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DNA analysis of the lectotype specimen
of *Ulva nematoidea* Bory (Ulvaceae, Chlorophyta)
determines its synonymy with *Ulva lactuca* L.

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DNA analysis of the lectotype specimen of *Ulva nematoidea* Bory (Ulvaceae, Chlorophyta) determines its synonymy with *Ulva lactuca* L.

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ABSTRACT

Ulva nematoidea Bory is a currently accepted species distributed in the south eastern Pacific Ocean from Mexico to Chile. Its identity however remains unknown because no DNA sequences have been obtained from the type specimen. To determine its identity and taxonomic status, we performed high-throughput sequencing on a fragment of the lectotype specimen of *U. nematoidea*. Genetic analyses of the *rbcL*, *tufA* and nuclear ITS DNA found that *U. nematoidea* is identical in sequence to *U. lactuca* L. These results indicate that *U. nematoidea* is a synonym of *U. lactuca* and further highlight the need for sequencing additional type specimens of *Ulva* L.

KEY WORDS

Ulvaceae,
DNA analysis,
new synonym.

RÉSUMÉ

L'analyse de l'ADN du spécimen lectotype d'Ulva nematoidea Bory (Ulvaceae, Chlorophyta) détermine sa synonymie avec Ulva lactuca L.

Ulva nematoidea Bory est une espèce actuellement acceptée répartie dans le sud-est de l'océan Pacifique, du Mexique au Chili. Son identité reste cependant inconnue car aucune séquence d'ADN n'a été obtenue à partir du spécimen type. Pour déterminer son identité et son statut taxonomique, nous avons effectué un séquençage à haut débit sur un fragment du spécimen lectotype d'*U. nematoidea*. Les analyses génétiques de l'ADN *rbcL*, *tufA* et ITS nucléaire ont révélé que *U. nematoidea* a une séquence identique à *U. lactuca* L. Ces résultats indiquent que *U. nematoidea* est un synonyme de *U. lactuca* et soulignent davantage la nécessité de séquencer des spécimens types supplémentaires d'*Ulva* L.

MOTS CLÉS

Ulvaceae,
analyse ADN,
synonyme nouveau.

INTRODUCTION

Ulva nematoidea Bory was described from specimens from Concepción, Chile collected by Dumont d'Urville while aboard *La Coquille* on his “voyage autour du monde” in 1822-1825 (Bory 1828) (Fig. 1). The species was said to be elegant and to have lacinate fronds that were simple, elongate, and undulate. Bory (1828) noted that *U. nematoidea* closely resembled *U. fasciata* Delile, but concluded that the latter was slightly more forked and a little less wavy. Since its proposal by Bory, the taxonomy of *U. nematoidea* has been a matter of debate. The name was considered a synonym of *U. lactuca* L. or *U. fasciata* by some earlier workers (Montagne 1839; Kützinger 1849; Agardh 1883; De Toni 1889), but was accepted as a distinct species based on morpho-anatomical examination by later phycologists (Wynne 2002; Pedroche *et al.* 2005; Norris 2010). *Ulva nematoidea* currently includes the heterotypic synonym *U. costata* (M.Howe) Hollenberg *nomen illegitimum* (basonym: *U. fasciata* f. *costata* M.Howe), with a type locality of the Chincha Islands, Peru. *Ulva costata* (M.Howe) Hollenberg is a later homonym of *U. costata* Wollny (1881), with a type locality of Helgoland. The accepted distribution of *U. nematoidea* is Mexico (Pedroche *et al.* 2005; Norris 2010; Norris *et al.* 2017), Peru (Dawson *et al.* 1964; Ávila-Peltroche & Padilla-Vallejos 2020), and Chile (Santelices 1989; Ramírez & Santelices 1991). The lectotype of *U. nematoidea*, PC0042814 (Fig. 1), was designated by Wynne (2002). On the type sheet, in Bory's hand, is written “*Ulva multifida* Bory Côtes du Chili à la Concepcion rapportés par Durville”. Wynne (2002) mentioned the possibility that Bory recognized that his manuscript name, “*Ulva multifida* Bory” already had been published as *Ulva multifida* J.E.Smith (1808), but that name is illegitimate because it is a later homonym of *Ulva multifida* Turner (1801), the basonym of *Cutleria multifida* Greville (1830).

Recently, DNA sequencing of numerous type specimens of *Ulva* by Hughey *et al.* (2018, 2019, 2021a, b) has shown that most morpho-anatomical studies failed to accurately identify species of *Ulva*. To date, DNA from the type collections of *U. nematoidea* have not been analyzed, and attempts to sequence DNA from recent field collected specimens morpho-anatomically identified as *U. nematoidea* were unsuccessful (Chávez-Sánchez *et al.* 2019). Thus, we performed high-throughput sequencing on the lectotype specimen of *U. nematoidea* to determine the correct application of the name.

MATERIAL AND METHODS

DNA from the lectotype specimen of *U. nematoidea* was extracted following the protocol of Hughey *et al.* (2019) and the precautionary guidelines for analyzing herbarium specimens outlined by Hughey & Gabrielson (2012). The 150 bp PE Illumina library was constructed using the



FIG. 1. — Lectotype specimen of *Ulva nematoidea* Bory (PC0042814) from Concepción, Chile. Scale bar: 2 cm.

KAPA HyperPrep Kit (Roche, Basel, Switzerland) and sequenced by Quick Biology Inc. (Pasadena, California, United States). The data were trimmed using the Trim Adapters and Trim Low Quality default settings with the BBDuk plugin in Geneious Prime version 2019.1.3 (Biomatters Limited, Auckland, New Zealand). The trimmed reads were mapped to the complete chloroplast genome of *U. lactuca* (GenBank accession number: MH730972) and to an internal transcribed spacer 1 and 2 *U. lactuca* sequence (ITS, GenBank accession number: MT887233) using the Map to Reference function with the default settings (Medium-Low Sensitivity/Fast, iterate up to five times) in Geneious Prime to obtain the *rbcL*, *tufA*, and ITS sequences of *U. nematoidea*. The *U. nematoidea* *rbcL* sequence was aligned to representative *Ulva* sequences (Table 1)

TABLE 1. — Information for GenBank sequences used in the *rbcL* phylogenetic analysis of *Ulva nematoidea* Bory.

GenBank name	Currently recognized name	Specimen voucher/ sample code	Collection information	<i>rbcL</i> GenBank accessions	Source
<i>Enteromorpha compressa</i>	<i>Ulva compressa</i> L.	Not stated	Portaferry, Strangford Lough, Ireland	AY255859	Hayden & Waaland 2004
<i>Enteromorpha procera</i>	<i>Ulva procera</i> (K.Ahlner) H.S.Hayden, Blomster, Maggs, P.C.Silva, Stanhope & Waaland	Not stated	Not stated	AY255863	Hayden <i>et al.</i> 2003
<i>Gemina letterstedtioidea</i>	<i>Gemina letterstedtioidea</i> V.J.Chapman	WELT A027326	Bollons I., Antipodes Islands, New Zealand	EF110069	Heesch <i>et al.</i> 2009
<i>Percursaria percursa</i>	<i>Percursaria percursa</i> (C.Agardh) Rosenv.	UWCC MA230	Not stated	AF499674	Hayden & Waaland 2002
<i>Ulva adhaerens</i>	<i>Ulva adhaerens</i> Matsumoto & S.Shimada	TNS:AL:183435	Kanagawa, Sajima, Tenjin-jima, Japan	AB894328	Matsumoto & Shimada 2015
<i>Ulva aragoensis</i>	<i>Ulva aragoensis</i> (Bliding) Maggs	HER 2 TC	Herzliya, Israel	MG704815	Krupnik <i>et al.</i> 2018
<i>Ulva arasakii</i>	<i>Ulva arasakii</i> Chihara	SAP 095062	Miyagi, Shizugawa, Japan	AB097621	Shimada <i>et al.</i> 2003
<i>Ulva australis</i>	<i>Ulva australis</i> Aresch.	LK-029	Flinders, Victoria, Australia	EU933953	Kraft <i>et al.</i> 2010
<i>Ulva australis</i>	<i>Ulva australis</i>	S A2025, lectotype of <i>U. australis</i>	Port Adelaide, Australia	LC331300	Hanyuda & Kawai 2018
<i>Ulva californica</i>	<i>Ulva californica</i> Wille	WTU 344796	Moss Landing Harbor, Monterey County, California, USA	AY422557	Hayden & Waaland 2004
<i>Ulva chaugulii</i>	<i>Ulva chaugulii</i> M.G. Kavale & M.A. Kazi	ARC-U-303A	Vayangani, India	KP710829	Kazi <i>et al.</i> 2016
<i>Ulva conglobata</i>	<i>Ulva conglobata</i> Kjellman	UPS A588132/3, lectotype of <i>U. conglobata</i> f. <i>conglobata</i> , specimen #1	Yokohama, Goto or Amakusa, Japan	MT815850	Hughey <i>et al.</i> 2021b
<i>Ulva expansa</i>	<i>Ulva expansa</i> (Setchell) Setchell & N.L.Gardner	UC98481, holotype	Monterey, Monterey County, California, USA	MH731009	Hughey <i>et al.</i> 2018
<i>Ulva fasciata</i>	<i>Ulva lactuca</i> L.	GALW 0015524	Faial, Azores, Portugal	EU484418	Loughnane <i>et al.</i> 2008
<i>Ulva fasciata</i>	<i>Ulva lactuca</i>	SAP:095075	Kochi, Usa, Japan	AB097633	Shimada <i>et al.</i> 2003
<i>Ulva fasciata</i>	<i>Ulva lactuca</i>	TNS AL183430	Kanagawa, Sajima, Tenjin-jima, Japan	AB894323	Shimada <i>et al.</i> 2003
<i>Ulva fenestrata</i>	<i>Ulva fenestrata</i> Postels & Ruprecht	UBC A57002, LE fragment of holotype	Kamchatka Peninsula, Siberia, Russia	MK456393	Hughey <i>et al.</i> 2019
<i>Ulva flexuosa</i>	<i>Ulva flexuosa</i> Wulfen	SAP 095057	Wakayama, Tajiri, Japan	AB097619	Shimada <i>et al.</i> 2003
<i>Ulva flexuosa</i>	<i>Ulva flexuosa</i> subsp. <i>pilifera</i> (Kützinger) M.J.Wynne	L 0054611	Tennstedt, Thüringen, Germany	HM447571	Mareš <i>et al.</i> 2011
<i>Ulva gigantea</i>	<i>Ulva gigantea</i> (Kütz.) Bliding	Strain U101	France	MT160562	Fort <i>et al.</i> 2021
<i>Ulva iliohaha</i>	<i>Ulva iliohaha</i> H.L.Spalding & A.R.Sherwood	ARS08535, holotype of <i>U. iliohaha</i>	64 m depth from French Frigate Shoals, NWHI, Hawaii, United States	KT932995	Spalding <i>et al.</i> 2016
<i>Ulva intestinalis</i>	<i>Ulva intestinalis</i> L.	WTU 344772	Sheep Bay, Valdez-Cordova County, Alaska, USA	AY422552	Hayden & Waaland 2004
<i>Ulva lacinulata</i>	<i>Ulva lacinulata</i> (Kützinger) Wittrock	Herbarium Kützinger L 0054997, herein designated lectotype of <i>Phycoseris lacinulata</i>	Lesina, Croatia	MW543061	Hughey <i>et al.</i> 2021a
<i>Ulva lactuca</i>	<i>Ulva lactuca</i>	LINN 1275-24 #5, lectotype	Indo-Pacific	MK456395	Hughey <i>et al.</i> 2019
<i>Ulva lactuca</i>	<i>Ulva lactuca</i>	L 0054996, lectotype of <i>Ulva lobata</i>	Chile	MH730972	Hughey <i>et al.</i> 2019
<i>Ulva lactuca</i>	<i>Ulva lactuca</i>	NC01-331	Ile des Pins, La piscine, New Caledonia	MK456402	Hughey <i>et al.</i> 2019
<i>Ulva lactuca</i>	<i>Ulva lactuca</i>	JW4711	Queensland, Australia	MK456401	Hughey <i>et al.</i> 2019
<i>Ulva limnetica</i>	<i>Ulva limnetica</i> Ichihara & S.Shimada	P36	Okinawa, Ishigaki Is., Omoto, Japan	AB425968	Ichihara <i>et al.</i> 2009
<i>Ulva linza</i>	<i>Ulva linza</i> L.	SAP 095061	Tokushima, Yoshino river, Japan	AB097620	Shimada <i>et al.</i> 2003
<i>Ulva muscoides</i>	<i>Ulva muscoides</i> Clemente	Unknown	Los Toruños, Puerto Real, Cádiz, Spain	AY422563	Hayden & Waaland 2004

TABLE 1. — Continuation.

GenBank name	Currently recognized name	Specimen voucher/ sample code	Collection information	<i>rbcL</i> GenBank accessions	Source
<i>Ulva nematoidea</i>	<i>Ulva lactuca</i>	PC0042814, lectotype of <i>Ulva nematoidea</i>	Concepción, Chile	OL542489	This Study
<i>Ulva ohiohilulu</i>	<i>Ulva ohiohilulu</i> H.L.Spalding & A.R.Sherwood	ARS08539	Waikīkī, South O'ahu, Hawaii, United States	KT932996	Spalding <i>et al.</i> 2016
<i>Ulva ohnoi</i>	<i>Ulva ohnoi</i> Hiraoka & S.Shimada	KU-MACC:KU-3321	Tosa Bay, Tosa, Kochi Prefecture, Japan, in Kobe University Macro- Algal Culture Collection	AP018696	Suzuki <i>et al.</i> 2018
<i>Ulva prolifera</i>	<i>Ulva prolifera</i> O.F.Müller	WTU 344780	Red Hill Marina, Salton Sea, Imperial County, California, USA	AY422554	Hayden & Waaland 2004
<i>Ulva pseudocurvata</i>	<i>Ulva pseudocurvata</i> Koeman & Hoek	EOO0685122	Ythan estuary, Aberdeenshire, Scotland	AY255869	Hayden <i>et al.</i> 2003
<i>Ulva reticulata</i>	<i>Ulva reticulata</i> Forsskål	WTU 344825	Lipoa Street, Kihei, Maui County, Hawaii, USA	AY422568	Hayden & Waaland 2004
<i>Ulva rigida</i>	<i>Ulva rigida</i> C.Agardh	Agardh Herbarium no 14294, lectotype specimen of <i>Ulva rigida</i>	Cádiz, Spain	MW543060	Hughey <i>et al.</i> 2021a
<i>Ulva</i> sp.	<i>Ulva</i> sp.	WTU 344782	Coast Guard Cove, Humboldt Bay, Humboldt County, California, USA	AY422561	Hayden & Waaland 2004
<i>Ulva</i> sp.	<i>Ulva clathratioides</i> L.G.Kraft, Kraft & R.F.Waller	LK-009	Williamstown, Victoria, Australia	EU933940	Kraft <i>et al.</i> 2010
<i>Ulva</i> sp.	<i>Ulva conglobata</i>	TNS:AL:183434	Kanagawa, Sajima, Tenjin- jima, Japan	AB894326	Matsumoto & Shimada 2015
<i>Ulva stenophylla</i>	<i>Ulva stenophylla</i> Setchell & N.L.Gardner	WTU 344829	Seattle, Washington, USA	AY255874	Hayden <i>et al.</i> 2003
<i>Ulva stenophylloides</i>	<i>Ulva stenophylloides</i> L.G.Kraft, Kraft & R.F.Waller	LK-024	Point Lonsdale, Victoria, Australia	EU933950	Kraft <i>et al.</i> 2010
<i>Ulva sublittoralis</i>	<i>Ulva sublittoralis</i> Segawa	zk1-3	Kagoshima, Mage island offshore, Japan	AB741535	Ichihara <i>et al.</i> 2013
<i>Ulva taeniata</i>	<i>Ulva taeniata</i> (Setchell) Setchell & N.L.Gardner	WTU 344833	Point Loma, San Diego, San Diego County, California, USA	AY422566	Hayden & Waaland 2004
<i>Ulva tanneri</i>	<i>Ulva tanneri</i> H.S.Hayden & Waaland	WTU 344770	South Point, Cabrillo, Monterey, California, USA	AF499672	Hayden & Waaland 2002
<i>Ulva tepida</i>	<i>Ulva tepida</i> Masakiyo & S.Shimada	MIC 3 TA	Michmoret, Israel	MG704820	Krupnik <i>et al.</i> 2018
<i>Ulvaria obscura</i> var. <i>blyttii</i>	<i>Ulvaria obscura</i> var. <i>blyttii</i> (Areschoug) Bliding	WTU 344838	Padilla Bay National Estuarine Research Reserve, Skagit County, Washington, USA	AF499673	Hayden & Waaland 2002
<i>Umbraulva olivascens</i>	<i>Umbraulva olivascens</i> (P.J.L.Dangeard) G.Furnari	WTU 344837	Portaferry, Strangford Lough, N. Ireland	AY255876	Hayden <i>et al.</i> 2003

online (<https://mafft.cbrc.jp/alignment/server/>) using the MAFFT auto strategy (Katoh & Standley 2013; Katoh *et al.* 2019). The RAxML phylogenetic analysis was executed with Geneious Prime with the GTR + gamma substitution model and 1000 rapid bootstrap replicates. The Bayesian analysis (Ronquist & Huelsenbeck 2003) was performed using the same model with default settings in Geneious Prime. The tree was visualized with TreeDyn 198.3 at Phylogeny.fr (Dereeper *et al.* 2008).

RESULTS

High-throughput sequencing of the lectotype specimen of *U. nematoidea* yielded 24 424 274 reads. Mapping of the reads resulted in nearly complete *rbcL* (1365 bp, GenBank accession number: OL542489) and *tufA* (1161 bp, GenBank accession number: OL542490) gene sequences as well as the ITS 1 and 2 regions (739 bp, GenBank accession number: OL583932). Nucleotide BLAST analysis of the

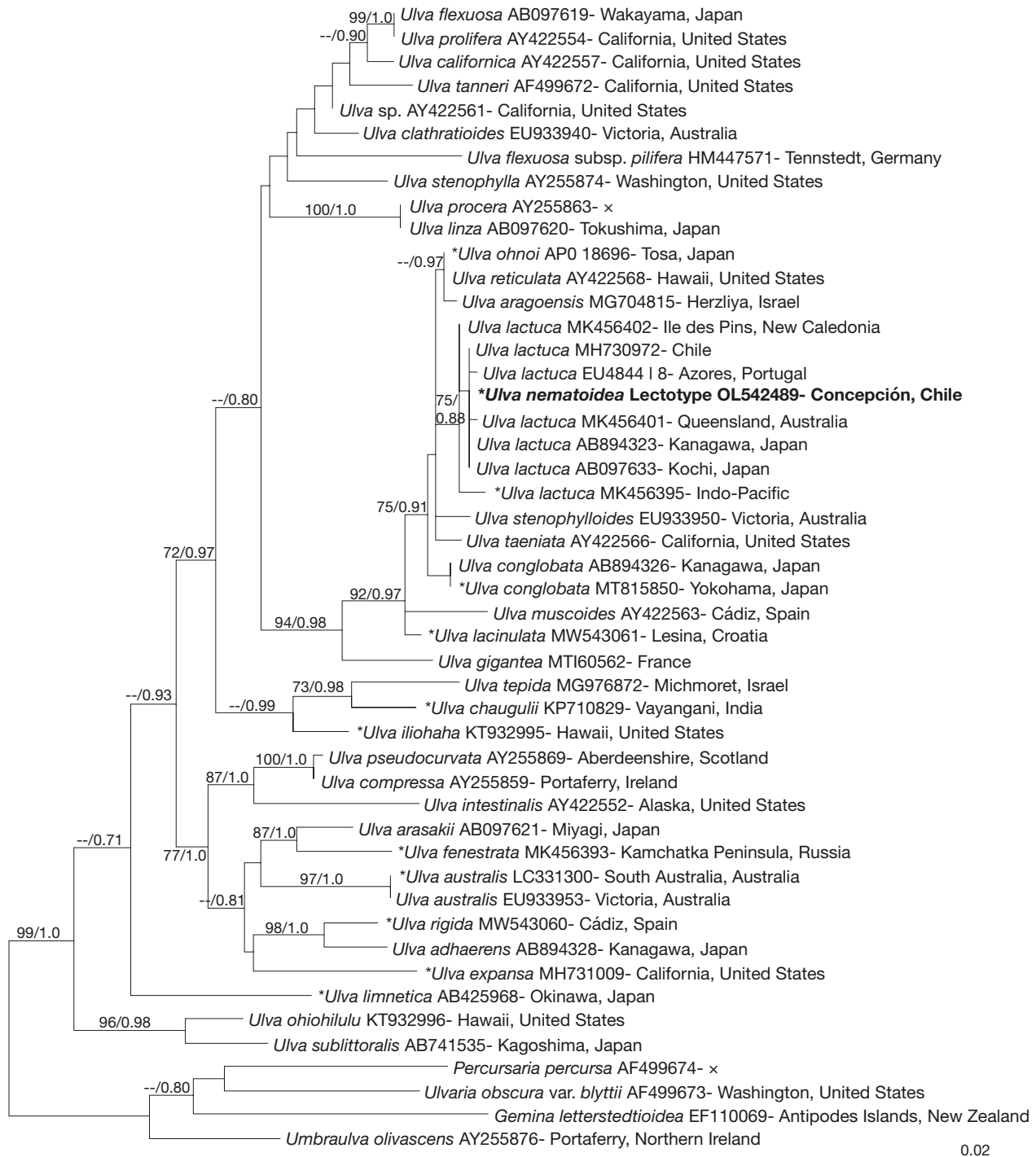


FIG. 2. — RAxML phylogram based on *rbcL* gene sequences showing the evolutionary relationship of *Ulva nematoidea* Bory (GenBank accession number: OL542489) to representative Ulvaceae. Bootstrap support values based on 1000 replicates/Bayesian posterior probabilities are cited at the nodes. x indicates no locality given. -- or blank nodes indicate less than 70% bootstrap support or less than 0.70 posterior probability. * denotes the sequence was generated from type material. The legend below represents the scale for nucleotide substitutions.

three *U. nematoidea* markers found more than 100 identical sequences in GenBank identified as *U. lactuca* and *U. fasciata* (*U. fasciata* is a heterotypic synonym of *U. lactuca*, Hughey *et al.* 2019). The sequence from the lectotype of *U. nematoidea* was identical to 58 *rbcL*, 44 *tufA*, and six ITS sequences in GenBank. Phylogenetic analysis of the *rbcL*

gene sequence of the lectotype of *U. nematoidea* resolved the lectotype in a moderately supported clade with *U. lactuca* (Fig. 2).

On the basis of genetic evidence from three markers, we propose the synonymy of *U. nematoidea* under the earlier name, *U. lactuca*.

Family ULVACEAE J.V.Lamouroux ex Dumortier
Genus *Ulva* L.

Ulva lactuca L.

Species plantarum 2: 1163 (Linnaeus 1753). — Lectotype: LINN 1275-24.

Ulva fasciata Delile, *Description de l'Égypte* [...] *Histoire naturelle*, vol. 2: 297 (Delile 1813). — *Ulva lactuca* f. *fasciata* (Delile) Hering in Krauss, *Flora* 29: 215 (Krauss 1846). — Epitype: UC2050475 supporting the lectotype PC0119343.

Ulva nematoidea Bory, *Voyage autour du monde, exécuté par ordre du Roi, sur la corvette de Sa Majesté, La Coquille, pendant les années 1822, 1823, 1824 et 1825*: 190 (Bory 1828). — Lectotype: PC0042814. **Syn. nov.**

Phycoseris lobata Kützing, *Botanische Zeitung* 5: 54 (Kützing 1847). — *Ulva lobata* (Kützing) Harvey, *The Botany of the Antarctic Voyage of H.M. Discovery Ships Erebus and Terror, in the years 1839-1843, under the Command of Captain Sir James Clark Ross*, vol. 2: 265 (Harvey 1855). — *Ulva fasciata* var. *lobata* (Kützing) Piccone, *Algae del viaggio di circumnavigazione della Vettor Pisani*: 23 (Piccone 1886). — Lectotype: L 0054996.

Ulva rotundata Bliding, *Botaniska Notiser* 121: 566. (Bliding 1968). — Holotype: LD 2129253.

DISCUSSION

Montagne (1839) initially and correctly attributed *U. nematoidea* to *U. lactuca*, but later accepted it as a distinct species, although with reservations (Montagne 1846), stating in reference to *U. nematoidea* and *U. fasciata* (translated from French) “I can assure you that I have seen in the same tuft individuals displaying the characteristics that the author attributes to each of the two species”. Montagne (1854) eventually accepted *U. nematoidea* (as *Phycoseris fasciata* (Delile) Montagne) without reservation. Kützing (1849), as *P. fasciata*, Agardh (1883) and De Toni (1889) all recognized *U. nematoidea* as a synonym of *U. fasciata*. This synonymy held until Etcheverry (1986), without comment, applied the name *U. nematoidea* to plants from Chile. This taxonomic opinion was adopted by others (Wynne 2002; Pedroche *et al.* 2005; Norris 2010). The data here, and from previous studies, show (Hughey *et al.* 2018, 2019, 2021a, b) that the correct application of an *Ulva* binomial requires sequencing type material. DNA sequences obtained from numerous *Ulva* type specimens continue to indicate that morpho-anatomical techniques fail to accurately identify species of *Ulva*.

Ulva fasciata f. *costata* was excluded from the above list of heterotypic synonyms because no type material has been successfully sequenced to confirm its synonymy. We attempted to PCR amplify DNA from an isoelectotype specimen (UC197872), but those attempts failed. Dr Robert E. Coker, the collector of the seaweeds treated by Howe (1914), preserved his collections in formaldehyde, which is known to damage DNA (Grafstrom *et al.* 1983). To resolve the identity of *U. fasciata* f. *costata*, HTS should be attempted on type material, or Sanger sequencing or HTS on topotype material from the Chincha Islands, Peru.

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