A TAXONOMIC REVIEW OF *SARGASSUM*
(FUCALES, PHAEOPHYCEAE), WITH AN EMPHASIS ON THE
AUSTRALIAN SPECIES

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Abstract

The taxonomy of the common and conspicuous brown algal genus *Sargassum* C. Agardh, with 76 species in Australia and 336 worldwide, was investigated at a range of scales using genetic and morphological data. New DNA sequences derived from Australian collections were supplemented by co-author contributions from South Africa, Madagascar, New Zealand, New Caledonia, Japan, Netherlands and France. Variation in the loci *cox3*, *rbcL*-S spacer and ITS-2, as well as a morphological assessment of new and herbarium collections, led to a number of substantial changes to the taxonomy of *Sargassum* and its four currently recognized subgenera. Neither the genus *Sargassum*, nor its most early-diverged subgenus, *Sargassum* subgenus *Phyllotricha*, were resolved as monophyletic taxa. To correct this, species of *Sargassum* subgenus *Phyllotricha* were transferred either to the newly resurrected genus *Phyllotricha* Areschoug or to the genus *Sargassopsis* Trevisan. These species were well differentiated, with the exception of *Sargassum decurrens* and *Sargassum peronii*, and the latter was placed in synonymy with the former. The separation of *Sargassum* subgenera *Arthrophycus* and *Bactrophycus*, previously distinguished primarily by their disjunct distributions, was not supported by the genetic or morphological data. Species of *Sargassum* subgenus *Arthrophycus* were genetically and morphologically nested within *Sargassum* subgenus *Bactrophycus* section *Halochloa* (Kützing) Endlicher, and were transferred accordingly. *Sargassum* section *Halochloa* species, particularly from the southern hemisphere, could not be easily differentiated, with intraspecific variation equal to or greater than intraspecific variation in all but one case (*Sargassum incisifolium*).

The final subgenus treated was *Sargassum* subgenus *Sargassum*. As the most species rich and widespread subgenus, a geographically broad-scale approach, as was undertaken with the other subgenera, was not feasible. Instead this effort was concentrated in a floristic survey of the previously poorly known north-western Australian members of the brown algal order Fucales, which was composed largely of *Sargassum* subgenus *Sargassum* species. Seventeen species of Fucales were recorded for north-western Australia, 10 of which were in *Sargassum* subgenus *Sargassum*. The floristic treatment includes full descriptions of each taxonomic level, incorporating current nomenclature, morphology, keys, and numerous figures, and represents the first detailed account of the Fucales of tropical Western Australia. As part of this study, a number of range extensions were recorded, as well as new records for Australia.
and a new species, *Sargassum rastum* R.Dixon & Huisman. In addition, the phylogenetic analyses of the north-western Australian species confirmed recent revisions at the sectional level of *Sargassum* subgenus *Sargassum* taxonomy.

The present study has reassessed the taxonomy of *Sargassum* using a combination of detailed morphological examination and molecular analyses, the latter incorporating a triple-loci approach. The investigation confidently differentiated many Australian *Sargassum* species, yet indicated that to unequivocally resolve species level boundaries in the genus, a greater collection and sequencing effort is required.
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**Originality Statement**

This work contains no material which has been accepted for the award of any other degree or diploma in any university or other tertiary institution to Rainbo Rita Mae Dixon and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text.

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Chapter 1 Introduction

The brown algae, or Phaeophyceae, are a monophyletic class within the Stramenopiles (Baldauf 2008), unique in the group for having complex multicellular thalli. The nearest eukaryote lineages with comparably complex multicellular thalli (Metazoans, Fungi, Archaeplastida) are evolutionarily distant and structurally very different (Charrier et al. 2007). Brown algae occur in marine and, less commonly, freshwater environments, from deeper than 90 m depths to the upper intertidal zone (Littler et al. 1985). In this project I investigated the taxonomy and evolutionary relationships of the marine brown algal genus Sargassum C. Agardh and related genera in the order Fucales. The Fucales is a distinctive group that includes the majority of the conspicuous brown algae. It is one of the most diverse of the brown algal orders, with 590 recorded species (Guiry & Guiry 2015), second only to the Ectocarpales with 787 species. Fucales first arose at the end of the Upper Cretaceous (approx. 65Mya) (Silberfeld et al. 2010), and have a biphasic life history with a much reduced gametophyte (Chapman 1995).

Sargassum species occur globally in both tropical and temperate marine waters. They are usually found along coastlines growing on rock or in drifting rafts, the latter most famously in the Sargasso Sea of the south-eastern United States. In tropical waters, Sargassum species are often the dominant canopy-forming macroalgae. Their structure involves a conical or creeping holdfast that supports upright axes giving rise to leaf-like laterals, vesicles (spherical floats) and receptacles (reproductive branches). Sargassum can grow over 2 metres tall in sheltered (e.g. lagoonal) areas, although on reef crests and in intertidal zones they are typically much smaller and often under 30 cm in height.

Taxonomic background

Since its inception, Sargassum has proved to be taxonomically challenging. Many of the early species were described based on fragmentary material (Womersley 1956; pers. obs.), and as such did not enable a full understanding of the species’ morphological range and limits. Moreover, many morphological variants were described in a large number of varieties and forms (Grunow 1915, 1916), further complicating the taxonomy. The following is a brief introduction to the taxonomic history of the Sargassum subgenera (expanded in later chapters).
**Sargassum** [with type *Sargassum bacciferum* (Turner) C.Agardh] was described by Carl Adolph Agardh (1820), who included 59 species and subdivided the genus into several groups on the basis of receptacle position and leaf characters. In 1848, Agardh’s son, Jacob Georg Agardh, added and described further species and arranged the genus into three sections, each subdivided into tribes; *Pterophycus* J.Agardh (with tribe *Pterocaulon*), *Arthrophycus* J.Agardh (with tribes *Schizophylla*, *Holophylla* and *Heterophylla*), and *Eusargassum* J.Agardh (with tribes *Carpophylla*, *Glandularia*, *Biserrulae*, *Siliquosae*, *Acanthocarpa*, *Acinaria* and *Ligularia*). J. Agardh (1889) later reorganized the genus into five subgenera; *Phyllotricha* (Areschoug) J.Agardh (with tribes *Heteromorphae*, *Cladomorphae*, *Phyllomorphae*, *Pteromorphae* and *Dimorphae*), *Schizophycus* J.Agardh, *Arthrophycus* J.Agardh, *Bactrophycus* J.Agardh and *Sargassum* J.Agardh (with tribes *Zygocarpicae*, *Carpophyllae*, *Glomerulatae*, *Biserrulae*, *Fruticoliferae*, *Cymosae* and *Racemosae*). This subgeneric arrangement formed the basis of *Sargassum* classification until only recently, with significant modifications occurring only in the last 10 years with the advent of molecular tools. At the outset of the present study, four subgenera were current, *Phyllotricha*, *Arthrophycus*, *Bactrophycus* and *Sargassum*.

**Sargassum in Australia**

The genus *Sargassum* currently has 339 accepted taxa (species and infraspecific) worldwide, including 76 accepted in Australia (Guiry & Guiry 2015). Since J.Agardh’s (1889) monograph of the genus, which included many Australian species, the genus has been treated in several monographs and checklists in Australia. Womersley (1958) recorded seven *Sargassum* species from the Northern Territory, and later gave a detailed account of the southern Australian *Sargassum* (including southern Western Australia, South Australia and Victoria), recognising 16 species and transferring 10 species into synonymy (Womersley 1987). Based on literature records, Lewis (1985) reported 57 *Sargassum* species from northern Australia (including northern Western Australia, Northern Territory and Queensland). In Western Australia, regional checklists recorded 30 current species in total, with eight from Rottnest Island (Huisman & Walker 1990), nine species from the Houtman Abrolhos Islands (Huisman 1997), five species from Shark Bay (Kendrick *et al.* 1990), and three species from the Dampier Archipelago (Huisman & Borowitzka 2003). In Queensland, Phillips (1997) recorded 49 species from across the State and Kraft (2009) included a detailed account that recognised 12
Sargassum species from Lord Howe Island (LHI) and the Southern Great Barrier Reef, five of which were newly described. In New South Wales, 19 species were recorded from the coastal mainland (Millar & Kraft 1994) and eight from Norfolk Island (Millar 1999). The ranges of many of the Sargassum species overlap across these regions, owing to their dispersal capabilities, including the ability to drift over large distances of 600-900 km (Norton 1992) while remaining viable (Critchley et al. 1983, Yatsuya 2008). This is particularly evident in tropical species, where several are widely distributed throughout the Indo-Pacific, and to a lesser extent in temperate species with pan-southern Australian distributions.

**Classical vs. molecular assisted taxonomic approaches**

Virtually all systematic work on Australian Sargassum to the present has employed morphology-based alpha taxonomy. Further afield molecular-assisted studies have transferred some of the common Indo-Pacific species into synonymy (Mattio & Payri 2008, 2009, Mattio et al. 2009), altering known Australian species diversity as a result. Our understanding of Sargassum is slowly improving with growing molecular datasets assisting morphological study. As a result, diagnostic concepts of many Sargassum species have expanded to encompass a wider range of morphotypes (Mattio et al. 2008, 2009, 2010, Mattio & Payri 2009, Cho et al. 2012). From what has been revealed in these studies, it is clear there is much to uncover about the many species and geographic regions that have not been subject to molecular investigation. Australia is of particular interest for this reason, as it has 76 current Sargassum taxa, and three of the four current subgenera (Guiry & Guiry 2015), yet the few molecular-assisted studies thus far that have included Australian Sargassum are severely limited. Prior to the present work only two studies to date applied molecular techniques to Australian samples. Benzie et al. (2000) investigated allozyme variation to genetically identify Sargassum species of the Great Barrier Reef; the authors proposed several synonyms but these were later recognised as distinct species and retained (Mattio et al. 2009a, 2009b). Benzie et al. (2000) also suggested evolutionary proximity of species later shown to be widely divergent (Draisma et al. 2010). The only other study to include Australian collections incorporated just one sample for subgeneric comparison (Phillips & Fredericq 2000). Both studies are thus of limited value in assessing the taxonomy of Australian Sargassum and do not enable any firm conclusions regarding species limits. The need for revision is now increasingly evident with recent transfers leaving taxonomic groups no longer defined by sensible morphological
argument. For example, *Sargassum decurrens* (R.Brown ex Turner) C.Agardh of *S.* subgenus *Phyllotricha* was singularly transferred to *Sargassopsis* based on molecular data, however, its habit is in close agreement with residual *Phyllotricha* species. What then is the correct taxonomic placement of the remaining seven *S.* subgen. *Phyllotricha* species? Given the many changes occurring in this group elsewhere, the Australian *Sargassum* are acutely in need of revision.

**Statement of the problem**

A multidimensional molecular and morphological approach is needed to determine species diversity and evolutionary relationships of *Sargassum* within Australia; particularly incorporating the most reliable molecular techniques to test and understand the diversity described in morphological studies.

**Purpose of the study**

This study proposes to explore the diversity and systematics of Australian *Sargassum*, incorporating collections from further afield to assist in exploring the systematics of the entire genus.

**Significance of the study**

*Sargassum* is one of the largest, most conspicuous marine brown algae, and an important ecological habitat (Jobe & Brooks 2009, Kraft 2009). The genus currently poses an arduous challenge in identification to species and to subgeneric rank in the subgenus *Sargassum*. This is the first comprehensive Australian work to incorporate molecular sequencing methods in the treatment of *Sargassum* and related genera in the Fucales. The combined approach of molecular-assisted taxonomy allows for both the revision of our classical morphological understanding and also analysis of the genetic results ensuring any proposed phylogenetic schema make sense when morphological characters are incorporated.

**Primary research questions**

The aim of this study is to explore the taxonomy and systematics of *Sargassum*, testing the current generic, subgeneric, section and species boundaries.
The study will first focus on S. subgenus *Phyllotricha*, endemic to Australia and New Zealand.

The second part will focus on the subgenera *Arthrophycus* and *Bactrophycus*, which have morphological similarities but as presently constituted are separated geographically by tropical equatorial waters.

Lastly the study takes a more geographically targeted approach investigating the Fucales species of north-western Australia. In this region S. subgenus *Sargassum* species are the most conspicuous and diverse of the brown macroalgae.

**Research design**

Collections were made opportunistically across southern Australia and into the tropics by the author (R.R.M.D.), supervisor (J.M.H.) as well as volunteers and collaborators. Fieldtrips organized by the Western Australian Museum (to the Kimberley in 2009-2013) and CReefs (to Ningaloo Reef and the Great Barrier Reef 2008-2010) amassed a large proportion of the tropical collections. Southern Australian collections were gathered over several fieldtrips from 2008-2010.

Non-Australian material for Chapter 3 was primarily sourced via collaborator L. Mattio. Methods for morphological identification include a wide variety of literature, primarily accessed from the South Australian Herbarium, Murdoch University and Adelaide University libraries. The molecular methodology involved Sanger sequencing of three loci from different areas of the genome, the nuclear mRNA internal transcribed spacer 2 (ITS-2), the mitochondrial cytochrome oxidase 3 (*cox3*) and the chloroplast derived ribulose 1,5-bisphosphate carboxylase/oxygenase large and small partial subunits including the spacer (*rbcL*-S spacer).

**Theoretical framework**

This study adopted current methodologies with regard to subsample collection in silica, the DNA extraction protocol, and loci chosen for investigation. Mattio *et al.* (2008, 2009) demonstrated the ability of a triple marker approach (ITS-2, *cox3*, *rbcL*-S) to discriminate between species and identify synonyms in *Sargassum* of New Caledonia and the central and eastern Pacific Ocean. Draisma *et al.* (2010) and Cho *et al.* (2012) furthered this, by adding more loci to better resolve the deeper evolutionary relationships. The genetic work in the
present study was carried out partly in the Wildlife Genetics Lab (Murdoch University) and partly at the Evolutionary Biology Unit, University of Adelaide.

**Assumptions limitations and scope**

In molecular systematic work one assumes the observed genetic variation of loci under investigation is equivalent to studying the actual variation between organisms. The greater amount of unlinked genetic information available, the closer we can get to realizing this assumption. The three loci studied here are from vastly separate areas of the genome, the nucleus, mitochondrion and chloroplast, however they represent a minute fraction of the organism’s total genetic material. It was assumed that these loci would show sufficient genetic variation for species-level discrimination of Australian taxa. Given most Australian species have not been sequenced previously, and the subgenera *Phyllotricha* and *Arthrophycus* have very little to nothing known about their genetic variability, this was a point of uncertainty and potential limitation. The focus of this study was the collection, sequencing, and morphological and molecular analyses of the Australian *Sargassum* flora. This was refined for the scope of a Ph.D. project, particularly in regards to the treatment of *S.* subgenus *Sargassum*, which focuses in more detail on the regional flora of north-western Australia.

**Summary**

This study contributes to our knowledge of the Australian marine flora, exploring the systematics of a large and common, yet little understood brown algal genus. The story of *Sargassum* unfolds with a substantial new DNA sequence dataset assisting morphological analyses, leading to a revision of the taxonomy and systematics of this group.

**References**


Chapter 2  A morphological and molecular study of austral Sargassum (Fucales, Phaeophyceae) supports the recognition of Phyllotricha at genus level, with further additions to the genus Sargassopsis.

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Abstract

*Sargassum* subgenus *Phyllotricha* currently includes seven species restricted to Australian and New Zealand coasts. A recent study of *Cystoseira* and other Sargassaceae genera based on mitochondrial 23S DNA and chloroplast-encoded *psbA* sequences resulted in the most widely distributed species of subgenus *Phyllotricha*, *Sargassum decurrens*, being transferred to the reinstated monospecific *Sargassopsis* Trevisan. The fate of the residual six *Phyllotricha* species, however, was not considered. The present study examines these *Phyllotricha* species, alongside other *Sargassum* subgenera, *Sargassopsis*, *Sirophysalis trinodis* (formerly *Cystoseira trinodis*) and the New Zealand endemic *Carpophyllum* Greville, using morphological evidence and the molecular phylogenetic markers *cox3*, ITS-2 and the *rbcL–S* spacer. Our results suggest both the genus *Sargassum* and *Sargassum* subgenus *Phyllotricha* are polyphyletic as currently circumscribed. Four *S. subgen.* *Phyllotricha* species, i.e. *S. sonderi*, *S. decipiens*, *S. varians* and *S. verruculosum*, form a monophyletic group sister to the genus *Carpophyllum*, and *S. peronii* is genetically identical to *S. decurrens* with regard to all three loci. We propose the resurrection of the genus *Phyllotricha* Areschoug, with type species *Phyllotricha sonderi*, and include the new combinations *Phyllotricha decipiens*, *Phyllotricha varians* and *Phyllotricha verruculosum*. *Sargassum peronii*, *S. heteromorphum* and *S. kendrickii* are transferred to *Sargassopsis* and *Sargassum peronii* is considered a synonym of *Sargassopsis decurrens*.

Introduction

“The identification of Sargassums is a task of no small magnitude, nor is it one to be undertaken without due concern for the probable uncertainty of its outcome” (W. A. Setchell, November 1931)

*Phyllotricha* (with type *P. sonderi* [J. Agardh] J. Agardh) was first described as a genus by Areschoug (1854), but then subsequently relegated to a section, then subgenus, of the widespread brown alga *Sargassum* C. Agardh by J. Agardh (1873, 1889). Areschoug’s original spelling was widely used up to and including Grunow (1915), but most workers have used the orthographic variant *Phyllotrichia* (e.g., Womersley 1954, 1987, Goldberg & Huisman 2004, Draisima et al. 2010, Mattio & Payri 2011). This variant was seemingly first introduced by Setchell & Gardner (1924: 739), without explanation, then also by Setchell
(1931), who initially listed J. Agardh’s subgenera with the original spelling (p. 244), but subsequently used the variant in his key (p. 247). Setchell’s excellent introduction to Sargassum and its subgenera was cited by Womersley (1954), where the variant spelling was used throughout and undoubtedly led to its entrenched use from then on. On-line resources including the ‘Index Nominorum Genericorum’ (botany.si.edu/ing/), Paul Silva’s ‘Index Nominum Algarum’ (ucjeps.berkeley.edu/INA.html) and Guiry & Guiry’s ‘Algaebase’ (http://www.algaebase.org/), however, all give the original correct spelling.

Sargassum subgen. Phyllotricha (Areschoug) J. Agardh as originally conceived was one of J. Agardh’s (1889) five subgenera alongside S. subgen. Schizophycus J. Agardh, S. subgen. Arthrophyccus J. Agardh, S. subgen. Bactrophyccus J. Agardh and S. subgen. Sargassum J. Agardh. It included 15 species subdivided into five ‘tribus’ based on variation in axes and lateral shape and orientation: (i) Heteromorphae (2 species), (ii) Cladomorphae (3 species), (iii) Phyllomorphae (4 species), (iv) Pteromorphae (4 species), and (v) Dimorphae (2 species).

Lucas (1935) added Sargassum howeanum A. H. S. Lucas from Lord Howe Island and Womersley (1954), in merging Sargassum subgen. Schizophycus, added another two species, Sargassum pinnatifidum Harvey and Sargassum patens C. Agardh. Five members of subgenus Phyllotricha have been represented in molecular phylogenetic studies to date (Sargassum decurrens [R. Brown ex Turner] C. Agardh, Sargassum boryi C. Agardh, S. howeanum, Sargassum piluliferum [Turner] C. Agardh and Sargassum yendoi Okamura & Yamada), but none still remain in the group. Sargassum boryi is now a synonym of Sargassopsis decurrens, (R. Brown ex Turner) Trevisan and S. howeanum, S. piluliferum and S. yendoi were removed to Sargassum subgenus Sargassum based on molecular affinities (Stiger et al. 2003, Yoshida et al. 2004, Mattio & Payri 2009, Draisma et al. 2010). Until recently, the most well known and commonly recorded species of S. subgen. Phyllotricha was S. decurrens, a species distributed across tropical and temperate regions of the east Indian and western Pacific Oceans. The molecular study of Draisma et al. (2010), however, revealed that Sargassum is polyphyletic if S. decurrens is included, and to remedy this they reinstated the genus Sargassopsis Trevisan, including only Sargassopsis decurrens. Draisma et al.’s study was based on mt23S DNA and psbA sequences of species from a broad range of Sargassaceae genera, some closely related to Sargassum such as Cystoseira C. Agardh, Anthophycus Kützing, Carpophyllum Greville, Myagropsis Kützing and Nizamuddinia P. C. Silva, the first three of which were clearly nested in a group with Sargassum and S. decurrens. This
additionally resulted in the transfer of the widespread *Cystoseira trinodis* (Forsskål) C. Agardh to the newly reinstated *Sirophysalis* Kützing. *Sirophysalis trinodis* (Forsskål) Kützing was found most closely related to remaining *Sargassum* species (Draisma et al. 2010).

Previous molecular phylogenetic work on interspecific boundaries within *Sargassum* focused primarily on species in the subgenera *Bactrophycus* and *Sargassum*, using *Turbinaria* J. V. Lamouroux as an outgroup and including *S. decurrens* of subgenus *Phyllotricha*, which always formed a clade sister to other *Sargassum* subgenera (Stiger et al. 2000, Yoshida et al. 2004, Mattio et al. 2008, 2009, 2010, Mattio & Payri 2009). The reinstatement of *Sargassopsis* by Draisma et al. (2010) revealed the importance of including a wide range of closely related outgroup taxa when studying taxonomic groups with high morphological variability such as occur in the Sargassaceae, because it is not always clear which features are taxonomically informative.

*Sargassum* subgen. *Phyllotricha* currently includes seven species: *S. peronii* C. Agardh, *S. heteromorphum* J. Agardh, *S. sonderi* (J. Agardh) J. Agardh, *S. decipiens* (R. Brown ex Turner) J. Agardh, *S. varians* Sonder, *S. verruculosum* C. Agardh, and *S. kendrickii* N. A. Goldberg & Huisman, all of which occur in Australia (Womersley 1954, 1987, Goldberg & Huisman 2004). From a morphological perspective, the habit of *Sargassopsis decurrens* is in close agreement with residual *Phyllotricha* species, all having primary laterals emerging from the main axis as foliar expansions that are pinnate and flattened throughout or become cylindrical above bearing leaves, bladders and receptacles. This begs the obvious question, also raised by Mattio & Payri (2011) and Draisma et al. (2010), vis., what is the correct taxonomic placement of the remaining seven *S. subgen. Phyllotricha* species?

The aim of this study, therefore, is to understand the evolutionary relationships and species boundaries within *S. subgen. Phyllotricha* using morphological and molecular data. Collections made over the past 3 years were studied in terms of morphology alongside historical collections and analysed using the molecular markers ITS-2, *cox3*, and the *rbcL–S* spacer. These markers have been widely used in *Sargassum* and many sequences are available from GenBank, providing a good basis of comparison.

**Materials and methods**

*Collecting, preservation and morphological analysis:* Samples were collected between 2006
and 2010 on fieldtrips on the Australian and New Zealand coasts. Collections were made while snorkelling, SCUBA diving, and walking over intertidal rock platforms during low tide. Herbarium vouchers of all specimens were made as pressed sheets (Table 2:1), and, where possible, a reproductive branch was retained in 4% formalin. Subsamples of fertile branches, or an apical section of axes were dried in silica gel for molecular analysis. All morphological variants obtained were anatomically and morphologically analysed under a Zeiss 47 50 52-9901 (Jena, Germany) dissecting microscope and a Nikon Eclipse 80i compound light microscope (Nikon, Tokyo, Japan). Morphological criteria used for the identification of specimens were based on Womersley (1954, 1987), Goldberg & Huisman (2004), outlined in Table 2:2. Photographs of type specimens were also studied at AD. Herbarium specimens were lodged at PERTH, AD and WELT.

Molecular analyses: Representatives of each morphospecies were selected for molecular analysis, as detailed in Table 2:1. Prior to DNA extraction, tissues were frozen in liquid nitrogen, or in a freeze dryer overnight, and disrupted with a TissueLyser II (Qiagen Ltd., Crawley, UK). DNA was extracted using the Plant DNeasy Minikit according to manufacturer’s instructions (Qiagen Ltd., Crawley, UK), or by AGRF (Adelaide) using the Nucleospin Plant II system (Machery-Nagel GmbH & Co, Düren, Germany) using the SDS buffer set option. DNA was purified using GeneClean III (Qbiogene, Cambridge, UK). The nuclear ITS-2, mitochondrial cox3 and the chloroplast partial rbcLS-operon markers were PCR amplified in 25 µL reactions composed of 1X GeneAmp PCR Buffer (Applied Biosystems, Carlsbad, CA, USA), 3 mM MgCl2, 0.32 M Betaine, 100 µM of each dNTP, 0.2 µM each forward and reverse primer and 0.72 U AmpliTaq Gold (Applied Biosystems) or Taq TI (FisherBiotec, Wembley, WA, Australia) and 1 µL of 1:10 diluted DNA template. Amplifications were run on the Palm Cycler (Corbett Research, Sydney, Australia) with an initial denaturation at 95°C for 5–9 min followed by 30 cycles of 94°C for 40 s, 55°C (ITS-2), 50°C (rbcL–S spacer) or 45°C (cox3) for 40 s and 72°C for 45 s, terminated by 72°C for 7 min. PCR products were cleaned on a vacuum manifold plate and commercially sequenced by Macrogen (Seoul, South Korea) and AGRF. Primers for ITS-2, cox3 and the rbcL–S spacer followed those used by Mattio et al. (2008). The three individual loci were aligned separately in Geneious Pro v.5.5.2 (Drummond et al. 2010), and manually corrected. All analyses were run on the individual alignments as well as a concatenated alignment of the three markers. Maximum likelihood (ML) analyses were conducted in PAUP* (Swofford 2002) using the
model of evolution and parameters obtained from jModelTest (Guindon & Gascuel 2003, Posada 2008). The concatenated analysis used a GTR + G model with base frequencies (A = 0.26390, C = 0.21990, G = 0.22930, T = 0.2869), Nst = 6, rate matrix = (1.3778, 4.2329, 1.3778, 1.0000, 4.2329) and gamma distribution shape (a = 0.577) G. For each analysis 1,000 separate searches with random sequence additions using the tree bisection-reconnection (TBR) branch-swapping algorithm were completed. Node support for the ML analysis was assessed using non-parametric bootstrapping (Felsenstein 1985) using 500 resamplings as implemented in PAUP*.

Bayesian inference was performed with BEAST v.1.6.1 (Drummond et al. 2006, Drummond & Rambaut 2007), the concatenated dataset had the GTR + G substitution model, a coalescent constant size tree prior and a strict clock model. Markov Chain Monte Carlo runs were done for 50 million generations, sampled every 5000th generation and tree files were calculated with branch lengths in substitutions. These were monitored in Tracer v.1.5 (Rambaut & Drummond 2007), a 10% burn-in was removed in TreeAnnotator v.1.6.1 (Drummond & Rambaut 2007) and final trees were created in FigTree v.1.3.1 (Drummond and Rambaut 2007).

To distinguish between *Sargassum*, and *Sargassopsis* in abbreviations, the former will be referred to as ‘S.’, the latter ‘Ss.’

**Results**

Six *S.* subgen. *Phyllotricha* species were collected and identified based on morphological characters summarised in Table 2:2. *Sargassum peronii* and *Ss. decurrens* were found co-occurring in tropical Western Australia and *Ss. decurrens* extended south to Cape Naturaliste, W. A. The remaining *Phyllotricha* species were found in temperate waters from Rottnest Island, W. A., around southern Australia (including Tasmania).

Morphological identification of all specimens was congruent with the molecular data. Thirty-eight sequences each of *cox3*, *rbcL–S* spacer and ITS-2 were included in the phylogenetic analyses. These represent three samples of *Ss. decurrens*, two samples that are intermediate in form between *Ss. decurrens* and *S. peronii*, eight samples of *S.* subgenus *Phyllotricha* (one *S. heteromorphum*, three *S. peronii*, one *S. sonderi*, one *S. decipiens*, two *S. varians* and one *S. verruculosum*), five *Carpophyllum*, four *S.* subgenus *Arthrophycus*, 10 *S.* subgenus
Sargassum, three Sirophysalis trinodis (Forsskål) Kützing, one Turbinaria gracilis Sonder, and one Landsburgia quercifolia J. D. Hooker & Harvey, with the latter two species used as outgroups. The alignments contained 566 nt positions of ITS-2 sequences, 541 nt of cox3 and 192 nt of the rbcL–S spacer region (flanked by 527 nt of rbcL, and 68 nt of rbcS). The ITS-2 alignment had most variation with 70.8% variable sites, including 60.1% variable in the ingroups. The cox3 and rbcL–S spacer alignments had 30.3% and 20.1% variable sites respectively, with 25.7% and 14% variable in the ingroups. The concatenated ML consensus tree in Figure 2:1 shows posterior probability values taken from Bayesian trees with the same topology. Phylograms from individual loci (available from author) differed slightly from the concatenated analyses as outlined below. Six well supported ingroups formed in all analyses, (i) S. subgen. Sargassum and (ii) S. subgen. Arthropycus, which formed sister groups, (iii) Sirophysalis trinodis was sister to those above, (iv) S. subgen. Phyllotricha species, with the exception of S. peronii and S. heteromorphum, formed a monophyletic group sister to (v) Carpophyllum, and (vi) Ss. decurrens, S. peronii and S. heteromorphum, which were identical on all three loci except S. heteromorphum, differing by one nucleotide in cox3 and four nucleotides in rbcL–S spacer sequences.

Discussion

Our results indicate that Sargassum and S. subgenus Phyllotricha are both polyphyletic. Sargassum subgenus Sargassum and S. subgenus Arthropycus grouped into monophyletic sister taxa with Sirophysalis trinodis the nearest related neighbour. Sargassum subgenus Phyllotricha formed two distinct groups, the first a monophyletic sister to Carpophyllum and the second with Sargassopsis. The first S. subgen. Phyllotricha group included four species (S. decipiens, S. sonderi, S. varians, S. verruculosum) including S. sonderi, the type species of Phyllotricha. Taxonomically, this presents three options, either: (i) Recognize a more broadly conceived Sargassum containing Sirophysalis, S. subgen. Phyllotricha and Carpophyllum; (ii) Reinstate Phyllotricha Areschoug (1854) at genus level; or (iii) Include four species of S. subgen. Phyllotricha in Carpophyllum. Considering the overall complexity of the genus Sargassum and the morphological differences between the taxa concerned (outlined below), as well as the recent revisions of Sargassaceae, with four genera reinstated (including Sargassopsis and Sirophysalis) and one new genus established by Draisma et al. (2010), it seems appropriate to recognize this genetic and morphological variability at genus level and
reinstate *Phyllotricha*. Aside from the type, *P. sonderi*, Areschoug included one other member in the original *Phyllotricha* diagnosis, *Phyllotricha spartioides* (Turner) Areschoug, presently considered a synonym of *Cystophora moniliformis* (Esper) Womersley & Nizamuddin. We therefore propose to resurrect the genus *Phyllotricha* with type species *P. sonderi*, and additionally include the species *Phyllotricha decipiens*, *Phyllotricha varians*, and *Phyllotricha verruculosum*. Although *P. verruculosum* had low ML bootstrap, the following values supported its placement within *Phyllotricha*: 66 in the concatenated analysis, 61 in the ITS-2, <50 in the *rbc*L–S spacer and <50 in the *cox*3 analysis, and the BI analyses had mostly high posterior probability support values for this branch: 1 in the concatenated, 0.9868 in the ITS-2, 0.9813 in the *rbc*L–S spacer and <0.5 in the *cox*3 analysis. Furthermore, the morphological affinity of *S. verruculosum* to other *Phyllotricha* species is unquestionable. *Phyllotricha* species have a short primary axis arising from the holdfast, giving rise to indeterminate primary branches that bear laterals, vesicles and reproductive structures (Fig. 2:2A). In *Carpophyllum* the primary axis arising from the holdfast gives rise directly to determinate laterals (Fig. 2:2B).

The resurrection of the genus *Sargassopsis* (Draisma et al. 2010) including *Ss. decurrens* was supported. The morphologically similar *S. peronii* was genetically identical to *Ss. decurrens* and we propose that the former be synonymised with the latter. Womersley (1954, 1987: 345) distinguished *S. peronii* by the presence of basally constricted, nearly always simple laterals, and *S. decurrens* by laterals that are always divided without constrictions. J. Agardh’s (1889) drawings fail to distinguish clearly the differences between the two species. Observed specimens were compared with descriptions and photographs of the type specimens of *Ss. decurrens*, *S. peronii* and their synonyms (*Ss. decurrens* holotype in BM, photograph AD-A70490; *Sargassum scabripes* J. Agardh holotype in LD, photograph AD-A70491 [synonym of *S. decurrens*]; *S. peronii* type in PC, photograph AD-A73384; *S. peronii* Turner’s specimen in Kew AD-A73380; *S. boryi* type in LD, photograph AD-A73385 [synonym of *S. peronii*]). Both forms appear to be extremes along a continuum of intermediate forms, represented by specimens from this study in Figure 2:3. Given that all sequences of the two species generated were identical across the three loci, the synonymy of *S. peronii* is proposed below. *Sargassum heteromorphum* was also genetically similar to *Ss. decurrens*. Morphologically the two species
differ primarily in their vesicle and receptacle size, however their axes and lateral constructions are identical, thus the addition of *S. heteromorphum* to *Sargassopsis* is proposed. *Sargassum kendrickii* was not collected during this study owing to its restricted distribution, recorded only in the Recherche Archipelago, W. A. at depths greater than 10 m. While no fresh material could be obtained for molecular analysis, morphological examination of the type voucher (PERTH 07037422), and specimens of *Sargassum flindersii* Womersley (2004: 205–206) in AD, found to represent the earlier described *S. kendrickii*, were in agreement with *Sargassopsis*. The combination *Sargassopsis kendrickii* is proposed with *S. flindersii* placed in synonymy.


The proposed taxonomic changes and morphological distinctions between genera of *Phyllotricha* and *Sargassopsis* are presented below, followed by a key to the five genera presented in this study.

**Proposed taxonomic changes and morphological distinctions in *Phyllotricha***

**Reinstatement and new combinations:**


*Phyllotricha varians* (Sonder) R.R.M.Dixon & Huisman, comb. nov.
**Basionym:** *Sargassum varians* Sonder, *Nova algarum genera et species, quas in itinere ad oras occidentales Novae Hollandiae*, collegit L.Priess, Ph. Dr., *Botanische Zeitung* 3: 51 (1845). T.: W.A.

*Phyllotricha verruculosum* (C.Agardh) R.R.M. Dixon & Huisman, comb. nov. *Basionym:* *Sargassum verruculosum* C.Agardh, *Species algarum* ... 26 (1820). T.: King George Sound, W.A.

**Distinction between Phyllotricha and Carpophyllum**

In *Carpophyllum* the holdfast is a flattened extension of the singular primary axis (which is itself flattened in all species except *C. angustifolium*) that creeps over the substrate bearing a few peripheral rhizoids (Fig. 2:2C). The primary axis also gives rise directly to vegetative and reproductive laterals, whereas *Phyllotricha* has a discoid-conical holdfast (rarely becoming divided forming haptera) producing one or several primary axes that give rise to primary branches from which the laterals arise (Fig. 2:2A).

**Distinction between Phyllotricha and Sargassum:** In *Phyllotricha* the basal laterals are usually branched, most commonly in a pinnate arrangement. Primary branches may be terete, compressed or angular but never triquetrous. A few *Sargassum* species also have occasional branched lower laterals [e.g., *Sargassum linearifolium* (Turner) C. Agardh] but they are never pinnate, and the plants are also distinct in their complex densely clustered receptacles and spinous axes.

**Proposed taxonomic changes and morphological distinctions in Sargassopsis**

*Synonymies and new combinations:*


Sargassopsis kendrickii (N.A.Goldberg & Huisman) R.R.M.Dixon & Huisman, comb. nov.


Distinction between Sargassopsis, Phyllotricha and Sargassum: In Sargassopsis primary branches are compressed and leaf-like, often described as winged, with a central midrib and complanate, distichous laterals. Primary branches in Phyllotricha and Sargassum, if thinly compressed, are not leaf-like.

Key to the genera Sargassum, Sargassopsis, Phyllotricha and Carpophyllum

1. Primary axis directly giving rise to determinate laterals, often with a creeping rhizoidal holdfast ..............................................................Carpophyllum

1. Primary axes producing several primary branches that give rise to vegetative laterals……2

2. Primary branches compressed and leaf-like, winged with a central midrib giving rise to complanate distichous laterals.................................................................Sargassopsis

2. Primary branches terete, angular or compressed, not leaf-like.................................3

3. Lower laterals nearly always branched, most commonly in a pinnate arrangement; primary branches never triquetrous, and if compressed, give rise to retroflex laterals.................................................................Phyllotricha

3. Lower laterals entire, or if branched, they are never pinnate and are born on plants with densely clustered, branched receptacles (Sargassum linearifolium).................................4

4. Vesicles usually born on chains, primary branches terete and spinous, leafy laterals with highly acute apices.................................................................Sirophysalis trinodis

5. Vesicles always singular.................................................................Sargassum
Acknowledgements

We would like to thank the following people, programs and institutions who helped make this study possible: the Australian Census of Coral Reef Life (CReefs) and the Western Australian Museum for field and financial support. The Australian Postgraduate Award and Australian Biological Resources Study for financial support to RRMD and JMH. Many thanks to Lydiane Mattio, Mike Bunce, Joe Zuccherello, Nicole White and Morten Allentoft for assistance with molecular work. To Kyatt Dixon, Gary Saunders, Gerry Kraft, Gareth Belton, Shawn Smith, David Vize, Sean Flynn and Mark Langdon for field assistance and specimen contributions.

Figure legends

Table 2:1. Samples analysed in this study. DNA sequences with GenBank accession numbers in bold were generated by R.R.M.D. in the present study. The new sequences were submitted to GenBank by R.R.M.D.


Fig 2:1. Sargassum and related genera Maximum Likelihood consensus tree based on cox3, rbcL–S and ITS-2 sequence data combined with bootstrap (left) and BI posterior probability (right) values at nodes, with ‘#’ indicating a bootstrap value of 100% and ‘–’ indicating values of less than 50% bootstrap, 0.5 posterior probability.

Fig 2:2. (A and B) Schematic morphology of Phyllotricha (A) and Carpophyllum (B). (C) Carpophyllum holdfast, scale bar = 10 mm (J. Buchanan).

Fig 2:3. The range in morphology of Sargassopsis decurrens. (A) AD-A85922, clear basal constrictions on lateral branches, all laterals entire (none divided). (B) PERTH 08286256, slight to negligible basal constrictions on lateral branches, laterals divided in upper branches only. (C) PERTH 08286280, lateral branches divided yet leaf-like. (D) IRD1602, lateral branches divided, becoming filiform (photo: L. Mattio).
Figure 2:2
Table 2:1. Samples analysed in this study

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<td>(Turner) C.Agardh</td>
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<td><em>Sargassum paradoxum</em></td>
<td>PERTH 08286485</td>
<td>Figure of Eight I., W.A.</td>
<td>R.R.M. Dixon</td>
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<tr>
<td>(R.Brown ex Turner) Gaillon</td>
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<tr>
<td>(R.Brown ex Turner) Gaillon</td>
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<tr>
<td><em>Sargassum spinuligerum</em></td>
<td>AD-A88645</td>
<td>Ningaloo Reef, W.A.</td>
<td>R.R.M. Dixon &amp; C.F. Gurgel</td>
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<tr>
<td>Sonder</td>
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<tr>
<td><em>Sargassum spinuligerum</em></td>
<td>AD-A88644</td>
<td>Ningaloo Reef, W.A.</td>
<td>R.R.M. Dixon &amp; C.F. Gurgel</td>
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<tr>
<td>Sonder</td>
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<td></td>
<td></td>
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<tr>
<td>J.Agardh</td>
<td></td>
<td></td>
<td></td>
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<tr>
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<td>R.R.M. Dixon</td>
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<td>J.M. Huisman</td>
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<tr>
<td>C.Agardh</td>
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<td></td>
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<tr>
<td><em>Sargassopsis decurrens</em></td>
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<td></td>
</tr>
<tr>
<td>(R.Brown ex Turner) Trevisan</td>
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<td><em>Sargassopsis decurrens</em></td>
<td>AD-A89508B</td>
<td>Ningaloo Reef, W.A.</td>
<td>R.R.M. Dixon &amp; C.F. Gurgel</td>
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<td>(R.Brown ex Turner) Trevisan</td>
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<td><em>Sargassopsis decurrens</em></td>
<td>PERTH 08286280</td>
<td>Adele I., W.A.</td>
<td>R.R.M. Dixon</td>
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<tr>
<td>(R.Brown ex Turner) Trevisan</td>
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</tr>
<tr>
<td>Species</td>
<td>Accession</td>
<td>Location</td>
<td>Collector</td>
<td>Ref 1</td>
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<td>----------------------------------------------</td>
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<tr>
<td>Sargassopsis decurrens (R. Brown ex Turner) Trevisan</td>
<td>IRD1526</td>
<td>New Caledonia</td>
<td>L. Mattio</td>
<td>EU10080 3.1</td>
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<td>Sargassopsis decurrens (R. Brown ex Turner) Trevisan</td>
<td>IRD1602</td>
<td>New Caledonia</td>
<td>L. Mattio</td>
<td>EU88226 7.1</td>
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<td>IRD4010</td>
<td>New Caledonia</td>
<td>L. Mattio</td>
<td>EU88226 6.1</td>
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<td>R.R.M. Dixon &amp; G.S. Belton</td>
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<td>R.R.M. Dixon &amp; G.S. Belton</td>
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<tr>
<td>Carpophyllum maschalocarpum (Turner) Greville</td>
<td>WELT A031309</td>
<td>Pukerua Bay, NZ</td>
<td>J. Buchanan</td>
<td>JN637977</td>
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<tr>
<td>Carpophyllum plumosum (A. Richard) J. Agardh</td>
<td>WELT A031824</td>
<td>Riversdale, Wairarapa, NZ</td>
<td>J. Buchanan</td>
<td>JN637979</td>
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<td>Riversdale, Wairarapa, NZ</td>
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<td>Carpophyllum angustifolium J. Agardh</td>
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<td>Waterfall Reef, Leigh, NZ</td>
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<td>JN637980</td>
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<td>Carpophyllum flexuosum (Esper) Greville</td>
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<td>JN637976</td>
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<td>Turbinaria gracilis Sonder</td>
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<td>Adele I., W.A.</td>
<td>R.R.M. Dixon</td>
<td>JN243839</td>
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<tr>
<td>Landsburgia quercifolia J.D. Hooker &amp; Harvey</td>
<td>WELT A031933</td>
<td>Wellington, NZ</td>
<td>J. Buchanan</td>
<td>JN637978</td>
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<table>
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<tr>
<th>Feature</th>
<th><em>Sargassopsis decurrens</em> (R.Brown ex Turner) V.B.A.Trevisan</th>
<th><em>Sargassum peronii</em> C.Agardh</th>
<th><em>Sargassum sonderi</em> (J.Agardh) J.Agardh</th>
<th><em>Sargassum decipiens</em> (R.Brown ex Turner) J.Agardh</th>
</tr>
</thead>
<tbody>
<tr>
<td>Height</td>
<td>10–20 (–50) cm</td>
<td>To 80 cm</td>
<td>10–50 cm</td>
<td>10–50 cm</td>
</tr>
<tr>
<td>Colour</td>
<td>Medium brown</td>
<td>Brown</td>
<td>Medium brown</td>
<td>Medium brown</td>
</tr>
<tr>
<td>Holdfast</td>
<td>Discoid-conical, 5–15 mm across, one to several stipes</td>
<td>Discoid-conical</td>
<td>Discoid-conical, 5–20 mm across, one</td>
<td>Discoid-conical 3–5 (–18) mm across, one (–3)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>to several stipes</td>
<td>stipes</td>
</tr>
<tr>
<td>Primary axis</td>
<td>Simple to branched, slightly compressed, verrucose, 1–12 cm</td>
<td>Slightly compressed,</td>
<td>Occasionally branched, sub-terete</td>
<td>Simple to branched sub-terete at base,</td>
</tr>
<tr>
<td></td>
<td>long, 2–4 mm broad</td>
<td>verrucose, to 10 cm long, 1–3</td>
<td>top, 2–22 cm long, 2–6 mm broad</td>
<td>compressed at top, 2–15 cm long</td>
</tr>
<tr>
<td>Primary branch</td>
<td>(One to several) Distichous, complanately branched,</td>
<td>(Several) Distichous, pinnate</td>
<td>(2–12) Radially branched, much</td>
<td>(2–8) Radially branched, densely clustered</td>
</tr>
<tr>
<td></td>
<td>compressed with prominent midrib and lateral wings, 5–15 mm</td>
<td>with a prominent midrib and</td>
<td>divided, angular but not compressed</td>
<td>laterals below (esp. when sterile), angular,</td>
</tr>
<tr>
<td></td>
<td></td>
<td>broadly winged axes, to 40 cm</td>
<td>axes, 5–40 cm long, 0.75–1.5 mm diam.</td>
<td>2–40 cm long, 1.5–2 mm diam.</td>
</tr>
<tr>
<td>Basal laterals</td>
<td>Alternate, simple or becoming branched 1–3 times below,</td>
<td>Alternate, simple or</td>
<td>Pinnate 3–6 (–10) cm long, with linear</td>
<td>Simple or once or twice divided, compressed to</td>
</tr>
<tr>
<td></td>
<td>more above, not or slightly basally constricted,</td>
<td>occasionally branched but</td>
<td>branchlets 1–3 cm long, 2–4 (–5) mm</td>
<td>subterete, 1–4 cm long, 0.5–2 mm broad</td>
</tr>
<tr>
<td></td>
<td>tapering to apex, 1–4 cm long, 10 mm broad</td>
<td>variable with some simple</td>
<td>broad</td>
<td></td>
</tr>
<tr>
<td>Upper laterals</td>
<td>Simple or divided, to 2 cm long and 3–4 mm broad</td>
<td>Simple or rarely divided, up</td>
<td>Deeply pinnate, becoming filiform</td>
<td>Much branched with filiform, terete ramuli,</td>
</tr>
<tr>
<td></td>
<td></td>
<td>to 2 cm long, 3–4 mm broad</td>
<td>above, terete to compressed, 1–3 cm</td>
<td>1–3 cm long</td>
</tr>
<tr>
<td>Vesicles</td>
<td>Borne in axes of laterals or upper ramuli, subspherical</td>
<td>Borne regularly in axes of</td>
<td>Petiolate, subsperical 1–2 (–3) mm</td>
<td>Petiolate, subsperical to ovoid, 1–2 (–3) mm</td>
</tr>
<tr>
<td></td>
<td>3–6 mm diam., mutic or rarely with a slender mucro 2–10</td>
<td>each lateral on main and</td>
<td>in diam. mutic or with a slender</td>
<td>in diam., with a short or longer mucro</td>
</tr>
<tr>
<td></td>
<td>mm long</td>
<td>secondary branches, spherical,</td>
<td>apical mucro</td>
<td></td>
</tr>
<tr>
<td>Receptacles</td>
<td>In racemose clusters on upper ramuli, petiolate, simple</td>
<td>Distichous, simple to</td>
<td>In racemose clusters on upper ramuli,</td>
<td>In racemose clusters on upper ramuli, petiolate,</td>
</tr>
<tr>
<td></td>
<td>or once divided, terete, smooth, linear-lanceolate, 2–8</td>
<td>furcate, terete, smooth,</td>
<td>petiolate, simple, shorty</td>
<td>petiolate, lanceolate to elongate-ovoid,</td>
</tr>
<tr>
<td></td>
<td>mm long, 0.4–1 mm diam.</td>
<td>linear-lanceolate, 3–8 mm</td>
<td>lanceolate, smooth, 1–2 mm long, 500–800</td>
<td>occasionally branched, 1–7 mm long 300–1200 µm</td>
</tr>
<tr>
<td></td>
<td></td>
<td>long, 0.5–1 mm broad</td>
<td>µm diam.</td>
<td></td>
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31
<table>
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<tr>
<th>Feature</th>
<th>Sargassum varians Sonder</th>
<th>Sargassum verruculosum C.Agardh</th>
<th>Sargassum heteromorphum J.Agardh</th>
<th>Sargassum kendrickii N.A.Goldberg &amp; Huisman</th>
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</thead>
<tbody>
<tr>
<td>Height</td>
<td>10–50 cm</td>
<td>10–100 cm</td>
<td>10–45 cm</td>
<td>To 35 cm</td>
</tr>
<tr>
<td>Colour</td>
<td>Medium to dark brown</td>
<td>Medium to dark brown</td>
<td>Dark brown</td>
<td>Light to medium brown</td>
</tr>
<tr>
<td>Holdfast</td>
<td>Discoid-conical 5–20 mm across, one (to a few) stipes</td>
<td>Discoid-conical, becoming divided or hapteroid, 2–20 mm across, 2–10 mm high</td>
<td>Discoid-conical, becoming lacerate, 5–15 mm across with one (–3) stipes</td>
<td>Discoid-conical 12–24 mm across with a single stipe</td>
</tr>
<tr>
<td>Primary axis</td>
<td>Sub-terete to compressed, 2–10 cm long, 2–4 mm broad</td>
<td>Terete, 1–6 mm long, 2–3 mm broad</td>
<td>Terete, 0.5–2 cm long 1–3 mm broad</td>
<td>Terete, 18–20 mm long, 2–7 mm broad</td>
</tr>
<tr>
<td>Primary branch</td>
<td>(2–4) Compressed, leaf-like, with central midrib, 5–40 cm long, 3–5 (–7) mm wide</td>
<td>(2–6) Smooth, subterete, 10–90 cm long, 1–1.5 (–3) mm diam.</td>
<td>(1–3) Compressed, complanately branched below, with midrib, 10–40 cm long, 5–10 mm wide</td>
<td>(4–9) Terete, radial, 10–33 cm long, 3–5 mm wide</td>
</tr>
<tr>
<td>Basal laterals</td>
<td>Retroflex, compressed, simple becoming pinnate, margins smooth to curly, apices rounded to acute, 3–13 cm long, 2–10 mm wide</td>
<td>Retroflex, irregularly pinnate 3–5 cm long with branches 1–3 (–4) mm broad</td>
<td>Alternately pinnate, linear with rounded to acute apices, 2–5 cm long below 3–6 (–9) mm broad</td>
<td>Slightly twisted at base, alternately branched, broad, pinnate, margins serrated, 5.5–13 cm long, 2–6 mm broad</td>
</tr>
<tr>
<td>Upper laterals</td>
<td>Irregularly radial, a sharp transition from the lower laterals, pinnate with filiform ramuli, 0.5–2 cm long</td>
<td>Densely branched, filiform, rigidly subdichotomous to laxly pinnate when older, (1–) 2–3 cm long</td>
<td>Becoming filiform, terete to compressed, irregularly branched, 2–5 cm long and 200–500 (–800) µm broad</td>
<td>Alternate, flattened, pinnate, costate, alternate simple spiny ramuli 3–9 mm long, 3–5 mm broad</td>
</tr>
<tr>
<td>Vesicles</td>
<td>Petiolate, subspherical, smooth, 2–10 mm diam. mutic or with a slender mucro to 2 mm long</td>
<td>Petiolate, subspherical, smooth, 4–10 mm diam. mutic or with short slender mucro to 1 mm long</td>
<td>Born on upper ramuli, petiolate, subsperical 1–3 mm diam. with a short, acute apical mucro</td>
<td>absent</td>
</tr>
<tr>
<td>Receptacles</td>
<td>In dense clusters, simple or divided at apices, ovoid to lanceolate, verrucose, 1–3 mm long, 0.5–1 mm diam.</td>
<td>Simple to occasionally branched, lanceolate, slightly torulose, with short petioles, 3–5 mm long, 400–800 µm diam.</td>
<td>In racemose clusters, terete, lanceolate, simple or divided, verrucose, sessile or pedicellate, 1.5–4 mm long, 0.3–1.2 mm diam.</td>
<td>In open clusters with short pedicels, torulose, 2–6 mm long, 1 mm broad</td>
</tr>
</tbody>
</table>
References


Mattio, L. & Payri, C.E. 2009. Taxonomic revision of *Sargassum* species (Fucales, Phaeophyceae) from New Caledonia based on morphological and molecular analyses. *Journal*
of Phycology 45: 1374–1388.


The previous chapter treated *Sargassum* subgen. *Phyllotricha*, the earliest subgenus to diverge from the rest of *Sargassum*. This study found that *Sargassum* was polyphyletic with *Phyllotricha* included and so the subgenus was raised and resurrected to the level of genus (*Phyllotricha* Areschoug). The next chapter continues the study of *Sargassum*, focusing on the subgenera *Arthrophycus* and *Bactrophycus*, with particular attention to their southern hemisphere species.
Chapter 3  North meets south – Taxonomic and biogeographic implications of a phylogenetic assessment of *Sargassum* subgenera *Arthrophycus* and *Bactrophycus* (Fucales, Phaeophyceae)

Rainbo R.M. Dixon¹, Lydiane Mattio²,³, John M. Huisman¹,⁴, Claude E. Payri³, John J. Bolton² and C. Frederico D. Gurgel⁵,⁶,⁷


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⁶State Herbarium of South Australia, Plant Biodiversity Centre, Hackney Road, G.P.O. Box 1047, Adelaide, SA 5001, Australia

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Statement of Authorship

North meets south – Taxonomic and biogeographic implications of a phylogenetic assessment of Sargassum subgenera Arthrophycus and Bactrophycus (Fucales, Phaeophyceae)


Dixon, R.R.M. (Candidate)

Contributed to initial manuscript conceptualization, collection and curation of specimens, DNA extraction, sequencing, data analysis, GenBank sequence submission, acted as lead author in drafting initial manuscript, coordinated addressing reviewers comments, prepared figures and tables.

I hereby certify that the statement of contribution is accurate

Signature: [Signature] Date: 14/07/15

Mattio, L.

Contributed to initial manuscript conceptualization and initial drafting, collection and curation of specimens, DNA extraction, sequencing, commented on and edited subsequent manuscript drafts.

I hereby certify that the statement of contribution is accurate

Signature: [Signature] Date: 04/03/2015

Huisman, J.M.

Contributed to initial manuscript conceptualization and initial drafting, collection and curation of specimens, commented on and edited subsequent manuscript drafts.

I hereby certify that the statement of contribution is accurate

Signature: [Signature] Date: 03/03/2015
Payri, C.E.

Contributed collection and curation of specimens, commented on and edited manuscript drafts.

I hereby certify that the statement of contribution is accurate

Signature: ___________________________ Date: 03/03/2015

Bolton, J.J.

Contributed collection and curation of specimens, commented on and edited manuscript drafts.

I hereby certify that the statement of contribution is accurate

Signature: ___________________________ Date: 03/03/2015

Gurgel, C.F.D.

Contributed to initial manuscript conceptualization, fieldwork, training and supervision in the DNA laboratory, commented on and edited manuscript drafts.

I hereby certify that the statement of contribution is accurate

Signature: ___________________________ Date: 07/03/2015
Abstract

The *Sargassum* subgenera *Bactrophycus* and *Arthrophycus* were considered to be geographically restricted to the northern and southern hemispheres, respectively. Phylogenetic analyses of 19 *Sargassum* subgenus *Bactrophycus* species and eight *Sargassum* subgenus *Arthrophycus* species, based on a concatenated dataset of the loci ITS-2, *cox3* and the *rbcL*-S spacer, showed that they formed a single clade, with *Arthrophycus* species nested within *Bactrophycus* section *Halochloa*. We merged the two subgenera as subgenus *Bactrophycus* and transferred “*Arthrophycus*” species to *Sargassum* section *Halochloa*. The genus now includes only the two subgenera, *Sargassum* and *Bactrophycus*, and both were found at temperate and subtropical latitudes; only subgenus *Sargassum* occurred at low latitudes near the equator, whereas subgenus *Bactrophycus* had an antitropical, disjunct distribution.

Introduction

*Sargassum* C. Agardh is a conspicuous canopy-forming marine brown algal genus found from cool-temperate to tropical latitudes worldwide. Several taxonomic rearrangements of the genus, guided by molecular data, have been proposed during the last two decades, these resulting in the reinstatement of old genera, the relegation of many species to synonymy, and the refinement of the original broad generic concept (Agardh 1820; Agardh 1848, 1889) (Mattio et al. 2010; Dixon et al. 2012). Currently the genus contains the three widely accepted subgenera *Arthrophycus* J. Agardh, *Bactrophycus* J. Agardh and *Sargassum* [commonly referred to prior to the 1980s as the subgenus *Eusargassum* (Tseng et al. 1985)], and 335 species (Guiry & Guiry 2013). The dynamic taxonomic history of the genus is best exemplified by revisions to sections of *Sargassum* subgenus *Sargassum* (Mattio et al. 2010; Mattio 2013), and to species of subgenus *Phyllotricha*, the latter now apportioned between the reinstated genera *Sargassopsis* Trevisan and *Phyllotricha* Areschoug (Draisma et al. 2010; Dixon et al. 2012). No studies to date have addressed both the molecular and morphological relationships between the current subgenera.

Agardh (1848) initially designated *Arthrophycus* as a section of *Sargassum* but later (1889) elevated it to a subgenus, at the same time creating the additional subgenera *Bactrophycus*, *Eusargassum*, *Phyllotricha* and *Schizophycus*. He distinguished *Arthrophycus* from *Bactrophycus* solely on the basis of receptacle morphology and credited them with 20 and 14
species respectively. *Bactrophycus* was characterized as having receptacles that are ‘simple siliquaeform and unarmed,’ whereas, those of *Arthrophycus* are ‘often compound, in branch axils, racemose or rarely sub-cymose, either terete and often unarmed or angular and often dentate’ (Agardh 1889). Yoshida (1983), however, demonstrated that many *Bactrophycus* species have a variable receptacle morphology that can frequently overlap with that of *Arthrophycus*. This and other morphological uncertainties have led to several transfers between the two subgenera. For example, *S. mcclurei* Setchell was first attributed to *Arthrophycus* (Setchell 1933), then transferred to *Bactrophycus* (Tseng et al. 1985), and most recently placed in subgenus *Sargassum* (Stiger et al. 2000).

Subgenus *Bactrophycus* was subdivided into four sections by Yoshida (1983): *Halochloa*, *Repentia*, *Spongocarpus* and *Teretia*. Tseng (1985) shortly afterward described a fifth section, *Phyllocystae*, based on vesicle morphology, but this was later transferred to subgenus *Sargassum* based on molecular implications (Stiger et al. 2000; Yoshida et al. 2002). Stiger et al. (2003) added section *Hizikia* to the subgenus, and Mattio & Payri (2011) merged sections *Repentia* and *Halochloa*. As a result, *Bactrophycus* currently contains 23 species arranged in the four sections *Halochloa*, *Hizikia*, *Spongocarpus* and *Teretia*. *Halochloa* species have predominantly triquetrous or sharply compressed (ancipitous) main branches that are basally retroflex, and receptacles that are triquetrous, angular, or compressed, rarely smooth. *Teretia* species have angulate main branches and receptacles that are always terete. *Spongocarpus* species lack primary branches entirely, and branches arise in the axils of subtending leaves, while *Hizikia* species have entirely terete leaves (Yoshida 1983, as *Hizikia fusiformis*). Several *Bactrophycus* species are widely used in food and medicine and are of economic value in Asia, such as *Sargassum fusiforme* (Harvey) Setchell (known as *Hijiki* in Japan), and

*Sargassum fulvllum* (Turner) C.Agardh (known as *Hondawara* in Japan and *Mojaban* or *Mom* in Korea (Madlener 1977).

Few taxonomic revisions have been proposed for *Arthrophycus*, although Womersley (1987) has presented an alpha-taxonomic monograph of the temperate-Australian species that make up the bulk of that section. Nine species are currently recognised (Agardh 1889; Womersley 1987; Cho et al. 2012), only four of which have featured in molecular studies to date (Phillips & Fredericq 2000; Mattio & Payri 2009; Dixon et al. 2012). The most recent result of molecular analyses was the transfer by Cho et al. (2012) of *S. fallax* from *Arthrophycus* to
Bactrophycus sect. Halochloa. Cho et al. (2012) provided no morphological details; however, our observations of the morphological similarities between Halochloa and S. fallax in axes and receptacle shape support this transfer.

Setchell (1931) was the first to suggest the biogeographic segregation of the subgenera, stating that Bactrophycus ‘is distinctly a group of East-Asiatic waters’; whereas, Arthrophycus species are ‘confined to the austral, or southern regions’. Yoshida (1983) furthered this, recognising the uncertainties in distinguishing between the subgenera using morphology, and attributed species to the two subgenera based on their geographical distribution ‘until [more] comparative studies are made’. Like Setchell, Yoshida considered species of Arthrophycus to be restricted to the southern hemisphere and those of Bactrophycus to the northern hemisphere (Yoshida 1983, 1989). East Asia is a hotspot of diversity for Bactrophycus (Tseng et al. 1985; Yoshida 1983, 1989), with all known species represented in Japan, while Arthrophycus species are known from Australia, New Zealand and southern Africa (Womersley 1987; Adams 1994; Silva et al. 1996). Based on preliminary molecular analyses, Mattio & Payri (2011) suggested that Arthrophycus and Bactrophycus may represent a single subgenus. Concordant with Mattio & Payri (2011) and Cho et al.’s (2012) molecular studies casting doubt on the separation of the two subgenera, members of both Arthrophycus and Bactrophycus share defining taxonomic features, i.e. triquetrous and ancipitous stems, and angular spinous receptacles. These were probably overlooked in the past as a result of the biogeographical biases of Setchell (1931) and Yoshida (1983).

Given the numerous uncertainties regarding their separation, the primary aim of the present study was to investigate the phylogenetic relationships between Arthrophycus and Bactrophycus, in order to evaluate whether their continued independent status is warranted.

Materials and methods

Specimens of Arthrophycus and Bactrophycus spp. were collected from Australia, New Zealand, South Africa, southern Madagascar, southern Mozambique, Japan (all regions in which they are native) as well as Europe (where S. muticum is introduced). A portion of the samples were processed in New Caledonia and South Africa by the second author and the remainder processed in Australia by the first author. Vouchers are lodged at the Bolus Herbarium, University of Cape Town (BOL), the Institut de Recherche pour le
Développement in New Caledonia (NOU-IRD), the State Herbarium of South Australia (AD), and the Western Australian Herbarium (PERTH). For morphology based identification, receptacle structure was examined using dissecting microscopes, and specimens were identified based on traditional characters, as described in Hooker & Harvey (1845), Agardh (1848, 1889), Womersley (1987), Adams (1994) and Yoshida (1983, 1998). Identifications were confirmed by direct comparison with type specimens or by comparison with images of type specimens, including Bryan Womersley’s type photo collection at AD and type photos from Global Plants http://plants.jstor.org/ or by requests to herbaria where necessary.

The nuclear ITS-2, mitochondrial cox3 and the chloroplast rbcL-S spacer (with partial rbcL and rbcS) were chosen for analysis using primers outlined in Mattio et al. (2008). The Japanese samples were PCR amplified using the methods of Mattio & Payri (2009) and sequenced by Macrogen (Macrogen Inc., Seoul, Korea). Australian samples were PCR amplified and sequenced using the methods from Dixon et al. (2012). The southwest Indian Ocean samples were processed at the Central Analytical Facility (Stellenbosch University, South Africa) and were PCR amplified and sequenced using the methods from Mattio et al. (2013).

In addition to sequences obtained for the present study, those published by Mattio et al. (2008), Mattio & Payri (2009), Mattio et al. (2009), Silberfeld et al. (2010) and Cho et al. (2012) were downloaded from GenBank. Each locus (ITS-2, rbcL-S and cox3) was aligned separately in Geneious Pro v.5.5.6 (Drummond et al. 2010) and manually corrected. Analyses were run on individual markers as well as a three-marker concatenated dataset. Models of evolution and parameters were obtained from jModelTest (Guindon & Gascuel 2003; Posada 2008) and were as follows: ITS-2, GTR+G, rbcL-S and cox3, GTR+I+G, concatenated, GTR+I. Bayesian Inference was performed with BEAST v.1.7.1 (Drummond et al. 2006; Drummond & Rambaut 2007) using estimated base frequencies, 4 C categories to model among-site rate heterogeneity, a relaxed lognormal molecular clock, a coalescent tree prior with a randomly generated starting tree, and run for 50 million generations. Every 5,000th generation was sampled and tree files were generated with branch lengths in substitutions. BEAST outputs were analysed in Tracer v1.5.0 (Rambaut & Drummond 2007) and the consensus tree created in TreeAnnotator, with 10% of the trees discarded as burn-in, then visualised in FigTree v1.3.1 (Drummond & Rambaut 2007).
Results

In total 11 *Bactrophycus* and seven *Arthrophycus* species were collected and identified during the present study. Of *Arthrophycus*, the following species were analysed: *Sargassum paradoxum* (R. Brown ex Turner) Gaillon, *Sargassum vestitum* (R. Brown ex Turner) C. Agardh, *Sargassum lacerifolium* (Turner) C. Agardh and *Sargassum tristichum* Sonder as described in Womersley (1987 from southern Australia), *Sargassum vigorosum* (from south-western Australia), *Sargassum sinclairii* (from New Zealand) and *Sargassum incisifolium* (from South Africa). Three morphotypes were not identified to species and were referred to as ‘*Sargassum sp.*’ Two further species, *Sargassum erosum* J.Agardh and *Sargassum globulariifolium* J.Agardh (both from New South Wales, Australia) were studied from herbarium vouchers in AD and type material from LD. The remaining *Arthrophycus* species, *Sargassum ensifolium* (C.Agardh) J.Agardh and *Sargassum laevigatum* J.Agardh were not available for study.

A total of 151 sequences from three loci were newly obtained from 57 samples collected in South Africa, southern Madagascar, Australia, New Zealand, Japan and Europe (Table 3:1). To this dataset were added sequences of *Bactrophycus* specimens from Korea (Cho *et al.* 2012). The concatenated dataset included 122 ITS-2 (nuclear), 104 *rbcL*-S (plastid) and 114 *cox3* (mitochondrial) sequences representing seven of the nine known *Arthrophycus* species and 20 of the 23 known *Bactrophycus* species, derived from a wide range of their known geographical distribution. Specimen numbers, collection details (or publication) and GenBank accessions are listed in Table 3:1.

Results of all analyses were broadly congruent, as was indicated by the concatenated dataset consensus tree that resulted from the Bayesian Inference analysis (Fig. 3:1). All four sections of *Bactrophycus* (*Halochloa*, *Hizikia*, *Teretia* and *Spongocarpus*) were represented as distinct and well-supported clades (PP = 1), with the exception of the monospecific section *Hizikia*, for which only one sequence was available. All *Arthrophycus* sequences appeared as a monophyletic group nested within the *Halochloa* clade. Resolution within this group was very poor, with only *S. incisifolium* well supported out of the eight *Arthrophycus* species represented. The remaining *Arthrophycus* sequences formed a well-supported monophyletic lineage sister to *S. incisifolium*. This group included 15 samples attributed to seven species, although there was little within-group branch support (<0.9 posterior probability) leaving these
species genetically unresolved.

Discussion

The triple-marker approach using ITS-2, cox3 and rbcL-S has been widely employed for phylogenetic studies of Sargassum and has led to a number of recent major taxonomic revisions (e.g. Mattio & Payri 2011; Cho et al. 2012; Dixon et al. 2012). Our results (Fig. 3:1) show that Arthropycus isolates, including a representative of the type species S. incisifolium (formerly known as Sargassum heterophyllum) nest as a monophyletic group within a clade representing Bactrophycus sect. Halochloa. Distinguishing Bactrophycus from Arthropycus species on grounds other than biogeography has long proved a challenge for taxonomists, and the features by which the two were originally separated are no longer defensible. A comparison of stem and receptacle morphology in species of Arthropycus and Bactrophycus sect. Halochloa revealed consistent similarities. All share predominantly triquetrous or strongly compressed (ancipitous) main branches that are basally retroflex, and receptacles that are triquetrous, angular, or compressed and usually spinous.

Given the morphological observations detailed above and the implications of our molecular-phylogenetic results, we propose that all species of Arthropycus and Bactrophycus section Halochloa be considered part of a single taxon. Although ‘Arthropycus’ appeared earlier in the literature than ‘Bactrophycus’, it was first coined as a section name (Agardh 1848) and therefore does not have priority outside this rank (ICN Art. 11.2, McNeill et al. 2012). Both ‘Arthropycus’ and ‘Bactrophycus’ were first used at subgenus level by Agardh (1889) and therefore have equal priority. Of the two, we have preferred ‘Bactrophycus’ in recognition of its greater diversity and widespread economic use in Asia. In doing so, we establish priority for this name (ICN Art. 11.5, McNeill et al. 2012).

Halochloa was initially described as a genus by Kützing (1843) and later recognised as a section of Sargassum by Yoshida (1983). Yoshida (1983) wrote ‘stat. nov.’, indicating that he regarded himself as the first to employ the name at this taxonomic level, and the section is commonly cited as Sargassum sect. Halochloa (Kützing) Yoshida (1983). However, this name is nomenclaturally superfluous, as Endlicher (1843) had previously included Halochloa as a section in Sargassum, thus predating section Arthropycus J.Agardh (1848). We therefore adopt Sargassum section Halochloa (Kützing) Endlicher as the name for the taxon that
includes the previous ‘Halochloa’ and now all ‘Arthrophycus’ species. With the recent transfer of section Repentia to Halochloa (Mattio & Payri 2011), section Halochloa of Bactrophycus now contains a total of 28 species from Australia/New Zealand, southern Africa, and East Asia.

A further result of our phylogenetic analyses is the nesting of Sirophysalis trinodis (Forsskål) Kützing (formerly Cystoseira trinodis Forsskål) within the Sargassum clade. This species was transferred from Cystoseira C. Agardh to the reinstated Sirophysalis Kützing by Draisma et al. (2010), who found the former to be polyphyletic. In our analyses Sirophysalis trinodis appears sister to subgenus Sargassum (Fig. 3:1), although with low support, and its position within Sargassum changes depending on the number of taxa and other variables of the BEAST run (data not shown). The paraphyly of Sirophysalis trinodis within Sargassum was consistent throughout all concatenated analyses performed. Morphological differences between Sirophysalis and Sargassum, namely the chained vesicles and apical receptacles in Sirophysalis compared to singular vesicles and axial receptacles in Sargassum, are significant, and for the present we defer any taxonomic revisions based on this result. Resolving this issue will require a comprehensive molecular analysis of the family Sargassaceae.

**Species boundaries within Sargassum section Halochloa**

The results of our phylogenetic analyses and new taxonomic proposal generate conflict with traditional morphological delineation of Halochloa species. In total, 115 sequences for 18 species belonging to this taxon was analysed, resulting in a poorly resolved cluster, this being especially true for the sequences representing the seven Australasian species (Fig. 3:1). Of the other species represented in Halochloa, only Sargassum micracanthum, S. incisifolium and S. tristichum were well supported. The remaining species were either polyphyletic (perhaps due to poor identification) or represented by singletons, and they exhibited low divergence. Similar shallow resolution had been observed previously for east-Asian species of Halochloa alone using either a one-marker (ITS-2, Stiger et al. 2000, 2003) or four-marker (ITS-2 + rbcL + psaA + cox3, Cho et al. 2012) approach. Low genetic divergence in Sargassum has commonly been attributed to a recent and rapid radiation with incomplete lineage sorting (Phillips et al. 2005; Mattio & Payri 2009).

The anatomical observations and measurements of recent collections, historical vouchers and
type material (Table 3:2) were made on morphotypes that were clearly referable to particular species but there were numerous specimens with intermediate morphologies. Several species concepts also cover a range of forms that encompass the critical features of other species, but whether these all-encompassing morphologies result from ecological factors, hybridization, or a genuine admixture of species is not clear. The lack of genetic variation observed in Australian and New Zealand members of *Halochloa*, as well as their overlapping morphologies, suggests that fewer species are present than currently recognised. Due to the relatively small sample size and the lack of genetic diversity across all three markers tested, we believe that the present study does not provide sufficient information for a final assessment of species boundaries. A range of other markers such as the mitochondrial COI, mt23S and adjacent spacer (mtsp) (Draisma *et al*. 2010; Mattio *et al*. 2010) and the chloroplast *rbcL* and *psaA* (Cho *et al*. 2012) have been tested on closely-related species of *Sargassum* but likewise did not provide better resolution. Where recent speciation events are occurring, genetic structure takes time to diverge (Nice & Shapiro 1999; Wang *et al*. 2008). Further marker discovery is necessary, although this may not yield a substantial increase in sequence divergence.

**Taxonomic Summary**

*Sargassum subgenus Bactrophycus J.Agardh 1889*


HETEROTYPIC SYNONYM: *Sargassum subgenus Arthrophycus* J.Agardh, 1848: 275, 286.

*Sargassum (Bactrophycus) section Halochloa* (Kützing) Endlicher 1843


SYNONYMS: *Sargassum section Arthrophycus* J.Agardh, 1848: 275, 286.

*Sargassum (Bactrophycus) section Halochloa* (Kützing) Yoshida, 1983: 113, 166, *nom. superfl*.

**Biogeographic implications**

The separation of subgenus *Bactrophycus* (of the northern hemisphere) from subgenus *Arthrophycus* (of the southern hemisphere) based on geographical distribution, as suggested
by Setchell (1931) and Yoshida (1983, 1989), is evidently not taxonomically defensible. Yet
the separation of these formerly independent taxa by a broad expanse of equatorial waters
from which both are now absent is of interest from a biogeographic viewpoint. Most of the
Arthrophyllum species occur in Australia (Agardh 1889; Grunow 1915; Womersley 1987).
Exceptions are the New Zealand-endemic Sargassum sinclairii (Adams 1994) and the South
African (Stegenga et al. 1997), southern Mozambique (Silva et al. 1996) and southern
Madagascar (this paper) Sargassum incisifolium. The absence of S. incisifolium in Mauritius
was noted by Mattio et al. (2013) and the single record from India (Srinivasan 1967) remains
unconfirmed. A large part of the northern hemisphere Bactrophyllum species occur in cool- to
cold-temperate regions of Japan, Korea, China and the southern Pacific coast of Russia (Tseng
1985; Yoshida 1983, 1989). Other species have been recorded from South East Asia but they
largely represent taxa since revised and transferred to Sargassum subgenus Sargassum (e.g.
Sargassum quin honense and Sargassum mcclurei, see Mattio & Payri 2011) or doubtful
records (see Yoshida 1983, 1989; Silva et al. 1987). A few subtropical collections have been
made of both Arthrophyllum and Bactrophyllum species from fringe regions of the tropics that
have some temperate elements; e.g. Ningaloo Reef in Western Australia, southern
Mozambique and north-east South Africa (this study), Ryukyu Island (Tsuda & Kamura
1991), Hong- Kong (Setchell 1933), Taiwan (Anon 2012), and the northern Philippines (Silva
et al. 1987). The lower latitudinal records of Bactrophyllum in the northern and southern
hemispheres are approximately 118° N and 218° S, respectively (Silva et al. 1987; this study),
and it is likely that only species of Sargassum subgenus Sargassum occur in equatorial tropical
regions (Yoshida 1989; Mattio et al. 2009).

The results of the present paper, and the taxonomic changes proposed, necessitate a
reconsideration of the distribution of Bactrophyllum. Bactrophyllum sect. Halochloa
consequently now contains species from temperate to subtropical regions of both the northern
(East Asia: Korea, China – incl. Taiwan, the northern Philippines and Japan) and southern
(south-west Indian Ocean: South Africa, Mozambique and Madagascar; Australia and New
Zealand) hemispheres (Fig 3:2). This antitropical and disjunct distribution is peculiar and
raises the question of how the closely related members of section Halochloa came to exist in
such distant regions. The nesting of a southern hemisphere Halochloa clade within the East-
Asiatic clade (itself nested in the East-Asiatic subgenus Bactrophyllum clade) suggests that the
common ancestor to members of section Halochloa was probably present in east Asia and
crossed the tropics only once, resulting in the observed antitropical distribution. Present day antitropical distributions in marine organisms are usually attributed to trans-equatorial migration during glacial periods when tropical waters were cooler (e.g. Ekman 1953; Lindberg 1991; Hilbish et al. 2000; Burridge 2002; Mabuchi et al. 2004). According to Lindberg (1991), at least two major periods of transequatorial exchange have occurred. The larger of the two took place during the late Pliocene (about 3.1 Ma), while a smaller exchange occurred during the Pleistocene glaciations. Considering the low level of accumulated divergence between the northern and southern hemisphere Halochloa taxa, a Pliocene (or earlier) exchange is unlikely.

Randall (1981) suggests that the sea-surface temperature may have only cooled one to two degrees C during the Pleistocene. Bactrophycus species can tolerate a wide range of physical stresses (Chu et al. 2012), including significant seawater-temperature variation [e.g. 10–25°C for Sargassum horneri (Choi et al. 2008), and up to 31°C for Sargassum macrocarpum (Haraguchi et al. 2005), and may remain viable while floating for long periods of time (Thiel & Gutow 2005; Yatsuya et al. 2008). A temperature change of only 1 or 2°C, combined with a narrower tropical region, such as occurred during the Pleistocene, may have been enough to allow limited dispersal through the tropics. Other hypotheses could include dispersal through the tropics via deeper and cooler tropical habitats, such as those discussed by Graham et al. (2007) for kelps, followed by vicariance when the climate became warmer.

Migration from Australia to the southwest Indian Ocean region could have occurred secondarily. The presence of Halochloa in both the south-western and eastern Indian Ocean may be due to the migration from western Australia via the North Equatorial Current, using localized upwelling habitats as stepping stones in epochs when tropical waters were cooler (Hommersand 1986). The alternative hypothesis is via the Antarctic Circumpolar Current (ACC), which is known to disperse floating macroalgae such as Durvillaea antarctica (Chamisso) Hariot and Macrocystis pyrifera (Linnaeus) C. Agardh clockwise around Antarctica (Waters 2008; Fraser et al. 2009; Macaya & Zuccarello 2010), and may have aided the dispersal of section Halochloa from Australia to South Africa via South America. The absence of Halochloa in Chile may seem somewhat inconsistent with this hypothesis, although ice scour may be a contributing cause for this phenomenon as it is known to have removed large areas of algae during the Last Glacial Maximum (18,000 to 21,000 yr ago).
(Macaya & Zuccarello 2010). A reliable molecular clock and (paleo)niche modelling is needed to discuss these and further hypotheses on the biogeography of section *Arthropycus*.

**Acknowledgements**

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**Figure captions**

Figure 3:1. *Sargassum* and related genera Bayesian Inference consensus tree based on concatenated *cox3*, *rbcL*-S and ITS-2 sequence data with BI posterior probability values greater than 0.9 displayed. FJ = Fiji; FP = French Polynesia; Fr = France; HI = Hawaii; JP = Japan; Mad = Madagascar; NC = New Caledonia; NL = Netherlands; NZ = New Zealand; SAf = South Africa; SAu = South Australia; SK = South Korea; Tas = Tasmania; Van = Vanuatu; WAu = Western Australia.

Figure 3:2. World distribution of *Sargassum* subgenus *Bactrophycus*.

Table 3:1. Collections used in this study. All samples DNA sequences given a citation were previously published on GenBank. DNA sequences with GenBank accession numbers in bold were generated by R.R.M.D. Those with GenBank accession numbers followed by ‘*’ were generated by co-authors or other contributors and published for the first time in the present study. The new sequences were submitted to GenBank by R.R.M.D.

Figure 3:1
Figure 3:2
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### Sargassum paradoxum (R. Brown ex Turner) Gaillon

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### Sargassum sinclairii J.D.Hooker & Harvey

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<td>KF281771 KF281968 KF281913</td>
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<td>C.Agardh</td>
<td>PERTH 08404178; Canal Rocks (33.6694 S, 114.9947 E), Western Australia; R.R.M. Dixon &amp; K.R. Dixon; Nov. 2009</td>
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**Sargassum nigrifolium** Yendo

PF1420; Cho et al. 2012

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IRD5215; Japan, Mitohama, Misaki; F. Mineur; Oct. 2010

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PF1359; Cho et al. 2012

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**Sargassum ringgoldianum** Harvey

IRD5221; Japan, Mitohama, Misaki; F. Mineur; Oct. 2010

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GENT-HV1951; Japan, Shikoku, Kochi Prefecture, Tosakure; H. Verbruggen & F. Mineur; 2009

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GENT-HV2083; Japan, Honshu, Shizuoka Prefecture, Shimoda; H. Verbruggen & F. Mineur; 2009

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SGAD0909016; Japan, Oishi, Yura, Sumoto, Awaji island; S.G.A. Draisma; Sept. 2009

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GENT-HV2005; Japan, Shikoku, Tokushima Prefecture, Izari; H. Verbruggen & F. Mineur; 2009

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GENT-HV2008; Japan, Shikoku, Tokushima Prefecture, Izari; H. Verbruggen & F. Mineur; 2009

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**Sargassum sagamianum** Yendo

PF1033; Cho et al. 2012

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**Sargassum serratifolium** (C.Agardh) C.Agardh

PF1439; Cho et al. 2012

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**Sargassum siliquastrum** (Mertens ex Turner) C.Agardh

PF1423; Cho et al. 2012

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**Sargassum yamadae** Yoshida & T.Konno

PF1430; Cho et al. 2012

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**Sargassum yezoense** (Yamada) Yoshida & T.Konno

PF1350; Cho et al. 2012

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**Sargassum cf. yamamotoi** Yoshida

GENT-HV2004; Japan, Shikoku, Tokushima Prefecture, Izari; H. Verbruggen & F. Mineur; 2009

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**S. sect. Hizikia**

**Sargassum fusiforme** (Harvey) Setchell

PF589; Cho et al. 2012

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**S. sect. Spongocarpus**
| Sargassum horneri (Turner) C.Agardh | IRD5219; Japan, Mitohama, Misaki; F. Mineur; Oct. 2010 | KF281783* KF281979* KF281925* |
| GENT-HV2037; Japan, Honshu, Wakajama Prefecture, Shirahama; H. Verbruggen & F. Mineur; 2009 | KF281799* KF281989* KF281941* |
| SGAD0909002A; Japan, Higashiura, Awaji Island; S.G.A. Draisma; Sept. 2009 | KF281797* – KF281939* |
| SGAD0909002B; Japan, Higashiura, Awaji Island; S.G.A. Draisma; Sept. 2009 | KF281798* – KF281940* |
| PF958; Cho et al. 2012 | JF931688 JF931740 JF931860 |
| PF1005; Cho et al. 2012 | JF931695 JF931747 JF931861 |
| Sargassum sp. 1 (HV1880, SGAD10) | GENT-HV1880; Japan, Shikoku, Ehime Prefecture, Ikata; H. Verbruggen & F. Mineur; 2009 | – KF281992* KF281944* |
| S. sect. Teretia | |
| Sargassum confusum C.Agardh | GENT-HV2010; Japan, Shikoku, Tokushima Prefecture, Izari; H. Verbruggen & F. Mineur; 2009 | KF281801* KF281991* KF281943* |
| IRD5240; Japan, Mitohama, Misaki; F. Mineur; Oct. 2010 | KF281789* – KF281931* |
| PF1372; Cho et al. 2012 | JF931682 JF931734 JF931852 |
| Sargassum fulvellum (Turner) C.Agardh | PF634; Cho et al. 2012 | JF931689 JF931741 JF931853 |
| Sargassum hemiphyllum (Turner) C.Agardh | PF584; Cho et al. 2012 | JF931692 JF931744 JF931854 |
| Sargassum miyabei Yendo | GENT-HV2007; Japan, Shikoku, Tokushima Prefecture, Izari; H. Verbruggen & F. Mineur; 2009 | KF281791* KF281985* KF281933* |
| IRD5220; Japan, Mitohama, Misaki; F. Mineur; Oct. 2010 | KF281792* KF281986* KF281934* |
| SGAD09090018; Japan, Oishi, Yura, Sumoto, Awaji island; S.G.A. Draisma; Sept. 2009 | KF281793* – KF281935* |
| Sargassum muticum (Yendo) Fensholt | PF1452; Cho et al. 2012 | JF931701 JF931753 JF931856 |
| PF1010; Cho et al. 2012 | JF931703 JF931755 JF931857 |
| Sargassum Miyabei Yendo | GENT-ODC1702; France, Roscoff; O. De Clerck & F. Steen; July 2008 | KF281781* KF281977* KF281923* |
### Sargassum sp. 1 (HV1880, SGAD10)

**Sargassum sp. 1**

NV “SGADNL”, Neetherlands, Zeelandbrug, Oosterschelde; S.G.A. Draisma; 1999

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### Sargassum thunbergii (Mertens ex Roth) Kuntze

**Sargassum thunbergii**

PF531; Cho et al. 2012

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**Sargassum patens**

PF1407; Cho et al. 2012

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### S. subgen. Sargassum

#### S. sect. Binderiana

**Sargassum aquifolium** (Turner) C.Agardh

IRD1582; Mattio et al. 2009

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**Sargassum patens**

PF1407; Cho et al. 2012

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**Sargassum ilicifolium** (Turner) C.Agardh

IRD3940; Mattio & Payri 2010

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**S. sect. Ilicifolia**

**Sargassum ilicifolium** (Turner) C.Agardh

IRD1618; Mattio et al. 2009

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**Sargassum patens**

PF1407; Cho et al. 2012

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</table>
**Phyllotricha varians** (Sonder)
R.R.M.Dixon & Huisman

PERTH 08286388; Dixon et al. 2012  
**JN243836**  **JN243795**  **JN243824**

PERTH 08286329; Dixon et al. 2012  
**JN243837**  **JN243796**  **JN243823**

**Sargassopsis decurrens** (R.Brown ex Turner) Trevisan

IRD1526; Mattio et al. 2008  
**EU100803**  **EU100822**  **EU100773**

IRD1602; Mattio et al. 2010  
**EU882267**  **EU882247**  **EU882258**

IRD4010; Mattio et al. 2010  
**EU882266**  **EU882246**  **EU882257**

PERTH 08286256; Dixon et al. 2012  
**JN243832**  **JN243791**  **JN243819**

AD-A85922; Dixon et al. 2012  
**JN243833**  **JN243792**  **JN243820**

PERTH 07700865; Dixon et al. 2012  
**JN243834**  **JN243793**  **JN243821**

**Sargassopsis heteromorphum** (J.Agardh)
R.R.M.Dixon & Huisman

AD-A93883; Dixon et al. 2012  
**JN243828**  **JN243799**  **JN243801**

**Sirophysalis trinodis** (Forsskål) Kützing

AD-A87712; Great Australian Bight (31.5453 S, 131.3750 E), South Australia; C.F. Gurgel & R.N. Baldock; Sept. 2008  

–  
**KF281961**  **KF281906**

AD-A87719; Great Australian Bight (31.5453 S, 131.3750 E), South Australia; C.F. Gurgel & R.N. Baldock; Sept. 2008  
**KF281765**  **KF281962**  **KF281907**

AD-A88230; Ningaloo Reef (21.8733 S, 113.9979 E), Western Australia, R.R.M. Dixon; June 2008  
**KF281761**  **KF281953**  **KF281898**

AD-A88639; Ningaloo Reef (22.6754 S, 113.6839 E), Western Australia; C.F. Gurgel & R.R.M. Dixon; May 2009  
**KF281763**  **KF281956**  **KF281901**

AD-A88643C; Ningaloo Reef (22.6655 S, 113.6540 E), Western Australia; C.F. Gurgel & R.R.M. Dixon; May 2009  

–  
**KF281957**  **KF281902**

AD-A88661; Ningaloo Reef (22.6712 S, 113.6424 E), Western Australia; R.R.M. Dixon; May 2009  
**KF281764**  **KF281958**  **KF281903**

AD-A89509; Ningaloo Reef (21.9120 S, 113.9618 E), Western Australia; M. Blazewicz-Paszkowycz; June 2008  
–  
**KF281951**  **KF281896**
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<td>AD-A90004</td>
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<tr>
<td>AD-A90167</td>
<td>Dixon et al. 2012</td>
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<td>AD-A92128</td>
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<td>AD-A92146</td>
<td>Dixon et al. 2012</td>
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<td>IRD4574</td>
<td>New Caledonia; C.E. Payri; Mar. 2009</td>
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<td>PERTH 08436010</td>
<td>Barrow I., Western Australia; anon; Aug. 2009</td>
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<tr>
<td>PERTH 08436029</td>
<td>Barrow I., Western Australia; anon; Aug. 2009</td>
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**Turbinaria conoides** (J. Agardh) Kützing

<table>
<thead>
<tr>
<th>Accession</th>
<th>Location</th>
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<th>Year</th>
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</thead>
<tbody>
<tr>
<td>PERTH 08286248</td>
<td>Dixon et al. 2012</td>
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**Turbinaria ornata** (Turner) J. Agardh

<table>
<thead>
<tr>
<th>Accession</th>
<th>Location</th>
<th>Collectors</th>
<th>Year</th>
</tr>
</thead>
<tbody>
<tr>
<td>IRD1536</td>
<td>Mattio et al. 2009</td>
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**Myagropsis myagroides** (Mertens ex Turner) Fensholt

<table>
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<th>Location</th>
<th>Collectors</th>
<th>Year</th>
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<td>PF1024</td>
<td>Cho et al. 2012</td>
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<tr>
<td>PF1052</td>
<td>Cho et al. 2012</td>
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</tr>
<tr>
<td>PF089</td>
<td>Cho et al. 2012</td>
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<table>
<thead>
<tr>
<th><strong>Thallus</strong></th>
<th><strong>Holdfast</strong></th>
<th><strong>Main branch</strong></th>
<th><strong>Leaves (primary)</strong></th>
<th><strong>Leaves (secondary)</strong></th>
<th><strong>Vesicles</strong></th>
<th><strong>Receptacles</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Sargassum paradoxum</em> (R.Brown ex Turner) Gaillon 1828: 355</td>
<td>20–100(-150) cm discoid 5-15(-25) mm across</td>
<td>robust, triquetrous, tristichous</td>
<td>simple, lanceolate L; W (mm)</td>
<td>linear L; W (mm)</td>
<td>subspherical with small terminal leaflet</td>
<td>female terete below, slightly compressed or triquetrous above with no or few spines L; W (mm)</td>
</tr>
<tr>
<td><em>Sargassum fallax</em> Sonder 1845: 52</td>
<td>20-100 cm discoid 5-20 mm across</td>
<td>triquetrous, tristichous</td>
<td>simple, lanceolate L; 50–200; 20–30</td>
<td>20–50; 3–10</td>
<td>subspheiral, mucronate or with terminal leaflet present</td>
<td>dioecious or monocious</td>
</tr>
<tr>
<td><em>Sargassum vestitum</em> (R.Brown ex Turner) C.Agardh 1820: 24</td>
<td>10-150 cm long discoid 5-15 mm across</td>
<td>moderately robust, triquetrous, tristichous</td>
<td>simple, lanceolate L; 40-100(-250); 5-15(-20)</td>
<td>10-30; 10-30</td>
<td>ovoid to ellipsoid with small mucro or terminal leaflet present</td>
<td>in dense racemose clusters</td>
</tr>
<tr>
<td><em>Sargassum tristichum</em> Sonder 1845: 51</td>
<td>10-60 cm discoid-conical 5-20 mm across</td>
<td>moderately robust, triquetrous, tristichous</td>
<td>simple, lanceolate L; 30-70(-100); 5-15</td>
<td>10-30; 1-5(-8)</td>
<td>subspheiral with small occasionally compressed mucro present</td>
<td>dense clusters, simple, compressed or triquetrous above with prominent spines along the ridges</td>
</tr>
<tr>
<td><em>Sargassum lacerifolium</em> (Turner) C.Agardh 1820: 15</td>
<td>10-60 cm discoid-conical</td>
<td>robust, triquetrous, tristichous</td>
<td>simple, lanceolate L; 40-100; (10-15)30</td>
<td>20-80; 2-10</td>
<td>subspheiral with terminal leaflet present</td>
<td>single or clustered in upper laterals</td>
</tr>
</tbody>
</table>

### Leaves

- **shape**
  - *Sargassum paradoxum*: simple, lanceolate
  - *Sargassum fallax*: simple, lanceolate
  - *Sargassum vestitum*: simple, lanceolate
  - *Sargassum tristichum*: simple, lanceolate
  - *Sargassum lacerifolium*: simple, lanceolate

- **margin**
  - *Sargassum paradoxum*: entire, strongly undulate or serrate
  - *Sargassum fallax*: entire, becoming slightly to moderately serrate
  - *Sargassum vestitum*: smooth, entire
  - *Sargassum tristichum*: entire to wavy or serrulate
  - *Sargassum lacerifolium*: slightly to deeply incised

- **midrib**
  - *Sargassum paradoxum*: conspicuous
  - *Sargassum fallax*: conspicuous
  - *Sargassum vestitum*: conspicuous
  - *Sargassum tristichum*: conspicuous
  - *Sargassum lacerifolium*: conspicuous

- **pedicel**
  - *Sargassum paradoxum*: retroflex
  - *Sargassum fallax*: reflex
  - *Sargassum vestitum*: reflex
  - *Sargassum tristichum*: cuneate
  - *Sargassum lacerifolium*: cuneate

- **base**
  - *Sargassum paradoxum*: asymmetrical
  - *Sargassum fallax*: asymmetrical
  - *Sargassum vestitum*: attenuate
  - *Sargassum tristichum*: asymmetrical
  - *Sargassum lacerifolium*: asymmetrical

- **apex**
  - *Sargassum paradoxum*: obtuse or acute
  - *Sargassum fallax*: obtuse or acute
  - *Sargassum vestitum*: obtuse or acute
  - *Sargassum tristichum*: obtuse or acute
  - *Sargassum lacerifolium*: obtuse or acute

### Vesicles

- **shape**
  - *Sargassum paradoxum*: linear
  - *Sargassum fallax*: linear
  - *Sargassum vestitum*: linear-lanceolate
  - *Sargassum tristichum*: linear-lanceolate
  - *Sargassum lacerifolium*: linear-lanceolate

- **pedicel diameter (mm)**
  - *Sargassum paradoxum*: 3–10
  - *Sargassum fallax*: 3–10
  - *Sargassum vestitum*: 5–10
  - *Sargassum tristichum*: 3–10
  - *Sargassum lacerifolium*: 3–10

### Receptacles

- **shape**
  - *Sargassum paradoxum*: female terete clusters
  - *Sargassum fallax*: terete and short-lanceolate or compressed above, usually simple, occasionally with a sterile awn
  - *Sargassum vestitum*: dense clusters, simple, compressed or triquetrous above with prominent spines
  - *Sargassum tristichum*: simple, clustered in upper laterals
  - *Sargassum lacerifolium*: simple, distinctly triquetrous usually with prominent spines

- **L; W (mm)**
  - *Sargassum paradoxum*: (3)-5–10(-15); 0.7–1.5
  - *Sargassum fallax*: 2.5(4); 0.3-0.9
  - *Sargassum vestitum*: (1)-2-3(-5); 0.5-1(-2)
  - *Sargassum tristichum*: 2-5(-8); 1-1.5(-2)
  - *Sargassum lacerifolium*: (2)-5-10(-17); (1-2)-3

- **reproduction**
  - *Sargassum paradoxum*: dioecious or monocious
  - *Sargassum fallax*: dioecious or monocious
  - *Sargassum vestitum*: dioecious or monocious
  - *Sargassum tristichum*: dioecious or monocious
  - *Sargassum lacerifolium*: dioecious or monocious

---

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<table>
<thead>
<tr>
<th>Type information</th>
<th>Reference</th>
<th>Type</th>
<th>locality</th>
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<tbody>
<tr>
<td><strong>Reference</strong></td>
<td>Womersley</td>
<td>Womersley</td>
<td>Womersley</td>
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<tr>
<td><strong>Type locality</strong></td>
<td>probably Tasmania or Kent Is., Bass Strait</td>
<td>Western Australia Kent Is., Bass Strait</td>
<td>Western Australia</td>
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<td>Type: BM00056352 (Robert Brown, #s.n.), BM000563348 (Robert Brown, #159)</td>
<td>BM000563352 (Robert Brown, #s.n.), BM000563348 (Robert Brown, #159)</td>
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<td>Type:</td>
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<td>BM000562941 (Johann August Ludwig Preiss, #s.n.)</td>
<td>BM000563352 (Robert Brown, #s.n.), BM000563348 (Robert Brown, #159)</td>
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<tr>
<td><strong>Sargassum erosum</strong> J.Agardh 1889:</td>
<td><strong>Sargassum vigorosum</strong> P.C.Silva 1996:</td>
<td><strong>Sargassum sinclairii</strong> J.D.Hooker &amp; Harvey 1845:</td>
<td><strong>Sargassum incisifolium</strong> (Turner) C.Agardh 1820:</td>
</tr>
<tr>
<td>-----------------------------------</td>
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<td>-----------------------------------</td>
</tr>
<tr>
<td>74, pl. XXIII: figs 1–6</td>
<td>706</td>
<td>522</td>
<td>14–15 to 50 cm, fairly rigid</td>
</tr>
<tr>
<td><strong>Thallus</strong></td>
<td></td>
<td></td>
<td>approx 1 ft.</td>
</tr>
<tr>
<td>22–45 cm</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Holdfast</strong></td>
<td><strong>Main branch</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>discoid-conical</td>
<td>triquetrous</td>
<td></td>
<td></td>
</tr>
<tr>
<td>conical</td>
<td>obovate</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Leaves (primary)</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>shape</td>
<td>emerging on side plane</td>
<td>lanceolate</td>
<td>emerged on side plane</td>
</tr>
<tr>
<td>L; W (mm)</td>
<td>24–50; 3–12</td>
<td>to 100 mm long</td>
<td>100; 15–20; (1.5)–2–3 ‘inches’</td>
</tr>
<tr>
<td>margins</td>
<td>entire or lightly serrate</td>
<td>lobed or toothed</td>
<td>entire</td>
</tr>
<tr>
<td>midrib</td>
<td>conspicuous</td>
<td>smooth to dentate</td>
<td>smooth to dentate</td>
</tr>
<tr>
<td>pedicel</td>
<td>thin, vanishing</td>
<td>thin, vanishing</td>
<td>thin, vanishing</td>
</tr>
<tr>
<td>base</td>
<td>retroflex</td>
<td>attenuate</td>
<td>retroflex</td>
</tr>
<tr>
<td>apex</td>
<td>asymmetrical</td>
<td>obtuse</td>
<td>cuneate-attenuate</td>
</tr>
<tr>
<td><strong>Leaves (secondary)</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>shape</td>
<td>linear-obovate</td>
<td>lanceolate</td>
<td>lanceolate to obovate</td>
</tr>
<tr>
<td>L; W (mm)</td>
<td>14–48; 2–8</td>
<td>5–25; 0.5–5</td>
<td>20–32; 4–13</td>
</tr>
<tr>
<td>margins</td>
<td>serrate</td>
<td>entire or slightly toothed</td>
<td>entire or slightly serrate</td>
</tr>
<tr>
<td>midrib</td>
<td>vanishing</td>
<td>remotely serrated</td>
<td>remotely serrated</td>
</tr>
<tr>
<td>apex</td>
<td>obtuse</td>
<td>obtuse to acute</td>
<td>obtuse to acute</td>
</tr>
<tr>
<td><strong>Vesicles</strong></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>shape</td>
<td>pyriform-elliptical</td>
<td>globose</td>
<td>spherical, awned or with apical</td>
</tr>
<tr>
<td>L; W (mm)</td>
<td>absent</td>
<td>awned</td>
<td>leaves long</td>
</tr>
<tr>
<td>pedicel diameter (mm)</td>
<td>present</td>
<td>slender</td>
<td>1.5–3</td>
</tr>
<tr>
<td></td>
<td>3–5</td>
<td>present</td>
<td>5–10</td>
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<tr>
<td><strong>Receptacles</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>shape</td>
<td>smooth to triquetrous, spinoi or</td>
<td>stalked, swollen, turbinate, lobed</td>
<td>laceolate, compressed or</td>
</tr>
<tr>
<td>L; W (mm)</td>
<td>with undulate margin</td>
<td>or toothed edges</td>
<td>triquetrous, bumpy to spinous</td>
</tr>
<tr>
<td>reproduction</td>
<td>1-3; 0.25-1</td>
<td>or with 3-4 apical spines above</td>
<td></td>
</tr>
<tr>
<td></td>
<td>monoecious</td>
<td>L:W 2-3:1</td>
<td>in axes of young leaves smooth,</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>terete, to compressed, spinous</td>
</tr>
<tr>
<td></td>
<td>1-6; 0.5-1.25</td>
<td></td>
<td>above L:W 2-3:1</td>
</tr>
</tbody>
</table>

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**Notes:**

- **Sargassum erosum** has a thallus ranging from 22–45 cm, with a holdfast and main branch described.
- **Sargassum vigorosum** has a thallus up to 40 cm, with a holdfast and main branch described.
- **Sargassum sinclairii** has a thallus up to 50 cm, with a holdfast and main branch described.
- **Sargassum incisifolium** has a thallus up to 50 cm, with a holdfast and main branch described.
- **Sargassum globulariifolium** has a thallus approx 1 ft, with a holdfast and main branch described.
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<tr>
<th>Type information</th>
<th>Reference</th>
<th>Type locality</th>
<th>Herbarium accession</th>
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<tbody>
<tr>
<td><strong>Type</strong></td>
<td>Agardh 1889: 74</td>
<td>Port Jackson, Port Stevens, N.S.W. Australia</td>
<td>BM000562940 (Ferdinand Jacob Heinrich von Mueller, #s.n.)</td>
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<td><strong>information</strong></td>
<td>Agardh 1889: 66-67; Grunow 1915: 355</td>
<td>Swan River, Western Australia</td>
<td>LD No. 2015-2011</td>
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<td><strong>Reference</strong></td>
<td>Adams 1994: 118, Hooker and Harvey 1845b: 522</td>
<td>Bay of Islands, New Zealand</td>
<td>BM000519551 (Joseph Dalton Hooker, #s.n.), BM000563661 (Anon., #s.n.), BM000563053 (Joseph Dalton Hooker, #s.n.) TCD0000075 (Drége, Jean François, #s.n.), TCD0000072 (W.H.Harvey #sn), TCD000007</td>
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<tr>
<td><strong>Type locality</strong></td>
<td>Cap. Bonae Spei. Illawarra, Port Jackson, Sydney</td>
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<tr>
<td><strong>Herbarium</strong></td>
<td>Jstor, Agardh 1889</td>
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<tr>
<td><strong>accession</strong></td>
<td>Agardh 1889: 69</td>
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**Type locality**
- Port Jackson, Port Stevens, N.S.W. Australia
- Swan River, Western Australia
- Bay of Islands, New Zealand
- Cap. Bonae Spei. Illawarra, Port Jackson, Sydney

**Herbarium accession**
- BM000562940 (Ferdinand Jacob Heinrich von Mueller, #s.n.)
- LD No. 2015-2011
- BM000519551 (Joseph Dalton Hooker, #s.n.), BM000563661 (Anon., #s.n.), BM000563053 (Joseph Dalton Hooker, #s.n.)
- TCD0000075 (Drége, Jean François, #s.n.), TCD0000072 (W.H.Harvey #sn), TCD000007
References


Hooker, J.D. & Harvey, W.H. 1845. Algae Novae Zelandiae; being a catalogue of all of the species of algae yet recorded as inhabiting the shores of New Zealand, with characters and brief descriptions of the new species discovered during the voyage of H. M. discovery ships “Erebus” and “Terror” and of others communicated to Sir W. Hooker by D. Sinclair, the Rev. Colenso, and M. Raoul. *London Journal of Botany* 4: 521–551.


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Herendeen, P.S., Knapp S., Marhold, K., Prado, J., Prud’homme Van Reine W.F., Smith
G.F., Wiersema, J.H. & Turland, N.J. 2012. *International code of nomenclature for algae,
fungi and plants* (Melbourne code) adopted by the eighteenth international botanical

Nice, C.C. & Shapiro, A.M. 1999. Molecular and morphological divergence in the
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Phillips, N. & Fredericq, S. 2000. Biogeographic and phylogenetic investigations of the
Pantropical genus *Sargassum* (Fucales, Phaeophyceae) with respect to Gulf of Mexico

*Sargassum* (Fucales, Phaeophyceae) using portions of the *rbcL*-S operon. *Phycological
Research* 53: 1–10.

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Adjoining paragraph

The previous chapter focused on the *Sargassum* subgenera *Arthrohycus* and *Bactrophycus* and resulted in the transfer of subgenus *Arthrohycus* to subgenus *Bactrophycus* section *Halochloa*. With the results of the second chapter also transferring all species of *S. subgen. Phyllotricha* outside the genus (to the genera *Phyllotricha* and *Sargassopsis*), the genus *Sargassum* is left with just two remaining subgenera, *Bactrophycus* and *Sargassum*. *Sargassum* is by far the largest of all the subgenera and an Australia-wide treatment was beyond the scope of this thesis. Instead part of a regional floristic monograph is presented here, of which the majority of species belong to *Sargassum subgen. Sargassum*. The next chapter investigates the biodiversity of the order Fucales in north-western Australia.
Chapter 4  Fucales

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Fucales


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I hereby certify that the statement of contribution is accurate

Signature: ___________________________ Date: 14/07/15

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Contributed to initial manuscript conceptualization and initial drafting, collection and curation of specimens, prepared figures and tables, commented on and edited subsequent manuscript drafts.

I hereby certify that the statement of contribution is accurate

Signature: ___________________________ Date: 03/03/2015
**Fucales Bory, Cryptogamie 62 (1827), as Fuci.**

Type: Fucaceae Adans.

Thallus large, bushy, frondose, many growing in beds. Growth from a conspicuous apical cell that is usually sunken in a terminal pit, persistent throughout the life of the plant; in some species the apical cell dividing with great precision and forming a typical plant body of dichotomous branching laterals radially arranged around axes. Cells containing several discoid plastids, lacking pyrenoids. Colourless vesicles containing fucosan, a tannin-like compound, are very common in outer cell layers, meristematic cells and reproductive cells, accounting for the dark brown colour of many plants. Reproductive organs developing within unisexual or bisexual conceptacles, embedded in apices of vegetative branches or on specialised branchlets (receptacles). Reproduction oogamous; oogonia with 1–8 uninucleate eggs; antheridia producing 64–128 small biflagellate sperms; liberation of eggs and sperms followed by fertilisation. Zygotes developing into new diploid plants. Life history diplohaplontic, heteromorphic; gametophyte phase reduced to the immediate post-meiotic formation of gametes.

This large order of seven families is found mainly in temperate seas. Together with the Laminariales (the kelps, not in N.W.A.), it includes the majority of large, conspicuous brown seaweeds; one family, five genera and 16 species in N.W.A.

Taxonomic designations at species, section and subgeneric level were assisted by molecular sequence data (Fig. 4:1). Collections were subsampled, preserved in silica, and representatives of each morphospecies were prepared and sequenced at the nuclear internal transcribed spacer (ITS-2), mitochondrial cytochrome oxidase 3 (cox3) and the chloroplast partial rbcL-S operon, following Dixon et al. (2012). The three individual loci were aligned separately in Geneious Pro v.5.5.6 (Drummond et al. 2010) and manually corrected. All analyses were run on the individual alignments as well as a concatenated alignment of the three markers. Maximum Likelihood (ML) analyses were conducted in PhyML (Guindon et al. 2010) using the model of evolution and parameters obtained from jModelTest (Guindon & Gascuel, 2003; Posada, 2008). Bayesian Inference was performed with BEAST v.1.7.1 (Drummond et al., 2006; Drummond & Rambaut, 2007), the concatenated dataset had the GTR + G substitution model, a coalescent constant size tree prior and a strict clock model. Markov Chain Monte Carlo runs were done for 50 million generations, sampled every
5000th generation and tree files were calculated with branch lengths in substitutions. These were monitored in Tracer v.1.5 (Rambaut & Drummond, 2007), a 10% burn-in was removed in TreeAnnotator v.1.6.1 (Drummond & Rambaut, 2007) and final trees were created in FigTree v.1.3.1 (Drummond & Rambaut, 2007). In the specimens examined sections of the following treatment, the GenBank accession numbers for DNA sequences associated with the collections are placed in bold where those sequences have been generated by R.R.M.D. Where GenBank accession number are followed by ‘*’ they have not been published/presented in the preceeding chapters of this thesis.

**SARGASSACEAE**


Type: *Sargassum* C.Agardh


Thallus erect, moderately large, from a discoid-conical holdfast, or stoloniferous with 1 or a few simple terete to compressed stipes bearing primary branches radially, distichously or tristichously. Primary branches themselves usually richly branched, with filiform leaf-like or obconical determinate laterals. Vesicles usually present, discrete or within ramuli. Structure parenchymatous, with a medulla, cortex and surface meristoderm. Receptacles seasonal on upper parts of branches, axillary or developed from laterals, simple or branched, terete to compressed or flat, smooth, verrucose or spinous. Conceptacles scattered or marginal, unisexual or bisexual; oogonia sessile, with a single egg; antheridia sessile or on branched paraphyses [modified from Womersley (1987: 418)].

A cosmopolitan family of 32 genera. The previously segregated *Cystoseiraceae* Kütz. is included here in the Sargassaceae based on the DNA sequence studies of Rousseau & De Reviers (1999), Harvey & Goff (2006) and Cho *et al.* (2006). Five genera are known from N.W.A.
KEY TO GENERA

1 Leaves distinctly turbinate, usually with marginal spines; vesicles present or absent, if present immersed in the outer part of the leaf .................................................. 5. TURBINARIA

1: Leaves triquetrous or terete and greatly reduced; vesicles discrete or in chains, or formed within lateral branches .......................................................... 2

2 Receptacles axillary; vesicles discrete, not in chains (1:) ........................................ 3

2: Receptacles not axillary; vesicles in chains or formed within lateral branches ....... 4

3 Thallus bilateral, with distinctly flattened axes (2) ......................... 2. SARGASSOPSIS

3: Thallus radial, with terete, triquetrous or flattened axes...................... 3. SARGASSUM

4 Thallus with triquetrous leaf-like laterals; vesicles, if present, not in chains (2:) ..... .......................................................... 1. HORMOPHYSA

4: Thallus without triquetrous leaf-like laterals; vesicles formed in chains of up to 4 .......................................................... 4. SIROPHYSALIS

1. HORMOPHYSA

Hormophya Kütz., Phycol. General. 359 (1843); from the Greek hormos (a chain) and physa (a bubble), presumably in reference to the arrangement of vesicles.

Type: H. triquetra (L.) Kütz. [= H. cuneiformis (J.F.Gmel.) P.C.Silva]

Thallus usually 10–40 cm tall, with a short stipe from a discoid-conical holdfast, bearing several ±straight primary branches. Primary branches with triquetrous interrupted wings and similar laterals arising from the branch rachis. Vesicles present within the primary and lateral branches, elongate, developing in the medulla. Growth from a single apical cell in an apical depression. Structure a central medulla of compact elongate cells and an extensive cortex of isodiametric cells decreasing in size to the surface phaeoplastic meristoderm; cryptostomata scattered over the entire frond. Conceptacles scattered throughout the thallus, but best developed in the walls of the
vesicles and thicker parts, bisexual; oogonia with a single egg [after Womersley (1987: 354)].

The monotypic Hormophysa is found throughout the tropical and subtropical Indo-Pacific, also extending to warm-temperate waters. Several names have been applied to forms of the type species (Papenfuss, 1968), which was commonly recorded as H. triquetra until Silva (Silva et al., 1987) investigated the nomenclature of the genus and updated the species name. Hormophysa is characterised by its triquetrous winged axes, the upper parts of which contain conceptacles and internal vesicles.


For a full list of synonyms, see Silva et al. (1996).


Thallus medium to dark brown, to 33 cm tall; holdfast to 8 mm wide. Primary branches smooth, terete, with triquetrously arranged lateral wings 10–60 mm long and 4–7 mm wide; vesicles forming centrally within the medulla of upper branches. Wings occasionally absent from a thallus or branch, the axes then appearing moniliform, or with one wing absent or reduced to spines; in that case the axes appearing as elongate leaves similar to *Sargassum*. Secondary branches 15–80 mm long, with serrated lateral wings 5–25 mm long and 0.5–9.0 mm wide. Vesicles elongate, 3.5–5.5 mm long, 1.0–2.5 mm wide. Cryptostomata dark, numerous, scattered over laterals. Thalli monoecious, with conceptacles scattered over the upper laterals. Oogonia sessile,
ovoid and broadly based, 40–110 μm long, 30–90 μm wide; antheridia on short simple or branched paraphyses, elongate-ovoid, 18–22 μm long, 11–15 μm wide. Fig. 4:2A. Pl. 4:1A.

Widespread in tropical and subtropical parts of the Indian and western Pacific Oceans. In Australia known from north of Rottnest Island, W.A., presumably across northern Australia to Qld; also in the upper Spencer Gulf, S.A.; epilithic in the intertidal and subtidal.

Specimens examined: North LeRoy Beach, Ningaloo, 2 m, 19 May 2010, G.S.Belton & C.F.D.Gurgel (AD A91693); Ningaloo, on sand and rock in lagoon, 7 m, 20 May 2010, G.S.Belton & C.F.D.Gurgel (AD A91730); Bateman Bay, Ningaloo, on limestone in sand, 6 m, 26 June 2010, R.R.M.Dixon (PERTH 08436509); Whites Beach, Barrow Is., 9 Feb. 2008, J.M.Huisman (PERTH 08436754); Turtle Is., intertidal, 13 May 2008, J.M.Huisman (PERTH 08436533); just off mainland shore opposite Haycock Is., northern Dampier Archipelago, 24 Aug. 1979, M.L.Cambridge (AD A51772); Montgomery Reef, intertidal, 22 Oct. 2009, R.R.M.Dixon [PERTH 08435928 (GenBank: KF281802)].

Our collections of Hormophysa cuneiformis include a range of morphological variation, from broadly foliose to having reduced (or absent) leaf-like laterals. At one extreme, the laterals lack wings entirely and appear moniliform. This was the form described by Mertens (1819: 189) as Fucus nodularius Mert. and examined in detail by Allender & Smith (1978). In another form, the wings are reduced to occasional spines on terete axes that also bear elongate leaf-like laterals. This form is highly reminiscent of Sargassum and was only attributed to Hormophysa following the discovery of specimens with some branches that were typically triquetrous. While most have clearly triquetrous axes, a few are triquetrous only on parts of the thallus, with the occasional spine, or a reduced third wing.

2. SARGASSOPSIS

Sargassopsis Trevis., Atti Riunione Sci. Ital. 4: 332–335 (1843); presumably named for its likeness to Sargassum.

T: S. decurrens (R.Br. ex Turner) Trevis.

Thallus erect from a discoid-conical holdfast, with 1–several subterete or terete primary axes bearing distichous pinnate or alternate primary branches giving rise to complanate laterals with or without basal constrictions. Vesicles axillary, spherical or
subspherical. Receptacles axillary, racemose, sessile or pedicellate, simple or branched, terete, lanceolate, smooth or verrucose. Conceptacles scattered, unisexual or bisexual.

*Sargassopsis* was resurrected by Draisma *et al.* (2010) for *Sargassum decurrens* after DNA sequence data showed *Sargassum* was polyphyletic with *S. decurrens* included. Two further species have been recognised [*S. heteromorphum* (C.Agardh) R.R.M.Dixon & Huisman and *S. kendrickii* (N.A.Goldberg & Huisman) R.R.M.Dixon & Huisman], while *Sargassopsis peronii* (C.Agardh) Trevis. has been placed into synonymy with *S. decurrens* by Dixon *et al.* (2012), giving the genus a total of three species. Only *S. decurrens* is known from N.W.A.


Thallus pale to medium brown, to 80 cm tall, with a discoid-conical holdfast 5–15 mm wide, usually giving rise to a single primary axis that is simple or branched, slightly
compressed, verrucose, with branch residues, to 12 cm long and 2–4 mm wide. Primary branches distichous, with a prominent midrib and lateral wings, 5–15 mm wide. Primary laterals complanate with primary branches, alternate, simple or divided, with or without a basal constriction, 2–5 cm long and up to 10 mm wide, tapering evenly toward the apex. Secondary branches arising in axils, alternate, distichous, with simple or divided laterals to 2 cm long and 3–4 mm wide. Cryptostomata irregularly arranged or in vague straight lines (on smaller laterals). Vesicles borne in axils, spherical, with a short stalk, to 6 mm diam., mutic or with a slender mucro 2–10 mm long. Receptacles on upper ramuli, stalked, simple or once-divided, terete, smooth, linear-lanceolate, 3–8 mm long, 0.5–1.0 mm diam. Fig. 4:2C–E. Pl. 4:2A.

Known from Bahrain, Iran, Kuwait, Qatar, Saudi Arabia, the United Arab Emirates, Pakistan and east to New Caledonia. In Australia it occurs from Cape Naturaliste, W.A., around northern Australia to Keppel Bay, Qld. Also in the upper Spencer Gulf, S.A.; epilithic in the subtidal, usually forming beds.


Sargassopsis decurrens is a common species in lagoons and other sheltered habitats in N.W.A. Moreover, it is one of the more readily identified Sargassaceae as its foliose, complanate, winged primary branches clearly distinguish it from all other Fucales in the region. The recent placement of S. peronii in synonymy with S. decurrens (Dixon et al. 2012) expands the morphological variability of this species to include specimens with simple and divided secondary laterals. Its disjunct distribution, and that of Hormophyta cuneiformis, both with potentially relict occurrences in the Great Australian Bight, S.A., might be explained by future population biogeographic reasearch. However, for S. decurrens this potential is limited by the availability of collections, as southern Australian specimens are few and mostly found in drift.
Sargassum C.Agardh, Spec. Alg. 1: 1 (1820), nom. cons.; from the Spanish sargazo (seaweed, a term used by navigators to describe floating algae).

Type: *S. bacciferum* (Turner) C.Agardh [= *S. natans* (L.) Gaillon]

Thallus erect, from a discoid-conical or stoloniferous holdfast with 1–few simple terete or compressed stipes bearing primary branches radially or distichously. Primary branches seasonal, usually richly branched distichously, tristichously or radially; basal laterals compressed, often leaf-like, entire or with spinous margins. Vesicles usually present, discrete. Structure with a medulla, cortex and a superficial meristoderm. Receptacles axillary, simple or branched, terete to compressed, smooth, verrucose or spinous. Conceptacles scattered, unisexual or bisexual. Receptacles solitary or arranged in an alternate, racemose or cymose inflorescence [after Womersley (1987: 418)].

Identification of *Sargassum* species can be difficult, especially in the absence of reproductive structures. However, several of the N.W.A. species, such as *S. paradoxum* and *S. polycystum*, have distinctive vegetative features. The genus is undergoing considerable taxonomic revision following studies by Lydiane Mattio and associates (mostly tropical Indo-Pacific species) and the first author of the present treatment (mostly Australian taxa). Two subgenera are currently recognised, these being differentiated primarily by stem and leaf morphology (Dixon *et al.* 2014).

A genus of at least 800 named taxa, of which more than 335 are currently accepted (Guiry & Guiry, 2013); 11 species in N.W.A., 10 in subgenus *Sargassum* and one (*S. paradoxum*) in subgenus *Bactrophycus*. Lord Howe Island and Southern Great Barrier Reef support 12 *Sargassum* species (Kraft, 2009); however, only two taxa are shared by eastern Australia and N.W.A. Little molecular work has been carried out on eastern Australian taxa, a group in need of critical reassessment.

**KEY TO THE SPECIES OF SARGASSUM**

1 Branches triquetrous; leaves retroflex (subg. *Bactrophycus*) .1. *S. paradoxum*

1: Branches terete or compressed; leaves not retroflex (subg. *Sargassum*) ................. 2
2 Plants delicate, usually adhering to paper; branches subterete; leaves or vesicles
arising directly from receptacles (sect. Zygocarpicae) ........................................... 3
2: Plants not as above ........................................................................................................ 4
3 Leaves always simple; colour uniform.............................................................. 10. S. carpophyllum
3: Leaves occasionally divided, darker at apices ............................................ 11. S. flavicans
4 Branch axes strongly compressed, smooth, arising from main axis (sect.
Binderiana) ...................................................................................................................... 5
4: Branch axes usually terete or subterete; if compressed, arising directly from the
holdfast............................................................................................................................ 7
5 Apices of primary laterals acute; receptacles cymose, subterete and spinous ....
........................................................................................................................................ 4. S. swartzii
5 Apices of primary laterals usually obtuse; receptacles leaf-like to compressed and
spinous .................................................................................................................................. 6
6 Receptacles compressed, leaf-like and simple, rarely divided ........... 3. S. ligulatum
6: Receptacles subterete to moderately compressed in dense cymose glomerules,
often divided............................................................................................................... 2. S. aequifolium
7 Leaves always simple; branch axes sparsely to densely spinous, or covered in short
determinate branchlets (sect. Polycystae) .............................................................. 8
7: Leaves simple or divided; branch axes usually smooth, rarely with spines........... 9
8 Branch axes bearing short dense determinate subterete clavate laterals to 6 mm
long; plants resembling Rastafarian dreadlocks .................................................. 8. S. rastum
8: Plants not as above; leaves can be short and filiform, but at medium density with
visible axes throughout; vesicles mostly spherical, often abundant 7. S. polycystum
9 Receptacles smooth to verrucose, not spinous; leaves often divided (sect.
Sargassum) ................................................................................................................ 9. S. linearifolium
9: Receptacles spinous; leaves simple, ovate to oblanceolate (sect. Ilicifolia) ........ 10
10 Branch axes terete or compressed; receptacles simple, terete or subterete, often
spinous (females)........................................................................................................... 5. S. ilicifolium
10: Branch axes markedly compressed, arising directly from the holdfast;
receptacles associated with vesicles or rarely a leaf, occasionally winged,
spinous ........................................................................................................................ 6. S. marginatum
Sargassum subg. Bactrophycus


Type: *S. horneri* (Turner) C.Agardh


The synonymy of subg. *Arthrophycus* with subg. *Bactrophycus* is discussed by Dixon *et al.* (2014).

Thalli with branch axes 3-sided (triquetrous). Lower laterals leaf-like, usually dark brown, markedly larger than upper laterals of fertile fronds [after Womersley (1987)].

1. **Sargassum paradoxum** (R.Br. ex Turner) Gaillon, Résumé Thalassioph. 355 (1828)


Thallus medium to dark brown, to 50 cm tall; holdfast discoid-conical, smooth, to 25 mm wide, giving rise to 1–3 primary axes, terete with occasional scars to 14 mm long, 3.0–3.5 mm diam. Primary branches densely whorled, angular, triquetrous, 2.0–4.5 mm diam. Primary leaves retroflex, lanceolate, 60–150 mm long, 14–23 mm wide, bent back, slightly ruffled, with undulating curls, serrulate; apices obtuse; base symmetrical, narrowly cuneate with minute scattered cryptostomata. Secondary branches angular, triquetrous, whorled, 1.5–2.5 mm diam. Secondary leaves whorled, lanceolate, 12–26 mm long, 3–8 mm wide, serrulate; apices obtuse; base asymmetrical, cuneate. Vesicles spherical, 2.0–3.5 mm diam., with a short apical mucro to 2 mm long. Receptacles monoecious, solitary or in racemose clusters, verrucose, flattened, leaf-like, 4–11 mm long, 1.5–2.0 mm wide, 0.4–0.5 mm thick. Conceptacles unisexual; oogonia round or oval, 100–145 µm long, 82–118 µm wide; antheridia elongate, stalked or sessile, 15–20 µm long, 7–9 µm wide. Fig. 4:3A–D.

Known from North West Cape, W.A. south to Westernport Bay, Vic. and around Tas.; epilithic in the subtidal.

**Specimens examined:** Bateman Bay Lagoon, Ningaloo, 5 m, 26 June 2010, R.R.M. Dixon [PERTH 08436002 (Genbank: KF281769, KF281966, KF281911)]; Simpson Is., Exmouth Gulf, 29 Aug. 1995, B.Schaffelke (PERTH 08404135).

*Sargassum paradoxum* was formerly known only from south-eastern Australia (S.A., Vic. and Tas.) with, according to Womersley (1987), doubtful records from further north at Eden, New South Wales (May, 1939: 202) and Geraldton, Western Australia (De Toni & Forti, 1923: 66). One of the N.W.A. specimens (PERTH 08436002) was collected from limestone substratum in the Ningaloo Reef lagoon, and another discovered among older collections (PERTH 08404135), confirming the northern extent of this species on the west coast.

**Sargassum subg. Sargassum**

*Sargassum* C.Agardh subg. *Sargassum*

Thalli with branch axes angular to terete, not 3-sided. Lower laterals usually leaf-like but slender in some species (rarely linear with a single branch), usually light to medium brown, markedly to only slightly larger than upper laterals [after Womersley (1987)].
**Sargassum sect. Binderiana**


Type: _S. binderi_ Sond. [= _S. aquifolium_ (Turner) C.Agardh]

Thallus bearing strongly flattened axes that are distichously arranged in 1 plane. Leaves elongate, spatulate, with an attenuated base and dentate margins; cryptostomata small to large, mostly aligned on each side of the midrib. Vesicles on a long stalk, spherical to obovoid, smooth or with a short mucro, a foliar appendage or crown, or differentiated into phyllocysts (leaf-like laterals with an internal cavity). Receptacles mostly bisexual, arranged in dense cymose glomerules, with serrate margins [after Mattio _et al._ (2010: 902)].

2. **Sargassum aquifolium** (Turner) C.Agardh, _Spec. Alg._ 1: 12–13 (1820)


_Sargassum biserrula_ J.Agardh, _Spec. Gen. Ord. Alg._ 318 (1848). T: “in mari Indico ad littora Hindostaniae (Wigt [Wight] in Hb. Hookerii sub. n:o 238 et 240!” _n.v._ [Note: According to Mattio _et al._ (2010) the holotype is TCD 1118 (Wight No 240) from the West Indies. This is an error and should be East Indies. Moreover, Agardh listed two specimens and did not nominate a holotype. Thus, Mattio _et al._’s use of holotype is an error to be corrected to lectotype.]

_Sargassum echinocarpum_ Grev., _Algae Orient._ 274–275, pl. 5, upper figs 1–7 (1848), _nom. illeg._, _non_ _S. echinocarpum_ J.Agardh; _S. odontocarpum_ Sond., _Alg. Trop. Austral._ 43 (1871). T: “in mari Indico” [India] _R.Wight_ in herb. no. 18; holo: E; iso: BM 000563654 _n.v._

Thallus medium brown, 10–45 cm tall, with a discoid-crustose holdfast 7–11 mm wide. Primary axes terete, smooth, 3–4 mm long, 1.25–2.00 mm diam. Primary branches smooth to wrinkled, compressed, with sharp edges, 2–4 mm wide. Primary laterals alternate, linear-lanceolate to ovate-elongate, 13–30 mm long, 5–11 mm wide; margins undulate to deeply dentate; apices obtuse; base subsymmetrical, cuneate, arising directly from the stem and lacking a distinct stalk; margins vanishing 80% of the way to the apex. Secondary branches smooth, compressed 1–3 mm diam. Secondary laterals alternate, oblanceolate to ovate, 15–37 mm long, 8–15 mm wide; margins serrate to dentate; apices obtuse or acute; base cuneate, subsymmetrical; cryptostomata prominent. Vesicles subspherical to elongate, smooth, 3–6 mm diam., often with a small apical mucro. Receptacles monoecious, subterete to moderately compressed in dense cymose glomerules, 2–5 mm long, 0.75–2.00 mm wide, spinous, often divided. Conceptacles bisexual; oogonia oval, 105–160 µm long, 60–200 µm wide; antheridia trapezoid, oval or elongate, 14–24 µm long, 8–20 µm wide. Fig. 4:4A–D. Pl. 4:2B.

Widespread in the tropical Indo-Pacific. In Australia known from Coral Bay northwards, presumably around northern Australia to Qld and Norfolk Island (Mattio & Payri, 2009b).


*Sargassum* sect. *Binderiana* is characterised by strongly flattened axes that are distichously arranged in one plane, and leaves that are spathulate and elongate with an
attenuated base (Mattio et al., 2010). Three of the four currently accepted species are known from N.W.A.; the exception is the East Asian S. patens C.Agardh.

Mattio et al. (2010) noted three types of reproductive organs with intermediate morphologies for S. aquifolium: (1) predominantly female receptacles with a tendency to be flat, stocky and dentate; (2) bisexual receptacles that are glomerulate and spiny; and (3) predominantly male receptacles, more likely to be slender and cylindrical with only very few spinules. N.W.A. specimens resemble the second type, with all observed receptacles bisexual, subterete and spinous.

Many names have recently been transferred to S. aquifolium based on similarities in the morphology of axes, leaves and vesicles, as well as DNA sequence analyses (Mattio et al., 2009a, 2010). Sargassum ligulatum, endemic to Western Australia, and sequenced for the first time in the current study, is closely related to, but genetically distinct from S. aquifolium (Fig. 4:1). The morphological comparison presented here is based largely on the sequenced specimens.

3. Sargassum ligulatum C.Agardh, Syst. Alg. 297 (1824)

T: “ad litus occidentale Novae Hollandiae” [W.A.]; holo: LD 2405 (Herb. Agardh) n.v.


Thallus pale to medium brown, 15–50 cm tall, with a conical holdfast 10–23 mm diam. Primary axes terete to subterete, smooth, 3–7 mm long, 2.0–2.5 mm diam. Primary branches smooth or wrinkled, flattened, with sharp edges, 3–6 mm wide, 1.0–1.5 mm thick. Primary laterals alternate, linear-lanceolate, 25–100 mm long, 17–20 mm wide; margins undulate to serrate; apices obtuse; base subsymmetrical, narrowly cuneate, arising directly from the stem and lacking a distinct stalk. Secondary branches smooth to wrinkled, compressed, 2–3 mm diam. Secondary laterals linear-lanceolate to lanceolate, 10–70 mm long, 8–20 mm wide; margins serrate to dentate; apices acute or obtuse; base cuneate, subsymmetrical; cryptostomata prominent. Vesicles spherical, mutic, 3.0–9.5 mm diam., with a flattened or leaf-like stalk usually
longer than the vesicle, occasionally extending into the vesicle as a small wing or thickened rib; cryptostomata large and raised. Receptacles monoecious, compressed and leaf-like, solitary, cymose or subalternate, 4–15 mm long, 2–4 mm wide, occasionally intermixed with leaves and vesicles, simple or once-divided, with rounded apices, either smooth or spinous across the margins. Conceptacles bisexual; oogonia egg-shaped, 75–160 µm long, 70–120 µm wide; antheridia egg-shaped, on long stalks, 14–30 µm long, 7–20 µm wide. Fig. 4:5.

Known only from the west coast of W.A.


*Sargassum ligulatum* is characterised by the simple or once-divided, flattened leaf-like receptacles. The closely related *S. aquifolium* has spinous, subterete receptacles usually in dense glomerules (in N.W.A. specimens), while *S. oligocystum* Mont. has more divided receptacles. The presence of *S. oligocystum* was not confirmed in N.W.A. However, a specimen collected in 1995 (PERTH 06890342) had a higher level of receptacle division than was observed in other *S. ligulatum* material. This sample has not yet been sequenced due to its age. When *S. oligocystum* sequences become available (none are currently published), preferably from the type locality (Sumatra, Indonesia), this sample should be revisited for comparison.
4. **Sargassum swartzii** C.Agardh, *Spec. Alg.* 1: 11 (1820)


*Sargassum wightii* Grev. ex J.Agardh, *Spec. Gen. Ord. Alg.* 329 (1848), as *wigtii*.  T: “ad oras Hindostaniae [India], Herb. Hooker 246, 248”.  [Note: According to Mattio *et al.* (2010), syntypes are TCD 1120, 1121, these bearing the numbers 246 and 248, which appear to be Wight’s numbering rather than Hooker’s. Other specimens labelled similarly are BM 000563524, while the Greville Herbarium in E also holds a specimen (E 00270739) annotated as “Holotype” (by Nizamuddin).]


Thallus medium brown, to 60 cm tall, with a smooth compressed primary axis 1.5–2.0 mm wide. Primary branches smooth, flat, 2–5 mm wide, with sharp edges. Secondary branches smooth, compressed, 0.5–1.5 mm wide. Lower laterals lanceolate, variable in size, similar to upper laterals in some specimens (e.g. PERTH 08435871) or conspicuously larger, then 4–6 cm long, 6–10 mm broad (PERTH 08436207); upper laterals becoming linear, serrate to dentate; apices acute; bases cuneate, subsymmetrical, 9–44 mm long, 1.5–8.0 mm wide. Vesicles ellipsoidal to subellipsoidal, smooth or with scattered cryptostomata, occasionally with a short mucro, (1.25–) 2.00–6.00 mm diam.; stalk narrow, compressed, usually shorter than the vesicle. Receptacles monoecious, arranged in cymes or short subracemose clusters, 1–3 times divided, verrucose, terete to subterete, bearing numerous spines and irregular branches, (0.75–) 1.00–3.00 mm long, 0.30–0.75 mm diam. Conceptacles monoecious; oogonia round to egg-shaped; 90–220 µm long, 73–210 µm wide; antheridia stalked, 16–27 µm long, 9.0–13.5 µm wide.  Fig. 4:4E–H.

Widespread in the tropical Indo-Pacific. Known from W.A. north of Coral Bay, and also from Qld.

**Specimens examined:** Ningaloo, on coral bommie inside lagoon, 7 m, 10 June 2008, *C.F.D.Gurgel & R.R.M.Dixon* (AD A89608); S end of LeRoy Beach, N of Point Cloates, Ningaloo, 1 m, 21 May 2009, *C.F.D.Gurgel* (AD A90143); North Turtle Is., drift, 13 May
At first glance, *S. swartzii* might be mistaken for *S. aquifolium*, both having flattened primary branches and lanceolate laterals with prominent cryptostomata and spinous, subterete receptacles. The former is characterised by its narrower leaves with mostly acute apices, smaller vesicles with shorter, narrower stalks, smaller receptacles and larger oogonia. However, the vegetative morphology of both *S. aquifolium* and *S. swartzii* has been shown to vary considerably, making specimen identification challenging without the support of molecular data.

**Sargassum sect. Ilicifolia**


Type: *S. ilicifolium* (Turner) C.Agardh.

Thallus bearing cylindrical to compressed axes, occasionally twisted, alternately and spirally arranged. Leaves broadly spatulate, with a cuneate or rounded unequal base; cryptostomata thin, numerous, dispersed, rarely aligned; margins serrate to dentate. Vesicles spherical to obovoid, smooth, supported by a short stalk, with an ear-like or simple spine-like micro. Receptacles bearing spine-like protuberances, mostly unisexual and showing a male/female dimorphism [emended after Mattio *et al.* (2010: 901)].


**Sargassum subfalcatum** var. *montebellense* Grunow, in E.Askenasy, *Forschungs. Gazelle* 4(2): 27 (1888);


Thallus thick and bushy, to 2 m tall, with a crustose-scuteellate or creeping holdfast to 18 mm diam. which is usually covered in epiphytes and sand; in some plants giving rise directly to small leaves. Stipe terete, smooth or with branch scars, to 10 mm tall, 1.0–2.5 mm diam. Primary branches smooth, terete or slightly compressed, 1.0–2.5 mm diam. Secondary branches radial, smooth, except when covered in branch scars, subterete, 0.5–2.0 mm diam. Primary leaves ovate, lanceolate or oblanceolate, 20–75 mm long, 6–22 mm wide; margins entire to serrate; apices obtuse, rarely acute. Secondary leaves arising in an alternate pattern on stem, often in pairs, ovate, spathulate or lanceolate, (5–) 10–59 mm long, 3–20 mm wide, medium to dark brown, with a dentate to almost entire margin; distal edge of leaf can be simple or divided into two, forming a cup shape; apices obtuse; midrib percurrent; base asymmetrical, cuneate; cryptostomata scattered, variable in size. Vesicles mostly spherical, some elongate or ovoid, smooth, 2–7 mm diam., each with a compressed to leaf-like stalk the same length as the vesicle or slightly shorter. Plants monoecious or dioecious. Receptacles simple or once-branched, in racemose or cymose inflorescences; male receptacles smooth, subterete, 2–9 mm long, 0.5–1.0 mm diam.; female receptacles spinous, compressed, 2.0–6.5 mm long, 1–2 mm diam.; monoecious receptacles subterete to compressed, with marginal spines, 3–12 mm long, 1.0–1.5 mm diam. Conceptacles mostly unisexual; oogonia 160–230 µm long, 130–160 µm wide; antheridia oval, stalked, 11–21 µm long, 7–13 µm wide. Fig. 4:6A–C.
Pantropical from East Africa across the Indo-Pacific to Tonga. In Australia, known from Geraldton (W.A.) around northern Australia to southern Qld.


Frequently cast up on the shore, the abundant *S. ilicifolium* is possibly the largest *Sargassum* in N.W.A. In protected shallow bays and lagoons plants reach their greatest length (around 2 metres), while on exposed reef tops they tend to be short, robust and often have divided apices. N.W.A. specimens exhibit the three different receptacle morphologies also seen in Pacific *S. ilicifolium* and *S. aquifolium* (see the discussion of *S. aquifolium*, above). Therefore, they are most reliably identified by
means of axis and leaf morphology (Mattio et al., 2010). *Sargassum ilicifolium* can be distinguished from *S. aquifolium* by having axes that are subterete or slightly compressed rather than flattened, and with edges and leaves that have fine, rather than large coarse cryptostomata. Two varieties have been described from N.W.A., viz. *S. ilicifolium* var. *montebellense* (Grunow) Grunow and *S. ilicifolium* var. *oocystoides* Grunow. Although examination of Grunow’s type material is required to verify these taxa, given the morphological variability in *S. ilicifolium* they are not recognised here.


Thallus medium to dark brown, bushy and erect, to 23 cm tall, with a discoid holdfast to 9 mm diam. Primary branches growing directly from the holdfast, 4–7, smooth, compressed, to 20 cm long, 1.5–2.5 mm wide. Secondary branches alternate, compressed or subterete, to 15 cm long and 1 mm wide. Primary laterals ovate to lanceolate, serrate, with rounded apices and a cuneate base, usually asymmetrical, 12–55 mm long, 9–13 mm wide; midrib fading between half-way to a few millimetres below the apex; stalk flat, 1.5–2.0 mm wide, merging into the leaf blade; cryptostomata small, scattered. Secondary leaves distinctly obovate, with rounded apices and asymmetrical bases, serrate, 8–20 mm long, 5–8 mm wide; midrib fading well before apices; cryptostomata small, scattered. Vesicles spherical, smooth, mutic, 1–3 mm diam. Plants monoecious. Receptacles clustered in stalked inflorescences associated with vesicles or (rarely) a leaf, clavate to compressed, spiny and occasionally winged, 2–6 mm long. Fig. 4:6G, H.

Known from the Kimberley region, W.A., and Great Keppel Island, Qld; also in India, Sri Lanka, Indonesia and probably also Vanuatu and the Solomon Islands (Mattio et al., 2009a).


These are the first Australian records of Sargassum marginatum, and the first sequences of this species in GenBank. Although Agardh (1889) placed S. marginatum in Sargassum sect. Acanthocarpicae, the section was shown to be polyphyletic and was subdivided into several new or newly ranked sections (Mattio et al., 2010), leaving the taxonomic position of many species in doubt. We include S. marginatum in sect. Ilicifolia, while a number of ‘Sargassum sp.’ records from the Solomon Islands, Vanuatu and New Caledonia (Mattio et al., 2009b), assigned to sect. Ilicifolia, closely match the N.W.A. vouchers in their morphology and sequences. We suggest these also be designated S. marginatum, expanding its distribution eastward into the South Pacific.

Sargassum sect. Polycystae


Type: S. polycystum C.Agardh

Holdfast disc-like or conical. Lower part of main axis giving rise to stolon-like horizontal branches. Stolon branches smooth, cylindrical to flattened and branched, often bearing secondary haptera from which a new plantlet can arise. Upper parts of secondary branches densely clothed with leaves, vesicles and receptacles. Leaves always simple [after Mattio et al. (2009a)].

Stolon-like horizontal branches are rare in N.W.A. specimens.

7. Sargassum polycystum C.Agardh, Syst. Alg. 304 (1824)


Thallus medium brown, to 39 cm tall, with a discoid-conical, lobed or creeping holdfast to 30 mm wide, giving rise to 1–several terete primary axes (with radial scars) to 50 mm long, 1–3 mm diam. Primary branches terete to subterete, smooth to densely spinous, 0.6–2.0 mm diam.; spines simple or divided, with acute, obtuse or centrally depressed apices, 0.25–1.00 mm long. Primary laterals linear, ovate, lanceolate or botuliform, 2–85 mm long, 0.3–10 mm wide; margins smooth to serrulate; apices acute or obtuse. Secondary branches borne radially 1–5 mm apart, terete, 0.4–1.5 mm diam., smooth or with blunt or centrally depressed radial spines/protuberances that are 0.2–0.6 (–1.5) mm long. Secondary laterals linear to linear-lanceolate, 4–40 mm long, 0.5–4.5 mm wide; margins entire, serrulate or serrate; apices acute or obtuse; midrib ending just below the apex; cryptostomata often prominent, raised. Vesicles often clustered, with a short stalk to 1 mm long, spherical to slightly elongate toward the
base, 0.6–2.0 (–3.0) mm diam. Inflorescences cymose or racemose clusters of up to 3 receptacles, always associated with vesicles and occasionally leaves. Receptacles usually dioecious, terete, smooth to verrucose, simple, 1–5 mm long, 0.4–1.0 mm diam., giving rise to other receptacles or sterile awns; apices rounded, flat and uneven, or acute. Conceptacles usually unisexual; oogonia sessile, oval, 140–230 µm long, 80–135 µm diam.; antheridia on short or long stalks, oval, 8.0–13.5 µm long, 6–9 µm wide. Fig. 4:7A–D.

Known from N.W.A. and Qld; also in the Canary Islands, Africa, and in the tropical Indo-Pacific Ocean as far east as Tonga.

Sargassum polycystum exhibits a broad range of vegetative morphological phenotypes due largely to the recent addition of S. myriocystum to its synonymy (Mattio et al., 2009a). Stems are also highly variable, from completely smooth to heavily spinous. Cryptostomata are nearly always large and prominent, and the small and numerous vesicles are invariably associated with receptacles. Sargassum baccularia (Mert.) C.Agardh, from eastern Australia and Asia, resembles the smooth-stemmed specimens of S. polycystum from N.W.A. (e.g. AD A88646 and PERTH 08435596). However, a study of the two species in Malaysia (Wong et al., 2004) found them to be morphologically and genetically distinct.

8. Sargassum rastum1 R.R.M.Dixon & Huisman, sp. nov.


Thallus medium or dark brown, to 17 cm tall, arising from a crustose or occasionally lobed holdfast 7–16 mm wide. Primary branches 5–16, resembling Rastafarian dreadlocks arising clustered together directly from the base, terete, 45–160 mm long, 0.75–1.00 mm diam. Primary laterals subterete, clavate, broader near the apex, tapering toward the base, densely clustered, obscuring the view of the axes beneath, 2–6 mm long, 0.2–0.6 mm wide. Secondary branches determinate, 5–52 mm long, 0.75–1.00 mm diam., dense, terete, linear or clavate, curling inwards at the apex. Vesicles, when present, densely clustered in upper branches, elliptical to elongate, with thick compressed or subterete pedicels, 1.5–2.5 mm long, 1.0–1.5 mm diam., usually with a short mucro. Fertile plants not seen. Fig. 4:7E, F. Pl. 4:2D.

Widespread in N.W.A; epilithic in the intertidal and shallow subtidal.


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1 The published version (‘rasta’) was an incorrect orthographic variant that will be corrected in a later publication.
This alga was first identified as *Cystoseira* sp. in field surveys in N.W.A. Dense bushy projections, giving axes the appearance of dreadlocks, could be either stunted laterals or pronounced stem spines, the latter similar in both *Siropphysalis trinodis* (formerly *Cystoseira trinodis*) and *Sargassum polycystum*. Molecular analyses place *S. rastum* in sect. *Polycystae*, and it differs from the closely related *S. polycystum* and other members of the section by its dense and comparatively short laterals. The genetic distinction between *S. polycystum* and *S. rastum* in N.W.A. was present in all three loci studied (Fig. 4:1), thus demonstrating an unambiguous, species-level separation.

Named for the appearance of the thallus, which is reminiscent of the dreadlock hairstyle favoured by Rastafarians. The epithet was first suggested by Gary Kendrick.

**Sargassum sect. Sargassum**

*Sargassum* C.Agardh sect. *Sargassum*.

Leaves and vesicles well differentiated; leaves not basally retroflex; receptacles usually compound, cylindrical, smooth, arranged in cymes or racemes [after Mattio et al. (2010)].


Sargassum carpophyllum auct. non J.Agardh, sensu Sond., Linnaea 672 (1853).

Sargassum vulgare auct. non C.Agardh, sensu Sond., Linnaea 673 (1853).


Thallus medium to dark brown, to 45 cm tall, with a discoid-conical holdfast, occasionally scutellate, 7–35 mm wide, with a single terete stipe to 50 mm long, 1.5–3.0 mm diam. Primary branches subterete to compressed, smooth or striated, 0.5–2.5 mm diam., with occasional short spines, with rounded or pointed tips, 0.50–1.75 mm long. Primary laterals lanceolate, simple or divided up to 3 times, 8–50 mm long, 4–10 mm wide, the margins often ruffled and serrulate, smooth or serrate; apices usually obtuse; midrib percurrent or terminating near the apex. Secondary branches compressed, smooth to striated, 0.30–1.75 mm diam. Secondary laterals linear, lanceolate, simple or divided up to 4 times, 10–45 mm long, (2–) 3–11 mm wide; margins serrate to serrulate and often undulate. Vesicles spherical to slightly elongate, with a compressed or subterete stalk, 1.5–4.5 mm diam. Receptacles dioecious, simple, branched or in dense clusters, smooth to verrucose, with rounded or acute apices that are often darker, 1.0–5.5 mm long, 0.25–0.50 mm diam. Conceptacles unisexual; oogonia oval, 209–273 µm long, 180–218 µm wide; antheridia oval, 18–30 µm long, 9–18 µm wide. Fig. 4:3E–I.

Known from temperate and tropical coasts throughout Australia; also from East Africa and India to New Caledonia.

Specimens examined: S of Coral Bay, Ningaloo, 6 m, on limestone, 10 June 2010, R.R.M.Dixon (PERTH 08399751, 08435936); Coral Bay back reef, Ningaloo, 3 m, 20 June 2010, R.R.M.Dixon (PERTH 08399573, 08436134); Ned’s Beach, Ningaloo, drift, C.F.D.Gurgel 9.6.8.3.3 & R.R.M.Dixon (AD A89570); Ningaloo, S of Tantabiddi, 4 m, on coral rubble and sand, back reef bommies, 10 June 2008, C.F.D.Gurgel & R.R.M.Dixon [AD A89596 (GenBank: KF281886*)]; Ningaloo, on a coral bommie in lagoon, 7 m, 10 June 2008, C.F.D.Gurgel & R.R.M.Dixon [AD A89607 (GenBank: KF281887*)]; Ningaloo, near Tantabiddi, 4 m under navigation buoy, 13 June 2008, R.R.M.Dixon & C.F.D.Gurgel [AD A89626 (Genbank: KF281888*)]; loc. id., 13 June 2008, R.R.M.Dixon & C.F.D.Gurgel [AD
Womersley (1987) characterised southern Australian *S. linearifolium* by its spinous axes, heavily branched receptacles, and narrow, often furcate laterals. This was in contrast with *S. spinuligerum*, which had predominantly smooth axes and broader laterals that were rarely furcate. Many N.W.A. specimens appear intermediate between the two, having occasionally spinous axes and furcate laterals that are broader than usually seen in *S. linearifolium*. Genetically, there is no species-level distinction between specimens of *S. linearifolium* and *S. spinuligerum* from N.W.A., the Great Australian Bight, New Caledonia and Tanzania in the loci *cox*3, ITS-2, and the *rbcL*-S spacer. Womersley (1987: 441) noted the similarity in reproductive features between specimens of southern Australian *S. spinuligerum* and *S. linearifolium* and hinted at the possibility of morphological intergrades. We include *S. spinuligerum* in synonymy with *S. linearifolium*, the only species of sect. *Sargassum* in N.W.A.

**Sargassum sect. Zygocarpicae**


Type: *S. carpophyllum* J.Agardh

Thalli fine, delicate, usually flattened completely and adhering to paper in herbarium presses. Receptacles associated with leaves and/or vesicles.


Thallus pale to medium brown, to 46 cm tall, with a discoid-conical holdfast c. 12 mm wide giving rise to 1 or 2 terete stipes to 15 mm long and 1–2 mm diam. covered in radial branch scars. Primary branches subdistichous, compressed to subterete, smooth to slightly striated, 0.5–1.0 mm diam. Lower laterals lanceolate, serrulate to serrate, 25–45 mm long, 4.5–6.0 mm wide; apices obtuse; midrib vanishing just below the apex. Secondary branches distichous, subterete to compressed, smooth to striated, 0.5–1.5 mm diam. Upper laterals lanceolate or ovate-lanceolate, serrate-dentate, 10–30 mm long, 1.5–5.0 mm wide; apices usually obtuse; midrib prominent, vanishing just below the apex; base cuneate, asymmetrical, with prominent scattered cryptostomata. Vesicles spherical to slightly elongate, smooth, mutic or with 1–4 short foliar appendages, 1–3 mm diam., with terete or winged stalks. Reproductive branches zygocarpic; vesicles and leaves arising directly from receptacles (Fig. 4:8B). Receptacles monoecious, simple or loosely branched, smooth, terete, with rounded to acute apices, 1–3 mm long, 0.25–0.50 mm diam. Conceptacles unisexual; oogonia oval or bean-shaped, 68–102 µm long, 45–60 µm wide; antheridia possibly sessile 9–15 µm long, 5.5–11.0 µm wide.   Fig. 4:8A–C.

Known from several localities in the Indian and western Pacific Oceans, including N.W.A. and Qld.

The most delicate of the N.W.A. species, *S. carpophyllum* is characterised by the leaves and vesicles arising directly from receptacles and by the absence of divided leaves. Boundaries have not yet been resolved for the N.W.A. species of sect. *Zygocarpicae*, as sequences are available only for *S. carpophyllum*.

11. **Sargassum flavicans** (Mert.) C.Agardh, *Spec. Alg.* 1: 18 (1820)


Thallus pale brown, delicate, to 35 cm tall, with a discoid-crustose holdfast 5–8 mm wide giving rise to 1–3 terete primary axes covered in short branch scars 1–2 mm diam. Primary branches subterete to flattened when pressed, smooth or striated, with occasional cryptostomata, 0.8–1.5 mm diam. Primary laterals alternate, lanceolate, serrulate, occasionally divided, 22–45 mm long, 2–6 mm wide; apices obtuse or acute; base cuneate, subsymmetrical; cryptostomata small. Secondary branches alternate, compressed, smooth, 0.3–1.0 mm diam. Secondary laterals alternate, lanceolate, serrulate, occasionally bifid, 5–42 mm long, 1.5–8.0 mm wide; apices obtuse or acute with darker tips when immature. Vesicles smooth, spherical, 1.5–3.5 mm diam., occasionally with a spiny winged margin or mucro; stalk terete or flattened and leaf-like. Receptacles in tight cymose clusters associated with leaves and vesicles, smooth, globose, 0.25–0.50 mm long, 0.10–0.15 mm wide; all specimens immature. *Fig. 4*: 8D, E.

Known from several localities in the Indian and western Pacific Oceans. In Australia also reported as drift from the N.T. (Womersley, 1951) and Qld (Cribb, 1996).

**Specimens examined**: Disaster Reef, Broome, 8 m, 15 June 2001, *J.M.Huisman & M.van Keulen* (PERTH 08279209, 08279195, 08279187).

The N.W.A. specimens appear to be wholly compatible with the illustrations provided by Agardh (1889). Occasionally divided leaves and the co-occurrence of vesicles and leaves within (zygocarpic) inflorescences are diagnostic for this species.

4. SIROPHYSALIS

*Sirophysalis* Kütz., *Phycol. General*. 368 (1843); from the Greek *seira* (a chain) and *physo* (bladder), presumably in reference to the chains of vesicles.

Type: *S. muricata* (C.Agardh) Kütz. [= *S. trinodis* (Forssk.) Kütz.]

Thallus coarse and cartilaginous, to 50–100 cm long. Primary axes erect from a discoid-crustose holdfast, bearing numerous seasonal primary branches that are lightly to heavily spinous. Primary laterals radial, much larger than upper laterals, lanceolate with acute apices. Vesicles intercalary in upper ramuli, often in a linear series of 2–5.

A recently resurrected, monotypic genus (Draisma et al., 2010).

*Sirophysalis trinodis* (Forssk.) Kütz., *Spec. Alg.* 603 (1849)

*Fucus trinodis* Forssk., *Fl. Aegypt.-Arab.* 192 (1775); *Cystoseira trinodis* (Forssk.) C.Agardh, *Spec. Alg.* 1: 67–68 (1820); *Cystophyllum trinode* (Forssk.) J.Agardh, *Spec. Gen. Ord. Alg.* 1: 230 (1848). T: “Ad littora urbis TÔr” [Tor, Sinai Peninsula, Egypt], *P.Forsskål*; holo: C [Note: Børgesen (1932: 12) indicated a single specimen from Tor was present in Herb. Forsskål (C), which can therefore be regarded as the holotype].


_Sirophysalis binodis_ Kütz., _Tab. Phycol._ 22, pl. 59, fig. 2 (1860); _Cystophyllum muricatum_ (C.Agardh) J.Agardh var. _binode_ (Kütz.) De Toni, _Syll. Alg._ 3: 154 (1895). T: Australia; holo: n.v.


Thalli medium brown, to 65 cm tall, with a solitary or clustered growth form, erect from a crustose holdfast 7.5–10.0 mm wide. Primary axis terete, branched, covered in scars from previously shed laterals, 13–19 mm long, 2–4 mm wide. Primary branches radial, terete, crowded, 1.0–1.5 mm diam., with sparse to very crowded narrow spines with acute forked or infundibuliform, 0.25–0.40 mm long. Secondary branches radial, terete, 0.5–1.0 mm diam., with spines 0.3–0.4 mm long. Lower laterals linear-lanceolate to broadly lanceolate, 12–120 mm long, 1.5–15.0 mm wide; margins smooth to serrulate; apices acute; midrib percurrent; cryptostomata scattered and numerous. Upper laterals distinctly smaller, linear-lanceolate, 12–65 mm long, 0.5–15.0 mm wide; apices tapering to a very narrow point; midrib percurrent; base sharply cuneate, oblique with pedicels 0.25–0.50 mm; cryptostomata minute, scattered or in rows. Vesicles slightly elongate, 0.5–2.5 mm diam., solitary or in chains of 2–4 embedded mid-leaf or crowned with a linear-serrate leaf. Receptacles alternate on determinate reproductive branches, often associated with vesicles, smooth to coarse, terete or slightly compressed, simple or divided up to twice, with vesicles arising mid-receptacle in some plants. Monoecious with bisexual conceptacles. Fig. 4:2F–H. Pl. 4:3C.

Known from Egypt to South Africa, Pakistan, India and Sri Lanka and east to Indonesia, New Caledonia and Chile. Occurs in W.A., S.A., N.T., Qld and Lord Howe Island; it is possibly a recent adventive in Tas. (Sanderson, 2000).

**Specimens examined:** 1.5 km W of Tantabiddi boat ramp, Ningaloo Reef, 2–5.5 m, 8 June 2008, _M.Blazewicz-Paszkwowycz_ (AD A89509); Ningaloo Reef, Tantabiddi, to 2 m, under

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Many plants collected in the recent surveys of N.W.A. match the description of Cystophyllum nothum Grunow from the Montebello Islands. Grunow commented on the difficulty assigning this species to Cystophyllum or Sargassum, as it had affinities to both. Agardh (1889) placed it in synonymy with Cystoseira trinodis (Forssk.) C.Agardh along with several other Cystophyllum species. The C. nothum morphotype specimens in this study were identified in the field as Sargassum sp. due to their likeness in stem, vesicle and receptacle structure. However, molecular data confirm they represent just one of many morphotypes of Sirophysalis trinodis. Molecular phylogenetic studies show this species to be closely related to Sargassum (Draisma et al., 2010; Dixon et al., 2012, 2014).

5. TURBINARIA

Turbinaria J.V. Lamour., Dict. Class. Hist. Nat. 5: 71 (1825); from the Latin turbinatus (top-shaped, conical), in reference to the shape of the vesiculate determinate laterals.

Type: T. turbinata (L.) Kuntze

Thallus erect from a spreading base of branched fibrous ‘roots’. Percurrent axes surrounded by unbranched laterals consisting of a short stalk expanding to flared, fleshy, wedge-shaped or obconically turbinate leaves (Taylor, 1964: 476), in most species enclosing a hollow vesicle. Receptacles dendroid, axillary on fertile laterals; conceptacles monoecious, containing small clusters of antheridia and eggs [after Kraft (2009)].
**Turbinaria** is a mainly tropical Indo-Pacific genus of 23 species (Guiry & Guiry, 2013). Three species are known from Australia, and all occur in N.W.A. The Western Australian endemic *T. gracilis* Sond. extends south to Cape Leeuwin, and the widespread *T. ornata* and *T. conoides* usually occur in shallow habitats across tropical Australia and the Indo-Pacific. Each of the N.W.A. species has a broad range of morphological variation that overlaps between species, making it a challenge to distinguish them. This treatment focuses heavily on specimens identified with the aid of DNA sequence data in addition to those that were not sequenced. The key does not accommodate *T. ornata* specimens that lack crown teeth, or those of *T. gracilis* that lack lobes. Such anomalies are largely indistinguishable by traditional methods, and they require DNA sequence analyses for accurate identification.

**KEY TO THE SPECIES OF TURBINARIA**

1. Laterals less than 10 mm diam. .................................................................1. *T. conoides*

1:

2. Laterals mostly greater than 10 mm diam. ..................................................2

2:

2. Laterals deeply lobed, mostly with smooth margins, but occasionally dentate (*l:*:) ........

.................................................................................................................................................2. *T. gracilis*

2:

2. Laterals with a double margin of spines, generally not deeply lobed ........3. *T. ornata*

1. **Turbinaria conoides** (J.Agardh) Kütz., *Tab. Phycol.* 24, pl. 66, fig. 2e, f (1860)


Illustrations: F.T.Kützing, *op. cit.* 24, pl. 66, fig. 2; C.K.Tseng, *Common Seaweeds of China* 241, pl. 121, fig. 3 (1983).

Thallus to 14 cm tall; erect axes densely branched from a creeping holdfast. Erect axes subterete, smooth, 1.00–1.25 mm diam. Primary branches radial, giving rise to leafy obconical laterals that are rounded to slightly triangular from above, with smooth to dentate margins, 8.75–9.50 mm diam. Receptacles digitate, simple or forked, in dense racemose clusters, verrucose, terete, with rounded apices, 2.0–3.5 mm long, 0.50–0.75 mm diam. Fig. 4:9A, B.

Widespread in the tropical Indo-Pacific. In Australia known from N.W.A. and Qld; attached to subtidal reefs and rocks.
Specimen examined: Adele Is., Kimberley, to 14 m on coral reef, 14 Oct. 2009, R.R.M.Dixon [PERTH 08286248 (Genbank: JN243839, JN243798, JN243826)].

The N.W.A. specimen of *T. conoides* has partially serrate lateral margins; elsewhere this species is usually smooth-margined (Tseng, 1983: 241).

2. Turbinaria gracilis Sond., *Bot. Zeitung (Berlin)* 3: 352 (1845)

T: “ad oras occidentales Novae Hollandiae” [W.A.], J.A.L.Preiss (Silva et al., 1996: 712); holo: n.v.


Thallus to 50 cm tall, the erect axes closely branched in small plants, sparingly branched in larger plants. Laterals 5–16 mm long, including the subterete stalk, (4–) 6–15 mm wide, the turbinate upper part rounded to deeply lobed, with ±entire or serrulate to dentate margins. Stalk 0.75–1.50 mm diam., flattened below, becoming angulate above. Vesicles ranging from a near dominance of the leaf to a vestigial float. Inflorescence (2–) 5–14 mm long, attached near the stalk base, almost racemose. Receptacles 1–3 (–5) mm long, terete, smooth, simple or forked. Fig. 4:9C, E.

Known from Hamelin Bay, W.A. and around northern Australia to Qld.

N.W.A. specimens match the illustrations and descriptions in Taylor (1964: 480) and Kützing (1860: 25, pl. 70). Plants differ from *T. ornata* in having a deeply lobed distal marginal blade that is often smooth rather than dentate.


T: not designated.


Thallus to 30 cm tall; axes erect simple or branched. Laterals, including stalk, 7–21 mm long, 5–21 mm wide, usually dentate and with a large central vesicle crowned by occasional coarse erect teeth. Stalk terete to angular, 0.5–1.0 mm diam. at the base, thickening towards the apex. Some plants with flattened laterals and stalks; vesicle vestigial and margins entire, resembling the shape of a gingko leaf. Inflorescences 3–9 mm long, arising in the basal third of the vesicle, with racemose receptacles 1–4 mm long, terete with rounded apices.  
Pl. 4:1B.

Widespread in tropical seas. In W.A. known from the tropics south to the Houtman Abrolhos Islands.


The N.W.A. specimens are very similar to those reported from elsewhere (e.g. Taylor, 1964: 483). The range of leaf asymmetry described by Taylor is also observed in these specimens; thus, leaves can be crowned equally on all sides, or be moderate to highly asymmetrical, with one side entirely vestigial, resembling a gingko leaf. Taylor (1964)

**Plate legends**

Figure 4:1. Fucales phylogenetic tree using Bayesian Inference of concatenated *cox3*, ITS-2 and *rbcl*-S spacer sequence data. Branch values in posterior probabilities, only those >0.8 included as reliable. ‘*’ indicates a species from NW Australia.


of vesicles and receptacles. Scales: A, G = 2 cm; B = 5 mm; C = 1 cm; D–F = 2 mm; H–J = 1 mm.


Plate 4:2. *Sargassum* and *Sirophysalis*.
Figure 4:3
Figure 4:4
Figure 4:7
Plate 4:1
Plate 4:2
References


Papenfuss, G.F. 1968. The history, morphology and taxonomy of Hormophysa (Fucales: Cystoseiraceae), *Phytomorphology* 17: 42–47.


Chapter 5 Discussion

This taxonomic and systematic study on Australian members of the brown algal genus *Sargassum* and its close relatives employed morphological and molecular techniques to investigate generic, subgeneric and species level boundaries, assisted by analyses of sequences from the nuclear, mitochondrial and chloroplast genomes; ITS-2, *cox3* and *rbcL*-S. The resulting phylogeny indicated the genus *Sargassum* as presently constituted is polyphyletic, with closely related genera nested within. The morphological data confirmed several new taxonomic transfers proposed at the species, subgeneric and generic level. An understanding of *Sargassum* and the family Sargassaceae reflecting both evolutionary relationships and morphological variation is the basis of sound biodiversity measurements, the foundation of ecological studies, and can accurately inform environmental decision making.

Significant findings

The first two papers in this study investigated phylogenetic relationships and species boundaries in the two lesser-known *Sargassum* subgenera; *Phyllotricha* and *Arthropycus*. The first (Chapter 2) identified and confirmed that *Sargassum* was polyphyletic if subgenus *Phyllotricha* was included. *Sargassum* subgenus *Phyllotricha* was divergent from the remaining *Sargassum* and formed two genetic groups, these morphologically distinguishable by their primary axis and lateral branch construction. Previous studies demonstrated that *Phyllotricha* was sister with the rest of *Sargassum* (Stiger *et al.* 2003, Mattio 2009a, 2009b) and Draisma *et al.* (2010) identified polyphyly in *Sargassum*; however, the molecular study provided a *Phyllotricha* sample size of one, and omitted morphological data. The present study included species not previously sequenced and a morphological investigation providing a more comprehensive assessment of the generic level divergence in *Sargassum*. To remedy the polyphyly in *Sargassum*, *S.* subgen. *Phyllotricha* was restored to genus level as *Phyllotricha* Areschoug and several *Sargassum* species were transferred to it (those with primary branches radially branched and not leaf-like). The remaining *S.* subgen. *Phyllotricha* spp. were transferred to the recently resurrected genus *Sargassopsis* (those with distichous leaf-like primary branches). The genetic variation within species of the former *S.* subgenus *Phyllotricha* was sufficient to recognize species-level variation and, for the most part, concurred with the current morphological-based taxonomy; thus, most existing species were retained (albeit transferred to another genus), and just one reduced to synonymy.
The investigation into Sargassum subgenera Arthropycus and Bactrophycus (Chapter 3) found the two taxa were not genetically or morphologically distinct, and their past and contemporary recognition was essentially based solely on their geographical distribution. Molecular analyses demonstrated that species of S. subgenus Arthropycus were genetically nested within S. subgenus Bactrophycus section Halochloa, and this study proposed to transfer them accordingly, subsuming the name Arthropycus. This outcome had been alluded to by Cho et al. (2012) who transferred one member of S. subgen. Arthropycus (S. fallax) to S. subgen. Bactrophycus on the basis of genetic data. This newly circumscribed S. subgenus Bactrophycus has an antitropical and disjunct distribution, being present in the temperate to subtropical northwestern Pacific Ocean and the temperate to subtropical southern Indo-Pacific, but not at all in tropical equatorial waters. The precise biogeographic history of the subgenus is unclear, however the monophyly and lack of genetic diversity of southern hemisphere Bactrophycus suggests a single dispersal event from the northern hemisphere population southward. Species delimitation within the southern hemisphere Halochloa was inconclusive due to a lack of genetic resolution. The South African/Madagascan Sargassum incisifolium was the only southern hemisphere species supported by the available genetic data. Previous molecular studies into S. subgen. Bactrophycus also reported the low genetic polymorphism in the section Halochloa, attributing it as a result of the recent rapid radiation of the group (Stiger et al. 2000, Cho et al. 2012).

The third aspect of this study constitutes a chapter of the book Algae of Australia: Marine Benthic Algae of North-western Australia, I. Green and Brown Algae (Australian Biological Resources Study and CSIRO Publishing) and focused on the north-western Australian Fucales (Chapter 4). This section was based on extensive new collections made throughout tropical Western Australia. The order Fucales in this region is composed of five genera: Hormophysa, Sargassopsis, Sargassum, Sirophysalis and Turbinaria. Of these, Sargassum comprised 10 of the 16 species, and all but one of these was in subgenus Sargassum. The results confirm the sectional level revisions of subgenus Sargassum by Mattio et al. (2010), adding Australian species to each section. Species level genetic variation could largely be elucidated in the north-western Australia S. subgenus Sargassum and much of the classical taxonomic work was validated. A number of new species to the area were added as range extensions, including Sargassum marginatum (known previously from India, Sri Lanka and Indonesia), Sargassum paradoxum (known previously from
temperate Australia), *Sargassum aquifolium* (common and includes several previously recognised species as synonyms), and the new species *Sargassum rastum* R.R.M.Dixon & Huisman (described here). The pre-study estimates of *Sargassum* diversity in the Australian north-west, based on species records in the broader region (WA, NT, Qld, Indonesia), suggested that approximately 30 taxa (specific and infraspecific) would occur in the area. Many of these were not found in the collections, their ranges possibly not extending to northern Western Australia, and others (particularly those based originally on features now recognized as variable) are undoubtedly included within the descriptions of species recorded. In the latter group, the few that were described from the study area were noted and accounted for, however those with a type locality removed from the area were omitted.

**Taxonomic character evaluation**

In classical taxonomy, the weighting of morphological characters and their taxonomic relevance was largely speculative. An enormous amount of respect must be awarded to those undertaking taxonomic assessments with only morphological observations at hand, particularly in the genus *Sargassum*. It is remarkable how much of the classic taxonomy remains current today after the more objective molecular techniques have scrutinized them. In this section the relative value of various morphological characters is reassessed given the results of this study.

(**= highly useful, **= somewhat useful, *= not very useful)**

***Stem (axes) morphology:*** Whether terete, compressed or triangular, stem cross-section morphology was nearly always conserved at a subgeneric or sectional level. For example, all section *Halochloa* species had a triangular (or highly angular) stem, and all section *Binderiana* species had a compressed stem. Only *Sargassum* section *Ilicifolia* had variable stem morphology; most species had a terete to subterete stem although *S. marginatum* had a flattened stem.

***Leaf morphology varied considerably in size and often shape within species yet was nonetheless a useful diagnostic feature. Eg. *Sargassum ilicifolium* exhibited an oblancoolate paddle-shaped leaf, with an obtuse-angled leaf apex. However, the leaf morphology would otherwise vary considerably from serrulate to cristate in the margins with a single or divided leaf apex. In *S. linearifolium* the leaves were simple or divided up to three times; however, the general shape was always linear-lanceolate, often with a
rounded apex. In summary the general leaf shape was a very useful character, but the size, marginal texture, and ability to divide were often not.

**Vesicles were useful taxonomic features. In Australian Halochloa spp. the vesicles are nearly always crowned by a leaf, and also in Sirophysalis, where there were often a chain of vesicles. Other species had winged vesicles (i.e. with a leaf-like projection out to the side), an apical mucro (spine), conspicuously large cryptostomata, or were perfectly spherical. Vesicles were always useful in aiding identification.***

***Receptacles: While receptacles varied considerably within species, they were also taxonomically useful. The shape and structural features (i.e. apical foliage) of receptacles far outweigh textural properties (i.e. spiny vs. smooth). Size can also be highly variable within species, possibly depending on age or environmental factors. The foliar, or zygocarpic nature of receptacles is important at the species level, yet is not necessarily diagnostic at the sectional level, with species across many sections producing zygocarpic and non-zygocarpic inflorescences (Polycystae, Zygocarpicae and Ilicifolia).***

*Holdfast: The holdfast is not a particularly useful species-level taxonomic feature in Sargassum. It can vary widely within species, from discoid, conical, crustose, scutellate or creeping.

**Implications**

These findings elucidate a number of issues present in Sargassum taxonomy and systematics, particularly in clarifying subgeneric level evolutionary relationships. Sargassum is taxonomically revised from a genus with four subgenera to two: Sargassum and Bactrophycus. At the species level there is less diversity than previously recognised. Molecular results highlight that intra-specific morphological variation can be considerable, at the same time that inter-specific variation may appear subtle. Knowing which morphological characters are taxonomically relevant is imperative. The challenges facing Sargassum taxonomists in the past have been alleviated considerably with a new understanding of the taxonomy that is now clearly reflected in morphology, and also a realization of the limitations in some areas of our knowledge of species boundaries. Diagnostic descriptions and comprehensive keys to the Sargassaceae genera (p. 91) and Sargassum species of north-western Australia are provided (p. 99–100) as well as morphological data on southern hemisphere Bactrophycus spp. (p. 75–78). The implications of this work are far-reaching, with many of the included Sargassum species
distributed across the Indo-Pacific. This work greatly contributes to the limited knowledge of these species, many of which are sequenced for the first time, and for which there were previously only inadequate descriptions and limited images available in the literature.

Together the three published works have reconstructed the taxonomy of *Sargassum* in Australia and the region, tackling each subgenus individually and to varying degrees. The works are a resource to present and future taxonomists, systematists, ecologists, environmental contractors and educators alike in species identification and evaluating evolutionary relationships within the Sargassaceae.

**Limitations**

At the time this study was planned and lab work undertaken, multi-locus genetic studies included two to rarely four loci. It was understood that most species investigated could be reasonably resolved if a number of well chosen markers were investigated. The inconclusive species boundaries shown in Australian subgenus *Bactrophycus* exemplifies that despite significant levels of variation presented in one subgenus or section, closely related groups are not always so well resolved. Similar results have emerged elsewhere in the brown algae and also within *Sargassum*, published during the course of this study (Mattio & Payri 2011). Several other molecular markers have been tested for their ability to resolve species boundaries in challenging groups within the brown algae (Mattio & Payri 2010) yet none have outperformed those used here. This study would have greatly benefited from more data; collections and sequence data. The northwestern Australian *Sargassum* flora was well collected and sequenced due to the support of the Western Australian Museum, CReefs and BOLD. The study of temperate subgenus *Sargassum* was incomplete at the time of submission due to a lack of resources for the extra lab work.

**Future work**

*Sargassum* is a genus generally feared by most self-respecting phycologists for the challenges it poses in identification. As is true for most difficult taxa, prior to molecular sequencing it seemed that greater exposure to the genus often led only to greater confusion, as the boundaries of seemingly informative characters blurred into one another. While this study may have helped that situation somewhat, there is still a large portion of the country that was not covered, and aspects that did not always reveal conclusive results. To complete the picture of Australian *Sargassum* taxonomy, future work includes extending the study of *S.* subgenus *Sargassum* into temperate waters and across to eastern and
northern Australia. In doing this it will also be necessary to develop and incorporate new molecular methods to increase the amount of the genome under investigation, increasing the number of loci, include single copy coding nuclear markers and Single Nucleotide Polymorphism (SNP) data using High Throughput Sequencing (HTS) technologies. This will reduce the sequencing costs while greatly increasing the amount of data produced. It is also important to incorporate the latest analysis programs – Structure, *Beast, etc. allowing a better understanding of species boundaries and population genetics. The most important future contribution will be the development of user-friendly tools for the identification of *Sargassum* Australia-wide, for example in the form of an interactive key.

**Conclusion**

A large, widespread, ecologically significant canopy-forming alga like *Sargassum* deserves to be fully understood. In Australia there are 66 current species (Cowan 2006, Guiry & Guiry 2015), and while the genus may be easily recognisable with its leaf-like laterals and numerous vesicles (air-floats), species recognition can border on agony for a non-specialist charged with the task. Understanding a species’ taxonomy is not only personally rewarding, on a broader scale the knowledge is crucial for undertaking accurate environmental, ecological or biogeographic science and sound political decision making.

**References**


