
Ten new species of *Ulva* (Ulvophyceae, Chlorophyta) discovered in New Caledonia: genetic and morphological diversity, and bloom potential

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Abstract :

Ulva is a green macroalgal genus with rich species diversity and worldwide distribution. While current knowledge on *Ulva* diversity focuses on temperate regions, genetic and morphological data in tropical and subtropical areas are scarce and the species richness is not clearly defined. The genus is known for its bloom-forming ability that can induce green tides leading to severe environmental and economic damage. In the last two decades, several important blooms of *Ulva* spp. have occurred in New Caledonia, requiring further investigations to identify the species involved. As knowledge of New Caledonian *Ulva* diversity is limited, an update to the *Ulva* spp. inventory in the area is essential. Based on *Ulva* specimens collected throughout New Caledonia (Grande Terre, Isle of Pines and Loyalty Islands), we (1) reassessed species diversity using species delimitation methods, (2) analysed morpho-anatomical characters to identify species and/or enrich their diagnosis, and (3) reconstructed a multilocus phylogeny (ITS, *rbcL*, *tufA*) of the genus. We found 21 secondary species hypotheses (SSHs) among our dataset, from which five were successfully assigned to *U. lactuca*, *U. ohnoi*, *U. tepida*, *U. meridionalis* and *U. taeniata*. Ten SSHs were defined as new species for which we provided taxonomic description, and six other SSHs were singletons that will need to be data-enriched for better interpretation. Our concatenated multilocus matrix included 61 *Ulva* species. Of these, 15 species were found in New Caledonia and were moderately to strongly supported. Among the *Ulva* species found in New Caledonia, seven are known to be bloom-forming which highlights the need for strict regulation and regular monitoring of water quality, particularly in areas exposed to strong nutrient input where these species can form green tides. Highlights *Ulva* diversity in New Caledonia was reassessed with 15 species highlighted. Ten new species have been discovered in New Caledonia. Indigenous species caused recent green tides in New Caledonia.

Highlights

► *Ulva* diversity in New Caledonia was reassessed with 15 species highlighted. ► Ten new species have been discovered in New Caledonia. ► Indigenous species caused recent green tides in New Caledonia.

Keywords : Anatomy, diversity, green tides, marine, Pacific, phylogeny, rbcL, species delimitation, tropical, Ulvales

INTRODUCTION

With more than 400 species described, *Ulva* Linnaeus is the most cosmopolitan genus of the order Ulvales Blackman & Tansley (Guiry & Guiry, 2021). Among them, only 85 species are currently taxonomically accepted. The genus *Ulva* groups together foliose forms, known as sea lettuce, and tubular forms, formerly known as the genus *Enteromorpha* which has been placed in synonymy following the DNA-based work of Hayden *et al.* (2003).

Ulva species are ubiquitous in marine, brackish, and freshwater environments and, as nitrophilic organisms, they can be indicative of eutrophic environments (Kraft *et al.*, 2010). They are characterised by high metabolic and growth rates due to their high area/volume ratio which promotes gas and nutrient exchanges with the external environment and improves their nutrient and carbon uptake (Rosenberg & Ramus, 1984; Teichberg *et al.*, 2010). It confers on species a strong ability to proliferate and form blooms, which can lead to green tides (Blomster *et al.*, 1998; Smetacek & Zingone, 2013).

Green tides have several potential impacts on ecosystems and human health, notably through shading other light dependent organisms and releasing toxins (e.g. hydrogen sulphide) into the atmosphere and sediments (Yabe *et al.*, 2009; Teichberg *et al.*, 2010; Lyons *et al.*, 2014). During the last two decades, green tides have often resulted in important economic losses and environmental issues, as the Yellow Sea events have shown in China (Ye *et al.*, 2011; Liu *et al.*, 2013). Several species of *Ulva* are known to bloom, such as *U. australis* Areschoug (Japan, Yoshida *et al.*, 2015; Korea, Lee *et al.*, 2019; Park, 2014), *U. chaugulii* M.G.Kavale & M.A.Kazi (China, Xie *et al.*, 2020), *U. compressa* Linnaeus (US east coast, Melton & Lopez-Bautista, 2021), *U. fenestrata* Postels & Ruprecht (Florida, Lapointe *et al.*, 2006), *U. lactuca* Linnaeus (Korea, Lee *et al.*, 2019), *U. linza* Linnaeus (China, Kang *et al.*, 2016), *U. meridionalis* R.Horimoto & S.Shimada (China, Xie *et al.*, 2020), *U. ohnoi* M.Hiraoka & S.Shimada (Japan, Hiraoka *et al.*, 2004; Australia, Lawton *et al.*, 2013; Korea, Lee *et al.*, 2019; Florida, Melton *et al.*, 2016), *U. prolifera* O.F.Müller (China, Lee *et al.*, 2019), *U. pseudo-ohnoi* H.W.Lee, J.C.Kang & M.S.Kim (Korea, Lee *et al.*, 2019), *U. reticulata* Forsskål (Japan, Hiraoka *et al.*, 2019), *U. rigida* C.Agardh (Ireland, Wan *et al.*, 2017; US east coast, Melton & Lopez-Bautista, 2021), *U. pseudorotundata* Cormaci, G.Furnari & Alongi (Ireland, Wan *et al.*, 2017), and *U. tepida* Y.Masakiyo & S.Shimada (Australia, Phillips *et al.*, 2016; Western Indian Coast, Bast *et al.*, 2014; China, Xie *et al.*, 2020). Nevertheless, the species identified at the origin of green tides can be subject to misidentifications due to the high cryptic diversity and morphological plasticity in the genus.

In New Caledonia, the shoreline of the city of Noumea has experienced several green tides over the past 25 years, caused by *U. ohnoi* blooms related to poor wastewater management. The species was initially identified by C. Payri based on morphology and confirmed by DNA analysis by F. Mineur (unpublished data). Tubular *Ulva* blooms are also common, with annual occurrences reported by the local population during the rainy warm season on sandy shallow habitats located along the shoreline of the Ouvea atoll (Loyalty Islands) and on the sandy terraces of the barrier reef of Grande Terre (Fig. 1). These seaweeds are locally known by fishermen since rabbitfish (*Siganus lineatus*) are frequently found in the same habitat. However, in January 2018, an important green tide event occurred in the Poé-Gouaro-Déva (PGD) area located on the west coast of Grande Terre. The PGD area is a hotspot of tourism activities and one of the Caledonian lagoons registered as a UNESCO World Heritage site. This green tide was caused by an unknown tubular species characterised by a morphology unmistakably corresponding to the genus *Ulva* (Fig. 1). Since then, other peaks of high abundance of this unidentified species have been reported (Brisset *et al.*, 2021). The identity of the species involved is needed to provide clues to the cause of blooms, since not all *Ulva* species have the same sensitivity and response to environmental changes (Pérez-Lloréns *et al.*, 1996; Malta *et al.*, 1999; Taylor *et al.*, 2001).

However, *Ulva* diversity in New Caledonia is poorly documented with only four species reported: *Ulva compressa* Linnaeus (Garrigue & Tsuda, 1988; Payri, 2007), *U. lactuca* Linnaeus (as *Ulva fasciata* Delile; Garrigue & Tsuda, 1988; Payri, 2007), *U. intestinalis* Linnaeus (Garrigue & Tsuda, 1988; Payri, 2007), and *U. paradoxa* C.Agardh (Payri, 2007). The extent of *Ulva* diversity in New Caledonia is still unknown, and this prevents an accurate identification of the species involved in the green tides that occurred in PGD. At the regional scale, *Ulva* has been deeply studied in Australia (e.g. Kirkendale *et al.*, 2013, Huisman, 2015, Kraft *et al.*, 2010) and New Zealand (e.g. Chapman, 1956; Heesch, 2009), with 23 (including 9 in Lord Howe Island) and 20 taxonomically valid species recorded, respectively (Guiry & Guiry, 2021). Nevertheless, most of these species are of temperate origin and might not necessarily correspond to those found in New Caledonia. The natural distribution of most *Ulva* species at the global scale is poorly known and difficult to estimate due to the biofouling ability of the genus (Callow *et al.*, 1997; Flagella *et al.*, 2007). Indeed, this allows the spread and introduction of *Ulva* species through human-mediated dispersal (e.g. passive transport in ballast water or on the hulls of ships) to many areas outside their natural ranges (Mineur *et al.*, 2006; Phillips *et al.*, 2016) where they can become invasive species. The identification of *Ulva* species is challenged by a strong phenotypic

plasticity (Guidone *et al.*, 2013; Xie *et al.*, 2020) and morphogenesis differences (Wichard *et al.*, 2015), as well as high cryptic diversity within the genus (Melton *et al.*, 2016; Hughey *et al.*, 2019; Steinhagen *et al.*, 2019a), all of which have led to morphological-based misidentification and taxonomic errors (Hayden & Waaland 2004; Ogawa *et al.*, 2013; Cui *et al.*, 2018; Hughey *et al.*, 2019; Fort *et al.*, 2021). For a long time, most *Ulva* specimens were named according to their morphological and anatomical resemblance to European species (Kraft *et al.*, 2010). Since then, some studies argue that the use of temperate and boreal species epithets to name tropical and subtropical *Ulva* species is inappropriate (O'Kelly *et al.*, 2010) and that the latter often correspond to new cryptic or closely resembling species (Heesch *et al.*, 2009; Kraft *et al.*, 2010). Species identification based on morphology is therefore noted as a source of misidentification, and several authors have highlighted the need for molecular-based species determination (Guidone *et al.*, 2013; Wichard *et al.*, 2015; Kang *et al.*, 2019). The combination of both molecular and morphological species determination allows highlighting species complexes and accurately refining species boundaries, as it was the case for the *linza-prolifera-procera* (LPP) complex (Shimada *et al.*, 2008) and the “European clade” of *U. prolifera* (Cui *et al.*, 2018). In addition, other studies have also highlighted the need to analyse herbarium material in order to assign species names correctly (e.g. Hughey *et al.*, 2019; Steinhagen *et al.*, 2019a).

To update the inventory of the New Caledonian flora and resolve the identity of the tubular species from PGD blooms, we analysed *Ulva* specimens from different areas in New Caledonia through DNA and morphological analyses. Additional specimens from our collections, housed at the phycological herbarium (NOU), were also considered to extend analyses to other areas, along with available data in GenBank. Through this study, we then proposed to 1) reassess the diversity of *Ulva* species using species delimitation methods, 2) identify these species by conducting morpho-anatomical analyses, and 3) determine the relationships between these species by reconstructing a multilocus (ITS, *rbcL*, *tufA*) phylogeny. On this basis, we then defined a shortlist of *Ulva* species present in New Caledonia that are known to generate green tides, locally or elsewhere.

Material and Methods

Sampling

A total of 147 *Ulva* specimens from New Caledonia, including 60 sampled in the blooming area of the Poé-Gouaro-Déva (PGD) lagoon were considered in this study (Fig. 1). Additional

specimens from opportunistic sampling in French Polynesia (11) and Papua New Guinea (1) were included in the analyses (see Table S1 for more details). Some of the specimens were collected by SCUBA during marine flora surveys between 2004 and 2015 and preserved as dry herbarium sheets with fragments preserved in silica gel or 95° ethanol. The samples from PGD were collected from the intertidal to subtidal zones and preserved in a solution of seawater and 5% formaldehyde for morphological analyses, and in 95° ethanol and silica gel for subsequent DNA analyses. Most of the specimens (vouchers) from which fragments were analysed were pressed and dried as herbarium sheets. All specimens were deposited in NOU (herbarium abbreviation follows Thiers (2021), continuously updated).

DNA extraction, PCR amplification, and sequencing

Total genomic DNA from each fragment preserved in ethanol and/or silica gel, or taken directly from the herbarium sheets, was extracted using the cetyl trimethyl ammonium bromide (CTAB) extraction protocol (Doyle & Doyle, 1987) modified by the Research Group Phycology of the University of Ghent (Belgium). Based on the literature, three markers were selected and amplified: the nuclear-encoded rDNA internal transcribed spacer (ITS) and the two chloroplast markers, *rbcL* (encoding the large subunit of the ribulose 1,5-bisphosphate carboxylase/oxygenase) and *tufA* (encoding the elongation factor Tu). ITS displays high mutation rates, high variability, and proved to be useful in *Ulva* species phylogeny (Hayden *et al.*, 2003; Shimada *et al.*, 2003; Hayden & Waaland, 2004; Hiraoka *et al.*, 2004). *rbcL* has previously solved several taxonomic issues within the *Ulva* genus, and *tufA* has high interspecific divergence (Saunders & Kucera, 2010). The primers ITS1a/ITS2d were used for the amplification of the ITS gene, RH1/1385R and RH1/*rbcL*590 for the *rbcL* gene, and *tufA*-F/*tufA*-R and HtufA-F/HtufA-R for the *tufA* gene (Table S2). The reaction mix was prepared for a total volume of 25 µL containing 2 µL of DNA, 1 µL each of forward and reverse primer, 8.5 µL of milliQ water, and 12.5 µL of AmpliTaq Gold 360 Master Mix (Applied Biosystems, Foster City, California, USA). The Polymerase Chain Reaction (PCR) was performed according to the specific program for each primer (see Table S3). PCR products were checked by electrophoresis and sent to GenoScreen (Lille, France) for Sanger sequencing. Sequences were edited and aligned with the Geneious 7.0.6 software (<http://www.geneious.com>, Kearse *et al.*, 2012).

Phylogenetic reconstruction

In the first step, phylogenetic reconstructions were performed for each marker to account for the general topology of the genus and the phylogenetic position of our specimens and to identify them at the species level, when possible (see Figures S1 to S3). As much as possible and to avoid misidentification, only sequences from type material or material from type locality available on GenBank were added to our sequences (i.e. 45 ITS, 55 *rbcL* and 32 *tufA* sequences; cf. Table S4). Sequences of *Umbraulva amamiensis* (Tanaka) Bae & I.K.Lee, *U. dangeardii* M.J.Wynne & G.Furnari, and *U. japonica* (Holmes) Bae & I.K.Lee, were added as outgroups.

In the second step, a concatenated multilocus matrix was constructed. For this multilocus analysis, we selected only one representative per species for GenBank sequences. We only included specimens with at least two of the three markers available, and selected only one representative of species per collecting locality. Partition finder v. 1.1.0 (Lanfear *et al.*, 2012) was used to identify the best partition scheme and evolutionary models associated under the Akaike Information Criterion (AIC).

Maximum likelihood (ML) trees were reconstructed with RAXML (Stamatakis, 2014) through the CIPRES web portal (Miller *et al.*, 2010), with the “rapid bootstrapping and search for the best-scoring ML tree” algorithm, the GTRGAMMA model, and 1,000 replicates of bootstraps (bs). Ultrametric gene trees were reconstructed using BEAST v2.6.3 (Drummond *et al.*, 2012). Two independent analyses of 40, 20, and 40 million generations were run for ITS, *rbcL*, and *tufA*, respectively, and sampled every 1,000 generations. A relaxed lognormal molecular clock (Drummond *et al.*, 2006) with a coalescent constant size tree prior was used to estimate trees. The convergence of the Markov Chains Monte Carlo (MCMC) and the effective sample size (ESS) values of each run were checked using the software Tracer v.1.5 (Rambaut & Drummond, 2007). The outputs were then combined with Log Combiner, after removing the first 10% generations as burn-in, and the Maximum Clade Credibility Tree (MCCT) was calculated using Tree Annotator (both programs are included in the BEAST package). Bayesian inference (BI) on the concatenated multilocus matrix was carried out by MrBayes 3.1.2 (Huelsenbeck & Ronquist, 2001). The matrix was analysed under nine partitions (by genes and by codon positions) with the following evolution model: GTR+I+G, GTR+G, GTR+I+G for ITS, GTR+I+G, GTR+I+G, HKY+I+G for *rbcL* and GTR+I+G, GTR+I+G, HKY+I+G for *tufA*. Two independent runs of 20 million generations, sampled every 1,000 generations, were performed. The first two million generations were discarded as burn-in. The convergence of the two runs and sufficient parameter estimation were also

checked in Tracer 1.7.13 (Rambaut & Drummond, 2007) before computing a consensus topology and the posterior probabilities.

Species delimitation analyses

Three methods of species delimitations were applied on each gene dataset: the General Mixed Yule Coalescent (GMYC; Pons *et al.*, 2006), the Assemble Species by Automatic Partitioning (ASAP; Puillandre *et al.*, 2021), and the Poisson Tree Process (PTP, Zhang *et al.*, 2013).

GMYC was used on BEAST ultrametric gene trees with the single threshold method, using the package “splits” in R (R Development Core Team, 2021); ASAP was applied directly on alignments with the simple distance model through the ASAP website (<https://bioinfo.mnhn.fr/abi/public/asap/asapweb.html#>); PTP was applied on MCCT trees with 500,000 generations sampling every 1000 generations, through the Exelixis Lab web server (<http://sco.h-its.org/exelixis/web/software/PTP/index.html>).

Through the species delimitation approach, we compared the different primary species hypotheses (PSHs) and defined secondary species hypotheses (SSHs) based on congruence between the different markers and methods. Then, the SSHs were confirmed with morpho-anatomical observations, and when possible, assigned a species name. In case of conflicts, a majority rule was applied, and the most prevalent PSH was selected as SSH. To aid understanding, the term “clade” is used in the presentation of the exploratory results to designate the SSHs, which will be defined at the end of the analyses.

Morpho-anatomical analyses

Morpho-anatomical observations were made using formalin-preserved or herbarium specimens. Occasionally, if previous storage was not available, observations were performed on ethanol-preserved specimens. The observations were carried out on specimens belonging to each New Caledonian clade obtained through the species delimitation analysis to identify and assign them known species names or highlight potential new species and enrich their diagnoses. Observations of morphological characters were based on original diagnoses and previous studies (e.g. Kraft *et al.*, 2010; Horimoto *et al.*, 2011; Masakiyo & Shimada, 2014; Krupnik *et al.*, 2018; Xie *et al.*, 2020; Melton & Lopez-Bautista, 2021). Analyses consisted of external morphology observations and measurements (size, blade or tubular shape, presence or absence of branching along the axe), thallus structure (thickness, disposition of the cells), and cell features and contents (length, width, general shape, pyrenoids, chloroplasts disposal). External morphology was observed with a binocular microscope (Wild M3Z) fitted with a

Canon EOS 700D camera (Canon, Tokyo, Japan). Microscopic characters were observed using an Axio Imager A2 microscope (ZEISS, Oberkochen, Germany) fitted with a Canon EOS 100D camera (Canon, Tokyo, Japan).

RESULTS

Species delimitation analyses and identification

A total of 428 sequences were analysed in this study, including 296 newly produced (i.e. 105 ITS, 123 *rbcL*, and 68 *tufA* sequences). A total of 143 sequences have been submitted to the GenBank under accession numbers MZ870605-MZ870654 for ITS sequences, MZ870655-MZ870689 for *tufA* sequences and MZ902934-MZ902991 for *rbcL* sequences (see Table S1).

Species delimitation analyses resulted in a different number of clades depending on the markers (Fig. 2). For the ITS dataset, a total of 21 PSHs were delimited by all three methods with a similar partition scheme. For *rbcL*, a total of 20 PSHs were defined by GMYC and ASAP, and 19 PSHs by PTP. Differences between method partitions were observed in GMYC and PTP lumping the clades 7+ 11+ 12 into one PSH. ASAP lumped the clades 1+ 9, 7+ 12+ 14, and 17+ 18 into unique PSHs. PTP lumped the clades 8+ 19+ 20 into one PSH. Finally, the *tufA* dataset was divided into 15, 12 and 13 PSHs by GMYC, ASAP, and PTP, respectively. GMYC and PTP split the clade 3 into two PSHs, while ASAP considered the clades 3+ 4 as one PSH. GMYC split the clade 4 into two PSHs and lumped the clades 7+ 8 into one PSH. The clades 7+ 12+ 14 were lumped into one PSH with PTP. ASAP also lumped the clades 7+ 11+ 12+ 14 and 17+ 18 into unique PSHs.

Among the notable incongruences between datasets, (i) Clade 4 in the *rbcL* dataset with all three methods and with the GMYC method on the *tufA* dataset was split into two PSHs (NOU218801 was separated from the rest of the samples). Clade 4 was defined as one PSH in the *tufA* dataset with the other methods as well as for the ITS dataset by all methods. Morpho-anatomical observations confirmed us that the specimen NOU218801 was similar to the others included in clade 4. Thus, clade 4 was considered as a unique SSH, identified as *U. tepida*; (ii) Clade 3 was split into two PSHs in the ITS dataset (i.e. NOU218803 apart) and also in the *tufA* dataset with GMYC and PTP, but not into the same partitions as the former (i.e. NOU218867 and the GenBank sequences apart from the rest). The morpho-anatomical verification of the specimens among the clade, particularly NOU218803 and NOU218867, revealed that all of them were similar and matched the original description of *U. meridionalis* (Horimito & Shimada, 2011); (iii) The morpho-anatomical observations of the specimens

from clades 7, 11, 12, and 14 confirmed four distinct taxa and validated the results obtained for the ITS marker with the three methods, as well as on the *tufA* gene with the GMYC method; (iv) Clades 6, 8, 15, 17, 18, 19, 20, and 21 were confirmed as different undescribed taxa with morpho-anatomical observations; (v) A sample from Texas (TM268 from Melton & Lopez-Bautista, 2021; as *Ulva* sp. 2) was close to clade 16 and, depending on the species delimitation method, it was or was not included within the clade. Nevertheless, Melton & Lopez-Bautista (2021) did not provide a detailed description of their *U.* sp. 2, except a few photographs and the number of pyrenoids (one vs 1-3 in our samples). Therefore, until more information can be acquired, we chose to consider *Ulva* sp. 2 *sensu* Melton & Lopez-Bautista (2021) and clade 16 (composed of our samples) as two distinct entities.

Following the SSHs definition process, 21 SSHs were identified among our samples, including six singletons. Among them, four SSHs were characterised by distromatic blade morphologies, while the 17 remaining were tubular throughout the entire thallus with one cell layer. Morpho-anatomical observations and measurements of the specimens observed for each SSH are reported in Supplementary Information (Table S5). Morphological observations, as well as GenBank sequences, led to the identification of five known species including three blade-forming species, *Ulva lactuca*, *U. ohnoi*, and *U. taeniata* (Setchell) Setchell & N.L.Gardner, and two tubular species, *U. meridionalis*, and *U. tepida*. To determine if the 10 remaining SSHs corresponded to existing species, the following decision procedure was applied (see also Table S6). Among the remaining 80 taxonomically valid species (i.e. excluding the five species identified in our dataset), 41 had available genetic sequences and represented species that are phylogenetically different from our 10 SSHs. From the remaining 39 species, for which we had no genetic information, 27 corresponded to foliose forms, while our 10 unidentified SSHs were tubular. This left only 12 existing, unsequenced species to which they could be assigned, and for which we therefore carefully reviewed all original diagnoses and descriptions. The 10 unidentified SSHs in our study did not match any of these descriptions and diagnoses (see arguments in Table S6), and we considered that they represent new species, described below. Singletons were not considered as potential new species, due to the lack of representative's specimens and sequences.

Multilocus Phylogeny

The three-locus concatenated matrix was composed of 2980 base pairs (bp) (ITS: 700 bp; 1357 bp; *tufA*: 923 bp). ML and BI phylogenetic reconstructions were congruent for the position of our clades and samples, except for the specimen NOU218235 (clade 10). The *Ulva*

genus was well supported (bs= 100; PP= 1) and most *Ulva* species represented in the phylogeny were moderately to strongly supported (seven species with bs= 100 and PP= 1, three other species strongly supported (bs> 90; PP> 0.95) and four species moderately supported (bs> 75 and PP> 0.90); Fig. 3). *Ulva ohnoi* (SSH 2) was strongly supported in BI (PP=0.99) but not in ML (bs= 66). SSH 11 was not well supported in both methods (bs= 69; PP= 0.75), probably due to the presence of a specimen represented only by a *rbcL* sequence (NOU218792), which was retained in the analysis to avoid a singleton. Deeper nodes have moderate to low support, thus we will not detail other species relationships here.

Five known species included specimens from New Caledonia, namely *Ulva lactuca* (bs= 96; PP= 0.90; Isle of Pines), *U. meridionalis* (bs= 100; PP= 1; Grande Terre), *U. ohnoi* (bs= 66; PP= 0.99; Grande Terre, Isle of Pines, and Lifou of Loyalty Is.), *U. tepida* (bs= 93; PP= 0.96; Isle of Pines, Grande Terre, and Lifou of Loyalty Is.), and *U. taeniata* (Isle of Pines and Lifou of Loyalty Is.). This latter species was not fully resolved probably because it was composed of specimens for which we could only obtain *rbcL* sequences (NOU218096; NOU214119) but that we nevertheless included in the analysis, as they were the only representatives of *U. taeniata* in our collection. *Ulva lactuca*, *U. meridionalis*, and *U. tepida* were also found in French Polynesia (Tahiti and Marquises Is.).

The genus was completed by ten other SSHs and six singletons that did not fit with any species sequences available on GenBank. The singleton NOU218769 (SSH 5) was from French Polynesia, and SSH 16 (bs= 92; PP= 1) was composed of both French Polynesian and New Caledonian samples (western coast). The SSH 7 (bs = 82; PP = 0.98) was composed of specimens from western and north-eastern New Caledonia and one sample from Papua New Guinea. All other SSHs were found only and exclusively in New Caledonia and are detailed as follows: SSH 8 (bs= 100; PP= 1) was composed of specimens from western and north-eastern Grande Terre and Isle of Pines; SSH 12 (bs= 100; PP= 0.95) from north-western Grande Terre; SSH 13 (bs= 100; PP= 1) from north-eastern and north-western Grande Terre; SSH 14 (bs= 100; PP= 1) was composed of samples from western and north-eastern Grande Terre; SSH 17 (bs= 100; PP= 1) from western Grande Terre; SSH 18 (bs= 100; PP= 1) from western Grande Terre and Isle of Pines; SSH 11 (bs = 63; PP= 0.75), SSH 6 (bs= 100; PP= 1), and the singleton SSHs 15, 19, 20, and 21 were from PGD only (western Grande Terre).

New species from the Pacific

Ulva arbuscula Lagourgue & Payri sp. Nov, Fig. 4-12 (SSH 13)

Description: Tuft of large and fine tubular filaments, 0.5 to 2 cm tall, anchored by a rhizoidal base. Larger filaments flattened, 200-960 µm in diameter, while the thinner are 60 to 80 µm in diameter. Branching from the base and then, along the large filaments as nodes of branching. In surface view, cells are aligned or sometimes in a mosaic, forming a compact and welded assembly. Cells measure 10 to 30 µm in length, 10 to 28 µm wide, and 10 to 20 µm high. In transversal section, filaments composed of one layer of cells taller than wide. 1-4 to multiple pyrenoids per cell.

Holotype: NOU218800. Collected by C. Peignon on 1st July 2020. Housed at NOU.

Type locality: New Caledonia, eastern coast of Grande Terre, Poindimié area, Tibarama islet.

Etymology: In reference to the resemblance of the thallus to a small bush or shrub.

Habitat: High intertidal zone on beach rock mostly on coral islet.

Distribution: New Caledonia.

List of vouchers and representative genetic sequences (holotype in bold): New Caledonia, Tibarama islet, 2020: **NOU218800** (ITS: **MZ870607**; *rbcL*: **MZ902936**); New Caledonia, Tiam'Bouene islet, 2020: NOU218805 (*rbcL*: MZ902953).

Ulva pennata Lagourgue & Payri **sp. nov.**, **Fig. 13-20** (SSH 8)

Description: Feather-like thallus, up to 3 cm tall, composed of main filaments with numerous close and thin ramifications in rows. Filaments entangled in small clumps of 1-5 cm wide. Diameter of main filaments from 160 to 350 µm, those of ramifications 40 to 50 µm. Cells are aligned, square to rectangular in surface view. Cell dimensions of 15 to 30 µm in length, 11 to 30 µm wide, and 20 to 25 µm high. 1-3 pyrenoids per cell.

Holotype: NOU218731. Collected by S. Gobin on 5th February 2019. Housed at NOU.

Type locality: New Caledonia, western coast of Grande Terre, Poé-Gouaro-Déva.

Etymology: In reference to the feather-like aspect formed by the filaments arranged on either side of the main axis.

Habitat: On subtidal sandy terraces or attached to high- to mid-intertidal coral rubble.

Distribution: New Caledonia.

List of vouchers and representative genetic sequences (limited to 2 per locality; holotype in bold): New Caledonia: Poé-Gouaro-Déva, 2019; NOU218723 (ITS: MZ870614; *rbcL*: MZ902944; *tufA*: MZ870660) and **NOU218731** (ITS: **MZ921397**; *rbcL*: **MZ936429**; *tufA*: **MZ921402**); New Caledonia, Saint Vincent, 2020; NOU218825 (ITS: MZ870651; *rbcL*: MZ902988); New Caledonia, Amoss Pass, 2004: NOU218700 (ITS: MZ870633; *rbcL*: MZ902968); New Caledonia, Isle of Pines, 2007: NOU218711 (ITS: MZ870644; *rbcL*:

MZ902981; *tufA*: MZ870683); New Caledonia, Ouvea, 2020: NOU218818 (ITS: MZ921395; *rbcL*: MZ936427) and NOU218820 (ITS: MZ870648; *rbcL*: MZ902985).

Ulva planiramosa Lagourgue & Payri **sp. nov.**, **Fig. 21-29** (SSH 12)

Description: Profusely basally branched thallus, up to 2.5 cm tall, fixed by a rhizoidal base, and composed of intricate tubular filaments of three different sizes. Branches present at the base and along the larger and flattened filaments. Large filaments 430 to 690 μm in diameter, medium filaments 130 to 240 μm in diameter, thin filaments 60 to 70 μm in diameter. Cells are square to rectangular or polygonal and aligned or arranged in a mosaic in surface view. Cell sizes from 10 to 30 μm in length and 10 to 20 μm width. Tubes are composed of one layer of cells of 15 to 20 μm high. Chloroplasts are lattice-like. 1-4 pyrenoids per cell.

Holotype: NOU218807. Collected by C. Peignon on 28th June 2020. Housed at NOU.

Type locality: New Caledonia, eastern coast of Grande Terre, Hienga islet.

Etymology: In reference to its flat filaments (Latin: *plani*).

Habitat: High intertidal zone on beach rock mostly on coral islets.

Distribution: New Caledonia.

List of vouchers and representative genetic sequences (holotype in bold): New Caledonia, Hienga islet, 2020: **NOU218807** (ITS: **MZ870630**; *rbcL*: **MZ902965**; *tufA*: **MZ870671**); New Caledonia, Bayes islet, 2020: NOU218802 (ITS: MZ870617; *rbcL*: MZ902948).

Ulva batuffolosa Lagourgue & Payri **sp. Nov.**, **Fig. 30-39** (SSH 7)

Description: Thallus forming a compact, yellowish-green mass of spaghetti shaped filaments, varying from a few to several tens of centimetres tall. Profusely branched tubular filaments throughout with short uniseriate ramifications forming hooked-like or spinous filaments. Filaments from 50 to 280 μm in diameter, tapering towards the apex. Ramifications along the filaments are 15-50 μm in diameter. In surface view, cells are square to rectangular or polygonal, sometimes with rounded edges, aligned or in a mosaic arrangement and forming a cohesive assembly. Filaments composed of one layer of cells in transversal section. Cells dimensions are 12 to 30 μm in length, 10 to 20 μm in width, and 15 to 30 μm high. Chloroplasts are lattice-like. 1-4 pyrenoids per cell.

Holotype: NOU218754. Collected by S. Gobin in July 2019. Housed at NOU.

Type locality: New Caledonia, western coast of Grande Terre, Poé-Gouaro-Déva.

Etymology: The name comes from the Italian “*batuffolo*” which means messy hair in reference to the tufts of very entangled filaments.

Habitat: Intertidal and subtidal substratum, attached on shallow rocks and corals or epiphytes on seagrass and seaweeds. Occasionally drifting at bottom proximity over sandy terraces.

Distribution: New Caledonia, Papua New Guinea.

List of vouchers and representative genetic sequences (limited to 2 per locality; holotype in bold): New Caledonia, Bois de Fer islet, 2020: NOU218810 (*rbcL*: MZ902937; *tufA*: MZ870656); New Caledonia, Moindou, 2020: NOU218849 (ITS: MZ921392; *rbcL*: MZ936423), NOU218850 (ITS: MZ870631; *rbcL*: MZ902966); New Caledonia, Poé-Gouaro-Déva, 2019: **NOU218754** (ITS: **MZ870641**; *rbcL*: **MZ902977**; *tufA*: **MZ870679**), NOU218759 (ITS: MZ921396; *rbcL*: MZ936428; *tufA*: MZ921401); 2020: NOU218784 (ITS: MZ921391; *rbcL*: MZ936422; *tufA*: MZ921399); Papua New Guinea, Madang, 2012: NOU218860 (*tufA*: MZ921398).

Ulva tentaculosa Lagourgue & Payri **sp. nov.**, **Fig. 40-45** (SSH 16)

Description: Light green tuft of tubular filaments radiating from the base, 0.5 to 4 cm tall. Large and flattened filaments from 350 to 780 µm in diameter, ramify sparsely into thinner and tubular filaments (40 to 100 µm in diameter). In surface view, cells are square, rectangular to polygonal, aligned or in mosaic. Cell size 10 to 21 µm length, 10 to 20 µm width, and 20 to 22 µm high. Filaments composed of one layer of cells in transversal section. 3-4 pyrenoids per cell.

Holotype: NOU218829. Collected by C.E. Payri on 12th July 2020. Housed at NOU.

Type locality: New Caledonia, western coast of Grande Terre, Cap Goulevain.

Etymology: In reference to the tentacle-like branches of the filaments.

Habitat: High intertidal zone, on coral debris.

Distribution: New Caledonia and French Polynesia.

List of vouchers and representative genetic sequences (limited to 2 per locality): New Caledonia: Cap Goulevain, 2020: **NOU218829** (*rbcL*: **MZ902954**; *tufA*: **MZ870666**); French Polynesia, Mangareva, Gatawake bay 2020: NOU218840 (ITS: MZ870616; *rbcL*: MZ902946; *tufA*: MZ870662) and NOU218841 (ITS: MZ870628; *rbcL*: MZ902961).

Ulva finissima Lagourgue & Payri **sp. nov.**, **Fig. 46-51** (SSH 11)

Description: Thallus composed of a mass of vermicelli-like filaments, 2 cm tall. Filaments very thin (20 to 40 µm in diam.) and unbranched. Filaments composed of 4 cells per row. In transversal section, one layer of cells arranged around a very small lumen. Cells square to

rectangular, aligned, and 8 to 12 μm in length, 10 to 18 μm in width, and 15 to 18 μm in height. 1-4 pyrenoids per cell.

Holotype: NOU218760. Collected by S. Gobin in July 2019. Housed at NOU.

Type locality: New Caledonia, western coast of Grande Terre, Poé-Gouaro-Déva.

Etymology: In reference to its very fine filaments.

Habitat: Shallow water on rocks or epiphytes on seagrass. The species was part of the bloom cortege of *U. batuffolosa*.

Distribution: New Caledonia.

List of vouchers and representative genetic sequences (holotype in bold): New Caledonia, Poé-Gouaro-Déva: 2019: **NOU218760** (ITS: **MZ870652**; *rbcL*: **MZ902989**; *tufA*: **MZ870687**); 2020: NOU218792 (*rbcL*: MZ902947).

Ulva pluriramosa Lagourgue & Payri **sp. nov.**, **Fig. 52-57** (SSH 6)

Description: Thallus corresponds to thin clumps of a few (1-2) cm tall composed of tubular filaments ramified throughout. Filaments 20 to 120 μm in diameter. Cells square or rectangular, aligned in surface view. Cell dimensions are 10 to 30 μm in length, 10 to 15 μm wide, and 20 μm high. Filaments composed of one layer of cells in transversal section. 1-2 pyrenoids per cell.

Holotype: NOU218730. Collected by S. Gobin on 5th February 2019. Housed at NOU.

Type Locality: New Caledonia, western coast of Grande Terre, Poé-Gouaro-Déva.

Etymology: In reference to the numerous ramifications on the filaments.

Habitat: On eroded corals in shallow water.

Distribution: New Caledonia.

List of vouchers and representative genetic sequences (limited to 2 per locality; holotype in bold): New Caledonia, Poé-Gouaro-Déva, 2019: **NOU218730** (ITS: **MZ870647**; *rbcL*: **MZ902984**) and NOU218738 (ITS: MZ870638; *rbcL*: MZ902974; *tufA*: MZ870677).

Ulva scolopendra Lagourgue & Payri **sp. nov.**, **Fig. 58-63** (SSH 18)

Description: Light green to yellowish-green tuft composed of entangled filaments with numerous short ramifications all along, up to 8 cm tall. The ramifications alternate, almost perpendicular to the main filament, uniseriate, straight, and spinous or bent. Filaments highly branched at the apices, giving a fan-like appearance, and taper towards the apex. Main filaments from 100 to 320 μm in diameter, while ramifications are 30 to 40 μm in diameter. In surface view, cells rectangular and aligned, with centrally concentrated chloroplast. Cell

dimensions are 25 to 50 µm length, 20 to 50 µm wide, and 20 to 30 µm high. Tubular filaments composed of one layer of cells in transversal section. 2-4 pyrenoids per cell.

Holotype: NOU218811. Collected by R. Legendre on 18th January 2020. Housed at NOU.

Isotype: NOU218813. Collected by R. Legendre on 18th January 2020. Housed at NOU.

Type locality: New Caledonia, Isle of Pines.

Etymology: In reference to its millipede-like filaments.

Habitat: Forming diffuse mat on sandy bottom on barrier reef.

Distribution: New Caledonia.

List of vouchers and representative genetic sequences (types sequences in bold): New Caledonia, Poé, 2019: NOU218725 (ITS: MZ870608; *rbcL*: MZ902938), NOU218753 (ITS: MZ870626; *rbcL*: MZ902958); New Caledonia, Moindou, 2020: NOU218851 (ITS: MZ870620; *rbcL*: MZ902951); New Caledonia, Isle of Pines, 2020: **NOU218811** (*rbcL*: MZ936426), **NOU218813** (ITS: MZ870636; *rbcL*: MZ902970; *tufA*: MZ870675).

Ulva siganiphyllia Lagourgue & Payri **sp. nov.**, **Fig. 64-68** (SSH 17)

Description: Tuft of tubular filaments forming a light green, velvet-like mass up to 5 cm tall. Large filaments with numerous thinner, ramified filaments. Main tubular filaments of 150 to 260 µm in diameter. Ramifications spinous or hook-shaped, 30 to 40 µm in diameter, tapering towards the apex to 20 µm. Cells are aligned, most square, some rectangular. Cell dimensions are 15 to 40 µm in length, 20 to 30 µm wide, and 15 to 25 µm high. In transversal section, cells in one layer. 1-2 pyrenoids per cell.

Holotype: NOU218822. Collected by M. Dumas on 7th July 2020. Housed at NOU.

Type locality: New Caledonia, western coast of Grande Terre, Saint-Vincent.

Etymology: The species is called in reference to its local name “*Herbe à picot*”: “sigani” to refer to the fish name *Siganus* and “phyllia” is from the Greek “*phýllon*” meaning leaf.

Habitat: Forming large masses on sandy, 10 m depth terraces of barrier reefs, locally and seasonally very abundant.

Distribution: New Caledonia.

List of vouchers and representative genetic sequences (limited to 2 per locality; holotype in bold): New Caledonia, Saint-Vincent, 2020: **NOU218822** (ITS: MZ870627; *rbcL*: MZ902959) and NOU218824 (ITS: MZ870619; *rbcL*: MZ902950).

Ulva spumosa Lagourgue & Payri **sp. Nov.**, **Fig. 69-75** (SSH 14)

Description: Thallus composed of profusely branched tubular filaments throughout giving a tree aspect, 0.2-10 cm tall. Numerous ramifications along the filament of 1 to 2 orders, alternate to opposite. Main filaments of 40 to 80 µm in diameter, composed of 2 to 4 cell rows. Ramifications tapering, those of first order composed of 2 cell rows and 20 to 30 µm in diameter, while those of second order are uniseriate and 10 to 15 µm in diameter. Basal filaments are larger, 250 to 340 µm. Filaments composed of 1 to 2 cells, square to rectangular, aligned. Cell dimensions: 10 to 32 µm in length, 12 to 20 µm width, and 20 µm high. In transversal section, cells arranged in one layer. 2-3 pyrenoids per cell.

Holotype: NOU218856. Collected by C.E. Payri on 16th September 2020. Housed at NOU

Type locality: New Caledonia, eastern coast of Grande Terre, Ponerihouen.

Etymology: In reference to its resemblance to moss.

Habitat: Shallow water on rocky substrata.

Distribution: New Caledonia.

List of vouchers and representative genetic sequences (holotype in bold): New Caledonia, Poé-Gouaro-Déva, 2019: NOU218726 (ITS: MZ921393; *rbcL*: MZ936424); New Caledonia, Houailou, 2019: NOU218756 (ITS: MZ870612; *rbcL*: MZ902942; *tufA*: MZ870659); New Caledonia, Kone, 2004: NOU218704 (ITS: MZ870613; *rbcL*: MZ902943); New Caledonia, Ponerihouen, 2020: NOU218855 (ITS: MZ921394; *rbcL*: MZ936425; *tufA*: MZ921400) and **NOU218856 (ITS: MZ870621; *rbcL*: MZ902952; *tufA*: MZ870664)**; New Caledonia, Ouanne Islet, 2020: NOU218806 (ITS: MZ870622; *tufA*: MZ870665).

DISCUSSION

Species diversity in New Caledonia and new insights on species ranges

In the present study, *Ulva* is a strongly supported monophyletic group (bs= 100; PP= 1), which is consistent with what was previously established by Hayden *et al.* (2003). Most *Ulva* species represented in the phylogeny were moderately to strongly supported. Deeper nodes were not strongly supported, which can be explained by the lack of species due to our tight selection of representative sequences (from type material or locality). The existence of yet undescribed and/or unsequenced species may also have contributed to some of the relatively low bootstrap values in our phylogenetic tree. *Ulva* species diversity is still incomplete and resolving interspecific relationships will therefore require additional type material sequences, as well as sampling of understudied regions to uncover the missing diversity and obtain more robust phylogenies. However, the lack of robustness in deep nodes in the phylogeny remains

of minor concern for the purpose of this study, since it neither prevented the assessment of species diversity in New Caledonia, nor in most cases, relationships between species.

From the set of specimens mostly from New Caledonia and to a lesser extent from French Polynesia, 21 different species have been genetically identified, from which ten are distinct from any previously sequenced *Ulva* species (plus six supplementary singleton entities). Through our step-by-step decision procedure (cf. Table S6), including the comparison with the diagnosis of existing species (whether they are from tropical or temperate regions), we deduced that these ten species were new. Only two existing species diagnoses could not be found, those of *Ulva instestinaloides* and *U. patengensis*. Both species appear to have a restricted range to their type locality (Netherlands and Bangladesh, respectively; Guiry & Guiry, 2021). We therefore believe that our specimens found in New Caledonia, are unlikely to correspond to these two species. Nevertheless, more information on *U. instestinaloides* and *U. patengensis* would allow us to confirm this conclusion.

Otherwise, it is the first time that the “Californian” species *U. taeniata* and the “Japanese” species *U. meridionalis* and *U. tepida* were reported in New Caledonia, which raises questions about the arrival processes and pathways in this area. *U. ohnoi* had been reported in New Caledonia as early as 1996 during a major green tide, although this record was unpublished. Finally, it is noteworthy that the ten new species from New Caledonia branch together into a group only composed of species with tropical origins (i.e. *U. iliohaha*, *U. kraftiorum*, and *U. sp2* from Melton & Lopez-Bautista (2021); Fig. 3). Further studies are needed to confirm these tropical affinities, and/or their possible unique origin.

The earlier records of *Ulva* species from New Caledonia were *Ulva compressa*, *U. lactuca* (as *Ulva fasciata* Delile), *U. intestinalis*, and *U. paradoxa* (Garrigue & Tsuda, 1988; Payri, 2007). *Ulva lactuca* (Payri *et al.*, 2000, Payri & N’Yeurt 1997) and *U. rigida* (Payri & N’Yeurt 1997) were previously reported in French Polynesia. All these identifications were based on morphology with the exception of *Ulva lactuca* which has already been genetically confirmed in New Caledonia by Hughey *et al.* (2019). Apart from *U. lactuca*, none of the species previously mentioned in New Caledonia and French Polynesia were found in our genetic analyses. The DNA sequences available from GenBank for these species are far from our specimens in the phylogenetic tree (see Fig. 2). These results confirm that tropical species named from temperate species may have been taxonomic errors, as already reported by O’Kelly *et al.* (2010).

Our investigation expands the distribution areas of several species. First, we demonstrated that *U. meridionalis* and *U. tepida*, which until now had only been observed in the Southwestern Pacific (Australia, Queensland; Phillips *et al.*, 2016), have a distribution area that extends further east, with specimens now recorded in New Caledonia and the Central Pacific (French Polynesia). Second, our study fills a gap in the distribution area of *U. taeniata*, which might be cosmopolitan in the Pacific. Indeed, *U. taeniata* (type locality: California) was observed from the Hawaiian Islands (Abbott & Huisman, 2004) to the Western Pacific in Australia (Womersley, 1984; Scott, 2017), New Zealand (Chapman, 1956; Womersley, 1984), and New Caledonia (this study).

Differences in species distribution ranges have been observed. Some species have a very wide distribution area, including the overlap between New Caledonia and French Polynesia (e.g. *U. meridionalis* and *U. tepida*). In contrast, twice as many undescribed species show restricted distribution. Aside from the singletons, *U. pluriramosa*, *U. pennata*, *U. finissima*, *U. planiramosa*, *U. arbuscula*, *U. spumosa*, *U. scolopendra* corresponded to specimens only sampled in New Caledonia and, for some of them, restricted to one locality (e.g. PGD for *U. finissima* or northern Grande Terre for *U. arbuscula*). These restricted distribution ranges, however, may be due to sampling bias rather than endemism. Nowhere in New Caledonia or Polynesia have all these species co-occurred, but several species have nevertheless been found in the same locality. Notably nine and five different *Ulva* species were reported at PGD and Isle of Pines, respectively, but not always during the same period or year.

Combining molecular and morphological analyses to reassess species diversity

Through this study, we confirmed that *Ulva* species show a strong intraspecific morphological plasticity (e.g. size cells difference) that made the morphological identification challenging, and it was difficult to determine clear diagnostic taxonomic characters, as highlighted in previous works (Kraft *et al.*, 2010; Guidone *et al.*, 2013; Kirkendale *et al.*, 2013; Wichard *et al.*, 2015; Kang *et al.*, 2019). For example, the number of pyrenoids, which has long been considered an important discriminatory character (Bliding, 1968; Koeman & van den Hoek, 1981; Coat *et al.*, 1998), was found to be unreliable to accurately delimit *Ulva* species (Tanner, 1986; Phillips, 1988), as it may fluctuate significantly among seasons for a given species (Malta *et al.*, 1999; on *Ulva lactuca*). Similarly, the branching pattern within a species can vary according to the salinity or to the light intensity (De Silva & Burrows, 1973; Reed & Russell, 1978; Leskinen *et al.*, 2004; Gao *et al.*, 2016). In addition, in our study *Ulva* species,

particularly the *Enteromorpha*-like ones, have shown external morphology crypticity, which hampers their identification *in situ* and requires deeper morpho-anatomical analyses to distinguish them, as already highlighted by Hughey *et al.* (2019) or Steinhagen *et al.* (2019b). Even if this study confirms the difficulty to establish relevant diagnostic morphological characters for the genus *Ulva*, we think that the combination of different taxonomic characters often helps species identification or delimitation (e.g. branching patterns and cells or filaments size). However, morphological-based identification (or delimitation) remains laborious if not coupled with molecular analyses and has previously generated a large number of *Ulva* species (408) from which nearly 80% were placed in synonymy (Guiry & Guiry, 2021). The integration of type data (i.e. genetic and/or morphological data from holotypes, lectotypes or isotypes) and the consideration of original diagnoses are essential to identify species and better assess the diversity present in a dataset. This is the approach we have taken in this study.

Another issue that must be considered when blasting sequences for species identification is the high frequency of incorrect species names assigned to published genetic sequences. Sulpice & Fort (2020) estimated that 21% entries of *Ulva* in GenBank are misannotated (including 65% of *U. lactuca* sequences). This trend was confirmed in the present study, with many assignments found doubtful and thus, not used in the analyses. A major revision and correction of the sequence assignments available on GenBank, as well as the localities reported on Algaebase, would be necessary to better identify the diversity of the genus and the distribution of its species.

Origin, blooming capacity, and species involved in the green tides in New Caledonia

The flora of New Caledonia is mostly composed of undescribed species that are likely to be indigenous. Most non-indigenous species originate in the Pacific or Indo-Pacific, with similar temperature ranges, i.e. tropical or subtropical: *U. meridionalis*, *U. ohnoi* (cf. Hiraoka *et al.*, 2004; referring to Ohno, 1988), and *U. lactuca* (cf. Hughey *et al.*, 2019), with the exception of *U. tepida* and *U. taeniata* which are from temperate waters. All these previously described species have wide distribution ranges and their presence in New Caledonia may be the result of natural dispersion and/or vessel traffic, similar to the expansion of *U. ohnoi* and *U. australis* from Japan to the Mediterranean Sea (Flagella *et al.*, 2010) and Australia (Hanyuda *et al.*, 2018), respectively. Although the current data do not allow us to discriminate these potential pathways, their presence in New Caledonia calls for stricter regulation and management of water quality, as all of them (except *U. taeniata*) have already generated

green tides inducing significant costs for coastal societies and ecosystems (Hiraoka *et al.*, 2004; Lawton *et al.*, 2013; Bast *et al.*, 2014; Phillips *et al.*, 2016; Lee *et al.*, 2019, Xie *et al.*, 2020). In addition, three of the new species (*Ulva batuffolosa*, *U. pennata*, and *U. siganiphyllia*) caused blooming events in New Caledonia between 2018 and 2021. None of the indigenous nor non-indigenous species are currently considered as invasive, although we have to be cautious about the presence of species known for their invasive potential elsewhere (more so in temperate waters).

The specimens at the origin of the green tides at PGD in 2018 and 2019 (except July 2019) correspond to *Ulva batuffolosa* sp. nov., which, to date, has only been found in New Caledonia and Papua New Guinea. In New Caledonia, at the PGD site, the species forms compact clusters of algae that entangle in coral and seagrass beds, or drift near the bottom under the impulsion of water currents. These clusters stretch and can reach several decimetres in length. Other species were present among the bloom cortege (e.g., *Ulva finissima*, *Boodlea* sp., *Cladophora* sp., and *Chaetomorpha* sp.), but *Ulva batuffolosa* always remained the dominant species. The 2018 green tide at PGD was triggered by a massive input of nutrients in the lagoon due to the excessive use of fertilizers in this area (pers. comm.). In other sites in New Caledonia or Papua New Guinea, this species is present but has not caused any blooms to our knowledge.

Other algal bloom events are periodically reported in New Caledonia during the hot and rainy season in Ouvea (Loyalty Islands) and PGD involving *Ulva pennata* sp. nov., or along the south-western Grande Terre with *Ulva siganiphyllia* sp. nov., locally known as “*Herbe à picots*”. The cause of these blooms by these indigenous species is not yet documented, but their periodic nature, mostly during the rainy season and nearly absent during the dry season (Brisset *et al.*, 2021), suggests that nutrient input in the lagoon through water runoff may trigger the proliferation.

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10 T.J., and S.V.W. Sampling authorizations were delivered by La Province Sud (N°4406-

11 2018/ARR/DENV). Other samples were collected during scientific campaigns described
12 below: New Caledonia: Loyalty Islands, 2005: R/V Alis, BSM-LOYAUTE,

13 [10.17600/5100030](#) ; Isle of Pines, 2001; 2005: R/V Alis, BIODIP, [10.17600/5100100](#); 2007:

14 R/V Alis, CORALCAL-1, [10.17600/7100020](#); French Polynesia, 2008: Moorea-biocode;

15 2011: Marquises, Pakaihi i te Moana expedition; Papua New Guinea, 2012: R/V Alis,

16 NUIGUINI campaign, [10.17600/12100070](#)

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20

21 **Disclosure statement**

22 No potential conflict of interest was reported by the authors.

23

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Supplementary information

Table S1: List of the specimens included in this study, with sample IDs, species identification, location of sampling, GenBank accession numbers (or BOLD sequence ID in grey for those not submitted), and the corresponding SSH number, as well as the sequences used in the multilocus phylogeny.

Table S2: Primers used for amplification of the ITS, *rbcL* and *tufA* markers, corresponding DNA fragment size and references.

Table S3: PCR programs used according to the marker amplified.

Table S4: List of specimens from GenBank database included in our phylogenetic analyses, with voucher names, collection localities, sequence accession numbers for ITS, *rbcL* and *tufA* genes, and reference studies.

Table S5: Morpho-anatomical observations and measures of the specimens studied in each SSH.

Table S6: Decision aid to ascertain whether our tubular specimens correspond to new species or not: presence or absence of genetic data (0/1); if not, diagnosis found (x) and comparison of morphological characters; if not and in the last case, consultation of herbarium (x) to check external morphology. Arguments justifying our decision are also reported. NA: not attributable.

Table S1 : List of the specimens included in this study, with sample IDs, species identification, location of sampling, GenBank accession numbers (or BOLD sequence ID in grey for those not submitted), and the corresponding SSH number, as well as the sequences used in multilocus and time-calibrated phylogenies.

Herbarium ID	Vouchers	Species	Collect Locality	BOLD	GenBank accession numbers (or Bold)			# SSH (Clade)	Used in concatenated phylogeny
					ITS	<i>rbcL</i>	<i>tufA</i>		
NOU217270	IDP05_0102	<i>Ulva ohnoi</i>	New Caledonia, Isles of Pines	ULV001-21	MZ870605	MZ902934		2	v
NOU218015	IDP05_0823	<i>Ulva lactuca</i>	New Caledonia, Isles of Pines	ULV003-21		ULV003-21		1	
NOU218096	IDP05_0912	<i>Ulva taeniata</i>	New Caledonia, Isles of Pines	ULV004-21		MZ902962		9	v
NOU218690	LIF18_005	<i>Ulva tepida</i>	New Caledonia, Loyalties Islands, Lifou	ULV005-21	ULV005-21	ULV005-21	ULV005-21	4	
NOU218691	LIF18_006	<i>Ulva tepida</i>	New Caledonia, Loyalties Islands, Lifou	ULV006-21	MZ870615	MZ902945	MZ870661	4	v
NOU218692	LIF18_007	<i>Ulva tepida</i>	New Caledonia, Loyalties Islands, Lifou	ULV007-21	ULV007-21	ULV007-21	ULV007-21	4	
NOU218693	LIF18_008	<i>Ulva tepida</i>	New Caledonia, Loyalties Islands, Lifou	ULV008-21	ULV008-21	ULV008-21	ULV008-21	4	
NOU218694	LIF18_009	<i>Ulva tepida</i>	New Caledonia, Loyalties Islands, Lifou	ULV009-21		ULV009-21	ULV009-21	4	
NOU218695	LIF18_010	<i>Ulva tepida</i>	New Caledonia, Loyalties Islands, Lifou	ULV010-21		ULV010-21		4	
NOU218696	LIF18_011	<i>Ulva tepida</i>	New Caledonia, Loyalties Islands, Lifou	ULV011-21		ULV011-21	ULV011-21	4	
NOU218697	LIF18_012	<i>Ulva tepida</i>	New Caledonia, Loyalties Islands, Lifou	ULV012-21		ULV012-21		4	
NOU218698	LIF18_013	<i>Ulva tepida</i>	New Caledonia, Loyalties Islands, Lifou	ULV013-21	ULV013-21	ULV013-21	ULV013-21	4	
NOU218700	NC04_771	<i>Ulva pennata</i>	New Caledonia, Amoss Pass	ULV014-21	MZ870633	MZ902968		8	v
NOU218704	NC04_857	<i>Ulva spumosa</i>	New Caledonia, Kone	ULV015-21	MZ870613	MZ902943		14	v
NOU214119	NC05_0309	<i>Ulva taeniata</i>	New Caledonia, Loyalties Islands, Lifou, Cap des Pins	ULV016-21		MZ902990		9	v
NOU218235	NC05_1289	<i>Ulva</i> sp.	New Caledonia, Corne Sud	ULV017-21		MZ902960		10	v

NOU218705	NC06_600a	<i>Ulva ohnoi</i>	New Caledonia, Noumea, Anse Vata beach	ULV018-21		ULV018-21		2	
NOU218706	NC06_600b	<i>Ulva tepida</i>	New Caledonia, Noumea, Anse Vata beach	ULV019-21	MZ870646	MZ902983		4	v
NOU218707	NC07_645a	<i>Ulva tepida</i>	New Caledonia, Isles of Pines, Kodjeu	ULV020-21		ULV020-21		4	
NOU218708	NC07_645b	<i>Ulva tepida</i>	New Caledonia, Isles of Pines, Kodjeu	ULV021-21		ULV021-21		4	
NOU218709	NC07_646a	<i>Ulva ohnoi</i>	New Caledonia, Isles of Pines, Kodjeu	ULV022-21		MZ902972		2	v
NOU218710	NC07_646b	<i>Ulva ohnoi</i>	New Caledonia, Isles of Pines, Kodjeu	ULV023-21	ULV023-21			2	
NOU218711	NC07_651	<i>Ulva pennata</i>	New Caledonia, Isles of Pines, Kodjeu	ULV024-21	MZ870644	MZ902981	MZ870683	8	v
NOU218712	NC07_655a	<i>Ulva ohnoi</i>	New Caledonia, Moindou	ULV025-21		ULV025-21		2	
NOU218713	NC07_655b	<i>Ulva ohnoi</i>	New Caledonia, Moindou	ULV026-21			ULV026-21	2	
NOU218715	NC07_657	<i>Ulva meridionalis</i>	New Caledonia, Moindou	ULV027-21		ULV027-21	ULV027-21	3	
NOU218716	NC07_656	<i>Ulva ohnoi</i>	New Caledonia, Moindou	ULV028-21		ULV028-21		2	
NOU218717	NC18_001	<i>Ulva ohnoi</i>	New Caledonia, Loyalties Islands, Lifou, Chépénéhé	ULV029-21	MZ870650	MZ902987	MZ870686	2	v
NOU218719	NC19_004	<i>Ulva batuffolosa</i>	New Caledonia, Poe	ULV030-21	ULV030-21	ULV030-21		7	
NOU218720	NC19_005	<i>Ulva batuffolosa</i>	New Caledonia, Poe	ULV031-21	ULV031-21	ULV031-21		7	
NOU218721	NC19_006	<i>Ulva pennata</i>	New Caledonia, Poe	ULV032-21	ULV032-21	ULV032-21		8	
NOU218723	NC19_008	<i>Ulva pennata</i>	New Caledonia, Poe	ULV033-21	MZ870614	MZ902944	MZ870660	8	v
NOU218724	NC19_010	<i>Ulva batuffolosa</i>	New Caledonia, Poe	ULV034-21	ULV034-21	ULV034-21		7	
NOU218725	NC19_015	<i>Ulva scolopendra</i>	New Caledonia, Poe	ULV035-21	MZ870608	MZ902938		18	v
NOU218726	NC19_016	<i>Ulva spumosa</i>	New Caledonia, Poe	ULV036-21	MZ921393	MZ936424		14	
NOU218727	NC19_017	<i>Ulva pennata</i>	New Caledonia, Poe	ULV037-21	ULV037-21	ULV037-21	ULV037-21	8	
NOU218728	NC19_019	<i>Ulva batuffolosa</i>	New Caledonia, Poe	ULV038-21	ULV038-21			7	
NOU218729	NC19_022	<i>Ulva pluriramosa</i>	New Caledonia, Poe	ULV039-21	MZ870654	MZ902991		6	v

NOU218730	NC19_024	<i>Ulva pluriramosa</i>	New Caledonia, Poe	ULV040-21	MZ870647	MZ902984		6	v
NOU218731	NC19_032	<i>Ulva pennata</i>	New Caledonia, Poe	ULV041-21	MZ921397	MZ936429	MZ921402	8	
NOU218732	NC19_033	<i>Ulva pennata</i>	New Caledonia, Poe	ULV042-21	ULV042-21	ULV042-21	ULV042-21	8	
NOU218733	NC19_034	<i>Ulva pennata</i>	New Caledonia, Poe	ULV043-21		ULV043-21	ULV043-21	8	
NOU218734	NC19_035	<i>Ulva pennata</i>	New Caledonia, Poe	ULV044-21	ULV044-21	ULV044-21	ULV044-21	8	
NOU218735	NC19_038	<i>Ulva</i> sp.	New Caledonia, Poe	ULV045-21	MZ870639	MZ902975	MZ870678	20	v
NOU218736	NC19_041	<i>Ulva pennata</i>	New Caledonia, Poe	ULV046-21		ULV046-21		8	
NOU218737	NC19_042	<i>Ulva pluriramosa</i>	New Caledonia, Poe	ULV047-21	ULV047-21	ULV047-21		6	
NOU218738	NC19_043	<i>Ulva pluriramosa</i>	New Caledonia, Poe	ULV048-21	MZ870638	MZ902974	MZ870677	6	v
NOU218739	NC19_046	<i>Ulva batuffolosa</i>	New Caledonia, Poe, Domaine de Deva	ULV049-21	ULV049-21	ULV049-21		7	
NOU218740	NC19_047	<i>Ulva batuffolosa</i>	New Caledonia, Poe, Domaine de Deva	ULV050-21	ULV050-21	ULV050-21		7	
NOU218742	NC19_049	<i>Ulva meridionalis</i>	New Caledonia, Poe, Domaine de Deva	ULV051-21	ULV051-21	ULV051-21	ULV051-21	3	
NOU218743	NC19_050	<i>Ulva meridionalis</i>	New Caledonia, Poe, Domaine de Deva	ULV052-21	MZ870645	MZ902982	MZ870684	3	v
NOU218744	NC19_051	<i>Ulva</i> sp.	New Caledonia, Poe, Domaine de Deva	ULV053-21	MZ870625	MZ902957		21	v
NOU218745	NC19_060	<i>Ulva tepida</i>	New Caledonia, Noumea, Anse Vata beach	ULV054-21		ULV054-21	ULV054-21	4	
NOU218746	NC19_061	<i>Ulva ohnoi</i>	New Caledonia, Noumea, Magenta beach	ULV055-21		MZ902964	MZ870670	2	v
NOU218747	NC19_062	<i>Ulva tepida</i>	New Caledonia, Noumea, Magenta beach	ULV056-21	MZ870649	MZ902986	MZ870685	4	v
NOU218748	NC19_063	<i>Ulva batuffolosa</i>	New Caledonia, Poe, Domaine de Deva	ULV057-21	ULV057-21	ULV057-21		7	
NOU218749	NC19_064	<i>Ulva tepida</i>	New Caledonia, Bourail, Roche percee	ULV058-21	ULV058-21	ULV058-21	ULV058-21	4	
NOU218751	NC19_065b	<i>Ulva spumosa</i>	New Caledonia, Poe	ULV060-21	ULV060-21		ULV060-21	14	
NOU218752	NC19_066	<i>Ulva ohnoi</i>	New Caledonia, Poe	ULV061-21		ULV061-21		2	
NOU218753	NC19_067	<i>Ulva scolopendra</i>	New Caledonia, Poe	ULV062-21	MZ870626	MZ902958		18	v
NOU218754	NC19_068	<i>Ulva batuffolosa</i>	New Caledonia, Poe	ULV063-21	MZ870641	MZ902977	MZ870679	7	v

NOU218755	NC19_069	<i>Ulva meridionalis</i>	New Caledonia, Bourail, Roche percee	ULV064-21	ULV064-21	ULV064-21	ULV064-21	3	
NOU218756	NC19_070	<i>Ulva spumosa</i>	New Caledonia, Houailou	ULV065-21	MZ870612	MZ902942	MZ870659	14	v
NOU218757	NC19_071	<i>Ulva batuffolosa</i>	New Caledonia, Poe, Domaine de Deva	ULV066-21	ULV066-21	ULV066-21	ULV066-21	7	
NOU218758	NC19_072	<i>Ulva batuffolosa</i>	New Caledonia, Poe, Domaine de Deva	ULV067-21	ULV067-21	ULV067-21	ULV067-21	7	
NOU218759	NC19_073	<i>Ulva batuffolosa</i>	New Caledonia, Poe, Domaine de Deva	ULV068-21	MZ921396	MZ936428	MZ921401	7	
NOU218760	NC19_074	<i>Ulva finissima</i>	New Caledonia, Poe, Domaine de Deva	ULV069-21	MZ870652	MZ902989	MZ870687	11	v
NOU218768	NJ18_003	<i>Ulva ohnoi</i>	New Caledonia, La Roche	ULV070-21	MZ870624	MZ902956	MZ870668	2	v
NOU218769	PF_689	<i>Ulva</i> sp.	French Polynesia, Tahiti	ULV071-21	MZ870642	MZ902979	MZ870681	5	v
NOU218770	PF_690	<i>Ulva meridionalis</i>	French Polynesia, Tahiti	ULV072-21	MZ870623	MZ902955	MZ870667	3	v
NOU218771	PF_691	<i>Ulva tepida</i>	French Polynesia, Tahiti	ULV073-21		MZ902973	MZ870676	4	v
NOU218772	PF_692	<i>Ulva lactuca</i>	French Polynesia, Tahiti	ULV074-21	MZ870634	MZ902969	MZ870673	1	v
NOU218773	TER_Ia	<i>Ulva ohnoi</i>	New Caledonia, Fort Teremba	ULV075-21	ULV075-21			2	
NOU218774	TER_II	<i>Ulva ohnoi</i>	New Caledonia, Fort Teremba	ULV076-21	ULV076-21			2	
NOU218777	CP09_19_2	<i>Ulva batuffolosa</i>	New Caledonia, Poe	ULV077-21			ULV077-21	7	
NOU218778	190220_2AE	<i>Ulva batuffolosa</i>	New Caledonia, Poe	ULV078-21		ULV078-21		7	
NOU218779	190220_2AEb	<i>Ulva batuffolosa</i>	New Caledonia, Poe	ULV079-21	MZ870609	MZ902939	MZ870657	7	v
NOU218781	190220_2B2E	<i>Ulva batuffolosa</i>	New Caledonia, Poe	ULV080-21		ULV080-21	ULV080-21	7	
NOU218782	190220_3E	<i>Ulva batuffolosa</i>	New Caledonia, Poe	ULV081-21	ULV081-21			7	
NOU218784	190220E	<i>Ulva batuffolosa</i>	New Caledonia, Poe	ULV082-21	MZ921391	MZ936422	MZ921399	7	
NOU218785	A102J2E	<i>Ulva batuffolosa</i>	New Caledonia, Poe	ULV083-21	ULV083-21	ULV083-21	ULV083-21	7	
NOU218786	A105J2E	<i>Ulva batuffolosa</i>	New Caledonia, Poe	ULV084-21	ULV084-21	ULV084-21	ULV084-21	7	
NOU218787	A105SAI05EA	<i>Ulva batuffolosa</i>	New Caledonia, Poe	ULV085-21	ULV085-21		ULV085-21	7	
NOU218789	A113SAI13E	<i>Ulva</i> sp.	New Caledonia, Poe	ULV086-21	MZ870640	MZ902976		19	v

NOU218790	A115SAI15E	<i>Ulva</i> sp.	New Caledonia, Poe	ULV087-21	MZ870637	MZ902971		15	v
NOU218792	B21S2E	<i>Ulva finissima</i>	New Caledonia, Poe	ULV088-21		MZ902947		11	v
NOU218793	B21S8_E_A	<i>Ulva batuffolosa</i>	New Caledonia, Poe	ULV089-21	ULV089-21	ULV089-21	ULV089-21	7	
NOU218795	B27J2E	<i>Ulva pennata</i>	New Caledonia, Poe	ULV091-21	MZ870610	MZ902940		8	v
NOU218796	B41STQ3EA	<i>Ulva batuffolosa</i>	New Caledonia, Poe	ULV092-21	ULV092-21			7	
NOU218797	B41STQ3EB	<i>Ulva batuffolosa</i>	New Caledonia, Poe	ULV093-21	ULV093-21	ULV093-21		7	
NOU218798	B42S15E	<i>Ulva batuffolosa</i>	New Caledonia, Poe	ULV094-21	ULV094-21			7	
NOU218799	CHP1	<i>Ulva ohnoi</i>	New Caledonia, islet Double	ULV095-21	MZ870618	MZ902949	MZ870663	2	v
NOU218800	CHP10	<i>Ulva arbuscula</i>	New Caledonia, islet Tibarama	ULV096-21	MZ870607	MZ902936		13	v
NOU218801	CHP11	<i>Ulva tepida</i>	New Caledonia, islet Nana	ULV097-21		MZ902978	MZ870680	4	v
NOU218802	CHP12	<i>Ulva planiramosa</i>	New Caledonia, islet Bayes	ULV098-21	MZ870617	MZ902948		12	v
NOU218803	CHP2	<i>Ulva meridionalis</i>	New Caledonia, islet Double	ULV099-21	MZ870653		MZ870688	3	v
NOU218805	CHP4	<i>Ulva arbuscula</i>	New Caledonia, islet Tiam'Bouene	ULV100-21		MZ902953		13	v
NOU218806	CHP5a	<i>Ulva spumosa</i>	New Caledonia, islet Ouanne	ULV101-21	MZ870622		MZ870665	14	x
NOU218807	CHP6	<i>Ulva planiramosa</i>	New Caledonia, islet Hienga	ULV102-21	MZ870630	MZ902965	MZ870671	12	v
NOU218810	CHP9	<i>Ulva batuffolosa</i>	New Caledonia, islet Bois de Fer	ULV103-21		MZ902937	MZ870656	7	v
NOU218811	CP20_001	<i>Ulva scolopendra</i>	New Caledonia, Isle of Pines	ULV104-21		MZ936426		18	
NOU218813	CP20_003	<i>Ulva scolopendra</i>	New Caledonia, Isle of Pines	ULV105-21	MZ870636	MZ902970	MZ870675	18	v
NOU218814	CP20_004	<i>Ulva ohnoi</i>	New Caledonia, Noumea, Hippodrome	ULV106-21	MZ870632	MZ902967	MZ870672	2	v
NOU218818	CP20_010	<i>Ulva pennata</i>	New Caledonia, Ouvea	ULV107-21	MZ921395	MZ936427		8	
NOU218819	CP20_011	<i>Ulva pennata</i>	New Caledonia, Ouvea	ULV108-21	ULV108-21	ULV108-21		8	
NOU218820	CP20_012	<i>Ulva pennata</i>	New Caledonia, Ouvea	ULV109-21	MZ870648	MZ902985		8	v
NOU218821	CP20_013	<i>Ulva pennata</i>	New Caledonia, Ouvea	ULV110-21	ULV110-21	ULV110-21		8	

NOU218822	NC20_10	<i>Ulva siganiphyllia</i>	New Caledonia, Saint Vincent, Barrier reef	ULV111-21	MZ870627	MZ902959		17	v
NOU218823	NC20_11	<i>Ulva siganiphyllia</i>	New Caledonia, Saint Vincent, Barrier reef	ULV112-21		ULV112-21		17	
NOU218824	NC20_12	<i>Ulva siganiphyllia</i>	New Caledonia, Saint Vincent, Barrier reef	ULV113-21	MZ870619	MZ902950		17	v
NOU218825	NC20_13b	<i>Ulva pennata</i>	New Caledonia, Saint Vincent, Barrier reef	ULV114-21	MZ870651	MZ902988		17	v
NOU218826	NC20_15	<i>Ulva meridionalis</i>	Cap Goulevain	ULV115-21	ULV115-21	ULV115-21		3	
NOU218827	NC20_16	<i>Ulva tepida</i>	Cap Goulevain	ULV116-21		ULV116-21		4	
NOU218828	NC20_17	<i>Ulva tepida</i>	Cap Goulevain	ULV117-21	MZ870611	MZ902941	MZ870658	4	v
NOU218829	NC20_18	<i>Ulva tentaculosa</i>	Cap Goulevain	ULV118-21		MZ902954	MZ870666	16	v
NOU218832	NC20_22	<i>Ulva meridionalis</i>	Cap Goulevain	ULV119-21	MZ870643	MZ902980	MZ870682	3	v
NOU218833	SABL1	<i>Ulva tentaculosa</i>	French Polynesia, Gambier Is., Gatawake bay	ULV120-21	ULV120-21	ULV120-21		16	
NOU218834	SABL2	<i>Ulva tentaculosa</i>	French Polynesia, Gambier Is., Gatawake bay	ULV121-21	MZ870606	MZ902935		16	v
NOU218835	SABL3	<i>Ulva tentaculosa</i>	French Polynesia, Gambier Is., Gatawake bay	ULV122-21	ULV122-21	ULV122-21		16	
NOU218836	SABL4	<i>Ulva tentaculosa</i>	French Polynesia, Gambier Is., Gatawake bay	ULV123-21		ULV123-21		16	
NOU218837	SABL5	<i>Ulva tentaculosa</i>	French Polynesia, Gambier Is., Gatawake bay	ULV124-21	ULV124-21			16	
NOU218838	SAN1	<i>Ulva tentaculosa</i>	French Polynesia, Gambier Is., Gatawake bay	ULV125-21	ULV125-21	ULV125-21		16	
NOU218839	SAN2	<i>Ulva tentaculosa</i>	French Polynesia, Gambier Is., Gatawake bay	ULV126-21	ULV126-21	ULV126-21		16	
NOU218840	SAN3	<i>Ulva tentaculosa</i>	French Polynesia, Gambier Is., Gatawake bay	ULV127-21	MZ870616	MZ902946	MZ870662	16	v
NOU218841	SAN4	<i>Ulva tentaculosa</i>	French Polynesia, Gambier Is., Gatawake bay	ULV128-21	MZ870628	MZ902961		16	v
NOU218844	E11_1	<i>Ulva batuffolosa</i>	New Caledonia, Poe	ULV129-21	MZ870629	MZ902963	MZ870669	7	v
NOU218845	E11_5	<i>Ulva batuffolosa</i>	New Caledonia, Poe	ULV130-21			ULV130-21	7	
NOU218846	E11_8	<i>Ulva batuffolosa</i>	New Caledonia, Poe	ULV131-21	ULV131-21	ULV131-21		7	
NOU218847	E11_11	<i>Ulva meridionalis</i>	New Caledonia, Poe	ULV132-21		ULV132-21	ULV132-21	3	
NOU218849	MOIN262	<i>Ulva batuffolosa</i>	New Caledonia, Moindou	ULV133-21	MZ921392	MZ936423		7	

NOU218850	MOIN263	<i>Ulva batuffolosa</i>	New Caledonia, Moindou	ULV134-21	MZ870631	MZ902966		7	v
NOU218851	MOIN264	<i>Ulva scolopendra</i>	New Caledonia, Moindou	ULV135-21	MZ870620	MZ902951		18	v
NOU218852	MOIN265	<i>Ulva batuffolosa</i>	New Caledonia, Moindou	ULV136-21	ULV136-21	ULV136-21		7	
NOU218853	MOIN266	<i>Ulva batuffolosa</i>	New Caledonia, Moindou	ULV137-21	ULV137-21	ULV137-21		7	
NOU218854	MOIN269	<i>Ulva batuffolosa</i>	New Caledonia, Moindou	ULV138-21		ULV138-21		7	
NOU218855	NC20_23	<i>Ulva spumosa</i>	New Caledonia, Ponerihouen	ULV139-21	MZ921394	MZ936425	MZ921400	14	
NOU218856	NC20_24	<i>Ulva spumosa</i>	New Caledonia, Ponerihouen	ULV140-21	MZ870621	MZ902952	MZ870664	14	v
NOU218860	PHV_809	<i>Ulva batuffolosa</i>	Papua New-Guinea, Madang	ULV142-21			MZ921398	7	
NOU215143	MQ11_028	<i>Ulva lactuca</i>	Frend Polynesia, Marquises	ULV143-21	ULV143-21			1	
NOU215229	MQ11_198	<i>Ulva lactuca</i>	Frend Polynesia, Marquises	ULV144-21	ULV144-21			1	
NOU215262	MQ11_263	<i>Ulva lactuca</i>	Frend Polynesia, Marquises	ULV145-21	ULV145-21			1	
NOU215308	MQ11_345	<i>Ulva meridionalis</i>	Frend Polynesia, Marquises	ULV146-21			MZ870655	3	v
NOU215309	MQ11_346	<i>Ulva meridionalis</i>	Frend Polynesia, Marquises	ULV147-21			ULV147-21	3	
NOU215325	MQ11_365	<i>Ulva lactuca</i>	Frend Polynesia, Marquises	ULV148-21	MZ870635		MZ870674	1	v
NOU218867	CP08_1001	<i>Ulva meridionalis</i>	French Polynesia, Moorea	ULV149-21			MZ870689	3	v

Figure S1: Maximum Clade Credibility Tree (MCCT) obtained from the BEAST analysis with the ITS dataset (unique haplotypes).

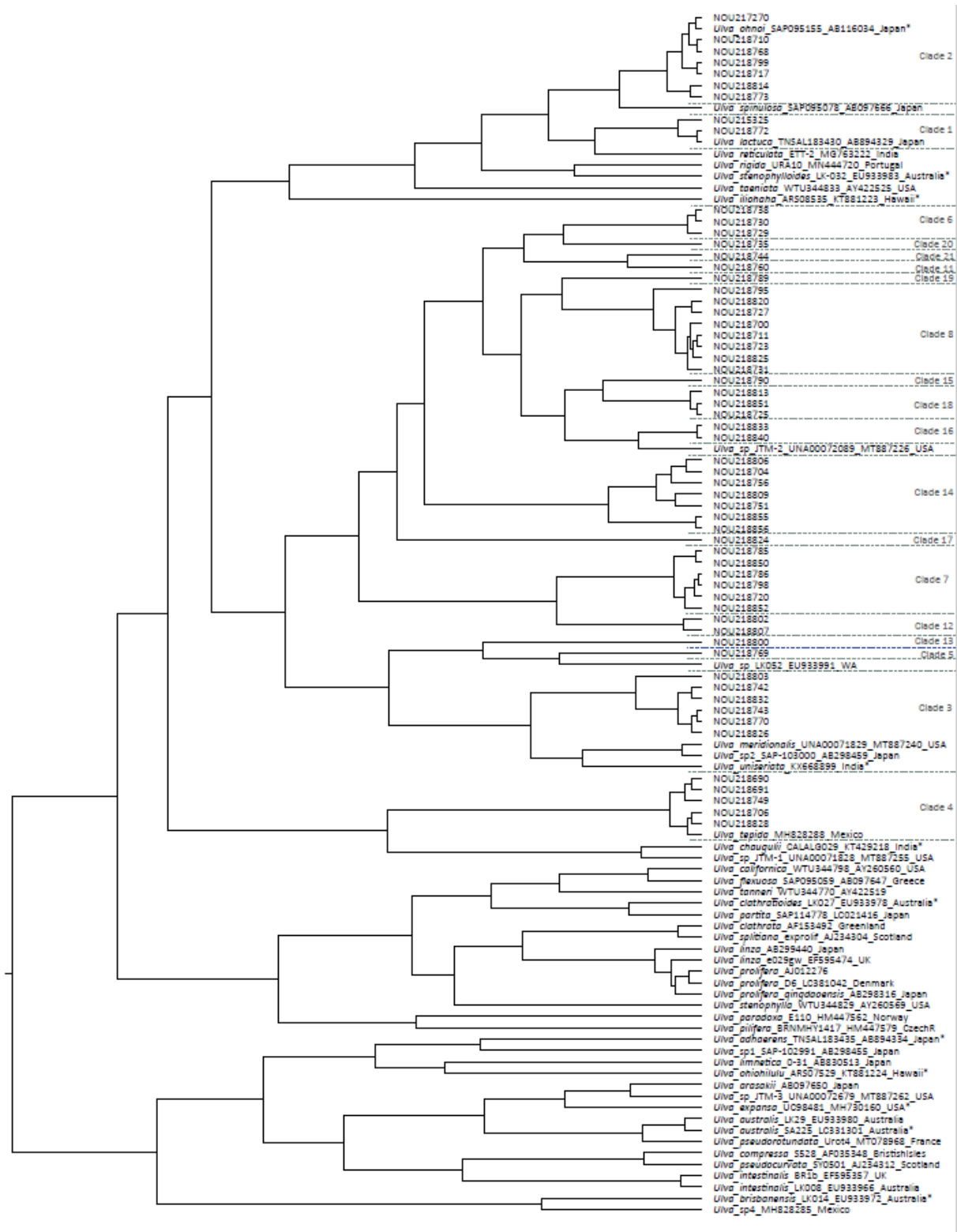


Figure S2: Maximum Clade Credibility Tree (MCCT) obtained from the BEAST analysis with the *rbcL* dataset (unique haplotypes).

Table S2 : Primers used for amplification of the ITS, *rbcL* and *tufA* markers, corresponding DNA fragment size and references.

Primers	Gene	DNA Fragment size (pb)	References
ITS1a/ITS2D	ITS	500 à 600	Leskinen & Pamilo (1997)
<i>rbcL</i> -RH1/ <i>rbcL</i> -1385R	<i>rbcL</i>	1200 à 1300	Hayden et al. (2003)
<i>rbcL</i> -RH1/ <i>rbcL</i> 590	<i>rbcL</i>	500 à 600	Hayden et al. (2003)
<i>tufA</i> -F/ <i>tufA</i> -R	<i>tufA</i>	800 à 900	Famà et al. (2002)
H <i>tufA</i> -F/H <i>tufA</i> -R	<i>tufA</i>	700 à 800	Famà et al. (2002)

Table S3: PCR programs used according to the marker amplified.

Thermocycling	Markers		
	<i>TufA</i>	<i>rbcL</i>	ITS
Initial denaturation	10 min.; 95°C	10 min.; 95°C	10 min.; 95°C
Cycles number	35		
Denaturation	1 min.; 95°C	1 min. 10 sec.; 94°C	1 min. 10 sec.; 94°C
Hybridation	1 min.; 52°C	50 sec.; 54°C	50 sec.; 54°C
Elongation	2 min.; 72°C	1 min. 30 sec.; 72°C	1 min. 30 sec.; 72°C
Final elongation	10 min.; 72°C	10 min.; 72°C	10 min.; 72°C

Table S4 : List of specimens from GenBank database included in our phylogenetic analyses, with voucher names, collection localities, sequence accession numbers for ITS, *rbcL* and *tufA* genes, and reference studies.

Species	Voucher	Locality	<i>tufA</i>	<i>rbcL</i>	ITS	Reference	Notes
<i>Ulva adhaerens</i>	TNS,AL,183435	Japan, Kanagawa, Sajima, Tenjin-jima		AB894328	AB894334	Matsumoto & Shimada, 2015	type material
<i>Ulva adhaerens</i>	MSK-GA00075	Korea, Seogwipo, Munseom	MT978122	MT978113		Lee et al., 2020	
<i>Ulva aragoensis</i>	HER_2_TC	Israel	MG976875	MG704815		Krupnik et al., 2018	
<i>Ulva australis</i>	S,A2025	Port Adelaide, Australia		LC331300	LC331301	Hanyuda & Kawai, 2018	Lame
<i>Ulva australis</i>	LAK45	Port Lincoln, South Australia	JN029262			Kirkendale et al., 2011	
<i>Ulva australis</i>	LK29	Flinders, Victoria, Australia		EU933953	EU933980	Kraft et al., 2008	
<i>Ulva arasaki</i>	SAP_095062	Japan, Miyagi, Shizugawa		AB097621	AB097650	Shimada et al., 2003	
<i>Ulva arasaki</i>		Japan, Ibaraki, Japan	AB561079			Matsumoto et al., 2011	
<i>Ulva brisbanensis</i>	LK-014	Brisbane, QLD, Australia		EU933945	EU933972	Kraft et al., 2008	
<i>Ulva californica</i>	GWS021868	SA, California, Jade Cove	KM255023			Saunders, 2014	
<i>Ulva californica</i>	WTU344798, isolate Ucal99-26	USA, Casa Cove, La Jolla, CA		AY255866	AY260560	Hayden et al., 2003	
<i>Ulva chaugulii</i>	CAL/ALG./029	India			KT429218	Kazi and Kavale, 2015	Holotype material
<i>Ulva chaugulii</i>	ARC-U-303A	India, Vayangani		KP710829		Kazi & Kavale, 2015	
<i>Ulva clathrata</i>	623	Ireland		AY255862		Hayden et al., 2003	
<i>Ulva clathrata</i>	EclaGL	Greenland, Disko Island			AF153492	Malta et al., 1999	
<i>Ulva clathratioides</i>	LK027	Point Lonsdale, Victoria, Australia		EU933951	EU933978	Kraft et al., 2008	
<i>Ulva clathratioides</i>	GWS015137	Australia, Tasmania, Snug Park	JN029343			Kirkendale et al., 2011	
<i>Ulva compressa</i>	Sample NO. 528	British Isles			AF035348	Blomster et al., 1998	
<i>Ulva compressa</i>		Portaferry, Strangford Lough, N. Ireland		AY255859		Hayden et al., 2003	
<i>Ulva compressa</i>	S_79	Germany, Schleswig-Holstein, Wackerballig	MF979661			Steinhagen et al., 2019	
<i>Ulva conglobota</i>	A-588132/3, specimen 1	Yokohama, Goto or Amakusa		MT815850		Hughey et al., 2020	type material
<i>Ulva curvata</i>		Lewes, DE, USA		AF189071		Sherwood et al., 2000	
<i>Ulva expansa</i>	UC98481	Monterey, California	MH731007	MH731009	MH730160	Hughey et al., 2018	Type material
<i>Ulva fenestrata</i>	UBC A57002 LE	Kamchatka Peninsula, Siberia, Russia	MK456404	MK456393		Hughey et al., 2019	type material
<i>Ulva flexuosa</i>	Isolate VE7	Adriatic sea, Italy	HE600177	HE600158		Wolf et al., 2008	Filamenteuse
<i>Ulva flexuosa</i>	SAP_095059	Greece, Tessaaloniki			AB097647	Shimada et al., 2002	
<i>Ulva gigantea</i>	U44	France	MT160698	MT160588		Fort et al., 2020	

<i>Ulva howensis</i>	GWS023394	Australia, New South Wales, Far Rocks, Signal Point, Lord Howe	JN029312	JN082216		Kirkendale et al., 2011	
<i>Ulva iliohaha</i>	ARS08535	Hawaii	KT932976	KT932995	KT881223	Spalding et al., 2015	type material
<i>Ulva intestinalis</i>	BR1b	United Kingdom	EF595335		EF595357	Rinkel et al., 2012	
<i>Ulva intestinalis</i>	LK-008	Australia, Cape Otway, VIC		EU933939	EU933966	Kraft et al., 2008	
<i>Ulva lactuca</i>	NC01-331	IDP, NC		MK456402		Hughey et al., 2019	Lectotype specimen of <i>Ulva lobata</i> (Kutzing) Harvey = <i>Phycoseris lobata</i> (Kutzing 1847)
<i>Ulva lactuca</i>	L0054996	Chile	MH730972	MH730972		Hughey et al., 2019	
<i>Ulva lactuca</i>	TNS_AL_183430	Japan, Kanagawa, Sajima, Tenjin-jima		AB894323	AB894329	Matsumoto & Shimada, 2015	
<i>Ulva lactuca</i>	No 1275-24 5	Indo-Pacific		MK456395		Hughey et al., 2019	Holotype
<i>Ulva limnetica</i>	0-31	Japan, Fukui, Wakasa, Lake Suigetsu		AB830525	AB830513	Ogawa et al., 2013	
<i>Ulva linza</i>	SAP_102983 (ULKMM2)	Japan, Kochi, Murotsu, Port of Murotsu			AB299440	Cui et al., 2018	
<i>Ulva linza</i>	CAM1057	PortaFerry, Ireland,		MG704800		Krupnik et al., 2018	
<i>Ulva linza</i>	e029gw	United Kingdom, East Cornwall, Greenaway	EF595300		EF595474	Rinkel et al., 2012	
<i>Ulva meridionalis</i>	RH010	Japan, Okinawa, Ishigaki island, Todoroki River		AB598812		Horomito et al., 2011	type locality
<i>Ulva meridionalis</i>	UNA00071829, TM1	UsA, Cedar Point, AL	MT859761	MT882752	MT887240	Melton et al., 2020	
<i>Ulva ohiohilulu</i>	ARS07528	Hawaii, USA	KT932977		KT881224	Spalding et al., 2015	Holotype
<i>Ulva ohiohilulu</i>	ARS08539	Hawaii, USA		KT932996		Spalding et al., 2015	
<i>Ulva ohnoi</i>	SAP_095155	Japan, Kochi, Tosa		AB116040	AB116034	Hiraoka et al., 2004	Type material
<i>Ulva ohnoi</i>	KU-3321	Japan	AP018696			Suzuki et al., 2018	
<i>Ulva paradoxa</i>	E110	Norway			HM447562		
<i>Ulva paradoxa</i>	BRNM HY 141	Czech Republic		HM447565		Mares et al., 2010	
<i>Ulva paradoxa</i>	UNA00072559, TM637	Nags Head, NC, USA	MT859880		MT882777	Melton & Lopez-Bautista., 2020	
<i>Ulva partita</i>	SAP,114778	Japan, Kochi		LC021415	LC021416	Ichiara et al., 2015	
<i>Ulva pilifera</i>	CB164	Italy, Lake Ganzirri, Messina	KM212027			Bertuccio et al., 2014	
<i>Ulva pilifera</i>	BRNMHY1417	Czech Republic		HM447566	HM447579	Mares et al., 2010	
<i>Ulva prolifera</i>	D6	Denmark, offing of Lolland Island			LC381042	Hiraoka et al., unpublished	
<i>Ulva prolifera</i>	A00278, E24	Sweden			AJ012276	Leskinen & Pamilo, 1997	

<i>Ulva prolifera sbs qingdaoensis</i>	SAP-102944 (C455)	Japan, Iwate, Yamada		AB298316	Cui et al., 2018		
<i>Ulva pseudocurvata</i>	SY0501	Ythan Estuary, Aberdeenshire, Scotland		AJ234312	Tan et al., 1999		
<i>Ulva pseudocurvata</i>	EOO0685 1 2	Ythan Estuary, Aberdeenshire, Scotland		AY255869	Hayden et al., 2003		
<i>Ulva pseudoohnoi</i>	MSK-U41-JD-SM-D-03	Korea, Jeju, Jongdal	MT625015	MT624844	Lee et al., 2019		
<i>Ulva pseudorotundata</i>	U60	Ireland	MT160725	MT160615	Fort et al.,2020		
<i>Ulva pseudorotundata</i>	U.rot.4	France, Roscoff		MT078968	Coat et al., 1998		
<i>Ulva reticulata</i>	ETT-2	India, Ettikulam	MG963806	MG763222	Rani & Bast, 2018, unpublished		
<i>Ulva reticulata</i>	DBIS30	India, Tamil Nadu coast		MT478094	Nara et al., 2020		
<i>Ulva rigida</i>	URA10	Portugal, Aveiro		MN450427	MN444720	Califano & Wichard, 2020	
<i>Ulva rigida</i>	U72	Portugal	MT160738		Fort et al.,2020		
<i>Ulva shanxiensis</i>	SAS06035	China, Shanxi	KJ617036		Chen et al., 2015		
<i>Ulva spinulosa</i>	SAP,095078	Japan,Kochi, Fubenhama		AB097636	AB097666	Shimada et al., 2003	
<i>Ulva sp</i>	LK052	Australia, Brunei Bay, WA		EU933963	EU933991	Kraft et aL, 2008	
<i>Ulva sp4</i>		Japan		AB598814			
<i>Ulva sp1</i>	SAP_102991, TT006	Japan, Okinawa, Onna		AB298455		Shimada et al., 2008	
<i>Ulva sp2</i>	SAP_103000, NY140	Japan, Okinawa, Ishigaki		AB298459		Shimada et al., 2008	
<i>Ulva sp3</i>	HLM-Ch-UI-3001	Mexico, Baja California Sur		MH853472	MH828285	Melton & Lopez-Bautista, 2020	
<i>Ulva sp. JTM1</i>	UNA00071828	USA, Dauphin Island, AL		MT887255		Melton & Lopez-Bautista, 2020	
<i>Ulva sp. JTM2</i>	UNA00072089	USA, Aransas Pass, TX		MT887226		Melton & Lopez-Bautista, 2020	
<i>Ulva sp. JTM3</i>	UNA00072679	USA, Rudee Inlet, VA		MT887262		Melton & Lopez-Bautista, 2020	
<i>Ulva splitiana</i>	SY0301	Ythan Estuary, Aberdeenshire, Scotland		AJ234304		Tan et al., 1999	
<i>Ulva stenophylla</i>	GWS040576	USA, Washington	KX281910			Saunders, 2016	
<i>Ulva stenophylla</i>	WTU344829	Shilshole Bay, Seattle, King county, WA, USA		AY255874	AY260569	Hayden et al, 2003	
<i>Ulva stenoiphylloides</i>	LK-024	Australia, Point Lonsdale, VIC		EU933950	EU933977	Kraft et al., 2008	type material
<i>Ulva sublittoralis</i>	zk1-3	Japan,Kagoshima, Mage island offshore		AB741535		Ichihara et al., 2012	
<i>Ulva taeniata</i>	WTU344833, isolate Utae99-17	Perkins Park, Monterey, CA. USA		AY422566	AY422525	Hayden & Waaland, 2003	
<i>Ulva tanneri</i>	WTU344770	South Point Cabrillo, Monterey, CA, USA		AF499672	AY422519	Hayden & Waaland, 2003	
<i>Ulva tanneri</i>	GWS021582	USA, California, Sea Lion Point South, Point Lobos State Reserve	KM255002			Saunders, 2014	
<i>Ulva tepida</i>	HLM-Ch-UI-3004	Mexico, Baja California		MH853474	MH828288	Melton et al., 2018	
<i>Ulva tepida</i>	MIC_3_TA	Israël	MG976864	MG704820		Krupnik et al., 2018	

<i>Ulva torta</i>	S_138	Germany, Schleswig-Holstein, Nordstrand	MH538694			Steinhagen et al., 2019
<i>Ulva torta</i>	UNA00072517	USA, Surf City, NC	MT859834	MT887244		Melton et al., 2018
<i>Ulva torta</i>	UNA00072083	USA, Goose Island, TX	MT859827	MT882745		Melton et al., 2018
<i>Ulva uniseriata</i>	FB-2017, isolate DIA	India		KX668899		Bast, 2016 type material
Outgroups						
<i>Umbraulva amamiensis</i>	KU-d21923	Japan, Kagoshima, Yakushima	LC507140			Kawai et al., 2020
<i>Umbraulva amamiensis</i>	SAP_095052	Japan, Tokushima, Kaifu Australia, New South Wales, Yellow Rock, Lord Howe		AB097614	AB097640	Shimada et al., 2003
<i>Umbraulva dangeardii</i>	GWS023894		JN029359			Kirkendale et al., 2013
<i>Umbraulva dangeardii</i>	F11623	Carna, County Galway, Ireland			AJ234322	Tan et al., 1999
<i>Umbraulva dangeardii</i>	CAM_1062_Hayling	Israeli Mediterranean Sea		MG704796		Krupnik et al., 2018
<i>Umbraulva japonica</i>	SAP_095050	Japan, Shizuoka, Shimoda		AB097612	AB097638	Shimada et al., 2003
<i>Umbraulva japonica</i>	GWS018246	South Korea, Cheju-do, Rocky Reef at Lighthouse "Point" Piyangdo Island	JN029346			Kirkendale et al., 2011

Table S5 (first part) : Morpho-anatomical observations and measures of the specimens studied in each SSH.

# Vouchers	# NOU	# SSH	Storing	External morphology (Foliose/Tubular)	Extern aspect of filaments	Margin	Branching mode	Ø of branches (µm)	mean or delta	surface cells arrangement & shape
NC19-060	NOU218745	4	F	T	Large and thin filaments	NA	From the basal part	400, 250, 70	large: 100 to 500 thin: 20 to 50	polygonal with rounded edges; mostly in mozaic but aligned in some areas
LIF18-001	NOU218690	4	F	T	Large and thin filaments	NA	From the basal part; Basal filaments with rhizoids	100, 230		polygonal; wome with round edges; in mozaic
CHP11	NOU218801	4	E	T	Dense and short tuft composed of large and thin filaments	NA	From the basal part	100, 100, 50, 60; base (young ramifications): 20, 30		polygonal; some rectangular; aligned in thin branches, in mozaic in large filaments
NC07-645a	NOU218707	4	H	T	Large and thin filaments	NA	From the basal part	500		polygonal; in mozaic
NC19-049	NOU218742	3	F	T	Tuft lighth green of large filaments and other thinner	NA	From the basal part	340, 340 apex= 290 large flmt= 1,6mm	340 (290apex) to 830 (1600)	rectangular or polygonal
NC07-657	NOU218715	3	H	T	Tuft lighth green of large filaments and other thinner	NA	From the basal part	750, 830		polygonal
CP08-001	NOU218867	3	E	T	Tuft lighth green of large filaments (almost flat aspect) and other thinner	NA	From the basal part	720, 760		
PF-689	NOU218769	5	F	T	Large filaments with ramifications in thinner filaments	NA	along filaments; "node" of branching	1240, 550 thin branches = 120, 200, 200, 150	550 to 1240 (large flmts) 120 to 200 (branches)	square to polygonal; welded
CHP04	NOU218805	13	E	T	Flat and large filaments and other filaments thinner	NA	From the basal part; Nodes of branching on some filaments	960, 200, 300	gros:200 to 960 branches: 60 to 80	very welded; more or less aligned
CHP10	NOU218800	13	E	T	Flat and large filaments and other filaments thinner	NA	From the basal part; Nodes of branching on some filaments	570, 910, 660, thin flmts: 80,70,60		in mozaic

NC19-038	NOU218735	20	F	T	Large filaments with ramifications in thinner filaments; node of branching	NA	Branching along filaments; nodes of branching	370, 780		square, rectangular or some polygonal; aligned tightly
CHP6	NOU218807	12	E	T	Filaments of 3 different sizes; Large filaments with ramifications of thinner filaments	NA	from basal part; filaments without ramifications : monolinear	(1) 690, 660 (2) 240, 140	(1) 430 to 690 (2) 130 to 240 (3) 60 to 70	square to polygonal in mosaic disposal of chloroplast lattice-like
CHP12	NOU218802	12	E	T	Large filaments with ramifications of thinner filaments	NA	from basal part; filaments without ramifications : monolinear	(1) 690, 430, 650 (2) 160, 130, 150 (3) 60, 70		rectangular to polygonal; aligned or in mosaic
MOIN263	NOU218850	7	E	T	filaments thin, "sphagettis-like"	NA	Branching along the filaments	tapering 50-> 40; 120 -> 100 ramfct°: 20, 25, 15, 40	80 to 280 branches: 30, 50	rectangular; aligned
NC19-068	NOU218754	7	E	T	filaments thin, "sphagettis-like"	NA	young and short ramifications along filaments	280, 180, 220,		square to rectangular to polygonal with round edges; aligned or mozaic; disposal of chloroplast lattice-like
NC19-047	NOU218740	7	F	T	filaments thin, "sphagettis-like"	NA	Branching along the filaments	80, 90, 120, 110 ramif: 30, 40, 40		aligned in rows
NC19-005	NOU218720	7	F	T	filaments thin, "sphagettis-like"	NA	Branching along the filaments	80, 70, 90 ramif: 50, 30		polygonal, square or rectangular; aligned
NC19-034	NOU218733	8	F	T	Feather-like thallus, filaments very branched and even more at their apex	NA	Main axis with ramifications all along	350, 290	160 to 350 (main flmt) branches: 40 to 50	square to rectangular; aligned;

B27J2E	NOU218795	8	E	T	Feather-like thallus, filaments very branched and even more at their apex	NA	Main axis with ramifications all along	300, 240, branches: 50, 40		square to rectangular or some polygonal; aligned tightly
AI13SAI13E	NOU218789	19	E	T	Large filaments with thinner branched filaments	NA	Along filaments; feather like at the apex (numerous ramifications)	tapering: 140 -> 120, 720 -> 710 ramifications: 100, 70, 100, 120, 180 -> 60, 20, 10 (apex)	120 to 720 apex 10 to 60	square to rectangular; aligned;
NC19-074	NOU218760	11	E	T	Filaments very thin; "vermicelli-like" and entangled	NA	no branching	40, 40, 30, 30, 20	20 to 40	square to rectangular; aligned
NC20-24	NOU218856	14	E	T	Tuft of very branched filaments giving a tree aspect	NA	numerous branching along filaments (primary and secondary ramifications/ramification of first and second order); alternate branching	flmt I ^R : 40, 50 flmt II ^R tapering; 30, 20, 30, 20, 20 -> 10, 10, 15	flmt I ^R : 40 to 50	square, rectangular; aligned; one to 2 rows per filaments
NC04-857	NOU218704	14	H	T	Tuft of very branched filaments giving a tree aspect	NA	numerous branching along filaments (primary and secondary ramifications/ramification of first and second order); opposite and alternate branching ~"tree" aspect	flmt I ^R : 50 -> 40 flmt II ^R : 30, 30 flmt III ^R : 10, 15 Basal flmts: 340, 250	flmt II ^R : 20 to 30 flmt III ^R : 10 to 15	square to rectangular; aligned
NC19-051	NOU218744	21	F	T	Thin filaments "spaghetthis-like"	NA	branching from basis and along axes; Irregular branching; One large filaments; other thinner and uniseriate	large: 320 others: 80, 70, 40, 50		polygonal; aligned or in mosaic; chloroplasts in the centre
NC05-1289	NOU218235	10	H	F	Foliose	irregular; Spines at the margin	NA			polygonal cells; mosaic
NC05-309	NOU214119	9	H	F	Foliose	irregular; Spines at the margin	from the basal part			polygonal cells; round edges; in mosaic; chloroplasts lattice-like

IDP05-912	NOU218096	9	H	F	Foliose	irregular; Spines at the margin	from the basal part			cells more angular; in mosaic; chloroplast lattice-like
NC19-024	NOU218730	6	F	T	Thin filaments	NA	all along the filaments	20 to 70 (branches?)		rectangular or square (in the branches) aligned;
SAN1	NOU218838	16	E	T	Flat and large filaments with thinner and tubular filaments branching	NA	all along the filaments	430, 350, 650, 780 branches: 40, 60, 80, 100	350 to 780 ramif: 40 to 100	polygular; in mosaic or aligned in some areas
SABL2	NOU218834	16	E	T	Flat and large filaments with thinner and tubular filaments branching	NA	all along the filaments	480, 440 branches: 60, 40, 40		square to rectangular; aligned
NC20-10	NOU218822	17	E	T	Velvet appearance; Thin filaments entangled	NA	Branching all long the filaments; Spinous or hook-like ramifications	250, 260 branches: 40,40,30 -> 20 = tapering	150 to 260 20 to 40	most are square, some rectangular; aligned
CP20-001	NOU218811	18	E	T	Thin filaments with numerous ramifications	NA	all along the filaments; Ramifications uniseriate and spinous or straight and perpendicular at the base of filaments; fan aspect at the apex (numerous short ramification)	tapering: 160, 150, 130, 100, 50 branches: 40, 30	main: 100 to 320 (tapering) branches: 30 to 40	aligned
MOIN264	NOU218851	18	E	T	Tuft light green composed of very ramified filaments	NA	all along and around the filaments; Spinous or bent ramifications	260, 270, 40, 40, 30 (tapering)		rectangular; aligned
CP20-003	NOU218813	18	E	T	Tuft light green composed of very ramified filaments	NA	all along and around the filaments; alternate branching Spinous or bent ramifications	150, 140, 200, 40, 30, 40		rectangular; aligned; chloroplast in the center
NC19-067	NOU218753	18	F	T	Filaments with branches and smaller ramifications	NA	all along and around the filaments; Spinous or bent ramifications	280, 320		rectangular cells; aligned; chloroplast in the center

AI15SAI15 E	NOU218790	15	E	T	masse flmt très branchus	NA	branching all along; nodes of ramification on large filaments (constrictions point from which several thin filaments arise); accumulation of chloroplasts in the nodes; Branches uniseriate, then multiseriate; Apex feather-like	main filament tapering: 540 -> 110 branches: 50, 40, 50, 30 -> 12	main filament: 540 to 110 (tapering) branches: 12 to 50	polygonal; in mosaic
NC19-061	NOU218746	2		F	NA	Irregular; outgrowths of one or two cells at the margin	NA			rectangular to round; spaced
CP20-004	NOU218814	2		F	NA		NA			polygonal; in mosaic
PF692	NOU218772	1		F	NA	Irregular; Spines and outgrowth at the margin	NA			polygonal with round edges or round or oval cells; coherent cells sheet

Table S5 (following) : Morpho-anatomical observations and measures of the specimens studied in each SSH.

# Vouchers	# NOU	Cell dimensions in surface view (µm)	mean dim.; delta	# of pyrenoids	# layers in CT (1/2)	thickness CT if > 1 layer; or filament diameter (µm)	mean/ delta	Cells dimension (L* H; µm)	mean/ delta (L* H µm)	Species	
NC19-060	NOU218745	11*8, 12*10, 15*11, 15*10, 12*8, 12*11, 10*11, 11*12, 12*15, 18*15	large fitms: L: 12 to 18 l: 15 to 28 fins fitms: L: 9 to 15 l: 8 to 12	1-2	1	130, 80, 80, 140	800 to 140	20*20, 15*20, 20*20, 15*20, 20*20, 10*20, 15*20, 10*20, 15*20, 15*20	L: 15 to 20 H: 10 to 20	<i>U. tepida</i>	
LIF18-001	NOU218690	18*25, 11*22, 10*20, 10*20, 9*18, 10*21, 11*28, 10*18, 11*20			1						<i>U. tepida</i>
CHP11	NOU218801	10*11, 10*15, 10*13, 11*18, 11*20, 12*20		inconspicuous (1?)	1						<i>U. tepida</i>
NC07-645a	NOU218707	10*12, 10*11, 10*12			1						<i>U. tepida</i>
NC19-049	NOU218742	30*11, 20*8, 13*21, 12*21, 17*28, 20*11, 12*10, 9*20	L: 9 to 20 l: 12 to 30	1-3, 1-4	1	200, 720, 500, 390, 200, 250, 400	200 to 720	20*30, 20*30, 18*28, 18*30, 15*25, 15*25, 10*25, 10*25, 12*25	L: 10 to 20 H: 25 to 30	<i>U. meridionalis</i>	
NC07-657	NOU218715	20*15		inconspicuous	1					<i>U. meridionalis</i>	
CP08-001	NOU218867	20*20, 20*15, 21*11, 18*11, 15*21		1-4	1					<i>U. meridionalis</i>	
PF-689	NOU218769	21*20, 21*20, 22*5, 10*20, 18*22	L: 10 to 22 l: 5 to 22	1	1	330, 560	330 to 560	25*40, 30*25, 25*20, 15*20, 20*20, 25*20	L: 15 to 30 H: 20	<i>U. sp.</i> (singleton)	
CHP04	NOU218805	10*12, 11*15, 15*10, 15*20, 10*15, 10*11, 15*12, 12*10	L: 10 to 30 l: 10 to 28	1-2, 1-4	1	160, 190, 300, 250, 350	190 to 350	18*35, 15*30, 20*40, 12*35, 10*30, 10*30, 15*30, 20*30, 20*20, 18*10, 10*20, 10*10, 12*20,	L: 10 to 20 H: 20 to 40	<i>U. sp.</i>	
CHP10	NOU218800	20*10, 15*20, 22*20, 11*20, 21*10, 20*28, 15*20, 30*10, 20*15, 20*11		1-3 et > 4 (numerous l)	1	270				<i>U. sp.</i>	
NC19-038	NOU218735	20*24, 25*20, 20*20, 15*20, 20*20,	L: 15 to 25 l: 20 to 25	1-2	1		30, 27	20*20, 18*20, 30*30, 20*20, 25*20, 30*20, 30*25	L: 18 to 30 H: 20 to 30	<i>U. sp.</i> (singleton)	
CHP6	NOU218807	20*20, 20*20, 20*20, 18*20, 20*18, 10*15, 11*15, 20*15, 30*10, 12*18, 15*15	L: 10 to 30 l: 10 to 20	1-2	1	250, 350, 710, 750	250 to 750	20*20, 20*20, 28*20, 22*0, 25*20, 20*18, 20*15, 18*18, 30*18, 20*18	L: 18 to 30 H: 15 to 20	<i>U. sp.</i>	

CHP12	NOU218802	15*20, 10*20, 20*18, 15*20, 20*30, 30*11, 30*12, 28*15, 30*10, 28*11		1-3, 1-4	1					<i>U. sp.</i>
MOIN263	NOU218850	25*22, 22*21, 20*20, 15*20, 21*20, 25*20, 25*20, 28*20	L: 12 to 30 l: 10 to 20	1-2, 1-3, 1-4	1	70, 110, 130, 120	70 to 280	20*20, 12*20, 20*21, 10*20, 20*30, 25*25, 20*20, 20*20	L: 10 to 32 H: 15 to 30	<i>U. sp.</i>
NC19-068	NOU218754	20*20, 22*20, 12*12, 20*18, 18*20, 28*20, 20*15, 22*18, 20*20, 25*20		1-2	1	220, 200, 150, 240, 280, 150		20*18, 18*20, 25*15, 32*28, 25*20, 20*25, 30*25, 30*30, 20*22, 30*28		<i>U. sp.</i>
NC19-047	NOU218740	22*11, 20*15, 20*15, 30*11, 20*15, 20*20, 20*11, 20*15, 20*10, 25*20, 20*18, 20*20, 30*18, 20*15		1-3						<i>U. sp.</i>
NC19-005	NOU218720	25*18, 22*18, 20*15, 20*12, 20*20		1-2	1	80, 80	20*20, 20*20, 20*20, 30*20, 10*20, 15*20, 20*20, 20*20	<i>U. sp.</i>		
NC19-034	NOU218733	25*30, 22*20, 22*15, 21**11, 21*11, 30*21, 22*20, 25*20, 28*20, 30*30	L: 15 to 30 l: 11 to 30	1-3, 1-2	1	240, 160, 210		15*25, 30*20, 30*20, 20*20, 20*20, 20*25, 20*25, 20*20, 20*20	L: 15 to 30 H: 20 to 25	<i>U. sp.</i>
B27J2E	NOU218795	15*30, 18*30, 20*20, 25*30, 18*20		1-2						<i>U. sp.</i>
AI13SAI13E	NOU218789	20*20, 15*30, 25*20, 30*20, 22*25, 25*25, 12*22, 22*20, 20**20, 15*28, 22*20	L: 15 to 30 l: 20 to 30	1-2, 1-3 (with a circle in the centre)	1	250, 250, 170	170 to 250	20*18, 25*20, 28*20, 30*30, 28*18	L: 20 to 30 H: 18 to 30	<i>U. sp.</i> (singleton)
NC19-074	NOU218760	10*15, 10*18, 11*18, 12*15, 11*12, 10*11, 10*10, 8*11, 8*10	L: 8 to 12 l: 10 to 18	1-2, 1-3, 1-4	1	40, 30, 30, 20	20 to 40	18*10, 15*10, 18*10, 18*10	L: 15 to 18 H: 10	<i>U. sp.</i>
NC20-24	NOU218856	20*20, 30*15, 25*20, 30*20, 32*25, 22*18, 25*18, 30*20, 20*20, 18*18	L: 10 to 32 l: 12 to 20	1-2, 1-3	1	50, 70, 80, 75, 40, 30, 30, 40, 25, 35	30-80 up to 340	20*20, 20*20, 20*20, 20*20, 20*20	L: 12 to 20 H: 20	<i>U. sp. cf. polyclada</i>

NC04-857	NOU218704	10*20, 20*12, 15*15, 22*18, 12*20, 18*20		1-2	1	340, 250		20*20, 12*20, 15*20, 12*20, 20*20, 20*20		<i>U. sp. cf. U. polyclada</i>	
NC19-051	NOU218744	gros: 11*25, 15*25, 30*20, 30*12, 30*10, autres: 20*8, 18*21, 20*20, 25*22	L: 11 to 30 l: 8 to 25	1 ou 1-2	1	80, 60		20*20, 20*20, 30*20, 30*20, 20*20, 25*15, 15*15	L: 22 to 30 H: 20	<i>U. sp.</i> (singleton)	
NC05-1289	NOU218235	1521, 12*30, 11*20, 20*21, 15*21		1-3, 1-4	2	60, 60		18*12, 20*15, 20*18, 18*15			
NC05-309	NOU214119	19*22, 20*29, 20*30, 18*20, 20*30,	L: 10 to 30 l: (8,11)15 to 30	1-2, 1-3	2	70, 60		20*22, 18*25, 20*20, 21*30,, 20*28, 20*30, 22*30, 25*30, 20*30	L: 18 to 25 H: 20 to 30	<i>U. taeniata</i>	
IDP05-912	NOU218096	20*20, 22*20, 30*15, 15*8, 10*11		1-2	2					<i>U. taeniata</i>	
NC19-024	NOU218730		10 to 15 10 to 30		1	120		22*20, 22*20, 30*20, 20*20, 22*20, 25*20	L: 20 to 25 H: 20		
SAN1	NOU218838	20*10, 21*12, 10*12, 12*11, 20*11, 20*18, 12*12, 12*15, 18*20, 20*20	L: 10 to 21 l: 10 to 20	1-3, 1-4	1	270, 100, 100	70 to 400	15*20, 18*20, 12*20, 18*20, 20*22, 10*20, 10*20, 10*20, 15*20	L: 10 to 20 H: 20 to 22	<i>U. sp.</i>	
SABL2	NOU218834	20*18, 20*15, 20*10, 20*20, 20*18		1-3, 1-4	1	400, 230, 120, 70, 230, 220		11*20, 18*20, 20*22, 18*22, 18*20, 20*20, 15*20, 20*20		<i>U. sp.</i>	
NC20-10	NOU218822	25*30, 22*31, 30*30, 18*20, 15*20, 20*30, 22*30, 40*20, 30*20, 30*20	L: 15 to 40 l: 20 to 30	1-2	1	180, 150, 150, 170, 220, 200		15*20, 20*20, 20*20, 15*20, 20*20, 25*20, 30**25, 15*15	L: 15 to 30 H: 15 to 25	<i>U. sp.</i> ("Herbe à picots")	
CP20-001	NOU218811	30*30, 30*30, 25*30, 30*25, 30*40	L: 25 to 50 l: 20 to 50							<i>U. sp.</i>	
MOIN264	NOU218851	40*28, 40*25, 40*30, 38*30, 38**32, 25*40, 25*50, 30*35, 28*50		1-3, 1-4							<i>U. sp.</i>
CP20-003	NOU218813	45*20, 40*20, 50*20, 40*20, 30*25, 50*35, 30*40, 20*30		1-2	1	110, 140, 120, 190, 210		20*28, 20*30, 15*30, 30*28, 20*28, 22*20, 32*30, 20*20, 20*20, 20*20	L: 15 to 30 H: 20 to 30	<i>U. sp.</i>	
NC19-067	NOU218753	35*40, 30*50, 30*40, 60*30, 30*38, 40*35									<i>U. sp.</i>
AI15SAI15E	NOU218790	30*25, 30*25, 40*28, 35*30, 40*28, 25*30, 30*30, 30*25, 40*25	L: 30 to 40 l: 25 to 40	1-2	1	30, 40, 35, 12		40*30, 20*30, 40*35, 40*38, 50*40, 440*30, 40*35, 35*30	L: 20 to 50 H: 30 to 40	<i>U. sp.</i> (singleton)	
NC19-061	NOU218746	8*10, 10*10, 8*8, 8*10, 10*11, 10*15	L: 8 to 10 l: 8 to 15	1-3	2	100, 100 (cell-wall: 10, 20		allongées: htr: 35, 30 largeur: 15, 12, 10, 12, 15	L: 10 to 15	<i>U. ohnoi</i>	

									H: 30 to 35	
CP20-004	NOU218814			1-3, 1-4 (coarse)		50 (cell-wall: 10)		15*20, 20*15, 20*20, 10*20, 12*20, 10*20, 10*20, 15*20	L:10 to 20	<i>U. ohnoi</i>
PF692	NOU218772	10*20, 10*20, 20*10, 20*10, 25*20	L: 10 to 25 l: 10 to 20	1-2		40, 45, 50		H: 20,22 L: 12, 15, 10, 20, 15, 12	L: 10 to 20 H: 20 to 22	<i>U. lactuca</i>

Table S6 : Decision aid to ascertain whether our tubular specimens correspond to new species or not: presence or absence of genetic data (0/1); if not, diagnosis found (x) and comparison of morphological characters; if not and in the last case, consultation of herbarium (x) to check external morphology. Arguments justifying our decision are also reported. NA: not attributable.

Species	Date description	GenBank sequence	Diagnosis available	Herbarium image consulted	External morphology	Argument
<i>Ulva adhaerens</i>	2015	1			Foliose	NA
<i>Ulva anandii</i>	1993	0	x		Foliose	NA
<i>Ulva arasaki</i>	1969	1			Foliose	NA
<i>Ulva ardreana</i>	2013	0	x		Foliose	NA
<i>Ulva atroviridis</i>	1938	0	x		Foliose	NA
<i>Ulva australis</i>	1854	1			Foliose	NA
<i>Ulva beytentis</i>	1966	0	0	x	Foliose	NA
<i>Ulva brevistipita</i>	1956	0	x		Foliose	NA
<i>Ulva bulbosa</i>	1805	0	0	x	Foliose	NA
<i>Ulva californica</i>	1899	1			Foliose	NA
<i>Ulva chapmanii</i>	2021	0	x		Foliose	NA
<i>Ulva chaugulii</i>	2016	1			Foliose	NA
<i>Ulva conglobata</i>	1897	1			Foliose	NA
<i>Ulva costata</i>	1881	0	0	x	Foliose	NA
<i>Ulva covelongensis</i>	1969	0	x		Foliose	NA
<i>Ulva crassimembrana</i>	2003	0	x		Foliose	NA
<i>Ulva curvata</i>	1889	1			Foliose	NA
<i>Ulva dangeardii</i>	1959	0	x		Foliose	NA
<i>Ulva expansa</i>	1920	1			Foliose	NA
<i>Ulva fenestrata</i>	1840	1			Foliose	NA
<i>Ulva geminoidea</i>	1956	0	x		Foliose	NA
<i>Ulva gigantea</i>	1969	1			Foliose	NA
<i>Ulva grandis</i>	1977	0	x		Foliose	NA
<i>Ulva iliohaha</i>	2016	1			Foliose	NA
<i>Ulva lactuca</i> *	1753	1			Foliose	Corresponds to SSH1
<i>Ulva laingii</i>	1956	0	x		Foliose	NA
<i>Ulva limnetica</i>	2009	1			Foliose	NA
<i>Ulva linza</i>	1753	1			Foliose	NA
<i>Ulva linzoides</i>	2014	0	x		Foliose	NA
<i>Ulva maeotica</i>	2011	0	x		Foliose	NA
<i>Ulva nematoidea</i>	1828	0	x		Foliose	NA
<i>Ulva ohiohilulu</i>	2016	1			Foliose	NA
<i>Ulva ohnoi</i>	2004	1			Foliose	Corresponds to SSH2
<i>Ulva papenfussii</i>	1969	0	x		Foliose	NA
<i>Ulva parva</i>	1956	0	x		Foliose	NA
<i>Ulva phyllosa</i>	1960	0	x		Foliose	NA
<i>Ulva profunda</i>	1928	0	x		Foliose	NA
<i>Ulva pseudocurvata</i>	1981	1			Foliose	NA
<i>Ulva pseudohnoi</i>	2019	1			Foliose	NA
<i>Ulva pseudolinza</i>	2003	0	x		Foliose	NA
<i>Ulva pseudorotundata</i>	2014	1			Foliose	NA

<i>Ulva ranunculata</i>	2000	0	x		Foliose	NA
<i>Ulva reticulata</i>	1775	1			Foliose	NA
<i>Ulva rhacodes</i>	1960	0	x		Foliose	NA
<i>Ulva rigida</i>	1823	1			Foliose	NA
<i>Ulva saifullahii</i>	1993	0	x		Foliose	NA
<i>Ulva sorensenii</i>	1956	0	x		Foliose	NA
<i>Ulva spinulosa</i>	1936	1			Foliose	NA
<i>Ulva stenophylla</i>	1920	1			Foliose	NA
<i>Ulva stenophylloides</i>	2010	1			Foliose	NA
<i>Ulva sublittoralis</i>	1938	1			Foliose	NA
<i>Ulva taeniata</i>	1920	1			Foliose	Corresponds to SSH9
<i>Ulva tanneri</i>	2003	1			Foliose	NA
<i>Ulva quilonensis</i>	1995	0	x		Foliose	NA
<i>Ulva acanthophora</i>	2003	0	x		Tubular	thallus green, tubular, elongated, curved, wavy (or flexible), besieged by numerous curved spines; cell granules randomly distributed, diam 1/200-1/180" Long 4" and more; lat. 1/3- 1/2" SSH18 have filaments with curved spines but the rest of the description do not match.
<i>Ulva aragoënsis</i>	2018	1			Tubular	Genetically distinct
<i>Ulva brisbanensis</i>	2010	1			Tubular	Genetically distinct
<i>Ulva chaetomorphoides</i>	2003	0	x		Tubular	Tubular but ramifications rares, most often at the apices; 3 rows of cells; ramifications: 1 to 2 rows of cells; 2 pyrenoids, rarely 3 None of our specimens have rare ramifications; either numerous, or none
<i>Ulva clathrata</i>	1811	1			Tubular	Genetically distinct
<i>Ulva clathratioides</i>	2010	1			Tubular	Genetically distinct
<i>Ulva compressa</i>	1753	1			Tubular	Genetically distinct
<i>Ulva croatica</i>	2014	0	x		Tubular	Tubular; solitary filaments, unbranched or at the base, narrows branches Could have corresponded to SSH11 (unbranched) but filaments aren't solitary in these specimens, but arranged in tuft; All the other SSHs are branched
<i>Ulva cruciata</i>	2017	0	x		Tubular	Tubular; branching mostly a single series of cells ; monosiphonous ; rounded cells SSH 11 could have corresponded to "monosiphonous" but it is unbranched and its filaments are not

						composed of one serie of cells; SSH 18 has uniseriate ramifications but these latter are spinous, straight or bent and cells are not rounded; The other SSHs do not match
<i>Ulva flexuosa</i>	1803	1			Tubular	Genetically distinct
<i>Ulva gracillima</i>	2018	0	x		Tubular	Fresh water
<i>Ulva hookeriana</i>	2003	0	x		Tubular	Thallus dark green, compressed, flat, linear, ramified with reduce basis, regrouped into large subsets (1/3-1/2" wide), stooped or slightly erect branches None of our SSHs match the description (those composed of flat filaments are not dark green nor regrouped into large subsets)
<i>Ulva howensis</i>	2007	1			Tubular	Genetically distinct
<i>Ulva intestinalis</i>	1753	1			Tubular	Genetically distinct
<i>Ulva kraftiorum</i>	2015	1	x		Tubular	Genetically distinct
<i>Ulva kyllini</i>	2003	0	x		Tubular	Tubular; unbranched except on basal part à; Filaments 0.5-3mm; several rows of cells; 16-14 um Unbranched like SSH11 but filaments much wider (0,5; 3 mm vs 40,30 um); All other SSHs are branched
<i>Ulva meridionalis</i>	2011	1			Tubular	Corresponds to SSH3
<i>Ulva paradoxa</i>	1817	1			Tubular	Genetically distinct
<i>Ulva partita</i>	2015	1			Tubular	Genetically distinct
<i>Ulva pilifera</i>	2018	1			Tubular	Genetically distinct
<i>Ulva polyclada</i>	2007	0	x		Tubular	SSH 14 ressembles to U. polyclada but specimens do not form individual thalli and plastes have smooth margin with few pyrenoids instead of crenelate plastes with multiples pyrénoids in U. polyclada.
<i>Ulva prolifera</i>	1778	1			Tubular	Genetically distinct
<i>Ulva radiata</i>	2003	0	x		Tubular	cellulis intra stratum cuticulare conspicuum adparenter rotundatis, verticaliter elongatis obovatis. Not observed in our samples
<i>Ulva ralfsii</i>	1863	0	x		Tubular	unbranched, like SSH11 but flmt and cells sizes > those of SSH11
<i>Ulva shanxiensis</i>	2015	1			Tubular	Genetically distinct
<i>Ulva splitiana</i>	2014	1			Tubular	Genetically distinct
<i>Ulva tepida</i>	2014	1			Tubular	Corresponds to SSH4

<i>Ulva torta</i>	1842	1			Tubular	Genetically distinct
<i>Ulva uniseriata</i>	2019	1			Tubular	Genetically distinct
<i>Ulva intestinaloides</i>	1982	0	0			Informations needed
<i>Ulva patengensis</i>	1981	0	0			Informations needed

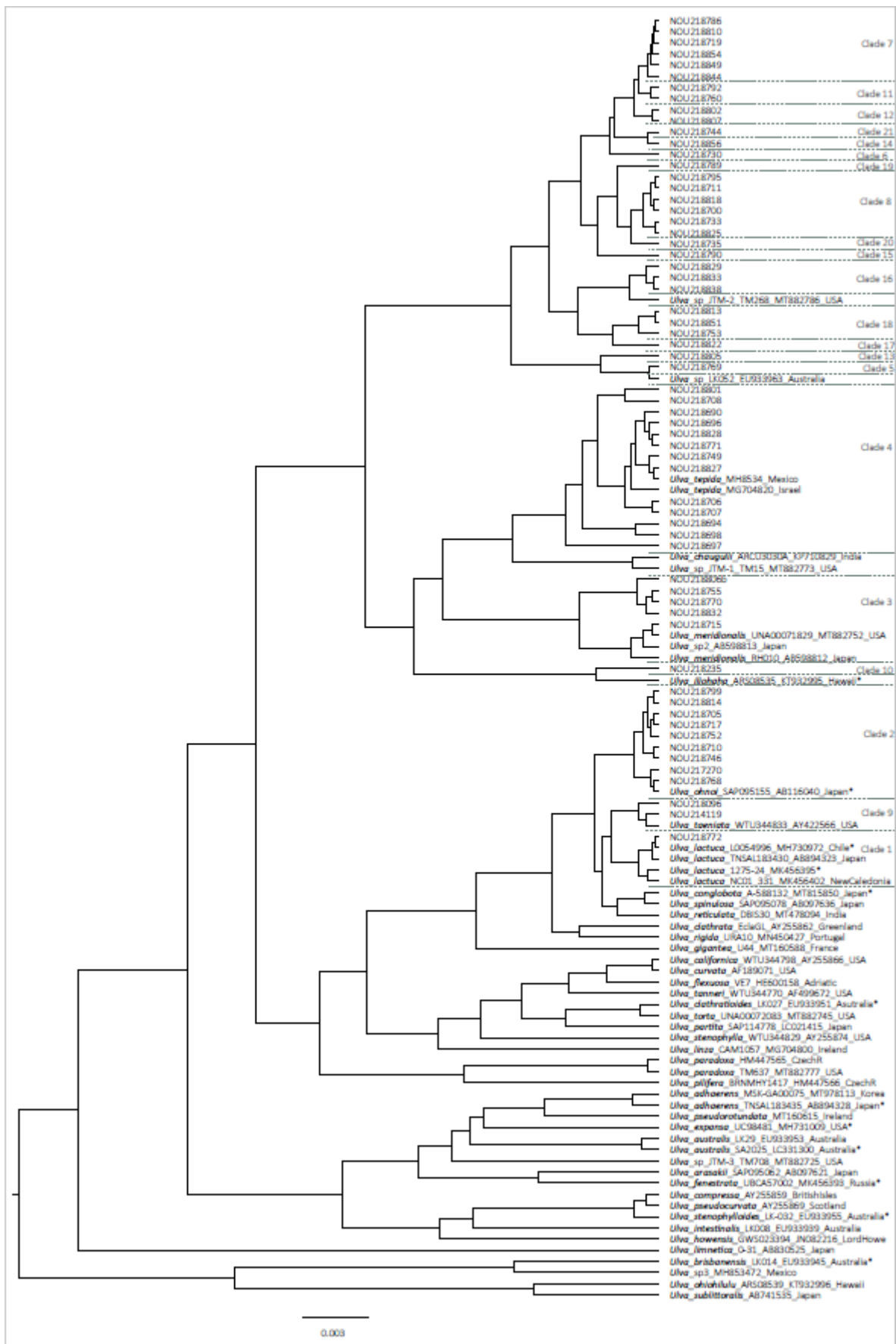
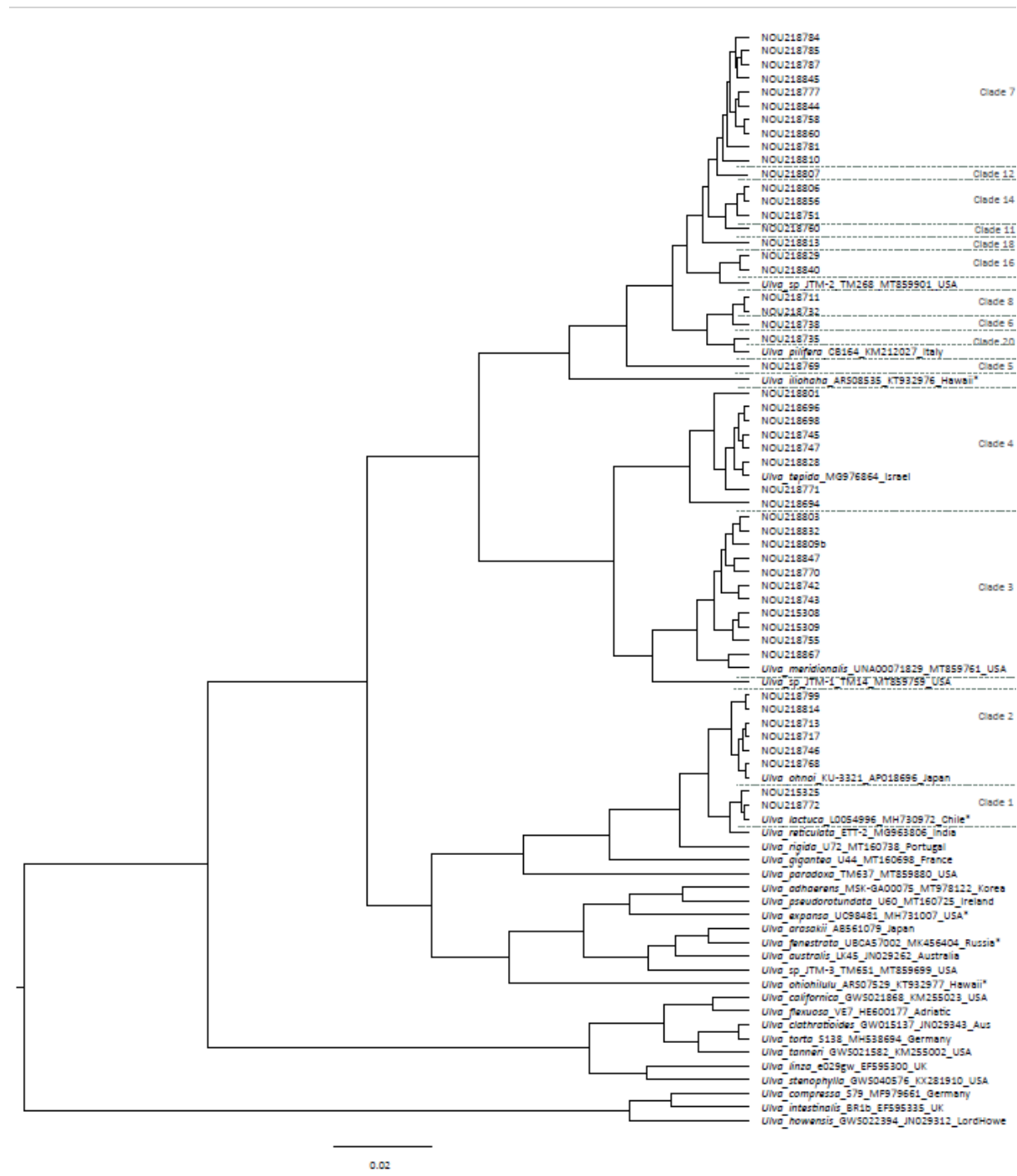


Figure S3: Maximum Clade Credibility Tree (MCCT) obtained from the BEAST analysis with the *tufA* dataset (unique haplotypes).



Author contributions

L. Lagourgue: treatment and analyses of molecular data (species delimitation, phylogeny), morphological analyses, taxonomic diagnosis, original concept and drafting of manuscript; S. Gobin: samples collection, acquisition of genetic sequences, morphological observations; M. Brisset; samples collection, acquisition of genetic sequences and editing manuscript; S.

Vandenberghe: acquisition of genetic sequences; C. Bonneville: acquisition of genetic sequences and editing manuscript; T. Jauffrais: samples collection and editing manuscript; S. Van Wynsberge: conception of the ELADE project, samples collection and editing manuscript. C.E. Payri: samples collection, morphological analyses, original concept and editing of manuscript.

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254

Figures

Figure 1: A-B: *In situ* photographs of tubular *Ulva* spp. cover at Poé-Gouaro-Déva (PGD), in February 2019 on coral colony (A) and in July 2019 on a sandy plain (B). **C:** Map of the sampling localities in New Caledonia around the Grande Terre, the Isle of Pines, and the Loyalty Islands. Scales bars: Fig.1A, 30 cm; Fig. 1B, 50 cm. Images rights: S. Andrefouët & S. Van Wynsberge.

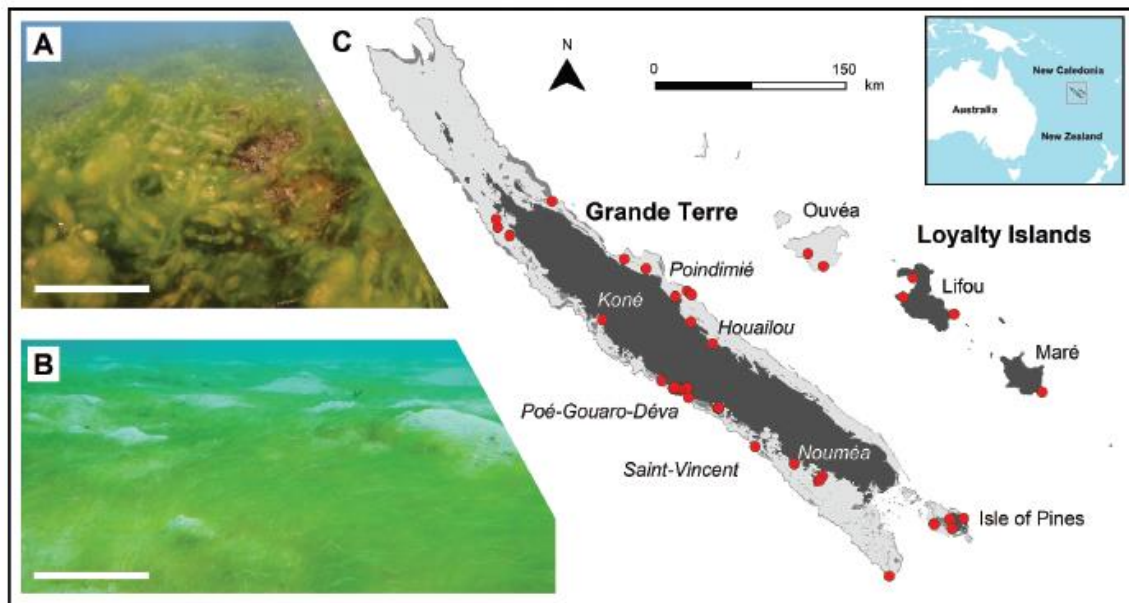


Figure 2: Results of the species delimitation methods reported on the multi-locus (ITS, *rbcL*, *tufA*) phylogeny of *Ulva* genus. Bootstraps and posterior probabilities (bs/PP) are indicated at tree nodes only if supported. Sequence names followed by an asterisk represent sequences from type material. In bold, *Ulva* species or SSHs known to be bloom-forming. At the right, species delimitation results for the methods GMYC, ASAP, and PTP on three markers (the number of PSHs resulting with each method is provided between brackets). Black bars indicate partitions retained as SSHs, while grey bars indicate different partition schemes not retained. Stripes indicate missing sequences. Species assignment and/or SSH number is provided on the right.

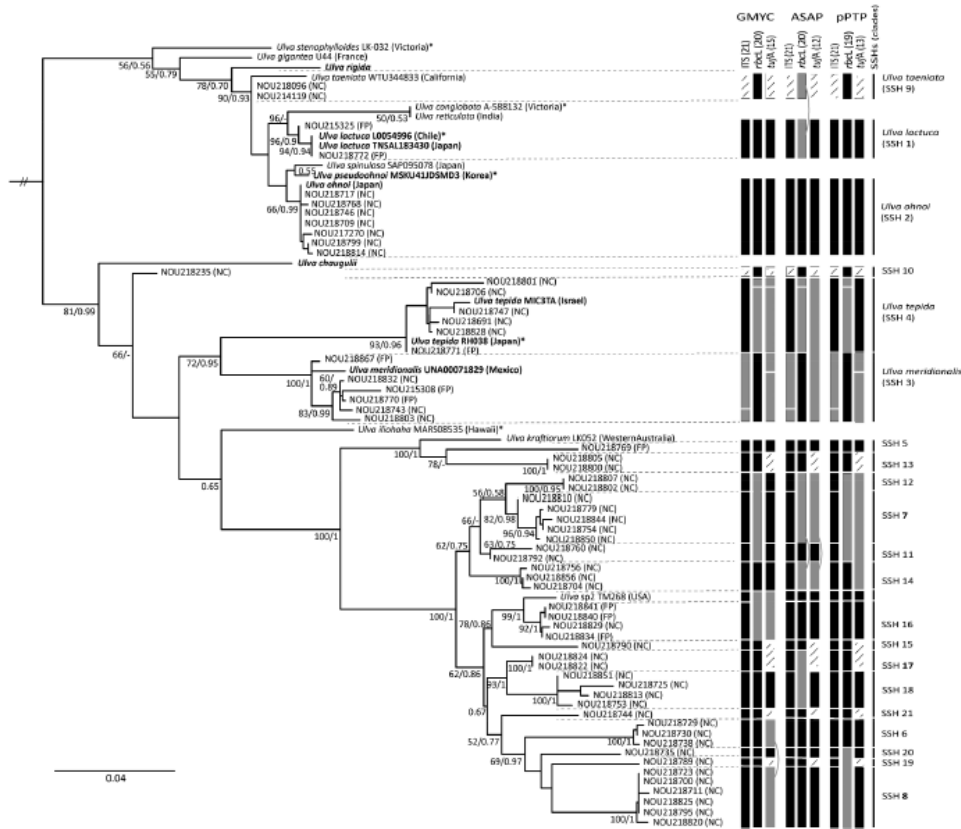


Figure 3: Multilocus phylogeny (ITS, *rbcL*, *tufA*) of *Ulva* genus. Bootstraps and posterior probabilities (bs/PP) are indicated at nodes only if supported. Sequence names followed by an asterisk represent sequences from type material. Bloom-forming *Ulva* species are in bold. On the right, dark green bars represent species with tropical and subtropical type locality and light blue ones indicate species with temperate type locality (or sampling locality for undescribed SSHs).

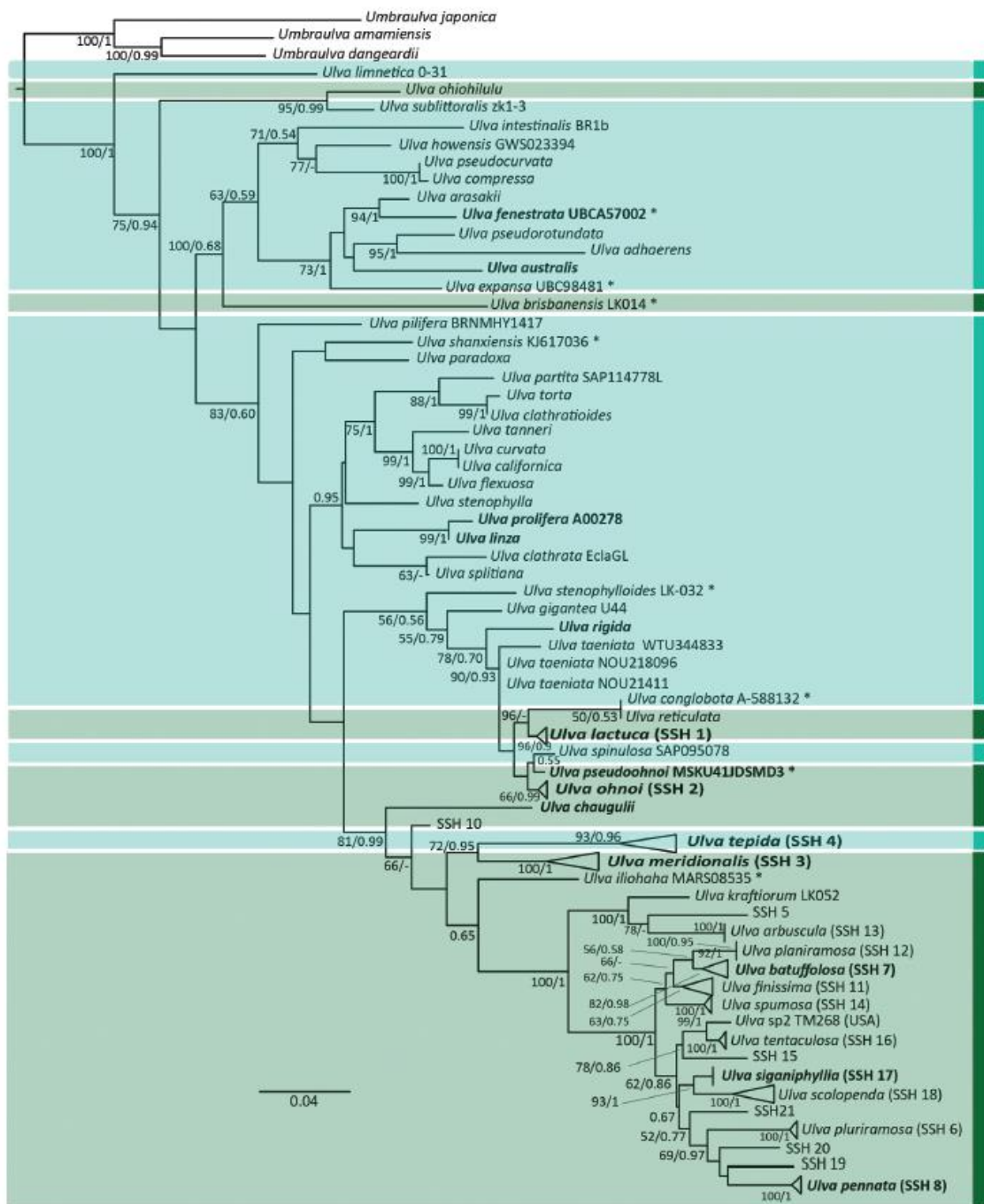


Figure 4-20: 4-12 *Ulva arbuscula*: **4:** External habit (NOU218805); **5:** Basal branching pattern (NOU218800); **6:** Node of branching, i.e. several branches originate at the same level on the filament (C: NOU218800); **7:** Young ramifications (NOU218805); **8-9:** Aligned to lezardous cells arrangement (E: NOU218805; F: NOU218800); **10-11:** Transversal sections: thin filament (10), large and flattened filament (11) (NOU218805); **12:** Pyrenoids (NOU218805); **12-20:** *Ulva pennata*: **13-16:** Feather-like thallus (13: NOU218727; 14: NOU218731; 15-16: NOU218732); **17:** Axes with numerous whorls of ramifications

(NOU218795); **18** : Aligned cells in surface view (NOU218733) ; **19** : 2-3 pyrenoids per cells (NOU218733) ; **20** : Transversal section of filament (NOU218733). Scales bars: Fig. 4, 6 mm; Fig. 5, 1.4 mm; Fig. 6, 250 μ m; Fig. 7, 200 μ m; Fig. 8, 60 μ m; Fig. 9, 50 μ m; Fig. 10, 44 μ m; Fig. 11, 87.5 μ m; Fig. 12, 22 μ m; Fig. 13-14, 1.75 mm; Fig. 15, 2 mm; Fig. 16, 800 μ m; Fig. 17, 390 μ m; Fig. 18, 83 μ m; Fig. 19, 23 μ m; Fig. 20, 50 μ m.

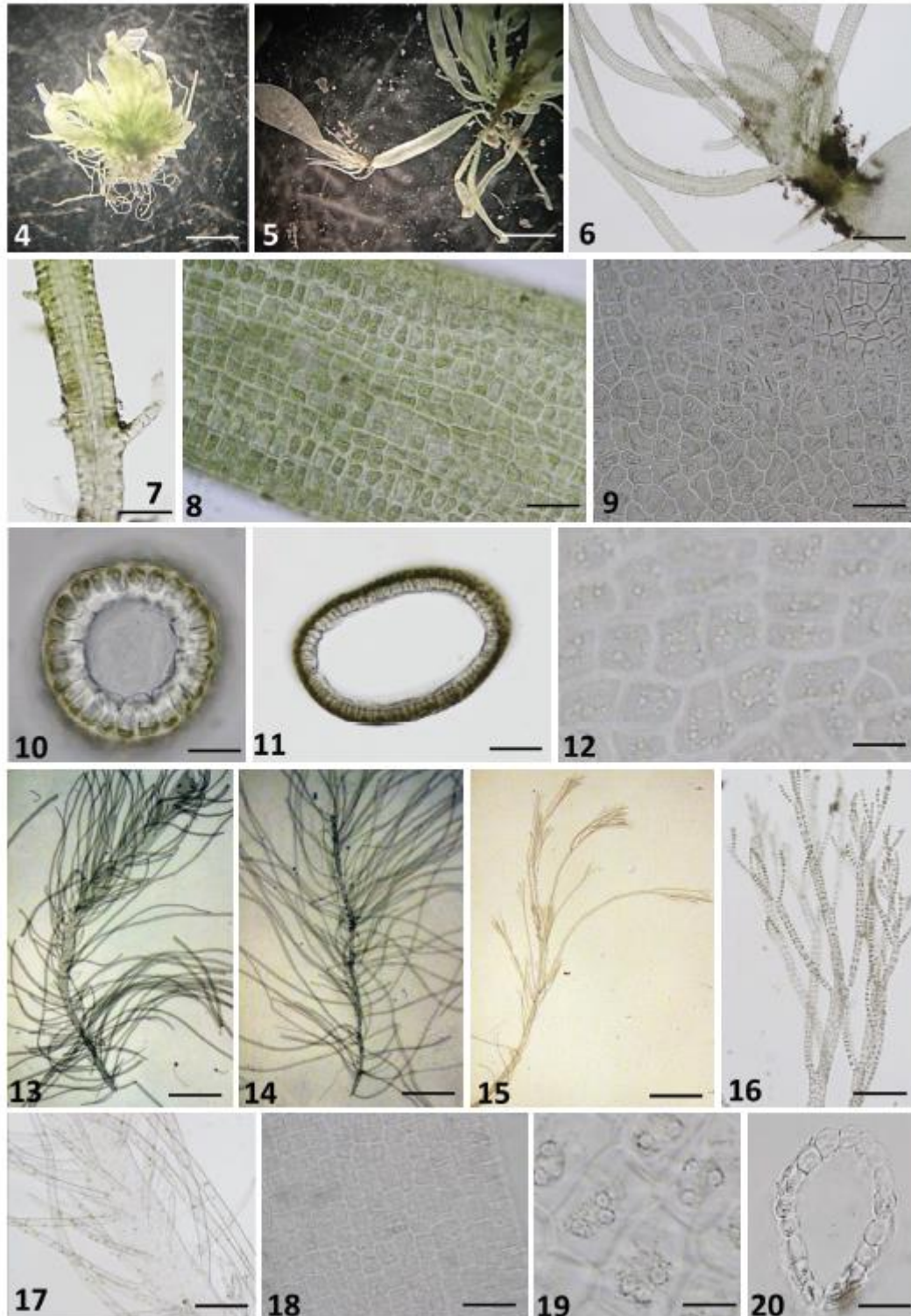


Figure 21-39 : 21-29: *Ulva planiramosa*: 21: External habit (NOU218807); **22:** Characteristic flat filaments (NOU218807); **23:** Basal branching (NOU218802) ; **24-25:** Filaments ramification and branching patterns (NOU218802); **26:** Surface view of cell alignment of square to rectangular shape; **27:** Cells with lattice-like chloroplast disposition (NOU218807); **28:** Transversal section (NOU218807); **29:** Pyrenoids (NOU218802); **30-39:** *Ulva batuffolosa* **30:** External habit (NOU218850), **31:** Filament's ramifications (NOU218850); **32:** Hook-shaped ramifications (NOU218850); **33:** Spinous ramification (NOU218850; **34:** Close-up ramification (NOU218754); **35:** Cell shape and arrangement (NOU218850); **36:** Pyrenoids (NOU218754); **37-39:** Transversal sections (37-38: NOU218798; 39: NOU218850). Scale bars: Fig. 21, 5 mm; Fig. 22, 2.3 mm; Fig. 23, 1.38 mm; Fig. 24, 345 μm ; Fig. 25, 243 μm ; Fig. 26, 160 μm ; Fig. 27, 50 μm ; Fig. 28, 180 μm ; Fig. 29, 17 μm ; Fig. 30, 800 μm ; Fig. 31, 180 μm ; Fig. 32, 267 μm ; Fig. 33, 63 μm ; Fig. 34, 122 μm ; Fig. 35, 67 μm ; Fig. 36, 33 μm ; Fig. 37-38, 63 μm ; Fig. 39, 33 μm .

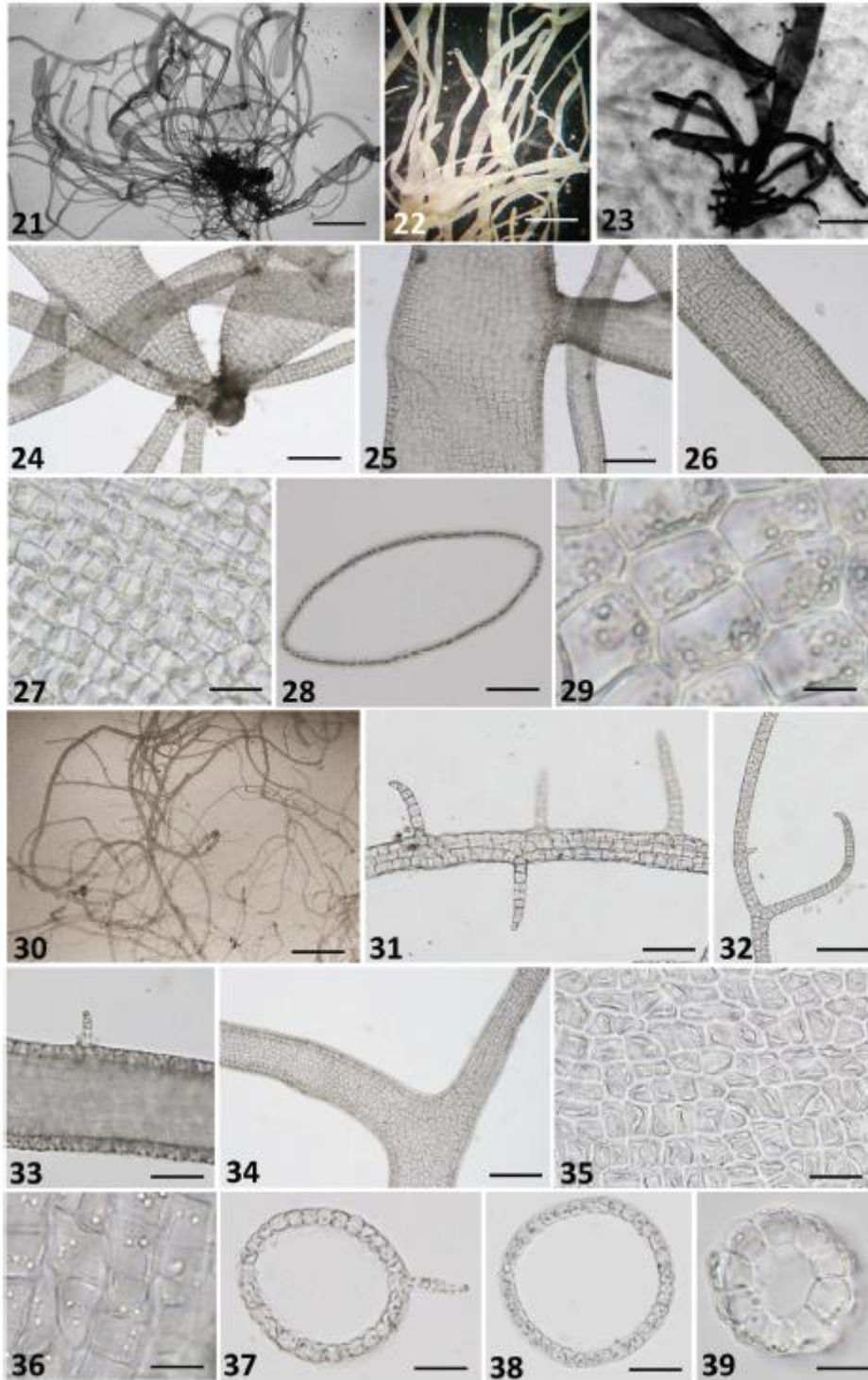


Figure 40-51: 40-45: *Ulva tentaculosa*: 40: External habit of filaments (NOU218829); 41: A large filament with thin ramifications (NOU218838); 42: Aligned cells in surface view (NOU218838); 43: Transversal section (NOU218838); 44-45: Pyrenoids (44: NOU218838; 45: NOU218834); 46-51: *Ulva finissima* (NOU218760): 46 : External habit of the thallus composed of entangled filaments ; 47: Unbranched filaments; 48: In surface view, cells are

aligned in 2 rows; **49-50** : Transversal section showing the 4 cells arranged around a small lumen **51**: 2-3 pyrenoids per cell. Scale bars: Fig. 40, 5 mm; Fig. 41, 330 μm ; Fig. 42, 67 μm ; Fig. 43, 100 μm ; Fig. 44, 25 μm ; Fig. 45, 40 μm ; Fig. 46, 800 μm ; Fig. 47, 133 μm ; Fig. 48, 15 μm ; Fig. 49, 15 μm ; Fig. 50, 13 μm ; Fig. 51, 15 μm .

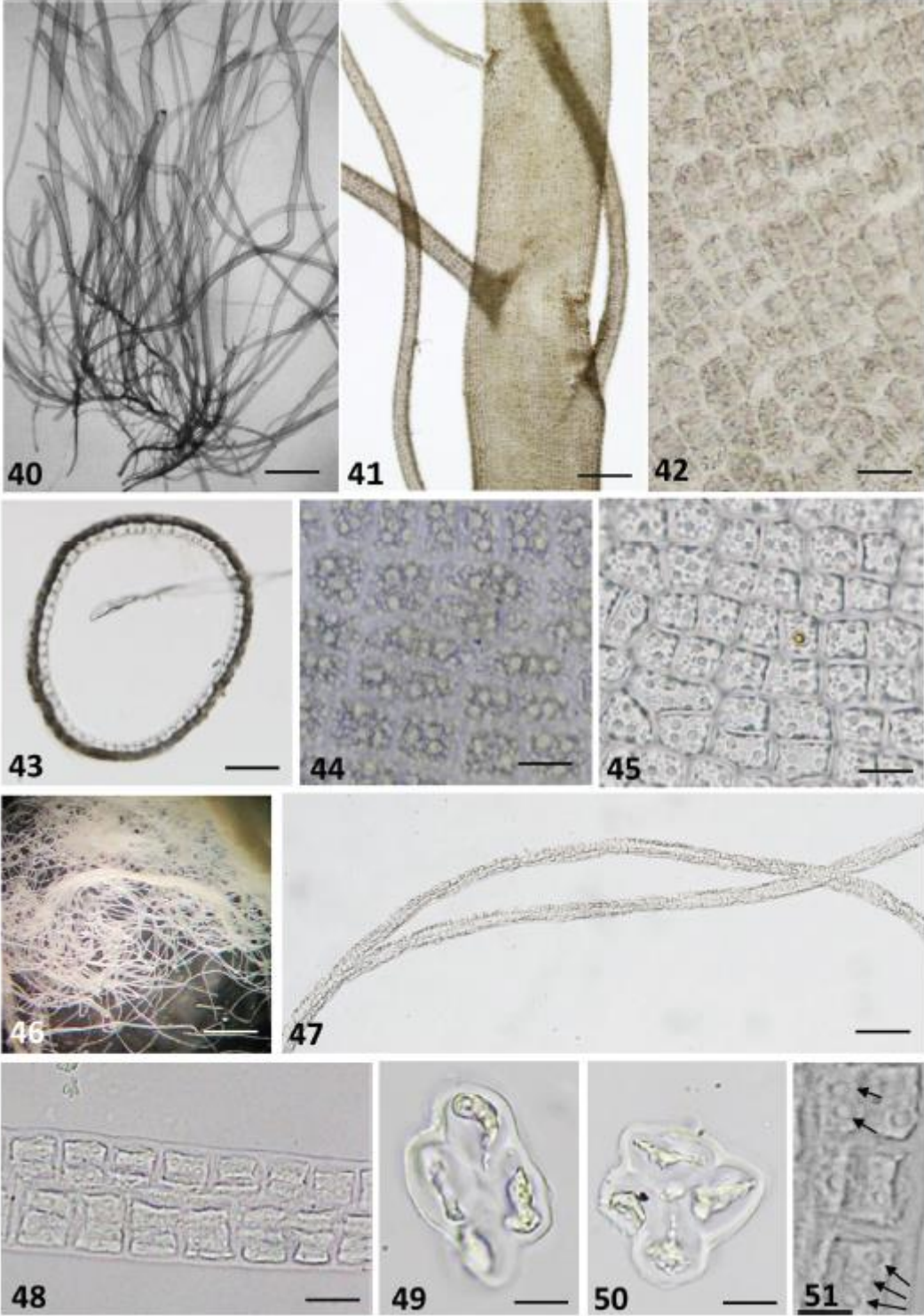


Figure 52-63: **52-57:** *Ulva pluriramosa* (NOU218730); **52:** Habit; **53:** Branched filaments; **54:** Uniseriate young ramification; **55:** Alignment of rectangular cells; **56:** 1-2 pyrenoids, **57:** transversal section; **58-63:** *Ulva scolopendra*. **58:** External habit (Herbarium specimen; NOU218811); **59:** Millipede-like filaments (NOU218846); **60:** Filament with short and spinous ramifications (NOU218811); **61:** Filament with bent ramifications (NOU218851); **62:** Rectangular and aligned cells with centrally concentrated chloroplast in surface view; **63:** Transversal view of filaments (NOU218813); Scale bars: Fig. 52, 4 mm; Fig. 53, 62,5 µm; Fig. 54, 30 µm; Fig. 55, 16.7 µm; Fig. 56, 25 µm; Fig. 57, 40 µm; Fig. 58, 2 cm; Fig. 59, 1.3 mm; Fig. 60, 215 µm; Fig. 61, 105 µm; Fig. 62, 20 µm; Fig. 63, 56 µm.

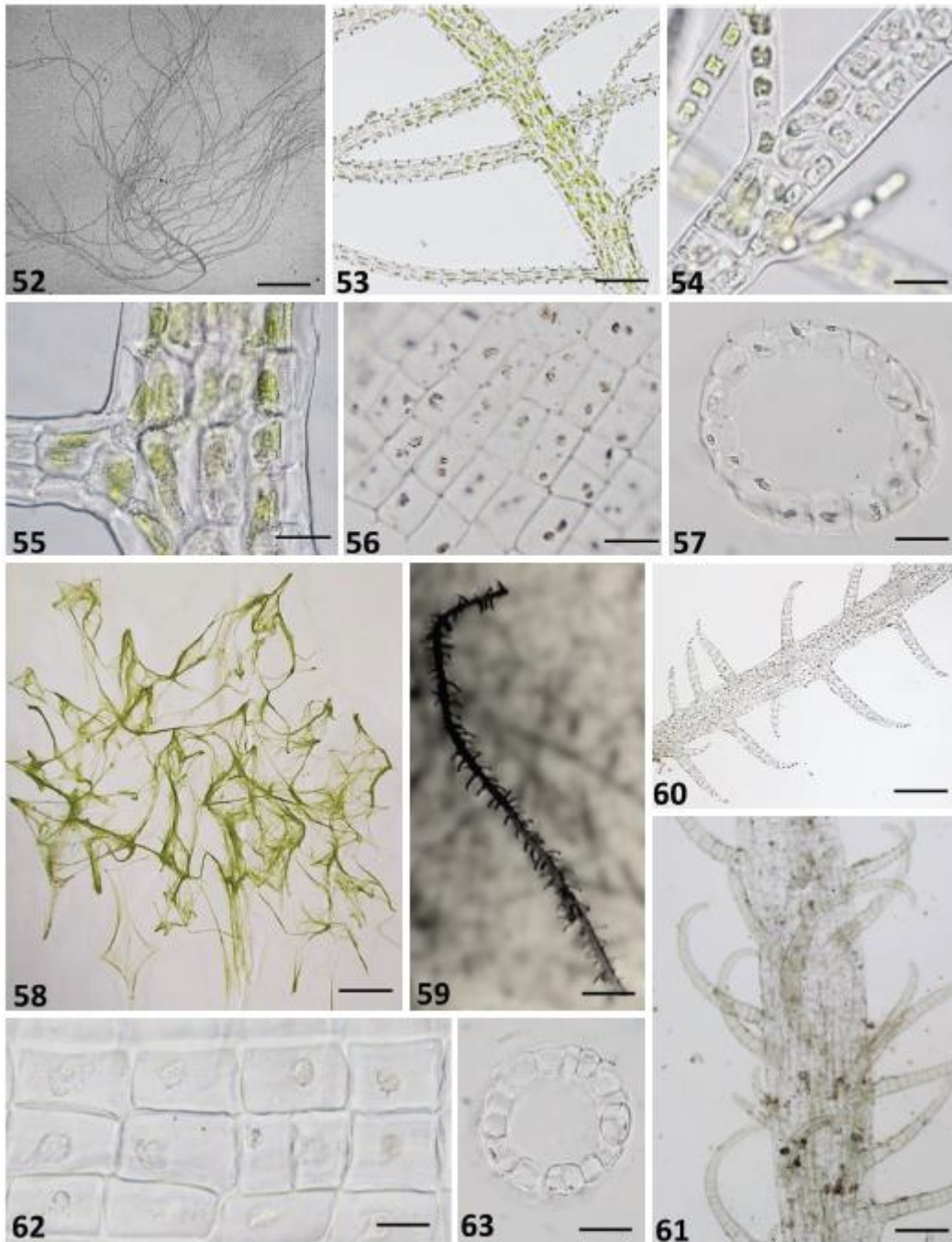


Figure 64-75: **64-68:** *Ulva siganiphyllia* (NOU218822): **64:** External habit (Herbarium specimen); **65:** Main filament with multiple ramifications; **66:** Hook-shaped, thin ramification; **67:** Pyrenoids; **68:** One layer of cells composing tubular filaments; **69-75:** *Ulva spumosa* **69:** External habit of the thallus composed of entangled and branched filaments (NOU218856) ; **70-71:** Filaments branching to 1 and 2 orders (70: NOU218704; 71: NOU218856); **72:** Uniseriate ramification from two cell rows filament; **73:** 2 and 3 pyrenoids; **74-75:** Transversal section with cells arranged in one layer (72-75: NOU218856). Scales bars:

Fig. 64, 2.3 mm; Fig. 65, 117 μm ; Fig. 66, 167 μm ; Fig. 67, 19 μm ; Fig. 68, 55 μm ; Fig. 69, 1 mm; Fig. 70-71, 200 μm ; Fig. 72, 55.5 μm ; Fig. 73, 8 μm ; Fig. 74-75, 20 μm .

