens representative of the complanata group (EDM 13, EDM24) and FHL23-44 were placed within the Alariacaece clade sister to a sequence of *Pleurophycus gardneri* from GenBank. This complanata group/*P. gardneri* clade is highly supported (bootstrap value = 99). These specimens are topologically distant from *S. latissima* and *H. nigripes*, which are resolved in the Laminaraceae clade.

In a direct comparison of ITS 1 region the GenBank *P. gardneri* to those of complanata group/FHL23-44 the only divergences were two single site insertion-deletion mutations (indels), and an area of one large (or seven non-contiguous) indels in the *Pleurophycus* sequence depending upon how this region is aligned (Fig. 8a). The ITS 2 region differed by two indels and one base pair substitution between the EDM13, EDM24, FHL23-44, and GenBank *P. gardneri* sequences (Fig. 8b).

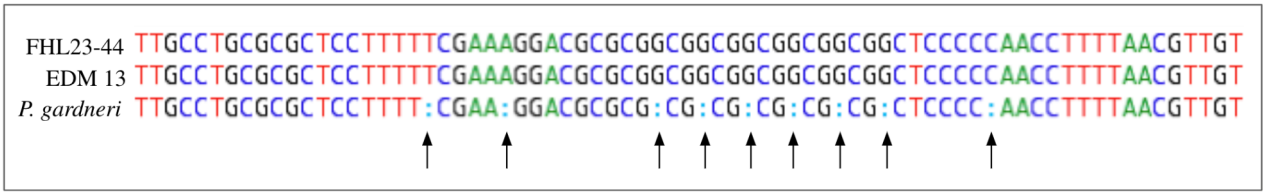


**Figure 8a.** Snapshots of Sequencher alignments of the ITS1 regions of complanata group specimens and the only existing sequence of *P. gardneri* highlighting the areas of divergence. Arrows indicate the sites of single nucleotide deletions.

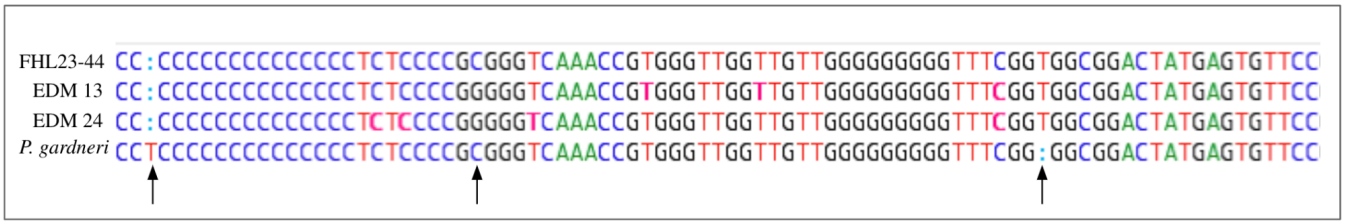


**Figure 8b.** Snapshots of Sequencher alignments of the ITS2 regions of complanata group specimens and the only existing sequence of *P. gardneri* with arrows highlighting the areas of sequence disagreement.

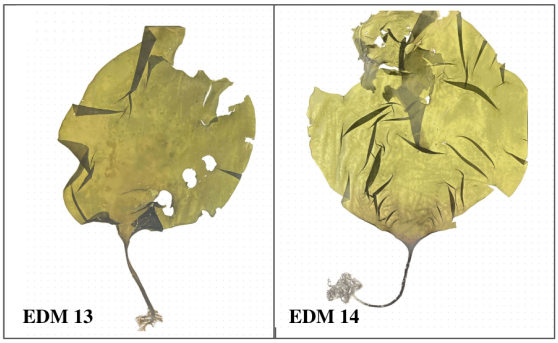


**Figure 9.** Visual comparison of EDM 13 (complanata group) and EDM 14 (*S. latissima*). Note the similar morphologies.

## Discussion

My hypothesis was that the *S. complanata* would show no major genetic variation from *S. latissima*, and data would support the new combination *Saccharina latissima f. complanata* with the Basionym *Laminaria saccharina f. complanata* Setchell and Gardner. The data show that the answer is more nuanced, as genetic sequencing placed *S. complanata* in an entirely different genus. I now suggest two plausible, yet mutually exclusive, interpretations that these specimens of the complanata group are 1) either a new species in the genus *Pleurophycus* or 2) a morphological form of *Pleurophycus gardneri*, *P. gardneri f. complanata*.

On one hand, the similarity in the ITS 1 & 2 regions of the complanata group and the P. *gardneri* sequence, which differ only by a few sites, suggests the existence of *P. gardneri f. Complanata* (Fig 8a,b). These differences could be understood as single nucleotide polymorphisms or similar mutations that can be present from alga to alga within the same species. In addition, specimen FHL23-44 had a defined, broad midrib indicative of *P. gardneri* and yet ITS sequences that match the complanata group at all but one site. This further blurs the

lines between *P. gardneri* species and the complanata group, consistent with the hypothesized existence of *P. gardneri f. complanata* (Fig 5c.).

On the other hand, the high level of conservation seen in the ITS 1 & 2 sequences between specimens of the same species of the Laminariales order, such as *S. latissima* an *H. nigripes*, could indicate that the small changes in the ITS sequences between the complanata group and *P. gardneri* are enough to classify these two groups as different species (Fig. 6). The idea of two *Pleurophycus* species is also supported by the absence of a thick, broad midrib in all complanata group specimens (except for FHL23-44). Although morphological variation within species is a common phenomenon in the Laminaraceae family, there have been no reported instances of *gardneri* specimens lacking a defined midrib. This supports the interpretation of *S. complanata* as a new midrib-less *Pleurophycus* species, separate from *P. gardneri*.

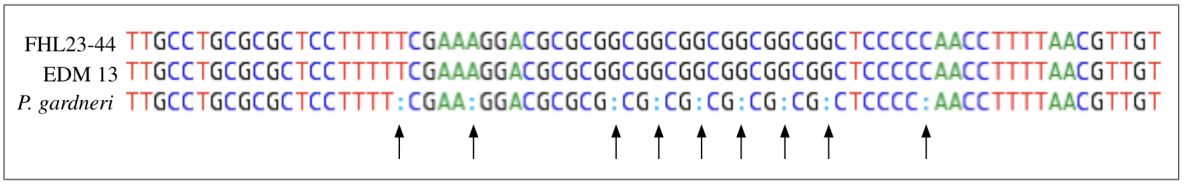


**Figure 8a.** Snapshots of Sequencher alignments of the ITS1 regions of complanata group specimens and the only existing sequence of *P. gardneri* highlighting the areas of divergence. Arrows indicate the sites of single nucleotide deletions.

Apart from the *pleurophycus-complanata* enigma, my results do offer some bits of certainty. First, it is clear that morphological observations alone cannot be relied upon to consistently classify different species of kelp (particularly within the Laminariaceae and Alariaceae families) with high accuracy. There is too much variability of the stipe length, blade thickness, shape, presence/absence of midrib between individuals within the species and overlap of so called 'distinct' morphological traits between different species to align with 'classic'

descriptions of these *Saccharina* species (and now possibly *Pleurophycus*). This is well demonstrated in the comparison of the species EDM13 and EDM14 (Fig. 9). From a morphological perspective using both Setchell & Gardners descriptions and Gabrielson's 2012 key, EDM13 and EDM14 would both be classified as *S. complanata* (Gabrielson, 2012; Setchell, 1919). However, ITS 1 sequences classify EMD13 as part of the complanata group and EDM14 as a *S. latissima*, placing two nearly identical looking kelp into two different families/genera/species. Similarly, specimen FHL23-44 has a defined, broad midrib indicative of *P. gardneri* and yet ITS sequences match the complanata group (Fig. 5c, 6).

Finally, I can confidently say that future studies expanding on these findings, as well as the results from studies like Lane et al. (2006) and Starko et al. (2021), that aim to fully understand the Laminariales phylogenetic relationships, are desperately needed. Additional sequence data at multiple loci from a variety of *Pleurophycus gardneri, S. latissima*, and *S. complanata* are needed to further unravel the mystery of *Saccharina complanata*. One vital step for future investigations would be tracking down and sequencing vouchers of the type specimens of *S. latissima, S. complanata,* and *P. gardneri*.

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This research study would not have been possible without the support of my Marine Botany instructors, Dr. Thomas Mumford and Dr. Wilson Freshwater. As someone who was new to marine biology at the start of this research project I was inspired by y'alls passion for the study of algae/phycology. Tom, thank you for letting me work on this project and your contagious determination to figure out the *complanata* mystery. Wilson, thank you for all your time, energy, and hours spent on this project. I am grateful for your support throughout this entire process. In addition, Sarah Tanja, the teaching assistant for Marine Botany, was an integral resource for

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