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Systematics of Ulvaceae (Ulvales, Ulvophyceae) and the genus *Ulva* L. based on nuclear and chloroplast sequence data

Hillary Seth Hayden

A dissertation submitted in partial fulfillment of the
requirements for the degree of

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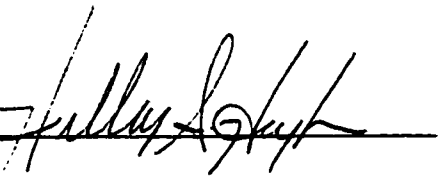
Signature 

Date 20 July 2001

University of Washington
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Hillary Seth Hayden

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Abstract

Systematics of Ulvaceae (Ulvales, Ulvophyceae) and the genus *Ulva* L. based on nuclear and chloroplast sequence data

Hillary Seth Hayden

Chairperson of the Supervisory Committee:
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Systematic hypotheses for Ulvaceae were tested using sequences for the chloroplast gene encoding the large subunit of RUBISCO (*rbc*L) and nuclear small subunit ribosomal DNA (18S rDNA). Ulvaceae *sensu* Floyd and O'Kelly (1990), including *Percursaria*, *Ulvaria* and a complex of closely related species of *Chloropelta*, *Enteromorpha* and *Ulva*, is supported. Morphological synapomorphies for the family include the early development of vegetative thalli and motile cell ultrastructure. Method of flagellate release and gross morphology are not systematically reliable characters. The Ulvales and Ulotrichales *sensu* Floyd and O'Kelly (1990) are monophyletic. *Blidingia* and *Kornmannia* are allied with the former and *Capsosiphon* with the latter, though relationships among these and other taxa in these orders remain uncertain.

Sequences of the internal transcribed spacers of nuclear ribosomal DNA (ITS nrDNA) and *rbc*L were analyzed to test the monophyly of the cosmopolitan genera *Ulva* and *Enteromorpha*. Phylogenetic analyses indicate that neither *Ulva* nor *Enteromorpha* are monophyletic; however, with the exception of *Ulva olivascens*, all

sampled *Ulva* and *Enteromorpha* form a strongly supported clade. Within this clade, there are smaller clades comprised of all distromatic, all tubular, and both distromatic and tubular species; however, few morphological synapomorphies defining these clades can be identified, given the simple morphology and high degree of phenotypic plasitcity in these algae.

A phylogeny of *Ulva* and *Enteromorpha* in the northeast Pacific was reconstructed to test existing species hypotheses. ITS nrDNA and *rbc*L sequences were determined for accessions from the northeast Pacific, Australia, Chile, Hawaii and Japan and were combined with existing sequences for European taxa for analysis. Species were inferred based on monophyly of sampled sequences, and secondarily, sequence divergence. Three species of *Enteromorpha* and seven species of *Ulva* are inferred to occur in this region: *E. intestinalis*, *E. linza*, *E. prolifera*, *U. californica*, *U. lactuca*, *U. lobata*, *U. pseudocurvata*, *U. rigida*, *U. stenophylla* and *U. taeniata*. Three of these appear to be polyphyletic: *E. linza*, *E. prolifera* and *U. taeniata*. The presence of an eighth species, *U. rotundata*, is uncertain. The monospecific genus *Chloropelta* is nested among *Ulva* and *Enteromorpha* species. *Chloropelta caespitosa* is recognized as *Ulva caespitosa*.

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I would also like to thank the organizations that provided funding for this project, including the Department of Botany, Padilla Bay National Estuarine Research Reserve, Phycological Society of America and National Science Foundation. In this vein, I would like to specifically thank Dr. Charles O'Kelly for his guidance in grant writing.

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Finally, I would like to thank my family and friends for being there when I needed them and for helping me to think about things other than this project every now and then.

Dedication

I would like to dedicate this dissertation to my late aunt, Eleanore Lourdes Hayden, who was a dedicated educator and a pioneer in the field of child psychiatric nursing. I am honored to have known her and am grateful to have had her as a role model throughout my pursuit of this degree. Her tremendous strength, and her ability to find beauty and humor in the world in the face of great adversity, continue to inspire me.

General Introduction

The Ulvaceae (Ulvales, Ulvophyceae) are a morphologically simple group of cosmopolitan, macroscopic algae including *Ulva*, one of the first seaweed genera named by Linnaeus (1753). Members of this family, especially *Ulva* (sea lettuce) and *Enteromorpha* (gut weed), are among the most familiar marine algal genera. They are prevalent in coastal ecosystems providing nutrients and habitat to invertebrates and fishes, and they are able to grow rapidly in response to eutrophication producing nuisance "green tides" (Schramm & Nienhuis 1996). Notwithstanding their early scientific record, ubiquitous distribution, and impacts on human activities, little is known about the evolutionary history of the family. Further, Ulvaceae is the type family for the class Ulvophyceae. The validity and circumscription of this class is still under debate, and there are fewer molecular sequences and phylogenetic analyses for this class than for any other green algal class (Zechman et al. 1999). This dissertation explores questions of phylogeny for Ulvaceae and the genus *Ulva* using a molecular systematic approach. Molecular data provide an additional character set to test systematic hypotheses and address questions of character evolution.

Evolutionary relationships among putative Ulvaceae genera are poorly understood due to a limited diagnostic character set (Theriot 1989). Fourteen genera have been allied with *Ulva* since Thuret (1854) emended the Ulvaceae to include green algae with foliose and tubular morphologies, and classification of the family has undergone numerous changes as a result of culture and electron microscopic studies (Kunieda

1934, Fritsch 1935, Chapman 1952, Papenfuss 1960, Bliding 1963, 1968, Kornmann 1965, 1973, Yoshida 1970, Gayral 1971, Round 1971, Tatewaki 1972, Vinogradova 1974, Abbott and Hollenberg 1976, Kornmann and Sahling 1977, Tanner 1979, Silva 1982, Bold and Wynne 1985, Floyd and O'Kelly 1984a, 1984b, 1990, van den Hoek et al. 1995, Gabrielson et al. 2000). Four genera, *Chloropelta*, *Enteromorpha*, *Ulva* and *Ulvaria* are commonly included in the family in recent classifications; however, the systematic positions of four other genera, *Blidingia*, *Capsosiphon*, *Kornmannia* and *Percursaria*, remain controversial due to conflicting variations in morphological, developmental, life history and ultrastructural characters. Relationships among these genera are investigated in Chapter I using sequence data from the chloroplast gene encoding the large subunit of RUBISCO (*rbc*L) and nuclear small subunit ribosomal DNA (18S rDNA).

Ulva and *Enteromorpha* Link are two of the most common nearshore algal genera with approximately 50 and 35 currently recognized species, repectively. *Ulva* includes green seaweeds with distromatic blades, and *Enteromorpha* includes the tubular green seaweeds. The presence of intermediate forms between *Ulva* and *Enteromorpha*, culture studies showing flexibility of form (e.g., Gayral 1967, Bonneau 1977), and recent molecular data (e.g., Tan et al. 1999) suggest that these generic constructs are artificial. Additionally, *Chloropelta*, a monotypic genus described by Tanner (1980), has been considered a close relative of *Ulva*. *Chloropelta caespitosa*, a diminutive, distromatic alga, was separated from *Ulva* based on developmental features; however, initial phylogenetic analyses (Chapter I) suggested that this genus

is not distinct from *Ulva*. The monophyly of *Ulva*, *Enteromorpha* and *Chloropelta* is tested in Chapter II using sequences from the internal transcribed spacer regions and 5.8S gene of nuclear ribosomal DNA (ITS nrDNA) and the *rbc*L gene.

Species delineation in *Ulva* and *Enteromorpha* is known to be difficult because there is a lack of distinguishing morphological characters and high degree of phenotypic plasticity in these algae (e.g., Setchell & Gardner 1903, Vinogradova 1974, Tanner 1979, van den Hoek et al. 1995). *Ulva* species are simple, distromatic blades without distinct branching patterns, reproductive structures and other characters used to infer evolutionary relationships in many other green algal and plant genera. *Enteromorpha* species are monostromatic tubes which also lack many diagnostic morphological characters. Species descriptions in these genera are based on a small set of characters, many of which are quantitative in nature, including gross morphology (thallus shape, size, thickness), cytology (cell size, pyrenoid number) and germling ontogeny (e.g., number of cells in uniseriate germling at first longitudinal division). Delimitation of character states for quantitative characters is difficult in these and other taxa (Stevens 1991), and this difficulty has contributed to the challenge of inferring systematic relationships among *Ulva* and *Enteromorpha* species. Species hyptheses for northeast Pacific *Ulva*, *Enteromorpha* and *Chloropelta* are tested in Chapter 3 using ITS nrDNA and *rbc*L sequences.

The results of this dissertation research have implications for the phylogeny and classification of the Ulvaceae and related taxa. Further, they provide a clearer understanding of the species diversity and distribution of *Ulva*, *Enteromorpha* and

Chloropelta in the northeast Pacific and indicate areas for further systematic study of these ubiquitous green seaweeds.

Chapter I:

Phylogenetic systematics of the Ulvaceae (Ulvales, Ulvophyceae) using nuclear and chloroplast sequences

Introduction

The Ulvaceae (Ulvales, Ulvophyceae) are a morphologically simple group of cosmopolitan macroalgae. The type genus *Ulva* (sea lettuce) was one of the first seaweed genera named by Linnaeus (1753) and is among the most familiar marine algal genera. Ulvaceous algae are ubiquitous and abundant in intertidal and nearshore subtidal areas where they provide habitat and nutrients to marine invertebrates and fishes (Lobban and Harrison 1997). In eutrophic estuaries and harbors they grow rapidly, often causing biofouling and "green tides," i.e., vast accumulations of green algal biomass following a bloom. Biofouling increases drag on marine vessels leading to high fuel consumption and costly maintenance (Fletcher 1980). Green tides disrupt marine ecosystems and interfere with fishing and shellfish harvests (Schramm and Nienhuis 1996). Notwithstanding their long scientific record, predominance in coastal habitats, and impact on human activities, evolutionary relationships among these seaweeds remain poorly understood.

Fourteen genera have been allied with *Ulva* since Thuret (1854) emended the Ulvaceae to include green algae with foliose and tubular morphologies, and classification of the family has undergone numerous changes as a result of culture and

electron microscopic studies (Kunieda 1934, Fritsch 1935, Chapman 1952, Papenfuss 1960, Bliding 1963, 1968, Kornmann 1965, 1973, Yoshida 1970, Gayral 1971, Round 1971, Tatewaki 1972, Vinogradova 1974, Abbott and Hollenberg 1976, Kornmann and Sahling 1977, Tanner 1979, Silva 1982, Bold and Wynne 1985, Floyd and O'Kelly 1984a, 1984b, 1990, van den Hoek et al. 1995, Gabrielson et al. 2000). In recent treatments four genera are considered members of the family, *Chloropelta*, *Enteromorpha*, *Ulva*, and *Ulvaria* (Table 1.1). These genera are characterized by: 1) an isomorphic, diplohaplontic life history in which gametangia and sporangia are identical in structure and development; 2) motile cells which exit singly through a pore in the sporangial or gametangial cell wall; 3) motile cells with bilobed terminal caps, proximal sheaths consisting of two equal subunits and rhizoplasts in specific arrays; and 4) germinating cells which develop from uni-to multiseriate filaments, to monostromatic tubular germlings anchored by rhizoids (Bliding 1963, 1968, Tanner 1980, O'Kelly and Floyd 1984). Germlings remain tubular, at least in part, in *Enteromorpha* (Kapraun 1970) or collapse to form distromatic blades in *Ulva* (Løvlie 1964). Tubular germlings tear open to form monostromatic blades in *Ulvaria* (Dube 1967), or in *Chloropelta*, one division of cells in the tubular germling followed by its rupture produces a distromatic, peltate blade (Tanner 1980).

Ulva and *Enteromorpha* traditionally were considered sister taxa, though generic boundaries have been questioned, given the existence of species with intermediate morphology and culture studies showing flexibility of form between blade and tubular thalli (Silva 1952, Gayral 1967, Bonneau 1977, Provasoli and Pintner 1980). Recent

phylogenetic analyses of the internal transcribed spacer regions of ribosomal DNA (ITS rDNA) suggest that these genera are polyphyletic (Blomster et al. 1999, Tan et al. 1999, Woolcott and King 1999, Hayden Chap. 2). This result, based on a single DNA region, is further evaluated here using multiple data sets. Tanner (1979) suggested that *Chloropelta* is most similar to *Ulvaria* on the basis of developmental similarities. The present study is the first to reconstruct phylogeny for this genus.

The systematic positions of four additional genera, *Blidingia*, *Capsosiphon*, *Kornmannia* and *Percursaria*, are controversial. All were placed in Ulvaceae in early classification schemes (Thuret 1854, Blackman and Tansley 1902). However, as life history and developmental differences became clearer, these genera were divided between two (Kunieda 1934, Papenfuss 1960, Yoshida 1970, Abbott and Hollenberg 1976) or more families (Chapman 1952, Kornmann 1965, Bliding 1968, Gayral 1971, Vinogradova 1974, Silva 1982, Bold and Wynne 1985). Most recently, Floyd and O'Kelly (1990) considered motile cell ultrastructure along with life history and developmental features in their treatment of the class Ulvophyceae (Table 1.2). They included *Percursaria* in Ulvaceae *sensu stricto* but grouped *Blidingia* and *Kornmannia* with the genus *Pseudendoclonium* (*sensu* Nielsen 1980) in an informal "*Blidingia* group" in the Ulvales (Table 1.1). They considered *Capsosiphon* to be allied with taxa of the sister order Ulotrichales *sensu* Floyd and O'Kelly (1984). Further, they expanded the concept of the Ulvales to include microscopic species with branched filamentous thalli, algae traditionally placed in the Chaetophorales. They grouped most of these genera in the family Ulvellaceae (e.g., *Acrochaete*, *Tellamia*, *Ulvella*), and

placed others in informal groups. Their revision of the Ulvales was generally followed by van den Hoek et al. (1995) but not by others (Scagel et al. 1993, Gabrielson et al. 2000).

Few studies using molecular data have addressed phylogeny of ulvaceous algae beyond investigating relationships among species of *Enteromorpha* and *Ulva*. Zechman et al. (1990, 1999) included two species of *Enteromorpha* and *Ulva* in phylogenetic studies of the class Ulvophyceae based on morphology and small (18S). and large (26S) subunit rDNA sequences. Van Oppen (1995) reconstructed phylogeny for a small set of ulotrichalean genera using 18S rDNA sequences. Two species of *Enteromorpha* and one species of *Ulva* were used for outgroup comparison. Sherwood et al. (2000) investigated the phylogenetic position of the Prasiolales (Chlorophyta) using the chloroplast–encoded gene for the large subunit of RUBISCO (*rbc*L) and 18S rDNA sequences. Two species from both the Ulvales and Ulotrichlaes were included to represent these orders. All of these studies support the close association of the Ulvales and Ulotrichales, though the studies by Zechman et al. (1990, 1999) and Sherwood et al. (2000) suggest that the Ulvophyceae is not monophyletic. In their trees, the Ulvales and Ulotrichales are separated from a clade formed by the remaining ulvophycean orders; however, relationships among these orders and the Chlorophyceae and Trebouxiophyceae are not well supported and remain uncertain (Zechman 1999, Sherwood et al. 2000). Due to limited taxon sampling, these studies provide little information about relationships among ulvacean

taxa. The present paper explores phylogeny and tests systematic hypotheses for *Ulva* and related genera using 18S rDNA and *rbc*L sequence data.

Materials and Methods

Samples. Taxa used in this study (Table 1.3) included (approximate percentage of total species in genus is in parentheses): two *Blidingia* (20%), one *Capsosiphon* (33%), one *Chloropelta* (100%), one *Kornmannia* (100%), one *Percursaria* (50%), five *Ulva/Enteromorpha* (5%) and one *Ulvaria* (50%). Additional samples from the Ulvales and Ulotrichales included *Acrosiphonia duriuscula*, *Acrosiphonia* sp., *Gloeotilopsis planctonica*, *Gloeotilopsis sarinoidea*, *Monostroma grevillei*, *Monostroma nitidum*, *Pseudendoclonium fucicola*, *Pseudoneochloris marina*, *Tellamia contorta* and *Ulothrix zonata*. The Trebouxiophytes *Chlorella vulgaris* and *Myrmecia biatorellae* were included as outgroups. The Trebouxiophyceae are the presumed nearest class to the Ulvophyceae (Zechman et al. 1999), and these sequences introduced the shortest outgroup branches of all available taxa. The 18S rDNA dataset includes seventeen new sequences plus eight previously published sequences (Huss and Sogin 1989, Friedl and Zeltner 1994, van Oppen 1995, Freidl 1996, Watanabe et al. 2000). All sequences in the *rbc*L dataset are new.

Algae were field-collected or obtained as unialgal cultures from collections (Table 1.3). Unialgal cultures were grown in taxon-specified media and temperatures in glass culture vessels under 30 – 50 $\mu mol(photons) \cdot m^{-2} \cdot s^{-1}$ on a 16L:8D hour photoperiod

cycle. Field-collected *Chloroptelta caespitosa*, *Ulva californica* and *Ulva fenestrata* collections were grown as unialgal cultures under similar conditions to confirm identification. Other field collections were preserved in 50 – 70 mg of silica gel following identification. *Pseudendoclonium fucicola* and *Tellamia contorta* were obtained as unialgal cultures from Dr. Charles J. O'Kelly at Bigelow Laboratories. Vouchers for field collections were deposited in the University of Washington Herbarium (WTU) (Appendix G).

DNA extraction. For silica gel preserved collections, 14 – 18 mg of material were rehydrated in 200 ml of ddH_2O at 4°C for 10 minutes prior to DNA extraction. Total DNA was extracted from rehydrated or fresh culture material using a modified CTAB method (Doyle and Doyle 1990, Hughey and Hommersand 1999).

PCR amplification and sequencing. Total genomic DNA (10 – 20 ng) was added to six 25 µl PCR reactions each containing 2.5 µl 10X PCR Buffer II (PE Applied Biosystems), 1.5 mM $MgCl_2$, 0.8 mM dNTPs (GibcoBRL), 0.3 Units AmpliTaq DNA Polymerase (PE Applied Biosystems) and 0.8 mM of each primer. PCR amplification was carried out in a PTC-100 Programmable Thermal Controller (MJ Research, Inc.). 18S rDNA was amplified with a set of primers from van Oppen (1995) (forward AB1: GGAGGATTAGGGTCCGATTCC and reverse TW4: CTTCCGTCAATTCCTTTAAG). These primers amplified a 753 bp fragment, excluding primers, spanning the variable 4 and flanking regions. The reaction profile included an initial denaturation at 94°C for 3 min, followed by 35 cycles of 1 min at

94°C, 1 min at 50°C and 2 min at 72°C. The *rbc*L gene was amplied using primers from Manhart (1994) (forward RH1: ATGTCACCACAAACAGAAACTAAAGC and reverse 1385R: AATTCAAATTTAATTTCTTTCC). These primers amplified the first 1358 bp of the *rbc*L gene excluding primers. This fragment excludes the variable 3' terminus and represents 98% of the gene. The reaction profile included an initial denaturation at 94°C for 3 minutes, followed by 35 cycles of 1 min at 94°C, 2 min at 45°C and 3 min at 65°C. PCR products were run on 1.5% agarose gels (SeaKem® LE, FMC Bioproducts), stained in a solution of 0.5 mg/ml ethidium bromide and visualized under UV light. Products were pooled then purified using a PEG-8000 precipitation (Sigma Corp.).

Purified PCR products were sequenced using a dideoxy chain termination protocol with the ABI Prism BigDye Terminator Cycle Sequencing Ready Reaction Kit (PE Applied Biosystems). Internal sequencing primers for the *rbc*L gene were designed by the author. Both strands of PCR products were sequenced on an automated DNA sequencer (ABI 377).

Phylogenetic analysis. Sequences were aligned using Clustal X (Thompson et al. 1997) and edited by eye. Conserved rRNA secondary structure was used to refine the 18S rDNA data set alignment (Van de Peer et al. 2000). Maximum parsimony (MP) and maximum likelihood (ML) analyses were performed for each data set and for a combined data matrix using PAUP* version 4.0b8 (Swofford 1999). Prior to analyses of combined data, the incongruence length difference test (ILD) of Farris et al. (1994), implemented in PAUP* as the partition homogeneity test, was performed using a

partition for 18S rDNA versus *rbc*L data (p = 0.77). An ILD test was also performed for the *rbc*L data set using a partition for each of the three codon positions (p = 1.00). Given the nonsignificant result of this ILD test, analyses were performed using all codon positions. In MP analyses nucleotide positions and character state changes were weighted equally. Gaps were coded as missing data. Heuristic searches were performed with tree bisection-reconnection (TBR), MULTREES and steepest descent options in effect. Ten replicate searches with randomized taxon input were conducted using the random stepwise-addition option. Nonparametric bootstrap analysis (Felsenstein 1985) with 500 replicates was performed to estimate branch support.

Prior to likelihood searches, several parameters were estimated using PAUP*. Bias in nucleotide base composition across taxa was analyzed using a chi-square test of homogeneity of base frequency (p = 0.90). Base frequencies, substitution bias, proportion of invariable sites and site-to-site rate heterogeneity were estimated under likelihood criterion from an optimal parsimony topology (Swofford 1996) and then fixed to those values in ML searches. Substitution bias was modeled by the general time-reversible model (GTR, Yang 1994a), and the proportion of invariable sites was estimated (Hasegawa et al. 1985). Rate heterogeneity was modeled using the gamma distribution method (Yang 1994b) with four discrete rate categories and a single shape parameter (alpha). Heuristic searches were conducted with the same set of options in effect as in MP searches. A total of 100 bootstrap replications were performed under the ML criterion to estimate branch support (Felsenstein 1985).

Results

Analyses of 18S rDNA sequences. The final alignment of 764 nucleotides required the insertion of ten short gaps in regions of 18S rDNA that have been identified as highly variable across eukaryotes (Van der Peer et al. 2000). Nine nucleotide positions were excluded prior to analyses because they could not be aligned with confidence (Appendix A).

MP analysis yielded 21 most parsimonious trees of 247 steps (CI excluding uniformative characters = 0.649, RI = 0.849, not shown). There were 137 variable sites in the analyzed data set, 102 were phylogenetically informative. The topology of one optimal MP tree was identical to that of the tree produced by ML analysis (-lnL = 2390.997) (Fig. 1.1). In this tree, and in the MP trees, three clades are resolved which correspond to taxonomic groupings of Floyd and O'Kelly (1990): Ulvaceae comprised of *Chloropelta*, *Enteromorpha*, *Percursaria*, *Ulva* and *Ulvaria*; Ulvales including Ulvaceae plus *Blidingia*, *Kornmannia*, *Pseudendoclonium* and *Tellamia*; and Ulotrichales with *Capsosiphon*. Bootstrap support under ML and MP criteria is relatively strong for Ulvaceae, moderate for the Ulvales and weak for the Ulotrichales. Within Ulvales, *Percursaria percursa* is sister to the clade comprised of *Chloropelta*, *Enteromorpha* and *Ulva* (*C-E-U*) though support for this relationship is not robust. The clade comprised of *Blidingia*, *Kornmannia*, *Pseudendoclonium* and *Tellamia* (*B-K-P-T*) and two smaller clades, one comprised of *Pseudendoclonium fucicola* and *Tellamia contorta* and the other with the *Blidingia* accessions, are stongly supported.

Within the Ulotrichales, branches are not well-supported in both the MP and ML analyses, except the branch leading to the two *Acrosiphonia* accessions. *Monostroma grevillei* groups with *Ulothrix zonata* rather than *M. nitidum*, though bootstrap support for this clade is relatively weak.

Divergence of 18S rDNA sequences ranges from 0% to 1.9% in Ulvaceae, 0.0% (among *Blidingia* species) to 8.2% in Ulvales, 0.7% to 4.2% in Ulotrichales. The largest divergence (10.1%) among 18S rDNA sequences occurs between outgroup *Myrmecia biatorellae* and taxa in Ulvaceae. In MP trees, low sequence divergence among ulvacean taxa resulted in different branching topologies within this clade; however, neither *Enteromorpha* nor *Ulva* is monophyletic in any optimal tree. The topology of the ML tree (Fig. 1.1) also suggests that these genera are polyphyletic.

Analysis of rbcL sequences. The *rbc*L data set included 19 of the 24 taxa in the 18S rDNA analyses. The *rbc*L gene could not be amplified in the *Capsosiphon fulvescens* collection from Nova Scotia, and efforts to obtain additional *Capsosiphon* from the field or culture collections were unsuccessful. Amplification difficulties also occurred with accessions of *Blidingia* and *Monostroma nitidum*. Several reverse primers for the 3' region were designed, but no primer combination was effective in amplifying the majority of the gene. As a result, only 500 nucleotides from the 5' region are included for these taxa. The final alignment of 1358 nucleotides included one gap representing a single codon located in the *rbc*L gene as amino acid 91 (positions 244 – 246 in the present alignment) (Appendix B). Translation of the DNA sequence indicated that a proline residue was present in *Kornmannia leptoderma*, the ulotrichalean taxa and

Chlorella vulgaris. An alanine residue was present in *Myrmecia biatorellae*. This amino acid residue was inferred to be a deletion in the remaining 12 ingroup taxa. This amino acid is present in the *rbc*L gene of most green algae, including charophytes (Manhart 1994), chlorophytes (Yang et al. 1986, Yoshinaga et al. 1998), prasinophytes (Daugbjerg et al. 1995), trebouxiophytes (Sherwood et al. 2000) and some ulvophytes (Kono et al. 1991); however, a three-base gap also is inferred at this position in other Ulvales sequenced to date (Sherwood et al. 2000).

MP analysis resulted in two optimal trees of 1106 steps (CI excluding uniformative characters = 0.492, RI = 0.575) (Fig. 1.2). A total of 475 characters were variable, 342 of these were phylogenetically informative. The two optimal trees differed from each other only in the position of *Pseudoneochloris marina* (sister to Ulvales versus basal in Ulotrichales). The tree resulting from the ML analysis (-lnL = 6877.522, not shown) had a similar topology to the MP trees, except with respect to the position of *Kornmannia leptoderma*. In the MP analysis, this taxon is sister to the *Blidingia* clade (Fig. 1.2); however, in the ML analysis it is sister to the *Blidingia-Pseudendoclonium-Tellamia* (*B-P-T*) clade which is similar to 18S rDNA results (Fig. 1.1). As in the 18S rDNA analyses, the Ulvaceae *sensu* Floyd and O'Kelly (1990) are strongly supported by both analyses. Additionally, several clades within the family are strongly supported. One internal clade includes one species each of *Chloropelta*, *Enteromorpha* and *Ulva*, while a second contains the remaining *Enteromorpha* and *Ulva* species. The *C-E-U* clade is strongly supported, and *Ulvaria* is sister to this clade. *Percursaria* is basal in the Ulvaceae. The branch leading to the Ulvales is

moderately supported in the *rbc*L analyses. The Ulotrichales have <50% bootstrap support in both analyses, though support for the Ulotrichales minus *Pseudoneochloris marina* is strong. The ranges of *rbc*L sequence divergence within clades are as follows: Ulvaceae 0.6%- 4.8%, Ulvales 0.8%-14.3%, and Ulotrichales 9.7%-12.6%. The greatest sequence divergence (20%) occurs between outgroup *Myrmecia biatorellae* and *Blidingia minima* var. *vexata*.

Analysis of combined 18S rDNA and rbcL sequences. The alignment of combined. data included all taxa with *rbc*L positions coded as missing data for the taxa noted above. In general, bootstrap support for branches is greater in analyses of combined data than in analyses of either individual data set. Two trees of 1359 steps resulted from MP analysis (CI excluding uninformative characters = 0.518, RI = 0.653, not shown). Of the 2113 characters analyzed in the combined data set, 440 were parsimony informative. With respect to relationships of taxa outside the Ulotrichales clade, these MP trees were similar to those resulting from MP analysis of the *rbc*L data alone (Fig. 1.2). In particular, *Kornmannia leptoderma* was sister to the *Blidingia* clade. The topological difference between the two MP trees occurred in the Ulotrichales clade. In one tree *Monostroma grevillei* was sister to the *Gloeotilopsis* clade. In the second tree, this taxon formed a clade with *Ulothrix zonata*, and this clade was sister to the *Gloeotilopsis* clade; however, the node joining *Monostroma grevillei* and *Ulothrix zonata* was only weakly supported (55%).

The tree resulting from ML analysis of the combined data (-lnL=9431.828) is shown in Figure 1.3. As in previous analyses, the Ulvaceae and the *B-K-P-T* clade are

well supported. *Kornmannia leptoderma* is basal in the latter clade similar to trees resulting from analyses of 18S rDNA (Fig. 1.1) and ML analysis of the *rbc*L data (not shown). Additionally, the Ulvales is strongly supported. In contrast to previous trees, *Pseudoneochloris marina* is sister to the Ulvales, and *Monostroma nitidum* is basal in the clade comprised of *Monostroma grevillei*, *Ulothrix zonata*, and the *Gloeotilopsis* and *Acrosiphonia* species; however, bootstrap support under both MP and ML criteria is weak for these relationships. Given the instability of *Pseudoneochloris marina*, this taxon was deleted, and the combined data set was reanalyzed using MP criterion to assess the affect of its removal on support for the Ulotrichales (not shown). Bootstrap support increased to 79% for the branch leading to *Capsosiphon fulvescens* and the remaining Ulotrichalean algae. Other nodes in the reanalyzed data set had comparable support to initial analyses.

Additionally, the instability of *Kornmannia leptoderma*, and its possession of an amino acid in the *rbc*L gene which is absent in other Ulvales, prompted the use of topological constraints to investigate tree lengths with *Kornmannia* positioned outside the Ulvales. The Ulvales (minus *Kornmannia*) were constrained as monophyletic, although relationships within the Ulvales and among *Kornmannia* and ulotrichalean taxa were unconstrained. A heuristic search with similar parameters to previous searches resulted in five most parsimonius trees that were 15 steps longer than unconstrained trees. In these trees (not shown), *Kornmannia leptoderma* was sister to the Ulvales. A statistical test of competing topolgies (*Kornmannia* within Ulvales versus sister to Ulvales) was not conducted since computationally simple tests for this

purpose, i.e., the Kishinio-Hasegawa test (1989), have been shown to be invalid when one of the competing topologies is the optimal solution, as in the present case (Goldman et al 2000).

Discussion

Trees inferred from phylogenetic analyses of 18S rDNA and *rbc*L sequences are generally congruent and have implications for the phylogeny and classification of the Ulvaceae and related taxa.

Ulvaceae. The clade comprised of *Chloropelta*, *Enteromorpha*, *Percursaria*, *Ulva* and *Ulvaria* received strong bootstrap support in all analyses. These results are consistent with Floyd and O'Kelly's (1990) proposal for Ulvaceae, in which these genera, and the genus *Letterstedtia*, are members of the family. Areschoug (1851) separated *Letterstedtia* from *Ulva* on the growth of lateral, "pinnate leaflets" along the thallus margin; however, Papenfuss (1960) argued that *Letterstedtia* is not distinct enough from *Ulva* to warrant generic status. His hypothesis remains to be tested, but it appears unlikely that this genus will be upheld given present results for other genera separated from *Ulva* on the basis of morphology.

Most recent classification schemes of Ulvaceae include *Percursaria* (Papenfuss 1960, Gayral 1964, 1971, Vinogradova 1974, Floyd and O'Kelly 1990), but some place this genus in a separate family (Bliding 1968, Kornmann and Sahling 1977, Silva 1982). Bliding (1968) erected the monotypic Percursariaceae based on distinctive

developmental features observed in *P. percursa*. In the present study, *P. percursa* is sister to the *C-E-U* clade in the 18S rDNA tree (Fig. 1.1) and is sister to the clade comprised of *C-E-U* plus *Ulvaria* in *rbc*L and combined data trees (Figs. 1.2 and 1.3). Using monophyly as the basis for taxonomy, the Percursariaceae is rejected by the 18S rDNA tree but is neither supported nor rejected by the *rbc*L and combined data trees; however, there is strong bootstrap support in all analyses for the clade including *Percursaria*, *Ulvaria* and the *C-E-U* clade and relatively weak support for the clade comprised of the *C-E-U* clade plus *Ulvaria*. Further, it is possible that *Percursaria* is closer to *C-E-U* taxa than *Ulvaria* given the 18S rDNA tree. In this case, the Ulvaceae would be paraphyletic if the Percursariaceae were accepted. Based on these findings, *Percursaria* is considered a member of the Ulvaceae following Floyd and O'Kelly (1990).

Systematists have long considered *Enteromorpha* and *Ulva* to be valid genera despite evidence to the contrary. In her culture studies of European *Ulva* species, Gayral (1967) observed the development of both tubular and blade thalli from single populations of zoospores and parthenogenetic gametes. Bonneau (1977) observed the development of plants possessing distromatic, partially distromatic and completely tubular thalli from swarmers released from a single isolate of *Ulva lactuca*. Provasoli and Pintner (1980) showed that *Ulva* cultures can form uniseriate filaments when axenic or tubular thalli when grown with certain bacteria. Bonneau (1977) and Provasoli and Pintner (1980) agreed that there were no valid criteria for recognizing two genera. Tan et al. (1999) tested their hypothesis using phylogenetic analysis of

ITS rDNA sequences. This analysis revealed mixed clades of *Ulva* and *Enteromorpha* and led Tan et al. (1999) to suggest that there may be a reversible morphogenetic switch controlling gross morphology in these algae. Two clades each with representatives of both *Enteromorpha* and *Ulva* are strongly supported in *rbc*L and combined data analyses. These data are further evidence that these genera are not distinct evolutionary entities. Relationships among these closely related taxa are not resolved by 18S rDNA due to an absence of phylogenetic signal.

There is strong support for the grouping of *Chloropelta caespitosa* with *Ulva californica* and *Enteromorpha prolifera* in the *rbc*L and combined data analyses. Tanner (1980) erected the genus *Chloropelta* on the basis of its unique developmental pattern, which is very distinctive in culture (pers. obs.). On the basis of molecular data, *Chloropelta* cannot be recognized at the generic level. It is premature to assess phylogenetic affinities of *C. caespitosa* to particular species of *Enteromorpha* and *Ulva* given the small number of representative taxa in the current study. Research using phylogenetic analysis of molecular data and a larger sampling of taxa is underway to address this issue (Hayden, this dissertation, Chap. 2).

Ulvales. The Ulvales are well supported in most analyses, though certain relationships are not resolved within this clade. Floyd and O'Kelly (1990) considered *Blidingia*, *Kornmannia*, *Pseudendoclonium* and *Tellamia* as members of families or informal groups distinct from the Ulvaceae (O'Kelly and Floyd 1984, Floyd and O'Kelly 1990). *Blidingia*, *Kornmannia* and *Pseudendoclonium* (*sensu* Nielsen) were placed in an informal "*Blidingia* group" (Floyd and O'Kelly 1990) because these genera

are typified by small zoospores having very reduced features. *Tellamia*, a filamentous alga found within the periostracum of *Littorina obtusata* (Nielsen and McLachlan 1986), was considered a member of the Ulvellaceae, a family of minute algae lacking rhizoplasts in their motile cells. Based on molecular data, *Pseudendoclonium fucicola* is more closely related to *Tellamia contorta* than to *Blidingia* and *Kornmannia*. This suggests that Floyd and O'Kelly's "*Blidingia* group" is not monophyletic. Phylogenetic analyses are equivocal with respect to the relationship between *Kornmannia leptoderma* and species of *Blidingia*. These genera were considered by Bliding (1968) and Gayral (1971) to be closely related based on cytology and certain life history and thallus developmental features. Conversely, Golden and Cole (1986) erected the monotypic Kornmanniaceae (Ulotrichales) citing unique pyrenoid (Hori 1973) and life history traits. O'Kelly and Floyd (1984) considered *Kornmannia* as *incertae sedis* based on these unique features but later placed this genus in their informal "*Blidingia* group" (Floyd and O'Kelly 1990) based on motile cell ultrastrucure and early thallus development.

Kornmannia leptoderma shares the presence of an additional amino acid with representative ulotrichalean and outgroup genera yet sequence data consistently ally this taxon with ulvalean genera with strong bootstrap support. The position of *Kornmannia* in this clade and the lack of an additional amino acid residue in other Ulvales suggests that either two independent deletions occurred (along branches leading to the *B-P-T* clade and the Ulvaceae) or an amino acid was lost prior to diversification of the Ulvales and independently regained in *Kornmannia*. An alternative tree topolgy

which would explain sequence evolution among these algae would place the branch leading to *Kornmannia* between the Ulotrichales and Ulvales. Under this hypothetical scenario, an amino acid would be lost prior to the diversification of the Ulvales but after the branch leading to *Kornmannia* (i.e., one loss versus two losses or a loss followed by an independent gain). However, constrained trees which result in *K. leptoderma* assuming an intermediate position between the Ulotrichales and Ulvales are 15 steps longer than unconstrained trees.

Within the *B-K-P-T* clade the position of *Kornmannia leptoderma* is relatively unstable. It is sister to *Blidingia* in MP analyses of *rbc*L (Fig. 1.2) and combined data (not shown), and it is sister to the *B-P-T* clade in all other unconstrained analyses. The instability of this taxon may be due, in part, to the relatively small selection of representative Ulvales sequences in this study. Limited taxon sampling likely contributes to relatively long branches in this clade. Relationships among these genera should be reconsidered after more taxa have been sampled.

Ulotrichales. Floyd and O'Kelly (1990) allied *Capsosiphon* with *Gayralia* and *Trichosarcina* in their informal "*Gayralia* group" of the Ulotrichales. The present study supports their hypothesis that *Capsosiphon* is a member of the Ulotrichales though its position in this order remains unclear. *Capsosiphon* does not appear to have a close association with *Ulothrix* as Migita (1967) and O'Kelly and Floyd (1984) proposed. The placement of *Capsosiphon* in Ulvaceae was based primarily on the morphology and development of its tubular thalli (Bliding 1935, Papenfuss 1960, Chihara 1967). Chapman (1952) elevated the genus to familial rank

(Capsosiphonaceae, Ulvales) given observed cytological and structural differences between thalli of *Capsosiphon* and other Ulvaceae. Detailed life history studies revealed that the sexual life history of *C. fulvescens* (Migita 1967, Yoshida 1970) and *C. groenlandicum* (as *Monostroma groenlandicum*, Tatewaki 1972) includes an alternation of tubular gametophytes with cyst-like sporophytes. The cyst-like sporophyte, or *Codiolum* sporophyte, is characteristic of genera in the Ulotrichales. Relationships among Ulotrichalean genera have been investigated using molecular data. (Friedl and Zeltner 1994, van Oppen 1995, Friedl 1996); however, species of *Capsosiphon* have not been included in these studies. The addition of new taxa in molecular-based phylogenies should produce a clearer picture of the relationship of *Capsosiphon* to other genera of the Ulotrichales.

Although the systematic position of *Pseudoneochloris marina* was not a focus of this study, this taxon's instability in trees is noteworthy. Watanabe et al. (2000) described this coccoid green alga based on ultrastructure and 18S rRNA sequence data. In their study, *P. marina* grouped with Ulvophycean taxa as sister to the genus *Acrosiphonia* or nested between this genus and a clade of Ulotrichalean taxa; however, as in the present study, the position of this taxon was not well supported. Additional taxon sampling may help resolve its systematic position among the Ulotrichales. Also noteworthy is the apparent polyphyly of *Monostroma*. Some evidence for this has already been discussed by Van Oppen (1995). A comprehensive study of this genus is warrented given her results and those from the present study.

Character assessment. Few characters have been available for systematic studies of these morphologically simple green algae. An inclusive list of traits considered in assessing relationships among genera includes sexual life history pattern, sporangial and gametangial structure and development, ultrastructure of motile cells and method of their release, and development and morphology of vegetative thalli. Consideration of these traits has led to an array of conflicting systematic hypotheses and classification schemes. The evolution of these traits and their ability to diagnose natural groupings can be evaluated given robust phylogenetic trees.

Sexual life history pattern and sporangial and gametangial structure and development have been used to separate genera at the ordinal level (Kornmann 1965, Floyd and O'Kelly 1984). Clades that reflect this separation are resolved by molecular data. Interestingly, the consideration of sexual life history pattern has led to conflicts in systematic hypotheses for *Kornmannia*. In *K. leptoderma*, a macroscopic sporophyte comprised of monostromatic blades growing from a basal disc of tissue alternates with a discoid gametophyte (Yamada and Tatewaki 1965). This seemingly unique heteromorphic life cycle is a primary character used to group this taxon with the Ulotrichales (Golden and Cole 1986), yet the heteromorphic life cycle of the Ulotrichales includes a *Codiolum* sporophyte which is absent in *K. leptoderma*. Additionally, a life cycle similar to that of *K. leptoderma* (i.e., a macroscopic sporophyte and discoid gametophyte) was observed in *Blidingia minima* (Tatewaki and Iima 1984), a species in which an isomorphic life history is known (Tatewaki 1972). The loss of upright thalli from the discoid gametophyte of *K. leptoderma* may

simply represent a reduction in an essentially isomorphic life history rather than the evolution of a novel heteromorphic pattern. Given this interpretation, an isomorphic sexual life history pattern should be considered a synapomorphy of the Ulvales.

Features of motile cell ultrastructure and method of motile cell release have been considered in the diagnosis of orders and families for these algae (Floyd and O'Kelly 1984, O'Kelly and Floyd 1984, Floyd and O'Kelly 1990). Groupings of taxa based on ultrastructural traits are consistent with clades resolved by molecular data while those based on the method of motile cell release are not. A vesicle surrounding motile cells during their release from sporangia and gametangia has been observed in *Percursaria percursa* (Kornmann 1956, Bliding 1963) but is absent in other ulvalean genera. O'Kelly and Floyd (1984) suggested that the vesicle is a plesiomorphic trait because it is derived from an electron-dense wall, or capsule, of the mother cell present in both ulvalean and ulotrichalean genera. In most Ulvales, the capsule remains attached to the mother cell wall; however, this layer functions as a vesicle surrounding exiting motile cells in many Ulotrichales, a function which may have been regained in *Percursaria*. Molecular evidence is in accordance with this view.

Development and morphology of vegetative thalli have been used to delineate the Ulvaceae and genera in this family. Trees inferred from molecular data suggest that certain developmental traits diagnose monophyletic groups while others do not. One synapomorphy, the early developmental pattern of sporophytes and gametophytes, defines the family. In all observed Ulvacean taxa, zygotes, spores and parthenogenetic gametes germinate into uniseriate filaments which later become biseriate. In

Percursaria, upright thalli are composed of biseriate filaments. In the remaining Ulvaceae, filaments become multiseriate and then tubular.

Generic boundaries have been based on the fate of the tubular germling, i.e., germlings remain tubular in *Enteromorpha*, collapse to form distromatic blades in *Ulva*, or tear open to form monostromatic blades in *Ulvaria*, etc. Although the delineation of genera on this basis is very appealing, it does not appear to have phylogenetic significance in all cases. The splitting open of the monostromatic tube appears to be a synapomorphy for *Ulvaria*; however, the existence of non-overlapping clades with mixtures of *Chloropelta*, *Enteromorpha* and *Ulva* species suggests that other developmental steps are not systematically reliable. A second developmental trait that does not appear to be reliable is the growth of upright filaments from a basal cushion of tissue. This was one of the primary characters that led Bliding (1968) to separate *Percursaria* from the Ulvaceae; however, growth from a basal disc also occurs in *Blidingia*, *Kornmannia* and *Monostroma*. The position of these genera in phylogenetic trees suggest that this trait has evolved several times in this group of green algae.

Conclusions

18S rDNA and *rbc*L sequence data are valuable for testing systematic hypotheses for the Ulvaceae and related taxa. With few exceptions, Floyd and O'Kelly's (1990) hypotheses for these genera are further supported by the molecular evidence presented here. A monophyletic Ulvaceae includes *Percursaria*, *Ulvaria* and a complex of

closely related species which should be considered *Ulva*. The Ulvales and Ulotrichales are distinct evolutionary lineages. *Blidingia* and *Kornmannia* are allied with the former, *Capsosiphon* with the latter. The Ulvales are characterized by an isomorphic life history pattern, gametangia and sporangia that are identical in structure and development, motile cells with bilobed terminal caps and proximal sheaths consisting of two equal subunits. The initial development of vegetative thalli and the presence of rhizoplasts in specific arrays diagnose a monophyletic Ulvaceae. Method of motile cell release and the gross morphology of vegetative thalli are not systematically reliable characters. The present finding that molecular data support groupings based on motile cell characters and refute those based on vegetative morphology is similar to that from studies of the Ulotrichales (Friedl and Zeltner 1994, van Oppen 1995).

Table 1.1. Selected classification schemes for Ulvaceae and related genera. Only genera included in the present study are listed for Floyd and O'Kelly (1990). (Modified from Tanner 1979).

Papenfuss (1960)	Gayral (1964)	Bliding (1968)	Vinogradova (1974)	Kornmann & Sahling (1977)	Floyd & O'Kelly (1990)
CHLOROPHYCEAE	**CHLOROPHYCEAE**	**CHLOROPHYCEAE**	**CHLOROPHYCEAE**	**CHLOROPHYCEAE**	**ULVOPHYCEAE**
Ulotrichales	**Ulotrichales**	**Ulvales**	**Ulvales**	**Ulvales**	**Ulvales**
Ulvaceae	Capsosiphonaceae	Capsosiphonaceae	Capsosiphonaceae	Capsosiphonaceae	Ulvellaceae
Capsosiphon	*Capsosiphon*	*Capsosiphon*	*Capsosiphon*	*Capsosiphon*	*Tellamia*
		Percursariaceae		Percursariaceae	
		Percursaria		*Percursaria*	
	Ulvaceae	Ulvaceae	Ulvaceae	Ulvaceae	Ulvaceae
Percursaria	*Percursaria*		*Percursaria*		*Percursaria*
Enteromorpha	*Enteromorpha*	*Enteromorpha*	*Enteromorpha*	*Enteromorpha*	*Enteromorpha*
Ulva	*Ulva*	*Ulva*	*Ulva*	*Ulva*	*Ulva*
	Ulvaria	*Ulvaria*	*Ulvaria*		*Ulvaria*
Rhizenteron					*Chloropelta*
					"*Blidingia* group"
					Pseudendoclonium
Blidingia	*Blidingia*			*Blidingia*	*Blidingia*
				Kornmannia	*Kornmannia*
Feldmannodora	*Ulvopsis*			**CODIOLOPHYCEAE**	**Ulotrichales**
Monostromataceae	Monostromataceae	Monostromataceae	Monostromataceae	Monostromataceae	Monostromataceae
		Blidingia	*Blidingia*		
Monostroma (including *Ulvaria*)	*Monostroma*	*Monostroma*	*Monostroma*	*Monostroma*	*Monostroma*
		Kornmannia	*Kornmannia*		
			Gomontia		
			Gayraliaceae		"*Gayralia* group"
			Gayralia		*Capsosiphon*
			Protomonostroma		
					Ulotrichaceae
					Ulothrix

Table 1.2. Summary of characters used to diagnose the Ulvales, Ulotrichales and families within the Ulvales based on Bliding (1968), Floyd and O'Kelly (1984) and O'Kelly and Floyd (1984).

Character		
	Ulvales	**Ulotrichales**
Life History	Isomorphic; gametangia and sporangia identical in structure and development	Heteromorphic in most genera; structure and development of gametophyte-borne gametangia/sporangia different from sporophyte-borne sporangia
Flagellate release	Singly, through pore in sporangial/gametangial cell wall	Usually en masse from gametophytes, surrounded by vesicle of modified cell wall material; through simple, unelevated hole
Flagellate ultrastructure	Bilobed terminal caps; proximal sheath with 2 equal subunits and having the same structure on basal bodies	Simple, overlapping terminal caps; wedge-shaped proximal sheaths subtending upper basal bodies
	Ulvaceae	**Ulvellaceae**
Thallus morphology	Parenchymatous	Filamentous or pseudoparenchymatous
Thallus development	Zygotes/spores -> uni-to multiseriate filaments -> monostromatic tubular germlings anchored by rhizoids	N/A
Flagellate ultrastructure	Rhizoplasts in specific arrays	Rhizoplasts absent

Table 1.3. Species sampled in this study.

Taxon	Source [a]	GenBank [b]
Ulvophyceae		
Acrosiphonia duriuscula (Ruprecht) Yendo	Watanabe et al. unpub.	AB049418
Acrosiphonia sp. Agardh	Zechman and Chapman unpub.	U03757
Blidingia minima (Nägeli *ex* Kützing) Kylin var. *minima*	Bolinas Beach, CA	
Blidingia minima var. *vexata* (Setchell *et* Gardner) J. Norris	Vancouver Is., British Columbia	
Capsosiphon fulvescens (C. Agardh) Setchell *et* Gardner	Monks Head Beach, Nova Scotia	
Chloropelta caespitosa Tanner	Monterey, CA	
Enteromorpha intestinalis (L.) Nees	Vancouver Is., British Columbia	
Enteromorpha prolifera (O. F. Müller) J. Agardh	Blakely Is., WA	
Gloeotilopsis planctonica Iyengar *et* Philipose	SAG 29.93	Z28970
Gloeotilopsis sarinoidea (as *Protoderma sarinoidea* [Groover *et* Bold] Tupa)	Friedl (1996)	Z47998
Kornmannia leptoderma (Kjellman) Bliding	Vancouver Is., British Columbia	
Monostroma grevillei (Thuret) Wittrock	Tan and Sluiman unpub.	AF015279
Monostroma nitidum Wittrock	Shirahama, Japan	
Percursaria percursa (C. Agardh) Rosenvinge	UWCC MA230	
Pseudendoclonium fucicola (Rosenvinge) R. Nielsen	Boothbay Harbor, ME	
Pseudoneochloris marina Watanabe, Himizu, Lewis *et* Floyd	UTEX 1445	U41102
Tellamia contorta Batters	San Juan Is., WA	
Ulva californica Wille	San Juan Is., WA	
Ulva fenestrata Postels *et* Ruprecht	San Juan Is., WA	
Ulva lactuca L.	Strangford Lough, Ireland	
Ulvaria obscura var. *blyttii* (Areschoug) Bliding	Padilla Bay, WA	
Ulothrix zonata (F. Weber *et* D. Mohr) Kützing	SAG 38.86	Z47999
Trebouxiophyceae		
Chlorella vulgris Beijerinck	SAG 211-11b	X13688
Myrmecia biatorellae Boye-Petersen	SAG 8.82	

[a] CCMP, Provasoli-Guillard National Center for Culture of Marine Phytoplankton; SAG, Sammlung von Algenkulturen der Universität Göttingen (Culture Collection of Algae at the University of Göttingen); UTEX, Culture Collection of Algae at the University of Texas; UWCC, University of Washington Culture Collection.

[b] Available GenBank accession numbers for 18S rDNA sequences.

Figure 1.1. Phylogenetic tree inferred from a heuristic search using maximum likelihood of 18S rDNA sequence data (-lnL = 2390.997). Family and orders are based on Floyd and O'Kelly (1990). Horizontal branch lengths are proportional to the mean number of nucleotide substitutions per site. Numbers associated with nodes indicate bootstrap values using maximum likelihood (100 replicate samples) followed by values for maximum parsimony (500 replicate samples), respectively; – indicates a bootstrap value less than 50% for an analysis. Nodes with bootstrap values of less than 50% in both analyses are not labeled.

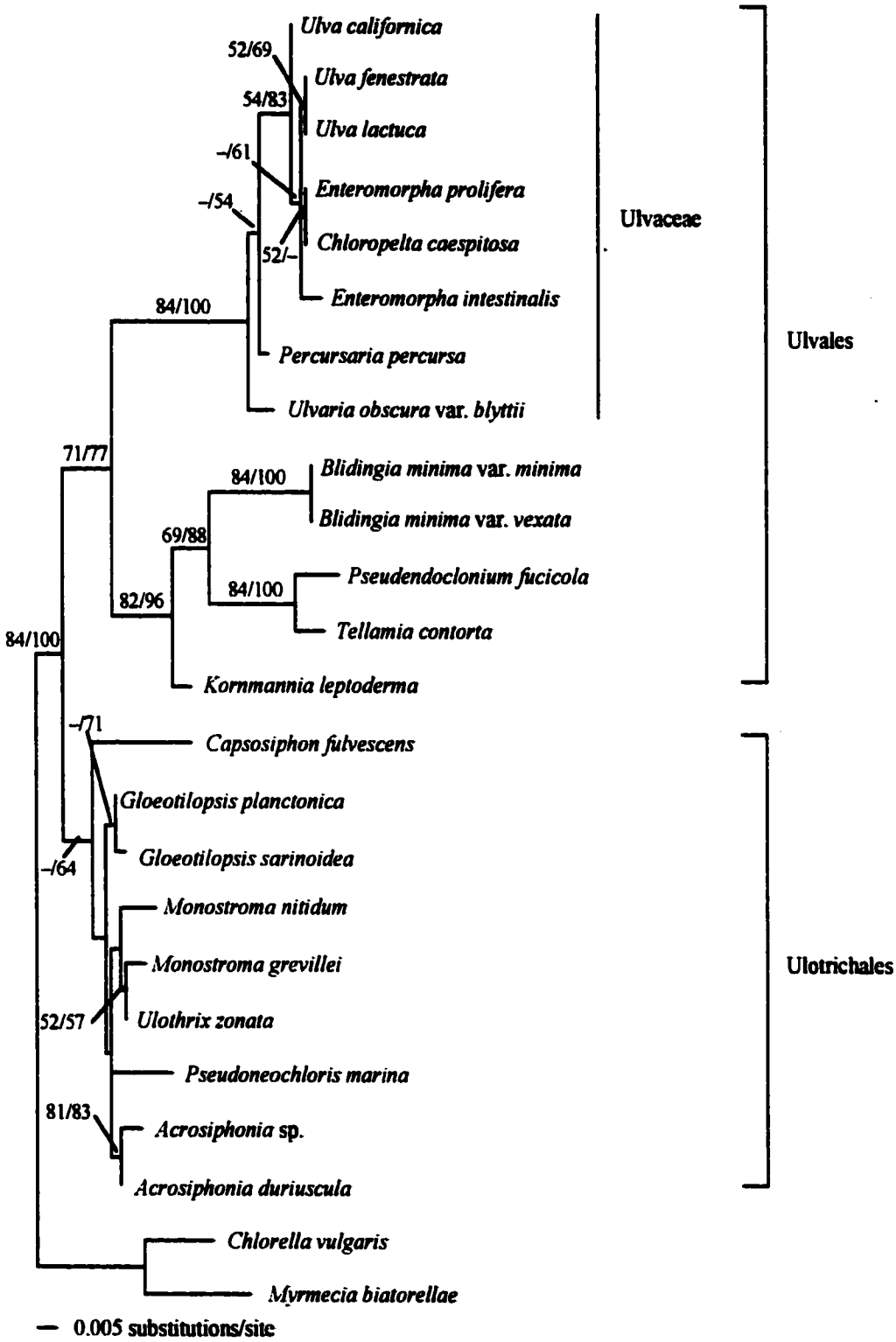

Ulva californica
52/69
Ulva fenestrata
54/83
Ulva lactuca
-/61
Enteromorpha prolifera
-/54
Chloropelta caespitosa
52/-
Enteromorpha intestinalis
84/100
Percursaria percursa
Ulvaria obscura var. blyttii
Ulvaceae
Ulvales
71/77
84/100
Blidingia minima var. minima
Blidingia minima var. vexata
69/88
84/100
Pseudendoclonium fucicola
82/96
Tellamia contorta
84/100
Kornmannia leptoderma
-/71
Capsosiphon fulvescens
Gloeotilopsis planctonica
Gloeotilopsis sarinoidea
-/64
Monostroma nitidum
Monostroma grevillei
52/57
Ulothrix zonata
Pseudoneochloris marina
81/83
Acrosiphonia sp.
Acrosiphonia duriuscula
Ulotrichales
Chlorella vulgaris
Myrmecia biatorellae
0.005 substitutions/site

Figure 1.2. Phylogram based on maximum parsimony analysis of *rbc*L sequences. Tree shown is one of two equally parsimonious trees recovered in a heuristic search. Nodes are labeled with bootstrap values for maximum likelihood (100 replicate samples) and maximum parsimony (500 replicate samples), respectively; – indicates a bootstrap value less than 50% for an analysis. Nodes with bootstrap values of less than 50% in both analyses are not labeled. An asterisk (*) notes nodes which collapse in the strict consensus tree. Tree length = 1106 steps; CI excluding uninformative characters = 0.492, RI = 0.575. Scale bar for 50 nucleotide changes shown at bottom.

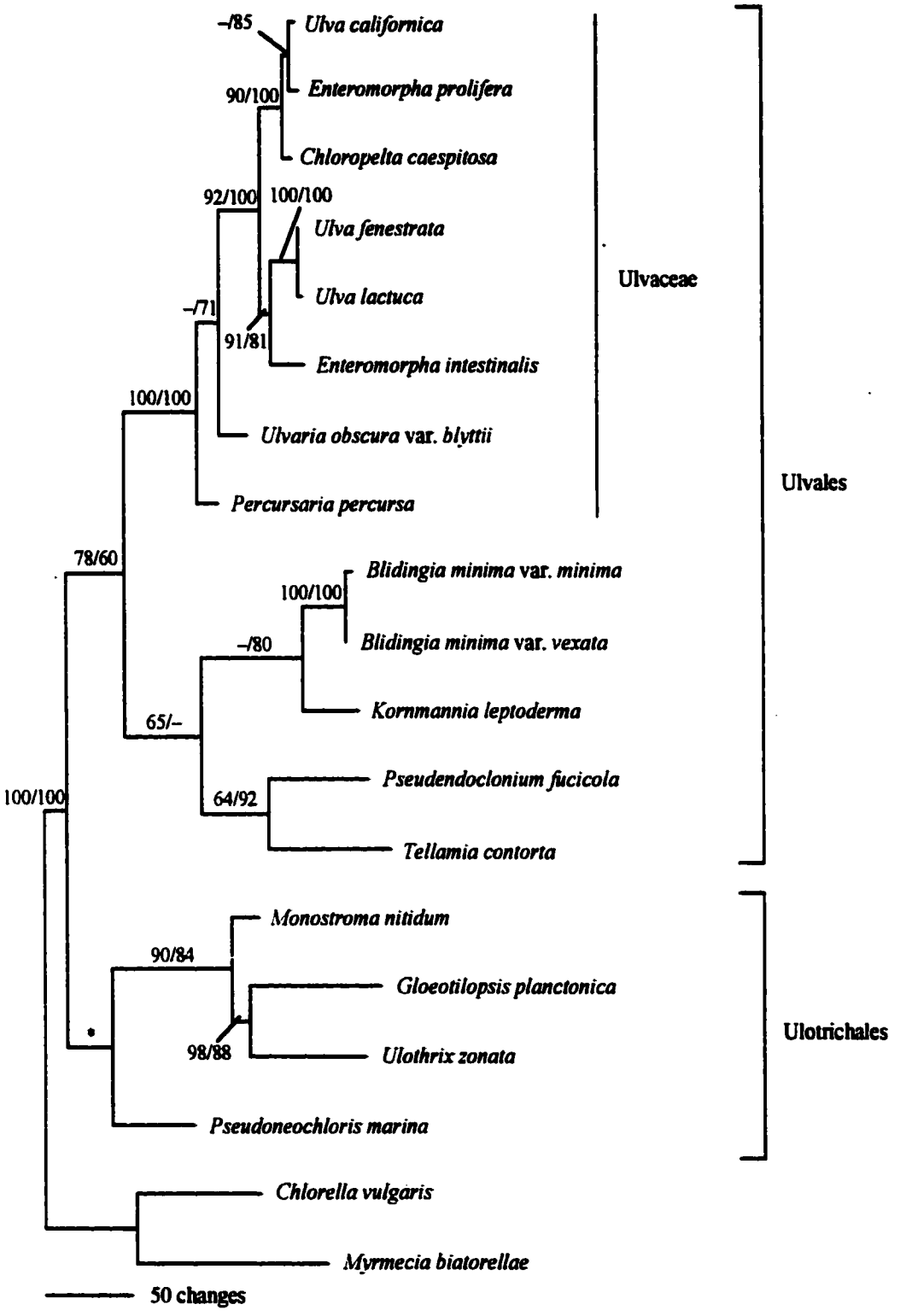
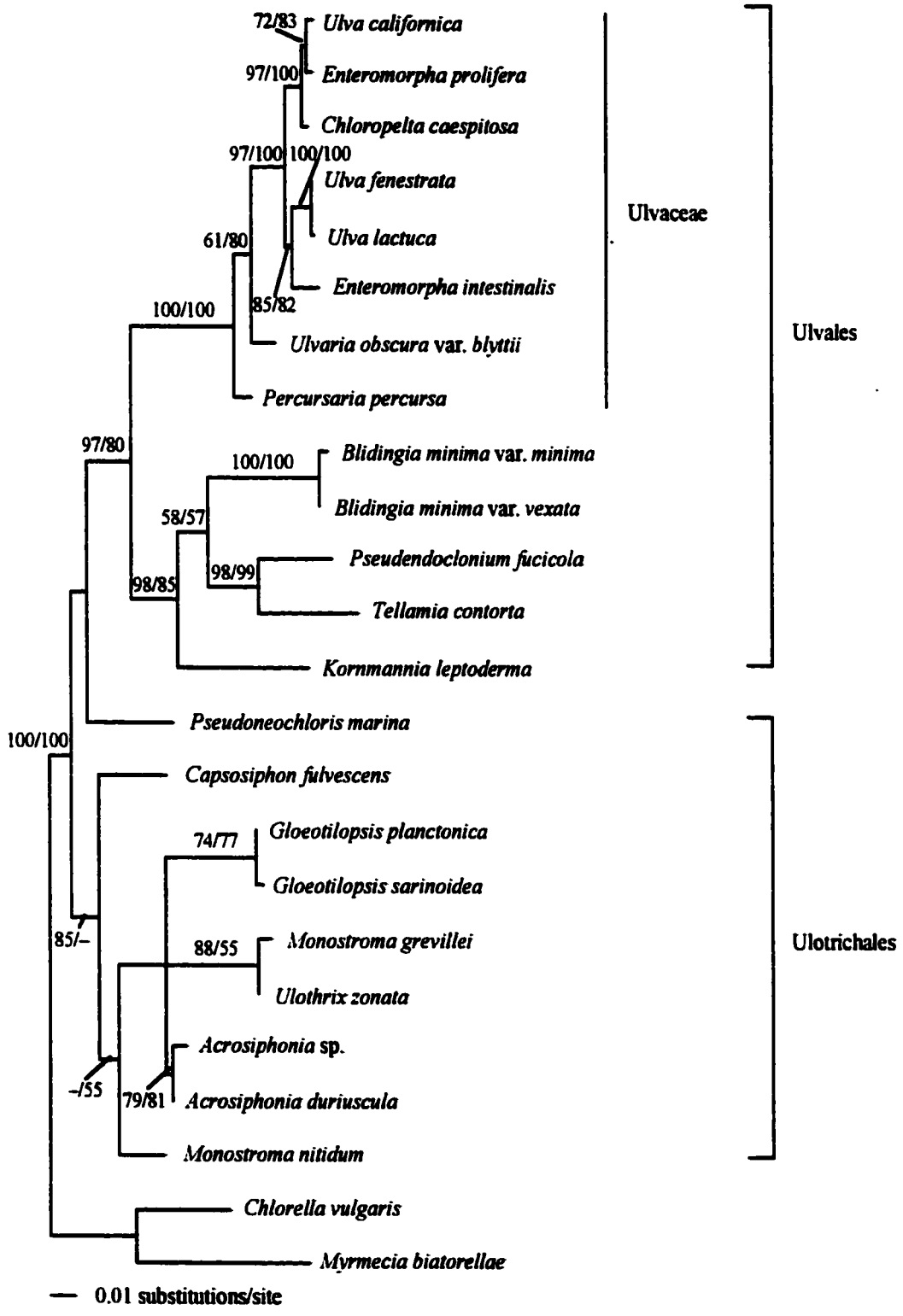

–/85
Ulva californica
Enteromorpha prolifera
90/100
Chloropelta caespitosa
92/100
100/100
Ulva fenestrata
Ulva lactuca
–/71
91/81
Enteromorpha intestinalis
Ulvaceae
100/100
Ulvaria obscura var. blyttii
Percursaria percursa
Ulvales
78/60
Blidingia minima var. minima
100/100
Blidingia minima var. vexata
–/80
Kornmannia leptoderma
65/–
Pseudendoclonium fucicola
100/100
64/92
Tellamia contorta
Monostroma nitidum
90/84
Gloeotilopsis planctonica
98/88
Ulothrix zonata
Ulotrichales
Pseudoneochloris marina
Chlorella vulgaris
Myrmecia biatorellae
50 changes

Figure 1.3. Phylogenetic tree inferred from a heuristic search using maximum likelihood of combined 18S rDNA and *rbc*L sequence data (-lnL = 9431.828). Horizontal branch lengths are proportional to the mean number of nucleotide substitutions per site. Nodes are labeled with bootstrap values for maximum likelihood (100 replicate samples) followed by values for maximum parsimony (500 replicate samples), respectively; – indicates a bootstrap value less than 50% for an analysis. Nodes with bootstrap values of less than 50% in both analyses are not labeled.


72/83
Ulva californica
97/100
Enteromorpha prolifera
Chloropelta caespitosa
97/100
100/100
Ulva fenestrata
Ulvaceae
61/80
Ulva lactuca
Enteromorpha intestinalis
85/82
100/100
Ulvaria obscura var. blyttii
Ulvales
Percursaria percursa
97/80
100/100
Blidingia minima var. minima
Blidingia minima var. vexata
58/57
Pseudendoclonium fucicola
98/99
98/85
Tellamia contorta
Kornmannia leptoderma
Pseudoneochloris marina
100/100
Capsosiphon fulvescens
74/77
Gloeotilopsis planctonica
Gloeotilopsis sarinoidea
85/–
88/55
Monostroma grevillei
Ulotrichales
Ulothrix zonata
Acrosiphonia sp.
–/55
79/81
Acrosiphonia duriuscula
Monostroma nitidum
Chlorella vulgaris
Myrmecia biatorellae
0.01 substitutions/site

Chapter II:

Evidence for polyphyly of *Ulva* and *Enteromorpha* (Ulvaceae, Ulvales) from nuclear and chloroplast sequences

Introduction

"*Ulva* is distinguished from *Enteromorpha* on the basis of its distromatic blade, which in certain species (e.g., *Ulva linza*) may become tubular at the margins and thus approach the situation in *Enteromorpha* wherein at least the adult thalli are markedly tubular and hence monostromatic. This criterion is sometimes difficult to apply, and opinion is divided as to whether such species as *U. linza* should be referred to *Ulva* or *Enteromorpha*. There is perhaps something to be said in favor of those early workers who treated *Enteromorpha* as a section of *Ulva*." Silva (1952)

"A given swarmer population [of *U. lactuca*] may produce all *Enteromorpha*-like plants, all distromatic *Ulva* plants, a mixture of both types, or plants displaying both morphologies on the same plant." Bonneau (1977)

"The similarity of the abnormal filamentous uniseriate growth of *Ulva* and *Enteromorpha* and the fact that even with bacterial reinfection the *Ulva*-58 [isolate] produces at best thalli similar to *Enteromorpha* support the conclusion of Bonneau (1977) that there are at present no valid criteria for the maintenance of *Ulva* and *Enteromorpha* as separate genera." Provasoli and Pintner (1980)

Despite such comments, the cosmopolitan algal genera *Ulva* and *Enteromorpha* have been maintained to the present day (e.g., Gabrielson et al. 2000, Graham and Wilcox 2000). The separation is convenient, because the majority of currently recognized species can be readily assigned to one genus or the other based on morphology. The genus *Ulva* was one of the first named by Linnaeus (1753) and

initially included a variety of unrelated algae. In the 1800s its members were split into several genera. *Ulva* was maintained for green seaweeds with distromatic blades, and *Enteromorpha* was established for tubular green seaweeds (Link 1820). Since then, more than 140 *Ulva* and 135 *Enteromorpha* species, with additional subspecific taxa, have been described worldwide (Guiry 2001, Silva 2001); however, approximately 50 *Ulva* and 35 *Enteromorpha* species are currently recognized (Guiry 2001).

Several lines of evidence suggest that these generic constructs are artificial. Species with intermediate forms, such as *E. linza* with an *Enteromorpha*-like tubular base and *Ulva*-like distromatic blade distally, exist in nature, and several culture studies have revealed flexibility between tubular and blade morphologies. Gayral (1959, 1967) reported the development of tubular, or partially tubular, thalli in cultures of some *Ulva* species. Bonneau (1977) observed clonal progeny of *U. lactuca* with distromatic, partially distromatic or completely tubular blades, as well as individuals that were completely distromatic in one area of the blade and tubular in another. Føyn (1960, 1961) produced stable phenotypic mutants of *U. mutabilis* with tubular fronds that were capable of successful mating with wild-type individuals. Additionally, axenic culture experiments have revealed similarities that span generic boundaries. Absent of native bacteria, *Ulva* and *Enteromorpha* cultures resulted in similar abnormal morphologies (Provasoli 1965, Berglund 1969, Kapraun 1970, Fries 1975, Provasoli and Pintner 1980).

Molecular phylogenies corroborate results from culture experiments. Three molecular studies which include more than one or two representatives of each genus

have been published (Blomster et al. 1999, Tan et al. 1999, Woolcott and King 1999). In these studies, clades comprised of both *Ulva* and *Enteromorpha* taxa were resolved in phylogenetic trees based on the internal transcribed spacer regions and 5.8S gene of nuclear ribosomal DNA (ITS nrDNA). However, despite the morphological flexibility among conspecifics and clones observed in culture studies, phylogenetic studies show that thallus form has been fixed in naturally occurring lineages. For example, in Tan et al. (1999) some clades included geographically distinct isolates that are clearly recognizable as species of *Ulva* or *Enteromorpha*. One strongly supported clade included collections of *E. intestinalis* from Scotland and British Columbia, Canada, and another included representatives of several species of *Ulva* from England, Scotland, France, and North America. Similar results are revealed in studies of ITS nrDNA in *Ulva* and *Enteromorpha* from eastern Australia (Woolcott and King 1999), Ireland (Blomster et al. 1999) and the northeast Pacific (Hayden, this dissertation, Chap. 3).

Tan et al. (1999) is the most extensive of the molecular papers to date with 21 *Ulva* and *Enteromorpha* species sampled. Based on their ITS nrDNA trees, the authors proposed that *Enteromorpha* be collapsed into *Ulva*. However, Woolcott and King (1999) studying taxa from eastern Australia noted that preliminary results based on the more conserved RUBISCO large subunit gene (*rbc*L) supported separation of the two genera. Compared to these studies, the present study includes an increased number of taxa with broader geographical distribution, and phylogenetic analysis of both ITS nrDNA and the chloroplast-encoded *rbc*L gene. Empirical and theoretical studies show the need to obtain sequence data from several independent loci, because

individual gene trees may not represent the evolutionary history of the taxa being studied due to natural phenomena such as introgression and lineage sorting (Wendel and Doyle 1998). Although phylogenetic studies of seed plants often include sequences from two or more genes (Soltis and Soltis 1998), the use of multiple genes is still relatively rare in the phycological literature (e.g., only two of 37 systematic papers using sequence data published in the *Journal of Phycology* in 1999 and 2000 included analysis of more than one gene sequence).

Additionally, this study includes a sample of *Chloropelta*, a monotypic genus described by Tanner (1980), which has been considered a close relative of *Ulva*. *Chloropelta caespitosa*, a diminutive, distromatic alga, was separated from *Ulva* based on developmental features. Initial phylogenetic analyses using small subunit rDNA and *rbc*L sequences and a small number of *Ulva* and *Enteromorpha* taxa suggested that this genus is not distinct from *Ulva* (Hayden Chap. 1). An accession is included here to further investigate its relationship to *Ulva* and *Enteromorpha*.

In this study, trees are constructed from 1) ITS nrDNA sequences for currently available species of *Ulva* and *Enteromorpha*; 2) *rbc*L sequences for a subset of taxa; and 3) a combined analysis. The phylogeny of these genera is discussed based on the comparison of these independent data sets.

Materials and Methods

One *Chloropelta*, eighteen *Ulva* and ten *Enteromorpha* accessions were included in the ITS nrDNA analyses, while a subset of one *Chloropelta*, thirteen *Ulva* and seven *Enteromorpha* were included in the *rbc*L analyses (Table 2.1). Several taxa were chosen for outgroup comparison based on prior molecular analyses of the relationships of Ulvales genera (Hayden Chap. 1) (approximate number of species in each genus is noted in parentheses): *Blidingia minima* var. *minima* (5), *Kornmannia leptoderma* (1), *Percursaria percursa* (2) and *Ulvaria obscura* var. *blyttii* (2). All outgroups were used in the *rbc*L analysis; however, *B. minima* var. *minima* and *K. leptoderma* were excluded from ITS nrDNA analyses, since large sections of the spacers in these taxa were unalignable with ingroup taxa. Fifteen of the thirty ingroup ITS nrDNA sequences and all ingroup sequences in the *rbc*L data set are new.

Northeast Pacific collections (Table 2.1) were placed in culture, when possible. Unialgal cultures were grown in Guillard's f/2 enriched seawater at 15°C in glass culture vessels under 30 – 50 $\mu mol \cdot m^{-2} \cdot s^{-1}$ on a 16 light:8 dark photoperiod cycle. *Ulva* collections from Australia, Chile, Hawaii, Spain and Japan were received as silica gel preserved specimens. Vouchers for all collections were deposited in the University of Washington Herbarium (WTU) (Appendix G). DNA extraction from dried specimens was preceded by a rehydration step in which 14 – 18 mg of material were rehydrated in 200 ml of ddH2O at 4°C for ten minutes. Total DNA was extracted from fresh culture or rehydrated material using a modified CTAB method (Doyle and Doyle 1990,

Hughey and Hommersand 1999). Genomic DNA for eight European taxa was supplied by Dr. Christine Maggs at The Queen's University of Belfast, Ireland, in order to sequence the *rbc*L gene. ITS nrDNA sequences for these taxa were published elsewhere (Table 2.1).

Total genomic DNA (10 – 20 ng) was added to six 25 µl PCR reactions each containing 2.5 µl 10X PCR Buffer II (PE Applied Biosystems), 1.5 mM $MgCl_2$, 0.8 mM dNTPs (GibcoBRL), 0.3 Units AmpliTaq DNA Polymerase (PE Applied Biosystems) and 0.8 mM of each primer. ITS nrDNA reactions also contained 5% DMSO (Sigma Corp.). PCR amplification was carried out in a PTC-100 Programmable Thermal Controller (MJ Research, Inc.). Primers used to amplify and sequence ITS nrDNA and the *rbc*L gene are listed in Table 2.1. PCR primers for the ITS regions were modified from Blomster et al. (1998). A fragment containing ITS 1, ITS 2 and the 5.8S ribosomal subunit was amplified using primers 18S1505 and ENT26S, which bind to the 18S and 26S ribosomal subunits, respectively. The reaction profile included an initial denaturation at 94°C for 5 min, followed by 1 min at 94°C and 3 min at 60°C for 30 cycles, and a final 10 min extension at 60°C (Blomster et al. 1998). The *rbc*L gene was amplified using primers from Manhart (1994). These primers amplified the first 1358 bp of the *rbc*L gene excluding primers. This fragment excludes the variable 3' terminus and represents 98% of the gene. The reaction profile included an initial denaturation at 94°C for 3 minutes, followed by 35 cycles of 1 min at 94°C, 2 min at 45°C and 3 min at 65°C. PCR products were run on 1.5% agarose gels (SeaKem® LE, FMC Bioproducts), stained in a solution of 0.5 mg/ml ethidium

bromide (Gibco BRL) and visualized under UV light. Products were pooled then purified using a PEG-8000 precipitation (Sigma Corp.). Purified PCR products were sequenced using a dideoxy chain termination protocol with the ABI Prism BigDye Terminator Cycle Sequencing Ready Reaction Kit (PE Applied Biosystems). Both strands of PCR products were sequenced on an automated DNA sequencer (ABI 377).

RUBISCO sequences were aligned using Clustal X (Thompson et al. 1997) and edited by eye. ITS nrDNA regions were aligned manually using Se-Al version 1.0a1. All positions of ITS 1 and ITS 2 that could not be aligned with confidence were removed prior to analyses. Maximum parsimony (MP) and maximum likelihood (ML) analyses were performed for each data set using PAUP* version 4.0b8 (Swofford 1999). A MP analysis was also conducted for a combined data set. In MP analyses, all characters and character state changes were weighted equally. Gaps were coded as missing data. Heuristic searches were performed with tree bisection-reconnection (TBR), MulTrees and steepest descent options in effect. Ten replicate searches with randomized taxon input were conducted to avoid local optima of most parsimonious trees. To compare relative support for branches, 1000 bootstrap replications (Felsenstein 1985) were performed using heuristic searches with simple taxon addition, TBR and MulTrees options in effect.

Prior to likelihood searches, several parameters were estimated using PAUP*. Base frequencies, transition to transversion ratio (Hasegawa et al. 1995), proportion of invariable sites and site-to-site rate heterogeneity were estimated under maximum likelihood criterion from an optimal parsimony topology (Swofford et al. 1996) and

then fixed to those values in ML searches. Rate heterogeneity was modeled using the gamma distribution method (Yang 1994) with four discrete rate categories and a single shape parameter (alpha). A heuristic search was conducted using an optimal starting tree from MP analyses with TBR, MulTrees and steepest descent options in effect.

Results

Manual alignment of ITS 1, ITS 2 and 5.8S nrDNA resulted in 612 nucleotide positions. Boundaries for the 5.8S gene were defined according to Thompson and Herrin (1994). The 5' end of ITS 1 and the 3' end of ITS 2 were determined according to van de Peer et al. (2000) and Wuyts et al. (2001), respectively. The lengths of the spacers ranged from 154 – 218 bp in ITS 1 and 162 – 184 bp in ITS 2 among the surveyed taxa. A total of 141 characters were excluded from the spacers prior to analyses because positional homology could not be determined in five areas of the alignment (Appendix C). In contrast, the 5.8S nrDNA gene was 158 bp in all surveyed taxa and had only fourteen variable characters. The lengths of the spacers and the 5.8S gene are comparable to other taxa in the Ulvophyceae (Bakker et al. 1995a, Bakker et al. 1995b, van Oppen 1995, Friedl 1996). MP and ML analyses were conducted using 471 aligned characters from the spacers and the 5.8S gene.

Alignment of *rbc*L sequences required the addition of a single gap of three nucleotides in all sequences except the outgroup *Kornmannia leptoderma* (Appendix D). The additional amino acid in *K. leptoderma* is present in other green algae

sequenced to date (e.g., Yang et al. 1986, Kono et al. 1991, Manhart 1994, Sherwood et al. 2000), with the exception of other Ulvales (Sherwood et al. 2000, Hayden Chap. 1). The final *rbc*L alignment included 1357 characters.

The alignment of combined data included all accessions with *rbc*L positions coded as missing data for the taxa in which this gene was not sequenced (Table 2.1).

MP analysis of ITS nrDNA data resulted in 90 optimal trees of 347 steps. Of the 471 characters analyzed, 324 were constant and 108 were parsimony informative. The strict consensus of most parsimonious trees is shown in Figure 2.1a. The ML analysis resulted in a single tree (Fig 2.2) which is generally similar to the strict consensus tree based on ITS nrDNA sequences (Fig. 2.1a). Differences between trees can be seen in the clades comprised of *U. lactuca*, *U. australis*, etc., and *U. stenophylla*, *E. prolifera*, etc. and the positions of *E. flexuosa* and *Enteromorpha* sp. II; however, these differences are not significant for the purposes of the present investigation.

MP analysis of the *rbc*L data set resulted in six optimal trees of 473 steps. The strict consensus tree is shown in Figure 2.1b. Of the 1357 characters analyzed, 1066 characters were constant and 138 were parsimony informative. Clades with bootstrap values of 50% or greater in the consensus tree (Fig. 2.1b) were also resolved in the ML tree (Fig. 2.3) with one exception. In the ML tree *U. olivascens* rather than *Ulvaria obscura* var. *blyttii* is basal in the clade that is sister to the remaining *Ulva* and *Enteromorpha* species.

Prior to the MP analysis of combined data, the incongruence length difference test (ILD) of Farris et al. (1994), implemented in PAUP* as the partition homogeneity

test, was performed using a partition for ITS nrDNA versus *rbc*L data (p = 0.99). A heuristic search resulted in 117 trees of 824 steps (Fig. 2.4). A total of 1828 characters were included in the analysis, 246 were parsimony informative. Clades resolved in the combined data consensus tree (Fig. 2.4) are similar to those in the ITS nrDNA and *rbc*L consensus trees (Fig. 2.1), but they have higher bootstrap values. In all trees a clade comprised of all *Ulva* and *Enteromorpha* species except *U. olivascens* is strongly supported. The topology of the deepest branches within this clade varies between trees; however, in all analyses there are well supported clades which contain both *Ulva* and *Enteromorpha* species. Examples of such clades include: 1) *E. compressa* and *U. pseudocurvata*; 2) these taxa plus *E. intestinalis* and *E. intestinaloides*; *U. californica* and *Enteromorpha* sp. I; 3) these taxa plus *C. caespitosa*; and 4) *E. muscoides* plus several species of *Ulva*. Several additional clades have moderate to strong bootstrap values in all consensus trees. These are comprised of either *Ulva* or *Enteromorpha* species.

Estimated sequence divergence in the ITS nrDNA data set ranged from 0% between *U. fasciata* and *U.* sp. II to nearly 18% between *Percursaria percursa* and some species of *Ulva* and *Enteromorpha*. The *U. olivascens* sequence was ~7% divergent from *Ulvaria obscura* var. *blyttii* and *P. percursa* and was more than 13% divergent from other *Ulva* and *Enteromorpha* sequences. The greatest divergence among ingroup taxa (minus *U. olivascens*) was 13.3% between *U. taeniata* and *E. compressa*. Divergence among species found in mixed *Ulva* and *Enteromorpha* clades varied. There was 0.2% divergence between *E. compressa* and *U. pseudocurvata* and ~6%

between these taxa and *E. intestinalis*. Sequence divergence was 1.3% between *U. californica* and *Enteromorpha* sp. I, ~3% between these taxa and *C. caespitosa*, and 5.0% — 6.5% between *E. muscoides* and closely related *Ulva* taxa.

Sequence divergence values in the *rbc*L data set were generally lower than those observed in the ITS nrDNA data set. They ranged from 0.1% between two pairs of taxa, *U. lactuca* L./*U. fenestrata* and *E. compressa*/*U. pseudocurvata*, to nearly 14% between ingroup taxa and the two outgroups, *K. leptoderma* and *B. minima* var. *minima*. *Ulva olivascens* was less than 3% divergent from *Ulvaria obscura* var. *blyttii* and *P. percursa* and 3.7% — 4.4% divergent from other *Ulva* and *Enteromorpha* taxa. In mixed clades, there was 1.9% sequence divergence between *E. intestinalis* and either *E. compressa* or *U. pseudocurvata*. Divergence was 0.5% between *U. californica* and *Enteromorpha* sp. I, 0.7% — 0.8% between *C. caespitosa* and these taxa, and 0.9% — 1.6% between *E. muscoides* and related *Ulva* species. The greatest sequence divergence among ingroup taxa (minus *U. olivascens*) was 3.6%.

Discussion

With the exception of *U. olivascens*, *Ulva* and *Enteromorpha* together form a strongly supported clade in all analyses. These results combined with earlier findings from molecular (Blomster et al. 1999, Tan et al. 1999, Woolcott and King 1999) and culture studies (Gayral 1959, 1967, Føyn 1960, 1961, Løvlie 1964, Provasoli 1965, Berglund 1969, Kapraun 1970, Fries 1975, Bonneau 1977, Provasoli and Pintner 1980)

provide strong evidence that neither *Ulva* nor *Enteromorpha* is monophyletic. Using monophyly as a basis for taxonomy, *Ulva* and *Enteromorpha* should not be recognized as separate genera. Since *Ulva* is the older name, *Enteromorpha* should be reduced to a synonym.

Additionally, *Chloropelta caespitosa* is nested among *Ulva* taxa. Tanner (1979, 1980) described *C. caespitosa* on the basis of its unique developmental pattern which is very distinctive in culture (pers. obs.). Early in development cells in the tubular germling undergo one division producing a distromatic tubular germling not seen in other Ulvaceae. Rupture of the tube produces a distromatic, peltate blade. Despite its unique development, *C. caespitosa* groups with *U. californica* and *Enteromorpha* sp. I in all trees, and bootstrap support for this grouping is strong in strict consensus trees. Thus, *Chloropelta* should also be reduced to a synonym of *Ulva*.

In the ensuing discussion, the clade comprised of *Ulva* (minus *U. olivascens*), *Enteromorpha* and *Chloropelta* taxa will be referred to as the *Ulva* clade. *Ulva olivascens* should be moved from *Ulva* to a new genus. Evidence for this revision is discussed further below.

Cryptic clades among Ulva *and* Enteromorpha. Within the *Ulva* clade several clades with distromatic and tubular species received strong support. *E. compressa* and *U. pseudocurvata* are allied with 100% bootstrap support in trees from all analyses. *E. compressa* is common in the British Isles and is morphologically similar to the type species of *Enteromorpha*, *E. intestinalis*. These two species have been shown to be distinct evolutionary entities using crossing experiments (Larsen 1981) and

phylogenetic analysis of ITS nrDNA sequences (Blomster et al. 1998). *Ulva pseudocurvata* is a typical *Ulva* species with a distromatic, medium to light green membranaceous blade (Koeman and van den Hoek 1981). ITS nrDNA sequence divergence among isolates of these two species was similar to levels of divergence within clearly monospecific groupings, such as geographically distinct collections of *E. intestinalis* and *E. compressa* (up to 2.3%) (Blomster et al. 1998). Distances between *rbc*L sequences among conspecifics range from 0.0% to 0.4% (Hayden, this dissertation, Chap. 3). Thus, divergence between *E. compressa* and *U. pseudocurvata* in the *rbc*L gene (< 0.1%) is also within the range of conspecifics.

Another mixed pair that is well supported in both trees is *U. californica* and *Enteromorpha* sp. I. *U. californica* is a distromatic species found along the Pacific coast of North America from the Alaska Peninsula to Baja California. Morphology and culture studies have revealed that while this species has a wide range of environmentally-influenced blade forms, it shows a distinctive developmental pattern which clearly separates it from other species of *Ulva* (Tanner 1979, 1986). These developmental characteristics are the presence of a germination tube and the early development of an extensive basal system of rhizoids (Tanner 1986). *Enteromorpha* sp. I, a tubular alga with a branched morphology similar to *E. prolifera*, has a similar distribution to that of *U. californica* (Hayden, this dissertation, Chap. 3). Divergence between these taxa is 1.3% and 0.5% for ITS nrDNA and *rbc*L sequences, respectively. These values are not much greater than those for *E. compressa* and *U. pseudocurvata*.

One explanation for these observations is that these paired taxa represent two phases in the life history of a single species. However, an isomorphic life history has been observed in *E. compressa* (Bliding 1968), *U. pseudocurvata* (Koeman and van den Hoek 1981) and *U. californica* (Tanner 1979, 1986). Further, sexual life history (isomorphic vs. heteromorphic) is used to delimit the Ulvales and Ulotrichales (Kornmann 1965), and its use at this taxonomic level is supported by molecular and ultrastructural data (Floyd and O'Kelly 1984, Hayden Chap. 1). Thus, an alternation of heteromorphic generations in this clade is unlikely. An alternative explanation is that these paired taxa may be in the early stages of diverging from one another and changes have occurred in the genome in area(s) that control blade versus tubular morphology before many changes have occurred in other regions. Some sequence divergence between these taxa is already apparent. In Tan et al. (1999) the monophyly of *E. compressa* based on ITS nrDNA is strongly supported. Similarly, geographically distinct isolates of *U. californica* form a clade, as do isolates of *Enteromorpha* sp. I in ITS nrDNA and *rbc*L trees (Hayden, this dissertation, Chap. 3).

Tan et al. (1999) hypothesized that a reversible morphogenetic switch (or switches) controls gross morphology in these algae: the switch from a blade to a tube morphology (or vice versa) is activated infrequently in nature perhaps by various environmental cues, and it is more frequent in culture due to stresses unique to artificial systems. It is clear from the position of *Ulva* and *Enteromorpha* taxa in the present trees and those of Tan et al. (1999) that gross morphology has been fixed in certain naturally occurring lineages for relatively long periods of time. It is unclear whether

the same mechanism(s) is involved in culture experiments. Culture studies citing flexibility of form show *Ulva* taxa with tubular or globular morphologies (Løvlie 1964, Gayral 1959, 1967, Bonneau 1977, Føyn 1960, 1961), but there are no culture studies which show *Enteromorpha* with distromatic morphologies. Further, observations of cultures made by the present author suggest that altered morphologies in cultures of *Ulva* are not uncommon (Hayden, this dissertation, Chap. 3). With the exception of *Percursaria*, all ulvacean taxa pass through a tubular stage in development (Hayden Chap. 1). Distromatic species growing without exposure to wave action, desiccation or other environmental factors may not develop normally beyond the tubular stage. Species of *Ulva* have been observed in culture without mention of altered morphology (e.g., Bliding 1963, 1968, Kapruan 1970, Tanner 1979). It is possible that certain culture conditions foster normal development, or that some species are capable of normal development in culture while others are not. Further research, including field outplanting of culture material, may help to resolve these issues and lead to a better understanding of the mechanism(s) underlying morphology in these algae.

Morphological synapomorphies. Notwithstanding questions concerning generic status, *Ulva* and *Enteromorpha* are known to be taxonomically difficult due to a lack of distinguishing morphological characters and high degree of phenotypic plasticity (van den Hoek et al. 1995). Characters commonly used to distinguish species are listed in Table 2.3. Few of these traits are qualitative (i.e., present versus absent), rather most are descriptive or quantitative and have considerable overlap. Studies focused on the variability of vegetative characters have demonstrated that some of these characters

are too variable for taxonomic use (Vinogradova 1974, Titlyanov et al. 1975, Steffensen 1976, Tanner 1979, Phillips 1988). Generally speaking, identification of a particular taxon requires a combination of traits. Phenotypic plasticity, coupled with the fact that a change in form from blade to tube or vice versa may have allometric consequences in quantitative traits (Tan et al. 1999), presents considerable challenge for identifying morphological synapomorphies defining clades in molecular trees. The difficulty in identifying morphological synapomorphies for clades in molecular-based trees is not unique to this group of algae (e.g., Stiller and Waaland 1993).

A comparison of traits for surveyed species revealed few synapomorphies. Given that clades are not defined on the basis of distromatic versus tubular morphology, it is not surprising that they are also not defined by the type of blade (e.g., expanded versus linear) or tube (e.g., branched versus unbranched). Other characters are too conserved, e.g., mode of reproduction (Floyd and O'Kelly 1984, Hayden Chap. 1) or too variable, e.g., cell size, number of pyrenoids (Tanner 1979, Phillips 1988). These results reinforce the need for great caution when using morphological characters in comparative, taxonomic or systematic studies in this and other groups of morphologically simple algae. Of the characters listed in Table 2.3, only two potential synapomorphies were identified. *E. compressa*, *U. pseudocurvata*, *E. intestinalis* and *E. intestinaloides* are all described as having "hood" or "cup"-shaped chloroplasts which are predominantly oriented apically in cells of the middle and apical regions (Blomster et al. 1998, Koeman and van den Hoek 1981, Koeman and van den Hoek 1982). Some taxa, such as *U. lactuca* and *U. rigida*, have been observed to have

similarly shaped chloroplasts in these thallus regions, but their chloroplasts are variously oriented rather than apically oriented (Koeman and van den Hoek 1981). Other taxa have chloroplasts which completely fill cells in surface view. Neither of the latter chloroplast conditions appears to delimit clades. Studies by Britz and Briggs (1976, 1983) and Mishkind et al. (1979) showed that chloroplasts in some *Ulva* species migrate to different positions in cells according to a circadian rhythm. Such movement was not detected in certain Ulvales, including an alga identified as *E. intestinalis* (Britz and Briggs 1976). These studies may suggest that chloroplast position is too variable for use in systematic studies. Conversely, the presence of diurnal variation in chloroplast position may prove to be a synapomorphy; however, at present this phenomena has been studied in only a limted number of taxa.

Ulva species in the clade with *E. muscoides* (Fig. 1) share the presence of microscopic teeth along the blade margin. *E. muscoides* has a tubular morphology and therefore lacks a blade margin; however, one of the diagnostic characters for this species is the presence of "spine-like" short branchlets throughout the thallus (Bliding 1963, Blomster et al. 1999). These branchlets have a broad base composed of several cells and a narrow tip which typically ends in a single cell. Their appearance is reminiscent of marginal teeth observed in *Ulva* species, though the suggestion that these structures are homologous is highly speculative. Marginal dentition has been described in two other surveyed taxa, *U. rotundata* (Bliding 1968) and *U. australis* (Phillips 1988, Woolcott and King 1999), a finding which suggests that this trait has evolved more than once in these algae.

Comparison with other molecular studies. Relationships of taxa in the present trees are generally congruent with those in Tan et al. (1999) and Blomster et al. (1999), though the latter study included only nine *Ulva* and *Enteromorpha* species. Differences in the positions of three taxa between the present study and that of Tan et al. (1999) are noteworthy. In the present study, *U. olivascens* is allied with the designated outgroups, *Ulvaria* and *Percursaria*, and these three taxa comprise the sister group to the *Ulva* clade in the *rbc*L trees. In Tan et al. (1999) *U. olivascens* occupied a basal position among the sampled *Ulva* and *Enteromorpha* leading to the conclusion that all *Ulva* and *Enteromorpha* species form a clade. However, *Ulvaria* and *Percursaria* were not included in their study, rather *Blidingia* (Ulvales) and *Gloeotilopsis* (Ulotrichales) served as the sole outgroups and introduced a relatively long branch into the ITS nrDNA-based trees.

Ulva olivascens, found in the northeast Atlantic and Mediterranean, was named for its characteristic olive green thallus (Dangeard 1951). Other traits which distinguish this taxon include the presence of 1) relatively large cells in the mature plant, 2) characteristically rounded cells in apical regions, and 3) a marginal region of sterile cells distal to zoosporangia that detaches in "threadlike masses" following reproductive cell release (Bliding 1968, Burrows 1991). Given its distromatic blade, the inclusion of this taxon in *Ulva* has not been questioned. Nonetheless, *U. olivascens* can be clearly separated from other *Ulva* taxa based on the above morphological traits. Identification based on morphology is not as straightforward with many *Ulva* species (e.g., Tanner 1986, van den Hoek 1995). At present, there are no clear morphological traits that

would suggest affinities of *U. olivascens* to *Ulvaria* or *Percursaria* other than its early development which is typically ulvacean (Bliding 1968). Based on molecular and morphological evidence, *U. olivascens* should be moved from *Ulva* to a new monotypic genus.

The positions of two additional *Ulva* species, *U. fenestrata* and *U. californica*, differ in the present trees compared to those in Tan et al. (1999). Their collection of *U. fenestrata* was allied with *U. armoricana*, and their collection of *U. californica* appeared in a clade of multiple geographically distinct collections of *U. lactuca*, the type species of *Ulva*. In the present trees the close relationship of *U. fenestrata* and *U. lactuca* is strongly supported. Sequence divergence values between these taxa are within the range of conspecifics, 0.5% and 0.1% for ITS nrDNA and *rbc*L, respectively (Blomster 1998, 1999, Hayden Chap. 3). A study of *Ulva* and *Enteromorpha* from the northeast Pacific includes collections of *U. californica* and *U. fenestrata* from throughout their distribution ranges (Hayden, this dissertation, Chap. 3). In that study the relationships of these species to others are similar to those in the present trees. This suggests that the *U. californica* and *U. fenestrata* collections in Tan et al. (1999) were misidentified. Given the morphological plasticity exhibited by these taxa, overlapping distribution ranges and ecology (Tanner 1979, 1986, Gabrielson 2000), it is not unreasonable that an individual of *U. californica* would be misidentified as *U. fenestrata*. Further, the definitive characters which separate these species are developmental, yet there is no indication that these species were placed in culture prior to identification for the Tan et al. paper. The true identity of the *U. fenestrata*

collection in Tan et al. (1999) is less certain, but it appears in a strongly supported clade with *U. armoricana* and *U. scandinavica*. In the present ITS nrDNA trees relationships among these taxa are not well resolved and sequence divergence values are low (<0.4%). Relationships among these taxa warrant further investigation.

Conclusions

In addressing the question of monophyly of *Ulva* and *Enteromorpha*, results from phylogenetic analyses of the *rbc*L gene are similar to those from ITS nrDNA in this and previous studies. Neither *Ulva* nor *Enteromorpha* is monophyletic; however, with the exception of *U. olivascens*, taxa from these genera together form a strongly supported clade. Since *Ulva* is the older genus, *Enteromorpha* should be reduced to a synonym. Despite its unique development, *Chloropelta caespitosa* is nested within this clade; thus, it should also be reduced to a synonym of *Ulva*. Conversely, *Ulva olivascens* does not group with other *Ulva* species in phylogenetic trees and can be clearly separated from other *Ulva* taxa on the basis of morphological traits. This taxon should be moved from *Ulva* to a new genus.

Within the *Ulva* clade, there are smaller clades comprised of all distromatic, all tubular, and both distromatic and tubular species; however, few morphological synapomorphies defining these clades can be identified, given the simple morphology and high degree of phenotypic plasticity in these algae. Certain clades contain distromatic and tubular species that exhibit sequence divergence values within the range

of conspecifics. A plausible explanation is that these taxa are in the early stages of diverging from one another and changes have occurred in areas of the genome that control gross morphology before many changes have occurred in other regions. Although the controls for gross morphology (tubular versus distromatic blade) in these algae remain unclear, it is likely that the mechanism underlying relatively rare changes in nature is different from that for more frequent changes in culture. Given that all Ulvaceae, except *Percursaria*, pass through a tubular stage in development, it is reasonable to postulate that changes from blade to tube morphology observed in *Ulva* cultures are artifactual.

Table 2.1. Details for sampled taxa. GenBank accession numbers for previously published ITS nrDNA sequences are listed.

Taxon	Collection information or ITS rDNA sequence origin	ITS rDNA
Chloropelta caespitosa Tanner	Kobe, Hyogo Pref., Japan. 22 Mar 2000. Coll. H. Kawai	
Enteromorpha compressa (L.) Nees	Blomster et al. 1998	AF035350
E. flexuosa (Wulfen) J. Agardh	Leskinen & Pamilo 1997	AJ234306
E. intestinalis (L.) Nees	Blomster et al. 1998	AF035342
E. intestinaloides Koeman *et* van den Hoek	Tan et al. 1999	AJ234303
E. linza (L.) J. Agardh	Humboldt Bay, CA USA. 19 Jun 2000. Coll. H.S. Hayden & F. Shaunessey	
E. muscoides (Clemente y Rubio) Cremades	Blomster et al. 1999	AF127170
E. procera Ahlner	Coll. J. Blomster	
E. prolifera (O.F. Müller,) J. Agardh	Tan et al. 1999	AJ234304
E. sp. I	Bodega Bay, CA, USA. 17 Jun 2000. Coll. H.S. Hayden	
E. sp. II	Tan et al. 1999	AJ234308
Ulva armoricana Dion, de Reviers *et* Coat	Coat et al. 1998	
U. australis Areschoug	Woolcott & King 1999	AF099726
U. californica Wille *in* Collins, Holden *et* Setchell	La Jolla, CA, USA. 14 Jun 1999. Coll. H.S. Hayden	
U. fasciata Delile	Kihei, Maui, USA. 6 Feb 2000. Coll. L. Hodgson	
U. fenestrata Postels *et* Ruprecht	San Juan Is., WA, USA. 15 Jun 1998. Coll. H.S. Hayden & D.J. Garbary	
U. lactuca L.	Tan et al. 1999	AJ234310
U. lobata (Kützing) Setchell *et* Gardner	Newport, OR, USA. 16 May 1999. Coll. H.S. Hayden & A. Whitmer	
U. olivascens P.A. Dangeard	Portaferry, Strangford Lough, N. Ireland. 5 May 2000. Coll. C.A. Maggs	
U. pertusa Kjellman	Tan et al. 1999	AJ234321
U. pseudocurvata Koeman *et* van den Hoek	Tan et al. 1999	AJ234312
U. rigida C. Agardh	Càdiz, Spain. Coll. C.A. Maggs	

Table 2.1. Continued.

Taxon	Collection information or ITS rDNA sequence origin	ITS rDNA
U. rotundata Bliding	Coat et al. 1998	
U. scandinavica Bliding	Tan et al. 1999	AJ234317
U. sp. I	Coihuin, Puerto Montt, Chile. 17 Oct 2000. Coll. J.R. Waaland	
U. sp. II	Tamarama, Syndey, NSW. 9 Aug 1999. Coll. G. Zuccarello	
U. sp. III	Newport Beach, CA, USA. 15 Jun 1999. Coll. H.S. Hayden & S. Murray	
U. stenophylla Setchell *et* Gardner	Seattle, WA, USA. 2 Jun 2000. Coll. H.S. Hayden	
U. taeniata (Setchell *in* Collins, Holden *et* Setchell) Setchell *et* Gardner	Monterey, CA, USA. 17 Jun 1999. Coll. H.S. Hayden	
Outgroups		
Blidingia minima (Nägeli *ex* Kützing) Kylin var. *minima*	Bolinas, CA, USA. 16 Jun 2000. Coll. H.S. Hayden	
Kornmannia leptoderma (Kjellman) Bliding	Vancouver Is., B.C., Canada. 29 Jun 1999. Coll. H.S. Hayden	
Percursaria percursa (C. Agardh) Rosenvinge	UWCC MA230	
Ulvaria obscura var. *blyttii* (Areschoug) Bliding	Padilla Bay, WA, USA. 25 Apr 1997. Coll. H.S. Hayden	

Table 2.2. Primers used in this study for PCR amplification and sequencing.

Primer	Sequence	Target	Direction
18S1505	5' TCTTTGAAACCGTATCGTGA 3'	ITS 1	Forward
18S1763[a]	5' GGTGAACCTGCGGAGGGATCATT 3'	ITS 1	Forward
5.8S30	5' GCAACGATGAAGAACGCAGC 3'	ITS 2	Forward
5.8S142	5' TATTCCGACGCTGAGGCAG 3'	ITS 1	Reverse
ENT26S[b]	5' GCTTATTGATATGCTTAAGTTCAGCGGGT 3'	ITS 2	Reverse
RH1[c]	5' ATGTCACCACAAACAGAAACTAAAGC 3'	rbcL	Forward
rbc571	5' TGTTTACGAGGTGGTCTTGA 3'	rbcL	Forward
rbc590	5' TCAAGACCACCTCGTAAACA 3'	rbcL	Reverse
1385r[c]	5' AATTCAAATTTAATTTCTTTCC 3'	rbcL	Reverse

[a] Modified from Blomster et al. 1998
[b] Blomster et al. 1998
[c] Manhart 1994

Table 2.3. Characters used to delimit species of *Ulva* and *Enteromorpha* based on Koeman and van den Hoek (1981) and Bliding (1963, 1968). Characters noted with (E) and (U) are used only in *Enteromorpha* and *Ulva*, respectively.

Character
Gross morphology, including color and texture of mature plant
Structure of plant base
Arrangement and shape of cells in surface view
Structure of branch tips (E)
Number of pyrenoids per cell
Shape of chloroplast in surface view
Cell size at base, middle and apex of thallus
Height-to-width ratio of cells in cross section (U)
Thallus thickness (U)
Morphology of young germling
Mode of reproduction
Ecology

Figure 2.1. Comparison of strict consensus trees derived from (A) nuclear ribosomal ITS sequence data and (B) the chloroplast-encoded *rbc*L gene. Bootstrap percentages (1000 replicate samples) are shown above branches.

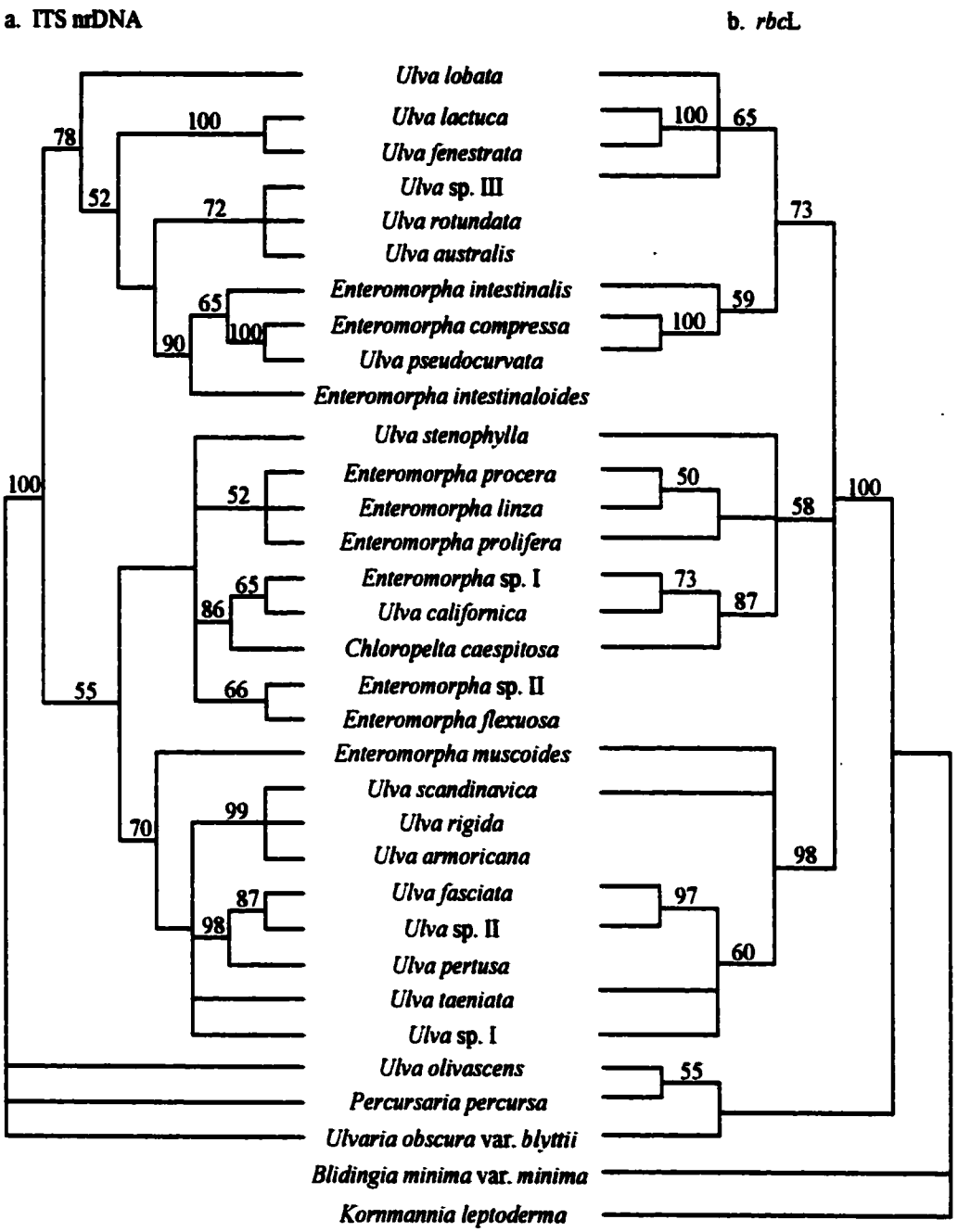

a. ITS nrDNA
b. rbcL
Ulva lobata
Ulva lactuca
Ulva fenestrata
Ulva sp. III
Ulva rotundata
Ulva australis
Enteromorpha intestinalis
Enteromorpha compressa
Ulva pseudocurvata
Enteromorpha intestinaloides
Ulva stenophylla
Enteromorpha procera
Enteromorpha linza
Enteromorpha prolifera
Enteromorpha sp. I
Ulva californica
Chloropelta caespitosa
Enteromorpha sp. II
Enteromorpha flexuosa
Enteromorpha muscoides
Ulva scandinavica
Ulva rigida
Ulva armoricana
Ulva fasciata
Ulva sp. II
Ulva pertusa
Ulva taeniata
Ulva sp. I
Ulva olivascens
Percursaria percursa
Ulvaria obscura var. blyttii
Blidingia minima var. minima
Kornmannia leptoderma

Figure 2.2. Phylogram of sampled taxa based on ML analysis of ITS nrDNA sequences (-lnL = 2424.316).

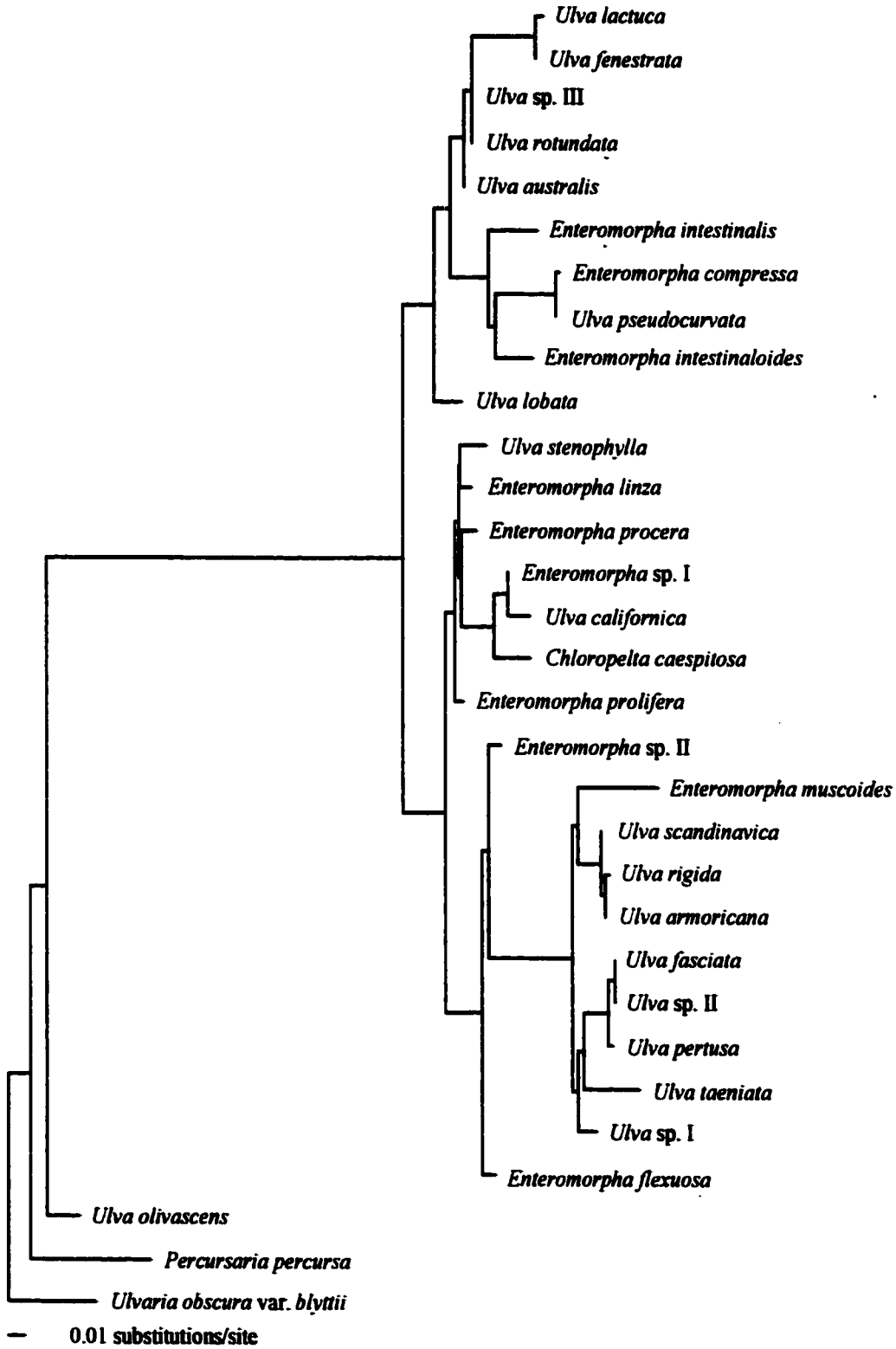

Ulva lactuca
Ulva fenestrata
Ulva sp. III
Ulva rotundata
Ulva australis
Enteromorpha intestinalis
Enteromorpha compressa
Ulva pseudocurvata
Enteromorpha intestinaloides
Ulva lobata
Ulva stenophylla
Enteromorpha linza
Enteromorpha procera
Enteromorpha sp. I
Ulva californica
Chloropelta caespitosa
Enteromorpha prolifera
Enteromorpha sp. II
Enteromorpha muscoides
Ulva scandinavica
Ulva rigida
Ulva armoricana
Ulva fasciata
Ulva sp. II
Ulva pertusa
Ulva taeniata
Ulva sp. I
Enteromorpha flexuosa
Ulva olivascens
Percursaria percursa
Ulvaria obscura var. blyttii
0.01 substitutions/site

Figure 2.3. Phylogram of a subset of sampled taxa based on ML analysis of *rbc*L sequences (-lnL = 4435.492).

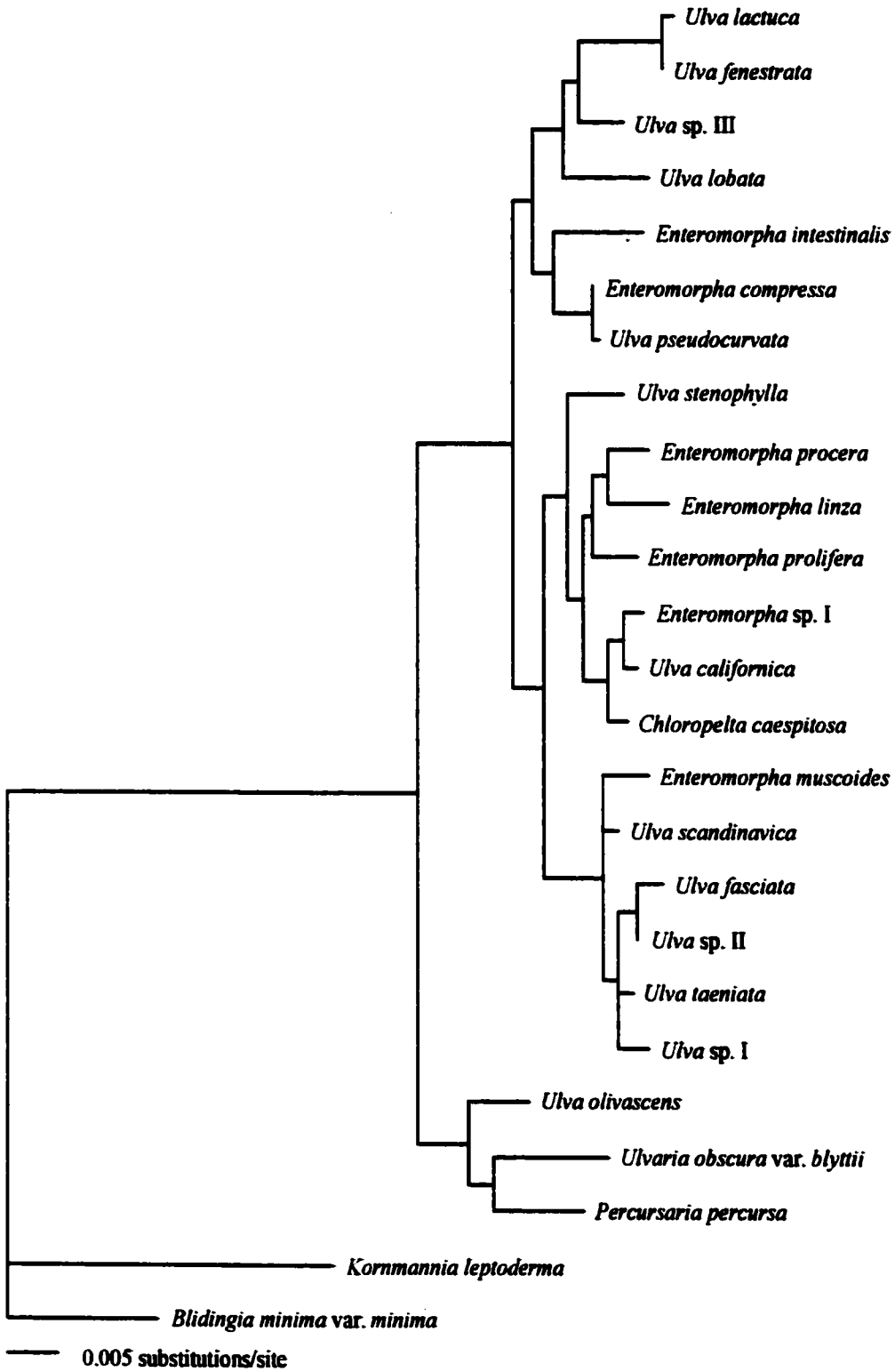
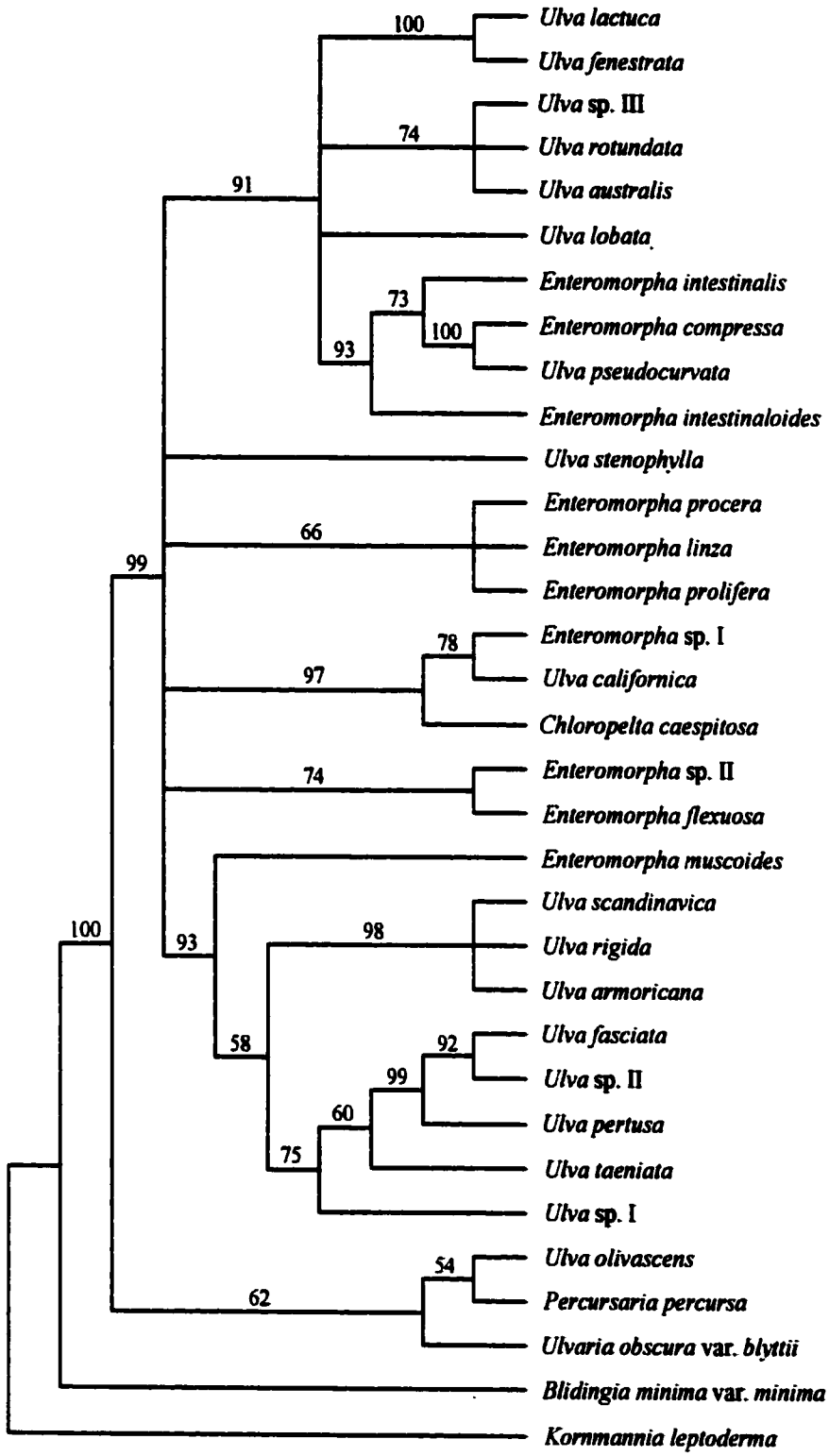

Ulva lactuca
Ulva fenestrata
Ulva sp. III
Ulva lobata
Enteromorpha intestinalis
Enteromorpha compressa
Ulva pseudocurvata
Ulva stenophylla
Enteromorpha procera
Enteromorpha linza
Enteromorpha prolifera
Enteromorpha sp. I
Ulva californica
Chloropelta caespitosa
Enteromorpha muscoides
Ulva scandinavica
Ulva fasciata
Ulva sp. II
Ulva taeniata
Ulva sp. I
Ulva olivascens
Ulvaria obscura var. blyttii
Percursaria percursa
Kornmannia leptoderma
Blidingia minima var. minima
0.005 substitutions/site

Figure 2.4. Strict consensus of 117 most parsimonious trees of 824 steps from the analysis of combined ITS nrDNA and *rbc*L sequences. Bootstrap percentages (1000 replicate samples) are shown above branches.


100
Ulva lactuca
Ulva fenestrata
Ulva sp. III
74
Ulva rotundata
91
Ulva australis
Ulva lobata
Enteromorpha intestinalis
73
Enteromorpha compressa
100
93
Ulva pseudocurvata
Enteromorpha intestinaloides
Ulva stenophylla
Enteromorpha procera
66
Enteromorpha linza
99
Enteromorpha prolifera
78
Enteromorpha sp. I
97
Ulva californica
Chloropelta caespitosa
74
Enteromorpha sp. II
Enteromorpha flexuosa
Enteromorpha muscoides
Ulva scandinavica
100
98
93
Ulva rigida
Ulva armoricana
58
92
Ulva fasciata
99
Ulva sp. II
60
Ulva pertusa
75
Ulva taeniata
Ulva sp. I
54
Ulva olivascens
62
Percursaria percursa
Ulvaria obscura var. blyttii
Blidingia minima var. minima
Kornmannia leptoderma

Chapter III:

A molecular systematic study of *Ulva*, *Enteromorpha* and *Chloropelta* (Ulvaceae, Ulvales) from the northeast Pacific

Introduction

Species of the morphologically simple green algal genera *Ulva* L. and *Enteromorpha* Link are ubiquitous members of marine intertidal floras worldwide. They are found in a diversity of habitats from exposed rocky shores to protected bays and estuaries where they can thrive attached to solid substrata or while floating freely. Many species tolerate wide ranges of salinity, temperature and water quality and grow rapidly in nutrient-rich habitats causing "green tides" and marine fouling (Fletcher 1996). *Ulva* and *Enteromorpha* species are also common in experimental systems where they have been used as model organisms for studies of algal physiology (e.g., Johnston 1991, Vershinin and Kamnez 1996, Larsson and Axelsson 1999), spore adhesion (e.g, Dillon et al. 1989, Fletcher and Callow 1992), and as bioindicators of marine pollution (e.g., Ho 1990, Favero et al. 1996).

The genus *Ulva* was one of the first named by Linnaeus (1753) and initially included many unrelated algae. In the 1800s its members were split into several genera. *Ulva* was maintained for green seaweeds with distromatic blades, and *Enteromorpha* was established for tubular green seaweeds (Link 1820). Since then, more than 140 *Ulva* and 135 *Enteromorpha* species, with additional subspecific taxa, have been described worldwide (Guiry 2001, Silva 2001). The actual number of species is uncertain; however, approximately 50 *Ulva* and 35 *Enteromorpha* species are currently recognized (Guiry 2001).

Initially, *Ulva* and *Enteromorpha* species were described entirely on morphological and anatomical characters. Although these seaweeds are morphologically simple, they exhibit considerable plasticity in response to environmental factors (Vinogradova 1974, Titlyanov et al. 1975, Steffensen 1976, Tanner 1979) which likely has contributed to the large number of described specific and subspecific taxa. Later, researchers incorporated characters considered to be more stable, including details of reproduction, development and hybridization potential, in combination with morphological and anatomical features to delimit species (Føyn 1955, Cauro 1958, Dangeard 1958, 1959, Chihara 1968, 1969, Bliding 1963, 1968, Kapraun 1970, Vinogradova 1974, Tanner 1979, Koeman and van den Hoek 1981, Hoeksema and van den Hoek 1983, Womersley 1984, Phillips 1988). These studies resulted in extensive revisions, yet this group of algae continues to be systematically and taxonomically difficult (van den Hoek et al. 1995, Gabrielson et al. 2000).

Molecular data are increasingly being used to test systematic hypotheses for difficult groups, such as *Enteromorpha* and *Ulva*. While these data provide insight into genetic variation, delineating species boundaries remains difficult and arbitrary. Many competing species concepts have been proposed (e.g, Mayr 1969, Van Valen 1976, Cracraft 1989). While a discussion regarding the relative merits of these is beyond the scope of the present paper, it is important to recognize the concept and criteria employed to delimit species (Luckow 1995). The present analysis follows the phylogenetic species concept described by Donoghue (1985) in which species, like other taxonomic units, are recognized as monophyletic groups based on shared derived

characters. Sequence divergence between taxa in monophyletic groups is used as a secondary criterion for determining boundaries for species rank. Such an approach has been taken in the green algae (though perhaps not explicitly stated) using sequences of the fast-evolving internal transcribed spacers of nuclear rDNA (ITS nrDNA) in cases where morphological traits are highly variable. For example, Marks and Cummings (1996) delimited freshwater species of *Cladophora* Kützing (Ulvophyceae) in which they found no correlation between ITS genotypes and morphology, habitat and geographical distribution. Blomster et al. (1998) delimited two morphologically similar species of *Enteromorpha*, *E. intestinalis* and *E. compressa* (see Table 3.2 for authorities), though they were unable to correlate ITS nrDNA data with either sample morphology or geographical distribution.

The first major treatments of *Ulva* and *Enteromorpha* in the northeast Pacific (Setchell and Gardner 1920a, 1920b) recognized thirteen species of *Ulva* and sixteen species of *Enteromorpha* from Alaska to southern California. Subsequent studies in this region recognized some additional taxa while reducing others to synonyms (Doty 1947, Scagel 1966, Chihara 1968, Hollenberg 1971, Norris 1971, Tanner 1979). Tanner (1979) conducted a comprehensive study of *Ulva* from northern British Columbia to southern California. He recognized six species of *Ulva* and reduced six others to synonyms. He also described a monotypic genus, *Chloropelta*, based on developmental features (Tanner 1980). His species concepts are followed today (e.g., Gabrielson et al. 2000). Assignment of local *Enteromorpha* to species (Scagel 1966, Abbott and Hollenberg 1976, Gabrielson et al. 2000) is based primarily on studies of

European taxa (Bliding 1963, 1968, Kornmann and Sahling 1977, Blomster et al. 1998, 1999). Currently, six species of *Ulva* and seven species of *Enteromorpha* are recognized from southeast Alaska to southern California (Table 3.1) (Abbott and Hollenberg 1976, Gabrielson et al. 2000).

The present study uses molecular data to test species hypotheses for northeast Pacific *Ulva*, *Enteromorpha* and *Chloropelta*. Though previous molecular studies indicate that *Ulva* and *Enteromorpha* are polyphyletic (Tan et al. 1999, Hayden, this dissertation, Chap. 2), generic names are maintained here pending completion of a taxonomic revision (Silva et al. in prep). Taxa were sampled from Valdez, AK to San Diego, CA, additional Pacific locales outside this region and Europe. Sequences from two genomic regions were sampled based on their utility in previous studies, ITS nrDNA (e.g., Blomster et al. 1998, 1999) and the large subunit of the chloroplast-encoded RUBISCO gene (*rbc*L) (e.g., Nozaki 1999, Hayden, this dissertation, Chap. 2). ITS nrDNA and *rbc*L sequences were analyzed separately and simultaneously. Combining data sets increases the number of characters available for analysis. A larger number of characters can increase phylogenetic signal over noise caused by homoplasy in independent data sets, and thus, results in a more accurate estimate of the true phylogeny (e.g., Olmstead and Sweere 1994, Steane et al. 1999).

The results of the present study provide a clearer understanding of the species diversity and distribution of *Ulva*, *Enteromorpha* and *Chloropelta* in the northeast Pacific and indicate areas for further systematic study of these ubiquitous green seaweeds.

Materials and Methods

Collection and identification of samples. Northeast Pacific *Ulva*, *Enteromorpha* and *Chloropelta* were sampled at sites in Alaska, British Columbia, Washington, Oregon and California from 1997 to 2000 (Table 3.2). Effort was made to collect samples from type localities, or locations near them. Geographical coordinates were recorded using a hand-held GPS unit (Garmin 45). Habitat information was also recorded, including a description of available substrata, wave exposure and dominant algae (Dethier 1990).

Each sample consisted of several morphologically similar thalli collected from an area of less than 25 cm^2. Samples were wrapped in damp paper towels and stored in plastic bags in the dark at 4 to 15° C until detailed laboratory observations could be made. Algae were identified to species using the following references: *Chloropelta* (Tanner 1980), *Ulva* (Tanner 1979, 1986), and *Enteromorpha* (Bliding 1963, Scagel 1966, Abbot and Hollenberg 1976 and Blomster et al. 1998, 1999). Morphological characters used for identification were: 1) thallus habit (color, shape, length, width, branching pattern, form of attachment); 2) features of cells in surface and transectional views (shape, height, width, arrangement); 3) thallus thickness; 4) number of pyrenoids per cell; 5) chloroplast position in cells; 6) ecology (habitat type, location of sample in intertidal); and 7) miscellaneous features (e.g., presence of microscopic teeth along blade margin in certain *Ulva* species). Cell dimensions and thallus thickness were measured with an ocular micrometer at 400 – 1000x magnification. Several pieces of thalli from identified samples were either dried in silica gel for molecular research or placed in culture as described below. The remaining material was pressed for herbarium specimens.

When possible, collections were placed in culture to observe reproductive and developmental characters, including spore and gamete dimensions, presence of a germination tube, number of cells in germling at first longitudinal division and basal development. Fertile material was field collected, or reproduction was induced in pieces of vegetative thalli using a modified protocol from Tanner (1979). Unialgal cultures were grown in Guillard's f/2 enriched seawater at 15°C in 500 ml glass culture vessels under 30 – 50 $\mu mol \cdot m^{-2} \cdot s^{-1}$ cool white fluorescents on a 16 light:8 dark photoperiod cycle.

Additional collections from Australia, Chile, Hawaii, Spain and Japan were received as silica gel preserved specimens. Vouchers for these and field collections were deposited in the University of Washington Herbarium (WTU) (Appendix G). These collections were compared to herbarium specimens, including many of the type specimens, from the northeast Pacific and other areas. These herbarium specimens, particularly those from Tanner (1979), were valuble for interpreting species descriptions, published distributions, and geographical and seasonal variation.

Outgroup taxa were chosen based on results from previous studies of the Ulvaceae (Hayden, this dissertation, Chap. 1, Chap. 2). These studies indicate that *Ulva olivascens* should be moved from *Ulva* to a new monotypic genus. It is included here to serve as an additional outgroup and will not be discussed further.

DNA extraction, PCR amplification and sequencing. DNA extraction from dried specimens was preceded by a rehydration step in which 14 – 18 mg of material were rehydrated in 200 ml of ddH2O at 4°C for ten minutes. Total DNA was extracted from fresh culture or rehydrated material using a modified CTAB method (Doyle and Doyle 1990, Hughey and Hommersand 1999). Genomic DNA for eight European taxa was supplied by Dr. Christine Maggs at The Queen's University of Belfast, Ireland in

order to sequence the *rbc*L gene. ITS nrDNA sequences for these taxa were published elsewhere (Table 3.2).

Total genomic DNA (10 – 20 ng) was added to six 25 µl PCR reactions each containing 2.5 µl 10X PCR Buffer II (PE Applied Biosystems), 1.5 mM $MgCl_2$, 0.8 mM dNTPs (GibcoBRL), 0.3 Units AmpliTaq DNA Polymerase (PE Applied Biosystems) and 0.8 mM of each primer. ITS nrDNA reactions also contained 5% DMSO (Sigma Corp.). PCR amplification was carried out in a PTC-100 Programmable Thermal Controller (MJ Research, Inc.). Primers used to amplify and sequence ITS nrDNA and the *rbc*L gene follow Hayden (Chap. 2). The reaction profile for ITS nrDNA included an initial denaturation at 94°C for 5 min, followed by 1 min at 94°C and 3 min at 60°C for 30 cycles, and a final 10 min extension at 60°C (Blomster et al. 1998). The reaction profile for *rbc*L included an initial denaturation at 94°C for 3 minutes, followed by 35 cycles of 1 min at 94°C, 2 min at 45°C and 3 min at 65°C. PCR products were run on 1.5% agarose gels (SeaKem® LE, FMC Bioproducts), stained in a solution of 0.5 mg/ml ethidium bromide (Gibco BRL) and visualized under UV light. Products were pooled then purified using a PEG-8000 precipitation (Sigma Corp.). Purified PCR products were sequenced using a dideoxy chain termination protocol with the ABI Prism BigDye Terminator Cycle Sequencing Ready Reaction Kit (PE Applied Biosystems). Both strands of PCR products were sequenced on an automated DNA sequencer (ABI 377).

Phylogenetic analysis. Sequences for *rbc*L were aligned using Clustal X (Thompson et al. 1997) and edited by eye. ITS nrDNA sequences were aligned manually using Se-Al version 1.0a1Fat because they contained numerous substitutions and indels. Three regions of ITS 1 and two of ITS 2 were unalignable across all taxa; however, sequences within four of these regions were alignable within subsets of taxa.

In the final alignment these subsets were offset with corresponding gaps in unaligned sequences following the method of Steane et al. (1999). Using this method, all reliable data can be used to resolve relationships within subgroups as well as between these groups for higher level resolution. One region in ITS 1 that could not be aligned with confidence (positions 539-546) was removed prior to all analyses (Appendix E). Pairwise percentage sequence divergence values were calculated separately for ITS nrDNA and *rbc*L sequences. For the ITS nrDNA data set, only those regions alignable across all taxa were included in calculations; thus, divergence values are approximate.

Maximum parsimony (MP) analyses were performed for the ITS nrDNA, *rbc*L and combined data sets using PAUP* version 4.0b8 (Swofford 1999). Prior to analyses of combined data, the incongruence length difference test (ILD) of Farris et al. (1994), implemented in PAUP* as the partitions homogeneity test, was performed using a partition for ITS nrDNA versus *rbc*L data ($p = 0.44$). Nucleotide positions and character state changes were weighted equally and gaps were coded as missing data in all analyses. In analyses of the independent data sets, heuristic searches were performed with tree bisection-reconnection (TBR), MulTrees and steepest descent options in effect. Ten replicate searches with randomized taxon input were conducted using the random stepwise-addition option to avoid local optima of most parsimonious trees. In analyses of combined data, heuristic searches were performed with TBR and steepest descent (MulTrees off) with 100 replicate searches of randomized taxon input. The ITS nrDNA, *rbc*L and combined data sets were bootstrapped 1000 times (Felsenstein 1985), using closest addition sequence, TBR and steepest descent (MulTrees off), to assess relative support for branches.

The MulTress option was turned off in parsimony analysis of the combined data and in bootstrap analyses because saving multiple minimal trees for branch swapping

proved to be computationally prohibitive. DeBry and Olmstead (2000) and Mort et al. (2000) showed that bootstrap analysis with reduced search effort did not inflate bootstrap values. Rather, it resulted in generally lower bootstrap values for nodes with less than 90% bootstrap support (DeBry and Olmstead 2000) or similar bootstrap values (Mort et al. 2000) as more rigorous searches.

Results

Boundaries of ITS 1, ITS 2 and 5.8S nrDNA follow Hayden (Chap. 2). The length of these combined regions ranged from 492 – 540 nucleotides for surveyed taxa. The aligned sequence length without offsetting the highly variable regions in ITS 1 and ITS 2 (see Material and Methods) was 478 nucleotide positions. The alignment including offset regions was 1055 positions (Appendix E). Size ranges of ITS 1, ITS 2 and the 5.8S gene are comparable with other taxa in the Ulvophyceae (Bakker et al. 1995a, 1995b, van Oppen 1995, Friedl 1996). Alignment of *rbc*L sequences resulted in 1354 nucleotides, which includes 98% of the gene, and required no gaps (Appendix F). This length is similar to most *Ulvales* sequenced to date and differs from other Ulvophyceae by one amino acid (see Hayden, this dissertation, Chap. 1).

Estimated sequence divergence of ITS nrDNA ranged from 0% among conspecifics to 11.9 – 16.8% between ingroup and outgroup taxa. The G + C content of sequences ranged from 59.9 – 66.4%. Nucleotide bias in ribosomal DNA has been shown to confound phylogenetic analysis based on those sequences by grouping taxa with similarly-biased compositions when they do not share a recent common ancestor (Hasegawa and Hashimoto 1993); however, a chi-squared test of homogeneity of base frequencies across surveyed taxa was not significant ($p = 1.0$). Divergence values in

the *rbc*L data set ranged from 0% among conspecifics to 3.7 – 4.9% between ingroup taxa and designated outgroups.

Parsimony analysis of 478 nucleotide positions of ITS nrDNA, which excluded the highly variable regions, yielded 30 equally most parsimonious trees (MPT) of 367 steps (Fig 3.1a, CI excluding uninformative sites = 0.578, RI = 0.886). Parsimony analysis of *rbc*L sequences resulted in 16 MPT of 320 steps (Fig. 3.1b, CI excluding uninformative sites = 0.565, RI = 0.889). The ITS nrDNA and *rbc*L trees are similar though not identical. Strict consensus trees show that many similar well supported nodes (> 80% bootstrap values) are resolved in both analyses (Fig. 3.2); however, some nodes are strongly supported in one tree and are weakly supported or unresolved in the other. These "soft incongruencies" (Seelanan et al. 1997) explain much of the topological differences between trees. For example, the clade comprised of *U. fenestrata*I OR and *U. fenestrata* CCA appears in two different locations in the strict consensus trees, but its position in the *rbc*L based tree is not well supported. The remaining topological differences can be explained by differences in surveyed taxa.

The results of the ILD test indicated that the length of the original partition (ITS nrDNA versus *rbc*L) was not significantly different from random partitions of characters from the combined data set. Given this result, the two data sets were combined for further phylogenetic analysis. Parsimony analysis of combined data, including 478 nucleotide positions of ITS nrDNA plus 1354 *rbc*L positions, resulted in 95 trees of 695 steps (Fig. 3, CI = 0.540, RI = 0.884). Of the 1832 positions, 235 were parsimony informative. The tree based on combined data is more resolved than the ITS nrDNA or *rbc*L based trees, and bootstrap values in the combined data tree are generally higher.

Sequences in the highly variable regions of ITS 1 and ITS 2 were alignable within five clades in the combined data tree (Fig. 3.3, I – V). Clade I was subdivided into smaller groups of taxa (Ia – If) for alignment in one region of ITS 1 in which sequences were not clearly alignable across all Clade I taxa. Outgroups were aligned together as a separate group (VI). This method of aligning variable sequence regions within subgroups incorporates assumptions about relationships among taxa. Thus, primarily moderate and well supported nodes were used to delimit alignment groupings. Clades I – V and Clade I subgroups received >50% bootstrap support in the separate and combined data trees with the exception of Clade I which received <50% bootstrap support in the *rbc*L tree, and Clade II which does not exist in the *rbc*L tree because the gene was not sequenced in these taxa. The combined data set was reanalyzed including these aligned regions. Of the 2401 positions included, 299 were parsimony informative. MP analysis resulted in 98 trees of 860 steps (not shown, CI excluding uniformative sites = 0.570, RI = 0.885). The topology of the tree based on the re-analyzed data set was similar to that resulting from analysis of the smaller combined data set (Fig. 3.3). Bootstrap values in the two trees also were similar though support for certain nodes was slightly higher (e.g., Clade III) or lower (e.g., Clade II) in the tree based on the reanalyzed data.

Discussion

Phylogenetic analysis of ITS nrDNA, *rbc*L and combined sequences yielded similar trees. In all analyses, monophyly of both *Ulva* and *Enteromorpha* is rejected though the union of these taxa is supported. This result is consistent with previous studies (Blomster et al. 1999, Tan et al. 1999, Woolcott and King 1999) and is discussed

further in Hayden (this dissertation, Chap. 2). *Chloropelta caespitosa* is nested within this clade of *Ulva* and *Enteromorpha*.

Numerous clades are well-supported, particularly in the combined data tree. Some of these clades are comprised of geographic isolates of recognizable taxa, such as *U. californica* and *E. intestinalis*. Sequence divergence values within these clades are relatively low, up to 0.7% in ITS nrDNA and up to 0.4% in *rbc*L. This range for ITS nrDNA sequences is comparable to that in a previous study of *E. muscoides* (Blomster et al. 1999) and is smaller than that in a previous study of *E. intestinalis* and *E. compressa* in which intraspecific divergence was as large as 2.3% (Blomster 1998).

Other well supported terminal clades are comprised of multiple taxa, such *as U. lactuca* with *U. fenestrata*. To address this discord, each of the currently recognized northeast Pacific *Ulva*, *Enteromorpha* and *Chloropelta* species are discussed below. Percent bootstrap support values for clades in the tree based on the combined data set (Fig. 3.3) are noted in parentheses. A list of northeast Pacific taxa recognized in this study is provided in Table 3.3.

Ulva californica. Tanner (1979, 1986) investigated morphological variation in *U. californica* through morphological studies of field and herbarium material and culture studies. He concluded that *U. californica* is a distinct species with a wide range of thallus size and habit from a tufted, cuneate form which grows in the upper littoral zone to a lanceolate to oblanceolate blade which grows in the mid littoral zone. As a result, he synonymized two taxa with *U. californica*, *U. angusta* Setchell and Gardner and *U. scagelii* Chihara (Tanner 1986). Plants fitting the descriptions for typical *U. californica*, *U. angusta and U. scagelii*, were collected for the present study. Phylogenetic analysis yielded a strongly supported (100%) clade comprised of all these collections. Within this clade there is little sequence divergence in either ITS

nrDNA (<0.4%) or *rbc*L (<0.1%). Thus, molecular data support Tanner's conclusions. Interestingly, *Ulva* sp. from Scotland groups with *U. californica* accessions. Prior to this study, this species was believed to be present only in the northeast Pacific.

Tanner (1986) considered *U. californica* to be a distinct species based on its development in culture. This species produces a germination tube and extensive basal rhizoidal discs, though Tanner found that these traits can be influenced by growth conditions. These traits were observed in all cultured samples in this clade, including *U. californica* SCA which was collected near the type locality in La Jolla, CA.

Ulva fasciata. *Ulva fasciata* is a warm water species occurring in tropical and subtropical waters around the world. Although Tanner (1979) included this taxon in his treatment of northeast Pacific *Ulva*, he did not collect this species from the field and based conclusions on two herbarium specimens from southern California. Algae fitting the description of *U. fasciata* were not observed in warmer California waters during the present study; however, samples were obtained from Hawaii and the Texas Gulf Coast. This species is morphologically similar to *U. taeniata* (discussed below) though environmental conditions have been shown to influence thallus morphology (Mshigeni and Kajumulo 1979). Setchell and Gardner (1920a, 1920b) separated *U. taeniata* from *U. fasciata* based on blade morphology. Tanner (1979) followed Setchell and Gardner and further distinguished these taxa using anatomical characters. Molecular data support this separation. The clade comprised of *U. fasciata* collections and *Ulva* sp. II from Australia is well supported (92%). Further, divergence among these collections is <0.3% for ITS nrDNA and <0.4% for *rbc*L sequences, whereas divergence between *U. fasciata* and *U. taeniata* sequences is >4.0% for ITS nrDNA and >0.5% for *rbc*L. *Ulva pertusa* from Korea groups with *U. fasciata* with strong

bootstrap support (99%) and little sequence divergence, just 0.6% in ITS nrDNA. *Ulva pertusa* is reported to occur in the northwest Pacific and Indian Ocean. Based on the limited sampling of *U. pertusa* (only 1 sequence is available in GenBank), it is unclear whether these taxa are conspecific.

Ulva fenestrata. Postels and Ruprecht (1840) established *U. fenestrata* based on algae with perforated, expanded blades collected in Kamchatka. Although subsequent research suggested that the perforations are a result of herbivory (Vinogradova 1974, Tanner 1979), Tanner (1979) recognized this species and considered all expanded blades in the northeast Pacific to be *U. fenestrata*, a view which has persisted to the present day (Gabrielson 2000). Algae identified as *U. fenestrata* from the northeast Pacific appear in several clades: *U. fenestrata* from Alaska to northern California and *U. lactuca* from Europe in Clade Ia (100%); *U. fenestrata* from southern California, Japan and *U. rotundata* from Europe in Clade Ib (100%); *U. fenestrata* from central California and Oregon in Clade Ic (100%); *U. fenestrata* from southern California and *U. pseudocurvata* and *E. compressa* from Europe in Clade If (100%); and *U. fenestrata* from Oregon (Tan et al. 1999) in Clade IV (95%). Divergence among taxa in Clades Ia, Ib, Ic and If is <0.5% for ITS nrDNA and <0.2% in *rbc*L sequences. In Clade IV sequence divergence among *U. fenestrata* and several European taxa is <0.7% for ITS nrDNA sequences. Strong bootstrap values for these clades coupled with low sequence divergence among taxa within them suggest that there are several genetically distinct algae in the northeast Pacific currently recognized as *U. fenestrata*.

Tan et al. (1999) sequenced several geographically distinct isolates of *U. lactuca*, the type species of *Ulva*. One of these was included here for comparison purposes. In Clade Ia, algae identified as *U. fenestrata* group with this *U. lactuca*. According to Setchell and Gardner (1920b), *U. lactuca* is distributed from Alaska to the Gulf of

California and *U. fenestrata* is distributed from southeast Alaska to Puget Sound, WA. Abbott and Hollenberg (1976) included *U. lactuca* in their treatment of the California flora. Doty (1947), Scagel (1966) and Tanner (1979) recognized *U. fenestrata* but not *U. lactuca* in their studies of *Ulva* from Alaska to Orgeon. Bliding (1968) considered *U. lactuca* to have a northern distribution in Europe. Tanner (1979) conducted a very limited hybridization experiment with European *U. lactuca* and northeast Pacific *U. fenestrata* and interpreted a delay in fusion and a small number of fused gametes as a negative mating response (following Bliding 1963). Based on results from this study, Tanner's conclusion that *U. lactuca* does not occur in the northeast Pacific is rejected. Phylogenetic analyses suggest that some algae in this region considered to be *U. fenestrata* are conspecific with *U. lactuca*.

Algae in Clade Ia represent what is considered typical northeast Pacific *U. fenestrata* except *U. fenestrata*III OR and *U. fenestrata* BC which are small plants from the upper littoral zone. These two accessions fit Tanner's (1979) concept of northeast Pacific *U. conglobata* which he suggested may be a high intertidal form of *U. fenestrata*. Current results are consistent with this view. The presence of *U. californica*II OR among *U. fenestrata* rather than *U. californica* suggests that it was misidentified by Tan et al. (1999). Given the morphological plasticity exhibited by *U. fenestrata* and *U. californica*, overlapping distribution ranges and ecology (Tanner 1979, 1986, Gabrielson 2000), it is not unreasonable that an individual of *U. californica* would be misidentified as *U. fenestrata*. Further, the definitive characters which separate these species are developmental, yet there is no indication that these species were placed in culture prior to identification for the Tan et al. (1999) paper.

In Clade Ib, *U. fenestrata* collections from southern California and Japan group with *U. rotundata* from Europe. This result is surprising given that *U. rotundata* is

considered to be restricted to the northeast Atlantic and Mediterranean. Bliding (1968) established *U. rotundata* based on its large, rounded cells and its development in culture in which the upper thallus grows into a rounded disc with a well-developed stipe. Subsequent authors (Hoeksema and van den Hoek 1983, Coat et al. 1998) further noted that *U. rotundata* thalli have a "metallic gloss" not present in other *Ulva* species. Collections from southern California did not follow the developmental pattern noted in Bliding (1968). A metallic gloss also was not recorded; however, this trait may have been overlooked since this character was not noted in any accounts of northeast Pacific *Ulva*. The anatomy of the cells and thallus thickness of the southern California collections is consistent with *U. rotundata*; however, there is considerable overlap in these characters across *Ulva* taxa (Vinogradova 1974, Titlyanov et al. 1975, Steffensen 1976, Tanner 1979, Phillips 1988). Sequence divergence between algae in Clade Ib and the sister Clade Ia is >3.5% and >1.9% for ITS nrDNA and *rbc*L, respectively. These divergence values are greater than those considered for conspecifics in this group of algae. Thus, Clade Ib is comprised of a distinct *Ulva* species. Given discrepancies in developmental characters, additional comparative studies of European *U. rotundata* and algae fitting the description of *U. fenestrata* from southern California are necessary.

Clade Ic is comprised of two collections, obovate plants collected from the lower littoral zone in Oregon (*U. fenestrata*I OR) and tufted plants collected from the upper littoral zone in central California (*U. fenestrata* CCA). Prior to Tanner's (1979) study which was used to provide provisional names to accessions in this study, northeast Pacific *Ulva* specimens with expanded blades were divided into several species, including *U. expansa*, *U. fenestrata*, *U. lactuca* and *U. lobata*. Thallus habit and ecology of *U. fenestrata*I OR is similar to Setchell and Gardner's (1920b) description

and collections of *U. lobata*. Further, the anatomy of this collection is similar to *U. fenestrata* CCA and overlaps that of *U. lobata*, though the same caveat applies here as with *U. rotundata* discussed above. Phylogenetic analyses suggest that these algae are distinct from other expanded-type samples. Based on this evidence, these algae are considered *U. lobata* contrary to Tanner's (1979) suggestion that this taxon be synonymized with *U. fenestrata*. Morphological differences between these collections are likely a result of environmental conditions since there is a general trend in *Ulva* toward smaller thalli where desiccation is greater (Tanner 1986, Hayden pers. obs.).

In Clade If, ITS nrDNA and *rbc*L sequences for *U. fenestrata*I SCA are identical to those of *U. pseudocurvata* from Europe. As with *U. lactuca*, Tan et al. (1999) sequenced several samples of this taxon. *U. fenestrata*I SCA was collected as a drift specimen from mudflats in Newport Bay, CA. It is typical of *Ulva* frequently encountered in protected bays in the northeast Pacific (pers. obs.), but these blades are atypical of *U. fenestrata sensu* Setchell and Gardner (1920b). The thallus morphology and anatomy of *U. fenestrata*I SCA overlaps with that described for *U. pseudocurvata* (Koeman and van den Hoek 1980); however, the characteristically curved nature *of U. pseudocurvata* thalli was not readily apparent in this collection since the base of the plant is absent. Reproductive and developmental characters could not be compared for these taxa because pieces of the *U. fenestrata*I SCA thallus persisted in a vegetative state in culture despite light and temperature alterations. Given that sequences for these taxa are identical and that the morphology of *U. fenestrata*I SCA is atypical for *U. fenestrata sensu* Setchell and Gardner (1920b), it is reasonable to refer this alga to *U. pseudocurvata*. Until now, this taxon has been considered a northeast Atlantic species.

Finally, the Oregon collection of *U. fenestrata* from Tan et al. (1999) which appears in Clade IV is closely related to several European taxa, including *U. armoricana*, *U. rigida* and *U. scandinavica*. Given this divergent position in the trees, this collection is likely misidentified. Suggestions for its identity are discussed further below.

Ulva rigida. Setchell and Gardner (1920b) and more recent authors (Abbott and Hollenberg 1976, Scagel 1966, Tanner 1979) considered *U. rigida* to be a member of the northeast Pacific marine flora. This species was described by C. Agardh (1822) based on material from southern Spain and is very common in some areas along northeast Atlantic shores (Hoeksema and van den Hoek 1983). A sample of *U. rigida* from the type locality (UrigEU) was obtained for this study. It appears in a strongly supported clade (92%) with a sample of *U. rigida* from Chile, *U. fenestrata* from Oregon (Tan et al. 1999) and two other European taxa. Divergence values among sequences in this clade are within the range for conspecifics. Divergence in ITS nrDNA sequences is 1% between *U. rigida* CE and other taxa in this clade but is 0.2% among *U. rigida* EU, *U. armoricana* EU and *U. scandinavica* EU. Divergence in *rbc*L sequences is 0.2% between *U. rigida* CE and *U. scandinavica* EU. This result is consistent with a previous molecular study including these *U. armoricana*, *U. fenestrata* and *U. scandinavica* sequences and different *U. rigida* samples (Tan et al. 1999). The separation of these taxa is based on very few molecular and morphological characters (Bliding 1968, Coat et al. 1998, Dion et al. 1998), and observed morphological and anatomical differences are likely environmentally influenced. Given these findings, *U. armoricana* and *U. scandinavica* should be reduced to synonyms of the older *U. rigida*. The presence of an Oregon collection in this clade (*U. fenestrata* IV OR) suggests that *U. rigida* is present in the northeast Pacific.

Ulva stenophylla. Setchell and Gardner (1920a) described *U. stenophylla* based on morphologically distinct plants growing in the lower littoral and upper sublittoral zones in central California. Subsequent authors recognized this species (e.g., Doty 1947, Scagel 1966, Tanner 1979, Gabrielson et al. 2000), though there was some confusion initially over its identity due to inaccuracies in the original description and an atypical holotype (Smith 1944, Abbott and Hollenberg 1976, Tanner 1979). Although its linear thallus with undulate margins and planular central axis makes *U. stenophylla* one of the easier species to identify in the northeast Pacific, it was difficult to find in the field and only one collection was made during the present study.

U. stenophylla WA is basal in Clade III in phylogenetic trees based on combined data. The branch leading to it has a sufficient number of changes to suggest that it is distinct from other surveyed taxa, and it is recognized here as a separate species. *Ulva stenophylla* has been reported in the northeast Pacific from Vancouver Is., British Columbia to Santa Barbara County, CA (Gabrielson et al. 2000).

Ulva taeniata. Setchell and Gardner (1920a) established *U. taeniata* based on algae with long, simple or segmented, dentate thalli found in central California. They described a second species, *U. dactylifera*, for smaller algae with similar morphology but slightly different anatomy found in southern California. A third species with similar morphology but a more distinct midrib, *U. costata*, was described by Hollenberg (1971). Tanner (1979) suggested that *U. dactylifera* and *U. costata* were conspecific with *U. taeniata* and that observed differences were due to environmental conditions (thallus size) or the physiological state of cells (thickened midrib). He has been followed by recent authors (Scagel 1993, Gabrielson et al. 2000). Collections of taxa in this assemblage were made in central and southern California, including at the type locality in Monterey, CA. Algae fitting the description for this taxon were not

encountered north of Monterey, CA; however, *U. taeniata* has been reported as far north as southern British Columbia (Gabrielson 2000). Sequence from an Oregon collection from a previous study (Tan et al. 1999) was included as a more northern representative.

Sequences from these collections appear in two clades, one comprised of the California collections and the other of the Oregon collection and *Ulva* sp. from Chile. Although neither of these clades have strong support in the combined analysis trees, *U. taeniata*I SCA and *U. taeniata* CCA are grouped with strong support in the ITS nrDNA tree (Fig. 3.2a). ITS nrDNA data is lacking for *U. taeniata*II SCA, but it groups with the other California samples in *rbc*L trees (Fig. 3.1b and 3.2b). Sequence divergence among these three collections is within the range of conspecifics. *Ulva taeniata* CCA has morphology typical of *U. taeniata* and was collected from the type locality. *Ulva taeniata*II SCA is more typical of *U. dactylifera*, though some specimens have a more distinct midrib similar *to U. costata*. *Ulva taeniata*I SCA was initially identified as *U. rigida*, since it lacks lacinae; however, these algae were growing higher in the intertidal than most *U. taeniata* and may have been dwarfed by stress due to desiccation. Given these observations, Tanner's suggestion for synonymy of *U. costata* and *U. dactylifera* with *U. taeniata* appears to be supported by molecular data.

Sequence divergence between the two clades of *U. taeniata* is 3.5% for ITS nrDNA and 0.7% for *rbc*L which are outside the ranges of conspecifics. Further, the habit of the Chilean *Ulva* is different from the typical California *U. taeniata*. The former has a blade that is simple and broad whereas the latter has blades divided into several long divisions that are deeply ruffled and often twisted. The herbarium specimen for the Oregon accession was not observed; however, the collector confirmed that this

accession has a morphology typical of *U. taeniata* (G. Hansen, pers. comm.). Based on the molecular and morphological evidence, *U. taeniata* appears to be polyphyletic.

Enteromorpha intestinalis. *Enteromorpha intestinalis* was among the sixteen *Enteromorpha* taxa recognized by Setchell and Gardner (1920a, 1920b), and it is recognized in the northeast Pacific flora to the present day (Gabrielson et al. 2000). A recent study of European *E. intestinalis* showed this taxon to be genetically distinct from the morphologically similar *E. compressa* (Blomster et al. 1998). The present study, including *E. intestinalis* collections from Alaska, British Columbia, northern California and Europe, further supports this conclusion. These collections group with strong bootstrap support (100%). Sequence divergence among them is near the upper limit for conspecifics in this study, up to 0.7% in ITSnrDNA and to 0.4% in *rbc*L sequences, but this ITS nrDNA value is within the bounds observed by Blomster et al. (1998). This taxon is common in the northeast Pacific, particularly in freshwater seeps in the upper littoral zone.

Enteromorpha linza. Setchell and Gardner (1920b) considered *E. linza* to be a member of *Ulva* and thus reported the occurrence of *Ulva linza* in the northeast Pacific. This alga is very common in this region; however, PCR amplification difficulties prevented the inclusion of more than one sample in the present study. *Enteromorpha linza* NCA groups with *E. linza*, *E. procera* and *E. prolifera* from Europe and Japan, but support for the node uniting these taxa is weak (58%). Sequence divergence between *E. linza* NCA and the remaining taxa in this clade is approximately 2.0% for ITS nrDNA and >1.5% for *rbc*L. Although the ITS nrDNA value is within the range for *E. intestinalis* and *E. compressa* (Blomster et al. 1998), the *rbc*L value is well above divergence among conspecifics observed in the present study. This suggests that northeast Pacific *E. linza* may not be conspecific with European *E.*

linza; however, additional European and northeast Pacific samples should be sequenced to confirm this finding. European *E. linza* groups with *E. procera* from Europe and Japan with strong bootstrap support (100%). This result is surprising given the different morphologies of these two taxa, yet is consistent with a previous study including only the European samples (Tan et al. 1999).

Enteromorpha prolifera. Setchell and Gardner (1920b) reported the presence of *E. prolifera* in the northeast Pacific, and it has been reported by numerous recent authors (e.g., Doty 1947, Abbott and Hollenberg 1976, Gabrielson et al. 2000). It is relatively common in this region in protected bays and estuaries and can become quite prevalent in these environments in late summer in Puget Sound, WA (Hayden and Waaland 1998, 1999). Collections of *E. prolifera* from Washington and northern and southern California form a well supported clade (94%); however, this clade does not include the European sample of *E. prolifera*, which is only distantly related. The northest Pacific collections of *E. prolifera*, particularly *E. prolifera* WA and *E. prolifera* NCA, are typical *E. prolifera sensu* Abbott and Hollenberg (1976) and Gabrielson et al. (2000). When compared to the European literature, these accesssions fit the description of *E. prolifera* subsp. *radiata* (Bliding 1963) which is recognized in a more recent study by Koeman and van den Hoek (1982) as *E. radiata* J. Agardh. Given this similarity, it is hypothesized that these accessions represent *E. radiata*; however, no molecular data are available at present for European *E. radiata* to test this hypothesis.

The remaining *Enteromorpha* species reported in the northeast Pacific, *E. compressa*, *E. flexuosa*, *E. muscoides* and *E. torta*, were not encountered during the present study. Sequences for all but *E. torta* were included for comparison from European collections. One unidentified collection, *Enteromorpha* sp. NCA did not group strongly with any other surveyed taxa. In ITS nrDNA trees it groups with

European *E. prolifera* but only with weak support. Sequence divergence between *Enteromorpha* sp. NCA *and E. prolifera* EU is 1.3% for ITS nrDNA and 1.4% for *rbc*L. Thus, its identity remains uncertain.

Chloropelta caespitosa. Tanner (1979, 1980) established the monotypic *Chloropelta* on the basis of its unique developmental pattern which is very distinctive in culture (pers. obs.). In *C. caespitosa*, cells in the tubular germling undergo one division producing a distromatic tubular germling not seen in other Ulvaceae. Rupture of the tube produces a distromatic, peltate blade. *Chloropelta caespitosa* has been reported from as far away as South Africa and Japan, but its distribution in the northeast Pacific was considered restricted to southern California until the present study. *Chloropelta caespitosa* CCA was collected in Monterey. Although it was not discernable from neighboring *U. californica* in the field, its peltate blade was identified upon closer inspection, and its development in culture confirmed identification. Development was not observed in *C. caespitosa* from Japan.

Despite its unique development, *C. caespitosa* is nested in the *Ulva* clade, and thus, cannot be recognized at the generic level. *Chloropelta caespitosa* is recognized here as a distinct species based on strong bootstrap support (100%) for the node uniting the California and Japan collections and the relatively large divergence values between sequences for these collections and other surveyed taxa — >3% for ITS nrDNA and >0.7% for *rbc*L.

Conclusions

The focus of the present study was to test species hypotheses and to gain a better understanding of species diversity of *Ulva*, *Enteromorpha*, and *Chloropelta* in the

northeast Pacific. To date, it is the largest study of *Ulva* and *Enteromorpha* using molecular data and the first to use more than one gene region in phylogenetic analyses. The results provide insights into the systematics of these taxa and point to areas for additional research.

Many of the species recognized by early and more recent treatments for this region are resolved by molecular data. This demonstrates the value of these data in species delimitations in these morphologically simple algae. In particular, molecular data were useful for discerning species among *Ulva* with expanded-type thalli. Tanner's (1979). hypothesis that all northeast Pacific expanded-type *Ulva* are *U. fenestrata* is rejected. Rather, several species, recognized by earlier authors, can be distinguished. However, his hypotheses for *U. californica* and *U. taeniata* are supported.

The present phylogenetic analyses revealed unanticipated conspecific taxa, such as European *U. rotundata* and *U. fenestrata* from southern California. Strong bootstrap values for such clades and low sequence divergence within them suggests that more detailed studies of these taxa are warranted. Phylogenetic analyses also revealed that closely related taxa can be morphologically similar (e.g., *U. fasciata* and *U. taeniata*) or very different (e.g., *U. californica* and northeast Pacific *E. prolifera*). This is in accord with previous studies which showed that it is difficult to identify morphological and developmental traits reflecting interspecific relationships (Tan et al. 1999, Hayden, this dissertation, Chap. 2).

Another result of this study is the finding that *Ulva* and *Enteromorpha* species are more widely distributed than may have been recognized previously. Many species described in Europe are inferred to occur here (e.g., *U. lactuca* and *E. intestinalis*) and vice versa (e.g., *U. californica*). Given their tolerance for wide ranges of salinity, temperature and water quality, it is not surprising that these species are widely

distributed. Further, given their role as fouling organisms, these algae may move around the globe via human activities such as shipping and commercial shellfish transport (J. Olsen, pers. comm.). Such large distribution ranges signify the need for studies of individual taxa to incorportate samples from more than one geographic region. Although this may require added effort on the part of the investigator, more restricted studies may lead to false conclusions.

Based on results from the present study, three species of *Enteromorpha* are inferred to occur in this region: *E. intestinalis*, *E. linza*, and *E. prolifera* (but see Table 3.3 for additional comments). Other *Enteromorpha* species reported in this region were not encountered during the present study. Seven species of *Ulva* were observed: *U. californica*, *U. lactuca*, *U. lobata*, *U. pseudocurvata*, *U. rigida*, *U. stenophylla* and *U. taeniata*. The presence of an eighth species, *U. rotundata*, is uncertain. The monospecific genus *Chloropelta* is not distinct from *Ulva* and *Enteromorpha*. *Chloropelta caespitosa* is recognized as *Ulva caespitosa*.

Table 3.1. Species of *Chloropelta*, *Enteromorpha* and *Ulva* currently recognized in the northeast Pacific.

Taxon
Chloropelta caespitosa Tanner [a]
Enteromorpha compressa (L.) Nees [b, c]
Enteromorpha flexuosa (Wulfen) J. Agardh [b, c]
Enteromorpha intestinalis (L.) Nees [b, c]
Enteromorpha linza (L.) J. Agardh [b, c]
Enteromorpha muscoides (Clemente y Rubio) Cremades [c]
Enteromorpha prolifera (O.F. Müller.) J. Agardh [b, c]
Enteromorpha torta (Mertens) Reinbold [c]
Ulva californica Wille *in* Collins, Holden *et* Setchell [a, b, c]
Ulva fasciata Delile [a]
Ulva fenestrata Postels *et* Ruprecht [a, c]
Ulva rigida C. Agardh [a, b]
Ulva stenophylla Setchell *et* Gardner [a, b, c]
Ulva taeniata (Setchell *in* Collins, Holden *et* Setchell) Setchell *et* Gardner [a, b, c]

[a] Tanner (1979)
[b] Abbott and Hollenberg (1976)
[c] Gabrielson et al. (2000)

Table 3.2. Species and sample names of *Chloropelta*, *Enteromorpha* and *Ulva* with source, collection details and GenBank accession numbers for published ITS nrDNA sequences. Collections were identified according to the following sources: *Chloropelta* (Tanner 1980), *Enteromorpha* (Bliding 1963, Scagel 1966, Abbott and Hollenberg 1976, and Blomster et al. 1998, 1999) and *Ulva* (Tanner 1979, 1986). The geographical area from which each sample was collected is indicated in the sample name: AK, Alaska; AU, Australia; BC, British Columbia; NCA, northern California, CCA, central California; SCA, southern California; CE, Chile; EU, Europe; JN, Japan; KA, Korea; OR, Oregon; TX, Texas; WA, Washington. CCA includes Marin Co. south through San Luis Obispo Co. ITS nrDNA sequences of European samples are from source references.

Sample name	Species	Source	Collection locality	Collection date	Latitude, longitude	ITS nrDNA
Chloropelta caespitosa CCA	*Chloropelta caespitosa* Tanner	Field collection	South Point Cabrillo, Monterey, Monterey Co., CA	17 Jun. 99	36°36.6' N, 121°53.7' W	
Chloropelta caespitosa JN	*C. caespitosa*	Field collection by H. Kawai	Kobe, Hyogo Pref., Japan	22 Mar. 00	34°43' N, 135°19' W	
Enteromorpha compressa EU	*Enteromorpha compressa* (L.) Nees	Blomster et al. 1998	Portaferry, Strangford Lough, N. Ireland	12 Apr. 96	54°22.7' N, 5°34.6' W	AF035350
Enteromorpha flexuosa EU	*E. flexuosa* (Wulfen) J. Agardh	Tan et al. 1999	Sweden	na	na	AJ234306
Enteromorpha intestinalis AK	*E. intestinalis* (L.) Nees	Field collection by T. Klinger	Sheep Bay, Valdez-Cordova Co., AK	8 Jul. 97	60°39.7' N, 146°0.5'W	
Enteromopha intestinalis BC	*E. intestinalis*	Field collection	Botany Bay, Vancouver Is., BC	29 Jun. 99	48°31.7' N, 124°27.2' W	

Table 3.2. Continued.

Sample name	Species	Source	Collection locality	Collection date	Latitude, longitude	ITS nrDNA
Enteromorpha intestinalis NCA	*E. intestinalis*	Field collection	Bodega Head, Sonoma Co., CA	17 Jun. 00	38°18.2' N, 123°3.9' W	
Enteromorpha intestinalis EU	*E. intestinalis*	Blomster et al. 1998	Woolwich, Thames, London, England	9 Nov. 96	51°30.0' N, 0°5.0'W	AF035342
Enteromorpha intestinaloides EU	*E. intestinaloides* Kocman *et* van den Hoek	Tan et al. 1999	Dunbar, East Lothian, Scotland	na	56°0' N, 2°31' W	AJ234303
Enteromorpha linza NCA	*E. linza* (L.) J. Agardh	Field collection	Coast Guard Cove, Humboldt Bay, Humboldt Co. CA	19 Jun. 00	40°45.8' N, 124°13.2' W	
Enteromorpha linza EU	*E. linza*	Tan et al. 1999	Ythan estuary, Aberdeenshire, Scotland	na	57°7' N, 2°6' W	AJ000203
Enteromorpha muscoides EU	*E. muscoides* (Clemente y Rubio) Cremades	Blomster et al. 1999	Los Toruños, Puerto Réal, Cádiz, Spain	2 May 98	36°30.0' N, 6°20.0' W	AF127170
Enteromorpha procera EU	*E. procera* Ahlner	Field collection by J. Blomster	Suomenlinna, Helsinki, Findland	na	60°36' N, 21°25' E	na
Enteromorpha procera JN	*E. procera*	Field collection by H. Kawai	Osaka Bay, Japan	26 Apr. 00	35°57' N, 137°16'E	

Table 3.2. Continued.

Sample name	Species	Source	Collection locality	Collection date	Latitude, longitude	ITS nrDNA
Enteromorpha prolifera WA	*E. prolifera* (O.F. Müller.) J. Agardh	Field collection	Blakely Is., San Juan Co., WA	13 Aug. 97	48°33.7' N, 122°48.0' W	
Enteromorpha prolifera NCA	*E. prolifera*	Field collection	Westside Rd., Bodega Bay, Sonoma Co., CA	17 Jun. 00	38°18.6' N, 123°3.6' W	
Enteromorpha prolifera SCA	*E. prolifera*	Field collection by D.M. Dexter	Red Hill Marina, Salton Sea, Imperial Co., CA	5 Feb. 00	33°22.5' N, 116°0.3' W	
Enteromorpha prolifera EU	*E. prolifera*	Tan et al. 1999	Ythan estuary, Aberdeenshire, Scotland	na	57°7' N, 2°6' W	AJ234304
Enteromorpha sp. NCA	*Enteromorpha* sp.	Field collection	Coast Guard Cove, Humboldt Bay, Humboldt Co. CA	19 Jun. 00	40°45.8' N, 124°13.2' W	
Enteromorpha sp. EU	*Enteromorpha* sp.	Tan et al. 1999	Ythan estuary, Aberdeenshire, Scotland	na	57°7' N, 2°6' W	AJ234308
Ulva armoricana EU	*Ulva armoricana* Dion, de Reviers *et* Coat	Coat et al. 1998	Roscoff, France	na	48°43.0' N, 4°1.0' W	na
Ulva californica BC	*U. californica* Wille *in* Collins, Holden *et* Setchell	Field collection	Botany Bay, Vancouver Is., BC	29 Jun. 99	48°31.7' N, 124°27.2' W	

Table 3.2. Continued.

Sample name	Species	Source	Collection locality	Collection date	Latitude, longitude	ITS nrDNA
Ulva californica WA	*U. californica*	Field collection	Cattle Point, San Juan Is., San Juan Co., WA	15 Jun. 98	48°27.0' N, 122°57.7' W	
*Ulva californica*I OR	*U. californica*	Field collection	Fogarty Creek, Lincoln Co., OR	14 May 99	44°50.4' N, 124°3.2' W	
*Ulva californica*II OR	*U. californica*	Tan et al. 1999	Otter Crest, Lincoln, Co., OR	na	44°45.7'N, 124°3.8' W	AJ234315
*Ulva californica*I NCA	*U. californica*	Field collection	Coast Guard Cove, Humboldt Bay, Humboldt Co. CA	19 Jun. 00	40°45.8' N, 124°13.2' W	
*Ulva californica*II NCA	*U.californica*	Field collection	Coast Guard Cove, Humboldt Bay, Humboldt Co., CA	19 Jun. 00	40°45.8' N, 124°13.2' W	
*Ulva californica*I CCA	*U. californica*	Field collection	South Point Cabrillo, Monterey, Monterey Co., CA	17 Jun. 99	36°36.6' N, 121°53.7' W	
*Ulva californica*II CCA	*U.californica*	Field collection	Moss Landing Harbor	18 Jun. 99	36°48.5' N, 121°47.2' W	
Ulva californica SCA	*U. californica*	Field collection	Casa Cove, La Jolla, San Diego Co., CA	14 Jun. 99	32°50.9' N, 117°16.7' W	

Table 3.2. Continued.

Sample name	Species	Source	Collection locality	Collection date	Latitude, longitude	ITS nrDNA
Ulva fasciata TX	*U. fasciata* Delile	LB1859, UTEX culture collection	Port Aransas, Nueces Co., TX	na	27°50.0' N, 97°3.7 W	
*Ulva fasciata*I HI	*U. fasciata*	Field collection by L. Hodgson	Kihei, Maui Co., HI	6 Feb. 00	20°47.0' N, 156°28.0' W	
*Ulva fasciata*II HI	*U. fasciata*	Field collection by L. Hodgson	Maalaea, Maui Co., HI	6 Feb. 00	20°47.8' N, 156°30.9' W	
Ulva fenestrata AK	*U. fenestrata* Postels *et* Ruprecht	Field collection	Petersburg, Wrangell-Petersburg Co., AK	6 Sep. 98	56°48.8' N, 132°57.6' W	na
Ulva fenestrata BC	*U. fenestrata*	Field collection	Botanical Beach, Vancouver Is., BC	30 Jun. 99	48°32.0' N, 124°26.0' W	
Ulva fenestrata WA	*U. fenestrata*	Field collection	Cattle Point, San Juan Is., San Juan Co., WA	15 Jun. 98	48°27.0' N, 122°57.7' W	
*Ulva fenestrata*I OR	*U. fenestrata*	Field collection	North Jetty, Yaquina Bay State Park, Lincoln Co., OR	16 May 99	44°37.4' N, 124°3.7' W	
*Ulva fenestrata*II OR	*U. fenestrata*	Field collection	Fogarty Creek, Lincoln Co., OR	14 May 99	44°50.4' N, 124°3.2' W	

Table 3.2. Continued.

Sample name	Species	Source	Collection locality	Collection date	Latitude, longitude	ITS nrDNA
*Ulva fenestrata*III OR	*U. fenestrata*	Field collection	Seal Rock, Lincoln Co., OR	15 May 99	44°30.0' N, 124°5.0' W	
*Ulva fenestrata*IV OR	*U. fenestrata*	Tan et al. 1999	North Boardman State Park, OR	na	na	AJ234316
Ulva fenestrata NCA	*U. fenestrata*	Field collection	Coast Guard Cove, Humboldt Bay, Humboldt Co. CA	19 Jun. 00	40°45.8' N, 124°13.2' W	
Ulva fenestrata CCA	*U. fenestrata*	Field collection	San Simeon, San Luis Obispo Co., CA	16 Jun. 99	35°36.9' N, 121°9.0' W	
*Ulva fenestrata*I SCA	*U. fenestrata*	Field collection	North Star Beach, Newport, Orange Co., CA	15 Jun. 99	33°37.5' N, 117°53.6' W	
*Ulva fenestrata*II SCA	*U. fenestrata*	Field collection	Lower Newport Bay, Newport, Orange Co., CA	15 Jun. 99	33°37.1' N, 117°56.0' W	
*Ulva fenestrata*III SCA	*U. fenestrata*	Field collection	Perez Cove, Mission Bay, San Diego Co., CA	14 Jun. 99	32°46.0' N, 117°13.8' W	
*Ulva fenestrata*IV SCA	*U. fenestrata*	Field collection	Bird Rock, La Jolla, San Diego Co., CA	14 Jun. 99	32°48.9' N, 117°16.4'W	
Ulva fenestrata JN	*U. fenestrata*	Field collection by H. Kawai	Yura, Hyogo Pref., Japan	21 Mar. 00	34°17' N, 134°57' E	

Table 3.2. Continued.

Sample name	Species	Source	Collection locality	Collection date	Latitude, longitude	ITS nrDNA
Ulva lactuca EU	*U. lactuca* L.	Tan et al. 1999	Ballyhenry Is., Strangford Lough, N. Ireland	na	54°25.9' N, 5°31.9' W	AJ234310
Ulva pertusa KA	*U. pertusa* Kjellman	Tan et al. 1999	Guryongpo, East Coast, Korea	na	na	AJ234321
Ulva pseudocurvata EU	*U. pseudocurvata* Koeman *et* van den Hoek	Tan et al. 1999	Ythan estuary, Aberdeenshire, Scotland	na	57°7' N, 2°6' W	AJ234312
Ulva reticulata HI	*U. reticulata* Forsskål	Field collection by L. Hodgson	Lipoa St., Kihei, Maui Co., HI	6 Feb. 00	20°47.0' N, 156°28.0' W	na
Ulva rigida EU	*U. rigida* C. Agardh	Field collection by C.A. Maggs	Cádiz, Spain	na	36°30' N, 6°20' W	
Ulva rigida CE	*U. rigida*	Field collection by J.R. Waaland	Pelluco Beach, SE of Puerto Montt, Chile	17 Oct. 00	41°28' S, 72°56' W	
Ulva rotundata EU	*U. rotundata* Bliding	Coat et al. 1998	Roscoff, France	na	48°43.0' N, 4°1.0' W	na
Ulva scandinavica EU	*U. scandinavica* Bliding	Tan et al. 1999	Langstone Harbor, Portsmouth, England	na	50°46' N, 1°4' W	AJ234317
Ulva stenophylla WA	*U. stenophylla* Setchell *et* Gardner	Field collection	Shilshole Bay, Seattle, King Co., WA	2 Jun. 00	47°41.4' N, 122°24.0' W	

Table 3.2. Continued.

Sample name	Species	Source	Collection locality	Collection date	Latitude, longitude	ITS nrDNA
Ulva taeniata OR	*U. taeniata* (Setchell *in* Collins, Holden *et* Setchell) Setchell *et* Gardner	Tan et al. 1999	Seal Rock, Lincoln Co., OR	na	44°30.0' N, 124°5.0' W	AJ234320
Ulva taeniata CCA	*U. taeniata*	Field collection	Perkins Park, Monterey, Monterey Co., CA	17 Jun. 99	36°37.6' N, 121°55.1' W	
*Ulva taeniata*I SCA	*U. taeniata*	Field collection	Point Loma, San Diego, San Diego Co., CA	14 Jun. 99	32°41.7' N, 117°15.3' W	
*Ulva taeniata*II SCA	*U. taeniata*	Field collection	Point Loma, San Diego, San Diego Co., CA	14 Jun. 99	32°41.7' N, 117°15.3' W	na
Ulva sp. AU	*Ulva* sp.	Field collection by G. Zuccarello	Tamarama, Sydney, Australia	9 Aug. 99	33°53' S, 151°12' E	
Ulva sp. CE	*Ulva* sp.	Field collection by J.R. Waaland	Coihuin, SE of Puerto Montt, Chile	17 Oct. 00	41°28 S, 72°56' W	
Ulva sp. EU	*Ulva* sp.	Tan et al. 1999	Stromness Harbour, Orkney, Scotland	na	59°0' N, 3°0' W	AJ234323

Table 3.2. Continued.

Sample name	Species	Source	Collection locality	Collection date	Latitude, longitude	ITS nrDNA
Percursaria percursa	*P. percursa* (C. Agardh) Rosenvinge	UWCC MA230, UW culture collection	na	na	na	
Ulva olivascens	*U. olivascens* P.A. Dangeard	Field collection by C.A. Maggs	Portaferry, Strangford Lough, N. Ireland	5 May 00	54°22.7' N, 5°34.6' W	
Ulvaria obscura var. *blyttii*	*U. obscura* var. *blyttii* (Areschoug) Bliding	Field collection	Padilla Bay National Estuarine Research Reserve, Skagit Co., WA	25 Apr. 97	48°28.7 N, 122°30.2' W	

Table 3.3. Species of *Enteromorpha* and *Ulva* recognized in the present study, and their observed distribution in the northeast Pacific. Abbreviations are as in Table 3.2.

Taxon	Northeast Pacific Distribution	Comments
Enteromorpha intestinalis	Alaska to southern California	see Blomster et al. 1998
Enteromorpha linza	Alaska to southern California	polyphyletic taxon, northeast Pacifc and European *E. linza* not conspecific
Enteromorpha prolifera	Washington to southern California	polyphyletic taxon, northeast Pacific and European *E. prolifera* not conspecific, northeast Pacific accessions similar to *E. radiata sensu* Koeman and van den Hoek 1982
Ulva californica	British Columbia to southern California	synonymy of *U. angusta* and *U. scagelii* is supported, also in Europe, see Tanner 1986
Ulva caespitosa	central California	*comb. nov.*, see Tanner 1980 (as *Chloropelta caespitosa*)
Ulva fasciata	not observed in this region	
Ulva lactuca	Alaska to central California	*U. fenestrata sensu* Tanner 1979, see Bliding 1968
Ulva lobata	Oregon to central California	*U. fenestrata sensu* Tanner 1979, see Setchell and Gardner 1920a, 1920b
Ulva pseudocurvata	southern California	see Koeman and van den Hoek 1981
Ulva rigida	Oregon	*U. armoricana* and *U. scandinavica* are probable synonyms, see Bliding 1968
Ulva rotundata	southern California?	European sample is conspecific with several *U. fenestrata* SCA *sensu* Tanner 1979, but developmental traits are inconsistent
Ulva stenophylla	Washington	see Tanner 1979
Ulva taeniata	Oregon to southern California	polyphyletic taxon

Figure 3.1. (A) One of 30 most parsimonious trees of 367 steps derived from cladistic analysis of ITS nrDNA sequence data (478 nucleotide positions). (B) One of 16 most parsimonious trees of 320 steps resulting from cladistic analysis of *rbc*L sequences. Numbers above branches equal branch lengths. Collections were identified according to the following sources: *Chloropelta* (Tanner 1980), *Enteromorpha* (Bliding 1963, Scagel 1966, Abbott and Hollenberg 1976, and Blomster et al. 1998, 1999) and *Ulva* (Tanner 1979, 1986). Geographical abbreviations are as in Table 3.2. The clade comprised of *U. fenestrata*I OR and *U. fenestrata* CCA appears twice because it occupies different locations in the two trees.

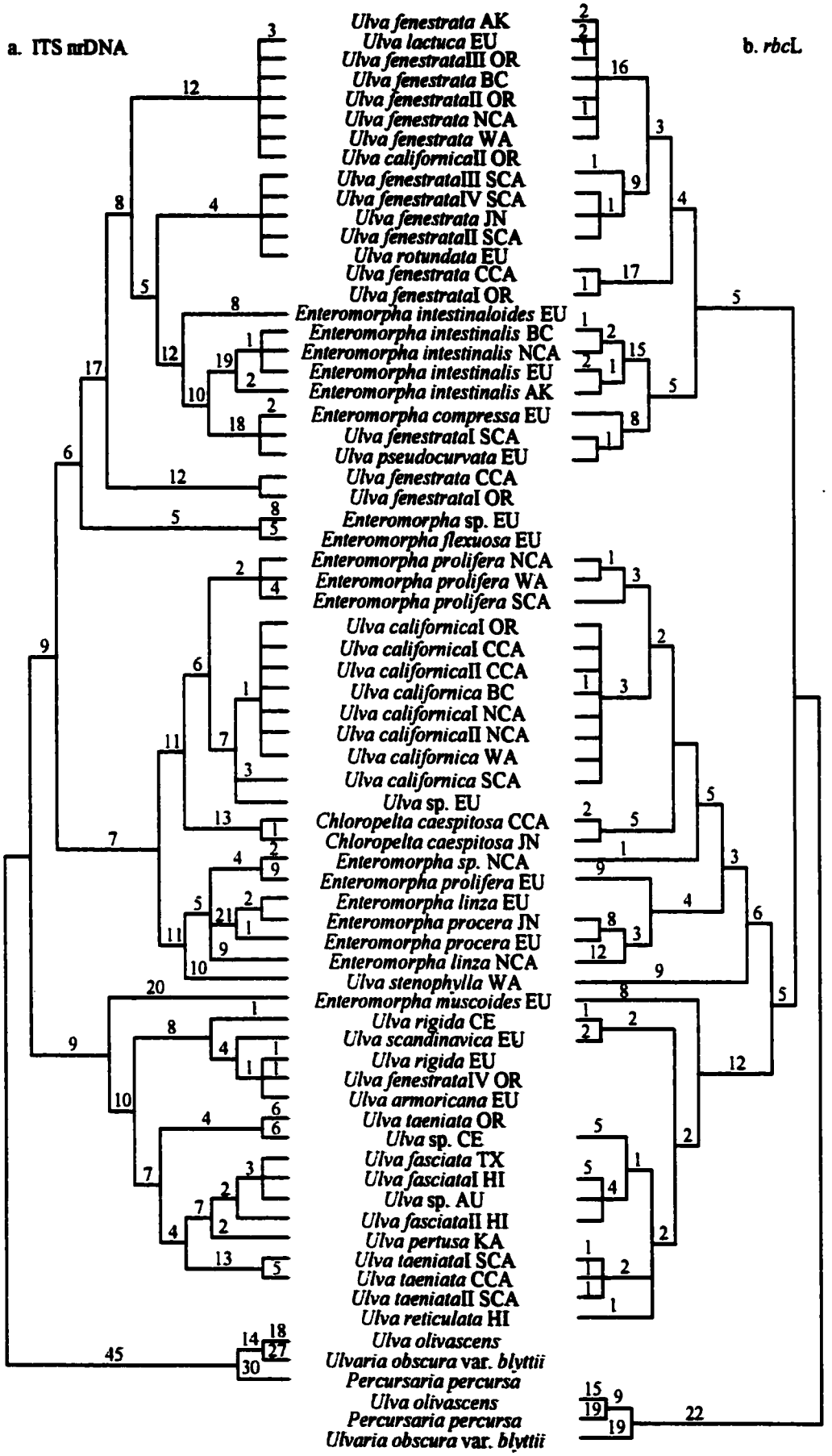

a. ITS nrDNA
b. rbcL
Ulva fenestrata AK
Ulva lactuca EU
Ulva fenestrataIII OR
Ulva fenestrata BC
Ulva fenestrataII OR
Ulva fenestrata NCA
Ulva fenestrata WA
Ulva californicaII OR
Ulva fenestrataIII SCA
Ulva fenestrataIV SCA
Ulva fenestrata JN
Ulva fenestrataII SCA
Ulva rotundata EU
Ulva fenestrata CCA
Ulva fenestrataI OR
Enteromorpha intestinaloides EU
Enteromorpha intestinalis BC
Enteromorpha intestinalis NCA
Enteromorpha intestinalis EU
Enteromorpha intestinalis AK
Enteromorpha compressa EU
Ulva fenestrataI SCA
Ulva pseudocurvata EU
Ulva fenestrata CCA
Ulva fenestrataI OR
Enteromorpha sp. EU
Enteromorpha flexuosa EU
Enteromorpha prolifera NCA
Enteromorpha prolifera WA
Enteromorpha prolifera SCA
Ulva californicaI OR
Ulva californicaI CCA
Ulva californicaII CCA
Ulva californica BC
Ulva californicaI NCA
Ulva californicaII NCA
Ulva californica WA
Ulva californica SCA
Ulva sp. EU
Chloropelta caespitosa CCA
Chloropelta caespitosa JN
Enteromorpha sp. NCA
Enteromorpha prolifera EU
Enteromorpha linza EU
Enteromorpha procera JN
Enteromorpha procera EU
Enteromorpha linza NCA
Ulva stenophylla WA
Enteromorpha muscoides EU
Ulva rigida CE
Ulva scandinavica EU
Ulva rigida EU
Ulva fenestrataIV OR
Ulva armoricana EU
Ulva taeniata OR
Ulva sp. CE
Ulva fasciata TX
Ulva fasciataI HI
Ulva sp. AU
Ulva fasciataII HI
Ulva pertusa KA
Ulva taeniataI SCA
Ulva taeniata CCA
Ulva taeniataII SCA
Ulva reticulata HI
Ulva olivascens
Ulvaria obscura var. blyttii
Percursaria percursa
Ulva olivascens
Percursaria percursa
Ulvaria obscura var. blyttii

Figure 3.2. Comparison of strict consensus trees derived from (A) ITS nrDNA (478 nucleotide positions) and (B) *rbc*L sequences. Bootstrap percentages (> 50%) are shown above branches. Species identification and geographical abbreviations are as in Table 3.2. The clade comprised of *U. fenestrata*I OR and *U. fenestrata* CCA appears twice because it occupies different locations in the two trees.

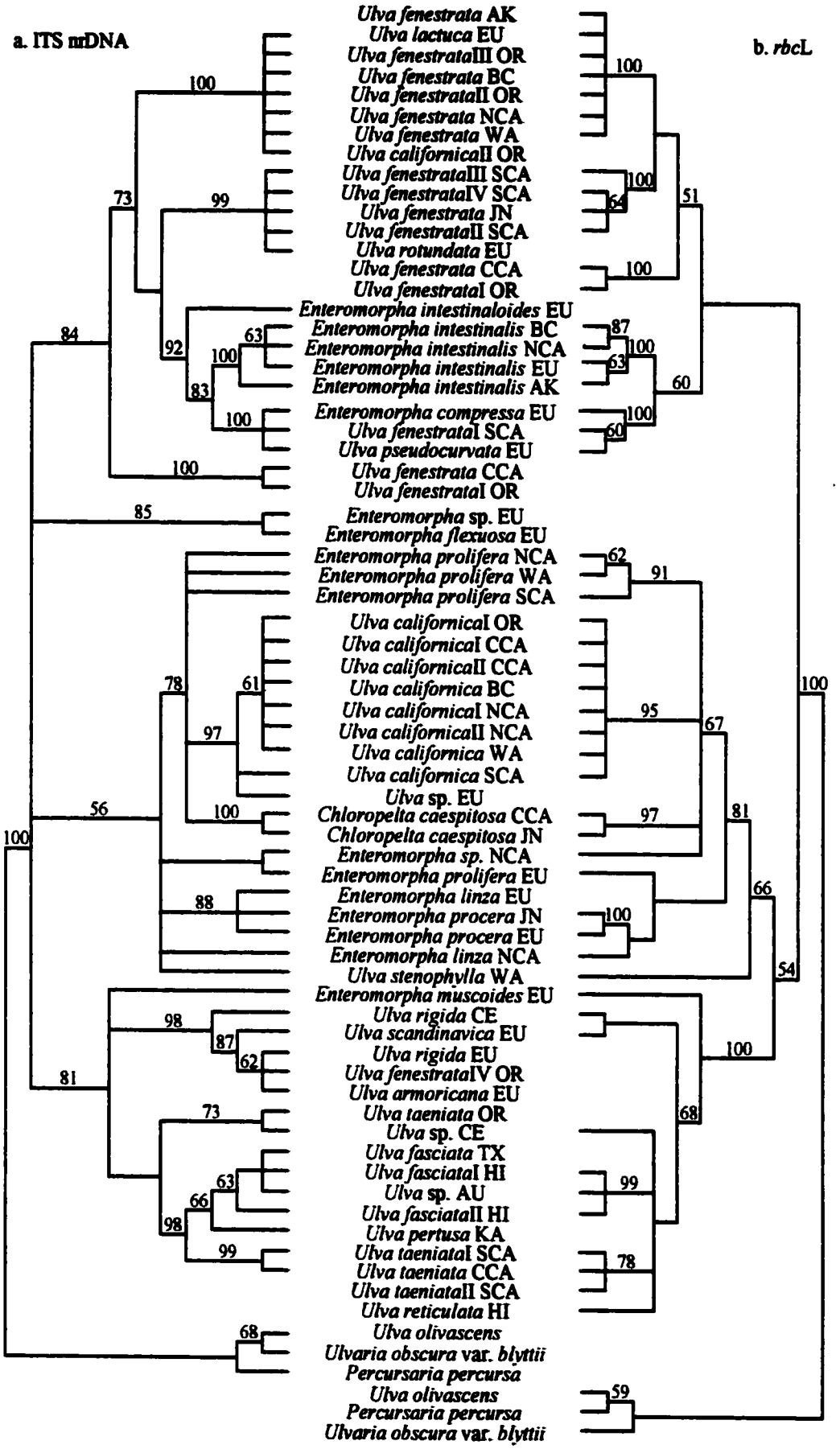
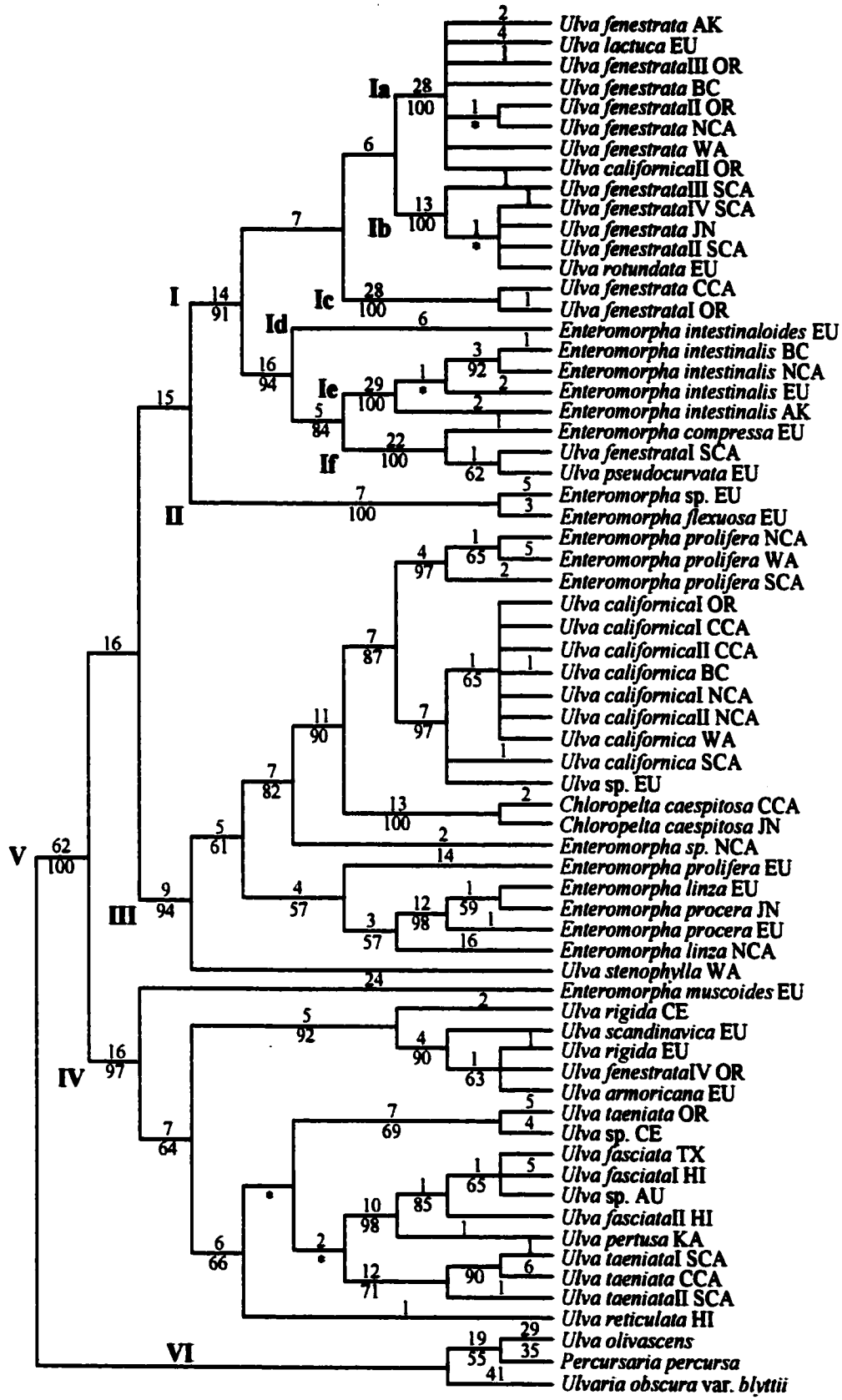

a. ITS nrDNA
b. rbcL
Ulva fenestrata AK
Ulva lactuca EU
Ulva fenestrataIII OR
Ulva fenestrata BC
Ulva fenestrataII OR
Ulva fenestrata NCA
Ulva fenestrata WA
Ulva californicaII OR
Ulva fenestrataIII SCA
Ulva fenestrataIV SCA
Ulva fenestrata JN
Ulva fenestrataII SCA
Ulva rotundata EU
Ulva fenestrata CCA
Ulva fenestrataI OR
Enteromorpha intestinaloides EU
Enteromorpha intestinalis BC
Enteromorpha intestinalis NCA
Enteromorpha intestinalis EU
Enteromorpha intestinalis AK
Enteromorpha compressa EU
Ulva fenestrataI SCA
Ulva pseudocurvata EU
Ulva fenestrata CCA
Ulva fenestrataI OR
Enteromorpha sp. EU
Enteromorpha flexuosa EU
Enteromorpha prolifera NCA
Enteromorpha prolifera WA
Enteromorpha prolifera SCA
Ulva californicaI OR
Ulva californicaI CCA
Ulva californicaII CCA
Ulva californica BC
Ulva californicaI NCA
Ulva californicaII NCA
Ulva californica WA
Ulva californica SCA
Ulva sp. EU
Chloropelta caespitosa CCA
Chloropelta caespitosa JN
Enteromorpha sp. NCA
Enteromorpha prolifera EU
Enteromorpha linza EU
Enteromorpha procera JN
Enteromorpha procera EU
Enteromorpha linza NCA
Ulva stenophylla WA
Enteromorpha muscoides EU
Ulva rigida CE
Ulva scandinavica EU
Ulva rigida EU
Ulva fenestrataIV OR
Ulva armoricana EU
Ulva taeniata OR
Ulva sp. CE
Ulva fasciata TX
Ulva fasciataI HI
Ulva sp. AU
Ulva fasciataII HI
Ulva pertusa KA
Ulva taeniataI SCA
Ulva taeniata CCA
Ulva taeniataII SCA
Ulva reticulata HI
Ulva olivascens
Ulvaria obscura var. blyttii
Percursaria percursa
Ulva olivascens
Percursaria percursa
Ulvaria obscura var. blyttii

Figure 3.3. One of 95 most parsimonious trees of 695 steps resulting from cladistic analysis of combined ITS nrDNA (478 nucleotide positions) and *rbc*L sequences. Branch lengths are indicated above branches and bootstrap percentages (> 50%) are shown below. Asterisks note branches which collapse in the strict consensus tree. Roman numerals I-VI correspond to clades in which subsets of taxa were aligned in highly variable regions of ITS 1 and ITS 2 (see Appendix E). Groups Ia – If are subgroups within Clade I which correspond to alignment groupings for positions 219 – 420. Species identification and geographical abbreviations are as in Table 3.2.


Ulva fenestrata AK
Ulva lactuca EU
Ulva fenestrataIII OR
Ulva fenestrata BC
Ulva fenestrataII OR
Ulva fenestrata NCA
Ulva fenestrata WA
Ulva californicaII OR
Ulva fenestrataIII SCA
Ulva fenestrataIV SCA
Ulva fenestrata JN
Ulva fenestrataII SCA
Ulva rotundata EU
Ulva fenestrata CCA
Ulva fenestrataI OR
Enteromorpha intestinaloides EU
Enteromorpha intestinalis BC
Enteromorpha intestinalis NCA
Enteromorpha intestinalis EU
Enteromorpha intestinalis AK
Enteromorpha compressa EU
Ulva fenestrataI SCA
Ulva pseudocurvata EU
Enteromorpha sp. EU
Enteromorpha flexuosa EU
Enteromorpha prolifera NCA
Enteromorpha prolifera WA
Enteromorpha prolifera SCA
Ulva californicaI OR
Ulva californicaI CCA
Ulva californicaII CCA
Ulva californica BC
Ulva californicaI NCA
Ulva californicaII NCA
Ulva californica WA
Ulva californica SCA
Ulva sp. EU
Chloropelta caespitosa CCA
Chloropelta caespitosa JN
Enteromorpha sp. NCA
Enteromorpha prolifera EU
Enteromorpha linza EU
Enteromorpha procera JN
Enteromorpha procera EU
Enteromorpha linza NCA
Ulva stenophylla WA
Enteromorpha muscoides EU
Ulva rigida CE
Ulva scandinavica EU
Ulva rigida EU
Ulva fenestrataIV OR
Ulva armoricana EU
Ulva taeniata OR
Ulva sp. CE
Ulva fasciata TX
Ulva fasciataI HI
Ulva sp. AU
Ulva fasciataII HI
Ulva pertusa KA
Ulva taeniataI SCA
Ulva taeniata CCA
Ulva taeniataII SCA
Ulva reticulata HI
Ulva olivascens
Percursaria percursa
Ulvaria obscura var. blyttii
Ia
Ib
Ic
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Ie
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I
II
III
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VI

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Appendix A. Sequence alignment in NEXUS format for 18S rDNA data used in Chapter 1. Nine positions were excluded from analyses, including positions 291, 292, 300, 301, 302 and 312 – 315.

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#NEXUS

BEGIN DATA;
DIMENSIONS  NTAX=24 NCHAR=764;
FORMAT DATATYPE=DNA  MISSING=? GAP=-  INTERLEAVE ;
MATRIX

[                                  10        20        30        40        50        60        70        80        90       100]
[                                   .         .         .         .         .         .         .         .         .        .]

Ulva_californica                   GGAGAGGGAGCCTGAGAAACGGCTACCACATCCAAGGAAGGCAGCAGGCGCGCAAATTACCCAATCCTGACACAGGGAGGTAGTGACAA----------  [89]
Ulva_fenestrata                    GGAGAGGGAGCCTGAGAAACGGCTACCACATCCAAGGAAGGCAGCAGGCGCGCAAATTACCCAATCCTGACACAGGGAGGTAGTGACAA----------  [89]
Ulva_lactuca                       GGAGAGG?AGCCTGAGAAACGGCTACCACATCCAAGGAAGGCAGCAGGCGCGCAAATTACCCAATCCTGACACAGGGAGGTAGTGACAA----------  [89]
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Blidingia_minima_var._minima       GGAGAGGGAGCCTGAGAAACGGCTACCACATCCAAGGAAGGCAGCAGGCGCGCAAATTACCCAATCCTGACACAGGGAGGTAGTGACAA----------  [89]
Blidingia_minima_var._vexata       GGAGAGGGAGCCTGAGAAACGGCTACCACATCCAAGGAAGGCAGCAGGCGCGCAAATTACCCAATCCTGACACAGGGAGGTAGTGACAA----------  [89]
Kornmannia_leptoderma              GGAGAGGGAGCCTGAGAAACGGCTACCACATCCAAGGAAGGCAGCAGGCGCGCAAATTACCCAATCCTGACACAGGGAGGTAGTGACAA----------  [89]
Pseudendoclonium_fucicola          GGAGAGGGAGCCTGAGAAACGGCTACCACATCCAAGGAAGGCAGCAGGCGCGTAAATTACCCAATCCTGACACAGGGAGGTAGTGACAA----------  [89]
Tellamia_contorta                  GGAGAGGGAGCCTGAGAAACGGCTACCACATCCAAGGAAGGCAGCAGGCGCGTAAATTACCCAATCCTGACACAGGGAGGTAGTGACAA----------  [89]
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Mymecia_biatorellae                GGAGAGGGAGCCTGAGAGACGGCTACCACATCCAAGGAAGGCAGCAGGCGCGCAAATTACCCAATCCTGACACAGGGAGGTAGTGACAA----------  [89]

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Ulvaria_obscura_var._blyttii       TAAATATCAATTCTGGGCCACAT--GGTCCGGTAATTGGAATGAGTACAATGTAAACGCCTTAACGAGGATCCATTGGAGGGCAAGTCTGGTGCCAGCAG  [187]
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Blidingia_minima_var._vexata       AAAATATCAATACTGGGCCTTCT--GGTCCGGTAATTGGAATGAGTACAATTTAAATCCGTTAACGAGGATCCATTGGAGGGCAAGTCTGGTGCCAGCAG  [187]
Kornmannia_leptoderma              AAAATATCAATACTGGGCCTTCT--GGTCCGGTAATTGGAATGAGTACAATTTAAATCCGTTAACGAGGATCCATTGGAGGGCAAGTCTGGTGCCAGCAG  [187]
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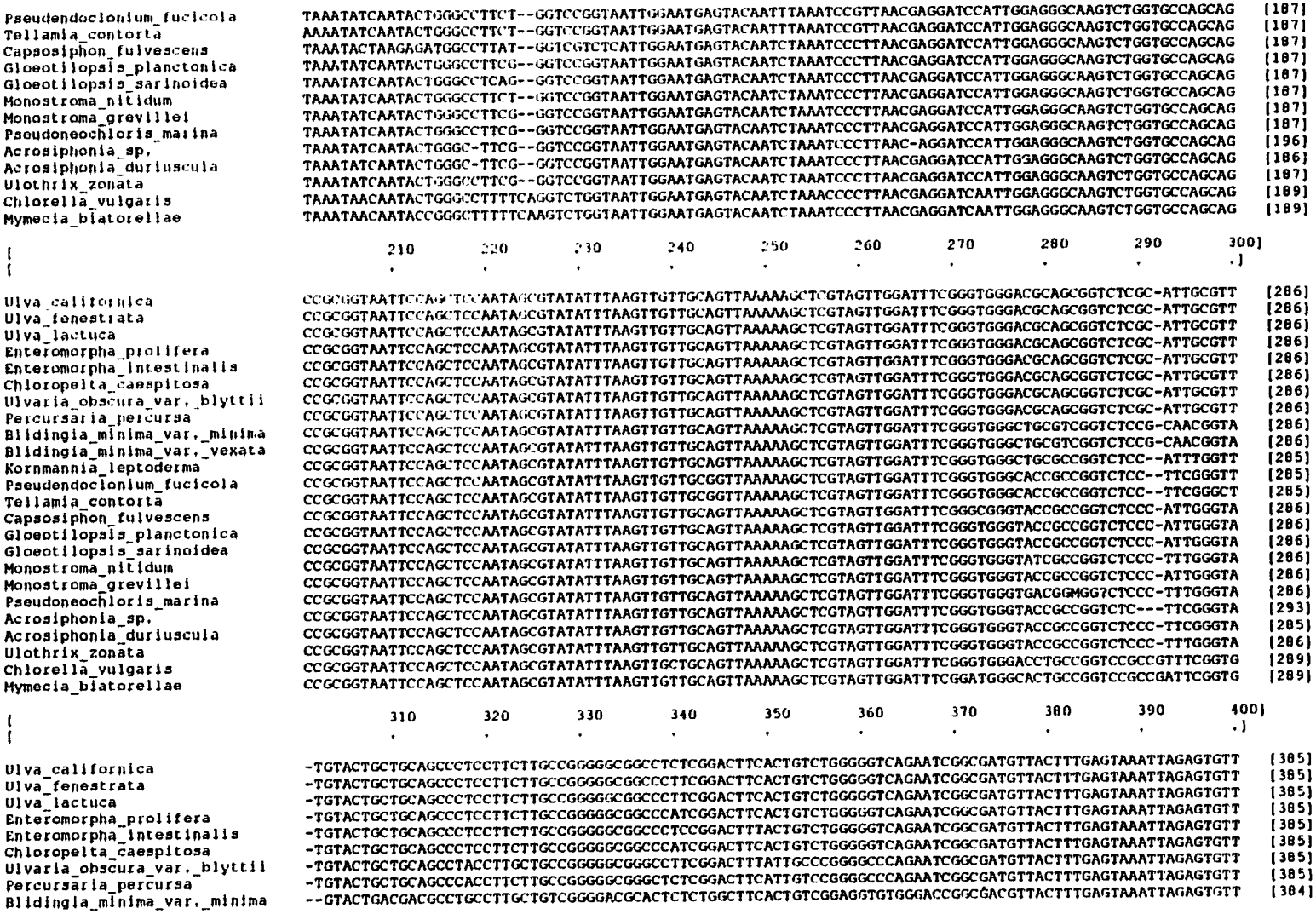
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Mymecia_biatorellae TAAATAACAATACCGGGCTTTTTCAAGTCTGGTAATTGGAATGAGTACAATCTAAATCCCTTAACGAGGATCAATTGGAGGGCAAGTCTGGTGCCAGCAG [189]
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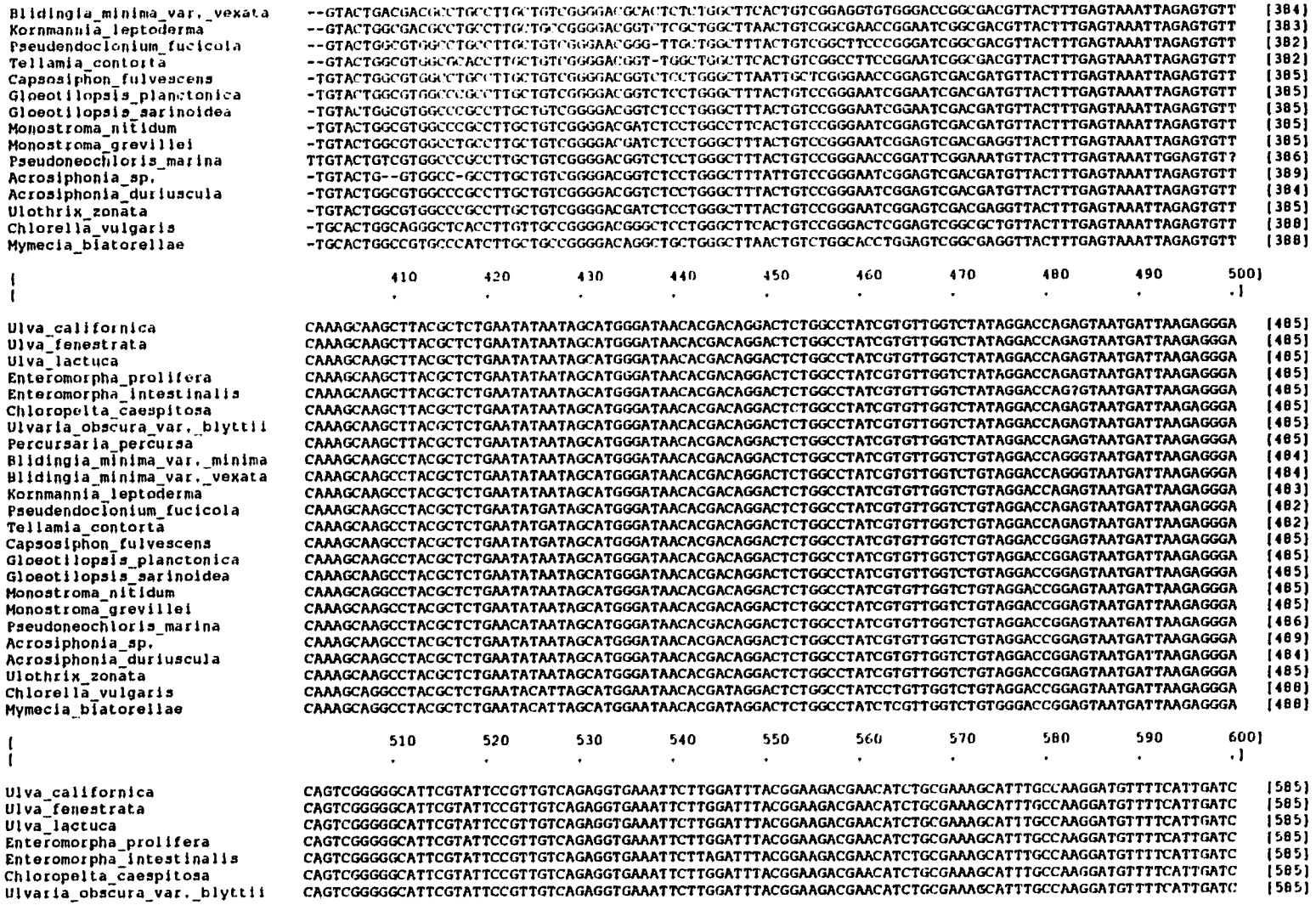
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Acrosiphonia_sp. CAAAGCAAGCCTACGCTCTGAATATAATAGCATGGGATAACACGACAGGACTCTGGCCTATCGTGTTGGTCTGTAGGACCGGAGTAATGATTAAGAGGGA [489]
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Ulothrix_zonata CAAAGCAAGCCTACGCTCTGAATATAATAGCATGGGATAACACGACAGGACTCTGGCCTATCGTGTTGGTCTGTAGGACCGGAGTAATGATTAAGAGGGA [485]
Chlorella_vulgaris CAAAGCAGGCCTACGCTCTGAATACATTAGCATGGAATAACACGATAGGACTCTGGCCTATCCTGTTGGTCTGTAGGACCGGAGTAATGATTAAGAGGGA [488]
Mymecia_biatorellae CAAAGCAGGCCTACGCTCTGAATACATTAGCATGGAATAACACGATAGGACTCTGGCCTATCTCGTTGGTCTGTGGGACCGGAGTAATGATTAAGAGGGA [488]
510 520 530 540 550 560 570 580 590 600
Ulva_californica CAGTCGGGGGCATTCGTATTCCGTTGTCAGAGGTGAAATTCTTGGATTTACGGAAGACGAACATCTGCGAAAGCATTTGCCAAGGATGTTTTCATTGATC [585]
Ulva_fenestrata CAGTCGGGGGCATTCGTATTCCGTTGTCAGAGGTGAAATTCTTGGATTTACGGAAGACGAACATCTGCGAAAGCATTTGCCAAGGATGTTTTCATTGATC [585]
Ulva_lactuca CAGTCGGGGGCATTCGTATTCCGTTGTCAGAGGTGAAATTCTTGGATTTACGGAAGACGAACATCTGCGAAAGCATTTGCCAAGGATGTTTTCATTGATC [585]
Enteromorpha_prolifera CAGTCGGGGGCATTCGTATTCCGTTGTCAGAGGTGAAATTCTTGGATTTACGGAAGACGAACATCTGCGAAAGCATTTGCCAAGGATGTTTTCATTGATC [585]
Enteromorpha_intestinalis CAGTCGGGGGCATTCGTATTCCGTTGTCAGAGGTGAAATTCTTAGATTTACGGAAGACGAACATCTGCGAAAGCATTTGCCAAGGATGTTTTCATTGATC [585]
Chloropelta_caespitosa CAGTCGGGGGCATTCGTATTCCGTTGTCAGAGGTGAAATTCTTGGATTTACGGAAGACGAACATCTGCGAAAGCATTTGCCAAGGATGTTTTCATTGATC [585]
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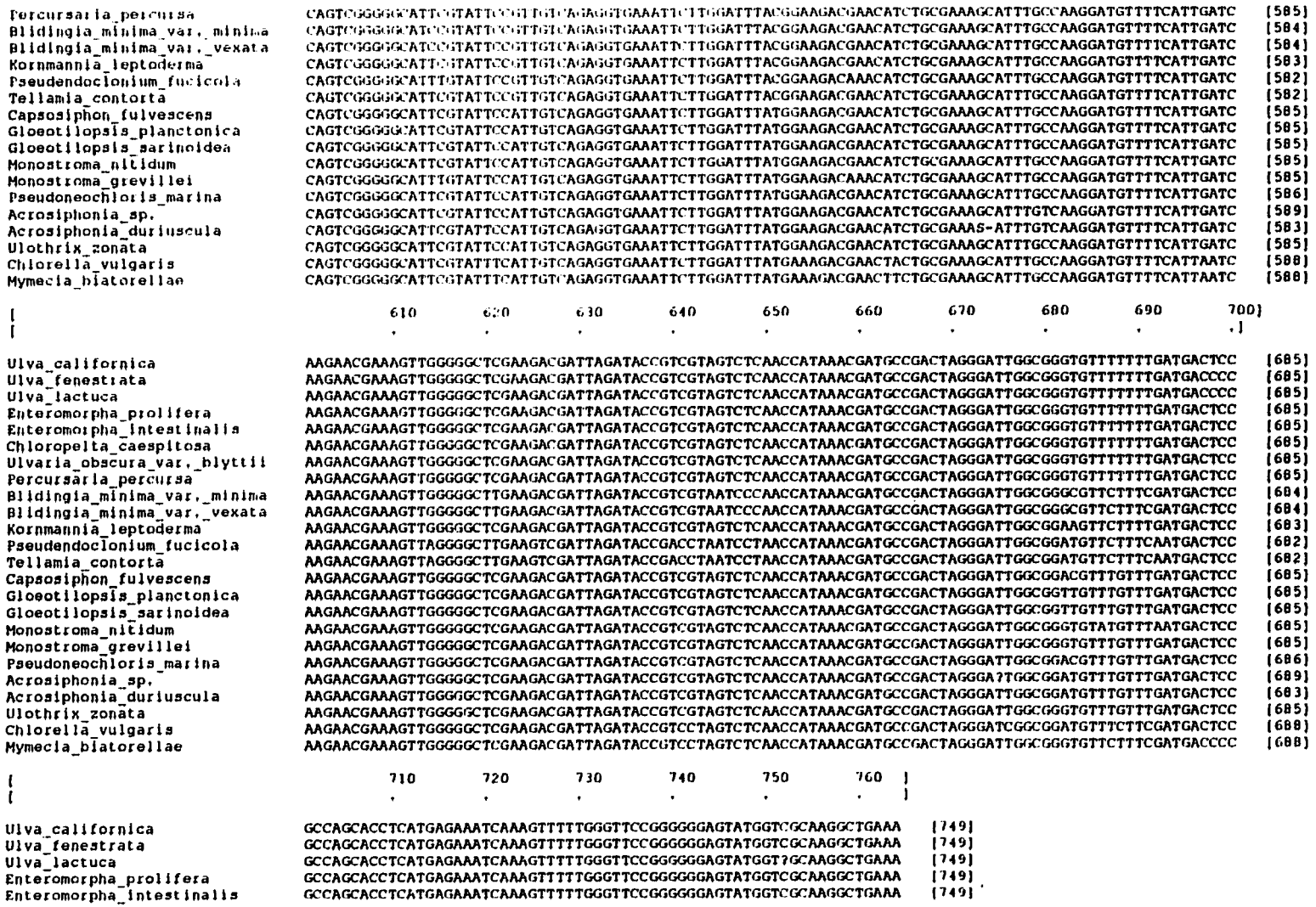
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Kornmannia_leptoderma CAGTCGGGGGCATTCGTATTCCGTTGTCAGAGGTGAAATTCTTGGATTTACGGAAGACGAACATCTGCGAAAGCATTTGCCAAGGATGTTTTCATTGATC [583]
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Tellamia_contorta CAGTCGGGGGCATTCGTATTCCGTTGTCAGAGGTGAAATTCTTGGATTTACGGAAGACGAACATCTGCGAAAGCATTTGCCAAGGATGTTTTCATTGATC [582]
Capsosiphon_fulvescens CAGTCGGGGGCATTCGTATTCCATTGTCAGAGGTGAAATTCTTGGATTTATGGAAGACGAACATCTGCGAAAGCATTTGCCAAGGATGTTTTCATTGATC [585]
Gloeotilopsis_planctonica CAGTCGGGGGCATTCGTATTCCATTGTCAGAGGTGAAATTCTTGGATTTATGGAAGACGAACATCTGCGAAAGCATTTGCCAAGGATGTTTTCATTGATC [585]
Gloeotilopsis_sarinoidea CAGTCGGGGGCATTCGTATTCCATTGTCAGAGGTGAAATTCTTGGATTTATGGAAGACGAACATCTGCGAAAGCATTTGCCAAGGATGTTTTCATTGATC [585]
Monostroma_nitidum CAGTCGGGGGCATTCGTATTCCATTGTCAGAGGTGAAATTCTTGGATTTATGGAAGACGAACATCTGCGAAAGCATTTGCCAAGGATGTTTTCATTGATC [585]
Monostroma_grevillei CAGTCGGGGGCATTTGTATTCCATTGTCAGAGGTGAAATTCTTGGATTTATGGAAGACAAACATCTGCGAAAGCATTTGCCAAGGATGTTTTCATTGATC [585]
Pseudoneochloris_marina CAGTCGGGGGCATTCGTATTCCATTGTCAGAGGTGAAATTCTTGGATTTATGGAAGACGAACATCTGCGAAAGCATTTGCCAAGGATGTTTTCATTGATC [586]
Acrosiphonia_sp. CAGTCGGGGGCATTCGTATTCCATTGTCAGAGGTGAAATTCTTGGATTTATGGAAGACGAACATCTGCGAAAGCATTTGTCAAGGATGTTTTCATTGATC [589]
Acrosiphonia_duriuscula CAGTCGGGGGCATTCGTATTCCATTGTCAGAGGTGAAATTCTTGGATTTATGGAAGACGAACATCTGCGAAAS-ATTTGTCAAGGATGTTTTCATTGATC [583]
Ulothrix_zonata CAGTCGGGGGCATTCGTATTCCATTGTCAGAGGTGAAATTCTTGGATTTATGGAAGACGAACATCTGCGAAAGCATTTGCCAAGGATGTTTTCATTGATC [585]
Chlorella_vulgaris CAGTCGGGGGCATTCGTATTTCATTGTCAGAGGTGAAATTCTTGGATTTATGAAAGACGAACTACTGCGAAAGCATTTGCCAAGGATGTTTTCATTAATC [588]
Mymecia_biatorellae CAGTCGGGGGCATTCGTATTTCATTGTCAGAGGTGAAATTCTTGGATTTATGAAAGACGAACTTCTGCGAAAGCATTTGCCAAGGATGTTTTCATTAATC [588]
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Ulva_californica AAGAACGAAAGTTGGGGGCTCGAAGACGATTAGATACCGTCGTAGTCTCAACCATAAACGATGCCGACTAGGGATTGGCGGGTGTTTTTTTGATGACTCC [685]
Ulva_fenestrata AAGAACGAAAGTTGGGGGCTCGAAGACGATTAGATACCGTCGTAGTCTCAACCATAAACGATGCCGACTAGGGATTGGCGGGTGTTTTTTTGATGACCCC [685]
Ulva_lactuca AAGAACGAAAGTTGGGGGCTCGAAGACGATTAGATACCGTCGTAGTCTCAACCATAAACGATGCCGACTAGGGATTGGCGGGTGTTTTTTTGATGACCCC [685]
Enteromorpha_prolifera AAGAACGAAAGTTGGGGGCTCGAAGACGATTAGATACCGTCGTAGTCTCAACCATAAACGATGCCGACTAGGGATTGGCGGGTGTTTTTTTGATGACTCC [685]
Enteromorpha_intestinalis AAGAACGAAAGTTGGGGGCTCGAAGACGATTAGATACCGTCGTAGTCTCAACCATAAACGATGCCGACTAGGGATTGGCGGGTGTTTTTTTGATGACTCC [685]
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Ulvaria_obscura_var._blyttii AAGAACGAAAGTTGGGGGCTCGAAGACGATTAGATACCGTCGTAGTCTCAACCATAAACGATGCCGACTAGGGATTGGCGGGTGTTTTTTTGATGACTCC [685]
Percursaria_percursa AAGAACGAAAGTTGGGGGCTCGAAGACGATTAGATACCGTCGTAGTCTCAACCATAAACGATGCCGACTAGGGATTGGCGGGTGTTTTTTTGATGACTCC [685]
Blidingia_minima_var._minima AAGAACGAAAGTTGGGGGCTTGAAGACGATTAGATACCGTCGTAATCCCAACCATAAACGATGCCGACTAGGGATTGGCGGGCGTTCTTTCGATGACTCC [684]
Blidingia_minima_var._vexata AAGAACGAAAGTTGGGGGCTTGAAGACGATTAGATACCGTCGTAATCCCAACCATAAACGATGCCGACTAGGGATTGGCGGGCGTTCTTTCGATGACTCC [684]
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Pseudendoclonium_fucicola AAGAACGAAAGTTAGGGGCTTGAAGTCGATTAGATACCGACCTAATCCTAACCATAAACGATGCCGACTAGGGATTGGCGGATGTTCTTTCAATGACTCC [682]
Tellamia_contorta AAGAACGAAAGTTAGGGGCTTGAAGTCGATTAGATACCGACCTAATCCTAACCATAAACGATGCCGACTAGGGATTGGCGGATGTTCTTTCAATGACTCC [682]
Capsosiphon_fulvescens AAGAACGAAAGTTGGGGGCTCGAAGACGATTAGATACCGTCGTAGTCTCAACCATAAACGATGCCGACTAGGGATTGGCGGACGTTTGTTTGATGACTCC [685]
Gloeotilopsis_planctonica AAGAACGAAAGTTGGGGGCTCGAAGACGATTAGATACCGTCGTAGTCTCAACCATAAACGATGCCGACTAGGGATTGGCGGTTGTTTGTTTGATGACTCC [685]
Gloeotilopsis_sarinoidea AAGAACGAAAGTTGGGGGCTCGAAGACGATTAGATACCGTCGTAGTCTCAACCATAAACGATGCCGACTAGGGATTGGCGGTTGTTTGTTTGATGACTCC [685]
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Monostroma_grevillei AAGAACGAAAGTTGGGGGCTCGAAGACGATTAGATACCGTCGTAGTCTCAACCATAAACGATGCCGACTAGGGATTGGCGGGTGTTTGTTTGATGACTCC [685]
Pseudoneochloris_marina AAGAACGAAAGTTGGGGGCTCGAAGACGATTAGATACCGTCGTAGTCTCAACCATAAACGATGCCGACTAGGGATTGGCGGACGTTTGTTTGATGACTCC [686]
Acrosiphonia_sp. AAGAACGAAAGTTGGGGGCTCGAAGACGATTAGATACCGTCGTAGTCTCAACCATAAACGATGCCGACTAGGGA?TGGCGGATGTTTGTTTGATGACTCC [689]
Acrosiphonia_duriuscula AAGAACGAAAGTTGGGGGCTCGAAGACGATTAGATACCGTCGTAGTCTCAACCATAAACGATGCCGACTAGGGATTGGCGGATGTTTGTTTGATGACTCC [683]
Ulothrix_zonata AAGAACGAAAGTTGGGGGCTCGAAGACGATTAGATACCGTCGTAGTCTCAACCATAAACGATGCCGACTAGGGATTGGCGGGTGTTTGTTTGATGACTCC [685]
Chlorella_vulgaris AAGAACGAAAGTTGGGGGCTCGAAGACGATTAGATACCGTCCTAGTCTCAACCATAAACGATGCCGACTAGGGATCGGCGGATGTTTCTTCGATGACTCC [688]
Mymecia_biatorellae AAGAACGAAAGTTGGGGGCTCGAAGACGATTAGATACCGTCCTAGTCTCAACCATAAACGATGCCGACTAGGGATTGGCGGGTGTTCTTTCGATGACCCC [688]
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Ulva_californica GCCAGCACCTCATGAGAAATCAAAGTTTTTGGGTTCCGGGGGGAGTATGGTCGCAAGGCTGAAA [749]
Ulva_fenestrata GCCAGCACCTCATGAGAAATCAAAGTTTTTGGGTTCCGGGGGGAGTATGGTCGCAAGGCTGAAA [749]
Ulva_lactuca GCCAGCACCTCATGAGAAATCAAAGTTTTTGGGTTCCGGGGGGAGTATGGT?GCAAGGCTGAAA [749]
Enteromorpha_prolifera GCCAGCACCTCATGAGAAATCAAAGTTTTTGGGTTCCGGGGGGAGTATGGTCGCAAGGCTGAAA [749]
Enteromorpha_intestinalis GCCAGCACCTCATGAGAAATCAAAGTTTTTGGGTTCCGGGGGGAGTATGGTCGCAAGGCTGAAA [749]

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Ulvaria_obscura_var._blyttii    GCCAGCACCTCATGAGAAATCAAAGTTTTTGGGTTCCGGGGGGAGTATGGTCGCAAGGCTGAAA   [749]
Percursaria_percursa            GCCAGCACCTCATGAGAAATCAAAGTTTTTGGGTTCCGGGGGGAGTATGGTCGCAAGGCTGAAA   [749]
Blidingia_minima_var._minima    GCCAGCACCTCATGAGAAATCAAAGTTTTTGGGTTCCGGGGGGAGTATGGTCGCAAGGCTGAAA   [748]
Blidingia_minima_var._vexata    GCCAGCACCTCATGAGAAATCAAAGTTTTTGGGTTCCGGGGGGAGTATGGTCGCAAGGCTGAAA   [748]
Kornmannia_leptoderma           GCCAGCACCTCATGAGAAATCAAAGTTTTTGGGTTCCGGGGGGAGTATGGTCGCAAGGCTGAAA   [747]
Pseudendoclonium_fucicola       GCCAGCACCTCATGAGAAATCAAAGTTTTTGGGTTCCGGGGGGAGTATGGTCGCAAGGCTGAAA   [746]
Tellamia_contorta               GCCAGCACCTCATGAGAAATCAAAGTTTTTGGGTTCCGGGGGGAGTATGGTCGCAAGGCTGAAA   [746]
Capsosiphon_fulvescens          GCCAGCACCTCATGAGAAATCAAAGTTTTTGGGTTCCGGGGGGAGTATGGTCGCAAGGCTGAAA   [749]
Gloeotilopsis_planctonica       GCCAGCACCTTATGAGAAATCAAAGTTTTTGGGTTCCGGGGGGAGTATGGTCGCAAGGCTGAAA   [749]
Gloeotilopsis_sarinoidea        GCCAGCACCTTATGAGAAATCAAAGTTTTTGGGTTCCGGGGGGAGTATGGTCGCAAGGCTGAAA   [749]
Monostroma_nitidum              GCCAGCACCTTATGAGAAATCAAAGTTTTTGGGTTCCGGGGGGAGTATGGTCGCAAGGCTGAAA   [749]
Monostroma_grevillei            GCCAGCACCTTATGAGAAATCAAAGTTTTTGGGTTCCGGGGGGAGTATGGTCGCAAGGCTGAAA   [749]
Pseudoneochloris_marina         GCCAGCACCTTATGAGAAATCAAAGTTTTTGGGTTCCGGGGG-AGTATGGTCGCAAGGCTGAAA   [749]
Acrosiphonia_sp.                GCCAGCACCTTATGAGAAATCAAAGTTTTTGGGTTCCGGGGGGAGTATGGTCGCAAGGCTGAAA   [753]
Acrosiphonia_duriuscula         GCCAGCACCTTATGAGAAATCAAAGTTTTTGGGTTCCGGGGGGAGTATGGTCGCAAGGCTGAAA   [747]
Ulothrix_zonata                 GCCAGCACCTTATGAGAAATCAAAGTTTTTGGGTTCCGGGGGGAGTATGGTCGCAAGGCTGAAA   [749]
Chlorella_vulgaris              GCCGGCACCTTATGAGAAATCAAAGTTTTTGGGTTCCGGGGGGAGTATGGTCGCAAGGCTGAAA   [752]
Myrmecia_biatorellae            GCCAGCACCTTATGAGAAATCAAAGTTTTTGGGTTCCGGGGGGAGTATGGTCGCAAGGCTGAAA   [752]
;
END;


BEGIN CODONS;
CODESET * UNTITLED = Universal: all ;
END;

BEGIN ASSUMPTIONS;
        OPTIONS  DEFTYPE=unord PolyTcount=MINSTEPS ;
END;
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Appendix B. Sequence alignment in NEXUS format for *rbc*L data used in Chapter 1.

```
#NEXUS

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FORMAT DATATYPE=DNA  MISSING=? GAP=-  INTERLEAVE ;
MATRIX

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[                                .         .         .         .         .         .         .         .         .        .]

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Ulva_fenestrata                  AGGTACTGGCTTTAAAGCTGGTGTAAAAGATTACCGTTTAACTTATTACACGCCTGATTATCAAGTAAAAGATACTGATATTTTAGCAGCGTTTCGTATG   [100]
Ulva_lactuca                     AGGTACTGGCTTTAAAGCTGGTGTAAAAGATTACCGTTTAACTTATTACACGCCTGATTATCAAGTAAAAGATACTGATATTTTAGCAGCGTTTCGTATG   [100]
Enteromorpha_prolifera           AGGTACTGGCTTTAAAGCTGGTGTAAAAGATTACCGTTTAACTTATTACACGCCTGATTATCAAGTAAAAGATACTGATATTTTAGCAGCGTTCCGTATG   [100]
Enteromorpha_intestinalis        AGGTACTGGCTTTAAAGCTGGTGTAAAAGATTACCGTTTAACTTATTACACGCCTGATTATCAAGTAAAAGATACTGATATTTTAGCAGCGTTTCGTATG   [100]
Chloropelta_caespitosa           AGGTACTGGCTTTAAAGCTGGTGTAAAAGATTACCGTTTAACTTATTACACGCCTGATTATCAAGTAAAAGATACTGATATTTTAGCAGCGTTCCGTATG   [100]
Ulvaria_obscura_var._blyttii     AGGTACTGGCTTTAAAGCTGGTGTAAAAGATTACCGTTTAACTTATTACACACCTGATTATCAAGTAAAAGATACTGATATTTTAGCAGCATTCCGTATG   [100]
Percursaria_percursa             AGGTACTGGCTTTACAGCTGGTGTAAAAGACTACCGTTTAACTTATTACACACCTGATTATCAAGTAAAAGATACTGATATTTTAGCAGCATTTCGTATG   [100]
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Blidingia_minima_var._vexata     GGGAACGGGTTTTAAGGCTGGTGTTAAAGACTATCGTTTAACTTATTATACACCAGATTATCAAGTAAAAGATACGGATATTTTAGCGGCATTCCGTATG   [100]
Kornmannia_leptoderma            TGGAACGGGTTTTAAAGCGGGTGTTAAAGATTATCGTTTAACATACTATACGCCAGACTATCAAGTAAAAGATACTGATATTCTTGCGGCATTCCGTATG   [100]
Pseudendoclonium_fucicola        GGGAACAGGCTTTAAGGCTGGTGTAAAAGACTACCGATTAACGTACTACACACCTGACTATCAAGTAAAAGATACAGATATTTTAGCGGCGTTCCGTATG   [100]
Tellamia_contorta                AGGAACAGGCTTTAAGGCTGGTGTAAAAGATTACCGTTTAACGTACTACACACCTGACTATCAAGTTAAAGATACAGATATCTTAGCAGCATTCCGTATG   [100]
Monostrom_nitidum                AGGAACAGGCTTTAAAGCTGGTGTAAAAGATTACCGTTTAACTTATTA?ACACC?GATTATCAAGTTAAAGATACAGATATTCTTGCTGCATTCCGTATG   [100]
Gloeotilopsis_planctonica        AGGAACAGGCTTTAAAGCTGGTGTAAAAGATTATCGTTTAACGTATTACACTCCTGATTATCAAGTAAAAGACACGGATATTCTTGCAGCCTTCCGTATG   [100]
Pseudoneochloris_marina          AGGAACTGGCTTTAAAGCTGGTGTAAAAGACTACCGTCTAACTTATTATACACCTGATTACCAAGTAAAAGATACTGATATTTTAGCAGCATTCCGTATG   [100]
Ulothrix_zonata                  AGGAACAGGCTTTAAAGCTGGTGTAAAAGACTACCGCTTAACTTACTACACACCTGACTACCAAGTAAAAGATACAGATATTCTTGCAGCTTTCCGTATG   [100]
Chlorella_vulgaris               AGGTGCTGGGTTTAAAGCAGGTGTTAAAGACTACCGTTTAACTTACTATACTCCTGATTACCAACCAAAAGACACTGATATTCTTGCAGCGTTCCGTATG   [100]
Mymecia_biatorellae              AAGTGCTGGCTTTAAAGCAGGTGTAAAAGATTATCGTTTAACATACTACACTCCAGACTATCAAGTTAAAGAAACTGATATTCTTGCAGCTTTCCGTATG   [100]

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Ulva_fenestrata                  ACTCCTCAACCAGGAGTACCAGCAGAAGAAGCAGGTGCAGCTGTTGCTGCTGAATCATCAACAGGTACTTGGACAACTGTATGGACTGATGGTTTAACAT   [200]
Ulva_lactuca                     ACTCCTCAACCAGGAGTACCAGCAGAAGAAGCAGGTGCAGCTGTTGCTGCTGAATCATCAACAGGTACTTGGACAACTGTATGGACTGATGGTTTAACAT   [200]
Enteromorpha_prolifera           ACTCCTCAACCAGGAGTACCAGCAGAAGAAGCAGGTGCAGCTGTTGCTGCTGAATCATCAACAGGTACTTGGACAACTGTATGGACTGATGGTTTAACAT   [200]
Enteromorpha_intestinalis        ACTCCTCAACCAGGAGTACCAGCAGAAGAAGCAGGTGCAGCTGTTGCTGCTGAATCATCAACAGGTACTTGGACAACTGTATGGACTGATGGTTTAACAT   [200]
Chloropelta_caespitosa           ACTCCTCAACCAGGAGTACCAGCAGAAGAAGCAGGTGCAGCTGTTGCTGCTGAATCATCAACAGGTACTTGGACAACTGTATGGACTGATGGTTTAACAT   [200]
Ulvaria_obscura_var._blyttii     ACTCCTCAACCAGGAGTACCAGCAGAAGAAGCTGGTGCAGCTGTTGCTGCTGAATCATCAACAGGTACTTGGACAACTGTATGGACTGATGGTTTAACAT   [200]
Percursaria_percursa             ACTCCTCAACCAGGAGTACCAGCAGAAGAAGCAGGTGCAGCTGTTGCTGCTGAATCATCAACAGGTACTTGGACAACTGTATGGACTGATGGTTTAACAT   [200]
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Blidingia_minima_var._vexata     ACTCCACAACCTGGAGTACCTGCTGAAGAAGCAGGAGCAGCTGTAGCAGCCGAATCATCAACAGGAACTTGGACAACGGTTTGGACAGATGGTTTAACTT   [200]
Kornmannia_leptoderma            ACACCACAACCAGGTGTTCCTTCAGAGGAAGCAGGTGCAGCAGTAGCAGCTGAATCATCAACAGGTACATGGACTACTGTATGGACTGATGGATTAACAA   [200]
Pseudendoclonium_fucicola        ACACCACAACCTGGTGTACCAGCTGAAGAAGCAGGTGCAGCAGTAGCGGCTGAATCATCAACAGGTACTTGGACAACTGTATGGACTGATGGATTAACAT   [200]
Tellamia_contorta                ACACCACAACCAGGTGTACCACCAGAAGAGGCAGGAGCTGCGGTAGCGGCTGAGTCATCAACTGGGACTTGGACAACTGTATGGACTGATGGATTAACAT   [200]
Monostrom_nitidum                ACTCC?CAACC?GGCGTACCGGTTGAAGAAGCTGGTGCAGCTGT?GCTGCAGAATCATCAACAGGAAC?TGG?CAACTGTATGGACAGATGGTTTAACTT   [200]
Gloeotilopsis_planctonica        ACTCCTCAACCAGGAGTACCTGTAGAAGAAGCTGGAGCTGCCGTTGCAGCAGAATCAAGTACAGGAACGTGGACAACTGTATGGACAGATGGTTTAACAT   [200]
Pseudoneochloris_marina          ACACCTCAACCAGGTGTACCAGCTGAAGAAGCAGGTGCAGCAGTTGCAGCTGAATCATCTACAGGTACTTGGACAACTGTATGGACTGATGGTTTAACTT   [200]
Ulothrix_zonata                  ACTCCTCAACCAGGAGTACCCGTTGAAGAAGCTGGAGCAGCGGTTGCTGCA?AATCAAGTACTGGAACGTGGACTACTGTATGGACTGATGGTTTAACTT   [200]
Chlorella_vulgaris               ACTCCTCAACCAGGTGTTCCACCAGAAGAAGCGGGTGCGGCAGTAGCAGCAGAATCATCAACTGGTACTTGGACGACTGTATGGACTGATGGTTTAACTA   [200]
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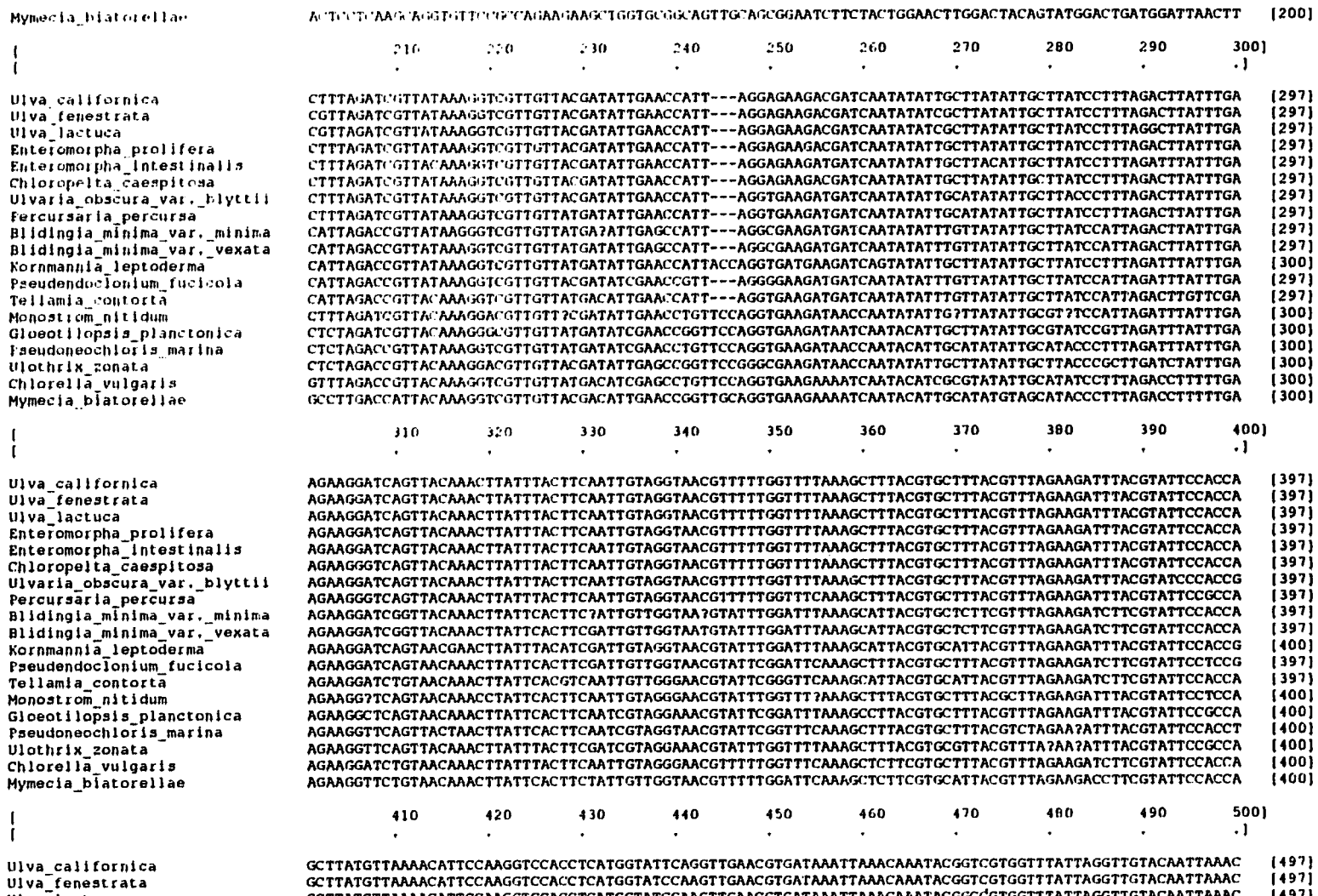
Mymecia_biatorellae
[200]
[210 220 230 240 250 260 270 280 290 300]
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Ulva_californica CTTTAGATCGTTATAAAGGTCGTTGTTACGATATTGAACCATT---AGGAGAAGACGATCAATATATTGCTTATATTGCTTATCCTTTAGACTTATTTGA [297]
Ulva_fenestrata CGTTAGATCGTTATAAAGGTCGTTGTTACGATATTGAACCATT---AGGAGAAGACGATCAATATATCGCTTATATTGCTTATCCTTTAGACTTATTTGA [297]
Ulva_lactuca CGTTAGATCGTTATAAAGGTCGTTGTTACGATATTGAACCATT---AGGAGAAGACGATCAATATATCGCTTATATTGCTTATCCTTTAGGCTTATTTGA [297]
Enteromorpha_prolifera CTTTAGATCGTTATAAAGGTCGTTGTTACGATATTGAACCATT---AGGAGAAGACGATCAATATATTGCTTATATTGCTTATCCTTTAGACTTATTTGA [297]
Enteromorpha_intestinalis CTTTAGATCGTTACAAAGGTCGTTGTTACGATATTGAACCATT---AGGAGAAGATGATCAATATATTGCTTACATTGCTTATCCTTTAGATTTATTTGA [297]
Chloropelta_caespitosa CTTTAGATCGTTATAAAGGTCGTTGTTACGATATTGAACCATT---AGGAGAAGACGATCAATATATTGCTTATATTGCTTATCCTTTAGACTTATTTGA [297]
Ulvaria_obscura_var._blyttii CTTTAGATCGTTATAAAGGTCGTTGTTACGATATTGAACCATT---AGGTGAAGATGATCAATATATTGCATATATTGCTTACCCTTTAGACTTATTTGA [297]
Percursaria_percursa CTTTAGATCGTTATAAAGGTCGTTGTTATGATATTGAACCATT---AGGTGAAGATGATCAATATATTGCATATATTGCTTATCCTTTAGACTTATTTGA [297]
Blidingia_minima_var._minima CATTAGACCGTTATAAGGGTCGTTGTTATGA?ATTGAGCCATT---AGGCGAAGATGATCAATATATTTGTTATATTGCTTATCCATTAGACTTATTTGA [297]
Blidingia_minima_var._vexata CATTAGACCGTTATAAAGGTCGTTGTTATGATATTGAGCCATT---AGGCGAAGATGATCAATATATTTGTTATATTGCTTATCCATTAGACTTATTTGA [297]
Kornmannia_leptoderma CATTAGACCGTTATAAAGGTCGTTGTTATGATATTGAACCATTACCAGGTGATGAAGATCAGTATATTGCTTATATTGCTTATCCTTTAGATTTATTTGA [300]
Pseudendoclonium_fucicola CATTAGACCGTTATAAAGGTCGTTGTTACGATATCGAACCGTT---AGGGGAAGATGATCAATATATTTGTTATATTGCTTATCCATTAGATTTATTTGA [297]
Tellamia_contorta CATTAGACCGTTACAAAGGTCGTTGTTATGACATTGAACCATT---AGGTGAAGATGATCAATATATTTGTTATATTGCTTATCCATTAGACTTGTTCGA [297]
Monostrom_nitidum CTTTAGATCGTTACAAAGGACGTTGTT?CGATATTGAACCTGTTCCAGGTGAAGATAACCAATATATTG?TTATATTGCGT?TCCATTAGATTTATTTGA [300]
Gloeotilopsis_planctonica CTCTAGATCGTTACAAAGGGCGTTGTTATGATATCGAACCGGTTCCAGGTGAAGATAATCAATACATTGCTTATATTGCGTATCCGTTAGATTTATTTGA [300]
Pseudoneochloris_marina CTCTAGACCGTTATAAAGGTCGTTGTTATGATATCGAACCTGTTCCAGGTGAAGATAACCAATACATTGCATATATTGCATACCCTTTAGATTTATTTGA [300]
Ulothrix_zonata CTCTAGACCGTTACAAAGGACGTTGTTACGATATTGAGCCGGTTCCGGGCGAAGATAACCAATATATTGCTTATATTGCTTACCCGCTTGATCTATTTGA [300]
Chlorella_vulgaris GTTTAGACCGTTACAAAGGTCGTTGTTATGACATCGAGCCTGTTCCAGGTGAAGAAAATCAATACATCGCGTATATTGCATATCCTTTAGACCTTTTGA [300]
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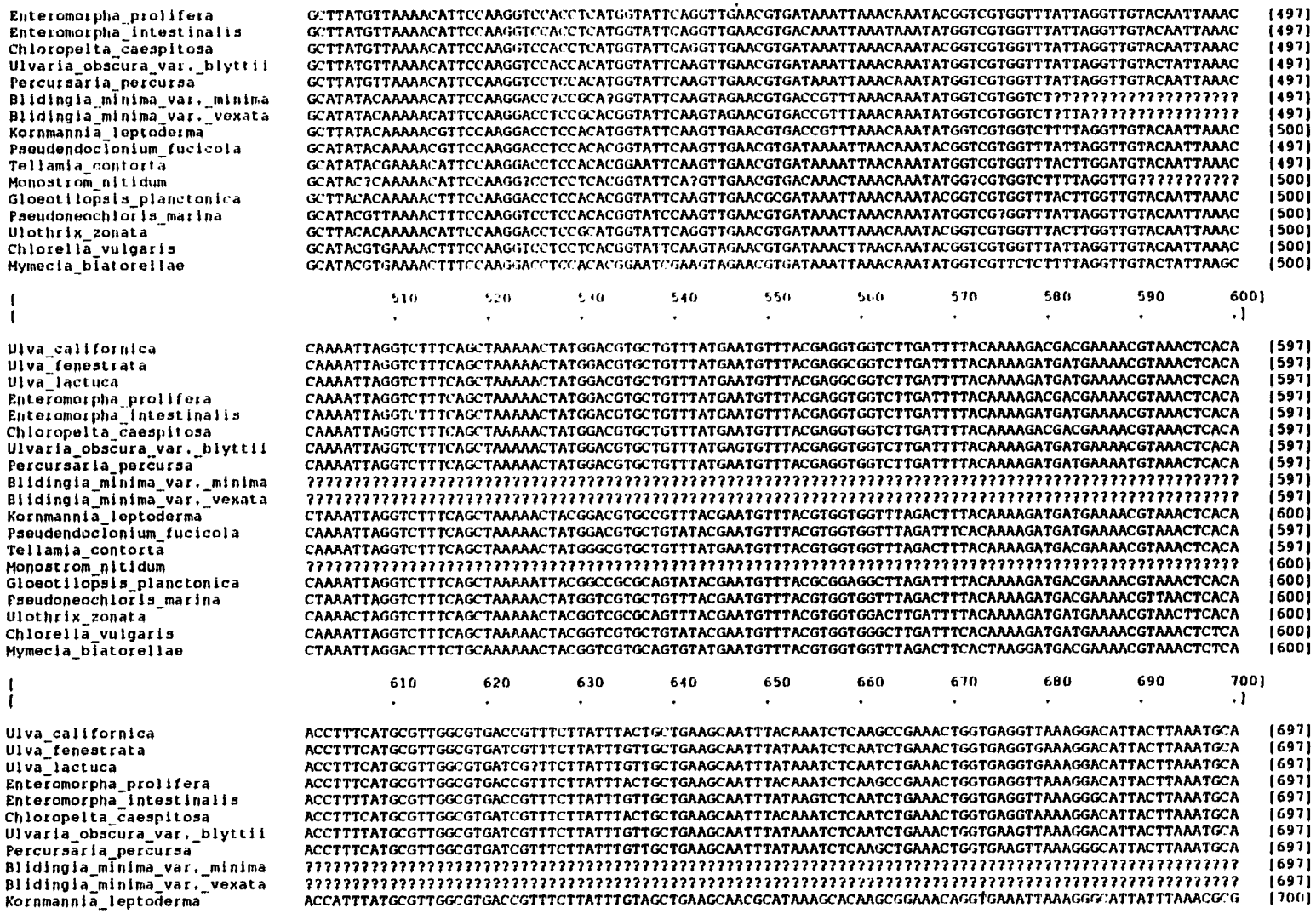
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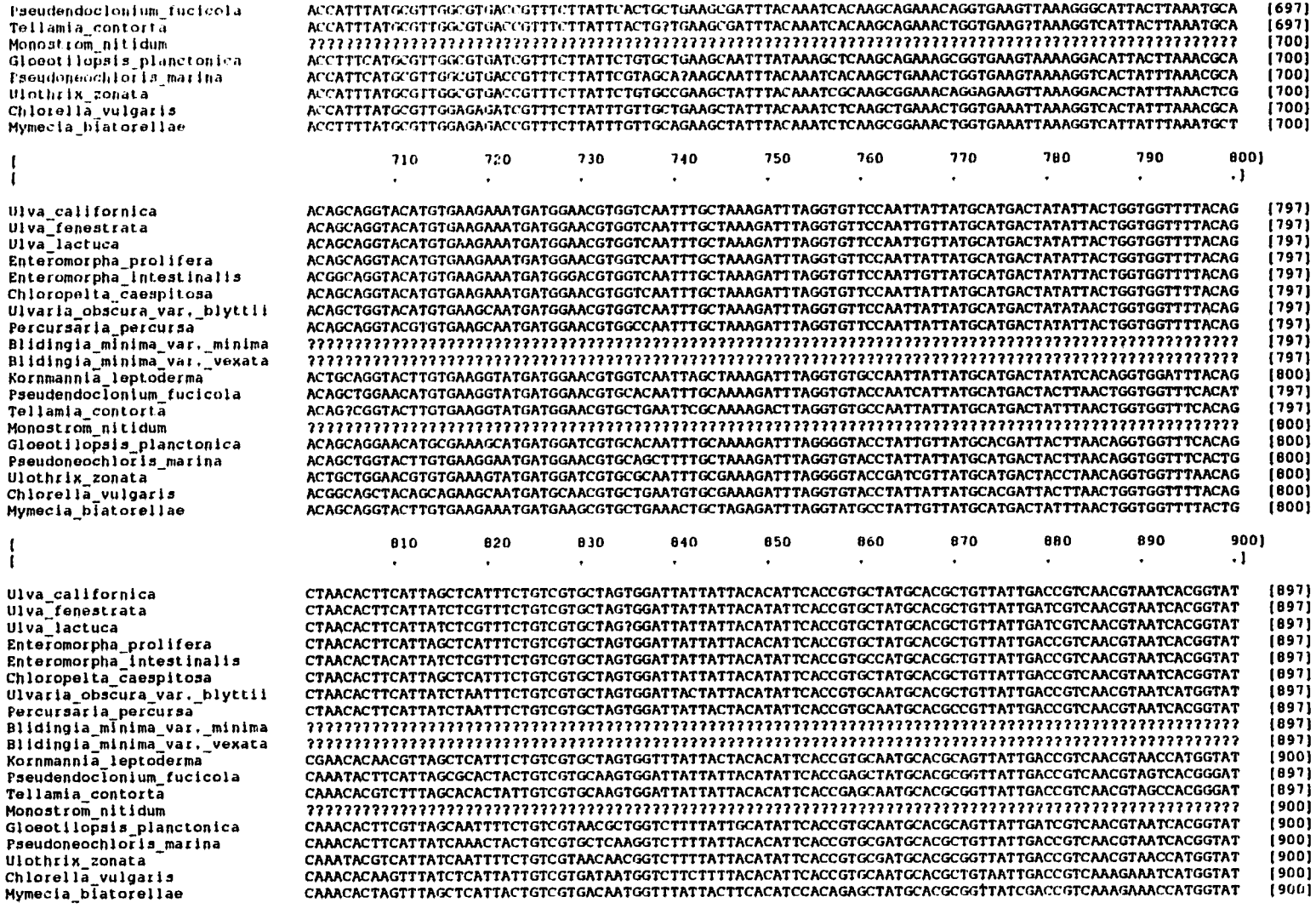
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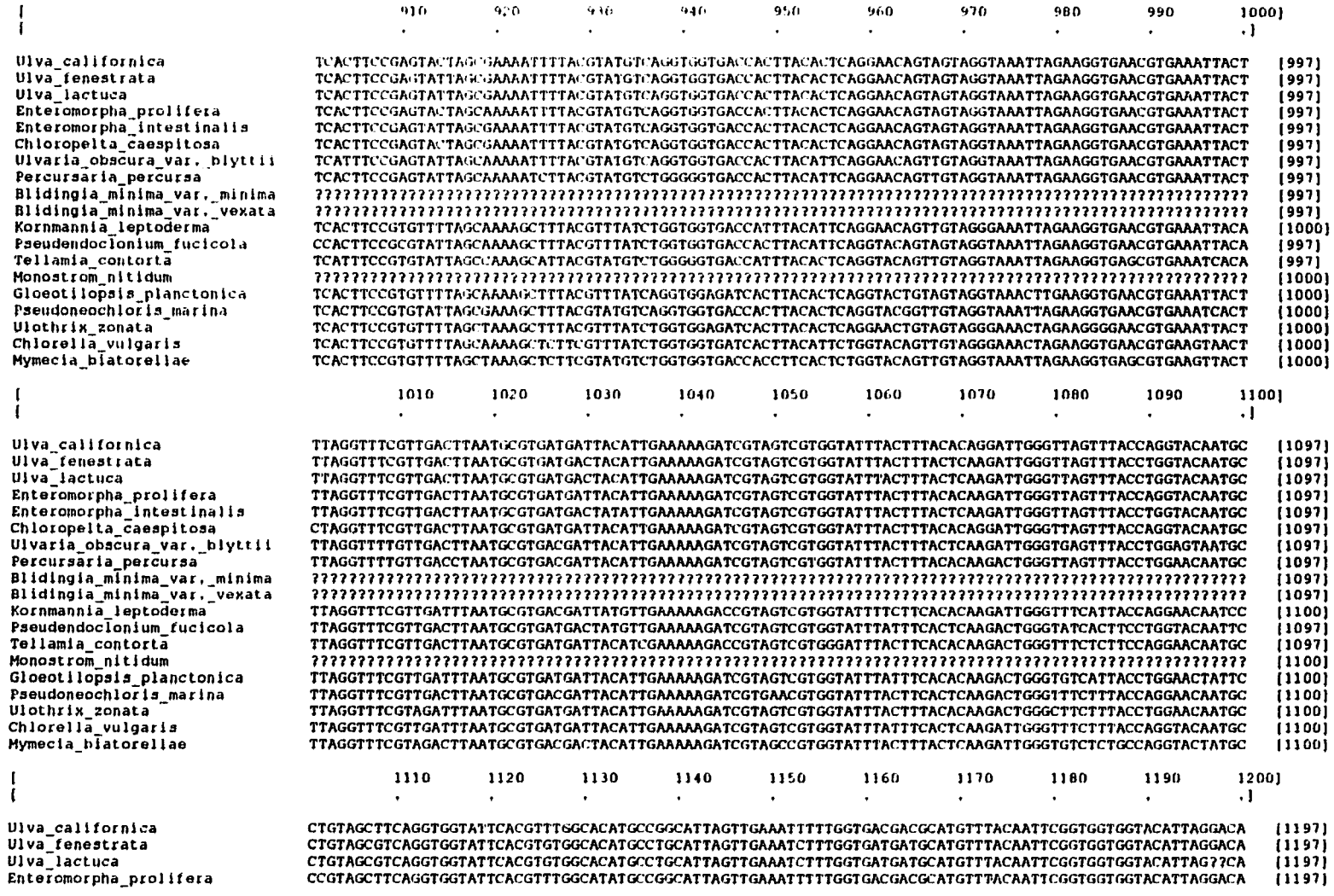
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Ulvaria_obscura_var._blyttii TTAGGTTTTGTTGACTTAATGCGTGACGATTACATTGAAAAAGATCGTAGTCGTGGTATTTACTTTACTCAAGATTGGGTGAGTTTACCTGGAGTAATGC [1097]
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Blidingia_minima_var._vexata ?? [1097]
Kornmannia_leptoderma TTAGGTTTCGTTGATTTAATGCGTGACGATTATGTTGAAAAAGACCGTAGTCGTGGTATTTTCTTCACACAAGATTGGGTTTCATTACCAGGAACAATCC [1100]
Pseudendoclonium_fucicola TTAGGTTTCGTTGACTTAATGCGTGATGACTATGTTGAAAAAGATCGTAGTCGTGGTATTTATTTCACTCAAGACTGGGTATCACTTCCTGGTACAATTC [1097]
Tellamia_contorta TTAGGTTTCGTTGACTTAATGCGTGATGATTACATCGAAAAAGACCGTAGTCGTGGGATTTACTTCACACAAGACTGGGTTTCTCTTCCAGGAACAATGC [1097]
Monostrom_nitidum ?? [1100]
Gloeotilopsis_planctonica TTAGGTTTCGTTGATTTAATGCGTGATGATTACATTGAAAAAGATCGTAGTCGTGGTATTTATTTCACACAAGACTGGGTGTCATTACCTGGAACTATTC [1100]
Pseudoneochloris_marina TTAGGTTTCGTTGACTTAATGCGTGACGATTACATTGAAAAAGATCGTGAACGTGGTATTTACTTCACTCAAGACTGGGTTTCTTTACCAGGAACAATGC [1100]
Ulothrix_zonata TTAGGTTTCGTAGATTTAATGCGTGATGATTACATTGAAAAAGATCGTAGTCGTGGTATTTACTTTACACAAGACTGGGCTTCTTTACCTGGAACAATGC [1100]
Chlorella_vulgaris TTAGGTTTCGTTGATTTAATGCGTGATGATTACATTGAAAAAGATCGTAGTCGTGGTATTTATTTCACTCAAGATTGGGTTCTTTACCAGGTACAATGC [1100]
Mymecia_biatorellae TTAGGTTTCGTAGACTTAATGCGTGACGACTACATTGAAAAAGATCGTAGCCGTGGTATTTACTTTACTCAAGATTGGGTGTCTCTGCCAGGTACTATGC [1100]
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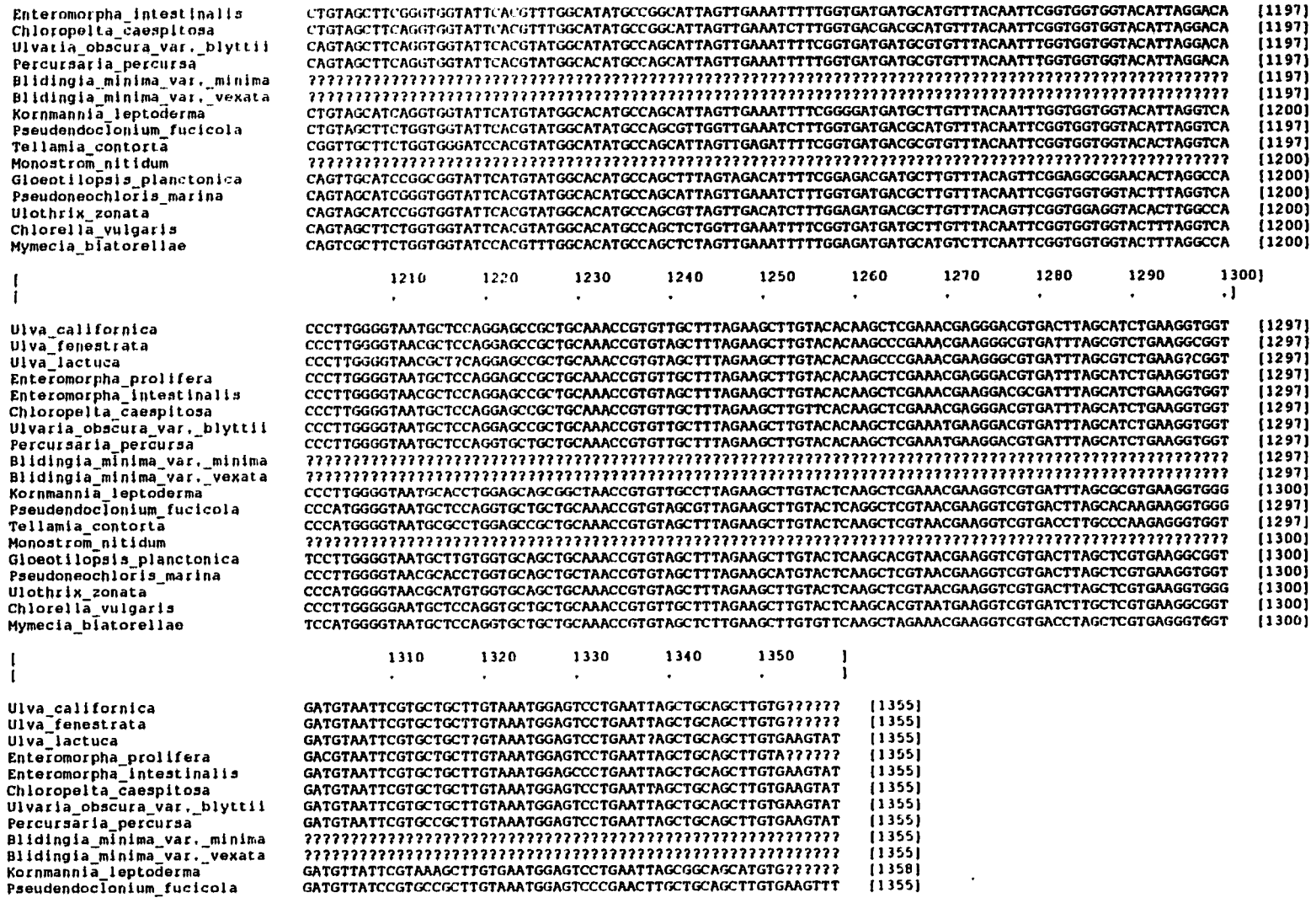
Ulva_californica CTGTAGCTTCAGGTGGTATTCACGTTTGGCACATGCCGGCATTAGTTGAAATTTTTGGTGACGACGCATGTTTACAATTCGGTGGTGGTACATTAGGACA [1197]
Ulva_fenestrata CTGTAGCGTCAGGTGGTATTCACGTGTGGCACATGCCTGCATTAGTTGAAATCTTTGGTGATGATGCATGTTTACAATTCGGTGGTGGTACATTAGGACA [1197]
Ulva_lactuca CTGTAGCGTCAGGTGGTATTCACGTGTGGCACATGCCTGCATTAGTTGAAATCTTTGGTGATGATGCATGTTTACAATTCGGTGGTGGTACATTAG??CA [1197]
Enteromorpha_prolifera CCGTAGCTTCAGGTGGTATTCACGTTTGGCATATGCCGGCATTAGTTGAAATTTTTGGTGACGACGCATGTTTACAATTCGGTGGTGGTACATTAGGACA [1197]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Ulvaria_obscura_var._blyttii CAGTAGCTTCAGGTGGTATTCACGTATGGCATATGCCAGCATTAGTTGAAATTTTCGGTGATGATGCGTGTTTACAATTTGGTGGTGGTACATTAGGACA [1197]
Percursaria_percursa CAGTAGCTTCAGGTGGTATTCACGTATGGCACATGCCAGCATTAGTTGAAATTTTGGTGATGATGCGTGTTTACAATTTGGTGGTGGTACATTAGGACA [1197]
Blidingia_minima_var._minima ?? [1197]
Blidingia_minima_var._vexata ?? [1197]
Kornmannia_leptoderma CTGTAGCATCAGGTGGTATTCATGTATGGCACATGCCAGCATTAGTTGAAATTTTCGGGGATGATGCTTGTTTACAATTTGGTGGTGGTACATTAGGTCA [1200]
Pseudendoclonium_fucicola CTGTAGCTTCTGGTGGTATTCACGTATGGCATATGCCAGCGTTGGTTGAAATCTTTGGTGATGACGCATGTTTACAATTCGGTGGTGGTACATTAGGTCA [1197]
Tellamia_contorta CGGTTGCTTCTGGTGGGATCCACGTATGGCATATGCCAGCATTAGTTGAGATTTTCGGTGATGACGCGTGTTTACAATTCGGTGGTGGTACACTAGGTCA [1197]
Monostrom_nitidum ?? [1200]
Gloeotilopsis_planctonica CAGTTGCATCCGGCGGTATTCATGTATGGCACATGCCAGCTTTAGTAGACATTTTCGGAGACGATGCTTGTTTACAGTTCGGAGGCGGAACACTAGGCCA [1200]
Pseudoneochloris_marina CAGTAGCATCGGGTGGTATTCACGTATGGCACATGCCAGCATTAGTTGAAATCTTTGGTGATGACGCTTGTTTACAATTCGGTGGTGGTACTTTAGGTCA [1200]
Ulothrix_zonata CAGTAGCATCCGGTGGTATTCACGTATGGCACATGCCAGCGTTAGTTGACATCTTTGGAGATGACGCTTGTTTACAGTTCGGTGGAGGTACACTTGGCCA [1200]
Chlorella_vulgaris CAGTAGCTTCTGGTGGTATTCACGTATGGCACATGCCAGCTCTGGTTGAAATTTTCGGTGATGATGCTTGTTTACAATTCGGTGGTGGTACTTTAGGTCA [1200]
Mymecia_biatorellae CAGTCGCTTCTGGTGGTATCCACGTTTGGCACATGCCAGCTCTAGTTGAAATTTTTGGAGATGATGCATGTCTTCAATTCGGTGGTGGTACTTTAGGCCA [1200]
1210 1220 1230 1240 1250 1260 1270 1280 1290 1300
Ulva_californica CCCTTGGGGTAATGCTCCAGGAGCCGCTGCAAACCGTGTTGCTTTAGAAGCTTGTACACAAGCTCGAAACGAGGGACGTGACTTAGCATCTGAAGGTGGT [1297]
Ulva_fenestrata CCCTTGGGGTAACGCTCCAGGAGCCGCTGCAAACCGTGTAGCTTTAGAAGCTTGTACACAAGCCCGAAACGAAGGGCGTGATTTAGCGTCTGAAGGCGGT [1297]
Ulva_lactuca CCCTTGGGGTAACGCT?CAGGAGCCGCTGCAAACCGTGTAGCTTTAGAAGCTTGTACACAAGCCCGAAACGAAGGGCGTGATTTAGCGTCTGAAG?CGGT [1297]
Enteromorpha_prolifera CCCTTGGGGTAATGCTCCAGGAGCCGCTGCAAACCGTGTTGCTTTAGAAGCTTGTACACAAGCTCGAAACGAGGGACGTGATTTAGCATCTGAAGGTGGT [1297]
Enteromorpha_intestinalis CCCTTGGGGTAACGCTCCAGGAGCCGCTGCAAACCGTGTAGCTTTAGAAGCTTGTACACAAGCTCGAAACGAAGGACGCGATTTAGCATCTGAAGGTGGT [1297]
Chloropelta_caespitosa CCCTTGGGGTAATGCTCCAGGAGCCGCTGCAAACCGTGTTGCTTTAGAAGCTTGTTCACAAGCTCGAAACGAGGGACGTGATTTAGCATCTGAAGGTGGT [1297]
Ulvaria_obscura_var._blyttii CCCTTGGGGTAATGCTCCAGGAGCCGCTGCAAACCGTGTTGCTTTAGAAGCTTGTACACAAGCTCGAAATGAAGGACGTGATTTAGCATCTGAAGGTGGT [1297]
Percursaria_percursa CCCTTGGGGTAATGCTCCAGGTGCTGCTGCAAACCGTGTTGCTTTAGAAGCTTGTACACAAGCTCGAAATGAAGGACGTGATTTAGCATCTGAAGGTGGT [1297]
Blidingia_minima_var._minima ?? [1297]
Blidingia_minima_var._vexata ?? [1297]
Kornmannia_leptoderma CCCTTGGGGTAATGCACCTGGAGCAGCGGCTAACCGTGTTGCCTTAGAAGCTTGTACTCAAGCTCGAAACGAAGGTCGTGATTTAGCGCGTGAAGGTGGG [1300]
Pseudendoclonium_fucicola CCCATGGGGTAATGCTCCAGGTGCTGCTGCAAACCGTGTAGCGTTAGAAGCTTGTACTCAGGCTCGTAACGAAGGTCGTGACTTAGCACAAGAAGGTGGG [1297]
Tellamia_contorta CCCATGGGGTAATGCGCCTGGAGCCGCTGCAAACCGTGTAGCTTTAGAAGCTTGTACTCAAGCTCGTAACGAAGGTCGTGACCTTGCCCAAGAGGGTGGT [1297]
Monostrom_nitidum ?? [1300]
Gloeotilopsis_planctonica TCCTTGGGGTAATGCTTGTGGTGCAGCTGCAAACCGTGTAGCTTTAGAAGCTTGTACTCAAGCACGTAACGAAGGTCGTGACTTAGCTCGTGAAGGCGGT [1300]
Pseudoneochloris_marina CCCTTGGGGTAACGCACCTGGTGCAGCTGCTAACCGTGTAGCTTTAGAAGCATGTACTCAAGCTCGTAACGAAGGTCGTGACTTAGCTCGTGAAGGTGGT [1300]
Ulothrix_zonata CCCATGGGGTAACGCATGTGGTGCAGCTGCAAACCGTGTAGCTTTAGAAGCTTGTACTCAAGCTCGTAACGAAGGTCGTGACTTAGCTCGTGAAGGTGGG [1300]
Chlorella_vulgaris CCCTTGGGGGAATGCTCCAGGTGCTGCTGCAAACCGTGTTGCTTTAGAAGCTTGTACTCAAGCACGTAATGAAGGTCGTGATCTTGCTCGTGAAGGCGGT [1300]
Mymecia_biatorellae TCCATGGGGTAATGCTCCAGGTGCTGCTGCAAACCGTGTAGCTCTTGAAGCTTGTGTTCAAGCTAGAAACGAAGGTCGTGACCTAGCTCGTGAGGGTGGT [1300]
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Ulva_californica GATGTAATTCGTGCTGCTTGTAAATGGAGTCCTGAATTAGCTGCAGCTTGTG?????? [1355]
Ulva_fenestrata GATGTAATTCGTGCTGCTTGTAAATGGAGTCCTGAATTAGCTGCAGCTTGTG?????? [1355]
Ulva_lactuca GATGTAATTCGTGCTGCT?GTAAATGGAGTCCTGAAT?AGCTGCAGCTTGTGAAGTAT [1355]
Enteromorpha_prolifera GACGTAATTCGTGCTGCTTGTAAATGGAGTCCTGAATTAGCTGCAGCTTGTA?????? [1355]
Enteromorpha_intestinalis GATGTAATTCGTGCTGCTTGTAAATGGAGCCCTGAATTAGCTGCAGCTTGTGAAGTAT [1355]
Chloropelta_caespitosa GATGTAATTCGTGCTGCTTGTAAATGGAGTCCTGAATTAGCTGCAGCTTGTGAAGTAT [1355]
Ulvaria_obscura_var._blyttii GATGTAATTCGTGCTGCTTGTAAATGGAGTCCTGAATTAGCTGCAGCTTGTGAAGTAT [1355]
Percursaria_percursa GATGTAATTCGTGCCGCTTGTAAATGGAGTCCTGAATTAGCTGCAGCTTGTGAAGTAT [1355]
Blidingia_minima_var._minima ?? [1355]
Blidingia_minima_var._vexata ?? [1355]
Kornmannia_leptoderma GATGTTATTCGTAAAGCTTGTGAATGGAGTCCTGAATTAGCGGCAGCATGTG?????? [1358]
Pseudendoclonium_fucicola GATGTTATCCGTGCCGCTTGTAAATGGAGTCCCGAACTTGCTGCAGCTTGTGAAGTTT [1355]

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Tellamia_contorta               GACGTTATCCGTGCCGCATGTAAATGGAGCCCAGAATTAGCGGCTGCATGTGAGGTAT   [1355]
Monostrom_nitidum               ??????????????????????????????????????????????????????????   [1358]
Gloeotilopsis_planctonica       GACGTTATTCGCGCTGCTTGTAAGTGGAGTCCTGAATTAGCTGCTGCTTGTGAAGT??   [1358]
Pseudoneochloris_marina         GACGTAATTCGTGCCGCTTGTCGCTGGAGTCCTGAACTAGCAGCAGCTTGTGAAGT??   [1358]
Ulothrix_zonata                 GATGTAATTCGTGCGGCTTGCAAATGGAGTCCTGAATTAGCAGCTGCTTGTGAAGTTT   [1358]
Chlorella_vulgaris              GATGTAATCCGTGCAGCGTGCAAATGGAGTCCTGAATTAGCTGCAGCGTGTGAAGTTT   [1358]
Mymecia_biatorellae             GACGTTATTCGTGCTGCTTGCAAGTGGAGTCCTGAATTAGCTGCTGCTTGTGAAGTTT   [1358]
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END;


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                2: 3-1356\3,
                3: 1-1357\3;
CODESET * UNTITLED = Universal: all ;
END;

BEGIN ASSUMPTIONS;
        OPTIONS  DEFTYPE=unord PolyTcount=MINSTEPS ;
END;
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Appendix C. Sequence alignment in NEXUS format for ITS nr rDNA data used in Chapter 2. A total of 141 positions were excluded from analyses, including positions 36 – 76, 107 – 155, 169 – 174, 415 – 436, and 457 – 479.

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#NEXUS

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FORMAT DATATYPE=DNA  MISSING=? GAP=-  INTERLEAVE ;
MATRIX

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Ulva_lactuca                ??????ATCAAACCAACCCCAGC?AACCTGCGGGCTC----------------------------------CGGCCCGCC---GTACAC?GTAACCGC?   [62]
Ulva_fenestrata             AAACCGATCAAACCAACCCCAGAGAACCTGCGGGCTC----------------------------------CGGCCCGCC---GTACAC-GGAACCGCC   [61]
Ulva_sp._III                AAACCGATCAAACCAATCCCAGAGAACTTGCGGGCTT----------------------------------CGGCCCGCC---GTATAC-GGAACCGCC   [61]
Ulva_rotundata              AAACCGATCAAACCAATCCCAGAGAACTTGCGGGCTT----------------------------------CGG-CCGC----GTATAC-GGAACCGCC   [59]
Ulva_australis              ????????????????????????????????????????????????????????????????????????????????????????????????????   [100]
Ulva_lobata                 AAACCGATCAAACCAATCCCTGAGAACCTGCGGGCTT----------------------------------CGGCCCGCC---GTATAC-GGAACCGCC   [61]
Enteromorpha_intestinalis   AAACCGATCAAACCAACCCCAGCGAACTTGCGGGCC----GCTCTC----------------------GTGGTGGCCCGC?---GTATTC-GGAACCGCC   [70]
Enteromorpha_compressa      AAACCGATCAAACCAACCCCAGAGCACTTGTGGGCGCCGCGCCTCCCCC-------------GGGGGGAGCGGCGTCCGCC---GTTTTC-GGAACCGCC   [83]
Ulva_pseudocurvata          AAACCGATCAAACCAACCCCAGAGCACTTGCGGGCGCCGCGCCTCCCCC-------------GGGGGGAGCGGCGTCCGCC---GTTTTC-GGAACCGCC   [83]
Enteromorpha_intestinaloides AAACCGATCAAACCAACCCCAGAGCACTTGCGGGCCT----------------------------------CGGCCCGCC---GTATTC-GGAACCGCC   [61]
Ulva_stenophylla            AAACCGATCAAACCAAACACTGAGCACCTGCGGGCGCC-CGCCTCCCAC------------GGGGGGCGGGGCGGTCCGCC---GTTTACAGGATCCGCC   [84]
Enteromorpha_procera        AAACCGATCAAACCAATCACAGAGCACCTGCGGGCGCT-CGCTCCCCTC------------GGGGGGCGAGGGCCCGCC---GTTTACAGGATCCGCC   [82]
Enteromorpha_linza          AAACCGATCAAACCAATCACAGAGCACCTGCGGGCGCT-CACGCCGGTCCCCTC--GGGGGCTGGGGTGGGGCGGTCCGCC---GTTTACAGGATCCGCC   [94]
Enteromorpha_sp._I          AAACCGATCAAACCAATCACAGAGCACCTGCGGGCGCT-CACCTCCCCCGTTC---GCGGGGTGGGGTGGGGCGGTCCGCC---GTTTACAGGAGCCGCC   [93]
Enteromorpha_prolifera      AAACCGATCAAACCAATCACAGAGCACCTGCGGGCGCT-CACCTCCCCCCTCA---CGGGGGCGGGGTGGGGCGGTCCGCC---GTTTACAGGATCCGCC   [93]
Enteromorpha_sp._II         AAACCGATCAATCCAATCACAGAGCACCTGCGGGCGCT-CACCTCCCTTGT----------GGGGGTGGGGCGGTCCGCC---GTTTACAGGATCCGCC   [85]
Chloropelta_caespitosa      AAACCGATCAAACCAATCACAGAGCACTTGCGGGCGCT-CACCTCCTCCCGTCCG-CGGGGGTGGGGTGGGGCGGCCCGCC---GTTTATTGGGACCGCC   [95]
Ulva_californica            AAACCGATCAAACCATTCACAGAGCACCTGCGGGCGCT-CACCTCCCCCGTTTGC-GCGGGGTGGGGTGGGGCGGTCCGCC---GTTTACAGGAGCCGCC   [95]
Enteromorpha_flexuosa       AAACCGATCAAACCAATCACAGAGCACCTGCGGGCGCT-CACCTCCCTTGC----------GGGGGGTGGGGCGGCCCGCC---GTTTACAGGATCCGCC   [86]
Enteromorpha_muscoides      AAACCGATCAATCCACTCACAGAGCACCAGCGGGCTT----------------------------------GCCCGCCGTAGTTT---GGGTCCGCC   [60]
Ulva_scandinavica           AAACCGATCAATCCACTCACAGAGCACCAGCGGG-TT----------------------------------CGCCCCGCCGTAGTTTT--GGATCCGCC   [62]
Ulva_rigida                 AAACCGATCAATCCACTCACAGAGCACCAGCGGGGTT----------------------------------CGCCCCGCCGTAGTTTT--GGATCCGCC   [63]
Ulva_armoricana             AAACCGATCAATCCACTCACAGAGCACCAGCGGGGTT----------------------------------CGCCCCGCCGTAGTTTT--GGATCCGCC   [63]
Ulva_fasciata               AAACCGATCAATCCACTCACAGAGCACCAGCGGGCCC----------------------------------CGGCCCGCCGTAGTTT---GGATCCGCC   [62]
Ulva_sp._II                 AAACCGATCAATCCACTCACAGAGCACCAGCGGGCCC----------------------------------CGGCCCGCCGTAGTTT---GGATCCGCC   [62]
Ulva_taeniata               AAACCGATCAATCCACCCACAGAGCACCAGCGGGCCC----------------------------------GCCCGCCGTAGTTT---GGATCCGCC   [60]
Ulva_pertusa                AAACCGATCAATCCACTCACAGAGCACCAGCGGGCCC----------------------------------CGGCCCGCCGTAGTTT---GGATCCGCC   [62]
Ulva_sp._I                  AAACCGATCAATCCACTCACAGAGCACCAGCGGGCTT----------------------------------GCCCGCCGTAGTTT---GGATCCGCC   [60]
Ulva_olivascens             AAACCGATCAAACCATCCACAGCGAACCCGCGGGCTCC----------------GGCCCGCCGTCTGCGCTC-GCGCCG-------GGGGGCTCCGC   [73]
Ulvaria_obscura_var._blyttii AAACCGATCAAACCATCCACAGCGAACTAGCGGGCCCCTCCCCCCCGGG---GGTGTGGCCTGCCGTCTGCGCTCTGCGGCGCCGTTTCGGCGGCTCCGC   [97]
Percursaria_percursa        AAACCGATCAAACCATCCCCAGCGAACCAGCGGGCCCCGCCGGCGAGAGCCGGAGGGGGCGCGCCGTCTGCGTCCTGTCCCC-GGT---GCGCGCTCCGC   [96]

[                                 110       120       130       140       150       160       170       180       190       200]
[                                   .         .         .         .         .         .         .         .         .         .]

Ulva_lactuca                -GGCGGGGGCTTAACC----------------------------------CCCCCCGCCGCG-CGGCGCCGA--AACCCATGAAACCGCCCGCCCTGAAG   [124]
Ulva_fenestrata             -GGCGGGGGCTTAACC----------------------------------CCCCCCGCCGCG-CGGCGCCGA--AACCCATGAAACCGCCCGCCCTGAAG   [123]
Ulva_sp._III                CGGTGGGGGCGGGGCC----------------------------CCCTCCCCCCGCCGAG-CGGCGCCGAC-AACCCATGAAACCCTCCGCCCTGAAG   [129]
Ulva_rotundata              CGGTGGGGGCGGGGGG--------------------GACATCCCCCCCCTCCCCCCGCCGAG-CGGCGCCGAG-AACCCATGAAACCCTCCGCCCTGAAG   [137]
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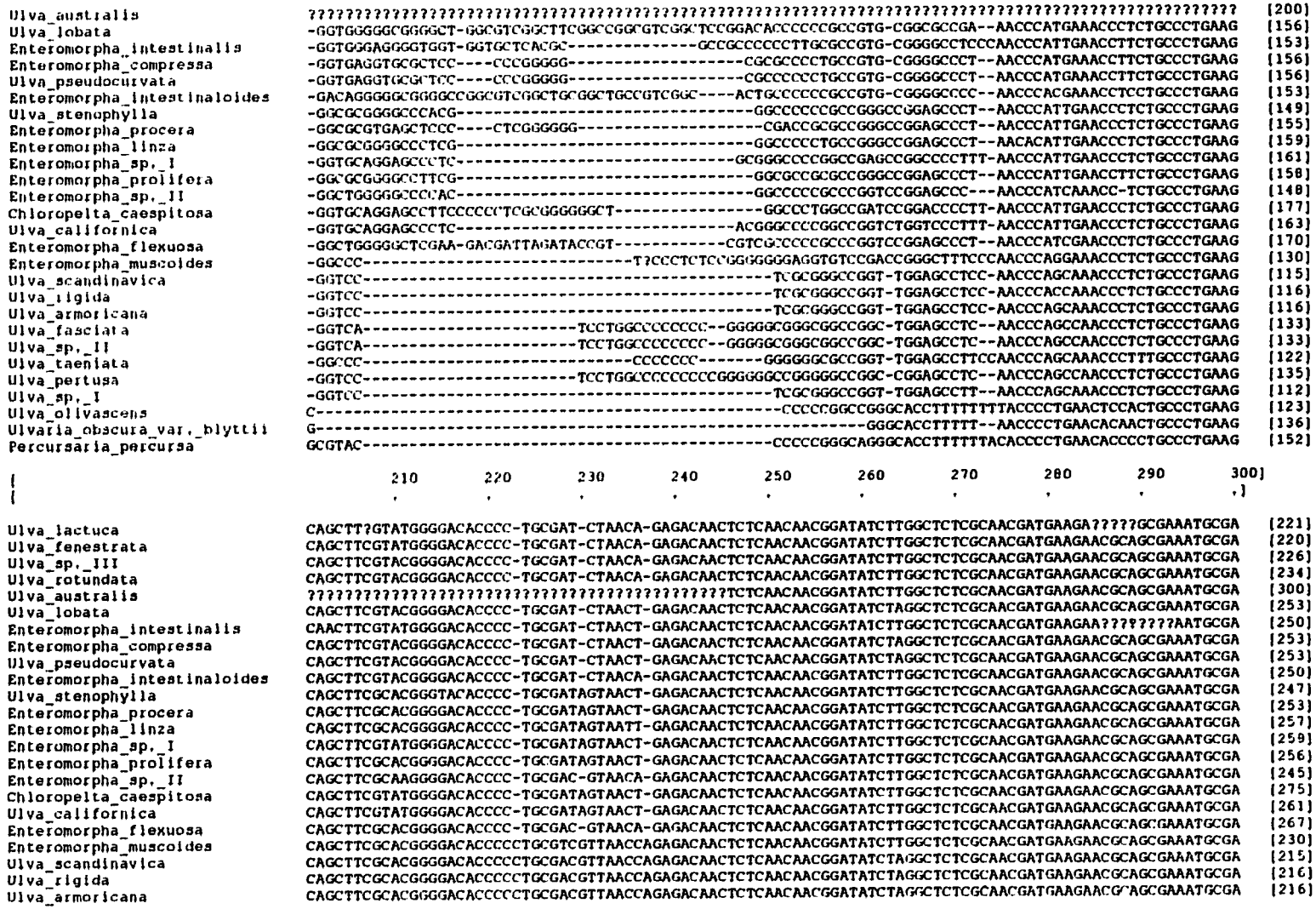
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Enteromorpha_linza
Enteromorpha_sp._I
Enteromorpha_prolifera
Enteromorpha_sp._II
Chloropelta_caespitosa
Ulva_californica
Enteromorpha_flexuosa
Enteromorpha_muscoides
Ulva_scandinavica
Ulva_rigida
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300
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Ulva_fenestrata
Ulva_sp._III
Ulva_rotundata
Ulva_australis
Ulva_lobata
Enteromorpha_intestinalis
Enteromorpha_compressa
Ulva_pseudocurvata
Enteromorpha_intestinaloides
Ulva_stenophylla
Enteromorpha_procera
Enteromorpha_linza
Enteromorpha_sp._I
Enteromorpha_prolifera
Enteromorpha_sp._II
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Enteromorpha_flexuosa
Enteromorpha_muscoides
Ulva_scandinavica
Ulva_rigida
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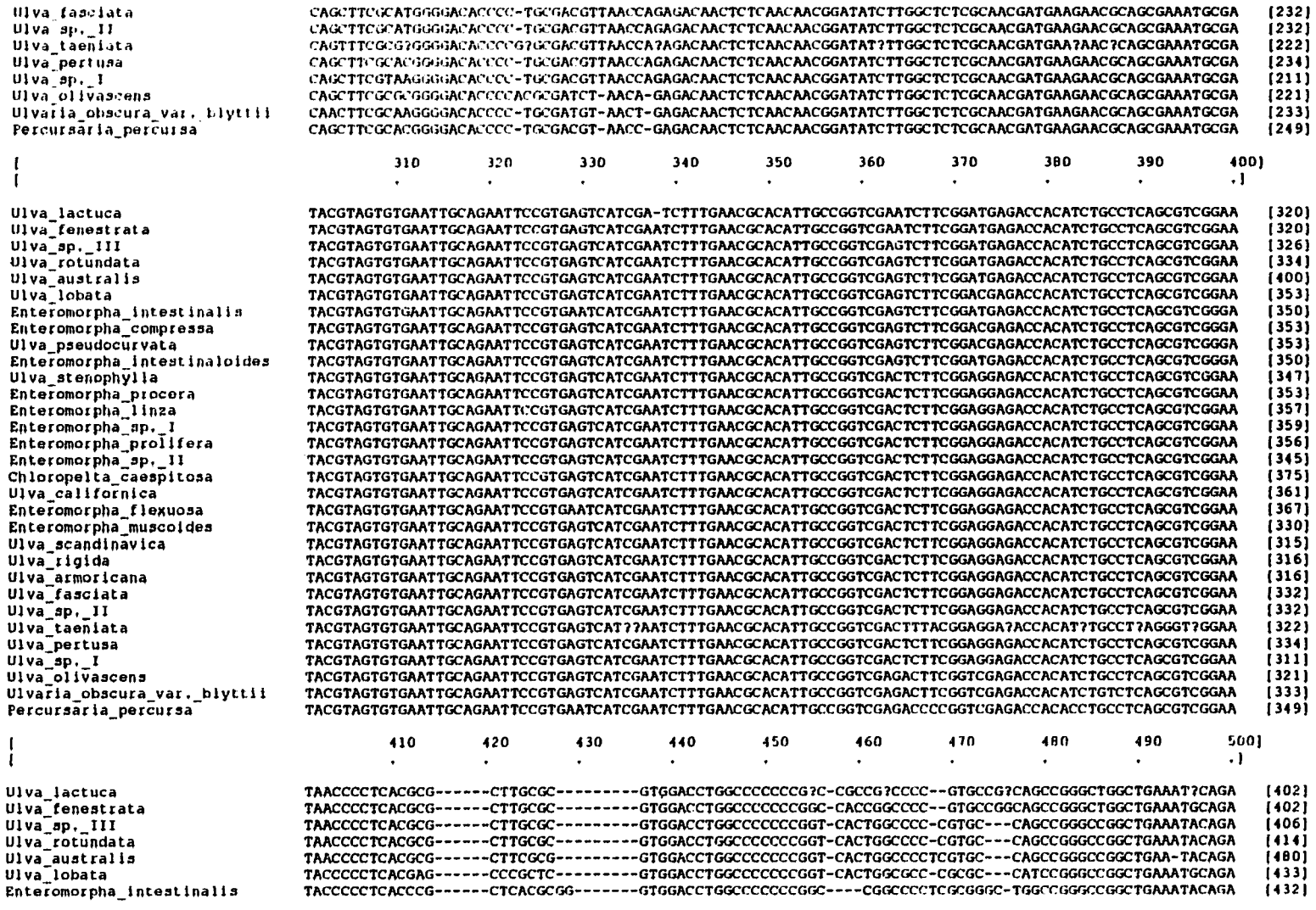
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Ulva_sp._II CAGCTTCGCATGGGGACACCCC-TGCGACGTTAACCAGAGACAACTCTCAACAACGGATATCTTGGCTCTCGCAACGATGAAGAACGCAGCGAAATGCGA [232]
Ulva_taeniata CAGTTTCGCG?GGGGACACCCC?GCGACGTTAACCA?AGACAACTCTCAACAACGGATAT?TTGGCTCTCGCAACGATGAA?AAC?CAGCGAAATGCGA [222]
Ulva_pertusa CAGCTTCGCACGGGGACACCCC-TGCGACGTTAACCAGAGACAACTCTCAACAACGGATATCTTGGCTCTCGCAACGATGAAGAACGCAGCGAAATGCGA [234]
Ulva_sp._I CAGCTTCGTAAGGGGACACCCC-TGCGACGTTAACCAGAGACAACTCTCAACAACGGATATCTTGGCTCTCGCAACGATGAAGAACGCAGCGAAATGCGA [211]
Ulva_olivascens CAGCTTCGCGCGGGGACACCCCACGCGATCT-AACA-GAGACAACTCTCAACAACGGATATCTTGGCTCTCGCAACGATGAAGAACGCAGCGAAATGCGA [221]
Ulvaria_obscura_var._blyttii CAACTTCGCAAGGGGACACCCC-TGCGATGT-AACT-GAGACAACTCTCAACAACGGATATCTTGGCTCTCGCAACGATGAAGAACGCAGCGAAATGCGA [233]
Percursaria_percursa CAGCTTCGCACGGGGACACCCC-TGCGACGT-AACC-GAGACAACTCTCAACAACGGATATCTTGGCTCTCGCAACGATGAAGAACGCAGCGAAATGCGA [249]
[310 320 330 340 350 360 370 380 390 400]
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Ulva_fenestrata TACGTAGTGTGAATTGCAGAATTCCGTGAGTCATCGAATCTTTGAACGCACATTGCCGGTCGAATCTTCGGATGAGACCACATCTGCCTCAGCGTCGGAA [320]
Ulva_sp._III TACGTAGTGTGAATTGCAGAATTCCGTGAGTCATCGAATCTTTGAACGCACATTGCCGGTCGAGTCTTCGGATGAGACCACATCTGCCTCAGCGTCGGAA [326]
Ulva_rotundata TACGTAGTGTGAATTGCAGAATTCCGTGAGTCATCGAATCTTTGAACGCACATTGCCGGTCGAGTCTTCGGATGAGACCACATCTGCCTCAGCGTCGGAA [334]
Ulva_australis TACGTAGTGTGAATTGCAGAATTCCGTGAGTCATCGAATCTTTGAACGCACATTGCCGGTCGAGTCTTCGGATGAGACCACATCTGCCTCAGCGTCGGAA [400]
Ulva_lobata TACGTAGTGTGAATTGCAGAATTCCGTGAGTCATCGAATCTTTGAACGCACATTGCCGGTCGAGTCTTCGGACGAGACCACATCTGCCTCAGCGTCGGAA [353]
Enteromorpha_intestinalis TACGTAGTGTGAATTGCAGAATTCCGTGAATCATCGAATCTTTGAACGCACATTGCCGGTCGAGTCTTCGGATGAGACCACATCTGCCTCAGCGTCGGGA [350]
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Enteromorpha_intestinaloides TACGTAGTGTGAATTGCAGAATTCCGTGAGTCATCGAATCTTTGAACGCACATTGCCGGTCGAGTCTTCGGATGAGACCACATCTGCCTCAGCGTCGGGA [350]
Ulva_stenophylla TACGTAGTGTGAATTGCAGAATTCCGTGAGTCATCGAATCTTTGAACGCACATTGCCGGTCGACTCTTCGGAGGAGACCACATCTGCCTCAGCGTCGGAA [347]
Enteromorpha_procera TACGTAGTGTGAATTGCAGAATTCCGTGAGTCATCGAATCTTTGAACGCACATTGCCGGTCGACTCTTCGGAGGAGACCACATCTGCCTCAGCGTCGGAA [353]
Enteromorpha_linza TACGTAGTGTGAATTGCAGAATTCCGTGAGTCATCGAATCTTTGAACGCACATTGCCGGTCGACTCTTCGGAGGAGACCACATCTGCCTCAGCGTCGGAA [357]
Enteromorpha_sp._I TACGTAGTGTGAATTGCAGAATTCCGTGAGTCATCGAATCTTTGAACGCACATTGCCGGTCGACTCTTCGGAGGAGACCACATCTGCCTCAGCGTCGGAA [359]
Enteromorpha_prolifera TACGTAGTGTGAATTGCAGAATTCCGTGAGTCATCGAATCTTTGAACGCACATTGCCGGTCGACTCTTCGGAGGAGACCACATCTGCCTCAGCGTCGGAA [356]
Enteromorpha_sp._II TACGTAGTGTGAATTGCAGAATTCCGTGAGTCATCGAATCTTTGAACGCACATTGCCGGTCGACTCTTCGGAGGAGACCACATCTGCCTCAGCGTCGGAA [345]
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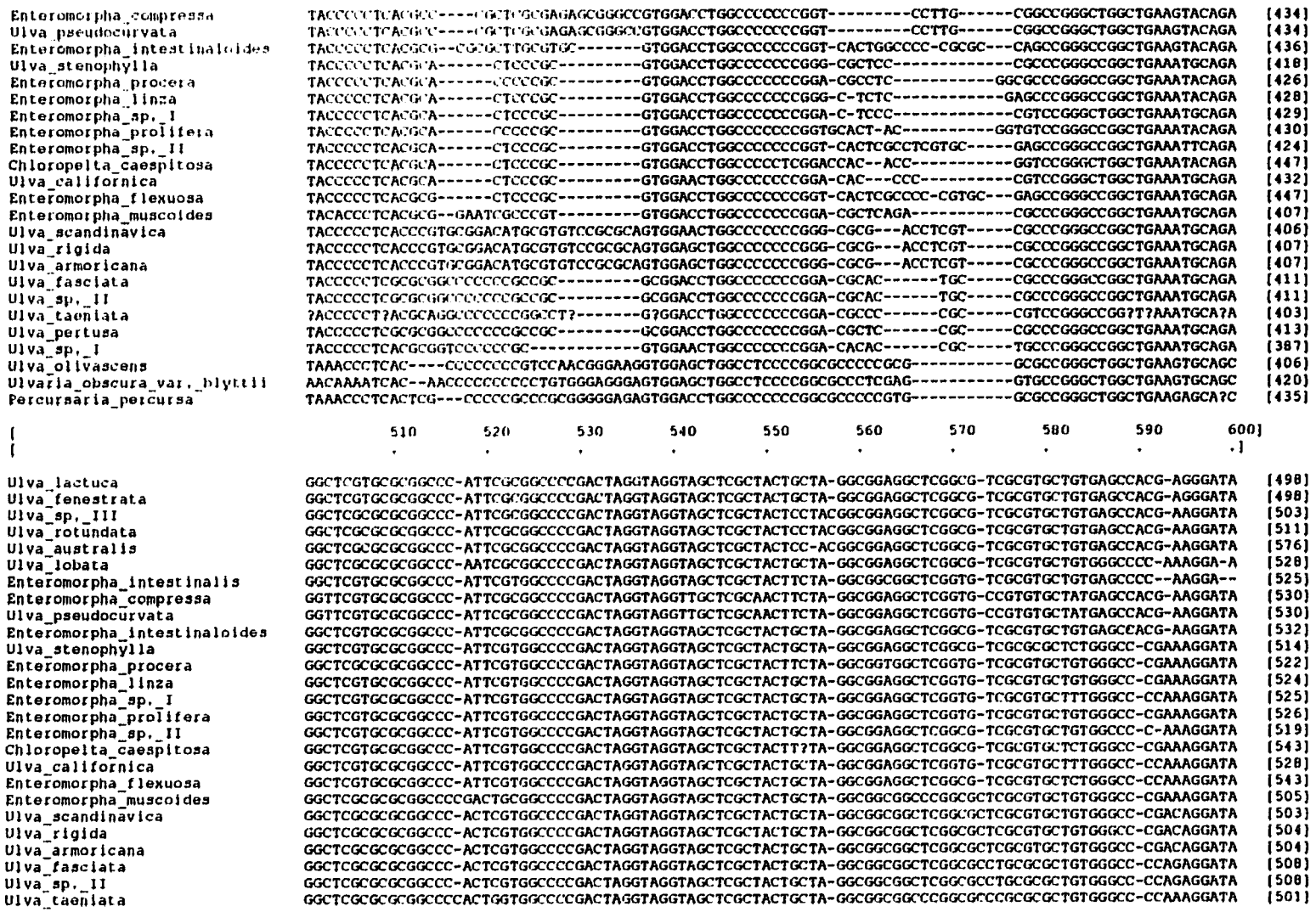
Ulva_californica TACGTAGTGTGAATTGCAGAATTCCGTGAGTCATCGAATCTTTGAACGCACATTGCCGGTCGACTCTTCGGAGGAGACCACATCTGCCTCAGCGTCGGAA [361]
Enteromorpha_flexuosa TACGTAGTGTGAATTGCAGAATTCCGTGAATCATCGAATCTTTGAACGCACATTGCCGGTCGACTCTTCGGAGGAGACCACATCTGCCTCAGCGTCGGAA [367]
Enteromorpha_muscoides TACGTAGTGTGAATTGCAGAATTCCGTGAGTCATCGAATCTTTGAACGCACATTGCCGGTCGACTCTTCGGAGGAGACCACATCTGCCTCAGCGTCGGAA [330]
Ulva_scandinavica TACGTAGTGTGAATTGCAGAATTCCGTGAGTCATCGAATCTTTGAACGCACATTGCCGGTCGACTCTTCGGAGGAGACCACATCTGCCTCAGCGTCGGAA [315]
Ulva_rigida TACGTAGTGTGAATTGCAGAATTCCGTGAGTCATCGAATCTTTGAACGCACATTGCCGGTCGACTCTTCGGAGGAGACCACATCTGCCTCAGCGTCGGAA [316]
Ulva_armoricana TACGTAGTGTGAATTGCAGAATTCCGTGAGTCATCGAATCTTTGAACGCACATTGCCGGTCGACTCTTCGGAGGAGACCACATCTGCCTCAGCGTCGGAA [316]
Ulva_fasciata TACGTAGTGTGAATTGCAGAATTCCGTGAGTCATCGAATCTTTGAACGCACATTGCCGGTCGACTCTTCGGAGGAGACCACATCTGCCTCAGCGTCGGAA [332]
Ulva_sp._II TACGTAGTGTGAATTGCAGAATTCCGTGAGTCATCGAATCTTTGAACGCACATTGCCGGTCGACTCTTCGGAGGAGACCACATCTGCCTCAGCGTCGGAA [332]
Ulva_taeniata TACGTAGTGTGAATTGCAGAATTCCGTGAGTCAT??AATCTTTGAACGCACATTGCCGGTCGACTTTACGGAGGA?ACCACAT?TGCCT?AGGGT?GGAA [322]
Ulva_pertusa TACGTAGTGTGAATTGCAGAATTCCGTGAGTCATCGAATCTTTGAACGCACATTGCCGGTCGACTCTTCGGAGGAGACCACATCTGCCTCAGCGTCGGAA [334]
Ulva_sp._I TACGTAGTGTGAATTGCAGAATTCCGTGAGTCATCGAATCTTTGAACGCACATTGCCGGTCGACTCTTCGGAGGAGACCACATCTGCCTCAGCGTCGGAA [311]
Ulva_olivascens TACGTAGTGTGAATTGCAGAATTCCGTGAGTCATCGAATCTTTGAACGCACATTGCCGGTCGAGACTTCGGTCGAGACCACATCTGCCTCAGCGTCGGAA [321]
Ulvaria_obscura_var._blyttii TACGTAGTGTGAATTGCAGAATTCCGTGAGTCATCGAATCTTTGAACGCACATTGCCGGTCGAGACTTCGGTCGAGACCACATCTGTCTCAGCGTCGGAA [333]
Percursaria_percursa TACGTAGTGTGAATTGCAGAATTCCGTGAATCATCGAATCTTTGAACGCACATTGCCGGTCGAGACCCCGGTCGAGACCACACCTGCCTCAGCGTCGGAA [349]
[410 420 430 440 450 460 470 480 490 500]
Ulva_lactuca TAACCCCTCACGCG------CTTGCGC---------GTGGACCTGGCCCCCCCG?C-CGCCG?CCCC--GTGCCG?CAGCCGGGCTGGCTGAAAT?CAGA [402]
Ulva_fenestrata TAACCCCTCACGCG------CTTGCGC---------GTGGACCTGGCCCCCCCGGC-CACCGGCCCC--GTGCCGGCAGCCGGGCTGGCTGAAATGCAGA [402]
Ulva_sp._III TAACCCCTCACGCG------CTTGCGC---------GTGGACCTGGCCCCCCCGGT-CACTGGCCCC-CGTGC---CAGCCGGGCCGGCTGAAATACAGA [406]
Ulva_rotundata TAACCCCTCACGCG------CTTGCGC---------GTGGACCTGGCCCCCCCGGT-CACTGGCCCC-CGTGC---CAGCCGGGCCGGCTGAAATACAGA [414]
Ulva_australis TAACCCCTCACGCG------CTTCGCG---------GTGGACCTGGCCCCCCCGGT-CACTGGCCCCTCGTGC---CAGCCGGGCCGGCTGAA-TACAGA [480]
Ulva_lobata TACCCCCTCACGAG------CCCGCTC---------GTGGACCTGGCCCCCCCGGT-CACTGGCGCC-CGCGC---CATCCGGGCCGGCTGAAATGCAGA [433]
Enteromorpha_intestinalis TACCCCCTCACCCG------CTCACGCGG-------GTGGACCTGGCCCCCCCGGC----CGGCCCCTCGCGGGC-TGGCCGGGCCGGCTGAAATACAGA [432]


Enteromorpha_compressa
Ulva_pseudocurvata
Enteromorpha_intestinaloides
Ulva_stenophylla
Enteromorpha_procera
Enteromorpha_linza
Enteromorpha_sp._I
Enteromorpha_prolifera
Enteromorpha_sp._II
Chloropelta_caespitosa
Ulva_californica
Enteromorpha_flexuosa
Enteromorpha_muscoides
Ulva_scandinavica
Ulva_rigida
Ulva_armoricana
Ulva_fasciata
Ulva_sp._II
Ulva_taeniata
Ulva_pertusa
Ulva_sp._I
Ulva_olivascens
Ulvaria_obscura_var._blyttii
Percursaria_percursa
510
520
530
540
550
560
570
580
590
600
Ulva_lactuca
Ulva_fenestrata
Ulva_sp._III
Ulva_rotundata
Ulva_australis
Ulva_lobata
Enteromorpha_intestinalis
Enteromorpha_compressa
Ulva_pseudocurvata
Enteromorpha_intestinaloides
Ulva_stenophylla
Enteromorpha_procera
Enteromorpha_linza
Enteromorpha_sp._I
Enteromorpha_prolifera
Enteromorpha_sp._II
Chloropelta_caespitosa
Ulva_californica
Enteromorpha_flexuosa
Enteromorpha_muscoides
Ulva_scandinavica
Ulva_rigida
Ulva_armoricana
Ulva_fasciata
Ulva_sp._II
Ulva_taeniata

```
Ulva_pertusa                    GGCTCGCGCGCGGCCC-ACTCGTGGCCCCGACTAGGTAGGTAGCTCGCTACTGCTA-GGCGGCGGCTCGGCGCCTGCGCGCTGTGGGCC-CCAGAGGATA   [510]
Ulva_sp._I                      GGCTCGCGCGCGGCCC-ACTCGTGGCCCCGACTAGGTAGGTAGCTCGCTACTGCTA-GGCGGCGGCTCGGCGCCCGCGTGCTGTGGGCC-CCAAAGGATA   [484]
Ulva_olivascens                 GGCTCGCGCGCGGACCCATTCCGGGCCCCGACTAGGTAGGTAGCTCGCTACTGCTA-GGCGGCGGC-CGGGTCCGAGGCGCTCTGGGCC-CG-CAGGA-A   [501]
Ulvaria_obscura_var._blyttii    GGCTCGCGCTCGGACCCACTTTGGGCCCCGACTAGGTAGGTAGCTCGCTACTGCTA-GCCGGCGGC-CGGGACCGACGCGCTCTGGGCC-CG-CAGGA-A   [515]
Percursaria_percursa            GGCTCGCGCACGGACCCGTT-GGGGCCCCGACTAGGTAGGTAGCTCGCTACTGCTA-GCCGGCGGC-CGGGCCCGCGGCGCTCTGGGCC-CG-CAGGA-A   [529]

[                                       610]
[                                        .  ]

Ulva_lactuca                    C-CCATCCAT??    [509]
Ulva_fenestrata                 C-CCATCCATTC    [509]
Ulva_sp._III                    C-CCA-CTATTC    [513]
Ulva_rotundata                  C-CCA-CTAT??    [521]
Ulva_australis                  CATC--CTATTC    [506]
Ulva_lobata                     CATCATCCATTC    [540]
Enteromorpha_intestinalis       CATC-CTT-TCC    [535]
Enteromorpha_compressa          C-TAACTT-TCC    [540]
Ulva_pseudocurvata              C-TAACTT-TCC    [540]
Enteromorpha_intestinaloides    C-CCG-TT-TCC    [541]
Ulva_stenophylla                C-CCATCCATTC    [525]
Enteromorpha_procera            C-CAATCCAT??    [533]
Enteromorpha_linza              C--CATCCATTC    [534]
Enteromorpha_sp._I              C-CCATCCATTC    [536]
Enteromorpha_prolifera          T-CCATCCATTC    [537]
Enteromorpha_sp._II             C--CATCCATTC    [529]
Chloropelta_caespitosa          C-CCATCCATTC    [554]
Ulva_californica                C-CCATCCATTC    [539]
Enteromorpha_flexuosa           C--CATCCATTC    [553]
Enteromorpha_muscoides          ACCCCCTCATTC    [517]
Ulva_scandinavica               ACCC-CTCATTC    [514]
Ulva_rigida                     ACCC-CTCATTC    [515]
Ulva_armoricana                 ACCC-CTCAT??    [515]
Ulva_fasciata                   ACC--CCCATTC    [518]
Ulva_sp._II                     ACC--CCCATTC    [518]
Ulva_taeniata                   ACC--CCCATTC    [511]
Ulva_pertusa                    ACCC-CCCATTC    [521]
Ulva_sp._I                      ACCC-CATATTC    [495]
Ulva_olivascens                 CC---ACTATTC    [510]
Ulvaria_obscura_var._blyttii    CCC---TTTTTC    [524]
Percursaria_percursa            CCCCCACTATTC    [541]
;
END;


BEGIN CODONS;
CODESET * UNTITLED = Universal: all ;
END;

BEGIN ASSUMPTIONS;
        OPTIONS  DEFTYPE=unord PolyTcount=MINSTEPS ;
END;
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Appendix D. Sequence alignment in NEXUS format for *rbc*L data used in Chapter 2.

```
#NEXUS

BEGIN DATA;
DIMENSIONS  NTAX=25 NCHAR=1357;
FORMAT DATATYPE=DNA  MISSING=? GAP=-  INTERLEAVE ;
MATRIX

[                          10        20        30        40        50        60        70        80        90       100]
[                           .         .         .         .         .         .         .         .         .        .]

Ulva_lactuca               GGTACTGGCTTTAAAGCTGGTGTAAAAGATTACCGTTTAACTTATTACACGCCTGATTATCAAGTAAAAGATACTGATATTTTAGCAGCGTTTCGTATGA   [100]
Ulva_fenestrata            GGTACTGGCTTTAAAGCTGGTGTAAAAGATTACCGTTTAACTTATTACACGCCTGATTATCAAGTAAAAGATACTGATATTTTAGCAGCGTTTCGTATGA   [100]
Ulva_sp._III               GGTACTGGCTTTAAAGCTGGTGTAAAAGATTACCGTTTAACTTATTACACGCCTGATTATCAAGTAAAAGATACTGATATTTTAGCAGCGTTTCGTATGA   [100]
Ulva_lobata                GGTACTGGCTTTAAAGCTGGTGTAAAAGATTACCGTTTAACTTATTACACGCCTGATTATCAAGTAAAAGATACTGATATCTTAGCAGCGTTTCGTATGA   [100]
Enteromorpha_intestinalis  GGTACTGGCTTTAAAGCTGGTGTAAAAGATTACCGTTTAACTTATTACACGCCTGATTATCAAGTAAAAGATACTGATATTTTAGCAGCGTTTCGTATGA   [100]
Enteromorpha_compressa     GGTACTGGCTTTAAAGCTGGTGTAAAAGATTACCGTTTAACTTATTACACGCCTGATTATCAAGTAAAAGATACTGATATTTTAGCAGCGTTTCGTATGA   [100]
Ulva_pseudocurvata         GGTACTGGCTTTAAAGCTGGTGTAAAAGATTACCGTTTAACTTATTACACGCCTGATTATCAAGTAAAAGATACTGATATTTTAGCAGCGTTTCGTATGA   [100]
Ulva_stenophylla           GGTACTGGCTTTAAAGCTGGTGTAAAAGATTACCGTTTAACTTATTACACGCCTGATTATCAAGTAAAAGATACTGATATTTTAGCAGCGTTCCGTATGA   [100]
Enteromorpha_procera       GGTACTGGCTTTAAAGCTGGTGTAAAAGATTACCGTTTAACTTATTACACGCCTGATTATCAAGTAAAAGATACTGATATTTTAGCAGCGTTCCGTATGA   [100]
Enteromorpha_prolifera     GGTACTGGCTTTAAAGCTGGTGTAAAAGATTACCGTTTAACTTATTACACGCCTGACTATCAAGTAAAAGATACTGATATTTTAGCAGCGTTCCGTATGA   [100]
Enteromorpha_linza         GGTACTGGCTTTAAAGCTGGTGTAAAAGATTACCGTTTAACTTATTACACGCCTGATTATCAAGTAAAAGATACTGATATTTTAGCAGCTTTCCGTATGA   [100]
Enteromorpha_sp._I         GGTACTGGCTTTAAAGCTGGTGTAAAAGATTACCGTTTAACTTATTACACGCCTGATTATCAAGTAAAAGATACTGATATTTTAGCAGCGTTCCGTATGA   [100]
Chloropelta_caespitosa     GGTACTGGCTTTAAAGCTGGTGTAAAAGATTACCGTTTAACTTATTACACGCCTGATTATCAAGTAAAAGATACTGATATTTTAGCAGCGTTCCGTATGA   [100]
Ulva_californica           GGTACTGGCTTTAAAGCTGGTGTAAAAGATTACCGTTTAACTTATTACACGCCTGATTATCAAGTAAAAGATACTGATATTTTAGCAGCGTTCCGTATGA   [100]
Enteromorpha_muscoides     GGTACTGGCTTTAAAGCTGGTGTAAAAGATTACCGTTTAACTTATTACACGCCTGATTATCAAGTAAAAGATACTGATATTTTAGCAGCATTCCGTATGA   [100]
Ulva_scandinavica          GGTACTGGCTTTAAAGCTGGTGTAAAAGATTACCGTTTAACTTATTACACGCCTGATTATCAAGTAAAAGATACTGATATTTTAGCAGCATTCCGTATGA   [100]
Ulva_fasciata              GGTACTGGCTTTAAAGCTGGTGTAAAAGATTACCGTTTAACTTATTACACGCCTGATTATCAAGTAAAAGATACTGATATTTTAGCAGCATTTGGTATGA   [100]
Ulva_sp._II                GGTACTGGCTTTAAAGCTGGTGTAAAAGATTACCGTTTAACTTATTACACGCCTGATTATCAAGTAAAAGATACTGATATTTTAGCAGCATTTCGTATGA   [100]
Ulva_taeniata              GGTACTGGCTTTAAAGCTGGTGTAAAAGATTACCGTTTAACTTATTACACGCCTGATTATCAAGTAAAAGATACTGATATTTTAGCAGCATTCCGTATGA   [100]
Ulva_sp._I                 GGTACTGGCTTTAAAGCTGGTGTAAAAGATTACCGTTTAACTTATTACACGCCTGATTATCAAGTAAAAGATACTGATATTTTAGCAGCATTCCGTATGA   [100]
Ulva_olivascens            GGTACTGGCTTTAAAGCTGGTGTAAAAGATTACCGTTTAACTTATTACACACCTGATTATCAAGTAAAAGATACTGATATTTTAGCAGCATTTCGTATGA   [100]
Ulvaria_obscura_var._blyttii GGTACTGGCTTTAAAGCTGGTGTAAAAGATTACCGTTTAACTTATTACACACCTGATTATCAAGTAAAAGATACTGATATTTTAGCAGCATTCCGTATGA   [100]
Percursaria_percursa       GGTACTGGCTTTACAGCTGGTGTAAAAGACTACCGTTTAACTTATTACACACCTGATTATCAAGTAAAAGATACTGATATTTTAGCAGCATTTCGTATGA   [100]
Kornmannia_leptoderma      GGAACGGGTTTTAAAGCGGGTGTTAAAGATTATCGTTTAACATACTATACGCCAGACTATCAAGTAAAAGATACTGATATTCTTGCGGCATTCCGTATGA   [100]
Blidingia_minima_var._minima GGAACGGGTTTTAAGGCTGGTGTTAAAGACTATCGTTTAACTTATTATACACCAGATTATCAAGTAAAAGA?ACGGATATTTTAGCGGCATTCCGTATGA   [100]

[                         110       120       130       140       150       160       170       180       190       200]
[                           .         .         .         .         .         .         .         .         .        .]

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Ulva_fenestrata            CTCCTCAACCAGGAGTACCAGCAGAAGAAGCAGGTGCAGCTGTTGCTGCTGAATCATCAACAGGTACTTGGACAACTGTATGGACTGATGGTTTAACATC   [200]
Ulva_sp._III               CTCCTCAACCAGGAGTACCGGCAGAAGAAGCAGGTGCAGCTGTTGCTGCTGAATCATCAACAGGTACTTGGACAACTGTATGGACTGATGGTTTAACATC   [200]
Ulva_lobata                CTCCTCAACCAGGGGTACCTGCAGAAGAAGCAGGTGCAGCTGTTGCTGCTGAATCATCAACAGGTACTTGGACAACTGTATGGACTGATGGTTTAACATC   [200]
Enteromorpha_intestinalis  CTCCTCAACCAGGAGTACCAGCAGAAGAAGCAGGTGCAGCTGTTGCTGCTGAATCATCAACAGGTACTTGGACAACTGTATGGACTGATGGTTTAACATC   [200]
Enteromorpha_compressa     CTCCTCAACCAGGAGTACCAGCAGAAGAAGCAGGTGCAGCTGTTGCTGCTGAATCATCAACAGGTACTTGGACAACTGTATGGACTGATGGTTTAACATC   [200]
Ulva_pseudocurvata         CTCCTCAACCAGGAGTACCAGCAGAAGAAGCAGGTGCAGCTGTTGCTGCTGAATCATCAACAGGTACTTGGACAACTGTATGGACTGATGGTTTAACATC   [200]
Ulva_stenophylla           CTCCTCAACCAGGAGTACCAGCAGAAGAAGCAGGTGCAGCTGTTGCTGCTGAATCATCGACAGGTACTTGGACAACTGTATGGACTGATGGTTTAACATC   [200]
Enteromorpha_procera       CTCCTCAACCAGGAGTACCGGCAGAAGAAGCAGGTGCAGCTGTTGCTGCTGAATCATCAACAGGTACTTGGACAACTGTATGGACTGATGGTTTAACATC   [200]
Enteromorpha_prolifera     CTCCTCAACCAGGAGTACCAGCAGAAGAAGCAGGTGCAGCTGTTGCTGCTGAATCATCAACAGGTACTTGGACAACTGTATGGACTGATGGTTTAACATC   [200]
Enteromorpha_linza         CTCCTCAACCAGGAGTACCAGCAGAAGAAGCAGGTGCAGCTGTTGCTGCTGAATCATCAACAGGTACTTGGACAACTGTATGGACTGATGGTTTAACATC   [200]
Enteromorpha_sp._I         CTCCTCAACCAGGAGTACCAGCAGAAGAAGCAGGTGCAGCTGTTGCTGCTGAATCATCAACAGGTACTTGGACAACTGTATGGACTGATGGTTTAACATC   [200]
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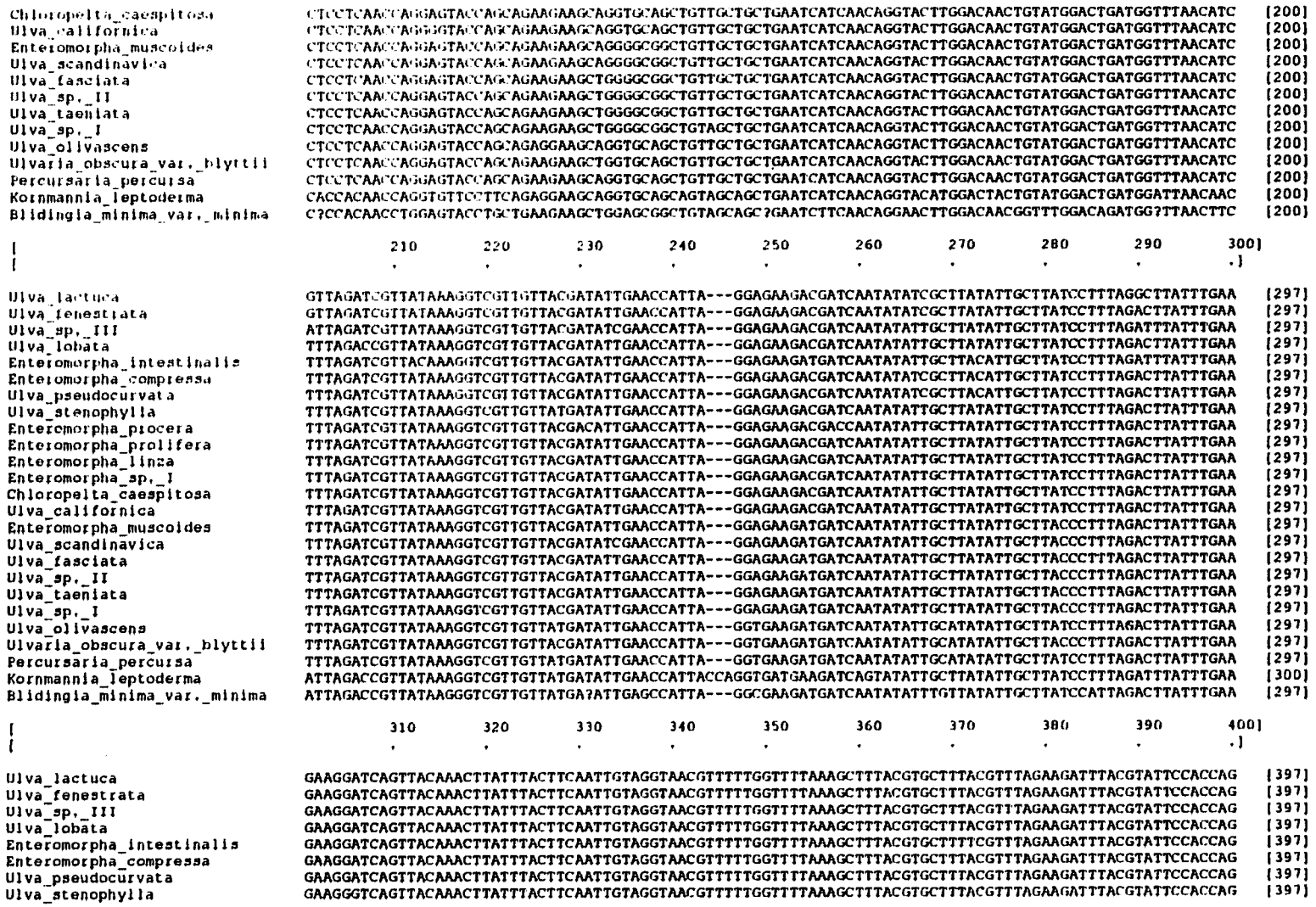
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Ulva_californica CTCCTCAACCAGGGTACCAGCAGAAGAAGCAGGTGCAGCTGTTGCTGCTGAATCATCAACAGGTACTTGGACAACTGTATGGACTGATGGTTTAACATC [200]
Enteromorpha_muscoides CTCCTCAACCAGGAGTACCAGCAGAAGAAGCAGGGGCGGCTGTTGCTGCTGAATCATCAACAGGTACTTGGACAACTGTATGGACTGATGGTTTAACATC [200]
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Ulva_fasciata CTCCTCAACCAGGAGTACCAGCAGAAGAAGCTGGGGCGGCTGTTGCTGCTGAATCATCAACAGGTACTTGGACAACTGTATGGACTGATGGTTTAACATC [200]
Ulva_sp._II CTCCTCAACCAGGAGTACCAGCAGAAGAAGCTGGGGCGGCTGTTGCTGCTGAATCATCAACAGGTACTTGGACAACTGTATGGACTGATGGTTTAACATC [200]
Ulva_taeniata CTCCTCAACCAGGAGTACCAGCAGAAGAAGCTGGGGCGGCTGTTGCTGCTGAATCATCAACAGGTACTTGGACAACTGTATGGACTGATGGTTTAACATC [200]
Ulva_sp._I CTCCTCAACCAGGAGTACCAGCAGAAGAAGCTGGGGCGGCTGTAGCTGCTGAATCATCAACAGGTACTTGGACAACTGTATGGACTGATGGTTTAACATC [200]
Ulva_olivascens CTCCTCAACCAGGAGTACCAGCAGAGGAAGCAGGTGCAGCTGTTGCTGCTGAATCATCAACAGGTACTTGGACAACTGTATGGACTGATGGTTTAACATC [200]
Ulvaria_obscura_var._blyttii CTCCTCAACCAGGAGTACCAGCAGAAGAAGCTGGTGCAGCTGTTGCTGCTGAATCATCAACAGGTACTTGGACAACTGTATGGACTGATGGTTTAACATC [200]
Percursaria_percursa CTCCTCAACCAGGAGTACCAGCAGAAGAAGCAGGTGCAGCTGTTGCTGCTGAATCATCAACAGGTACTTGGACAACTGTATGGACTGATGGTTTAACATC [200]
Kornmannia_leptoderma CACCACAACCAGGTGTTCCTTCAGAGGAAGCAGGTGCAGCAGTAGCAGCTGAATCATCAACAGGTACATGGACTACTGTATGGACTGATGGATTAACAAC [200]
Blidingia_minima_var._minima C?CCACAACCTGGAGTACCTGCTGAAGAAGCTGGAGCGGCTGTAGCAGC?GAATCTTCAACAGGAACTTGGACAACGGTTTGGACAGATGG?TTAACTTC [200]
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Ulva_fenestrata GTTAGATCGTTATAAAGGTCGTTGTTACGATATTGAACCATTA---GGAGAAGACGATCAATATATCGCTTATATTGCTTATCCTTTAGACTTATTTGAA [297]
Ulva_sp._III ATTAGATCGTTATAAAGGTCGTTGTTACGATATCGAACCATTA---GGAGAAGACGATCAATATATTGCTTATATTGCTTATCCTTTAGATTTATTTGAA [297]
Ulva_lobata TTTAGACCGTTATAAAGGTCGTTGTTACGATATTGAACCATTA---GGAGAAGACGATCAATATATTGCTTATATTGCTTATCCTTTAGACTTATTTGAA [297]
Enteromorpha_intestinalis TTTAGATCGTTACAAAGGTCGTTGTTACGATATTGAACCATTA---GGAGAAGATGATCAATATATTGCTTACATTGCTTATCCTTTAGATTTATTTGAA [297]
Enteromorpha_compressa TTTAGATCGTTATAAAGGTCGTTGTTACGATATTGAACCATTA---GGAGAAGACGATCAATATATCGCTTACATTGCTTATCCTTTAGACTTATTTGAA [297]
Ulva_pseudocurvata TTTAGATCGTTATAAAGGTCGTTGTTACGATATTGAACCATTA---GGAGAAGACGATCAATATATCGCTTACATTGCTTATCCTTTAGACTTATTTGAA [297]
Ulva_stenophylla TTTAGATCGTTATAAAGGTCGTTGTTATGATATTGAACCATTA---GGAGAAGACGATCAATATATTGCTTATATTGCTTATCCTTTAGACTTATTTGAA [297]
Enteromorpha_procera TTTAGATCGTTATAAAGGTCGTTGTTACGACATTGAACCATTA---GGAGAAGACGACCAATATATTGCTTATATTGCTTATCCTTTAGACTTATTTGAA [297]
Enteromorpha_prolifera TTTAGATCGTTATAAAGGTCGTTGTTACGATATTGAACCATTA---GGAGAAGACGATCAATATATTGCTTATATTGCTTATCCTTTAGACTTATTTGAA [297]
Enteromorpha_linza TTTAGATCGTTATAAAGGTCGTTGTTACGATATTGAACCATTA---GGAGAAGACGATCAATATATTGCTTATATTGCTTATCCTTTAGACTTATTTGAA [297]
Enteromorpha_sp._I TTTAGATCGTTATAAAGGTCGTTGTTACGATATTGAACCATTA---GGAGAAGACGATCAATATATTGCTTATATTGCTTATCCTTTAGACTTATTTGAA [297]
Chloropelta_caespitosa TTTAGATCGTTATAAAGGTCGTTGTTACGATATTGAACCATTA---GGAGAAGACGATCAATATATTGCTTATATTGCTTATCCTTTAGACTTATTTGAA [297]
Ulva_californica TTTAGATCGTTATAAAGGTCGTTGTTACGATATTGAACCATTA---GGAGAAGACGATCAATATATTGCTTATATTGCTTATCCTTTAGACTTATTTGAA [297]
Enteromorpha_muscoides TTTAGATCGTTATAAAGGTCGTTGTTACGATATTGAACCATTA---GGAGAAGATGATCAATATATTGCTTATATTGCTTACCCTTTAGACTTATTTGAA [297]
Ulva_scandinavica TTTAGATCGTTATAAAGGTCGTTGTTACGATATCGAACCATTA---GGAGAAGATGATCAATATATTGCTTATATTGCTTACCCTTTAGACTTATTTGAA [297]
Ulva_fasciata TTTAGATCGTTATAAAGGTCGTTGTTACGATATTGAACCATTA---GGAGAAGATGATCAATATATTGCTTATATTGCTTACCCTTTAGACTTATTTGAA [297]
Ulva_sp._II TTTAGATCGTTATAAAGGTCGTTGTTACGATATTGAACCATTA---GGAGAAGATGATCAATATATTGCTTATATTGCTTACCCTTTAGACTTATTTGAA [297]
Ulva_taeniata TTTAGATCGTTATAAAGGTCGTTGTTACGATATTGAACCATTA---GGAGAAGATGATCAATATATTGCTTATATTGCTTACCCTTTAGACTTATTTGAA [297]
Ulva_sp._I TTTAGATCGTTATAAAGGTCGTTGTTACGATATTGAACCATTA---GGAGAAGATGATCAATATATTGCTTATATTGCTTACCCTTTAGACTTATTTGAA [297]
Ulva_olivascens TTTAGATCGTTATAAAGGTCGTTGTTATGATATTGAACCATTA---GGTGAAGATGATCAATATATTGCATATATTGCTTATCCTTTAGACTTATTTGAA [297]
Ulvaria_obscura_var._blyttii TTTAGATCGTTATAAAGGTCGTTGTTACGATATTGAACCATTA---GGTGAAGATGATCAATATATTGCTTACCCTTTAGACTTATTTGAA [297]
Percursaria_percursa TTTAGATCGTTATAAAGGTCGTTGTTATGATATTGAACCATTA---GGTGAAGATGATCAATATATTGCATATATTGCTTATCCTTTAGACTTATTTGAA [297]
Kornmannia_leptoderma ATTAGACCGTTATAAAGGTCGTTGTTATGATATTGAACCATTACCAGGTGATGAAGATCAGTATATTGCTTATATTGCTTATCCTTTAGATTTATTTGAA [300]
Blidingia_minima_var._minima ATTAGACCGTTATAAGGGTCGTTGTTATGA?ATTGAGCCATTA---GGCGAAGATGATCAATATATTTGTTATATTGCTTATCCATTAGACTTATTTGAA [297]
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Ulva_fenestrata GAAGGATCAGTTACAAACTTATTTACTTCAATTGTAGGTAACGTTTTTGGTTTTAAAGCTTTACGTGCTTTACGTTTAGAAGATTTACGTATTCCACCAG [397]
Ulva_sp._III GAAGGATCAGTTACAAACTTATTTACTTCAATTGTAGGTAACGTTTTTGGTTTTAAAGCTTTACGTGCTTTACGTTTAGAAGATTTACGTATTCCACCAG [397]
Ulva_lobata GAAGGATCAGTTACAAACTTATTTACTTCAATTGTAGGTAACGTTTTTGGTTTTAAAGCTTTACGTGCTTTACGTTTAGAAGATTTACGTATTCCACCAG [397]
Enteromorpha_intestinalis GAAGGATCAGTTACAAACTTATTTACTTCAATTGTAGGTAACGTTTTTGGTTTTAAAGCTTTACGTGCTTTTCGTTTAGAAGATTTACGTATTCCACCAG [397]
Enteromorpha_compressa GAAGGATCAGTTACAAACTTATTTACTTCAATTGTAGGTAACGTTTTTGGTTTTAAAGCTTTACGTGCTTTACGTTTAGAAGATTTACGTATTCCACCAG [397]
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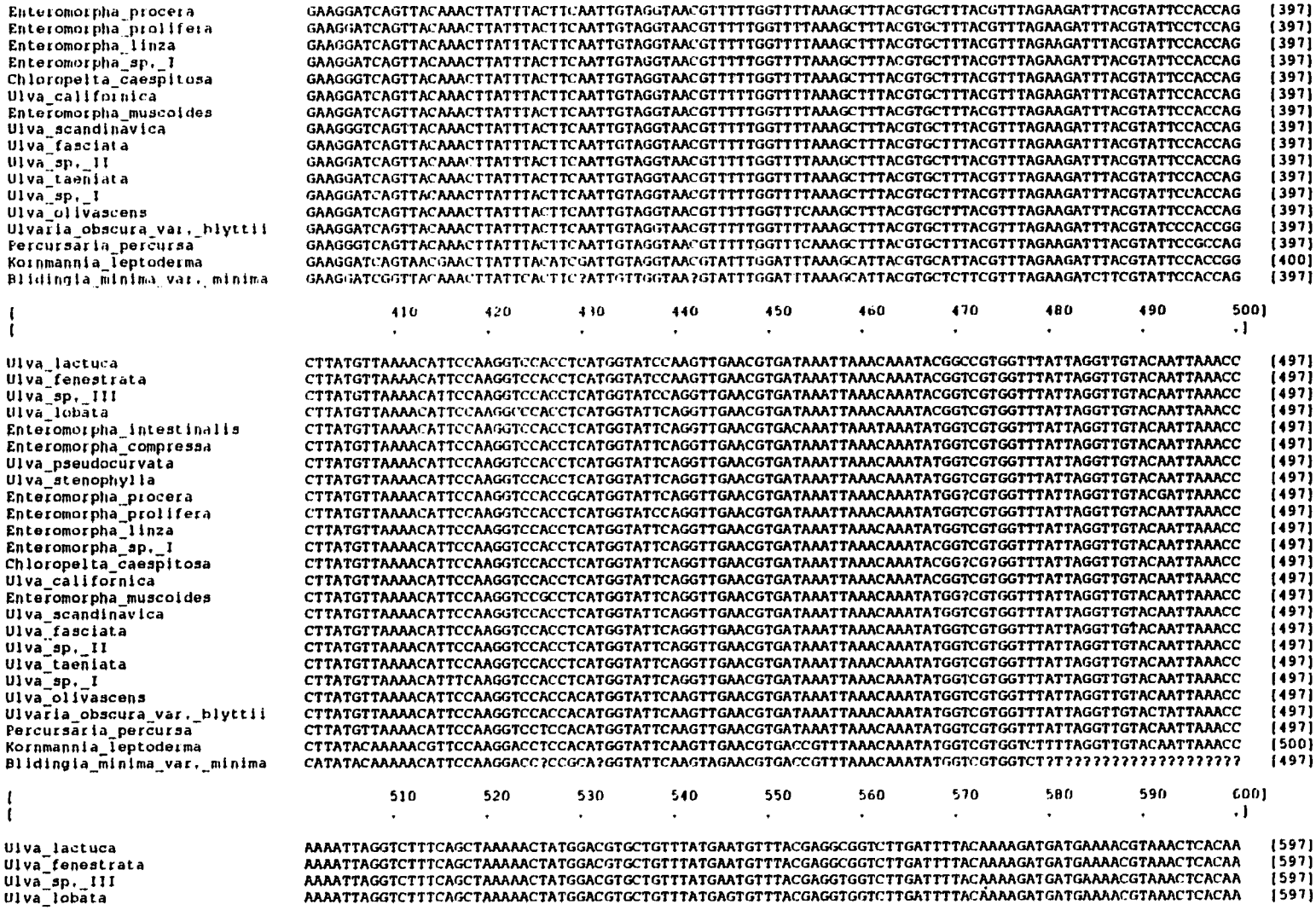
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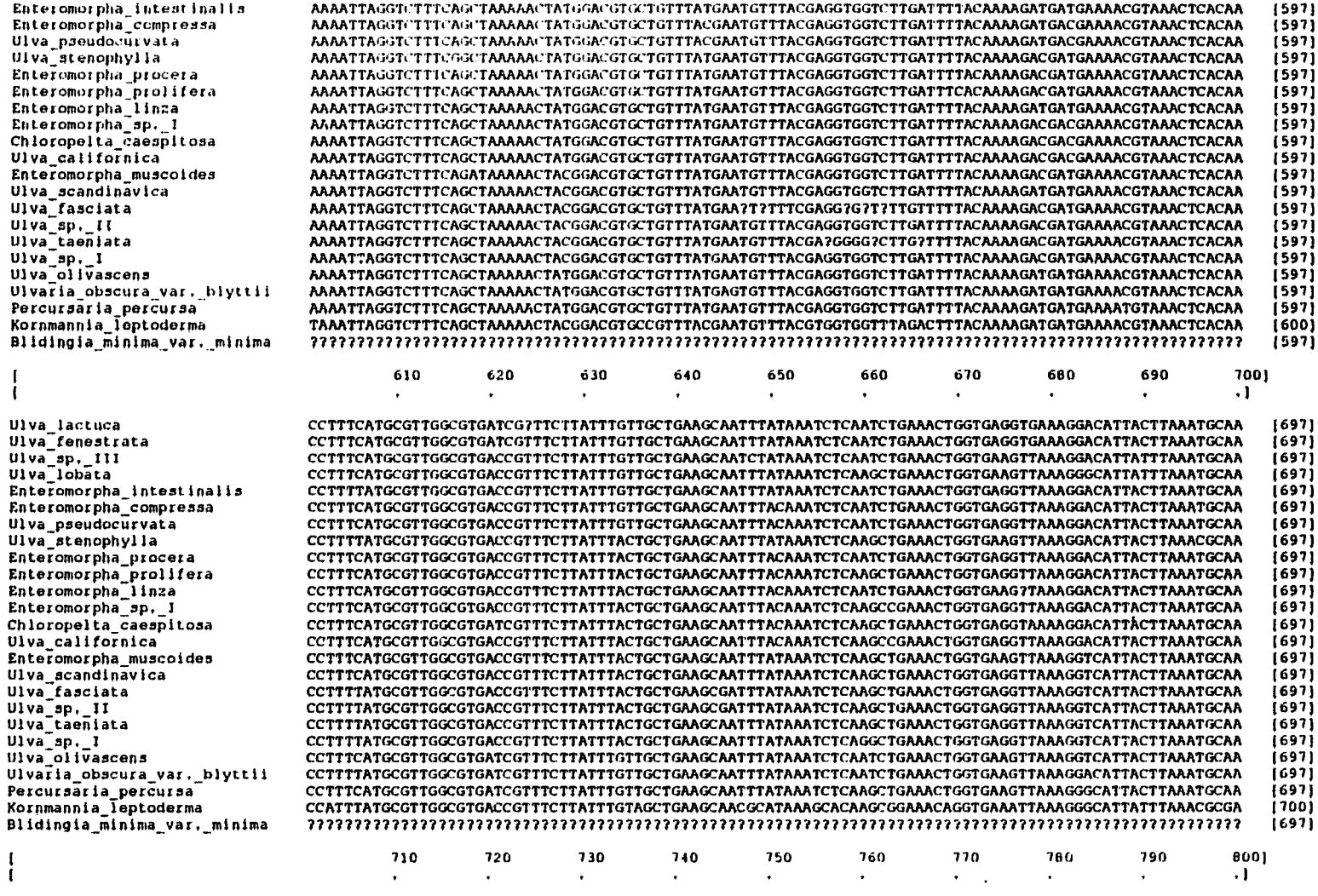
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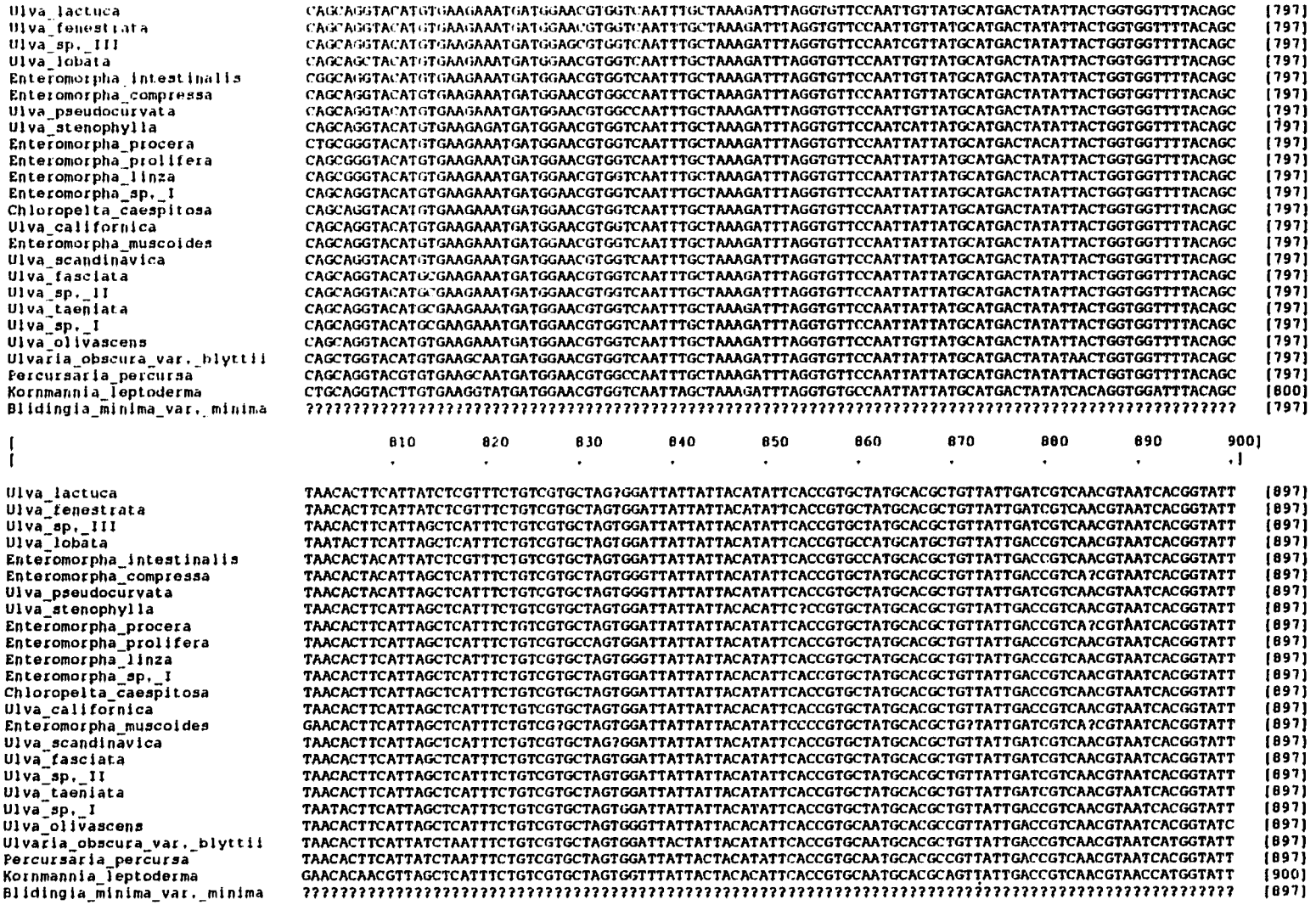
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Ulva_taeniata TAACACTTCATTAGCTCATTTCTGTCGTGCTAGTGGATTATTATTACATATTCACCGTGCTATGCACGCTGTTATTGATCGTCAACGTAATCACGGTATT [897]
Ulva_sp._I TAATACTTCATTAGCTCATTTCTGTCGTGCTAGTGGATTATTATTACATATTCACCGTGCTATGCACGCTGTTATTGACCGTCAACGTAATCACGGTATT [897]
Ulva_olivascens TAACACTTCATTAGCTCATTTCTGTCGTGCTAGTGGGTTATTATTACACATTCACCGTGCAATGCACGCCGTTATTGACCGTCAACGTAATCACGGTATC [897]
Ulvaria_obscura_var._blyttii TAACACTTCATTATCTAATTTCTGTCGTGCTAGTGGATTACTATTACATATTCACCGTGCAATGCACGCTGTTATTGACCGTCAACGTAATCATGGTATT [897]
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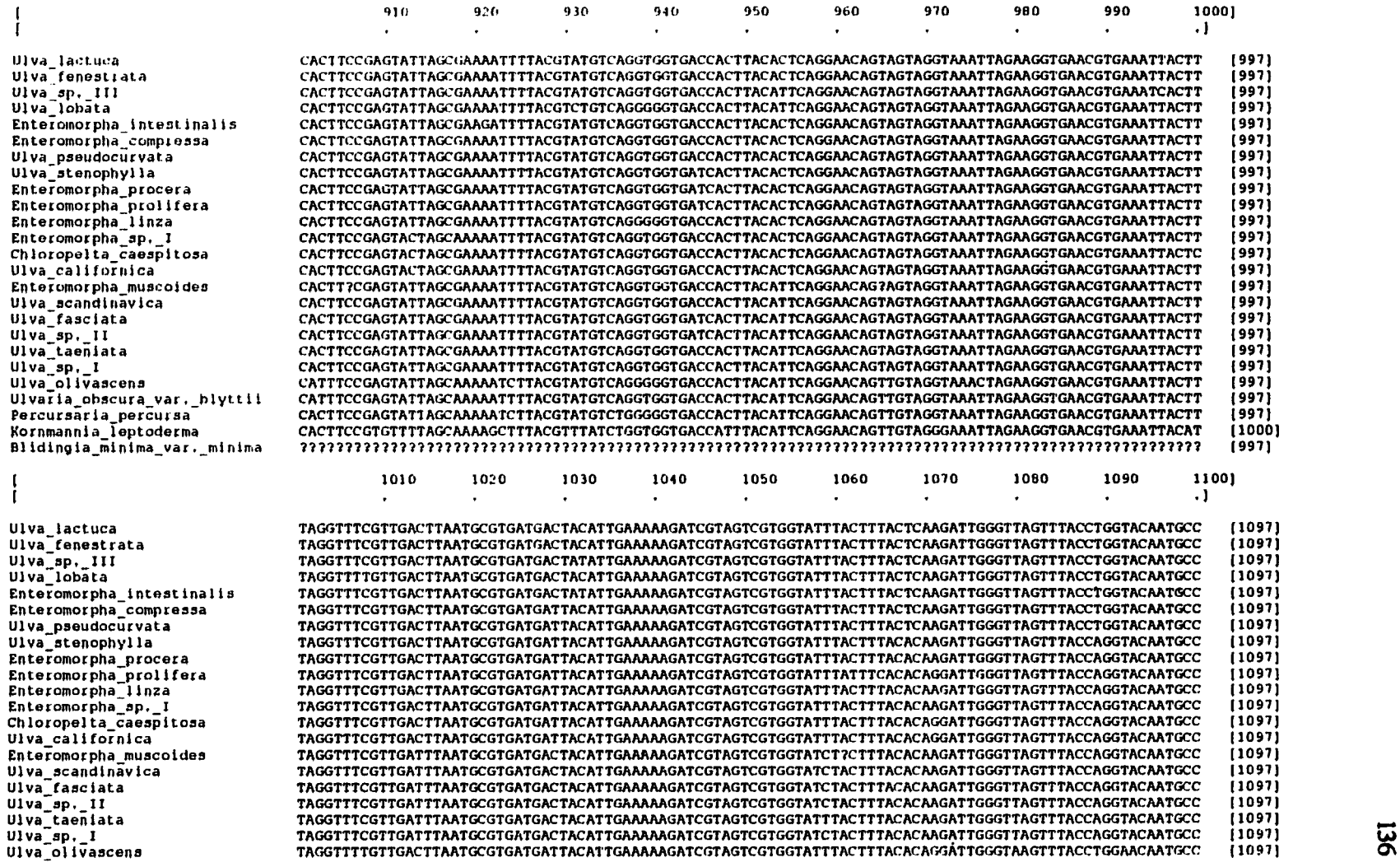
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Ulva_pseudocurvata CACTTCCGAGTATTAGCGAAAATTTTACGTATGTCAGGTGGTGACCACTTACACTCAGGAACAGTAGTAGGTAAATTAGAAGGTGAACGTGAAATTACTT [997]
Ulva_stenophylla CACTTCCGAGTATTAGCGAAAATTTTACGTATGTCAGGTGGTGATCACTTACACTCAGGAACAGTAGTAGGTAAATTAGAAGGTGAACGTGAAATTACTT [997]
Enteromorpha_procera CACTTCCGAGTATTAGCGAAAATTTTACGTATGTCAGGTGGTGATCACTTACACTCAGGAACAGTAGTAGGTAAATTAGAAGGTGAACGTGAAATTACTT [997]
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Ulva_taeniata CACTTCCGAGTATTAGCGAAAATTTTACGTATGTCAGGTGGTGACCACTTACATTCAGGAACAGTAGTAGGTAAATTAGAAGGTGAACGTGAAATTACTT [997]
Ulva_sp._I CACTTCCGAGTATTAGCGAAAATTTTACGTATGTCAGGTGGTGACCACTTACATTCAGGAACAGTAGTAGGTAAATTAGAAGGTGAACGTGAAATTACTT [997]
Ulva_olivascens CATTTCCGAGTATTAGCAAAAATCTTACGTATGTCAGGGGGTGACCACTTACATTCAGGAACAGTTGTAGGTAAACTAGAAGGTGAACGTGAAATTACTT [997]
Ulvaria_obscura_var._blyttii CATTTCCGAGTATTAGCAAAAATTTTACGTATGTCAGGTGGTGACCACTTACATTCAGGAACAGTTGTAGGTAAATTAGAAGGTGAACGTGAAATTACTT [997]
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Kornmannia_leptoderma CACTTCCGTGTTTTAGCAAAAGCTTTACGTTTATCTGGTGGTGACCATTTACATTCAGGAACAGTTGTAGGGAAATTAGAAGGTGAACGTGAAATTACAT [1000]
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Ulva_sp._III TAGGTTTCGTTGACTTAATGCGTGATGACTATATTGAAAAAGATCGTAGTCGTGGTATTTACTTTACTCAAGATTGGGTTAGTTTACCTGGTACAATGCC [1097]
Ulva_lobata TAGGTTTTGTTGACTTAATGCGTGATGACTACATTGAAAAAGATCGTAGTCGTGGTATTTACTTTACTCAAGATTGGGTTAGTTTACCTGGTACAATGCC [1097]
Enteromorpha_intestinalis TAGGTTTCGTTGACTTAATGCGTGATGACTATATTGAAAAAGATCGTAGTCGTGGTATTTACTTTACTCAAGATTGGGTTAGTTTACCTGGTACAATGCC [1097]
Enteromorpha_compressa TAGGTTTCGTTGACTTAATGCGTGATGATTACATTGAAAAAGATCGTAGTCGTGGTATTTACTTTACTCAAGATTGGGTTAGTTTACCTGGTACAATGCC [1097]
Ulva_pseudocurvata TAGGTTTCGTTGACTTAATGCGTGATGATTACATTGAAAAAGATCGTAGTCGTGGTATTTACTTTACTCAAGATTGGGTTAGTTTACCTGGTACAATGCC [1097]
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Enteromorpha_procera TAGGTTTCGTTGACTTAATGCGTGATGATTACATTGAAAAAGATCGTAGTCGTGGTATTTACTTTACACAAGATTGGGTTAGTTTACCAGGTACAATGCC [1097]
Enteromorpha_prolifera TAGGTTTCGTTGACTTAATGCGTGATGATTACATTGAAAAAGATCGTAGTCGTGGTATTTATTTCACACAGGATTGGGTTAGTTTACCAGGTACAATGCC [1097]
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Chloropelta_caespitosa TAGGTTTCGTTGACTTAATGCGTGATGATTACATTGAAAAAGATCGTAGTCGTGGTATTTACTTTACACAGGATTGGGTTAGTTTACCAGGTACAATGCC [1097]
Ulva_californica TAGGTTTCGTTGACTTAATGCGTGATGATTACATTGAAAAAGATCGTAGTCGTGGTATTTACTTTACACAGGATTGGGTTAGTTTACCAGGTACAATGCC [1097]
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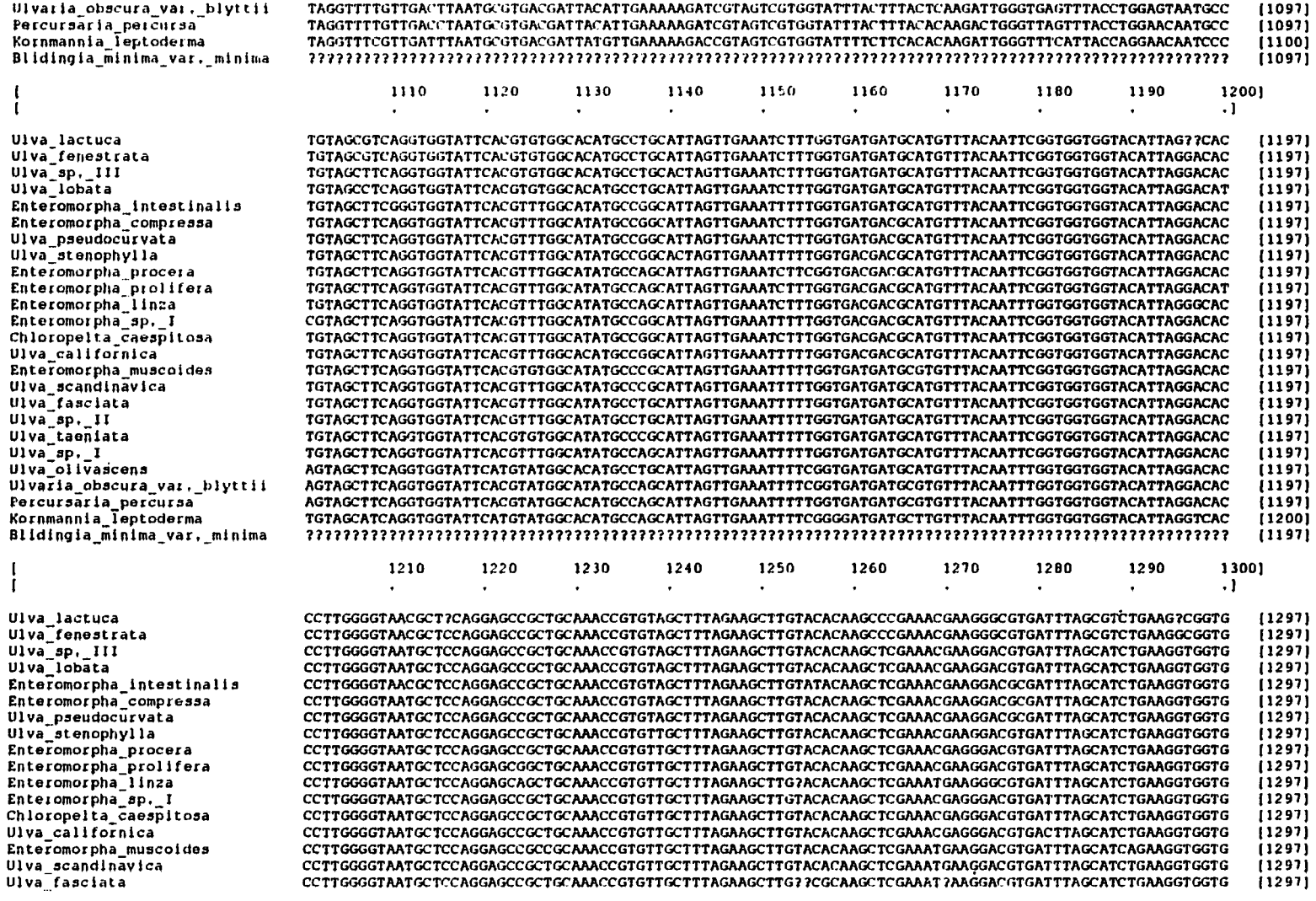
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Ulva_fenestrata TGTAGCGTCAGGTGGTATTCACGTGTGGCACATGCCTGCATTAGTTGAAATCTTTGGTGATGATGCATGTTTACAATTCGGTGGTGGTACATTAGGACAC [1197]
Ulva_sp._III TGTAGCTTCAGGTGGTATTCACGTGTGGCACATGCCTGCACTAGTTGAAATCTTTGGTGATGATGCATGTTTACAATTCGGTGGTGGTACATTAGGACAC [1197]
Ulva_lobata TGTAGCCTCAGGTGGTATTCACGTGTGGCACATGCCTGCATTAGTTGAAATCTTTGGTGATGATGCATGTTTACAATTCGGTGGTGGTACATTAGGACAT [1197]
Enteromorpha_intestinalis TGTAGCTTCGGGTGGTATTCACGTTTGGCATATGCCGGCATTAGTTGAAATTTTTGGTGATGATGCATGTTTACAATTCGGTGGTGGTACATTAGGACAC [1197]
Enteromorpha_compressa TGTAGCTTCAGGTGGTATTCACGTTTGGCATATGCCGGCATTAGTTGAAATCTTTGGTGATGACGCATGTTTACAATTCGGTGGTGGTACATTAGGACAC [1197]
Ulva_pseudocurvata TGTAGCTTCAGGTGGTATTCACGTTTGGCATATGCCGGCATTAGTTGAAATCTTTGGTGATGACGCATGTTTACAATTCGGTGGTGGTACATTAGGACAC [1197]
Ulva_stenophylla TGTAGCTTCAGGTGGTATTCACGTTTGGCATATGCCGGCACTAGTTGAAATTTTTGGTGACGACGCATGTTTACAATTCGGTGGTGGTACATTAGGACAC [1197]
Enteromorpha_procera TGTAGCTTCAGGTGGTATTCACGTTTGGCATATGCCAGCATTAGTTGAAATCTTCGGTGACGACGCATGTTTACAATTCGGTGGTGGTACATTAGGACAC [1197]
Enteromorpha_prolifera TGTAGCTTCAGGTGGTATTCACGTTTGGCATATGCCAGCATTAGTTGAAATCTTTGGTGACGACGCATGTTTACAATTCGGTGGTGGTACATTAGGACAT [1197]
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Chloropelta_caespitosa TGTAGCTTCAGGTGGTATTCACGTTTGGCATATGCCGGCATTAGTTGAAATCTTTGGTGACGACGCATGTTTACAATTCGGTGGTGGTACATTAGGACAC [1197]
Ulva_californica TGTAGCTTCAGGTGGTATTCACGTTTGGCACATGCCGGCATTAGTTGAAATTTTTGGTGACGACGCATGTTTACAATTCGGTGGTGGTACATTAGGACAC [1197]
Enteromorpha_muscoides TGTAGCTTCAGGTGGTATTCACGTGTGGCATATGCCCGCATTAGTTGAAATTTTTGGTGATGATGCGTGTTTACAATTCGGTGGTGGTACATTAGGACAC [1197]
Ulva_scandinavica TGTAGCTTCAGGTGGTATTCACGTTTGGCATATGCCCGCATTAGTTGAAATTTTTGGTGATGATGCATGTTTACAATTCGGTGGTGGTACATTAGGACAC [1197]
Ulva_fasciata TGTAGCTTCAGGTGGTATTCACGTTTGGCATATGCCTGCATTAGTTGAAATTTTTGGTGATGATGCATGTTTACAATTCGGTGGTGGTACATTAGGACAC [1197]
Ulva_sp._II TGTAGCTTCAGGTGGTATTCACGTTTGGCATATGCCTGCATTAGTTGAAATTTTTGGTGATGATGCATGTTTACAATTCGGTGGTGGTACATTAGGACAC [1197]
Ulva_taeniata TGTAGCTTCAGGTGGTATTCACGTGTGGCATATGCCCGCATTAGTTGAAATTTTTGGTGATGATGCATGTTTACAATTCGGTGGTGGTACATTAGGACAC [1197]
Ulva_sp._I TGTAGCTTCAGGTGGTATTCACGTTTGGCATATGCCAGCATTAGTTGAAATTTTTGGTGATGATGCATGTTTACAATTCGGTGGTGGTACATTAGGACAC [1197]
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Percursaria_percursa AGTAGCTTCAGGTGGTATTCACGTATGGCACATGCCAGCATTAGTTGAAATTTTTGGTGATGATGCGTGTTTACAATTTGGTGGTGGTACATTAGGACAC [1197]
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Ulva_fenestrata CCTTGGGGTAACGCTCCAGGAGCCGCTGCAAACCGTGTAGCTTTAGAAGCTTGTACACAAGCCCGAAACGAAGGGCGTGATTTAGCGTCTGAAGGCGGTG [1297]
Ulva_sp._III CCTTGGGGTAATGCTCCAGGAGCCGCTGCAAACCGTGTAGCTTTAGAAGCTTGTACACAAGCTCGAAACGAAGGACGTGATTTAGCATCTGAAGGTGGTG [1297]
Ulva_lobata CCTTGGGGTAATGCTCCAGGAGCCGCTGCAAACCGTGTAGCTTTAGAAGCTTGTACACAAGCTCGAAACGAAGGACGTGATTTAGCATCTGAAGGTGGTG [1297]
Enteromorpha_intestinalis CCTTGGGGTAACGCTCCAGGAGCCGCTGCAAACCGTGTAGCTTTAGAAGCTTGTATACAAGCTCGAAACGAAGGACGCGATTTAGCATCTGAAGGTGGTG [1297]
Enteromorpha_compressa CCTTGGGGTAATGCTCCAGGAGCCGCTGCAAACCGTGTAGCTTTAGAAGCTTGTACACAAGCTCGAAACGAAGGACGCGATTTAGCATCTGAAGGTGGTG [1297]
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Ulva_stenophylla CCTTGGGGTAATGCTCCAGGAGCCGCTGCAAACCGTGTTGCTTTAGAAGCTTGTACACAAGCTCGAAACGAAGGACGTGATTTAGCATCTGAAGGTGGTG [1297]
Enteromorpha_procera CCTTGGGGTAATGCTCCAGGAGCCGCTGCAAACCGTGTTGCTTTAGAAGCTTGTACACAAGCTCGAAACGAGGGACGTGATTTAGCATCTGAAGGTGGTG [1297]
Enteromorpha_prolifera CCTTGGGGTAATGCTCCAGGAGCGGCTGCAAACCGTGTTGCTTTAGAAGCTTGTACACAAGCTCGAAACGAAGGACGTGATTTAGCATCTGAAGGTGGTG [1297]
Enteromorpha_linza CCTTGGGGTAATGCTCCAGGAGCAGCTGCAAACCGTGTTGCTTTAGAAGCTTG?ACACAAGCTCGAAATGAAGGGCGTGATTTAGCATCTGAAGGTGGTG [1297]
Enteromorpha_sp._I CCTTGGGGTAATGCTCCAGGAGCCGCTGCAAACCGTGTTGCTTTAGAAGCTTGTACACAAGCTCGAAACGAGGGACGTGATTTAGCATCTGAAGGTGGTG [1297]
Chloropelta_caespitosa CCTTGGGGTAATGCTCCAGGAGCCGCTGCAAACCGTGTTGCTTTAGAAGCTTGTACACAAGCTCGAAACGAGGGACGTGATTTAGCATCTGAAGGTGGTG [1297]
Ulva_californica CCTTGGGGTAATGCTCCAGGAGCCGCTGCAAACCGTGTTGCTTTAGAAGCTTGTACACAAGCTCGAAACGAGGGACGTGACTTAGCATCTGAAGGTGGTG [1297]
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Ulva_fasciata CCTTGGGGTAATGCTCCAGGAGCCGCTGCAAACCGTGTTGCTTTAGAAGCTTG??CGCAAGCTCGAAAT?AAGGACGTGATTTAGCATCTGAAGGTGGTG [1297]

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Ulva_sp._I                     CCTTGGGGTAATGCTCCAGGAGCCGCTGCAAACCGTGTTGCTTTAGAAGCTTGTACACAAGCTCGAAATGAAGGACGTGATTTAGCATCTGAAGGTGGTG   [1297]
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Kornmannia_leptoderma          CCTTGGGGTAATGCACCTGGAGCAGCGGCTAACCGTGTTGCCTTAGAAGCTTGTACTCAAGCTCGAAACGAAGGTCGTGATTTAGCGCGTGAAGGTGGGG   [1300]
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|                                        .           .           .           .           .        |

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Ulva_sp._III                   ATGTAATTCGTGCTGCTTGTAAATGGAGTCCTGAATTAGCTGCAGCTTGTGAAGTAT   [1354]
Ulva_lobata                    ATGTAATTCGTGCTGCTTGTAAATGGAGTCCTGAATTAGCTGCAGCTTGTGAAGTAT   [1354]
Enteromorpha_intestinalis      ATGTAATTCGTGCTGCTTGTAAATGGAGCCCTGAATTAGCTGCAGCTTGTGAAGTAT   [1354]
Enteromorpha_compressa         ATGTAATTCGTGCTGCTTGTAAATGGAGTCCTGAATTAGCTGCAGCTTGTGAAGTAT   [1354]
Ulva_pseudocurvata             ATGTAATTCGTGCTGCTTGTAAATGGAGTCCTGAATTAGCTGCAGCTTGTGAAGTAT   [1354]
Ulva_stenophylla               ATGTAATTCGTGCTGCTTGTAAATGGAGTCCTGAATTA?CTGCAGCTTGTGAAGTAT   [1354]
Enteromorpha_procera           ATGTAATTCGTGCTGCTTGTAAATGGAGTCCTGAATTAGCTGCAGCTTGTGAAGTAT   [1354]
Enteromorpha_prolifera         ATGTAATTCGTGCTGCTTGTAAATGGAGTCCTGAATTAGCTGCAGCTTGTGAAGTAT   [1354]
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Enteromorpha_sp._I             ACGTAATTCGTGCTGCTTGTAAATGGAGTCCTGAATTAGCTGCAGCTTGTGAAGTAT   [1354]
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Ulva_californica               ATGTAATTCGTGCTGCTTGTAAATGGAGTCCTGAATTAGCTGCAGCTTGTGAAGTAT   [1354]
Enteromorpha_muscoides         ATGTAATTCGTGCTGCT?GTAAATGGAGTCCTGAATTAGCTGCAGC?TGTGAAGTAT   [1354]
Ulva_scandinavica              ATGTAATTCGTGCTGCTTGTAAATGGAGTCCTGAATTAGCTGCAGCTTGTGAAGTAT   [1354]
Ulva_fasciata                  ATGTAATTCGTGCTGCTTGTAAATGGAGTCCTGAATTAGCTGCAGCTTGTGAAGTAT   [1354]
Ulva_sp._II                    ATGTAATTCGTGCTGCTTGTAAATGGAGTCCTGAATTAGCTGCAGCTTGTGAAGTAT   [1354]
Ulva_taeniata                  ATGTAATTCGTGCTGCTTGTAAATGGAGTCCTGAATTAGCTGCAGCTTGTGAAGTAT   [1354]
Ulva_sp._I                     ATGTAATTCGTGCTGCTTGTAAATGGAGTCCTGAATTAGCTGCAGCTTGTGAAGTAT   [1354]
Ulva_olivascens                ATGTAATTCGTGCTGCTTGTAAATGGAGTCCTGAATTAGCTGCAGCTTGTGAAGTAT   [1354]
Ulvaria_obscura_var._blyttii   ATGTAATTCGTGCTGCTTGTAAATGGAGTCCTGAATTAGCTGCAGCTTGTGAAGTAT   [1354]
Percursaria_percursa           ATGTAATTCGTGCCGCTTGTAAATGGAGTCCTGAATTAGCTGCAGCTTGTGAAGTAT   [1354]
Kornmannia_leptoderma          ATGTTATTCGTAAAGCTTGTGAATGGAGTCCTGAATTAGCGGCAGCATGTGAAGTGT   [1357]
Blidingia_minima_var._minima   ??????????????????????????????????????????????????????????   [1354]
;
END;


BEGIN CODONS;
CODESET * UNTITLED = Universal: all ;
END;

BEGIN ASSUMPTIONS;
        OPTIONS  DEFTYPE=unord PolyTcount=MINSTEPS ;
END;
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Appendix E. Sequence alignment in NEXUS format for ITS nrDNA data used in Chapter 3. Highly variable regions of ITS 1 and ITS 2 include positions 36 – 189, 220 – 521, 539 – 546, 788 – 859, 880 – 920. Positions 539 – 546 were excluded from all analyses.

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FORMAT DATATYPE=DNA  MISSING=? GAP=-  INTERLEAVE ;
MATRIX

[                          10        20        30        40        50        60        70        80        90       100]
[                          .         .         .         .         .         .         .         .         .         .]

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Ulva_fenestrataIII_OR      AAACCGATCAAACCAACCCCAGAGAACCTGCGGGCTCCGGC----------------------------------------------- [41]
Ulva_fenestrata_BC         AAACCGATCAAACCAACCCCAGAGAACCTGCGGGCTCCGGC----------------------------------------------- [41]
Ulva_fenestrataII_OR       ??????????AACCAACCCCAGAGAACCTGCGGGCTCCGGC----------------------------------------------- [41]
Ulva_fenestrata_NCA        AAACCGATCAAACCAACCCCAGAGAACCTGCGGGCTCCGGC----------------------------------------------- [41]
Ulva_fenestrata_WA         AAACCGATCAAACCAACCCCAGAGAACCTGCGGGCTCCGGC----------------------------------------------- [41]
Ulva_fenestrata_AK         ???????????????????????????????????????????????????????????????????????????????????? [100]
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Ulva_fenestrataIII_SCA     AAACCGATCAAACCAATCCCAGAGAACTTGCGGGCTTCGGC----------------------------------------------- [41]
Ulva_fenestrataIV_SCA      AAACCGATCAAACCAATCCCAGAGAACTTGCGGGCTTCGGC----------------------------------------------- [41]
Ulva_fenestrata_JH         AAACCGATCAAACCAATCCCAGAGAACTTGCGGGCTTCGGC----------------------------------------------- [41]
Ulva_fenestrataII_SCA      AAACCGATCAAACCAATCCCAGAGAACTTGCGGGCTTCGGC----------------------------------------------- [41]
Ulva_rotundata_EU          AAACCGATCAAACCAATCCCAGAGAACTTGCGGGCTTCGG------------------------------------------------ [40]
Ulva_fenestrata_CCA        ????????????????????CCCTGA?AACCTGCGGGCTTCGGC----------------------------------------------- [41]
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Enteromorpha_intestinalis_BC AAACCGATCAAACCAACCCCAGCGAACTTGCGGGC--CG-C-TCTC----------GTGGTGGC----------------------------- [50]
Enteromorpha_intestinalis_NCA AAACCGATCAAACCAACCCCAGCGAACTTGCGGGC--CG-C-TCTC----------GTGGTGGC----------------------------- [50]
Enteromorpha_intestinalis_AK AAACCGATCAAACCAACCCCAGCGAACTTGCGGGC--CG-C-TCTC----------GTGGTGGC----------------------------- [50]
Enteromorpha_intestinalis_EU AAACCGATCAAACCAACCCCAGCGAACTTGCGGGC--CG-C-TCTC----------GTGGTGGC----------------------------- [50]
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Enteromorpha_flexuosa_EU   AAACCGATCAAACCAATCACAGAGCACCTGCGGGC----------------------------GCTCACCTCCCTTGCGGGGGGTGGGGCGGC----- [65]
Enteromorpha_prolifera_NCA AAACCGATCAAACCAATCACAGAGCACCTGCGGGC----------------------------------------------------------GCTCA [40]
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Enteromorpha_prolifera_WA  AAACCGATCAAACCAATCACAGAGCACCTGCGGGC----------------------------------------------------------GCTCA [40]
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Ulva_californicaII_CCA     AAACCGATCAAACCAATCACAGAGCACCTGCGGGC----------------------------------------------------------GCTCA [40]
Ulva_californica_BC        AAACCGATCAAACCAATCACAGAGCACCTGCGGGC----------------------------------------------------------GCTCA [40]
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Ulva_californicaII_NCA     AAACCGATCAAACCAATCACAGAGCACCTGCGGGC----------------------------------------------------------GCTCA [40]
Ulva_californica_WA        AAACCGATCAAACCAATCACAGAGCACCTGCGGGC----------------------------------------------------------GCTCA [40]
Ulva_sp._EU                AAACCGATCAAACCAATCACAGAGCACCTGCGGGC----------------------------------------------------------GCTCA [40]
Chloropelta_caespitosa_CCA AAACCGATCAAACCAATCACAGAGCACTTGCGGGC----------------------------------------------------------GCTCA [40]
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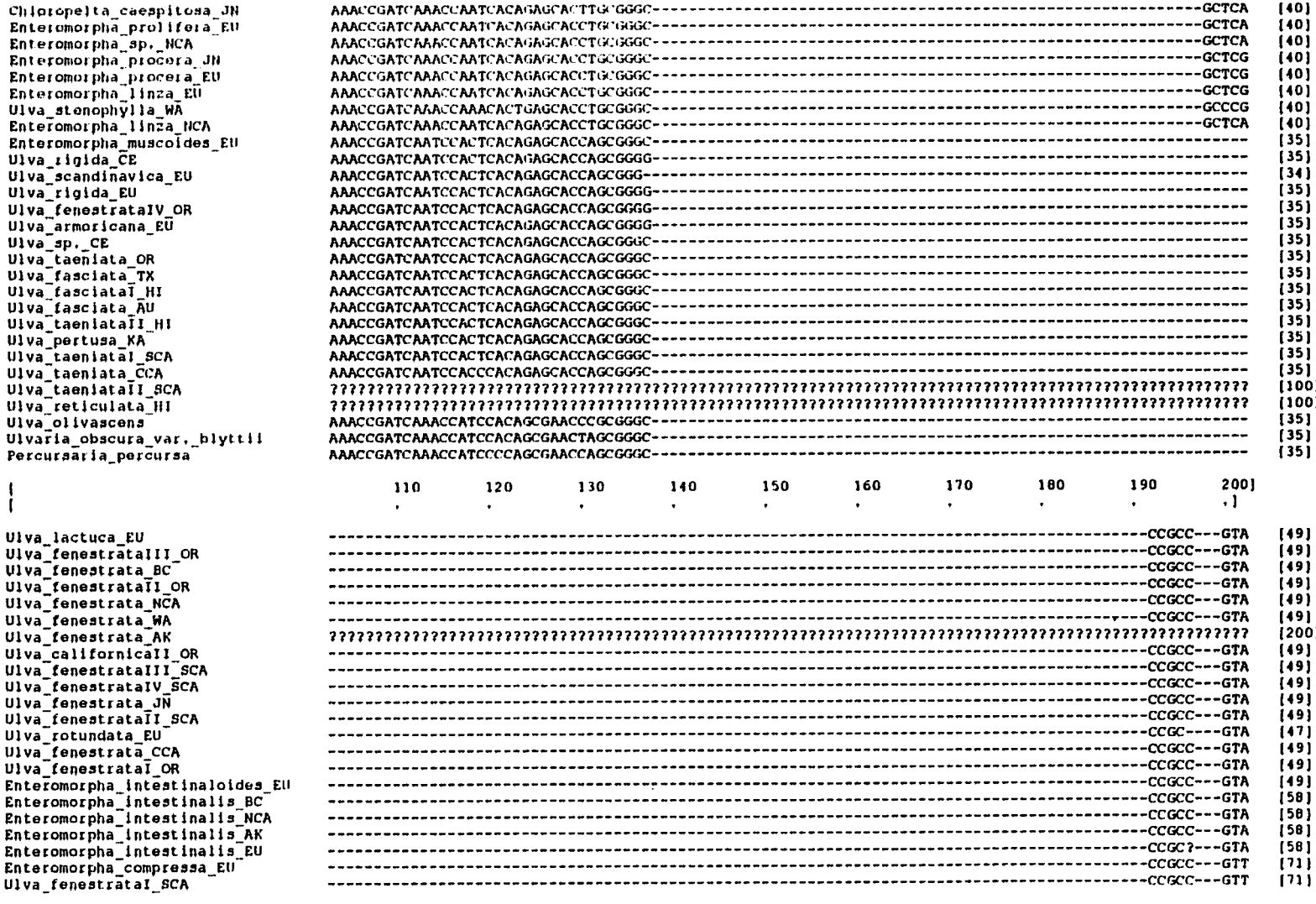
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Ulva_pertusa_KA AAACCGATCAATCCACTCACAGAGCACCAGCGGGC---------- [35]
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Ulva_fenestrata_AK ?? [200]
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Ulva_fenestrataIV_SCA ----------CCGCC---GTA [49]
Ulva_fenestrata_JN ----------CCGCC---GTA [49]
Ulva_fenestrataII_SCA ----------CCGCC---GTA [49]
Ulva_rotundata_EU ----------CCGC----GTA [47]
Ulva_fenestrata_CCA ----------CCGCC---GTA [49]
Ulva_fenestrataI_OR ----------CCGCC---GTA [49]
Enteromorpha_intestinaloides_EU ----------CCGCC---GTA [49]
Enteromorpha_intestinalis_BC ----------CCGCC---GTA [58]
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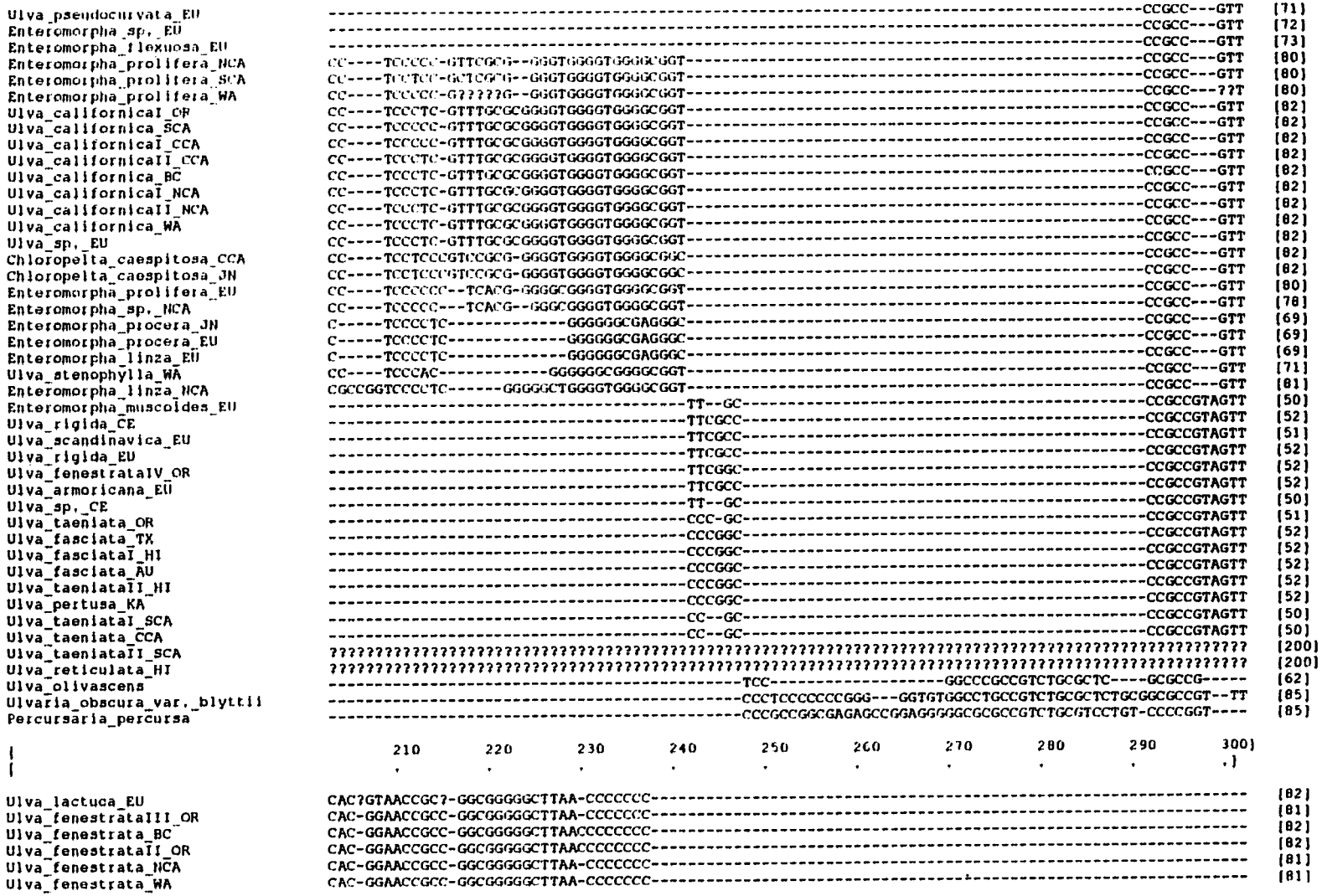
Enteromorpha_intestinalis_EU ----------CCGC?---GTA [58]
Enteromorpha_compressa_EU ----------CCGCC---GTT [71]
Ulva_fenestrataI_SCA ----------CCGCC---GTT [71]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Enteromorpha_prolifera_SCA
Enteromorpha_prolifera_WA
Ulva_californicaI_OR
Ulva_californica_SCA
Ulva_californicaI_CCA
Ulva_californicaII_CCA
Ulva_californica_BC
Ulva_californicaI_NCA
Ulva_californicaII_NCA
Ulva_californica_WA
Ulva_sp._EU
Chloropelta_caespitosa_CCA
Chloropelta_caespitosa_JN
Enteromorpha_prolifera_EU
Enteromorpha_sp._NCA
Enteromorpha_procera_JN
Enteromorpha_procera_EU
Enteromorpha_linza_EU
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Enteromorpha_muscoides_EU
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Ulva_taeniataII_HI
Ulva_pertusa_KA
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Ulva_olivascens
Ulvaria_obscura_var._blyttii
Percursaria_percursa
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290
300
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Ulva_fenestrata_NCA
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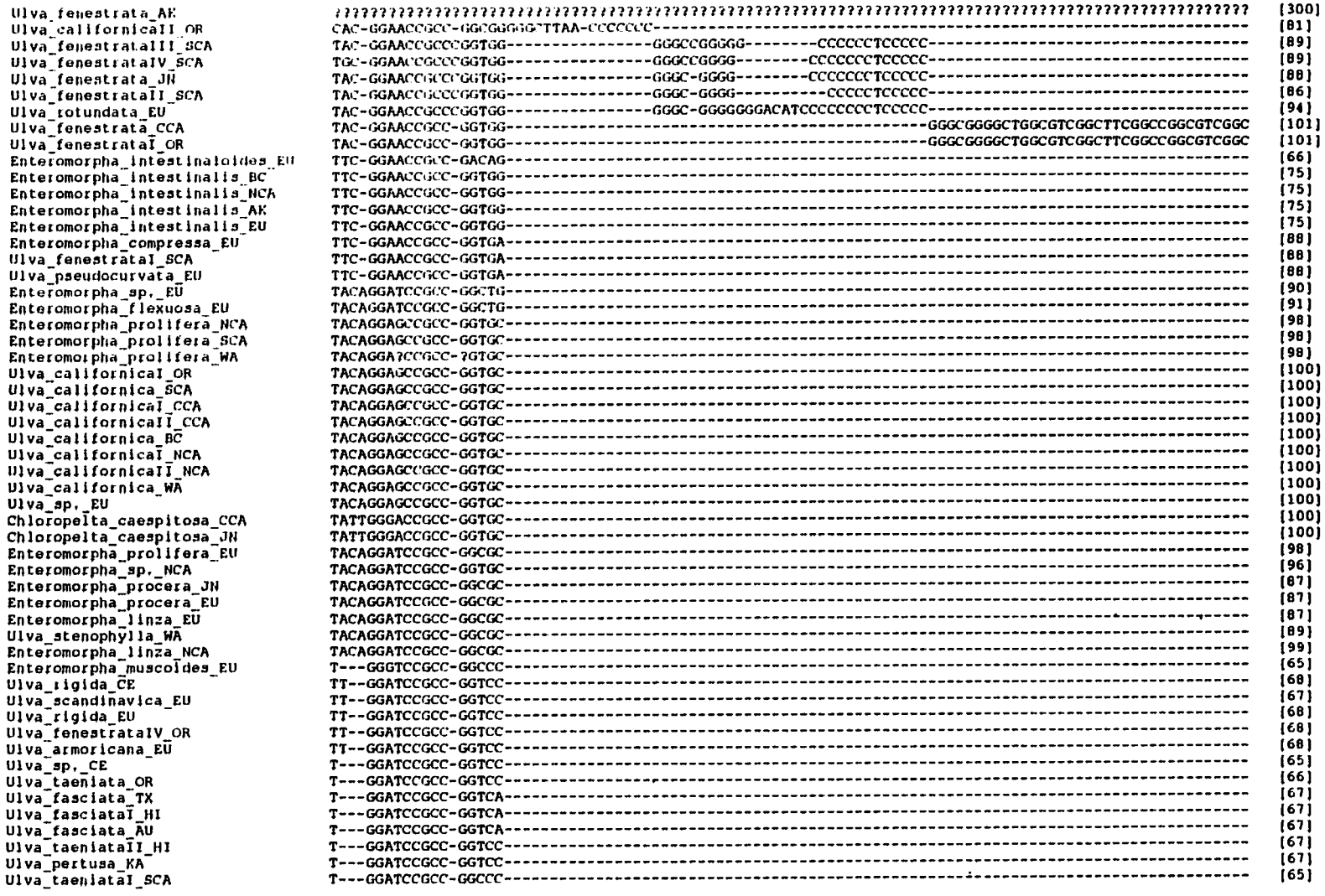
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Ulva_fenestrataIV_SCA TGC-GGAACCGCCCGGTGG----------GGGCCGGGG--------CCCCCCCTCCCCC---------- [89]
Ulva_fenestrata_JN TAC-GGAACCGCCCGGTGG----------GGGC-GGGG--------CCCCCCCTCCCCC---------- [88]
Ulva_fenestrataII_SCA TAC-GGAACCGCCCGGTGG----------GGGC-GGGG---------CCCCCTCCCCC---------- [86]
Ulva_rotundata_EU TAC-GGAACCGCCCGGTGG----------GGGC-GGGGGGGACATCCCCCCCCTCCCCC---------- [94]
Ulva_fenestrata_CCA TAC-GGAACCGCC-GGTGG----------GGGCGGGGCTGGCGTCGGCTTCGGCCGGCGTCGGC [101]
Ulva_fenestrataI_OR TAC-GGAACCGCC-GGTGG----------GGGCGGGGCTGGCGTCGGCTTCGGCCGGCGTCGGC [101]
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Enteromorpha_intestinalis_BC TTC-GGAACCGCC-GGTGG---------- [75]
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Enteromorpha_intestinalis_EU TTC-GGAACCGCC-GGTGG---------- [75]
Enteromorpha_compressa_EU TTC-GGAACCGCC-GGTGA---------- [88]
Ulva_fenestrataI_SCA TTC-GGAACCGCC-GGTGA---------- [88]
Ulva_pseudocurvata_EU TTC-GGAACCGCC-GGTGA---------- [88]
Enteromorpha_sp._EU TACAGGATCCGCC-GGCTG---------- [90]
Enteromorpha_flexuosa_EU TACAGGATCCGCC-GGCTG---------- [91]
Enteromorpha_prolifera_NCA TACAGGAGCCGCC-GGTGC---------- [98]
Enteromorpha_prolifera_SCA TACAGGAGCCGCC-GGTGC---------- [98]
Enteromorpha_prolifera_WA TACAGGA?CCGCC-?GTGC---------- [98]
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Enteromorpha_linza_EU TACAGGATCCGCC-GGCGC---------- [87]
Ulva_stenophylla_WA TACAGGATCCGCC-GGCGC---------- [89]
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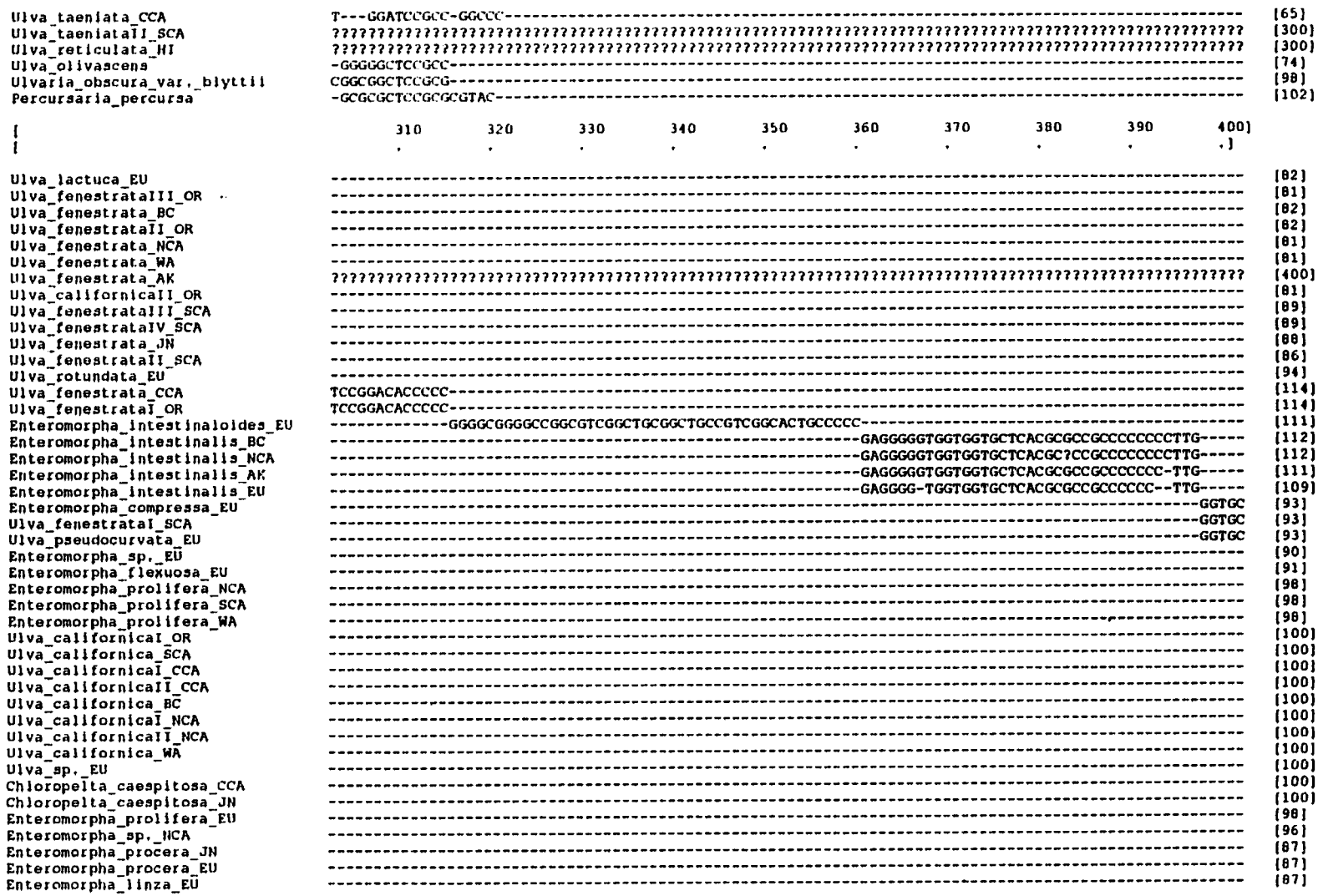
Enteromorpha_muscoides_EU T---GGGTCCGCC-GGCCC---------- [65]
Ulva_rigida_CE TT--GGATCCGCC-GGTCC---------- [68]
Ulva_scandinavica_EU TT--GGATCCGCC-GGTCC---------- [67]
Ulva_rigida_EU TT--GGATCCGCC-GGTCC---------- [68]
Ulva_fenestrataIV_OR TT--GGATCCGCC-GGTCC---------- [68]
Ulva_armoricana_EU TT--GGATCCGCC-GGTCC---------- [68]
Ulva_sp._CE T---GGATCCGCC-GGTCC---------- [65]
Ulva_taeniata_OR T---GGATCCGCC-GGTCC---------- [66]
Ulva_fasciata_TX T---GGATCCGCC-GGTCA---------- [67]
Ulva_fasciataI_HI T---GGATCCGCC-GGTCA---------- [67]
Ulva_fasciata_AU T---GGATCCGCC-GGTCA---------- [67]
Ulva_taeniataII_HI T---GGATCCGCC-GGTCC---------- [67]
Ulva_pertusa_KA T---GGATCCGCC-GGTCC---------- [67]
Ulva_taeniataI_SCA T---GGATCCGCC-GGCCC---------- [65]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Ulva_reticulata_HI ?? [300]
Ulva_olivascens -GGGGGCTCCGCC---------- [74]
Ulvaria_obscura_var._blyttii CGGCGGCTCCGCG---------- [98]
Percursaria_percursa -GCGCGCTCCGCGCGTAC---------- [102]
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[. . . . .]
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Ulva_fenestrataIII_OR ---------- [81]
Ulva_fenestrata_BC ---------- [82]
Ulva_fenestrataII_OR ---------- [82]
Ulva_fenestrata_NCA ---------- [81]
Ulva_fenestrata_WA ---------- [81]
Ulva_fenestrata_AK ?? [400]
Ulva_californicaII_OR ---------- [81]
Ulva_fenestrataIII_SCA ---------- [89]
Ulva_fenestrataIV_SCA ---------- [89]
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Ulva_fenestrataII_SCA ---------- [86]
Ulva_rotundata_EU ---------- [94]
Ulva_fenestrata_CCA TCCGGACACCCCC---------- [114]
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Enteromorpha_compressa_EU ----------GGTGC [93]
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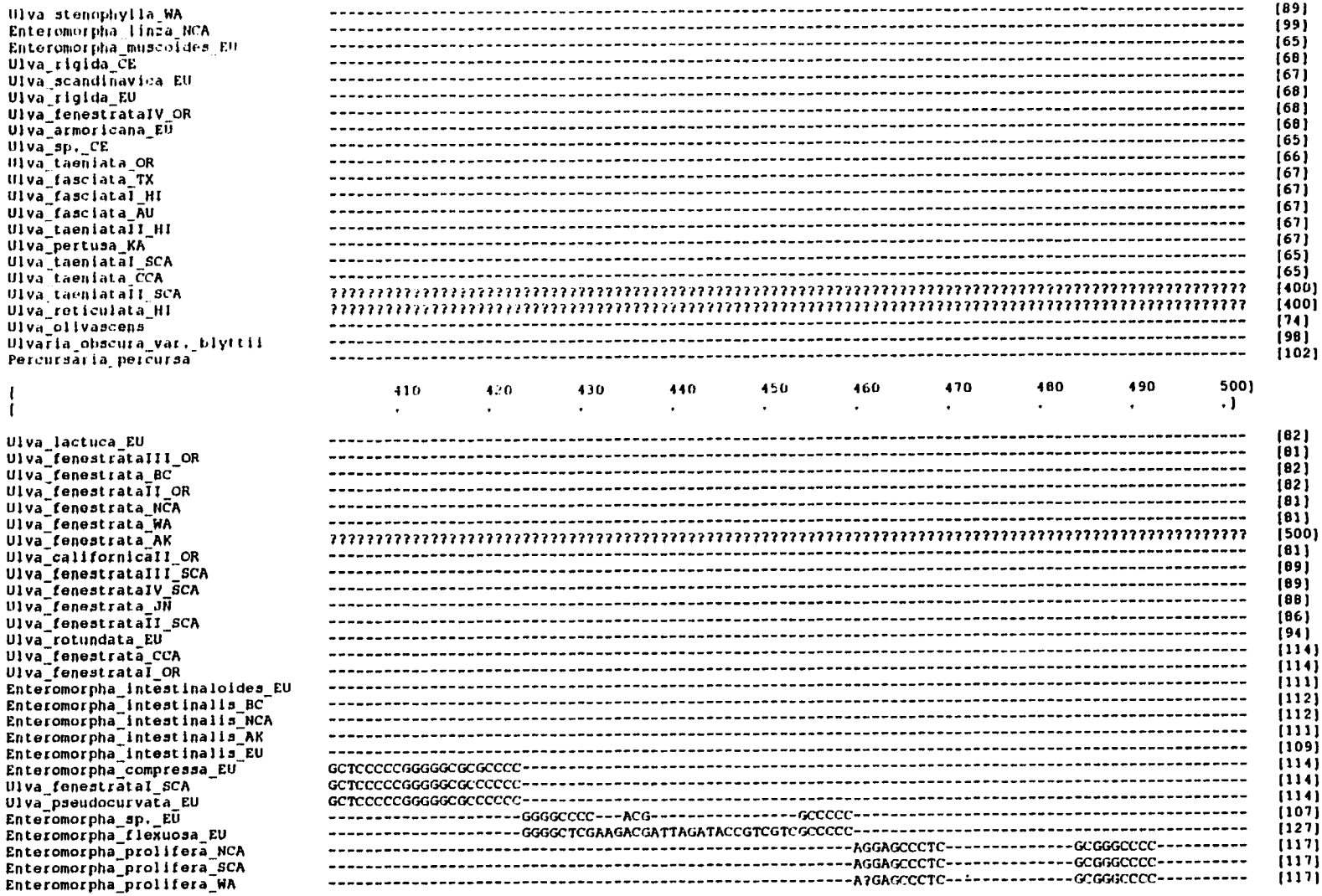
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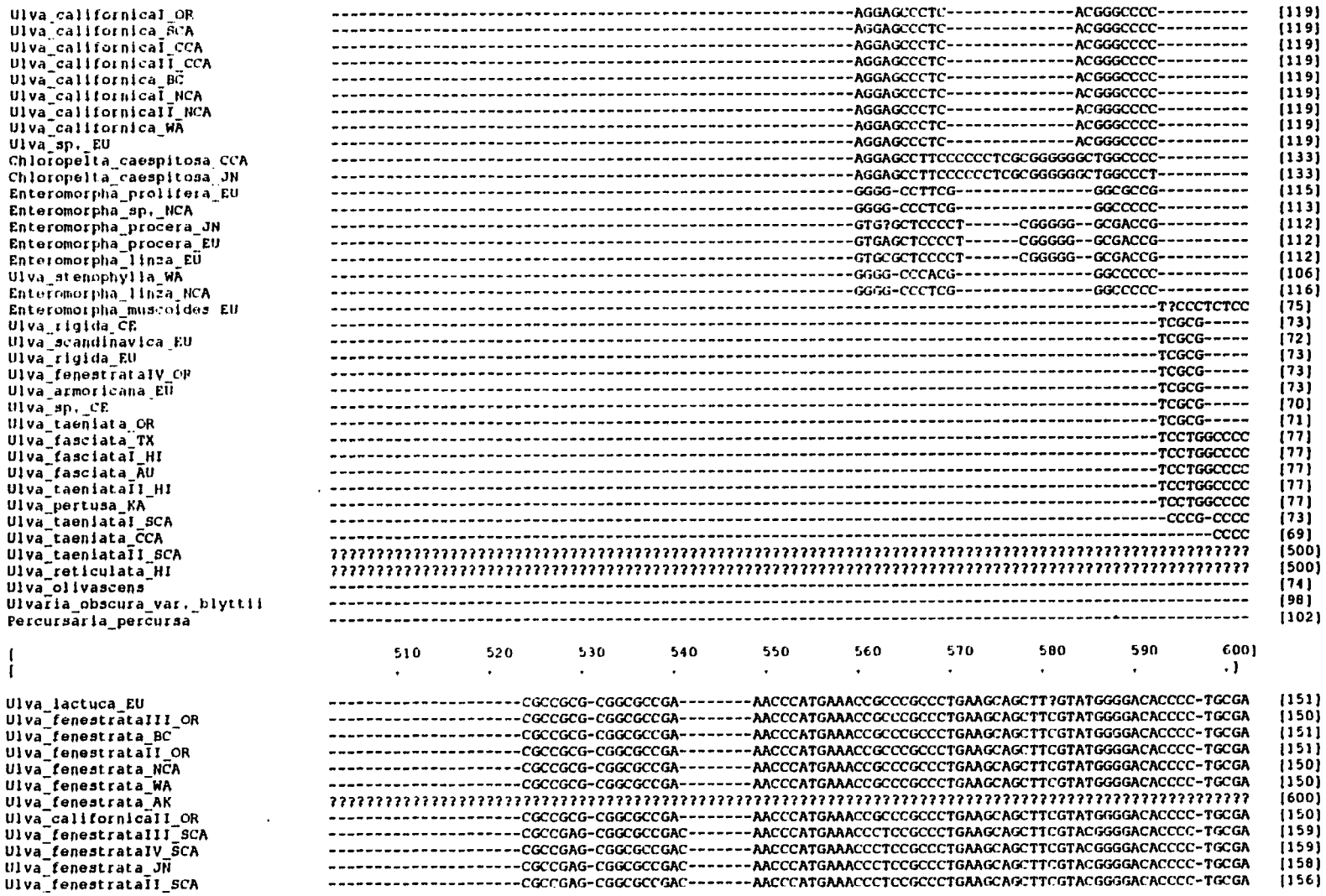
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Ulva_sp._EU
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Chloropelta_caespitosa_JN
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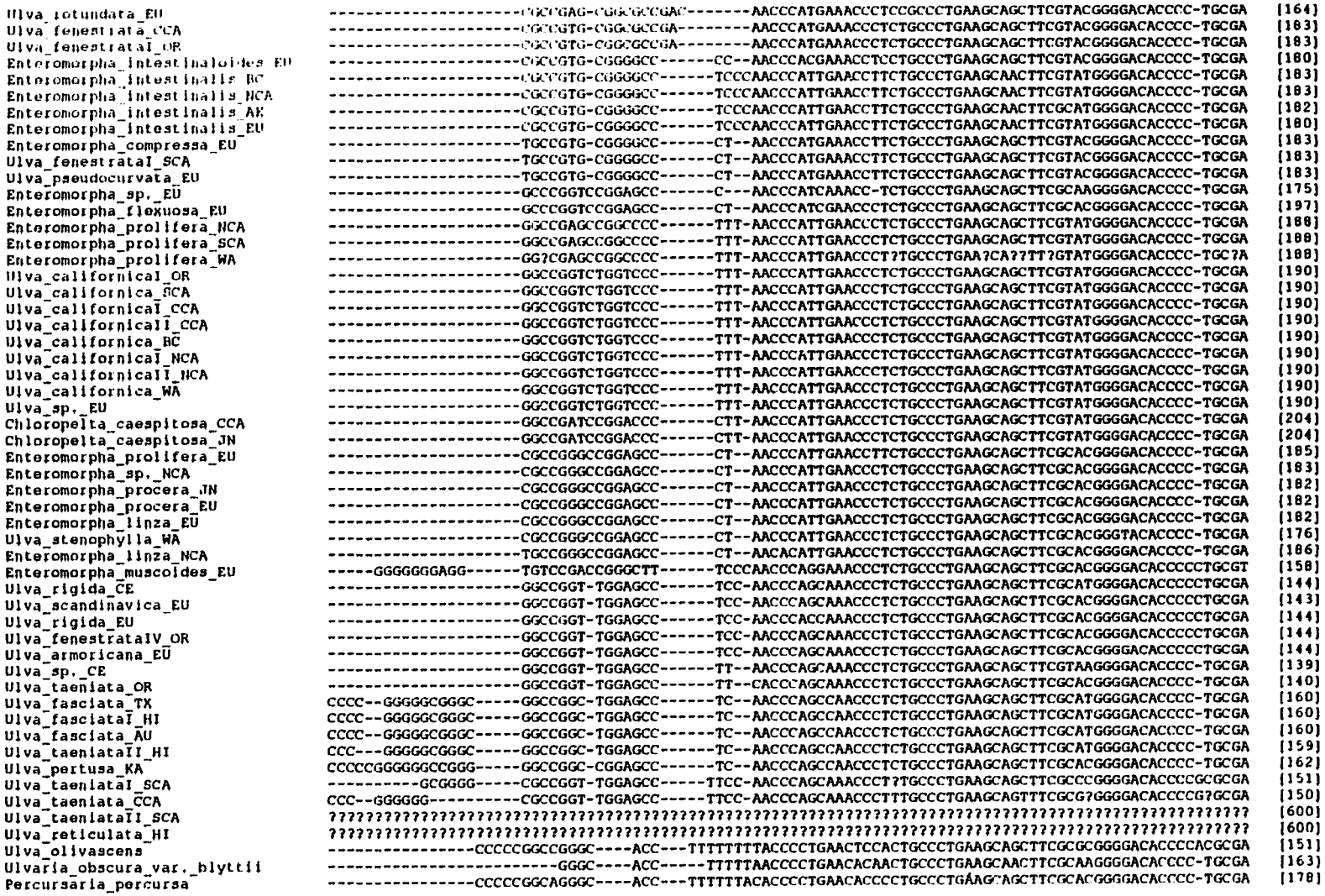

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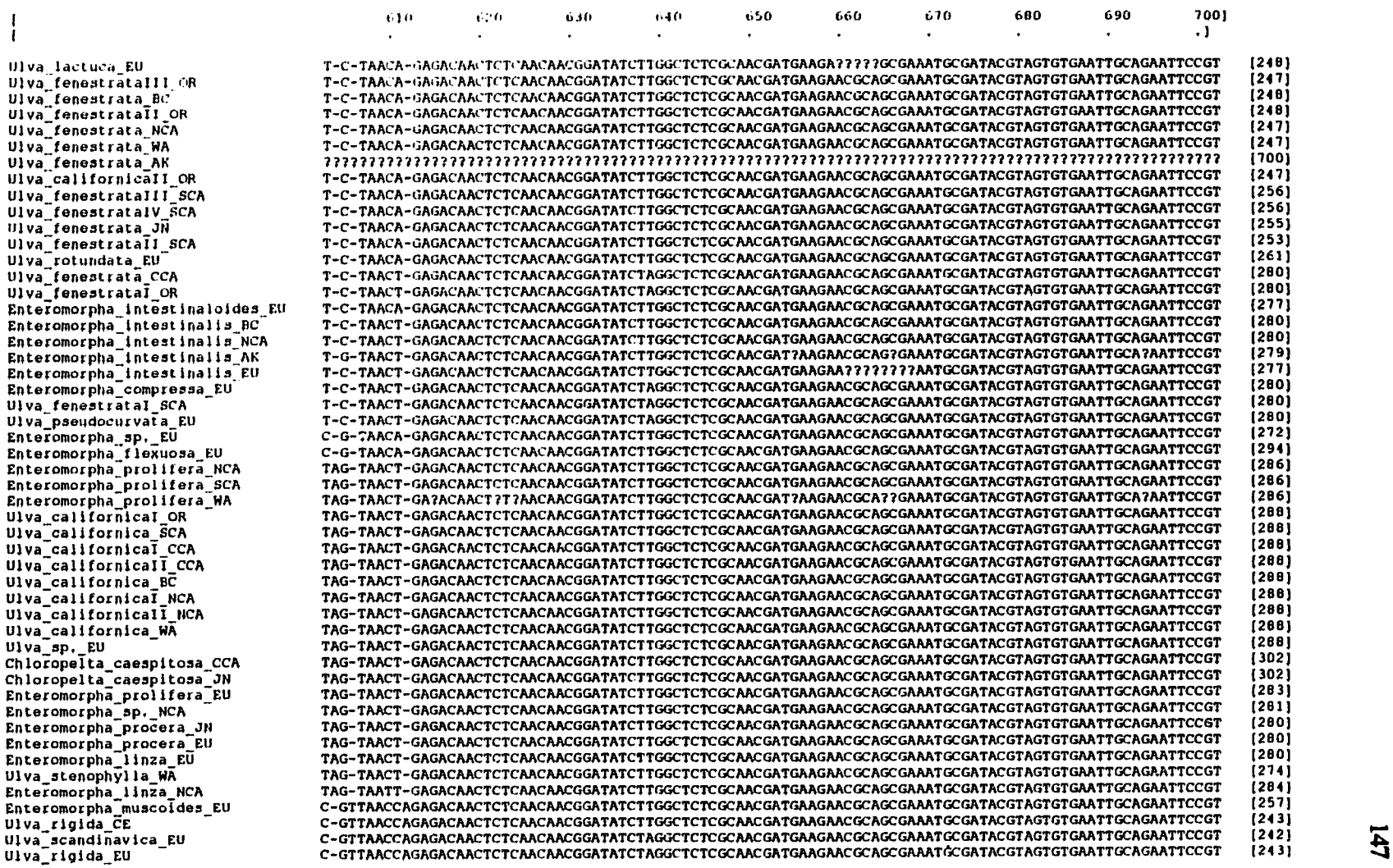
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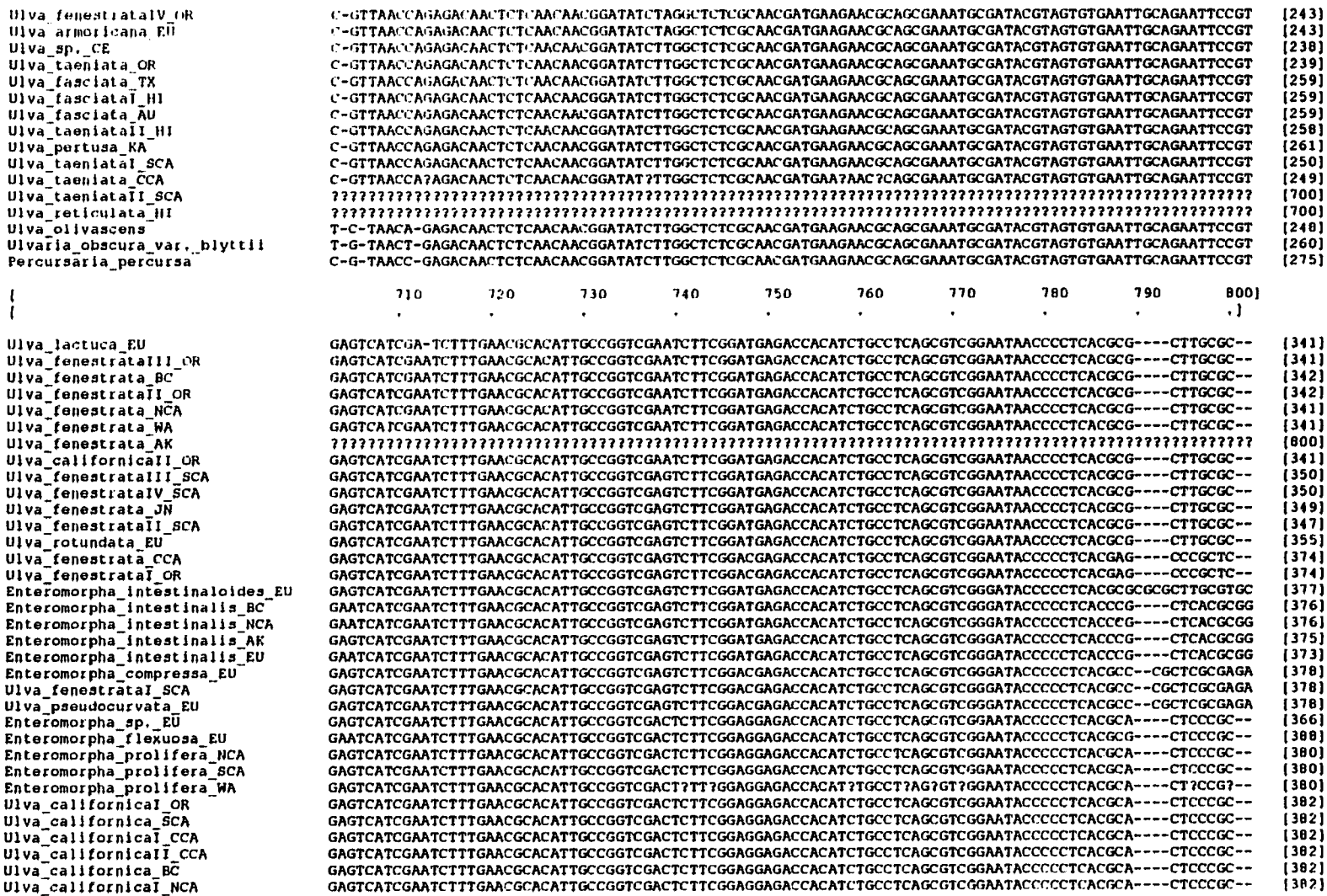
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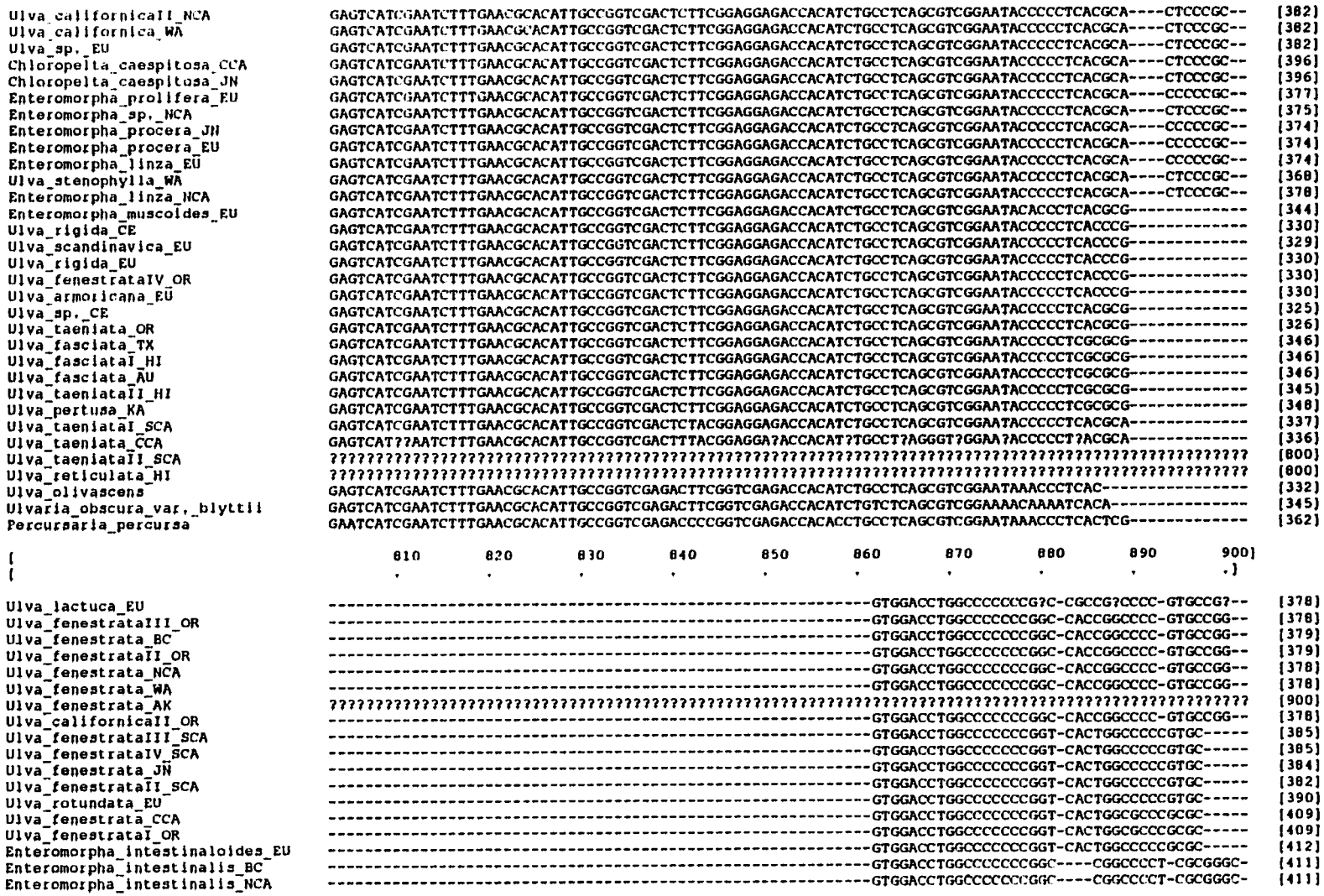
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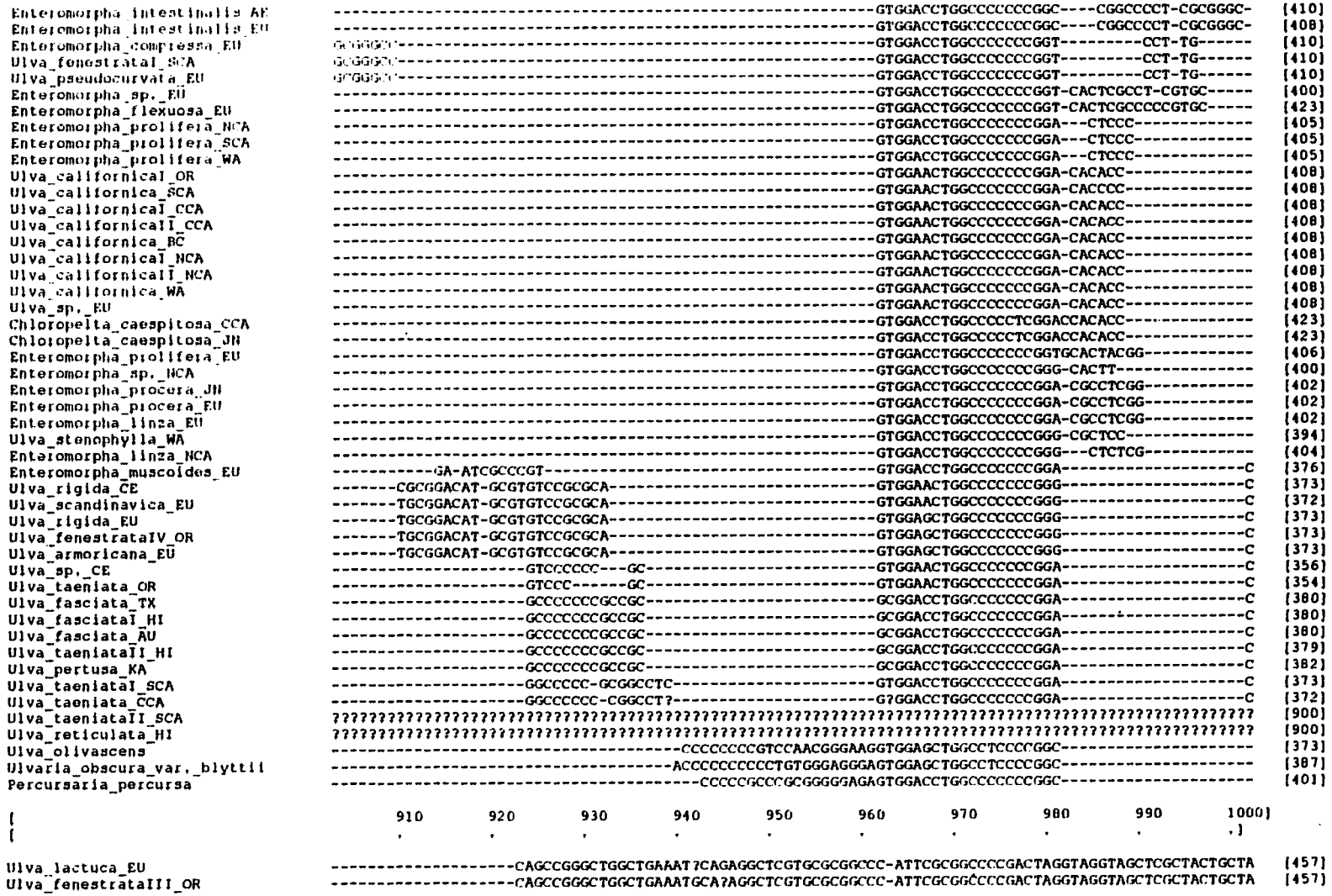
Ulva_fenestrataIII_SCA ----------GTGGACCTGGCCCCCCCGGT-CACTGGCCCCCGTGC----- [385]
Ulva_fenestrataIV_SCA ----------GTGGACCTGGCCCCCCCGGT-CACTGGCCCCCGTGC----- [385]
Ulva_fenestrata_JN ----------GTGGACCTGGCCCCCCCGGT-CACTGGCCCCCGTGC----- [384]
Ulva_fenestrataII_SCA ----------GTGGACCTGGCCCCCCCGGT-CACTGGCCCCCGTGC----- [382]
Ulva_rotundata_EU ----------GTGGACCTGGCCCCCCCGGT-CACTGGCCCCCGTGC----- [390]
Ulva_fenestrata_CCA ----------GTGGACCTGGCCCCCCCGGT-CACTGGCGCCCGCGC----- [409]
Ulva_fenestrataI_OR ----------GTGGACCTGGCCCCCCCGGT-CACTGGCGCCCGCGC----- [409]
Enteromorpha_intestinaloides_EU ----------GTGGACCTGGCCCCCCCGGT-CACTGGCCCCCGCGC----- [412]
Enteromorpha_intestinalis_BC ----------GTGGACCTGGCCCCCCCGGC----CGGCCCCT-CGCGGGC- [411]
Enteromorpha_intestinalis_NCA ----------GTGGACCTGGCCCCCCCGGC----CGGCCCCT-CGCGGGC- [411]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Ulva_pseudocurvata_EU [410]
Enteromorpha_sp._EU [400]
Enteromorpha_flexuosa_EU [423]
Enteromorpha_prolifera_NCA [405]
Enteromorpha_prolifera_SCA [405]
Enteromorpha_prolifera_WA [405]
Ulva_californicaI_OR [408]
Ulva_californica_SCA [408]
Ulva_californicaI_CCA [408]
Ulva_californicaII_CCA [408]
Ulva_californica_BC [408]
Ulva_californicaI_NCA [408]
Ulva_californicaII_NCA [408]
Ulva_californica_WA [408]
Ulva_sp._EU [408]
Chloropelta_caespitosa_CCA [423]
Chloropelta_caespitosa_JN [423]
Enteromorpha_prolifera_EU [406]
Enteromorpha_sp._NCA [400]
Enteromorpha_procera_JN [402]
Enteromorpha_procera_EU [402]
Enteromorpha_linza_EU [402]
Ulva_stenophylla_WA [394]
Enteromorpha_linza_NCA [404]
Enteromorpha_muscoides_EU [376]
Ulva_rigida_CE [373]
Ulva_scandinavica_EU [372]
Ulva_rigida_EU [373]
Ulva_fenestrataIV_OR [373]
Ulva_armoricana_EU [373]
Ulva_sp._CE [356]
Ulva_taeniata_OR [354]
Ulva_fasciata_TX [380]
Ulva_fasciataI_HI [380]
Ulva_fasciata_AU [380]
Ulva_taeniataII_HI [379]
Ulva_pertusa_KA [382]
Ulva_taeniataI_SCA [373]
Ulva_taeniata_CCA [372]
Ulva_taeniataII_SCA [900]
Ulva_reticulata_HI [900]
Ulva_olivascens [373]
Ulvaria_obscura_var._blyttii [387]
Percursaria_percursa [401]
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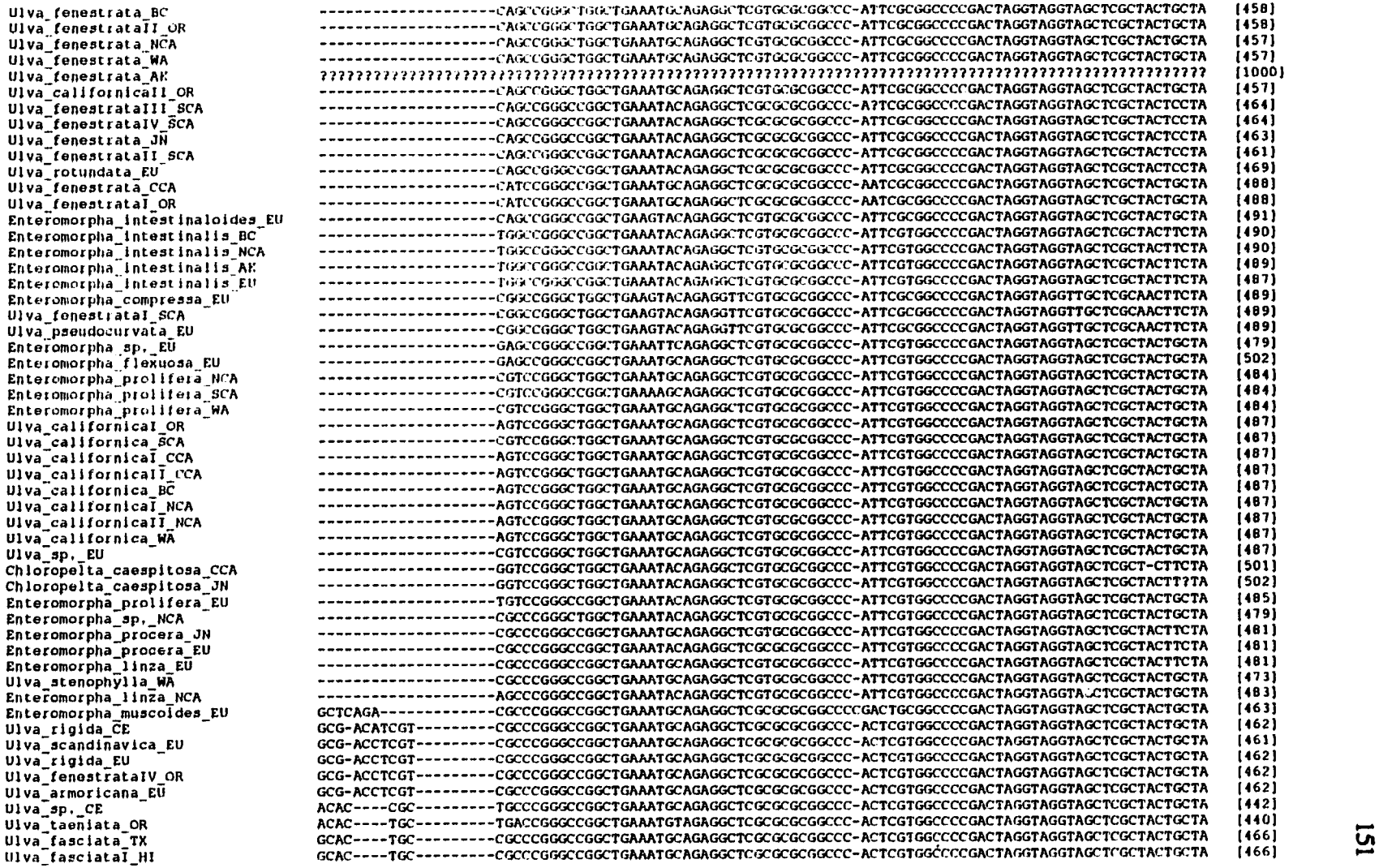
Ulva_fenestrataIII_OR [457]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Ulva_fenestrataII_OR ----------CAGCCGGGCTGGCTGAAATGCAGAGGCTCGTGCGCGGCCC-ATTCGCGGCCCCGACTAGGTAGGTAGCTCGCTACTGCTA [458]
Ulva_fenestrata_NCA ----------CAGCCGGGCTGGCTGAAATGCAGAGGCTCGTGCGCGGCCC-ATTCGCGGCCCCGACTAGGTAGGTAGCTCGCTACTGCTA [457]
Ulva_fenestrata_WA ----------CAGCCGGGCTGGCTGAAATGCAGAGGCTCGTGCGCGGCCC-ATTCGCGGCCCCGACTAGGTAGGTAGCTCGCTACTGCTA [457]
Ulva_fenestrata_AK ?? [1000]
Ulva_californicaII_OR ----------CAGCCGGGCTGGCTGAAATGCAGAGGCTCGTGCGCGGCCC-ATTCGCGGCCCCGACTAGGTAGGTAGCTCGCTACTGCTA [457]
Ulva_fenestrataIII_SCA ----------CAGCCGGGCCGGCTGAAATACAGAGGCTCGCGCGCGGCCC-A?TCGCGGCCCCGACTAGGTAGGTAGCTCGCTACTCCTA [464]
Ulva_fenestrataIV_SCA ----------CAGCCGGGCCGGCTGAAATACAGAGGCTCGCGCGCGGCCC-ATTCGCGGCCCCGACTAGGTAGGTAGCTCGCTACTCCTA [464]
Ulva_fenestrata_JN ----------CAGCCGGGCCGGCTGAAATACAGAGGCTCGCGCGCGGCCC-ATTCGCGGCCCCGACTAGGTAGGTAGCTCGCTACTCCTA [463]
Ulva_fenestrataII_SCA ----------CAGCCGGGCCGGCTGAAATACAGAGGCTCGCGCGCGGCCC-ATTCGCGGCCCCGACTAGGTAGGTAGCTCGCTACTCCTA [461]
Ulva_rotundata_EU ----------CAGCCGGGCCGGCTGAAATACAGAGGCTCGCGCGCGGCCC-ATTCGCGGCCCCGACTAGGTAGGTAGCTCGCTACTCCTA [469]
Ulva_fenestrata_CCA ----------CATCCGGGCCGGCTGAAATGCAGAGGCTCGCGCGCGGCCC-AATCGCGGCCCCGACTAGGTAGGTAGCTCGCTACTGCTA [488]
Ulva_fenestrataI_OR ----------CATCCGGGCCGGCTGAAATGCAGAGGCTCGCGCGCGGCCC-AATCGCGGCCCCGACTAGGTAGGTAGCTCGCTACTGCTA [488]
Enteromorpha_intestinaloides_EU ----------CAGCCGGGCCGGCTGAAGTACAGAGGCTCGTGCGCGGCCC-ATTCGCGGCCCCGACTAGGTAGGTAGCTCGCTACTGCTA [491]
Enteromorpha_intestinalis_BC ----------TGGCCGGGCCGGCTGAAATACAGAGGCTCGTGCGCGGCCC-ATTCGTGGCCCCGACTAGGTAGGTAGCTCGCTACTTCTA [490]
Enteromorpha_intestinalis_NCA ----------TGGCCGGGCCGGCTGAAATACAGAGGCTCGTGCGCGGCCC-ATTCGTGGCCCCGACTAGGTAGGTAGCTCGCTACTTCTA [490]
Enteromorpha_intestinalis_AK ----------TGGCCGGGCCGGCTGAAATACAGAGGCTCGTGCGCGGCCC-ATTCGTGGCCCCGACTAGGTAGGTAGCTCGCTACTTCTA [489]
Enteromorpha_intestinalis_EU ----------TGGCCGGGCCGGCTGAAATACAGAGGCTCGTGCGCGGCCC-ATTCGTGGCCCCGACTAGGTAGGTAGCTCGCTACTTCTA [487]
Enteromorpha_compressa_EU ----------CGGCCGGGCTGGCTGAAGTACAGAGGTTCGTGCGCGGCCC-ATTCGCGGCCCCGACTAGGTAGGTTGCTCGCAACTTCTA [489]
UlvaI_fenestrataI_SCA ----------CGGCCGGGCTGGCTGAAGTACAGAGGTTCGTGCGCGGCCC-ATTCGCGGCCCCGACTAGGTAGGTTGCTCGCAACTTCTA [489]
Ulva_pseudocurvata_EU ----------CGGCCGGGCTGGCTGAAGTACAGAGGTTCGTGCGCGGCCC-ATTCGCGGCCCCGACTAGGTAGGTTGCTCGCAACTTCTA [489]
Enteromorpha_sp._EU ----------GAGCCGGGCCGGCTGAAATTCAGAGGCTCGTGCGCGGCCC-ATTCGTGGCCCCGACTAGGTAGGTAGCTCGCTACTGCTA [479]
Enteromorpha_flexuosa_EU ----------GAGCCGGGCCGGCTGAAATGCAGAGGCTCGTGCGCGGCCC-ATTCGTGGCCCCGACTAGGTAGGTAGCTCGCTACTGCTA [502]
Enteromorpha_prolifera_NCA ----------CGTCCGGGCTGGCTGAAATGCAGAGGCTCGTGCGCGGCCC-ATTCGTGGCCCCGACTAGGTAGGTAGCTCGCTACTGCTA [484]
Enteromorpha_prolifera_SCA ----------CGTCCGGGCCGGCTGAAAAGCAGAGGCTCGTGCGCGGCCC-ATTCGTGGCCCCGACTAGGTAGGTAGCTCGCTACTGCTA [484]
Enteromorpha_prolifera_WA ----------CGTCCGGGCTGGCTGAAATGCAGAGGCTCGTGCGCGGCCC-ATTCGTGGCCCCGACTAGGTAGGTAGCTCGCTACTGCTA [484]
UlvaI_californicaI_OR ----------AGTCCGGGCTGGCTGAAATGCAGAGGCTCGTGCGCGGCCC-ATTCGTGGCCCCGACTAGGTAGGTAGCTCGCTACTGCTA [487]
Ulva_californica_SCA ----------CGTCCGGGCTGGCTGAAATGCAGAGGCTCGTGCGCGGCCC-ATTCGTGGCCCCGACTAGGTAGGTAGCTCGCTACTGCTA [487]
Ulva_californicaI_CCA ----------AGTCCGGGCTGGCTGAAATGCAGAGGCTCGTGCGCGGCCC-ATTCGTGGCCCCGACTAGGTAGGTAGCTCGCTACTGCTA [487]
UlvaI_californicaII_CCA ----------AGTCCGGGCTGGCTGAAATGCAGAGGCTCGTGCGCGGCCC-ATTCGTGGCCCCGACTAGGTAGGTAGCTCGCTACTGCTA [487]
Ulva_californica_BC ----------AGTCCGGGCTGGCTGAAATGCAGAGGCTCGTGCGCGGCCC-ATTCGTGGCCCCGACTAGGTAGGTAGCTCGCTACTGCTA [487]
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UlvaI_californicaII_NCA ----------AGTCCGGGCTGGCTGAAATGCAGAGGCTCGTGCGCGGCCC-ATTCGTGGCCCCGACTAGGTAGGTAGCTCGCTACTGCTA [487]
Ulva_californica_WA ----------AGTCCGGGCTGGCTGAAATGCAGAGGCTCGTGCGCGGCCC-ATTCGTGGCCCCGACTAGGTAGGTAGCTCGCTACTGCTA [487]
Ulva_sp._EU ----------CGTCCGGGCTGGCTGAAATGCAGAGGCTCGTGCGCGGCCC-ATTCGTGGCCCCGACTAGGTAGGTAGCTCGCTACTGCTA [487]
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Chloropelta_caespitosa_JN ----------GGTCCGGGCTGGCTGAAATACAGAGGCTCGTGCGCGGCCC-ATTCGTGGCCCCGACTAGGTAGGTAGCTCGCTACTT??TA [502]
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Enteromorpha_sp._NCA ----------CGCCCGGGCTGGCTGAAATACAGAGGCTCGTGCGCGGCCC-ATTCGTGGCCCCGACTAGGTAGGTAGCTCGCTACTGCTA [479]
Enteromorpha_procera_JN ----------CGCCCGGGCCGGCTGAAATGCAGAGGCTCGTGCGCGGCCC-ATTCGTGGCCCCGACTAGGTAGGTAGCTCGCTACTTCTA [481]
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Enteromorpha_linza_NCA ----------AGCCCGGGCCGGCTGAAATACAGAGGCTCGTGCGCGGCCC-ATTCGTGGCCCCGACTAGGTAGGTAGCTCGCTACTGCTA [483]
Enteromorpha_muscoides_EU GCTCAGA----------CGCCCGGGCCGGCTGAAATGCAGAGGCTCGCGCGCGGCCCCGACTGCGGCCCCGACTAGGTAGGTAGCTCGCTACTGCTA [463]
Ulva_rigida_CE GCG-ACATCGT---------CGCCCGGGCCGGCTGAAATGCAGAGGCTCGCGCGCGGCCC-ACTCGTGGCCCCGACTAGGTAGGTAGCTCGCTACTGCTA [462]
Ulva_scandinavica_EU GCG-ACCTCGT---------CGCCCGGGCCGGCTGAAATGCAGAGGCTCGCGCGCGGCCC-ACTCGTGGCCCCGACTAGGTAGGTAGCTCGCTACTGCTA [461]
Ulva_rigida_EU GCG-ACCTCGT---------CGCCCGGGCCGGCTGAAATGCAGAGGCTCGCGCGCGGCCC-ACTCGTGGCCCCGACTAGGTAGGTAGCTCGCTACTGCTA [462]
Ulva_fenestrataIV_OR GCG-ACCTCGT---------CGCCCGGGCCGGCTGAAATGCAGAGGCTCGCGCGCGGCCC-ACTCGTGGCCCCGACTAGGTAGGTAGCTCGCTACTGCTA [462]
Ulva_armoricana_EU GCG-ACCTCGT---------CGCCCGGGCCGGCTGAAATGCAGAGGCTCGCGCGCGGCCC-ACTCGTGGCCCCGACTAGGTAGGTAGCTCGCTACTGCTA [462]
Ulva_sp._CE ACAC----CGC---------TGCCCGGGCCGGCTGAAATGCAGAGGCTCGCGCGCGGCCC-ACTCGTGGCCCCGACTAGGTAGGTAGCTCGCTACTGCTA [442]
Ulva_taeniata_OR ACAC----TGC---------TGACCGGGCCGGCTGAAATGTAGAGGCTCGCGCGCGGCCC-ACTCGTGGCCCCGACTAGGTAGGTAGCTCGCTACTGCTA [440]
Ulva_fasciata_TX GCAC----TGC---------CGCCCGGGCCGGCTGAAATGCAGAGGCTCGCGCGCGGCCC-ACTCGTGGCCCCGACTAGGTAGGTAGCTCGCTACTGCTA [466]
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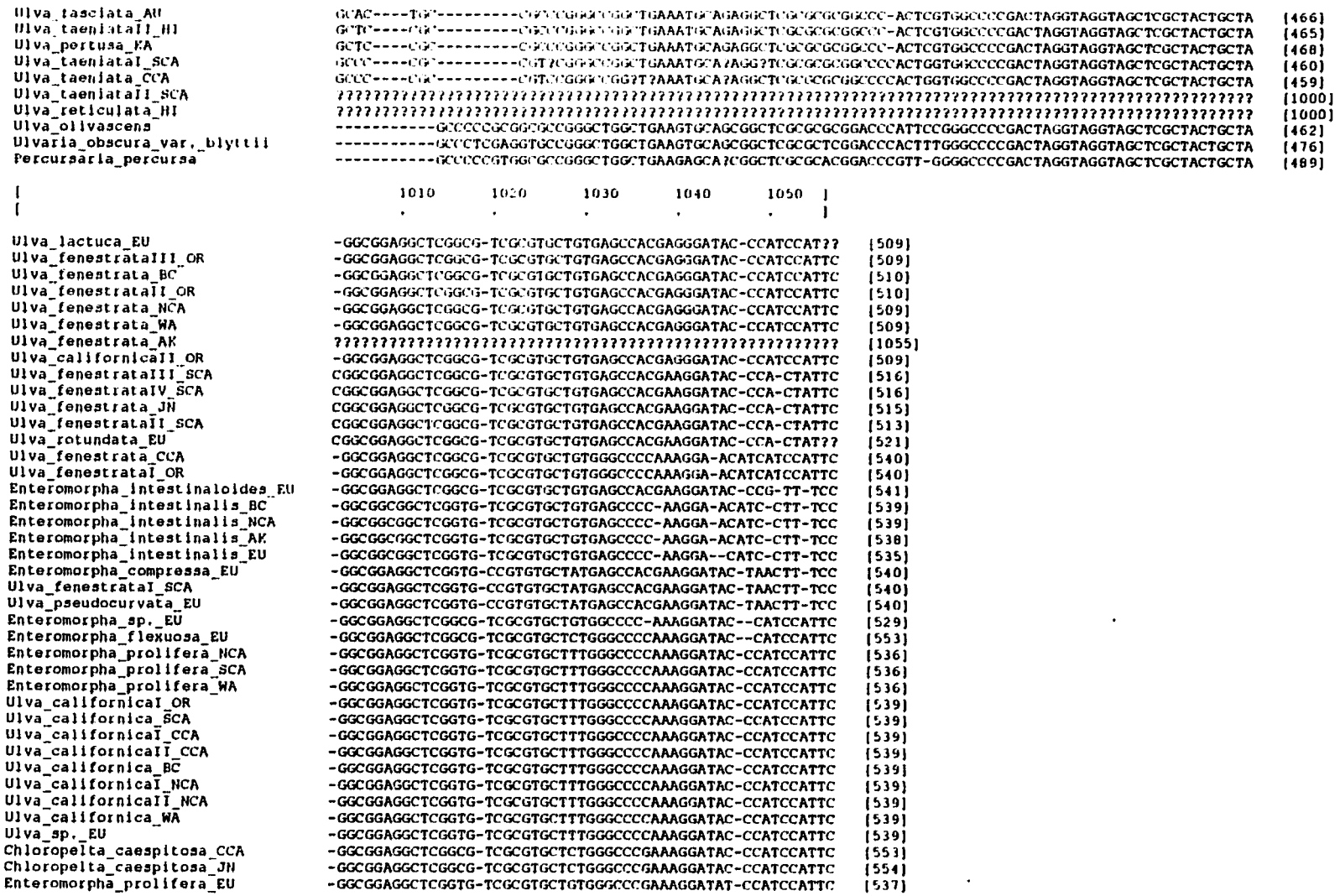
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Ulva_taeniataI_SCA
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Ulva_reticulata_HI
Ulva_olivascens
Ulvaria_obscura_var._blyttii
Percursaria_percursa
1010
1020
1030
1040
1050
Ulva_lactuca_EU
Ulva_fenestrataIII_OR
Ulva_fenestrata_BC
Ulva_fenestrataII_OR
Ulva_fenestrata_NCA
Ulva_fenestrata_WA
Ulva_fenestrata_AK
Ulva_californicaII_OR
Ulva_fenestrataIII_SCA
Ulva_fenestrataIV_SCA
Ulva_fenestrata_JN
Ulva_fenestrataII_SCA
Ulva_rotundata_EU
Ulva_fenestrata_CCA
Ulva_fenestrataI_OR
Enteromorpha_intestinaloides_EU
Enteromorpha_intestinalis_BC
Enteromorpha_intestinalis_NCA
Enteromorpha_intestinalis_AK
Enteromorpha_intestinalis_EU
Enteromorpha_compressa_EU
Ulva_fenestrataI_SCA
Ulva_pseudocurvata_EU
Enteromorpha_sp._EU
Enteromorpha_flexuosa_EU
Enteromorpha_prolifera_NCA
Enteromorpha_prolifera_SCA
Enteromorpha_prolifera_WA
Ulva_californicaI_OR
Ulva_californica_SCA
Ulva_californicaI_CCA
Ulva_californicaII_CCA
Ulva_californica_BC
Ulva_californicaI_NCA
Ulva_californicaII_NCA
Ulva_californica_WA
Ulva_sp._EU
Chloropelta_caespitosa_CCA
Chloropelta_caespitosa_JN
Enteromorpha_prolifera_EU

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Enteromorpha_sp._NCA                -GGCGGAGGCTCGGTG-TCGCGTGCTGTGGGCCCGAAAGGATAT--CATCCATTC   [530]
Enteromorpha_procera_JN             -GGCGGTGGCTCGGTG-TCGCGTGCTGTGGGCCCGAAAGGATAC-CAATCCATTC   [533]
Enteromorpha_procera_EU             -GGCGGTGGCTCGGTG-TCGCGTGCTGTGGGCCCGAAAGGATAC-CAATCCAT??   [533]
Enteromorpha_linza_EU               -GGCGGTGGCTCGGTG-TCGCGTGCTGTGGGCCCGAAAGGATAC-CAATCCATTC   [533]
Ulva_stenophylla_WA                 -GGCGGAGGCTCGGCG-TCGCGCGCTCTGGGCCCGAAAGGATAC-CCATCCATTC   [525]
Enteromorpha_linza_NCA              -GGCGGAGGCTCGGTG-TCGCGTGCTGTGGGCCCGAAAGGATAC--CATCCATTC   [534]
Enteromorpha_muscoides_EU           -GGCGGCGGCCCGGCGCTCGCGTGCTGTGGGCCCGAAAGGATAACCCCCTCATTC   [517]
Ulva_rigida_CE                      -GGCGGCGGCTCGGCGCTCGCGTGCTGTGGGCCCGAAAGGATAACCC-CTCATTC   [515]
Ulva_scandinavica_EU                -GGCGGCGGCTCGGCGCTCGCGTGCTGTGGGCCCGACAGGATAACCC-CTCATTC   [514]
Ulva_rigida_EU                      -GGCGGCGGCTCGGCGCTCGCGTGCTGTGGGCCCGACAGGATAACCC-CTCATTC   [515]
Ulva_fenestrataIV_OR                -GGCGGCGGCTCGGCGCTCGCGTGCTGTGGGCCCGACAGGATAACCC-CTCATTC   [515]
Ulva_armoricana_EU                  -GGCGGCGGCTCGGCGCTCGCGTGCTGTGGGCCCGACAGGATAACCC-CTCAT??   [515]
Ulva_sp._CE                         -GGCGGCGGCTCGGCGCCCGCGTGCTGTGGGCCCCAAAGGATAACCC-CATATTC   [495]
Ulva_taeniata_OR                    -GGCGGCGGCTCGGCGCCCGCGTGCTGTGGGCCCCAAAGGATAACCC-CCC-CCC   [492]
Ulva_fasciata_TX                    -GGCGGCGGCTCGGCGCCTGCGCGCTGTGGGCCCCAGAGGATAACC--CCCATTC   [518]
Ulva_fasciataI_HI                   -GGCGGCGGCTCGGCGCCTGCGCGCTGTGGGCCCCAGAGGATAACC--CCCATTC   [518]
Ulva_fasciata_AU                    -GGCGGCGGCTCGGCGCCTGCGCGCTGTGGGCCCCAGAGGATAACC--CCCATTC   [518]
Ulva_taeniataII_HI                  -GGCGGCGGCTCGGCGCCTGCGCGCTGTGGGCCCCAGAGGATAACCC-CCCATTC   [518]
Ulva_pertusa_KA                     -GGCGGCGGCTCGGCGCCTGCGCGCTGTGGGCCCCAGAGGATAACCC-CCCATTC   [521]
Ulva_taeniataI_SCA                  -GGCGGCGGCCCGGCGCCCGCGCGCTGTGGGCCCCAAAGGATAACC--CCCATTC   [512]
Ulva_taeniata_CCA                   -GGCGGCGGCCCGGCGCCCGCGCGCTGTGGGCCCCAAAGGATAACC--CCCATTC   [511]
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Ulva_reticulata_HI                  ??????????????????????????????????????????????????????   [1055]
Ulva_olivascens                     -GGCGGCGGC-CGGGTCCGAGGCGCTCTGGGCCCG-CAGGA-ACC---ACTATTC   [510]
Ulvaria_obscura_var._blyttii        -GCCGGCGGC-CGGGACCGACGCGCTCTGGGCCCG-CAGGA-ACC---CTTTTTC   [524]
Percursaria_percursa                -GCCGGCGGC-CGGGCCCGCGGCGCTCTGGGCCCG-CAGGA-ACCCCCACTATTC   [540]
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CHARPARTITION ITS_rbcL = ITS: 1-1055, rbcL: 1056-2409;

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CODESET * UNTITLED = Universal: all ;
END;

BEGIN ASSUMPTIONS;
        OPTIONS  DEFTYPE=unord PolyTcount=MINSTEPS ;
END;
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Appendix F. Sequence alignment in NEXUS format for *rbc*L data used in Chapter 3.

```
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DIMENSIONS  NTAX=66 NCHAR=1354;
FORMAT DATATYPE=DNA  MISSING=? GAP=-  INTERLEAVE ;
MATRIX

[                                   10        20        30        40        50        60        70        80        90       100]
[                                   .         .         .         .         .         .         .         .         .        .]

Ulva_lactuca_EU                     GGTACTGGCTTTAAAGCTGGTGTAAAAGATTACCGTTTAACTTATTACACGCCTGATTATCAAGTAAAAGATACTGATATTTTAGCAGCGTTTCGTATGA [100]
Ulva_fenestrataIII_OR               GGTACTGGCTTTAAAGCTGGTGTAAAAGATTACCGTTTAACTTATTACACGCCTGATTATCAAGTAAAAGATACTGATATTTTAGCAGCGTTTCGTATGA [100]
Ulva_fenestrata_BC                  GGTACTGGCTTTAAAGCTGGTGTAAAAGATTACCGTTTAACTTATTACACGCCTGATTATCAAGTAAAAGATACTGATATTTTAGCAGCGTTTCGTATGA [100]
Ulva_fenestrataII_OR                GGTACTGGCTTTAAAGCTGGTGTAAAAGATTACCGTTTAACTTATTACACGCCTGATTATCAAGTAAAAGATACTGATATTTTAGCAGCGTTTCGTATGA [100]
Ulva_fenestrata_NCA                 GGTACTGGCTTTAAAGCTGGTGTAAAAGATTACCGTTTAACTTATTACACGCCTGATTATCAAGTAAAAGATACTGATATTTTAGCAGCGTTTCGTATGA [100]
Ulva_fenestrata_WA                  GGTACTGGCTTTAAAGCTGGTGTAAAAGATTACCGTTTAACTTATTACACGCCTGATTATCAAGTAAAAGATACTGATATTTTAGCAGCGTTTCGTATGA [100]
Ulva_fenestrata_AK                  GGTACTGGCTTTAAAGCTGGTGTAAAAGATTACCGTTTAACTTATTACACGCCTGATTATCAAGTAAAAGATACTGATATTTTAGCAGCGTTTCGTATGA [100]
Ulva_californicaII_OR               ???????????????????????????????????????????????????????????????????????????????????????????????? [100]
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Ulva_fenestrataIV_SCA               GGTACTGGCTTTAAAGCTGGTGTAAAAGATTACCGTTTAACTTATTACACGCCTGATTATCAAGTAAAAGATACTGATATTTTAGCAGCGTTTCGTATGA [100]
Ulva_fenestrata_JN                  GGTACTGGCTTTAAAGCTGGTGTAAAAGATTACCGTTTAACTTATTACACGCCTGATTATCAAGTAAAAGATACTGATATTTTAGCAGCGTTTCGTATGA [100]
Ulva_fenestrataII_SCA               GGTACTGGCTTTAAAGCTGGTGTAAAAGATTACCGTTTAACTTATTACACGCCTGATTATCAAGTAAAAGATACTGATATTTTAGCAGCGTTTCGTATGA [100]
Ulva_rotundata_EU                   ???????????????????????????????????????????????????????????????????????????????????????????????? [100]
Ulva_fenestrata_CCA                 GGTACTGGCTTTAAAGCTGGTGTAAAAGATTACCGTTTAACTTATTACACGCCTGATTATCAAGTAAAAGATACTGATATCTTAGCAGCGTTTCGTATGA [100]
Ulva_fenestrataI_OR                 GGTACTGGCTTTAAAGCTGGTGTAAAAGATTACCGTTTAACTTATTACACGCCTGATTATCAAGTAAAAGATACTGATATCTTAGCAGCGTTTCGTATGA [100]
Enteromorpha_intestinaloides_EU     ???????????????????????????????????????????????????????????????????????????????????????????????? [100]
Enteromorpha_intestinalis_BC        GGTACTGGCTTTAAAGCTGGTGTAAAAGATTACCGTTTAACTTATTACACGCCTGATTATCAAGTAAAAGATACTGATATTTTAGCAGCGTTTCGTATGA [100]
Enteromorpha_intestinalis_NCA       GGTACTGGCTTTAAAGCTGGTGTAAAAGATTACCGTTTAACTTATTACACGCCTGATTATCAAGTAAAAGATACTGATATTTTAGCAGCGTTTCGTATGA [100]
Enteromorpha_intestinalis_AK        GGTACTGGCTTTAAAGCTGGTGTAAAAGATTACCGTTTAACTTATTACACGCCTGATTATCAAGTAAAAGATACTGATATTTTAGCAGCGTTTCGTATGA [100]
Enteromorpha_intestinalis_EU        GGTACTGGCTTTAAAGCTGGTGTAAAAGATTACCGTTTAACTTATTACACGCCTGATTATCAAGTAAAAGATACTGATATTTTAGCAGCGTTTCGTATGA [100]
Enteromorpha_compressa_EU           GGTACTGGCTTTAAAGCTGGTGTAAAAGATTACCGTTTAACTTATTACACGCCTGATTATCAAGTAAAAGATACTGATATTTTAGCAGCGTTTCGTATGA [100]
Ulva_fenestrataI_SCA                GGTACTGGCTTTAAAGCTGGTGTAAAAGATTACCGTTTAACTTATTACACGCCTGATTATCAAGTAAAAGATACTGATATTTTAGCAGCGTTTCGTATGA [100]
Ulva_pseudocurvata_EU               GGTACTGGCTTTAAAGCTGGTGTAAAAGATTACCGTTTAACTTATTACACGCCTGATTATCAAGTAAAAGATACTGATATTTTAGCAGCGTTTCGTATGA [100]
Enteromorpha_sp._EU                 ???????????????????????????????????????????????????????????????????????????????????????????????? [100]
Enteromorpha_flexuosa_EU            ???????????????????????????????????????????????????????????????????????????????????????????????? [100]
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Enteromorpha_prolifera_SCA          GGTACTGGCTTTAAAGCTGGTGTAAAAGATTACCGTTTAACTTATTACACGCCTGATTATCAAGTAAAAGATACTGATATTTTAGCAGCGTTCCGTATGA [100]
Enteromorpha_prolifera_WA           GGTACTGGCTTTAAAGCTGGTGTAAAAGATTACCGTTTAACTTATTACACGCCTGATTATCAAGTAAAAGATACTGATATTTTAGCAGCGTTCCGTATGA [100]
Ulva_californicaI_OR                GGTACTGGCTTTAAAGCTGGTGTAAAAGATTACCGTTTAACTTATTACACGCCTGATTATCAAGTAAAAGATACTGATATTTTAGCAGCGTTCCGTATGA [100]
Ulva_californica_SCA                GGTACTGGCTTTAAAGCTGGTGTAAAAGATTACCGTTTAACTTATTACACGCCTGATTATCAAGTAAAAGATACTGATATTTTAGCAGCGTTCCGTATGA [100]
Ulva_californicaI_CCA               GGTACTGGCTTTAAAGCTGGTGTAAAAGATTACCGTTTAACTTATTACACGCCTGATTATCAAGTAAAAGATACTGATATTTTAGCAGCGTTCCGTATGA [100]
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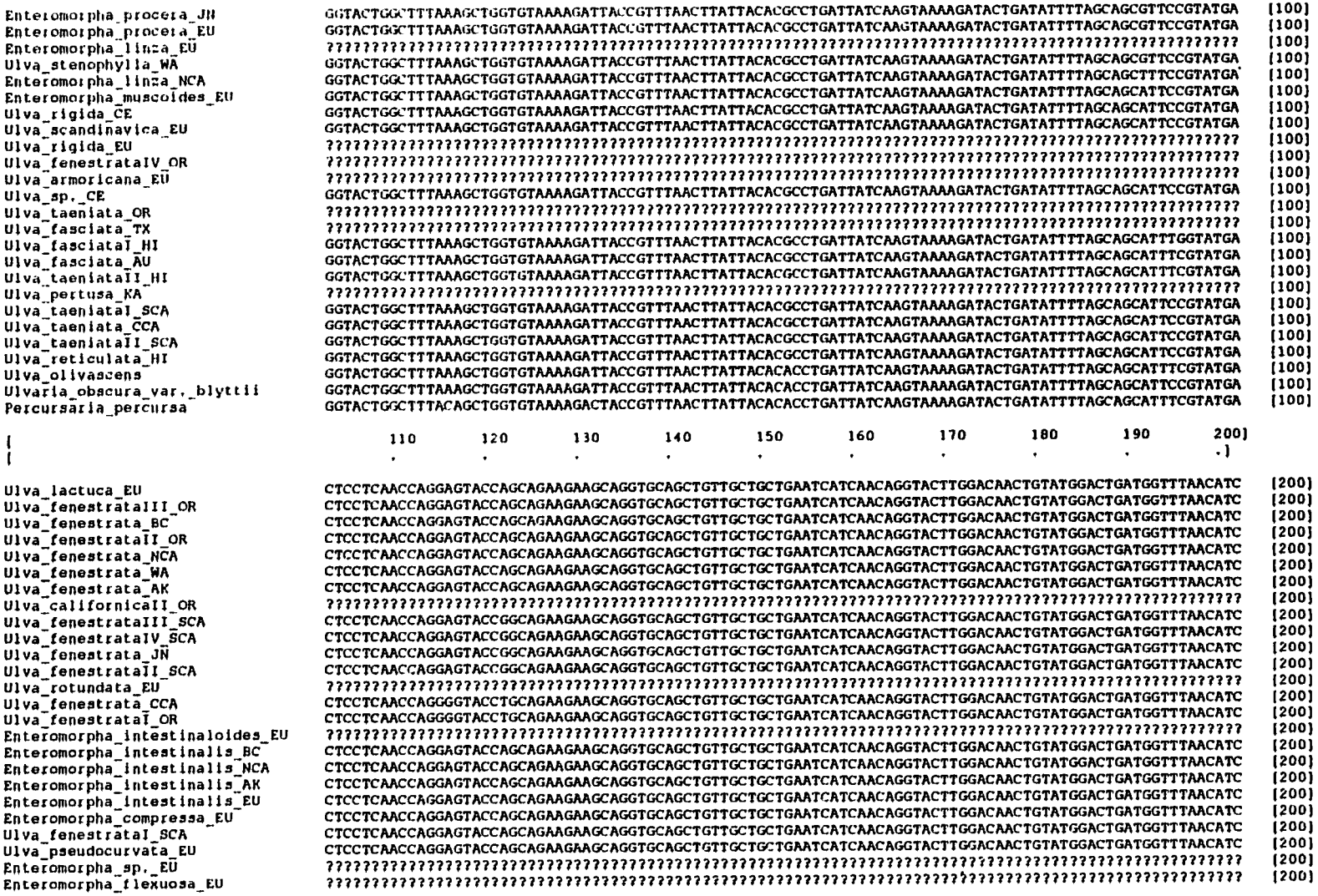
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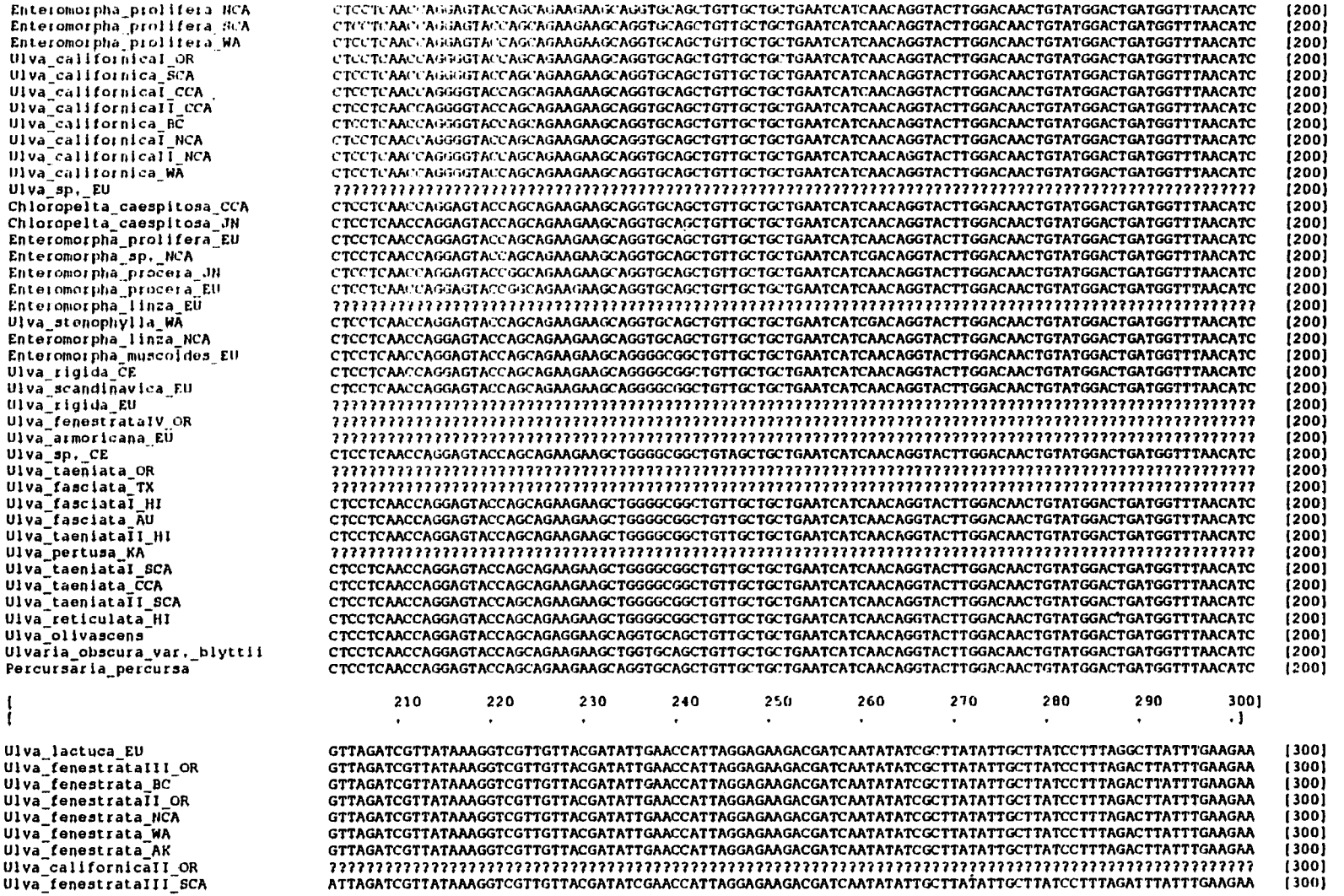
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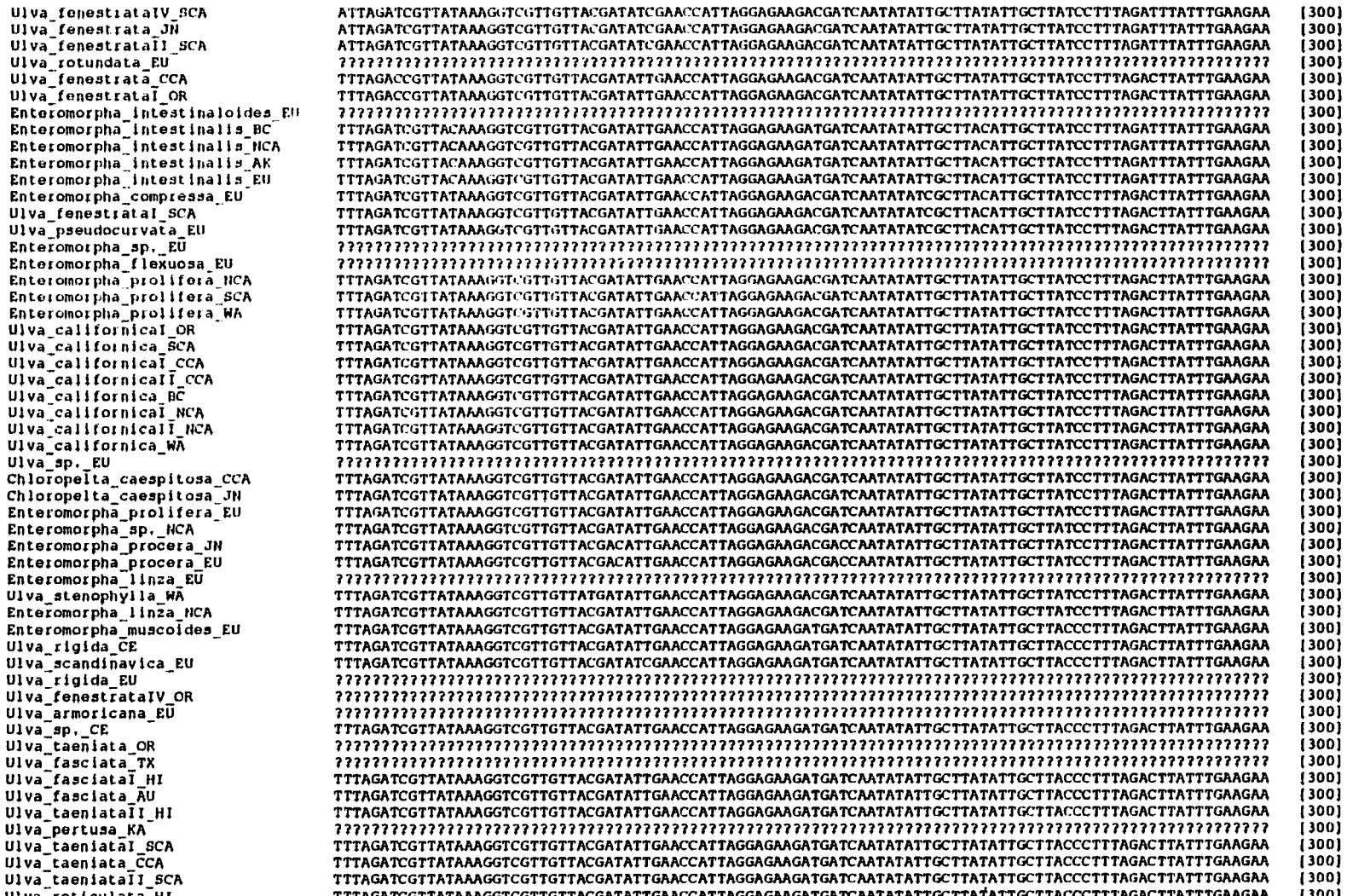
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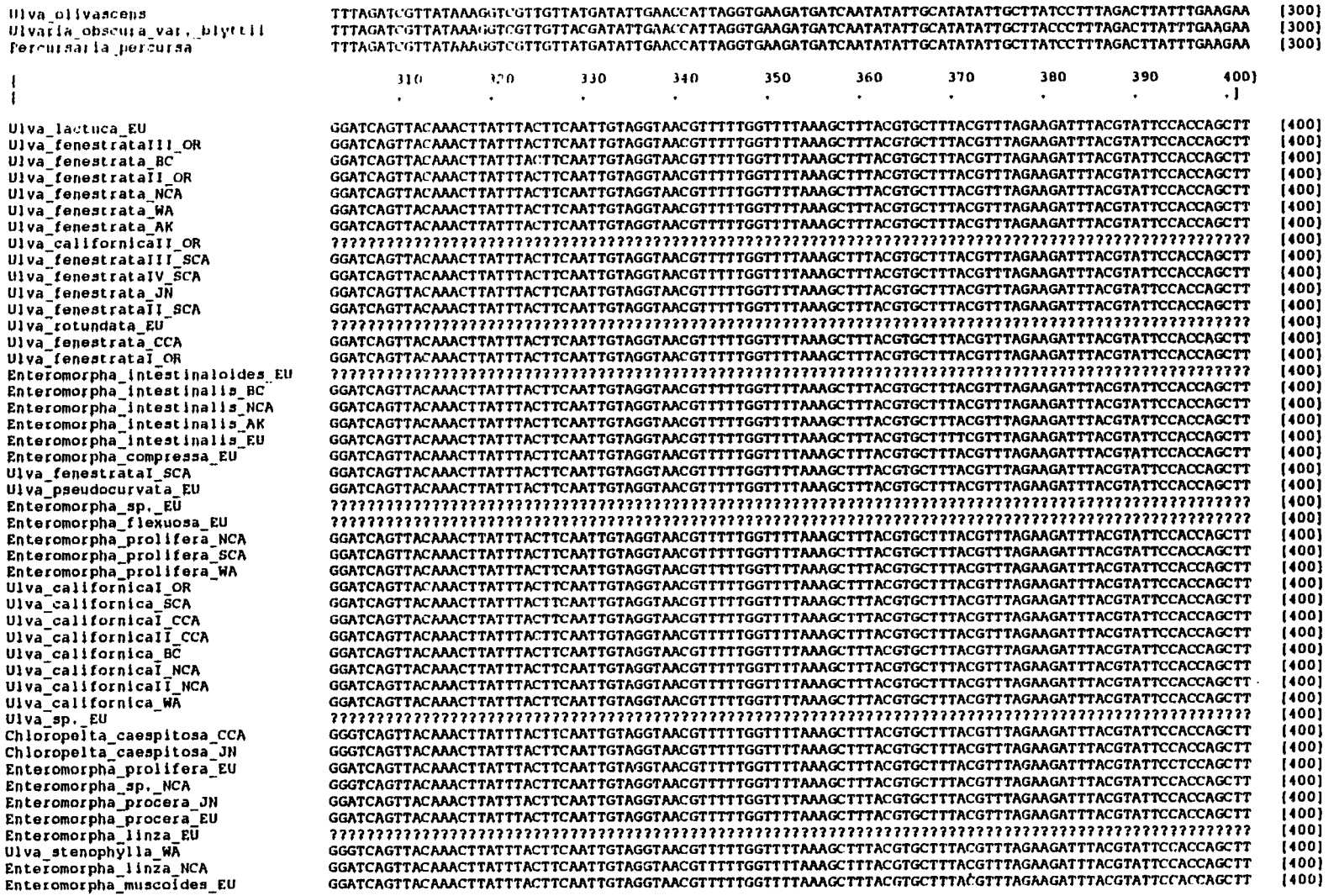
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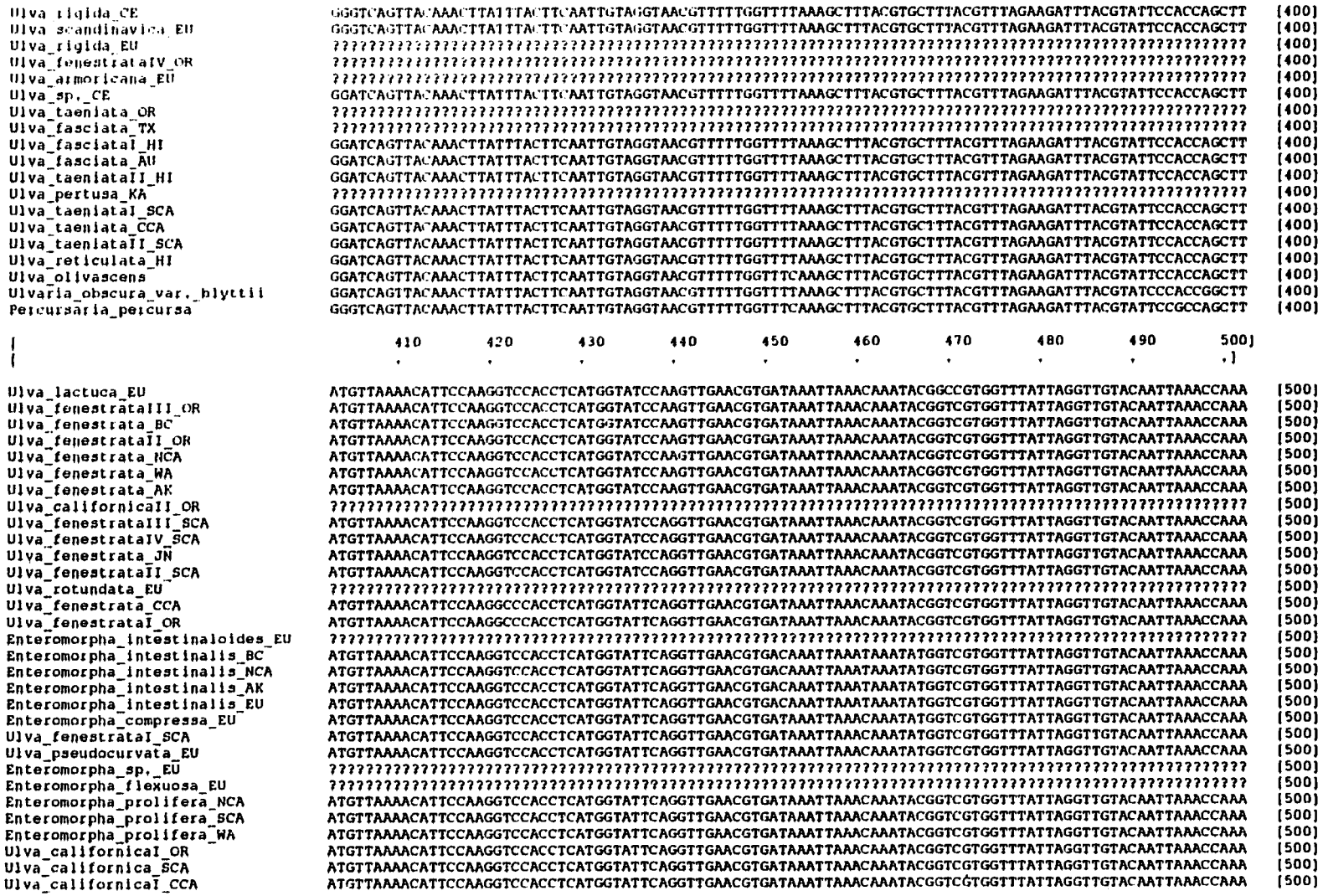
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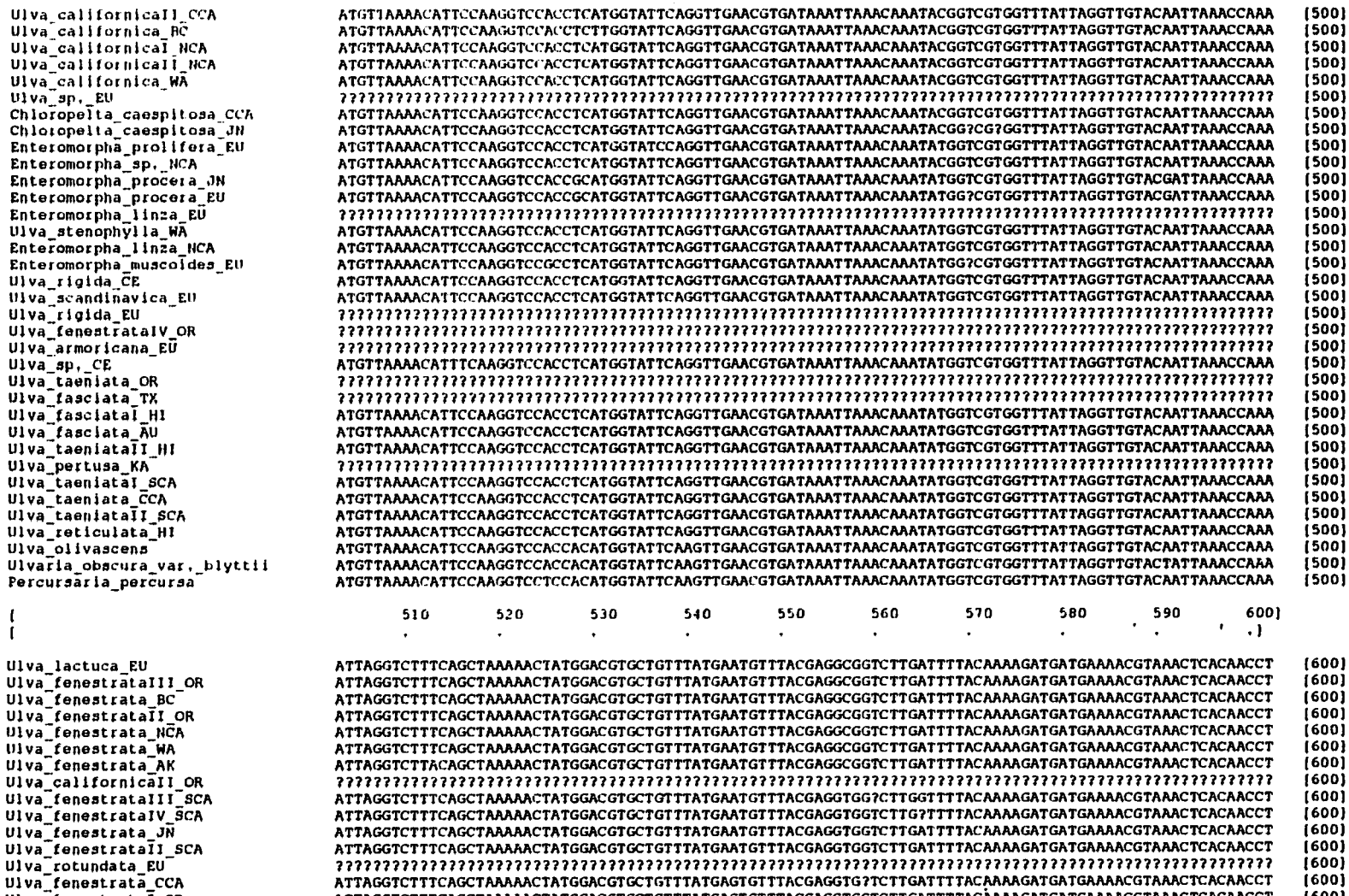
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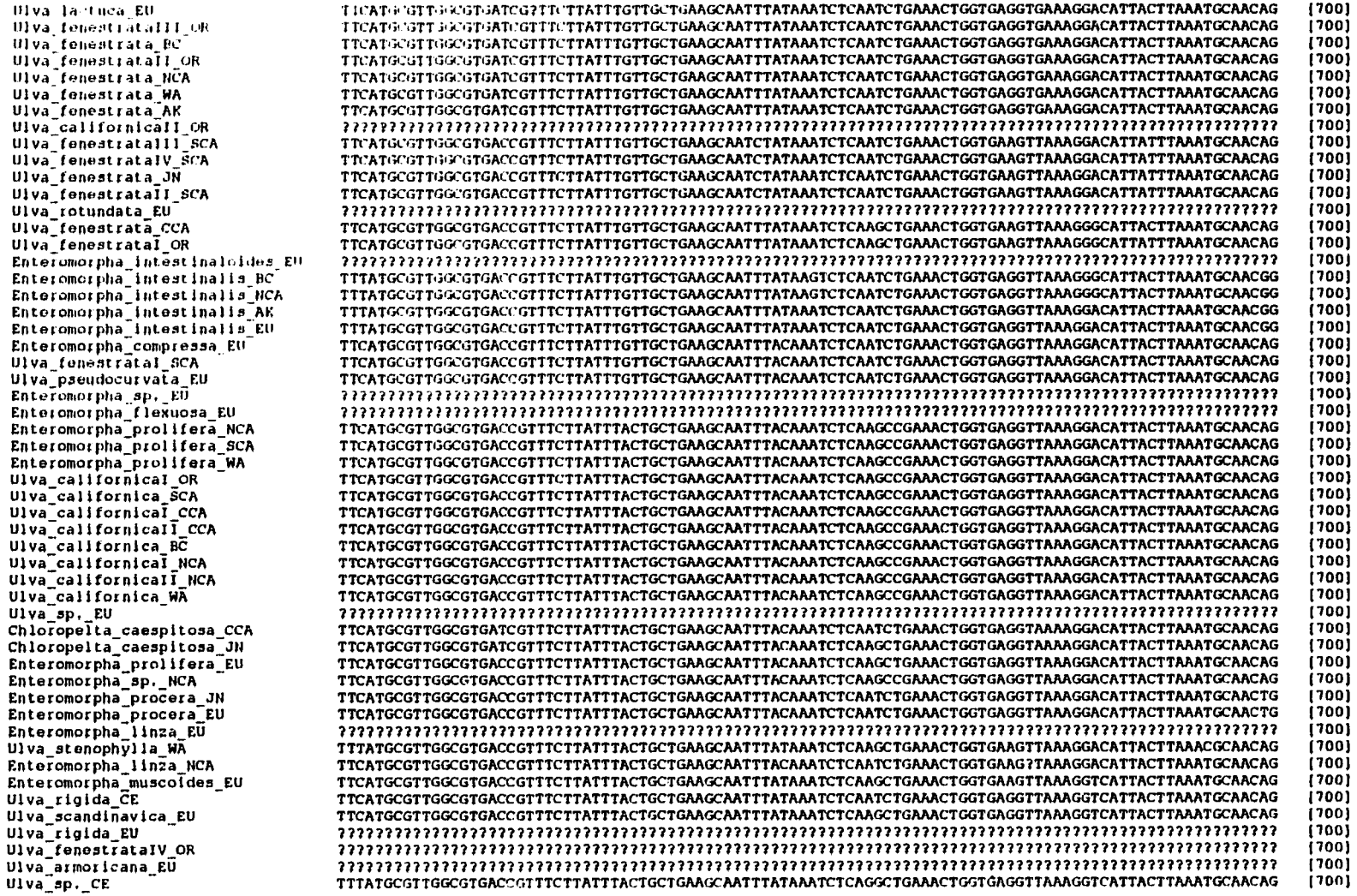
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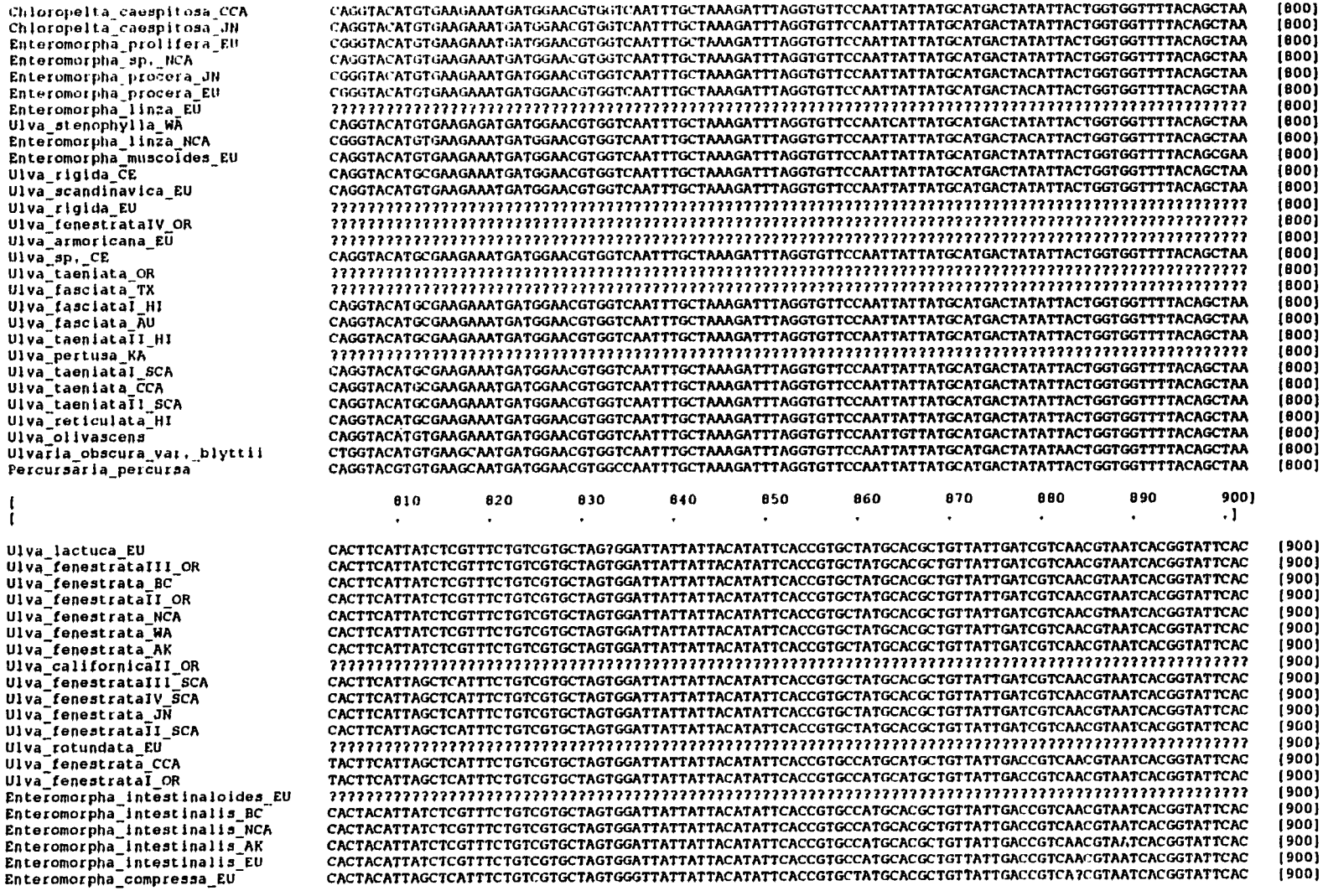

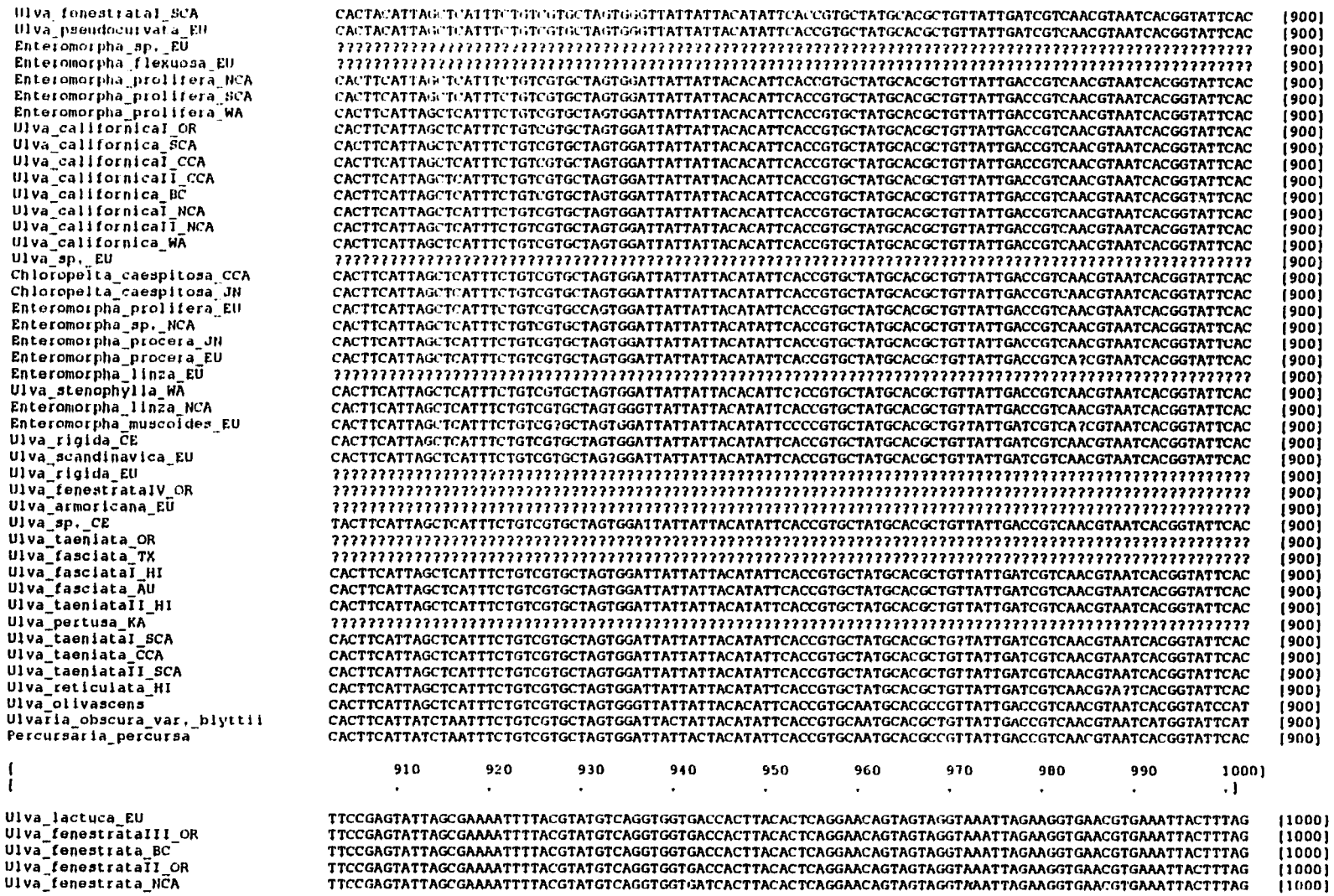
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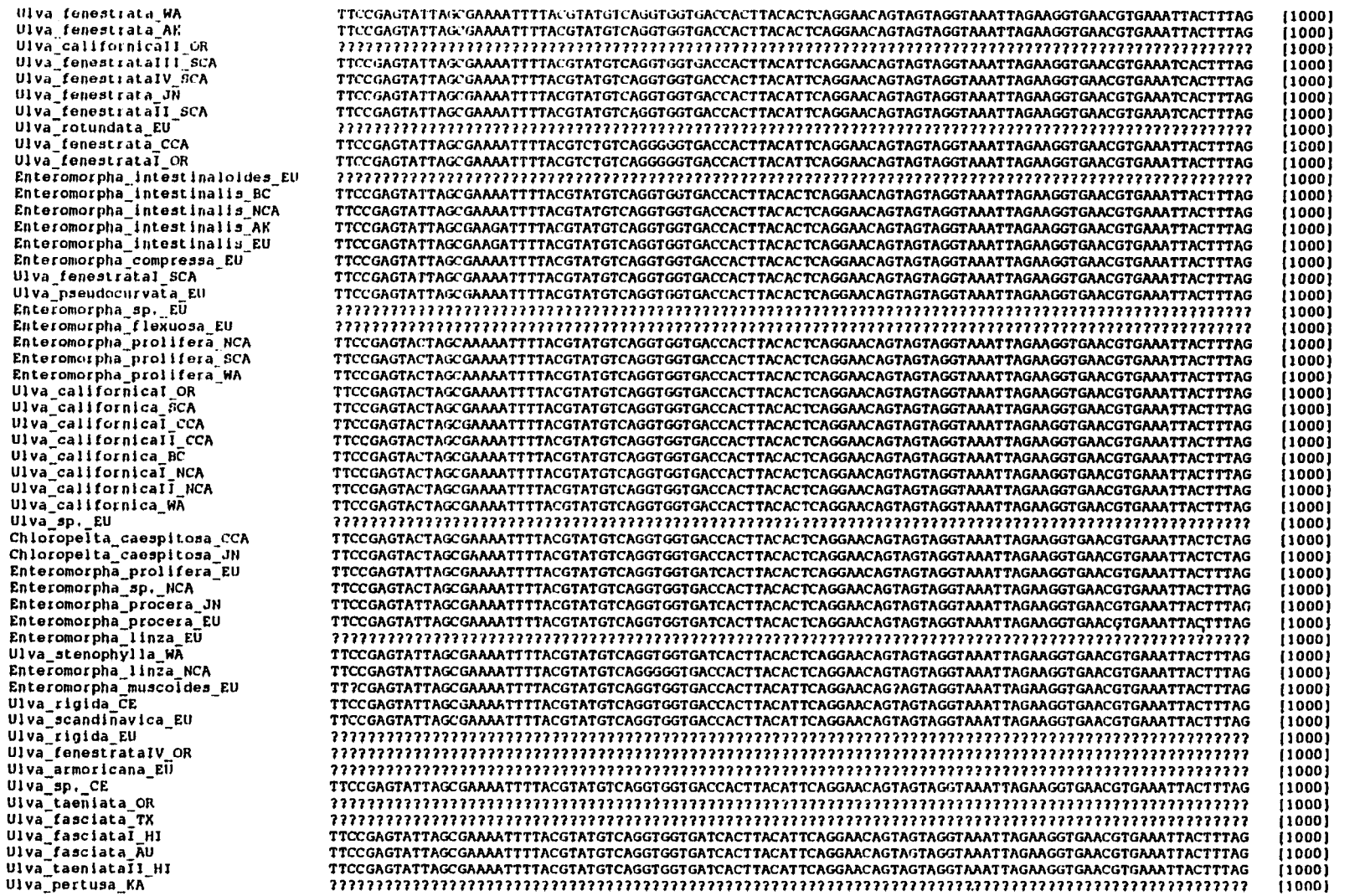
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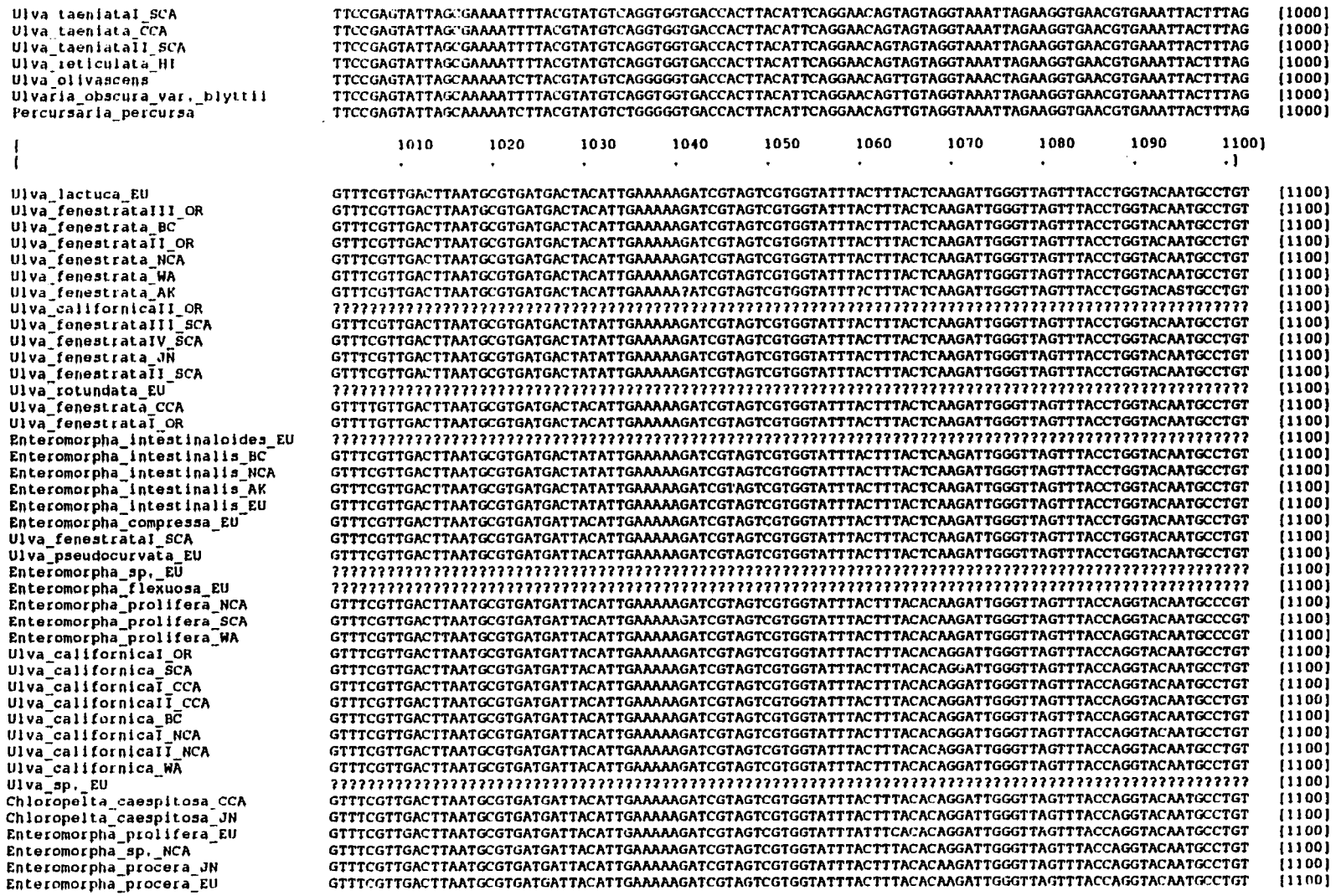
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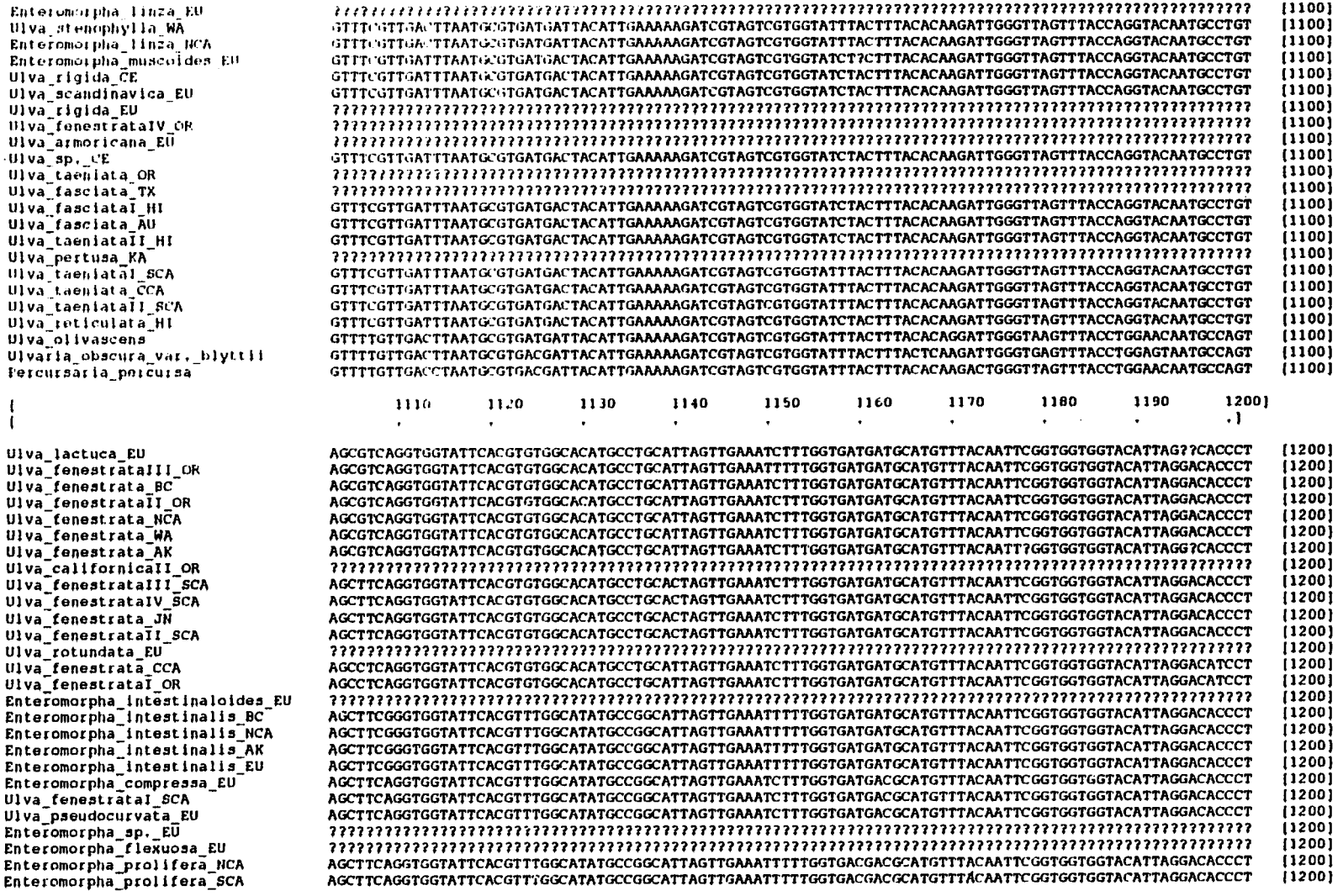
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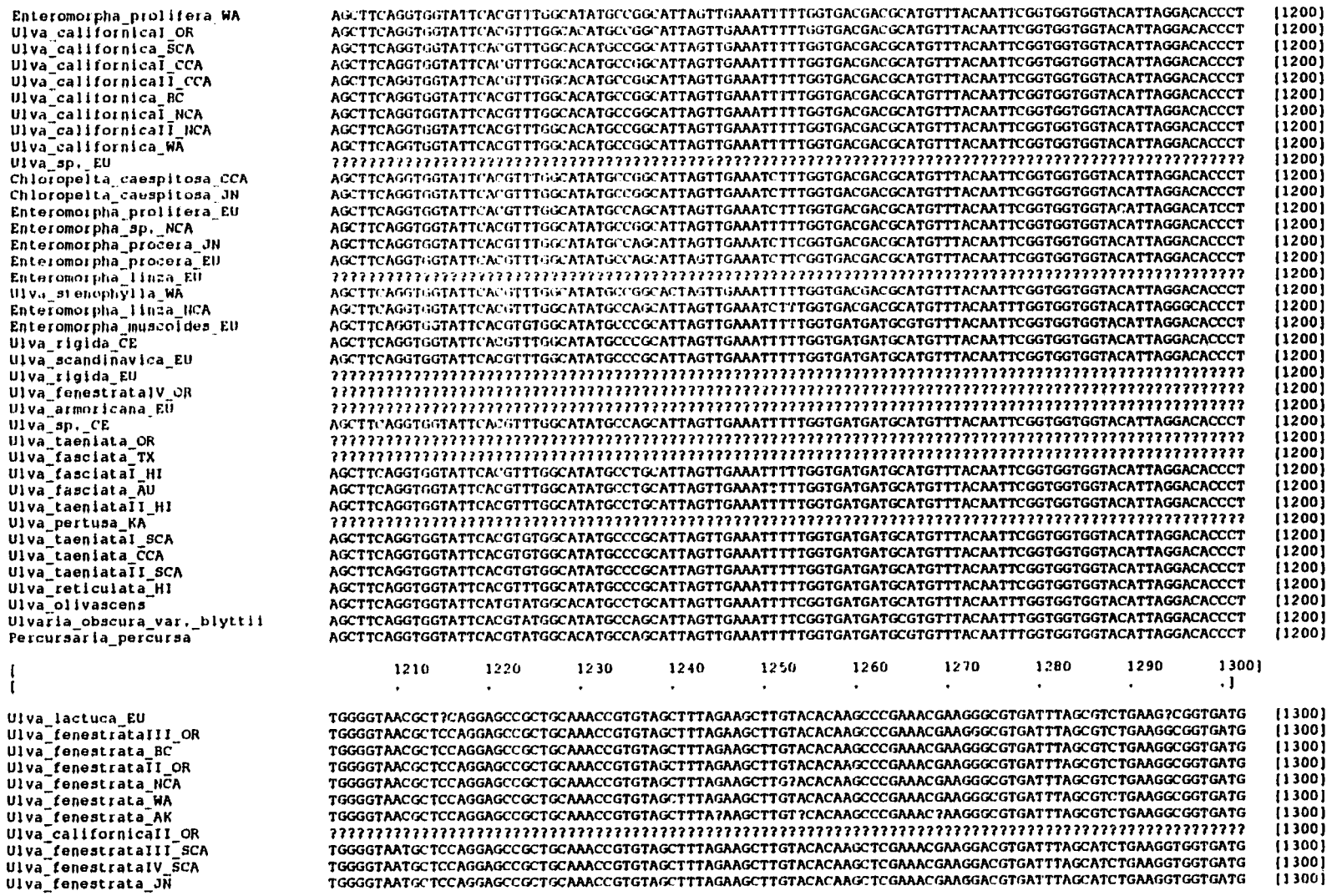
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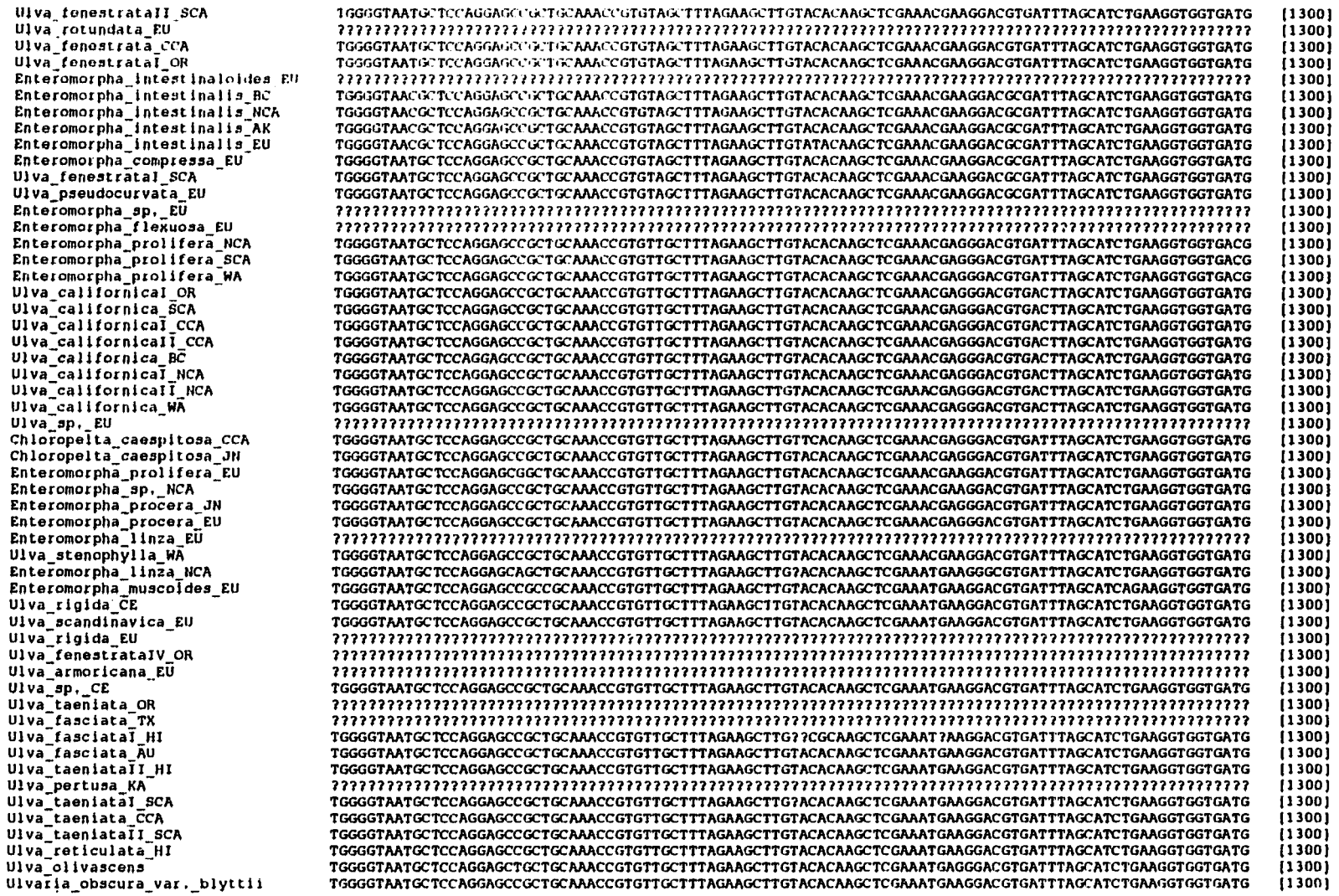
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Enteromorpha_intestinalis_NCA TAATTCGTGCTGCTTGTAAATGGAGCCCTGAATTAGCTGCAGCTTGTGAAGTAT   [1354]
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Enteromorpha_intestinalis_EU  TAATTCGTGCTGCTTGTAAATGGAGCCCTGAATTAGCTGCAGCTTGTGAAGTAT   [1354]
Enteromorpha_compressa_EU     TAATTCGTGCTGCTTGTAAATGGAGTCCTGAATTAGCTGCAGCTTGTGAAGTAT   [1354]
Ulva_fenestrataI_SCA          TAATTCGTGCTGCTTGTAAATGGAGTCCTGAATTAGCTGCAGCTTGTGAAGTAT   [1354]
Ulva_pseudocurvata_EU         TAATTCGTGCTGCTTGTAAATGGAGTCCTGAATTAGCTGCAGCTTGTGAAGTAT   [1354]
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Enteromorpha_flexuosa_EU      ????????????????????????????????????????????????????   [1354]
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Enteromorpha_prolifera_SCA    TAATTCGTGCTGCTTGTAAATGGAGTCCTGAATTAGCTGCAGCTTGTGAAGTAT   [1354]
Enteromorpha_prolifera_WA     TAATTCGTGCTGCTTGTAAATGGAGTCCTGAATTAGCTGCAGCTTGTAAGTAT-   [1353]
Ulva_californicaI_OR          TAATTCGTGCTGCTTGTAAATGGAGTCCTGAATTAGCTGCAGCTTGTGAAGTAT   [1354]
Ulva_californica_SCA          TAATTCGTGCTGCTTGTAAATGGAGTCCTGAATTAGCTGCAGCTTGTGAAGTAT   [1354]
Ulva_californicaI_CCA         TAATTCGTGCTGCTTGTAAATGGAGTCCTGAATTAGCTGCA?CTTGT?A?????   [1354]
Ulva_californicaII_CCA        TAATTCGTGCTGCTTGTAAATGGAGTCCTGAATTAGCTGCAGCTTGTGAAGTAT   [1354]
Ulva_californica_BC           TAATTCGTGCTGCTTGTAAATGGAGTCCTGAATTAGCTGCAGCTTGTGAAGTAT   [1354]
Ulva_californicaI_NCA         TAATTCGTGCTGCTTGTAAATGGAGTCCTGAATTAGCTGCAGCTTGTGAAGTAT   [1354]
Ulva_californicaII_NCA        TAATTCGTGCTGCTTGTAAATGGAGTCCTGAATTAGCTGCAGCTTGTGAAGTAT   [1354]
Ulva_californica_WA           TAATTCGTGCTGCTTGTAAATGGAGTCCTGAATTAGCTGCAGCTTGTGAAGTAT   [1354]
Ulva_sp._EU                   ????????????????????????????????????????????????????   [1354]
Chloropelta_caespitosa_CCA    TAATTCGTGCTGCTTGTAAATGGAGTCCTGAATTAGCTGCAGCTTGTGAAGTAT   [1354]
Chloropelta_caespitosa_JN     TAATTCGTGCTGCTTGTAAATGGAGTCCTGAATTAGCTGCAGCTTG????????   [1354]
Enteromorpha_prolifera_EU     TAATTCGTGCTGCTTGTAAATGGAGTCCTGAATTAGCTGCAGCTTGTGAAGTAT   [1354]
Enteromorpha_sp._NCA          TAATTCGTGCTGCTTGTAAATGGAGTCCTGAATTAGCTGCAGCTTGTGAAGTAT   [1354]
Enteromorpha_procera_JN       TAATTCGTGCTGCTTGTAAATGGAGTCCTGAATTAGCTGCAGCTTGTGAAGTAT   [1354]
Enteromorpha_procera_EU       TAATTCGTGCTGCTTGTAAATGGAGTCCTGAATTAGCTGCAGCTTGTGAAGTAT   [1354]
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Ulva_stenophylla_WA           TAATTCGTGCTGCTTGTAAATGGAGTCCTGAATTA?CTGCAGCTTGTGA?????   [1354]
Enteromorpha_linza_NCA        TAATCCGTGCTGCTTGTAAATGGAGTCCTGAATTA?CTGCAGCTTG????????   [1354]
Enteromorpha_muscoides_EU     TAATTCGTGCTGCT?GTAAATGGAGTCCTGAATTAGCTGCAGC?TGTGAAGTAT   [1354]
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Ulva_scandinavica_EU          TAATTCGTGCTGCTTGTAAATGGAGTCCTGAATTAGCTGCAGCTTGTGAAGTAT   [1354]
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Ulva_fenestrataIV_OR            ????????????????????????????????????????????????????????????  [1354]
Ulva_armoricana_EU              ????????????????????????????????????????????????????????????  [1354]
Ulva_sp._CE                     TAATTCGTGCTGCTTGTAAATGGAGTCCTGAATTAGCTGCAGCTTGTGAAGTAT          [1354]
Ulva_taeniata_OR                ????????????????????????????????????????????????????????????  [1354]
Ulva_lasciata_TX                ????????????????????????????????????????????????????????????  [1354]
Ulva_fasciataI_HI               TAATTCGTGCTGCTTGTAAATGGAGTCCTGAATTAGCTGCAGCTTGTGAAGTAT          [1354]
Ulva_fasciata_AU                TAATTCGTGCTGCTTGTAAATGGAGTCCTGAATTAGCTGCAGCTTGTGAAGTAT          [1354]
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Ulva_pertusa_KA                 ????????????????????????????????????????????????????????????  [1354]
Ulva_taeniataI_SCA              TAATTCG?GCTGCTTGTAAATGGAGTCCTGAATTAGCTGCAGCTTGTGAAGTGT          [1354]
Ulva_taeniata_CCA               TAATTCGTGCTGCTTGTAAATGGAGTCCTGAATTAGCTGCAGCTTGTGAAGTAT          [1354]
Ulva_taeniataII_SCA             TAATTCGTGCTGCTTGTAAATGGAGTCCTGAATTAGCTGCAGCTTGTGAAGTAT          [1354]
Ulva_reticulata_HI              TAATTCGTGCTGCTTGTAAATGGAGTCCTGAATTAGCTGCAGCTTGTGAAGTAT          [1354]
Ulva_olivascens                 TAATTCGTGCTGCTTGTAAATGGAGTCCTGAATTAGCTGCAGCTTG????????          [1354]
Ulvaria_obscura_var._blyttii    TAATTCGTGCTGCTTGTAAATGGAGTCCTGAATTAGCTGCAGCTTGTGAAGTAT          [1354]
Percursaria_percursa            TAATTCGTGCCGCTTGTAAATGGAGTCCTGAATTAGCTGCAGCTTGTGAAGTAT          [1354]
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CHARPARTITION ITS_rbcL = ITS: 1-1055, rbcL: 1056-2409;

BEGIN CODONS;
CODESET * UNTITLED = Universal: all ;
END;

BEGIN ASSUMPTIONS;
        OPTIONS  DEFTYPE=unord PolyTcount=MINSTEPS ;
END;
```

Appendix G. Sample code and name for algae in the present study with collection details and University of Washington Herbarium accession numbers. The geographical location from which each sample was collected is indicated in the sample name: AK, Alaska; AU, Australia; BC, British Columbia; NCA, northern California, CCA, central California; SCA, southern California; CE, Chile; EU, Europe; JN, Japan; KA, Korea; OR, Oregon; TX, Texas; WA, Washington. (CCA includes Marin Co. south through San Luis Obispo Co.) Abbreviations for culture collections: CCMP, Provasoli-Guillard National Center for Culture of Marine Phytoplankton; SAG, Sammlung von Algenkulturen der Universität Göttingen (Culture Collection of Algae at the University of Göttingen); UTEX, Culture Collection of Algae at the University of Texas; UWCC, University of Washington Culture Collection.

Sample code	Sample name	Source	Collection locality	Collection date	Latitude, longitude	Accession no.
Bvex99-64	*Blidingia minima* var. *vexata*	Field collection	Botany Bay, Vancouver Is., BC	29 Jun. 99	48°31.7' N, 124°27.2' W	344767
Bmin00-2	*Blidingia minima* var. *minima*	Field collection	Bolinas, CA	16 Jun. 00	37°54.1' N, 122°41.5 W	344768 344769
Ccae99-40	*Chloropelta caespitosa* CCA	Field collection	South Point Cabrillo, Monterey, Monterey Co., CA	17 Jun. 99	36°36.6' N, 121°53.7' W	344770
UconHK	*Chloropelta caespitosa* JN	Field collection by H. Kawai	Kobe, Hyogo Pref., Japan	22 Mar. 00	34°43' N, 135°19' W	na
CfDG	*Capsosiphon fulvescens*	Field collection by D. Garbary	Monks Head Beach, Nove Scotia	15 Aug. 98	na	344771
CvSAG	*Chlorella vulgaris*	SAG 211-11b	na	na	na	na
Ecom543	*Enteromorpha compressa* EU	Blomster et al. 1998	Portaferry, Strangford Lough, N. Ireland	12 Apr. 96	54°22.7' N, 5°34.6' W	na
EfleSW	*Enteromorpha flexuosa* EU	Tan et al. 1999	Sweden	na	na	na

Appendix G. Continued.

Sample code	Sample name	Source	Collection locality	Collection date	Latitude, longitude	Accession no.
EintTK	*Enteromorpha intestinalis* AK	Field collection by T. Klinger	Sheep Bay, Valdez-Cordova Co., AK	8 Jul. 97	60°39.7' N, 146°0.5'W	344772
Eint99-53	*Enteromopha intestinalis* BC	Field collection	Botany Bay, Vancouver Is., BC	29 Jun. 99	48°31.7' N, 124°27.2' W	344773
Eint00-6	*Enteromorpha intestinalis* NCA	Field collection	Bodega Head. Sonoma Co., CA	17 Jun. 00	38°18.2' N, 123°3.9' W	344774 344775
Eint585	*Enteromorpha intestinalis* EU	Blomster et al. 1998	Woolwich, Thames, London, England	9 Nov. 96	51°30.0' N, 0°5.0'W	na
EintestSc	*Enteromorpha intestinaloides* EU	Tan et al. 1999	Dunbar, East Lothian, Scotland	na	56°0' N, 2°31' W	na
Elin00-14	*Enteromorpha linza* NCA	Field collection	Coast Guard Cove, Humboldt Bay, Humboldt Co. CA	19 Jun. 00	40°45.8' N, 124°13.2' W	344776 344777
ElinSc	*Enteromorpha linza* EU	Tan et al. 1999	Ythan estuary, Aberdeenshire, Scotland	na	57°7' N, 2°6' W	na
Emus623	*Enteromorpha muscoides* EU	Blomster et al. 1999	Los Toruños, Puerto Réal, Cádiz, Spain	2 May 98	36°30.0' N, 6°20.0' W	na
Eproc615	*Enteromorpha procera* EU	Field collection by J. Blomster	Suomenlinna, Helsinki, Findland	na	60°36' N, 21°25' E	na
EproHK	*Enteromorpha procera* JN	Field collection by H. Kawai	Osaka Bay, Japan	26 Apr. 00	35°57' N, 137°16'E	na
EproBI	*Enteromorpha prolifera* WA	Field collection	Blakely Is., San Juan Co., WA	13 Aug. 97	48°33.7' N, 122°48.0' W	344778

Appendix G. Continued.

Sample code	Sample name	Source	Collection locality	Collection date	Latitude, longitude	Accession no.
Epro00-7	*Enteromorpha prolifera* NCA	Field collection	Westside Rd., Bodega Bay, Sonoma Co., CA	17 Jun. 00	38°18.6' N, 123°3.6' W	344779
EproSS	*Enteromorpha prolifera* SCA	Field collection by D.M. Dexter	Red Hill Marina, Salton Sea, Imperial Co., CA	5 Feb. 00	33°22.5' N, 116°0.3' W	344780 344781
EprolSc	*Enteromorpha prolifera* EU	Tan et al. 1999	Ythan estuary, Aberdeenshire, Scotland	na	57°7' N, 2°6' W	na
Esp00-17	*Enteromorpha* sp. NCA	Field collection	Coast Guard Cove, Humboldt Bay, Humboldt Co. CA	19 Jun. 00	40°45.8' N, 124°13.2' W	344782 344783
EcylSc	*Enteromorpha* sp. EU	Tan et al. 1999	Ythan estuary, Aberdeenshire, Scotland	na	57°7' N, 2°6' W	na
GpSAG	*Gloeotilopsis planctonica*	SAG 29.93	na	na	na	na
Klep99-52	*Kornmannia leptoderma*	Field collection	Botany Bay, Vancouver Is., BC	29 Jun. 99	48°31.7' N, 124°27.2' W	344784 344785
MbSAG	*Myrmecia biatorellae*	SAG 8.82	na	na	na	na
MnHK	*Monostroma nitidum*	Field collection by H. Kawai	Shirahama, Japan	4 Jun. 00	na	na
PmUT	*Pseudoneochloris marina*	UTEX LB1445	na	na	na	na
PfCO	*Pseudendoclonium fucicola*	Culture collect. C. O'Kelly	Boothbay Harbor, ME	na	na	na

Appendix G. Continued.

Sample code	Sample name	Source	Collection locality	Collection date	Latitude, longitude	Accession no.
TcCO	*Tellamia contorta* Batters	Culture collect. C. O'Kelly	San Juan Is., WA	na	na	na
UzSAG	*Ulothrix zonata*	SAG 38.86	na	na	na	na
UarmFr	*Ulva armoricana* EU	Coat et al. 1998	Roscoff, France	na	48°43.0' N, 4°1.0' W	na
Ucal99-48	*Ulva californica* BC	Field collection	Botany Bay, Vancouver Is., BC	29 Jun. 99	48°31.7' N, 124°27.2' W	344786 344787 344788
UcalWA	*Ulva californica* WA	Field collection	Cattle Point, San Juan Is., San Juan Co., WA	15 Jun. 98	48°27.0' N, 122°57.7' W	344789
Ucal99-5	*Ulva californica*l OR	Field collection	Fogarty Creek, Lincoln Co., OR	14 May 99	44°50.4' N, 124°3.2' W	344790
UcalifOR	*Ulva californica*ll OR	Tan et al. 1999	Otter Crest, Lincoln, Co., OR	na	44°45.7'N, 124°3.8' W	na
Ucal00-13	*Ulva californica*l NCA	Field collection	Coast Guard Cove, Humboldt Bay, Humboldt Co. CA	19 Jun. 00	40°45.8' N, 124°13.2' W	344791 344792
Ucal00-15	*Ulva californica*ll NCA	Field collection	Coast Guard Cove, Humboldt Bay, Humboldt Co., CA	19 Jun. 00	40°45.8' N, 124°13.2' W	344793 344794
Ucal99-41	*Ulva californica*l CCA	Field collection	South Point Cabrillo, Monterey, Monterey Co., CA	17 Jun. 99	36°36.6' N, 121°53.7' W	344795
Ucal99-47	*Ulva californica*ll CCA	Field collection	Moss Landing Harbor	18 Jun. 99	36°48.5' N, 121°47.2' W	344796 344797

Appendix G. Continued.

Sample code	Sample name	Source	Collection locality	Collection date	Latitude, longitude	Accession no.
Ucal99-26	*Ulva californica* SCA	Field collection	Casa Cove, La Jolla, San Diego Co., CA	14 Jun. 99	32°50.9' N, 117°16.7' W	344798
UfasUT	*Ulva fasciata* TX	UTEX LB1859	Port Aransas, Nueces Co., TX	na	27°50.0' N, 97°3.7 W	na
UfasHI	*Ulva fasciata*I HI	Field collection by L. Hodgson	Kihei, Maui Co., HI	6 Feb. 00	20°47.0' N, 156°28.0' W	344799
UtaeHI	*Ulva fasciata*II HI	Field collection by L. Hodgson	Maalaea, Maui Co., HI	6 Feb. 00	20°47.8' N, 156°30.9' W	344800
UlJ22	*Ulva* sp. AU	Field collection by G. Zuccarello	Tamarama, Sydney, Australia	9 Aug. 99	33°53' S, 151°12' E	344801
Ufen4AK	*Ulva fenestrata* AK	Field collection	Ferry dock, Petersburg, Wrangell-Petersburg Co., AK	6 Sep. 98	56°48.8' N, 132°57.6' W	344802 344803 344804
Ufen99-58	*Ulva fenestrata* BC	Field collection	Botanical Beach, Vancouver Is., BC	30 Jun. 99	48°32.0' N, 124°26.0' W	344805
UfenWA	*Ulva fenestrata* WA	Field collection	Cattle Point, San Juan Is., San Juan Co., WA	15 Jun. 98	48°27.0' N, 122°57.7' W	344806 344807
Usp99-11b	*Ulva fenestrata*I OR	Field collection	North Jetty, Yaquina Bay State Park, Lincoln Co., OR	16 May 99	44°37.4' N, 124°3.7' W	344808 344809 344810
Ufen99-2	*Ulva fenestrata*II OR	Field collection	Fogarty Creek, Lincoln Co., OR	14 May 99	44°50.4' N, 124°3.2' W	344811 344812 344813

Appendix G. Continued.

Sample code	Sample name	Source	Collection locality	Collection date	Latitude, longitude	Accession no.
Ufen99-8	*Ulva fenestrata* III OR	Field collection	Seal Rock, Lincoln Co., OR	15 May 99	44°30.0' N, 124°5.0' W	344814
UfenOr	*Ulva fenestrata* IV OR	Tan et al. 1999	North Boardman State Park, OR	na	na	na
Ufen00-16	*Ulva fenestrata* NCA	Field collection	Coast Guard Cove, Humboldt Bay, Humboldt Co. CA	19 Jun. 00	40°45.8' N, 124°13.2' W	344815 344816
Ufen99-37	*Ulva fenestrata* CCA	Field collection	San Simeon, San Luis Obispo Co., CA	16 Jun. 99	35°36.9' N, 121°9.0' W	344817
Ufen99-34	*Ulva fenestrata* I SCA	Field collection	North Star Beach, Newport, Orange Co., CA	15 Jun. 99	33°37.5' N, 117°53.6' W	344818
Ufen99-35	*Ulva fenestrata* II SCA	Field collection	Lower Newport Bay, Newport, Orange Co., CA	15 Jun. 99	33°37.1' N, 117°56.0' W	344819 344820 344821
Ufen99-20	*Ulva fenestrata* III SCA	Field collection	Perez Cove, Mission Bay, San Diego Co., CA	14 Jun. 99	32°46.0' N, 117°13.8' W	344822 344823
Usp99-21	*Ulva fenestrata* IV SCA	Field collection	Bird Rock, La Jolla, San Diego Co., CA	14 Jun. 99	32°48.9' N, 117°16.4'W	344824
UperHK	*Ulva fenestrata* JN	Field collection by H. Kawai	Yura, Hyogo Pref., Japan	21 Mar. 00	34°17' N, 134°57' E	na
Ulac519	*Ulva lactuca* EU	Tan et al. 1999	Ballyhenry Is., Strangford Lough, N. Ireland	na	54°25.9' N, 5°31.9' W	na
UperKO	*Ulva pertusa* KA	Tan et al. 1999	Guryongpo, East Coast, Korea	na	na	na

Appendix G. Continued.

Sample code	Sample name	Source	Collection locality	Collection date	Latitude, longitude	Accession no.
Upseudol	*Ulva pseudocurnata* EU	Tan et al. 1999	Ythan estuary, Aberdeenshire, Scotland	na	57°7' N, 2°6' W	na
UretHI	*Ulva reticulata* HI	Field collection by L. Hodgson	Lipoa St., Kihei, Maui Co., HI	6 Feb. 00	20°47.0' N, 156°28.0' W	344825
UrigCM	*Ulva rigida* EU	Field collection by C.A. Maggs	Cádiz, Spain	na	36°30' N, 6°20' W	344826
U2JRW	*Ulva rigida* CE	Field collection by J.R. Waaland	Pelluco Beach, southeast of Puerto Montt, Chile	17 Oct. 00	41°28' S, 72°56' W	344827 344828
UrotFr	*Ulva rotundata* EU	Coat et al. 1998	Roscoff, France	na	48°43.0' N, 4°1.0' W	na
UscalEn	*Ulva scandinavica* EU	Tan et al. 1999	Langstone Harbor, Portsmouth, England	na	50°46' N, 1°4' W	na
Uste00-1	*Ulva stenophylla* WA	Field collection	Shilshole Bay, Seattle, King Co., WA	2 Jun. 00	47°41.4' N, 122°24.0' W	344829
UtaeOr	*Ulva taeniata* OR	Tan et al. 1999	Seal Rock, Lincoln Co., OR	na	44°30.0' N, 124°5.0' W	na
Utae99-43	*Ulva taeniata* CCA	Field collection	Perkins Park, Monterey, Monterey Co., CA	17 Jun. 99	36°37.6' N, 121°55.1' W	344830 344831 344832
Utae99-17	*Ulva taeniata*I SCA	Field collection	Point Loma, San Diego, San Diego Co., CA	14 Jun. 99	32°41.7' N, 117°15.3' W	344833
Utae99-18	*Ulva taeniata*II SCA	Field collection	Point Loma, San Diego, San Diego Co., CA	14 Jun. 99	32°41.7' N, 117°15.3' W	344834

Appendix G. Continued.

Sample code	Sample name	Source	Collection locality	Collection date	Latitude, longitude	Accession no.
U3JRW	*Ulva* sp. CE	Field collection by J.R. Waaland	Coihuin, southeast of Puerto Montt, Chile	17 Oct. 00	41°28 S, 72°56' W	344835 344836
UspSc	*Ulva* sp. EU	Tan et al. 1999	Stromness Harbour, Orkney, Scotland	na	59°0' N, 3°0' W	na
PpUW	*Percursaria percursa*	UWCC MA230	na	na	na	na
UoliCM	*Ulva olivascens*	Field collection by C.A. Maggs	Portaferry, Strangford Lough, N. Ireland	5 May 00	54°22.7' N, 5°34.6' W	344837
UoPB3-10	*Ulvaria obscura* var. *obscura*	Field collection	Padilla Bay National Estuarine Research Reserve, Skagit Co., WA	25 Apr. 97	48°28.7 N, 122°30.2' W	344838 344839

Curriculum Vitae

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PAPERS AND PUBLICATIONS:

Hayden, H.S. and J.R. Waaland. 2000. Systematics of Ulvaceae (Ulvophyceae, Chlorophyta) using nuclear and chloroplast DNA sequences. . *J. Phycol.* 36(3): 87 suppl.

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