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Linnaeus was right all along: *Ulva* and *Enteromorpha* are not distinct genera

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Ulva, one of the first Linnaean genera, was later circumscribed to consist of green seaweeds with distromatic blades, and *Enteromorpha* Link was established for tubular forms. Although several lines of evidence suggest that these generic constructs are artificial, *Ulva* and *Enteromorpha* have been maintained as separate genera. Our aims were to determine phylogenetic relationships among taxa currently attributed to *Ulva*, *Enteromorpha*, *Umbraulva* Bae *et* I.K. Lee and the monotypic genus *Chloropelta* C.E. Tanner, and to make any nomenclatural changes justified by our findings. Analyses of nuclear ribosomal internal transcribed spacer DNA (ITS nrDNA) (29 ingroup taxa including the type species of *Ulva* and *Enteromorpha*), the chloroplast-encoded *rbc*L gene (for a subset of taxa) and a combined data set were carried out. All trees had a strongly supported clade consisting of all *Ulva*, *Enteromorpha* and *Chloropelta* species, but *Ulva* and *Enteromorpha* were not monophyletic. The recent removal of *Umbraulva olivascens* (P.J.L. Dangeard) Bae *et* I.K. Lee from *Ulva* is supported, although the relationship of the segregate genus *Umbraulva* to *Ulvaria* requires further investigation. These results, combined with earlier molecular and culture data, provide strong evidence that *Ulva*, *Enteromorpha* and *Chloropelta* are not distinct evolutionary entities and should not be recognized as separate genera. A comparison of traits for surveyed species revealed few synapomorphies. Because *Ulva* is the oldest name, *Enteromorpha* and *Chloropelta* are here reduced to synonymy with *Ulva*, and new combinations are made where necessary.

Key words: *Chloropelta*, *Enteromorpha*, nuclear ribosomal internal transcribed spacer DNA (ITS nrDNA), *rbc*L, *Ulva*, *Umbraulva*

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 & Pintner, 1980)

Despite evidence to the contrary, the cosmopolitan algal genera *Ulva* L. and *Enteromorpha* Link have been maintained to the present day (e.g. Gabrielson *et al.*, 2000; Graham & Wilcox, 2000). The

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separation is convenient, because the majority of currently recognized species can be readily assigned to one genus or the other on the basis of morphology. The genus *Ulva* was one of the first named by Linnaeus (1753) and initially included a variety of unrelated algae. In the nineteenth century its members were split into several genera. Green seaweeds with distromatic blades were maintained in *Ulva*, and tubular green seaweeds were moved to *Enteromorpha* (Link, 1820). Papenfuss (1960) argued that Linnaeus based his diagnosis of *Ulva* on *Enteromorpha intestinalis* (the type species of *Enteromorpha*) so that the names *Ulva* and *Enteromorpha* should both be typified by *E. intestinalis*, but the type of *Ulva* is now conserved with *Ulva lactuca* L. (Greuter *et al.*, 2000). Of the more than 140 *Ulva* and 135 *Enteromorpha* species described worldwide (Index Nominum Algarum, 2002), approximately 50 *Ulva* and 35 *Enteromorpha* species are currently recognized (Guiry & NicDonncha, 2002).

Several lines of evidence suggest that these generic constructs are artificial. Species exist in nature that have intermediate forms, such as *E. linza* with an *Enteromorpha*-like tubular base and *Ulva*-like distromatic blade distally, 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. In the absence of native bacteria, *Ulva* and *Enteromorpha* cultures displayed similar abnormal morphologies (Provasoli, 1965; Berglund, 1969; Kapraun, 1970; Fries, 1975; Provasoli & Pintner, 1980).

Most molecular phylogenies corroborate results from culture experiments. Four studies that include more than one or two representatives of each genus have been published (Blomster *et al.*, 1999; Tan *et al.*, 1999; Woolcott & King, 1999; Malta *et al.*, 1999). Among these, Tan *et al.* (1999) is the most extensive with 21 *Ulva* and *Enteromorpha* species sampled primarily from Europe. Based on nuclear ribosomal internal transcribed spacer DNA (ITS nrDNA) trees, the authors proposed that *Enteromorpha* be collapsed into *Ulva*. Other ITS nrDNA studies of European taxa (Blomster *et al.*, 1999; Malta *et al.*, 1999) supported their findings. However, preliminary results for taxa from eastern Australia based on the more conserved plastid-encoded RUBISCO large subunit gene (*rbc*L) supported separation of the two genera (Woolcott & King, 1999).

The aims of the present study were to determine the phylogenetic relationships of taxa currently attributed to *Ulva* and *Enteromorpha* and to make any nomenclatural changes justified by our findings. To do this, we included the type species of *Ulva* and *Enteromorpha*, and sampled from a broad geographical area. We also sampled two species formerly included in *Ulva* – *Umbraulva olivascens* (P.J.L. Dangeard) Bae *et* I.K. Lee and *Chloropelta caespitosa* C.E. Tanner – to investigate their relationship to *Ulva* and *Enteromorpha* taxa. We obtained sequences of ITS nrDNA for all 29 ingroup taxa; the chloroplast-encoded *rbc*L gene was sequenced for a subset of taxa, for which combined analyses were also carried out.

Materials and methods

Northeast Pacific collections (Table 1) were isolated into culture when possible. Unialgal cultures were grown in Guillard's f/2 enriched seawater at 15°C in glass culture vessels under 30–50 μmol m^{-2} s^{-1} in a 16 h light:8 h dark photoregime. *Ulva* collections from Australia, Chile, Hawaii, Spain and Japan were received as silica-gel-preserved specimens. Vouchers for collections were deposited in the University of Washington Herbarium (**WTU**). Herbarium studies of type and other relevant material were carried out in the Natural History Museum London (**BM**) and the Dillenian Herbarium, Oxford University (**OXF**). All herbarium abbreviations are as listed in the Index Herbariorum (http://www.nybg.org/bsci/ih/ih.html).

One *Chloropelta*, one *Umbraulva*, 17 *Ulva* and 10 *Enteromorpha* accessions were included in ITS nrDNA analyses. *rbc*L sequences were available only from algal samples collected by the present authors, with the exception of *Ulva rigida* for which amplification difficulties were experienced. Thus, a subset of one *Chloropelta*, one *Umbraulva*, 12 *Ulva* and seven *Enteromorpha* samples were included in *rbc*L analyses (Table 1). Taxa were chosen for outgroup comparison on the basis of prior molecular analyses of generic relationships in the Ulvales (Hayden & Waaland, 2002). In each case the type species of the genus was studied, as follows (with approximate number of species in each genus 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, but *B. minima* var. *minima* and *K. leptoderma* were excluded from ITS nrDNA analyses because large sections of the spacers in these taxa were unalignable with ingroup taxa.

DNA extraction from silica-gel-preserved specimens was preceded by a rehydration step in which 14–18 mg of material was rehydrated in 200 μl of double-distilled, UV-treated water at 4°C for 10 min. Total DNA was extracted from fresh cultured or rehydrated material

Table 1. Details of the sampled taxa

Taxon	Collection information or ITS rDNA sequence origin	ITS rDNA	*rbc*L
Chloropelta caespitosa C.E. Tanner	Kobe, Hyogo Pref., Japan. 22 Mar 2000. Coll. H. Kawai	AY260556	AY255858
Enteromorpha clathrata (Roth) Greville	Blomster *et al.* 1999 (as *E. muscoides*)	AF127170	AY255862
E. compressa (L.) Nees	Blomster *et al.* 1998	AF035350	AY255859
E. flexuosa (Wulfen) J. Agardh	Leskinen & Pamilo 1997	AJ234306	na
E. intestinalis (L.) Nees	Blomster *et al.* 1998	AF035342	AY255860
E. intestinaloides Koeman *et* van den Hoek	Tan *et al.* 1999	AJ234303	na
E. linza (L.) J. Agardh	Humboldt Bay, CA USA, 19 Jun 2000. Coll. H.S. Hayden & F. Shaunessey	AY260557	AY255861
E. procera Ahlner	Coll. J. Blomster	AY260558	AY255863
E. prolifera (O.F. Müller.) J. Agardh	Tan *et al.* 1999	AJ234304	AY255864
Enteromorpha sp. I	Bodega Bay, CA, USA. 17 Jun 2000. Coll. H.S. Hayden	AY260559	AY255865
Enteromorpha sp. II	Tan *et al.* 1999	AJ234308	na
Ulva armoricana Dion, de Reviers *et* Coat	Coat *et al.* 1998	na	na
U. australis Areschoug	Woolcott & King 1999	AF099726	na
U. californica Wille *in* Collins, Holden *et* Setchell	La Jolla, CA, USA. 14 Jun 1999. Coll. H.S. Hayden	AY260560	AY255866
U. fasciata Delile	Kihei, Maui, USA. 6 Feb 2000. Coll. L. Hodgson	AY260561	AY255867
U. fenestrata Postels *et* Ruprecht	San Juan Is., WA, USA. 15 Jun 1998. Coll. H.S. Hayden & D.J. Garbary, MA715	AY260562	AF499668
U. lactuca L.	Tan *et al.* 1999	AJ234310	AF499669
U. lobata (Kützing) Setchell *et* Gardner	Newport, OR, USA. 16 May 1999. Coll. H.S. Hayden & A. Whitmer, MA716[a]	AY260563	AY255868
U. pertusa Kjellman	Tan *et al.* 1999	AJ234321	na
U. pseudocurvata Koeman *et* van den Hoek	Tan *et al.* 1999	AJ234312	AY255869
U. rigida C. Agardh	Cádiz, Spain. Coll. J. Berges	AY260565	na
U. rotundata Bliding	Coat *et al.* 1998	na	na
U. scandinavica Bliding	Tan *et al.* 1999	AJ234317	AY255870
Ulva sp. I	Coihuin, Puerto Montt, Chile. 17 Oct 2000. Coll. J.R. Waaland	AY260566	AY255871
Ulva sp. II	Tamarama, Sydney, NSW. 9 Aug 1999. Coll. G. Zuccarello	AY260567	AY255872
Ulva sp. III	Newport Beach, CA, USA. 15 Jun 1999. Coll. H.S. Hayden & S. Murray	AY260568	AY255873
U. stenophylla Setchell *et* Gardner	Seattle, WA, USA. 2 Jun 2000. Coll. H.S. Hayden, MA721[a]	AY260569	AY255874
U. taeniata (Setchell *in* Collins, Holden *et* Setchell) Setchell *et* Gardner	Monterey, CA, USA. 17 Jun 1999. Coll. H.S. Hayden, MA722[a]	AY262335	AY255875
Umbraulva olivascens (P.J.L Dangeard) Bae *et* I.K. Lee	Portaferry, Strangford Lough, N. Ireland. 5 May 2000. Coll. C.A. Maggs	AY260564	AY255876
Outgroups			
Blidingia minima (Nägeli *ex* Kützing) Kylin var. *minima*	Bolinas, CA, USA. 16 Jun 2000. Coll. H.S. Hayden	na	AF499675
Kornmannia leptoderma (Kjellman) Bliding	Vancouver Is., B.C., Canada. 29 Jun 1999. Coll. H.S. Hayden	na	AF499661
Percursaria percursa (C. Agardh) Rosenvinge	MA230[a]	AY260570	AF499658
Ulvaria obscura var. *blyttii* (Areschoug) Bliding	Padilla Bay, WA, USA. 25 Apr 1997. Coll. H.S. Hayden	AY260571	AF499657

[a] Cultures are in the University of Washington Culture Collection (UWCC).

using a modified CTAB method (Doyle & Doyle, 1990; Hughey *et al.*, 2001). *rbc*L sequences of eight European taxa were obtained from genomic DNA previously used for ITS nrDNA sequences published elsewhere (Table 1).

Total genomic DNA (10–20 ng) was added to six 25 μl PCR reactions each containing final concentrations of 1 × PCR Buffer II (PE Applied Biosystems), 1.5 mM $MgCl_2$, 0.8 mM dNTPs (GibcoBRL), 0.3 U AmpliTaq DNA Polymerase (PE Applied Biosystems) and 0.8 mM of each primer. ITS nrDNA reactions also contained 5% DMSO (Sigma). Six reactions were performed in order to produce more product and to avoid sequence errors resulting from PCR amplification. PCR amplification was carried out in a PTC-100 Programmable Thermal Controller (MJ Research, NJ, USA). Primers used to amplify and sequence ITS nrDNA and the *rbc*L gene are listed in Table 2. A fragment containing ITS1, ITS2 and the 5.8S ribosomal subunit was amplified using primers 18S1505 and ENT26S, which anneal 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 1357 bp of the *rbc*L gene excluding primers. This

Table 2. Primers used in this study for PCR amplification and sequencing

Primer	Sequence	Target
18S1505[a]	5′ TCTTTGAAACCGTATCGTGA 3′	ITS1
18S1763[b]	5′ GGTGAACCTGCGGAGGGATCATT 3′	ITS1
5.8S30[a]	5′ GCAACGATGAAGAACGCAGC 3′	ITS2
5.8S142[a]	5′ TATTCCGACGCTGAGGCAG 3′	ITS1
ENT26S[c]	5′ GCTTATTGATATGCTTAAGTTCAGCGGGT 3′	ITS2
RH1[d]	5′ ATGTCACCACAAACAGAAACTAAAGC 3′	*rbc*L
rbc571[a]	5′ TGTTTACGAGGTGGTCTTGA 3′	*rbc*L
rbc590[a]	5′ TCAAGACCACCTCGTAAACA 3′	*rbc*L
1385r[d]	5′ AATTCAAATTTAATTTCTTTCC 3′	*rbc*L

[a] Primer name includes gene abbreviation and approximate position to which primer anneals in *Ulva*.
[b] Modified from Blomster *et al.* (1998).
[c] Blomster *et al.* (1998).
[d] Manhart (1994).

fragment excludes the variable 3′ terminus and represents 95% of the gene. The reaction profile included an initial denaturation at 94°C for 3 min, 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^{-1} ethidium bromide (Gibco BRL) and visualized under UV light. Products were pooled then purified using a polyethylene glycol (PEG) precipitation (Sigma). Briefly, an equal volume of a 20% PEG – 8000/2.5M NaCl stock solution was added to pooled PCR product. Following mixing, solutions were incubated at 37°C for 15 min and microcentrifuged for 15 min. The supernatant was removed and the DNA pellet was washed twice in 80% cold ethanol, dried down and resuspended in double-distilled, UV-treated water for sequencing. 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).

Sequences for the *rbc*L gene 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 ITS1 and ITS2 that could not be aligned with confidence were removed prior to analyses. Sequence divergence values were calculated using uncorrected ‘p’ distances. 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; however, a ML analysis of the combined data was not performed due to computational limitations. Prior to analysis of the combined data, the incongruence length difference test (ILD) of Farris *et al.* (1994), implemented in PAUP* as the partition homogeneity test, was performed. This test assesses heterogeneity among user-designated partitions, e.g. genes or codon positions. A non-significant result indicates that user-designated data partitions are not significantly different from random partitions of the combined data set. Congruent data partitions may then be combined in a single phylogenetic analysis (de Queiroz *et al.*, 1995; Huelsenbeck *et al.*, 1996). In MP analyses, all characters and character state changes were weighted equally and 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, proportion of invariable sites and site-to-site rate heterogeneity were estimated under maximum likelihood criteria from an optimal parsimony topology (Swofford *et al.*, 1996). These parameters were then set to estimated values in ensuing ML searches. Based on these estimations, substitution bias was modelled by the general time-reversible model (Yang, 1994*a*) with invariable sites (Hasegawa *et al.*, 1985), and rate heterogeneity was modelled using the gamma distribution method (Yang, 1994*b*) with four discrete rate categories and a single shape parameter (alpha) (model GTR + I + G). A heuristic search was conducted using an optimal starting tree from MP analyses with TBR, MulTrees and steepest descent options in effect.

Results

MP and ML analyses were conducted using 471 aligned characters from the spacers and the 5.8S gene. Boundaries for the 5.8S gene were defined according to Thompson & Herrin (1994). The 5′ end of ITS1 and the 3′ end of ITS2 were determined according to van de Peer *et al.* (2000) and Wuyts *et al.* (2001), respectively. The ITS1 spacer ranged in length from 154 to 218 bp and the ITS2 from 162 to 184 bp among the surveyed taxa. A total of 141 characters were excluded from the spacers prior to analyses because positional homology could not be confidently determined. In contrast, the 5.8S nrDNA gene was 158 bp in all surveyed taxa and had only 14 variable sites. The lengths of the spacers and the 5.8S gene are comparable to those of other taxa in the Ulvophyceae (Bakker *et al.*, 1995*a*, *b*; van Oppen, 1995; Friedl, 1996).

Alignment of *rbc*L sequences required the addition of a single gap of three nucleotides in all sequences relative to the outgroup *Kornmannia leptoderma*. 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 & Waaland, 2002). The final *rbc*L alignment included 1357 characters.

The ILD test using partitions for *rbc*L versus ITS nrDNA was non-significant ($p = 0.99$); thus, data sets were combined in a single analysis. The alignment of combined data included all taxa, and *rbc*L positions were coded as missing data for the taxa in which this gene was not sequenced (Table 1).

MP analysis of ITS nrDNA data resulted in 90 optimal trees of 347 steps. There were 147 variable sites in the analysed data set, and 108 sites were parsimony-informative. The strict consensus of most-parsimonious trees is shown in Fig. 1*a*. The ML analysis resulted in a single tree (Fig. 2) which is similar to the strict consensus tree based on ITS nrDNA sequences (Fig. 1*a*). Minor differences between trees can be seen in the clades comprising *U. lactuca*, *U. australis*, etc., and *U. stenophylla*, *E. prolifera*, etc. and the positions of *E. flexuosa* and *Enteromorpha* sp. II.

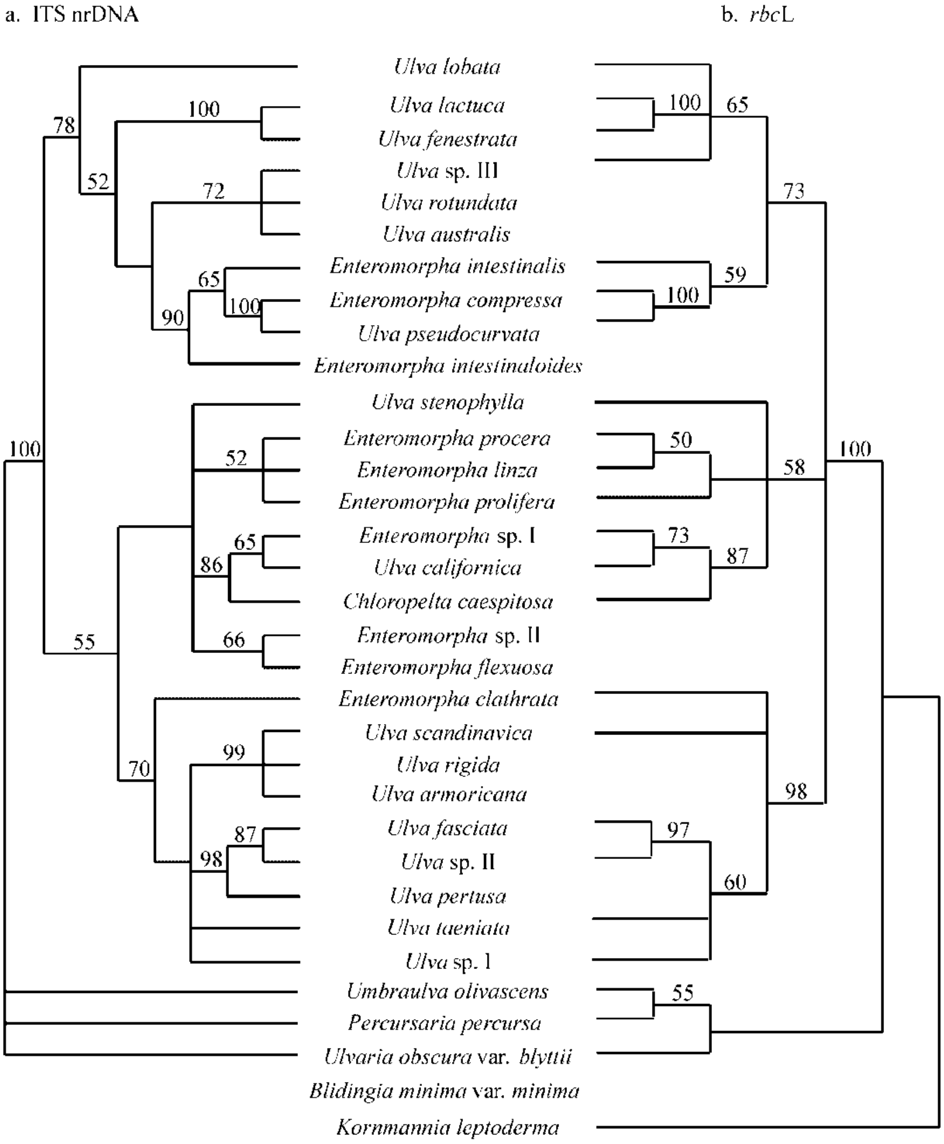

Fig. 1. Comparison of strict consensus trees derived from (*a*) nuclear ribosomal ITS sequence data and (*b*) the chloroplast-encoded *rbc*L gene. Bootstrap percentages (1000 replicates samples) are shown above branches. Nodes with bootstrap values of less than 50% are not labelled.

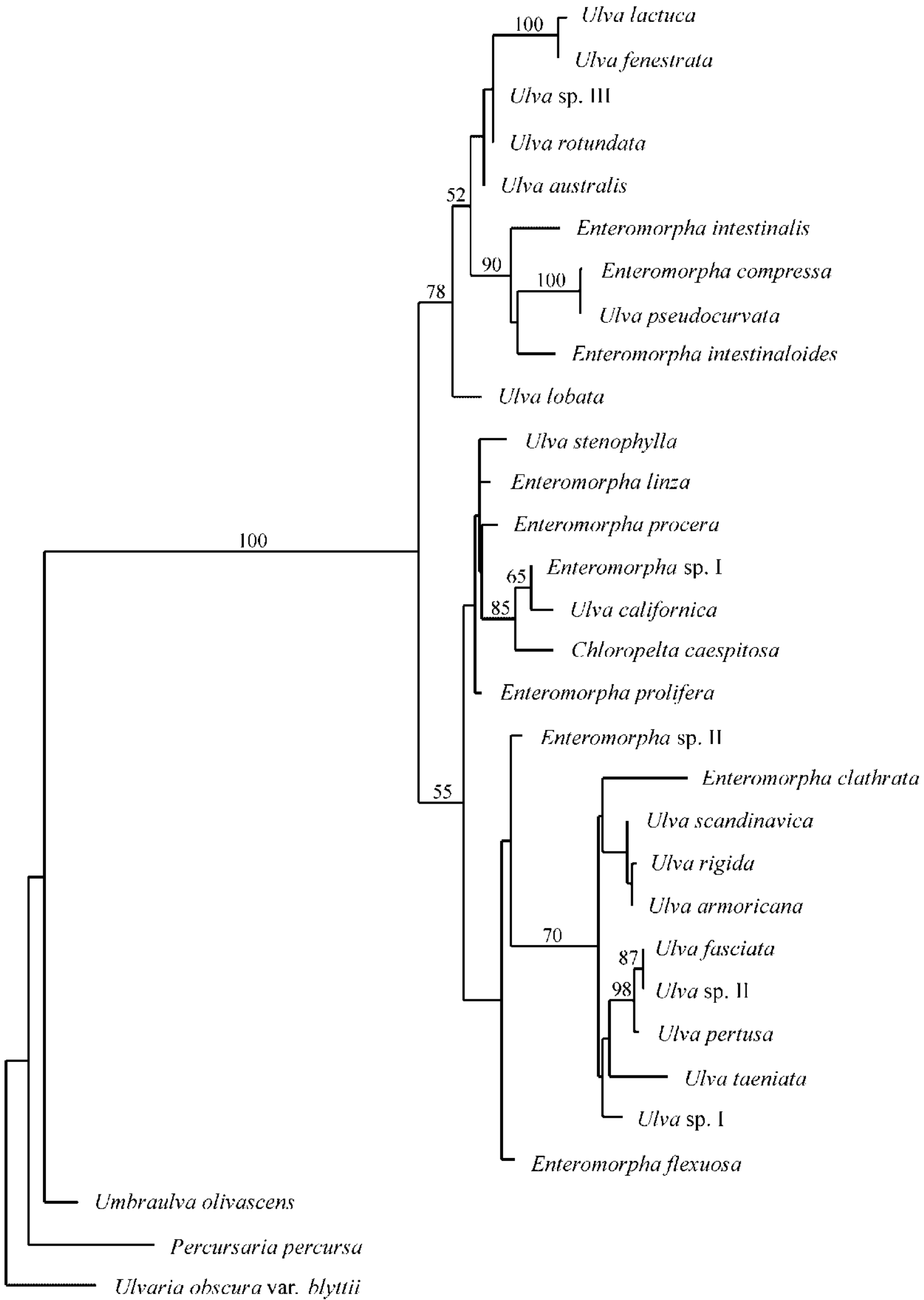

Fig. 2. Phylogram of sampled taxa based on ML analysis of ITS nrDNA sequences ($-\ln L = 2424.316$). Bootstrap percentages (1000 replicates samples) are shown above branches. Nodes with bootstrap values of less than 50% are not labelled.

MP analysis of the *rbc*L data set resulted in six optimal trees of 473 steps. The strict consensus tree is shown in Fig. 1*b*. There were 291 variable sites in the data set, and 138 sites were parsimony-informative. Clades with bootstrap values of 50% or greater in the consensus tree (Fig. 1*b*) were also resolved in the ML tree (Fig. 3) with one exception. In the ML tree *Umbraulva olivascens* rather than *Ulvaria obscura* var. *blyttii* is basal in the clade that is sister to the remaining *Ulva* and *Enteromorpha* species.

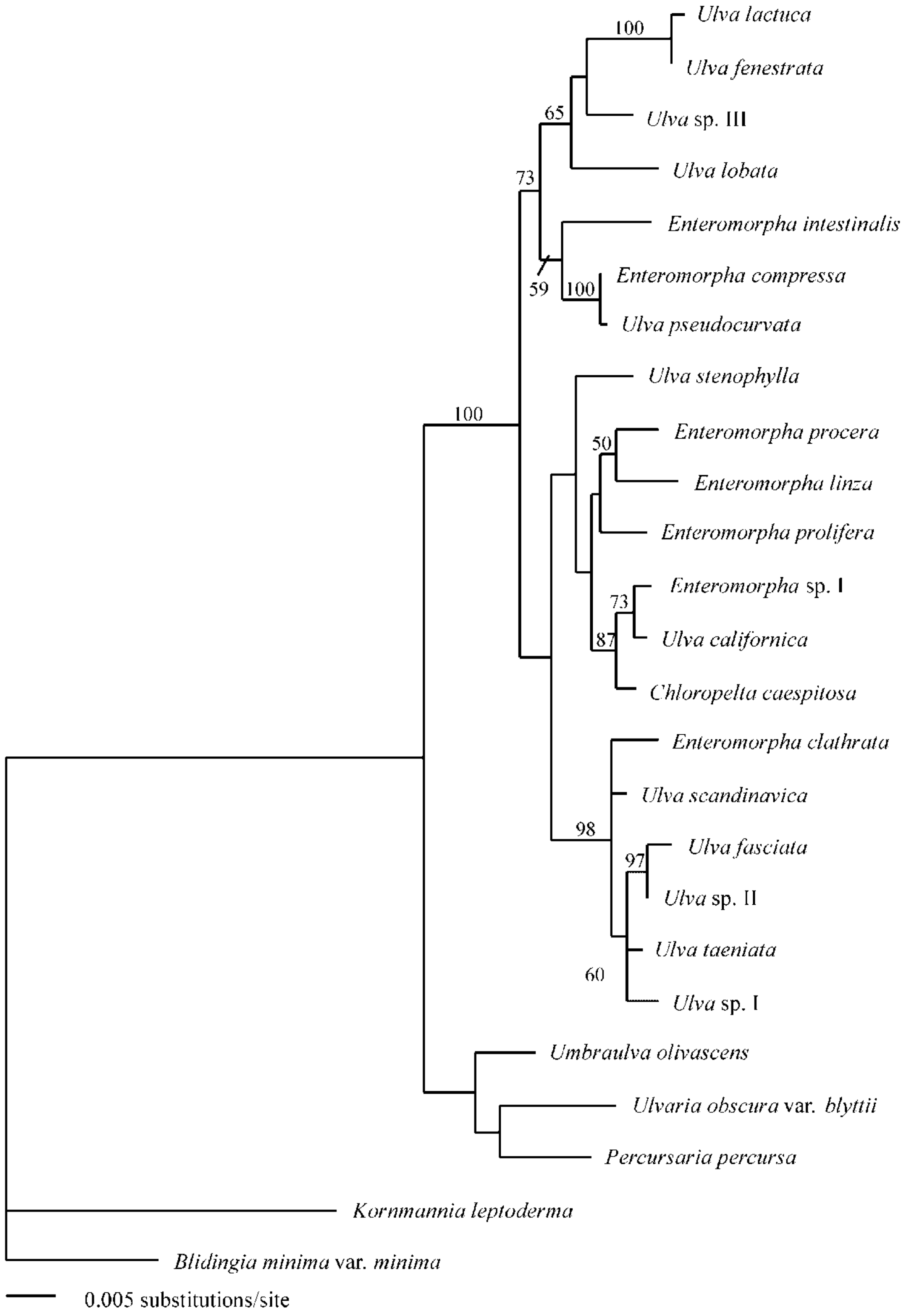

Fig. 3. Phylogram of a subset of sampled taxa based on ML analysis of *rbc*L sequences (−lnL = 4435.492). Bootstrap percentages (1000 replicates samples) are shown above branches. Nodes with bootstrap values of less than 50% are not labelled.

MP analysis of the combined data resulted in 117 trees of 824 steps (Fig. 4). A total of 1828 characters were included in the analysis, of which 246 were parsimony-informative. Clades resolved in the combined data consensus tree (Fig. 4) are similar to those in the ITS nrDNA and *rbc*L consensus trees (Fig. 1) but they have higher bootstrap values. In all trees a clade consisting of all *Ulva* and *Enteromorpha* species is strongly supported. The topology of the deepest branches within this clade varies among trees; however, in all analyses there are well-supported clades which

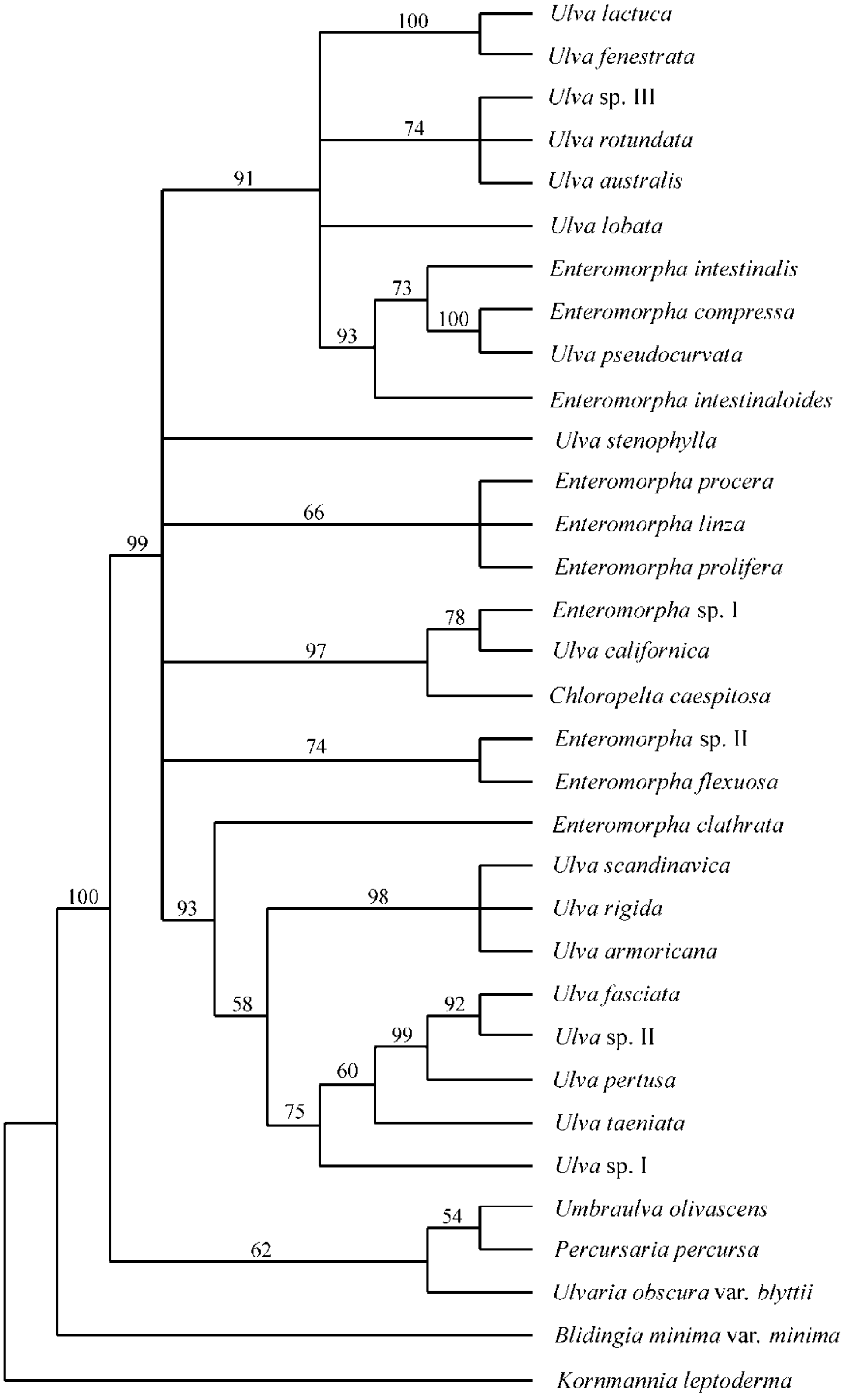

Fig. 4. Strict consensus of 117 most parsimonious trees of 824 steps from the analysis of combined ITS nrDNA and *rbc*L sequences. Bootstrap percentages (1000 replicate samples are shown above branches. Nodes with bootstrap values of less than 50% are not labelled.

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*; (3) *U. californica* and *Enteromorpha* sp. I; (4) these taxa plus *Chloropelta caespitosa*; and (5) *E. clathrata* plus several species of *Ulva*. Several additional clades that have moderate to strong bootstrap values in all consensus trees contain either *Ulva* or *Enteromorpha* species.

Sequence divergence among the ITS nrDNA sequences ranged from 0 between *U. fasciata* and *Ulva* sp. II to nearly 18% between *Percursaria percursa* and some species of *Ulva* and *Enteromorpha*. The *Umbraulva olivascens* sequence was approximately 7% divergent from *Ulvaria obscura* var. *blyttii* and *P. percursa* and more than 13% divergent from *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 approximately 6% between these taxa and *E. intestinalis*. Sequence divergence was 1.3% between *U. californica* and *Enteromorpha* sp. I, approximately 3% between these taxa and *C. caespitosa*, and 5.0–6.5% between *E. clathrata* 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* /*U. fenestrata* and *E. compressa*/*U. pseudocurvata*, to nearly 14% between ingroup taxa and the two outgroups, *K. leptoderma* and *B. minima* var. *minima*. *Umbraulva olivascens* was less than 3% divergent from *Ulvaria obscura* var. *blyttii* and *P. percursa* and 3.7–4.4% divergent from *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. clathrata* and related *Ulva* species. The greatest sequence divergence among ingroup taxa (minus *U. olivascens*) was 3.6%.

Discussion

Ulva and *Enteromorpha* together form a strongly supported clade in all analyses, but they are not monophyletic. These results, combined with earlier findings from molecular (Blomster *et al*., 1999; Tan *et al*., 1999) and culture studies (Gayral, 1959, 1967; Føyn, 1960, 1961; Løvlie, 1964; Provasoli, 1965; Berglund, 1969; Kapraun, 1970; Fries, 1975; Bonneau, 1977; Provasoli & Pintner, 1980), provide strong evidence that *Ulva* and *Enteromorpha* are not distinct evolutionary entities and should not be recognized as separate genera.

Additionally, *Chloropelta caespitosa* is nested among *Ulva* and *Enteromorpha* taxa. Tanner (1979, 1980) described *C. caespitosa* on the basis of its unique developmental pattern. Early in development, cells in the tubular germling undergo one division producing a distromatic tubular germling not seen in other Ulvaceae. Rupture of the apical end of the germling and continued growth eventually result in a peltate distromatic blade (Tanner, 1980). Despite its unique development, which is very distinctive in culture (Hayden, personal observation), *C. caespitosa* groups with *U. californica* and *Enteromorpha* sp. I from California in all trees, and bootstrap support for this grouping is strong (Fig. 4). Thus, the type and only species of *Chloropelta* should also be transferred to *Ulva*. However, because the resulting binomial would be a later homonym of *Ulva caespitosa* Withering (Bot. Arr. Veg. Gt. Brit.: 735. 1776), the basionym of *Catenella caespitosa* (Withering) L. Irvine (*J. Mar. Biol. Assoc. UK*, 56: 590. 1976), the following substitute name is proposed:

> *Ulva tanneri* H.S. Hayden & J.R. Waaland, nom. nov.
> Replaced name: *Chloropelta caespitosa* C.E. Tanner (*J. Phycol.*, 16: 130, figs 2–49. 1980).

In the ensuing discussion, the clade comprising *Ulva*, *Enteromorpha* and *Chloropelta* taxa will be referred to as the *Ulva* clade. *Umbraulva olivascens* is discussed further below.

Mixed clades of Ulva *and* Enteromorpha

Within the *Ulva* clade several subclades consisting of both 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*; however, 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 & 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, 2001). Thus, divergence between *E. compressa* and *U. pseudocurvata* in the *rbc*L gene (< 0.1%) is also within the range of conspecifics.

Another mixed *Ulva* and *Enteromorpha* pair that is well supported in trees is *U. californica* and *Enteromorpha* sp. I from California. *U. californica* is a distromatic species found along the Pacific coast of North America from the Alaska Peninsula to Baja California. Morphological 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, 2001). Divergence between these taxa is 1.3% and 0.5% for ITS nrDNA and *rbc*L sequences, respectively – values 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 & van den Hoek, 1981) and *U. californica* (Tanner, 1979, 1986). Further, the type of sexual life history is used to delimit the Ulvales (isomorphic) from the Ulotrichales (heteromorphic) (Kornmann, 1965), and its use at this taxonomic level is supported by molecular and ultrastructural data (Floyd & O'Kelly, 1984; Hayden & Waaland, 2002). Thus, an alternation of heteromorphic generations in this clade is unlikely. An alternative explanation is that these pairs represent separate species and that observed low sequence divergences are due either to recent speciation, i.e. they are in the early stages of diverging from one another, or to other factors, such as convergent evolution. Data supporting their status as individual species exist. In Tan *et al.* (1999) the monophyly of *E. compressa* accessions is strongly supported by ITS nrDNA analyses. 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, 2001). Thus, these taxa are considered separate species.

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 lineages. 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 although monostromatic sheets are formed under green tide conditions (Blomster *et al.*, 2002) there are no culture studies which show *Enteromorpha* with distromatic morphologies. Further, observations of cultures suggest that altered morphologies in cultures of *Ulva* are not uncommon (Hayden, personal observation). With the exception of *Percursaria*, all ulvacean taxa pass through a tubular stage in development. Distromatic species growing without exposure to wave action, desiccation or other environmental factors may not develop normally beyond the tubular stage. Some culture studies of *Ulva* species have not reported altered morphology (e.g. Bliding, 1963, 1968; Kapraun, 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

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 & O'Kelly, 1984) or too variable, e.g. cell size, number of pyrenoids (Tanner, 1979; Phillips, 1988). The difficulty in identifying morphological synapomorphies for clades in molecular-based trees is not unique to this group of seaweeds (e.g. Stiller & Waaland, 1993). 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. Characters commonly used to distinguish species are listed in Table 3. Of these characters, 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 & van den Hoek, 1981, 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 & van den Hoek, 1981). Other taxa have chloroplasts which completely fill cells in

Table 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 colour 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

surface view. Neither of the latter chloroplast positions appears to delimit clades. Studies by Britz & Briggs (1976, 1983) and Mishkind *et al.* (1979) showed that chloroplasts in some *Ulva* species migrate within the cells according to a circadian rhythm. Such movement was not detected in certain Ulvales, including an alga identified as *E. intestinalis* (Britz & Briggs, 1976). These studies may suggest that chloroplast position is too variable for use in systematic studies. Conversely, the presence of diurnal changes in chloroplast position may prove to be a synapomorphy, but at present this phenomenon has been studied in only a limited number of taxa.

Ulva species in the clade with *E. clathrata* (Fig. 4) share the presence of microscopic teeth along the blade margin. *E. clathrata* 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, as *E. muscoides*). 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 (Dion *et al.*, 1998); however, marginal dentition has been described in two other surveyed taxa – *U. rotundata* (Bliding, 1968) and *U. australis* (Phillips, 1988; Woolcott & King, 1999) – which were not placed in the same clade as *E. clathrata*, suggesting 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), although the latter study included a relatively small number of *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, *Umbraulva 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* (as *Ulva 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.

Umbraulva olivascens, found in the northeast Atlantic and Mediterranean, was named for its characteristic olive-green thallus (Dangeard, 1951, 1961, as *Ulva olivascens*). Other traits which distinguish this taxon from *Ulva* species 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). 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), and the relationship between these three taxa requires further investigation.

The positions of two additional *Ulva* species, *U. fenestrata* and *U. californica*, differ in the present trees compared with those in Tan *et al.* (1999). Tan *et al.* (1999) found that *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, 2001). A study of *Ulva* and *Enteromorpha* from the northeast Pacific including collections of *U. californica* and *U. fenestrata* from throughout their distribution ranges found similar relationships of these species to others (Hayden, 2001). 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, and overlapping distribution ranges and ecology (Tanner, 1979, 1986; Gabrielson *et al.*, 2000), it is not unreasonable that an individual of *U. californica* would be misidentified as *U.*

Table 4. Valid *Enteromorpha* binomials with authorities, in current usage (Wynne, 1998; Guiry & NicDonncha, 2002) or otherwise of interest as indicated, with existing binomials in *Ulva*, new combinations in *Ulva*, or explanations why binomials in *Ulva* are blocked (Index Nominum Algarum, 2002). Infraspecific taxa are omitted

Binomial in *Enteromorpha* Basionym (if different) Binomial in *Ulva*	Type locality; *collector* Type material (with relevant reference if any) Type or other authentic material examined	Taxonomic notes (non-type material examined)
Enteromorpha acanthophora Kützing (1849) Sp. Alg.: 479 *Ulva acanthophora* (Kützing) comb. nov.	Bay of Islands, New Zealand; *J.D. Hooker* Type: **L** 938.19.134 (Womersley, 1956)	Currently placed in synonymy with *E. clathrata* but we concur with Adams (1994) that New Zealand material might be distinct (*E. acanthophora*, **BM**, Chatham Islands, H.E. Maltby xi 1905)
Enteromorpha atroviridis (‘*atro-viridis*’) (Levring) M.J. Wynne (1986) Nova Hedwigia 43: 324 *Ulva atroviridis* Levring (1938) Lunds Univ. Årsskr. N.F. Avd. 2, 34(9): 4, fig. 2; pl. 1: fig. 1	Hotel Rocks, Port Nolloth, Cape Province, South Africa Type: **GB** (Wynne, 1986)	South African endemic resembling *E. linza* (Wynne, 1986; Stegenga *et al*., 1997)
Enteromorpha bulbosa (Suhr) Montagne (1846) Voy. Bonite, Crypt. Cell.: 33 *Solenia bulbosa* Suhr (1839) Flora 22: 72, pl. IV: fig. 46 *Solenia bulbosa* Suhr was transferred to *Ulva* by Trevisan (Fl. Eugan.: 51. 1842), but *Ulva bulbosa* (Suhr) Trevisan is a later homonym of *Ulva bulbosa* Palisot de Beauvois (Fl. Oware 1: 20, pl. XIII: fig. 1. 1805) from Ghana, of uncertain identity	Peru Type: **L** 1391 sheet 40 (Ricker, 1987) Material examined: **BM**, Peru, ex herb. Montagne	Highly morphologically variable, from tubular to cornucopia-like (Ricker, 1987). Many putative synonyms. As the *Ulva* binomial cannot be used, a synonym is chosen here. The most appropriate geographically is *E. hookeriana* Kützing (see below)
Enteromorpha chaetomorphoides Børgesen (1911) Bot. Tidsskr. 31: 149, fig. 12 *Ulva chaetomorphoides* (Børgesen) comb. nov.	Bovoni Lagoon, St Thomas, Virgin Islands Holotype: **C** (Bliding, 1963)	Very finely branched material, often growing with *Rhizoclonium*. (**BM**, Puerto Rico, various collections)
Enteromorpha clathrata (Roth) Greville *Conferva clathrata* Roth (1806) Cat. bot. III: 175–8	Type locality: Fehmarn, SW Baltic (original material missing) Neotype: **LD** 137737 from Landskoma, Baltic Oresund, 1829 (Blomster *et al*., 1999; illustrated in Bliding 1963, figs 69a, b)	Heterotypic synonyms include: *E. crinita* Nees (1820) Hor. Phys. Berol.: Index [2] *E. muscoides* (Clemente) J. Cremades in J. Cremades & J.L. Pérez-Cirera (1990) Anales Jard. Bot. Madrid 47: 489, based on *Ulva muscoides* Clemente (1807) Ensayo sobre las Variedades de la Vid: 320 (erroneously regarded as the oldest valid name by Blomster *et al*., 1999) *E. ramulosa* (J.E. Smith) Carmichael *Enteromorpha welwitschii* J. Agardh (1883) Alg. Syst. 3: 143. Tagus R. near Aldea, Portugal; *Welwitsch*, Phyc. Lusitan. 289. Syntypes: **BM** *Enteromorpha gelatinosa* Kützing (1849) Sp. Alg.: 482. Canary Islands, Despreaux non *Ulva gelatinosa* Kützing (1856) Tab. Phyc. VI, Tab. 32

(*continued*)

Table 4. (*continued*)

Binomial in *Enteromorpha* Basionym (if different) Binomial in *Ulva*	Type locality; *collector* Type material (with relevant reference if any) Type or other authentic material examined	Taxonomic notes (non-type material examined)
Enteromorpha compressa (Linnaeus) Nees (1820) Hor. Phys. Berol.: Index [2] *Ulva compressa* Linnaeus (1753) Sp. Pl. 2: 1163	Bognor, Sussex, England? Typotype (= epitype): **OXF**. Lectotype: Dillenius (1742: pl. 9, fig. 8; Blomster *et al*., 1998)	Heterotypic synonyms: *Enteromorpha usneoides* J. Agardh (1883) Alg. Syst. 3: 159 [misnumbered 157] (Blomster *et al*., 1998) *Enteromorpha complanata* Kützing 1845: 248; see Silva *et al*. (1996)
Enteromorpha crassimembrana V.J. Chapman (1956) J. Linn. Soc. London, Bot. 55: 424, fig. 74 *Ulva crassimembrana* (V.J. Chapman) comb. nov.	Cape Maria van Diemen, New Zealand Type: **AKU** (Chapman, 1956)	Known only from northern North I., New Zealand (Adams, 1994)
Enteromorpha flexuosa (Wulfen) J. Agardh (1883) Alg. Syst. 3: 126 *Ulva flexuosa* Wulfen (1803) Crypt. Aquat.: 1., new name for *Conferva flexuosa* Roth 1800 (nom. illeg.; see Silva *et al.,* 1996, p. 732)	Duino, near Trieste, Italy Holotype: **W**, Wulfen no. 23 (Bliding, 1963)	Heterotypic synonym: *Enteromorpha tubulosa* (Kützing) Kützing, based on *Enteromorpha intestinalis* var. *tubulosa* Kützing (1845) Phycol. Germ.: 247 (Bliding, 1963)
Enteromorpha hookeriana Kützing (1849) Sp. Alg.: 480 *Ulva hookeriana* (Kützing) comb. nov.	Berkeley Sound, Falkland Islands; *J.D. Hooker* Type: **L**? Isotype: **BM**, iv 1842	Currently treated as a synonym of *Enteromorpha bulbosa* (Suhr) Montagne, which cannot be transferred to *Ulva* due to a prior homonym (see above)
Enteromorpha intestinalis (Linnaeus) Nees (1820) Hor. Phys. Berol.: Index [2] *Ulva intestinalis* Linnaeus (1753) Sp. Pl. 2: 1163	Woolwich, London, England? Typotype (= epitype): **OXF.** Lectotype: Dillenius (1742: pl. 9, fig. 7; Blomster *et al*., 1998)	Type species of *Enteromorpha* Link (1820) Algae in Nees, Hor. Phys. Berol.: 5 nom. cons. vs. *Splaknon* Adanson 1763, nom. rej.
Enteromorpha intestinaloides R.P.T. Koeman & C. van den Hoek (1982) Arch. Hydrobiol. Suppl. 63 [Algol. Stud. 32]: 321, figs. 115–129 *Ulva intestinaloides* (R.P.T. Koeman & C. van den Hoek) comb. nov.	Westkapelle, Netherlands; *R.P.T. Koeman* (iv.1976) Holotype: **L**; Isotype: **GRO** (Koeman & van den Hoek, 1982)	Differs morphologically and ecologically from *E. intestinalis* (Koeman & C. van den Hoek, 1982)
Enteromorpha kylinii Bliding 1948: 199–204, figs 1–3 *Ulva kylinii* (Bliding) comb. nov.	Kristineberg, Swedish west coast Holotype: **LD** (Bliding, 1963)	Recorded widely from NE Atlantic and elsewhere (e.g. Coppejans, 1995; Silva *et al*., 1996; Furnari *et al*., 1999)
Enteromorpha lingulata J. Agardh (1883) Alg. Syst. 3: 143 Cannot be transferred to *Ulva* because of the prior existence of *Ulva lingulata* A.P. de Candolle (in Lamarck & de Candolle, 1805, Fl. Franc. ed. 3, 2: 14), of uncertain identity but most likely referable to *Hypoglossum hypoglossoides*	North Atlantic; Gulf of Mexico; Tasmania; New Zealand Syntypes: **L** 13522 to 13576 (some European, mostly from Australia; Bliding, 1963)	Recorded widely in Atlantic and Pacific Oceans (e.g. Silva *et al*., 1996; Wynne, 1998) Type material investigated by Bliding (1963) was conspecific with or closely related to *Enteromorpha flexuosa* (Wulfen) J. Agardh so a new name is not proposed here
Enteromorpha linza (Linnaeus) J. Agardh (1883) Alg. Syst. 3: 134. *Ulva linza* Linnaeus (1753) Sp. Pl. 2: 1163.	Sheerness, Kent, England Epitype: **OXF**. Lectotype: Dillenius (1742: pl. 9, fig. 6), *Tremella marina fasciata* (L.M. Irvine, note dated xii 1966, in Herb. **OXF**)	

(*continued*)

Table 4. (*continued*)

Binomial in *Enteromorpha* Basionym (if different) Binomial in *Ulva*	Type locality; *collector* Type material (with relevant reference if any) Type or other authentic material examined	Taxonomic notes (non-type material examined)
Enteromorpha muscoides (Clemente) J. Cremades in J. Cremades & J.L. Pérez-Cirera (1990) Anales Jard. Bot. Madrid 47: 489. *Ulva muscoides* Clemente (1807) Ensayo sobre las Variedades de la Vid: 320.	Cádiz, Algeciras, Spain; *Clemente* Lectotype: **MA**-Algae 1713 (Blomster *et al*., 1999).	Heterotypic synonyms include: *E. clathrata* (Roth) Greville; *E. crinita* Nees; *E. ramulosa* (J.E. Smith) Carmichael (see Blomster *et al*., 1999) *Enteromorpha welwitschii* J. Agardh (1883) Alg. Syst. 3: 143. Tagus R. near Aldea, Portugal; *Welwitsch*, Phyc. Lusitan. 289. Syntypes: **BM**. *Enteromorpha gelatinosa* Kützing (1849) Sp. Alg.: 482. Canary Islands, Despreaux. non *Ulva gelatinosa* Kützing (1856) Tab. Phyc. VI, Tab. 32
Enteromorpha paradoxa (C. Agardh) Kützing (1845) Phycol. Germ.: 247. *Ulva paradoxa* C. Agardh (1817), new name, Syn. Alg. Scand.: XXII. *Conferva paradoxa* Dillwyn 1809 (illeg.)	Bangor, Wales Lectotype: **LD** 13702 (Bliding, 1960, fig. 43a–d; Womersley, 1984) Typified by the type of *Conferva paradoxa* Dillwyn (1809) Conf. Syn. 70, suppl. pl. F.	*Enteromorpha flexuosa* subsp. *paradoxa* (C. Agardh) Bliding (1963); recognized at species level by Womersley (1984) Heterotypic synonym: *E. plumosa* Kützing (Bliding, 1963)
Enteromorpha procera Ahlner (1877) Bidr. Enteromorpha: 40, fig. 5. *Ulva procera* (Ahlner) comb. nov.	Sweden Type: **S.** Should be typified with material of *E. procera* f. *denudata* Ahlner Bidr. Enteromorpha: 42 (Bliding's '*E. ahlneriana* Typus III'; Bliding, 1963)	*Enteromorpha ahlneriana* Bliding (1944) Bot. Not. 1944: 338, 355 is an illegitimate new name for *E. procera* Ahlner
Enteromorpha prolifera (O.F. Müller) J. Agardh (1883) Alg. Syst. 3: 129. *Ulva prolifera* O.F. Müller (1778) Fl. Dan. 5(13): 7, pl. DCCLXIII(1)	Nebbelund, Lolland Island, Denmark Type lost (Womersley, 1984). In the absence of material, we hereby designate by Fl. Dan. pl. DCCLXIII(1) as lectotype.	Heterotypic synonyms: *Enteromorpha salina* Kützing 1845: 247 (Guiry & NicDonncha, 2002) *Enteromorpha torta* (Mertens) Reinbold (Burrows, 1991)
Enteromorpha pseudolinza R.P.T. Koeman & C. van den Hoek (1982) Arch. Hydrobiol. Suppl. 63 [Algol. Stud. 32]: 302, figs. 50–69 *Ulva pseudolinza* (R.P.T. Koeman & C. van den Hoek) comb. nov.	Den Helder, Netherlands; *R.P.T. Koeman* (vi.1975) Holotype: **L**	
Enteromorpha radiata J. Agardh 1883: 156 *Ulva radiata* (J. Agardh) comb. nov.	Arctic Norway, *Berggren* Lectotype: **LD** 14233 (Bliding, 1963)	*Enteromorpha prolifera* subsp. *radiata* (J. Agardh) Bliding (1963, p. 56) Recognized in NE Atlantic: Coppejans (1995); Stegenga *et al*. (1997)
Enteromorpha ralfsii Harvey (1851) Phycol. Brit. 3: pl. CCLXXXII *Ulva ralfsii* (Harvey) Le Jolis (1863) Mém. Soc. Imp. Sci. Nat. Cherbourg 10: 54	Bangor, North Wales; *J. Ralfs* No types in **TCD** (Bliding, 1963) nor in **BM**. Lectotype: Harvey (1851) Phycol. Brit. 3: pl. CCLXXXII	
Enteromorpha simplex (K.L. Vinogradova) R.P.T. Koeman & C. van den Hoek (1982, p. 42) *E. prolifera* f. *simplex* K.L. Vinogradova 1974, Ul'vovye Vodorosli SSSR: 99, pl. XXXIII: 5–12 *Ulva simplex* (K.L. Vinogradova) comb. nov.	Kandalakshski Zaliv, Beloye More, Murmansk Oblast, Russia; *K.L. Vinogradova* (8.viii.1967) Holotype: **LE**	

Table 5. _Enteromorpha_ binomials that are currently regarded as synonyms of other valid names, not in current usage, and/or not valid. Infraspecific taxa are omitted. Binomials indicated by an asterisk lack valid binomials in _Ulva_, so if they were to be recognized at the species level in this genus they would require transfer to _Ulva_. Binomials in parentheses are either not valid or not legitimate. Binomials in square brackets are currently placed in genera other than _Enteromorpha_. For taxa shown in bold, transfer to _Ulva_ is blocked by pre-existing _Ulva_ binomials (for details see Index Nominum Algarum)

(_E. adriatica_ Bliding)
*_E. africana_ Kützing
(_E. ahlneriana_ Bliding)
E. angusta (Setchell & Gardner) M.S. Doty
(_E. aragoensis_ Bliding)
*_E. arctica_ J. Agardh
E. attenuata (C. Agardh) Greville
[_E. aureola_ (C. Agardh) Kützing][a]
*_E. basiramosa_ Fritsch
*_E. bayonnensis_ P.J.L. Dangeard
(_E. bertolonii_ Montagne)
*_E. biflagellata_ Bliding
(_E. byssoides_ Nees)
*_E. caerulescens_ Harvey
*_E. canaliculata_ Batters
E. capillaris M. Noda
[*_E. chadefaudii_ J. Feldmann][b]
*_E. chartacea_ Schiffner
*_E. chlorotica_ J. Agardh
*_E. clathrata_ (Roth) Greville (see Table 4)
E. clavata Wollny
[*_E. coarctata_ Kjellman][b]
(_E. comosa_ J. Agardh)
*_E. complanata_ Kützing (see Table 4)
*_E. confervacea_ (Kützing) Kützing
*_E. confervicola_ DeNotaris
(_E. constricta_ (J. Agardh) S.M. Saifullah & M. Nizamuddin)
*_E. corniculata_ Kützing
E. cornucopiae (Lyngbye) Carmichael
*_E. coziana_ P.J.L. Dangeard
*_E. crinita_ Nees (see Table 4)
E. crispa (Kützing) Kützing
E. crispata (Bertoloni) Piccone
*_E. cruciata_ Collins
(_E. cylindracea_ J. Blomster)
E. dangeardii H. Parriaud
*_E. denudata_ (Ahlner) Hylmö
*_E. echinata_ (Roth) Nees
*_E. ectocarpoidea_ Zanardini
E. erecta (Lyngbye) Carmichael
E. fascia Postels & Ruprecht (see Table 4)
E. fasciculata P.J.L. Dangeard
*_E. firma_ Schiffner
*_E. flabellata_ P.J.L. Dangeard
*_E. fucicola_ (Meneghini) Kützing
E. fulvescens (C. Agardh) Greville
(_Enteromorpha fulvescens_ Schiffner)
(_E. gayraliae_ P.J.L. Dangeard)
E. gelatinosa Kützing (see Table 4)
*_E. gracillima_ G.S. West
[_E. grevillei_ Thuret][c]
[*_E. groenlandica_ (J. Agardh) Setchell & Gardner][a]
*_E. gujaratensis_ S.R. Kale
[_E. gunniana_ J. Agardh][b]
(_E. hendayensis_ P.J.L. Dangeard & H. Parriaud)
*_E. hirsuta_ Kjellman
*_E. hookeriana_ Kützing (see Table 4)
E. hopkirkii M'Calla _ex_ Harvey
*_E. howensis_ Lucas
*_E. intermedia_ Bliding
(_E. juergensii_ Kützing)
(_E. jugoslavica_ Bliding)
E. lanceolata (Linnaeus) Rabenhorst
*_E. limosa_ A. Parriaud
E. linkiana Greville
(_E. linziformis_ Bliding)
*_E. littorea_ Kützing
E. livida W.J. Hooker
(_E. longissima_ P.J.L. Dangeard)
*_E. maeotica_ Proshkina-Lavrenko
*_E. marchantiae_ Setchell & N.L. Gardner
[_E. marginata_ J. Agardh][b]
[_E. micrococca_ Kützing][b]
*_E. microphylla_ Foslie
[*_E. minima_ Nägeli ex Kützing][b]
(_E. multiramosa_ Bliding)
E. muscoides (Clemente) J. Cremades (see Table 4)
*_E. musciformis_ P.J.L. Dangeard
[*_E. nana_ (Sommerfelt) Sjöstedt][b]
*_E. nizamuddinii_ K. Aisha & M. Shameel
*_E. novae-hollandiae_ (Kützing) Kützing
E. opposita J. Agardh
*_E. ovata_ F. Thivy & V. Visalakshmi _ex_ H.V. Joshi & V. Krishnamurthy
Enteromorpha pacifica Montagne
*_E. pallescens_ Schiffner
[_E. percursa_ (C. Agardh) Greville][d]
*_E. perestenkoae_ K.L. Vinogradova
*_E. peruviana_ Montagne
*_E. pilifera_ Kützing
E. plumosa Kützing (see Table 4)
*_E. polyclados_ (Kützing) Kützing
(_Enteromorpha pulcherrima_ Holmes & Batters)
E. quaternaria Ahlner
*_E. ramellosa_ Kützing
E. ramulosa (J.E. Smith) Carmichael (see Table 4)
[_E. rhacodes_ Holmes][e]
(_E. rivularis_ P.J.L. Dangeard)
*_E. roberti-lamii_ H. Parriaud
(_E. rugosa_ Nees)
*_E. saifullahii_ K. Aisha & M. Shameel
*_E. salina_ Kützing (see Table 4)
(_E. sancti-joannis_ P.J.L. Dangeard)
*_E. saxicola_ Simmons
(*_E. scopulorum_ (P.J.L. Dangeard) J.P. Villot)
*_E. spermatoidea_ (Kützing) Kützing
*_E. spinescens_ Kützing
(_E. stipitata_ P.J.L. Dangeard)
E. subulata (Wulfen) Nees
*_E. szegediensis_ Gyorffy & Kol
E. torta (Mertens) Reinbold (see Table 4)
[*_E. tuberculosa_ P.J.L. Dangeard][b]
*_E. tubulosa_ (Kützing) Kützing (see Table 4)
E. utricularis (Roth) Nees
E. vexata (Setchell & Gardner) M.S. Doty
(_E. vulgaris_ Edmondston)
*_E. welwitschii_ J. Agardh (see Table 4)

[a] Species of _Capsosiphon_ (Burrows, 1991).
[b] Species of _Blidingia_ (Womersley, 1956, 1964; Burrows, 1991; Benhissoune _et al_., 2001).
[c] Species of _Monostroma_ (Burrows, 1991).
[d] Species of _Percursaria_ (Bliding, 1963).
[e] Species of _Ulva_ (Silva _et al_., 1996).

fenestrata. 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

Within the *Ulva* clade, there are smaller clades consisting 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 possible explanation is that these taxa are in the early stages of diverging from one another. 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 artefactual.

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, taxa from these genera together form a strongly supported clade. Since *Ulva* is the older genus, *Enteromorpha* is reduced to synonymy, as shown in Table 4. Despite its unique development, *Chloropelta caespitosa* is nested within this clade; thus, it also is transferred to *Ulva*.

The nomenclatural changes are therefore proposed as shown in Table 4; binomials in *Enteromorpha* that are not currently recognized at the species level in *Enteromorpha* are listed in Table 5.

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References

ADAMS, N.M. (1994). *Seaweeds of New Zealand. An Illustrated Guide*. Canterbury University Press, Christchurch, New Zealand.

AGARDH, C.A. (1817). *Synopsis algarum Scandinaviae*. Lund.

AGARDH, J.G. (1883). Till algernes systematik. Nya bidrag, 3. *Lunds Univ.Års-Skrift, Afd. Math. Naturvetensk*., **19:** 177 pp.

AHLNER, K. (1877). *Bidrag till kännedomen om de svenska formerna af algslägtet* Enteromorpha. Akademisk afhandling, Uppsala, Sweden.

BAE, E.H. & LEE, I.K. (2001). *Umbraulva*, a new genus based on *Ulva japonica* (Holmes) Papenfuss (Ulvaceae, Chlorophyta). *Algae*, **16:** 217–231.

BAKKER, F.T., Olsen, J.L. & Stam, W.T. (1995*a*). Evolution of nuclear rDNA ITS sequences in the *Cladophora albida/sericea* clade (Chlorophyta). *J. Mol. Evol*., **40:** 640–651.

BAKKER, F.T., OLSEN, J.L. & STAM, W.T. (1995*b*). Global phylogeography in the cosmopolitan species *Cladophora vagabunda* (Chlorophyta) based on nuclear rDNA internal transcribed spacer sequences. *J. Phycol*., **30:** 197–208.

BENHISSOUNE, S., BOUDOURESQUE, C.-F. & VERLAQUE, M. (2001). A checklist of marine seaweeds of the Mediterranean and Atlantic coasts of Morocco. I. Chlorophyceae Wille s. l. *Bot. Mar*., **44:** 171–182.

BERGLUND, H. (1969). On the cultivation of multicellular marine green algae in axenic culture. *Svensk Bot. Tidskr*., **63:** 251–264.

BLIDING, C. (1948). *Enteromorpha kylini*, eine neue Art aus der Schwedischen Westküste. *Fys. Sällsk. Lund Förhandl*., **18:** 199–204.

BLIDING, C. (1963). A critical survey of European taxa in Ulvales, Part I. *Capsosiphon*, *Percursaria*, *Blidingia*, *Enteromorpha*. *Bot. Not. Suppl*., **8:** 1–160.

BLIDING, C. (1968). A critical survey of European taxa in Ulvales, Part II. *Ulva*, *Ulvaria*, *Monostroma*, *Kornmannia*. *Bot. Not*., **121:** 534–629.

BLOMSTER, J., MAGGS, C.A., & STANHOPE, M.J. (1998). Molecular and morphological analysis of *Enteromorpha intestinalis* and *E. compressa* (Chlorophyta) in the British Isles. *J. Phycol*., **34:** 319–340.

BLOMSTER, J., MAGGS, C.A. & STANHOPE, M.J. (1999). Extensive intraspecific morphological variation in *Enteromorpha muscoides* (Chlorophyta) revealed by molecular analysis. *J. Phycol*., **35:** 575–586.

BLOMSTER, J., BÄCK, S., FEWER, D.P., KIIRIKKI, M., LEHVO, A., MAGGS, C.A. & STANHOPE, M.J. (2002). Novel morphology in *Enteromorpha* (Ulvophyceae) forming green tides. *Am. J. Bot*., **89:** 1756–1763.

BONNEAU, E.R. (1977). Polymorphic behavior of *Ulva lactuca* (Chlorophyta) in axenic culture. I. Occurence of *Enteromorpha*-like plants in haploid clones. *J. Phycol*., **13:** 133–140.

BØRGESEN, F. (1911). Some Chlorophyceae from the Danish West Indies. *Bot. Tidsskr*., **31:** 127–152.

BRITZ, S.J. & BRIGGS, W.R. (1976). Circadian rhythms of chloroplast orientation and photosynthetic capacity in *Ulva*. *Plant Physiol*., **58:** 22–27.

BRITZ, S.J. & BRIGGS, W.R. (1983). Rhythmic chloroplast migration in the green alga *Ulva*: dissection of movement mechanism by differential inhibitor effects. *J. Cell Biol*., **31:** 1–8.

Burrows, E.M. (1991). *Seaweeds of the British Isles*, vol. 2. *Chlorophyta*. British Museum (Natural History), London.

Chapman, V.J. (1956). The marine algae of New Zealand. 1. Myxophyceae and Chlorophyceae. *J. Linn. Soc. Bot.*, **55:** 333–501.

Clemente [y Rubio], S. de Rojas (1807). *Ensayo sobre las variedades de la vid commun que vegetan en Andalucia*. Madrid.

Coat, G., Dion, P., Noailles, M.-C., De Reviers, B., Fontiane, J.-M., Berger-Perrot, Y. & Loiseaux-De Goër, S. (1998). *Ulva armoricana* (Ulvales, Chlorophyta) from the coasts of Brittany (France). II. Nuclear rDNA ITS sequence analysis. *Eur. J. Phycol.*, **33:** 81–86.

Coppejans, E. (1995). *Flore algologique des côtes du Nord de la France et de la Belgique*. Jardin Botanique National de la Belgique, Meise.

Cremades, J. & Pérez-Cirera, J.L. (1990). Nuevas combinaciones de algas bentónicas marinas, como resultado del estudio del herbario de Simón de Rojas Clemente y Rubio (1777–1827). *Anal. Jard. Bot. Madrid*, **47:** 489–492.

Dangeard, P. (1951). Sur une espèce d'*Ulva* des nos côtes atlantiques (*U. olivacea* n. sp.). *Le Botaniste*, **35:** 27–34.

Dangeard, P. (1958). Observations sur quelques Ulvacées du Maroc. *Le Botaniste*, **42:** 5–63.

Dangeard, P. (1961). Le problème de l'espèce avec référence au groupe des Ulvacées. *Le Botaniste*, **44:** 21–36.

de Queiroz, A., Donoghue, M.J. & Kim, J. (1995). Separate versus combined analysis of phylogenetic evidence. *Annu. Rev. Ecol. Syst.*, **28:** 657–681.

Dillwyn, L.W. (1802–9). *British Confervae*. London.

Dion, P., de Reviers, B. & Coat, G. (1998). *Ulva armoricana* sp. nov. (Ulvales, Chlorophyta) from the coasts of Brittany (France). I. Morphological identification. *Eur. J. Phycol.*, **33:** 73–80.

Doyle, J.J. & Doyle, J.L. (1990). Isolation of plant DNA from fresh tissue. *Focus,* **12:** 13–15.

Farris, J.S., Kallersjo, M., Kluge, A.G. & Bult, C. (1994). Testing significance of incongruence. *Cladistics*, **10:** 315–319.

Felsenstein, J. (1985). Confidence limits on phylogenies: an approach using the bootstrap. *Evolution*, **39:** 137–195.

Floyd, G.L. & O'Kelly, C.J. (1984). Motile cell ultrastructure and the circumscription of the orders Ulotrichales and Ulvales (Ulvophyceae, Chlorophyta). *Am. J. Bot.*, **71:** 111–120.

Føyn, B. (1960). Sex-linked inheritance in *Ulva*. *Biol. Bull.*, **118:** 407–411.

Føyn, B. (1961). Globose, a recessive mutant in *Ulva mutabilis*. *Bot. Mar.*, **3:** 60–64.

Friedl, T. (1996). Evolution of the polyphyletic genus *Pleurastrum* (Chlorophyta): inferences from nuclear-encoded ribosomal DNA sequences and motile cell ultrastructure. *Phycologia*, **35:** 456–469.

Fries, L. (1975). Some observations of the morphology of *Enteromorpha linza* (L.) J. Ag. and *Enteromorpha compressa* (L.) Grev. in axenic culture. *Bot. Mar.*, **18:** 251–253.

Furnari, G., Cormaci, M. & Serio, D. (1999). Catalogue of the benthic marine macroalgae of the Italian coast of the Adriatic Sea. *Bocconea*, **12:** 1–214.

Gabrielson, P.W., Widdowson, T.B., Lindstrom, S.C., Hawkes, M.J. & Scagel, R.F. (2000). *Keys to the Benthic Marine Algae and Seagrasses of British Columbia, southeast Alaska, Washington and Oregon*. Department of Botany, University of British Columbia, Vancouver.

Gayral, P. (1959). Premières observations et réflexions sur des Ulvacées en culture. *Le Botaniste*, **43:** 85–100.

Gayral, P. (1967). Mise au point sur les Ulvacées (Chlorophycées), particulièrement sur les résultats de leure étude en laboratoire. *Le Botaniste*, **50:** 205–251.

Graham, L.E. & Wilcox, L.W. (2000). *Algae*. Prentice-Hall, Upper Saddle River, NJ.

Greuter, W. *et al*., (2000). *International Code of Botanical Nomenclature (Saint Louis Code)*. Koeltz Scientific Books, Königstein, Germany.

Guiry, M.D. & NicDonncha, E. (2002). *AlgaeBase*. World Wide Web electronic publication. www.algaebase.com (30 May 2002).

Harvey, W.H. (1846–1851). *Phycologia Britannica*. Reeve, London.

Hasegawa, M., Kishino, H. & Yano, T. (1985). Dating the human–ape split by a molecular clock of mitochondrial DNA. *J. Mol. Evol.*, **22:** 160–174.

Hayden, H.S. (2001). Systematics of Ulvaceae (Ulvales, Ulvophyceae) and the genus *Ulva* L. based on nuclear and chloroplast sequence data. PhD dissertation, University of Washington, Seattle.

Hayden, H.S. & Waaland, J.R. (2002). Phylogenetic systematics of the Ulvaceae (Ulvales, Ulvophyceae) using chloroplast and nuclear sequences. *J. Phycol.*, **38:** 1200–1212.

Huelsenbeck, J.P., Bull, J.J. & Cunningham, C.W. (1996). Combining data in phylogenetic analyses. *Trends Evol. Ecol.*, **43:** 288–291.

Hughey, J.R., Silva, P.C. & Hommersand, M.H. (2001). Solving taxonomic and nomenclatural problems in Pacific Gigartinaceae (Rhodophyta) using DNA from type material. *J. Phycol.*, **37:** 1091–1109.

Index Nominum Algarum (2002). University Herbarium, University of California, Berkeley. Compiled by Paul Silva. Available online at http://ucjeps.herb.berkeley.edu/INA.html

Kapraun, D.F. (1970). Field and cultural studies of *Ulva* and *Enteromorpha* in the vicinity of Port Aransas, Texas. *Contrib. Mar. Sci.*, **15:** 205–285.

Koeman, R.P.T. & van den Hoek, C. (1981). The taxonomy of *Ulva* (Chlorophyceae) in The Netherlands. *Br. J. Phycol.*, **16:** 9–53.

Koeman, R.P.T. & van den Hoek, C. (1982). The taxonomy of *Enteromorpha* Link, 1820 (Chlorophyceae) in the Netherlands. I. The section *Enteromorpha*. *Arch. Hydrobiol. Suppl.*, **63:** 279–330.

Kono, M., Satoh, H., Okabe, Y., Abe, Y., Nakayama, K. & Okada, M. (1991). Nucleotide sequence of the large subunit of ribulose-1,5-bisphosphate carboxylase/oxygenase from the green alga *Bryopsis maxima*. *Plant Mol. Biol.*, **17:** 505–508.

Kornmann, P. (1965). Ontogenie und Lebenszyklus der Ulotrichales in phylogenetischer sicht. *Phycologia*, **14:** 163–172.

Kützing, F.T. (1845). *Phycologia Germanica*. Nordhausen.

Kützing, F.T. (1849). *Species Algarum*. Leipzig.

Kützing, F.T. (1856). *Tabulae Phycologicae* ... VI. Nordhausen.

Lamarck, J.B. de & De Candolle, A.P. (1805). *Flore française*, 3rd edn. Paris.

Larsen, J. (1981). Crossing experiments with *Enteromorpha intestinalis* and *E. compressa* from different European localities. *Nord. J. Bot.*, **1:** 128–136.

Le Jolis, A. (1863). Liste des Algue Marines de Cherbourg. *Mém. Soc. Imp. Sci. Nat. Cherbourg*, **10:** 6–168.

Leskinen, E. & Pamilo, P. (1997). Evolution of the ITS sequences of ribosomal DNA in *Enteromorpha* (Chlorophyceae). *Hereditas*, **126:** 17–23.

Levring, T. (1938). Verzeichnis einiger Chlorophyceen und Phaeophyceen von Südafrika. *Lunds Univ. Årsskr. N.F. Avd. 2*, **34**(9): 25pp.

Link, H.F. (1820). Epistola de algis aquatics in genera disponendis. In *Horae Physicae Berolinensis* (Nees von Esenbeck, C.D., editor). Bonn, 1–8.

Linnaeus, C. (1753). *Species planarum, exhibentes plantas rite cognitas, ad genera relatas, cum differentiis specificus, nominibus trivialibus, synonymis selectis, locis natalibus, secundum systema sexuale digestas*. Ed. 1. Vols. 1–2, Salvii, Stockholm. Vol. 1, pp [i–xii] 1–560. Vol. 2, pp. [i], 561–1200, [1–30 index].

Løvlie, A. (1964). Genetic control of division rate and morphogenesis in *Ulva mutabilis* Føyn. *C. R. Trav. Lab. Carlsberg*, **34:** 77–168.

Malta, E.-J., Draisma, S.G.A. & Kamermans, P. (1999). Free-floating *Ulva* in the southwest Netherlands: species or morphotypes? A morphological, molecular and ecological comparison. *Eur. J. Phycol.*, **34:** 443–454.

Manhart, J.R. (1994). Phylogenetic analysis of green plant *rbc*L sequences. *Mol. Phylogenet. Evol.*, **3:** 114–127.

Mishkind, M., Mauzerall, D. & Beale, S.I. (1979). Diurnal variation *in situ* of photosynthetic capacity in *Ulva* is caused by a dark reaction. *Plant Physiol.*, **64:** 896–899.

Montagne, J.F.C. (1846). Phyceae. In *Voyage autour du monde exécuté pendant les années 1836 et 1837 sur la corvette* 'La Bonite' *commandée par M. Vaillant. Botanique*. Vol. 1: *Cryptogames cellulaires et vasculaires* (Gaudichaud, C., editor), 1 – 112. Paris.

Müller, O.F. (1778). *Flora Danica*, pls 760 – 780.

Nees, C.G. (1820). *Horae physicae berolinenses*. Bonn.

Papenfuss, G.F. (1960). On the genera of the Ulvales and the status of the order. *J. Linn. Soc. (Bot.)*, **56:** 303 – 318.

Phillips, J.A. (1988). Field, anatomical and developmental studies on southern Australian species of *Ulva* (Ulvaceae, Chlorophyta). *Aust. Syst. Bot.*, **1:** 411 – 456.

Provasoli, L. (1965). Nutritional aspects of seaweed growth. *Proc. Can. Soc. Plant Physiol.*, **6:** 26 – 27.

Provasoli, L. & Pintner, I.J. (1980). Bacteria induced polymorphism in an axenic laboratory strain of *Ulva lactuca* (Chlorophyceae). *J. Phycol.*, **16:** 196 – 201.

Ramírez, M.E. & Santelices, B. (1991). *Catalogo de las algas marinas bentónicas de la costa temperada del Pacífico de Sudamérica*. Monografías Biológicas no. 5, Pontificia Universidad Católico de Chile. Publicaciones Periódicas, Vicerrectoría Académica.

Ricker, R.W. (1987). *Taxonomy and Biogeography of Macquarie Island Seaweeds*. British Museum (Natural History), London.

Sherwood, A.R., Garbary, D. J. & Sheath, R.G. (2000). Assessing the phylogenetic position of the Prasiolales (Chlorophyta) using *rbc*L and 18S rRNA gene sequence data. *Phycologia*, **39:** 139 – 146.

Silva, P.C. (1952). A review of nomenclatural conservation in the algae from the point of view of the type method. *Univ. Calif. Publ. Bot.*, **25:** 241 – 324.

Silva, P.C., Basson, P.W. & Moe, R.L. (1996). Catalogue of the benthic marine algae of the Indian Ocean. *Univ. Calif. Publ. Bot.*, **79:** 1 – 1259.

Soltis, D.E. & Soltis, P.S. (1998). Choosing an approach and an appropriate gene for phylogenetic analysis. In *Molecular Systematics of Plants II, DNA Sequencing* (Soltis, D.E., Soltis, P.S. & Doyle, J.J., editors). Kluwer Academic, Boston, MA.

Steffensen, D.A. (1976). Morphological variation in *Ulva* in the Avon-Heathcote Estuary, Christchurch. *N. Z. J. Mar. Freshwater Res.*, **10:** 329 – 341.

Stegenga, H., Bolton, J.J. & Anderson, R.J. (1997). *Seaweeds of the South African West Coast*. Bolus Herbarium, University of Cape Town, Cape Town.

Stiller, J.W. & Waaland, J.R. (1993). Molecular analysis reveals cryptic diversity in *Porphyra* (Rhodophyta). *J. Phycol.*, **29:** 506 – 517.

Suhr, J.N. von (1839). Beiträge zur Algenkunde. *Flora, Jena*, **22:** 65 – 75.

Swofford, D.L. (1999). *PAUP* Phylogenetic Analysis Using Parsimony (*and other methods)*, version 4. Sinauer Associates, Sunderland, Mass.

Swofford, D.L., Olsen, G.J., Waddell, P.J. & Hillis, D.M. (1996). Phylogenetic inference. In *Molecular Systematics* (Hillis, D.M., Moritz, C. & Mable, B.K., editors), pp. 407 – 514. Sinauer Associates, Sunderland, Mass.

Tan, I.H., Blomster, J., Hansen, G., Leskinen, E., Maggs, C.A., Mann, D.G., Sluiman, H.J. & Stanhope, M.J. (1999). Molecular phylogenetic evidence for a reversible morphogenetic switch controlling the gross morphology of two common genera of green seaweeds, *Ulva* and *Enteromorpha*. *Mol. Biol. Evol.*, **16:** 1011 – 1018.

Tanner, C.E. (1979). The taxonomy and morphological variation of distromatic ulvaceous algae (Chlorophyta) from the northeast Pacific. PhD dissertation, Department of Botany, University of British Columbia, Vancouver.

Tanner, C.E. (1980). *Chloropelta* gen. nov., an ulvaceous green alga with a different type of development. *J. Phycol.*, **16:** 128 – 137.

Tanner, C.E. (1986). Investigations of the taxonomy and morphological variation of *Ulva* (Chlorophyta): *Ulva californica* Wille. *Phycologia*, **25:** 510 – 520.

Thompson, A.J. & Herrin, D.L. (1994). A chloroplast group I intron undergoes the first step of reverse splicing into host cytoplasmic 5.8 S rRNA. *J. Mol. Biol.*, **236:** 455 – 468.

Thompson, J.D., Gibson, T.J., Plewnial, F., Jeanmougin, F. & Higgons, D.G. (1997). The ClustalX windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. *Nucleic Acids Res.*, **24:** 4876 – 4882.

Titlyanov, E.A., Glebova, N.T. & Kotlyarova, L.S. (1975). Seasonal changes in structure of the thalli of *Ulva fenestrata* P. *et* R. *Ekologiya*, **6:** 320 – 324.

Trevisan, V.B.A. (1842). *Prospetto della flora Euganea*. Padua.

van de Peer, Y., De Rijik, P., Wuyts, J., Winkelmans, T. & De Wachter, R. (2000). The European small subunit ribosomal RNA database. *Nucleic Acids Res.*, **28:** 175 – 176.

van den Hoek, C., Mann, D.G. & Jahns, H.M. (1995). *Algae: An Introduction to Phycology*. Cambridge University Press, Cambridge.

van Oppen, M.J.H. (1995). Tracking trails by cracking codes. PhD dissertation, University of Groningen, The Netherlands.

Vinogradova, K.L. (1974). *Ul 'vovye vodorosli (Chlorophyta) morej SSSR*. Nauka, Leningrad.

Wendel, J.F. & Doyle, J.J. (1998). Phylogenetic incongruence: window into genome history and molecular evolution. In *Molecular Systematics of Plants II, DNA Sequencing* (Soltis, D.E., Soltis, P.S. & Doyle, J.J., editors). Kluwer Academic, Boston, Mass.

Womersley, H.B.S. (1956). A critical survey of the marine algae of Southern Australia. I. Chlorophyta. *Aust. J. Mar. Freshwater Res.*, **7:** 343 – 383.

Womersley, H.B.S. (1984). *The Marine Benthic Flora of Southern Australia*, part I. Government Printer, South Australia, Adelaide.

Woolcott, G.W. & King, R.J. (1999). *Ulva* and *Enteromorpha* (Ulvales, Ulvophyceae, Chlorophyta) in eastern Australia: comparison of morphological features and analyses of nuclear rDNA sequence data. *Aust. Syst. Bot.*, **12:** 709 – 725.

Wulfen, F.X. (1803) Cryptogama Aquatica. *Arch. Bot. (Römer)*, **3:** 1 – 64.

Wuyts, J., De Rijik, P., Van de Peer, Y., Winkelmans, T. & De Wachter, R. (2001). The European large subunit ribosomal RNA database. *Nucleic Acids Res.*, **29:** 175 – 177.

Wynne, M.J. (1986). Report on a collection of benthic marine algae from the Namibian coast (southwestern Africa). *Nova Hedwigia*, **43:** 311 – 355.

Wynne, M.J. (1998). A checklist of benthic marine algae of the tropical and subtropical western Atlantic: first revision. *Nova Hedwigia*, **116:** 1 – 155.

Yang, R.C., Dove, M., Seligy, V.L., Lemieux, C., Turmel, M. & Narang, S.A. (1986). Complete nucleotide sequence and mRNA-mapping of ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCo) from *Chlamydomonas moewusii*. *Plant Mol. Biol.*, **10:** 259 – 270.

Yang, Z. (1994*a*). Estimating the pattern of nucleotide substitution. *J. Mol. Evol.*, **39:** 105 – 111.

Yang, Z. (1994*b*). Maximum likelihood phylogenetic estimation from DNA sequences with variable rates over sites: approximate methods. *J. Mol. Evol.*, **39:** 306 – 314.